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# Interactive effects of temporal correlations, spatial heterogeneity and dispersal on population persistence

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It is an ecological truism that population persistence depends on a population's growth rate when rare. To understand the interplay between temporal correlations, spatial heterogeneity and dispersal on persistence, an analytic approximation for this growth rate is derived for partially mixing populations. Partial mixing has two effects on population growth. In the absence of temporal correlations in relative fitness, greater movement to patches with, on average, higher relative fitness increases population growth rates. In the absence of spatial heterogeneity in the average relative fitnesses, lower dispersal rates enhance population growth when temporal autocorrelations of relative fitness within a patch exceed temporal cross-correlations in relative fitness between patches. This approximation implies that metapopulations whose expected fitness in every patch is less than 1 can persist if there are positive temporal autocorrelations in relative fitness, sufficiently weak spatial correlations and the population disperses at intermediate rates. It also implies that movement into lower quality habitats increases the population growth rate whenever the net temporal variation in *per capita* growth rates is sufficiently larger than the difference in the means of these *per capita* growth rates. Moreover, temporal autocorrelations, whether they be negative or positive, can enhance population growth for optimal dispersal strategies.

**Keywords:** metapopulation persistence; spatial heterogeneity; temporal correlations; source-sink dynamics

## 1. INTRODUCTION

Populations, whether they be viral particles, biochemicals, plants or animals, experience temporal and spatial variation in environmental factors such as temperature, precipitation, resource availability and predation risk. Since these environmental factors influence survivorship and reproduction, individuals can modulate their fitness (i.e. the mean number of offspring produced during their lifetime) by dispersing across space. Hence, interactions between movement and spatio-temporal heterogeneities determine how quickly a population grows or declines. Understanding the precise nature of these interactive effects is a central issue in population biology and has received increasing attention from theoretical, empirical and applied perspectives (Petchey *et al.* 1997; Lundberg *et al.* 2000; Gonzalez & Holt 2002; Schmidt 2004; Roy *et al.* 2005; Boyce *et al.* 2006; Matthews & Gonzalez 2007).

Temporal fluctuations in environmental conditions can lead to fluctuations in population growth rates. For a given mean population growth rate, one expects that extinction risk increases with temporal variation in the growth rates. This expectation is supported by numerous models (Lewontin & Cohen 1969; Turelli 1978; Lande 1993; Halley & Iwasa 1999), experimental studies with

brine shrimp and water fleas (Belovsky *et al.* 1999; Drake & Lodge 2004) and a statistical analysis of over 500 time series from the global population dynamics database (GPDD; Inchausti & Halley 2003). If environmental conditions in successive years are positively correlated (i.e. positively autocorrelated), populations experience longer bouts of similar conditions resulting in environmental variation amplifying over time (Lawton 1988). Intuitively, one expects that these positive autocorrelations increase extinction risk as populations are less likely to survive through long runs of poor environmental conditions than short runs of poor conditions, a prediction supported by experimental studies with the collembolan *Folsomia candida* (Pike *et al.* 2004) and the time-series analysis of the GPDD (Inchausti & Halley 2003). Theoretical studies, however, have shown that positive autocorrelations can decrease or increase extinction risk depending on additional structural features of the environmental noise (Schwager *et al.* 2006), the time frame over which extinction risk is evaluated (Heino *et al.* 2000), and density-dependent feedbacks within the population (Ripa & Lundberg 1996; Petchey *et al.* 1997; Laakso *et al.* 2004; Schwager *et al.* 2006).

Unlike temporal heterogeneity, which in itself, negatively impacts persistence of a closed population, spatial variation in individual fitness enhances population growth for dispersal limited populations (Holt 1985; Dushoff & Levin 1995; Melbourne *et al.* 2007). Intuitively, spatial variation implies individuals experience

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higher fitnesses in some patches, and dispersal limitation ensures that individuals remain sufficiently long in these patches to achieve faster population growth. Dispersal can dilute this inflationary effect as individuals from more productive habitats typically disperse to lower quality patches (Hastings 1983; Adler 1992; Kirkland *et al.* 2006; Schreiber & Lloyd-Smith 2009). For example, the invasion of the woody weed, *Mimosa pigra*, in tropical Australia exhibited fast growth in favourable wetland patches, but exhibited slower growth regionally owing to the separation of wetlands by unfavorable eucalyptus savannas (Lonsdale 1993). Positive correlations between habitat quality and movement can marginalize the dilutionary effect of dispersal (Chesson 1982; Schreiber & Lloyd-Smith 2009). Alternatively, patterns of reproduction and movement that eventually lead to individuals or their descendants returning to their patch of origination also marginalizes the negative impact of dispersal on persistence (Hastings & Botsford 2006).

When there is spatial and temporal variation in environmental factors, dispersal can inflate population growth rates at a regional scale and, thereby, enhance persistence (Metz *et al.* 1983; Lundberg *et al.* 2000; Roy *et al.* 2005). For environmental variation uncorrelated in space and time, Metz *et al.* (1983) showed that highly dispersive populations exhibit a higher growth rate than sedentary populations. Therefore, populations can persist even when their *per capita* growth rates are, on average, negative everywhere (Jansen & Yoshimura 1998; Bascompte *et al.* 2002; Roy *et al.* 2005). Intuitively, independence in space increases the likelihood that some local populations experience favourable environmental conditions, and local populations experiencing less favourable conditions are rescued by dispersing individuals. Spatial correlations in temporal fluctuations dilute this rescue effect by synchronizing dynamics across space (Liebhold *et al.* 2004). In contrast, theoretical studies suggest that positive temporal autocorrelations enhance persistence of coupled sink populations (Gonzalez & Holt 2002; Schmidt 2004; Roy *et al.* 2005). This prediction was demonstrated in a recent experimental study with metapopulations of *Paramecium aurelia* (Matthews & Gonzalez 2007).

While it is an ecological truism to say that understanding metapopulation persistence requires understanding metapopulation growth rates when populations are rare, prior theoretical work has only examined these rates for well-mixed populations (Metz *et al.* 1983; Jansen & Yoshimura 1998; Bascompte *et al.* 2002) or for small environmental fluctuations (Wiener & Tuljapurkar 1994). However, many populations experience large stochastic fluctuations and are dispersal limited, in which case the metapopulation growth rate is determined by a nonlinear interplay between dispersal limitation, temporal correlations and spatial heterogeneity. To gain general insights about this interplay, a biologically interpretable expression for the metapopulation growth rate for partially mixed populations is derived. This expression provides a framework to address a variety of fundamental questions in population biology. For example, in patchy networks, how do temporal correlations and spatial heterogeneity interact with dispersal to influence persistence? When does movement into lower quality habitats enhance population growth?

## 2. MODEL AND ANALYSIS

Let us consider a population that lives in an environment with  $n$  discrete patches. Let  $N_t^i$  be the number of individuals in patch  $i$  at time  $t$ . The fitness of an individual in patch  $i$  is  $f_t^i$  at time  $t$ . Let  $d_{ij}$  be the fraction of the population from patch  $j$  that disperse to patch  $i$ . Under these assumptions, the population dynamics are given by

$$\begin{aligned} N_{t+1}^i &= \left(1 - \sum_{k \neq i} d_{ki}\right) f_t^i N_t^i + \sum_{j \neq i} d_{ij} f_t^j N_t^j \\ &= \sum_{j=1}^n d_{ij} f_t^j N_t^j. \end{aligned} \quad (2.1)$$

To write this model more compactly, let  $\mathbf{F}_t$  be the diagonal matrix with diagonal entries  $f_t^1, \dots, f_t^n$ ,  $\mathbf{D}$  be the matrix whose  $i$ - $j$ th entry is given by  $d_{ij}$  and  $\mathbf{N}_t = (N_t^1, \dots, N_t^n)'$  be the vector population abundances where  $'$  denotes transpose. With this notation, equation (2.1) simplifies to

$$\mathbf{N}_{t+1} = \mathbf{D}\mathbf{F}_t\mathbf{N}_t.$$

While this model does not include density dependence, one can view it as a linearization of a density-dependent model about the extinction equilibrium and, therefore, equation (2.1) determines how metapopulations grow when rare (Benaïm & Schreiber 2009).

The time evolution of the fitness in each patch is assumed to be stationary. If there is no dispersal into or out of patch  $i$ , then the population size at time  $t$  in patch  $i$  is  $N_t^i = f_{t-1}^i \dots f_0^i N_0^i$ . Owing to this multiplicative nature of population growth, the long-term fate of the population is determined by the expected value,  $\mathbb{E}[\log f^i]$ , of the logarithmic fitnesses  $\log f_t^i$ . Namely, in the absence of dispersal, the population size in patch  $i$  at time  $t$  is approximately  $N_0^i e^{\mathbb{E}[\log f^i]t}$ , where  $e^{\mathbb{E}[\log f^i]}$  is the geometric mean of  $f^i$ . For this reason,  $\mathbb{E}[\log f^i]$  is called the *population growth rate in (isolated) patch i*.

When all patches are connected by dispersal (i.e.  $\mathbf{D}$  is irreducible and aperiodic) and  $\mathbb{E}[\log^+ \|\mathbf{D}\mathbf{F}\|] < \infty$  where  $\|\cdot\|$  is any matrix norm, a random version of the Perron Frobenius theorem (Tuljapurkar 1990) implies that there is a quantity,  $M = \lim_{t \rightarrow \infty} (1/t) \mathbb{E}[\log \|\mathbf{D}\mathbf{F}_t \dots \mathbf{D}\mathbf{F}_1\|]$ , such that

$$M = \lim_{t \rightarrow \infty} \frac{1}{t} \log(N_t^1 + \dots + N_t^n) \quad \text{with probability 1} \quad (2.2)$$

whenever  $N_0^i > 0$  for at least one patch. As the total population size at time  $t$  is approximately  $e^{Mt}$ ,  $M$  is called the *metapopulation growth rate*. If  $M > 0$ , then the population grows exponentially and persists, while  $M < 0$  implies that the population goes exponentially quickly to extinction.

Metz *et al.* (1983) derived an explicit expression for  $M$  when the fraction of the population going to patch  $i$  is independent of their initial position (i.e.  $d_{ij} = v_i$  for all  $j$ ). This dispersal pattern occurs when individuals enter a common migrant pool prior to dispersing their final destination. For these populations, hereafter called *well mixed*, the spatial average of the fitnesses in year  $t$  is

$$S_t = \sum_{i=1}^n v_i f_t^i,$$

and the metapopulation growth rate is the expected value (i.e. temporal average) of the logarithm of the spatially averaged fitnesses:

$$M = \mathbb{E}[\log S]. \quad (2.3)$$

Owing to the concavity of the log function, Jensen's inequality (Ruel & Ayres 1999) applied to the spatial and temporal averages of  $\mathbb{E}[\log S]$  yields

$$\log\left(\sum_{i=1}^n v_i \mathbb{E}[f^i]\right) > \mathbb{E}[\log S] > \sum_{i=1}^n v_i \mathbb{E}[\log f^i]. \quad (2.4)$$

The second inequality in equation (2.4) implies that dispersal can mediate persistence as  $\mathbb{E}[\log S]$  can be positive despite all local growth rates  $\mathbb{E}[\log f^i]$  being negative. However, the first inequality in equation (2.4) implies that dispersal-mediated persistence for well-mixed populations requires that the expected fitness  $\mathbb{E}[f^i]$  is greater than 1 in at least one patch.

For well-mixed populations, the metapopulation growth rate in equation (2.3) does not depend on the autocorrelation of  $f_t^i$  in consecutive years. Their effects only come to light when the populations are not well mixed, which here after I call *partially mixed*. To understand these effects, imagine that a fraction  $a$  of the population in patch 1 no longer emmigrates to patch 2 (i.e.  $d_{21} = v_2 - a$ ,  $d_{11} = v_1 + a$  and  $d_{ij} = v_i$  for all other  $i, j$ ). Define  $R_t^i = f_t^i/S_t$  to be the *relative fitnesses* of non-dispersive individuals in patch  $i$  to dispersive individuals. Appendix A in the electronic supplementary material shows that

$$M \approx \mathbb{E}[\log S] + a v_1 \mathbb{E}[(R_{t+1}^1 - R_{t+1}^2)R_t^1], \quad (2.5)$$

whenever  $a$  is sufficiently small. To interpret this approximation, one can rewrite the expectation of the right-most term as

$$\mathbb{E}[(R_{t+1}^1 - R_{t+1}^2)R_t^1] = \mathbb{E}[R^1 - R^2] \mathbb{E}[R^1] + \text{Cov}[R_{t+1}^1 - R_{t+1}^2, R_t^1].$$

The sign of the first term,  $\mathbb{E}[R^1 - R^2] \mathbb{E}[R^1]$ , is proportional to the difference in the temporal averages of the relative fitness for the two patches. In the absence of temporal correlations, this term implies that the reduction of movement of individuals from patch 1 to patch 2 enhances the metapopulation growth rate when the relative fitness of individuals in patch 1 is, on average, greater than the relative fitness of individuals in patch 2 (i.e.  $\mathbb{E}[R^1] > \mathbb{E}[R^2]$ ). The second term,  $\text{Cov}[R_{t+1}^1 - R_{t+1}^2, R_t^1] = \text{Cov}[R_{t+1}^1, R_t^1] - \text{Cov}[R_{t+1}^2, R_t^1]$ , equals the difference between the *autocovariance of relative fitness* in patch 1 in successive years and the *cross-covariance between the relative fitnesses* of the two patches in successive years. This difference is positive when the autocovariance exceeds the cross-covariance, i.e. years of relatively high fitness in patch 1 are followed by years where the relative fitness in patch 2 is lower than the relative fitness in patch 1. Under these circumstances, reduced movement from patch 1 to patch 2 can enhance the metapopulation growth rate.

In general, any departure from a well-mixed population can be expressed as  $d_{ji} = v_j - a_{ji}$  for  $i \neq j$  and  $d_{ii} = v_i + \sum_{j=1}^n a_{ji}$ . In which case, the metapopulation

growth rate can be approximated by

$$M \approx \mathbb{E}[\log S] + \sum_{ij} a_{ji} v_i \mathbb{E}[(R_{t+1}^i - R_{t+1}^j)R_t^i]. \quad (2.6)$$

To illustrate the utility of this approximation, applications to a patch network model and a source-sink model are given.

### (a) A population network

Here, I consider a generalization of a simple yet instructive model introduced by Bascompte *et al.* (2002) and apply it to the acorn woodpecker (*Melanerpes formicivorus*) data analysed by Stacey & Taper (1992). In this model, a fraction  $d$  of the population disperse and go to any of the other patches with equal likelihood (i.e.  $d_{ij} = 1 - d$  and  $d_{ij} = d/(n-1)$  for  $i \neq j$ ). The fitness of an individual within any patch has mean  $\mathbb{E}[f]$  and coefficient of variation CV. The spatial correlation between fitnesses of individuals living in neighbouring patches is  $\rho_{\text{space}}$ . The temporal autocorrelation coefficient between consecutive years on the same patch (i.e.  $f_t^i$  and  $f_{t+1}^i$ ) is  $\rho_{\text{time}}$ . Appendix B in the electronic supplementary material shows how such a model with these spatial correlations and temporal autocorrelations can be constructed for any temporal distribution of fitnesses (e.g. the acorn woodpecker data).

If there are sufficiently many patches (simulations suggest 20 or more), then the metapopulation growth rate can be approximated using equation (2.6) as follows:

$$M \approx \log \mathbb{E}[f] + \text{CV}^2 \left( (1-d)\rho_{\text{time}} - \frac{\rho_{\text{space}}}{2} \right) \quad (2.7)$$

for  $d$  sufficiently large,

and  $\rho_{\text{space}}$  sufficiently small (electronic supplementary material, appendix B). Equation (2.7) implies that the metapopulation growth rate decreases linearly with the spatial correlation  $\rho_{\text{space}}$ . In contrast,  $M$  increases linearly with the temporal autocorrelation  $\rho_{\text{time}}$ . Both of these effects are proportional to the squared CV of fitness. Moreover, the effect of temporal autocorrelations is proportional to the fraction of non-dispersing individuals: a reduction of movement increases  $M$  if there are positive temporal autocorrelations, and reduces  $M$  if there are negative temporal autocorrelations.

For low dispersal rates (i.e.  $d \approx 0$ ), equation (2.7) is not an appropriate approximation for  $M$ . However, Benaïm & Schreiber (2009, proposition 3) show that  $M$  is continuous with respect to  $d$ . Hence,

$$M \approx \mathbb{E}[\log f] \quad \text{for } d \text{ sufficiently small.} \quad (2.8)$$

Thus, as  $\log \mathbb{E}[f] > \mathbb{E}[\log f]$ , dispersal enhances  $M$  whenever spatial correlations are sufficiently weak.

This network model is parameterized with the demographic data for the acorn woodpecker population in Water Canyon, New Mexico (Stacey & Taper 1992). This population exhibited high variability in adult survivorship (from 38 to 71%) and reproductive rates (0.05 to 4 young per breeding pair) over a 10-year period. During this period, the average fitness of a female was  $\mathbb{E}[f] \approx 0.987$ . Consequently, in the absence of immigration, this population would go extinct quickly. However, if there are multiple patches (e.g. canyons), then approximation (2.7) predicts that coupling these patches by dispersal alters the metapopulation growth

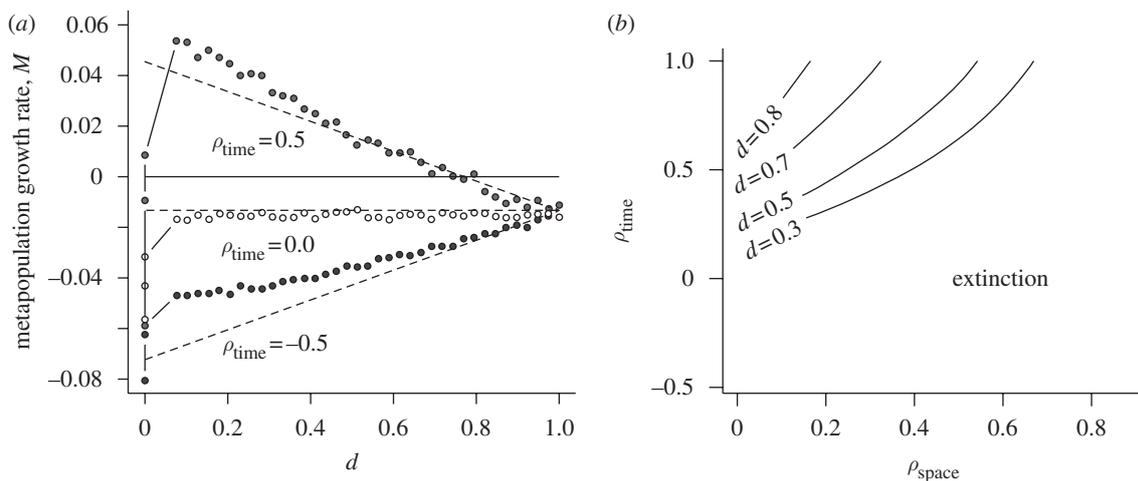


Figure 1. Persistence for a 30-patch network with local demography given by the acorn woodpecker data analysed by Stacey & Taper (1992). (a) The metapopulation growth rate  $M$  is plotted as a function fraction of individuals dispersing,  $d$ , with no spatial correlation ( $s = 0$ ) and temporal correlations as indicated. Plotted circles correspond to numerically estimated values of  $M$  and dashed lines corresponds to the analytic approximation (2.7) of  $M$ . (b) Zero contours of  $M$  for different fractions of dispersing individuals. Extinction (i.e.  $M < 0$ ) occurs in the regions below the contour lines. Computations performed with R (R Development Core Team 2008).

rate and may mediate persistence (figure 1a). When fitnesses are uncorrelated in time and in space, the metapopulation growth rate is  $\log \mathbb{E}[f] \approx -0.013$  for highly dispersive populations, but  $\mathbb{E}[\log f] \approx -0.070$  for sedentary populations. Thus, while dispersal increases the metapopulation growth rate in the absence of temporal autocorrelations, dispersal fails to mediate persistence. Negative temporal autocorrelations worsen the situation by reducing the metapopulation growth rate for all dispersal rates. As predicted by equation (2.7) and (2.8), positive temporal autocorrelations increase  $M$  and result in  $M$  being positive at intermediate dispersal rates (upper curve in figure 1a). Finally, as predicted by equation (2.7), spatial correlations inhibit persistence: persistence is impossible at high spatial correlations and possible at low spatial correlations provided there are sufficiently strong temporal correlations (figure 1b).

### (b) Source–sink dynamics

Patchy landscapes form geographical mosaics consisting of source and sink habitats. Source habitats, call them habitat type 1, sustain populations without immigration, i.e.  $\mathbb{E}[\log f^1] > 0$ . Sink habitats, call them habitat type 2, cannot support populations without immigration, i.e.  $\mathbb{E}[\log f^2] < 0$ . Let  $d_1$  be the fraction of the source population dispersing to sink habitats, and  $d_2$  the fraction of the sink population dispersing to source habitats.

Appendix C in the electronic supplementary material demonstrates that the maximal metapopulation growth rate is realized when some individuals move from sink to source habitats. When a few individuals disperse from source to sink habitats, equation (2.5) implies

$$M \approx \mathbb{E}[\log f^1] + d_1 \left( \mathbb{E} \left[ \frac{f^2}{f^1} \right] - 1 \right) \quad (2.9)$$

(electronic supplementary material, appendix C). Approximation (2.9) implies that if the ratio of fitness in sink habitats to fitness in source habitats is, on average,

greater than 1, then movement into sink habitats increases the metapopulation growth rate.

To better understand how spatial and temporal correlations between the growth rates in the two habitats influence metapopulation growth, assume  $\log f_t^i$  are normally distributed with means  $\mu_i$  and variances  $\sigma_i^2$ . Let  $\rho_{\text{space}}$  be the spatial correlation between  $\log f_t^1$  and  $\log f_t^2$ . Appendix C in the electronic supplementary material shows that dispersal into sink habitats increases the metapopulation growth rate if and only if

$$\sigma_1^2 + \sigma_2^2 - 2\rho_{\text{space}}\sigma_1\sigma_2 > 2(\mu_1 - \mu_2). \quad (2.10)$$

Since  $\sigma_1^2 + \sigma_2^2 - 2\rho_{\text{space}}\sigma_1\sigma_2$  equals the temporal variance of  $\log f_t^1 + \log f_t^2$ , inequality (2.10) implies that if the difference in the means of within-patch growth rates is less than one-half of the net temporal variation in *per capita* growth rates, then some dispersal into sink habitats maximizes the metapopulation growth rate. Since the net temporal variance decreases with the spatial correlation between the within-patch growth rates, spatial correlations decrease the optimal metapopulation growth rate and reduce the movement of optimal dispersers into sink habitats (figure 2a–b).

Although temporal autocorrelations do not influence whether or not movement into sink habitat is optimal, these autocorrelations have two effects on the optimal dispersal strategy and optimal metapopulation growth rate (figure 3). Since temporal autocorrelations provide information about future conditions within patches, these autocorrelations, whether they be negative or positive, increase the optimal metapopulation growth rate (figure 3a). As predicted by approximation (2.6), optimal metapopulation growth occurs at lower dispersal rates when there are positive autocorrelations, and at higher dispersal rates when there are negative autocorrelations (figure 3b).

### 3. DISCUSSION

Metapopulation growth is determined by a complex interplay between dispersal and spatio-temporal

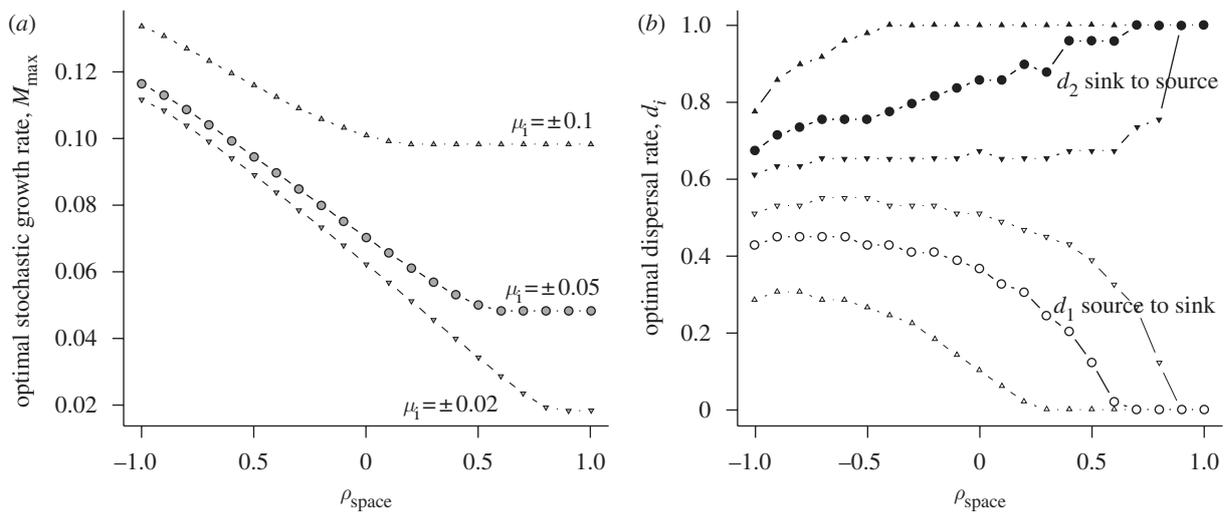


Figure 2. Effects of spatial correlations on optimal movement patterns and metapopulation growth in source–sink environments. (a) The optimal metapopulation growth rates plotted as a function of the spatial correlation  $\rho_{\text{space}}$  between the within-patch growth rates  $\log f_i^t$ . Average *per capita* growth rates in source and sink habitats are  $\mu_1 = \mathbb{E}[\log f^1] > 0$  and  $\mu_2 = \mathbb{E}[\log f^2] < 0$ , respectively. *Per capita* growth rates are temporally uncorrelated with variance 0.25. (b) The dispersal rates yielding the optimal metapopulation growth rate are plotted.

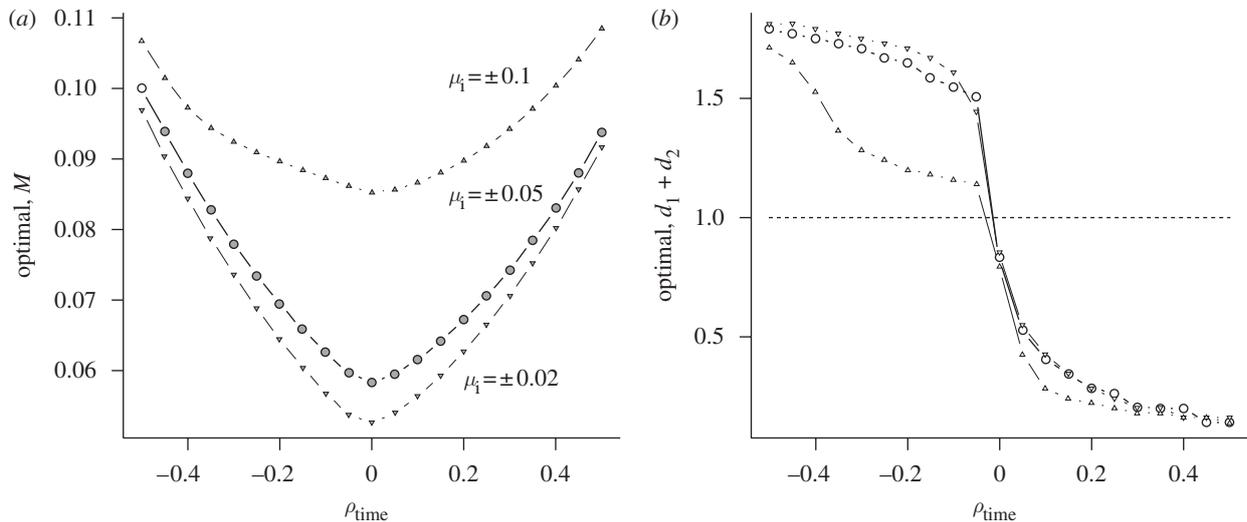


Figure 3. Effects of temporal autocorrelations on optimal movement patterns and metapopulation growth in source–sink environments. (a) The optimal metapopulation growth rates plotted as a function of the temporal autocorrelation  $\rho_{\text{time}}$  of within-patch growth rates  $\log f_i^t$ . Average *per capita* growth rates in source and sink habitats are  $\mu_1 = \mathbb{E}[\log f^1] > 0$  and  $\mu_2 = \mathbb{E}[\log f^2] < 0$ , respectively. *Per capita* growth rates  $\log f_i^t$  are spatially uncorrelated with variance 0.25. (b) The sum of the dispersal rates yielding the optimal metapopulation growth rate are plotted. The dashed line corresponds to a well-mixed population, i.e.  $d_1 = 1 - d_2$ .

fluctuations. While temporal fluctuations and dispersal in spatial heterogeneous habitats in themselves reduce metapopulation growth rates, dispersal in the presence of spatial and temporal fluctuations can enhance metapopulation growth. For well-mixed populations, temporal fluctuations enhance the metapopulation growth rate whenever they are sufficiently uncorrelated in space. However, temporal autocorrelations in these fluctuations have no effect on the growth rate (Metz *et al.* 1983; Jansen & Yoshimura 1998; Bascompte *et al.* 2002). Since many populations are limited by dispersal, I provided a biologically interpretable expression for the growth rate for partially mixed populations. This expression highlights how spatio-temporal heterogeneity influences persistence of dispersal limited populations

and determines movement patterns that maximize growth rates.

For well-mixed populations, the metapopulation growth rate equals the logarithmic average of the spatially averaged fitnesses (Metz *et al.* 1983; Jansen & Yoshimura 1998; Bascompte *et al.* 2002). Equivalently, exponentiating this growth rate yields the geometric mean of the spatially averaged fitnesses. Here, I have shown that partial mixing modifies this growth rate by two terms involving the relative fitnesses of an individual remaining in a patch versus a dispersing individual. In the absence of temporal correlations, the first of these terms implies that remaining in patches with, on average, higher relative fitness enhances the metapopulation growth rate. The second of these terms equals the difference between the

temporal autocovariance of relative fitness within a patch and the temporal cross-covariance in relative fitnesses between patches. If the autocovariances are greater than the cross-covariances, then lower dispersal rates enhance metapopulation growth rates, otherwise higher dispersal rates enhance metapopulation growth. The ultimate effect of partial mixing on metapopulation growth depends on the combined effects of the spatial variation in the mean within-patch fitnesses (the first term) and the differences in the temporal autocovariances and cross-covariances (the second term).

It is useful to contrast the approximations developed here with work of Chesson (2000) and Roy *et al.* (2005). By summing population abundances across all patches, these authors show that equation (2.5) reduces to

$$\langle N_{t+1}^i \rangle = \langle f_t^i \rangle + n \text{Cov}[f_t^i, p_t^i] \langle N_t^i \rangle,$$

where  $\langle N^i \rangle = 1/n \sum_{i=1}^n N^i$  is the spatial average of the population abundances,  $p_t^i = N_t^i / \sum_j N_t^j$  is the proportion of the population living in patch  $i$  at time  $t$  and  $\text{Cov}[f_t^i, p_t^i]$  is the *fitness-density covariance*: covariance between the fitnesses  $\{f_t^1, \dots, f_t^n\}$  and the relative abundances  $\{p_t^1, \dots, p_t^n\}$  at time  $t$ . Equation (2.2) implies that the metapopulation growth rate  $M$  satisfies

$$M = \lim_{T \rightarrow \infty} \frac{1}{T} \sum_{t=1}^T \log \langle f_t^i \rangle + n \text{Cov}[f_t^i, p_t^i] \text{ with probability 1.} \quad (2.11)$$

Hence, the metapopulation growth rate is larger when the fitness-density covariance tends to be positive. Since the long-term behaviour of the fitness-density covariance depends non-trivially on the details of how individuals disperse between patches and the spatial-temporal structure of the within-patch fitnesses, the analytic approximations of  $M$  in conjunction with equation (2.11) can be used to understand the effects of partial mixing and spatial-temporal heterogeneity on the fitness-density covariance.

#### (a) *Effects of dispersal and spatio-temporal heterogeneity on metapopulation persistence*

Prior work has shown that metapopulation persistence does not require patches that sustain populations without immigration (Metz *et al.* 1983; Jansen & Yoshimura 1998; Bascompte *et al.* 2002; Schmidt 2004; Roy *et al.* 2005). This initially counter intuitive phenomena stems from Lewontin & Cohen's (1969) observation that 'even though the expectation of population size may grow infinitely large with time, the probability of extinction may approach unity, owing to the difference between the geometric and arithmetic mean.' A population restricted to a patch is extinction prone when the geometric mean of the fitness is less than 1 (i.e. the mean *per capita* growth rate  $\mathbb{E}[\log f_i]$  is negative). Alternatively, the average population size across many independent realizations grows when the arithmetic mean is greater than 1. For populations dispersing freely between many patches and experiencing spatially uncorrelated fluctuations, this arithmetic mean of fitness determines the metapopulation growth rate (Metz *et al.* 1983; Bascompte *et al.* 2002). In which case, environmental conditions yielding Lewontin & Cohen's surprising prediction for within-patch dynamics

yield conditions where sink populations coupled by dispersal persist (Jansen & Yoshimura 1998). More generally, an application of Jensen's inequality reveals that a positive growth rate for well-mixed populations requires that the arithmetic mean of fitness is greater than 1 in at least one patch.

When environmental fluctuations have positive temporal autocorrelations and the population is partially mixing, the metapopulation growth rate can be positive despite the arithmetic mean of fitness being less than 1 in every patch. In particular, for partially mixed population networks (see equation (2.7)), the metapopulation growth rate increases linearly with temporal autocorrelations and the squared coefficient of variation of the fluctuations. These results combined with equation (2.11) also imply that positive temporal autocorrelations increase the fitness-density covariance for partially mixed populations. Intuitively, partial mixing allows the population to build up in patches experiencing longer runs of better conditions, which in conjunction with positive temporal autocorrelations generates a positive fitness-density covariance. Furthermore, in the presence of these positive autocorrelations, the analysis reveals that the maximal metapopulation growth rate occurs at intermediate dispersal rates, thereby confirming results of Roy *et al.* (2005) and extending recent work of Roy & Holt (in press). Roy & Holt (in press), derived approximations for the expected metapopulation growth rate (i.e.  $\bar{M} = \lim_{t \rightarrow \infty} (1/t) \log \mathbb{E}[\sum_i N_t^i]$ ) when local fitness randomly varies only between two values: zero and a positive value. For these models, the metapopulation growth rate  $M$  is not well defined (i.e.  $M = -\infty$ ). However, for less extreme distributions of fitness (e.g. the models considered here), Jensen's inequality implies that  $\bar{M} > M$  and, consequently,  $\bar{M} > 0$  is necessary but not sufficient for persistence. Consistent with my results, Roy & Holt found that positive temporal correlations make the fitness-density covariance positive and, thereby, inflate the value of  $\bar{M}$ .

Consistent with many earlier findings (Harrison & Quinn 1989; Palmqvist & Lundberg 1998; Bascompte *et al.* 2002; Roy *et al.* 2005), I found that the metapopulation growth rate decreases linearly with spatial correlations. Consequently, spatial correlations can negate the inflationary effects of temporal autocorrelations and increase extinction risk.

All of the aforementioned predictions are consistent with recent experimental work on metapopulations of *P. aurelia* (Matthews & Gonzalez 2007). These populations experienced a negative *per capita* growth rate at 4°C and a positive *per capita* growth rate at 18°C. To generate different spatio-temporal patterns of fluctuations in the *per capita* growth rates, Matthews & Gonzalez randomly varied temperatures in patches (i.e. glass flasks) between these two temperatures. Across all treatments, populations connected by dispersal had higher metapopulation growth rates than uncoupled populations. In spatially correlated environments, metapopulation growth rates were negative and several of the replicants went extinct within 50 days, the length of the experiment. In spatially uncorrelated environments, populations coupled by dispersal always persisted for 50 days and exhibited a higher metapopulation growth rate when temporal correlations were positive.

Given the ubiquity of temporal correlations in important environmental variables (Vasseur & Yodzis 2004), the inflationary effects of temporal autocorrelations are potentially relevant for many natural populations. Consider, for example, the acorn woodpecker (*M. formicivorus*) population studied by Stacey & Taper (1992). A decade's worth of data in the 1970s reveals that the fitness of this acorn woodpecker population is highly variable with an arithmetic mean less than 1. A population viability analysis predicts that in the absence of immigration, this population would go extinct within two decades (Stacey & Taper 1992). Hence, immigration is essential for its continued persistence in the past three decades. The analysis presented here suggests that a metapopulation with the same unsustainable local demography can persist provided it exhibits low dispersal rates and experiences positive temporal autocorrelations in environmental factors. While this explanation is unlikely to solely account for the persistence of the acorn woodpeckers, it may play a contributing role.

### (b) Effects of spatial heterogeneity and fluctuations on optimal dispersal patterns

In stable environments, populations maximize their growth rate by dispersing exclusively into source habitats (Holt 1985). However, when habitat quality fluctuates over time, populations can increase their growth rate by dispersing into sink habitats (Holt 1997; Schreiber & Saltzman 2009). For example, Holt (1997) showed that if the fitness in the source fluctuates with equal probability between two values whose geometric mean equals 1 (i.e.  $\mathbb{E}[\log f^1] = 0$ ), then movement into sinks with constant fitness  $f^2 < 1$  is selectively advantageous if  $f^2 \mathbb{E}[f^1] > 1$ . For any temporal distributions of fitness in source and sink habitats, I demonstrate that movement into sink habitats increases the metapopulation growth rate whenever the fitnesses in the sink relative to the fitness in source is, on average, greater than 1 (i.e.  $\mathbb{E}[f_t^2/f_t^1] > 1$ ). When fitnesses are log-normally distributed, movement into sink habitats maximizes growth when the net temporal variation in within-patch growth rates is sufficiently greater than the difference between the means of these growth rates. Intuitively, larger differences in mean habitat quality favour movement into sink habitats only if there are larger fluctuations in the habitat qualities.

For dispersal patterns that maximize the metapopulation growth rate, temporal autocorrelations, whether they be negative or positive, enhance metapopulation growth. For positively autocorrelated environments, optimal dispersal patterns involve lower rates of movement. Schmidt (2004) found a related result for individuals that played a win-stay and lose-shift dispersal strategy in environments with positive temporal autocorrelations. For negatively autocorrelated environments, optimal dispersal patterns involve higher rates of movement. Interestingly, for metapopulations experiencing high levels of spatial symmetry (e.g. the population network considered here or the networks considered by Roy *et al.* 2005), the inflationary effect of negative autocorrelations on metapopulation growth vanishes for optimal dispersal strategies, while the inflationary effect of positive autocorrelations is maintained. However, as most

metapopulations exhibit spatial asymmetries (e.g. source-sink structures), it is likely that negative temporal autocorrelations can mediate persistence as well as maintain sink populations.

### (c) Extensions and challenges

While the models considered here do not include density dependence or demographic stochasticity, the results presented here do apply to models incorporating these additional complexities. If the metapopulation growth rate defined here is positive for a linearization of a density dependent model about the extinction state, the work of Benaïm & Schreiber (2009) implies that the metapopulation persists in the sense of stochastic boundedness (Chesson 2000; Ellner 1984). Namely, with high probability, the metapopulation tends to stay bounded away from extinction. Conversely, if the metapopulation growth rate is negative for the linearized model, then the metapopulation goes to extinction at an exponential rate. Similarly, the theory of multi-type branching processes in random environments (Tanny 1981) coupled with our results imply that if the metapopulation growth rate is negative for populations experiencing demographic stochasticity, then extinction occurs with probability 1. Conversely, when the metapopulation growth rate is positive, persistence occurs with positive probability. Finding explicit expressions for these extinction probabilities is a challenging problem worthy of further investigation. A greater challenge is to understand how the simultaneous inclusion of density dependence and demographic stochasticity influences the distribution of times to extinction.

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