Chapter 4

Stochastic Modeling

4.1 Stochastic Model

The stochastic simulations are carried out in a continuous-time Monte Carlo simulation using the Gillespie algorithm (Gillespie, 1977). Generally, we calculate what happens over a series of time steps, where in each time step one individual is either born, dies, or migrates between nodes. We keep track of the number of individuals in each patch and determine what happens at each time step based on the probability of each state transition: birth, death, or migration.

The births and deaths b_i and d_i respectively, for a population N_i in each node, were chosen as:

$$b_i = rN_i \tag{4.1}$$

$$d_i = r\frac{N_i^2}{K} \tag{4.2}$$

This choice is easily related back to the logistic ODE in Equation 1.1. We can expand the equation and rearrange the terms as:

$$\frac{dN}{dt} = rN - r\frac{N^2}{K} \tag{4.3}$$

where the birth and death rates are represented by the positive and negative terms respectively.

The total migration rate M is defined as the total number of individuals in the state vector. This is because each individual has a possibility of migrating. However, the majority of migrations are self-loops, which do not result in any population transfer. Notice this migration rate is defined as the total migration rate for the implementation of the Monte Carlo simulation, and is different from v, the parameter which relates to individuals that actually migrate out of a node.

$$M = \sum_{i=1}^{n} N_i \tag{4.4}$$

Transitioning between different population states is a Poisson process with a mean rate of R_{tot}. R_{tot} is equal to the sum of all birth, death, and migration rates,

$$R_{tot} = \sum_{i}^{n} b_i + \sum_{i}^{n} d_i + \sum_{i}^{n} N_i$$

and the time between events is then exponentially distributed with mean R_{tot}^{-1}.

The algorithm to simulate a biotic invasion is implemented as described: First, initialize the state vector s_t as described for the deterministic models. At each time step, record the values in each patch in s_t. To generate the time to the next event τ, we first draw a uniformly distributed random number u, between 0 and 1. This is converted to an exponentially drawn number by equation

$$\tau = \frac{\ln(\frac{1}{u})}{R_{tot}} \tag{4.5}$$

After we have found the time step, we determine whether a birth, death, or migration event has occurred. This is done by assigning a numerical range to each event proportional to the fraction of its rate over the total rate R_{tot}, then seeing where u falls after normalizing it to the width of the range. We repeat the process of drawing uniform random numbers and placing them within a range to determine which patch or patches are involved in

the event that occurs. For birth and death this involves drawing one number with each node having an equal chance of being chosen. For migration this involves drawing two numbers, one for the outbound node and one for the inbound node, with the width of the range we assign each node equal to the corresponding value in the transition matrix $\mathbf{P}$.

To generate a plot of population vs. time that we can compare against the deterministic model, we run the algorithm described above for 1000 years.

4.1.1 Results

In the introduction we stated that a large proportion of invasive species introductions do not establish stable colonies, and that those that do experience a lag period before growing. However, in the deterministic model analysis section, we showed that the extinct state of our population growth function is unstable. This means deterministically we would expect any introduction to grow to carrying capacity. The difference between the deterministic model and biological reality is that in reality stochastic effects can play a large role in a colony's establishment. Stochastic effects are particularly significant in populations with a small number of individuals and migration rates, both of which are properties of invasive species introductions.

Here we present some results from the comparison of the deterministic ODE model and the stochastic Monte Carlo simulation. The following are multi-panel plots of 1000-year simulations of the deterministic model (solid line) and the stochastic model (dashed line) with constant parameter values $K = 500$, $b = d = 0.01$. These figures illustrate the increasing magnitude of stochastic effects at low population levels and migration rates.

We note that in all of these simulations, the overall pattern is that all populations reach equilibrium. This is reasonable because our birth and death processes mimic the logistic growth function, which has an unstable extinct state. At low population, the migration out of a patch is negligible, so the probability of a series of chance events driving a new population experiencing logistic growth to extinction is incredibly small
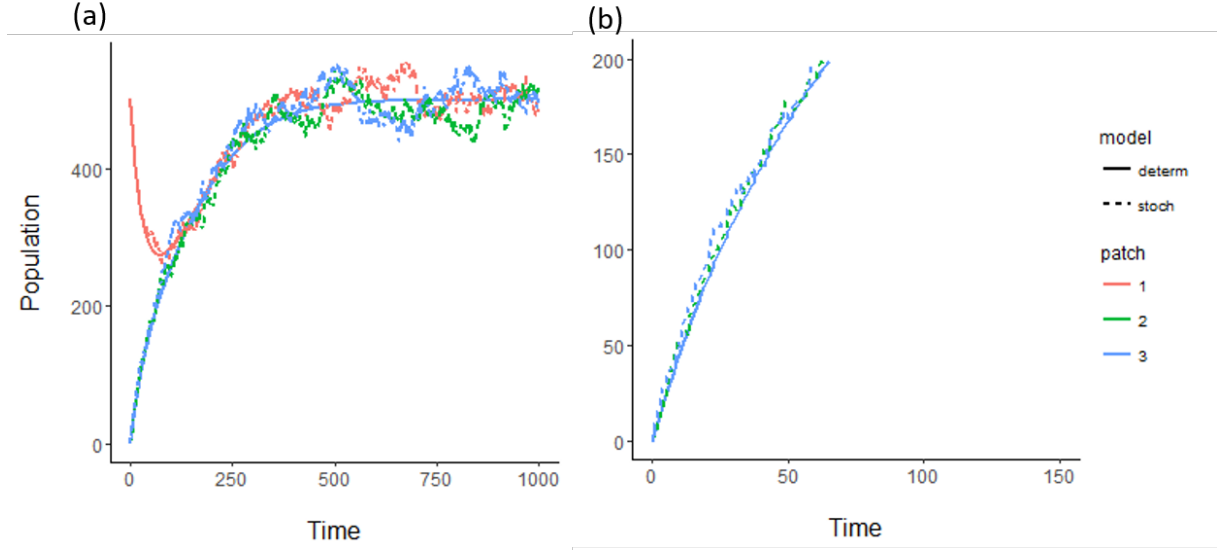
Figure 4.1: Migration rate $v = 0.01$. Plot (a) shows the entire 1000-year trajectory of each population patch while plot (b) shows a shorter time frame where stochastic effects are most apparent. Other parameters $K = 500$, $r = 0.01$.
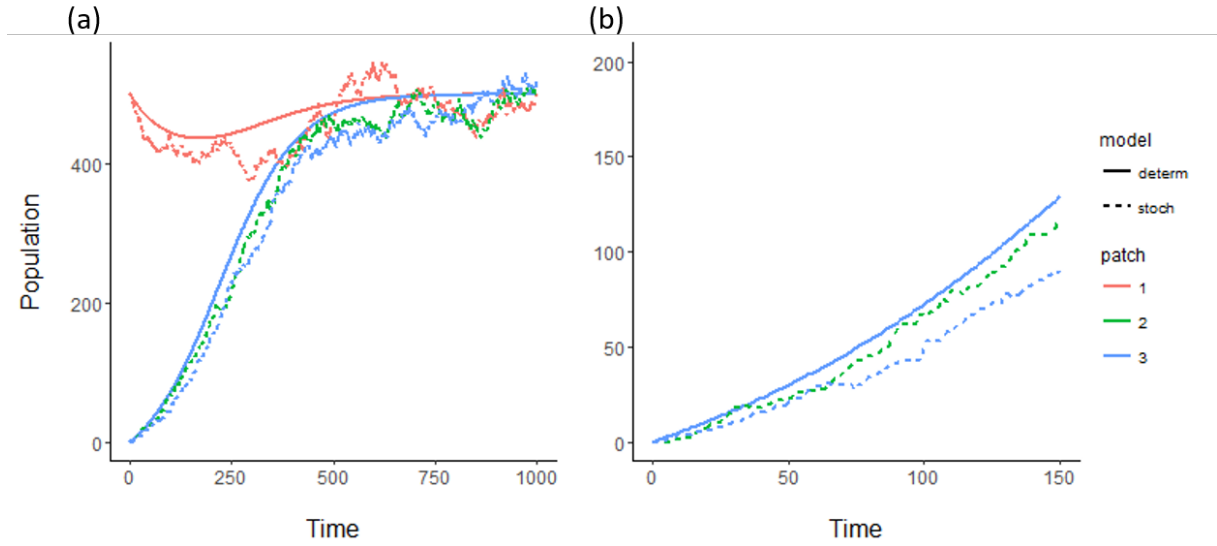

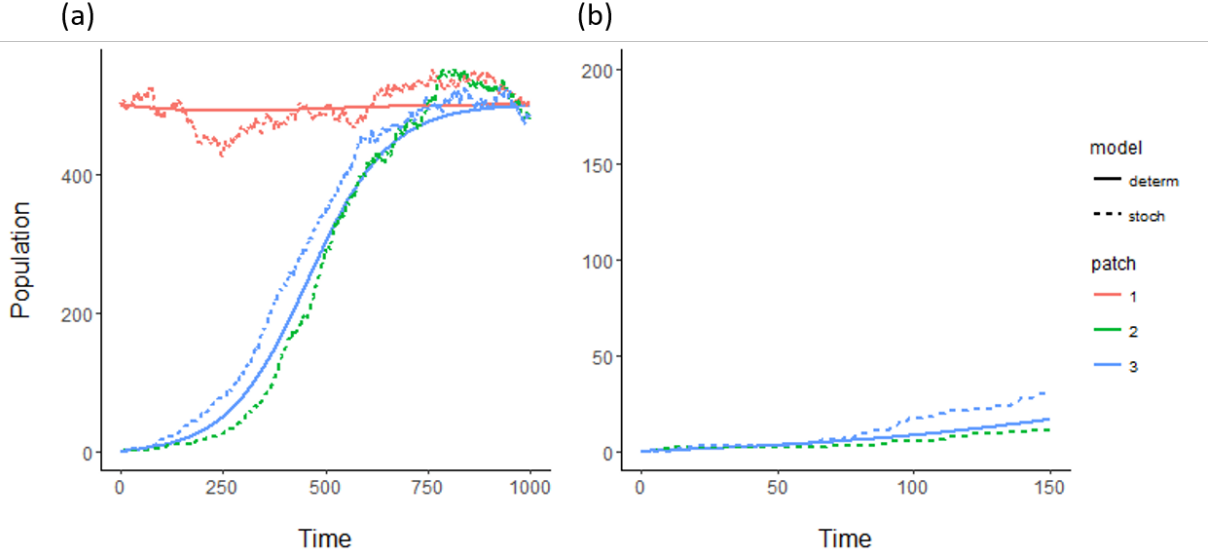Figure 4.2: Migration rate $v = 0.001$, other parameters $K = 500$, $r = 0.01$.

Figure 4.3: Migration rate $v = 0.0001$, other parameters $K = 500$, $r = 0.01$.

when there is a source feeding into it. As a result the stochastic model more or less traces the deterministic model with small perturbations.

However, these figures show that the fit between the deterministic and stochastic model breaks down over certain time and parameter regimes. Specifically the regime where stochastic effects are most apparent is in the initial lag period before logistic growth is high, when population is low and population dynamics are primarily controlled by migration. While in the deterministic model, the populations grow at the same rate, this is not true of the stochastic model. Due to low migration rates and birth rates at low population, if one patch happens to receive an introduction early one, its population will grow much more rapidly than the others, as seen in Figure 4.4.

Previously we discussed Allee effects as more biologically realistic logistic growth models. The subject of Allee effects in stochastic simulations is discussed as a possible topic of future work.
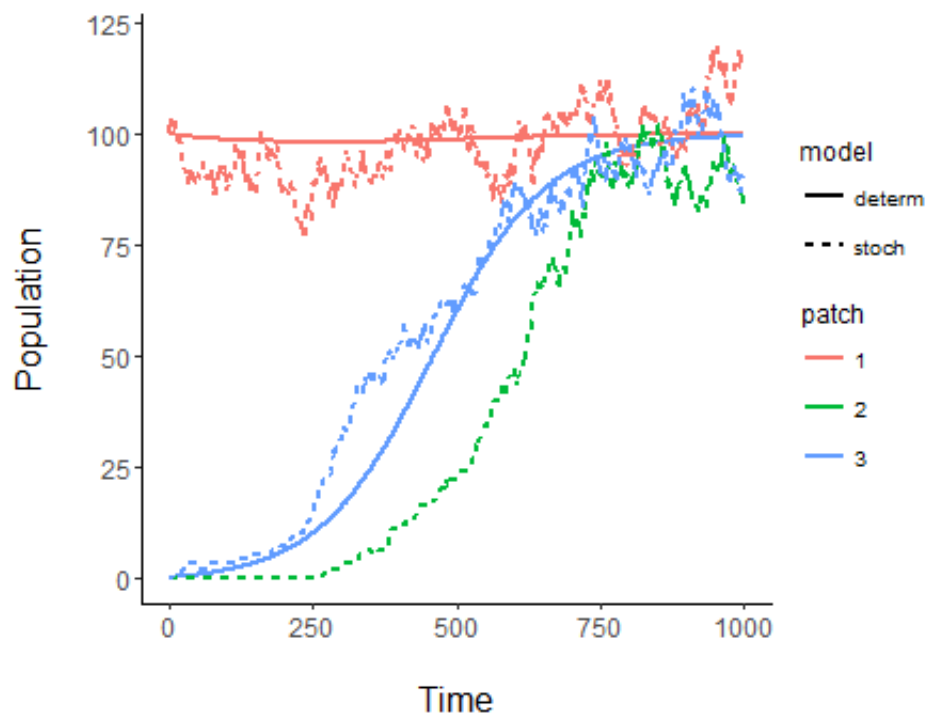
Figure 4.4: Migration rate $v = 0.0001$, other parameters $K = 100$, $r = 0.01$. This plot shows that patch dynamics can become highly varied when the population sizes are low.

Chapter 5

Conclusions

5.1 Summary

In this section we will summarize the results of this thesis. We first developed our n dimensional deterministic network model and analyzed it. We found the fixed points and stability of the 1 dimensional system, which is simply logistic growth of a single population, to be the same for our discrete map in Equation 2.4 as the stability of the original continuous logistic equation (1.1) from which it was derived. For populations with a positive growth rate r, we find that the extinct state is unstable while there is a stable fixed point at the carrying capacity K. We presented a portion of the analysis of the 2 dimensional system, though did not include calculations for a positive non-zero fixed point due to its complexity. We found that the stability result for the extinct state held in the more complex 2 dimensional system, so that the extinct state is unstable. For modeling higher dimensional networks, we relied on numerical simulations.

We implemented deterministic and stochastic versions of this model in R. We explained how the discrete time map we developed in Equation 2.4 differs from the integrated ODE model in Equation 2.16 in dependence on parameters v and possibly r. We found that the discrepancy is negligible for relevant parameter values in this study and leave it for future

work to determine the exact ~~mapping of the parameters v and r~~ between the discrete time and continuous time models.

We found that the results from the numerical simulations on the stochastic model generally followed a growth pattern expected from our analysis of steady states in our deterministic network model. We identified regimes where stochastic effects were most relevant: low migration rate and population. However, we found that long-term qualitative behavior of the deterministic and stochastic models agreed. Any node that received an introduction grew its population to the carrying capacity. Allee effects would be a good direction to take future work, recalling that the stability of the extinct state switches from unstable to stable with the introduction of a strong Allee effect.

We introduced small world networks and used them to study the effects of random dispersal events on the transient properties of a biotic invasion. We measured the speed of an invasion by measuring a metric called time to establishment. This was the time it took for an invasive population establish on the diametrically opposite node from where the invasion began. We recorded the normalized and absolute time to establishment for multiple parameter sets at increasing values of p, the rewiring probability of the small world network generator. We found that the normalized time to establishment generally decreases in relation to rewiring probability, which we hypothesize relates to a decrease in characteristic path length with increasing p, resulting in an increasing number of long distance connections between nodes, thought to be a significant component of invasive species dispersal. Further work in this area could include investigation into characteristic path length, clustering coefficient, and other network properties and how they influence spread dynamics.

5.2 Future Work

5.2.1 Allee Effect

We previously introduced the Allee effect as an extension of the logistic growth equation. The resulting ODE incorporating an Allee effect into logistic growth is defined in Equation 1.2. We noted that there is a difference in steady states between this model and the original ODE in Equation 1.1. In the Allee model, there are three fixed points: 0, A (the Allee threshold), and K. Recall that $0 < A < K$. The extinct state, 0 is stable, the Allee threshold is unstable, and the carrying capacity is stable.

The difference in steady states and stability underly a significant difference between our current stochastic model and a biologically realistic one. In real landscapes introduced populations do not necessarily tend towards carrying capacity; instead, many small populations fail to establish. This effect is described by the change in steady state stability of a logistic growth model under an Allee effect. A future direction for research would be the implementation and analysis of a growth function incorporating an Allee effect. Updating the continuous time Monte Carlo simulation using birth and death rates associated with that model would likely yield interesting results when tested under low migration rate and low population.

5.2.2 Networks

In the small world section we noted that the normalized time to establishment metric we tested followed the same shape as the normalized mean clustering coefficient. It might be fruitful to further investigate how clustering affects spread dynamics and also what other network properties might be important in the same respect. It is not intuitively clear why clustering coefficient would impact time to establishment and so the connection may be a coincidence or related to a confounding variable, perhaps another network property that is dependent on node clustering.

Another topic of interest in many networks is the presence of hubs. Hubs, defined non-technically, are nodes which experience a large volume of of incoming and outgoing traffic relative to other nodes. As discussed in the introduction in Chapter 1, in Floerl et al. (2009), once an invasive species has established in a hub, it plays a large role in the spread of that species to many secondary locations, having considerable impact on the overall spread dynamics. Hubs in network models have a direct real world significance, corresponding to regions that experience large volumes of traffic, such as population and shipping centers. For example, in Kaluza et al. (2010), researchers found that highly trafficked ports were on coastlines that had high numbers of marine invasive species. Hubs as hotspots for the spread of invasive species could be a promising direction for future research. This type of research could be particularly useful for environmental managers, who could employ this type of knowledge to best allocate limited resources to transport hubs where they would have the largest impact.

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