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Dispersal Increases Spatial Synchrony of Populations but Has Weak Effects on Population Variability: A Meta-analysis

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ABSTRACT: The effects of dispersal on spatial synchrony and population variability have been well documented in theoretical research, and a growing number of empirical tests have been performed. Yet a synthesis is still lacking. Here, we conducted a meta-analysis of relevant experiments and examined how dispersal affected spatial synchrony and temporal population variability across scales. Our analyses showed that dispersal generally promoted spatial synchrony, and such effects increased with dispersal rate and decreased with environmental correlation among patches. The synchronizing effect of dispersal, however, was detected only when spatial synchrony was measured using the correlation-based index, not when the covariance-based index was used. In contrast to theoretical predictions, the effect of dispersal on local population variability was generally nonsignificant, except when environmental correlation among patches was negative and/or the experimental period was long. At the regional scale, while low dispersal stabilized metapopulation dynamics, high dispersal led to destabilization. Overall, the sign and strength of dispersal effects on spatial synchrony and population variability were modulated by taxa, environmental heterogeneity, type of perturbations, patch number, and experimental length. Our synthesis demonstrates that dispersal can affect the dynamics of spatially distributed populations, but its effects are context dependent on abiotic and biotic factors.

Keywords: dispersal, spatial synchrony, stability, meta-analysis.

Introduction

One of the most fundamental results in spatial ecology is that spatially distributed populations can have dramatically different dynamics when they are linked by dispersal than when they are isolated (Abbott 2011). In a spatial context, two dynamical characteristics are particularly relevant to the persistence of populations: temporal variability (e.g., the ratio of standard deviation to mean population size over time) and spatial synchrony (i.e., coherence in population temporal dynamics among local patches). Simple metapopulation models predicted that dispersal could decrease the temporal variability of local populations while increasing their spatial synchrony (Kendall et al. 2000; Wang et al. 2015). Such locally stabilizing and spatially synchronizing effects of dispersal are intuitive to understand and thus well accepted (Abbott 2011), but more complex models revealed that the effects of dispersal could depend on various biotic and abiotic factors, such as the rate and mode of dispersal, temporal and spatial environmental autocorrelation, and species interactions (Taylor 1998; Ylikarjula et al. 2000; Fox et al. 2017; Stark et al. 2021).

Metapopulation models predict that dispersal tends to synchronize spatially distinct populations via exchanges of individuals among habitat patches (Ranta et al. 1998; Lande et al. 1999; Liebhold et al. 2004). While the synchronizing effect of dispersal has been demonstrated to be robust across a broad range of scenarios, its magnitude, and occasionally direction, are context dependent (Bjørnstad et al. 1999; Paradis et al. 1999; Fontaine and Gonzalez 2005). Early studies, which used different metapopulation models to understand the interplay between dispersal and spatial environmental correlation, showed additive (Ripa 2000), subadditive (Kendall et al. 2000), or neutral (Palmqvist and Lundberg 1998) influences on spatial synchrony. Moreover, density dependency, symmetry, and other properties of dispersal have also been suggested to affect the outcome of dispersal-induced synchrony (Münkemüller and Johst 2008; Dey et al. 2014). In particular, when dispersal is highly asymmetric between patches, dispersal can contribute to decreasing spatial synchrony even in single-species metapopulations (Wang et al. 2015). Furthermore,

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in metacommunities consisting of multiple species, the effect of dispersal can be complicated by its interplay with local species interactions, making it difficult to draw conclusions about dispersal effects on spatial synchrony (Hauzy et al. 2010; Townsend and Gouhier 2019).

The effect of dispersal on population temporal variability is also context dependent (Briggs and Hoopes 2004; Zelnik et al. 2019). Briggs and Hoopes (2004) summarized three possible stabilizing mechanisms of dispersal: statistical stabilization by summing over asynchronous fluctuations, decoupling immigration from local density in systems with asynchronous fluctuations and weakly coupled dynamics, and nonlinear spatial averaging associated with static self-organized spatial patterning. These mechanisms regulate spatial population dynamics and have the potential to influence local and metapopulation variability differentially. At the local scale, dispersal could decrease population variability via recolonization of declining patches and/or replacement of less adapted individuals (Abbott 2011; Gokhale et al. 2018). While such local stabilizing effects of dispersal had been documented in metapopulation models, metacommunity models revealed that the interplay between dispersal and local species interactions could lead to positive or nonlinear dispersal–local variability relationships (Gouhier et al. 2010; Gramlich et al. 2016). At the regional scale, a nonlinear relationship between dispersal rate and variability has often been reported (Earn 2000; Dey and Joshi 2006; Yaari et al. 2012). That is, while low to intermediate dispersal tends to decrease regional population variability, high dispersal tends to increase regional variability. Such nonlinear relationships have been reported for both metapopulations (Palmqvist and Lundberg 1998; Stark et al. 2021) and metacommunities (Loreau et al. 2003; Shanafelt et al. 2015).

Because regional population variability is determined by both local population variability and spatial synchrony (Wang and Loreau 2014), one can expect an intrinsic link between dispersal effects on spatial synchrony and population variability at local and regional scales. Indeed, theoretical models have clarified that the dispersal effect on regional variability depends on how the local stabilizing effect of dispersal balances its spatially synchronizing effect (Abbott 2011; Wang et al. 2015). Such a perspective has been widely adopted in recent metapopulation studies, where the effects of dispersal on spatial synchrony as well as local and regional variability are often explored collectively (Gupta et al. 2017; Laan and Fox 2020; Luo et al. 2021).

Despite the large body of theoretical research, empirical tests on the effect of dispersal on metapopulation dynamics remain limited. One difficulty is to implement the desired levels of dispersal and maintain them for multiple generations, especially in in situ experiments and/or for populations with active dispersal (Grainger and Gilbert 2016; Fox et al. 2017). That said, experimental efforts have been accumulating since the 1990s, using mainly microcosm experiments with fast population turnover and passive dispersal (e.g., protists; Altermatt et al. 2015). In this study, we synthesize findings from these experiments and perform quantitative meta-analyses to examine dispersal effects on spatial synchrony and population variability at different spatial scales. We also examine how the effects of dispersal are modulated by different biotic and abiotic factors, including dispersal rate, taxa and species diversity of the experimental organisms, environmental heterogeneity, and type of perturbations. We also explore the possible influences of three methodological characteristics, namely, the number of patches, experimental length, and the definition of spatial synchrony. We end with a discussion about our results in light of theoretical insights and their implications for future studies.

Methods

Literature Search

Our literature search was based on two approaches. First, we searched the ISI Web of Science database for publications that investigated the impact of dispersal on spatial synchrony and/or temporal variability, with March 2021 as the cutoff date. We utilized the combination of three different strings (table S1) because the amount of relevant theoretical research was much larger than that of empirical research. Second, we searched the ISI Web of Science and the Dryad Data Repository to compile raw time-series data from studies that manipulated dispersal but did not calculate its effects on synchrony or variability (table S1).

Altogether, we obtained 1,204 and 2,130 articles for synchrony and variability, respectively, and 76 data sets from Dryad. Studies were included if they met the following criteria. First, the study reported results from manipulative experiments with at least three replicates in both control (without dispersal) and treatment (with dispersal) groups. Second, dispersal was manipulated directly and performed within the same metapopulation or metacommunity. We excluded experiments that inferred dispersal indirectly (e.g., according to dispersal-related species traits) or used external species pool as the source of immigrants. Third, we also excluded experiments comparing variability in fragments to that in continuous habitat, where dispersal effects may be confounded with area change. Fourth, for studies that reported raw data but did not measure synchrony or variability, we included those with sufficient information for deriving these metrics (e.g., time-series abundance/biomass/density data of each replicate and each patch to measure synchrony and local variability).

Our final data set consisted of 24 studies in total, including 19 studies (7 data sets) for dispersal-synchrony analysis, 17 studies (8 data sets) for dispersal-local variability analysis, and 15 studies (8 data sets) for dispersal-regional variability analysis. For studies that reported synchrony and/or variability measures, we extracted their values from text, tables, or figures using WebPlotDigitizer (Rohatgi 2021). For those with original time-series data, we quantified synchrony and variability using commonly adopted indices (see below).

Quantification of Spatial Synchrony and Population Variability

Most studies included in our analyses measured spatial synchrony by the mean correlation coefficient of population growth rates across patches ($\bar{\rho}_{\mathrm{r}}$, with the subscript "r" representing growth rates), while the correlation coefficient of population sizes ($\bar{\rho}_{\mathrm{x}}$, with the subscript "x" representing population sizes) was also used in a few studies (table 1). Recent theory also proposed a new covariance-based index of spatial synchrony (φ; table 1), which provides a scaling factor from local variability to regional variability and is thus more relevant to variability analysis (Wang et al. 2019). Although this covariance-based index was not used in any experiment in our data set, we calculated the different indices of spatial synchrony ($\bar{\rho}_{\mathrm{r}}$, $\bar{\rho}_{\mathrm{x}}$, and φ) using the raw data we collected and explored whether dispersal effects differ between different indices (for details, see "Statistical Analysis").

Population variability was mostly measured using the coefficient of temporal variation (CV), that is, the ratio of standard deviation to the mean of population sizes (or population density or biomass). Local variability was represented by the average of CVs across patches ($\mathrm{CV_L}$, with the subscript "L" representing the local scale), and regional variability was represented by CV of total metapopulation/metacommunity size ($\mathrm{CV_R}$, with the subscript "R" representing the regional scale; table 1). In

Table 1: Definitions of spatial synchrony and population variability indices

Symbol	Description
$x_{i,t}$	Abundance/biomass/density of patch i at time t
$r_{i,t} = \log x_{i,t+1} - \log x_{i,t}$	Population growth rate in patch i between t and $t+1$, measured by the difference in log-transformed abundance/biomass/density
μ_i	Temporal mean abundance/biomass/density of patch i
v_{ij}	Temporal covariance between abundances/biomasses/densities of patch i and j
$\mu_\Sigma = \sum_i \mu_i$	Temporal mean abundance/biomass/density of the whole metapopulation/metacommunity
$v_\Sigma = \sum_{ij} v_{ij}$	Temporal variance of the whole metapopulation/metacommunity
	Variability index
$\mathrm{CV}_i = \frac{\sqrt{v_{ii}}}{\mu_i}$	Temporal variability of patch i, measured by the coefficient of temporal variation
$\mathrm{CV_L} = \frac{\sum_{i=1}^{N} \mathrm{CV}_i}{N}$	Local variability measured by the mean variability (CV_i) across patches
$\mathrm{CV_R} = \frac{\sqrt{v_\Sigma}}{\mu_\Sigma}$	Regional variability measured by the coefficient of temporal variation of metapopulation/metacommunity biomass
	Synchrony index
$\bar{\rho}_{\mathrm{r}} = \frac{2}{N(N-1)} \sum_{i=1}^{N} \sum_{j=i+1}^{N} \rho_{(\mathrm{r}_i, \mathrm{r}_j)}$	Spatial synchrony measured by the mean correlation coefficient of growth rates ($r_{i,t}$) across all patch pairs
$\bar{\rho}_{\mathrm{x}} = \frac{2}{N(N-1)} \sum_{i=1}^{N} \sum_{j=i+1}^{N} \rho_{(\mathrm{x}_i, \mathrm{x}_j)}$	Spatial synchrony measured by the mean correlation coefficient of abundance/biomass/density ($x_{i,t}$) across all patch pairs
$\varphi = \frac{\sqrt{v_\Sigma}}{\sum_{i=1}^{N} \sqrt{v_i}}$	Spatial synchrony measured by a covariance-based index, which follows the definition in Wang et al. (2019)

addition, a few studies also used temporal standard deviation or variance to represent variability.

Effect Size of Dispersal

Within each study, we regarded experimental units with no (or lower) dispersal as the control group (C) and those with (higher) dispersal as the treatment group (T). For experiments with multiple levels of treatment (e.g., different dispersal rates) and/or combinations of different factors (e.g., dispersal × temperature), we calculated the effect size of dispersal for each treatment level or combination. Because in our data set spatial synchrony was mostly calculated by correlation coefficients that are bounded within $(-1, 1)$, we quantified the effect size of dispersal on spatial synchrony by its raw mean difference between treatment ($\bar{Y}_{\mathrm{T}}$) and control ($\bar{Y}_{\mathrm{C}}$) groups:

$$D = \bar{Y}_{\mathrm{T}} - \bar{Y}_{\mathrm{C}}, \tag{1}$$

where a positive value of D indicates a positive effect of dispersal on spatial synchrony and vice versa. The variance of D was calculated as (Cooper et al. 2009)

$$v_D = \frac{S_{\mathrm{C}}^2}{N_{\mathrm{C}}} + \frac{S_{\mathrm{T}}^2}{N_{\mathrm{T}}}, \tag{2}$$

where S_{C}^2, N_{C}, S_{T}^2, and N_{T} represent the sample variance (S_{C}^2 and S_{T}^2) and sample size (N_{C} and N_{T}) for control and treatment groups, respectively.

To quantify the effect size of dispersal on population variability, we used the log response ratio (LRR) to facilitate comparisons among studies using different measures of variability (e.g., CV and variance):

$$\mathrm{LRR} = \ln \bar{Y}_{\mathrm{T}} - \ln \bar{Y}_{\mathrm{C}}. \tag{3}$$

A positive value represents a positive effect of dispersal on variability (i.e., a destabilizing effect) and vice versa. The variance of LRR was calculated as (Lajeunesse 2011)

$$v_{\mathrm{LRR}} = \frac{S_{\mathrm{C}}^2}{N_{\mathrm{C}}\bar{Y}_{\mathrm{C}}^2} + \frac{S_{\mathrm{T}}^2}{N_{\mathrm{T}}\bar{Y}_{\mathrm{T}}^2}. \tag{4}$$

Biotic and Abiotic Moderators

To understand how abiotic and biotic moderators might influence the effect size of dispersal, we examined a number of moderators that were highlighted by theoretical studies and/or previous syntheses (table S2). Specifically, we recorded the following information when available.

1. *Dispersal rate*. Dispersal rate represents the mean proportion of medium/culture/individuals transferred between patches during experimental dispersal events.

2. *Taxa*. Five levels were defined according to the habitat and taxonomy of the species contributing to the majority of community biomass: terrestrial animals, aquatic animals, bacteria (only aquatic), plants (only aquatic), and protists (only aquatic).

3. *Diversity*. Three levels were defined according to whether the synchrony/variability metrics captured the dynamics of single species, multiple species from the same trophic level (single trophic), or multiple species from different trophic levels (multitrophic). Note that species that were introduced into the experimental system as food resources were not considered.

4. *Environmental heterogeneity*. Five levels were defined according to the spatiotemporal heterogeneity of the abiotic and biotic environment. For experiments with temporally constant environmental conditions, we classified them into spatially homogeneous (HOM) and spatially heterogeneous (SPA) systems. For those with temporally varying environmental conditions, we classified them on the basis of the between-patch correlation in the temporal pulses: negatively correlated (TEM_-), positively correlated (TEM_+), and uncorrelated (TEM_0).

5. *Perturbations*. Three levels were defined following the original publication: no perturbation, abiotic perturbation (e.g., chemical stressor), and biotic perturbation (e.g., introduction of parasite).

6. *Number of patches*. Because more than half of experimental metapopulations or metacommunities in our data set included two patches, we defined two discrete levels: two patches and more than two patches.

7. *Experimental length*. Two levels were defined according to the number of generations for the dominant taxa: short (2.5–45 generations) and long (120–1,000 generations). We have converted the original number of generations into two levels because their distribution is highly uneven. Detailed classification and descriptions for these variables are given in table S2.

Statistical Analysis

Separate meta-analyses were conducted to test the effects of dispersal on spatial synchrony, local variability, and regional variability. As multiple effect sizes were obtained from the same study, we adopted two approaches to account for different sources of nonindependence between effect sizes in subsequent analyses. The first source of nonindependence was attributed to the common control group to calculate multiple effect sizes. To account for such nonindependence, we constructed the sampling variance-covariance matrix (Cheung 2015), where the variance elements remained the same as in equations (2) and (4) but the covariance elements (off-diagonals) due to the shared control were calculated as $S_{\mathrm{C}}^2/N_{\mathrm{C}}$ for D (Cooper et al. 2009) and $S_C^2/N_C\bar{Y}_C^2$ for LRR (Lajeunesse 2011). The second source of nonindependence was due to the nested structure of observed effect sizes (e.g., multiple factorial experiment design), which could be accommodated by including publication as a random effect (Nakagawa and Santos 2012). All analyses were performed using the rma.mv function from the metafor package (Viechtbauer 2010) in R (ver. 4.1.0; R Core Team 2021).

We first estimated the overall mean effect size of dispersal across all studies using a random effects model (Cooper et al. 2009). To assess the heterogeneity in effect sizes across studies, the Q statistic was computed and tested against a χ^2 distribution (with $n-1$ df, where n is the sample size; Koricheva et al. 2013). Because the Q statistic is sensitive to the sample size, we also reported the I^2 statistic, that is, the percentage of total variation that is attributed to between-study heterogeneity, which takes a value within 0%–100% (Higgins and Thompson 2002). We assessed publication bias by checking funnel plot asymmetry visually and by conducting the modified Egger's regression test for nonindependent effect size estimates (Nakagawa and Santos 2012). We found no evidence of publication bias by both the funnel plot and Egger's test ($P > .1$ for spatial synchrony and local and regional variability; fig. S2).

To test the influence of moderators on dispersal effects, we first conducted a mixed effects metaregression to examine the relationship between dispersal rate and effect size. We compared linear and quadratic models for local and regional variability to account for potential nonlinearity, using Akaike's information criterion corrected for small sample sizes (AICc). We then examined the categorical moderators (see table 1) using mixed effects models. Each categorical moderator was included as a fixed effect, and the between-group heterogeneity was estimated by Q_M. A large Q_M indicates significant differences across different levels of the moderator (Borenstein 2009). The differences were then determined by Tukey's all-pair comparisons using the multcomp package in R, and adjusted P values from multiple comparisons were reported (Hothorn et al. 2008). To account for potential confounding effects among different moderators, we also conducted a full model analysis including all moderators (Viechtbauer 2007). Note that experimental length was excluded from this full model because information on this variable was available for only half of all studies. The most supported model was selected on the basis of AICc, using the glmulti package in R (Calcagno and Mazancourt 2010). As the glmulti function performs model section using the maximum likelihood method, we refitted selected models by the restricted maximum likelihood method to estimate the coefficients. Then we assigned each moderator in the best models an importance value, which equaled the sum of weights (based on AICc) across models in which the moderator was included (Crawford et al. 2019). An importance value greater than 0.8 indicates that the moderator significantly contributes to explaining the variation in effect sizes, and marginal R^2 was calculated to quantify the proportion of variation explained by fixed effects (Nakagawa and Schielzeth 2013).

Last, to examine the sensitivity of our results to the definition of spatial synchrony, we recalculated three synchrony indices using the raw data we collected, namely, the mean correlation coefficient of population growth rates ($\bar{\rho}_r$), the mean correlation coefficient of population sizes ($\bar{\rho}_x$), and the covariance-based index (φ; see table 1). We calculated the effect size of dispersal by the raw mean difference for these indices ($D_{\bar{\rho}_r}$, $D_{\bar{\rho}_x}$, and D_φ). Because the covariance-based index (φ) takes positive values (with a range of 0~1), we also quantified the effect size of dispersal on φ using the log response ratio (LRR_φ) to test the potential influence of different effect size measures (i.e., D vs. LRR). Then, based on the four effect sizes calculated as described above, we conducted a mixed effects model analysis with the type of effect size (defined as a categorical variable of four levels: $D_{\bar{\rho}_r}$, $D_{\bar{\rho}_x}$, D_φ, and LRR_φ) as the fixed effect and study as the random effect. We estimated the mean of each effect size and compared them using Tukey's all-pair comparisons.

Results

Dispersal-Synchrony Relationships

Our analysis revealed an overall positive effect of dispersal on spatial synchrony, with mean effect size $D = 0.22$ (95% confidence interval [CI] $= 0.080$ to 0.359, $P = .002$; fig. 1*A*). These effect sizes exhibited high variation ($Q = 1{,}266$, $P < .0001$; $I^2 = 91.7\%$), ranging from -0.696 to 1.442. The effect of dispersal on synchrony increased as the dispersal rate increased ($Q_M = 109$, $P < .0001$; fig. 2*A*). Dispersal increased spatial synchrony of animal species in terrestrial ecosystems ($D = 0.430$, 95% CI $= 0.068$ to 0.792, $P = .020$), but it had no effect on animal species in aquatic ecosystems ($D = 0.150$, 95% CI $= -0.205$ to 0.505, $P = .409$) or bacterial species ($D = 0.146$, 95% CI $= -0.219$ to 0.510, $P = .433$). Also, dispersal increased spatial synchrony in single-trophic systems ($D = 0.297$, 95% CI $= 0.106$ to 0.487, $P = .002$) and experimental systems consisting of two patches ($D = 0.291$, 95% CI $= 0.110$ to 0.472, $P = .002$) but had no effect in experimental systems with multiple trophic levels ($D = -0.007$, 95% CI $= -0.359$ to 0.344, $P = .967$) or more than two patches ($D = 0.122$, 95% CI $= -0.089$ to 0.333, $P = .257$). Moreover, dispersal effects exhibited significant between-group heterogeneity among different

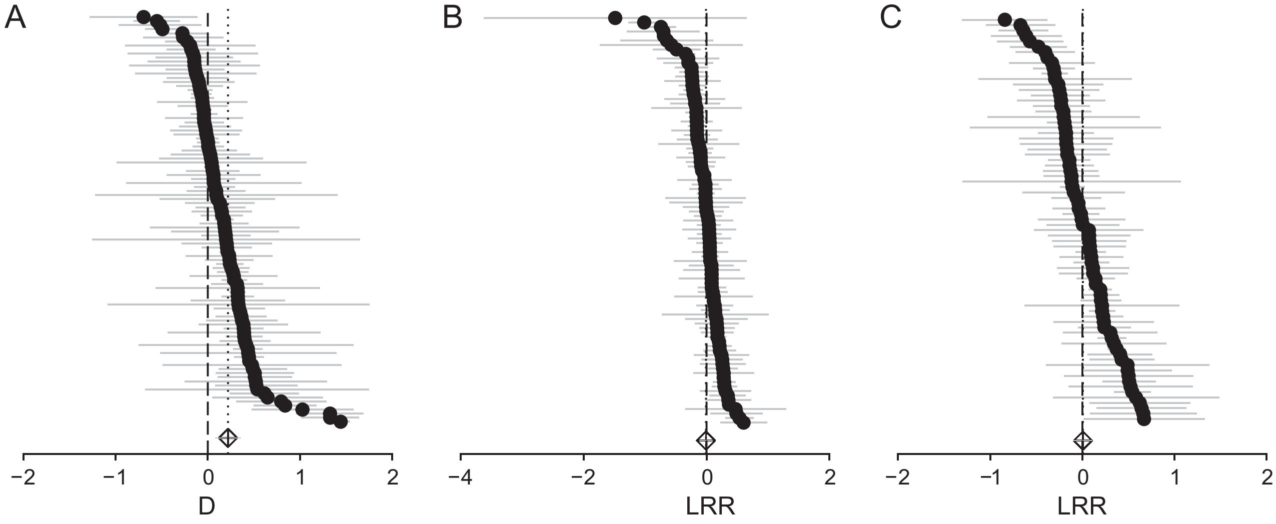

Figure 1: Effect sizes of dispersal on spatial synchrony (*A*; $n = 101$), local variability (*B*; $n = 91$), and regional variability (*C*; $n = 75$). Each black circle represents an individual effect size for one level of treatment, and the gray line represents the corresponding 95% confidence intervals. The black circles are ranked from the smallest (*top*) to the largest (*bottom*) effect sizes. Diamonds represent the overall weighted mean effect sizes, estimated from random effects models. LRR = log response ratio.

categories of environmental heterogeneity ($Q_M = 164$, $P < .0001$) and perturbations ($Q_M = 25$, $P < .0001$; table S3). Specifically, in temporally constant environments, dispersal had positive effects on spatial synchrony in both spatially homogeneous and heterogeneous systems ($D_{HOM} = 0.386$, 95% CI = 0.207 to 0.565, $P < .0001$; $D_{SPA} = 0.366$, 95% CI = 0.190 to 0.543, $P < .0001$), and the effect sizes were not different from each other (Tukey's comparison: $z = 0.728$, $P = .940$; fig. 3). In temporally fluctuating environments, dispersal had strong synchronizing effects in asynchronous environments ($D_{TEM-} = 1.034$, 95% CI = 0.812 to 1.256, $P < .0001$) but no effect when environmental factors (e.g., PH, temperature) fluctuated synchronously or independently ($D_{TEM+} = 0.039$, 95% CI = −0.145 to 0.224, $P = .676$; $D_{TEM_0} = -0.036$, 95% CI = −0.212 to 0.141, $P = .692$). Compared with systems without perturbations, the effect of dispersal on synchrony was significantly greater in the presence of biotic perturbations ($z = 4.985$, $P < .0001$). Last, the synchronizing effect of dispersal was significant in long experiments

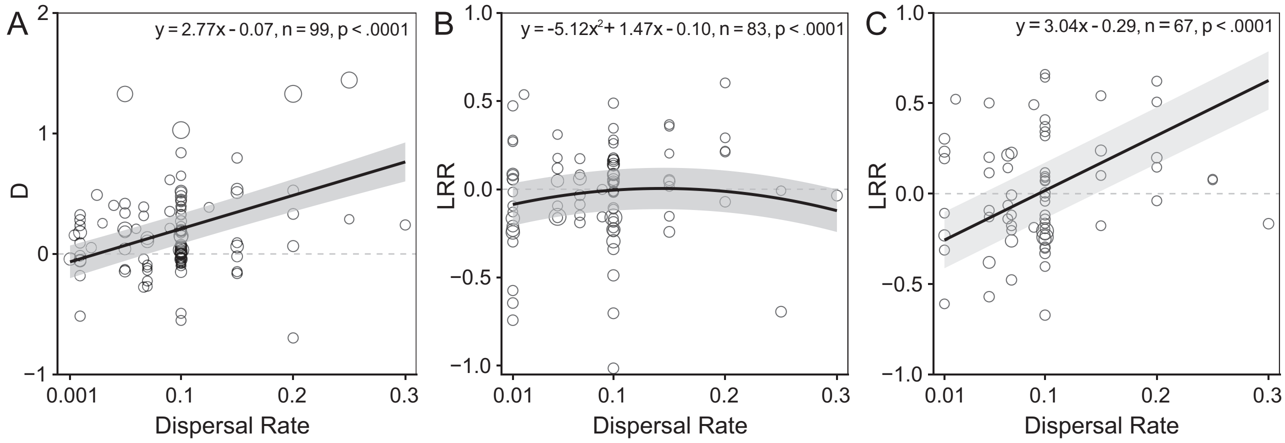

Figure 2: Relationships between dispersal rate and the effect size of dispersal on spatial synchrony (*A*), local availability (*B*), and regional variability (*C*). Each circle represents an individual effect size, scaled by its weight in the metaregression model. Black lines or curves show fitted results from mixed effects metaregression models, and shading indicates 95% confidence intervals. Note that studies that did not report dispersal rate were excluded.

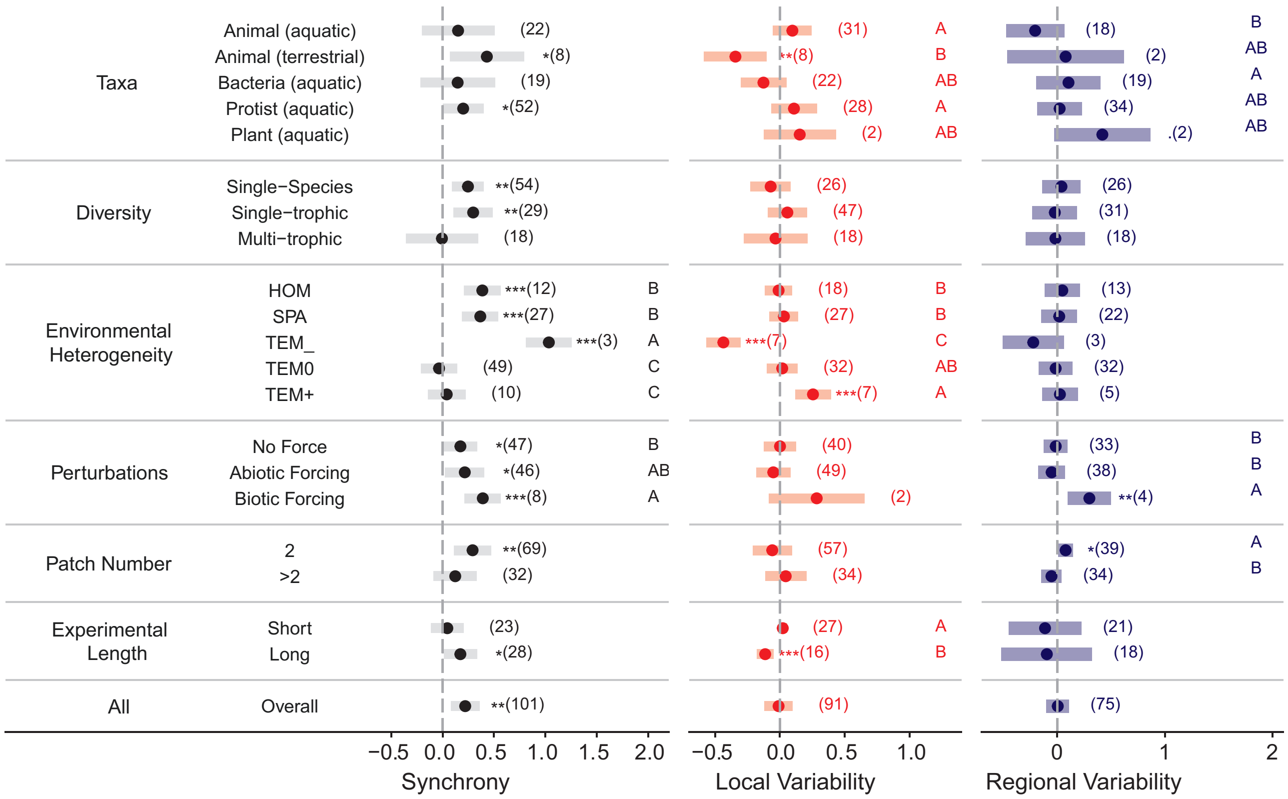

Figure 3: Mean (circles) and 95% confidence intervals (shading) of the effect size of dispersal for each level of categorical moderators, estimated from separate mixed effects models for spatial synchrony, local variability, and regional variability. Numbers in parenthesis denote the sample sizes for corresponding levels. Letters indicate significant differences among different levels of the moderator (Tukey's all-pair comparisons, $P < .05$). Significance levels indicate difference from zero: $^{***}P < .001$, $^{**}P < .01$, $^{*}P < .05$, $^{\cdot}P < .1$.

($D = 0.172$, 95% CI $= 0.011$ to 0.333, $P = .036$) but not in short ones ($D = 0.045$, 95% CI $= -0.114$ to 0.204, $P = .580$).

Results from the full model that included all abiotic and biotic moderators were generally consistent with univariate mixed effects models except that the effect of dispersal on synchrony for animal species (in both terrestrial and aquatic systems) was significantly lower than that for protists after accounting for all other moderators ($P < .05$; table S4). Dispersal rate, environmental heterogeneity, and perturbations were the most important determinants of dispersal effects in the optimal metaregression model based on AICc, which together explained 30.8% of the total variance ($Q_M = 305$, $P < .0001$; table S5).

With raw data from eight studies, we compared the four measures of dispersal effects on spatial synchrony using different definitions of synchrony or effect size (i.e., $D_{\bar{\rho}_r}$, $D_{\bar{\rho}_x}$, D_{φ}, and LRR_{φ}). Results from the mixed effects model revealed a significant difference among these four indices ($Q_M = 105$, $P < .0001$; fig. 4). While dispersal had positive effects on the two correlation-based measures of synchrony ($D_{\bar{\rho}_r} = 0.085$, 95% CI $= 0.004$ to 0.166, $P = .041$; $D_{\bar{\rho}_x} = 0.243$, 95% CI $= 0.161$ to 0.325, $P < .0001$), it had no effect on covariance-based measures ($D_{\varphi} = 0.024$, 95% CI $= -0.050$ to 0.098, $P = .524$; $\mathrm{LRR}_{\varphi} = 0.024$, 95% CI $= -0.050$ to 0.099, $P = .526$). Moreover, dispersal had stronger effects on the correlation of population size than that of population growth rate ($z = 5.819$, $P < .001$; fig. 4).

Dispersal-Variability Relationships

At the local scale, the average effect size of dispersal on population variability was not different from zero (LRR $= -0.01$, 95% CI $= -0.118$ to 0.099, $P = .864$; fig. 1*B*), due to high variation among individual effect sizes ($Q = 937$, $P < .0001$; $I^2 = 89.9\%$). Both linear and quadratic models revealed a significant relationship between dispersal rate and effect size (linear model: $Q_M = 11$, $P = .0001$; quadratic model: $Q_M = 43$, $P < .0001$). Although AICc indicated that the quadratic model better fitted the data, both models explained low fractions of the total variance (linear

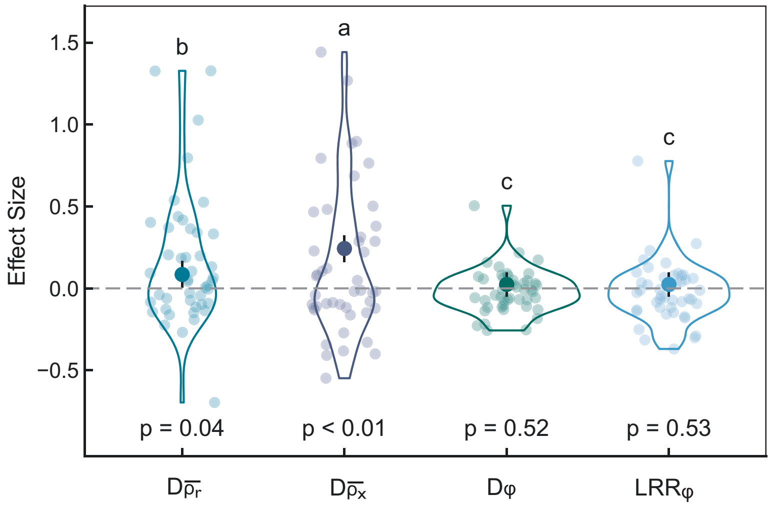

Figure 4: Mean effect size estimates (circles) with 95% confidence intervals (black bars) for different measures of spatial synchrony and effect size (table 1): $D_{\bar{\rho}_r}$, raw mean difference in correlation coefficient of population growth rates; $D_{\bar{\rho}_x}$, raw mean difference in correlation coefficient of population sizes; D_{φ}, raw mean difference in the covariance-based synchrony index; and LRR$_{\varphi}$, log response ratio for the covariance-based synchrony index. Light circles represent the distribution of individual effect sizes ($n = 45$ for each measure). Different letters on top indicate significant difference between different measures (Tukey's all-pair comparisons, $P < .05$).

model: $R^2 = 0.270\%$, AICc = 452.275; quadratic model: $R^2 = 0.971\%$, AICc = 427.145; fig. 2*B*). Analyses of between-group heterogeneity revealed significant differences in dispersal effects among different system taxa ($Q_{\mathrm{M}} = 14$, $P = .007$), environmental heterogeneity ($Q_{\mathrm{M}} = 234$, $P < .0001$), and experiment length ($Q_{\mathrm{M}} = 14$, $P = .0002$). Specifically, dispersal decreased local population variability of animal species in terrestrial ecosystems (LRR = −0.342, 95% CI = −0.585 to −0.100, $P = .006$) but had no significant effect on other taxa. In temporally fluctuating environments, dispersal decreased local population variability when habitat patches exhibited negative temporal correlations ($\mathrm{LRR}_{\mathrm{TEM}-} = -0.435$, 95% CI = −0.568 to −0.303, $P < .0001$) but increased it under positive correlations ($\mathrm{LRR}_{\mathrm{TEM}+} = 0.256$, 95% CI = 0.118 to 0.394, $P = .0003$). In temporally constant environments, however, dispersal had no effect on local variability regardless of spatial heterogeneity ($z = -0.672$, $P = .959$; fig. 3). Also, dispersal was found to decrease local population variability in long experiments, but it had no effect in short ones ($\mathrm{LRR}_{\mathrm{Short}} = 0.023$, 95% CI = −0.009 to 0.054, $P = .159$; $\mathrm{LRR}_{\mathrm{Long}} = -0.113$, 95% CI = −0.178 to −0.048, $P = .001$; $z = -3.678$, $P = .0002$). Moreover, the effect size of dispersal did not vary with diversity ($Q_{\mathrm{M}} = 2$, $P = .418$), type of perturbations ($Q_{\mathrm{M}} = 3$, $P = .176$), or patch number ($Q_{\mathrm{M}} = 1$, $P = .354$; table S3). Our multivariate analyses revealed that the best model with the lowest AICc included dispersal rate (quadratic), environmental variability, and taxa as explanatory variables, which together explained 27% of the total variance in dispersal effects on local variability ($Q_{\mathrm{M}} = 285$, $P < .0001$; table S5).

Likewise, dispersal had no overall effect on population variability at the regional scale (LRR = 0.005, 95% CI = −0.099 to 0.110, $P = .921$; fig. 1*C*), with large variation across studies ($Q = 1{,}086$, $P < .0001$; $I^2 = 80.3\%$). Meta-regression models revealed a linear positive relationship between dispersal rate and effect size ($P < .0001$, AICc = 293.796), whereas the quadratic term was nonsignificant ($P = .098$, AICc = 295.808). These models also showed contrasting dispersal–regional variability relationships under weak and strong dispersal, with the negative effect sizes at low dispersal rates (e.g., 0.01) indicating stabilizing effects and the positive effect sizes at high dispersal rates (e.g., 0.2) indicating destabilizing effects (fig. 2*C*). Between-group heterogeneity analyses revealed significant effects only for the number of patches ($Q_{\mathrm{M}} = 5$, $P = .028$) and perturbations ($Q_{\mathrm{M}} = 11$, $P = .004$). That is, experimental systems consisting of two patches exhibited a significant positive effect of dispersal on regional variability, but its effect was weaker and nonsignificant in experiments with more than two patches ($z = 2.197$, $P = .028$; fig. 3). Also, we found that dispersal increased regional variability in systems with biotic perturbations (LRR = 0.299, 95% CI = 0.097 to 0.500, $P = .004$). Our multivariate analyses generally supported the above univariate models except that dispersal significantly decreased regional variability in asynchronous environments when all moderators were included

($P = .043$; table S4). The best model with the lowest AICc highlighted the influences of dispersal rate, perturbations, and number of patches as well as taxa and environmental heterogeneity ($Q_M = 633, P < .0001, R^2 = 29.3\%$; table S5).

Discussion

Our meta-analysis of metapopulation/metacommunity experiments showed that dispersal generally promoted spatial synchrony, but its effects on population variability were weak and often idiosyncratic. The sign and strength of dispersal effects were modulated by ecological factors such as dispersal rate, taxa, environmental heterogeneity, type of perturbations, patch number, and experimental length. The overall weak effect sizes of dispersal (even on spatial synchrony), as well as their context dependency, are in line with the positive and negative effects of dispersal predicted by various metapopulation models (e.g., Earn 2000; Kendall et al. 2000; Abbott 2011; Wang et al. 2015). For spatial synchrony, we also found that the effect of dispersal differed among different definitions of synchrony.

In accordance with predictions from many theoretical models (Abbott 2011), our results showed that dispersal had overall positive effects on spatial synchrony, and such effects increased with increasing dispersal rate. The synchronizing effects of dispersal were found to be strongest when temporal environmental fluctuations were negatively correlated across patches and weak under uncorrelated or positively correlated fluctuations. This result is consistent with model predictions by Kendall et al. (2000), which revealed a negative interaction between dispersal and the temporal correlation in environment fluctuations across patches, suggesting a stronger effect of dispersal in less synchronous environments. The weak synchronizing effects of dispersal in spatially uncorrelated environments might be explained by some unconsidered attributes of environmental fluctuation, such as its intensity and autocorrelation (Palmqvist and Lundberg 1998; Gouhier et al. 2010; Desharnais et al. 2018). Besides, we found that dispersal had larger synchronizing effects in the presence of biotic forcing, such as predators and parasites. One explanation is that the interplay between trophic interaction and dispersal can generate parallel mortality and/or phase-lock predator-prey cycles, which strongly promotes spatial synchrony (Bjørnstad et al. 1999; Vogwill et al. 2009; Tadiri et al. 2018).

Contrary to the widely accepted locally stabilizing effects of dispersal, we found no overall effect of dispersal on local population variability (fig. 1*B*). Although there existed a significant quadratic relationship between dispersal rate and effect size, the magnitude was modest along the gradient of dispersal rate (fig. 2*B*). Our analyses showed that dispersal had stabilizing effects when temporal environmental fluctuations were negatively correlated across patches, but it had destabilizing effects when environmental correlation was positive (fig. 3). This result is in line with the prediction of metapopulation models that the locally stabilizing effects of dispersal were stronger (weaker) in negatively (positively) correlated environments, although it contrasts with the universal stabilizing effects predicted by these models (Wang et al. 2015). When patches are isolated, the negatively correlated fluctuations could generate spatially and temporally varying sink conditions (Steiner et al. 2013). In such cases, dispersal could ensure different species/individuals to survive and maintain relatively stable populations in local patches (Loreau et al. 2003).

At the regional scale, dispersal was found to have no overall effect on population variability, which can be partially explained by the contrasting effects of low versus high dispersal (fig. 2*C*). This result corroborates theoretical predictions that while low dispersal may stabilize metapopulation dynamics, high dispersal could lead to a lower stability and higher extinction risk of the metapopulation (Earn 2000; Dey and Joshi 2006). Moreover, we found that dispersal increased regional population variability in the presence of biotic forcing. This might again be explained by the strong synchronizing effects of dispersal when interacting with trophic interactions (Vasseur and Fox 2009), which results in coherent dynamics across populations and hence large regional-scale fluctuations.

Our findings that dispersal increased spatial synchrony but had little effect on local and regional population variability seem contradictory at first glance because the effect of dispersal on regional variability should be determined by its effects on spatial synchrony and local variability (Wang et al. 2015). While such an expectation is derived from the mathematical partitioning of regional variability into local variability and spatial synchrony (Wang et al. 2019), most studies in our data set defined variability and/or synchrony in different ways from the partitioning framework. In particular, whereas the partitioning framework defined spatial synchrony using a covariance-based index (φ), most experimental studies we collected reported correlation-based indices. Consistent with a previous study showing that different definitions of synchrony might lead to contradictory conclusions (Thibaut and Connolly 2013), our analyses showed that dispersal had positive effects on the correlation-based measure of spatial synchrony ($\bar{\rho}_r$ and $\bar{\rho}_x$) but no effect on the covariance-based measure (φ; fig. 4). One possible explanation for the contrasting effects of dispersal is that while increasing the temporal correlation across patches (Wang et al. 2015), dispersal can simultaneously increase the spatial evenness of populations (Lecomte et al. 2004; Bowler and Benton 2011), which contributes to decreasing the covariance-based synchrony φ (Thibaut and Connolly 2013; Wang and Loreau 2014). We note that our analyses also applied different definitions of local variability and different approaches to quantifying dispersal effects sizes for synchrony (D) and variability (LRR), but these choices had little impact on our results (fig. S3; table S6).

Interestingly, we found that experimental practices (e.g., experimental length and number of patches) also influenced the effect size of dispersal. Both the locally stabilizing and the spatially synchronizing effects of dispersal were easier to discover in longer experiments, for example, those lasting for more than 120 generations of focal species (fig. 3). In shorter ones, the effects of dispersal were always nonsignificant. This result is consistent with findings from a recent theoretical study (Luo et al. 2021): because dispersal has contrasting effects on spatial synchrony and local population variability at long versus short timescales, the empirical relationships between dispersal and spatial synchrony or local population variability can differ qualitatively with experimental duration. We also found strong, positive dispersal effects on spatial synchrony and regional variability in two-patch metapopulations. These results were consistent with theoretical insights that smaller spatial systems (e.g., two-patch metapopulations) allowed fewer refugia opportunities and were easier to be synchronized, which increased the risk of regional extinction (Yaari et al. 2012; Gupta et al. 2017).

Two limitations associated with our meta-analyses need to be acknowledged. First, the sample size was relatively small, reflecting the limited experimental efforts investigating dispersal-synchrony/variability relationships compared with theoretical efforts. The incomplete information on some moderators also forced us to exclude some studies from our analysis (e.g., when testing the influence of experimental length). Consequently, our analyses have examined only the separate effects of moderators, leaving their interactions to be addressed in future studies. Second, the dispersal rate in our analysis was simply the (mean) proportion of individuals transferred per dispersal event, while the standardized dispersal rate commonly used in relevant theoretical models represents the proportion of immigrants per generation. We were unable to standardize the dispersal rates because of the lack of information on generation time.

Conclusion and Future Directions

Our synthesis of existing experimental efforts provides support for and against some widely accepted predictions of spatial ecological theory. Consistent with theoretical predictions, we found that dispersal generally promoted correlation-based spatial synchrony, and such effects increased with dispersal rate and decreased with environmental correlation among patches. That said, the synchronizing effects of dispersal were nonsignificant if spatial synchrony was measured using a covariance-based index. Inconsistent with theoretical predictions, we found that dispersal had overall weak effects on local population variability except when environmental correlation among patches was negative and/or the experimental period was long. Taken together, the spatially synchronizing and locally stabilizing effects of dispersal were only partially supported by experiments, which is likely due to the context dependence of dispersal effects on biotic and abiotic drivers.

Our study suggests several future avenues to reconcile theoretical and experimental insights into the effect of dispersal. First, there is an urgent need for a more refined protocol about how metapopulation and metacommunity experiments should be conducted and reported. Because the effects of dispersal can be timescale dependent, as suggested by recent theory (Luo et al. 2021) and verified by our results, experiments should be maintained for a sufficiently long time to ensure robust statistical inference. The low bound of experimental length (e.g., the minimum number of generations) can be determined using a simulation-based statistical power analysis (Luo et al. 2021). Also, detailed information about focal species, treatments, and metrics (e.g., measures of spatial synchrony) should also be reported to facilitate synthesis. Second, future experiments and theoretical models should better characterize the reality of the dispersal process in natural populations, for example, density dependency and inter- and intraspecific variation (Clobert et al. 2012; Fronhofer et al. 2018). In particular, while most experiments included in our meta-analysis simulated passive dispersal via manually exchanging individuals/medium among artificial patches, dispersal can be an active process and driven by local conditions such as resource availability and predation risk, especially for animals (Fronhofer et al. 2018). Balancing the reality and tractability of dispersal manipulations may present a major challenge in future experiments. Last, an integrated approach of experiment and theory may allow researchers to better exploit the multigenerational sampling data and uncover the underlying processes (Ives et al. 2004), which would help to achieve a practical spatial theory.

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Statement of Authorship

S.W. conceived the study; Q.Y. collected the data and performed statistical analyses, with help from P.H. and S.W.; Q.Y. and S.W. wrote the first draft of the manuscript; and all authors contributed substantially to the interpretation of the results and revision of the manuscript.

Data and Code Availability

Data and R code are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.4xgxd25c8; Yang et al. 2022).

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