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ORIGINAL PAPER

Beyond connectivity: how the structure of dispersal influences metacommunity dynamics

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Abstract Dispersal within metacommunities can play a major role in species persistence by promoting asynchrony between communities. Understanding this role is crucial both for explaining species coexistence and managing landscapes that are increasingly fragmented by human activities. Here, we demonstrate that spatial patterning of dispersal connections can drastically alter both the tendency toward asynchrony and the effect of asynchrony on metacommunity dynamics commonly used to infer the potential for persistence. We also demonstrate that changes in dispersal connections in strictly homogeneous predator-prey metacommunities can generate an extremely rich variety of dynamics even when previously investigated properties of connectivity such as the magnitude and distribution of dispersal among patches are held constant. Furthermore, the dynamics we observe depend strongly on initial conditions. Our results illustrate the effectiveness of measures of spatial structure for predicting asynchrony and its effects on community dynamics, providing a deeper understanding of the relationship between spatial structure and species persistence in metacommunities.

Keywords Metacommunities · Dispersal · Synchronization · Stability · Connectivity · Fluctuations · Consumer-resource interactions

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Introduction

Modern ecology has demonstrated that spatial processes play a major role in community functioning. Spatially extended communities ("metacommunities") differ fundamentally from the classical conception of individual well-mixed communities (Leibold et al. 2004) as their component parts (patches) can exhibit differing dynamics ("synchrony"), while still interacting through dispersing organisms. Asynchrony can include a range of dynamical differences depending on operational definition, from variation in the timing of otherwise identical community dynamics to dramatic shifts in equilibrium values or limit cycle amplitudes. Asynchronous dynamics have many dramatic effects on metacommunities, enabling the persistence of extinction-prone species through rescue effects (Brown and Kodric-Brown 1977), reducing population variability through averaging (Maser et al. 2007), and otherwise buffering the effects of perturbations (Buckling et al. 2000; Chesson and Huntly 1997) relative to isolated communities. As the key feature governing the effects of space on community dynamics, understanding the conditions necessary for asynchrony to occur is a crucial goal of metacommunity ecology (Gouhier et al. 2010; Steiner et al. 2011), and has implications for conservation, reserve design, and biological control (Crooks and Sanjayan 2006; Murdoch et al. 2003). It has been well demonstrated that high dispersal tends to synchronize communities and thereby remove the effects of space from metacommunities (Hastings 1993; Koelle and Vandermeer 2005). However, the structure of dispersal connections ("spatial structure") between community patches determines the amount of dispersal necessary to synchronize a metacommunity (Arenas et al. 2008), playing a central although less understood role in governing metacommunity dynamics.

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A complete theory on the dynamics of ecological communities therefore requires that the effect of spatial structure on metacommunity synchronization be fully described. Thus far it has been well established that synchronization is strongly influenced by the number of dispersal connections, or "connectivity," (Liebhold et al. 2004; Paradis et al. 1999; Holyoak and Lawler 1996) and the evenness of their distribution among patches, or the "degree" of each patch (Watts and Strogatz 1998; Holland and Hastings 2008; Gilarranz and Bascompte 2012). As a result, connectivity and related measures have been the focus in studies of structure and dynamics (Bunn et al. 2000; Marleau et al. 2014; Plitzko and Drossel 2015; Saunders et al. 1991; Taylor et al. 1993). However, such measures remove information about the patterning of connections among communities such as how often communities share neighbors, form tightly interconnected neighborhoods, and how distant communities are from these neighborhoods (Arenas et al. 2008). The patterning of connections among communities also includes many properties which may be unintuitive but play an important role dynamically such as the spectral properties of the connectivity matrix (Barahona and Pecora 2002). Because these elements of structure are more challenging to measure and observe, they are often overlooked and as a result the role of the patterning of connections in metacommunity synchronization has not been well described. Moreover, overlooking these features risks confounding the effects of connectivity and the patterns of connections on synchronization. Identifying the unique contribution of the patterning of connections among communities is therefore necessary to understand how spatial structure determines synchronization in metacommunities.

Here, we demonstrate the unique effects of dispersal connection patterning on the tendency of metacommunities to synchronize, independent of connectivity or degree distribution. To accomplish this, we consider a set of "regular" spatial structures with the same number of connections between each patch and a completely even distribution of these connections among patches. The set of regular spatial structures we consider are therefore perfectly equivalent in terms of measures of connectivity, specifically the total number of connections and the evenness of their distribution among communities. Nevertheless, alternative measures describing the pattern of connections, such as the frequency of clustering and topological distance between communities, do differ among these structures and have been shown to influence synchronization (Arenas et al. 2008; Barahona and Pecora 2002; Watts and Strogatz 1998). We further asses the role of the pattern of connections among communities in synchronization by comparing the dynamics of a simple metacommunity model on regular structures with equal connectivity but varying patterns of connection. We consider a simple case of community dynamics, a predator-prey model, to focus on the role of spatial processes. Furthermore, by holding parameter values equal across all patches, we guarantee that each patch is identical to every other across all spatial structures, as each patch has the same number of dispersal connections and local dynamics. These metacommunities are therefore completely homogeneous and highly prone to synchrony.

We explore the role of the patterning of dispersal connections on synchronization by analyzing the reaction of these metacommunities with regular spatial structures to a range of asynchronous initial conditions, simulating a spatially heterogeneous perturbation. These tests reveal the tendency of individual structures to either synchronize or switch to asynchronous states following perturbation, highlighting the role of connectivity-independent structure. We further determine how asynchrony influences the dynamics of communities, particularly how well asynchrony stabilizes an unstable predator-prey interaction at both the regional and local scales. Through this analysis, we hope to further reveal the deeply complex relationship between spatial structure and community interactions, a topic of central importance for understanding metacommunity ecology and explaining the spatial dynamics observed in nature.

Methods

To simulate metacommunity dynamics, we chose a Rosenzweig-MacArthur predator-prey model (Rosenzweig and MacArthur 1963) with dispersal:

$$\frac{dH_i}{d\tau} = rH_i\left(1 - \frac{H_i}{K}\right) - \frac{aP_iH_i}{b + H_i} + D\sum_{j=1}^{n} L_{ij}H_j \tag{1}$$

$$\frac{dP_i}{d\tau} = \frac{caP_iH_i}{b + H_i} - mP_i + D\sum_{j=1}^{n} L_{ij}P_j \tag{2}$$

where H_i and P_i are the prey and predator abundances, respectively, in patch i, K is the prey's carrying capacity, a is the predator's attack rate, b is the half-saturation coefficient of the predator's functional response, c is the conversion rate of consumed prey to predator offspring, m is predator mortality, D is dispersal rate (equal for both species). The matrix L_{ij} is a negative Laplacian describing the structure of dispersal between patches; an off-diagonal element L_{ij}, $(i \neq j)$ indicates the presence (1) or absence (0) of dispersal from patch j to patch i and a diagonal element L_{ii} is the negative sum of off-diagonal elements for column i, reflecting the total amount of emigration from patch i. In our networks, dispersal is always bi-directional $(L_{ij} = L_{ji})$.

To further simplify model analyses, we employ a non-dimensional form of Eqs. 1 and 2 (Holland and Hastings 2008):

$$\frac{dh_i}{dt} = h_i(1-\theta h_i) - \frac{p_i h_i}{1+h_i} + \delta \sum_{j=1}^{n} L_{ij} h_j \tag{3}$$

$$\frac{dp_i}{dt} = \frac{\phi p_i h_i}{1+h_i} - \eta p_i + \delta \sum_{j=1}^{n} L_{ij} p_j \tag{4}$$

This model retains the same dynamics, but is rescaled in terms of ratios of initial parameters. This reduces the number of parameters while highlighting the relationships which drive dynamics. Time is rescaled in terms of the prey instantaneous per-capita growth rate ($\tau = rt$). As a result, dynamics are determined exclusively by the predator-prey conversion rate relative to prey growth($\phi = ca/r$), prey self-regulation ($\theta = b/K$), predator mortality relative to prey growth ($\eta = m/r$), dispersal relative to prey growth ($\delta = D/r$), and spatial structure (L) which remains unchanged from the previous equations. To complete the substitution predator and prey abundances are rescaled ($h = H/b$, $p = aP/rb$). To focus on the effects of changing spatial structure, we constrained dynamics to parameter values analyzed in Holland and Hastings (2008) corresponding to high-amplitude oscillations ($\phi = 5, \theta = .3, \eta = 1$). In nature these dynamics would correspond to a highly extinction prone, unstable predator-prey pair, and are therefore ideal for observing the effect of spatial stabilizing mechanisms on species interactions. Similarly, a single value of dispersal was used ($\delta = .018$). Preliminary simulations showed little effect of dispersal beyond the expected trend of increasing asynchrony with lower dispersal. Thus, we selected a relatively high level of dispersal where asynchrony is possible but not universal to emphasize the effects of structure on asynchrony.

Spatial structure

We explore the effects of spatial properties on asynchrony and community dynamics by varying spatial structure L. Specifically, we isolate properties of spatial structure independent of connectivity by using only regular structures. These regular structures are all constructed with ten patches and four connections per patch, for which fifty-six distinct structures are possible. Thus, connectivity and related measures do not vary among these structures. Other properties expected to play a role in synchronization do vary among these structures, however, specifically mean path length and transitivity (Arenas et al. 2008). Path length is the shortest number of dispersal connections an organism must cross to get from one patch to another, one for directly connected patches, two for those which share a neighbor but no direct connection, etc. Mean path length is the average of path lengths between all patches, and reflecting how isolated patches are from each other. Similarly, transitivity is the proportion of connected patches which share a neighbor to those which do not, measuring the tendency of patches within a structure to form tightly interconnected clusters. These measures were calculated for our networks using the igraph package in R (Csardi and Nepusz 2006).

We also characterize spatial structure using spectral theory, which utilize the eigenvalues (λ) and eigenvectors (ν) of the spatial structure matrix as a Laplacian matrix, $-L$. Specifically, the ratio of the largest eigenvalue to the smallest non-zero eigenvalue $\left(\frac{\lambda_{max}}{\lambda_2}\right)$ can be used to determine the stability of a metacommunity's synchronized state (Barahona and Pecora 2002). This has been shown for any general model of coupled dynamics $\frac{dX_i}{dt} = F(X_i) - \delta \sum_{j=1}^{n}(-L_{ij})H(X_j)$, where $F(X_i)$ is the change in X due to local processes in patch i, and $H(X_j)$ describes the effect of interaction with patch j. The synchronized state of this model is S, such that $X_i(t) = S(t)$ for all times t when all patches are synchronized. To determine the stability of this state, a small perturbation ξ is introduced (which is a vector with an element for each patch) and separated into the components of the eigenvectors of the Laplacian ν by solving the linear system $\xi = \sum_{i=1} \zeta_i \nu_i$. Then, the change in each eigenvector is given by $\nu_i(t) = \zeta_i e^{[F'(S(t)) - \delta\lambda_i H'(S(t))]t}$ where $F'(S(t))$ and $H'(S(t))$ are the Jacobian matrices describing the effects of of local dynamics F and dispersal interactions H on S at time t.

Following this, the term $[F'(S(t)) - \delta\lambda_i H'(S(t))]$ is the master stability function, and if it is greater than zero at any time the ith eigenmode is unstable, as perturbations of the ith eigenvector will always increase over time. For synchrony to be stable across all eigenvectors, $[F'(s) - \delta\lambda_i H'(s)]$ must be less than zero for all λ_i, the range of which can be found from the maximum (λ_{max}) and smallest non-zero eigenvalue (λ_2). Due to the Laplacian's zero row-sum, the zero eigenvalue is associated with an eigenvector with all elements equal and corresponds to synchrony; thus, change in this eigenvector is ignored. The greater the range of asynchronous eigenvalues is in terms of the ratio between λ_{max} and λ_2, the more likely at least one value falls in the range where $[F'(S(t)) - \delta\lambda_i H'(S(t))]$ is less than zero regardless of the exact model used (Barahona and Pecora 2002). While the ratio $\frac{\lambda_{max}}{\lambda_2}$ is commonly used in the literature, we use the inverse $\frac{\lambda_2}{\lambda_{max}}$ to characterize our structures, as this has a more linear distribution among the structures we consider. Following this we expect structures with smaller values of $\frac{\lambda_2}{\lambda_{max}}$ to be more prone to asynchronous dynamics.

Simulation methods

We ran the model with each of the fifty-six regular network structures with ten patches and four connections per patch to determine their tendency for asynchrony and resulting dynamics. Asynchrony was initially introduced through variation in initial population abundance. For structure, two hundred replicates of dynamics were simulated and analyzed. A range of randomly generated initial conditions was used to determine the relative frequency of synchrony and the range of asynchronous state possible for each structure. Variation in the initial distribution was introduced for each replicate by randomly selecting abundances from the uniform interval $[.9\hat{x}, 1.1\hat{x}]$, where $\hat{x}$ is the unstable fixed-point equilibrium density of species x: for prey (h), $\hat{h} = \eta/(\phi - \eta)$ and for predators (p), $\hat{p} = (1 + \hat{h})(1 - \theta\hat{h})$. Dynamics were simulated for 20000 time steps, by which point greater than 95% of simulations had reached equilibrium. Dynamics were simulated by solving the model system with the R implementation (library deSolve) of the FORTRAN Odepack solver lsoda (Soetaert et al. 2010). Select simulations were also checked using the ode45 method of the deSolve library, with no differences found.

For each simulation, we measured a number of characteristics of metacommunity dynamics, particularly those describing the ability of both species to persist. As there is only a single tightly-coupled predator-prey pair, oscillations and variability are highly correlated between both species allowing us to simplify analysis by focusing on one species for which we chose the prey. First, we consider variability as a measure of extinction risk, and measured the variability of prey in terms of the coefficient of variation (standard deviation divided by the mean) in the final 2000 time steps of each simulation. This was done both for the total regional abundance of the metacommunity, which shows the effects of averaging in asynchronous states, and for the local abundances of patches to describe the appearance and stabilizing properties of dynamical heterogeneity. Finally, asynchrony was measured in terms of correlations between patch dynamics (ρ_{ij}), measured by the Pearson product-moment correlation coefficient. Given the deterministic nature of our simulations we use a strict definition for synchrony, $\rho_{ij} = 1$, considering patches with any form of dynamical differences to be asynchronous. For asynchronous equilibria, patches are grouped into synchronized "clusters" (Holland and Hastings 2008) and characterized by the number of clusters present; synchronous states having one cluster, and purely asynchronous states having as many clusters as patches, or ten.

Source code in R for all methods available at github.com/SMHayes/Beyond-connectivity.

Results

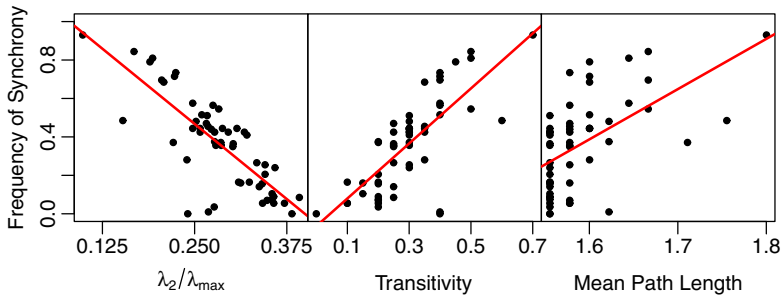
Frequency of asynchrony

We observed a substantial amount of variation in the frequency of synchrony among metacommunities with regular spatial structures. Differences in the frequency of synchrony and the utility of mean path length, transitivity, and the eigenratio $\frac{\lambda_2}{\lambda_{max}}$ in predicting them are summarized in Fig. 1. Of these measures, the eigenratio $\frac{\lambda_2}{\lambda_{max}}$ appears to be the best individual predictor of a metacommunity structure's tendency to synchronize. A combined model using all predictors was considered; however, within our regular networks, these measures are strongly correlated with one another; $\rho(\frac{\lambda_2}{\lambda_{max}}$, Transitivity) = .795, $\rho(\frac{\lambda_2}{\lambda_{max}}$, Mean Path Length) = .834, and ρ(Transitivity, Mean Path Length) = .720. As a result of this multicollinearity, there is little difference between the predictive power of all measures combined and $\frac{\lambda_2}{\lambda_{max}}$ alone.

As expected, synchrony was very common among our metacommunties given the high degree of homogeneity inherent in regular spatial structures. Nevertheless, a number of spatial structures were highly resistant to synchronization, and in general, the tendency toward synchrony varied considerably among structures. This presents a clear demonstration that the spatial variation among these networks plays a significant role in their dynamics despite no differences in connectivity both at the level of the entire structure and between individual patches. While the eigenratio $\frac{\lambda_2}{\lambda_{max}}$ appears to capture much of the dynamically relevant variation, a great deal remains unexplained even when mean path length and transitivity are included.

Asynchronous dynamics

Despite the strict homogeneity of our metacommunities, as each community is identical and connected to exactly four other communities, we observe a substantial range of different types of stable asynchronous dynamics, in which patches differentiate into several different internally synchronized dynamical regimes ("clusters"). We illustrate several examples of these dynamics in Fig. 2 and compare them with the synchronous equilibrium (a) which is identical for all structures. Synchronous dynamics are characterized by extremely high-amplitude oscillations and significant periods of low abundance for both species. Unsurprisingly, asynchronous dynamics have universally lower variability than the synchronous state. Additionally, asynchronous dynamics typically feature at least one synchronized cluster with oscillations of much higher average abundance and lower amplitude than the metacommunity average. These



Effects	Model 1	Model 2	Model 3
β_1 Eigenratio	-.797	-	-
β_2 Transitivity	-	.751	-
β_3 Mean Path Length	-	-	.559
R^2	.635	.564	.313

Fig. 1 Predictive value of measures of spatial structure on metacommunity synchrony. Here, the frequency out of 160 simulations that resulted in synchronized dynamics are plotted against structural descriptors for each of 56 unique metacommunity structures. Standardized coefficients were obtained by fitting simple linear regression models for each predictor as implemented using the lm command in the R package "stats". The associated R^2 values estimate how much variation in each metacommunity's frequency of synchrony is accounted for by the given measures of spatial structure. The eigenratio $\frac{\lambda_2}{\lambda_{max}}$ is the single best predictor of synchrony based on R^2

patches in many cases are phase-locked and adjacent to several high-amplitude patches (Fig. 2b, d, e). In these cases, their maxima can be seen to occur just before the maxima of high-amplitude patches, when abundances of high-amplitude patches are very low. Dispersal is therefore having a relatively high net negative effect on the low-amplitude patches during their maxima, as migrants are sent to the high-amplitude patches at their minima at a much higher rate than they are received. This trend then switches following the low-amplitude patches' maxima, with dispersal having a net positive effect as the high-amplitude patches increase toward their maxima. Asynchronous patterns can also be more complex, exhibiting complex multi-point limit cycles (Fig. 2c) and secondary low-frequency oscillations (Fig. 2e).

A full summary of the frequency and variability of asynchronous dynamics produced by each regular spatial structure is presented in Fig. 3. The variability of predator-prey oscillations are universally lower for asynchronous equilibrium at both the local scale (Coefficient of variation of prey .22 − 1.40 for asynchrony, 1.66 for synchrony) and regional scale (coefficient of variation of prey .43 − 1.36

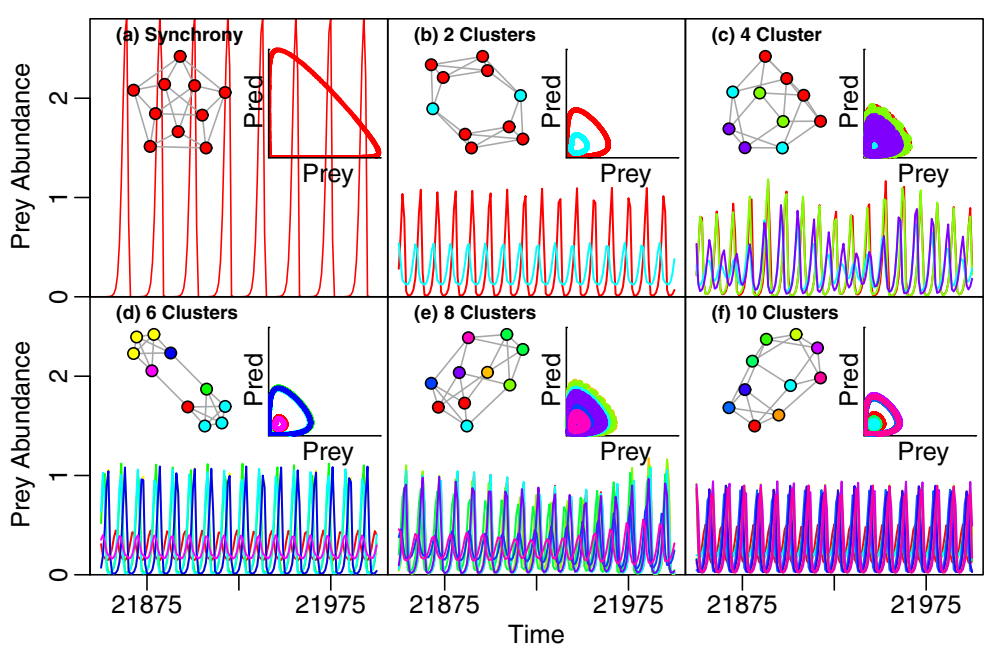


Fig. 2 Examples of the different classes of dynamical behavior observed in our simulations, where patches with the same colors exhibit identical dynamics. While the dynamics of synchronized metacommunities (**a**) are identical among all examples of their class at equilibrium, metacommunities with asynchronous equilibria (**b**–**f**) vary widely both in their dynamics and pattern of spatial clustering

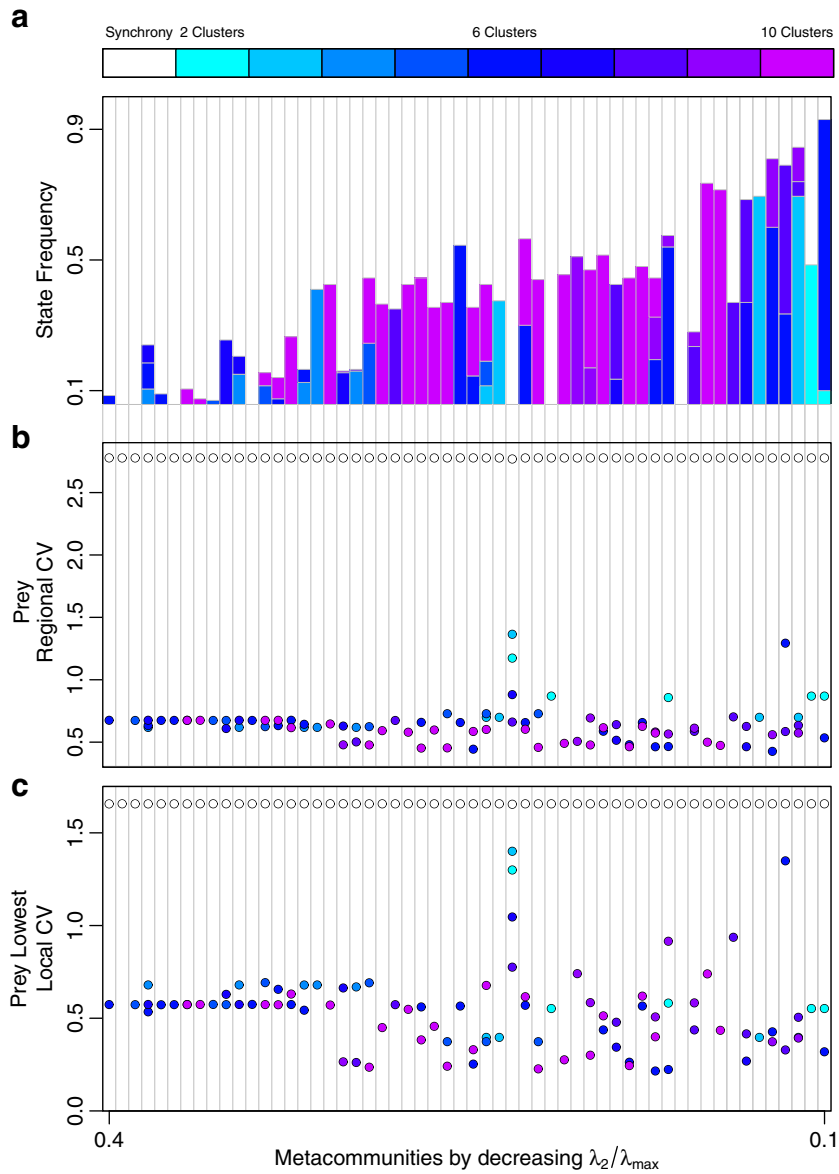


Fig. 3 Illustration of the dynamical variation observed as a result of variation in metacommunity spatial structure and initial conditions. The *y*-axis shows each metacommunity structure ranked by decreasing eigenratio. In (**a**), we show differences in the frequency of all observed spatial patterns of asynchrony, noting that many structures produce multiple types of stable spatial patterns. In (**b**) and (**c**), we show the effect of these various spatial patterns on the total regional and lowest observed local variability of the prey species calculated at the final 2000 time steps of each simulation. The completely synchronized state is always more variable than partially synchronized states, yet the degree to which variability is reduced due to asynchrony varies depending on the spatial structure of a given metacommunity, the pattern of clustering, and whether the local or regional scale is considered

for asynchrony, 2.78 for synchrony). While this is expected, the degree to which asynchronous equilibrium states vary relative to each other is surprising. Additionally, we note that different asynchronous equilibria vary in their effect on the regional and local scales. Specifically, states with two to three clusters typically have higher regional variability (Fig. 3b) than higher clusters states, but many have patches with equal or lower local variability (Fig. 3c). This suggests that the variability of asynchronous states are being influenced by multiple mechanisms acting at different spatial scales, and the degree to which each mechanism plays a role varies depending on structure and pattern of clustering.

Any given spatial structure may produce multiple types of asynchronous patterns with varying numbers of synchronized clusters (Fig. 3). This leads, somewhat surprisingly, to considerable differences in the pattern of asynchrony and predator-prey dynamics produced even by the same dispersal structure. While a single structure may produce multiple types of dynamics, each asynchronous regime is tied to a specific pattern of clusters. The patterns possible are constrained by the structure of dispersal, specifically in that all patches belonging to a synchronized cluster are connected to the same types and numbers of patches belonging to other synchronized clusters. For example, in the case of Fig. 2b, teal patches are always connected to four red patches, and red patches to three red patches and one teal patch. This guarantees that patches which are synchronized experience the same fluctuations as a result of dispersal. Thus, the structure of dispersal connections within the metacommunity is influencing not only the frequency of asynchrony, but also the variability of asynchronous dynamics by constraining how partially synchronized clusters can be distributed.

Altogether, it is extremely challenging to predict the variation in asynchronous dynamics we observe from spatial structure alone. In Fig. 3a, it is clear that while the total frequency of asynchronous dynamics decrease with the eigenratio of the structure, the number of clusters observed in these patterns is highest at intermediate levels. Because lower cluster states often have higher regional variability, this means that patches with intermediate values of the eigenratio also have the lowest regional variability. However this does not hold for local variability. Furthermore, the actual variability of each structure will vary dramatically depending on the specific pattern of clustering realized.

Discussion

Our results demonstrate that the tendency of metacommunities to synchronize is strongly influenced by the pattern of connections among community patches, even when connectivity and degree distribution are held constant. This is an important step to better understanding how metacommunity dynamics are influenced by spatial structure given the focus on connectivity in the literature (Bunn et al. 2000; Marleau et al. 2014; Plitzko and Drossel 2015; Saunders et al. 1991; Taylor et al. 1993). We further illustrate that differences in the pattern of connections and initial conditions among communities lead to the emergence of a wide array of stable asynchronous dynamics, leading to substantial differences in the potential persistence of an unstable predator-prey interaction at both the regional metacommunity and local patch level, despite the otherwise strict homogeneity of our metacommunities in which each community is identical and connected to exactly four other community patches. Our study is the first to produce this range of dynamical variation as a result of such subtle changes in spatial structure; this contrasts with earlier work that has only produced comparable variation through heterogeneity in connectivity or degree distribution (Holland and Hastings 2008; Gilarranz and Bascompte 2012), differences in dispersal among species (de Roos et al. 1998), or alteration of community dynamics in more complex models (Marleau et al. 2014; Hata et al. 2014). The appearance of this striking range of dynamical variation, both in the frequency and and quality of asynchrony among metacommunities shows the important role of the pattern of connections among local communities in shaping the regional dynamics of metacommunities.

Emergent asynchrony in nature

The emergence of complex asynchronous dynamics from homogeneous metacommunities makes inferences about habitat quality based on community dynamics challenging. As our results demonstrate, differences between communities may be driven by spatial patterns imposed by the structure of dispersal rather than any environmental effects, or a combination of both. Without accounting for the effects of spatial structure, approaches assuming that species distributions are driven primarily by environmental features may fail to accurately identify the importance of habitat patches for conservation or predict the effects of environmental changes on species (Keith et al. 2008; Swab et al. 2012). When spatial heterogeneity is produced through pattern formation, the structure as a whole is responsible for determining what patterns are possible and the resulting effects on species. Conservation planning which includes the addition or removal of habitat or connections between them must then consider the importance of these mechanisms.

Additionally, we have demonstrated that while asynchrony generally provides enhanced stability for a community relative to synchrony, its effect varies depending on the spatial pattern of asynchrony. The relative strength of stabilizing effects vary both at the regional scale, as through spatial averaging and rescue effects, and at the local scale through dispersal subsidies depending on the patterns promoted by the spatial structure of the metacommunity. Plans to promote stability at the metacommunity level then must move beyond how to maintain asynchrony, but also consider the patterns of asynchrony and their overall effect on community dynamics.

Emergence of asynchronous dynamics

The emergence of the asynchronous equilibria we observe is an example of pattern formation, wherein stable heterogeneity emerges from a homogeneous system (Turing 1952). In these cases, variation in initial conditions provides a source of heterogeneity which is stabilized by the underlying structure of the environment and movement within it. While these are typically studied in the context of Turing instabilities, wherein spatial processes also destabilize the synchronized homogeneous state, alternative mechanisms for the formation of spatial patterns have been described (Cahn and Hilliard 1958; Liu et al. 2013), and they can occur in systems with locally stable homogeneous states (Wolfrum 2012). The patterns we observe are surprising because they are equivalent to the special case of traveling wave patterns as their equilibria are limit cycles rather than fixed points, which typically require at least three species to occur (Turing 1952; Hata et al. 2014). Here they can arise with only two species because the interaction between the predator and prey is already prone to oscillation (Yang et al. 2004). These dynamics are a prime example of emergent behavior, wherein the interactions between the components of a system give rise to collective dynamics which cannot be predicted by understanding the parts alone (Anderson and

et al 1972). Despite each community patch in our simulations being identical when viewed individually, utilizing the same parameter values and connecting to precisely four other patches, they can generate entirely different dynamics depending on the structure of the greater metacommunity and their position within it.

We describe the effects of this emergent asynchrony on the dynamics of metacommunities at both the local and regional scale. Total regional variability (Fig. 3b) is determined both by the variability of individual patches and an additional reduction due to spatial averaging effects that result from phase differences among communities' limit cycles in our simulations (Goldwyn and Hastings 2008). Spatial averaging effects occur on the regional scale of the metacommunity, reducing total regional variability and extinction risk by buffering population minima with dispersal from populations at different points in their limit cycle (Briggs and Hoopes 2004; Maser et al. 2007). Spatial averaging does not cause changes at the local scale, however, and alone cannot be responsible for the differences in the dynamics among communities in the same metacommunity that we observe, as in Fig. 3c. These differences are created by an additional interaction with the non-linearity of species' interactions, which causes the same relative amount of dispersal to have different effects on communities depending on their current position in their limit cycle. Dispersal can therefore simulate the effects of changing prey growth or predator attack rates and change the shape of communities' limit cycles (de Roos et al. 1998; Briggs and Hoopes 2004). The effect of dispersal on the shape of the limit cycle depends on the magnitude of dispersal between communities, which is increased by differences among communities. This feedback then causes the emergence of a heterogeneous spatial pattern if a stable pattern of differences among patches can be reached.

Spatial structure determines the emergence of stable asynchronous patterns from our homogeneous metacommunities primarily by constraining the spatial patterns possible. As discussed, in all observed spatial patterns all patches in a synchronized cluster are connected to the same type and number of other synchronized clusters. This arrangement is otherwise known as a balanced equivalence relation or balanced coloring, and is strictly required for the pattern of asynchrony to be stable (Theorem 6.5, (Stewart et al. 2003). The number and corresponding pattern of these balanced colorings is specific to the underlying spatial structure, dictating the number of synchronized clusters, a property which has been previously suggested to be the major determinant in differences between asynchronous metacommunities (Holland and Hastings 2008). However, we observe that metacommunities with different numbers of clusters can have identical stability properties and vice versa (Fig. 3). Beyond influencing the synchronization of individual patches, structure also constrains how synchronized clusters of unique dynamics interact with one another. This indirectly determines the magnitude of dispersal experienced by each patch, a key driver of differences in the variability and limit cycles of each patch.

Conclusion

Overall, we find that characteristics of metacommunity spatial structure independent of connectivity play a crucial role in determining dynamics not only by influencing asynchrony frequency, but also by constraining the action of asynchrony's stabilizing mechanisms. Our findings strongly suggest a need to both move beyond connectivity as the focus of spatial structure and to move beyond the presence or absence of synchrony to understand metacommunity dynamics. The spatial patterning of partially synchronized clusters is a major determinant of the effect of space on interactions between species. Considering that spatial structure is being dramatically altered as a result of human development and the importance of these mechanisms for maintaining stability of communities and persistence of species, a deeper understanding of the relationship between spatial structure, patterns of synchrony, and metacommunity dynamics is absolutely necessary both from a theoretical and conservation perspective.

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