# Canonical functions for dispersal-induced synchrony

## Ottar N. Bjørnstad[1*] and Benjamin Bolker[2]

[1]*National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, CA 93106, USA*
(*bjornsta@nceas.ucsb.edu*)
[2]*Department of Zoology, University of Florida, Gainesville, FL 32611, USA* (*bolker@zoo.ufl.edu*)

Two processes are universally recognized for inducing spatial synchrony in abundance: dispersal and correlated environmental stochasticity. In the present study we seek the expected relationship between synchrony and distance in populations that are synchronized by density-independent dispersal. In the absence of dispersal, synchrony among populations with simple dynamics has been shown to echo the correlation in the environment. We ask what functional form we may expect between synchrony and distance when dispersal is the synchronizing agent. We formulate a continuous-space, continuous-time model that explicitly represents the time evolution of the spatial covariance as a function of spatial distance. Solving this model gives us two simple canonical functions for dispersal-induced covariance in spatially extended populations. If dispersal is rare relative to birth and death, then covariances between nearby points will follow the dispersal distance distribution. At long distances, however, the covariance tails off according to exponential or Bessel functions (depending on whether the population moves in one or two dimensions). If dispersal is common, then the covariances will follow the mixture distribution that is approximately Gaussian around the origin and with an exponential or Bessel tail. The latter mixture results regardless of the original dispersal distance distribution. There are hence two canonical functions for dispersal-induced synchrony.

**Keywords:** moment equations; spatial dynamics; autocorrelation; diffusion kernel;
dispersal distance distribution

## 1. INTRODUCTION

Environmental correlation and movement of individuals are the two main classes of processes that synchronize dynamics (Ranta *et al*. 1997, 1998). Moran (1953) provided the first theoretical description of regionalization through environmentally correlated forcing. The 'Moran theorem' states that local populations sharing a common structure of density dependence will be synchronized according to the pattern of regional covariation in the density-independent force (Royama 1992; Ranta *et al*. 1995; Lande *et al*. 1999). Strictly speaking, the Moran theorem only holds for populations governed by linear dynamics (see, for example, Grenfell *et al*. 1998; Bjørnstad *et al*. 1999; Bjørnstad 2000), but it appears to work as a heuristic for systems with simple dynamics (Lande *et al*. 1999). The patterns of regional correlation in climatic factors have, in this way, a potential for providing the functional form for synchrony in population dynamics (Sutcliffe *et al*. 1996; Williams & Liebhold 2000). In the following, we explore whether there exists a 'canonical function' to describe the pattern among populations that are synchronized through individual movement rather than environmental correlation. By 'canonical function' we mean an *a priori* family of functions to use when quantifying synchrony in systems where dispersal is thought important. Our study is directly motivated by a practical problem. The last few years have seen a large number of empirical enquiries into regional synchronization (reviewed in Bjørnstad *et al*. 1999; Koenig 1999). Most of these studies have relied on non-parametric, i.e. curve-free, descriptions of how synchrony changes with distance.

An important reason for this is a lack of theoretical justification for any particular functional form (Bjørnstad *et al*. 1999). Our study is a first step towards filling this gap.

Synchrony and regionalization are usually studied by describing patterns (and temporal changes in patterns) of spatial covariance (Bolker & Pacala 1997, 1999; Bjørnstad *et al*. 1999; Lande *et al*. 1999; Kendall *et al*. 2000). We initially consider a very simple scenario of a regional population that is distributed across a large (continuous) area. The individuals comprising the population are assumed to disperse according to some dispersal distance distribution, $\kappa$. We then consider the more complicated situation that occurs in the presence of local dynamics. We model the system using moment equations to show that there are two canonical functions for dispersal-induced synchrony. If dispersal is rare relative to birth and death, then the local synchrony has approximately the same shape as the dispersal distance distribution. If dispersal is frequent, then the local synchrony is Gaussian ($\propto \exp(-cr^2)$), where $c$ is some constant and $r$ is distance). The tails (i.e. more distant synchrony) follow an exponential function ($\propto \exp(-c'r)$) in one dimension or a Bessel function in two dimensions in all cases. The Bessel function tails off faster than the exponential, but is otherwise closely related. Because we seek a full analytical solution, the treatment is necessarily fairly technical. We have, however, relegated many of the gory technicalities to a sequence of appendices (Appendices A–D).

Recent studies have produced a distinguished literature on the synchronizing effects of dispersal on metapopulations (i.e. where the regional population is divided into discrete, internally homogenous subpopulations) through simulation (Ranta *et al*. 1997, 1998) or mathematical

*Author for correspondence.

analyses (Lande *et al.* 1999; Kendall *et al.* 2000). These studies have generally not provided analytical solutions to the functional form describing how covariance may be expected to drop with distance. Following the recent work of Bolker and co-workers (Bolker & Pacala 1997, 1999; Bolker *et al.* 2000), we use moment equations to supplement the current theory by explicitly modelling (i) spatial covariance in abundance, (ii) how the covariance decays with distance, (iii) how this covariance function will evolve through time, and (iv) the covariance function when populations experience both dispersal and stochastic growth.

## 2. SPATIAL COVARIANCE

Synchrony is usually quantified by considering two populations at different locations $\mathbf{x}$ and $\mathbf{y}$ and how their abundances $\mathcal{N}(\mathbf{x})$ and $\mathcal{N}(\mathbf{y})$ covary. (The location descriptors, $\mathbf{x}$ and $\mathbf{y}$ are written in bold-face type to signify that they may be in a two-dimensional space.) We assume that the organisms live in a homogenous environment, so that the covariance depends on the distance, $r = |\mathbf{x} - \mathbf{y}|$, separating the two populations. Note that this technical definition of homogeneity (Cressie 1991) does not preclude some kinds of exogenous (environmental) heterogeneity, but it does mean that there are no special places in the environment, such as refuges from predation, that we must track separately (see Bjørnstad *et al.* (1999) for a population ecological discussion). The covariance $C(r)$ is defined as

$$C(r) = \langle \mathcal{N}(\mathbf{x})\mathcal{N}(\mathbf{y}) \rangle - \langle \mathcal{N}(\mathbf{x}) \rangle \langle \mathcal{N}(\mathbf{y}) \rangle, \tag{1}$$

where angled brackets denote the expectation over space. The scaled covariance, or spatial correlation, is a common measure of synchrony. In this case, the covariance is scaled by the variance $\sigma^2$, defined by

$$\sigma^2 = C(0) = \langle \mathcal{N}(\mathbf{x})^2 \rangle - \langle \mathcal{N}(\mathbf{x}) \rangle^2. \tag{2}$$

Understanding synchrony involves understanding how the covariance varies with the distance (or spatial lag), how the covariance function evolves in time, and the equilibrium shape of the covariance as a function of lag. We investigate the effect of dispersal on these aspects of spatial dynamics. We first solve a simple continuous-time, continuous-space redistribution model without population dynamics. Next, we introduce stochastic local dynamics, using the results from the simpler model to help interpret the outcome in a system with both population dynamics and redistribution.

## 3. THE REDISTRIBUTION MODEL

To develop a model for how dispersal induces and shapes the spatial covariance in abundance, we consider a randomly distributed initial population that disperses in continuous time. If it moves, an individual is assumed to be redistributed according to a dispersal distance distribution or 'dispersal kernel', $\kappa(r)$. This kernel describes the probability that a moving individual will travel to a location a distance $r$ away. We assume that each individual first decides to move or not, with a density-independent rate $p$ per unit time, and upon moving it redistributes

(instantaneously) according to $\kappa(r)$. We consider the simple case of density-independent emigration and immigration in a homogenous region. The expected emigration per unit time from location $\mathbf{x}$ with $\mathcal{N}(\mathbf{x})$ individuals is thus $p\mathcal{N}(\mathbf{x})$: the expected immigration is $\int_{\mathbf{y} \neq \mathbf{x}} p\mathcal{N}(\mathbf{y})\kappa(r)\mathrm{d}\mathbf{y}$. In a homogeneous landscape the expected number of individuals at each location is identical. Because we have not yet introduced local dynamics, there is no change in the regional population size. If we take a spatial average, therefore, the expected emigration must balance the immigration.

The temporal change in the covariance can be expressed in terms of convolutions of the distance distribution with the covariance functions. In one dimension, the convolution of two distributions $A$ and $B$ is given by

$$(A \times B)(r) = \int_{-\infty}^{\infty} A(x)B(x - r) \, \mathrm{d}x. \tag{3}$$

In two dimensions, the expression is more complicated (equation (A2)), but the meaning is identical and all conclusions carry over. Heuristically, convolving the spatial covariance with the dispersal distribution corresponds to filtering or 'smearing' the spatial covariance; for example, if the dispersal distribution is uniform (up to some maximum distance), the convolution corresponds to taking a moving average of the covariance.

To understand the connection between movement and convolution of the covariance with the dispersal kernel, consider a pair of individuals that are situated a distance $r$ apart. Their mutual presence contributes to the positive covariance at spatial lag $r$. If one individual moves, then the contribution will shift to the post-dispersal distance between them. The expected post-dispersal covariance is thus spread according to the dispersal kernel over all possible new spatial lags. This weighted sum of densities across all new locations is exactly the convolution of the pre-dispersal covariance and the dispersal kernel.

We let all individuals follow our simple rule (density-independent movement at rate $p$, followed by dispersal according to $\kappa$). The equations for how the variance $\sigma^2$ and covariance $C(r)$ evolve through time are then (Appendix B)

$$\frac{\mathrm{d}V}{\mathrm{d}t} = -2pV + (\kappa \times C)(0) \approx -2pV, \tag{4a}$$

$$\frac{\mathrm{d}C(r)}{\mathrm{d}t} = 2p(-C(r) + (\kappa \times C)(r) + \kappa(r)V\Delta x), \tag{4b}$$

where, for notational convenience, $V = \sigma^2 - \langle \mathcal{N} \rangle$ represents the variance minus the mean. The equation for the variance (equation (4a)) leads to (approximately) an exponential decay. Thus, starting from a completely random distributed regional population, the spatial variance will decrease as mixing occurs. Equation (4b) describes how local (and thereby average) spatial covariance first increases and then decreases as the regional population becomes homogenized. The build-up occurs as individuals from initially dense locations spread out across the neighbourhood to form clusters. Later, the local covariance is eroded as redistribution continues.

We can solve the Fourier-transformed equations analytically (Appendix B, §(d)):
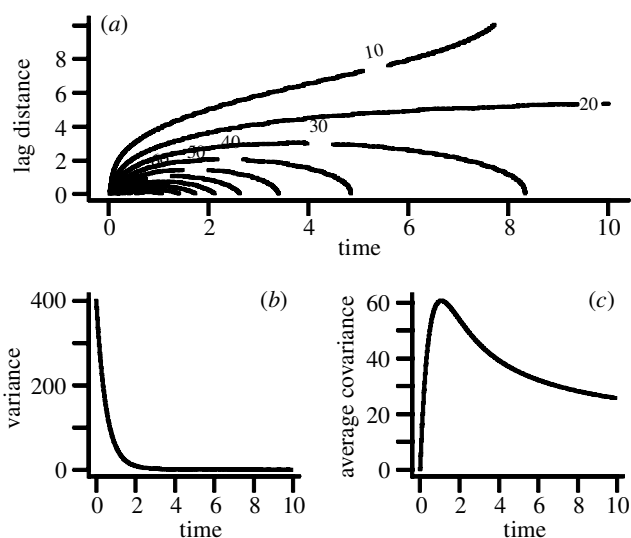
Figure 1. Numerical integration of the variance–covariance equations (4) shows how the the covariance function changes through time. (*a*) Contours of the covariance as a function of spatial lag and time. Contours for small spatial lags and intermediate times ($t = 0.5$–2) show high covariance, while those for large time contours show a smaller and more distributed covariance. (*b*) The decay in spatial variance with time. (*c*) The average covariance first builds up and then declines with time. The build-up is due to individuals from initial high-density locations diffusing out to form high-density clusters that later dissipate with further movement. The figure is based on a one-dimensional arena of total length 10, $\Delta x = 0.05$, $p = 1$, and a standard exponential dispersal kernel $\kappa = \exp(-|x|)/2$.

$$V(t) = V(0)\,\exp(-2pt), \tag{5a}$$

$$\tilde{C}(q, t) = e^{-2pt}(\tilde{\kappa}(q)V(0) + ke^{2p\tilde{\kappa}t}), \tag{5b}$$

where a tilde denotes the Fourier transform, and $q$ is the spatial frequency. Unfortunately, it is not easy to express the analytic solution to the covariance function (5*b*), except in terms of the Fourier transform (or spatial power spectrum). While we cannot find closed-form solutions for the inverse Fourier transform of equations (5), we can integrate the original equations numerically (Appendix D). Figure 1 summarizes the space–time evolution of the variance and covariance for a specific set of parameters, and illustrates the initial build-up and then smearing out of the spatial covariance (figure 1*a*). During this transition, the spatial variance undergoes an approximately exponential decay (figure 1*b*) and the average covariance among all the populations first increases and then dissipates (figure 1*c*).

While we have not managed to find closed forms for the inverse Fourier transform of solutions (5) directly, we can Taylor-expand the power spectrum solution (Appendix B, §(d)). The power spectrum contains a term of the form $\exp(2\tilde{\kappa})$, which we can back-transform after Taylor-expansion to

$$1 + (2pt)\kappa + \frac{1}{2}(2pt)^2(\kappa \times \kappa) + \ldots + \frac{1}{n!}(2pt)^n\kappa^{\times n} + \ldots, \quad (6)$$

where $\kappa^{\times n}$ denotes the $n$-fold convolution of the dispersal kernel with itself. This shows that in the
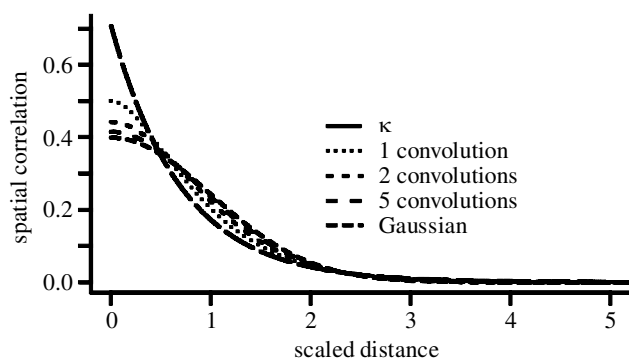


Figure 2. Normalized spatial covariance functions from the continuous-space model after different numbers of dispersal events (convolutions). The dispersal kernel $\kappa$ used in this example is the standard exponential dispersal kernel $\kappa = \exp(-|x|)/2$.

redistribution model, the covariance is a mixture of different *n*-folded convolutions of the original dispersal distribution $\kappa$. The mixture reflects the distributions of individuals that have moved different numbers of times. The first-order term in equation (6) will dominate when $t$ is small. However, as time goes by, the higher-order terms in the expansion (6) gain more and more weight, until eventually all individuals have moved many times, and the covariance is dominated by the the $\kappa^{\times n}$ term.

## 4. CANONICAL FORMS: REDISTRIBUTION

The results for the continuous-time system provide a complete analytical solution for the magnitude and shape of the spatial covariance through time in systems governed by density-independent dispersal. However, because we can only express the inverse Fourier transform of equations (5) as a sum of convolutions, the challenge of understanding the shape of the covariance function partially remains. We can interpret the changing shape of the covariance function by considering the movement within pairs of individuals. As discussed above, when one moves, the covariance becomes convolved once by the dispersal kernel, $\kappa$. When both move, or when one moves twice, the covariance is convolved with $\kappa$ twice. Hence, as time passes, and all individuals are separated by many movement events, the initial covariance becomes convolved with the dispersal kernel many times. Because any function convolved with itself many times becomes approximately Gaussian, the change of weighting of terms in equation (6) is associated with a transition in functional forms (figure 2). The low-order terms dominating the covariance function initially have the same shape as the dispersal distance distribution, while the high-order terms dominating the covariance function for later times are Gaussian.

The pure redistribution model thus predicts that the spatial covariance function will take the form of the dispersal kernel initially (or if the system is frequently disrupted) and the form of the Gaussian covariance function later.

## 5. LOCAL DYNAMICS

When considering population redistribution only (no local dynamics), two canonical functions for synchrony arose. Individuals in real populations, of course, experience reproduction and population growth as well as redistribution. Let us therefore assume that the individuals reproduce and die according to some density-dependent per-capita growth function, $R(\mathcal{N})$. We further assume that the population growth is affected by (spatially and temporally uncorrelated) environmental stochasticity of magnitude $\sigma_R^2$. The model for the local dynamics is then

$$\frac{d\mathcal{N}(\mathbf{x})}{dt} = \underbrace{\mathcal{N}(\mathbf{x})R(\mathcal{N}(\mathbf{x}))}_{\substack{\text{local population}\\ \text{dynamics}}} \underbrace{-p\mathcal{N}(\mathbf{x}) + p\int \kappa(|\mathbf{x}-\mathbf{z}|)\mathcal{N}(\mathbf{z})d\mathbf{z}}_{\text{movement}}$$
$$+ \underbrace{\sigma_R \frac{dB(\mathbf{x})}{dt}}_{\text{noise}},\qquad(7)$$

where $dB(\mathbf{x})/dt$ is (as is customary in stochastic differential models for population growth, e.g. Øksendal (1989) and Lande *et al.* (1999)), the derivative of a random walk.

If we Taylor-expand the per-capita growth function around the spatial average density $\langle\mathcal{N}\rangle$ and discard higher-order terms (Appendix C), we arrive at an equation for the covariance

$$\frac{dC(r)}{dt} = 2((R(\langle\mathcal{N}\rangle) + \langle\mathcal{N}\rangle R'(\langle\mathcal{N}\rangle)C(r) - pC(r))$$
$$+ p(\kappa \times C)(r)) + \sigma_R^2\delta(r),\qquad(8)$$

where $\delta(r)$ is the correlation function of the environmental noise. Because our objective is to understand the effect of dispersal, we assume environmental noise to be spatially uncorrelated: that is, $\delta(r)$ is a delta-function that is non-zero only at the origin. Note, how equation (8) resembles the equation for the spatial covariance given by Lande *et al.* (1999) despite the derivation being different (Appendix C).

At equilibrium, $R(\langle\mathcal{N}\rangle) = 0$ and the strength of population regulation is $-\langle\mathcal{N}\rangle R'(\langle\mathcal{N}\rangle)$. This quantity, which we denote by $\gamma$, measures how efficient density dependence is at suppressing local fluctuations away from the equilibrium (Lande *et al.* 1999). (For example, if local dynamics follow the logistic equation, then $\gamma$ equals the intrinsic growth rate.) We can rewrite equation (8) at equilibrium as

$$\frac{dC(r)}{dt} = 2C(r)(\gamma - p) + p(\kappa \times C(r)) + \sigma_R^2\delta(r).\qquad(9)$$

If we Fourier transform, solve for the equilibrium covariance (in the frequency domain), Taylor-expand and back-transform (see § 3) we obtain

$$C^* = \frac{\sigma_R^2}{2(\gamma + p)}\left(1 + \sum_{i=n}^{\infty}\left(\frac{p}{\gamma + p}\right)^i \kappa^{\times n}\right),\qquad(10)$$

where, as before, $\kappa^{\times n}$ is the $n$-fold convolution of $\kappa$ with itself.

Equation (10) for the covariance in the redistribution-and-growth model is somewhat different from that found

for pure redistribution (equation 3). However, once again, the shape of the spatial covariance is a weighted sum of $n$-hop covariances—the covariances of pairs of individuals that are separated by $n$ dispersal events. As before, few-hop components are shaped like the dispersal kernel, while many-hop components are Gaussian. In the previous models, the balance between these two shapes was governed by the elapsed time since redistribution started. In the case of local population dynamics, it is governed by the relative importance of population redistribution and population regulation, $p/(\gamma + p)$. Strong regulation will tend to 'reset the clock' so that most individuals are effectively separated by fewer dispersal events.

## 6. CANONICAL FORM: LOCAL DYNAMICS

While it is mathematically complete to express the exact shape of the equilibrium covariance as a summation of $n$-hop covariances (equation (10)), we would also like a more heuristic description of this shape in different limits. There are two obvious limiting cases: (i) regulation is strong relative to redistribution, and (ii) redistribution is important (frequent) relative to regulation.

If $p \ll \gamma$ (strong regulation), there will be many birth-and-death events for every movement event. Most pairs of individuals that are near each other will be separated by only a few moves. The shape of the covariance is then very similar to the shape of the dispersal kernel. If, in contrast, $p \gg \gamma$, there will be many movement events for every birth and death. The local synchrony, i.e. the covariance near the origin, is then weighted towards Gaussian shapes. (Note, however, that exponential (in one dimension) and Bessel (in two dimensions) dispersal kernels break with this general pattern; see § 7.) Figure 3 illustrates how either the Gaussian or the dispersal kernel will dominate the local synchrony. For a variety of dispersal kernels, synchrony will approximate a Gaussian function when dispersal dominates but will inherit its shape from $\kappa$ if population growth dominates.

There are thus two canonical functions for synchrony also in the presence of local dynamics. There is an interesting difference, however, in the presence of population growth. For long spatial lags (more than a few times the average dispersal distance) most individuals are separated by many dispersal events. Therefore, as before, the spatial covariance (equation (10)) will be weighted towards many-hop covariances. Each particular $n$-hop component will tend towards the Gaussian shape (as soon as $n$ is not very small), but with different variances. The overall covariance will thus be a mixture of Gaussian distributions with increasing variances. This leads to tails that are exponential (one dimension) or Bessel (two dimensions). The two canonical functions arising from equation (10) both have exponential/Bessel tails but are locally dominated by (i) the dispersal kernel (when local dynamics dominates) and (ii) the Gaussian (when movement dominates).

## 7. DISCUSSION

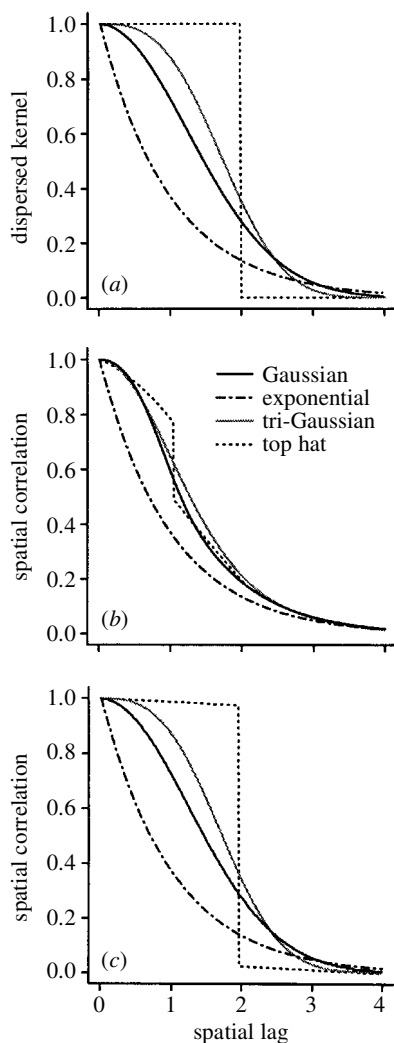We have undertaken a theoretical investigation of how spatial synchrony (and covariation) results from

Figure 3. Synchrony from dispersal and local dynamics.
(*a*) Dispersal distributions: 'top hat' ($\kappa(r) = 1/\rho$, if $r < \rho$,
otherwise zero), 'tri-Gaussian' ($\kappa(r) \propto \exp(cr^3)$), Gaussian
and exponential. All distributions are scaled to $\kappa(0) = 1$,
and unit average dispersal distance. (*b*) Equilibrium spatial
distributions for common movement: $m/(\gamma + m) = 0.8$. Both
the top hat and Gaussian distributions lead to Gaussian
shapes near the origin and exponential tails; the exponential
distribution leads to an exponential everywhere.
(*c*) Equilibrium spatial distributions for rare movement:
$m/(\gamma + m) = 0.05$. All equilibrium distributions have
approximately the same shapes as the dispersal distribution
locally, but with exponential tails. The figure is based on a
one-dimensional arena. In two dimensions the tails will follow
a Bessel function, but all else will be equal.

individual dispersal. We have addressed this by consid-
ering a homogeneous region of initially randomly distrib-
uted individuals that disperse according to some dispersal
kernel. In the absence of local dynamics, dispersal is
shown to reduce the spatial variance. The route to spatial
homogeneity is through locally high correlation that
subsequently smears out spatially and decays temporally.
The covariance function initially resembles the dispersal
kernel, but subsequently converges on the Gaussian covar-
iance function. When we introduce local population
growth, the form of the covariance function depends on
the balance between density-dependent regulation and
frequency of dispersal. With strong regulation, synchrony

will take the form of the dispersal distance distribution
(but with an exponential or Bessel tail). When movement
dominates, synchrony takes the form of a very particular
mixture distribution that is Gaussian near the origin but
with an exponential or Bessel tail. There are thus two
natural, or canonical, functions for dispersal-induced
synchrony.

We need to note that there is an exception to this rule.
In the presence of local dynamics, exponential (one
dimension) or Bessel (two dimensions) distribution
kernels remain exponential or Bessel regardless of the
strength of regulation (figure 3). Note that the Bessel
function tails off slightly faster than the exponential, but
is otherwise closely related. (In fact, this function can be
approximated as $r^{-1/2}e^{-cr}$, where $c$ is some constant; see,
for example, Turchin 1998.)

The dispersal distance distribution features centrally in
our attempts to understand spatial synchrony. Turchin
(1998) reviews how individual movement translates into
various theoretical redistribution kernels. We will not try
to repeat this discussion here. It is, however, useful to
discuss three prototypical models pertaining to dispersal
kernels resulting from simple rules of movement (in the
absence of reproduction).

(i) If individuals perform a random walk (many short
    uncorrelated jumps) for a fixed length of time, the
    kernel $\kappa$ will be Gaussian (both in the one- and two-
    dimensional case). (A motivation for this may be
    found by a direct analogy to the above redistribution
    model (§ 3).)
(ii) If individuals move with a constant velocity
    outward, in a random direction with a constant stop-
    ping probability, the kernel $\kappa$ will follow an
    exponential distribution (in both one and two
    dimensions).
(iii) If individuals undergo a random walk with constant
    stopping probability, the kernel $\kappa$ will follow an
    exponential distribution if the individuals live in a
    one-dimensional habitat, but will follow a Bessel
    distribution in two dimensions (Metz & Van den
    Bosch 1995).

While many other special cases are conceivable and
may be of interest, we use these three to explain why the
exponential (or Bessel) and the Gaussian distributions are
plausible functional forms for the dispersal distance distri-
bution. (Note that Buechner's (1987) geometric model is the
discrete version of the exponential distribution. For
further discussion, see for example, Portnoy & Willson
(1993) and Turchin (1998).)

Our study was specifically framed to highlight plausible
functional forms for the spatial covariance in abundance
that results from dispersal. Obviously, real populations
extend across a heterogeneous environment. This hetero-
geneity may induce covariance in its own right. There are
a suite of other factors that affect spatial covariance and
synchrony. Regionally correlated climatic forcing is one
that has received much attention recently (see § 1).
Related to that, a number of studies ask how nonlinear
population regulation interplays with synchronizing
agents (Grenfell *et al.* 1998; Ranta *et al.* 1998; Bjørnstad
2000). This interaction will certainly be an important
area of future research.

We make the simplifying assumption that environmental noise is spatially uncorrelated: that is, $\delta(r)$ is a delta-function of magnitude $\sigma_R^2$ at the origin, and zero elsewhere. We chose this to understand the effect of dispersal. Having said that, all calculations will directly generalize to spatially correlated noise. We are currently studying how we may use such more general formulations to 'deconvolve' the signals of dispersal and correlated environments in spatio-temporal abundance data.

Tilman & Kareiva (1997) characterized space as the 'last frontier' in ecology. By deriving canonical forms for the spatial covariance function arising from density-independent dispersal, we hope to have helped push the frontier on, one small step.

## APPENDIX A. CONVOLUTIONS

The one-dimensional convolution is defined as in equation (3). It combines two spatial variables or kernels by taking the integral of their product for every value of the spatial lag, $r$. Convolution is equivalent to smoothing one kernel using the second kernel as a moving window. The most general definition of the convolution is

$$(A \times B)(r) = \int_{|\mathbf{y} - \mathbf{x}| = r} A(\mathbf{x}) B(\mathbf{y}) \, d\mathbf{y}. \tag{A1}$$

The two-dimensional convolution is defined in polar coordinates as

$$(A \times B)(r) = \int \int A(r') B(R(r, r', \theta)) r' \, dr' \, d\theta, \tag{A2}$$

where $R(r, r', \theta) = \sqrt{r^2 + r'^2 - 2rr' \cos \theta}$ is the length of the third side of a triangle with sides of length $r$ and $r'$ forming an angle $\theta$. The notation of the two-dimensional convolution looks ugly, but the meaning of convolutions remains the same in any dimension.

## APPENDIX B. REDISTRIBUTION MODEL

### (a) *Definitions*

In this appendix we derive the continuous-time, continuous-space redistribution model for changes in covariance. To do so, we start from a definition of changes in (small) discrete patches of size $\Delta x$ that take place during a (small) discrete time-step $\Delta t$. We then take the limit $\Delta x \to 0$, $\Delta t \to 0$ to derive the desired continuous-time, continuous-space model. (Note that in contrast to the standard derivation of diffusion equations (e.g. Okubo 1980), we do not have to be particularly careful how we take the space and time limits.) Using the process described in the text for movement of individuals between discrete patches in the environment, the probability of

dispersal from a patch located at $\mathbf{y}$ to a patch of size $\Delta x$ located at $\mathbf{x}$ in time interval $\Delta t$ is

$$p\mathcal{N}(\mathbf{y}) \kappa(|\mathbf{y} - \mathbf{x}|) \Delta x \Delta t. \tag{B1}$$

The change in $\langle \mathcal{N}(\mathbf{x}) \rangle$ in $\Delta t$ is

$$(-1) \cdot p\mathcal{N}(\mathbf{x}) + (+1) \cdot \sum_{\mathbf{y}} p\mathcal{N}(\mathbf{y}) \kappa(|\mathbf{y} - \mathbf{x}|) \Delta x, \tag{B2}$$

which has expectation zero for spatial homogeneity ($\langle \mathcal{N}(\mathbf{x}) \rangle = \langle \mathcal{N}(\mathbf{y}) \rangle = \langle \mathcal{N} \rangle$) because $\kappa$, as a probability distribution function, is normalized to unity.

### (b) *Change in covariance*

To find the laws governing the change in the covariance, we calculate the change in $\langle \mathcal{N}(\mathbf{x}) \mathcal{N}(\mathbf{y}) \rangle$ for $\mathbf{x} \neq \mathbf{y}$. In so doing it is important to keep track of jumps from $\mathbf{x}$ to $\mathbf{y}$ separately from jumps between $\mathbf{x}$ and $\mathbf{y}$ to all other locations (denoted by $\mathbf{z}$) in the habitat $\Omega$. The change in $\langle \mathcal{N}(\mathbf{x}) \mathcal{N}(\mathbf{y}) \rangle$ is then

$$\Big\langle - p\mathcal{N}(\mathbf{x})\mathcal{N}(\mathbf{y})(1 - \kappa(|\mathbf{x} - \mathbf{y}|)\Delta x)$$
$$\text{(dispersal from } \mathbf{x}, \textit{not} \text{ to } \mathbf{y})$$
$$- p\mathcal{N}(\mathbf{y})\mathcal{N}(\mathbf{x})(1 - \kappa(|\mathbf{y} - \mathbf{x}|)\Delta x)$$
$$\text{(dispersal from } \mathbf{y}, \textit{not} \text{ to } \mathbf{x})$$
$$+ p \sum_{\mathbf{z} \in \Omega, \mathbf{z} \neq \mathbf{y}} \kappa(|\mathbf{z} - \mathbf{x}|) \mathcal{N}(\mathbf{z})\mathcal{N}(\mathbf{y}) \Delta x$$
$$\text{(dispersal from not-}\mathbf{y} \text{ to } \mathbf{x})$$
$$+ p \sum_{\mathbf{z} \in \Omega, \mathbf{z} \neq \mathbf{x}} \kappa(|\mathbf{z} - \mathbf{y}|) \mathcal{N}(\mathbf{z})\mathcal{N}(\mathbf{x}) \Delta x$$
$$\text{(dispersal from not-}\mathbf{x} \text{ to } \mathbf{y})$$
$$+ p\mathcal{N}(\mathbf{x})(-\mathcal{N}(\mathbf{y}) + \mathcal{N}(\mathbf{x}) - 1)\kappa(|\mathbf{x} - \mathbf{y}|)\Delta x$$
$$\text{(dispersal from } \mathbf{x} \text{ to } \mathbf{y})$$
$$+ p\mathcal{N}(\mathbf{y})(-\mathcal{N}(\mathbf{x}) + \mathcal{N}(\mathbf{y}) - 1)\kappa(|\mathbf{x} - \mathbf{y}|)\Delta x \Big\rangle.$$
$$\text{(dispersal from } \mathbf{y} \text{ to } \mathbf{x})$$
$$\tag{B3}$$

The term $(-\mathcal{N}(\mathbf{x}) + \mathcal{N}(\mathbf{y}) - 1)$ in the last line comes from subtracting the old density product $\mathcal{N}(\mathbf{x})\mathcal{N}(\mathbf{y})$ from the new value $(\mathcal{N}(\mathbf{x}) + 1)(\mathcal{N}(\mathbf{y}) - 1)$, after one individual has moved from $\mathbf{y}$ to $\mathbf{x}$ (an analogous argument applies in the second-to-last line). Assuming homogeneity (interchanging $\mathbf{x}$ and $\mathbf{y}$ as convenient) and simplifying, equation (B3) becomes

$$2p\Big\langle - \mathcal{N}(\mathbf{x})\mathcal{N}(\mathbf{y}) + \sum_{\mathbf{z} \in \Omega} \kappa(|\mathbf{z} - \mathbf{x}|)\mathcal{N}(\mathbf{z})\mathcal{N}(\mathbf{y}) \Delta x$$
$$- \mathcal{N}(\mathbf{x})\kappa(|\mathbf{x} - \mathbf{y}|)\Delta x \Big\rangle. \tag{B4}$$

Note that the sum in the convolution omits the point $\mathbf{z} = \mathbf{y}$. Using the definitions in the main text we then obtain

$$\Delta C(|\mathbf{y} - \mathbf{x}|) = 2p(-C(|\mathbf{y} - \mathbf{x}|) + (\kappa \times C)(|\mathbf{y} - \mathbf{x}|)$$
$$+ \kappa(|\mathbf{y} - \mathbf{x}|)(\sigma^2 - \langle \mathcal{N} \rangle)\Delta x)\Delta t. \tag{B5}$$

Letting $\Delta t$ go to zero, and defining $V = \sigma^2 - \langle \mathcal{N} \rangle$ as the cumulant or 'extra-Poisson variance' we get an infinite

set of ordinary differential equations for $C(r)$, one for each value of $r$:

$$\frac{\mathrm{d}C(r)}{\mathrm{d}t} = 2p(-C(r) + (\kappa \times C)(r) + \kappa(r)V\Delta x). \quad \text{(B6)}$$

If we let $\Delta x \to 0$ then we can drop the last term on the right-hand side and obtain the partial differential equation governing the change in covariance with time in a continuous-time, continuous-space setting,

$$\frac{\partial C(r)}{\partial t} = 2p(-C(r) + (\kappa \times C)(r)). \quad \text{(B7)}$$

In some of our numeric work (Appendix D), we have found that as $C$ becomes very small the $\kappa(r)V\Delta x$ term in equation (B6) can no longer be safely ignored. In these cases we use equation (B6) instead of (B7). See Appendix D for more details.

### (c) *Change in variance*

We derive a separate equation for the variance, $\sigma^2 = C(0)$, by writing

$$\langle p\mathcal{N}(\mathbf{x})(-2\mathcal{N}(\mathbf{x}) + 1) \qquad \text{(one jumps away)}$$

$$+ p \sum_{\mathbf{z} \in \Omega} \kappa(|\mathbf{z} - \mathbf{x}|)\mathcal{N}(\mathbf{z})(2\mathcal{N}(\mathbf{x}) + 1)\Delta x\rangle; \quad \text{(B8)}$$

$$\text{(one jumps in from } \mathbf{z})$$

without loss of generality we have set $\kappa(0) = 0$ (because $p$ governs whether an individual jumps or not). Equation (B8) is easily rewritten as

$$p\langle(-2\mathcal{N}(\mathbf{x})^2 + \mathcal{N}(\mathbf{x})) + \sum_{\mathbf{z} \in \Omega} \kappa(|\mathbf{z} - \mathbf{x}|)(2\mathcal{N}(\mathbf{z})\mathcal{N}(\mathbf{x})$$

$$+ \mathcal{N}(\mathbf{z}))\Delta x\rangle, \quad \text{(B9)}$$

which simplifies to

$$\Delta \sigma^2 = 2p(-\sigma^2 + \langle \mathcal{N} \rangle + \bar{C})\Delta t, \quad \text{(B10)}$$

where $\bar{C} = (\kappa \times C)(0) = \Sigma_{\mathbf{z} \in \Omega}\kappa(|\mathbf{z}|)C(|\mathbf{z}|)\Delta x$.

Dividing both sides by $\Delta t$ and taking a continuous-time limit, we obtain

$$\frac{\mathrm{d}\sigma^2}{\mathrm{d}t} = 2p(-\sigma^2 + \langle \mathcal{N} \rangle + \bar{C}). \quad \text{(B11)}$$

If need be, we may drop the $\bar{C}$ term because it is of order $\Delta x$ relative to the other terms in the equation. Thus we may re-express the variance in terms of $V = \sigma^2 - \langle \mathcal{N} \rangle$ as

$$\frac{\mathrm{d}V}{\mathrm{d}t} \approx -2pV. \quad \text{(B12)}$$

### (d) *Solution*

Equation (B12) is easy to solve ($V(t) = V(0)\exp(-2pt)$). Applying a Fourier transform to equation (B6) turns the convolution into a product (James 1995),

$$\frac{\mathrm{d}\tilde{C}(q)}{\mathrm{d}t} = (\tilde{\kappa} - 1)\tilde{C} + \tilde{\kappa}V(t), \quad \text{(B13)}$$

where a tilde denotes the Fourier-transformed variables. The solution to this linear first-order differential equation is

$$\tilde{C}(q, t) = \tilde{\kappa}(q)V(0)\mathrm{e}^{-2pt} + (\tilde{C}(0, q) - 1)\mathrm{e}^{-2p(1-\tilde{\kappa})t}. \quad \text{(B14)}$$

If the initial condition is a random spatial distribution, then $\tilde{C}(0, q)$ is constant with respect to $q$. Denoting this initial condition as $1 + k$, we rewrite the solution as

$$\tilde{C}(q, t) = \mathrm{e}^{-2pt}(\tilde{\kappa}(q)V(0) + k\mathrm{e}^{2p\tilde{\kappa}t}). \quad \text{(B15)}$$

To obtain an approximation to equation (B15) in original coordinates (i.e. back-transforming from the Fourier solution), we note that the Taylor expansion of $\exp(2p\tilde{\kappa}t)$ is

$$1 + (2pt)\tilde{\kappa} + \frac{1}{2}(2pt)^2\tilde{\kappa}^2 + \ldots + \frac{1}{n!}(2pt)^n\tilde{\kappa}^n + \ldots. \quad \text{(B16)}$$

Because the Taylor expansion is linear, we can back-transform (B16) to equation (6).

## APPENDIX C. LOCAL DYNAMICS

Equation (7) describes the dynamics of local populations governed by density-dependent growth $\mathcal{N}R(\mathcal{N})$ and coupled by dispersal. We measure the environmental correlation in the noise as $\langle \mathrm{d}B(\mathbf{x})\mathrm{d}B(\mathbf{y})\rangle = \delta(\mathbf{x} - \mathbf{y})$. In this study we make the simplifying assumption that environmental noise is spatially uncorrelated (see §7): that is, $\delta(\mathbf{x} - \mathbf{y})$ is a delta-function that is non-zero only at the origin and integrates to unity. If $\mathrm{d}B$ is independent of all other quantities, we can calculate the change in the joint product $\mathrm{d}(\langle \mathcal{N}(\mathbf{x})\mathcal{N}(\mathbf{y})\rangle)/\mathrm{d}t$ (and discarding terms of order $\mathrm{d}t^2$),

$$\frac{\langle \mathrm{d}(\mathcal{N}(\mathbf{x})\mathcal{N}(\mathbf{y}))\rangle}{\mathrm{d}t} = \langle \mathcal{N}(\mathbf{x}) \cdot \mathcal{N}(\mathbf{y})R(\mathcal{N}(\mathbf{y}))\rangle$$

$$+ \langle \mathcal{N}(\mathbf{y}) \cdot \mathcal{N}(\mathbf{x})R(\mathcal{N}(\mathbf{x}))\rangle + \sigma_R^2\delta(\mathbf{x} - \mathbf{y}). \quad \text{(C1)}$$

Given homogeneity, i.e. $\mathcal{N}$ forms an isotropic stationary random field ($\mathbf{x}$ and $\mathbf{y}$ are exchangeable; $\langle \mathcal{N}(x)\rangle = \langle \mathcal{N}(y)\rangle = \langle \mathcal{N}\rangle$) and subtracting $\mathrm{d}\langle \mathcal{N}\rangle^2/\mathrm{d}t$ as in Appendix B, we can write

$$\frac{\mathrm{d}C(|\mathbf{x} - \mathbf{y}|)}{\mathrm{d}t} = 2\langle \mathcal{N}(\mathbf{x}) \cdot \mathcal{N}(\mathbf{y})R(\mathcal{N}(\mathbf{y}))\rangle$$

$$+ 2\langle \mathcal{N}\rangle\frac{\mathrm{d}\langle \mathcal{N}\rangle}{\mathrm{d}t} - \sigma_R^2\delta(\mathbf{x} - \mathbf{y}). \quad \text{(C2)}$$

To simplify $\langle \mathcal{N}(\mathbf{x}) \cdot \mathcal{N}(\mathbf{y})R(\mathcal{N}(\mathbf{y}))\rangle$ we Taylor-expand $R$ around $\langle \mathcal{N}\rangle$ and obtain

$$R(\mathcal{N}(\mathbf{y})) \approx R(\langle \mathcal{N}\rangle) + R'(\langle \mathcal{N}\rangle)(\mathcal{N}(\mathbf{y}) - \langle \mathcal{N}\rangle)$$

$$+ 1/2R''(\langle \mathcal{N}\rangle)(\mathcal{N}(\mathbf{y}) - \langle \mathcal{N}\rangle)^2, \quad \text{(C3)}$$

where $R'$ and $R''$ represent the first and second derivative of $R( )$ with respect to $\langle \mathcal{N}\rangle$, respectively. In addition, we have to expand out and simplify all terms of the form $\langle \mathcal{N}(\mathbf{x})\mathcal{N}(\mathbf{y})\rangle$, $\langle \mathcal{N}(\mathbf{x})\mathcal{N}(\mathbf{y})^2\rangle$, and $\langle \mathcal{N}(\mathbf{x})\mathcal{N}(\mathbf{y})^3\rangle$. The expectation of $\mathcal{N}(\mathbf{x})\mathcal{N}(\mathbf{y})$ is, as before, $C(|\mathbf{x} - \mathbf{y}|) + \langle \mathcal{N}\rangle^2$. The higher-order products are more tedious, but nevertheless straightforward to simplify in terms of higher moments $M$.

$$M_{\mathbf{xyz}} = \langle(\mathcal{N}(\mathbf{x}) - \bar{\mathcal{N}})(\mathcal{N}(\mathbf{y}) - \bar{\mathcal{N}})(\mathcal{N}(\mathbf{z}) - \bar{\mathcal{N}})\rangle. \quad \text{(C4)}$$

We get the full expressions for $\langle \mathcal{N}(\mathbf{x})\mathcal{N}(\mathbf{y})^2\rangle$ and $\langle \mathcal{N}(\mathbf{x})\mathcal{N}(\mathbf{y})^3\rangle$ by writing out the definition for $M_{\mathbf{xy}^2}$ and

$M_{\mathbf{xy}^3}$ and expanding the right-hand sides. We can then write equation (C2) as

$$
\begin{aligned}
\frac{\mathrm{d}C(|\mathbf{x} - \mathbf{y}|)}{\mathrm{d}t} = 2\bigg( & R(\langle N \rangle)C(|\mathbf{x} - \mathbf{y}|) + R'(\langle N \rangle)(M_{\mathbf{xy}^2} \\
& + \langle N \rangle C(|\mathbf{x} - \mathbf{y}|)) + \frac{R''(\langle N \rangle)}{2}(M_{\mathbf{xy}^3} \\
& + \langle N \rangle M_{\mathbf{xy}^2}) - p\,C(|\mathbf{x} - \mathbf{y}|) \\
& + p(\kappa \times C)(|\mathbf{x} - \mathbf{y}|)\bigg) + \sigma_R^2 \delta(\mathbf{x} - \mathbf{y}). \quad (C5)
\end{aligned}
$$

Dropping the higher moment terms—essentially, assuming that the variances and higher-order moments of the density at $\mathbf{x}$ are independent of the density at $\mathbf{y}$—gives us equation (8). Note, that in contrast to the redistribution case, we have to resort to moment closure to obtain a solution to the redistribution-and-growth problem (Bolker & Pacala 1997, 1999; Bolker *et al.* 2000).

Because equation (8) has only linear expressions and convolutions of $C$, Fourier transforming as in Appendix B, §(d) is easy. Note that the delta-function involving exogenous population fluctuations, $\sigma_R^2 \delta(\mathbf{x} - \mathbf{y})$, becomes a constant $\sigma_R^2$ when we transform. Solving for the equilibrium $C$ when $\langle N \rangle$ is at equilibrium (so that $R(\langle N \rangle) = 0$) gives

$$
\begin{aligned}
\tilde{C}^*(q) &= \frac{\sigma_R^2}{2(-\langle N \rangle R'(\langle N \rangle)\langle N \rangle + p) - 2p\tilde{\kappa}(q)} \\
&= \frac{\sigma_R^2}{2(\gamma + p) - 2p\tilde{\kappa}(q)} \\
&= \frac{\sigma_R^2}{2(\gamma + p)}\frac{1}{(1 - (p/\gamma + p))\tilde{\kappa}(q)}, \quad (C6)
\end{aligned}
$$

which, upon expanding according to $(1 - X)^{-1} = 1 + \Sigma_{n=1}^{\infty} X^n$, gives the equilibrium solution in the space domain (10).

## APPENDIX D. NUMERIC INTEGRATION

We numerically integrated the covariance equations using **xtc**, a one-dimensional PDE integrator written by Bard Ermentrout that runs on Unix workstations (available from http://www2.pitt.edu/~phase/). A typical input file for our system is available from the authors.

As mentioned above, we found it useful to retain terms of order $\Delta x$ in the equations when integrating equation (4) numerically. This is because although $C$ is negligible relative to $V$ for small $t$, it decreases more slowly than the exponential decline of $V$; if we run simulations for long enough, $V$ eventually becomes so small that we have to take $C$ into account to obtain an accurate answer.

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