Global dynamics of diffusive animal movement models under habitat degradation, destruction, and fragmentation: eigenvalue problems and geometry at the landscape scale

by

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Abstract

Habitat loss is a significant problem and the leading cause of species extinctions and decreases in biodiversity worldwide. This issue is primarily driven by human activities, making it crucial to understand the consequences of our actions as a global community. The empirical study of habitat loss is complex, expensive, and time-consuming. Moreover, habitat is being lost at an accelerating rate, and so there is a substantial need for a timely assessment of the impacts of habitat loss. Fortunately, mathematical modelling allows us to assess the impacts of different aspects of habitat loss in a general setting, applicable to numerous species in various environmental scenarios.

In this dissertation, we delve into three critical aspects of habitat loss: habitat degradation, habitat destruction, and habitat fragmentation. By employing the framework of reaction-diffusion equations, we investigate the global dynamics of single and multi-species models under different forms of habitat loss. This analysis includes a detailed exploration of the global dynamics of time-dependent single and multi-species models using tools from the theory of partial differential equations and the theory of monotone flows. We develop robust modelling frameworks specific to habitat loss processes derived from a careful consideration of the ecological definitions of these forms of habitat loss. Of significance is a rigorous, analytical connection between the degradation and destruction formulations through an asymptotic limit. This connection between habitat degradation and destruction appears to be the first of its kind, establishing a connection consistent with the observation that the level of degradation of different habitats lies on a spectrum, ranging from *intact* to *destroyed*.

A central object of study in this analysis is the so-called principal eigenvalue, which, in our context, provides a theoretical net growth rate of the population, at least for small population sizes. By examining these principal eigenvalues, we can assess habitat fragmentation's impact independently of or in conjunction with habitat degradation and destruction. This results in a fitness index intimately dependent on the arrangement and geometry of the degraded/destroyed regions. Compared to existing measures of habitat fragmentation, our approach offers a mechanistic and species-oriented tool, providing unique insights into the effect of fragmentation on diffusive species while also providing a robust framework for translation to other environmental factors or non-diffusive movement mechanisms.

Importantly, this framework is versatile enough to be applied to both the landscape and patch scales. It is essential to note that fragmentation is often studied at the patch scale, which can lead to misleading conclusions regarding the overall impact of habitat fragmentation. Since habitat fragmentation is sometimes measured empirically in ways incompatible with our fitness index metric, we also examine the impacts of habitat fragmentation on the theoretical total abundance of a population, considered for both single- and multi-species models.

In all assessment methods, we consider fragmentation as an arrangement and a process. By doing so, we take into account the spatial distribution of habitats and the changes that may occur over time, relating more closely to habitat fragmentation as it occurs in the natural world. In turn, this allows us to analyze habitat loss's consequences more comprehensively and generate more accurate conclusions about the effects on species populations.

This dissertation presents a detailed and thorough investigation of habitat loss and its impacts on species, focusing on the connections between habitat degradation, destruction, and fragmentation. By employing mathematical modelling and the framework of reaction-diffusion equations, we are able to study the global dynamics of single and multi-species models under different scenarios of habitat loss. This work provides numerous assessment tools and viable hypotheses which can be tested and verified, either experimentally or in the field, giving precise mechanisms and, ultimately, answers to some of the most pressing questions surrounding the complex effects of habitat loss.

Preface

This dissertation is broken into three main chapters which consider habitat degradation, habitat destruction, and habitat fragmentation. The second chapter, concerning habitat *degradation*, is based on the work published with my current supervisors, Dr. Hao Wang & Dr. Zhongwei Shen. This was published in the Journal of Mathematical Biology in 2022 [104]. In the present work, the results are generalized further to include cases not previously considered.

The third chapter, concerning habitat *destruction*, is based on work also done with my current supervisors. Similar to the degradation chapter, the work of chapter three provides more detail than would otherwise be found in publication. There is also a direct development of the theory for linear equations in the 'destruction' setting, which is less appropriate for a scientific paper, but is great to include in a dissertation setting.

The fourth chapter, concerning habitat *fragmentation*, contains the most recent results obtained during the final year of my doctoral degree. This chapter is a slight departure from the previous two in that the mathematical analysis is less developed, and so we appeal to the use of numerical simulation to complement the analytical insights. As one may soon read, this is a requirement if we really want to study fragmentation in an ecologically meaningful way, as analytical results are incredibly challenging to obtain for 'geometric' problems in partial differential equations in general.

Throughout this work, a number of numerical simulations are used to compliment the analytical insights. All of these are done using the MATLAB software.

As a final note, shifting to first person momentarily, this work is centred in the field of *mathematical biology*; yet, I must admit that *biology* or *ecology* was never particularly motivating, at least prior the start of my doctoral degree. My background, both in my undergraduate degree and in my master's degree, was in the theoretical analysis of partial differential equations. While there was always a loose connection to biological, chemical, or physical phenomena, this was not the selling point of the work, so to speak. I do not think I appreciated it at the time, but the analysis and the analysis alone was the motivating factor of my work.

Starting my PhD at the University of Alberta, I have since had the pleasure of working with some of the top experts in mathematical biology the field has to offer. Through these interactions I have, I believe, begun to understand how mathematics can be connected and used to describe the natural world in greatly diverse ways. In my own work, this includes a deeper understanding of the types of problems I am familiar with mathematically, but had never studied from the perspective of *yes, but what do these analytical results tell us*? I had not even seen a simple derivation of the heat equation before taking a graduate level Mathematical Biology course at the University of Alberta. In hindsight, this feels somewhat embarrassing.

The point of all of this is: the thesis you are about to read, whether intentional or not, seems to reflect my own personal journey, moving from a very theoretical standpoint to a much more applied point of view. This is not to say that the work *actually* becomes more applied as we progress; indeed, this does not seem to be the case. Instead, what is reflected as the thesis progresses is my own change in attitude towards these problems. This paradigm shift has been an important one, and I hope that it is reflected in this work.

To Atticus

For teaching me everything I need to know about ~~math~~ life.

You are not controlling the storm, and you are not lost in it. You are the storm.

– Sam Harris.

Who would have guessed reading and writing would pay off?

– Homer Simpson.

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The process of understanding is a collective one, and I am deeply grateful to all those who have contributed to my intellectual growth and development. I could not have done this without the people I have been fortunate enough to be surrounded by. I am honoured to have learned from you all.

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Chapter 1

Introduction

1.1 On "Habitat Loss"

Habitat loss is one of, if not the contributing factor to the loss of biodiversity worldwide [65], including birds [115], mammals [3], reptiles [51], amphibians [114], invertebrates [26], and plants [69]. While some forms of habitat loss are naturally occurring (e.g., flooding, geological processes, other substantial weather events), the unfortunate reality is that the majority of habitat loss is a result of human activity [25], [97], [98], especially through deforestation, agricultural development and urbanization, but also through resource extraction, pollution, climate change, trawling, and more. On one hand, we have a broad understanding of the impacts of habitat loss on local species populations. This can be seen through some prototypical mathematical models that capture the relative effects of habitat loss on competing species ([116] is a classic example), as well as empirical studies that span decades [18], [97]. As a result of reduced biodiversity, cascading effects include decreased pollination and seed dispersal, decreased climate regulation, and diminished pest and disease control [29]. On the other hand, when seeking more precise descriptions of the relative impacts of differing forms of habitat loss, such as *degradation*, *destruction*, and *fragmentation*, there are many competing ideas.

Perhaps the lack of clarity stems from a lack of consistency in terms and definitions used across disciplines and research areas. On the empirical side, for example, the definition(s) of *habitat loss*, as well as the related concepts commonly used to describe and study these phenomena, (e.g., habitat, patch model, landscape scale, measurement effects, etc.), are not so clear. Indeed, some authors have noted these issues explicitly and the downstream effects these oversights can have [72]. In some cases, different empirical studies and setups result in different directions of effect. This is best exemplified by differing mechanisms and interpretations of habitat fragmentation [39], [46], [49]. Ultimately, this leads to further confusion, especially for policymakers, when the science that should be informing their decisions is inconclusive at worst, and not entirely convincing at best. To further exacerbate these issues, this lack of consistency has spilled into the modelling literature as well. Given the accelerated rate of habitat loss worldwide [25], we may not have the time to appeal to continued data collection and observation; the timescales at which negative effects are realized may not be commensurate with the timescales of data collection, or more importantly, the timescales at which we may meaningfully respond as a human collective.

Why should we care?

We first ignore the question of what habitat loss is, exactly, and instead focus on why we should care about its consequences in a more broad sense. The argument is obvious: humans, as a species, are a part of the natural world and benefit from the resources it provides. These benefits are referred to as *ecosystem services* in the ecological literature [22]. We have become incredibly efficient at using the resources on offer. This has led to a massive increase in population (we are currently around 8 billion people; in 1992, the year I was born, there were around 5.5 billion people; in 1951, $<$ 75 years ago, there were around 2.6 billion people).

Unfortunately, however, this increase in efficiency comes with costs, and these costs are conveniently delayed, often at a time scale that allows for downplaying of consequences through arrogance, willful ignorance, or both. Humans, generally speaking, like (and sometimes, admittedly, *need*) *stuff*. Once a population has determined that it likes a certain *thing*, economic theory suggests that a “free market” will minimize the cost associated with producing said *thing* through competition, supply, demand, and so on, allowing many people to enjoy said *thing* at a minimal cost. Alas, this minimization procedure does not often take into account other negative consequences of such processes, let alone address potential long term consequences. This minimization of cost, as a consequence, is not often innovative, but instead transfers the cost to others elsewhere, both in space or in time. This point is made eloquently in *Nature's Services: Societal Dependence On Natural Ecosystems* [22] over two decades ago:

> "In the space of a single human lifetime, society finds itself suddenly confronted with a daunting complex of trade-offs between some of its most important activities and ideals. Recent trends raise disturbing questions about the extent to which today's people may be living at the expense of their descendants, casting doubt upon the cherished goal that each successive generation will have greater prosperity. Technological innovation may temporarily mask a reduction in earth's potential to sustain human activities; in the long run, however, it is unlikely to compensate for a massive depletion of such fundamental resources as productive land, fisheries, old-growth forests, and biodiversity."

We then beg the question, *how* do these negative effects of habitat loss actualize? The general hypothesis, now widely agreed upon, is that habitat loss is the primary contributing factor to the global decline in biodiversity. Biodiversity refers simply to the variety and variability of organisms, ranging from the gene level to the ecosystem level. This decrease in diversity is a direct consequence of habitat loss, and the realized negative effects described above are symptoms of this decline. These interactions are not well understood, so it is not possible to give concrete answers in a general sense to questions such as *when will this species go extinct?*, or *how much land can we remove before extirpation of a local population?*. However, we present a few case studies to highlight some of the underlying mechanisms we see these negative effects.

- **Bananas:** Banana crops suffer from disease outbreaks due to the use of *crop monocultures.* This means that, since the banana population in crops are very homogeneous (genetically speaking), disease outbreaks are much more likely, which reduces yield, alters appearance, shelf life, and marketability; debilitates the host plant, or at worst, kills the plants [100]. The conversion of natural ecosystems to monocultural plantations (an example of minimizing cost and maximizing yields), has devastating effects on the local environment.

- **Coffee beans:** Climate change, a broad form of habitat degradation, can affect coffee bean production through a reduction in quality and yield, as well as increased exposure and sensitivity to certain insects and diseases [40].
- **Climate regulation:** Forests and tropical forests are well-known for their role in carbon capture [6], [73]; a removal of these ecosystems naturally reduces their capacity to continue to do so! Forests are also useful in temperature regulation, regulating freshwater flows, and more [6]; indeed, forests' interactions with carbon should be seen "*as one co-benefit of reforestation strategies designed to protect and intensify the hydrologic cycle and associated cooling*" [30].
- **Loss of pollinators:** Pollinators provide an essential service to ecosystems, and habitat loss is a primary driver of their decline [101]. While pollination can occur naturally through, e.g., wind, a majority of plants rely on animals. The destruction of the habitat of pollinators has the downstream effect of drastically impacting cultivated and wild plants alike.

Hence, habitat loss does not directly affect humans nearly as often as it does indirectly through other negative consequences[3], and these consequences do not impact everyone equally. To better parse these complexities, mathematical modelling offers a unique perspective to better understand the consequences of habitat loss on species and biodiversity in general.

How to model habitat loss

In the present work, the phenomenon we are most interested in is that of *habitat loss*; but, this is somewhat misleading, as habitat loss is *not* a single, well-defined occurrence [82]. It is the author's opinion that clarifications are desperately needed

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[3] This is not to discount special cases, such as indigenous tribes that live in tropical forests: deforestation practices directly affect their population by destroying their home [102].

due to gaps in the connection between the mathematical and ecological study of habitat loss. Admittedly, the following is by no means a *new* argument, at least at the meta level; such points have been raised a number of times for habitat loss specifically [32], [33], [39], [44], [46], [49], but also in other areas of ecology [57]. Yet, there is still a lack of clarity in the wider literature. For this reason, we take a detour to elucidate some common points of confusion.

First, a non-trivial question to ask is: what is *habitat*? As asserted in [49], [57], habitat is sometimes used synonymously with concepts of *vegetation type* or *landscape features* more generally. Understanding that this has evidently led to ambiguity and confusion, we opt for a more precise definition.

Definition 1.1.1 (Habitat [57]). *The resources and conditions present in an area that produce occupancy - including survival and reproduction - by a given organism. Habitat is organism-specific; it relates the presence of a species, population, or individual (animal or plant) to an area's physical and biological characteristics.*

We refer to a general region of interest as a landscape, with the distinction being that a given landscape is independent of the species occupying it. Our models will be formulated at the *landscape* scale, with some regions comprised of *habitat* as defined above, and other regions comprised of *non-habitat.*

In particular, we note that habitat is *not* mere vegetation type or structure; it is the accumulation of particular landscape features required by an organism to survive and reproduce. Given an area where an organism is provided with resources (food, water, shelter, etc.) that allow it to survive, it is habitat. This perspective will be important when we develop our models later.

We now ask: what is habitat loss? Even those far removed from its study can imagine that habitat loss must be related to the removal of natural habitat by some means - it is in the term itself, the habitat is lost! For example, on February 6, 2023, the top Google search result from *The National Wildlife Federation* provides the following description:

> "Habitat loss—due to destruction, fragmentation, or degradation of habitat—is the primary threat to the survival of wildlife in the United States.

> When an ecosystem has been dramatically changed by human activities—such as agriculture, oil and gas exploration, commercial development, or water diversion—it may no longer be able to provide the food, water, cover, and places to raise young that wildlife need to survive."[56]

The second search result, found on Wikipedia[2], gives the following description:

> "Habitat destruction (also termed habitat loss and habitat reduction) is the process by which a natural habitat becomes incapable of supporting its native species. The organisms that previously inhabited the site are displaced or dead, thereby reducing biodiversity and species abundance."[55]

One may note that neither provides a *definition* of habitat loss, which may indeed be intentional. Between these two descriptions, there are notable similarities and distinctions. The similarities between the two are *changes to natural habitat* and *the impact these changes have on local species*. This is a good start, perhaps, as it aligns with the intuitive understanding of habitat loss described earlier; but, there are several key differences that produce more questions than answers.

In the first definition, we immediately notice three subcategories of habitat loss, namely *degradation*, *destruction*, and *fragmentation*. This appears to be at odds with the second definition, where habitat *loss* is equivalently termed habitat *reduction* or habitat *destruction*, while degradation and fragmentation are nowhere to be found. Similarly, the first definition attributes habitat loss directly to human activities while the second does not. Human activities are understood to be a primary driver of habitat loss [25], [106] (in some sense that will be made clearer), but can also be a consequence of events less directly connected to human activity (forest fires are one such example). The second definition of habitat loss does not make such an anthropomorphic distinction. Furthermore, the first definition leaves some ambiguity as to what extent species need to be affected by habitat changes in order for the habitat to be considered

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[2] Of course, one should delve into the citations provided for these definitions rather than working directly from Wikipedia - this is not the purpose of this exercise; instead, we are looking at what a layperson may first find should one do their own research

"lost". On the other hand, the second definition appears to *require* local species to be displaced or wiped out entirely for the habitat to be considered lost.

Keen readers may tacitly claim that this is a strawman argument: these descriptions were pulled from a google query, and so surely do not represent the more academic exploration of habitat loss from the ecologists' point of view. To conclude this point more concretely, Table 1.1 compiles a handful of definitions used for some key terms introduced here. This includes *habitat loss*, *habitat degradation*, *habitat destruction*, *habitat fragmentation* and *habitat fragmentation per se*. Note that these definitions were taken from papers that included them in an explicit way. This table, similar to those found in [49] or [57], highlights more clearly the concern: these definitions are woefully inconsistent at best and contradictory at worst! What is even more unfortunate, perhaps, is the fact that *many* references studying these phenomena *do not even provide a working definition of the term*!

This discussion is not all encompassing, but highlights some of the potential issues when trying to model these processes using mathematical tools: we require underlying assumptions and precise definitions of the processes being modelled. Initially, what we find instead are *descriptions of the consequences of environmental modification on species*. In such a case, habitat loss is, by definition, the end result of species decline upon modification of the habitat (presumably in a negative way). This may be a suitable formulation for an ecologist, but it is wholly inadequate and outright misleading from a modelling perspective. If the mathematician has an idea of what habitat loss is, but their idea is inconsistent with the idea that the ecologist holds, it becomes very difficult to utilize interdisciplinary communication. In fact, this mismatch may even invalidate the model to begin with! Of even more consequence, perhaps, are cases where models are meant to be connected to observations of empirical data - a mismatch between a model formulation and data collection casts doubt on any concrete conclusions drawn.

The general thrust being made here is simple: before diving into deeper scientific questions and insights, we must first clearly define our terms so that we all know what we are talking about! If terms cannot be clearly well defined, this aspect should also

Term	Definition provided	Ref.
Habitat loss	“A change to an area that prevents a species from living there (e.g., conversion of forest to crop field)”	[72]
	“... a process whereby habitat is destroyed over time.”	[37]
	“When natural land cover is converted to anthropogenic land cover.”	[39]
Habitat degradation	“Of the surviving habitat, much is being degraded in various ways—such as by habitat fragmentation, increased edge effects, selective logging, pollution, overhunting, altered fire regimes, and climate change.”	[82]
	“Habitat degradation is often a slow transformation from optimal to sub-optimal habitat, wherein habitat quality is reduced and habitats are less able to provide the appropriate conditions (i.e., resources) for individual survival and population persistence.”	[65]
Habitat destruction	“Habitat destruction occurs when a natural habitat, such as a forest or wetland, is altered so dramatically that it no longer supports the species it originally sustained. Plant and animal populations are destroyed or displaced, leading to a loss of biodiversity.”	[82]
Habitat fragmentation	“...is heterogeneity in its simplest form: the mixture of habitat and non- habitat. However, the effects of habitat fragmentation is also dependent on the composition of non-habitat. The matrix of non-habitat may have a positive, negative, or neutral effect on adjacent habitat... Thus, to define habitat fragmentation adequately, habitat must first be defined at a scale relevant to the species being examined.”	[49]
	“The breaking apart of habitat into several smaller pieces. Habitat fragmentation results in both habitat loss and fragmentation per se.”	[72]
	“When a large expanse of habitat is transformed into a number of smaller patches of smaller total area, isolated from each other by a matrix of habitats unlike the original’”	[122]
	“Altered spatial configuration of habitat for a given amount of habitat loss.”	[46]
	“Fragmentation is defined (literally) as the breaking apart of habitat; note fragmentation does not imply loss of habitat.”	[36]
	“Habitat fragmentation, by definition, is the “breaking apart” of continuous habitat, such as tropical forest or semi-arid shrubland, into distinct pieces.	[82]
	“...often thought of as a process involving both the loss and the breaking apart of habitat.”	[37]
	“...a landscape-level process in which a specific habitat is progressively subdivided into smaller and more isolated fragments.”	[74]
Habitat fragmentation *per se*	“Habitat fragmentation independent of habitat amount.”	[39]
	“...if there is no habitat loss, [fragmentation per se] comprises the altered spatial configuration of habitat, such that remaining patches are smaller but more numerous.”	[20]
	“...significant responses to fragmentation independent of the effects of habitat amount (here-after referred to as habitat fragmentation).”	[37]

Table 1.1: A compilation of definitions of common terms found and used in the literature.

be highlighted explicitly rather left vague and up to interpretation. For this reason, we will take a moment to explore some of the key terms found in the literature surrounding habitat loss, primarily from the perspective of the ecologist. This exploration will lead us to a handful of *postulates*, which are useful guiding tenets or heuristics that are ecologically reasonable while providing guidance into how one may incorporate key aspects of habitat loss in a mathematical setting.

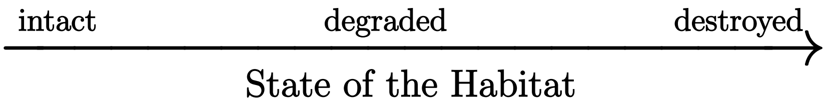
Despite their shortcomings, these descriptions of habitat loss still give us some useful information. In particular, the first definition highlights three (possibly distinct) processes closely related to habitat loss. We define these more clearly now.

Definition 1.1.2 (Habitat Degradation [82]). *A general term describing any set of processes resulting in a decrease in quality of habitat.*

Definition 1.1.3 (Habitat Destruction [82]). *When a natural habitat is altered so dramatically that it no longer supports the species it originally sustained.*

What may be useful to note is the following caveat: total destruction of a natural habitat is much less common than one might think. Instead, habitat quality is often reduced while simultaneously increasing its level of heterogeneity. This process can take a long time, and so it is difficult to say exactly when the habitat has become "destroyed" except for in very extreme cases. This suggests that the line between degradation and destruction is fuzzy, and these are instead two ends of a spectrum, ranging from *not at all degraded* to *completed degraded.* At the point of total degradation, the habitat can be considered destroyed. This is the convention we will use throughout this manuscript when we discuss habitat degradation and/or destruction. Furthermore, this will align in a favorable way with model formulations to be introduced later. In this sense, definitions 1.1.2 and 1.1.3 will be agreeable to a majority of biologists/ecologists while also providing an implicit mechanism suitable for mathematical description.

<u>**Postulate One:**</u> Habitat degradation and habitat destruction lie on a spectrum.



Another interesting distinction gleaned from this discussion is the alteration of habitat, and the *impact* said alteration(s) have on local species. From the ecologists' perspective, some argue that one cannot and should not separate these two aspects [33], [72]. The difference here is therefore purely mathematical: from the modelling point of view, it is conceptual to describe habitat loss independent of the effect on species. One can imagine a scenario in which habitat is "lost" by some means, but some subset of local species (bacteria, insects) are more/less affected than others (large mammals). This suggests that not only does the process of habitat degradation/destruction lie on a spectrum, but it is also species dependent: properties of the population itself may determine whether a particular instance of habitat loss is better or worse than another, leading to the following.

Postulate Two: Habitat and habitat quality, however described, is species dependent. The exact same observable characteristic(s) of a given landscape (food, water, shelter, availability of space, etc.) may be ideal for some species while terrible for another. In this sense, habitat loss in any form should not be viewed in a vacuum.

This distinction between habitat loss *independent of impact*, and habitat loss *as it effects local species*, becomes more important when one considers habitat fragmentation. Fragmentation, in a general sense, is defined as follows.

Definition 1.1.4 (Fragment (noun) [47]). *A part broken off or detached; an isolated, unfinished or incomplete part.*

Definition 1.1.5 (Fragment (verb) [47]). *To collapse or break into fragments; to divide into fragments: disunify*

Definition 1.1.6 (Fragmentation [47]). *The act or process of fragmenting; the state of being fragmented.*

Habitat fragmentation, as previously discussed, is a much more precarious term. A common definition of habitat fragmentation is the following.

Definition 1.1.7 (Habitat Fragmentation (vague)).

- *A process by which large and contiguous habitats get divided into smaller, isolated patches of habitats [33], [38];*

- *Landscape transformation that includes the breaking of large habitat into smaller pieces [48].*

Funnily enough, the first definition, taken again from Wikipedia, follows the term "*more specifically*"; the comedy here being that this is not very specific at all! The second definition from another author is similar. While they capture the rough idea behind habitat fragmentation, it is a difficult definition to work with from a modelling perspective. A slightly more useful definition, perhaps, is the following.

Definition 1.1.8 (Habitat Fragmentation (more precise) [33])**.** *The process during which a large expanse of habitat is transformed into a number of smaller patches of smaller total area isolated from each other by a matrix of habitats unlike the original.*

Readers should be careful here: the use of the term *habitat* above does not appear to be the same as that used here. Instead, they probably mean something closer to *vegetation type.*

We distinguish the previous definitions from the following, also commonly found in the ecological literature.

Definition 1.1.9 (Habitat Fragmentation *per se*)**.** *Changes in habitat configuration that result from the breaking apart of existing habitat, independent of other forms of habitat loss (e.g., habitat degradation or destruction).*

In particular, when we refer to habitat fragmentation *per se*, we are discussing the arrangement of the regions of habitat alone, independent of other forms of habitat loss (degradation or destruction). More precisely, this point of view considers the study of the effects of the mere *arrangement* for a given total amount of habitat. There is much debate on the use and validity of studying such perspectives in detail, however we take motivation from [44]: rather than dismissing one definition in favor of the other, we will explore habitat fragmentation from multiple perspectives as they can provide complimentary results and insights. This motivates our third postulate.

Postulate Three: Habitat fragmentation can be viewed in two distinct ways: in the sense of *as an arrangement*, and in the sense of *as a process.*

Studying habitat fragmentation *as an arrangement*, as suggested, considers the effect of shape and geometry of habitat in a given landscape. The *effect* part of the study can be varied and sometimes quite complicated; we discuss this in more detail in Chapter 4. Some critics suggest that this point of view is not a good representation of habitat fragmentation as it occurs in the natural world. For a more ecologically minded perspective, we also study habitat fragmentation *as a process*: this is the idea that, through the process of habitat degradation and destruction, fragmentation occurs *as an inevitable consequence*. The end result of a fragmented landscape is therefore an epiphenomenon. We expand upon this in Chapter 4.

We then take the general term *habitat loss* to be as follows.

Definition 1.1.10 (Habitat Loss)**.** *Any combination of one or more of the processes of habitat degradation, destruction or fragmentation.*

In this way, habitat loss remains somewhat vague, but its constituent components are better defined.

1.2 Preliminaries

In this section, we highlight some of the standard notations and conventions used throughout the dissertation. We also explore some of the abstract theory used to prove later results. This *preliminaries* section will focus on all of the mathematical tools to be used in this thesis in detail. This includes key definitions, theorem statements, lemmas, and propositions. What will be lacking is a detailed repetition of proofs for many of these statements. In some cases, if the key ingredients are enlightening and not overly cumbersome, some further detail or insights may be provided. In other cases, the technical nature of the results and their proofs can be incredibly tedious, outweighing any novel insights one may gain through the exposition of a proof. In such cases, at minimum two different references should be provided for further reading and additional context. Ultimately, a judgement call will be made, balancing the big picture with the technical details. Sometimes, when a proof technique is very similar, we will prove only the "more challenging" case(s). In particular, we provide proofs for results that may essentially follow from existing arguments, but do not themselves have a nice reference to point to.

1.2.1 Function spaces

We briefly introduce some notations and conventions. Spoiler alert: this work deals with partial differential equations, almost exclusively of parabolic or elliptic type. Naturally, this involves a few key components: space, time, derivatives, and their relationships. Functions will be denoted by the usual letters (u,v,w,z,f,g, etc.). Unless otherwise clear, we write $u = u(x,t)$ to denote dependence on a point $x \in \mathbb{R}^N$ with dimension $N \geq 1$, and on a point $t \in [0,\infty)$. Derivatives will be written as $\frac{\partial}{\partial x}$, $\frac{\partial^2}{\partial x^2}$, etc. Sometimes we may use subscripts, i.e., $\frac{\partial u}{\partial t} =: u_t$, $\frac{\partial u}{\partial x} =: u_x$, and so on. We denote by $\nabla = (\frac{\partial}{\partial x_1}, \dots, \frac{\partial}{\partial x_N})$ the gradient. We denote by $\Delta = \sum_{i=1}^{N} \frac{\partial^2}{\partial x_i^2}$ the Laplacian. We then denote by $\Omega \subset \mathbb{R}^N$ a smooth (C^2 unless otherwise specified), bounded domain. $\overline{\Omega}$ denotes the closure of the domain, while $\partial\Omega$ denotes the boundary. Q_T will occasionally denote the (open) parabolic cylinder $\Omega \times (0,T)$ for some fixed time $T > 0$, while $\overline{Q}_T$ will denote the closed cylinder. When dealing with integrals, we often suppress the variable of integration when the context is clear. In most cases, the domain over which we integrate provides the required context.

Continuous function spaces

In *classical* PDE theory, we work with smooth solutions, which are understood to be solutions sufficiently differentiable in the classical sense. We highlight some of these spaces and their basic properties here.

Continuous functions in space only

$C^k(\Omega)$ ($C^k(\overline{\Omega})$) denotes the set of all functions having continuous derivatives up to order k in Ω ($\overline{\Omega}$). $C^0(\Omega)$ and $C^0(\overline{\Omega})$ will be denoted simply by $C(\Omega)$ and $C(\overline{\Omega})$, respectively.

If we denote by $\alpha = (\alpha_1, \dots, \alpha_n)$ a *multi-index* for non-negative integers α_i satisfying $|\alpha| = \alpha_1 + \cdots + \alpha_n$, we can define a norm on $C^k(\overline{\Omega})$ by

$$\|u\|_{C^k(\overline{\Omega})} = \sum_{|\alpha| \leq k} \sup_{x \in \Omega} |D^\alpha u|,$$

where

$$D^\alpha u = \frac{\partial^{|\alpha|} u}{\partial x_1^{\alpha_1} \cdots \partial x_n^{\alpha_n}}.$$

It is readily verified that $C^k(\overline{\Omega})$ endowed with this norm is a Banach space (see, for example, [1]). Note that when $k = 0$, we have the space of all continuous functions, denoted simply by $C(\Omega)$, with the usual sup-norm

$$|u|_{C(\Omega)} = \sup_{x \in \Omega} |u(x)|.$$

Definition 1.2.1. *Given a function $u(x)$ defined over Ω, we define the support of the function u by*

$$\operatorname{supp}(u) = \overline{\{x \in \Omega : u(x) \neq 0\}}.$$

Definition 1.2.2. *Denote by $C_0^k(\Omega)$ the set of all functions belonging to $C^k(\Omega)$ with compact support in Ω.*

To generalize these spaces of continuous functions a little bit, one may introduce the following semi-norm for a function u defined on Ω:

$$\sup_{x,y \in \Omega, x \neq y} \frac{|u(x) - u(y)|}{|x - y|^\alpha},$$

for any $\alpha \in (0,1)$. We then consider the Hölder class, denoted by $C^\alpha(\overline{\Omega})$, the set of all functions such that the norm

$$\|u\|_{C^\alpha(\Omega)} = \|u\|_{C(\Omega)} + \sup_{x,y \in \Omega, x \neq y} \frac{|u(x) - u(y)|}{|x - y|^\alpha}$$

is finite. We then define the function space for any non-negative integer k

$$C^{k,\alpha}(\overline{\Omega}) = \{u : D^\beta u \in C^\alpha(\overline{\Omega}) \text{ for any multi-index } \beta \text{ such that } |\beta| \leq k\},$$

with the associated norms built in an analogous way. Of particular interest are the spaces $C^{1,\alpha}(\overline{\Omega})$ and $C^{2,\alpha}(\overline{\Omega})$, the set of functions that are once (or twice) differentiable, with its first (or second) derivative being Hölder continuous.

Finally, we say that a subset Ω' is *compactly contained* within Ω, denoted $\Omega' \Subset \Omega$, if $\overline{\Omega'}$ is compact and $\overline{\Omega'} \subset \Omega$. If given any subdomain $\Omega' \Subset \Omega$ there holds $u \in C^{k,\alpha}(\overline{\Omega'})$, we say that $u \in C^{k,\alpha}(\Omega)$. The space $C^{0,\alpha}(\Omega)$ is exactly the Hölder space $C^{\alpha}(\Omega)$.

As noted previously, all spaces are Banach when equipped with the norms introduced here. Also note that in the case when $\alpha = 1$, the Hölder class is referred to as a *Lipschitz* class.

Finally, for functions on Hilbert spaces, we have the following standard result. Its statement is found in [8], for example.

Proposition 1.2.1. *Let H be a Hilbert space. Denote the inner product on H by $\langle \cdot, \cdot \rangle$ and the corresponding norm by $\|\cdot\|$. Let T be a compact, symmetric operator on H. If*

$$\eta_1 = \sup \{\langle Tu, u\rangle : \|u\| = 1\} > 0,$$

then η_1 is an eigenvalue of T, i.e. there exists $u_1 \in H \setminus \{0\}$ so that $Tu_1 = \eta_1 u_1$.

Continuous functions in space and time

In the case where our domain is a parabolic cylinder, we introduce similar spaces that are convenient for the study of second order parabolic equations. Given two points $A = (x,t), B = (y,s) \in Q_T$, define the *parabolic distance* between A and B as

$$d(A,B) = \left(|x-y|^2 + |t-s|\right)^{1/2}.$$

Then, given a function defined on Q_T, we introduce the semi-norm

$$\sup_{A,B \in Q_T, A \neq B} \frac{|u(A) - u(B)|}{d^{\alpha}(A,B)}$$

for any $\alpha \in (0,1)$. We denote by $C^{\alpha,\alpha/2}(\overline{Q}_T)$ the space of all functions such that the norm

$$\|u\|_{C^{\alpha,\alpha/2}(\Omega)} = \|u\|_{C(Q_T)} + \sup_{A,B \in Q_T, A \neq B} \frac{|u(A) - u(B)|}{d^{\alpha}(A,B)}$$

is finite, where $\|\cdot\|_{C(Q_T)}$ is now the sup-norm over Q_T. We then define the following space appropriate for second order parabolic partial differential equations.

Definition 1.2.3. *For any non-negative integer k and any $\alpha \in (0,1)$, we define the space*

$$C^{2+\alpha,1+\alpha/2}(\overline{Q}_T) = \{u : D^\beta u, \tfrac{\partial u}{\partial t} \in C^{\alpha,\alpha/2}(\overline{Q}_T) \text{ for any } \beta \text{ such that } |\beta| \leq 2\}$$

endowed with the norm

$$\|u\|_{C^{2+\alpha,1+\alpha/2}(Q_T)} = \left\|\tfrac{\partial u}{\partial t}\right\|_{C^{\alpha,\alpha/2}(Q_T)} + \sum_{|a|\leq 2} \|D^\alpha u\|_{C^{\alpha,\alpha/2}(Q_T)}.$$

Sobolev spaces in the domain Ω

Here we remind readers of some basic facts and definitions for the theory of Sobolev spaces. We discuss the case of a spatial domain only. The more complicated case of t-anisotropic Sobolev spaces [123] is discussed after.

When a classical, smooth setting is not appropriate, it is common to appeal to notions of *integrability* and *weak derivatives*. This naturally involves the theory of *Sobolev spaces*. For $1 \leq p < \infty$, define the norm

$$\|f\|_{L^p(\Omega)} = \left(\int_\Omega |f|^p\right)^{1/p}.$$

We then denote by $L^p(\Omega)$ the space of all integrable functions (in the sense of Lebesgue, see [1, Ch. 1]) such that its L^p-norm remains finite. In the case of $p = \infty$, $L^\infty(\Omega)$ is understood to be the set of functions that are essentially bounded, i.e. the set of functions such that

$$\text{esssup}(u) = \inf\{c \in \mathbb{R} : u(x) \leq c \text{ for almost every } x \in \Omega\}$$

remains finite. In this case, $\|u\|_{L^\infty(\Omega)} \equiv \text{esssup}(u)$. For continuous functions, we have that

$$\lim_{p\to\infty} \|f\|_{L^p(\Omega)} = \|f\|_{L^\infty(\Omega)}.$$

The space $L^p(\Omega)$ can be obtained through the completion of $C^\infty(\Omega)$ with respect to the norm $\|\cdot\|_{L^p(\Omega)}$. If, given any $K \Subset \Omega$ there holds $\|f\|_{L^p(K)} < \infty$, we say that f belongs to $L^p_{loc}(\Omega)$.

Definition 1.2.4. *Suppose* $u \in L^1_{loc}(\Omega)$ *and* $i = 1, \dots, N$. *If there exists functions* $g_i \in L^1_{loc}(\Omega)$ *such that*

$$\int_\Omega g_i \phi = -\int_\Omega u \frac{\partial \phi}{\partial x_i}$$

holds for any function $\phi \in C_0^\infty(\Omega)$, *we say that* g_i *is a* weak derivative *of* u. *In such a case, we then write*

$$\frac{\partial u}{\partial x_i} = g_i.$$

In the definition above, the function ϕ is commonly referred to as a *test function.* Using this framework, we now have notions of weak gradients and higher. This is a key ingredient that allows one to develop notions of solutions that are not necessarily classical.

We are then able to introduce higher order Sobolev spaces. If a function has k weak derivatives (through repeated application of Definition 1.2.4), we say that it belongs to the space $W^k(\Omega)$. We define the following Sobolev space.

Definition 1.2.5. *Let* k *be a non-negative integer and* $p \geq 1$. *Then we denote by* $W^{k,p}(\Omega)$ *the class of functions*

$$W^{k,p}(\Omega) = \{u \in W^k(\Omega) : D^\alpha u \in L^p(\Omega) \text{ for all } |\alpha| \leq k\}$$

endowed with the norm

$$\|u\|_{W^{k,p}(\Omega)} = \left(\int_\Omega \sum_{|\alpha| \leq k} |D^\alpha u|^p \right)^{1/p}.$$

For all $p > 1$, $W^{k,p}(\Omega)$ is a Banach space. Finally, we have the following space of functions that "vanish along the boundary" in a weak sense.

Definition 1.2.6. *Denote by* $W_0^{k,p}(\Omega)$ *the closure of* $C_0^\infty(\Omega)$ *in* $W^{k,p}(\Omega)$.

Remark 1.2.1. *In the definitions above, when one takes* $p = 2$ *we have a Hilbert space with an inner product given by the norm. It is customary to denote these spaces as* $H^k(\Omega)$. *Of particular interest are the spaces* $H^1(\Omega)$ *and* $H_0^1(\Omega)$.

We also have the following Poincaré-type inequality for functions which vanish on a set of positive measure. This is Theorem 4.4.2 in *Weakly Differentiable functions* by Ziemer [125], modified as to align with the notation used here.

Proposition 1.2.2. *Suppose* $\Omega \subset \mathbb{R}^N$ *is bounded. Suppose* $u \in H^1(\Omega)$ *has the property that*

$$\int_E \nabla u = \int_E u = 0,$$

where $E \subset \Omega$ *is a measurable set of positive (Lebesgue) measure. Then, there exists a constant* $C = C(\Omega)$ *so that*

$$\|u\|_{L^2(\Omega)} \leq C \|\nabla u\|_{L^2(\Omega)} .$$

This is usually presented in the case of $H^1_0(\Omega)$, the set of functions whose trace vanishes on $\partial\Omega$. In Chapter 3, we will require the same inequality for functions which vanish on some set contained within Ω.

Sobolev spaces in the domain Q_T

We now introduce the so-called t-anisotropic Sobolev spaces for problems that depend on time. The most important space is $W^{2,1}_p(\Omega)$, also appropriate for the study of second order parabolic equations.

Definition 1.2.7. *For any* $p \geq 1$ *we define the space*

$$W^{2,1}_p(Q_T) = \left\{u : D^\alpha u, \tfrac{\partial u}{\partial t} \in L^p(Q_T) \textit{ for every } |\alpha| \leq 2\right\}$$

endowed with the norm

$$\|u\|_{W^{2,1}_p(Q_T)} = \left(\iint_{Q_T} \left(\sum_{|\alpha|\leq 2} |D^\alpha u|^p + \left|\tfrac{\partial u}{\partial t}\right|^p\right) dxdt\right)^{1/p}$$

$W^{2,1}_p(\Omega)$ is also a Banach space. There are additional special cases for $W^{k,m}_p$ when k, m are 0 or 1. There are also precise definitions for smooth functions vanishing along $\partial\Omega \times (0,T)$ or along $\partial\Omega \times (0,T) \cup \overline{\Omega} \times \{t = 0\}$. For these cases, we refer to [123, Ch.

1.4.1]. Here, we will simply refer to such functions as test functions where the context will be clear.

What will be useful for later chapters is the special space $V_2(Q_T)$, which is also found to be a Banach space.

Definition 1.2.8. *Let* $L^\infty(0,T;L^2(\Omega))$ *be the set of all functions for which almost every* $t \in (0,T)$, $u \in (\cdot,t) \in L^2(\Omega)$ *with* $\|u(\cdot,t)\|_{L^2(\Omega)}$ *bounded. We denote by* $V_2(Q_T)$ *the set* $L^\infty(0,T;L^2(\Omega)) \cap W_2^{1,0}(Q_T)$ *endowed with the norm*

$$\|u\|_{V_2(Q_T)} = \sup_{t\in(0,T)} \|u(\cdot,t)\|_{L^2(\Omega)} + \|\nabla u\|_{L^2(Q_T)}.$$

There are many fine and useful properties of these function spaces, including properties of weak derivatives, equivalencies under certain hypotheses, density and compactness properties, interpolation inequalities, relations to less regular boundary conditions, and so on. We do not expand any further here, instead referring to [1], [123] for further insights. When these properties may be used, we provide references as appropriate.

1.2.2 Inequalities, convergence and embeddings

In this section we compile some useful inequalities, along with convergence and embedding results.

Inequalities

We have the following, *Cauchy's inequality with epsilon*: given $\varepsilon > 0$ and $a, b \geq 0$ there holds

$$ab \leq \frac{\varepsilon}{2}a^2 + \frac{1}{2\varepsilon}b^2$$

Its generalization, *Young's inequality with epsilon*, is as follows: given any $\varepsilon > 0$, $a, b \geq 0$, and $p, q > 1$ satisfying $\frac{1}{p} + \frac{1}{q} = 1$, there holds

$$ab \leq \frac{\varepsilon}{p}a^p + \frac{\varepsilon^{-q/p}}{q}b^q.$$

This inequality allows one to prove Hölder's inequality.

Proposition 1.2.3 (Hölder's inequality). *Let $p, q > 1$ satisfy $\frac{1}{p} + \frac{1}{q} = 1$. If $f \in L^p(\Omega)$ and $g \in L^q(\Omega)$, then $fg \in L^1(\Omega)$ and*

$$\|fg\|_{L^1(\Omega)} \leq \|f\|_{L^p(\Omega)} \|g\|_{L^q(\Omega)} .$$

Select convergence results

Here we highlight some standard convergence results. First is the Arzelà-Ascoli Theorem.

Theorem 1.2.1 (Arzelà-Ascoli Theorem). *Suppose a sequence of real-valued functions $f_n(x)$ are uniformly bounded and equicontinuous on $\overline{\Omega}$. Then, there exists a uniformly convergent subsequence.*

Similarly, we have Dini's theorem.

Theorem 1.2.2 (Dini's Theorem). *Suppose a sequence of real-valued functions $\{f_n(x)\}_{n \in \mathbb{N}}$ are monotone (increasing or decreasing) and converge pointwise in $\overline{\Omega}$. If the limit function is also continuous, the convergence is uniform.*

Embeddings

Let X and Y be Banach spaces such that $X \subset Y$. Recall that we say X is *compactly embedded* in Y, denoted by $X \Subset Y$, provided that i. $\|u\|_Y \leq C \|u\|_X$ for some C independent of u; and ii. each bounded sequence in X is precompact in Y. We have the following two standard embedding theorems.

Theorem 1.2.3 (Sobolev embedding). *Let $\Omega \subset \mathbb{R}^N$ be a smooth, bounded domain and $p > Nk$. Then, $W^{1,p}(\Omega) \subset C^{\alpha}(\overline{\Omega})$ for any $0 < \alpha \leq 1 - N/p$, and for any function $u \in W^{1,p}(\Omega)$, there holds*

$$\|u\|_{C^{\alpha}(\overline{\Omega})} \leq C(N, p, \Omega) \|u\|_{W^{1,p}(\Omega)} .$$

Furthermore, the embedding is compact.

Theorem 1.2.4 (t-anisotropic Sobolev embedding). *Let $\Omega \subset \mathbb{R}^N$ be a smooth, bounded domain and $p > (N+2)/2$. Then, $W_p^{2,1}(Q_T) \subset C^\alpha(\overline{Q}_T)$ for any $0 < \alpha \leq 2-(N+2)/p$, and for any function $u \in W_p^{2,1}(Q_T)$, there holds*

$$\|u\|_{C^{\alpha,\alpha/2}(\overline{Q}_T)} \leq C(N,p,Q_T) \|u\|_{W_p^{2,1}(\Omega)}.$$

Furthermore, the embedding is compact.

A simple example

Here we briefly explore a simple example demonstrating the application of the Sobolev embedding theorem. Consider the equation

$$u_t = du_{xx} + u(m(x) - u)$$

in a bounded domain Q_T subject to appropriate boundary conditions. In classical PDE theory, one assumes that $m \in C^\alpha(\overline{\Omega})$ for some $\alpha \in (0,1)$ in order to obtain a classical solution $u \in C^{2+\alpha,1+\alpha/2}(Q_T)$. Suppose instead that we merely assume $m(x) \in L^\infty(\Omega)$. Classical theory no longer applies, but we may regularize m by m_ε so that m_ε is smooth for every $\varepsilon > 0$, and $m_\varepsilon \to m$ in $L^p(\Omega)$ as $\varepsilon \to 0^+$ for any $p \geq 1$. The corresponding solution, denoted by u_ε, is then classical. It is possible to obtain uniform bounds on u_ε, independent of ε. This shows that $u_\varepsilon \in W_p^{2,1}(Q_T)$ for any $p \geq 1$ by the L^p-theory of parabolic equations. Hence, there exists a convergent subsequence, converging to a weak solution of the original problem. Using Theorem 1.2.4, we may choose p as large as we like to conclude that in fact $u \in C^{1+\alpha,(1+\alpha)/2}(\overline{Q}_T)$ for any $\alpha \in (0,1)$. This shows that the solution is differentiable in space, with its derivative Hölder continuous, but with (perhaps) no second derivative (in a classical sense)!

1.2.3 Monotone dynamical systems

In this section, we highlight some of the standard abstract results applied to monotone dynamical systems, and more specifically continuous monotone dynamical systems. We focus on continuous-time order-preserving flows as this will be the primary use of these tools here. For further precision and details, we refer readers to [68], [124]. We hope to provide a reminder and some context for more familiar readers.

We begin with some standard definitions and their notations. Let X be a Banach space with $Y \subset X$. A subset K of X is said to be a cone if $K + K \subset X$, $\lambda K \subset K$ for all $\lambda \geq 0$, and $K \cap (-K) = \{0\}$. We will assume a cone has non-empty interior unless otherwise specified. There is then an ordering induced by the cone K. For each $u, v \in K$, we write $u \geq v$ if $u - v \in K$; $u > v$ if $u - v \in K^+$; $u \gg v$ if $u - v \in K^{++}$, where $K^+ = K \setminus \{0\}$ and K^{++} is the interior of the set K, i.e., the set consisting of all points $x_0 \in K$ such that there exists an open ball around x_0 contained within K.

A simple but instructive example is the space $X := C(\overline{\Omega})$. Then, $C^+(\overline{\Omega})$ is simply the set of non-negative continuous functions on Ω. $C^{++}(\overline{\Omega})$ is the set of *strictly positive* functions in Ω. For $w^1, w^2 \in C(\overline{\Omega})$, the following ordering is often used in literature.

$$\begin{aligned} w^1 \leq w^2 \quad &\text{iff} \quad w^2 - w^1 \in C^+(\overline{\Omega}), \\ w^1 < w^2 \quad &\text{iff} \quad w^2 - w^1 \in C^+(\overline{\Omega}) \setminus \{0\}, \\ w^1 \ll w^2 \quad &\text{iff} \quad w^2 - w^1 \in C^{++}(\overline{\Omega}). \end{aligned}$$

Note that the cone we work in depends on the problem we study; the ordering above is appropriate for homogeneous Neumann boundary data, but is not sufficient for homogeneous Dirichlet boundary data.

We now present some important theorems concerning compact, positive operators, their spectral radius, and connections to eigenvalues. Let T be a linear operator on a Banach space X. T is called positive if $T(K) \subset K$. Denote by $\sigma(T)$ the spectrum of T and $\operatorname{spr}(T)$ the spectral radius of T. We have the following theorems of Krein-Rutman, both found in e.g., [68, Ch. I.7].

Theorem 1.2.5 (Krein-Rutman I)**.** *Suppose an operator $T : X \to X$ is compact and positive. Assume that $\lambda = \operatorname{spr}(T) > 0$. Then λ is an eigenvalue of T with eigenfunction $\psi > 0$.*

Assume now that K has nonempty interior. An operator T is called strongly positive if $T(K^+) \subset K^{++}$. We have the second theorem.

Theorem 1.2.6 (Krein-Rutman II)**.** *Suppose the operator T is compact and strongly positive. Then $\lambda = \operatorname{spr}(T) > 0$, and λ is the unique eigenvalue of T having a positive* *eigenfunction* ψ*. Furthermore,* $\psi \gg 0$ *and* λ *is algebraically simple. Finally,* $|r| < \lambda$ *for all* $r \in \sigma(T)$*,* $r \neq \lambda$*.*

Finally, we have the following result for the inhomogeneous problem. We assume $h \in X^+$ and consider the solution of the equation

$$\gamma u + Tu = h \quad \text{in } X^+.$$

Theorem 1.2.7 (Krein-Rutman III)**.** *Assume the hypotheses of Theorem 1.2.6 hold. Then*

(i) *There exists a unique solution* $u \in X^{++}$ *solving the inhomogeneous problem for every* $\gamma > \lambda$*; there is no positive solution for any* $\gamma \leq \lambda$*.*

(ii) *If* $\gamma = \lambda$*, there is no solution at all.*

We next recall the definition of a semi-flow. A semi-flow is a continuous map $S = S(t, u) : \mathrm{Dom}(S) \subset [0, \infty) \times Y \to Y$ such that $\mathrm{Dom}(S)$ is open in $[0, \infty) \times Y$ and satisfies the following three properties:

i.) $S(0, u) = u, \quad \forall u \in Y;$

ii.) $S(t, S(t', u)) = S(t + t', u)$ for any $t, t' \geq 0$, $u \in \mathrm{Dom}(S(t + t'))$;

iii.) $S(t, u)$ is strongly continuous in (t, u).

Property ii. is often referred to as the semigroup property. The map S is called *strictly order preserving* (resp. strongly order-preserving) if for any $t > 0$, $u < v$ implies that $S(t, u) < S(t, v)$ (resp. $S(t, u) \ll S(t, v)$). Note that in some references, the term *order-preserving* is exchanged with *monotone*. Hence the term *monotone dynamical systems.*

Beyond monotonicity, there is the notion of subhomogeneity.

Definition 1.2.9 (Subhomogeneous function)**.** *A continuous function* $f : X \to X$ *is said to be* subhomogeneous *if* $f(\lambda u) \geq \lambda f(u)$ *for any* $u \in X$ *and* $\lambda \in [0, 1]$*;* strictly subhomogeneous *if* $f(\lambda u) > \lambda f(u)$ *for any* $u \in X$ *with* $u \gg 0$ *and* $\lambda \in (0, 1)$*; and* strongly subhomogeneous *if* $f(\lambda u) > \lambda f(u)$ *for any* $u \in X$ *with* $u \gg 0$ *and* $\lambda \in (0, 1)$*.*

We now present a useful "threshold dynamics"-type theorem in the language of [124] (the precise theorem statement is given in [124, Thm. 2.3.4]). Similar results and further discussion can be found in [68].

Theorem 1.2.8 (Threshold dynamics)**.** *Suppose a continuous map $f : X^+ \to X^+$ is either strongly monotone and strictly subhomogeneous, or monotone and strongly subhomogeneous. Suppose further that f is asymptotically smooth, and every orbit in X^+ is bounded. Finally, suppose that $f(0) = 0$ and that $Df(0)$ is compact and strongly positive. Then the following threshold dynamics hold.*

- *If* $\operatorname{spr}(Df(0)) \leq 1$*, then every orbit in* X^+ *converges to* 0*;*
- *If* $\operatorname{spr}(Df(0)) > 1$*, then there exists a unique fixed point* $u^* \gg 0$ *such that every orbit in* X^+ *converges to* u^**.*

To give some additional context, we also state the following two theorems from [68] concerning subhomogeneous continuous time semiflows. Denote by $[u_1, u_2]$ the *order interval* $\{u \in C(\overline{\Omega}) : u_1 \leq u \leq u_2\}$.

Theorem 1.2.9 (Monotone theorem I)**.** *Let $u_1 < u_2$ be equilibrium points of the strictly order-preserving semiflow S, and let $X = [u_1, u_2]$.*

Assume $[0, \infty) \times X \subset \operatorname{Dom}(S)$ and that $S(t, X)$ is relatively compact for each $t > 0$. Then either

(i) *there is a further equilibrium in X, or*

(ii) *there is a strictly monotone entire orbit $\gamma = \{z_t : t \in \mathbb{R}\}$ connecting u_1 and u_2, i.e., $z_{t+\tau} = S(\tau, z_t)$ for every $t \in \mathbb{R}$, $\tau \in [0, \infty)$, and either*

$$x_t < x_{t+\tau},\ \forall t \in \mathbb{R},\ \tau > 0, \quad \textit{and} \ \lim_{t \to -\infty} z_t = u_1,\ \lim_{t \to \infty} z_t = u_2,$$

or

$$x_t > x_{t+\tau},\ \forall t \in \mathbb{R},\ \tau > 0, \quad \textit{and} \ \lim_{t \to \infty} z_t = u_1,\ \lim_{t \to -\infty} z_t = u_2$$

For the next theorem, we also require the notion of *subequilibria* and *superequilibria.*

Definition 1.2.10 (Subequilibria & Superequilibria)**.** *A point $u \in X$ is called a subequilibrium (superequilibrium) of the continuous dynamical system S if $u \leq S(t,u)$ ($u \geq S(t,u)$) for all $t \in [0,T)$, where $0 < T = T(u)$ is the (possibly infinite) maximal existence time of the flow S. A point u is a strict subequilibrium (superequilibrium) if it is a subequilibrium (superequilibrium), but not an equilibrium.*

Theorem 1.2.10 (Monotone theorem II)**.** *Let S be strongly order-preserving, and let $v_1 < v_2$ be subequilibrium and superequilibrium, respectively. Let $V := [v_1, v_2]$, and assume that $[0,\infty) \times V \subset \mathrm{Dom}(S)$ and that $S(t,V)$ is relatively compact for each $t > 0$. Finally, assume each equilibrium in V is stable. Then all positive semiorbits in V converge, i.e. $\omega(v) = \{v^*\}$, v^* equilibrium, for all $v \in V$. In addition, the set $\mathcal{E}$ of equilibria of S in V is totally ordered and connected.*

The language is sometimes difficult to parse so we will use the same simple example to demonstrate its use.

Return to a simple example

We return again to the equation

$$u_t = du_{xx} + u(m(x) - u)$$

in Ω, subject to appropriate boundary conditions. The abstract Theorem 1.2.8 can be applied to this problem to conclude that there exists a unique steady state $u^*_{d,m}$ if and only if the sign of a principal eigenvalue is negative, otherwise 0 is the only steady state. Using the maximum principle, we can show that the PDE generates a strongly monotone flow. Furthermore, since the reaction term is concave in the variable u, it is also strongly subhomogeneous, and so the PDE generates a strongly monotone subhomogeneous flow.

The "asymptotic smoothness" property follows from the regularizing effect the PDE operator has. In this case, the operator takes a merely continuous function and returns a twice differentiable function (if $m(x) \in C^\alpha(\overline{\Omega})$). Using standard methods one can show that solutions remain uniformly bounded for all time due to the strict concavity of the reaction term.

It is easy to verify that $u(x, 0) \equiv 0$ implies that $u(x, t) = 0$ for all $t > 0$. Compactness again follows from the regularity of the PDE operator (in this case, a simple diffusion operator). Since the PDE has the "infinite propagation speed" property, i.e., solutions with non-negative, non-trivial initial data are strictly positive for any $t > 0$, the PDE is strongly positive.

Thus, the PDE map $S(t; u_0(x))$, taking a continuous function $u_0(x) = u(x, 0)$ as an input, returning a solution to the given problem satisfies all of the conditions of Theorem 1.2.8. In practice, the higher order terms (diffusion, advection) relate to compactness properties of the PDE map S. On the other hand, properties of the low order term (generally $f(x, u)$, in this case the logistic form $u(m(x) - u)$) provide monotonicity or subhomogeneity properties of the PDE map S.

As it turns out, the dichotomy between $[0, 1]$ and $(1, \infty)$ in this case can be made equivalent to the sign of a principal eigenvalue. This eigenvalue corresponds to the linearization of the time-dependent problem about the trivial steady state. This eigenvalue, in turn, depends on the diffusion rate d and the heterogeneity $m(x)$, giving insights into the nature of persistence for diffusing species.

1.2.4 Maximum principles, comparison principles, and Hopf's lemma

In this section, we highlight briefly the two main "types" of solutions we work with. The first is the *classical* solution, which is sufficiently differentiable to plug directly into the relevant equation and satisfies it everywhere in Ω or Q_T. The second is the *weak* solution (in our case, this often turns out to be a *strong* solution). Also of note is the *mild* solution, though we do not use this notion in the present work and will not focus deeply on the theory of semigroups.

Elliptic equations

Suppose we are given a general, second order linear elliptic operator:

$$Lu := -\sum_{i,j=1}^{N} a_{ij} \frac{\partial^2 u}{\partial x_i \partial x_j} + \sum_{i=1}^{N} b_i \frac{\partial u}{\partial x_i} + cu. \tag{1.1}$$

We always assume that $a_{ij}(x)$, $b_i(x)$, $c(x)$ belong to $L^\infty(\Omega)$, $a_{ij} = a_{ji}$, and that there exists constants $0 < \lambda \leq \Lambda$ so that

$$\lambda \left|\xi\right|^2 \leq \sum_{i,j=1}^{N} a_{ij}(x)\xi_i\xi_j \leq \Lambda \left|\xi\right|^2, \quad \forall \xi \in \mathbb{R}^N,\ x \in \Omega.$$

This lower bound is commonly referred to as a *uniform ellipticity* condition, which essentially ensures a "non-degeneracy" condition on the highest order term of the operator L. We may then consider equations of the form

$$Lu = f \quad \text{ in } \Omega,$$

where $f(x)$ is some given, suitably smooth function. A quintessential tool in the study of PDE is the so-called *maximum principle*, see e.g., [123, Ch. 8], [95, Ch. 2], [8, Ch.]. In what follows, $\frac{\partial}{\partial \nu}$ denotes the outward unit normal vector to the boundary $\partial\Omega$.

Theorem 1.2.11 (Maximum principle for elliptic equations)**.** *Let* $c(x) \geq 0$, *and* $a_{ij}(x)$, $b_i(x)$, $c(x)$ *belong to* $L^\infty(\Omega)$. *Suppose that* $u \in C^2(\Omega)$ *satisfies* $Lu \leq 0$ *in* Ω. *Then,*

- *If* u *attains a non-negative maximum* $M \geq 0$ *at any point* $x_0 \in \Omega$, *then* $u \equiv M$ *in all of* Ω.
- *Suppose further that* $u \in C(\overline{\Omega})$ *and that* Ω *satisfies the interior ball condition (i.e., every point* $x_0 \in \partial\Omega$ *lies on the boundary of a ball* $B_\rho(y_0) \subset \Omega$*). If* $u = M$ *at some point* $x_0 \in \partial\Omega$ *for which* $\frac{\partial u}{\partial \nu}$ *exists, then either* $\frac{\partial u}{\partial \nu} > 0$ *at* x_0 *or* $u \equiv M$ *in* Ω.

The second part of this theorem ensuring the *strict* positivity of the outward facing normal

Note that our general assumption that $\partial\Omega$ is of class C^2 ensures the interior ball condition holds automatically; less regular domains, such as those with cusps, can still satisfy an interior ball condition.

The maximum principle has many consequences. Of particular use is the *comparison principle*, which now incorporates some information along the boundary. In this work, we primarily consider only the homogeneous *Dirichlet* or *Neumann* boundary condition:

$$B_D u := u = 0 \text{ on } \partial\Omega, \quad \text{or} \quad B_N u := \frac{\partial u}{\partial \nu} = 0 \text{ on } \partial\Omega.$$

Then, we can formulate the boundary value problem

$$\begin{cases} Lu = f & \text{in } \Omega, \\ B_i u = 0 & \text{on } \partial\Omega, \end{cases} \tag{1.2}$$

where $i = D, N$ and $f(x)$ is a given, suitably smooth function. We then have the following.

Theorem 1.2.12 (Comparison principle for elliptic equations). *Suppose* $c(x) \geq 0$ *and* $b_i(x)$, $c(x)$ *belong to* $L^\infty(\Omega)$. *Suppose that* $u, v \in C^2(\Omega) \cap C(\overline{\Omega})$ *satisfy* $Lu \leq Lv$ *in* Ω, *and* $B_i u \leq B_i v$ *along* $\partial\Omega$ *for* $i = D$ *or* N. *Then there holds*

$$u(x) \leq v(x) \quad \forall x \in \Omega.$$

Remark 1.2.2. *This theorem statement was taken from [123, Ch. 8.1] which is valid only for the Dirichlet boundary condition. The same is true for a Neumann boundary condition (or a Robin boundary condition, not discussed here), in which case we reference [95] or [8] and the references therein.*

As we will explore in the next section, often the requirements for these results are too strong.

Parabolic equations

Here we compile the analogous results to the previous section for the case of second order parabolic problems. In this case, the operator is still of the form given in (1.1), but now $a_{ij} = a_{ij}(x,t)$, $b_i = b_i(x,t)$, $c = c(x,t)$, each of which are assumed bounded in Q_T. It is still assumed that a_{ij} satisfies the uniform ellipticity condition for all $(x,t) \in Q_T$.

We then consider solutions to the equation

$$u_t + Lu = f \quad \text{in } Q_T$$

where $f = f(x,t)$ is some given, appropriately smooth function. We have first the maximum principle.

Theorem 1.2.13 (Maximum principle for parabolic equations)**.** *Suppose* $a_{ij}(x,t)$*,* $b_i(x,t)$*,* $c(x,t)$ *belong to* $L^\infty(\Omega)$*. Suppose that* $u \in C^{2,1}(Q_T)$ *satisfies* $u_t + Lu \leq 0$ *in* Ω*. Then,*

- *If* u *attains a non-negative maximum* $M \geq 0$ *at any point* $(x_0, t_0) \in Q_T$*, then* $u \equiv M$ *in all of* $\Omega \times (0, t_0]$*.*
- *Suppose further that* $u \in C(\overline{\Omega} \times (0,T))$ *and that* Ω *satisfies the interior ball condition (i.e., every point* $x_0 \in \partial\Omega$ *lies on the boundary of a ball* $B_\rho(y_0) \subset \Omega$*). If* $u = M$ *at some point* $(x_0, t_0) \in \partial\Omega \times (0,T)$ *for which* $\frac{\partial u}{\partial \nu}$ *exists, then either* $\frac{\partial u}{\partial \nu} > 0$ *at* (x_0, t_0) *or* $u \equiv M$ *in* $\Omega \times (0, t_0)$*.*

Then, we can formulate the parabolic initial-boundary value problem analogous to problem (1.2):

$$\begin{cases} u_t + Lu = f(x,t) & \text{in } \Omega \times (0,T), \\ B_i u(x,t) = 0 \text{ on } \partial\Omega \times (0,T), \\ u(x,0) = u_0(x) \gneq 0 \text{ in } \overline{\Omega} \end{cases} \tag{1.3}$$

where $i = D, N$ as before, and $f(x,t)$ is a given. We then have the following.

Theorem 1.2.14 (Comparison principle for parabolic equations)**.** *Suppose* $a_{ij}(x,t)$*,* $b_i(x,t)$*,* $c(x,t)$ *belong to* $L^\infty(\Omega)$*. Suppose that* $u, v \in C^{2,1}(Q_T) \cap C(\overline{Q}_T)$ *satisfy* $u_t + Lu \leq v_t + Lv$ *in* Q_T*, and* $B_i u \leq B_i v$ *along* $\partial\Omega \times (0,T)$ *for* $i = D$ *or* N*. Then there holds*

$$u(x,t) \leq v(x,t) \quad \forall (x,t) \in Q_T.$$

Similar results under weaker conditions

As we will explore in the next section, often the conditions for maximum/comparison principles are too strict, particularly when we consider solutions that may not be differentiable in the usual sense. As it turns out, strong maximum principle-type results still hold for *weak* and *strong* solutions, where differential inequalities are now understood in the weak or almost everywhere sense. For the case of elliptic equations, we state the so-called Aleksandrov maximum principle, with statement taken from [52, Ch. 9.1]. We modify the statement slightly for the conventions used here.

Theorem 1.2.15 (Aleksandrov maximum principle)**.** *Suppose* $u \in W^{2,N}(\Omega)$ *satisfies* $-Lu \leq 0$ *and* $c = 0$ *(*$c \geq 0$*). Then* u *cannot achieve a maximum (nonnegative maximum) in* Ω *unless it is a constant.*

In the case of parabolic equations, we state the result found in [4, Theorem 1]. We again modify the statement slightly to align with the conventions used here.

Theorem 1.2.16 (Aleksandrov maximum principle for parabolic equations)**.** *Suppose that* $u(x,t), v(x,t) \in C^{1,1}(Q_T)$*. Suppose that there exists a point* $(x_0, t_0) \in Q_T$ *such that* $u(x_0,t_0) = v(x_0,t_0)$ *and that* $u \leq v$ *in* Q_{t_0}*. Suppose further that* u *and* v *satisfy*

$$u_t - Lu \leq 0 \leq v_t - Lv$$

in Q_{t_0} *in the weak sense. Then,* $u \equiv v$ *in* Q_{t_0}*.*

Remark 1.2.3. *Actually, the result in [4] is much more general, allowing for nonlinearity at the highest order. We do not require such machinery generally; the value is in the decreased regularity assumptions on the functions. Notice that we require* u *and* v *to satisfy some differential inequalities (similar to the classical case), but now they hold only in a* weak sense*. We elaborate further on this point in the subsequent section.*

Essentially, so long as the appropriate differential inequalities are satisfied, even in a weaker sense, we have the same results as those found in Theorem's 1.2.11-1.2.13.

We also state the following result, commonly known as Hopf's lemma. This lemma is of particular use when applying the maximum principle and considering boundary points. Of note is the lack of regularity required: the result holds for strong solutions (see the following section for details!). Since our solutions are not always classical such considerations are necessary. The statement is taken from [103, Theorem 1.1]

Theorem 1.2.17 (A general Hopf's lemma)**.** *Let* $\Omega \subset \mathbb{R}^N$ *be a smooth bounded domain,* $a_{ij} \in C^{\alpha}(\Omega)$ *with* $a_{ij}(x) = a_{ji}(x)$*,* $1 \leq i,j \leq N$*,* $x \in \Omega$*, and* $\sum_{i,j=1}^{N} a_{ij}(x)\xi_i\xi_j > 0$ *for* *all $x \in \Omega$ and $\xi \in \mathbb{R}^N \setminus 0$. Assume that $u \in C^1(\Omega)$ solves, in the weak sense,*

$$-\sum_{i,j=1}^{N} \partial_{x_i}(a_{ij}(x)\partial_{x_j}u) + \sum_{i=1}^{N} b_i(x)\partial_{x_i}u + c(x)u \geq 0, \quad \text{in } \Omega,$$

where $b_i \in L^\infty(\Omega)$ for $1 \leq i \leq N$, $c \in L^\infty(\Omega)$, and $c(x) \geq 0$ a.e. in Ω. Suppose that for $x_0 \in \partial\Omega$ there exists a ball $B \subset \Omega$ with $x_0 \in \partial B$ where $u = u(x) > u(x_0)$ for $x \in B$. If $u(x_0) \leq 0$ then

$$\frac{\partial u}{\partial \nu}(x_0) < 0,$$

where ν is the outward unit normal at x_0.

Remark 1.2.4. *Note that in the statement above, the operator is in* divergence form*. This is different from L introduced in (1.1), which is* not *in divergence form. This can cause some confusion, however, we note that under appropriate smoothness assumptions on the coefficients they are equivalent. In particular, we always consider $a_{ij}(x) \equiv d_i\delta_{ij}$, where δ_{ij} is the Kronecker-Delta function and $d_i > 0$ is a constant. Hence, the two forms are equivalent for our purposes.*

1.2.5 Notions of *solutions* to PDEs

Here we explore which kind of solutions we expect to obtain in this work.

Classical solutions of elliptic equations

Definition 1.2.11 (Classical solution)**.** *We call a function $u(x)$ a* classical solution *of problem (1.2) if it belongs to $C^{2+\alpha}(\Omega) \cap C(\overline{\Omega})$ for some $\alpha \in (0,1)$, satisfies the equation everywhere in Ω, and satisfies the boundary condition pointwise everywhere along $\partial\Omega$.*

From this definition, we see that a classical solution is the easiest to work with, at least in one sense: all derivatives are the usual derivatives that we are familiar with from calculus I, and the equation is satisfied in an intuitive way. This is different from the notion of weak and strong solutions. Notice that in this case, the operator L is taken in divergence form. As stated previously, this will not make a difference for our purposes since a_{ij} will be constant for each of its entries; despite this, it is worth noting that in general, weak formulations are a little more natural for equations in divergence form.

Weak and strong solutions of elliptic equations

In most cases of interest, regularity assumptions required for classical solutions are much too restrictive. It is nice to be able to work with less regular functions and still have a notion of a solution in a meaningful way. To this end, we use the notion of *weak derivative* introduced previously. In particular, weak solutions are made well-defined through integration by parts.

Definition 1.2.12 (Weak solution (elliptic case)). *A function $u(x)$ belonging to $H^1(\Omega)$ is said to be a* weak solution *of the equation $Lu = f$ in Ω if, given any test function $\phi \in C_0^\infty(\Omega)$, there holds*

$$\int_\Omega \left(\sum_{i,j=1}^{N} a_{ij}(x) \frac{\partial u}{\partial x_j} \frac{\partial \phi}{\partial x_i} + \sum_{i=1}^{N} b_i(x) \frac{\partial u}{\partial x_i} \phi + c(x) u \phi \right) dx = \int_\Omega f \phi dx. \tag{1.4}$$

If, in addition, $u \in H_0^1(\Omega)$, u is said to be a weak solution to the boundary value problem (1.2) *with $B_D = 0$.*

Remark 1.2.5. *In the definition above, if $u \in H_0^1(\Omega)$, u is said to vanish along $\partial\Omega$ in the sense of the trace. The trace theorem is an important result that allows one to consider functions taking values on "sets of measure zero". Indeed, from the point of view of Ω, $\partial\Omega$ has measure zero since it is $N-1$-dimensional! In the case of Dirichlet boundary conditions, this is obtained somewhat directly. In the case of Neumann boundary conditions, a similar perspective is taken, with the Neumann boundary condition satisfied in some integral sense.*

We highlight the trace theorem here for convenience. The following is taken from [31, Ch. 5].

Theorem 1.2.18 (Trace theorem I). *Let Ω have a C^1 boundary and fix $p \geq 1$. Then, given any $u \in W^{1,p}(\Omega)$, there exists a bounded linear operator $T : W^{1,p}(\Omega) \mapsto L^p(\partial\Omega)$ such that*

- $Tu = u|_{\partial\Omega} \quad if \quad u \in W^{1,p}(\Omega) \cap C(\overline{\Omega})$; *and*

- $\|Tu\|_{L^p(\partial\Omega)} \leq C \|u\|_{W^{1,p}(\Omega)}$,

where C *depends only on* p *and* Ω.

In some references, the statement is more "direct" for the Hilbert space $H^1(\Omega)$, and so we state this version as well, taken from [123, Ch. 1].

Theorem 1.2.19 (Trace theorem II)**.** *Let* Ω *have a* C^2 *boundary. Then, any* $u \in H^1(\Omega)$ *has a trace* Tu *along* $\partial\Omega$ *such that* $Tu \in L^2(\partial\Omega)$*, which is to say, there exists a function* $Tu \in L^2(\partial\Omega)$ *satisfying*

$$\lim_{n\to\infty} \int_{\partial\Omega} |u_n - Tu|^2 \, dS = 0,$$

where $\{u_n\}_{n\in\mathbb{N}} \subset C^1(\overline{\Omega})$ *is an arbitrary sequence converging to* u *in* $H^1(\Omega)$.

Further discussion on traces can be found in, e.g., [8, Ch. 1.6].

In the definition of a weak solution, we make no assumption on the regularity of the solution beyond $H^1(\Omega)$. In many cases, the regularity can be improved so that the solution, while not classical, may still have some classical differentiability or integrability properties. This motivates the definition of a *strong solution*.

Definition 1.2.13 (Strong solution (elliptic case))**.** *A function* $u \in W^{2,p}(\Omega)$ *is said to be a* strong solution *to the equation* $Lu = f$ *if* u *satisfies the equation almost everywhere in* Ω*. If, in addition,* $u \in H_0^1(\Omega)$*,* u *is said to be a strong solution of the boundary value problem* (1.2) *with* $i = D$.

Remark 1.2.6. *Similar to the case of weak solutions, analogous formulations exist for the case of Neumann boundary conditions. In fact, in the case of homogeneous Neumann boundary data, both weak and strong solutions are defined through the identity* (1.4) *with* $H_0^1(\Omega)$ *replaced by the larger space* $H^1(\Omega)$*. These distinctions are covered in detail in [89, Ch. IV].*

Classical solutions of parabolic equations

We now highlight the analogous results to the previous section for the parabolic case. All results are almost identical aside from a handful of technical details that change. Overall, the philosophy to develop notions of classical, weak, and strong solutions remains the same.

Definition 1.2.14. *We call a function* $u(x,t)$ *a* classical solution *of problem* (1.3) *if it belongs to* $C^{2+\alpha,1+\alpha/2}(Q_T) \cap C(\overline{Q}_T)$ *for some* $\alpha \in (0,1)$*, satisfies the equation everywhere in* Q_T*, satisfies the boundary condition pointwise along* $\partial\Omega$ *for all* $t > 0$*, and there holds* $\lim_{t\to 0^+} u(x,t) = u_0(x)$ *pointwise in* $\overline{\Omega}$*.*

Weak and strong solutions of parabolic equations

As in the case of elliptic equations, requirements for classical solutions are often too restrictive. Using the same notion of weak differentiability, we have the following definition of a weak solution.

Definition 1.2.15 (Weak solution (parabolic case))**.** *A function* $u(x,t)$ *belonging to* $H^1(Q_T) := W_2^{1,1}(Q_T)$ *is said to be a* weak solution *of the equation* $u_t + Lu = f$ *in* Q_T *if, given any test function* $\phi \in C_0^\infty(Q_T)$*, there holds*

$$\iint_{Q_T} \left(u_t\phi + \sum_{i,j=1}^{N} a_{ij} \frac{\partial u}{\partial x_j}\frac{\partial \phi}{\partial x_i} + \sum_{i=1}^{N} b_i \frac{\partial u}{\partial x_i}\phi + cu\phi \right) dx = \int_\Omega f\phi dx. \tag{1.5}$$

If, in addition, $u(\cdot,t) \in H_0^1(\Omega)$ *for almost every* $t \in (0,T)$*,* u *is said to be a weak solution to the boundary value problem* (1.3) *with* $B_D u = 0$*.*

Remark 1.2.7. *As in the case of elliptic equations, we may treat the homogeneous Neumann boundary condition though choosing test functions from the space* $H^1(Q_T)$*. Furthermore, as in the case of elliptic equations, boundary conditions are considered satisfied in the sense of the trace. This notion extends to satisfying the initial data in the sense of the trace.*

For convenience we highlight some trace theorems for parabolic problems. In what follows, we denote by ∂Q_T the set $\partial\Omega \times (0,T) \cup \overline{\Omega} \times \{t = 0\}$.

Theorem 1.2.20. *Let Ω have a C^2 boundary. Given any function $u \in H^1(Q_T)$, u has a trace $Tu \in L^2(\partial Q_T)$.*

We conclude with the notion of strong solution for parabolic problems.

Definition 1.2.16. *A function $u \in W_p^{2,1}(Q_T)$ is said to be a* strong solution *of the equation $u_t + Lu = f$ if u satisfies the equation almost everywhere in Q_T. If, in addition, $u(\cdot, t) \in H_0^1(\Omega)$ for almost every $t \in (0,T)$, and $\lim_{t\to 0^+} u(x,t) = u_0(x)$ in the sense of the trace, u is said to be a strong solution of the initial-boundary value problem (1.3) with $i = D$.*

Remark 1.2.8. *As in the case of elliptic equations, most textbooks consider in detail only the case of Dirichlet boundary data. The analogous formulation for the homogeneous Neumann problem follows by replacing $H_0^1(Q_T)$ with $H^1(Q_T)$, the details of which can be found in, e.g., [89, Ch. VI].*

1.2.6 Schauder Theory for elliptic and parabolic equations

To complement the material introduced in previous sections, we now state some results sometimes generally referred to as the *Schauder theory* of elliptic and parabolic equations. This theory provides conditions which ensure the existence and uniqueness of a classical solution to linear, second order elliptic and parabolic equations. Additionally, we have the so-called *Schauder estimates* for these classical solutions.

Elliptic equations

Theorem 1.2.21 (Existence of classical solutions (elliptic case))**.** *Assume $\alpha \in (0,1)$, and a_{ij},b_i,c, f belong to $C^\alpha(\overline{\Omega})$ with $c \geq 0$. Then, problem (1.2) admits a unique classical solution $u \in C^{2,\alpha}(\Omega) \cap C(\overline{\Omega})$.*

Theorem 1.2.22 (Schauder estimates (elliptic case))**.** *Assume $\alpha \in (0,1)$, and a_{ij},b_i,c belong to $C^\alpha(\overline{\Omega})$. Suppose also that $f \in C^\alpha(\overline{\Omega})$. If $u \in C^{2,\alpha}(\Omega) \cap C(\overline{\Omega})$ is a classical solution to problem (1.2), then*

$$\|u\|_{C^{2,\alpha}(\Omega)} \leq C \left(\|f\|_{C^\alpha(\Omega)} + \|u\|_{C(\Omega)} \right)$$

for some constant $C > 0$ depending on N, α, Ω, and the C^α-norms of a_{ij}, b_i, c.

Parabolic equations

Theorem 1.2.23 (Existence of classical solutions (parabolic case))**.** *Assume* $\alpha \in (0,1)$, *and* a_{ij},b_i,c, f *belong to* $C^{\alpha}(\overline{\Omega})$*. Then, problem* (1.3) *admits a unique classical solution* $u \in C^{2+\alpha,1+\alpha/2}(Q_T) \cap C(\overline{Q}_T)$*.*

Theorem 1.2.24 (Schauder estimates (parabolic case))**.** *Assume* $\alpha \in (0,1)$, *and* a_{ij},b_i,c *belong to* $C^{\alpha,\alpha/2}(\overline{Q}_T)$*. Suppose also that* $f \in C^{\alpha,\alpha/2}(\overline{Q}_T)$*. If* $u \in C^{2+\alpha,1+\alpha/2}(Q_T)\cap C(\overline{Q}_T)$ *is a classical solution to problem* (1.3)*, then*

$$\|u\|_{C^{2+\alpha,1+\alpha/2}(Q_T)} \leq C\left(\|f\|_{C^{\alpha,\alpha/2}(Q_T)} + \|u\|_{C(Q_T)}\right)$$

for some constant $C > 0$ *depending on* N, α, Ω, *and the* C^{α}*-norms of* a_{ij}, b_i, c.

1.2.7 L^p-theory for elliptic and parabolic equations

We conclude with the weak and strong analogues to the Schauder theory briefly presented in the previous section. In these cases, the Hölder condition on the right hand side is exchanged for an L^p condition. For the case of weak solutions, we state some theorems from the L^2-theory of elliptic and parabolic equations. Then we state results for the L^p-theory versions leading to strong solutions.

Theorem 1.2.25 (L^2-existence for linear elliptic equations)**.** *Suppose* $b_i \equiv 0$ *and that* $c \geq 0$*. Then, given any function* $f \in L^2(\Omega)$*, the following hold.*

- *There exists a unique weak solution* $u \in H_0^1(\Omega)$ *solving problem* (1.2) *with* $i = D$*.*
- *If, in addition,* $c \not\equiv 0$ *in* Ω*, then there exists a unique weak solution* $u \in H^1(\Omega)$ *solving problem* (1.2) *with* $i = N$*.*

Remark 1.2.9. *This result for the case of Dirichlet boundary conditions (homogeneous or otherwise) can be found in, e.g., [31, Theorem 3 Ch. 6.2] or [123, Theorem 2.3.2]. The result for Neumann boundary data (homogeneous or otherwise) can be found in [89, Ch. IV]. In the case where* $c \equiv 0$*, the problem reduces to* Poisson's equation*, which is easier and can be treated separately. Actually, this is precisely Problem 4 in [31, Ch. 6.6].*

Remark 1.2.10. *If the condition $b_i \equiv 0$ is violated, Theorem 1.2.25 is still true; in this case, the equation solved must be written as $Lu + \mu u$ for some $\mu \in \mathbb{R}$. Then, there exists a $\gamma \geq 0$ so that Theorem 1.2.25 holds for all $\mu \geq \gamma$. This can be found in the two Theorems referenced in the previous remark. Essentially, the first order terms ruin the symmetry of the operator L, and so the "usual" techniques (Riesz's representation theorem or variational methods) do not apply.*

Along with the existence of a solution, we also obtain the following estimates for the solution obtained.

Theorem 1.2.26 (L^2-type estimates for linear elliptic equations)**.** *Suppose the hypotheses of Theorem 1.2.25 hold. Then, there exists a constant $C > 0$ such that the solution u satisfies*

$$\|u\|_{H^1(\Omega)} \leq C \|f\|_{L^2(\Omega)},$$

where the constant C is independent of f. If $\partial\Omega$ has a C^2 boundary, then there further holds

$$\|u\|_{H^2(\Omega)} \leq C \left(\|f\|_{L^2(\Omega)} + \|u\|_{H^1(\Omega)} \right),$$

for some $C > 0$ independent of f and u.

Remark 1.2.11. *The first estimate is obtained rather directly with limited regularity requirements on $\partial\Omega$. Usually, the second estimate is presented as an "interior estimate" first, holding only in any compact subset $\Omega' \Subset \Omega$. Since we always assume Ω has a smooth enough boundary, we jump straight to the punchline: we obtain H^2-estimates in terms of the data f and lower order norms of the solution u. For the Dirichlet problem, we refer to [123, Ch. 2]. For the homogeneous Neumann problem, we refer to [89, Ch. IV.3].*

Theorem 1.2.27 (L^2-existence for linear parabolic equations)**.** *Suppose $a_{ij}, b_i, c \in L^\infty(Q_T)$. For simplicity, we assume that a_{ij} are independent of t. Suppose also that $u_0 \in H^1(\Omega)$. Then, given any function $f \in L^2(Q_T)$, the following hold.*

- *There exists a unique weak solution solving problem (1.3) with $i = N$.*

- *Suppose further that $u_0 \in H_0^1(\Omega)$. Then, there exists a unique weak solution u solving problem (1.3) with $i = D$.*

Remark 1.2.12. *For the homogeneous Neumann boundary data case, we refer to [89, Ch. VI]. For the homogeneous Dirichlet boundary data case, we refer to [123, Theorem 3.5.1].*

Theorem 1.2.28 (L^2-type estimates for linear parabolic equations)**.** *Suppose the hypothesis of Theorem 1.2.27 hold and that $\partial\Omega$ is C^2.. Then, there exists a constant $C > 0$ such that the solution u satisfies*

$$\|u\|_{W_2^{2,1}(Q_T)} \leq C \left(\|f\|_{L^2(\Omega)} + \|u_0\|_{H^1(\Omega)} \right).$$

Remark 1.2.13. *Unlike the case of elliptic equations, we choose to jump straight to the global regularity estimate in $W_2^{2,1}(Q_T)$ rather than starting in some weaker space, like $W^{1,0}(Q_T)$. These results exist, but compiling the varying technical details is cumbersome and distracting to the main goal.*

Finally, we conclude with the so-called L^p-theory of elliptic and parabolic equations. In this case, we increase the requirement on the right hand side, which improves the space in which solutions are obtained from $W^{2,2}(\Omega)$ and $W_2^{2,1}(Q_T)$ to $W^{2,p}(\Omega)$ and $W_p^{2,1}(Q_T)$. In particular, this is most useful when applying the Sobolev embedding theorems (Theorem 1.2.3 and 1.2.4). For the following theorems, we now present the existence and apriori estimates in the same place.

Theorem 1.2.29 (L^p-theory for linear elliptic equations)**.** *Suppose that $a_{ij}, b_i, c \in L^\infty(\Omega)$, $c \geq 0$, and $a_{ij} \in C(\overline{\Omega})$. Assume $p > 1$ and that $\partial\Omega$ is C^2. Then, given any function $f \in L^p(\Omega)$, there exists a unique strong solution $u \in W^{2,p}(\Omega)$ solving problem (1.2). Furthermore, the solution u satisfies*

$$\|u\|_{W^{2,p}(\Omega)} \leq C \left(\|f\|_{L^p(\Omega)} + \|u\|_{L^p(\Omega)} \right),$$

for some $C > 0$ independent of f and u.

Theorem 1.2.30 (L^p-theory for linear parabolic equations)**.** *Suppose that $a_{ij}, b_i, c \in L^\infty(Q_T)$ and $a_{ij} \in C(\overline{Q}_T)$. Assume $p > 1$, that $\partial\Omega$ is C^2, and $u_0 \in W^{2,p}(\Omega)$. Then,* *given any function $f \in L^p(Q_T)$, there exists a unique strong solution $u \in W_p^{2,1}(Q_T)$ solving problem (1.3). Furthermore, the solution u satisfies*

$$\|u\|_{W_p^{2,1}(Q_T)} \leq C \left(\|f\|_{L^p(Q_T)} + \|u_0\|_{W^{2,p}(\Omega)} + \|u\|_{L^p(Q_T)} \right),$$

for some $C > 0$ independent of f and u.

Remark 1.2.14. *These results contain so-called global estimates over the entire domain Ω. Generally, one first obtains interior estimates for any compact subset $\Omega' \Subset \Omega$. For general L^p-estimates, we refer to [119]. In it, interior estimates are obtained for some general second order linear elliptic and parabolic equations (note that they do not contain first order terms in the operator, i.e., $b_i \equiv 0$). One may then apply a local flattening of the boundary technique in order to prove these estimates are in fact global across the whole domain Ω, where the smoothness requirement of $\partial\Omega$ is what allows one to perform this "trick". This is covered in detail for the Dirichlet case in [123, Ch. 9.1] (for elliptic) and [123, Ch. 9.2] (for parabolic). For the case of Neumann boundary conditions, one may use the interior estimates found in [119], along with the approaches used in [89] (to handle the Neumann boundary condition) and the methods of [123, Ch. 9] (to handle the local flattening of the boundary).*

1.2.8 Monotone methods for nonlinear elliptic and parabolic equations

We conclude with a brief discussion of so called *monotone methods* in proving the well-posedness of certain general nonlinear problems. It is important to note that this sense of "monotone" is different than the "theory of monotone flows". In the present setting, *monotone* refers to the construction of monotonic sequences of sub/super solutions. For quasilinear parabolic and elliptic equations, particularly those with nonlinearity in the reaction term only, we can prove the existence/uniqueness of solutions based on some rather reasonable conditions on the right hand side (particularly, Assumptions 2.2.1-2.2.2).

These results are well-known and not original here. For the purpose of this presentation, we follow references such as [123] or [95]. We use sub/super solutions in the classical sense, applying the classical comparison principle, Theorem's 1.2.12 and 1.2.14, to show that the generated sequences are indeed monotone. Paired with Dini's theorem and the Schauder estimates, we prove the sequences converge to a solution to the original problem. In some cases, this solution is unique; other times, we obtain at least two solutions that are ordered.

The result we present here is for the case of a scalar parabolic problem. The elliptic case is similar with some important modifications. More precisely, notice the non-negativity of $c(x)$ in Theorem 1.2.12; there is no such requirement for parabolic equations, an essential difference between the two. This is what may lead to a lack of uniqueness in the steady state problem.

Beyond scalar equations, these monotone methods can also be applied to systems of elliptic and parabolic equations. In these cases, the differential inequalities may change depending on the nature of the interaction on the right hand side. The three common cases are *quasimonotone nonincreasing*, *quasimonotone nondecreasing*, or *mixed quasimonotone*. We focus only on the nonincreasing case, since this corresponds to competitive systems.

We now introduce the notion of *sub* and *super* solutions. Actually, we have already seen this for linear equations in Theorems 1.2.12 and 1.2.14, where u and v are respectively sub and super solutions. Note that in some references these are called *lower* and *upper* solutions. Suppose we are given the following nonlinear problem:

$$\begin{cases} u_t - \Delta u = f(u), & \text{in} \quad Q_T, \\ B_i u = 0, & \text{on} \quad \partial\Omega \times (0,T), \\ u(x,0) = u_0(x), & \text{in} \quad \overline{\Omega}, \end{cases} \tag{1.6}$$

for some non-trivial initial data $u_0(x)$ and $i = B$ or $i = N$. We assume that $f(u)$ is at least Lipschitz continuous in its argument.

Definition 1.2.17. *A function $\underline{u}$ $(\overline{u})$ belonging to $C^{2,1}(\overline{Q}_T)$ is called a* sub *(*super*) solution of problem* (1.6) *if it satisfies*

$$w_t - \Delta w \leq \ (\geq)\ f(w) \quad \textit{in} \quad Q_T,$$

satisfies

$$B_i w \leq \ (\geq)\ 0 \quad \textit{on} \quad \partial\Omega \times (0,T),$$

and satisfies $w(x,0) \leq\ (\geq)\ u_0(x)$ *in* $\overline{\Omega}$.

Sometimes we say that $\underline{u}$, $\overline{u}$ are *ordered* if $\underline{u} \leq \overline{u}$ in $\overline{Q}_T$. Notice that a solution is both a sub and super solution. Since f is Lipschitz, there exists a constant $\underline{c} > 0$ so that

$$f(u) - f(v) \geq -\underline{c}(u - v) \tag{1.7}$$

whenever $u \geq v$. If we consider functions lying between our sub and super solutions, this means that the function

$$F(u) := \underline{c}u + f(u)$$

is monotone nondecreasing for $\underline{u} \leq u \leq \overline{u}$. Later, we will actually assume that f is differentiable and is therefore Lipschitz. We then set up an iteration scheme via

$$w_t^n - \Delta w^n + \underline{c}w^n = F(w^{n-1}), \quad \text{in} \quad Q_T, \tag{1.8}$$

$$B_i w^n = 0, \quad \text{on} \quad \partial\Omega \times (0,T), \tag{1.9}$$

$$w^n(x,0) = u_0(x), \quad \text{in} \quad \overline{\Omega}, \tag{1.10}$$

where we choose our initial iterate $w^0(x,t) \in C^{\alpha,\alpha/2}(\overline{Q}_T)$ for some $\alpha \in (0,1)$. Since the right hand side is known, classical theory (e.g., Theorem 1.2.23) ensures the existence of a unique classical solution $w^1(x,t)$. Bootstrapping this process, we have a classical solution for each $n \geq 1$. Putting some of these pieces together, the natural initial iterates we might choose are given by $\underline{w}^0 := \underline{u}$ and $\overline{w}^0 := \overline{u}$. These initiate our upper and lower sequences which, with some care, can be shown to converge to a true (classical) solution of the original problem. This is what we find in the following statement, modified from [123, Ch. 12.1.3].

Theorem 1.2.31. *Let* $\underline{w}$ *and* $\overline{w}$ *be ordered supersolution and subsolution of problem* (1.6)*, respectively, and assume* f *is Lipschitz continuous. Then, the upper sequence* $\{\overline{w}^n\}_{n\geq 0}$ *converges monotonically from above to a solution* $\overline{w}^\infty$ *and the lower sequence* $\{\underline{w}\}_{n\geq 0}$ *converges monotonically from below to a solution* $\underline{w}^\infty$*, and* $\underline{w}^\infty(x,t) \leq \overline{w}^\infty(x,t)$ *in* Q_T*; in fact,* $\underline{w}^\infty = \overline{w}^\infty$ *is the unique solution.*

Since the proof is somewhat instructive for future sections, we provide the key details here.

Proof. **Step 1: monotonicity.** First we show that the iterates $\{\underline{w}^n\}_{n\geq 0}$, $\{\overline{w}^n\}_{n\geq 0}$ are monotone increasing and decreasing, respectively. We show the second case only, with the first following in a similar fashion. Set $z := \overline{u} - \overline{w}^1 = \overline{w}^0 - \overline{w}^1$. Then, we compute directly to find that

$$z_t - \Delta z + \underline{c}z \geq F(\overline{u}) - F(\overline{w}^0) = 0 \quad \text{in} \quad Q_T,$$

since $\overline{u} = \overline{w}^0$. The maximum principle implies that $z \geq 0$ in Q_T, since we also have that $B_i z \geq 0$ along $\partial\Omega \times (0,T)$ and $z(x,0) = 0$. Therefore,

$$\overline{w}^1 \leq \overline{w}^0 \quad \text{in } \overline{Q}_T.$$

Arguing in the other direction yields $\underline{w}^0 \leq \underline{w}^1$. Then we set $\tilde{z} := \overline{w}^1 - \underline{w}^1$. $\tilde{z}$ satisfies

$$\tilde{z}_t - \Delta\tilde{z} = F(\overline{u}) - F(\underline{u}) \geq 0 \quad \text{in} \quad Q_T,$$

which holds since $\underline{u} \leq \overline{u}$ by assumption and $F(w)$ is nondecreasing for all $\underline{u} \leq w \leq \overline{u}$. Since $B_i\tilde{z} = 0$ and $\tilde{z}(x,0) = 0$, the maximum principle again yields that $\tilde{z} \geq 0$, and so

$$\underline{w}^1 \leq \overline{w}^1 \quad \text{in} \quad \overline{Q}_T.$$

We now proceed inductively. Assume that for some $k \geq$ there holds

$$\underline{w}^{n-1} \leq \underline{w}^n \leq \overline{w}^n \leq \overline{w}^{n-1}.$$

Set $\hat{z} := \overline{w}^n - \overline{w}^{n+1}$. Then $\hat{z}$ satisfies

$$\hat{z}_t - \Delta\hat{z} = F(\overline{w}^{n-1}) - F(\overline{w}^n) \geq 0 \quad \text{in} \quad Q_T,$$

which follows from the non-increasing property of F and the inductive hypotheses. We again have that $B_i\hat{z} \geq 0$ with $\hat{z}(x,0) = 0$, and so

$$\overline{w}^{n+1} \leq \overline{w}^n \quad \text{in } \overline{Q}_T$$

by the maximum principle. Similarly, we find that $\underline{w}^n \leq \underline{w}^{n+1}$ in $\overline{Q}_T$. One repeats the procedure one last time to obtain that $\underline{w}^{n+1} \leq \overline{w}^{n+1}$, which proves the desired monotone property of the respective sequences.

Step 2: convergence. We now show that these sequences converge, and in fact converge to a solution of problem (1.6). We show the result for $\{\underline{w}^n\}_{n\geq 0}$. Since F is monotone nonincreasing and Lipschitz, the (pointwise) monotone convergence of $\underline{w}^n \nearrow \underline{w}^\infty$ as $n \to \infty$ implies that $F(\underline{w}^n) \to F(\underline{w}^\infty)$ as $n \to \infty$. Since the initial iterate is smooth, each iterate is itself smooth, i.e.,

$$\underline{w}^n, \overline{w}^n \in C^{2+\alpha,1+\alpha/2}(Q_T),$$

for each $n \geq 1$, which holds by the existence Theory Theorem 1.2.23. In fact, by the Schauder estimates for parabolic equations there holds

$$\|\underline{w}^n\|_{C^{2+\alpha,1+\alpha/2}(Q_T)} \leq C\left(\|u_0\|_{C^{2+\alpha,1+\alpha/2}(Q_T)} + \|\underline{w}^{n-1}\|_{C^{2+\alpha,1+\alpha/2}}\right),$$

for some $C > 0$, independent of n. This implies that $\{\underline{w}^n\}_{n\geq 0}$ is uniformly bounded in $C^{2+\alpha,1+\alpha/2}$, and hence $\underline{w} \to \underline{w}^\infty$ is indeed a solution to problem (1.6). Notice that in this step we use the monotone property of the sequences generated. This completes the proof of the first part of the theorem.

Step 3: uniqueness. Since f is Lipschitz continuous, $\underline{w}^\infty - \overline{w}^\infty$ satisfies

$$(\underline{w}^\infty - \overline{w}^\infty)_t - \Delta(\underline{w}^\infty - \overline{w}^\infty) = f(\underline{w}^\infty) - f(\overline{w}^\infty) \geq -\underline{c}(\underline{w}^\infty - \overline{w}^\infty) \quad \text{in} \quad Q_T,$$

for some $\underline{c} \geq 0$. With $B_i(\underline{w}^\infty - \overline{w}^\infty) = \underline{w}^\infty(x,0) - \overline{w}^\infty(x,0) = 0$, the maximum principle implies that

$$\underline{w}^\infty - \overline{w}^\infty \geq 0 \quad \text{in} \quad \overline{Q}_T$$

and so $\underline{w}^\infty = \overline{w}^\infty$, completing the proof. □

Remark 1.2.15. *Under weaker conditions on the function f, we may lose the uniqueness of the solution. Instead, we have that any other solution $\tilde{w}$ lying between the sub/super solution pair satisfies $\underline{w}^\infty \leq \tilde{w} \leq \overline{w}^\infty$. Additionally, the* ordered *property of the sub/super solutions is not necessary! They are necessarily ordered by virtue of the equation that they solve, see Chapter 2.*

Some further discussion is warranted. As we have just proven, a Lipschitz condition is sufficient to ensure that the solution to the time-dependent problem is unique. The same cannot be said for the elliptic equation without additional hypotheses on the function f. The next theorem will require in addition that the constant $\underline{c}$ in the Lipschitz condition (1.7) be non-negative. Looking at **Step 3** of the previous proof, we see where this requirement will be necessary: for parabolic equations, the sign of the low order coefficient $c(x,t)$ does not affect the fact of the maximum principle.

Furthermore, the use of monotone sequences, let alone the use of classical sub/super solution pairs, is not a requirement for a similar result to hold. Just as we introduced notions of weak derivatives and weak/strong solutions, we may consider weak/strong sub/super solutions. In such cases, equality in (1.4) or (1.5) can be replaced with $\leq$ and$\geq$ for sub and super solutions, respectively. It is weak if the integral inequality holds for any test function belonging to the appropriate space. It is strong if the integration by parts is unnecessary so that the equation holds almost everywhere in the domain. Using these notions of sub/super solutions, one may emulate the techniques used in the previous proof. The main ingredient that changes is the application of the maximum principle for strong or weak solutions. To do away with the monotone property, we use the Bolzano–Weierstrass theorem in place of the monotone convergence theorem: every bounded subsequence has a convergent subsequence. Compactness properties of the spaces in which the sequences are bounded allow one to extract a subsequence that converges in some nice way. This is the strategy used in the following proof, modified from a handful of results found in [95, Ch. 3] concerning elliptic equations.

Theorem 1.2.32. *Suppose $\underline{w}, \overline{w}$ are strong sub/super solutions to the steady state for problem (1.6). Then, the upper and lower sequences $\{\underline{w}_n\}_{n\geq 1}$ and $\{\overline{w}_n\}_{n\geq 1}$ given by the iteration scheme (1.8) with initial iterates $\underline{w}$ and $\overline{w}$, respectively, are monotone in the sense that $\{\underline{w}_n\}_{n\geq 1}$ is nondecreasing and $\{\overline{w}_n\}_{n\geq 1}$ is non-increasing. Furthermore, $\underline{w}^n \leq \overline{w}^n$ for each $n \geq 0$. Therefore, the monotone pointwise limits*

$$\lim_{n\to\infty} \underline{w}^n = \underline{w}^\infty \quad \text{and} \quad \lim_{n\to\infty} \overline{w}^n = \overline{w}^\infty$$

exist; they are each a strong steady state solution to problem (1.6). Finally, there exists *another solution w^* lying in $\underline{w} \leq w^* \leq \overline{w}$, then $\underline{w}^\infty \leq w^* \leq \overline{w}^\infty$.*

Remark 1.2.16. *When we have the homogeneous Neumann boundary condition, we must further assume that $\underline{c} \not\equiv 0$ in Q_T; otherwise, the* iterates *we generate may not have a* unique *classical solution. In fact, the problem has a continuum of constant solutions.*

We omit the proof as we use the same techniques in Chapter 2. The technical details are similar to the proof of Theorem 1.2.23; the difference is in the arguments for the convergence step, appealing instead to Sobolev theory and the Sobolev embedding theorem. Then, we can bootstrap to prove that the sequence converges in $C^{1+\alpha,(1+\alpha)/2}(\overline{Q}_T)$; continuing further, we obtain a classical solution via Schauder estimates. The monotonicity of the sequences still holds, giving us convergence of the entire sequence. Repeating these arguments, one can prove that any other solution must lie between the lower and upper limits.

In future chapters, we apply a similar technique; however, we do not get convergence of the entire sequence. The subsequence extracted still produces a strong solution, however, and the solution is unique under appropriate conditions on the right hand side. These results as presented are meant to give insights into the big picture for monotone methods. Further discussion on the uniqueness problem for elliptic equations can be found in [95, Ch. 3.3]. The following condition is sufficient to guarantee the uniqueness of the solution:

$$f(u) \leq f(v) \quad \text{whenever} \quad \underline{w} \leq v \leq u \leq \overline{w}.$$

Finally, we comment that similar existence-comparison theorems exist for coupled equations of reaction-diffusion type. The sense in which functions are sub/super solutions in the competitive case is given in Chapters 2 and 3, see the proof of Theorem 2.5.2. Some useful references include [123, Ch. 12] and [95, Ch. 3], where weaker conditions on the reaction term f and more general operators are considered.

1.2.9 Existing mathematical works

We take a moment to highlight briefly some of the existing literature most related to the present work. Here, we emphasize works focusing primarily on the analysis of reaction-diffusion equations of the form to be studied in the present work; within each chapter, we will highlight in more detail efforts made to model habitat loss specifically.

In the mathematical context, we are studying the effects of environmental heterogeneity on diffusing species in a reaction-diffusion equation setting. This area has been well studied, and so we do not expect to be comprehensive here. Instead, we highlight some of the key works by authors who have frontiered this perspective, especially in application to biological systems. Key textbook references include [8], [90], [93], [94], [109].

For a single species, the pioneering work of Cantrell & Cosner explore in the late 1980's and early 1990's exemplifies the utility of diffusive logistic equations in heterogeneous environments. In [13], properties of a principal eigenvalue with sign-indefinite weight is considered, an application of results obtained in [7], [43]. In [12], a diffusive logistic model with sign-indefinite weight is considered, providing a foundational framework on which all subsequent results essentially follow. Their analysis uses the study of the principal eigenvalue to determine local stability of trivial steady states. Subsequent works, including [14]–[17], explore further the effects of environmental heterogeneity on diffusing species.

Later, multi-species models are considered, either in a cooperative or competitive setting. [28] considers a n-species population model, where differing phenotypes represent differing dispersal strategies, while all other traits remain identical. This led to the classic result *"the slower diffuser always wins!"*, which is robust in a temporally static but non-homogeneous landscape. This concept has been widely explored since then, including further study of the 2-species competition case and time-periodic environments, see [70], [71].

More recently, a rather complete description of the global dynamics of a 2-species competition model has been described by He and Ni in a series of papers, see [59], [60], [64] and [61], [81]. These works provide a complete description of the global dynamics under biologically relevant environmental properties, such as one species with a heterogeneous environment while the other has a homogeneous environment. These works, while general, rely again on the study of a principal eigenvalue, and so the stability criteria are often abstract, and impossible to verify in many cases. For this reason, a direct application to habitat loss is not possible: mathematical generality is favoured, perhaps at the cost of precise, quantitative information.

Different from existing works, we seek to combine the mathematical rigour of previous efforts with the biological precision of more ecologically minded efforts to gain deep insight into the effects and relative impacts of different processes of habitat loss. This will follow from our three postulates introduced previously, beginning with habitat degradation, followed by habitat destruction, and finally, habitat fragmentation.

Chapter 2

Habitat Degradation

In this chapter, we present some novel habitat degradation models using reaction-diffusion equations. Continuing from the introduction, we introduce some additional key ecological terms to solidify the connection between the model and ecological insights. We discuss briefly some existing efforts to model habitat loss in a general sense, noting that they are not necessarily specific enough to distinguish between different forms of habitat loss described thus far. In Section 2.2, we derive our PDE model using postulates and definitions given thus far. In Section 2.3, we take a detour to establish some of the technical background we will need to fully determine the global dynamics of the time-dependent system. In Section 2.4, we discuss the scalar equation subject to habitat degradation. This includes well-posedness results, comparison principles, and a full description of the global dynamics. Finally, we discuss a two-species competition model with habitat degradation in Section 2.5. In order to fully analyze the problem, we make some biologically reasonable simplifications. We prove the well-posedness of the problem as well as some comparison-principal type results for competitive systems. We are then able to fully describe the global dynamics. We present some numerical simulations to demonstrate some of our theorem statements, particularly in the two-species competition model case, in Section 2.6. We conclude with a discussion of the results and related implications in Section 2.7.

2.1 Preface

Habitat degradation, as defined in Chapter 1, is the gradual deterioration of habitat quality. As noted in [44], "*in [a] degraded habitat, a species may decline, occur at a lower density, or may be unable to breed*". In contrast to obvious habitat destruction, habitat degradation is sometimes more difficult to detect because of the timescale at which effects are realized, and some species with longer lifespans may persist in an area for a long period of time before extirpation. Moreover, habitat degradation is implicitly linked to habitat *quality*; often, habitat quality is not explicitly considered for landscape-level habitat analysis. Consider the following quote from [65]:

> The exclusion of habitat quality from many landscape-level habitat analyses likely results from the difficulty in measuring habitat characteristics and reliably associating those conditions with demographic outcomes. Habitat quality is often multi-faceted, affecting multiple population outcomes (e.g., survival and reproduction), difficult to directly describe with remotely sensed imagery and evaluate alongside measures of habitat amount and fragmentation (Johnson, 2007). Consequently, habitat quality is often omitted or more subjectively represented in habitat management or conservation planning.

Hence, we have significant motivation to study the effects of habitat degradation with a little more nuance. Mathematical modelling offers unique insights into such subtleties.

Evidently, essential to the definition of habitat degradation is an understanding of habitat *quality*. We adhere to the following.

Definition 2.1.1 (Habitat quality [57]). *The ability of the environment to provide conditions appropriate for individual and population persistence. It should be considered a continuous variable, ranging from low to medium to high, based on resources available for survival, reproduction, and population persistence, respectively.*

Recalling that habitat is species-specific, habitat quality is also intrinsically species-specific in this context. We also have a rough ordering of priority: low-quality habitat may allow for survival alone; medium-quality habitat will facilitate reproduction; high-quality habitat facilitates persistence of the population. In this sense, terms like "bad habitat" or "unsuitable habitat" are somewhat oxymoronic; if a 'habitat' is bad, it is not habitat by definition. Alternatively, habitat is *good by definition*.

2.2 Model derivation

Our focus in this section is on providing a heuristic derivation of the modelling framework to be used in describing habitat degradation. Taking motivation from Section 1.1, we aim to incorporate postulates one and two: habitat degradation and destruction lie on a spectrum, and this level of impact is dependent on the species considered. We then cast this problem in the context of partial differential equations and explore the predictions made by this simple model. We consider first the case of a single species and then formulate the reaction-diffusion system between two competing species.

To start, we assume that there is some landscape given by a bounded region. For simplicity, we will assume that the landscape can be divided into two distinct regions: the undisturbed region, unaltered by processes of habitat loss, and the modified region, assumed to be degraded by some natural or anthropomorphic process. We will assume that it is "business as usual" in the undisturbed region, with the population dynamics described by some reasonable functional form. We then assume that there is a negative impact on the species in the degraded region, and so the population level will either remain static or decrease in these regions. This negative impact, which is implicitly dependent on the species considered, will be described by the parameter $c \geq 0$. This parameter will be a key aspect of our analysis. This parameter can be thought of in two ways: as a net death rate in those regions, a consequence of the modified habitat, or as the inverse of the *resilience* of a species in terms of its ability to withstand modifications to its environment. This perspective is important for future discussions, as pests are often species that are rather resilient to environmental change, putting them at a competitive advantage compared to other native species [27], [105], [108].

To this end, fix $\Omega \subset R^N$, $N \geq 1$. This will be our landscape occupied by the local species. Note carefully that, should we refer to Ω as *habitat*, we are assuming implicitly that *it once was habitat.* We assume that the species move according to diffusive movement at a constant rate $d > 0$. In the absence of birth/death processes, we assume the total population remains fixed. This yields a zero-flux boundary condition, which in this case corresponds to a homogeneous Neumann boundary condition (such as in problem (1.2) with boundary operator B_N). To model the effects of habitat degradation, we assume the following according to our previous descriptions:

(i) The habitat Ω is split into two regions such that $\Omega = G \cup B$. G denotes the undisturbed region(s), while B denotes the region(s) of degraded habitat. We always assume that $0 < |B| < |\Omega|$, where $|\cdot|$ denotes the Lebesgue measure.

(ii) In region G, the population grows according to a logistic growth or similarly shaped functional response (to be made precise below).

(iii) In region B, the population declines at rate $c \geq 0$.

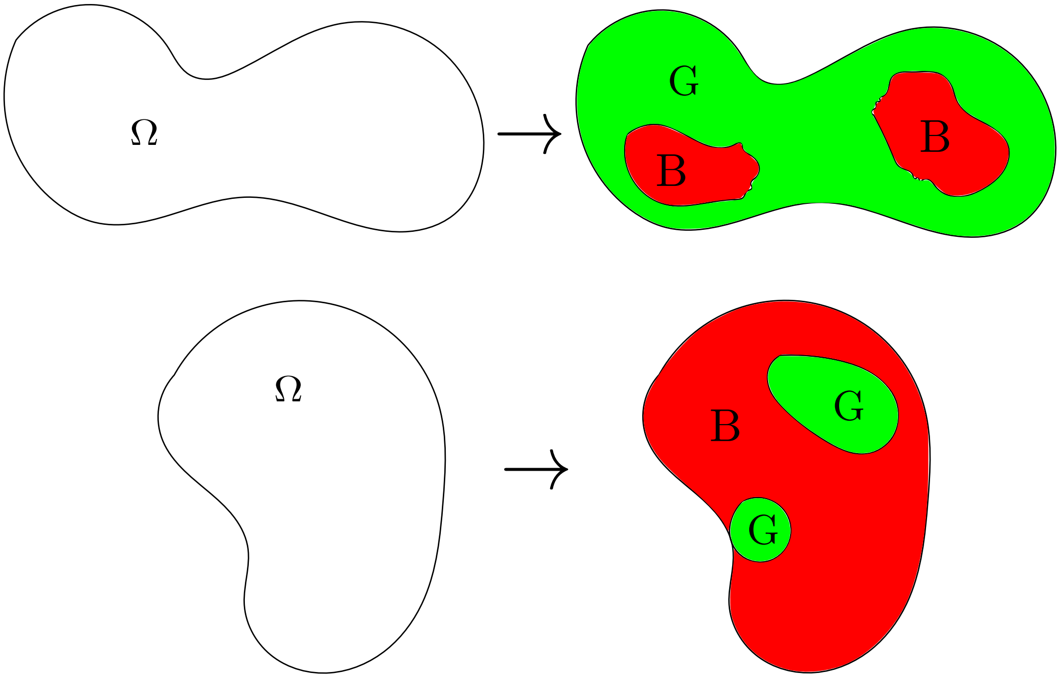


Figure 2.1: A two-dimensional representation of assumption (i), where the whole domain Ω is broken into disjoint subdomains representing the undisturbed region of habitat "G" and the degraded region of habitat "B". The regions can be of any (fixed) shape or size, as long as both regions have positive area.

These assumptions give us a simple setting to explore the impacts of a degraded habitat on diffusing species. Assumption (i) simply ensures that there are both better and worse quality regions within the available habitat; of course, this is a simplification. In the natural world, these boundaries may not be so well defined. One may then debate whether the region B is indeed *habitat* in our present context; on one hand, species will persist in these regions due to the nature of the PDE model. Therefore, we may interpret the region B is a *low-quality* habitat. On the other hand, if the entire landscape is made of only the region B, the species goes extinct; in this case, B is no longer habitat by definition, as it can no longer sustain the local population(s). Assumption (ii) is the "business as usual" assumption in the good region G. (iii) is the assumption of, at worst, a non-positive impact the degraded habitat has on local species. This satisfies postulates one and two, where c is the net (negative) result on the population growth, and the level of impact ranges from $c = 0$ (completely neutral) to $c = \infty$ (completely lethal). We should take care, however, as assumptions (ii)-(iii) implicitly assume that forms of "competition" (intraspecific competition in the single species case) do not take place in the degraded region B. This is more or less reasonable depending on the actual mechanism of competition. In the case of interference competition (i.e. competition that occurs directly between individuals), the species may still interact within a degraded area of habitat. This could be through direct acts of aggression in order to prevent other individuals (within the same species) from accessing their mating partner. In this case, the intraspecific competition might be considered independent of the quality of the habitat, and so assumption (iii) may not be reasonable. Alternatively, if the interference competition occurs in order to maintain access to a specific resource, such as water or territory necessary for survival, it is assumed that the degraded region(s) do not contain such resources, and so competition is no longer necessary in these regions. Similarly, in the case of exploitative competition (i.e. competition that occurs indirectly between individuals), the use of a necessary resource by one species results in less resource for other species. In the degraded region(s), there are no such resources available, and so it is reasonable to assume that there is no competitive interaction.

Denote by $\mathbb{1}_K(x)$ the indicator function of a set $K \subset \mathbb{R}^N$, that is,

$$\begin{cases} \mathbb{1}_K(x) = 1 & \text{for } x \in K, \\ \mathbb{1}_K(x) = 0 & \text{otherwise.} \end{cases}$$

Then, we can formulate the single species model as follows:

$$\begin{cases} w_t = d\Delta w + \mathbb{1}_G f(x,w) - c\mathbb{1}_B w & \text{in } \Omega \times (0,T), \\ w(x,0) = w_0(x) \gneqq 0 & \text{in } \overline{\Omega}, \\ \frac{\partial w}{\partial \nu} = 0 & \text{on } \partial\Omega \times (0,T), \end{cases} \tag{2.1}$$

In general, we always assume that the reaction term satisfies

Assumption 2.2.1. *$f(x,w) \in C^{\alpha,1}(\overline{\Omega} \times \mathbb{R}^+)$, $f(0) = 0$, and there exists $U > 0$ so that $f(x,w) < 0$ for all $w > U$, for all $x \in \Omega$,*

along with one of the following:

Assumption 2.2.2. *For any $x \in \Omega$ there holds $f(x,\lambda w) \geq \lambda f(x,w)$ for all $w \in \mathbb{R}^+$ and $\lambda \in (0,1)$. Moreover, there exists an open set $\Gamma \Subset G$ such that the inequality is strict, i.e., $f(x,\lambda w) > \lambda f(x,w)$ for all $x \in \Gamma$.*

Assumption 2.2.3. *For any $x \in \Omega$ there holds*

$$(1-\lambda)f(x,w_1) + \lambda f(x,w_2) \lneqq f(x,(1-\lambda)w_1 + \lambda w_2)$$

for any $w_1 \neq w_2$ and $\lambda \in (0,1)$. In fact, since f is assumed differentiable in the variable w, this is equivalent to the function being bounded by its Taylor approximation:

$$f(x,w_2) \leq f(x,w_1) + f'(x,w_1)[w_2 - w_1]$$

for any $x \in \Omega$ and any w_1,w_2 belonging to $\mathbb{R}^+$.

Assumption 2.2.1 is a standard regularity condition for well-posedness, though the notation may not be standard. Here, $C^{\alpha,1}$ means that for each $w \geq 0$ fixed, $f(x,\cdot)$ is Hölder continuous with exponent α, and for each $x \in \overline{\Omega}$ fixed, $f(\cdot,w)$ is differentiable. It also assumes that if the population is zero there is no birth or death, and that the population growth becomes negative for sufficiently large population sizes. Technically, this condition is a minimal requirement ensuring the existence of a non-trivial steady. The first part of Assumption 2.2.2 is sometimes referred to as a subhomogeneity condition [124, Ch. 2.3] in the variable w. In particular, a subhomogeneity condition automatically implies that $f(x,w) \leq f'(x,0)w$ for all $w > 0$. Assumption 2.2.3 is a standard concavity condition in the variable w. Notice that concavity implies subhomogeneity. We can see this through a few examples. One example of a function satisfying assumptions 2.2.1 and (2.2.2) but not (2.2.3)) is

$$f(x,w) = w(e^{-w} - \gamma)$$

for $\gamma \in (0,1)$. An example of a function satisfying all assumptions is the logistic growth form $w(1-w)$. Since we allow environmental heterogeneity in the good region G, we may more generally consider

$$f(x,w) = w(m(x) - w)$$

for some function $m(x) \in C^{\alpha}(\overline{\Omega})$.

Scalar problems are, generally, easier to analyse than systems, and so we can treat more general forms of the reaction term f. For the competition system, we instead assume a simple Lotka-Volterra form of reaction. In this case, the habitat degradation competition-diffusion model can be written as follows:

$$\begin{cases} u_t = d_1 \Delta u + \mathbb{1}_G u(1 - u - \gamma_1 v) - c_1 \mathbb{1}_B u & \text{in} \quad Q_T, \\ v_t = d_2 \Delta v + \mathbb{1}_G v(1 - \gamma_2 u - v) - c_2 \mathbb{1}_B v & \text{in} \quad Q_T. \end{cases}$$

Through this construction, we still split the domain into two (almost) disjoint regions - assumption (i). We see logistic growth and competition in the undisturbed habitat G, while both species experience mortality in region B at rates $c_i \geq 0$, $i = 1, 2$ - assumptions (ii) and (iii), respectively. In particular, we note that c_1 is not necessarily equal to c_2, even if each population exists in the same environment. This moves towards addressing the subtlety in the effect of altered habitat on species, as it depends on the species and their individual traits. For simplicity, we assume the rate of competition is equal, that is, $\gamma_1 = \gamma_2 = 1$, so as to isolate the effects of degradation on the interacting species alone. We take species u as the slower diffuser and species v as the faster diffuser so that $0 < d_1 \leq d_2$ are held fixed. This assumption can be made without loss of generality since the system has some nice symmetry properties. The Neumann problem may now be more conveniently written as follows:

$$\begin{cases} u_t = d_1\Delta u + u[m_{c_1} - \mathbb{1}_G(u+v)] & \text{in} \quad Q_T, \\ v_t = d_2\Delta v + v[m_{c_2} - \mathbb{1}_G(u+v)] & \text{in} \quad Q_T, \\ u(\cdot,0) = u_0 \gneqq 0, \;\; v(\cdot,0) = v_0 \gneqq 0, & \text{in} \quad \overline{\Omega}, \\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0 & \text{on} \quad \partial\Omega \times (0,T), \end{cases} \tag{2.2}$$

where

$$m_{c_i}(x) := \mathbb{1}_G(x) - c_i \mathbb{1}_B(x), \quad i = 1, 2. \tag{2.3}$$

Our goal now is to investigate the global dynamics of the scalar equation (2.1) as they depend on d, c, along with its associated steady state. We can then perform a detailed analysis of the competition-diffusion system (2.2) depending on the relation between the parameters d_i and c_i, resulting in a complete description of the global dynamics.

In order to use the tools of monotone dynamical systems, we must first introduce some relevant eigenvalue problems. As it turns out, these problems will allow us to determine the precise local stability of all of the steady states.

Existing results

We now introduce some comparisons to existing habitat loss modelling efforts. First and foremost, it should be noticed that this model is spatially explicit, and so it explicitly captures the impact that heterogeneity has on competing species. As a comparison, one may consider a classic habitat loss model given in [116] in which n species compete for a shared resource. The model is given as a system of ordinary differential equations, and is therefore spatially homogeneous. The species are ordered in terms of their competitiveness, i.e. superior species can occupy the area of inferior species, whereas inferior species cannot occupy an area held by a superior competitor. The destruction is described in terms of the proportion of available habitat remaining, i.e. the total available habitat is 1, and the proportion of available habitat is $1 - D$, where D is the proportion of total habitat that has been removed. Such models do not consider the effect (whether positive or negative) of configuration or fragmentation, as there is no distinction between possible configurations. Furthermore, this type of model is more accurately described as a habitat *destruction* model (as opposed to habitat *degradation* model), as it is assumed the lost region is no longer viable in any way for any species, and so no consideration is given to the precise quality of the lost habitat. This framework has been investigated extensively, including other effects not considered here, such as variation in patch quality [54] or the Allee effect [19]. Such constructions align more closely with the habitat amount hypothesis, see [34].

More generally, it has been a popular approach to model habitat loss through metapopulations, or multiple patches, as introduced by Levins in 1969 [83]. Such modelling efforts vary in their construction, application and complexity, see for example, [66], [77], [92] or more recently [88]. In [66], for example, a single-species metapopulation model is used to explore the effect of immigration rates between patches on population persistence. While an implicit heterogeneity of the landscape is built into the model, the relation to habitat fragmentation is also implicit as a consequence. Arrangement is not considered as much as the exchange between neighbouring patches, and the cost of moving between patches (if any) must be determined apriori, rather than as a consequence of the model formulation itself. An important development described in [77] is the *rate* at which habitat is lost; when investigating extinctions thresholds, as is common in these metapopulation models generally, one implicitly assuming a rate at which the habitat is lost. Whether this rate is fast or slow has a dramatic impact on the time it takes for extinction/extirpation to occur. Similar to some of the conclusions drawn later in this Chapter, [92] concludes that the systematic removal of habitat can favor ‘weedy’ species, emphasizing the counter-intuitive effects that habitat loss can have on competing species. The more recent work [88] considers similar modelling frameworks, where individual patches may now variation in habitat quality over time, with the binary ‘suitable’ and ‘unsuitable’ perspective as a special case. Nevertheless, all metapopulation models suffer from the same drawback of implicit spatial structure and uniformity within and between patches. These models are mathematically similar to the ODE habitat loss model prototype described previously, and so suffer from similar drawbacks. However, even in the cases where the models differ (both mathematically and conceptually) in a more significant way, the precise measurement of “habitat loss” is often obscured, or at least inconsistent across modelling efforts. One may refer to [72], which highlights some of the measures that may be used in these contexts. This includes measures such as number of patches, mean patch size, mean patch isolation, or total edge amount. Depending on the modelling framework, any combination of these measures can be interpreted as habitat loss or fragmentation. This results in confusion, as highlighted by Figure 3 in [72]. Roughly speaking, one can hold any variable fixed and alter the remaining variables positively or negatively in order to draw widely varying conclusions regarding the sustainability of species. One benefit of using a spatially explicit model is that all of these factors are encapsulated within the model, with the drawback being an increased difficulty in performing analysis for any particularly chosen configuration. Such drawbacks may be overcome through the use of numerical simulation, however.

Some authors have proposed spatially explicit models comparable to that presented here [112], however, the analysis involves simplifications in order to make comparisons to the spatially homogeneous ODE model. Such simplifications include an appeal to a one dimensional model only, writing the spatially dependent solution in its Fourier series expansion. After dropping higher order terms, one retains only the linear terms, reducing to the form of an ordinary differential equation. Such efforts are valuable in determining the disparity between spatially homogeneous and spatially heterogeneous models; however, they still lack the explicit spatial structure required to study habitat fragmentation.

In the form of (2.2), the mathematical model most closely resembles existing models investigating the effect of heterogeneous environments, see chapter 4 in [93] and the references therein, and more recently [61]–[63], which provide a rather complete picture of the global dynamics under fairly mild assumptions on the heterogeneity appearing in the system. Additionally, readers are directed to some interesting results found in [8] where the authors consider a one dimensional habitat $(0, 1)$ with heterogeneity of the form

$$m_a(x) := \begin{cases} -1 & \text{in } [0, a), \\ k & \text{in } [a, a + L), \\ -1 & \text{in } [a + L, 1]. \end{cases}$$

Then, the authors investigate the optimal location of the favorable region given by the parameter a. This is done for both Dirichlet and Neumann boundary conditions, and a more general investigation is given in [9]–[11]. Such works provide some motivation and insight into the investigation presented here, but tend to focus on the particular locations of favorable habitat patches in single species models rather than the impact of the measure of detriment within the favorable and unfavorable regions.

We now investigate the long-term behaviour and properties of the steady states corresponding to problem (2.2) depending on the parameters appearing within the model. In particular, we explore changes in stability based on the parameters c_i, which measures the effect of the degraded region on the competing species u and v.

2.3 Eigenvalue problems with a sign-indefinite weight

In this section, we highlight some of the key results from the study of eigenvalue problems. These solutions, and in particular the principal eigenvalue/eigenfunction pair, is closely related to the stability properties of solutions to the scalar equation. In fact, from our assumptions made thus far, our solution process is a strongly monotone dynamical system. The threshold dynamics found in theorems such as Theorem 1.2.8 will depend critically on the sign of a particular principal eigenvalue. Then, we can use the same monotone theory to determine the global dynamics of the competition system. Therefore, a detailed description of the local stability of possible steady states through these eigenvalues is critical to our analysis. To study the eigenvalue problem allowing us to apply Theorem 1.2.8 to problem (2.1), we first introduce a closely related auxiliary eigenvalue problem. Originally studied by Brown and Lin [7], this problem is often referred to as an "*eigenvalue problem with sign-indefinite weight*". Further references and discussion can be found in [8]. A warning: this problem, while important, is more of a technical piece of information useful for our analysis rather than a meaningful ecologically connected concept.

2.3.1 The first problem

Let $m \in L^\infty(\Omega)$ and consider the problem

$$\begin{cases} \Delta\psi + \lambda m\psi = 0 & \text{in} \quad \Omega, \\ \frac{\partial\psi}{\partial\nu} = 0 & \text{on} \quad \partial\Omega. \end{cases} \tag{2.4}$$

If there exists a value $\lambda_1(m) \in \mathbb{R}$ and a *positive* function $\psi_1 \in H^1(\Omega)$ solving (2.4) in the weak sense, we call $\lambda_1(m)$ the principal eigenvalue to problem (2.4). The following is a well-known result. Manes and Micheletti originally discussed this problem under Dirichlet boundary data in [84] (in French), while Brown and Lin [7] discussed the more subtle case of homogeneous Neumann boundary data yielding the result below. A rather complete discussion of this problem can be found in [8], where the authors discuss the more general case of Robin-like boundary data. The main result we will use here is the following, which can be found in, e.g., [93, Chapter 4], [8, Ch. 2], a result of the conclusion reached in [7].

Proposition 2.3.1. *Let $m \in L^\infty(\Omega)$ be non-constant. Problem (2.4) has a nonzero principal eigenvalue $\lambda_1(m)$ if and only if m changes sign (on sets of positive measure) and $\int_\Omega m \neq 0$. More precisely,*

(i) $\int_\Omega m < 0 \Rightarrow \lambda_1(m) > 0$ *;*

(ii) $\int_\Omega m > 0 \Rightarrow \lambda_1(m) < 0$*;*

(iii) $\int_\Omega m = 0 \Rightarrow 0$ *is the only principal eigenvalue;*

(iv) $\lambda_1(h) > \lambda_1(k)$ *if* $h \lneqq k$*;*

(v) $\lambda_1(h_n) \to \lambda_1(h)$ *if* $h_n \to h$ *in* $L^\infty(\Omega)$*.*

Since the proof of this theorem uses tools that are very similar to those used in the proof of Theorem 3.4.1, we omit it here.

One can see how this eigenvalue problem might relate to the population models we want to analyse. Since we have assumed that both sets B and G have positive measure, the heterogeneity for the competition system will always change sign in Ω (m_{c_i} is 1 in G and $-c$ in B). Thus we will always have a principal eigenvalue, the sign of which is determined only by the sign of $|G| - c\,|B|$. For the general scalar equation, it is slightly more complicated, where the function we care about will be the linearization about 0, i.e., $\mathbb{1}_G f'(x,0) - c\mathbb{1}_B$. Yet, we still have an easily verifiable formula given by

$$\int_G f'(x,0)dx - c\,|B|\,,$$

the sign of which determines the sign of $\lambda_1(\mathbb{1}_G f'(x,0) - c\mathbb{1}_B)$. This will become important in later sections. Implicit in this formulation is the shape and geometry of the sets G and B, but we save this discussion for Chapter 4.

Notice that this problem features only the environmental heterogeneity, but not the rate of diffusion d. In the following section, we introduce the primary eigenvalue problem of interest. This will incorporate information from Theorem 2.3.1 and the size of d, with precise asymptotic information as $d \to 0^+$ or as $d \to \infty$.

2.3.2 The second problem

From the construction of our original problem, we see that there are two primary pieces of information at play given a fixed habitat Ω: the first is the heterogeneity of the environment, given by $\mathbb{1}_G f(x,w) - c\mathbb{1}_B w$, and the second is the diffusion rate $d > 0$. The eigenvalue problem introduced in this section corresponds directly to the local stability of a steady state via a linearization process. The sign of this new principal eigenvalue can be characterized by the principal eigenvalue of problem (2.4). In particular, when we linearize about the trivial steady state, the principal eigenvalue is the net growth rate of the entire population over the entire domain for small population sizes. A necessary condition for the persistence of the population will be net positive growth for small population sizes. Before we get ahead of ourselves, let us introduce the problem and the main results to be used in subsequent analysis.

Let $m \in L^\infty(\Omega)$ and consider the following eigenvalue problem:

$$\begin{cases} d\Delta\phi + m\phi + \mu\phi = 0 & \text{in} \quad \Omega, \\ \frac{\partial\phi}{\partial\nu} = 0 & \text{on} \quad \partial\Omega. \end{cases} \tag{2.5}$$

We call $\mu_1(d,m)$ a principal eigenvalue for problem (2.5) whenever there exists a positive solution $\phi_1 \in H^1(\Omega)$. It is well-known that this problem has a unique principal eigenvalue admitting the variational characterization:

$$\mu_1(d,m) = \inf \left\{ \int_\Omega \left[d\, |\nabla \phi|^2 - m\phi^2 \right] dx : \phi \in H^1(\Omega), \int_\Omega \phi^2 dx = 1 \right\}. \tag{2.6}$$

The following proposition highlights some of the classical properties of this eigenvalue as related to problem 2.4.

Proposition 2.3.2. *Suppose $m \in L^\infty(\Omega)$ is not a constant function. Then the following hold.*

(i) $\int_\Omega m \geq 0 \;\Rightarrow\; \mu_1(d,m) < 0$ *for all* $d > 0$.

(ii) $\int_\Omega m < 0 \;\Rightarrow\; \begin{cases} \mu_1(d,m) < 0, & \textit{if} \quad d < \lambda_1^{-1}(m), \\ \mu_1(d,m) = 0, & \textit{if} \quad d = \lambda_1^{-1}(m), \\ \mu_1(d,m) > 0, & \textit{if} \quad d > \lambda_1^{-1}(m). \end{cases}$

(iii) $\mu_1(d,m)$ *is strictly increasing and concave with respect to* $d > 0$.

(iv) $\mu_1(d,m) < \mu_1(d,\tilde{m})$ *whenever* $m \gneqq \tilde{m}$.

(v) $\mu_1(d,m)$ *satisfies the following limiting behaviour:*

$$\lim_{d\to 0^+} \mu_1(d,m) = -\max_\Omega m \qquad \textit{and} \qquad \lim_{d\to\infty} \mu_1(d,m) = -\,|\Omega|^{-1} \int_\Omega m$$

(vi) $\mu_1(d,m_n) \to \mu_1(d,m)$ *whenever* $m_n \to m$ *in* $L^\infty(\Omega)$.

Similar to before, the proof of this result uses similar techniques in proving Proposition 3.4.2, and so we omit the details here. Points (i)-(v) appear in [93], however point (vi) is not explicitly discussed. Point (v) is proven in [68] when $m_n \to m$ in $C(\overline{\Omega})$, whereas a weakened regularity case (with respect to $L^p(\Omega)$, $p > N/2$) is discussed in detail in [23], [45], [67], for example.

Returning to our previous discussion, we recall that if $m = \mathbb{1}_G f'(x,0) - c\mathbb{1}_B$, the principal eigenvalue corresponds to a growth rate for small population sizes. From the convention used here, $-\mu_1(d,m)$ is therefore the net growth rate of the population near m. This gives a concrete connection to the ecological impact of the environmental heterogeneity on a diffusing species: (i) if the average heterogeneity is non-negative, the net growth of the population is positive for all $d > 0$; (ii) if the average heterogeneity is negative, the net growth rate may be positive or negative depending on the size of the diffusion rate d. We notice the sign of the net growth rate changes precisely when $d = \lambda_1(m)$. This is the direct connection between $\mu_1(d, m)$ and $\lambda_1(m)$; (iv) tells us that better environments increase the net growth rate; (v) tells us that the net growth rate is continuous with respect to changes in the environment. Each of these facts gives a preliminary verification that the model is consistent with what we often observe in the natural world; (iii) is less intuitive, but suggests that a slower rate of diffusion is advantageous for population survival when the resources are held fixed in time. This is less universally true than the other properties, but can be understood biologically as well: suppose $m(x)$ is the resource density in Ω. When the diffusion rate is very large, the species are moving so quickly that they use only the average resource density available. This is made precise by the limiting behaviour as $d \to \infty$ found in point (vi): in the limit, the net growth rate is exactly the average of the resources available given by $m(x)$. In this case, if the average resource density is negative, the population will decay. On the other hand, as $d \to 0^+$, the net growth rate is the maximum value of the resource function $m(x)$. Thus, as long as there are resources *somewhere* in Ω, the net population growth will also remain positive for small enough rates of diffusion. Therefore, in this modelling paradigm, a slower rate of diffusion somehow allows the population to concentrate around resource peaks, or at the very least, utilize the best resource areas between the faster movers.

2.4 The scalar equation

We now have the tools to explore in detail the well-posedness and global dynamics of problem (2.1). We first prove the well-posedness of the time-dependent problem under biologically reasonable assumptions. Since the system is nonlinear, we must prove some comparison principle results that allow us to apply a monotone method to obtain a global solution. This monotone method is similar to the ideas presented in Section 1.2.8. There are some areas of care, however, since our right hand side is, in general, discontinuous. Therefore, the classical theory presented in Section 1.2 is not directly applicable. Instead we appeal to the notion of strong solutions, using regularity results to ensure that the solution obtained is smooth enough to apply the monotone dynamical theory. We then prove a similar existence theorem for the steady state problem depending on the sign of a principal eigenvalue. We then apply the monotone theory to obtain the global threshold dynamics, followed by a special case to be used in the study of the competition system.

2.4.1 Well-posedness

We start with the definition of a strong solution of the time-dependent problem (2.1) and its associated steady state (i.e., when we take $w_t \equiv 0$), which differ slightly from the notion of strong solution introduced in Section 1.2.

Definition 2.4.1. (1) *A* strong solution *on Q_T to (2.1) is a solution which belongs to $W_p^{2,1}(Q_T) \cap C([0,T]; C(\overline{\Omega}))$ for all $p \geq 1$, satisfies the equation almost everywhere in Q_T and satisfies the boundary condition everywhere on $\partial\Omega$ for all $t \in (0,T)$. A* global strong solution *is a strong solution on $[0,T)$ for all $T > 0$.*

(2) *A* steady state *to (2.1) is a solution which belongs to $W^{2,p}(\Omega)$ for all $p \geq 1$, satisfies the equation almost everywhere in Ω and satisfies the boundary condition everywhere on $\partial\Omega$.*

Remark 2.4.1. *Since we may choose p as large as we like, the boundary condition is satisfied in the classical sense due to the Sobolev embedding, Theorem's 1.2.3 and 1.2.4.*

Recall that we denote by $C^{++}(\overline{\Omega})$ the interior of the cone $C^{+}(\overline{\Omega})$ with the ordering $\leq, <, \ll$ introduced in Section 1.2. We state the following comparison principle whose proof, being much simpler than that of Proposition 2.5.1 for the competition system, is omitted.

Proposition 2.4.1. *Suppose $F(x,w) \in C^{\alpha,1}(\overline{\Omega} \times \mathbb{R}^+)$ satisfies Assumption 2.2.2. Suppose $w^1, w^2 \in W_p^{2,1}(Q_T) \cap C([0,T); C(\overline{\Omega}))$ for any $p \geq 1$, and satisfy*

$$\begin{cases} w_t^1 \leq d\Delta w^1 + \mathbb{1}_G F(x,w^1) - c\mathbb{1}_B w^1 & a.e. \ in \quad \Omega \times (0,T), \\ \frac{\partial w^1}{\partial \nu} \leq 0 & on \quad \partial\Omega \times (0,T), \end{cases}$$

$$\begin{cases} w_t^2 \geq d\Delta w^2 + \mathbb{1}_G F(x,w^2) - c\mathbb{1}_B w^2 & a.e. \ in \quad \Omega \times (0,T), \\ \frac{\partial w^2}{\partial \nu} \geq 0 & on \quad \partial\Omega \times (0,T). \end{cases}$$

(1) *If $w^1(\cdot,0) \leq w^2(\cdot,0)$, then $w^1(\cdot,t) \leq w^2(\cdot,t)$ for all $t \in (0,T)$.*

(2) *Suppose, in addition, $w^1, w^2 \in C^1((0,T); C(\overline{\Omega}))$. If $w^1(\cdot,0) \leq w^2(\cdot,0)$ and $w^1(\cdot,0) \not\equiv w^2(\cdot,0)$, then $w^1(\cdot,t) \ll w^2(\cdot,t)$ for all $t \in (0,T)$.*

Similarly, we have the following comparison theorem for non-negative steady states.

Proposition 2.4.2. *Suppose $F(x,w) \in C^{\alpha,1}(\overline{\Omega} \times \mathbb{R}^+)$ satisfies Assumption 2.2.2. Suppose $w^1, w^2 \in W^{2,p}(\Omega)$ for any $p \geq 1$ are non-negative and satisfy*

$$\begin{cases} -d\Delta w^1 \leq \mathbb{1}_G F(x,w^1) - c\mathbb{1}_B w^1 & a.e. \ in \quad \Omega, \\ \frac{\partial w^1}{\partial \nu} \leq 0 & on \quad \partial\Omega, \end{cases}$$

$$\begin{cases} -d\Delta w^2 \geq \mathbb{1}_G F(x,w^2) - c\mathbb{1}_B w^2 & a.e. \ in \quad \Omega, \\ \frac{\partial w^2}{\partial \nu} \geq 0 & on \quad \partial\Omega. \end{cases}$$

Then, $w^1 \leq w^2$. Moreover, there holds either $w^1 < w^2$ or $w^1 \equiv w^2$.

Proof. We argue by contradiction: suppose that $w^1 \leq w^2$ were false. Set $\alpha^* := \inf\{\alpha > 1 : w^1 \leq \alpha w^2\}$. The continuity of w^1 and w^2 implies that $\alpha^* > 1$ and $w^1 \leq \alpha^* w^2$, and that there exists a point $x_0 \in \overline{\Omega}$ such that $w^1(x_0) = \alpha^* w^2(x_0)$.

Since $F(x,w)$ satisfies $\alpha^* F(\cdot,w) \geq F(\cdot,\alpha^* w)$ for $w > 0$ by Assumption 2.2.2, we find $-d\Delta(\alpha^* w^2) \geq \mathbb{1}_G F(x,\alpha^* w^2) - c\mathbb{1}_B \alpha^* w^2$. In particular, w^1 and $\alpha^* w^2$ are an ordered sub/super solution pair according to the differential inequalities found in the statement of the proposition.

If $x_0 \in \Omega$, Theorem 1.2.16 (from [4, Theorem 1]) implies that $w^1 \equiv \alpha^* w^2$ in Ω. Then, $0 < w^2 < w^1$ due to $\alpha^* > 1$, and hence,

$$0 = -d\Delta(w^1 - \alpha^* w^2) \leq \mathbb{1}_G(F(x,w^1) - \alpha^* F(x,w^2)) < \mathbb{1}_G(F(x,w^1) - F(x,\alpha^* w^2)) = 0$$

in $\Gamma \Subset G$ by Assumption 2.2.2, a contradiction. If $x_0 \in \partial\Omega$, Hopf's lemma gives $\frac{\partial}{\partial\nu}(w^1 - \alpha^* w^2) > 0$ at x_0, in contradiction to the boundary conditions assumed. Hence, $w^1 \leq w^2$.

Repeating the previous steps using the maximum principle and Hopf's lemma, we find that either $w^1 < w^2$ or $w^1 \equiv w^2$ in $\overline{\Omega}$. This completes the proof. $\square$

We now prove the following Theorem concerning the well-posedness of problem (2.1).

Theorem 2.4.1. *For any initial data $w_0 \in C^+(\overline{\Omega})$, (2.1) admits a unique global strong solution $w \in C^\alpha([0,\infty); C^+(\overline{\Omega})) \cap C^1((0,\infty); C^+(\overline{\Omega}))$ for any $\alpha \in (0,1)$.*

Proof of Theorem 2.4.1. The proof essentially follows regularization arguments and standard theory. In what follows, we remind readers that $Q_T := \Omega \times (0,T)$ for some $T > 0$ fixed. Note that the uniqueness of global strong solutions follows immediately from Proposition 2.4.1 point (2).

We now show existence. We first approximate $\mathbb{1}_G$ and $\mathbb{1}_B$ by the functions $\mathbb{1}_G^\varepsilon$ and $\mathbb{1}_B^\varepsilon$ belonging to $C^\infty(\Omega)$ (through mollification, for example), so that $\mathbb{1}_G^\varepsilon \to \mathbb{1}_G$ and $\mathbb{1}_B^\varepsilon \to \mathbb{1}_B$ in $L^p(\Omega)$ for any $p \geq 1$. We first prove the existence of a positive classical solution $w_\varepsilon(x,t)$ for each $\varepsilon > 0$. We then argue that in the limit as $\varepsilon \to 0^+$, we retain a strong solution $w(x,t)$ to problem (2.1) for some $T > 0$ fixed. It is then easy to show that the solution is in fact global and will in fact be globally bounded.

In what follows, we essentially use a sub/super solution argument. First, 0 is clearly a subsolution since $f(x,0) = 0$. Then, by Assumption 2.2.1, there exists $M \gg 1$ so that $f(x,U) < 0$ for all $x \in \Omega$ for any $U > M$, and so M is a supersolution. By Theorem 1.2.31, there exists a classical solution $w_\varepsilon(x,t)$ for every $\varepsilon > 0$. By the uniqueness of the classical solution, it is also a strong solution. Since $f(x,U) \leq f'(x,0)U$ for all $U \geq 0$, Gronwall's inequality implies that there exists constants $C, \gamma > 0$ so that $w_\varepsilon(x,t) \leq Ce^{\gamma t}$ for all $t > 0$, and so $w_\varepsilon(x,t)$ is a global solution. By the same sub/super solution argument, there holds $0 \leq w_\varepsilon(x,t) \leq M$ for all $t \in (0,\infty)$, and so $w_\varepsilon(x,t)$ is globally bounded. Notice also that these bounds holds uniformly in ε as well. Therefore, the right hand side is uniformly bounded in $L^\infty(Q_T)$. In particular, $\mathbb{1}_G^\varepsilon f(x,w_\varepsilon) - c\mathbb{1}_B^\varepsilon w_\varepsilon$

belongs to $L^p(Q_T)$ for any $p \geq 1$. By Theorem 1.2.4, the right hand side is therefore bounded in $W_p^{2,1}(Q_T)$, and so there exists a subsequence which we do not relabel such that

$$w_\varepsilon \to w \quad \text{strongly in } W^{1,0}(Q_T), \quad \text{weakly in } W_p^{2,1}(Q_T),$$

and by Theorem 1.2.4, $w_\varepsilon \to w$ in $C^{1+\alpha,(1+\alpha)/2}(Q_T)$ for any $\alpha \in (0,1)$. Therefore, since $\mathbb{1}_G^\varepsilon$, $\mathbb{1}_B^\varepsilon$ are uniformly bounded in ε, it is not difficult to show that Δw_ε is a Cauchy sequence in $L^p(Q_T)$. The completeness of L^p implies that $\Delta w_\varepsilon \to \Delta w$ strongly in $L^p(Q_T)$, and so $w_\varepsilon \to w$ strongly in $W_p^{2,1}(Q_T)$. Note that there is a bit of a jump here: we have estimates on Δw_ε, but not on $D^2 w_\varepsilon$, which includes the mixed derivatives as well. This is not difficult to overcome since

$$\int_\Omega (\Delta w_\varepsilon)^2 = \int_\Omega \left(\sum_{i=1}^N \frac{\partial^2 w_\varepsilon}{\partial x_i^2} \right)^2 = \int_\Omega \left(\sum_{i,j=1}^N \left(\frac{\partial^2 w_\varepsilon}{\partial x_i \partial x_j} \right)^2 \right) = \int_\Omega (D^2 u)^2,$$

which is obtained via integration by parts. The regularity of w_ε for each $\varepsilon > 0$ justifies the calculation, and so w is indeed the unique strong solution to problem (2.1).

Again, by Gronwall's inequality and Assumption 2.2.1, we find that $w(x,t)$ is global and uniformly bounded in time. Furthermore, $w \in C^{(1+\alpha)/2}([0,\infty); C(\overline{\Omega}))$. The regularity of w is an immediate consequence of [111, Theorem 3]. Indeed, since $w_0 \in C^+(\overline{\Omega})$ and $(x,t) \mapsto \mathbb{1}_G(x) f(x, w(x,t)) - c\mathbb{1}_B(x) w(x,t)$ is Hölder continuous in time, $\frac{\partial w}{\partial t}$ exists and is uniformly continuous on $(0,\infty) \times \overline{\Omega}$. Hence, $w \in C^1((0,\infty); C(\overline{\Omega}))$.

We verify that w satisfies the Neumann boundary condition. Since $w_\varepsilon \to w$ in $C^{1+\alpha}(\overline{\Omega})$ as $\varepsilon \to 0$, we see for any fixed $t > 0$ and $x_0 \in \partial\Omega$

$$\begin{aligned} \left| \frac{\partial w}{\partial \nu}(x_0, t) \right| &\leq \left| \frac{\partial}{\partial \nu}(w(x_0,t) - w_\varepsilon(x_0,t)) \right| + \left| \frac{\partial w_\varepsilon}{\partial \nu}(x_0,t) \right| \\ &= \left| \lim_{x \to x_0} \frac{(w - w_\varepsilon)(x_0,t) - (w - w_\varepsilon)(x,t)}{x - x_0} \right| \leq \| w - w_\varepsilon \|_{C^1(\overline{\Omega})} . \end{aligned}$$

Taking $\varepsilon \to 0$ shows that $\frac{\partial w}{\partial \nu} = 0$ for all $x \in \partial\Omega$ and $t > 0$. This completes the proof. □

Similarly, we have the following Theorem for the existence and uniqueness of non-trivial steady states.

Theorem 2.4.2. *Denote by $\mu_1(d, \mathbb{1}_G f'(x,0) - c\mathbb{1}_B)$ the principal eigenvalue to problem* (2.5). *If $\mu_1(d, \mathbb{1}_G f'(x,0) - c\mathbb{1}_B) < 0$, then there exists a unique positive steady state $w^*_{d,c} \in W^{2,p}(\Omega)$ solving problem* (2.1). *If $\mu_1(d, \mathbb{1}_G f'(x,0) - c\mathbb{1}_B) \geq 0$, then 0 is the only steady state solving problem* (2.1).

Proof of Theorem 2.4.2. Denote by ϕ_1 the positive eigenfunction to problem (2.5) associated with $\mu_1(d, \mathbb{1}_G f(x,w) - c\mathbb{1}_B)$. We treat first the case when $\mu_1 < 0$. We compute directly to see that

$$-d\Delta(\varepsilon\phi_1) = \varepsilon\phi_1(\mathbb{1}_G f'(x,0) - c\mathbb{1}_B + \mu_1) \leq \mathbb{1}_G f(x, \varepsilon\phi_1) - c\mathbb{1}_B\phi_1,$$

which holds for all ε sufficiently small since $-\mu_1 > 0$. Similarly, $M \gg 1$ is a supersolution by Assumption 2.2.2. By Theorem 2.4.2 and Theorem 1.2.31, there exists a unique positive solution $w^*_{d,c}$ satisfying $\varepsilon\phi_1 \leq w^*_{d,c} \leq M$ for all $x \in \overline{\Omega}$.

Suppose now that $\mu_1 > 0$ and there exists a strong solution $w^*_{d,c}$ that is positive somewhere in Ω. We compute directly to see that

$$-d\Delta(\varepsilon\phi_1) = \varepsilon\phi_1(\mathbb{1}_G f'(x,0) - c\mathbb{1}_B + \mu_1) \geq \mathbb{1}_G f'(x, \varepsilon\phi_1) - c\mathbb{1}_B\varepsilon\phi_1,$$

which holds for all $\varepsilon > 0$ sufficiently small by the subhomogeneity of f. Hence, for all $\varepsilon > 0$ sufficiently small, Theorem 2.4.2 guarantees that $w^*_{d,c} \leq \varepsilon\phi_1$. Since ε was arbitrary, choosing ε small enough contradicts the positivity of the steady state. This proves the second part of the theorem, completing the proof. □

Remark 2.4.2. *In Theorem 2.4.2, the steady state is a strong solution belonging to the class $W^{2,p}(\Omega)$ for any $p \geq 1$. In particular, choosing p sufficiently large yields that in fact $w^*_{d,c} \in C^{1+\alpha}(\overline{\Omega})$ for any $\alpha \in (0,1)$ by the Sobolev embedding Theorem 1.2.3.*

2.4.2 Global dynamics

We now prove the following theorem concerning the global dynamics of (2.1). Recall that $-\mu_1(d, \mathbb{1}_G f'(x,0) - c\mathbb{1}_B)$ can be understood as the net growth rate for small population sizes, obtained through a linearization of (2.1) about 0.

Theorem 2.4.3. *Suppose $w_0 \in C^+(\overline{\Omega}) \setminus \{0\}$ and that $f(x,w) \in C^{\alpha,1}(\overline{\Omega} \times \mathbb{R}^+)$ satisfies Assumption 2.2.2. Then, we observe the following global dynamics.*

(i) *Suppose that* $\mu_1(d, \mathbb{1}_G f'(x,0) - c\mathbb{1}_B) < 0$. *Then,* $w(\cdot,t) \to w^*_{d,c}$ *in* $C(\overline{\Omega})$ *as* $t \to \infty$, *where* $w^*_{d,c}$ *is the unique positive steady state to problem* (2.1) *obtained in Theorem 2.4.2.*

(ii) *Suppose that* $\mu_1(d, \mathbb{1}_G f'(x,0) - c\mathbb{1}_B) \geq 0$. *Then,* $w(\cdot,t) \to 0$ *in* $C(\overline{\Omega})$ *as* $t \to \infty$.

In the following proof we apply some of the existence/regularity results we have obtained thus far, Propositions 2.4.1 and 2.4.2, and the abstract Theorem 1.2.8.

Proof of Theorem 2.4.3. The existence and uniqueness of a global strong solution follows from Theorem 2.4.1.

To prove this result, we apply some of the theory of monotone flows presented in Section 1.2.

Denote by $\{\Phi_t\}_{t\geq 0}$ the semiflow on $C^+(\overline{\Omega})$ generated by solutions of (2.1). Let $u_0 \in C^+(\overline{\Omega}) \setminus \{0\}$. Replacing u_0 by $\Phi_1 u_0$, we may assume without loss of generality that $u_0 \in C^{++}(\overline{\Omega})$.

Claim 1: When $\mu_1(d, \mathbb{1}_G f'(x,0) - c\mathbb{1}_B) < 0$, (2.1) admits a unique positive steady state $w^*_{d,m}$ by Theorem 2.4.2. Denote by ϕ_1 the associated positive eigenfunction. Notice that $\Phi_t(0) = 0$ and $\Phi_t(w^*_{d,c}) = w^*_{d,c}$.

Fix ε so small and M so large that $\varepsilon\phi_1 \leq u_0 \leq M$. Then, $\Phi_t(\varepsilon\phi_1) \leq \Phi_t u_0 \leq \Phi_t M$ for all $t \geq 0$ thanks to Proposition 2.4.1. In fact, choosing $\varepsilon \ll 1$ so that

$$\mu_1 + \mathbb{1}_G \left(f'(x,0) - \frac{f(x,\varepsilon\phi_1)}{\varepsilon\phi_1} \right) \leq 0,$$

we have by Proposition 2.4.1 that $\varepsilon\phi \leq \Phi_t(\varepsilon\phi)$, and so $\varepsilon\phi$ is a strict subequilibrium by the subhomogeneity of f. Similarly, choosing M large enough so that $f(x,U) < 0$ for all $U > M$, Proposition 2.4.1 again gives that $\Phi_t(M) \leq M$. M is therefore a strict superequilibrium. By Theorem 1.2.9, $\Phi_t(\varepsilon\phi_1)$ is increasing in t and converges pointwise to the positive steady state $\underline{w}^*_{d,m_c}$ as $t \to \infty$, and $\Phi_t M$ is decreasing in t and converges pointwise to a positive steady state $\overline{w}^*_{d,c}$ as $t \to \infty$. Proposition 2.4.2 guarantees that $\underline{w}^*_{d,c} = \overline{w}^*_{d,c}$ since the positive steady state is unique. By Dini's theorem, the convergence holds in $C(\overline{\Omega})$. It follows that $\Phi_t u_0 \to w^*_{d,c}$ in $C(\overline{\Omega})$ as $t \to \infty$.

If $\mu_1(d, \mathbb{1}_G f'(x,0) - c\mathbb{1}_B) \geq 0$, then 0 is the only steady state to (2.1). Indeed, it follows that for each $M \gg 1$, $\Phi_t M$ is decreasing in t and converges in $C(\overline{\Omega})$ to 0 as $t \to \infty$. Fixing M so large that $u_0 \leq M$, we conclude that $\Phi_t u_0 \to 0$ in $C(\overline{\Omega})$ as $t \to \infty$. This completes the proof. □

A special case

We briefly treat a special case of the more general theorem proved here. This is the form explored in [104].

When $f(x,w) = w(1-w)$, $\mathbb{1}_G f'(x,0) - c\mathbb{1}_B = \mathbb{1}_G - c\mathbb{1}_B$. Theorem 2.4.3 tells us that the persistence of a single species depends on the sign of the principal eigenvalue $\mu_1(d, \mathbb{1}_G - c\mathbb{1}_B)$, which depends directly on the size and shape of the region B, the diffusion rate d, and the level of impact c in the region B. In particular, given any size or location of destroyed habitat, one can always choose c sufficiently small such that $\int_\Omega m dx = |G| - c|B| > 0$ so long as $|G| > 0$ (see Lemma 2.4.1). From Proposition 2.3.2, we see that this is enough to ensure that $\mu_1 < 0$. Notice that the same cannot be said concerning extinction if we take c large! That is to say, we do not necessarily have that $\mu_1(d, \mathbb{1}_G - c\mathbb{1}_B) > 0$ for some $c \gg 1$. This implies that given any configuration of good and bad regions, there is always a value c sufficiently small such that the species' population persists.

This observation motivates consideration of the special case when $c = 0$. Our nonlinear term becomes $w(\mathbb{1}_G - \mathbb{1}_G w) = \mathbb{1}_G w(1-w)$. In this form, $w \equiv 1$ is the only steady state, and hence, $w \to 1$ as $t \to \infty$ for any nontrivial initial data. This is an interesting result as it indicates that as long as there is *some* region where the growth rate of the species is positive (in this case, in the region G at rate 1), the species will reach carrying capacity *everywhere*. This point will become important later when discussing a similar limiting case of the full system (2.2).

Let us make this rigorous and concrete. In what follows, $\mu_1(d, m_c)$ denotes the principal eigenvalue to problem (2.5) with $m = \mathbb{1}_G - c\mathbb{1}_B$.

Lemma 2.4.1. *Suppose that* $\int_G f'(x,0) > 0$. *Then, there exists* $c^* = c^*(d) \in (0, \infty]$ *such that* $\mu_1(d, \mathbb{1}_G f'(x,0) - c\mathbb{1}_B) < 0$ *if and only if* $c \in [0, c^*)$.

Proof. Direct computation shows that $\int_\Omega (\mathbb{1}_G f'(x,0) - c\mathbb{1}_B) = \int_G f'(x,0) - c\,|B| \geq 0$ for all $0 \leq c \leq \int_G f'(x,0)$. It follows from Proposition 2.3.2 (i) that $\mu_1(d, \mathbb{1}_G f'(x,0) - c\mathbb{1}_B) < 0$ for all $c \in [0, \int_G f'(x,0)]$.

By Proposition 2.3.2 (iv) and (v), the function $c \mapsto \mu_1(d, \mathbb{1}_G f'(x,0) - c\mathbb{1}_B)$ is increasing and continuous on $[0,\infty)$. Thus, if $\lim_{c\to\infty} \mu_1(d, \mathbb{1}_G f'(x,0) - c\mathbb{1}_B) > 0$, then there is a unique $c^* \in (0,\infty)$ such that $\mu_1(d, \mathbb{1}_G f'(x,0) - c\mathbb{1}_B) = 0$ when $c = c^*$, and $\mu_1(d, \mathbb{1}_G f'(x,0) - c\mathbb{1}_B) < 0$ if and only if $c \in [0, c^*)$. If $\lim_{c\to\infty} \mu_1(d, \mathbb{1}_G f'(x,0) - c\mathbb{1}_B) \leq 0$, then $\mu_1(d, \mathbb{1}_G f'(x,0) - c\mathbb{1}_B) < 0$ for all $c \in [0,\infty)$. In this case, $c^* = \infty$. □

The following is an immediate consequence which we note for later use.

Corollary 2.4.1. *Suppose $f(x,w) = w(1-w)$. Then, $f'(x,0) = 1$, $\int_G f'(x,0) = |G|$, and so $\mu_1(d, m_c) < 0$ for all $c \in [0, \frac{|G|}{|B|}]$.*

Let $c^* = c^*(d)$ be as in Lemma 2.4.1. Theorem 2.4.1 ensures that problem (2.1) admits a unique positive steady state $w^*_{d,c}$ for each $c \in [0, c^*)$. We prove the following result.

Lemma 2.4.2. *There holds $w^*_{d,c} < w^*_{d,0}$ in $\overline{\Omega}$ for all $c \in (0, c^*)$. Furthermore, $w^*_{d,c} \to w^*_{d,0}$ in $C(\overline{\Omega})$ as $c \to 0$.*

Proof. We write w^*_c for $w^*_{d,c}$ as the context for the current proof should be clear.

Notice that for any $c \in (0, c^*)$, $w^*_c \lneqq w^*_0$ by Proposition 2.4.2. Theorem 1.2.16 then implies that $w^*_c < w^*_0$ in Ω. If $w^*_c(x_0) = w^*_0(x_0)$ for some $x_0 \in \partial\Omega$, Hopf's lemma implies that $\frac{\partial w^*_c}{\partial \nu}(x_0) > 0$, which contradicts the boundary condition satisfied by w^*_c, and so $w^*_c < w^*_0$ in $\overline{\Omega}$ for all $c \in (0, c^*)$.

By Proposition 2.4.2, w^*_c is increasing as c decreases. Hence, the pointwise limits $w^* := \lim_{c\to 0} w^*_c$ exist in $\overline{\Omega}$, and $0 < w^* \leq w^*_0$ in $\overline{\Omega}$. We now show that $w^* \equiv w^*_0$.

Since w^*_0 is bounded for all $c \in [0, c^*)$, $|\mathbb{1}_G f(x, w^*_c) - c\mathbb{1}_B w^*_c| \leq M < \infty$ for all $c \in [0, c^*)$. In particular, the right hand side belongs to $L^p(\Omega)$ for any $p \geq 1$. Theorem 1.2.29 then tells us that in fact $\sup_{c\in[0,c^*)} w^*_c \in W^{2,p}(\Omega)(\Omega)$ for any $p \geq 1$. Thus, the compactness of $W^{2,p}(\Omega)$ (i.e., the Rellich–Kondrachov compactness theorem [31, Ch. 5]) yields the existence of a subsequence such that

$$w^*_c \to w^*, \quad \nabla w^*_c \to \nabla w^* \quad \text{strongly in } L^p(\Omega) \text{ as } c \to 0.$$

Note that, since $w_c^*(x)$ is monotone increasing for each $x \in \Omega$ as $c \to 0$, the limit point is unique, and so we are guaranteed that the limit is exactly w^*.

Consequently, if we multiply the equation for w_c^* against a test function ϕ and integrate by parts, we immediately find that w^* is a weak solution solving the same problem as w_0^*. The Sobolev embedding ensures that in fact $w^* \in C^{1+\alpha}(\overline{\Omega})$ for any $\alpha \in (0,1)$, and so the weak solution is in fact a strong solution. Uniqueness of the strong solution tells us that $w_0^* = w^*$. Finally, Dini's theorem ensures that $w_c^* \to w_0^*$ uniformly in Ω, completing the proof. $\square$

We then have the following corollary for later use.

Corollary 2.4.2. *Suppose* $f(x,w) = w(1-w)$*. Then,* $w_0^* \equiv 1$ *in* Ω*,* $w_c^* < 1$ *for all* $c \in (0, c^*)$*, and* $w_c^* \to 1$ *uniformly in* Ω *as* $c \to 0^+$*.*

2.5 A competitive system

With the results proved in the previous section, we are now ready to tackle the competitive system. Since the system is more complicated than the scalar equation, we consider the special form of reaction given in problem (2.2). We essentially apply the same theory to the system, but there are now possibly four (or more) steady states. Therefore, we must discuss the appropriate cone in which to work so that we generate a strong monotone flow, and we must determine precisely the local stability of possible steady states. We begin to address the first piece of the puzzle now.

2.5.1 Comparison principles for competitive systems

In what follows, the orderings $\leq_K$, $<_K$ and $\ll_K$ denote the *skew orderings* for competitive systems: for $u_1, u_2, v_1, v_2 \in C(\overline{\Omega})$,

$$(u_1, v_1) \leq_K (u_2, v_2) \quad \text{iff} \quad u_2 - u_1 \in C^+(\overline{\Omega}) \quad \text{and} \quad v_1 - v_2 \in C^+(\overline{\Omega}),$$

$$(u_1, v_1) <_K (u_2, v_2) \quad \text{iff} \quad u_2 - u_1 \in C^+(\overline{\Omega}) \setminus \{0\} \quad \text{and} \quad v_1 - v_2 \in C^+(\overline{\Omega}) \setminus \{0\},$$

$$(u_1, v_1) \ll_K (u_2, v_2) \quad \text{iff} \quad u_2 - u_1 \in C^{++}(\overline{\Omega}) \quad \text{and} \quad v_1 - v_2 \in C^{++}(\overline{\Omega}).$$

Thus, we work in the cone $(X^+) \times (-X^+) = (C(\overline{\Omega}^+) \times (-C(\overline{\Omega}))$ so that our competitive system can be treated as a cooperative system. We now present an analogue to the comparison theorem for scalar problems, Theorem 2.4.1. The approach to proving the result can easily be translated to a proof for the scalar case.

Proposition 2.5.1. *Let* $T \in (0,\infty)$. *Suppose that* $\underline{u}$, $\overline{u}$, $\underline{v}$, $\overline{v}$ *belong to* $W_p^{2,1}(Q_T) \cap C([0,T);C(\overline{\Omega}))$ *for any* $p \geq 1$ *with* $\overline{u}(\cdot,0), \overline{v}(\cdot,0) \geq 0$ *and satisfy the conditions:*

$$\begin{aligned} &\underline{u}_t - d_1\Delta\underline{u} \leq \underline{u}(m_{c_1} - \mathbb{1}_G(\underline{u}+\overline{v})) \quad a.e.\ in \quad \Omega\times(0,T),\\ &\underline{v}_t - d_2\Delta\underline{v} \leq \underline{v}(m_{c_2} - \mathbb{1}_G(\overline{u}+\underline{v})) \quad a.e.\ in \quad \Omega\times(0,T),\\ &\overline{u}_t - d_1\Delta\overline{u} \geq \overline{u}(m_{c_1} - \mathbb{1}_G(\overline{u}+\underline{v})) \quad a.e.\ in \quad \Omega\times(0,T),\\ &\overline{v}_t - d_2\Delta\overline{v} \geq \overline{v}(m_{c_2} - \mathbb{1}_G(\underline{u}+\overline{v})) \quad a.e.\ in \quad \Omega\times(0,T),\\ &\qquad\frac{\partial\underline{u}}{\partial\nu} \leq \frac{\partial\overline{u}}{\partial\nu} \quad on \quad \partial\Omega\times(0,T),\\ &\qquad\frac{\partial\underline{v}}{\partial\nu} \leq \frac{\partial\overline{v}}{\partial\nu} \quad on \quad \partial\Omega\times(0,T). \end{aligned}$$

Then, the following hold.

(1) If $(\underline{u}(\cdot,0),\overline{v}(\cdot,0)) \leq_K (\overline{u}(\cdot,0),\underline{v}(\cdot,0))$, *then* $(\underline{u}(\cdot,t),\overline{v}(\cdot,t)) \leq_K (\overline{u}(\cdot,t),\underline{v}(\cdot,t))$ *for all* $t \in (0,T)$.

(2) Suppose in addition $\underline{u}$, $\overline{u}$, $\underline{v}$, $\overline{v}$ *belong to* $C^1((0,\infty);C(\overline{\Omega}))$. *If* $(\underline{u}(\cdot,0),\overline{v}(\cdot,0)) <_K (\overline{u}(\cdot,0),\underline{v}(\cdot,0))$, *then*

$$(\underline{u}(\cdot,t),\overline{v}(\cdot,t)) \ll_K (\overline{u}(\cdot,t),\underline{v}(\cdot,t)), \quad \forall t \in (0,T).$$

Proof. (1) First, we claim that $\overline{u},\overline{v} \geq 0$ holds necessarily. Consider $w = -\overline{u}$. Then by assumption, w satisfies

$$w_t - d_1\Delta w \leq \beta(t)w, \tag{2.7}$$

for some nonnegative $\beta(t)$, the existence of which follows from $\underline{v},\overline{u} \in C([0,T);C(\overline{\Omega}))$. Set $w^- = \max\{0,-\overline{u}\}$. Multiplying (2.7) by w^-, integrating the resulting inequality over Ω and integrating by parts yields that $\frac{1}{2}\frac{d}{dt}\int_\Omega (w^-)^2dx \leq \beta(t)\int_\Omega (w^-)^2dx$. From the Gronwall inequality and the nonnegativity at $t=0$, we obtain $w^- \equiv 0$. The same argument applies to $\overline{v}$, and hence $\overline{u},\overline{v} \geq 0$.

Now, set $w_1 := \underline{u} - \overline{u}$ and $w_2 = \underline{v} - \overline{v}$. We show that $w_i^+ := \max\{0, w_i\} \equiv 0$ for $i = 1, 2$. Setting $f_1(x, u, v) = u(m_{c_1} - \mathbb{1}_G(u + v))$ and $f_2(x, u, v) = v(m_{c_2} - \mathbb{1}_G(u + v))$, we estimate

$$\begin{aligned}
&\frac{1}{2}\frac{d}{dt}\int_\Omega \left[(w_1^+)^2 + (w_2^+)^2\right] dx \\
&\leq \int_\Omega \left[w_1^+\left(d_1\Delta w_1 + f_1(x, \underline{u}, \overline{v}) - f_1(x, \overline{u}, \underline{v})\right) + w_2^+\left(d_2\Delta w_2 + f_2(x, \overline{u}, \underline{v}) - f_2(x, \overline{u}, \underline{v})\right)\right] dx \\
&\qquad \leq \int_\Omega w_1^+\left(f_1(x, \underline{u}, \overline{v}) - f_1(x, \overline{u}, \underline{v})\right) dx + \int_\Omega w_2^+\left(f_2(x, \overline{u}, \underline{v}) - f_2(x, \overline{u}, \underline{v})\right) dx,
\end{aligned} \tag{2.8}$$

where we used the assumed differential inequalities in the first inequality, and integrated by parts and dropped non-positive gradient terms in the second inequality.

We now write

$$\begin{aligned}
f_1(x, \underline{u}, \overline{v}) - f_1(x, \overline{u}, \underline{v}) &= \underline{u}(m_{c_1} - \mathbb{1}_G(\underline{u} + \overline{v})) - \overline{u}(m_{c_1} - \mathbb{1}_G(\overline{u} + \underline{v})) \\
&= m_{c_1}(\underline{u} - \overline{u}) - \mathbb{1}_G\left((\underline{u} + \overline{u})(\underline{u} - \overline{u}) + \overline{v}(\underline{u} - \overline{u}) - \overline{u}(\underline{v} - \overline{v})\right) \\
&= (m_{c_1} - \mathbb{1}_G(\underline{u} + \overline{u} + \overline{v}))w_1 + \mathbb{1}_G\overline{u}w_2, \\
f_2(x, \overline{u}, \underline{v}) - f_2(x, \overline{u}, \underline{v}) &= (m_{c_2} - \mathbb{1}_G(\underline{v} + \overline{v} + \overline{u})w_2 + \mathbb{1}_G\overline{v}w_1.
\end{aligned}$$

Inserting these into (2.8) yields

$$\begin{aligned}
&\frac{1}{2}\frac{d}{dt}\int_\Omega \left[(w_1^+)^2 + (w_2^+)^2\right] dx \\
&\leq \int_\Omega (m_{c_1} - \mathbb{1}_G(\underline{u} + \overline{u} + \overline{v}))(w_1^+)^2 dx + \int_\Omega (m_{c_2} - \mathbb{1}_G(\underline{v} + \overline{v} + \overline{u})(w_2^+)^2 dx \\
&+ \int_\Omega \left(\overline{u}w_1^+w_2 + \overline{v}w_2^+w_1\right) dx \\
&\leq \int_\Omega \left[(m_{c_1} - \mathbb{1}_G\underline{u})(w_1^+)^2 + (m_{c_2} - \mathbb{1}_G\underline{v})(w_2^+)^2\right] dx + \int_\Omega (\overline{u} + \overline{v})w_1^+w_2^+ dx.
\end{aligned}$$

Notice that in the second inequality we have used that $\overline{u}, \overline{v} \geq 0$ so that $\overline{u}w_1^+w_2 = \overline{u}w_1^+(w_2^+ - w_2^-) \leq \overline{u}w_1^+w_2^+$. A similar inequality holds for $\overline{v}w_2^+w_1$.

Next, applying Young's inequality to the mixed term yields

$$\begin{aligned}
&\frac{1}{2}\frac{d}{dt}\int_\Omega \left[(w_1^+)^2 + (w_2^+)^2\right] dx \\
&\leq \int_\Omega (m_{c_1} - \mathbb{1}_G\underline{u} + (\overline{u} + \overline{v})/2)(w_1^+)^2 dx + \int_\Omega (m_{c_2} - \mathbb{1}_G\underline{v} + (\overline{u} + \overline{v})/2)(w_2^+)^2 dx \\
&\leq \beta(t)\int_\Omega \left[(w_1^+)^2 + (w_2^+)^2\right] dx,
\end{aligned}$$

where the existence of such a function $\beta(t)$ again follows from the fact that all sub/super solution pairs belong to $C([0,T), C(\overline{\Omega}))$. Gronwall's inequality then gives

$$\int_\Omega \left((w_1^+)^2 + (w_2^+)^2\right) dx \leq e^{2\int_0^t \beta(s)ds} \int_\Omega \left((w_1^+(0))^2 + (w_2^+(0))^2\right) dx = 0,$$

since $w_1^+(0) = \max\{0, \underline{u}(x,0) - \overline{u}(x,0)\} = 0$ and $w_2^+(0) = \max\{0, \underline{v}(x,0) - \overline{v}(x,0)\} = 0$ by assumption. Consequently, $w_i^+ = 0$, and hence $w_i \leq 0$ a.e. in Q_T for each i, i.e. $\underline{u} \leq \overline{u}$ and $\underline{v} \leq \overline{v}$ a.e. in Q_T. Finally, by the Sobolev embedding Theorem 1.2.4, all quantities are continuous in $\overline{Q}_T$, and hence the inequality holds everywhere in Q_T. This completes the proof of the first part of the theorem.

(2) Next, notice the Sobolev embedding ensures that $\underline{u}, \overline{u}, \underline{v}, \overline{v} \in C^1(\overline{\Omega})$ for all $t \in (0,T)$. If in addition we assume that $\underline{u}, \overline{u}, \underline{v}, \overline{v} \in C^1((0,T); C(\overline{\Omega}))$, we may apply the strong maximum principle Theorem 1.2.16 as follows. Since $w_1 \leq 0$, the hypothesis of Theorem 1.2.16 is satisfied. Suppose there exists a point $(x_0, t_0) \in Q_T$ such that $w_1 = 0$. By Theorem 1.2.16, it must be the case that $w_1 \equiv 0$ in Ω for all $t \in (0, t_0)$. This contradicts the continuity of $w_1(\cdot, t)$ and the fact that $w_1(x,0) = \underline{u}(x,0) - \overline{u}(x,0) < 0$ for some $x \in \Omega$. Hence, $w_1 < 0$ for all $(x,t) \in Q_T$, i.e. $\underline{u} < \overline{u}$ for all $(x,t) \in Q_T$.

We now consider points on the boundary ∂Q_T. Suppose that there exists $x_0 \in \partial\Omega$ such that $w_1(x_0, t_0) = 0$ for some $t_0 > 0$. Hopf's lemma (the parabolic version of Theorem 1.2.17) then guarantees that $\frac{\partial w_1}{\partial \nu} > 0$, which is clearly in contradiction to the assumption that $\frac{\partial w_1}{\partial \nu} = \frac{\partial \underline{u}}{\partial \nu} - \frac{\partial \overline{u}}{\partial \nu} \leq 0$. Hence, $\underline{u} < \overline{u}$ for all $(x,t) \in \overline{\Omega} \times (0,T)$.

The same procedure yields that $\underline{v} < \overline{v}$ using instead that $\underline{u} \leq \overline{u}$ from (1) and the boundary conditions for $\underline{v}, \overline{v}$. This completes the proof of the second part, and concludes the proof of the theorem. □

We also have the following existence-comparison theorem for the elliptic system, which is partially an analogue of Proposition (2.5.1). In this case, we actually have more since we strengthen our assumption: a comparison theorem holds, but we also obtain solutions to the elliptic system through a monotone iteration scheme. This is similar to the strategy explored in Section 1.2, but the complexity is increased due to the coupled system. On the other hand, the form of the reaction terms are appropriately *quasimonotone* [123, Ch. 12], and so the sequences generated are monotone.

Proposition 2.5.2. *Suppose that $\underline{u}$, $\overline{u}$, $\underline{v}$, $\overline{v}$ belong to $W^{2,p}(\Omega)$ for any $p \geq 1$ and satisfy the conditions:*

$$\begin{aligned}
-d_1\Delta\underline{u} &\leq \underline{u}(m_{c_1} - \mathbb{1}_G(\underline{u}+\overline{v})) \quad a.e.\ in \quad \Omega,\\
-d_2\Delta\underline{v} &\leq \underline{v}(m_{c_2} - \mathbb{1}_G(\overline{u}+\underline{v})) \quad a.e.\ in \quad \Omega,\\
-d_1\Delta\overline{u} &\geq \overline{u}(m_{c_1} - \mathbb{1}_G(\overline{u}+\underline{v})) \quad a.e.\ in \quad \Omega,\\
-d_2\Delta\overline{v} &\geq \overline{v}(m_{c_2} - \mathbb{1}_G(\underline{u}+\overline{v})) \quad a.e.\ in \quad \Omega,\\
\frac{\partial\underline{u}}{\partial\nu} &\leq \frac{\partial\overline{u}}{\partial\nu} \quad on \quad \partial\Omega,\\
\frac{\partial\underline{v}}{\partial\nu} &\leq \frac{\partial\overline{v}}{\partial\nu} \quad on \quad \partial\Omega.
\end{aligned}$$

If $\underline{u}$, $\overline{u}$, $\underline{v}$, $\overline{v}$ satisfy $(\underline{u},\overline{v}) \leq_K (\overline{u},\underline{v})$, then

- *there exist steady states $(\underline{u}^*,\overline{v}^*)$ and $(\overline{u}^*,\underline{v}^*)$ to (2.2) such that*

$$(\underline{u},\overline{v}) \leq_K (\underline{u}^*,\overline{v}^*) \leq_K (\overline{u}^*,\underline{v}^*) \leq_K (\overline{u},\underline{v});$$

- *any steady state $(\hat{u},\hat{v})$ to (2.2) obeying $(\underline{u},\overline{v}) \leq_K (\hat{u},\hat{v}) \leq_K (\overline{u},\underline{v})$ must satisfy*

$$(\underline{u}^*,\overline{v}^*) \leq_K (\hat{u},\hat{v}) \leq_K (\overline{u}^*,\underline{v}^*).$$

Proof. The proof follows from "standard" iterative arguments for quasimonotone systems and Theorem 1.2.16 in place of the classical maximum principle. The scalar case was considered in Section 1.2.8.

First, let K be so large that $F_1(x,u,v) := Ku+u(m_{c_1}-\mathbb{1}_G(u+v))$ and $F_2(x,u,v) := Kv + v(m_{c_2} - \mathbb{1}_G(u+v))$ are non-decreasing in the arguments u and v, respectively. We then iterate through the process

$$\begin{aligned}
-d_1\Delta u_k + Ku_k &= F_1(x,u_{k-1},v_{k-1}),\\
-d_2\Delta v_k + Kv_k &= F_2(x,u_{k-1},v_{k-1}).
\end{aligned}$$

subject to homogeneous Neumann boundary data along $\partial\Omega$.

We use our sub/super solution pairs $(\underline{u},\overline{v}) = (\underline{u}_0,\overline{v}_0)$ and $(\overline{u},\underline{v}) = (\overline{u}_0,\underline{v}_0)$ as initial iterates to create monotonic sequences satisfying

$$\underline{u} \leq \underline{u}_k \leq \underline{u}_{k+1} \leq \overline{u}_{k+1} \leq \overline{u}_k \leq \overline{u}, \quad \underline{v} \leq \underline{v}_k \leq \underline{v}_{k+1} \leq \overline{v}_{k+1} \leq \overline{v}_k \leq \overline{v},$$

in Ω for all $k \geq 1$. We follow a similar procedure as that outlined in, e.g., [123, Ch. 12] or [95].

We show the details for $(\underline{u}_k, \overline{v}_k)$ with the same approach applying to $(\overline{u}, \underline{v})$. Since $\underline{u}, \overline{v}$ belong to $W^{2,p}(\Omega)$, they are uniformly bounded in $\overline{\Omega}$ by the Sobolev embedding. Hence,

$$F_1(x, \underline{u}, \overline{v}), F_2(x, \underline{u}, \overline{v}) \in L^\infty(\Omega).$$

By the existence result Theorem 1.2.29, there exists a unique positive strong solution $\underline{u}_1, \overline{v}_1 \in W^{2,p}(\Omega)$. Set $w_1 = \underline{u} - \underline{u}_1$ and $z_1 = \overline{v}_1 - \overline{v}$. By the assumptions in the statement of the theorem there holds

$$-d_1 \Delta w_1 + K w_1 \leq F_1(x, \underline{u}, \overline{v}) - F_1(x, \underline{u}, \overline{v}) = 0,$$

and $\frac{\partial w_1}{\partial \nu} \leq 0$ along $\partial\Omega$. Similarly, $-d_2 \Delta z_1 \leq 0$. By the comparison principle we have that $w_1 = \underline{u} - \underline{u}_1 \leq 0$ and $z_1 = \overline{v}_1 - \overline{v} \leq 0$.

Consider now $w_k = \underline{u}_k - \underline{u}_{k+1}$ and $z_k = \overline{v}_{k+1} - \overline{v}_k$. Assume $w_i, z_i \leq 0$ up to $i = k-1$. We proceed inductively. First we have that

$$-d_1 \Delta w_k + K w_k = F_1(x, \underline{u}_{k-1}, \overline{v}_{k-1}) - F_1(x, \underline{u}_{k-2}, \overline{v}_{k-2}).$$

Write the right hand side as

$$F_1(x, \underline{u}_{k-1}, \overline{v}_{k-1}) - F_1(x, \underline{u}_{k-1}, \overline{v}_{k-2}) + F_1(x, \underline{u}_{k-1}, \overline{v}_{k-2}) - F_1(x, \underline{u}_{k-2}, \overline{v}_{k-2}) \leq 0,$$

which holds by the non-increasing property of F_1 and the fact that our iterates are positive. The same argument holds for z_k.

Using the same setup, one can show that $\overline{u}_k \geq \overline{u}_{k+1}$ and $\underline{v}_{k+1} \geq \underline{v}_{k+1}$ for every k.

Finally, we consider $w_k = \underline{u}_k - \overline{u}_k$. By assumption, $w_0 \leq 0$. For $k \geq!$, w_k satisfies

$$(w_k)_t - d_1 \Delta w_k + K w_k = F_1(x, \underline{u}_{k-1}, \overline{v}_{k-1}) - F_1(x, \overline{u}_{k-1}, \underline{v}_{k-1})$$

Assume the above holds up to $k-1$. Using the same rearrangement used previously along with the fact that $\overline{v}_{k-1} - \underline{v}_{k-1}$, it is not difficult to obtain $w_k \leq 0$. The same argument holds for $z_k = \underline{v}_l - \overline{v}_k$. Hence, the monotonicity of our sequences holds for all k.

Since the sequences are monotone and uniformly bounded, the following pointwise limits exist

$$\lim_{k\to\infty} \underline{u}_k = \underline{u}^*, \quad \lim_{k\to\infty} \overline{u}_k = \overline{u}^*, \quad \lim_{k\to\infty} \underline{v}_k = \underline{v}^*, \quad \lim_{k\to\infty} \overline{v}_k = \overline{v}^*,$$

and are uniformly bounded in $W^{2,p}(\Omega)$ for any $p \geq 1$. Thus, the compactness of $W^{2,p}(\Omega)$ yields a subsequence that we do not relabel which converges strongly in $W^{1,p}(\Omega)$ and weakly in $W^{2,p}(\Omega)$. Since each $F_i(x,u,v)$ are Lipschitz continuous in the arguments u, v, we find that the pairs $(\underline{u}^*, \overline{v}^*)$ and $(\overline{u}^*, \underline{v}^*)$ are steady state solutions to problem (2.2) in the weak sense. Furthermore, by the Sobolev embedding we have convergence in $C^{1+\alpha}(\overline{\Omega})$. In particular, the boundary condition is satisfied everywhere along $\partial\Omega$. Again by the regularity of F_i in the arguments u, v, we can show that the convergence is strong in $W^{2,p}(\Omega)$ and $(\underline{u}^*, \overline{v}^*)$ and $(\overline{u}^*, \underline{v}^*)$ are strong solution pairs to problem (2.1).

The ordering relation of these solutions obtained then follows immediately due to the ordering of the original sequences.

Finally, if (u^*, v^*) is any other solution lying between the original sub/super solutions pairs, choosing $(\underline{u}_0, \overline{v}_0) = (u^*, v^*)$ yields $\underline{u}^* \leq u^*$ and $\overline{v}^* \geq v^*$. A similar argument yields $\overline{u}^* \geq u^*$ and $\underline{v}^* \leq v^*$, completing the proof. □

We conclude this subsection with the following simple result.

Corollary 2.5.1. *If a coexistence steady state* $(\tilde{u}, \tilde{v})$ *to* (2.2) *exists, there must hold* $(\tilde{u}, \tilde{v}) \in C^{++}(\overline{\Omega}) \times C^{++}(\overline{\Omega})$.

Proof. It is easy to see that $(0, v^*) \leq_K (\tilde{u}, \tilde{v}) \leq_K (u^*, 0)$ from Proposition 2.5.2. The result then follows from of Proposition 2.5.1 (2) with $(\underline{u}, \overline{v}) = (0, v^*)$ and $(\overline{u}, \underline{v}) = (u^*, 0)$. □

2.5.2 Well-posedness

Using the results of the previous section, we are now ready to prove the well-posedness of the time-dependent competition system. Furthermore, the solution process generates a strongly monotone flow on the space $(C^+(\overline{\Omega}) \times (-C^+(\overline{\Omega}))$. We have the following theorem.

Theorem 2.5.1. *For any initial data* $(u_0, v_0) \in C^+(\overline{\Omega}) \times C^+(\overline{\Omega})$*, there exists a unique global strong solution* (u, v) *to* (2.2) *satisfying*

$$(u, v) \in [C^{\alpha}([0, \infty); C^+(\overline{\Omega})) \cap C^1((0, \infty); C^+(\overline{\Omega}))]^2$$

for any $\alpha \in (0, 1)$*. Moreover, solutions to problem* (2.2) *are strongly monotone in the sense that if* $(u_0, v_0), (\tilde{u}_0, \tilde{v}_0) \in C^+(\overline{\Omega}) \times C^+(\overline{\Omega})$ *are such that* $(u_0, v_0) <_K (\tilde{u}_0, \tilde{v}_0)$*, then* $(u(\cdot, t), v(\cdot, t)) \ll_K (\tilde{u}(\cdot, t), \tilde{v}(\cdot, t))$ *for all* $t > 0$

Proof of Theorem 2.5.1. We may repeat the same process given in the scalar case in order to deduce some preliminary regularity results. To this end, regularize by $\mathbb{1}_G^{\varepsilon}$, $\mathbb{1}_B^{\varepsilon}$. It is easy to see that 0 is a subsolution while M suitably large is a supersolution for both equations u and v. By a standard monotone iteration schemes (see Section 1.2.8) we deduce the existence of a unique classical solution $(u_\varepsilon, v_\varepsilon) \in C^{2+\alpha, 1+\alpha/2}(Q_T) \cap C(\overline{Q}_T)$ for each $\varepsilon > 0$ fixed. Furthermore, $u_\varepsilon, v_\varepsilon$ are uniformly bounded in ε since M is a supersolution for all $\varepsilon > 0$. Thus, $F_i(x, u_\varepsilon, v_\varepsilon)$ are uniformly bounded in $L^\infty(Q_T)$, and so by Theorem 1.2.30 $(u_\varepsilon, v_\varepsilon)$ are uniformly bounded in $W_p^{2,1}(Q_T)$ for any $p \geq 1$. Choosing p large enough we have that in fact $(u, v) \in [C^{1+\alpha, (1+\alpha)/2}(\overline{\Omega} \times [0, T))]^2$ for any $\alpha \in (0, 1)$ by the Sobolev embedding. It is easy to verify the boundary condition as in the scalar equation case due to the convergence in $C^1(\overline{\Omega})$.

Next we show that solutions are positive and global. First, we assert that the solution (u, v) is non-negative. To see this, note that the equation for each solution can be written as

$$u_t = d_1 \Delta u + u F_1(t),$$
$$v_t = d_2 \Delta v + v F_2(t),$$

where $F_i(t) = m_i - \mathbb{1}_G(u + v)$ are bounded by some nonnegative function $\beta(t)$ for any $T > 0$. Multiplying each equation by $u^- = \max\{0, -u\}$ and $v^- = \max\{0, -v\}$ respectively and integrating over Ω, we find that

$$\frac{1}{2} \frac{d}{dt} \int_\Omega \left[(u^-)^2 + (v^-)^2\right] dx \leq \beta(t) \int_\Omega \left[(u^-)^2 + (v^-)^2\right] dx.$$

The result then follows from Gronwall's inequality and the fact that $u^-(\cdot,0) = v^-(\cdot,0) = 0$.

Next, if one considers the pair $(\overline{u}, \underline{v}) = (Me^{\gamma t}\phi_1, 0)$ where ϕ_1 is the first eigenfuction solving (2.5) corresponding to $\mu_1(d_1, m_{c_1})$, it is easy to see that

$$\overline{u}_t - d\Delta\overline{u} \geq \overline{u}(m_{c_1} - \mathbb{1}_G(\overline{u} + \underline{v})),$$

so long as $\gamma \geq \mu_1(d_1, m_{c_1})$. Hence, u is exponentially bounded in time and thus necessarily exists globally. Furthermore, we see that $u(x,t) > 0$ in $\overline{\Omega}$ for all $t > 0$ so long as $u_0(x) = u(x,0) > 0$ somewhere in Ω. A similar argument holds for $v(x,t)$ when one considers $(\underline{u}, \overline{v}) = (0, Me^{\gamma t}\hat{\phi}_1)$ where $\hat{\phi}_1$ corresponds to $\mu_1(d_2, m_{c_2})$ and γ is chosen such that $\gamma + \mu_1(d_2, m_{c_2}) \geq 0$.

We may now improve the regularity in the time variable for application in the following section. Most important in this argument is the Hölder continuity of the solution in the variable t. This allows us to apply [111, Theorem 3] once again: since $u_0 \in C(\Omega)$ and $(x,t) \mapsto u(x,t)[m_{c_1} - \mathbb{1}_G(u(x,t) + v(x,t))]$ is Hölder continuous with exponent α in the variable t, we may conclude that $\frac{\partial u}{\partial t}$ exists and is uniformly continuous on $(0,\infty)$. Similarly, we conclude that $\frac{\partial v}{\partial t}$ exists and is also uniformly continuous on $(0,\infty)$. Consequently, the unique strong solution (u,v) belongs to $[C^\alpha([0,\infty); C(\overline{\Omega})) \cap C^1((0,\infty); C(\overline{\Omega}))]^2$.

With the sufficient regularity obtained, an application of Proposition 2.5.1 (2) immediately gives us the strong monotonicity of the system in $(C(\overline{\Omega}) \times (-C(\overline{\Omega}))$, completing the proof. □

2.5.3 Global dynamics

We now state one of the main results of this chapter. Denote by $\mu_1(d_1, m_{c_1})$ (resp. $\mu_1(d_2, m_{c_2})$) the principal eigenvalue associated with the linearization of (2.1) at 0 with $(d,m) = (d_1, m_{c_1})$ (resp. $(d,m) = (d_2, m_{c_2})$). See Proposition 2.3.2 for details.

By Theorem 2.4.1, we have a unique positive steady state when the principal eigenvalue is negative. Whenever $\mu_1(d_1, m_{c_1}) < 0$, denote by u^* the unique positive steady state of (2.1) with $(d,m) = (d_1, m_{c_1})$. Similarly, whenever $\mu_1(d_2, m_{c_2}) < 0$, denote by v^* the unique positive steady state of problem (2.1) with $(d, m) = (d_2, m_{c_2})$. The following result provides a full description of the global dynamics of the competition system (2.2) depending on d_i and c_i.

Theorem 2.5.2. *Let $0 < d_1 < d_2$. Then the following hold (with all convergences hold in $C(\overline{\Omega}) \times C(\overline{\Omega})$).*

(1) *Suppose $\mu_1(d_1, m_{c_1}) \geq 0$ and $\mu_1(d_2, m_{c_2}) \geq 0$. Then, $(u, v) \to (0, 0)$ as $t \to \infty$.*

(2) *Suppose $\mu_1(d_1, m_{c_1}) < 0$ and $\mu_1(d_2, m_{c_2}) \geq 0$. Then, $(u, v) \to (u^*, 0)$ as $t \to \infty$.*

(3) *Suppose $\mu_1(d_1, m_{c_1}) \geq 0$ and $\mu_1(d_2, m_{c_2}) < 0$. Then, $(u, v) \to (0, v^*)$ as $t \to \infty$.*

(4) *Suppose $\mu_1(d_1, m_{c_1}) < 0$ and $\mu_1(d_2, m_{c_2}) < 0$. Then, there exist critical values $0 < \underline{c}_2^* < \overline{c}_2^* < c_1$ such that the following results hold.*

   (i) If $c_2 \in (\overline{c}_2^*, \infty)$, then $(u, v) \to (u^*, 0)$ as $t \to \infty$.

   (ii) If $c_2 \in (\underline{c}_2^*, \overline{c}_2^*)$, then $(u, v) \to (\tilde{u}, \tilde{v})$ as $t \to \infty$, where $(\tilde{u}, \tilde{v})$ is the unique coexistence steady state of (2.2).

   (iii) If $c_2 \in (0, \underline{c}_2^*)$, then $(u, v) \to (0, v^*)$ as $t \to \infty$.

   Furthermore, $\underline{c}_2^*$ and $\overline{c}_2^*$ are given by the unique zero of the functions $c_2 \mapsto \mu_1(d_1, m_{c_1} - \mathbb{1}_G v^*)$ and $c_2 \mapsto \mu_1(d_2, m_{c_2} - \mathbb{1}_G u^*)$, respectively. That is,

$$c_2 = \underline{c}_2^* \iff \mu_1(d_1, m_{c_1} - \mathbb{1}_G v^*) = 0 \quad \text{and} \quad c_2 = \overline{c}_2^* \iff \mu_1(d_2, m_{c_2} - \mathbb{1}_G u^*) = 0.$$

Remark 2.5.1. *Note that in the description of $\underline{c}_2^*$, the dependence of $\mu_1(d_1, m_{c_1} - \mathbb{1}_G v^*)$ on c_2 is given implicitly by the dependence of v^* on c_2. This is in contrast to $\overline{c}_2^*$ where the dependence is more explicit, seen directly by the presence of m_{c_2}.*

We also prove the following limiting case extending point (iii) of Theorem 2.5.2.

Theorem 2.5.3. *Let $0 < d_1 < d_2$ and $c_2 = 0 < c_1$. Then,*

$$(u, v) \to (0, v^*) \quad \text{in} \quad C(\overline{\Omega}) \times C(\overline{\Omega}) \quad \text{as} \quad t \to \infty.$$

To complete the picture of potential asymptotic outcomes, we highlight the following limiting cases when either the diffusion coefficients are identical, or the level of degradation for each species is identical.

Theorem 2.5.4. *Suppose that* $d_1, d_2 > 0$ *and* $c_1 = c_2 = 0$. *Then, there exists a curve of steady states of the form* $\{(\sigma, 1-\sigma) : \sigma \in [0,1]\}$. *Furthermore, the linearization about the semi-trivial steady states* $(1,0)$ *and* $(0,1)$ *have a zero eigenvalue, that is, the semi-trivial steady states are neutrally stable.*

Theorem 2.5.5. *Suppose that* $d_1 = d_2 > 0$, *and* u^* *and* v^* *exist. The following hold.*

(1) *If* $c_1 < c_2$, *then* $(u,v) \to (u^*, 0)$ *in* $C(\overline{\Omega}) \times C(\overline{\Omega})$ *as* $t \to \infty$.

(2) *If* $c_1 > c_2$, *then* $(u,v) \to (0, v^*)$ *in* $C(\overline{\Omega}) \times C(\overline{\Omega})$ *as* $t \to \infty$.

This result is of notable significance due to its implications for the sustainability of multiple species' populations. This result suggests that, under the introduction of any amount of degraded habitat, if one species is particularly resilient in the degraded region, not only will it survive, but it will drive the other species to extinction! Moreover, this result holds for any such $0 < d_1 < d_2$. *Hence, under the introduction of variable heterogeneity, the slower diffuser may not always win!* In fact, in the limiting case, as long as species u experiences some level of mortality in some region of Ω, *species* v *always drives species* u *to extinction! The remarkable fact is that this holds for any* $c_1 > 0$, *for any region* B, *regardless of how small* c_1 *or the region* B *might be.* This behaviour can be observed in the numerical results of Section 2.6.

In order to prove Theorem 2.5.2, we use the following crucial result.

Proposition 2.5.3. *Let* $d_1, d_2 > 0$ *and* $c_1, c_2 \geq 0$ *be such that* $\mu_1(d_i, m_{c_i}) < 0$ *for* $i = 1, 2$. *Suppose that every coexistence steady state of* (2.2), *if exists, is asymptotically stable. Then one of the following alternatives holds.*

(a) There exists a unique coexistence steady state of (2.2) *which is globally asymptotically stable.*

(b) System (2.2) *has no coexistence steady state, and one of* $(u^*, 0)$ *or* $(0, v^*)$ *is globally asymptotically stable, while the other is unstable.*

For notational simplicity, we omit Neumann boundary conditions whenever no confusion is caused.

Proof of Theorem 2.5.2 (1)-(3). We address cases (1)-(3) together since they are the most straightforward. Denote by (u, v) the unique global strong solution to (2.2) with initial data $(u_0, v_0) \in [C^+(\overline{\Omega}) \setminus \{0\}]^2$.

(1) Suppose $\mu_1(d_i, m_{c_i}) > 0$ for $i = 1, 2$. Define $(\underline{u}, \overline{v}) := (0, w_2)$ and $(\overline{u}, \underline{v}) := (w_1, 0)$ in $\overline{\Omega} \times [0, \infty)$, where w_1 and w_2 are respectively solutions to (2.1) with $(d, m) = (d_1, m_{c_1})$ and $(d, m) = (d_2, m_{c_2})$ subject to the initial conditions $w_1(\cdot, 0) = u_0$ and $w_2(\cdot, 0) = v_0$. By Theorem 2.4.3, $w_i(\cdot, t) \to 0$ in $C(\overline{\Omega})$ as $t \to \infty$ for $i = 1, 2$.

Direct computation shows that the differential inequalities in Proposition 2.5.1 hold, that is, $(\underline{u}, \overline{v})$ and $(\overline{u}, \underline{v})$ are respectively a sub solution and a super solution of (2.2). We conclude from Proposition 2.5.1 that $0 \leq u \leq \overline{u}$ and $0 \leq v \leq \overline{v}$ in $\overline{\Omega}$ for all $t > 0$. Hence, $(u, v) \to (0, 0)$ in $C(\overline{\Omega}) \times C(\overline{\Omega})$ as $t \to \infty$, completing the proof of part (1).

Next we prove the result for case (3). Case (2) follows in an identical fashion. Suppose that $\mu_1(d_1, m_{c_1}) \geq 0$ while $\mu_1(d_2, m_{c_2}) < 0$ so that v^* exists.

Let w be the unique solution of (2.1) with $(d, m) = (d_1, m_{c_1})$ and initial data $w_0 = u_0$. Theorem 2.4.3 (ii) ensures that $w \to 0$ in $C(\overline{\Omega})$ as $t \to \infty$. Obviously, w satisfies

$$w_t - d_1 \Delta w \geq w(m_{c_1} - \mathbb{1}_G(w + v)) \quad \text{a.e. in} \quad \Omega \times (0, \infty),$$

and hence, $u \leq w$ by Proposition 2.4.1. It follows that $u \to 0$ in $C(\overline{\Omega})$ as $t \to \infty$, and thus, for any $0 < \varepsilon \ll 1$, there is $t_\varepsilon \gg 1$ such that $0 \leq u \leq \varepsilon$ in $\overline{\Omega}$ for all $t \geq t_\varepsilon$. Let z_ε be the strong solution to the following auxiliary problem

$$\begin{cases} z_t = d_2 \Delta z + z(m_{c_2} - \mathbb{1}_G(z + \varepsilon)) & \text{in} \quad \Omega \times (t_\varepsilon, \infty), \\ z(\cdot, t_\varepsilon) = v(\cdot, t_\varepsilon) & \text{in} \quad \overline{\Omega}. \end{cases}$$

Proposition 2.4.1 yields that $z_\varepsilon \leq v$ for all $t \geq t_\varepsilon$.

Recall that $\mu_1(d_2, m_{c_2}) < 0$. By Proposition 2.3.2 (iii), we may choose ε so small that $\mu_1(d_2, m_{c_2} - \varepsilon \mathbb{1}_G) < 0$. Then, the following equation:

$$d_2 \Delta z^* + z^*(m_{c_2} - \mathbb{1}_G(z^* + \varepsilon)) = 0 \quad \text{in} \quad \Omega$$

admits a unique positive solution z_ε^*. It follows from Theorem 2.4.3 that $z_\varepsilon \to z_\varepsilon^*$ in $C(\overline{\Omega})$ as $t \to \infty$.

Finally, let $\overline{v}$ solve

$$\begin{cases} \overline{v}_t = d_2 \Delta \overline{v} + \overline{v}(m_{c_2} - \mathbb{1}_G \overline{v}) & \text{in} \quad \Omega \times (0, \infty), \\ \overline{v}(\cdot, 0) = v_0 & \text{in} \quad \overline{\Omega}. \end{cases}$$

By Theorem 2.4.3, $\overline{v} \to v^*$ as $t \to \infty$. Note that by Proposition 2.4.1, $v \leq \overline{v}$ in $\overline{\Omega}$ for all $t > 0$. Combining these results, we deduce that

$$z_\varepsilon^* = \lim_{t \to \infty} z_\varepsilon \leq \liminf_{t \to \infty} v \leq \limsup_{t \to \infty} v \leq \lim_{t \to \infty} \overline{v} = v^*, \quad \forall 0 < \varepsilon \ll 1.$$

We conclude by showing that $z_\varepsilon^* \to v^*$ in $C(\overline{\Omega})$ as $\varepsilon \to 0$. Actually, the exact same argument as that used in the proof of Theorem 2.4.2 applies except we replace c with ε. Dini's theorem proves the uniform convergence over $\overline{\Omega}$. Furthermore, the convergence holds in $C^{1+\alpha}(\overline{\Omega})$ for any $\alpha \in (0,1)$, and so the boundary condition is satisfied everywhere on $\partial\Omega$.

It follows that z_0^* is a strong solution satisfying the same equation as v^*. The uniqueness of solutions implies that $z_0^* = v^*$ in $\overline{\Omega}$. Sending ε to zero completes the proof of part (3), and we are done. $\square$

The rest of this section is devoted to the proof of Theorem 2.5.2 (4) with the short proof of Theorem 2.5.3 presented afterward. In what follows, we analyze in detail the local stability of the steady states. Since $\mu_1(d_i, m_{c_i}) < 0$ for $i = 1, 2$, we have at least three steady states: $(0,0)$, $(u^*, 0)$, and $(0, v^*)$. In particular, recall that Lemma 2.4.2 applies to u^* and v^* with respect to c_1 and c_2, respectively.

Lemma 2.5.1. *Suppose* $c_1 > 0$ *and* $\mu_1(d_1, m_{c_1}) < 0$. *Then there exists a critical value* $\overline{c}_2^* \in (0, c_1)$ *such that the following hold:*

(i) if $c_2 \in (0, \overline{c}_2^*)$, *then* $(u^*, 0)$ *is unstable;*

(ii) if $c_2 \in (\overline{c}_2^*, c_1)$, *then* $(u^*, 0)$ *is linearly stable.*

Furthermore, $\overline{c}_2^*$ *satisfies* $\overline{c}_2^* > \overline{c}_2 := \frac{|G| - \int_G u^*}{|B|} > 0$.

Proof. Consider the following eigenvalue problem associated to the linearization of (2.2) about $(u^*, 0)$:

$$\begin{cases} d_1\Delta\psi_1 + (m_{c_1} - 2\mathbb{1}_G u^*)\psi_1 - \mathbb{1}_G u^*\psi_2 + \lambda\psi_1 = 0 & \text{in} \quad \Omega, \\ d_2\Delta\psi_2 + (m_{c_2} - \mathbb{1}_G u^*)\psi_2 + \lambda\psi_2 = 0 & \text{in} \quad \Omega. \end{cases} \tag{2.9}$$

In particular,

$$d_2\Delta\psi_2 + (m_{c_2} - \mathbb{1}_G u^*)\psi_2 + \lambda\psi_2 = 0 \quad \text{in} \quad \Omega, \tag{2.10}$$

and so all eigenvalues are real.

Since $|G| > \int_G u^*$ due to Lemma 2.4.2, we deduce $\int_\Omega (m_{c_2} - \mathbb{1}_G u^*) = |G| - \int_G u^* - c_2\,|B| \geq 0$ for all $c_2 \leq \bar{c}_2$, where $\bar{c}_2$ is as in the statement. It follows from Proposition 2.3.2 that

$$\mu_1(d_2, m_{c_2} - \mathbb{1}_G u^*) < 0, \quad \forall c_2 \leq \bar{c}_2, \tag{2.11}$$

where $\mu_1(d_2, m_{c_2} - \mathbb{1}_G u^*)$ is the first eigenvalue of (2.10).

Assume $c_2 \leq \bar{c}_2$ and let ψ_2 be the positive eigenfunction associated to $\lambda := \mu_1(d_2, m_{c_2} - \mathbb{1}_G u^*) < 0$. We solve for ψ_1 in the first equation of (2.9) given by

$$d_1\Delta\psi_1 + (m_{c_1} - 2\mathbb{1}_G u^*)\psi_1 - \mathbb{1}_G u^*\psi_2 + \lambda\psi_1 = 0 \quad \text{in} \quad \Omega. \tag{2.12}$$

Since $\mu_1(d_1, m_{c_1} - 2\mathbb{1}_G u^*) > \mu_1(d_1, m_{c_1} - \mathbb{1}_G u^*) = 0$ and $\lambda < 0$, the operator given by

$$d_1\Delta + (m_{c_1} - 2\mathbb{1}_G u^*) + \lambda : C(\overline{\Omega}) \to C(\overline{\Omega}), \tag{2.13}$$

is invertible. This together with the third theorem of Krein-Rutman, Theorem 1.2.7, imply that (2.12) admits a unique positive solution. Hence, λ is a negative eigenvalue to the problem (2.9) and $(u^*, 0)$ is unstable.

So far, we have shown that $(u^*, 0)$ is unstable for $c_2 \in (0, \bar{c}_2]$. We extend this interval to $(0, \bar{c}_2^*)$ for some $\bar{c}_2^* > \bar{c}_2$. First, if we choose $c_2 = c_1$ so that $m_{c_2} = m_{c_1}$, we see from Proposition 2.3.2 (iii) that $\mu_1(d_2, m_{c_2} - \mathbb{1}_G u^*) > \mu_1(d_1, m_{c_2} - \mathbb{1}_G u^*) = 0$. This together with (2.11) and the monotonicity of $c_2 \mapsto \mu_1(d_2, m_{c_2} - \mathbb{1}_G u^*)$ yields the existence of a unique value $\bar{c}_2^* \in (\bar{c}_2, c_1)$ such that $\mu_1(d_2, m_{c_2} - \mathbb{1}_G u^*) = 0$. In particular, $\mu_1(d_2, m_{c_2} - \mathbb{1}_G u^*) < 0$ for all $c_2 \in (0, \bar{c}_2^*)$. Hence, the operator (2.13) is again invertible for all $c_2 \in (0, \bar{c}_2^*)$ and so $(u^*, 0)$ is unstable. This proves part (i) of the proposition.

It remains to show that $(u^*, 0)$ is linearly stable for all $c_2 \in (\overline{c}_2^*, c_1)$. Referring back to the eigenvalue problem (2.9), if $\psi_2 \not\equiv 0$, then λ must satisfy $\lambda \geq \mu_1(d_2, m_{c_2} - \mathbb{1}_G u^*) > 0$, as $c_2 \in (\overline{c}_2^*, c_1)$. On the other hand, if $\psi_2 \equiv 0$, one considers only

$$d_1 \Delta \psi_1 + (m_{c_1} - 2\mathbb{1}_G u^*)\psi_1 + \lambda \psi_1 = 0 \quad \text{in} \quad \Omega,$$

and notices that $\lambda \geq \mu_1(d_1, m_{c_1} - 2\mathbb{1}_G u^*) > \mu_1(d_1, m_{c_1} - \mathbb{1}_G u^*) = 0$. In either case, all eigenvalues of (2.9) are positive, and thus, $(u^*, 0)$ is linearly stable for all $c_2 \in (\overline{c}_2^*, c_1)$. This completes the proof of part (ii). □

We now prove the analogous result for the local stability of $(0, v^*)$.

Lemma 2.5.2. *Let $c_1 > 0$ and $\mu_1(d_2, m_{c_2}) < 0$. There exists a critical value $\underline{c}_2^* \in (0, c_1)$ such that the following hold:*

- *(i) if $c_2 \in (0, \underline{c}_2^*)$, then $(0, v^*)$ is linearly stable;*
- *(ii) if $c_2 \in (\underline{c}_2^*, c_1)$, then $(0, v^*)$ is unstable.*

Furthermore, $\underline{c}_2^*$ satisfies $\underline{c}_2^* > \underline{c}_2 := \sup\{c_2 > 0 : v^* \geq u^* \text{ in } G\} > 0$.

Proof. Consider the following eigenvalue problem associated to the linearization of (2.2) about $(0, v^*)$:

$$\begin{cases} d_1 \Delta \psi_1 + (m_{c_1} - \mathbb{1}_G v^*)\psi_1 + \lambda \psi_1 = 0 & \text{in} \quad \Omega, \\ d_2 \Delta \psi_2 + (m_{c_2} - 2\mathbb{1}_G v^*)\psi_2 - \mathbb{1}_G v^* \psi_1 + \lambda \psi_2 = 0 & \text{in} \quad \Omega. \end{cases} \tag{2.14}$$

By Corollary 2.4.2, $u^* < 1$ in $\overline{\Omega}$, and $v^* \to 1$ in $C(\overline{\Omega})$ as $c_2 \to 0$, and thus, $u^* \leq v^*$ in G for every c_2 sufficiently small. Hence, $\underline{c}_2$ is well-defined. From Proposition 2.3.2 (iv) it follows that

$$\mu_1(d_1, m_{c_1} - \mathbb{1}_G v^*) > \mu_1(d_1, m_{c_1} - \mathbb{1}_G u^*) = 0, \quad \forall c_2 \in (0, \underline{c}_2).$$

If $\psi_1 \not\equiv 0$, then $\lambda \geq \mu_1(d_1, m_{c_1} - \mathbb{1}_G v^*) > 0$. If $\psi_1 \equiv 0$, then $\lambda \geq \mu_1(d_2, m_{c_2} - 2\mathbb{1}_G v^*) > \mu_1(d_2, m_{c_2} - \mathbb{1}_G v^*) = 0$. In either case, all eigenvalues of (2.14) are positive for $c_2 \in (0, \underline{c}_2)$, and so $(0, v^*)$ is linearly stable for $c_2 \in (0, \underline{c}_2)$.

We now extend the interval $(0, \underline{c}_2)$ to $(0, \underline{c}_2^*)$. Notice that if we choose $c_2 = c_1$, then

$$\mu_1(d_1, m_{c_1} - \mathbb{1}_G v^*) = \mu_1(d_1, m_{c_2} - \mathbb{1}_G v^*) < \mu_1(d_2, m_{c_2} - \mathbb{1}_G v^*) = 0,$$

and hence there exists a critical value $\underline{c}_2^* > \underline{c}_2$ such that $\mu_1(d_1, m_{c_1} - \mathbb{1}_G v^*) = 0$. Consequently, $(0, v^*)$ is linearly stable for all $c_2 \in [0, \underline{c}_2^*)$.

Finally, we show that $(0, v^*)$ is unstable for all $c_2 > \underline{c}_2^*$. Referring back to the linearized system (2.14), set $\lambda = \mu_1(d_1, m_{c_1} - \mathbb{1}_G v^*) < 0$ and denote by ψ_1 the corresponding eigenfunction. We now solve for ψ_2. This follows immediately from the fact that the operator $d_2\Delta + (m_{c_2} - 2\mathbb{1}_G v^*) + \lambda$ is invertible since $\mu_1(d_2, m_{c_2} - 2\mathbb{1}_G v^*) > 0$ and $\lambda < 0$, i.e., we apply the third Krein-Rutman theorem once again. Hence, (2.14) has a negative eigenvalue for all $c_2 > \underline{c}_2^*$ and so $(0, v^*)$ is unstable. This completes the proof. □

Next, we state a result asserting that every coexistence steady state is linearly stable, whenever it exists. This key result in conjunction with Proposition 2.5.3 will allow us to prove the subsequent Lemma, which results in conclusions of global asymptotic stability.

Lemma 2.5.3. *Suppose* $0 < d_1 < d_2$ *and* $0 \le c_2 < c_1$. *Then, any coexistence steady state of* (2.2), *whenever it exists, is linearly stable.*

Proof. We adapt the proof of [61, claim (S)]. Let $(\tilde{u}, \tilde{v})$ be a coexistence steady state of (2.2). Then, $(0, \tilde{v}) \ll_K (\tilde{u}, 0)$ by Corollary 2.5.1. Consider the eigenvalue problem associated to the linearization of (2.2) about $(\tilde{u}, \tilde{v})$:

$$\begin{cases} d_1\Delta\psi_1 + (m_{c_1} - \mathbb{1}_G(\tilde{u} + \tilde{v}) - \mathbb{1}_G\tilde{u})\psi_1 - \mathbb{1}_G\tilde{u}\psi_2 + \lambda\psi_1 = 0 & \text{in} \quad \Omega, \\ d_2\Delta\psi_2 + (m_{c_2} - \mathbb{1}_G(\tilde{u} + \tilde{v}) - \mathbb{1}_G\tilde{v})\psi_2 - \mathbb{1}_G\tilde{v}\psi_1 + \lambda\psi_2 = 0 & \text{in} \quad \Omega. \end{cases} \tag{2.15}$$

Denote by (ϕ_1, ϕ_2) the eigenfunction pair associated to the principal eigenvalue λ_1, whose existence and simplicity is ensured by the second Krein-Rutman theorem, Theorem 1.2.6. We may choose ϕ_1, ϕ_2 such that $(0,0) \ll_K (\phi_1, \phi_2)$, that is, $(\phi_1, \phi_2) \in (X^+) \times (-X^+)$, and $\|\phi_1\|_2^2 + \|\phi_2\|_2^2 = 1$. Direct calculations give

$$d_1\nabla \cdot \left(\tilde{u}^2\nabla\left(\frac{\phi_1}{\tilde{u}}\right)\right) = \mathbb{1}_G\tilde{u}^2(\phi_1 + \phi_2) - \lambda_1\tilde{u}\phi_1 \quad \text{in} \quad \Omega.$$

Multiplying the above identity by $\frac{\phi_1^2}{\tilde{u}^2}$ and integrating over Ω, we find

$$-2d_1\int_\Omega \tilde{u}\phi_1\left|\nabla\left(\frac{\phi_1}{\tilde{u}}\right)\right|^2 dx = \int_G \phi_1^2(\phi_1+\phi_2)dx - \lambda_1\int_\Omega \frac{\phi_1^3}{\tilde{u}}dx.$$

Similarly, there holds

$$-2d_2\int_\Omega \tilde{v}\phi_2\left|\nabla\left(\frac{\phi_2}{\tilde{v}}\right)\right|^2 dx = \int_G \phi_2^2(\phi_1+\phi_2)dx - \lambda_1\int_\Omega \frac{\phi_2^3}{\tilde{v}}dx.$$

Combining these two identities, we find

$$\begin{aligned}-\lambda_1\int_\Omega\left(\frac{\phi_1^3}{\tilde{u}}-\frac{\phi_2^3}{\tilde{v}}\right)dx &= -2d_1\int_\Omega \tilde{u}\phi_1\left|\nabla\left(\frac{\phi_1}{\tilde{u}}\right)\right|^2 dx - \int_G \phi_1^2(\phi_1+\phi_2)dx\\ &\quad + 2d_2\int_\Omega \tilde{v}\phi_2\left|\nabla\left(\frac{\phi_2}{\tilde{v}}\right)\right|^2 dx + \int_G \phi_2^2(\phi_1+\phi_2)dx\\ &\le -\int_G(\phi_1+\phi_2)(\phi_1^2-\phi_2^2)dx = -\int_G(\phi_1+\phi_2)^2(\phi_1-\phi_2)dx \le 0.\end{aligned}$$

This implies that $\lambda_1 \ge 0$ with equality if and only if $\frac{\phi_1}{\tilde{u}} \equiv \text{const}$, $\frac{\phi_2}{\tilde{v}} \equiv \text{const}$ and $\phi_1 = -\phi_2$.

If $(\tilde{u},\tilde{v})$ is not linearly stable, then $\lambda_1 = 0$. It follows that $\tilde{u} = k\tilde{v}$ for some $k > 0$, which together with the system satisfied by $(\tilde{u},\tilde{v})$ gives

$$\begin{cases} d_1\Delta\tilde{u} + \tilde{u}(m_{c_1} - \mathbb{1}_G(1+k^{-1})\tilde{u}) = 0 & \text{in } \Omega,\\ d_2\Delta\tilde{v} + \tilde{v}(m_{c_2} - \mathbb{1}_G(1+k)\tilde{v}) = 0 & \text{in } \Omega.\end{cases}$$

Clearly, $w^* := (1+k^{-1})\tilde{u} = (1+k)\tilde{v}$ satisfies

$$\begin{cases} d_1\Delta w^* + w^*(m_{c_1} - \mathbb{1}_G w^*) = 0 & \text{in } \Omega,\\ d_2\Delta w^* + w^*(m_{c_2} - \mathbb{1}_G w^*) = 0 & \text{in } \Omega.\end{cases}$$

Hence, w^* satisfies $(d_2-d_1)\Delta w^* - \mathbb{1}_B(c_1-c_2)w^* = 0$ in Ω, leading to $w^* = 0$ in Ω. This contradicts the positivity of $\tilde{u}$ and $\tilde{v}$. In conclusion, $\lambda_1 > 0$, and hence, $(\tilde{u},\tilde{v})$ is linearly stable. □

Lemma 2.5.3 allows us to show an additional property of the quantities $\underline{c}_2^*$ and $\overline{c}_2^*$: they are ordered. This gives us an existence/non-existence result for a positive coexistence steady state.

Lemma 2.5.4. *It holds $\underline{c}_2^* < \overline{c}_2^*$. Moreover,* *(i) If* $c_2 \in [0, \underline{c}_2^*) \cup (\overline{c}_2^*, \infty)$*, there is no coexistence steady state;*

(ii) If $c_2 \in (\underline{c}_2^*, \overline{c}_2^*)$*, then there exists a unique coexistence steady state.*

Proof. First, we claim that $\underline{c}_2^* < \overline{c}_2^*$. Suppose otherwise. We then consider two cases: $\underline{c}_2^* > \overline{c}_2^*$ and $\underline{c}_2^* = \overline{c}_2^*$.

In the first case, whenever $c_2 \in (\overline{c}_2^*, \underline{c}_2^*)$, both $(u^*, 0)$ and $(0, v^*)$ are linearly stable according to Lemmas 2.5.1 and 2.5.2. Such a case is contradictory to Proposition 2.5.3.

Suppose now that $\underline{c}_2^* = \overline{c}_2^*$. Let c_2 be exactly this value. Note that v^* is fixed corresponding to c_2, whereas u^* is fixed and independent of c_2. From the definition of $\underline{c}_2^*$ and $\overline{c}_2^*$, we find simultaneously that

$$\mu_1(d_1, m_{c_1} - \mathbb{1}_G v^*) = 0 = \mu_1(d_2, m_{c_2} - \mathbb{1}_G u^*)$$

for some eigenfunctions ψ_1, ψ_2, while $0 = \mu_1(d_1, m_{c_1} - \mathbb{1}_G u^*) = \mu_1(d_2, m_{c_2} - \mathbb{1}_G v^*)$ with eigenfunctions u^* and v^*, respectively. In other words, the following equations are satisfied:

$$\begin{aligned} &d_1 \Delta \psi_1 + (m_{c_1} - \mathbb{1}_G v^*)\psi_1 = 0, \qquad && d_1 \Delta u^* + u^*(m_{c_1} - \mathbb{1}_G u^*) = 0, \\ &d_2 \Delta \psi_2 + (m_{c_2} - \mathbb{1}_G u^*)\psi_2 = 0, \qquad && d_2 \Delta v^* + v^*(m_{c_2} - \mathbb{1}_G v^*) = 0, \end{aligned}$$

From the variational characterization of these eigenvalues, we have that

$$\begin{aligned} 0 &\le \int_\Omega \left[d_2 |\nabla \phi|^2 - \phi^2 (m_{c_2} - \mathbb{1}_G u^*) \right] dx, \quad \forall \phi \in H^1(\Omega) : \phi \not\equiv 0, \\ 0 &= \int_\Omega \left[d_2 |\nabla v^*|^2 - (v^*)^2 (m_{c_2} - \mathbb{1}_G v^*) \right] dx, \end{aligned} \tag{2.16}$$

and also

$$\begin{aligned} 0 &\le \int_\Omega \left[d_1 |\nabla \phi|^2 - \phi^2 (m_{c_1} - \mathbb{1}_G v^*) \right] dx, \quad \forall \phi \in H^1(\Omega) : \phi \not\equiv 0, \\ 0 &= \int_\Omega \left[d_1 |\nabla u^*|^2 - (u^*)^2 (m_{c_2} - \mathbb{1}_G u^*) \right] dx. \end{aligned} \tag{2.17}$$

Note that the inequalities above are strict when ϕ is any function other than the principal eigenfunction. Hence, if we choose $\phi = v^*$ in the first equation appearing in (2.16) and take the difference of the two, we find that $\int_G (v^*)^2 (u^* - v^*) > 0$. Similarly, if we choose $\phi = u^*$ in the first equation appearing in (2.17) and take the difference of the two, we obtain $\int_G (u^*)^2(v^* - u^*) > 0$. Adding these two quantities, we find

$$0 < \int_G (v^*)^2(u^* - v^*)dx + \int_G (u^*)^2(v^* - u^*)dx = -\int_G (u^* - v^*)^2(u^* + v^*)dx \leq 0,$$

which is a contradiction. Hence, $\underline{c}_2^* \neq \overline{c}_2^*$, and so combining these two cases implies that $\underline{c}_2^* < \overline{c}_2^*$ must hold.

(i) Let $0 \leq c_2 < \underline{c}_2^*$. Suppose on the contrary that there exists a coexistence steady state $(\tilde{u}, \tilde{v})$. In this case, $(0, v^*)$ is linearly stable by Lemma 2.5.2, while $(\tilde{u}, \tilde{v})$ is globally asymptotically stable by Lemma 2.5.3 and Proposition 2.5.3, leading to a contradiction.

A similar argument holds when $c_2 > \overline{c}_2^*$.

(ii) Suppose $c_2 \in (\underline{c}_2^*, \overline{c}_2^*)$. Then, both $(u^*, 0)$ and $(0, v^*)$ are unstable, and hence, Proposition 2.5.3 ensures the existence of a unique coexistence steady state. This completes the proof. □

We are ready to prove Theorem 2.5.2 (4).

Proof of Theorem 2.5.2 (4). By Lemmas 2.5.1, 2.5.2 and 2.5.4, there holds $\underline{c}_2^* < \overline{c}_2^* < c_1$.

(i) Suppose $c_2 \in (\overline{c}_2^*, c_1)$. By Lemma 2.5.1, $(u^*, 0)$ is linearly stable. Since $c_2 > \underline{c}_2^*$, Lemma 2.5.2 implies that $(0, v^*)$ is unstable. By Lemma 2.5.4, there is no coexistence steady state. From Proposition 2.5.3, we conclude that $(u^*, 0)$ is globally asymptotically stable.

(ii) Suppose $c_2 \in (\underline{c}_2, \overline{c}_2^*)$. Then, both $(u^*, 0)$ and $(0, v^*)$ are unstable. By Lemma 2.5.4, there exists a unique coexistence steady state, and is hence globally asymptotically stable by Proposition 2.5.3.

(iii) Suppose $c_2 \in (0, \underline{c}_2^*)$. Then, $(0, v^*)$ is linearly stable by Lemma 2.5.2. By Lemma 2.5.1, $(u^*, 0)$ is unstable, and by Lemma 2.5.4, there is no coexistence steady state. Hence, Proposition 2.5.3 implies that $(0, v^*)$ is globally asymptotically stable. □

Theorem 2.5.3 follows almost immediately from the previous results.

Proof of Theorem 2.5.3. It is easy to see that when $c_2 = 0 < c_1$, $(u^*, 0)$ is unstable while $(0, v^*)$ is linearly stable. From Lemma 2.5.4, we see that there cannot exist a coexistence steady state when $c_2 = 0$. Hence, $(0, v^*)$ is globally asymptotically stable by Proposition 2.5.3. □

Proof of Theorem 2.5.4. In this case, our system becomes

$$\begin{cases} u_t = d_1 \Delta u + \mathbb{1}_G u(1 - u - v), \\ v_t = d_2 \Delta v + \mathbb{1}_G v(1 - u - v). \end{cases}$$

Clearly, constant steady states consist of $\{(\sigma, 1 - \sigma) : \sigma \in [0, 1]\}$. Linearizing about the steady state $(u^*, 0) = (1, 0)$ gives

$$\begin{cases} d_1 \Delta \psi_1 - \mathbb{1}_G \psi_1 - \mathbb{1}_G \psi_2 + \lambda \psi_1 = 0, \\ d_2 \Delta \psi_2 + \lambda \psi_2 = 0. \end{cases}$$

Obviously, $\lambda = 0$ is an eigenvalue with an eigenfuntion $(\psi_1, \psi_2) = (1, -1)$. The same argument applies to $(0, v^*) = (0, 1)$, showing this state also has a zero eigenvalue. □

Proof of Theorem 2.5.5. The proof is identical to the case when $c_1 = c_2$ and $d_1 < d_2$. More precisely, the result follows from the monotonicity of the eigenvalue $\mu_1(d, m_c)$ with respect to c. □

2.6 Numerical simulation

In Figure 2.2 we find a region plot showing the globally asymptotically stable steady state in the c_2-d_2 plane. Using MATLAB's `pdepe` function, we solve the time-dependent problem for the coupled system (u, v) and compute the L^1-norm of the solution, now close to a steady state after sufficient time has passed. We then compute separately the solution in the absence of a competitor, that is, the solutions $(\tilde{u}, 0)$ and $(0, \tilde{v})$ each corresponding to its scalar equation counterpart. We then plot a "*relative total abundance*", which compares the abundance of each population in the competitive system (u, v) relative to the total abundance in absence of a competitor given by the solutions $(\tilde{u}, 0)$ and $(0, \tilde{v})$.

In this example, we fix $d_1 = c_1 = 1$ for population u; the black vertical line denotes $c_1 = 1$. Note that since d_1, c_1 are held fixed, we need compute the total abundance at steady state for $(\tilde{u}, 0)$ only once! On the other hand, we must compute the total abundance at steady state of $(0, \tilde{v})$ for each fixed value in the (c_2, d_2) plane. The landscape is given by $\Omega = (0, 10)$, the habitat by $G = (0, 4) \cup (6, 10)$, and the degraded region by $B = (4, 6)$. The quantities $\underline{c}_2^*, \overline{c}_2^*$ are the quantities defined in Theorem 2.5.2. The subplot is a cross-section of the case when $d_2 = 10$. This figure can be found in [104].

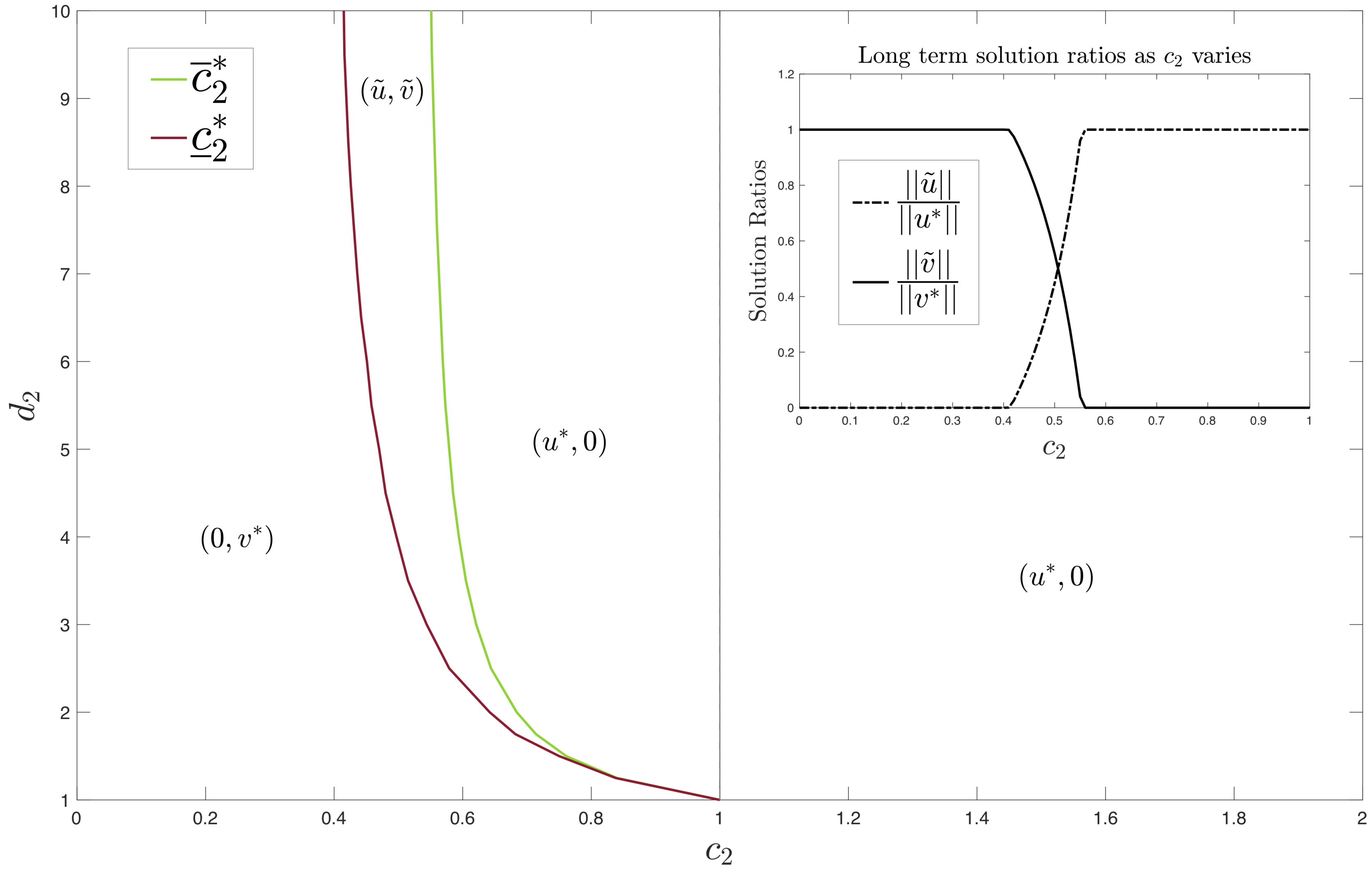


Figure 2.2: Numerical validation of Theorem 2.5.2.

2.7 Discussion

In this chapter we developed a habitat degradation model using reaction-diffusion equations. We consider both the scalar (single-species) case as well as a two-species competition case. Different from existing works, we include ecologically relevant components not commonly considered in tandem: a diffusive movement mechanism with explicit spatial heterogeneity and species-dependent habitat quality. Our main result, Theorem 2.5.2, highlights the importance of species-dependent habitat quality as a consideration. It is found that, for any degraded area B with positive Lebesgue measure, a sufficiently resilient species (e.g., $c_2 \ll 1$) will *always* displace the slower diffuser! This result is robust in that any size or shape for the region B facilitates this result. This is exemplified by the key thresholds $0 < \underline{c}_2^* < \overline{c}_2^* < c_1$, where $c_2 < \underline{c}_2^*$ ensures that population v always displaces population u, $c_2 > \overline{c}_2^*$ returns to the classical case where population u always displaces population v, and intermediate values of c_2 guarantee the global asymptotic stability of the coexistence steady state. Of course, the relative *size* of these thresholds in relation to 0 or c_1 certainly depend directly on the geometric properties of the region B. These quantities are of significant importance. First, they demonstrate explicitly that a resilience to environmental change can act as a viable evolutionary strategy. This is in contrast to classical results suggesting an evolution towards slow dispersal rates [28]. Of note is the potential for application across differing species, rather than merely across different phenotype expression within the same species as in the aforementioned reference. Moreover, these thresholds highlight the importance of considering species-specific traits. Typically, it is assumed in many works that sharing the same landscape or environment means that we can take the same function $m(x)$ to describe the spatially-dependent growth rates of two competing species. On the contrary, given that habitat itself is a species-specific concept, we need consider the existing landscape *and its relation to the needs of each competitor*. This is of further interest when considering questions of conservation, where the removal of existing habitat while maintaining some subset of said habitat may counter-intuitively lead to the displacement of the "stronger" competitor due to an unforeseen or disregarded resiliency of the "weaker" species. This also gives a mechanism by which invasive species can easily displace native species through a lack of natural mortality or an enhanced ability to occupy less resource-rich areas of the landscape.

To prove this main result, we describe completely the global dynamics of the scalar equation and establish useful existence-comparison results. Due to the lack of regularity of the environment (i.e., we have discontinuities along the boundary ∂B), we must appeal to notions of strong solutions. Fortunately, the regularity of the obtained solutions is sufficient to apply the theory of monotone flows.

Important in this analysis is the detailed study of the sign of some principal eigenvalues. These eigenvalues, corresponding to a linearization about 0 (and other steady states for the competition system), determine the local stability of the steady states. The framework developed here allows for a precise description of these principal eigenvalues. This extends some of the existing mathematical literature in an interesting way. In classical works studying two-species competition-diffusion models, it is assumed that the environmental heterogeneity is identical for each species. It is then found that the slower diffuser always wins, indicating an evolutionary selection pressure for slower dispersal rates [28]. However, this perspective assumes the *only difference between agents is the diffusion rate*. This is almost certainly quite rare in the natural world; more nuance is desirable. We extend this result, showing that slow diffusion is still beneficial to survival, but that resilience to environmental changes can also facilitate persistence. This offers an alternative strategy to slower rates of diffusion: higher rates of resilience in a modified habitat. In works such as [59], [60], [64], [81], similar descriptions of the global dynamics are established; however, they are somewhat limited in their ecological application due to the assumptions required for their results to hold. For example, in [59], [60], [64], the environmental heterogeneity must be non-negative. This setting is inadequate for the study of habitat loss and its effect on interacting populations. We extend this literature by establishing similar results for functions that may be negative in some regions. Furthermore, their results are established in an abstract setting: their conclusions follow from an assumption of the sign of a principal eigenvalue *a priori*! That is, the set of parameters for which coexistence or mutual exclusion is a possibility may be empty. This is concerning for ecological application, as we do not have an explicit understanding of how these principal eigenvalues behave. We extend such results by considering a configuration that can be studied in detail (indicator functions with 'good' or 'bad' regions only), giving explicit behaviour as it depends on parameters in the model, while also remaining general enough to be applied across a wide variety of species and environmental scenarios. Of significance is the fact that there is *always* a parameter window in which coexistence is guaranteed; the trade-off between dispersal rates and levels of resilience can promote biodiversity, at least from the point of view of this simplified analysis.

Of further interest is the behaviour of the critical values $\underline{c}_2^*$ and $\overline{c}_2^*$. Is it possible to increase the size of this window indefinitely? That is, can the parameter regime for which coexistence is guaranteed be made arbitrarily large? Can we obtain bounds above for $\overline{c}_2^*$ or below for $\underline{c}_2^*$? In describing either of these quantities, we gain information for the principal eigenvalue which tells us more information about whether a population may persist or be extirpated.

From our analysis, we also begin to observe some general heuristics when judging the impacts of habitat loss. In the case of habitat degradation, we have a necessary condition for population persistence: the total resources in the region G must be greater than $c\,|B|$. This indicates that we can first facilitate persistence by either improving habitat quality (decreasing the value of c), or by decreasing the size of the degraded region B. In practice, we can ideally reduce *both*.

There are limitations to the perspective. We make a big assumption on the nature of the movement of the organism. Diffusive movement is widely applicable, but is not universal [8], [94]. Different movement mechanisms, such as advection or spatially dependent diffusion, may be ecologically relevant in many cases and may alter the results established here. We also assume that competition (either intra- or inter-) occurs only in the good region G. We justified this earlier; it may be interesting to study the case when competition occurs across the entire landscape, even within the degraded region B. Unfortunately, our results rely on the convergence of the steady state $u^* \to 1^-$ as $c \to 0^+$, which no longer holds if the competition occurs across the entire domain. More precisely, this convergence result is what allows us to determine precisely the sign of all relevant principal eigenvalues. It is not immediately obvious how this will translate, and so we leave this question for future efforts.

Chapter 3

Habitat Destruction

In this chapter, we move towards a novel habitat destruction model under a similar framework. Continuing to take motivation from our introductory discussion, we use heavily Postulate One: *habitat degradation and habitat destruction lie on a spectrum.* We first discuss briefly some modelling context, noting that existing works discussed in Chapter 2 are also appropriate examples here; therefore we do not discuss other efforts in much more detail. In Section 3.2, we derive our habitat destruction model from some basic ecological principles. In Section 3.3, we introduce some further technical preliminaries necessary to study the destruction problem in detail. As in the degradation models, eigenvalue problems are a key tool for analysis; Section 3.4 introduces the relevant eigenvalue problems for this new setting, and also includes an important convergence result between the degradation eigenvalue problem and the destruction eigenvalue problem. We then study the scalar habitat destruction problem in Section 3.5. This includes well-posedness, comparison principles, and a complete description of the global dynamics, and a connection between the dynamics of the degradation problem and the dynamics of the destruction problem. Most importantly, we prove Theorem 3.5.10, which provides an analytical connection between our habitat degradation problem and the habitat destruction problem in an asymptotic limit. In Section 3.6, we analyze the two-species competition model in the destruction setting, and then prove another convergence result between the degradation and destruction systems. Section 3.7 includes some numerical demonstrations of these results. We conclude with a discussion of the broad impacts and insights of these results in Section 3.8.

3.1 Preface

Habitat destruction, as defined in Chapter 1, suggests that the habitat has been altered so dramatically that it can no longer sustain the species it once did. In contrast to mere degradation, destruction is the most extreme case: species cannot survive there at any level. While easier to identify in practice due to its drastic appearance, its effects are comparably drastic, and paradoxically may still take much time for a local species to feel the full effects. Therefore, following the model formulations of Chapter 2, we propose similar models that now feature regions of *truly destroyed* habitat. In this case, our destroyed regions fall squarely within *non-habitat*; a question of *quality* is no longer relevant. It is as bad as it can possibly be! This motivates our following derivation process.

3.2 Model derivation

We now propose a new model meant to capture habitat destruction. To this end, we appeal once again to postulate one: levels of degradation lie on a spectrum, with increasing degradation leading to destruction. If degradation is measured by some parameter, such as $c \geq 0$ in the habitat degradation model derived in Section 2.2, we logically ask the question: *what happens in the limit as* $c \to \infty$*?*. In a reasonable habitat degradation model, this limit should correspond to a habitat destruction model, at least in some sense.

We then try to intuit what problem might be solved in such a limit. Denote by $w_c(x,t)$ the solution to the scalar degradation problem (2.1). We make the following observations:

- $w_c(x,t) \geq 0$ in Q_T for all $c \geq 0$.
- $w_c(x,t)$ is monotonically decreasing in Q_T with respect to c.
- $w_c(x,t) \leq w_0(x,t)$ in Q_T for all $c \geq 0$.

The first fact follows from the maximum principle. The second fact will follow from a refinement of Lemma 2.4.2. The third fact follows from the second. It is therefore quite reasonable to assume that there is a well-defined limiting problem corresponding to the case when $c = +\infty$.

We then make a slight jump using a relatively simple observation. If we multiply the equation for w_c by w_c and integrate by parts, we have

$$\frac{d}{dt}\int_\Omega \tfrac{1}{2}w_c^2 = -d\int_\Omega |\nabla w_c|^2 + \int_G f(x,w_c)w_c - c\int_B w_c^2$$

Rearranging and integrating from 0 to T gives further that

$$c\iint_{B\times(0,T)} w_c^2 = \iint_{G\times(0,T)} f(x,w_c)w_c - d\iint_{Q_T} |\nabla w_c|^2 - \int_\Omega w_c(x,t)\Big|_0^T.$$

Therefore, dropping the negative terms and using the boundedness of w_c, we find that

$$\|w_c\|_{L^2(B\times(0,T))} \leq Mc^{-1/2}$$

for some $M > 0$ independent of c. Consequently, at least on the bounded interval $(0, T)$, our solution w_c vanishes in the region B as $c \to \infty$. Hence, whatever problem the limit solves, it should always be zero in the destroyed region B. We therefore formulate a potential habitat *destruction* problem as

$$\begin{cases} w_t = d\Delta w + f(x,w), & \text{in} \quad \Omega\setminus\overline{B}\times(0,\infty), \\ \frac{\partial w}{\partial \nu} = 0, & \text{on} \quad \partial\Omega\times(0,\infty), \\ w = 0, & \text{on} \quad \partial B\times(0,\infty). \end{cases} \tag{3.1}$$

In this way, the habitat destruction problem is described by a reaction-diffusion equation subject to homogeneous Neumann boundary data on the outer boundary $\partial\Omega$, but also features interior sub-region(s) with homogeneous Dirichlet boundary data along ∂B, that is, there is a hostile boundary within the available habitat Ω. Note that while intuitive, it is not immediately clear that this is the correct problem to study. Problem (3.1) will be our candidate for the limiting problem as $c \to \infty$ in problem (2.1).

In addition to studying connections between these scalar problems, we also want to investigate again the corresponding competition destruction system. The degradation competition system given by 2.2 has the following analogous competition destruction system:

$$\begin{cases} u_t = d_1\Delta u + f_1(x,u,v), & \text{in} \quad \Omega\setminus\overline{B}\times(0,T), \\ v_t = d_2\Delta v + f_2(x,u,v), & \text{in} \quad \Omega\setminus\overline{B}\times(0,T), \\ \frac{\partial u}{\partial\nu} = \frac{\partial v}{\partial\nu} = 0, & \text{on} \quad \partial\Omega\times(0,T), \\ u = v = 0, & \text{on} \quad \partial B\times(0,T). \end{cases} \tag{3.2}$$

One may consider general forms of the functions f_i with minimal changes to existing methods to study the global dynamics of this problem. However, since we also wish to provide concrete, analytical connections between these degradation and destruction problems, we take the prototypical Lotka-Volterra form of competition in a heterogeneous environment

$$f_1(x,u,v) = u(m(x) - u - v), \qquad f_2(x,u,v) = v(m(x) - u - v), \tag{3.3}$$

where $m \in C^\alpha(\overline{\Omega}\setminus B)$ for some $\alpha \in (0,1)$.

We now seek to connect problems (2.1) and (3.1), (2.2) and (3.2) as well as their respective steady states, through a limit as the level of degradation c in the region B becomes arbitrarily large.

From Chapter 2, we already understand that the global dynamics for such problems can be understood via the theory of monotone flows. This naturally led to a detailed study of some related eigenvalue problems. Thus, we have two tasks before discussing the time-dependent problem: first, we must develop the corresponding eigenvalue problems to (3.1), obtaining results similar to those found in Section 2.3. This will allow us to describe the global dynamics of problems (3.1) and (3.2), assuming that we have a reasonable solution process to work with. Second, if we want to produce an analytical connection between the degradation and destruction problems, it will prove very useful to first prove some convergence results between corresponding eigenvalues and eigenfunctions. These are the results we obtain in Section 3.4. Before we can tackle these, however, we first require some technical preliminaries concerning assumptions and appropriate function spaces to work in.

3.3 Technical preliminaries

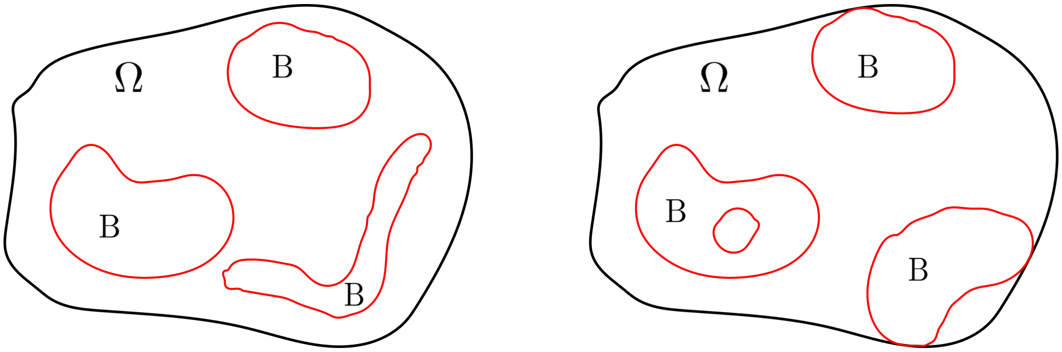
Assumptions

We begin the assumptions for the bad habitat B and the growth rate function f appearing in (2.1). In contrast to the habitat degradation problem, we now require some technical conditions on the geometry of the set B. This is not a significant restriction as we may approximate an open set B by a smooth set B' such that the sets differ by an arbitrarily small amount (in symmetric difference, for example). The assumption for the set B is the following.

Assumption 3.3.1. *$B \Subset \Omega$ is an open subset with smooth boundary, comprised of finitely many disjoint components, each of which are themselves simply connected.*

Biologically, such a condition is in correspondence with the "cookie cutter" interpretation of habitat loss [98], [99], which suggests that habitat loss is "*like a cookie cutter stamping out poorly mixed dough*". Mathematically, this assumption ensures that the inner boundary ∂B does not touch the outer boundary $\partial\Omega$, and more importantly ensures that B does not "split" the domain Ω into disjoint components in the case of spatial dimension > 1. In two dimensions, for example, an annulus is not an allowable configuration in our setting; despite this, it is worth noting that in such a case where the domain is split, one may consider each separate component individually. In the case of the annulus, one would treat the outer region as we do in the current work, while the inner region is merely a circle with hostile boundary, which can be treated through classical methods. Readers may also note that this restriction is used in the destruction case, but such a restriction is not necessary in the case of a fixed level of degradation. Some sample configurations, both allowable and not, can be found in Figure 3.1.

The assumptions on the growth rate $f : (\overline{\Omega}\backslash B) \times [0, \infty) \to \mathbb{R}$ will remain the same as in assumptions 2.2.1 and (2.2.3)) but now holding only in the set $\Omega \setminus \overline{B}$. Unfortunately, an assumption of mere subhomogeneity is not sufficient to obtain uniform estimates in time. Hence, we require the stronger condition of concavity, but we note the places where subhomogeneity is sufficient. Similar to the scalar degradation case, we assume



(a) Allowable (b) Not Allowable

Figure 3.1: A visual depiction of allowable and not allowable configurations of the region B. In (a), all regions are simply connected, have regular enough boundary, and there is distance between the edges of B and the edge of Ω. In (b), one region features a hole and is therefore not acceptable; another touches the boundary of Ω at exactly two points, essentially cutting off a chunk of Ω which is also not allowed. The third touches the edge of Ω at a single point; For technical reasons, we cannot allow this either.

some standard regularity requirements for the reaction term in each argument. The positivity of $f'(\cdot, 0)$ somewhere in $\Omega \setminus \overline{B}$ is necessary to ensure that a positive steady state may exist; without this condition, the only steady state will be the trivial one. Paired with the regularity of the domains Ω and B, we also have regularity up to the boundary $\partial\Omega$ and up to ∂B for problem (3.1). The concavity condition ensures that the flow induced by the differential equation is strongly monotone, and ensures the uniqueness of the positive steady state, whenever it exists. More importantly, at least in the current context, we require a strict concavity condition to obtain convergence from the time dependent problem to the corresponding steady state, uniform in the variable c. Some prototypical examples of functions satisfying these hypotheses can be found in Chapter 2.

Assumptions 3.3.1, 2.2.1, and 2.2.3 are always assumed in what follows whenever B and f are involved.

Some new function spaces

Despite the amount of function spaces introduced in Section 1.2, we require yet further function spaces to study these new problems. In the remainder of this section, we introduce these function spaces over the domain $\Omega \setminus \overline{B}$ and their relation to similar spaces over the entire domain Ω. We remind readers that we denote by $\partial/\partial\nu$ the unit outward facing normal vector along either $\partial\Omega$ or, in this chapter, ∂B. To be clear: the outward facing normal vector on ∂B is outward facing from within $\Omega \setminus B$; in other words, the *inner* facing normal vector from within the set B.

We denote by $C^1_B(\Omega)$ the space

$$C^1_B(\Omega) := \left\{ v \in C^1(\overline{\Omega} \setminus B) : v|_{\partial B} = 0 \right\},$$

and consider $H^1_B(\Omega)$ to be the closure of the space $C^1_B(\Omega)$ with respect to the usual H^1-norm over $\Omega \setminus \overline{B}$. In this way, $H^1_B(\Omega)$ can be thought of as similar to the space $H^1_0(\Omega)$, with functions now vanishing along ∂B in the trace sense. More precisely, it can be checked that

$$H^1_B(\Omega) = \left\{ u \in H^1(\Omega \setminus \overline{B}) : \mathbf{T}u = 0 \right\},$$

where $\mathbf{T}$ denotes the trace operator extending the notion of restricting a function on $\Omega \setminus B$ to ∂B. This follows from some of the standard arguments used in, e.g., [123, Ch. 1.5.2], which gives some equivalencies between functions that vanish in the sense of the trace and the space $H^1_0(\Omega)$.

For any $u \in C^1_B(\Omega)$ or $H^1_B(\Omega)$, we always identify it with its zero extension into B. If $u \in H^1_B(\Omega) \cap C(\overline{\Omega \setminus \overline{B}})$, then u is continuous over all of Ω. Furthermore, if $u \in H^1_B(\Omega)$, then the resulting function belongs to $H^1(\Omega)$, where its weak derivative identical in $\Omega \setminus B$ and identically zero in B. This follows from problem 18 in [31, Ch. 5].

Conversely, if $u \in H^1(\Omega)$ with $u = 0$ a.e. in B, then $u|_\Omega \in H^1_B(\Omega)$. Therefore, we identify $H^1_B(\Omega)$ with $\{u \in H^1(\Omega) : u = 0 \text{ a.e. in } B\}$, and simply write

$$H^1_B(\Omega) = \left\{ u \in H^1(\Omega) : u = 0 \text{ a.e. in } B \right\}.$$

We wish to emphasize that these results crucially rely on the smoothness of ∂B and the fact that $B \Subset \Omega$.

Recall that for $T > 0$, we write $Q_T := \Omega \times (0, T)$. Similarly, we write $Q_{B,T} := (\Omega \setminus \overline{B}) \times (0, T)$, and define $H^1_B(Q_T)$ to the closure of $\{v \in C^1((\Omega \setminus B) \times [0, T]) : v(\partial B \times [0, T]) = 0\}$

under the usual H^1-norm over $(\Omega \setminus \overline{B}) \times (0,T)$. Similarly, there holds

$$H^1_B(Q_T) = \left\{u \in H^1(Q_{B,T}) : \mathbf{T}u = 0\right\} = \left\{u \in H^1(Q_T) : u = 0 \text{ a.e. in } B \times (0,T)\right\}.$$

We have already introduced the spaces $L^2(Q_T)$ and $H^1(Q_T)$ in Section 1.2. We similarly consider $H^1_B(Q_T)$ to be the completion of the set of all smooth functions v vanishing in a neighbourhood of $\partial B \times (0,T)$ with respect to the $H^1(Q_T)$ norm. Similar to the previous discussion, we have the following observation: if $v \in H^1(Q_T)$ is such that $v \equiv 0$ in $B \times (0,T)$, then $v \in H^1_B(Q_T)$. This result follows from the same arguments made in the purely spatial case, see [123, Ch. 1.5.3]. In particular, when ∂B is smooth any function belonging to $H^1(Q_T)$ has a trace on $\partial B \times (0,T)$ (e.g. [123, Theorem 1.5.3])). Then, one may modify the proof of [123, Theorem 1.5.4] to obtain the desired result.

3.4 Eigenvalue problems in domains with holes

3.4.1 The first problem (reprise)

Motivated by the form of problem (3.1), we formulate the associated *destruction* eigenvalue problem as follows:

$$\begin{cases} \Delta\psi + \lambda m\psi = 0, & \text{in} \quad \Omega \setminus \overline{B}, \\ \frac{\partial \psi}{\partial \nu} = 0, & \text{on} \quad \partial\Omega, \\ \psi = 0, & \text{on} \quad \partial B, \end{cases} \tag{3.4}$$

where $m \in L^\infty(\Omega \setminus B)$. Different from problem (2.4), we note that 0 is NOT a principal eigenvalue of (3.4) due to the zero Dirichlet boundary condition on ∂B, which actually causes some essential differences between (2.4) and (3.4). Also different from problem (2.4), there is always a principal eigenvalue. If problem (3.4) is to be connected to problem (2.4) through a limit, we observe that for any set satisfying $|B| > 0$ we may always choose $c \gg 1$ sufficiently large so that

$$\int_\Omega (\mathbb{1}_G m - c\mathbb{1}_B) = -c\,|B| + \int_G m < 0.$$

By Proposition 2.3.1, we therefore have the existence of a value $c^* > 0$ such that a principal eigenvalue $\lambda_1(c)$ exists for every $c \geq c^*$. Consequently, it seems reasonable to expect the following result, an analogue of problem (2.4) for the destruction case.

Proposition 3.4.1. *Suppose* $m \in L^\infty(\Omega \setminus \overline{B})$ *is positive on a set of positive Lebesgue measure. Then,* (3.4) *admits a unique positive principal eigenvalue* $\lambda_1(m, B)$*, which is simple and given by*

$$\lambda_1(m,B) = \inf_{\psi \in H^1_B(\Omega)} \left\{ \frac{\int_{\Omega\setminus\overline{B}} |\nabla\psi|^2}{\int_{\Omega\setminus\overline{B}} m\psi^2} : \int_{\Omega\setminus\overline{B}} m\psi^2 > 0 \right\}.$$

Moreover, $\lambda_1(m, B)$ *is monotone in the following sense:*

(i) *for any* B_1, B_2 *such that* $B_1 \subset B_2$*,* $\lambda_1(m, B_1) \le \lambda_1(m, B_2)$ *with strict inequality whenever* $B_2 \setminus \overline{B_1}$ *has positive measure;*

(ii) *for any* $m_1, m_2 \in L^\infty(\Omega \setminus B)$ *satisfying* $m_1 \le m_2$*,* $\lambda_1(m_1, B) \ge \lambda_1(m_2, B)$ *with strict inequality whenever* $m_1 \not\equiv m_2$*.*

Such existence results can be obtained from the more general abstract framework found in [121, Chapter 3], for example. A direct proof is provided here for our case, which mimics closely the case of homogeneous Dirichlet boundary conditions along $\partial\Omega$, see [7].

Proof of Theorem 3.4.1. First, recall that the norms $\|\nabla u\|_{L^2(\Omega\setminus\overline{B})}$ and $\|u\|_{H^1(\Omega\setminus\overline{B})}$ are equivalent by Poincaré's inequality. We now justify an application of Proposition 1.2.1. For any $u, v \in H^1_B(\Omega)$ fixed, we define the symmetric quadratic form $(u, v) \to \int_{\Omega\setminus\overline{B}} muv$ on the space $H^1_B(\Omega) \times H^1_B(\Omega)$. The Riesz representation theorem [31, Ch. D.3] guarantees the existence of an operator T such that $\langle Tu, v\rangle = (u, v)$, where $\langle\cdot,\cdot\rangle$ denotes the inner product on $H^1_B(\Omega)$ given by

$$\langle u, v\rangle = \int_{\Omega\setminus\overline{B}} \nabla u \nabla v.$$

Furthermore, it is easy to verify that T is symmetric since $(u, v) \mapsto \int_{\Omega\setminus\overline{B}} muv$ is symmetric. Since m is bounded, Hölder's inequality shows that T is bounded:

$$|\langle Tu, v\rangle| = \int_{\Omega\setminus\overline{B}} muv \le \|m\|_{L^\infty(\Omega\setminus\overline{B})} \|u\|_{L^2(\Omega\setminus\overline{B})} \|v\|_{L^2(\Omega\setminus\overline{B})} .$$

We now show that the operator T is compact. Suppose $\{u_n\}$ is a bounded sequence in $H^1_B(\Omega)$. Since $H^1_B(\Omega)$ is Hilbert, the sequence converges weakly in $H^1_B(\Omega)$ to some element $u \in H^1_B(\Omega)$, i.e. $u_n \rightharpoonup u$ in $H^1_B(\Omega)$. Since the space $H^1_B(\Omega)$ embeds compactly in $L^2_B(\Omega)$, we have that $u_n \to u$ strongly in $L^2_B(\Omega)$. The Cauchy-Schwarz inequality then implies that $Tu_n \to Tu$ in $H^1_B(\Omega)$:

$$\begin{aligned}
\|Tu_n - Tu\|^2_{H^1(\Omega\setminus\overline{B})} &= \langle Tu_n - Tu, Tu_n - Tu\rangle \\
&= \int_{\Omega\setminus\overline{B}} m(u_n - u)(Tu_n - Tu) \\
&\leq \|m\|_{L^\infty(\Omega\setminus\overline{B})} \|u_n - u\|_{L^2(\Omega\setminus\overline{B})} \|Tu_n - Tu\|_{L^2(\Omega\setminus B)} \\
&\leq C\,\|m\|_{L^\infty(\Omega\setminus B)} \|u_n - u\|_{L^2(\Omega\setminus\overline{B})} \|Tu_n - Tu\|_{H^1(\Omega\setminus\overline{B})} .
\end{aligned}$$

Hence, T is compact. Consequently, under the assumption that $\Omega' := \{x \in \Omega\setminus\overline{B} : m(x) > 0\}$ is a set of positive measure, we may choose $\tilde{u} \in H^1_B(\Omega)$ to be a function which is positive on Ω' and zero elsewhere so that

$$\langle T\tilde{u}, \tilde{u}\rangle = \int_{\Omega\setminus\overline{B}} m(x)\tilde{u}^2 = \int_{\Omega'} m(x)\tilde{u}^2 > 0.$$

Proposition 1.2.1 then ensures that there exists a principal eigenvalue $\eta_1 > 0$ and corresponding eigenfuntion ψ_1 for T such that $T\psi_1 = \eta_1\psi_1$. We then assert that ψ_1 can be chosen to be strictly positive in $\overline{\Omega}\setminus B$. Indeed, the usual bootstrapping argument allows one to show that $\psi_1 \in L^p(\Omega\setminus B)$ for any $p \geq 1$, and so the Sobolev embedding ensures that in fact $\psi_1 \in C^{1+\alpha}(\overline{\Omega}\setminus B)$ for any $\alpha \in (0,1)$. To see this, notice that since $m\psi_1 \in L^2(\Omega\setminus\overline{B})$, $\psi_1 \in W^{2,2}(\Omega\setminus\overline{B})$ by the L^p-theory of elliptic equations, Theorem 1.2.29. Using the Sobolev embedding Theorem 1.2.3, we have that $\psi_1 \in L^q(\Omega\setminus\overline{B})$ for some $q > 2$. We then repeat the process, concluding that $\psi_1 \in W^{2,q}(\Omega\setminus\overline{B})$. Eventually we conclude that $\psi_1 \in C^\alpha(\overline{\Omega\setminus\overline{B}})$ and so ψ_1 is bounded and belongs to $W^{2,p}(\Omega\setminus\overline{B})$ for every $p \geq 1$.

Then, ψ_1 is a strong solution solving problem 3.4 for $\lambda = \eta_1^{-1}$. We then consider the positive and negative parts $\psi_1^+ = \max\{\psi_1, 0\}$ and $\psi_1^- = \max\{-\psi_1, 0\}$. Each belongs to $H^1_B(\Omega)$ and are thus both weak solutions to the same problem. Using the same notation for $m^{+/-}$, we may then write

$$-\Delta\psi_1^+ + m^-\psi_1^+ = \lambda_1 m^+\psi_1^+ \geq 0,$$

and so the strong maximum principle and the regularity of $\partial\Omega$, ∂B ensure that $\psi_1^{+/-}$ are sign definite or constant. Due to the boundary condition along ∂B, the latter is impossible and so we choose $\psi_1 = \psi_1^+$ to be our eigenfunction. Further, $\partial\psi_1/\partial\nu < 0$ along $\partial\Omega$.

Uniqueness follows immediately. Indeed, suppose ψ_1, ψ_2 are eigenfunctions corresponding to η_1^{-1}. Then, for each $\beta \in \mathbb{R}$, $\psi_1 + \beta\psi_2$ is also an eigenfunction of definite sign. We may then choose β so that

$$\int_{\Omega\setminus B} (\psi_1 + \beta\psi_2) = 0,$$

in which case $\psi_1 + \beta\psi_2 = 0$, and hence ψ_1 and ψ_2 are linearly dependent. The first part of the proof is completed by setting $\lambda_1(m, B) = 1/\eta_1$. A standard scaling argument allows one to deduce the variational formulation as presented in the statement of the theorem, following directly from Proposition 1.2.1.

With the variational formulation at hand, the monotonicity of $\lambda_1(m, B)$ with respect to subsets follows immediately once one realizes that $\psi \in H^1_{B_2}(\Omega) \Rightarrow \psi \in H^1_{B_1}(\Omega)$ whenever $B_2 \subset B_1$, and so a simple choice in test function yields the desired result: in the variational formulation of $\lambda_1(m, B_1)$, choose the principal eigenfunction corresponding to $\lambda_1(m, B_2)$ as your test function.

Similarly, the variational formulation allows one to conclude that whenever $m_1 \leq m_2$, the eigenfunction corresponding to m_2 is a valid test function for the eigenvalue corresponding to m_1. The strict inequality follows from the uniqueness of the eigenfunction. This completes the proof. □

3.4.2 The second problem (reprise)

Similar to Section 2.3, we formulate the associated destruction eigenvalue problem as

$$\begin{cases} d\Delta\phi + m\phi + \mu\phi = 0, & \text{in} \quad \Omega \setminus \overline{B}, \\ \frac{\partial\phi}{\partial\nu} = 0, & \text{on} \quad \partial\Omega, \\ \phi = 0, & \text{on} \quad \partial B, \end{cases} \tag{3.5}$$

where $m \in L^\infty(\Omega \setminus \overline{B})$. This can be viewed as the destruction analogue to problem (2.5). We again recall the previous degradation result, which characterized the principal eigenvalue depending directly on the average of the environmental heterogeneity. Since we are taking $c \to \infty$, we remove the possibility of the principal eigenvalue to problem

(3.5) to be negative for *all* $d > 0$. Instead, we have a threshold depending on d where the sign may change; this is comparable to the standard Dirichlet eigenvalue problem. We have the following result.

Proposition 3.4.2. *Problem* (3.5) *admits a principal eigenvalue* $\mu_1(d, m, B)$. *It is simple and given by*

$$\mu_1(d, m, B) = \inf_{\phi \in H^1_B(\Omega)} \left\{ \int_{\Omega \setminus \overline{B}} \left(d \left| \nabla \phi \right|^2 - m\phi^2 \right) \ : \ \int_{\Omega \setminus \overline{B}} \phi^2 = 1 \right\}.$$

Moreover, $\mu_1(d, m, B)$ *enjoys the following properties:*

(i) $d \mapsto \mu_1(d, m, B)$ *is strictly increasing on* $(0, \infty)$; *in fact, it is strictly concave on* $(0, \infty)$.

(ii) $\mu_1(d, m_2, B) < \mu_1(d, m_1, B)$ *if* $m_2 \gneqq m_1$.

(iii) $m \leq 0 \Rightarrow \mu_1(d, m, B) > 0$ *for all* $d > 0$.

(iv) $m > 0$ *on some nontrivial subset* $\Rightarrow \begin{cases} \mu_1(d, m, B) < 0, & \textit{if} \quad d < \frac{1}{\lambda_1(m,B)}, \\ \mu_1(d, m, B) = 0, & \textit{if} \quad d = \frac{1}{\lambda_1(m,B)}, \\ \mu_1(d, m, B) > 0, & \textit{if} \quad d > \frac{1}{\lambda_1(m,B)}. \end{cases}$

(v) *If* $m_n \to m$ *in* $C(\overline{\Omega} \setminus B)$, *then* $\mu_1(d, m_n, B) \to \mu_1(d, m, B)$ *as* $n \to \infty$.

Proof of Theorem 3.4.2. We take for granted the variational formulation of the principal eigenvalue, which follows from the theory of symmetric, compact operators on Hilbert spaces. We focus instead on the properties of $\mu_1(d, m, B)$ as it depends on the rate of diffusion, the environmental heterogeneity, and the set B.

Fix m and B. If $0 < d_1, d_2$, the variational form of μ_1 allows us to write

$$\alpha\mu_1(d_1, m, B) + (1 - \alpha)\mu_1(d_2, m, B) \leq \int_{\Omega \setminus \overline{B}} (\alpha d_1 + (1 - \alpha)d_2) \left| \nabla \psi \right|^2 - m\psi^2,$$

for any $\alpha \in (0, 1)$ and any $\psi \in H^1_B(\Omega)$. Since ψ was arbitrary, we take the infimum to conclude that

$$\alpha\mu_1(d_1, m, B) + (1 - \alpha)\mu_1(d_2, m, B) \leq \mu_1(\alpha d_1 + (1 - \alpha)d_2, m, B),$$

where strict inequality follows from the uniqueness of the eigenfunction. This proves (i).

Point (ii) follows from the same reasoning, using the variational formulation and choosing the correct test function to show that $\mu_1(d, m_2, B) \leq \mu_1(d, m_1, B)$. Strict inequality follows from the uniqueness of the eigenfunction.

For $m \leq 0$, the positivity of the eigenvalue follows immediately from the variational form, proving point (iii).

Suppose now that $m > 0$ on some nontrivial subset. By Theorem 3.4.1 it follows that the principal eigenvalue $\lambda_1(m, B) > 0$ exists. Choosing $\phi_1 \in H^1_B(\Omega)$ the corresponding eigenfunction, the variational form of $\mu_1(d, m, B)$ gives us that

$$\mu_1(d, m, B) \leq (d\lambda_1 - 1) \int_{\Omega \setminus \overline{B}} m\phi_1^2.$$

Since $\int_{\Omega \setminus \overline{B}} m\phi_1^2 > 0$, we see that $\mu_1(d, m, B) \leq 0$ whenever $d\lambda_1 - 1 \leq 0$. This proves the first part of (iv).

Similarly, we choose $\psi_1 \in H^1_B(\Omega)$, the principal eigenfunction to $\mu_1(d, m, B)$, in the variational form of $\lambda_1(m, B)$ to find that

$$\lambda_1(m, B) \leq \frac{\mu_1(d, m, B) + 1}{d}.$$

Choosing $d = \lambda_1^{-1}(m, B)$ and combining with the previous result yields $\mu_1(d, m, B) = 0 \iff \lambda_1^{-1}(m, B) = d$, proving the second part of (iv). The third part follows immediately, completing the proof of part (iv).

Finally, if $m_n \to m$ in $C(\overline{\Omega} \setminus B)$, there exists a sequence $\{\varepsilon_n\}_{n \in \mathbb{N}}$ so that $-\varepsilon_n \leq m - m_n \leq \varepsilon_n$ for each n, and $\varepsilon_n \searrow 0$ as $n \to \infty$. Then, using the fact that $\mu_1(d, m \pm \varepsilon, B) = \mu_1(d, m, B) \mp \varepsilon$, we find that $|\mu_1(d, m, B) - \mu_1(d, m_n, B)| \leq \varepsilon_n$. Sending $n \to \infty$ yields (v), completing the proof. $\square$

3.4.3 Connections with Section 2.3

Now that we have the degradation and destruction eigenvalue problems formulated and some of their properties described, we are ready to prove rigorously some convergence results between these sets of problems.

Denote by $\lambda_{1,c} := \lambda_1(m_c)$ the principal eigenvalue to problem (2.4) with $m := m_c = \mathbb{1}_G m(x) - c\mathbb{1}_B$. Denote by $\psi_{1,c}$ the corresponding eigenfunction for each $c \geq 0$ fixed. Here, $m \in L(\Omega \backslash B)$ can be considered a bounded function over all of Ω via an extension by zero in B. Denote by $\lambda_{1,\infty} := \lambda_1(m, B)$ the principal eigenvalue to problem (3.4) and by $\psi_{1,\infty}$ its corresponding eigenfunction. The following result establishes a connection between these eigenpairs.

Theorem 3.4.1. *The following hold.*

(i) *There exists a unique $c_* > 0$ such that the function $c \mapsto \lambda_{1,c}$ is strictly increasing on (c_*, ∞), and $\lim_{c\to\infty} \lambda_{1,c} = \lambda_{1,\infty}$.*

(ii) $\lim_{c\to\infty} \psi_{1,c} = \psi_{1,\infty}$ *in $H^1(\Omega)$ under the normalization $\int_\Omega m_c \psi_{1,c}^2 = \int_{\Omega\backslash B} m\psi_{1,\infty}^2 = 1$.*

Proof of Theorem 3.4.1. Since the proof is almost identical to the proof of Theorem 3.4.2, and arguably a bit easier, we outline only the key steps. First, it is easy to deduce that $\lambda_{1,c}$ is strictly increasing and bounded above by $\lambda_{1,\infty}$. As a result, its limit exists and is given by the supremum, denoted by λ_∞. Then, we find that $\psi_{1,c}$ is uniformly bounded in $H^1(\Omega)$ and thus has a convergent subsequence, weakly in $H^1(\Omega)$ and strongly in $L^2(\Omega)$. Denote this by ψ_∞. Furthermore, $\psi_{1,c} \to 0$ a.e. in B, and so the candidate function $\psi_\infty \in H^1_B(\Omega)$ as argued previously. We may then show that $\lambda_{1,\infty} \leq \lambda_\infty$ by the weak lower semicontinuity of the norm. This implies that $\nabla\psi_{1,c} \to \nabla\psi_\infty$ in norm, and hence the convergence is in fact strong. Uniqueness of the eigenfunction allows one to conclude that $\psi_\infty = \psi_{1,\infty}$, and the proof is complete. □

Our second result, while similar to Theorem 3.4.1, is of more consequence in an ecological sense. This result establishes a connection between the principal eigenpairs of (2.5) and (3.5) in the limit as $c \to \infty$, which corresponds directly to a linearization of the scalar problem. Denote by $\mu_{1,c} := \mu_1(d, m)$ the principal eigenvalue to problem 2.5 with $m := m_c(x)$ as previously defined. Denote by $\phi_{1,c}$ its corresponding eigenfunction. Denote by $\mu_{1,\infty} := \mu_1(d, m, B)$ the principal eigenvalue to problem (3.5). We prove the following.

Theorem 3.4.2. *The following hold.*

(1) *The function $c \mapsto \mu_{1,c}$ is strictly increasing on* $(0,\infty)$, *and* $\lim_{c\to\infty} \mu_{1,c} = \mu_{1,\infty}$. *In fact, $\mu_{1,c}$ is strictly concave on* $(0,\infty)$.

(2) $\lim_{c\to\infty} \phi_{1,c} = \phi_{1,\infty}$ *in* $H^1(\Omega)$ *under the normalization* $\|\phi_{1,c}\|_{L^2(\Omega)} = \|\phi_{1,\infty}\|_{L^2(\Omega\setminus\overline{B})} = 1$.

Proof of Theorem 3.4.2. Since $m_{c_1} \geq m_{c_2}$ for $c_1 \leq c_2$, Theorem 2.3.2 (iv) guarantees that $\mu_{1,c_1} \geq \mu_{1,c_2}$ with strict inequality whenever $c_1 < c_2$. This shows $\mu_{1,c}$ is increasing. Then, we compute directly via the variational form to obtain for any $\alpha \in (0,1)$

$$\alpha\mu_{1,c_1} + (1-\alpha)\mu_{1,c_2} \leq \int_\Omega \left(d\left|\nabla\psi\right|^2 - m_{(1-\alpha)c_1+\alpha c_2}\psi^2\right)$$

for any $\psi \in H^1(\Omega)$ satisfying $\|\psi\|_{L^2(\Omega)} = 1$. Taking the infimum over functions $\psi \in H^1(\Omega)$ and noting again the uniqueness of the principal eigenvalue, we find that $\mu_{1,c}$ is strictly concave with respect to c.

Since $\phi_{1,\infty} \in H^1_B(\Omega)$, $\phi_{1,\infty} \in H^1(\Omega)$ by zero extension in B. It follows from the variational form (2.6) and the normalization $\int_\Omega \phi_{1,\infty}^2 = 1$ that

$$\mu_{1,c} \leq \int_\Omega \left(d\left|\nabla\phi_{1,\infty}\right|^2 - m_c\phi_{1,\infty}^2\right) = \int_{\Omega\setminus\overline{B}} \left(d\left|\nabla\phi_{1,\infty}\right|^2 - m\phi_{1,\infty}^2\right) = \mu_{1,\infty},$$

where the second equality is a result of the eigen-equation satisfied by $\mu_{1,\infty}$ and $\phi_{1,\infty}$. Thus, $\mu_{1,c}$ is strictly increasing, strictly concave and uniformly bounded by $\mu_{1,\infty}$. Hence, a unique $\mu_\infty := \lim_{c\to\infty}\mu_{1,c}$ exists and is finite. It is clear that we must have $\mu_\infty \leq \mu_{1,\infty}$.

From the eigen-equation satisfied by $\mu_{1,c}$ and $\phi_{1,c}$ (or (2.6) with the understanding that the infimum is attained at $\phi_{1,c}$),

$$d\int_\Omega \left|\nabla\phi_{1,c}\right|^2 = \mu_{1,c} + \int_\Omega m_c\phi_{1,c}^2 \leq \mu_\infty + \|m\|_{L^\infty(\Omega\setminus\overline{B})},$$

where we have thrown away the negative term and used the normalization $\int_\Omega \phi_{1,c}^2 = 1$. Hence, $\{\phi_{1,c}\}_{c\geq 0}$ is uniformly bounded in $H^1(\Omega)$. Consequently, there exists a subsequence (still denoted by $\phi_{1,c}$) and some $\phi_\infty \in H^1(\Omega)$ such that

$$\lim_{c\to\infty}\phi_{1,c} = \phi_\infty \quad \text{weakly in } H^1(\Omega) \quad \text{and} \quad \text{strongly in } L^2(\Omega). \tag{3.6}$$

Notice also that

$$c\int_B \phi_{1,c}^2 = \mu_{1,c} + \int_{\Omega\setminus\overline{B}} m\phi_{1,c}^2 - d\int_\Omega |\nabla\phi_{1,c}|^2 \le \mu_\infty + \|m\|_{L^\infty(\Omega\setminus\overline{B})},$$

leading to $\int_B \phi_{1,c}^2 \le \frac{1}{c}\left(\mu_\infty + \|m\|_{L^\infty(\Omega\setminus\overline{B})}\right) \to 0$ as $c \to \infty$. This together with the strong convergence in (3.6) implies $\int_B \phi_{1,\infty}^2 = 0$. Hence, $\phi_\infty = 0$ a.e. in B, and so, $\phi_\infty \in H^1_B(\Omega)$ by the discussion in Section 3.3. Furthermore, since $\int_\Omega \phi_{1,c}^2 = 1$, the strong convergence in (3.6) implies that $\int_\Omega \phi_\infty^2 = 1$. Hence, ϕ_∞ is nonzero and is a valid test function in the variational characterization of $\mu_{1,\infty}$.

We now show that $\mu_{1,\infty} \le \mu_\infty$. Since $\mu_{1,\infty}$ has the variational characterization given in Proposition 2.3.2, we find

$$\mu_{1,\infty} = \inf_{\phi\in H^1_B(\Omega)} \left\{ \int_{\Omega\setminus\overline{B}} \left(d\,|\nabla\phi|^2 - m\phi^2\right) \;:\; \int_{\Omega\setminus\overline{B}} \phi^2 = 1 \right\}.$$

This together with the weak lower semicontinuity of the norm $\|\cdot\|_{L^2(\Omega)}$ and (3.6) leads to

$$\begin{aligned}
\mu_{1,\infty} &\le \int_{\Omega\setminus\overline{B}} d\,|\nabla\phi_\infty|^2 - \int_{\Omega\setminus\overline{B}} m\phi_\infty^2 \\
&= \int_\Omega d\,|\nabla\phi_\infty|^2 - \int_\Omega m_c\phi_\infty^2 \\
&\le \liminf_{c\to\infty} \int_\Omega d\,|\nabla\phi_{1,c}|^2 - \lim_{c\to\infty}\int_\Omega m_c\phi_{1,c}^2 = \liminf_{c\to\infty} \mu_{1,c} = \mu_\infty.
\end{aligned}$$

Hence,

$$\mu_\infty = \lim_{c\to\infty} \mu_{1,c} = \mu_{1,\infty}. \tag{3.7}$$

In particular, this implies that ϕ_∞ solves the same eigenvalue problem as $\phi_{1,\infty}$, and hence, $\phi_\infty = \phi_{1,\infty}$ by the uniqueness of the eigenfunction and the normalization.

It remains to show $\lim_{c\to\infty} \nabla\phi_{1,c} = \nabla\phi_\infty$ in $L^2(\Omega)$ so that $\lim_{c\to\infty}\phi_{1,c} = \phi_\infty$ in $H^1(\Omega)$. Notice that

$$\begin{aligned}
d\int_\Omega \left(|\nabla\phi_{1,c}|^2 - |\nabla\phi_\infty|^2\right) &= \mu_{1,c} - \mu_{1,\infty} + \int_{\Omega\setminus\overline{B}} m(\phi_{1,c}^2 - \phi_\infty^2) - c\int_B \phi_{1,c}^2 \\
&\le \mu_{1,c} - \mu_{1,\infty} + \int_{\Omega\setminus\overline{B}} m(\phi_{1,c}^2 - \phi_\infty^2).
\end{aligned}$$

Letting $c \to \infty$ in the above inequality, we see from (3.7) and the strong convergence in (3.6) that $\limsup_{c\to\infty} \int_\Omega |\nabla \phi_{1,c}|^2 \le \int_\Omega |\nabla \phi_\infty|^2$. As $\liminf_{c\to\infty} \int_\Omega |\nabla \phi_{1,c}|^2 \ge \int_\Omega |\nabla \phi_\infty|^2$ due to the weak lower semicontinuity of the norm $\|\cdot\|_{L^2(\Omega)}$ and the weak convergence in (3.6), we find $\lim_{c\to\infty} \int_\Omega |\nabla \phi_{1,c}|^2 = \int_\Omega |\nabla \phi_\infty|^2$, which together with the weak convergence in (3.6) yields $\lim_{c\to\infty} \nabla \phi_{1,c} = \nabla \phi_{1,\infty}$ in $L^2(\Omega)$ (i.e., weak convergence plus convergence in norm implies strong convergence in a Hilbert space). This completes the proof. $\square$

Uniform upper and lower bounds of principal eigenfunctions

These convergence results, while essential to the study of the degradation and destruction models, are not sufficient on their own. While we have solutions belonging to $H^1(\Omega)$ and $H^1(\Omega \setminus \overline{B})$, we seek a stronger result, namely some uniform L^∞-bounds on the eigenfunctions with respect to c.

Denote by $\mu_{1,c} := \mu_1(d, \mathbb{1}_G m - c\mathbb{1}_B)$ the principal eigenvalue with eigenfunction ϕ_c solving problem (3.5), normalized so that $\|\phi_c\|_{L^2(\Omega)} = 1$. We prove the following technical lemmas which give some uniform boundedness estimates from above and below on ϕ_c with respect to $c \gg 1$.

Lemma 3.4.1. *Given any subset $K \Subset \overline{\Omega} \setminus \overline{B}$, there holds*

$$0 < \inf_{c\gg 1} \inf_K \phi_c \le \sup_{c\gg 1} \sup_K \phi_c < \infty.$$

Proof. By a slight modification of the proof of Theorem 3.4.2,

$$\lim_{c\to\infty} \phi_c = \phi_\infty \quad \text{in} \quad H^1(\Omega), \tag{3.8}$$

where $\phi_\infty \in H^1_B(\Omega)$ is the first eigenfunction solving problem (3.5) normalized so that $\|\phi_\infty\|_{L^2(\Omega\setminus B)} = 1$. Since $m \in L^\infty(\Omega \setminus B)$ and $\phi_\infty = 0$ on ∂B (in the sense of the trace), L^p-theory of elliptic equations applies. This is a similar argument to that used in the proof of Theorem 3.4.1. The Sobolev embedding, Theorem 1.2.3, ensures that for all $c \gg 1$, $\phi_c \in L^q(\Omega \setminus \overline{B})$ for some $q > 2$. We repeat until we may choose $q > N$ which guarantees that $\phi_\infty \in C(\overline{\Omega} \setminus B)$.

Without loss of generality, we may assume K has a smooth boundary. Then, from the L^2-theory of elliptic equations, (essentially Theorem 1.2.29, or the improved global regularity case for Theorem 1.2.25), $\{\phi_c\}_{c\gg 1}$ is bounded in $H^2(K)$. Repeated application of the L^p-estimates yields that in fact $\{\phi_c\}_{c\gg 1}$ is bounded in $W^{2,p}(K)$ for any $p \geq 1$, since $m \in L^\infty(\Omega \setminus B)$ does not depend on c. By the Sobolev embedding Theorem 1.2.3, $\{\phi_c\}_{c\gg 1}$ is bounded in $C^{1,\alpha}(\overline{K})$ for some $\alpha \in (0,1)$, and so, $\lim_{c\to\infty} \phi_c = \phi_\infty$ in $C(\overline{K})$ thanks to the Arzelà-Ascoli theorem and (3.8). Since $0 < \inf_K \phi_c \leq \sup_K \phi_c < \infty$, the conclusion of the lemma follows. $\square$

We now obtain the global L^∞ estimate.

Lemma 3.4.2. *There holds* $\sup_{c\gg 1} \sup_\Omega \phi_c < \infty$.

Proof. From Lemma 3.4.1, we see that $\{\phi_c\}_{c\gg 1}$ is uniformly bounded from above for any $K \Subset \overline{\Omega}\backslash\overline{B}$. The delicacy in this case comes in deriving a uniform upper bound on ϕ_c in a neighbourhood of B. Unlike the previous methods applied, we cannot use the same bootstrapping arguments since $\mathbb{1}_{\Omega\backslash B} m - c\mathbb{1}_B$ becomes unbounded in $L^p(\Omega)$ as $c \to \infty$ for any $p \geq 1$. For this reason, we appeal to an application of the Moser iteration technique. While somewhat technical in the calculations, the result is a brilliant one. To this end, we seek to obtain a bound of the form

$$\|\phi_c\|_{L^{2N^k/(N-2)^k}(B_{R_{k+1}}(x_0))} \leq C_k \|\phi_c\|_{L^{2N^{k-1}/(N-2)^{k-1}}(B_{R_k}(x_0))}, \tag{3.9}$$

for some constants C_k such that their product $\prod_{n=1}^\infty C_n$ is bounded independent of $c \gg 1$, and $B_{R_{k+1}}(x_0) \Subset B_{R_k}(x_0)$ concentric balls of particular radii R_k defined below. In the above estimate, $N \geq 3$ is the spatial dimension. The cases $N = 1, 2$ are simpler and the explicit calculations are omitted. Briefly, one notices that for $p = 2$, the Sobolev embedding gives a stronger result when $N = 1, 2$. For $N = 1$, we obtain boundedness essentially for free (in fact, we obtain Hölder continuity from a $W^{1,2}(\Omega)$ estimate!). For $N = 2$, we are in the case where $N = p$, and so $W^{1,2}(\Omega) \subset L^q(\Omega)$ for any $1 \leq q < \infty$. For $N \geq 3$, the best we can do is a $L^q(\Omega)$ estimate for $q = 2N/(N-2)$, as we explore in detail now.

Step 1 By Theorem 3.4.2, $\{\mu_{1,c}\}_{c\gg 1}$ is bounded and $\lim_{c\to\infty}\phi_c = \phi_\infty$ in $H^1(\Omega)$ for some $\phi_\infty \in H^1_B(\Omega)$, considered as an element in $H^1(\Omega)$ by zero extension.

Since $B \Subset \Omega$, there is $R > 0$ such that the R-neighbourhood of B is compactly contained in Ω. Fix an arbitrary point $x_0 \in \overline{B}$. Then, $B_R(x_0) \Subset \Omega$. We drop the dependence on x_0 moving forward for notational brevity. Choose a cut-off function $\eta \in C_0^\infty(B_R)$ so that $0 \le \eta \le 1$ in B_R, $\eta = 1$ in $B_{R(1-1/N)}$, and $|\nabla\eta| \le 4N^2/R(N-2)$. Multiplying the equation for ϕ_c by $\eta^2\phi_c$ and integrating by parts yields

$$d\int_{B_R} |\nabla\phi_c|^2\eta^2 \le 2d\int_{B_R}\eta\,|\nabla\phi_c|\,|\nabla\eta|\,\phi_c + \int_{B_R}\eta^2(\mathbb{1}_{\Omega\setminus B}m - c\mathbb{1}_B + \mu_{1,c})\phi_c^2. \tag{3.10}$$

Applying Young's inequality to the first term on the right hand side of (3.10) side yields

$$\begin{aligned} 2d\int_{B_R}\eta\,|\nabla\phi_c|\,|\nabla\eta|\,\phi_c &\le \frac{d}{2}\int_{B_R}\eta^2\,|\nabla\phi_c|^2 + 2d\int_{B_R}\phi_c^2\,|\nabla\eta|^2 \\ &\le \frac{d}{2}\int_{B_R}\eta^2\,|\nabla\phi_c|^2 + 2d\left(\frac{4N^2}{R(N-2)}\right)^2\int_{B_R}\phi_c^2. \end{aligned}$$

Combining this with (3.10), using the boundedness of m, $\{\mu_{1,c}\}_{c\gg 1}$, and dropping the negative term, we are left with

$$\frac{d}{2}\int_{B_R}|\nabla\phi_c|^2\eta^2 \le \left(2d\left(\frac{4N^2}{R(N-2)}\right)^2 + \|m\|_{L^\infty(\Omega\setminus B)} + |\mu_{1,c}|\right)\int_{B_R}\phi_c^2 \le C_0\int_{B_R}\phi_c^2. \tag{3.11}$$

Since $\eta\phi_c \in H^1_0(B_R)$, the Sobolev inequality and Poincaré's inequality yields

$$\|\eta\phi_c\|_{L^{2N/(N-2)}(B_R)} \le C\,\|\eta\phi_c\|_{H^1(B_R)} \le C\,\|\nabla(\eta\phi_c)\|_{L^2(B_R)},$$

where C may change between inequalities but does not depend on $c \gg 1$. Using the fact that $\nabla(\eta\phi_c) = \nabla\eta\phi_c + \nabla\phi_c\eta$ paired with the estimate (3.11), we see that

$$\begin{aligned} \frac{d}{4}\|\nabla(\eta\phi_c)\|^2_{L^2(B_R)} &\le \frac{d}{2}\int_{B_R}(|\nabla\eta|^2\phi_c^2 + |\nabla\phi_c|^2\eta^2) \\ &\le \frac{d}{2}\left(\frac{4N^2}{R(N-2)}\right)^2\int_{B_R}\phi_c^2 + C_0\int_{B_R}\phi_c^2 \le C_0\,\|\phi_c\|^2_{L^2(B_R)}, \end{aligned}$$

where again C_0 may change from line to line but remains independent of $c \gg 1$. Finally, using the fact that $\eta = 1$ in $B_{R(1-1/N)}$ we obtain the estimate

$$\|\phi_c\|_{L^{2N/(N-2)}(B_{R(1-1/N)})} \le C_1\,\|\phi_c\|_{L^2(B_R)}, \tag{3.12}$$

where C_1 depends on all quantities thus far but can be chosen independent of $c \gg 1$.

Step 2 We seek to show the induction step. Set $\alpha_k = (N/(N-2))^{k-1}$ for integer $k \geq 1$ and consider the sequence of radii $R_k = \frac{R}{2}(1+\alpha_k^{-1})$ so that $R_1 = R$ and $R_\infty := \lim_{k\to\infty} R_k = R/2$. Note that we have established (3.9) for $k=1$ (namely, (3.12)), where C_1 is as defined above. Then, we consider a sequence of cut-off functions $\eta_k \in C_0^\infty(B_{R_k})$ so that $0 \leq \eta_k \leq 1$, $\eta_k = 1$ in $B_{R_{k+1}}$, and $|\nabla \eta_k| \leq 4/(R_k - R_{k+1}) = 4N\alpha_k/R$. Multiplying the equation for ϕ_c by $\eta^2 \phi_c^{2\alpha_k - 1}$, integrating by parts and throwing away negative terms yields

$$\begin{aligned}\frac{d(2\alpha_k-1)}{\alpha_k^2}\int_{B_{R_k}} \left|\nabla \phi_c^{\alpha_k}\right|^2 \eta_k^2 \leq 2d\int_{B_{R_k}} \eta_k \left|\nabla \phi_c\right| \left|\nabla \eta_k\right| \phi_c^{2\alpha_k-1} \\ + \left(\|m\|_{L^\infty(\Omega\setminus B)} + |\mu_{1,c}|\right)\int_{B_{R_k}} \phi_c^2.\end{aligned} \tag{3.13}$$

We again control the first term on the right hand side via Young's inequality and absorb into the left hand side. To this end, we compute

$$\begin{aligned}2d\int_{B_{R_k}} \eta_k \left|\nabla \phi_c\right| \phi_c^{2\alpha_k-1}\left|\nabla \eta_k\right| &= \frac{2d}{\alpha_k}\int_{B_{R_k}} \eta_k \left|\nabla \phi_c^{\alpha_k}\right| \phi_c^{\alpha_k}\left|\nabla \eta_k\right| \\ &\leq \frac{d(2\alpha_k-1)}{2\alpha_k^2}\int_{B_{R_k}} \left|\nabla \phi_c^{\alpha_k}\right|^2 \eta_k^2 + \frac{2d}{2\alpha_k-1}\int_{B_{R_k}} \phi_c^{2\alpha_k}\left|\nabla \eta_k\right|^2 \\ &\leq \frac{d(2\alpha_k-1)}{2\alpha_k^2}\int_{B_{R_k}} \left|\nabla \phi_c^{\alpha_k}\right|^2 \eta_k^2 + \frac{32dN^2\alpha_k^2}{R^2(2\alpha_k-1)}\int_{B_{R_k}} \phi_c^{2\alpha_k}.\end{aligned}$$

Combining this result with (3.13) leaves

$$\frac{d(2\alpha_k-1)}{2\alpha_k^2}\int_{B_{R_k}} \left|\nabla \phi_c^{\alpha_k}\right|^2 \eta_k^2 \leq \left(\|m\|_{L^\infty(\Omega\setminus B)} + |\mu_{1,c}| + \frac{32dN^2\alpha_k^2}{R^2(2\alpha_k-1)}\right)\left\|\phi_c^{\alpha_k}\right\|^2_{L^2(B_{R_k})}. \tag{3.14}$$

Notice again that $\eta_k\phi_c^{\alpha_k}$ belongs to $H_0^1(B_{R_k})$. Therefore, applying the Sobolev inequality, Poincaré's inequality and the fact that $\nabla(\eta_k\phi_c^{\alpha_k}) = \nabla\eta_k\phi_c^{\alpha_k} + \eta_k\nabla(\phi_c^{\alpha_k})$ gives us that

$$\frac{d(2\alpha_k-1)}{4\alpha_k^2}\left\|\eta_k\phi_c^{\alpha_k}\right\|^2_{L^{2N/(N-2)}(B_{R_k})} \leq \frac{d(2\alpha_k-1)}{2\alpha_k^2}\int_{B_{R_k}} \left(\left|\nabla\eta_k\right|^2\phi_c^{2\alpha_k} + \left|\nabla\phi_c^{\alpha_k}\right|^2\eta_k^2\right),$$

and so combining this estimate with (3.14) and using that $\eta_k \equiv 1$ in $B_{R_{k+1}}$ yields

$$\tfrac{d(2\alpha_k-1)}{4\alpha_k^2}\left\|\phi_c^{\alpha_k}\right\|^2_{L^{2N/(N-2)}(B_{R_{k+1}})} \le \left(\|m\|_{L^\infty(\Omega\setminus B)} + |\mu_{1,c}| + \tfrac{32dN^2\alpha_k^2}{R^2(2\alpha_k-1)} + \tfrac{8dN^2(2\alpha_k-1)}{R^2}\right)\left\|\phi_c^{\alpha_k}\right\|^2_{L^2(B_{R_k})}. \tag{3.15}$$

An elementary manipulation gives that

$$\left\|\phi_c^{\alpha_k}\right\|_{L^{2N/(N-2)}(B_{R_{k+1}})} = \|\phi_c\|^{\alpha_k}_{L^{2\alpha_{k+1}}(B_{R_{k+1}})}, \quad \left\|\phi_c^{\alpha_k}\right\|_{L^2(B_{R_k})} = \|\phi_c\|^{\alpha_k}_{L^{2\alpha_k}(B_{R_k})}. \tag{3.16}$$

Finally, rearranging (3.15) and using (3.15) we obtain the final estimate

$$\|\phi_c\|_{L^{2\alpha_{k+1}}(B_{R_{k+1}})} \le C_k \|\phi_c\|_{L^{2\alpha_k}(B_{R_k})},$$

where C_k is a constant depending on all quantities used throughout this procedure but can be chosen independent of c, and is dominated by a term of order $(\alpha_k^4/(2\alpha_k-1)^2)^{1/2\alpha_k} \sim (\alpha_k)^{1/\alpha_k}$ for k large.

Step 3 We complete the limiting process. The uniformity in c is clear; on the other hand, upon iteration we find that

$$\|\phi_c\|_{L^{2N^k/(N-2)^k}(B_{R_{k+1}})} \le \prod_{n=1}^{k} C_n \|\phi_c\|_{L^2(B_{R_k})}, \tag{3.17}$$

and so we now ensure that the product of the constants C_k are bounded. First, note that there exists a constant A depending on $\|m\|_{L^\infty(\Omega)}, |\mu_{1,c}|, d, N, R$ but independent of c, k so that

$$C_k \le (A\alpha_k)^{1/\alpha_k}.$$

Here, the constant A can be obtained by extracting the highest order terms (with respect to powers of α_k) and estimating the remaining terms from above, which are already known to be uniformly bounded. Then, we use the fact that $\prod_{n=1}^{\infty} C_n < \infty \iff \sum_{n=1}^{\infty}\log(C_n) < \infty$. Using the bound above and some elementary calculation, we see that

$$\sum_{n=1}^{\infty}\log(C_n) \le \sum_{n=1}^{\infty}\frac{(n-1)\log(A^{1/(n-1)}\sigma)}{\sigma^{n-1}} < \infty,$$

where $\sigma = N/(N-2) > 1$ ensures the convergence. Thus, (3.17) is bounded, and taking $k \to \infty$ yields

$$\|\phi_c\|_{L^\infty(B_{R/2}(x_0))} \leq M \|\phi_c\|_{L^2(B_R(x_0))} .$$

Since $x_0 \in \overline{B}$ was arbitrary, we have that ϕ_c is uniformly bounded on some set B' such that $B \Subset B'$. Combining this with Lemma 3.4.1, we conclude that $\sup_{c \gg 1} \sup_{\Omega} \phi_c$ is bounded. This completes the proof. □

3.5 The scalar equation

3.5.1 Well-posedness

In this section we focus now on building solutions to problem (3.1). We begin with the definition of a solution in this context.

Definition 3.5.1. (1) *A* classical solution *on $Q_{B,T}$ to problem* (3.1) *is a solution belonging to $C^{2+\alpha,1+\alpha/2}((\Omega \setminus \overline{B}) \times (0,\infty)) \cap C^+((\overline{\Omega} \setminus B) \times [0,\infty))$ satisfying the equation everywhere in $\Omega \setminus \overline{B}$, satisfying $w_\infty = 0$ everywhere along ∂B, and $\partial w_\infty / \partial \nu = 0$ everywhere along $\partial \Omega$.*

(2) *A* steady state *to problem* (3.1) *is a solution belonging to $C^{2+\alpha}(\Omega \setminus \overline{B}) \cap C(\overline{\Omega} \setminus B)$ satisfying the equation everywhere in $\Omega \setminus \overline{B}$ and boundary conditions everywhere along $\partial\Omega$ and ∂B.*

Remark 3.5.1. *Notice that, different from the degradation problem, we actually assume sufficient regularity on the function $f(x,w)$ restricted to $\Omega \setminus \overline{B}$. This will guarantee the existence of a classical solution.*

Before we can prove the existence of such a solution, we briefly develop some of the theory for linear parabolic equations in domains with holes.

Second order linear parabolic equations in domains with holes

In order to discuss the well-posedness of problem (3.1), we must first highlight some of the standard theory for linear equations of the same form. For our purposes, it is sufficient to establish some standard theory for the following problem:

$$\begin{cases} w_t = d\Delta w + c(x,t)w + f(x,t), & \text{in } \Omega \setminus \overline{B} \times (0,T), \\ \frac{\partial w}{\partial \nu} = 0, & \text{on } \partial\Omega \times (0,T), \\ w = 0, & \text{on } \partial B \times (0,T), \\ w(x,0) = w_0 \gneqq 0, & \text{in } \overline{\Omega} \setminus B. \end{cases} \tag{3.18}$$

We first state the following strong maximum principle, plus a comparison theorem for the nonlinear problem. The maximum principle result is identical to the classical case, except we must treat both cases along $\partial\Omega$ and ∂B, using the "Neumann" boundary arguments along $\partial\Omega$, and the "Dirichlet" boundary arguments along ∂B.

Theorem 3.5.1. *Suppose $w \in C^{2,1}(\overline{Q}_{B,T})$ satisfies*

$$\begin{cases} w_t - d\Delta w + c(x,t)w \geq 0, & \text{in } Q_{B,T}, \\ \frac{\partial w}{\partial \nu} \geq 0, & \text{on } \partial\Omega \times (0,T), \\ w \geq 0, & \text{on } \partial B \times (0,T), \\ w(x,0) \gneqq 0, & \text{in } \overline{\Omega} \setminus B, \end{cases}$$

where $c(x,t)$ is bounded in $Q_{B,T}$. Then $w(x,t) \geq 0$ in $\overline{Q}_{B,T}$, and $w(x,t) > 0$ in $\overline{\Omega} \setminus \overline{B}$ unless it is identically zero.

Theorem 3.5.2. *Suppose that $\underline{w}, \overline{w}$ belong to $C^{2+\alpha,1+\alpha/2}(\overline{Q}_{B,T})$ with $\underline{w}(\cdot,0), \overline{w}(\cdot,0) \geq 0$ and satisfy the following:*

$$\begin{cases} \underline{w}_t - d\Delta \underline{w} \leq f(x,\underline{w}), & \text{in } Q_{B,T}, \\ \overline{w}_t - d\Delta \overline{w} \geq f(x,\overline{w}), & \text{in } Q_{B,T}, \\ \frac{\partial \underline{w}}{\partial \nu} \leq \frac{\partial \overline{w}}{\partial \nu}, & \text{on } \partial\Omega \times (0,T), \\ \underline{w} \leq \overline{w} & \text{on } \partial B \times (0,T). \end{cases}$$

If $\underline{w}(\cdot,0) \leq \overline{w}(\cdot,0)$, then $\underline{w}(x,t) \leq \overline{w}(x,t)$ for all $(x,t) \in Q_{B,T}$. Furthermore, if $\underline{w}(\cdot,0) \lneqq \overline{w}(\cdot,0)$, then $\underline{w}(x,t) < \overline{w}(x,t)$ for all $(x,t) \in \overline{\Omega} \setminus \overline{B} \times (0,T)$.

Remark 3.5.2. *This result is essentially identical to that found in Theorem 2.4.1 of the previous chapter. The key differences are that the inequalities now hold in the classical sense, and we must satisfy an inequality along both boundary portions.*

Proof. This result follows from a standard argument, see e.g. [95, Ch. 2 Lemma 3.6], where one uses the fact that the nonlinearity $f(x,\cdot)$ is a C^1-function. First, one deduces that $\underline{w} \leq \overline{w}$ in $Q_{B,T}$ via Theorem (3.5.1). Next, one uses the Neumann boundary condition along $\partial\Omega$ to conclude that the inequality must be strict. The strong maximum principle implies that $\underline{w} - \overline{w} = 0$ cannot occur for an interior point $(x_0, t_0) \in Q_{B,T}$, and so $\underline{w} < \overline{w}$ in $Q_{B,T}$. Then, one makes use of Hopf's lemma to conclude that $\underline{w} - \overline{w} = 0$ cannot occur along $\partial\Omega$, since this would imply that $\frac{\partial(\underline{w}-\overline{w})}{\partial\nu} > 0$, a contradiction. This completes the proof. □

Next, we establish the following existence result.

Theorem 3.5.3. *Suppose $\partial\Omega$ and ∂B are smooth and $w_0(x) \in H^1_B(\Omega) \cap C^\alpha(\overline{\Omega})$ for some $\alpha \in (0,1)$. Suppose also that $f(x,t), c(x,t) \in C^\alpha(\overline{Q}_{B,T})$. Then there exists a unique classical solution $w(x,t) \in C^{2+\alpha,1+\alpha/2}(\overline{Q}_{B,T}) \cap H^1_B(\Omega)$ solving problem (3.18). In addition, $\frac{\partial w}{\partial\nu} < 0$ along ∂B.*

Proof. The well-posedness of the linear problem follows from standard arguments with essentially no change aside from building weak solutions from the space $H^1_B(\Omega)$. For this reason we highlight the key steps only.

First, we note that $-d\Delta + m(x)$ is a self adjoint operator on $H^1_B(\Omega)$ and is furthermore compact. The compactness follows from Poincaré's inequality and the boundedness of $m(x)$. By the theory of self adjoint, compact operators in a Hilbert space, we have that the eigenfunctions of $-d\Delta + m(x)$ form an orthogonal basis for the space $H^1_B(\Omega)$. Actually, this is just the spectral theorem, see [31, Ch. D.6, Theorem 7].

Next, we apply the Galerkin method using the aforementioned eigenfunctions as our basis in order to deduce the existence of weak solutions to problem (3.18), see e.g. [31, Ch. 7.1]. In particular, we first assume that $f \in C^\infty(\overline{Q}_{B,T})$ in order to deduce the existence of a solution $w \in C^\infty(\overline{Q}_{B,T}) \cap H^1_B(\Omega)$. Uniqueness of this solution follows from the usual argument, i.e. assume there are two solutions and apply the maximum principle.

With the existence of a smooth solution, we then take an approximating sequence $f_\varepsilon(x,t) \in C^\infty(\overline{Q}_{B,T})$ so that $f_\varepsilon \to f \in C^{\alpha,\alpha/2}(\overline{Q}_{B,T})$ as $\varepsilon \to 0$. An application of Schauder estimates (Theorem 1.2.24) then yields the existence of a unique solution

$$w(x,t) \in C^{2+\alpha,1+\alpha/2}(Q_{B,T}) \cap C(\overline{Q}_{B,T}) \cap H^1_B(\Omega)$$

which also satisfies the boundary conditions in the classical sense. Finally, since $w > 0$ in $Q_{B,T}$ and $u = 0$ along ∂B, u attains its minimum value (of 0) along ∂B. Since w is not constant, the maximum principle then implies that $\frac{\partial w}{\partial \nu} < 0$ along ∂B. This completes the proof. $\square$

Finally, we may use a standard method of sub/super solutions applied to the problem (3.1) in order to deduce the existence and uniqueness of solutions for this nonlinear problem. This is summarized in the following theorem.

Theorem 3.5.4. *Suppose there exists functions $\underline{u}, \overline{u}$ satisfying the hypotheses of Theorem 3.5.2 in $Q_{B,T}$. Then there exists a unique solution $\underline{u} \leq u \leq \overline{u}$ solving problem* (3.1) *in $(0, T)$, and this solution is in fact global. Furthermore, $\frac{\partial u}{\partial \nu} < 0$ along ∂B.*

Proof of Theorem 3.5.4. The proof follows from a standard monotone iteration procedure. See the proof of Proposition 3.5.6, which uses the same technique for the elliptic system. The only modification is an application of the existence theory for linear equations developed above. $\square$

Second order linear elliptic equations in domains with holes

Similar arguments and results hold for the corresponding elliptic (or steady state) problems. We highlight two key results here to be used later.

Theorem 3.5.5. *Suppose that $\underline{w}, \overline{w}$ belong to $C^{2+\alpha}(\overline{\Omega} \setminus B)$ and satisfy the following:*

$$\begin{cases} -d\Delta \underline{w} \leq f(x, \underline{w}), & \text{in } \Omega \setminus \overline{B}, \\ -d\Delta \overline{w} \geq f(x, \overline{w}), & \text{in } \Omega \setminus \overline{B}, \\ \frac{\partial \underline{w}}{\partial \nu} \leq \frac{\partial \overline{w}}{\partial \nu}, & \text{on } \partial\Omega, \\ \underline{w} \leq \overline{w} & \text{on } \partial B. \end{cases}$$

Then $\underline{w} \leq \overline{w}$. Furthermore, either $\underline{w} < \overline{w}$ or else $\underline{w} < \overline{w}$.

Theorem 3.5.6. *Let $\mu_{1,\infty}$ be the principal eigenvalue to problem 3.5 for $m \equiv f'(x, 0)$. Then we have the following dichotomy.*

(1) *Suppose $\mu_{1,\infty} < 0$. Then,* (3.1) *admits a unique positive steady state w^*_∞.*

(2) *Suppose* $\mu_{1,\infty} \geq 0$. *Then,* $w^*_\infty \equiv 0$ *is the only steady state solving problem* (3.1).

Proof of Theorem 3.5.6. When $\mu_{1,\infty} < 0$, the existence of a positive steady state $w^* \in X^{++}$ follows from a sub/super solution argument. In such a case, $\varepsilon\phi_{1,\infty}$ acts as a sub solution for any $\varepsilon \ll 1$, where we choose ε small enough so that $f'(\cdot, 0) - \frac{f(\cdot,\varepsilon\phi_{1,\infty})}{\varepsilon\phi_{1,\infty}} \leq -\mu_1(\infty)$. Choosing $M \gg 1$ as a super solution, we apply the existence theorem for monotone elliptic problems Theorem 1.2.32. Therefore, there exists a steady state w^* satisfying $\varepsilon\phi_{1,\infty} \leq w^* \leq M$. The concavity of f in the argument w (actually, subhomogeneity is sufficient) ensures that the steady state is unique and so $w^* \equiv w^*_\infty$ is the positive steady state solving problem (3.1).

In the case that $\mu_{1,\infty} \geq 0$, we may choose $\varepsilon\phi_{1,\infty}$ as a super solution. Since $\varepsilon > 0$ was arbitrary, sending $\varepsilon \to 0$ yields (2). This completes the proof. □

3.5.2 Global dynamics

For the global dynamics of the destruction problem, there are three perspectives we take. First, we naturally want to describe the global dynamics for the scalar destruction problem (3.1). Second, we seek to describe fully the global dynamics of the degradation problem in relation to the principal eigenvalue $\mu_{1,\infty}$. In Chapter 2, we fully described the global dynamics of the degradation problem in Theorem 2.4.3. We will reformulate this result in the context of the current chapter. Third, we finish with a uniform connection between these in a global sense. We begin with the global dynamics of the habitat destruction problem.

Theorem 3.5.7. *Assume* $0 \lneq w_\infty(\cdot, 0) \in C^1_B(\overline{\Omega})$. *The following hold.*

(i) *If* $\mu_{1,\infty} < 0$, *then Theorem 3.5.6 ensures that* (3.1) *admits a unique positive steady state* w^*_∞. *Then,* $w_\infty \to w^*_\infty$ *in* $C(\overline{\Omega} \setminus B)$ *as* $t \to \infty$;

(ii) *If* $\mu_{1,\infty} \geq 0$, *Theorem 3.5.6 guarantees that* 0 *is the only steady state to* (3.1). *Then,* $w_\infty \to 0$ *in* $C(\overline{\Omega} \setminus B)$ *as* $t \to \infty$.

Remark 3.5.3. *Notice the similarities with Theorem 2.4.3. Indeed, these theorems are essentially "equivalent" in their respective settings.*

Proof. This result follows from similar arguments made in the proof of Theorem 3.5.8, but there are some technical issues to address due to the Dirichlet boundary condition along the boundary ∂B. To address this, we set $X := C^1_B(\overline{\Omega})$ and recall the strong partial order on X generated by the cone $X^+ = \{v \in X : v \geq 0\}$ with interior

$$X^{++} = \left\{ v \in X : v > 0 \text{ in } \overline{\Omega} \setminus \overline{B} \text{ and } \frac{\partial v}{\partial \nu} < 0 \text{ on } \partial B \right\}.$$

The global existence, uniqueness and regularity of solutions to (3.1) with initial data in X^+ follow from Theorem 3.5.3. The comparison principle ensures that (3.1) generates a strongly monotone flow on X^{++}. In contrast to the degradation problem, the destruction problem requires information about the normal derivative on the boundary. Luckily, we have the required result, stated at the end of Theorem 3.5.3.

When $\mu_{1,\infty} < 0$, the existence of a positive steady state $w^* \in X^{++}$ follows from Theorem 3.5.6. Since problem (3.1) generates a strongly monotone flow in X^{++}, we then conclude that w^* is globally attractive for any initial data $u_0 \in X^+ \setminus \{0\}$ through an application of Theorems 1.2.9-1.2.10. This is essentially an identical argument to that used in the proof of Theorem 2.4.3.

When $\mu_{1,\infty} \leq 0$, 0 is the only steady state solving problem (3.1) by Theorem 2.4.2. Hence, 0 is globally attractive and the proof is complete. □

Remark 3.5.4. *It is worth mentioning that the concavity assumption is not essential for Theorem's 3.5.7 and 3.5.7 to hold. Indeed, a weaker condition of subhomogeneity (Assumption 2.2.2) is sufficient. In fact, concavity is only needed when taking the limit* $c \to \infty$.

3.5.3 Connecting the asymptotic behaviour of degradation and destruction

We now state a result connecting the dynamics of the degradation problem (2.1) and the destruction problem (3.1). In this case, we are not yet concerned about uniform behaviour necessarily.

Theorem 3.5.8. *The following hold for each* $c \in (0, \infty)$.

(i) *If* $\mu_{1,c} < 0$*, then* (2.1) *admits a unique positive steady state* $w_c^* \in W^{2,p}(\Omega)$ *for any* $p \geq 1$*, and* $w_c(\cdot, t) \to w_c^*$ *in* $C(\overline{\Omega})$ *as* $t \to \infty$ *whenever* $w_c(0, \cdot) \not\equiv 0$*;*

(ii) *If* $\mu_{1,c} \geq 0$*, then* 0 *is the only steady state solution to* (2.1) *and* $w_c(\cdot, t) \to 0$ *in* $C(\overline{\Omega})$ *as* $t \to \infty$*.*

Moreover,

- *if* $\mu_{1,\infty} \leq 0$*, then* (i) *holds for any* $c \in (0, \infty)$*;*
- *if* $\mu_{1,\infty} > 0$*, then there exists a unique* $c^* > 0$ *such that* (ii) *holds for all* $c \in (c^*, \infty)$*.*

Proof. The proof of this result follows from results found in Chapter 2. We include the additional arguments as necessary.

The first part of the theorem follows directly from Theorem 2.4.3.

The "Moreover" part follows directly from Theorem 3.4.2 (1). That is, since $\mu_{1,c}$ is increasing and bounded above by $\mu_{1,\infty}$, we have two cases. In the first case, $\mu_{1,c} < \mu_{1,\infty} \leq 0$, and the result follows. In the second case, the monotone convergence of $\mu_{1,c} \to \mu_{1,\infty}$ implies the existence of a unique value c_* so that $\mu_{1,c} > 0$ for all $c \in (c_*, \infty)$. The second conclusion follows, completing the proof. $\square$

3.5.4 Uniform convergence between degradation and destruction

Finally, we are ready to establish a connection between the scalar degradation and destruction problems. We prove the following two results, the first for the steady state problems, and the second for the time-dependent problems.

Theorem 3.5.9. *The following hold.*

(1) *Suppose* $\mu_{1,\infty} < 0$ *so that Theorem* (3.5.6) *ensures that problem* (3.1) *admits a unique positive steady state* w_∞^**. Then, problem* (2.1) *admits a unique positive steady state* w_c^* *for all* $c \gg 1$*, and there holds*

$$\lim_{c \to \infty} w_c^* = w_\infty^* \quad \textit{in} \quad C(\overline{\Omega}).$$

(2) *Suppose* $\mu_{1,\infty} > 0$ *so that Theorem* (3.5.6) *guarantees that* $w_\infty^* \equiv 0$ *is the only steady state solving problem* (3.1). *Then, there exists a unique* $c^* > 0$ *such that* $w_c^* \equiv 0$ *is the only steady state solving problem* (2.1) *for all* $c \in (c^*, \infty)$.

(3) *Suppose* $\mu_{1,\infty} = 0$. *Then,* $w_c^* > 0$ *exists for all* $c > 0$ *by Theorem 2.4.3, and* $w_c^* \to 0$ *in* $C(\overline{\Omega})$ *as* $c \to \infty$.

Theorem 3.5.10. *Assume that* $\mu_{1,\infty} \neq 0$. *Let* w_c *and* w_∞ *be the unique solutions to problems* (2.1) *and* (3.1), *respectively, with the initial data satisfying* $0 \lneq w_c(\cdot, 0) = w_\infty(\cdot, 0) \in C^1_B(\overline{\Omega})$ *and* $\operatorname{supp}(w_\infty(\cdot, 0)) \Subset \overline{\Omega} \setminus \overline{B}$. *Then,*

$$\lim_{c \to \infty} w_c = w_\infty \quad \textit{uniformly in} \quad \overline{\Omega} \times [0, \infty).$$

The proof of Theorem 3.5.9

In this section we prepare for and provide the proof of Theorem 3.5.9. To do so, we use a monotonicity argument, Dini's theorem, and uniqueness of the steady state. First we establish the following monotonicity result.

Lemma 3.5.1. *Assume* $\mu_{1,\infty} < 0$. *Then, for any* $0 < \underline{c} < \bar{c}$, *there holds* $w_\infty^* \leq w_{\bar{c}}^* < w_{\underline{c}}^*$ *in* $\overline{\Omega}$.

Proof. Note that since $\mu_{1,\infty} < 0$, w_c^* exists for all $c > 0$. Then, it is easy to see that $w_{\bar{c}}^* \leq w_{\underline{c}}^*$ by the concavity of $f(x, \cdot)$ and the strong maximum principle for strong solutions, e.g., Theorem 1.2.16. The strong maximum principle and Hopf's lemma imply that either $w_{\bar{c}}^* < w_{\underline{c}}^*$ or $w_{\bar{c}}^* \equiv w_{\underline{c}}^*$ in $\overline{\Omega}$. By the uniqueness of the steady state solution, the second cannot hold, and the strict inequality follows.

Let $c > 0$. Note that both w_c^* and w_∞^* satisfy

$$\begin{cases} 0 = d\Delta w + f(x, w), & \text{in} \quad \Omega \setminus \overline{B}, \\ \frac{\partial w}{\partial \nu} = 0, & \text{on} \quad \partial\Omega. \end{cases}$$

As $w_\infty^* = 0 < w_c^*$ on ∂B, we apply Theorem 3.5.2 to conclude $w_\infty^* \leq w_c^*$ in $\overline{\Omega} \setminus B$. Since w_∞^* is identified with its extension by zero in B, we automatically have that $w_\infty^* < w_c^*$ in $\overline{B}$ by the positivity of w_c^*. Hence, $w_\infty^* \leq w_c^*$ in $\overline{\Omega}$, and the proof is complete. □

We now establish Theorem 3.5.9. Its proof is instructive for the more difficult parabolic analog, Theorem 3.5.10, as we require fewer estimates to conclude our desired result.

Proof of Theorem 3.5.9. The existence and uniqueness of positive steady states follow from Theorems 3.5.6 and 3.5.8. We consider three cases separately.

Case 1: Suppose first that $\mu_{1,\infty} < 0$. Lemma 3.5.1 asserts that $\{w_c^*\}_{c\gg 1}$ is a decreasing sequence of functions and is uniformly bounded below by w_∞^*. Hence, the pointwise limit $w^* := \lim_{c\to\infty} w_c^*$ exists in $\overline{\Omega}$ and is nontrivial. This is our candidate solution to the limiting problem.

Multiplying the equation satisfied by the steady state w_c^* by itself and integrating over Ω, we obtain

$$d\int_\Omega |\nabla w_c^*|^2 = \int_{\Omega\setminus B} f(\cdot, w_c^*)w_c^* - c\int_B (w_c^*)^2 \le \|f'(\cdot,0)\|_{L^\infty(\Omega\setminus\overline{B})}\, \|w_c^*\|^2_{L^2(\Omega)}, \tag{3.19}$$

where used Assumption 2.2.3 in the inequality (actually, subhomogeneity is sufficient here). Hence, $\{w_c^*\}_{c\gg 1}$ is uniformly bounded in $H^1(\Omega)$. Consequently, there exists a subsequence, still denoted by w_c^*, such that

$$\lim_{c\to\infty} w_c^* = w^* \quad \text{strongly in } L^2(\Omega) \quad \text{and} \quad \text{weakly in } H^1(\Omega). \tag{3.20}$$

In particular, for any $\phi \in H_B^1(\Omega)$ (considered as an element in $H^1(\Omega)$ after zero extension in B), we have $-c\int_B w_c^*\phi = 0$ for all $c \gg 1$, and

$$\lim_{c\to\infty} d\int_\Omega \nabla w_c^* \nabla\phi = d\int_\Omega \nabla w^*\nabla\phi, \quad \lim_{c\to\infty}\int_\Omega f(\cdot, w_c^*)\phi = \int_\Omega f(\cdot, w^*)\phi.$$

Therefore, w^* satisfies $-d\Delta w^* = f(x, w^*)$ in $\Omega\setminus\overline{B}$ in the weak sense.

We now show that $w^* \in H_B^1(\Omega)$. We see from the equality in (3.19) that

$$c\int_B (w_c^*)^2 \le \|f'(\cdot,0)\|_{L^\infty(\Omega\setminus\overline{B})}\int_\Omega (w_c^*)^2.$$

As $\sup_{c\gg 1}\int_\Omega (w_c^*)^2 < \infty$, we arrive at $\lim_{c\to\infty}\int_B (w_c^*)^2 = 0$. It then follows from the convergence in (3.20) or the monotone convergence theorem that $\int_B (w^*)^2 = 0$, and hence, $w^* = 0$ a.e. in B. In particular, $w^* \in H_B^1(\Omega)$.

Combining these results, we conclude from the elliptic regularity theory that w^* is a steady state to (3.1), and therefore, $w^* = w^*_\infty$ by the uniqueness of positive steady states. As $w^* \in C(\overline{\Omega})$, we conclude the result from Dini's theorem, and thus, complete the proof. $\square$

Remark 3.5.5. *Unfortunately, we cannot expect a stronger notion of convergence in the entire space* Ω *in a classical sense than what was shown above. Informally, this can be made intuitive if one considers the fact that* $\frac{\partial w^*_\infty}{\partial \nu}$ *is negative along* ∂B *while* w^*_∞ *is identically zero inside of* B*. Hence, we expect the classical derivative of* w^*_∞ *to be discontinuous along* ∂B*. However, stronger notions of convergence are readily established away from the boundary of* B *through the usual arguments.*

Preparing for the proof of Theorem 3.5.10

In this section we prepare for the proof of Theorem 3.5.10. In order to do so, we prove convergence in a number of steps, treating separately the convergence in $\Omega \setminus \overline{B}$, $\overline{B}$, as well as the time intervals $(0, T]$ and (T, ∞). The strategy is to abuse the monotonicity of the family of solutions w_c, w^*_c with respect to parameter c. This is similar to the proof of Theorem 3.5.9, but the time dependence makes things a little more delicate. The following schematic gives an overview of how this result is proved.

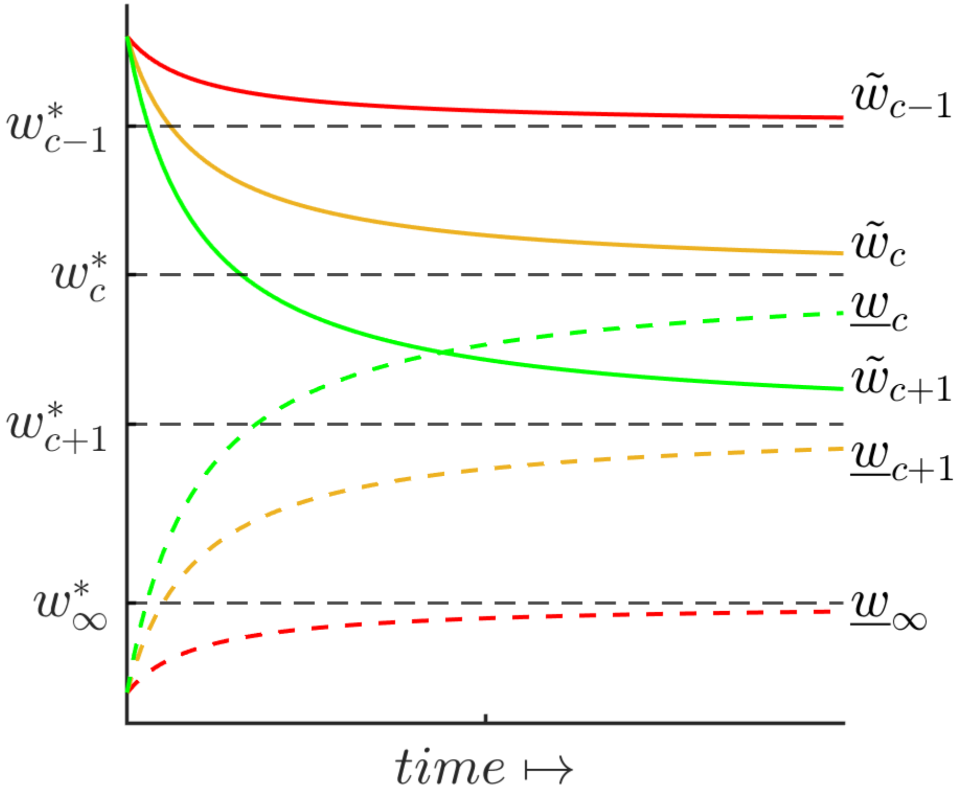


Figure 3.2: A schematic showing the strategy to prove uniform convergence in the scalar case. First, we have the monotonicity of the steady states (dashed lines, decreasing in c). We see monotonicity of the time-dependent sub/super solutions (in c). From above, we have a *decreasing* property in both time and c for sufficiently large initial data (solid red, orange, green, respectively). From below, solutions are increasing (in time) for sufficiently small initial data (dashed red, orange and green), however this is counteracted by the decreasing nature in c (dashed green, orange, red, respectively). To overcome this, we use $\underline{w}_\infty$ as the lower bound, which converges in time independent of c.

We establish the following monotonicity result.

Lemma 3.5.2. *Denote by $w_c(x,t)$ the unique solution to problem (2.1) for $c > 0$. Assume $0 < \underline{c} < \bar{c}$. If $w_{\underline{c}}(\cdot, 0) = w_{\bar{c}}(\cdot, 0) \in C^+(\overline{\Omega}) \setminus \{0\}$, then $w_{\underline{c}} > w_{\bar{c}} > 0$ in $\overline{\Omega} \times (0, \infty)$.*

Proof. Set $w := w_{\bar{c}} - w_{\underline{c}}$ and $w^+ := \max\{0, w\}$. Note that $w_{\bar{c}}$ and $w_{\underline{c}}$ are bounded. This together with the regularity assumption on f implies the existence of some $K > 0$

such that

$$\frac{1}{2}\frac{d}{dt}\int_\Omega (w^+)^2 = -d\int_\Omega \left|\nabla w^+\right|^2 + \int_\Omega w^+(f(\cdot, w_{\bar{c}}) - f(\cdot, w_{\underline{c}})) \le K\int_\Omega (w^+)^2.$$

Gronwall's inequality implies that $w^+ = 0$ a.e. in Q_T and hence $w_{\bar{c}} \le w_{\underline{c}}$ holds in all of Q_T by the smoothness of the solutions. Then, since $w_c \in C^1((0,\infty); C^+(\overline{\Omega}))$, the strong maximum principle for strong solutions applies, e.g., Theorem 1.2.16. In particular, if there exists a point $(x_0, t_0) \in Q_T$ such that $w = 0$, it follows that $w \equiv 0$ in Ω for all $t \in (0, t_0)$, a contradiction to the uniqueness of solutions. Finally, if there exists a point $x_0 \in \partial\Omega$ such that $w(x_0, t_0) = 0$ for some $t_0 > 0$, Hopf's lemma implies that $\frac{\partial w}{\partial \nu}(x_0, t_0) > 0$, a contradiction to the homogeneous Neumann boundary condition satisfied by w along $\partial\Omega$. Hence, $w < 0 \Rightarrow w_{\bar{c}} < w_{\underline{c}}$ in $\overline{\Omega} \times (0,\infty)$. The conclusion $w_{\bar{c}} > 0$ in $\overline{\Omega} \times (0,\infty)$ follows from similar arguments and the proof is complete. $\square$

As an immediate consequence of Theorem 3.5.8 and Lemma 3.5.2, we have the following result.

Corollary 3.5.1. *Suppose $\mu_{1,\infty} > 0$. Then, for any initial data $w_c(0,\cdot) \in C^+(\Omega) \setminus \{0\}$ independent of $c \gg 1$, there holds*

$$\lim_{t\to\infty} \sup_{c \gg 1} \|w_c(\cdot, t)\|_{C(\overline{\Omega})} = 0.$$

Proof. By Theorem 3.5.8, there is $c^* \gg 1$ such that $\lim_{t\to\infty} \|w_{c^*}(\cdot, t)\|_{C(\overline{\Omega})} = 0$. The result then follows from the monotonicity result Lemma 3.5.2: $w_c(x,t) \le w_{c^*}$ for all $c \in (c^*, \infty)$. This completes the proof. $\square$

The next result addresses the uniform convergence over finite time intervals.

Lemma 3.5.3. *If $w_c(\cdot, 0) = w_\infty(\cdot, 0) \in H^1_B(\Omega) \cap C^+(\overline{\Omega})$ for all $c \gg 1$ and $\mathrm{supp}(w_\infty(\cdot, 0)) \Subset \overline{\Omega} \setminus \overline{B}$, then for each $T > 0$,*

$$\lim_{c\to\infty} w_c = w_\infty \textit{ uniformly in } \overline{\Omega} \times [0,T].$$

Proof. Fix $T > 0$ and denote by w_0 the common initial data. The proof is done within four steps.

Step 1 We show the existence of some $M = M(T) > 0$ such that

$$\iint_{Q_T} \left(w_c^2 + |\nabla w_c|^2 + \left| \frac{\partial w_c}{\partial t} \right|^2 \right) \leq M, \quad \forall c \gg 1. \tag{3.21}$$

Due to the lack of smoothness of the solution w_c, we first mollify the indicator functions on the right hand side of (2.1) so that the approximate solution belongs to $H^1(Q_T)$. To this end, we set $\varepsilon_0 := \frac{1}{2}\mathrm{dist}(\partial\Omega, \partial B)$ and define for each $\varepsilon \in (0, \varepsilon_0)$ the sets:

$$B^\varepsilon = \left\{ x \in \overline{\Omega} : \mathrm{dist}(x, B) < \varepsilon \right\}, \quad B_\varepsilon = \left\{ x \in B : \mathrm{dist}(x, \partial B) > \varepsilon \right\}.$$

Note that $B_\varepsilon \Subset B \Subset B^\varepsilon \Subset \Omega$. We regularize $\mathbb{1}_{\Omega\setminus B}$ such that

$$\mathbb{1}^\varepsilon_{\Omega\setminus B} = 1 \text{ in } \Omega \setminus B^\varepsilon, \quad \mathbb{1}^\varepsilon_{\Omega\setminus B} = 0 \text{ in } B, \quad 0 \leq \mathbb{1}^\varepsilon_{\Omega\setminus B} \leq 1 \text{ in } B^\varepsilon \setminus B,$$

and $\lim_{\varepsilon\to 0} \mathbb{1}^\varepsilon_{\Omega\setminus B} = \mathbb{1}_{\Omega\setminus B}$ in $L^2(\Omega)$. Similarly, we regularize $\mathbb{1}_B$ such that

$$\mathbb{1}^\varepsilon_B = 1 \text{ in } B_\varepsilon, \quad \mathbb{1}^\varepsilon_B = 0 \text{ in } \Omega \setminus B, \quad 0 \leq \mathbb{1}^\varepsilon_B \leq 1 \text{ in } B \setminus B_\varepsilon,$$

and $\lim_{\varepsilon\to 0} \mathbb{1}^\varepsilon_B = \mathbb{1}_B$ in $L^2(\Omega)$. Consider (2.1) with $\mathbb{1}_{\Omega\setminus B}$ and $\mathbb{1}_B$ replaced by $\mathbb{1}^\varepsilon_{\Omega\setminus B}$ and $\mathbb{1}^\varepsilon_B$, respectively, that is

$$\begin{cases} w_t = d\Delta w + \mathbb{1}^\varepsilon_{\Omega\setminus B} f(x, w) - c\mathbb{1}^\varepsilon_B w, & \text{in} \quad \Omega \times (0, \infty), \\ \frac{\partial w}{\partial \nu} = 0, & \text{on} \quad \partial\Omega \times (0, \infty). \end{cases} \tag{3.22}$$

Denote by w_c^ε the unique solution of (3.22) satisfying the initial data $w_c^\varepsilon(\cdot, 0) = u_0$. Note that the standard L^2-theory of parabolic equations, e.g., Theorem 1.2.25, ensures that

$$\lim_{\varepsilon\to 0} w_c^\varepsilon = w_c \quad \text{in} \quad W_2^{2,1}(Q_T), \tag{3.23}$$

and that $\frac{\partial w_c^\varepsilon}{\partial t} \in H^1(Q_T)$ for each $\varepsilon > 0$.

We establish some uniform-in-ε estimates of w_c^ε. First, we differentiate $\|w_c^\varepsilon\|^2_{L^2(\Omega)}$ with respect to time and integrate by parts to obtain:

$$\begin{aligned} \frac{d}{dt} \|w_c^\varepsilon\|^2_{L^2(\Omega)} &= 2 \int_\Omega w_c^\varepsilon \left(d\Delta w_c^\varepsilon + \mathbb{1}^\varepsilon_{G\setminus B} f(\cdot, w_c^\varepsilon) - c\mathbb{1}^\varepsilon_B \right) \\ &\leq 2 \int_\Omega |f(\cdot, w_c^\varepsilon) w_c^\varepsilon| \leq 2 \|f'(\cdot, 0)\|_{L^\infty(\Omega\setminus\overline{B})} \int_\Omega (w_c^\varepsilon)^2. \end{aligned}$$

Gronwall's inequality implies that $\|w_c^\varepsilon(\cdot,t)\|^2_{L^2(\Omega)} \leq e^{M_0 T} + \|w_0\|^2_{L^2(\Omega)}$, where $M_0 := 2\|f'(\cdot,0)\|_{L^\infty(\Omega\backslash B)}$. Integrating with respect to time yields

$$\|w_c^\varepsilon\|^2_{L^2(Q_T)} \leq T(e^{M_0 T} + \|w_0\|^2_{L^2(\Omega)}). \tag{3.24}$$

We now seek to estimate higher order terms. Clearly, w_c^ε satisfies

$$\iint_{Q_T} \left(\frac{\partial w_c^\varepsilon}{\partial t} v + d\nabla w_c^\varepsilon \cdot \nabla v\right) = \iint_{Q_T} \left(\mathbb{1}^\varepsilon_{\Omega\backslash B} f(\cdot, w_c^\varepsilon) - c\mathbb{1}^\varepsilon_B w_c^\varepsilon\right) v, \quad \forall v \in H^1(Q_T). \tag{3.25}$$

Setting $v = w_c^\varepsilon$ in (3.25), legal by the regularity of w_c^ε, we have

$$\begin{aligned} \int_0^T \frac{d}{dt}\|w_c^\varepsilon\|^2_{L^2(\Omega)} + d\|\nabla w_c^\varepsilon\|^2_{L^2(Q_T)} &= \iint_{Q_{B,T}} f(\cdot, w_c^\varepsilon) w_c^\varepsilon - c\iint_{B\times(0,T)} (w_c^\varepsilon)^2 \\ &\leq \|f'(\cdot,0)\|_{L^\infty(\Omega\backslash\overline{B})} \|w_c^\varepsilon\|^2_{L^2(Q_T)}. \end{aligned}$$

Note that $\sup_{\varepsilon\in(0,\varepsilon_0)} \sup_{c\gg 1} \|w_c^\varepsilon\|_{L^2(Q_T)} < \infty$ by (3.24). Setting

$$M_1 = M_1(T) := \|f'(\cdot,0)\|_{L^\infty(\Omega\backslash\overline{B})} \sup_{\varepsilon\in(0,\varepsilon_0)} \sup_{c\gg 1} \|w_c^\varepsilon\|^2_{L^2(Q_T)} + \|u_0\|^2_{L^2(\Omega)},$$

we find the uniform bounds

$$\sup_{0\leq t\leq T} \|w_c^\varepsilon(\cdot,t)\|^2_{L^2(\Omega)} \leq M_1, \quad \|\nabla w_c^\varepsilon\|^2_{L^2(Q_T)} \leq \frac{M_1}{d}, \quad \forall c \gg 1 \text{ and } \varepsilon \in (0,\varepsilon_0), \tag{3.26}$$

We now seek to obtain estimates on $\frac{\partial w_c^\varepsilon}{\partial t}$. Setting $v = \frac{\partial w_c^\varepsilon}{\partial t}$ in (3.25), made possible due to the mollification procedure, we deduce

$$\begin{aligned} \iint_{Q_T} \left|\frac{\partial w_c^\varepsilon}{\partial t}\right|^2 &= -\frac{d}{2}\iint_{Q_T} \frac{\partial}{\partial t}|\nabla w_c^\varepsilon|^2 + \iint_{Q_T} \mathbb{1}^\varepsilon_{\Omega\backslash B} f(\cdot, w_c^\varepsilon)\frac{\partial w_c^\varepsilon}{\partial t} - \frac{c}{2}\iint_{Q_T} \mathbb{1}^\varepsilon_B \frac{\partial}{\partial t}(w_c^\varepsilon)^2 \\ &\leq -\frac{d}{2}\left(\|\nabla w_c^\varepsilon(\cdot,T)\|^2_{L^2(\Omega)} - \|\nabla u_0\|^2_{L^2(\Omega)}\right) + \frac{1}{2}\iint_{Q_T}\left|\frac{\partial w_c^\varepsilon}{\partial t}\right|^2 + \frac{1}{2}\|f(\cdot, w_c^\varepsilon)\|^2_{L^2(Q_{B,T})} \\ &\quad - \frac{c}{2}\int_B \mathbb{1}^\varepsilon_B\left((w_c^\varepsilon)^2(\cdot,T) - u_0^2\right) \\ &\leq \frac{d}{2}\|\nabla u_0\|^2_{L^2(\Omega)} + \frac{1}{2}\iint_{Q_T}\left|\frac{\partial w_c^\varepsilon}{\partial t}\right|^2 + \frac{1}{2}\|f'(\cdot,0)\|^2_{L^\infty(\Omega\backslash\overline{B})}\|w_c^\varepsilon\|^2_{L^2(Q_T)}, \end{aligned}$$

where we have applied Young's inequality, thrown away the negative terms, and used the fact that $u_0 \equiv 0$ in B. Setting

$$M_2 = M_2(T) := d\|\nabla u_0\|^2_{L^2(\Omega)} + \|f'(\cdot,0)\|^2_{L^\infty(\Omega\backslash\overline{B})} \sup_{\varepsilon\in(0,\varepsilon_0)} \sup_{c\gg 1} \|w_c^\varepsilon\|^2_{L^2(Q_T)},$$

we find

$$\iint_{Q_T} \left| \frac{\partial w_c^\varepsilon}{\partial t} \right|^2 \leq M_2, \quad \forall c \gg 1 \text{ and } \varepsilon \in (0, \varepsilon_0). \tag{3.27}$$

Passing to the limit $\varepsilon \to 0$ in (3.26) and (3.27), we conclude (3.21) from (3.23).

Step 2 By (3.21), there is a subsequence, still denoted by w_c, and a function $U \in H^1(Q_T)$ such that

$$\begin{aligned} &\lim_{c\to\infty} w_c = U \quad \text{in} \quad L^2(Q_T), \\ &\lim_{c\to\infty} \frac{\partial w_c}{\partial t} = \frac{\partial U}{\partial t} \quad \text{weakly in} \quad L^2(Q_T), \\ &\lim_{c\to\infty} \nabla w_c = \nabla U \quad \text{weakly in} \quad L^2(Q_T). \end{aligned} \tag{3.28}$$

Note that in light of Lemma 3.5.2, U must be the pointwise and monotone limit of w_c as $c \to \infty$. We show $U = 0$ a.e. in $B \times (0, T)$ so that $U \in H^1_B(Q_T)$.

Recall that $\phi_{1,c}$ is a positive eigenfunction of (2.5) associated with the principal eigenvalue $\mu_{1,c}$. The normalization $\|\phi_{1,c}\|_{L^2(\Omega)} = 1$ is fixed. Set $w_c := Me^{-\mu_{1,c}t}\phi_{1,c}$ for some $M > 0$ to be determined. Direct computations yield

$$(w_c)_t - d\Delta w_c = (\mathbb{1}_{\Omega\setminus B} f'(\cdot, 0) - c\mathbb{1}_B) w_c \geq \mathbb{1}_{\Omega\setminus B} f(\cdot, w_c) - c\mathbb{1}_B w_c,$$

where we used in the inequality the fact that $f(\cdot, u) \leq f'(\cdot, 0)u$ for any $u \geq 0$ due to Assumption 2.2.3 (subhomogeneity is sufficient). Obviously, $\frac{\partial w_c}{\partial \nu} = 0$ on $\partial\Omega$.

Theorem 3.4.2 (2) says $\lim_{c\to\infty} \phi_{1,c} = \phi_{1,\infty}$ in $H^1(\Omega)$, where we recall that $\phi_{1,\infty}$ is a positive eigenfunction of (3.5) associated with the principal eigenvalue $\mu_{1,\infty}$ and satisfies the normalization $\|\phi_{1,\infty}\|_{L^2(\Omega\setminus\overline{B})} = 1$. This together with $\frac{\partial \phi_{1,\infty}}{\partial \nu} < 0$ on ∂B and the conditions on u_0 ensures the existence of $M \gg 1$ such that $u_0 \leq M\phi_{1,c}$ for all $c \gg 1$ by Lemma 3.4.1. For such a M, we apply the comparison principle to conclude that $w_c \leq w_c$ in $\overline{\Omega} \times [0, \infty)$ for all $c \gg 1$. This together with Theorem 3.4.2 and the fact $\phi_{1,\infty} \in H^1_B(\Omega)$ yields

$$\limsup_{c\to\infty} \int_0^T \int_B w_c^2 \leq \limsup_{c\to\infty} M^2 \int_0^T e^{-2\mu_{1,c}t} dt \int_B \phi_{1,c}^2 = 0.$$

We then conclude from the monotone convergence theorem or the convergence in (3.28) that $U = 0$ a.e. in $B \times (0, T)$, and hence, $U \in H^1_B(Q_T)$.

Step 3 We show $U = w_\infty$ on $\overline{\Omega} \times [0,T]$. Note that w_c satisfies

$$\iint_{Q_T} \left(\frac{\partial w_c^\varepsilon}{\partial t} v + d\nabla w_c^\varepsilon \cdot \nabla v \right) = \iint_{Q_T} \left(\mathbb{1}^\varepsilon_{\Omega\backslash B} f(\cdot, w_c^\varepsilon) - c\mathbb{1}^\varepsilon_B w_c^\varepsilon \right) v, \quad \forall v \in H^1(Q_T). \tag{3.29}$$

For $v \in C^1([0,T]; H^1_B(\Omega))$ with $v(T) = 0$, we see from (3.29) that

$$-\iint_{Q_{B,T}} \frac{\partial v}{\partial t} w_c + \iint_{Q_{B,T}} \nabla w_c \cdot \nabla v = \iint_{Q_{B,T}} f(\cdot, w_c) v + \int_{\Omega\backslash B} u_0 v(\cdot, 0). \tag{3.30}$$

Note from (3.29) and (3.28) that U satisfies

$$\iint_{Q_{B,T}} \left(\frac{\partial U}{\partial t} v + d\nabla U \cdot \nabla v \right) = \iint_{Q_{B,T}} f(\cdot, U) v, \quad \forall v \in H^1_B(Q_T). \tag{3.31}$$

In particular, for $v \in C^1([0,T]; H^1_B(\Omega))$ with $v(T) = 0$,

$$-\iint_{Q_{B,T}} \frac{\partial v}{\partial t} U + \iint_{Q_{B,T}} \nabla U \cdot \nabla v = \iint_{Q_{B,T}} f(\cdot, w_\infty) v + \int_{\Omega\backslash B} U(\cdot, 0) v(\cdot, 0). \tag{3.32}$$

Comparing (3.30) and (3.32) and taking $c \to \infty$, we find that indeed $U(\cdot, 0) = u_0$ by the arbitrariness of $v(\cdot, 0)$.

Consequently, we have shown that U satisfies (3.31) and $U(\cdot, 0) = u_0$. This is actually a weak formulation of (3.1). Moreover, as the pointwise and monotone limit of w_c as $c \to \infty$, U must be bounded. We show that the weak formulation admits at most one bounded solution, and then, $U = w_\infty$ on $\overline{\Omega} \times [0,T]$.

To this end, we make note of the following fact (see e.g. [123, Lemma 3.1.2]): given a function $w \in H^1_B(Q_T)$ such that $w(\cdot, 0) = 0$, there holds

$$\int_{\Omega\backslash\overline{B}} w^2(\cdot, t) = 2\int_0^t \int_{\Omega\backslash\overline{B}} w \frac{\partial u}{\partial t} \quad \text{a.e.} \quad t \in (0,T). \tag{3.33}$$

Suppose now that there are two bounded solutions $u_1, u_2 \in H^1_B(Q_T)$ satisfying the weak formulation (3.31) and the same initial data belonging to $H^1_B(\Omega) \cap C^+(\overline{\Omega})$, which is assumed to hold in the trace sense. Set $w := u_1 - u_2$ and note that $w(\cdot, 0) = 0$ in $\overline{\Omega} \setminus B$. Then, w satisfies

$$\iint_{Q_{B,T}} \left(\frac{\partial w}{\partial t} v + d\nabla w \cdot \nabla v \right) = \iint_{Q_{B,T}} (f(\cdot, u_1) - f(\cdot, u_2)) v, \quad \forall v \in H^1_B(Q_T).$$

Take $v = w^+ \in H^1_B(Q_T)$ and apply (3.33) and the Lipschitz continuity of $f(x,\cdot)$ to obtain

$$\frac{1}{2}\int_{\Omega\setminus\overline{B}}(w^+)^2(\cdot,t) \leq M \iint_{Q_{B,T}}(w^+)^2.$$

The integral form of Gronwall's inequality implies that $\int_{\Omega\setminus B}(w^+)^2 = 0$ for a.e. $t \in (0,T)$. Repeating the procedure for $v = w^-$, we conclude that $w = 0$ a.e. and the uniqueness follows.

Step 4 As U is the monotone limit of w_c as $c \to \infty$ and $U = w_\infty$ is continuous in $\overline{\Omega}\times[0,T]$ when extended by zero in B, we conclude from Dini's theorem that $w_c \to w_\infty$ uniformly in $\overline{\Omega}\times[0,T]$ as $c \to \infty$. This completes the proof. □

Now, we treat infinite time intervals.

Lemma 3.5.4. *Assume* $\mu_{1,\infty} < 0$. *If* $w_c(\cdot,0) = w_\infty(\cdot,0) \in H^1_B(\Omega)\cap C^+(\overline{\Omega})$ *for all* $c \gg 1$ *and* $\operatorname{supp}(w_\infty(\cdot,0)) \Subset \overline{\Omega}\setminus\overline{B}$, *then there exist* $r > 0$ *and* $M = M(w_\infty) > 0$ *such that*

$$\|w_c(\cdot,t) - w_c^*\|_{C(\overline{\Omega})} \leq Me^{-rt} + \|w_\infty^* - w_c^*\|_{C(\overline{\Omega})}, \quad \forall t > 0 \text{ and } c \gg 1.$$

Proof. The conclusion of the lemma follows from the following two steps. Denote by $w_{00} := w_c(\cdot,0) = w_\infty(\cdot,0)$ the common initial data.

Step 1 We show the existence of $r_1 > 0$ and $M_1 = M_1(u_0) > 0$ such that

$$w_c(\cdot,t) - w_c^* \leq M_1 e^{-r_1 t}, \quad \forall t \geq 0 \text{ and } c \gg 1.$$

By Theorem 3.5.8, w_c^* exists for all $c > 0$. Denote by $\mu_1(d, \mathbb{1}_{\Omega\setminus B}f'(\cdot,w_c^*) - c\mathbb{1}_B)$ the principal eigenvalue of (2.5) with $m := \mathbb{1}_{\Omega\setminus B}f'(\cdot,w_c^*) - c\mathbb{1}_B$, and by $\hat{\psi}_c$ the associated positive eigenfunction satisfying the normalization $\int_\Omega \hat{\psi}_c^2 = 1$. Notice that $\mu_1(d, \mathbb{1}_{\Omega\setminus B}f'(\cdot,w_c^*) - c\mathbb{1}_B) > 0$ for any $c \in (0,\infty)$ due to the concavity of $f(x,\cdot)$. Actually, subhomogeneity is sufficient, since subhomogeneity implies that

$$\frac{f(x,w_c^*)}{w_c^*} \leq f'(0),$$

and so Proposition 2.3.2 (iv) implies that

$$\mu_1(d, \mathbb{1}_{\Omega\setminus B} f'(\cdot, w_c^*) - c\mathbb{1}_B) > 0 = \mu_1(d, \mathbb{1}_{\Omega\setminus B} f(x, w_c^*) - c\mathbb{1}_B),$$

where the second equality follows from the existence of a unique steady state.

We claim that

$$\liminf_{c\to\infty} \mu_1(d, \mathbb{1}_{\Omega\setminus B} f'(\cdot, w_c^*) - c\mathbb{1}_B) > 0. \tag{3.34}$$

Denote by $\mu_1(\mathbb{1}_{\Omega\setminus B} f'(\cdot, w_\infty^*) - c\mathbb{1}_B)$ the principal eigenvalue of (2.5) with $m = \mathbb{1}_{\Omega\setminus B} f'(\cdot, w_\infty^*) - c\mathbb{1}_B$. By a minor modification of the proof of Theorem 3.4.2, it is not difficult to find that

$$\lim_{c\to\infty} \mu_1(d, \mathbb{1}_{\Omega\setminus B} f'(\cdot, w_\infty^*) - c\mathbb{1}_B) = \mu_1(d, f'(\cdot, w_\infty^*), B), \tag{3.35}$$

where $\mu_1(d, f'(\cdot, w_\infty^*), B)$ is the principal eigenvalue of (3.5) with $m = f'(\cdot, w_\infty^*)$.

By the variational characterization of $\mu_1(d, \mathbb{1}_{\Omega\setminus B} f'(\cdot, w_\infty^*) - c\mathbb{1}_B)$, we find

$$\begin{aligned}\mu_1(d, \mathbb{1}_{\Omega\setminus B} f'(\cdot, w_\infty^*) - c\mathbb{1}_B) &\le d\int_\Omega \left|\nabla\hat{\psi}_c\right|^2 - \int_\Omega \hat{\psi}_c^2(\mathbb{1}_{\Omega\setminus B} f'(\cdot, w_\infty^*) - c\mathbb{1}_B)\\ &= \mu_1(d, \mathbb{1}_{\Omega\setminus B} f'(\cdot, w_c^*) - c\mathbb{1}_B) + \int_{\Omega\setminus B} \hat{\psi}_c^2(f'(\cdot, w_c^*) - f'(\cdot, w_\infty^*)).\end{aligned}$$

Theorem 3.5.9 and the normalization $\int_\Omega \hat{\psi}_c^2{=}1$ imply that $\lim_{c\to\infty}\int_{\Omega\setminus B}\hat{\psi}_c^2(f'(\cdot, w_c^*) - f'(\cdot, w_\infty^*)) = 0$. It then follows from (3.35) that

$$\begin{aligned}\mu_1(d, \mathbb{1}_{\Omega\setminus\overline{B}} f'(\cdot, w_\infty^*), B) &= \liminf_{c\to\infty} \mu_1(d, \mathbb{1}_{\Omega\setminus B} f'(\cdot, w_\infty^*) - c\mathbb{1}_B)\\ &\le \liminf_{c\to\infty} \mu_1(d, \mathbb{1}_{\Omega\setminus B} f'(\cdot, w_c^*) - c\mathbb{1}_B).\end{aligned}$$

Since $\mu_1(d, \mathbb{1}_{\Omega\setminus\overline{B}} f'(\cdot, w_\infty^*), B) > 0$, the claim (3.34) follows.

Since w_{00} is continuous and compactly supported in $\overline{\Omega}\setminus\overline{B}$, and $\{\hat{\psi}_c\}_{c\gg 1}$ is locally uniformly positive in $\overline{\Omega}\setminus\overline{B}$ by Lemma 3.4.1, there exists $\tilde{M}_1 > 0$ such that $u_0 \le \tilde{M}_1\hat{\psi}_c$ for all $c \gg 1$. Set

$$W_c := \tilde{M}_1 e^{-\mu_1(d, \mathbb{1}_{\Omega\setminus B} f'(\cdot, w_c^*) - c\mathbb{1}_B)t}\hat{\psi}_c.$$

It is straightforward to check that W_c satisfies

$$(W_c)_t - d\Delta W_c = (\mathbb{1}_{\Omega\setminus B} f'(\cdot, w_c^*) - c\mathbb{1}_B)W_c \quad \text{in} \quad \Omega\times(0,\infty).$$

Note that $\tilde{w}_c := w_c - w_c^*$ obeys

$$(\tilde{w}_c)_t - d\Delta\tilde{w} = \mathbb{1}_{\Omega\setminus B}(f(\cdot, w_c) - f(\cdot, w_c^*)) - c\mathbb{1}_B w_c \leq (\mathbb{1}_{\Omega\setminus B} f'(\cdot, w_c^*) - c\mathbb{1}_B) w_c$$

in $\Omega \times (0, \infty)$, where we used the concavity of f in the inequality. Obviously, both W_c and $\tilde{w}_c$ satisfy the homogeneous Neumann boundary condition on $\partial\Omega$. Since $\tilde{w}_c(\cdot, 0) = w_{00} - w_c^* \leq \tilde{M}_1 \hat{\psi}_c = W_c(\cdot, 0)$, we apply the comparison principle to arrive at $w_c \leq W_c$. Note that Lemma 3.4.2 yields $\sup_{c\gg1} \sup_\Omega \hat{\psi}_c < \infty$. Hence, setting $r_1 := \liminf_{c\to\infty}\{\mu_1(f'(\cdot, w_c^*) - c\mathbb{1}_B\} - \delta > 0$ for some fixed $0 < \delta \ll 1$ and $M_1 := \tilde{M}_1 \sup_{c\gg1} \sup_\Omega \hat{\psi}_c + 1$, we find $w_c(\cdot, t) - w_c^* \leq M_1 e^{-r_1 t}$ for all $t \geq 0$ and $c \gg 1$.

Step 2 We show the existence of $r_2 > 0$ and $M_2 = M_2(u_0) > 0$ such that

$$w_c^* - w_c(\cdot, t) \leq M_2 e^{-r_2 t} + \|w_\infty^* - w_c^*\|_{C(\overline{\Omega})}, \quad \forall t \geq 0 \text{ and } c \gg 1.$$

As we are treating the lower bound for w_c, we may assume without loss of generality that $u_0 \leq u_\infty^*$. Note that Lemma 3.5.2 ensures that $w_\infty \leq w_c$ for all $c \gg 1$, leading to

$$w_c^* - w_c(\cdot, t) \leq \|w_\infty^* - w_c^*\|_{C(\overline{\Omega})} + w_\infty^* - w_\infty(\cdot, t), \quad \forall t \geq 0 \text{ and } c \gg 1, \tag{3.36}$$

where w_∞ solves (3.1) with initial data u_0. Hence, it suffices to derive an exponential-in-time upper bound for $w_\infty^* - w_\infty(\cdot, t)$.

We claim that there exist $t_0 \gg 1$ and $v \in L^\infty(\Omega)$ such that

$$0 \lneqq v \leq w_\infty(\cdot, t) \quad \text{in} \quad \Omega \setminus \overline{B}, \quad \forall t \geq t_0. \tag{3.37}$$

Indeed, since Theorem 3.5.7 ensures that $w_\infty(\cdot, t) \to w_\infty^*$ uniformly in $\overline{\Omega} \setminus B$ as $t \to \infty$, for some fixed $V \Subset \Omega \setminus \overline{B}$ there is $t_0 \gg 1$ such that $\inf_{V\times(t_0,\infty)} w_\infty > 0$. The claim follows readily.

Set $F(w) := \frac{f(\cdot, w_\infty^*) - f(\cdot, w)}{w_\infty^* - w}$. We show $r_2 := \mu_1(d, F(v), B)) > 0$. Indeed, since $w_\infty(\cdot, t) \leq w_\infty^*$ for all $t \geq 0$ by the choice of the initial data w_{00}, we find $v \leq w_\infty^*$ from (3.37). It follows from the concavity of f that $F(v) \leq F(0)$. Noticing that $\mu_1(d, F(0), B) = 0$ (as w_∞^* is exactly the associated eigenfunction), we deduce from Lemma 3.4.2 (ii) and $v \gneqq 0$ (by (3.37)) that $r_2 = \mu_1(d, F(v), B) > \mu_1(d, F(0), B) = 0$.

Set $W_\infty := M_2 e^{-r_2(t-t_0)}\hat{\psi}_\infty$ in $\Omega \setminus \overline{B} \times [t_0,\infty)$, where $\hat{\psi}_\infty$ is the positive eigenfunction of (2.4) with $m = F(w^*_\infty, v)$ associated with the principal eigenvalue $r_2 = \mu_1(d, F(v), B)$, and $M_2 > 0$ is such that $w^*_\infty \le M_2\hat{\psi}_\infty$. Such a M_2 exists due to the positivity of w^*_∞ and $\hat{\psi}_\infty$ in $\overline{\Omega} \setminus \overline{B}$ and the negativity of the outer normal derivative of w^*_∞ and $\hat{\psi}_\infty$ along ∂B. It is straightforward to check that W_∞ satisfies

$$(W_\infty)_t - d\Delta W_\infty = F(v)W_\infty \quad \text{in} \quad (\Omega \setminus \overline{B}) \times (t_0,\infty),$$

while $w := w^*_\infty - w_\infty$ satisfies

$$w_t - d\Delta w = \left(\frac{f(x,w^*_\infty) - f(x,w_\infty)}{w^*_\infty - w_\infty}\right) w \le F(v)w \quad \text{in} \quad (\Omega \setminus \overline{B}) \times (t_0,\infty),$$

where the inequality follows from (3.37) and the concavity of f. Obviously, both W_∞ and w satisfy the homogeneous Neumann boundary condition on $\partial\Omega$ and homogeneous Dirichlet boundary condition on ∂B. Since $w(\cdot,t_0) \le w^*_\infty \le M_2\hat{\psi}_\infty = W_\infty(\cdot,t_0)$, we apply the comparison principle to find $w(\cdot,t) \le W_\infty(\cdot,t)$ for $t \ge t_0$. This can be readily extended to hold for all $t \ge 0$ by making M_2 larger if necessary. The conclusion in this step then follows from (3.36). □

We are ready to prove Theorem 3.5.10.

Proof of Theorem 3.5.10. Clearly, for any $T > 0$,

$$\begin{aligned} A_c &:= \sup_{t\in(0,\infty)} \|w_c(\cdot,t) - w_\infty(\cdot,t)\|_{C(\overline{\Omega})} \\ &\le \sup_{t\in(0,T]} \|w_c(\cdot,t) - w_\infty(\cdot,t)\|_{C(\overline{\Omega})} + \sup_{t\in(T,\infty)} \|w_c(\cdot,t) - w_\infty(\cdot,t)\|_{C(\overline{\Omega})} \\ &=: A^1_c(T) + A^2_c(T). \end{aligned} \tag{3.38}$$

By Lemma 3.5.3,

$$\lim_{c\to\infty} A^1_c(T) = 0, \quad \forall T > 0. \tag{3.39}$$

To treat $A^2_c(T)$, we consider two cases. Denote again by w_{00} the common initial data.

Case 1: $\mu_{1,\infty} > 0$**.** It follows from Corollary 3.5.1 and Theorem 3.5.7 (ii) that $\lim_{T\to\infty}\lim_{c\to\infty} A^2_c(T) = 0$, which together with (3.38) and (3.39) yields $\lim_{c\to\infty} A_c = 0$.

Case 2: $\mu_{1,\infty} < 0$ Obviously, for any $T > 0$,

$$\begin{aligned} A_c^2(T) &\le \sup_{t\in(T,\infty)} \|w_c(\cdot,t) - w_c^*\|_{C(\overline{\Omega})} + \|w_c^* - w_\infty^*\|_{C(\overline{\Omega})} + \sup_{t\in(T,\infty)} \|w_\infty^* - w_\infty(\cdot,t)\|_{C(\overline{\Omega})} \\ &=: \tilde{A}_c^1(T) + \tilde{A}_c^2 + \tilde{A}^3(T). \end{aligned}$$

By Lemma 3.5.4, there exist $r > 0$ and $M = M(w_{00}) > 0$ such that $\tilde{A}_c^1(T) \le Me^{-rT} + \tilde{A}_c^2$ for all $T > 0$ and $c \gg 1$. Since $\lim_{c\to\infty} \tilde{A}_c^2 = 0$ by Theorem 3.5.9 and $\lim_{T\to\infty} \tilde{A}^3(T) = 0$ by Theorem 3.5.7 (1), we find $\lim_{T\to\infty} \lim_{c\to\infty} A_c^2(T) = 0$, which together with (3.38) and (3.39) yields $\lim_{c\to\infty} A_c = 0$.

□

3.6 A competitive system

In this section, we prove the uniform convergence of a competition system subject to habitat degradation, problem (3.2), to a competition system subject to habitat destruction, problem (2.2). To make the problem more tractable, we assume that $0 < d_1 < d_2$ and take the prototypical form given in (3.3). As in the scalar case, we reserve the notation (u_∞, v_∞) for the unique solution to problem (3.2) and denote by (u_c, v_c) the unique solution to problem (2.2) for each $c > 0$.

The main result of this section is the following.

Theorem 3.6.1. *Suppose* $0 < d_1 < d_2$, $\mu_{1,\infty}(d_1) \neq 0$ *and* $\mu_{1,\infty}(d_2) \neq 0$. *Denote by* (u_c, v_c) *and* (u_∞, v_∞) *the unique solutions to problems* (2.2) *and* (3.2), *respectively, with the initial data satisfying* $0 \lneqq u_c(\cdot,0) = u_\infty(\cdot,0) \in C_B^1(\overline{\Omega})$ *and* $0 \lneqq v_c(\cdot,0) = v_\infty(\cdot,0) \in C_B^1(\overline{\Omega})$ *such that* $\mathrm{supp}(u_c(\cdot,0)) \Subset \overline{\Omega} \setminus \overline{B}$ *and* $\mathrm{supp}(v_c(\cdot,0)) \Subset \overline{\Omega} \setminus \overline{B}$. *Then,*

$$\lim_{c\to\infty} (u_c, v_c) = (u_\infty, v_\infty) \quad \textit{uniformly in} \quad \overline{\Omega} \times (0,\infty).$$

Similar to the scalar case, we set for $d > 0$ and $c > 0$,

$$\mu_{1,c}(d) := \mu_1(d, \mathbb{1}_{\Omega\setminus B} m - c\mathbb{1}_B) \quad \text{and} \quad \mu_{1,\infty}(d) := \mu_1(d, m, B).$$

By Theorem 3.4.1 (1), $c \mapsto \mu_{1,c}(d)$ is increasing and $\lim_{c\to\infty} \mu_{1,c}(d) = \mu_{1,\infty}(d)$.

To this end, we first reformulate a previous result, namely Theorem 2.5.2, suited to the current context. This provides a similar result to Theorem 3.5.8, connecting the asymptotic behaviour of the degradation and destruction scalar problems, but not necessarily in a uniform sense.

Theorem 3.6.2. *Consider problem* (2.2) *with fixed* $c > 0$.

(1) *If* $\mu_{1,c}(d_1) < 0$, *then the semi-trivial steady state* $(u_c^*, 0)$ *exists, and for any initial data* $u_0, v_0 \in C^+(\overline{\Omega}) \setminus \{0\}$, *there holds*

$$\lim_{t\to\infty}(u_c(\cdot,t), v_c(\cdot,t)) = (u_c^*, 0) \quad \textit{in} \quad C(\overline{\Omega}) \times C(\overline{\Omega}).$$

Furthermore, if $\mu_{1,\infty}(d_1) < 0$, *then* $\mu_{1,c}(d_1) < 0$ *for all* $c \in (0, \infty)$.

(2) *If* $\mu_{1,c}(d_1) \geq 0$, *then the only steady state is the trivial one, and for any initial data* $u_0, v_0 \in C^+(\overline{\Omega}) \setminus \{0\}$, *there holds*

$$\lim_{t\to\infty}(u_c(\cdot,t), v_c(\cdot,t)) = (0, 0) \quad \textit{in} \quad C(\overline{\Omega}) \times C(\overline{\Omega}).$$

Furthermore, if $\mu_{1,\infty}(d_1) > 0$, *then there exists* C *sufficiently large so that* $\mu_{1,c}(d_1) > 0$ *for all* $c \in (C, \infty)$.

Proof. This result follows directly from the proof of Theorem 2.5.2 when $c_1 = c_2$.

Roughly, one proves that problem (2.2) induces a strongly monotone flow. From the assumption of $0 < d_1 < d_2$ and identical resource distribution, one can then show that $(u_c^*, 0)$ is locally stable while $(0, v_c^*)$ is unstable, whenever it exists. Recall that the existence of non-trivial $(0, v_c^*)$ is given by the sign of $\mu_{1,c}(d_2)$ as found in Theorem 3.5.8. One can then show that there are no coexistence steady states. The conclusion then follows from the theory of monotone flows, e.g., Theorems 1.2.9-1.2.10. □

A similar result holds for the competition destruction problem. We omit the details of the proof as they are essentially the same as the proof of Theorem 3.6.2, with the only change being the cone due to the homogeneous Dirichlet condition along ∂B.

Theorem 3.6.3. *Consider problem* (3.2). *If* $\mu_{1,\infty}(d_1) < 0$, *then the semi-trivial steady state* $(u_\infty^*, 0)$ *exists, and for any initial data* $0 \lneq u_0, v_0 \in C_B^1(\overline{\Omega})$,

$$\lim_{t\to\infty}(u_\infty(\cdot,t), v_\infty(\cdot,t)) = (u_\infty^*, 0) \quad \textit{in} \quad C(\overline{\Omega}) \times C(\overline{\Omega}).$$

In the following, we seek to prove Theorem 3.6.1. Unlike the scalar problem, however, it is no longer expected that $c \mapsto (u_c, v_c)$ is decreasing. This is due to the interplay between the *decrease* in m_c as c increases, and the competition between species; for, if u_c is decreasing, $-u_c$ is *increasing* in the equation for v_c. This is a subtle but important difference between the degradation system and its corresponding scalar equation. Despite this, we are still able to prove a uniform convergence result in a number of steps. Taking motivation from the scalar case, we consider separately the intervals $(0, T)$ and $[T, \infty)$. We first prove convergence in an arbitrary, finite time interval.

Lemma 3.6.1. *For any initial data* $(u_c(\cdot, 0), v_c(\cdot, 0))$ *and* $(u_\infty(\cdot, 0), v_\infty(\cdot, 0))$ *satisfying the same assumptions as in Theorem 3.6.1, it holds that for each* $T > 0$*,*

$$\lim_{c\to\infty} (u_c, v_c) = (u_\infty, v_\infty) \quad \textit{uniformly in} \quad \overline{\Omega} \times [0, T].$$

Proof. Denote by $\tilde{u}_c, \tilde{v}_c$ the unique solutions to problem (2.1) with $d = d_1$, $f = f_1(\cdot, \cdot, 0)$, $\tilde{u}_c(\cdot, 0) = u_c(\cdot, 0)$ and $d = d_2$, $f = f_2(\cdot, 0, \cdot)$, $\tilde{v}_c(\cdot, 0) = v_c(\cdot, 0)$, respectively. We finish the proof within four steps.

Step 1 We show that $\gamma := \max\left\{\sup_{c\gg1} \sup_{\overline{\Omega}\times[0,\infty)} \tilde{u}_c, \sup_{c\gg1} \sup_{\overline{\Omega}\times[0,\infty)} \tilde{v}_c\right\} < \infty$ and

$$e^{-\gamma t}\tilde{u}_c \leq u_c \leq \tilde{u}_c \quad \text{and} \quad e^{-\gamma t}\tilde{v}_c \leq v_c \leq \tilde{v}_c \quad \text{in} \quad \overline{\Omega} \times [0, \infty), \quad \forall c \gg 1.$$

We first demonstrate $\gamma < \infty$. Lemma 3.5.2 implies that $\tilde{u}_c \leq \tilde{u}_1$ in $\overline{\Omega} \times [0, \infty)$ for all $c \geq 1$. Since $\tilde{u}_1$ is bounded thanks to Assumption 2.2.1, we find $\sup_{c\gg1} \sup_{\overline{\Omega}\times[0,\infty)} \tilde{u}_c < \infty$. A similar argument yields $\sup_{c\gg1} \sup_{\overline{\Omega}\times[0,\infty)} \tilde{v}_c < \infty$. Hence, $\gamma < \infty$.

For the two-sided inequalities of u_c and v_c to hold, it suffices to show that for each $c \gg 1$, $(\underline{u}, \overline{v}) := (e^{-\gamma t}\tilde{u}_c, \tilde{v}_c)$ and $(\overline{u}, \underline{v}) := (\tilde{u}_c, e^{-\gamma t}\tilde{v}_c)$ are respectively subsolution and supersolution thanks to the comparison principle.

Clearly,

$$\underline{u}_t - d_1\Delta\underline{u} = -\gamma\underline{u} + \underline{u}(\mathbb{1}_{\Omega\setminus B}m - c\mathbb{1}_B - \tilde{u}_c) \leq \underline{u}(\mathbb{1}_{\Omega\setminus B}m - c\mathbb{1}_B - e^{-\gamma t}\tilde{u}_c - \tilde{v}_c) = f_1(x, \underline{u}, \overline{v}),$$

where $\gamma \geq \tilde{v}_c$ is used in the inequality, and

$$\overline{u}_t - d_1\Delta\overline{u} = \overline{u}(\mathbb{1}_{\Omega\setminus B}m - c\mathbb{1}_B - \overline{u}) \geq \overline{u}(\mathbb{1}_{\Omega\setminus B}m - c\mathbb{1}_B - \overline{u} - \underline{v}) = f_1(x, \overline{u}, \underline{v}),$$

where we used $\overline{v}\underline{u} > 0$ in the inequality. Similarly, we find that $\underline{v}$ and $\overline{v}$ obey $\underline{v}_t \leq d_2\Delta\underline{v} + f_2(x, \overline{u}, \underline{v})$ and $\overline{v}_t \geq d_2\Delta\overline{v} + f_2(x, \underline{u}, \overline{v})$, respectively. Obviously, $\underline{u}$, $\overline{u}$, $\underline{v}$ and $\overline{v}$ satisfy the homogeneous Neumann boundary condition on $\partial\Omega$.

Step 2 We show that

$$\lim_{c\to\infty}(u_c, v_c) = (u_\infty, v_\infty) \quad \text{uniformly in} \quad (\overline{\Omega} \setminus B) \times [0, T].$$

Recall that $Q_{B,T} := (\Omega \setminus \overline{B}) \times (0, T)$. We introduce the following auxiliary problem:

$$\begin{cases} u_t = d_1\Delta u + f_1(x, u, v), & \text{in} \quad Q_{B,T}, \\ v_t = d_2\Delta v + f_2(x, u, v), & \text{in} \quad Q_{B,T}, \\ \frac{\partial u}{\partial \nu} = 0 = \frac{\partial v}{\partial \nu}, & \text{on} \quad \partial\Omega \times (0, T), \\ u = u_c, & \text{on} \quad \partial B \times (0, T), \\ v = v_c, & \text{on} \quad \partial B \times (0, T). \end{cases} \tag{3.40}$$

Since u_c and v_c are Hölder continuous, this problem is well-posed (see, for example, [95, Ch. 8] for a treatment of time dependent boundary data; see also [80, Ch. III, §5]). Denote by $(\hat{u}_c, \hat{v}_c)$ the unique solution of (3.40) with initial data $(\hat{u}_c(\cdot, 0), \hat{v}_c(\cdot, 0)) = (u_c(\cdot, 0), v_c(\cdot, 0))$.

Uniqueness of solutions ensures that $(\hat{u}_c, \hat{v}_c) = (u_c, v_c)$ in $\Omega \setminus \overline{B}$ for $t \in [0, T)$, and hence, $\hat{u}_c \leq \tilde{u}_c\gamma$ and $\hat{v}_c \leq \tilde{v}_c \leq \gamma$ in $Q_{B,T}$ for all $c \gg 1$. In particular, this implies that $\{f_i(\cdot, \hat{u}_c, \hat{v}_c)\}_{c\gg 1}$, $i = 1, 2$ are uniformly bounded in $L^p(Q_{B,T})$ for any $p \geq 1$. Theorem 1.2.30 along with Ehrling-Nirenberg-Gagliardo's interpolation inequality (see, e.g. [123, Theorem 1.3.1] or [1, Theorem 5.2]) ensure that $\{\hat{u}_c\}_{c\gg 1}$ and $\{\hat{v}_c\}_{c\gg 1}$ are uniformly bounded in $W_p^{2,1}(Q_{B,T})$ for any $p \geq 1$. The Sobolev embedding Theorem 1.2.4 then implies the existence of a subsequence, still denoted by $(\hat{u}_c, \hat{v}_c)$, which converges to $(\hat{u}_\infty, \hat{v}_\infty)$ in $C^{1+\alpha,(1+\alpha)/2}(Q_{B,T})$ as $c \to \infty$ for any $\alpha \in (0, 1)$.

We then proceed with the usual bootstrapping argument. Since $f_i(x, \hat{u}_c, \hat{v}_c)$, $i = 1, 2$ are Hölder continuous in $Q_{B,T}$, interior Schauder estimates for parabolic equations (see, for example, [123, Theorem 7.2.5]; this is similar to Theorem 1.2.24 which gives global estimates) ensure that $\{\hat{u}_c\}_{c\gg 1}$ and $\{\hat{v}_c\}_{c\gg 1}$ are uniformly bounded in $C^{2+\alpha,1+\alpha/2}(Q_{B,T})$ for some $\alpha \in (0, 1)$. We may then deduce the existence of a further subsequence (still labelled by c) such that

$$\Delta \hat{u}_c \to \Delta \hat{u}_\infty, \quad \nabla \hat{u}_c \to \nabla \hat{u}_\infty, \quad \hat{u}_c \to \hat{u}_\infty,$$
$$\Delta \hat{v}_c \to \Delta \hat{v}_\infty, \quad \nabla \hat{v}_c \to \nabla \hat{v}_\infty, \quad \hat{v}_c \to \hat{v}_\infty,$$

in $C^{\beta,\beta/2}(Q_{B,T})$ as $c \to \infty$ for any $\beta \in (0, \alpha)$.

We now show that the limit $(\hat{u}_\infty, \hat{v}_\infty)$ satisfies the same initial data and boundary conditions as the solution (u_∞, v_∞) solving (3.2). We provide the details for $\hat{u}_\infty$ with the same arguments holding for $\hat{v}_\infty$. Note that since $B \Subset \Omega$, the boundary data along $\partial\Omega$ is trivially satisfied. From **Step 1** we have already shown that $e^{-\gamma t}\tilde{u}_c \le \hat{u}_c = u_c \le \tilde{u}_c$ in $Q_{B,T}$ for all $c \gg 1$. In the limit, we therefore have that

$$0 \le \limsup_{\substack{x \in \Omega \setminus \overline{B} \\ x \to x_0}} \hat{u}_\infty(x,t) \le \lim_{\substack{x \in \Omega \setminus \overline{B} \\ x \to x_0}} \tilde{u}_\infty(x,t) = 0, \quad \forall (x_0, t) \in \partial B \times [0, T].$$

Hence, $\hat{u}_\infty = 0$ on $\partial B \times [0, T]$. Similarly, we also find that

$$\tilde{u}_\infty(\cdot, 0) = \lim_{t \to 0^+} e^{-\gamma t}\tilde{u}_\infty(\cdot, t) \le \lim_{t \to 0^+} \hat{u}_\infty(\cdot, t) \le \lim_{t \to 0^+} \tilde{u}_\infty(\cdot, t) = \tilde{u}_\infty(\cdot, 0),$$

and so $\hat{u}_\infty(\cdot, 0) = u_c(\cdot, 0)$. Thus, we find that in fact $(\hat{u}_\infty, \hat{v}_\infty)$ belong to $C^{2+\alpha, 1+\alpha/2}(Q_{B,T}) \cap C(\overline{Q}_{B,T})$ for some $\alpha \in (0, 1)$, and is a solution to problem (3.2). The uniqueness of solutions then implies that $(\hat{u}_\infty, \hat{v}_\infty) = (u_\infty, v_\infty)$.

Step 3 Since Theorem 3.5.10 gives that $\tilde{u}_c, \tilde{v}_c \to 0$ uniformly in $\overline{B} \times [0, T]$ as $c \to \infty$, we find from **Step 1** that $\lim_{c \to \infty}(u_c, v_c) = (u_\infty, v_\infty)$ uniformly in $\overline{B} \times [0, T]$. The result then follows from **Step 2**. □

We conclude with the proof of Theorem 3.6.1.

Proof of Theorem 3.6.1. Again, we denote by $\tilde{u}_c, \tilde{v}_c$ the unique solutions to problem (2.1) with $d = d_1$, $f = f_1(\cdot, \cdot, 0)$, $\tilde{u}_c(\cdot, 0) = u_c(\cdot, 0)$ and $d = d_2$, $f = f_2(\cdot, 0, \cdot)$, $\tilde{v}_c(\cdot, 0) = v_c(\cdot, 0)$, respectively. Denote by $\tilde{u}_\infty, \tilde{v}_\infty$ the unique solutions to problem (3.1) with $d = d_1$, $f = f_1(\cdot, \cdot, 0)$, $\tilde{u}_c(\cdot, 0) = u_c(\cdot, 0)$ and $d = d_2$, $f = f_2(\cdot, 0, \cdot)$, $\tilde{v}_c(\cdot, 0) = v_c(\cdot, 0)$, respectively. By Theorem 3.5.10, $\lim_{c \to \infty} \tilde{u}_c = \tilde{u}_\infty$ and $\lim_{c \to \infty} \tilde{v}_c = \tilde{v}_\infty$ uniformly in $\overline{\Omega} \times [0, \infty)$. Set

$$A_c^u := \sup_{t \in [0,\infty)} \|u_c(\cdot, t) - u_\infty(\cdot, t)\|_{C(\overline{\Omega})} \quad \text{and} \quad A_c^v := \sup_{t \in [0,\infty)} \|v_c(\cdot, t) - v_\infty(\cdot, t)\|_{C(\overline{\Omega})}.$$

To treat A_c^u and A_c^v as $c \to \infty$ and in consideration of the fact that $\mu_{1,\infty}(d_1) < \mu_{1,\infty}(d_2)$, we consider three cases: $\mu_{1,\infty}(d_1) > 0$, $\mu_{1,\infty}(d_1) < 0 < \mu_{1,\infty}(d_2)$, and $\mu_{1,\infty}(d_2) < 0$.

Case 1: $\mu_{1,\infty}(d_1) > 0$: It is straightforward to check that $(0, \tilde{v}_c)$ and $(\tilde{u}_c, 0)$ are subsolution and supersolution, respectively. The comparison principle then yields

$$u_c \le \tilde{u}_c, \quad v_c \le \tilde{v}_c, \quad \forall c \gg 1. \tag{3.41}$$

Similarly, $u_\infty \le \tilde{u}_\infty$ and $v_\infty \le \tilde{v}_\infty$. It is evident that, for any $T > 0$,

$$\begin{aligned} A_c^u &\le \sup_{t\in[0,T]} \|u_c(\cdot,t) - u_\infty(\cdot,t)\|_{C(\overline{\Omega})} + \sup_{t\in(T,\infty)} \Big(\|\tilde{u}_c(\cdot,t)\|_{C(\overline{\Omega})} + \|\tilde{u}_\infty(\cdot,t)\|_{C(\overline{\Omega})} \Big) \\ &=: A_c^{u,1}(T) + A_c^{u,2}(T). \end{aligned}$$

Lemma 3.6.1 yields that $\lim_{c\to\infty} A_c^{u,1}(T) = 0$ for any $T > 0$. As $\lim_{c\to\infty} \tilde{u}_c = \tilde{u}_\infty$ uniformly in $\overline{\Omega} \times [0,\infty)$ thanks to Theorem 3.5.10, we arrive at $\lim_{c\to\infty} A_c^{u,2}(T) = 2\sup_{t\in(T,\infty)} \|\tilde{u}_\infty(\cdot,t)\|_{C(\overline{\Omega})}$. Since $\mu_{1,\infty}(d_1) > 0$, Theorem 3.5.7 ensures that

$$\lim_{t\to\infty} \|\tilde{u}_\infty(\cdot,t)\|_{C(\overline{\Omega})} = 0,$$

leading to $\lim_{T\to\infty} \lim_{c\to\infty} A_c^{u,2}(T) = 0$. Hence, $\lim_{c\to\infty} A_c^u = 0$.

Since $\mu_{1,\infty}(d_2) > \mu_{1,\infty}(d_1) > 0$, an identical approach shows that $\lim_{c\to\infty} A_c^v = 0$, concluding the proof of case 1.

Case 2: $\mu_{1,\infty}(d_1) < 0 < \mu_{1,\infty}(d_2)$. In this case, (3.41) still holds. Since $\mu_{1,\infty}(d_2) > 0$, we apply Corollary 3.5.1 to arrive at $\lim_{t\to\infty} \sup_{c\gg1} \|\tilde{v}_c(\cdot,t)\|_{C(\overline{\Omega})} = 0$. Hence, for each $0 < \delta \ll 1$, there is $T_\delta \gg 1$ such that $\sup_{c\gg1} \|v_c(\cdot,t)\|_{C(\overline{\Omega})} \le \delta$ for all $t \ge T_\delta$.

Consider the following auxiliary problem:

$$\begin{cases} u_t = d_1\Delta u + u(\mathbb{1}_{\Omega\setminus B} m - u - \delta) - c\mathbb{1}_B u, & \text{in} \quad \Omega \times (T_\delta, \infty), \\ \frac{\partial u}{\partial \nu} = 0, & \text{on} \quad \partial\Omega \times (T_\delta, \infty). \end{cases} \tag{3.42}$$

Denote by u_c^δ the unique solution of (3.42) with the initial condition $u_c^\delta(\cdot, T_\delta) = u_c(\cdot, T_\delta)$.

First, we claim that

$$u_c^\delta \le u_c \quad \text{in} \quad \overline{\Omega} \times [T_\delta, \infty), \quad \forall c \gg 1. \tag{3.43}$$

Indeed, since $-v_c \geq -\delta$, there holds

$$(u_c)_t - d_1 \Delta u_c = u_c(\mathbb{1}_{\Omega\setminus B} m - u_c - v_c) - c\mathbb{1}_B u_c \geq u_c(\mathbb{1}_{\Omega\setminus B} m - u_c - \delta) - c\mathbb{1}_B u_c.$$

Then, as $u_c(\cdot, T) = u_c^{\delta}(\cdot, T)$, (3.43) follows from the comparison principle.

Second, we claim that for $\delta > 0$ sufficiently small (in fact, $\delta < -\mu_{1,\infty}(d_1)$ is sufficient), there exists a non-trivial steady state $u_c^{\delta,*}$ corresponding to problem (3.42) that is globally attractive. To see this, we note that

$$\mu_1(d_1, \mathbb{1}_{\Omega\setminus B} m - \delta - c\mathbb{1}_B) = \mu_{1,c}(d_1) + \delta \leq \mu_{1,\infty}(d_1) + \delta < 0,$$

where the first inequality follows from Theorem 3.4.2(1). Our second claim then follows from Theorem 3.5.8. Moreover, we have that $\lim_{c\to\infty} u_c^{\delta,*} = u_\infty^{\delta,*}$ in $C(\overline{\Omega})$ by Theorem 3.5.9, where $u_\infty^{\delta,*}$ is the unique positive steady state of (3.1) with $d = d_1$ and $f(x,u) = u(m(x) - \delta - u)$.

Third, we claim that

$$\lim_{\delta\to 0^+} u_\infty^{\delta,*} = u_\infty^* \quad \text{uniformly in } \overline{\Omega}. \tag{3.44}$$

Indeed, using the comparison principle, it is not difficult to see that $u_\infty^{\delta,*}$ is increasing with respect to δ, and is bounded above by u_∞^*. Clearly, the pointwise limit $\lim_{\delta\to 0^+} u_\infty^{\delta,*} = u_\infty^{0,*}$ exists and is non-trivial. Uniqueness of solutions ensures that $u_\infty^{0,*} = u_\infty^*$. Dini's theorem ensures that the convergence is indeed uniform, and so (3.44) holds. In fact, these arguments are almost identical to those used in the proof of Lemma 2.4.2. We omit further details.

We now treat A_c^u and A_c^v. Since $\mu_{1,\infty}(d_2) > 0$, we can follow the arguments as in **Case 1** to conclude that $\lim_{c\to\infty} A_c^v = 0$. For A_c^u, we see that for any $T > 0$,

$$A_c^u \leq \sup_{t\in[0,T]} \|u_c(\cdot,t) - u_\infty(\cdot,t)\|_{C(\overline{\Omega})} + \sup_{t\in(T,\infty)} \|u_c(\cdot,t) - u_\infty(\cdot,t)\|_{C(\overline{\Omega})} =: A_c^{u,1}(T) + A_c^{u,2}(T).$$

By Lemma 3.6.1, $\lim_{c\to\infty} A_c^{u,1}(T) = 0$ for any $T > 0$. We now estimate $A_c^{u,2}(T)$. It follows from (3.41) and (3.43) that $0 \leq u_c - u_c^{\delta} \leq \tilde{u}_c - u_c^{\delta}$ in $\overline{\Omega} \times [T_\delta, \infty)$, leading to

$$\left\|u_c(\cdot,t) - u_c^{\delta}(\cdot,t)\right\|_{C(\overline{\Omega})} \leq \left\|\tilde{u}_c(\cdot,t) - u_c^{\delta}(\cdot,t)\right\|_{C(\overline{\Omega})}, \quad \forall t \geq T_\delta.$$

Thus, for $T \geq T_\delta$,

$$\begin{aligned}
A_c^{u,2}(T) &\leq \sup_{t\in(T,\infty)} \left\| u_c(\cdot,t) - u_c^\delta(\cdot,t) \right\|_{C(\overline{\Omega})} + \sup_{t\in(T,\infty)} \left\| u_c^\delta(\cdot,t) - u_\infty(\cdot,t) \right\|_{C(\overline{\Omega})} \\
&\leq \sup_{t\in(T,\infty)} \left\| \tilde{u}_c(\cdot,t) - u_c^\delta(\cdot,t) \right\|_{C(\overline{\Omega})} + \sup_{t\in(T,\infty)} \left\| u_c^\delta(\cdot,t) - u_\infty(\cdot,t) \right\|_{C(\overline{\Omega})} \\
&=: \tilde{A}_{c,\delta}^{u,1}(T) + \tilde{A}_{c,\delta}^{u,2}(T).
\end{aligned}$$

From our second claim and Theorem 3.5.10, we have for $T \geq T_\delta$,

$$\begin{aligned}
\lim_{c\to\infty} \tilde{A}_{c,\delta}^{u,1}(T) &= \sup_{t\in(T,\infty)} \left\| \tilde{u}_\infty(\cdot,t) - u_\infty^\delta(\cdot,t) \right\|_{C(\overline{\Omega})}, \\
\lim_{c\to\infty} \tilde{A}_{c,\delta}^{u,2}(T) &= \sup_{t\in(T,\infty)} \left\| u_\infty^\delta(\cdot,t) - u_\infty(\cdot,t) \right\|_{C(\overline{\Omega})}.
\end{aligned}$$

Given Theorem 3.5.7, we let $T \to \infty$ to find that

$$\begin{aligned}
\lim_{T\to\infty} \lim_{c\to\infty} \tilde{A}_{c,\delta}^{u,1}(T) &= \left\| \tilde{u}_\infty^* - u_\infty^{\delta,*} \right\|_{C(\overline{\Omega})} = \left\| u_\infty^* - u_\infty^{\delta,*} \right\|_{C(\overline{\Omega})}, \\
\lim_{T\to\infty} \lim_{c\to\infty} \tilde{A}_{c,\delta}^{u,2}(T) &= \left\| u_\infty^{\delta,*} - u_\infty^* \right\|_{C(\overline{\Omega})},
\end{aligned}$$

where we used the fact that $\tilde{u}_\infty^* = u_\infty^*$. It then follows from (3.44) that

$$\lim_{\delta\to0^+} \lim_{T\to\infty} \lim_{c\to\infty} \left(\tilde{A}_{c,\delta}^{u,1}(T) + \tilde{A}_{c,\delta}^{u,2}(T) \right) = 0.$$

Hence, $\lim_{T\to\infty} \lim_{c\to\infty} A_c^{u,2}(T) = 0$, resulting in $\lim_{c\to\infty} A_c^u = 0$. In conclusion, $\lim_{c\to\infty}(A_c^u + A_c^v) = 0$, which completes the proof in this case.

Case 3: $\mu_{1,\infty}(d_2) < 0$ This is the most difficult case since we do not have direct control via $\tilde{u}$ or $\tilde{v}$. Instead, we carefully construct new sub/super solutions to show that $v_c \to 0$, and then proceed as in **Case 2**. As in the previous cases, we focus on the large time interval (T,∞) for some $T \gg 1$ fixed since convergence in any finite time interval $[0,T]$ follows from Lemma 3.6.1.

To this end, we still choose $(\overline{u}, \underline{v}) = (\tilde{u}_c, 0)$, which satisfies the appropriate differential inequalities as shown in Theorem 3.5.10, **Case 1**. We then set $(\underline{u}, \overline{v}) = (\hat{u}_c, \hat{v}_c)$, where $\hat{v}_c$ solves

$$\begin{cases} (\hat{v}_c)_t - d_2\Delta\hat{v}_c = \hat{v}_c(\mathbb{1}_{\Omega\setminus B}m - c\mathbb{1}_B + \sigma - u_c^* - \hat{v}_c), & \text{in } \Omega\times(T,\infty), \\ \hat{v}_c(\cdot,T) = v_c(\cdot,T), & \text{in } \overline{\Omega}, \\ \frac{\partial\hat{v}_c}{\partial\nu} = 0, & \text{on } \partial\Omega\times(T,\infty), \end{cases} \tag{3.45}$$

and $\hat{u}_c$ solves

$$\begin{cases} (\hat{u}_c)_t - d_1\Delta\hat{u}_c = \hat{u}_c(\mathbb{1}_{\Omega\setminus B}m - c\mathbb{1}_B - \hat{v}_c - \hat{u}_c), & \text{in } \Omega\times(T,\infty), \\ \hat{u}_c(\cdot,T) \le u_c(\cdot,T), & \text{in } \overline{\Omega}, \\ \frac{\partial\hat{u}_c}{\partial\nu} = 0, & \text{on } \partial\Omega\times(T,\infty). \end{cases} \tag{3.46}$$

In (3.45), $0 < \sigma \ll 1$ is held fixed to be chosen independent of c. Without loss of generality, we may assume that $\hat{u}_c(\cdot,T) \le u_c^*$ for all $c \gg 1$. The comparison principle readily yields that $\hat{u}_c(\cdot,t) \le u_c^*$ for all $t \ge T$ and $c \gg 1$. Moving forward, we suppress the dependence of $(\hat{u}_c,\hat{v}_c)$ on σ.

We first claim that for σ sufficiently small,

$$\lim_{t\to\infty}\sup_{c\gg1}\|\hat{v}_c(\cdot,t)\|_{C(\overline{\Omega})} \to 0. \tag{3.47}$$

To see this, let $\tilde{w}_c$ solve

$$\begin{cases} (\tilde{w}_c)_t - d_2\Delta\tilde{w}_c = \tilde{w}_c(\mathbb{1}_{\Omega\setminus B}m - c\mathbb{1}_B + \sigma - u_\infty^* - \tilde{w}_c), & \text{in } \Omega\times(T,\infty), \\ \tilde{w}_c(\cdot,T) = \varphi(\cdot), & \text{in } \overline{\Omega}, \\ \frac{\partial\tilde{w}_c}{\partial\nu} = 0, & \text{on } \partial\Omega\times(T,\infty), \end{cases} \tag{3.48}$$

where $\varphi \in C^+(\Omega)$ satisfies $\sup_{c\gg1} v_c(\cdot,T) \le \varphi(cdot)$, which is possible due to the fact that $\sup_{c\gg1}\|v_c(\cdot,T)\|_{C(\overline{\Omega})} < \infty$ by Lemma 3.5.2. Then, since $u_\infty^* < u_c^*$ for all $c \gg 1$, the comparison principle yields $\hat{v}_c(\cdot,t) \le \tilde{w}_c(\cdot,t)$ for all $t \ge T$ and $c \gg 1$. Moreover, we have that

$$\mu_1(d_2, m_c - u_\infty^*) \le \mu_1(d_2, m_c - u_c^*)$$

by Proposition (2.3.2)(iii). Furthermore, Lemma 3.4.2 yields

$$\lim_{c\to\infty}\mu_1(d_2, m_c - u_\infty^*) \nearrow \mu_1(d_2, m - u_\infty^*, B) > \mu_1(d_1, m - u_\infty^*, B) = 0,$$

where $\mu_1(d_2, m - u_\infty^*, B)$ is the principal eigenvalue to problem (2.5) with $d = d_2$ and $f_u(x,0) = m - u_\infty^*$. Hence, for c sufficiently large, there exists $0 < \sigma \ll 1$ so that

$$\mu_1(d_2, m_c - u_c^*) - \sigma = \mu_1(d_2, m_c - u_c^* + \sigma) > 0,\ \forall c \gg 1. \tag{3.49}$$

Choosing $c^* \gg 1$ fixed and $\sigma \ll 1$ small enough so that (3.49) holds, we set

$$\tilde{W} = Me^{-\mu_1(d_2, m_{c^*} - u_{c^*}^* + \sigma)t}\psi_{c^*},$$

where ψ_{c^*} is the corresponding eigenfunction to $\mu_1(d_2, m_{c^*} - u^*_{c^*} + \sigma)$. One readily obtains that $\tilde{W}$ is a super solution to w_{c^*} by choosing $M \gg 1$ so that

$$\varphi(\cdot) \leq W(\cdot, T).$$

Hence, $\lim_{t\to\infty} \|\tilde{w}_{c^*}\|_{C(\overline{\Omega})} \leq \lim_{t\to\infty} \left\|\tilde{W}\right\|_{C(\overline{\Omega})} = 0$. Finally, by Lemma 3.5.2, it is not difficult to see that $\tilde{w}_c$ is decreasing with respect to c. Consequently, for all $c \geq c^*$, we have that

$$\hat{v}_c(\cdot, t) \leq \tilde{w}_c(\cdot, t) \leq w_{c^*}(\cdot, t),$$

and so it follows that

$$\lim_{t\to\infty} \sup_{c\gg1} \|\hat{v}(\cdot, t)\|_{C(\overline{\Omega})} \leq \lim_{t\to\infty} \sup_{c\gg1} \|w_c(\cdot, t)\|_{C(\overline{\Omega})} \leq \lim_{t\to\infty} \left\|\tilde{W}_{c^*}\right\|_{C(\overline{\Omega})} = 0,$$

and (3.47) holds.

Next, notice that while $\hat{u}_c$ depends on $\hat{v}_c$, $\hat{v}_c$ remains independent of $\hat{u}_c$ and so (3.45)-(3.46) do not comprise a fully coupled system of equations.

Through construction, $\underline{u}$ trivially satisfies

$$\underline{u}_t - d_1 \underline{u} = \underline{u}(\mathbb{1}_{\Omega\setminus B} m - c\mathbb{1}_B - \underline{u} - \overline{v}). \tag{3.50}$$

For $\overline{v}$ we then compute

$$\begin{aligned} \overline{v}_t - d_2 \overline{v} = \overline{v}(\mathbb{1}_{\Omega\setminus B} m - c\mathbb{1}_B + \sigma - u^*_c - \overline{v}) &\geq \overline{v}(\mathbb{1}_{\Omega\setminus B} m - c\mathbb{1}_B - \underline{u} - \overline{v}) \\ \iff u^*_c \leq \underline{u} + \sigma = \hat{u}_c + \sigma. & \end{aligned} \tag{3.51}$$

Since (3.47) holds, we may choose $T = T(\delta) \gg 1$ independent of c so that $\overline{v}(\cdot, t) \leq \delta$ for all $t \geq T$, for any given $\delta > 0$ fixed. We then proceed as in **Case 2** to show that (3.51) holds for T sufficiently large, for all $c \gg 1$.

To this end, for a (possibly new) value $\delta > 0$ satisfying $0 < \delta \ll \sigma \ll 1$, we construct yet another solution $\hat{u}^\delta_c$ solving problem (3.42) with $\hat{u}^\delta_c(\cdot, T) = \hat{u}_c(\cdot, T)$. Arguing as we did to show (3.43) in the proof of **Case 2**, one similarly finds that

$$\hat{u}^\delta_c(\cdot, t) \leq \hat{u}_c(\cdot, t) \leq u^*_c(\cdot), \quad \forall t \geq T, \ \forall c \gg 1, \tag{3.52}$$

and for δ small enough there exists a unique non-trivial steady state $u_c^{\delta,*}$ such that $\hat{u}_c^{\delta}(\cdot,t) \to u_c^{\delta,*}(\cdot)$ in $C(\overline{\Omega})$ as $t \to \infty$ for all $c \gg 1$. Note that (3.52) also gives us

$$0 \leq u_c^*(\cdot) - \hat{u}_c(\cdot,t) \leq u_c^*(\cdot) - \hat{u}_c^{\delta}(\cdot,t) \Rightarrow \|u_c^*(\cdot) - \hat{u}_c(\cdot,t)\|_{C(\overline{\Omega})} \leq \left\|u_c^*(\cdot) - \hat{u}_c^{\delta}(\cdot,t)\right\|_{C(\overline{\Omega})},$$

for all $t \geq T$, for all $c \gg 1$. We then estimate as follows:

$$\left\|u_c^*(\cdot) - \hat{u}_c^{\delta}(\cdot,t)\right\|_{C(\overline{\Omega})} \leq \left\|u_c^* - u_c^{\delta,*}\right\|_{C(\overline{\Omega})} + \left\|u_c^{\delta,*}(\cdot) - \hat{u}_c^{\delta}(\cdot,t)\right\|_{C(\overline{\Omega})} =: A_c^{\delta,1} + A_c^{\delta,2}(t). \tag{3.53}$$

By Theorem (3.52) and the subsequent remarks, there exists $T \gg 1$ such that for all $t \geq T$, $c \gg 1$, there holds

$$A_c^{\delta,2}(t) \leq \frac{\sigma}{2}.$$

Estimating now $A_c^{\delta,2}$ we find

$$A_c^{\delta,1} \leq \|u_c^* - u_\infty^*\|_{C(\overline{\Omega})} + \left\|u_\infty^* - u_\infty^{\delta,*}\right\|_{C(\overline{\Omega})} + \left\|u_\infty^{\delta,*} - u_c^{\delta,*}\right\|_{C(\overline{\Omega})} =: I_1 + I_2 + I_3. \tag{3.54}$$

By Theorem 3.5.9, we may choose C sufficiently large so that

$$I_1 + I_3 \leq \frac{\sigma}{4} \quad \forall c \geq C.$$

Similarly, by (3.44) we may choose δ sufficiently small so that

$$I_2 \leq \frac{\sigma}{4}.$$

Combining these results, we find that

$$\left\|u_c^*(\cdot) - \hat{u}_c^{\delta}(\cdot,t)\right\|_{C(\overline{\Omega})} \leq A_c^{\delta,1} + A_c^{\delta,2}(t) \leq \sigma \quad \forall t \geq T,\ \forall c \gg 1.$$

Finally, we are able to conclude that

$$u_c^*(\cdot) - \hat{u}_c(\cdot,t) \leq \left\|u_c^*(\cdot) - \hat{u}_c^{\delta}(\cdot,t)\right\|_{C(\overline{\Omega})} \leq \sigma$$

for all $t \geq T$, for all $c \gg 1$, and so (3.51) indeed holds.

Combining (3.50) and (3.51) and noting the ordering of the initial data, the comparison principle yields that

$$\begin{aligned} \hat{u}_c^{\delta}(\cdot,t) \leq \hat{u}_c(\cdot,t) = \underline{u} \leq & u_c(\cdot,t) \leq \overline{u} = \tilde{u}_c(\cdot,t), \\ 0 = \underline{v} \leq & v_c(\cdot,t) \leq \overline{v} = \hat{v}_c(\cdot,t), \quad \forall t \geq T,\ \forall c \gg 1. \end{aligned} \tag{3.55}$$

We are now prepared to estimate A_c^u, A_c^v. Obviously,

$$A_c^v \leq \sup_{t\in[0,T]} \|v_c(\cdot,t) - v_\infty(\cdot,t)\|_{C(\overline{\Omega})} + \sup_{t\in(T,\infty)} \|v_c(\cdot,t) - v_\infty(\cdot,t)\|_{C(\overline{\Omega})} =: A_c^{v,1}(T) + A_c^{v,2}(T), \tag{3.56}$$

Lemma 3.6.1 gives that $\lim_{c\to\infty} A_c^{u,1}(T) = 0$ and $\lim_{c\to\infty} A_c^{v,1}(T) = 0$.

We continue now to estimate $A_c^{v,2}(T)$. Using (3.55), we may write for any $c \geq C$

$$\begin{aligned} A_c^{v,2}(T) &\leq \sup_{t\in(T,\infty)} \left(\|\hat{v}_c(\cdot,t)\|_{C(\overline{\Omega})} + \|v_\infty(\cdot,t)\|_{C(\overline{\Omega})} \right) \\ &\leq \sup_{t\in(T,\infty)} \left(\|\hat{v}_C(\cdot,t)\|_{C(\overline{\Omega})} + \|v_\infty(\cdot,t)\|_{C(\overline{\Omega})} \right), \end{aligned}$$

where the second inequality follows from the monotonicity of $\hat{v}_c(\cdot,\cdot)$ given by Lemma 3.5.2. From (3.47) and Theorem 3.6.3, we may then take the limit as $T\to\infty$ to obtain

$$\lim_{T\to\infty} A_c^{v,2}(T) \leq \lim_{T\to\infty} \sup_{t\in(T,\infty)} \left(\|\hat{v}_C(\cdot,t)\|_{C(\overline{\Omega})} + \|v_\infty(\cdot,t)\|_{C(\overline{\Omega})} \right) = 0.$$

We now treat $A_c^{u,2}(T)$ using (3.55) once more:

$$\begin{aligned} A_c^{u,2}(T) &\leq \sup_{t\in(T,\infty)} \left\| u_c(\cdot,t) - \hat{u}_c^\delta(\cdot,t) \right\|_{C(\overline{\Omega})} + \sup_{t\in(T,\infty)} \left\| \hat{u}_c^\delta(\cdot,t) - u_\infty(\cdot,t) \right\|_{C(\overline{\Omega})} \\ &\leq \sup_{t\in(T,\infty)} \left\| \tilde{u}_c(\cdot,t) - \hat{u}_c^\delta(\cdot,t) \right\|_{C(\overline{\Omega})} + \sup_{t\in(T,\infty)} \left\| \hat{u}_c^\delta(\cdot,t) - u_\infty(\cdot,t) \right\|_{C(\overline{\Omega})} \end{aligned} \tag{3.57}$$

By Theorem 3.5.10, we may take the limit as $c\to\infty$ in (3.57) to find

$$\begin{aligned} \lim_{c\to\infty} A_c^{u,2}(T) &\leq \lim_{c\to\infty} \left(\sup_{t\in(T,\infty)} \left\| \tilde{u}_c(\cdot,t) - \hat{u}_c^\delta(\cdot,t) \right\|_{C(\overline{\Omega})} + \sup_{t\in(T,\infty)} \left\| \hat{u}_c^\delta(\cdot,t) - u_\infty(\cdot,t) \right\|_{C(\overline{\Omega})} \right) \\ &= \sup_{t\in(T,\infty)} \left\| \tilde{u}_\infty(\cdot,t) - \hat{u}_\infty^\delta(\cdot,t) \right\|_{C(\overline{\Omega})} + \sup_{t\in(T,\infty)} \left\| \hat{u}_\infty^\delta(\cdot,t) - u_\infty(\cdot,t) \right\|_{C(\overline{\Omega})}, \end{aligned}$$

where $\tilde{u}_\infty$ solves problem (3.1) with $d = d_1$, $f = \tilde{u}_\infty(m - \tilde{u}_\infty)$ and $\hat{u}_\infty^\delta$ solves problem (3.1) with $d = d_1$ and $f = \hat{u}_\infty(m - \delta - \hat{u}_\infty)$. Note that in this step, we must also choose δ small enough so that Assumption 2.2.1 holds. Taking now $T\to\infty$, we further obtain by Theorem's 3.5.10 and 3.6.3 that

$$\begin{aligned} \lim_{T\to\infty} \lim_{c\to\infty} A_c^{u,2}(T) &\leq \lim_{T\to\infty} \left(\sup_{t\in(T,\infty)} \left\| \tilde{u}_\infty(\cdot,t) - \hat{u}_\infty^\delta(\cdot,t) \right\|_{C(\overline{\Omega})} + \sup_{t\in(T,\infty)} \left\| \hat{u}_\infty^\delta(\cdot,t) - u_\infty(\cdot,t) \right\|_{C(\overline{\Omega})} \right) \\ &= \left\| u_\infty^* - \hat{u}_\infty^{\delta,*} \right\|_{C(\overline{\Omega})} + \left\| \hat{u}_\infty^{\delta,*} - u_\infty^* \right\|_{C(\overline{\Omega})} \\ &= 2 \left\| \hat{u}_\infty^{\delta,*} - u_\infty^* \right\|_{C(\overline{\Omega})} \end{aligned}$$

Finally, by (3.44), we may take $\delta \to 0^+$ to get the final estimate

$$\lim_{T\to\infty}\lim_{c\to\infty} A_c^{u,2}(T) \le \lim_{\delta\to 0^+} 2\left\|\hat{u}_\infty^{\delta,*} - u_\infty^*\right\|_{C(\overline{\Omega})} = 0.$$

Combining all estimates, we are able to conclude that

$$\lim_{c\to\infty}\left(A_c^u + A_c^v\right) = 0,$$

completing the proof of **Case 3**, and the Theorem is proven. □

3.7 Numerical simulation

In Figure 3.3, we observe numerical validation of Theorem 3.5.9. Actually, these profiles are obtained using MATLAB's `pdepe` function after running long enough to reach a steady state. Then we plot the solution profile as the parameter c increases. As in the degradation case, we fix the domain $\Omega = (0, L)$ with a single degraded region $B = (4, 6)$ in the centre of Ω. The habitat quality is 1 everywhere in $G = (0, 4) \cup (6, 10)$.

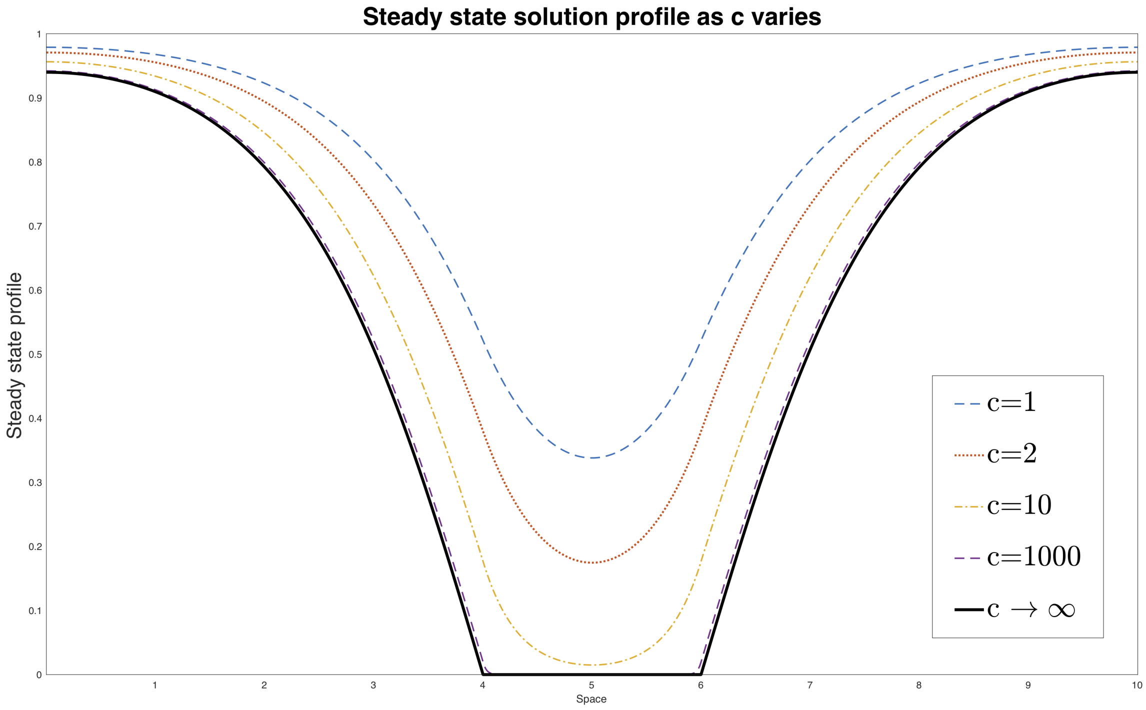


Figure 3.3: A simulation demonstrating Theorem 3.5.9 in one spatial dimension.

Note that we do not consider the simulation of results for the competition system. Indeed, the dynamic results are a little less interesting in this case (population u always wins), and so it will look essentially identical to Figure 3.3 above.

3.8 Discussion

In this chapter we developed a habitat destruction model using reaction-diffusion equations. This was formulated from two perspectives. The first, coming from the definition of habitat *destruction* appealed to in this work, we conceptualize a model in a 'domain with holes'. These holes represent the destroyed region of habitat, prescribed a homogeneous Dirichlet boundary condition along the inner boundary of the hole ∂B. The second perspective, coming from Postulate One (*degradation and destruction lie on a spectrum*), involves taking a limit as $c \to \infty$ in the degradation problem of Chapter 2; naturally this should correspond to a habitat destruction problem. As was established analytically, these two perspectives are equivalent. These constitute the key results of this chapter: the uniform convergence between the habitat degradation model developed in Chapter 2 and the new habitat destruction model developed here. This result is proven for a general right-hand side in the parabolic scalar case; a similar result holds for the elliptic steady states. Of note is the fact that this convergence holds uniformly in time. For the competition case, we appeal to a standard Lotka-Volterra competition model. As far as we can tell, this is the first modelling perspective establishing a mathematically rigorous connection between the process of habitat degradation and habitat destruction.

To study the habitat destruction problem in the first perspective (independent of any connection with the degradation model), we had to develop some fundamental theory. These developments are new in that they do not appear to exist in any present texts, at least in an explicit way. However, these developments do follow from existing theory of Hilbert spaces and standard 'energy method'/Galerkin approximation techniques. This establishes a well-posedness theory for linear equations in domains with holes. Nevertheless, in Chapter 4, this development will prove very useful in that it indicates where and why, exactly, our assumptions on the set B are required. This is particularly relevant for the question of habitat *fragmentation*.

Related to the convergence the parabolic and elliptic problems are the convergence results between the related eigenvalue problems. As we have seen in the last two chapters, an understanding of the global dynamics depends critically on the behaviour of these principal eigenvalues. A significant portion of this chapter was dedicated to exactly this. In Section 3.4, we introduce the relevant principal eigenvalue corresponding to the habitat destruction problem. The properties of these new eigenvalue problems are closely related to the eigenvalue problems introduced in Chapter 2. Indeed, a precise convergence result is established between both the principal eigenvalues and the corresponding eigenfunctions. This is the steppingstone required to connect the global dynamics of the degradation problem with the global dynamics of the destruction problem, and ultimately, to prove the uniform convergence between these solution sets. Also of note is the uniform upper and lower bounds of the principal eigenfunctions as they depend on the parameter c. This result, while intuitive, is highly non-trivial in the end. An application of the Moser iteration technique seems to be the only applicable method to obtain these bounds.

The results found in this chapter are also ecologically relevant. On the surface, they validate the modelling perspective: increasing degradation leads to regions with a population density of zero. This is in agreement with what many consider to be the *definition* of habitat loss: *the habitat is altered so dramatically that it can no longer sustain the species it once did.* In this case, the extirpation of species is a *consequence* of habitat destruction and the modelling formulation used. This gives a 'lower bound' on the likelihood for persistence of a population: if the principal eigenvalue of the *destruction* problem indicates persistence, the population will always survive in a degraded region. This may seem like a trivial fact, but it is also robust. Moreover, to establish this and to demonstrate it rigorously in any modelling setting is a challenge not often taken on.

In addition, we can make a comparison to the results obtained in Chapter 2: when the habitat is merely degraded at some level, coexistence is always a possibility for some parameter regimes. In contrast to the results of the present chapter, we find that when a habitat is destroyed, coexistence is *never* a possibility, and we recover the 'slower diffuser always wins!' result. While interesting, this is a consequence of the fact that we assume the environmental heterogeneity in the remaining good region $\Omega \setminus B$ is identical for each population. As noted previously, this may be too restrictive to draw broad conclusions. It may then be of interest to combine the perspective of the last two chapters: one may consider 'good' and 'degraded' regions, in addition to destroyed regions. Trade-offs in resilience and dispersal rates may then facilitate coexistence, even in the habitat destruction setting. We leave such explorations for future work.

Inside of these results are some rather technical assumptions on the set B. Unlike Chapter 2, we now require the boundary of B to be smooth and to be compactly contained in the landscape Ω. The reason is simple enough: our analysis requires some distance between the boundary of B and the boundary of Ω. With some further technical arguments, it is likely that such conditions can be weakened significantly. In increasing order of difficulty, one may consider less regular sets B, allow ∂B to touch $\partial\Omega$ at a single point, and then allow ∂B to touch $\partial\Omega$ along an interval. One difficulty is that along this shared portion, the problem may become ill-posed due to the 'double' boundary condition (homogeneous Neumann and Dirichlet at the same time). For this reason, one may need to modify the problem further to study such cases in detail.

Related to this, we require some rather strong assumptions on the initial data. In particular, we must have that the initial data start with zero population density in the destroyed region B. This is again more of a technical requirement and does not limit its ecological application. Despite this, it may be possible to prove a similar convergence result on the *open* interval (δ, T) for any $\delta > 0$. Such compatibility conditions are common in the study of PDE, and so such restrictions are not entirely unexpected (e.g., the initial data satisfying a homogeneous Dirichlet boundary condition for convergence up to $t = 0$ in a standard Dirichlet problem setting). We leave a further study of such technicalities for future work.

Chapter 4

Habitat Fragmentation

In the last two chapters, we studied in detail the global dynamics of some reaction-diffusion equations and systems. This chapter is a departure from this level of mathematical analysis, opting now for a combination of analytical insights which are complementary to some numerical insights. This is of necessity, in some sense, as the analytical challenges of the problems we are about to explore are significant. More precisely, we seek to investigate the impacts of habitat *fragmentation* in this chapter. Under any reasonable definition of habitat fragmentation, this naturally leads to the study of the influence of the size and geometry of the degraded/destroyed region B.

First, we discuss in more detail some of the conceptual and practical challenges that arise when studying habitat fragmentation. In Section 4.1, we discuss some challenges from the perspective of an ecologist. We then discuss how these confusions appear to have bled into the modelling literature, and how we might remedy this (possibly growing) disconnect. In Section 4.2 we describe some of the existing measures used to assess fragmentation in a quantitative way. We will not use these formulations in any direct way; however they provide insights into the kinds of qualitative behaviour of fragmentation that researchers explore. Essential to our exploration will again be some principal eigenvalues, all of which have been introduced in Chapters 2-3; we prove some analytical results concerning the geometry of the region B and changes in principal eigenvalues in Section 4.3. These results are rather technical, and no effort is made to connect to the ecological application there. In Section 4.4, we finally explore how to assess the impact of habitat fragmentation using the setting of partial differential equations. Recall from Chapter 1 Postulate Three: habitat fragmentation can be studied *as an arrangement* or *as a process* [33]. There are actually further distinctions to make: in each setting, we may consider so-called species-oriented measures or pattern-oriented measures. We construct one measure for each, namely, the SOFFI score and POFI score, respectively. A third approach, somewhat removed from the first two, will assess the impact of fragmentation from the perspective of population sizes. We construct two measures for this perspective: the TAFI score for single-species models, and the R-TAFI score for multiple-species models. In Sections 4.5-4.6, we explore in detail each of these measures *as an arrangement* and *as a process*, respectively. These sections include some analytical insights, but the most detailed and interesting information will come from numerical simulations. We conclude with a discussion and broad implications of these results in Section 4.7.

4.1 Preface

In Chapter 1, we introduced three primary components of habitat loss: degradation, destruction, and *fragmentation*. From this discussion and the subsequent results of Chapters 2-3, we found that while habitat degradation and destruction are intimately linked, assumed to lie on a shared spectrum and then rigorously connected through an asymptotic limit, the process of habitat fragmentation is more distinct. In some sense, habitat fragmentation is an epiphenomenon: as a natural habitat undergoes a process of degradation and destruction, it contemporaneously becomes fragmented. It is the process of habitat removal itself that results in a fragmented landscape[1].

This fact can, it seems, lead to some confusion in the literature. The following references provide insights into the robust nature of the debates: [32], [33], [39], [44], [46], [49]. These works motivate the discussion found here.

In particular, such confusions are found in the disconnect between modelling efforts seeking to describe and quantify habitat fragmentation in some meaningful way, and the perspectives and insights provided by ecologists most interested in the preservation

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[1] Note carefully that we distinguish habitat fragmentation as a consequence of habitat loss from natural changes in the heterogeneity of the environment.

of species. From the point of view of the ecologist, there are a number of challenges when using field studies and data to assess the impacts of fragmentation:

- **Lack of consensus.** There does not appear to be a consensus on what we mean by *habitat fragmentation* (this point was discussed at length in Section 1.1), let alone which *measure* is most useful to assess impacts of habitat fragmentation. One commonly used approach includes measuring and comparing population-level fitness quantities, such as net population growth rates or total abundances under different landscape circumstances (quality or arrangement) [44]. The importance of the distinction between measuring a growth rate versus the total abundance will become evident shortly.

- **Scale matters.** Many data are collected at the *patch* scale rather than the *landscape* scale: if a landscape is made up of many smaller, roughly distinct patches, data collected within these smaller patches making up the entire landscape matrix may not accurately reflect the trends at the landscape scale [33], [39]. This naturally leads to inconsistencies in modelling when it is not clear whether a model is appropriate for the patch or landscape scale.

- **Data collection can be challenging.** Fitness alone is difficult to quantify and measure. For example, we cannot easily measure the growth rate of a population directly, particularly in natural ecosystems [2]; instead, we often count the number of instances of a particular species in a given area (methods include a mark-recapture study, using (births-deaths)/(time) to estimate a net growth rate, recording changes in population sizes over time, or using a laboratory setting. Some useful resources in this regard are [117] and [78]). This is expensive and time-consuming work, therefore making it difficult to repeat for a large number of species. This in turn makes generalization difficult. Pairing these challenges with the complex dynamics of habitat fragmentation as it occurs in the natural world introduces a second challenge highlighted below.

- **How to connect with fragmentation.** Even once a fitness measure is obtained or data collected, one must introduce a mechanism to connect with habitat fragmentation. This could focus on the particular species, its unique traits, and reasonable assumptions on what is required for its survival. On the other hand, one could describe independently different arrangements of habitat, and then correlate this with collected data statistically. This approach is explored in [58] and [120]; we expand on this point and discuss some of their insights momentarily.

- **Context matters.** It is not clear that measuring population growth rates and total abundances will tell us the same thing; actually, it may be unreasonable to assume that they would in the first place. To see this, one may consider a single population that is in decline from a previously thriving population; the total abundance may be very high while their net population change is negative. This can lead to a number of logical errors. First, if one models habitat fragmentation with the output a predicted growth rate, while the data is total abundance, one must take care in connecting these pieces of information directly. Second, it leads to a logical inconsistency if we do not clarify what is meant by a "better" or "worse" outcome: if population u under arrangement B_1 has a smaller growth rate but larger total abundance than population v under arrangement B_2, fragmentation could be "better" or "worse" for one population depending on what we care about. This is highly relevant for both industry and conservation efforts: a struggling population would benefit more from maximizing its growth rate, while industry may prefer to maximize yield.

- **Confounding factors.** Even if the issues raised above are addressed, many existing measures of fragmentation correlate highly with total available habitat [33], [120]. This raises issues when studying in more realistic, less idealized scenarios, where habitat arrangement and amount are varied simultaneously. Untangling their relative effects then becomes an additional challenge [35].

These challenges are explored in more detail in [74], asserting *"...most manipulative and mensurative fragmentation experiments have not provided clear insights into the ecological mechanisms and effects of habitat fragmentation."*. Furthermore, habitat fragmentation is evidently intimately related to the species under consideration, and the environment in which they live. Hence, we have substantial motivation to construct novel and informative modelling techniques which

i.) Make predictions and hypotheses derived from biologically reasonable first principles that can be rigorously tested; derivation should be mechanistic.

ii.) Assess impacts of habitat fragmentation in a general enough setting that a wide range of species can be considered.

iii.) Assess the impacts of fragmentation in combination with other environmental factors.

iv.) Are accessible to mathematical biologists and ecologists. Such tools should complement existing efforts and experimental findings.

Generally, a *species-area* approach is utilized to study the effects of habitat loss [34]; this does not consider the configuration of the landscape, however, which introduces confounding factors and unclear results [32].

From this discussion, we are inspired to take motivation from [44]: rather than choosing a particular perspective and ignoring others, we aim to study the problem of habitat fragmentation from two distinct perspectives, wherein we consider two further standpoints within each overarching perspective. This will be comparable to our efforts to study habitat degradation and destruction on a (continuous) spectrum, in some sense. The modelling of habitat fragmentation can be broken roughly into two categories. One end of this spectrum is *species-oriented* approaches. This approach focuses heavily on the species and their individualistic responses to their environment, and in our case, their response to environmental change. These approaches study exogenous threats (habitat loss), endogenous threats (behaviour changes, biological changes, species interactions), stochastic threats (environmental, genetic), or extinction proneness (interaction between species attributes and processes that threaten). On one hand, this perspective is useful in that it considers explicitly the individual traits of a species; on the other hand, it is limited in scope as it is impossible to do this for every species across widely varying landscapes.

On the other end of the spectrum are the *pattern-oriented* approaches. These cases essentially focus on classifying different patterns as geometric objects through some measure, then connecting this quantification with habitat fragmentation through, e.g., statistical correlations with empirical data [44]. These approaches study native vegetation (amount, size and structure of patches), edge effects, landscape connectivity, and the interaction between matrix and landscape heterogeneity. This perspective may be easier to apply in some cases, offering more flexibility and multiple perspectives through numerous measures available; yet a lack of mechanistic connection to the species considered makes generalization difficult, or even misleading [44].

These two approaches can be used in a complementary fashion, each providing different insights or providing alternative hypotheses to be tested and verified. Note that this distinction and exposition, while closely related to the study of habitat fragmentation "as an arrangement" versus "as a process", is not equivalent. To be clear, one may apply a species-oriented *or* pattern-oriented approach to either fragmentation "as a process" or fragmentation "as an arrangement".

Before we explore these ideas in more detail, we briefly explore some existing perspectives for measuring the impacts of habitat fragmentation.

4.2 Existing methodologies to assess impacts of fragmentation

In this section we present some of the existing measures of fragmentation, most of which are from the perspective of a 'pattern-oriented' approach. While there are many ecological studies assessing the impacts of fragmentation from a 'species-oriented' approach, there are limited works presently in the literature that study this from a rigorous mathematical perspective. For this reason, we direct most of our attention to the general trends found in statistical approaches.

We present primarily some of the ideas found in [58] and [120]. Suppose we are given a population growth rate for two identical populations under different arrangements of habitat, but with the total available habitat kept equal. One must first determine which arrangement is "more" or "less" fragmented. Then we can correlate these quantifications with the measured fitness levels to determine the impact of a fragmented landscape. In the first paper, authors present and compare a handful of common analytical tools that measure the level of fragmentation of a two-colored image; the second paper, appearing over a decade after the first, performs a similar analysis, but with many variations of the measures found in the first. As described earlier, they then perform an analysis of correlations *between each fragmentation measure*.

In [58], they do not connect these measures to ecological findings necessarily; instead, they look for correlations between measures, indicating which measures tell us something *unique* about the landscape, or which measures may be superfluous. These measures are therefore deemed *pattern-oriented* approaches, since they do not connect directly to any particular species or individual traits. The purpose of the presentation here is not to give a detailed account of their findings, but rather to gain some perspective into what kind of qualities or properties are commonly used to assess "fragmentation".

Edge density: The total length of patch edge per unit area within a landscape [87]. In principle, one imagines that as the edge length per unit area increases, the landscape is more fragmented. This measure is, however, susceptible to misinterpretation as it is sensitive to the resolution of the map used (think of fractal-like objects, which can have infinite edge length and finite area).

Contagion: Describes to what extent pixels are clustered. In [58], it is calculated as the sum of two probabilities: *"the probability that a pixel belongs to cover type i, equivalent to the proportional representation of the cover type on the map, and the conditional probability that, given a pixel is type i, that one of the neighbouring cells is cover type j"* [87]. This measure will be relevant to later constructions of fragmented landscapes in the present work, where this concept of contagion motivates our construction of simulated, fragmented landscapes.

Mean nearest neighbour distance: Defines an average edge-to-edge distance between a given patch and its nearest neighbouring patch. This measure does *not* use patch area, and the distance is calculated based *only* on the closest other patch.

Mean proximity index: A *proximity index* measures the level of isolation of a patch within a group of patches. The determining factor is the search radius, which determines which neighbouring patches are included in the calculation. The value is given by a sum of the ratio of patch size to nearest neighbour edge-to-edge distance. The *mean proximity index* is then the average of the proximity index over all patches. Note that, different from the mean nearest neighbour distance, patch size is incorporated.

Perimeter-area fractal dimension: Provides information on the roughness of a patch edge. It is calculated as a slope of a ratio of the log of the perimeter and area of each patch [87]. This measure actually lies between 1 and 2, where values closer to 2 indicate a more complex patch edge. The average across all patches is then calculated.

Mass fractal dimension: Calculates the complexity of the entire landscape, rather than of individual patches. The measure describes how the relationship between the number of pixels of a given landcover type in a pre-sized box changes with respect to changes in the size of the box.

Many additional measures can be obtained through modification of these prototypical measures, each of which are studied in detail in [58].

The authors then used simulated landscapes to explore what each measure predicts for a level of fragmentation. In most cases, this is done for two landcover types only (good or bad). The authors found that correlations were highest between any combination of edge density, contagion, and mass fractal dimension, which implies that these three measures roughly tell us the same thing. This is perhaps unsurprising based on the nature of the construction of the measures. Edge density and contagion over increasing land removal were almost exactly inversely proportional. In [120], a huge number of other fragmentation measures, mostly modifications of similar forms to those found here, are considered (see [120, Table 1], listing over 50 different measures).

While an interesting and useful contribution, the issues raised previously permeate these approaches. Some authors even assert that classifying all of these measures can be a daunting task [118], with endless modifications available. Related to the *mass fractal dimension* are other perspectives that seek to measure fragmentation through a single index. One rudimentary tool was developed in [5]. Others include "image-classification" approaches, which measure fragmentation via the complexity (in a computer science sense) of an image. This can be studied using compression algorithms, for example, where a more "fragmented" landscape has higher complexity and therefore takes more space to store [118]. This is more of a "top-down" approach, similar to the approach we will develop here.

Finally, there are a handful of modelling efforts falling under a more *species-oriented* approach. The first is [113], where a PDE approach is used. While the original formulation features explicit spatial structure, simplifying assumptions are used to reduce it to ordinary differential equations. To achieve this, the authors write the solution to their one-dimensional PDE as a Fourier series expansion, retain only the first term and drop all higher order terms (i.e., a linearization procedure). This first mode satisfies an ordinary differential equation which they then analyze. We instead seek to retain an explicit spatial structure due to the important connection it has to habitat fragmentation. More recently, [21] develops what they refer to as the *Preston function*, which describes *triphasic species–area relationships for contiguous regions.* This Preston function comes from a spatially neutral model, and the authors construct new formulas that relate it to several new fragmentation scenarios. They apply their measure to real and simulated landscapes to determine species-area relationships as they also depend on spatial arrangements. The potential drawback to this approach is that the results may be biased due to its derivation from a spatially neutral setting, requiring the distribution of the species considered to be 'statistically similar to those of neutral species', limiting its scope.

Our ultimate goal in this chapter is to develop robust assessment tools. In what follows, we develop some fragmentation measures using tools and results obtained in Chapters 2-3. The primary object of study will be the associated eigenvalue problems, and in particular, changes in the size of the principal eigenvalue with respect to changes in the lost region B. As it turns out, the principal eigenvalue obtained via a linearization procedure (about 0) is directly related to the intrinsic growth rate of the population, at least for small population sizes [8], [94]. Hence, studying changes in this population growth rate allows one to make direct connections between the geometric properties of a degraded/destroyed region and the fitness of the population. Therefore, we take a moment to explore some technical analytical results. We then connect these results to some fragmentation indices developed in Section 4.4. Due to the level of complexity in studying such problems analytically, we use numerical simulation to gain further insights.

4.3 Properties of principal eigenvalues as a function of $B \Subset \Omega$

In this section, we explore properties of the principal eigenvalues for problems 2.4, 2.5, 3.4 and 3.5. We focus primarily on demonstrating some results for $\lambda_1(m, B)$; similar results follow for all other eigenvalue problems. As we soon find, these proofs depend critically on certain properties of the principal eigenvalue $\lambda_1(m, B)$, all of which are satisfied by the other eigenvalue problems as well.

For tractability, we simplify the problem and consider only $\lambda_1(B) := \lambda_1(1, B)$, the special case where the habitat quality is 1 everywhere in $\Omega \setminus B$. Note that in such a case, the connection to $\mu_1(d, 1, B)$, the principal eigenvalue to problem (3.5), is rather direct.

Continuity of $\lambda_1(B)$ with respect to B

We prove the following theorem regarding the continuity of $\lambda_1(B)$ with respect to the set B, in some sense. Denote by $B_r(x_0)$ the ball of radius $r > 0$ about the point $x_0 \in \Omega$. Recall that the Hausdorff distance between two subsets of Euclidean space is given by

$$d(A_1, A_2) = \inf \left\{ r > 0 : A_2 \subset F_r(A_1) \text{ and } A_1 \subset F_r(A_2) \right\},$$

where $F_r(A) := \cup_{x \in A} B_r(x)$ is the so called "r-fattening" of the set A. We have the following continuity result with proof following modification of the techniques used in [42, Theorem 1.6].

Theorem 4.3.1. *Suppose A, A_n are closed subsets compactly contained in Ω such that $d(A, A_n) \to 0$ as $n \to \infty$. Denote by $\lambda_1(A_n)$, $\lambda_1(A)$ the principal eigenvalues to* *problem* (3.4) *with* $B := A_n$, $n \in \mathbb{N}$, *and* $B := A$, *respectively. Denote by* ψ_1^n, ψ_1 *the corresponding eigenfunctions. Then it is true that*

$$\lim_{n\to\infty} |\lambda_1(A) - \lambda_1(A_n)| = 0.$$

Furthermore, there holds

$$\lim_{n\to\infty} \psi_1^n = \psi_1 \quad \textit{strongly in} \quad H^1(\Omega).$$

Proof. Let $A_\varepsilon = F_\varepsilon(A)$ for some $\varepsilon > 0$ and assume that $d(A, A_n) \to 0$ as $n \to \infty$. Then for any fixed $\varepsilon > 0$, there exists $\overline{n}$ large enough so that $A_n \subset A_\varepsilon$ for all $n \geq \overline{n}$. Obviously $A \subset A_\varepsilon$ holds by definition, and so we then have that

$$H^1_{A_\varepsilon}(\Omega) \subset H^1_{A_n}(\Omega) \cap H^1_A(\Omega). \tag{4.1}$$

Consequently, $\lambda_1(A_n) \leq \lambda_1(A_\varepsilon)$ by Proposition 3.4.1 (i) for all $n \geq \overline{n}$.

By the density of $C^1_A(\Omega)$ in $H^1_A(\Omega)$ (by definition; recall that under our regularity assumptions for the hole in Ω, $H^1_A(\Omega)$ can be identified through the completion of $C^1_A(\Omega)$ with respect to the H^1-norm), there exists a function $\psi_1^\delta \in C^\infty(\Omega)$, which vanishes in a neighbourhood of A, and is H^1-close to ψ_1, i.e.

$$\left\|\psi_1 - \psi_1^\delta\right\|^2_{H^1(\Omega)} \leq \delta,$$

for each $\delta > 0$. Furthermore, we may choose ε small enough so that the support of ψ_1^δ is contained within $\overline{\Omega} \setminus A_\varepsilon$. This implies that $\psi_1^\delta \in H^1_{A_\varepsilon}(\Omega) \subset H^1_{A_n}(\Omega)$, and ψ_1^δ is a valid test function in the variational characterization of $\lambda_1(A_n)$:

$$\begin{aligned}
\lambda_1(A_n) &\leq \left\|\nabla\psi_1^\delta\right\|^2_{L^2} \\
&\leq \|\nabla\psi_1\|^2_{L^2} + \left\|\nabla\psi_1^\delta - \nabla\psi_1\right\|^2_{L^2} \\
&\leq \lambda_1(A) + \delta.
\end{aligned}$$

Repeating this process for the eigenfunction ψ_1^n associated to $\lambda_1(A_n)$ (which is possible due to (4.1)), we find that

$$\lambda_1(A) \leq \lambda_1(A_n) + \delta.$$

Note that, as $A, A_n \subset A_\varepsilon$, we may choose δ depending only on A_ε. Combining these results we conclude that

$$|\lambda_1(A) - \lambda_1(A_n)| \leq \delta,$$

as desired.

Next, since $\lambda_1(A_n) \to \lambda_1(A)$, under a unit L^2-normalization we find that

$$\|\nabla \psi_1^n\|_{L^2(\Omega)}^2 = \lambda_1(A_n) < \infty,$$

and so $\{\psi_1^n\}_{n=1}^\infty$ is uniformly bounded in $H^1(\Omega)$. A subsequence therefore exists (which we still denote by n) such that $\psi_1^n \to \psi_\infty$ strongly in $L^2(\Omega)$ and weakly in $H^1(\Omega)$, for some $\psi_1^\infty \in H_A^1(\Omega)$. In particular, $\psi_1^\infty \equiv 0$ a.e. in A by the strong convergence in $L^2(\Omega)$. By the variational characterization of $\lambda_1(A)$ and the weak lower semicontinuity of the norm, we then observe that

$$\lambda_1(A) \leq \|\nabla \psi_1^\infty\|_{L^2}^2 \leq \liminf_{n\to\infty} \|\nabla \psi_1^n\|_{L^2}^2 \leq \lim_{n\to\infty} \lambda_1(A_n) = \lambda_1(A),$$

and so $\psi_1^\infty \equiv \psi_1$ by the uniqueness of the eigenfunction. This completes the proof. □

We have the following corollary for problem (3.5).

Corollary 4.3.1. *Under the same assumptions, Theorem 4.3.1 also holds for* $\mu_1(d, m, B)$, *the principal eigenvalue for problem* (3.5).

This result holds for the degradation eigenvalue problems as well. Note that in this case the result is somewhat trivial: the convergence result $\mu_1(d, m_n) \to \mu_1(d, m)$ for $m_n \to m$ in $C(\overline{\Omega})$ actually holds if m_n converges in $L^p(\Omega)$ for $p > N/2$ [8], [43]. Hence, the continuity of $\lambda_1(\mathbb{1}_G m - c\mathbb{1}_B)$ and $\mu_1(d, \mathbb{1}_G m - c\mathbb{1}_B)$ with respect to B follows immediately whenever

$$\lim_{n\to\infty} \|\mathbb{1}_{A_n} - \mathbb{1}_A\|_{L^p(\Omega)} = 0$$

for any $p \geq 1$. This is a different form of convergence than in the Hausdorff sense; one may replace Hausdorff with convergence in the sense of *symmetric difference*, i.e., the (Lebesgue) measure of the set $(A_1 \setminus A_2) \cup (A_2 \setminus A_1)$. The technicalities surrounding different measures with respect to different metrics in different spaces are quite complex and beyond the scope of the present work; for this reason, we focus less on true *rigour* and more on the big picture as it applies to biological application. This does leave room for future work, however, as such an exploration may yield different insights into the measures which we use to assess fragmentation.

Differentiability of $\lambda_1(A)$ under certain deformations

In this section, we prove (using essentially existing results) that the function $\lambda_1(A)$ is differentiable with respect to perturbations of the set A. The sense in which this differentiability holds is the following: consider a smooth map $V : \mathbb{R}^N \to \mathbb{R}^N$ referred to as the *deformation field*. Then, we consider perturbations of the set A of the form

$$A_t := (Id + tV)(A) = \{x + tV(x),\ x \in A\}\,.$$

Then the following theorem holds.

Theorem 4.3.2. *The function $\lambda_1(A_t)$ is differentiable with respect to t at $t = 0$ and has the form*

$$\frac{d}{dt}\lambda_1(A_t)\bigg|_{t=0} = \lambda_1'(A) = -\int_{\partial A}\left(\frac{\partial\psi_1}{\partial\nu}\right)^2\langle V,\nu\rangle\, dS,$$

where ψ_1 is the normalized eigenfunction associated to $\lambda_1(A)$ and ν denotes the outer normal vector to ∂A.

Remark 4.3.1. *This result is emblematic of Hadamard's variational formula and related formulations, see [53]. The pairing $\langle V,\nu\rangle$ plays the role of the usual outward facing unit normal vector, denoted by $\partial/\partial\nu$ throughout the present work. The more abstract form $\langle V,\nu\rangle$ is somewhat complicated; we avoid most of the technical details but provide appropriate references and key steps in the following proof.*

Proof. The proof of this result follows from identical computations found in the [41]. Actually, our setting is much simpler. We highlight the key steps only, leaving out technical computations.

First, one shows the differentiability of $\lambda_1(A_t)$ *and* its associated eigenfunction ψ_t at $t = 0$ through an application of the implicit function theorem ([41, Lemma 2.1]) and the Fredholm alternative. Such a result also follows from the more abstract theory developed in [75, Chapter 5], but the following approach is more direct. Essentially, one applies the IFT to the map

$$g(t) = (\lambda_1(A_t), \psi_t) \in \mathbb{R} \times H^1_{A_t}(\Omega).$$

From our previous results, $g(0) = (\lambda_1(A), \psi_1)$ and is continuous at zero. Using the weak formulation of solutions to the eigenvalue problem for $t > 0$ and the IFT, it follows that $g(t)$ is differentiable at $t = 0$, that is, $\lambda_1(A_t)$ and ψ_t are differentiable at zero (see the proof of [41, Lemma 2.7]). This does not, however, immediately give us the form for $\lambda'(A)$ found in the theorem.

Once differentiability is established, one formulates the associated PDE to which $\psi' := \frac{\partial \psi_t}{\partial t}\big|_{t=0}$ is a solution. In fact, ψ' solves

$$\begin{cases} \Delta\psi' + \lambda_1'\psi_1 + \lambda_1\psi', & \text{in} \quad \Omega, \\ \frac{\partial \psi'}{\partial \nu} = 0, & \text{on} \quad \partial\Omega, \\ \psi' = -\frac{\partial \psi_1}{\partial \nu}\langle V, \nu\rangle, & \text{on} \quad \partial A, \end{cases}$$

where $\langle \cdot, \cdot \rangle$ denotes a pairing along ∂A between the deformation field V and the normal vector ν. Again, this formulation is somewhat complicated, so we refer to the detailed discussion in [53] regarding the interpretation of $\langle V, \nu\rangle$. Roughly, it is defined as *the rate of deformation of the surface ∂A in the instantaneous normal direction.* Also note that in the derivation of this problem, the normal derivative $\partial\psi_1/\partial\nu$ actually appears as the gradient $\nabla\psi_1$ along ∂A; therefore, the gradient along ∂A is actually in the direction of the normal, and so they are equivalent along ∂A.

Once it is verified that ψ' satisfies the problem above, we multiply by a test function $\psi \in H^1(\Omega)$ with unit L^2-norm. Integrating over Ω yields

$$\int_\Omega \Delta\psi'\psi + \lambda_1' \int_\Omega \psi_1\psi + \lambda_1 \int_\Omega \psi'\psi = 0.$$

Substitute $\psi := \psi_1$ and apply Green's second identity to obtain

$$\lambda_1' + \int_\Omega \psi'\Delta\psi_1 + \lambda_1 \int_\Omega \psi'\psi_1 + \int_{\partial A} \psi' \frac{\partial \psi_1}{\partial \nu} = 0,$$

where all other boundary terms vanish, and we have used that ψ_1 has unit L^2-norm. Substituting the equation satisfied by $\Delta\psi_1$ and the boundary condition along ∂A satisfied by ψ', we obtain the result found in the theorem statement. □

This result yields the following interesting corollary.

Corollary 4.3.2. *Consider $\Omega = B_R(0)$ for some $R > 0$. Then the hole $A := B_r(0)$ for $0 < r < R$ fixed is critical in the sense that $\lambda_1'(A) = 0$ for all divergence free deformations of A. Furthermore, $B_r(0)$ is a global maximum with respect to translations of the set $B_r(0)$ such that $B_r(0) \subset\subset B_R(0)$.*

Proof. First, one immediately finds that when $A = B_r(0)$, $\Omega = B_R(0)$, solutions to the problem are radially symmetric. Hence, $\frac{\partial \psi_1}{\partial \nu} = C > 0$ for some constant C all along ∂A. Hence, using the formula for $\lambda_1'(B_r(0))$ obtained in Theorem 4.3.2 we have

$$\begin{aligned}\lambda_1'(B_r(0)) &= -\int_{\partial A} \left(\frac{\partial \psi}{\partial \nu}\right)^2 \langle V, \nu\rangle \, dS \\ &= -C^2 \int_{\partial A} \langle V, \nu\rangle \, dS = 0,\end{aligned}$$

since V is a divergence free vector field.

Next, we consider transformations of the form $A_t := B_r(-t, 0, \dots, 0)$, i.e. a translation of the ball in the first coordinate. Note that due to symmetry of the problem under translations, we may consider without loss of generality translations in one coordinate direction along that particular axis. In two dimensions, this is simply the ball of radius r centred at the point $(t, 0)$ for $0 < t < R - r$. Note the upper bound on t ensures that $A_t \subset\subset \Omega$.

We now construct a test function for any appropriately chosen translation based on the radially symmetric solution ψ_0 corresponding to $\lambda_1(A_0) = \lambda_1(B_r(0))$. To this end, take ψ_0 and define $\tilde{\psi} = \psi_0(-t, 0, \dots, 0)$ so that $\tilde{\psi} \equiv 0$ in a (fixed) translated hole $B_{r,t} := B_r(-t, 0, \dots, 0)$. Then we extend $\tilde{\psi}$ to $\mathbb{R}^N$ by a constant value, where the constant is given by $\max_{x \in \overline{\Omega}} \psi_0$. We can better understand the approach through Figure 4.1.

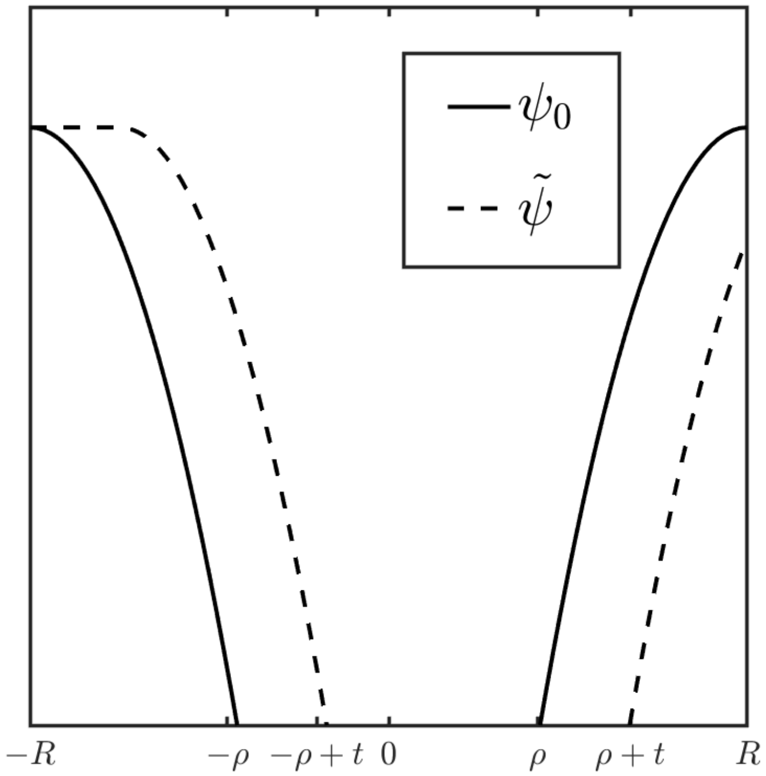

Figure 4.1: A schematic demonstrating the idea behind the proof of Corollary 4.3.2. The solid curve denotes the eigenfunction ψ_0 when the hole $B_\rho(t)$ is placed exactly in the centre $t = 0$. The dashed curve denotes the shifted eigenfunction $\tilde{\psi}$. On the right side, we 'lose' some of the eigenfunction. On the left side, we extend the eigenfunction by a constant value. This is our test function. Then, since the (weak) gradient of this test function is identically *zero* in the extended region, it contributes nothing in the variational characterization of the eigenvalue.

Claim: $\max_{x\in\overline{\Omega}} \psi_0 = \max_{x\in\partial B_R(0)} \psi_0$, and so this extension is continuous on $B_R(0)$. In particular, $\tilde{\psi} \in H^1_{B_{r,t}}(B_R(0))$ and is thus a valid test function on this space.

The proof of this claim can be seen as follows. Since ψ_0 is radially symmetric, denote by $\phi(s)$ the solution solving $\phi'' + s^{-1}\phi' + \lambda_1\phi = 0$ subject to $\phi'(R) = \phi(r) = 0$. By the positivity of ϕ in Ω and the boundary condition at r, one readily finds that an interior minimum is impossible. Suppose now that an interior maximum occurs at some point $s_0 \in (r, R)$. Because an interior minimum is impossible, there is no other such maximum in (s_0, R). Then, on the interval $(s_0 - \varepsilon, R)$ we would find

$$\begin{aligned} \phi'(s) &> 0 \text{ on } (s_0 - \varepsilon, s_0); \\ \phi'(s_0) &= 0; \\ \phi'(s) &< 0 \text{ on } (s_0, R); \\ \phi'(R) &= 0. \end{aligned}$$

Then,

$$\phi''(R) = \lim_{h \to 0} \frac{\phi'(R) - \phi'(R-h)}{h} = -\lim_{h \to 0} \frac{\phi'(R-h)}{h} > 0,$$

for h small. This is a contradiction, since $\phi''(R) = -\lambda_1 \phi(R) < 0$. Hence, no interior maximum exists and $\max_{x \in \overline{\Omega}} \psi_0 = \max_{x \in \partial B_R(0)} \psi_0$.

We now estimate as follows: since $\tilde{\psi} \equiv \mathit{const.}$ in $B_R(0) \setminus B_{R,t}$, we find that

$$\begin{aligned} \int_{B_R(0)} \left|\nabla \tilde{\psi}\right|^2 dx &= \int_{B_R(0) \setminus B_{R,t}} \left|\nabla \tilde{\psi}\right|^2 dx + \int_{B_R(0) \cap B_{R,t}} \left|\nabla \tilde{\psi}\right|^2 dx \\ &\leq \int_{B_R(0) \setminus B_{R,t}} \left|\nabla \psi_0\right|^2 dx + \int_{B_R(0) \cap B_{R,t}} \left|\nabla \tilde{\psi}\right|^2 dx \\ &= \int_{B_R(0)} \left|\nabla \psi_0\right|^2 dx. \end{aligned}$$

Next, by the claim above, since $\psi_0 \leq \tilde{\psi}$ in $B_R(0) \setminus B_{R,t}$, we have that

$$\int_{B_R(0)} \psi_0^2 dx \leq \int_{B_R(0)} \tilde{\psi}^2 dx.$$

Consequently, from the variational characterization of $\lambda_1(B_{r,t})$, we have that

$$\begin{aligned} \lambda_1(B_{r,t}) &\leq \frac{\int_\Omega \left|\nabla \tilde{\psi}\right|^2}{\int_\Omega \tilde{\psi}^2} \\ &\leq \frac{\int_{B_R(0)} \left|\nabla \psi_0\right|^2}{\int_{B_R(0)} \psi_0^2} \\ &= \lambda_1(B_r(0)). \end{aligned}$$

Furthermore, since $\tilde{\psi}$ is *not* an eigenfunction of the translated problem, this inequality is strict. Hence, $\lambda_1(B_{r,t}) < \lambda_1(B_r(0))$ for any $t > 0$. In particular, this implies that $\lambda_1(B_r(0))$ is a maximum among translated balls within a larger ball. □

We can also prove the following result which provides the asymptotic behaviour of the principal eigenvalue $\lambda_1(B_\rho)$ as $\rho \to R^-$.

Theorem 4.3.3. *Suppose* $N = 2$. *Fix* $R > 0$ *with* $0 < \varepsilon_0 \leq \rho < R$. *Then there holds*

$$\lambda_1(B_\rho(0)) \geq \max\left\{\frac{1}{(R-\rho)^2} - \frac{1}{2}\left(M^2 + \varepsilon_0^{-1}\right),\ 0\right\},$$

where $M = M(R) := \max_{x \in \partial B_R(0)} \psi_1$. *In particular, since* ψ_1 *is uniformly bounded for all* $\rho \in (\varepsilon_0, R)$,

$$\lambda_1(B_\rho(0)) \sim (R-\rho)^{-2}$$

as $\rho \to R^-$.

Actually, this result will follow from a relatively elementary result: a Poincaré-type inequality that is a property of the underlying space $H^1_\rho(B_R(0))$.

Lemma 4.3.1. *For any* $\psi \in H^1_\rho(B_R(0))$ *it is true that*

$$\int_\rho^R \phi^2 dr \leq (R-\rho)^2 \int_\rho^R |\phi'|^2\, dr.$$

Proof. Let $r \in (0, \rho)$. Using the fundamental theorem of calculus and applying Hölder's inequality we can write

$$\begin{aligned} |\phi(r)|^2 &= \left|\int_\rho^r \phi' ds\right|^2 \\ &\leq (r-\rho)\int_\rho^r |\phi'|^2\, ds \\ &\leq (R-\rho)\int_\rho^R |\phi'|^2\, ds. \end{aligned}$$

Hence, if we integrate this with respect to r we find

$$\begin{aligned} \int_\rho^R \phi^2 dr &\leq \int_\rho^R \left((R-\rho)\int_\rho^R |\phi'|^2\, ds\right) dr \\ &= (R-\rho)^2 \int_\rho^R |\phi'|^2\, ds, \end{aligned}$$

and the result is proved. $\square$

We now prove Theorem 4.3.3.

Proof of Theorem 4.3.3. Set $\Omega := B_R(0) \subset \mathbb{R}^2$, $A := B_\rho(0) \subset \mathbb{R}^2$ with $0 < \rho < R$. Then, the solution to our eigenvalue problem is radially symmetric, and our eigenvalue problem can be written as follows through a polar-coordinate transform:

$$\begin{cases} r^2\phi'' + r\phi' + \lambda_1 r^2 \phi = 0, & \text{in} \quad (\rho, R), \\ \phi'(R) = 0, \\ \phi(\rho) = 0. \end{cases}$$

The abstract framework in Chapter 3 guarantees the existence of a principal eigenvalue $\lambda_1(B_\rho(0))$ with eigenfunction ψ_1. Choose ψ_1 with unit L^2-norm. Since $\rho > 0$, $\lambda_1 > 0$ by Theorem 3.4.1.

Dividing both sides of the equation by r^2, multiplying by ψ_1 and integrating by parts on the second order derivative term yields

$$\lambda_1(B_\rho(0)) = \int_\rho^R |\psi_1'|^2 - \int_\rho^R \frac{1}{r}\left(\frac{\psi_1^2}{2}\right)'.$$

Note that we have only λ_1 on the left-hand side by the normalization of the eigenfunction. Applying the Lemma and integrating by parts once more, we find

$$\lambda_1(B_\rho(0)) \geq (R-\rho)^{-2} - \frac{1}{2}\left(\psi_1^2(R) + \int_\rho^R \left(\frac{\psi_1}{r}\right)^2\right).$$

Finally, using the normalization of ψ_1 once more along with the fact that $0 < \varepsilon_0 \leq \rho$ to obtain

$$\lambda_1(B_\rho(0)) \geq (R-\rho)^{-2} - \frac{1}{2}\left(\psi_1^2(R) + \varepsilon_0^{-1}\right),$$

and the proof is complete. □

We have the following consequence, relating the previous result to behaviour of $\mu_1(d, 1, B_\rho(0))$.

Corollary 4.3.3. *Fix $d > 0$. Then, there exists $\rho^* = \rho^*(d) > 0$ such that*

$$\mu_1(d, 1, B_\rho(0)) > 0$$

for all $\rho \in (\rho^*, R)$.

Proof. The result follows from the asymptotic behaviour of $\lambda_1(B_\rho(0))$ as $\rho \to R^-$ and Theorem 3.4.2. In fact, ρ^* is given by the unique value such that

$$\lambda_1(B_{\rho^*}(0)) = d,$$

whose existence for any $d > 0$ follows from the monotonicity properties of λ_1 and the fact that $\lambda_1(B_\rho(0)) \searrow 0$ as $\rho \to 0$. $\square$

We now state an interesting result found in [8] which applies to the degradation problem (2.4). We modify the statement to fit the notation used here.

Theorem 4.3.4. *Let $m_n(x) \in L^\infty(\Omega)$ for each $n = 1, 2, \ldots$. Suppose further that there is a constant M_1 so that $\|m_n\|_{L^\infty(\Omega)} \leq M_1$ for all n. Denote the positive principal eigenvalue of problem (2.4) with $m = m_n(x)$ by $\lambda_1(m_n)$. We have $\lambda_1(m_n) \to \infty$ as $n \to \infty$ if and only if there exists $M_0 > 0$ such that*

$$\int_\Omega m_n(x)\, dx \leq -M_0 \quad \text{for all } n.$$

and

$$\limsup_{n\to\infty} \int_\Omega m_n \psi \leq 0$$

for all $\psi \in L^1(\Omega)$ with $\psi \geq 0$ a.e.

This has interesting implications for the problem of habitat fragmentation, which we explore in the following sections. Before we get there, notice that combined with Proposition 2.3.2 we can conclude that if $\lambda_1(m_n) \to +\infty$, then $\liminf_{n\to\infty} \mu_1(d, m_n) > 0$ for all $d > 0$. This provides a simple mechanism by which "chopping up" the landscape into good and bad regions can cause deterministic extinction if the average habitat quality is non-positive!

4.4 'Species-oriented' versus 'pattern-oriented' approaches

Previously, we used a reaction-diffusion equation approach to model habitat degradation and habitat destruction, both in a single species model and in a two-species competition model. In those results, we obtain very general rules that are consistent with our current understanding of habitat loss and its impact on biodiversity. This indicates that, roughly, the models make predictions that are consistent with our understanding of these two aspects of habitat loss. In particular, the models are successful in that they predict species extirpation *as a consequence of habitat loss.*

At the heart of this analysis was the nature of the problems themselves (they are continuous-in-time monotone dynamical systems) and a detailed study of local stability. The local stability, as it was, depended precisely on the sign of a principal eigenvalue μ_1: $\mu_1 < 0$ predicted persistence, while $\mu_1 > 0$ predicted extinction. If we set $r_1 := -\mu_1$, r_1 is the average net growth rate over the entire landscape Ω, at least for small population sizes[1]. Depending on the form of the reaction term, we may decay to zero, grow indefinitely, or saturate at some threshold, generally given by the carrying capacity. Therefore, this growth rate can be used as a proxy to assess the fitness of a population: $r_1 > 0$ is a fit population, while $r_1 < 0$ is not; a population with growth rate $\tilde{r}_1$ satisfying $\tilde{r}_1 > r_1 > 0$ is more fit than the first. In the ecological literature, this is just one method to assess the fitness of a population [50], [110]. Therefore, we propose that this principal eigenvalue as it depends on the subset B can be used as a proxy for assessing impacts of fragmentation. The sense in which we mean *fragmentation* will depend on the measure we use, which we describe shortly and will connect directly to our discussion of habitat fragmentation.

To construct our measure, we let

$$\tilde{\mu}_1(d, \tilde{m}, c, B) := \mu_1(d, \mathbb{1}_G \tilde{m} - c\mathbb{1}_B)$$

be the principal eigenvalue to problem (2.5) with $m := \mathbb{1}_G \tilde{m} - c\mathbb{1}_B$. m describes the habitat quality in G, while the region B is assumed degraded at some level $c \geq 0$. Each of our measures will be built from the following quantity:

$$\Gamma(d, \tilde{m}, c, B) := \max\{-\tilde{\mu}_1(d, \tilde{m}, c, B), 0\}. \tag{4.2}$$

The preliminary measure (4.2) simply says:

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[1] Recall that this quantity in the given form is obtained through a linearization about the trivial steady state.

- Larger values of Γ imply a relatively more fit population.
- A value of 0 implies population decline, indicating deterministic extirpation.

We refer to Γ generally as a *Fitness Index* (FI) due to its ability to measure fitness (through a theoretical population growth rate) in relation to some key biological parameters (diffusion rate d, habitat quality $\tilde{m}$, level of degradation in destroyed habitat c, and the geometry of the set B).

Through construction, this is very much a *species-oriented* measure. It depends on key parameters that are species-dependent, but more notably, it does not make an effort to differentiate between particularly *bad* arrangements of habitat in a landscape. This is in contrast to the usual *pattern-oriented* approaches, where *any* configuration can, in principle, be classified and compared in a less coarse fashion. We are able to take such liberties because, unlike most other habitat fragmentation models, we have a direct and mechanistic connection to the growth rate of the population via the PDE model[2]. Of course, it is not difficult to modify the definition above to compare the theoretical growth rates directly whether positive or negative; we are instead interested in cases where it is possible to facilitate population persistence or predict population decline through the properties of the set B alone. Also note that, as opposed to the destruction perspective of Chapter 3, we choose the degradation perspective of Chapter 2 as the foundation of our framework. This is due to the generality of the problem (the destruction case can be obtained through the limit as $c \to +\infty$, as shown in Chapter 3) and the weaker assumptions on the set B.

We now simplify the setting to further isolate the effects of fragmentation alone. Similar to the competition-degradation system case, we take $\tilde{m} = 1$ so that the habitat quality is fixed to 1 in the region G. Denote by ω the set of subsets

$$\omega := \{B \subset \mathbb{R}^N : B \Subset \Omega\}$$

and by ω_α the set of subsets

$$\omega_\alpha := \{B \in \omega : |B| = \alpha \in (0, |\Omega|)\}.$$

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[2] In such a case, we would take $\tilde{m} = f'(x, 0)$, the linearization of the reaction term at zero.

Species-Oriented Fragmentation Fitness Index (SOFFI)

Our proposed Species-Oriented Fragmentation Fitness Index (SOFFI) is a function $\mathbb{R}^+ \times \mathbb{R}^+ \times \omega \mapsto [0, 1)$ defined by

$$\text{SOFFI}(d, c, B) := \Gamma(d, 1, c, B), \tag{4.3}$$

with a focus on changes to the set B. Notice that as $|B| \to 0^+$ in measure, SOFFI $\to 1^-$ for any $d > 0$ and $c \geq 0$, giving the upper bound found in the range. The lower bound follows from the definition of Γ. These results and others are found in Theorem 4.5.1. This inherits the same interpretation as Γ: the larger the SOFFI, the more fit the population is predicted to be in that particular habitat arrangement. Through construction, the measure is *species-oriented* in three ways: an assumption of diffusive movement of the population, a variable rate of diffusion, and a variable level of impact in the degraded regions.

Pattern-Oriented Fragmentation Index (POFI)

On the other hand, the fitness index Γ can be modified to construct *pattern-oriented* measures. In this case, we seek to remove some of the dependence on biological parameters in addition to some normalization procedure. This way, the measure depends *primarily on properties of the set B while neutralizing the influence of other species-dependent parameters.* We can remove two of the biologically related components, however it is important to note that we cannot remove the assumption of diffusive movement!

To this end, we fix the diffusion rate $d = |\Omega|^{2/N}$ and the degradation level at $c = 0$. This way we study the problem at an approximately fixed scale, so that we do not bias the measure towards small domains[3] and the average of the environmental heterogeneity remains positive, guaranteeing the positivity of the measure by Proposition 2.3.2. Then, we restrict ourselves to the space ω_α. As shown in [42, Theorem 1.2] for

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[3] Since we can rescale space through a rescaling of diffusion, using the volume of the domain to the power $2N$ where N is the spatial dimension, we keep the measure roughly fixed across diffusion rates. For example, if $\Omega = (0, L)$ or $(0, L) \times (0, L)$, $d = L^2$ so it is as if we study the problem in $(0, 1)$ or $(0, 1) \times (0, 1)$, respectively.

a different but closely related problem, there is evidence to suggest that, given any $\alpha \in (0, |\Omega|)$ fixed, there exists a set $B^*_\alpha \subset \Omega$ such that

$$\mathrm{SOFFI}(|\Omega|^{2/N}, 0, B) \leq \mathrm{SOFFI}(|\Omega|^{2/N}, 0, B^*_\alpha),$$

for any other subset $B \in \omega_\alpha$. In ecological terms, *there exists an optimal habitat maximizing the* SOFFI *score.* Our Pattern-Oriented Fragmentation Index (POFI) is a function $\omega_\alpha \mapsto (0, 1]$ defined by

$$\mathrm{POFI}(B) := \frac{\mathrm{SOFFI}(|\Omega|^{2/N}, 0, B)}{\mathrm{SOFFI}(|\Omega|^{2/N}, 0, B^*_\alpha)}. \tag{4.4}$$

POFI removes much of the novelty of the species-dependent properties included in SOFFI, however we must note that *the measure is intrinsically species-oriented in some capacity since the measure assumes a diffusive movement mechanism!*

Total abundance as a measure of fragmentation

In other cases, such as the competition systems previously explored, the eigenvalue problems are not as easy to study, either analytically or numerically. This is because the stability now depends on eigen-*systems*, in which case tools like the *variational characterization* of the principal eigenvalue do not exist. As an alternative, one may assess the ‘fitness’ of a population through the total abundance at a steady state. **There are two important caveats to make here:**

- Total abundance is *not* a standard measurement of fitness. Fitness is generally understood in the sense of an ability to reproduce, survival, reproductive rates, and the ability for a population to persist [96]. A population with high total abundance but low reproductive output may be less fit than expected (especially if the population is in decline, for example).

- Total abundance predictions are sometimes inherently at odds with the population growth rate measure of fitness, at least in the present setting: as the population is at a temporally constant steady state, the change in total population is *zero*! This indicates a population-level fitness of “zero” from the perspective of population growth rates.

Despite these caveats, total abundance *is* sometimes used to assess ecosystem health [24], [107]. The Biodiversity Intactness Index (BII) gives a score between 0 and 100, indicating the percentage of population decline in some region, where we compare to a presumed population before human-induced habitat loss. This could, in principle, be used for a single species, but seems to generally be used in systems with multiple species coexisting (hence the *biodiversity* aspect of the index). Due to the straightforward mathematical formulation this provides, we study this perspective in some detail as well.

Suppose we are given a population density $u_{d,c,B}(x)$, assumed at steady state, where c, B indicate the dependence on the level of degradation $c \geq 0$ and the properties of the set B. Assume we have a theoretical population density $u^*(x)$ representing the outcome when there is *no disturbance to the habitat.* More precisely, u^* corresponds to the case when $|B| = 0$, and so is never identically zero so that persistence is always a possibility. Our Total Abundance Fragmentation Index (TAFI) is then a function $C(\overline{\Omega})^+ \times C(\overline{\Omega})^+ \mapsto [0,1]$ defined by

$$\mathrm{TAFI}(u_{d,c,B}, u^*) := \frac{\int_\Omega u_{d,c,B} dx}{\int_\Omega u^* dx}. \tag{4.5}$$

Since $0 \leq u_{d,c,B} \leq u^*$ in Ω, the range of TAFI follows. Beyond the reasoning above, we study this perspective in some detail since it is commensurate with some experimental methodologies (such as measure incidence rates of a given species in some area) and is of general interest to the understanding of the consequences of habitat fragmentation.

There are some other changes in perspective (as opposed to the BII) that may make this a more reasonable, *relative* fitness measure of the population: in the case of a competition system, we can compare the theoretical population abundance of each population in the competition system relative to the theoretical population abundance of all populations. This gives a *relative* measure of population fitness between two (or more) populations by comparing their relative incidence rates as they depend on habitat quality and arrangement. Given a j-species competition model for $j \geq 2$, denote by $u_i^*(x)$ the population abundance of population i at steady state. The Relative-Total

Abundance Fragmentation Index for each population u_i is then

$$\text{R-TAFI}(u_i^*) = \frac{\int_\Omega u_i^* dx}{\sum_{k=1}^{j} \int_\Omega u_k^* dx}.$$

R-TAFI may be considered as a BII measure for reaction-diffusion equations.

In the following two sections, we explore the predictions and hypotheses produced from these fragmentation measures. In all perspectives, we are able to consider habitat fragmentation *as an arrangement* as well as habitat fragmentation *as a process.*

4.5 Assessing the impact of fragmentation as an arrangement

In this section, we focus on assessing the impact of fragmentation *as an arrangement.* As described in Chapter 1, studying habitat fragmentation as an arrangement alone is sometimes referred to as habitat fragmentation *per se.* This is a perspective where we study the effect of arrangement *independent of total available habitat* [33].

To suit this perspective, we will work in landscapes with degraded region $B \subset \Omega$ such that the total area of B is fixed. **Therefore, in this section we always assume:**

$$B \in \omega_\alpha \quad \text{for some} \quad \alpha \in (0, |\Omega|).$$

This way, the total available habitat $\Omega \setminus B$ is held fixed, and there is always *some* amount of habitat lost. We will then assess the differing impacts for habitats of different configurations of B, isolating the effect of changes in arrangement of habitat and non-habitat. Due to the complexity of this geometric problem, we study it both numerically and analytically where possible.

4.5.1 Species-oriented approach

We begin with the species-oriented measure SOFFI. We state first some analytical results which can be verified and explored further later using numerical techniques.

Analytical insights

First, we connect some properties of the principal eigenvalue to the SOFFI measure. We have the following properties.

Theorem 4.5.1. *Assume $d > 0$, $c \geq 0$. The following hold.*

1.) *For d, c fixed,* $\mathrm{SOFFI}(d, c, B) \in [0, 1)$.

2.) $\mathrm{SOFFI}(d, c, B)$ *is decreasing in both d and c. If $B_1 \subset B_2$,* $\mathrm{SOFFI}(d, c, B_1) > \mathrm{SOFFI}(d, c, B_2)$.

3.) *For d, c fixed,* $\mathrm{SOFFI}(d, c, B) \to 1^-$ *as $|B| \to 0^+$ in measure (i.e., as $\alpha \to 0^+$).*

4.) *If $|G| > c\alpha$ for G, c fixed,* $\mathrm{SOFFI}(d, c, B) \in (0, 1)$ *for all $d > 0$. Moreover,* $\lim_{d \to 0^+} \mathrm{SOFFI}(d, c, B) = 1$ *and* $\lim_{d \to \infty} \mathrm{SOFFI}(d, c, B) = |G| - c\alpha$.

5.) *If $|G| < c\alpha$ for G, c fixed,* $\lim_{d \to 0^+} \mathrm{SOFFI}(d, c, B) = 1$. *Furthermore, there exists a $d^* > 0$ such that*

   - $\mathrm{SOFFI}(d, c, B) \in (0, 1)$ *for all $d \in (0, d^*)$;*
   - $\mathrm{SOFFI}(d, c, B) = 0$ *for all $d^* \in (d^*, \infty)$*

6.) *If $|G| = c\alpha$ for G, c fixed, then* $\mathrm{SOFFI}(d, c, B) \in (0, 1)$ *for all $d > 0$, but* $\lim_{d \to \infty} \mathrm{SOFFI}(d, c, B) = 0$.

7.) *Fix d, B and let $\mu_1(d, 1, B)$ be the principal eigenvalue to problem* (3.5). *We have the following.*

   - *If $\mu_1(d, 1, B) < 0$, then* $\inf_{c > 0} \mathrm{SOFFI}(d, c, B) \in (0, 1)$.
   - *If $\mu_1(d, 1, B) > 0$, there exists $c^* > 0$ such that* $\mathrm{SOFFI}(d, c, B) \in (0, 1)$ *for all $c < c^*$, and* $\mathrm{SOFFI}(d, c, B) = 0$ *for all $c > c^*$.*

8.) *Fix d, c. We have the following.*

   - *Suppose $|G| > c\alpha$. Then* $\mathrm{SOFFI}(d, c, B) \in (0, 1)$ *for any configuration $B \in \omega_\alpha$.*

- *Suppose* $|G| < c\alpha$. *Then there exists a sequence of habitats* $\{B_n\}_{n\in\mathbb{N}}$ *with fixed volume such that* $\mathrm{SOFFI}(d, c, B_n) \to 0$ *as* $n \to \infty$*; in fact, there exists a sequence such that* $\mathrm{SOFFI}(d, c, B_n) = 0$ *for all* $n \geq \overline{n} \geq 0$.

Proof. Each of these properties follow from properties of $\mu_1(d, m)$ found in Proposition 2.3.2 and the definition of SOFFI. □

Ecological interpretations of SOFFI's properties

All of these properties are ecologically relevant and fall within the scope of works such as [58]: we want to know, and more importantly *understand*, the limits of any given measure of fragmentation. Unlike many existing fragmentation measures, these results provide detailed hypotheses that can be verified experimentally, at least in principle. We interpret each of the statements in Theorem 4.5.1.

1.) The range of values possible for SOFFI lies between $[0, 1)$. It is important to know the range of values our index might take; between 0 and 1 is simple and interpretable. This could, in practice, be normalized as is desired, so the range is somewhat arbitrary in this sense.

2.) SOFFI is decreasing with respect to increased degradation. This is an entirely expected behaviour: as habitat quality decreases, the score should also decrease. On the other hand, SOFFI is also decreasing with respect to d. This is a consequence of the assumed movement mechanism. Since the movement is diffusive at a constant rate, increased diffusion spreads out the population uniformly through the domain (this can be shown rigorously). This means that the species use the average amount of available resources. In contrast, smaller rates of diffusion allow the population to concentrate around the peaks of resources or around areas of high-quality habitat; we see this in the limiting behaviour as $d \to 0$.

3.) If we remove the entire degraded region, SOFFI reaches a value of 1. A value of 1 corresponds to an undisturbed habitat, in which case d and c have no influence. This is reasonable as diffusion has no effect in a homogeneous landscape[1]. Since the

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[1] With homogeneous Neumann boundary conditions.

degraded region B does not exist, c never appears in the equation.

4.) If the average landscape quality is positive, SOFFIis positive for any positive rate of diffusion. In such cases, one can compare fitness levels based on the relative sizes of their SOFFI scores.

5.) If the average landscape quality is negative, there is a diffusion rate at which SOFFI becomes zero. This is consistent with a previous property: if increased diffusion causes a homogeneously distributed population, agents spend as much time in the good regions as in the bad. Since the overall landscape quality is negative, eventually increasing diffusion results in a zero SOFFI score.

6.) If the average landscape quality is exactly zero, the SOFFI score is always positive, but increased diffusion leads to a smaller and smaller SOFFI score.

7.) We proved some limiting analytical results in Chapter 3 concerning convergence between the degradation and destruction eigenvalue problems. Hence, we have information for large values of c depending on the sign of a different principal eigenvalue. This is also reasonable: based on information known in the 'worst case' scenario, we can determine whether the SOFFI score will always remain positive for larger and larger c, or if it will eventually reach a zero SOFFI score.

8.) We also have some information based on arbitrary configurations of B. If the average habitat quality is positive, then the SOFFI score will *always* be positive! On the other hand, a negative average habitat quality always has bad enough configurations that ensure a zero SOFFI score. This is interesting as it connects quite directly to the habitat amount hypothesis: the easiest way to ensure a positive SOFFI score is to ensure that the amount of habitat G is sufficiently large! Therefore, SOFFI may be most informative for edge cases where little habitat G remains, or the degradation level c is particularly high.

Applications of the SOFFI score

From these explanations, it is now even more evident the species-oriented nature of the SOFFI score. All of these properties tell us valuable information about the impacts of habitat arrangements in a general sense, depending precisely on a few key biological parameters. However, we are also interested in more precise examples, in which case we appeal to some of the analytical results proved in the previous sections of this chapter.

Example 1. 'Placement of a factory' This this example, we evaluate the behaviour of the SOFFI score with a ball inside of a ball in two spatial dimensions. Fix $R > 0$, $0 < \rho < R$, and $t \in [0, R - \rho)$. We then take

$$\Omega := B_R(0), \quad B := B_\rho(t),$$

and so

$$|\Omega| = \pi R^2, \quad |B| = \alpha = \pi \rho^2.$$

We then explore changes in SOFFI with respect to the parameter $c \geq 0$, $d > 0$, and the location of $B_\rho(t)$ depending on the centre t. Recall that due to the symmetry of this problem, we consider only translations along the x_1-axis. The range of t ensures that $B \Subset \Omega$. See Figure 4.2.

First, we make some analytical observations following from [93, Ch. 4 Prop. 4.4]:

$$\lim_{d \to 0^+} \mathrm{SOFFI}(d, c, B_\rho(t)) = 1, \quad \text{and} \quad \lim_{d \to \infty} \mathrm{SOFFI}(d, c, B) = \frac{R^2 - c\rho^2}{R^2}.$$

This holds for any $c, \rho > 0$ fixed. We also expect a global minimum across all $t \in (0, R - \rho)$ when $t = 0$. This follows from the fact that the principal eigenvalue is maximized across translations when it is exactly in the centre of $B_R(0)$. Finally, $\mathrm{SOFFI}(d, c, B_\rho(t))$ is obviously decreasing with respect to c for $d, \rho > 0$ fixed.

We observe the following behaviour numerically. This problem is solved using the PDE Modeler applet in MATLAB. For technical reasons, we explore this problem from two separate perspectives.

First, in Figure 4.3 we fix the centre $t = 0$ and observe changes in the SOFFI score with respect to the size of the inner radius ρ, and the level of impact c within the degraded region. We find that for any level $c \in (0, 1)$, the SOFFI score is approximately 1 (its maximal possible value, indicated by the color yellow) when the degraded region is not too large. We then find a sharp drop-off when the inner radius is greater than ~ 0.4, quickly decreasing to a minimal value of 0 (indicated by the color blue). The contour lines contain labels indicating the changing intermediate values.

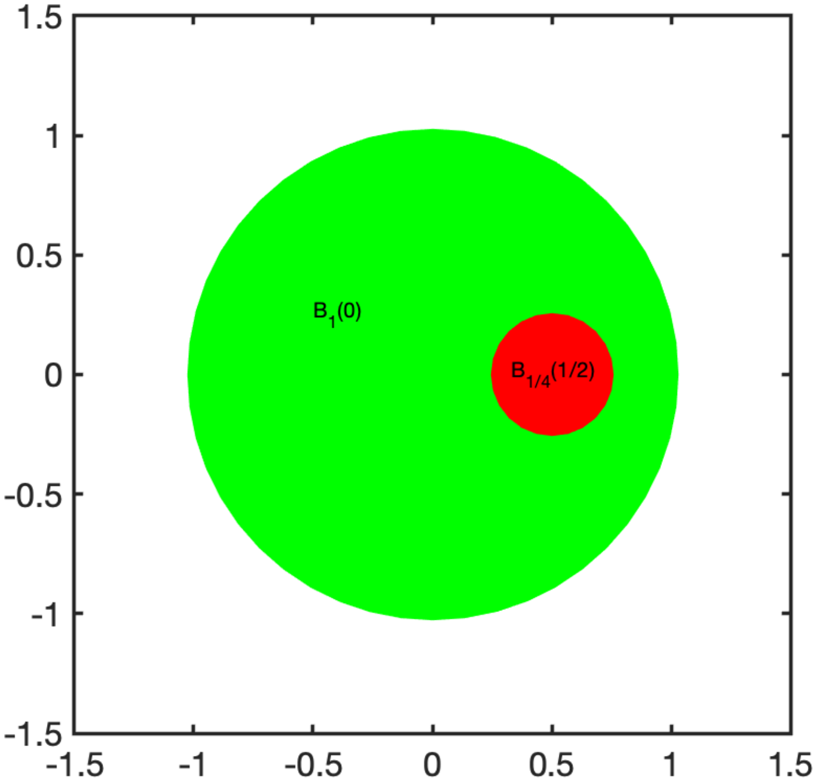


Figure 4.2: Schematic demonstrating the placement of a factory, depicted in red, in a habitat $\Omega = B_1(0)$. In this example, the factory is placed at $1/2$ with radius $1/4$.

Second, in Figure 4.4 we consider the destruction case ($c = +\infty$) and observe changes in the SOFFI score with respect to the location t of the inner region and the size of the destroyed region ρ. As in Figure 4.3, yellow denotes areas of maximal values whereas blue denotes areas of minimal values, and labelled contour lines indicate changes in intermediate values. We restrict ourselves to $0 < t < 1 - \rho$ so that $B_\rho(t) \Subset B_1(0)$. As expected, the radius of the ball has a drastic effect on the SOFFI score. This is somewhat an artifact of the fact that we are in the destruction case. More informative is the impact of the centre t: the SOFFI score is increased if we move the destroyed region *away* from the centre of the domain.

Example 2. 'Increasing fragmentation' In this example, we explore changes

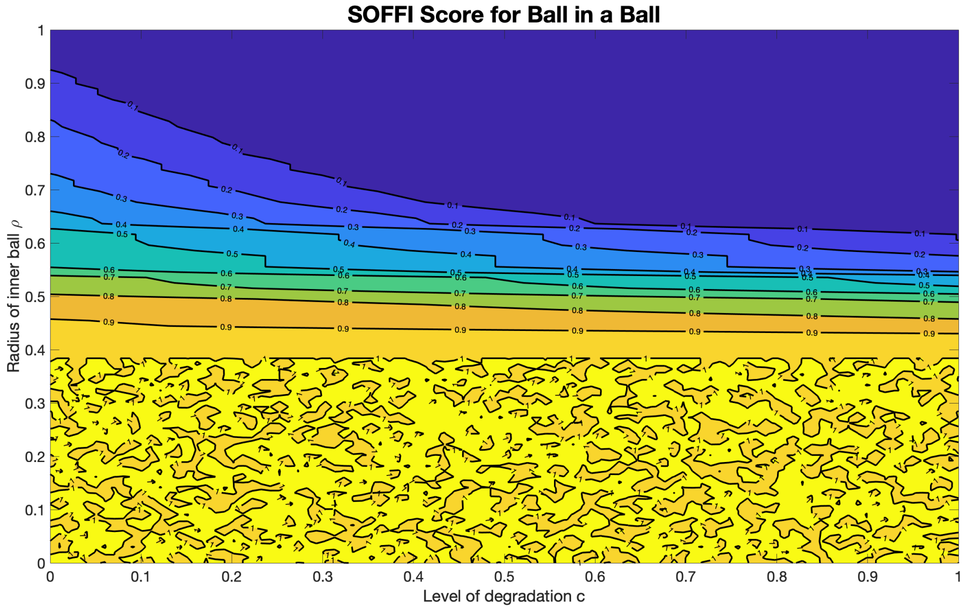


Figure 4.3: SOFFI **Score Example 1a.** A numerical simulation of the SOFFI score as it depends on c and ρ. Note that the centre $t = 0$ is fixed. Note also that the noise found in the lower half of the plot is due to small variations coming from numerical error. In the raw data, all values found below $\rho \sim 0.4$ are within 10^{-6} of the maximal value 1.

in the SOFFI score when B is a set of the form

$$B_k := \bigcup_{0 \leq i \leq k-1} \left(\frac{2i}{2^k}, \frac{2i+1}{2^k} \right),$$

in $\Omega = (0,1)$, for some $k \in \mathbb{N}$. If $k = 1$, $B_1 = (0, \frac{1}{2})$. If $k = 2$, $B_2 = (0, 1/4) \cup (1/2, 3/4)$. Therefore, the total area of B_k is fixed (it is exactly 1/2 of the area of the total landscape), but as k increases, B_k becomes more and more divided. In some sense, it is becoming more fragmented in terms of its arrangement alone.

One prototypical example of an environment that has this behaviour is $\sin(2k\pi x)$. In our setting, we will study the same kind of periodic function which is instead constant 1 in $(0,1) \setminus B_k$, and is constant $-c$ in B_k for some $c \geq 0$. In fact, numerically we may approximate this by

$$m_k(x; c) := (\max\{\sin(2k\pi x),\ 0\})^{1/n} - c\,(\max\{-\sin(2k\pi x),\ 0\})^{1/n}$$

for some $n \gg 1$ and $k \in \mathbb{N}$ fixed.

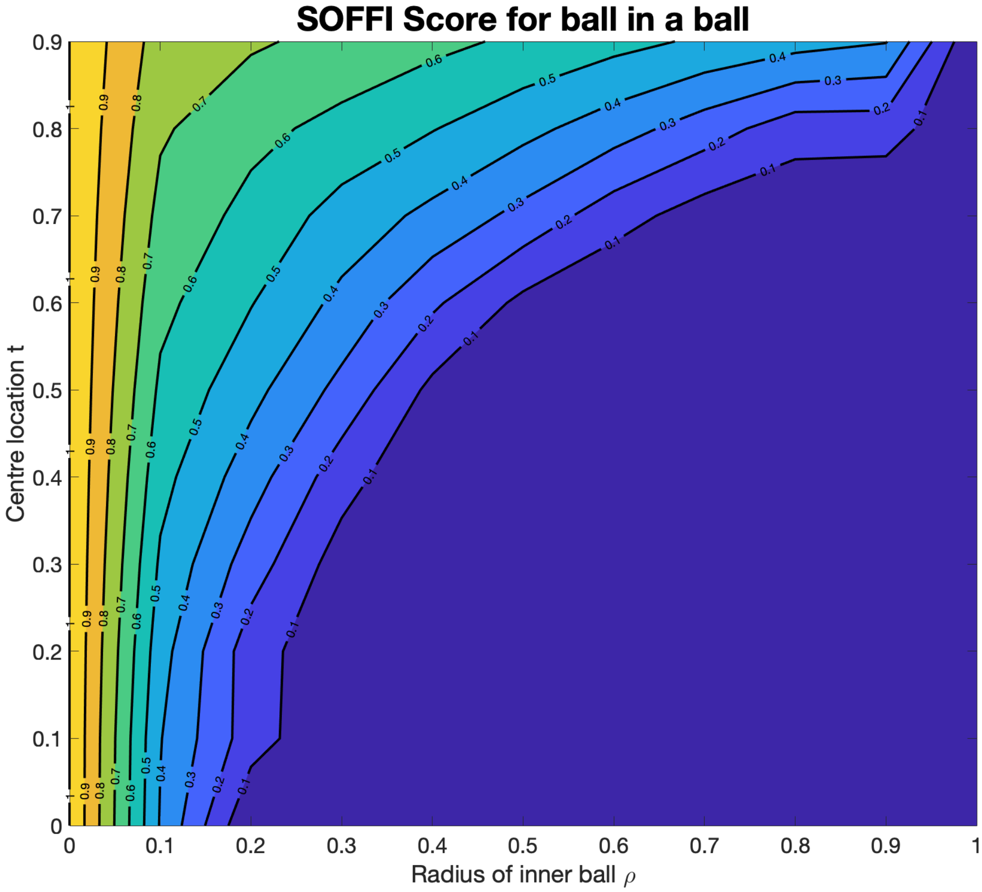


Figure 4.4: SOFFI **Score Example 1b.** A numerical simulation of the SOFFI score as it depends on t and ρ. In this case the level of degradation is infinite, i.e., $c = \infty$. Also note that we consider only $0 < t < 1 - \rho$, and so the figure is symmetric about this line.

In Figure 4.5, we observe changes in SOFFI score ranging from 1 resource peak 8 resource peaks. As expected, the score is decreasing as c increases for any level of fragmentation. More interestingly, perhaps, is the compounding effect that the level of degradation and the level of fragmentation has: it is much worse when *both* factors are high, rather than only degraded or only fragmented.

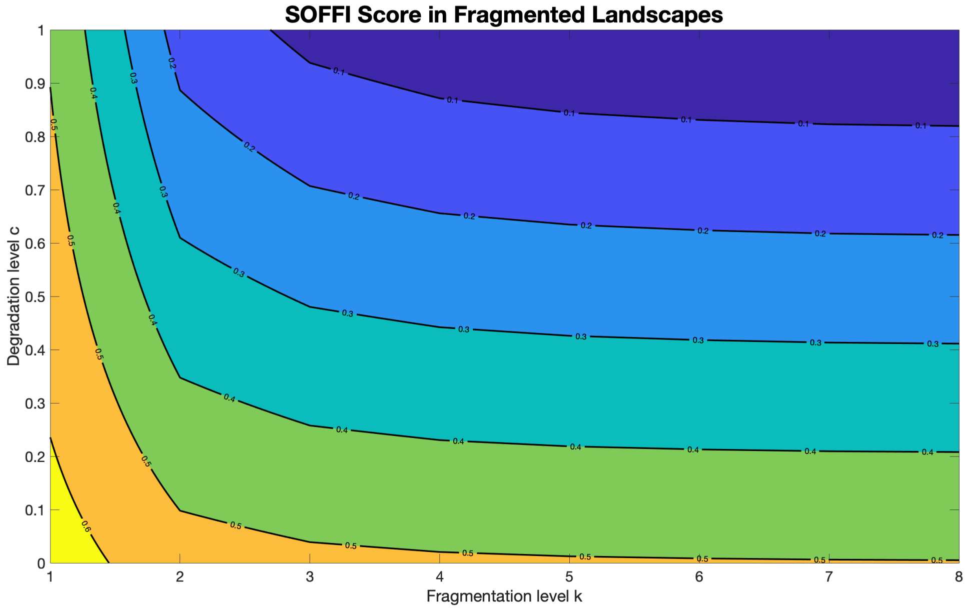


Figure 4.5: SOFFI **Score Example 2.** A numerical simulation of the SOFFI score as it depends on the degradation level c and the fragmentation level k. In this case, we have up to $k = 8$ patches of habitat.

4.5.2 Pattern-oriented approach

We now complete a similar analysis for the pattern-oriented measure POFI. This will be a little easier since the results are similarly obtained (POFI is made from SOFFI, after all).

Analytical insights

We again start with some analytical properties of POFI. Notice that in comparison to the analytical results for SOFFI, we are much more limited in our analytical insights. This is because we now focus exclusively on the geometric properties of B.

Theorem 4.5.2. *The following hold.*

1.) *For any* $B \in \omega_\alpha$ *with* $\alpha \in (0, |\Omega|)$ *fixed,* $\mathrm{POFI}(B) \in (0, 1]$.

2.) $\mathrm{POFI}(B) \to 1^-$ *as* $|B| \to 0^+$ *(i.e. as* $\alpha \to 0^+$*).*

3.) $\mathrm{POFI}(B) \to 0^+$ *as* $|B| \to |\Omega|^-$.

4.) *For each* $\alpha \in (0, |\Omega|)$ *fixed, there exists a sequence* $\{B_k\}_{k\geq 1}$ *such that*

$$\mathrm{POFI}(B_k) \to \frac{|G|}{|\Omega| \cdot \mathrm{SOFFI}(B^*_\alpha)}$$

as $k \to \infty$*.*

Proof. The first three results follow directly from properties of the principal eigenvalue. The fourth property follows from the limiting property of the principal eigenvalue as $d \to \infty$ and a rescaling argument. That is, a sequence of increasingly fragmented landscapes can be made equivalent to sending the diffusion rate to infinity. □

Ecological interpretations of POFI's properties

We may interpret these results ecologically as follows.

1.) The range and interpretation of POFI is very similar to SOFFI. The main difference is that POFI now provides a ratio describing how far away the arrangement B is from an optimal arrangement B^*. A POFI score of 1 implies that there are no changes in the arrangement that could improve outcomes; the smaller the POFI value, the further it is from an optimal configuration.

2.) As the degraded region vanishes, POFI has a score of 1. This makes sense as no degraded region is optimal for species survival!

3.) As the degraded region fills the entire landscape, the POFI score tends to zero. This makes sense as if there is no habitat left, the species cannot survive!

4.) This result is somewhat convoluted, but we attempt to explain here. Since $|B| > 0$ is fixed, $\frac{|G|}{|\Omega|}$ is always smaller than one. Therefore, by chopping up the degraded region in a pathological way, you can force the numerator of POFI to tend towards this ratio (the average habitat quality, in fact). This is, in some sense, the 'worst case' scenario for a degraded region of fixed volume α when the level of degradation is neutral ($c = 0$). Hence, the smaller the total available habitat Γ, the smaller the theoretical limits of the measure POFI.

4.5.3 Total abundance approach

Unlike the previous two approaches, this total abundance approach is somewhat more difficult to study analytically as it actually involves the qualitative study of the steady state to an elliptic reaction-diffusion equation. Therefore, we simplify our setting in similar ways as in the species- and pattern-oriented approaches. We do this for a single-species setting and a multi-species setting.

The single species case

First, we assume that $u_{c,B}$ is the steady state to problem (2.1) with $d > 0$, $f(x,u) = u(1-u)$ and $c \geq 0$. Then, for $B \in \omega_\alpha$ fixed, $u_{c,B}$ solves

$$-d\Delta u^* = u^*(\mathbb{1}_G - c\mathbb{1}_B - \mathbb{1}_G u^*).$$

Furthermore, we can guarantee the existence of a unique, non-trivial steady state whenever $\mu_1(d,1,B) < 0$, where $\mu_1(d,1,B)$ is the principal eigenvalue to problem (3.5). Then, we notice that if either $c = 0$ or $|B| = 0$, $u^* \equiv 1$ is the unique steady state. In fact, as proven in Chapter 2, for fixed B there holds $u_{c,B} \to 1$ uniformly in Ω as $c \to 0^+$. Therefore, in our setting the denominator of the TAFI score is

$$\int_\Omega u^* dx = |\Omega|,$$

and so TAFI reduces to the average population density of $u_{c,B}$ over the landscape Ω:

$$\text{TAFI}(u_{c,B}, 1) = \frac{1}{|\Omega|}\int_\Omega u_{c,B} dx.$$

As it turns out, this is a popular object of study, see [85], [86], [91], [93] and the references therein. In particular, we make note of two important facts:

- Maximizing the total population is **not** equivalent to maximizing the growth rate of the population. That is to say, information gained from a linearization procedure near zero *is almost entirely disconnected from the solution behaviour at steady state.* From the perspective of linearization, we do not ‘see’ steady state behaviour at all.

- Unlike the growth rates via principal eigenvalues, it is not clear (and is in fact not true) that the total abundance is monotone with respect to any parameters aside from c. Of course, we know that the steady states are monotonically decreasing with respect to c by Lemma 3.5.1.

Therefore, questions of total abundance require different approaches of analysis. We highlight a few basic properties now.

Analytical insights

We have the following theorem regarding some properties of the TAFI score.

Theorem 4.5.3. *Suppose $d > 0$, $c \geq 0$ and $B \in \omega_\alpha$. The following hold.*

1.) *For any d, c, B fixed,* $\mathrm{TAFI}(u_{d,c,B}) \in [0,1]$.

2.) *For any c, B fixed, there holds*

  - $\lim_{d\to 0^+} \mathrm{TAFI}(u_{d,c,B})) = \frac{|G|}{|\Omega|}$;
  - $\lim_{d\to\infty} \mathrm{TAFI}(u_{d,c,B})) = \max\{1 - c\frac{|B|}{|G|},\ 0\}$

3.) *For any d, B fixed there holds* $\lim_{c\to 0^+} \mathrm{TAFI}(u_{d,c,B}) = 1$.

4.) *For any d, B fixed, there holds for some $\varepsilon_0 > 0$*

$$\lim_{c\to\infty} \mathrm{TAFI}(u_{d,c,B}) \geq \varepsilon_0 > 0 \quad \Longleftrightarrow \quad \mu_1(d,1,B) < 0,$$

where $\mu_1(d,1,B)$ is the principal eigenvalue to problem (3.5) with $m \equiv 1$ in G.

5.) *For any d, c fixed,* $\mathrm{TAFI}(u_{d,c,B}) \to 1$ *as* $|B| \to 0^+$.

6.) *For any d, c and $\alpha \in (0, |\Omega|)$ fixed, there exists a set $B^* \in \omega_\alpha$ such that* $\mathrm{TAFI}(u_{d,c,B^*}) \geq \mathrm{TAFI}(u_{d,c,B})$ *for any other $B \in \omega_\alpha$.*

We will also observe the following fact: there exist configurations which are *more fragmented* from the perspective of SOFFI, but has a *higher* TAFI *score than the least fragmented arrangement.* This demonstrates analytically a fundamental and important difference between the perspective of population growth rates and total population sizes.

Remark 4.5.1. *We wish to highlight that, while deep and interesting results exist regarding the maximization of total abundance [85], [91], their depth is somewhat reliant on particular assumptions. This means that, in terms of more general application or insights to be gained, we are restricted in making generalizations. For example, results assume the heterogeneity is non-negative [86] (so* $c = 0$ *is the only possibility in our setting), and the form of reaction must be precisely* $u(m(x) - u)$*, which is slightly different than the format found here (i.e., competition occurs across the entire domain rather than only in the region* G*).*

Ecological interpretations of TAFI's properties

These properties can be interpreted ecologically as follows.

1.) The range of TAFI lies between 0 and 1; closer to 0 indicates a less 'fit' population, while closer to 1 indicates a more 'fit' population.

2.) For c, B fixed, we have precise values of TAFI when diffusion is arbitrarily small or large. When $d \to 0^+$, the TAFI score is simply the ratio of total available habitat over the total size of the landscape. When $d \to \infty$, TAFI may vanish. When $c|B| < |G|$, the TAFI score remains positive. This gives an interesting heuristic in regard to fragmentation: regardless of the arrangement, we can either reduce the size of the degraded region or reduce the level of impact within the degraded region (or both) to improve outcomes for local species.

3.) If the level of degradation in B is neutral ($c = 0$), the TAFI score is maximized.

4.) We can relate the uniform positivity of the TAFI score with the negativity of the principal eigenvalue in the destruction case. This simply says that, if TAFI is positive in the *worst possible scenario*, it will be positive for any other fixed value $c > 0$.

5.) The TAFI score is maximized if the degraded region does not exist, which is a biologically reasonable expectation.

6.) Similar to previous suggestions, there exist works that study the existence of optimal regions B^* maximizing the total abundance.

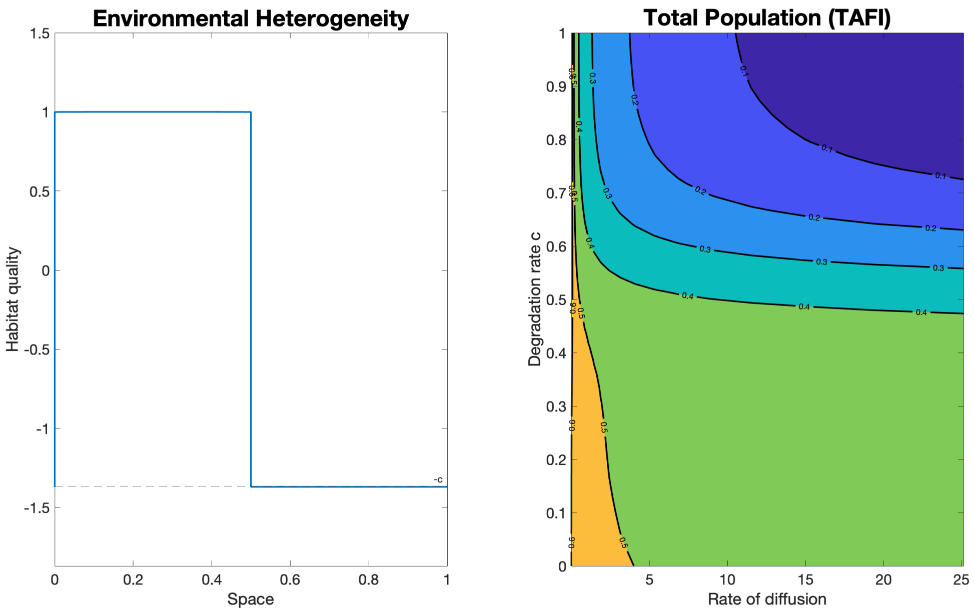


Figure 4.6: A numerical simulation of the TAFI score as it depends on d and c. In this case, we have just 1 large patch of habitat.

Applications of the TAFI score

Example 2. ‘Increasing fragmentation’

As in the case of SOFFI, we know that the optimal scenario is when $k = 1$. When $c = 0$, $m_k(x; 0)$ is given by

$$m_k(x; 0) = (\max\{\sin(2k\pi x),\ 0\})^{1/n}.$$

We can observe the following behaviour across 4 plots. We fix the fragmentation level k for each (choosing $k = 1, 2, 3, 8$). We plot the resulting TAFI score as a function of rate of diffusion (parameter d) and the level of degradation (parameter c). Since our domain is fixed as $\Omega = (0, 1)$, our normalization factor is exactly 1, and the TAFI score is simply the total abundance.

The multi-species case

We also have the R-TAFI score for multi-species models. In our case, we appeal again to a two-species model under habitat degradation as in Chapter 2. Since the complexity

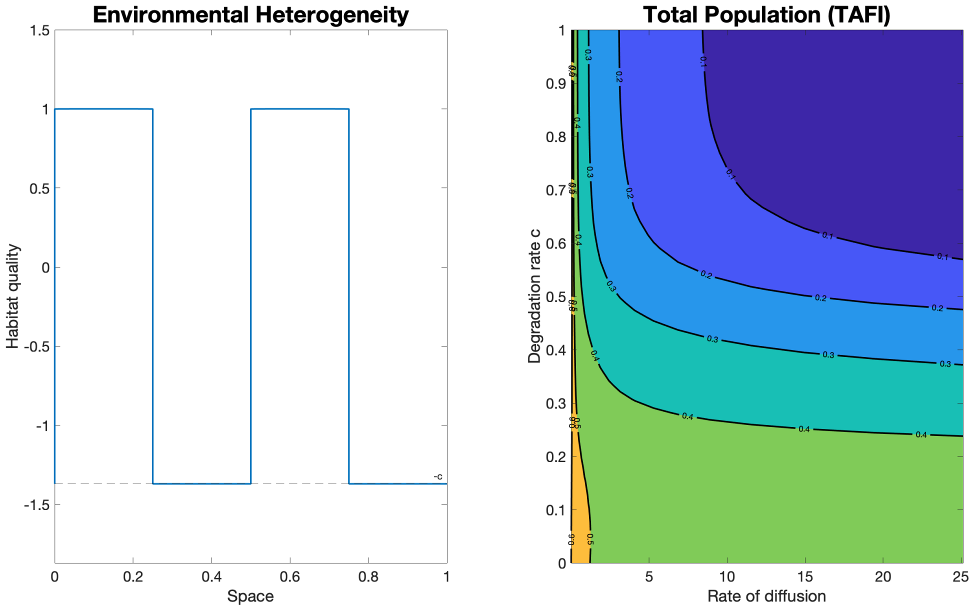


Figure 4.7: A numerical simulation of the TAFI score as it depends on d and c. In this case, we have 2 smaller patches of habitat.

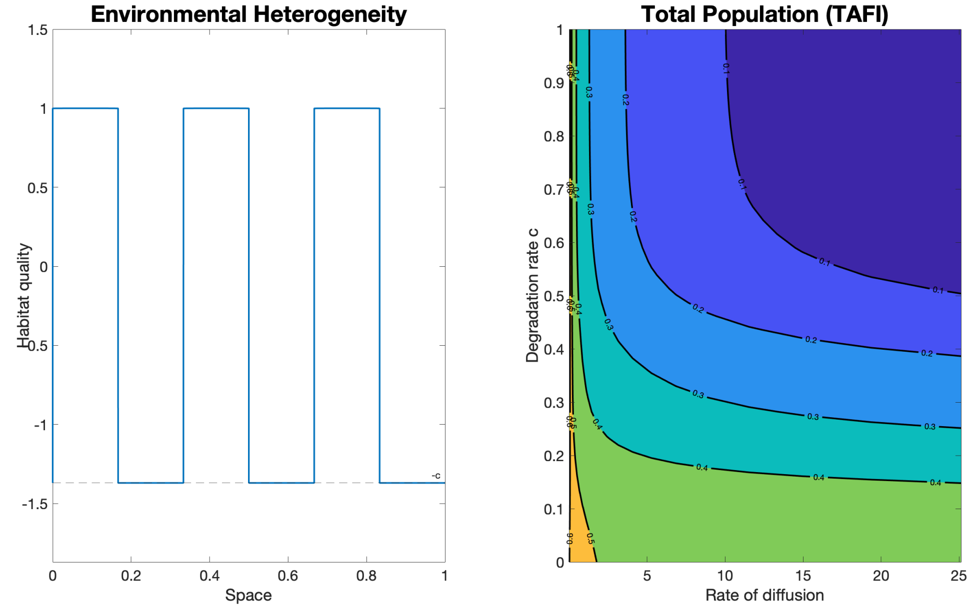


Figure 4.8: A numerical simulation of the TAFI score as it depends on d and c. In this case, we have 3 smaller patches of habitat.

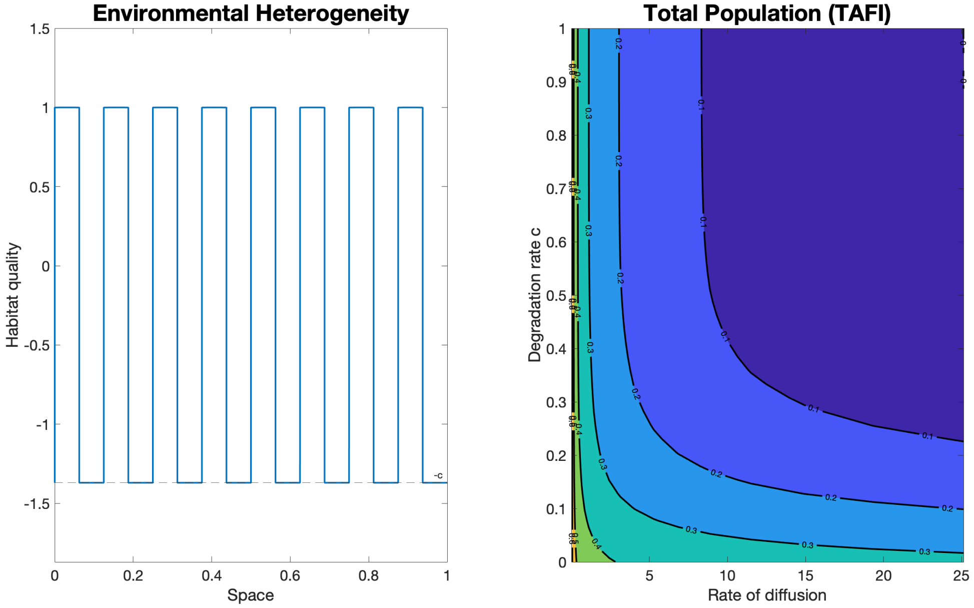


Figure 4.9: A numerical simulation of the TAFI score as it depends on d and c. In this case, we have 8 very small patches of habitat.

of multi-species models is significantly higher than that of single-species models, the only real analytical insight we can determine assuredly is the following.

Theorem 4.5.4. *Suppose* (u_{c_1}, v_{c_2}) *is the unique steady state to problem* (2.2) *with* $0 < d_1 < d_2$ *fixed,* $B \Subset \Omega$ *fixed, and* $0 < c_2 < c_1$ *for some* $c_1 > 0$ *fixed. Then, there exists* $0 < \underline{c}_2 < \bar{c}_2 < c_1$ *such that*

- *For all* $c_2 > \bar{c}_2$, $\text{R-TAFI}(u_{c_1}) = 1$ *and* $\text{R-TAFI}(v_{c_2}) = 0$*;*
- *For all* $c_2 < \underline{c}_2$, $\text{R-TAFI}(u_{c_1}) = 0$ *and* $\text{R-TAFI}(v_{c_2}) = 1$*;*
- *For all* $c_2 \in (\underline{c}_2, \bar{c}_2)$, $0 < \text{R-TAFI}(u_{c_1}), \text{R-TAFI}(v_{c_2}) < 1$.

Proof. The proof follows directly from the global dynamics established in Theorem 2.5.2. ☐

This result suggests a continuum of possibilities. We explore this numerically now.

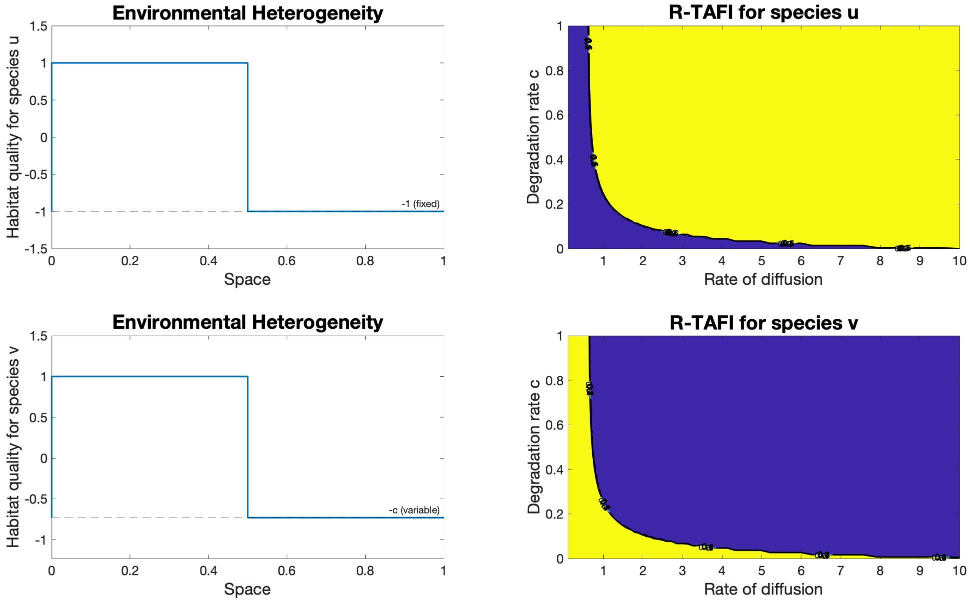


Figure 4.10: A numerical simulation of the R-TAFI score as it depends on d and c_2. In this case, we have 1 patch of habitat.

Applications of the R-TAFI score

In this section, we use a numerical exploration to investigate Theorem 4.5.4. In this case, we appeal to the R-TAFI score as we now have two populations. We use the same environmental setup as in the single species case, but we now fix the degradation level $c_1 = 1$ and diffusion rate $d_1 = 0.1$ for population u, while population v has a degradation level $c_2 := c$ varying between 0 and 1 and diffusion rate d_2 varying between 0.1 and 10. In Figures 4.10-4.13, we observe changes in the R-TAFI score as it depends on the rate of diffusion and the level of degradation for population v.

4.6 Assessing the impact of fragmentation as a process

The perspective taken in Section 4.5 most accurately corresponds to habitat fragmentation *per se*: we are interested in separating the effects of *removal* of habitat and the *arrangement* of habitat. Inherent in this standpoint is essentially the consideration of

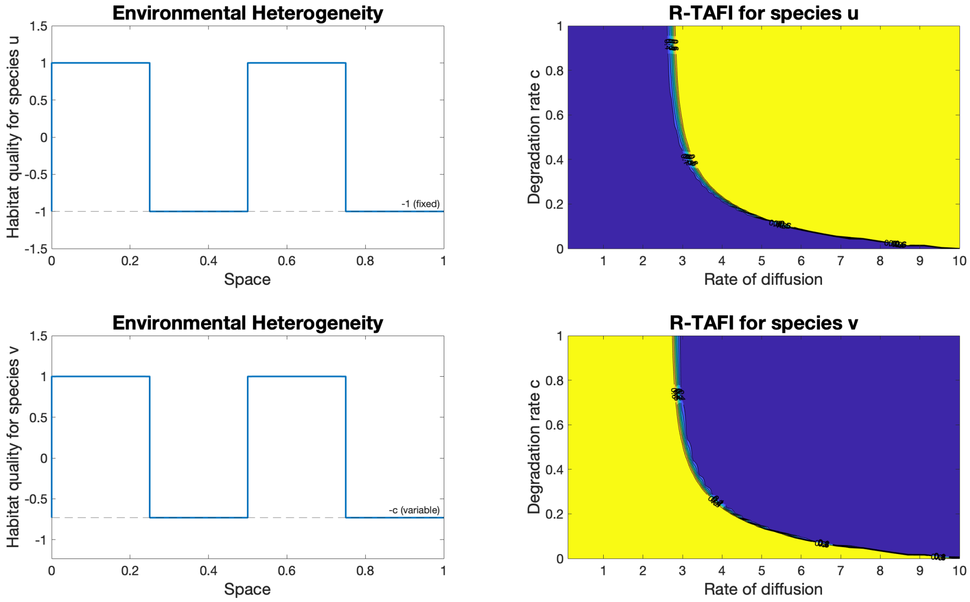


Figure 4.11: A numerical simulation of the R-TAFI score as it depends on d and c_2. In this case, we have 2 smaller patches of habitat.

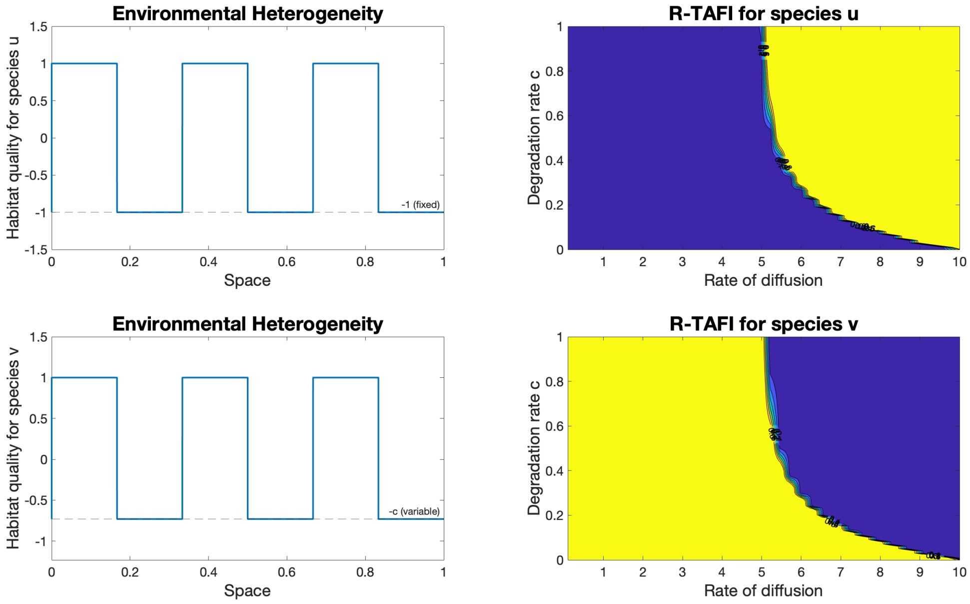


Figure 4.12: A numerical simulation of the R-TAFI score as it depends on d and c_2. In this case, we have 3 smaller patches of habitat.

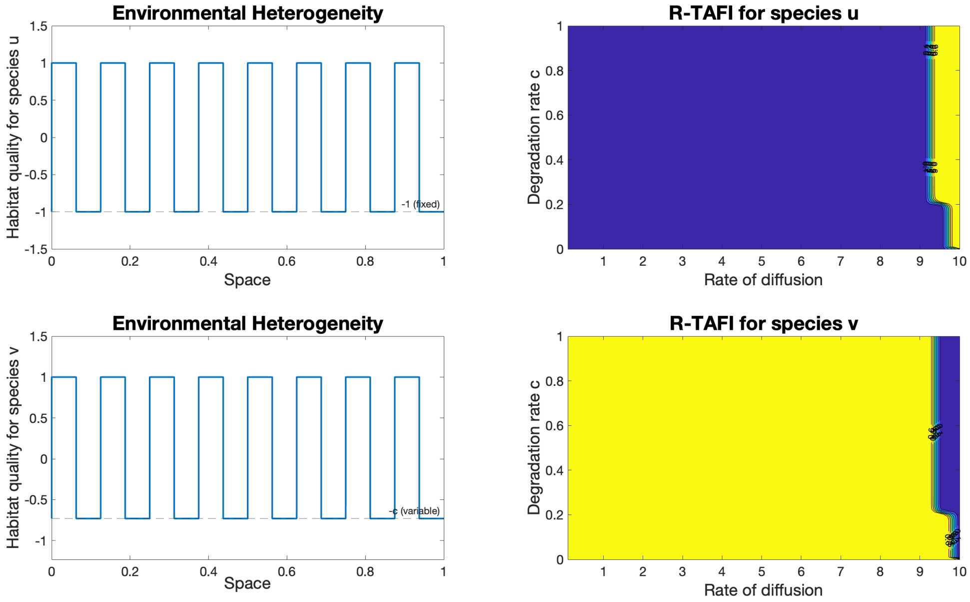


Figure 4.13: A numerical simulation of the R-TAFI score as it depends on d and c_2. In this case, we have 8 very small patches of habitat.

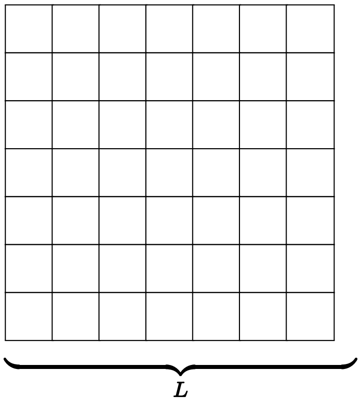
snapshots in time. In some applications, this may be precisely the insights desirable, such as optimization of yield under well-controlled environmental conditions. There are limitations to this point of view, especially from an ecological perspective: habitat fragmentation, while intimately tied to the geometry of the patterns generated, is more often an ecological process occurring over some period of time. An intact habitat is gradually broken apart into disjoint, less connected patches lying within some environmental matrix. As described in [33], assessment of fragmentation as an arrangement generally implies four effects of fragmentation (as a process) on the resulting landscape patterns observed: a reduction in total habitat *amount*, increases in *number* of distinct habitat patches, a decrease in the *size* of habitat patches, and an increase in *isolation* of habitat patches. This is what much of the measures/approaches discussed in Section 4.2 consider, sometimes in tandem but often only one effect at a time. This motivates a completely different approach to assessing fragmentation while using the same tools developed in the previous section. In particular, we are motivated by the following supposition found in [33]:

> "Habitat can be removed from a landscape in many different ways, resulting in many different spatial patterns (Figure 2). Do some patterns represent a higher degree of fragmentation than others, and does this have implications for biodiversity? If the answer to either of these questions is "no," then the concept of fragmentation is redundant with habitat loss. The assertion that habitat fragmentation means something more than habitat loss depends on the existence of effects of fragmentation on biodiversity that can be attributed to changes in the pattern of habitat that are independent of habitat loss. Therefore, many researchers define habitat fragmentation as an aspect of habitat configuration."

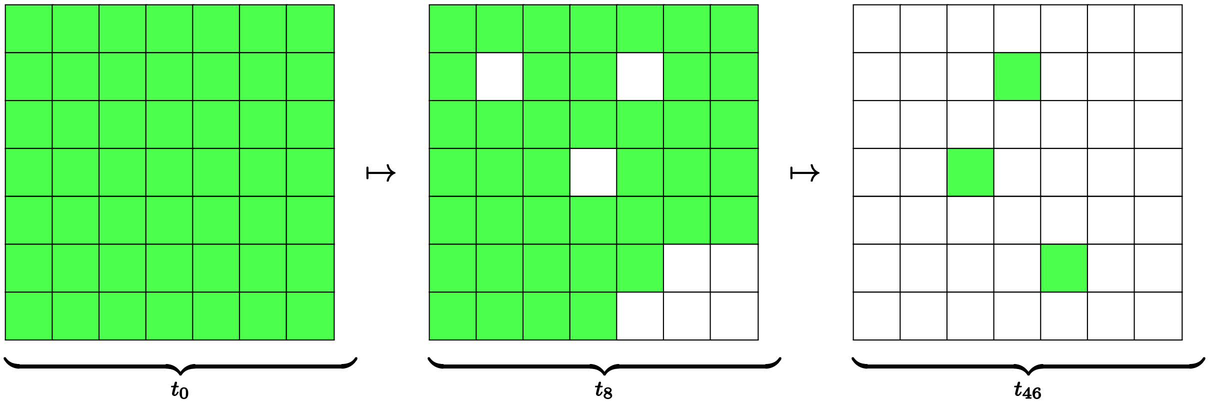
Using some of our measures developed, we will show that the answer to each of the key questions raised above is *yes!*, and that habitat fragmentation as a by-product of habitat loss is indeed meaningful and worth further exploration, both theoretically and empirically. Furthermore, our approach remains at the landscape scale, and so we are able to investigate the impacts of habitat fragmentation beyond mere patch-level effects.

To achieve this, rather than considering snapshots in time and comparing the predictions of different measures (the pattern-oriented approach), we now *start* with an entirely intact landscape: the entire domain Ω is habitat for the species under consideration. We then systematically remove patches of habitat of a prescribed size. This process replaces habitat with degraded/destroyed regions, resulting in a (potentially) fragmented habitat. The nature of the process of removal of patches is what determines whether or not it is 'fragmented'. Naturally, this results in a discrete "time series" of sorts, where each successive time-step indicates another chunk has been removed. This process more accurately reflects habitat fragmentation as it occurs most commonly in the natural world [33], and allows us to study the effects of habitat fragmentation over time.

Let us make this more practical for our purposes. It is important to first note that an analytical study of this setup is quite impractical. It is already difficult to study arrangements of fixed sizes; studying sequences of arrangements of varying sizes complicates things further. Hence, we develop this idea with numerical implementation in mind. To this end, we consider the fixed habitat $\Omega := (0, L) \times (0, L)$, a square of side length $L > 0$. We then 'discretize' the habitat into N^2 patches of side length L/N. For example, we may have a domain of length L and choose $N = 7$ so that we have exactly $7^2 = 49$ discrete patches of length $L/7$:



We can then generate sequences of *habitat matrices* indexed by $1 \leq k \leq N^2$. This sequence is always at most of length N^2, for at step N^2, the final patch of habitat is removed, and the species must undergo deterministic extinction by definition (i.e., there is no habitat left to facilitate persistence!). For example, we may have a sequence as follows. At time-step t_0, the entire landscape is comprised of habitat (denoted by green blocks). At timestep t_8, we have 8 patches removed; at t_{46}, we have 46 patches removed (or, $N^2 - 46 = 3$ patches remain).



We then study the changes in our previously developed measures of fragmentation as this sequence of habitat matrices evolves. Our general strategy in this section is thus:

1. Generate sequences of habitat matrices of length (at most) N^2;
2. Compute measures of fragmentation at each time step k, $1 \leq k \leq N^2$;
3. Compare results and explore implications for habitat fragmentation.

4.6.1 Fragmentation as a process and the SOFFI score

In what follows, we develop a strategy for Step 1 for the SOFFI score. This will be slightly different from the approach taken for the total abundance approaches.

Step 1. Habitat matrix generation

Built into the approach described above is the generation of these sequences of habitat matrices. We develop a method to generate such sequences here. In fact, our approach takes inspiration from the so-called *contagion* measure of habitat fragmentation.

First, we fix two sequences of square matrices $\{M^k\}_{1 \leq k \leq N^2}$,$\{H^k\}_{1 \leq k \leq N^2}$ of size N. H^k will denote the habitat matrix at step t_k, where H^0 is simply the ones matrix (all entries have value 1, indicating the entire landscape is habitat). The matrix M^k will be an auxiliary probability matrix for the time step t_k: each entry $M_{i,j}$, $1 \leq i, j \leq N$, corresponds to the entry $H_{i,j}$. We then systematically prescribe probabilities to each entry $M_{i,j}$. Note that this requires $\sum_{i,j=1}^{N} M_{ij} = 1$ (in practice we achieve this through normalization). These probabilities then correspond to the likelihood that a given patch within H will be removed. For example, if we have $M_{i,j} = 1/N^2$ for every i, j, it is equally probable that *any* patch of H could be removed. Deviating from this may make a certain patch more or less likely to be removed at the next time step. Once a matrix entry $(\tilde{i}, \tilde{j})$ of H is chosen, based on the probability matrix M, the entry $H_{\tilde{i},\tilde{j}}$ is changed from a value of 1 to a value of 0 (it is now degraded at some level). $(\tilde{i}, \tilde{j})$ is then assigned a value of zero in M, indicating that it has a probability of zero to be chosen at any subsequent step; biologically, this assumes that the patch has been degraded or destroyed and does not become habitat again at any future step.

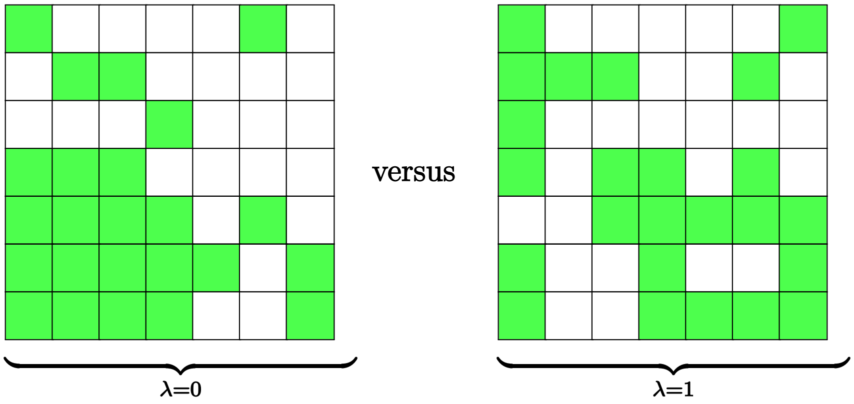
This algorithm generates a sequence of matrices $\{H^k\}_k$, $1 \leq k \leq N^2 - 1$, where we remove the final entry as we need not compute any measure for the trivial case of *no habitat available.* Note that, at each time step t_k, we generate a *new* probability matrix with $N^2 - k$ non-zero entries. This new probability matrix then determines the patch to be removed at the subsequent time step, and the process repeats.

One may now ask: what does this have to do with fragmentation? Of course, we also need some method to prescribe these probabilities to each entry of M. This is where the concept of *contagion* returns. We first introduce a parameter $\lambda \in (0, 1)$, which will be our level of 'fragmentation' in the matrix H. We initialize the algorithm with an equal probability across all matrix entries. That is, M^0 is a matrix with a value of $1/N^2$ in each entry. The first patch is therefore removed randomly with a uniform distribution. Once the entry $(\tilde{i}, \tilde{j})$ is chosen to be removed, the habitat matrix H^1 is the matrix with all 1's except for the single entry $(\tilde{i}, \tilde{j})$, now assigned a value of 0.

We then generate the next probability matrix M^1, where $(\tilde{i}, \tilde{j})$ now has a value of 0 (it is removed and cannot be chosen again). This leaves $N^2 - 1$ patches to be assigned a probability. We then use the parameter λ to determine how likely it is that the *next patch removed is adjacent to a previously removed patch.* This is similar to contagion, but in the reverse direction. The endpoints are easiest to demonstrate the idea: when $\lambda = 0$, there is 'zero' fragmentation, and therefore there is a probability of 1 that the next patch removed will be adjacent to a previously removed patch. Thus, $\lambda = 0$ logically corresponds to a *no fragmentation* case, since the matrix H^k will have a connected degraded region at any time step t_k through construction. On the other hand, when $\lambda = 1$, there is 'the most' fragmentation, and therefore there is an equal probability that *any* block could be removed at the next time step. This logically corresponds to a much more fragmented habitat, since the patches removed are more uniformly distributed throughout the landscape. Then, we may vary $\lambda \in (0, 1)$ continuously, corresponding to *less fragmented* (values closer to 0) or *more fragmented* (values closer to 1).

In our case, our algorithm is built as follows. In H^k, there are k entries with 0. We then classify patches as *adjacent* or *not adjacent*. In our simulations, we classify adjacent patches as either left/right, above/below, or on a diagonal from a removed patch. Adjacent patches are assigned a probability lying between 1 (when $\lambda = 0$) and $1/(N^2 - k)$ (when $\lambda = 1$). All non-adjacent patches are assigned a probability lying between 0 (when $\lambda = 0$) and $1/(N^2 - k)$ (when $\lambda = 1$). The parameter λ controls the scaling between these two edge cases. In some sense, we have built a rather dichotomous algorithm: there are only two probability values, with all adjacent patches receiving the same value and all non-adjacent patches receiving the same value.

The following shows the outcome of a single simulation for $\lambda = 0$ (no fragmentation) versus $\lambda = 1$ (most fragmentation). In it, we fix $N = 7$ and show time-step t_{25} (approximately half of the habitat removed).



From this simplified example, we see that the $\lambda = 0$ case has a more ‘connected’ habitat remaining compared to the $\lambda = 1$ case. Hence, we see that this algorithm does roughly what we want it to do: as lambda increases from 0 to 1, the habitat sequences generated move from ‘less fragmented’ to ‘more fragmented’

Step 2. Computation of fragmentation measures

Once we have our sequence of habitat matrices, we must next compute the measures which are meant to assess the impact of fragmentation. For now, we focus on an application of the SOFFI score. We first note a few facts. In the following, we abuse notation slightly and denote by $\text{SOFFI}(d, c, H^k)$ the SOFFI score at step k, where we understand that H^k corresponds to the domain Ω with k patches removed.

Proposition 4.6.1. *Suppose $d > 0$, $c \geq 0$ are fixed. Then, there holds*

- $\text{SOFFI}(d, c, H^0) = 1$, *and* $\text{SOFFI}(d, c, H^{N^2}) = 0$.
- $\text{SOFFI}(d, c, H^k) \geq \text{SOFFI}(d, c, H^{k+1})$ *for every* $k = 1, 2, \ldots, N^2$. *Furthermore, if* $c = 0$ *the inequality is strict.*
- $\text{SOFFI}(d, 0, H^k) > 0$ *for all* $k = 1, 2, \ldots, N^2 - 1$.

Proof. The first property follows directly from the definition of SOFFI and properties of the principal eigenvalue. The monotonicity in item two follows from Theorem 4.5.1 2.), where the strict inequality can be observed from Theorem 4.5.2 1.) and Theorem 4.5.2 1.). The final property can be observed from Theorem 4.5.2 1.). □

These properties, while somewhat trivial mathematically, are important to note for the ecological interpretation of results: when there is no habitat removed, SOFFI $= 1$. When the entire habitat is removed, we of course have SOFFI $= 0$. In this setup, SOFFI is monotonically decreasing as habitat is removed; this is consistent with our understanding of the impact of habitat loss on a single species. The third property says that if the removed habitat is neutral to the species, our SOFFI score will always predict persistence; extirpation is only possible when the entire habitat is removed.

Different from the previous section, we no longer use the *PDEModeler* app from MATLAB. Due to the number of repetitions required, we instead construct a simple discretization of the Laplacian (using a second order central difference scheme and 'ghost nodes' to handle the Neumann boundary condition). We then solve for the principal eigenvalue of the discrete problem using Newton's iterative method, setting up N^2 equations for the discretized problem and the final equation through normalization of the eigenvalue (i.e., $N^2 + 1$ equations and $N^2 + 1$ unknowns). Note that we must take some care at this step: Newton's method, while brilliant, can have some stability issues [76], especially for larger, more sparse matrices (such as in our case). Based on some rudimentary testing[1], this becomes an issue with small diffusion rates and/or finer mesh scales. To avoid this, we choose our diffusion rate and domain size not too small and not too large, respectively.

Step 3. Comparison of results

We now present the outcomes found for this setup for the SOFFI score. We first fix $N = 10$, so that we have a habitat matrix H with $N^2 = 100$ patches. We compute the SOFFI score every $1 - 5$ steps, depending on the case, to save decrease computation time. This is reasonable due to the continuity of SOFFI with respect to changes in B, which follows from the continuity of the principal eigenvalue. We fix our habitat length $L = 1$, and choose a mesh of 4 for each patch; therefore, the *true* mesh when we solve for the principal eigenvalue is ~ 0.025 (i.e., $\sim L/(4N) = 0.025$.

We compare the SOFFI score across a number of variables. First, we are most interested in changes with respect to the parameter λ as well as changes with respect to the number of blocks removed. Therefore, we first plot the SOFFI score versus the number of patches removed over the values $\lambda = 0.0, 0.25, 0.5, 0.75, 1.0$. We also observe changes with respect to the level of impact in the removed regions. This is described by the parameter c, and so we consider cases $c = 0, 0.1, 1.0, 10.0$. We hold the diffusion rate fixed at $d = 0.1$, which is $1/10$ the size of the domain[2]. Finally, we note an important caveat: since the habitat matrices are generated in a probabilistic way, we cannot rely on a single sequence to garner meaningful insights. To overcome this, we repeat the process for a number of trials. In the following, we run 30 trials for each fixed value λ. We then take an average of the SOFFI score across all trials. This

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[1] The author readily admits numerical analysis is not the focus of this work; instead, we point out that this method does not appear to be universally useful in this context. The issue seems to stem from *other* eigenvalues being rather close to the principal eigenvalue, in which case the iterates may return an incorrect (but close) result. This occurs most obviously when the diffusion rate is taken small ($\ll 10^{-1}$) and the spatial mesh must be chosen small enough to compensate. We avoid such cases here to keep in mind the big picture. To study these edge cases, alternative methods may be used to extract the principal eigenvalue

[2] A further note on the choice of diffusion rate: since we know the limiting behaviour of the principal eigenvalue as $d \to 0^+$ or $d \to \infty$, we do not want to choose d too small or too large. More precisely, for $d \ll 1$, our SOFFI score will remain close to 1; for $d \gg 1$, our SOFFI score will remain close to the average habitat quality. Such limiting cases can mask the influence of fragmentation alone.

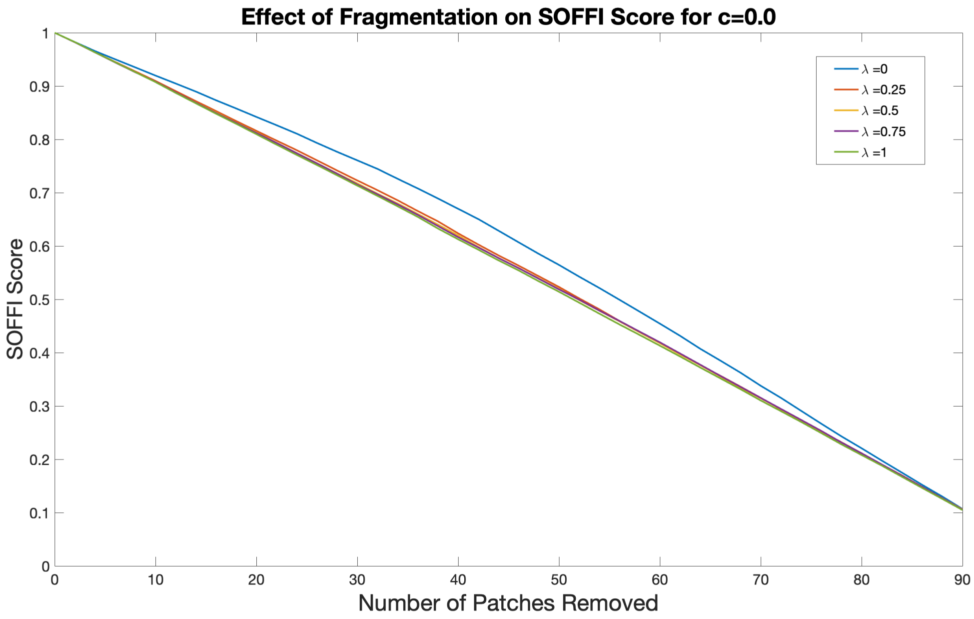

Figure 4.14: A numerical simulation of the SOFFI score as it depends on the number of patches removed. The level of degradation in the removed patches is fixed at $c = 0.0$.

is meant to remove bias due to the random removal of patches. These results are found in Figures 4.14-4.17, where the only change across figures is the level of degradation c within the region B.

4.6.2 Fragmentation as a process and total abundance

Of interest is also the assessment of fragmentation as a process in relation to total abundance. As previously noted, the habitat arrangement optimizing the growth rate (i.e., maximizing the SOFFI score) is *not necessarily* the same as the arrangement maximizing the total abundance. For this reason, we briefly explore the effect of fragmentation as a process on two competing species.

Unlike the SOFFI score, the TAFI or R-TAFI scores require that we calculate the total abundance at steady state. In a square domain, this can be rather involved. For this reason, we take the same approach in a one-dimensional spatial domain: given the domain $(0, L)$ for $L > 0$ fixed, break the habitat into N pieces of length L/N and systematically remove a patch, with $\lambda \in (0, 1)$ a parameter determining how connected

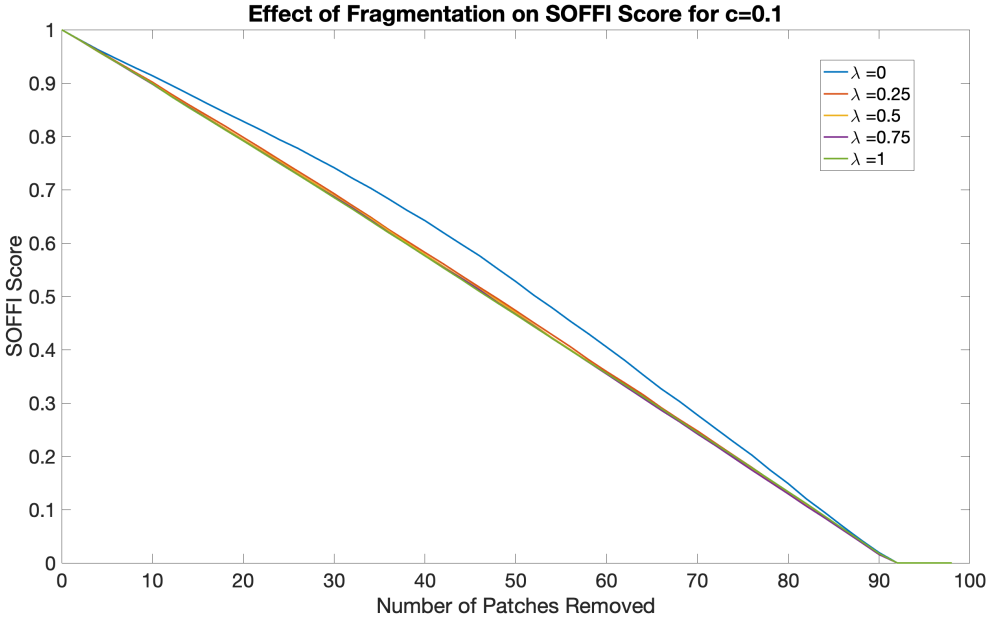

Figure 4.15: A numerical simulation of the SOFFI score as it depends on the number of patches removed. The level of degradation in the removed patches is fixed at $c = 0.1$.

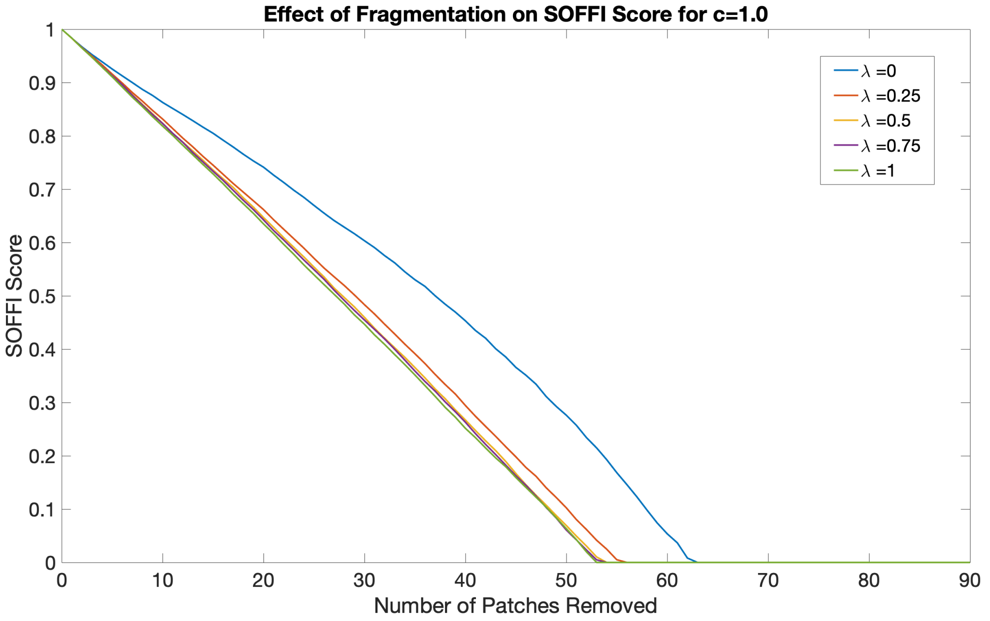

Figure 4.16: A numerical simulation of the SOFFI score as it depends on the number of patches removed. The level of degradation in the removed patches is fixed at $c = 1.0$.

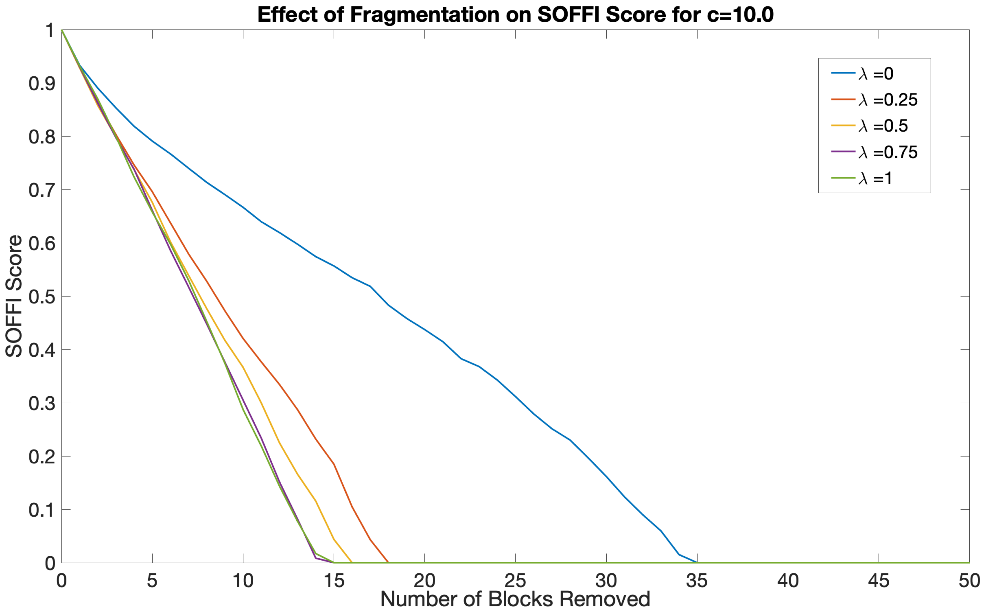

Figure 4.17: A numerical simulation of the SOFFI score as it depends on the number of patches removed. The level of degradation in the removed patches is fixed at $c = 10.0$.

the habitat will be at each time step.

Once a sequence of habitats H^k, $0 \leq k \leq N$, has been generated, we calculate the total abundance at steady state for each time step. Carefully note the distinction between the time step t_k, which refers to the current state of the landscape, and the time dependence of the problem we look at. This may seem contradictory, since the steady state is obtained by letting $t \to \infty$ in the parabolic problem. On the other hand, when the reaction term is concave (like the logistic form used in these examples), the rate of convergence is exponential in time. Hence, this setup is most reasonable if the landscape changes are occurring on a timescale slower than the population dynamics. We then calculate the TAFI (single-species case) and R-TAFI score of each population (two-species case), plotting the score versus the number of patches removed, identical to the SOFFI score case.

The TAFI score

Note that we already have insights into one property of the TAFI score under this configuration: since the environmental heterogeneity is monotonically *decreasing* (we always *remove* patches), the TAFI score *will always be monotonically decreasing.* This is mathematically obvious but has significant ecological implications: *habitat fragmentation as a process is always bad for a single species.* The same is not necessarily true for the multi-species case, since a decrease in competition could improve the overall habitat quality, even though habitat is being degraded/destroyed! What we are more interested in are differences between less fragmented cases ($\lambda = 0$) and more fragmented cases ($\lambda = 1$).

In Figures 4.18-4.20, we observe an interesting departure from the SOFFI score predictions. First, note that we do not include the case of neutral degradation ($c = 0$) due to Theorem 4.5.3 point 3.): in this case, the TAFI score is always 1. We show the cases $c = 0.1$, $c = 1.0$, and $c = 10.0$. Unlike the SOFFI score, we find that when the degradation level is low (Figure 4.18), fragmentation as measured by λ is actually a *good* thing! For $\lambda > 0$, intermediate levels of lost habitat ($\sim 15 - 35$ patches removed) actually increases the total abundance substantially compared to the no fragmentation case ($\lambda = 0$). This is most pronounced at $\sim 25 - 30$ patches removed, where fragmentation alone can account for an almost 40% decrease in abundance. We then see that when a large portion of the habitat has been removed ($\sim 36 - 37$ patches removed), the relationship reverts back to what was found for the SOFFI score.

When we increase the level of degradation from 0.1 to 1.0 and 10.0, we find that this phenomenon disappears completely! Of course, the TAFI score decreases when c increases; what is more interesting is the difference between fragmentation regimes. This is most pronounced in Figure 4.20, where the no fragmentation regime decreases in a roughly linear fashion, while increasing λ results in a roughly ordered decrease in TAFI score. This time, the differences are apparent with as little as $\sim 5 - 10$ patches removed! When $\sim 10 - 15$ patches are removed, fragmentation alone can account for an almost 90% decrease in abundance. As expected, when enough blocks are removed (> 30), the TAFI score is zero, indicating deterministic extinction. This behaviour is

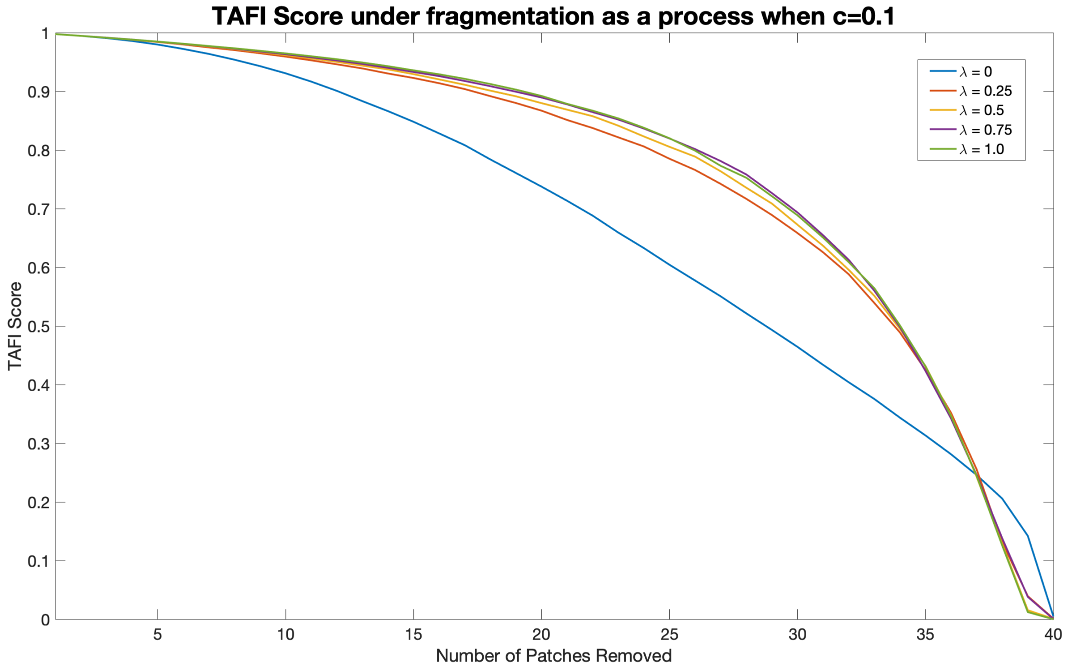

Figure 4.18: A numerical simulation of the TAFI score as it depends on the number of patches removed. The level of degradation in the removed patches is fixed at $c = 0.1$. The diffusion rate is fixed at $d = 0.1$ in a domain $\Omega = (0, L)$.

now consistent with predictions made by the SOFFI score.

The R-TAFI score

We now repeat this process for the R-TAFI score. Recall that R-TAFI is a *relative* measure. In the case of two competing species, it is a zero-sum game: if population u is thriving, population v is necessarily *not* thriving. Therefore, in Figures 4.21-4.25, we plot only the R-TAFI score for population u. The R-TAFI score for population v is obtained by taking $\text{TAFI}(v) = 1 - \text{TAFI}(u)$. We fix the diffusion rates as $d_1 = 0.1 < d_2 = 1.0$ so that u is always the slower diffuser. We fix the degradation level for population u at $c_1 = 1.0$ and consider cases when $c_2 < c_1$ so that population v is the more resilient population. We study the problem in the domain $\Omega = (0, L)$ with $N = 12$ (12 patches to remove). We again run 30 trials for each value of λ and take the average of the R-TAFI scores.

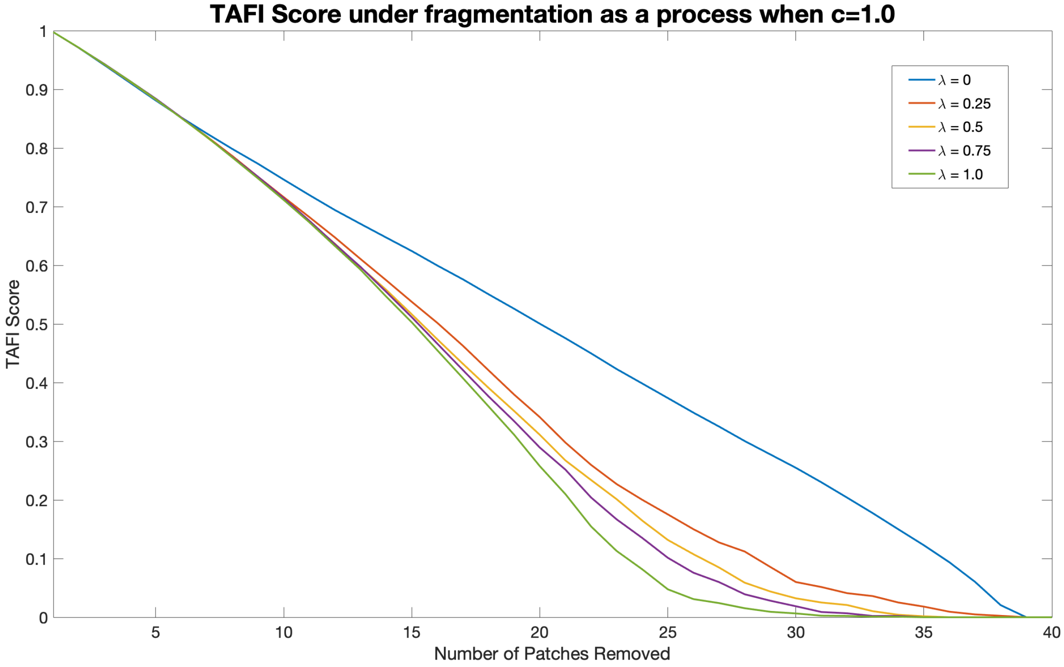

Figure 4.19: A numerical simulation of the TAFI score as it depends on the number of patches removed. The level of degradation in the removed patches is fixed at $c = 1.0$. The diffusion rate is again fixed at $d = 0.1$ in a domain $\Omega = (0, L)$.

First, we know that for 0 patches removed, both populations persist. This is actually the kinetics (ODE) case, since the environment is homogeneous, and the boundary condition is homogeneous Neumann. Importantly, we note that **population u will survive up to step t_{11}. This means that when the R-TAFI score decreases, we eliminate the possibility that both u and v go extinct simultaneously.**

Beginning with Figure 4.21, we observe that when $1 - 3$ patches are removed, population v is the winner (R-TAFI$(u) = 0 \Rightarrow$ R-TAFI$(v) = 1$). We then find that when fragmentation is low ($\lambda = 0$, blue line), we have coexistence for $4 - 10$ patches removed. Once 8 patches are removed, R-TAFI$(u) > 0.5$ and so population u becomes the 'winner'. Under increasing fragmentation, we also find coexistence, but population u is at much lower levels. In this sense, fragmentation appears to favor population v.

As the degradation level c increases from 0.25 to 0.9 in Figures 4.22-4.25, we find some potentially expected behaviour: as population v approaches a similar level of

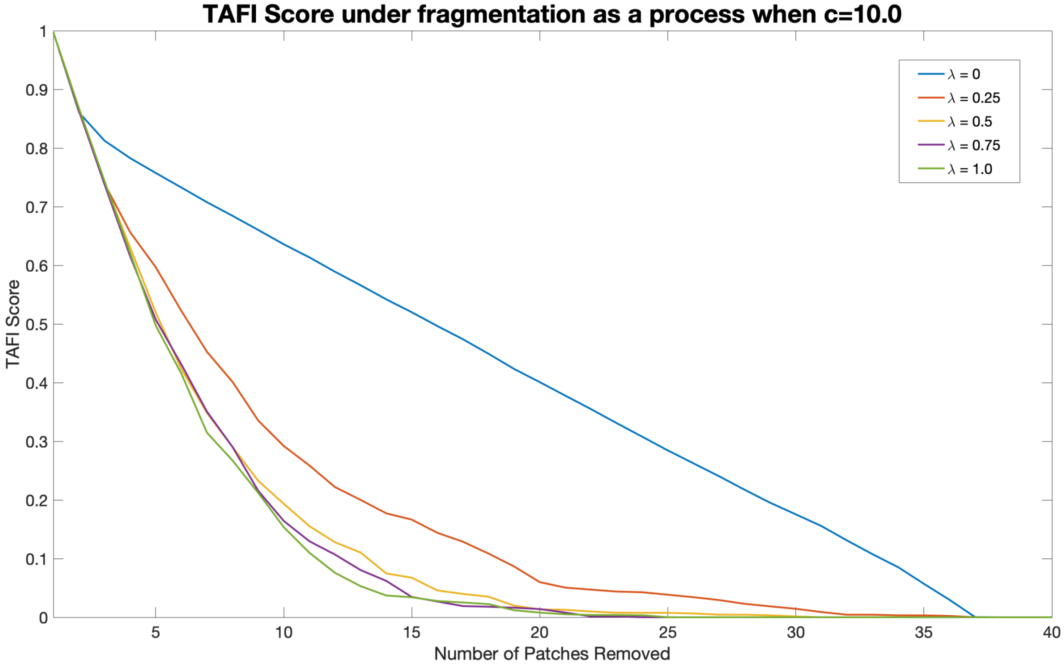

Figure 4.20: A numerical simulation of the TAFI score as it depends on the number of patches removed. The level of degradation in the removed patches is fixed at $c = 10.0$. The diffusion rate is again fixed at $d = 0.1$ in a domain $\Omega = (0, L)$.

resilience as population u (i.e., as c_2 approaches $c_1 = 1$), population u should eventually start to increase in its R-TAFI score. Indeed, this is what we observe, where population u wipes out population v for $1 - 11$ patches removed. What is interesting, though, is the change in behaviour when almost all patches are removed: we again begin to see coexistence! In Figure 4.25, we find that coexistence is only facilitated when $\lambda > 0$. When the degraded region is entirely connected, population u sees the benefit. This trend holds across all figures: when $\lambda = 0$, coexistence is not facilitated at all when too many patches are removed. On the other hand, when λ is positive (indicating the habitat is at least somewhat fragmented), coexistence is much more likely to occur. Population v seems to benefit the most under low- or high-habitat loss scenarios with fragmentation. Conversely, population u seems to benefit most under intermediate habitat loss and no fragmentation.

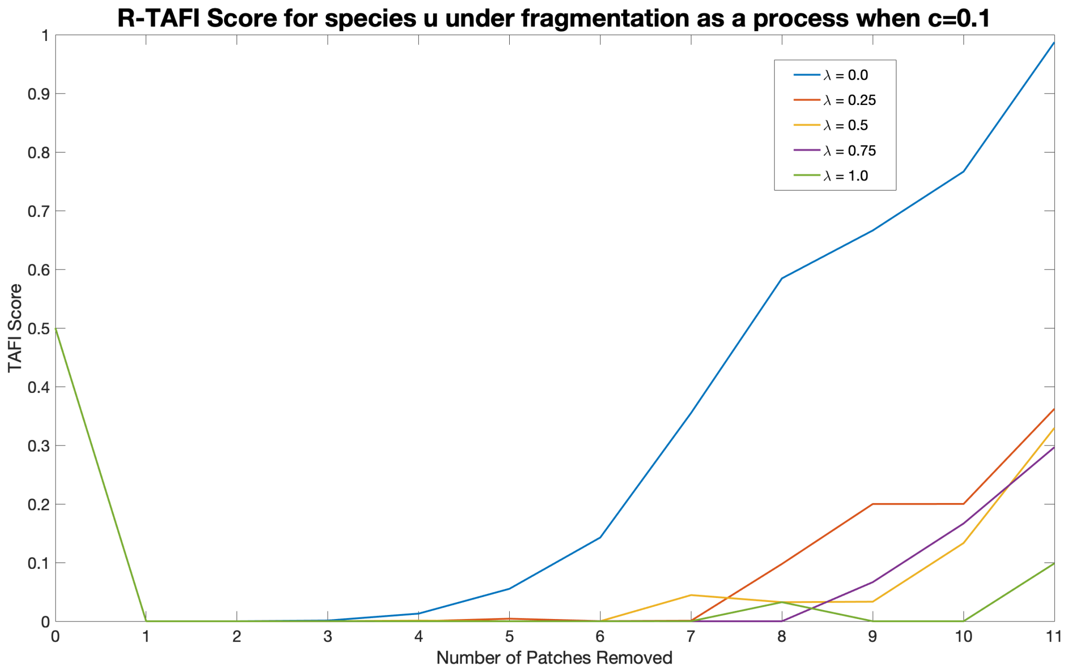

Figure 4.21: A numerical simulation of the R-TAFI score as it depends on the number of patches removed. The level of degradation in the removed patches for population v is fixed at $c = 0.1$.

4.7 Discussion

This chapter has been dense with both numerical and analytical investigation. Here, we aim to bring all of our findings together in a concise and interpretable fashion. Fundamentally, we are interested in the following question: *is habitat fragmentation good or bad for species*? As has been made evident, this question is ill-posed: habitat fragmentation is not universally *good* or *bad* as context matters! Instead, we reframe the question as: *under what circumstances can habitat fragmentation be good, bad, or neutral for diffusive species*? We answer this question from the numerous perspectives explored earlier.

4.7.1 When is habitat fragmentation neutral?

We first discuss cases where fragmentation is neutral. Through construction, fragmentation is generally *not* neutral, since we are removing habitat. However, through

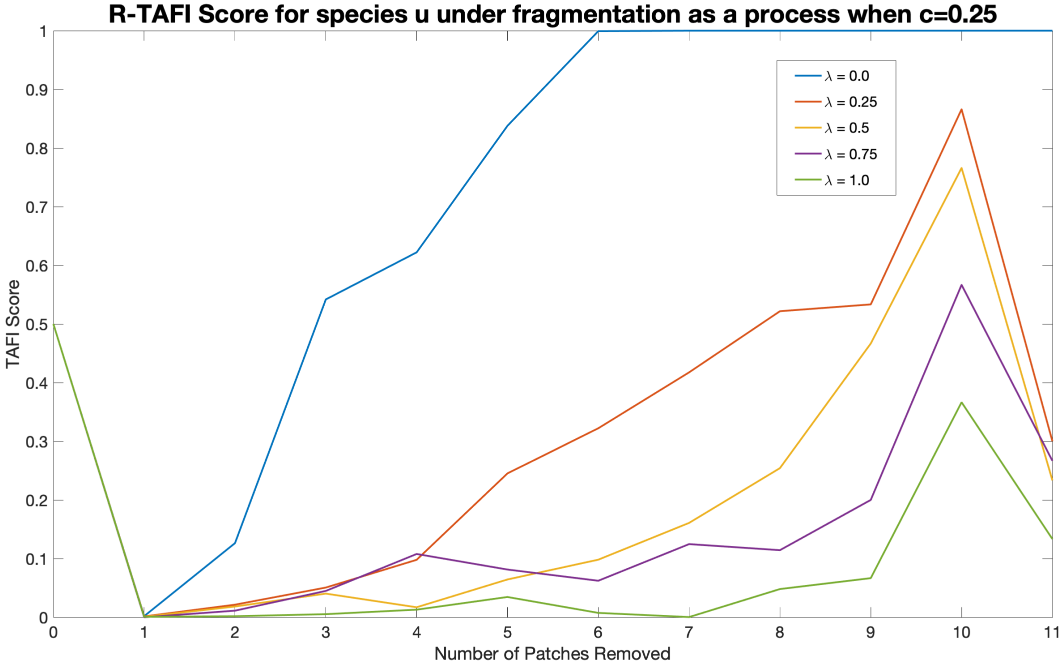

Figure 4.22: A numerical simulation of the R-TAFI score as it depends on the number of patches removed. The level of degradation in the removed patches for population v is fixed at $c = 0.25$.

simulation we observe some cases where habitat alteration does not cause significant changes in our assessment measures.

In Figure 4.3, we consider the SOFFI score in a landscape $B_1(0)$ and degraded region $B_\rho(0)$ for $0 < \rho < 1$. We use a contour plot to view the SOFFI score with respect to changes in the size of the degraded region (ρ) and the level of degradation in the degraded region (c). We notice that the level of degradation c matters much less than the *size* of the degraded region: if the inner radius is below ~ 0.4, the SOFFI score is ~ 1 (its maximal possible value). In this simple example, we observe that **for 'fragmentation' in the arrangement sense, total habitat is more important than habitat quality**.

A similar observation can be made from Figure 4.4. In this case, we have a completely destroyed region of radius ρ within the domain $B_1(0)$. This time, we consider the effect of moving the location of the destroyed region, given by the parameter t. We

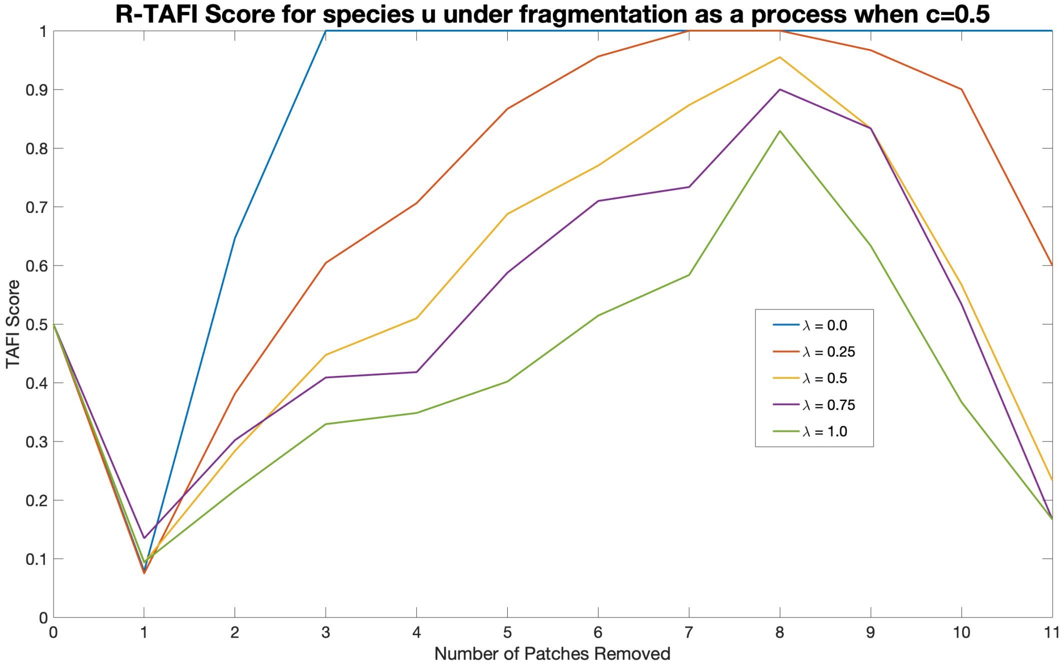

Figure 4.23: A numerical simulation of the R-TAFI score as it depends on the number of patches removed. The level of degradation in the removed patches for population v is fixed at $c = 0.5$.

find that for small destroyed regions ($\rho < 0.1$), the location of the destroyed region has little effect (the SOFFI score is roughly constant over vertical cross-sections when ρ is small). complementing the previous insight, this indicates that **for 'fragmentation' as an arrangement, the location of a destroyed region matters much less for small regions**.

In Figures (4.6)-(4.9), we find an example of fragmentation *per se*: the total available habitat remains fixed while the arrangement alone changes. In this case, we examine changes in the TAFI score (identical to the total population in this particular scenario). In these figures, we observe that for small rates of diffusion ($d < 1$), increasing fragmentation has little effect on the TAFI score (it remains near 0.5). This is consistent with Theorem 4.5.3 point 2.), which says that as $d \to 0^+$, TAFI $\to |G| \,/\, |\Omega| = 0.5$. Similarly, we observe that for low levels of degradation (when c is small), the level of fragmentation has less impact; this is observed in Figures (4.6)-(4.8) across all diffusion

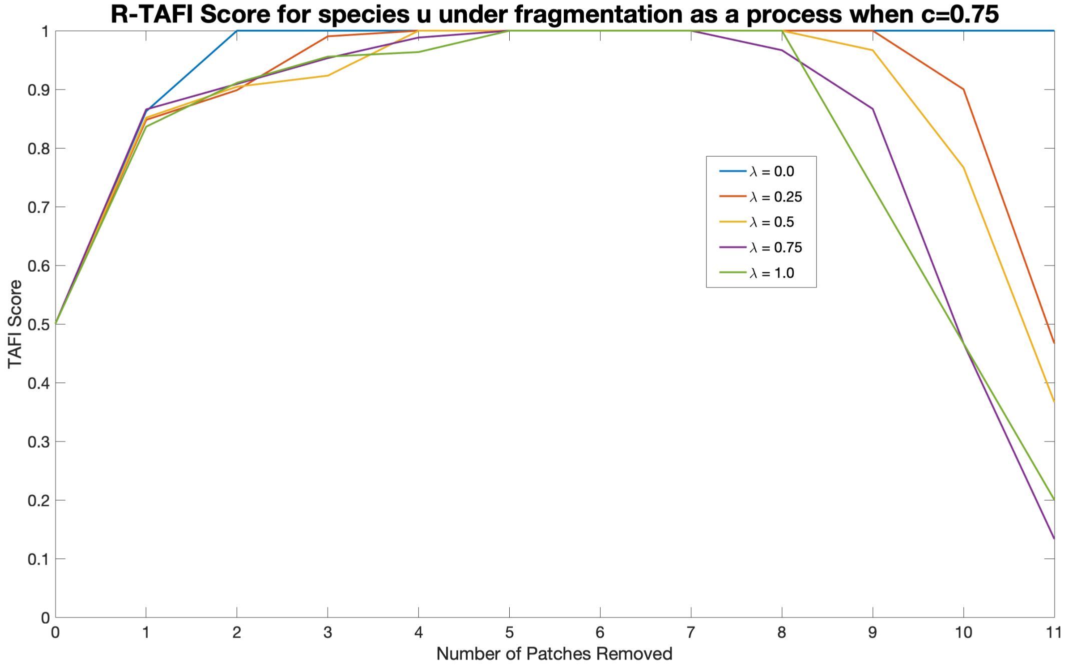

Figure 4.24: A numerical simulation of the R-TAFI score as it depends on the number of patches removed. The level of degradation in the removed patches for population v is fixed at $c = 0.75$.

rates and $c < 0.2$. Of course, this trend breaks down in the limit as the number of distinct patches increases arbitrarily.

Similar conclusions are drawn when studying habitat fragmentation as a process. In Figure 4.14, we observe that the SOFFI score, while decreasing, always remains positive. This is consistent with item three of Proposition 4.6.1. But this is not exactly what should interest us most: instead, we are interested in differences between different values of λ. In particular, when $c = 0$, the SOFFI score decreases approximately proportional to the amount of available habitat. All values of λ produce approximately the same result. This is not necessarily an example of fragmentation being *neutral*; instead, it indicates that *for low levels of degradation, the total available habitat matters more than the arrangement of the habitat patches.*

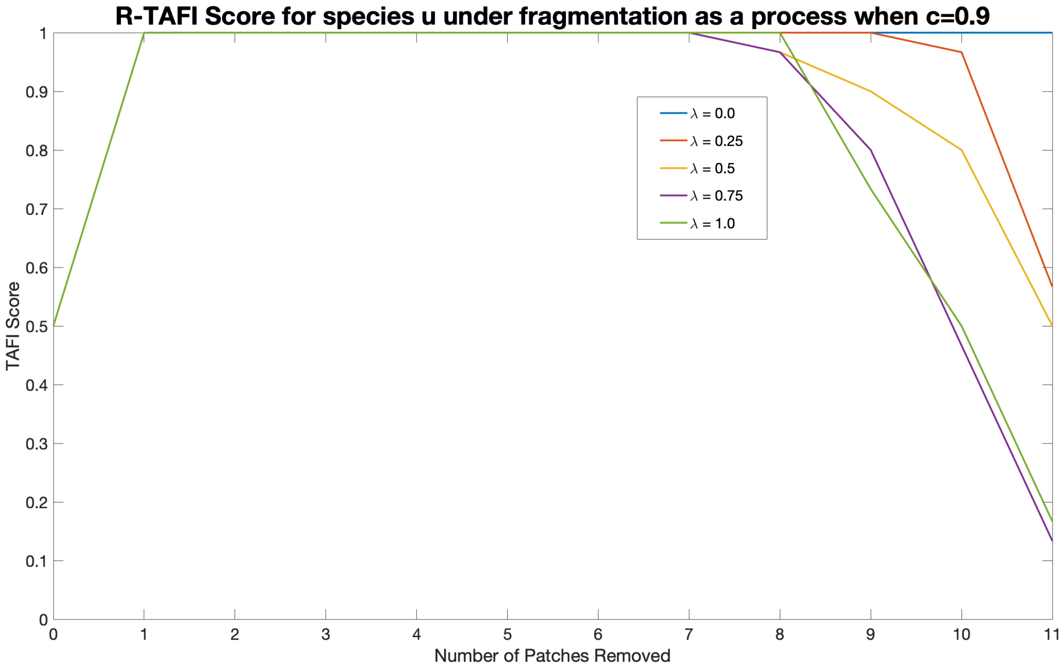

Figure 4.25: A numerical simulation of the R-TAFI score as it depends on the number of patches removed. The level of degradation in the removed patches for population v is fixed at $c = 0.9$.

4.7.2 When is habitat fragmentation bad?

On the other hand, we have many more insights into when fragmentation is particularly negative for a population. In Figure 4.3, we find that when the inner radius grows beyond 0.4 (i.e., when the degraded region occupies more than $\sim 20 - 25\%$ of the landscape), there is a sharp drop off of the SOFFI score. Somewhat obviously, the higher the level of degradation, the sharper the drop off.

Similarly, Figure 4.4 indicates that the location of a destroyed region can make a significant difference in outcomes: when the destroyed region has radius > 0.1 (i.e., when the degraded region occupies more than $\sim 1 - 2\%$ of the landscape), the centre value t can actually determine the difference between extinction and persistence as predicted by the SOFFI score. Of course, the dramatic effect is amplified by the fact that the level of degradation in this region is arbitrarily large. For finite values of c, one expects the contour plot to stretch to the right (more areas of orange and yellow).

In Figure 4.5, we observe a roughly decreasing SOFFI score with respect to both level of degradation c and the level of fragmentation k. Recall that in this case, we study habitat fragmentation *per se*, since the total available habitat remains fixed while levels of fragmentation and degradation increase. The decrease in SOFFI score is more dramatic over increasing degradation at higher levels of fragmentation. When the landscape is less fragmented, the impact of degradation level is less pronounced. This suggests that **the negative effects of degradation are amplified by fragmentation *per se***.

We observe a similar trend in Figures 4.6-4.9: increasing the level of fragmentation *per se* dramatically increases the size of the *blue* regions, indicating an increase in parameter regions with 0 SOFFI score. This is most pronounced in Figure 4.9, where almost the entire parameter region has a SOFFI score less than $\sim 0.2 - 0.3$. This suggests the same conclusion: **the negative effects of degradation are amplified by fragmentation *per se***.

The negative effects of habitat fragmentation are, perhaps, most evident in the progression from Figure 4.14 to Figure 4.17. When the level of degradation is neutral ($c = 0$), the SOFFI score decreases in a way that is proportional to the total available habitat. That is, it is decreasing in a similar way across different fragmentation levels (as described by the parameter $\lambda \in (0, 1)$). As the level of degradation increases, the difference between the no fragmentation case ($\lambda = 0$) and the high fragmentation case ($\lambda = 1$) is quite dramatic. This is most pronounced in Figure 4.17: we observe that in the low fragmentation case, the SOFFI score is zero after ~ 35 patches are removed. This is in contrast to the case $\lambda = 1$, where the SOFFI score is zero after only ~ 15 patches are removed! In this setting, the significant difference between these values of λ indicates a significant difference due to fragmentation alone. Therefore, **the level of degradation greatly amplifies the impact of habitat fragmentation as a process**.

When we consider instead the effect of fragmentation on total abundance, we find trends similar to those described above under certain scenarios. For a single species, we use the TAFI score. In Figures 4.19-4.20, it is evident that fragmentation at any level ($\lambda > 0$) is much worse than the zero-fragmentation case ($\lambda = 0$). This is most pronounced in Figure 4.20 where fragmentation alone can account for a $\sim 90\%$ decrease in total abundance. Therefore, **the level of degradation greatly amplifies the impact of fragmentation on total abundance as measured by the** TAFI **score**.

For the case of two competing species, we appeal to the R-TAFI score. As previously discussed, fragmentation appears to have a negative effect on the relative abundance of population u (the slower diffuser). However, this case is more complicated than the single species case, as the success of population u and the impact of fragmentation now depend intimately on the level of impact felt by population v. As expected from our analytical results, when $c_2 \ll 1$, we expect population v to thrive. This is observed clearly in Figure 4.21, where population v is the winner for $1 - 7$ patches removed. Interestingly, R-TAFI(u) is increasing when the amount of habitat lost is high; note that this benefit is decreased when fragmentation is high.

The story becomes more interesting as the impact felt by population v increases. As c approaches 1, R-TAFI(u) starts to increase. This is expected, as a worse environment for population v is a good thing for population u. However, the increase found for population u depends significantly on the level of fragmentation. For example, in Figures 4.22-4.23, we see that the zero-fragmentation case has a much higher R-TAFI score than any case with fragmentation. Specifically, in Figure 4.23, the zero-fragmentation case has population u wiping out population v for 3 or more patches removed. When $\lambda > 0$, there is *always* coexistence, except for when $\lambda = 0.25$ and $7 - 8$ patches are removed. Therefore, **habitat fragmentation is generally worse for the slower, less resilient population**.

4.7.3 When is habitat fragmentation good?

As found in the discussion thus far, we primarily observe habitat fragmentation to have a negative impact on a population. This is easy enough to understand in some sense. When we consider only a single species, habitat fragmentation as a process is **always** bad. This is simply due to the fact that habitat is being removed, and so we expect all of our measures to decrease. This trend appears to hold for fragmentation as a pattern: fragmentation, even when controlling for the total amount of habitat, is negative in the sense that the SOFFI score decreases. Does this mean that we have created a tautology? Habitat fragmentation is bad, essentially by definition? In the cases mentioned above, the answer is perhaps *yes*. There are cases where this does not hold, however.

First, habitat fragmentation, while negative for the SOFFI and POFI scores, may actually improve the TAFI or R-TAFI scores. This is due to the disconnect between *persistence* and *total abundance*: as noted previously, maximizing the SOFFI score is *not* necessarily the same as maximizing the TAFI score. This is observed in Figure 4.18. In this case, the level of degradation is mild ($c = 0.1$). We then see that any level of fragmentation actually *increases* the TAFI score quite a bit, at least when the amount of habitat loss is high. For example, when $25 - 30$ patches are removed, the fragmentation cases ($\lambda > 0$) can account for a $\sim 45\%$ increase in total abundance! This effect seems to disappear at high habitat loss or high levels of degradation.

Of particular interest are the more complicated cases of interacting species. In our case, we explore the influence of habitat fragmentation on a two-species competition model. In Figures 4.10-4.13, we explore the effects of fragmentation *per se*. In each successive plot, the total available habitat remains the same, while the number of patches increases. Notice first that this measure does not portray any negative effect on the total population of either u or v; it is a relative measure! What we *do* find, however, is that **increasing fragmentation *per se* increasing the size of the parameter region which predicts species v as the survivor!** This is in stark contrast to the classic result *the slower diffuser always wins!*. It is well-known that for reaction-diffusion equations, a smaller rate of diffusion is preferable. However, when the faster diffuser (species v in this case) has even a slight advantage in the degraded region (i.e., if c is even slightly less than 1), we observe that the range of diffusion rates for which population v out-competes population u grows significantly as the landscape becomes more fragmented. Furthermore, it also appears that the window for coexistence increases as fragmentation increases. This point may deserve further attention, as it is more likely not monotone (i.e., there exists some 'optimal' level of fragmentation maximizing the size of the window $(\underline{c}, \bar{c})$.

We find similar behaviour when we measure the R-TAFI score as a process. In contrast to the impacts for population u, who generally does *not* benefit from habitat fragmentation, fragmentation alone can be the difference between persistence and extirpation. This is most clearly found in Figure 4.23: when there is no fragmentation ($\lambda = 0$), population u *always wins* when 3 or more patches are removed. On the other hand, when there is some level of fragmentation ($\lambda > 0$), coexistence is more often a possibility than not. Therefore, **fragmentation is generally better for the faster, more resilient population**.

This is a particularly enlightening point, especially when paired with the insights gained for a single-species model: habitat fragmentation can be good *or* bad, but the mechanism by which fragmentation is *good* appears to require the presence of other species. In our case, it appears that despite the habitat quality decreasing for *both* populations u and v, since the decrease in quality affects population u more than it affects population v, this may result in a 'net' increase in habitat quality! This can actually be observed mathematically: consider the reaction term for population v:

$$f(x, u, v) = v(\mathbb{1}_G - c\mathbb{1}_B - \mathbb{1}_G(u + v)).$$

In it, the habitat 'quality' is given by $\mathbb{1}_G - c\mathbb{1}_B$. This quantity appears in many of our theorems, giving insights into the local stability at zero. However, with a slight change in perspective, the habitat quality may just as well include the presence of competitors. In such a case, the habitat quality is

$$\mathbb{1}_G - c\mathbb{1}_B - \mathbb{1}_G u.$$

Thus, if population u is *decreasing* due to increased fragmentation (we found exactly this behaviour in the scalar case!), $-u$ is *increasing*. Therefore, *the habitat quality for species v may be increasing when population u is decreasing*! We should remind readers again of an important point: this investigation depends closely on the diffusive assumption for animal movement. We carefully note that other movement mechanisms may result in drastically different predictions.

When is fragmentation...	Scenario	Evidence
Bad	Fragmentation as an arrangement. The level of degradation is high; increasing fragmentation amplifies the degradation effects.	Figure 4.5; decrease in SOFFI score amplified with fragmentation. Figures (4.6)-(4.9); decrease in TAFI score amplified with fragmentation.
Bad	Fragmentation as a process. The level of degradation increases; increasing fragmentation amplifies affect of habitat loss.	Figures 4.14-4.17; as c increases, difference between SOFFI score in a low fragmentation regime versus a high fragmentation is increased. The required number of patches removed to reach a score of zero is substantially less in high fragmentation regimes.
Bad	Fragmentation as a process. The level of degradation increases, fragmentation amplifies negative effects.	Figures 4.19-4.20; as c increases, significant differences arise in the fragmented versus not fragmented cases.
Bad	Fragmentation as an arrangement, two-species competition model. The level of fragmentation increases; likelihood of survival decreased for the less resilient, slower diffuser.	Figures 4.10-4.13; as fragmentation increases, the parameter region for which species u (slower diffuser) persists decreases dramatically in size. This is demonstrated using the R-TAFI score.
Bad	Fragmentation as a process, two-species competition model. As fragmentation increases, the slower, less resilient population generally has a lower R-TAFI score.	Figures 4.21-4.21; as fragmentation increases, the R-TAFI score for population u is generally lower than the no fragmentation case.
Neutral	Fragmentation as an arrangement. Size and location of a ball in a ball with varying level of degradation; size of ball is small or level of degradation is low.	Figures 4.3-4.4. Size of degraded region much more impactful than level of degradation; position of destroyed region matters less for small region sizes. Note that this neutrality is more a consequence of amount of area lost.
Neutral	Fragmentation as an arrangement. Total resource held fixed, fragmentation increasing, level of degradation is low.	Figures 4.6-4.9; as fragmentation increases, TAFI score is constant for low levels of degradation.
Good	Fragmentation as a process, single species model. Degradation is mild-moderate.	Figure 4.18; higher levels of fragmentation increase the TAFI score.
Good	Fragmentation as an arrangement, two-species competition model. The level of fragmentation increases; likelihood of survival increased for the more resilient, faster diffuser.	Figures 4.10-4.13; as fragmentation increases, the parameter region for which species v (faster diffuser) persists increases dramatically in size. This is demonstrated using the R-TAFI score.
Good	Fragmentation as a process, two-species competition model. As fragmentation increases, the faster, more resilient population generally has a higher R-TAFI score.	Figures 4.21-4.21; as fragmentation increases, the R-TAFI score for population v is generally higher than the no fragmentation case. In fact, fragmentation alone can account for persistence versus extirpation.

Table 4.1: A broad summary of the impacts of habitat fragmentation.

We summarize these findings in Table 4.1, providing direct answers to some of the questions raised by ecologists and the nature of the impact of habitat fragmentation.

4.7.4 Concluding remarks

In this chapter, we discussed in detail some of the challenges associated with studying habitat fragmentation. Of particular concern is the wide variety of definitions and terminologies used in the literature. In the worst cases, the same term is used for entirely distinct processes. This lack of clarity bleeds into the modelling literature, with many authors not providing clear terminology. Interpreting results becomes much more difficult as a consequence. As evidenced by works such as [39] and [46], interpretations and outcomes of fragmentation impacts are sometimes contradictory and often confusing.

To combat this, we distinguish two perspectives: habitat fragmentation *as an arrangement* and *as a process*. We propose 4 distinct, but closely related, measures of fragmentation. Using tools developed and used in Chapters 2-3, these measures developed are closer to the *species-oriented* perspective, including species-specific quantities, such as diffusion rates and varying resilience to landscape changes. The first two indices, SOFFI and POFI, are presented as measures of *fitness* since they relate directly to the net growth rate of the population. The SOFFI score is easiest and most useful to interpret. The POFI score, meant to remove some of the species-specific qualities, is more of a theoretical object, providing a proof of concept that these measures can be modified to fit more closely with pattern-oriented approaches. To complement these, we also introduce the TAFI and the R-TAFI, relative measures of total abundance. In the single species (TAFI) case, it is relative to the maximal theoretical population size should there be *no* habitat disturbance. In the multi-species case (R-TAFI), it is relative to the total abundance of all populations.

Using these scores, we assess the impact of fragmentation as a pattern and as a process. By approaching the problem from several angles, we are able to tease apart some general trends that appear to hold across all cases. These findings are summarized in Table 4.1.

Due to the lack of consistency in conclusions found in the existing literature, we do not expect this problem to have an easy answer. The results obtained here reflect this quite clearly: arguing whether habitat fragmentation is good or bad is moot. Instead, we reframe the question as *when is habitat fragmentation good, bad, or neutral*? We find that, in almost all cases, the impact of habitat fragmentation is amplified by higher levels of degradation. On the other hand, low levels of degradation with high fragmentation can sometimes be a good thing, even in the single species case. We then observe that habitat fragmentation effects are much more complicated when there are interacting species: depending on the species-specific features (dispersal rates, resilience levels), fragmentation can be the difference between extirpation and persistence.

These results, while not definitive or necessarily conclusive, provide many mechanisms by which the variability in fragmentation effects can be explained. We hope that these results stimulate some new avenues of study, leaning more towards mechanistic and species-specific perspectives for wide application and assessment.

Chapter 5

Conclusion

5.1 Discussion and broad impact

Much of the main conclusions drawn and insights gained in this work are discussed in detail at the end of each chapter, so we do not seek to repeat them here. Instead, we will discuss some of the overarching themes of the dissertation and aim to connect back to some of the original goals of this work from Chapter 1.

As has been argued, habitat loss is a timely issue which needs to be better understood before it can be fully addressed. Habitat loss is inevitable, and so we are highly motivated to study its impacts now so we can mitigate its impacts on biodiversity and sustainability in the future. Moreover, habitat loss is a highly complex process with many counter-intuitive components and impacts. Part of this complexity is inherent in the problem; the rest of this complexity is perhaps a consequence of ambiguity in both the mathematical and ecological literature. Before addressing habitat loss from a modelling perspective, we must first define it in a way that is amicable to analytical study. This is what was argued in Chapter 1.

In Chapter 2, we introduced a habitat degradation model following the precise definitions found in the preceding chapter. From the discussion of Chapter 2, we conclude that the habitat degradation model developed offers valuable insights into the dynamics of some ecological systems subject to habitat degradation. The inclusion of ecologically relevant components, such as a diffusive movement mechanism with explicit spatial heterogeneity and species-dependent habitat quality, has allowed for a more nuanced understanding of the impacts of habitat degradation on interacting populations. The main result of the chapter, a complete description of the global dynamics of a competition-diffusion system, highlights the importance of species-dependent habitat quality as a consideration. This indicates that a sufficiently resilient species will always displace the slower diffuser, and this result is highly robust in that it holds true for a degraded region of any size or shape. Different from existing mathematical works studying similar problems, we fully describe the asymptotic behaviour with less abstraction. In particular, we found that for any fixed configuration, there is always a window giving coexistence of the competing species.

The framework developed in this chapter also extends existing mathematical literature in an interesting way, offering an alternative strategy to slower rates of diffusion through higher rates of resilience in a modified habitat. The chapter's results show that slow diffusion is still beneficial to survival, but that resilience to environmental changes can also facilitate persistence.

These insights offer a promising avenue for promoting biodiversity through a trade-off between dispersal rates and levels of resilience. This is in contrast to classical results, such as '*the slower diffuser always wins!*' result: even moderately different species-specific qualities can drastically change the dynamical outcomes. This is best understood through the detailed study of the principal eigenvalue, which contains all of the necessary information to draw such strong conclusions. Significant effort was given towards obtaining these sharp results.

While the assumptions on the nature of the movement of the organism and the extent of competition may have its limitations, the insights provided by this model can inform strategies for facilitating population persistence in the face of habitat degradation. In practice, improving habitat quality and reducing the size of the degraded region are both promising approaches. The habitat degradation model offers valuable insights into the impacts of habitat degradation on ecological systems and highlights the importance of considering species-dependent habitat quality in these analyses.

Using our three postulates, we then formulate a habitat destruction model from two different perspectives, as explored in Chapter 3. First, from the definition of habitat destruction given here, we construct a habitat destruction model giving rise to reaction-diffusion equations ‘in domains with holes’. Then, from our understanding that habitat degradation and destruction lies on a spectrum, we consider an asymptotic limit as the level of degradation becomes arbitrarily high. As it turns out, these two perspectives are equivalent, giving some consistency to the models’ development.

From the discussion of Chapter 3, we can conclude that the habitat destruction model developed also offers some valuable ecological insights, complementing the results of Chapter 2. First, we prove a uniform convergence between the habitat degradation model and the new habitat destruction model in a single-species setting. Beyond its mathematical interest, this is the first convergence result of its kind, providing a direct connection between the processes of habitat degradation and habitat destruction. In the limit, we obtain a problem that is comparable to a classical Dirichlet problem, suggesting that there is an equivalent ‘critical domain size’ result to be obtained. More interestingly, the convergence between these problems suggests a critical domain size even in the degradation setting. We also establish a convergence result between the degradation and destruction competition systems, indicating that in a destroyed habitat, the slower diffuser regains the competitive advantage. In other words, variable responses to habitat degradation are required to facilitate coexistence. Within these results is a direct connection between the asymptotic behaviour of the solutions, obtained via a detailed study of the associated principal eigenvalue problems.

These results demonstrate the importance of understanding the behaviour of principal eigenvalues as they relate to the global dynamics of ecological systems. Indeed, the intrinsic growth rate of a population is given by the negative of this eigenvalue, giving a direct connection to a populations’ fitness. The uniform convergence established between the principal eigenvalues and corresponding eigenfunctions of the degradation and destruction problems offers a steppingstone for connecting the global dynamics of the two models, as well as for determining the likelihood of population persistence in degraded or destroyed regions.

While Chapter 3’s assumptions on the nature of the set B and the initial data are more limited than those of Chapter 2, the insights provided by the model can still inform strategies for mitigating the impacts of habitat loss on ecological systems. As previously discussed, these are technical assumptions that may potentially be weakened with further effort. In either case, these technical requirements do not detract from the broad conclusions made.

Synthesizing these results and referring again to the arguments made in Chapter 1, we begin to develop a unique approach to assess the impacts of habitat fragmentation. We sought to study this aspect of habitat loss both as a process and as an arrangement. The key tool to do so is, again, the associated principal eigenvalue.

In Chapter 4, we made a slight departure from the previous chapters, focusing more closely on ecologically relevant scenarios of habitat fragmentation. This chapter highlights the importance of clarifying terminology and definitions in ecological research, especially when we seek to model these processes mathematically. By distinguishing between habitat fragmentation as an *arrangement* and as a *process*, and by proposing several measures of fragmentation, Chapter 4 provides a framework for assessing fragmentation impacts in a more rigorous and mechanistic way. The measures developed adopt both a species-oriented and a pattern-oriented approach, an attempt to broaden the possible application of these measures, rather than close one off to a particular perspective already existing in the ecological literature. The key measures introduced, the SOFFI and POFI scores, give a single quantity between 0 and 1, indicating the population's fitness. Despite its simplicity, its derivation from first principles relies on an assumption of diffusive movement; while this is a strong assumption to make, it also provides very rich and complex information about a given landscape. Importantly, the measure captures implicitly many of the key properties (edge length, edge density, contagion, etc.) of fragmentation that ecologists care about. Given the mechanistic beginnings, this approach is readily generalized to other movement mechanisms beyond diffusion.

Using these scores, we assessed fragmentation as a pattern and as a process. As a pattern, we provide analytical insights based off of the analytical properties of the principal eigenvalue. These give general rules to promote a populations' fitness, stated as an abstract theorem, and then explained in simpler terms. As a process, it was found that fragmentation (as simulated via 'contagion') is negative for a population's fitness.

Despite its utility, it is also recognized that assessing fragmentation through growth rates is not always commensurate with empirical studies of habitat fragmentation. Indeed, many studies collect data indicating a total population abundance rather than a growth rate. Hence, we introduce two additional measures, the TAFI and R-TAFI scores, which provide a relative total abundance compared to some theoretical 'optimal state'. This is motivated again by existing measures found in the ecological literature, such as the *biodiversity intactness index.* In both cases, it was found that fragmentation can sometimes be *good* for increasing the total abundance of a population; however, this was heavily dependent on the *level* of impact in the degraded region.

These findings suggest that the impact of habitat fragmentation on a species depends intimately on 1. what metric is being used to assess said impacts, and 2. what the quality of the habitat and surrounding matrix is. We summarized differing scenarios in a table, providing viable answers to some of the toughest questions surrounding the seemginly contradictory conclusions reached in some of the existing ecological literature.

These results combine to provide a nuanced overarching view into all of the processes which comprise *habitat loss.* As discussed in Chapter 1, we have substantial motivation to study the broad impacts of habitat loss of species. Due to the complexity of this problem, mathematical modelling offers an alternative to costly and time-consuming field studies. In [79], the authors state "*Not only is research on the impacts of alien species necessary to understand why some species are more disruptive than others and why some systems are more susceptible to being disturbed by alien species, but it is also of practical importance in determining how limited management resources should be allocated.*" Whether studying invasive species or otherwise, this is of significant importance: we must strive to optimize our conservation efforts. The results found here provide a number of mechanisms by which we can understand more deeply the impacts of habitat loss.

5.2 Future directions

From the work found in this document, there are many different directions one might take to extend these insights further. We discuss briefly future directions for each perspective somewhat separately.

Degradation

For the degradation models of Chapter 2, there are a few directions one might consider. First, we consider a *binary* classification of the landscape, defining regions of *habitat* (G) and *non-habitat* (B). This is, of course, a simplification. One may retain the novelty of the 'indicator function' approach and it potential for precise analytical insights by considering a higher-grain perspective. For example, one might separate multiple 'good' regions $G_1, \ldots, G_k$ and bad regions $B_1, \ldots, B_j$, $k, j \geq 1$, each of which are (almost) disjoint, whose union comprise the entire landscape Ω. Then, we can assign different constant habitat quality values in each G_i, and different degradation levels in each B_i. This will increase the difficulty of analytical study but may also provide insights that cannot be captured in a binary setting.

Related to this point is the assumption that the 'good' regions and 'bad' regions overlap exactly for the two competing species. Instead, one may consider a shared 'bad' region B, but then species specific growth rates in subsets of G; that is to say, there may be separate regions of habitat for each species. This would almost certainly further promote coexistence through niche differentiation.

Finally, one may consider competing species with 3 or more interacting populations. This would provide richer insights into questions of biodiversity, but it is unlikely that the global dynamics can be established in a general setting. In particular, competition models with 3 or more interacting populations no longer fall under the umbrella of monotone dynamical systems, and so alternative methods must be utilized.

Destruction

Similar to some future directions for the degradation model, it would be interesting to consider the combined effects of habitat degradation and fragmentation. That is, we assumed a unit growth rate in the undisturbed region(s) $\Omega \setminus B$. It would be interesting to consider a good region G and a *moderately* degraded region B' such that $G \cup B' = \Omega$. This would, of course, decrease the likelihood for persistence, but it may also facilitate coexistence in the competition model.

Aside from broadening the biological application, it would be of mathematical interest to determine where our technical assumptions are necessary, and where they might be weakened. In particular, it may be useful to weaken the condition on the initial data so that it can be positive over the entire domain. It would also be of great interest to prove an exponential rate of convergence in time, independent of the parameter c. We come *close* to this result, but the devil is always in the details. It is very difficult to use sub/super solution arguments to obtain uniform estimates of the rate of convergence to a steady state across all values of c.

For the competitive system, it is likely possible to consider a more general right-hand side satisfying appropriate monotonicity conditions. The form $u(m - u - v)$ is prototypical for competition in the sense that

$$\frac{\partial f}{\partial u} = m - 2u - v, \qquad \frac{\partial f}{\partial v} = -u,$$

and so both are decreasing in the argument u. This is usually a sufficient condition to apply the theory of monotone flows (i.e., we require a 'cooperative' system or something equivalent).

Fragmentation

This chapter holds some of the most interesting avenues for future study. First, the influence of the size and geometry of the degraded/destroyed region B on the size/sign of principal eigenvalues is of mathematical interest and can also provide ecological insights. The existence of an optimal hole, for example, is of great interest for conservation efforts. As was demonstrated, *optimal* is relative to what you care about: *optimal for population growth rates* does not always agree with *optimal for total abundance.*

Several measures of habitat fragmentation were developed, but the application was in the setting of simulated landscapes or particular forms of heterogeneity. While general trends were found, these insights are likely biased by the nature of the simulated landscape considered. It would be interesting to apply these measures to fragmented landscapes that are generated by different means and determine if the same conclusions can be reached.

Finally, it would be a significant contribution to the literature if we could apply these measures to *real* habitat loss data. Even a cursory image search for ‘deforestation satellite images’ gives an idea of what shapes/patterns we might expect. It would be useful to develop algorithms to translate such satellite imagery to a ‘black-and-white’ pixelated matrix. Then, we can classify each pixel as ‘habitat’ or ‘non-habitat’ and feed this landscape matrix into the measures developed in this dissertation. This would be the most ecologically appropriate, as habitat fragmentation is a process that occurs in the natural world in a less algorithmic way than mere simulated landscapes.

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