

Intraspecific Variation and Species Coexistence

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ABSTRACT: We use a two-species model of plant competition to explore the effect of intraspecific variation on community dynamics. The competitive ability ("performance") of each individual is assigned by an independent random draw from a species-specific probability distribution. If the density of individuals competing for open space is high (e.g., because fecundity is high), species with high maximum (or large variance in) performance are favored, while if density is low, species with high typical (e.g., mean) performance are favored. If there is an interspecific mean-variance performance trade-off, stable coexistence can occur across a limited range of intermediate densities, but the stabilizing effect of this trade-off appears to be weak. In the absence of this trade-off, one species is superior. In this case, intraspecific variation can blur interspecific differences (i.e., shift the dynamics toward what would be expected in the neutral case), but the strength of this effect diminishes as competitor density increases. If density is sufficiently high, the inferior species is driven to extinction just as rapidly as in the case where there is no overlap in performance between species. Intraspecific variation can facilitate coexistence, but this may be relatively unimportant in maintaining diversity in most real communities.

Keywords: coexistence, competition, drift, individual variation, neutral theory, trade-off.

The importance of niche differences in promoting species coexistence has played a central role in ecological theory (MacArthur and Levins 1967; Levin 1970; MacArthur 1972; Tilman 1982, 1988; Chesson 2000). Niche differences

can often be formulated in terms of interspecific trade-offs in the ability to exploit different environments or resources (MacArthur 1972; Tilman 1982), in the susceptibility to different predators or pathogens (Janzen 1970; Connell 1971), or between different aspects of performance, such as competitive and colonizing abilities (Skelam 1951; Levins and Culver 1971; Horn and MacArthur 1972; Hastings 1980; Tilman 1994). An alternative explanation for species coexistence is provided by neutral theory, which has demonstrated that diversity can be maintained by immigration or speciation in stochastic models in which all individuals are ecologically equivalent, so that species abundances are subject to neutral drift (Hubbell 1997, 2001; Chave 2004).

Inferences about the importance of different trade-offs in structuring community dynamics are often based on interspecific comparisons of key aspects of individual performance, such as growth and mortality (Horn 1971; Bazzaz 1979; Kitajima 1994; Pacala et al. 1994; Lusk and Smith 1998; Kobe 1999; Davies 2001). These comparisons are typically based on species means and treat intraspecific variation as noise (Clark et al. 2003). However, rather than sampling errors, intraspecific variation (fig. 1) may reflect important individual-level differences due, for example, to adaptive genetic variation (Williams 1975) or variable (and possibly unmeasurable) features of the environment (Clark et al. 2003). Regardless of its underlying cause, intraspecific variation might in some cases overwhelm interspecific differences along a given niche axis (Clark et al. 2003). Hubbell (2005) suggests that broad interspecific overlap in performance (fig. 1B) could lead to neutral community dynamics, whereas Clark et al. (2003) argue that such overlap might render interspecific differences along a given trade-off axis "too weak to matter" (p. 29), so that additional trade-offs are required for coexistence. While these interpretations differ, both view intraspecific variation as a force that blurs interspecific differences.

The notion that intraspecific variation could blur interspecific differences is intuitively appealing, but how strong is the effect? Consider a simplistic example where seeds of two plant species (call them "species 1" and "species 2") disperse into an open site that is the size of a single adult. Assume that individual seeds vary along a

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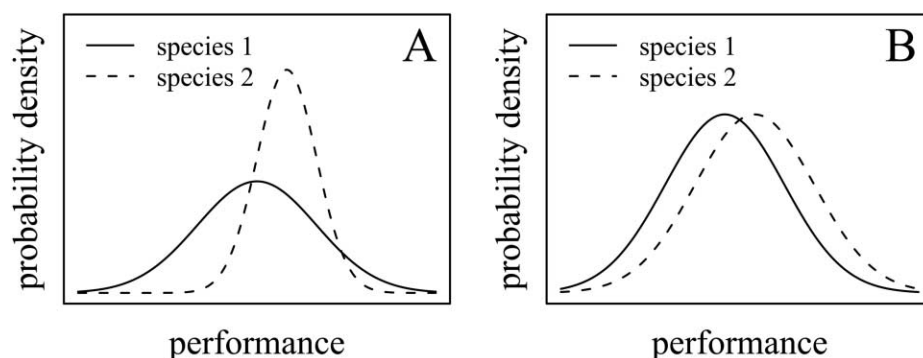


Figure 1: *A*, Gaussian distributions of individual performance for two species with a mean-variance trade-off. Species 2 has the higher mean performance but the lower variance. *B*, Gaussian distributions of individual performance for a superior and an inferior species. Both species have the same variance; species 2's mean performance is 0.5 standard deviations higher than species 1's.

single performance axis (from weak to strong competitors) and that the site is captured by the single best-performing seed that arrives. Furthermore, assume that species 2 has the higher mean seed quality (i.e., higher mean individual performance) but that the two species' probability distributions of individual performance are otherwise identical. The probability that species 2 wins the site depends on the amount of intraspecific variation relative to the mean interspecific difference and also on the number of arriving seeds of each species (app. A in the online edition of the *American Naturalist*). If both species have n arriving seeds, then, for a given n , the probability that species 2 wins the site decreases (to a minimum of $1/2$) as intraspecific variation increases (fig. 2). Alternatively, for a given level of intraspecific variation, the probability that species 2 wins the site increases with n . If n is sufficiently large, then species 2 is nearly assured of winning the site, regardless of the level of intraspecific variation (fig. 2).

The preceding example suggests that we should be cautious in attempting to infer community dynamics from distributions of individual performance alone. The example supports the claim that intraspecific variation can blur interspecific differences but also demonstrates that the strength of the effect depends on the density of competitors.

In this article, we use a two-species model of plant competition to explore the effect of intraspecific variation on community dynamics. The model builds on the example above but allows for stochasticity in seed rain and focuses on landscape-scale (rather than single-site) dynamics. Throughout, we assume that variation in performance reflects fixed, nonheritable properties of individuals. (In "Discussion," we outline special conditions under which environmentally induced variation may be treated as if it were due to properties of individuals.) Like the

example above, the model exhibits a range of behaviors, depending on the density of individuals competing for open space. If there is an interspecific mean-variance trade-off in individual performance (fig. 1A), then high competitor density favors the high-variance species, low density favors the high-mean species, and intermediate density leads to stable coexistence. In the absence of this trade-off, one species is superior (fig. 1B). In this case, the dynamics shift toward what would be expected in the neutral case as intraspecific variation increases and/or as competitor density decreases. For any competitor density, if intraspecific variation is sufficiently high, then the competitive dynamics between a superior and an inferior species are nearly neutral. Alternatively, for any level of intraspecific variation, if competitor density is sufficiently high, the inferior species goes extinct rapidly relative to the neutral case.

A Plant Competition Model with Intraspecific Variation

We seek a minimally complex model that allows us to explore the interacting effects of intraspecific variation and competitor density on community dynamics. Consider a landscape comprised of a number of identical sites that are either vacant or occupied by one adult. Assume that all adults are identical, so that individual variation is expressed only in juveniles, which vary along a single performance axis (from weak to strong competitors). Each juvenile is assigned a performance value by an independent random draw from a species-specific probability distribution (fig. 1). Because we consider only two life stages (juvenile and adult), all aspects of juvenile performance (germination, growth, and survival) are subsumed by a single index, which we refer to as "seed quality." We con-

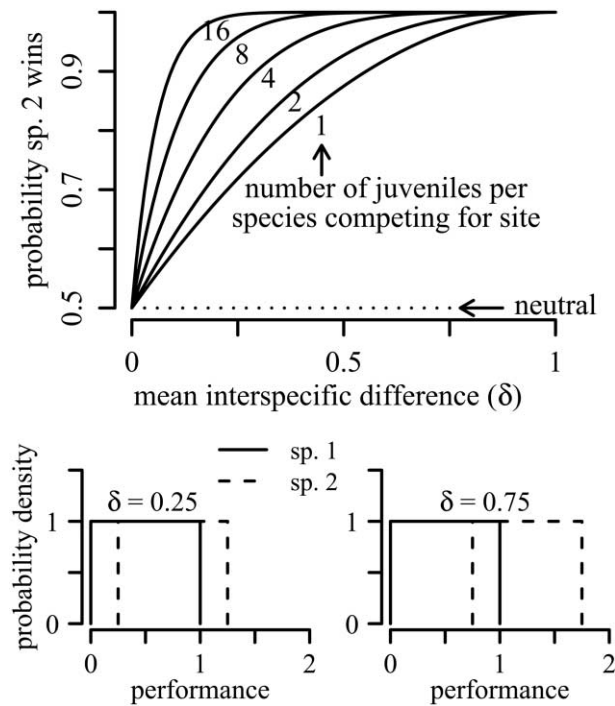


Figure 2: The probability that an open site is won by the superior of two species increases with the number of juveniles per species that compete for the site (n) and with the mean interspecific performance difference (δ). In this example, the amount of intraspecific variation relative to the mean interspecific difference decreases linearly with δ , which is scaled so that $\delta = 0$ represents the case where both species have the same performance distribution and $\delta = 1$ the case where the inferior species' maximum performance is equal to the superior species' minimum performance (i.e., no interspecific overlap). The site winner is the single juvenile with the highest performance among $2n$ random draws (n draws from each species' distribution). For any $\delta > 0$, if n is sufficiently large, then the superior species is likely to win the site. For analytical tractability, both species are assumed to have uniform performance distributions with equal variance. The lower panels show examples of performance distributions for two values of δ .

sider seed quality to be a fixed property of an individual until it dies or becomes an adult.

Each year, each adult produces b seeds and has probability μ of dying. The total number of seeds produced each year by species i is bx_iN , where x_i is the proportion of sites occupied by species i adults and N is the total number of sites in the landscape. For large N and assuming random dispersal, the distribution of seed rain (number of seeds landing on a site) is Poisson, with mean bx_i . Hereafter, we assume Poisson seed rain unless stated otherwise. Of the seeds arriving at an open site in a given year, assume that only the best one survives and that it immediately becomes an adult; seeds landing on occupied sites die. In the large- N limit, the stochastic model can be summarized by the following deterministic difference equation:

$$x_{i,t+1} = (1 - \mu)x_{i,t} + \left[1 - (1 - \mu) \sum_j x_{j,t}\right] W_{i,t}, \quad (1)$$

where $x_{i,t}$ and $x_{i,t+1}$ are the proportion of sites occupied by, or the "adult density" of, species i at years t and $t + 1$, respectively; the term in brackets is the proportion of sites open for colonization; and $W_{i,t}$ is the probability that species i wins an open site, which depends on b , $x_{j,t}$, and the species-specific seed quality distributions. Hereafter, we omit the subscript " t " except when needed for clarity. Total adult density, $X = \sum_j x_j$, has a globally stable equilibrium, \hat{X} , with $\hat{X} > 0$ if $b > \mu$ (app. B in the online edition of the *American Naturalist*; fig. 3). With Poisson seed rain, $\sum_j W_j = 1 - e^{-bX}$. The model just described can accommodate any number of species, but in this article, we restrict our attention to the two-species case.

Analytical Results

For some special cases, we have obtained analytical results for the behavior of the stochastic model, which becomes deterministic in the large- N limit (eq. [1]). In the following section, we compare these analytical results to stochastic simulations of the model, where we are not restricted to special cases. We first present a general invasion criterion: to invade when rare, species i must have a higher per capita probability of winning an open site than the resident j

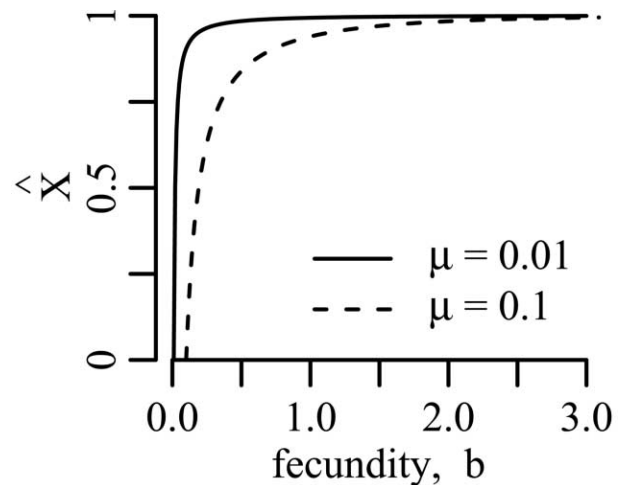


Figure 3: Equilibrium total adult density, \hat{X} , approaches 1 (all sites occupied) if fecundity b (seeds per adult) is high relative to adult mortality μ . Conversely, $\hat{X} \rightarrow 0$ as $b \rightarrow \mu$ (app. B in the online edition of the *American Naturalist*). We calculated \hat{X} by numerically solving equation (1) for total plant density, $X \equiv \sum_j x_j = (1 - \mu)X + [1 - (1 - \mu)X]W$, where $W = 1 - e^{-bX}$ is the probability that at least one seed, of any species, arrives at an open site, assuming Poisson seed rain.

(app. C in the online edition of the *American Naturalist*):

$$\frac{\tilde{W}_i}{\tilde{x}_i} > \frac{\hat{W}_j}{\hat{x}_j}. \quad (2)$$

Hereafter, we use the tilde (\sim) and the hat ($\hat{}$) to refer to invading and equilibrium populations, respectively. We can gain insight into the model's behavior by considering the high and low mean seed rain limits, where mean seed rain, $b\hat{X}$, is the expected total number of seeds arriving at an open site (i.e., the density of individuals competing for open space). Mean seed rain increases with fecundity, b , both directly and through the effect of b on \hat{X} (fig. 3).

We first examine the high-seed rain case. Let c be seed quality (or seed "competitive ability") and $f(c)$ be a probability density function (PDF). In appendix C, we show that for sufficiently high mean seed rain, species i is dominant (i.e., it can invade but cannot be invaded by species j) if there is some seed quality, c' , beyond which $f_i(c) \geq f_j(c)$, with strict inequality for at least some open set on $c > c'$. Loosely translated, this means that high seed rain favors the species with the higher maximum possible seed quality, or, if the seed quality distributions are unbounded (e.g., Gaussian), the species whose PDF has the fatter right tail (e.g., species 1 in fig. 1A). The conditions for species i 's dominance hold for uniform PDFs if species i has the higher maximum seed quality and for Gaussian PDFs if species i has the higher variance. If the PDFs have the same shape and variance but different means, the conditions hold if species i has the higher mean (e.g., species 2 in figs. 1B, 2).

Next, consider the case where mean seed rain, $b\hat{X}$, is low enough that nearly all open sites receive zero, one, or two seeds. In this case, the condition for species i 's dominance is that the probability that a single species i seed beats a single species j seed is greater than 1/2 (app. C). For probability distributions that are uniform or symmetric and unimodal (e.g., Gaussian), this condition is satisfied if and only if the mean seed quality of species i is greater than that of species j (app. C). More generally, species i will dominate at low seed rain if it has the higher typical seed quality, where the precise definition of "typical" will depend on the shapes of the seed quality distributions.

The above results imply that if there is an interspecific mean-maximum (or mean-variance) seed quality trade-off (fig. 1A), then the species with the higher mean dominates at low seed rain, while the species with the higher maximum (or variance) dominates at high seed rain. In appendix D in the online edition of the *American Naturalist*, we show that this trade-off leads to stable coexistence

at intermediate seed rain. Our coexistence proof involves demonstrating negative frequency dependence, but we do not yet have an intuitive explanation for why the frequency dependence occurs. A special case of our model is analogous to a competition-colonization trade-off, which provides a partial explanation for coexistence (app. D).

Finally, we note that if there is no interspecific mean-maximum (or mean-variance) seed quality trade-off and if the seed quality distributions are symmetric and of the same shape (e.g., both are Gaussian), then one species is dominant (it can invade but cannot be invaded by the competing species) for positive mean seed rain, $b\hat{X} > 0$ (app. E in the online edition of the *American Naturalist*).

Probability of Winning an Open Site

To study the model in more detail, we require expressions for W_i , the probability that species i wins an open site. In a two-species system, we have

$$\begin{aligned} W_i &= P(n_i > 0, n_j > 0, c_i^* > c_j^*) + P(n_i > 0, n_j = 0) \\ &= W_i^* + (1 - e^{-bx_i})e^{-bx_j}, \end{aligned} \quad (3)$$

where n_i is the number of species i seeds arriving at an open site and c_i^* is the quality of species i 's best seed arriving at an open site. The second term in equation (3) is the probability that species i wins by default under Poisson seed rain. The first term is the probability that seeds of both species are present and that species i wins,

$$\begin{aligned} W_i^* &= \sum_{n_i=1}^{\infty} \sum_{n_j=1}^{\infty} \left[\frac{e^{-bx_i}(bx_i)^{n_i}}{n_i!} \frac{e^{-bx_j}(bx_j)^{n_j}}{n_j!} \right. \\ &\quad \times \left. \int_{-\infty}^{\infty} n_i f_i(c_i) [F_i(c_i)]^{n_i-1} \int_{-\infty}^{c_i} n_j f_j(c_j) [F_j(c_j)]^{n_j-1} dc_j dc_i \right], \end{aligned} \quad (4)$$

where $f_i(c)$ is the PDF for species i 's seed quality and $F_i(c)$ is the cumulative density function, that is, the probability that a seed's quality is less than c . Terms of the form $nf(c)[F(c)]^{n-1}$ are the probability densities that a species' best seed at an open site has quality c . To see this, note that $n-1$ seeds all have quality lower than c with probability $[F(c)]^{n-1}$ and that there are n ways for this to happen. The double integral is the probability that species i wins an open site, given particular values of Poisson seed rain n_i and n_j , which are summed over all values greater than 0.

There is no closed-form expression for $F(c)$ for most

common continuous probability distributions, precluding a closed form for W_i . However, for the special case of uniformly distributed seed quality, we have $f(c) = 1/(c^{\max} - c^{\min})$ and $F(c) = (c - c^{\min})/(c^{\max} - c^{\min})$. We now consider two scenarios of competition between species with uniform seed quality distributions, relying on closed forms for W_i (app. F in the online edition of the *American Naturalist*). In the first scenario, there is an interspecific mean-maximum performance trade-off. We illustrate the general results presented above that low seed rain favors the species with the higher mean performance, high seed rain favors the species with the higher maximum, and coexistence occurs at intermediate seed rain. In the second scenario, we consider competition between a superior and an inferior species, and we focus on how the extinction rate of the inferior species depends on mean seed rain (i.e., competitor density) and on the level of intraspecific variation.

Uniform Seed Quality Distributions with a Mean-Maximum Trade-Off

Figure 4A shows an example of species with a mean-maximum seed quality trade-off, where species 1 has the higher maximum and species 2 has the higher mean. To examine invasion success as a function of mean seed rain, we rewrite the invasion criterion (eq. [2]) as

$$\tilde{R}_i \equiv \frac{\tilde{W}_i/\tilde{x}_i}{\tilde{W}_j/\tilde{x}_j} > 1. \quad (5)$$

Using the closed forms for W_i (app. F), we can obtain closed forms for \tilde{R}_i (app. G in the online edition of the

American Naturalist) and determine the mean seed rain values that allow species 1 and 2 to invade (fig. 4B). Species 2 can invade but cannot be invaded by species 1 at low seed rain. At high seed rain, the converse is true, and at intermediate seed rain, both species can invade a resident population of the other species (fig. 4B; app. D).

Figure 4C shows combinations of mean seed rain and species 2's mean seed quality, \bar{c}_2 , leading to dominance of either species or to coexistence. The range of mean seed rain values resulting in coexistence expands as \bar{c}_2 increases (fig. 4C; note logarithmic Y-axis) and as species 2's seed quality range, $c_2^{\max} - c_2^{\min}$, decreases (results not shown).

Uniform Seed Quality Distributions with a Superior and an Inferior Species

If species 2 has both the higher mean and the higher maximum seed quality, then it can invade but cannot be invaded by species 1 for positive mean seed rain, $b\hat{X} > 0$ (app. E). In this case, the interesting question is how fast species 1 is driven to extinction. If we perturb the system from the stable equilibrium, $(\hat{x}_1, \hat{x}_2) = (0, \hat{X})$, then the timescale of extinction of species 1 is determined by the eigenvalues of the stability matrix (May 1974).

At the high-seed rain limit (or, equivalently, the high-fecundity limit), the eigenvalues for the present case (superior and inferior species with uniform seed quality distributions) are $1 - \mu$ and 0; that is, species 1's extinction rate depends only on the adult mortality rate because species 2 wins all open sites. This result holds as long as species 2 has the higher maximum seed quality; if mean seed rain is high enough, then regardless of the level of intraspecific

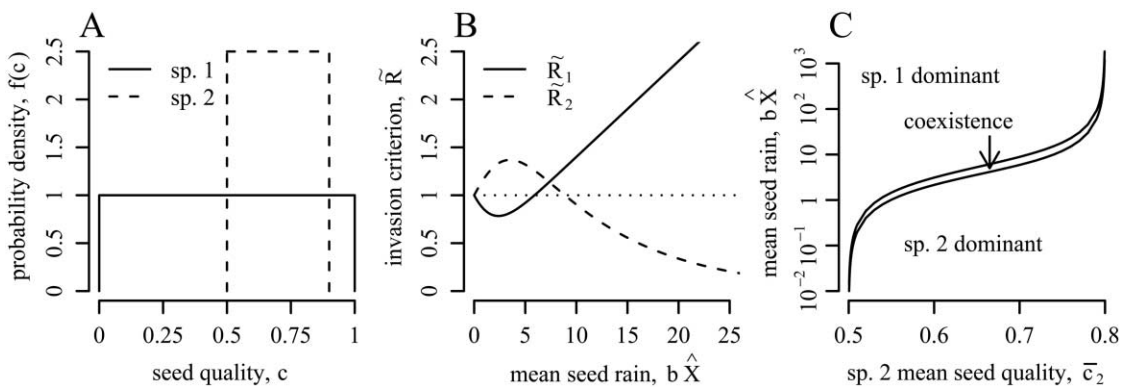


Figure 4: A, Uniform probability density functions of seed quality with a mean-maximum trade-off: $c_1^{\min} = 0$, $c_1^{\max} = 1$, $c_2^{\min} = 0.5$, and $c_2^{\max} = 0.9$. B, Analytical results (assuming an infinite landscape) for the performance distributions in A: dominance of species 2 at low mean seed rain, dominance of species 1 at high mean seed rain, and coexistence at intermediate seed rain. Species i can invade if $\tilde{R}_i > 1$ (eq. [G1]), with coinvasion occurring where both curves are above the dotted line. C, Combinations of mean seed rain and species 2 mean seed quality, \bar{c}_2 , leading to dominance of species 1 (with $c_1^{\min} = 0$ and $c_1^{\max} = 1$), coexistence, or dominance of species 2 (with $c_2^{\max} - c_2^{\min} = 0.4$). The seed rain coexistence region expands as \bar{c}_2 increases (note logarithmic Y-axis). The example in A and B corresponds to $\bar{c}_2 = 0.7$ in C.

cific variation, any advantage in maximum seed quality translates into a large effective advantage (fig. 5A). This population-level result, where seed rain is a Poisson random variable, mirrors our previous result for a single open site where we ignored stochasticity in seed rain (fig. 2).

At the low-seed rain limit (or, equivalently, the low-fecundity limit), both eigenvalues are 1; that is, the system is neutral to first order, regardless of the seed quality parameters (fig. 5A), because seeds of both species rarely co-occur at open sites. Note that neither species can persist at this limit, because $\hat{X} \rightarrow 0$ as $b \rightarrow \mu$ (fig. 3; app. B). But as long as mean seed rain is not too close to 0 (i.e., b not too close to μ), coexistence time should increase as mean seed rain decreases and the dynamics become more nearly neutral (fig. 5B).

Stochastic Simulations

To determine the sensitivity of our analytical results to demographic stochasticity and the shape of the seed quality distributions, we ran stochastic simulations with uniform and Gaussian seed quality distributions. Each combination of landscape size (100 or 1,000 sites), adult mortality rate ($\mu = 0.01$ or 0.1), fecundity (see below), and seed quality parameters (see below) was simulated 1,000 times. In all cases, results for $\mu = 0.01$ and 0.1 were qualitatively similar, and we report results only for $\mu = 0.01$. At the beginning of each simulation, each species occupied half of the sites. Each year (time step) consisted of mortality followed by colonization. Mortality was implemented by converting each occupied site to an open site with probability μ . Colonization was implemented as follows: for each species at each open site, the number of arriving seeds was a random draw from a Poisson distribution with mean $b\hat{x}_i$, where \hat{x}_i is the proportion of sites that species i occupied before mortality. The quality of each seed was a random draw from a species-specific probability distribution. Open sites were immediately converted to occupied sites of the species with the highest seed quality present or remained open if no seeds arrived.

We simulated scenarios with a mean-variance trade-off and scenarios with a superior and an inferior species (same variance, different means). In the former scenarios, we considered coexistence to occur if both species persisted for 1,000 generations, where a generation is defined as $1/\mu$ years. Simulations with a superior and an inferior species were run until one species went extinct.

Species with a Mean-Variance Seed Quality Trade-Off

For the uniform seed quality distributions in figure 4A, our analytical results (eq. [G1] in the online edition of the *American Naturalist*) predict coinvasion for $5.9 < b\hat{X} <$

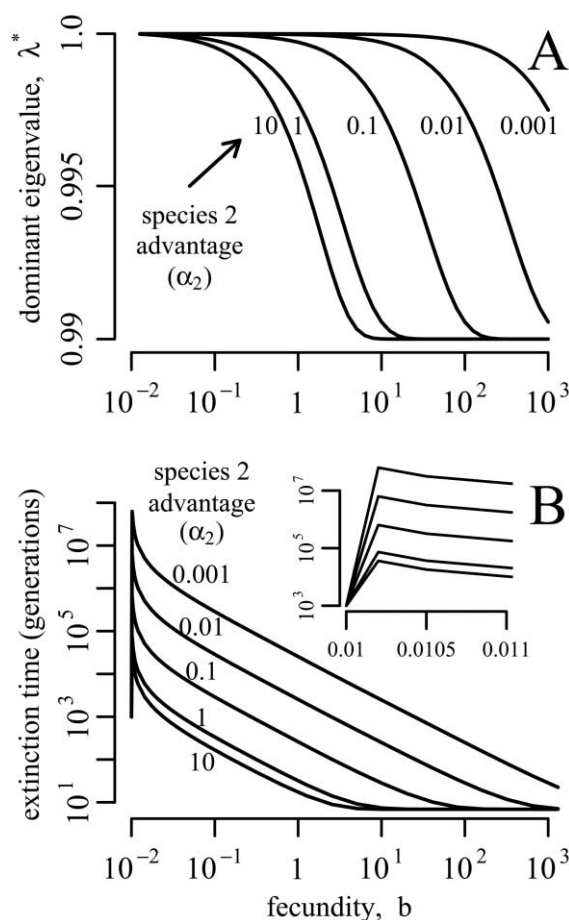


Figure 5: The effective advantage of the superior species increases as fecundity, b (seeds per adult), increases and intraspecific variation decreases. Species 1 and 2 have uniform seed quality distributions with equal variance; α_2 is species 2's mean seed quality advantage in standard deviation units. Larger values of α_2 reflect lower levels of intraspecific variation relative to the mean interspecific difference; the performance distributions are nonoverlapping if $\alpha_2 > 12^{1/2}$. A, At high fecundity, species 1's extinction rate, which depends on the dominant eigenvalue (λ^*) of the stability matrix at the equilibrium $(\hat{x}_1, \hat{x}_2) = (0, \hat{X})$, is independent of $\alpha_2 > 0$ and is limited only by the adult mortality rate: $\lim_{b \rightarrow \infty} \lambda^* = 1 - \mu$, with $\mu = 0.01$ in this example. In contrast, the system is neutral to first order at the low-fecundity limit: $\lim_{b \rightarrow \mu} \lambda^* = 1$. B, Extinction time (one generation = $1/\mu$ time steps) in deterministic simulations of equation (1) in a landscape of $N = 1,000$ sites (extinction was considered to occur if the proportion of sites occupied by species 1 fell below $N/2$). As fecundity increases from $b = \mu = 0.01$, where both species are driven to extinction, species 1's extinction time first increases (because b is low enough for the dynamics to be nearly neutral yet high enough for persistence of species 2) and then decreases as species 2's effective advantage increases. The inset expands the region of the plot near $b = \mu$.

8.9, exclusion of species 1 below this range, and exclusion of species 2 above this range (fig. 4B). We tested these predictions (which assume an infinite landscape) with stochastic simulations by varying fecundity, b , from 5 to 10

in increments of 0.5. For these combinations of b and μ (0.01 or 0.1), $\hat{X} > 0.999$ (fig. 3), so predictions for $b\hat{X}$ can be evaluated by varying b . Coexistence rarely occurred in landscapes of 100 sites, where demographic stochasticity should be important, although the relative performance of the two species was consistent with the analytical predictions; that is, the species with the higher mean seed quality dominated at low b , and the species with the higher maximum dominated at high b (fig. 6A). In landscapes of 1,000 sites, coexistence occurred across most of the analytically predicted fecundity range (fig. 6B). To aid in interpreting the simulation results, we calculated the expected equilibrium density, \hat{x} , of each species by numerically solving for the equilibria to equation (1) using equations (F4) and (F5) in the online edition of the *American Naturalist*. Coexistence tended to occur when expected abundance (\hat{x} times the number of sites) was relatively high for both species (fig. 6B).

To examine the behavior of the model with Gaussian seed quality distributions, we set $\bar{c}_1 = 0$, $\sigma_1^2 = 1$, $\bar{c}_2 = 0.5$, and $\sigma_2^2 = 0.25$, as in figure 1A. The analytical results

were borne out: species 2 (higher mean seed quality) was dominant at low b , species 1 (higher variance) was dominant at high b , and coexistence occurred for intermediate b in the larger landscapes (fig. 6C, 6D).

Superior and Inferior Species

For systems with uniform or Gaussian seed quality distributions, we examined cases where both species had the same variance but species 2's mean was higher by α_2 standard deviations. Smaller values of α_2 correspond to higher levels of intraspecific variation relative to the mean interspecific difference. We used stochastic simulations to determine how the proportion of contests won by species 2 and the mean extinction time depend on landscape size (100 or 1,000 sites), mortality rate ($\mu = 0.01$ or 0.1), fecundity ($b = 0.01, 0.1, 1, 10, 100$, or 1,000 seeds per adult), and species 2's mean advantage ($\alpha_2 = 0, 0.001, 0.01, 0.1, 1$, or 10 standard deviations). Results for both landscape sizes were qualitatively similar; results for only the larger landscapes are presented.

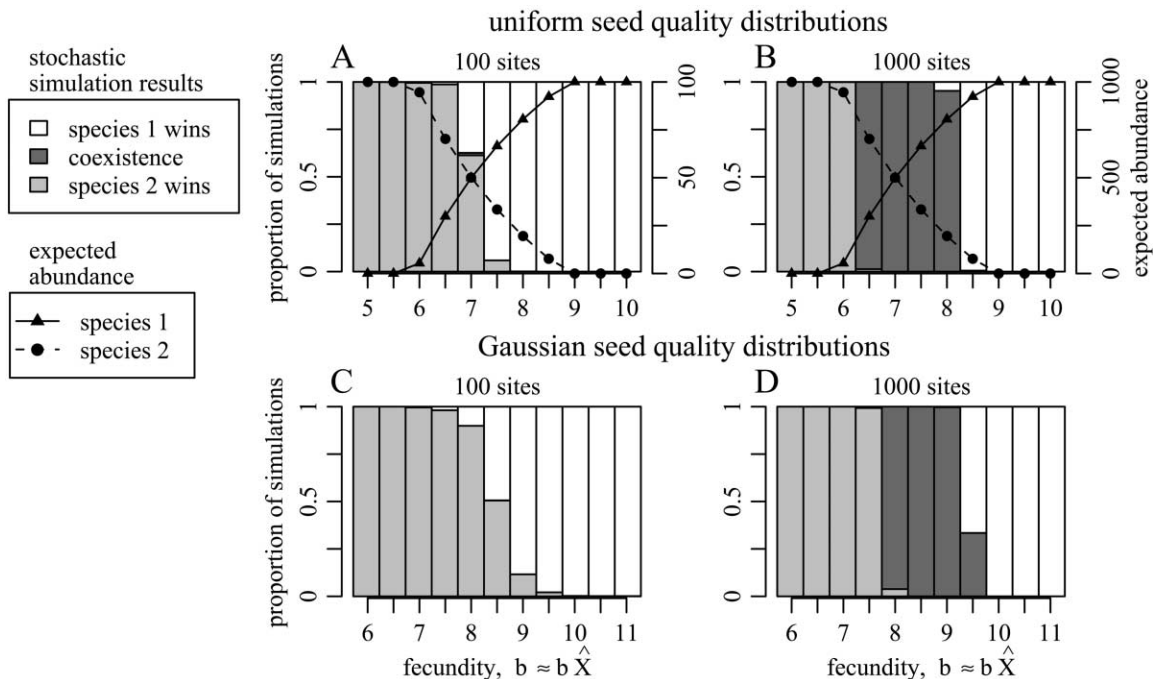


Figure 6: Stochastic simulation results agree with the analytical predictions of dominance of species 2 (higher mean seed quality) at low fecundity, dominance of species 1 (higher maximum, or variance in, seed quality) at high fecundity, and coexistence at intermediate fecundity; demographic stochasticity prevents coexistence in small landscapes (100 sites). A, B, Stochastic simulations for uniform distributions shown in figure 4A. Coexistence occurs across most of the analytically predicted seed rain range (fig. 4B) in the larger landscapes (1,000 sites). Expected abundance was calculated by numerically solving equation (1) (using the closed forms in app. F in the online edition of the *American Naturalist*) for equilibrium adult densities and then multiplying these by the number of sites. C, D, Simulations for the Gaussian distributions shown in figure 1A, with $\bar{c}_1 = 0$, $\sigma_1^2 = 1$, $\bar{c}_2 = 0.5$, and $\sigma_2^2 = 0.25$. Mortality rate, μ , is 0.01 for all panels; results were similar for $\mu = 0.1$. Fecundity (b ; seeds per adult) and mean seed rain ($b\hat{X}$; seeds per open site) are approximately equal in these simulations because $\hat{X} \approx 1$ (fig. 3).

As expected, each species won about half of the neutral contests ($\alpha_2 = 0$), regardless of landscape size or the shape of the seed quality distributions (fig. 7A, 7B). For neutral contests, mean extinction time was shortest at the lowest fecundity ($b = \mu$) and rose quickly to an asymptote with increasing b (fig. 7C, 7D). This pattern follows from the relationship between equilibrium total adult density, \bar{X} , and b : both species are driven to extinction ($\bar{X} \rightarrow 0$) as $b \rightarrow \mu$ (app. B), and \bar{X} rises quickly to its asymptotic value of 1 with increasing b (fig. 3).

Our analytical results for the model with uniform distributions predict that for $\alpha_2 > 0$, the dynamics should be independent of α_2 for b near μ and for high b (fig. 5). For b near μ , the dynamics should be nearly neutral for any α_2 , with both species driven to extinction if $b = \mu$. In contrast, for sufficiently high b , species 1 (with the lower mean seed quality) should be rapidly excluded relative to the neutral case, regardless of the level of intraspecific variation (fig. 5).

As predicted, the simulated dynamics appeared neutral for all α_2 at the lowest fecundity ($b = \mu$) for both uniform and Gaussian cases. For a given $\alpha_2 > 0$, the dynamics became increasingly nonneutral as b increased, but the transition from neutral dynamics to dominance of species 2 with increasing b was slower in the Gaussian than in the uniform cases (fig. 7). The prediction that the dynamics should be independent of $\alpha_2 > 0$ at high b , with species 1 being rapidly excluded, was clearly borne out in the simulations with uniform distributions (fig. 7A, 7C). In the simulations with Gaussian distributions (fig. 7B, 7D), the increasingly nonneutral dynamics with increasing b suggest that the same result (i.e., dynamics independent of α_2 for $\alpha_2 > 0$) would be obtained for sufficiently high b .

Discussion

In this article, we have examined a two-species model of plant competition in which each individual's performance

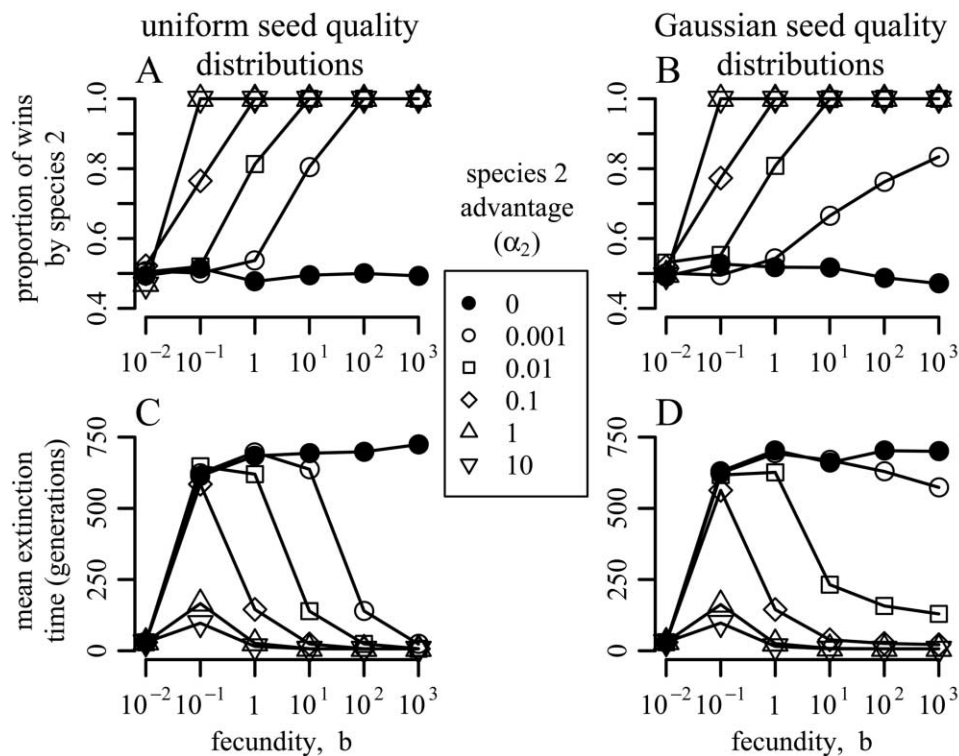


Figure 7: Stochastic simulations with both uniform (A, C) and Gaussian (B, D) seed quality distributions show that the tendency for species 1 (the inferior species) to be rapidly excluded increases with fecundity. Species 2's mean seed quality is higher than species 1's mean by α_2 standard deviations; both species have the same variance. For a given mean difference, increasing the amount of intraspecific variation leads to broader overlap in the performance distributions (smaller α_2) and shifts the dynamics toward the neutral case ($\alpha_2 = 0$). However, for any $\alpha_2 > 0$, if fecundity is sufficiently high, then species 1 is driven to extinction just as rapidly as in the case where there is no interspecific overlap in performance (uniform case with $\alpha_2 = 10$). For all panels, mortality rate is $\mu = 0.01$, and landscape size is $N = 1,000$ sites; results were qualitatively similar for the four cases with $\mu = 0.1$ or 0.01 and $N = 100$ or $1,000$. Fecundity (b ; seeds per adult) and mean seed rain ($b\bar{X}$; seeds per open site) are roughly equal for $b \geq 1$ and $\mu \leq 0.1$ (fig. 3).

is assigned by an independent random draw from a species-specific probability distribution and open space is captured by the best-performing individual arriving at a site. Under these conditions, high density of individuals competing for open space favors the species with the higher maximum (or larger variance in) performance, low density favors the species with the higher typical (e.g., mean) performance, and intermediate density promotes stable coexistence if there is an interspecific mean-maximum (or mean-variance) trade-off (fig. 1A). In the absence of trade-offs, one species is superior (fig. 1B). In this case, intraspecific variation shifts the dynamics toward what would be expected in the neutral case, but the strength of this effect diminishes as the density of individuals competing for open space increases. For any level of intraspecific variation, if competitor density is sufficiently high, then the inferior species will go extinct just as rapidly as in the case where there is no overlap in performance (i.e., the case in which all individuals of the superior species outperform all individuals of the inferior species). These results demonstrate that a given set of performance distributions can lead to qualitatively different community dynamics, depending on competitor density. Therefore, we should be cautious in attempting to infer dynamics from performance distributions alone.

Because competitor density has a strong effect on the dynamics of our model, it is desirable to know how these densities compare to those in real communities. Unfortunately, it is difficult to connect models as simple as ours to the real world. Our model assumes that all sites are identical and that competition for open space is an instantaneous process following seed dispersal. Here, competitor density is the number of seeds per open site. What is the analogous quantity in real communities, where "open space" comes in many varieties? Even if we were to focus on a particular kind of open site, it is difficult to quantify competitor density in real communities. Consider, for example, canopy gaps in forests that are captured by saplings that were already present before the gap formed (i.e., "advanced regeneration"). The number of individuals competing for a gap could be defined as the number of juveniles present when the gap formed, the number in a particular size class, or the number (including, perhaps, those that died before the gap formed) in a particular cohort or group of cohorts. Each of these definitions has merit, and each would provide a different answer.

Although it is difficult to compare competitor density in our model to that in nature, our results suggest that the capacity for intraspecific variation to blur interspecific differences may often be weak. In our model, if species with the same variance in performance but different means compete in a landscape of 1,000 adult sites and the mean number of juveniles (of both species combined) competing

per open site is at least 1, then intraspecific variation has little effect on the dynamics unless species mean performances differ by less than 0.1 standard deviations (fig. 7). In other words, unless intraspecific variation is so great that the means differ by less than 0.1 standard deviations, the dynamics are similar to the case in which there is no interspecific overlap in performance. This result holds whether distributions of individual performance are uniform (fig. 7C) or Gaussian (fig. 7D), assuming that at least one juvenile (on average) is present per open site in a landscape of at least 1,000 adult sites. If the performance distributions are Gaussian, to have a 90% chance of detecting a mean difference of 0.1 standard deviations would require sample sizes of more than 1,700 per species. Because sample sizes are typically much smaller than this, our results suggest that failure to detect a statistically significant difference between species means does not imply that species do not differ importantly in the parameter in question. Conversely, if field data do reveal a statistically significant mean difference in an important aspect of performance, then our model suggests that the difference is likely to matter; that is, if species differences are apparent in field data, then coexistence is unlikely in the absence of an interspecific trade-off.

Generality of Our Results

Our analytical results were obtained under simplifying assumptions (e.g., infinite landscape size, uniform performance distributions) that allowed for closed-form solutions of the stochastic model. Stochastic simulations revealed that the stabilizing effect of the mean-variance trade-off was not strong enough to allow for long-term coexistence in small landscapes (100 sites; fig. 6A, 6C), where demographic stochasticity should be important. None of our other analytical results changed qualitatively in stochastic simulations with uniform or Gaussian performance distributions. These two distributions (the former having no tails and the latter having infinite tails) should bracket many of the cases in real systems. We note, however, that some of our results do depend on the shapes of the performance distributions. We have derived general conditions to predict the competitive dominant in the limiting low- and high-density cases (app. C). But only under certain conditions (e.g., all species have Gaussian performance distributions) do these general results lead to simple predictions based on means and variances. If the performance distributions are skewed, for example, then the dominant species at low density is not necessarily the species with the highest mean.

Our model can accommodate any number of species, but we have restricted our analysis to the two-species case. Our results for competition between a superior and

an inferior species should apply qualitatively to the n -species case in which variance in performance is a non-decreasing function of mean performance (e.g., species have the same variance but different means). We would expect drift to become more important among similar species as diversity increases and each species becomes more recruitment limited (Hurtt and Pacala 1995); but if we were to pool the worse half and the better half of the species into two groups, then we would expect these groups to have dynamics similar (with respect to each other) to those observed here for two species. In contrast to the superior/inferior species scenario, where generalization to the n -species case seems straightforward, we do not know how an interspecific mean-variance performance trade-off (i.e., variance in performance is a decreasing function of mean performance) would play out in a multispecies community. This would be an interesting subject for future work.

Our model involves a number of additional simplifications that could limit the generality of our results. We now discuss three assumptions that seem particularly important: global seed dispersal, "winner-takes-all" competition, and uncorrelated variation among individuals.

Global dispersal. Our model accounts for fecundity limitation and stochasticity in seed rain but ignores the distance-dependent component of recruitment limitation (Ribbens et al. 1994; Clark et al. 1998; Nathan and Muller-Landau 2000). Exploring how local dispersal affects our results would be an interesting topic for future research. In particular, we do not know whether our coexistence result (stable coexistence at intermediate density in the presence of a mean-variance trade-off) holds under local dispersal.

Winner-takes-all competition. The effect of intraspecific variation on community dynamics depends on the nature of competition. In our model, competition for each open site is limited to a discrete set of individuals, with the competitive environment varying from site to site because of stochasticity in the number and quality of individual competitors. Each site is captured in its entirety by the single best-performing individual present. This winner-takes-all form of competition allows the effects of intraspecific variation to be manifested strongly. These effects may disappear in models with different assumptions about the nature of competition. For example, consider a model in which each open site is partitioned in proportion to the relative competitive abilities (c) of the individuals present; that is, species j captures a proportion of each open site equal to $\sum_i c_{ij} / \sum_{ik} c_{ik}$, where c is assumed to be positive, the numerator sums the performances of species j individuals present at the site, and the denominator sums over all individuals of all species present. Under many circum-

stances, we would expect intraspecific variation to have little or no effect on the dynamics of this system.

Our model is a variant of the discrete-cell model described by Skellam (1951) and subsequently modified by numerous authors (e.g., Chesson and Warner 1981; Shmida and Ellner 1984; Pacala and Tilman 1994; Hurtt and Pacala 1995; Moko and Iwasa 2000; Hubbell 2001). This model is a useful caricature for light-limited plant communities, where competition is strongly size asymmetric, and the winner-takes-all assumption seems reasonable. Sale (1977) argues that this model is also applicable to territorial coral reef fishes. Our results may not apply to other types of systems.

Uncorrelated variation among individuals. Our model assumes that individual performance is nonheritable and behaves as an independent random draw from a species-specific probability distribution. Nonheritable variation in performance may be caused by numerous environmental factors, including predators/herbivores, disease, and spatial variation in resources, temperature, wind, etc. Most environmental factors that affect individual performance can generate variation that is uncorrelated among individuals, as well as structured variation. Our results apply only to the component of variation that is uncorrelated among individuals (i.e., unstructured variation).

To see that structured and unstructured environmentally induced variation can lead to different dynamics, consider the setting assumed by our model, in which juveniles compete for sites, each of which is the size of a single adult. Furthermore, assume that all variation in juvenile performance is due to species-specific responses to the environment. First, consider the case where all sites are identical but each site is comprised of many spatially uncorrelated microsites. In this case, microsite effects on juvenile performance will generate variation that is independent among individuals, and the dynamics will be the same as in our model (where variation is assumed to reflect intrinsic properties of individuals). In the second case, assume that within each site, microsites are identical, but that the environment varies among sites. In this case, variation will be correlated among the individuals competing for a site, which will be captured by the species present that performs best in that environment. Our model does not apply to this situation. Here, coexistence would depend on interspecific trade-offs across environments (e.g., Denslow 1980; Tilman 1982; Pacala and Tilman 1994; Moko and Iwasa 2000; Silvertown 2004).

Intraspecific Variation and Species Coexistence

The preceding examples demonstrate that it is important to specify exactly what is meant by "intraspecific" or "individual" variation. It is perhaps obvious to some readers

that these terms should refer only to the component of variation that is due to (1) properties of individuals (and is thus uncorrelated among them) or (2) environmentally induced variation that operates at the scale of individuals (and thus can be treated as if it were due to individual properties). We do not object to this usage, but in light of the variety of ways that variation can arise and the variety of ways that it can affect dynamics, it seems important to clarify exactly what is meant by these terms in a given context.

Our results demonstrate two ways in which random independent intraspecific variation can facilitate species coexistence. First, if one species competes against a second species that has a lower mean but a higher variance in individual performance, then stable coexistence occurs over some range of intermediate competitor density. Second, if superior and inferior species compete (e.g., the same variance in individual performance but different means), then intraspecific variation can blur the interspecific differences; that is, the dynamics shift toward what would be expected in the neutral case as the amount of intraspecific variation increases. Here, intraspecific variation acts as an equalizing mechanism that can prolong unstable coexistence or, if stabilizing mechanisms are also present, facilitate stable coexistence (Chesson 2000).

Although random independent variation can facilitate coexistence, we do not know whether this is an important factor in most real communities. First, stable coexistence of two species with a mean-variance performance trade-off occurs only over a limited range of competitor densities (fig. 4C). Even if competitor density is within this range, the stabilizing effect of this trade-off appears to be relatively weak (i.e., long-term coexistence rarely occurred in small landscapes, where demographic stochasticity is important; fig. 6). Furthermore, we do not know if this trade-off can lead to multispecies coexistence. Second, although random independent intraspecific variation can blur interspecific differences between superior and inferior competitors, the strength of this effect diminishes as competitor density increases. In our model, the capacity for intraspecific variation to blur interspecific differences is weak even for modest competitor densities unless there is so much variation that species means would be difficult to distinguish from field data. Finally, much of the intraspecific variation in nature is structured (Kobe 1996, 2006; Wright et al. 1998; Ogle et al. 2006), and this structured variation may in some cases overwhelm the effect of unstructured variation on community dynamics. Understanding the combined effects of different forms of variation (e.g., variation that is uncorrelated among individuals vs. variation that is spatially structured) on community dynamics is an important area for future work.

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Appendix A from J. W. Lichstein et al., “Intraspecific Variation and Species Coexistence”

(Am. Nat., vol. 170, no. 6, p. 807)

Single-Site Competition with n Draws from Each of Two Uniform Performance Distributions

We derive an expression for the probability that a superior species wins a single site, where the site winner is the individual with the highest performance, or “competitive ability” (c), among n random draws from each of two species’ performance distributions. Both performance distributions are assumed to be uniform, with finite width w . Without loss of generality, we assume that species 1 has minimum performance of 0. Species 1’s probability density function (PDF) is thus $f_1(c) = 1/w$ for $0 \leq c \leq w$ and $f_1(c) = 0$ otherwise, with cumulative density function (CDF) $F_1(c) = c/w$ for $0 \leq c \leq w$, $F_1(c) = 0$ for $c < 0$, and $F_1(c) = 1$ for $c > w$. Species 2 has PDF $f_2(c) = 1/w$ for $\delta \leq c \leq \delta + w$ and $f_2(c) = 0$ otherwise, and it has CDF $F_2(c) = (c - \delta)/w$ for $\delta \leq c \leq \delta + w$, $F_2(c) = 0$ for $c < \delta$, and $F_2(c) = 1$ for $c > \delta + w$.

We assume that $\delta \geq 0$. The neutral case is $\delta = 0$, where both species capture the site with probability 1/2. If $\delta > 0$, species 2 is the superior species. If $\delta \geq w$, there is no overlap in the performance distributions, so species 2 wins the site with probability 1. For $0 < \delta < w$, the probability that species 2 wins the site is $P_2 = \theta_2 + 1 - [1 - (\delta/w)]^n$, where θ_2 is the probability that species 2 wins with a performance no greater than w (species 1’s maximum possible performance) and $1 - [1 - (\delta/w)]^n$ is the probability that species 2 has at least one individual with performance greater than w . For θ_2 , we have

$$\begin{aligned} \theta_2 &= \int_{\delta}^w n f_2(c_2) [F_2(c_2)]^{n-1} \int_0^{c_2} n f_1(c_1) [F_1(c_1)]^{n-1} dc_1 dc_2 \\ &= \int_{\delta}^w \left(\frac{n}{w} \right) \left(\frac{c_2 - \delta}{w} \right)^{n-1} \int_0^{c_2} \left(\frac{n}{w} \right) \left(\frac{c_1}{w} \right)^{n-1} dc_1 dc_2 = \left(\frac{n}{w^{2n}} \right) \int_{\delta}^w c_2^n (c_2 - \delta)^{n-1} dc_2, \end{aligned}$$

which is easily solved for a given n . To see that θ_2 , and therefore P_2 , depends only on n and the ratio δ/w , we define $x \equiv c_2/\delta$ and rewrite θ_2 in terms of x :

$$\theta_2 = \left(\frac{n}{w^{2n}} \right) \int_1^{w/\delta} (\delta x)^n (\delta x - \delta)^{n-1} \delta dx = n \left(\frac{\delta}{w} \right)^{2n} \int_1^{w/\delta} x^n (x - 1)^{n-1} dx.$$

Appendix B from J. W. Lichstein et al., “Intraspecific Variation and Species Coexistence”

(Am. Nat., vol. 170, no. 6, p. 807)

Global Stability of Total Adult Density

Total adult density is $X \equiv \sum_i x_i$. From equation (1),

$$X_{t+1} = (1 - \mu)X_t + [1 - (1 - \mu)X_t]W_t, \quad (B1)$$

where W_t , the probability that at least one seed lands on an open site, is $1 - e^{-bX_t}$, assuming Poisson seed rain. At equilibrium, $\hat{X} = (1 - \mu)\hat{X} + [1 - (1 - \mu)\hat{X}]\hat{W}$. We now show that if $b > \mu$ and X_t and μ are within their biologically meaningful ranges ($0 \leq X_t \leq 1$ and $0 < \mu < 1$), then there is a globally stable equilibrium, $\hat{X} > 0$, in the interval $0 < X_t \leq 1$. We first show that there is at least one equilibrium by the following three properties of $g(X_t) \equiv X_{t+1}$: first, $g(0) = 0$; second, $g'(0) = 1 + b - \mu > 1$, where $g'(X_t) \equiv dX_{t+1}/dX_t$; and third, $g(1) = 1 - \mu e^{-b} < 1$. Together, these three properties ensure that $g(X_t)$ crosses the line $X_{t+1} = X_t$ at least once. That there is only one such equilibrium follows from the fact that $g(X_t)$ is concave down: $g''(X_t) \equiv d^2X_{t+1}/dX_t^2 = -be^{-bX_t}\{2(1 - \mu) + b[1 - X_t(1 - \mu)]\} < 0$. That this equilibrium is globally stable follows from the fact that $g(X_t)$ is monotonically increasing: $g'(X_t) = [1 - (1 - \mu)X_t]be^{-bX_t} + (1 - \mu)e^{-bX_t} > 0$. It is easy to show with graphical methods (e.g., Murray 1993, p. 38) that if there is a unique equilibrium, \hat{X} , and $g(X_t)$ is concave down and monotonically increasing, then X_t will monotonically approach \hat{X} from either direction.

Note that $\lim_{b \rightarrow \infty} g(1) = 1$, so $\lim_{b \rightarrow \infty} \hat{X} = 1$. In contrast, if $b < \mu$, then $g'(0) = 1 + b - \mu < 1$, which, together with the properties $g(0) = 0$ and $g''(X_t) < 0$, shows that in this case, $g(X_t) < X_t$ for $0 < X_t \leq 1$, and so the globally stable equilibrium is $\hat{X} = 0$.

Appendix C from J. W. Lichstein et al., “Intraspecific Variation and Species Coexistence”

(Am. Nat., vol. 170, no. 6, p. 807)

Invasion Criteria

General Invasion Criterion

Species i (with $\tilde{x}_i \approx 0$) can invade species j (with $\hat{x}_j = \hat{X}$) if $(\tilde{x}_{i,t+1} - \tilde{x}_{i,t})/\tilde{x}_{i,t} > 0$, or, from equation (1), if

$$-\mu + [1 - (1 - \mu)\hat{x}_j] \frac{\tilde{W}_i}{\tilde{x}_i} > 0. \quad (C1)$$

For the resident at equilibrium, $\hat{x}_j = (1 - \mu)\hat{x}_j + [1 - (1 - \mu)\hat{x}_j]\hat{W}_j$, so

$$-\mu + [1 - (1 - \mu)\hat{x}_j] \frac{\hat{W}_j}{\hat{x}_j} = 0. \quad (C2)$$

Combining equations (C1) and (C2) gives the general invasion criterion (eq. [2]).

Low-Seed Rain (Low-Fecundity) Invasion Criterion

Consider the case where mean seed rain, $b\hat{X}$, is low enough (b close to μ) that nearly all open sites receive no, one, or two seeds and we can ignore the few sites receiving more than two seeds. The invasion criterion (eq. [2]) for species i is, then,

$$\frac{P(n_i = n_j = 1)P(c_i > c_j) + P(n_i = 1 \text{ or } 2)P(n_j = 0)}{\tilde{x}_i} > \frac{P(n_i = n_j = 1)P(c_j > c_i) + P(n_j = 1 \text{ or } 2)P(n_i = 0)}{\hat{x}_j},$$

where $P(n_i = k)$ is the probability that species i has k seeds at an open site, and $P(c_i > c_j)$ is the probability that a single random draw from species i 's seed quality distribution is better than a single draw from species j 's distribution. With Poisson seed rain, the invasion criterion is

$$e^{-b(\tilde{x}_i + \hat{x}_j)} \hat{x}_j P(c_i > c_j) + \frac{\tilde{x}_i}{2} > e^{-b(\tilde{x}_i + \hat{x}_j)} \tilde{x}_i P(c_j > c_i) + \frac{\hat{x}_j}{2}.$$

Substituting $\tilde{x}_i \approx 0$ and $e^{-b(\tilde{x}_1 + \tilde{x}_2)} = e^{-b\hat{X}} \approx 1$ (because $b\hat{X} \approx 0$) gives $P(c_i > c_j) > 1/2$ as the invasion criterion. Coinvasion is not possible in the low-seed rain case, because if $P(c_i > c_j) > 1/2$, then $P(c_j > c_i) < 1/2$.

We now show that if the seed quality probability density functions (PDFs) are symmetric about their mean, then $\bar{c}_i > \bar{c}_j$ (i.e., species i has the higher mean seed quality) implies $P(c_i > c_j) \geq 1/2$, which becomes a strict inequality, $P(c_i > c_j) > 1/2$, under certain conditions, including cases where the PDFs are uniform or symmetric and unimodal. First, note that

$$P(c_i > c_j) = \int_{-\infty}^{\infty} f_i(c) F_j(c) dc = \int_{-\infty}^{\infty} f_i(2\bar{c}_i - c) F_j(2\bar{c}_i - c) dc,$$

where $f_i(c)$ is the PDF for species i 's seed quality, $F_j(c)$ is the cumulative density function (CDF) for species j 's seed quality, and \bar{c}_i is species i 's mean seed quality. Equality of the above two integrals implies that they are equal to their mean:

$$P(c_i > c_j) = \frac{1}{2} \int_{-\infty}^{\infty} f_i(c) F_j(c) + f_i(2\bar{c}_i - c) F_j(2\bar{c}_i - c) dc.$$

Symmetry of $f_i(c)$ implies $f_i(c) = f_i(2\bar{c}_i - c)$, so we can rewrite the above as

$$P(c_i > c_j) = \frac{1}{2} \int_{-\infty}^{\infty} f_i(c) [F_j(c) + F_j(2\bar{c}_i - c)] dc.$$

Symmetry of $f_j(c)$ implies $F_j(c) + F_j(2\bar{c}_j - c) = 1$, so

$$P(c_i > c_j) = \frac{1}{2} \int_{-\infty}^{\infty} f_i(c) \{1 + [F_j(2\bar{c}_i - c) - F_j(2\bar{c}_j - c)]\} dc = \frac{1}{2} + \frac{1}{2} \int_{-\infty}^{\infty} f_i(c) [F_j(2\bar{c}_i - c) - F_j(2\bar{c}_j - c)] dc \geq \frac{1}{2}$$

if $\bar{c}_i > \bar{c}_j$. The above expression becomes a strict inequality, $P(c_i > c_j) > 1/2$, if the PDFs are uniform or symmetric and unimodal or if the PDFs are symmetric and there is some range of c for which both $f_i(c) > 0$ and $f_j(c) > 0$.

High–Seed Rain (High-Fecundity) Invasion Criterion

We can express the invasion criterion (eq. [2]) on a per seed basis, because both species have the same per adult fecundity, b ; for species i to invade, it must have a higher per seed probability of winning an open site than the resident. Species i 's per seed probability of winning an open site in a resident j environment is

$$Z_{ij} = \int_{-\infty}^{\infty} f_i(c) \Phi_j(c) dc, \quad (C3)$$

where $\Phi_j(c)$ is the CDF for the quality of the best species j seed present at a given open site:

$$\Phi_j(c) = \sum_{n=0}^{\infty} P(n) [F_j(c)]^n, \quad (C4)$$

where $P(n)$ is the probability that species j has n seeds present at an open site, $F_j(c)$ is the CDF for the quality of a single species j seed, and $[F_j(c)]^n$ is the probability that all n species j seeds have quality lower than c . In appendix D, we make use of the fact that Φ is a concave-up function of $F(c)$ if $P(n) > 0$ for some $n > 1$, as occurs for any reasonable distribution of n . Under Poisson seed rain with mean y , equation (C4) is

$$\Phi_j(c) = \sum_{n=0}^{\infty} \frac{e^{-y} y^n}{n!} [F_j(c)]^n = e^{y[F_j(c)-1]}. \quad (C5)$$

The criterion for species i to invade a resident j is $Z_{ij} > Z_{jj}$, or, from equations (C3) and (C5),

$$\int_{-\infty}^{\infty} f_i(c) e^{y F_j(c)} dc > \int_{-\infty}^{\infty} f_j(c) e^{y F_j(c)} dc, \quad (C6)$$

which holds for sufficiently high mean seed rain, y , if there is some c' such that $f_i(c) \geq f_j(c)$ for $c > c'$, with strict inequality for some open set on $c > c'$. To see this, we rewrite equation (C6) as

$$\int_{-\infty}^{c'} [f_i(c) - f_j(c)] e^{yF_j(c)} dc + \int_{c'}^{\infty} [f_i(c) - f_j(c)] e^{yF_j(c)} dc > 0.$$

If $f_i(c) \geq f_j(c)$ for $c > c'$, with strict inequality for some open set on $c > c'$, then the second integral is positive, and, because $F_j(c)$ increases with c , the second integral will be greater in magnitude than the first integral (which can be negative) if y is sufficiently high. Thus, if $f_i(c) \geq f_j(c)$, with strict inequality for some open set on $c > c'$, then species i is dominant (it can invade but cannot be invaded by species j) at high mean seed rain. For bounded (e.g., uniform) PDFs, the conditions for species i 's dominance hold if species i has the higher maximum seed quality. For Gaussian PDFs, the conditions hold if species i has the larger variance.

The above results for the low- and high-seed rain cases imply that if there is an interspecific mean-maximum or mean-variance seed quality trade-off, the identity of the dominant species switches with seed rain, with the high-mean species dominant at low seed rain and inferior at high seed rain.

Appendix D from J. W. Lichstein et al., “Intraspecific Variation and Species Coexistence”

(Am. Nat., vol. 170, no. 6, p. 807)

Coexistence of Species with a Mean-Variance Performance Trade-Off

Our model assumes that both species have random, global dispersal and the same adult fecundity and mortality rates; therefore, $Z_{ii} = Z_{jj}$, where Z_{ii} is species i 's per seed probability of winning an open site in its own resident environment (see eq. [C3]). We now show that the mean of the two invading species' per seed probabilities of winning an open site is always greater than the resident per seed probability of winning an open site: $(Z_{ij} + Z_{ji})/2 > Z_{ii}$. The implication of this result is that if the identity of the dominant species switches as mean seed rain, $y \equiv b\hat{X}$, varies from low to high values (as occurs when there is an interspecific mean-maximum or mean-variance seed quality trade-off; see app. C) and if the Z 's are continuous functions of y , then there must be some value of y at which $Z_{ij} = Z_{ji} > Z_{ii}$; that is, either species can invade when rare.

We now show that $(Z_{ij} + Z_{ji})/2 > Z_{ii}$, or $Z_{ij} + Z_{ji} - 2Z_{ii} > 0$. For convenience, we assume that $f_i(c)$ and $f_j(c)$, the seed quality PDFs, are continuous on $(-\infty, \infty)$. From equation (C3),

$$Z_{ij} + Z_{ji} - 2Z_{ii} = \int_{-\infty}^{\infty} f_i \Phi_j dc + \int_{-\infty}^{\infty} f_j \Phi_i dc - 2 \int_{-\infty}^{\infty} f_i \Phi_i dc = \int_{-\infty}^{\infty} (f_j - f_i) \Phi_i dc + \int_{-\infty}^{\infty} f_i (\Phi_j - \Phi_i) dc, \quad (D1)$$

where f_i is shorthand for $f_i(c)$ and Φ_i is shorthand for $\Phi_i(c)$, the CDF of the quality of the best species i seed present at an open site (see eq. [C4]). For the first integral in equation (D1), integration by parts gives

$$\int_{-\infty}^{\infty} (f_j - f_i) \Phi_i dc = \Phi_i (F_j - F_i) \Big|_{-\infty}^{\infty} - \int_{-\infty}^{\infty} (F_j - F_i) \Phi_i' f_i dc = - \int_{-\infty}^{\infty} (F_j - F_i) \Phi_i' f_i dc, \quad (D2)$$

where F_i is shorthand for $F_i(c)$ and $\Phi_i' \equiv d\Phi_i/dc$. The term $\Phi_i (F_j - F_i) \Big|_{-\infty}^{\infty}$ is 0 because $\lim_{c \rightarrow -\infty} F_i(c) = \lim_{c \rightarrow -\infty} F_j(c) = 0$, and $\lim_{c \rightarrow \infty} F_i(c) = \lim_{c \rightarrow \infty} F_j(c) = 1$. Combining equations (D1) and (D2), we have

$$Z_{ij} + Z_{ji} - 2Z_{ii} = - \int_{-\infty}^{\infty} (F_j - F_i) \Phi_i' f_i dc + \int_{-\infty}^{\infty} f_i (\Phi_j - \Phi_i) dc = \int_{-\infty}^{\infty} f_i \{ \Phi_j - [\Phi_i + (F_j - F_i) \Phi_i'] \} dc. \quad (D3)$$

By viewing Φ as a function of F (see eq. [C4]) and using the notation $\Phi(F_i) \equiv \Phi_i$, we see that the term in square brackets in equation (D3) is the value of $\Phi(F)$ predicted at $F = F_j$ by linear extrapolation from the point tangent to $\Phi(F)$ at $F = F_i$. Because $\Phi(F)$ is concave up (see app. C), the term in square brackets is positive, so the coinvasion criterion, $Z_{ij} + Z_{ji} - 2Z_{ii} > 0$, holds.

An important factor limiting the generality of our proof is our assumption that the invader and the resident experience the seed rain environment in the same way; that is, the probability of competing for an open site against n resident seeds is the same for an invading seed and for a randomly chosen resident seed. Clearly, this is the case for Poisson seed rain, where each seed is randomly and independently dispersed. The assumption also holds if there is spatial heterogeneity in mean seed rain because of factors such as topography or wind, if these factors affect all seeds equally. The assumption will not hold if there is within-species clustering, for example, due to local dispersal or to dispersal of fruits containing multiple seeds.

Thus far, we have demonstrated only coinvasion. In the special case where the higher-mean species has zero variance in seed quality and its competitor has uniformly distributed seed quality, it is easy to show that coinvasion implies a globally stable internal equilibrium. We have not proved that this result applies in general, but we suspect that it does, for the following reasons. First, there is no apparent mechanism in our model for species to overshoot their target density. Second, simulations suggest that parameter combinations that lead to coinvasion also lead to a stable internal equilibrium (results not shown).

Why does coexistence occur in this model? The above proof relies on negative frequency dependence: the mean of the two invading species’ per capita probabilities of winning an open site is always greater than the resident per capita probability of winning an open site. Unfortunately, we do not have an intuitive explanation for why this frequency dependence occurs. Nevertheless, we can gain some insight as to how coexistence occurs in our model by considering competition between species 1, with uniformly distributed seed quality on $(0, 1)$, and species 2, with fixed seed quality c_2 , where $1/2 = \bar{c}_1 < c_2 < 1$. A proportion c_2 of species 1’s seeds can never win an open site if a species 2 seed is present, and a proportion $1 - c_2$ of species 1’s seeds can never be beaten by a species 2 seed. Define species 1* as identical to species 1 but without the inferior seeds; that is, species 1* has fecundity $(1 - c_2)b$, and all of its seeds are superior to species 2 seeds. Species 1* and 2 constitute a system with a competition-colonization trade-off, in which species 1* is the stronger competitor but the weaker colonizer (species 2 has fecundity b). This trade-off can lead to stable coexistence (see references in the introduction to this article). The preceding caricature of our model is not entirely correct; we should not ignore species 1’s inferior seeds, because any sites that these seeds capture will reduce the space available to species 2 and will also produce some superior seeds. Nevertheless, viewing the mean-variance seed quality trade-off as a competition-colonization trade-off provides some intuition as to how coexistence occurs in our model. This is only a partial explanation of the coexistence mechanism. A more complete explanation will likely depend on understanding the root cause of the frequency dependence.

Appendix E from J. W. Lichstein et al., “Intraspecific Variation and Species Coexistence”

(Am. Nat., vol. 170, no. 6, p. 807)

Competitive Dominance in Systems Lacking a Mean-Variance Performance Trade-Off

Here, we show that if the seed quality distributions for species i and j are symmetric and have the same shape (e.g., both are Gaussian), then species i is dominant (it can invade but cannot be invaded by species j) for positive mean seed rain ($b\hat{X} > 0$) if $\bar{c}_i > \bar{c}_j$ and $\sigma_i^2 \geq \sigma_j^2$ or if $\bar{c}_i \geq \bar{c}_j$ and $\sigma_i^2 > \sigma_j^2$, where \bar{c} is mean seed quality and σ^2 is variance in seed quality.

We first show that species i is dominant if $\bar{c}_i > \bar{c}_j$ and $\sigma_i^2 = \sigma_j^2$. From equation (C3), the invasion criterion for species i is

$$\int_{-\infty}^{\infty} f_i(c)\Phi_j(c)dc > \int_{-\infty}^{\infty} f_j(c)\Phi_j(c)dc = \int_{-\infty}^{\infty} f_i(c)\Phi_i(c)dc, \quad (\text{E1})$$

where $\Phi(c)$ is defined in equation (C4) and the equality on the right follows from our assumptions that both species have randomly dispersed seeds and that all adults have the same fecundity and mortality rate. If $\bar{c}_i > \bar{c}_j$ and $\sigma_i^2 = \sigma_j^2$ and if $f_i(c)$ and $f_j(c)$ have the same shape, then $F_j(c) > F_i(c)$ for all c , which implies that $\Phi_j(c) > \Phi_i(c)$ for all c . Thus, inequality (E1) holds, and species i can invade. A similar argument shows that species j cannot invade.

We now show that species i is dominant if $\bar{c} = \bar{c}_i = \bar{c}_j$ and $\sigma_i^2 > \sigma_j^2$. Species i 's per seed probability of winning an open site in a species j environment is

$$\begin{aligned} \int_{-\infty}^{\infty} f_i(c)\Phi(F_j(c))dc &= \int_{-\infty}^{\infty} f_i(2\bar{c} - c)\Phi(F_j(2\bar{c} - c))dc \\ &= \int_{-\infty}^{\infty} f_i(c)\Phi(1 - F_j(c))dc = \int_{-\infty}^{\infty} f_i(c)\frac{\Phi(F_j(c)) + \Phi(1 - F_j(c))}{2}dc, \end{aligned}$$

where $\Phi(F_i(c)) \equiv \Phi_i(c)$ and $\Phi(1 - F_i(c)) \equiv \Phi_i(2\bar{c} - c)$; that is, we view Φ as a function of F or $1 - F$ rather than as a function of c . The third integral above follows from the fact that $f(c) = f(2\bar{c} - c)$ and $F(c) + F(2\bar{c} - c) = 1$ if the PDFs are symmetric, and the fourth integral follows from the fact that the first and third integrals are equal to their mean. We now rewrite species i 's invasion criterion (eq. [E1]) as

$$\int_{-\infty}^{\infty} f_i\frac{\Phi(F_i) + \Phi(1 - F_i)}{2}dc > \int_{-\infty}^{\infty} f_i\frac{\Phi(F_i) + \Phi(1 - F_i)}{2}dc, \quad (\text{E2})$$

where f and F are shorthand for $f(c)$ and $F(c)$, respectively. Note that F and $1 - F$ are the same distance δ from $F(\bar{c}) = 1/2$; that is, $|F - 1/2| = |1 - F - 1/2| = \delta$. Furthermore, because the PDFs have the same shape, the conditions $\bar{c} = \bar{c}_i = \bar{c}_j$ and $\sigma_i^2 > \sigma_j^2$ imply that $\delta_j > \delta_i$ for all $c \neq \bar{c}$, with $\delta_j = \delta_i = 0$ for $c = \bar{c}$. Here, $\Phi(F)$ is a

concave-up function (app. D), so $\delta_j \geq \delta_i$ implies $\bar{\Phi}_j \equiv [\Phi(F_j) + \Phi(1 - F_j)]/2 \geq \bar{\Phi}_i$ (with equality occurring only for $c = \bar{c}$), which implies that inequality (E2) is true; that is, species i can invade. By a similar argument, species j cannot invade.

We have now shown that species i is dominant if $\bar{c}_i > \bar{c}_j$ and $\sigma_i^2 = \sigma_j^2$ or if $\bar{c}_i = \bar{c}_j$ and $\sigma_i^2 > \sigma_j^2$. To complete the proof that species i is dominant if $\bar{c}_i > \bar{c}_j$ and $\sigma_i^2 \geq \sigma_j^2$ or if $\bar{c}_i \geq \bar{c}_j$ and $\sigma_i^2 > \sigma_j^2$, we need only to show dominance when $\bar{c}_i > \bar{c}_j$ and $\sigma_i^2 > \sigma_j^2$; that is, inequality (E2) holds if $\bar{c}_i > \bar{c}_j$. To see this, note that if $\bar{c}_i > \bar{c}_j$, then, for a given c , $\bar{\Phi}_i$ is even smaller relative to $\bar{\Phi}_j$ than in the case where $\bar{c}_i = \bar{c}_j$, because $F_i(c)$ decreases as \bar{c}_i increases.

Appendix F from J. W. Lichstein et al., ‘Intraspecific Variation and Species Coexistence’

(Am. Nat., vol. 170, no. 6, p. 807)

Probability of Winning an Open Site with Uniform Seed Quality Distributions

Without loss of generality, we transform the seed quality axis so that species 1's seed quality distribution is uniform on $(0, 1)$. This simplifies the derivation of W_i but has no effect on the dynamics of the model. Species 1's probability density function (PDF) is thus $f_1(c) = 1$ for $0 \leq c \leq 1$ and $f_1(c) = 0$ otherwise, with cumulative density function (CDF) $F_1(c) = c$ for $0 \leq c \leq 1$, $F_1(c) = 0$ for $c < 0$, and $F_1(c) = 1$ for $c > 1$. For species 2, $c_2^{\min} = L$ and $c_2^{\max} = U$, with PDF $f_2(c) = 1/(U - L)$ for $L \leq c \leq U$ and $f_2(c) = 0$ otherwise, and CDF $F_2(c) = (c - L)/(U - L)$ for $L \leq c \leq U$, $F_2(c) = 0$ for $c < L$, and $F_2(c) = 1$ for $c > U$. Because of the discontinuities in f_i and f_2 , there are two distinct uniform cases, depending on whether or not one species' PDF is ‘nested’ within that of the other species.

Nested Distributions

Here, we derive W_i for the nested case (e.g., fig. 4A), with $0 < L < U < 1$. We first derive W_1 , the probability that species 1 wins an open site. The probability that seeds of both species are present at an open site and that species 1 wins is $W_1^* \equiv P(n_1 > 0, n_2 > 0, c_1^* > c_2^*)$, where n_i is the number of species i seeds arriving to an open site and c_i^* is the quality of species i 's best arriving seed. Because of the discontinuities in f_i and f_2 , we break W_1^* into two pieces: $W_1^* = W_{1a}^* + W_{1b}^*$, where $W_{1a}^* \equiv P(n_1 > 0, n_2 > 0, U \geq c_1^* > c_2^*)$, and $W_{1b}^* \equiv P(n_1 > 0, n_2 > 0, c_1^* > U \geq c_2^*)$. From equation (4),

$$W_{1a}^* = \sum_{n_1=1}^{\infty} \sum_{n_2=1}^{\infty} \frac{e^{-bx_1}(bx_1)^{n_1}}{n_1!} \frac{e^{-bx_2}(bx_2)^{n_2}}{n_2!} \int_L^U n_1 f_1 F_1^{n_1-1} \int_L^{c_1} n_2 f_2 F_2^{n_2-1} dc_2 dc_1,$$

where f_i and F_i are shorthand for $f_i(c)$ and $F_i(c)$, respectively. Rearranging gives

$$W_{1a}^* = \int_L^U \int_L^{c_1} f_1 f_2 \sum_{n_1=1}^{\infty} \frac{e^{-bx_1}(bx_1)^{n_1}}{n_1!} n_1 F_1^{n_1-1} \sum_{n_2=1}^{\infty} \frac{e^{-bx_2}(bx_2)^{n_2}}{n_2!} n_2 F_2^{n_2-1} dc_2 dc_1.$$

Note that terms of the form $\theta \equiv \sum_{n=1}^{\infty} [e^{-bx}(bx)^n/n!] n F^{n-1}$ can be rewritten as

$$\theta = e^{-bx} b x e^{bx F} \sum_{n=1}^{\infty} \frac{e^{-bx F} (bx F)^{n-1}}{(n-1)!} = e^{bx(F-1)} b x \sum_{n=0}^{\infty} \frac{e^{-bx F} (bx F)^n}{n!} = e^{bx(F-1)} b x. \quad (F1)$$

Substituting for θ_i , f_i , and F_i gives

$$W_{1a}^* = \frac{b^2 x_1 x_2}{U - L} \int_L^U \int_L^{c_1} e^{bx_1(c_1-1)} e^{bx_2(c_2-U)/(U-L)} dc_2 dc_1. \quad (F2)$$

Here, W_{1b}^* is the probability that $n_2 > 0$ and $c_1^* > U$:

$$W_{1b}^* = (1 - e^{-bx_2}) \sum_{n_1=1}^{\infty} \frac{e^{-bx_1} (bx_1)^{n_1}}{n_1!} \int_U^1 n_1 f_1 F_1^{n_1-1} dc_1,$$

which, if we rearrange as above and substitute for θ_1 (eq. [F1]), f_1 , and F_1 , gives

$$W_{1b}^* = (1 - e^{-bx_2}) bx_1 \int_U^1 e^{bx_1(c_1-1)} dc_1. \quad (F3)$$

It is straightforward to obtain closed forms for equations (F2) and (F3), giving a closed form for W_1 :

$$W_1 = \frac{x_2(e^{-b[x_1(1-L)+x_2]} - e^{-bx_1(1-U)}) + [x_1(U-L) + x_1](1 - e^{-b(x_1+x_2)})}{x_1(U-L) + x_2}. \quad (F4)$$

The derivation for W_2 is similar to that for W_1 , but unlike W_1^* , W_2^* need not be broken into two pieces, because f_2 is nested within f_1 . A closed form for W_2 is

$$W_2 = \frac{x_2(e^{-bx_1(1-U)} - e^{-b[x_1(1-L)+x_2]})}{x_1(U-L) + x_2}. \quad (F5)$$

Nonnested Distributions

We present W_1 and W_2 for the case where $c_1^{\min} = 0$, $c_1^{\max} = 1$, $1 > c_2^{\min} = L \geq 0$, and $c_2^{\max} = U > 1$. Closed forms for W_i in the nonnested case can be obtained in a manner similar to that for the nested case above by changing the limits of integration. In the nonnested case, W_i^* (eq. [4]) must be broken into two pieces for species 2 but not for species 1. Closed forms are

$$W_1 = \frac{x_1(U-L)e^{-bx_2(U-1)/(U-L)} - [x_1(U-L) + x_2(1 - e^{bx_1L})]e^{-b(x_1+x_2)}}{x_1(U-L) + x_2} \quad (F6)$$

and

$$W_2 = \frac{x_1(U-L)(1 - e^{-bx_2(U-1)/(U-L)}) + x_2(1 - e^{-b[x_1(1-L)+x_2]})}{x_1(U-L) + x_2}. \quad (F7)$$

Appendix G from J. W. Lichstein et al., “Intraspecific Variation and Species Coexistence”

(Am. Nat., vol. 170, no. 6, p. 807)

Invasion Criteria for Nested Uniform Seed Quality Distributions

Without loss of generality, we assume that species 1 has $c_1^{\min} = 0$ and $c_1^{\max} = 1$, and species 2 has $c_2^{\min} > 0$ and $c_2^{\max} < 1$ (e.g., fig. 4A). The invasion criteria, expressed as ratios (eq. [5]), are, from equations (F4) and (F5),

$$\tilde{R}_1 = \frac{e^{b\hat{X}}[b\hat{X}(1 - \bar{c}_2 - r_2/2) + r_2] + b\hat{X}(\bar{c}_2 - r_2/2) - r_2}{e^{b\hat{X}} - 1} > 1$$

and

$$\tilde{R}_2 = \frac{e^{b\hat{X}(\bar{c}_2 - r_2/2)}(e^{b\hat{X}r_2} - 1)}{r_2(e^{b\hat{X}} - 1)} > 1, \quad (\text{G1})$$

where $r_2 = c_2^{\max} - c_2^{\min}$ and we have substituted the global attractor \hat{X} for the resident \hat{x}_i . For particular values of fecundity (b) and adult mortality (μ), we can numerically solve for \hat{X} (fig. 3). It is then straightforward to calculate \tilde{R}_i from equation (G1).

We now examine \tilde{R}_i at the seed rain limits to confirm our general results (app. C). At the high-seed rain limit, we have $\lim_{b\hat{X} \rightarrow \infty} \tilde{R}_1 = \infty$ and $\lim_{b\hat{X} \rightarrow \infty} \tilde{R}_2 = 0$. Thus, species 1, with the higher maximum seed quality, is dominant at this limit. For the low-seed rain limit ($b \rightarrow \mu$), we Taylor expand \tilde{R}_1 and \tilde{R}_2 around $b\hat{X} = 0$. A third-order expansion gives $\tilde{R}_1 \approx 1 + b\hat{X}(\bar{c}_1 - \bar{c}_2)$ and $\tilde{R}_2 \approx 1 + b\hat{X}(\bar{c}_2 - \bar{c}_1)$. Thus, the species with the higher mean seed quality is dominant near the low-seed rain limit.