

# Building a better metaweb: predicting spatiotemporally explicit plant-pollinator networks

[Michael D. Catchen](#)<sup>1,2</sup> [Andrew Gonzalez](#)<sup>1,2</sup> [Samuel M. Flaxman](#)<sup>3</sup>

<sup>1</sup> McGill University <sup>2</sup> Québec Centre for Biodiversity Sciences <sup>3</sup> University of Colorado at Boulder

## Correspondance to:

Michael D. Catchen — [michael.catchen@mail.mcgill.ca](mailto:michael.catchen@mail.mcgill.ca)

# 1 Introduction

2 Human activity is changing the face of Earth, leaving landscapes that are fragmented and patchy.

3 It is well understood that landscape structure influences ecosystem processes (**cite?**). Understanding how  
4 landscape structure affects ecological processes remains a fundamental goal of ecological research.

5 Landscape connectivity can mitigate the negative effects of habitat loss on ecosystem functioning, through  
6 corridors (Resasco 2019).

7 As a result understanding how habitat structure effects the movement and dispersal of organisms, and  
8 how this scales up to explain the abundance and distribution of species across space, is a primary aim of  
9 landscape ecology. Models in landscape ecology—analytic, computational, and statistical— have long  
10 used diffusion to approximate model how organisms move or disperse between habitat patches (Hastings  
11 1978; **Okubo2001DifEco?**).

12 What does it mean that model uses diffusion? The way in which organisms move from one habitat patch  
13 to another, via active or passive dispersal, is inherently stochastic. Diffusion approximates this stochastic  
14 process by assuming the that stochastic process of movement of organisms between two locations is equal  
15 to its expected value at every time point—ignoring any temporal variation in dispersal. However, here we  
16 show that in some cases this assumption creates artificially synchronized dynamics across space.

17 Why is it important we understand when dispersal is a valid approximation of dispersal? In order to  
18 design landscapes that mitigate biodiversity loss and its effects (Albert *et al.* 2017), we need models to  
19 understand how landscape structure affects ecological processes. Understanding when dispersal is  
20 well-approximated by diffusion, and when it isn't, is important because diffusion models are much less  
21 computationally expensive.

22 We do this by using a simulation model with two parts: 1) a spatial graph model of both stochastic  
23 dispersal and diffusion, and 2) a Ricker model of local population dynamics. We then show that there are  
24 two regimes: one under which diffusion creates highly synchronized dynamics where stochastic dispersal  
25 doesn't, and one under which diffusion and stochastic dispersal produce similar distributions of  
26 synchrony. We show that the boundaries between these regimes is caused by both the modularity of the  
27 dispersal network and demographic parameters. We show that what distinguishes these regimes is  
28 whether the primary source of variation in population dynamics is either dispersal or demography.

## 30 **Methods**

31 Here, we present a model of metapopulation dynamics on spatial graphs. This model contains three parts:  
 32 a model of landscape connectivity, a model of local population dynamics, and a model of dispersal. We use  
 33 this model to simulate time-series of metapopulation abundances using both diffusion and stochastic  
 34 models of dispersal, and then measure the synchrony of population dynamics between populations. By  
 35 comparing the synchrony created by stochastic dispersal and diffusion models, we show there are two  
 36 distinct regimes: a regime where diffusion well approximates stochastic dispersal, and a regime where it  
 37 does not.

### 38 **Landscape connectivity model**

39 Spatial graphs have long been used to model a system of habitat patches (nodes) connected by dispersal  
 40 (edges, which combined form a landscape (Urban & Keitt 2001; Minor & Urban 2008; Dale & Fortin 2010).

41 // have to define connectivity

42 To describe how the edges of this spatial graph describe dispersal,  
 43 we model landscape connectivity as a combination of two different factors: the probability than any  
 44 individual migrates during its lifetime,  $m$ , and the conditional distribution over spatial nodes of where an  
 45 individual goes ( $j \in L$ ), given both that it migrates  $m$  and where it started ( $i \in L$ ), which we call the  
 46 dispersal potential and denote

$$\Phi_{ij} = P(i \rightarrow j|m)$$

47 The dispersal potential can be modeled several ways. In empirical systems, the relative cost of movement  
 48 from one point to another is often estimated with resistance surfaces [spear\_use\_2010]. Here we model  
 49 the dispersal potential using isolation-by-distance (IBD), which assumes the relative probability of  
 50 dispersal from location  $i$  to location  $j$  is inversely proportional to the distance between them,  $d_{ij}$ , and the  
 51 strength of this IBD relationship,  $\alpha$ , which is treated as an intrinsic value of a species dispersal capacity.

52 The form of the IBD relationship (historically called the dispersal kernel) we consider an exponential with  
 53 decay-strength  $\alpha$  and a cutoff value  $\epsilon$  (Hanski 1994; Grilli *et al.* 2015).

$$f(d_{ij}, \alpha, \epsilon) = \begin{cases} e^{-\alpha d_{ij}} & \text{if } e^{-\alpha d_{ij}} > \epsilon \text{ and } i \neq j \\ 0 & \text{else} \end{cases}$$

54 Then, to construct a dispersal potential  $\Phi_{ij}$  with a kernel  $f(d_{ij}, \alpha)$ , we normalize:

$$\Phi_{ij} = \frac{f(d_{ij}, \alpha, \epsilon)}{\sum_k f(d_{ik}, \alpha, \epsilon)}$$

55 Note that the sum of each row of  $\Phi$ , forms a probability distribution, i.e.  $\sum_j \Phi_{ij} = 1 \ \forall i$ , meaning the  
 56 probability that an individual leaves its original population given that it migrates is 1. In some cases, for a  
 57 given location  $i$ , the dispersal kernel  $f(d_{ij}, \alpha, \epsilon)$  could be 0 for all  $j$ , in which case  $\Phi_{ii}$  is set to 1 to enforce  
 58 this condition. In all other cases,  $\Phi_{ii} = 0$ . Also note that if  $\alpha = 0$ , the dispersal potential is a uniform  
 59 distribution over other locations. In Figure ??, we can see the same set of points plotted spatial graphs  
 60 plotted representing the same set of populations across differing values of isolation-by-distance strength,  $\alpha$ .

## 61 **Local population dynamics model**

62 We model local population dynamics using the Ricker Model. At each timestep, the abundance  $N_i$  at  
 63 location  $i$  is drawn as

$$N_i(t + 1) \sim \text{Poisson}\left(N_i(t)\lambda R e^{-\chi N_i(t)}\right)$$

64 where  $\chi$  represents the strength of mortality of surviving until adulthood,  $R$  is the probability that an adult  
 65 reproduces (0.9 for all results presented here), and where  $\lambda$  is the mean number of offspring for each  
 66 individual that reproduces—yielding three total parameters:  $\theta = \{\lambda, R, \chi\}$ . We consider the simplest  
 67 variation on the model, which only includes demographic stochasticity, however it is straightforward to  
 68 extend this to other forms of stochasticity (**Melbourne2008ExtRis?**).

## 69 Dispersal Models

### 70 Stochastic Dispersal

71 To simulate stochastic dispersal, the number of migrants leaving a given location is stochastically drawn  
72 each timestep as  $m_i \sim \text{Binomial}(N_i, m)$  for each location  $i$ . For every migrating individual we randomly  
73 draw where that individual goes from the distribution of potential destinations  $\Phi^{(i)}$ .

### 74 Diffusion

75 To simulate diffusion dispersal, we incorporate the local Ricker Model into a reaction-diffusion model. If  
76 the probability that an individual disperses before reproducing is  $m$ , then we can define a diffusion matrix  
77  $D$  as

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

78 where  $D_{ij}$  is now the expected value an individual born in  $i$  reproduces in  $j$ . The dispersal dynamics of the  
79 diffusion model are described by the mapping

$$N_i(t + 1) = \sum_j D_{ji} N_j(t)$$

80 which can be combined into the local Ricker model from above as reaction-diffusion model by computing  
81 diffusion before each round of local dynamics.

$$N_i(t + 1) \sim \text{Poisson}\left(\lambda R e^{-\chi\left(\sum_j D_{ji} N_j(t)\right)} \cdot \sum_j D_{ji} N_j(t)\right)$$

### 82 Measuring Synchrony

83 In ecology and other fields, the crosscorrelation function, (CC), has long been used as a measure of the  
84 synchrony between two time-series. Here, with a metapopulation, we consider the mean crosscorrelation

85 in abundances between all pairs of populations, which we call Pairwise-Crosscorrelation (PCC) and  
86 compute as

$$\text{PCC} = \frac{1}{(N_p - 1)^2} \sum_{i \neq j} CC(\vec{N}_i, \vec{N}_j)$$

87 where  $\vec{N}_i$  is the time-series of abundances at population  $i$ .

## 88 Results

89 We first consider how synchrony, measured by PCC, changes as a function of the intrinsic dispersal  
90 probability  $m$ . In figure fig. 2, we see how PCC changes in response to  $m$  at varying levels of both  
91 landscape connectivity  $\alpha$  and intrinsic growth rate  $\lambda$ . We see that under some combinations of  $\alpha$ ,  $\lambda$ , and  $m$   
92 both stochastic dispersal (green) and diffusion (orange) produce similar levels of synchrony, however at  
93 some parameter values diffusion artificially creates more synchronous dynamics than stochastic dispersal.

94 [Figure 2 about here.]

95 At low  $\lambda$ , the diffusion model produces increasingly synchronized population dynamics as migration  
96 increases; however, the stochastic dispersal model produces effectively no synchrony regardless of  
97 migration rate. As  $\lambda$  increases, we see two phenomena: 1) the distribution of PCC for both diffusion and  
98 stochastic model begin to move closer to one another, and 2) the shift from non-synchronized to  
99 synchronized dynamics becomes more “critical,” meaning it rapidly jumps to near PCC = 1.0 as  $m$   
100 increases. As we increase  $\lambda$ , the gap between the diffusion and stochastic PCC distributions shrinks. As  $\alpha$ ,  
101 the modularity of the habitat networks, increases, we see the difference in PCC between diffusion and  
102 stochastic dispersal models shrink, but the amount of variance in this estimate increases and we increase  
103 the modularity of the habitat network ( $\alpha$ ). In this case, the spatial configuration of habitat patches, and  
104 how the dispersal structure of a randomly generated habitat network changes with  $\alpha$ , is driving greater  
105 variation in the amount of synchrony observed at a given set of parameter values.

106 To better understand this, we consider “mapping” this difference in the parameter space defined by  
107 varying levels of landscape connectivity  $\alpha$  and intrinsic growth rate  $\lambda$  at “snapshots” of various value of  
108 intrinsic dispersal rate  $m$  (fig. 3). Dispersal rate is often treated as a property intrinsic to a species.

[Figure 3 about here.]

110 Why is it that we see a response to  $\lambda$ ? Consider what we know about the Ricker model, By comparing the  
 111 synchrony created by stochastic dispersal and diffusion models, we show there are two distinct regimes: a  
 112 regime where diffusion well approximates stochastic dispersal, and a regime where it does not.  
 113 higher  $\lambda$  without changing other parameters means the mean population size increases. As the mean  
 114 population size increases, the size of the sampling distribution of dispersers at each timestep increases,  
 115 and we expect this distribution to converge to  $\Phi$  as the number of migrants increases toward infinity.  
 116 We conclude by emphasizing the difference in simulation time between these models, especially as the  
 117 number of spatial locations increases. This is compounded by stochastic dispersal's runtime is sensitive to  
 118 the intrinsic migration probability  $m$ . At higher value of  $m$ , more dispersal events occur,

[Figure 4 about here.]

## 120 Discussion

121 When developing models to understand and predict how landscape structure effects ecological processes,  
 122 diffusion can be a convenient abstraction to speed up computation in some cases.

123 Here we show that diffusion can artificially synchronize dynamics across space.

124 Spatial synchrony of population dynamics is generally of interest. Dispersal induced synchrony can  
 125 increase population stability, up until a certain threshold where the dynamics become so highly  
 126 synchronized that they increase extinction risk (Abbott 2011).

127 The point goes beyond synchrony. The major point we intend to make here is that if one is developing an  
 128 ecological model that involves organisms moving across space, it is imperative to test whether stochastic  
 129 and diffusion dispersal produce similar results. Diffusion can often be a valuable abstraction that make  
 130 computation faster. "Understanding the scope and proper domain of each abstraction" (Levins &  
 131 Lewontin 1987) One way to view this is diffusion ignores temporal variation in dispersal.

132 Another important consideration for this work is what is meant by a "location" within our model.  
 133 Although we frame this in terms of habitat patches, what an individual point in a spatial network

134 represents is a convenient abstract to represent the spatial dimension of ecological processes. We argue the  
135 dispersal potential, by using probabilistic framework to represent dispersal, is a way to describe landscape  
136 structure at any scale.

- 137 • Spatial graph models as tool for modeling ecological processes across space and as generative  
138 models.
- 139 • Emergent properties and the role of stochasticity

## 140 **Acknowledgments**

## 141 **References**

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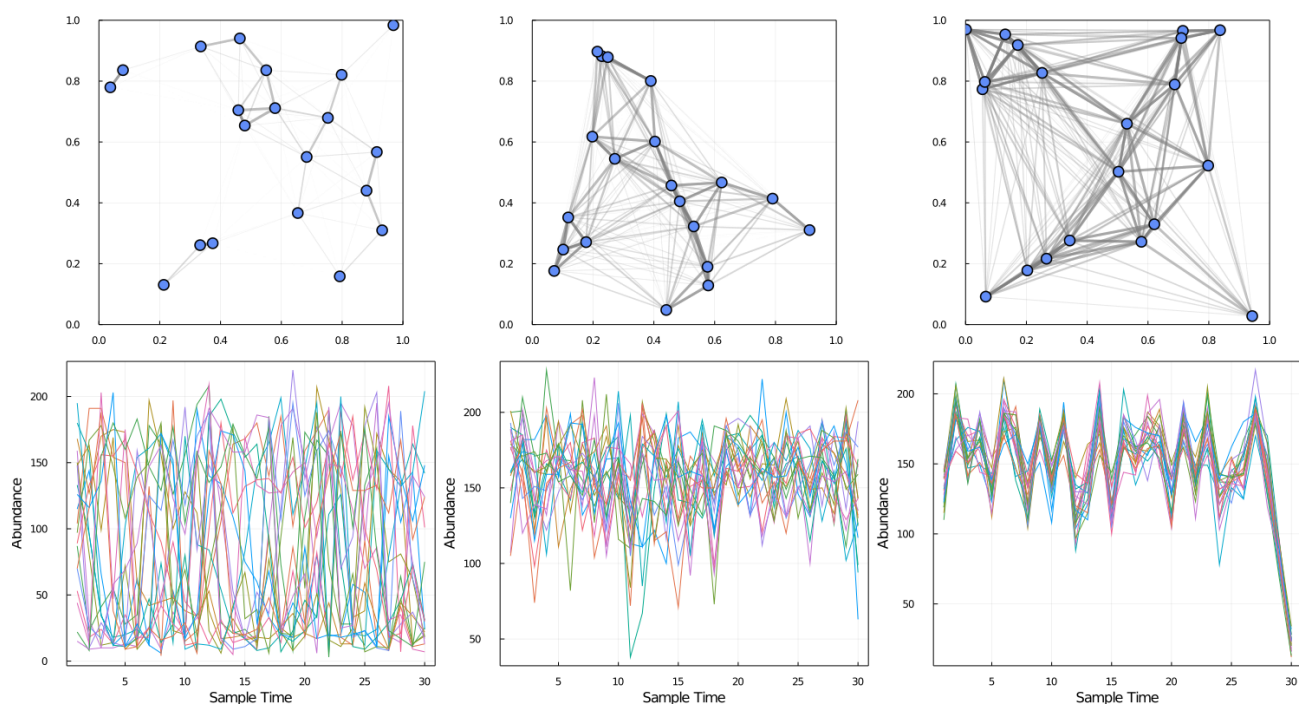


Figure 1: TODO Caption

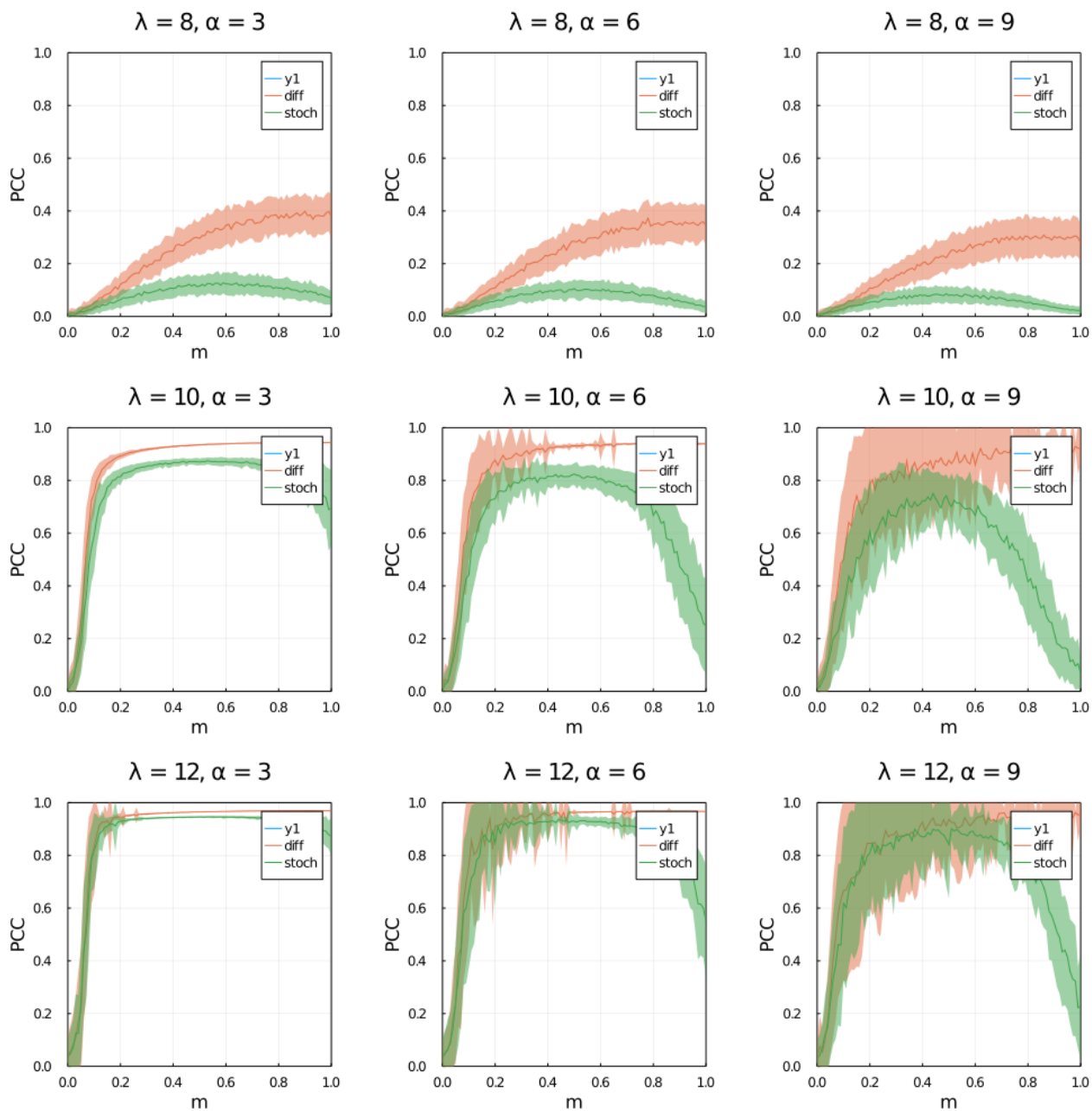


Figure 2: TODO Caption

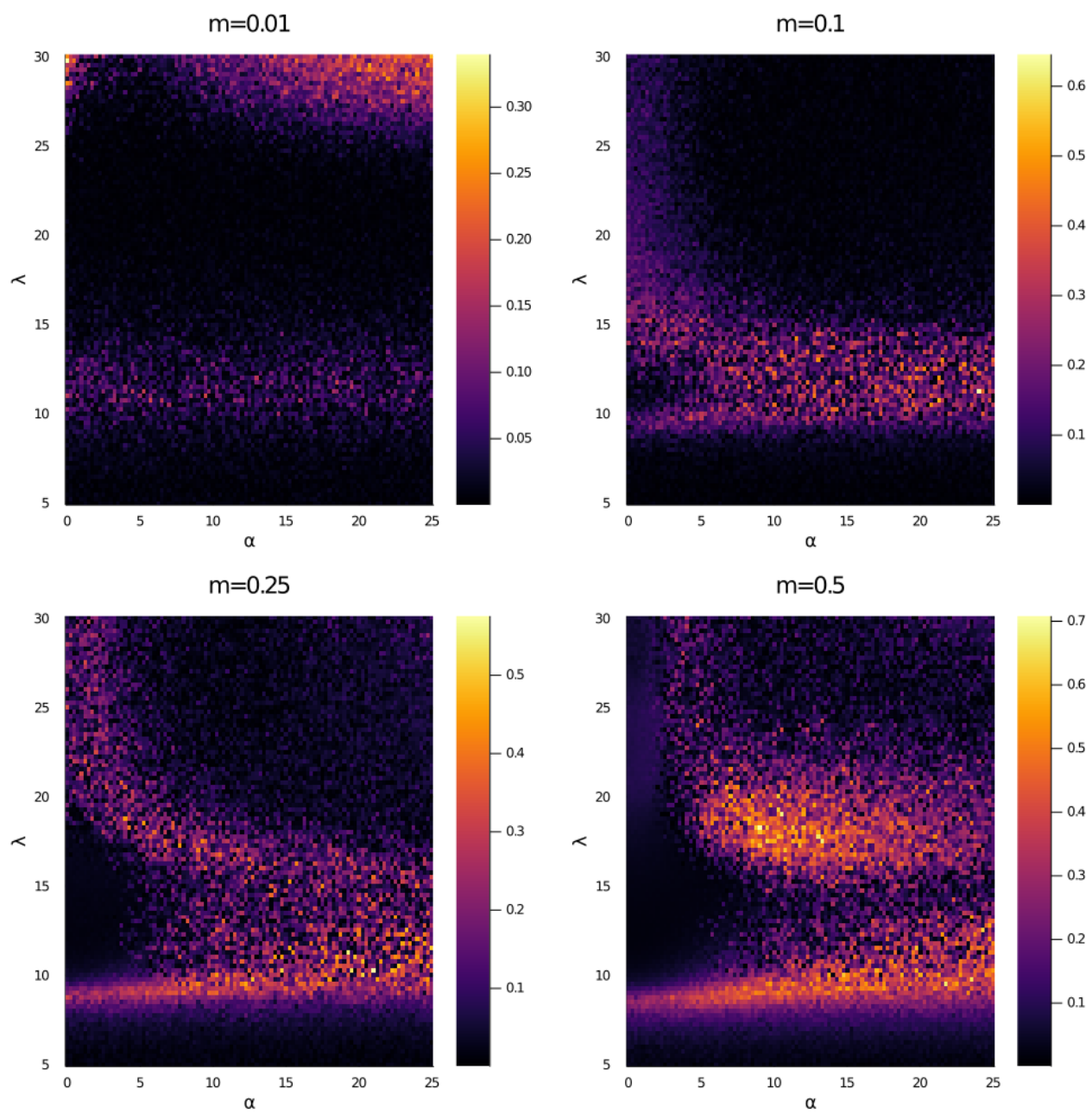


Figure 3: TODO Caption

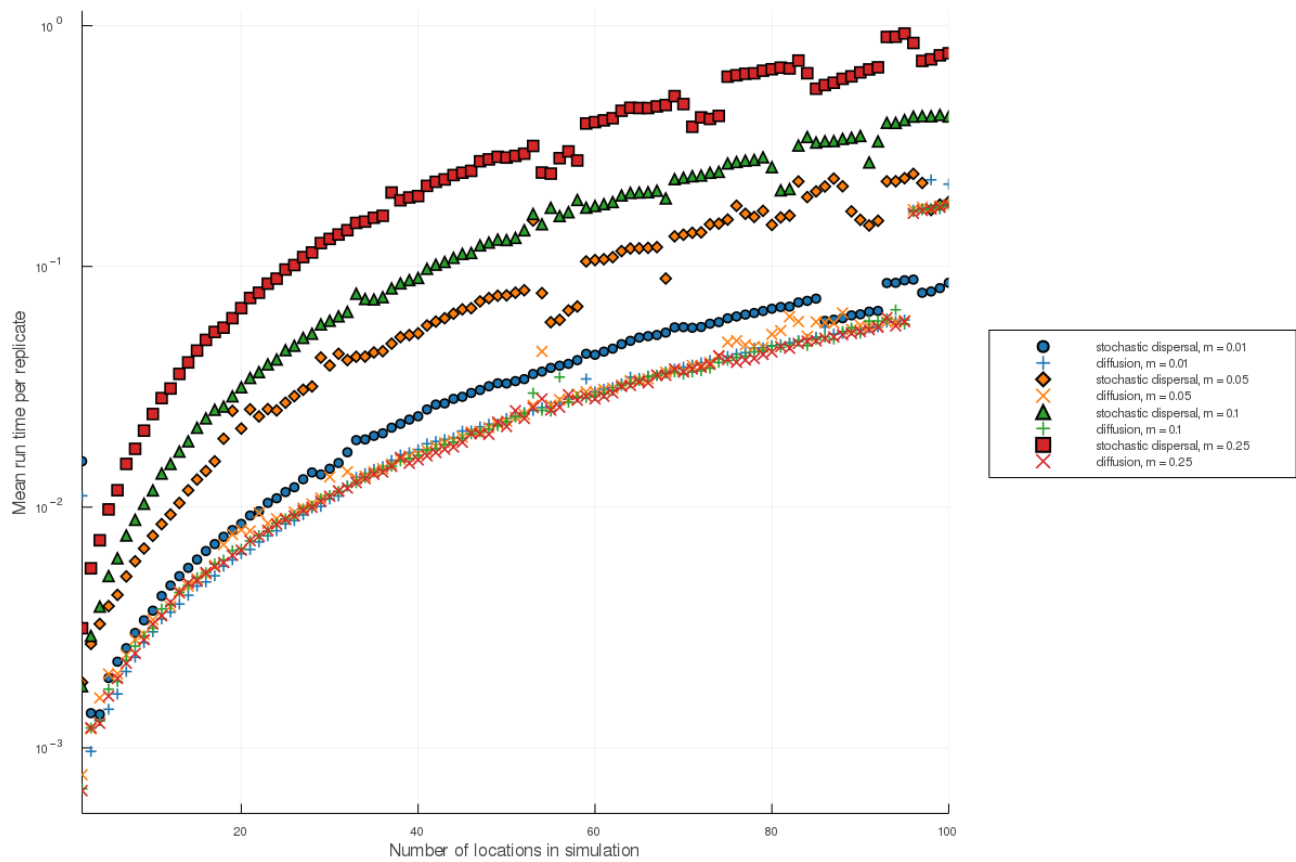


Figure 4: TODO Caption