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Fitness Dependent Dispersal in Intraguild Predation Communities

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FITNESS DEPENDENT DISPERSAL IN INTRAGUILD PREDATION COMMUNITIES

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A model of a three species intraguild predation community is proposed. The model is realized as a system of cross-diffusion equations which allow the intraguild prey species to adjust its motility based on local resource and intraguild predator densities. Solutions to the cross-diffusion system are shown to exist globally in time and the existence of a global attractor is proved. Abstract permanence theory is used to study conditions for coexistence in the ecological community. The case where the intraguild prey disperses randomly is compared to the case where the intraguild prey disperses conditionally on local ecological fitness and it is shown that the ability of the intraguild prey to persist in the ecological community is enhanced if the intraguild prey utilizes a movement strategy of avoiding areas with negative fitness. A finite element scheme is used to numerically simulate solutions to the system and confirm the analytical results.

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Contents

Chapter 1

Introduction

In December, 2008, the Proceedings of the National Academy of Sciences ran a 76 page special issue highlighting the field of movement ecology (Vol 105, No. 49). In [20] the authors claim there are roughly $26,000$ papers in the literature that refer to organismal movement. Clearly, movement of organisms has been an area of intense interest for the ecological community; however, there is still a considerable amount of work to be done in using precise mathematical models for non-random organismal movement. In particular, one important direction is examining how non-random movement strategies at the organism level affect the population dynamics in an ecological community.

In this thesis I examine one particular ecological community module: intraguild predation. Intraguild predation refers to an interaction where two species compete for a resource and one of these species preys on the other; it is a blend of competition and predator-prey dynamics. In the model we develop herein, we explicitly model the dynamics of three species: the resource, the intraguild prey and the intraguild predator. We will examine how non-random dispersal strategies employed by the intraguild prey affect community population dynamics.

Intraguild predation has been observed in wide variety of ecological communities including: avian [17], [37], [36], both large and small mammals [14], [33], [41], reptile [9], insect [29], fish [21] and bacteria [30]. In fact, any ecosystem with a complex food web is likely to have examples of intraguild predation within it. In [7] a database of 113 food webs was analyzed for presence of intraguild predation and it was found to be present at high frequencies throughout.

One of the earliest attempts to rigorously model intraguild predation (IGP) was by Holt and Polis in [19] where basic ODE models were developed for the three species community. One of the conclusions reached in [19] was that their model with strong IGP was particularly prone to species exclusion, even though communities with strong IGP seem widespread in nature. Holt and Polis suggested numerous lines of future research on mechanisms to stabilize coexistence states in IGP communities. One of these was to allow for a heterogeneous environment.

Dr. Priyanga Amarasekare at the UCLA Department of Ecology was the first to model IGP in a heterogeneous environment; first with random movement [5], and then with non-random movement strategies (density, habitat and fitness dependent were all considered) [6]. Both of these models use an environment consisting of 3 distinct patches, each with a different level of resource productivity. The dynamic equations take the the form of an ODE for each species in each patch. Due to the size of the system (9 equations) all conclusions were based on numerical simulations of the systems. In this thesis we will model the IGP system using a system of partial differential equations that model space explicitly as a continuous two dimensional region. The system will only have 3 equations, so it will be much more feasible to understand the dynamics using analytical techniques.

Numerous papers in ecology and biology journals have appeared citing examples where the intraguild prey (IGPrey) employs nonrandom dispersal in foraging behaviors and habitat selection in an apparent effort to reduce its risk of predation [29], [37], [36], [14], [33], [41]. In the model we develop in this thesis, the IGPrey will employ non-random dispersal strategies that account for local resource availability and predation risk. We assume that the resource and intraguild predator (IGPredator) will disperse randomly. We will analyze what effects the non-random dispersal strategies have on the long-term population dynamics in the community.

There has been some past work modeling IGP communities that have incorporated negative penalties into the functional response terms of the IGPrey in areas of increased IGPredator density in an effort to model prey vigilance, adaptive foraging, and other anti-predation behavior [22], [32]. This differs significantly from the model we propose below where we model space explicitly and allow the IGPrey to actively avoid areas that it judges to be “bad”.

Chapter 2

A Model for Intraguild Predation with IGPrey Movement Strategies

2.1 Development of Model

We will use a system of partial differential equations to model the population dynamics of the three species as functions of space, x, and time, t. The domain for the space variable x describes a point in a two dimensional region, $\Omega \subseteq \mathbb{R}^2$, with smooth boundary denoted by $\partial\Omega$. Throughout this thesis we will only be considering the case of a reflective boundary, i.e. no-flux boundary conditions.

We will assume that the resource and IGPredator disperse through random movement that will be modeled by pure diffusion. The IGPrey's dispersal will be modeled with a cross-diffusion term that depends on local resource and IGPredator densities. One of the earliest ecological models to employ cross-diffusion to model conditional dispersal was proposed by Shigesada, Kawasaki and Teramoto in [38]. They proposed a PDE system with cross-diffusion to model two interacting species that have a propensity to avoid crowding from both interspecifics and conspecifics:

$$\begin{aligned}\frac{\partial u_1}{\partial t} &= \Delta\left[\left(\alpha_1 + \beta_{11}u_1 + \beta_{12}u_2\right)u_1\right] \ , \\ \frac{\partial u_2}{\partial t} &= \Delta\left[\left(\alpha_2 + \beta_{21}u_1 + \beta_{22}u_2\right)u_2\right] \ , \end{aligned} \tag{2.1}$$

The parameters β_{11} and β_{22} are called self-diffusion pressures and represent the propensity to avoid conspecifics. β_{12} and β_{21} are called cross-diffusion pressures and indicate the degree to which interspecifics avoid each other. It was shown in [38] that for certain parameter choices a system of this form can lead to spatial segregation of the populations. Since this model was first proposed, numerous other models (e.g. [23], [35], [28] and [34]) employing cross-diffusion to model interacting populations in ecological communities have been proposed and analyzed (but not an intraguild predation community module).

One of the main difficulties with cross-diffusion models is proving that solutions do not become unbounded in finite time (which is clearly an undesirable property for systems modeling population dynamics). Cross-diffusion systems are a special case of quasilinear parabolic systems.

In a series of papers, [2], [4] and [3] Herbert Amann proved some key results for systems of quasilinear parabolic equations. Amann considered systems of the form

$$\begin{aligned}\frac{\partial u}{\partial t} + \mathcal{A}(t,u)u &= f(x,t,u,\partial u) && \text{in } \Omega \times \mathring{J}, \\ \mathcal{B}(t,u)u &= 0 && \text{on } \partial\Omega \times \mathring{J}, \\ u(x,0) &= u_0 && \text{on } \Omega.\end{aligned} \tag{2.2}$$

where $\mathcal{A}$ is a normally elliptic operator for all $u \in G \subseteq \mathbb{R}^N$, $\mathring{J}$ is the interior of the maximal interval of existence, and $\mathcal{B}(t,u)$ is an appropriate boundary operator (note this is a system of N component equations). Some regularity conditions are also imposed on f (see [3] for full details). Let $C^k_{\mathcal{B}}$ be functions in $C^k(\overline{\Omega}, \mathbb{R}^N)$, $0 \leq k \leq 2$, satisfying the prescribed boundary conditions required of $\mathcal{B}$. Let $\mathcal{G}^k = \{u \in C^k_{\mathcal{B}}; u(\overline{\Omega}) \subseteq G\}$. Then we can state Amann's culminating result:

Theorem 2.1.1 (Theorem 1 [3])**.** *Given any $u_0 \in \mathcal{G}^2$, there exists a unique classical solution defined on a maximal interval of existence, $J(u_0)$*

$$u(\cdot, u_0) \in C(J(u_0), \mathcal{G}^0) \cap C(\mathring{J}(u_0), C^2(\overline{\Omega}, \mathbb{R}^N)) \cap C^1(\mathring{J}(u_0), C(\overline{\Omega}, \mathbb{R}^N))$$

of the quasilinear parabolic system (2.2)*. Moreover, u is a global solution, that is $J(u_0) = [0, \infty)$, provided $u(J(u_0) \cap [0,T], u_0)$ is, for each $T \in \mathring{J}(u_0)$, bounded away from $\partial\mathcal{G}$ and bounded in $H^{s,p}$ for some $p > n$ with $p \geq 2$ and some s with*

$$1 < s < \min\{(1 + 1/p), (2 - n/p)\}.$$

If f is affine in the gradient, we can choose s=1.

In the theorem above, $H^{s,p}$ is a fractional order Sobolev space when s is noninteger. The "affine in the gradient" condition on f requires that if f involves ∇u terms, that it is linear in these terms. The system we will construct below will satisfy this condition, so we will be able to use the Sobolev space $W^{1,p}$ in this theorem. In combination with this result, Corollary 7.4 of [4] shows that in the case where $\mathcal{A}$ and $\mathcal{B}$ are not time-dependent (2.2) generates a semiflow on $W^{1,p}$. We will come back to this in Chapter 4. Amann goes on to prove in Theorem 3 of [3] that in some special cases of $\mathcal{A}(u)$

weaker *a priori* bounds on u are sufficient for global existence. Namely, if $\mathcal{A}(u)$ is an upper-triangular differential operator, i.e. the rth-component equation only depends on the components $u_r, u_{r+1}, \ldots, u_N$, then knowing that $u(\cdot, t)$ is bounded away from $\partial\mathcal{G}$ and bounded in L^∞ for each $T \in \mathring{J}(u_0)$ is sufficient to conclude that the solution is global (i.e. $J(u_0) = [0, \infty)$).

We will assume that the *motility* of the IGPrey is given by a function $M(u, w)$ that is twice differentiable in both of its arguments and is uniformly bounded below for all $u, w \geq 0$. This will be sufficient to make $\mathcal{A}(u)$ normally elliptic. Our assumption that the resource and IGPredator disperse randomly means that we can write our system as an upper-triangular system, and hence, we will have some powerful global existence results at our disposal. We will continue this discussion in Chapter 3.

The term motility refers to the function $\mu(x)$ in the diffusion equation

$$\frac{\partial u}{\partial t} = \Delta[\mu(x)u] \ \text{ in } \Omega \ . \tag{2.3}$$

This form of diffusion arises from specific assumptions made in the random-walk formulation prior to taking the diffusion limit. The assumption that the chance of moving from a location is a function only of the conditions at the current location leads to this kind of diffusion limit. The more classical diffusion equation

$$\frac{\partial u}{\partial t} = \nabla \cdot (d(x)\nabla u) \ \text{ in } \Omega \ , \tag{2.4}$$

uses a *diffusivity* function $d(x)$, and is a result of assuming that the chance of departing a given location depends on averaging conditions between the point of departure and the point of arrival and then taking the diffusion limit. See [42] for a discussion of the derivations of these two diffusion models.

For models of organismal movement, it makes sense to think that the choice of whether to move or not should be based on local conditions, and not necessarily an averaging of conditions between point of arrival and departure. Since Shigesada, Kawasaki and Teramoto introduced their cross-diffusion model in [38], the use of density dependent motility functions has seen widespread use in ecological modeling.

In order for the IGPrey to benefit from a non-random dispersal strategy, there should be some sort of environmental heterogeneity present (especially since we will be imposing no-flux boundary conditions). In the case of no-flux boundary conditions and a homogeneous environment, we could expect to see spatially constant equilibrium solutions. We will incorporate heterogeneity into our model by varying resource productivity throughout the domain Ω. This naturally leads to the concept of "good" and "bad" habitat regions *vis a vis* areas without sufficient resources to support a consumer vs. areas with sufficient resource productivity levels. We will assume that the resource follows logistic growth with spatially varying reproduction rate and carrying capacity in the absence of the two consumer species.

We will assume that both consumer species, the IGPrey and the IGPredator, have their population levels decline due to natural mortality in the absence of the resource or prey (i.e. they are not generalist). We will also impose self-limiting growth terms to represent crowding effects.

All predation/consumption terms will use Holling Type II functional responses (saturating functional responses). (From here out we will use the vocabulary of predator/prey interactions as opposed to resource/consumer, even for consumption of the resource species.) This type of functional response is derived by assuming that the predator must spend a certain amount of time handling any prey that it has encountered in its search, and thus there is a upper bound on the amount of prey per unit time that a predator can consume, regardless of the local prey density.

2.2 The Model Equations

We are finally ready to state our model equations. As mentioned above, Ω is assumed to be a domain in $\mathbb{R}^2$ with smooth boundary. We will use $u(x,t)$ to denote the density of the resource species, $v(x,t)$ for the IGPrey and $w(x,t)$ for the IGPredator. The full system of equations is:

$$\begin{aligned} \frac{\partial u}{\partial t} &= d_1 \Delta u + f(x,u,v,w)\, u \\ \frac{\partial v}{\partial t} &= \Delta \left[M(u,w) v \right] + g(u,v,w)\, v \\ \frac{\partial w}{\partial t} &= d_3 \Delta w + h(u,v,w)\, w \quad \text{in } \Omega, \\ u(x,0) &= u_0(x)\,,\ v(x,0) = v_0(x)\,,\ w(x,0) = w_0(x), \\ \frac{\partial u}{\partial n} &= \frac{\partial v}{\partial n} = \frac{\partial w}{\partial n} = 0 \quad \text{on } \partial\Omega\,, \end{aligned} \tag{2.5}$$

where the per-capita growth rates (or "fitness" functions), f, g and h are given by

$$f(x,u,v,w) = r(x) - \omega_1 u - \frac{a_1 v}{1 + h_1 a_1 u} - \frac{a_2 w}{1 + h_2 a_2 u} \tag{2.6}$$

$$g(u,v,w) = \frac{e_1 a_1 u}{1 + h_1 a_1 u} - \frac{a_3 w}{1 + h_3 a_3 v} - \mu_1 - \omega_2 v \tag{2.7}$$

$$h(u,v,w) = \frac{e_2 a_2 u}{1 + a_2 h_2 u} + \frac{e_3 a_3 v}{1 + h_3 a_3 v} - \mu_2 - \omega_3 w\,. \tag{2.8}$$

The constants d_1, and d_3 are the motility of the resource and IGPredator respectively. The function $M(u, w)$ is the motility of the IGPrey. It is assumed that the IGPrey changes its movement strategy based on the local density of the resource as well as the IGPredator. Specific choices for the function M are discussed in later chapters. Any choice for M will need to be twice differentiable in u and w. In addition, there must be a positive constant d such that

$$M(u, w) \geq d > 0\,. \tag{2.9}$$

The function $r(x)$ is the spatially varying resource productivity which affects both resource growth rate and carrying capacity (the local carrying capacity in the absence of v and w would be $r(x)/\omega_1$). We assume that $r(x)$ is $C^\alpha(\overline{\Omega})$ for some $\alpha \in (0, 1)$ and that $r(x) > 0$ on Ω.

The parameters μ_1 and μ_2 are the natural mortality rates of the IGPrey and IGPredator and ω_1, ω_2 and ω_3 are the self-limiting/crowding coefficients for each species.

The a_i parameters are the attack rates, the h_i's are the handling times and the e_i's are the conversion efficiencies of each predation/consumption functional response.

We will assume that a_i, h_i, e_i, μ_i, ω_i and d_i are all positive for $i = 1, 2, 3$. In addition, we will assume that

$$\frac{e_1}{h_1} > \mu_1 \quad \text{and} \quad \frac{e_2}{h_2} + \frac{e_3}{h_3} > \mu_2\,, \tag{2.10}$$

or else it would not be possible for the energetic gains from any amount of resources and prey consumption to exceed the mortality rates of the IGPrey and IGPredator.

Note that we have imposed Neumann conditions in (2.5). These are actually no-flux conditions for the system. It is clear that the boundary flux of the resource and IGPredator are merely $\frac{\partial u}{\partial n}$ and $\frac{\partial w}{\partial n}$ respectively. However, for the IGPrey the flux across the boundary is

$$\frac{\partial}{\partial n}(M(u,w)v) = M(u,w)\frac{\partial v}{\partial n} + v\frac{\partial M}{\partial u}\frac{\partial u}{\partial n} + v\frac{\partial M}{\partial w}\frac{\partial w}{\partial n}\,. \tag{2.11}$$

We see from (2.11) that if $\frac{\partial v}{\partial n} = 0$ in addition to the conditions already imposed on u and w then we will have no-flux for the v-component equation as well. Conversely, in order to achieve no-flux in the v equation and maintain no-flux in the u and w equations we would have to impose $\frac{\partial v}{\partial n} = 0$. Thus, no-flux and Neumann boundary conditions are equivalent for (2.5).

We will now prove that for nonnegative initial conditions in $W^{1,p}(\Omega)$ (2.5) has unique solutions that are global (exist for $t \in [0, \infty)$).

Chapter 3

Global Existence and the Global Attractor

3.1 Abstract Theory

In Chapter 1 we stated results from Amann concerning the existence of unique global solutions to (2.5) under certain *a priori* conditions. The G used to state Amann's results will be an open neighborhood of the positive octant in $\mathbb{R}^3$ in our case, so $\mathcal{G}$ will consist of triples of continuous functions that take function values in this neighborhood. Amann's result requires that $(u(t), v(t), w(t))$ is bounded away from $\partial\mathcal{G}$ and that $\|u(t)\|_\infty, \|v(t)\|_\infty$ and $\|w(t)\|_\infty$ are bounded on $[0, T)$ for all $T > 0$. Being bounded away from $\partial\mathcal{G}$ is not a problem, as it is a result of the system (2.5) having nonnegative solutions for all nonnegative initial data (which we will show below). However, the *a priori* L^∞ bounds can be difficult to establish.

In [25], Dung Le studies a two component cross-diffusion system and improves on Amann's result for this specific case. Le considers a two species system where each species exhibits random diffusion and self-diffusion, but only one of the species exhibits cross-diffusion. He shows that if an L^∞ *a priori* bound can be established on the species without cross-diffusion terms and a L^n *a priori* bound can be established for the species with cross-diffusion (where n is the number of space dimensions), then the solutions exist globally in time. Moreover, he shows that the Hölder norms of the solution components are ultimately uniformly bounded (definition given below), leading to the existence of a global attractor for the system. This result is what we will use to prove global existence for solutions to (2.5) and establish the existence of a global attractor, which will be a key component of the analysis in Chapter 4. We will need a precise definition for ultimately uniformly bounded, taken from [25].

Definition 3.1.1. *Given an initial boundary value problem or the form* (2.5)*, define*

$$\Theta = \{J_{\vec{\xi}} \times \vec{\xi} \mid \vec{\xi} \in [W_+^{1,p}(\Omega)]^3\}$$

where $J_{\vec{\xi}} \subseteq \mathbb{R}_+$ *is the maximal interval of existence for the solution of* (2.5) *with initial conditions* $(u_0, v_0, w_0) = \vec{\xi}$*. Let* $\mathcal{P}$ *be the set of functions* $\omega : \Theta \to \mathbb{R}_+$ *such that there exists a continuous function* $C_0(\|\vec{\xi}\|)$ *satisfying*

$$\omega(t, \vec{\xi}) \leq C_0(\|\vec{\xi}\|), \quad \text{for all } \vec{\xi} \in [W_+^{1,p}(\Omega)]^3, \text{ and } t \in J_{\vec{\xi}}.$$

Additionally, if $J_{\vec{\xi}} = [0, \infty)$ *there exists a positive constant* C_∞ *such that*

$$\limsup_{t\to\infty} \omega(t, \vec{\xi}) \leq C_\infty \quad \text{for all } \xi \in [W_+^{1,p}(\Omega)]^3.$$

Then $\mathcal{P}$ *is the set of ultimately uniformly bounded functions with respect to* (2.5)*.*

We will use *a priori* bounds on the solutions to (2.5) to show that appropriate functions, frequently norms of solutions to (2.5) or functions thereof, are in $\mathcal{P}$.

Although the system we are considering here has three components instead of two, Le's results may be directly extended to our system (mainly because our extra component is a standard reaction-diffusion equation). Since we are considering a domain in $\mathbb{R}^2$ we will need to show that $\|u\|_\infty \in \mathcal{P}$, $\|v\|_2 \in \mathcal{P}$ and $\|w\|_\infty \in \mathcal{P}$.

3.2 *A Priori* Bounds

We are considering solutions to (2.5) with non-negative initial conditions in $[W^{1,p}(\Omega)]^3$ for some $p > 2$. It is relatively easy to show that the L^∞ norms of the u and w components are in $\mathcal{P}$. We do this by bounding the reaction terms and then using the comparison principle for second order parabolic equations, which states:

Theorem 3.2.1 (Theorem 1.19 of [11]). *Suppose that L is a uniformly elliptic operator of the form*

$$L = \sum_{i,j=1}^{n} a_{ij}(x,t)\frac{\partial^2}{\partial x_i \partial x_j} + \sum_{i=1}^{n} b_i(x,t)\frac{\partial}{\partial x_i}$$

with $|a_{ij}(x,t)|$ and $|b_i(x,t)|$ uniformly bounded on $\Omega \times (0,T]$. Suppose that $f(x,t,u)$, $\frac{\partial f(x,t,u)}{\partial u} \in C(\overline{\Omega} \times [0,T] \times \mathbb{R})$. If $\overline{u}, \underline{u} \in C^{2,1}(\overline{\Omega} \times (0,T]) \cap C(\overline{\Omega} \times [0,T])$ with

$$\begin{aligned} \frac{\partial \overline{u}}{\partial t} - L\overline{u} &\geq f(x,t,\overline{u}) \quad \text{in } \Omega \times (0,T], \\ \frac{\partial \underline{u}}{\partial t} - L\underline{u} &\leq f(x,t,\underline{u}) \quad \text{in } \Omega \times (0,T], \end{aligned}$$

$\overline{u}(x,0) \geq \underline{u}(x,0)$ on Ω and $\frac{\partial \overline{u}}{\partial n} \geq \frac{\partial \underline{u}}{\partial n}$ on $\partial\Omega \times (0,T]$, then either $\overline{u} \equiv \underline{u}$ or $\overline{u} > \underline{u}$ on $\Omega \times (0,T]$.

We call the $\overline{u}$ and $\underline{u}$ of Theorem 3.2.1 a *supersolution* and a *subsolution* respectively of the semilinear parabolic equation

$$\frac{\partial u}{\partial t} = Lu + f(x,t,u) \ \text{ in } \Omega, \quad \text{and } \frac{\partial u}{\partial n} = 0 \ \text{ on } \partial\Omega\,. \tag{3.1}$$

Note that a solution to (3.1) is also both a subsolution and a supersolution to the equation, so we are able to compare solutions to sub or supersolutions via Theorem 3.2.1.

To establish that $\|u\|_\infty \in \mathcal{P}$, we can drop the predation terms from the u-component equation of (2.5) to obtain the differential inequality

$$\frac{\partial u}{\partial t} \leq d_1\Delta u + r(x)u - \omega_1 u^2 \ \text{ in } \Omega, \quad \text{and } \frac{\partial u}{\partial n} = 0 \ \text{ on } \partial\Omega\,. \tag{3.2}$$

Thus, u is a subsolution to the initial boundary value problem

$$\begin{aligned} \frac{\partial \hat{u}}{\partial t} &= d_1\Delta\hat{u} + r(x)\hat{u} - \omega_1\hat{u}^2 \ \text{ in } \Omega, \\ \frac{\partial \hat{u}}{\partial n} &= 0 \ \text{ on } \partial\Omega\,, \quad \hat{u}(x,0) = u_0(x)\,, \end{aligned} \tag{3.3}$$

which is a standard heterogeneous diffusive logistic equation. The solution, $\hat{u}$, to (3.3) converges to a unique globally attracting equilibrium by Proposition 3.3 of [11]. Theorem 3.2.1 implies that either $u \equiv \hat{u}$ or $u < \hat{u}$ on $\Omega \times (0,\infty)$. Therefore, $\|u\|_\infty \in \mathcal{P}$. Similarly we can bound the reaction terms in the w component equation by

$$w\left(\frac{e_2a_2u}{1+h_2a_2u} + \frac{e_3a_3v}{1+a_3h_3v} - \mu_2 - \omega_2 w\right) \leq w\left(\frac{e_2}{h_2} + \frac{e_3}{h_3} - \mu_2 - \omega_2 w\right)\,. \tag{3.4}$$

Hence w satisfies the differential inequality

$$\frac{\partial w}{\partial t} \leq d_3 \Delta w + w \left(\frac{e_2}{h_2} + \frac{e_3}{h_3} - \mu_2 - \omega_2 w \right) . \tag{3.5}$$

The argument we used for the u-component above applies again; w is also a subsolution to a diffusive logistic equation whose solution is known to have a unique globally attracting positive equilibrium (because we have assumed $\frac{e_2}{h_2} + \frac{e_3}{h_3} > \mu_2$), hence $\|w\|_\infty \in \mathcal{P}$.

Because of the presence of the cross-diffusion terms in the v equation, it becomes much more difficult to establish that $\|v\|_2 \in \mathcal{P}$. We can trace the argument made by Le in [25] where he considers a particular 2-dimensional example at the end of the paper. We begin by establishing the following Lemma.

Lemma 3.2.1. *$\|v\|_1 \in \mathcal{P}$ and $\int_t^{t+1} \|v(s)\|_2^2 \, ds \in \mathcal{P}$.*

Proof. We begin by integrating both sides of the equation for the v component over Ω (the Laplacian term drops out due to the no flux boundary conditions)

$$\begin{aligned} \frac{d}{dt} \int_\Omega v \, dx &= \int_\Omega v \left(\frac{e_1 a_1 u}{1 + h_1 a_1 u} - \frac{a_3 w}{1 + h_3 a_3 v} - \mu_1 - \omega_2 v \right) dx \\ &\leq \frac{e_1}{h_1} \int_\Omega v \, dx - \omega_2 \int_\Omega v^2 \, dx \\ &\leq \frac{e_1}{h_1} \int_\Omega v \, dx - \frac{\omega_2}{|\Omega|} \left(\int_\Omega v \, dx \right)^2 . \end{aligned} \tag{3.6}$$

Therefore, $\|v\|_1$ is a subsolution to a logistic equation that has all solutions with positive initial conditions converging to $\frac{e_1|\Omega|}{h_1\omega_2}$ as $t \to \infty$, so $\|v\|_1 \in \mathcal{P}$.

Rearranging the first inequality in (3.6) we see that

$$\int_\Omega v^2\,dx \le \frac{e_1}{\omega_2 h_1}\int_\Omega v\,dx - \frac{1}{\omega_2}\frac{d}{dt}\int_\Omega v\,dx\ , \tag{3.7}$$

and integrating this from t to $t+1$ yields

$$\begin{aligned}\int_t^{t+1}\int_\Omega v(x,s)^2\,dx\,ds &\le \frac{e_1}{\omega_2 h_1}\int_t^{t+1}\int_\Omega v(x,s)\,dx\,ds + \frac{1}{\omega_2}\int_\Omega [v(x,t)-v(x,t+1)]\,dx\\ &\le \frac{e_1}{\omega_2 h_1}\int_t^{t+1}\int_\Omega v(x,s)\,dx\,ds + \frac{1}{\omega_2}\int_\Omega v(x,t)\,dx\ .\end{aligned} \tag{3.8}$$

Since $\|v\|_1 \in \mathcal{P}$, we have $\int_t^{t+1}\|v(s)\|_1\,ds \in \mathcal{P}$, so (3.8) implies $\int_t^{t+1}\|v(s)\|_2^2\,ds \in \mathcal{P}$. □

It will be useful to have the following side calculation in the material to follow:

$$\begin{aligned}\int_\Omega v\Delta\left[M(u,w)v\right]\,dx &= \int_\Omega v\nabla\cdot\left(M\nabla v + M_u v\nabla u + M_w v\nabla w\right)\,dx\\ &= -\int_\Omega M|\nabla v|^2 + M_u v\nabla u\cdot\nabla v + M_w v\nabla w\cdot\nabla v\,dx\,.\end{aligned} \tag{3.9}$$

Now, return to the v component equation, multiply by v and integrate, use (3.9) and drop the negative reaction terms to arrive at the inequality

$$\frac{1}{2}\frac{d}{dt}\int_\Omega v^2\,dx + \int_\Omega M|\nabla v|^2\,dx \le -\int_\Omega M_u v\nabla u\cdot\nabla v + M_w v\nabla w\cdot\nabla v\,dx + \int_\Omega \frac{e_1 a_1 u v^2}{1+h_1 a_1 u}\,dx\,. \tag{3.10}$$

Use the fact that $M(u,w) \geq d$ and bound the terms on the right hand side from above to obtain

$$\frac{1}{2}\frac{d}{dt}\int_\Omega v^2\,dx + d\int_\Omega |\nabla v|^2\,dx \leq \int_\Omega |M_u v\nabla u\cdot\nabla v| + |M_w v\nabla w\cdot\nabla v|\,dx + \frac{e_1}{h_1}\int_\Omega v^2\,dx\,. \tag{3.11}$$

We will need to make use of the Gagliardo-Nirenberg Inequality in the form found in [31]:

Theorem 3.2.2 (Gagliardo-Nirenberg). *Let Ω be a domain in $\mathbb{R}^n$ with smooth boundary and let u belong to $L^q(\Omega)$ and its derivatives of order m, $D^m u$, belong to $L^r(\Omega)$, $1 \leq q, r \leq \infty$. For the derivatives $D^j u$, $0 \leq j < m$, the following inequalities hold:*

$$\|D^j u\|_p \leq C\left(\|D^m u\|_r^a \|u\|_q^{1-a} + \|u\|_{\tilde{q}}\right) \tag{3.12}$$

where

$$\frac{1}{p} = \frac{j}{n} + a\left(\frac{1}{r} - \frac{m}{n}\right) + (1-a)\frac{1}{q} \quad \text{and} \quad \tilde{q} > 0\ ,$$

for all a in the interval

$$\frac{j}{m} \leq a \leq 1$$

(the constant, C, depending only on n, m, j, q, r, a and Ω), with the following exception: If $1 < r < \infty$, and $m - j - \frac{n}{r}$ is a non-negative integer, then (3.12) holds only for a satisfying $\frac{j}{m} \leq a < 1$.

Recall that we are considering a domain $\Omega \subseteq \mathbb{R}^2$. This will be an important fact whenever we apply Theorem 3.2.2 (although these same results will also hold for

$\Omega \subseteq \mathbb{R}^1$). We will apply this theorem with different choices of m, j, q, r, a and $\tilde{q}$. For now, choose $p = r = 2$, $j = 0$, $a = 1/2$ and $m = q = \tilde{q} = 1$ to get

$$\begin{aligned} \|v\|_2^2 &\leq C\|\nabla v\|_2 \, \|v\|_1 + C\|v\|_1^2 \\ &= C(\sqrt{\varepsilon}\|\nabla v\|_2) \left(\frac{\|v\|_1}{\sqrt{\varepsilon}} \right) + C\|v\|_1^2 \\ &\leq \frac{C\varepsilon}{2}\|\nabla v\|_2^2 + \frac{C}{2\varepsilon}\|v\|_1^2 + C\|v\|_1^2 \,. \end{aligned} \tag{3.13}$$

Throughout the following calculations C will be a constant and $\omega(t)$ will be a function with $\limsup_{t\to\infty} \omega(t)$ bounded, and they both may change from line to line. We have already shown that $\|v\|_1 \in \mathcal{P}$, so by choosing ε small enough in (3.13) we have

$$\frac{e_1}{h_1} \int_\Omega v^2 \, dx \leq \frac{d}{2} \int_\Omega |\nabla v|^2 \, dx + \omega(t) \,. \tag{3.14}$$

Since $\|u\|_\infty$ and $\|w\|_\infty$ are in $\mathcal{P}$ and M_u and M_w are continuous functions of u and w we have M_u and M_w in $\mathcal{P}$ as well. Using this fact and substituting (3.14) into (3.11) we find that

$$\frac{d}{dt} \int_\Omega v^2 \, dx + d \int_\Omega |\nabla v|^2 \, dx \leq \omega(t) \int_\Omega |v \nabla u \cdot \nabla v| + |v \nabla w \cdot \nabla v| \, dx + \omega(t) \,. \tag{3.15}$$

We now need a bound for $\int_\Omega |v\nabla u \cdot \nabla v|\, dx$ and $\int_\Omega |v\nabla w \cdot \nabla v|\, dx$. We begin with the latter expression

$$
\begin{aligned}
\int_\Omega |v\nabla w \cdot \nabla v|\, dx &\leq \int_\Omega |\nabla v||v\nabla w|\, dx \\
&\leq \frac{\varepsilon_1}{2}\int_\Omega |\nabla v|^2\, dx + \frac{1}{2\varepsilon_1}\int_\Omega v^2|\nabla w|^2\, dx \\
&\leq \frac{\varepsilon_1}{2}\|\nabla v\|_2^2 + \frac{1}{2\varepsilon_1}\|v\|_4^2\|\nabla w\|_4^2\,.
\end{aligned} \tag{3.16}
$$

To get a bound on $\|v\|_4$ we can use the Gagliardo-Nirenberg Inequality (3.12) again but with $j = 0$, $p = 4$, $m = \tilde{q} = 1$, $a = 1/2$ and $q = r = 2$

$$
\|v\|_4^2 \leq C\|\nabla v\|_2\|v\|_2 + C\|v\|_1^2\,. \tag{3.17}
$$

Recall that $\|v\|_1 \in \mathcal{P}$, so substituting (3.17) in (3.16) results in

$$
\begin{aligned}
\int_\Omega |v\nabla w \cdot \nabla v|\, dx &\leq \frac{\varepsilon_1}{2}\|\nabla v\|_2^2 + \frac{C}{2\varepsilon_1}\|\nabla v\|_2\|v\|_2\|\nabla w\|_4^2 + \omega(t)\|\nabla w\|_4^2 \\
&\leq \left(\frac{\varepsilon_1}{2} + \frac{C\varepsilon_2}{4\varepsilon_1}\right)\|\nabla v\|_2^2 + \frac{C}{4\varepsilon_1\varepsilon_2}\|v\|_2^2\|\nabla w\|_4^4 + \omega(t)\|\nabla w\|_4^2\,.
\end{aligned} \tag{3.18}
$$

Choose $\varepsilon_2 = \frac{2\varepsilon_1^2}{C}$ so that the $\|\nabla v\|_2^2$ terms in (3.18) are controlled by ε_1. This same argument gives the analogous bound for $\int_\Omega |v\nabla u \cdot \nabla v|\, dx$ where $\|\nabla w\|_4^4$ is replaced by $\|\nabla u\|_4^4$. Now, choose ε_1 small and t_0 large so that $2\varepsilon_1\omega(t) \leq d$ when $t \geq t_0$. Then (3.18) and the analogous bound for $\int_\Omega |v\nabla u \cdot \nabla v|\, dx$ gives

$$
\omega(t)\int_\Omega |v\nabla u \cdot \nabla v| + |v\nabla w \cdot \nabla v|\, dx \leq d\int_\Omega |\nabla v|^2\, dx + C(1 + \|v\|_2^2)(\|\nabla u\|_4^4 + \|\nabla w\|_4^4) \tag{3.19}
$$

for $t \geq t_0$. Substitute (3.19) into (3.15) and cancel the $d\int_\Omega |\nabla v|^2\,dx$ terms to obtain

$$\frac{d}{dt}\|v\|_2^2 \leq C\|v\|_2^2\left(\|\nabla u\|_4^4 + \|\nabla w\|_4^4\right) + C(1 + \|\nabla u\|_4^2 + \|\nabla w\|_4^2) \text{ for } t \geq t_0\,. \tag{3.20}$$

At this point, we will need to make use of the Uniform Gronwall Lemma as found in [39]:

Lemma 3.2.2 (Uniform Gronwall Lemma)**.** *Let $g, h, y,$ be three positive locally integrable functions on (t_0, ∞) such that y' is locally integrable on (t_0, ∞), and which satisfy*

$$\frac{dy}{dt} \leq gy + h \quad \textit{for} \quad t \geq t_0,$$

and,

$$\int_t^{t+r} g(s)\,ds \leq a_1, \quad \int_t^{t+r} h(s)\,ds \leq a_2, \quad \int_t^{t+r} y(s)\,ds \leq a_3, \quad \textit{for} \quad t \geq t_0$$

where $r, a_1, a_2, a_3,$ are positive constants. Then,

$$y(t+r) \leq \left(\frac{a_3}{r} + a_2\right)e^{a_1}, \;\; \forall t \geq t_0.$$

From Lemma 3.2.1 we know that $\int_t^{t+1}\|v(s)\|_2^2\,ds \in \mathcal{P}$; so, if we can now show that $\int_t^{t+1}\|\nabla u(s)\|_4^4\,ds$ and $\int_t^{t+1}\|\nabla w(s)\|_4^4\,ds \in \mathcal{P}$, then we can use the Uniform Gronwall Lemma on (3.20) to conclude that $\|v\|_2^2 \in \mathcal{P}$ (and hence $\|v\|_2 \in \mathcal{P}$) as desired.

We will begin by considering the expression involving the w component. Using the Gagliardo-Nirenberg inequality, (3.12), with $j = \tilde{q} = 1$, $p = 4$, $m = r = 2$, $q = \infty$ and $a = 1/2$ yields

$$\|\nabla w\|_4^4 \leq C\|w\|_{2,2}^2\|w\|_\infty^2 + C\|w\|_1^4. \tag{3.21}$$

Furthermore, from standard elliptic theory we have the standard *a priori* bound for weak solutions of $\Delta w = f$

$$\|w\|_{2,2} \leq C(\|f\|_2 + \|w\|_2) \ = C(\|\Delta w\|_2 + \|w\|_2). \tag{3.22}$$

We can view the solution to our parabolic problem as solving an elliptic equation at each snapshot in time, hence at any moment in time we have

$$\|w\|_{2,2} \leq C(\|\Delta w\|_2 + \|w\|_2) \ . \tag{3.23}$$

We will show that $\int_t^{t+1} \|\Delta w\|_2^2 \, ds \in \mathcal{P}$ and then conclude from (3.21) and (3.23) that $\int_t^{t+1} \|\nabla w\|_4^4 \, ds \in \mathcal{P}$. First we will show that $\|\nabla w\|_2^2 \in \mathcal{P}$. Adding w to both sides of the w-component equation yields the equality

$$\frac{\partial w}{\partial t} + w = d_3 \Delta w + w\, h + w \ . \tag{3.24}$$

Multiply both sides of (3.24) by $-2d_3\Delta w$ and integrate over Ω to get

$$\begin{aligned}
-2\int_\Omega d_3 \Delta w \left(\frac{\partial w}{\partial t} + w\right) dx &= -2\int_\Omega d_3\Delta w \,(d_3\Delta w + w\, h + w)\ dx \\
&= -2\int_\Omega d_3^2 (\Delta w)^2 \, dx - 2\int_\Omega d_3 \Delta w (w\, h + w)\, dx \\
&\leq -2\int_\Omega d_3^2 (\Delta w)^2 \, dx + \int_\Omega d_3^2 (\Delta w)^2 \, dx + \int_\Omega (w\, h + w)^2 \, dx \\
&\leq \int_\Omega (w\, h + w)^2 \, dx \, .
\end{aligned} \tag{3.25}$$

But, $\|w\|_\infty \in \mathcal{P}$ which implies $\|w\|_p \in \mathcal{P}$ for all $1 \le p \le \infty$. Also $-\mu_2 - \omega_3 w \le h \le \frac{e_2}{h_2} + \frac{e_3}{h_3}$, so $\|h\|_\infty \in \mathcal{P}$ as well. Therefore, $\int_\Omega (w\,h + w)^2\,dx \in \mathcal{P}$. We also have

$$\begin{aligned}\int_\Omega \frac{\partial w}{\partial t}\Delta w\,dx &= \int_\Omega \nabla\cdot\left(\frac{\partial w}{\partial t}\nabla w\right) - \nabla\left(\frac{\partial w}{\partial t}\right)\cdot\nabla w\,dx \\ &= -\int_\Omega \left(\frac{d}{dt}\nabla w\right)\cdot\nabla w\,dx \\ &= -\frac{1}{2}\frac{d}{dt}\int_\Omega |\nabla w|^2\,dx\ .\end{aligned} \tag{3.26}$$

Therefore,

$$-2d_3\int_\Omega \Delta w\left(\frac{\partial w}{\partial t} + w\right)\,dx = d_3\frac{d}{dt}\int_\Omega |\nabla w|^2\,dx + 2d_3\int_\Omega |\nabla w|^2\,dx\ . \tag{3.27}$$

Inserting (3.27) into (3.25) and dividing by d_3 we get

$$\frac{d}{dt}\int_\Omega |\nabla w|^2\,dx + 2\int_\Omega |\nabla w|^2\,dx \le \omega(t)\ . \tag{3.28}$$

Integrate the inequality above in time to conclude that $\|\nabla w\|_2^2 \in \mathcal{P}$. Now we can begin to show $\int_t^{t+1}\|\Delta w(s)\|_2^2\,ds \in \mathcal{P}$. Note that

$$\int_\Omega \frac{\partial w}{\partial t}\Delta w\,dx = d_3\int_\Omega (\Delta w)^2\,dx + \int_\Omega (w\,h)\Delta w\,dx \tag{3.29}$$

so,

$$\int_\Omega \frac{\partial w}{\partial t}\Delta w\,dx \ge \int_\Omega (w\,h)\Delta w\,dx\,. \tag{3.30}$$

Now, go back to the w-component equation, multiply both sides by $(w\,h)$, integrate over Ω and apply (3.30) to obtain the inequality

$$\int_\Omega \frac{\partial w}{\partial t}(w\,h)\,dx = \int_\Omega d_3(w\,h)\Delta w\,dx + \int_\Omega (w\,h)^2\,dx \le d_3\int_\Omega \frac{\partial w}{\partial t}\Delta w\,dx + \int_\Omega (w\,h)^2\,dx\ . \tag{3.31}$$

Once again, start with the w-component equation, but this time multiply both sides by $\frac{\partial w}{\partial t}$, integrate over Ω, and apply (3.31) to reach

$$\int_\Omega \left(\frac{\partial w}{\partial t}\right)^2\,dx = \int_\Omega d_3\frac{\partial w}{\partial t}\Delta w\,dx + \int_\Omega \frac{\partial w}{\partial t}(w\,h)\,dx \le 2d_3\int_\Omega \frac{\partial w}{\partial t}\Delta w\,dx + \int_\Omega (w\,h)^2\,dx \tag{3.32}$$

at which point we can use (3.26) to get

$$\int_\Omega \left(\frac{\partial w}{\partial t}\right)^2\,dx \le -d_3\frac{d}{dt}\int_\Omega |\nabla w|^2\,dx + \int_\Omega (w\,h)^2\,dx \tag{3.33}$$

Integrate (3.33) from t to $t+1$ to find

$$\begin{aligned}\int_t^{t+1}\left\|\frac{\partial w}{\partial t}(s)\right\|_2^2\,ds &\le d_3\int_\Omega |\nabla w(x,t)|^2 - |\nabla w(x,t+1)|^2\,dx + \int_t^{t+1}\|w(s)h(s)\|_2^2\,ds\\ &\le d_3\|\nabla w(t)\|_2^2 + \int_t^{t+1}\|w(s)h(s)\|_2^2 ds\ .\end{aligned} \tag{3.34}$$

We already have $\|\nabla w\|_2^2 \in \mathcal{P}$, hence $\int_t^{t+1}\left\|\frac{\partial w}{\partial t}(s)\right\|_2^2\,ds \in \mathcal{P}$. Now, return to the w-component equation, subtract $(w\,h)$ from both sides, square both sides of the resulting equation, and integrate over Ω and from t to $t+1$ to obtain

$$\begin{aligned}\int_t^{t+1}\int_\Omega (d_3\Delta w)^2\,dx &= \int_t^{t+1}\int_\Omega\left(\frac{\partial w}{\partial t} - w\,h\right)^2 dx\\ &\le 2\int_t^{t+1}\int_\Omega\left(\frac{\partial w}{\partial t}\right)^2 dx + 2\int_t^{t+1}\int_\Omega w^2h^2\,dx\,.\end{aligned} \tag{3.35}$$

Both terms on the right hand side are in $\mathcal{P}$, so $\int_t^{t+1}\|\Delta w(s)\|_2^2\,ds \in \mathcal{P}$. We can conclude from (3.21) and (3.23) that $\int_t^{t+1}\|\nabla w(s)\|_4^4\,ds \in \mathcal{P}$.

The corresponding analysis for the u component is slightly trickier. Following the argument for w we can arrive at an inequality which corresponds to (3.28), namely

$$d_1\frac{d}{dt}\int_\Omega |\nabla u|^2\,dx + 2d_1\int_\Omega |\nabla u|^2\,dx \le \int_\Omega (u\,f + u)^2\,dx\,. \tag{3.36}$$

We have that f satisfies

$$-\omega_1 u - a_1 v - a_2 w \le f \le r(x)\,. \tag{3.37}$$

Clearly f is bounded above by $r(x)$. However, an upper bound on f^2 will involve v. As such, it is not necessarily in $\mathcal{P}$. However, from (3.37) there is an $\omega(t)$ such that

$$\int_\Omega f^2\,dx \le \int_\Omega \omega(t)(1+v)^2\,dx\,. \tag{3.38}$$

We established in Lemma 3.2.1 that $\|v\|_1$ and $\int_t^{t+1}\|v(s)\|_2^2\,ds$ are in $\mathcal{P}$. Hence, $\int_t^{t+1}\|f(s)\|_2^2\,ds \in \mathcal{P}$. This will be a strong enough bound on f to use the Uniform Gronwall Lemma on (3.36) if we can also show $\int_t^{t+1}\|\nabla u(s)\|_2^2\,ds \in \mathcal{P}$. This is accomplished by multiplying the u-component equation by u integrating over Ω and integrating in time to obtain

$$\frac{1}{2}\int_t^{t+1} \frac{d}{ds}\int_\Omega u^2\, dx\, ds = -d_1 \int_t^{t+1} \int_\Omega |\nabla u|^2\, dx\, ds + \int_t^{t+1} \int_\Omega u^2\, f\, dx\, ds\,. \tag{3.39}$$

Using the fact that $\|u\|_\infty \in \mathcal{P}$ and rearranging yields

$$d_1 \int_t^{t+1} \int_\Omega |\nabla u|^2\, dx\, ds \leq \omega(t) + \omega(t) \int_t^{t+1} \int_\Omega f\, dx\, ds\,. \tag{3.40}$$

Therefore, $\int_t^{t+1} \|\nabla u(s)\|_2^2\, ds \in \mathcal{P}$ and the Uniform Gronwall Lemma applied to (3.36) yields $\|\nabla u\|_2^2 \in \mathcal{P}$. The inequality for the u-component that is analogous to (3.33) is

$$\int_\Omega \left(\frac{\partial u}{\partial t}\right)^2 dx \leq -d_1 \frac{d}{dt}\int_\Omega |\nabla u|^2\, dx + \int_\Omega (u\, f)^2\, dx\ . \tag{3.41}$$

Integrating this from t to $t+1$ yields

$$\int_t^{t+1} \left\|\frac{\partial u}{\partial t}(s)\right\|_2^2 ds \leq d_1 \|\nabla u(t)\|_2^2 + \int_t^{t+1} \|u(s) f(s)\|_2^2\, ds\ . \tag{3.42}$$

We need to use the fact that $\int_t^{t+1} \|f(s)\|_2^2\, ds \in \mathcal{P}$ again (along with $\|u\|_\infty \in \mathcal{P}$) to conclude $\int_t^{t+1} \|u(s) f(s)\|_2^2\, ds \in \mathcal{P}$. Therefore the right hand side of (3.42) is all ultimately uniformly bounded and $\int_t^{t+1} \left\|\frac{\partial u}{\partial t}(s)\right\|_2^2 ds \in \mathcal{P}$. Return to the u-component equation, subtract $(u\, f)$ from both sides, square the resulting equation and integrate over Ω and t to $t+1$ to arrive at

$$\int_t^{t+1}\int_\Omega (d_1\Delta u)^2\,dx\,ds = \int_t^{t+1}\int_\Omega \left(\frac{\partial u}{\partial t} - u\,f\right)^2 dx\,ds$$
$$\leq 2\int_t^{t+1}\left\|\frac{\partial u}{\partial t}(s)\right\|_2^2 ds + 2\int_t^{t+1}\|u(s)f(s)\|_2^2\,ds\ . \tag{3.43}$$

We have shown that the right hand side above is in $\mathcal{P}$, so $\int_t^{t+1}\|\Delta u(s)\|_2^2\,ds \in \mathcal{P}$ and we can finally conclude from (3.20), (3.21) and (3.23) that $\|v\|_2 \in \mathcal{P}$.

3.3 Existence And The Global Attractor

Now that we have the appropriate *a priori* bounds on the components of our system, we can use the main result of Dung Le [25] to conclude global existence of solutions and the existence of a global attractor. Le's result concerns the system

$$\frac{\partial u}{\partial t} = \nabla\cdot(Q(u)\nabla u) + F(u,v)$$
$$\frac{\partial v}{\partial t} = \nabla\cdot(P(u,v)\nabla v + R(u,v)\nabla u) + G(u,v)\quad \text{for } x\in\Omega\subseteq\mathbb{R}^n, t>0\ , \tag{3.44}$$

with Neumann or Robin type boundary conditions and initial conditions in $W^{1,p}(\Omega)$ with $p>n$. (We have switched the u and v from Le's original paper so that this system matches with (2.5) more directly). It is assumed that P, Q and R are differentiable in their variables and that there exists a positive constant d and continuous function Φ such that

$$Q(u) \geq d > 0\,, \tag{3.45}$$

$$P(u,v) \geq d > 0\,, \tag{3.46}$$

$$|R(u,v)| \leq \Phi(u)v\,. \tag{3.47}$$

Also, the partial derivatives with respect to u and v can be majorized by some powers of u and v. The assumption on the reaction terms is that there exists a nonnegative continuous function $C(u)$ such that

$$|F(u,v)| \leq C(u)(1+v)\,, \quad G(u,v)v^p \leq C(u)(1+v^{p+1})\,, \tag{3.48}$$

for all $u, v \geq 0$ and $p > 0$. His main result states:

Theorem 3.3.1 ([25] Theorem 2.2)**.** *Assume* (3.45) - (3.48) *hold. Let* (u, v) *be a nonnegative solution to* (3.44) *with its maximal existence interval* I*. If* $\|u(t)\|_\infty$ *and* $\|v(t)\|_n$ *are in* $\mathcal{P}$*, then there exists* $\nu > 1$ *such that*

$$\|u(t)\|_{C^\nu(\overline{\Omega})}\,,\ \|v(t)\|_{C^\nu(\overline{\Omega})} \in \mathcal{P}\,. \tag{3.49}$$

The proof of this theorem relies on using the $L^n(\Omega)$ *a priori* bound on v, the $L^\infty(\Omega)$ bound on u and single-equation regularity results for quasi-linear parabolic equations from [24] to get $C^{\alpha,\alpha/2}(\overline{\Omega})$ bounds on u for some $\alpha > 0$. With this bound on u and conditions (3.45) - (3.48), Le is able to then show that v is in $L^q(\Omega)$ for all

$1 \leq q < \infty$. This is then used to prove a stronger regularity result for u that, in turn, yields stronger regularity for v.

This idea can be applied to our system, (2.5), with little modification. Since u and w have standard diffusion operators, classical parabolic regularity theory can be applied using the *a priori* $L^2(\Omega)$ bound on v, and the $L^\infty(\Omega)$ bounds on u and w. The resulting regularity results for u and w can then be used to prove v is in $L^q(\Omega)$ for all $1 \leq q < \infty$, which is then used to prove increased regularity for u and w and so forth. In fact, any number of additional components could be added to the system, as long as none of them have cross-diffusion terms in their differential operators.

It is still necessary to verify that our choice of reaction terms and the conditions we have imposed on $M(u, w)$ satisfy (3.45)-(3.48). Writing the Laplacian term in the v component equation in a form analogous to (3.44) yields

$$\Delta[M(u, w)v] = \nabla \cdot \left(M(u, w)\nabla v + v\frac{\partial M}{\partial u}\nabla u + v\frac{\partial M}{\partial w}\nabla w \right) . \tag{3.50}$$

The conditions equivalent to (3.45)-(3.47) are that $M(u, w) \geq d > 0$ and that $M(u, w)$ has continuous partial derivatives up to second order. It is easy to verify that the reaction terms defined by (2.6)-(2.8) satisfy the constraints analogous to (3.48). We will need a nonnegative continuous function $C(u, w)$ such that f, g and h satisfy

$$|u\, f(x, u, v, w)| \leq C(u, w)(1 + v)\,, \tag{3.51}$$

$$g(u, v, w)v^{p+1} \leq C(u, w)(1 + v^{p+1})\,, \tag{3.52}$$

$$|w\, h(u, v, w)| \leq C(u, w)(1 + v) \;. \tag{3.53}$$

Returning to (2.6)-(2.8) we see that

$$|u\,f(x,u,v,w)| \leq (\overline{r} + \omega_1 u + a_1 v + a_2 w)u\,, \tag{3.54}$$

$$g(u,v,w)v^{p+1} \leq \frac{e_1}{h_1}v^{p+1}\,, \tag{3.55}$$

$$|w\,h(u,v,w)| \leq \left(\frac{e_2}{h_2} + \frac{e_3}{h_3} + \mu_2 + \omega_3 w\right) w\ , \tag{3.56}$$

where $\overline{r} = \max_{x\in\Omega} r(x)$. Clearly there exists a $C(u,w)$ that will satisfy the constraints (3.51)-(3.53). It is worth noting that although we make use of the saturating functional responses to achieve the bounds in (3.55) and (3.56), non-saturating functional response terms will satisfy Le's conditions as well. We can now formally state a global existence theorem for (2.5).

Theorem 3.3.2. *Suppose Ω is a bounded domain in $\mathbb{R}^2$ with smooth boundary. Let $h_1, h_2, h_3, \mu_1, \mu_2, \omega_1, \omega_2, \omega_3, d_1$ and d_3 be positive constants, $r(x) > 0$ for $x \in \overline{\Omega}$ and $M(u,w) \geq d > 0$ for some $d > 0$ and all $u, w \geq 0$. Then for all nonnegative intial data $(u_0(x), v_0(x), w_0(x)) \in [W^{1,p}(\Omega)]^3$ with $p > 2$, (2.5) has a unique nonnegative classical solution, $(u(x,t), v(x,t), w(x,t))$, that exists globally in time. Furthermore, (2.5) induces a semiflow on $\left[W_+^{1,p}(\Omega)\right]^3$ which possesses a global attractor and there is a constant $\nu > 1$ such that*

$$\|u(\cdot,t)\|_{C^\nu(\overline{\Omega})},\ \|v(\cdot,t)\|_{C^\nu(\overline{\Omega})}, \|w(\cdot,t)\|_{C^\nu(\overline{\Omega})} \in \mathcal{P}. \tag{3.57}$$

Proof. We can conclude from the *a priori* bounds proved in Section 3.2 and the generalization of Theorem 2.2 of [25] discussed above that for nonnegative initial conditions in $W^{1,p}(\Omega)$, $p > 2$, there is a unique classical solution, (u,v,w) to (2.5) that exists globally in time. The fact that (2.5) induces a semiflow on $\left[W_+^{1,p}(\Omega)\right]^3$ is a result of Amann's in [4]. The global attractor comes from the fact that $C^{\nu}(\overline{\Omega})$ embeds compactly in $W^{1,p}(\Omega)$ and the bound (3.57) which results from the generalizatoin of Le's main result of [25], Theorem 3.3.1, to three components. $\square$

Chapter 4

Permanence

In this Chapter we investigate the effect of the IGPrey's movement strategy, M, on the conditions for coexistence in the system (2.5). In particular, we would like to see if a biologically feasible movement strategy can result in coexistence but a movement by random diffusion would result in v being excluded from the system. We will first establish sufficient conditions for coexistence and then investigate how specific choices of M will affect these criteria.

4.1 The Semi-Flow Framework

We will examine the conditions for coexistence of the three species through the lens of abstract permanence theory. Saying that the system (2.5) exhibits ecological permanence means that for all initial conditions where no component is identically zero, there is an asymptotic floor and ceiling for each component, i.e. there are constants $C_1, C_2, t' > 0$ such that

$$C_1 \leq u(x,t), v(x,t), w(x,t) \leq C_2 \ \text{ for all } x \in \Omega,\ t > t'\,. \tag{4.1}$$

Permanence can also be studied via the mathematical theory of semi-dynamical systems. Suppose (Y, d) is a complete metric space and π is a semiflow on Y. Assume that Y can be written as $Y = Y_0 \cup \partial Y_0$ where Y_0 is open in Y and both Y_0 and ∂Y_0 are forward invariant under π. Then we say π is permanent if there is a bounded subset U that is bounded away from ∂Y_0 and

$$\inf_{u \in U} d(\pi(y_0, t), u) \to 0 \text{ as } t \to \infty \ \text{ for all } y_0 \in Y_0\,. \tag{4.2}$$

For the appropriate metric space, Y, permanence of the semiflow implies ecological permanence of the system (see Section 4.6 of [11]). We will use this abstract version of permanence to study the asymptotic dynamics of (2.5)

Amann proved in [4] that the system (2.5) with $\Omega \subseteq \mathbb{R}^n$ generates a semiflow, π, on $[W^{1,p}(\Omega)]^3$ for $p > n$ (in our case we have $n = 2$). We showed in the previous Chapter that solutions to (2.5) are actually ultimately uniformly bounded in $[C^\nu(\overline{\Omega})]^3$ for some $\nu > 1$. We know that $C^\nu(\overline{\Omega})$ embeds compactly in $C^1(\overline{\Omega})$ and $C^1(\overline{\Omega})$ embeds continuously in $W^{1,p}(\Omega)$. Therefore, $[C^\nu(\overline{\Omega})]^3$ is compactly embedded in $[W^{1,p}(\Omega)]^3$. This compact embedding along with (3.57) tells us two critical points about the semiflow, π:

1. π is dissipative (orbits are ultimately uniformly bounded in $[W^{1,p}(\Omega)]^3$) and,

2. $\pi(\cdot, t) : [W^{1,p}(\Omega)]^3 \to [W^{1,p}(\Omega)]^3$ is a compact map for $t > 0$.

We will actually want to set up the semiflow on the subset of $[W^{1,p}(\Omega)]^3$ corresponding to nonnegative functions. It makes sense to speak of nonnegative functions in $W^{1,p}(\Omega)$ for $p > 2$ because $W^{1,p}(\Omega)$ embeds continuously in $C(\overline{\Omega})$. Let Y be defined by

$$Y = \left[W_+^{1,p}(\Omega)\right]^3 \equiv \{(u, v, w) \in \left[W^{1,p}(\Omega)\right]^3 \mid u\,,\ v\,,\ w \geq 0 \text{ for all } x \text{ in } \overline{\Omega}\}\,,$$

with $\|(u, v, w)\|_Y = \|u\|_{1,p} + \|v\|_{1,p} + \|w\|_{1,p}$. Y is a complete metric space and is forward invariant under π. This invariance is a direct result of the maximum principle for parabolic equations ([11], Corollary 1.18). The global existence result of Amann in [3] states that for all initial conditions in $[W^{1,p}(\Omega)]^3$, the solution trajectories to (2.5), $(u(t), v(t), w(t))$, are in $[C^2(\overline{\Omega})]^3$ for all $t \in (0, \infty)$; so, the maximum principle can be directly applied to the u and w equations by viewing the per capita growth rates as time-dependent coefficients of a parabolic operator. To apply the maximum principle to the v equation, we can first rewrite the equation as

$$\begin{aligned}\frac{\partial v}{\partial t} &= M(u, w)\Delta v + 2\nabla M(u, w) \cdot \nabla v \\ &\quad + \left(\frac{e_1 a_1 u}{1 + a_1 h_1 u} - \mu_1 - \omega_2 v - \frac{a_3 w}{1 + a_3 h_3 w} + \Delta M(u, w)\right) v\,, \qquad (4.3)\end{aligned}$$

and recall that $M(u, w) \geq d > 0$ and M has continuous derivatives up to second order. In fact, the maximum principle gives a stronger result than the forward invariance of Y. It states that if any component has an initial condition that is not identically zero, then that component will be strictly positive on $\overline{\Omega}$ for all $t > 0$.

The classic result of Billotti and LaSalle [8] states that if Y is a complete metric space, and π a semiflow on Y such that π is dissipative and $\pi(\cdot, t')$ is compact for some $t' > 0$, then π possesses a global attractor in Y. As shown above, this is the case for our semiflow coming from (2.5). Let $\mathcal{A}$ denote the global attractor for π in Y.

Let $\mathring{Y}$ denote the interior of Y, i.e. the triples of functions that are strictly positive on $\overline{\Omega}$, and $\partial\mathring{Y}$ be its boundary, the nonnegative triples where at least one component vanishes at some point x in Ω.

For any set, U, define the epsilon ball around U, $\mathcal{B}(U, \varepsilon)$, by

$$\mathcal{B}(U, \varepsilon) = \left\{ x \in Y \mid \inf_{x' \in U} \|x - x'\|_Y < \varepsilon \right\} ; \tag{4.4}$$

and, the distance from a point x in Y to the set U by

$$d(x, U) = \inf_{x' \in U} \|x - x'\|_Y . \tag{4.5}$$

$\mathcal{A}$ is a global attractor for π, so for any bounded U in Y there exists a t_U such that $\pi(U, t_U) \subseteq \mathcal{B}(\mathcal{A}, \varepsilon)$. Therefore, to investigate long-term dynamics of (2.5) it is only necessary to consider what happens to initial data in $\mathcal{B}(\mathcal{A}, \varepsilon)$, so we define

$$\tilde{X} = \overline{\pi(\mathcal{B}(\mathcal{A}, \varepsilon), [t_0, \infty))} \tag{4.6}$$

where the overline represents the closure in Y, $\varepsilon > 0$ and $t_0 > 0$. Since, $\pi(\cdot, t) : Y \to Y$ is compact for $t \geq t_0$ and we have taken the closure of the resulting set, $\tilde{X}$ is compact. Then take

$$X = \pi(\tilde{X}, t') \tag{4.7}$$

for some $t' > 0$ (this guarantees that all elements of X with a component equal to zero somewhere on $\overline{\Omega}$ will have that component zero everywhere in $\overline{\Omega}$). Finally, set

$S = X \cap \partial \mathring{Y}$. As in Theorem 4.1 of [11] we have that $\tilde{X}$, X and S are compact and $\tilde{X}$, X, S and $X \setminus S$ are forward invariant under π. Note that as per the discussion of the maximum principle above, S will consist of triples with at least one component identically zero, whereas $X \setminus S$ will consist of triples that are all strictly positive on $\overline{\Omega}$. We will need two additional definitions before we state the acyclicity test for permanence. Let $\omega(y)$ denote the omega limit set of a point y under the semiflow π, and let $\alpha(u)$ be the alpha limit set (if it exists). For any set U in Y, define

$$\omega(U) = \bigcup_{u \in U} \omega(u)\,, \tag{4.8}$$

which is actually a non-standard definition for the omega limit set of a set, but it is what we will need below. If U is a compact invariant subset of X, we define the stable set of U, $W^s(U)$, by

$$W^s(U) = \{u \in X \mid \omega(u) \neq \emptyset,\, \omega(u) \subseteq U\}\ . \tag{4.9}$$

and the unstable set of U by

$$W^u(U) = \{u \in X \mid \omega(u) \neq \emptyset,\, \alpha(u) \subseteq U\}\ . \tag{4.10}$$

If U_1 and U_2 are two compact invariant subsets of Y, we will say that U_1 is *chained* to U_2 and write $U_1 \to U_2$ if there exists a $u \notin U_1 \cup U_2$ such that $u \in W^u(U_1) \cap W^s(U_2)$, i.e. there is a full orbit, $\gamma(u)$ passing through u with that connects to U_1 as $t \to -\infty$ and connects to U_2 as $t \to \infty$. We say a collection of compact invariant sets, $\{U_1, \ldots, U_m\}$ forms a *chain* if

$$U_1 \to U_2 \to \ldots \to U_m\,,$$

and we say the collection forms a *cycle* if $U_m = U_1$.

The acyclicity test for permanence, Theorem 4.1 of [18], states that in order to establish permanence for the system we must show that there are pairwise disjoint compact invariant subsets of S, $\mathcal{A}_1, ..., \mathcal{A}_k$, such that:

1. $\omega(S) = \bigcup_{i=1}^{k} \mathcal{A}_i$,

2. no subcollection of $\{\mathcal{A}_1, ..., \mathcal{A}_k\}$ forms a cycle,

3. $\mathcal{A}_i$ is isolated with respect to π and π_S (the semiflow which results from restricting π to S), and

4. $W^s(\mathcal{A}_i) \cap (X \setminus S) = \emptyset$ for each $i = 1, ..., k$.

In order to test 4 above, the following Lemma is useful:

Lemma 4.1.1. *If $u \in X$ and U is a compact invariant subset of X such that $u \in W^s(U)$, then*

$$\lim_{t \to \infty} d(\pi(u,t), U) = 0\,. \tag{4.11}$$

Proof. Suppose $\lim_{t\to\infty} d(\pi(u,t), U) \neq 0$. Then there exist an $\varepsilon > 0$ and $\{t_n\}_{n=1}^{\infty}$ with $t_n \to \infty$ such that $d(\pi(u,t_n), U) \geq \varepsilon$. Take any $t' > 0$. Since π is dissipative on X, we know that $\{u_n\} \equiv \{\pi(u, t_n - t')\}$ is defined and bounded for n large enough so that $t_n > t'$. Furthermore, $\pi(\cdot, t')$ is a compact map so $\pi(u, t_n) = \pi(u_n, t')$ has a convergent subsequence $\pi(u, t_{n_k})$ that converges to some point $y \in X$. Therefore, $y \in \omega(u)$; but, $u \in W^s(U)$ implies that $\omega(u) \subseteq U$ which means that $y \in U$. This contradicts the fact that $d(y, U) \geq \varepsilon$. $\square$

4.2 Invasibility Criteria

First, we need to compute $\omega(S)$. We will show below that $\omega(S)$ can be comprised of up to four isolated invariant compact sets, $\mathcal{A}_1, \ldots, \mathcal{A}_4$, which we will compute below. For each of these sets we will need to develop sufficient criteria so that $W^s(\mathcal{A}_i) \cap (X \setminus S) = \emptyset$. This will be done using principal eigenvalues of various linearizations of of (2.5). Consider the linear elliptic boundary value problem

$$\nabla \cdot (d(x)\nabla\phi) + m(x)\phi = \sigma\phi \;\text{ in } \Omega, \quad \frac{\partial\phi}{\partial n} = 0 \;\text{ on } \partial\Omega\,. \tag{4.12}$$

We say that $\hat{\sigma}$ is the *principal eigenvalue* of (4.12) if it is the largest value of σ such that (4.12) has a solution. Classical elliptic theory states that there is always a principal eigenvalue and that the corresponding solution (or eigenfunction), ϕ is unique up to a scalar multiple and positive on Ω (see Chapter 2 of [11] for a full discussion). We will see below that principal eigenvalues play a critical role in determining stable and unstable sets. If the left hand side of (4.12) results from linearizing a system about a particular point, then the sign of $\hat{\sigma}$ will determine if small perturbations from the point of linearization will grow ($\hat{\sigma} > 0$) or shrink ($\hat{\sigma} < 0$).

We can also talk about principal eigenvalues for equations of the form

$$\nabla \cdot (d(x)\nabla\phi) + \Lambda m(x)\phi = 0 \;\text{ in } \Omega, \quad \frac{\partial\phi}{\partial n} = 0 \;\text{ on } \partial\Omega\,. \tag{4.13}$$

In this case, the principal eigenvalue, $\hat{\Lambda}$, is the smallest value of Λ for which (4.13) possesses a solution. Again, the corresponding eigenfunction will be positive on Ω. Theorems 2.5 and 2.6 of [11] draw a connection between these two types of principal eigenvalues:

Theorem 4.2.1 (Theorem 2.5 and Theorem 2.6 [11]). *Suppose* $\int_\Omega m(x)\,dx < 0$*, then then the principal eigenvalue,* $\hat{\Lambda}$*, of* (4.13) *is positive. Furthermore, the principal eigenvalue,* $\hat{\sigma}$*, of*

$$\nabla \cdot (d(x)\nabla\phi) + \Lambda m(x)\phi = \sigma\phi \quad in\ \Omega, \quad \frac{\partial\phi}{\partial n} = 0 \quad on\ \partial\Omega \tag{4.14}$$

is positive if and only if $0 < \Lambda < \hat{\Lambda}$*.*

If $\int_\Omega m(x)\,dx > 0$ *then the principal eigenvalue,* $\hat{\sigma}$*, of* (4.14) *is positive for all* $\Lambda > 0$*.*

Now, let's begin to compute $\omega(S)$. Clearly, $(0,0,0)$ is an equilibrium point in our system. Set $\mathcal{A}_1 = (0,0,0)$. If the resource is entirely absent from the system, the resulting $v - w$ subsystem has the form

$$\begin{aligned}
&\frac{\partial v}{\partial t} = \Delta\left[M(w)v\right] - \left(\mu_1 + \omega_2 v + \frac{a_3 w}{1 + a_3 h_3 v}\right) v \\
&\frac{\partial w}{\partial t} = d_3 \Delta w + \left(\frac{e_3 a_3 v}{1 + a_3 h_3 v} - \mu_2 - \omega_3 w\right) w \quad \text{in } \Omega\,, \\
&\frac{\partial v}{\partial n} = \frac{\partial w}{\partial n} = 0 \quad \text{on } \partial\Omega\,.
\end{aligned} \tag{4.15}$$

The dynamics of this system are not immediately evident. Even though the reaction terms in the first equation of (4.15) are always strictly negative, the nonlinear diffusion prevents a comparison principle type of argument. However, we can make use of the compact global attractor to conclude that all solutions of (4.15) with non-negative initial conditions converge to the extinction state $(0,0)$. To do this, we will show that for any non-negative initial conditions, the solutions to (4.15) converge to $(0,0)$ in $\left[L^1(\Omega)\right]^2$, and then use the compact global attractor to conclude the convergence is actually in X. Multiply the first equation in (4.15) by e_3, add it to the second equation and integrate over Ω (applying the divergence theorem to eliminate the Laplacian terms) to obtain

$$\frac{d}{dt}\int_{\Omega}(e_3v+w)\,dx=-\int_{\Omega}\mu_1e_3v+\omega_2e_3v^2+\mu_2w+\omega_3w^2\,dx\ . \tag{4.16}$$

We can drop the quadratic terms from the right hand side and set $k=\min\{\mu_1,\mu_2\}$ to get the inequality

$$\frac{d}{dt}\|e_3v+w\|_1\leq -k\|e_3v+w\|_1\ , \tag{4.17}$$

and then conclude that $\|e_3v+w\|_1\to 0$ as $t\to\infty$, hence $\|v\|_1,\|w\|_1\to 0$ individually. We know that $\pi(\cdot,t)$ is compact for $t>0$, so for any nonnegative initial conditions, and sequence of solution points at time t_n, (v_n,w_n), where $t_n\to\infty$ there is a convergent subsequence in X. However, this convergent subsequence must be converging to $(0,0)$ in $[L^1(\Omega)]^2$ which implies that it is converging to $(0,0)$ in X as well. Since every sequence of solution points has a subsequence converging to $(0,0)$ in X, the solution trajectory must be converging to $(0,0)$ in X as well. We can conclude that $(0,0,0)$ attracts all initial conditions where the resource is absent.

With both the IGPrey and IGPredator absent, (2.5) reduces to a diffusive logistic equation with heterogeneous growth rate

$$\frac{\partial u}{\partial t}=d_1\Delta u+r(x)u-\omega_1u^2 \text{ in } \Omega,\quad \frac{\partial u}{\partial n}=0 \text{ on } \partial\Omega\,. \tag{4.18}$$

This equation is well understood, see [11] Section 3.2 for details. Since $r(x)>0$ on Ω and we have Neumann boundary conditions, any solution to (4.18) with initial condition $u_0(x) \geq 0$, u_0 not identically zero, will converge to a positive globally attracting equilibrium u^*. Set $\mathcal{A}_2 = (u^*, 0, 0)$.

Next, consider the $u - v$ subsystem that arises when the IGPredator is absent

$$\begin{aligned}\frac{\partial u}{\partial t} &= d_1 \Delta u + u \left(r(x) - \omega_1 u - \frac{a_1 v}{1 + h_1 a_1 u} \right) \\ \frac{\partial v}{\partial t} &= \Delta \left[M(u, 0) v \right] + v \left(\frac{e_1 a_1 u}{1 + h_1 a_1 u} - \mu_1 - \omega_2 v \right) \text{ in } \Omega, \\ \frac{\partial u}{\partial n} &= \frac{\partial v}{\partial n} = 0 \quad \text{on } \partial\Omega\,.\end{aligned} \tag{4.19}$$

We will show below that this system will exhibit permanence if v is able to invade $(u^*, 0)$, which will be the case if the principal eigenvalue σ_1 of

$$\Delta \left[M(u^*, 0) v_1 \right] + \left(\frac{e_1 a_1 u^*}{1 + h_1 a_1 u^*} - \mu_1 \right) v_1 = \sigma_1 \, v_1 \text{ in } \Omega, \quad \frac{\partial v_1}{\partial n} = 0 \text{ on } \partial\Omega \tag{4.20}$$

is positive. If this is the case, then there exists a compact invariant set $\mathcal{A}_3$ in $\left[C^1_+(\overline{\Omega}) \right]^2$ bounded away from the boundary that attracts all initial data of the form $(u_0, v_0, 0)$ with $u_0(x)\,,\, v_0(x) \geq 0$ and neither u_0 nor v_0 identically zero.

Lemma 4.2.1. *If* $\sigma_1 > 0$ *in* (4.20)*, then the system defined in* (4.19) *exhibits permanence in* $\left[W^{1,p}_+(\Omega) \right]^2$.

Proof. The proof is similar to that found in [26] and [27]. Let $Y_3 = \left[W^{1,p}_+(\Omega) \right]^2$, and π_3 be the semi-dynamical system corresponding to (4.19) on Y_3. We will use $\mathring{Y}_3$ to denote the interior of Y_3 and $\partial \mathring{Y}_3$ to denote the boundary of $\mathring{Y}_3$. As was the case for the full system there is a global attractor, $\mathcal{A}_{\pi_3}$ for π_3 and analogous to (4.6) and (4.7) we can define $\tilde{X}_3 = \overline{\pi_3(\mathcal{B}(\mathcal{A}_{\pi_3}, \varepsilon), [t_0, \infty))}$ and $X_3 = \pi_3(\tilde{X}_3, t')$ and set $S_3 = X_3 \cap \partial \mathring{Y}_3$.

To apply the acyclicity test for permanence to π_3 we will need to consider $\omega(S_3)$. For all initial conditions of the form $(u_0, 0)$ where u_0 is positive somewhere in $\overline{\Omega}$ we have $\pi((u_0, 0), t) \to (u^*, 0)$ as $t \to \infty$ (the resulting equation is a standard diffusive logistic equation). For initial conditions of the form $(0, v_0)$ we have $\pi((0, v_0), t) \to (0, 0)$ as $t \to \infty$. This is because when $u \equiv 0$ we have $M = M(0, 0)$ which is a constant on $\overline{\Omega}$, so (4.19) reduces to a standard reaction-diffusion equation for v with reaction terms of the form $-\mu_1 v - \omega_2 v^2$. All solutions to this equation converge to $v \equiv 0$ as $t \to \infty$ (standard comparison arguments can be employed using a spatially constant super-solution). Therefore, $\omega(S_3) = \{(0, 0), (u^*, 0)\}$ which is clearly isolated and acyclic, therefore π_3 is permanent if

$$W^s((0,0)) \cap (X_3 \setminus S_3) = \emptyset \text{ and,} \tag{4.21}$$

$$W^s((u^*,0)) \cap (X_3 \setminus S_3) = \emptyset\ . \tag{4.22}$$

Suppose there exists a $(u_0, v_0) \in W^s((0,0)) \cap (X_3 \setminus S_3)$. Let $(u(t), v(t)) = \pi_3((u_0, v_0), t)$. Then, by Lemma 4.1.1 $\lim_{t\to\infty} \|u(t)\|_{1,p} + \|v(t)\|_{1,p} = 0$. Let σ_r be the principal eigenvalue of

$$d_1 \Delta \psi_r + r(x)\psi_r = \sigma_r \psi_r \ \text{ in } \Omega, \quad \frac{\partial \psi_r}{\partial n} = 0 \text{ on } \partial\Omega\,, \tag{4.23}$$

which is positive because $r(x) > 0$ on Ω. Multiply the u-component equation in (4.19) by ψ_r and integrate over Ω to obtain

$$\frac{d}{dt}\int_\Omega u\psi_r\, dx = \int_\Omega d_1\psi_r \Delta u + u\psi_r r(x) - u\psi_r\left(\omega_1 u + \frac{a_1 v}{1 + h_1 a_1 u}\right) dx\,. \tag{4.24}$$

Use the Divergence Theorem twice on the Laplacian term to move the differentiation onto the ψ_r factor and use (4.23) to get

$$\frac{d}{dt}\int_\Omega u\psi_r\,dx = \int_\Omega \sigma_r u\psi_r - u\psi_r\left(\omega_1 u + \frac{a_1 v}{1+h_1a_1u}\right)dx\,. \tag{4.25}$$

Let $\xi = \frac{\sigma_r}{2(\omega_1+a_1)}$ so that

$$\omega_1 u + \frac{a_1 v}{1+a_1h_1u} \leq \frac{\sigma_r}{2} \tag{4.26}$$

for all $(u,v)\in\mathcal{B}((0,0),\xi)$. There is a $t'>0$ such that $(u(t),v(t))\in\mathcal{B}((0,0),\xi)$ for all $t>t'$. Therefore

$$\frac{d}{dt}\int_\Omega u\psi_r\,dx \geq \frac{\sigma_r}{2}\int_\Omega u\psi_r\,dx \;\text{ for } t\geq t'\,. \tag{4.27}$$

Thus, for $t\geq t'$ we have $\|u\psi_r\|_1$ growing at least exponentially without bound. However,

$$\|u\psi_r\|_1 \leq \|u\|_\infty\|\psi_r\|_1 \leq C\|u\|_{1,p}\|\psi_r\|_1\,, \tag{4.28}$$

so $\|u\|_{1,p}$ must be growing at least exponentially as well. This contradicts $\|u\|_{1,p}\to 0$.

Now, to show that $W^s((u^*,0))\cap(X_3\setminus S_3)=\emptyset$ we will employ a similar technique and make use of the fact that $\sigma_1>0$ in (4.20). Suppose $(u_0,v_0)\in W^s((u^*,0))\cap(X_3\setminus S_3)$ and let $(u(t),v(t))=\pi_3((u_0,v_0),t)$. Then we must have $\|u(t)-u^*\|_{1,p}+\|v(t)\|_{1,p}\to 0$ as $t\to\infty$. Multiply the v-component equation of (4.19) by $M(u^*,0)v_1$, multiply the eigenvalue equation (4.20) by $M(u,0)v$ and then integrate over Ω to get

$$\begin{aligned}\frac{d}{dt}\int_\Omega M(u^*,0)v_1 v\,dx &= \int_\Omega M(u^*,0)v_1\Delta[M(u,0)v]\,dx\\ &\quad+\int_\Omega M(u^*,0)v_1 v\left(\frac{e_1a_1u}{1+h_1a_1u}-\mu_1-\omega_2 v\right)\,,\end{aligned} \tag{4.29}$$

and

$$\sigma_1 \int_\Omega M(u,0)v_1 v\,dx = \int_\Omega M(u,0)v\Delta[M(u^*,0)v_1]\,dx + \int_\Omega M(u,0)v_1 v\left(\frac{e_1a_1u^*}{1+h_1a_1u^*} - \mu_1\right). \quad (4.30)$$

Apply the Divergence Theorem once to each integral with Laplacian term in (4.29) and (4.30) and then subtract (4.30) from (4.29) and factor the resulting right hand side to obtain

$$\frac{d}{dt}\int_\Omega M(u^*,0)v_1 v\,dx = \int_\Omega M(u^*,0)v_1 v\left[\frac{e_1a_1u}{1+h_1a_1u} - \mu_1 - \omega_2 v - \frac{M(u,0)}{M(u^*,0)}\left(\frac{e_1a_1u^*}{1+h_1a_1u^*} - \mu_1\right) + \sigma_1\frac{M(u,0)}{M(u^*,0)}\right]dx \quad (4.31)$$

Now, set $K = \max_\Omega M(u^*,0)$ and choose $\xi > 0$ such that

$$\frac{e_1a_1u}{1+h_1a_1u} - \mu_1 - \omega_2 v - \frac{M(u,0)}{M(u^*,0)}\left(\frac{e_1a_1u^*}{1+h_1a_1u^*} - \mu_1\right) \geq \frac{-\sigma_1 d}{2K} \quad (4.32)$$

for all $(u,v) \in \mathcal{B}((u^*,0),\xi)$. Let $t' > 0$ be such that $(u(t),v(t)) \in \mathcal{B}((u^*,0),\xi)$ for all $t > t'$. Then from (4.31) and (4.32) we have

$$\frac{d}{dt}\int_\Omega M(u^*,0)v_1 v\,dx \geq \frac{\sigma_1 d}{2K}\int_\Omega M(u^*,0)v_1 v\,dx \ \text{ for } t > t' \quad (4.33)$$

which means that $\|M(u^*,0)v_1 v\|_1$ grows at least exponentially for all $t > t'$. However,

$$\|M(u^*,0)v_1 v\|_1 \leq \|v\|_\infty \|M(u^*,0)v_1\|_1 \leq C\|v\|_{1,p}\|M(u^*,0)v_1\|_1 \quad (4.34)$$

so $\|v(t)\|_{1,p} \to \infty$ which is a contradiction. The last inequality above comes from the fact that for $p > n$ we have that $W^{1,p}(\Omega)$ is continuously embedded in $L^\infty(\Omega)$, so there exists a constant C such that $\|\cdot\|_\infty \le C\|\cdot\|_{1,p}$.

Therefore, all conditions for (4.19) are satisfied. $\square$

Now consider the $u-w$ subsystem that arises when the IGPrey is absent

$$\begin{aligned}
\frac{\partial u}{\partial t} &= d_1\Delta u + u\left(r(x) - \omega_1 u - \frac{a_2 w}{1+h_2a_2u}\right)\\
\frac{\partial w}{\partial t} &= d_3\Delta w + w\left(\frac{e_2a_2u}{1+h_2a_2u} - \mu_2 - \omega_3 w\right) \text{ in } \Omega\,,\\
\frac{\partial u}{\partial n} &= \frac{\partial w}{\partial n} = 0 \quad \text{on } \partial\Omega\,.
\end{aligned} \tag{4.35}$$

This is a standard system of the type considered in [11]. As in [11], Section 4.5, (4.35) will be permanent if w is able to invade $(u^*, 0)$, which will be the case if the principal eigenvalue σ_2 of

$$d_3\Delta w_2 + \left(\frac{e_2a_2u^*}{1+h_2a_2u^*} - \mu_2\right)w_2 = \sigma_2 w_2 \text{ in } \Omega, \quad \frac{\partial w_2}{\partial n} = 0 \text{ on } \partial\Omega \tag{4.36}$$

is positive. If this is the case, then there exists a compact invariant set $\mathcal{A}_4$ in the $u-w$ plane that is bounded away from the axes that attracts all initial data of the form $(u_0, 0, w_0)$ with $u_0(x)\,,\, w_0(x) \ge 0$ and neither u_0 nor w_0 identically zero. (Alternatively, a proof analogous to Lemma 4.2.1 could be used to show permanence in (4.35).)

If σ_1 and σ_2 are positive, then $\omega(S) = \mathcal{A}_1 \cup \mathcal{A}_2 \cup \mathcal{A}_3 \cup \mathcal{A}_4$ (see Figure 4.1). Clearly no subcollection of $\mathcal{A}_i$'s can form a cycle due to the attracting nature of $\mathcal{A}_3$ and $\mathcal{A}_4$ and the global stability of $\mathcal{A}_2$ in the resource only subsystem. We must now establish

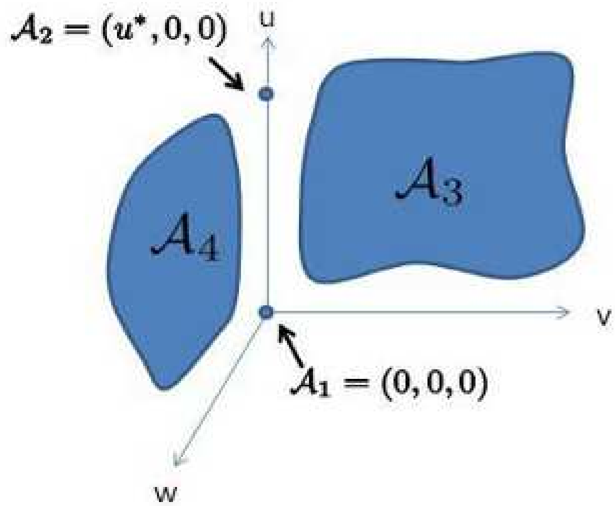

Figure 4.1: A sketch of the boundary attractors. Note that in reality each "axis" in the figure is an infinite dimensional Banach space.

that all $\mathcal{A}$'s are isolated with respect to π and π_S and that

$$W^s(\{(0,0,0)\}) \cap (X \setminus S) = \emptyset$$
$$W^s(\{(u^*,0,0)\}) \cap (X \setminus S) = \emptyset$$
$$W^s(\mathcal{A}_3) \cap (X \setminus S) = \emptyset$$
$$W^s(\mathcal{A}_4) \cap (X \setminus S) = \emptyset\,.$$

The first two cases follow from an argument along the lines of the proof of Lemma 4.2.1 or by a comparison argument as found in Lemma 4.5 of [11]. $W^s(\{(0,0,0)\}) \cap (X \setminus S) = \emptyset$ is a direct consequence of $r(x) > 0$ and $W^s(\{(u^*,0,0)\}) \cap (X \setminus S) = \emptyset$ follows from either $\sigma_1 > 0$ or $\sigma_2 > 0$. The last two cases require more care. Begin by considering $W^s(\mathcal{A}_3)$.

Lemma 4.2.2. *Suppose there exists a continuous function* $\tilde{h}(x)$ *such that* $\tilde{h}(x) \leq h(u, v, 0)$ *for all* $(u, v, 0) \in \mathcal{A}_3$ *and the principal eigenvalue* σ_3 *of*

$$d_3 \Delta w_3 + \tilde{h}(x)\, w_3 = \sigma_3\, w_3 \tag{4.37}$$

is positive. Then $W^s(\mathcal{A}_3) \cap (X \setminus S) = \emptyset$.

Proof. Suppose there exists $(u_0, v_0, w_0) \in X_0$ such that

$$\lim_{t \to \infty} d\left((u(t), v(t), w(t)), \mathcal{A}_3\right) = 0\,.$$

Choose $\xi > 0$ such that $\tilde{h}(x) \leq h(u, v, w) + \frac{\sigma_3}{2}$ for all $(u, v, w) \in \mathcal{B}(\mathcal{A}_3, \xi)$. Take t_0 such that $d((u, v, w), \mathcal{A}_3) \leq \xi$ for all $t \geq t_0$. Now multiply the w component equation of (2.5) by w_3, multiply (4.37) by w, integrate both equations, apply the divergence theorem, and subtract to get

$$\frac{d}{dt} \int_\Omega w\, w_3\, dx = \int_\Omega w\, w_3 (\sigma_3 + h(u, v, w) - \tilde{h}(x))\, dx\,. \tag{4.38}$$

For $t > t_0$ we have $\sigma_3 + h(u, v, w) - \tilde{h}(x) \geq \frac{\sigma_3}{2}$, so

$$\frac{d}{dt} \int_\Omega w\, w_3\, dx \geq \frac{\sigma_3}{2} \int_\Omega w\, w_3\, dx \text{ for } t > t_0\,. \tag{4.39}$$

This implies that $\|ww_3\|_1$ grows without bound, and

$$\|ww_3\|_1 \leq \|w\|_\infty \|w\|_1 \leq C \|w\|_{1,p} \|w\|_1\,, \tag{4.40}$$

which contradicts $(u, v, w) \in \mathcal{B}(\mathcal{A}_3, \xi)$ for $t \geq t_0$. Therefore, $W^s(\mathcal{A}_3) \cap (X \setminus S) = \emptyset$. $\square$

The argument for $W^s(\mathcal{A}_4)$ is similar, but the diffusion pressure, M, further complicates matters.

Lemma 4.2.3. *Suppose there exists a continuous function $\tilde{b}(x)$ such that $\tilde{b}(x) \leq \frac{g(u,0,w)}{M(u,w)}$ for all $(u, 0, w) \in \mathcal{A}_4$ and the principal eigenvalue σ_4 of*

$$\Delta v_4 + \tilde{b}(x)\, v_4 = \sigma_4\, v_4 \;\; \text{in } \Omega, \quad \frac{\partial v_4}{\partial n} = 0 \;\; \text{on } \partial\Omega\,, \tag{4.41}$$

is positive. Then $W^s(\mathcal{A}_4) \cap (X \setminus S) = \emptyset$.

Proof. As in the proof for $W^s(\mathcal{A}_3)$, assume there is a $(u_0, v_0, w_0) \in X_0$ such that

$$\lim_{t\to\infty} d((u(t), v(t), w(t)), \mathcal{A}_4) = 0\,.$$

Choose $\xi > 0$ such that

$$\tilde{b}(x) \leq \frac{g(u,v,w)}{M(u,w)} + \frac{\sigma_4}{2} \tag{4.42}$$

for all $(u, v, w) \in \mathcal{B}(\mathcal{A}_4, \xi)$. Take t_0 such that $d((u, v, w), \mathcal{A}_4) \leq \xi$ for all $t > t_0$. Multiply the v component equation of (2.5) by v_4 and multiply (4.41) by $M(u, w)v$ and integrate over Ω to obtain

$$\frac{d}{dt}\int_\Omega v_4 v\, dx = \int_\Omega v_4 \Delta[M(u,w)v]\, dx + \int_\Omega v_4 v\, g(u,v,w)\, dx \tag{4.43}$$

and

$$\int_\Omega M(u,w) v \Delta v_4\, dx + \int_\Omega M(u,w)\tilde{b}(x) v_4 v\, dx - \sigma_4 \int_\Omega M(u,w) v_4 v\, dx = 0\,. \tag{4.44}$$

Apply the divergence theorem twice to the first term in (4.44) and subtract (4.44) from (4.43) to get

$$\frac{d}{dt}\int_\Omega v\,v_4\,dx = \sigma_4\int_\Omega M(u,w)v\,v_4\,dx + \int_\Omega\Big(g(u,v,w)-\tilde{b}M(u,w)\Big)\,v\,v_4\,dx\,. \quad (4.45)$$

From (4.42) we have that $g(u,v,w)-\tilde{b}M(u,w) \geq -\frac{\sigma_4 M(u,w)}{2}$ for all $t > t_0$, and we have also assumed that M is such that $M(u,w) \geq d > 0$ for all $u,w \geq 0$. Therefore, $\|v\|_\infty$ and hence $\|v\|_{1,p}$ must grow without bound which contradicts $(u,v,w) \in \mathcal{B}(\mathcal{A},\xi)$, so $W^s(\mathcal{A}_4) \cap (X \setminus S) = \emptyset$. □

Note that if $\mathcal{A}_4$ is a single equilibrium point, $(\hat{u},\hat{w})$, then the condition that there exists an $x_0 \in \Omega$ such that $g^*(u(x_0),w(x_0)) > 0$ for all $(u,0,w) \in \mathcal{A}_4$ reduces to the simpler statement $g^*(\hat{u},\hat{w}) > 0$ at some point in Ω.

We can now synthesize these results into a theorem.

Theorem 4.2.2. *If the parameters of* (2.5) *are such that the principal eigenvalue of* (4.20)*,* σ_1*, and the principal eigenvalue of* (4.36)*,* σ_2*, are positive then there exists boundary attractors,* $\mathcal{A}_3$ *and* $\mathcal{A}_4$ *in the* $u-v$ *and* $u-w$ *planes respectively bounded away from the axes. Furthermore, if there exists continuous functions* $\tilde{h}(x)$ *and* $\tilde{b}(x)$ *satisfying the conditions of Lemma 4.2.2 and Lemma 4.2.3 that yield positive* σ_3 *and* σ_4 *respectively, then* (2.5) *exhibits ecological permanence; and,* (2.5) *possesses a componentwise positive equilibrium point.*

Proof. For σ_1 and σ_2 positive we have shown that $\omega(S) = \mathcal{A}_1 \cup \mathcal{A}_2 \cup \mathcal{A}_3 \cup \mathcal{A}_4$ which are all compact isolated invariant sets. Furthermore, we know that $\mathcal{A}_1$ is chained to $\mathcal{A}_2, \mathcal{A}_3$ and $\mathcal{A}_4$. $\mathcal{A}_2$ is chained to $\mathcal{A}_3$ and $\mathcal{A}_4$; and, $\mathcal{A}_3$ and $\mathcal{A}_4$ are not chained to any other $\mathcal{A}_i$. Therefore, the set $\{\mathcal{A}_1,\mathcal{A}_2,\mathcal{A}_3,\mathcal{A}_4\}$ is acyclic. Furthermore, if there exists

$\tilde{h}(x)$ and $\tilde{b}(x)$ that make σ_3 and σ_4 positive respectively, then $W^s(\mathcal{A}_i) \cap (X \setminus S) = \emptyset$ for $i = 1, 2, 3$ and 4, which would imply by the acyclicity theorem that (2.5) is permanent.

Theorem 4.6 of [11] states that if a system exhibits permanence, then the existence of at least one componentwise positive equilibrium point is guaranteed. $\square$

We will now investigate how the function M affects these eigenvalues. Looking at (4.36) we see that M has no effect on σ_2. Examining (4.37) it appears that M does not affect σ_3 either, but this is misleading. In fact, M can change the set $\mathcal{A}_3$ and hence change $\tilde{h}$ and in turn influence σ_3. This is a very indirect relationship, and not much analysis can be done without further assumptions that give more information about $\mathcal{A}_3$. However, in the special case that M is independent of u, σ_3 will be independent of M.

To examine the effect of M on σ_1 and σ_4 it is useful to obtain the variational formulations of these eigenvalues. We can use the fact that $M \geq d > 0$ to make the change of variables $\psi = M(u^*, 0)v_1$ in (4.20) to get the equivalent equation

$$\Delta\psi + \frac{1}{M(u^*, 0)} \left(\frac{e_1 a_1 u^*}{1 + h_1 a_1 u^*} - \mu_1 \right) \psi = \frac{\sigma_1}{M(u^*, 0)} \psi \text{ in } \Omega, \quad \frac{\partial \psi}{\partial n} = 0 \text{ on } \partial\Omega \,. \tag{4.46}$$

From (4.46) we see that σ_1 has variational characterization

$$\sigma_1 = \max_{\psi \in W^{1,2}(\Omega)} \frac{-\displaystyle\int_\Omega |\nabla \psi|^2 \, dx + \int_\Omega \frac{1}{M(u^*, 0)} \left(\frac{e_1 a_1 u^*}{1 + h_1 a_1 u^*} - \mu_1 \right) \psi^2 \, dx}{\displaystyle\int_\Omega \frac{1}{M(u^*, 0)} \psi^2 \, dx} \tag{4.47}$$

(see [11] Section 2.2).

The variational formula for σ_4 is standard and requires no change of variable, namely

$$\sigma_4 = \max_{\psi \in W^{1,2}(\Omega)} \frac{-\displaystyle\int_\Omega |\nabla \psi|^2 \, dx + \int_\Omega \tilde{b}(x)\psi^2 \, dx}{\displaystyle\int_\Omega \psi^2 \, dx} . \tag{4.48}$$

4.3 Fitness Dependent Dispersal

Without knowing the specific details of the equilibrium point $(u^*, 0, 0)$ and the boundary attractor $\mathcal{A}_4$ it may seem that the variational formulations (4.47) and (4.48) for σ_1 and σ_4 are not very helpful. However, if M is chosen in an appropriate form, we can make some useful observations on the effect of M. It is useful to think of M as a perturbation away from a random diffusion movement strategy with motility d_2. We will show that if the IGPrey can increase its motility to a sufficiently high level in areas where its linearized fitness is negative while maintaining a low level of motility in areas where the linearized fitness is positive, then the IGPrey will be able to invade the $u - w$ subsystem. This type of movement amounts to the IGPrey avoiding areas where resources are scarce and predation risk is high and feeling less diffusion pressure in areas with abundant resources and low predation risk. In order for this type of strategy to be biologically feasible, the IGPrey must be capable of assessing the local level of resource availability and the frequency of predator encounters. Both of these assumptions are reasonable for a variety of species [36], [14], [33], [41].

The major assumption that we will make about M is that it is actually a twice differentiable function of the linearized fitness, $g(u, 0, w)$, which we will now refer to as g^*. We will examine a one parameter family of movement strategies, $\{M_\lambda(g^*)\}_{\lambda\geq 0}$ such that

$$M_0(g^*) = d_2 \text{ for all real } g^*, \tag{4.49}$$

$$M_\lambda(0) = d_2 \text{ for all } \lambda \geq 0, \tag{4.50}$$

$$d_2 \geq M_\lambda(g^*) \geq d \text{ for all } \lambda \text{ and } g^* > 0 \text{ and}, \tag{4.51}$$

$$M_\lambda(g^*) \geq d_2 \text{ and } \lim_{\lambda\to\infty} M_\lambda(g^*) = \infty \text{ for all } g^* < 0. \tag{4.52}$$

Condition (4.49) says that $\lambda = 0$ corresponds to random diffusion with diffusion coefficient d_2. Condition (4.50) says that the motility in regions of zero linearized fitness is d_2 regardless of λ. (4.51) describes the motility in areas of positive linearized fitness. In these areas, v may have lower motility, but may never have values that drop below the level d. When the linearized fitness is negative, λ increasing toward infinity will result in ever higher motility for v. In this sense, higher values of λ make the IGPrey more sensitive to "bad" areas, i.e. areas where the linearized fitness is negative. With higher values of λ, the IGPrey will experience an increased diffusive pressure in these "bad" areas. We will examine what happens to σ_1 and σ_4 as λ increases from 0.

For each $x \in \Omega$, define $G(x) \subset \mathbb{R}$ by

$$G(x) = \{r \in \mathbb{R} \mid g^*(u(x), w(x)) = r \text{ for some } (u, 0, w) \in \mathcal{A}_4\}. \tag{4.53}$$

We will now prove that $G(x)$ is a compact set in $\mathbb{R}$ for every $x \in \overline{\Omega}$. Fix $x \in \overline{\Omega}$ and let $\{r_n\} \subseteq G(x)$ and $\{(u_n, w_n)\} \subseteq \mathcal{A}_4$ such that $g^*(u_n(x), w_n(x)) = r_n$ for all n. We know that $\mathcal{A}_4$ is compact in $[C^1(\overline{\Omega})]^2$, so there exists a subsequence, $\{(u_{n_k}, w_{n_k})\}$, that converges in $[C^1(\overline{\Omega})]^2$. This implies that the subsequence $\{r_{n_k}\}$ converges in $\mathbb{R}$ to the limit of $\{g^*(u_{n_k}(x), w_{n_k}(x))\}$, hence $\{r_n\}$ is compact. It is also important to note that $G(x)$ does not depend on the movement strategy since $\mathcal{A}_4$ arises from the $u - w$ subsystem, which is independent of M. Thus $G(x)$ is not influenced by λ in any way. Define

$$\zeta_\lambda(x) = \min_{r \in G(x)} \frac{r}{M_\lambda(r)} \,. \tag{4.54}$$

Note that for each $x \in \Omega$ the minimum in the definition of ζ_λ is attained because $G(x)$ is compact.

Lemma 4.3.1. *The function $\zeta_\lambda(x)$ defined by* (4.54) *is continuous on $\overline{\Omega}$.*

Proof. Fix $x_0 \in \overline{\Omega}$ and suppose ζ_λ is not continuous at x_0. Then there is an $\varepsilon > 0$ and a sequence $\{x_n\}_{n=1}^{\infty} \subseteq \overline{\Omega}$ such that $x_n \to x_0$ and $|\zeta_\lambda(x_n) - \zeta_\lambda(x_0)| > \varepsilon$ for all n. Let $\{(u_n, w_n)\} \subseteq \mathcal{A}_4$ be such that

$$\zeta_\lambda(x_n) = \frac{g^*(u_n(x_n), w_n(x_n))}{M_\lambda(g^*(u_n(x_n), w_n(x_n)))} \quad \text{for } n = 0, 1, \dots \,. \tag{4.55}$$

Since $\mathcal{A}_4$ is compact there is a subsequence, $\{(u_{n_k}, w_{n_k})\}$, that converges (in $[C^1(\overline{\Omega})]^2$) to some function pair $(\hat{u}, \hat{w})$ in $\mathcal{A}_4$. Choose K large enough so that

$$\left| \frac{g^*(u_0(x_{n_k}), w_0(x_{n_k}))}{M_\lambda(g^*(u_0(x_{n_k}), w_0(x_{n_k})))} - \zeta_\lambda(x_0) \right| < \varepsilon \text{ for all } k \geq K \,, \tag{4.56}$$

$$\left| \frac{g^*(\hat{u}(x_{n_k}), \hat{w}(x_{n_k}))}{M_\lambda(g^*(\hat{u}(x_{n_k}), \hat{w}(x_{n_k})))} - \frac{g^*(\hat{u}(x_0), \hat{w}(x_0))}{M_\lambda(g^*(\hat{u}(x_0), \hat{w}(x_0)))} \right| < \frac{\varepsilon}{2} \text{ for all } k \geq K \,, \tag{4.57}$$

and

$$\left| \frac{g^*(\hat{u}(x_{n_k}), \hat{w}(x_{n_k}))}{M_\lambda(g^*(\hat{u}(x_{n_k}), \hat{w}(x_{n_k})))} - \zeta_\lambda(x_{n_k}) \right| < \frac{\varepsilon}{2} \text{ for all } k \geq K \,. \tag{4.58}$$

Fix $k \geq K$. Suppose $\zeta_\lambda(x_{n_k}) > \zeta_\lambda(x_0) + \varepsilon$. Then (4.56) implies that

$$\frac{g^*(u_0(x_{n_k}), w_0(x_{n_k}))}{M_\lambda(g^*(u_0(x_{n_k}), w_0(x_{n_k})))} < \zeta_\lambda(x_{n_k}) \tag{4.59}$$

which contradicts the minimality of $\zeta_\lambda(x_{n_k})$ for $r \in G(x_{n_k})$. Now, suppose $\zeta_\lambda(x_0) > \zeta_\lambda(x_{n_k}) + \varepsilon$. Then (4.57) and (4.58) imply that

$$\frac{g^*(\hat{u}(x_0), \hat{w}(x_0))}{M_\lambda(g^*(\hat{u}(x_0), \hat{w}(x_0)))} < \zeta_\lambda(x_0) \tag{4.60}$$

which contradicts the minimality of $\zeta_\lambda(x_0)$ for $r \in G(x_0)$.

Therefore, we must have that $\zeta_\lambda(x)$ is continuous on $\overline{\Omega}$. $\square$

If $\int_\Omega \zeta_\lambda(x)\, dx > 0$ we can use $\tilde{b}(x) = \zeta_\lambda(x)$. Then $\tilde{b} \leq \frac{g^*(u,w)}{M_\lambda(g^*(u,w))}$ for all $(u, 0, w) \in \mathcal{A}_4$ and $\int_\Omega \tilde{b}(x)\, dx > 0$, so the principal eigenvalue σ_4 of (4.41) will be positive and v will be able to invade the boundary attractor $\mathcal{A}_4$ if the movement strategy M_λ is adopted. So, we will examine conditions that guarantee $\int_\Omega \zeta_\lambda\, dx > 0$.

Lemma 4.3.2. *Let $G(x)$ be given by* (4.53) *and define $\Omega_1 = \{x \in \Omega \mid \min G(x) > 0\}$. If* (2.5) *is such that Ω_1 has positive measure and $\{M_\lambda(g^*)\}_{\lambda \geq 0}$ satisfies* (4.49) - (4.52), *then there exists a Λ such that $\int_\Omega \zeta_\lambda\, dx > 0$ for all $\lambda \geq \Lambda$.*

Proof. Define $\Omega_2 = \Omega \setminus \Omega_1$. Because $\mathcal{A}_4$ is bounded in $C(\overline{\Omega})$ and g^* is continuous, there exists a $K > 0$ such that $g^*(u, w) \geq -K$ for all $(u, 0, w) \in \mathcal{A}_4$, so $\Omega_2 = \{x \in \Omega \mid -K \leq \min G(x) \leq 0\}$. Note that $\zeta_\lambda(x) > 0$ on Ω_1 and $\zeta_\lambda(x) \leq 0$ on Ω_2. Break $\int_\Omega \zeta_\lambda\, dx$ into two parts via

$$\int_\Omega \zeta_\lambda\, dx = \int_{\Omega_1} \min_{r \in G(x)} \frac{r}{M_\lambda(r)}\, dx + \int_{\Omega_2} \min_{r \in G(x)} \frac{r}{M_\lambda(r)}\, dx \tag{4.61}$$

and analyze each piece separately. Begin with the Ω_1 integral. Since $|\Omega_1| > 0$ there exists a positive integer, k, such that $|\Omega_{1,k}| > 0$ where $\Omega_{1,k} = \{x \in \Omega_1 \mid \min G(x) > \frac{1}{k}\}$. By (4.51) we have

$$\int_{\Omega_1} \min_{r \in G(x)} \frac{r}{M_\lambda(r)}\, dx \geq \frac{1}{d_2} \int_{\Omega_1} \min_{r \in G(x)} r\, dx \geq \frac{|\Omega_{1,k}|}{d_2 k} = C > 0\,. \tag{4.62}$$

Now, fix any $x \in \Omega_2$. For any $\delta \in (0, K)$ we have

$$0 \geq \min_{r \in G(x)} \frac{r}{M_\lambda(r)} \geq \min_{r \in [-K,-\delta]} \frac{r}{M_\lambda(r)} + \min_{r \in (-\delta,0]} \frac{r}{M_\lambda(r)} \tag{4.63}$$

because the minimizing choice of $r \in G(x)$ must fall in either the interval $[-K, -\delta]$ or $(-\delta, 0]$ and both terms are nonpositive. So

$$\int_{\Omega_2} \min_{r \in G(x)} \frac{r}{M_\lambda(r)}\, dx \geq \int_{\Omega_2} \min_{r \in [-K,-\delta]} \frac{r}{M_\lambda(r)}\, dx + \int_{\Omega_2} \min_{r \in (-\delta,0]} \frac{r}{M_\lambda(r)}\, dx\,. \tag{4.64}$$

Now, choose δ such that $\frac{\delta|\Omega|}{d_2} < \frac{C}{2}$ and then choose Λ such that $\frac{K}{M_\lambda(r)} < \frac{C}{2|\Omega|}$ for all $\lambda \geq \Lambda$ and $r \in [-K, -\delta]$. Such a Λ exists because $\lim_{\lambda \to \infty} M_\lambda(r) = \infty$ for each $r \in [-K, -\delta]$ and this interval is compact. Consequently, we will have

$$\int_{\Omega_2} \min_{r \in (-\delta,0]} \frac{r}{M_\lambda(r)}\, dx \geq \frac{1}{d_2} \int_{\Omega_2} \min_{r \in (-\delta,0]} r\, dx \geq \frac{-\delta|\Omega_2|}{d_2} > \frac{-\delta|\Omega|}{d_2} > -\frac{C}{2} \tag{4.65}$$

and, for $\lambda \geq \Lambda$

$$\int_{\Omega_2} \min_{r \in [-K,-\delta]} \frac{r}{M_\lambda(r)}\, dx \geq \int_{\Omega_2} \min_{r \in [-K,-\delta]} \frac{-K}{M_\lambda(r)}\, dx > \int_{\Omega_2} -\frac{C}{2|\Omega|}\, dx > -\frac{C}{2}\,. \tag{4.66}$$

Combining (4.61), (4.62) and (4.64) - (4.66) we can conclude that $\int_\Omega \zeta_\lambda \, dx > 0$ for all $\lambda \geq \Lambda$. $\square$

As an immediate consequence of Lemma 4.3.2 we can state one of the main results of this thesis:

Theorem 4.3.1. *Suppose* $\{M_\lambda(g^*)\}_{\lambda \geq 0}$ *satisfies* (4.50) - (4.52). *If there exists a point* $x_0 \in \Omega$ *with* $g^*(u(x_0), w(x_0)) > 0$ *for all* $(u, w) \in \mathcal{A}_4$ *and* $M(u, w) = M_\lambda(g^*(u, w))$ *for sufficiently large* λ, *then* v *will be uniformly persistent in* (2.5) *for all initial conditions,* (u_0, v_0, w_0), *with* u_0 *and* v_0 *not identically zero.*

Proof. The assumption that $g^*(u(x_0), w(x_0)) > 0$ for all $(u, 0, w) \in \mathcal{A}_4$ is equivalent to saying that $\zeta_\lambda(x_0) > 0$. Since $\zeta_\lambda(x)$ is a continuous function, we have that Ω_1 (as defined in Lemma 4.3.2) has positive measure, which means there is a Λ such that $\int_\Omega \zeta_\lambda(x) \, dx > 0$ for all $\lambda \geq \Lambda$. Taking $\tilde{b}(x) = \zeta_\lambda(x)$ gives $\sigma_4 > 0$ in Lemma 4.2.3.

Note that $w > 0$ and $u < u^*$ for all $(u, 0, w) \in \mathcal{A}_4$ so $g^*(u^*, 0) > g^*(u, w)$ for all $(u, 0, w) \in \mathcal{A}_4$, hence $\frac{g(u^*,0)}{M_\lambda(g^*(u^*,0))} > \zeta_\lambda(x)$ so $\int_\Omega \frac{g(u^*,0)}{M_\lambda(g^*(u^*,0))} \, dx > 0$ and we can conclude from (4.46) that $\sigma_1 > 0$.

Since $\sigma_1, \sigma_4 > 0$ we have $W^s(\{(0,0,0)\}) \cap (X \setminus S) = \emptyset$, $W^S(\{(u^*,0,0)\}) \cap (X \setminus S) = \emptyset$ and $W^s(\mathcal{A}_4) \cap (X \setminus S) = \emptyset$. If we knew that $W^s(\mathcal{A}_3) \cap (X \setminus S) = \emptyset$ we could conclude that (2.5) was permanent. However, even if $W^s(\mathcal{A}_3) \cap (X \setminus S) \neq \emptyset$ we can still conclude that v persists for all initial conditions with u_0 and v_0 positive somewhere in Ω.

If $w_0 \equiv 0$, then $\pi((u_0, v_0, 0), t) \to \mathcal{A}_3$, which is uniformly bounded away from the plane $\{v \equiv 0\}$, so v will be uniformly persistent.

If $w_0 > 0$ somewhere in Ω, then we must deconstruct the proof of the acyclicity theorem, Theorem 4.1 of [18]. This proof reveals that if v is not uniformly persistent then one of the boundary attractors, $\mathcal{A}_i$, in the plane $\{v \equiv 0\}$ ($i = 1, 2$ or 4) would need to satisfy either $(H1)$ or $(H2)$ stated below:

$(H1)$ $W^s(\mathcal{A}_i) \cap (X \setminus S) \neq \emptyset$

$(H2)$ There exists a $j \in \{1, 2, 3, 4\}$, $j \neq i$ such that $\mathcal{A}_j$ is chained to $\mathcal{A}_i$ by an orbit in S *and* $\mathcal{A}_j$ satisfies either $(H1)$ or $(H2)$ as well.

We know that $W^s(\mathcal{A}_1) \cap (X \setminus S) = \emptyset$, $W^S(\mathcal{A}_2) \cap (X \setminus S) = \emptyset$ and $W^s(\mathcal{A}_4) \cap (X \setminus S) = \emptyset$, so anytime one of $\mathcal{A}_1, \mathcal{A}_2$ or $\mathcal{A}_4$ is required to satisfy either $(H1)$ or $(H2)$ it must satisfy $(H2)$. We know that $\mathcal{A}_3$ is not chained to any other boundary attractor because $\mathcal{A}_3$ attracts all boundary points in a neighborhood in S of itself, hence $W^u(\mathcal{A}_3) = \mathcal{A}_3$. Therefore, we can never have $j = 3$ in $(H2)$. So, we start with an $\mathcal{A}_i$, $i = 1, 2$ or 4, that satisfies $(H2)$. This gives an $\mathcal{A}_j$, $j = 1, 2$ or 4, $j \neq i$, which must also satisfy $(H2)$. This goes on *ad infinitum* creating an infinite chain comprised solely of $\mathcal{A}_1$, $\mathcal{A}_2$ and $\mathcal{A}_4$, which implies there is a subset of $\{\mathcal{A}_1, \mathcal{A}_2, \mathcal{A}_4\}$ that forms a cycle, a contradiction.

Therefore, we have that v is uniformly persistent in (2.5) if there is a $x_0 \in \Omega$ with $g^*(u(x_0), w(x_0)) > 0$ for all $(u, 0, w) \in \mathcal{A}_4$ and we take $M(u, w) = M_\lambda(g^*(u, w))$ for $\lambda \geq \Lambda$. $\square$

Ecologically speaking, Theorem 4.3.1 states that if there is a region in the habitat such that the linearized fitness of the IGPrey is positive for all (u, w) in the attractor of the $u - w$ subsystem, then the IGPrey adopting a movement strategy of sufficiently high motility in areas that have negative linearized fitness can allow the IGPrey to invade and persist. Of course, an arbitrarily large motility may not be feasible for any given species of IGPrey.

The use of linearized fitness, $g^*(u,w)$, instead of actual fitness, $g(u,v,w)$, is not based on an ecological consideration, but rather a mathematical necessity. The permanence analysis would be very similar if we were using g instead of g^* because they are equivalent when $v = 0$ and the invasion analysis for v deals with a neighborhood of this region.

The main mathematical difficulty actually comes when establishing global existence and is due to the saturating functional response of the IGPredator consuming the IGPrey. Suppose we were to use $M(u,v,w) = M(g(u,v,w))$, then

$$\Delta[M(u,v,w)v] = \nabla \cdot [(M + vM_v)\nabla v + vM_u \nabla u + vM_w \nabla w] \tag{4.67}$$

and we cannot be sure that $M + vM_v = M + vM'(g)\frac{\partial g}{\partial v}$ is bounded below away from zero, which is crucial to proving global existence. Note that $M'(g) \leq 0$ so the problem arises when it is possible to have $\frac{\partial g}{\partial v} > 0$, which would allow $M + vM_v$ to be negative for certain positive values of v. This is the case with our choice of g because of the $-\frac{a_3 w}{1+a_3 h_3 v}$ term in g.

4.4 Examples Of Dispersal Strategies

We will now give three examples of movement strategy families that satisfy (4.49) - (4.52): exponential, piecewise polynomial and exponentially smoothed. Our first example uses a family of negative exponential functions

$$M_\lambda(g^*) = (d_2 - d)e^{-\lambda g^*} + d\,. \tag{4.68}$$

Clearly (4.68) satisfies all of the required conditions on $\{M_\lambda\}$.

Suppose we would like a movement strategy that assumes a constant motility throughout regions where $g^* \geq 0$, but that increases linearly with respect to $|g^*|$ when $g^* < 0$. Such a family of strategies would have the form

$$M_\lambda(g^*) = \begin{cases} d_2 & \text{for } g^* \geq 0\,, \\ -\lambda g^* + d_2 & \text{for } g^* < 0\,. \end{cases} \tag{4.69}$$

This has discontinuous first and second derivatives at $g^* = 0$. However, we could connect these linear functions over an interval near $g^* = 0$ using a function that matches the first and second derivatives of the linear functions on each end of the matching region. Such a family is given below using $(-1/\lambda, 0)$ as the matching region and a degree 5 polynomial (6 degrees of freedom are needed, 3 for each connecting point) to connect the linear functions

$$M_\lambda = \begin{cases} d_2 & \text{for } g^* \geq 0\,, \\ -3(\lambda g^*)^5 - 8(\lambda g^*)^4 - 6(\lambda g^*)^3 + d_2 & \text{for } \frac{-1}{\lambda} < g^* < 0\,, \\ -\lambda g^* + d_2 & \text{for } g^* \leq \frac{-1}{\lambda}\,. \end{cases} \tag{4.70}$$

We can verify that $M_\lambda(g^*)$ is $C^2(\mathbb{R})$ by direct calculation. At $g^* = 0$ we have $\lim_{g^* \to 0^-} M_\lambda'(g^*) = \lim_{g^* \to 0^-} M_\lambda''(g^*) = 0$ and $\lim_{g^* \to 0^-} M_\lambda(g^*) = d_2$ which matches the constant function defining M_λ to the right of $g^* = 0$. At $g^* = -1/\lambda$ we have

$$\lim_{g^* \to (-1/\lambda)^+} M_\lambda(g^*) = -3(-1)^5 - 8(-1)^4 - 6(-1)^3 + d_2 = 1 + d_2\ , \tag{4.71}$$

$$\lim_{g^* \to (-1/\lambda)^+} M'_\lambda(g^*) = -15\lambda(-1)^4 - 32\lambda(-1)^3 - 18\lambda(-1)^2 = -\lambda \tag{4.72}$$

and

$$\lim_{g^* \to (-1/\lambda)^+} M''_\lambda(g^*) = 60\lambda^2(-1)^3 - 96\lambda^2(-1)^2 + 36\lambda^2\lambda(-1) = 0\ . \tag{4.73}$$

All of these match the corresponding values as we approach $g^* = -1/\lambda$ from the left. In addition, (4.70) clearly satisfies conditions (4.49) - (4.52).

Another approach to approximating a piecewise defined function like (4.69) is to multiply by a smoothing function. Suppose we have $M_\lambda(g^*) = f_\lambda(g^*) + d_2$ for $g^* < 0$ where $f_\lambda \in C^\infty((-\infty, 0))$ and $\lim_{g^* \to 0^-} f_\lambda(g^*) = 0$ and $M_\lambda(g^*) = d_2$ for $g^* \geq 0$, but M_λ is not C^2 at $g^* = 0$. We can approximate this family of movement strategies by multiplying f_λ by a function of the form e^{k/g^*}. We will show below that as long as f_λ does not have derivatives that blow up in particularly nasty ways at $g^* = 0$, the resulting product will have all of its derivatives equal to 0 at $g^* = 0$ (in particular, bounded derivatives would certainly qualify as would any derivatives that blow-up at 0 like g^{*-N} for some $N > 0$). We will then have the following family in $C^\infty(\mathbb{R})$:

$$M_\lambda(g^*) = \begin{cases} d_2 & \text{for } g^* \geq 0\,, \\ f_\lambda(g^*)e^{k/g^*} + d_2 & \text{for } g^* < 0\ . \end{cases} \tag{4.74}$$

To see that (4.74) defines a function that is infinitely smooth at 0, consider the nth derivative of M_λ as $g^* \to 0^-$

$$\frac{d^n}{dg^{*n}} M_\lambda(g^*) = \sum_{i=0}^{n} C_i f_\lambda^{(i)}(g^*) \frac{d^{n-i}}{dg^{*n-i}}(e^{k/g^*}) = \sum_{i=0}^{n} f_\lambda^{(i)}(g^*) P_i(1/g^*) e^{k/g^*}\ , \tag{4.75}$$

where the C_i's are constant and the $P_i(1/g^*)$'s are polynomials in $1/g^*$. We can conclude from (4.75) that a sufficient condition for $M_\lambda(g^*) \in C^\infty(\mathbb{R})$ is

$$\lim_{g^* \to 0^-} \frac{f_\lambda^{(n)}(g^*)}{{g^*}^N e^{-k/g^*}} = 0 \ \text{ for all } n \geq 1,\ N \geq 1\,. \tag{4.76}$$

Note that the denominator in (4.76) is increasing to ∞ at an exponential rate. This allows for a very wide class of f's to be used. Note that if $f_\lambda(g^*) + d_2$ satisfies (4.49)-(4.52) for $g^* \leq 0$ then so will the function defined by (4.74).

We will see in later chapters that an additional condition, namely

$$\frac{d}{dg^*}\left(\frac{g^*}{M_\lambda(g^*)}\right) > 0 \tag{4.77}$$

becomes important when determining the local stability of certain bifurcating branches of solutions (see Section 5.5). We also make use of this inequality when making a practical persistence type of argument in Chapter 6. Note that (4.68) does not satisfy this condition; and, (4.70) fails to do so if $d_2 < 6^5/5^4 \approx .415$. However, depending on f_λ and the choice of k, (4.74) can satisfy this condition (we will see a specific example in Chapter 6).

Chapter 5

Bifurcation From The Resource Only Equilibrium

5.1 Bifurcation in the $u-w$ Subsystem

Consider the equilibrium problem for the $u-w$ subsystem

$$\begin{gathered} d_1\Delta u + u\left(r(x) - \omega_1 u - \frac{a_2 w}{1+h_2 a_2 u}\right) = 0 \\ d_3\Delta w + w\left(\frac{e_2 a_2 u}{1+h_2 a_2 u} - \mu_2 - \omega_3 w\right) = 0 \ \text{ in } \Omega\,, \\ \frac{\partial u}{\partial n} = \frac{\partial w}{\partial n} = 0 \ \text{ on } \partial\Omega\,. \end{gathered} \tag{5.1}$$

Let $(u^*, 0)$ denote the unique semi-trivial equilibrium to (5.1). For e_2 sufficiently small, (5.1) cannot have any coexistence equilibrium states because the per capita growth rate in the w component equation is negative on all of Ω when

$$e_2 < \mu_2 h_2\ . \tag{5.2}$$

If this were the case, then integrating the w-component equation and using the no-flux boundary condition would yield

$$\int_\Omega w\left(\frac{e_2a_2u}{1+h_2a_2u}-\mu_2-\omega_3w\right)dx=0\,, \tag{5.3}$$

but if $w>0$ and $e_2<\mu_2h_2$ then the integral above is negative, which would be a contradiction. Therefore, if $e_2<\mu_2h_2$ the only nonnegative solution to the w-component equation is $w\equiv 0$.

We will examine (5.1) using e_2 as a bifurcation parameter to see when and how coexistence states bifurcate from the semi-trivial solution, $(u^*,0)$. Write (5.1) as

$$F(e_2,(u,w))=\vec{0} \tag{5.4}$$

where $F:\mathbb{R}\times\left[C_N^{2,\alpha}(\overline{\Omega})\right]^2\to\left[C^\alpha(\overline{\Omega})\right]^2$ for $\alpha\in(0,1)$ such that $r(x)\in C^\alpha(\overline{\Omega})$. Note that $F(e_2,(u^*,0))=\vec{0}$ for all e_2. The Crandall-Rabinowitz bifurcation theorem ([12] Theorem 1.7) states that if e_2^* is such that $F_{(u,w)}(e_2^*,(u^*,0))$ is a Fredholm operator with

$$\dim N(F_{(u,w)}(e_2^*,(u^*,0)))=\operatorname{codim} R(F_{(u,w)}(e_2^*,(u^*,0)))=1\ ; \tag{5.5}$$

and, if $N(F_{(u,w)}(e_2^*,(u^*,0)))=\langle\vec{y_0}\rangle$ with

$$F_{e_2,(u,w)}(e_2^*,(u^*,0))\vec{y_0}\notin R(F_{(u,w)}(e_2^*,(u^*,0)))\ , \tag{5.6}$$

then e_2^* is a bifurcation point for $(u^*,0)$. This means that there are a $\delta>0$ and continuously differentiable functions $e_2:(-\delta,\delta)\to\mathbb{R}$ and $(\hat{u},\hat{w}):(-\delta,\delta)\to\left[C_N^{2,\alpha}(\overline{\Omega})\right]^2$ with $e_2(0)=e_2^*$ and $(\hat{u}(0),\hat{w}(0))=(0,0)$ such that if $e_2=e_2(s)$ and

$(u, w) = (u^*, 0) + s\vec{y_0} + s(\hat{u}(s), \hat{w}(s))$ then $F(e_2(s), (u^*, 0) + s\vec{y_0} + s(\hat{u}(s), \hat{w}(s))) = 0$ for $s \in (-\delta, \delta)$. Furthermore, the entire solution set for $F(e_2, (u, w)) = 0$ in a small neighborhood of $(e_2^*, (u^*, 0))$ in $\mathbb{R} \times \left[C_N^{2,\alpha}(\overline{\Omega})\right]^2$ is the line $(e_2, (u^*, 0))$ and the curve $(e_2(s), (u^*, 0) + s\vec{y_0} + s(\hat{u}(s), \hat{w}(s))$ [12].

First, we will examine $N(F_{(u,w)}(e_2, (u^*, 0)))$. We have

$$F_{(u,w)}(e_2, (u^*, 0)) \begin{pmatrix} \psi_1 \\ \psi_2 \end{pmatrix} = \begin{pmatrix} d_1 \Delta\psi_1 + r(x)\psi_1 - 2\omega_1 u^* \psi_1 - \frac{a_2 u^*}{1 + a_2 h_2 u^*}\psi_2 \\ -d_3 \Delta \psi_2 + \mu_2 \psi_2 - \frac{e_2 a_2 u^*}{1 + a_2 h_2 u^*}\psi_2 \end{pmatrix} \tag{5.7}$$

Writing $F_{(u,w)}(e_2, (u^*, 0))\vec{\psi} = 0$ in system form and rearranging yields

$$\begin{aligned} d_1 \Delta\psi_1 + r(x)\psi_1 - 2\omega_1 u^* \psi_1 &= \frac{a_2 u^*}{1 + a_2 h_2 u^*}\psi_2 \\ -d_3 \Delta \psi_2 + \mu_2 \psi_2 &= \frac{e_2 a_2 u^*}{1 + a_2 h_2 u^*}\psi_2 \quad \text{in } \Omega, \\ \frac{\partial \psi_1}{\partial n} = \frac{\partial \psi_2}{\partial n} &= 0 \quad \text{on } \partial\Omega\,. \end{aligned} \tag{5.8}$$

Let

$$L_1 u = -d_3 \Delta u + \mu_2 u \;\; \text{and} \;\; m(x) = \frac{a_2 u^*}{1 + a_2 h_2 u^*}\;. \tag{5.9}$$

Then existence/uniqueness theory for elliptic equations implies that L_1^{-1} exists and $L_1^{-1} : C^\alpha(\overline{\Omega}) \to C^{2,\alpha}(\overline{\Omega})$ is a bounded linear operator ([16] Theorem 6.31). Additionally, $C^{2,\alpha}(\overline{\Omega})$ embeds compactly into $C^\alpha(\overline{\Omega})$, so $L_1^{-1} : C^\alpha(\overline{\Omega}) \to C^\alpha(\overline{\Omega})$ is compact. In fact, the strong maximum principle guarantees that L_1^{-1} maps nonnegative functions that are not identically zero into functions that are positive on all of $\overline{\Omega}$ which means that L_1^{-1} is a strongly positive compact linear operator on $C^\alpha(\overline{\Omega})$, and so is $L_1^{-1} \circ m(x)$. The Krein-Rutman Theorem (see [1] Theorem 3.2 for example) implies that there is a unique maximal eigenvalue for $L_1^{-1} \circ m(x)$ that is real and simple with positive eigenfunction. The ψ_2 equation in (5.8) can be rewritten as

$$\frac{1}{e_2}\psi_2 = L_1^{-1}(m(x)\psi_2) \;\text{ in } \Omega \;\text{ and }\; \frac{\partial \psi_2}{\partial n} = 0 \text{ on } \partial\Omega \,. \tag{5.10}$$

The smallest value of e_2 that can yield a solution for (5.10) is the reciprocal of the maximal eigenvalue of $L^{-1} \circ m(x)$, so it is simple and the corresponding solution, ψ_2, will be positive on Ω. This is the smallest possible value of e_2 that could yield a bifurcation. Call this value e_2^* and fix $e_2 = e_2^*$ and let ψ_2 be the positive eigenfunction corresponding to e_2^*.

Now, examine the first equation in (5.8). Let σ be the principal eigenvalue of

$$d_1\Delta z + [r(x) - 2\omega_1 u^*]z = \sigma z \;\text{ in } \Omega \,,\; \frac{\partial z}{\partial n} = 0 \text{ on } \partial\Omega \,. \tag{5.11}$$

Then, multiply the resource only equilibrium equation (4.18) by z, multiply (5.11) by u^* integrate over Ω and subtract to get

$$\int_\Omega z[d_1\Delta u^* + (r(x) - \omega_1 u^*)u^*] - u^*[d_1\Delta z + (r(x) - 2\omega_1 u^*)z]\, dx = -\sigma \int_\Omega u^* z\, dx \,. \tag{5.12}$$

The Laplacian terms drop out after integrating by parts twice, leaving

$$\int_\Omega \omega_1 (u^*)^2 z\, dx = -\sigma \int_\Omega u^* z\, dx \,. \tag{5.13}$$

Hence $\sigma < 0$. This means that the operator $L_2 u = d_1\Delta u + (r(x) - 2\omega_1 u^*)u$ is invertible.

So,

$$N(F_{(u,w)}(e_2^*,(u^*,0))) = \left\langle \begin{pmatrix} L_2^{-1}\left(\frac{a_2u^*}{1+a_2h_2u^*}\psi_2\right) \\ \psi_2 \end{pmatrix} \right\rangle \tag{5.14}$$

Computing $R(F_{(u,w)}(e_2^*,(u^*,0)))$ is somewhat more difficult. We will resort to using Fredholm theory and will show that

$$R(F_{(u,w)}(e_2^*,(u^*,0))) = C^\alpha(\overline{\Omega}) \times \left\{ f \in C^\alpha(\overline{\Omega}) \mid \int_\Omega f\,\psi_2\,dx = 0 \right\}.$$

We will examine for which $\vec{f} = \begin{pmatrix} f_1 \\ f_2 \end{pmatrix}$ the equation

$$\begin{pmatrix} d_1\Delta\psi_1 + r(x)\psi_1 - 2\omega_1 u^*\psi_1 - \frac{a_2u^*}{1+a_2h_2u^*}\psi_2 \\ -d_3\Delta\psi_2 + \mu_2\psi_2 - \frac{e_2a_2u^*}{1+a_2h_2u^*}\psi_2 \end{pmatrix} = \begin{pmatrix} f_1 \\ f_2 \end{pmatrix} \tag{5.15}$$

is solvable. The following argument is adapted from [15]. Let

$$Lu = -d_3\Delta u + \mu_2 u - e_2^* m(x)u\ . \tag{5.16}$$

For some $\rho > 0$ such that $\rho + \mu_2 - e_2^* m(x) > 0$ on $\overline{\Omega}$ define

$$L_\rho w = -d_3\Delta w + \mu_2 w - e_2^* m(x)w + \rho w \tag{5.17}$$

and, for u, $v \in H^1(\Omega)$, define

$$B_\rho[u\,,\,v] = \int_\Omega d_3\nabla u\cdot\nabla v + [\rho + \mu_2 - e_2^* m(x)]\,uv\,dx\ . \tag{5.18}$$

Then $B_\rho[u\,,\,v]$ is an inner product on $H^1(\Omega)$. Let $\tilde{f} \in L^2(\Omega)$ and define $l_{\tilde{f}}(v) = \langle \tilde{f}\,,\,v\rangle_{L^2(\Omega)}$ for $v \in H^1(\Omega)$. Then $l_{\tilde{f}}$ is a bounded linear functional on $H^1(\Omega)$. The Riesz Representation Theorem implies there exists a unique $u \in H^1(\Omega)$ such that $B_\rho[u\,,\,v] = \langle \tilde{f}\,,\,v\rangle$ for all $v \in H^1(\Omega)$. Note that this u is a weak solution of $L_\rho u = \tilde{f}$, so we can denote u by $L_\rho^{-1}\tilde{f}$. Now, consider the equation

$$Lu = f_2\ . \tag{5.19}$$

This is equivalent to

$$L_\rho u = \rho u + f_2\ . \tag{5.20}$$

So, u is a weak solution of $Lu = f_2$ if and only if $B_\rho[u\,,\,v] = \langle \rho u + f_2\,,\,v\rangle$ for all $v \in H^1(\Omega)$. This is the case if and only if

$$\begin{aligned} u &= L_\rho^{-1}(\rho u + f_2) \\ &= \rho L_\rho^{-1}u + L_\rho^{-1}f_2 \\ &= Ku + h \end{aligned} \tag{5.21}$$

where $Ku = \rho L_\rho^{-1}u$ and $h = L_\rho^{-1}f_2$. This K is a bounded operator from $L^2(\Omega)$ to $H^1(\Omega)$ and hence is a compact operator when viewed from $L^2(\Omega)$ to $L^2(\Omega)$. To see this, let $g \in L^2(\Omega)$. From (5.18) there exists a $\beta > 0$ such that

$$\begin{aligned}\beta\|Kg\|^2_{H^1(\Omega)} &\leq B_\rho[Kg\,,\,Kg] \\ &= \rho B_\rho[L_\rho^{-1}g\,,\,Kg] \\ &= \rho\langle g\,,\,Kg\rangle \\ &\leq \rho\|g\|_{L^2(\Omega)}\|Kg\|_{L^2(\Omega)} \\ &\leq \rho\|g\|_{L^2(\Omega)}\|Kg\|_{H^1(\Omega)}\ . \end{aligned} \tag{5.22}$$

So

$$\|Kg\|_{H^1(\Omega)} \leq \frac{\rho}{\beta}\|g\|_{L^2(\Omega)}\ . \tag{5.23}$$

Because K is compact for $L^2(\Omega) \to L^2(\Omega)$, $(I - K)$ is Fredholm index 0 as a map from $L^2(\Omega) \to L^2(\Omega)$. Recall that $Lu = 0$ if and only if $u \in \langle\psi_2\rangle$. But $Lu = 0$ if and only if $(I - K)u = 0$, hence $N(I - K) = \langle\psi_2\rangle$ as well. The Fredholm alternative implies that for any $h \in L^2(\Omega)$ the equation

$$(I - K)u = h \tag{5.24}$$

has a solution if and only if $\langle h\,,\,v\rangle = 0$ for all $v \in N(I - K^*)$ (where K^* denotes the adjoint of K). We will now show that $N(I - K^*) = \langle\psi_2\rangle$. First, we will show that $K = K^*$ as an operator from $L^2(\Omega) \to L^2(\Omega)$. Let $g, h \in C^\alpha(\overline{\Omega})$ be given. Define u, $v \in C^{2,\alpha}(\overline{\Omega})$ by

$$u = \frac{1}{\rho}Kg \;\text{ and }\; v = \frac{1}{\rho}Kh\ , \tag{5.25}$$

which implies

$$g = L_\rho u \;\text{ and }\; h = L_\rho v\ . \tag{5.26}$$

The operator L_ρ is formally self-adjoint, so

$$\langle L_\rho u \,,\, v\rangle = \langle u \,,\, L_\rho v\rangle \ . \tag{5.27}$$

Use (5.25) and (5.26) to rewrite (5.27) as

$$\langle g \,,\, \frac{1}{\rho}Kh\rangle = \langle \frac{1}{\rho}Kg \,,\, h\rangle \tag{5.28}$$

$$\Longrightarrow\ 0 = \langle (K-K^*)g \,,\, h\rangle \ \text{ for all } g,h \in C^\alpha(\overline{\Omega}) \ . \tag{5.29}$$

Since $C^\alpha(\overline{\Omega})$ is dense in $L^2(\Omega)$ (5.29) must hold for any $h \in L^2(\Omega)$ as well. Hence $Kg = K^*g$ for all $g \in C^\alpha(\overline{\Omega})$ and we can appeal to density again to conclude $K = K^*$ as an operator for $L^2(\Omega) \to L^2(\Omega)$. Therefore, $N(I-K^*) = N(I-K) = \langle \psi_2\rangle$. So we have that $Lu = f_2$ is solvable if and only if $\langle h \,,\, \psi_2\rangle = 0$ where $h = L_\rho^{-1} f_2 = \frac{1}{\rho}Kf_2$. So, f_2 in the range of L if and only if

$$\begin{aligned} 0 &= \frac{1}{\rho}\langle Kf_2 \,,\, \psi_2\rangle \\ &= \frac{1}{\rho}\langle f_2 \,,\, K^*\psi_2\rangle \\ &= \frac{1}{\rho}\langle f_2 \,,\, \psi_2\rangle \end{aligned} \tag{5.30}$$

where the last line follows from the fact that $K = K^*$ and $K\psi_2 = \psi_2$. From (5.30) we have that there exists a ψ_2 that solves the second component equation of (5.15) if and only if $\int_\Omega f_2\psi_2\,dx = 0$. Assume this is the case. Then, the first component equation of (5.15) can be written as

$$d_1\Delta\psi_1 + r(x)\psi_1 - 2\omega_1 u^*\psi_1 = \frac{a_2u^*}{1+a_2h_2u^*}\psi_2 + f_1 \ . \tag{5.31}$$

The left hand side of (5.31) is invertible, so this equation will be solvable for any choice of f_1. We can finally conclude that

$$R(F_{(u,w)}(e_2^*,(u^*,0))) = C^\alpha(\overline{\Omega}) \times \left\{ f \in C^\alpha(\overline{\Omega}) \mid \int_\Omega f\,\psi_2\,dx = 0 \right\}.$$

Finally, in order to assert that the Crandall-Rabinowitz bifurcation theorem applies, we need to show that

$$F_{e_2,(u,w)}(e_2^*,(u^*,0)) \begin{pmatrix} L_2^{-1}\left(\frac{a_2u^*}{1+a_2h_2u^*}\psi_2\right) \\ \psi_2 \end{pmatrix} \notin R(F_{(u,w)}(e_2^*,(u^*,0))) \,. \tag{5.32}$$

Differentiating $F_{(u,w)}(e_2^*,u^*,0)$ (see (5.7)) with respect to e_2 we see that

$$F_{e_2,(u,w)}(e_2^*,u^*,0) \begin{pmatrix} \phi_1 \\ \phi_2 \end{pmatrix} = \begin{pmatrix} 0 \\ \frac{a_2u^*}{1+a_2h_2u^*}\phi_2 \end{pmatrix} \,. \tag{5.33}$$

If (5.32) fails, then we have $\int_\Omega \frac{a_2u^*}{1+a_2h_2u^*}\psi_2^2\,dx = 0$ which is a contradiction. The Crandall-Rabinowitz bifurcation theorem now applies to F at $(e_2^*,u^*,0)$ and we can conclude there is a parameterized curve of solutions to (5.4) passing through $(e_2^*,u^*,0)$ such that this curve and the semi-trivial solution are the only solutions in a neighborhood of $(e_2^*,u^*,0)$.

5.2 Bifurcation in the $u-v$ Subsystem

The analysis for the bifurcation from the resource only equilibrium in the $u-v$ subsystem is nearly identical to the analysis of the $u-w$ subsystem. The only real difference is that the $u - v$ system should be transformed first by the substitution $z = M(u)v$ so that the resulting system is a semi-linear elliptic system,

$$\begin{aligned} d_1\Delta u + \left(r(x) - \omega_1 u - \frac{a_1 z}{M(u)(1 + a_1 h_1 u)}\right) u &= 0 \\ \Delta z + \left(\frac{e_1 a_1 u}{1 + a_1 h_1 u} - \mu_1 - \frac{\omega_2}{M(u)} z\right) \frac{z}{M(u)} &= 0 \quad \text{in } \Omega, \\ \frac{\partial u}{\partial n} = \frac{\partial z}{\partial n} &= 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{5.34}$$

This system linearized at $(u^*, 0)$ and applied to the vector $\begin{pmatrix} \phi_1 \\ \phi_2 \end{pmatrix}$ yields

$$\begin{aligned} d_1\Delta\phi_1 + r(x)\phi_1 - 2\omega_1 u^*\phi_1 &= \frac{a_1 u^*}{M(u^*)(1 + a_1 h_1 u^*)}\phi_2 \\ -\Delta\phi_2 + \frac{\mu_1}{M(u^*)}\phi_2 &= \frac{e_1 a_1 u^*}{M(u^*)(1 + a_1 h_1 u^*)}\phi_2 \quad \text{in } \Omega, \\ \frac{\partial\phi_1}{\partial n} = \frac{\partial\phi_2}{\partial n} &= 0 \quad \text{on } \partial\Omega\,. \end{aligned} \tag{5.35}$$

As in the case of the $u - w$ subsystem, the operator on the left hand side of the second equation of (5.35) has an inverse that is a positive compact operator (in the appropriate space) and the right hand side is a bounded positive operator, leading to a maximal principal eigenvalue, $\frac{1}{e_1^*}$, of the equation written in terms of the inverse operator and a corresponding positive eigenfunction. This gives a minimal eigenvalue, e_1^*, for the weighted eigenvalue problem in (5.35) (the second equation). This e_1^* becomes the candidate for bifurcation and the rest of the analysis proceeds in an identical manner as the $u - w$ case.

5.3 Local Stability of the $u - w$ Coexistence State

Let $s \in (-\delta, \delta)$ parameterize the curve of solutions to (5.1) guaranteed to exist by the Crandall-Rabinowitz bifurcation theorem, [12] Theorem 1.7, and write

$$u(s) = u^* + s\psi_1 + \hat{u}(s)\,,$$
$$w(s) = s\psi_2 + \hat{w}(s)\,,$$

where $\hat{u}(s)$ and $\hat{w}(s)$ are both $o(|s|)$. We also have $e_2(s) : (-\delta, \delta) \to \mathbb{R}$ with $e_2(0) = e_2^*$. In [13], Crandall and Rabinowitz prove that if $F, e_2^*, (u^*, 0), \vec{y_0}, \delta, e_2(s)$ and $(u(s), w(s))$ are as in Section 5.1, then there are an interval I and continuously differentiable functions $\sigma(e_2) : I \to \mathbb{R}$, $\vec{\psi}(e_2) : I \to \left[C_N^{2,\alpha}(\overline{\Omega})\right]^2$, $\mu(s) : (-\delta, \delta) \to \mathbb{R}$ and $\vec{\tau}(s) : (-\delta, \delta) \to \left[C_N^{2,\alpha}(\overline{\Omega})\right]^2$ such that

$$F_{(u,w)}(e_2, (u^*, 0))\vec{\psi}(e_2) = \sigma(e_2)\vec{\psi}(e_2) \text{ and} \tag{5.36}$$
$$F_{(u,w)}(e_2(s), (u(s), w(s)))\vec{\tau}(s) = \mu(s)\vec{\tau}(s)\,. \tag{5.37}$$

Furthermore, near $s = 0$ the functions $\mu(s)$ and $-se_2'(s)\sigma'(e_2^*)$ have the same zeros and their signs are the same when they are not zero. If $\mu(s)$ is negative for s small and positive (positive s corresponds to positive solutions since $\psi_2 > 0$), then the branch of solutions bifurcating from $(e_2^*, (u^*, 0))$ will be locally stable (in terms of linearized stability). The $\sigma(e_2)$ eigenvalues in (5.36) are monotonically increasing in e_2 (refer back to (5.8) to see the full equations and the dependence on e_2) so $\sigma'(e_2^*) > 0$. Therefore, if $e_2'(0) < 0$ the bifurcating branch of solutions will be unstable for small positive s and if $e_2'(0) > 0$ the bifurcating branch of solutions will be locally stable for small positive s. We will now calculate $e_2'(0)$.

We can write the w component equation of the $u-w$ subsystem using the notation $h(s) = h(e_2(s), u(s), w(s))$ as

$$0 = d_3 \Delta w(s) + w(s) h(s) \ , \tag{5.38}$$

and differentiate with respect to s

$$0 = d_3 \Delta(\psi_2 + \hat{w}'(s)) + h(s)(\psi_2 + \hat{w}'(s)) + w(s) h'(s) \ . \tag{5.39}$$

Substituting $s = 0$ in (5.39) and using $w(0) = 0$ and the fact that ψ_2 satisfies

$$0 = d_3 \Delta \psi_2 + h(0) \psi_2 \tag{5.40}$$

yields

$$0 = d_3 \Delta \hat{w}'(0) + h(0) \hat{w}'(0) \ . \tag{5.41}$$

Hence $\hat{w}'(0) = k\psi_2$ for some k. However, from the results of Crandall and Rabinowitz, we can assume that $(\hat{u}'(0), \hat{w}'(0))$ lies in the range of $F_{(u,w)}(e_2^*, u^*, 0)$, hence k must be zero and $\hat{w}'(0) \equiv 0$. If we follow a similar approach and differentiate the u equation with respect to s and set $s = 0$ we find

$$0 = d_1 \Delta \hat{u}'(0) + r(x) \hat{u}'(0) - 2\omega_1 u^* \hat{u}'(0) \ . \tag{5.42}$$

As discussed before, the operator above is invertible and hence $\hat{u}'(0) \equiv 0$ as well.

Now, differentiate (5.39) once more with respect to s and again set $s = 0$ to get

$$0 = d_3 \Delta \hat{w}''(0) + h(0)\hat{w}''(0) + 2\psi_2 h'(0) \ . \tag{5.43}$$

We can calculate $h'(0)$ explicitly,

$$\begin{aligned} h'(0) &= \left.\frac{\partial h}{\partial e_2}\right|_{s=0} e_2'(0) + \left.\frac{\partial h}{\partial u}\right|_{s=0} u'(0) + \left.\frac{\partial h}{\partial w}\right|_{s=0} w'(0) \\ &= \frac{a_2 u^*}{1 + a_2 h_2 u^*} e_2'(0) + \frac{a_2 e_2^*}{(1 + a_2 h_2 u^*)^2} \psi_1 - \omega_3 \psi_2 \ . \end{aligned} \tag{5.44}$$

Substitute (5.44) into (5.43), multiply by ψ_2 and integrate over Ω to obtain

$$\begin{aligned} 0 = d_3 \int_\Omega & \psi_2 \Delta \hat{w}''(0) + h(0)\hat{w}''(0)\psi_2 \\ &+ 2\psi_2^2 \left(\frac{a_2 u^*}{1 + a_2 h_2 u^*} e_2'(0) + \frac{a_2 e_2^*}{(1 + a_2 h_2 u^*)^2} \psi_1 - \omega_3 \psi_2 \right) dx \ . \end{aligned} \tag{5.45}$$

Apply the divergence theorem twice to the Laplacian term and use the fact that ψ_2 satisfies (5.40) to eliminate the terms involving $\hat{w}''(0)$. We can break up the remaining terms into separate integrals, divide by the common factor of 2, and use the fact that $e_2'(0)$ is constant over Ω to get

$$0 = e_2'(0) \int_\Omega \frac{a_2 u^* \psi_2^2}{1 + a_2 h_2 u^*} \, dx + \int_\Omega \frac{a_2 e_2^* \psi_1 \psi_2^2}{(1 + a_2 h_2 u^*)^2} \, dx - \int_\Omega \omega_3 \psi_2^3 \, dx \ . \tag{5.46}$$

Therefore,

$$e_2'(0) = \frac{\displaystyle\int_\Omega \omega_3 \psi_2^3 - \frac{a_2 e_2^* \psi_1 \psi_2^2}{(1 + a_2 h_2 u^*)^2} \, dx}{\displaystyle\int_\Omega \frac{a_2 u^* \psi_2^2}{1 + a_2 h_2 u^*} \, dx} \ . \tag{5.47}$$

Note that $u(s)$ is a strict subsolution to the semi-trivial equilibrium equation with solution u^* when $s \in (0, \delta)$, so $u(s) < u^*$ for $s \in (0, \delta)$ which implies $\psi_1 < 0$ on Ω. Therefore, (5.47) tells us that $e_2'(0) > 0$, and the local stability of the coexistence solution is guaranteed for $s \in (0, \delta)$.

The results of the analysis in Sections 5.1 and 5.3 can be summarized in a theorem.

Theorem 5.3.1. *There is a critical value e_2^*, and $\delta > 0$ such that when $e_2 \leq e_2^*$ there is no positive equilibrium of* (4.35) *and when $e_2 \in (e_2^*, e_2^* + \delta)$ there is a positive equilibrium of* (4.35) *that is locally stable.*

Proof. The bifurcation of a locally stable branch of positive equilibrium solutions at e_2^* was shown in Sections 5.1 and 5.3. What is left to show is that there are no positive solutions to (5.1) when $e_2 \leq e_2^*$.

Fix $e_2 \leq e_2^*$ and suppose $(\hat{u}, \hat{w})$ is a positive equilibrium solution to (4.35). A standard comparison argument yields $\hat{u} < u^*$ on Ω, hence

$$\frac{e_2 a_2 \hat{u}}{1 + a_2 h_2 \hat{u}} - \mu_1 < \frac{e_2^* a_2 u^*}{1 + a_2 h_2 u^*} - \mu_1 \,. \tag{5.48}$$

Since there is a positive function, ψ_2, that solves the second equation of (5.8), we know that the principal eigenvalue, σ, of

$$d_3 \Delta \phi + \left(\frac{e_2^* a_2 u^*}{1 + a_2 h_2 u^*} - \mu_1 \right) \phi = \sigma \phi \tag{5.49}$$

is zero. Therefore, the principal eigenvalue, $\hat{\sigma}$ of

$$d_3 \Delta \hat{\phi} + \left(\frac{e_2 a_2 \hat{u}}{1 + a_2 h_2 \hat{u}} - \mu_1 \right) \hat{\phi} = \hat{\sigma} \hat{\phi} \tag{5.50}$$

must be negative. Proposition 3.1 of [11] rules out the possibility of a positive solution to

$$d_3\Delta\hat{w} + \hat{w}\left(\frac{e_2 a_2 \hat{u}}{1 + a_2 h_2 \hat{u}} - \mu_1 - \omega_3 \hat{w}\right) = 0\,, \tag{5.51}$$

so no positive equilibrium solutions of (4.35) are possible. □

5.4 Comparison of Random Diffusion and Fitness Dependent Dispersal

In the previous section we saw that a locally stable positive equilibrium to (4.35) bifurcates from $(u^*, 0)$ at $e_2 = e_2^*$. We will now look at criteria for v to invade this equilibrium point for the cases $\lambda = 0$, i.e. $M(u, w) = d_2$, and λ large to see the effect of the fitness dependent dispersal strategy.

For $M(u, w) = d_2$, v will be able to invade the resource only equilibrium if the principal eigenvalue, σ_1 of

$$d_2\Delta v_1 + \left(\frac{e_1 a_1 u^*}{1 + a_1 h_1 u^*} - \mu_1\right) v_1 = \sigma_1 v_1 \text{ in } \Omega, \quad \frac{\partial v_1}{\partial n} = 0 \text{ on } \partial\Omega\,, \tag{5.52}$$

is positive. Recall the notation $g^*(u, w) = \frac{e_1 a_1 u}{1 + a_1 h_1 u} - \mu_1 - a_3 w$. If $\int_\Omega g^*(u^*, 0)\, dx > 0$ then σ_1 will be positive regardless of the value of d_2. However, if $\int_\Omega g^*(u^*, 0)\, dx < 0$ then σ_1 will be positive if and only if $\frac{1}{d_2} > \Lambda_1^+(g^*(u^*, 0))$ (see Theorem 2.6 in [11]) where $\Lambda_1^+(m(x))$ is the positive principal eigenvalue of

$$\Delta\psi + \Lambda m(x) = 0 \text{ in } \Omega, \quad \frac{\partial \psi}{\partial n} = 0 \text{ on } \partial\Omega\,, \tag{5.53}$$

which is guaranteed to exist by Theorem 2.5 of [11] for any $m(x)$ that changes signs in Ω and has $\int_\Omega m(x)\, dx < 0$. Assume that d_2 satisfies this condition and consider the bifurcating branch of positive solutions to (5.1), $(u(s), w(s))$, for $s > 0$ small enough so that the local stability is maintained and $g^*(u(s), w(s))$ is positive somewhere in Ω. We know that $u(s) < u^*$ and $w(s) > 0$ in $\overline{\Omega}$, so $g^*(u(s), w(s)) < g^*(u^*, 0)$ and

$$\Lambda_1^+\left(g^*(u(s), w(s))\right) > \Lambda_1^+\left(g^*(u^*, 0)\right) \ . \tag{5.54}$$

If d_2 is such that

$$\Lambda_1^+\left(g^*(u(s), w(s))\right) > \frac{1}{d_2} > \Lambda_1^+\left(g^*(u^*, 0)\right) \ , \tag{5.55}$$

then the IGPrey will be able to invade the resource only equilibrium, but will not be able to invade the locally stable positive $u - w$ coexistence state.

Compare this to the situation when λ is large, i.e. the IGPrey is employing a movement strategy that avoids areas with negative linearized fitness. We saw in Theorem 4.3.1 that v will be able to invade this $u - w$ coexistence state if $g^*(u(s), w(s)) > 0$ at any point in Ω (which we have assumed is the case) if λ is sufficiently large.

If $g^*(u(s), w(s))$ is negative on all of Ω, then the IGPrey will not be able to invade the coexistence state regardless of movement strategies employed. This would be equivalent to saying the entire domain is "bad" for the IGPrey.

5.5 Stability of the $u - v$ Coexistence State

We will follow the same procedure used to analyze the local stability of the coexistence state in the $u - w$ subsystem. Let $s \in (-\delta, \delta)$ parameterize this curve of solutions and write

$$u(s) = u^* + s\phi_1 + \tilde{u}(s)\,,$$
$$z(s) = s\phi_2 + \tilde{z}(s)\,,$$

where $\tilde{u}(s)$ and $\tilde{z}(s)$ are both $o(|s|)$. We also have $e_1(s) : (-\delta, \delta) \to \mathbb{R}$ with $e_1(0) = e_1^*$. We can use the procedure from the preceding section to calculate $e_1'(0)$ and draw conclusions about the local stability of the coexistence equilibrium. We can write the z component equation of the $u - z$ subsystem using the notation

$$g^*(e_1, u) = \frac{e_1 a_1 u}{1 + a_1 h_1 u} - \mu_1 \tag{5.56}$$

and

$$k(s) = \frac{g^*(e_1(s), u(s))}{M(g^*(e_1(s), u(s)))} - \frac{\omega_2}{M(g^*(e_1(s), u(s)))^2} z(s)\ . \tag{5.57}$$

Then the z-component equation is

$$0 = \Delta z(s) + z(s)k(s)\ . \tag{5.58}$$

Differentiate this with respect to s to get

$$0 = \Delta(\phi_2 + \tilde{z}'(s)) + k(s)(\phi_2 + \tilde{z}'(s)) + z(s)k'(s)\,, \tag{5.59}$$

with a companion equation for $\tilde{u}'(s)$. The argument employed for the $u - w$ subsystem transfers here without modification. We find that $\tilde{z}'(0) \equiv 0$ and $\tilde{u}'(0) \equiv 0$. We can differentiate (5.59) with respect to s one more time and evaluate at $s = 0$ to obtain

$$0 = d_3 \Delta \tilde{z}''(0) + k(0)\tilde{z}''(0) + 2\phi_2 k'(0) \ , \tag{5.60}$$

where

$$k'(0) = \frac{\partial}{\partial u^*}\left(\frac{g^*(e_1^*, u^*)}{M(g^*(e_1^*, u^*))}\right)\phi_1 + \frac{a_1 u^*}{1 + a_1 h_1 u^*} e_1'(0) - \omega_2 \phi_2 \ . \tag{5.61}$$

Substitute (5.61) into (5.60), multiply by ϕ_2 and integrate over Ω to obtain

$$\begin{aligned} 0 = \int_\Omega & \phi_2 \Delta \tilde{z}''(0) + k(0)\tilde{z}''(0)\phi_2 \\ & + 2\phi_2^2 \left(\frac{\partial}{\partial u^*}\left(\frac{g^*(e_1^*, u^*)}{M(g^*(e_1^*, u^*))}\right)\phi_1 + \frac{a_1 u^*}{1 + a_1 h_1 u^*} e_1'(0) - \omega_2 \phi_2\right) dx \ . \end{aligned} \tag{5.62}$$

Apply the divergence theorem twice to the Laplacian term and use the fact that ϕ_2 satisfies (5.35) to eliminate the terms involving $\tilde{z}''(0)$. We can break up the remaining terms into separate integrals, divide by the common factor of 2, and use the fact that $e_1'(0)$ is constant over Ω to get

Therefore,

$$e_1'(0) = \frac{\displaystyle\int_\Omega \frac{\omega_2 \phi_2^3}{M(g^*(e_1^*, u^*))^2} - \frac{\partial}{\partial u^*}\left(\frac{g^*(e_1^*, u^*)}{M(g^*(e_1^*, u^*))}\right)\phi_1 \phi_2^2 \, dx}{\displaystyle\int_\Omega \frac{a_1 u^* \phi_2^2}{1 + a_1 h_1 u^*} \, dx} \ . \tag{5.63}$$

Note that $u(s)$ is a strict subsolution to the semi-trivial equilibrium equation with solution u^* when $s \in (0, \delta)$, so $u(s) < u^*$ for $s \in (0, \delta)$ which implies $\phi_1 < 0$ on Ω. If we assume condition (4.77), then $\frac{\partial}{\partial u^*}\left(\frac{g^*(e_1^*, u^*)}{M(g^*(e_1^*, u^*))}\right) > 0$ (because $\frac{\partial g^*}{\partial u} > 0$) and we can conclude from (5.63) that $e_1'(0) > 0$, and the local stability of the coexistence solution is guaranteed for $s \in (0, \delta)$.

However, if condition (4.77) is not satisfied, the analysis of Section 5.2 remains valid and we can guarantee that the bifurcation point exists; but, we are not able to determine its stability from (5.63) and it is possible to have a subcritical bifurcation at $(e_1^*, (u^*, 0))$. The results of the analysis in Sections 5.2 and 5.5 are summarized in the following theorem.

Theorem 5.5.1. *Suppose* $M(u, w) = M(g^*(u, w))$ *and* $\frac{d}{dg^*}\left(\frac{g^*}{M(g^*)}\right) > 0$. *Then there exists a* $\delta > 0$ *and critical value* e_1^* *such that if* $e_1 \leq e_1^*$ *there are no positive equilibrium solutions to* (4.19) *and if* $e_1 \in (e_1^*, e_1^* + \delta)$ *there is a positive equilibrium solution to* (4.19) *that is locally stable.*

Proof. The existence of the locally stable bifurcating branch of equilibrium solutions was shown in Sections 5.2 and 5.5. The proof of the nonexistence of positive equilibrium solutions when $e_1 \leq e_1^*$ makes use of the fact that $\frac{\partial}{\partial u}\left(\frac{g^*(u,0)}{M(g^*(u,0))}\right) > 0$; but other than this, is identical to the proof for the $u - w$ subsystem in Section 5.3. $\square$

Chapter 6

The Effect of λ on IGPredator Invasibility

6.1 A Sufficient Condition for the IGPredator to Invade When λ is Large

We will now examine a sufficient condition for the IGPredator to invade any equilibrium points of the $u - v$ subsystem when λ is sufficiently large. Consider the equilibrium equations for the $u - v$ subsystem for a particular value of λ:

$$
\begin{gathered}
d_1 \Delta u_\lambda + \left(r(x) - \omega_1 u_\lambda - \frac{a_1 v_\lambda}{1 + a_1 h_1 u_\lambda} \right) u_\lambda = 0 \\
\Delta \left[M_\lambda(u_\lambda) v_\lambda \right] + \left(\frac{e_1 a_1 u_\lambda}{1 + a_1 h_1 u_\lambda} - \mu_1 - \omega_2 v_\lambda \right) v_\lambda = 0 \;\text{ in } \Omega, \\
\frac{\partial u_\lambda}{\partial n} = \frac{\partial v_\lambda}{\partial n} = 0 \;\text{ on } \partial\Omega\,,
\end{gathered}
\tag{6.1}
$$

where

$$M_\lambda(u_\lambda) = \begin{cases} -\lambda g^* e^{d_2/(\lambda g^*)} + d_2 & \text{when } g^* < 0 \\ \\ d_2 & \text{when } g^* \geq 0 \end{cases} \quad \text{and,} \tag{6.2}$$

$$g^*(u_\lambda) = \frac{e_1 a_1 u_\lambda}{1 + a_1 h_1 u_\lambda} - \mu_1, \tag{6.3}$$

and where we use the convention that $M_0 \equiv d_2$. This choice for M_λ is the exponentially smoothed (as in (4.74)) version of (4.69). As in the discussion of (4.74), this function (viewed as a function of $g^* \in \mathbb{R}$) is $C^\infty(\mathbb{R})$. The exponential terms are chosen so that condition (4.77) is satisfied,

$$\frac{d}{dg^*}\left(\frac{g^*}{M_\lambda(g^*)}\right) = \frac{M_\lambda(g^*) - g^* M_\lambda'(g^*)}{M_\lambda(g^*)^2}\,, \tag{6.4}$$

and for $g^* < 0$, $\lambda > 0$

$$\begin{aligned} M_\lambda(g^*) - g^* M_\lambda'(g^*) &= -\lambda g^* e^{d_2/(\lambda g^*)} + d_2 - g^*\left(\frac{d_2}{g^*} e^{d_2/(\lambda g^*)} - \lambda e^{d_2/(\lambda g^*)}\right) \\ &= d_2 - d_2 e^{d_2/(\lambda g^*)} > 0\,. \end{aligned} \tag{6.5}$$

Satisfying (4.77) will be used to establish the practical persistence type bounds we are going to develop for the solutions of (6.1) below. Satisfying this condition has the added benefit of making the positive solution to (6.1) locally stable for values of e_1 in $(e_1^*, e_1^* + \delta)$. We also should note that $g^{*\prime}(u) = \frac{e_1 a_1}{(1+a_1 h_1 u)^2} > 0$, so another consequence of the calculations in (6.4) and (6.5) is that $\frac{dM_\lambda}{du} < 0$ when $g^* < 0$ and $\lambda > 0$.

Set

$$u_c = \frac{\mu_1}{e_1 a_1 - a_1 h_1 \mu_1} \tag{6.6}$$

so that $g^*(u_c) = 0$. We will assume that $e_1 \geq e_1^*$ so that positive solutions to (6.1) exist. We know that $e_1^* > h_1\mu_1$ so $u_c > 0$. To analyze the ability of the IGPredator to invade solutions of (6.1) it will help to make the substitution $z_\lambda = M_\lambda(u_\lambda)v_\lambda$ in (6.1) to get an equivalent $u - z$ system:

$$\begin{aligned} d_1\Delta u_\lambda + \left(r(x) - \omega_1 u_\lambda - \frac{a_1 z_\lambda}{M_\lambda(u_\lambda)(1 + a_1 h_1 u_\lambda)}\right) u_\lambda = 0 \\ \Delta z_\lambda + \left(\frac{e_1 a_1 u_\lambda}{1 + a_1 h_1 u_\lambda} - \mu_1 - \frac{\omega_2}{M_\lambda(u_\lambda)} z_\lambda\right) \frac{z_\lambda}{M_\lambda(u_\lambda)} = 0 \ \text{ in } \Omega, \\ \frac{\partial u_\lambda}{\partial n} = \frac{\partial z_\lambda}{\partial n} = 0 \ \text{ on } \partial\Omega. \end{aligned} \tag{6.7}$$

Ultimately, we want to construct a pair of functions $(\underline{u}, \underline{v})$ such that for all $\varepsilon > 0$, $h(u_\lambda, v_\lambda, 0) \geq h(\underline{u}, \underline{v}, 0) - \varepsilon$ for λ sufficiently large. We can then establish sufficient criteria for the IGPredator to invade the equilibrium point (u_λ, v_λ) when λ is large. We will construct $(\underline{u}, \underline{v})$ via a practical persistence type argument as in [10]. First we will construct a $\overline{z}$ such that $\overline{z} \geq z_\lambda$ for all $\lambda \geq 0$. We will then use this to construct a monotone family of lower solutions to the u_λ equation, $\{\underline{u}_\lambda\}_{\lambda \geq 0}$, such that $\underline{u}_\lambda$ is converging pointwise to a function $\underline{u}$. We can then use the $\underline{u}_\lambda$'s to construct lower solutions, $\underline{z}_\lambda$, to the z_λ equation, which again limit to a function, $\underline{z}$, as $\lambda \to \infty$. Finally, the lower solution pairs, $(\underline{u}_\lambda, \underline{z}_\lambda)$ can be used to construct lower solutions to the v_λ equation which limit to a function $\underline{v}$ as $\lambda \to \infty$. Functional analysis arguments are employed to strengthen the convergence so that these limiting functions can be used in an eigenvalue analysis of the IGPredator's invasibility criteria for large λ.

Let u^* represent the resource only semi-trivial equilibrium to (6.1) (which is independent of λ). Clearly $u_\lambda \leq u^*$ for all $\lambda \geq 0$ and hence $g^*(u_\lambda) \leq g^*(u^*)$ for all $\lambda \geq 0$.

Define

$$\overline{u} = \max_{x\in\Omega} u^*(x) \;\text{ and }\; \overline{z} = \frac{d_2 g(\overline{u})}{\omega_2} = \frac{d_2}{\omega_2}\left(\frac{e_1 a_1 \overline{u}}{1 + a_1 h_1 \overline{u}} - \mu_1\right) . \tag{6.8}$$

Then

$$\Delta\overline{z} + \left(\frac{e_1 a_1 u_\lambda}{1 + a_1 h_1 u_\lambda} - \mu_1 - \frac{\omega_2}{M_\lambda(u_\lambda)}\overline{z}\right)\frac{\overline{z}}{M_\lambda(u_\lambda)} \le 0$$

because the term in parenthesis is negative whenever $g^*(u_\lambda) < 0$ and when $g^*(u_\lambda) \ge 0$ we have $M_\lambda(u_\lambda) = d_2$ and $g^*(u_\lambda) \le \max_\Omega g^*(u^*)$. Thus, $\overline{z}$ is a supersolution to the z_λ equation for all $\lambda \ge 0$. We can obtain a subsolution, $\underline{u}_\lambda$, to the u_λ equation in (6.7) by replacing z_λ with $\overline{z}$ and letting $\underline{u}_\lambda$ be the solution of

$$d_1\Delta\underline{u}_\lambda + \left(r(x) - \omega_1\underline{u}_\lambda - \frac{a_1\overline{z}}{M_\lambda(\underline{u}_\lambda)}\right)\underline{u}_\lambda = 0 \text{ in } \Omega,\; \frac{\partial \underline{u}_\lambda}{\partial n} = 0 \text{ on } \partial\Omega \tag{6.9}$$

when a positive solution exists, and 0 otherwise. There will be a positive solution to (6.9) for sufficiently large values of λ. To see this, linearize (6.9) about the trivial solution and examine the resulting eigenvalue equation

$$d_1\Delta\phi + \left(r(x) - \frac{a_1\overline{z}}{M_\lambda(0)}\right)\phi = \sigma\phi \text{ in } \Omega,\; \frac{\partial\phi}{\partial n} = 0 \text{ on } \partial\Omega. \tag{6.10}$$

As $\lambda \to \infty$, $M_\lambda(0) \to \infty$, so for large λ, (6.10) will have a positive principal eigenvalue and a standard comparison argument will guarantee that (6.9) admits a positive solution. This solution is unique because

$$\frac{\partial}{\partial\underline{u}_\lambda}\left(r(x) - \omega_1\underline{u}_\lambda - \frac{a_1\overline{z}}{M_\lambda(\underline{u}_\lambda)}\right) = -\omega_1 + \frac{a_1\overline{z}M_\lambda'(\underline{u}_\lambda)}{M_\lambda(\underline{u}_\lambda)^2} < 0 \;; \tag{6.11}$$

see [11], Proposition 3.3.

We can now use the fact that $\frac{d}{du}\frac{g(u)}{M_\lambda(u)} \geq 0$ and $\underline{u}_\lambda \leq u_\lambda$ for all $\lambda \geq 0$ to construct subsolutions to the z_λ equation. Let $\underline{z}_\lambda$ be the unique positive solution to

$$\Delta \underline{z}_\lambda + \frac{g(\underline{u}_\lambda)}{M_\lambda(\underline{u}_\lambda)}\underline{z}_\lambda - \frac{\omega_2}{M_\lambda(u^*)^2}\underline{z}_\lambda^2 = 0 \text{ in } \Omega, \ \frac{\partial \underline{z}_\lambda}{\partial n} = 0 \text{ on } \partial\Omega \tag{6.12}$$

if such a solution exists, and $\underline{z}_\lambda \equiv 0$ otherwise. If we want (6.12) to admit a positive solution for large values of λ, we will assume some extra conditions on the parameters of our system. This analysis will be deferred until the end of Chapter 6.

Now, we will see that the subsolutions we have constructed to (6.7), $(\underline{u}_\lambda, \underline{z}_\lambda)$, are monotone increasing in λ and bounded above by $(u^*, \overline{z})$. The key observation is that $\frac{d}{d\lambda}M_\lambda(u) \geq 0$. With this in mind, let $\lambda_1 < \lambda_2$ and examine (6.9). We see that $\underline{u}_{\lambda_1}$ will be a subsolution to the equation for $\underline{u}_{\lambda_2}$ and hence $\underline{u}_{\lambda_1} \leq \underline{u}_{\lambda_2}$. Knowing that $\underline{u}_\lambda$ increases in λ and examining (6.12) we see that the quantity $\frac{g(\underline{u}_\lambda)}{M_\lambda(\underline{u}_\lambda)}$ is increasing in λ. This is because the region in which $g(\underline{u}_\lambda) \geq 0$ is expanding as λ increases and within this region g is increasing in λ and $M_\lambda = d_2$. In the region where $g(\underline{u}_\lambda) < 0$, we have to be a little more careful as the function definition of M_λ is changing in λ as well. It will help to write M_λ and $\underline{u}_\lambda$ as functions that depend on a variable λ and use the chain rule to compute

$$\frac{d}{d\lambda}\left(\frac{g(\underline{u}_\lambda)}{M_\lambda(\underline{u}_\lambda)}\right) = \frac{d}{d\lambda}\left(\frac{g(\underline{u}(\lambda)}{M(\lambda, g(\underline{u}(\lambda)))}\right) = \frac{-g}{M(\lambda,g)^2}\frac{\partial M}{\partial \lambda} + \frac{\partial}{\partial g}\left(\frac{g}{M(\lambda,g)}\right)\frac{dg}{d\underline{u}}\frac{d\underline{u}}{d\lambda}. \tag{6.13}$$

We have $\frac{\partial M}{\partial \lambda} \geq 0$, $\frac{\partial}{\partial g}\left(\frac{g}{M(\lambda,g)}\right) > 0$ (condition (4.77)), $\frac{dg}{d\underline{u}} \geq 0$ and $\frac{d\underline{u}}{d\lambda} \geq 0$ for $g < 0$; so, (6.13) gives $\frac{d}{d\lambda}\left(\frac{g(\underline{u}_\lambda)}{M_\lambda(\underline{u}_\lambda)}\right) \geq 0$ for $g < 0$. The quadratic term in (6.12) is negative and the denominator is increasing in λ, hence this whole term is increasing in λ as well. Therefore, $\underline{z}_\lambda$ is increasing in λ.

Since $\underline{u}_\lambda$ and $\underline{z}_\lambda$ are increasing and bounded above, they must be converging pointwise to some functions $\underline{u}$ and $\underline{z}$ on $\overline{\Omega}$. We can see that this convergence is actually much stronger by rewriting (6.9) and (6.12) as

$$\underline{u}_\lambda = (-\Delta+1)^{-1}\left(\underline{u}_\lambda + \frac{\underline{u}_\lambda}{d_1}\left(r(x) - \omega_1\underline{u}_\lambda - \frac{a_1\overline{z}}{M_\lambda(\underline{u}_\lambda)}\right)\right) \tag{6.14}$$

$$\underline{z}_\lambda = (-\Delta+1)^{-1}\left(\left(1 + \frac{g(\underline{u}_\lambda)}{M_\lambda(\underline{u}_\lambda)}\right)\underline{z}_\lambda - \frac{\omega_2}{M_\lambda(u^*)^2}\,\underline{z}_\lambda^2\right) \tag{6.15}$$

and use the fact that $(-\Delta+1)^{-1}$ is a bounded linear operator from $C(\overline{\Omega})$ to $C_N^{1+\alpha}(\overline{\Omega})$ for all $\alpha \in (0,1)$. Take any $\{\lambda_n\}_{n=1}^\infty$ converging to ∞, and observe that the corresponding solution pairs $\{(\underline{u}_{\lambda_n}, \underline{z}_{\lambda_n})\}$ are bounded in $C(\overline{\Omega}) \times C(\overline{\Omega})$ (and so are the resulting right hand sides of (6.14) and (6.15)). Hence $\{(\underline{u}_{\lambda_n}, \underline{z}_{\lambda_n})\}$ is bounded in $C^{1+\alpha}(\overline{\Omega}) \times C^{1+\alpha}(\overline{\Omega})$ which compactly embeds in $C^{1+\beta}(\overline{\Omega}) \times C^{1+\beta}(\overline{\Omega})$ for $0 < \beta < \alpha$. Therefore, there exists a subsequence of $\{(\underline{u}_{\lambda_n}, \underline{z}_{\lambda_n})\}$ that converges in $C^{1+\beta}(\overline{\Omega}) \times C^{1+\beta}(\overline{\Omega})$ to $(\underline{u}, \underline{z})$ (because the limit in $C^{1+\beta}(\overline{\Omega}) \times C^{1+\beta}(\overline{\Omega})$ must agree with the pointwise limit). We can conclude that $\|(\underline{u}_\lambda, \underline{z}_\lambda) - (\underline{u}, \underline{z})\|_{C^{1+\beta}(\overline{\Omega})\times C^{1+\beta}(\overline{\Omega})} \to 0$ as $\lambda \to \infty$. This follows from the fact that if the limit were not 0, then we could select a sequence of λ_n's approaching ∞ and an $\varepsilon > 0$ such that $\|(\underline{u}_{\lambda_n}, \underline{z}_{\lambda_n}) - (\underline{u}, \underline{z})\|_{C^{1+\beta}(\overline{\Omega})\times C^{1+\beta}(\overline{\Omega})} > \varepsilon$ for all λ_n yet it still has a subsequence that converges to $(\underline{u}, \underline{z})$. This is clearly a contradiction.

To develop sufficient criteria for the successful invasion of an equilibrium, (u_λ, v_λ), of the u-v subsystem by the IGPredator, we will need a lower bound for the v_λ's. Define

$$\underline{v}_\lambda = \begin{cases} \dfrac{\underline{z}_\lambda}{d_2} & \text{where } \underline{u}_\lambda > u_c, \\[2ex] 0 & \text{otherwise.} \end{cases} \tag{6.16}$$

Because $v_\lambda = \frac{z_\lambda}{M_\lambda(u_\lambda)}$ and $\underline{u}_\lambda \le u_\lambda$ we have $v_\lambda = \frac{z_\lambda}{d_2}$ whenever $\underline{u}_\lambda > u_c$. Combine this with the fact that $\underline{z}_\lambda \leq z_\lambda$ and we get $\underline{v}_\lambda \leq v_\lambda$. Let

$$\underline{v} = \begin{cases} \dfrac{z}{d_2} & \text{where } \underline{u} > u_c, \\ 0 & \text{otherwise.} \end{cases} \tag{6.17}$$

Now, we have $(\underline{u}_\lambda, \underline{v}_\lambda)$ increasing pointwise to the bounded functions $(\underline{u}, \underline{v})$. The IGPredator functional response function, $h(u, v, w)$, is continuous and increasing in both the u and v variables, hence $h(\underline{u}_\lambda, \underline{v}_\lambda, 0)$ is increasing pointwise to $h(\underline{u}, \underline{v}, 0)$. We can now state a sufficient condition for the IGPredator to be able to invade a $u - v$ equilibrium point when λ is large.

Theorem 6.1.1. *Consider the principal eigenvalue, σ, of*

$$d_3 \Delta\phi + h(\underline{u}, \underline{v}, 0)\phi = \sigma\phi \text{ in } \Omega, \text{ and } \frac{\partial \phi}{\partial n} = 0 \text{ on } \partial\Omega, \tag{6.18}$$

that is given by

$$\sigma = \max_{\substack{\psi \in W^{1,2}(\Omega) \\ \|\psi\|_2 = 1}} \left(-d_3 \int_\Omega |\nabla \psi|^2 \, dx + \int_\Omega h(\underline{u}, \underline{v}, 0)\psi^2 \, dx \right). \tag{6.19}$$

If $\sigma > 0$ then there exists a $\Lambda > 0$ such that for $\lambda \geq \Lambda$, w_λ will be able to invade the $(u_\lambda, v_\lambda, 0)$ equilibrium.

Proof. Let $\hat{\psi}$ be the unique positive maximizer of of (6.19). Then $h(\underline{u}_\lambda, \underline{v}_\lambda, 0)\hat{\psi}^2$ is a measureable function that is increasing in λ and converging pointwise to $h(\underline{u}, \underline{v}, 0)\hat{\psi}^2$. The Lebesgue Monotone Convergence Theorem implies that

$$\lim_{\lambda \to \infty} \int_\Omega h(\underline{u}_\lambda, \underline{v}_\lambda, 0)\hat{\psi}^2 \, dx = \int_\Omega h(\underline{u}, \underline{v}, 0)\hat{\psi}^2 \, dx \,. \tag{6.20}$$

Choose Λ large enough so that for all $\lambda \geq \Lambda$ we have

$$\int_\Omega h(\underline{u}_\lambda, \underline{v}_\lambda, 0)\hat{\psi}^2\,dx \geq \int_\Omega h(\underline{u}, \underline{v}, 0)\hat{\psi}^2\,dx - \frac{\sigma}{2}\,. \tag{6.21}$$

Take $\lambda \geq \Lambda$ and let σ_λ be the principal eigenvalue of

$$d_3\Delta\phi_\lambda + h(u_\lambda, v_\lambda, 0)\phi_\lambda = \sigma_\lambda\phi_\lambda\,. \tag{6.22}$$

If this eigenvalue is positive, then w can invade the equilibrium point $(u_\lambda, v_\lambda, 0)$. The variational formula for σ_λ gives

$$\begin{aligned}
\sigma_\lambda &= \max_{\substack{\psi\in W^{1,2}(\Omega)\\ \|\psi\|_2=1}} \left(-d_3\int_\Omega |\nabla\psi|^2\,dx + \int_\Omega h(u_\lambda, v_\lambda, 0)\psi^2\,dx\right)\\
&\geq \max_{\substack{\psi\in W^{1,2}(\Omega)\\ \|\psi\|_2=1}} \left(-d_3\int_\Omega |\nabla\psi|^2\,dx + \int_\Omega h(\underline{u}_\lambda, \underline{v}_\lambda, 0)\psi^2\,dx\right)\\
&\geq -d_3\int_\Omega |\nabla\hat{\psi}|^2\,dx + \int_\Omega h(\underline{u}_\lambda, \underline{v}_\lambda, 0)\hat{\psi}^2\,dx\\
&\geq -d_3\int_\Omega |\nabla\hat{\psi}|^2\,dx + \int_\Omega h(\underline{u}, \underline{v}, 0)\hat{\psi}^2\,dx - \frac{\sigma}{2}\\
&= \frac{\sigma}{2} > 0\,.
\end{aligned} \tag{6.23}$$

$\square$

As discussed above, we might wish to guarantee that the $\underline{z}_\lambda$'s are non-zero for sufficiently large λ. This will be the case if there exists a region in Ω with positive measure such that $\underline{u}_\lambda > u_c$ for all large λ. Let $\overline{r} = \max_{x \in \Omega} r(x)$. Then, if

$$\overline{r} - \omega_1 u_c - \frac{a_1 \overline{z}}{d_2} \leq 0 \tag{6.24}$$

we will have $\underline{u}_\lambda \leq u_c$ everywhere for all λ. This follows from the fact that if (6.24) is satisfied, then u_c is a supersolution to the $\underline{u}_\lambda$ equation, (6.9), for all λ. So, a necessary condition for $\underline{z}_\lambda > 0$ for λ large is

$$\overline{r} > \omega_1 u_c + \frac{a_1 \overline{z}}{d_2} \ . \tag{6.25}$$

In fact, this condition is also sufficient if d_1 is sufficiently small and λ sufficiently large. To show this, fix x and consider the equation

$$r(x) = \omega_1 \xi + \frac{a_1 \overline{z}}{M_\lambda(\xi)} \ . \tag{6.26}$$

This will have a unique positive solution (depending on λ) for all $x \in \overline{\Omega}$ when λ is large. Call this solution $\xi_\lambda(x)$. We know there is a unique solution because the left hand side is independent of λ and the right hand side is increasing (at least linearly) in ξ (because $M_\lambda(\xi)$ is decreasing in ξ) and can be made arbitrarily small at $\xi = 0$ by choosing λ large. Now, Proposition 3.16 of [11] applies to (6.9) giving the result:

Lemma 6.1.1. *For a fixed $\lambda > 0$ such that $\xi_\lambda(x)$, the solution to* (6.26)*, is a positive function on Ω, the solution, $\underline{u}_\lambda$, to* (6.9) *is such that $\underline{u}_\lambda \to \xi_\lambda(x)$ uniformly on any closed subset of Ω as $d_1 \to 0$.*

Proof. This is a direct application of Proposition 3.16 in [11]. □

If (6.25) is satisfied, then $\xi_\lambda(x) > u_c$ in a neighborhood of the point where $r(x)$ attains its maximum value; and, for small enough d_1 Lemma 6.1.1 implies that we will have $\underline{u}_\lambda > u_c$ at this point as well.

We can use (6.6) to express u_c in terms of the original system parameters, and use the fact that $\overline{u} \leq \frac{\overline{r}}{\omega_1}$ to get the bound

$$\omega_1 u_c + \frac{a_1 \overline{z}}{d_2} \leq \frac{\omega_1 \mu_1}{a_1(e_1 - h_1\mu_1)} + \frac{a_1}{\omega_2}\left(\frac{e_1 a_1 \overline{r}}{\omega_1 + a_1 h_1 \overline{r}} - \mu_1\right) . \tag{6.27}$$

So, for (6.25) to be satisfied, it would be sufficient to have

$$\overline{r} > \frac{\omega_1 \mu_1}{a_1(e_1 - h_1\mu_1)} + \frac{a_1}{\omega_2}\left(\frac{e_1 a_1 \overline{r}}{\omega_1 + a_1 h_1 \overline{r}} - \mu_1\right) . \tag{6.28}$$

This is a quadratic inequality in $\overline{r}$, and a more transparent condition that disentangles the system parameters may be desired. This can be obtained by noting that

$$\frac{e_1 a_1 \overline{r}}{\omega_1 + a_1 h_1 \overline{r}} < \frac{e_1}{h_1} \tag{6.29}$$

which can be used to get another, more clear, condition that will imply (6.25), namely

$$\overline{r} > \frac{\omega_1 \mu_1}{a_1 h_1(e_1 - \mu_1 h_1)} + \frac{a_1(e_1 - \mu_1 h_1)}{\omega_2 h_1} . \tag{6.30}$$

To recap, in order for $z_\lambda > 0$ for any value of λ it is necessary for (6.25) to hold. In addition, if d_1 is sufficiently small, then (6.25) is a sufficient condition for $z_\lambda > 0$ for large values of λ. Furthermore, conditions (6.28) and (6.30) imply (6.25) (and are easier to verify directly from system parameters).

Chapter 7

Numerical Approximation

7.1 A Finite Element Discretization

We will make use of a finite element discretization scheme that is the system analogue to the single equation scheme described in Chapter 13 of [40]. Let Ω be a plane convex domain with smooth boundary and $J = (0, T]$. The numerical scheme derived in [40] is for the parabolic problem

$$u_t - \nabla \cdot (a(u)\nabla u) = f(u) \ \text{ in } \Omega,\ t \in J, \tag{7.1}$$
$$u = 0 \ \text{ on } \partial\Omega,\ t \in J;\ u(\cdot, 0) = u_0 \ \text{ in } \Omega\,.$$

We are dealing with a system of equations, but the analysis is valid unchanged (merely more cumbersome notation). Our system has explicit x dependence in what would be the $f(u)$ term on the right hand side, but again the analysis is unchanged. In fact, although not explicitly stated, the analysis treats f as a function from the function space of u into a Hilbert space (usually the dual space to the space of test functions employed in the finite element discretization). The fact that [40] treats Dirichlet conditions instead of Neumann again is insignificant, as Neumann conditions arise naturally in the finite element discretization via dropping boundary integrals that arise from using the Divergence Theorem.

It is necessary to assume that a and f are smooth functions such that

$$0 < d \leq a(x,\xi) \leq M, \quad \left|\frac{\partial}{\partial \xi} a(x,\xi)\right| + \left|\frac{\partial}{\partial \xi} f(x,\xi)\right| \leq B, \tag{7.2}$$

for $x \in \overline{\Omega}$ and ξ in a neighborhood of the solution of (7.1) (the neighborhood being taken in $C(\overline{\Omega})$). We have assumed that $M(u,w)$ is twice differentiable and bounded below by d, and we showed in Chapter 3 that solutions to our system have $C^{1+\alpha}(\overline{\Omega})$ norms that are bounded in time by a constant depending on our initial conditions, so (7.2) is satisfied for our problem.

Let $\mathcal{T}_h$ be a triangulation of Ω with $\max_{\tau \in \mathcal{T}_h} \operatorname{diam}(\tau) \leq h$ and let S_h the the corresponding finite dimensional space of continuous functions on Ω that are linear when restricted to any $\tau \in \mathcal{T}_h$ (the piecewise linear approximating functions). Define $u_{0,h}$ to be the approximating function of u_0 in S_h (by projecting it onto the finite basis of S_h). Let k be the constant time-step size for the time discretization. The discretized version of problem (7.1) is to find $\{U^n\}_{t_n \in J} \subseteq S_h$ such that

$$\langle \bar{\partial} U^n, \chi \rangle + \langle a(U^n) \nabla U^n, \nabla \chi \rangle = \langle f(U^n), \chi \rangle, \ \forall \chi \in S_h, t_n \in J, \tag{7.3}$$

where $U^0 = u_{0,h}$ and $\bar{\partial} U^n = \frac{U^n - U^{n-1}}{k}$. However, (7.3) is still a nonlinear system, and therefore not an efficient means of obtaining an approximate solution. The first method used to derive a linear system that approximates the solution to (7.1) replaces the $a(U^n)$ and $f(U^n)$ terms in (7.3) with $a(U^{n-1})$ and $f(U^{n-1})$, yielding the linear system

$$\langle \bar{\partial} U^n, \chi \rangle + \langle a(U^{n-1}) \nabla U^n, \nabla \chi \rangle = \langle f(U^{n-1}), \chi \rangle, \ \forall \chi \in S_h, t_n \in J\,. \qquad (7.4)$$

The following error estimate applies to (7.4):

Theorem 7.1.1 (Theorem 13.3 [40])**.** *Let U^n and u be the solutions to* (7.4) *and* (7.1) *respectively. Then under the appropriate regularity assumptions for u we have*

$$\|U^n - u(t_n)\|_2 \leq C \|u_{0,h} - u_0\|_2 + C(u)(h^2 + k)\,, \quad \textit{for } t_n \in \bar{J}\,. \qquad (7.5)$$

The error estimate above is quadratic in terms of the triangulation size h, but only linear with respect to the time step size. Quadratic accuracy in time can be achieved by using a Crank-Nicolson time stepping scheme. Let $\hat{U}^n = \frac{U^n + U^{n-1}}{2}$ for $n \geq 1$ and $\bar{U}^n = \frac{3}{2} U^{n-1} - \frac{1}{2} U^{n-2}$ for $n \geq 2$. The system

$$\langle \bar{\partial} U^n, \chi \rangle + \langle a(\bar{U}^n) \nabla \hat{U}^n, \nabla \chi \rangle = \langle f(\bar{U}^n), \chi \rangle, \ \forall \chi \in S_h, t_n \in J \qquad (7.6)$$

is linear and yields quadratic accuracy in time (see Theorem 7.9 below). However, we need both U^0 and U^1 to begin computing U^n via (7.6). This is accomplished by defining $U^{1,0}$ to be the solution of the linear system

$$\left\langle \frac{U^{1,0} - U^0}{k}, \chi \right\rangle + \left\langle a(U^0) \nabla \left(\frac{U^{1,0} - U^0}{2} \right), \nabla \chi \right\rangle = \langle f(U^0), \chi \rangle\,, \ \forall \chi \in S_h\,; \qquad (7.7)$$

and, U^1 determined by the solution of

$$\left\langle \bar{\partial} U^1, \chi \right\rangle + \left\langle a\left(\frac{U^{1,0} - U^0}{k}\right) \nabla \hat{U}^1, \nabla \chi \right\rangle = \left\langle f\left(\frac{U^{1,0} - U^0}{k}\right), \chi \right\rangle \,, \ \forall \chi \in S_h \,. \quad (7.8)$$

The error estimate (which is quadratic in space, h, and time, k) is given by the following theorem:

Theorem 7.1.2 (Theorem 13.5 [40]). *Let U^n be the solution of* (7.6)*, with U^1 coming from solving* (7.7) *and* (7.8) *and u the solution of* (7.1)*. Then, under the appropriate regularity assumptions for u, we have*

$$\|U^n - u(t_n)\|_2 \leq C\|u_{0,h} - u_0\|_2 + C(u)\|h^2 + k^2\|_2, \quad \textit{for } t_n \in \bar{J} \,. \qquad (7.9)$$

The scheme described in Theorem 7.1.2 was implemented using the Python programming language and the finite element package GetFEM++ which is a free GNU license finite element library written for C++ with implementations in C++, Matlab, Python and Scilab (http://download.gna.org/getfem/html/homepage).

7.2 Numerical Results

Numerical solutions were run using a long thin rectangle, $\Omega = \{(x, y) \in [0, 1] \times [0, .025]\}$ for the domain. The environmental heterogeneity was taken as a function of x only:

$$r(x, y) = \cos(2\pi x) + 2.4 \,. \qquad (7.10)$$

The finite element nodes were spaced $h = .025$ units apart and the time step, k, was .05. The rest of the parameters used were:

$d_1 = .01$	$d_2 = .05$	$d_3 = .001$
$e_1 = 1$	$a_1 = 1$	$h_1 = .1$
$e_2 = .5$	$a_2 = 1$	$h_2 = .1$
$e_3 = .2$	$a_3 = 2$	$h_3 = .1$
$\omega 1 = 1$	$\omega 2 = .3$	$\omega 3 = .4$
$\mu 1 = .1$	$\mu 2 = .4$	

These parameters were chosen so that:

- the IGPredator and resource have low random dispersal rates;
- the IGPredator cannot subsist locally on the resource productivity in the center of the domain, but the IGPrey can; and,
- the IGPredator is very hostile towards the IGPrey ($a_3 = 2$), but the IGPredator gains little from the consumption of the IGPrey ($e_3 = .2$).

This creates a situation where the $u - w$ subsystem has low IGPredator density in the center of the domain and a much higher density towards the edges that in turn makes $g^*(u, w)$ positive in the center of the domain and negative towards its edges. When the IGPrey dispersed randomly with diffusion coefficient d_2, these parameters resulted in the IGPrey being driven to extinction for all initial values tried. For all of the initial values used, the u and w components converged to the equilibrium pictured in Figure 7.1. Along with the resource and IGPredator equilibrium levels, Figure 7.1 shows the function $g^*(u,w)$ at this equilibrium.

This is the situation that was discussed in Section 5.4, where $\int_\Omega g^*(u,w)\,dx < 0$ and $\frac{1}{d_2} < \Lambda_1^+(g^*(u,w))$. Recall, the IGPrey can invade this equilibrium with random dispersal if and only if $\frac{1}{d_2} > \Lambda_1^+(g^*(u,w))$.

Methodically varying d_2 to estimate the value of $\Lambda_1^+(g^*(u,w))$ yielded an estimate of $\Lambda_1^+(g^*(u,w)) \approx 500$, or a critical value for d_2 of .002 for these parameters.

Figures 7.2 and 7.3 show coexistence equilibrium states for the system with all of the same parameters as Figure 7.1 except that the IGPrey is using fitness dependent dispersal. The specific choice for $M_\lambda(u,w)$ was the exponentially smoothed piecewise linear function

$$M_\lambda(g^*) = \begin{cases} d_2 & \text{for } g^* \geq 0\,, \\ -\lambda g^* e^{d_2/(\lambda g^*)} + d_2 & \text{for } g^* < 0\,, \end{cases} \tag{7.11}$$

(with $d_2 = .05$ as in the previous case). Figure 7.2 results from choosing $\lambda = 3$ and Figure 7.3 results from choosing $\lambda = 1.5$ (notice the scale diffrences for the v and M_λ graphs in these two figures). In both cases, the IGPrey has nearly constant density in the region where $g^* \geq 0$ and then decays sharply outside of this region. Larger values of λ result in higher IGPrey densities in this "good" region.

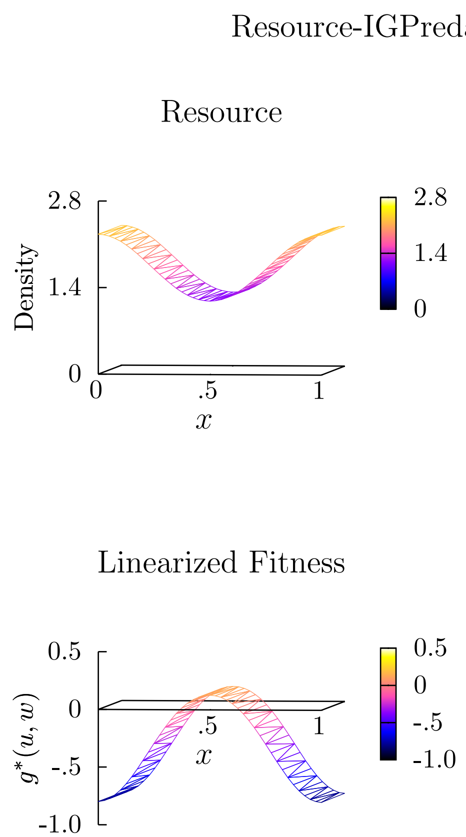

Figure 7.1: An equilibrium solution where the IGPrey has been driven to extinction. There is a narrow region in the center of Ω where $g^*(u,w) > 0$.

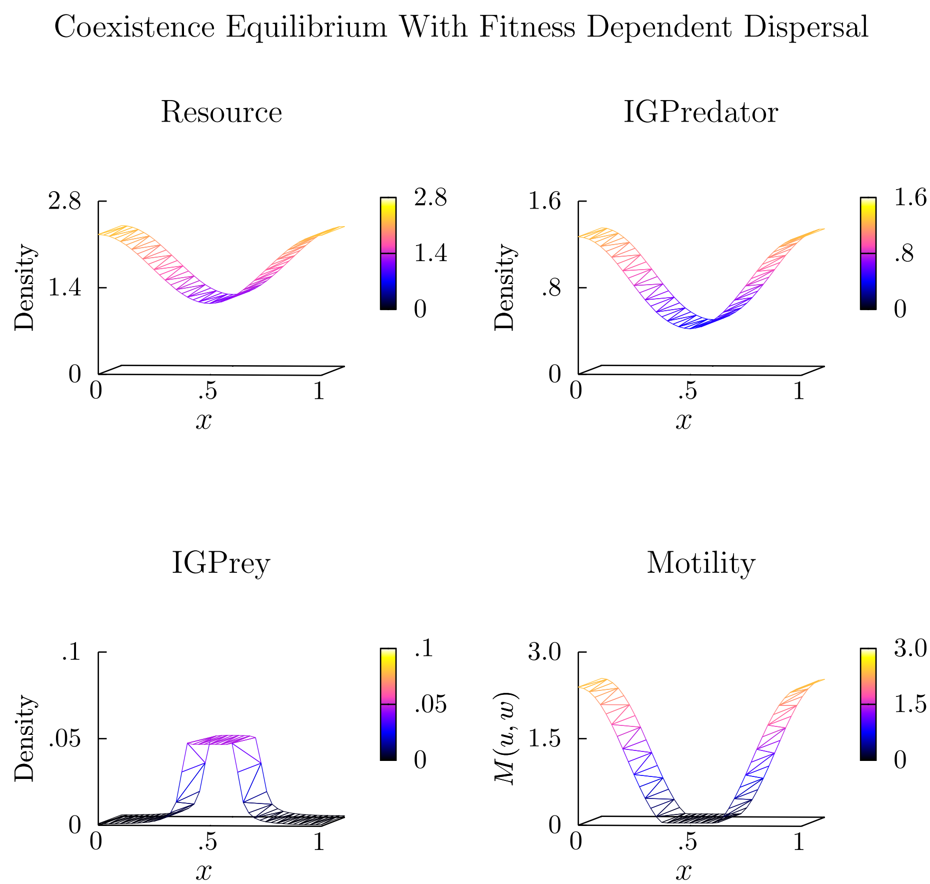

Figure 7.2: The coexistence equilibrium resulting from the IGPrey employing the fitness dependent movement strategy (7.11) with $\lambda = 3$.

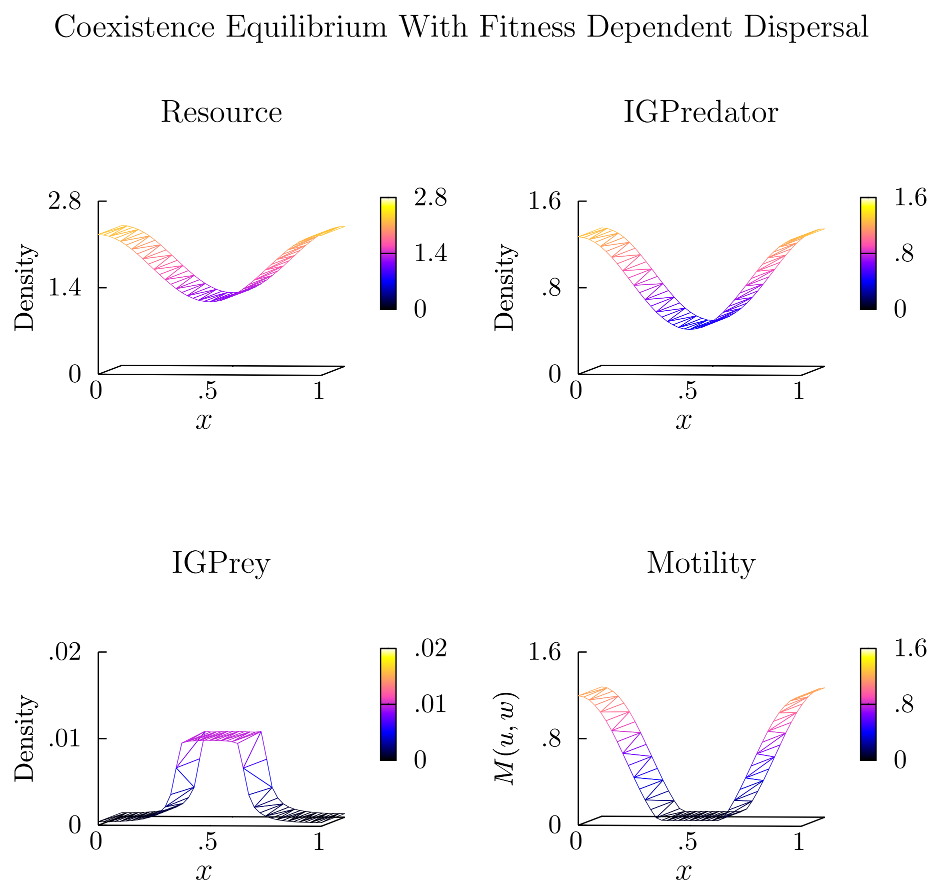

Figure 7.3: The coexistence equilibrium resulting from the IGPrey employing the fitness dependent movement strategy (7.11) with $\lambda = 1.5$.

Chapter 8

Conclusion

We have proposed a model for studying the effects of fitness dependent dispersal in an intraguild predation community module. We used a cross-diffusion system to model the population dynamics of the resource, IGPrey and IGPredator, under the assumption that the resource and IGPredator dispersed through the environment randomly and the IGPrey employed a movement strategy based on population densities of the resource and IGPredator.

In Chapter 3, we showed that the model system we developed has global solutions for any choice of movement strategy, $M(u, w)$ that was bounded below away from zero for nonnegative u and w and is twice differentiable.

In Chapter 4, we used a semiflow framework to study ecological permanence for the model. We restricted our choices of $M(u, w)$ to strategies that were a function of the IGPrey's fitness (linearized about $v \equiv 0$). We saw that if the strategy increased motility sufficiently in response to negative fitness, then the IGPrey would be uniformly persistent as long as there was some point in the domain that had positive fitness for all resource-IGPredator configurations arising from the global attractor of the $u - w$ subsystem.

This result seems complementary to the result from standard reaction-diffusion equations that if there is a point in the habitat where the species has positive fitness and the random diffusion level is small enough, then the species will persist under no-flux boundary conditions (see Proposition 3.16 of [11]). In that instance, small motility throughout the domain leads to coexistence because the loss due to *flux into the "bad" areas is small.* In our model with nonrandom dispersal, persistence is the result of a high motility in the "bad" region, i.e. *the flux out of the "bad" region is large.*

Chapter 5 showed that the conversion efficiencies, e_1 and e_2, could be used as bifurcation parameters to study the subsystems arising when the IGPredator or IG-Prey is absent. We showed that there were critical levels, e_1^* and e_2^*, at which locally stable (with some restrictions on M) positive equilibria bifurcated from the semi-trivial equilibrium state $(u^*, 0)$. We went on to show how the criteria for v invading this locally stable equilibrium of the $u - w$ subsystem differed in the case of random diffusion vs. fitness dependent dispersal.

The last piece of analytical study of (2.5) came in Chapter 6, where we investigated the effect of fitness dependent dispersal on the IGPredator's ability to invade a $u - v$ subsystem equilibrium. We developed sufficient criteria for the IGPredator to invade for all M of the type we have been considering.

The finite element numerical scheme developed in Chapter 7 provided simulation results confirming that fitness dependent dispersal could facilitate coexistence in cases where random diffusion failed to do so.

Recall that Holt and Polis in [19] used a Lotka-Volterra ODE model to study an intraguild predation community. They found that coexistence was most common when resource productivity was at an intermediate level. By introducing spatial heterogeneity into the system through a spatially varying resource productivity, we were able to examine the effects of nonrandom dispersal strategies for the IGPrey. We found that fitness dependent dispersal could enhance the IGPrey's ability to invade and persist in the system as long as there was some region in the environment where the resource/predation trade-off was sufficiently favorable (positive fitness). This is likely to occur when the environment has a large variation in resource productivity. The numerical simulations of Chapter 7 demonstrate an example where the resource varies significantly and the coexistence is attained through a partial segregation of the IGPrey and IGPredator. The IGPrey occupied the area with lower resource productivity (where its competitive ability gave it an advantage) and the IGPredator was more concentrated in areas of high resource productivity (where it was able to subsist at high enough density to cause significant predation pressure on the IGPrey). Priyanga Amarasekare found a similar segregation effect for fitness dependent dispersal in an ODE patch model with varying resource productivity [6].

This type of spatial heterogeneity can lead to coexistence with random diffusion as well; however, the segregation effect of the IGPrey's fitness dependent dispersal strategy leads to a significantly broader range of parameter values where coexistence can occur (because it is less likely to be driven to extinction). This suggests that an interplay between environmental and behavioral factors may be the reason why intraguild predation communities exhibit robust coexistence.

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