

How the Spatial Scales of Dispersal, Competition, and Environmental Heterogeneity Interact to Affect Coexistence

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ABSTRACT: Spatial coexistence depends on a variety of biological and physical processes, and the relative scales of these processes may promote or suppress coexistence. We model plant competition in a spatially varying environment to show how shifting scales of dispersal, competition, and environmental heterogeneity affect coexistence. Spatial coexistence mechanisms are partitioned into three types: the storage effect, nonlinear competitive variance, and growth-density covariance. We first describe how the strength of each of these mechanisms depends on covariances between population densities and between population densities and the environment, and we then explain how changes in the scales of dispersal, competition, and environmental heterogeneity should affect these covariances. Our quantitative approach allows us to show how changes in the scales of biological and physical processes can shift the relative importance of different classes of spatial coexistence mechanisms and gives us a more complete understanding of how environmental heterogeneity can enable coexistence. For example, we show how environmental heterogeneity can promote coexistence even when competing species have identical responses to the environment.

Keywords: coexistence, competition, dispersal, kernels, spatial heterogeneity, spatial scale.

Regional-scale ecological dynamics depend on biological and physical processes occurring at several spatial scales,

and changes in the relative scales of these processes can significantly alter regional-scale dynamics (Lande et al. 1999; Levin 2000; Bolker 2003; E. W. Seabloom, O. N. Björnstad, B. M. Bolker, and O. J. Reichman, unpublished manuscript). In particular, spatial mechanisms of coexistence in communities of sessile organisms such as plants depend on the scales of environmental heterogeneity, competition between and within species, and dispersal. Other studies have shown how the balance between scales of interspecific and intraspecific competition (Murrell and Law 2003), between scales of competition and dispersal (Bolker and Pacala 1999), or between scales of dispersal and environmental heterogeneity (Snyder and Chesson 2003) can affect competitive outcome, but researchers are only now beginning to consider all three spatial scales (E. W. Seabloom, O. N. Björnstad, B. M. Bolker, and O. J. Reichman, unpublished manuscript).

Species coexist if each species can increase when rare (Gotelli 1995). This article concentrates on species' recovery rates as the foundation of coexistence and explains how different spatial coexistence mechanisms increase or decrease that recovery rate. In order to consider multiple coexistence mechanisms, variable scales of dispersal and competition, and environmental variability across a range of spatial scales, we have relied on three tools: spatial interaction kernels, Fourier analysis, and a partitioning of the invader growth rate. Spatial interaction kernels are functions that define how the strengths of biological processes change with distance. For example, competition kernels define how the competitive effect of one individual on another declines with their distance apart, while dispersal kernels define the probability that a seed disperses a given distance. Fourier analysis, presented in more detail in "Our Mathematical Approach," simplifies the analysis of the interaction between different kernels. It also allows us to consider arbitrary patterns of environmental variation without having to choose a particular form in advance. Finally, we partition spatial mechanisms of coexistence into three broad classes—the storage effect, nonlinear competitive variance, and growth-density covariance—and explain how each is promoted or

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suppressed by the interplay of competition, dispersal, and environmental heterogeneity (Chesson 2000a).

This partitioning allows us to explore the relative importance of multiple coexistence mechanisms acting simultaneously. It also provides a more complete understanding of how spatial variability in environmental conditions promotes coexistence. For example, previous analyses of spatial coexistence have focused on source-sink dynamics, where different species thrive in different locations and dispersal from favorable locations subsidizes populations in unfavorable locations. Our analysis will show that environmental heterogeneity can promote coexistence even when species experience identical patterns of environmental favorability.

The rest of the article is organized as follows. We present our model of the local scale dynamics in “Local Dynamics: The Lottery Model” and shift to the regional scale in “The Regional Growth Rate and Coexistence.” We then briefly outline our mathematical approach in “Our Mathematical Approach.” In “Resident Population Distribution,” we calculate the equilibrium spatial distribution of a single species, which we use in later analyses of invasibility. We use the invasibility criterion for coexistence so that two species coexist if each species in monoculture can be invaded by the other species. “Spatial Variation Mechanisms” is broken into subsections devoted to the storage effect, nonlinear competitive variance, and growth-density covariance. This article intends to provide an intuitive understanding of how these spatial coexistence mechanisms work while at the same time providing the full mathematical justification for the mathematically inclined. To facilitate these dual aims, “Spatial Variation Mechanisms” contains descriptions for both audiences. In particular, each subsection includes a narrative description of what is going on based on the mathematical insights presented earlier in the subsection. We present a hypothetical example of two competing annual plants in “A Hypothetical Example” and discuss what we would expect for each species as invader, while in “The Scale of Environmental Variability,” we briefly discuss the sensitivities of the storage effect, nonlinear competitive variance, and growth-density covariance to different spatial scales of environmental variability. The main body of the article concludes with “Discussion.” Derivations of the quantitative expressions for each term are presented in the appendix in the online edition of the *American Naturalist*, as is a summary of the basic framework developed by Chesson (2000a).

Local- and Regional-Scale Dynamics

Local Dynamics: The Lottery Model

For specificity, we base our analysis on the lottery model, one of the standard examples for competition theory, anal-

ogous to the Lotka-Volterra model for predator-prey dynamics or the contact process for spatial spread (Chesson and Warner 1981; Comins and Noble 1985; Chesson 2000a; Moko and Iwasa 2000). We use a version of the lottery model based on annual plant communities, with dispersing juveniles that compete in continuous space to become sessile, semelparous adults. For simplicity, we define our model in one-dimensional space; however, our conclusions do not change in higher dimensions.

In the classical lottery model (Chesson and Warner 1981), the environment is assumed to have an important role in determining the number of seeds at a location through effects on reproduction. Once at a location, however, all seeds are assumed to have an equal chance of success. Thus, the success of any individual seed is inversely related to the total number of seeds present. In the presence of spatial environmental variation, however, the competitive ability of a seed may depend on environmental conditions at the seed’s location. Thus, we assume that the success of a seed of species j is not constant but is proportional to environmental response $E_j(x)$, a spatially varying, species-specific quantity reflecting the effects of the environment for location x and species j . By extension of the lottery idea, a seed’s success again diminishes as the density of neighboring seeds increases, but the competitive effect of a neighbor now declines with distance and depends on the neighbor’s environmental response. We now write this verbal account in terms of formulas and then return to discuss environmental response and competition in greater detail.

If a species j seed lands at location x at time t , where it has environmental response $E_j(x)$ and experiences competition $C_j(x, t)$, then the probability that it will establish itself and produce seeds is defined to be $E_j(x)/C_j(x, t)$. We assume that an adult of species j produces F_j seeds (species j has per capita fecundity F_j). The per capita local finite growth rate ($\lambda_j(x, t)$) then equals the probability of establishment times the per capita fecundity, making the number of species j seeds produced at x between times t and $t + 1$ equal to

$$\lambda_j(x, t)n_j(x, t), \quad (1)$$

where

$$\lambda_j(x, t) = \frac{F_j E_j(x)}{C_j(x, t)}.$$

(Alternatively, we may assume that $C_j(x, t)$ represents competitive processes after establishment, so $E_j(x)$ represents the probability of establishment, and per capita fecundity is reduced to $F_j/C_j(x, t)$ by competition. The mathematical

development here covers both possibilities or any combination of them.)

After the seeds are produced, they disperse with a species-specific probability $k_j(z)$ of traveling a distance z . Thus, the number of seeds landing at location x at time $t + 1$ ($n_j(x, t + 1)$) is equal to the number of seeds produced at location y between times t and $t + 1$ times the probability of dispersing from y to x , summed over all y , or

$$n_j(x, t + 1) = \int_{-\infty}^{\infty} k_j(x - y)(\lambda_j(y, t)n_j(y, t))dy. \quad (2)$$

To fully specify the model, we need to define the environmental response (E_j) and competition (C_j) of species j . Environmental response $E_j(x)$ can be any demographic parameter that is sensitive to the environment; in the context of annual plants, $E_j(x)$ might represent a germination probability. We assume that a species' environmental response varies in space but not in time. We are therefore considering environmental variation that can be treated in models as static, to a good approximation, such as aspect, exposure, and soil type. Different species may respond to different environmental variables or may respond differently to the same environmental variables, and so $E_j(x)$ is species specific.

We define competition as the multiple by which the local growth rate is decreased in the presence of neighbors: $C_j(x, t) = (\lambda_j(x, t) \text{ without neighbors})/(\lambda_j(x, t) \text{ with neighbors})$. We assume that competition $C_j(x, t)$ depends on how far away the neighbors of the focal plant are, what species they belong to, and how favorable their environments are. Individuals in favorable environments may grow larger or germinate earlier and thus have a greater competitive effect. We account for the effect of the environment on competition in a simple way by weighting the densities of the competitors by their environmental responses. Thus, the local competitive contribution of species k is $E_k(x)n_k(x)$.

The effect of competitors also declines with distance from the focal individual, and so the local competitive contribution of species k is weighted by competition kernel $U_{jk}(z)$, which represents the effect of a species k individual on a species j individual at a distance z . The shape of the kernel will depend on the range of the competition between the two species. For example, short-range competition leads to a narrow competition kernel. Competitors close to the focal individual contribute strongly to the total competition experienced by an individual, while those further away contribute only weakly (fig. 1, left). Long-range competition is represented by a low, broad kernel, so in-

dividuals over a wide area around the focal individual contribute similarly to the total competition experienced by the focal individual (fig. 1, right). Without loss of generality, we assume that the competition kernel integrates to 1. Under this assumption, the total competitive effect of species k on the focal individual is a weighted average of the local competitive effects:

$$\int_{-\infty}^{\infty} U_{jk}(x - y)(E_k(y)n_k(y))dy. \quad (3)$$

A weighted average of this kind, of the form $\int_{-\infty}^{\infty} K(x - y)N(y)dy$, is called a convolution, represented by $(K * N)(x)$; equation (3) would be expressed as $(U_{jk} * (E_k n_k))(x)$.

Finally, we must sum the competitive effects from different species of competitor k . Thus, the total competition experienced by an individual of species j at location x is

$$C_j(x) = \sum_k U_{jk} * (E_k n_k)(x). \quad (4)$$

The Regional Growth Rate and Coexistence

Coexistence is defined over some spatial extent, most sensibly the scale at which the community is effectively closed (Chesson 2000b). We call this scale the regional scale, and any measure of coexistence must deal with regional-scale densities and growth rates rather than with densities and dynamics at a particular spot. We define the regional-scale population density as the spatial average of the local population density (\bar{n}) and define the regional scale growth rate at time t , $\tilde{\lambda}(t)$, as the regional density at time $t + 1$ divided by the regional scale density at time t : $\tilde{\lambda}(t) = \bar{n}_j(t + 1)/\bar{n}_j(t)$. Thus, the regional scale dynamics are given by

$$\bar{n}_j(t + 1) = \tilde{\lambda}_j(t)\bar{n}_j(t). \quad (5)$$

We can relate the regional-scale growth rate to the local growth rate by noting that $n_j(x, t + 1)$ and $\lambda_j(x, t)n_j(x, t)$ must have the same spatial average because dispersal only redistributes offspring. Thus, $\tilde{\lambda}_j(t) = \bar{n}_j(t + 1)/\bar{n}_j(t) = \overline{\lambda_j(t)n_j(t)}/\bar{n}_j(t)$. Defining relative population density $v_j(x, t)$ as the local population density scaled by the average population density, $v_j(x, t) = n_j(x, t)/\bar{n}_j(t)$, we see that $\tilde{\lambda}_j$ is equal to $\overline{\lambda_j(t)v_j(t)}$. Thus, the regional-scale growth rate is the average of the local growth rate weighted by the relative population density, so locations with higher population densities contribute more to the regional-scale

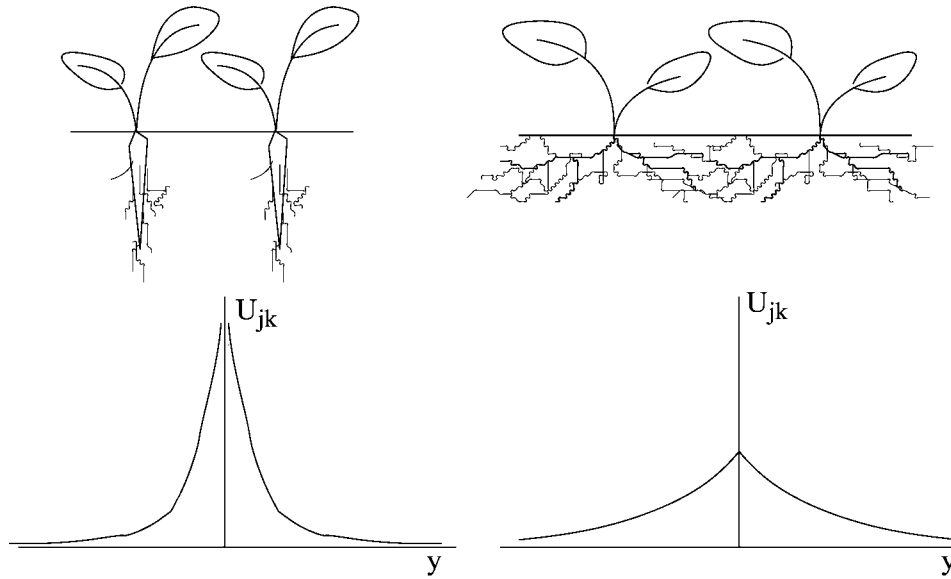


Figure 1: Short- and long-range competition kernels. The competition kernel $U_{jk}(y)$ indicates how much a competitor of species k affects an individual of species j if they are separated by distance y . All competition kernels are normalized to 1 (the area under the curve equals 1), which means that the total strength of competition is the same for all pairs of species. If both species have taproots and largely vertical growth habits, then competition will tend to be short range, and the competition kernel will be narrower, as in the figure on the left. On the other hand, if one or both plants have laterally spreading roots or sprawling growth habits, then competition will tend to be longer range, and the competition kernel will be wider, as in the figure on the right. Some forms of apparent competition, such as shared pathogens or herbivores, may also produce long-range competition.

growth rate. Finally, we note that $\overline{\lambda_j(t)v_j(t)}$ can be split into $\overline{\lambda_j(t)}\overline{v_j(t)} + \text{Cov}(\lambda_j, v_j)(t)$. The average of $v_j(x, t)$ is 1 by definition, and so

$$\tilde{\lambda}_j(t) = \overline{\lambda_j(t)} + \text{Cov}(\lambda_j, v_j)(t). \tag{6}$$

We use the standard mutual invasibility criterion for coexistence, which states that species coexist if each species can increase from a regionally low density (“invade”) in the presence of its competitors (the “residents”), which are not constrained to low density. Thus, the species coexist if each species has a sufficiently high regional-scale recovery rate from low density ($\tilde{\lambda}_i > 1$). We will use subscript i to denote invader quantities and subscript r to denote resident quantities, while subscript j represents generic species quantities.

Following Chesson (2000a), we partition $\tilde{\lambda}_i$ into the sum of nonspatial coexistence mechanisms ($\tilde{\lambda}'_i$), the storage effect (ΔI), nonlinear competitive variance (ΔN), and growth-density covariance ($\Delta \kappa$):

$$\tilde{\lambda}_i \approx \tilde{\lambda}'_i + \Delta I - \Delta N + \Delta \kappa. \tag{7}$$

The terms ΔI , ΔN , and $\Delta \kappa$ are quantitative measures of the contributions of the storage effect and so forth to the

invader’s regional-scale growth rate. When they increase the growth rate (ΔI and $\Delta \kappa$ positive, ΔN negative), they help the invader to persist in the presence of its competitors. The storage effect, nonlinear competitive variance, and growth-density covariance all depend on environmental variability and are stabilizing terms that, if strong enough, can overcome fitness differences and permit coexistence as discussed by Chesson (2000b). We discuss each in detail in “Spatial Variation Mechanisms” and in the appendix. Their most general forms are summarized in “Summary of the Basic Framework” in the appendix and presented in detail by Chesson (2000a). We do not discuss nonspatial coexistence mechanisms in the body of the article, but we do present a calculation of $\tilde{\lambda}'_i$ for the lottery model in “Nonspatial Coexistence Mechanisms” in the appendix.

Our Mathematical Approach

Fourier transforms, our primary tool for this analysis, partition variance into contributions from different spatial scales by reexpressing functions as sums of sine and cosine waves at different spatial frequencies, ω , proportional to 1 over the period of the sine or cosine. The Fourier transform of a spatial function $f(x)$ is denoted $\tilde{f}(\omega)$.

Two properties make Fourier transforms especially useful for this problem. First, the contributions of different spatial scales are additive, so we can study single scales of environmental variation without worrying that we may be missing interactions between scales. Second, spatial variances and covariances, which form the heart of the storage effect, nonlinear competitive variance, and growth-density covariance, have very simple representations in terms of Fourier transforms in which convolutions are reduced to products.

Covariances figure prominently in our analysis. A covariance (e.g., $\text{Cov}(E_j, C_j)$) is the product of the correlation between two quantities times the product of their standard deviations. A covariance can therefore be large if either the correlation is large or the standard deviations are large. The correlation can be taken between two quantities evaluated at the same location (e.g., $E_j(x)$ and $C_j(x)$) or between quantities evaluated at points a certain distance (“lag”) apart (e.g., $E_j(x)$ and $C_j(y)$, where the lag is $x - y$). The covariances in the expressions for ΔI , ΔN , and $\Delta \kappa$ are unlagged.

The details of our calculations are left to the appendix. However, a few words are necessary here to render the notation of the final results intelligible. For simplicity, we perform an invasibility analysis for only two species. We proceed by considering small deviations of the environmental response and the relative population density from their average values, $\epsilon_j(x) \equiv E_j(x)/\bar{E}_j - 1$ and $u_j(x) \equiv \nu_j(x) - 1$, where the variation in E is assumed to be small and the variation in ν is assumed to be of the same order of magnitude.

Resident Population Distribution

The resident’s equilibrium spatial distribution in the absence of the invader determines the competitive landscape for both the resident and the invader. In “Preliminary Calculations” in the appendix, we show that the equilibrium spatial distribution of $u_r(x, t)$, the deviation of the resident relative population density from its spatial average, equals the convolution of the environmental deviation $\epsilon_r(x)$ with another kernel, $M(z)$:

$$u_r(x) = \int_{-\infty}^{\infty} M(x - y)\epsilon_r(y)dy = (M * \epsilon_r)(x). \quad (8)$$

The kernel $M(z)$ gives the response of the resident population density to environmental variation a distance z away; in equation (8), $u_r(x)$ is calculated by weighting the resident environmental variation at y by $M(x - y)$ and integrating over y . We leave the expression for $M(x - y)$

to the appendix and note simply that it depends on resident dispersal and resident-resident competition. We more commonly use the Fourier transform of equation (8). Fourier transforms turn convolutions into products, giving the convenient expression

$$\tilde{u}_r(\omega) = \tilde{M}(\omega)\tilde{\epsilon}_r(\omega). \quad (9)$$

When $\tilde{M}(\omega)$ is large, it will amplify the effects of $\tilde{\epsilon}_r(\omega)$, so resident density has a large response and varies strongly at frequency ω , and when $\tilde{M}(\omega)$ is small, it will dampen the effects of $\tilde{\epsilon}_r(\omega)$, and resident density will have only a weak response. The full resident population distribution is then the sum of its responses at all frequencies.

The response function $\tilde{M}(\omega)$ is hump shaped. This means that resident density can best track environmental variation (larger populations in more favorable areas, smaller populations in less favorable areas) within the range of frequencies defining the extent of the hump, which is determined by the interplay between resident dispersal and resident-resident competition. The peak becomes higher and more pronounced as the scale of resident dispersal becomes shorter and the scale of resident-resident competition becomes longer (see fig. 2), indicating that resident population density is best able to track the resident environmental response when the environment varies at an intermediate scale, resident dispersal is short range, and resident-resident competition is long range, a pattern found in other studies as well (Roughgarden 1974; Gurney and Nisbet 1976). Short-range dispersal seems an obvious requirement for close tracking of the environment because local retention will cause the population density to build up in favorable areas. Long-range competition means that individuals in unfavorable areas compete not only with the few neighbors that share their environment but also with the many individuals in nearby favorable environments, driving population troughs even lower. Similarly, the competition of individuals in favorable areas is averaged over both high- and low-density areas, reducing their competitive load and allowing population peaks to rise still higher (see also Roughgarden 1974).

This allows us to understand why $\tilde{M}(\omega)$ is hump shaped. Population density will not be able to track very short scale environmental variation because plants gather their resources and disperse their seeds over some area, and these processes cause the plant to experience an average of its local environment. Environmental variation over too short a scale gets averaged out. On the other hand, resident population density also has a limited ability to track large-scale variation. When environmental heterogeneity is at a scale that is much larger than the scale of competition,

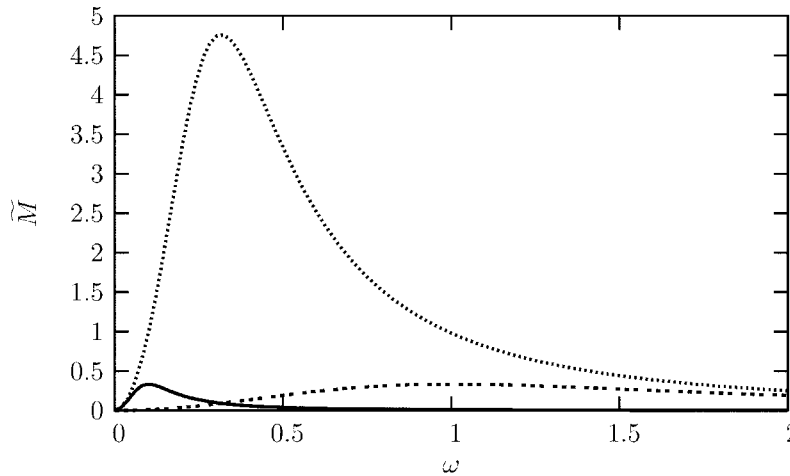


Figure 2: Resident population density’s response to environmental variation. The response function $\tilde{M}(\omega)$ shows how resident relative population density responds to environmental variation at different spatial frequencies ω via the equation $\tilde{u}_i(\omega) = \tilde{M}(\omega)\tilde{\epsilon}_i(\omega)$. The response to multiple frequencies of variation is the sum of the responses to single frequencies. The function $\tilde{M}(\omega)$ is hump shaped, indicating that resident population density responds most strongly to intermediate frequencies of variation. The peak in $\tilde{M}(\omega)$ becomes higher and sharper as resident dispersal becomes shorter range and resident-resident competition becomes longer range, reflecting the resident population density’s increased ability to track environmental variation at these frequencies. Laplacian kernels were used for resident dispersal and resident-resident competition: $k_r(x) = 1/(2a_r)\exp(-|x|/a_r)$, $U_r(x) = 1/(2b_r)\exp(-|x|/b_r)$. The characteristic dispersal scale, given by the mean of $|x|$, is thus a_r , and the characteristic scale of competition is b_r . (See the end of “Storage Effect.”) For the solid line, both dispersal and competition are relatively long range, with a_r and $b_r = 10.0$, while for the light dotted line, dispersal and competition are both short range, with a_r and $b_r = 1.0$. The heavy dotted line shows the combination that makes $\tilde{M}(\omega)$ the largest: short-range dispersal ($a_r = 1.0$) and long-range competition ($b_r = 10.0$).

individuals in crowded, favorable locations experience little release of competitive pressure. Likewise, individuals in sparsely populated, unfavorable areas are not suppressed by those in crowded areas. Because populations cannot track environmental conditions, environmental variation does not increase spatial variation in population density. The ability of the residents to track their environment at various spatial scales will affect how the strengths of our coexistence mechanisms change with the scale of environmental heterogeneity because, as we shall see, all of these coexistence mechanisms rely on variation in resident population density.

Spatial Variation Mechanisms

Storage Effect

Whenever the effects of the environment and competition on local growth interact (i.e., their combined effect cannot be expressed as a sum of a function of the environment and a function of competition), the invader’s regional-scale growth rate depends on the covariance of E and C (Chesson 2000a). For example, in our model, $\lambda_i(x) = FE_i(x)/C_i(x)$, which cannot be written in the form $\lambda_i(x) = f(E_i) + g(C_i)$, and so $\tilde{\lambda}_i$ will depend on $\text{Cov}(E_i, C_i)$. The storage effect incorporates both the

strength of the interaction and the covariance. While the strength of the interaction is often the same for both residents and invaders, their environment-competition covariances typically differ. A common resident species will be crowded by conspecifics in favorable areas, so competition is strong (C_i is large) where the environment is favorable (E_i is large), and thus $\text{Cov}(E_i, C_i)$ is large and positive. We consider only the initial growth of the invader from a globally low density, so the invader is too sparsely distributed to compete much with itself. Additionally, if it prefers different environmental conditions than the residents or if it competes with residents over a broad area, then neither will it experience much of an increase in competition with residents. Hence, the invader frequently experiences little increase in competition when in a favorable area, so $\text{Cov}(E_i, C_i)$ is small. The storage effect thus represents the degree to which invaders, relative to residents, are able to exploit favorable areas without encountering increased competition.

For our spatial lottery model, the storage effect (ΔI) is given by

$$\Delta I = F_r \text{Cov}(E_r, C_r) - F_i \text{Cov}(E_i, C_i), \tag{10}$$

where we evaluate the competition terms with invader density set to 0 and F_r and F_i are the resident and invader

Table 1: Response of storage effect components to dispersal and competition scales

Component of ΔI	Invader dispersal	Resident dispersal	Resident-resident competition	Resident-invader competition
$\text{Cov}(E_p, C_r)$	NA	Shorter	Shorter	NA
$\text{Cov}(E_p, C_i)$	NA	Shorter	Longer	Shorter

Note: For each component of ΔI , shorter indicates that the component increases as the length scale grows shorter, and longer indicates that the component increases as that length scale grows longer. NA means that that biological process does not affect the quantity in question.

fecundities. (See “Derivation of ΔI ” in the appendix for a derivation.) Thus, the storage effect is here simply the difference of the covariances between environment and competition for the resident and the invader, weighted by their fecundities.

To understand the factors affecting the covariances in these models, we can expand the environment-competition covariances in terms of covariances involving ϵ_j ($j = i, r$), the relative deviation of the environmental response from its spatial average, and u_r , the deviation of the resident equilibrium relative population density from 1, its spatial average. Here,

$$\text{Cov}(E_p, C_r) \approx [U_{rr} * (\text{Cov}(\epsilon_r, u_r) + \text{Cov}(\epsilon_r, \epsilon_r))], \quad (11)$$

$$\text{Cov}(E_i, C_i) \approx [U_{ir} * (\text{Cov}(\epsilon_i, u_r) + \text{Cov}(\epsilon_i, \epsilon_r))], \quad (12)$$

where we evaluate the competition terms with invader density set to 0. The covariances on the right-hand side are evaluated at a range of lags—giving the relationships between resident density fluctuations and resident and invader environmental fluctuations at different distances apart—and are then convolved with competition kernel U_{jr} . The whole expression is then evaluated at $x = 0$ to give the unlagged covariance $\text{Cov}(E_j, C_j)$. (See “Derivation of ΔI ” for a derivation of eqq. [11], [12].)

Equations (11) and (12) show that environment-competition covariances for both resident and invader depend on covariances of the resident and invader environments with the resident density ($\text{Cov}(\epsilon_j, u_r)$) and with the resident environment ($\text{Cov}(\epsilon_j, \epsilon_r)$), reflecting the fact that competition depends on both the local resident density and the resident’s environment, as expressed in equation (4).

The covariance of invader or resident environment ϵ_j with resident environment ϵ_r will be larger when either ϵ_j or ϵ_r varies more and when ϵ_j and ϵ_r are correlated (which is necessarily true for the covariance of the resident environment with itself). The covariances with resident density will be larger when the resident population density varies more. As shown in “Resident Population Distribution,” resident density varies more when resident dis-

persal is short range and resident-resident competition is long range. These covariances are then convolved with (averaged over) the competition kernels U_{rr} and U_{ir} . The larger the spatial scale of the competition, the more the averaging will tend to blur the covariances, making them smaller. Table 1 summarizes the effects of dispersal and competition scales on $\text{Cov}(E_i, C_i)$ and $\text{Cov}(E_p, C_r)$.

The size of the storage effect will depend on both the magnitude and the sign of $\text{Cov}(E_i, C_i)$. From the above, we see that the magnitude of $\text{Cov}(E_i, C_i)$ will be maximized when resident dispersal is short range and resident-resident competition is long range, increasing the variation in resident density (u_r), and when resident-invader competition is short range (U_{ir} narrow), preserving the covariance. The case of $\text{Cov}(E_p, C_r)$ is a little trickier. Making resident dispersal short range will always increase $\text{Cov}(E_p, C_r)$. However, U_{rr} has competing effects. Short-range resident-resident competition preserves the covariances of resident environmental response with itself and with resident density but reduces the variation in resident density, whereas long-range competition increases variation but diminishes the covariances. In the end, preserving the covariances is the more important effect so that $\text{Cov}(E_p, C_r)$ is maximized when resident-resident competition is short range. (In “Derivation of ΔI ,” we show that $\text{Cov}(E_p, C_r)$ is equal to an integral over ω , whose integrand is approximately equal to $1 - 6 \text{Var}(k_r) \text{Var}(U_{rr})\omega^2$ in the range that dominates the integral. Thus, $\text{Cov}(E_p, C_r)$ is decreased when we increase the range of either resident dispersal or resident-resident competition.)

The difference between $\text{Cov}(E_p, C_r)$ and $\text{Cov}(E_i, C_i)$ determines the storage effect (ΔI), and so ΔI will be larger when $\text{Cov}(E_i, C_i)$ is small and positive or large and negative. It is not clear in this formulation when $\text{Cov}(E_i, C_i)$ will be positive or negative. However, if we consider environmental variation at a single spatial frequency, we can show that $\text{Cov}(E_i, C_i)$ is positive when the invader and resident environments are in phase—meaning that both species tend to favor the same environments—and negative when they are out of phase. (See “Derivation

of ΔI .”) The net effects of changing dispersal and competition scales on ΔI are summarized in table 2.

We can use the above mathematical insights to construct an intuitive picture of what is happening. For the storage effect to benefit the invader, the covariance between environment and competition must be larger (more positive) for the resident than it is for the invader so that the resident’s growth is more strongly limited when it is in a favorable environment. This can happen in two ways.

If, on average, residents and invaders prefer different environments, residents will be dense in areas that are environmentally unfavorable for the invader. In order for the invaders to benefit from this spatial pattern, the competitive effect of the residents on the invaders must be short range (U_{ir} must be narrow). This ensures that invaders in a favorable location will incur minimal competition from nearby clusters of residents. Thus, if we were considering a resident that germinated best in clay-rich soils and an invader that fared better in sandy soils, the invader would benefit more from the storage effect if both species had relatively compact growth habits and root masses so that invaders in sandy patches did not compete too much with residents in nearby clay patches. In addition, if the resident environment varies strongly (so that maximizing $\text{Cov}(E_r, C_r)$ is more important than maximizing $|\text{Cov}(E_i, C_i)|$), then resident-resident competition must be sharply focused (short range) so that resident growth is strongly limited in particularly favorable areas. However, if the resident environment is not varying strongly (so that maximizing $|\text{Cov}(E_i, C_i)|$ becomes more important), long-range resident-resident competition can help to focus resident population density into the (moderately) more favorable areas, leaving low-density areas for invaders to exploit. Returning to our example, this means that if the resident were very sensitive to soil conditions,

with high germination rates when soil conditions were just right, then the invader would benefit if residents competed mostly with their immediate neighbors so that resident competition was strong in areas with high germination rates and the number of residents that reach maturity was limited. On the other hand, if resident germination rates varied only weakly with environmental conditions, then variation in soil type alone would not cause the resident to cluster much in favorable areas. However, long-range competition between residents, caused perhaps by laterally reaching root systems or low, sprawling growth, would amplify the resident’s response to environmental variation and cause it to cluster in the higher germination areas, freeing up space for the invader.

If residents and invaders grow best in similar habitats, the storage effect (ΔI) will be maximized when resident-resident competition is short range and resident-invader competition is diffuse/long range. This boosts the invader growth rate because residents in favorable areas limit themselves more than they limit invaders. Suppose, for example, that both the resident and invader germinated best in clay-rich soil. The invader would then tend to be mixed in among the residents. However, if the resident had a taproot while the invader had diffuse, laterally spreading roots, with a similar overall volume, then the competitive pressure on the resident would be determined largely by its crowded immediate neighborhood, while the invader would experience an average of both the crowded local surroundings and potentially less crowded areas farther away.

In either case, short-range resident dispersal strengthens the storage effect. This concentrates the resident population in favorable areas, increasing crowding and strengthening the covariance between resident environment and competition.

Table 2: Response of lottery model growth rate components to dispersal and competition scales

Component of $\tilde{\lambda}_i$	Invader dispersal	Resident dispersal	Resident-resident competition	Resident-invader competition
Storage effect (ΔI)	NA	Shorter	Shorter Inconsistent	Longer (E_i and E_r in phase) Shorter (E_i and E_r out of phase)
Nonlinear competition variance (magnitude) ($ \Delta N $) ^a	NA	Shorter	Longer	Shorter
Growth-density covariance ($\Delta\kappa$)	Shorter	Inconsistent Inconsistent ^c	Inconsistent ^b Inconsistent ^d	Inconsistent (E_i and E_r in phase) Shorter (E_i and E_r out of phase)

Note: For each component of $\tilde{\lambda}_i$, shorter indicates that the component increases as the length scale grows shorter, and longer indicates that the component increases as that length scale grows longer. NA means that that biological process does not affect the quantity in question. Inconsistent means that the effect of that spatial scale depends on the spatial scales and relative magnitudes of resident and invader environmental variation.

^a ΔN will be positive if $\text{Var}(C_r) > \text{Var}(C_i)$ and negative if the reverse is true.

^b Unless resident dispersal and resident-invader competition are both long range, in which case, shorter.

^c Unless resident-invader competition is short range and resident-resident competition is long range, in which case, shorter.

^d Longer if resident-invader competition is short range or otherwise inconsistent.

To understand how this measure, which applies to persistence of an individual species in competition with another species, affects species coexistence, we need to convert it into a community measure. Chesson (2003) shows how this is done by taking a weighted average of ΔI over all species as invader. Here (and in the other Δ measures discussed later), the weights are equal to 1, and the average is the ordinary average.

Figure 3 shows an example of how the strength of the storage effect changes with the scale of environmental heterogeneity. Because the contributions of different spatial scales are additive, it makes sense to consider resident and invader environments varying at a single spatial frequency, ω_e . In figures 3 and 4, the resident environment is $E_r(x) = \ln [B_r \sin(\omega_e x)]$, and the invader environment is $E_i(x) = \ln [B_i \sin(\omega_e x + \phi)]$. (Because of the quotient structure of λ_j in the lottery model, the assumptions listed in “Summary of the Basic Framework” about the size of perturbations in E and C are best met if environmental response is measured on a logarithmic scale.) Resident and invader environments are in phase when $\phi = 0$ and precisely out of phase when $\phi = \pi$. Figure 3 plots the storage effect (ΔI) as a function of the wavelength of the environmental heterogeneity, $2\pi/\omega_e$. In figure 3, as in figure 4, Laplacian forms are used for the dispersal and competition kernels: $k_j(x) = 1/(2a_j) \exp(-|x|/a_j)$, $U_{jr}(x) = 1/(2b_{jr}) \exp(-|x|/b_{jr})$. The scale parameters a_j and b_{jr} have

units of length and give an indication of the width of the kernel. For example, the mean dispersal distance of species j , $\int_{-\infty}^{\infty} |x|k_j(x)dx$, is a_j .

Nonlinear Competitive Variance

If growth drops off rapidly as competition initially increases from 0 but then reaches an asymptotic rate that is insensitive to further increases, then an organism in a highly variable competitive landscape will be able to take advantage of rare opportunities for quick growth with little risk of offsetting losses. Conversely, if growth is insensitive to low levels of competition but drops off rapidly when competition becomes high, then a species with the same mean level of competition will perform better if it is exposed to uniformly intermediate levels of competition and escapes damaging extremes. Nonlinear competitive variance gauges the relative abilities of the invader and resident to take advantage of rare opportunities and avoid damaging extremes.

Mathematically, the benefits or perils of varying competition arise from averages of nonlinear functions. The regional growth rate is an average of the local growth rate over a landscape in which the strength of competition varies. Because nonlinear functions weight their arguments unevenly, the average of a nonlinear function ($\overline{\lambda(C)}$) does not equal the nonlinear function of the average ($\lambda(\overline{C})$),

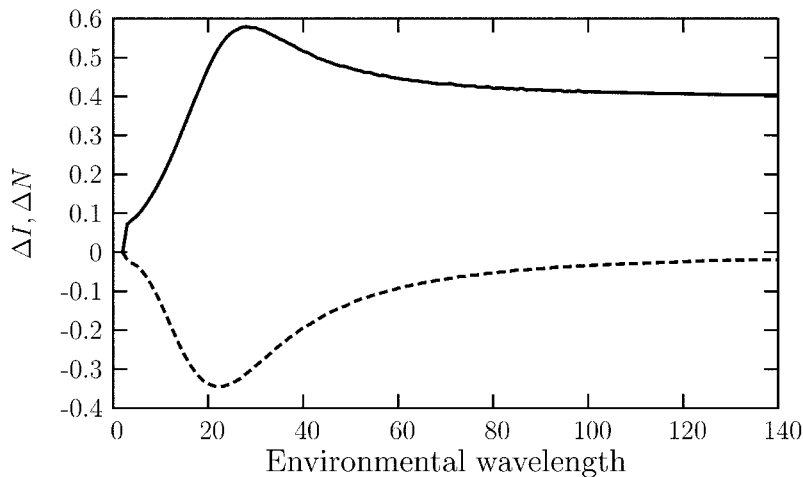


Figure 3: Storage effect and nonlinear competitive variance plotted against environmental wavelength for a sinusoidally varying environment. The strength of the storage effect is indicated by the solid line, and the dotted line shows the strength of nonlinear competitive variance. Invader dispersal is long range ($a_i = 10.0$), and resident dispersal is short range ($a_r = 2.0$), while resident-invader competition is short range ($b_{ir} = 2.0$), and resident-resident competition is long range ($b_{rr} = 5.0$). The phase difference ϕ between resident and invader environments equals π . Here and in figure 4, $F_i = F_r = 1$, $B_r = B_i = 0.6$, and the wavelength of the environmental heterogeneity, $2\pi/\omega_e$, is given on the X-axis. To create this figure and figure 4, the local dynamics according to equation (2) were simulated on a computer, and ΔI , ΔN , and $\Delta \kappa$ were calculated by measuring variances and covariances according to their definitions in equations (A36), (A57), and (A63) in the online-only appendix. These plots of ΔI and so forth therefore do not include the $O(\sigma^2)$ approximations made in the final expressions for these quantities.

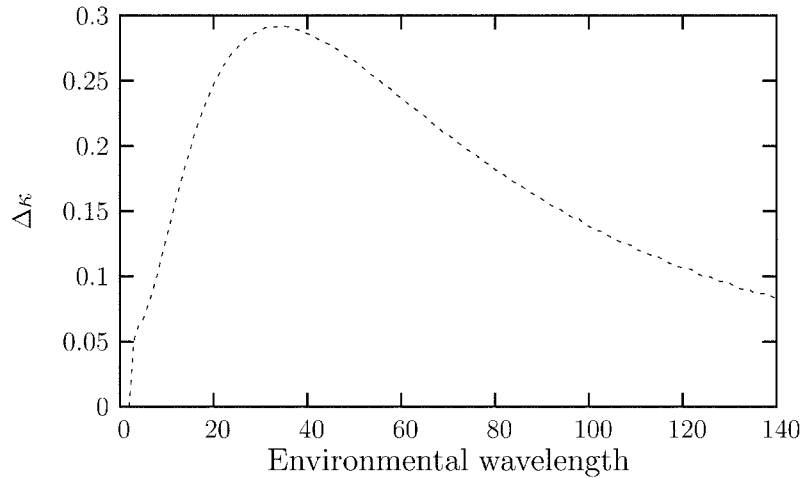


Figure 4: Growth-density covariance plotted against environmental wavelength for a sinusoidally varying environment. Invader dispersal is short range ($a_i = 2.0$), while resident dispersal is long range ($a_r = 100.0$). The competition kernels are identical and long range ($b_r = b_i = 10.0$). The phase difference ϕ is 0. All other parameters are as given in figure 3. (Because the calculation of growth-density covariance can be sensitive to finite domain size, its strength has been shown separately from those of the storage effect and nonlinear competitive variance, using parameter values that minimize that sensitivity.)

which means that the regional growth rate in a varying environment may be greater or less than the regional growth rate in a constant environment with the same mean. If the local growth rate decreases rapidly with competition and then levels off (rare opportunities, few risks), then greater variation in competition will boost the regional (average) growth rate. For example, in this model, the local growth rate is proportional to $1/C$. The growth rate is very large for small C , providing opportunities for rapid growth, but it declines only slowly as C increases beyond a certain point. Figure 5 shows a graphical demonstration of this for the simplistic case where competition takes only two values.

Nonlinear competitive variance depends both on the nonlinearity of the local growth rate and on the variance of competition. In “Derivation of ΔN ” in the appendix, we show that for our model,

$$\Delta N = \text{Var}(C_r) - \text{Var}(C_i), \quad (13)$$

where we evaluate both competition terms with invader density set to 0. The coefficients before the variances (unity) come from the way in which local growth depends nonlinearly on competition and are the same because λ is proportional to $1/C$ for both species. The competition variances will be different, however, if the species have different competition kernels. (See “Derivation of ΔN ” for a derivation of the general expression for nonlinear competitive variance.)

In this model, the resident and invader growth rates look like figure 5a, not figure 5b. When competition is low, the growth rate increases rapidly with further declines in competition, but when competition is high, the growth rate declines only slowly as competition increases. Both species therefore benefit from variable competitive environments. The invader gains an advantage when its competitive environment varies more than the resident’s does, as shown by equation (13). (Recall that ΔN enters the expression for the regional invader growth rate with a minus sign: $\tilde{\lambda}_i = \tilde{\lambda}'_i + \Delta I - \Delta N + \Delta \kappa$.)

The invader will have a larger competition variance than the resident when the resident density varies strongly (because resident population density is the source of competition) and resident-invader competition is more narrowly focused than resident-resident competition, so invaders close to peaks of resident density experience high competition, and invaders further from peaks of resident density experience low competition. This is reflected in the mathematical expressions for $\text{Var}(C_r)$ and $\text{Var}(C_i)$ in the lottery model, derived in “Derivation of ΔN ”:

$$\text{Var}(C_r) \approx \text{Var}[U_{rr} * (u_r + \epsilon_r)], \quad (14)$$

$$\text{Var}(C_i) \approx \text{Var}[U_{ir} * (u_r + \epsilon_r)]. \quad (15)$$

(The contribution to competition from a single point is normally the product of resident density and environment, $n_r(x)E_r(x)$, but to a satisfactory approximation for variance

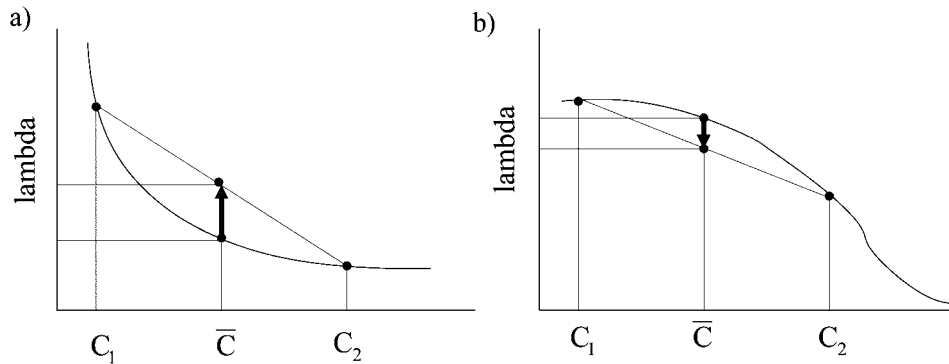


Figure 5: Effects of varying competition on the average growth rate. We assume a uniform environmental response and plot local growth as a function of competition. When competition equals \bar{C} everywhere, then local growth takes the same value everywhere, and the spatial average of the growth rate can be read directly from the graph. However, if each location has either competition C_1 or C_2 , such that the average competition is \bar{C} , then the average growth rate increases (if growth vs. competition is concave-up) or decreases (if growth vs. competition is concave-down) by the amount of the bold arrow. (For the simplistic case in which competition takes only two values with equal probability, the average growth rate is found by taking the midpoint of the line segment connecting the growth rates at high and low competition.) Intuitively, the average growth rate increases when competition varies if the increase in the growth rate at low competition is not offset by the decrease in the growth rate at higher competition.

calculations, the effects of density and environment can be treated as additive, $u_r + \epsilon_r$.) Looking at the expression for $\text{Var}(C_r)$, we see that if resident-resident competition is diffuse so that $U_{rr}(x)$ is a low, broadly peaked function, then the convolutions with U_{rr} will smear out most of the variation in u_r and ϵ_r , leaving the variance small. Similarly, looking at $\text{Var}(C_i)$, if resident-invader competition is narrowly focused so that $U_{ir}(x)$ is a sharply peaked function, then the convolutions with U_{ir} will preserve much of the variation in u_r and ϵ_r , allowing the variance to be substantial. Of course, there must be variation in u_r , the resident population density, to preserve. As explained in “Resident Population Distribution,” the resident population density varies more strongly as the spatial scale of resident dispersal decreases and the spatial scale of resident-resident competition increases, so long-range resident-resident competition increases the magnitude of nonlinear competitive variance in two ways. The effects of different scales of dispersal and competition are summarized in table 2, while figure 3 shows an example of how the strength of nonlinear competitive variance changes with the scale of environmental heterogeneity.

“Derivation of ΔN ” contains a Fourier representation of ΔN (eq. [A67]). The expression for ΔN vanishes if $\tilde{U}_{rr} = \tilde{U}_{ir}$; thus, the two competition kernels, U_{ir} and U_{rr} , must be different for ΔN to be nonzero. This requirement occurs because the growth rates for both species are nonlinear in C in the same way (the two are not relatively nonlinear), and so ΔN arises entirely from differences in their competitive variances, which come in turn from differences in their competition kernels.

Constructing an intuitive picture from the mathematics, short-range resident dispersal and long-range resident-resident competition cause the resident population distribution to respond more sensitively to resident environmental variation, leaving low-density areas in which invaders will experience low competition and high growth rates. Although this process also creates high-density areas in which invaders experience high competition because of the way in which local growth is nonlinear in competition ($\lambda \propto 1/C$), these high-competition areas do not decrease the local growth rates as much as the low competition areas increase them. Short-range resident-invader competition ensures that the competitive pressure on invaders comes mostly from the local resident density and environment and not from an average over high- and low-density areas. Long-range resident-resident competition, in addition to increasing variability in resident population density, means that residents are less able to take advantage of their own low-density areas because competitive pressure on residents comes from a broad spatial region that may encompass both high- and low-density zones.

Nonlinear competitive variance will promote the coexistence of the community if the average of ΔN over all species as invader is negative (Chesson 2003). The average of ΔN will of course be negative if it is negative for both species individually. Looking at the Fourier representation of ΔN (eq. [A67]), we can see that this will happen if competition within species is longer range than competition between species ($\tilde{U}_{11}(\omega)$ and $\tilde{U}_{22}(\omega)$ narrow and $\tilde{U}_{12}(\omega)$ and $\tilde{U}_{21}(\omega)$ broad). (This situation was also found

to promote coexistence by Murrell and Law [2003], though for a different reason. See “Discussion.”) This may be possible if there is long-range apparent competition due to specialist predators or pathogens.

Growth-Density Covariance

Growth-density covariance ($\Delta\kappa$) measures the degree to which the resident and invader populations accumulate in favorable locations. While population buildup must ultimately lead to crowding and a reduced growth rate, for questions of coexistence, we consider only the initial recovery of invader populations from regionally low densities, and so population retention in favorable locations is beneficial for the invader.

For the lottery model, growth-density covariance is given by the difference in the covariance between local growth rate λ and relative population density ν for residents and invaders:

$$\Delta\kappa = \text{Cov}(\lambda_i, \nu_i) - \text{Cov}(\lambda_r, \nu_r), \quad (16)$$

where again, λ_j and ν_j are calculated with invader density set to 0 and the covariances are evaluated at 0 lag. (See “Derivation of $\Delta\kappa$ ” in the appendix for a derivation of eq. [16]. For the most general form, see the review of the general framework in “Summary of the Basic Framework.”) $\text{Cov}(\lambda_j, \nu_j)$ will be positive if relative population density ν_j is high where growth rate λ_j is high, so $\Delta\kappa$ will be positive if population density concentrates in high-growth areas to a greater extent for the invader than for the resident.

For this model, $\text{Cov}(\lambda_i, \nu_i)$ is proportional to the integral of the product of $\tilde{k}_i(\omega)/[1 - \tilde{k}_i(\omega)]$ and $\tilde{R}(\omega)$, where $\tilde{R}(\omega)$ depends on the Fourier transform of resident-invader competition ($\tilde{U}_{ir}(\omega)$), the response of the resident to its environment ($\tilde{M}(\omega)$), and the Fourier transforms of the resident and invader environments ($\tilde{\epsilon}_r(\omega)$ and $\tilde{\epsilon}_i(\omega)$). (See “Derivation of $\Delta\kappa$ ” for the full expression.) Meanwhile,

$$\begin{aligned} \text{Cov}(\lambda_r, \nu_r) \approx \\ \text{Cov}(\epsilon_r, u_r) - [U_{rr} * (\text{Cov}(\epsilon_r, u_r) + \text{Cov}(u_r, u_r))], \end{aligned} \quad (17)$$

where, as with ΔI , the covariances that are convolved with the competition kernel U_{rr} are functions of a lag and the entire convolution is evaluated at 0. (See “Derivation of $\Delta\kappa$ ” for a derivation.)

We can derive some simple insights from these expressions. The resident growth-density covariance, $\text{Cov}(\lambda_r, \nu_r)$, is approximately equal to the covariance between the resident environment and the resident relative density, $\text{Cov}(\epsilon_r, u_r)$. The other terms, $U_{rr} * (\text{Cov}(\epsilon_r, u_r) +$

$\text{Cov}(u_r, u_r)$), are generally small because if resident-resident competition is short range, u_r will not vary much (see “Our Mathematical Approach”), but if resident-resident competition is long range, then the two covariances will be averaged away by their convolution with the broadly peaked competition kernel U_{rr} . The statement $\text{Cov}(\lambda_r, \nu_r) \approx \text{Cov}(\epsilon_r, u_r)$ means that the residents will accumulate in favorable locations ($\text{Cov}(\lambda_r, \nu_r)$ will be larger) if the residents can track their environment well, which requires short-range dispersal and long-range competition with each other, as discussed in “Resident Population Distribution.”

In the integral for invader growth-density covariance, $\tilde{k}_i(\omega)/(1 - \tilde{k}_i(\omega))$ becomes very large for $\omega \ll 1/(\text{Var}(k_i))^{1/2}$, so the smaller $\text{Var}(k_i)$ is, the greater the range of frequencies is over which $\tilde{k}_i(\omega)/(1 - \tilde{k}_i(\omega))$ is large. The standard deviation of the invader dispersal kernel, $(\text{Var}(k_i))^{1/2}$, can be thought of as representing typical invader dispersal distances, so $\text{Cov}(\lambda_i, \nu_i)$ can be quite large when invader dispersal is short range ($\text{Var}(k_i)$ small) and environmental variation is present at scales much larger than typical dispersal distances ($\omega \ll 1/(\text{Var}(k_i))^{1/2}$). (This is discussed further in Snyder and Chesson 2003.) Although we have reached this result mathematically, it is not surprising that short-range dispersal helps the invader to accumulate in favorable locations.

What is less clear are the roles of resident-resident and resident-invader competition and resident dispersal in determining $\text{Cov}(\lambda_i, \nu_i)$. This is difficult to tease out analytically, but plotting $\tilde{R}(\omega)$ for different combinations of phase difference between resident and invader environments, magnitudes of resident and invader environments, and dispersal and competition scales reveals some patterns for the case when resident- and invader-favorable areas are largely distinct. In this case, short-range resident-invader competition increases $\text{Cov}(\lambda_i, \nu_i)$. Short-range resident dispersal also increases $\text{Cov}(\lambda_i, \nu_i)$, although if resident-invader competition is long range and resident-resident competition is short range, the effect is minimal. Long-range resident-resident competition increases $\text{Cov}(\lambda_i, \nu_i)$, although if resident dispersal and resident-invader competition are long range, the effect is again minimal.

The effects of changing the spatial scales of dispersal and competition on the components of $\Delta\kappa$ are summarized in table 3. In practice, the size of $\text{Cov}(\lambda_i, \nu_i)$ often dominates $\text{Cov}(\lambda_r, \nu_r)$, both because of the size of \tilde{R} and because of the amplifying effect of $\tilde{k}_i/(1 - \tilde{k}_i)$. The net effects of changing dispersal and competition scales are summarized in table 2.

Let us use these mathematical insights to construct an intuitive picture of what is happening. Short-range invader dispersal increases $\Delta\kappa$ by helping the invader population

Table 3: Response of growth-density components to dispersal and competition scales

Component of $\Delta\kappa$	Invader dispersal	Resident dispersal	Resident-resident competition	Resident-invader competition
$Cov(\lambda_i, \nu_i)$	Shorter	Inconsistent Shorter ^a	Inconsistent Longer ^b	Inconsistent (E_i and E_r in phase) Shorter (E_i and E_r out of phase)
$Cov(\lambda_r, \nu_r)$	NA	Shorter	Longer	NA

Note: For each component of $\Delta\kappa$, shorter indicates that the component increases as the length scale grows shorter, and longer indicates that the component increases as that length scale grows longer. NA means that that biological process does not affect the quantity in question. Inconsistent means that the effect of that spatial scale depends on the spatial scales and relative magnitudes of resident and invader environmental variation.

^a Minimal effect if resident-invader competition is long range and resident-resident competition is short range.

^b Minimal effect if resident dispersal and resident-invader competition are both long range.

to accumulate in favorable locations. The other situations about which we can say something definite occur when residents and invaders prefer different environments, so any peaks of resident density are offset from the areas most favorable to invaders. Short-range resident-invader competition reduces the competitive effect of residents in favorable areas on invaders in their own favorable areas, increasing λ_i there and thereby increasing $Cov(\lambda_i, \nu_i)$ and $\Delta\kappa$. Resident population density can be focused in favorable resident areas, reducing its presence in favorable invader areas, if resident dispersal is short range or resident-resident competition is long range, as explained in “Resident Population Distribution.” However, because this increases $Cov(\lambda_r, \nu_r)$ in addition to $Cov(\lambda_i, \nu_i)$, the net effect on $\Delta\kappa$ depends on which covariance dominates. At least for the Laplacian kernels that we have used, long-range resident-resident competition consistently increases $\Delta\kappa$ when resident and invader environments are out of phase, whereas the effects of short-range resident dispersal depend on the magnitudes and spatial scales of resident and invader environments.

Figure 4 shows an example of how the strength of growth-density covariance changes with the scale of environmental heterogeneity. Growth-density covariance will promote coexistence in the community as a whole if the average of $\Delta\kappa$ over all species as invader is positive (Chesson 2003).

A Hypothetical Example

Suppose that we are investigating coexistence between two annual plant species. One, which we shall call dandelion-like, has light, winged seeds able to travel long distances, prefers sandy soil, and has a taproot. The other, which we shall call lupine-like, also has a taproot but has heavy seeds that remain close to the parent plant and prefers clay-rich soil. It also has a specialist insect predator. If we suppose that competition is largely for underground resources,

competition between dandelion-like individuals and between dandelion-like and lupine-like individuals should be short range because their root systems do not have much lateral extent. Direct competition between lupine-like individuals will also be short range, but the presence of the insect predator will add apparent competition. Let us suppose that the insect is fairly mobile so that total competition between lupine-like individuals is long range. What do we expect ΔI , ΔN , and $\Delta\kappa$ will look like for each of these two species as invader?

When the dandelion-like species is the invader, invader dispersal is long range, so we expect little growth-density covariance. Resident-invader competition is short range, resident-resident competition is long range, and E_i and E_r are out of phase. Looking at table 2, we see that the short-range resident-invader competition should increase the size of the storage effect, although the effect of resident-resident competition is unclear. Meanwhile, nonlinear competitive variance could be substantial. Because resident-resident competition is longer range than resident-invader competition, ΔN will be negative, benefiting the invader. Figure 6 shows ΔI , ΔN , and $\Delta\kappa$ plotted against environmental wavelength for a sinusoidally varying environment.

Now consider the lupine-like species as the invader. Invader dispersal is short range, so growth-density covariance may be substantial. In this case, resident-resident and resident-invader competition are both short range. Let us suppose that these competition kernels are actually the same. In this case, there will be no nonlinear competitive variance. As before, the short-range resident-invader competition will increase the storage effect. The values of ΔI and $\Delta\kappa$ are plotted against environmental wavelength in figure 7.

The Scale of Environmental Variability

Nonlinear competitive variance, the storage effect, and growth-density covariance each peak at intermediate scales

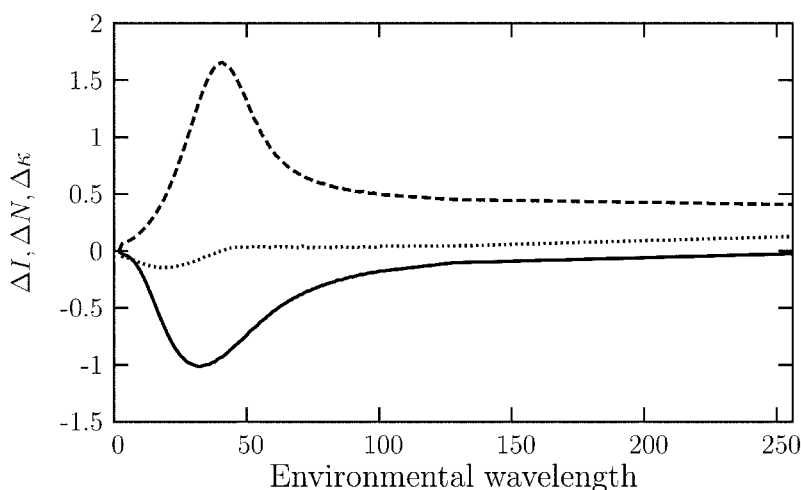


Figure 6: Regional-scale growth rate components plotted against environmental wavelength for the dandelion-like species as invader. ($a_i = 100.0$, $a_r = 2.0$, $b_r = 2.0$, $b_r = 10.0$, phase difference $\phi = \pi$. All other parameters are as in fig. 3.) The light dotted line shows the storage effect, the solid line shows nonlinear competitive variance, and the heavy dotted line shows growth-density covariance.

of environmental heterogeneity because they all rely on variation in resident density (u_r appears in the expressions for ΔN , ΔI , and $\Delta \kappa$), and resident density varies only in response to environmental heterogeneity at intermediate spatial scales. For relative nonlinearity, it is clear why this should be so because relative nonlinearity arises from variance in competition, which comes from variance in resident density. Likewise, the storage effect relies on covariance between resident environmental response and resident competition and hence on covariance between resident environment and resident density. Growth-density covariance ($\Delta \kappa$) is more complicated. At first glance, it would seem as though the less resident density varies, the stronger $\Delta \kappa$ would be because $\Delta \kappa$ is large when the invader population is concentrated in favorable locations and the resident population is more evenly distributed. However, growth-density covariance measures how strongly the invader population is concentrated in areas with a high growth rate, which is a result not only of a large environmental response but also of low competition. When resident density varies a little bit, it affords opportunities for lower competition and larger invader growth rates.

Discussion

Our models show how different scales of dispersal, competition, and environmental heterogeneity can interact to promote or suppress spatial mechanisms of coexistence. We connect these spatial scales to their effects on coexistence in two steps: we express the invader's regional-

scale growth rate in terms of various covariances and then show how these covariances are strengthened or weakened by changes in biological and physical scales.

We have also presented an extension of relative nonlinearity, a previously known mechanism of coexistence. Both relative nonlinearity and its extension, nonlinear competitive variance, result from a variable competitive landscape and growth that is a nonlinear function of competition. Distinguishing the two involves the concept of limiting factors (Levin 1970). Both C_i and C_r are limiting factors because the invader and resident growth rates depend on them and they reflect competition. When competition kernels are the same for all pairs of species ($U_{11} = U_{12} = U_{21} = U_{22}$), then invader competition and resident competition become equal ($C_i = C_r = C$), and λ_i and λ_r are functions of the same limiting factor, C . Relative nonlinearity applies when the growth rates of different species are different nonlinear functions of the same limiting factors. For example, if the growth rate of species 1 were $\lambda_{1,x} = E_{1,x}/C$ and the growth rate of species 2 were $\lambda_{2,x} = E_{2,x}/C^2$, then there would be relative nonlinearity. Nonlinear competitive variance allows the growth rates of different species to be nonlinear functions of different limiting factors. This could mean the same nonlinear function of different factors, which is the case here. Because invader and resident competition involve different competition kernels, C_i and C_r are different limiting factors, and so λ_i and λ_r are the same nonlinear function (the reciprocal function) of different limiting factors. The nonlinear competitive variance that we have here depends on the fact that C_i and C_r have different variances and that each of

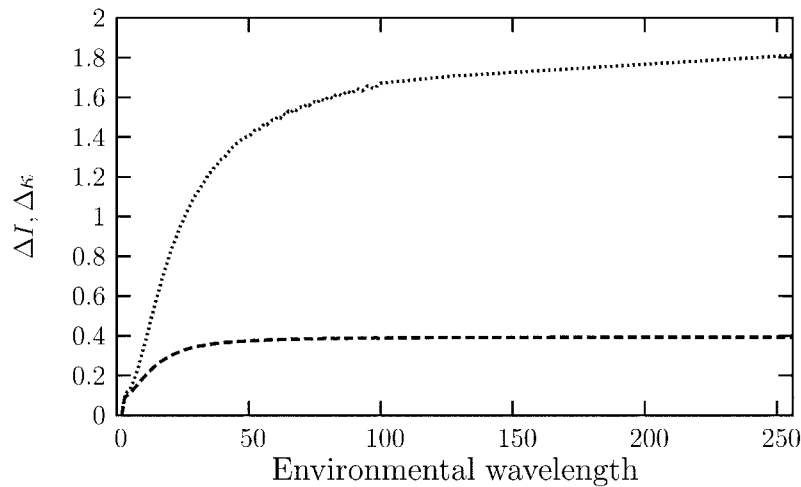


Figure 7: Regional-scale growth rate components plotted against environmental wavelength for the lupine-like species as invader. ($a_i = 2.0$, $a_r = 100.0$, $b_{ir} = b_{rr} = 2.0$, phase difference $\phi = \pi$. All other parameters are as in fig. 3.) The light dotted line shows the storage effect, and the heavy dotted line shows growth-density covariance.

them have nonlinear effects on growth. More details are given in “Derivation of ΔN .”

Connections with Existing Literature

By partitioning the invader’s regional-scale growth rate into contributions from different classes of coexistence mechanisms, we are able not only to indicate the relative importances of different mechanisms in different circumstances but also to give a more complete understanding of how environmental heterogeneity can promote coexistence. Most discussions of coexistence in heterogeneous environments have been framed in terms of source-sink dynamics or a “spatial mass effect” (Shmida and Whittaker 1981; Shmida and Ellner 1984). (Classically, a sink refers only to a place in which the local finite growth rate λ_{jx} is <1 even in the absence of competition; however, we use this term more loosely to refer to any place in which λ_{jx} is <1 .) It is assumed that species’ responses to the environment are dissimilar, so different locations favor different species, and a species’ most favorable locations act as a source, subsidizing less favorable areas where the population would ordinarily decline. However, we have shown that environmental heterogeneity can promote coexistence when species’ environmental responses are similar or even identical, as long as they experience competition on different spatial scales. A species can gain an advantage by being less limited by competition in its favorable areas (ΔI) or by being better at retaining its population in favorable areas ($\Delta \kappa$). It is even possible for environmental variation itself to promote coexistence, whether species

have similar or different responses, as long as the two species experience different variation in competition (ΔN). Pacala and Roughgarden (1982) give an example of coexistence via growth-density covariance when the species have similar habitat preferences. They discuss a two-patch model in which both the resident and invader have a higher carrying capacity in patch 1 than in patch 2. Short-range dispersal in the context of this model means local retention, while long-range dispersal means dispersal into the other patch. In the absence of dispersal between patches, high competition from the resident would make both patches sinks for the invader, but resident dispersal causes a net flow of residents to the patch with the lower carrying capacity (patch 2), lowering interspecific competition enough in patch 1 for the invader to survive there. This patch may then become a source of invaders for patch 2. In a second example, the invader could survive in both patches in the absence of dispersal, but resident dispersal raises the resident population in patch 2, potentially increasing the invader’s competition there to the point that patch 2 becomes a sink for the invader. The invader can then persist only if it has sufficient local retention (i.e., short-range dispersal) in patch 1.

Of course, if species have dissimilar environmental responses, source-sink dynamics can arise, and these can be created by either the storage effect or growth-density covariance. Which mechanism is active depends on the details of how the environmental response affects local growth λ_{jx} . The storage effect measures the covariance between the different effects of environmental response and competition on growth. If environmental response has

no direct effect on growth but instead changes λ_{jx} only indirectly via its effect on competition, defined as the fractional reduction of the growth rate in the presence of neighbors, then there can be no storage effect, although growth-density covariance is possible. A number of the articles that discuss coexistence via source-sink dynamics demonstrate growth-density covariance (Muko and Iwasa 2000; Amarasekare and Nisbet 2001; Codeço and Grover 2001; Levine and Rees 2002). (A further discussion of growth-density covariance in existing articles can be found in "Synthesis of Spatial Mechanisms" in Snyder and Chesson 2003.) Other source-sink discussions feature a storage effect (Shmida and Ellner 1984; Chesson 1985; Comins and Noble 1985) or a combination of both (Mouquet and Loreau 2002).

Another well-known spatial coexistence mechanism is the competition-colonization trade-off (Tilman 1994), in which a far-dispersing inferior competitor is able to persist by being better at colonizing newly available habitat. Long-distance dispersal is beneficial to the invader when there is a competition-colonization trade-off but is not a feature of any of the spatial coexistence mechanisms we have discussed. The reason for this is that we consider fixed spatial environmental variation only—there are no temporal fluctuations in environmental conditions to open up new habitat—and we assume that the resident has reached a stable equilibrium where the effects of demographic stochasticity are negligible; the resident will not become locally extinct because of either cyclic dynamics or chance demographic events. Because there is no new habitat to exploit, long-distance dispersal can cause the invader to experience a net loss of population only from the most favorable areas.

We are unaware of any studies showing that spatial relative nonlinearity or nonlinear competitive variance has played a significant role in coexistence. This is unsurprising. Nonlinear competitive variance requires a nonzero spatial scale for competition, and few studies have considered the scale of competition. When competition occurs only at a point (zero-length scale), then only relative nonlinearity is possible, and, as already discussed by Chesson (2000a), relative nonlinearity is unlikely to be a prominent spatial coexistence mechanism, although its analog for temporal variation can be important (Abrams 2004).

A few articles have considered the spatial scales of both dispersal and competition. Our work is most closely related to that of Murrell and Law (2003), who include both dispersal and competition kernels, although the environment is homogeneous. Murrell and Law make the scales of intraspecific competition equal ($U_{rr}(x) = U_{ii}(x)$) and the scales of interspecific competition equal ($U_{ir}(x) = U_{ri}(x)$) and find that when species have identical dispersal kernels and life-history parameters, the species coexist if interspecific competition occurs on a shorter scale than intra-

specific competition. This matches our finding that if interspecific competition occurs on a shorter scale than intraspecific competition, nonlinear competitive variance (ΔN) will increase the regional-scale invasion rates of both species. Local dispersal drives both species to aggregate, and diffuse intraspecific competition does little to oppose the formation of conspecific clusters. This means that there are gaps in resident density for the invader to exploit and that the invader is able to track these gaps. Meanwhile, shorter scale interspecific competition prevents residents from having too strong an effect on the interiors of invader clusters. Although there is no environmental heterogeneity, this coexistence mechanism is effectively a form of growth-density covariance, in which the invaders track not a favorable physical environment but enemy-free space. Of course, in this form, coexistence will be promoted as resident-resident competition becomes longer, not shorter, because that is what causes gaps for the invaders to inhabit.

This work is also connected with that of Bolker (2003), who considers the effects of environmental heterogeneity along with dispersal and competition kernels. Although Bolker does not explicitly address coexistence, he does note that short-range dispersal allows more offspring to be retained in favorable environments and thereby becomes more advantageous as environmental heterogeneity increases. This again is a form of growth-density covariance.

Testing the Robustness of Our Conclusions

We have shown how ΔI , ΔN , and $\Delta \kappa$ respond to changes in the spatial scales of dispersal, competition, and environmental variation in the lottery model. While the lottery model is a useful caricature of several biological systems, it is important to ask how well our conclusions generalize to systems with fundamentally different dynamics. We have tried to show that our mathematical conclusions make intuitive sense: it is reasonable, for example, that short-range dispersal allows the invader to accumulate in favorable locations and thus increases growth-density covariance. This gives us hope that our conclusions are likely to be broadly valid. Nonetheless, how would one go about testing these ideas?

One approach is theoretical. One could use different models or simply different definitions of competition and proceed mathematically as we have here to see whether our conclusions remain valid. The second approach is empirical. This approach, which is already in use (Melbourne et al. 2004; Sears 2004), begins by defining a model for the population dynamics of an experimental system in terms of an empirically defined E and C . (Having λ proportional to E/C is generally a good choice, at least within one life-history stage.) One then makes experimental measurements of ν , E , and C for both the invader and the

resident as they vary over a landscape so that the relevant variances and covariances can be determined and ΔI , ΔN , and $\Delta \kappa$ estimated.

In articles by Melbourne et al. (2004) and Sears (2004), a species that had recently been driven to low density served as the invader, while a common species served as the resident. These studies begin with a slight modification of the model used here in which C is measured at different points in space by standard neighbor-removal experiments (Goldberg et al. 1999); E is characterized as an effect on fecundity, and natural spatial variation in the environment is measured and detected on the basis of plant performance in the absence of neighbors. Measuring the spatial distributions of both invader and resident allows one to estimate ν_i and ν_r . Having obtained C , E , and ν for each species, it is possible to measure all of the covariances and variances in the expressions for ΔI , ΔN , and $\Delta \kappa$. Measuring the effects of nonlinear competitive variance has not yet been attempted because it was not understood before the work in this manuscript, but in principle, it is not of greater difficulty than measuring the other effects discussed here.

The storage effect and growth-density covariance will promote persistence of a species if their corresponding measures (ΔI and $\Delta \kappa$) are positive. Thus, measuring ΔI and $\Delta \kappa$ to see whether they are significantly positive is a test of the hypothesis that these mechanisms contribute to persistence of that species. Similarly, nonlinear competitive variance contributes to persistence if ΔN is negative, and so one should test whether ΔN is significantly negative.

The true power of our approach, however, lies in its ability to distinguish both the absolute and the relative degrees to which different mechanisms are contributing to coexistence and not simply to determine their presence or absence. By quantifying the strengths of different mechanisms, we can also determine the degree to which environmental variation may be diminishing persistence by different mechanisms. For example, if the resident has a stronger tendency to aggregate in high-growth areas than the invader, then $\Delta \kappa$ will be negative.

This study has focused on the contributions of environmental variation on persistence as the root of coexistence, and coexistence is certainly promoted when environmental variation increases the regional-scale growth of all species as invader. It is also possible, however, that a mechanism promotes coexistence in the community as a whole by giving a boost to a subordinate species (positive ΔI or $\Delta \kappa$, negative ΔN) while disadvantaging a dominant (negative ΔI or $\Delta \kappa$, positive ΔN). One can determine whether there is an overall coexistence-promoting effect by combining separate species values into an overall community level Δ value, using a weighted average over species (Chesson 2003). As mentioned above, the weights are 1

in the models given here, so the weighted average is an ordinary average. Evidence against the hypothesis that the mechanism contributes to coexistence in the community in this way consists of finding a negative community-level value of ΔI or $\Delta \kappa$ or a positive community-level value of ΔN .

In this article, we have a range of predictions about the ways that the scales of dispersal, competition, and environmental variation affect the strength of these coexistence mechanisms. Testing hypotheses of this sort has not been attempted yet but is not infeasible and might be done as an extension of the above procedures for determining mechanism strength. We give just one example of how this might be done to test predictions about scales of environmental variation. We give just one example of how scales might be manipulated. Soil temperatures at and before the time of rainfall are known to be important environmental factors affecting germination of annual plants (Baskin and Baskin 1998). Shading has major effects on soil temperature and can vary dramatically in space. In Southwestern deserts with both winter and summer annual communities, standing dead grass, which is spatially variable, affects shading of winter annuals during the fall germination season (P. Chesson, personal observation). This shading is conveniently subject to manipulation and in principle allows flexible manipulation of the scale of environmental factors. Scales of competition might be investigated by using species with root systems of different spatial extents, and dispersal can be manipulated by bagging plants and hand dispersing seeds. We admit that there are many challenges in performing such experiments, but they are not infeasible and in principle allow the effects of interacting scales on the coexistence mechanisms presented here to be tested. Further development of such experimental designs, their field implementation, and the statistical tests associated with them are the subjects of this article and future work of P. Chesson and collaborators.

Among other advantages, investigating species coexistence by partitioning growth rates into terms corresponding to different mechanisms is especially suited to empirical investigation because it allows multiple mechanisms to be considered simultaneously in a single system, and the quantification of different mechanisms leads immediately to assessment of their relative importance. More subtle hypotheses about the factors affecting these relative importances can then be considered theoretically and potentially experimentally in the future.

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