reached the environmental carrying capacity, the birth rate matches the death rate and growth halts.

Recall that the parameter r is the intrinsic rate of growth for the population N. Though negative growth rates are possible, the populations we are modeling under typical logistic growth have positive growth rates associated with them. In terms of invasive species populations, the results of our fixed point analysis reveal that once an invasive is introduced to a new location, it will tend to grow until it reaches its carrying capacity. However, in more intricate models, this will not always be the case. For example, introduction of a strong Allee effect will induce a negative growth rate at low population densities, making the zero fixed point stable.

2.3 Model Formulation in Higher Dimensions

In this section we define a general form of the model in n dimensions. With multiple populations, patch dynamics depend on both within-node logistic growth as well as immigration and emigration between nodes.

The migration rates between the nodes are determined by the transition matrix $\mathbf{P}$,

$$\mathbf{P} = \begin{bmatrix} p_{11} & \cdots & p_{1j} & \cdots & p_{1n} \\ \vdots & \ddots & & & \vdots \\ p_{i1} & & p_{ij} & & p_{in} \\ \vdots & & & \ddots & \vdots \\ p_{ni} & \cdots & p_{nj} & \cdots & p_{nn} \end{bmatrix} \tag{2.8}$$

where element p_{ij} represents the proportion of population in patch j transferred from patch j to patch i in a single time step. The columns of $\mathbf{P}$ sum to 1, meaning that the outgoing population from each node is conserved. In addition, not all of the population is transferred out. The diagonal elements, p_{jj}, are the proportion of population within each patch that is sent back to itself at each time step.

We use a directed network graph to illustrate the connections defined by the transition matrix in a 3-patch model in Figure 2.1.

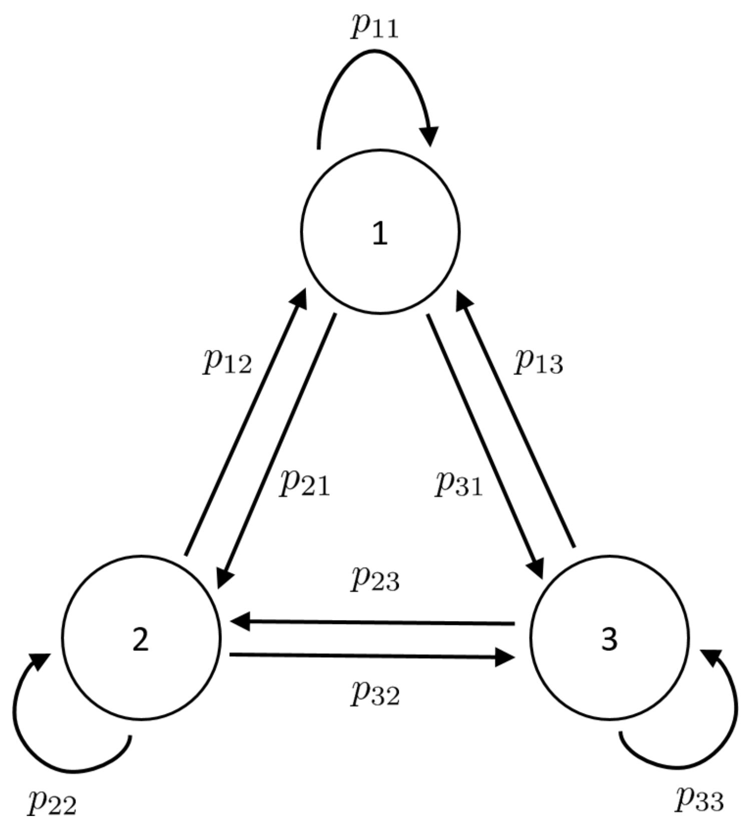

Figure 2.1: This is a connected network model in 3 dimensions. Each patch is connected with both its neighbors and itself, with edge weights denoted by p_{ij} which represent the proportion of population transfered from patch j to i in a single year.

The population of each node at each time t is stored in the state vector $\mathbf{s}_t$, an n

dimensional column vector defined as

$$\mathbf{s}_t = \begin{bmatrix} s_{t,1} \\ \vdots \\ s_{t,i} \\ \vdots \\ s_{t,n} \end{bmatrix} \tag{2.9}$$

where element $s_{t,i}$ represents the number of individuals in node i in year t.

We define a mapping of state vector $\mathbf{s}_t$ from year t to $t+1$ as

$$\mathbf{s}_{t+1} = \mathbf{P}\mathbf{g}(\mathbf{s}_t) \tag{2.10}$$

with the vector function

$$\mathbf{g}(\mathbf{s}_t) = \begin{bmatrix} g(s_{t,1}) \\ \vdots \\ g(s_{t,i}) \\ \vdots \\ g(s_{t,n}) \end{bmatrix} \tag{2.11}$$

Thus by applying the growth function defined in Equation 2.4 element-wise to each patch in $\mathbf{s}_t$ and multiplying the transition matrix $\mathbf{P}$ by the resulting column vector $\mathbf{g}(\mathbf{s}_t)$, we have our n dimensional determinstic network model of population growth and spread on the network.

2.4 Analysis of 2-Dimensional System

With the new notation in mind, we can describe the most general case of a two-patch system for analysis:

$$s_{t+1,1} = f_1(\mathbf{s}_t) = \frac{p_{11}s_{t,1}e^r}{1+\frac{s_{t,1}(e^r-1)}{K}} + \frac{p_{12}s_{t,2}e^r}{1+\frac{s_{t,2}(e^r-1)}{K}} \tag{2.12}$$

$$s_{t+1,2} = f_2(\mathbf{s}_t) = \frac{p_{22}s_{t,2}e^r}{1 + \frac{s_{t,2}(e^r-1)}{K}} + \frac{p_{21}s_{t,1}e^r}{1 + \frac{s_{t,1}(e^r-1)}{K}} \tag{2.13}$$

Similarly to the 1-dimensional analysis, we want to find the fixed points of the above system, s_1^* and s_2^*. We define s_i^* as the fixed point value of patch i in the state vector, where $f_i(s_i^*) = s_i^*$. Checking for the fixed points as we did before, we find that the extinct state at $(0,0)$ remains. Intuitively following the results from the 1-dimensional analysis, we predict the existence of a stable positive non-zero state. If we assume symmetry in our transition matrix, meaning in this case that $p_{11} + p_{12} = 1$ and $p_{21} + p_{22} = 1$, we find the fixed point to be (K, K), as predicted. Without this assumption of symmetry, in the model's most general form, we solve a complicated polynomial expression to arrive at an analytical form for the positive fixed point. We do not attempt to solve it here.

2.4.1 Stability Analysis

As in the 1-d analysis, we investigate the stability of the extinct state. From Strogatz (2014), we may be able to characterize the stability of this fixed point from the Jacobian matrix J, below, which describes our system of equations:

$$J = \begin{bmatrix} \frac{\partial f_1}{\partial s_1} & \frac{\partial f_1}{\partial s_2} \\ \frac{\partial f_2}{\partial s_1} & \frac{\partial f_2}{\partial s_2} \end{bmatrix}$$

We can characterize the stability of the extinct state by determining the eigenvalues of the Jacobian evaluated at that point. We evaluate the Jacobian at $(s_1^*, s_2^*) = (0,0)$ below:

$$J_{0,0} = \begin{bmatrix} p_{11}e^r & p_{12}e^r \\ p_{21}e^r & p_{22}e^r \end{bmatrix}$$

We allow the carrying capacity K to be equal to one. As a result, the population terms are taken to represent a fraction of the total carrying capacity.

Setting up the characteristic equation for the Jacobian,

$$(p_{11}e^r - \lambda)(p_{22}e^r - \lambda) - p_{21}e^r p_{12}e^r = 0$$

we solve for the eigenvalues using the quadratic equation,

$$\lambda_+, \lambda_- = \frac{e^r \left(p_{11} + p_{22} \pm \sqrt{(p_{11} - p_{22})^2 + 4p_{21}p_{12}}\right)}{2} \tag{2.14}$$

where λ_+ denotes the root derived from adding the quantity under the square root, and λ_- denotes the result of subtracting it. We note that in our model, movement between nodes conserves population such that the column sums of the transition matrix $\mathbf{P}$ are equal to 1. Thus, $p_{11} = 1 - p_{21}$ and $p_{22} = 1 - p_{12}$. Substituting these into Equation 2.14, we get:

$$\lambda_+, \lambda_- = \frac{e^r \left(p_{11} + p_{22} \pm (2 - p_{11} - p_{22})\right)}{2} \tag{2.15}$$

We can simplify this to get an expression for each eigenvalue:

$$\lambda_+ = e^r$$

$$\lambda_- = e^r(p_{11} + p_{22} - 1)$$

Recall that the elements of $\mathbf{P}$ represent the proportion of population transferred between nodes. As such, they are bounded between 0 and 1. Because $0 \leq p_{11} \leq 1$ and $0 \leq p_{22} \leq 1$, it follows that $-1 \leq p_{11} + p_{22} - 1 \leq 1$. Thus the magnitude of λ_- will always be a fraction of λ_+. To determine stability, we need only look at the magnitude of the larger eigenvalue, λ_+. If the magnitude of λ_+ is less than 1, then the fixed point is stable, and conversely if the magnitude of λ_+ is greater than 1, the fixed point is unstable. Setting up the inequality $\lambda_+ > 1$, we find that for $r > 0$, the fixed point at $(0, 0)$ is unstable. We have then shown that in 2-D, the extinct state is unstable when the growth rate r is positive.

2.5 Numerical Methods

Due to the complexity of analyzing the general network model in higher dimensions, in this section we introduce the deterministic models we use for numerical simulations. This includes the discrete map as well as an integrated ODE model.

2.5.1 Discrete Map

The discrete map defined by Equation 2.10 was implemented in R directly and was used for all results in the small world network section in Chapter 3.

2.5.2 ODE Model

We used an integrated ODE model to compare against the stochastic model in the stochastic modeling section. To see whether our discrete map derivation agrees with the original ODE model, we generate an integrated ODE model using the 'deSolve' package with the logistic equation (1.1) which we modify to incorporate the immigration and emigration terms derived from the transition matrix $\mathbf{P}$ in Equation 2.8. We define this as:

$$\frac{dN_i}{dt} = rN_i\left(1 - \frac{N_i}{K}\right) + \sum_{j=1, j\neq i}^{n} \mathbf{P}_{ij}N_j - \sum_{j=1, j\neq i}^{n} \mathbf{P}_{ji}N_i \tag{2.16}$$

The term $\mathbf{P}_{ij}N_j$ is the number of individuals patch j sends to patch i. The immigration term then, is the sum of $\mathbf{P}_{ij}N_j$ over all patches j that are not the patch in question, i. Emigration is defined similarly, though it is the sum of all outgoing individuals, $\mathbf{P}_{ji}N_i$ over all patches that are not the original patch i.

The values of p_{ij} in the transition matrix are filled using the migration rate v, which is a newly introduced parameter specified prior to beginning a simulation. In our simulations, we assume that edges between nodes are equally weighted with value v. Recall element p_{ij} is the proportion of population each patch transfers out over a yearly time step. For every edge p_{ij} where there exists a connection, we set its weight to v. Because the population is conserved, the values along the matrix diagonal values are set by the equation:

$$P_{jj} = 1 - k_j v$$

where k_j is the out degree of patch j. An example of a network generated with migration rate v is shown in Figure 2.2.

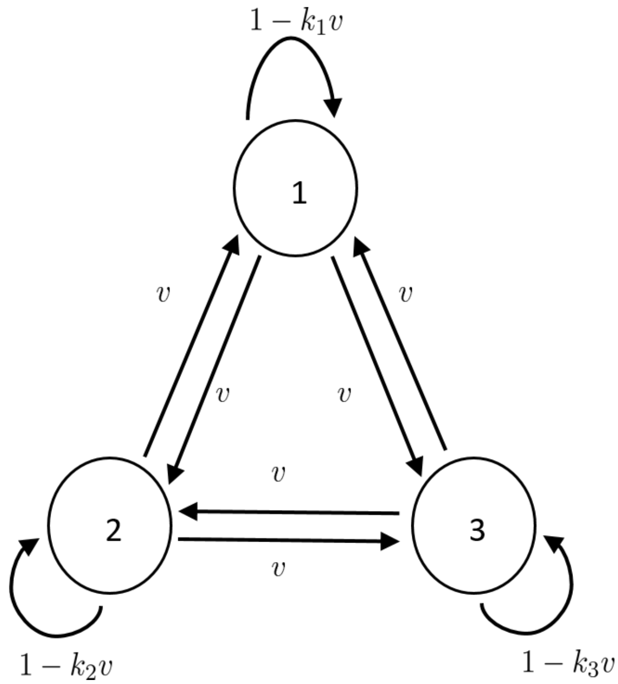

Figure 2.2: Figure showing a sample network with edges equally weighted. The parameter v is the migration rate between nodes and k_j is the outdegree of the node j.

To simulate a biotic invasion over a given time period, we initialize the state vector as $\mathbf{s}_0 = \vec{0}$. Then, we set the value of the patch where the invasion begins in $\mathbf{s}$ equal to carrying capacity K, and all other patches equal to 0. Then we apply the particular model: discrete map, integrated ODE, or Monte Carlo, which will be introduced later, for the given time period. We discuss the agreement of the deterministic models: the discrete map and the integrated ODE, in the following section.

2.5.3 Deterministic Model Agreement

The discrete map model in Equation 2.10 differs from the ODE model presented in Equation 2.16 in how population is distributed. In the former discrete time model, population is grown according to the growth function, Equation 2.11, before migration is calculated at the end of each time step according to the transition matrix. In the continuous time integrated ODE model, population growth and migration are calculated concurrently. This creates a small discrepancy between the models, which can be assumed to be negligible for our purposes. Consider the equation $\frac{dN_i}{dt} = -vN_i$, which represents the population loss term due to outbound migration on node i. Integrating over the course of one year gives us the equation $N_i(t+1) = e^{-v}N_i(t)$. The corresponding system in our discrete map model is $N_i(t+1) = (1-v)N_i(t)$. Note that at low values of v, which we use in this study, $e^{-v} \approx 1 - v$. Agreement of the model for typical parameter values are shown in Figure 2.3 and disagreement at large parameter values are shown in Figure 2.4. The calculation of migration in the integrated ODE model is not as straightforward as the multiplicative relationship in the discrete map model presented in Equation 2.10. Its dependence on v and potentially r are unclear, though we observe that at the typically small values chosen in this study, there is agreement between the two deterministic models presented.

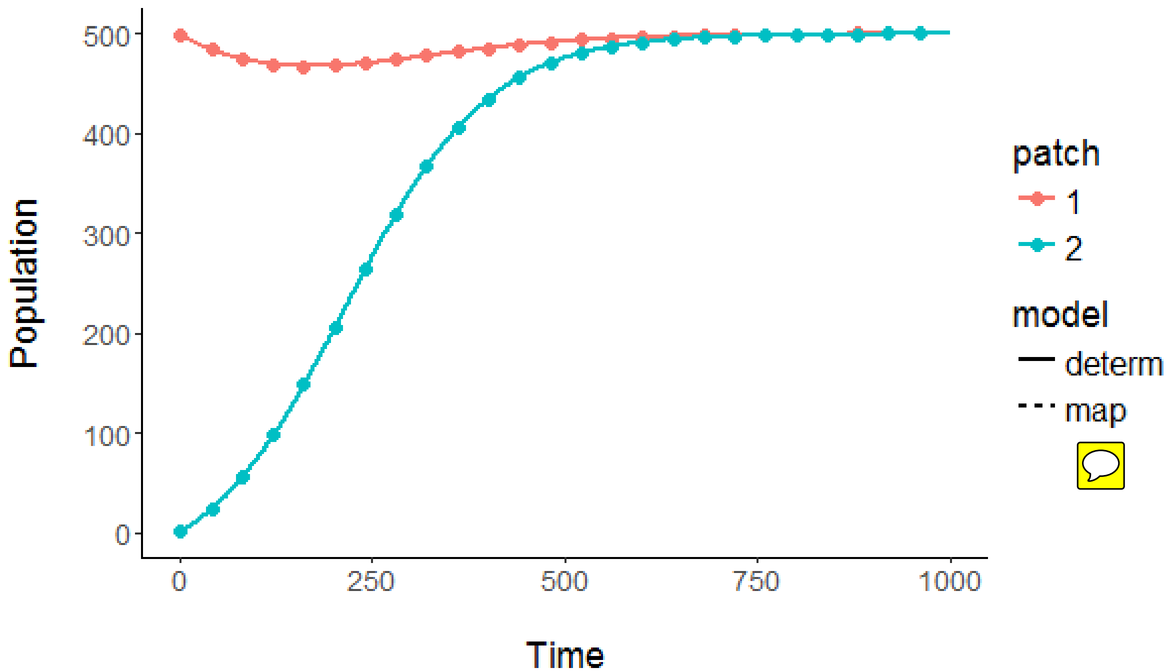

Figure 2.3: Figure showing the agreement between the ODE model and the discrete map at typical parameter values. The solid lines are the abundances in the ODE model, and are overlaid with points every 40 time steps from the discrete map model. The parameter values given are listed: $n = 2$ patches, migration rate $v = 0.001$, birth rate $r = 0.01$, and carrying capacity $K = 500$, over a course of 1000 time steps.

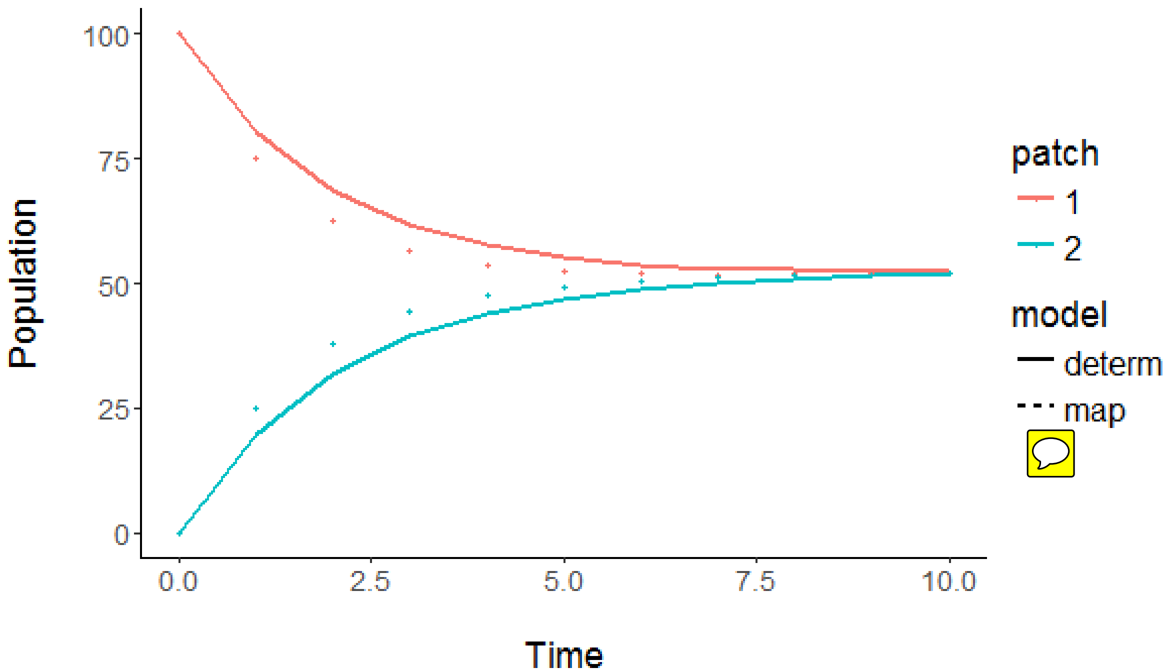

Figure 2.4: Figure showing discrepancy between the ODE model and the discrete map at large v values. The parameter values given are listed: $n = 2$ patches, migration rate $v = 0.25$, birth rate $r = 0.01$, and carrying capacity $K = 100$, over a course of 10 time steps.