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## Research

# The effects of dispersal on spatial synchrony in metapopulations differ by timescale

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Understanding the processes that stabilize species populations is a fundamental question in ecology and central to conservation biology. In metapopulations, dispersal can act as a 'double edged' sword for species stability by simultaneously decreasing local population variability (thereby decreasing local extinction risk) while increasing spatial synchrony (thereby increasing landscape-level extinction risk). These dynamics may operate at different timescales, complicating efforts to assess their relative importance for long-term stability. Here, we use a simple metapopulation model to understand how dispersal affects population variability and spatial synchrony across timescales. Our model shows that dispersal has contrasting effects at short versus long timescales on the variability and synchrony of populations. For populations that exhibit slow recovery when perturbed (i.e. under-compensatory growth), dispersal decreases local population variability while increasing spatial synchrony at long timescales. In contrast, at short timescales dispersal increases local population variability while decreasing spatial synchrony. For populations that recover via damped oscillation when perturbed (i.e. over-compensatory growth), the effects of dispersal are all opposite to those for populations with under-compensatory growth, at both short and long timescales. The timescale-dependent effect of dispersal has important implications for empirical studies. Specifically, studies conducted over short periods may only observe population variability increasing and spatial synchrony decreasing with dispersal, whereas the opposite patterns may predominate over longer periods. Our results provide novel insights on the dynamics underlying the role of dispersal and highlight the importance of time series length in empirical studies of metapopulations.

Keywords: dispersal, metapopulation, over-compensatory growth, spatial synchrony, stability, timescale, time series length, under-compensatory growth

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## Introduction

The field of spatial ecology has highlighted that the fate of a local population may be fundamentally tied to connection with surrounding populations. This idea has been formalized in the concept of metapopulation, defined as a collection of spatially separate populations that interact through dispersal (Levins 1969, Hanski 1999). Early conceptualizations of metapopulation theory highlighted that dispersal is central to the stability of metapopulations. For instance, in a stochastic environment where populations fluctuate constantly through time, dispersal can provide stabilizing effects by dampening the temporal variability of individual populations (Briggs and Hoopes 2004). On the other hand, dispersal can also generate spatial population synchrony (i.e. temporal correlation between local populations), such that all populations rise and fall at the same time (Liebhold et al. 2004). Synchronized fluctuations can be destabilizing, even causing increased extinction of the entire metapopulation (Heino et al. 1997, Earn et al. 2000). Consequently, the overall effect of dispersal on metapopulation stability is determined by the balance between its locally stabilizing and spatially synchronizing effects (Higgins 2009, Abbott 2011, Wang et al. 2015, Fox 2017).

The stabilizing and synchronizing effects of dispersal have been shown to depend on endogenous and exogenous factors, particularly the species' intrinsic growth rates and spatial correlation in the environment. A population's growth rate determines the rate at which it can independently recover from perturbation. Higher rates of dispersal, for instance, are often required to stabilize or rescue a local population with a lower growth rate (Wang et al. 2015, Zelnik et al. 2019). At the landscape level, spatial environmental correlation can cause spatial population synchrony (Moran 1953) and also modulate the role of dispersal, such that the synchronizing effect of dispersal is relatively weaker in a spatially correlated environment (Kendall et al. 2000, Ripa 2000, Liebhold et al. 2004). Thus, dispersal, local population growth rate and environmental correlation interact and jointly shape the stability and synchrony in metapopulations (Kendall et al. 2000, Wang et al. 2015). As these factors operate at different timescales (i.e. periods of fluctuations, such as annual dispersal events or decadal climate oscillations), the combination of these drivers may differentially affect population dynamics and spatial synchrony across timescales.

The timescale-specific patterns of population dynamics have long been acknowledged in ecological studies. Empirical studies reported that natural populations often exhibit positively autocorrelated temporal dynamics (Pimm and Redfearn 1988, Halley 1996, Inchausti and Halley 2001). Theoretical models showed that population growth rate and the timescale structure of environmental fluctuations have significant influences on the timescale-specific patterns of population dynamics (Ripa and Lundberg 1996, Kaitala et al. 1997, Petchey et al. 1997). Specifically, populations with low growth rates converge gradually to its equilibrium when perturbed (referred to as 'under-compensatory growth';

Ruokolainen et al. 2009), resulting in population dynamics with positive temporal autocorrelation. In contrast, populations with high growth rates overshoot the equilibrium when perturbed (referred to as 'over-compensatory growth'), resulting in population dynamics with negative autocorrelation. Moreover, the timescale structure of environmental fluctuations can generate similar patterns in population dynamics, e.g. populations living in a positively autocorrelated environment tend to exhibit positive autocorrelation (Kaitala et al. 1997, García-Carreras and Reuman 2011).

In a spatial context, the importance of timescale has become evident for understanding synchronous fluctuations of populations across space. Recent theory clarifies that spatial population synchrony measured at a specific timescale can be driven by spatial environmental correlation at the same timescale (Sheppard et al. 2016, Desharnais et al. 2018). Such theoretical insights have provided new opportunities to detect the drivers of spatial population dynamics in nature (Sheppard et al. 2016, 2019, Anderson et al. 2019). For instance, by showing the timescale-specific synchrony of both aphid populations and a number of climatic factors, Sheppard et al. (2016) discovered that winter temperature was a major driver of the spatial synchrony of aphid phenology. Theory also indicated that the presence of dispersal could alter the effect of environmental correlation in shaping the timescale-specific patterns of spatial synchrony (Desharnais et al. 2018). But an important and understudied problem is how dispersal itself shapes spatial synchrony across timescales. In particular, while dispersal can increase the stability and spatial synchrony of local populations (Abbott 2011), whether such effects are consistent across timescales is unknown.

Here we investigate how dispersal interacts with population growth rate and environmental noise to regulate population variability and synchrony at different timescales, as well as their empirical implications. In particular, if dispersal affects population variability and synchrony differently at different timescales (on a frequency domain), we expect that the empirical relationships between dispersal and population variability or synchrony may vary with the time series length (on a time domain), because short time series can only capture dynamics at short timescales but long ones can capture dynamics at both short and long timescales. Specifically, we use two-patch metapopulation models and employ Fourier transforms (Brillinger 2001, Bloomfield 2004) to uncover the timescale-specific patterns of population variability and spatial synchrony in the frequency domain. We first examine whether dispersal has different effects on population variability or spatial synchrony at short versus long timescales, and test whether these effects differ when populations exhibit under- and over-compensatory growth. We then use simulated time series to investigate relationships of dispersal with population variability and spatial synchrony, and test whether these relationships depend on time series length. Our analyses derived new predictions on the timescale-dependent effects of dispersal, and we conclude with a discussion on the theoretical and practical implications of our results.

## Methods

### The metapopulation model

We consider a two-patch discrete-time metapopulation model, in which population dynamics are governed by a Ricker growth function, environmental stochasticity and dispersal:

$$x_i{'}\left(t\right) = \left(1-d\right) \times x_i\left(t\right) + d \times x_j\left(t\right) \qquad (1a)$$

$$x_i\left(t+1\right) = x_i{'}\left(t\right) \times \exp\left(r_i\left(1 - \frac{x_i{'}\left(t\right)}{K_i}\right) + \varepsilon_i\left(t\right)\right) \qquad (1b)$$

Here, $x_i(t)$ and $x_i{'}(t)$ denote the population size in patch $i$ recorded before and after the dispersal process, respectively. $K_i$ and $r_i$ are the carrying capacity and intrinsic growth rate in patch $i$, and $d$ is the dispersal rate. $\varepsilon = (\varepsilon_1, \varepsilon_2)^T$ is two-dimensional Gaussian white noise with component variances 0.01 and correlation coefficient $\rho$, which describes the response of population growth rate to environmental fluctuations. We calculate population variability and synchrony based on $x_i(t)$ to avoid the immediate influence of dispersal (de Raedt et al. 2019; but see Desharnais et al. 2018). Previous studies that considered both $x_i(t)$ and $x_i{'}(t)$ showed that these two types of models generated qualitatively similar effects of dispersal on synchrony and variability (Wang et al. 2015).

In our model, we consider the intrinsic growth rates ($r_i$) to be within the interval (0,2), such that local populations always have stable equilibria $K_i$. When $0 < r_i < 1$, a local population exhibits under-compensatory growth and converges monotonically to its steady state when disturbed. When $1 < r_i < 2$, the local population exhibits over-compensatory growth and oscillates but eventually converges to its steady state when disturbed (Ruokolainen et al. 2009, McCann 2012).

### Synchrony and variability: overall and timescale-specific measures

We measure the temporal variability by the squared coefficient of variation (CV$^2$), i.e. the ratio of temporal variance (var($x$)) to the squared mean ($\overline{x}^2$) of population size. Given a time series of metapopulation dynamics, we calculate population variability ($V_P$) by the average temporal variability of the two local populations, i.e. $V_P = (\mathrm{CV}^2(x_1) + \mathrm{CV}^2(x_2))/2$; we calculate metapopulation variability ($V_M$) by the temporal variability of total metapopulation size ($V_M = (\mathrm{CV}^2(x_1 + x_2))$. The spatial synchrony ($\phi$) is defined as the temporal correlation between the two populations (i.e. $\phi = \mathrm{cor}(x_1, x_2)$). To be distinguishable from the timescale-specific metrics below, we refer to these metrics as overall (meta)population variability and overall synchrony.

We then derive the timescale-specific metrics for variability and synchrony based on discrete Fourier transformation (Shumway and Stoffer 2017). Specifically, the sample variance of population $i$ can be decomposed into the sum of timescale-specific terms: $\mathrm{var}(x_i) = \Sigma_\sigma I_{ii}(\sigma)$, where $I_{ii}(\sigma)$ denotes the power spectrum of time series $x_i$ at the time scale $\sigma \in \left\{\dfrac{T}{T-1}, \dfrac{T}{T-2}, \ldots, \dfrac{T}{2}, T\right\}$ (Zhao et al. 2020), corresponding to the frequency $f = T/\sigma$ in other contexts (Halley 1996). Similarly, the sample covariance between populations $i$ and $j$ could be decomposed into sum of timescale-specific terms: $\mathrm{cov}(x_i, x_j) = \Sigma_\sigma I_{ij}(\sigma)$, where $I_{ij}(\sigma)$ denotes the cospectrum between the time series $x_i$ and $x_j$. For a timescale $\sigma$, we define $V_P\left(\sigma\right) = \dfrac{1}{2}\left(\dfrac{I_{11}\left(\sigma\right)}{\overline{x}_1^2} + \dfrac{I_{22}\left(\sigma\right)}{\overline{x}_2^2}\right)$ as the timescale-specific measure of population variability, and

$$V_M\left(\sigma\right) = \frac{\left(I_{11}\left(\sigma\right) + I_{22}\left(\sigma\right) + 2I_{12}\left(\sigma\right)\right)}{\left(\overline{x}_1 + \overline{x}_2\right)^2}$$ as the timescale-specific measure of metapopulation variability. By definition, the overall population and metapopulation variability can be expressed as the sum of timescale-specific population and metapopulation variability, respectively, i.e. $V_P = \Sigma_\sigma V_P(\sigma)$ and $V_M = \Sigma_\sigma V_M(\sigma)$. We also define $\phi\left(\sigma\right) = \dfrac{I_{12}\left(\sigma\right)}{\sqrt{I_{11}\left(\sigma\right) \times I_{22}\left(\sigma\right)}}$ as a timescale-specific measure of synchrony used by Desharnais et al. (2018). The denominator of this metric serves to normalize by the power spectrum of the two time series, so $\phi(\sigma)$ is a timescale-specific measure of synchrony that is independent of timescale-specific patterns of variance (Desharnais et al. 2018). Note that the sum of $\phi(\sigma)$ across timescales does not equal the overall synchrony $\phi$.

### Analytic investigation

We solve analytically our model (1) in a spatially homogeneous case, i.e. the two patches have same environmental conditions ($r_1 = r_2 = r$, $K_1 = K_2 = K$), using a linearization approximation around the equilibrium (Supporting information). Note that the linearization approximation requires that the equilibrium is asymptotically stable ($0 < r < 2$) and the environmental stochasticity is not very strong (Loreau and de Mazancourt 2013, Wang et al. 2015). For the overall metrics of variability and synchrony, previous studies have provided analytic solutions for $\phi$, $V_P$ and $V_M$ (Abbott 2011, Wang et al. 2015). These solutions show that dispersal decreases the variability of local populations but increases spatial synchrony; these two effects cancel out at the larger metapopulation scale, such that dispersal has no effect on the stability of the metapopulation. Given the homogeneity assumption of our model, we also have: $V_M = V_P \times (1 + \phi)/2$ (Wang et al. 2015). For the timescale-specific metrics, we can similarly linearize the model and use filter theory of time series (Reinsel 1993) to derive the analytic solutions for $\phi(\sigma)$, $V_P(\sigma)$ and $V_M(\sigma)$ as functions of timescale, growth rate, dispersal and timescale-specific variance/synchrony of environmental noise (Supporting information; Desharnais et al.

2018). We note that the analytical solutions of timescale-specific variability and synchrony correspond to Fourier transforms of infinite time series (Supporting information). To visualize and compare with simulation results based on finite time series of length $L$, we rescaled the timescale-specific variability and synchrony by: $z'(\sigma) = \dfrac{z(\sigma)}{L}$, where $z(\sigma)$ denotes $\phi(\sigma)$, $V_P(\sigma)$ or $V_M(\sigma)$ (Supporting information). Following Sheppard et al. (2016), we used the threshold $\sigma = 4$ between short and long timescales. We note that the timescale $\sigma$ corresponds to the reciprocal of frequency (on a frequency domain), which is different from the time series length $L$ (on a time domain).

## Simulations

We first simulated the nonlinear dynamics described by Eq. 1 in homogenous landscapes with the same values of $r$ and $K$ in the two patches. We did so across a range of parameter values, systematically varying intrinsic growth rate ($r = 0.45$, 0.55, ..., 1.55), dispersal ($d = 0$, 0.05, 0.1, ..., 0.5) and spatial correlation in the environment ($\rho = -0.9$, $-0.8$, ..., 0.8, 0.9). For each set of parameters, we set the initial values of population sizes as the carrying capacities $K$ and ran the simulations for 1000 time steps to ensure that populations reach their stationary states and then recorded time series of the following 200 time steps. With the simulated time series, we applied the discrete Fourier transform (using the function 'fft' in Matlab) to derive the timescale specific metrics of variability and synchrony.

The length of time series may affect our ability to detect timescale-specific patterns of variability and synchrony and their relation with ecological factors (Inchausti and Halley 2002). To investigate this, we simulated metapopulation dynamics to stationary states ($T = 1000$) and then record time series with different lengths or number of time steps. We also examined how the 'observed' relationships (i.e. based on our simulated data) between dispersal and over-all synchrony or variability might differ between short (five timesteps) and long (60 timesteps) time series.

We then performed further simulations to test whether our results hold in landscapes with spatial heterogeneity, temporally autocorrelated environmental noises and more patches. We first simulated heterogeneous metapopulations with asymmetric population growth rates ($r_1 \neq r_2$) or carrying capacity ($K_1 \neq K_2$). We then consider cases where the environmental noise is temporally autocorrelated. Specifically, we define the noise term by a first-order autoregressive process (AR(1)): $\varepsilon_i(t) = q\varepsilon_i(t-1) + \xi_i(t)$, where $\xi_i(t)$ are white noises and $0 \leq q < 1$, $i = 1$, 2. A larger autoregression coefficient $q$ will result in a higher temporal autocorrelation. Lastly, we simulated a 16-patch metapopulation model with local population growth characterized by Eq. 1b and global dispersal, i.e. an emigrant from one patch has equal probabilities of immigrating into the other 15 patches.

## Results

### Analytic approximations for homogeneous metapopulations

We derive analytic solutions for timescale-specific metrics of synchrony and variability in homogenous two-patch landscapes (Supporting information). In the case that the environmental noise has the same power spectrum ($I_0$) and spatial synchrony ($\rho$) at all timescales, the timescale-specific solutions for spatial synchrony ($\phi(\sigma)$), population variability ($V_P(\sigma)$) and metapopulation variability ($V_M(\sigma)$) can be simplified as (Supporting information, Eq. B14–B16):

$$\phi(\sigma) = \frac{(1-\alpha)\rho + \alpha}{(1-\alpha) + \alpha\rho} \tag{2}$$

$$V_P(\sigma) = \frac{\left[(1-\alpha) + \alpha\rho\right] \times I_0}{1 + (1-r)^2 - 2(1-r) \times \cos(2\pi/\sigma)} \tag{3}$$

$$V_M(\sigma) = \frac{1}{2} \times \frac{(1+\rho) \times I_0}{1 + (1-r)^2 - 2(1-r) \times \cos(2\pi/\sigma)} \tag{4}$$

where

$$\alpha(\sigma) = \frac{2d(1-r)\cos(2\pi/\sigma) - (1-d)(1-r)}{\left((1-2d)(1-r)\right)^2 + 2(1-2d)(1-r) \times \cos(2\pi/\sigma) + 1}.$$

The above solutions clarify how the timescale-specific patterns of synchrony and variability depend on population dynamical parameters. In particular, the timescale-specific variability for both local populations and metapopulations increase as the timescale ($\sigma$) increases when population dynamics are under-compensatory ($r < 1$), and they both decrease as $\sigma$ increases when population dynamics are over-compensatory ($r > 1$) (Fig. 1; Supporting information). Similarly, at short timescales, synchrony and both population and metapopulation variability all increase as $r$ increases; at long timescales, all these synchrony and variability metrics decrease as $r$ increases (Fig. 1; Supporting information).

The effect of dispersal on synchrony and variability depends on the timescale considered and the population growth rate (Fig. 2). When $r < 1$, dispersal increases spatial synchrony and decreases population variability at long timescales, but it has just the inverse effects at short timescales. When $r > 1$, dispersal has the opposite effects on spatial synchrony and population variability at both short and long timescales. In the absence of dispersal, spatial synchrony equals $\rho$ at all timescales (Fig. 2b, e). Additionally, dispersal has no effect on the metapopulation variability at all timescales (Fig. 2c, f).
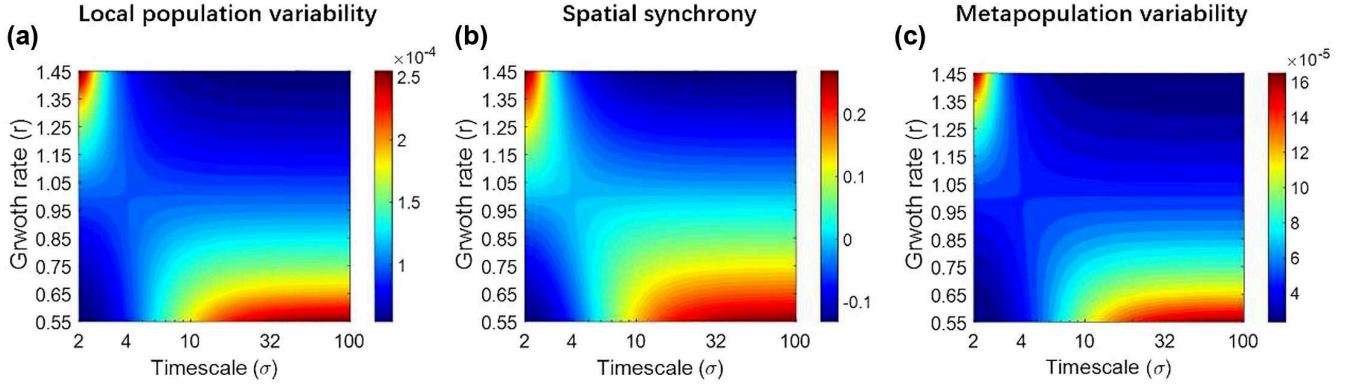
Figure 1. Timescale-specific population variability ($V_P(\sigma)$, a), spatial synchrony ($\phi(\sigma)$, b) and metapopulation variability ($V_M(\sigma)$, c) as functions of timescale ($2 \leq \sigma \leq 100$) and growth rate ($r$), derived from analytic approximations. Parameters: $\rho = 0$, $d = 0.2$, $K = 10$, var($\epsilon$) = 0.01.

The correlation of environmental noises ($\rho$) has positive effect on spatial synchrony and metapopulation variability at all timescales, regardless of the magnitude of $r$ (Supporting information). But the effects of environmental correlation on local population variability differ between under- and over-compensatory systems (Supporting information). When $r < 1$, local population variability increases as $\rho$ increases at long timescales, but it decreases slightly as $\rho$ increases at short timescales. When $r > 1$, the opposite is true. See the Supporting information for analytic investigations on the dependency of $V_P$, $\phi$ and $V_M$ on parameters $d$, $\sigma$ and $\rho$.

## Variability and synchrony in simulated metapopulations

Our simulations of homogeneous metapopulations reveal similar patterns as the analytic solutions, provided sufficiently long time series (e.g. 200 timesteps). In particular, dispersal has contrasting effects on variability and synchrony at short and long timescales, which depend on whether population growth follows under- or over-compensatory dynamics. In under-compensatory systems ($r < 1$), spatial synchrony increases and population variability decreases, as dispersal increases, at long timescales; in contrast, spatial synchrony
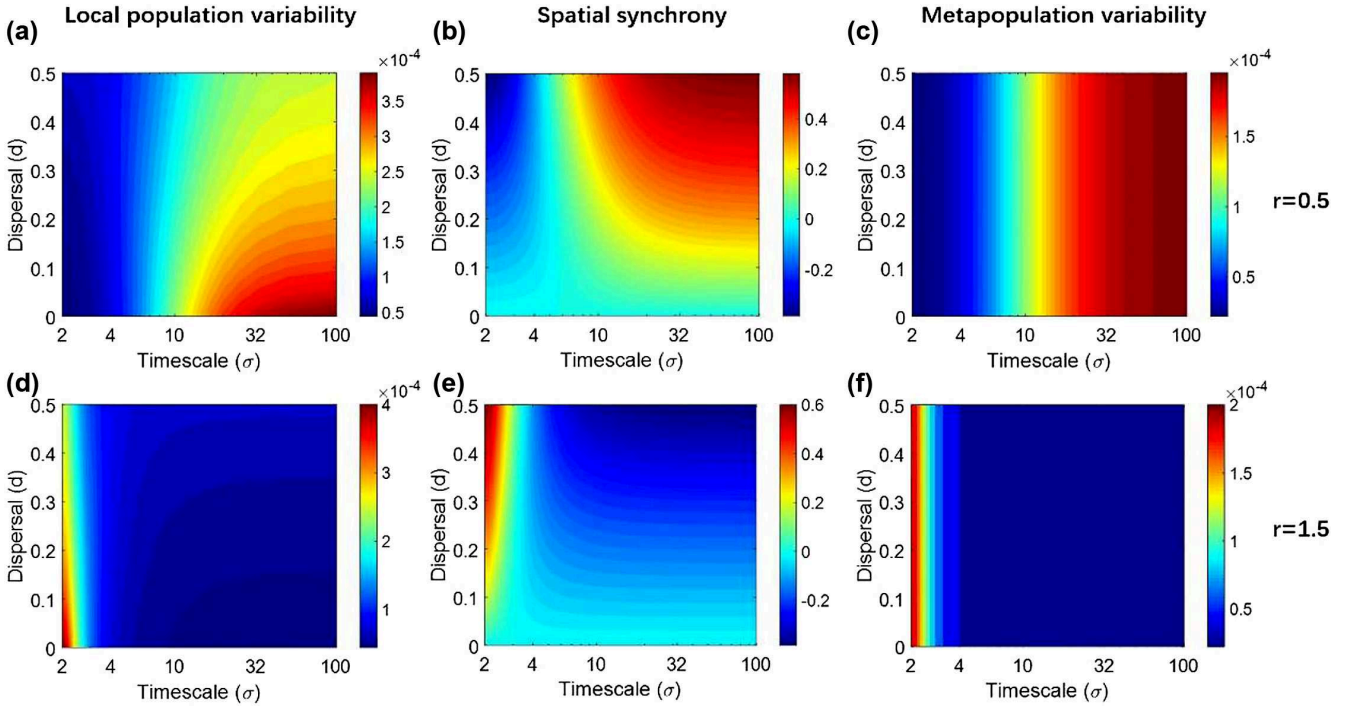


Figure 2. Timescale-specific population variability ($V_P(\sigma)$), spatial synchrony ($\phi(\sigma)$) and metapopulation variability ($V_M(\sigma)$) as functions of timescale and dispersal rate ($d$), derived from analytic approximations. Note that spatial synchrony always equals 0 when $d = 0$, which is invisible in the figure. Parameters are set with $r = 0.5$ (under-compensatory, a–c), 1.5 (over-compensatory, d–f) and $\rho = 0$, $K = 10$, var($\epsilon$) = 0.01.

decreases and population variability increases, as dispersal decreases, at short timescales (Supporting information). In over-compensatory systems ($r > 1$), the effects of dispersal are opposite at both short and long timescales (Supporting information). In these homogeneous metapopulations, dispersal has no effect on metapopulation variability at all timescales, regardless of $r$ (Supporting information). Besides, the (meta)population variability and synchrony all increase with $r$ at short timescales, and they decrease with $r$ at long timescales (Supporting information). The environmental correlation generally increases metapopulation variability and synchrony, except for population variability at short timescales when $r < 1$, or at long timescales when $r > 1$ (Supporting information). All these effects of dispersal, growth rate and environmental correlation are consistent with analytic solutions (Fig. 1, 2, Supporting information).

We then explore how the length of time series may influence their relationships with dispersal and intrinsic growth rate. The length of time series used for calculations directly influence the empirical relationship between dispersal and overall synchrony or population variability, even though the time series are generated from the same underlying model and only differ in their length. Specifically, given a long time series (length = 60), the overall synchrony increases, and overall population variability decreases, as dispersal increases, no matter whether local populations exhibit under- or over-compensatory dynamics (Fig. 3d–e). However, given a short time series (length = 5), the overall

spatial synchrony decreases and the overall population variability increases, as dispersal increases, when populations exhibit under-compensatory growth (i.e. $r < 1$); opposite patterns are observed when populations exhibit over-compensatory growth (i.e. $r > 1$) (Fig. 3a–b). In other words, when populations exhibited under-compensatory dynamics, dispersal has contrasting effects on spatial synchrony or population variability in short versus long time series. Lastly, the metapopulation variability exhibits no relation with dispersal, regardless of the time series length or whether populations follow under- or over-compensatory dynamics (Fig. 3c–f).

Similarly, the overall synchrony or (meta)population variability also exhibit contrasting relationships with the intrinsic growth rate ($r$) in short versus long time series. Given a long time series (length = 60), the overall synchrony and (meta)population variability all exhibit U-shape curves with $r$ (Supporting information), consistent with theoretical predictions (Wang et al. 2015). However, given a short time series (length = 5), the overall synchrony and (meta)population variability all increase monotonically with $r$ (Supporting information). Besides, the overall synchrony and (meta)population variability generally exhibit positive relationships with the environmental correlation, except that the variability of under-compensatory populations decreases slightly with $\rho$ in short time series (Supporting information).

To examine how additional ecological complexity alter the above results obtained from homogeneous metapopulations
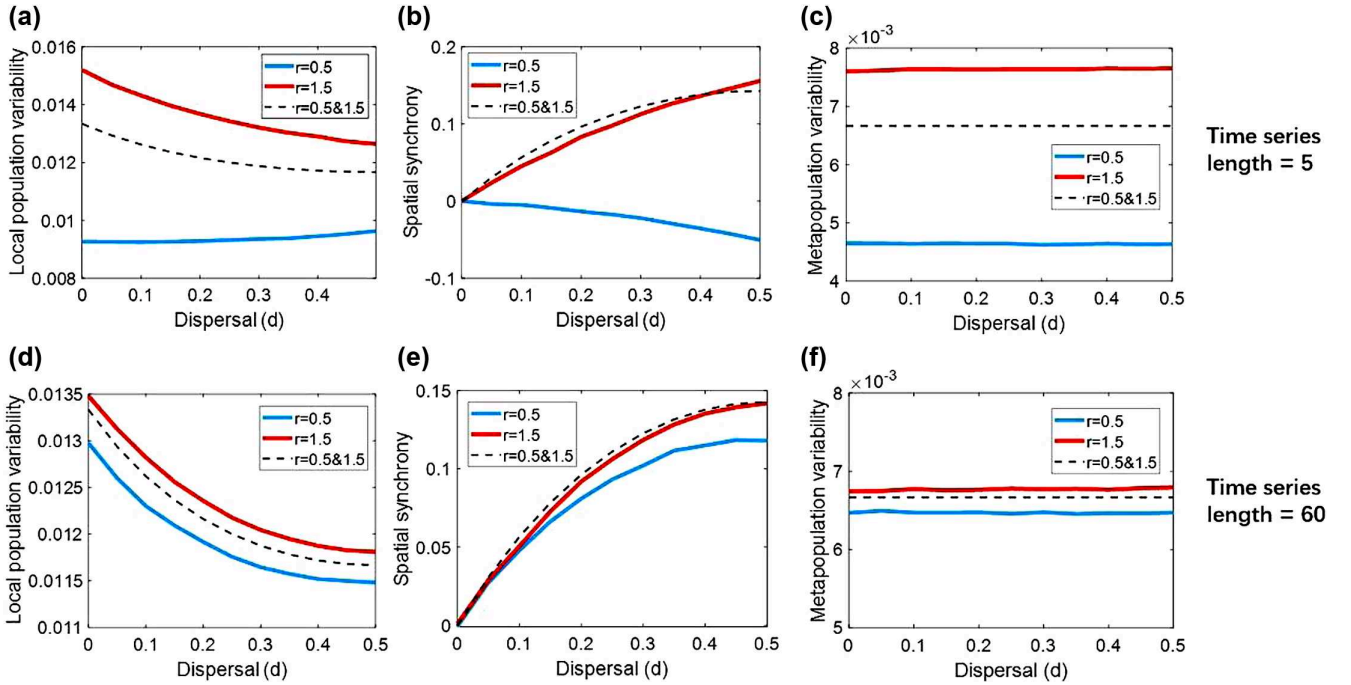


Figure 3. Effect of dispersal on local population variability (a, d), spatial synchrony (b, e) and metapopulation variability (c, f) calculated from short (a–c) and long (d–f) time series. Blue and red lines represent models with under- and over-compensatory population growth ($r = 0.5$ or 1.5), respectively. Dash lines represent respectively analytical solutions of variability and synchrony derived in Wang et al. (2015) (note that solutions are the same when $r = 0.5$ and 1.5). Parameters: $\rho = 0$, var($\epsilon$) = 0.1, $K = 10$. The results represent the average across 500 000 (length = 5) or 50 000 (length = 60) simulated communities.
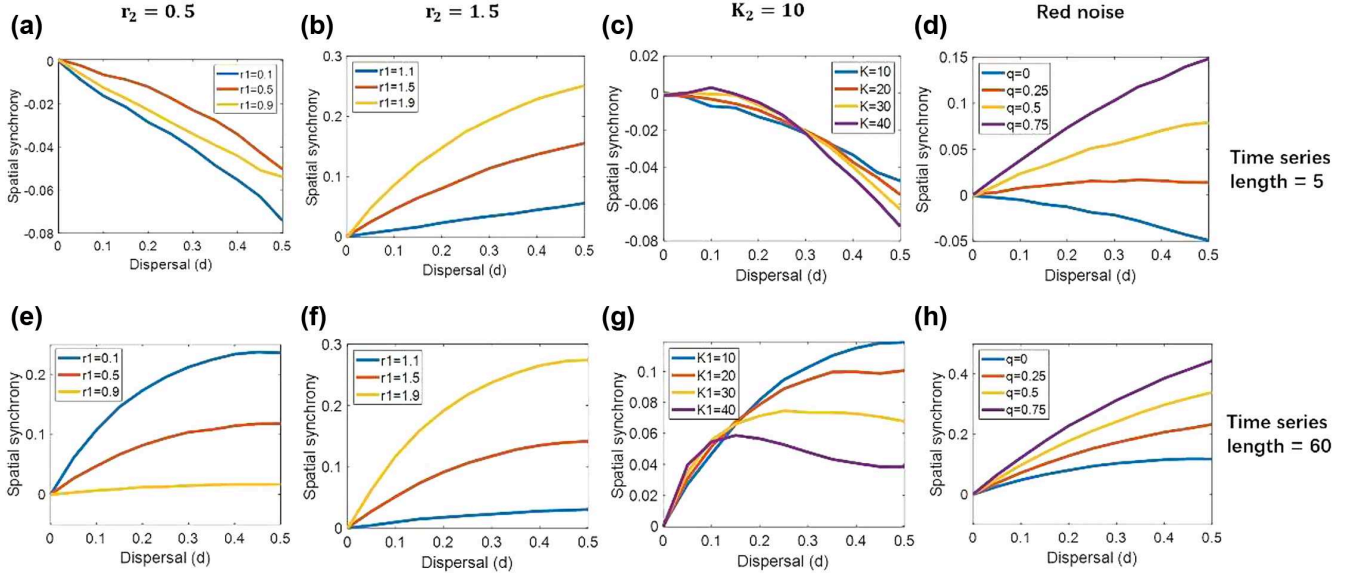
Figure 4. Effect of dispersal on spatial synchrony calculated from short (a–d), and long (e–h) time series under four scenarios: spatial heterogeneity in the intrinsic rate of under-compensatory grown (a, e), spatial heterogeneity in the intrinsic rate of over-compensatory grown (b, f), spatial heterogeneity in the carrying capacity (c, g) and temporally autocorrelated environmental noise (i.e. red noise; d, h). Parameters are set as follows when not specified: $\rho = 0$, $var(\epsilon) = 0.1$, $r = 0.5$, $K = 10$. The results represent the average across 500 000 (length = 5) or 50 000 (length = 60) simulated communities.

with white noises, we simulate population dynamics in heterogeneous landscapes or in temporally autocorrelated environments (Fig. 4). In heterogeneous landscapes where the two patches differ in their intrinsic growth rates ($r$) or carrying capacities ($K$), spatial synchrony at all timescales generally increase as dispersal increases in over-compensatory systems ($r > 1$); in under-compensatory systems ($r < 1$), spatial synchrony decreases as dispersal increases in short time series, and it increased as dispersal increases in long time series (Fig. 4). Such patterns also hold if the environmental fluctuations exhibited temporal autocorrelation. That said, if the environmental autocorrelation is very strong, spatial synchrony always increases with dispersal, regardless of the time series length (Fig. 4). Moreover, our simulations using 16-patch models exhibited similar time length dependency of spatial asynchrony–dispersal relationship as 2-patch ones (Supporting information). In all these heterogenous or autocorrelated scenarios, the overall population variability exhibits opposite patterns compared to those of overall synchrony (Supporting information). Overall, we find our results derived from two-patch homogeneous metapopulations with white noise are generally consistent in larger or heterogeneous metapopulations or with temporally autocorrelated environmental variability.

## Discussion

Our study demonstrates that dispersal has contrasting effects on spatial synchrony and population variability at short versus long timescales. We show that the well-documented locally stabilizing and spatially synchronizing effects of dispersal

operate only at particular timescales, and opposite effects can arise at other timescales. We present analytic predictions for two-patch homogeneous metapopulations, which are shown by simulations to hold in broader context with spatial heterogeneity and environmental autocorrelation. One implication of the timescale-dependent effects of dispersal is that the empirical relationship between dispersal and spatial synchrony or population variability can exhibit opposite patterns, simply because of different time series lengths. Our findings have important implications for experimental and observational studies that seek to understand the role of dispersal in structuring and sustaining metapopulations.

### Contrasting effects of dispersal at short versus long timescales

The effects of dispersal on population variability and synchrony have been widely explored in metapopulation models. Previous models showed that dispersal is a 'double-edged sword' for metapopulation stability by decreasing local population variability but also increasing spatial synchrony (Hudson and Cattadori 1999, Kendall et al. 2000, Abbott et al. 2011, Wang et al. 2015). While such local stabilizing and spatially synchronizing effects of dispersal are well understood, our model demonstrates that these two effects are timescale-dependent and, moreover, such timescale-dependency relies on the nature of population growth of the species of interest.

For populations exhibiting under-compensatory growth (i.e. slow recovery after being perturbed), the local stabilizing and spatially synchronizing effects of dispersal operate mainly at long timescales. At short timescales,
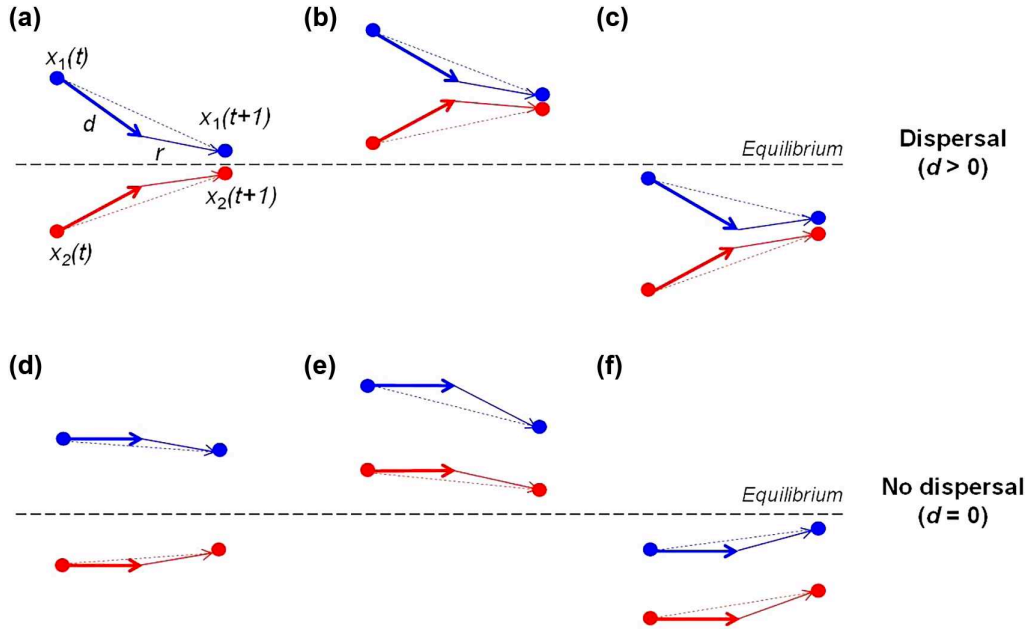
Figure 5. An illustration on the dispersal-induced negative synchrony at short timescales in under-compensatory systems: with (a–c) and without (d–f) dispersal. Each panel represents the dynamics of two populations (blue and red) during one time step. Three different scenarios of the initial states are shown in (a, d), (b, e) and (c, f). Starting from a different population size (i.e. $x_1(t)$ and $x_2(t)$), each population experiences first dispersal ($d$) and then local growth ($r$), indicated by the thick and thin arrows, respectively. The dashed lines indicate the overall changes during one time step. Strong dispersal reduces the difference between the two populations via a statistical averaging effect, and then the intrinsic growths moves the population size towards the equilibrium. Note that in a highly under-compensatory systems, the effects of intrinsic growth are moderate in one time step. Overall, the two populations always exhibit a negative correlation during one time step (between $t$ and $t+1$) in the presence of dispersal (a–c), and either positive (e–f) or negative (d) correlations in the absence of dispersal.

counterintuitively, dispersal destabilizes local populations and desynchronizes population dynamics across patches (Fig. 2a–c). Such counterintuitive effects can be understood from the interaction between environmental fluctuations and the statistical averaging effect of dispersal (Briggs and Hoopes 2004). For example, consider a starting point where the two patches have different population sizes due to environmental fluctuations (Fig. 5). During the next step, dispersal will decrease the population size in one patch and increase it in the other, followed by relatively moderate changes in population size driven by local under-compensatory population growth in both patches (Fig. 5a–c). Therefore, in the short term, dispersal causes different population sizes to converge toward intermediate values, which generates a negative correlation between populations and thus decreases spatial synchrony (Fig. 5a–c). But in the absence of dispersal, local population growth causes different population sizes to converge toward the equilibrium, where a negative temporal correlation between the two populations emerges only if the population size in one patch is larger, and that in the other patch is smaller than the equilibrium (Fig. 5d–f). In contrast, for populations exhibiting over-compensatory growth (i.e. dampening oscillatory recovery after being perturbed), the interaction between environmental fluctuations and the averaging effects of dispersal leads to opposite effects of dispersal across timescales:

dispersal has local stabilizing and spatially synchronizing effects at short timescales, and opposites effects at long timescales (Fig. 2d–f; see the Supporting information for illustration).

Although previous studies have revealed both under- and over-compensatory growth in natural populations, the former was found to be far more common than the latter (Fagan et al. 2010, Cortés 2016). In these under-compensatory populations, the contrasting effects of dispersal at short versus long timescales lead to an increasing trend of spatial synchrony with timescales, even if spatial environmental correlation is constant at all timescales (Fig. 2). Such an increasing trend of spatial synchrony with timescale is consistent with observations from recent empirical studies, which revealed a higher spatial synchrony at longer timescales in gypsy moth defoliation (Walter et al. 2017), zooplankton abundances (Anderson et al. 2019) and the productivity of terrestrial vegetation and marine phytoplankton (Defriez and Reuman 2017a, b, Sheppard et al. 2019). One explanation for the higher spatial synchrony at longer timescales was the stronger spatial environmental correlation at long timescales (Sheppard et al. 2016, 2019, Desharnais et al. 2018). Our theoretical results, however, provide an alternative explanation from endogenous processes via the interaction between dispersal and under-compensatory growth dynamics.

## Time series length matters in metapopulation studies

The contrasting effects of dispersal at short versus long timescales lead to a sample size dependency of the empirical relationship between dispersal and population variability or synchrony. For populations with under-compensatory growth, short time series would reveal a positive effect of dispersal on the overall population variability and a negative effect on overall spatial synchrony, which is the opposite of predictions derived from long time series or analytic solutions (Fig. 3; Abbott 2011, Wang et al. 2015). Such a contrast can be explained by the fact that short time series represented information mainly at short timescales, at which dispersal has opposite effects from long timescales (Fig. 5). In comparison, long time series cover information at both short and long timescales, which reflect the combined effect of dispersal across all timescales. Sample size dependency also applies to other factors that exhibit contrasting effects at short and long timescales – for instance population growth rate (Supporting information).

Such a sample size dependency has two implications for ecological research. First, to understand the effect of dispersal (and other factors), comparison between metapopulation experimental studies should be made among experiments with similar time series length and between species with similar types of growth (e.g. over- or under-compensatory). A growing number of metapopulation experiments has been conducted to test the effect of dispersal on spatial synchrony and population variability, which revealed a range of effect sizes and directions (Dey and Joshi 2006, Steiner et al. 2011, 2013, Thompson et al. 2015). Our results suggest that different time series length might complicate across-study comparison and account for the idiosyncratic conclusions in the literature. Smeti et al. (2016), for example, conducted an experiment of phytoplankton metapopulations that spanned 15–30 generations and found no significant effects of dispersal on spatial asynchrony. Our results suggested that the short experimental period may explain the reported insignificant effect of dispersal. Second, because the goal of understanding variability and synchrony is to eventually predict the long-term persistence of populations, we argue that sufficiently long time series should be used to reveal the long-term, or 'theoretically expected', relationship between dispersal and population dynamics. An important question remains: 'How long of a time series is necessary for experimental research to reveal the 'theoretically expected' relationship?

Determining a 'critical time series length' is particularly useful for metapopulation study design as well as cross-study comparisons. We suggest that a tentative time series length may be derived by conducting a simulation-based statistical power analysis. Specifically, based on prior knowledge on the dynamical parameters of the focal species (e.g. intrinsic growth rate), one can simulate metapopulation models with different experimental setting (e.g. gradients of dispersal, environmental noise, number of replicates, etc.) and numerically determine the minimum time series length for exhibiting a positive dispersal–spatial synchrony relationship with a given accuracy (Supporting information). Our preliminary analyses show that a longer time series or more replicates are required for metapopulations with under-compensatory dynamics ($r < 1$), a lower environmental correlation between patches and replicates ($\rho$) and a narrower gradient of dispersal rate, whereas the variance of environmental noise ($\sigma^2$) has only moderate influence (Supporting information). We encourage such kind of power analysis before starting a metapopulation study or conducting meta-analyses of spatial synchrony.

## Conclusion

The past decades of metapopulation research have made significant progress in understanding the role of dispersal in population variability and synchrony (Abbott et al. 2011). To date, however, studies have generally used overall measures of variability and synchrony that integrate information over a wide range of timescales, which potentially overlooked the timescale dependence of dispersal effects. Our study demonstrates that dispersal has contrasting effects on population variability and synchrony at short versus long timescales. A timescale-specific perspective not only extends our understanding of dispersal impacts on metapopulations, but also has important implications for how we interpret the results from empirical studies utilizing time series of different lengths. In particular, the length of time series itself is sufficient to generate contrasting conclusions about the relationship between dispersal and spatial synchrony. Future studies are needed to explore the implications of the timescale-dependent effects of dispersal for population extinction probability and to examine how time series length may affect the empirical relationship between dispersal and spatial synchrony in empirical data. Our study highlights the importance of accounting for the time series length when comparing results among studies of spatial synchrony. This is in line with recent calls to account for spatial scale when comparing results among studies of biodiversity and stability (Chase and Knight 2013, Wang et al. 2017). Our findings add to a growing body of work supporting the idea that long-term, continual data collection (e.g. the long-term ecological research; LTER) is needed to advance population ecology (Clutton-Brock and Sheldon 2010, Gaiser et al. 2020), because ecological cause-and-effect inferences can be qualitatively altered by time series length.

## Author contributions

**Mingyu Luo**: Conceptualization (lead); Formal analysis (lead); Methodology (lead); Writing – original draft (lead); Writing – review and editing (lead). **Daniel Reuman**: Conceptualization (equal); Methodology (equal); Writing – review and editing (equal). **Lauren M. Hallett**: Conceptualization (equal); Methodology (equal); Writing – review and editing (equal). **Lauren Shoemaker**: Conceptualization (equal); Methodology (equal); Writing – review and editing (equal). **Lei Zhao**: Conceptualization (equal); Writing – review and editing (equal). **Max C. N. Castorani**: Conceptualization (equal); Writing – review and editing (equal). **Joan C. Dudney**: Conceptualization (equal); Writing – review and editing (equal). **Laureano A. Gherardi**: Conceptualization (equal); Writing – review and editing (equal). **Andrew L. Rypel**: Conceptualization (equal); Writing – review and editing (equal). **Lawrence W. Sheppard**: Conceptualization (equal); Writing – review and editing (equal). **Jonathan A. Walter**: Conceptualization (equal); Writing – review and editing (equal). **Shaopeng Wang**: Conceptualization (lead); Methodology (lead); Supervision (lead); Writing – original draft (lead); Writing – review and editing (lead).

## Data availability statement

This paper is based on theoretical analyses and does not contain any data.

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