Mathematical Modelling of Population Dynamics in Complex and Fragmented Environments

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by
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“Important thing in science is not so much to obtain new facts as to discover new ways of thinking about them.”

Sir William Bragg
Abstract

Understanding the effect of the global environmental change on the dynamics of ecosystems and populations is a major challenge in contemporary science, and mathematical modelling is widely recognised as an efficient research tool to address it. In particular, habitat fragmentation has become a key concern in ecology over the past 20 years as it is thought to increase the threat to biodiversity that causes species extinction worldwide. Mathematical modelling helps to understand the effect of complex and fragmented habitat on population dynamics.

The objective of this thesis is to address several issues related to the problem of habitat fragmentation and shed light onto population dynamics using mathematical modelling and computer simulations in several domains of different shape. Chapter 1 gives an introduction and literature review. Chapter 2 provides a single species model, i.e., two-dimensional reaction-diffusion equation (taking the Allee effect into account) in order to determine how the boundaries impact the population persistence using various domain shapes and sizes with different strengths of the Allee effect. Chapter 3 considers a domain of a more complicated shape, i.e. two large uniform habitats connected by a narrow corridor with a "stepping stone" in the middle, and investigates the survival rates of a population already at risk of extinction. This includes varying factors, such as patch size, Allee effect strength and patch location. Patterns and rates of invasive species spread in a complex environment have been a focus of attention in Chapter 4, where we are considering the spatiotemporal dynamics of an alien species affected by a predator.

Since the purpose of this work is to reveal the factors affecting species survival in small and fragmented habitats, critical domain problem for the reaction-telegraph equation model is introduced in Chapter 5. Telegraph equation is sometimes thought to be a more adequate model of population dynamics as it takes into account directional persistence of individual animal movement. Chapter 6 provides conclusions and an outline of possible future work.
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To my lovely son

Saleh
Chapter 1

Introduction

1.1 Biological Invasions

Biological invasion is a very common phenomenon. It is the process by which non-native living organisms, plants, animals or even microbes, are introduced into a new ecological range beyond their original range [47, 51, 81, 134, 137, 150, 186]. Over a long time, the subject of biological invasion has been of public interest. This is partly because of the fast accelerating number of invasive species. Many scholars and researchers have developed profound interest in invasive species. This is evident by the increasing number of publications on biological invasions, not just in the field of academics, but equally to a wider audience e.g. Section 1.4 in [99]. Biological invasions have had profound impact on the ecosystem, and are currently recognized as a significant part of the global environmental change [47, 81, 116, 134, 162, 186].

1.1.1 Classical examples of biological invasion

- Rats and Cats on Ocean Islands.

One of the oldest biological invasions was the invasion of rats, which keep on infesting places till now. Rats’ invasions are not deliberate but brought accidentally on boats and ships [113]. Their invasion has negative effects on native species [11, 15] and, in some cases, they cause the extinction of a species too. In
the 1960s, black rats established their colony on Big South Cape Island, Southland (New Zealand). Their arrival on this island caused the extinction of two endemic birds’ species, while a species of bat and three endemic birds were almost gone in approximately two years [15].

When rat infestation came to its extreme, domestic cats known as *Felis catus* were introduced as a solution because they are rat predators. Additionally, they were considered as pets, which was another reason for their biological invasion on the islands. This solution for eradication of pest through the invasion of another animal species rather than chemical means was one of its kind. But this solution failed badly and results were far worse. Domestic cats’ invasion proved fatal for endemic species of the Island as they did not attack rats [26, 113]; instead they hunted native species. The reason behind this behaviour was that native species were not familiar with cats before and did not know how to protect themselves [46]. It has been reported that at that time cats were introduced into over fifty islands. The cats hunted native species resulting in the huge loss of sea and land birds’ colonies, their population, and even in some islands species were eradicated too. Kerguelen Island is the true example of the discussed fact where cats multiplied hugely and brought disaster for birds species. Therefore, cats are responsible for the loss and extinction of many birds in these islands, with an estimated killing of 2 million petrels yearly [28]. Apart from birds, they cause threat to other animal species such as reptiles native to those islands [25] and island foxes, which can be defeated by cats easily and cause their extinction [36, 37, 99].

The above examples of cat and rats’ invasion are a true phenomenon of biological invasion and show a few important after effects. It can be noted that when an alien species is introduced in a given ecosystem, it may out compete the native species and lead to their extinction. Hence, alien species cannot be controlled by natural means. These results were not expected before, which ended in the extinction of species. So, to learn about possible results of biological invasion, a species can be assessed by a mathematical model or even to know the reason of specific outcomes a mathematical model can be used [99].
However, the invasion on an island and on a continent is different due to the geographical area. Islands are smaller in sizes and alien species, if survived, can spread easily and the results can be seen more rapidly. But the case is different on continents, where there is a wider area and spreading of species and their effect can be seen in a greater time. Invasion on continents shows a spatial aspect clearly [99].

- **Distribution of Grey Squirrel in the UK.**

Another very important example of biological invasion is the Grey Squirrels in the UK which is called *Sciurus carolinensis*, scientifically. They were first introduced in 1876 by a victorian banker. The reason why they were added is not clear, but perhaps they were deemed attractive and decorative in the grounds of stately homes. Unaware of the fact that these non-native squirrels can be a threat to native red squirrels, people started to bringing more grey squirrels from America and set them free in different areas of the UK [99]. These species have since spread and colonized most of England and Wales. The grey squirrels are estimated to continue spreading in the United Kingdom at an annual rate of 7.7 kilometres (See Fig. 1.1) [120, 187]. One advantage that has favoured the spread of grey squirrels in Britain and Scotland is the absence of natural predators. With an approximated population of 2,520,000 in the United Kingdom, grey squirrels overshadow their red counterparts which is called *Sciurus vulgaris* [166]. According to the wildlife trusts the populations of red squirrels are currently estimated at approximately 140,000 [185]. The grey squirrel exists as the major threat to the endurance of the native red squirrel population. Both species of the squirrels apparently do not pose threat to each other, but grey squirrels impacted the native species negatively and lead them to extinction. Since they are larger compared to the red squirrels, they can store up to about four times more fat [39], so they have a greater chance of surviving tougher winter conditions than their red counterpart. Moreover, grey squirrels are more competitive due to their capability to produce many offsprings and survive at higher densities. The decline of the red squirrel is attributable to the presence of the grey squirrel in areas where they are introduced [21, 38, 165].
The range of grey squirrel is attributable to the decline in the population of the red squirrel. The grey squirrel has the squirrel pox virus that infects and kills the red ones [103].

Grey squirrels are more adventurous as well as happier eaters on the ground, unlike their red counterparts that spend most of their lives on coniferous trees. They spread through many routes including corridors of the landscape features such as river corridors, roads or road verges, tracks or paths and field edges [52, 172, 173, 184].

Moreover, they damaged the native flora and fauna. For the flora (plants), it has been found that grey squirrels debark trees, destroy gardens and orchids [172]. To the animals, (Fauna), they target birds’ nests for eggs and fledglings. The total economic damage of the grey squirrels in the United Kingdom is estimated to be in the millions of pounds [99].

After realizing the seriousness of the situation, measures have been taken to control the situation, such as the act of 1981 according to wildlife [185], it is not permitted to set a grey squirrel free if caught but can be destroyed humanely. Areas where the red squirrels are allowed to eradicate grey squirrels so that the reds can survive and grow. Moreover, there is another group of squirrels known as
black squirrels (the subgroup of greys) which are thought to help in the reduction of grey ones as they are strong competitors [99].

- **Invasion of Muskrat in Eastern Europe.**

  One of the well known examples of biological invasions is the muskrat *Ondatra zibethica*. They started to spread in Europe in early 20th century when a small number of these muskrats escaped the farm. Within decades they grew and spread across the whole Europe. In 1951 Skellam attempted to quantify the spread rate of muskrat and to derive mathematical approaches for modeling species [168, 162].

- **Gypsy moth (Lymantria dispar) in North America.**

  The distribution and spread of *Lymantria dispar* in North America are also one of the famous examples of biological invasion. This moth was brought by an amateur entomologist from France. It escaped in 1870 and started multiplying in Boston and soon spread all over the North-East of the USA. Its infestation harmed agriculture sector a lot and subsequently economy too. However, to stop this insect from increasing in numbers, measures were introduced in the 20th century [100].

- **Invasion of Zooplankton in the Black Sea.**

  Other classical examples from recent years is the spread of Zooplankton known scientifically as *Mnemiopsis leidyi* in the Black Sea [179]. It came to the
Black Sea accidentally by the cargo ships returning from Carribean sea region. They were released with the water ballasts in 1980 near Odessa port and in 1988 the species started to multiply fast. Within a few months this species biologically invaded the whole sea, leaving native fish in danger. It is also reported that at the time of quick spread some of the commercial species of fish were near to extinction. Examining such biological invasion and similar networks is difficult, yet there are ways which help in analyzing them [99].

- **Spread of Fallopia japonica in the UK.**

  *Fallopia japonica* known as Japanese knotweed is the example of herb invasion in the United Kingdom. Native to Eastern Asia, Japanese knotweed is a large plant perennial in nature, came to the UK as an ornamental plant due to its beauty [30, 91]. It has stems which are hollow like bamboo and can reach up to 3 to 4 meters. It has the property of colonizing waste places and roadsides. Due to its invasive root system, this plant is devastating and damages buildings, roads, concrete foundations, retaining walls, flood defences, and paving [91].

  Japanese knotweed’s root system is unique with the capacity to withstand low temperatures down to $-35^\circ C$ and spreads 7 meters horizontally and 3 meters vertically. These unique characteristics make it highly difficult to remove through excavation. Moreover, it resists the cutting as it spreads more and forms colonies when cut. Its roots and stems have a tendency to re-sprout vigorously. Japanese knotweed can easily be dispersed through water, helping it to invade and grow within new habitats. Its quick adaptation into new ecosystems makes it a threat to infrastructure and other plants [99].

- **Cordgrass (Spartina alterniflora) in the US.**

  Cordgrass is an invasive plant found on the Pacific coast of the United States, particularly in California and Washington State. This species has also become an *ecosystem engineer* due to its harmful effects on the tidal mudflats [20, 40]. It eliminates saltmarsh vegetation and native eelgrass beds. Cordgrass traps sediments and changes local hydrology by forming deep channels and high
zones. The value of marshlands and tidal mudflats is in being chief habitats for many juvenile fish and bird species, which are greatly degraded by the invasion of Cordgrass [122].

1.1.2 Invasion Stages

The biological invasion is not a simple event. Upon the introduction in a new ecosystem, the introduced species go through a number of stages before they become harmful to the native species. Even though the stages might vary from one researcher to another, there is always a point of agreement between the researchers, that there are three principal stages of invasion that an introduced species has to go through before it is able to impose environmental and economic injury. The first stage is the introduction of a specific species into another ecosystem, either purposefully or accidentally. The introduced individuals can either die, leading to the end of the scenario, or survive, adapt and begin reproduction [99]. The second stage is the survival and reproduction of introduced species, that is how it establishes itself in a new environment.
Lastly, when first two stages are achieved then the third stage comes which is the geographical spread of the new species. In this stage, species start to grow over a wider area than the place of introduction. If there is a suitable mechanism of species spatial redistribution, only then the geographical spread of alien species is possible. The biological invasion requires a mechanism of species transport. For a given type of transport, its relevance to the invasion of species depends not only on the magnitude of the typical travelled distance but also on the process of species establishment at new locations [134].

For example, repeated long-distance relocations typical for many bird species usually occur without shifting species range such as a flock of birds may fly a thousand miles for the sake of spending winters in a warmer place and each next spring it returns to exactly the same pond or forest to produce a new family. On the other hand, the daily roundabout motion of animals that occurs on a much smaller scale can end up in a steady increase in the species range and, as a result, make the invasion of species possible [134].

Further, the consequence of species invasion is different for different forms of transport. The effect of trade and tourism is expected to bring about new introductions far away from the region invaded already, while small-scale migrations and random self-motion of individuals lead to a gradual growth of the range [134]. Moreover, every biological invasion stage is unique and has its own related problems, thus needing specific modeling approaches. It is to be noted that geographical spread is not only the result of biological invasion but when species colonize or recolonize they do spread with time too. However, the mechanism can be the same for both reasons of spread and allows the researchers to study with the same modeling techniques e.g. as was done by Lubina and Levin [102]. On the whole, the biological invasion is a complicated phenomenon and consists of many different characteristics and consequences.

These are just a few examples out of many thousands of plants and animals invasions in different parts of the world. Bringing about the destruction of some native species and great biodiversity loss, biological invasion can be a very serious
threat to the native ecological communities. They frequently bring economic losses due to the damage produced by the alien pests to aquaculture, agriculture and forestry in the invaded areas [99].

At present, one of the main reasons for the loss of biodiversity all over the world is an invasion of alien species that every so often results in virtual eradication of some native species. Therefore, biological invasion usually has immense effect on the native ecological community. It often causes great damage to aquaculture in the case of marine ecosystems or agriculture, and hence it may also end in large economic failures. Even though not all the cases of biological invasion are documented equally well, it is a very common phenomenon and its occurrence has increased considerably over the last decades [134].

Since biological invasion springs from the interplay between many socioeconomic, biological and environmental factors, it is thus very important to understand this highly challenging and complex phenomenon. Some properties common in nature are thought to be true of all biological invasions despite the wide range of invaded ecosystems and possibly even wider range of traits of alien species [99].

1.2 Mathematical models: an overview

There is abundant experimental and observational information available about invasive species, including an extensive range of models that are potentially useful for characterising biological invasion. Yet the tools and methods commonly applied in ecology, for example field data, are insufficient for a complete analysis of biological invasions. Whilst traditional ecology methods do generate interesting results and significant conclusions, there is no experimental repeatability, which is key in scientific studies. Analysing the data collected from particular studies results in hypothesis formation.

Hypotheses need to be verified and validated, which is achieved by experimenting under controlled conditions. Consequently, invasion ecology is ill suited to hypothesis testing. To do so would demand that a species that is potentially or
already a confirmed dangerous pest, be released. Whilst difficult to predict, the probable corollary of releasing such a species is harm to biodiversity and the environment. Adverse effects could even extend to the well-being of humans, which would make the research contentious and a challenge to defend. The greatest challenge, however, is presented by the natural changes in the environment; controlling the conditions is unfeasible. For example, how would researchers be able to recreate the same weather pattern repeatedly?

In theoretical ecology, mathematical modelling is for sure a powerful research tool that can be helpful by creating a virtual environment. However, not all models are the same, varying in accordance with the mathematics employed and the study’s aim. The data derived from the models can supplement field data to arrive at results that are more comprehensive.

Population dynamics is one of ecology’s most interesting topics, not least because populations of biological species are in a constant state of flux; as individuals are born then die, populations change over time. The assumption of the simplest population models is spatial homogeneity, which result in non-spatial models with population density as function of time but not of space. The use of continuous- or discrete-time models is determined by whether or not the populations have overlapping generations. Continuous-time models are used in this thesis, thus ordinary differential equations, which give a relevant framework [89, 116].

\[
\frac{du_i}{dt} = F_i(u) \quad i = 1, 2, \ldots, n
\]

Where \( u_i \) is the population density of the \( i \)th species at time \( t \), \( n \) is the number of species and functions, and \( F_i \) describes population changes due to births and deaths.

A continuous-time single-species model is represented by \( n = 1 \). This important model, defined as the dynamics of the continuous single-species population model, is the rate of population growth and is a function of the population density
Chapter 1 Introduction

This model has be described by several authors, i.e. Petrovskii and Li, [134],

\[
\frac{du}{dt} = F(u) = uf(u)
\]  

where \( f(u) \) is the per capita growth rate that can also depend on the population density. Here the right-hand side is assumed to take into account both population multiplication and natural mortality.

It is the factors influencing population growth, of function \( F \) that determines the properties of the model. Population models have a long history, with one of the earliest being the one introduced by Malthus in 1798, which supposed a density independent form of \( f(u) = F(u)/u = \alpha = \) constant resulting in unbounded, exponential growth for a positive value of the constant, \( \alpha > 0 \). Except over relatively short time frames when exponential growth can occur, it is improbable for any \( t \), for real population growth to approach an exponential. As a consequence of increasing population density, there are fewer life-supporting resources available to individuals. Ultimately, the scarcity of resources leads to an increase the mortality rate and a decrease in birth rate. Therefore, the effect of populations becoming dense is that the growth rate slows and potentially goes into reverse.

Mathematical expression of this phenomenon says that where \( u \) is large, \( f(u) \) should be negative. Thus, Eq. (1.2) must have a positive steady state, which is represented by \( K \), i.e., \( f(K) = 0 \). Furthermore, this is a stable steady state, as the argument above indicates, \( f(u) < 0 \) for \( u > K \) and \( f(u) > 0 \) for a range of values \( u < K \). The steady state of the population density \( K \), can be referred to as the carrying capacity of the environment to support the given population, for convenience, it is usually called just 'carrying capacity' [116].

The simplest choice of function \( f \) that meets the requirements above allowing for intraspecific competition, specifically \( f(u) = \alpha (1 - \frac{u}{K}) \) of Eq. (1.2), results in the logistic growth model.

\[
\frac{du}{dt} = \alpha u \left(1 - \frac{u}{K}\right).
\]  

(1.3)
The maximum per capita growth rate occurs at $u = 0$ and decreases monotonically for $u > 0$. Eq. (1.3) has been valuable in theoretical population dynamics, as it is the simplest-possible model for presenting realistic population.

Yes, there is no reason why the per capita growth $f(u)$ should exactly have a linear function. As an alternative, a rather more general explanation of the populace growth in the single-species model can be considered:

$$F(u) > 0 \text{ for } 0 < u < K, \quad F(u) < 0 \text{ for } u > K,$$

(1.4)

$$F'(0) = \alpha > 0, \quad F'(u) < \alpha \text{ for } u > 0.$$  

(1.5)

Function $F$, satisfying conditions in Eqs. (1.4-1.5) is called a "generalised logistic growth". In the logistic growth model there is a monotonous decline in the per capita growth rate; yet this does not always hold true, as demonstrated by numerous populations experiencing reductions in the per capita growth rate when the population density is low (Allee effect). Furthermore, when the densities are especially low, the per capita growth can become negative. This gives rise to the somewhat general description of the growth function $F(u)$, which in the case of the strong Allee effect can appear as Fig. 1.6.
In general, it is not correct to assume that the per capita growth rate is a monotonically decreasing function of the population density. An alternative form of density-dependence occurs when the maximum per capita growth rate is achieved for a particular intermediate density (see Fig. 1.4). This shift is the Allee effect; Allee dynamics describes the associated population dynamics [6, 22, 24, 32, 34, 43, 44, 74, 80, 97, 136, 171].

When population growth becomes negative for small population densities, theoretical studies tend to distinguish between the "weak" Allee effect (see Fig. 1.5), and the "strong" Allee effect (see Fig. 1.6). A several description of the growth function $F(u)$ in the case of the strong Allee effect is given follows:

$$F(u) < 0 \text{ for } 0 < u < \beta, \text{ and } u > K, \quad (1.6)$$

$$F(u) > 0 \text{ for } \beta < u < K, \quad (1.7)$$

Here, parameter $\beta$ corresponds to a particular threshold population density and an unstable equilibrium. Model (1.6-1.7) is often parametrized as a cubic polynomial [97, 43]. For further details, see Chapter 2.

$$\frac{du}{dt} = \alpha u \left(1 - \frac{u}{K}\right)(u - \beta) \quad (1.8)$$

Figure 1.5: Sketch of the growth function $F(u)$ in case of the weak Allee effect
In this model, when $0 < \beta < K$ the Allee effect is strong, and weak when $-K < \beta < 0$ The Allee effect is absent when $\beta < -K$.

Ecosystems typically include multiple, interacting species. As such, the general model in Eq. (1.1) has $n > 1$. A two-species system is inevitably the next level of complexity and the dynamics of such a system can be described by two coupled ODEs:

$$\frac{du}{dt} = P(u, v), \quad \frac{dv}{dt} = Q(u, v)$$

(1.9)

in which $P$ and $Q$ represent the respective growth rates of species $u$ and $v$.

A range of biological situations is described by model (1.9). Interspecies interactions can easily be categorised in terms of the functional properties of $P$ and $Q$:

$$\frac{du}{dt} < 0, \quad \frac{dv}{dt} < 0$$

(1.10)

$$\frac{du}{dt} > 0, \quad \frac{dv}{dt} > 0$$

(1.11)

$$\frac{du}{dt} < 0, \quad \frac{dv}{dt} > 0$$

(1.12)

It is worth noting here that when the conditions in (1.12) are met, they always describe predator-prey interactions; yet these interactions may exhibit complex
density-dependence relationships. See Chapter 4 for further detail.

Furthermore, as a new species is introduced into an environment, it starts to establish itself. At this point, the key biological invasion issue is that of survival. Will the population rapidly become extinct after introduction because of a fundamental incompatibility with the new environment? Or will the population density increase over time?

It may be assumed that the outcome is determined by the introduced species' population size. Theoretically, just a single mating pair of animals or seed can instigate successful biological invasion. Examples of well-documented, successful invasions include muskrats (*Ondatra zibethicus*) in central Europe [168] and the Japanese beetle (*Popillia japonica*) in northeast USA [51]. These early twentieth century invasions are reported to have arisen from only a few animals being released. Intuitively, more members in large populations of any given species are more likely to survive when the population is large than when it is small. The Allee effect presents a challenge to small populations becoming successfully established.

Usually, alien species start to spread once it has become established at its introductory location. A model is required to explore the theoretical spread of the species. The most straightforward model is the one-dimensional equation with linear growth and diffusion.

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + \alpha u$$

where $\alpha$ is the linear growth rate and $D$ is the diffusion coefficient, and $0 < x < L$ where $L$ is the domain length.

Consequently, the population goes extinct if $L < L_{Cr}$, where $L_{Cr} = \pi \sqrt{\frac{D}{\alpha}}$, and it grows boundlessly if $L > L_{Cr}$. Yet, unlimited growth is an artefact of the Malthusian model. It would not occur in reality; instead, the population growth would follow the dynamics outlined earlier.

The population spread can be modelled by the reaction-diffusion equation
with nonlinear growth. Reaction-diffusion models that have nonlinear dynamics are often have travelling wave solution.

Established on a mathematical framework of reaction-diffusion equations, the reaction-diffusion model was introduced eighty years ago in the seminal work by Fisher and Kolmogorov [58, 87], supplemented by Skellam and Turing [168, 176]. The model demonstrated its effectiveness in studying population dynamics and general mathematical biology (See [23, 67, 72, 106, 162, 181]). In recent times, there has been increased interest in spatially explicit reaction-diffusion equations, which have been used as the basis for mathematical models of biological invasions [119].

This model, in particular, gave rise to the idea of a self-organised travelling population front, which is fundamental to the theory of biological invasions; it has been a template for spread pattern of invasive species for many years.

Many invasions have illustrated the dynamic feature of spread at a constant speed [102, 162, 168]. These observations strengthen the role of the reaction-diffusion model as an adequate means to describe invasive species spread. The reaction-diffusion equation in an unbounded one-dimensional space is,

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + F(u), \quad (1.14)$$

where $D$ is the diffusion coefficient and $F(u)$ is the per capita growth rate.

There is good agreement between empirical invasion studied empirically, and the ecologically relevant models such as that which predicts travelling wave solution [134, 162, 181]. How fast will the invasive species progress? This is the basic question applicable to all biological invasions. Another question is: To what extent can mathematical models predict the progress of invasive species? When the Allee effect is not present [58, 168, 87], travelling fronts spread at an asymptotic rate of spread equal to

$$C^* = 2 \sqrt{F'(0) D} \quad (1.15)$$
On the other hand, when the Allee effect is included, the speed of invasion is reduced [97].

Eq. (1.14) can be readily extended to the case of several interacting species

\[
\frac{\partial u_i}{\partial t} = D_i \frac{\partial^2 u_i}{\partial x^2} + F_i(u_1, u_2, ..., u_m), \quad i = 1, 2, ..., m, \quad (1.16)
\]

where \(D_i\) is the diffusion coefficient and \(F_i(u)\) is growth rate function for species \(i\). Consequently, a community of two interacting species with population densities \(u_1\) and \(u_2\) and growth functions \(F_1\) and \(F_2\), respectively, can be described by two coupled PDEs:

\[
\frac{\partial u_1(x, t)}{\partial t} = D_1 \left( \frac{\partial^2 u_1}{\partial x^2} + \frac{\partial^2 u_1}{\partial y^2} \right) + F_1(u_1, u_2), \quad (1.17)
\]

\[
\frac{\partial u_2(x, t)}{\partial t} = D_2 \left( \frac{\partial^2 u_2}{\partial x^2} + \frac{\partial^2 u_2}{\partial y^2} \right) + F_2(u_1, u_2). \quad (1.18)
\]

In reality, species spread normally takes place in two dimensions, To make the models (1.17-1.18) closer to reality, we will consider the system below:

\[
\frac{\partial u_1(x, y, t)}{\partial t} = D_1 \left( \frac{\partial^2 u_1}{\partial x^2} + \frac{\partial^2 u_1}{\partial y^2} \right) + F_1(u_1, u_2), \quad (1.19)
\]

\[
\frac{\partial u_2(x, y, t)}{\partial t} = D_2 \left( \frac{\partial^2 u_2}{\partial x^2} + \frac{\partial^2 u_2}{\partial y^2} \right) + F_2(u_1, u_2). \quad (1.20)
\]

For unspecified function \(F_1\) and \(F_2\), Eqs. (1.19-1.20) can describe many different systems with different properties. In this work, we are mostly interested in a prey predator system. The relevant parametrization of functions \(F_1\) and \(F_2\) will be discussed in Chapter 4.

Understanding the mechanisms of interacting species are not always easy and different cases can be linked to the effect of different factors. For instance, in a realistic 2D system, a standard invasion scenario is where the front separates the invaded area behind the front from the uninvaded areas in front of the front. A completely different scenario is called "patchy invasion" where the spread takes place via the spatial dynamics of separate patches of high population density with a very low density between them, and a continuous population front does not exist...
at any time (see Fig. 1.7). Patchy invasion has been studied theoretically in much
detail using diffusion-reaction models, e.g. see Chapter 12 in [106].

![Figure 1.7: Scenario of patchy invasion](image)

Reaction-diffusion models have been used with success for a broad range of
taxa [7, 162, 168]. However, whilst diffusion models are able to portray the basic
concept of range expansion, the combination of dispersal and population growth
has led to criticisms of the models unnecessarily complicating animal movement
[167, 175].

Another assumption of reaction-diffusion equations is that animals move
isotropically. That is, all individuals move in all directions at equal speeds and do
not exhibit preferences for directions. Yet, clearly, this is not the case in reality.

The scope of interest of biological invasion models is not limited to pre-
dicting the rate at which invasive species spread. The spatiotemporal patterns
that are detected in natural populations are the main feature of biological inva-
sions [27]. Whilst the mechanisms that support pattern formations have yet to
be fully elucidated, hypotheses have been proposed. For example, examples of spatial patterns in reaction-diffusion systems have been attributed to Turing and diffusive-like instabilities [155, 176]. Although there are some ecological examples to hand, Turing type patterns attract controversy due to their spatially periodic tendencies [86].

Moreover, observed first by Dunbar in 1983 [48] as damped regular oscillations, spatiotemporal patterns may appear in the wake of travelling fronts in the diffusive Lotka-Volterra system. Later research found that emerging chaotic patterns could arise from the propagating travelling fronts [127, 158, 159, 161].

Where population growth is damped by the strong Allee effect, qualitatively similar dynamics of patchy distribution have been detected in reaction-diffusion systems [114, 127, 136]. This will be the focus of Chapter 4.

1.3 Thesis outline

This work investigate the effect of fragmented and complex habitats on population dynamics within the introduced framework of partial differential equations.

This thesis is organized as follows. Chapter 1 gives a general background on biological invasion with brief introduction for the mathematical modelling of invasion.

Chapter 2 explores the ways in which population dynamics are affected by the shape and size of fragmented habitats. We show that both domain size and shape have crucial effect on population survival.

Chapter 3 continues the study of complex shaped effects. We have shown that population might survive and even spread in a complex habitat that already has an extinction effect on the population, by applying patch with better environmental conditions (a stepping stone) inside the domain subject to different factors (patch size, Allee effect strength and patch location).

In Chapter 4, we have introduced the spatiotemporal dynamics of an alien species affected by a predator in a domain where two large uniform habitats are
Chapter 1 Introduction

connected by a narrow corridor. Mathematically, our system consists of two coupled reaction-diffusion equations. The results indicate that the corridor tends to slow down the spread and it shows the effect of narrow corridor with simple analytical estimates for the critical width of the corridor. Finally, we show how the corridor may become a source of a secondary invasion.

Chapter 5 deals with the critical domain problem for the reaction-telegraph equation model of population dynamics. For the linear problem, the expression for the critical domain size is obtained analytically. The non linear problem (with logistic growth and strong Allee effect) is studied in numerical simulations.

Chapter 6 gives conclusions of the work done and possible future work.
Chapter 2

The effect of size and shape on population persistence in fragmented habitats

2.1 Introduction

Due to ill-planned human action and unsustainable exploitation of resources, fragmentation of ecological habitats is becoming more common and has become a process that can negatively affect the survival rates of many species [54, 68, 140, 152]. Consequently, for the past two decades, the study of population dynamics with regards to fragmented habitats has become an issue of considerable importance for conservationists and other parties interested in certain species survival [29, 54]. The ecological effects of fragmentation have received increasing attention in many recent studies focused on the issue of habitat fragmentation and related aspects (e.g., formation of habitat boundary ecosystem) [54, 57, 140, 145]. Mathematical models confirming that small and fragmented populations are more likely to go extinct have been developed and used as a result thereof [43, 65, 66, 93, 94, 144].

The effects of the fragmentation processes on habitats can be observed in two ways: either in the short-term (including modifications of habitat shapes,
changes in population sizes, and the emerging structures at the edges of the fragments) or in the long-term (including population genetic transformations and extinction of species that have either low growth rate or complex life cycles) [17]. Furthermore, fragmentation can have either a direct or indirect impact on different types of plant and animal species. Generally speaking, plants and animals react in one of three ways to habitat fragmentation: i) they can respond positively (e.g. by an increase in the population size of pioneer species of plants, modifications in species composition, and changes in distribution and biotic interactions); ii) negatively (such as by experiencing a decrease in the population size, as it happens for many species), or neutrally (meaning that fragmentation has no observable effect on them). This latter example can be seen in the case of the fragmentation of the habitat of Los Tuxtlas, Mexico, where a continuous forest covering $1000\text{km}^2$ showed no difference in the population size of a particular plant species both prior to and after fragmentation [17]. As a rule, the effect of habitat fragmentation is felt strongest by plant species, especially those whose seeds are disseminated by animals.

In the ecosystems science, a major area of study has been the effect of fragmentation on population dynamics. A wide range of effects has been discovered, revealing the influence of various factors including (1) fragment size, (2) edge effects, (3) fragment shape, (4) isolation, and (5) the characteristics of the environment “matrix” surrounding the fragments (e.g. native vegetation type such as deforested areas, cattle pasture, agricultural crops, urban areas, etc.) [17, 29, 31, 53, 54]. However, the dynamics have in some cases proven difficult for biologists to study and evaluate, for various reasons including (1) the response time of populations to fragmentation, (2) the biogeographical position of the species under study, and (3) synergism between different processes (e.g., between fragmentation and harvesting, or fragmentation and climatic change). For these reasons, mathematical modelling is used extensively. In this Chapter, we use mathematical modelling and simulation to study the effects of fragmentation on population dynamics as a function of (1) edge effects, (2) fragment size, and (3) fragment shape.
**Edge Effects.** One important outcome of habitat fragmentation is the emergence of the habitat edges. Ewers and Didham [53] explained this by referring to those sections of a fragment that have been modified by outside agents and, therefore, implicitly experienced edge effects. These effects manifest themselves in the manner in which two neighbouring ecosystems interact through the common boundary [57]. As noted by Ewers and Didham [53], habitat fragmentation increases the chances of changes to occur. This is seen most prominently closer to the edge. Habitat edges play a key role not only in regulating the flow of organisms but also in permitting the invasion of external influences, such as fire and non-native species. Closeness to the fragment edge has an impact on the persistence and survival of animal and plant species as well as on their interactions. The survival and persistence of animal and plant species and their subsequent interactions are also influenced when they are nearer to the fragment edge [17].

**Fragment Size.** Fragment size has been identified by numerous researchers as the most important spatial feature that has a significant effect on the biodiversity in a fragmented landscape [29, 53, 92]. Expansive areas are generally good for the survival and proliferation of plants and animals. As a result thereof, the extent to which a species is susceptible to potential extinction increases with a decrease in the fragment size.

**Fragment Shape.** Ecological interactions are known to go differently in areas adjacent to the habitat border than in the core areas [31, 95]. On the other hand, for a given area of the habitat, domains of complex shape tend to have longer boundary and/or smaller core areas. One can conjecture that the population dynamics (in particular, the likelihood of population survival) should dependent on the habitat shape. Indeed, the connection between the shape of the fragment and the richness of the population species living therein was noticed in some earlier work [115], although the measures to determine the importance of the shape of the fragment remained largely speculative.

In order to predict the changes in population dynamics or community structure resulting from a change in landscape structure, it is necessary to understand
the interrelationship between the essential components [49]. The interplay between the fragment size and fragment shape has a decisive influence on the area of a habitat fragment that is likely to feel the impact of the edge effects [53]. Moreover, as was mentioned above, whether animal and plant species will survive or not is often determined by the proximity to fragment edges [17]. On the other hand, it was also observed that, under certain circumstances, plant and animal populations may be favourably influenced by habitat fragments of large size and with an irregular shape [17]. This favourable influence of complex shapes on species of plants and animals may be explained by the fact that, compared to more compact fragments, they permit colonisation by different populations with greater frequency. Ewers and Didham [53] clarified that intensified colonisation is made possible because of the larger total edge length possessed by the fragments with a complex shape.

To gain an understanding of this influence, different fragment shapes will be analysed, with a particular focus on the existence of critical patch size effects, taking into account three different normalisations of the population growth rates [97]. Since the critical patch size of a population is the minimum size of habitat necessary for population persistence, its estimation is clearly crucial for understanding population dynamics. The earliest investigation of critical patch size was performed by Skellam [168] and Kierstead & Slobodkin [84]. They derived the critical size for continuous-time models displaying exponential growth and simple diffusion, i.e., for the following equation:

\[
\frac{\partial u}{\partial t} = D \nabla^2 u + \alpha u,
\]

(2.1)

where \(\alpha\) is the linear growth rate and \(D\) is the coefficient of diffusion. Having considered Eq. (2.1) in a one-dimensional habitat with length \(L\), they obtained the following formula:

\[
L_{Sr} = \pi \sqrt{\frac{D}{\alpha}}.
\]

(2.2)

The species survives if \(L > L_{Sr}\), but will be at risk of becoming extinct if \(L < L_{Sr}\).
In the case of a two-dimensional square domain \( L \times L \), the condition of population survival is given by:

\[
L > L_{Sr} = \pi \sqrt{\frac{2D}{\alpha}},
\]

Formula (2.3) is easy to derive (by considering the eigenvalues of the problem) and it is apparently far too simple in the context of real landscapes. A shape of greater complexity is likely to be more realistic. Based on this observation, the following point can be deduced: the variety of shapes manifested by different habitats can result in wide variations in critical patch size and, consequently, wide variations in the efficiency of population survival.

In this study we will analyse three fragment shapes, namely, H-shaped, cross-shaped and square. A numerical solution of the two-dimensional reaction-diffusion equation (taking the Allee effect into account) will be employed to analyse the critical sizes of these habitat shapes for a single species. We will discuss (a) possible explanations for the critical habitat sizes of these shapes using different normalisations of the population growth rates, and (b) the effect of shape complexity in determining whether a population persists or goes extinct.

### 2.2 Mathematical Model

Our model is given by the following reaction-diffusion equation [50, 89, 116, 134, 181]:

\[
\frac{\partial u}{\partial t} = D\nabla^2 u + F(u),
\]

where \( u \) is the population density, \( D \) is the diffusion coefficient, \( \nabla^2 \) is the Laplacian defined as \( \frac{\partial^2}{\partial x^2} \) for the one-dimensional (1D) case and \( \left[ \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2} \right] \) for the two-dimensional (2D) case, and \( F(u) \) is the population growth rate.

Assuming that the growth rate is dampened by the Allee effect [97, 128] (as indeed is often the case [43, 34]), the per capita growth rate is dome-shaped and hence can be approximated with a square polynomial, which results in the
cubic-polynomial expression for the growth rate $F$:

$$F(u) = \gamma u (1 - u) (u - \beta),$$  \hspace{1cm} (2.5)

where $\gamma$ is a coefficient which can be regarded as the characteristic growth rate. Note that the carrying capacity $K = 1$. Parameter $\beta$ is known as the Allee threshold or threshold density and can be used to estimate how strong the Allee effect is. The Allee effect is considered weak when $-1 < \beta < 0$ and is considered strong when $0 < \beta$ [97]. Here the values $0.5 < \beta < 1$ are sensible but not interesting because for these values a sufficiently large perturbation of the upper steady state $u = 1$ would normally lead to the population extinction in the spatial system (2.4) (for more details see [99, p. 72]).

Note that every different choice of parameters $\gamma$ and $\beta$ corresponds, generally speaking, to a different population. In order to study the effect of habitat’s size and shape on different populations, one should be able to compare those different populations in a sensible way. Sensible comparison between two populations defined by two arbitrary parameter pairs, say $(\gamma_1, \beta_1)$ and $(\gamma_2, \beta_2)$ is difficult, if at all possible. Indeed, different $\gamma$ and $\beta$ result in the growth rate of a different shape, and so what? In order to resolve this generic difficulty, Lewis & Kareiva [97] suggested to fix a certain feature of the population growth so that variation of the parameters would leave it unchanged. (For instance, such a feature can be the maximum growth, i.e. the maximum value of function $F(u)$ for $0 < u < 1$.) Introducing this constraint would introduce a relation between $\gamma$ and $\beta$, hence rendering only one of them being independent (say, $\beta$) and the other one becoming its function, say $\gamma(\beta)$. Following [97], we therefore consider three different options:

1. The simplest constraint is to assume that $\gamma$ always has a fixed value:

$$\gamma = \text{constant.}$$  \hspace{1cm} (2.6)

For the sake of simplicity, below we consider $\gamma = 1$. 
2. In the case that the growth rate \( F(u) \) as given by Eq. (2.5) is constrained to attain a fixed maximum value of 1, then it is readily seen that

\[
F_{\text{max}} = \frac{\gamma}{27} \left[ 2(\beta^2 - \beta + 1)^{\frac{3}{2}} + 2\beta^3 - 3\beta^2 - 3\beta + 2 \right] = 1
\]

(can be derived from \( F'(u^*) = 0 \) and \( F(u^*) = F_{\text{max}} \)), from which follows:

\[
\gamma = \frac{27}{2} \left[ 2((1 + \beta)^2 - 9\beta/2)(1 + \beta) + ((1 + \beta)^2 - 3\beta)^{\frac{3}{2}} \right]. \tag{2.7}
\]

3. In the case the maximum per capita growth rate is assumed to have a constant value of 1, then is:

\[
f_{\text{max}} = \frac{\gamma}{4} (1 - \beta)^2 = 1
\]

(which can be derived from \( F(u)/u_{\text{max}} = 1 \)), from which follows:

\[
\gamma = \frac{4}{(1 - \beta)^2}. \tag{2.8}
\]

In the next section, in order to reveal the effect of the size and shape, the 2D dynamics of the spatial system (2.4) will be considered in the domain of three different shapes (H-shaped, cross-shaped, and a simple square) subject to the different constraints (2.6-2.8).

### 2.3 Results of computer simulations

In this Section, we will present the results of the numerical simulations. Eq. (2.4) is solved numerically by finite differences using the explicit scheme. The values of the grid steps \( \delta x \) and \( \delta t \) are chosen to be sufficiently small in order to avoid numerical artifacts. Furthermore, before proceeding to the numerical simulations, the equations are required to be supplemented with boundary and initial conditions. At the boundary \( \Gamma \) of the domain, we use the ‘zero-function’ Dirichlet condition, i.e. \( u(\mathbf{r}, t) = 0 \) for \( \mathbf{r} \in \Gamma \). For the initial values, we use \( u(x, y, 0) = u_0 = \text{constant} \) in
the interior of the domain. The growth rate was chosen in line with Eqs. (2.6-2.8). The diffusivity is fixed as $D = 1$.

We first consider a special case where the growth rate is linear, i.e. where the dynamics is described by Eq. (2.1). For the square-shaped domain, the critical size is given by Eq. (2.3). As the next level of geometrical complexity, we consider Eq. (2.1) in a cross shaped domain (see Fig. 2.1) which is obtained from the square-shaped $L \times L$ domain by removing equal $l \times l$ squares from its every corner (where, obviously, $0 < l < 0.5L$). Numerical simulations show that there indeed exists the critical size that tends to decrease with the increase in the growth rate $\alpha$; see Figs. 2.2 and 2.3.

![Figure 2.1: A sketch of the solution of the reaction-diffusion equation in the 2D cross-shaped domain.](image)

We then consider the specific question whether it may be possible to match the critical size of the cross-shaped domain with that of the square where the results are known; see Eq. (2.3). Intuitively, the matching factor should take into account the area removed at the corners of the original square, which leads to the following heuristic relation between the critical size of the cross-shaped domain and that of the square:

$$L_{Cr} = L_{Sr} \left[ 1 - 4\zeta^2 \right],$$

(2.9)

where $L_{Sr}$ is the critical size of the square (as is given by Eq. (2.3)), $L_{Cr}$ represents the critical size of the cross-shaped domain and $\zeta = l/L$, so that $0 < \zeta < 0.5$. The simple formula (2.9) gives very good result when $\zeta$ is not large; (see Fig. 2.2). The
agreement is becoming somewhat worse when $\zeta$ approaches its maximum possible value 0.5. We mention here that the matching relation (2.9) can be made more accurate by introducing the correcting term, say $\rho(\zeta)$:

$$L_{Cr} = L_{Sr} \left[ \frac{1}{1 - 4\zeta^2} + \rho(\zeta) \right]. \quad (2.10)$$

In particular, we have found that the following choice of function $\rho(\zeta)$:

$$\rho(\zeta) = -584\zeta (-0.5 + \zeta) \left( -0.004 + 0.074\zeta - 0.528\zeta^2 + \zeta^3 \right), \quad (2.11)$$

makes the matching relation (2.10) almost precise; (see Fig. 2.3). The correcting term in (2.11) appears as a result of fitting the computational data with polynomial.

The linear population growth considered above, although providing a good approximation in case the population density is not large and there is no strong Allee effect, is not realistic if considered in a more general case. We therefore proceed now to a more general model (2.4) with the growth rate given by (2.5) with one of the scaling relations (2.6-2.8). In this case, there is no analytical solution to the critical size problem and the system is studied through extensive numerical simulations. The results obtained for the two different shapes (i.e. square and
Chapter 2 *The effect of habitat’s size and shape on populations*

![Graph showing the effect of habitat size and shape on population growth](image)

**Figure 2.3:** Critical size of cross-shaped domain obtained at different values of linear growth rate $\alpha$. The solid curves show the critical size as given by the numerical simulations and the dashed-and-dotted curves show the critical size as given by Eqs. (2.10-2.11) for (1) $\zeta = 0.1$, (2) $\zeta = 0.2$, (3) $\zeta = 0.3$ and (4) $\zeta = 0.4$.

The domain $L$ and the three different choices for $\gamma(\beta)$ are shown in Figs. 2.4-2.6. The critical relation between $L$ and $\beta$ is shown by the solid curve (obtained numerically); the parameters from above the curve correspond to population survival, the parameters from below the curve correspond to population extinction. We therefore observe that the general system (2.4-2.5) exhibits essentially the same tendency with regard to the domain shape as the linear system (2.1): for the same value of $L$ and $\beta$, the critical size of the cross-shaped domain is always larger than the critical size of the square-shaped domain. This clearly manifests the importance of the domain shape for population survival. We also observe that the critical size tends to increase with an increase in the strength of the Allee effect (quantified by parameter $\beta$). Interestingly, the rate of increase appears to depend on the choice of the scaling relation for $\gamma$. In particular, when $\gamma$ is scaled as (2.8) (i.e. to keep the same value of the maximum per capita growth), the critical size is approximately constant for $\beta < 0$ where the Allee effect is weak.

In order to further reveal the effects of the domain geometry on the population dynamics, now we are going to consider the domain of a different shape. For convenience, we refer to it as the ‘H-shaped’ domain; (see Fig. 2.7). There are therefore two large sub-domains (Habitat 1 and Habitat 2) and the narrow passage connecting them. Our choice of this shape is motivated by the biological...
Figure 2.4: The structure of the parameter plane $(\beta, L)$. The parameters from above the solid curve correspond to population survival and the parameters from below the curve correspond to extinction. The population growth rate is scaled according to Eq. (2.6). (a) Square shaped domain, (b) cross-shaped domain with $(l/L = 0.3)$.

Figure 2.5: The structure of the parameter plane $(\beta, L)$, obtained when the population growth rate is scaled according to Eq. (2.7). (a) Square shaped domain, (b) cross-shaped domain with $(l/L = 0.3)$.

Figure 2.6: The structure of the parameter plane $(\beta, L)$, obtained when the population growth rate is scaled according to Eq. (2.8). (a) Square shaped domain, (b) cross-shaped domain with $(l/L = 0.3)$. 
observations pointing out at the importance of corridors for the population dynamics [17]. We will consider the overall size of the domain to be large enough \((L = 100)\), so that the size of Habitats 1 and 2 are overcritical; hence, the population would not be endangered in either of them. Our aim is to reveal the effect of the passage. We choose the initial conditions differently from the above, namely \(u_0 = 1\) in Habitat 1 and \(u_0 = 0\) in the rest of the domain, i.e. in Habitat 2 and the passage. As before, the Dirichlet boundary conditions \(u(r, t) = 0\) are used at the domain boundary. Our primary interest here is to reveal how the parameters of the passage, i.e. its length and width, can affect the population spread from Habitat 1 to Habitat 2.

\[ u_0 = 1 \text{ in Habitat 1 and } u_0 = 0 \text{ in the rest of the domain, i.e. in Habitat 2 and the passage.} \]

\[ D = 1 \text{ and } \beta = 0.1, \text{ and } \gamma(\beta) \text{ is given by Eq. (2.6).} \]

**Figure 2.7:** A sketch of the solution of the 2D reaction-diffusion equation affected by the domain shape, in particular, by the parameters (i.e. width and length) of the passage between the two large sub-domains.

**Figure 2.8:** The simulation results showing the spread of the population to Habitat 2 in case of (a) shorter passage with (length, width)=\((4.6, 7)\) and (b) population blocking for a longer passage with (length, width)=\((5, 7)\). Other parameters are \(D = 1\) and \(\beta = 0.1\), and \(\gamma(\beta)\) is given by Eq. (2.6).
Figure 2.8 shows some typical simulation results. Having fixed the passage width as 7, we observe that the population spills over to habitat 2 for the passage length 4.6 but is blocked by the passage when its length is equal to 5. The existence of the critical passage length is thus demonstrated. Intuitively, we can therefore expect that the population is going to be blocked for a sufficiently narrow or sufficiently long passage but could spill over to Habitat 2 otherwise. This expectation is generally confirmed by our simulation results; see Fig. 2.9.

Additionally, we observe that there exists a critical value \( w_{cr} \) of the passage width, \( w_{cr} \approx 7.8 \), \( w_{cr} \approx 3.0 \) and \( w_{cr} \approx 3.6 \) for Fig. 2.9a, b and c, respectively. In case the width is larger than \( w_{cr} \), the population cannot be blocked whatever is the length of the passage. Note that the critical width appears to be about 2.5 times larger.

Figure 2.9: Parameter plane (width, length) of the H-shaped domain obtained for \( D = 1 \) and \( \beta = 0.1 \) (see Fig 2.7). The solid curve shows the critical relationship between the width and length of the passage. For the parameters from below the line, the population invades through the passage. For the parameters from above the line, the passage is blocked. Here (a), (b) and (c) correspond to the the population growth rate \( \gamma \) scaled according to Eq. (2.6), Eq. (2.7), and Eq. (2.8), respectively.
2.4 Discussion and concluding remarks

In this Chapter, we have considered the effect of the domain size and shape on the population dynamics, in particular, on the population survival in case the overall size of the habitat is small. We have addressed this problem theoretically using the single species model described by a scalar reaction-diffusion equation. Relevant properties of the solution such as either $u(r,t) \to 0$ for $t \to \infty$ uniformly over the domain (extinction) or otherwise (survival) were revealed in extensive computer simulations with various domain shapes and sizes, the strength of the Allee effect and different scaling (parametrisation) of the growth rate. Having analyzed the simulation results in the special case of the linear growth rate, we found a simple formula to match the critical size of the cross-shaped domain to that of the square, thus making the corresponding problem analytically tractable.

Having considered three different parametrisations for the population growth rate $\gamma$, see Eqs. (2.6-2.8), we have found that the features of the critical size dependence on the strength of the Allee effect are sensitive to the way how different populations are compared. In particular, in the square-shaped domain, in the range $-1 < \beta < 0$ (i.e. when the Allee effect is weak) the critical size increases almost linearly in case of parametrisation (2.7) but remains approximately constant in case of parametrisation (2.8).

As was previously discussed, both the size and shape of the habitat have a significant influence on the population dynamics, in particular on its survival. We have shown that, although the size of the domain is important, in reality it is actually the interplay between the size and shape of a given domain that determines the survival of its population. One important finding of our study is that the critical size of the cross-shaped domain is always larger than the corresponding critical size of the square-shaped domain. It suggests that the likelihood of the population survival is higher in fragmented habitats of simple shapes. This conclusion agrees
well with the empirical observation that the probability of population persistence in fragments with complex shapes can sometimes be reduced [19, 85]. Similarly, the fraction of the habitat area that is affected by the edge effects is known to be determined by the connection between the shape and the size of the habitat [17]. Thus, our study provides a relevant theoretical framework for the interpretation of empirical observations on the population dynamics on fragmented habitats that can be used in further studies on this important research topic.
Chapter 3

Effect of complex landscape geometry on the invasive species spread: invasion with stepping stones

3.1 Introduction

Invasive species are known to be a major problem in ecology, resulting in significant biodiversity loss worldwide [47, 150] and causing serious problems for agriculture, forestry and fishery worth billions of dollars annually [81, 137]. For these reasons, biological invasion has been a major focus of intense empirical and theoretical research for several decades [51, 142, 186] with the number of papers growing with time nearly exponentially [143]. In particular, a variety of invasion scenarios have been identified [73, 74, 136, 162], and considerable progress has been made in understanding how various factors can affect the rate and pattern of species spread into space [99]. Having said that, due to the high complexity of the phenomenon (cf. [149]), many questions remain open and many issues are lacking clarity [35].

Factors affecting the spread, as well as appropriate models and tools to study the invasive species spread, depend on the spatial and temporal scales at
which the phenomenon is considered. In particular, this bears upon the role of the environmental heterogeneity. Much of the theoretical research has been concerned with invasive spread occurring either in large spatially-uniform areas or in an environment with a small-scale heterogeneity (e.g. in the form of environmental noise). Relevant modelling frameworks are given by reaction-diffusion equations [72, 97, 121, 134, 162, 168, 181], stochastic models [96, 98] including stochastic reaction-diffusion equations [60, 101, 178], and integral-difference equations [88, 90, 118].

Whichever particular model is used to study the invasive spread, it is usually considered in an unbounded space, hence neglecting the effect of domain boundaries. However, the assumption of the environmental heterogeneity is restricted to a certain timescale and ceases to be valid when the spreading alien population approaches the limits of the corresponding geographic range. On a larger scale, invasive spread can be considered in a fragmented, ‘discrete’ environment where disjoint habitats are connected by dispersal; relevant modelling framework includes coupled map lattices [42, 80, 111] and networks [154].

Interestingly, the intermediate case of environmental heterogeneity occurring on a ‘not too large’ spatial scale, e.g. where the typical spatial size of the heterogeneity is the same as the typical scale of the spreading alien population (e.g. as is given by the variance of the dispersal kernel) has been rarely considered. In particular, the effect of domain (habitat) boundaries on the invasive species spread remains poorly understood, especially in case of a nontrivial landscape geometry. Meanwhile, in a somewhat different ecological context, the importance of the boundaries and the habitats shape for the population dynamics is widely recognized [17]. In Chapter 2, we addressed the above problem by considering invasive spread in a dumbbell-shaped domain where two large habitats are connected by a narrow passage or corridor and showed that the effect of the corridor can be nontrivial and counterintuitive [4].

In this Chapter, we consider a spatial system with a more complex geometry, where the corridor is not uniform but includes a patch with different
properties. In case the environment inside the patch is more favourable for the population (e.g. resulting in a higher growth rate or lower mortality rate) than the rest of the corridor, such a patch can play the role of a ‘stepping stone’ for the invading population [14, 75, 79, 151].

The main goal of this study is to reveal the relation between the ecologically meaningful factors such as the stepping stone patch size, location, and the environment quality inside the patch that can hamper or promote invasive species spread in a complex landscape. This Chapter is organized as follows. In Section 3.2, we introduce our modelling framework and consider the effect of stepping stones in a simple one-dimensional system. In Section 3.3, we consider the effect of stepping stones in a hypothetical two-dimensional H-shaped domain. In Section 3.4, we extend our approach by considering the effect of stepping stones on invasion success in a keyhole-shaped domain. Section 3.5 provides discussion and conclusions.

3.2 Stepping stone in 1D case

In order to make an inceptive insight into some generic properties of invasive spread with stepping stones, we begin with a simple one-dimensional (1D) system.

3.2.1 Model

We consider a single-species reaction-diffusion model where the local population growth is hampered by the Allee effect. In the case of an 1D space, the model is given by the following equation [97, 116, 182]:

\[
\frac{\partial u(x,t)}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + \gamma u(1 - u)(u - \beta(x)),
\]

where \( u \) is the population density of the alien species at position \( x \) and time \( t \), \( D \) is the diffusion coefficient, \( \gamma \) is a coefficient which can be regarded as the characteristic growth rate (for convenience we keep \( \gamma = 1 \), its meaning will become
clear in Section 3.3.3). Note that the carrying capacity is scaled to one and $\beta$ is the measure of the strength of the Allee effect to which we will refer as the Allee threshold. The Allee effect is called weak for $-1 < \beta \leq 0$ and strong for $0 < \beta < 1$ [182].

In case the population dynamics is considered in a spatially uniform environment, $\beta$ is a constant parameter. In an unbounded space, the generic solution of Eq. (3.1) relevant to biological invasion (i.e. for appropriately chosen initial conditions) is then a travelling population front [97, 116]; see Fig. 3.1. Invasion is successful (the front propagates towards the areas where the invasive species is absent, i.e. to the right in Fig. 3.1) if $\beta < 0.5$ and invasion fails (the population front retreats, i.e. propagates to the left in Fig. 3.1) if $0.5 < \beta < 1$ [116]. Below we will refer to the case $\beta > 0.5$ as a ‘very strong’ Allee effect. In case the spatial domain is bounded but sufficiently large, strictly speaking the travelling front solution of Eq. (3.1) is not valid any more yet it provides “an intermediate asymptotics” [13]: a good approximation of the actual solution (for relevant initial and boundary conditions) for the time range when the front is sufficiently far away from the domain boundaries.

In the present study, in order to account for the effect of environmental heterogeneity, we consider $\beta$ to be a function of space. More specifically, we
consider the system where the spatial domain is split into a succession of several subdomains or habitats – say, Habitats A, B, C, D and E (see Fig. 3.2) that differ by their quality. We assume that the quality of the environment is quantified by a single parameter, i.e. by the strength of the Allee effect. Correspondingly, Habitat $X$ is described by the Allee threshold $\beta_X$ and by its length $L_X$, $X = A, \ldots, E$, where $L_A + L_B + L_C + L_D + L_E = L$ and $L$ is the overall length of the domain.

**Figure 3.2:** Sketch of the domain structure: (a) a wide ‘barrier’ of unfavourable environment (with a very strong Allee effect, $0.5 < \beta < 1$), as given by combined Habitats A & B & C, separates the invaded Habitat A from potentially invadable but inaccessible Habitat E behind the barrier; (b) the same as in (a) but now with a ‘stepping stone’ of favourable environment (Habitat C) in the middle of the barrier.

In our choice of values $\beta_X$, we focus on the situation where the invasive species in its spread has approached a ‘bad’ area with unfavorable conditions (environment of poor quality) where the Allee effect is very strong, $0.5 < \beta < 1$; see combined habitats A, B and C in Fig. 3.2a. In case the length of this unfavorable area is small, i.e. smaller than a certain critical value [125], the propagating population front will eventually overcome the bad area (sometimes subject to a considerable delay [124]) and continue spreading on the other side, i.e. into favourable Habitat E. In case the length of the unfavorable area is larger than the critical value, the propagating population front will stop at the interface between Habitats A and B, even though the environment behind this barrier is favourable again [125]. The question that we consider here is: How may this situation may change if there is a domain with favorable conditions (e.g. a weak Allee effect,
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\[ \beta < 0 \] which we call a ‘stepping stone’ inside the unfavorable area, (see Habitat C in Fig. 3.2b).

We assume that the invasive species spreads from left to right; correspondingly, for the initial condition, we consider the situation that the invasive species is present at its carrying capacity in Habitat A but absent from all other habitats, that is

\[ u(x,0) = 1 \quad \text{for} \quad 0 \leq x \leq L_A, \quad u(x,0) = 0 \quad \text{for} \quad L_A < x < L. \quad (3.2) \]

For the conditions at the external domain boundaries, we consider the zero-flux Neumann condition at the left-hand side boundary:

\[ \frac{\partial u(0,t)}{\partial x} = 0, \quad (3.3) \]

because the areas at \( x < 0 \) (that are not include explicitly into the model) are already inhabited by the alien species; see the lines above Eq. (3.2), and the Dirichlet-type zero function at the right-hand side boundary, because at \( x > L \) the species is absent (it has not arrived there yet):

\[ u(L,t) = 0. \quad (3.4) \]

3.2.2 Simulation results

Equation (3.1) with \( \beta(x) \) defined as a piecewise-constant function (cf. Fig. 3.2) was solved by finite differences\(^1\). The steps of the numerical grid were chosen sufficiently small to avoid numerical artifacts and it was checked that the results do not change with a further decrease of the grid step sizes.

Having performed extensive simulations for various parameter values, we

\(^1\)Equation (3.1) was solved in each of the habitats separately and the solutions were then matched together using the conditions of continuity of the function and of the flux at the boundaries separating the habitats.
have identified three essentially different invasion regimes that are shown schematically in Fig. 3.3. In Case 1, the population stops at the boundary between Habitats A and B. The population is at approximately its carrying capacity in A but quickly decays to zero outside of Habitat A. In Case 2, the population spills over to Habitat C and establishes there at the population density approximately equal to the carrying capacity, but is blocked at the boundary between Habitats C and D, hence never spilling over to Habitat E (except for an exponentially thin tail). In Case 3, the population first overcomes unfavorable Habitat B and establishes itself in favorable Habitat C (stepping stone) and then eventually spills over to favorable Habitat E. We mention here that, depending on parameter values there may be minor variation in the above scenarios, e.g. the density profile shown in Case 2 may not have the trough or, on the contrary, the density profile shown in Case 3 may have a trough located in Habitat D. Since our main goal is to distinguish between the successful invasion (population overcomes the bad area) from invasion failure (population is blocked by the bad area), here we do not pay any attention to those relatively minor details of the population profile.

We consider $L_C$ and $\beta_C$ as controlling parameters of the problem and make...
a more detailed insight into how the properties of the stepping stone Habitat C affect the dynamics of the invasive spread. Our specific goal is to reveal for what parameter values the blocked invasion (Case 1 in Fig. 3.3) changes to successful invasion (Case 3 in Fig. 3.3). Apparently, the invading population cannot spill over to Habitat E behind the barrier before establishing in Habitat C first, therefore one point to understand is when Case 1 changes to Case 2. This question is addressed through extensive numerical simulations where we fix parameters as $L_A = L_B = 15$, $\beta_A = \beta_E = 0.3$, $\beta_B = \beta_D = 0.6$ and $L_D = 4$ and vary $\beta_C$ and $L_C$ in a broad range of values. The corresponding structure of the parameter plane $(\beta_C, L_C)$ is shown in Fig. 3.4a. It is readily seen that, for Habitat C to be invaded, either its length must be sufficiently large or the Allee effect must be sufficiently weak (i.e. the quality of the environment should be sufficiently high).

![Figure 3.4: Map in parameter plane $(\beta_C, L_C)$ where the domains above and below the curve correspond to different invasion scenarios obtained for (a) $L_D = 4$ and (b) $L_D = 3$. Other parameters are $\beta_{A,E} = 0.3$, $\beta_{B,D} = 0.6$ and $L_A = L_B = 15$.](image)

For the parameter values of Fig. 3.4a, the population cannot proliferate to Habitat E as it is blocked by unfavourable Habitat D. Hence the expectation is that, provided the population establishes in Habitat C, the success of its further spread depends on the parameters of Habitat D, in particular on its length. Intuitively, one can expect that the spread can only be blocked if $L_D$ is sufficiently large. In case $L_D$ is not large enough, successful establishment in Habitat C should inevitably lead to a successful spread to Habitat E, i.e. Case 2 would change to
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Case 3. This intuitive expectation is confirmed by simulation results. Figure 3.4b shows parameter plane \((\beta_C, L_C)\) obtained for a smaller value \(L_D = 3\), other parameters being the same as in Fig. 3.4. It is readily seen that for this value of \(L_D\) Case 2 cannot happen: whenever the population spreads to Habitat C, it spreads to Habitat E too.

![Figure 3.5: Critical size of Habitat D as a function of the strength of the Allee effect in stepping stone Habitat C (solid curve). For parameters above the curve the population spreads to Habitat E, for parameters below the curve the spread is blocked by bad Habitat D.](image)

Numerical simulations performed for various values of \(L_D\) reveal that, for other parameter values fixed as above, the critical length of Habitat D is approximately 3.7. However, this value is likely to depend on the strength of the Allee effect in the stepping-stone Habitat C. In order to have a more detailed look into this issue, we now fix the length of Habitat C as \(L_C = 8\) along with other parameters and vary the length of Habitat D. Figure 3.5 shows the structure of parameter plane \((\beta_C, L_D)\). It is readily seen that the dynamics does depend on the strength of the Allee effect, albeit slightly, the main controlling parameter being the length of the bad area \(L_D\).

### 3.3 Stepping stones in 2D case

The results of the previous section provide a first insight into the problem, in particular showing that the outcome of the invasive spread (i.e. success or failure)
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Figure 3.6: Sketch of the 2D computational domain to study the effect of the favourable patch ('stepping stone', shown by the yellow square) on the invasion success.

depends on a subtle interplay between the parameters of the bad area and those of the stepping stone patch, in particular its location and the strength of the Allee effect inside the patch. However, one feature of the dynamics that is completely missed out by the 1D system is the possibility of the spreading population to overcome the bad area by going around it. In this section, we are going to address this issue by considering the problem in a more appropriate 2D layout of the model.

In the 2D space \((x, y)\), the model is given by the following reaction-diffusion equation:

\[
\frac{\partial u(x, y, t)}{\partial t} = \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} + u(1 - u)(u - \beta(x, y)),
\]  

(3.5) (in dimensionless units) where notations have the same meaning as in Section 3.2.1.

We consider an H-shaped domain where two large rectangular sub-domains of the same size, Habitat 1 and Habitat 2 – are connected by a passage; see Fig. 3.6. At the boundary of the domain (including the passage boundaries) we use the zero-function Dirichlet type condition; from the ecological perspective, it implies that the areas outside of the H-shaped domain are extremely unfavourable.

Our goal is to consider how the invasion success can be affected by the existence of the stepping stone (cf. Fig. 3.6) – a patch with more favourable conditions than in the rest of the domain situated inside either the passage or one of the habitats. Inside the patch, we consider the Allee effect to be weak (except for
a few clearly stated special cases); elsewhere in the domain, we consider it to be strong. The strength of the Allee effect inside and outside the patch is quantified by the value of the Allee threshold as, respectively, $\beta_w (\leq 0)$ and $\beta_s (> 0)$.

The problem is studied by means of extensive numerical simulations. Equation (3.5) is solved numerically by finite differences. In most cases, we used the simple explicit scheme with mesh steps $\Delta x = \Delta y = 0.1$ and $\Delta t = 0.001$. In all simulations shown below, the overall size of the computational domain is $L = 50$. For the value of the Allee threshold, we fix $\beta_s = 0.1$ but vary $\beta_w$ using different values (normally, between 0 and $-1$) in different simulations.

### 3.3.1 Establishment

We first consider how the existence of a stepping stone can help the establishment of an alien species in a new environment. For this purpose, we consider the situation where the stepping stone is located inside Habitat 1 (see Fig. 3.6).

Let us begin with the special case where $\beta_w = \beta_s$ which means that, effectively, there is no stepping stone. We consider that the alien species is introduced into a small square-shaped area to which we for convenience refer as ‘IC-patch’. We assume that, immediately after the introduction, the alien species is distributed uniformly inside the patch with density $u_0$. Correspondingly, the initial conditions for Eq. (3.5) are as follows:

$$u(x, y, 0) = u_0 \quad \text{for} \quad (x, y) \in \text{IC-patch}, \quad u(x, y, 0) = 0 \quad \text{otherwise.} \quad (3.6)$$

It is well known that, in case the population growth is affected by the strong Allee effect, the species introduction into a finite area of a uniform space exhibits criticality. The species persists if and only if the initial population density is sufficiently large, i.e. larger than a certain critical value where the latter depends on the size of the IC-patch [99, 134]. Simulation results obtained for Eqs. (3.5–3.6) and the parameters of the passage as (length, $w$)=(12, 7.5) where $w$ is the width in
the case $\beta_w = \beta_s = 0.1$ are shown in Fig. 3.7a. It is readily seen that a smaller IC-patch does require a higher initial population density to ensure the survival of the alien population as the critical patch size is a monotonously decreasing function of the initial density.

**Figure 3.7**: Critical patch size as a function of the initial population density $u_0$ for different strengths of the Allee effect inside the stepping stone patch. The Allee effect is strong in (a), weak in (b,c) and absent in (d). Parameters of the passage are $(\text{length}, w) = (12, 7.5)$.

A question now arises as to how this situation may change if the place of the species introduction has more favourable environmental conditions than the rest of the domain (weak Allee effect), i.e. if the IC-patch effectively coincides with the stepping stone. We mention here that, unlike the case of a uniform space, the problem of species establishment in a nonuniform space has been poorly studied. Figure 3.7b-d shows simulation results obtained for a few different values of the Allee threshold $\beta_w$ inside the patch. We observe that the system possesses the properties similar to those shown in Figure. 3.7a: there exists a critical value of
the initial population density, the critical patch size is a decreasing function of the initial population density. Interestingly, for a sufficiently weak Allee effect inside the patch (cf. Figs. 3.7c,d), the critical patch size exhibits only a weak dependence on $u_0$ compared to the strong dependence when $\beta_w = -0.1$ or larger.

To further demonstrate the effect of the stepping stone on species establishment, Fig. 3.8 shows the dependence of the critical patch size on the strength of the Allee effect inside the patch. We observe that the weaker the Allee effect is, the smaller the critical patch size is (i.e. the more likely the alien species are to persist) and this effect is more prominent for smaller values of the initial population density.

### 3.3.2 Spread through the passage

In the rest of Section 3.3, we consider the situation where the alien species has already invaded Habitat 1. Correspondingly, the following initial conditions are used:

$$u(x, y, 0) = 1 \text{ for } (x, y) \in \text{Habitat 1}, \quad u(x, y, 0) = 0 \text{ otherwise.} \quad (3.7)$$

It has been shown in our previous work that, in case of a uniform environment ($\beta$ is constant everywhere inside the domain, no stepping stones), the
invasion success in the H-shaped geometry is fully determined by the size of the passage (see Figure 2.9a). The alien population spills over to Habitat 2 if either the width of the passage is sufficiently large or the length is sufficiently small; otherwise it is blocked by the passage. Here we are going to consider the effect of the stepping stone (cf. Fig. 3.9). Our aim is to reveal the relation between the factors that can affect the invasion success (the spill-over of the alien species to Habitat 2), namely, between the size of the patch, the patch location inside the passage (quantified by the distance $l_p$ between the patch and the entrance to the passage from Habitat 1), and the strength of the Allee effect inside the patch.

**Figure 3.9:** The H-shaped domain with the stepping stone located inside the passage.

**Figure 3.10:** Population density obtained at $t = 4000$. The population is blocked by the passage with (length, $w$) = (10, 7.5), no stepping stone; other parameters are given in the text.
It was observed in simulations that, in case of a successful spread, the population spill-over to Habitat 2 is usually established by about $t = 500$. Correspondingly, for all parameter values where invasion failure (spread blockage) is seen, in order to exclude long term transients, simulations are run until $t = 4000$.

We begin with the case where the size of the passage is $(\text{length}, \ w) = (10, 7.5)$. In the case where there is no stepping stone, the passage with these parameters is impassable, so that the alien species is blocked and never proliferates into Habitat 2; see Fig. 3.10. It is intuitively clear that a small stepping stone is unlikely to unblock the passage, and this is indeed what is seen in simulations. Figure 3.11 shows the results obtained for the same parameters as in Fig. 3.10 but now with a $2 \times 2$ patch with $\beta_w = -0.5$ located at the distance $l_p = 2.8$ from the passage entrance. It is readily seen that, for this patch size and location, the population spread remains blocked by the passage.

Interestingly, a patch with the same parameters as above but at a different location inside the passage can lead to different dynamics changing invasion failure to invasion success. Figure 3.12 show the results obtained in the case where $l_p = 2.9$, i.e. the patch is located just slightly further away from the passage entrance (other parameters are the same as in Fig. 3.11). It is readily seen that in this case the passage is unblocked and the population quickly spreads into Habitat 2.

In order to provide a comprehensive overview of the system’s properties it is therefore necessary to consider the dynamics subject to different parameter combinations. This has been achieved by means of extensive numerical simulations.

![Figure 3.11: Snapshots of the population distribution over space obtained for the passage size as (length, w) = (10, 7.5), patch size of 2 x 2 and the patch location l_p = 2.8.](image)
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(a) \( t = 100 \)  
(b) \( t = 300 \)  
(c) \( t = 400 \)

**Figure 3.12:** Snapshots of the population distribution over space obtained for the patch location \( l_p = 2.9 \), other parameters are the same as in Fig. 3.11.

Varying all relevant parameters over a broad range. Essential results are shown in Figs. 3.13-3.14. Figure 3.13 shows the map in the parameter plane \((\beta_w, l_p)\) obtained for several different sizes of the stepping stone patch. It is readily seen that, the larger the patch size is, the broader is the range of parameters where invasion is

![Figure 3.13](image-url)

**Figure 3.13:** Map in parameter plane \((\beta_w, l_p)\) showing parameter ranges where the invasion is successful (blue color) and parameter ranges where invasion is blocked by the passage (red color) for the stepping stones of different size. Parameters of the passage are \((\text{length}, w) = (12, 7.5)\).
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Figure 3.14: Map in parameter plane \((\beta_w, l_p)\) showing parameter ranges where the invasion is successful (blue color) and parameter ranges where invasion is blocked by the passage (red color) for the stepping stone \(2 \times 2\) and the passage of different size.

successful. For the patch size of \(5 \times 5\) or larger, invasion blocking is only possible for a few particular combination of parameter values such as values of \(\beta_w\) close to zero and the patch location close to either the passage entrance (i.e. close to Habitat 1) or to the passage exit (close to Habitat 2); see, respectively, the bottom-right and the top-right corners in Fig. 3.13d. For the stepping stone patch of a small size, see Figs. 3.13a and 3.13b, invasion can only be successful if the patch is located approximately in the middle of the passage, but not at the entrance to the passage. Note that, unless the patch size is large, e.g. equal to or larger than one half of the passage width (cf. Fig. 3.13c), an increase in \(\beta_w\) will always result in invasion blocking, even though the Allee effect in the patch is still weak and the conditions are favourable.

We want to mention that, for the parameters of Fig. 3.13, the passage
without the stepping stone would block the spread regardless of the strength of
the Allee effect inside the patch; see (see Fig. 2.9a). Therefore, the existence of
the stepping stone can unblock the otherwise impassable passage.

It is readily seen from Fig. 3.13 that, for the passage of a fixed size, the
parameter domain corresponding to successful invasion (cf. light-blue colored areas
in Fig. 3.13) grows steadily with an increase in the stepping stone patch size. When
the patch size approaches the width of the passage, the parameter range where
the invasion can be blocked shrinks to zero. A question can arise as to whether
the system’s dynamics actually depends on the ratio of the passage width and the
patch size rather than on these two parameters separately. In order to address
this question, we fix the size of the stepping stone patch at $2 \times 2$ and perform
simulations with the passage of different sizes. The results are shown in Fig. 3.14.
It is readily seen that the parameter domain of successful invasion shrinks along
with a decrease in the passage width, hence showing the tendency opposite to that
observed in Fig. 3.13.

### 3.3.3 Effects of different growth rate normalization

The above results were obtained under the assumption that the normalizing coeffi-
cient $\gamma$ in Eq. (3.1) is constant, i.e. not related to any other species traits. Although
this assumption is routinely used in mathematical ecology [50, 116, 162, 182], a
closer look reveals that it is in fact not well justified biologically. Indeed, it is
readily seen that in this case a change in the value of the threshold density $\beta$ leads
to a change in the maximum growth rate and the maximum per capita growth rate [97]. Meanwhile, the properties of the population growth rate at small popu-
lation densities (where the Allee effect is especially important) and at intermediate
population densities (where the maximum growth rate is reached) are often de-
termined by different factors and processes and hence are not necessarily directly
related. Therefore, as an alternative to the simple case $\gamma = 1$, now we are going to
consider a model where these processes are uncoupled. That requires normalizing
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coefficient to become a function of the Allee threshold, i.e. \( \gamma = \gamma(\beta) \), where the
particular function depends on what property is being preserved.

Namely, we consider the following two cases [97]:

- The maximum growth rate is kept constant (i.e. independent of \( \beta \)).
- The maximum per capita growth rate is kept constant.

(For more details see Eqs. (2.7) and (2.8) in Section 2.2).

We now perform simulations using the 2D model (3.5–3.7) with \( \gamma(\beta) \) given
by either (2.7) or (2.8) in the H-shaped domain with a stepping stone in the
passage; (see Fig. 3.9). Results are summarized in Figs. 3.15–3.16.

Figure 3.15 shows parameter plane \((\beta_w, l_p)\) of the stepping stone properties
obtained in the case of scaling (2.7) preserving the maximum growth rate and the
passage of the size (length, \( w \))=(5, 2.6). Without the stepping stone, the passage of
this size is impassable for the population; see (see Fig. 2.9b). It is readily seen from
Fig. 3.15 that, although the shape of the map is somewhat different, the general
tendencies remain essentially the same as in the case of \( \gamma = 1 \). The existence
of a stepping stone promotes successful spread as it can unblock the otherwise
impassable passage; the larger the stepping stone is, the more distinct this effect
is (i.e. the broader the corresponding parameter range is). For the stepping stone

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{fig3_15.png}
\caption{Map in parameter plane \((\beta_w, l_p)\) showing parameter ranges where
the invasion is successful (blue color) and parameter ranges where invasion is
blocked by the passage (red color) for the stepping stones of different size and
the normalizing coefficient \( \gamma \) chosen according to Eq. (2.7). Parameters of the
passage are (length, \( w \))=(5, 2.6).}
\end{figure}
of a small size (cf. Fig. 3.15a), it can only unblock the passage if it is located at a certain optimum location approximately in the middle of the passage.

Figure 3.16 shows parameter plane $(\beta_w, l_p)$ obtained for the stepping stones of different size in the case where $\gamma$ is given by Eq. (2.8) (hence preserving the maximum per capita growth rate). The size of the passage is $(\text{length}, w) = (5, 3.4)$; note that without the stepping stone this passage is impassable (see Fig. 2.9c). Just as before, we observe that the stepping stone can assist the spread by unblocking the passage. For smaller patches, there is a certain optimum location, but a larger patch unblocks the passage in a broader range of parameters.

### 3.4 2D case with cylindrical symmetry

In the previous section, we have considered the effect of the stepping stone inside an H-shaped habitat where the boundary of the domain is a piecewise straight line and all the corners have right angles. Obviously, for this ‘rectangular geometry’, Cartesian coordinates are most natural. Apparently, the domain of this shape is not a very general case. Since the goal of this chapter is to make an insight into the effects of habitat’s shape on the population dynamics, in particular on the success of invasive spread through the passage, a question arises as to how
the results obtained in the previous section may change in case of a domain of a
different shape. Correspondingly, in this section we consider a similar problem in
a domain with similar properties – i.e. two large habitats connected by a much
smaller one – but with a different shape and symmetry; see Fig. 3.17. The domain
thus consists of two large radial sectors of radius $R$ (see Habitat A and Habitat B
in Fig. 3.17a) and a circular-shaped central area or field of a much smaller radius
$r_c$, the latter thus playing the role similar to that of the passage in the rectangular
geometry. For convenience, below we will refer to this shape as a keyhole-shaped
domain.

In the polar coordinates, that is the natural coordinate system for the
domain of this shape, the reaction-diffusion equation (3.5) takes the following
form:

$$
\frac{\partial u(r, \phi, t)}{\partial t} = \frac{1}{r} \frac{\partial}{\partial r} \left( r \frac{\partial u}{\partial r} \right) + \frac{1}{r^2} \frac{\partial^2 u}{\partial \phi^2} + \gamma u \left( 1 - u \right) \left( u - \beta(r, \phi) \right),
$$

(3.8)

where $u \equiv u(r, \phi, t)$ is the population density at the location defined by the dis-
tance $r$ from the origin (i.e. from the center of the domain) and the polar angle
$\phi$.

Our primary interest here is to reveal how the parameters of the central
area, i.e. its radial size $r_c$ and angular size $\phi_c$, can affect the success of the popu-
lation spread from Habitat A to Habitat B. We begin with the case of a uniform
environment where $\beta = \beta_s = const$ throughout the domain ($0 < \beta_s < 0.5$, strong
Allee effect) and then proceed to the case with a stepping stone inside the central
area (see Fig. 3.17b), i.e. a patch where the Allee effect is weak ($-1 < \beta_w < 0$).

For the initial condition, as in Section 3.3, we assume that the alien species
propagates from left to right and has already invaded Habitat A but is yet absent
from the rest of the domain:

$$
u(r, \phi, 0) = 1 \quad \text{for} \quad (r, \phi) \in \text{Habitat 1}, \quad u(r, \phi, 0) = 0 \quad \text{otherwise.} \quad (3.9)
$$

For the boundary conditions, the Dirichlet boundary condition $u = 0$ is
used at the external boundary. Besides, we use the Neumann boundary condition at the origin, that is

\[
\frac{\partial u(0, \phi, t)}{\partial r} = 0, \quad (3.10)
\]

as is required by the specifics of the Laplacian in the polar coordinates [56, 141], and the periodic boundary conditions for the angular dependence:

\[
u(r, 0, t) = u(r, 2\pi, t), \quad \frac{\partial u(r, 0, t)}{\partial \phi} = \frac{\partial u(r, 2\pi, t)}{\partial \phi}. \quad (3.11)
\]

### 3.4.1 Simulation results

Equation (3.8) is solved numerically by finite differences using the implicit scheme with the grid steps \(\Delta r = 0.05\), \(\Delta \phi = \frac{\pi}{28}\) and \(\Delta t = 0.01\) and it was checked that these values are sufficiently small to avoid numerical artifacts.

Figure 3.18a shows the snapshot of the population density at \(t = 4000\) obtained for \(\beta = 0.1\) and the geometrical parameters of the domain chosen as \(\phi_c = \pi/2\) and \(r_c = 4.5\). It is readily seen that the population has proliferated

**Figure 3.17:** A sketch of the 2D computational domain with polar symmetry, (a) with a uniform environment inside the domain, (b) with a stepping stone patch (an area with better conditions, i.e. a weaker Allee effect) inside the central field.
through the passage (i.e. the central field) and successfully invaded Habitat B. However, the central field of a smaller size may become impassable for the invader. Figure 3.18b shows the snapshot of the population density obtained at $t = 4000$ for $r_c = 4.45$, other parameters being the same as above. Obviously, the spread is blocked by the passage. Therefore, for the given value of $\phi_c$, there is a critical value of the central field radius, say $r_c^*$, such that the invading population successfully spreads into Habitat B for $r_c > r_c^*$, but is blocked by the central field for $r_c < r_c^*$.

The question arises as to whether the above observation remains true for a different value of $\phi_c$ and, if yes, how the critical value $r_c^*$ depends on $\phi_c$. In order to address this question, simulations were run for values of $\phi_c$ and $r_c$ varied over a broad range. The results are summarized in Fig. 3.19. The critical radius decreases with an increase in $\phi_c$, tending to small values when $\phi_c$ approaches $\pi$. Note that, for $\phi_c \to 0$, Habitats A and B become degenerated, effectively shrinking to a line. With a decrease in $\phi_c$, as soon as the maximum width of the domain (approximately $\phi_c R$) becomes less than the critical size of a 1D system, Habitats A and B are not capable to support the population; see Section 3.2 in [99]. For this values of $\phi_c$ (shown by the dashed vertical line in Fig. 3.19), the population

![Figure 3.18](image_url)

**Figure 3.18**: Snapshots of the population density obtained at $t = 4000$ in the system without a stepping stone for (a) $r_c = 4.5$ and (b) $r_c = 4.45$. Other parameters are $\phi_c = \pi/2$ and $\beta = 0.1$. 
Figure 3.19: Parameter plane \((\phi_c, r_c)\) of the central field (see Fig. 3.17). The solid curve (obtained in numerical simulations) separates the parameter range where the invasion is successful (above the curve) from the parameter range where the invasion is blocked by the passage (below the curve). For values of \(\phi_c\) on the left of the vertical line, invasion fails for all \(r_c\).

We now proceed to the case where there is a favourable patch (stepping stone) inside the central field (see Fig. 3.17b). In order to attain generality, we consider different locations of the patch quantified by the distance along the horizontal symmetry axis in the direction of Habitat B between its center and the center of the domain – say, \(x_p\). As in the previous section, our aim is to determine the relation between the parameters of the patch, such as its location \(x_p\), its radius \(r_p\) and the value of the Allee effect \(\beta_w\) inside the patch, that can turn invasion failure into a successful spread.

Figure 3.20 shows the simulation results obtained in the domain with the geometrical parameters chosen as \(r_c = 3.5\) and \(\phi_c = \frac{\pi}{2}\) and the stepping stone patch of radius \(r_p = 1.8\) located at \(x_p = 15.45\) (i.e. well inside Habitat B). We recall that in the system without the stepping stone these values of the geometrical parameters result in the invasion failure (see Fig. 3.19). Apparently, the presence of the stepping stone with the given parameters does not change the dynamics, still...
resulting in the invasion failure. However, the stepping stone at a slightly different location, \( x_p = 15.4 \), does change the dynamics, turning the invasion failure into a successful spread; see Fig. 3.21.

**Figure 3.20**: Population density obtained in simulations of the system with a stepping stone of radius \( r_p = 1.8 \) located at the distance \( x_p = 15.4 \) along the horizontal symmetry axis. Other parameters are \( r_c = 3.5, \phi_c = \frac{\pi}{2}, \beta_s = 0.1 \) and \( \beta_w = -0.5 \).

**Figure 3.21**: Population density obtained in simulations of the system with a stepping stone of radius \( r_p = 1.8 \) located at the distance \( x_p = 14.4 \) along the horizontal symmetry axis. Other parameters are the same as in Fig. 3.20.

In order to obtain a systematic view of the effect of the stepping stone parameters on invasion success, we perform numerical simulations for a few values of the radius of the stepping stone patch varying the strength of the Allee effect inside the patch and the patch location in a broad range. The results are shown in Fig. 3.22. We observe that the effect of the stepping stone to assists the invasion
Invasion with stepping stones

Figure 3.22: Map in the parameter plane \((\beta_w, x_p)\) obtained for different values of the stepping stone radius showing parameter ranges where the population is blocked (red lines) and where it successfully spreads to Habitat B (blue lines). Other parameters are the same as in Figs. 3.20–3.21.

becomes greater with an increase in the stepping stone radius (note the growth of the light-blue area from Fig. 3.22a to Fig. 3.22d). For any given stepping stone radius, there is an optimum stepping stone location where it turns invasion failure into invasion success for a broader range of values of \(\beta_w\), i.e. for a stronger Allee effect. For instance, for the patch radius \(r_p = 1.9\), the stepping stone ensures the successful spread for the strength of the Allee effect up to \(\beta_w = -0.4\) if located between \(2 < x_p < 8\) (see the lower half of Fig. 3.22c), but only up to \(\beta_w = -0.7\) or less if located at \(x_p \geq 17\).

As in the case of rectangular geometry, we are now going to check how the results can be changed by a different choice of \(\gamma\) (see Section 3.3.3). Figure 3.23 summarizes the results obtained when constant \(\gamma\) is replaced by \(\gamma(\beta)\) given...
by Eq. (2.7). We observe that the structure of the parameter plane changes significantly. For a small patch, its location close to the center of the central field unblocks the passage (cf. the narrow light-blue stripe at the bottom of Figs. 3.23a and b). Interestingly, there is also a range of locations at a much larger distance (see the light-blue area in the top left corner in Figs. 3.23a and b); in this case, the stepping stone is located well inside Habitat B rather than in the central field. Along with an increase in the size of the stepping stone, the range of those locations inside Habitat B grows significantly (cf. Fig. 3.23c) eventually merging with the range of locations inside the central field (Fig. 3.23d).

Figure 3.23: Map in parameter plane \((\beta_w, x_p)\) obtained for \(\gamma\) given by Eq. (2.7) and different values of the stepping stone radius showing parameter ranges where the population is blocked (red lines) and where it successfully spreads to Habitat B (blue lines). Parameters of the central field are \(r_c = 1.5\) and \(\phi_c = \frac{\pi}{2}\), other parameters are the same as in Fig. 3.22.

Figure 3.24 shows parameter plane \((\beta_w, x_p)\) obtained when constant \(\gamma\) is replaced by \(\gamma(\beta)\) given by Eq. (2.8). Again, we observe that the structure of the plane is rather different from the one obtained in the case \(\gamma = 1\). For a smaller
Invasion with stepping stones

Figure 3.24: Map in parameter plane \((\beta_w, x_p)\) obtained for \(\gamma\) given by Eq. (2.8) and different values of the stepping stone radius showing parameter ranges where the population is blocked (red lines) and where it successfully spreads to Habitat B (blue lines). Radius the central field is \(r_c = 1.9\) and \(\phi_c = \frac{\pi}{2}\), other parameters are the same as in Fig. 3.23.

patch (Fig. 3.24a), the passage can only be unblocked if the stepping stone is situated at the narrow range of locations at the entrance to Habitat B. For a larger patch, this range of locations grows fast and changes its shape to include (for a sufficiently weak Allee effect inside the patch) a broad range of locations inside Habitat B (see Fig. 3.24b); in fact, for \(\beta_w \leq -0.7\), the stepping stone at almost any location unblocks the passage.

3.5 Discussion and conclusions

Biological invasion has been a focus of intense research for several decades because of severe consequences that alien species’ spread can cause to biodiversity, environment, forestry and agriculture [47, 51, 81, 137, 150, 186]. Once a new species is introduced and starts spreading, evaluation of the extent of the invadable area becomes an important issue. It is often addressed by means of species distribution modelling (SDM) which attempts to predict the future distribution of invasive species on the basis of the known distribution in their native range by revealing the correlation between the values of the population density and relevant environmental parameters (e.g. temperature, precipitation, soil type, land cover, etc.) [8]. However, the capability of SDM to correctly predict the extent of the actually
invaded area depends on various factors that can affect species dispersal, such as barriers. Meanwhile, it is well known that dispersal can be a limiting factor that affects species distribution and, sometimes (e.g. under the global climate change), their whole existence [153]. In other words, SDM generally succeeds (subject to the quality of available data) to identify the potential areas where the alien species can establish and persist, but it says very little about how the alien species will actually get there and whether it will get there at all.

Heterogeneity of the environment often reduces the space accessible to alien species spread to narrow corridors [174]. In conservation programs, corridors are generally regarded as a landscape feature that promotes species persistence [62]. In the context of the invasive spread, however, their effect is different as they tend to slow down the spread [4, 61] or even can block it altogether [3]. Although empirical research into the effect of corridors on invasive species spread remains meagre (arguably, because of considerable technical and methodological difficulties [61]), its tendency to hamper the spread was demonstrated in modelling studies using different models, e.g. see [3, 4, 61].

On the other hand, the importance of stepping stones for species dispersal has long been recognised [14]. It is usually considered as a feature promoting long-distance dispersal [151], i.e. dispersal on a large spatial scale (such as is given, for instance, by an archipelago of small islands [151]). In our study, we endeavored to consider the effect of stepping stones on a much smaller spatial scale by linking them to dispersal corridors. We considered a situation where the corridor connecting two large habitats has got a small area or patch inside that has more favourable conditions than the rest of the environment. In agreement with previous studies, we found that stepping stones promote species spread; the larger is the stepping stone patch, the more noticeable its effect is. However, we also found that their actual efficiency to promote the alien species spread depends significantly on the relation between three factors such as their size, the quality of the environment inside the patch (quantified here as the strength of the Allee effect) and their location. In particular, we found that there exists an optimum location of the
stepping stone where even a stepping stone of small size and with relatively poor environmental conditions can unblock the otherwise impassable corridor. We have shown (by considering H-shaped and keyhole-shaped domains) that this feature does not depend much on the details of the habitat’s geometry and hence is likely to be sufficiently general.

In this study, we have considered the effect of habitat boundaries in the context of landscape geometry, i.e. aiming to understand how the shape of natural landscape features can affect the spread of invasive species. However, we mention here that a similar problem arises in relation to invasive species control. Indeed, one way to control the spread used in practical applications is to create landscape features – “barriers” – inaccessible for the invader [156, 157]. Arguably, the effect of the boundaries of those human-made structures on the dynamics of the invading population is going to be the same as the effect of natural landscape structures, so that our analysis is fully relevant. Our results therefore may help to provide a more efficient design of the barriers.
Chapter 4

Patterns of invasive species spread in a landscape with a complex geometry: effect of interspecific interactions

4.1 Introduction

Biological invasion is a phenomenon that has a variety of important implications for ecology (in particular, through species extinctions and biodiversity loss), environment, human wellbeing, agriculture/aquaculture, and sometimes industries beyond agriculture [81, 137, 150]. For these reasons, it has been a focus of intense empirical and theoretical research for many decades [47, 142, 186]. Mathematical modelling is widely accepted as an effective tool to study biological invasion [69, 99, 162]. Indeed, in the situation when replicated studies are hardly possible\(^1\), mathematical models along with computer simulations provide a virtual laboratory where the effect of various factors can be refined and analyzed and different hypotheses can be tested safely and at a relatively low cost.\(^2\)

\(^1\)Not to mention the transient nature of the weather that makes it virtually impossible to reproduce the initial conditions, a repeated release of an alien species - potentially, a dangerous pest – would be highly controversial and possibly illegal.

\(^2\)The majority of this chapter has been published [4]
In studies on biological invasion, a central question is how the alien species proliferates into space away from the place of its introduction. In its turn, it evokes the question as to what is the pattern of spread. For several decades, a paradigm of invasive species spread was a travelling population front. A large amount of theoretical work has been done in order to evaluate the speed of the front propagation [9, 58, 87, 168] and to reveal how the propagation can be affected by various factors [16, 97, 121], in particular, by environmental heterogeneity [7, 80, 125, 164]. The travelling front paradigm was eventually complemented by an alternative pattern of spread known as patchy invasion [73, 114, 136, 135] which is often observed in nature [41, 100, 104] and predicted by various dispersal-growth models [96, 111, 147, 163]. In the patchy invasion scenario, there is no population front and species spread in space occurs through the dynamics of separate disconnected population patches.

Whether it is a population travelling front or a patchy spread, previous studies on biological invasions have overwhelmingly focused on an idealized case of species spread in an unbounded space. (In case of a simulation study, the domain is bounded but can be chosen ‘sufficiently large’ in order to imitate an unbounded space.) Even though the effect of environmental heterogeneity was considered in a number of studies, e.g. see the references above, the role of inaccessible areas and hence the effect of landscape geometry on the rate of spread have remained poorly understood. Meanwhile, such a role is likely to be very important. One real world example is the invasion of grey squirrels in the UK. Whilst they successfully colonized most of England and Wales, the rate of their spread being in good agreement with predictions of relevant mathematical models [16, 120], they have largely failed to spill over to central and northern Scotland, and the landscape geometry – as given by large areas that are not accessible to squirrels such as swamps or high mountain ranges – is thought to be a reason for that [183]. As another example, it was found in a study on the invasion of nutria in Iran that about one third of the country could potentially be colonized [55]. In reality, however, having been introduced about one hundred years ago to the sub-Caspian
region, this species remains confined to largely the same area. A closer look reveals that different parts of the potential range are poorly connected (e.g. due to the effect of mountain ranges inaccessible to nutria), which is likely to limit species dispersal.

In this chapter, we consider the effect of the landscape geometry on the invasive species spread by means of mathematical modelling and computer simulations. The “complexity” of the landscape geometry (as is relevant in the context of this study) is represented by a dumbbell-like, “H-shaped” spatial domain consisting of two large habitats connected by a narrow passage or corridor. The initial conditions correspond to the situation where the alien species is present in one of the habitats but not in the other. We are especially interested in the following questions:

- How much a narrow passage can slow down the spread? Can a sufficiently narrow passage block the spread completely so that the invading population would never spill over to the other side?

- Depending on species traits, invasive spread into open space is known to follow a few different scenarios (see Fig. 4.1). Can the effect of the passage change the invasion scenario, e.g. turning a propagating population front into patchy spread (or visa versa)?

- Can the effect of the passage depend on the invasion scenario (e.g. slowing down the spread in one case but not having much effect in another)?

It has been shown in our earlier work [3] that the success of the species invasion into the second habitat depends on the width and length of the corridor as well as demographic parameters such as the maximum growth rate and the strength of the Allee effect. However, the effect of the dynamical complexity on the invasive species spread, in particular due to interspecific interactions and pattern formation, has remained obscure. Here we show that the dynamical complexity can affect the invasion success significantly. In particular, we show that the effect of the corridor on the invasion success is significantly different depending on whether
the invasive species spreads following the travelling population front scenario or the patchy invasion scenario. We also show that a corridor that blocks the species spread can become a refuge for the alien species and can subsequently become a source of a secondary invasion.

4.2 Model

The choice of the mathematical model is a somewhat subtle issue [108, 123, 131]. From a biological standpoint, it might be tempting to account in detail for a variety of biological interactions that the invasive species is experiencing during its spread, e.g. interactions with all species of the native community. A corresponding model is likely to be very complicated. Such a model would be difficult to parameterize as the information about the feedbacks and functional responses as well as parameter values is usually meagre and incomplete. Moreover, the higher the complexity of the model is, the more difficult it may be to reveal the general properties of the phenomenon as they may become obscured by specific details. Since in this chapter our goal is to look into general properties of the dynamics rather than to study a particular case, the model should not be too complicated. However, it should not be too simple either as some important features of the invasion dynamics – such as, for instance, pattern formation [73, 106, 136, 161, 160, 163] – can be missing altogether due to the insufficient complexity of the model.

We therefore look for a model of an intermediate complexity. Arguably, an appropriate model is a prey-predator system. On the one hand, it obviously takes into account only some common, basic interactions, i.e. how the population dynamics of the alien species (regarded in this context as a prey) is affected by its predator where the predator can be a native species or can be introduced as a biological control agent, cf. [82, 129, 135]. On the other hand, a spatially explicit prey-predator model allowing for the population dispersal is known to have a complicated spatiotemporal dynamics [99, 106], its “realistic” properties being consistent with at least some field observations [73, 121].
A general prey-predator system is described by the following coupled diffusion-reaction equations [116, 121, 161]:

\[
\frac{\partial U(r, T)}{\partial T} = D_1 \nabla^2 U(r, T) + F(U) - f(U, V),
\]

\[
\frac{\partial V(r, T)}{\partial T} = D_2 \nabla^2 V(r, T) + \kappa f(U, V) - MV,
\]  

where \(U(r, T)\) and \(V(r, T)\) are, respectively, the prey and predator population densities at time \(T\) and position \(r = (X, Y)\), \(D_1\) and \(D_2\) are the corresponding diffusion coefficients, \(\kappa\) is the food utilization coefficient. Function \(F(U)\) is the growth rate of the prey, \(f(U, V)\) describes predation, and \(M\) is the predator mortality rate. A particular choice of functions \(F(U)\) and \(f(U, V)\) may vary depending on the species traits. We assume that the predator trophic response is of the Holling type II and choose the parametrization accordingly [116]:

\[
f(U, V) = \frac{AUV}{U + H},
\]

where \(A\) quantifies the predation rate and \(H\) is the half-saturation prey density.

With regard to the prey growth, there is considerable evidence that the Allee effect is common in the population dynamics [33, 34]. Correspondingly, we assume that the alien species is affected by the strong Allee effect and consider the following parametrization for its growth rate [97]:

\[
F(U) = GU (U - U_A) (K - U),
\]

where \(G\) is a coefficient related to the maximum per capita growth rate \(g\) as \(G = 4g/(K - U_A)^2\) [97], \(K\) is the carrying capacity, and the Allee threshold density \(U_A\) \((0 < U_A < K)\) is a parameter quantifying the strength of the Allee effect [121, 182].

Equations (4.1–4.2) with (4.3–4.4) contain a large number of parameters, which makes their numerical investigation cumbersome. However, if we choose new, dimensionless variables as \(u = U/K\), \(v = V/(\kappa K)\), \(t = aT\) where \(a = \)
\( \alpha K/H, \ x = X(a/D_1)^{1/2} \) and \( y = Y(a/D_1)^{1/2} \), Eqs. (4.1–4.2) turn to the following:

\[
\frac{\partial u(x, y, t)}{\partial t} = \left( \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} \right) + \gamma u (u - \beta) (1 - u) - \frac{uv}{1 + \alpha u}, \tag{4.5}
\]

\[
\frac{\partial v(x, y, t)}{\partial t} = \epsilon \left( \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} \right) + \frac{uv}{1 + \alpha u} - \delta v, \tag{4.6}
\]

where \( \alpha = K/H, \ \beta = U_A, \ \gamma = GHK/(\alpha K), \ \delta = M/a \) and \( \epsilon = D_2/D_1 \) are new (dimensionless) parameters. Properties of dimensionless solutions \( u \) and \( v \) therefore depend on five dimensionless combinations rather than on each of the nine original parameters separately.

Biological invasion usually starts with an introduction of a (small) number of individuals of an alien species into a certain location inside a new ecosystem [162]. Immediately after the introduction, the population density of the alien species is only non-zero inside a certain (small) area. Therefore, in order to account for the biological invasion, Eqs. (4.5–4.6) must be supplemented with initial conditions described by functions with a finite support. Here we consider the initial conditions as follows:

\[
u(x, y, 0) = \begin{cases} u_0 & \text{if } x_{11} < x < x_{12} \text{ and } y_{11} < y < y_{12} \\ 0 & \text{otherwise} \end{cases}
\tag{4.7}
\]

\[
v(x, y, 0) = \begin{cases} v_0 & \text{if } x_{21} < x < x_{22} \text{ and } y_{21} < y < y_{22} \\ 0 & \text{otherwise} \end{cases}
\tag{4.8}
\]

where \( u_0, v_0 \) the initial prey and predator densities, and parameters \( x_{ij} \) and \( y_{ij} \) \( (i, j = 1, 2) \) determine the initially occupied area.

### 4.3 Simulations and results

Equations (4.5–4.6) with the initial conditions (4.7–4.8) were solved numerically by finite-differences. In most cases we used the simple explicit scheme. The mesh
steps were chosen as $\Delta x = \Delta y = 0.4$ and $\Delta t = 0.03$; it is readily seen that they satisfy the Courant - Friedrichs - Lewy stability condition [146]. Having performed simulations for a few other values of the mesh steps, we checked that the above values are sufficiently small to avoid numerical artifacts.

![Figure 4.1: Snapshots of the spatial distribution of prey (i.e. the alien species) illustrating different scenarios of invasive spread as predicted by Eqs. (4.5–4.6) obtained in a square domain 200 $\times$ 200 for parameters (a) $\delta = 0.63$, (b) $\delta = 0.51$, (c) $\delta = 0.43$ and (d) $\delta = 0.37$. Other parameters are given in the text. Yellow color for high population density, green and light blue for intermediate values, dark blue for zero density.](image)

Although our main goal in this chapter is to study the effects of a complex geometry, we begin with a simple case when Eqs. (4.5–4.6) are considered in a square domain. The domain has size $L$ so that $0 < x < L$ and $0 < y < L$. At the boundary of the domain the Neumann-type no-flux conditions are imposed.
For any given parameter set, the simulation is stopped either just before or immediately after the spreading population reaches the domain boundary. In this way, the effect of the boundary conditions on the population dynamics inside the domain is minimized; correspondingly, the population spread imitates the spread in an open (unbounded) space.

Depending on the parameter values such as the predator mortality rate $\delta$ and/or the Allee threshold $\beta$, the prey-predator system (4.5–4.6) is known to exhibit different patterns of the population spread [106, 114, 181]. Having chosen $\delta$ as the controlling parameter, a brief visual overview of the patterns is shown in Fig. 4.1, where the results were obtained in a square domain $200 \times 200$ for parameters $\epsilon = 1$, $\gamma = 3.9$, $\alpha = 0.1$, $\beta = 0.2$, the initial conditions (4.7–4.8) with $u_0 = 1$, $v_0 = 0.2$, $x_{11} = 85$, $x_{12} = 105$, $x_{21} = 85$, $x_{22} = 95$, $y_{11} = 100$, $y_{12} = 105$, $y_{21} = 95$ and $y_{22} = 115$, and different values of $\delta$. Here and below, only the distribution of prey is shown as the distribution of predator exhibits similar features. Unless the initially inhabited domain is very small so that the alien population goes extinct due to the strong Allee effect [97], a somewhat trivial case that we do not consider here, the alien population spreads into the empty space away from the place of its introduction. This spread can follow the population front propagation scenario (Fig. 4.1a,b,c) with or without pattern formation in the wake or the patchy invasion scenario [135, 136] (Fig. 4.1d) where the population spread is not preceded by a travelling front propagation.

A practically important question is how high is the rate of invasive spread. It can be rephrased as follows: for a given location of the alien species introduction, how fast the invading species will arrive at a given location elsewhere? In a spatially uniform system, this question is linked to the question about the speed of the propagation of the travelling population front\(^3\): indeed, once the speed is known, a common sense estimate is $\text{time} = \frac{\text{distance}}{\text{speed}}$. However, it is intuitively clear that this simple argument is unlikely to remain valid in a case where

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\(^3\)The situation is somewhat more complicated in the case of patchy invasion or in the case where the invasive species employs a long-distance dispersal. In the former case there is no front and hence the definition of the speed is somewhat ambiguous [114], in the latter case the front can have variable speed [90].
the invasive spread takes place in a landscape with a complicated geometry where the spread can possibly be slowed down or block altogether by, for instance, the existence of narrow valleys or ‘corridors’.

In order to make an insight into possible effects of the corridors, we now consider a domain of a more complex shape, namely, H-shaped where two habitats (subdomains) of a rectangular shape are connected by a narrow passage or corridor. For the initial conditions, we consider the situation where the alien species is introduced to a certain location close to the center of the left-hand side habitat (which we also call Habitat 1 for convenience); see Fig. 4.2. For the boundary conditions, we consider the Neumann-type zero-flux condition along the whole boundary. One can expect that during the first stage of invasion, i.e. before the invading population reaches the boundary of Habitat 1, the dynamics should be essentially the same as in a domain of a simple shape or in an infinite space. Once the invading population reaches the entrance to the corridor, however, it becomes a new, different problem and the question arises as to whether the population spills over to the right-hand side habitat (which we call Habitat 2) for given length and width of the corridor and for a given pattern of spread, cf. Fig. 4.1.

Figure 4.2: A sketch of the H-shaped domain consisting of Habitat 1 at the left and Habitat 2 at the right connected by a narrow passage (corridor). The alien species is introduced in Habitat 1, the initially inhabited area is shown by a small yellow rectangle.
Figure 4.3: Snapshots of the spatial distribution of prey at different moments calculated for parameters $\epsilon = 1$, $\gamma = 3.9$, $\alpha = 0.1$, $\beta = 0.2$ and $\delta = 0.5$ and initial condition (4.7–4.8) with $u_0 = 1$, $v_0 = 0.2$, $x_{11} = 85.2$, $x_{12} = 105.2$, $x_{21} = 85.2$, $x_{22} = 95.2$, $y_{11} = 55.2$, $y_{12} = 60$, $y_{21} = 50$, $y_{22} = 70$ (note that $x$ is the vertical axis and $y$ is the horizontal one). Parameters of the corridor are $(\text{length, } w) = (10, 2.8)$. Yellow for high population density, dark blue for the zero density, green for intermediate density.

The case of the population spread with a uniform spatial population distribution behind the invasive front (Fig. 4.1a) is similar to the invasive spread in a single species model considered in [3]; we do not reconsider it here. We therefore begin with a more interesting case where invasion into a homogeneous space takes
Figure 4.4: Snapshots of the spatial distribution of prey at different moments calculated for parameters $\delta = 0.42$ and $(\text{length, } w) = (10, 6.4)$, other parameters and color coding are the same as in Fig. 4.3.

place via the propagation of the population front with spatiotemporal pattern formation in the wake (cf. Fig. 4.1b). The results shown in Fig. 4.3 are obtained for the parameters of the corridor as $(\text{length, } w) = (10, 2.8)$ where $w$ is the width. In the first stage of invasion, the population front propagates fast, apparently with the same speed as in an infinite space [99]. Once it reaches the entrance to the corridor, the spread slows down considerably: it takes the population about 100 extra time units to penetrate through the corridor, cf. the top-right and middle-left panels in Fig. 4.3. Eventually, the population spills over to Habitat 2 and invade
over the rest of the domain, see the bottom row in Fig. 4.3.

Interestingly, the corridor affects the pattern of spread. The spread of the invading population in Habitat 2 is accompanied by the formation of irregular asymmetric patterns in the wake of the propagating front, which apparently is a result of the asymmetry in the initial conditions. However, the population distribution behind the front in Habitat 2 exhibits a perfect circular symmetry, e.g. see the bottom-left panel in Fig. 4.3.
However, spilling over after a delay caused by the corridor is not the only possibility. The system can also exhibit a qualitatively different dynamics resulting in an invasion failure. Simulation results (not shown here for the sake of brevity) obtained for different parameters of the corridor reveal that the dynamics depend strongly on the size of the corridor, in particular on its width. An increase of the corridor width will not change the dynamics much resulting only in a decrease of the time required for the population to penetrate through. However, a decrease of the corridor width will eventually result in invasion blocking: as soon as the width is smaller than a certain critical value, the invading population is blocked in the passage and never spills over to Habitat 2.

In order to check whether the above situation is general or pattern-specific, we then performed simulations for a value of $\delta$ where the species spread in an open space takes place via the propagation of a solitary ring (see Fig. 4.1c). The results are shown in Fig. 4.4. It is readily seen that the population dynamics follows a similar scenario. In the first stage, the population spreads away from the place of its original introduction in the same manner as in an open space. Once the front reaches the entrance to the passage, the spread slows down; it takes about 40 time units to penetrate through to enter Habitat 2. (Interestingly, this time appears to be about twice shorter than in the previous case.) Once it spills over, the population spreads over Habitat 2 in a similar way as before. One difference from the corresponding pattern of spread in an open space is that a fraction of the population settles down inside the passage (this is well seen in the middle row of Fig. 4.4) and works as a source to generate a sequence of population fronts (spreading rings) into both habitats. As above, a successful spill-over through the corridor only happens if its width is not too narrow. Once the width becomes less than a certain critical value, the population is blocked in the passage and never penetrates to the other side.

Finally, we performed simulations for the value of $\delta$ where the alien population spreads in space according to the patchy invasion scenario (see Fig. 4.1d). The results are shown in Fig. 4.5. The dynamics exhibit features similar to those
observed in Figs. 4.3 and 4.4. The population first spreads from the place of its original location in exactly the same manner as in a domain of a simpler shape or in an open space. Once it approaches the entrance to the passage, it is delayed for a considerable time before it spills over to Habitat 2. Note that this delay is two orders of magnitude larger than in the previous cases. An explanation for this lies in the absence of the population front: because of the chaotic movement of the patches in space [114], it takes extra time for a patch to hit the entrance to the passage compared to the directional propagation of the front. Eventually, if the corridor width is greater than a certain critical value, the population spreads through the passage and invades Habitat 2 (as in the bottom row of Fig. 4.5). However, in the case of the corridor is not wide enough, the population is blocked and never penetrates to the other side (not shown here).

4.3.1 Propagation blocking

In order to get a more detailed insight into the existence of the corridor’s critical width and how its value depends on the predator mortality $\delta$ (considered as a controlling parameter) and hence on the type of species spread, we performed extensive computer simulations with different values of $w$ and $\delta$ keeping other parameters the same as above. For each parameter set, the code was run up to $t = 4000$. The results are shown in Fig. 4.6. We therefore observe that the critical width exhibits a non-monotone dependence on the predator mortality but tends to increase with a decrease in $\delta$.

An analytical estimation of the critical width is possible. Using the comparison principle for nonlinear partial differential equations [138, 180], it is readily seen that the following single-species model:

$$
\frac{\partial u(x, y, t)}{\partial t} = \left( \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} \right) + \gamma u(u - \beta)(1 - u),
$$

i.e. Eq. (4.5) without the last term on the right-hand side, is the upper bound for the prey-predator system (4.5–4.6). However, for the single-species model a simple
analytical estimate of the critical width can be easily obtained. Indeed, once the front arrives to the end of the passage and starts spilling into Habitat 2, it is of approximately circular shape (consistent with the numerical simulations above, e.g. see the middle-left panel in Fig. 4.3 and the middle-right panel in Fig. 4.5). For a circular propagating front of radius $R$ in a 2D system, its speed $c(R)$ is known to be related to the speed $c$ of the corresponding 1D front as

$$c(R) = c - \frac{D}{R}, \tag{4.10}$$

e.g. see [181]. For the front confined at the exit of the passage, $R = w/2$. Since the front is blocked, $c(R) = 0$. Equation (4.10) then turns into the following:

$$c - \frac{2D}{w} = 0. \tag{4.11}$$

For a scalar diffusion-reaction equation with the population growth parameterized by a cubic polynomial, the analytical expression for the speed of the front
propagation is well-known:

\[ c = \sqrt{\frac{DG}{2} (K - 2U_A)}, \tag{4.12} \]

e.g. see [99]. From (4.11) and (4.12), we therefore obtain:

\[ w_{cr} = \sqrt{\frac{8D}{G} \frac{1}{(K - 2U_A)}}, \tag{4.13} \]

or, in dimensional variables,

\[ w_{cr} = \frac{2\sqrt{2}}{(1 - 2\beta)\sqrt{\gamma}}. \tag{4.14} \]

For the parameters of Fig. 4.6, the estimate (4.14) gives \( w_{cr} \approx 2.3 \) which agrees well with the simulation results.

Now, a question can arise here as to how sensitive the above results are to the boundary conditions along the corridor. Indeed, it is well known that the critical behaviour of diffusion-reaction systems is generally sensitive to the boundary conditions; for instance, the solution of the critical size problem is essentially different in the cases of the Neumann (zero-flux) and Dirichlet (zero-density) conditions. In order to get an insight into this issue, we now consider the same H-shaped

\[ \text{Figure 4.7: Sketch of an H-shaped habitat with Dirichlet boundary conditions at the sides of the corridor.} \]
domain as above but with the Dirichlet zero-density conditions along the passage boundary; see Fig. 4.7. We mention here that, compared to the zero-flux condition, the zero-density boundary condition corresponds to a somewhat different situation. Instead of a narrow canyon (connecting two large valleys) where the population density can build up in the vicinity of the canyon wall, one can think, for instance, of a narrow ridge (e.g. connecting two mountain plateaus) where a casual step over the cliff would result in death - hence, the zero population density.

Having performed extensive computer simulations in the domain with the zero-density condition in the passage (Fig. 4.7), we obtain that the dynamics of the system is qualitatively the same as in the previous case of the zero-flux conditions. In particular, we obtained that for all invasion regimes (as in Fig. 4.1) the invading population spills over to Habitat 2 if the corridor width is large enough and is blocked if the corridor is too narrow. Dependence of the critical width on the predator mortality is shown in Fig. 4.8. Therefore, as well as in the previous case

![Figure 4.8](image.png)

**Figure 4.8:** Parameter plane \((w, \delta)\) in case of the Dirichlet zero-density conditions at the boundary of the corridor. Other parameters and boundary conditions are the same as above. For the parameters from above the green curve (obtained in simulations) the population spills over and invade Habitat 2, for the parameters from below the curve the population is blocked in the passage. Red line shows the analytical estimate (4.17).
we observe non-monotone dependence of \( w_{cr} \) on \( \delta \) with a tendency for the critical width to increase with a decrease in \( \delta \).

As above, it is possible to obtain a simple analytical estimate of the critical corridor width, although the argument and calculations are different. We recall that the single-species model is an upper bound for the prey-predator model, so a condition of population propagation blocking in the model (4.9) will be a sufficient condition of the propagation blocking in model (4.5–4.6). Consider the case of a long corridor. Consider the situation where the invasive species has penetrated through the corridor and successfully spilled over to Habitat 2. In this case, in the large time limit the population density profile across the corridor does not depend on its position along the corridor as long as the position is sufficiently far away from the corridor ends. The problem then becomes one-dimensional as the population density depends only on the coordinate across the corridor but not along the corridor. However, if considered in the 1D settings, this turns into the classical critical size problem (e.g. see Section 3.1 in [99]), that is, how large the domain must be to ensure the survival of the population inside. For the growth rate described by a cubic polynomial, its analytical solution is unknown. However, if we consider an upper bound of the growth rate as

\[
\gamma u (u - \beta) (1 - u) \leq gu \quad \text{for any} \quad u \geq 0, \quad (4.15)
\]

where \( g \) is the maximum per capita growth rate (see the lines below Eq. (4.4)), the expression for the critical size in the corresponding linear problem is well known:

\[
w_{cr} = \pi \sqrt{D/g}, \quad (4.16)
\]

and in the dimensionless variables:

\[
w_{cr} = \frac{2\pi}{(1 - \beta)\sqrt{\gamma}}. \quad (4.17)
\]
For the parameters used in simulations, the estimate (4.17) gives the value \( w_{cr} \approx 4 \), which appears to be in good agreement with numerical results; see Fig. 4.8.

Note that the mechanism of spread blocking is somewhat different in the two cases. For the zero-density conditions at the boundary of the passage, the population is blocked inside the passage (in a manner similar to how a subcritical size of the inhabited domain results in the population extinction). For the zero-flux conditions, however, the population cannot be blocked inside (except for the trivial case where \( \beta > 0.5 \)); instead, its propagation is blocked at the exit of the passage.

Finally, we want to emphasize here that both (4.14) and (4.17) are sufficient conditions of propagation blocking, but not necessary. Once \( w \leq w_{cr} \), the propagation will necessarily be blocked by the passage; however, \( w > w_{cr} \) does not guarantee that the population will spread into Habitat 2. In terms of the diagrams shown in Figs. 4.6 and 4.8, it means that the whole of the red line lies in the parameter range where the population spread is blocked in the prey-predator system (i.e. in the area marked by crosses).

### 4.3.2 Sensitivity of the patchy spread to the initial conditions

From the four invasion scenarios shown in Fig. 4.1, perhaps the patchy invasion poses the biggest challenge. The absence of a continuous propagating population front leads to a certain ambiguity in the definition of the extent of the invaded area [114]. Similarly, it introduces an uncertainty as to when exactly, for a given set of the initial conditions, the population reaches the entrance to the passage. It is not enough for the expanding ‘envelope’ (e.g. the location of the foremost patch, cf. [114]) to reach the entrance to the corridor; in order for the population to start penetrating through the corridor, there must be one of the patches that actually hits the entrance. However, since the spatiotemporal population dynamics during the patchy invasion is known to be chaotic, the movement of the patches is effectively random. In its turn, the exact location of the patches depends on
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Figure 4.9: Snapshots of different initial predator population distributions used in simulations: (a) (IC-1) $y_{11} = 55$, $y_{12} = 60$, $y_{21} = 50$ and $y_{22} = 70$; (b) (IC-2) $y_{11} = 32.8$, $y_{12} = 35.2$, $y_{21} = 30$ and $y_{22} = 40$; (c) (IC-3) $y_{11} = 27.6$, $y_{12} = 30$, $y_{21} = 25.2$ and $y_{22} = 35.2$. The initial conditions for the prey and other parameters are given in the text.

The initial population distribution. Therefore, one can expect that, altogether, the time that it takes the population to arrive at the passage entrance and to penetrate to the other side can vary significantly.

In order to get a more quantitative insight into this issue, we therefore performed simulations for a few different initial conditions changing the demographic parameters in the range where the patchy invasion occurs \([73, 114, 135]\). Specifically, we use $\gamma = 3.9$, $\alpha = 0.1$, $\beta = 0.2$ and $\delta = 0.37$. The parameters of the corridor are chosen as (length, $w$) = (10, 9.2). For the initial conditions, we fix the initial population densities as $u_0 = 1.2$ and $v_0 = 0.2$, and the initial distribution of prey as $x_{11} = 85.2$, $x_{12} = 105.2$, $x_{21} = 85.2$, $x_{22} = 95.2$, and consider a few different initial distributions of the predator; see Fig. 4.9.

For the above parameters and for each of the three initial distributions, the

<table>
<thead>
<tr>
<th>Boundary conditions in the passage</th>
<th>IC-1</th>
<th>IC-2</th>
<th>IC-3</th>
</tr>
</thead>
<tbody>
<tr>
<td>zero-flux (Neumann)</td>
<td>2340</td>
<td>460</td>
<td>5090</td>
</tr>
<tr>
<td>zero-density (Dirichlet)</td>
<td>4450</td>
<td>3970</td>
<td>1240</td>
</tr>
</tbody>
</table>

Table 4.1: approximate spill-over time required for the population to reach the corridor exit to Habitat 2 for different initial conditions (IC) and different conditions at the passage boundary (cf. Fig. 4.7).
population spread from the place of its introduction generally follows the scenario shown in Fig. 4.5 (we do not show the results for the sake of brevity). We first consider the case with the zero-flux conditions on the passage boundary. In each simulation run, we pick the time required for the population to reach Habitat 2, e.g. the ‘moment’ when the population has penetrated through the passage and starts spilling over into the open space on the other side, e.g. as shown in the middle-right panel in Fig. 4.5. The results are presented in Table 4.1. It is readily seen that the time varies quite significantly; in fact, by an order of magnitude. We then repeat simulations for the same parameters and the same sets of initial conditions but imposing the zero-density conditions at the passage boundary. As in the previous case, the spill-over time shows a considerable variation between different initial conditions.

### 4.3.3 Corridor as a refuge

Finally, we report on a curious invasion scenario that occurs in a certain range of the parameters of the corridor. Figure 4.10 shows snapshots of the prey distribution obtained for the demographic parameters chosen as $\gamma = 6.25$, $\alpha = 0.1$, $\beta = 0.2$ and $\delta = 0.5$. The parameters of the corridor are (length, $w$)= (10, 2.8) and the initial conditions are given by (4.7–4.8) with $u_0 = 1.0$, $v_0 = 0.2$, $x_{11} = 85.2$, $x_{12} = 105.2$, $x_{21} = 85.2$, $x_{22} = 95.2$, $y_{11} = 55.2$, $y_{12} = 60$, $y_{21} = 50$ and $y_{22} = 70$. The boundary condition are zero-flux along the whole boundary of the domain (including the passage). Apparently, for these parameters the population spreads into an open space via ring-shaped travelling fronts; see the top-left panel in Fig. 4.10. After the population has propagated through the passage, a number of travelling concentric fronts is produced on both sides of the passage; see the middle row in Fig. 4.10. Eventually, the fronts go away (cf. the bottom row in Fig. 4.10) and the alien population eventually goes extinct in the most of the domain – except for the passage. A close inspection reveals that there is a residual population that settled down inside the corridor; this is readily seen from Fig. 4.11 that also gives a magnified view of the passage. Since this residual population is still persistent
in the passage after a considerable time \((t = 9000\) in Fig. 4.11), we assume that it corresponds to a stationary solution of Eqs. \((4.5–4.6)\).

A question arises here as to what can be a response of this residual population to a change in the demographic parameters. Such a change can be the result of the alien species adaptation to their new environment, or it can be the result of some exogenous process, such as the global climate change. In either case, the question is whether the population will remain confined inside the passage or it goes extinct, or it may start spreading.

**Figure 4.10:** Dynamics of the system resulting in the formation of a stable steady state distribution of the prey species inside the passage that survives after the invading population goes extinct in the rest of the domain. Parameters and the initial conditions are given in the text.
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Figure 4.11: A magnified view of the steady state population distribution inside the passage.

Figure 4.12: Snapshots of the prey population density at time \( t = 9030 \) (left) and \( t = 9060 \) (right) after the value of the Allee threshold density was changed from the original value \( \beta = 0.2 \) to the new value \( \beta = 0.1 \) at the moment \( t = 9000 \) (see Fig. 4.11). The residual population that was confined in the passage for a long time now starts spreading into the Habitats 1 and 2.

Looking for an answer to the above question, we performed simulations using the residual population as the initial condition for another simulation run with a different value \( \beta_1 \) for the Allee threshold density. We obtain that for \( \beta_1 \) just slightly larger than \( \beta \), e.g. \( 0.2 < \beta_1 \leq 0.23 \), the population remains confined inside the passage and at any moment of time the spatial population distribution of the prey is similar to the one shown in Fig. 4.11. In case \( \beta_1 \) is sufficiently larger than \( \beta \), e.g. \( 0.24 \leq \beta_1 \leq 0.3 \), the residual population goes extinct. However, in case \( \beta_1 \) is sufficiently smaller than \( \beta \), e.g. \( 0.1 \leq \beta_1 \leq 0.16 \) the prey can start...
spreading away from the passage into both Habitats 1 and 2. As just one example, Fig. 4.12 show the results obtained in the case $\beta_1 = 0.1$. Note that the spread takes place following a different scenario compared to the original one; instead of the propagating ring (cf. top-left panel in Fig. 4.10), it now spreads through a propagating circular front with pattern formation in the wake. This is not surprising as $\beta$ is, along with the predator mortality, a parameter that controls the pattern of invasive spread [114, 130].

4.4 Discussion and conclusions

Factors affecting the patterns and rates of alien species spread have been a major focus of research for several decades. A vast majority of studies were concerned with the species proliferation into an “open space” – a relatively uniform environment where all areas, although not necessarily being equally favorable, are accessible to the invading population. However, a realistic landscape can often be strongly heterogeneous, combining areas accessible for the invader with inaccessible ones. The effect of the landscape geometry (as given by the size and shape of the inaccessible areas) remains poorly understood. In this Chapter, we addressed this problem by considering a mathematical model where the population dynamics of an alien species takes place in an H-shaped domain consisting of two large uniform habitats connected by a narrow passage or corridor. For the initial conditions, we considered that the alien species is introduced in a (small) area inside one of the habitats. Our goal was to reveal the effect of the corridor on the species spread, in particular whether the spread from one habitat to the other could be slowed down or blocked. In terms of the real-world landscape, such a system could account for an alien species spread through a narrow valley or an isthmus. To account for interspecific interactions, we considered a generic prey-predator model which is known to exhibit a rather complex, ‘realistic’ spatiotemporal dynamics and predicts a variety of different invasion scenarios [99, 106].
In reply to the questions bullet-pointed in the introduction, (see p.68) we obtained the following answers:

• The corridor does slow down the spread. It takes the spreading population extra time to penetrate through the passage. A sufficiently narrow corridor, i.e. its width being less than a certain critical value, blocks the spread so that the invasive population never spills over to the other habitat. Analytical estimates for the critical width are obtained, see Eqs. (4.14) and (4.17), that are in good agreement with numerical results;

• The corridor can modify the pattern of spread. An example of this is shown in Fig. 4.3 where the irregular spatiotemporal pattern emerging behind the propagating front in Habitat 1 changes to a regular (symmetric) spatial population distribution behind the front in Habitat 2. Interestingly, this is exactly opposite to the results of some earlier work [169] where the existence of inaccessible areas – but with a different geometry – changed a regular spatiotemporal pattern into a chaotic one. The regularizing effect of the corridor in our study can be readily explained: having propagated through the narrow passage, the population distribution at the exit to Habitat 2 becomes symmetric and effectively works as a symmetric initial condition for the population spread in Habitat 2;

• The delay of the spread caused by the corridor is significantly different depending on the pattern of spread. In particular, we obtained that it can be about two orders of magnitude larger in case of the patchy spread compared to the spread by the propagating continuous front.

Our results seem to send a potentially important message to the invasion management specialists. Since the corridor tends to impede the invasive species spread, it might be regarded as a possible control strategy. Although it apparently implies a significant alteration of the environment (e.g. to make a natural corridor more narrow), which is likely to be very expensive, we mention here that this
strategy is not unrealistic and some examples of large scale environment intervention with the goal to slow down the spread are well known [156]. Importantly, however, based on our results (especially see the last item from the above list) this cannot be a universal approach as its efficiency depends on the pattern of spread: whilst it slows down the invasion considerably in the case of patchy spread, the delay might be rather insignificant in the case of spread via a continuous front. In its turn, this observation highlights the need for a better understanding of the invasion patterns and their more efficient identification including advance adaptive monitoring [132].

Interestingly, although the corridor tends to impede the invasive species spread, it also can promote the invasion if considered on a longer time scale. Once the time is long enough to include an environmental change or species adaptation (e.g. through phenotypic evolution), the corridor can become a source of a secondary invasion (see Section 4.3.3) hence bringing the alien species back even when it may have already disappeared from the rest of the domain. If considered in the context of invasion management, this observation restricts the potential use of the corridor as a factor controlling invasion to a small-to-intermediate timescale. From the point of alien species monitoring, it also means that a special attention should be paid to landscape features that can act as corridors, because they may become a refuge for the alien pest.
Chapter 5

Critical Domain Problem for the Reaction–Telegraph Equation Model of Population Dynamics

5.1 Introduction

Habitat fragmentation due to the climate change and anthropogenic activities is regarded as a major threat to biodiversity worldwide [54]. Understanding the factors affecting species survival in small and fragmented habitats is therefore a problem of high practical importance [53, 57, 85]. Although being essentially an ecological problem, it can hardly be studied in full by only traditional ecological methods and tools. Replicated ecological experiments under controlled conditions required for an exhaustive empirical study are often impossible for a variety of reasons, e.g., due to high costs, potential damage to the environment, and irreproducibility of the weather conditions and initial species distribution, to name just a few.¹

Mathematical modelling has long been recognized as an efficient research tool in theoretical ecology that can be used as a supplement and sometimes even a substitute to a field experiment [107, 108]. Mathematical models along with

¹The majority of this chapter has been published [5]
computer simulations create a virtual laboratory where hypotheses can be tested and different scenarios can be followed under safe working conditions and at relatively low costs. In particular, the problem of population persistence in small habitats, often referred to as the problem of critical domain, has been studied almost exhaustively in terms of reaction–diffusion models [3, 83, 97, 126, 133].

The choice of an adequate model, however, is a subtle issue. Whilst reaction–diffusion models have been used extensively in mathematical ecology for several decades [58, 97, 106, 116, 168] helping to obtain a number of important insights and inferences, they have their limits and their relevance may sometimes become questionable. One point of criticism is that diffusion (Brownian motion) as a baseline animal movement pattern is not entirely realistic as the diffusively moving ‘animal’ can change its movement direction with a high frequency (i.e., with any two consequent turns infinitely close in time) and choose the new direction uniformly distributed over the circle. However, this is at odds with many observations as well as with common sense [139]: since the body of animals of all species has the front end and the rear end, they are more likely to choose the new movement direction (following re-orientation) close to the movement direction at the preceding moment. The corresponding movement pattern is known as the correlated random walk (CRW) [78] and the corresponding microscopic stochastic process as the telegraph process [77], and their mean-field counterpart is known as a telegraph equation [45, 64, 71, 105, 109]:

\[
\tau \frac{\partial^2 u}{\partial t^2} + \frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2},
\]

where \( u = u(x, t) \) is the population density at location \( x \) and time \( t \), \( D \) is the diffusion coefficient, and \( \tau \) is a characteristic time of the microscopic movement that quantifies directional persistence in individual animal movement. The precise meaning of parameter \( \tau \) can be slightly different depending on the details of the microscopic model; for instance, in the telegraph movement process, it is the time over which the animal moves without changing its movement direction [64, 71, 77].
Brownian motion thus corresponds to the limit $\tau \to 0$ when Eq. (5.1) turns into
the diffusion equation.

Equation (5.1) describes the evolution of the population density because of
animal movement. It does not take into account the contribution of births and
deaths. Interestingly, in order to include them into the model, it is not enough to
add the ‘reaction’ term (i.e., the population growth rate) – say, $F(u)$ – into the
right-hand side of Eq. (5.1) (as is done in the case of diffusive animal movement
[116]). An accurate account for birth and death events also modifies the factor in
front of the first order derivative on the left-hand side [71, 109]. The corresponding
model is known as the reaction–telegraph equation:

$$
\tau \frac{\partial^2 u}{\partial t^2} + [1 - \tau F'(u)] \frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + F(u). \tag{5.2}
$$

In order to obtain Eq. (5.2), one has to consider a stochastic movement of parti-
cles following the telegraph process (change in movement direction as a Poisson
process), combined with random birth/death processes [71, 109]. Here and below,
the prime denotes the derivative of a function with respect to its argument.

In this Chapter, we consider the properties of the reaction–telegraph equa-
tion in a bounded domain. In doing this, we are motivated by the ecological
problem of habitat fragmentation and its effect on species survival. Our main goal
is therefore to understand what the conditions are of species survival (i.e., when
$u(x,t)$ does not tend to zero uniformly over the domain in the large-time limit),
how they may differ from the predictions of the corresponding reaction–diffusion
model, and how they may depend on the type of density dependence in the pop-
ulation growth, e.g., the existence of the Allee effect.
5.2 Non-Conservative Property of the Telegraph Equation

In order to demonstrate that the telegraph equation has properties significantly different from the diffusion equation, we begin with a simple example. Consider Eq. (5.1) in a bounded domain $0 < x < L$ with the Neumann-type boundary conditions at the domain boundaries:

$$\frac{\partial u(0,t)}{\partial x} = 0, \quad \frac{\partial u(L,t)}{\partial x} = 0. \quad (5.3)$$

Integrating Eq. (5.1) over space and taking Eq. (5.3) into account, we readily obtain the equation for the total population size:

$$\tau M''(t) + M'(t) = 0, \quad (5.4)$$

where $M(t) = \int_0^L u(x,t)dx$. One solution of Eq. (5.4) is $M(t) = M_0 \exp(-t/\tau)$ so that, obviously, $M(t) \to 0$ for $t \to \infty$. Therefore, the population goes extinct in the large time limit regardless of its initial population size and regardless of the domain size. Note that, in the corresponding diffusion model, boundary conditions (5.3) correspond to impenetrable boundaries and the total mass is conserved, $M(t) = M_0 = const$, so that species extinction is impossible. This drastic difference between the predictions of the diffusion equation and telegraph equation is explained by the observation that, for the telegraph movement process, the flux is described differently from diffusion [109]; the flux is not proportional to the gradient of the population density (as given by the Fick law). Therefore, the boundary conditions as given by Eq. (5.3) that make the boundary impenetrable in the case of the diffusion process do not block the population flux in the case of the telegraph movement process.

In the context of the habitat fragmentation problem, which is the main focus of this Chapter, the domain is open rather than closed. As we will show in the next section, the difference between diffusion and the telegraph movement
process becomes somewhat less pronounced when the boundary conditions are of the Dirichlet-type and when the population reproduction is taken into account.

5.3 Telegraph Equation with Linear Growth

Once population multiplication is taken into account, telegraph equation becomes the reaction–telegraph equation; see Eq. (5.2). In case the per capita growth rate of the population can be regarded as density independent, i.e., \( F(u) = \alpha u \), Eq. (5.2) takes the following form:

\[
\tau \frac{\partial^2 u}{\partial t^2} + (1 - \alpha \tau) \frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + \alpha u,
\]  

(5.5)

where \( \alpha \) is the linear growth rate. The linear growth in Eq. (5.5) assumes that the individuals of the given species \( u \) do not interact; collective behaviours such as competition or cooperation are neglected. Although it is clearly not true in a general case, if the population density \( u \) is sufficiently small (e.g., because of the initial conditions), the linear growth function may provide a reasonable approximation to the true (nonlinear) growth rate; see [116] and also Section 2 in [99].

For the convenience of notation, we define new coefficients \( \omega_1 = \tau \) and \( \omega_2 = 1 - \tau F'(u) = 1 - \alpha \tau \). Eq. (5.5) then becomes

\[
\omega_1 \frac{\partial^2 u}{\partial t^2} + \omega_2 \frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + \alpha u.
\]  

(5.6)

We consider Eq. (5.6) in a bounded domain of length \( L \), i.e., \( 0 < x < L \). The environment outside of the domain is assumed to be unfavorable for the given species (in fact, very harsh), so that an animal that leaves the domain will die very soon without any chance of coming back. This is described by the following Dirichlet-type boundary conditions:

\[
(a) \quad u(0,t) = 0, \quad (b) \quad u(L,t) = 0.
\]  

(5.7)
Equation (5.6) is further complemented by the initial conditions:

(a) \( u(x, 0) = h_1(x) \), \hspace{1cm} (b) \( \frac{\partial u(x, 0)}{\partial t} = h_2(x) \), \hspace{1cm} 0 \leq x \leq L, \hspace{1cm} (5.8)

where \( h_1(x) \) and \( h_2(x) \) are certain functions, and \( h_1(x) \geq 0 \).

An analytical solution of the boundary problem given by Eqs. (5.6)–(5.8) can be found by the method of variable separation \([141, 56, 110]\), which we briefly revisit below. We look for a solution using the following anzatz:

\[ u(x, t) = X(x) T(t), \hspace{1cm} (5.9) \]

where \( X \) and \( T \) are certain functions to be determined. Having substituted it into Eq. (5.6), we obtain:

\[ \frac{\omega_1 T'' + \omega_2 T' - \alpha T}{T} = \frac{DX''}{X} = -\lambda, \hspace{1cm} (5.10) \]

where \( \lambda \) is a certain constant (since the left-hand side of Eq. (5.10) is a function of time \( t \) and the middle part is a function of \( x \)). From Eq. (5.10), we obtain:

\[ DX'' + \lambda X = 0, \hspace{1cm} (5.11) \]

\[ \omega_1 T'' + \omega_2 T' + (\lambda - \alpha) T = 0. \hspace{1cm} (5.12) \]

It is readily seen that Eq. (5.11) does not have non-trivial solutions for \( \lambda \leq 0 \) to satisfy boundary conditions given by Eq. (5.7), i.e., \( X(0) = X(L) = 0 \). For \( \lambda > 0 \), the solution for Eq. (5.11) is as follows:

\[ X(x) = A \cos \left( x \sqrt{\frac{\lambda}{D}} \right) + B \sin \left( x \sqrt{\frac{\lambda}{D}} \right), \hspace{1cm} (5.13) \]

where coefficients \( A \) and \( B \) are to be found. From \( X(0) = 0 \), we obtain \( A = 0 \), and from \( X(L) = 0 \) we obtain (assuming \( B \neq 0 \)) that \( \sin \left( L \sqrt{\frac{\lambda}{D}} \right) = 0 \). The latter
leads to the following expression for $\lambda$:

$$\lambda = \lambda_n = \left(\frac{\pi n}{L}\right)^2 D, \quad n = 1, 2, 3, \ldots.$$  \hspace{1cm} (5.14)

Obviously, solution $X_n(x)$ corresponding to a given $\lambda = \lambda_n$ is

$$X(x) = X_n(x) = B_n \sin\left(\frac{\pi nx}{L}\right), \quad n \geq 1.$$  \hspace{1cm} (5.15)

Correspondingly, the equation for $T_n(t)$ is

$$\omega_1 T_n'' + \omega_2 T_n' + (\lambda_n - \alpha) T_n = 0,$$  \hspace{1cm} (5.16)

with the characteristic polynomial

$$\omega_1 r^2 + \omega_2 r + (\lambda_n - \alpha) = 0.$$  \hspace{1cm} (5.17)

The roots of Eq. (5.17) are

$$r_{1,2} = \frac{-\omega_2 \pm \sqrt{\omega_2^2 - 4\omega_1 (\lambda_n - \alpha)}}{2\omega_1}.$$  \hspace{1cm} (5.18)

The properties of the solution essentially depend on the sign of the expression under the square root, i.e., on the following quantity:

$$R_n = \omega_2^2 - 4\omega_1 (\lambda_n - \alpha) = (\omega_2^2 + 4\omega_1 \alpha) - 4\omega_1 \lambda_n.$$  \hspace{1cm} (5.19)

Since $\lambda_n < \lambda_{n+1}, n = 1, 2, \ldots$, we observe that, if

$$\lambda_1 > \frac{(\omega_2^2 + 4\omega_1 \alpha)}{4\omega_1},$$  \hspace{1cm} (5.20)

then $R_n < 0$ for any $n$. In this case,

$$r_{1,2} = \frac{-\omega_2 \pm i\sqrt{|R_n|}}{2\omega_1},$$  \hspace{1cm} (5.21)
and the solution of Eq. (5.12) is

\[ T_n(t) = e^{(-\frac{\omega_2}{2\omega_1})t} \left[ A_n \cos \left( \frac{\sqrt{|R_n|}}{2\omega_1} t \right) + B_n \sin \left( \frac{\sqrt{|R_n|}}{2\omega_1} t \right) \right]. \quad (5.22) \]

The product \( X_n(x)T_n(t) \) gives a partial solution of Eq. (5.6). Since Eq. (5.6) is linear, a linear combination of solutions is also a solution. Therefore, the general solution of Eq. (5.6) allowing for the boundary conditions given by Eq. (5.7) is:

\[ u(x,t) = \sum_{n=1}^{\infty} \sin \left( \frac{\pi nx}{L} \right) e^{(-\frac{\omega_2}{2\omega_1})t} \left[ A_n \cos \left( \frac{\sqrt{|R_n|}}{2\omega_1} t \right) + B_n \sin \left( \frac{\sqrt{|R_n|}}{2\omega_1} t \right) \right], \quad (5.23) \]

where coefficients \( A_n \) and \( B_n \) are found from the initial conditions given by Eq. (5.8). Setting \( t = 0 \) in Eq. (5.23) and using the initial condition \( h_1(x) = u(x,0) \equiv 0 \) results in the requirement that

\[ u(x,0) = \sin \left( \frac{\pi nx}{L} \right) \equiv h_1(x), \quad 0 \leq x \leq L. \quad (5.24) \]

Recognizing that this is just a Fourier Sine Series for the function \( h_1(x) \), the constants \( A_n \) must be the coefficients of that Sine Series; therefore:

\[ A_n = \frac{2}{L} \int_{0}^{L} h_1(x) \sin \left( \frac{\pi nx}{L} \right) dx. \quad (5.25) \]

In order to make use of the second initial condition, we have to differentiate Eq. (5.23) with respect to time:

\[
\frac{\partial u(x,t)}{\partial t} = \sum_{n=1}^{\infty} \sin \left( \frac{\pi nx}{L} \right) \left[ A_n \cos \left( \frac{\sqrt{|R_n|}}{2\omega_1} t \right) + B_n \sin \left( \frac{\sqrt{|R_n|}}{2\omega_1} t \right) \right] e^{(-\frac{\omega_2}{2\omega_1})t} \left( \frac{-\omega_2}{2\omega_1} \right) \\
+ \sin \left( \frac{\pi nx}{L} \right) \left[ B_n \cos \left( \frac{\sqrt{|R_n|}}{2\omega_1} t \right) - A_n \sin \left( \frac{\sqrt{|R_n|}}{2\omega_1} t \right) \right] \frac{\sqrt{|R_n|}}{2\omega_1} e^{(-\frac{\omega_2}{2\omega_1})t},
\]
where $R_n$ is defined by Eq. (5.19). For $t = 0$, from the above equation, we obtain:

$$\frac{\partial u(x, 0)}{\partial t} = \sum_{n=1}^{\infty} \sin \left( \frac{\pi nx}{L} \right) \left[ - \frac{\omega_2}{2\omega_1} A_n + \sqrt{|R_n|} \frac{B_n}{2\omega_1} \right] \equiv h_2(x). \quad (5.26)$$

This is a Fourier Sine Series for $h_2(x)$ with coefficients as

$$- \frac{\omega_2}{2\omega_1} A_n + \frac{\sqrt{|R_n|}}{2\omega_1} B_n = \frac{2}{L} \int_0^L h_2(x) \sin \left( \frac{\pi nx}{L} \right) dx. \quad (5.27)$$

Therefore,

$$B_n = \frac{2\omega_1}{\sqrt{|R_n|}} \left[ \frac{2}{L} \int_0^L h_2(x) \sin \left( \frac{\pi nx}{L} \right) dx + \frac{\omega_2}{2\omega_1} A_n \right]. \quad (5.28)$$

Obviously, regardless the choice of the initial population distribution $h_1(x)$, the solution given by Eq. (5.23) describes a population decay eventually leading, in the large-time limit, to population extinction. This is in agreement with intuitive expectations: since $\lambda_n \sim L^{-2}$, the condition given by Eq. (5.20) means that the domain is ‘too small’ to support sustainable population dynamics for the given growth rate.

The situation changes if the size $L$ of the domain is sufficiently large (or the growth rate $\alpha$ is sufficiently large), i.e., the condition given by Eq. (5.20) does not hold. The solution of Eq. (5.16) then always contains oscillatory (trigonometric) and non-oscillatory (exponential) terms.

For the purposes of this chapter, it is sufficient to consider the situation where only $R_1 > 0$ and $R_n < 0$ for $n = 2, 3, \ldots$. In this case, the time-dependent part of the first term in Eq. (5.23) changes to

$$T_1(t) = A_ne^{r_1t} + B_ne^{r_2t}, \quad (5.29)$$

where

$$r_{1,2} = \frac{\omega_2}{2\omega_1} \left[ -1 \pm \left( 1 + \frac{2\omega_1}{\omega_2} (\alpha - \lambda_1) \right)^{1/2} \right]. \quad (5.30)$$
Let, respectively, $r_1$ correspond to plus and $r_2$ correspond to minus on the right-hand side of Eq. (5.30). Then, $r_1 < 0$ for any parameter values (as long as $R_1 > 0$) but $r_2$ can change its sign, so that

$$r_2 < 0 \text{ for } \lambda_1 > \alpha \quad \text{but} \quad r_2 > 0 \text{ for } \lambda_1 < \alpha. \quad (5.31)$$

Whilst $r_2 < 0$ corresponds to an exponential decay similar to that predicted by the solution given by Eq. (5.23), in case $r_2 > 0$, the first term in the solution of the problem in Eqs. (5.6)–(5.8) grows exponentially. Therefore, the properties of the solution change when the following critical relation between the parameters takes place:

$$\lambda_1 = \alpha. \quad (5.32)$$

From Eqs. (5.32) and (5.14), we arrive at the expression for the critical size of the domain:

$$L_{cr} = \pi \sqrt{\frac{D}{\alpha}}. \quad (5.33)$$

Interestingly, the expression of Eq. (5.33) for the critical domain size for the population dynamics described by the reaction–telegraph equation coincides with the critical domain size obtained for the linear reaction–diffusion equation, e.g., see Section 3.1 in [99]. Note that the critical size does not depend on the choice of the initial conditions.

The above result is further confirmed by numerical simulations. Figure 5.1 shows the critical domain size of the reaction–telegraph equation obtained for the initial conditions as in Eq. (5.8) with $h_1(x) \equiv 1$ and $h_2(x) \equiv 0$. To perform the simulations, the telegraph equation is solved by finite differences using an implicit method. Simulations were performed for a broad range of values for parameters $\omega_1$, $\omega_2$ and $\alpha$. It is readily seen that the simulation results are in a perfect agreement with the analytical result of Eq. (5.33). Although hardly surprising as such, this
agreement between the numerical and analytical results indicates high robustness of our numerical method that produces accurate results even in the case where $\omega_1$ and $\omega_2$ differ by two orders of magnitude (see green squares in Figure 5.1).

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure5.1.png}
\caption{Critical domain size of the reaction–telegraph equation obtained numerically at various values of linear growth rate $\alpha$ and various values of $\omega_1$ as shown by different symbols and different colors. The solid blue curve corresponds to Eq. (5.33). For parameters from below the curve, the population goes to extinction; for parameters from above the curve, the population exhibits unbounded growth.}
\end{figure}

Note that, in case the size of the domain is overcritical, i.e., $L > L_{cr}$ (or $\lambda_1 < \alpha$), the solution given by Eq. (5.23) of the problem (where $T_1(t)$ is given by Eq. (5.29) predicts an unbounded growth. This is an artefact of the linear population growth. In real population dynamics, as soon as the population density is large enough, nonlinear feedback (e.g., competition) would slow down the growth and eventually stabilize the dynamics. Understanding the effects of such feedback requires a more realistic model where the corresponding term in the reaction–telegraph equation is a nonlinear function of $u$. The critical domain problem for the nonlinear model is considered in the next section.
5.4 Telegraph Equation with Nonlinear Growth

In a more realistic case, the growth rate $F$ is a nonlinear function of the population density $u$. In this case, the reaction–telegraph equation has the following form:

\[
\omega_1 \frac{\partial^2 u}{\partial t^2} + \omega_2 \frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + F(u).
\]  

(5.34)

where, $\omega_2 = 1 - \omega_1 F'(u)$, for more details see Eq. (5.2) in Section 5.1.

Our goal here is, on the one hand, to apply the reaction–telegraph equation to determine the critical population size, and, on the other hand, to establish whether the reaction–telegraph equation and the reaction–diffusion equation have the same critical size and, if their critical size is different, to reveal how large the difference can be. In case of a nonlinear growth rate, the method of separation of variables cannot be used to analytically determine the critical size. Therefore, in order to address the above matters, computer simulations have been employed.

In simulations, we use the same Dirichlet-type boundary condition as above (see Eq. (5.7)). The initial conditions are used as in Eq. (5.8), where we now consider $h_1(x) \equiv K$, where parameter $K$ is the carrying capacity (see below). This initial condition can be interpreted ecologically that, prior to the habitat fragmentation, the population was in a spatially uniform steady state. Note that, whilst the meaning of $h_1(x)$ is straightforward (i.e., the initial distribution of the population density), the meaning of $\partial u(x,0)/\partial t$ is not obvious at all. Therefore, in order to avoid the ambiguity of interpretation, we set $h_2(x) \equiv 0$.

We consider two different types of the population growth. One of them is given by the logistic growth:

\[
F(u) = \alpha u \left(1 - \frac{u}{K}\right).
\]  

(5.35)

Below, we assume $K = 1$ without loss of generality as $K$ plays the role of a scaling parameter for the population density. In terms of the notations $\omega_1$ and $\omega_2$ introduced in Section 5.3, we observe that $\omega_1 = \tau$ and $\omega_2 = 1 - \omega_1 \alpha (1 - 2u)$. 

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Simulations were performed for different values of $\alpha$ varying in a broad range. For any given set of parameters $\alpha$ and $\omega_1$, Eq. (5.34) was solved numerically by finite differences (using the implicit method) in domains of different size $L$. By distinguishing between the simulation runs resulting in species extinction and those resulting in species persistence, the critical value of the domain size was established. The results are shown in Figure 5.2. In every panel of the figure, parameter values from below the curve(s) correspond to species extinction in the large-time limit (the domain is not large enough to support sustainable population dynamics), and parameter values from above the curve(s) correspond to species survival. It is readily seen that, for a small value of $\omega_1$, the critical domain size of the nonlinear reaction–telegraph equation nearly coincides with the critical domain size of the reaction–diffusion equation. This is perhaps not surprising as, intuitively, Eq. (5.34) with $\omega_1 \ll 1$ may be expected to approximate the diffusion equation. However, the difference between the two models become significant when either $\omega_1$ or $\alpha$ is sufficiently large. The diffusion equation and the telegraph equation then have a clearly different critical size. In case of $u < 0.5$, $\omega_2$ is a decreasing function of $\alpha$, so the largest difference between the models is reached for larger values of $\alpha$.

We therefore observe that, in all cases, the critical domain size of the reaction–telegraph equation appears to be larger than the critical size of the reaction–diffusion equation. In ecological terms, it indicates that survival in small domains is more problematic for species where animals consistently employ the movement pattern with a preferred movement direction (such as the CRW or the telegraph process).

We also consider the population growth with the strong Allee effect:

\[ F(u) = \alpha u (1 - u) (u - \beta), \quad (5.36) \]

where $\beta$ is a parameter, $0 < \beta < 1$. Correspondingly, we observe that now $\omega_1 = \tau$ and $\omega_2 = 1 - \omega_1 \alpha (-3u^2 + 2\beta u - \beta)$. Simulation results are shown in Figure 5.3.
Figure 5.2: Dependence of the critical domain size on parameter $\alpha$ in case the population growth is logistic (see Eq. (5.35)): (a) $\omega_1 = 0.01$; (b) $\omega_1 = 0.1$; (c) $\omega_1 = 0.5$; (d) $\omega_1 = 1$; (e) $\omega_1 = 2$; (f) $\omega_1 = 5$. The dashed black curve shows the results obtained for the reaction–telegraph Eq. (5.34), and the solid red curve shows the results obtained for the corresponding reaction–diffusion equation, i.e., (5.34) with $\omega_1 = 0$. Other parameters are $K = 1, D = 1$. 
Figure 5.3: Dependence of the critical domain size on parameter $\alpha$ in case the population growth is subject to the strong Allee effect (see Eq. (5.36)): (a) $\omega_1 = 0.1$; (b) $\omega_1 = 0.5$; (c) $\omega_1 = 1$; (d) $\omega_1 = 2$; (e) $\omega_1 = 5$; (f) $\omega_1 = 10$. The dashed orange curve shows the results for the reaction–telegraph Eq. (5.34), and the solid blue curve shows the results obtained for the corresponding reaction–diffusion equation, i.e., (5.34) with $\omega_1 = 0$. Other parameters are $K = 1$, $D = 1$, $\beta = 0.1$. 
Similarly to the above, we observe that the difference between the two models is small if $\omega_1 \ll 1$, but may become significant if $\omega_1$ is not small, and the difference tends to be larger for larger values of $\alpha$. As above, the critical size of the reaction–telegraph equation is always larger than the critical size of the reaction–diffusion equation.

5.5 Empirical Model: Telegraph Equation with a Cutoff

One property of the telegraph equation that can make its application to real-world population dynamics somewhat questionable is that it is not positively defined [70]. It means that, for a certain combination of parameters and for certain initial conditions, its solution can become negative, at least in some areas of the domain and for some intervals of time. In our simulations of the reaction–telegraph equation, we also observed this property. Although it does not seem to be a frequent phenomenon, it may indeed happen for some parameter values. By way of an example, the left column in Figure 5.4 shows the solutions of the reaction–telegraph equation with the logistic growth, where $u$ becomes negative at some locations close to the domain boundary. After being negative for a short time (several time steps in the finite-difference procedure), the solution becomes positive again. We mention here that this negativity of the solution is not a numerical artefact, as essentially the same behaviour is observed for smaller values of the mesh steps.

Questions arise here as to what may be the reason for the non-positivity and whether the model can possibly be amended to avoid this unrealistic behaviour. We mention here that the corresponding microscopic model that considers movement of individual ‘particles’ (e.g., animals) is positively defined [71]. The non-positivity of the solution is therefore an artefact of its mean-field counterpart rather than a genuine property of the movement–reproduction dynamics as such.

One empirical way to keep the solution nonnegative is to introduce a cutoff into the finite-difference method: as soon as $u^n_i = u(x_i, t_n) < 0$, we set $u^n_i = 0$. 
Figure 5.4: Solution of the reaction–telegraph equation with the logistic growth without cutoff (left, red curves) and with the cutoff of negative values (right, blue curves): (a) Time=0.2; (b) Time=0.5; (c) Time=1; (d) Time=20. Parameters are $\omega_1 = 4$ and $\omega_2 = 1 - \omega_1 F'(u)$. The circles mark the location of the areas where the solution becomes negative.
**Figure 5.5:** Solution of the reaction–telegraph equation with the Allee function without cutoff (left, red curves) and with the cutoff of negative values (right, blue curves): (a) Time=0.2; (b) Time=0.5; (c) Time=1; (d) Time=20. Parameters are $\omega_1 = 4$ and $\omega_2 = 1 - \omega_1 F'(u)$. The circles mark the location of the areas where the solution becomes negative.
Since we have observed in our simulations that, if the solution becomes negative, it only attains small values, one can expect that the perturbation introduced to the solution by the cutoff is likely to remain small. In order to look into this issue, for the same set of parameter values and initial conditions, we performed simulations with and without cutoff. We obtained that the solution of the reaction–telegraph equation was robust to the cutoff procedure and eventually produced almost the same distribution of the population density. The left column in Figure 5.4 shows the solution without cutoff and the right column shows the solution after a cutoff was implemented at $t = 0.5$. There is no visual distinction between the corresponding panels in the left and the right columns of the figure. Similar results are obtained in the case of the strong Allee effect as shown in Figure 5.5.

In order to get a more quantitative insight into the evolution of the perturbation introduced by the cutoff, we calculated the ‘error’—the difference between the solutions with and without cutoff—as a function of time and space. Figures (5.6 - 5.7) show the distribution of error over the domain at time $t = 0.5$ (i.e., immediately after the cutoff was done), as corresponds to the second row in Figures (5.4 - 5.5) respectively. The error is non-zero only in small areas close to the domain boundaries where the solution became negative. Figure 5.8a shows how the maximum error over the domain (i.e., the maximum of functions shown in Figure 5.6) evolves with time and logistic growth rate. It is readily seen that the maximum error promptly decays with time, eventually reaching very small values. Figure 5.8b shows the distribution of error over space at time $t = 20$, i.e., as corresponds to the bottom row in Figure 5.4. Furthermore, Figure 5.9(a-b) show the maximum error over the domain along with time and it shows the distribution of error over space at time $t = 20$, under the Allee effect function.
Figure 5.6: Distribution of the error $\| u - u_{\text{cutoff}} \|$ over space at $t = 0.5$, i.e., immediately after the cutoff was implemented. (Left) distribution over the whole domain $0 < x < L$; (Right) a magnified view of the part of the domain close to the left-hand side boundary.

Figure 5.7: Distribution of the error $\| u - u_{\text{cutoff}} \|$ over space at $t = 0.5$, (Left) distribution over the whole domain; (Right) a magnified view of the part of the domain close to the left-hand side boundary.
Figure 5.8: (Left) maximum error as a function of time; (Right) distribution of error $\| u - u_{cutoff} \|$ over the domain $0 < x < L$ at $t = 20$.

Figure 5.9: Graphs showing the error $\| u - u_{cutoff} \|$ corresponding to distribution space

5.6 $\delta$-type initial condition:

Different initial conditions can lead to different dynamics resulting in solutions with different properties. This section discusses the impact of $\omega_1$ on dynamic behaviour whilst also considering the Allee effect with Dirichlet boundary conditions, taking the form:

$$u(0,t) = 0, \quad u(L,t) = 0.$$  \hspace{1cm} (5.37)
For instance, when considering the problem of biological invasion, the initial condition has the form:

\[
  u(x, 0) = h_1(x) = \begin{cases} 
    u_0 & x \in \delta, \\
    0 & x \notin \delta,
  \end{cases}
\]

\[
  u_t = (x, 0) = h_2(x) = 0,
\]

with interval \( \delta \) as indicated in Figure 5.10.

![Figure 5.10: Sketch of the initial condition of \( \delta \)-type, with the length and \( u_0 \) being indicated](image)

The purpose is still to determine the critical size of the telegraph equation (i.e. 5.38). The problem of critical size now has a different meaning: we talk about the "size" of the initial distribution not the length of the domain. One important difference in the system properties is that for the logistic growth the population always survives regardless of the values \( u_0 \) and \( \delta \).

To this end, the simulation was conducted repeatedly with different \( \omega_1 \) values and constant value of Allee threshold \( \beta = 0.1 \). In accordance with Lewis [97], three distinct growth rate possibilities were taken into account; for more details see Eqs. (2.6), (2.7) and (2.8) in Section 2.2.
The parameter plane \((u_0, \text{Length})\) of the initial condition (5.38) is illustrated in Figure 5.11. Here (a), (b) and (c) correspond to population growth rate, which is shown on a scale of Eqs. (2.6-2.8).

![Figure 5.11](a) (b) (c)

**Figure 5.11:** The parameter plane \((u_0, \text{length})\) of the domain from Figure 5.10. The population growth rate scaled on the basis of (2.6-2.8) is shown in (a), (b) and (c). Parameter \(\omega_1\) is given in the figure legend, and \(\omega_2 = 1 - \omega_1\alpha(-3u^2 + 2\beta u - \beta)\). For parameters from domain 1 the population persists, for domain 2 it goes extinct.

Figure (5.11) clearly identifies that, in all cases, with an increase in \(\omega_1\) population survival becomes easier as the range of values of \(u_0\) and the length, for which survival is observed, becomes wider. Furthermore, when \(\omega_1\) has a very small value, for instance 0.01 or 0.1, the critical size of the telegraph equation is the same as the critical size of the diffusion equation. This is simply because, when \(\omega_1\) is very small, the second derivative part \(\frac{\partial^2 u}{\partial t^2}\) in Eq. (3.1) is very close to zero, and so the equation will turn into diffusion equation. Interestingly, the
strength of this effect of $\omega_1$ depends on the scaling of the growth rate, as detailed in Eqs.(2.6-2.8), the effect is the weakest when $\gamma = \text{constant}$ (cf.Eq.(2.6)) while, the strongest effect is when $\gamma$ scaling is Eq.(2.7).

Overall, the population with animal movement exhibiting directional persistence (telegraph equation) has a higher chance of survival than animals who move without directional persistence (diffusion equation).

5.7 Discussion and Conclusions

For several decades, the main mathematical framework for modelling animal movement and dispersal was based on the simple isotropic random walk model (SRW) which is unbiased in the sense that, at any moment, the walker can move in any possible direction [168]. This means that the movement direction taken at any given time is independent (uncorrelated) of the movement direction at the preceding moment. The CRW is an extension of the SRW that accounts for the persistence in the walker’s direction of movement [64, 71, 78, 109, 175]. Indeed, in most real-world systems, the walker is more likely to move in a direction similar to the previous one. This is known as persistence and it can be combined with a fixed speed of movement in the random walk process, resulting in the telegraph or velocity-jump processes [12, 18, 64, 177]. Our baseline model (5.1), i.e., the 1D telegraph equation is the mean-field counterpart for the simplest one-dimensional CRW; it includes SRW (the diffusive movement) as the limiting case when the persistence vanishes, i.e., for $\tau \to 0$.

Being thus a model presumably more adequate than the reaction–diffusion equation, questions arise as to what the properties of the reaction–telegraph equation can be in a relevant ecological context and how different they may be from those of the corresponding reaction–diffusion equation. In this chapter, we addressed these questions in the context of habitat fragmentation and species survival in small domains. Having considered the critical domain problem for the reaction–telegraph equation, we arrive at the following conclusions:
• In the case of a linear reaction term (i.e., linear population growth), we found that the critical domain size for the reaction–telegraph equation coincides with that of the corresponding reaction–diffusion equation. This seems to be a surprising result as intuitively the more directional animal movement described by the reaction–telegraph equation should result in a larger critical size.

• In the case of a nonlinear growth (either logistic or with a strong Allee effect), we found that the critical size of the reaction–telegraph equation is indeed somewhat larger than that of the corresponding reaction–diffusion equation. Thus, the difference between the two models arise as a result of a subtle interplay between the movement pattern and the nonlinearity of the population growth.

Our study has potentially important implications for ecology and nature conservation, in particular by means of providing better understanding of the effect that biologically meaningful factors (such as the animal movement pattern and the type of the growth rate) may have on the minimum domain size required to prevent extinctions. However, since the reaction–telegraph equation is widely used in various branches of science and engineering, our findings are likely to have broader range of applications. Traditionally, the telegraph equation was used to describe the voltage and current that can be found on electrical transmission line. In particular, the telegraph equation was studied by Lord Kelvin in relation to the signals that propagate across the transatlantic cable. The telegraph equation has also been used to model various problems in wave propagation and signal analysis more generally [76, 148], random walk theory [12], transport in heterogeneous porous media [18] and pulse transmission through a nerve axon [59, 117]. It also has applications in other fields, in particular, it has been used to model transport processes in physical, biological, social, and ecological systems [1, 2, 10, 63, 112, 148, 170]. Understanding the problem of critical size in those wide-ranging specific contexts is likely to result in exciting new research.
Chapter 6

Conclusions

Understanding the dynamics of species and communities in complex environments is a major focus in ecology. The problem has recently been exacerbated by the global climate change that tends to amend and reshape species habitats, and by anthropogenic activities that often result in habitat fragmentation. The latter is known to be the main factor that results in biodiversity loss worldwide.

In this thesis our main goal was to study the population dynamics in complex environments by means of mathematical modelling. Specifically, we focused on three inter-related questions:

1. How the size and shape of a species’ habitat affect its survival?

2. How the survival success in a small habitat may depend on animal’s movement behaviour?

3. How the spread of invasive species may be affected by a complex geometry of the environment (i.e. by the existence of barriers, corridors, stepping stone, etc.)?

The problems were studied using a combination of analytical tools of nonlinear dynamics and numerical simulations. To perform simulations, the equations were solved by finite differences. A nontrivial aspect of the numerical algorithm was the approximation of the complex shape of the habitat.
Chapter 1 provides a literature review on biological invasions and the underlying ecological mechanisms. Chapter 2 explores the ways in which population dynamics are affected by the shape and size of fragmented habitats. We have studied the properties of a single-species population dynamics in a 2D domain of a complicated shape (e.g. cross-shaped or H-shaped). Population growth is hampered by a strong Allee effect. We considered different relations between the per capita growth rate and the threshold density, which is thought to correspond to different evolutionary strategies. Our results indicate the following: (i) for domains of simple shape (e.g. rectangle), the effect of the critical patch size (amplified by the Allee effect) is similar to what is observed in 1D space, in particular, the likelihood of population survival is determined by the interplay between the domain size and the strength of the Allee effect; (ii) in domains of complicated shape, for the population to survive, the domain area needs to be larger than the area of the corresponding rectangle. Hence, it can be concluded that species survival depends on the details on the shape, not on the overall size of the domain as was previously thought.

In Chapter 3, we address the effect of the existence of stepping stones on the invasive species spread. We consider a reaction-diffusion model in a domain of a complex shape combining corridors and stepping stones. We show that the invasion success depends on a subtle interplay between the stepping stone size, location and the strength of the Allee effect inside. In particular, for a stepping stone of a small size, there is only a narrow range of locations where it can unblock the otherwise impassable corridor. The results are shown to remain essentially the same in domains with different symmetries and for different normalizations of the growth rate, which points out at their generality.

Chapter 4 addresses the effects of the landscape geometry (as given by the size and shape of inaccessible area) on the patterns and rates of invasive species spread in complex environment by considering the spatiotemporal dynamics of an alien species in a domain where two large uniform habitats are connected by a narrow corridor. We consider the case where the species is originally introduced
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into one of the habitats but not to the other. The alien species is assumed to be affected by a predator, so that mathematically our system consists of two coupled diffusion-reaction equations. We show that the corridor tends to slow down the spread: it takes the alien population an extra time to penetrate through the corridor, and this delay time can be significant in the case of patchy spread. We also show that a sufficiently narrow corridor blocks the spread; simple analytical estimates for the critical width of the corridor are obtained. Finally, we show that the corridor can become a refuge for the alien population. If considered on a longer timescale that includes species adaptation and/or climate change, the corridor may then become a source of a secondary invasion.

The models used in Chapter 2-4 consisted of reaction-diffusion equations. However, the reaction-diffusion framework is open to some criticism. A telegraph equation is believed to be an appropriate model of population dynamics as it accounts for the directional persistence of individual animal movement. Being motivated by the problem of habitat fragmentation, in Chapter 5 we consider the reaction-telegraph equation (i.e., telegraph equation combined with the population growth) on a bounded domain with the goal to establish the conditions of species survival. We first show analytically that, in the case of linear growth, the expression for the domain’s critical size coincides with the critical size of the corresponding reaction-diffusion model. We then consider two biologically relevant cases of nonlinear growth, i.e., the logistic growth and the growth with a strong Allee effect. Using extensive numerical simulations, we show that in both cases the critical domain size of the reaction-telegraph equation is larger than the critical domain size of the reaction-diffusion equation. Finally, we discuss possible modifications of the model in order to enhance the positivity of its solutions.

The results obtained in this thesis can be useful in the context of nature conservation, e.g. either helping to choose an efficient design of nature protection areas or to control/predict the spread of invasive species.

For the future work, we could extend the reaction-telegraph framework to 2D to fully understand the population dynamics. It would also be interesting to
study the critical domain problem for the other models of population dynamics such as Fokker-Planck diffusion reaction equation and Cahn-Hilliard equation.
Bibliography


