

DEPARTMENT OF BIOLOGICAL AND ENVIRONMENTAL SCIENCES

A COMPUTATIONAL MODEL OF METAPOPULATION DYNAMICS AND ORGANISM-MEDIATED NUTRIENT FLOW



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Raster image of nutrient concentration data from a realization of the simulation.

Abstract	2
Sammanfattning	
1 Introduction	
2 Background	
2.1 What defines a population?	5
2.2 Exponential and logistic growth	5
2.3 The Lotka-Volterra model	6
2.4 Spatially explicit and individual-based models	7
3 Aim and hypotheses	8
4 Materials and methods	9
4.1 Model description	9
4.1.1 Habitat	9
4.1.2 Individuals	9
4.1.2.1 Life cycle	11
4.1.2.2 Migration	13
4.1.3 Initialisation of the simulation	13
4.2 Experiment design	13
4.3 Analysis and sampling	14
5 Results	15
5.1 Metapopulation level	15
5.2 Patch level	16
5.3 Individual level	17
6 Discussion	19
6.1 Selfing, migration and maturity coefficient interactions	19
6.2 Population growth patterns	19
6.3 The case for and against self-compatibility	20
7 Conclusion	21
Acknowledgement	22
References	
S. Supporting information	
S.1.Tables	
S.2. Figures	

Abstract

The aim of this project was to assess, using *in-silico* experiments, how different life history characteristics, such as age at maturity and dispersal ability of individuals, influence the dynamics of a metapopulation. To achieve this, a novel model of a spatially explicit metapopulation, with organism-mediated nutrient flow between fragmented habitat patches, was implemented by means of computer simulations. The habitat is a two-dimensional grid plane. Each grid cell is a patch that can hold a population and nutrients. Nutrient flow is exclusively dependent on the migration of individuals between patches. The species is hermaphroditic and facultatively self-fertilising. Each individual requires two resources, *nutrients* and *energy*, for growth, migration, survival and reproduction. In the model, nutrients are acquired from the habitat, and they are, in part, used to produce energy. Time is modelled in discrete steps corresponding to the age of individuals. Within individual patches, the model assumes *nutrients* to be homogeneous, and mating to be random. Generations are overlapping. Unlike most population dynamics models, the carrying capacity and intrinsic growth rate are not explicitly defined in the current model. Instead, they are emergent model properties, influenced jointly by multiple model parameters. We assessed the model outcomes for different values of two parameters, namely, age at sexual maturity and the probability of migrating to a neighbouring patch. Initially, nutrients were distributed homogeneously across all patches, while only the four central patches were populated. We found complex metapopulation dynamics with local extinctions and recolonisations, wherein population size grew in a logistic fashion during recolonisation. A higher maturity age tended to result in a higher initial growth rate and higher carrying capacity, whereas a higher probability of migration tended to result in a higher initial growth rate and lower carrying capacity.

Keywords: computational model, population dynamics, metapopulation dynamics, nutrient flow, simulation, spatially explicit, individual-based

Sammanfattning

Detta projekts syfte var att via in-silico-experiment bedöma hur olika artspecifika life-historycharacteristics, det vill säga karakteristika såsom individernas minimiålder för reproduktion, samt deras förmåga att förflytta sig, påverkar dynamiken hos en metapopulation. För att uppnå detta syfte implementerade vi en ny modell av en spatialt explicit metapopulation, med organismdrivet näringsflöde mellan delar av ett fragmenterat habitat. Modellen implementerades genom datorsimuleringar. Habitatet är ett tvådimensionellt rutnät, där varje ruta kan hålla en population och näring. Näringsflödet mellan rutorna är helt beroende av individernas förflyttning. Arten är hermafroditisk och fakultativt självbefruktande. Var individ behöver två resurser, näringsämnen och energi, för tillväxt, förflyttning mellan rutor, överlevnad och fortplantning. I modellen upptar individerna näring från habitatet, vilket de sedan använder för tillväxt, reproduktion och produktionen av energi. I modellen simuleras tid i diskreta steg motsvarande individens ålder. Inom enskilda rutor antas det att näringsämnena är homogent fördelade, att parning sker slumpmässigt. Generationerna är överlappande. I kontrast till många andra modeller av populationsdynamik är varken carrying capacity, d.v.s. den övre gränsen för antalet individer som kan samexistera i habitatet, och intrinsic growth rate, d.v.s. den maximala populationstillväxten per capita, inte explicit definierade i vår modell. De är emergenta egenskaper som uppstår genom interaktionen mellan andra modellparametrar. Vi undersökte utfallen från ett antal värden hos två modellparametrar, minimiåldern för reproduktion och sannolikheten att en individ förflyttar sig till en angränsande ruta. I början av varje experiment fördelades näringsämnen homogent över alla rutor, medan individer endast placerades i de fyra rutorna i habitatets mitt. Vi observerade en komplex metapopulationsdynamik med lokala utdöenden och återkoloniseringar, med logistisk populationstillväxt. En högre reproduktionsålder resulterade i en snabbare populationstillväxt, samt en högre carrying capacity, medan en högre förflyttningssannolikhet resulterade i en populationstillväxt men en *lägre carrying capacity*.

1 Introduction

All biological populations are expected to go extinct. The fossil records confirm that extinctions have been occurring for as long as biological populations have existed. However, during certain points in earth's history, the rates of extinction have increased dramatically. To our knowledge, since life arose on this planet, there have been five major catastrophic losses of biodiversity (Barash 2012), excluding the great oxygenation event and other potential catastrophes in deep time (Och and Shields-Zhou 2012). We, humanity, may currently be on the brink of causing our planet's sixth mass extinction event (Ceballos, Ehrlich et al. 2015). To increase our chances of avoiding this, we need to understand the mechanisms that govern the behaviour of populations. This can be achieved through the study of *population dynamics* (Hastings 2013).

If given optimal conditions, populations have a tendency tend to grow. This is not always desirable, since both deadly infectious diseases, such as HIV/AIDS, and invasive species tend to follow this pattern as well. In the case of infectious diseases, they tend to initially spread to new hosts in a logistic fashion (Triambak, Mahapatra et al. 2021) and then decline, (as seen in Figure 2.1.1). This decline can be achieved through preventative measures, such as vaccination programmes and in the case of HIV/AIDS. the distribution and use of antiretroviral medication (Cohen, Chen et al. 2011) and barrier contraceptives, such as condoms (Pinkerton and Abramson 1997). To be



Figure 2.1.1. Number of Deaths from HIV/AIDS per 100 000 individuals in South Africa, between the years 1990 and 2010 Data from: (Global Burden of Disease Collaborative Network 2019). Showing signs of logistic growth followed by a decline.

able to understand the spread of disease (Bailey 1975, Panjer 1989, Greger 2007) and invasive species, (Andrew and Ustin 2010) good models are needed. This is also true in the context of conservation. With adequate models we are better able to predict and understand the processes that define the behaviours of, and interactions between populations, metapopulations and habitats. This knowledge can then aid in finding strategies to prevent harm.

Observations are necessary, but they can only tell us the past and current situation and by themselves, may not be sufficient to describe the processes that cause them. If we want to explain and understand our observations, and predict what could happen in the future, we first need to create a mathematical framework. By then performing experiments and analysing the results in the context of this framework, we can produce more accurate predictions. However, experiments can be costly and difficult to perform on large scales or over long periods of time. In some cases, these problems can be addressed through the use of *in-silico* experiments by means of computer simulations. Ideally, these simulations should be spatially explicit since the individuals of real species are spatially distributed. It is likely that a global extinction (extinction of the entire global metapopulation) is caused by a series of local extinctions (Chesson 2013, Yan, He et al. 2022).

Powerful methods have been developed to model the intricacies of the dynamics of naturally evolving populations. Three of the most widely used models of population dynamics are the exponential growth model (Malthus 1798), the logistic growth model (Bacaër 2011) and the Lotka-Volterra predator-prey model (Volterra 1928). Historically most models of population dynamics, such as those based on logistic growth or the Lotka-Volterra equations, have been spatially implicit and do not necessarily model metapopulation structure. These types of models are less computationally demanding and may be less specialised to specific contexts but can suffer in terms of realism, since natural populations and habitats have a spatial structure. These models typically include a carrying capacity that is explicitly set by the researcher. Instead of arbitrarily setting a carrying capacity in the model, it is necessary to understand how habitat quality (e.g. nutrient amount) and speciesspecific characteristics may jointly determine the maximal number of individuals of the focal species that are expected to be sustained in a given habitat (i.e. the species-specific carrying capacity).

As the ranges of organisms change or shrink due to climate change and habitat destruction (Morueta-Holme, Enquist et al. 2013) and as new diseases and invasive species spread, a greater insight into the processes that govern the persistence of local populations and global metapopulations in relation to their capacity of dispersal and nutrient transport is needed (Peller, Marleau et al. 2022). Predicting the likelihood of population persistence in these cases may be improved by the use of models that incorporate reciprocal interactions between populations, individual organisms, and their habitat. To increase our understanding of the metapopulation dynamics that can arise from the interactions between individuals, their species-specific life-history characteristics, populations and their habitat, we constructed a novel model of a hypothetical metapopulation and nutrient flow.

The origins of this project can be traced back to a sleepless night at the marine research laboratory in Kristineberg as summer turned to autumn in 2021.

This thesis is organised as follows. In chapter 2, a background on the mathematical basis and history of the most influential models of population dynamics is given. This is followed by a brief summary of spatially explicit and individual-based models. In chapter 3, the aims and hypotheses of the project described. In chapter 4, we explain our materials and methods. We give a detailed description of our model, followed by a description of the experiments that were performed with the model and our methods for analysis and sampling. In chapter 5 we provide the results from the experiments. In chapter 6 we discuss the results of the experiments and the model. In chapter 7 we give conclude with what we learned from the experiments and discuss the applicability, realism, and future plans for the model. Chapter 8 contains acknowledgements. In Chapter 10 figures, tables and matrices are provided.

2 Background

In this chapter, we will provide a short description of the definition of a population and metapopulation used in this thesis, then we will present a summary of a small selection of the most influential models in population dynamics.

2.1 What defines a population?

Here, a population is a group of individuals who share the same position. In reality, the definition of a population is dependent on the individuals in one population sharing some unique property that the individuals of other populations do not. Usually, this is based on geographic and genetic distance. The researcher must decide where to draw the line, to try to create the most informative grouping structure. A metapopulation is a collection of connected but distinct populations, in our model it is the collection of all populations in the model, in reality the constituents of a metapopulation depend on which populations the researcher chooses to group together. The demarcation between both populations and metapopulations can be difficult, but the concepts are very useful nevertheless (Wells and Richmond 1995).

In the next section of this chapter, we will summarise some of the most influential models and their history. We will also give a short explanation of important concepts that describe more recent advances in the field.

2.2 Exponential and logistic growth

As alluded to in the introduction, many powerful mathematical models of population dynamics have been constructed. Many of which have been instrumental in the development of the field of population dynamics. We will begin with the model of exponential growth.

One of the earliest mathematical models that are still in use today is the exponential growth model. The model produces growth that is dependent on the size of the population and can be used to model the growth of populations where there are no density dependent constraints on their growth (Malthus 1798). The first known use of the model in the context of population growth, was by the economist, cleric, and demographer Thomas R. Malthus, who in 1798 used it to predict the growth of the global human population.

Under the exponential-growth model, the population size N(t), depends on time t as follows:

$$N(t) = N_0 e^{rt} \,. \tag{1}$$

Here, N(t) is the population size, at time t, N_0 is the initial population size, r is the intrinsic growth rate (the maximum population growth per individual per unit time) and e is Euler's number, the base of the natural logarithm. A problematic result of this model is that the rate of population growth will accelerate indefinitely. Because of this, the model is only applicable within a certain range of values, after which the population size will approach infinity. The exponential model can be modified to produce the logistic model of growth (Bacaër 2011). Here, the population size is no longer free to grow indefinitely, and it is instead constrained by a maximum value, known as the *carrying capacity* (commonly denoted as K). This produces a curve with an initial exponential-like phase, followed by a linear phase to then taper off as the population size approaches the carrying capacity, as illustrated in Figure 2.2.1. Illustrative example of the logistic growth function with arbitrary values. The solution for different values of the intrinsic growth rate (r) are depicted in red, green, cyan, and purple ordered by increasing values of r

This model, and various extensions to it, has been extensively used to model natural populations, including the spread of infectious diseases (Triambak, Mahapatra et al. 2021). Under the logistic growth model, N(t), the population size at time t, is dependent on time, the intrinsic growth rate (r), the initial population size (N_0) and the carrying capacity (the maximum number of individuals the habitat can support, denoted as *K*), as follows:

$$N(t) = \frac{K}{1 + \left(\frac{K - N_0}{N_0}\right)e^{rt}}.$$
 (2)

As in the exponential growth function, *e* is the base of the natural logarithm.



2.3 The Lotka-Volterra model

ordered by increasing values of r

The equations that would come to be known as the Lotka-Volterra equations were developed by Doctor Alfred J. Lotka and Professor Vito Volterra in a series of publications, including the book Elements of physical biology (Lotka 1925), and the articles Fluctuations in the abundance of a species considered mathematically Variations (Volterra 1926) and Fluctuations of the Number of Individuals in Animal Species living together (Volterra 1928), and during the early 1900's, to describe the relationship between populations of predators and prey (Kingsland 2015). In the predator-prey equations, the prey population exhibits exponential growth in the absence of predators and is limited in the presence of predators. The relationship is described as follows:

$$\frac{dx}{dt} = \alpha x - \beta x y, \quad (3)$$
$$\frac{dy}{dt} = \delta x y - \gamma y, \quad (4)$$

where, t is the unit of time, x is the prey population density, y is the predator population density, α is maximum rate of growth for the prey population, β is the strength of the effect that the predator population has on the prey population, δ is the strength of the effect that the prey population has

on the predator population and γ is the death rate of the predator population. These equations are fully deterministic and tend to produce oscillatory-like behaviours that, depending on the parameters used, either continue indefinitely or result in the extinction of one or both of the populations.

Real predator-prey interactions often display this oscillatory-like behaviour (Hörnfeldt 1978), but the amplitude tends to be damped by other factors, such as constraints on the growth of the prey population (Lindström, Andrén et al. 1994).

2.4 Spatially explicit and individual-based models

A way to challenge the assumption of spatial homogeneity is to construct a spatially explicit model. These models involve the description of spatial structure. As the availability of computing power has increased, the use of spatially explicit models has become more common. Possibly because of them being better suited to answering questions that depend heavily on spatial structure (DeAngelis and Yurek 2017). Although a spatially explicit model is defined by its description of a spatial structure, the level of detail can be adapted to suit the context of its use. The individuals within the model can be modelled implicitly at the scale of populations or they may be modelled explicitly, as is the case with individual-based models.

Individual-based models explicitly describe the properties of each individual. This approach introduces more complexity, allowing for a greater level of detail, but requires more computing resources. A spatially explicit individual-based model describes the spatial relationships of both the organisms and features of their habitat. The changes in habitat in response to the population dynamics can feed back and critically impact the population dynamics, but to date our understanding of such a feedback has been poor. This thesis aims to increase this understanding by explicitly including in the models a feedback between a metapopulation and its habitat quality (i.e. nutrient level).

The next chapter summarises the aims and hypotheses of this thesis.

3 Aim and hypotheses

The aim of this project was to create a model of simulated organisms and set up *in silico* experiments to assess how different combinations of life history characteristics may influence local and global population persistence, extinction, and other dynamics of a metapopulation, particularly over timescales that are difficult to measure in non-artificial populations.

The spatially implicit and population-based models described in the background (Chapter 2) are immensely useful in describing and predicting the dynamics of natural populations, but they rely on many simplifying assumptions, some of which can be relaxed towards adding more realism. The pure mathematical approach becomes increasingly difficult to implement as more complexity is added. To implement models of larger and more complex systems, it may be preferable to use a bottom-up approach instead, where complexity can arise from many instances of simple components interacting with each other. We wanted to investigate the effects on the dynamics of metapopulations caused by organism-mediated nutrient flow, whereby relaxing the assumption that the properties of the habitat are unaffected by the population dynamics of its inhabitants. Our further aim was and to investigate how the life-history characteristic age at sexual maturity and the dispersal ability (probability of migration) of the individuals may influence their metapopulation dynamics.

For these reasons we constructed a spatially explicit individual-based model where the population dynamics influence the habitat by affecting the spatial distribution of nutrients and vice versa.

We expected that a higher probability of migration would lead to more rapid colonisation of the habitat and higher population persistence in local patches. Moreover, we expected that the metapopulation would experience logistic growth and that a lower age of sexual maturity would lead higher rates of initial growth and that lower maturity ages would lead to more rapid colonisation of new areas.

In the next chapter, we will provide a detailed description of our model, the experiments that we performed and our methods of sampling and analysis.

4 Materials and methods

Here we will explain the details of how the model functions, how it was implemented, and how we performed our analysis of the data.

4.1 Model description

The model is stochastic, spatially explicit, and individual-based. It describes a metapopulation, with organism-mediated nutrient flow between fragmented habitat patches. It was implemented by means of computer simulations. It is governed by a set of parameters, most of which will be explained in detail here (comprehensive list of the model parameters in table 1). Time is modelled in discrete units, which we will refer to as *time steps*. The time step is the shortest interval of time at which any process in the model can occur and is the rate at which the simulation updates. In the model, the *nutrients* serve as a generalised representation of the nutrients whose abundance we assume most strongly affect the population growth of primary producers, such as the phosphate ion. The nutrients and individuals in the model are contained within a closed system, with no net change in the total amount of nutrients and no migration from or to areas outside of the habitat boundaries.

The model was implemented in the $Unity^1$ game engine and the code was written in the $C\#^2$ programming language. The code for the grid was based on work by a programmer known as *Code-Monkey*³. The model is, to an extent, based on earlier versions of the model *blob bucket/cilioids*, created by the author of this text, first as a hobby and then as a supplementary part of the Ecotwin project (Strannegård, Engsner et al. 2022).

4.1.1 Habitat

The habitat is modelled as a two-dimensional plane divided into a grid of square cells with each cell representing one patch. The unit of length in the model is the edge length of the patch. The total number of patches is a model parameter, and it is here set to 256 (16x16). Each patch has the following properties: position in the habitat, area, amount of nutrients, number of individuals and number of gametes. The amount of nutrients is modelled as integers for simplicity and to make the simulation less computationally intense. The total amount of nutrients in the habitat is fixed and is chosen before the start of the simulation, making it a closed and isolated system. At the start of each simulations ran for the purposes of this thesis, the nutrients were distributed homogeneously over all patches of the habitat. In the model, it was assumed that nutrients can only be actively transported in the bodies of migrating individuals. The model could be viewed as an abyssal plain with little influx of nutrients where areas of higher amounts of nutrients are distant from each other, or as patches of grazing pastures separated by inhospitable barriers, such as roads, dense forests, or sandy beaches, if the organism prefers rocky coastal areas.

4.1.2 Individuals

The Individuals are assumed to be motile autotrophs or grazing primary consumers. Depending on the mode of reproduction parameter, the individuals are either hermaphroditic with external fertilisation or asexually reproducing. If the individuals are sexually reproducing, they can be either

¹ https://unity.com

² https://learn.microsoft.com/en-us/dotnet/csharp/tour-of-csharp/

³ https://unitycodemonkey.com/

facultatively self-fertilising or self-incompatible, i.e., obligate outcrossers. In the simulations performed here, individuals were assumed to be facultatively self-fertilising.

In the model, each individual requires two resources, *nutrients* and *energy*, for growth, migration, survival, and reproduction. It is assumed that the *nutrients* are acquired from the habitat and the individuals use them for reproduction, growth, and maintenance of their ability to produce *energy*. *Energy* is produced within the individual. It is used for migration, nutrient absorption, and all processes that require nutrients (see above) and it is directly required for survival. In the model, there are two ways that an individual can die (illustrated in **Error! Reference source not found.**). i.e., either if the *energy level* (E), reaches zero, or if the individual's age (A), reaches the *maximum age* (A_{max}). All processes within an individual occur independently of all other individuals. The nutrient level of the individual is denoted as L.



Figure 4.1.1. A visual representation of the two ways an individual can die. The smaller circle represents a juvenile and the larger circle represents an adult. The text boxes with overlayed colour represent conditions, with green signifying sufficient resource levels, and red signifying an absence of resources. If the individual has enough resources and has not reached its maximum age, it will remain alive, if it has zero nutrients, it will start to lose energy, once all energy is lost, the individual dies.

In each time step, all individuals produce a certain amount of energy. The amount of energy that is produced by the individual is determined by multiplying the variable *energy synthase integrity* (ε) with the parameter *base energy production* (E_{bp}).

The energy synthase integrity can range from zero to one and it requires both nutrients and energy to maintain. At a rate of once every two time steps, the energy synthase integrity decreases by a fixed amount (denoted by ε_a), as long as the energy synthase integrity is greater than ε_a . If it is greater than zero but smaller than ε_a the energy synthase integrity will be zero in the next time step.

Immediately after this, if the energy synthase integrity is smaller than one and the individual has sufficient nutrients and energy to restore it, the individual will expend a specific amount of energy (denoted as $E_{\epsilon c}$) and a specific amount of nutrients (denoted as $L_{\epsilon c}$) to restore the energy synthase integrity. This restoration, which increases the energy synthase integrity by ϵ_a can occur once every time step if the conditions above are met (. This means that every other time step, no decrease occurs, instead the model immediately proceeds to the restoration step. The rates at which these processes occur are model parameters that can be modified.

In addition, there is a fixed energy cost (denoted by E_{bc}) which is subtracted from the energy level of the individual at a rate of once every two time steps, given that the individual does not have an energy level of 0.

Note that nutrients are required for the energy synthase integrity (ε) to increase. Hence, if there are no available nutrients, ε will continue to decrease, and eventually the rate of energy production will be surpassed by the rate of energy loss, which will lead to the death of the individual.



4.1.2.1 Life cycle

Figure 4.1.2. A visualisation of the life cycle of the individuals.

The life cycle of the individuals is summarised in **Error! Reference source not found.** At age 0 the individual has a pre-determined amount of energy (E_0) and nutrients (L_0). Its nutrient level is equal to half of the nutrients that were present in the gametes it formed from, which is also equal to the nutrient requirement for producing one gamete. The other half is released into the habitat and E_0 is added to the individual in exchange. This process was introduced because individuals need an energy level higher than zero energy to survive and is justified by the fact that proteins can be used as a calorie source. The return of nutrients to the habitat that occurs when nutrients are expended, is meant to represent waste excretion.

In addition to energy, in the model we assigned to each individual its *maximum age*, A_{max} . *The maximum age* is assigned to each individual upon its birth by sampling a random number from a Gaussian distribution with a pre-defined mean and standard deviation (Table S.1.1 & S.1.2). During each subsequent step, the individual will absorb nutrients from its patch and grow. The amount of energy lost through nutrient absorption is defined by the *per nutrient absorption requirement* parameter (E_{LAC}). The individual can only hold a maximum amount of nutrients at a time, and we refer to this amount as the *maximum nutrients* parameter (L_{max}). Nutrients can only be absorbed when the nutrient level (L) is lower than L_{max} and only one nutrient can be absorbed per one time step.

Once an individual completes its growth stage, and reaches its *minimum maturity age*, M_{age}, it can reproduce. The individual reaches sexual maturity when the value of the *physical maturity* variable,

 M_{p} is equal to one, and the age of the individual is equal to the *minimum maturity age*, M_{age} . In the model, all individuals are assumed to have the same *maturity coefficient* parameter, M_{coef} (which we assume is a species-specific property), whereas they can differ by their minimum maturity age (M_{age}). Indeed, for each individual M_{age} is calculated by multiplying A_{max} of the individual with the *maturity coefficient* parameter, M_{coef} and then flooring that value to the closest integer:

$$M_{age} = \lfloor A_{max} M_{coef} \rfloor \qquad (5)$$

In eq. (5), $\lfloor a \rfloor$ denotes the maximal integer not larger than *a*.

In the model, individuals; growth is modelled as an increase of the *physical maturity variable* (M_p). It ranges from zero to one and will increase by a pre-determined amount (M_{growth}) each time step, given that the energy synthase variable has been restored to the value of one, and given that the nutrient and energy levels of the individual are higher than the *growth nutrient requirement* parameter (L_{growth}) and the *growth energy requirement* parameter (E_{growth}):

$$\label{eq:eq:star} \text{if} \begin{cases} \epsilon = 0 \\ E > E_{growth} \text{ and } M_p \leq 1 - M_{growth} \\ L \geq L_{growth} \end{cases}$$

then

 $dM_p = M_{growth}$ (6)

After reaching sexual maturity, the individual continues to reproduce for the remainder of its life, for as long as it has sufficient nutrients ($L \ge L_{gam}$) and energy ($E > E_{gam}$).

When an individual expends nutrients for growth and for the restoration of energy synthase, they are immediately excreted to the habitat.

In the experiments run for this thesis, the mode of reproduction was strictly sexual, meaning that reproduction only occurs through the production of gametes. The model can treat asexually reproducing individuals upon setting the parameter *mode of reproduction* parameter to *asexual* (this will be tackled in future work).

When a gamete is produced, the nutrients required for gamete production are transferred from the individual to the gamete and the energy required is subtracted from the energy level of the individual. The gamete remains in the patch for a specific number of time steps, defined by the *gamete persistence* parameter, G_p . During each time step that it remains in the patch, the gamete can potentially merge with another gamete in its patch, thereby producing a zygote, provided that there is at least one more gamete present in the patch. Pairs of gametes that can potentially interact and form a zygote are chosen uniformly at random from all gametes present in a given patch. When individuals are self-compatible, as is the case in the experiments performed for this thesis, all pairs of gametes produce viable zygotes. However, in the model version with self-incompatible individuals, only gametes coming from distinct parents are allowed to form zygotes. In this case, the incompatible gametes it formed from are removed from the simulation, and a juvenile individual is added to the patch. If a gamete has not fused with another gamete after G_p time steps, it is removed from the simulation and its nutrient content (L_{gam}) is returned to the patch.

Recall that each individual has a maximum age (A_{max}) that it can reach. However, an individual can die before reaching Amax if its energy drops to zero (see above). Upon death, the individual is removed from the simulation and the nutrients it had at the point of death are returned to the patch it died in.

4.1.2.2 Migration

An individual may migrate to a neighbouring patch at any point during its lifetime. At each time step, an individual that has sufficient energy, that is, if its energy level is higher than the minimum migration energy requirement ($E > E_{mig}$), it will migrate with the probability P_{mig} . Otherwise, it will not migrate.

An individual that does migrate in a given time step will migrate to one out of its eight neighbouring patches, all eight patches being equally likely. The patch that the individual migrates to is calculated by selecting a random index from eight two-dimensional migration vectors $\Delta \vec{U}$. (corresponding to separate columns in migration matrix Q; see **Error! Reference source not found.**). The selected migration vector ($\Delta \vec{U}$) is then added to the individual's *source vector* (i.e., the individual's current position vector in the grid, $\vec{U_0}$). If the resulting position vector lies outside of the habitat, migration is prevented. If the resulting position is within the habitat, the new position vector of the individual (\vec{U}) is set as the sum of the source vector and the migration vector. This means that the probability of remaining in the same patch is higher at the edges of the habitat.

Note that any migration event requires energy, denoted here by E_{mig} . Specifically, when an individual migrates, the energy amounting to E_{mig} is subtracted from the individual's energy prior to the migration.

4.1.3 Initialisation of the simulation

At time step zero, the total number of nutrients in the habitat is distributed to all patches according to a pre-defined distribution. The total number of individuals and their placement within the habitat is pre-defined as well. The first generation of individuals are added to the habitat as juveniles, with L = 0 and $E = E_0$. The simulation will then progress according to the parameters that have been set. More details about the initialisation and other simulation parameters are given in the next section

4.2 Experiment design

In the experiments, the habitat area was set to 16x16 patches, with 8192 nutrients distributed homogeneously over all patches. The initial population size was set to 64, where 16 individuals were placed in each of the four central patches of the habitat.

Two life-history characteristics were manipulated: the probability of migration (P_{mig}) and the minimum age at sexual maturity (determined by the parameter M_{coef}). Three values for each parameter were chosen and all unique combinations of these variables were assessed. The values chosen for the probability of migration were 2×10^{-4} , 4×10^{-4} and 8×10^{-4} . The values chosen for the maturity coefficient were 0.2, 0.4 and 0.8, corresponding to a minimum maturity age of 20%, 40% and 80% of the maximum age. For each combination of these parameter values, ten replicates were produced. In total, there were nine experiments with ten replicates.

Each experiment was run for 30 720 time steps. We had learned from pilot experiments that with the current parameters, the metapopulations tended to stabilise (in statistical sense) at around 30 000 time steps after the initialisation, or earlier. Due to stochastic nature of the realised population dynamics, we chose to trace the population dynamics also for several hundreds of timesteps upon reaching statistical equilibrium, and we deemed that a total of 30720 steps per simulation run is sufficient for this purpose. Every death and reproductive event was recorded and stored in memory as they occurred, but were transferred to permanent storage every 2048 time steps, meaning that 30 720 time steps were needed for the death and reproductive event data to be saved to disk 15

times. This was done to reduce the memory load associated with transferring large amounts of data and to not keep all data stored in RAM indefinitely. The output data from the simulations was stored as comma separated value files. All statistics, excluding death end reproduction data, were sampled once every 32 time steps. All simulation runs were created as server builds for *Microsoft Windows 10* and were run in parallel on six machines. Thirty realisations were run on a laptop lent to us by the University of Gothenburg and the remaining sixty realisations were run on five virtual machines rented from the cloud computing company *Paperspace*⁴.

4.3 Analysis and sampling

Although the model produces a larger number of statistics, we opted to analyse those that we deemed relevant to the experiments. The chosen statistics can be categorised into three levels: met-apopulation level, patch level and individual level.

The chosen metapopulation level statistics were the global population size, the global number of individuals produced via selfing, the global amount of free nutrients (that is, nutrients that are not locked in individuals or gametes) and the distribution of nutrients across the habitat.

The patch level statistics were the local population sizes, the local number of individuals produced via selfing, the local amount of free nutrients, the number of time steps that patches were continuously occupied (persistence time before a local extinction event), the number of time steps that the patches remained empty after a local extinction event (rescue time), and the number of time steps between the start of the experiment and the first colonisation event for each patch.

The individual level statistics were the ages at reproduction and death, the cause of death, the lifetime number of gametes produced and the lifetime amount of expended nutrients.

Global statistics were produced as tables with each variable being stored separately. Local statistics were sampled as individual snapshots of the habitat, to produce sequences of two-dimensional matrices where each index within each matrix represents one statistic in one patch at one point in time.

To gain a greater understanding of the local population dynamics, we analysed in more detail the dynamics of populations and nutrients in eight selected patches, that is, the patches extending from the top-right patch of the four central cells, index [8,8], to the rightmost edge patch of the habitat, [8,15].

The chosen time range to analyse the population when they had reached a longer-lasting quasiequilibrium was between t = 25 000 and t = 30 000. All data was sorted and analysed using the *dplyr* R-package (Wickham, François et al. 2018) and plotted with *ggplot2* (Wickham 2016) package in the *R* programming language. Raster images were generated from portions of the matrix data using the *grid* R-package and were animated using the open-source multimedia framework $FFmpeg^5$.

The results obtained are presented in the next chapter and they are further discussed in Chapter 6.

⁴ https://www.paperspace.com/

⁵ https://ffmpeg.org

5 Results

In this chapter we will present the results from the experiments.



5.1 Metapopulation level

Figure 5.1.1. The global population size for over time in one experiment for each replicate. Grey lines indicate the values in individual experiments, the red line indicates the mean value. ($M_{coef} = 0.2$, $P_{mig} = 2 \cdot 10^{-4}$)

The total population size of the metapopulation exhibited logistic growth in all experiments (**Error! Reference source not found.**).

Although this model does not have an explicitly defined carrying capacity, as is the case in the logistic growth model, we will refer to the size at which the population stabilises as the *carrying capacity*.

The initial growth rate and carrying capacity differed for different model parameters. Both the carrying capacity and the initial growth rate were larger for higher minimum maturity ages (compare the results for low (red, orange, olive lines), medium (light blue, cyan, dark green) and high minimum maturity ages (magenta, purple, dark blue) in Figure S.2.1).

We observed a higher initial rate of global population growth in the experiments with higher probabilities of migration. Conversely, the carrying capacity was lower for higher probabilities of migration (compare red vs. orange and olive, dark green vs. cyan and light blue, magenta vs. purple and dark blue in Figure S.2.1, as well as blue vs. green and red in Figure S.2.2).

Similarly, the average amount of free nutrients present in the habitat during the equilibrium state of the population differed between the experiments (Figure S.3.3). We observed that the effect on the mean amount of free nutrients at quasi-equilibrium seemed to be caused by an interaction between the probability of migration and the minimum maturity age. In the experiments with lower minimum maturity age, lower probabilities of migration were associated with a higher average amount, and a higher variability of, free nutrients, whereas the probability of migration seemed to have a weaker effect at higher maturity coefficients (red: lowest Pmig, blue: highest Pmig, in Figure S.3.4).

The distribution of nutrients throughout the habitat when the system had reached quasi-equilibrium did not display a clear spatial structure in any of the experiments.



5.2 Patch level

Figure 5.2.1. The mean time between the start of the experiment and the first colonisation event for each patch extending toward the habitat edge.

The population dynamics in all experiments corresponded to complex metapopulation dynamics with local extinctions and recolonisations. One way to quantify this metapopulation dynamics is to measure populations' persistence time before local extinction events, and the time needed for successful local recolonisation following an extinction event. As stated in the analysis section, we opted to analyse a subset of data from local patches, a line of eight patches, stretching from the center to the edge to serve as a one-dimensional representation of the habitat.

We found differences in the rate of expansion from the center towards the edge of the habitat. The time between the colonisation of each adjacent patch differed between all of the experiments, where a higher probability of migration and a higher minimum maturity age were associated with shorter and more consistent intervals of time between subsequent colonisations (Figure S.3.5.).

The mean local persistence time of populations in individual patches were found to be higher at higher maturity coefficient values (horizontal axis in Figure S.3.6) and at higher migration probabilities (blue in Figure S.3.6). The largest effect on the mean local persistence time was observed in response to manipulating the maturity coefficient where higher maturity coefficients were associated with higher persistence times. We found smaller but consistent effects, attributed to the probability of migration, on local population persistence at maturity coefficients of 0.4 and 0.2. No discernable differences in local population persistence, attributed to manipulation of the probability of migration, were found between the experiments with a maturity coefficient of 0.8 (Figure S.3.6). At statistical equilibrium, we found no differences in the mean persistence time between the eight patches of the same experiment.

The mean *rescue time*, i.e., the mean number of time-steps between local extinctions and subsequent recolonisations, was smaller at higher maturity coefficients and migration probabilities (Figure S.3.1).

Upon inspecting individual model realisations in a subset of habitat patches, we found that the population sizes were prone to more or less periodic (oscillatory-like) changes, which we will refer to as oscillations. Lower maturity coefficients and higher probabilities of migration were associated with oscillations of higher amplitude (Figure S.3.2).

Finally, the relative number of individuals produced via selfing were found to be higher during early phases of colonisation, especially at higher maturity coefficients. This phenomenon was observed both in local patches (Figure S.3.9, and Figure S.3.10) and on the global habitat scale (Figure S.3.11. Ratio of the number of individuals produced via selfing, to the ones produced by outcrossing, over time. Each colour represents one unique parameter combination. The shaded areas represent the 5th and 95th percentiles.

).

5.3 Individual level

Recall that individuals were assigned a maximum age after which they would die with certainty. However, the model allowed individuals to die before reaching this age due to a lack of energy. We assessed in each simulation the age at which individuals died and the underlying reason of death. Our results showed that a lower maturity coefficient and a higher migration probability was associated with a larger proportion of individuals dying due to a lack of energy (Figure S.3.12 & Figure S.2.14).

The total number of gametes produced per individual per lifetime was higher at low maturity coefficients (Figure S.2.15) .

We found that higher probabilities of migration were associated with a lower mean age at the first reproductive event (Figure S.3.15).

Higher probabilities of migration were associated with a higher mean number of migrations per individual per lifetime (Figure S.3.16).

Differences in the mean total amount of excreted nutrients per individual per lifetime between the experiments were found, with higher maturity coefficients being associated with less variance and higher mean amounts of total excreted nutrients (Figure S.3.17).

6 Discussion

In this chapter we will discuss the results of the experiments and the model as a whole. The experiments produced both results that were expected, and some that were quite unintuitive.

6.1 Selfing, migration and maturity coefficient interactions

The higher selfing ratio observed in recently colonised patches is expected and has been the subject of several previous studies (Eriksson and Rafajlović 2021). This is likely explained by a the individuals having fewer opportunities for outcrossing (Baker 1955).

In general, changes to the probability of migration did not produce very strong effects compared to those produced by manipulating the maturity coefficient. The reason for this may be that the range of values we chose was too limited. We did observe noticeable effects in some cases, however. The lower carrying capacity associated with a higher probability of migration may be caused by higher energy losses caused by more frequent migration. This is supported by the higher proportion of deaths attributed to a lack of energy in those groups (Figure S.3.12). A link between higher dispersal distances and a higher risk of mortality has been shown in experiments on natural populations as well (Johnson, Fryxell et al. 2009).

In the experiments with a low probability of migration, we saw that colonisation events only involving a single individual were more common. These individuals could only reproduce successfully through self-fertilisation, but to be able to self-fertilise, they would need to produce gametes at a rate high enough for their gametes to exist in the same span of time which we saw with the observed higher selfing ratio at high maturity coefficients. In essence they have a shorter, but more productive reproductive period, similar to that of long-lived semelparous organisms (Young and Augspurger 1991). The apparent relative success of the individuals with high maturity coefficients may in part be explained by this since they were more able to self-fertilise. Although the model does explicitly include trait evolution it may have captured parts of the processes that give self-compatible organisms an advantage (reproductive assurance) when expanding to new regions (Baker 1955). Even though all individuals in the model could theoretically self-fertilise, the ones that can produce gametes at a faster rate are more likely to do so, which could be interpreted as them being more self-compatible.

6.2 Population growth patterns

The logistic growth that we observed in the metapopulations indicate that the model is to some extent able to produce the effects that limited resources have on a growing population.

That the rate of initial growth, after the first generation, was higher in the experiments with lower maturity coefficients is explained by a mechanism similar to that in the Lotka-Volterra predatorprey model (Volterra 1928), but now with nutrients having the role of prey and the individuals having the role of predator. The mechanism is as follows: a high abundance of nutrients leads to a rapid increase in population size, which in turn leads to a depletion of freely available nutrients and this leads to a subsequent population crash. The rate at which the populations could grow if there were no constraints from nutrient availability, should be higher at lower maturity coefficients since they should have more opportunities to reproduce during their lifetime. However, in our experiments there *were* constraints on growth caused by nutrient availability, and what saw was that the population sizes experienced more extreme oscillations at lower maturity coefficients (*Error! Reference source not found.*). This may be explained by the individuals expending nutrients and energy at a faster rate, leading to short bursts of fast growth that are quickly followed by a crash in population size as the individuals are more vulnerable to a lack of nutrients. The positive relationship between probability of migration and mean number of gametes is unexpected, since in the model, the higher energetic costs associated with more migration, should leave less energy available for gamete production. We believe that this is due to higher rates of migration increasing the probability of individuals migrating to patches with lower competition for nutrients although further analyses are needed to confirm this.

It particularly interesting that despite of the identical habitat quality, different species-specific characteristics lead the metapopulation to stabilise at different equilibria whereby the population size stabilised around different carrying capacities.

6.3 The case for and against self-compatibility

Hermaphroditism is not the norm in the animal kingdom, but it is quite common among some taxa. (Jarne and Auld 2006). It is by far the most commonly employed reproductive strategy among seed plants, however. Many hermaphroditic organisms have evolved different strategies to prevent self-fertilisation, but a considerable number of taxa retain the ability to self-fertilise to varying degrees (Goodwillie, Kalisz et al. 2005).

There are both advantages and disadvantages to hermaphroditism and self-fertilisation. Hermaphroditism, even when selfing is prevented, can provide a greater access to mates, at lower population sizes, since any sexually mature individual is able to mate with any other sexually mature individual. In mixed mating systems, individuals can reproduce even if they have no access to mates (Baker 1955), but they are still able to outcross and avoid inbreeding when mates are available. The topic of self-fertilisation and inbreeding depression is very complex, however. Some studies have found that self-fertilisation might reduce inbreeding depression in some cases. The argument being that high rates of self-fertilisation tend to result in high homozygosity and individuals who are homozygous for deleterious alleles are more likely to suffer a fitness disadvantage, leading to a purging of these deleterious alleles from the population (Busch 2005). Although there are obvious benefits to mixed-mating systems, the disadvantages that come with self-fertilisation might be context dependent.

The model in this thesis does not account for genetics and therefore any potential fitness disadvantages that could arise from inbreeding are not present. We chose a mixed-mating system was chosen for two main reasons. It can be argued that self-compatibility may be the simplest way to model sexual reproduction, since there is no need to add sexes and rules that prevent self-fertilisation. We had previously seen in the model, that the self-compatible populations were able to persist over a wider range of parameter values, which made the experiments easier to set up. The model can be altered and built upon to include a genetic model that can take inbreeding depression into account and other modes of reproduction, which may give greater insight into the metapopulation dynamics of organisms whose life-history characteristics make them more vulnerable to extinction.

In the next chapter we will provide a conclusion to this thesis.

7 Conclusion

We delivered a novel model of metapopulation dynamics and nutrient flow that produced some results in line with our expectations and previous research, including logistic population growth, higher rates of self-fertilisation during early stages of colonisation (Rafajlović, Kleinhans et al. 2017, Eriksson and Rafajlović 2021). It also produced results that were unexpected, but that could potentially be explained by known processes. The periodic behaviour of the interaction between population size and nutrients on a patch level, could be interpreted as either negative densitydependence (Volterra 1928, Maron and Crone 2006, Hixon and Johnson 2009), Lotka-Volterra dynamics (Volterra 1928), or both. The higher rates of self-fertilisation associated with higher maturity ages seem to be akin to the reproductive strategy of semelparous organisms, where the resources required for reproduction are expended in a single massive reproductive event (Young and Augspurger 1991). We conclude that employing a bottom-up approach is a feasible way to produce realistic and highly complex metapopulation dynamics. We believe that the model can be expanded to give useful and more specific predictions in the future, both in the context of providing predictions for conservation and the spread of invasive species. Although the model should be explored further, to better gauge its explanatory power and applicability, we believe that the contribution of this study is a realistic model that can act as a base framework for a conceptual understanding of population dynamics. Moreover, we believe that the model can be further developed to include multiple interacting species, thereby establishing a framework to tackle the dynamics of communities. This is a key step to better understand and reveal potential threats to ecosystems or threatened populations and ecosystem functions.

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S. Supporting information

S.1.Tables

Parameter	Symbol	Value in experiments
Mode of reproduction		Sexual
Self-incompatibility		FALSE
Mean maximum age		256
Standard deviation of maximum age		32
Gamete nutrient requirement	L_{gam}	1
Gamete energy requirement	Egam	12
Maturity coefficient	M _{coef}	0.2, 0.4 & 0.8
Base energy production	E_{bp}	3
Maximum nutrients	L _{max}	16
Energy synthase repair cost, energy	$E_{\epsilon c}$	4
Energy synthase repair cost, nutrient	$L_{\epsilon c}$	1
Energy synthase decay & restore amount	ε	0.1
Migration energy requirement	E _{mig}	12
Migration probability	\mathbf{P}_{mig}	(2, 4 & 8) × 10 ⁻⁴
Growth nutrient requirement	Lgrowth	1
Growth energy requirement	Egrowth	2
Gamete persistence	$\mathbf{G}_{\mathbf{p}}$	8
Per nutrient absorption requirement	ELAC	0.1

Table S.1.1

Variable	Symbol
Maximum age	A _{max}
Minimum maturity age	M_{age}
Maturity	Mp
Age	А
Energy synthase integrity	3
Nutrient level	L
Energy level	Е

Table S.1.2. The model variables.





Figure S.2.1. Global population sizes over time. Each coloured line represents the mean population size over ten replicates for each unique parameter combination (see legend). The shaded ribbons span between the 5th and 95th percentile.



Figure S.2.2. Mean global population sizes over time at their respective equilibria. Error bars span between the 5th and 95th percentile.



Figure S.3.3. The mean number of free nutrients (i.e., nutrients that are not locked in individuals or gametes) as a function of time. Each coloured line represents the mean value over ten replicates and each colour represents a unique combination of parameter values as depicted in the figure legend. The ribbons span between the 5th and 95th percentile.



Figure S.3.4. The mean proportion, per parameter combination, of free nutrients relative to the total number of nutrients in the system, for different maturity coefficients (x-axis) and different probabilities of migration (indicated by different colours; see figure legend). Symbols show the mean over ten independent replicates, error bars span between the 5th and 95th percentile.



Figure S.3.5. The number of time-steps since the start of the simulations needed for a patch to be colonised, as a function of the distance from a central patch. Symbols show the mean over ten independent replicates, error bars span between the 5th and 95th percentile.



Figure S.3.6. The number of time steps from a colonisation event of a patch until its local extinction (y-axis) for different values of the maturity coefficient (x axis). Symbols show the mean over ten independent replicates, error bars span between the 5th and 95th percentile.



Figure S.3.1. Mean number of time-steps between local extinctions and recolonisations (y-axis) for different values of the maturity coefficient (x axis). Symbols show the mean over ten independent replicates, error bars span between the 5th and 95th percentile.



Figure S.3.2. Population sizes (y-axis) over time (x-axis) in a patch adjacent to an edge patch. The plot is showing the values in one single replicate for each parameter combination. Each panel corresponds to one unique parameter combination which is written in the grey labels beside the panels.



Figure S.3.9. Ratio of the number of individuals that were produced via selfing relative to the number of individuals produced via outcrossing (selfing ratio, y-axis) over time (x-axis), in a patch adjacent to an edge patch.. Each panel corresponds to one unique parameter combination which is written in the grey labels beside the panels.



Figure S.3.10. Raster image visualisation of the selfing ratio matrices sampled at intervals between t = 0 and t = 30720. The top left image is at t = 0 and the bottom right image is at t = 30720 Yellow: high selfing, blue: low selfing, black: unpopulated. The data is from one of the replicates of the experiment where Mcoef = 0.8 and $Pmig = 8 \cdot 10^{-4}$.





Figure S.3.11. Ratio of the number of individuals produced via selfing, to the ones produced by outcrossing, over time. Each colour represents one unique parameter combination. The shaded areas represent the 5th and 95th percentiles.



Figure S.3.12. The cause of death (x-axis), shown as percentages of the total number of deaths over the course of the experiments(y-axis) for all ten replicates. Each panel corresponds to one unique parameter combination which is written in the grey labels beside the panels.



Figure S.3.13. The distribution of age at the time of death for all ten replicates for each unique parameter combination. Vertical lines show the mean age at death, coloured by the cause of death. Black : mean age at death for all individuals, cyan: lack of energy, red: age. Each panel corresponds to one unique parameter combination which is written in the grey labels beside the panels.



Figure S.3.14. Mean number of gametes produced per individual per lifetime (y-axis) for different probabilities of migration (x axis). Symbols show the mean over ten independent replicates, colours show different values of the maturity coefficient.



Figure S.3.15. Mean age at first reproductive event per individual per lifetime with each point being a separate replicate (y-axis) for different probabilities of migration (x axis). Colours show different values of the maturity coefficient.,



Figure S.3.16. Mean number of migrations individual per lifetime (y-axis) for different probabilities of migration (x axis). Symbols show the mean over ten independent replicates, colours show different values of the maturity coefficient.



Figure S.3.17. The mean total nutrients excreted per individual per lifetime (y-axis) for different probabilities of migration (x axis). Symbols show the mean over ten independent replicates, colours show the different maturity coefficient values, error bars span between the 5th and 95th percentile.