Mean field approximations of spatial models of evolution

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Abstract

Mathematical models have been widely and successfully applied in understanding the interplay of population structure and the evolution of social behaviour. Here we ask whether helping and non-helping behaviour can coexist in social groups, and importantly, what ecological factors affect this coexistence. We use two types of modelling techniques to examine this question. The first is an individual based model based on the life cycle of social wasps and other colony founding species which compete for limited resource sites. The second is a coupled map lattice derived through a mean field approximation from the individual based model. Both techniques use simple ecological parameters, such as number of offspring, effect of division of labour and dispersal distance. Using these two techniques, we find that the spatial structure of populations is critically important in allowing helping behaviour to evolve. Our broad approach to investigating helping behaviour highlights the importance of spatial effects in the evolution of social behaviours.
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1 Introduction

The traditional way of studying single-species population models is done through differential equations or difference equations. The first such model, the logistic model, was introduced by Verhulst (1838):

\[
\frac{dN(t)}{dt} = rN(t)(K - N(t)) \frac{K}{K}
\]

where \( r \) is the rate of maximum population growth and \( K \) is the carrying capacity. The model is continuous in time, but the continuous equation can be modified to a discrete quadratic recurrence equation on the form

\[
x(t + 1) = rx(t)(1 - x(t))
\]

where \( x \equiv N/K \).

Another discrete time model was introduced by Ricker (1954). He proposed an equation to predict the number of fish that are caught through fishery, which gives the number of individuals \( N(t + 1) \) at generation \( t + 1 \) as a function of the number of individuals \( N(t) \) at time \( t \):

\[
N(t + 1) = N(t)e^{R(1-N(t)/K)}
\] (1)

Here \( R \) is interpreted as an intrinsic growth rate and \( K \) as the carrying capacity of the environment, as in the Verhulst model.

Numerous other models using differential and difference equations for studying population dynamics have been proposed (Nicholson, 1954; Hassell, 1975; Utida, 1967; Maynard, 1974; May et al., 1974). These classical population dynamical models are based on the assumption of homogeneous interactions among the individuals.

In most natural populations though, individuals only interact with neighbours from their own species or other species. With increasing computational capacity during the last 30 years, there has been a shift from the ‘top-down’ models discussed above, describing the overall population structure, to ‘bottom up’ individual based models capturing the local behaviour of the population (Brännström and Sumpter, 2005b; Sumpter and Broomhead, 2001). Individual based models are a class of computational models that simulate the actions and interactions of autonomous agents. There are many advantages of individual based models. One is that spatial structure can easily be captured in these models. However, it is hard to treat individual based models analytically. Therefore the interplay between analytical models and simulations is an important area of research.

The relationship between individual based models and dynamical systems has been widely investigated (Johansson and Sumpter, 2003; Sumpter and Broomhead, 2001). Royama presented a derivation of the Ricker model in equation (1) from an individual based model (Royama, 2012). However, many of these relationships rely on the lack of spatial structure.

Observations show that spatial structures are critically important in many ecological systems (Hassell et al., 1987; Jones et al., 1987). This has lead to the development of numerous methods such as mean field approximations and methods of moments, to capture the spatial structure of the individual based models (Bolker and Pacala, 1997). These different techniques all lead up to different analytical models. One of these is coupled map lattices.

Coupled map lattices were first introduced in 1980s to study the chaotic dynamics of spatially extended systems (Kaneko, 1984). A coupled map lattice has discrete space and
time, but a continuous state, and is therefore computationally and analytically easier to handle than partial differential equations. Coupled map lattices have been applied to a range of areas, including chemical reactions, convection, fluid flow and biological networks (Kaneko and Tsuda, 2001). In ecology, coupled map lattice models provide a framework for incorporating spatial structure into classical population dynamic models. Gyllenberg et al. (1993) and Hastings (1993) have both analysed the dynamics for the coupled logistic map. A coupled version of the Ricker map described in equation (1) has been developed and analysed qualitatively by Wysham and Hastings (2008), using tools from dynamical systems and crisis theory. Coupled map lattice models have also been studied as approximations of individual based models by Brännström and Sumpter (2005a).

From a biological perspective, an important advantage of individual based models is that exact observations of individuals interactions in a lifecycle can be included in a model. Empirical studies show that for many insects (Wilson, 1971; Costa, 2006), birds (Brown and Brown, 1996), microorganisms (Hibbing et al., 2010; Hall-Stoodley et al., 2004), and other species the population is distributed across resource sites, and then has a lifecycle involving the following phases: (1) competition for resource sites, (2) reproduction by one or more of these individuals and (3) dispersal of surviving offspring to new potential resource sites. One example is colony founding by ants and wasps. Early in their life, founding queens share a common nest, where they cooperate in excavation and divide labour (Jeanson et al., 2005; Fewell and Page Jr, 1999).

Cooperative behaviour like this gives rise to intriguing questions from an evolutionary perspective. Why should some individuals help and sacrifice their reproductive chances to other individuals? One way to answer this is through inclusive fitness theory (Hamilton, 1964): if individuals are genetically related, they get indirect benefits from cooperating. However, unrelated individuals also cooperate (Kolmer and Heinze, 2000; Sasaki et al., 1996).

In this thesis we use the techniques described in the beginning to try to answer this. First, we describe an individual based model based on the lifecycle presented above. Simulations of this model show that helping behaviour evolves as a result of resource competition. We then derive a coupled map lattice through a mean field approximation for an analytical analysis of the individual based model. For this part, we focus on how spatial structure is connected to the evolution of cooperation.

2 Model and Approximation

2.1 Individual Based Model

Individuals live on a $D \times D$ lattice with cyclic boundary conditions. There are $n = D \times D$ resource sites, and each resource site can support one reproductive individual, giving birth to $r$ offspring. There are two types of reproductive individuals: helpers, $Y$, and non-helpers, $X$. When competing for a resource site, the helpers always sacrifice the site to a non-helper. If more than one non-helper competes for a resource site, the helpers always sacrifice the site to a non-helper. If more than one non-helper competes for a resource site, they overexploit the site and reproduction fails. At a resource site with several helpers, the reproductive individual produces $h$ additional offspring for every non-reproducing helping individual at the resource site. This implies that a population consisting only of non-helpers exhibits scramble competition, while a population only consisting of helpers exhibits contest competition. After the reproduction phase, the offspring disperse and the process starts over again, as the life cycle is complete.
2.1.1 Competition and Reproduction

Mathematically, the competition phase and the reproduction phase can be described by interaction functions applied on every site. Index the sites by \((i,j)\). Let \(X^t_{ij}\) and \(Y^t_{ij}\) denote the number of non-helping and helping individuals at site \((i,j)\) at time \(t\) respectively. On each site at time \(t\), an interaction function \(\phi_x : \mathbb{Z}^2 \to \mathbb{Z}\) acts on \(X^t_{ij}\) and \(Y^t_{ij}\), and an interaction function \(\phi_y : \mathbb{Z}^2 \to \mathbb{Z}\) acts on \(X^t_{ij}\) and \(Y^t_{ij}\) where \(\phi_x\) and \(\phi_y\) is given by

\[
\phi_x(X_{ij}, Y_{ij}) = \begin{cases} 
  r + h \cdot Y_{ij} & \text{if } X_{ij} = 1 \\
  0, & \text{otherwise}
\end{cases}
\]  

(2)

and

\[
\phi_y(X_{ij}, Y_{ij}) = \begin{cases} 
  r + h \cdot (Y_{ij} - 1) & \text{if } X_{ij} = 0, Y_{ij} > 0 \\
  0, & \text{otherwise}
\end{cases}
\]  

(3)

2.1.2 Dispersal

In this model, we consider discrete generations: after the reproduction phase, the parents decease, resulting in \(X^{t+1}_{ij}\) non-helpers and \(Y^{t+1}_{ij}\) helpers at each site \((i,j)\). All these offspring disperse to random sites in a \((2s + 1) \times (2s + 1)\) Moore neighbourhood. The neighbourhood \(N(i,j,s)\) is given by the set of sites for which there exists a representation \((i',j') \in \mathbb{Z}^2\) such that \(|i - i'| \leq s\) and \(|j - j'| \leq s\). Since the lattice has cyclic boundary conditions, individuals leaving the lattice in one end, end up in the opposite part. Mathematically this means that we can identify two sites \((i,j)\) and \((i',j')\) if and only if \(D|(i - i')\) and \(D|(j - j')\).

![Figure 1: Illustration of the individual based model.](image)

(a) Helpers (green) and non helpers (red) are distributed within an array of resource sites. (b) The resource sites containing exactly one non-helper are occupied by that individual, irrespectively how many helpers there are. If a resource site contains more than one non-helper, all individuals die out. At the resource site containing only helpers, one randomly chosen helper occupies the site. (c) The occupier produces \(r = 4\) offspring which pass to the next generation. These offspring migrate (illustrated for only two sites) to sites chosen randomly within a \((2s + 1) \times (2s + 1)\) Moore neighbourhood, where \(s = 2\).

2.2 Mean Field Approximation

2.2.1 Competition and Reproduction

In the mean field approximation we want to approximate the individual based model with a deterministic discrete dynamical system of the form
\begin{align*}
x(t + 1) &= f(x(t), y(t)) \\
y(t + 1) &= g(x(t), y(t))
\end{align*}

where \(x(t)\) and \(y(t)\) denote the density of non-helpers and helpers at time \(t\) respectively.

In a mean field approximation, we neglect the spatial structure from the individual based model, and instead consider a well-mixed model. Johansson and Sumpter (2003) define a well-mixed model as a particular class of individual based models where there is mixing of individuals across the entire system between generations. Let \(X_t\) and \(Y_t\) denote the total number of non-helpers and helpers at time \(t\). Since we consider a well-mixed model, each non-helping individual is equally likely to be found at any of the resource sites. The same holds for the helping individuals. We can now define \(X_t\) and \(Y_t\) to be independently distributed random variables.

Since the individual based model is assumed to be well-mixed for this approximation, we can neglect that the resource sites are situated on a lattice, and instead consider the world as a set of \(n\) sites. The reproduction phase at each site \(i\) can be described as a function of the number of non-helpers, \(k\), and helpers, \(m\), using equations (2) and (3):

\[
\phi_x(k, m) = \begin{cases} 
  r + h \cdot m & \text{if } k = 1 \\
  0 & \text{otherwise}
\end{cases}
\]

and

\[
\phi_y(k, m) = \begin{cases} 
  r + h \cdot (m - 1) & \text{if } k = 0, m > 0 \\
  0 & \text{otherwise}
\end{cases}
\]

respectively.

Let \(K\) and \(M\) denote the total number of non-helpers and helpers respectively. Remember \(x(t)\) and \(y(t)\) are the density of the populations, so the total number of non-helpers at time \(t\) is given by \(K = n \cdot x(t)\) and \(M = n \cdot y(t)\). The functions \(f\) and \(g\), can be derived by finding the conditional expectations of non-helpers and helpers at the next generation, \(X_{t+1}\) and \(Y_{t+1}\), given that the current population of non-helpers and helpers are \(M\) and \(K\) respectively:

\[
f(x(t), y(t)) = \frac{1}{n} E[X_{t+1}|X_t = K, Y_t = M]
\]

\[
g(x(t), y(t)) = \frac{1}{n} E[Y_{t+1}|X_t = K, Y_t = M]
\]

The expected population of non-helpers at time \(t + 1\) is given by

\[
E[X_{t+1}|X_t = K, Y_t = M] = n \sum_{k=0}^{\infty} \sum_{m=0}^{\infty} P(k \text{ at site } i|K)P(m \text{ at site } i|M) \cdot \phi_x(k, m)
\]

and the expected population of helpers at time \(t + 1\) is given by

\[
E[Y_{t+1}|X_t = K, Y_t = M] = n \sum_{k=0}^{\infty} \sum_{j=0}^{\infty} P(k \text{ at site } i|K)P(m \text{ at site } i|M) \cdot \phi_y(k, m)
\]
Since the individuals are distributed uniformly at random between \( n \) sites, the probability that a particular site contains a particular non-helping individual is \( \frac{1}{n} \). Thus, the probability that there are \( k \) non-helping individuals at a particular site, given that the total number of non-helpers are \( K \), is

\[
P(k \text{ at site } i | K) = \left( \frac{K}{k} \right) \frac{1}{n} \left( 1 - \frac{1}{n} \right)^{K-k}
\]

For large \( n \), \( n!/(n-k)! \approx n^k \), so

\[
\left( \frac{K}{k} \right) \frac{1}{n} \left( 1 - \frac{1}{n} \right)^{K-k} \approx K^k \frac{1}{k!} \left( 1 - \frac{1}{n} \right)^{K-k}
\]

Now remember that \( K = n \cdot x(t) \), so

\[
\frac{K^k}{k!} \left( \frac{1}{n} \right)^k \left( 1 - \frac{1}{n} \right)^{K-k} = \frac{x(t)^k}{k!} \left( 1 - \frac{1}{n} \right)^{nx(t)-k}
\]

Since

\[
\lim_{n \to \infty} \left( 1 - \frac{1}{n} \right)^{nx(t)-k} = e^{-x(t)}
\]

the right-hand side of equation (5) goes to \( \frac{x(t)^k}{k!} e^{-x(t)} \) as \( n \to \infty \). Substituting this into the left-hand side of equation (4) yields

\[
P(k \text{ at site } i | K) = \frac{x(t)^k}{k!} e^{-x(t)}
\]

Hence, the number of non-helpers at a site is Poisson distributed with the population density as the rate parameter for large \( n \).

Obviously, the same derivation can be done for the helping population giving

\[
P(m \text{ at site } i | M) = \frac{y(t)^m}{m!} e^{-y(t)}
\]

for the helpers.

We can now use that \( \phi_x(k, m) = 0 \) for all \( k \neq 1 \) and \( \phi_y(k, m) = 0 \) for all \( k \neq 0 \). 

\[
E[X_{t+1}|X_t = K, Y_t = M] = n \sum_{k=0}^{\infty} \sum_{m=0}^{\infty} P(k \text{ at site } i | x)P(m \text{ at site } i | y(t)) \cdot \phi_x(k, m)
\]

\[
= n \sum_{m=0}^{\infty} x(t) e^{-x(t)} \cdot P(m \text{ at site } i | y(t)) \cdot \phi_x(1, m)
\]

\[
= x(t) e^{-x(t)} \sum_{m=0}^{\infty} P(m \text{ at site } i | y(t)) \cdot (r + h \cdot m)
\]

\[
= x(t) e^{-x(t)} \sum_{m=0}^{\infty} \frac{(y(t))^m}{m!} e^{-y(t)} \cdot (r + h \cdot m)
\]

\[
= x(t) e^{-x(t)} \left( \sum_{m=0}^{\infty} \frac{(y(t))^m}{m!} e^{-y(t)} \cdot r + \sum_{m=0}^{\infty} \frac{(y(t))^m}{m!} e^{-y(t)} \cdot h \cdot m \right)
\]

\[
= n(x(t) e^{-x(t)} (r + h \cdot y(t)))
\]
And similarly for the helpers we have:

\[
E[Y_{t+1}|X_t = K, Y_t = M] = n \sum_{k=0}^{\infty} \sum_{m=0}^{\infty} P(k \text{ at site } i|x(t))P(m \text{ at site } i|y(t)) \cdot \phi_y(k, m)
\]

\[
= n \sum_{m=0}^{\infty} e^{-x(t)}P(m \text{ at site } i|y(t)) \cdot \phi_y(0, m)
\]

\[
= ne^{-x(t)} \sum_{m=1}^{\infty} P(j \text{ at site } i|y(t)) \cdot (r + h(m - 1))
\]

\[
= ne^{-x(t)} \sum_{m=1}^{\infty} \frac{(y(t))^m}{m!} e^{-y(t)} \cdot (r + h(m - 1))
\]

\[
= ne^{-x(t)}((r - h)(1 - e^{-y(t)}) + y(t))
\]

Using that

\[
f(x(t), y(t)) = \frac{1}{n} E[X_{t+1}|X_t = K, Y_t = M]
\]

\[
g(x(t), y(t)) = \frac{1}{n} E[Y_{t+1}|X_t = K, Y_t = M]
\]

gives the following dynamical system:

\[
x(t + 1) = f(x(t), y(t)) = x(t)e^{-x(t)}(r + h \cdot y(t))
\]

\[
y(t + 1) = g(x(t), y(t)) = e^{-x(t)}((r - h)(1 - e^{-y(t)}) + h \cdot y(t))
\] (6)

2.2.2 Dispersal

The individual-based model has a clear spatial structure, with individuals living on a \(D \times D\) lattice. We now want to take this spatial structure into account in the mean field approximation. We start by dividing the lattice into two patches, \(P_1\) and \(P_2\), as seen in Figure 2 below.

![Diagram of lattice division into two patches](image)

Figure 2: Division of the lattice into two patches. The light grey area consists of the sites where dispersal to the other patch is possible, when the dispersal distance is \(s = 2\). The dark grey area shows the sites reachable by dispersal from the black site.
Let $s$ be the dispersal distance for the individuals, as described in section 2.1. We want to determine the dispersal rate $\delta$ as a function of the dispersal distance $s$. We use boundary conditions such that an individual in $P_1$ enters $P_2$ only when it crosses the border in the middle. When crossing the other borders, it re-enters $P_1$.

We now determine the dispersal rate, $\delta$, from $P_1$ to $P_2$. Since $P_1$ and $P_2$ are identical except for being laterally reversed, it suffices to determine the dispersal rate from $P_1$ to $P_2$ to find $\delta$. Index the sites by $(i,j)$, as in Figure 2. In $P_1$ we have $1 \leq i \leq D/2$ and $1 \leq j \leq D$.

The diffusion rate between $P_1$ and $P_2$ will be given by the probability that an individual $k$ is situated at site $(i,j)$ times the probability that it disperses to patch $P_2$, given that it is at site $(i,j)$, summed over all sites in $P_1$:

\[
\delta = \sum_{(i,j) \in P_1} P(k \text{ at site } (i,j) | k \text{ in } P_1) \cdot P(k \text{ disperse to } P_2 | k \text{ at site } (i,j))
\]

By assuming that the populations are well mixed within in $P_1$ and $P_2$, we can use that $P(k \text{ at site } (i,j) | k \text{ in } P_1)$ is given by $\frac{1}{D^2/2}$.

To determine $P(k \text{ disperse to } P_2 | k \text{ at site } (i,j))$, we want to find the number of sites in $P_1$ where $P_2$ is reachable by dispersal. This obviously depends on $s$. We have that

\[
P(k \text{ disperse to } P_2 | k \text{ at site } (i,j)) = \frac{(s+1)-i}{2s+1} \text{ when } i < s, \text{ and } 0 \text{ when } i > s.
\]

Thus, we have

\[
\delta = \sum_{(i,j) \in P_1} P(k \text{ at site } (i,j) | k \text{ in } P_1) \cdot P(k \text{ disperse to } P_2 | k \text{ at site } (i,j))
\]

\[
= \sum_{j=1}^{D} \sum_{i=1}^{D/2} \frac{1}{D^2/2} P(k \text{ disperse to } P_2 | k \text{ at site } (i,j))
\]

\[
= D \sum_{i=1}^{D/4} \frac{1}{D^2/2} P(k \text{ disperse to } P_2 | k \text{ at site } (i,j)) = 2D \sum_{i=1}^{D/4} \frac{(s+1)-i}{2s+1}
\]

\[
= \frac{s(s+1)}{D(2s+1)}
\]

When dispersal is global, i.e. $s = D$, and $D$ is large, we have

\[
\delta = \lim_{D \to \infty} \frac{D(D+1)}{D(2D+1)} = \frac{1}{2}
\]

With no dispersal, i.e. $s = 0$, we have that $\delta = \frac{1}{D} \to 0$ as $n \to \infty$. Hence, for lattices big enough, $0 \leq \delta \leq 1/2$.

As described in Section 2.1, individuals disperse after the reproduction phase. Since we assume that the populations are well-mixed within each patch, we can divide the population of non-helpers, $x$, and helpers, $y$ into two subpopulations, $x_1$ and $x_2$, and $y_1$ and $y_2$. 

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respectively and couple them with the diffusion parameter $\delta$. This gives a system

\begin{align*}
    x_1(t+1) &= (1 - \delta) \cdot f(x_1(t), y_1(t)) + \delta \cdot f(x_2(t), y_2(t)) \\
    y_1(t+1) &= (1 - \delta) \cdot g(x_1(t), y_1(t)) + \delta \cdot g(x_2(t), y_2(t)) \\
    x_2(t+1) &= (1 - \delta) \cdot f(x_2(t), y_2(t)) + \delta \cdot f(x_1(t), y_1(t)) \\
    y_2(t+1) &= (1 - \delta) \cdot g(x_2(t), y_2(t)) + \delta \cdot g(x_1(t), y_1(t))
\end{align*}

where $f$ and $g$ are given by (6).

3 Results and Analysis

3.1 Simulations

3.1.1 Individual Based Model

We now investigate under which circumstances helping behaviour can evolve in the individual based model. We first consider the case where helpers only sacrifice their resource site to a non-helping individual, and do not contribute to the reproductive capacity of the non-helpers, i.e. when $h = 0$. When dispersal is global (i.e. $s = D$), the non-helpers always outcompete the helpers. This is due to the fact that non-helpers always replace helpers when they compete for the same resource site. However, as seen in Figure 3b and 3c below, helping behaviour becomes a possible outcome when dispersal is local.

Figure 3: Spatial distributions of non-helpers (red) and helpers (green) after 1000 time steps of the model simulation when $s = 2$ for different values of $r$.

Figure 3 shows the spatial distribution of non-helpers (red) and helpers (green) after 1000 time steps for different values of $r$ when the dispersal distance, $s$, is set to 2. When $r = 30$ the whole population consists of non-helpers. The population of helpers dies out quickly and the population of non-helpers stabilizes. When $r = 65$, non-helpers and helpers coexist. The helpers are located at clusters as seen in Figure 3b. There is a clear spatial patterning in the positions of the helpers and non-helpers. The pattern is somewhat similar to an irregular chess board. The population dynamics of non-helpers is independent of the helpers, but is, due to scramble competition, sensitive for overcrowding. This results in empty spaces in the environment, that can be filled by the helpers. When $r = 110$ non-helpers become extinct as a result of overcrowding and the whole lattice is occupied by helpers.

The population dynamics is clearly dependent on the reproduction rate. For which values of $r$ does helping behaviour become a possible evolutionary outcome? In Figure 4
below, we varied the resource capacity \( r \) from 1 to 120 and plotted the density of helpers and non-helpers for each \( r \). There is a switching point when \( r \approx 40 \) when coexistence becomes possible. When \( r > 96 \), the non-helping individuals die out.

Figure 4: Population density of non-helpers (red) and helpers (green) as a function of the resource capacity \( r \). Simulation results for the last 500 time steps of a simulation run for 1000 time steps are presented for \( r \) ranging between 1 and 120.

3.1.2 Mean Field Approximation

We now ask if the mean field model shows the same behaviour for coexistence. First, we investigate the dynamics when the population only consists of non-helpers. The population dynamics is then given by

\[
x(t + 1) = r x(t) e^{-x(t)}
\]  

(7)

Figure 5 shows the bifurcation diagram for the non-helping population without dispersal, together with the Lyapunov exponent for the same system.

Figure 5: (a) Bifurcation diagram for the non-helping population when \( h = 0 \) for different values of \( r \) given in (7) and (b) Lyapunov exponent for the same equation for different values of \( r \).
The system has the steady states $x^* = 0$ and $x^* = \ln(r)$. The second steady state is a stable solution when $1 < r < e^2$, and undergoes a period-doubling bifurcation after that. For approximately $r > 14.7$ the dynamics of the non-helping population becomes chaotic. By setting $R = e^r$ and $K = \ln(r)$ we can rewrite equation (7) into equation (1).

### 3.1.3 Mean Field Approximation with Dispersal

When introducing dispersal between the two patches, we consider the total population of non-helpers, $x_1 + x_2$, and the difference in population size between the two patches, $x_1 - x_2$, as well as the total population of helpers, $y_1 + y_2$, and the difference in population size of helpers, $y_1 - y_2$. By doing this, we can classify all steady states into two types of solutions: in-phase solutions and out-of-phase solutions. In the in-phase solution, the two subpopulation sizes are always the same (i.e. $x_1 - x_2 = 0$ or $y_1 - y_2 = 0$), whereas in the out-of-phase solution the two subpopulations are always different (i.e. $x_1 - x_2 \neq 0$ or $y_1 - y_2 \neq 0$). When $\delta = 0$, the patches are uncoupled and behave as two independent systems. Within each patch the non-helpers will exhibit the same dynamics as in Figure 5a. However, when $\delta \neq 0$ the patches are coupled and the system behaves differently. Figure 6 and 7 show bifurcation diagrams for the total population and the difference in population of non-helpers and helpers for two different values of the dispersal rate, $\delta = 0.02$ and $\delta = 0.2$. 

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We see that the bifurcation plots of the helpers (Figure 6b and 6d) resemble the bifurcation plots of the non-helpers (Figure 6a and 6c) but in a smaller scale. We can also conclude that there is a stable equilibrium when $r > 53$, approximately. The bifurcation plots of the difference in population sizes indicate that this equilibrium is a period two out-of-phase solution.
From Figure 7b and 7d we can conclude that for $\delta = 0.2$, the system is in phase when $0 < r < 33$. Comparing Figure 6 with Figure 7 we see that the dispersal rate has an apparent influence on the dynamics of the system. Since the dispersal rate, $\delta$, is the coupling parameter between the patches, there are two interesting questions to be answered when considering $\delta$ as the bifurcation parameter. Firstly, how large must the dispersal rate be for the system to behave globally as a single patch? Secondly, how small must the dispersal rate be for the patches to behave independently of each other?

To answer these questions, Figure 8 shows bifurcation plots with $\delta$ as bifurcation parameter, when $r$ is fixed to 30.
Figures 8a and 8c show that there is a stable steady state when $0.01 < \delta < 0.19$ approximately. For these values of $\delta$, the populations in the patches are in an out-of-phase solution. When $\delta < 0.01$, the bifurcation plots for the difference in population sizes display chaotic behaviour. This suggests that for dispersal rates under 0.01 the coupling between the patches is so small that the patches behave independently. For $0.19 < d < 0.5$ the populations in the patches are in an in-phase solution. This is where the dispersal range is so large that the system starts behaving as a single patch. Thus we have one critical value $\delta_{c_1} \approx 0.01$ when the patches stop behaving independently, and another critical value $\delta_{c_2} \approx 0.19$ when the system starts to behave as a single patch.

Even though all the bifurcation diagrams above display coexistence between the non-helping and the helping population, the population density of the helping population is always less than 0.05. Can this be counted as coexistence between helpers and non-helpers? As seen in Figure 6a and 7a, in the bifurcation plots for the total non-helping populations, a lot of the points are plotted close to zero. In the individual based model with a $D \times D = 100 \times 100$ lattice, a population density of 0.0001 implies a population consisting of only one individual. Thus, all population densities under 0.0001 entails extinction in the simulations of the individual based model. By way of this, we introduce extinction for population
densities under 0.001 in the mean field model, to study the coexistence between the two species. Figure 9 shows heat maps for the density of non-helping (a) and helping population (b) in the mean field approximation without extinction, and the non-helping (c) and helping population (d) with extinction as a function of resource capacity $r$ and dispersal rate $\delta$.

![Heat maps](image)

Figure 9: Density of non-helpers (a) and helpers (b) as a function of resource capacity $r$ and dispersal rate $\delta$ for the mean field model without extinction. Density of non-helpers (a) and helpers (b) as a function of resource capacity $r$ and dispersal rate $\delta$ for the mean field model with extinction.

The overall pattern of these heat maps is that non-helpers always outnumber the helpers. One could argue that there is a region of coexistence for the mean field model without extinction, when $0.01 < \delta < 0.2$ and $r > 40$. For the mean field model with extinction, this corresponds to the region where $0.05 < \delta < 0.2$ and $20 < r < 38$. The population of non-helpers is always approximately 100 times larger than the population of helpers, even in this region where the population density of helpers is higher than on average.

### 3.1.4 Including Helping Behaviour

We now set $h > 0$ and consider the scenario when helpers not only sacrifice their own productivity, but also increase the reproductive capacity of the occupier at the resource site.
In the individual based model, helping initially increases the population of non-helpers, but as for high values of $r$, high values of $h$ lead to overcrowding of non-helpers. Since non-helpers exhibit scramble competition, overcrowding eventually makes them go extinct. Figure 10 shows that by increasing $h$ the proportion of non-helpers decreases.

Figure 10: Density of non-helpers (a) and helpers (b) as a function of resource capacity, $r$, and helping contribution, $h$.

A similar pattern was not found for the mean field approximation. Increasing helping behaviour had neither an apparent effect on the population dynamics in the mean field model without extinction nor in the model with extinction, as seen in Figure 11.
Figure 11: Density of non的帮助者 (a) and helpers (b) as a function of resource capacity $r$ and helping behaviour $h$.

To illustrate the difference between the models, a comparison of the time series for the individual based model and the mean field model for three different values of $r$ and two different values of $s$ and its corresponding $\delta$-value is found in Figure 12.
3.2 Stability Analysis

The numerical analysis in Section 3.1.3, showed that for the mean field approximation, non-helpers always outnumber the helpers. Furthermore, the helping contribution $h$ did not affect the dynamics notably. Nonetheless, the non-helping population displays interesting dynamics when varying the dispersal rate $\delta$, that cannot be fully understood from the bifurcation diagrams. In this section we will instead proceed with an analytical approach to the analysis of the coupled map lattice for single-species models. The analysis of the system soon becomes complicated, and will therefore not be carried out entirely.

In general, the coupled map lattice for a one species model with two patches can be described by the map

$$F(x_1, x_2) = \left( (1 - \delta)f(x_1) + \delta f(x_2), (1 - \delta)f(x_2) + \delta f(x_1) \right)$$

where $f(x)$ is determined by the local dynamics in each patch. To investigate the dynamics of the in-phase and out-phase solutions, start by changing coordinates to the total population size

$$s = x_1 + x_2$$

and the difference in population size between the two patches

$$d = x_1 - x_2$$

The map (8) in $s$ and $d$ is given by

$$\tilde{F}(s, d) = [s(t + 1), d(t + 1)]$$
where
\[ s(t + 1) = x_1(t + 1) + x_2(t + 1) \]
and
\[ d(t + 1) = x_1(t + 1) - x_2(t + 1) \]
Using this in equation (8) gives
\[ s(t + 1) = (1 - \delta)f(x_1) + \delta f(x_2) + (1 - \delta)f(x_2) + \delta f(x_1) = f(x_1) + f(x_2) \]
and
\[ d(t + 1) = (1 - \delta)f(x_1) + \delta f(x_2) + (1 - \delta)f(x_2) - (\delta f(x_1)) = (1 - 2\delta)(f(x_1) - f(x_2)) \]
Thus the coupled map takes the form
\[ \tilde{F}(s, d) = [f(x_1) + f(x_2), (1 - 2\delta)(f(x_1) - f(x_2))] \tag{10} \]
in terms of \( s \) and \( d \).

### 3.2.1 The Logistic Map

We now consider the coupled map lattice for the quadratic form of the logistic map
\[ f(x) = rx(1 - x) \]
as described by Hastings (1993) and Gyllenberg et al. (1993). To find the transformed map \( \tilde{F}(s, d) \), note that \( x_1 = \frac{s + d}{2} \) and \( x_2 = \frac{s - d}{2} \). This yields
\[ s(t + 1) = r \left( \frac{s(t) + d(t)}{2} \right) \left( 1 - \frac{s(t) + d(t)}{2} \right) + \frac{s(t) - d(t)}{2} \left( 1 - \frac{s(t) - d(t)}{2} \right) \]
and
\[ d(t + 1) = (1 - 2\delta) \left( r \frac{s(t) + d(t)}{2} \left( 1 - \frac{s(t) + d(t)}{2} \right) - r \frac{s(t) - d(t)}{2} \left( 1 - \frac{s(t) - d(t)}{2} \right) \right) \]
Which can be simplified to
\[ s(t + 1) = \frac{1}{2} r(s(t) - s^2(t) - d^2(t)) \tag{11} \]
and
\[ d(t + 1) = (1 - 2\delta)rd(t)(1 - s(t)) \tag{12} \]
So the map is given by
\[ \tilde{F}(s, d) = (r(s - s^2 - d^2), (1 - 2\delta)rd(1 - s)) \]
The Jacobian, \( D\tilde{F} \), to this system is given by
\[ D\tilde{F} = \begin{bmatrix} \frac{\partial s(t + 1)}{\partial s(t)} & \frac{\partial s(t + 1)}{\partial d(t + 1)} \\ \frac{\partial s(t + 1)}{\partial s(t)} & \frac{\partial d(t + 1)}{\partial s(t)} \end{bmatrix} = \begin{bmatrix} r(1 - 2s) & -2rd \\ -(1 - 2\delta)rd & (1 - 2\delta)r(1 - s) \end{bmatrix} \tag{13} \]
We start by considering the in-phase solution, i.e. when \( d = 0 \). The steady states for \((s, d) = (s^*, 0)\) is then given by the solutions to

\[
s^* = r(s^* - (s^*)^2)
\]

There are two steady states, given by \( s^* = 0 \) and \( s^* = 1 - \frac{1}{r} \). When evaluated at the non-zero steady state \((s^*, d^*) = (1 - 1/r, 0)\), the Jacobian becomes

\[
D\tilde{F}|_{(s^*, d^*)} = 
\begin{bmatrix}
2 - r & 0 \\
0 & (1 - 2\delta)(r - 1)
\end{bmatrix}
\]

The eigenvalues of \( D\tilde{F} \) are given by \( \lambda_1 = 2 - r \) and \( \lambda_2 = (1 - 2\delta)(r - 1) \). For this solution to be stable, \( |\lambda_1| < 1 \) and \( |\lambda_2| < 1 \). For the first eigenvalue this corresponds to \( 1 < r < 3 \). For the second eigenvalue we have \( |(1 - 2\delta)(r - 1)| < 1 \). This yields the following stable region for the in-phase solution

\[
\frac{r - 2}{2(r - 1)} < \delta < \frac{r}{2(r - 2)}
\]

Hastings (1993) analyse the out-of-phase period two solutions. He found numerically that the period two solutions have constant total population size, so he starts by looking at the existence and stability of solutions of the form

\[
s(t + 1) = s(t) \\
d(t + 2) = d(t)
\]

Using equation (11) and (12) we find

\[
d(t + 2) = r^2(1 - 2\delta)^2(d^2(t)1 - s(t))(1 - r(s(t) - \frac{s^2(t) + d^2(t)}{2}))
\]

This implies that either

\[
d^* = 0
\]

or

\[
1 = r^2(1 - 2\delta)^2(1 - s^*)(1 - r(s^* - \frac{s^{*2} + d^{*2}}{2}))
\]

(14)

The solution \( d^* = 0 \) corresponds to the in-phase solution, whereas solutions to equation (14) will give the out-of-phase solution. Since we have that \( s(t + 1) = s(t) \) for the out-of-phase solution, we can substitute (11) into equation (14). By doing this we find

\[
1 = r^2(1 - d\delta)(1 - s^{*2})
\]

which gives the solutions

\[
s^* = 1 - \frac{1}{r(1 - 2\delta)}
\]

and

\[
s^* = 1 + \frac{1}{r(1 - 2\delta)}
\]

For these steady states, the Jacobian determining the stability will be given by

\[
D\tilde{F}_2 = 
\begin{bmatrix}
\frac{\partial s(t+2)}{\partial s(t)} & \frac{\partial s(t+2)}{\partial d(t)} \\
\frac{\partial d(t+2)}{\partial s(t)} & \frac{\partial d(t+2)}{\partial d(t)}
\end{bmatrix}
\]
If we now write
\[ s(t + 2) = f_1(f_1(s(t), d(t))) \]
\[ d(t + 2) = f_2(f_2(s(t), d(t))) \]
the stability of these steady states can be determined by applying the chain rule
\[ \frac{\partial}{\partial t}(s(t) + 2) = f_1(f_1(s(t), d(t))) \]
\[ \frac{\partial}{\partial t}(d(t) + 2) = f_2(f_2(s(t), d(t))) \]
where \( D \tilde{F} \) is given by (13). From this, the region of stability can be found from
\[ \text{Det}(D \tilde{F}_2) = 1 \]
and
\[ \text{Tr}(D \tilde{F}_2) = \text{Det}(D \tilde{F}) \]
Hastings then continues the stability analysis numerically.

### 3.2.2 The Ricker Map

The mean field approximation of the individual based model in this thesis does not give the logistic map, but a certain type of the Ricker map. It has been shown that some properties of coupled map lattices are universal. For example, Amritkar and Gade (1993) have shown that for a certain range of dispersal rates, \((\delta_0, \delta_1)\), the period doubling sequence for any single chaotic map will be lifted to coupled systems in the form of spatiotemporal period doubling. Nevertheless, a more detailed analysis of the Ricker model should be carried out for better understanding of the system.

We now consider the map in our model, given by
\[ f(x) = rxe^{-x} \]
For the map \( f(x) = x e^{r(1-x)} \) Wysham and Hastings (2008) suggest a coordinate transformation of the form \( s = \frac{x_1 + x_2}{2} \) and \( d = \frac{x_1 - x_2}{2} \). With this change of coordinates, \( s \) represents the distance from the line \( x_1 = -x_2 \) and is, therefore, a measure of the amount in the direction of the diagonal, while \( d \) is a measure of the off-diagonal direction. However, we will use the same coordinate transformation as for the logistic map.

To find the map (10) in terms of \( s \) and \( d \), we follow the same procedure as for the logistic map:
\[ s(t + 1) = r x_1 e^{-x_1} + r x_2 e^{-x_2} \]
and
\[ d(t + 1) = (1 - 2\delta)(r x_1 e^{-x_1} - r x_2 e^{-x_2}) \]
(15)
Using that \( x_1 = \frac{s + d}{2} \) and \( x_2 = \frac{s - d}{2} \) we obtain
\[ s(t + 1) = r x_1 e^{-x_1} + r x_2 e^{-x_2} = \]
\[ = r(s + d)e^{-(s+d)} + r(s - d)e^{-(s-d)} = re^{-s}(e^{d} + e^{d}) + d(e^{d} - e^{d}) = \]
\[ = 2re^{-s}( \frac{e^{d} + e^{d}}{2} - d \frac{e^{d} - e^{d}}{2} ) \]
We can now rewrite the equation above as hyperbolic functions:

\[ s(t + 1) = 2re^{-s}(s \cosh(d) - d \sinh(d)) \]

and

\[ d(t + 1) = (1 - 2\delta)(r(s + d)e^{(s+d)} - r(s - d)e^{(s-d)}) = 2(1 - 2\delta)re^{-s}(d \cosh(d) - s \sinh(d)) \]

This yields the map

\[ \tilde{F}(s, d) = (2re^{-s}(s \cosh(d) - d \sinh(d)), 2(1 - 2\delta)re^{-s}(d \cosh(d) - s \sinh(d))) \]

Note the mistake made by Wysham and Hastings (2008): their map of the Ricker equation in terms of \( s \) and \( d \) is given by

\[ \tilde{F}(s, d) = \left( e^{r(1-s)}[s \cos(rd) - d \sin(rd)], (e^{r(1-s)}[d \cos(rd) - s \sin(rd)]) \right) \]

However, they only investigate the in-phase solution, i.e. solutions when \( d = 0 \). In this special case, \( \cosh(rd) = \cos(d) \) and \( \sinh(rd) = \sin(d) \), so the mistake in their derivation does no affect the outcome of the analysis. For a more general analysis of this system, also including the out-of-phase solutions, this mistake would lead to incorrect conclusions. Let \( D\tilde{F} \) denote the Jacobian of the map. By calculating the derivatives of the map we find

\[
D\tilde{F} = \begin{bmatrix}
2re^{-s}(\cosh(d)(1 - s) + d \sinh(d)) & -2re^{-s}(\sinh(d)(1 - s) + d \cosh(d)) \\
-2(1 - 2\delta)re^{-s}(\sinh(d)(1 - s) + d \cosh(d)) & 2(1 - 2\delta)re^{-s}(\cosh(d)(1 - s) + d \sinh(d))
\end{bmatrix}
\]

Let \( f_s = \frac{\partial f_1(s,d)}{\partial s} \) and \( f_d = \frac{\partial f_1(s,d)}{\partial d} \). From this we have the following symmetry

\[
D\tilde{F} = \begin{bmatrix}
 f_s(s,d) & f_d(s,d) \\
(1 - 2\delta)f_d(s,d) & (1 - 2\delta)f_s(s,d)
\end{bmatrix}
\]

If we now consider the in-phase solution, where \( d = 0 \), the Jacobian is given by

\[
D\tilde{F}(s,0) = \begin{bmatrix}
2re^{-s}(1 - s) & 0 \\
0 & 2(1 - 2\delta)re^{-s}(1 - s)
\end{bmatrix} = \begin{bmatrix}
f_s & 0 \\
0 & (1 - 2\delta)f_s(s)
\end{bmatrix}
\]

and the Jacobian of \( D\tilde{F}^{2k} \) when \( d = 0 \) is equal to

\[
D\tilde{F}^{2k}(s,0) = \begin{bmatrix}
\prod_{i=1}^{2k} f_s(s) & 0 \\
0 & (1 - 2\delta)^{2k}\prod_{i=1}^{2k} f_s(s)
\end{bmatrix}
\]

In Figure 5a, we see that \( f \) undergoes a period doubling cascade. From this, Wysham and Hastings argue that, as long as \( \delta << 1 \), the stability properties of the uncoupled Ricker map can be extended to the coupled system.

### 4 Conclusions

In this thesis we presented an individual based model to investigate how helping behaviour can evolve. We could conclude that, provided single individuals produce large numbers of offspring which emerge at the same time and disperse locally, helping behaviour can evolve.
As we saw in Figure 4, there is a shift from non-helping behaviour to helping behaviour as the evolutionary stable outcome when \( r \) increases. As non-helpers exhibit scramble competition, while helpers exhibit contest competition, interference between individuals leads to local extinction of non-helping individuals and invasion of helping individuals becomes possible. However, there is a large range of values of \( r \) where coexistence is possible. This result differs somewhat from that of Anazawa (2014) who found that for an individual based model, two species are more likely to coexist when they have the same competition type.

By means of the mean field the approximation we obtained a relationship between the individual based model and a dynamical system described in equations (6). When considering a population only consisting of non-helpers, the acquired equation is the well studied Ricker map found in equation (1). Both the relation between scramble competition and the Ricker map, as well as the dynamical properties of the Ricker map are well studied (Royama, 2012; Sumpter and Broomhead, 2001; Fisher et al., 1979; Thunberg, 2001). When considering populations of both non-helpers and helpers the dynamics became a lot more complicated.

To incorporate the spatial structure from the individual based model, we divided the lattice into two patches and derived the dispersal rate between the two patches. This resulted in a coupled map lattice. From this model we could conclude that migration has a stabilizing and synchronizing effect on the population dynamics. The critical values of the dispersal rate for this stabilizing effect were found to be \( d_{c1} \approx 0.01 \) and \( d_{c2} \approx 0.19 \). The same critical values were found by Hastings (1993) when studying the coupled logistic map, as discussed in the stability analysis of the logistic map. This indicates that critical values of the dispersal rate is a general property, not dependent on the inner dynamics of the patches. Quite contrary to what was found by Brännström and Sumpter (2005a) for their multiple patch model, increasing the dispersal distance does not influence the occurrence of period doubling bifurcations.

Subsequently, we investigated if this coupled map lattice was a good approximation of the individual based model. Comparing Figures 4, 9, 11 and 12 showed that the individual based model and the mean field approximation did not behave similarly. There are two possible explanations for this approximation being poor. Firstly, one could ask whether a division into only two patches is enough. Brännström and Sumpter (2005a) have divided the lattice into multiple patches. This certainly makes the analytical treatment of the model more complicated, but does not necessarily make the approximation better; the characteristics of low-dimensional coupled map lattices can be lifted to systems with large number of patches (Wysham and Hastings, 2008). Secondly, when incorporating diffusion into the model, the boundary conditions could well have been chosen in a different way. The choice of lattice topology and boundary conditions are interesting questions both when studying individual based models on its own, and when deriving mean field approximations. Berec (2002) has suggested different choices for this and discussed their consequences. These could be applied to this model, which perhaps could result in boundary conditions that give a better mean field approximation.

Including an extinction threshold into the mean field model did not enhance the similarity with the individual based model. Instead of an extinction threshold, it would be interesting to investigate the effect of an extinction and coexistence probability, as done by Anazawa (2014).

In spite of the limitations concerning the differences between the individual based model and the coupled map lattice model, this thesis has elucidated the need of a more rigorous framework for mean field approximations of more complicated species interactions. A more thorough stability analysis of the coupled map lattice model, as done by Wysham and
Hastings (2008), but for the two species system, remains to be done. Jánosi and Scheuring (1997) have studied a two species coupled map lattice model where dispersal is assumed to be density dependent. This is also an extension of our model that could be investigated.

For the individual based model, further extensions could include central concepts from evolutionary dynamics, such as inclusive fitness theory (Nowak and May, 1992; Lehmann et al., 2007; Nowak, 2006; Gardner et al., 2011). By using the relatedness between the individuals that can be determined in the individual based model, it would be possible to calculate cost, benefit and relatedness as a function of our model parameters. Adaptive dynamics models have lately been used to investigate the evolution of cooperation (Brännström and Dieckmann, 2005; Brännström et al., 2011). In an adaptive dynamics approach to our model, both the dispersal distance, $s$, and the reproductive rate, $r$, could be used as trait values. For example, evolutionary pressure should lead non-helpers to evolve longer dispersal range. Temporarily the evolutionary pressure should make both non-helpers and helpers increase the reproductive rate, but this should drive the non-helpers extinct in a long-term perspective. Increases in $s$ should favour non-helpers while increases in $r$ should favour helpers. This needs to be investigated further.
References


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