

Spatiotemporal population distributions and their implications for species coexistence in a variable environment

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Abstract

A population experiences environmental variation both directly, through effects on life history parameters such as fecundity, and indirectly, through effects on the population distributions of competitors and thus on the distribution of competition. Which spatial and temporal scales of environmental variation most influence the coexistence of two species thus depends in part on the degree to which the resident population responds to different scales of variation. In this paper, I calculate an approximation for a spatiotemporal population distribution as the result of a filter function convolved with the environmental variation. I find that there is no straightforward connection between spatial or temporal scales inherent to an organism's life history, such as mean lifetime or dispersal distance, and the population's sensitivity to variation at different scales. Rather, life history traits interact sensitively with the way environmental variation affects the organism. I comment on the implications for variation-mediated coexistence.

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1. Introduction

Which spatial and temporal scales of environmental variation most influence coexistence between two species with given life history strategies? More precisely, consider coexistence using the standard mutual invasibility criterion, which states that species coexist if each species can “invade” (increase from a regionally low density) in the presence of its competitors (the “residents”), which have reached a stationary distribution. Given an invader and a resident with particular life history strategies, which scales of environmental variation most encourage or discourage the persistence of the invader? Both temporal (Armstrong and McGehee, 1976; Abrams, 1984; Chesson and Warner, 1981; Chesson, 1994) and spatial (Pacala and Roughgarden, 1982; Comins and Noble, 1985; Chesson, 2000; Amarasekare, 2003; Abrams and Wilson, 2004) variation in environmental conditions can increase the growth rate of a low density species, thereby promoting coexistence, but

not all scales of variation are equally effective. A study of a California grassland showed that grasses and forbs can coexist when rainy years are followed by dry years (Levine and Rees, 2004), but in other cases, such rapid variation will be experienced as a kind of blur, effectively averaged over. For example, Collins et al. found that species richness in a tallgrass prairie was inversely proportional to the frequency of burning (Collins et al., 1995). Spatial variation on a scale larger than the invader's mean dispersal distance can increase the invader's regional growth rate (Snyder and Chesson, 2003), but intermediate-scale spatial variation may make a larger contribution under the right circumstances (Snyder and Chesson, 2004). Furthermore, existing studies on the effects of scale largely consider spatial or temporal variation separately, yet the effects of spatial and temporal variation may interact (Stratton and Bennington, 1998; Buckley et al., 2000). It is possible to calculate how much variation at a given spatial and temporal scale would contribute to an invader's long run growth rate, but we do not yet have an intuitive understanding of how the life history strategies of two competing species determine which scales most influence persistence at low density.

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A critical step in understanding the effects of temporal and spatial scale on coexistence is understanding how the density of the resident species responds to environmental variation at different spatial and temporal scales. Variation in resident density causes variation in competition, which can harm or help an invader. If environmental variation causes the resident population to accumulate in areas with environmental conditions that are favorable to the invader, then the invader will experience increased competition, to its disadvantage. If environmental variation prevents the resident from accumulating or causes it to accumulate in areas unfavorable to the invader, then the invader will experience decreased competition, to its benefit. Furthermore, simple variation in competition, regardless of its spatiotemporal distribution, may help an invader if a decrease in competition boosts its growth more than a comparable increase in competition depresses its growth, or may harm an invader if the reverse is true (“nonlinear competitive variance”, Snyder and Chesson, 2004). Environmental variation affects invader growth more strongly at some scales than at others in part because resident density is more sensitive to variation at some scales than at others, and variation in resident density has important consequences for the invader.

Put another way, the invader’s experience of the environment is partially mediated through the resident population distribution, which acts as a kind of filter for environmental variation. The resident population responds very weakly to environmental variation at certain scales. Invader competition therefore varies very little at these scales—they have been damped. The resident population responds strongly to environmental variation at other scales. Invader competition therefore varies strongly at these scales—they have been amplified. The invader experiences the environment both directly and indirectly: directly, through its own environmental response, and indirectly, through the resident population’s response to the environment and the effect of the resulting population distribution on competition.

Taking the metaphor of a filter literally, this paper shows how to approximate the resident population’s spatiotemporal distribution as the convolution of environmental variation and a filter function. Just as the electronic filters in a stereo can be adjusted to amplify the bass notes relative to the treble, this mathematical filter amplifies variation at some scales and damps it at others. This filter function can be transformed into a response function which measures the ability of the resident to track environmental variation (i.e. become aggregated in favorable areas) at different spatial and temporal scales. The invader’s growth rate depends on more than competition, but knowing how the resident is distributed is useful in creating heuristic predictions about whether an invader will grow or decline.

Comparing different response functions, I find that a population’s sensitivity to variation at different scales depends strongly on the way environmental variation

affects the organism. For example, the scales at which a population can track variation in germination are very different than the scales at which a population can track variation in adult fecundity. In addition, the spatial and temporal scales inherent in an organism’s life history can interact in unexpected ways with the manner in which environmental variation affects the organism. Naively, one might expect that the type of environmental variation would set the basic form of the response function, with that form modified in predictable ways by changes in life history parameters. For example, one would expect that increases in the spatial scale of dispersal or competition would cause the population to become less sensitive to variation at small spatial scales and that increases in life span would cause the population to become less sensitive to variation at small temporal scales. However, depending on the type of environmental variation, changes in life history parameters can cause striking qualitative changes in a population’s response function. For example, when germination varies, a change in seed survival can cause the response function to switch from depending almost entirely on the temporal scale of the variation to depending almost entirely on the spatial scale of the variation.

Because the resident’s response function plays an important role in determining which environmental scales most influence coexistence, these results have implications for studies that explore the connection between the scale of environmental variation, such as the spatial extent or temporal frequency of disturbance, and coexistence. We should expect, for example, that the effects of disturbance frequency and extent should depend on the timing of disturbance within the life cycle, since the life history parameters affected by disturbance (e.g., adult survival, seedling establishment) will depend in part on disturbance timing.

The rest of the paper proceeds as follows. Section 2 presents an annual plant model used to demonstrate the ideas in this paper. Section 3 discusses how the resident population density can be written in terms of a filter function convolved with the environmental variation and how the filter function can be transformed into a response function specifying the resident population’s sensitivity to variation at different scales. The full mathematical calculations are presented in the appendix. Section 4 relates the resident response function to invader growth rate and discusses some of the heuristic insights that can be gained by understanding how well the resident population density tracks environmental variation. Section 5 contrasts response functions that arise from variation in two different stages of the plant life cycle. The paper concludes with a discussion of response functions and their implications for variation-mediated coexistence in Section 6.

2. Example: an annual plant model

It will be easiest to develop these ideas within the context of a specific model. Consider the following model of an

annual plant with a seedbank. The number of seeds at location x in year t is $n_r(x, t)$. The subscript r serves as a reminder that we are considering the resident species. Seeds germinate with probability g_r and upon establishing themselves as adult plants produce a maximum number of seeds F_r (“fecundity”). However, seed production is reduced by competition, C_r , which is determined by a weighted average of the local seedling population, with weight function U_{rr} (“competition kernel”) defined so that more distant seedlings have less of a competitive effect. The seeds then disperse, traveling a distance z from their parent with probability $k_r(z)$. Seeds that fail to germinate survive with probability s_r until the following year, when they again have a chance to germinate. The density of seeds at location x in year $t + 1$ is then given by

$$n_r(x, t + 1) = \int_{-\infty}^{\infty} k_r(x - y) \lambda_{1r}(y, t) n_r(y, t) dy + \lambda_{2r}(x, t) n_r(x, t), \quad (1)$$

where $\lambda_{1r}(x, t)$, the per capita contribution of germinating seeds to next year’s seed bank, is given by

$$\lambda_{1r}(x, t) = \frac{F_r g_r}{C_r(x, t)}, \quad (2)$$

$\lambda_{2r}(x, t)$, the per capita contribution of non-germinating seeds to next year’s seed bank, is given by

$$\lambda_{2r}(x, t) = s_r(1 - g_r), \quad (3)$$

and competition $C_r(x, t)$ is given by

$$C_r(x, t) = \int_{-\infty}^{\infty} U_{rr}(x - y) g_r n_r(y, t) dy. \quad (4)$$

Integrals of this form are called convolutions and are denoted by the operator $*$. For example, Eq. (4) could be rewritten as $C_r(x, t) = U_{rr} * (g_r n_r)(x, t)$. For simplicity, I have written this model using one-dimensional space; however, I expect the qualitative results to remain true for two-dimensional space.

Environmental variation is felt through its effect on life history parameters such as fecundity or germination fraction. As a reminder of this, I refer to the varying life history parameter as the environmental response or simply “the environment” for short. For example, the appendix contains a derivation of the response function when environmental variation affects fecundity, so that fecundity is a function of space and time. I refer to fecundity as the environment and, as a further reminder, replace F_r with $E_r(x, t)$. Note that the environmental response has the subscript r . An invader may respond to the environment differently and will have its own environmental response, E_i . Section 5 compares response functions for variable fecundity and variable germination.

3. Filters and Fourier transforms

In this paper, I write the resident population density $n_r(x, t)$ in terms of a kernel convolved with the environ-

mental variation, and this kernel acts as a filter: environmental variation at some spatial and temporal scales is amplified while variation at other scales is damped. The filtering role of the kernel becomes clearer (and the mathematics becomes easier) when we use Fourier transforms to express population density and environmental variation as sums of sinusoids varying at different spatial and temporal frequencies. The Fourier transform $\tilde{f}(\omega)$ of a function of time $f(t)$ is the coefficient of the term that varies at temporal frequency ω . The Fourier transform $\tilde{f}(\omega)$ thus expresses how much variation there is in $f(t)$ at a given temporal frequency or, equivalently, at a given temporal period or scale, since the period of a sinusoid is 2π divided by its frequency. For example, if $\tilde{f}(\omega)$ starts out large for small ω and then decreases as ω becomes larger, then $f(t)$ varies a lot at low frequencies, corresponding to long time scales, and varies a little at high frequencies, corresponding to short time scales. In this paper, I take Fourier transforms with respect to both space and time, so that the transform is a function of spatial and temporal frequency.

Fourier transforms are especially useful in the present case because the Fourier transform of the convolution of two functions is the product of their Fourier transforms: $f * g(\omega) = \tilde{f}(\omega) \tilde{g}(\omega)$. The convolution that determines the population distribution thus becomes an equation of the form

$$\begin{aligned} & \left(\begin{array}{l} \text{Fourier transform} \\ \text{of population} \end{array} \right) (q, \omega) \\ &= \left(\begin{array}{l} \text{Response} \\ \text{function} \end{array} \right) (q, \omega) \left(\begin{array}{l} \text{Fourier transform} \\ \text{of environment} \end{array} \right) (q, \omega), \end{aligned}$$

where q is a spatial frequency and ω is a temporal frequency and where the “response function” is the Fourier transform of the kernel. Variation in population density at a given spatial and temporal frequency is thus equal to the variation in the environment at those frequencies times a factor given by the response function. The role of the response function as filter is now more apparent. Frequencies for which the magnitude of the response function is greater than one represent scales of environmental variation which are amplified in the resident population’s response. Frequencies for which the magnitude of the response function is less than one represent scales of environmental variation which are damped in the resident population’s response. Peaks and troughs in the magnitude of the response function represent spatial and temporal scales of environmental variation to which the resident population is especially sensitive. Areas where the magnitude of the response function is near zero represent scales to which the population is largely insensitive.

Response functions have been used in ecology to approximate a population’s response to static spatial variation (Roughgarden, 1974; Gurney and Nisbet, 1976; Snyder and Chesson, 2004; Anderson et al., 2005) or to

temporal variation such as seasonal changes (Nisbet and Gurney, 1982). The appendix shows how to use a response function to approximate a population's response to spatiotemporal variation by assuming that the environmental variation is small relative to the mean and linearizing the resident dynamics. (This first order approximation for the resident population density can be used to give a second order approximation to the resident and invader long run growth rates.) The relative population density, defined as $v_r(x, t) \equiv n_r(x, t)/\langle n_r \rangle_x(t)$, has a Fourier transform given by

$$\tilde{v}_r = R(q, \omega) e^{i\phi(q, \omega)} \tilde{\varepsilon}_r(q, \omega), \quad (5)$$

where $R(q, \omega) e^{i\phi(q, \omega)}$ is the response function and $\tilde{\varepsilon}_r(q, \omega)$ is the Fourier transform of the environmental variation normalized by its spatial average and adjusted to have spatial mean zero: $\varepsilon_r(x, t) \equiv E_r(x, t)/\langle E_r \rangle_x(t) - 1$. If there is no globally synchronized component to the environmental variation, so that $\langle E_r \rangle_x$ does not depend on time, then to the order of approximation used in this paper, the spatial average of n_r is also time-independent and $n_r(x, t) = \langle n_r \rangle_x v_r(x, t)$. Under these circumstances, $\tilde{n}_r(q, \omega) = \langle n_r \rangle_x \tilde{v}_r(q, \omega)$, so that Eq. (5) also describes the variation in $n_r(x, t)$. If $\langle E_r \rangle_x$ does depend on time, $\tilde{n}_r(q, \omega)$ is described by Eq. (5) plus terms that specify the variation in $\langle n_r \rangle_x$, which are governed by their own response function. This response function is derived in the appendix; however, for simplicity, this paper will focus on the response function for $v_r(x, t)$, effectively assuming that $\langle E_r \rangle_x$ is constant.

Fig. 1 compares the approximate relative density, determined by Eq. (5), to the real relative density, determined by a numerical solution of the resident dynamics (Eq. (1)). The approximation is generally quite good. It is worst for a species with long-range intraspecific competition, short-range dispersal, and long-lived seeds experiencing variation at a large spatial scale. Under these conditions, competition can become intense for plants in the middle of the environmentally favorable areas, and this creates a secondary dip in population density in the middle of these areas which is not predicted by the approximation. However, the population density does not vary much overall under these circumstances, so that the effects of this infidelity are limited. Of course, the approximation should also become worse as the environmental variation becomes large relative to the mean, since this perturbative approach assumes small variation.

The response function, $R(q, \omega) e^{i\phi(q, \omega)}$ is written in terms of an amplitude $R(q, \omega)$ and a phase angle $\phi(q, \omega)$. It is the amplitude which specifies a population's sensitivity to different scales of variation. A large amplitude means that the resident population varies strongly in response to environmental variation at spatial frequency q and temporal frequency ω . A small amplitude means that the resident population varies weakly in response to environmental variation at those frequencies. The phase angle $\phi(q, \omega)$ specifies the delay in the population's response to a

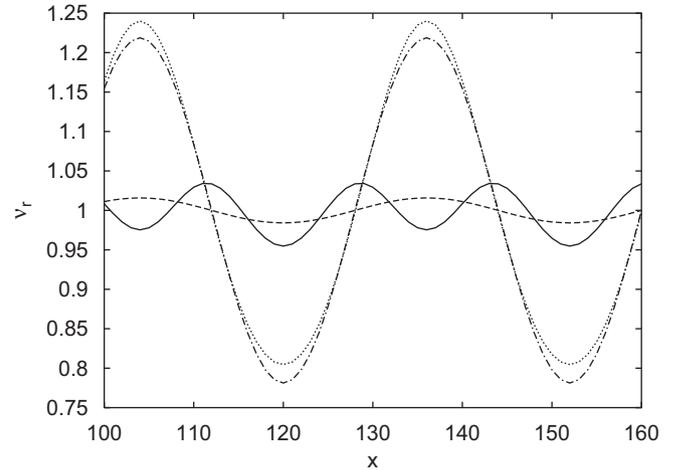


Fig. 1. Approximated and actual relative population density (v_r) as a function of location (x). Germination varies sinusoidally with spatial period 32, temporal period 8, amplitude 0.2, and spatiotemporal average 0.5. The population disperses according to a Laplacian kernel $k_r(x) = (\alpha_r/2)\exp(-\alpha_r|x|)$ with mean dispersal distance $1/\alpha_r$, and competes with itself according to a Laplacian kernel $U_{rr}(x) = (\beta_{rr}/2)\exp(-\beta_{rr}|x|)$ with characteristic competition distance $1/\beta_{rr}$. The approximation performs least well when the spatial period is large, seeds are long-lived, dispersal is short-range, and competition is long-range. This situation is depicted by the solid and dashed lines, for which $s_r = 0.9$, $\alpha_r = 1$, $\beta_{rr} = 0.1$. The solid line represents the true values, as found by numerically iterating Eq. (1), while the dashed line represents the approximation. The dotted and dash-dot lines show the true and approximate values, respectively, for short-range competition ($\beta_{rr} = 1$), with all other values remaining the same.

change in the environment: if $\varepsilon_r(x, t) = \sin(qx) \sin(\omega t)$, then $v_r(x, t) = R(q, \omega) \sin(qx) \sin(\omega t + \phi(q, \omega))$. (There is no spatial phase angle because dispersal and competition depend only on separation distance and do not have a preferred direction.) When the environment is changing very slowly (ω near zero), then ϕ is close to zero and there is little delay: $v_r(x, t) \approx R(q, \omega) \varepsilon_r(x, t)$. When locations alternate between good and bad years ($\omega = \pi$, the fastest possible variation), then $\phi = -\pi$, and the population is precisely out of phase with the environment: $v_r(x, t) = -R(q, \omega) \varepsilon_r(x, t)$. In this paper, I focus on the amplitude $R(q, \omega)$ and for simplicity refer to it as the response function. However, the reader should keep in mind that as the environmental variation becomes rapid ($\omega \rightarrow \pi$), the response function R acquires an overall minus sign. Fig. 2 shows an example of a sinusoidal signal that is modified by a complex response function.

4. How response functions determine growth rate

The connection between R and competition is generally straightforward. When $|R(q, \omega)|$ is large, the resident tracks variation at spatial frequency q and temporal frequency ω , becoming concentrated in favorable areas if R is positive and becoming concentrated in unfavorable areas if R is negative. Ordinarily, competition is high whenever the resident density is high, so that large $|R|$ signifies strong competition in either favorable or unfavorable areas,

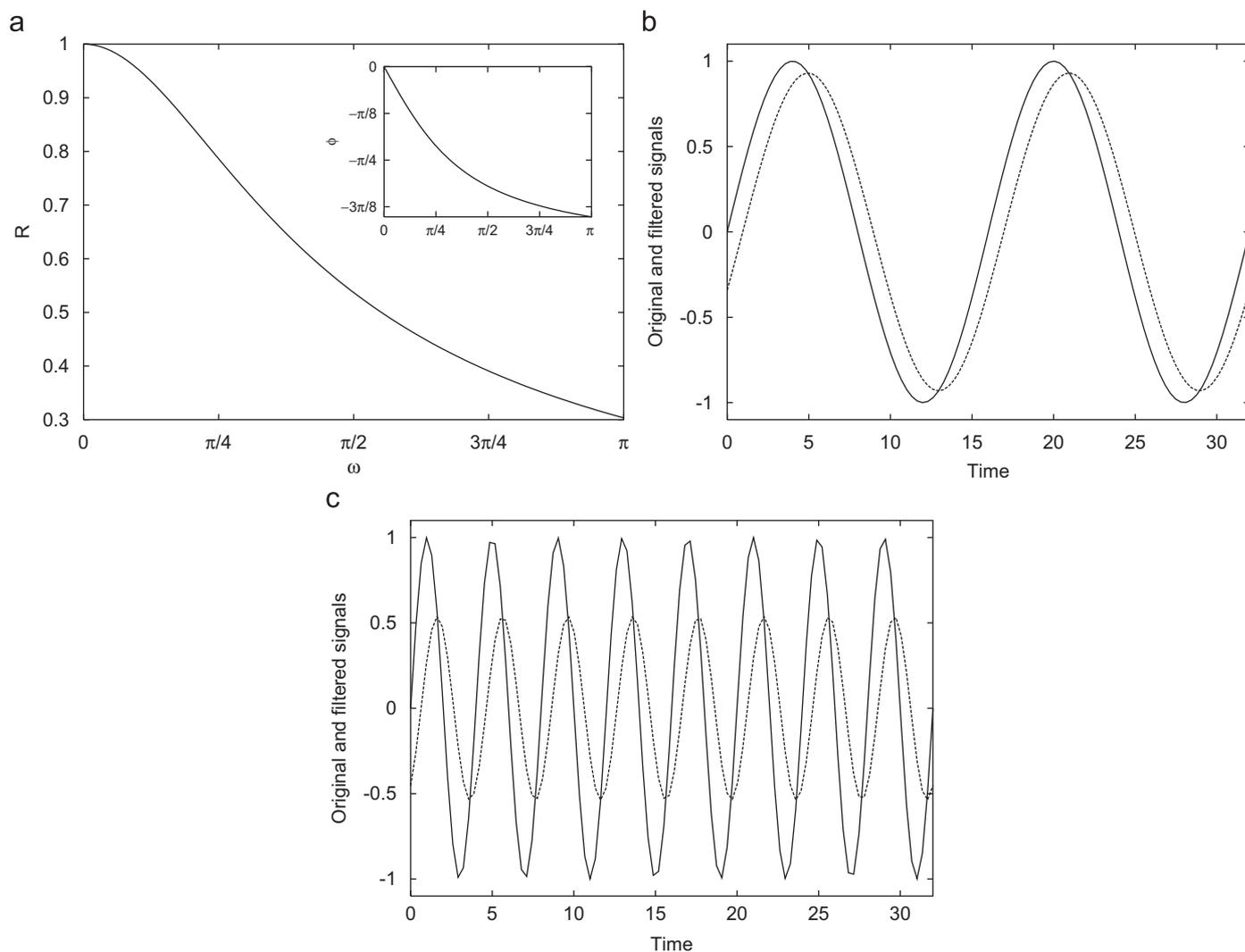


Fig. 2. The effect of a complex response function on a sinusoidal signal. Consider a sinusoidal signal $\sin(\omega_0 t)$ which is convolved with the kernel $\exp(-t), t \geq 0; 0, t < 0$. In the context of this paper, we can think of $\sin(\omega_0 t)$ as representing a temporally varying environment and the convolution of $\sin(\omega_0 t)$ as the resulting population dynamics. The Fourier transform of this kernel is $1/(1 + i\omega)$, which can be written as $R(\omega)\exp(i\phi(\omega))$, where $R(\omega) = 1/\sqrt{1 + \omega^2}$ and $\phi(\omega) = \tan^{-1}(-\omega)$. For “environmental variation” of the form $\sin(\omega_0 t)$, the resulting “population dynamics” is $R(\omega_0)\sin(\omega_0 t + \phi(\omega_0))$. Part (a) shows the amplitude and phase of the response function as a function of frequency ω . The decline of $R(\omega)$ with ω indicates that the population will vary less as the frequency of the environmental variation becomes higher. The decline of the phase $\phi(\omega)$ from zero to more negative values indicates that the delay between the environmental variation and the population’s response will grow longer as the frequency of the environmental variation becomes higher. This is demonstrated in parts (b) and (c), which show environmental variation (solid lines) and the resulting population dynamics (dashed lines) for low frequency variation ($\omega_0 = 2\pi/16$) in part (b) and high frequency variation ($\omega_0 = 2\pi/4$) in part (c).

depending on the sign of R . This relationship may not hold when population density is measured in a life history stage that is different from the stage where competition occurs. For example, in the model presented in Section 2, population density $n_r(x, t)$ refers to the density of resident seeds at location x at time t , but competition arises from seedlings whose density is given by the seed density times the germination fraction g_r . If environmental variation affects germination, so that germination fraction is a function of space and time, then R is negative at slow time scales when seed survival is high (Fig. 4), meaning that seeds tend to accumulate in areas with low germination. Seed density is low where germination is high and vice

versa, with the result that seedling density and the resulting competition vary only a little even though $|R|$ is large.

The connection between R and the invader’s long run growth rate, \bar{r}_i , is less clear. At a minimum, \bar{r}_i depends on $\langle \text{Cov}(n_i, n_r) \rangle_t$ (Are the residents and invaders concentrated in the same areas?), $\langle \text{Cov}(n_i, E_i) \rangle_t$ (Is the invader concentrated in an environment favorable to it?), $\text{Var}(n_r)_{x,t}$ (How much does the resident density vary?) (More variation increases \bar{r}_i if invader growth is a concave-up function of competition.), and $\langle \text{Cov}(n_r, E_i) \rangle_t$ (Are the residents concentrated in areas favorable to the invaders?). Calculating \bar{r}_i is, therefore, somewhat involved. However, there are three situations which tend to lead to higher long

run growth rates for the invader. In the first situation, the resident and invader each track environmental conditions well and prefer different habitats, so that they are spatially segregated. (The quantities $\text{Var}(n_r)_{x,t}$ and $\langle \text{Cov}(n_i, E_i)_{x,t} \rangle_I$ are positive, increasing \bar{r}_i , and $\langle \text{Cov}(n_i, n_r)_{x,t} \rangle_I$ and $\langle \text{Cov}(n_r, E_i)_{x,t} \rangle_I$ are negative, also increasing \bar{r}_i .) In the second situation, the resident is concentrated in unfavorable areas (“anti-tracking”) and the invader is more uniformly distributed. (Variance and covariances similar to the previous case.) It seems likely that species adapted to their environment will have evolved to avoid anti-tracking, but more recently introduced species may anti-track. In the third situation, which does not produce growth rates as high as the first two, the resident is unable to track environmental variation but the invader can. (The quantity $\langle \text{Cov}(n_i, E_i)_{x,t} \rangle_I$ is positive, increasing \bar{r}_i , and all of the other variances and covariances are small.) This tends to happen when environmental variation is relatively slow and the invader has shorter range dispersal than the resident, so that, averaged over time, the invader is better able to concentrate its population in favorable areas. This is a spatiotemporal version Chesson’s growth-density covariance mechanism (Chesson, 2000; Snyder and Chesson, 2003).

The most important spatial and temporal scales tend, therefore, to be those that allow one or both species to track environmental conditions. This paper has only discussed the resident’s spatiotemporal distribution, but it is possible to calculate the invader’s distribution in a similar fashion. (See, for example, the appendix of Snyder, 2006.) If the scales at which the resident becomes concentrated depend on life history strategy or the nature of the environmental variation, then the scales of variation which most affect coexistence are also likely to depend on these factors.

5. Comparison of various response functions

Figs. 3–6 show response functions (R) for sinusoidally varying fecundity or germination as a function of the spatial and temporal period of the environmental variation. Natural variation will not be sinusoidal, of course, but with the use of Fourier transforms, more complex patterns of variation can be broken into sums of sinusoids at different spatial and temporal frequencies (Section 3). Analyzing sinusoidal variation allows us to consider the effects of each component scale separately.

The differences among the response functions are striking. A population may be approximately equally sensitive to variation at all spatial scales, but not to all temporal scales (e.g. Fig. 4a, c). Likewise, it is possible for a population to be approximately equally sensitive to variation at all temporal scales but not to all spatial scales (e.g. Figs. 5a, c, 6a). It is also possible for a population to be differentially sensitive to both scales, so that the effects of spatial and temporal variation interact (e.g. Figs. 3d, 4b).

The response function is often positive but may be negative, as is the case for variable germination with high seed survival (Fig. 4). A large negative value for the response function means that the population is concentrated in unfavorable areas. Variation in germination can produce a negative response function because a favorable environment is one in which the germination fraction is high. If seeds are long-lived, this leaves seeds concentrated in areas where the germination fraction is low.

One apparently robust pattern occurs when dispersal is short range and competition is long range. As discussed in Snyder and Chesson (2004), the response function has a resonance peak, indicating that the resident population is especially sensitive to environmental variation at a small range of intermediate spatial scales. The peak occurs because short-range dispersal allows the population to accumulate in favorable areas and long-range competition reduces the competitive pressure in crowded favorable areas while increasing the pressure on individuals in adjacent unfavorable areas (Roughgarden, 1974; Snyder and Chesson, 2004). It seems likely that this resonance is a general phenomenon.

Nonetheless, it seems clear that the population’s response to variation at different spatial and temporal scales depends sensitively on how environmental variation affects the organism. Environmental variation that affects germination has a very different effect than environmental variation that affects fecundity. In addition, changes in life history parameters can produce unexpected results. For example, while an increase in the mean dispersal distance does make the population less sensitive to variation at small spatial scales, the same is not true of an increase in the spatial scale of competition, and the two spatial scales can interact to produce a resonance. Likewise, changes in seed survival produce only small, quantitative changes in sensitivity when fecundity varies, but produce radical changes when germination varies. (Compare Figs. 4 and 6.) The effects of life history parameters depend on how environmental variation affects the individuals and are likely to vary from situation to situation.

6. Discussion

When environmental conditions vary, the ability of a low-density species to persist in the presence of a competitor depends in large part on the competitor’s spatiotemporal distribution. This paper shows how we can think of a population’s distribution as the result of a mathematical filter applied to the environmental variation. The filter can be converted into a response function which shows the sensitivity of the population to variation at different spatial and temporal scales. Scales at which the response function is large represent spatial and temporal frequencies of variation to which the population is sensitive—the population will track environmental variation at these scales, possibly with some time delay. Scales at which the response function is small represent spatial and

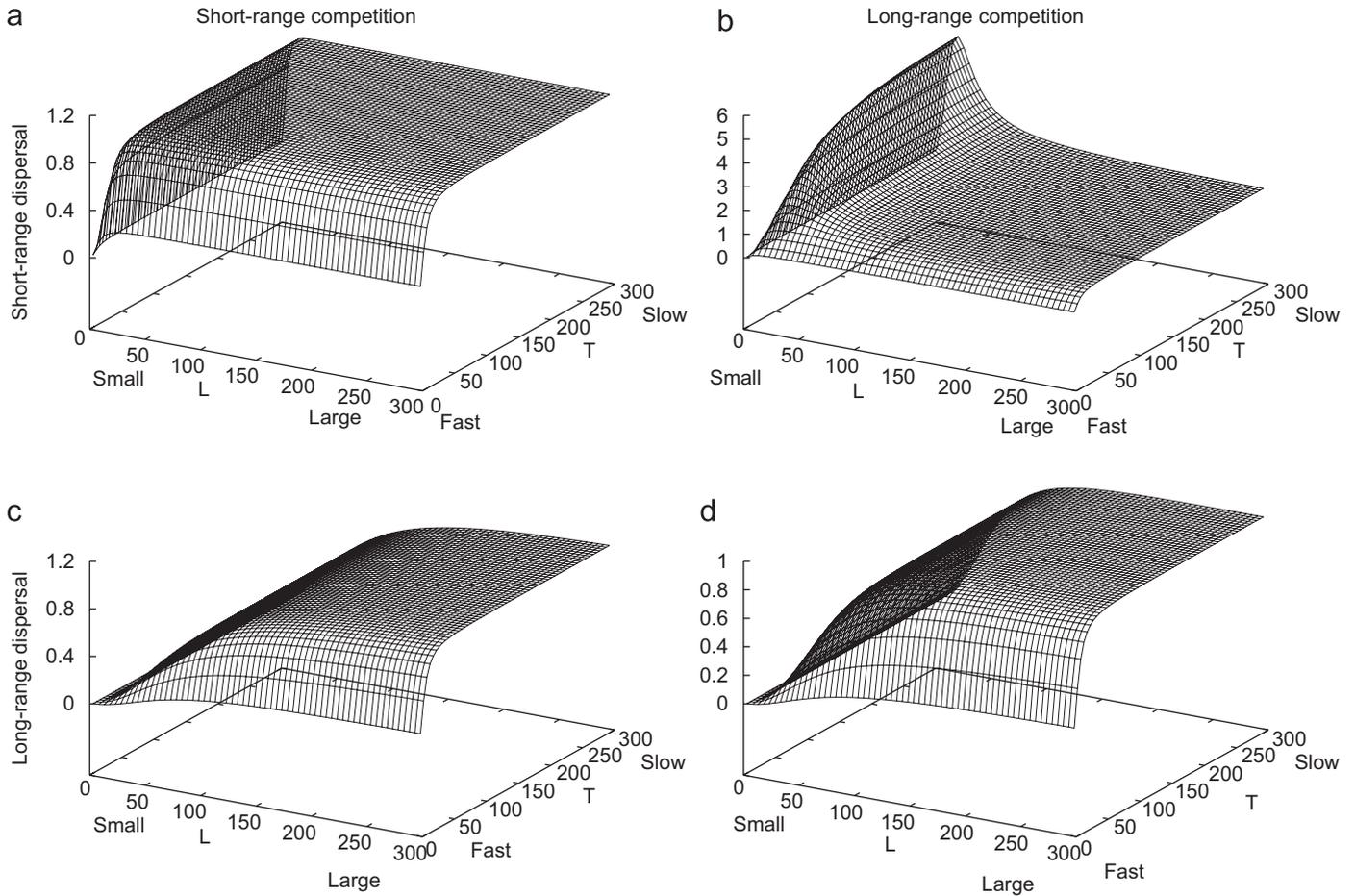


Fig. 3. Response functions for long-lived seeds ($s_r = 0.9$) and variable fecundity as a function of the spatial (L) and temporal (T) scale of the environmental variation. In these and the following figures, the environmental variation is sinusoidal in space and time with spatial period L (spatial frequency $q = 2\pi/L$) and temporal period T (temporal frequency $\omega = 2\pi/T$): $E(x, t) = \langle E \rangle_{x,t} + B \sin(2\pi x/L) \sin(2\pi t/T)$. The population disperses according to a Laplacian kernel $k_r(x) = \alpha_r/2 \exp(-\alpha_r|x|)$ with mean dispersal distance $1/\alpha_r$ and competes with itself according to a Laplacian kernel $U_{rr}(x) = \beta_{rr}/2 \exp(-\beta_{rr}|x|)$ with characteristic competition distance $1/\beta_{rr}$. (a) $1/\alpha_r = 1, 1/\beta_{rr} = 1$. (b) $1/\alpha_r = 1, 1/\beta_{rr} = 10$. (c) $1/\alpha_r = 10, 1/\beta_{rr} = 1$. (d) $1/\alpha_r = 10, 1/\beta_{rr} = 10$.

temporal frequencies to which the population is insensitive—the population is unable to track variation at these scales. Using an annual plant model, this paper demonstrates how to calculate the response function and presents response functions that arise from variation in two different stages in the plant’s life cycle.

Response functions help to explain how environmental variation affects invasion dynamics and species coexistence because response functions show where the resident population is clustered (in favorable or unfavorable areas) and to what degree, and this determines the competitive landscape experienced by the invaders. While the invader’s growth rate is not solely determined by competition, understanding how the residents are distributed can enable a heuristic understanding of patterns of invasibility and coexistence. For example, in their model of a California grassland, [Levine and Rees \(2004\)](#) described competition between a forb with long-lived seeds that accumulate in the seed bank and a competitively superior grass with short-lived seeds. In the first wet year after a dry year, the forb

population responds immediately, with many forb seeds in the seed bank germinating. In contrast, the response of the grass population lags. Having few seeds in the seed bank, the grass first must produce seeds, which then have the opportunity to germinate in the following year. Levine and Rees showed that if wet years are followed by dry years, then the grass anti-tracks the environment, becoming most populous in the dry years which follow wet years. This allows the competitively inferior forb to persist. In contrast, if wet years are followed by more wet years, the grass is able to track this slower variation, and the forb is excluded. If we were to calculate the response function of the grass, it would be negative for rapid variation and positive for slow variation.

In the above example, the inferior competitor is able to persist when dry years follow wet years because the superior competitor anti-tracks the environment under those conditions. The species in the role of invader also has an increased chance of persistence if it can track environmental conditions while, instead of anti-tracking the

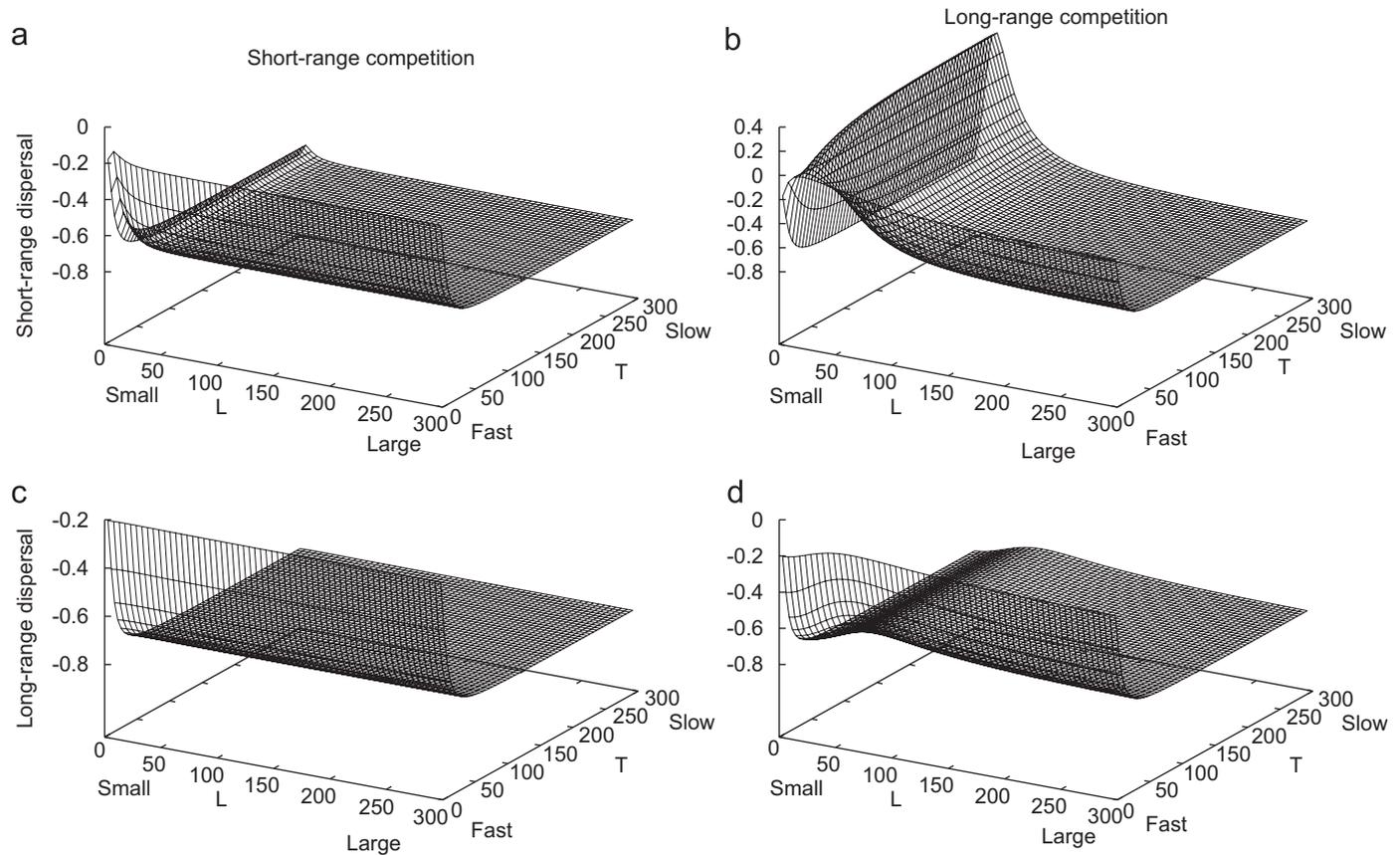


Fig. 4. Response functions for long-lived seeds ($s_r = 0.9$) and variable germination as a function of the spatial (L) and temporal (T) scale of the environmental variation. (a) $1/\alpha_r = 1, 1/\beta_{rr} = 1$. (b) $1/\alpha_r = 1, 1/\beta_{rr} = 10$. (c) $1/\alpha_r = 10, 1/\beta_{rr} = 1$. (d) $1/\alpha_r = 10, 1/\beta_{rr} = 10$.

environment, the resident is unable to track environmental conditions much at all. In the context of the example above, this would mean that the grass had a constant population in wet and dry years while the forb was populous only in wet years. Alternatively, if the two species prefer different environmental conditions, the invader is likely to do well if both species are able to track the environment. The success of a species in tracking conditions it finds favorable depends on the spatial and temporal scales of the environmental variation, and this dependence is encoded in its response function.

The invader's response function can be found in the same manner as the resident's; a calculation of the invader's response function can be found in the appendix of Snyder (2006). Determining the success of an invader is then a matter of using the expressions for $v_r(x, t)$, $v_i(x, t)$, and $\langle n_r \rangle_x(t)$ to find a second-order expression for the long term growth rate, defined as the geometric mean of the regional growth rate, $\tilde{\lambda}_i$. (See the appendix for a discussion of $\tilde{\lambda}_i$.) An example of these calculations can be found in the appendix of Schoolmaster and Snyder (2007), and a fuller treatment will be presented in a future paper.

One of the important insights response functions provide is that a population's sensitivity to variation at different scales depends strongly on the way environmental variation affects the organism. Comparing Figs. 3 and 4, for

example, we see that the response function may increase monotonically with spatial and temporal scale when fecundity varies but, for the same life history parameter values, depend only on temporal scale when germination varies.

Another important insight is that the way life history parameters affect a population's sensitivity to variation depends on how the environmental variation affects the organism. When I began this study, I expected that as the spatial and temporal scales inherent in an organism's life history grew, its sensitivity to small scale spatial and temporal variation would decrease. For example, as dispersal distance grew, I expected the population distribution to become more spatially uniform, averaging over the small scale spatial variation, and as the mean seed lifetime grew, I expected the population to become less sensitive to rapid temporal variation. These were, furthermore, the only effects I expected increases in dispersal or lifetime to produce. However, changes in life history parameters can interact with environmental variation in far more profound ways, depending on how environmental variation affects the organism. For example, when fecundity varies, increasing seed survival produces the expected decrease in sensitivity to rapid temporal variation. (Compare Figs. 3 and 5.) Yet when germination varies, a change in seed survival can cause the response function to switch from

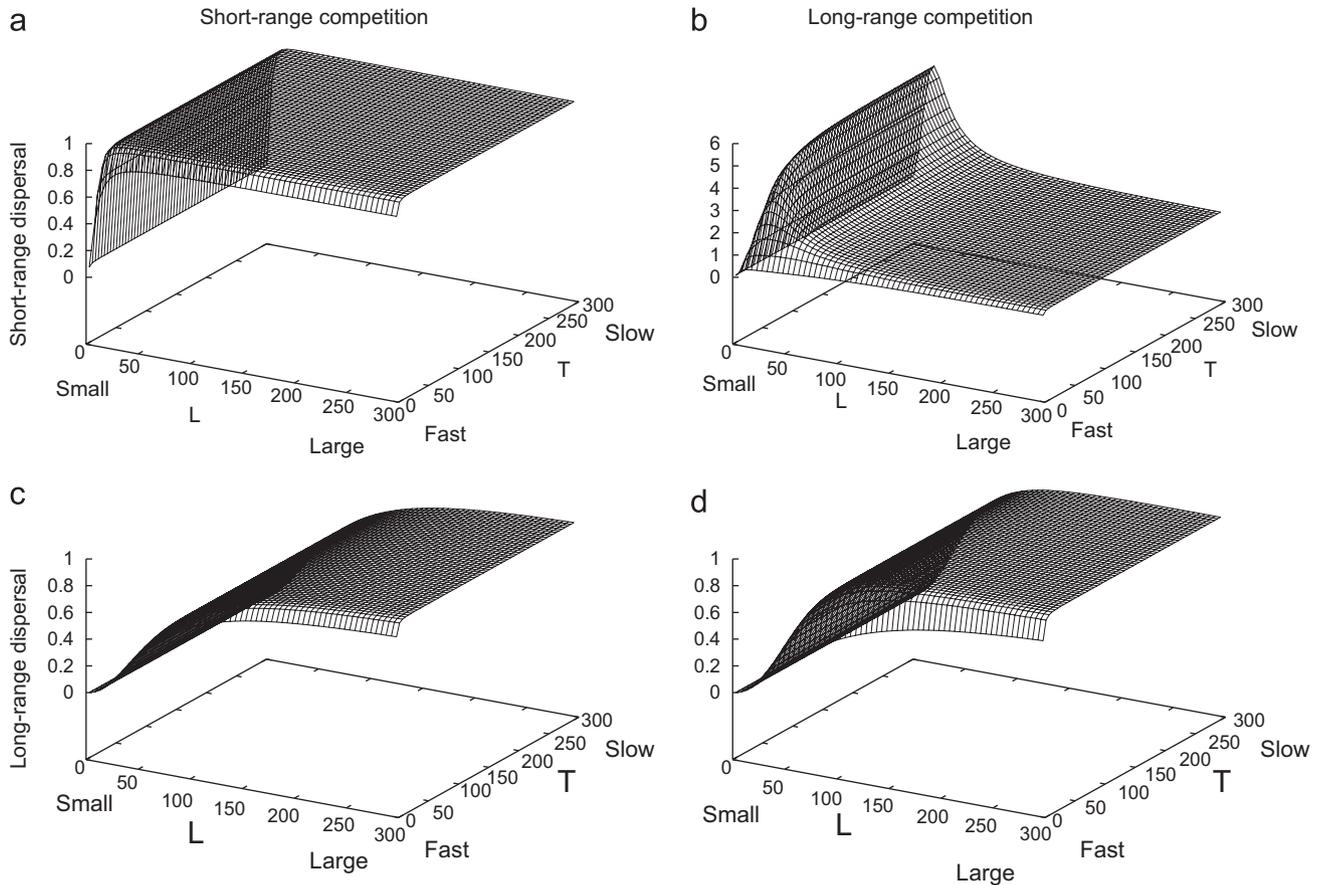


Fig. 5. Response functions for short-lived seeds ($s_r = 0.1$) and variable fecundity as a function of the spatial (L) and temporal (T) scale of the environmental variation. (a) $1/\alpha_r = 1, 1/\beta_{rr} = 1$. (b) $1/\alpha_r = 1, 1/\beta_{rr} = 10$. (c) $1/\alpha_r = 10, 1/\beta_{rr} = 1$. (d) $1/\alpha_r = 10, 1/\beta_{rr} = 10$.

depending almost entirely on the temporal scale of the variation to depending almost entirely on the spatial scale of the variation. (Compare Figs. 4 and 6.)

These differences in the response functions can lead to different patterns in the strength of coexistence mechanisms. Figs. 7a and b show $\sqrt{\bar{r}_{i=1}\bar{r}_{i=2}}$, the square root of the product of the long-run growth rates of each species as invader, as a function of the scales of variation in both germination and fecundity. Both species have a positive long-run growth rate as invader for all values shown, so that a large product means both species have large long-run growth rates as invaders. Neither species has a competitive advantage in the absence of environmental variability, and so $\sqrt{\bar{r}_{i=1}\bar{r}_{i=2}}$ gives a measure both of their mutual invasibility and of the degree to which variation at that scale contributes to coexistence. For these life history parameter values, mutual invasibility peaks for large-scale, slow variation in both germination and fecundity, although the peak is higher for variable fecundity. Rapid variation in germination also produces a peak in mutual invasibility, unlike rapid variation in fecundity. The reason that rapid variation in germination promotes coexistence and rapid variation in fecundity does not is because while the response function R is of similar magnitude for both forms of variation, it is negative for variable germination (Fig. 4c)

and positive for variable fecundity (Fig. 3c). Since the phase delay ϕ is near π for rapid variation, this means that the resident tracks variation in germination and anti-tracks variation in fecundity. The two species in this example prefer different habitats, so that resident tracking produces a negative covariance between invader competition and the environment (the competition experienced by the invader is higher in more favorable areas) and resident anti-tracking produces a positive covariance (the invader experiences low competition in areas it finds more favorable). Covariance between competition and the environment is an ingredient of the spatial storage effect (Chesson, 2000), which is what promotes coexistence in this example.

The results presented here have implications for the effects of disturbances on coexistence. Empirical tests of the effect of disturbance extent and frequency have had mixed results. Armstrong found that small size disturbances permit coexistence more readily than large ones (Armstrong, 1988), while Moloney and Levin (1996) found that size played only a minor role in their study. Moloney and Levin found that the frequency of disturbance played a key role in the population dynamics while McCabe and Gotelli (2000) found little effect of frequency (although they note that it might have been necessary to explore lower frequencies to see an effect). These conflicting results

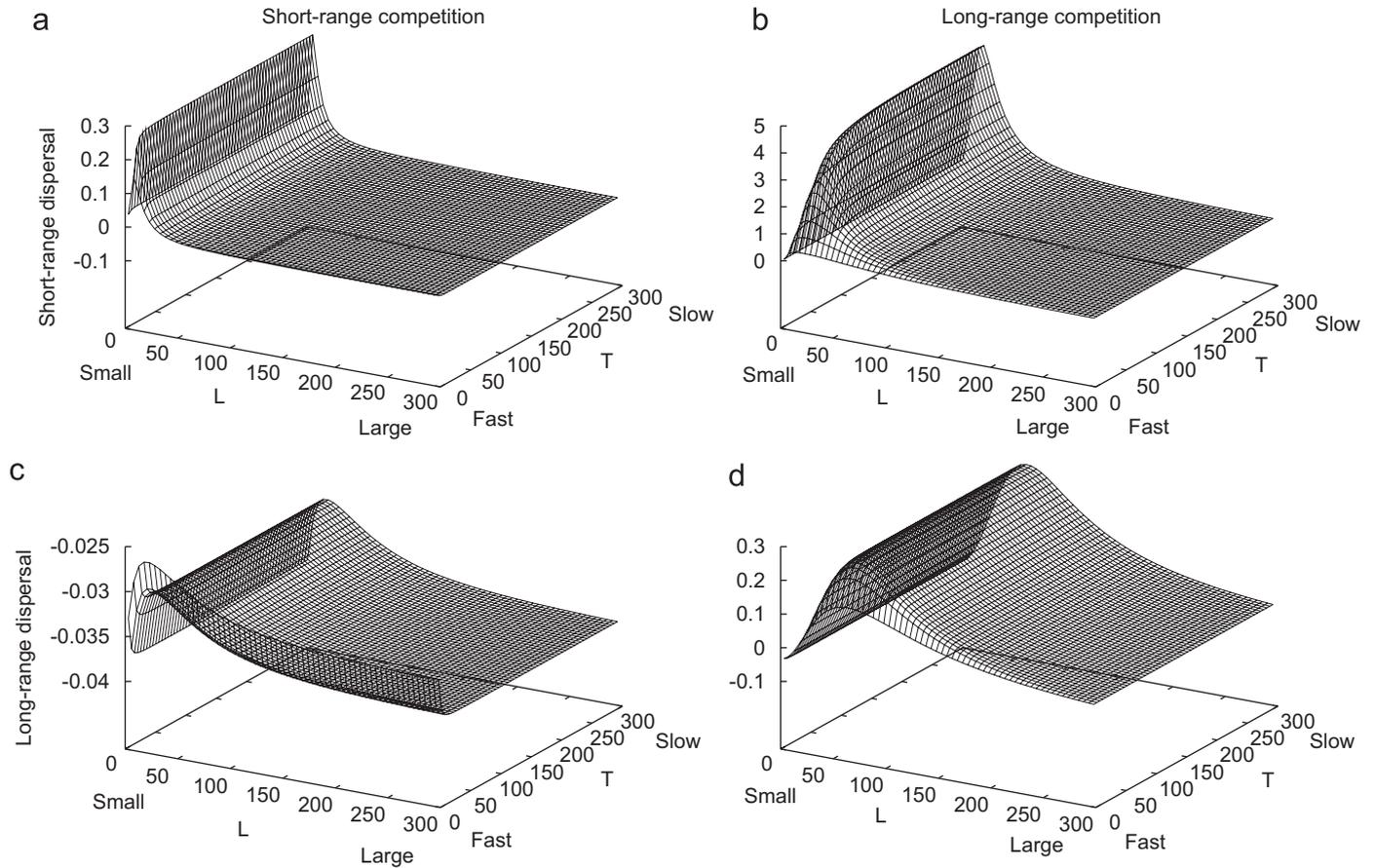


Fig. 6. Response functions for short-lived seeds ($s_r = 0.1$) and variable germination as a function of the spatial (L) and temporal (T) scale of the environmental variation. (a) $1/\alpha_r = 1, 1/\beta_{rr} = 1$. (b) $1/\alpha_r = 1, 1/\beta_{rr} = 10$. (c) $1/\alpha_r = 10, 1/\beta_{rr} = 1$. (d) $1/\alpha_r = 10, 1/\beta_{rr} = 10$.

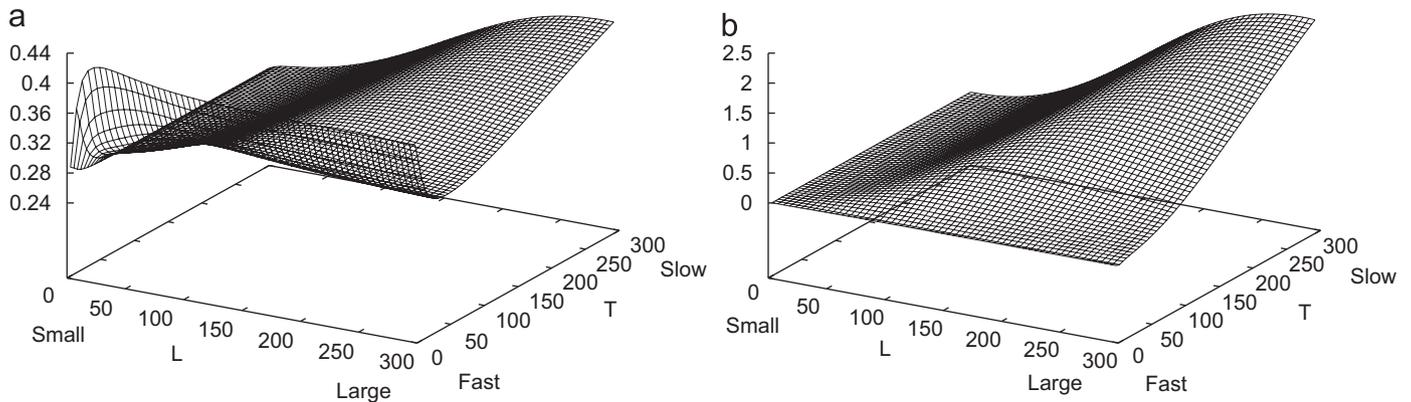


Fig. 7. Mutual invasibility for variable germination (a) and fecundity (b). This figure shows $\sqrt{\bar{r}_{i=1}\bar{r}_{i=2}}$, the square root of the product of the long-run growth rates of each species as invader, as a function of the spatial (L) and temporal (T) scales of environmental variation. Both species have a positive long-run growth rate as invader for all values shown, so that a large product means both species have large long-run growth rates as invaders. Neither species has a competitive advantage in the absence of environmental variability, and so $\sqrt{\bar{r}_{i=1}\bar{r}_{i=2}}$ gives a measure both of their mutual invasibility and of the degree to which variation at that scale contributes to coexistence. For both species, the mean fecundity, $\langle F \rangle_{x,r}$, equals 4, the mean germination fraction, $\langle g \rangle_{x,r}$, equals 0.36, and the amplitude of the environmental variation is 75% of the mean. Both species have long-distance dispersal ($\alpha_1 = \alpha_2 = 0.1$), short-range inter- and intra-specific competition ($\beta_{11} = \beta_{22} = \beta_{12} = \beta_{21} = 1$), and long-lived seeds ($s_1 = s_2 = 0.9$), and the two species prefer different environments: $\text{Corr}(E_1(x, t), E_2(x, t)) = -1$. For these life history parameter values, coexistence is promoted relatively strongly at large spatial and temporal scales for both variable fecundity and variable germination, although variable fecundity does so more strongly. (The vertical scales of the graphs are different.) Variable germination also promotes coexistence relatively strongly at small temporal scales.

are consistent with the current work, which suggests that we should not expect a particular range of spatial or temporal scales to be most effective in promoting

coexistence. The effects of disturbance size and frequency should depend both on life history characteristics and on the way that environmental variation affects the organisms.

The methods presented here are also relevant to the effect of disturbance timing, as early and late disturbances may cause variation in different life history parameters. For example, herbivory early in the growing season could cause effective variation in germination while herbivory late in the growing season could cause variation in fecundity. If variation in different life history parameters produces different response functions, we may be able to explain the results of disturbance timing by the effect of disturbance timing on the resident population distribution.

The work presented in this paper gives important insights into what determines which scales of environmental variation most influence species coexistence, but it does not tell the entire story. For example, the present work has made it clear that one cannot make simple statements such as “increasing the duration of one or more life stages causes the population to become less sensitive to variation at short temporal scales,” as one might intuitively suppose. Rather, one must account for the way that the type of environmental variation (does it affect fecundity? germination?) interacts with life history parameters. It is not clear, however, just how the form of the environmental variation determines the effect of life history parameters on a population’s sensitivity to variation. An intuitive understanding of how these factors work together would be very helpful.

Furthermore, to fully understand which scales most influence the coexistence of two species, we must take into account not only the distribution of the resident but also the distribution of the invader. Considering the resident’s distribution alone has already yielded useful insights, helping us to understand how invasibility in variable environments interacts with resident species turnover, for example (Schoolmaster and Snyder, 2007). Nonetheless, a fuller understanding is desirable. The coexistence of many species is thought to be mediated by disturbance or other forms of environmental variation. Understanding how the scales of that variation affect coexistence is important in understanding how these species coexist and how anthropogenic changes to disturbance regimes may affect them.

Acknowledgment

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Appendix A. Derivation of the resident response function

Let us derive the response function for variable fecundity. Assume that environmental variation, and therefore variation in population density and local growth rate, is of small amplitude so that we can write $E_r(x, t)$, $n_r(x, t)$, and $\lambda_r(x, t)$ in terms of their spatiotemporal averages plus perturbations of $O(\sigma)$.¹ Assume also that the deviations of

spatial averages from spatiotemporal averages are $O(\sigma)$. We first write $E_r(x, t)$, $n_r(x, t)$, and $\lambda_{kr}(x, t)$ in terms of perturbations away from their spatial averages:

$$E_r(x, t) = \langle E_r \rangle_x(t)(1 + \varepsilon_r(x, t)), \quad (\text{A.1})$$

$$n_r(x, t) = \langle n_r \rangle_x(t)(1 + u_r(x, t)), \quad (\text{A.2})$$

$$\lambda_{kr}(x, t) = \langle \lambda_{kr} \rangle_x(t)(1 + \zeta_{kr}(x, t)), \quad k = 1, 2, \quad (\text{A.3})$$

where $\langle \cdot \rangle_x$ denotes an average over space and the perturbations ε_r , u_r , and ζ_{kr} are $O(\sigma)$ and all have spatial and temporal averages equal to zero. We then write the spatial averages in terms of perturbations away from the spatiotemporal averages:

$$\langle E_r \rangle_x(t) = \langle E_r \rangle_{x,t}(1 + \Omega_r(t)), \quad (\text{A.4})$$

$$\langle n_r \rangle_x(t) = \langle n_r \rangle_{x,t}(1 + \eta_r(t)), \quad (\text{A.5})$$

$$\langle \lambda_{kr} \rangle_x(t) = \langle \lambda_{kr} \rangle_{x,t}(1 + h_{kr}(t)), \quad k = 1, 2, \quad (\text{A.6})$$

where $\langle \cdot \rangle_{x,t}$ denotes an average over time and space and Ω_r , η_r , and h_{kr} are $O(\sigma)$ and have temporal averages equal to zero. To $O(\sigma)$, then,

$$E_r(x, t) = \langle E_r \rangle_{x,t}(1 + \varepsilon_r(x, t) + \Omega_r(t)), \quad (\text{A.7})$$

$$n_r(x, t) = \langle n_r \rangle_{x,t}(1 + u_r(x, t) + \eta_r(t)), \quad (\text{A.8})$$

$$\lambda_{kr}(x, t) = \langle \lambda_{kr} \rangle_{x,t}(1 + \zeta_{kr}(x, t) + h_{kr}(t)), \quad k = 1, 2. \quad (\text{A.9})$$

Note that $\lambda_r(x, t) = \lambda_{1r}(x, t) + \lambda_{2r}(x, t)$ and so $\zeta_r(x, t) = \zeta_{1r}(x, t) + \zeta_{2r}(x, t)$ and $h_r(t) = h_{1r}(t) + h_{2r}(t)$. We will first derive an expression for $v_r(x, t) (= n_r(x, t)/\langle n_r \rangle_x(t))$ and then find an expression for $\langle n_r \rangle_x(t)$, and these will give us $u_r(t)$ and $\eta_r(t)$, respectively.

We begin by finding an expression for $v_r(x, t)$. As noted in Chesson (2000), $\langle n_r \rangle_x(t + 1) = \tilde{\lambda}_r \langle n_r \rangle_x(t)$, where $\tilde{\lambda}_r(t) = \langle \lambda_r \rangle_x(t) + \text{Cov}(\lambda_r, v_r)_x(t)$. We can convert Eq. (1), the equation for the dynamics of $n_r(x, t)$, into an equation for $v_r(x, t)$ by dividing both sides by $\langle n_r \rangle_x(t + 1)$ and replacing $\langle n_r \rangle_x(t + 1)$ by $\tilde{\lambda}_r(t) \langle n_r \rangle_x(t)$ on the righthand side:

$$v_r(x, t + 1) = k_r * \left(\frac{\lambda_{1r}}{\tilde{\lambda}_r} v_r \right)(x, t) + \left(\frac{\lambda_{2r}}{\tilde{\lambda}_r} v_r \right)(x, t). \quad (\text{A.10})$$

Using Eq. (A.8), the relative population density $v_r(x, t)$ can be written as $\frac{\langle n_r \rangle_{x,t}(1 + u_r(x, t) + \eta_r(t))}{\langle n_r \rangle_{x,t}(1 + \eta_r(t))}$. Taylor expanding to first order, $1/(1 + \eta_r) = 1 - \eta_r + O(\sigma^2)$, and so to $O(\sigma)$, $v_r(x, t) = 1 + u_r(x, t) + \eta_r(t) - \eta_r(t) = 1 + u_r(x, t)$. Using Eq. (A.9) to substitute for λ_{1r} and λ_{2r} , we can rewrite Eq. (A.10) as

$$\begin{aligned} 1 + u_r(x, t + 1) &= \frac{\langle \lambda_{1r} \rangle_{x,t}}{\tilde{\lambda}_r(t)} (1 + k_r * (u_r + \zeta_{1r})(x, t) + h_{1r}(t)) \\ &\quad + \frac{\langle \lambda_{2r} \rangle_{x,t}}{\tilde{\lambda}_r(t)} (1 + \zeta_{2r}(x, t) + u_r(x, t) \\ &\quad + h_{2r}(t)) + O(\sigma^2). \end{aligned} \quad (\text{A.11})$$

We might then replace $\tilde{\lambda}_r(t)$ by $\langle \lambda_r \rangle_x(t) + \text{Cov}(\lambda_r, v_r)_x(t)$. However, because ζ_r and u_r are $O(\sigma)$, the covariance is

¹By $g(x) = O(\sigma)$, I mean that $\frac{|g(x)|}{|\sigma|}$ can be made less than or equal to some positive constant K for σ small enough—i.e., if σ is appropriately small, $g(x)$ will be less than or equal to $K\sigma$.

$O(\sigma^2)$, and so to $O(\sigma)$, we can replace $\tilde{\lambda}_r(t)$ with $\langle \lambda_r \rangle_x(t) = \langle \lambda_r \rangle_{x,t}(1 + h_r(t))$. This gives us

$$\begin{aligned} 1 + u_r(x, t + 1) &= \frac{\langle \lambda_{1r} \rangle_{x,t}}{\langle \lambda_r \rangle_{x,t}}(1 + k_r * (u_r + \zeta_{1r})(x, t) \\ &\quad + h_{1r}(t) - h_r(t)) \\ &\quad + \frac{\langle \lambda_{2r} \rangle_{x,t}}{\langle \lambda_r \rangle_{x,t}}(1 + u_r(x, t) + \zeta_{2r}(x, t) \\ &\quad + h_{2r}(t) - h_r(t)) + O(\sigma^2). \end{aligned} \quad (\text{A.12})$$

Noting that $\frac{\langle \lambda_{1r} \rangle_{x,t}}{\langle \lambda_r \rangle_{x,t}} + \frac{\langle \lambda_{2r} \rangle_{x,t}}{\langle \lambda_r \rangle_{x,t}} = 1$ and $\langle \lambda_{1r} \rangle_{x,t} h_{1r}(t) + \langle \lambda_{2r} \rangle_{x,t} h_{2r}(t) = \langle \lambda_r \rangle_{x,t} h_r(t)$, we are left with

$$\begin{aligned} u_r(x, t + 1) &= \frac{\langle \lambda_{1r} \rangle_{x,t}}{\langle \lambda_r \rangle_{x,t}} k_r * (u_r + \zeta_{1r})(x, t) \\ &\quad + \frac{\langle \lambda_{2r} \rangle_{x,t}}{\langle \lambda_r \rangle_{x,t}} (u_r + \zeta_{2r})(x, t) + O(\sigma^2). \end{aligned} \quad (\text{A.13})$$

To proceed further, we must specify how the growth rate depends on resident density. Turning to Eqs. (2)–(4) from the model definition and using Eqs. (A.7) and (A.8) to express $E_r(x, t)$ and $n_r(x, t)$ in terms of small perturbations, we find that to $O(\sigma)$,

$$\begin{aligned} \lambda_{1r}(x, t) &= \frac{\langle E_r \rangle_{x,t}}{\langle n_r \rangle_{x,t}}(1 + \varepsilon_r(x, t) + \Omega_r(t) \\ &\quad - (U_{rr} * u_r)(x, t) - \eta_r(t)) + O(\sigma^2), \end{aligned} \quad (\text{A.14})$$

$$\lambda_{2r}(x, t) = s_r(1 - g_r), \quad (\text{A.15})$$

and so

$$\zeta_{1r}(x, t) = \varepsilon_r(x, t) - (U_{rr} * u_r)(x, t), \quad (\text{A.16})$$

$$\zeta_{2r}(x, t) = 0. \quad (\text{A.17})$$

Thus,

$$\begin{aligned} u_r(x, t + 1) &= \frac{\langle \lambda_{1r} \rangle_{x,t}}{\langle \lambda_r \rangle_{x,t}} k_r * (u_r + \varepsilon_r - U_{rr} * u_r)(x, t) \\ &\quad + \frac{\langle \lambda_{2r} \rangle_{x,t}}{\langle \lambda_r \rangle_{x,t}} u_r(x, t) + O(\sigma^2). \end{aligned} \quad (\text{A.18})$$

At this point it is useful to take the spatial Fourier transform, where the spatial transform and its inverse are given by

$$\begin{aligned} \tilde{f}(q, t) &= \int_{-\infty}^{\infty} f(x, t) e^{-iqx} dx, \\ f(x, t) &= \frac{1}{2\pi} \int_{-\infty}^{\infty} \tilde{f}(q, t) e^{iqx} dq, \end{aligned} \quad (\text{A.19})$$

the temporal transform by

$$\begin{aligned} \tilde{f}(x, \omega) &= \int_{-\infty}^{\infty} f(x, t) e^{-i\omega t} dt, \\ f(x, t) &= \frac{1}{2\pi} \int_{-\infty}^{\infty} \tilde{f}(x, \omega) e^{i\omega t} d\omega \end{aligned} \quad (\text{A.20})$$

and the spatiotemporal transform by the application of both a temporal and a spatial transform

$$\begin{aligned} \tilde{f}(q, \omega) &= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} f(x, t) e^{-i(qx + \omega t)} dx dt, \\ f(x, t) &= \frac{1}{(2\pi)^2} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \tilde{f}(q, \omega) e^{i(qx + \omega t)} dq d\omega. \end{aligned} \quad (\text{A.21})$$

The Fourier transform of a convolution is the product of the Fourier transforms of the convolved functions ($(f * g)(q) = \tilde{f}(q)\tilde{g}(q)$), and so, dropping the “ $+O(\sigma^2)$ ” reminder, the spatial Fourier transform of Eq. (A.18) is

$$\begin{aligned} \tilde{u}_r(q, t + 1) &= \left[\frac{\langle \lambda_{1r} \rangle_{x,t}}{\langle \lambda_r \rangle_{x,t}} \tilde{k}_r(q)(1 - \tilde{U}_{rr}(q)) + \frac{\langle \lambda_{2r} \rangle_{x,t}}{\langle \lambda_r \rangle_{x,t}} \right] \tilde{u}_r(q, t) \\ &\quad + \frac{\langle \lambda_{1r} \rangle_{x,t}}{\langle \lambda_r \rangle_{x,t}} \tilde{k}_r(q) \tilde{\varepsilon}_r(q, t). \end{aligned} \quad (\text{A.22})$$

The transformed population in year t , $\tilde{u}_r(q, t)$, depends on the previous year's population which depends in turn on populations still further back in time. Assuming that $\tilde{u}_r(q, t)$ reaches a stationary distribution independent of its initial condition, $\tilde{u}_r(q, t = 0)$, we can write

$$\tilde{u}_r(q, t) = \sum_{j=0}^{t-1} B_{ur}^{t-1-j}(q) B_{\varepsilon_r}(q) \tilde{\varepsilon}_r, \quad (q, t = j), \quad (\text{A.23})$$

where

$$B_{ur}(q) = \frac{\langle \lambda_{1r} \rangle_{x,t}}{\langle \lambda_r \rangle_{x,t}} \tilde{k}_r(q)(1 - \tilde{U}_{rr}(q)) + \frac{\langle \lambda_{2r} \rangle_{x,t}}{\langle \lambda_r \rangle_{x,t}}, \quad (\text{A.24})$$

$$B_{\varepsilon_r}(q) = \frac{\langle \lambda_{1r} \rangle_{x,t}}{\langle \lambda_r \rangle_{x,t}} \tilde{k}_r(q). \quad (\text{A.25})$$

Eq. (A.23) can be expressed as a discrete convolution in time

$$\tilde{u}_r(q, t) = \sum_{j=0}^{\infty} \tilde{M}(q, t - j) \tilde{\varepsilon}_r(q, j), \quad (\text{A.26})$$

where

$$\tilde{M}(q, n) = \begin{cases} B_{ur}^{n-1}(q) B_{\varepsilon_r}(q) & n > 0, \\ 0 & n \leq 0. \end{cases} \quad (\text{A.27})$$

Discrete Fourier transforms² turn discrete convolutions into products just as continuous Fourier transforms do with continuous convolutions, and so, taking the temporal Fourier transform, we reach the pleasingly simple form

$$\tilde{u}_r(q, \omega) = \tilde{M}(q, \omega) \tilde{\varepsilon}_r(q, \omega), \quad (\text{A.28})$$

²My convention for the discrete Fourier transform and its inverse is $\tilde{f}(x, \omega) = \lim_{N \rightarrow \infty} \sum_{t=-N/2}^{N/2-1} f(x, t) e^{-i\omega t}$, $f(x, t) = \lim_{N \rightarrow \infty} \frac{1}{N} \sum_{j=-N/2}^{N/2-1} \tilde{f}(x, \omega) e^{i\omega t}$, $\omega_j = \frac{2\pi j}{N}$.

where

$$\begin{aligned} \tilde{M}(q, \omega) &= \sum_{s=-\infty}^{\infty} \tilde{M}(q, s) e^{-i\omega s} = \sum_{s=1}^{\infty} B_{u_r}^{s-1}(q) B_{e_r}(q) e^{-i\omega s} \\ &= \frac{B_{e_r}(q)(e^{-i\omega} - B_{u_r}(q))}{1 + B_{u_r}^2(q) - 2B_{u_r}(q) \cos \omega}. \end{aligned} \quad (\text{A.29})$$

Switching to polar notation, we can rewrite $\tilde{M}(q, \omega)$ as $R(q, \omega) e^{i\phi(q, \omega)}$, where

$$\begin{aligned} R(q, \omega) &= [\text{Re}(\tilde{M}(q, \omega))^2 + \text{Im}(\tilde{M}(q, \omega))^2]^{1/2} \\ &= \frac{B_{e_r}(q)}{\sqrt{1 + B_{u_r}^2(q) - 2B_{u_r}(q) \cos \omega}}, \end{aligned} \quad (\text{A.30})$$

$$\begin{aligned} \phi(q, \omega) &= \tan^{-1} \left(\frac{\text{Im}(\tilde{M}(q, \omega))}{\text{Re}(\tilde{M}(q, \omega))} \right) \\ &= \tan^{-1} \left(\frac{-\sin \omega}{\cos \omega - B_{u_r}(q)} \right) \end{aligned} \quad (\text{A.31})$$

and where we extend the range of \tan^{-1} to $[0, 2\pi)$ by declaring ϕ to be in the first quadrant ($0 \leq \phi < \pi/2$) if both the numerator and the denominator of \tan^{-1} 's argument are positive, the second quadrant ($\pi/2 \leq \phi < \pi$) if the numerator is positive and the denominator negative, the third quadrant ($\pi \leq \phi < 3\pi/2$) if both numerator and denominator are negative, and the fourth quadrant ($3\pi/2 \leq \phi < 2\pi$) if the numerator is negative and the denominator positive.

For completeness' sake, let us find the values of $\frac{\langle \lambda_{1r} \rangle_{x,t}}{\langle \lambda_r \rangle_{x,t}}$ and $\frac{\langle \lambda_{2r} \rangle_{x,t}}{\langle \lambda_r \rangle_{x,t}}$. We take the spatiotemporal averages of the $O(\sigma)$ approximations for $\lambda_{1r}(x, t)$ (Eq. (A.14)) and $\lambda_{2r}(x, t)$ (Eq. (A.15)) and find

$$\langle \lambda_{1r} \rangle_{x,t} = \frac{\langle E_r \rangle_{x,t}}{\langle n_r \rangle_{x,t}}, \quad (\text{A.32})$$

$$\langle \lambda_{2r} \rangle_{x,t} = s_r(1 - g_r). \quad (\text{A.33})$$

The average value of λ_{1r} depends on the average resident population density, $\langle n_r \rangle_{x,t}$. We can use Eqs. (A.7) and (A.8) to Taylor expand Eq. (1), the equation for the population dynamics. Taking a spatiotemporal average, all of the $O(\sigma)$ terms vanish, so that to $O(\sigma)$,

$$\langle n_r \rangle_{x,t} = \left(\frac{\langle E_r \rangle_{x,t}}{\langle n_r \rangle_{x,t}} + s_r(1 - g_r) \right) \langle n_r \rangle_{x,t}, \quad (\text{A.34})$$

yielding

$$\langle n_r \rangle_{x,t} = \frac{\langle E_r \rangle_{x,t}}{1 - s_r(1 - g_r)}. \quad (\text{A.35})$$

Thus,

$$\langle \lambda_{1r} \rangle_{x,t} = 1 - s_r(1 - g_r), \quad (\text{A.36})$$

$$\langle \lambda_{2r} \rangle_{x,t} = s_r(1 - g_r) \quad (\text{A.37})$$

and

$$\langle \lambda_r \rangle_{x,t} \equiv \langle \lambda_{1r} \rangle_{x,t} + \langle \lambda_{2r} \rangle_{x,t} = 1. \quad (\text{A.38})$$

We can find an expression for $\langle n_r \rangle_x(t)$ with an approach similar to that for $v_r(x, t)$. As noted earlier, $\langle n_r \rangle_x(t + 1) = [\langle \lambda_r \rangle_x(t) + \text{Cov}(\lambda_r, v_r)_{x,t}(t)] \langle n_r \rangle_x(t)$. The covariance is $O(\sigma^2)$, and so to $O(\sigma)$,

$$\begin{aligned} \langle n_r \rangle_x(t + 1) &= \langle n_r \rangle_{x,t}(1 + \eta_r(t + 1)) \\ &= \langle \lambda_r \rangle_x(t) \langle n_r \rangle_x(t) \\ &= \langle n_r \rangle_{x,t} \langle \lambda_r \rangle_{x,t} (1 + h_r(t) + \eta_r(t)). \end{aligned} \quad (\text{A.39})$$

The resident population is assumed to have a stationary distribution, and so to $O(\sigma)$, the spatiotemporally averaged finite growth rate, $\langle \lambda_r \rangle_{x,t}$, must be 1, leaving

$$\eta_r(t + 1) = h_r(t) + \eta_r(t). \quad (\text{A.40})$$

Taking a spatial average of Eq. (A.14), we find that $h_r(t) =$

$$\begin{aligned} &\frac{\langle E_r \rangle_{x,t}}{\langle \lambda_r \rangle_{x,t} \langle n_r \rangle_{x,t}} (\Omega_r - \eta_r) = \frac{\langle E_r \rangle_{x,t}}{\langle n_r \rangle_{x,t}} (\Omega_r - \eta_r) \text{ to } O(\sigma), \text{ and so} \\ \eta_r(t + 1) &= \left(1 - \frac{\langle E_r \rangle_{x,t}}{\langle n_r \rangle_{x,t}} \right) \eta_r(t) + \frac{\langle E_r \rangle_{x,t}}{\langle n_r \rangle_{x,t}} \Omega_r(t). \end{aligned} \quad (\text{A.41})$$

Defining

$$B_\eta = 1 - \frac{\langle E_r \rangle_{x,t}}{\langle n_r \rangle_{x,t}}, \quad (\text{A.42})$$

$$B_\Omega = \frac{\langle E_r \rangle_{x,t}}{\langle n_r \rangle_{x,t}}, \quad (\text{A.43})$$

we can write

$$\eta_r(t) = \sum_{j=0}^{t-1} B_\eta^{t-1-j} B_\Omega \Omega_r(j). \quad (\text{A.44})$$

Paralleling the earlier derivation of $\tilde{u}_r(q, \omega)$, we write the above as a convolution in time and take the temporal Fourier transform to arrive at

$$\tilde{\eta}_r(\omega) = H(\omega) e^{i\chi(\omega)}, \quad (\text{A.45})$$

where

$$H(\omega) = \frac{B_\Omega}{\sqrt{1 + B_\eta^2 - 2B_\eta \cos \omega}} \quad (\text{A.46})$$

$$\chi(\omega) = \tan^{-1} \left(\frac{-\sin \omega}{\cos \omega - B_\eta} \right). \quad (\text{A.47})$$

Thus, in the most general case,

$$\begin{aligned} \tilde{n}_r(q, \omega) &= \langle n_r \rangle_{x,t} (\tilde{u}_r(q, \omega) + \tilde{\eta}_r(\omega)) \\ &= \langle n_r \rangle_{x,t} (R(q, \omega) e^{i\phi(q, \omega)} \tilde{e}_r(q, \omega) \\ &\quad + H(\omega) e^{i\chi(\omega)} \tilde{\Omega}_r(\omega)). \end{aligned} \quad (\text{A.48})$$

However, in the absence of globally synchronized variation, (i.e., $\langle E_r \rangle_x = \langle E_r \rangle_{x,t}$), $\tilde{\eta}_r(\omega)$ is zero, so that

$$\tilde{n}_r(q, \omega) = \langle n_r \rangle_{x,t} (R(q, \omega) e^{i\phi(q, \omega)} \tilde{e}_r(q, \omega)). \quad (\text{A.49})$$

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