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When does environmental variation most influence species coexistence?

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Abstract The ability of environmental variation to affect species coexistence is much studied, yet environmental variation is not always important. I present an approximate calculation for the long-run growth rate of a species in the presence of spatially and temporally correlated environmental variation. I then perform a factorial numerical experiment, varying the mean seed dispersal distances, competition radii, and overwinter seed survival probabilities for two competing species for an array of variational regimes, noting the effects on their long-run growth rates. I find, first, that purely spatial variation has a greater capacity for influence than variation with a temporal component. Second, spatiotemporal variation can promote coexistence as strongly as purely temporal variation or more so, given the right species traits. Third, if the environmental variation has a spatial component, traits which enable species to become spatially segregated promote coexistence most strongly. That is, it is the possibility of spatial segregation which gives spatial variation its large potential to promote coexistence.

Keywords Coexistence · Disturbance · Environmental variation · Colored noise · Life history traits

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Introduction

Whether in the form of resource pulses (Chesson et al. 2004), patchy disturbance (Moloney and Levin 1996), soil type variation (Reynolds et al. 1997), or other processes, the ability of environmental variation to affect species coexistence has been subject to much study, yet it is not always important. When do we expect environmental variation to have the most influence on species coexistence?

Environmental variation's influence should depend on the character of the variation. Positive temporal and spatial autocorrelation ("reddened noise") have been shown to have a strong influence on aspects of single-species dynamics such as extinction risk (Petchey et al. 1997; Heino 1998; Schwager et al. 2006) and spatial synchronization [e.g., the Moran effect (Moran 1953; Ranta et al. 1995)]. We should expect similar importance in the dynamics of interacting species.

The influence of environmental variation should also depend on the traits of the competing species. For example, in the presence of spatial variation, short-range dispersal can cause a population to become concentrated in favorable areas, increasing the likelihood that a species will persist (Bolker 2003; Snyder and Chesson 2003). Likewise, dormancy can allow desert seeds to take advantage of infrequent rainfall.

In this paper, I present an approximate calculation for the long-run growth rate of a species in the presence of reddened spatiotemporal noise ("An approximate expression for the long-run growth rate" section). Then, using a model of two competing annual plants, I introduce a factorial numerical experiment, varying the mean seed dispersal distance, competition radius, and overwinter seed survival probability for each species for an array of variational regimes ("Numerical experiment" section). For each combination of life history traits, I found the geometric mean of the changes that environmental variation produces in the long-run growth rates of each species at low density, a measure of the influence of variation on coexistence.

I find first that purely spatial variation has a greater capacity for influence than variation with a temporal component. Second, spatiotemporal variation can promote coexistence as strongly as purely temporal variation or more so, given the right species traits. Third, if the environmental variation has a spatial component, traits that enable species to become spatially segregated promote coexistence most strongly. That is, it is the possibility of spatial segregation which gives spatial variation its large potential to promote coexistence.

Model

Seeds of species j germinate with probability g_j and an adult plant can produce a maximum number of seeds F_j ("fecundity"). Either germination or fecundity may vary with fluctuating environmental conditions. As a reminder of this, I refer to whichever one is varying as "the environmental response" or simply "the environment" and denote it by $E_j(x,t)$. Seed production is reduced by competition, C_j, which is determined by a convolution of a competition kernel U_{jk} (for competition from species k) with the local seedling population (Eq. 2). The seeds then disperse, traveling a distance z from their parent with probability $k_j(z)$. Seeds that fail to germinate survive with probability s_j until the following year, when they again have a chance to germinate. The model assumes one-dimensional space. The density of seeds at location x in year $t+1$ is thus given by

$$n_j(x,t+1) = \int_{-\infty}^{\infty} k_j(x-y)\left(\frac{F_j g_j}{C_j} n_j\right)(y,t)\,dy + s_j(1-g_j)n_j(y,t). \tag{1}$$

I use the mutual invasibility criterion of coexistence, which states that two species will coexist if each can "invade" (increase from a regionally low density) in the presence of its competitors (the "residents"), which have reached a stationary distribution. The species in the role of the invader is denoted by subscript i and the resident by r. Making the standard assumption that the invader is at too low a density to contribute significantly to competition, the competition experienced by species j becomes

$$C_j(x,t) = \int_{-\infty}^{\infty} U_{jr}(x-y)(g_r n_r)(y,t)\,dy. \tag{2}$$

The numerical experiments were performed using Laplacian kernels: $k_j(z) = 1/(2a_j)\exp(-|z|/a_j)$ and $U_{jr}(z) = 1/(2b_{jr})\exp(-|z|/b_{jr})$, so that the mean dispersal distance is a_j and competition is relatively strong out to a distance of b_{jr}.

Variable definitions are summarized in Table 1.

Environmental correlation structure: As pointed out in Chesson (1985), all variation can be partitioned into a pure spatial component (PS), in which some locations are permanently more favorable than others; a pure temporal component (PT), in which favorability rises and falls in a globally synchronized way; and a pure spatiotemporal component (PST), in which the spatial average of environment $E(x,t)$ does not vary with time and the temporal average of $E(x,t)$ does not vary in space. For example, variation in aspect and soil type is PS on ecological time scales, while weather can produce PT variation as all locations become warmer, for example, or wetter. Interactions between weather and topography can produce variation with a PST component, with low-lying areas staying wetter for longer and south-facing slopes becoming warmer than north-facing ones. I assume that each component of the variation is exponentially correlated, so that for both species,

$$\begin{aligned}\mathrm{Cov}(E_j,E_j)_{x,t}(x',t') &= V_{PST}\exp\left(\frac{-|x'|}{\xi}\right)\exp\left(\frac{-|t'|}{\tau}\right)\\ &\quad + V_{PT}\exp\left(\frac{-|t'|}{\tau'}\right)\\ &\quad + V_{PS}\exp\left(\frac{-|x'|}{\xi'}\right), \quad j=1,2,\end{aligned} \tag{3}$$

where V_{PST} is the variance of the PST component, V_{PT} is the variance of the PT component, and V_{PS} is the variance of the PS component. Spatiotemporal covariance $\mathrm{Cov}(A,B)_{x,t}(x',t')$ equals $\langle (A(x,t) - \langle A\rangle_{x,t})(B(x+x',t+t') - \langle B\rangle_{x,t}\rangle_{x,t}$, with $\langle\cdot\rangle_{x,t}$ denoting an average over space and time and $\langle\cdot\rangle_x$ and $\langle\cdot\rangle_t$ denoting spatial and temporal averages, respectively. The temporal correlation lengths τ and τ' give a measure of environmental predictability: as τ and τ' become larger, environmental conditions remain similar for longer periods of time and are composed of a larger proportion of slow variation in the PST and PT variational components, respectively. Similarly, the spatial correlation lengths ξ and ξ' indicate the spatial scales over which

Table 1 Variable definitions

Variable	Definition
$n_j(x,t)$	Number of seeds of sp. j at location x at time t
F_j	Fecundity of sp. j
g_j	Germination fraction of sp. j
C_j	Competition experienced by sp. j
s_j	Seed survival probability for sp. j
$k_j(z)$	Dispersal kernel for sp. j
$U_{jk}(z)$	Kernel for competition experienced by sp. j from sp. k
a_j	Mean dispersal distance for sp. j
b_{jk}	Competition length for sp. j and k
$\bar{r}_j$	Long-run growth rate of sp. j
$E_j(x,t)$	Env. response (fecundity or germination) for sp. j
ξ	Spatial correlation length of PST component of env. var.
τ	Temporal correlation length of PST component of env. var.
ξ'	Spatial correlation length of PS component of env. var.
τ'	Temporal correlation length of PT component of env. var.
V_{PST}	Variance of PST component of env. var.
V_{PT}	Variance of PT component of env. var.
V_{PS}	Variance of PS component of env. var.
θ_{PST}	Phase angle for PST component of env. var.
θ_{PT}	Phase angle for PT component of env. var.
θ_{PS}	Phase angle for PS component of env. var.

environmental conditions are similar for the PST and PS variational components. As ξ and ξ' become larger, environmental variation includes proportionally more variation at larger spatial scales.

The PS, PT, and PST components of the environmental variation may come from various physical processes, and species may not have identical responses to these processes. For example, PS variation could arise from serpentine outcroppings, and one species might be adapted to serpentine soil and the other not. In such a case, the PS component for E_1 and E_2 would have a negative covariance. I model this by letting

$$\begin{aligned}\mathrm{Cov}(E_1, E_2)_{x,t}(x',t') &= \cos(\theta_{PST})V_{PST}\exp\left(\frac{-|x'|}{\xi}\right)\exp\left(\frac{-|t'|}{\tau}\right)\\ &\quad+\cos(\theta_{PT})V_{PT}\exp\left(\frac{-|t'|}{\tau'}\right)\\ &\quad+\cos(\theta_{PS})V_{PS}\exp\left(\frac{-|x'|}{\xi'}\right). \end{aligned} \tag{4}$$

Low values of phase angles θ_{PST}, θ_{PT}, and θ_{PS} indicate that species 1 and 2 prefer similar environmental conditions, while values near π indicate that the species prefer different environmental conditions—their environments are exactly out of phase.

Measuring environmental influence on coexistence : By providing favorable areas where a population may become concentrated, environmental variation can add to a species' long-run growth rate, yet this aggregation also increases local competition. The effect of variation on growth is ambiguous, and indeed, we will see that environmental variation both adds to and subtracts from the invader's long-run growth rate. I use the geometric mean of the changes to the invader long-run growth rates caused by environmental variation: $\sqrt{\Delta\bar{r}_{i=1}\Delta\bar{r}_{i=2}}$, where $\Delta\bar{r}_{i=1} = (\bar{r}_{i=1}$with variation)$-$($\bar{r}_{i=1}$ without variation) and similarly for species 2 and where $\sqrt{\Delta\bar{r}_{i=1}\Delta\bar{r}_{i=2}}$ is only defined for cases in which variation either increases or decreases the long-run growth rates of both species. The motivation is that the product will be large if the changes to the long-run growth rates of both species are large, and the square root is present to give the average the right scale. If we are interested specifically in variation that promotes coexistence, we consider only cases for which both $\Delta\bar{r}_{i=1}$ and $\Delta\bar{r}_{i=2}$ are positive. I will refer to $\sqrt{\Delta\bar{r}_{i=1}\Delta\bar{r}_{i=2}}$ as the "influence" of environmental variation.

An approximate expression for the long-run growth rate

An expression for $\bar{r}_j$: Let us take a perturbative approach to finding the long-run growth rate. Write environment $E_j(x,t)$ as

$$E_j(x,t)=\langle E_j\rangle_{x,t}(1+\varepsilon_j(x,t)+\Omega_j(t)),\ \langle\Omega_j\rangle_t=\langle\varepsilon_j\rangle_x=0, \tag{5}$$

where $\Omega_j(t)$ represents PT deviations of $E_j(x,t)$ away from its spatial average and $\varepsilon_j(x,t)$ represents the sum of PS and PST deviations from the spatiotemporal average. Assume that ε_j and Ω_j are $O(\sigma)$,[1] where σ is a small parameter. Let us now write the population density $n_j(x,t)$ as

$$n_j(x,t) = \langle n_j\rangle_{x,t}(1 + u_j(x,t) + \eta_j(t)), \quad \langle \eta_j\rangle_t = \langle u_j\rangle_x = 0, \tag{6}$$

where $\eta_j(t)$ represents PT deviations of $n_j(x,t)$ away from its spatial average and $u_j(x,t)$ represents PS and PST deviations from the spatiotemporal average. If ε_j and Ω_j are $O(\sigma)$, then so will u_j and η_j be: $O(\sigma)$ approximations for u_j and η_j are presented in Snyder (2006, 2007).

A population will temporarily increase if its regional growth rate $\widetilde{\lambda}_j$, the growth rate of the spatially averaged population, is positive. As discussed in Chesson (2000), the spatially averaged local dynamics,

$$\begin{aligned}\langle n_j\rangle_x(t+1) = \langle \lambda_j n_j\rangle_x(t) &= \langle \lambda_j\rangle_x(t)\langle n_j\rangle_x(t)\\ &\quad + \mathrm{Cov}(\lambda_j, n_j)_x(t),\end{aligned} \tag{7}$$

can be written in terms of a regional growth rate $\widetilde{\lambda}_j(t)$ by writing $\mathrm{Cov}(\lambda_j, n_j)_x$ as $\langle n_j\rangle_x \mathrm{Cov}(\lambda_j, \nu_j)_x$, where $\nu_j(x,t) = n_j(x,t)/\langle n_j\rangle_x(t)$, so that

$$\begin{aligned}\langle n_j\rangle_x(t+1) &= \left[\langle \lambda_j\rangle_x(t) + \mathrm{Cov}(\lambda_j, \nu_j)_x(t)\right]\langle n_j\rangle_x(t)\\ &= \widetilde{\lambda}_j(t)\langle n_j\rangle_x(t).\end{aligned} \tag{8}$$

However, in a time-varying environment, a population's ultimate fate is determined by its long-run growth rate, defined as the time average of the logarithm of the yearly growth rate (Lewontin and Cohen 1969). Thus,

$$\bar{r}_j = \langle \ln(\widetilde{\lambda}_j)\rangle_t = \langle \ln(\langle \lambda_j\rangle_x + \mathrm{Cov}(\lambda_j, \nu_j)_x)\rangle_t. \tag{9}$$

Assuming that $\widetilde{\lambda}_j$ is not too far from 1, we write $\bar{r}_j$ as $\langle \ln(1 + (\langle \lambda_j\rangle_x - 1) + \mathrm{Cov}(\lambda_j, \nu_j)_x)\rangle_t$ and expand the argument of the logarithm about 1, obtaining a second-order approximation for $\bar{r}_j$ by writing

$$\bar{r}_j \approx \left\langle \left(\langle \lambda_j\rangle_x - 1\right) + \mathrm{Cov}(\lambda_j, \nu_j)_x - \frac{1}{2}\left(\langle \lambda_j\rangle_x - 1\right)^2 \right\rangle_t, \tag{10}$$

where each of the terms should be approximated to $O(\sigma^2)$.

Let us suppose for the rest of this section that fecundity is varying, so that F_j becomes $E_j(x,t)$. Then, suppressing space and time arguments for concision,

$$\lambda_j = \frac{g_j\langle E_j\rangle_{x,t}(1 + \varepsilon_j + \Omega_j)}{g_r\langle n_r\rangle_{x,t}(1 + \eta_r + U_{jr} * u_r)} + s_j(1 - g_j). \tag{11}$$

Noting that $1/(1+x)$ can be Taylor expanded as $1 - x + x^2$ for small x, we write

$$\begin{aligned}\lambda_j = \frac{g_j\langle E_j\rangle_{x,t}}{g_r\langle n_r\rangle_{x,t}}\Big[&1 + \varepsilon_j + \Omega_j - \eta_r - U_{jr} * u_r - \varepsilon_j(\eta_r + U_{jr} * u_r)\\ &- \Omega_j(\eta_r + U_{jr} * u_r) + \eta_r^2 + (U_{jr} * u_r)^2 + 2\eta_r U_{jr} * u_r\Big]\\ &+ s_j(1 - g_j) + O\left(\sigma^3\right).\end{aligned} \tag{12}$$

Perturbations u_j and ε_j have been defined to have zero spatial average, so when we average over space, terms that are first order in u_j and ε_j vanish, while second-order terms become covariances and variances. Thus, to $O(\sigma^2)$,

$$\begin{aligned}\langle \lambda_j\rangle_x - 1 = \lambda_j^{(0)} - 1 + &\frac{g_j\langle E_j\rangle_{x,t}}{g_r\langle n_r\rangle_{x,t}}\\ &\times \left(\Omega_j - \eta_r - \mathrm{Cov}(\varepsilon_j, U_{jr} * u_r)_x - \Omega_j\eta_r + \eta_r^2\right.\\ &\left.+ \mathrm{Var}(U_{jr} * u_r)_x\right) + O(\sigma^4),\end{aligned} \tag{13}$$

where $\lambda_j^{(0)}$, the $O(\sigma^0)$ approximation for λ_j, is $\dfrac{g_j\langle E_j\rangle_{x,t}}{g_r\langle n_r\rangle_{x,t}} + s_j(1 - g_j)$ and

$$\begin{aligned}(\langle \lambda_j\rangle_x - 1)^2 = &\left(\lambda_j^{(0)} - 1\right)^2 + \left(\frac{g_j\langle E_j\rangle_{x,t}}{g_r\langle n_r\rangle_{x,t}}\right)^2 (\Omega_j - \eta_r)^2\\ &+ 2\left(\lambda_j^{(0)} - 1\right)\left(\frac{g_j\langle E_j\rangle_{x,t}}{g_r\langle n_r\rangle_{x,t}}\right)\\ &\times \left[\Omega_j - \eta_r - \mathrm{Cov}(\varepsilon_j, U_{jr} * u_r)_x - \Omega_j\eta_r + \eta_r^2\right.\\ &\left.+ \mathrm{Var}(U_{jr} * u_r)\right] + O(\sigma^4).\end{aligned} \tag{14}$$

Rewriting $\left(\lambda_j^{(0)} - 1\right) - \frac{1}{2}\left(\lambda_j^{(0)} - 1\right)^2$ as $\ln\left(\lambda_j^{(0)}\right)$ and taking time averages, Ω_j and η_r vanish, and we have

$$\begin{aligned}\bar{r}_j \approx \ln\left(\lambda_j^{(0)}\right) + &\frac{g_j\langle E_j\rangle_{x,t}}{g_r\langle n_r\rangle_{x,t}}\left(1 - \left(\lambda_j^{(0)} - 1\right)\right)\\ &\times \left(-\mathrm{Cov}(\varepsilon_j, U_{jr} * u_r)_{x,t} - \mathrm{Cov}(\Omega_j, \eta_r)_t\right.\\ &\quad\left.+ \mathrm{Var}(\eta_r)_t + \mathrm{Var}(U_{jr} * u_r)_{x,t}\right) - \frac{1}{2}\left(\frac{g_j\langle E_j\rangle_{x,t}}{g_r\langle n_r\rangle_{x,t}}\right)^2\\ &\times \left(\mathrm{Var}(\Omega_j)_t + \mathrm{Var}(\eta_r)_t - 2\mathrm{Cov}(\Omega_j, \eta_r)_t\right)\\ &+ \langle \mathrm{Cov}(\lambda_j, \nu_j)_x\rangle_t.\end{aligned} \tag{15}$$

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[1] By "$g(x)$ is $O(\sigma)$," I mean that $g(x)$ decreases rapidly enough with σ that $\left|\dfrac{g(x)}{\sigma}\right|$ can be made less than or equal to some positive constant K for σ small enough.

Turning our attention to the final term, $\langle \mathrm{Cov}(\lambda_j, \nu_j)_x \rangle_t$, we note that

$$\begin{aligned} \nu_j &= \frac{n_j}{\langle n_j \rangle_x} = \frac{\langle n_j \rangle_{x,t}(1 + u_j + \eta_j)}{\langle n_j \rangle_{x,t}(1 + \eta_j)} \\ &= (1 + u_j + \eta_j)\big(1 - \eta_j + O(\sigma^2)\big) \\ &= 1 + u_j + O(\sigma^2), \end{aligned} \tag{16}$$

and from Eq. 12,

$$\lambda_j = \frac{g_j \langle E_j \rangle_{x,t}}{g_r \langle n_r \rangle_{x,t}} \left[1 + \varepsilon_j + \Omega_j - \eta_r - U_{jr} * u_r\right] + O(\sigma^2). \tag{17}$$

Because they depend only on time, Ω_j and η_r will drop out of the spatial covariance, leaving

$$\langle \mathrm{Cov}(\lambda_j, \nu_j)_x \rangle_t = \frac{g_j \langle E_j \rangle_{x,t}}{g_r \langle n_r \rangle_{x,t}} \mathrm{Cov}(\varepsilon_j - U_{jr} * u_r, u_j)_{x,t}. \tag{18}$$

Equations 15 and 18 relate long-run growth rate to population distributions. In particular, variation in population can increase or decrease growth through the covariances or variances involving u or η. Population variation is driven by environmental variation, and, as discussed in Snyder (2007), populations have varying abilities to respond to environmental variation, depending on species traits and the characteristics of the variation. This means that the capacity of environmental variation to promote coexistence depends on its scale. In general, large-area, long-lasting variation plus the "tracking traits" discussed in Section Results produce the greatest variation in population density and the greatest modification of $\bar{r}$. Mathematically, this occurs because of a resonance in the population response: the amplitude of the resident population, u_r, approaches infinity as ω approaches zero (infinitely slow temporal variation), average dispersal distance (a) approaches zero, and the competition length (b) approaches infinity. (See Snyder and Chesson (2004) for more details.) The biological reasons for this are discussed in Section Results.

Finally, we can calculate $\langle n_r \rangle_{x,t}$ by taking a spatiotemporal average of the local dynamics: $\langle n_r \rangle_{x,t} = \langle \lambda_r n_r \rangle_{x,t}$. All of the $O(\sigma)$ terms vanish, so that to $O(\sigma)$,

$$\langle n_r \rangle_{x,t} = \left(\frac{g_r \langle E_j \rangle_{x,t}}{g_r \langle n_r \rangle_{x,t}} + s_r(1 - g_r) \right) \langle n_r \rangle_{x,t} \tag{19}$$

and thus,

$$\langle n_r \rangle_{x,t} = \frac{F_r}{1 - s_r(1 - g_r)} + O(\sigma^2). \tag{20}$$

Relationship to Chesson's variation-dependent coexistence mechanisms: It is also possible to calculate the invader's long-run growth rate by using a spatiotemporal extension of the calculations that Chesson has presented for PT variation (Chesson 1994) and PS variation (Chesson 2000) (Chesson, unpublished manuscript). Applying Eq. 15 to the invader's long-run growth rate ($j = i$), the spatial storage effect would contain $\mathrm{Cov}(\varepsilon_i, U_{ir} * u_r)_{x,t}$, and the temporal storage effect would contain $\mathrm{Cov}(\Omega_i, \eta_r)_t$. The terms $\mathrm{Var}(\eta_r)_t$ and $\mathrm{Var}(U_{ir} * u_r)_{x,t}$ would be gathered into relative nonlinearity/nonlinear competitive variance, and $\langle \mathrm{Cov}(\lambda_i, \nu_i)_x \rangle_t$ would be compared with $\langle \mathrm{Cov}(\lambda_r, \nu_r)_x \rangle_t$ to form growth-density covariance. The $\mathrm{Var}(\Omega_i)$ term would contribute to $\widetilde{\lambda}'_i$. The advantage of the current approach is that it produces a more consistent approximation. When one species has a competitive advantage in the absence of environmental variation, so that $\lambda_i^{(0)} \neq 1$, then Chesson's method leaves out some $O(\sigma^2)$ terms in the expression for $\bar{r}_i$ or misstates their coefficients. However, Chesson's partitioning of $\bar{r}_i$ into named coexistence mechanisms makes it easier to assign biological meanings to the terms that make up $\bar{r}_i$.

Calculating the constituent covariances: The easiest way to calculate the variances and covariances on which $\bar{r}_j$ depends is to use the Wiener–Khinchin theorem, the spatiotemporal version of which states that if $\langle f \rangle_{x,t} = \langle g \rangle_{x,t} = 0$, then $\mathrm{Cov}(f, g)_{x,t}$ is the inverse spatiotemporal Fourier transform of $\lim_{N \to \infty} \widetilde{f}^{(N)^*}(q, \omega)\widetilde{g}^{(N)}(q, \omega)/N^2$, where $\widetilde{f}^{(N)}(q, \omega)$ is the spatiotemporal Fourier transform taken with sums running from $-N/2$ to $N/2$ and superscript asterisk denotes the complex conjugate.

Thus, for example, noting that the Fourier transform of $A * B$ is $\widetilde{A}\widetilde{B}$,

$$\begin{aligned} &\mathrm{Cov}(\varepsilon_j, U_{jr} * u_r)_{x,t} \\ &\quad = U_{jr} * \mathrm{Cov}(\varepsilon_j, u_r)_{x,t} \\ &\quad = \lim_{N \to \infty} \frac{1}{N^2} \sum_{s=-N/2}^{N/2} \sum_{m=-N/2}^{N/2} \frac{\widetilde{U}_{jr}^{(N)}(q_s) \widetilde{\varepsilon}_j^{(N)^*}(q_s, \omega_m) \widetilde{u}_r^{(N)}(q_s, \omega_m)}{N^2} \\ &\quad = \lim_{N \to \infty} \frac{1}{(2\pi)^2} \int_{-\pi}^{\pi} \int_{-\pi}^{\pi} \frac{\widetilde{U}_{jr}^{(N)}(q) \widetilde{\varepsilon}_j^{(N)^*}(q, \omega) \widetilde{u}_r^{(N)}(q, \omega)}{N^2} dq\, d\omega, \end{aligned} \tag{21}$$

where $q_s = 2\pi s/N$ and similarly for ω_m .

In a stochastic environment, $\widetilde{\varepsilon}_j(q, \omega)$ and $\widetilde{u}_r(q, \omega)$ are unknown. However, to $O(\sigma)$ (which is all we need), $\widetilde{u}_r(q, \omega)$ can be written as a response function (also called a transfer function) $R(q,\omega)\exp(i\phi(q,\omega))$ times $\widetilde{\varepsilon}_r(q,\omega)$ (Snyder 2007). Thus,

$$\mathrm{Cov}(\varepsilon_j, U_{jr} * u_r)_{x,t} = \lim_{N\to\infty} \frac{1}{(2\pi)^2} \int_{-\pi}^{\pi}\int_{-\pi}^{\pi} \widetilde{U}_{jr}^{(N)}(q)\, R(q,\omega) e^{i\phi(q,\omega)} \times \frac{\widetilde{\varepsilon}_j^{(N)*}(q,\omega)\,\widetilde{\varepsilon}_r^{(N)}(q,\omega)}{N^2}\, dq\, d\omega. \tag{22}$$

Using the Wiener–Khinchin theorem again, we see that

$$\lim_{N\to\infty} \frac{\widetilde{\varepsilon}_j^{(N)*}(q,\omega)\,\widetilde{\varepsilon}_r^{(N)}(q,\omega)}{N^2} = \int_{-\pi}^{\pi}\int_{-\pi}^{\pi} \mathrm{Cov}(\varepsilon_j, \varepsilon_r)_{x,t}(x', t')\, dx'\, dt' \tag{23}$$

where $\mathrm{Cov}(\varepsilon_j, \varepsilon_r)_{x,t}(x', t')$ is given by Eq. 3.

Response functions for $\widetilde{u}_r$, $\widetilde{u}_i$, and $\widetilde{\eta}_r$ have been derived in the appendices of Snyder (2006, 2007).

Numerical experiment

Equations 15 and 18 show how an invader's long-run growth rate depends on its own distribution and that of its competitor. To relate growth to species traits and the scale of environmental variation, we must determine how traits and the environment affect population distributions. As discussed in Snyder (2007), the combined effect of species traits and environmental variation on population distributions is not always easy to predict, and so I test the effects of species and environmental characteristics on growth numerically, using both the approximation presented in the previous section and the unapproximated model equations (Eqs. 1 and 2). C code is available upon request for both the approximation and the full model. The figures show the results of the full model: where these differ from the predictions of the approximation, this is noted.

For a range of spatial and temporal correlation lengths (ξ, τ, ξ', and τ' = 0.5, 1, 2) and for a variety of species similarities (θ_{PST}, θ_{PS}, $\theta_{PT} = 0$ or π), I ran a seven-fold factorial "experiment," varying mean dispersal distances (a_1, a_2 = 0.5, 2, 10), competition lengths (b_{11}, b_{22}, $b_{12} = 0.5$, 2, 10), and seed survival probabilities (s_1, $s_2 = 0.1$, 0.9), and calculated the influence ($\sqrt{\Delta\bar{r}_{i=1}\Delta\bar{r}_{i=2}}$) for each combination of life history parameter values. The choices for the dispersal and competition kernel lengths represent distances mostly less than, mostly greater than, or much greater than the spatial correlation lengths. If we think of the spatial correlation length as representing a typical "patch" size, this means that spatial processes take place mostly within a patch, mostly between one or two patches, or between several patches. Similarly, the survival probabilities correspond to mean seed lifetimes longer than or shorter than temporal correlation lengths (mean lifetimes of 0.12 years and 90 years), so that seeds experience a mostly constant environment or live through several changes of environment.

I first focused on which suites of life history traits best enable environmental variation to promote coexistence. For each combination of environmental variables (ξ, τ, ξ', τ', θ_{PST}, θ_{PS}, θ_{PT}), I collected traits for both species (values of a_1, a_2, b_{11}, b_{22}, b_{12}, s_1, s_2) that produced an influence that was within 1% of the maximum value and for which variation benefited both species ($\Delta\bar{r}_i$ was positive for both species). Then, I considered the capacity of PST, PT, and PS variation to influence coexistence by examining the distributions of influence possible for each type of variation.

Results

Accuracy of the approximation: Equation 15 for long-run growth rate uses a first-order approximation for the population distributions, which is valid so long as the predicted population variation is small. However, when favorable areas are large and long-lasting (low spatial and temporal frequency), populations with appropriate traits (e.g., short-range dispersal) can become highly concentrated, and this large variation in population density causes higher-order terms to become important. The approximation may therefore overestimate variance in resident density. Estimates of the invader variance may be further overestimated because we assume that the invader has achieved a stationary spatial distribution when we calculate its low-density growth rate. However, growth in large, long-lasting areas can be so rapid that self-competition becomes significant before a stationary spatial distribution is reached—the invader ceases to be an invader before achieving a stationary distribution.

For these reasons, the approximation can overestimate the contribution to $\bar{r}$ from environmental variation at low spatial and temporal frequencies. In particular, the approximation greatly overestimates $\bar{r}$ under PS variation, although it is fairly accurate for PST variation. Fortunately, the conclusions of this paper are insensitive to this bias. While the approximation can overestimate the contribution of low frequencies to $\bar{r}$, it is still these frequencies that dominate $\bar{r}$'s value and it is still the same species traits that take advantage of variation at these frequencies.

Life history traits that enable environmental variation to promote coexistence: As long as there was some variation in space (PST, PS, PS + PT — anything but solely PT), a single suite of life history traits was dominant. For all spatial and temporal correlation lengths, regardless of whether the species preferred similar or different habitats, or whether germination or fecundity were varying, a single suite of life history traits best enabled environmental variation to promote coexistence (influence in the top 1%, $\Delta\bar{r}_{i=1}$ and $\Delta\bar{r}_{i=2}$ both positive). Both species had short-range dispersal ($a_1 = a_2 = 0.5$), long-range competition within species ($b_{11} = b_{22} = 10$), short-range competition between species ($b_{12}=0.5$), and short-lived seeds ($s_1=s_2=0.1$) (Fig. 1).

Why is this strategy so effective in promoting coexistence? First, the tracking strategy maximizes species' ability to track large-scale, slow variation. Short-range dispersal allows populations to accumulate in large, relatively long-lasting favorable areas. Long-range within-species competition reduces competitive pressure in these densely populated areas and increases pressure in nearby unfavorable areas, allowing populations in favorable areas to grow even more and further suppressing populations in unfavorable areas (Roughgarden 1974; Snyder and Chesson 2004). This aggregation then permits spatial segregation. By causing the resident population to become strongly aggregated, the tracking strategy opens up competitor-free areas where an invader may thrive. Short-range dispersal allows the invader population to accumulate in the interstices between resident clusters, and short-range between-species competition minimizes competition from nearby groups of residents. If both species prefer similar environments (θ_{PS} or $\theta_{PST}=0$), then areas with few residents contain suboptimal habitat, but the release from competition more than compensates: $\langle \mathrm{Cov}(n_i, n_r)_x \rangle_t$ is negative, indicating that the species are spatially segregated. Because the invader is able to concentrate its population in areas of low competition, $\langle \mathrm{Cov}(\lambda_i, \nu_i)_x \rangle_t$, the covariance between invader growth rate and relative population density increases, increasing $\bar{r}_i$. (When $\langle \mathrm{Cov}(n_i, n_r)_x \rangle_t$ is negative, so is the $\mathrm{Cov}(U_{ir} * u_r, u_i)$ term in Eq. 18, the expression for $\langle \mathrm{Cov}(\lambda_i, \nu_i)_x \rangle_t$.) Chesson calls this coexistence mechanism growth-density covariance (Chesson 2000). It is also a form of "heteromyopia," in which environmental variation drives resident clustering instead of demographic processes (Murrell and Law 2003).

This explanation of the tracking strategy's effectiveness makes clear that it depends on the relative scales of dispersal, competition, and spatial variation. In particular, populations need to be able to accumulate in favorable areas, which suggests that dispersal should be shorter than or equal to the spatial correlation length. What happens if we only consider mean dispersal

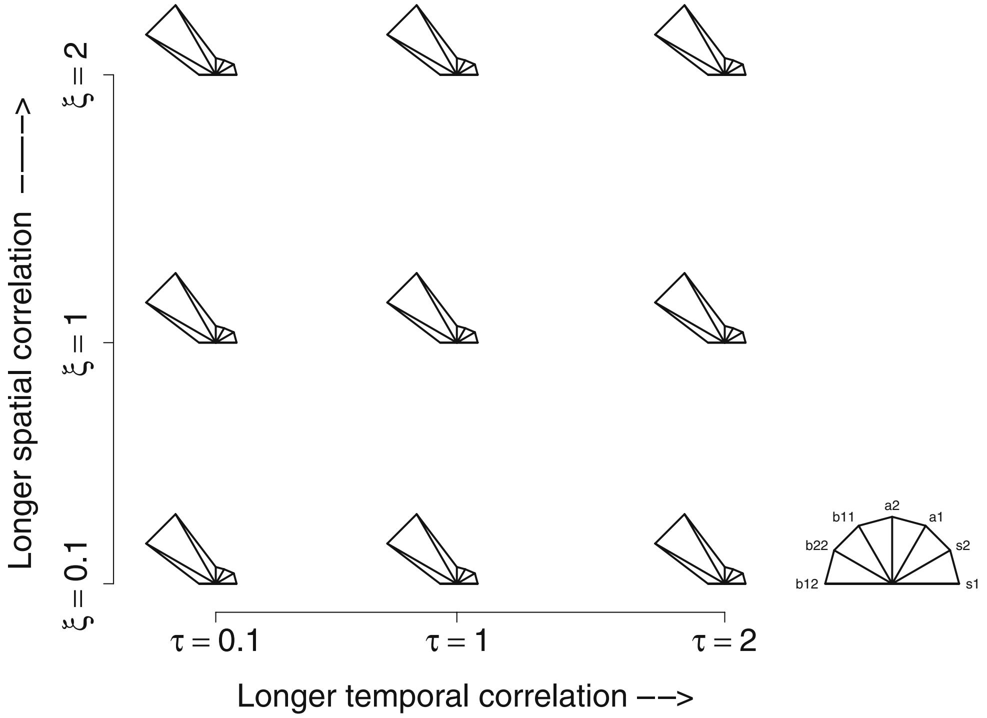
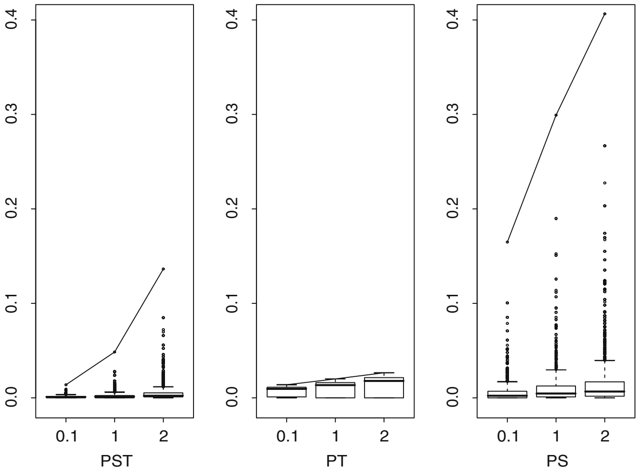


Fig. 1 Traits that most promote coexistence for PST variation in fecundity with different spatial and temporal correlation lengths. The plot is the same whether $\theta_{PST} = 0$ or π. Each glyph represents the suite of life history traits for which influence was in the top 1% and for which environmental variation benefitted both species as invaders ($\Delta\bar{r}_{i=1},\ \Delta\bar{r}_{i=2} > 0$). The length of each radial line represents the value of a parameter scaled to be between 0.2 and 1. The tracking strategy, discussed in the "Numerical experiment" section, maximizes influence in each case. These data were generated by simulations of the full, nonlinear dynamics. The same results were obtained for variable germination

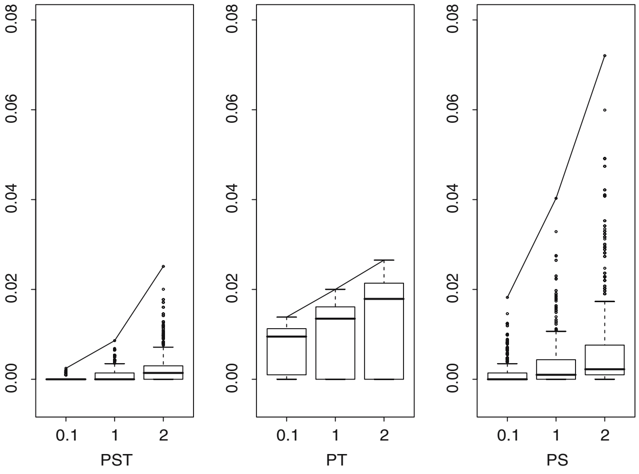
lengths of 2 and 10? Nothing changes if fecundity varies—the tracking strategy continues to maximize influence, with dispersal lengths of 2 instead of 0.5. If germination varies, however, the tracking strategy maximizes influence only if the spatial correlation length is 2, the same size as the shortest dispersal distance, and the temporal correlation length is greater than 0.1. The fact that limiting a spatial process, dispersal, changes the effectiveness of some *temporal* correlation lengths is consistent with the finding of Snyder (2007) that spatial and temporal traits are not always restricted to interacting with spatial and temporal variation, respectively.

The tracking strategy incorporates long-range, within-species competition and short-range between-species competition. This may be possible if, for example, both species are subject to a species-specific pest or disease, as in the Janzen–Connell hypothesis (Janzen 1970; Connell 1971). However, if competition is the result of overlapping resource depletion zones, then it may be more realistic to assume that the between-species competition distance lies somewhere between the within-species competition distances. If we constrain the between-species competition distance to be the average of the two within-species competition distances, we get results similar to the unconstrained case if the species prefer different environments. Coexistence is most promoted (influence in the top 1%, $\Delta\bar{r}_{i=1}$ and $\Delta\bar{r}_{i=2}$ both positive) when both species have short-range dispersal, short-range competition (within- and between-species), and small seed survival. The species are again spatially segregated. ($\langle \mathrm{Cov}(n_i, n_r)_x \rangle_t$ is always negative.) If the two species prefer similar environments, on the other hand, no one strategy dominates the top 1% of the influence values, the species are not spatially segregated, and influence is small: $\sqrt{\Delta\bar{r}_{i=1}\Delta\bar{r}_{i=2}}$ is typically around 10^{-3}, and even for PS, variation only reaches about 0.075 at its highest. As with unconstrained competition, environmental variation only has a large influence if species are spatially segregated.

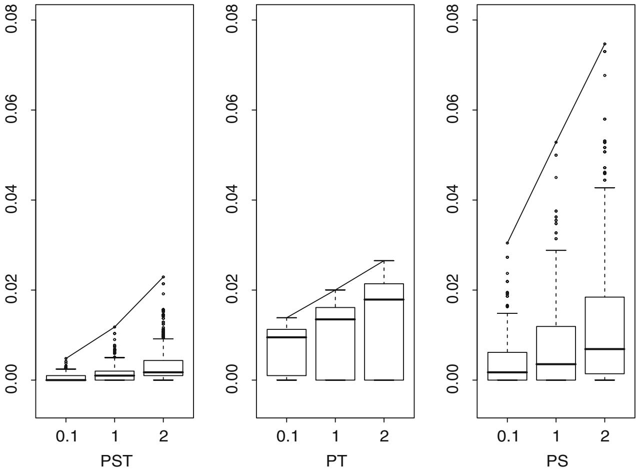
The capacity of different forms of environmental variation to influence coexistence: Both PS and PST variation have a greater capacity for influence (i.e., higher maximum influence) than PT variation (Fig. 2a); however, the tracking strategy is key. If we exclude a_1 and $a_2 = 0.5$, so that the shortest dispersal distance is 2,



a All data included



b Exclude shortest dispersal distance: $a_1,\ a_2 > 0.5$



c Constrain within-species competition distance: $b_{12} = (b_{11} + b_{22})/2$

Fig. 2 Influence ($\sqrt{\Delta\bar{r}_{i=1}\Delta\bar{r}_{i=2}}$) of PST, PT, and PS variation in fecundity. For each type of variation, boxplots are given for spatial and/or temporal correlation length equal to 0.1, 1, and 2. (For PST variation, $\xi = \tau = 0.1, 1, 2$.) Each boxplot represents the output of one of the numerical experiments described in the "Numerical experiment" section, which systematically varies dispersal distances, competition distances, seed survival probabilities, and phase angles (1,945 parameter combinations). The *lines* connect the maximum influences for each environment type. Only points for which variation helps both species ($\Delta\bar{r}_{i=1}, \Delta\bar{r}_{i=2} > 0$) or harms both species ($\Delta\bar{r}_{i=1}, \Delta\bar{r}_{i=2} < 0$) are used. The approximation presented in the "An approximate expression for the long-run growth rate" section overestimates the effect of large, slow variation. To avoid this bias, the data presented here were obtained by simulating the full, nonlinear dynamics. Each point is calculated using $\bar{r}$'s averaged over 50 realizations. These empirical results agree with the predictions of the approximation: PS variation has greater maximum influence than the others. PST can be made to have greater maximum influence than PT if dispersal distances are short enough and within-species competition is longer range than within-species competition. (Compare **a** with **b** and **c**.) Note the different scale on **a**. Similar results are obtained for variable germination

then PT variation's capacity exceeds PST's for all but the longest correlation length ($\xi = \tau = 2$) (Fig. 2b). This is also the case if we constrain the between-species competition distance to be the average of the within-species competition distances (Fig. 2c). However, PS variation retains the highest capacity for influence even with these changes. In sum, PS variation has a greater capacity for influence than variation with a temporal component, but spatiotemporal variation has the potential to be more influential than PT variation if most seeds can be retained within the natal "patch" (average dispersal distance less than or equal to the spatial correlation length) and the between-species competition length is shorter than the within-species competition lengths.

My intuition is that these results are likely to be true whenever organisms are able to aggregate in favorable areas and become spatially segregated (i.e., to employ something like the tracking strategy), though it is far from easy to prove. It is true that, when variation is PS, the long-run growth rate is an arithmetic mean of the local growth rates, while when variation is PT, the long-run growth rate is a geometric mean; however, it is not sufficient to note that arithmetic means are larger than geometric means, for resident densities may reasonably be higher under PS variation, so that the growth rates being averaged over are different for PS and PT variation. A safer, though nonrigorous, argument might be to say that variation-dependent coexistence mechanisms are driven by variation in population density, and it is easier for populations to become aggregated in favorable locations than in favorable times. Dispersal in space can be arbitrarily short-range, so that populations can become highly concentrated, whereas, even without dormancy, individuals must always "disperse" at least 1 year into the future.

Discussion

Variation-mediated coexistence has attracted ecologists' interest for years; yet, there has been little discussion of when environmental variation is likely to have a large influence on species coexistence. This paper presents a perturbative approach to calculating an invader's long-run growth rate in the presence of reddened spatiotemporal environmental variation plus a factorial numerical experiment in which the life history traits of a pair of annual plants are varied for an array of variational regimes. The results imply, first, that spatial variation has a greater capacity to influence coexistence than temporal or spatiotemporal variation; second, that spatiotemporal variation can promote coexistence as strongly as temporal variation, given the right species traits; and finally, that as long as environmental variation has some spatial component, traits that enable species to become spatially segregated promote coexistence most strongly. (Note that if variation occurs only in time, then spatial processes such as dispersal or competition become irrelevant: only dormancy can promote coexistence.) These segregation-enabling traits are those that allow species to track environmental variation ("tracking strategy"): short-range dispersal; short-range between-species competition; short-lived seeds; and, for the strongest tracking, long-range within-species competition—essentially a form of "heteromyopia" (Murrell and Law 2003), though here, population variation is exogenous rather than endogenous. This is not to say that spatial segregation necessarily results in coexistence. Rather, the way in which environmental variation can most strongly promote coexistence is if it results in spatial segregation.

Is the tracking strategy what we would expect to evolve? Not necessarily. This study highlights situations that maximize the fitness of both species as invader, while natural selection optimizes individual fitness.

Furthermore, physiological constraints typically prevent life history traits from evolving independently. Instead, we see tradeoffs between, for example, seed dormancy (a combination of seed survival and germination fraction) and seed weight, between dormancy and dispersal, and between dormancy and adult longevity (Rees 1993). Larger seeds can germinate in a wider variety of microsites (smaller variation in g) (Turnbull et al. 2005) and are produced in fewer numbers (smaller F) (Turnbull et al. 1999).

Although we cannot claim, based on this study, that species should evolve traits that would result in spatial segregation, segregation has been observed in a number of plant populations (Lopez-Pintor et al. 2003; Sanchez and Peco 2004; Allen and Shea 2006; Turnbull et al. 2007). Furthermore, spatial segregation has been shown experimentally to promote coexistence (Stoll and Prati 2001; Monzeglio and Stoll 2005).

Much of the attention paid to spatial segregation has been motivated by Tilman's argument that stronger competitors will be harmed by spatial segregation, while weaker competitors will benefit, because strong competitors experience greater self-limitation than weak competitors do (Tilman 1994). In a heterogeneous environment, however, spatial segregation permits both species to become concentrated in high-growth areas, either because they prefer different environmental conditions or because one is able to concentrate itself in favorable environments while the other is able to concentrate itself in areas of reduced competition.

Finally, I note that the capacity of environmental variation to promote coexistence depends on its scale (via the variances and covariances in the expression for $\bar{r}$) and that the tracking strategy promotes coexistence most strongly when temporal or spatial correlation lengths are relatively long—i.e., when favorable areas are larger than typical dispersal distances and last multiple generations. A number of studies have suggested that temporal correlation lengths may be less than 1 year ($\tau < 1$) in terrestrial systems (Steele 1985; Cyr and Cyr 2003; Vasseur and Yodzis 2004); however, relatively large spatial correlations (large on the scale of seed dispersal and resource-mediated competition) are likely to be ubiquitous. Spatial correlations can be produced by abiotic conditions such as rock outcroppings and variation in aspect or by biotic conditions such as the presence of shrubs or trees (e.g. Lopez-Pintor et al. 2003). This suggests that the tracking strategy discussed in this paper may be widespread.

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