

When can we approximate dispersal with diffusion in ecology?

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Abstract: A paper.

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?). Under-
4 standing how landscape structure affects ecological processes remains a fundamental goal of
5 ecological research.

6 Landscape connectivity can mitigate the negative effects of habitat loss on ecosystem function-
7 ing, through corridors (Resasco 2019).

8 As a result understanding how habitat structure affects the movement and dispersal of organisms,
9 and how this scales up to explain the abundance and distribution of species across space, is a
10 primary aim of landscape ecology. Models in landscape ecology—analytic, computational, and
11 statistical— have long used diffusion to approximate model how organisms move or disperse
12 between habitat patches (Okubo 2001; Hastings 1978).

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

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

24 We do this by using a simulation model with two parts: 1) a spatial graph model of both stochas-
25 tic dispersal and diffusion, and 2) a Ricker model of local population dynamics. We then show
26 that there are two regimes: one under which diffusion creates highly synchronized dynamics
27 where stochastic dispersal doesn't, and one under which diffusion and stochastic dispersal pro-
28 duce 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 (Dale and Fortin 2010; Minor and Urban 2008; Urban and Keitt 2001).

// 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

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

51 The dispersal potential can be modeled several ways. In empirical systems, the relative cost of
 52 movement from one point to another is often estimated with resistance surfaces [spear_use_2010].
 53 Here we model the dispersal potential using isolation-by-distance (IBD), which assumes the rel-
 54 ative probability of dispersal from location i to location j is inversely proportional to the distance
 55 between them, d_{ij} , and the strength of this IBD relationship, α , which is treated as an intrinsic
 56 value of a species dispersal capacity. The form of the IBD relationship (historically called the
 57 dispersal kernel) we consider an exponential with decay-strength α and a cutoff value ϵ (Grilli,
 58 Barabás, and Allesina 2015; Hanski 1994).

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

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

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

60 Note that the sum of each row of Φ , forms a probability distribution, i.e. $\sum_j \Phi_{ij} = 1 \quad \forall i$,
 61 meaning the probability that an individual leaves its original population given that it migrates is
 62 1. In some cases, for a given location i , the dispersal kernel $f(d_{ij}, \alpha, \epsilon)$ could be 0 for all j , in
 63 which case Φ_{ii} is set to 1 to enforce this condition. In all other cases, $\Phi_{ii} = 0$. Also note that if
 64 $\alpha = 0$, the dispersal potential is a uniform distribution over other locations. In Figure ??, we can
 65 see the same set of points plotted spatial graphs plotted representing the same set of populations
 66 across differing values of isolation-by-distance strength, α .

67 **Local population dynamics model**

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

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

where χ represents the strength of mortality of surviving until adulthood, R is the probability that an adult reproduces (0.9 for all results presented here), and where λ is the mean number of offspring for each individual that reproduces—yielding three total parameters: $\theta = \{\lambda, R, \chi\}$. We consider the simplest variation on the model, which only includes demographic stochasticity, however it is straightforward to 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 stochastically 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 α and intrinsic growth rate λ . We see that under some combinations of α , λ , 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 λ , 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 λ 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

107 to near $PCC = 1.0$ as m increases. As we increase λ , the gap between the diffusion and stochastic
108 PCC distributions shrinks. As α , the modularity of the habitat networks, increases, we see
109 the difference in PCC between diffusion and stochastic dispersal models shrink, but the amount
110 of variance in this estimate increases and we increase the modularity of the habitat network (α).
111 In this case, the spatial configuration of habitat patches, and how the dispersal structure of a
112 randomly generated habitat network changes with α , is driving greater variation in the amount
113 of synchrony observed at a given set of parameter values.

114 To better understand this, we consider “mapping” this difference in the parameter space de-
115 fined by varying levels of landscape connectivity α and intrinsic growth rate λ at “snapshots” of
116 various value of intrinsic dispersal rate m (fig. 3). Dispersal rate is often treated as a property
117 intrinsic to a species.

118 [Figure 3 about here.]

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

123 higher λ without changing other parameters means the mean population size increases. As
124 the mean population size increases, the size of the sampling distribution of dispersers at each
125 timestep increases, and we expect this distribution to converge to Φ as the number of migrants
126 increases toward infinity.

127 We conclude by emphasizing the difference in simulation time between these models, especially
128 as the number of spatial locations increases. This is compounded by stochastic dispersal’s run-
129 time is sensitive to the intrinsic migration probability m . At higher value of m , more dispersal
130 events occur,

131 [Figure 4 about here.]

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 proper domain of each abstraction” (Levins and 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

Acknowledgments

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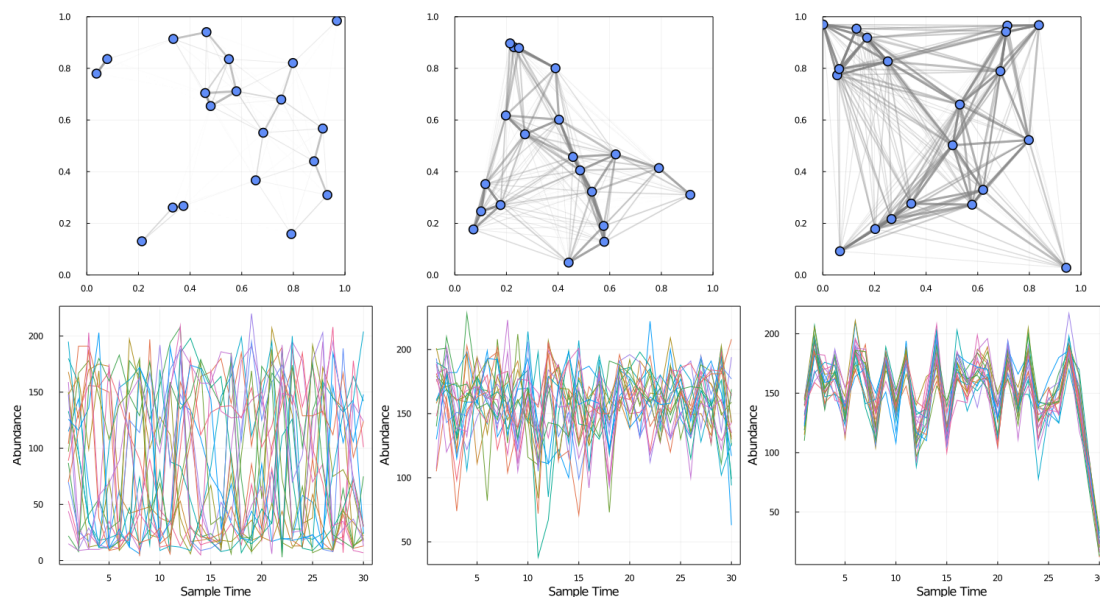


Figure 1: TODO Caption

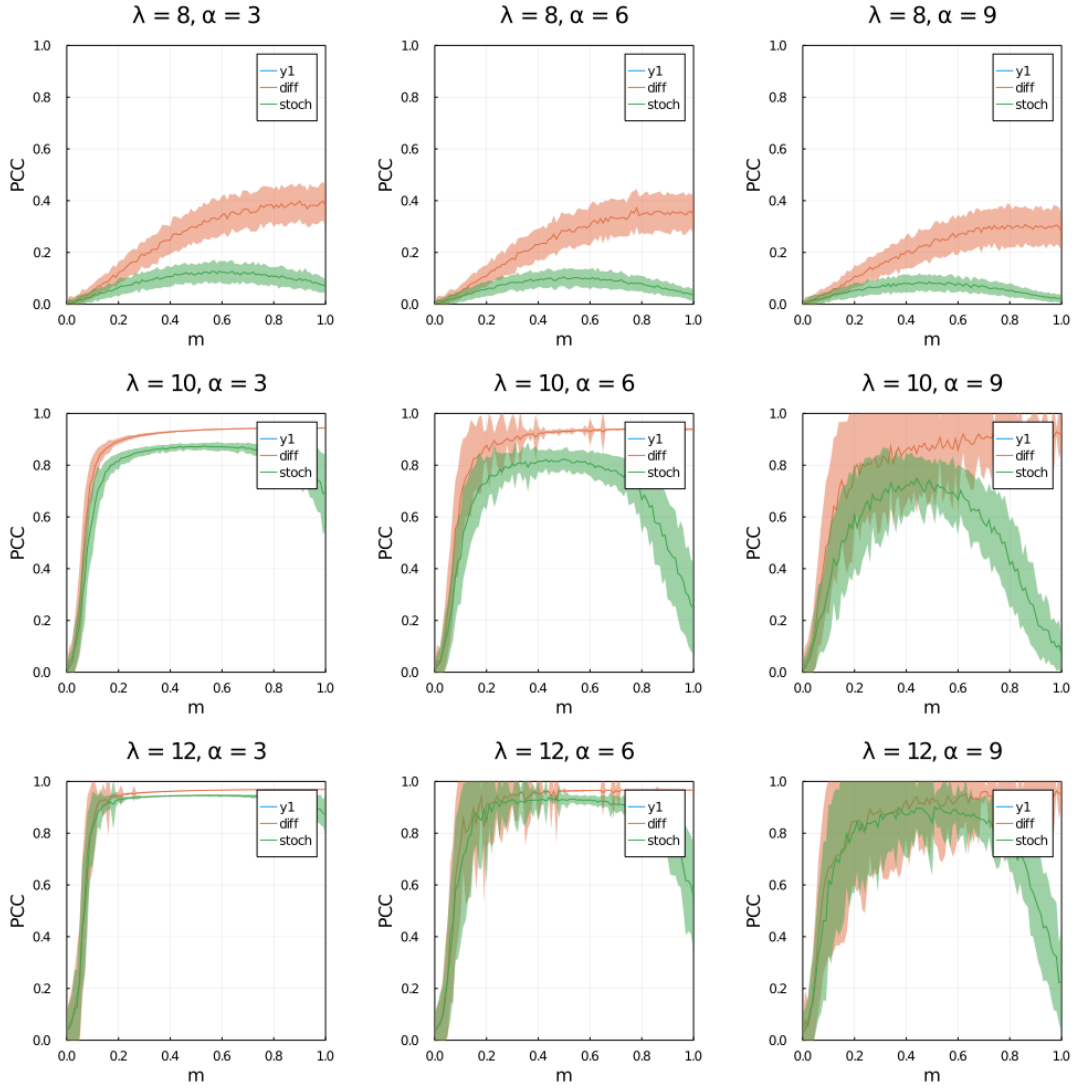


Figure 2: TODO Caption

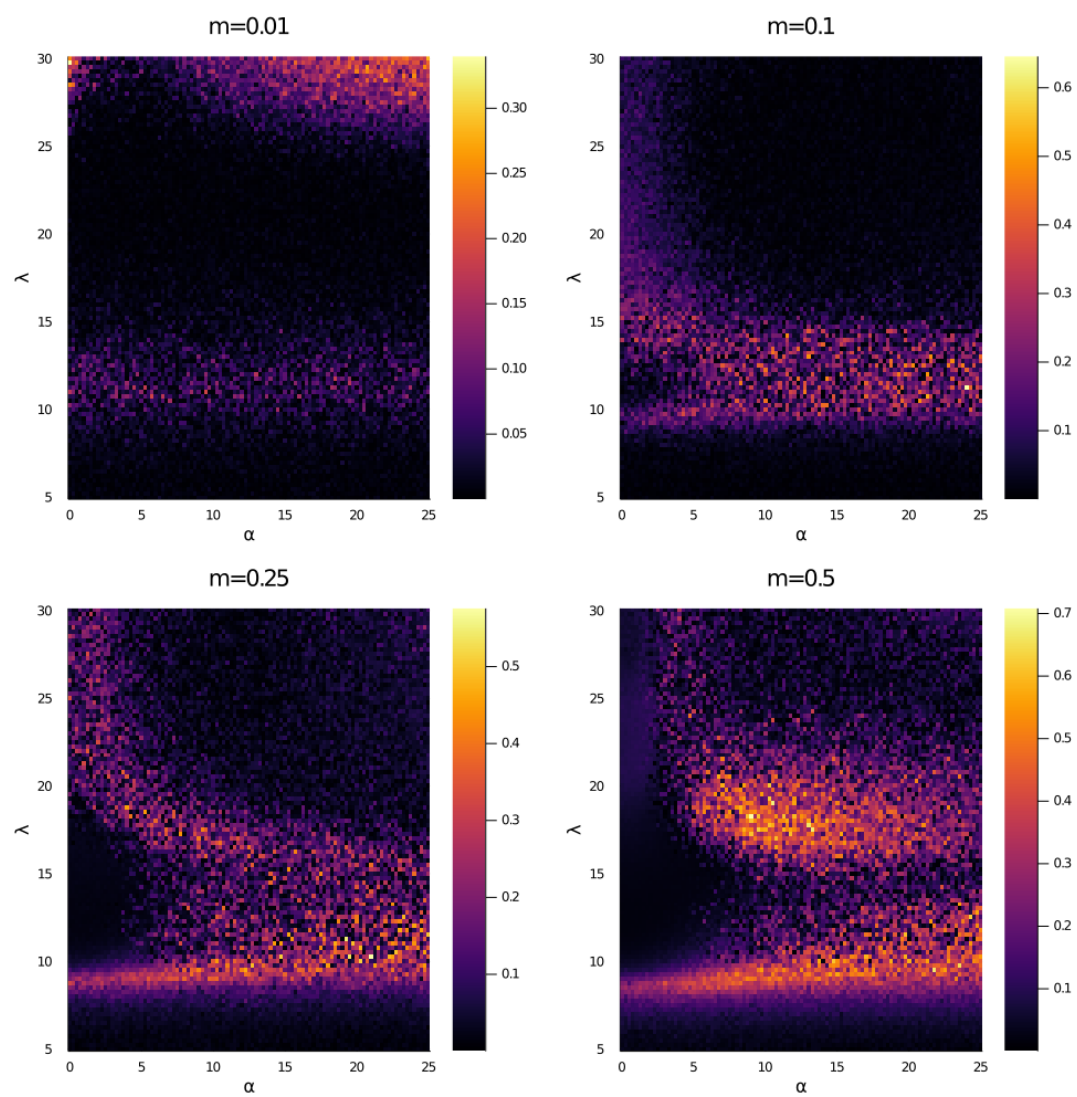


Figure 3: TODO Caption

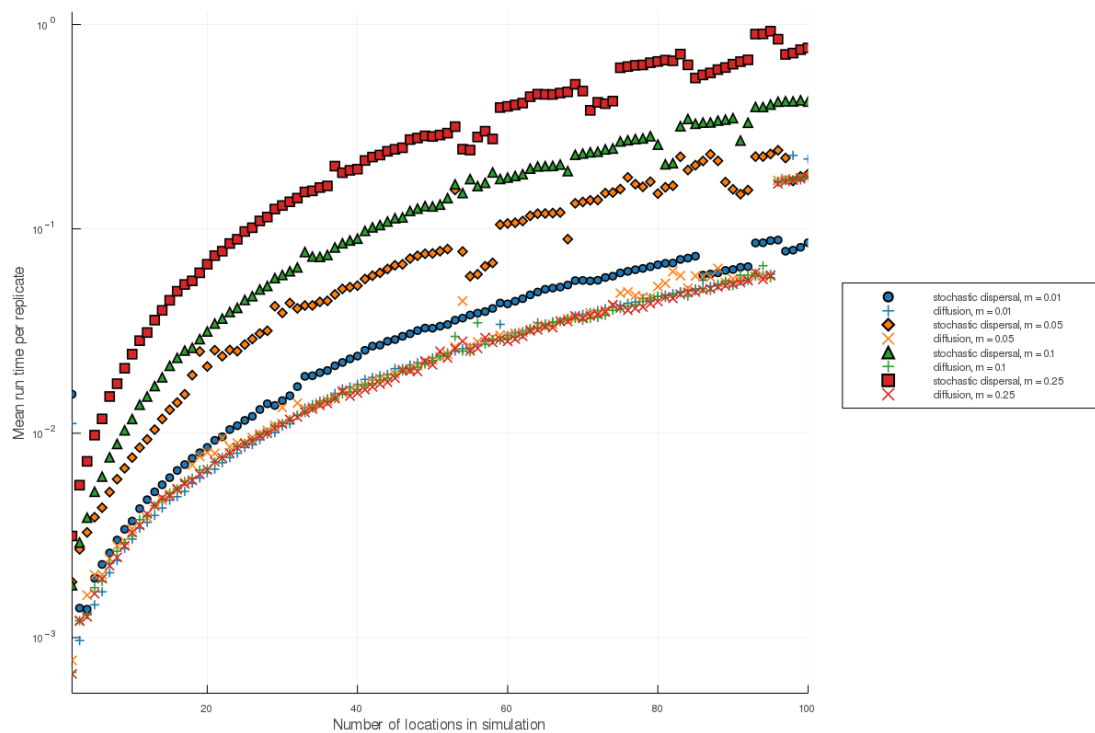


Figure 4: TODO Caption