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LETTER

Dispersal-induced desynchronization: from metapopulations to metacommunities

Katia Koelle* and John Vandermeer
The Department of Ecology and Evolutionary Biology, 2019 Kraus Natural Science Building, University of Michigan, 830 North University Avenue, Ann Arbor, MI 48109-1048, USA
**Correspondence: E-mail: kkoelle@umich.edu*

Abstract

The conceptualization of fragmented populations in terms of metapopulation theory has become standard over the last three decades. It is well known that increases in between-patch migration rates cause more synchronous population fluctuations and that this coherence increases the risk of global metapopulation extinction. Because species' migration rates and the probability of individuals surviving migration events depend on the effective distance between patches, the benefit of improving conservation corridors or the matrix between habitat patches has been questioned. As populations occur in the context of larger communities, moving from a metapopulation to a metacommunity model framework is a natural extension to address the generality of these conclusions. We show how considering a metacommunity can modify the conclusion that decreasing the effective distance between habitat patches (via improving matrix quality or other measures) necessarily increases the degree of metapopulation synchrony. We show that decreases in effective between-patch distance may deter population synchrony because of the simultaneous effect this change has on the migration patterns of other species. These results indicate that species interactions need to be considered when the effect of conservation measures on population synchrony, and ultimately persistence, is addressed.

Keywords

Coherence, coupled oscillators, dispersal, metacommunity, metapopulation models, synchrony.

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INTRODUCTION

Due to extensive fragmentation of many species' habitats, the dynamics of metapopulations have increasingly been studied both theoretically and empirically (Sih *et al.* 2000). Explicit consideration of local population dynamics has led to the general conclusion that synchrony, or coherence, in the fluctuations of the local populations is a likely consequence of interpatch migration (Hastings 1993; Ranta *et al.* 1995, 1997, 1998; Ruxton & Rohani 1998; Blasius *et al.* 1999; Sherratt *et al.* 2000; Shimada & Ishihama 2000) – an important result because synchronous fluctuations in subpopulations increase the risk of extinction of the entire metapopulation through generating temporally correlated extinction events and deterring the rescue effect (Harrison & Quinn 1989; Hanski 1991; Heino *et al.* 1997; Earn *et al.* 2000). The amount of dispersal that is capable of synchronizing a metapopulation's dynamics is known to depend on the local populations' extension in space, the specifics of the patches' density-dependent form, and the degree of coupling between the habitat patches. However, an unavoidable general qualitative pattern arises in all of these circumstances: an increase in dispersal rate inevitably leads to an increased degree of coherence. This synchrony-inducing effect of coupling between patches has highlighted the nonlinear effect of dispersal on global metapopulation persistence, with dispersal being considered a 'two-edged sword': a metapopulation whose local populations are too connected risks extinction because of synchrony, while a metapopulation whose populations are too isolated risks extinction because of low interpatch migration rates (Hudson & Cattadori 1999). Quantifying the optimal dispersal rate for the continued persistence of a metapopulation therefore becomes critical in a variety of practical applications, such as reserve design (Williams *et al.* 2004), or landscape conservation (Vandermeer & Carvajal 2001).

A more recent fusion of ideas from metapopulation theory and community ecology has generated an interest in metacommunity theory, where a metacommunity can be defined as a set of local communities on distinct habitat patches, linked by dispersal of one or more of its constituent species (Wilson 1992; Holt 1997). Although the most common focus of metacommunity theory has been to address species coexistence while metapopulation theory has focused on population persistence (Leibold *et al.* 2004; Leibold & Miller 2004), several studies have considered how the effects of interspecific interactions modulate the metapopulation dynamics of a focal species and vice versa (Hanski 1999). Of particular interest, Holt and colleagues have focused on the effect of metapopulation dynamics on food chain length (Holt 1977), while Caswell and Cohen have proposed a model of succession in which a species' patch colonization and extinction rate is ecosystem-dependent (Caswell & Cohen 1991).

Here we use a metacommunity framework to address population synchrony, specifically posing the question of how a fragmented population's persistence depends not only on its own between-patch migration rates, but also on the migration rates of the species with which it directly or indirectly interacts. We revisit the general conclusion from metapopulation theory that increased dispersal inevitably induces a greater degree of synchrony and demonstrate that adopting a metacommunity framework can modify the dominant pattern found in metapopulation theory. We show that the consequences of migration depend on the details of the food web in which the population in question is embedded. When proper account is taken of the migration patterns of the components in the food web we find that decreasing the effective distance between patches, via improvements in matrix quality for example, and thereby increasing all species' migration rates, may decrease the degree of population synchrony of a focal species present in the metacommunity.

METHODS

To address the effect of within-patch species interactions on between-patch population synchrony, we use a simple metacommunity model consisting of only two habitat patches, each of which harbors a tri-trophic food web. The three species community on each patch is given by a previously published model (Hastings & Powell 1991), and dispersal between the patches is modeled by including interhabitat migration of species x, y, and z. With species x being the basal species, species y being the intermediate species, and species z being the top species, the equations for patch 1 are:

$$\begin{aligned}\frac{dx_1}{dt} &= x_1(1-x_1) - f_x y_1 + m_x(s_x x_2 - x_1)\\ \frac{dy_1}{dt} &= f_x y_1 - f_y z_1 - d_y y_1 + m_y(s_y y_2 - y_1)\\ \frac{dz_1}{dt} &= f_y z_1 - d_z z_1 + m_z(s_z z_2 - z_1)\end{aligned} \qquad (1)$$

The functional responses are given by $f_x = \frac{a_x x_1}{1+b_x x_1}$ and $f_y = \frac{a_y y_1}{1+b_y y_1}$. Subscripts 1 and 2 refer to the populations residing on patch 1 and 2, respectively. Migration rates between patches are given by m_x, m_y, and m_z, and the probabilities of surviving migration are given by s_x, s_y, and s_z for species x, y, and z, respectively. Three analogous equations exist for patch 2, describing the population fluctuations of x_2, y_2, and z_2. The model is parameterized such that all three species' dynamics are oscillatory when the patches are completely isolated from one another. When migration of at least one of the species occurs, the two-patch system becomes a metacommunity, with local populations capable of exhibiting dispersal-induced synchrony. Between-patch survival probabilities and migration rates are dependent on a species' life-history characteristics as well as on the effective distance between habitat patches through which migration occurs. Conservation measures, including improvements in matrix quality between patches or the building of conservation corridors between patches, act to decrease the effective distance between patches that would otherwise be isolated by impervious space (Perfecto & Vandermeer 2002).

Extensive empirical results have identified the effects of distance on species' migration rates and survival probabilities. Here, we use two distinct dispersal models that provide alternative frameworks for addressing the consequences of changes in effective distance between patches on migration and survival rates, and in turn, on the degree of population synchrony. The first framework uses a leptokurtic redistribution kernel that models distance between patches as an input parameter affecting species' migration rates. Leptokurtic kernels describe the probability of an individual's offspring dispersing to a distance d as:

$$k(d) = (0.5\sqrt{c/D})e^{-d\sqrt{c/D}} \qquad (2)$$

with parameters c and D both greater than 0 (Neubert *et al.* 1995). A leptokurtic dispersal kernel for species' migration rates was chosen because empirical data suggest that for many species the functional relationship between the relative frequency of dispersal and distance from a source over a continuous landscape exhibits this shape (Makino *et al.* 1987; Willson 1993). Compared with a Gaussian redistribution kernel, the leptokurtic redistribution kernel has more frequent dispersal events to far distances. To use this empirically-based redistribution kernel in determining migration rates between habitat patches, we let migration rates between two habitat patches exhibit similarities to redistribution frequencies over continuous landscapes. For species x, the migration rate between two patches is thereby:

$$m_x = (0.5\sqrt{c_x/D_x})e^{-d\sqrt{c_x/D_x}} \tag{3}$$

where parameters c_x and D_x are species-specific. Similar migration kernels exist for species y and z. In this model, the probability of an individual of any species surviving migration is assumed to be one. The assumption of all emigrants becoming immigrants on other patches has the modelling advantage of functionally corresponding to previous theoretical single-species models that address metapopulation synchrony (e.g. Blasius *et al.* 1999; Earn *et al.* 2000).

Our second modelling framework is one explicitly formulated for metapopulation dynamics (Hanski 1999). This model has been successfully parameterized in metapopulations of butterflies, among other species (Hanski *et al.* 2000). It assumes that the migration rate of species from a patch is independent of the patch's connectivity. A patch's connectivity C is quantified by taking into consideration the distance between it and its neighbouring patches; patches with more proximal neighbours are more highly connected, all else being equal. Although not affecting migration rate, a patch's connectivity affects the survival probability of a migrating individual. Emigrants from a patch with high connectivity have a higher probability of surviving migration than emigrants from a patch with low connectivity. The probability of a species x surviving migration is then given by:

$$s_x = \frac{C^2}{\lambda_x + C^2} \tag{4}$$

where λ_x is a species-specific parameter. Survival probabilities for other species are similarly given.

These two frameworks present complementary approaches to modelling the consequences of changing the effective distance between patches on migration events. While the leptokurtic dispersal framework assumes that decreasing the effective interpatch distance increases the migration rates of species, not their survival probabilities, the connectivity framework assumes the opposite. Reality lies somewhere between these two extremes. By modelling these two extremes, however, we are confident that our analyses focusing on the effects of decreases in the effective distance between patches are sufficiently general.

To quantify the effect of migration on metapopulation synchrony, we use several synchrony measures. The first measure is the Pearson moment correlation coefficient (r), which has the benefit of being calculable from empirical data sampled at constant (usually yearly) time intervals. It is computed as described in (Bjørnstad *et al.* 1999a,b), with the emphasis being on synchrony of the population growth rates between neighbouring habitats, as opposed to synchrony of the population sizes. Field studies quantifying the degree of synchrony between patches have used this measure, resulting in the identification of general spatial patterns such as decreases in population synchrony as a function of distance between habitats (Hanski & Woiwod 1993; Bjørnstad *et al.* 1999a,b). Another measure to quantify changes in the degree of synchrony is the phase difference between population cycles. A population cycling at a natural frequency Ω can have its cycle decomposed into an amplitude A and a phase ϕ (Blasius *et al.* 1999). When sufficient migration causes two heterogeneous populations to become entrained (i.e. exhibiting the same frequencies Ω), their population peaks do not necessarily occur together. The populations can exhibit a degree of phase-locking, where at time t the phase ϕ of one population is different from the phase ϕ of the other population. This difference, calculated by computing the difference in phases ($\Delta\phi = \phi_1 - \phi_2$), measures the degree to which population sizes peak together. It is an alternative measure to the Pearson correlation coefficient r, but increases in r are usually accompanied by decreases in phase differences $\Delta\phi$ once populations are entrained.

A third way to visualize the degree of synchrony between two populations is to plot the size of one population against the size of the other population for all points in time. This visualization tool allows us to see whether low population sizes tend to occur at the same time. This graphical approach to assessing the degree of synchrony has the advantage of allowing us to focus on only a part of the time series. This is useful when the overall degree to which populations are synchronized is not of interest, for instance when we are more interested in ascertaining whether low populations sizes occur together (and thereby when there is a high chance of a regional or global extinction event). We, therefore, also illustrate some of our results by using these graphical plots.

Alternative ways to measure synchrony exist. For example, to address the effect of coherence on metapopulation persistence, Earn and colleagues computed the probability of metapopulation coherence using 10^4 simulations with different initial conditions. They define a coherent metapopulation as being one with the patches' population sizes being within 10% of each other after 10 iterations of a discrete-time model (Earn *et al.* 2000). We do not use this approach in assessing synchrony.

All simulations were run for 5000 units of time, with measures of synchrony being computed after the removal of transients (the first 2500 units of time). Initial conditions were chosen at random from population sizes of the unlinked patches.

RESULTS

We first illustrate the basic behaviour of the system with a simple time series subject to changes in migration pattern. Consider two habitat patches, with a tri-trophic community on each patch (eqn 1). First, the two isolated patches are initiated such that the top species z in both patches are oscillating, with some phase difference between them (from time T_0 to time T_1). At time T_1 a small amount of migration of the top species z is introduced, and later at time T_2 the migration of the top species ceases and migration of the basal species x is initiated. With migration of the top species (at T_1), the populations of the top species start synchronizing, as is evident by the trajectories converging on one another. With migration of only the basal species x (at T_2) the population trajectories of the top species z diverge with respect to one another, reversing the synchrony established during the migration of the top species z (Fig. 1a,b). This pattern is observed in tri-trophic metacommunities that exhibit stable limit cycle behavior (Fig. 1a) as well as in ones that exhibit chaotic dynamics (Fig. 1b).

According to theoretical and simulation studies within a metapopulation framework, an increase in the dispersal rate of any one of the species should result in increased population synchrony of that species. Yet, as can be seen in this simple example, this expectation does not hold for all of the species in the community. In particular, when the basal species x is the one migrating, not only do the top species subpopulations not synchronize in phase, there is a strong tendency toward anti-phase dynamics (Fig. 1a,b). A metapopulation's degree of synchrony and the magnitude of its phase differences are, therefore, affected by migration patterns not only of its own members, but also by the migration patterns of the species with which it interacts, directly or indirectly. It is these interactions that open the possibility for desynchronization to occur for subpopulations at the level of the metacommunity. We return to this basic behavioural pattern when we discuss the underlying mechanisms thought to be responsible for the observed pattern.

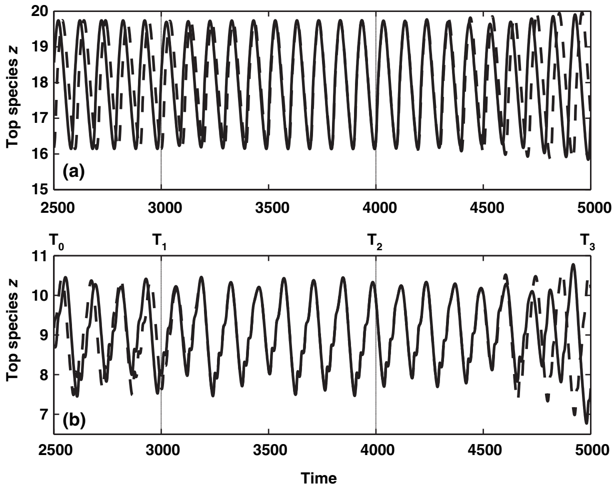

Figure 1 Time series of top species z in patch 1 (dashed) and top species z in patch 2 (solid). At time T_1 the isolated system was coupled by allowing migration of the top species z ($m_z > 0$). At time T_2 the coupling was changed such that the top species z no longer migrated, but the basal species x did ($m_x > 0$). (a) Population dynamics exhibiting stable limit cycle behaviour. Parameters for these time series are: $a_x = 2.17$, $a_y = 0.055$, $b_x = 1.25$, $b_y = 1.02$, $d_y = 0$, $d_z = 0.0058$, $m_y = 0$, $m_z = 0$ or 0.0025 (from T_1 to T_2), $m_x = 0$ or 0.02 (from T_2 to T_3). (b) Population dynamics exhibiting chaotic cycles. Parameters are: $a_x = 5$, $a_y = 0.1$, $b_x = 3$, $b_y = 2$, $d_y = 0.4$, $d_z = 0.01$, $m_y = 0$, $m_z = 0$ or 0.015 (from T_1 to T_2), $m_x = 0$ or 0.06 (from T_2 to T_3).

The behaviour of the system when only one component migrates (Fig. 1, T_1–T_2 and T_2 to T_3) is unrealistic in that all constituent species of a metacommunity are likely to migrate. Moreover, all species are likely to migrate more frequently or have a higher inter-patch survival probability as the effective distance between habitat patches decreases, via improvements in matrix quality or new conservation corridors. The patterns observed when all species' migration rates or survival rates change in response to changes in effective distance therefore need to be the focus of interest for conservation studies.

To determine the dynamics that arise from all species being affected by decreases in effective distance, or higher connectivity, between patches, we first use the leptokurtic dispersal framework described above. In this model, migration rates differ between species, but all monotonically increase with decreases in between-patch effective distances (Fig. 2a), and all migrants are assumed to survive migration events. When the effective distance between habitats is high, migration levels are low, and the all species subpopulations are highly in-phase synchronized, as indicated by both Pearson's correlation coefficient r (Fig. 2b) and the phase difference $\Delta\phi$ (Fig. 2c). However, as the effective distance between habitat patches decreases, via increases in matrix quality or the building of conservation corridors, full in-phase synchrony breaks down for both the basal species x and the intermediate species y, while the subpopulations of the top species z remain fully synchronized. These decreases in synchrony for two of the constituent species of the metacommunity indicate that conservation measures focusing on matrix quality improvements need not necessarily increase the risk of global metapopulation extinction through synchronization of subpopulations. In some metacommunities, therefore, the 'two-edged sword' of migration rates may become one-edged again.

Changes in correlations between any two subpopulations can be visualized by plotting the population size of one

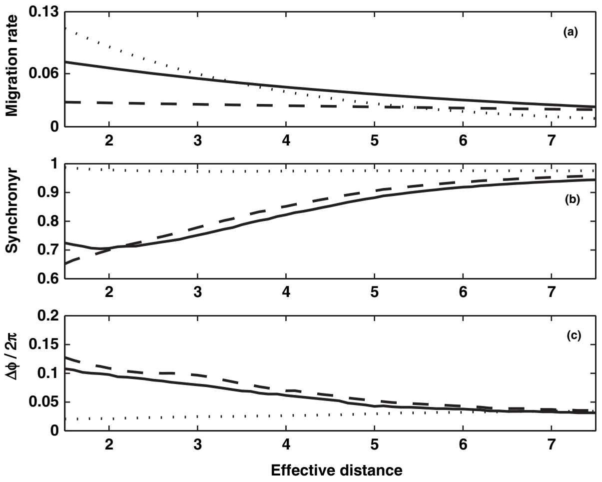

Figure 2 The effects of considering migration rates as a function of effective distance, using the leptokurtic dispersal kernel framework. (a) Migration rates of species x (solid), y (dashed), and z (dotted) comprising the metacommunity. (b) Population synchrony of the three metapopulations as a function of effective distance using Pearson's correlation coefficient r as the metric to quantify the extent of synchrony. Decreases in effective distance decrease the degree of synchrony for the basal species x and the intermediate species y, while increasing the degree of synchrony for the top species z. (c) The degree of population synchrony, as measured by the phase difference between the populations, as a function of effective distance. Decreases in effective distance increase the phase difference between the population cycles, for both the basal and the intermediate species, while slightly decreasing the phase difference between the top species populations. All simulations in which phase differences were computed exhibited fully entrained dynamics, such that there were no frequency differences present between populations on different patches. Ten replicate simulations were shown for each effective distance value, with similar results across replicates. Simulations had different initial conditions chosen at random from population sizes of the unlinked patches. Parameter values for the simulations are: $a_x = 5.0$, $a_y = 0.1$, $b_x = 2.25$ (patch 1), $b_x = 2.30$ (patch 2), $b_y = 2.0$, $d_x = 0.4$, $d_y = 0.01$ for the interspecific interactions, and $c_x = 0.1187$, $D_x = 3.0653$, $s_x = 1$, $c_y = 0.0165$, $D_y = 4.4477$, $s_y = 1$, $c_z = 0.3315$, $D_z = 1.9433$, and $s_z = 1$ for the parameters associated with migration.

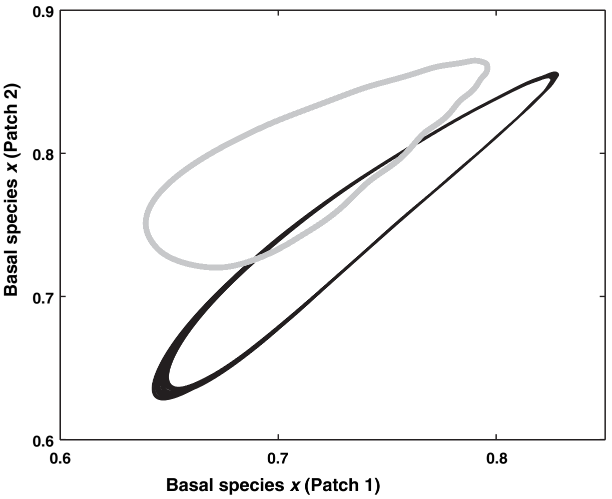

Figure 3 Changes in synchrony occurring via changes in migration rates. Population size of the basal species x on patch 2 (y-axis) plotted against the population size of the basal species on patch 1 (x-axis). The black projection is for an effective distance of $d = 7.0$ and the grey projection is for effective distance $d = 2.0$. Decreases in effective distance change the form of the phase-space attractor.

species on one patch against the population size of the species on the other patch. For the basal species, this projection indicates that at high effective distances between patches ($d = 7.0$), the subpopulations are highly synchronized (Fig. 3). At a lower effective distance between patches ($d = 2.0$), the subpopulations become less synchronized, although positive correlations between population sizes, as well as population growth rates, do still exist. Beyond decreases in overall synchrony, this projection indicates that that the shape of the attractor is dependent on the migration levels of the component species, resulting in less pronounced, and less synchronized, population minima at low effective distances.

Although decreases in effective distance, or higher connectivity between patches, can affect a metacommunity by increasing migration rates between patches, there are alternative effects of these changes on metacommunity rates. One such alternative effect is that increases in patch connectivity increases the survival rate of individuals migrating between patches (Hanski 1999) (eqn 4, Fig. 4a). Modelling this effect, while assuming constant species migration rates for any degree of patch connectivity, yields similar results: increases in patch connectivity can lead to reduced synchrony (Fig. 4b). In this example, not only do patch connectivity improvements reduce the degree of subpopulation synchrony for all component species, but there is a tendency towards high anti-phase synchrony.

We return to the first model formulation, in which migration rates depended on effective inter-patch distances, and complete survival of migrants was assumed. To determine whether the degree to which these results depend on the particular parameter values or dynamic regimes chosen, we investigated the pattern as a function of changing dynamic circumstances. We used the functional response parameter b_x in patch 2 as a vehicle for changing the dynamics of the metacommunity. The range of values of the parameter b_x was large enough to include both limit cycle and chaotic behaviour of the uncoupled system in patch 2. We simulated the model for a range of effective distances and a range of b_x values, and colour-coded the degree of synchrony between subpopulations of the basal

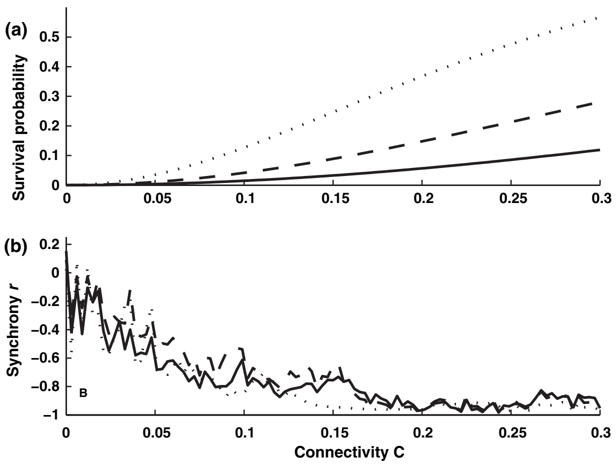

Figure 4 The effects of considering survival probabilities as a function of connectivity. (a) Survival probabilities s_x, s_y, and s_z of species x (solid), y (dashed), and z (dotted), respectively, comprising the metacommunity. Survival probabilites differ between species, but all are monotonically increasing functions of connectivity. (b) Population synchrony of the three metapopulations as a function of connectivity. Pearson's correlation coefficient r is used as the metric to quantify the extent of synchrony. Ten replicates were simulated for each matrix quality value, starting with different initial conditions (replicate simulations result in similar synchrony responses). Initial conditions were chosen at random from population sizes of the isolated patches. Parameter values for the simulations are: $m_x = 0.00068116$, $m_y = 0.2427$, $m_z = 0.0023$, $\lambda_x = 0.66641$, $\lambda_y = 0.23057$, and $\lambda_z = 0.068839$.

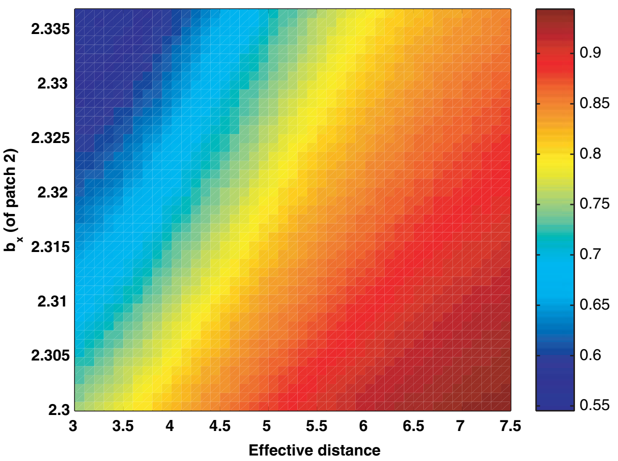

Figure 5 The generality of results across different dynamical regimes. As effective distance increases (x-axis) for a given value of b_x in patch 2 (y-axis), the degree of synchrony of the basal species x increases, as measured by Pearson's r. This decrease is evident for a range of b_x parameter values. The parameter range for b_x was chosen for its ability to generate both stable limit cycle behaviour and chaotic dynamics for patch 2 (in the absence of migration).

species (Fig. 5). The degree of synchrony clearly depends on the value of b_x, yet the underlying pattern remains consistent: decreases in synchrony can occur when the effective distance between patches is lowered through conservation measures.

Returning to the emerging pattern of desynchronization at lower effective distances when all species were migrating (Fig. 2b), we investigated the impact of changes in distance on the migration of each species separately (Fig. 6). When the basal species x is the only species migrating, there tends to be some degree of asynchrony resulting for all species ($r < 0$) (Fig. 6a), although it is minor for the basal species itself. The top species z becomes quickly asynchronized at any level of species x migration. Unlike migration of the basal species x, migration of the intermediate species y tends to strongly synchronize the subpopulations of the metacommunity ($r \approx 1$) (Fig. 6b). Furthermore, decreases in effective distance tend to more strongly synchronize the subpopulations, producing effects similar to those expected with one-species metapopulation models. Migration of only the top species z generates a considerably more complicated synchrony pattern (Fig. 6c). While decreases in effective distance serve to synchronize the dynamics of the top species, the degree of synchrony for the subpopulations of the basal species x and the subpopulations of the intermediate species y tend to decrease with decreases in distance. The general patterns from these simulations indicate that migration of the basal species induces asynchronous dynamics of the metacommunity's subpopulations, while migration of the intermediate species strongly synchronizes these subpopulations. Migration of the top species tends to synchronize the subpopulations ($r > 0$), but the effective distance largely determines the degree to which these subpopulations synchronize. These results are in agreement with the results shown in Fig. 1, in which the migration of the top species z alone produces synchronous population dynamics, while the migration of the basal species x alone produces asynchronous population dynamics, in both cases for the top species z.

DISCUSSION

In the above metacommunity models, oscillatory local population dynamics arise from two endogenous feedbacks, namely density-dependent growth and interspecific interactions. In one-species metapopulation studies that address metapopulation synchrony, oscillatory population dynamics arise only from intraspecific competition. In both metapopulation models and our metacommunity framework, decreases in effective distances between patches result in either increased migration rates or increased survival rates of individuals migrating between patches. However, our model explicitly considers that changes in effective distances

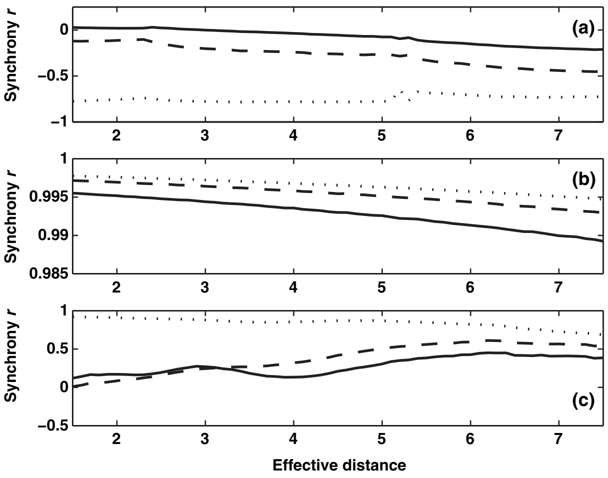

Figure 6 The synchronizing effects of considering migration of only one species at a time. The degree of synchrony was measured using Pearson's *r*. (a) The degree of synchrony for all three species (x = solid, y = dashed, z = dotted), resulting from the migration of only the basal species x. Any migration of species x leads to anti-phase dynamics of the constituent metapopulations. (b) The degree of synchrony for all three species resulting from the migration of only the intermediate species y. Decreases in effective distance increase the degree of synchrony of all three metapopulations, although there is a high degree of synchrony for any distance level. (c) The degree of synchrony for all three species resulting from the migration of only the top species z. Increased migration of species z at lower effective distances leads to increased population synchrony of species z itself, but also to non-monotonic effects on the between-patch synchrony of species x and of species y. Parameter values are as for Fig. 1.

between patches impact not only one focal species, but all of the species residing on the patches. Because these species are linked via direct or indirect interactions, increases in population synchrony do not necessarily result from conservation measures that lower the effective inter-patch distance. The origin of endogenous population cycling may, therefore, play an important role in understanding and predicting the effect of between-patch migration on population synchrony.

These numerical simulations show that increasing the migration rates of some species can have synchrony-deterring effects on a focal species. A qualitative interpretation of these results can be gained from a lower dimensional system. If we presume that the lower trophic level has extremely fast dynamics compared with the higher two levels, we can conceptualize the system as a pair of coupled consumer/resource oscillators, a formation that has been extensively analysed (Vandermeer 2004). If the consumer in one patch is linked to the resource in the other patch, and the effective migration between the two patches is not too large, we expect the oscillations in the two patches to become entrained in-phase. On the other hand, if the resource in one patch is linked to the resource in the other patch, such that the resources in the two patches compete with one another, we expect the oscillations in the two patches to become entrained in an anti-phase pattern (Vandermeer 2004). In our tri-trophic model if either the top species z or the intermediate species y is the only migrating species, the system is always in-phase coordinated ($r > 0$), while if only the basal species x migrates the system is always coordinated in a reversed or anti-phase fashion ($r < 0$). If coupling occurs via the intermediate species y, that is tantamount to allowing z_1 to eat a little bit of y_2 and z_2 to eat a little bit of y_1, which is the same as the consumer/resource connection in the consumer/resource coupled model (where z is the consumer and y is the resource). Thus we expect z_1 and z_2 to be in-phase, as observed. On the other hand, if coupling occurs via the basal species x, that is tantamount to allowing y_1 to eat a little of x_2 and y_2 to eat a little of x_1, which is the same as the resource/resource competition connection in the consumer/resource coupled model (where z is still consumer and y is still resource). Thus we expect z_1 and z_2 to be anti-phase, as observed.

The pattern in synchrony with a change in effective distance (Fig. 2) can thus be intuitively explained because we have three migration rates that vary. Because the component species have different sensitivities to changes in effective distance, the migration rate that dominates the dynamics changes with distance. The resulting degree of subpopulation synchrony is therefore determined by a combination of the three migration rates, as well as the way in which the species interact. Further research into the dynamics of coupled oscillators may be a way to approach a systematic study of why and when subpopulations may resist synchronization. The additional development of analytical approaches to study the effects of multiple species migrations on a focal species' degree of synchrony is necessary, such as the recently developed local stability analysis framework used to determine whether a system is spatially homogenous across multiple patches (Jansen & Lloyd 2000). Nevertheless, this research gives initial insight into the complex consequences that changes in effective distance may have on population synchrony.

Previous simulation studies have shown that the degree of metapopulation synchrony differs in models with two patches vs. a large number of patches (Ylikarjula *et al.* 2000). Extensions of this simple metacommunity model to more patches and to more complex webs of interactions are therefore necessary. Preliminary results indicate that metacommunities consisting of ten equally-coupled patches, each harbouring a community of seven species food webs (modelled with a web discussed in Fussmann & Heber 2002), exhibit similar desynchronization tendencies in certain parameter regions (results not shown). Migration-induced desynchronization therefore seems to be a robust phenomenon occurring for different kinds of species interactions, over various metacommunity sizes.

As we focused solely on the differential effects of distance on species migration and survival rates, and the synchronization patterns that emerge from the coupling of the patches, we do not explicitly address the question of effective distance, or matrix quality, on species extinction. While some previous research argues that enhanced coherence would decrease the probability of species persistence (Earn *et al.* 2000), other research suggests that dynamical phase-locking between patches, producing travelling waves on spatial landscapes, may play a stabilizing role in species persistence (Blasius *et al.* 1999). An evaluation of synchrony and its effect on species persistence is a natural extension to this metacommunity framework model.

Other mechanisms besides migration patterns may also cause metapopulation synchrony. For example, both correlated environmental forcing (the Moran effect) and nomadic predators are capable of synchronizing local population dynamics (Hudson & Cattadori 1999). Whether adopting a metacommunity framework can deter the synchronizing effects of these other two mechanisms is an interesting question that still needs to be addressed.

In light of the metacommunity results described above, we conclude that the pattern of dispersal-induced synchrony derived from metapopulation studies may not hold when populations are considered within the context of their structured, interacting communities. In terms of practical applications, whatever problem has been identified vis-à-vis metapopulation coherence, its details depend on how all the elements of the food web behave spatially. The problem of coherence, then, becomes similar to the problem of food web dynamics in general – conclusions based on knowledge of only a few connections may be misleading.

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