

# Risk spreading, connectivity, and optimal reserve spacing

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**Abstract.** Two important processes determining the dynamics of spatially structured populations are dispersal and the spatial covariance of demographic fluctuations. Spatially explicit approaches to conservation, such as reserve networks, must consider the tension between these two processes and reach a balance between distances near enough to maintain connectivity, but far enough to benefit from risk spreading. Here, we model this trade-off. We show how two measures of metapopulation persistence depend on the shape of the dispersal kernel and the shape of the distance decay in demographic covariance, and we consider the implications of this trade-off for reserve spacing. The relative rates of distance decay in dispersal and demographic covariance determine whether the long-run metapopulation growth rate, and quasi-extinction risk, peak for adjacent patches or intermediately spaced patches; two local maxima in metapopulation persistence are also possible. When dispersal itself fluctuates over time, the trade-off changes. Temporal variation in mean distance that propagules are dispersed (i.e., propagule advection) decreases metapopulation persistence and decreases the likelihood that persistence will peak for adjacent patches. Conversely, variation in diffusion (the extent of random spread around mean dispersal) increases metapopulation persistence overall and causes it to peak at shorter inter-patch distances. Thus, failure to consider temporal variation in dispersal processes increases the risk that reserve spacings will fail to meet the objective of ensuring metapopulation persistence. This study identifies two phenomena that receive relatively little attention in empirical work on reserve spacing, but that can qualitatively change the effectiveness of reserve spacing strategies: (1) the functional form of the distance decay in covariance among patch-specific demographic rates and (2) temporal variation in the shape of the dispersal kernel. The sensitivity of metapopulation recovery and persistence to how covariance of vital rates decreases with distance suggests that estimating the shape of this function is likely to be as important for effective reserve design as estimating connectivity. Similarly, because temporal variation in dispersal dynamics influences the effect of reserve spacing, approaches to reserve design that ignore such variation, and rely instead on long-term average dispersal patterns, are likely to lead to lower metapopulation viability than is actually achievable.

**Key words:** *connectivity; environmental covariance; population synchrony; reserve design; risk spreading; spatial population ecology.*

## INTRODUCTION

Spatial synchrony is an important determinant of the dynamics of spatially structured metapopulations (Royama 1992). In particular, spatial synchrony in the dynamics of subpopulations is particularly significant for their persistence, because the degree of synchrony is directly related to the likelihood of global extinction (Heino et al. 1997, Liebhold et al. 2004). This relationship between population synchrony and extinction means that processes determining the degree of synchrony in population fluctuations are critical for conservation (Kendall et al. 2000). Two important determinants of such synchrony are the degrees to which subpopulations are connected by dispersal (hereafter “connectivity”) and demographic responses to

environmental fluctuations are correlated between subpopulations (hereafter “environmental covariance”; Bjornstad et al. 1999, Liebhold et al. 2004). Connectivity and environmental covariance can counteract each other in space, and despite recognition of the potential trade-offs associated with these two phenomena (Hanski 1989), a general investigation of the effect of qualitatively different descriptions of the two processes on metapopulation dynamics has yet to be made. Such an investigation is critical for anticipating the likely demographic consequences of reserve spacing in networks of protected areas and, in particular, for determining the best balance between reserves being located close enough to each other ensure connectivity and far enough apart to provide some benefits from reduced environmental covariance.

The importance of connectivity to reserve design is well established (Botsford et al. 2001, Briers 2002, Williams et al. 2005). Recent reviews have highlighted

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empirical efforts to determine the efficacy of habitat corridors in terrestrial ecosystems (Gilbert-Norton et al. 2010), and dispersal distances in marine ecosystems (Jones et al. 2009). Metapopulation and reserve design models simplify connectivity, and for “functional connectivity” (*sensu* Tischendorf and Fahrig 2000, hereafter simply “connectivity”), dispersal kernels describe the probability of an individual propagule released from a particular location successfully arriving and settling at another location (Largier 2003). Most reserve design models make use of either Gaussian or Laplacian (back-to-back exponential) dispersal kernels (Botsford et al. 2009). The one study to date on the influence of dispersal kernel shape found no effect on population persistence, at least in the absence of advection (i.e., when the average dispersal distance of a propagule is zero, Lockwood et al. 2002). Here, we move beyond the case of a constant environment to determine whether this insensitivity to kernel shape changes in the presence of coincident distance decay of environmental covariance, or when there is temporal variation in connectivity.

A reasonable first order assumption to make regarding the connectivity of spatially distributed populations is that connectivity decreases with increasing distance (Okubo and Levin 1989, Almany et al. 2009). That is, individuals dispersing from one subpopulation are less likely to successfully settle in increasingly distant subpopulations. In a constant environment, this reduces the metapopulation growth rate when subpopulations are further apart, and reduces the potential for long-term metapopulation persistence. In a fluctuating environment, however, increasing distance between subpopulations may positively affect long-term metapopulation dynamics due to risk spreading. Birth and death rates fluctuate in response to environmental conditions, and are likely to covary to some extent in spatially structured metapopulations (Morris and Doak 2002, Boyce et al. 2006, Almany et al. 2009). For example, many common disturbances are patchy (e.g., oil spills, cyclones, disease/predator outbreaks, fire), and the correlation between the incidence of disturbance events will be higher for subpopulations close together than those far apart (McCarthy and Lindenmayer 1998, Morris and Doak 2002). Such a pattern of spatially correlated demographic responses decreases long-run metapopulation growth rates and metapopulation viability, and it increases the number of patches required for persistence (Harrison and Quinn 1989, Bascompte et al. 2002, Elkin and Possingham 2008, Schreiber 2010).

Reserve spacing must achieve a compromise between distances near enough to maintain connectivity, but far enough to benefit from risk spreading. Existing reserve design theory that has examined the trade-off between connectivity and environmental covariance has demonstrated that the optimal number of reserves, and optimal reserve spacing, depend on the relative rates of decay in the two processes (McCarthy et al. 2005, Wagner et al.

2007, Almany et al. 2009). These studies have used two basic alternative frameworks. One is a stochastic patch-occupancy framework, which models environmental covariance as the likelihood of a single catastrophe being large enough to cause extinction in both reserves (McCarthy et al. 2005, Wagner et al. 2007). Such models are best suited to cases where propagules disperse between patches sufficiently infrequently that their main demographic effect is to recolonize locally extinct subpopulations. The other is a metapopulation growth rate framework, which is more suitable when dispersers are potentially numerous enough to have significant effects on the rates of growth or decline of non-extinct subpopulations (Almany et al. 2009). Thus far, only exponential distance decay has been considered, which implies that dispersal and environmental covariance decay at constant respective rates, regardless of distance. Moreover, despite recognition of the importance of variable connectivity for reserve design, particularly in the marine context (Gaines et al. 2003, Largier 2003, Kaplan 2006), this body of theory has focused, to date, on constant connectivity.

Here, we investigate how the relationship between patch spacing and metapopulation persistence, and thus effective reserve design, depends on the functional forms of connectivity and environmental covariance, particularly where the relative rates of decay in these processes change with distance. We demonstrate that this relationship depends qualitatively on the shape of both the dispersal kernel and of the distance decay function for environmental covariance. We then examine how these patterns are influenced when connectivity itself fluctuates over time. Our discussion of these findings focuses on their implications for reserve design, as well as for the empirical study of populations of conservation concern.

#### MODEL AND METHODS

We use a metapopulation growth rate framework to investigate the trade-off between connectivity and environmental covariance. Specifically, we model a metapopulation in a one-dimensional habitat (e.g., along a coastline) with density-independent dynamics in discrete time, focusing on the special case of two subpopulations of semelparous individuals that grow, reproduce and die at each time step. To examine the effects of different relative rates of distance decay on metapopulation dynamics, we explicitly characterize decay functions for connectivity and environmental covariance that specify how these two processes change with distance, and we simulate metapopulation dynamics for a range of possible distances between the two subpopulations. To characterize distance decay in environmental covariance, we model per capita fecundities in each patch as correlated random variables, with the correlation a decreasing function of increasing distance. Similarly, to characterize distance decay in connectivity, we model dispersal as a decreasing function of increasing distance.

To determine both local retention and successful between-patch dispersal, propagules are released from the center of each patch and connectivity is determined by integrating a dispersal kernel,  $D(x|a, y)$ . This kernel is a function of dispersal distance  $x$  (defined as positive to the right, and negative to the left), advection ( $y$ ), and the diffusion coefficient ( $a$ ), and is integrated over a patch of width  $w$ . Note that advection refers to the mean direction and distance that a collection of propagules are transported (e.g., by winds or currents), and diffusion represents the variability in dispersal distances around that mean, due to idiosyncratic differences in how individual propagules are transported (Largier 2003). With these assumptions (and with patch A to the left of patch B), the dynamics of the subpopulations follow:

$$\begin{aligned} N_{A,t+1} &= f_{A,t} N_{A,t} \int_{x=-w/2}^{w/2} D(x|a, y) dx \\ &\quad + f_{B,t} N_{B,t} \int_{x=-w/2-x_p}^{-3w/2-x_p} D(x|a, y) dx \\ N_{B,t+1} &= f_{B,t} N_{B,t} \int_{x=-w/2}^{w/2} D(x|a, y) dx \\ &\quad + f_{A,t} N_{A,t} \int_{x=w/2+x_p}^{3w/2+x_p} D(x|a, y) dx \end{aligned} \quad (1)$$

where  $N_{i,t}$  is the number of adults in patch  $i$  (designated A or B) at time  $t$ ,  $f_{i,t}$  is the per capita fecundity of adults (which varies randomly over time), and  $x_p$  is the inter-patch distance.

Because we are interested in the effect of inter-patch distance on the trade-off between connectivity and environmental covariance, only dispersal between the two patches is considered: propagules either successfully reach and settle in the other patch, or die. This approximates systems where negligible population growth occurs outside of habitat patches (e.g., isolated patches surrounded by unsuitable habitat [Latore et al. 1998], or heavily harvested marine populations outside marine reserves [Almany et al. 2009]).

#### *Connectivity and the dispersal kernels*

To facilitate comparability with existing reserve design theory, we model connectivity with a dispersal kernel. This approach is particularly appropriate for organisms with a relatively sedentary adult phase and a dispersive phase that is substantially influenced by physical processes (e.g., directional transport by winds and currents), such as plants, arthropods, marine fishes, and invertebrates (Nathan and Muller-Landau 2000, Compton 2002, Strathmann et al. 2002). Dispersal kernels require a minimum of two parameters to represent the strength of advective and diffusive forces, respectively (Largier 2003). This approach also allows us

to separately investigate the effects of temporal variation in advective and diffusive processes.

To investigate the effect of dispersal kernel shape on metapopulation dynamics, we use two qualitatively different kernels to model dispersal: Gaussian and Laplacian. Gaussian dispersal arises from a simple diffusive process with simultaneous settlement at a fixed time after release (Neubert et al. 1995). For instance, many coral reef fish larvae have an obligate pre-settlement competency period in the plankton, followed by a very short period during which settlement occurs (e.g., Cowen et al. 2006). Indeed, fish dispersal models that incorporate such assumptions typically result in approximately Gaussian dispersal kernels (Siegel et al. 2003). Mathematically, Gaussian dispersal follows:

$$D(x) = \frac{1}{\sqrt{2\pi}a} e^{-\frac{(x-y)^2}{2a^2}}. \quad (2)$$

This function describes the probability of a propagule dispersing distance  $x$ ;  $y$  is the advection parameter, equal to the mean dispersal distance, and  $a$  is a scaling parameter that controls diffusion (and is equal to the standard deviation of the dispersal distance).

Alternatively, if propagules settle at a constant rate as soon as they are released (i.e., without an obligate pre-settlement period, such as seeds, spores, and many brooded marine larvae), dispersal should follow a Laplacian distribution (Neubert et al. 1995). For example, wind-dispersed plant seeds have been shown to exhibit dispersal kernels that are approximately Laplacian (e.g., Willson 1993). Laplacian dispersal follows:

$$D(x) = \frac{1}{2a} e^{-\frac{|x-y|}{a}} \quad (3)$$

where  $y$  is the mean advection distance;  $a$  is the diffusion coefficient, and is related to the standard deviation of the Laplacian kernel by  $a = \sigma_d/\sqrt{2}$ .

To examine how temporal variation in connectivity affects our results, we allow advection and diffusion to vary from year to year. To facilitate comparison with existing results, we follow existing reserve theory and use the Gaussian distribution to model temporal variation in advection (Kaplan 2006). However, because diffusion is constrained to be positive, temporal variation in diffusion was drawn from a lognormal distribution. We considered variation in these two components individually to determine their particular influences on the trade-off with environmental covariance in terms of optimal spacing and metapopulation growth.

#### *Environmental covariance functions*

Environmental covariance was modeled by drawing patch-level fecundities from a multivariate lognormal distribution, where the covariance of the fecundities declines with increasing distance between the patches. Two functions describing the distance decay in covariance of patch fecundities, amounting to different

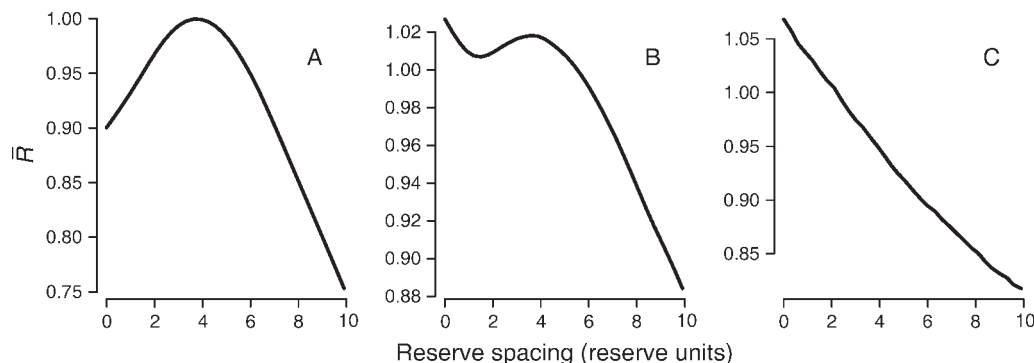


FIG. 1. Estimated long-term growth rate,  $\bar{R}$ , of a two-patch reserve system (metapopulation) as a function of reserve spacing. In all panels,  $E(\ln[f_A]) = E(\ln[f_B]) = 1.9$ ,  $\sigma_A^2 = \sigma_B^2 = 2.2$ , advection distance  $y = 0$ , and diffusion parameter  $a = 6$  ( $E(\ln[f_A])$  and  $E(\ln[f_B])$  represent the mean of log-fecundity in patches A and B respectively;  $\sigma_A^2$  and  $\sigma_B^2$  represent the variance of log-fecundity in patches A and B, respectively). (A) Gaussian dispersal and Gaussian covariance (range parameter  $\phi = 5$ ); (B) Laplacian dispersal and Gaussian covariance ( $\phi = 5$ ); (C) Laplacian dispersal and exponential covariance ( $\phi = 5\sqrt{3}$ ). Note that the case of Gaussian dispersal and exponential covariance is not illustrated in this figure, because it did not yield any additional qualitatively different outcomes beyond the three shown here.

qualitative descriptions of risk spreading, were used. Specifically, distance decay in the correlation of log-fecundity between patches was either exponential,

$$\rho_{A,B} = e^{\frac{(-x)}{\phi}} \quad (4)$$

or Gaussian,

$$\rho_{A,B} = e^{-\left(\frac{x}{\phi}\right)^2} \quad (5)$$

where  $x$  is the distance between the center of each subpopulation and  $\phi$  is the range parameter, which determines the rate at which correlation decays with increasing distance. The covariance in patch per capita fecundity was determined by

$$\text{COV}[\ln(f_{A,t}), \ln(f_{B,t})] = \rho_{A,B} \sigma_A \sigma_B \quad (6)$$

where  $\sigma_A$  and  $\sigma_B$  indicate the standard deviation of fluctuations in log-fecundity over time within patches.

#### Metapopulation dynamics

Metapopulation dynamics were modeled by averaging the results of 1000 repeated simulations for each inter-patch distance. For each simulation, subpopulations were initialized with 500 individuals and followed for 1000 years. To eliminate transient dynamics (which are sensitive to initial conditions), the first 100 simulated years were discarded, and a linear model was fitted to the remaining population sizes with time as the independent variable and the natural logarithm of the metapopulation abundance time series as the dependent variable. The slope of this line estimates the logarithm of the expected long-term metapopulation growth rate (Yoshimura and Jansen 1996). The mean of this quantity was calculated across all 1000 simulations for a given set of parameter values and patch spacing, and then back transformed to yield an estimate of the long-term metapopulation growth rate,  $\bar{R}$ . Given the large

number of simulations, this procedure yielded results indistinguishable from those obtained by estimating  $\bar{R}$  with autoregressive methods. Because this quantity is an estimate of the rate of recovery from decreases to low density, we used it as our principal measure of metapopulation persistence. However, because persistence also depends upon the temporal variance in the metapopulation growth rate, we also calculated quasi-extinction risk, which depends on this quantity (see Appendix A for details), to assess the robustness of our conclusions to the choice of a specific measure of metapopulation persistence.

For the figures in this paper, we chose baseline parameters based on two considerations. Firstly, we chose parameter values that produced  $\bar{R}$  values near unity, because it is metapopulations on the threshold of population growth or decline for which decisions about reserve spacing are likely to be most important. Secondly, we wanted to ensure that our baseline results illustrated all of the qualitatively different outcomes possible. Thus, for instance, we chose parameters for the dispersal and environmental covariance functions for which the decreases in successful dispersal and covariance in environmental fluctuations occurred over similar spatial scales. However, we also conducted extensive sensitivity analyses for each parameter, to understand how the values of particular parameters influenced the trade-off between dispersal and environmental covariance (Appendix B). All simulations were conducted using R (R Development Core Team 2008).

#### RESULTS

*Effect of different qualitative descriptions of dispersal and correlated environments.*—Simulations revealed three qualitatively different outcomes (Fig. 1). For a two-patch metapopulation, the long-run growth rate ( $\bar{R}$ ) may (1) be maximized at some intermediate inter-patch spacing (Fig. 1A); (2) show two local maxima, one for

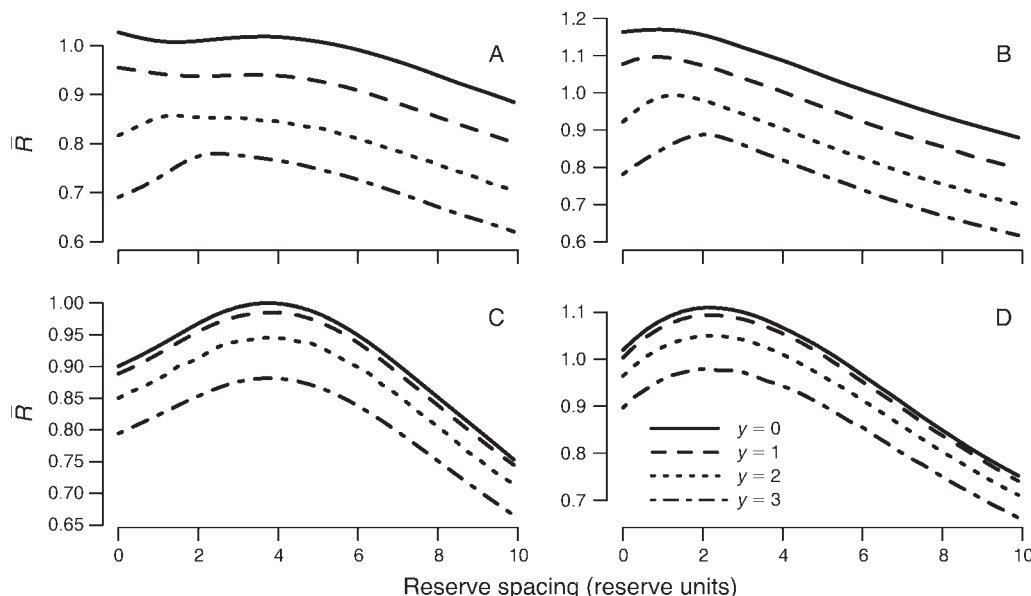


FIG. 2. Effect of changes to the advection distance ( $y$ ) on the trade-off between connectivity and environmental covariance shown for (A) Laplacian dispersal and Gaussian covariance, (B) Laplacian dispersal and exponential covariance, (C) Gaussian dispersal and covariance, (D) Gaussian dispersal and exponential covariance. All other parameter values are as in Fig. 1.

adjacent patches (reserve spacing = 0), and one for patches with some intermediate spacing (Fig. 1B); or (3) be maximized for adjacent patches (Fig. 1C).

A single peak at intermediate spacing occurs when the cost of decreasing connectivity is less than the benefits of reduced environmental covariance as distance between patches increases away from zero (Fig. 1A). Two local maxima in  $\bar{R}$  are possible where the relative rates of distance decay in the two processes change with distance. For example, as spacing increases away from zero under Laplacian dispersal and Gaussian covariance, the initial cost of reduced connectivity is greater than the benefits gained by the decrease in covariance, and metapopulation growth declines (Fig. 1B). For further increases in spacing, the benefits of reduced environmental covariance exceed the cost of lost connectivity, and a second peak in metapopulation growth is found at some intermediate spacing (Fig. 1B). Beyond the peak in metapopulation growth at intermediate spacing, connectivity is not sufficient to maintain metapopulation growth (despite there being very little environmental covariance), and  $\bar{R}$  decays with further increases in distance. Finally, if the cost of lost connectivity always exceeds the benefits of reduced environmental covariance, metapopulation growth rate peaks for adjacent patches, and declines monotonically with distance (Fig. 1C).

*Effect of advection and diffusion.*—Advection shifts the mode of the dispersal kernel away from zero. This reduces local retention, and results in an increase in connectivity from the upstream to the downstream patch, and a decrease in the opposite direction. As advection increases,  $\bar{R}$  decreases in magnitude overall. It

also peaks at greater distances for Laplacian dispersal, at a patch spacing approximately equal to the advection distance (Fig. 2A, B). Gaussian dispersal shows the same pattern of decreasing  $\bar{R}$  for increasing advection (Fig. 2C, D); however, the magnitude of the decrease is smaller due to a comparatively smaller reduction in local retention as advection increases. Additionally, the increase in downstream connectivity is not as great for Gaussian dispersal, and the distance at which metapopulation growth is maximized (hereafter “optimal spacing”) remains relatively unchanged (Fig. 2C, D).

Reducing diffusion makes the dispersal kernel more peaked - connectivity decays more steeply with increasing distance. This increases local retention, resulting in greater metapopulation growth rates, and increasing the likelihood of adjacent patches yielding the highest metapopulation growth (Fig. 3). Conversely, increasing diffusion reduces the benefits to adjacent patches, and dispersal success decays less quickly with increasing distance; thus, optimal spacing is more likely to occur at intermediate distances, and this distance is greater for larger values of the diffusion parameter (Fig. 3). Increasing diffusion also results in smaller maximum values of  $\bar{R}$ , and decreases the rate of decay in  $\bar{R}$  for widely spaced patches (Fig. 3).

*Effects of fecundity and covariance decay parameters.*—The qualitative relationship between patch spacing and metapopulation growth rate is sensitive to changes in parameter values that influence the relative rates of decay in connectivity and environmental covariance. For example, variation in per capita fecundity changes the magnitude of environmental covariance. Increasing the temporal variability of



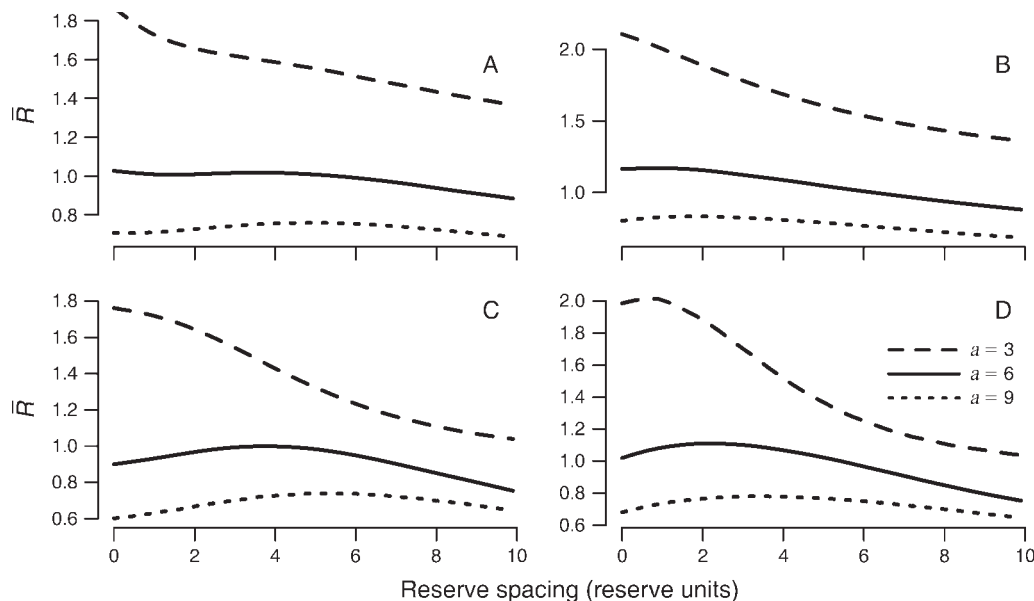


FIG. 3. Effect of increasing diffusion parameter ( $a$ ) on the trade-off between connectivity and environmental covariance shown for: (A) Laplacian dispersal and Gaussian covariance, (B) Laplacian dispersal and exponential covariance, (C) Gaussian dispersal and covariance, and (D) Gaussian dispersal and exponential covariance. All other parameter values are as in Fig. 1.

fecundity ( $\sigma$ ) increases its between-patch covariance (Eq. 6), and this increase in covariance is greatest for adjacent patches. For a given value of the covariance decay (range) parameter, the decrease in covariance of fecundity with a small increase in patch spacing is comparatively greater for larger values of  $\sigma$ . This enhances the benefits to risk spreading and the likelihood that metapopulation growth rate will be maximized at some intermediate distance (see Appendix B).

Changing the range parameter of the environmental covariance function changes the rate at which covariance decays. Increasing the range parameter ( $\phi$ ) decreases the rate at which environmental covariance decays with distance, and benefits to risk spreading increase more slowly with distance when  $\phi$  is bigger. Consequently, the reduced connectivity associated with increases in patch spacing increasingly outweigh any increased benefits due to risk spreading, and thus metapopulation growth rate is always maximized for adjacent patches beyond a threshold value of  $\phi$  (see Appendix B).

*Effect of temporal variation in connectivity on the trade-off with risk spreading.*—Year-to-year variation in connectivity qualitatively changes the trade-off between connectivity and environmental covariance, making intermediately spaced patches optimal in cases where, under constant connectivity, metapopulation growth rate peaked for adjacent patches (Fig. 4). Variation in diffusion tends to increase  $\bar{R}$  overall, but optimal spacing remains relatively unchanged. Variation in advection decreases  $\bar{R}$  overall, and optimal patch spacing either increases, or remains relatively unchanged.

Temporal variation in diffusion alone (Fig. 4A–C) shows qualitatively similar results to simulations with reduced constant diffusion (Fig. 3): benefits to adjacent patches increase,  $\bar{R}$  increases, and optimal spacing is slightly reduced for Gaussian dispersal and Gaussian covariance (Fig. 4A). This suggests that years with low diffusion outweigh years with high diffusion.

Temporal variation in advection (Fig. 4D–F) reduces the benefits to adjacent patches, and, overall, decreases metapopulation growth rates. Similar to the results of increased constant advection, optimal spacing increases for Laplacian dispersal, but remains relatively unchanged for Gaussian dispersal. Temporal variation in advection between two patches means that in any given year, connectivity is enhanced in one direction and impaired in the other. This variation in connectivity helps explain the decrease in  $\bar{R}$ : fluctuations in the contribution from the other patch will cause greater year-to-year variation in the patch growth rates, and thus a concomitant decrease in  $\bar{R}$ .

*Robustness of results.*—Changing the mean of log-fecundity does not qualitatively change the trade-off between connectivity and environmental covariance: the magnitude of  $\bar{R}$  increases for increasing fecundity, but optimal spacing remains relatively unchanged (see Appendix B).

Quasi-extinction probabilities showed similar results to those for  $\bar{R}$  (Appendix A). The three different qualitative outcomes for optimal spacing (Fig. A1) were reproduced, and the optimal patch spacing tended to be very similar for these two metrics in most cases. However, with temporal variation in connectivity, the benefits of risk spreading to quasi-extinction risk are

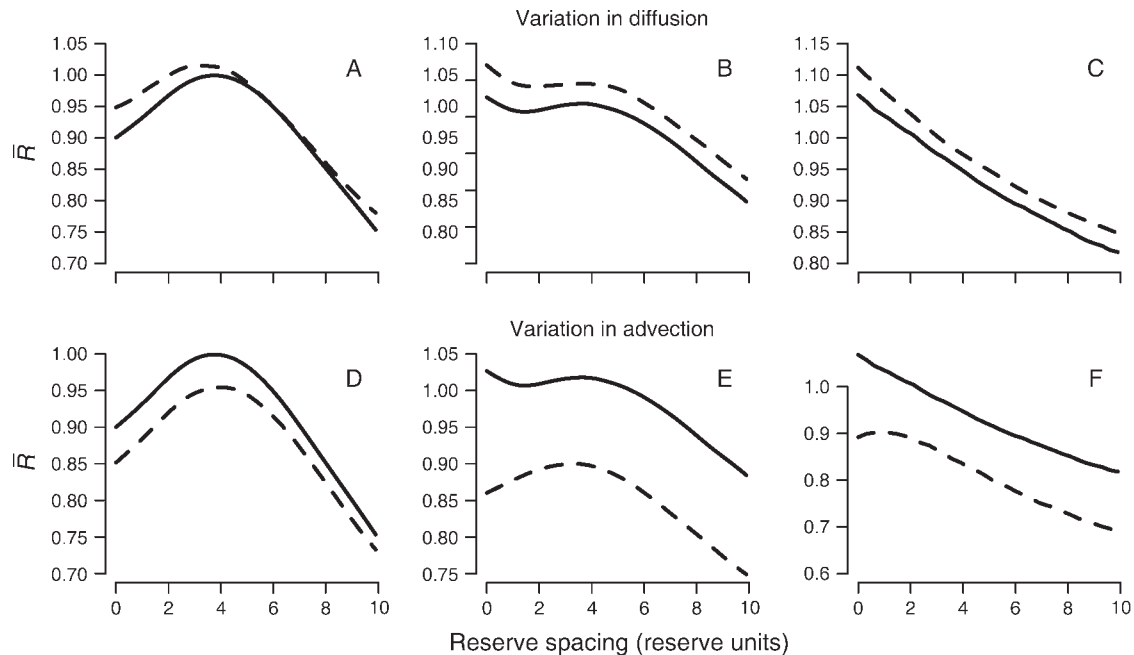


FIG. 4. Effect of temporal variation in connectivity on the estimated long-term growth rate of a two-patch reserve system (metapopulation) as function of reserve spacing. Panels A and D show Gaussian dispersal and Gaussian covariance; panels B and E show Laplacian dispersal and Gaussian covariance; and panels C and F show Laplacian dispersal and exponential covariance. Solid lines in all panels show the baseline results with constant connectivity (parameter values as per Fig. 1). Dashed lines in panels A–C show results of temporal variation in diffusion (diffusion is lognormally distributed with  $\mu_d = 6$ ,  $\sigma_d^2 = 4$ ); in panels D–F, dashed lines show variation in advection (advection is normally distributed with  $\mu_a = 0$ ,  $\sigma_a^2 = 4$ ). Note that  $\mu$  designates mean diffusion and advection ( $\mu_d$  and  $\mu_a$ , respectively) and  $\sigma^2$  designates the variance of diffusion and advection ( $\sigma_d^2$  and  $\sigma_a^2$ , respectively).

more pronounced to those for  $\bar{R}$  (Fig. A2–3). Accordingly, the peak at intermediate spacing is more pronounced than that observed for  $\bar{R}$ . This occurs because the variance in metapopulation growth rate, which increases quasi-extinction risk, tends to decrease as patch spacing increases away from zero as a consequence of the benefits of risk spreading. When  $\bar{R} > 1$ , this effect is more pronounced over shorter time frames, as the temporal variance is a particularly important determinant of quasi-extinction risk initially, before the metapopulation can realize its expected long-term growth away from the quasi-extinction boundary. Over longer time scales, the probability of quasi-extinction is increasingly dominated by the mean metapopulation growth rate, and the quasi-extinction risk of a two-patch metapopulation becomes qualitatively similar to our estimate of the long-term metapopulation growth rate  $\bar{R}$  (Fig. A1).

#### DISCUSSION

As reserves get farther apart, connectivity between them tends to be reduced, whereas environmentally-mediated fluctuations in within-patch vital rates, such as fecundity, tend to become less correlated between reserves. Our results highlight the importance of the countervailing effects of these two changes for metapopulation growth rates and metapopulation viability.

Optimal reserve spacing is determined by the relative rates of decay in connectivity and covariance in vital rates as reserve spacing increases. When connectivity itself does not fluctuate over time, optimal spacing may occur for adjacent reserves, or at some intermediate spacing, and where the relative rates of decay in connectivity and covariance change qualitatively with distance (in this study, where dispersal is Laplacian and environmental covariance is Gaussian), two local maxima in metapopulation growth rate (and corresponding local minima in quasi-extinction risk) are possible. In the present analysis, one of these maxima always occurs for adjacent patches. Temporal variation in connectivity qualitatively changes the trade-off. When this is driven by temporal variation in advection, benefits to adjacent reserves are reduced, optimal spacing is more likely to be intermediate, and metapopulation growth rates decrease. These results highlight the importance of understanding the relative shapes of the distance decay in connectivity and environmental covariance, as well as the importance of temporal variation in connectivity, for reserve design.

As far as we are aware, this is the first study to consider a trade-off between connectivity and environmental covariance in which the relative rates of decay can change with distance. Our demonstration of the sensitivity of optimal spacing to these changes supports

the hypothesis that these relative rates of distance decay are critical for reserve design (McCarthy et al. 2005, Almany et al. 2009). Optimal spacing is particularly sensitive to the relative rates of decay as spacing increases away from zero. This suggests that determining the scale over which demographic rates covary is as important as estimating connectivity for understanding metapopulation viability, and for reserve design. Indeed, these changes in relative rates of decay can give rise to two local maxima in the long-term metapopulation growth rate (and minima in quasi-extinction risk). In our baseline analyses, one peak always occurred for adjacent patches, but with non-zero advection, both local maxima can occur at intermediate distances, depending on the shape of the environmental covariance function (see Appendix C).

Existing reserve theory that has examined how the shape of the dispersal kernel influences critical patch size and metapopulation persistence has found qualitatively similar effects regardless of kernel shape (Lockwood et al. 2002). In contrast, we find that the shape of the kernel can alter optimal reserve spacing. Although our model differs from that of Lockwood et al. (2002) in several respects, the most likely explanation for our different findings is that we have included correlated responses to environmental fluctuations. By introducing a trade-off between the two processes undergoing distance decay, sensitivity of optimal spacing to the dispersal kernel's shape emerges, indicating that the entire distribution of dispersal distances is critical for metapopulation dynamics (Kot et al. 1996, Clark 1998, Levin et al. 2003).

Temporal variation in connectivity has been studied mainly in the marine context (Gaines et al. 2003, Largier 2003, Kaplan 2006). Our results indicate that for constant, non-zero advection, the shape of the dispersal kernel influences optimal spacing. For Laplacian dispersal, optimal spacing is approximately equal to advection distance; while optimal spacing remains relatively unchanged for Gaussian dispersal with non-zero advection. This extends earlier work (Kaplan 2006), which obtained similar findings for Laplacian dispersal in the special case of a homogenous environment (i.e., no spatial covariation of demographic rates). Extending our model to consider temporal variation in advection resulted in reduced long-term metapopulation growth rates overall, but it also reduced the benefits of adjacent patches disproportionately, such that optimal reserve spacing increased. Non-zero advection introduces asymmetric dispersal into the trade-off between connectivity and environmental covariance, and in this sense, our finding of reduced metapopulation growth rates overall with temporal variation in advection generalizes previous findings. Specifically, in a colonization-extinction model, without distance decay in environmental covariance, asymmetric dispersal decreases metapopulation viability (Vuilleumier and Possingham 2006). Similarly, in our model, the dispersal asymmetry

that accompanies temporal variation in advection increases quasi-extinction risk (and decreases metapopulation growth), suggesting that this earlier finding holds beyond the case of a homogenous environment. Our finding that temporal variation in advection reduces the benefits of adjacent reserves, relative to reserves that are farther apart, suggests that where reserve design fails to consider temporal variation in advection, reserves may be too close together.

Variation in diffusion increases metapopulation growth rates and leaves optimal spacing relatively unchanged. The increased metapopulation growth rates are a result of increased local retention; remaining in the natal patch ensures a contribution to the next generation, reduces variation in the patch growth rate, and thus increases the geometric mean growth rate of the metapopulation. This supports the hypothesis that where temporal or spatial environmental variation results in positively correlated demographic responses, a low dispersal strategy (high local retention) is favored, due to the greater average yield of non-dispersing offspring (Cohen and Levin 1991).

There is a growing body of research highlighting the ubiquity of asymmetric and fluctuating dispersal patterns in nature (e.g., Vuilleumier and Possingham 2006, Berkley et al. 2010, Salomon et al. 2010). Our findings indicate that these complexities are likely to have important implications for reserve networks that aim to enhance metapopulation persistence. Key traits of dispersive propagules such as shape, buoyancy, and behavior (Sponaugle et al. 2002, Vuilleumier and Possingham 2006, Clobert et al. 2009) will influence a species' susceptibility to dispersal vectors (winds and currents), and thus species are likely to differ in the extent to which fluctuations in the strength and direction of these vectors influences metapopulation persistence. For instance, in the marine environment, species with long pelagic larval periods and weak swimming ability are likely to be particularly susceptible to physical transport mechanisms, such as currents and eddies. For such species, averaging out temporal variation in the advection of propagules when determining optimal reserve spacing would be more likely to result in reserve spacings too close to maximize species persistence.

Both dispersal and environmental covariance influence population synchrony (Bjornstad et al. 1999, Liebhold et al. 2004). Extensive empirical efforts to estimate connectivity in both terrestrial and marine ecosystems (e.g., Jones et al. 2009, Gilbert-Norton et al. 2010) were prompted in part by reserve design theory that identified the importance of connectivity for the success of reserve networks. Our findings highlight the importance of understanding the spatial covariance of vital rates as well, particularly when it decays over spatial scales similar to the decay of dispersal. Although the spatial synchrony of metapopulations is determined in part by the distance decay of covariation in demographic rates, teasing apart the relative importance



of dispersal, environmental forcing (often termed the “Moran” effect), and local processes (e.g., density dependence, predation) from time series of metapopulation dynamics alone may generally be intractable (Benton et al. 2001, Abbott 2007). Consequently, direct estimation of the spatial covariance of vital rates is likely to be necessary, and could be incorporated, for example, as a component of reserve monitoring programs. For individual species of conservation concern (e.g., the Northern Spotted Owl; Glenn et al. 2011), and more generally, where long-term, large-scale monitoring efforts make use of mark–recapture techniques (e.g., Monitoring Avian Productivity and Survival [MAPS]; DeSante and Kaschube 2009), data on spatial variation in vital rates exists. Spatial variation in the mean and variance of survival probabilities have been estimated with such data (e.g., Saracco et al. 2010), and could be extended to estimate between-location covariances in vital rates. Calibration of such spatial covariances would allow for modeling studies tailored to particular species of conservation concern, focused on quantitative estimation of the consequences of different reserve configurations for metapopulation growth rates and quasi-extinction risk. Additionally, methods developed to account for uncertainty in reserve design (e.g., Halpern et al. 2006) could benefit from extensions that account for our present ignorance regarding this determinant of metapopulation growth rates. In particular, incorporating information about uncertainty in the spatial covariance in vital rates, and temporal variability in the shapes of dispersal kernels, would help to make reserve design more robust to these key determinants of metapopulation dynamics.

Our model of the trade-off between connectivity and environmental covariance is for a single species, and is most directly applicable to problems involving a species of high conservation or fisheries value. In contrast, reserve systems are often designed for the management of many species simultaneously. Nevertheless, some conservation plans have utilized guidelines derived from single species reserve design models (e.g., Botsford et al. 2001, White et al. 2010). One way to enhance the applicability of such models to multispecies conservation would be to calibrate and consider the dispersal kernels and environmental covariance functions for a range of species with representative life histories in such a framework. Such an approach would be most appropriate where species interactions are likely to be weak or highly diffuse. Alternatively, there have been some extensions of reserve design theory to consider interacting species explicitly (reviewed in Baskett et al. 2007). Extending such theory to incorporate the effects of interspecific differences in patterns of spatially correlated demographic rates is another important direction for future work.

Our results illustrate the importance of the trade-off between connectivity and environmental covariance for metapopulation dynamics, including designing reserves

or estimating the effects of an existing reserve design on particular species. Where the two processes decay over a similar scale, the relative rates of decay (i.e., the shape of the kernels) become important and both must be considered. The possibility of two local maxima in population growth rates, and two minima in quasi-extinction risk, highlights the potential for this trade-off to change sign at different distances; a finding that is likely to be particularly important for reserve spacing in systems with more than two reserves. Further, qualitative changes to the trade-off between connectivity and risk spreading, obtained when connectivity varies temporally, suggests that reserve design that ignores variation in the physical transport mechanisms operating in a given system may fail to meet conservation objectives by placing reserves either too close together or too far apart.

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## SUPPLEMENTAL MATERIAL

**Appendix A**

Methods and results of quasi-extinction analysis (*Ecological Archives* A022-019-A1).

**Appendix B**

Results of sensitivity analysis (*Ecological Archives* A022-019-A2).

**Appendix C**

The importance of the relative rates of decay for determining optimal spacing (*Ecological Archives* A022-019-A3).