

Spatio-Temporal Environmental Correlation and Population Variability in Simple Metacommunities

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Abstract

Natural populations experience environmental conditions that vary across space and over time. This variation is often correlated between localities depending on the geographical separation between them, and different species can respond to local environmental fluctuations similarly or differently, depending on their adaptation. How this emerging structure in environmental correlation (between-patches and between-species) affects spatial community dynamics is an open question. This paper aims at a general understanding of the interactions between the environmental correlation structure and population dynamics in spatial networks of local communities (metacommunities), by studying simple two-patch, two-species systems. Three different pairs of interspecific interactions are considered: competition, consumer–resource interaction, and host–parasitoid interaction. While the results paint a relatively complex picture of the effect of environmental correlation, the interaction between environmental forcing, dispersal, and local interactions can be understood via two mechanisms. While increasing between-patch environmental correlation couples immigration and local densities (destabilising effect), the coupling between local populations under increased between-species environmental correlation can either amplify or dampen population fluctuations, depending on the patterns in density dependence. This work provides a unifying framework for modelling stochastic metacommunities, and forms a foundation for a better understanding of population responses to environmental fluctuations in natural systems.

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Introduction

Natural populations experience fluctuating environmental conditions (such as temperature and precipitation). This variation occurs over time in local habitats, but there is also variation in conditions across space. Temporal variation is often positively autocorrelated, i.e., consecutive observations tend to be more similar to each other than those separated by longer time lags [1]. Similarly, more closely located areas tend to be more similar in their local environmental conditions, implying positive spatial autocorrelation. That is, environmental variation tends to be autocorrelated both over time and across space, which is expected to have both ecological and evolutionary consequences on biological systems [2]. Understanding how spatio-temporal patterns in environmental fluctuations, and those in species-specific responses to these fluctuations affect variability in population densities is an important challenge, when planning sustainable conservation and exploitation of natural populations. This is reflected in the recent interest in studying stochastic metacommunities both theoretically and empirically [3–7].

When considering the dynamics of populations and communities in a spatial context, the influence of local environmental fluctuations can be extended to other localities via individual dispersal between habitats. A common pattern is that increased migration between habitats stabilises local population dynamics that are not fully synchronised [3,8,9]. However, when the correlation between local environmental conditions increases (i.e.,

localities become more similar in their environments), the associated increase in population synchrony increases the extinction risk of the entire metapopulation [3,6,10,11]. Increasing local temporal autocorrelation in the environment can either increase or decrease population variability, depending on the strength of population density dependence, between-species interaction strength, and local community structure [12–16].

In general, species can differ in their responses to environmental fluctuations, e.g., depending on the similarity of their environmental tolerances [17–19]. When two species that are differently adapted to a common environmental variable come to interact, the arising between-species environmental correlation (ρ_S) – $\rho_S = 1$ means that responses are identical, $\rho_S = 0$ means responses are independent, and $\rho_S = -1$ indicates completely opposite responses – can affect population variability in closed communities [2,14,15,20]. In simple competitive communities increasing ρ_S dampens undercompensating population fluctuations, whereas overcompensating populations tend to increase in variability [14,15,21]. In multi-trophic food webs increased ρ_S can be associated with lower population variability [22], as well as increased food web persistence [23].

In the metacommunity context, where local communities are coupled together via dispersal of one or several species [24], the relative influence of between-patch (ρ_E) and between-species environmental correlation (ρ_S) on population variability remains unknown. This paper aims at filling this gap in ecological theory.

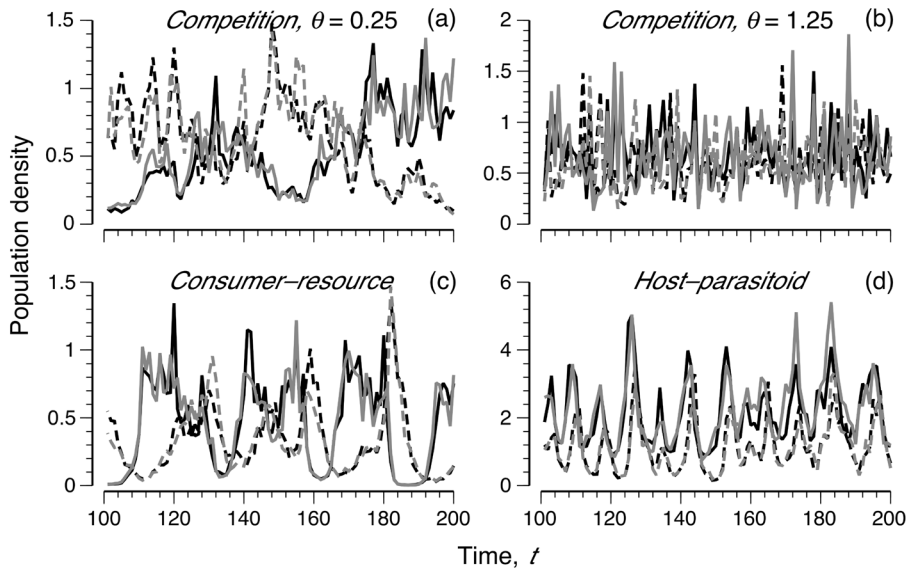


Figure 1. Examples of stochastic time series for two-species (species 1 solid, species 2 dashed), two-patch metacommunities (black lines for patch 1 and gray lines for patch 2). Local communities consist of either competitive communities with (a) undercompensating or (b) overcompensating populations, a (c) consumer–resource system (resource solid, consumer dashed), or a (d) host–parasitoid system (host solid, parasitoid dashed). Parameters: (a) $r = 1.5$, $\theta = 0.25$, $\alpha = 0.5$; (b) $r = 1.5$, $\theta = 1.25$, $\alpha = 0.5$; (c) $r = 1$, $K = 1$, $a = 2$, $R_0 = 1.25$, $e = 0.5$, $d = 0.25$; (d) $r = 2$, $q = 0.5$, $b = 0.5$. In all cases $m_{jk} = m = 0.25$, and environmental variation is white noise (zero mean and variance $\sigma^2 = 0.01$) affecting population per capita growth rates, independently between patches and species (i.e., $\rho_E = \rho_S = 0$). doi:10.1371/journal.pone.0072325.g001

population densities of $H_i^* = qr^{1/q} - 1/b(r-1)$ and $P_i^* = q(r^{1/q} - 1)/b$ [32] (an example time series for host–parasitoid dynamics is given in fig. 1d). This system is globally stable only if the equilibrium is stable (i.e., there is no stable limit cycle).

Linear analysis

For simplicity, environmental variation ε_{ik} is assumed to be serially uncorrelated ‘white’ noise, with a covariance matrix \mathbf{C} (see Appendix S1), describing the correlation in between-patch environmental fluctuations (between-patch environmental correlation, ρ_E) and how similarly the two species react to these fluctuations (between-species environmental correlation, ρ_S). When linearised around the equilibrium point, local population dynamics in each system can be described by the Jacobian matrix \mathbf{J} (Appendix S1), while dynamics in the global metacommunity are governed by matrix $\mathbf{B} = \mathbf{M}\mathbf{J}$, where \mathbf{M} is a dispersal matrix that describes the way individuals move between the local communities (Appendix S1). Given that equilibrium dynamics are stable in the absence of stochasticity (as required above), a linear approximation of the population variance-covariance matrix \mathbf{V} can be obtained as follows, assuming white noise [12]:

$$\text{Vec}(\mathbf{V}) = (\mathbf{I} - \mathbf{B} \otimes \mathbf{B})^{-1} \text{Vec}(\mathbf{C}), \quad (5)$$

where $\text{Vec}(\mathbf{V})$ is the vectorised variance-covariance matrix. The \otimes symbol indicates the Kronecker tensor product (producing all possible combinations between the elements in two matrices), \mathbf{I} is an identity matrix (ones on the main diagonal and zeros elsewhere), and $\text{Vec}(\mathbf{C})$ is the vectorised environmental covariance matrix. The diagonal elements of \mathbf{V} contain population variances V_{ii} , while the off-diagonal elements are between-population covariances V_{ij} .

While eqn. (5) is a useful tool for obtaining population variances (and covariances), it is not particularly useful for doing detailed analysis of the relationship between biological parameters and

environmental characteristics [15]. This can be in principle achieved via transforming the system described by \mathbf{B} to the coordinates along the eigenvectors of \mathbf{B} and back-transforming the resulting variances to gain variances in population densities [14,15,17]. For the first scenario, with interspecific competition (eqn. 2), population variance is readily obtained using this method (Appendix S1):

$$V_{ii} = \frac{\sigma^2}{\Theta^2} \left[\frac{(\rho_E + 1)(\rho_S - 1)}{\lambda_1^2 - 1} - \frac{(\rho_E + 1)(\rho_S + 1)}{\lambda_2^2 - 1} - \frac{(\rho_E - 1)(\rho_S - 1)}{\lambda_3^2 - 1} - \frac{(\rho_E - 1)(\rho_S + 1)}{\lambda_4^2 - 1} \right], \quad (6)$$

where σ^2 is the environmental variance, λ_i are the eigenvalues of \mathbf{B} (Appendix S1), and Θ is the order of \mathbf{B} (here $\Theta = 4$). Population variability is then found as $CV = (\alpha + 1)(V_{ii})^{1/2}/K$. From eqn. (6) it can be seen that the relative magnitude of λ_i affects the way ρ_E and ρ_S impact on population variance. However, the patterns in which the eigenvalues interact with environmental correlations are far more complex than those in isolated systems [14,15]. Eqn. (6) can be expanded to reveal the influence of model parameters on the relative importance of the interaction between different sources of environmental correlation ($\rho_E\rho_S$; Appendix S1, Figure S1, Text S1). This variance component becomes more important with increasing θ and r , less important with increasing α , and less (more) important with increasing m (when $m_{jk} = m$) when intrinsic dynamics are undercompensatory (overcompensatory).

Eqn. (6) gives the variance of local population fluctuations. The variance of global population variance, i.e., the variance of summed population densities (across patches) can be found by summing across the population variance-covariance matrix \mathbf{V} for each species:

$$V_{\Sigma X_i} = 2V_{ii} + 2V_{ij} = \frac{\sigma^2}{\theta^2} \left[\frac{(\rho_E + 1)(\rho_S - 1)}{\lambda_1^2 - 1} - \frac{(\rho_E + 1)(\rho_S + 1)}{\lambda_2^2 - 1} \right], \quad (7)$$

where V_{ii} is local population variance (eqn. 6) and V_{ij} is between-population covariance. Unlike V_{ii} , $V_{\Sigma X}$ is independent of the magnitude of dispersal, as the eigenvalues λ_1 and λ_2 are independent of m_{ik} . The remaining analysis concentrates on V_{ii} , which are used to calculate the population coefficient of variation, $CV_{ik} = (V_{ik})^{1/2}/X_{ik}^*$ (where X_{ik}^* is the equilibrium density of population i in patch k), a commonly used statistic for measuring population variability [33–35].

For systems in eqns. (3, 4) with consumer–resource and host–parasitoid dynamics, respectively, simple analytical expressions for population variances cannot be obtained. This is because the eigenvectors of the metacommunity Jacobian (\mathbf{B}) depend on model parameters, which leads to the covariance matrix for dynamics along the eigenvectors having non-zero off-diagonal elements. The interpretation of such values is not straightforward, as the variance along eigenvectors should be independent by definition [14]. Therefore the remaining analysis utilises eqn. (5) to generate numerical results for symmetric dispersal. Between-population synchrony (zero-lag cross-correlation) can be obtained from eqn. (5) as $COR(X_i, X_j) = V_{ij}/\sqrt{V_{ii}V_{jj}}$.

Stochastic simulations

Depending on the amplitude of environmental stochasticity, analytical predictions do not necessarily match simulation results [36]. The reliability of analytical results was evaluated by simulating spatial community dynamics for $t_{MAX} = 25000$ time steps (population densities initiated at random densities between (0, 1]) for each parameter combination (the first 5000 time steps were discarded before further analysis). The data was then used to calculate mean population variability for each species as the coefficient of variation [$CV_i = \sum_k (\sigma(X_{ik})/\mu(X_{ik}))/2$]. Each parameter combination was replicated 100 times. The procedure for stochastic simulation of the model communities, particularly the generation of environmental variables ε_{ik} , is described in detail in Text S1.

Results

A general pattern common to all scenarios examined here is that decreasing between-patch environmental correlation (ρ_E) decreases (local) population variability. This happens because increasingly asynchronous population fluctuations between patches become dampened by the act of dispersal; individuals dispersing from a large population to a small population bring both populations closer to their long-term means [9]. While varying ρ_E leads to an intuitive and expected result in all cases, the way ρ_E and the between-species environmental correlation (ρ_S) interact in driving population variability is more complicated. The interaction between ρ_E and ρ_S depends on the nature of local between-species interactions, as well as on the ecological role of the focal population (fig. 2). This namely boils down to whether forced synchronisation is amplified or dampened by species interactions.

Symmetric dispersal

In competitive metacommunities increasing ρ_S reduces the variability of populations with undercompensating dynamics (fig. 2a), and increases variability in association with overcompensating dynamics (fig. 2b). In addition, the effect of increasing ρ_E decreases with increasing (decreasing) ρ_S for undercompensating

(overcompensating) populations. These patterns arise because asynchronous local dynamics are amplified by undercompensating population responses to perturbations, whereas overcompensation amplifies synchronous dynamics [12,36].

As with the competitive communities, the species interaction can either amplify or dampen population fluctuations in exploitative communities ($C-R$ or $H-P$). In the consumer–resource system (top-down controlled) population variability increases with increasing ρ_S (fig. 2c, d). Here unstable dynamics are driven by overconsumption [30], while in the absence of consumption resources approach their carrying capacities. Negatively correlated local environmental responses between species ($\rho_S < 0$) lead to situations where resources are favoured and consumers are pressed by environmental conditions, which reduces the predation pressure and dampens population fluctuations. Conversely, increasingly positive ρ_S between the resource and the consumer promotes overconsumption, as the consumer is favoured when the resource is abundant. As in the $C-R$ system, the dynamical stability of the host–parasitoid system is controlled by the coupling strength between the two species (bottom-up controlled); in a persistent system the parasitoid is able to control the exponential growth of the host. This means that increasingly positive ρ_S will dampen population fluctuations by promoting this coupling, whereas increasingly negative ρ_S will increase the size of population fluctuations by decoupling host and parasitoid densities (fig. 2e, f).

Patterns in population variability are in qualitative agreement with those in between-patch (within-species) population synchrony (Text S1), which means that patterns in global population variability reflect those in local population variability. Increasing ρ_E is always synchronising. Instead, increasing ρ_S desynchronises (synchronises) populations in undercompensating (overcompensating) competitive systems (Figure S2a, b). In consumer–resource systems increasing ρ_S synchronises both resource and consumer dynamics between patches (Figure S2c, d), whereas host and parasitoid populations tend to become desynchronised (Figure S2e, f).

Asymmetric dispersal

Local population variabilities under asymmetric dispersal (figs. 3,4) are qualitatively similar to those observed under symmetric dispersal (fig. 2). While the relative effect of ρ_S depends on the between-species interaction, the relative effect of ρ_E on each population depends on its dispersal capacity; limited dispersal weakens the direct influence of ρ_E on the population variability of this species. Both of these factors affect the shape of the interaction between ρ_E and ρ_S . The interaction between m_{ik} and ρ_E is clearly seen in the competitive communities (fig. 3). While population variability at the species with a relatively high dispersal capacity (fig. 3b, d) remains practically the same as under symmetric dispersal (fig. 2a, b) (as the direct effect of ρ_E remains the same), the effect of ρ_E is weakened relative to ρ_S at the species with limited dispersal (fig. 3a, c). The same applies also in the consumer–resource and host–parasitoid systems, when the consumer (fig. 4f) or the host (fig. 4c) is limited in its dispersal capacity.

The relationship between dispersal potential and ρ_E does not hold in two special cases: under negative ρ_E , when either (1) the resource (in a $C-R$ system), or (2) the parasitoid (in a $H-P$ system), is limited in its dispersal. (1) Under these conditions ($\rho_E < 0$), resource fluctuations are dampened by increasing ρ_S (fig. 4a), despite of increased population synchrony. Under negative ρ_S the $\rho_E\rho_S$ term specifying the correlation between consumers and resource between patches is positive. Given that consumers are relatively well mixed between patches, high consumer dispersal from one patch coincides with high resource

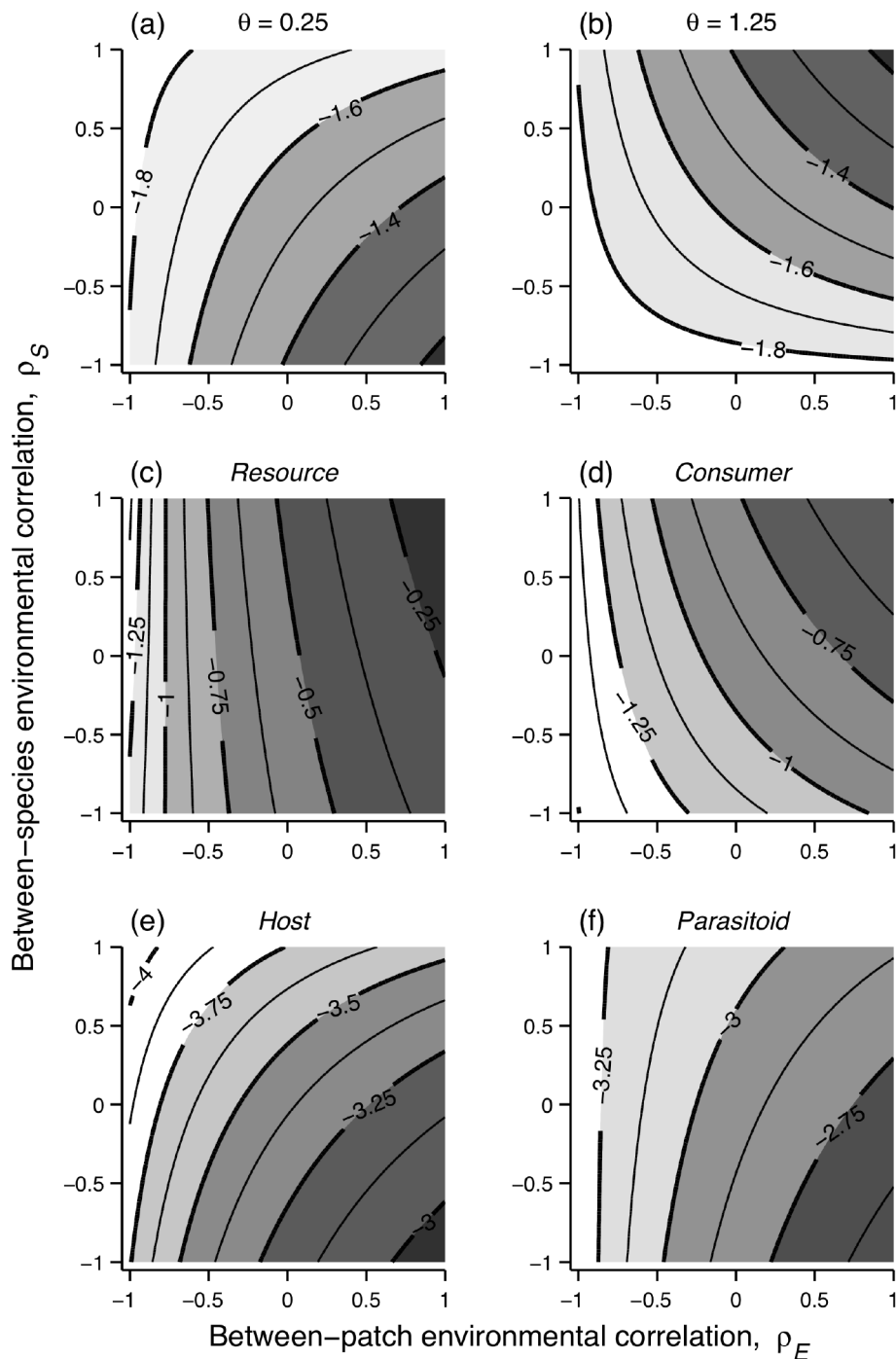


Figure 2. Population variability in simple two-species two-patch metacommunities depends on an interaction between the environmental correlation between patches (ρ_E describing the similarity in environmental conditions across space) and the local environmental correlation between species (ρ_S describing how similarly species respond to variation in local environmental conditions). This interaction further depends on the nature of the between-species interaction, as well as the ecological role of the focal population. In competitive communities (eqn. 2) species intrinsic dynamics are either (a) undercompensatory ($\theta=0.25$) or (b) overcompensatory ($\theta=1.25$). In exploitative communities (eqns. 3, 4) the interaction involves either (c, d) consumer–resource dynamics, or (e, f) host–parasitoid dynamics. The contours represent the logarithm of (local) population CV. Results are based on an intermediate level of symmetric dispersal for both species, $m_{ik} = m = 0.25$ (note that the effect of varying m is symmetrical around 0.5). Environmental variation is serially uncorrelated white noise, with zero mean and variance $\sigma^2 = 0.01$.

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growth in the other patch (immigration and density are coupled between species), which amplifies resource fluctuations. The same mechanism applies in the H – P system (fig. 4h); reduced ρ_S can

dampen parasitoid fluctuations when the host is relatively well mixed as high host immigration is associated with high parasitoid growth rates.

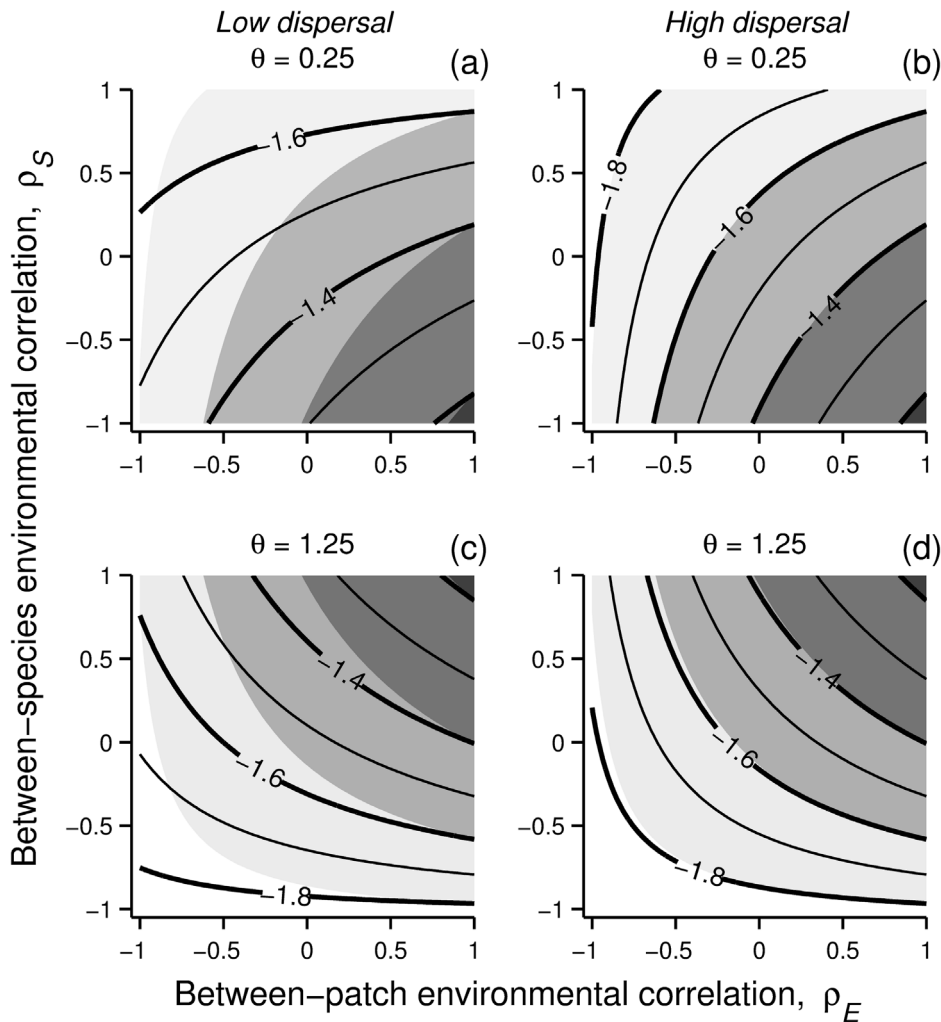


Figure 3. The effect of between-patch (ρ_E) and between-species (ρ_S) environmental correlation on population variability (log CV) in competitive metacommunities with asymmetric dispersal between species. The dispersal propensity is low ($m_{1k}=0.05$) for one species (a, c) and relatively high ($m_{2k}=0.25$) for the other (b, d). Populations have either undercompensatory ($\theta=0.25$; a, b) or overcompensatory ($\theta=1.25$; c, d) intrinsic dynamics. Contour lines represent (log) population CV under asymmetric dispersal, whereas the shading represents log CV under symmetric dispersal (with the same steps as the thick contour lines). Environmental variation is serially uncorrelated white noise, with zero mean and variance $\sigma^2=0.01$.

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Discussion

While the results presented here might appear complex at first glance, they can in the end be understood by common underlying mechanisms. In these symmetric systems (patches are identical), common environmental forcing between patches synchronises population dynamics even in the absence of dispersal – the so-called ‘Moran effect’ [37]. When patches are connected by dispersal, decreasing the correlation between local environmental conditions (ρ_E) dampens local population fluctuations due to a decoupling of immigration and population densities [9]. This stabilising effect of reduced ρ_E is in agreement with previous studies on metapopulation dynamics [3], as well as spatially extended food webs [5], and experimental work on competitive metacommunities [6,38]. The relative influence of ρ_E on population variability depends on a species dispersal potential, which explains why species can differ in their responses to variation in ρ_E under asymmetric dispersal.

Locally, between-species similarity in their responses to environmental fluctuations (ρ_S) affects the synchrony among local populations. Increasing local synchrony can either amplify or dampen population fluctuations, depending on the interaction between species. In competitive communities synchronous dynamics are amplified by increased density dependence (overcompensatory dynamics) [12,14,15,36]. A similar logic can be used to understand why the consumer – resources and host–parasitoid communities differ qualitatively in their responses to increasing ρ_S . Instability in the *C–R* system is driven by overconsumption by the consumer (top-down control) [30], when resource growth is density-dependent. Here increasing ρ_S promotes the consumer’s coupling to the resource, which amplifies population fluctuations. This differs from the result by Vasseur and Fox [22], who reported that increasing ρ_S between two intermediate consumers in a diamond-shaped food web reduces population variability, due cascading effects on the resource and the top predator.

Contrary to the *C–R* community, the run-away behaviour of the *H–P* model is driven by the host’s lack of density-dependence

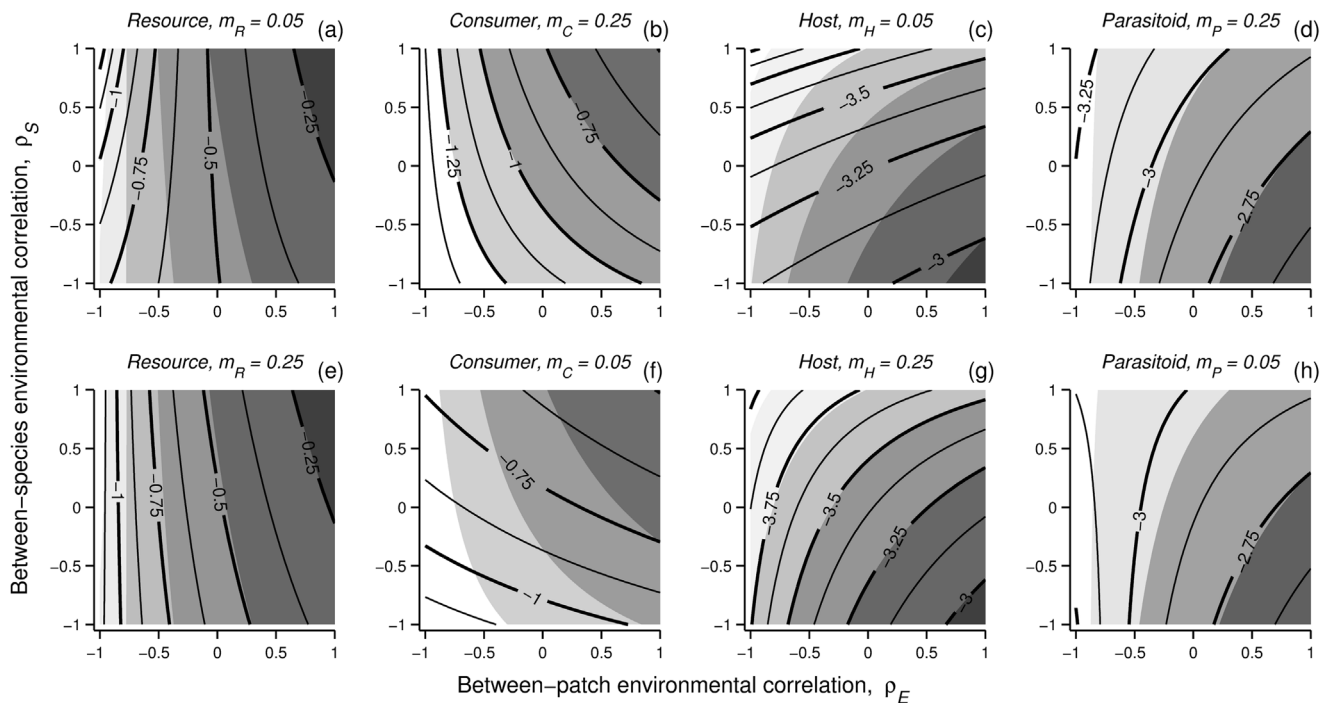


Figure 4. The effect of between-patch (ρ_E) and between-species (ρ_S) environmental correlation on population variability (log CV) in consumer–resource (a, b, e, f) and host–parasitoid (c, d, g, h) metacommunities with asymmetric dispersal between species. Contour lines represent (log) population CV under asymmetric dispersal, whereas the shading represents log CV under symmetric dispersal (with the same steps as the thick contour lines). Parameter values for C–R system: $r=1$, $K=1$, $a=2$, $R_0=1.25$, $e=0.5$, $d=0.25$. Parameter values for H–P system: $r=2$, $q=0.5$, $b=0.5$. Environmental variation is serially uncorrelated white noise, with zero mean and variance $\sigma^2=0.01$. doi:10.1371/journal.pone.0072325.g004

(bottom-up effect). Increasing ρ_S then promotes the parasitoids ability to track host growth, which reduces population variability. The importance of top-down control versus bottom-up effects in affecting the response of exploitative communities to forced synchronisation can be further highlighted by considering a host–parasitoid model with density-dependent host growth [25,39]. In such a case, the C–R and H–P models produce qualitatively matching results considering the influence of increasing between-species environmental correlation (Figure S3).

Interpreting environmental covariance

The between-patch environmental correlation (ρ_E) could be interpreted as the degree of spatial autocorrelation, as this measure is likely to vary, e.g., due to increasing spatial distance between patches [4,40]. Spatial autocorrelation in environmental conditions has been shown to play an important role, e.g., in population extinction risk [41–43]. In addition to spatial autocorrelation, temporal autocorrelation in local environmental conditions can also have important consequences for population extinction risk [2]. While this aspect was not considered here for simplicity, it is likely that temporal autocorrelation further affects the interaction between spatial correlation (ρ_E) and between-species environmental correlation (ρ_S), as it is known to interact with ρ_S in driving population variability in isolated communities [12,14,15], and to interact with ρ_E in competitive metacommunities in affecting population persistence [38]. Considering this alternative is beyond the scope of this paper, but the analytical methods used here are easily extended to account for temporally (serially) autocorrelated noise (Appendix S1) [12,14,15].

The magnitude of the between-species environmental correlation is likely to depend on external factors, namely the presence of

other species in the community. Without any adjustment to species behaviour, varying community composition can affect patterns in $\rho_S(i,j)$ (the environmental correlation between a pair of species i and j in a community), if species respond differently to fluctuations in environmental conditions (such as temperature or precipitation). However, on top of these intrinsic differences in species environmental responses, the $\rho_S(i,j)$'s can be further modified by individual behaviour. Interspecific competition can lead to changes in species resource utilization patterns [44–46] and if these resources are subject to environmental stochasticity, this can in turn result in variation in the $\rho_S(i,j)$'s. The presence of predators can be associated with altered patterns in prey habitat use [47]. This can affect the way prey is influenced by environmental fluctuations, potentially altering the correlation between environmental responses of the predator and the prey.

Extinction risk

In spatial systems, local population variability and global extinction risk are intimately related to patterns in population synchrony [3,8,10]. Extinction risk is generally increased by the Moran effect due to increased population synchrony [10]. Dispersal on the other hand can either synchronise or desynchronise local populations, depending on, e.g., spatial heterogeneity, local dynamics, and dispersal strategies [9,48,49].

Recently, Abbott [3] suggested that increasing population synchrony can either increase or decrease population variability, depending on the mechanism controlling the level of between-patch population synchrony; if synchrony varies due to population dispersal propensity or increased local growth rates, higher synchrony is stabilising, whereas other synchronising factors (such as increasing between-patch environmental correlation) tend to be

destabilising. This is in agreement of the present results. However, a previously unconsidered aspect is that local between-species environmental correlation can also affect population synchrony between patches. This is simply a statistical consequence of ρ_S affecting local population variances V_{ii} . When the variances are increased, while between-population covariances V_{ij} are unaffected, the between-species cross-correlation ($COR(X_i, X_j)$) necessarily decreases (by definition).

Dispersal asymmetry

Here I consider both symmetric and asymmetric dispersal between species, for completeness. Clearly, it is more realistic to assume that species differ in their dispersal potential. While predators are usually more mobile than their prey [50], many migratory species encounter sedentary predators in different habitats they visit [51]. Whether hosts or their parasitoids have higher dispersal capacities is likely to vary among taxa. For example, the Granville fritillary butterfly (*Melitaea cinxia*) has two parasitoids that differ in their dispersal capacity in comparison with their host. *Cotesia melitaeorum* is clearly less dispersive than the host, whereas *Hyposoter horticola* is at least as dispersive as the host [52].

For simplicity, species are here identical in the competitive communities. Thus, the identity of a dispersal-limited species is arbitrary. A logical outcome of dispersal limitation is that the relative influence of between-patch environmental correlation (ρ_E) on population variance is reduced. In the exploitative communities this also applies to the species that has more control over the local dynamics; the consumer in the *C-R* system and the host in the *H-P* system. With the other species (resource or parasitoid) dispersal limitation can lead to a qualitative change in the effect of increasing ρ_S under negative ρ_E . In the *C-R* system, for example, this arises because the immigration of the consumer is coupled with resource density. This is inline with the observation that decoupling between immigration and density (within species) dampens population fluctuations [9]. These results also support the finding that the identity of a mobile species in a food web can be important for food web dynamics in metacommunities [53].

Model assumptions and the robustness of results

I have here assumed that dispersal is a simple density independent reallocation of individuals [3,25,54]. It is, however, unlikely that individual dispersal strategies remain independent of their environments [55–60]. For example, spatial autocorrelation in environmental conditions can affect the evolution of dispersal modes [58,60], such that higher spatial autocorrelation selects for longer dispersal distance [60]. While all dispersal propensities are equally favoured in perfectly correlated environments, increasingly negative between-patch environmental correlation selects for intermediate dispersal propensities [58]. The environmental correlation structure can also affect acquisition of information used to make dispersal decision, which could affect the evolution of dispersal strategies [56]. Thus, incorporating other dispersal strategies that depend on population densities, local environmental conditions, or their combination [49] is an important direction for future research.

The analytical predictions from figure 2 were tested using extensive numerical simulations (Text S1). These results (Figure S4) show good qualitative agreement with the analytical model (fig. 2). This also applies to asymmetric dispersal (not shown). However, as the models considered here (eqns. 2–4) are all non-linear, the accuracy of the linearization around the system equilibrium (eqn. 5) is only accurate when perturbations around this equilibrium are relatively small. Therefore, increasing the size

of environmental fluctuations can potentially result in discrepancies between simulation and analytical results, as stronger forcing brings the system increasingly far away from the deterministic equilibrium [36]. As the environmental variance appears only as a linear scaling factor in eqn. (5), varying σ^2 has no qualitative effect on the analytical results.

An important assumption here is to only consider stable equilibrium dynamics. This is often assumed either to facilitate interpretation of resonance patterns between intrinsic dynamics and environmental forcing [36,61], or to apply linearisation of the system to generate analytical results [12,13]. However, non-equilibrium dynamics can have important consequences for spatial community dynamics under stochastic environments [5]. The influence of non-equilibrium dynamics was again tested with stochastic simulations, using the consumer–resource model with cyclic dynamics in the absence of stochasticity. The results from this simulation experiment (Figure S5) indicate that analytical results (fig. 2c, d) are not qualitatively sensitive to the assumption of stable equilibrium dynamics (at least under relatively weak noise). This is not very surprising, as the parameters used for stable dynamics are associated with dampened oscillations to equilibrium following perturbations. This means that under stochastic variation the system is constantly undergoing cyclic, transient dynamics, which is evident from figure 1c.

Implications

The analysis presented here makes predictions about the behaviour of extremely simple systems under stochastic environmental variation. These predictions, at least those considering symmetric dispersal, could be tested using existing procedures for experimental microcosms [38,62–64]. Between-patch environmental correlation would then be manipulated by simply tuning the correlation in, e.g., temperature [65] or light spectrum [64], between ‘patches’. Adjusting between-species environmental correlation would in turn require selecting a pair of species with desired differences in their adaptation along the focal environmental variable.

Predictions about the dynamics of populations and communities under spatio-temporal environmental variation are needed, e.g., for mitigation of climatic perturbations and planning sustainable population management across spatial landscapes. The present analysis is the first step towards a more general understanding of how metacommunities behave in stochastic environments. Considering the effect of spatial heterogeneity in patch quality [29,63,66–68] in association with the environmental covariance structure is an interesting direction for future research. A recent study demonstrated how spatial heterogeneity and spatially restricted harvesting can generate ecological traps, leading to global population extinction [69]. Although some work has been done on how exploitation interacts with spatial population processes in stochastic environments [8], more work is needed to better understand potential interactions between spatio-temporal environmental fluctuations and exploitation in spatial systems with between-patch dispersal. The works by Gouhier et al. [70] – showing that localised dispersal can generate non-stationary spatio-temporal patterns in population abundances, and Blowes and Connolly [40] – showing that the decay of between-patch environmental correlation with between-patch spatial distance can affect metapopulation persistence, make a promising step in this direction, both having direct implications to effective design of reserve networks.

Supporting Information

Figure S1 The dependency of the combined term $\rho_E\rho_S$ in the environmental covariance matrix C on its components ρ_E (between-patch environmental correlation) and ρ_S (between-species environmental correlation), see eqn. (A.3) in Appendix S1. (PDF)

Figure S2 Between-population synchrony in simple two-species two-patch metacommunities depends on an interaction between the environmental correlation between patches (ρ_E) and the local environmental correlation between species (ρ_S). In competitive communities species intrinsic dynamics are either (a) undercompensatory or (b) overcompensatory. In exploitative communities the interaction involves either (c, d) consumer–resource dynamics, or (e, f) host–parasitoid dynamics. The contours represent analytical approximations of the between-patch population cross-correlation for each species. Results are based on an intermediate level of symmetric dispersal for both species, $m_{ik} = m = 0.25$. Parameters: (a) $r = 1$, $\theta = 0.25$, $\alpha = 0.5$; (b) $r = 1$, $\theta = 1.25$, $\alpha = 0.5$; (c, d) $r = 1$, $K = 1$, $a = 2$, $R_0 = 1.25$, $e = 0.5$, $d = 0.25$; (e, f) $r = 2$, $q = 0.5$, $b = 0.5$. Environmental variation is serially uncorrelated white noise, with zero mean and variance $\sigma^2 = 0.01$. (PDF)

Figure S3 Population variability ($\log CV$), affected by between-patch (ρ_E) and between-species environmental correlation (ρ_S), in a host–parasitoid metacommunity. The local community dynamics are modelled as (Beddington et al., 1975; Ranta et al., 2008): $H_{t+1} = H_t \exp[r(1 - H_t/K) - bP_t]$, $P_{t+1} = cP_t[1 - \exp(-bH_t)]$, where r and K are the intrinsic growth rate and carrying capacity of the host (H), and b and c are the attack rate and conversion efficiency of the parasitoid (P). Parameters: $r = 1$, $K = 1$, $c = 2$, $b = 1$, $m_{ik} = m = 0.25$. Environmental variation is white noise (zero mean and variance $\sigma^2 = 0.01$). (PDF)

Figure S4 Analytically derived population variabilities ($\log CV$; red contour lines) match qualitatively with those resulting from stochastic simulations (black contour lines and shading). In competitive communities species intrinsic dynamics are either (a) undercompensatory or (b)

overcompensatory. In exploitative communities the interaction involves either (c, d) consumer–resource dynamics, or (e, f) host–parasitoid dynamics. The **black** contours represent the logarithm of simulated population CV , based on 100 independent replicates. Results are based on an intermediate level of symmetric dispersal for both species, $m_{ik} = m = 0.25$. Parameters: (a) $r = 1$, $\theta = 0.25$, $\alpha = 0.5$; (b) $r = 1$, $\theta = 1.25$, $\alpha = 0.5$; (c, d) $r = 1$, $K = 1$, $a = 2$, $R_0 = 1.25$, $e = 0.5$, $d = 0.25$; (e, f) $r = 2$, $q = 0.5$, $b = 0.5$. Environmental variation is serially uncorrelated white noise, with zero mean and variance $\sigma^2 = 0.01$, for both analytical and simulation results. Simulation-based CV -values have been scaled arbitrarily to better coincide with the corresponding analytically derived values. (PDF)

Figure S5 Population variability ($\log CV$), affected by between-patch (ρ_E) and between-species environmental correlation (ρ_S), in a consumer–resource metacommunity with cyclic local dynamics. Parameters: $r = 1$, $K = 1$, $a = 2$, $R_0 = 1.25$, $e = 0.5$, $d = 0.1$, $m_{ik} = m = 0.25$. The data (shaded contours) represents means over 100 replicates, while the contour lines give a smoothing of the original data. Environmental variation is serially uncorrelated white noise, with zero mean and variance $\sigma^2 = 0.01$. (PDF)

Appendix S1 Details on analytical treatment of environmental noise and population variance. (DOCX)

Text S1 Additional information on the environmental correlation structure, simulation methods, and additional results. (DOCX)

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Author Contributions

Conceived and designed the experiments: LR. Performed the experiments: LR. Analyzed the data: LR. Wrote the paper: LR.

References

- Vasseur DA, Yodzis P (2004) The color of environmental noise. *Ecology* 85: 1146–1152.
- Ruokolainen L, Lindén A, Kaitala V, Fowler MS (2009) Ecological and evolutionary dynamics under coloured environmental variation. *Trends Ecol & Evol* 24: 555–563.
- Abbott KC (2011) A dispersal-induced paradox: synchrony and stability in stochastic metapopulations. *Ecol Lett* 14: 1158–1169.
- Fox JW, Vasseur DA, Hausch S, Roberts J (2011) Phase locking, the Moran effect and distance decay of synchrony: experimental tests in a model system. *Ecol Lett* 14: 163–168.
- Gouhier TC, Guichard F, Gonzalez A (2010) Synchrony and stability of food webs in metacommunities. *Am Nat* 175: E16–E34.
- Steiner CF, Stockwell R, Kalaimani V, Aqel Z (2013) Population synchrony and stability in environmentally forced metacommunities. *Oikos* In press.
- Vasseur DA, Fox JW (2009) Phase-locking and environmental fluctuations generate synchrony in a predator–prey community. *Nature* 460: 1007–1010.
- Palmqvist E, Lundberg P (1998) Population extinctions in correlated environments. *Oikos* 83: 359–367.
- Briggs CJ, Hoopes MF (2004) Stabilizing effects in spatial parasitoid–host and predator–prey models: a review. *Theor Pop Biol* 65: 299–315.
- Heino M, Kaitala V, Ranta E, Lindström J (1997) Synchronous dynamics and rates of extinction in spatially structured populations. *Proc R Soc Lond B* 264: 481–486.
- Liebold A, Koenig WD, Björnstad ON (2004) Spatial synchrony in population dynamics. *Annu Rev Ecol Evol Syst* 35: 467–490.
- Greenman JV, Benton TG (2005) The impact of environmental fluctuations on structured discrete time population models: resonance, synchrony and threshold behaviour. *Theor Pop Biol* 68: 217–235.
- Ripa J, Heino M (1999) Linear analysis solves two puzzles in population dynamics: the route to extinction and extinction in coloured environments. *Ecol Lett* 2: 219–222.
- Ripa J, Ives AR (2003) Food web dynamics in correlated and autocorrelated environments. *Theor Pop Biol* 64: 369–384.
- Ruokolainen L, Ripa J (2012) The strength of species interactions modifies population responses to environmental variation in competitive communities. *J Theor Biol* 310: 199–205.
- Vasseur DA (2007) Populations embedded in trophic communities respond differently to coloured environmental noise. *Theor Pop Biol* 72: 186–196.
- Johansson J, Ripa J, Kuckländer N (2010) The risk of competitive exclusion during evolutionary branching: Effects of resource variability, correlation and autocorrelation. *Theor Pop Biol* 77: 95–104.
- Lehman CL, Tilman D (2000) Biodiversity, stability, and productivity in competitive communities. *Am Nat* 156: 534–552.
- Ruokolainen L, Ranta E, Kaitala V, Fowler MS (2009) Community stability under different correlation structures of species' environmental responses. *J Theor Biol* 261: 379–387.

20. Fowler MS, Ruokolainen L (2013) Colonization, covariance and colour: environmental and ecological drivers of diversity-stability relationships. *J Theor Biol* 324: 32–41.
21. Ruokolainen L, Fowler MS, Ranta E (2007) Extinctions in competitive communities forced by coloured environmental variation. *Oikos* 116: 439–448.
22. Vasseur DA, Fox JW (2007) Environmental fluctuations can stabilize food web dynamics by increasing synchrony. *Ecol Lett* 10: 1066–1074.
23. Borrvall C, Ebenman B (2008) Biodiversity and persistence of ecological communities in variable environments. *Ecol Complex* 5: 99–105.
24. Leibold M, Holyoak M, Mouquet N, Amarasekare P, Chase J, et al. (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* 7: 601–613.
25. Ranta E, Fowler MS, Kaitala V (2008) Population synchrony in small-world networks. *Proc R Soc B* 275: 435–442.
26. Ruokolainen L, Ranta E, Kaitala V, Fowler MS (2009) When can we distinguish between neutral and non-neutral processes in community dynamics under ecological drift? *Ecol Lett* 12: 909–919.
27. Maser GL, Guichard F, McCann KS (2007) Weak trophic interactions and the balance of enriched metacommunities. *J Theor Biol* 247: 337–345.
28. Ripa J (2000) Analysing the Moran effect and dispersal: their significance and interaction in synchronous population dynamics. *Oikos* 89: 175–187.
29. Petchey OL, Gonzalez A, Wilson HB (1997) Effects on population persistence: the interaction between environmental noise colour, intraspecific competition and space. *Proc R Soc Lond B* 264: 1841–1847.
30. Rip JMK, McCann KS (2011) Cross-ecosystem differences in stability and the principle of energy flux. *Ecol Lett* 14: 733–740.
31. Abrams PA, Ruokolainen L (2011) How does adaptive consumer movement affect population dynamics in consumer–resource metacommunities with homogeneous patches? *J Theor Biol* 277: 99–110.
32. May RM (1978) Host-parasitoid systems in patchy environments: a phenomenological model. *J Anim Ecol*: 833–844.
33. Gonzalez A, Descamps-Julien B (2004) Population and community variability in randomly fluctuating environments. *Oikos* 106: 105–116.
34. Hector A, Hautier Y, Saner P, Wacker L, Bagchi R, et al. (2010) General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. *Ecology* 91: 2213–2220.
35. Petchey OL (2000) Environmental colour affects aspects of single-species population dynamics. *Proc R Soc Lond B* 267: 747–754.
36. Ruokolainen L, Fowler MS (2008) Community extinction patterns in coloured environments. *Proc R Soc B* 275: 1775–1783.
37. Greenman JV, Benton TG (2001) The impact of stochasticity on the behaviour of nonlinear population models: synchrony and the Moran effect. *Oikos* 93: 343–351.
38. Matthews DP, Gonzalez A (2007) The inflationary effects of environmental fluctuations ensure the persistence of sink metapopulations. *Ecology* 88: 2848–2856.
39. Beddington JR, Free CA, Lawton JH (1975) Dynamic complexity in predator-prey models framed in difference equations. *Nature* 255: 58–60.
40. Blowes SA, Connolly SR (2012) Risk spreading, connectivity, and optimal reserve spacing. *Ecol Appl* 22: 311–321.
41. Engen S, Lande R, Sæther BE (2002) The Spatial Scale of Population Fluctuations and Quasi-Extinction Risk. *Am Nat* 160: 439–451.
42. Kallimanis AS, Kunin WE, Halley JM, Sgardelis SP (2005) Metapopulation extinction risk under spatially autocorrelated disturbance. *Conserv Biol* 19: 534–546.
43. Reed DH (2004) Extinction risk in fragmented habitats. *Anim Conserv* 7: 181–191.
44. Persson L (1986) Effects of reduced interspecific competition on resource utilization in perch (*Perca fluviatilis*). *Ecology* 67: 355–364.
45. Schoener TW (2011) The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. *Science* 331: 426–429.
46. Schoener TW (1974) Resource partitioning in ecological communities. *Science* 185: 27–39.
47. Werner EE, Gilliam JF, Hall DJ, Mittelbach GG (1983) An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64: 1540–1548.
48. Ruokolainen L, Abrams PA, McCann KS, Shuter BJ (2011) The roles of spatial heterogeneity and adaptive movement in stabilizing (or destabilizing) simple metacommunities. *J Theor Biol* 291: 76–87.
49. Amarasekare P (2007) Spatial dynamics of communities with intraguild predation: the role of dispersal strategies. *Am Nat* 170: 819–831.
50. McCann KS, Rooney N (2009) The more food webs change, the more they stay the same. *Phil Trans R Soc B* 364: 1789–1801.
51. Fryxell JM, Greever J, Sinclair ARE (1988) Why are migratory ungulates so abundant? *Am Nat*: 781–798.
52. Van Nouhuys S, Hanski I (2002) Colonization rates and distances of a host butterfly and two specific parasitoids in a fragmented landscape. *J Anim Ecol* 71: 639–650.
53. Koelle K, Vandermeer J (2005) Dispersal-induced desynchronization: from metapopulations to metacommunities. *Ecol Lett* 8: 167–175.
54. Ripa J (2000) Analysing the Moran effect and dispersal: their significance and interaction in synchronous population dynamics. *Oikos* 89: 175–187.
55. Avgar T, Mosser A, Brown GS, Fryxell JM (2013) Environmental and individual drivers of animal movement patterns across a wide geographical gradient. *J Anim Ecol* 82: 96–106.
56. Boecdi G, Heinonen J, Travis JM (2012) Uncertainty and the role of information acquisition in the evolution of context-dependent emigration. *Am Nat* 179: 606–620.
57. Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol Rev* 80: 205–225.
58. McPeck MA, Holt RD (1992) The evolution of dispersal in spatially and temporally varying environments. *Am Nat* 140: 1010–1027.
59. Schick RS, Loarie SR, Colchero F, Best BD, Boustany A, et al. (2008) Understanding movement data and movement processes: current and emerging directions. *Ecol Lett* 11: 1338–1350.
60. Travis JMJ (2001) The color of noise and the evolution of dispersal. *Ecol Res* 16: 157–163.
61. Schwager M, Johst K, Jeltsch F (2006) Does red noise increase or decrease extinction risk? Single extreme events versus series of unfavorable conditions. *Am Nat* 167: 879–888.
62. Fontaine C, Gonzalez A (2005) Population synchrony induced by resource fluctuations and dispersal in an aquatic microcosm. *Ecology* 86: 1463–1471.
63. Long ZT, Petchey OL, Holt RD (2007) The effects of immigration and environmental variability on the persistence of an inferior competitor. *Ecol Lett* 10: 574–585.
64. Stomp M, Huisman J, De Jongh F, Veraart AJ, Gerla D, et al. (2004) Adaptive divergence in pigment composition promotes phytoplankton biodiversity. *Nature* 432: 104–107.
65. Cohen AE, Gonzalez A, Lawton JH, Petchey OL, Wildman D, et al. (1998) A novel experimental apparatus to study the impact of white noise and 1/f noise on animal populations. *Proc R Soc Lond B* 265: 11–15.
66. Amarasekare P, Nisbet RM (2001) Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. *Am Nat* 158: 572–584.
67. Lindström T, Håkansson N, Wennberg U (2011) The shape of the spatial kernel and its implications for biological invasions in patchy environments. *Proc R Soc B* 278: 1564–1571.
68. Roy M, Holt RD, Barfield M (2005) Temporal autocorrelation can enhance the persistence and abundance of metapopulations comprised of coupled sinks. *Am Nat* 166: 246–261.
69. Abrams PA, Ruokolainen L, Shuter BJ, McCann KS (2012) Harvesting creates ecological traps: Consequences of invisible mortality risks in predator-prey metacommunities. *Ecology* 93: 281–293.
70. Gouhier TC, Guichard F, Menge BA (2013) Designing effective reserve networks for non-equilibrium metacommunities. *Ecol Appl* In press.