

1 **Phase Transitions in Landscape Connectivity**

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6 **Abstract**

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## 8 Introduction

### 9 Landscape connectivity intro

10 Ecological processes are inherently the product of interactions across all scales of biological  
11 organization [1]. This process of *emergence*, by which parts come together to form a whole  
12 with properties that don't exist among the individual parts, has been studied across a  
13 wide variety of disciplines [2] and is a ubiquitous phenomenon in complex systems. One  
14 potential cause of emergent behavior is *synchrony* among the individual parts of a complex  
15 system. When many independent parts come together to act as a whole, their dynamics  
16 become synchronized. This behavior is ubiquitous in biological systems across all scale of  
17 organization. From collections of cells acting together: the heart beating in rhythm [3],  
18 neurons firing in unison [4]—to behavior among organisms: the flash of fireflies [5] or the  
19 migration of birds [6]—to interactions between organisms: synchrony between abundances  
20 of predators and prey [? ], and of phenology [7, 8]. Synchrony, by definition, involves  
21 different entities changing over time in the same way. Within ecology, there has long been a  
22 focus on spatial synchrony, that is—how does spatial distribution of ecological entities affect  
23 whether they change together or separately? [9, 10, 11]. This is, in large part, due to the  
24 applied importance of understanding the effect of habitat loss on natural populations. Many  
25 theoretical studies have shown the two primary factors that develop spatial synchrony across  
26 space are dispersal and environmental covariance [12, 13]. Within this theory, one maxim  
27 that has developed is *Moran's rule*, which states that spatial synchrony is proportional to  
28 the covariance in the environmental conditions across space [14, 15].

29 A major goal of conservation is developing corridors to conserve landscape connectivity.  
30 Most measures of landscape connectivity used in the literature represent *structural* connec-  
31 tivity, meaning quantifying the structure of the landscape []. Structural connectivity stands  
32 in contrast with *functional* connectivity, which measures the connectivity of a given process  
33 [16, 17]. Here, in order to better understand functional connectivity, we use a simulation  
34 model to measure how synchrony across space changes as a function of landscape structure.  
35 We do this by developing a model of metapopulation dynamics on spatial graphs, which  
36 have long been used to model landscape connectivity [18? ? ], and analyze how synchrony

changes across space using the language of critical transitions.

Further, we show that increasing population synchrony reduces the variance in the generation-to-generation change in abundance, which is central in reducing the probability of metapopulation extinction (@lande\_risks\_1993, @lande\_extinction\_1998). This relationship suggests that promoting functional landscape connectivity can help mediate the probability of extinction for species facing significant habitat loss. We suggest using simulation models, such as those presented here, to aid in decision making regarding corridor placement.

## What are phase transitions?

### What are phase transitions?

When does a system change from one state to a different state? Due to the rapid changes induced on the planet by human activity, there has been recent focus on answering this question in ecology, especially the potential for changes in spatial structure to drive transitions between alternative stable states. Much of this theory has been aimed at the practical problem of being able to predicting the onset of transitions from time-series data [19, 20]. The bulk of the quantitative theory used to understand transitions between states is derived from statistical mechanics, where it was originally used to study phase-transitions in matter. In order to study phase transitions between regimes, we must first be clear on what these regimes are. As this theory was originally used to describe physical states of matter, the original regimes were solid, liquid, gas. However, as our understanding of condensed-matter has changed, so has the demarcation of what constitutes different states. In reality, the way in which particles come together to constitute matter is far more variable than these three categories. In such cases the ‘state’ of a collection of particles cannot be represented by a single categorical label, and so the theory of phase transitions as been adapted to model *continuous* phase transitions, where there is no clear demarcation point between different states [21]. This is useful for us in ecology, where the line between alternative ecosystem ‘states’ is even fuzzier.

We can formalize our understanding of phase transitions using the language of statistical

mechanics. We call the *order parameter* some measure of the system's state in space and time. The *control parameter*, then, is what causes the change in order parameter. When dealing with dynamics that are inherently stochastic, one tool often used in statistical mechanics is correlation functions which measure how well the order parameter is correlated in both space and time at a particular value of the control parameter [21]. For example, if we consider the population of a species inhabiting a landscape, where along the gradient of landscape connectivity, our control parameter, does that system go from consisting of one large, single, population, to many small, independent populations? We measure this qualitative shift from one system to many using *synchrony*, the correlation in the dynamics of abundance across space.

## 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.

### 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,  $\Phi_{ij}$ . 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,  $\alpha$ . 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  $\Phi_{ij}$  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.

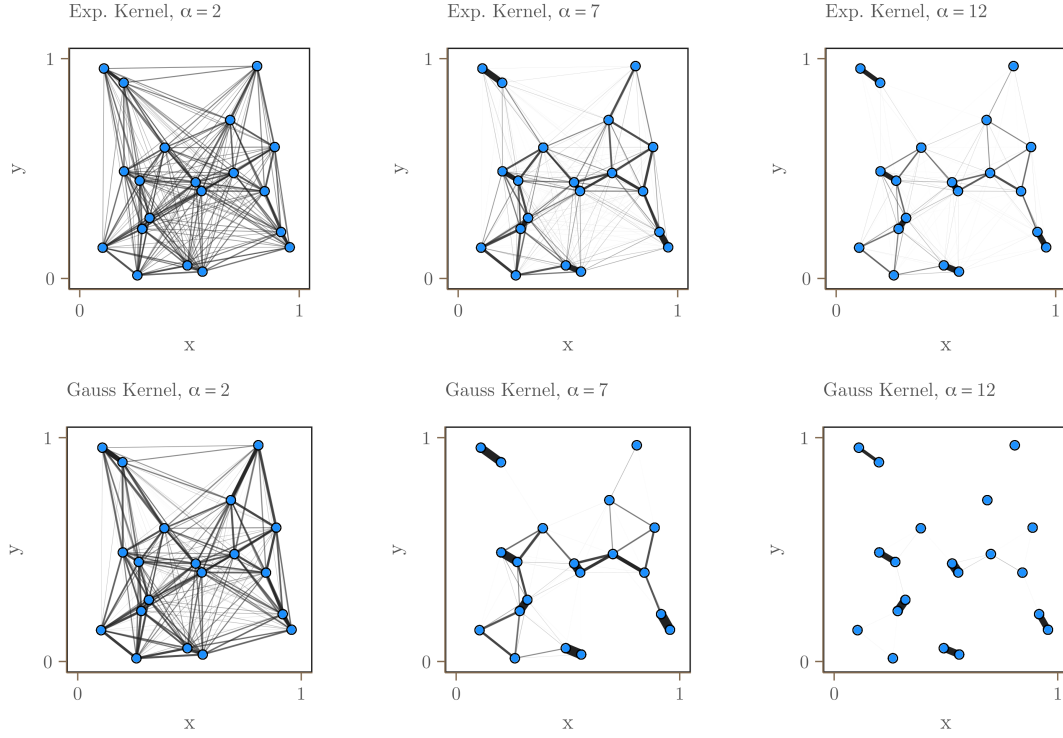


Figure 1: Sample output from tikzDevice

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

### 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  $L_i$ ,  $\lambda_i$  is the strength of density dependence in that population, and  $K_i$  is the carrying capacity of  $L_i$ .  $\sigma_p$  represents that standard deviation in abundance due to local stochasticity as a proportion of  $N_i$ . Here  $\sigma$  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  $\lambda_i$  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].

## 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,  $\Phi_{ij}$ , 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  $\Phi_{ij}$ , we can define the diffusion matrix  $D$  as

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

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

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

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

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

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

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

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

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

$$d\mathbf{N} = \mathbf{I}(D^T \mathbf{N}) \left( \mathbf{I} \mathbf{K}^{-1} (\mathbf{K} - D^T \mathbf{N}) \right) dt + \mathbf{I} \boldsymbol{\sigma} \mathbf{N} d\mathbf{W} \quad (2)$$

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



### 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.

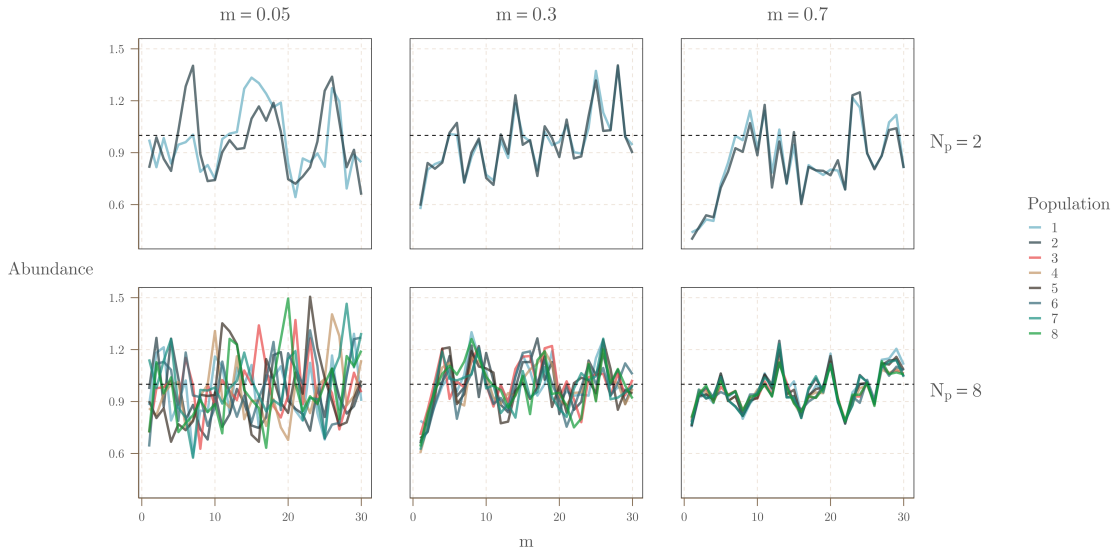


Figure 2: The abundance of 2 populations (top) and 8 populations (bottom) across time. Get the values of synchrony

### 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

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159 value of abundance for all populations from a uniform distribution,  $N_i \sim U(0, K_i)$ . We  
160 then integrate equation 2 forward 500 timesteps using the Euler–Maruyama method with  
161  $\Delta t = 0.1$ . After integrating forward, we compute the crosscorrelation coefficient,  $CC$  for  
162 each pair of populations  $i \neq j$ . Then, we compute the mean pairwise crosscorrelation for  
163 that replicate,  $PCC$ , and start the next replicate.

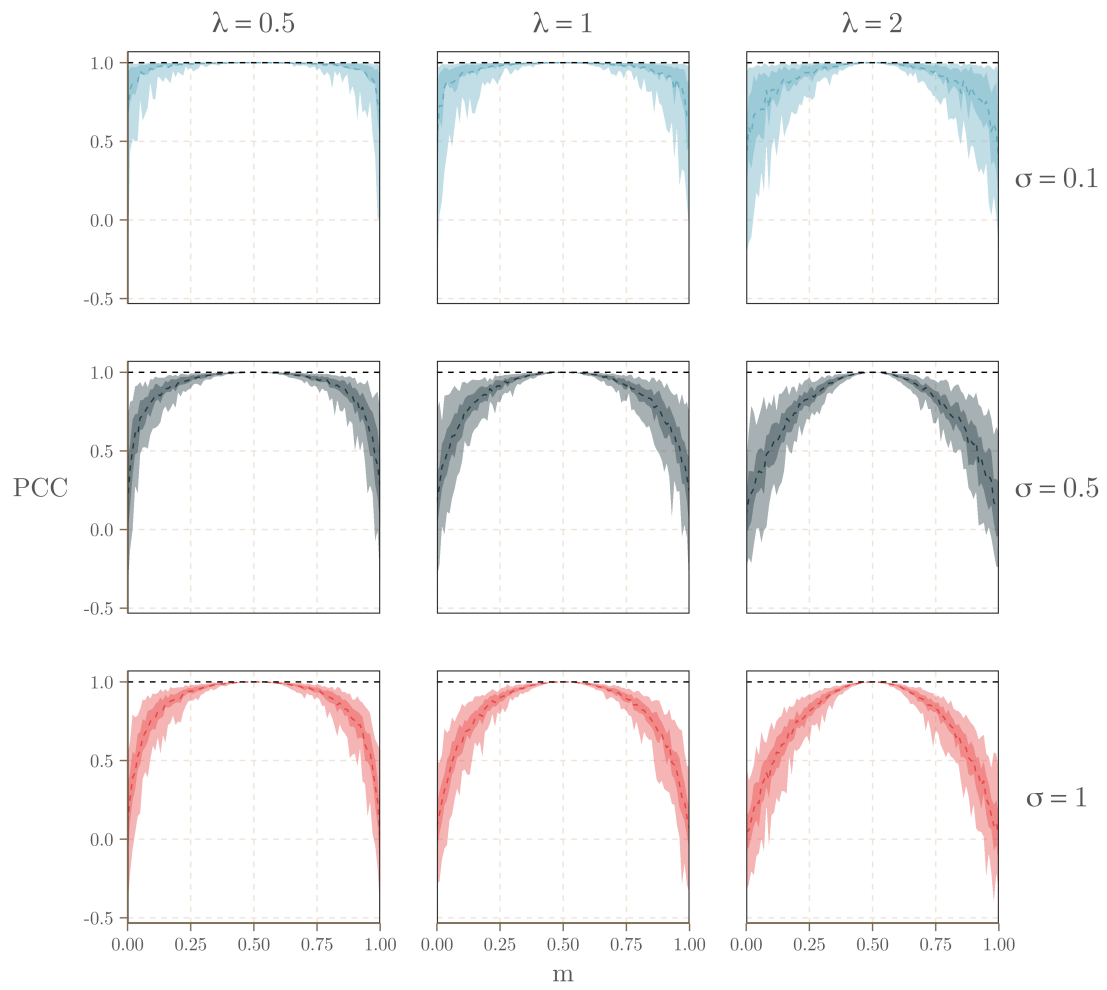


Figure 3

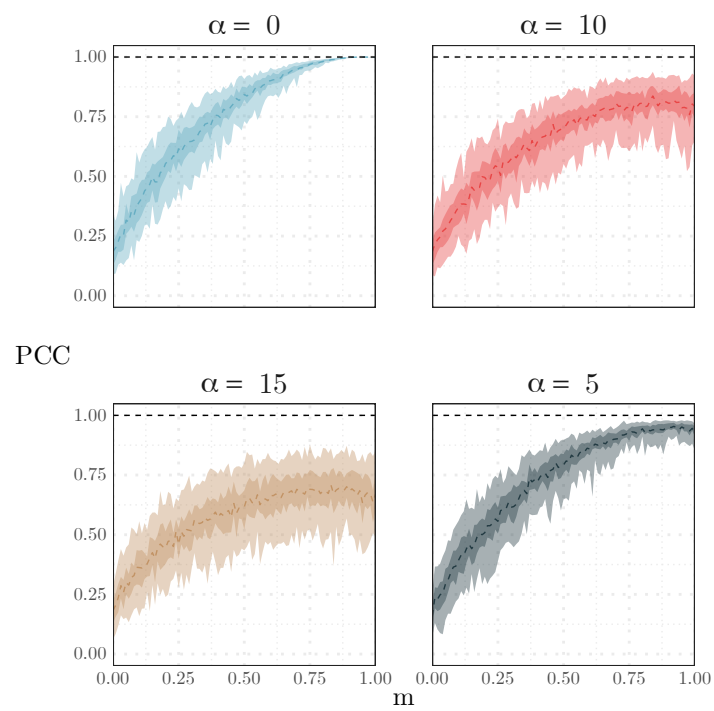


Figure 4

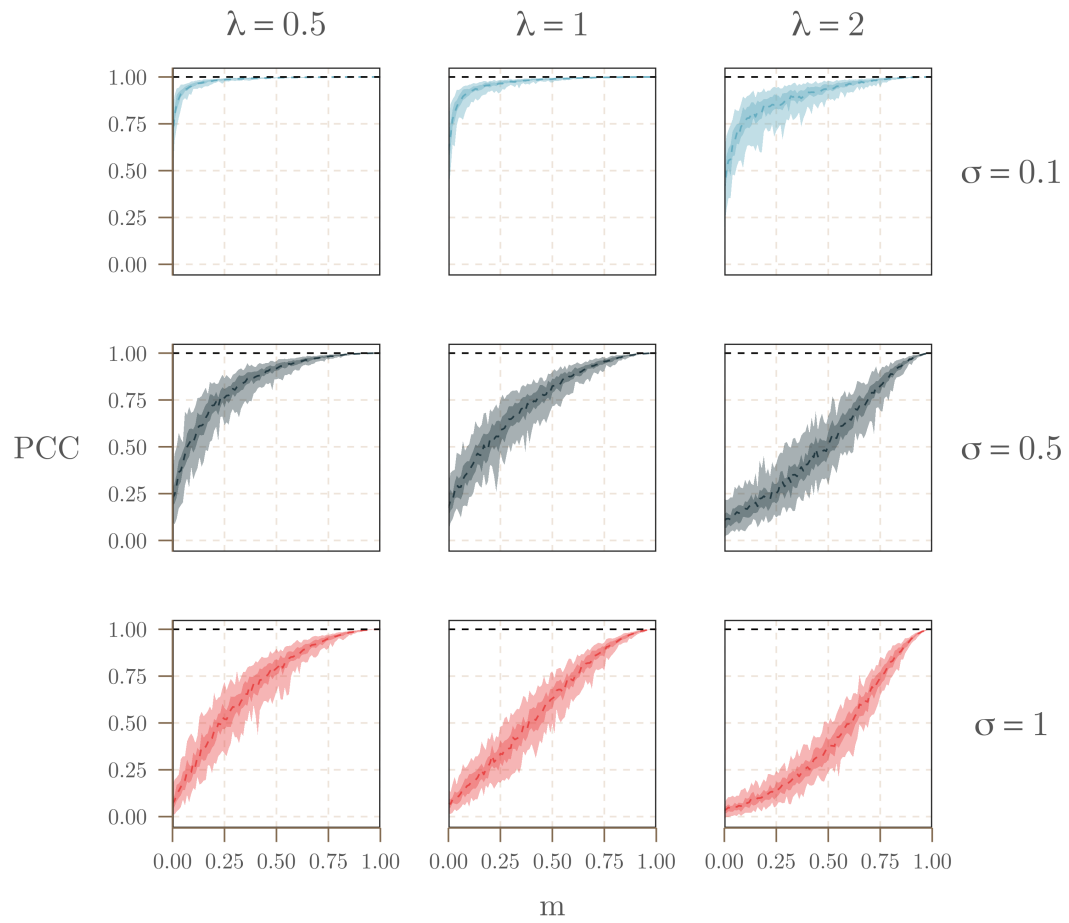


Figure 5

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