

1 **Critical Transitions in the Spatial Synchrony of**
2 **Metapopulation Dynamics**

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7 **Abstract**

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1 Introduction

Anthropogenic activity has rapidly reshaped Earth's habitats. To mitigate the known contribution of habitat loss to declining biodiversity [1], much attention has been paid to promoting *landscape connectivity*.

It is still mostly unknown how ecological systems respond to habitat loss and ensuing subdivision.

What is the spatial scale that constitutes a 'single' population? How does landscape connectivity effect the scale of spatial synchrony?

Review of synchrony and literature.

Connectivity and synchrony, how do we reduce extinction probability.

Ecological processes are inherently the product of interactions across all scales of biological organization [1]. This process of *emergence*, by which parts come together to form a whole with properties that don't exist among the individual parts, has been studied across a wide variety of disciplines [2] and is a ubiquitous phenomenon in complex systems. One potential cause of emergent behavior is *synchrony* among the individual parts of a complex system. When many independent parts come together to act as a whole, their dynamics become synchronized. This behavior is ubiquitous in biological systems across all scale of organization. From collections of cells acting together: the heart beating in rhythm [3], neurons firing in unison [4]—to behavior among organisms: the flash of fireflies [5] or the migration of birds [6]—to interactions between organisms: synchrony between abundances of predators and prey [7], and of phenology [7, 8].

Synchrony, by definition, involves different entities changing over time in the same way. Within ecology, there has long been a focus on spatial synchrony, that is—how does spatial distribution of ecological entities affect whether they change together or separately? [9, 10, 11]. This is, in large part, due to the applied importance of understanding the effect of habitat loss on natural populations. Many theoretical studies have shown the two primary factors that develop spatial synchrony across space are dispersal and environmental covariance [12, 13]. Within this theory, one maxim that has developed is *Moran's rule*,

51 which states that spatial synchrony is proportional to the covariance in the environmental
52 conditions across space [14, 15].

53 A major goal of conservation is developing corridors to conserve landscape connectivity.
54 Most measures of landscape connectivity used in the literature represent *structural* connec-
55 tivity, meaning quantifying the structure of the landscape []. Structural connectivity stands
56 in contrast with *functional* connectivity, which measures the connectivity of a given process
57 [16, 17]. Here, in order to better understand functional connectivity, we use a simulation
58 model to measure how synchrony across space changes as a function of landscape structure.
59 We do this by developing a model of metapopulation dynamics on spatial graphs, which
60 have long been used to model landscape connectivity [18? ?], and analyze how synchrony
61 changes across space using the language of critical transitions.

62 Further, we show that increasing population synchrony reduces the variance in the
63 generation-to-generation change in abundance, which is central in reducing the proba-
64 bility of metapopulation extinction (@lande_risks_1993, @lande_extinction_1998). This
65 relationship suggests that promoting functional landscape connectivity can help mediate
66 the probability of extinction for species facing significant habitat loss. We suggest using
67 simulation models, such as those presented here, to aid in decision making regarding
68 corridor placement.

69 1.1 What are phase transitions?

70 When does a system change from one state to a different state? Due to the rapid changes
71 induced on the planet by human activity, there has been recent focus on answering this
72 question in ecology, especially the potential for changes in spatial structure to drive transi-
73 tions between alternative stable states. Much of this theory has been aimed at the practical
74 problem of being able to predicting the onset of transitions from time-series data [19, 20].
75 The bulk of the quantitative theory used to understand transitions between states is derived
76 from statistical mechanics, where it was originally used to study phase-transitions in matter.
77 In order to study phase transitions between regimes, we must first be clear on what these
78 regimes are. As this theory was originally used to describe physical states of matter, the
79 original regimes were solid, liquid, gas. However, as our understanding of condensed-matter

80 has changed, so has the demarcation of what constitutes different states. In reality, the way
81 in which particles come together to constitute matter is far more variable than these three
82 categories. In such cases the ‘state’ of a collection of particles cannot be represented by a
83 single categorical label, and so the theory of phase transitions as been adapted to model
84 *continuous* phase transitions, where there is no clear demarcation point between different
85 states [21]. This is useful for us in ecology, where the line between alternative ecosystem
86 ‘states’ is even fuzzier.

87 We can formalize our understanding of phase transitions using the language of statistical
88 mechanics. We call the *order parameter* some measure of the system’s state in space and
89 time. The *control parameter*, then, is what causes the change in order parameter. When
90 dealing with dynamics that are inherently stochastic, one tool often used in statistical me-
91 chanics is correlation functions which measure how well the order parameter is correlated
92 in both space and time at a particular value of the control parameter [21]. For example,
93 if we consider the population of a species inhabiting a landscape, where along the gradient
94 of landscape connectivity, our control parameter, does that system go from consisting of
95 one large, single, population, to many small, independent populations? We measure this
96 qualitative shift from one system to many using *synchrony*, the correlation in the dynamics
97 of abundance across space.

2 The Model

Here we present a spatial graph model of landscape connectivity based on metapopulation theory [22, 23]. We model connectivity as a function of a few empirically estimable parameters, and then describe a stochastic model of metapopulation dynamics on these spatial graphs. We then simulate dynamics across a gradient of landscape connectivity parameters to measure transitions in the synchrony of population dynamics across space occur.

2.1 Modeling Landscape Connectivity with a Spatial Graph

Spatial graphs have long been used to model a system of habitat patches [24, 25, 26]. Here we model a system of populations, represented as a vector of vertices, \vec{L} in a spatial graph $G = (L, E)$. Here the edges E represent dispersal between populations. To define E , we choose to model landscape connectivity with respect to the process of metapopulation dynamics as a combination of two different factors: the probability than any individual migrates during its lifetime, m , and the conditional distribution over spatial nodes of where an individual goes, given that it migrates, $P(L_j|L_i)$, which we call the dispersal potential, Φ_{ij} . We can model the dispersal potential using a few methods. In empirical systems, this can be estimated with resistance surfaces, which provide relative weights of the difficulty of migration between points on a raster of land-cover type [27]. Theoretically, we model the dispersal potential using isolation-by-distance (IBD). The relative probability of dispersal between L_i to L_j is inversely proportional to the distance between them, d_{ij} , and the strength of this isolation-by-distance relationship, α . The functional form of this relationship, $f(d_{ij}, \alpha)$, has long been called the dispersal kernel [22]. Here we consider two different types of dispersal kernels: the exponential, $f(d_{ij}, \alpha) = e^{-\alpha d_{ij}}$, and Gaussian, $f(d_{ij}, \alpha) = e^{-\alpha^2 d_{ij}^2}$, which have both been considered as dispersal kernels in both theoretical and empirical work [22, 23].

To construct a dispersal potential Φ_{ij} with a kernel $f(d_{ij}, \alpha)$, we normalize:

$$\Phi_{ij} = P(V_j|V_i) = \frac{f(d_{ij}, \alpha)}{\sum_k f(d_{ik}, \alpha)}$$

Note that if $\alpha = 0$, then the value of both exponential and Gaussian kernels is the same for

all pairs of populations, and therefore the dispersal potential is a uniform distribution. In Figure 1, we can see spatial graphs plotted representing the same set of populations across differing values.

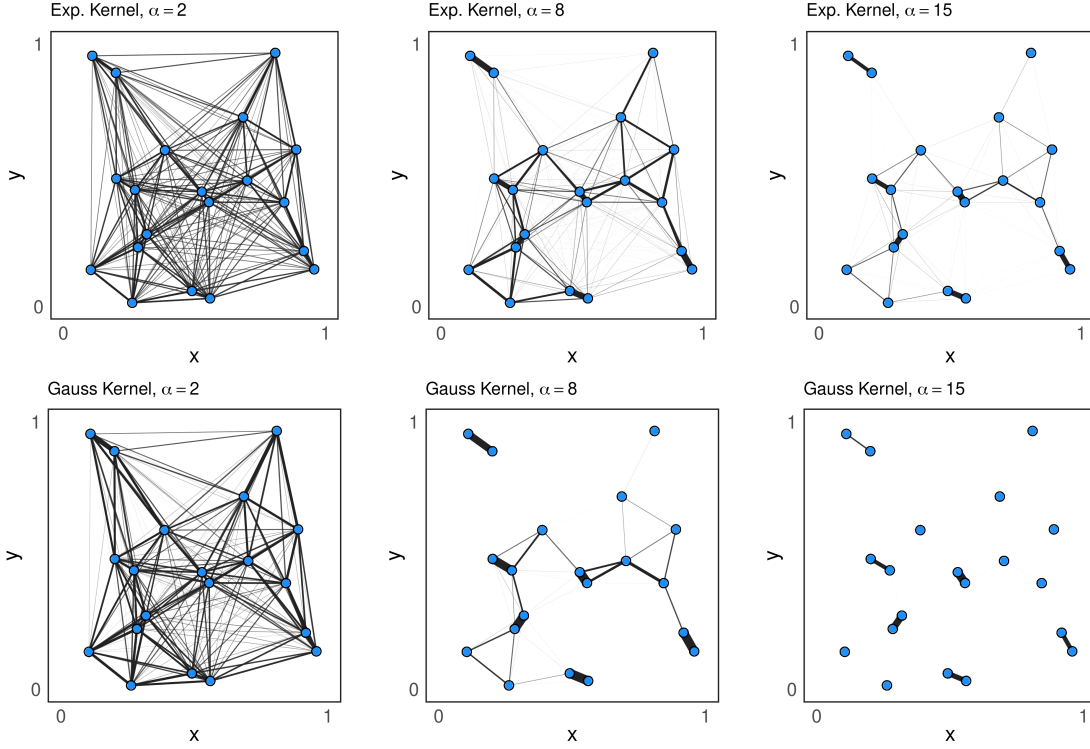


Figure 1: Sample output from tikzDevice

Now that we have a model of landscape connectivity, we turn to defining a model of metapopulation dynamics on these spatial graphs.

2.2 Local Dynamics

We model population dynamics within each local population L_i using the stochastic logistic model. The dynamics of the number of individuals N_i in population L_i are described by the stochastic differential equation (SDE)

$$dN_i = \lambda_i N_i \left(1 - \frac{N_i}{K_i} \right) dt + \sigma N_i dW$$

Here, N_i is the abundance of population L_i , λ_i is the strength of density dependence in that population, and K_i is the carrying capacity of L_i . σ_p represents that standard deviation in abundance due to local stochasticity as a proportion of N_i . Here σ represents an amalgamation of all factors contributing to local stochasticity in population dynamics, although it should be noted that the relative contribution of different factors to local stochasticity can drive significant variation in dynamics [28].

We can write this system as the matrix equation

$$d\mathbf{N} = \mathbf{I}\lambda\left(\mathbf{I}(\mathbf{K} - \mathbf{N})\mathbf{K}^{-1}\right)dt + \mathbf{I}\sigma\mathbf{N}d\mathbf{W} \quad (1)$$

For the sake of reducing the size of parameter space, here we consider all populations as having the same λ_i and K_i , however, future work could include exploring the source-sink dynamics in this system by varying intrinsic growth rates and carrying capacities across populations.

We use an SDE representation because they have been used to study phase transitions in stochastic systems before [29, 30], and they have many nice properties for inference. SDEs have also been used in ecology to study extinction dynamics before, as it is relatively straightforward to compute the mean time until extinction (MTE) using the Kolmogorov Backward Equation [31].

2.3 Diffusion on Spatial Graphs

When we model a landscape with a spatial graph, we have to decide how different nodes affect one another. The processes that connect landscapes are inherently stochastic. The probability that an individual migrates within its lifetime, m , and where it goes, Φ_{ij} , are both stochastic. Under some conditions, we can effectively model stochastic dynamics across space using diffusion models. In essence, a diffusion model assumes that at each timestep the system will change according to the expected value of stochastic dispersal. Diffusion models have seen widespread use in ecology and other fields [32, 33, 34].

Given our dispersal potential Φ_{ij} , we can define the diffusion matrix D as

$$D_{ij} = \begin{cases} 1 - m & \text{if } i = j \\ \Phi_{ij}m & \text{if } i \neq j \end{cases}$$

157 We can now represent the dynamics due to diffusion of this system as

$$\dot{N}_i = (1 - m)N_i + \sum_j \Phi_{ij}mN_j$$

158 In matrix notation, we can represent this diffusion model as

$$\frac{d\vec{N}}{dt} = D^T \vec{N}$$

159 We can then combine this with local dynamics as a reaction-diffusion model,

$$\frac{d\vec{N}}{dt} = g(D^T \vec{N})$$

160 where $g(x)$ is a function that represents the hypothesized mechanism of how the ecological
161 measurement evolves locally.

162 In principle, $g(x)$ can represent any ecological process of interest—for example if the state
163 space of x is allelic frequencies, $g(x)$ could describe genetic drift, or if x represents community
164 compositions across space, $g(x)$ could describe competition between species as a function of
165 environmental conditions, coevolutionary states across space, etc. Here, we consider $g(x)$
166 to be the stochastic logistic model (see previous section). Combining this with the diffusion
167 model yields the SDE

$$dN_i = \sum_j \left[D_{ji} \lambda_i N_i \left(1 - \frac{N_i}{K_i} \right) \right] dt + \sigma N_i dW_i \quad (2)$$

168 which will be the primary object of study in this paper.

2.4 Measuring Synchrony

As described above, measures of correlation in space and time are often used in the study of phase transitions. When the order parameter gains or loses correlation in space and time is used as an indicator of when a system changes qualitative phases. Within the context of ecology, the crosscorrelation function, CC , has long been used as a measure of synchronous dynamics [35]. Here, with a subdivided population, we consider the mean crosscorrelation compared across all populations, $PCC = \frac{1}{n^2} \sum_{i,j} CC(V_i, V_j)$. As an example, in 2, panel (a) show an example of low PCC, and panel (b) shows an example of high PCC.

Figure 2: The abundance of 2 populations (top) and 8 populations (bottom) across time. Get the values of synchrony

2.5 Simulating a Phase Transition across a Migration Gradient

Now we consider how synchrony changes as a function of p_m . Each run consists of the following parameters, $\theta = \{N_p, \lambda, \sigma_p, \vec{K}, p_m, \alpha\}$. For each unique set of parameters, we run 50 replicates across all values of $p_m = \{0.01, 0.02, \dots, 1.0\}$. For each replicate, we independently draw the location of N_p populations uniformly in $[0, 1]^2$. We draw the initial value of abundance for all populations from a uniform distribution, $N_i \sim U(0, K_i)$. We then integrate equation 2 forward 500 timesteps using the Euler–Maruyama method with $\Delta t = 0.1$. After integrating forward, we compute the crosscorrelation coefficient, CC for each pair of populations $i \neq j$. Then, we compute the mean pairwise crosscorrelation for that replicate, PCC , and start the next replicate.

3 Synchrony Across a Migration Gradient

Probability distribution of synchrony in a set of populations L given α and m .

There is symmetry in these distributions around $m = 1 - \frac{1}{|L|}$

Figure 3

Figure 4

Figure 5

190 4 Critical Transitions in Synchrony Across Space

191 4.1 Landscape Connectivity

192 4.2 Landscape Subdivision

193 Does eigenvector centrality predict synchrony?

194 5 Conclusion

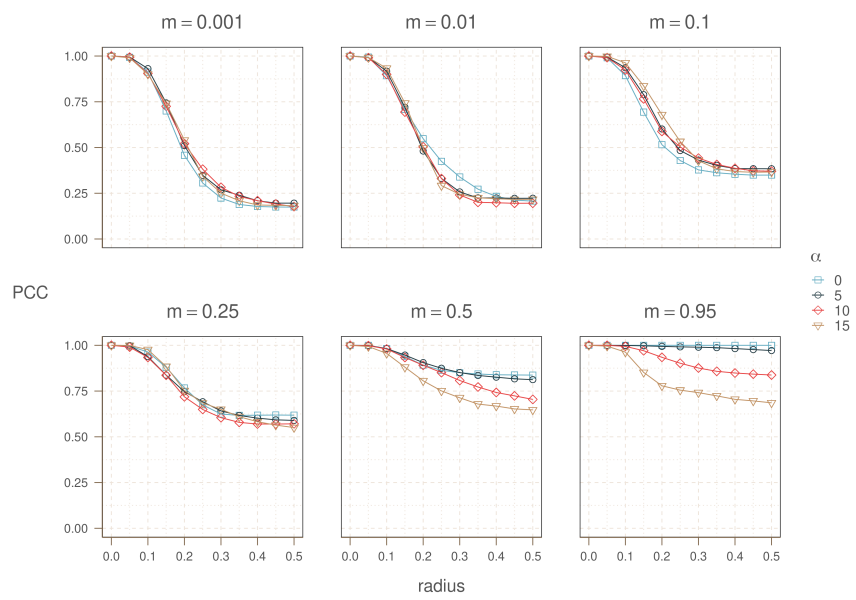


Figure 6

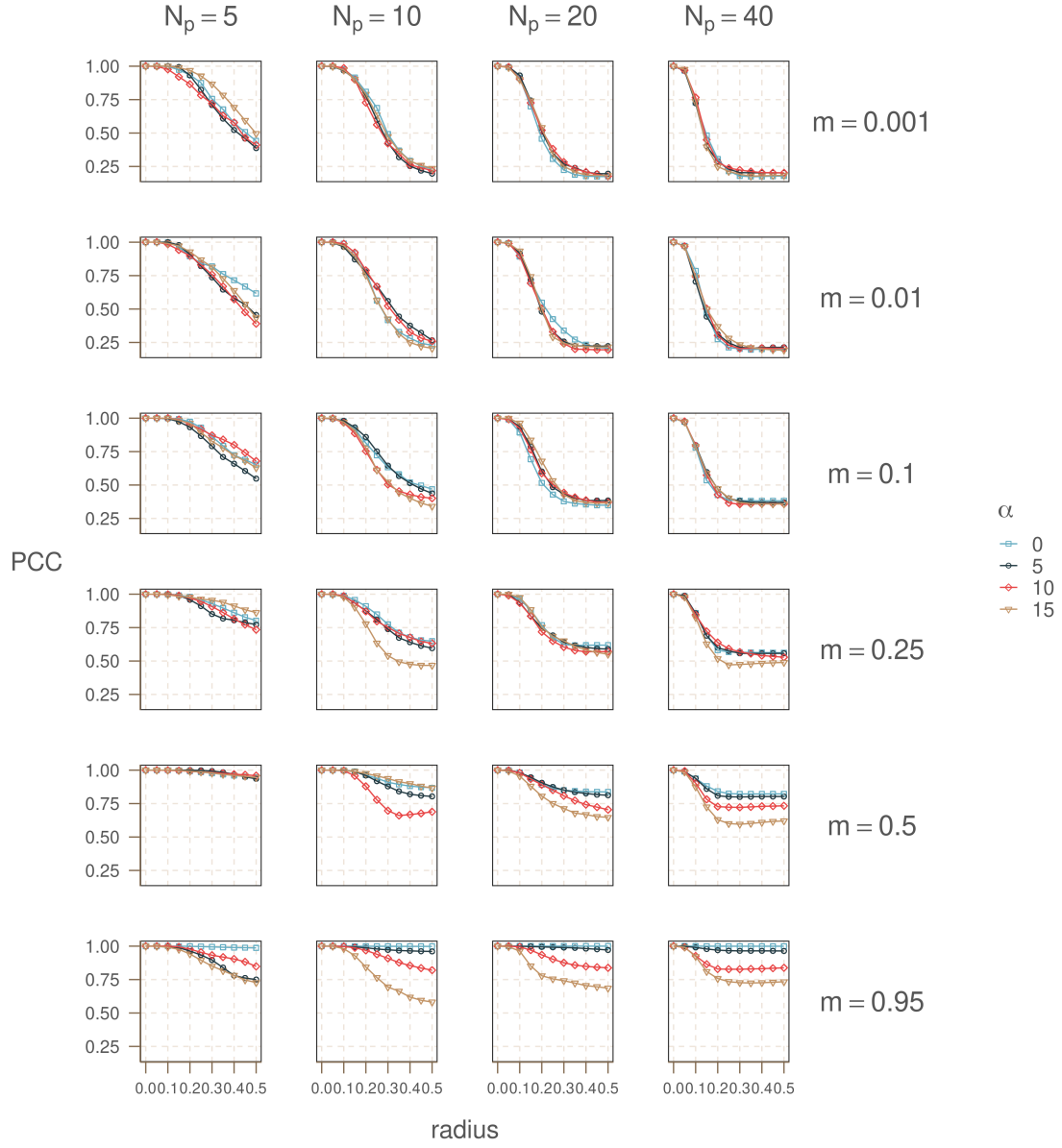


Figure 7

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