# Diffusion creates artificial synchronization of population dynamics on spatial networks

Michael D. Catchen [1,2]    Andrew Gonzalez [1,2]    Samuel M. Flaxman [3]

[1] McGill University    [2] Québec Centre for Biodiversity Sciences    [3] University of Colorado at Boulder

**Correspondance to:**

Michael D. Catchen — `michael.catchen@mail.mcgill.ca`

# Introduction

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

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

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

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

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

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

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

[Figure 1 about here.]

## Methods

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

### Landscape connectivity model

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

// have to define connectivity

To describe how the edges of this spatial graph describe dispersal,

we model landscape connectivity 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 ($j \in L$), given both that it migrates $m$ and where it started ($i \in L$), which we call the dispersal potential and denote

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

The dispersal potential can be modeled several ways. In empirical systems, the relative cost of movement from one point to another is often estimated with resistance surfaces [spear_use_2010]. Here we model the dispersal potential using isolation-by-distance (IBD), which assumes the relative probability of dispersal from location $i$ to location $j$ is inversely proportional to the distance between them, $d_{ij}$, and the 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).

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

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, $\alpha$.

## 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?**).

## Dispersal Models

### Stochastic Dispersal

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

### Diffusion

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

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

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

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

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

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

### Measuring Synchrony

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

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

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

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

## Results

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

[Figure 2 about here.]

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

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

Why is it that we see a response to $\lambda$? Consider what we know about the Ricker model,By comparing the synchrony created by stochastic dispersal and diffusion models, we show there are two distinct regimes: a regime where diffusion well approximates stochastic dispersal, and a regime where it does not.

higher $\lambda$ without changing other parameters means the mean population size increases. As the mean population size increases, the size of the sampling distribution of dispersers at each timestep increases, and we expect this distribution to converge to $\Phi$ as the number of migrants increases toward infinity.

We conclude by emphasizing the difference in simulation time between these models, especially as the number of spatial locations increases. This is compounded by stochastic dispersal's runtime is sensitive to the intrinsic migration probability $m$. At higher value of $m$, more dispersal events occur,

## Discussion

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

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

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

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

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

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

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

# References

Abbott, K.C. (2011). A dispersal-induced paradox: Synchrony and stability in stochastic metapopulations. *Ecology Letters*, 14, 1158–1169.

Albert, C.H., Rayfield, B., Dumitru, M. & Gonzalez, A. (2017). Applying network theory to prioritize multispecies habitat networks that are robust to climate and land-use change. *Conservation Biology*, 31, 1383–1396.

Dale, M.R.T. & Fortin, M.-J. (2010). From Graphs to Spatial Graphs. *Annual Review of Ecology, Evolution, and Systematics*, 41, 21–38.

Grilli, J., Barabás, G. & Allesina, S. (2015). Metapopulation Persistence in Random Fragmented Landscapes. *PLOS Computational Biology*, 11, e1004251.

Hanski, I. (1994). A Practical Model of Metapopulation Dynamics. *The Journal of Animal Ecology*, 63, 151.

Hastings, A. (1978). Global stability in Lotka-Volterra systems with diffusion. *Journal of Mathematical Biology*, 6, 163–168.

Levins, R. & Lewontin, R.C. (1987). *The Dialectical Biologist*. Harvard University Press, Cambridge, Mass.

Minor, E.S. & Urban, D.L. (2008). A Graph-Theory Framework for Evaluating Landscape Connectivity and Conservation Planning. *Conservation Biology*, 22, 297–307.

Resasco, J. (2019). Meta-analysis on a Decade of Testing Corridor Efficacy: What New Have we Learned? *Current Landscape Ecology Reports*, 4, 61–69.

159  Urban, D. & Keitt, T. (2001). Landscape Connectivity: A Graph-Theoretic Perspective. *Ecology*, 82,
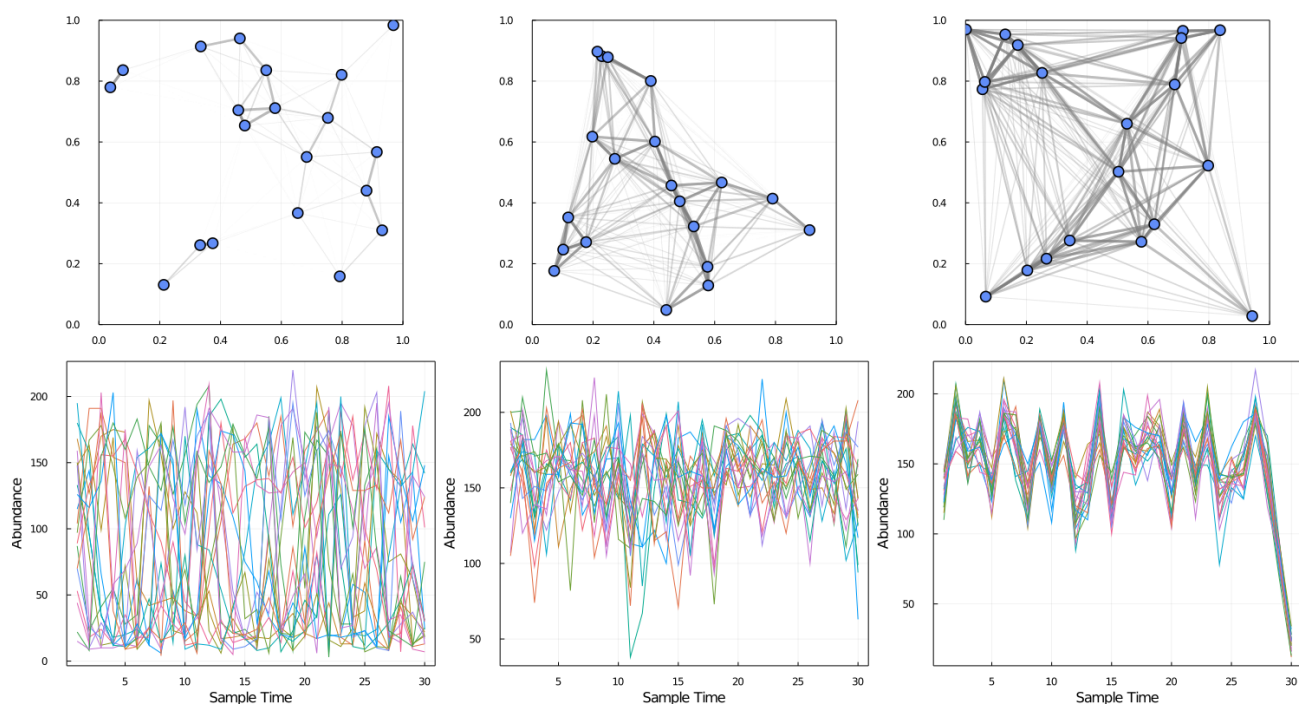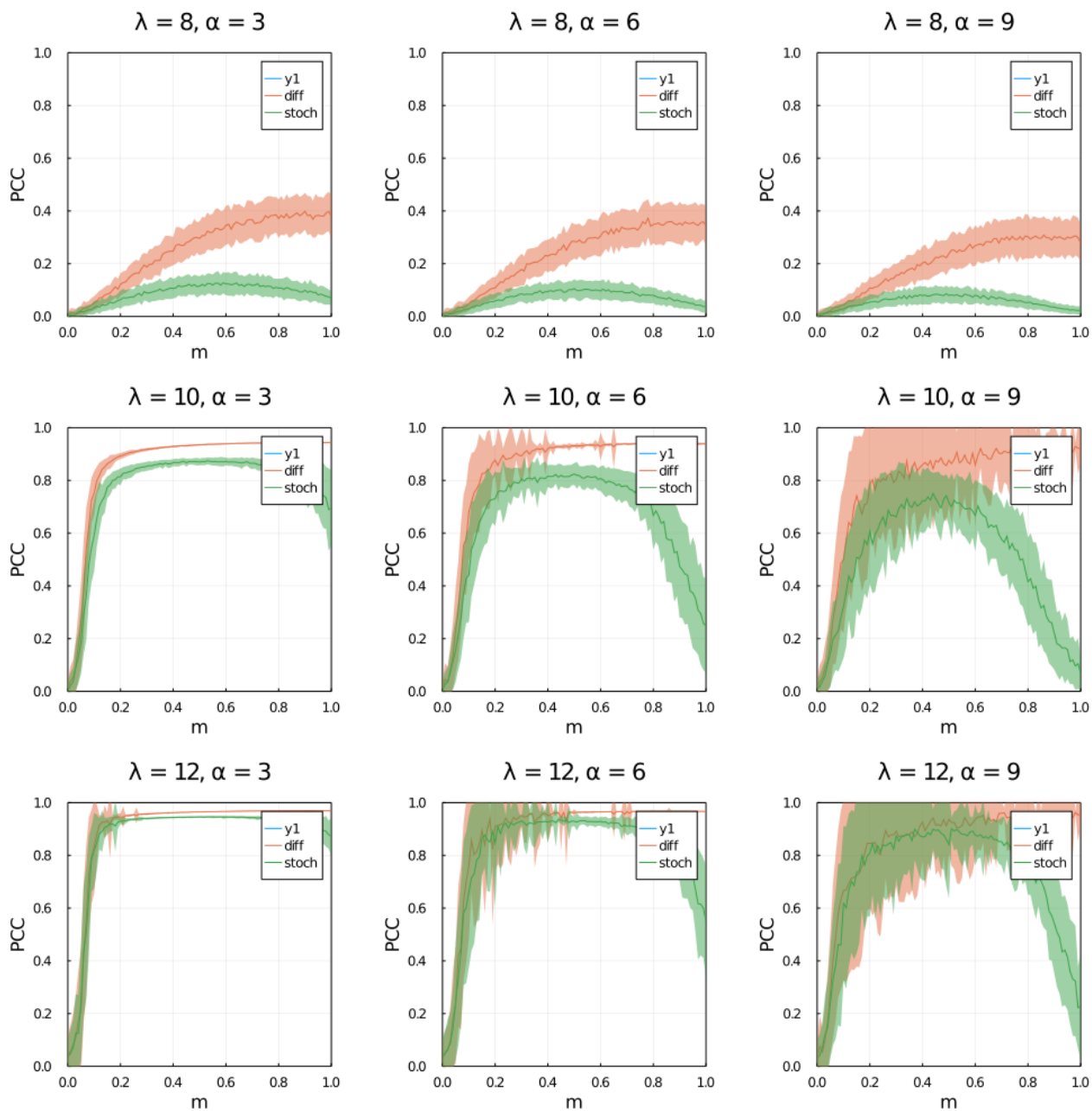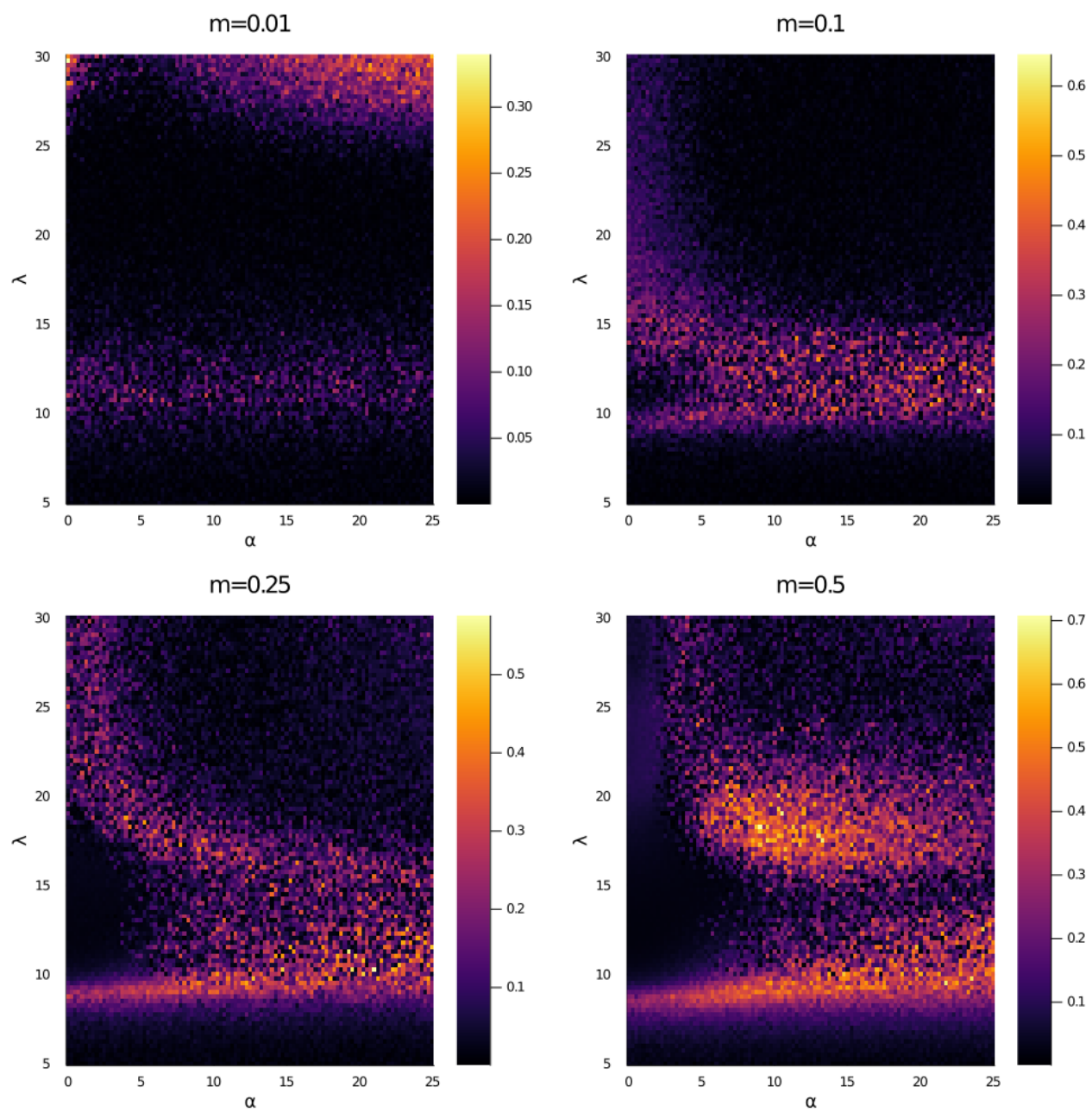
160      1205–1218.

Figure 1: TODO Caption

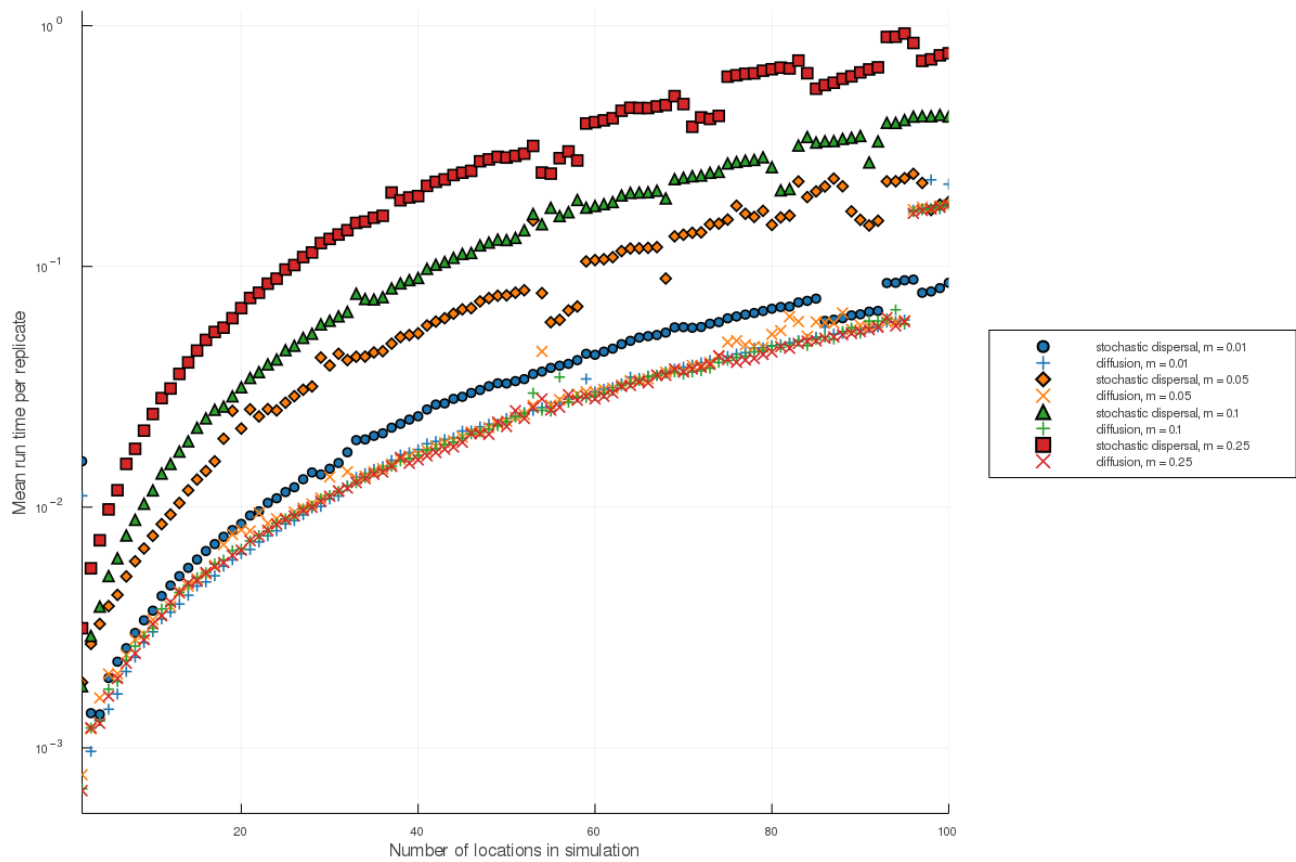Figure 2: TODO Caption

Figure 3: TODO Caption

Figure 4: TODO Caption