

Competition and Dispersal Delays in Patchy Environments

by

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Dedications

To my amazing father, Ayad Azer, and the most giving mother, Salwa Azer.

Supervisor: Dr. Pauline van den Driessche

ABSTRACT

Competition models for two species in a patchy environment are formulated as delay integro-differential equations that are coupled through competition and dispersal. Patches are identical, and dispersing species have an arbitrary distribution of dispersal times, different local dynamics and dispersal rates. The system is linearized around a non-negative steady state, and the resulting characteristic equation is analyzed. All solutions approach either a boundary equilibrium, or a spatially homogeneous or inhomogeneous steady state. High dispersal rates yield competitive exclusion and in some cases extinction. Numerical simulations are presented using a delta function distribution; thus all dispersing individuals have the same traveling time out of the patch. Biologically, high dispersal is usually a disadvantage. However, small dispersal rates (with certain parameter restrictions) can be an advantage to the dispersing species. Furthermore, as illustrated numerically, increasing the number of competitors to three yields oscillatory coexistence as a possible outcome to competition.

Supervisor: Dr. Pauline van den Driessche, (Department of Mathematics & Statistics)

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Chapter 1

Introduction and Literature Review

In ecological communities, an important role is played by competition, which has led to interest in competition models and their outcomes. A classical model of competition is due to Lotka (1932) and Volterra (1926); see for example [8, Chapter 12], [11, Section 3.5] and [7, Section 6.3]. The development given here follows that of [8]. Let N_1 and N_2 denote the densities of species 1 and 2, respectively. Let $r_i > 0$ and $K_i > 0$ denote the intrinsic growth rate and carrying capacity of species i , respectively, for $i = 1, 2$. Moreover, each species is assumed to grow logistically in the absence of the other according to the equations

$$\frac{dN_i(T)}{dT} = \frac{r_i}{K_i} N_i(T)(K_i - N_i(T)), \text{ for } i = 1, 2 \quad (1.1)$$

In including competition in the system (1.1), two additional interspecific

competition parameters are needed and they are denoted by α_{12} and α_{21} representing the effect of species 2 on species 1 and that of species 1 on species 2, respectively. This results in the classical Lotka-Volterra competition model equations

$$\begin{aligned}\frac{dN_1(T)}{dT} &= \frac{r_1}{K_1}N_1(T)(K_1 - N_1(T) - \alpha_{12}N_2(T)) \\ \frac{dN_2(T)}{dT} &= \frac{r_2}{K_2}N_2(T)(K_2 - N_2(T) - \alpha_{21}N_1(T))\end{aligned}\quad (1.2)$$

The above model is simplified by rescaling the variables and parameters as follows:

$$\begin{aligned}u_1 &= \frac{N_1}{K_1} & u_2 &= \frac{N_2}{K_2} \\ a_{12} &= \alpha_{12} \frac{K_2}{K_1} & a_{21} &= \alpha_{21} \frac{K_1}{K_2} \\ t &= r_1 T & \rho &= \frac{r_2}{r_1}\end{aligned}$$

This converts the system in (1.2) into the non-dimensional form

$$\begin{aligned}\frac{du_1}{dt} &= u_1(1 - u_1 - a_{12}u_2) \\ \frac{du_2}{dt} &= \rho u_2(1 - u_2 - a_{21}u_1)\end{aligned}\quad (1.3)$$

Global stability analysis of the non-dimensional system in (1.3) yields four possible outcomes summarized in Table 1.1, in which the positive steady state (u_1^*, u_2^*) represents coexistence of both species. The four possible outcomes are: competitive exclusion of species 2 with species 1 at its carrying capacity,

coexistence of both species at a value which is below their carrying capacities, initial condition dependent competitive exclusion, and competitive exclusion of species 1 with species 2 at its carrying capacity. The solutions of (1.3), with $u_i(0) > 0$, always approach a steady state, as the system has no limit cycle solutions. This can be easily proved using the Bendixson-Dulac negative criterion, as stated in [8, page 125]. Let

$$B(u_1, u_2) = \frac{1}{u_1 u_2} \quad (1.4)$$

then

$$\frac{\partial}{\partial u_1} \left(B \frac{du_1}{dt} \right) + \frac{\partial}{\partial u_2} \left(B \frac{du_2}{dt} \right) = -\frac{1}{u_2} - \frac{\rho}{u_1} < 0 \quad (1.5)$$

in the interior of the first quadrant, in which $u_1, u_2 > 0$. This ensures there are no closed orbits contained in the first quadrant. The conclusions of Table 1.1 now follow from an application of the Poincaré-Bendixson theorem, as in [8, page 137].

Realistically speaking, most species exist in patchy environments. Thus dispersal needs to be accounted for in the Lotka-Volterra competition model (1.2). This situation was studied by Takeuchi (1996); see [14, Chapter 5, Section 5.6]. The four-dimensional ordinary differential equation (ODE) model consists of 2 species denoted by N_1 and N_2 that compete between two non-identical patches (denoted by P and Q). Therefore, N_{ij} (for $i = 1, 2$ and $j = P, Q$) denotes the density of species i on patch j . Let r_{ij} and K_{ij} denote the growth rate and carrying capacity for species i on patch j , respectively. Moreover, denote the interspecific competition parameters on patch j by α_{12j}

	$a_{21} > 1$	$a_{21} < 1$
$a_{12} < 1$	<i>I: Competitive Exclusion (Species 1 wins)</i> (0, 0) - unstable (1, 0) - STABLE (0, 1) - unstable (u_1^*, u_2^*) - does not exist	<i>II: Coexistence</i> (0, 0) - unstable (1, 0) - unstable (0, 1) - unstable (u_1^*, u_2^*) - STABLE
$a_{12} > 1$	<i>III: Initial Condition Dependent Competitive Exclusion</i> (0, 0) - unstable (1, 0) - STABLE (0, 1) - STABLE (u_1^*, u_2^*) - unstable	<i>IV: Competitive Exclusion (Species 2 wins)</i> (0, 0) - unstable (1, 0) - unstable (0, 1) - STABLE (u_1^*, u_2^*) - does not exist

Table 1.1: Classical 2-species competition model: Summary of existence and global stability conditions for all steady states of (1.3)

and α_{21j} . Furthermore, let D_i be the dispersal rate for species i (the model given in [14, page 121] assumes that dispersal is both species and patch dependent). All parameters are assumed to be positive. The model equations are

$$\begin{aligned}
\frac{dN_{1P}}{dT} &= \frac{r_{1P}}{K_{1P}} N_{1P} (K_{1P} - N_{1P} - \alpha_{12P} N_{2P}) + D_1 [N_{1Q} - N_{1P}] \\
\frac{dN_{1Q}}{dT} &= \frac{r_{1Q}}{K_{1Q}} N_{1Q} (K_{1Q} - N_{1Q} - \alpha_{12Q} N_{2Q}) + D_1 [N_{1P} - N_{1Q}] \\
\frac{dN_{2P}}{dT} &= \frac{r_{2P}}{K_{2P}} N_{2P} (K_{2P} - N_{2P} - \alpha_{21P} N_{1P}) + D_2 [N_{2Q} - N_{2P}] \\
\frac{dN_{2Q}}{dT} &= \frac{r_{2Q}}{K_{2Q}} N_{2Q} (K_{2Q} - N_{2Q} - \alpha_{21Q} N_{1Q}) + D_2 [N_{2P} - N_{2Q}] \quad (1.6)
\end{aligned}$$

Possible boundary steady states of the system (1.6) are: $E_0 = (0, 0, 0, 0)$, $E_{N_1} = (\bar{N}_{1P}, \bar{N}_{1Q}, 0, 0)$, $E_{N_2} = (0, 0, \bar{N}_{2P}, \bar{N}_{2Q})$, which exist for any $D_i > 0$. Theorem 5.4.3 in [14] implies that E_{N_1} (E_{N_2}) is globally stable with respect to the positive N_1 (N_2) subspace. In addition, there may also exist a unique positive equilibrium point for the system in (1.6), in which case it is globally stable; see [14, page 121]. As proved by Takeuchi, for the case in which the patches are identical (i.e., $r_{iP} = r_{iQ} = r_i$, $K_{iP} = K_{iQ} = K_i$, $\alpha_{12P} = \alpha_{12Q} = \alpha_{12}$ and $\alpha_{21P} = \alpha_{21Q} = \alpha_{21}$, for $i = 1, 2$), the condition

$$\alpha_{21} < 1 < \frac{1}{\alpha_{12}} \quad (1.7)$$

ensures a positive equilibrium point exists for each patch. This is equivalent to $\alpha_{12} < 1$ and $\alpha_{21} < 1$ as in the classical case of competition between two species; see Table 1.1. Hence, competing species that disperse between two identical patches have a globally asymptotically stable equilibrium point for

any $D_i > 0$, $i = 1, 2$, provided the condition in (1.7) holds; see [14, page 124].

Another approach to analyzing competition models with dispersal was taken by Levin (1974), who analyzed the case of two species in two patches; see [10] and [16, Section 5.4.1]. As a special case of the model analyzed by Takeuchi [14], identical local dynamics and dispersal rates for the two species between the two patches are assumed. Therefore, $r_{ij} = r$, $K_{ij} = K$, $\alpha_{12j} = \alpha_{21j} = \alpha$ and $D_i = D$ denote growth rate, carrying capacity, inter-specific competition and dispersal rate, respectively, for $i = 1, 2$ and $j = P, Q$. As before, let N_{ij} denote the density of species i on patch j . The model equations are as in (1.6) with the above restrictions.

The assumption is made that the two species cannot coexist locally within a patch, i.e., $\alpha > 1$. In the case where $D = 0$, the model is the classical case of competition between two species and the outcome is similar to that obtained for the system in (1.2); thus only one species will be present in each patch. Due to the clear symmetry of this system, an obvious assumption is made in the case $D > 0$; assume $N_{1P} = N_{2Q}$ and $N_{2P} = N_{1Q}$. Using this assumption reduces the model equations to

$$\begin{aligned}\frac{dN_{1P}}{dT} &= \frac{r}{K}N_{1P}(K - N_{1P} - \alpha N_{2P}) + D[N_{2P} - N_{1P}] \\ \frac{dN_{2P}}{dT} &= \frac{r}{K}N_{2P}(K - N_{2P} - \alpha N_{1P}) + D[N_{1P} - N_{2P}]\end{aligned}\quad (1.8)$$

Replacing N_{1P} and N_{2P} by N_{2Q} and N_{1Q} , respectively, yields an identical pair of equations for patch Q . Adding the two right hand sides of (1.8) at

equilibrium gives

$$0 = N_{1P}^2 + N_{2P}^2 - KN_{1P} - KN_{2P} + 2\alpha N_{1P}N_{2P} \quad (1.9)$$

while subtracting them yields (for $N_{1P} \neq N_{2P}$)

$$N_{1P} + N_{2P} = \frac{K}{r}(r - 2D) \quad (1.10)$$

From (1.9) and (1.10), as D increases from 0, the two boundary equilibria move along the hyperbola (giving coexistence) until they coalesce with $N_{1P} = N_{2P} = \frac{K}{1+\alpha}$ and $D = \frac{r(\alpha-1)}{2(\alpha+1)}$. As proved in [16], the boundary equilibria are stable when $D = 0$, and remain so until slightly before the point of coalescence.

Biologically, the above results imply that for sufficiently small dispersal rates, the two species can coexist in this coupled patch model. However, as dispersal rates increase, ‘complete mixing’ occurs and the distinction between the two patches is lost. In this case, if $\alpha > 1$, coexistence is no longer possible, at least in a constant environment.

A model similar to the one presented in (1.6) is analyzed in a recent paper by Gourley and Kuang [4]. Species 1 and 2 have identical dispersal rates between the two patches denoted by P and Q , but have different local dynamics within each patch. This is a special case of the model discussed in (1.6) with $r_{ij} = K_{ij}$ and $\alpha_{12j} = \alpha_{21j} = 1$, for $i = 1, 2$ and $j = P, Q$. One conclusion of this paper, is that the boundary equilibria $(N_{1P}, N_{1Q}, 0, 0)$

and $(0, 0, N_{2P}, N_{2Q})$ are linearly stable to perturbations in which N_{2j} and N_{1j} remain zero, respectively, for $j = P, Q$. In the case $r_{2P} > r_{2Q}$, the winning strategy for species 1 as proved by Gourley and Kuang [4] is now summarized. If $r_{2P} > r_{2Q}$ and if species 1 widens the disparity between these birth rates (i.e., if species 1 adopts a higher birth rate in patch P , and a lower birth rate in patch Q), then species 1 will outcompete species 2, for a sufficiently large dispersal rate D .

In a paper by Hanski [5], a two species competition model with dispersal is discussed, in which the growth equations model the dynamics on fractions of patches containing species i , for $i = 1, 2$. Moreover, in a paper by Jansen and Lloyd [6], spatially homogeneous solutions of multi-patch systems are locally analyzed. Some work has also been done with delay competition models. An example of this is discussed in [1] in which the delay is introduced in the competition term.

Competition models in patchy environments discussed so far assume that dispersal is instantaneous. Realistically individuals that disperse take time to re-enter their patch. An arbitrary distribution of dispersal (travel) times between identical patches is introduced in this thesis.

Chapter 2 of this thesis is divided into two sections. The first section considers a one patch competition model with only one species dispersing. All steady states of the non-dimensional system are locally analyzed and the results are summarized in Theorem 2.1.4 and Table 2.1. Stated in this section

are some useful lemmas and tools used in the stability analysis throughout this thesis. In the second part of Chapter 2, the case with both species dispersing is locally analyzed and the results are summarized in Theorem 2.2.1 and Table 2.2. Chapter 3 considers a two patch model (identical patches) and is again divided into two main sections. The first section deals with the case of both species dispersing, while the second part considers the special case of only one species dispersing. The analytical and numerical results of both sections are summarized, for most spatially homogeneous and inhomogeneous steady states, in Theorem 3.1.1, Theorem 3.2.2, Table 3.1 and Table 3.2.

The general 2-species competition model is discussed in Chapter 4, in which both species disperse among an arbitrary number of identical patches. Local stability analysis of the boundary spatially homogeneous steady states is carried out and the results are summarized in Theorem 4.2.1. All analytical results are valid for an arbitrary distribution of dispersal times, and can be applied to special cases of the general models, such as constant travel time (as in the case of a delta function distribution explained below) and zero travel time (ODE models). To support analytical results for the models in which both species disperse, some numerical simulations were carried out, assuming a delta function distribution for dispersal times (i.e., all dispersing individuals take the same traveling time). The results along with supporting figures are discussed in the first part of Chapter 5. Some simulations are presented for models with 2 species dispersing among three patches, 2 species dispersing among two non-identical patches and 3 species dispersing

among two patches. The second part of Chapter 5 deals with the biological interpretations of the analytical and numerical results obtained.

Chapter 6 summarizes the conclusions of this thesis and suggests some open problems. Appendix A gives MatLab code which is used for numerical simulations of the one and two patch models with 2 species dispersing.

Chapter 2

One Patch Competition Model

2.1 Species 1 Disperses: Model Formulation

The total population densities of species 1 and 2 at time T are denoted by $N_1(T)$ and $N_2(T)$, respectively. Species 1 and 2 are assumed to have positive constant growth rates (the difference between birth and death rates) and carrying capacities, $r_1, K_1 > 0$ and $r_2, K_2 > 0$, respectively. For simplicity, we first assume that species 1 disperses at a rate $D_1 \geq 0$, while species 2 does not disperse at all. The interspecific competition parameter of species 2 on 1 is denoted by $\alpha_{12} > 0$, while that of species 1 on 2 is denoted by $\alpha_{21} > 0$. It is also reasonable to assume that different individuals in the species have different dispersal times, and also the traveling time varies between trips for a single individual. For this reason, a general probability density function, as in [12], denoted by $G_1(S) \geq 0$, is used to account for the time it takes an individual to disperse, given that the individual survives the trip. Hence, the product $G_1(S)dS$ is the probability that an individual disperses successfully,

departing at time T and completing the trip between time $T + S$ and time $T + S + dS$. Consequently,

$$\int_0^\infty G_1(S) dS = 1$$

Assume that for species 1, death during traveling is exponentially distributed with parameter $M_1 > 0$. The probability of an individual dying during a trip of duration S is represented by the cumulative distribution function $1 - e^{-M_1 S}$; see for example [2, Section 1.7]. Thus the probability that this individual survives the trip is $e^{-M_1 S}$, where M_1 is the death rate during travel. This distribution of travel times is incorporated into the first equation of the single patch model and the model equations are

$$\begin{aligned} \frac{dN_1(T)}{dT} &= \frac{r_1}{K_1} N_1(T) (K_1 - N_1(T) - \alpha_{12} N_2(T)) \\ &\quad + D_1 \left[\int_0^\infty G_1(S) e^{-M_1 S} N_1(T - S) dS - N_1(T) \right] \\ \frac{dN_2(T)}{dT} &= \frac{r_2}{K_2} N_2(T) (K_2 - N_2(T) - \alpha_{21} N_1(T)) \end{aligned} \quad (2.1)$$

In the absence of competition and dispersal, logistic growth is assumed; and if there is no dispersal (i.e., $D_1 = 0$) the above model is exactly the classical case of two competing species. It is useful to note that dispersing individuals do not participate in the competition and may die while traveling. In the above equation for species 1, the integral $\int_0^\infty G_1(S) e^{-M_1 S} N_1(T - S) dS$ realistically is $\int_0^{L_1} G_1(S) e^{-M_1 S} N_1(T - S) dS$ where L_1 is the longest life span of an individual in species 1. Note that, in Chapter 5, for the numerical simulations $G_1(S)$ is taken as a delta function, namely $G_1(S) = \delta(S - \mathcal{T})$.

We assume that initially $N_1(S) \geq 0$ for $S \in (-\infty, 0]$ with $N_1(0) > 0$ (and $N_1(S) = 0$ for $S \in (-\infty, -L_1)$); moreover $N_2(0) > 0$. Suppose that T_1 is the first positive time that $N_1(T) = 0$, then $\frac{dN_1(T_1)}{dT} > 0$. Thus $N_1(T) \geq 0$ for all T . Moreover, suppose T_2 is the first time that $N_2(T) = 0$, then $\frac{dN_2(T_2)}{dT} = 0$. This implies that $N_2(T) \geq 0$ for all T .

Assume also that $N_1(S) \leq K_1$ for $S \in (-\infty, 0]$ and $N_2(0) \leq K_2$. Let T_3 be the first time that $N_1(T) = K_1$, then $\frac{dN_1(T_3)}{dT} < 0$ implying that $N_1(T) \leq K_1$ for all T , and let T_4 be the first time that $N_2(T) = K_2$, then $\frac{dN_2(T_4)}{dT} \leq 0$ implying that $N_2(T) \leq K_2$ for all T .

Consequently, the non-negative region defined by

$$X_2 = \{(N_1, N_2) : 0 \leq N_i \leq K_i, \text{ for } i = 1, 2\}$$

is positively invariant and attracts all solutions, see [9, Chapter 2, Definition 3.5]. Therefore, it suffices to consider the dynamics of the system (2.1) on X_2 . Existence, for all $t \geq 0$, and uniqueness of the solution for the initial value problem follow from standard results; see for example [9, Chapter 2, Section 2.2].

2.1.1 Non-Dimensionalization

The analysis of the model is simplified by rescaling variables and parameters as follows:

$$\begin{aligned}
 u_1 &= \frac{N_1}{K_1} & u_2 &= \frac{N_2}{K_2} \\
 d_1 &= \frac{D_1}{r_1} & m_1 &= \frac{M_1}{r_1} \\
 a_{12} &= \alpha_{12} \frac{K_2}{K_1} & a_{21} &= \alpha_{21} \frac{K_1}{K_2} \\
 t &= r_1 T & s &= r_1 S & \rho &= \frac{r_2}{r_1}
 \end{aligned} \tag{2.2}$$

This converts (2.1) to the dimensionless form

$$\begin{aligned}
 \frac{du_1}{dt} &= u_1(1 - u_1 - a_{12}u_2) \\
 &\quad + d_1 \left[\int_0^\infty g_1(s) e^{-m_1 s} u_1(t-s) ds - u_1 \right] \\
 \frac{du_2}{dt} &= \rho u_2(1 - u_2 - a_{21}u_1)
 \end{aligned} \tag{2.3}$$

where $g_1(s)$ is the rescaled version of $G_1(S)$, namely $g_1(s) = \frac{1}{r_1} G_1(S)$, and the invariant region is

$$Y_2 = \{(u_1, u_2) : 0 \leq u_i \leq 1, \text{ for } i = 1, 2\}.$$

In these equations and in all that follows, it is understood that if time dependence is omitted, then the variable is evaluated at the current time t .

2.1.2 Determination of Steady States

Define

$$h_1 = 1 - d_1(1 - \tilde{g}_1(m_1)) \leq 1 \tag{2.4}$$

$$\tilde{g}_1(m_1) = \int_0^\infty g_1(s) e^{-m_1 s} ds \tag{2.5}$$

Here $\tilde{g}_1(m_1)$ is the (one-sided) Laplace transform of the travel time distribution $g_1(s)$. Note that for $m_1 > 0$, $\tilde{g}_1(m_1)$ is a positive, decreasing function with $\tilde{g}_1(0) = 1$. As for the dimensionless parameter h_1 , which is a measure of the difference between growth and dispersal, it decreases with increasing dispersal rate, and vice versa. In dimensional parameters, $h_1 = \frac{1}{r_1}(r_1 - D_1 + D_1\tilde{G}_1(M_1))$.

From the equations of the dimensionless system (2.3) at any steady state, the following relations are obtained:

$$u_1 = 0 \quad \text{or} \quad h_1 - u_1^* - a_{12}u_2^* = 0 \quad (2.6)$$

and

$$u_2 = 0 \quad \text{or} \quad 1 - u_2^* - a_{21}u_1^* = 0 \quad (2.7)$$

Solving for the steady states, four possible non-negative equilibria of the form $(\bar{u}_1, \bar{u}_2)$ are found, and they occur at the points:

$$\begin{aligned} & (0, 0) \qquad (h_1, 0) \text{ for } h_1 > 0 \qquad (0, 1) \\ & (u_1^*, u_2^*) = \left(\frac{h_1 - a_{12}}{1 - a_{12}a_{21}}, \frac{1 - a_{21}h_1}{1 - a_{12}a_{21}} \right) \end{aligned} \quad (2.8)$$

Here $u_1^* \leq h_1 \leq 1$, $u_2^* \leq 1$ and (u_1^*, u_2^*) is positive provided that $a_{12} < h_1$ and $a_{21}h_1 < 1$ (which implies that $a_{12}a_{21} < 1$), or $a_{12} > h_1$ and $a_{21}h_1 > 1$ (which implies that $a_{12}a_{21} > 1$). Thus in these cases $(u_1^*, u_2^*) \in Y_2$. Biologically these equilibria correspond to extinction of both species, competitive exclusion of species 2 with species 1 below its carrying capacity (due to dispersal), competitive exclusion of species 1 with species 2 at its carrying capacity, and coexistence of both species, respectively.

2.1.3 Local Stability Analysis For All Steady States

In order to proceed to analyze the dimensionless model (2.3), linear stability of each steady state in (2.8) is considered. As proved in Section 2.1, it suffices to analyze this system in Y_2 . Denote any non-negative equilibrium by $(\bar{u}_1, \bar{u}_2)$. The system is then linearized in the neighbourhood of this equilibrium, i.e., let $u_1 = \bar{u}_1 + v_1$ and $u_2 = \bar{u}_2 + v_2$, with $|v_i| \ll \bar{u}_i$, $i = 1, 2$. These relations are then substituted into the dimensionless model and after omitting all non-linear terms, the system (2.3) becomes

$$\begin{aligned} \frac{dv_1}{dt} &= v_1(1 - 2\bar{u}_1 - a_{12}\bar{u}_2) - a_{12}\bar{u}_1v_2 \\ &\quad + d_1\left[\int_0^\infty g_1(s)e^{-m_1s}v_1(t-s)ds - v_1\right] \\ \frac{dv_2}{dt} &= \rho v_2(1 - 2\bar{u}_2 - a_{21}\bar{u}_1) - \rho a_{21}\bar{u}_2v_1 \end{aligned}$$

Now, we look for solutions of the form:

$$v_1 = C_1 e^{\lambda t} \text{ and } v_2 = C_2 e^{\lambda t}$$

where C_1 and C_2 are arbitrary constants. Substituting these assumed solutions into the linearized equations gives

$$\begin{aligned} 0 &= C_1[1 - 2\bar{u}_1 - a_{12}\bar{u}_2 + d_1\tilde{g}_1(m_1 + \lambda) - d_1 - \lambda] - C_2a_{12}\bar{u}_1 \\ 0 &= C_1[-\rho a_{21}\bar{u}_2] + C_2[\rho(1 - 2\bar{u}_2 - a_{21}\bar{u}_1) - \lambda] \end{aligned} \quad (2.9)$$

where $\tilde{g}_1(m_1 + \lambda) = \int_0^\infty g_1(s)e^{-(m_1+\lambda)s}ds$. Thus the linearized coefficient matrix for (2.9) is

$A =$

$$\begin{pmatrix} 1 - 2\bar{u}_1 - a_{12}\bar{u}_2 + d_1\tilde{g}_1(m_1 + \lambda) - d_1 - \lambda & -a_{12}\bar{u}_1 \\ -\rho a_{21}\bar{u}_2 & \rho(1 - 2\bar{u}_2 - a_{21}\bar{u}_1) - \lambda \end{pmatrix}$$

Setting $\det(A) = 0$ assures that $(C_1, C_2) \neq (0, 0)$ and yields the following characteristic (quasi-polynomial) equation for λ ,

$$(1 - 2\bar{u}_1 - a_{12}\bar{u}_2 + d_1\tilde{g}_1(m_1 + \lambda) - d_1 - \lambda)(\rho(1 - 2\bar{u}_2 - a_{21}\bar{u}_1) - \lambda) = \rho a_{12} a_{12} \bar{u}_1 \bar{u}_2 \quad (2.10)$$

For most probability density functions $g(s)$ (including a delta distribution function as used in the numerical simulations in Chapter 5), equation (2.10) has an infinite number of roots. If all roots have negative real parts, then v_1 and v_2 tend to zero as $t \rightarrow \infty$, and the steady state $(\bar{u}_1, \bar{u}_2)$ is linearly asymptotically stable. On the other hand, if there is at least one root with positive real part, then $(\bar{u}_1, \bar{u}_2)$ is unstable. Precise definitions of linear asymptotic stability and instability and these statements are given in [9, Chapter 2, Definition 4.1, Theorem 4.1].

When applying this general linear analysis to the steady states in (2.8), the following three lemmas are used.

Lemma 2.1.1. *Let $\tilde{g}_1(m_1)$ be defined by (2.5). Then, for all $x \geq 0$ and $y \in \mathcal{R}$,*

$$|\tilde{g}_1(m_1 + x + iy)| \leq \tilde{g}_1(m_1) < 1$$

Proof:

$$\begin{aligned}
|\tilde{g}_1(m_1 + x + iy)| &= \left| \int_0^\infty g_1(s) e^{-m_1 s} e^{-xs} e^{-iys} ds \right| \\
&\leq \int_0^\infty |g_1(s) e^{-m_1 s}| |e^{-xs}| |e^{-iys}| ds \\
&\leq \int_0^\infty |g_1(s) e^{-m_1 s}| ds \\
&= \int_0^\infty g_1(s) e^{-m_1 s} ds \\
&= \tilde{g}_1(m_1) < 1
\end{aligned}$$

The second inequality follows since $|e^{-xs}| \leq 1$ for $x \geq 0$, and $|e^{-iys}| = 1$.

□

Lemma 2.1.2. *Let $\lambda - 1 + c + d_1 = \pm d_1 \tilde{g}_1(m_1 + \lambda)$ be a characteristic equation in λ where $c > h_1$ is a non-negative constant. Then $\operatorname{Re}(\lambda) < 0$ for all roots λ .*

Proof: Let $\lambda = x + iy$, where $y \in \mathcal{R}$ and suppose by contradiction that $x \geq 0$.

Then by taking the modulus of each side and squaring

$$\begin{aligned}
\lambda - 1 + c + d_1 &= \pm d_1 \tilde{g}_1(m_1 + \lambda) \\
\Rightarrow |x + iy - 1 + c + d_1|^2 &= |d_1 \tilde{g}_1(m_1 + \lambda)|^2 \\
&\leq d_1^2 \tilde{g}_1^2(m_1), \text{ by Lemma 2.1.1} \\
\Rightarrow (x - 1 + c + d_1)^2 + y^2 &\leq d_1^2 \tilde{g}_1^2(m_1) \\
\Rightarrow (x - 1 + c + d_1 - d_1 \tilde{g}_1(m_1))(x - 1 + c + d_1 + d_1 \tilde{g}_1(m_1)) &\leq -y^2 \\
\Rightarrow (x - h_1 + c)(x - h_1 + 2d_1 \tilde{g}_1(m_1) + c) &\leq -y^2
\end{aligned}$$

For $c > h_1$, the product on the left hand side of the above inequality is positive, whereas the right hand side is non-positive. This translates into

a contradiction to the original assumption that $x \geq 0$, and the lemma is proved. $\square$

The next result follows immediately from the Intermediate Value Theorem and monotonicity.

Lemma 2.1.3. *Let $f(x)$ be a real valued function that is differentiable on $[0, a]$ with $f(0) < 0$, $f(a) > 0$ and $f'(x) > 0$ for $x \in [0, a]$. Then there is a unique point $x \in (0, a)$ such that $f(x) = 0$.*

The linear stability analysis of (2.3) is summarized in the following result.

Theorem 2.1.4. *With h_1 defined by (2.4), the stability properties of all non-negative steady states of the system in (2.3) are given as follows:*

- (a) *The steady state $(0, 0)$ is always unstable*
- (b) *The steady state $(h_1, 0)$ is:*

$$\begin{aligned} \text{locally asymptotically stable if} \quad & a_{21}h_1 > 1 \\ \text{unstable if} \quad & a_{21}h_1 < 1 \end{aligned}$$

- (c) *The steady state $(0, 1)$ is:*

$$\begin{aligned} \text{locally asymptotically stable if} \quad & a_{12} > h_1 \\ \text{unstable if} \quad & a_{12} < h_1 \end{aligned}$$

- (d) *The steady state (u_1^*, u_2^*) given by (2.8) is:*

$$\begin{aligned} \text{locally asymptotically stable if} \quad & a_{12} < h_1 \text{ and } a_{21}h_1 < 1 \\ \text{unstable if} \quad & a_{12} > h_1 \text{ and } a_{21}h_1 > 1 \end{aligned}$$

Proof: In proving the statements of Theorem 2.1.4, the results obtained in (2.9) and (2.10) are applied to each steady state.

(a) *At the steady state $(0, 0)$:*

$$A(0, 0) = \begin{pmatrix} 1 + d_1 \tilde{g}_1(m_1 + \lambda) - d_1 - \lambda & 0 \\ 0 & \rho - \lambda \end{pmatrix}$$

Setting $\det(A(0, 0)) = 0$ gives $\lambda = \rho > 0$ as one solution and therefore $(0, 0)$ is always unstable.

(b) *At the steady state $(h_1, 0)$ for $h_1 > 0$:*

$$A(h_1, 0) = \begin{pmatrix} 1 - 2h_1 + d_1 \tilde{g}_1(m_1 + \lambda) - d_1 - \lambda & -a_{12}h_1 \\ 0 & \rho(1 - a_{21}h_1) - \lambda \end{pmatrix}$$

Setting $\det(A(h_1, 0)) = 0$ gives

$$\lambda = \rho(1 - a_{21}h_1) \quad (2.11)$$

$$\text{and} \quad \lambda = 1 - 2h_1 - d_1 + d_1 \tilde{g}_1(m_1 + \lambda) \quad (2.12)$$

From (2.11), if $a_{21}h_1 < 1$, then there exists a positive root and $(h_1, 0)$ is unstable. Thus, suppose that $a_{21}h_1 > 1$, then the root from (2.11) is negative. Equation (2.12) can be rewritten as

$$\lambda - 1 + 2h_1 + d_1 = d_1 \tilde{g}_1(m_1 + \lambda) \quad (2.13)$$

By Lemma 2.1.2, all the possible roots of (2.13) have negative real parts, and thus $(h_1, 0)$ is locally asymptotically stable.

(c) At the steady state $(0, 1)$:

$$A(0, 1) = \begin{pmatrix} 1 - a_{12} + d_1 \tilde{g}_1(m_1 + \lambda) - d_1 - \lambda & 0 \\ -\rho a_{21} & -\rho - \lambda \end{pmatrix}$$

Setting $\det(A(0, 1)) = 0$ gives $\lambda = -\rho < 0$, and the other solutions λ are roots of the equation

$$\lambda - 1 + a_{12} + d_1 = d_1 \tilde{g}_1(m_1 + \lambda) \quad (2.14)$$

If $a_{12} > h_1$, then $\operatorname{Re}(\lambda) < 0$ by Lemma 2.1.2, which in turn implies that $(0, 1)$ is locally asymptotically stable.

Now suppose that $a_{12} < h_1$ and let $\lambda = x \in \mathcal{R}$, then

$$x - 1 + a_{12} + d_1 = d_1 \tilde{g}_1(m_1 + x) \quad (2.15)$$

By letting $f(x) = x - 1 + a_{12} + d_1 - d_1 \tilde{g}_1(m_1 + x)$, equation (2.15) can be written as $f(x) = 0$. Then

$$\begin{aligned} f(0) &= -1 + a_{12} + d_1 - d_1 \tilde{g}_1(m_1) = a_{12} - h_1 < 0 \\ f(1) &= a_{12} + d_1 - d_1 \tilde{g}_1(m_1 + 1) > 0 \\ f'(x) &= 1 - d_1 \tilde{g}'(m_1 + x) > 0 \end{aligned}$$

Thus by Lemma 2.1.3 with $a = 1$, there exists a positive root x such that $f(x) = 0$, and so $(0, 1)$ is unstable. This proves Theorem 2.1.4(c).

(d) At the steady state (u_1^*, u_2^*) given by (2.8) for $a_{12}a_{21} \neq 1$:

$$A(u_1^*, u_2^*) = \begin{pmatrix} 1 - 2u_1^* - a_{12}u_2^* + d_1\tilde{g}_1(m_1 + \lambda) - d_1 - \lambda & -a_{12}u_1^* \\ -\rho a_{21}u_2^* & -\rho u_2^* - \lambda \end{pmatrix}$$

Setting $\det(A(u_1^*, u_2^*)) = 0$ gives

$$\begin{aligned} (1 - 2u_1^* - a_{12}u_2^* + d_1\tilde{g}_1(m_1 + \lambda) - d_1 - \lambda)(-\rho u_2^* - \lambda) &= \rho a_{12}a_{21}u_1^*u_2^* \\ \Rightarrow (\rho u_2^* + \lambda)(-1 + 2u_1^* + a_{12}u_2^* + d_1 + \lambda) - \rho a_{12}a_{21}u_1^*u_2^* & \\ &= d_1\tilde{g}_1(m_1 + \lambda)(\rho u_2^* + \lambda) \end{aligned} \quad (2.16)$$

Define

$$\begin{aligned} H(\lambda) &= (\rho u_2^* + \lambda)(-1 + 2u_1^* + a_{12}u_2^* + d_1 + \lambda) - \rho a_{12}a_{21}u_1^*u_2^* \\ \text{and } K(\lambda) &= (\rho u_2^* + \lambda)d_1\tilde{g}_1(m_1 + \lambda) \end{aligned}$$

The characteristic equation (2.16) can be expressed as

$$H(\lambda) = K(\lambda) \quad (2.17)$$

Using (2.6) yields

$$\begin{aligned} H(\lambda) &= (\rho u_2^* + \lambda)(u_1^* + d_1\tilde{g}_1(m_1) + \lambda) - \rho a_{12}a_{21}u_1^*u_2^* \\ &= \lambda^2 + \lambda(u_1^* + d_1\tilde{g}_1(m_1) + \rho u_2^*) + \rho u_1^*u_2^*(1 - a_{12}a_{21}) + \rho u_2^*d_1\tilde{g}_1(m_1) \end{aligned}$$

Clearly, $\lambda = 0$ is not a root of (2.17), since $H(0) = K(0) \iff a_{12}a_{21} = 1$. This is a clear contradiction, since in this case (u_1^*, u_2^*) does not exist. There are two cases to consider.

Case I: Suppose $a_{12} < h_1$ and $a_{21}h_1 < 1$ (which implies that $a_{12}a_{21} < 1$), and let $\lambda = x+iy$ with $x \geq 0$ and $x, y \in \mathcal{R}$. Then $|H(x+iy)|^2 = |K(x+iy)|^2$ implies

$$\begin{aligned} & \left| (x+iy)^2 + (x+iy)(u_1^* + d_1\tilde{g}_1(m_1) + \rho u_2^*) + \rho u_1^* u_2^* (1 - a_{12}a_{21}) + \rho u_2^* d_1\tilde{g}_1(m_1) \right|^2 \\ &= |(\rho u_2^* + x + iy)d_1\tilde{g}_1(m_1 + x + iy)|^2 \\ &\leq |\rho u_2^* + x + iy|^2 d_1^2 \tilde{g}_1^2(m_1) \\ &= [(\rho u_2^* + x)^2 + y^2] d_1^2 \tilde{g}_1^2(m_1) \end{aligned}$$

where the inequality comes from using Lemma 2.1.1.

Expanding and rearranging gives

$$\begin{aligned} & [x^2 - y^2 + x(u_1^* + \rho u_2^*) + \rho u_1^* u_2^* (1 - a_{12}a_{21}) + (\rho u_2^* + x)d_1\tilde{g}_1(m_1)]^2 \\ &+ y^2[(2x + u_1^* + \rho u_2^*)^2 + d_1^2 \tilde{g}_1^2(m_1) + 2(2x + u_1^* + \rho u_2^*)d_1\tilde{g}_1(m_1)] \\ &\leq (\rho u_2^* + x)^2 d_1^2 \tilde{g}_1^2(m_1) + y^2 d_1^2 \tilde{g}_1^2(m_1) \\ \Rightarrow & [x^2 - y^2 + x(u_1^* + \rho u_2^*) + \rho u_1^* u_2^* (1 - a_{12}a_{21})]^2 \\ &+ 2[x^2 + x(u_1^* + \rho u_2^*) + \rho u_1^* u_2^* (1 - a_{12}a_{21})](\rho u_2^* + x)d_1\tilde{g}_1(m_1) \\ &+ y^2[(2x + u_1^* + \rho u_2^*)^2 + 2(x + u_1^*)d_1\tilde{g}_1(m_1)] \\ &\leq 0 \end{aligned} \tag{2.18}$$

The left hand side of (2.18) is always positive whenever $x \geq 0$ and $1 > a_{12}a_{21}$.

This results in a contradiction, which in turn implies that $Re(\lambda) < 0$ for all roots λ ; hence (u_1^*, u_2^*) is locally asymptotically stable.

Case II: Suppose $a_{12} > h_1$ and $a_{21}h_1 > 1$ (which implies that $a_{12}a_{21} > 1$).

Take $\lambda = x \in \mathcal{R}$, then

$$H(x) = (\rho u_2^* + x)(u_1^* + d_1 \tilde{g}_1(m_1) + x) - \rho a_{12} a_{21} u_1^* u_2^*$$

and

$$K(x) = (\rho u_2^* + x) d_1 \tilde{g}_1(m_1 + x)$$

where, from (2.17), $H(x) = K(x)$. Note that this statement is not true if $\rho u_2^* + x = 0$, thus $\rho u_2^* + x \neq 0$. Dividing both expressions by $(\rho u_2^* + x)$ gives

$$\frac{H(x)}{\rho u_2^* + x} = u_1^* + d_1 \tilde{g}_1(m_1) + x - \frac{\rho a_{12} a_{21} u_1^* u_2^*}{\rho u_2^* + x}$$

and

$$\frac{K(x)}{\rho u_2^* + x} = d_1 \tilde{g}_1(m_1 + x)$$

Let $f(x) = \frac{H(x) - K(x)}{\rho u_2^* + x}$, then at the point $a = \rho u_2^*(a_{12} a_{21} - 1) > 0$

$$f(a) = d_1 \tilde{g}_1(m_1) + \rho u_2^*(a_{12} a_{21} - 1) - d_1 \tilde{g}_1(m_1 + \rho u_2^*(a_{12} a_{21} - 1)) > 0$$

$$f(0) = u_1^*(1 - a_{12} a_{21}) < 0$$

$$f'(x) = 1 + \frac{\rho a_{12} a_{21} u_1^* u_2^*}{(\rho u_2^* + x)^2} - d_1 \tilde{g}_1'(m_1 + x) > 0$$

Therefore by Lemma 2.1.3, there exists a positive root x of the equation (2.17), which implies that there is a root λ of (2.16) with $Re(\lambda) > 0$, and (u_1^*, u_2^*) is unstable.

This completes the proof of Theorem 2.1.4. □

A summary of existence and local stability conditions for $h_1 > 0$ are given in Table 2.1. For $h_1 \leq 0$, it follows from Box IV that $(0, 1)$ is stable and so species 2 outcompetes species 1.

$h_1 > 0$	$a_{21}h_1 > 1$	$a_{21}h_1 < 1$
$a_{12} < h_1$	<i>I: Competitive Exclusion (Species 1 wins)</i> (0, 0) - unstable $(h_1, 0)$ - STABLE (0, 1) - unstable (u_1^*, u_2^*) - does not exist	<i>II: Coexistence</i> (0, 0) - unstable $(h_1, 0)$ - unstable (0, 1) - unstable (u_1^*, u_2^*) - STABLE
$a_{12} > h_1$	<i>III: Initial Condition Dependent Competitive Exclusion</i> (0, 0) - unstable $(h_1, 0)$ - STABLE (0, 1) - STABLE (u_1^*, u_2^*) - unstable	<i>IV: Competitive Exclusion (Species 2 wins)</i> (0, 0) - unstable $(h_1, 0)$ - unstable (0, 1) - STABLE (u_1^*, u_2^*) - does not exist

Table 2.1: Summary of existence and local stability conditions for all steady states of the one patch model in (2.3) with only species 1 dispersing

2.2 When 2 Species Disperse

In some ecological situations, it may be more realistic to assume that both competitors disperse with different probability density functions. This situation is now analyzed showing how dispersal of species 2 modifies the previous results. It is also shown that extinction is possible for very high dispersal rates of both species. Incorporating a distribution of travel times for both species into the competition model gives the system

$$\begin{aligned}\frac{dN_1}{dT} &= \frac{r_1}{K_1} N_1 (K_1 - N_1 - \alpha_{12} N_2) \\ &\quad + D_1 \left[\int_0^\infty G_1(S) e^{-M_1 S} N_1(T-S) dS - N_1 \right] \\ \frac{dN_2}{dT} &= \frac{r_2}{K_2} N_2 (K_2 - N_2 - \alpha_{21} N_1) \\ &\quad + D_2 \left[\int_0^\infty G_2(S) e^{-M_2 S} N_2(T-S) dS - N_2 \right] \quad (2.19)\end{aligned}$$

Here, for the second species, D_2 , $G_2(S)$, and M_2 , are analogous to D_1 , $G_1(S)$, and M_1 in (2.1) and they represent dispersal rate, probability density function for dispersal, and the death rate of species 2 while traveling, respectively. In the previous section, L_1 , the longest life span of an individual of species 1, was introduced. Similarly, for species 2, the integral $\int_0^\infty G_2(S) e^{-M_2 S} N_2(T-S) dS$ realistically is $\int_0^{L_2} G_2(S) e^{-M_2 S} N_2(T-S) dS$ where L_2 is the longest life span of an individual in species 2.

Assume initially that $N_i(S) \geq 0$ for $S \in (-\infty, 0]$ with $N_i(0) > 0$ (and $N_i(S) = 0$ for $S \in (-\infty, -L_i)$) for $i = 1, 2$. Then, by a similar argument to

that given in Section 2.1, the non-negative region defined by

$$X_2 = \{(N_1, N_2) : 0 \leq N_i \leq K_i, \text{ for } i = 1, 2\}$$

is positively invariant and attracts all solutions; thus it suffices to consider the dynamics of the system (2.19) on X_2 . As before, existence for all $t \geq 0$ and uniqueness of the solution of the initial value problem follow from standard results; for an example, see [9, Chapter 2, Section 2.2].

The model in (2.19) is simplified by rescaling the new parameters as in (2.2) and also

$$d_2 = \frac{D_2}{r_2} \quad m_2 = \frac{M_2}{r_2} \quad g_2(s) = \frac{1}{r_1} G_2(S) \quad (2.20)$$

The model in (2.19) is converted into the non-dimensional form

$$\begin{aligned} \frac{du_1}{dt} &= u_1(1 - u_1 - a_{12}u_2) \\ &\quad + d_1 \left[\int_0^\infty g_1(s) e^{-m_1 s} u_1(t-s) ds - u_1 \right] \\ \frac{du_2}{dt} &= \rho u_2(1 - u_2 - a_{21}u_1) \\ &\quad + \rho d_2 \left[\int_0^\infty g_2(s) e^{-\rho m_2 s} u_2(t-s) ds - u_2 \right] \end{aligned} \quad (2.21)$$

This system is analyzed in the positively invariant region denoted by

$$Y_2 = \{(u_1, u_2) : 0 \leq u_i \leq 1, \text{ for } i = 1, 2\}$$

2.2.1 Steady States

Let h_1 and $\tilde{g}_1(m_1)$ be defined by (2.4) and (2.5), respectively, and define

$$h_2 = 1 - d_2(1 - \tilde{g}_2(\rho m_2)) \quad (2.22)$$

$$\tilde{g}_2(\rho m_2) = \int_0^\infty g_2(s) e^{-\rho m_2 s} ds, \quad (2.23)$$

Here $h_2 = \frac{1}{r_2}(r_2 - D_2 + D_2 \tilde{G}_2(\rho M_2))$ is the difference between growth and dispersal in species 2. Note that in the model of Section 2.1.1, $d_2 = 0 \iff h_2 = 1$.

The non-dimensional model in (2.21) has four possible non-negative steady states of the form $(\bar{u}_1, \bar{u}_2)$, and they occur at:

$$\begin{aligned} (0, 0) \quad & (h_1, 0) \text{ for } h_1 > 0 \quad (0, h_2) \text{ for } h_2 > 0 \\ (u_1^*, u_2^*) = & \left(\frac{h_1 - a_{12}h_2}{1 - a_{12}a_{21}}, \frac{h_2 - a_{21}h_1}{1 - a_{12}a_{21}} \right) \end{aligned} \quad (2.24)$$

Here $u_1^* \leq h_1 \leq 1$, $u_2^* \leq h_2 \leq 1$ and the steady state (u_1^*, u_2^*) is positive if $a_{12}h_2 < h_1$ and $a_{21}h_1 < h_2$ (which implies that $a_{12}a_{21} < 1$), or $a_{12}h_2 > h_1$ and $a_{21}h_1 > h_2$ (which implies that $a_{12}a_{21} > 1$). In these cases, $(u_1^*, u_2^*) \in Y_2$. As previously where only one species disperses, the equilibria have biological implications and the steady states in (2.24) correspond to extinction of both species, competitive exclusion of species 2 with species 1 below its carrying capacity (due to dispersal of species 1), competitive exclusion of species 1 with species 2 below its carrying capacity (due to dispersal of species 2), and coexistence of both species, respectively.

2.2.2 Local Stability Analysis

We proceed to analyze the system (2.21) in Y_2 through linearization in the neighbourhood of a non-negative steady state, denoted by $(\bar{u}_1, \bar{u}_2)$. Letting $u_1 = \bar{u}_1 + v_1$ and $u_2 = \bar{u}_2 + v_2$, with $|v_i| \ll \bar{u}_i$, $i = 1, 2$, converts (2.21) to the linearized system

$$\begin{aligned}
 \frac{dv_1}{dt} &= v_1(1 - 2\bar{u}_1 - a_{12}\bar{u}_2) - a_{12}\bar{u}_1v_2 \\
 &\quad + d_1\left[\int_0^\infty g_1(s)e^{-m_1s}v_1(t-s)ds - v_1\right] \\
 \frac{dv_2}{dt} &= \rho v_2(1 - 2\bar{u}_2 - a_{21}\bar{u}_1) - \rho a_{21}\bar{u}_2v_1 \\
 &\quad + \rho d_2\left[\int_0^\infty g_2(s)e^{-\rho m_2s}v_2(t-s)ds - v_2\right]
 \end{aligned} \tag{2.25}$$

We look for solutions of the form:

$$v_1 = C_1 e^{\lambda t} \text{ and } v_2 = C_2 e^{\lambda t}$$

where C_1 and C_2 are arbitrary constants. Substituting these solutions for v_1 and v_2 in the linearized equations gives

$$\begin{aligned}
 0 &= C_1[1 - 2\bar{u}_1 - a_{12}\bar{u}_2 + d_1\tilde{g}_1(m_1 + \lambda) - d_1 - \lambda] - C_2 a_{12}\bar{u}_1 \\
 0 &= C_1[-\rho a_{21}\bar{u}_2] + C_2[\rho(1 - 2\bar{u}_2 - a_{21}\bar{u}_1 + d_2\tilde{g}_2(\rho m_2 + \lambda) - d_2) - \lambda]
 \end{aligned} \tag{2.26}$$

where $\tilde{g}_2(\rho m_2 + \lambda) = \int_0^\infty g_2(s)e^{-(\rho m_2 + \lambda)s}ds$.

Letting $w_i = 1 - 2\bar{u}_i - d_i$ for $i = 1, 2$, the linearized coefficient matrix for (2.26) is

$$A = \begin{pmatrix} w_1 - a_{12}\bar{u}_2 + d_1\tilde{g}_1(m_1 + \lambda) - \lambda & -a_{12}\bar{u}_1 \\ -\rho a_{21}\bar{u}_2 & \rho(w_2 - a_{21}\bar{u}_1 + d_2\tilde{g}_2(\rho m_2 + \lambda)) - \lambda \end{pmatrix}$$

Setting $\det(A) = 0$ yields the following characteristic equation, with an infinite number of roots for λ ,

$$\begin{aligned} (w_1 - a_{12}\bar{u}_2 + d_1\tilde{g}_1(m_1 + \lambda) - \lambda)(\rho(w_2 - a_{21}\bar{u}_1 + d_2\tilde{g}_2(\rho m_2 + \lambda)) - \lambda) \\ = \rho a_{12} a_{21} \bar{u}_1 \bar{u}_2 \end{aligned} \quad (2.27)$$

Local stability analysis of (2.21) is summarized in the following theorem.

Theorem 2.2.1. *With h_1 and h_2 defined as in (2.4) and (2.22), respectively, the stability properties of the extinction and the competitive exclusion steady states of the system in (2.21) are given as follows:*

(a) *The steady state $(0, 0)$ is*

$$\begin{aligned} \text{locally asymptotically stable if } h_1, h_2 &< 0 \\ \text{unstable if } h_1 > 0 \text{ or } h_2 > 0 \end{aligned}$$

(b) *The steady state $(h_1, 0)$ is:*

$$\begin{aligned} \text{locally asymptotically stable if } a_{21}h_1 &> h_2 \\ \text{unstable if } a_{21}h_1 &< h_2 \end{aligned}$$

(c) *The steady state $(0, h_2)$ is:*

$$\begin{aligned} \text{locally asymptotically stable if } a_{12}h_2 &> h_1 \\ \text{unstable if } a_{12}h_2 &< h_1 \end{aligned}$$

Proof: In proving the conclusions of Theorem 2.2.1, the results obtained in (2.26) and (2.27) are applied to each steady state.

(a) *At the steady state $(0, 0)$:*

$$A(0, 0) = \begin{pmatrix} 1 + d_1\tilde{g}_1(m_1 + \lambda) - d_1 - \lambda & 0 \\ 0 & \rho(1 + d_2\tilde{g}_2(\rho m_2 + \lambda) - d_2) - \lambda \end{pmatrix}$$

Setting $\det(A(0, 0)) = 0$ gives two equations in λ .

$$\lambda - 1 + d_1 = d_1\tilde{g}_1(m_1 + \lambda) \quad (2.28)$$

$$\lambda - \rho + \rho d_2 = \rho d_2\tilde{g}_2(\rho m_2 + \lambda) \quad (2.29)$$

First consider (2.28). If $h_1 < 0$, then Lemma 2.1.2 for $c = 0$ implies $\operatorname{Re}(\lambda) < 0$. On the other hand, suppose $h_1 > 0$ and let $\lambda = x \in \mathcal{R}$, then from (2.28)

$$x - 1 + d_1 = d_1\tilde{g}_1(m_1 + x)$$

Let $f(x) = x - 1 + d_1 - d_1\tilde{g}_1(m_1 + x)$, then

$$f(0) = -1 + d_1 - d_1\tilde{g}_1(m_1) = -h_1 < 0$$

$$f(1) = d_1 - d_1\tilde{g}_1(m_1 + 1) > 0$$

$$f'(x) = 1 - d_1\tilde{g}'_1(m_1 + x) > 0$$

By Lemma 2.1.3, there exists a positive x satisfying $f(x) = 0$, which implies that there is a λ for (2.28) with $\operatorname{Re}(\lambda) > 0$ and so the steady state $(0, 0)$ is unstable.

Setting $\lambda = \rho\nu$ ($\rho > 0$) in (2.29) gives

$$\begin{aligned}\rho\nu - \rho + \rho d_2 &= \rho d_2 \tilde{g}_2(\rho m_2 + \rho\nu) \\ \Rightarrow \quad \nu - 1 + d_2 &= d_2 \tilde{g}_2(\rho m_2 + \rho\nu)\end{aligned}$$

This is identical to (2.28) with subscripts 1 and 2 interchanged. Thus results are identical to those obtained above with h_1 replaced by h_2 , and Theorem 2.2.1(a) is proved.

(b) *At the steady state $(h_1, 0)$ for $h_1 > 0$:*

$$A(h_1, 0) =$$

$$\begin{pmatrix} w_1 + d_1 \tilde{g}_1(m_1 + \lambda) - \lambda & -a_{12}h_1 \\ 0 & \rho(1 - a_{21}h_1 + d_2 \tilde{g}_2(\rho m_2 + \lambda) - d_2) - \lambda \end{pmatrix}$$

with $w_1 = 1 - 2h_1 - d_1$. Setting $\det(A(h_1, 0)) = 0$ gives two equations in λ .

$$\lambda - 1 + 2h_1 + d_1 = d_1 \tilde{g}_1(m_1 + \lambda) \quad (2.30)$$

$$\lambda - \rho(1 - a_{21}h_1 - d_2) = \rho d_2 \tilde{g}_2(\rho m_2 + \lambda) \quad (2.31)$$

By Lemma 2.1.2 for $c = 2h_1$, $Re(\lambda) < 0$ in (2.30). As for the equation in (2.31), let $\lambda = \rho\nu$, then

$$\nu - 1 + a_{21}h_1 + d_2 = d_2 \tilde{g}_2(\rho m_2 + \rho\nu) \quad (2.32)$$

If $a_{21}h_1 > h_2$, then by a result similar to that in Lemma 2.1.2, $Re(\nu) < 0$ which implies that $Re(\lambda) < 0$. This includes the case with $h_2 < 0$. Otherwise, if $a_{21}h_1 < h_2$ (which implies that $h_2 > 0$ since $h_1 > 0$) and $\nu = x \in \mathcal{R}$, then

let $f(x) = x - 1 + a_{21}h_1 + d_2 - d_2\tilde{g}_2(\rho m_2 + \rho x)$. This implies

$$\begin{aligned} f(0) &= -1 + a_{21}h_1 + d_2 - d_2\tilde{g}_2(\rho m_2) = a_{21}h_1 - h_2 < 0 \\ f(1) &= a_{21}h_1 + d_2 - d_2\tilde{g}_2(\rho m_2 + \rho) > 0 \\ f'(x) &= 1 - \rho d_2\tilde{g}_2'(\rho m_2 + \rho x) > 0 \end{aligned}$$

Therefore, by Lemma 2.1.3, there exists a positive root $x \in (0, 1)$ such that $f(x) = 0$. This implies that there is a λ with $\text{Re}(\lambda) > 0$ and so the steady state $(h_1, 0)$ is unstable.

(c) *At the steady state $(0, h_2)$ for $h_2 > 0$:*

$$A(0, h_2) =$$

$$\begin{pmatrix} 1 - a_{12}h_2 + d_1\tilde{g}_1(m_1 + \lambda) - d_1 - \lambda & 0 \\ -\rho a_{21}h_2 & \rho(w_2 + d_2\tilde{g}_2(\rho m_2 + \lambda)) - \lambda \end{pmatrix}$$

with $w_2 = 1 - 2h_2 - d_2$. Setting $\det(A(0, h_2)) = 0$ gives two equations in λ .

$$\lambda - 1 + a_{12}h_2 + d_1 = d_1\tilde{g}_1(m_1 + \lambda) \quad (2.33)$$

$$\lambda - \rho(1 - 2h_2 - d_2) = \rho d_2\tilde{g}_2(\rho m_2 + \lambda) \quad (2.34)$$

Setting $\lambda = \frac{\nu}{\rho}$ in (2.33) and $\lambda = \rho\nu$ in (2.34) and interchanging subscripts 1 and 2, this system is equivalent to (2.31) and (2.30). Therefore the results of Theorem 2.2.1(c) follow from those above for Theorem 2.2.1(b).

This completes the proof of Theorem 2.2.1. □

For this case with both species dispersing, local stability analysis of the coexistence steady state (u_1^*, u_2^*) , given by (2.24), using (2.27) has not been resolved (cf. one species dispersing). Existence and local stability of the steady states for $h_1, h_2 > 0$ are summarized in Table 2.2. If $h_1 \leq 0$ and $h_2 > 0$, then species 2 wins the competition (as in Box *IV*). However, if $h_1 > 0$ and $h_2 \leq 0$, then species 1 outcompetes species 2 (Box *I*). Furthermore, if $h_1, h_2 \leq 0$, then both species go extinct. Numerical results supporting stability/instability of this coexistence state, in Box *II/III*, are presented in Chapter 5.

$h_1, h_2 > 0$	$a_{21}h_1 > h_2$	$a_{21}h_1 < h_2$
	<i>I: Competitive Exclusion (Species 1 wins)</i>	<i>II: Coexistence?</i>
$a_{12}h_2 < h_1$	$(0, 0)$ - unstable $(h_1, 0)$ - STABLE $(0, h_2)$ - unstable (u_1^*, u_2^*) - does not exist	$(0, 0)$ - unstable $(h_1, 0)$ - unstable $(0, h_2)$ - unstable (u_1^*, u_2^*) - STABLE numerically
	<i>III: Initial Condition Dependent Competitive Exclusion</i>	<i>IV: Competitive Exclusion (Species 2 wins)</i>
$a_{12}h_2 > h_1$	$(0, 0)$ - unstable $(h_1, 0)$ - STABLE $(0, h_2)$ - STABLE (u_1^*, u_2^*) - unstable numerically	$(0, 0)$ - unstable $(h_1, 0)$ - unstable $(0, h_2)$ - STABLE (u_1^*, u_2^*) - does not exist

Table 2.2: Summary of existence and local stability conditions for all steady states of the two patch model in (2.21) with both species dispersing

Chapter 3

A Similar Competition Model With Two Patches

3.1 Two Patches: Dispersal of Both Species

In this nonlinear model, dispersing species travel between two patches denoted by P and Q ; thus N_{ij} represents the density of species i on patch j , for $i = 1, 2$ and $j = P, Q$. This notation is adopted from DeAngelis [3]. First, consider the general case in which both species disperse freely between the two patches. Species 1 and 2 are assumed to have different local dynamics and dispersal rates, and they interact competitively within the two patches, which in turn are coupled through dispersal. The system is closed, i.e., species must have left one patch in order to enter the other. Moreover, the two patches are assumed to be identical, so that for each species the parameters (growth rate, carrying capacity, interspecific competition constant, dispersal rate, and death rate due to dispersal) in the first patch are as-

sumed to be the same as those in the second patch. Detailed definitions and assumptions for the model parameters are as stated in Sections 2.1 and 2.2.

The model equations are

$$\begin{aligned}
\frac{dN_{1P}}{dT} &= \frac{r_1}{K_1} N_{1P} (K_1 - N_{1P} - \alpha_{12} N_{2P}) \\
&\quad + D_1 \left[\int_0^\infty G_1(S) e^{-M_1 S} N_{1Q} (T - S) dS - N_{1P} \right] \\
\frac{dN_{1Q}}{dT} &= \frac{r_1}{K_1} N_{1Q} (K_1 - N_{1Q} - \alpha_{12} N_{2Q}) \\
&\quad + D_1 \left[\int_0^\infty G_1(S) e^{-M_1 S} N_{1P} (T - S) dS - N_{1Q} \right] \\
\frac{dN_{2P}}{dT} &= \frac{r_2}{K_2} N_{2P} (K_2 - N_{2P} - \alpha_{21} N_{1P}) \\
&\quad + D_2 \left[\int_0^\infty G_2(S) e^{-M_2 S} N_{2Q} (T - S) dS - N_{2P} \right] \\
\frac{dN_{2Q}}{dT} &= \frac{r_2}{K_2} N_{2Q} (K_2 - N_{2Q} - \alpha_{21} N_{1Q}) \\
&\quad + D_2 \left[\int_0^\infty G_2(S) e^{-M_2 S} N_{2P} (T - S) dS - N_{2Q} \right] \quad (3.1)
\end{aligned}$$

Assume initially that $N_{ij}(S) \geq 0$ for $S \in (-\infty, 0]$ with $N_{ij}(0) > 0$ (and $N_{ij}(S) = 0$ for $S \in (-\infty, -L_i)$) for $i = 1, 2$ and $j = P, Q$; L_1 and L_2 are as defined in Chapter 2. Then by a similar argument as in Sections 2.1 and 2.2, $N_{ij}(T) \geq 0$ for all $T \geq 0$ and $N_{ij}(T) \leq K_i$ for $i = 1, 2$ and $j = P, Q$. Thus the region

$$X_4 = \{(N_{1P}, N_{1Q}, N_{2P}, N_{2Q}) : 0 \leq N_{ij} \leq K_i\}$$

is positively invariant and attracts all solutions, so it suffices to consider the dynamics on X_4 . Again, for all $t \geq 0$, existence and uniqueness of the solution of the initial value problem follow from standard results; see for example

[9, Chapter 2, Section 2.2].

The model equations in (3.1) can be simplified by rescaling the parameters as in (2.2) and (2.20) with $u_{ij} = \frac{N_{ij}}{K_i}$ for $i = 1, 2$ and $j = P, Q$; thus resulting in the non-dimensional system

$$\begin{aligned}
\frac{du_{1P}}{dt} &= u_{1P}(1 - u_{1P} - a_{12}u_{2P}) \\
&\quad + d_1 \left[\int_0^\infty g_1(s)e^{-m_1s}u_{1Q}(t-s)ds - u_{1P} \right] \\
\frac{du_{1Q}}{dt} &= u_{1Q}(1 - u_{1Q} - a_{12}u_{2Q}) \\
&\quad + d_1 \left[\int_0^\infty g_1(s)e^{-m_1s}u_{1P}(t-s)ds - u_{1Q} \right] \\
\frac{du_{2P}}{dt} &= \rho u_{2P}(1 - u_{2P} - a_{21}u_{1P}) \\
&\quad + \rho d_2 \left[\int_0^\infty g_2(s)e^{-\rho m_2s}u_{2Q}(t-s)ds - u_{2P} \right] \\
\frac{du_{2Q}}{dt} &= \rho u_{2Q}(1 - u_{2Q} - a_{21}u_{1Q}) \\
&\quad + \rho d_2 \left[\int_0^\infty g_2(s)e^{-\rho m_2s}u_{2P}(t-s)ds - u_{2Q} \right] \quad (3.2)
\end{aligned}$$

In the following sections this system is analyzed in the positively invariant region

$$Y_4 = \{(u_{1P}, u_{1Q}, u_{2P}, u_{2Q}) : 0 \leq u_{ij} \leq 1, \text{ for } i = 1, 2 \text{ and } j = P, Q\}$$

3.1.1 Steady States

Let h_1 , h_2 , $\tilde{g}_1(m_1)$, and $\tilde{g}_2(\rho m_2)$ be defined as in (2.4), (2.22), (2.5), and (2.23), respectively. Solving for the steady states of the form $(\bar{u}_{1P}, \bar{u}_{1Q}, \bar{u}_{2P}, \bar{u}_{2Q})$ of the non-dimensional system in (3.2) gives the following spatially homoge-

neous steady states $(\bar{u}_{1P}, \bar{u}_{1P}, \bar{u}_{2P}, \bar{u}_{2P})$ lying in Y_4 :

$$\begin{aligned}
 & (0, 0, 0, 0) \quad (h_1, h_1, 0, 0) \text{ for } h_1 > 0 \quad (0, 0, h_2, h_2) \text{ for } h_2 > 0 \\
 & (u_{1P}^*, u_{1P}^*, u_{2P}^*, u_{2P}^*) \text{ for } u_{1P}^* = u_1^* \text{ and } u_{2P}^* = u_2^* \\
 & \text{where } u_1^* \text{ and } u_2^* \text{ are defined as in (2.24)} \quad (3.3)
 \end{aligned}$$

Biologically, the steady states represent extinction of both species on the two patches, competitive exclusion of species 2 on both patches with species 1 below its carrying capacity (due to dispersal), competitive exclusion of species 1 on both patches with species 2 below its carrying capacity (due to dispersal), and coexistence of both species on the two patches with the same densities of species i on both patches, for $i = 1, 2$. These spatially homogeneous steady states are also called flat steady states [6].

The positive spatially inhomogeneous steady states in Y_4 are of the form $(u_{1P}^*, u_{1Q}^*, u_{2P}^*, u_{2Q}^*)$ and $(u_{1Q}^*, u_{1P}^*, u_{2Q}^*, u_{2P}^*)$, for $u_{1P}^* \neq u_{1Q}^*$ and $u_{2P}^* \neq u_{2Q}^*$. These have not been ruled out analytically, but were never found in numerical simulations of the system in (3.2). However, for special cases in which $d_1 = d_2$, $\tilde{g}_1(m_1) = \tilde{g}_2(\rho m_2)$ with $\rho = 1$, and $a_{12}, a_{21} > 1$, two positive inhomogeneous steady states were found and are stable for some initial conditions, as illustrated in Chapter 5.

3.1.2 Local Stability Analysis

Stability analysis of the non-dimensional system (2.21) in Y_4 is done by linearization in the neighbourhood of a non-negative equilibrium point, denoted by $(\bar{u}_{1P}, \bar{u}_{1Q}, \bar{u}_{2P}, \bar{u}_{2Q})$. Let $u_{ij} = \bar{u}_{ij} + v_{ij}$ with $|v_{ij}| \ll \bar{u}_{ij}$, for $i = 1, 2$ and

$j = P, Q$. Substituting these relations in (3.2) and omitting all non-linear terms gives

$$\begin{aligned}
\frac{dv_{1P}}{dt} &= v_{1P}(1 - 2\bar{u}_{1P} - a_{12}\bar{u}_{2P}) - a_{12}\bar{u}_{1P}v_{2P} \\
&\quad + d_1\left[\int_0^\infty g_1(s)e^{-m_1s}v_{1Q}(t-s)ds - v_{1P}\right] \\
\frac{dv_{1Q}}{dt} &= v_{1Q}(1 - 2\bar{u}_{1Q} - a_{12}\bar{u}_{2Q}) - a_{12}\bar{u}_{1Q}v_{2Q} \\
&\quad + d_1\left[\int_0^\infty g_1(s)e^{-m_1s}v_{1P}(t-s)ds - v_{1Q}\right] \\
\frac{dv_{2P}}{dt} &= \rho v_{2P}(1 - 2\bar{u}_{2P} - a_{21}\bar{u}_{1P}) - \rho a_{21}\bar{u}_{2P}v_{1P} \\
&\quad + \rho d_2\left[\int_0^\infty g_2(s)e^{-\rho m_2s}v_{2Q}(t-s)ds - v_{2P}\right] \\
\frac{dv_{2Q}}{dt} &= \rho v_{2Q}(1 - 2\bar{u}_{2Q} - a_{21}\bar{u}_{1Q}) - \rho a_{21}\bar{u}_{2Q}v_{1Q} \\
&\quad + \rho d_2\left[\int_0^\infty g_2(s)e^{-\rho m_2s}v_{2P}(t-s)ds - v_{2Q}\right] \quad (3.4)
\end{aligned}$$

We look for solutions of the form:

$$v_{ij} = C_{ij}e^{\lambda t} \text{ for } i = 1, 2 \text{ and } j = P, Q$$

where C_{ij} is an arbitrary constant. Substituting the assumed solutions into the linearized equations and setting $\bar{w}_{ij} = 1 - 2\bar{u}_{ij} - d_i$ for $i = 1, 2$ and $j = P, Q$ gives

$$\begin{aligned}
0 &= C_{1P}[\bar{w}_{1P} - a_{12}\bar{u}_{2P} - \lambda] + C_{1Q}[d_1\tilde{g}_1(m_1 + \lambda)] - C_{2P}[a_{12}\bar{u}_{1P}] \\
0 &= C_{1Q}[\bar{w}_{1Q} - a_{12}\bar{u}_{2Q} - \lambda] + C_{1P}[d_1\tilde{g}_1(m_1 + \lambda)] - C_{2Q}[a_{12}\bar{u}_{1Q}] \\
0 &= -C_{1P}[\rho a_{21}\bar{u}_{2P}] + C_{2P}[\rho(\bar{w}_{2P} - a_{21}\bar{u}_{1P}) - \lambda] + C_{2Q}[\rho d_2\tilde{g}_2(\rho m_2 + \lambda)] \\
0 &= -C_{1Q}[\rho a_{21}\bar{u}_{2Q}] + C_{2Q}[\rho(\bar{w}_{2Q} - a_{21}\bar{u}_{1Q}) - \lambda] + C_{2P}[\rho d_2\tilde{g}_2(\rho m_2 + \lambda)]
\end{aligned}$$

The linearized coefficient matrix can be written as $B - \lambda I$, where I is the 4×4 identity matrix and

$$B = \begin{pmatrix} \bar{w}_{1P} - a_{12}\bar{u}_{2P} & d_1\tilde{g}_1(m_1 + \lambda) & -a_{12}\bar{u}_{1P} & 0 \\ d_1\tilde{g}_1(m_1 + \lambda) & \bar{w}_{1Q} - a_{12}\bar{u}_{2Q} & 0 & -a_{12}\bar{u}_{1Q} \\ -\rho a_{21}\bar{u}_{2P} & 0 & \rho(\bar{w}_{2P} - a_{21}\bar{u}_{1P}) & \rho d_2\tilde{g}_2(\rho m_2 + \lambda) \\ 0 & -\rho a_{21}\bar{u}_{2Q} & \rho d_2\tilde{g}_2(\rho m_2 + \lambda) & \rho(\bar{w}_{2Q} - a_{21}\bar{u}_{1Q}) \end{pmatrix}$$

In proving the local stability for the steady states of the system in (3.2), the above matrix is considered at each of the equilibrium points. Theorem 3.1.1 summarizes the local stability results, which are the same as those for the one patch model (Theorem 2.2.1).

Theorem 3.1.1. *Let h_1 and h_2 be defined as in (2.4) and (2.22), respectively. The stability properties of the extinction and the competitive exclusion steady states in (3.2) are given as follows:*

(a) *The steady state $(0, 0, 0, 0)$ is*

$$\begin{aligned} \text{locally asymptotically stable if} \quad & h_1, h_2 < 0 \\ \text{unstable if} \quad & h_1 > 0 \quad \text{or} \quad h_2 > 0 \end{aligned}$$

(b) *The steady state $(h_1, h_1, 0, 0)$ is:*

$$\begin{aligned} \text{locally asymptotically stable if} \quad & a_{21}h_1 > h_2 \\ \text{unstable if} \quad & a_{21}h_1 < h_2 \end{aligned}$$

(c) *The steady state $(0, 0, h_2, h_2)$ is:*

$$\begin{aligned} \text{locally asymptotically stable if} \quad & a_{12}h_2 > h_1 \\ \text{unstable if} \quad & a_{12}h_2 < h_1 \end{aligned}$$

Proof:

(a) At the steady state $(0, 0, 0, 0)$:

$$B(0, 0, 0, 0) - \lambda I =$$

$$\begin{pmatrix} 1 - d_1 - \lambda & d_1 \tilde{g}_1(m_1 + \lambda) & 0 & 0 \\ d_1 \tilde{g}_1(m_1 + \lambda) & 1 - d_1 - \lambda & 0 & 0 \\ 0 & 0 & \rho - \rho d_2 - \lambda & \rho d_2 \tilde{g}_2(\rho m_2 + \lambda) \\ 0 & 0 & \rho d_2 \tilde{g}_2(\rho m_2 + \lambda) & \rho - \rho d_2 - \lambda \end{pmatrix}$$

The matrix is a direct sum and all that remains is to find the sign of $Re(\lambda)$ for each of the sub-matrices above.

Let

$$M(0, 0, 0, 0) = \begin{pmatrix} 1 - d_1 - \lambda & d_1 \tilde{g}_1(m_1 + \lambda) \\ d_1 \tilde{g}_1(m_1 + \lambda) & 1 - d_1 - \lambda \end{pmatrix}$$

Setting $\det(M(0, 0, 0, 0)) = 0$ gives the following equation in λ .

$$\begin{aligned} (1 - d_1 - \lambda)^2 &= d_1^2 \tilde{g}_1^2(m_1 + \lambda) \\ \Rightarrow 1 - d_1 - \lambda &= \pm d_1 \tilde{g}_1(m_1 + \lambda) \end{aligned} \quad (3.5)$$

There are two cases to consider.

Case I: Let $1 - d_1 - \lambda = -d_1 \tilde{g}_1(m_1 + \lambda)$, then

$$\lambda - 1 + d_1 = d_1 \tilde{g}_1(m_1 + \lambda) \quad (3.6)$$

This case is identical to the one discussed in the proof of Theorem 2.2.1

(a), and therefore for $h_1 < 0$, $Re(\lambda) < 0$ for all roots λ in (3.6), and

$h_1 > 0 \Rightarrow Re(\lambda) > 0$ for some λ in (3.6) and so the steady state $(0, 0, 0, 0)$ is unstable.

Case II: Let $1 - d_1 - \lambda = d_1 \tilde{g}_1(m_1 + \lambda)$, then

$$\lambda - 1 + d_1 = -d_1 \tilde{g}_1(m_1 + \lambda) \quad (3.7)$$

To determine the sign of $Re(\lambda)$ in (3.7), we only need to consider the case in which $h_1 < 0$, since for $h_1 > 0$ the steady state $(0, 0, 0, 0)$ is unstable as proved in Case I. Therefore, by Lemma 2.1.2, $h_1 < 0$ implies that $Re(\lambda) < 0$ for all roots λ in (3.7).

In conclusion, $Re(\lambda) < 0$ for all roots λ of (3.5) whenever $h_1 < 0$, while for $h_1 > 0$, $Re(\lambda) > 0$ for some λ in (3.5).

Next we consider the second sub-matrix of $B(0, 0, 0, 0) - \lambda I$. Let

$$L(0, 0, 0, 0) = \begin{pmatrix} \rho - \rho d_2 - \lambda & \rho d_2 \tilde{g}_2(\rho m_2 + \lambda) \\ \rho d_2 \tilde{g}_2(\rho m_2 + \lambda) & \rho - \rho d_2 - \lambda \end{pmatrix}$$

Setting $\det(L(0, 0, 0, 0)) = 0$ and letting $\lambda = \rho\nu$ gives

$$1 - d_2 - \nu = \pm d_2 \tilde{g}_2(\rho m_2 + \rho\nu) \quad (3.8)$$

This is identical to (3.5) with subscripts 1 and 2 interchanged. Note that the positive parameter ρ in $g_2(\rho m_2 + \rho\nu)$ does not affect the overall local stability results and therefore the statements of Theorem 3.1.1(a) follow by a similar argument as the one used above.

(b) At the steady state $(h_1, h_1, 0, 0)$: for $h_1 > 0$

$$B(h_1, h_1, 0, 0) =$$

$$\begin{pmatrix} 1 - 2h_1 - d_1 & d_1\tilde{g}_1(m_1 + \lambda) & -a_{12}h_1 & 0 \\ d_1\tilde{g}_1(m_1 + \lambda) & 1 - 2h_1 - d_1 & 0 & -a_{12}h_1 \\ 0 & 0 & \rho(1 - d_2 - a_{21}h_1) & \rho d_2\tilde{g}_2(\rho m_2 + \lambda) \\ 0 & 0 & \rho d_2\tilde{g}_2(\rho m_2 + \lambda) & \rho(1 - d_2 - a_{21}h_1) \end{pmatrix}$$

Again the matrix $B(h_1, h_1, 0, 0) - \lambda I$ reduces and we proceed to find the sign of $Re(\lambda)$ for each of the principal sub-matrices above. First, let

$$M(h_1, h_1, 0, 0) = \begin{pmatrix} 1 - 2h_1 - d_1 - \lambda & d_1\tilde{g}_1(m_1 + \lambda) \\ d_1\tilde{g}_1(m_1 + \lambda) & 1 - 2h_1 - d_1 - \lambda \end{pmatrix}$$

Setting $\det(M(h_1, h_1, 0, 0)) = 0$ gives

$$\begin{aligned} 1 - 2h_1 - d_1 - \lambda &= \pm d_1\tilde{g}_1(m_1 + \lambda) \\ \Rightarrow \lambda - 1 + 2h_1 + d_1 &= \pm d_1\tilde{g}_1(m_1 + \lambda) \end{aligned} \quad (3.9)$$

Therefore, by Lemma 2.1.2, $Re(\lambda) < 0$ for all roots λ in (3.9).

The second sub-matrix in $B(h_1, h_1, 0, 0) - \lambda I$ is:

$$L(h_1, h_1, 0, 0) = \begin{pmatrix} \rho(1 - d_2 - a_{21}h_1) - \lambda & \rho d_2\tilde{g}_2(\rho m_2 + \lambda) \\ \rho d_2\tilde{g}_2(\rho m_2 + \lambda) & \rho(1 - d_2 - a_{21}h_1) - \lambda \end{pmatrix}$$

Setting $(\det(L(h_1, h_1, 0, 0)) = 0$ and letting $\lambda = \rho\nu$, for $\rho > 0$, gives two characteristic equations

$$\nu - 1 + d_2 + a_{21}h_1 = \pm d_2\tilde{g}_2(\rho m_2 + \rho\nu) \quad (3.10)$$

For the case in which $a_{21}h_1 > h_2$, Lemma 2.1.2, with $c = a_{21}h_1$, implies that $Re(\lambda) < 0$.

Now suppose $0 < a_{21}h_1 < h_2$, and let $f(x) = x - 1 + d_2 + a_{21}h_1 - d_2\tilde{g}_2(\rho m_2 + \rho x)$. Then the equation $\nu - 1 + d_2 + a_{21}h_1 = d_2\tilde{g}_2(\rho m_2 + \rho\nu)$, in (3.10), can be expressed as $f(x) = 0$. This is exactly the case discussed in the proof of Theorem 2.2.1 (b), and therefore, by Lemma 2.1.3, there exists a positive root $x \in (0, 1)$ such that $f(x) = 0$. This implies there exists some λ with $Re(\lambda) > 0$ and so the steady state $(h_1, h_1, 0, 0)$ is unstable.

(c) *At the steady state $(0, 0, h_2, h_2)$: for $h_2 > 0$*

$$B(0, 0, h_2, h_2) =$$

$$\begin{pmatrix} 1 - d_1 - a_{12}h_2 & d_1\tilde{g}_1(m_1 + \lambda) & 0 & 0 \\ d_1\tilde{g}_1(m_1 + \lambda) & 1 - d_1 - a_{12}h_2 & 0 & 0 \\ -\rho a_{21}h_2 & 0 & \rho(1 - 2h_2 - d_2) & \rho d_2\tilde{g}_2(\rho m_2 + \lambda) \\ 0 & -\rho a_{21}h_2 & \rho d_2\tilde{g}_2(\rho m_2 + \lambda) & \rho(1 - 2h_2 - d_2) \end{pmatrix}$$

The matrix $B(0, 0, h_2, h_2) - \lambda I$ reduces to the two principal sub-matrices

$$M(0, 0, h_2, h_2) = \begin{pmatrix} 1 - d_1 - a_{12}h_2 - \lambda & d_1\tilde{g}_1(m_1 + \lambda) \\ d_1\tilde{g}_1(m_1 + \lambda) & 1 - d_1 - a_{12}h_2 - \lambda \end{pmatrix}$$

$$L(0, 0, h_2, h_2) = \begin{pmatrix} \rho(1 - 2h_2 - d_2) - \lambda & \rho d_2\tilde{g}_2(\rho m_2 + \lambda) \\ \rho d_2\tilde{g}_2(\rho m_2 + \lambda) & \rho(1 - 2h_2 - d_2) - \lambda \end{pmatrix}$$

Setting $(\det(M(0, 0, h_2, h_2)) = 0$ and $(\det(L(0, 0, h_2, h_2)) = 0$ gives

$$\lambda - 1 + d_1 + a_{12}h_2 = \pm d_1 \tilde{g}_1(m_1 + \lambda) \quad (3.11)$$

$$\lambda - \rho(1 - 2h_2 - d_2) = \pm \rho d_2 \tilde{g}_2(\rho m_2 + \lambda) \quad (3.12)$$

respectively.

Equations (3.11) and (3.12) with $\lambda = \rho\nu$, are identical to those in (3.10) and (3.9), respectively, with subscripts 1 and 2 interchanged. Therefore the results of Theorem 3.1.1(c) follow from those above in Theorem 3.1.1(b).

□

Existence and local stability conditions for the homogeneous steady states of the non-dimensional system (3.2) with $h_1, h_2 > 0$ are summarized in Table 3.1. For the case in which $h_1 > 0$ and $h_2 \leq 0$, species 1 outcompetes species 2 (as illustrated in Box *I*). Whereas, if $h_1 \leq 0$ and $h_2 > 0$, then species 2 wins the competition (Box *IV*). If $h_1, h_2 \leq 0$, then the extinction steady state $(0, 0, 0, 0)$ is the only stable spatially homogeneous steady state, while all others cease to exist. Numerical simulations (see Chapter 5) indicate that, with $u_{1P}^* = u_{1Q}^*$ and $u_{2P}^* = u_{2Q}^*$, the coexistence equilibrium is stable in Box *II* but unstable in Box *III*. Moreover, these simulations indicate that the inhomogeneous coexistence steady states $(u_{1P}^*, u_{1Q}^*, u_{2P}^*, u_{2Q}^*)$ and $(u_{1Q}^*, u_{1P}^*, u_{2Q}^*, u_{2P}^*)$, with $u_{1P}^* \neq u_{1Q}^*$ and $u_{2P}^* \neq u_{2Q}^*$, do not exist in the general system (3.2) except in very restricted cases (see Section 5.1.1 and Figure 5.12).

$h_1, h_2 > 0$	$a_{21}h_1 > h_2$	$a_{21}h_1 < h_2$
	<i>I: Competitive Exclusion (Species 1 wins)</i>	<i>II: Coexistence?</i>
$a_{12}h_2 < h_1$	$(0, 0, 0, 0)$ - unstable $(h_1, h_1, 0, 0)$ - STABLE $(0, 0, h_2, h_2)$ - unstable $(u_{1P}^*, u_{1P}^*, u_{2P}^*, u_{2P}^*)$ - DNE	$(0, 0, 0, 0)$ - unstable $(h_1, h_1, 0, 0)$ - unstable $(0, 0, h_2, h_2)$ - unstable $(u_{1P}^*, u_{1P}^*, u_{2P}^*, u_{2P}^*)$ - SN
	<i>III: Initial Condition Dependent Competitive Exclusion</i>	<i>IV: Competitive Exclusion (Species 2 wins)</i>
$a_{12}h_2 > h_1$	$(0, 0, 0, 0)$ - unstable $(h_1, h_1, 0, 0)$ - STABLE $(0, 0, h_2, h_2)$ - STABLE $(u_{1P}^*, u_{1P}^*, u_{2P}^*, u_{2P}^*)$ - UN †	$(0, 0, 0, 0)$ - unstable $(h_1, h_1, 0, 0)$ - unstable $(0, 0, h_2, h_2)$ - STABLE $(u_{1P}^*, u_{1P}^*, u_{2P}^*, u_{2P}^*)$ - DNE

Table 3.1: Summary of existence and local stability conditions for all spatially homogeneous steady states of the two patch model in (3.2) with both species dispersing. The abbreviations DNE, UN and SN denote does not exist, unstable numerically and stable numerically, respectively. † In special cases, two inhomogeneous steady states are found numerically and can be locally stable.

3.2 Dispersal of 1 Species

In the previous section, a general competition model is analyzed, where both species disperse between the two patches. A special case is the two patch model in which only species 1 disperses, i.e., $D_2 = 0$. The two patches are still assumed to be identical, while species 1 and 2 are assumed to have different local dynamics and dispersal rates. As before, the system is closed, i.e., species 1 must have left one patch in order to enter the other. The model equations are

$$\begin{aligned}
 \frac{dN_{1P}}{dT} &= \frac{r_1}{K_1} N_{1P} (K_1 - N_{1P} - \alpha_{12} N_{2P}) \\
 &\quad + D_1 \left[\int_0^\infty G_1(S) e^{-M_1 S} N_{1Q}(T - S) dS - N_{1P} \right] \\
 \frac{dN_{1Q}}{dT} &= \frac{r_1}{K_1} N_{1Q} (K_1 - N_{1Q} - \alpha_{12} N_{2Q}) \\
 &\quad + D_1 \left[\int_0^\infty G_1(S) e^{-M_1 S} N_{1P}(T - S) dS - N_{1Q} \right] \\
 \frac{dN_{2P}}{dT} &= \frac{r_2}{K_2} N_{2P} (K_2 - N_{2P} - \alpha_{21} N_{1P}) \\
 \frac{dN_{2Q}}{dT} &= \frac{r_2}{K_2} N_{2Q} (K_2 - N_{2Q} - \alpha_{21} N_{1Q})
 \end{aligned} \tag{3.13}$$

where N_{ij} for $i = 1, 2$, and $j = P, Q$, denotes the densities of species on the indicated patch. Initially $N_{ij}(S) \geq 0$ for $S \in (-\infty, 0]$ with $N_{ij}(0) > 0$ (and $N_{ij}(S) = 0$ for $S \in (-\infty, -L_1)$) for $i = 1, 2$ and $j = P, Q$. All other parameters and assumptions are as stated for the previous models.

Non-Dimensionalization of (3.13), as in the previous section, results in

the re-scaled model

$$\begin{aligned}
\frac{du_{1P}}{dt} &= u_{1P}(1 - u_{1P} - a_{12}u_{2P}) \\
&\quad + d_1 \left[\int_0^\infty g_1(s) e^{-m_1 s} u_{1Q}(t-s) ds - u_{1P} \right] \\
\frac{du_{1Q}}{dt} &= u_{1Q}(1 - u_{1Q} - a_{12}u_{2Q}) \\
&\quad + d_1 \left[\int_0^\infty g_1(s) e^{-m_1 s} u_{1P}(t-s) ds - u_{1Q} \right] \\
\frac{du_{2P}}{dt} &= \rho u_{2P}(1 - u_{2P} - a_{21}u_{1P}) \\
\frac{du_{2Q}}{dt} &= \rho u_{2Q}(1 - u_{2Q} - a_{21}u_{1Q})
\end{aligned} \tag{3.14}$$

This system is again analyzed in the positively invariant region denoted by

$$Y_4 = \{(u_{1P}, u_{1Q}, u_{2P}, u_{2Q}) : 0 \leq u_{ij} \leq 1, \text{ for } i = 1, 2 \text{ and } j = P, Q\}.$$

In contrast with the previous model in which both species disperse, this case in which $d_2 = 0$ gives rise to possibly 6 new equilibria in addition to the ones given in (3.3).

Let h_1 , h_2 , $\tilde{g}_1(m_1)$, and $\tilde{g}_2(\rho m_2)$ be defined as in (2.4), (2.22), (2.5), and (2.23), respectively. For the non-dimensional system in (3.14) the spatially homogeneous steady states of the form $(\bar{u}_{1P}, \bar{u}_{1Q}, \bar{u}_{2P}, \bar{u}_{2Q})$ in Y_4 are

$$\begin{aligned}
(0, 0, 0, 0) &\quad (h_1, h_1, 0, 0) \text{ for } h_1 > 0 &\quad (0, 0, 1, 1) \\
(u_{1P}^*, u_{1P}^*, u_{2P}^*, u_{2P}^*) &\text{ for } u_{1P}^* = u_1^* \text{ and } u_{2P}^* = u_2^* \\
&\quad \text{where } u_1^* \text{ and } u_2^* \text{ are defined as in (2.24)}
\end{aligned} \tag{3.15}$$

In biological terms, these steady states represent extinction of both species on the two patches, competitive exclusion of species 2 on both patches with species 1 below its carrying capacity (due to dispersal), competitive exclusion of species 1 with species 2 at its carrying capacity on both patches, and coexistence of both species with the same density of species i on both patches (for $i = 1, 2$), respectively.

Positive inhomogeneous steady states can occur in Y_4 and are of the form $(u_{1P}^*, u_{1Q}^*, u_{2P}^*, u_{2Q}^*)$ and $(u_{1Q}^*, u_{1P}^*, u_{2Q}^*, u_{2P}^*)$ for $u_{1P}^* \neq u_{1Q}^*$ and $u_{2P}^* \neq u_{2Q}^*$. Biologically, these steady states represent coexistence of both species with different densities of species i on both patches (for $i = 1, 2$) and are given by

$$\begin{aligned} u_{1P}^* &= \frac{p + \sqrt{p^2 - 4pd_1\tilde{g}_1(m_1)}}{2q} \\ u_{1Q}^* &= \frac{p - \sqrt{p^2 - 4pd_1\tilde{g}_1(m_1)}}{2q} \\ u_{2P}^* &= 1 - a_{21}u_{1P}^* \\ u_{2Q}^* &= 1 - a_{21}u_{1Q}^* \end{aligned}$$

in which $p = -1 + a_{12} + d_1 + d_1\tilde{g}_1(m_1) = a_{12} - h_1 + 2d_1\tilde{g}_1(m_1)$ must be positive and $q = a_{12}a_{21} - 1 > 0$. For this steady state to be biologically meaningful, $p \geq 4d_1\tilde{g}_1(m_1)$, i.e., $a_{12} - h_1 > 2d_1\tilde{g}_1(m_1)$, and the steady state must be in Y_4 .

In addition, other spatially inhomogeneous steady states can occur with at least one species going extinct on one or both patches; this is mainly due to the fact that species 2 does not disperse so the system is not symmetric. These steady states in Y_4 are

$$\begin{aligned}
& (0, 0, 1, 0) \qquad (0, 0, 0, 1) \\
& (\tilde{u}_{1P}, \tilde{u}_{1Q}, \tilde{u}_{2P}, 0) \text{ and } (\tilde{u}_{1Q}, \tilde{u}_{1P}, 0, \tilde{u}_{2P}) \text{ for } \tilde{u}_{1P} \neq \tilde{u}_{1Q}
\end{aligned} \tag{3.16}$$

In biological terms, the first two steady states represent competitive exclusion of species 1 on both patches and species 2 on Patch Q with species 2 on Patch P at its carrying capacity, and competitive exclusion of species 1 on both patches and species 2 on Patch P with species 2 on Patch Q at its carrying capacity, respectively. The steady state $(\tilde{u}_{1P}, \tilde{u}_{1Q}, \tilde{u}_{2P}, 0)$ represents competitive exclusion of species 2 on Patch Q with species 1 on both patches and species 2 on Patch P below their carrying capacities (due to dispersal), while $(\tilde{u}_{1Q}, \tilde{u}_{1P}, 0, \tilde{u}_{2P})$ represents competitive exclusion of species 2 on Patch P with species 1 on both patches and species 2 on Patch Q below their carrying capacities (due to dispersal). In order to be biologically meaningful, these steady states must lie in Y_4 and therefore $\tilde{u}_{1P}$ is any positive real root (< 1) of the cubic equation

$$\begin{aligned}
0 = & \tilde{u}_{1P}^3(a_{12}a_{21} - 1)^2 + 2\tilde{u}_{1P}^2(a_{12}a_{21} - 1)(1 - a_{12} - d_1) \\
& + \tilde{u}_{1P}[(1 - a_{12} - d_1)^2 + (a_{12}a_{21} - 1)(1 - d_1)d_1\tilde{g}_1(m_1)] \\
& + (1 - d_1)(1 - a_{12} - d_1)d_1\tilde{g}_1(m_1) - d_1^3\tilde{g}_1^3(m_1)
\end{aligned} \tag{3.17}$$

while $0 < \tilde{u}_{1Q} < 1$ and $0 < \tilde{u}_{2P} < 1$ are determined by

$$\begin{aligned}
\tilde{u}_{1Q} &= \frac{-(a_{12}a_{21} - 1)\tilde{u}_{1P}^2 - (1 - a_{12} - d_1)\tilde{u}_{1P}}{d_1\tilde{g}_1(m_1)}, \text{ and} \\
\tilde{u}_{2P} &= 1 - a_{21}\tilde{u}_{1P}
\end{aligned}$$

respectively. Note that the cubic equation (3.17) above is obtained from the system (3.14) at the steady state $(\tilde{u}_{1P}, \tilde{u}_{1Q}, \tilde{u}_{2P}, 0)$, by setting $\tilde{u}_{2P} = 1 - a_{21}\tilde{u}_{1P}$; thus yielding

$$\tilde{u}_{1P}(1 - a_{21} - d_1 + \tilde{u}_{1P}(a_{12}a_{21} - 1)) + d_1\tilde{g}_1(m_1)\tilde{u}_{1Q} = 0 \quad (3.18)$$

$$\tilde{u}_{1Q}(1 - \tilde{u}_{1Q} - d_1) + d_1\tilde{g}_1(m_1)\tilde{u}_{1P} = 0 \quad (3.19)$$

Dividing (3.18) by $\tilde{u}_{1P}$ and (3.19) by $\tilde{u}_{1Q}$ gives

$$1 - a_{21} - d_1 + \tilde{u}_{1P}(a_{12}a_{21} - 1) + d_1\tilde{g}_1(m_1)\frac{\tilde{u}_{1Q}}{\tilde{u}_{1P}} = 0 \quad (3.20)$$

$$1 - \tilde{u}_{1Q} - d_1 + d_1\tilde{g}_1(m_1)\frac{\tilde{u}_{1P}}{\tilde{u}_{1Q}} = 0 \quad (3.21)$$

Solving for $\tilde{u}_{1Q}$ in (3.20) and substituting this expression into (3.21) yields the desired cubic equation in (3.17).

Some of the above steady states are locally analyzed in the next section, and numerical simulations are then given.

3.2.1 Linear Stability Analysis of Equilibria

The non-dimensional system (3.14) in Y_4 is similar to the model in (3.2) with $d_2 = 0$. Therefore setting $d_2 = 0$ in (3.4) and assuming a solution of the form $v_{ij} = C_{ij}e^{\lambda t}$ for $i = 1, 2$ and $j = P, Q$ in which C_{ij} is an arbitrary constant, yields the linearized coefficient matrix $B - \lambda I$, where I is the 4×4 identity matrix and

$B =$

$$\begin{pmatrix} \bar{w}_{1P} - a_{12}\bar{u}_{2P} & d_1\tilde{g}_1(m_1 + \lambda) & -a_{12}\bar{u}_{1P} & 0 \\ d_1\tilde{g}_1(m_1 + \lambda) & \bar{w}_{1Q} - a_{12}\bar{u}_{2Q} & 0 & -a_{12}\bar{u}_{1Q} \\ -\rho a_{21}\bar{u}_{2P} & 0 & \rho(\bar{w}_{2P} - a_{21}\bar{u}_{1P}) & 0 \\ 0 & -\rho a_{21}\bar{u}_{2Q} & 0 & \rho(\bar{w}_{2Q} - a_{21}\bar{u}_{1Q}) \end{pmatrix}$$

with $\bar{w}_{ij} = 1 - 2\bar{u}_{ij} - d_i$ for $i = 1, 2$ and $j = P, Q$.

The following lemma is used in the linear stability analysis of some of the steady states.

Lemma 3.2.1. *Let V and W be any $n \times n$ matrices. Then*

$$\det \begin{pmatrix} V & W \\ W & V \end{pmatrix} = \det(V + W) \det(V - W)$$

Proof:

With I denoting the $n \times n$ identity matrix,

$$\begin{pmatrix} I & 0 \\ I & I \end{pmatrix} \begin{pmatrix} I & 0 \\ -I & I \end{pmatrix} = \begin{pmatrix} I & 0 \\ 0 & I \end{pmatrix}$$

it follows by similarity that

$$\begin{aligned} \det \begin{pmatrix} V & W \\ W & V \end{pmatrix} &= \det \left[\begin{pmatrix} I & 0 \\ I & I \end{pmatrix} \begin{pmatrix} V & W \\ W & V \end{pmatrix} \begin{pmatrix} I & 0 \\ -I & I \end{pmatrix} \right] \\ &= \det \begin{pmatrix} V - W & W \\ 0 & V + W \end{pmatrix} \\ &= \det(V + W) \det(V - W) \end{aligned}$$

□

The next theorem summarizes the local stability results for the steady states of the non-dimensional system in (3.14). In contrast to the case in which both species disperse, local stability of the coexistence steady state with $u_{1P}^* = u_{1Q}^*$ and $u_{2P}^* = u_{2Q}^*$ is resolved.

Theorem 3.2.2. *Let h_1 be defined as in (2.4). Then the following is a summary of the local stability results of the non-negative spatially homogeneous and the first two inhomogeneous steady states in (3.15) and (3.16), respectively, written as $(u_{1P}, u_{1Q}, u_{2P}, u_{2Q})$.*

- (a) *The steady state $(0, 0, 0, 0)$ is unstable*
- (b) *The steady state $(0, 0, 1, 0)$ is unstable*
- (c) *The steady state $(0, 0, 0, 1)$ is unstable*
- (d) *The steady state $(h_1, h_1, 0, 0)$ is:*

$$\begin{aligned} \text{locally asymptotically stable if} \quad & a_{21}h_1 > 1 \\ \text{unstable if} \quad & a_{21}h_1 < 1 \end{aligned}$$

- (e) *The steady state $(0, 0, 1, 1)$ is:*

$$\begin{aligned} \text{locally asymptotically stable if} \quad & a_{12} > h_1 \\ \text{unstable if} \quad & a_{12} < h_1 \end{aligned}$$

- (f) *The steady state $(u_{1P}^*, u_{1P}^*, u_{2P}^*, u_{2P}^*)$ is:*

$$\begin{aligned} \text{locally asymptotically stable if} \quad & a_{12} < h_1 \text{ and } a_{21}h_1 < 1 \\ \text{unstable if} \quad & a_{12} > h_1 \text{ and } a_{21}h_1 > 1 \end{aligned}$$

Proof:

Parts (a), (d) and (e) follow directly from Theorem 3.1.1 by setting $h_2 = 1$ (since $d_2 = 0$).

(b) *At the steady state $(0, 0, 1, 0)$:*

$$B(0, 0, 1, 0) - \lambda I = \begin{pmatrix} 1 - d_1 - a_{12} - \lambda & d_1 \tilde{g}_1(m_1 + \lambda) & 0 & 0 \\ d_1 \tilde{g}_1(m_1 + \lambda) & 1 - d_1 - \lambda & 0 & 0 \\ -\rho a_{21} & 0 & -\rho - \lambda & 0 \\ 0 & 0 & 0 & \rho - \lambda \end{pmatrix}$$

As before, setting $\det(B(0, 0, 1, 0) - \lambda I) = 0$ yields a characteristic equation with $\lambda = \rho > 0$ as a root, and so the steady state $(0, 0, 1, 0)$ is unstable.

(c) *At the steady state $(0, 0, 0, 1)$:*

$$B(0, 0, 0, 1) - \lambda I = \begin{pmatrix} 1 - d_1 - \lambda & d_1 \tilde{g}_1(m_1 + \lambda) & 0 & 0 \\ d_1 \tilde{g}_1(m_1 + \lambda) & 1 - d_1 - \lambda & 0 & 0 \\ 0 & 0 & \rho - \lambda & 0 \\ 0 & -\rho a_{21} & 0 & -\rho - \lambda \end{pmatrix}$$

Setting $\det(B(0, 0, 0, 1) - \lambda I) = 0$ again yields the positive root $\lambda = \rho$ of the resulting characteristic equation, and so the steady state $(0, 0, 0, 1)$ is unstable.

(f) At the steady state $(u_{1P}^*, u_{1P}^*, u_{2P}^*, u_{2P}^*)$:

$$B = \begin{pmatrix} w_{1P}^* - a_{12}u_{2P}^* & d_1\tilde{g}_1(m_1 + \lambda) & -a_{12}u_{1P}^* & 0 \\ d_1\tilde{g}_1(m_1 + \lambda) & w_{1P}^* - a_{12}u_{2P}^* & 0 & -a_{12}u_{1P}^* \\ -\rho a_{21}u_{2P}^* & 0 & \rho(w_{2P}^* - a_{21}u_{1P}^*) & 0 \\ 0 & -\rho a_{21}u_{2P}^* & 0 & \rho(w_{2P}^* - a_{21}u_{1P}^*) \end{pmatrix}$$

Here $w_{ij}^* = 1 - 2u_{ij}^* - d_i$ for $i = 1, 2$ and $j = P, Q$ with $d_2 = 0$.

Interchanging rows 2 and 3, and columns 2 and 3 yields the following matrix (which has the same determinant as B):

$$\begin{pmatrix} V & W \\ W & V \end{pmatrix} = \begin{pmatrix} w_{1P}^* - a_{12}u_{2P}^* & -a_{12}u_{1P}^* & d_1\tilde{g}_1(m_1 + \lambda) & 0 \\ -\rho a_{21}u_{2P}^* & \rho(w_{2P}^* - a_{21}u_{1P}^*) & 0 & 0 \\ d_1\tilde{g}_1(m_1 + \lambda) & 0 & w_{1P}^* - a_{12}u_{2P}^* & -a_{12}u_{1P}^* \\ 0 & 0 & -\rho a_{21}u_{2P}^* & \rho(w_{2P}^* - a_{21}u_{1P}^*) \end{pmatrix}$$

Moreover, using the steady state equation $1 - 2u_{2P}^* - a_{21}u_{1P}^* = -u_{2P}^*$, it follows that

$$V + W = \begin{pmatrix} w_{1P}^* - a_{12}u_{2P}^* + d_1\tilde{g}_1(m_1 + \lambda) & -a_{12}u_{1P}^* \\ -\rho a_{21}u_{2P}^* & -\rho u_{2P}^* \end{pmatrix}$$

and

$$V - W = \begin{pmatrix} w_{1P}^* - a_{12}u_{2P}^* - d_1\tilde{g}_1(m_1 + \lambda) & -a_{12}u_{1P}^* \\ -\rho a_{21}u_{2P}^* & -\rho u_{2P}^* \end{pmatrix}$$

By Lemma 3.2.1, $\det(B - \lambda I) = \det(V + W - \lambda I)\det(V - W - \lambda I)$, therefore the eigenvalues of the two 2×2 matrices $V + W$ and $V - W$ are considered.

The matrix $V + W - \lambda I$ is identical to the one analyzed in Theorem 2.1.4 (d) with $u_{1P}^* = u_1^*$ and $u_{2P}^* = u_2^*$. Therefore, $Re(\lambda) < 0$ for $a_{12} < h_1$ and $a_{21}h_1 < 1$ (i.e., $a_{12}a_{21} < 1$). For $a_{12} > h_1$ and $a_{21}h_1 > 1$, $Re(\lambda) > 0$, which in turn implies that the steady state $(u_{1P}^*, u_{1P}^*, u_{2P}^*, u_{2P}^*)$ is unstable. Consequently, for the matrix $V - W - \lambda I$, we only need to consider the case in which $a_{12} < h_1$ and $a_{21}h_1 < 1$ (i.e., $a_{12}a_{21} < 1$), since otherwise, the steady state is unstable.

Setting $\det(V - W - \lambda I) = 0$ yields

$$\begin{aligned} & (\lambda - 1 + 2u_{1P}^* + d_1 + a_{12}u_{2P}^* + d_1\tilde{g}_1(m_1 + \lambda))(\lambda + \rho u_{2P}^*) - \rho a_{12}a_{21}u_{1P}^*u_{2P}^* = 0 \\ \Rightarrow & (\lambda - 1 + 2u_{1P}^* + d_1 + a_{12}u_{2P}^*)(\lambda + \rho u_{2P}^*) - \rho a_{12}a_{21}u_{1P}^*u_{2P}^* \\ & = -d_1\tilde{g}_1(m_1 + \lambda)(\lambda + \rho u_{2P}^*) \quad (3.22) \end{aligned}$$

From the equations in (3.14) at the steady state,

$$-1 + u_{1P}^* + a_{12}u_{2P}^* + d_1 = d_1\tilde{g}_1(m_1)$$

Therefore (3.22) can be written as

$$\begin{aligned} & (\lambda + u_{1P}^* + d_1\tilde{g}_1(m_1))(\lambda + \rho u_{2P}^*) - \rho a_{12}a_{21}u_{1P}^*u_{2P}^* \\ & = -d_1\tilde{g}_1(m_1 + \lambda)(\lambda + \rho u_{2P}^*) \quad (3.23) \end{aligned}$$

Let

$$H(\lambda) = (\lambda + u_{1P}^* + d_1\tilde{g}_1(m_1))(\lambda + \rho u_{2P}^*) - \rho a_{12}a_{21}u_{1P}^*u_{2P}^*$$

$$\text{and} \quad K(\lambda) = -d_1\tilde{g}_1(m_1 + \lambda)(\lambda + \rho u_{2P}^*)$$

Then (3.23) can be written as $H(\lambda) = K(\lambda)$. Moreover, $\lambda = 0$ is not a root of (3.23); otherwise,

$$H(0) = K(0) \Rightarrow 2d_1\tilde{g}_1(m_1) + u_{1P}^*(1 - a_{12}a_{21}) = 0$$

which is impossible since $a_{12}a_{21} < 1$.

Let $\lambda = x+iy$ with $x \geq 0$ and $x, y \in \mathcal{R}$. Then $|H(x+iy)|^2 = |K(x+iy)|^2$ yields an expression that is identical (with u_{1P}^* and u_{2P}^* replacing u_1^* and u_2^* , respectively) to the one obtained in (2.18). Therefore, $Re(\lambda) < 0$ for all roots λ in (3.23). Hence Theorem 3.2.2 (f) is proved.

This completes the proof of Theorem 3.2.2.

□

A summary of existence and local stability for all steady states of the system (3.14) with $h_1 > 0$ is given in Table 3.2, and numerical simulations are given in the next chapter. These simulations indicate that the coexistence steady states with $u_{1P}^* \neq u_{1Q}^*$ and $u_{2P}^* \neq u_{2Q}^*$ are unstable in Box *III* and that they do not exist in Box *IV*. Note that from Section 3.2, these coexistence steady states do not exist in Box *I* or Box *II*, since

$$\begin{aligned} p > 4d_1\tilde{g}_1(m_1) &\Rightarrow -1 + a_{12} + d_1 - 3d_1\tilde{g}_1(m_1) > 0 \\ &\Rightarrow a_{12} - h_1 > 2d_1\tilde{g}_1(m_1) > 0 \end{aligned}$$

which is a contradiction to the necessary condition $a_{12} < h_1$ required for

Boxes *I* and *II*.

Moreover, numerical simulations indicate that the last two steady states in (3.16) are unstable in Boxes *II* and *IV* and do not exist in the other boxes. Note that here if $h_1 \leq 0$, then species 2 outcompetes species 1 (as in Box *IV*) and thus the steady state $(0, 0, 1, 1)$ is stable.

$h_1 > 0$	$a_{21}h_1 > 1$	$a_{21}h_1 < 1$
$a_{12} < h_1$	<i>I: Competitive Exclusion (Species 1 wins)</i> (0, 0, 0, 0) - unstable $(h_1, h_1, 0, 0)$ - STABLE (0, 0, 1, 1) - unstable $(u_{1P}^*, u_{1P}^*, u_{2P}^*, u_{2P}^*)$ - DNE (0, 0, 1, 0) - unstable (0, 0, 0, 1) - unstable $(u_{1P}^*, u_{1Q}^*, u_{2P}^*, u_{2Q}^*)$ - DNE $(u_{1Q}^*, u_{1P}^*, u_{2Q}^*, u_{2P}^*)$ - DNE $(\tilde{u}_{1P}, \tilde{u}_{1Q}, \tilde{u}_{2P}, 0)$ - DNEN $(\tilde{u}_{1Q}, \tilde{u}_{1P}, 0, \tilde{u}_{2P})$ - DNEN	<i>II: Coexistence?</i> (0, 0, 0, 0) - unstable $(h_1, h_1, 0, 0)$ - unstable (0, 0, 1, 1) - unstable $(u_{1P}^*, u_{1P}^*, u_{2P}^*, u_{2P}^*)$ - STABLE (0, 0, 1, 0) - unstable (0, 0, 0, 1) - unstable $(u_{1P}^*, u_{1Q}^*, u_{2P}^*, u_{2Q}^*)$ - DNE $(u_{1Q}^*, u_{1P}^*, u_{2Q}^*, u_{2P}^*)$ - DNE $(\tilde{u}_{1P}, \tilde{u}_{1Q}, \tilde{u}_{2P}, 0)$ - UN $(\tilde{u}_{1Q}, \tilde{u}_{1P}, 0, \tilde{u}_{2P})$ - UN
$a_{12} > h_1$	<i>III: Initial Condition Dependent Competitive Exclusion</i> (0, 0, 0, 0) - unstable $(h_1, h_1, 0, 0)$ - STABLE (0, 0, 1, 1) - STABLE $(u_{1P}^*, u_{1P}^*, u_{2P}^*, u_{2P}^*)$ - unstable (0, 0, 1, 0) - unstable (0, 0, 0, 1) - unstable $(u_{1P}^*, u_{1Q}^*, u_{2P}^*, u_{2Q}^*)$ - UN $(u_{1Q}^*, u_{1P}^*, u_{2Q}^*, u_{2P}^*)$ - UN $(\tilde{u}_{1P}, \tilde{u}_{1Q}, \tilde{u}_{2P}, 0)$ - DNEN $(\tilde{u}_{1Q}, \tilde{u}_{1P}, 0, \tilde{u}_{2P})$ - DNEN	<i>IV: Competitive Exclusion (Species 2 wins)</i> (0, 0, 0, 0) - unstable $(h_1, h_1, 0, 0)$ - unstable (0, 0, 1, 1) - STABLE $(u_{1P}^*, u_{1P}^*, u_{2P}^*, u_{2P}^*)$ - DNE (0, 0, 1, 0) - unstable (0, 0, 0, 1) - unstable $(u_{1P}^*, u_{1Q}^*, u_{2P}^*, u_{2Q}^*)$ - DNEN $(u_{1Q}^*, u_{1P}^*, u_{2Q}^*, u_{2P}^*)$ - DNEN $(\tilde{u}_{1P}, \tilde{u}_{1Q}, \tilde{u}_{2P}, 0)$ - UN $(\tilde{u}_{1Q}, \tilde{u}_{1P}, 0, \tilde{u}_{2P})$ - UN

Table 3.2: Summary of existence and local stability conditions for all steady states of the two patch model in (3.14) with only species 1 dispersing. The abbreviations DNE, DNEN and UN denote does not exist, does not exist numerically and unstable numerically, respectively.

Chapter 4

Multiple Patch Competition: A General Model

4.1 Model Formulation

This model assumes that two species interact competitively and disperse between an arbitrary number of identical patches denoted by $j = 1, \dots, n$, for $n \geq 2$. Individuals of the same species have the same traveling time distribution between patches, and each patch is coupled to every other patch. Let N_{ij} denote the density of species i on patch j , for $i = 1, 2$ and $j = 1, \dots, n$. As before, the growth rate and carrying capacity for each species are denoted by r_i and K_i , respectively, for $i = 1, 2$. All other parameters are as defined in Sections 2.1 and 2.2. The model equations are

$$\begin{aligned}
\frac{dN_{1j}}{dT} &= \frac{r_1}{K_1} N_{1j} (K_1 - N_{1j} - \alpha_{12} N_{2j}) \\
&\quad + D_1 \left[\frac{1}{n-1} \sum_{k=1, k \neq j}^n \int_0^\infty G_1(S) e^{-M_1 S} N_{1k} (T-S) dS - N_{1j} \right] \\
\frac{dN_{2j}}{dT} &= \frac{r_2}{K_2} N_{2j} (K_2 - N_{2j} - \alpha_{21} N_{1j}) \\
&\quad + D_2 \left[\frac{1}{n-1} \sum_{k=1, k \neq j}^n \int_0^\infty G_2(S) e^{-M_2 S} N_{2k} (T-S) dS - N_{2j} \right]
\end{aligned} \tag{4.1}$$

in which $j = 1, \dots, n$. As before, the system is assumed to be closed, i.e., individuals must have left one patch in order to enter another.

Assume initially that $N_{ij}(S) \geq 0$ for $S \in (-\infty, 0]$ with $N_{ij}(0) > 0$ (and $N_{ij}(S) = 0$ for $S \in (-\infty, -L_i)$) for $i = 1, 2$ and $j = 1, \dots, n$. Then by a similar argument as in Sections 2.1 and 2.2, $N_{ij}(T) \geq 0$ for all $T \geq 0$ and $N_{ij}(T) \leq K_i$ for $i = 1, 2$ and $j = 1, \dots, n$. Thus the region

$$X_{2n} = \{(N_{11}, \dots, N_{1n}, N_{21}, \dots, N_{2n}) : 0 \leq N_{ij} \leq K_i\}$$

is positively invariant and attracts all solutions, so it suffices to consider the dynamics on X_{2n} where $n \geq 2$ is the number of patches in the system. Again, for all $t \geq 0$, existence and uniqueness of the solution of the initial value problem follow from standard results; see for example [9, Chapter 2, Section 2.2].

Parameters in (4.1) can be rescaled as in (2.2) and (2.20) with $u_{ij} = \frac{N_{ij}}{K_i}$ for $i = 1, 2$ and $j = 1, \dots, n$. This results in the non-dimensional system

$$\begin{aligned}
\frac{du_{1j}}{dt} &= u_{1j}(1 - u_{1j} - a_{12}u_{2j}) \\
&\quad + d_1 \left[\frac{1}{n-1} \sum_{k=1, k \neq j}^n \int_0^\infty g_1(s) e^{-m_1 s} u_{1k}(t-s) ds - u_{1j} \right] \\
\frac{du_{2j}}{dt} &= \rho u_{2j}(1 - u_{2j} - a_{21}u_{1j}) \\
&\quad + \rho d_2 \left[\frac{1}{n-1} \sum_{k=1, k \neq j}^n \int_0^\infty g_2(s) e^{-\rho m_2 s} u_{2k}(t-s) ds - u_{2j} \right]
\end{aligned} \tag{4.2}$$

The dynamics of the system in (4.2) are analyzed below in the $2n$ region represented by

$$Y_{2n} = \{(u_{11}, \dots, u_{1n}, u_{21}, \dots, u_{2n}) : 0 \leq u_{ij} \leq 1, \text{ for } i = 1, 2 \text{ and } j = 1, \dots, n\}$$

4.2 Steady States and Local Stability Analysis

Let h_1 , h_2 , $\tilde{g}_1(m_1)$, and $\tilde{g}_2(\rho m_2)$ be defined as in (2.4), (2.22), (2.5), and (2.23), respectively, and the n -dimensional vector $\mathbf{h}_i = (h_i, \dots, h_i)$ for $i = 1, 2$. Steady states for the system in (4.2) are of the form $(\mathbf{u}_1, \mathbf{u}_2)$ in which the n -dimensional vector $\mathbf{u}_i = (u_{i1}, \dots, u_{in})$ represents the steady state densities of species i on all n (≥ 2) patches, for $i = 1, 2$. This non-dimensional system admits four non-negative spatially homogeneous steady states, lying in Y_{2n} , that are of the form $(\bar{\mathbf{u}}_1, \bar{\mathbf{u}}_2)$:

$$\begin{aligned}
& (\mathbf{0}, \mathbf{0}) \qquad (\mathbf{h}_1, \mathbf{0}) \text{ for } h_1 > 0 \qquad (\mathbf{0}, \mathbf{h}_2) \text{ for } h_2 > 0 \\
& (\mathbf{u}_1^*, \mathbf{u}_2^*) \text{ for } \mathbf{u}_1^* = (u_1^*, \dots, u_1^*) \text{ and } \mathbf{u}_2^* = (u_2^*, \dots, u_2^*) \\
& \text{where } u_1^* \text{ and } u_2^* \text{ are defined as in (2.24)} \qquad (4.3)
\end{aligned}$$

In biological terms, the steady states in (4.3) represent extinction of both species on all n patches, competitive exclusion of species 2 on all patches with species 1 below its carrying capacity (due to dispersal), competitive exclusion of species 1 on all n patches with species 2 below its carrying capacity (due to dispersal), and coexistence of both species with the same densities of each species on all n patches.

As in the two patch model discussed in Section 3.1, inhomogeneous steady states $(\mathbf{u}_1^*, \mathbf{u}_2^*)$ have not been ruled out analytically for the general system in (4.2) with $d_1 \neq d_2$ and $\tilde{g}_1(m_1) \neq \tilde{g}_2(\rho m_2)$.

Let $u_{ij} = \bar{u}_{ij} + v_{ij}$ with $|v_{ij}| \ll \bar{u}_{ij}$, for $i = 1, 2$ and $j = 1, \dots, n$. Thus linearization of the system in (4.2) in the neighbourhood of a non-negative equilibrium point, denoted by $(\bar{\mathbf{u}}_1, \bar{\mathbf{u}}_2)$ yields:

$$\begin{aligned}
\frac{dv_{1j}}{dt} &= v_{1j}(1 - 2\bar{u}_{1j} - a_{12}\bar{u}_{2j}) - a_{12}\bar{u}_{1j}v_{2j} \\
&\quad + d_1\left[\frac{1}{n-1} \sum_{k=1, k \neq j}^n \int_0^\infty g_1(s)e^{-m_1s}v_{1k}(t-s)ds - v_{1j}\right] \\
\frac{dv_{2j}}{dt} &= \rho v_{2j}(1 - 2\bar{u}_{2j} - a_{21}\bar{u}_{1j}) - \rho a_{21}\bar{u}_{2j}v_{1j} \\
&\quad + \rho d_2\left[\frac{1}{n-1} \sum_{k=1, k \neq j}^n \int_0^\infty g_2(s)e^{-\rho m_2s}v_{2k}(t-s)ds - v_{2j}\right]
\end{aligned} \tag{4.4}$$

for $j = 1, \dots, n$. We now seek solutions of the form:

$$v_{ij} = C_{ij}e^{\lambda t} \text{ for } i = 1, 2 \text{ and } j = 1, \dots, n$$

where C_{ij} is an arbitrary constant. Substituting the assumed solutions into the linearized equations and setting $\bar{w}_{ij} = 1 - 2\bar{u}_{ij} - d_i$ for $i = 1, 2$ and $j = 1, \dots, n$ gives

$$\begin{aligned}
0 &= C_{1j}[\bar{w}_{1j} - a_{12}\bar{u}_{2j} - \lambda] + \left[\frac{1}{n-1}d_1\tilde{g}_1(m_1 + \lambda)\right] \sum_{k=1, k \neq j}^n C_{1k} - C_{2j}[a_{12}\bar{u}_{1j}] \\
0 &= -C_{1j}[a_{21}\bar{u}_{2j}] + C_{2j}[\bar{w}_{2j} - a_{21}\bar{u}_{1j} - \frac{\lambda}{\rho}] + \left[\frac{1}{n-1}d_2\tilde{g}_2(\rho m_2 + \lambda)\right] \sum_{k=1, k \neq j}^n C_{2k}
\end{aligned}$$

Accordingly, the linearized coefficient matrix can be written as

$$B = \begin{pmatrix} C & D \\ E & F \end{pmatrix}$$

where C , D , E and F are $n \times n$ matrices given below. For I the $n \times n$ identity matrix,

$$C = -\lambda I +$$

$$\begin{pmatrix} \bar{w}_{11} - a_{12}\bar{u}_{21} & * & & & * \\ * & \bar{w}_{12} - a_{12}\bar{u}_{22} & * & \cdots & * \\ & * & \ddots & & \\ & \vdots & & \ddots & \\ * & * & \cdots & & \bar{w}_{1n} - a_{12}\bar{u}_{2n} \end{pmatrix}$$

Here, all off diagonal entries referred to by $*$ are $\frac{1}{n-1}d_1\tilde{g}_1(m_1 + \lambda)$. Similarly,

$$F = -\lambda I +$$

$$\begin{pmatrix} \rho(\bar{w}_{21} - a_{21}\bar{u}_{11}) & \diamond & & & \diamond \\ \diamond & \rho(\bar{w}_{22} - a_{21}\bar{u}_{12}) & \diamond & \cdots & \diamond \\ & \diamond & \ddots & & \\ & \vdots & & \ddots & \\ \diamond & \diamond & \cdots & & \rho(\bar{w}_{2n} - a_{21}\bar{u}_{1n}) \end{pmatrix}$$

in which the off diagonal entries, represented by $\diamond$ are $\frac{1}{n-1}\rho d_2\tilde{g}_2(\rho m_2 + \lambda)$.

The diagonal matrices D and E are as follows:

$$D = \begin{pmatrix} -a_{12}\bar{u}_{11} & 0 & \cdots & 0 \\ 0 & \ddots & & \\ & & \ddots & \\ 0 & \cdots & & -a_{12}\bar{u}_{1n} \end{pmatrix}$$

and

$$E = \begin{pmatrix} -\rho a_{21} \bar{u}_{21} & 0 & \cdots & 0 \\ 0 & \ddots & & \\ & & \ddots & \\ 0 & \cdots & & -\rho a_{21} \bar{u}_{2n} \end{pmatrix}$$

The coefficient matrix B is now applied to each of the spatially homogeneous steady states. Theorem 4.2.1 summarizes the local stability results. Note that the results of the following theorem are identical to the ones summarized in Theorem 3.1.1.

Theorem 4.2.1. *The stability properties of the extinction and the competitive exclusion steady states in (4.3) are given as follows:*

(a) *The steady state $(\mathbf{0}, \mathbf{0})$ is*

$$\begin{aligned} \text{locally asymptotically stable if} \quad & h_1, h_2 < 0 \\ \text{unstable if} \quad & h_1 > 0 \quad \text{or} \quad h_2 > 0 \end{aligned}$$

(b) *The steady state $(\mathbf{h}_1, \mathbf{0})$ is:*

$$\begin{aligned} \text{locally asymptotically stable if} \quad & a_{21} h_1 > h_2 \\ \text{unstable if} \quad & a_{21} h_1 < h_2 \end{aligned}$$

(c) *The steady state $(\mathbf{0}, \mathbf{h}_2)$ is:*

$$\begin{aligned} \text{locally asymptotically stable if} \quad & a_{12} h_2 > h_1 \\ \text{unstable if} \quad & a_{12} h_2 < h_1 \end{aligned}$$

Proof:

(a) At the steady state $(\mathbf{0}, \mathbf{0})$:

$$C(\mathbf{0}, \mathbf{0}) =$$

$$\begin{pmatrix} 1 - d_1 - \lambda & * & & & * \\ * & 1 - d_1 - \lambda & * & \cdots & * \\ & * & \ddots & & \\ & \vdots & & \ddots & \\ * & * & \cdots & & 1 - d_1 - \lambda \end{pmatrix}$$

in which the $*$ is used to represent all off-diagonal entries and they are $\frac{1}{n-1}d_1\tilde{g}_1(m_1 + \lambda)$.

$$F(\mathbf{0}, \mathbf{0}) =$$

$$\begin{pmatrix} \rho(1 - d_2) - \lambda & \diamond & & & \diamond \\ \diamond & \rho(1 - d_2) - \lambda & \diamond & \cdots & \diamond \\ & \diamond & \ddots & & \\ & \vdots & & \ddots & \\ \diamond & \diamond & \cdots & & \rho(1 - d_2) - \lambda \end{pmatrix}$$

Here, the off-diagonal entries $\diamond$ are $\frac{1}{n-1}\rho d_2\tilde{g}_2(\rho m_2 + \lambda)$. Moreover, $D(\mathbf{0}, \mathbf{0}) = E(\mathbf{0}, \mathbf{0}) = 0$, the $n \times n$ zero matrix.

Thus B is a direct sum and all that remains is to find the sign of $Re(\lambda)$ for each of $\det C = 0$ and $\det F = 0$ at $(\mathbf{0}, \mathbf{0})$. Here

$$\det C(\mathbf{0}, \mathbf{0}) = \begin{vmatrix} 1 - d_1 - \lambda & * & & & * \\ * & 1 - d_1 - \lambda & * & \cdots & * \\ & * & \ddots & & \\ & \vdots & & \ddots & \\ * & * & \cdots & & 1 - d_1 - \lambda \end{vmatrix}$$

Summing all rows and taking out the resulting common factor from row 1 gives

$$\det C(\mathbf{0}, \mathbf{0}) = (1 - d_1 + d_1 \tilde{g}_1(m_1 + \lambda) - \lambda) \times$$

$$\begin{vmatrix} 1 & 1 & \cdots & & 1 \\ * & 1 - d_1 - \lambda & * & \cdots & * \\ & * & \ddots & & \\ & \vdots & & \ddots & \\ * & * & \cdots & & 1 - d_1 - \lambda \end{vmatrix}$$

Subtracting the first column from all other columns and setting $\det C(\mathbf{0}, \mathbf{0}) = 0$ yields the following equation in λ :

$$(1 - d_1 + d_1 \tilde{g}_1(m_1 + \lambda) - \lambda) \left(1 - d_1 - \frac{d_1 \tilde{g}_1(m_1 + \lambda)}{n - 1} - \lambda\right)^{n-1} = 0 \quad (4.5)$$

$$\Rightarrow \quad \lambda - 1 + d_1 = d_1 \tilde{g}_1(m_1 + \lambda) \quad (4.6)$$

$$\text{or} \quad \lambda - 1 + d_1 = -\frac{d_1 \tilde{g}_1(m_1 + \lambda)}{n - 1} \quad (4.7)$$

Equation (4.6) is identical to (2.28) obtained in Theorem 2.2.1 (a). Thus, $Re(\lambda) < 0$ whenever $h_1 < 0$, whereas $h_1 > 0$ implies that $Re(\lambda) > 0$ for some

root λ in (4.6) and therefore the steady state $(\mathbf{0}, \mathbf{0})$ is unstable.

As for (4.7), the conclusion proved in Lemma 2.1.2 also applies to the more general case $\lambda - 1 + c + d_1 = \pm bd_1 \tilde{g}_1(m_1 + \lambda)$ in which b is a constant with $0 < b \leq 1$. In this case, $c > h_1 \geq 1 - d_1 \pm bd_1 \tilde{g}_1(m_1)$, which again results in a contradiction and the lemma is proved as in Lemma 2.1.2. Thus, for $b = \frac{1}{n-1}$, it follows that $Re(\lambda) < 0$ for all roots λ whenever $h_1 < 0$.

Interchanging subscripts 1 and 2 and replacing λ in the matrix $F(\mathbf{0}, \mathbf{0})$ with $\rho\nu$, then factoring out the positive constant ρ yields a matrix which is identical to $C(\mathbf{0}, \mathbf{0})$. Thus $Re(\lambda) > 0$ for some λ which is a root of the equation $\det F(\mathbf{0}, \mathbf{0}) = 0$ whenever $h_2 > 0$ and $Re(\lambda) < 0$ for all λ if $h_2 < 0$. This proves part (a) of the theorem.

(b) At the steady state $(\mathbf{h}_1, \mathbf{0})$ for $h_1 > 0$:

$$C(\mathbf{h}_1, \mathbf{0}) = -\lambda I + \begin{pmatrix} 1 - 2h_1 - d_1 & * & & & * \\ * & 1 - 2h_1 - d_1 & * & \cdots & * \\ & * & \ddots & & \\ & \vdots & & \ddots & \\ * & * & \cdots & & 1 - 2h_1 - d_1 \end{pmatrix}$$

Again, all off diagonal entries $*$ are $\frac{1}{n-1}d_1 \tilde{g}_1(m_1 + \lambda)$. Similarly, with $\lambda = \rho\nu$

$$F(\mathbf{h}_1, \mathbf{0}) = -\rho\nu I + \rho \times$$

$$\begin{pmatrix} 1 - a_{21}h_1 - d_2 & \diamond & & & \diamond \\ & \diamond & 1 - a_{21}h_1 - d_2 & \diamond & \cdots & \diamond \\ & & \diamond & \ddots & & \\ & & \vdots & & \ddots & \\ \diamond & \diamond & \cdots & & & 1 - a_{21}h_1 - d_2 \end{pmatrix}$$

The off diagonal entries, represented by $\diamond$ are $\frac{1}{n-1}d_2\tilde{g}_2(\rho m_2 + \rho\nu)$. The $n \times n$ diagonal matrix D is given by

$$D(\mathbf{h}_1, \mathbf{0}) = \begin{pmatrix} -a_{12}h_1 & 0 & \cdots & 0 \\ 0 & \ddots & & \\ & & \ddots & \\ 0 & \cdots & & -a_{12}h_1 \end{pmatrix}$$

and $E(\mathbf{h}_1, \mathbf{0}) = \mathbf{0}$, the $n \times n$ zero matrix. Therefore, the matrix B is reducible, thus only $\det C(\mathbf{h}_1, \mathbf{0}) = 0$ and $\det F(\mathbf{h}_1, \mathbf{0}) = 0$ need to be analyzed.

$\det C(\mathbf{h}_1, \mathbf{0}) =$

$$\begin{vmatrix} 1 - 2h_1 - d_1 - \lambda & * & & & * \\ * & 1 - 2h_1 - d_1 - \lambda & * & \cdots & * \\ & * & \ddots & & \\ & \vdots & & \ddots & \\ * & * & \cdots & & 1 - 2h_1 - d_1 - \lambda \end{vmatrix}$$

As in the proof of part (a), setting $\det C(\mathbf{h}_1, \mathbf{0}) = 0$ yields the following equation in λ :

$$(1 - 2h_1 - d_1 + d_1\tilde{g}_1(m_1 + \lambda) - \lambda)(1 - 2h_1 - d_1 - \frac{d_1\tilde{g}_1(m_1 + \lambda)}{n-1} - \lambda)^{n-1} = 0 \quad (4.8)$$

$$\Rightarrow \quad \lambda - 1 + 2h_1 + d_1 = d_1 \tilde{g}_1(m_1 + \lambda) \quad (4.9)$$

$$\text{or} \quad \lambda - 1 + 2h_1 + d_1 = -\frac{d_1 \tilde{g}_1(m_1 + \lambda)}{n - 1} \quad (4.10)$$

Since $2h_1 > h_1 > 0$, it follows from Lemma 2.1.2 and the remark in the proof of part (a) above, that $Re(\lambda) < 0$ for all roots λ in (4.9) and (4.10), respectively.

Similarly setting $\det F(\mathbf{h}_1, \mathbf{0}) = 0$ yields

$$\nu - 1 + a_{21}h_1 + d_2 - d_2 \tilde{g}_2(\rho m_2 + \rho \nu) = 0 \quad (4.11)$$

$$\nu - 1 + a_{21}h_1 + d_2 + \frac{d_2 \tilde{g}_2(\rho m_2 + \rho \nu)}{n - 1} = 0 \quad (4.12)$$

For $a_{21}h_1 > h_2$, Lemma 2.1.2 and the remark, in the proof of part (a), imply that $Re(\nu) < 0$ (i.e., $Re(\lambda) < 0$) for all roots ν of (4.11) and (4.12), respectively. Otherwise, if $a_{21}h_1 < h_2$, then, by Lemma 2.1.3, as in the proof of Theorem 2.2.1 (b), $Re(\lambda) > 0$ for some λ in (4.11) whenever $a_{21}h_1 < h_2$, and therefore, the steady state $(\mathbf{h}_1, \mathbf{0})$ is unstable.

(c) *At the steady state $(\mathbf{0}, \mathbf{h}_2)$ for $h_2 > 0$:* Results follow from (b) by symmetry, thus completing the proof. $\square$

Qualitatively, the behaviour of the system (4.2), as proved by Theorem 4.2.1, is similar to that of the two patch system (3.2), as summarized in Table 3.1. Due to the difficulty of the expressions in the $2n \times 2n$ matrix

B resulting from linearization about the positive steady state $(\mathbf{u}_1^*, \mathbf{u}_2^*)$, local stability analysis for this case is not yet resolved. As an example, some numerical simulations are presented in the next chapter for the case of 2 species dispersing among three patches. These show coexistence is possible for some parameter values.

Chapter 5

Simulations and Interpretations

5.1 Numerical Simulations

To support and complement analytical results, numerical simulations are carried out by integrating the non-dimensional systems using MatLab (dde23); see Appendix A. A delta function distribution for the probability density functions $g_i(s)$ is assumed, namely $g_i(s) = \delta(s - \tau)$ for $i = 1, 2$. This implies that all dispersing individuals have the same traveling time out of the patch, and thus for some fixed τ (in dimensionless time) with $0 < \tau < \min\{r_1 L_1, r_1 L_2\}$

$$\begin{aligned}\tilde{g}_1(m_1) &= \int_0^\infty g_1(s) e^{-m_1 s} ds = \int_0^\infty \delta(\tau - s) e^{-m_1 s} ds \\ &= e^{-m_1 \tau}\end{aligned}$$

and

$$\begin{aligned}\tilde{g}_2(\rho m_2) &= \int_0^\infty g_2(s) e^{-\rho m_2 s} ds = \int_0^\infty \delta(\tau - s) e^{-\rho m_2 s} ds \\ &= e^{-\rho m_2 \tau}\end{aligned}\tag{5.1}$$

For example, the non-dimensional equations for the one patch model with both species dispersing are explicitly given as:

$$\begin{aligned}\frac{du_1}{dt} &= u_1(1 - u_1 - a_{12}u_2) + d_1[e^{-m_1\tau}u_1(t - \tau) - u_1] \\ \frac{du_2}{dt} &= \rho u_2(1 - u_2 - a_{21}u_1) + \rho d_2[e^{-\rho m_2\tau}u_2(t - \tau) - u_2]\end{aligned}\quad (5.2)$$

For all densities, constant initial values in the interval $(0, 1)$ for $t \in [-\tau, 0]$ are assumed.

5.1.1 Identical Patches: Both Species Disperse

The analytical results for the case in which both species disperse are summarized in Table 2.2 (for one patch) and Table 3.1 (for two identical patches). As the ratio $\frac{h_1}{h_2}$ decreases, two different paths arise depending on the fixed value of $a_{12}a_{21} - 1$:

$$\text{Path } \mathcal{A} \text{ with } a_{12}a_{21} - 1 < 0: \text{Box } I \rightarrow \text{Box } II \rightarrow \text{Box } IV \quad (5.3)$$

$$\text{Path } \mathcal{B} \text{ with } a_{12}a_{21} - 1 > 0: \text{Box } I \rightarrow \text{Box } III \rightarrow \text{Box } IV \quad (5.4)$$

For Path $\mathcal{A}$, the fixed parameter values taken for illustration are $a_{12} = 0.5$, $a_{21} = 1.2$, $\rho = 1$, $m_1 = 1.5$, $m_2 = 1.3$ and $\tau = 0.3$, while d_1 increases and d_2 decreases. For the one patch model (system (2.21) with $\tilde{g}_i$ given by (5.1)), phaseplane diagrams (u_1, u_2) are presented for several initial conditions, while in the two patch model (system (3.2) with $\tilde{g}_i$ given by (5.1)), $(u_{1P}, u_{1Q}, u_{2P}, u_{2Q})$ are plotted against time t for one set of initial conditions. Simulations for the stability results stated in Tables 2.2 (for one patch) and

3.1 (for two identical patches) are illustrated in Figures 5.1 and 5.2 for Box *I* ($d_1 = 0.3$, $d_2 = 1.6$), Figures 5.3 and 5.4 for Box *II* ($d_1 = 1.2$, $d_2 = 0.9$) and Figures 5.5 and 5.6 for Box *IV* ($d_1 = 1.8$, $d_2 = 0.2$).

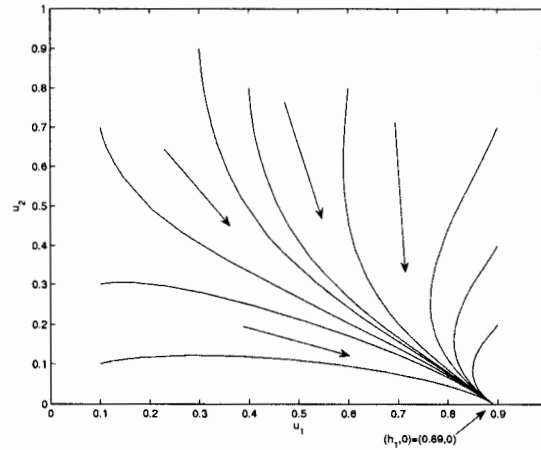


Figure 5.1: Phaseplane plot for Box *I* of Table 2.2, Path *A*, in which the dispersal rates used for this case are $d_1 = 0.3$ and $d_2 = 1.6$ implying $h_1 = 0.89$ and $h_2 = 0.48$. The steady state $(h_1, 0)$ is locally asymptotically stable

For the numerical simulations for Path *B* in Tables 2.2 and 3.1, the fixed parameter values taken in this case are $a_{12} = 0.8$, $a_{21} = 1.8$, $\rho = 1$, $m_1 = 1.5$, $m_2 = 1.3$ and $\tau = 0.3$, while again d_1 increases and d_2 decreases. For $d_1 = 0.3$ and $d_2 = 1.6$, the phaseplane diagrams for Box *I* are qualitatively similar to Figures 5.1 and 5.2. Figures 5.7 and 5.8 for Box *III* ($d_1 = 1.5$, $d_2 = 0.9$) show the initial condition dependent competitive exclusion. The figures corresponding to Box *IV* for $d_1 = 1.8$ and $d_2 = 0.2$, in Path *B*, are qualitatively similar to Figures 5.5 and 5.6.

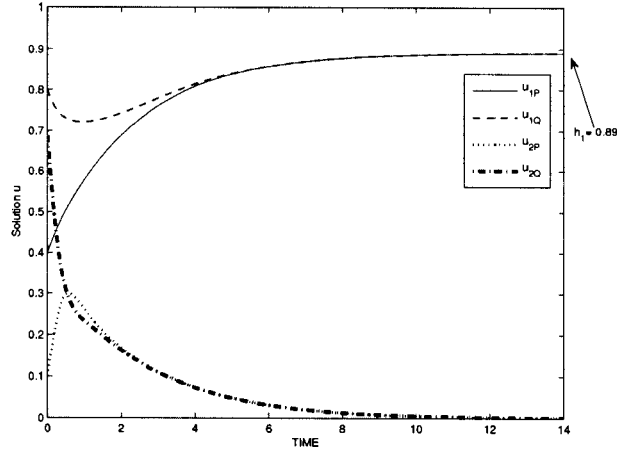


Figure 5.2: Competitive exclusion of species 2 as in Box *I* of Table 3.1, *PathA*, with $d_1 = 0.3$ and $d_2 = 1.6$ implying $h_1 = 0.89$ and $h_2 = 0.48$. The steady state $(h_1, h_1, 0, 0)$ is locally asymptotically stable

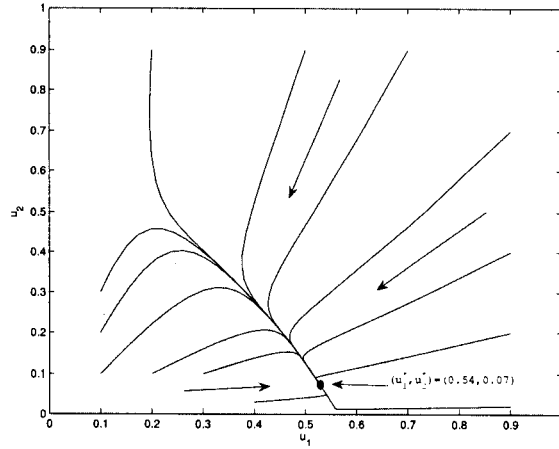


Figure 5.3: Phaseplane plot for Box *II* of Table 2.2, *PathA*. The dispersal rates used are $d_1 = 1.2$ and $d_2 = 0.9$ implying $h_1 = 0.57$ and $h_2 = 0.71$. The coexistence steady state $(u_1^*, u_2^*) = (0.54, 0.07)$ is locally asymptotically stable

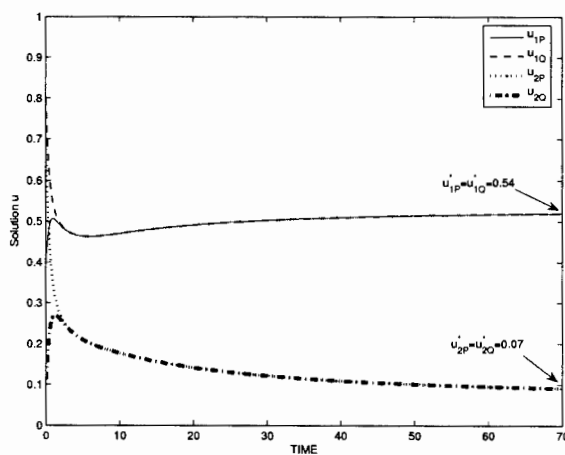


Figure 5.4: Plot for Box *II* of Table 3.1, *PathA*, in which the dispersal rates used for this case are the same as the ones used in Figure 5.3. The co-existence steady state $(u_{1P}^*, u_{1P}^*, u_{2P}^*, u_{2P}^*) = (0.54, 0.54, 0.07, 0.07)$ is locally asymptotically stable

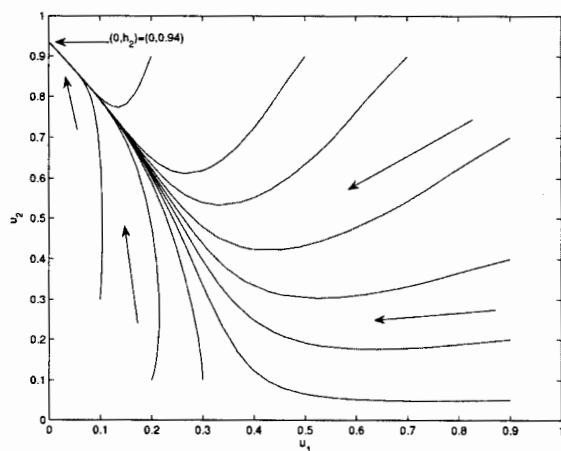


Figure 5.5: Phaseplane plot for Box *IV* of Table 2.2, *PathA*. Here $d_1 = 1.8$ and $d_2 = 0.2$ implying $h_1 = 0.35$ and $h_2 = 0.94$. The steady state $(0, h_2)$ is locally asymptotically stable

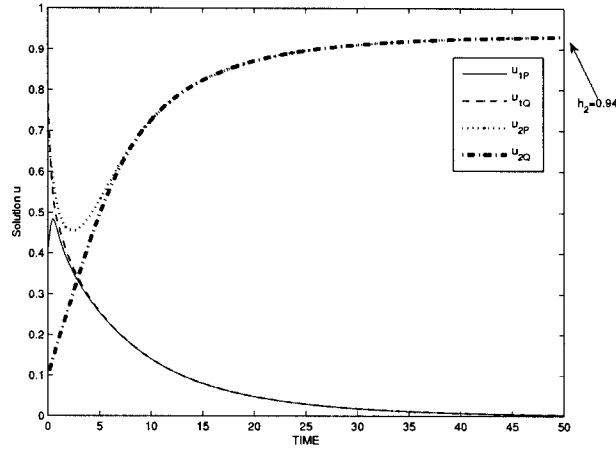


Figure 5.6: Very high dispersal rates for species 1 result in competitive exclusion as in Box IV of Table 3.1, *Path A*. Here the parameters taken are the same as those used in Figure 5.5. The steady state $(0, 0, h_2, h_2)$ is locally asymptotically stable

The results of the case in which species 1 disperses at a much higher rate than species 2, i.e., $h_1 < 0 < h_2$ (e.g., $d_1 = 3.5$, $d_2 = 0.4 \Rightarrow h_1 = -0.26$, $h_2 = 0.87$), are qualitatively the same as the ones presented in Figures 5.5 and 5.6. The case in which species 2 disperses at a much higher rate than species 1, i.e., $h_2 < 0 < h_1$ (e.g., $d_1 = 0.8$, $d_2 = 3.2$ implies $h_1 = 0.71$, $h_2 = -0.03$), is qualitatively the same as the ones presented in Figures 5.1 and 5.2. Furthermore, the case in which both species disperse at a very high rate, i.e., $h_1, h_2 < 0$ (e.g., $d_1 = 3.5$, $d_2 = 3.8 \Rightarrow h_1 = -0.26$, $h_2 = -0.23$), is presented in Figures 5.9 (for one patch) and 5.10 (for two identical patches). Note that, in agreement with Theorems 2.2.1(a) and 3.1.1(a), the only stable equilibria in this case are the steady states $(0, 0)$ and $(0, 0, 0, 0)$. Thus if both species disperse, it is possible for both to go extinct.

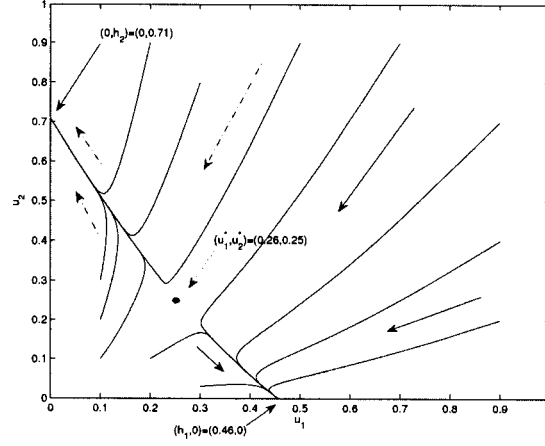


Figure 5.7: Phaseplane plot for Box *III* of Table 2.2, *PathB*, illustrating initial condition dependent competitive exclusion. The parameter values taken in this case are $d_1 = 1.5$ and $d_2 = 0.9$ which imply $h_1 = 0.46$ and $h_2 = 0.71$.

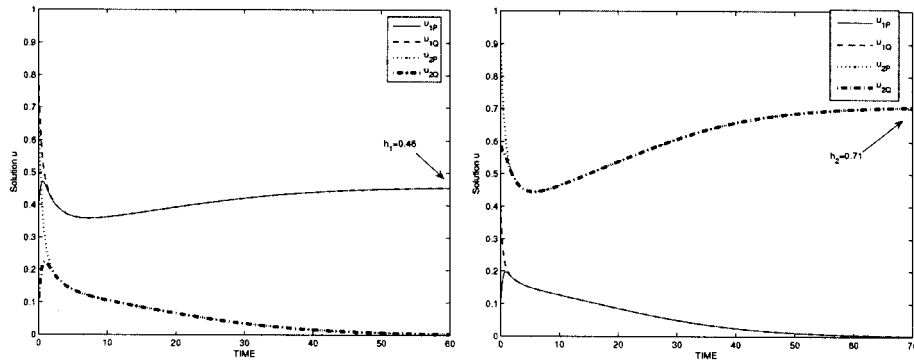


Figure 5.8: Initial condition dependent competitive exclusion as illustrated in Box *III* of Table 3.1, *PathB*, with $d_1 = 1.5$ and $d_2 = 0.9$ which imply $h_1 = 0.46$ and $h_2 = 0.71$.

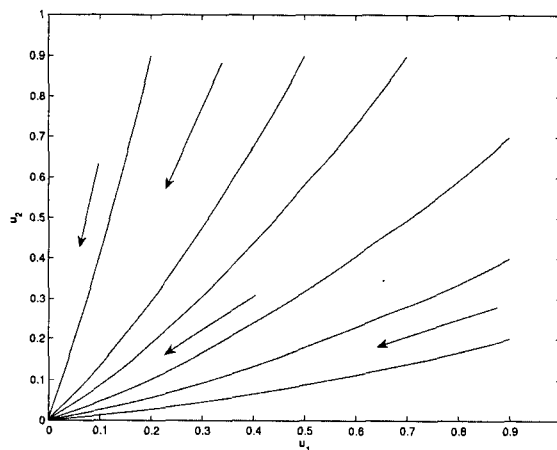


Figure 5.9: Very high dispersal rates of both species on one patch result in extinction. The parameters taken here are $d_1 = 3.5$ and $d_2 = 3.8$ ($h_1 = -0.26$ and $h_2 = -0.23$). The steady state $(0, 0)$ is locally asymptotically stable.

The two patch model is an example of the general multiple patch model discussed in Chapter 4. Increasing the number of patches to three yields similar results qualitatively. Figure 5.11 illustrates coexistence of the two species on all three patches. The parameter values taken are $a_{12} = 0.6$, $a_{21} = 0.2$, $m_1 = 0.5$, $m_2 = 0.7$, $\tau = 0.3$, $d_1 = 0.7$ and $d_2 = 0.3$).

As a special case of the two (identical) patch model, we assume that the two competing species have identical local dynamics, $d_1 = d_2 < 0.1$, $\tilde{g}_1(m_1) = \tilde{g}_2(\rho m_2)$ with $\rho = 1$ and $a_{12} \approx a_{21} > 1$. For a small set of parameter values, these restrictions can result in spatially inhomogeneous coexistence with small dispersal rates and travel delay (for some carefully chosen initial conditions). This is illustrated in Figure 5.12.

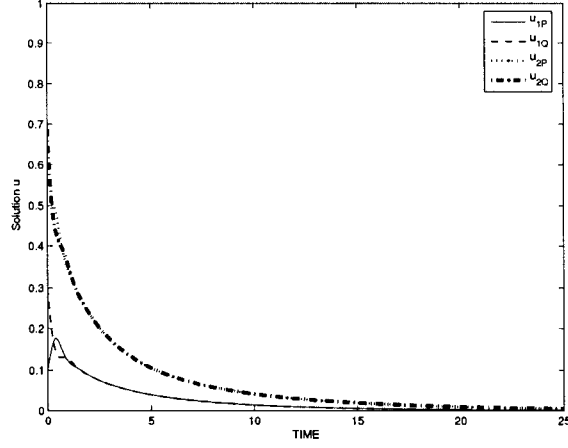


Figure 5.10: Very high dispersal rates of both species result in extinction on both patches. Here $d_1 = 3.5$ and $d_2 = 3.8$ ($h_1 = -0.26$ and $h_2 = -0.23$). The steady state $(0, 0, 0, 0)$ is locally asymptotically stable.

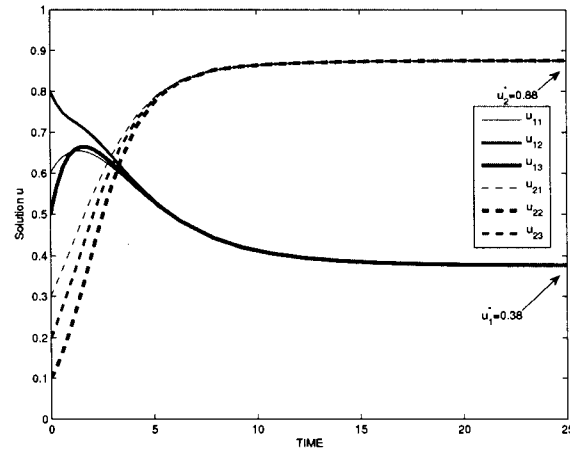


Figure 5.11: Coexistence of the two species on three patches as in (4.2) with $n = 3$, $d_1 = 0.7$ and $d_2 = 0.3$ ($h_1 = 0.902$ and $h_2 = 0.943$). Other parameters taken are $a_{12} = 0.6$, $a_{21} = 0.2$, $m_1 = 0.5$, $m_2 = 0.7$ and $\tau = 0.3$.

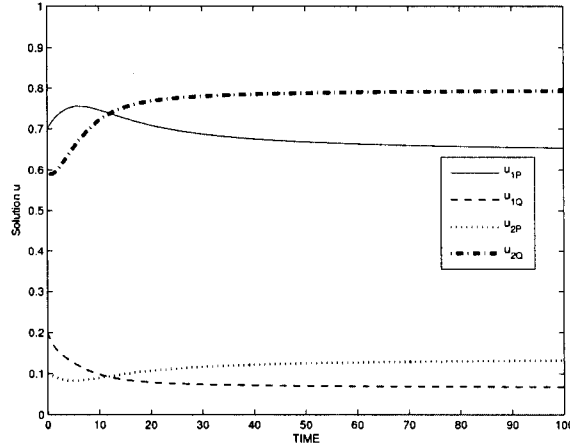


Figure 5.12: Stable inhomogeneous coexistence steady state for two species competing on two identical patches. Parameters taken are $d = 0.09$, $a_{12} = 2$, $a_{21} = 1.9$, $m = 0.5$ and $\tau = 0.3$.

Numerical simulations for the case in which only 1 species disperses are qualitatively similar to the general cases discussed above with the restriction $h_2 = 1$ (since $d_2 = 0$). In the two patch case, none of the new steady states introduced by $d_2 = 0$ are found to be stable.

5.1.2 Non-Identical Patches

Here we assume that the two patches denoted by P and Q are not identical, and thus local dynamics of each species differ greatly between patches. Let r_{ij} and K_{ij} denote the intrinsic growth rate and carrying capacity of species i on patch j , respectively, for $i = 1, 2$ and $j = P, Q$. For the numerical simulations of this case, a delta function distribution $\delta(S - \mathcal{T})$ is assumed. The model equations are

$$\begin{aligned}
\frac{dN_{1P}}{dT} &= \frac{r_{1P}}{K_{1P}} N_{1P} (K_{1P} - N_{1P} - \alpha_{12P} N_{2P}) \\
&\quad + D_1 [e^{-M_1 \mathcal{T}} N_{1Q} (T - \mathcal{T}) - N_{1P}] \\
\frac{dN_{1Q}}{dT} &= \frac{r_{1Q}}{K_{1Q}} N_{1Q} (K_{1Q} - N_{1Q} - \alpha_{12Q} N_{2Q}) \\
&\quad + D_1 [e^{-M_1 \mathcal{T}} N_{1P} (T - \mathcal{T}) - N_{1Q}] \\
\frac{dN_{2P}}{dT} &= \frac{r_{2P}}{K_{2P}} N_{2P} (K_{2P} - N_{2P} - \alpha_{21P} N_{1P}) \\
&\quad + D_2 [e^{-M_2 \mathcal{T}} N_{2Q} (T - \mathcal{T}) - N_{2P}] \\
\frac{dN_{2Q}}{dT} &= \frac{r_{2Q}}{K_{2Q}} N_{2Q} (K_{2Q} - N_{2Q} - \alpha_{21Q} N_{1Q}) \\
&\quad + D_2 [e^{-M_2 \mathcal{T}} N_{2P} (T - \mathcal{T}) - N_{2Q}] \tag{5.5}
\end{aligned}$$

Here the parameters α_{12j} and α_{21j} represent the interspecific competition on patch j , for $j = P, Q$.

The case with no travel delay ($\mathcal{T}$) is analyzed by Smith (1995); see [13, Chapter 4.4]. The ODE model (5.5) (with $\mathcal{T} = 0$) is numerically simulated using MatLab (ode23) with parameter values leading to coexistence. Depending on the local dynamics of each species, one species dominates the other in each patch but spatially inhomogeneous coexistence is still possible; this is illustrated in Figure 5.13.

For travel delay ($\mathcal{T} > 0$) and $M_i > 0$ ($i = 1, 2$), spatially inhomogeneous steady states may result, as for the ODE case, and is stable for some parameter values, as illustrated in Figure 5.14. Otherwise, solutions approach

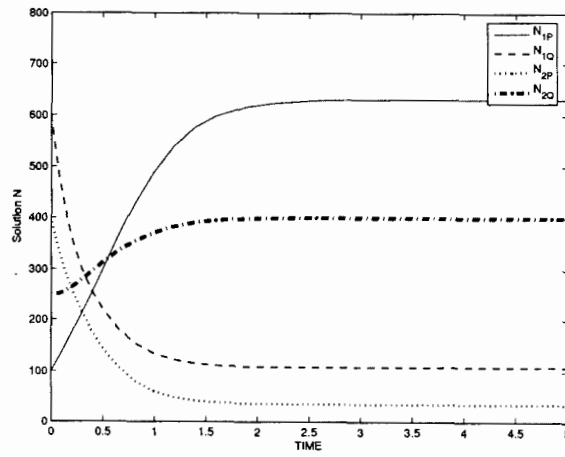


Figure 5.13: Spatially inhomogeneous coexistence steady state is stable for the ODE system, analyzed by Smith [13], of two species on two nonidentical patches. Here $D_1 = 0.3$, $D_2 = 0.5$, $r_{1P} = 3$, $r_{1Q} = 1.5$, $r_{2P} = 2$, $r_{2Q} = 5$, $K_{1P} = 700$, $K_{1Q} = 300$, $K_{2P} = 250$, $K_{2Q} = 500$, $a_{12P} = 0.3$, $a_{12Q} = 1.2$, $a_{21P} = 1.4$, $a_{21Q} = 0.5$, $m_1 = 0.5$ and $m_2 = 0.2$.

boundary steady states.

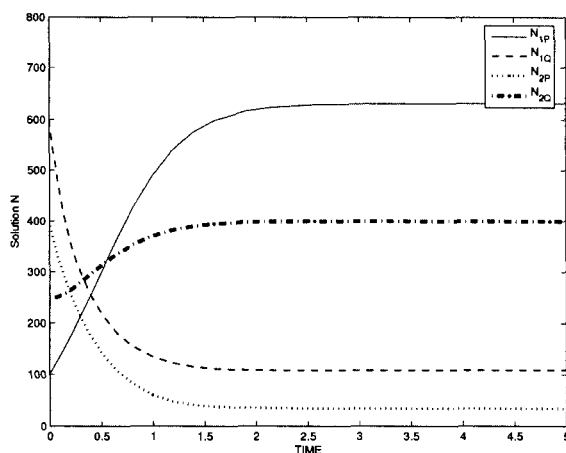


Figure 5.14: Both species competing on and dispersing among two nonidentical patches, with travel delay. Here $D_1 = 0.3$, $D_2 = 0.5$, $M_1 = 0.5$, $M_2 = 0.2$, $\mathcal{T} = 0.3$, $r_{1P} = 3$, $r_{1Q} = 1.5$, $r_{2P} = 2$, $r_{2Q} = 5$, $K_{1P} = 700$, $K_{1Q} = 300$, $K_{2P} = 250$, $K_{2Q} = 500$, $\alpha_{12P} = 0.3$, $\alpha_{12Q} = 1.2$, $\alpha_{21P} = 1.4$ and $\alpha_{21Q} = 0.5$.

5.1.3 More than Two Competitors: Are Oscillations Possible?

For the case in which only 2 species compete between the patches, all solutions approach a steady state. However increasing the number of competitors results in oscillations as a possible outcome for some parameter values. For the case in which 3 species compete among two patches, oscillatory coexistence is now possibly due to a Hopf Bifurcation; see Kuang [9, page 60]. With a delta function distribution for dispersal, the system of equations is given by:

$$\begin{aligned}
\frac{dN_{1P}}{dT} &= \frac{r_1}{K_1} N_{1P} (K_1 - N_{1P} - \alpha_{12} N_{2P} - \alpha_{13} N_{3P}) \\
&\quad + D_1 [e^{-M_1 \mathcal{T}} N_{1Q} (T - \mathcal{T}) - N_{1P}] \\
\frac{dN_{1Q}}{dT} &= \frac{r_1}{K_1} N_{1Q} (K_1 - N_{1Q} - \alpha_{12} N_{2Q} - \alpha_{13} N_{3Q}) \\
&\quad + D_1 [e^{-M_1 \mathcal{T}} N_{1P} (T - \mathcal{T}) - N_{1Q}] \\
\frac{dN_{2P}}{dT} &= \frac{r_2}{K_2} N_{2P} (K_2 - N_{2P} - \alpha_{21} N_{1P} - \alpha_{23} N_{3P}) \\
&\quad + D_2 [e^{-M_2 \mathcal{T}} N_{2Q} (T - \mathcal{T}) - N_{2P}] \\
\frac{dN_{2Q}}{dT} &= \frac{r_2}{K_2} N_{2Q} (K_2 - N_{2Q} - \alpha_{21} N_{1Q} - \alpha_{23} N_{3Q}) \\
&\quad + D_2 [e^{-M_2 \mathcal{T}} N_{2P} (T - \mathcal{T}) - N_{2Q}] \\
\frac{dN_{3P}}{dT} &= \frac{r_3}{K_3} N_{3P} (K_3 - N_{3P} - \alpha_{31} N_{1P} - \alpha_{32} N_{2P}) \\
&\quad + D_3 [e^{-M_3 \mathcal{T}} N_{3Q} (T - \mathcal{T}) - N_{3P}] \\
\frac{dN_{3Q}}{dT} &= \frac{r_3}{K_3} N_{3Q} (K_3 - N_{3Q} - \alpha_{31} N_{1Q} - \alpha_{32} N_{2Q}) \\
&\quad + D_3 [e^{-M_3 \mathcal{T}} N_{3P} (T - \mathcal{T}) - N_{3Q}] \tag{5.6}
\end{aligned}$$

Numerical simulations illustrate the oscillatory outcome for some carefully chosen parameter values [15, Example A] with $\mathcal{T} = 0.01$, as in Figure 5.15, in which the time axis is shown from 25 to 45.

5.2 Biological Interpretations

The results of the previous chapters with 1 or 2 species dispersing in the one and two patch models are now interpreted biologically; see [11] for an

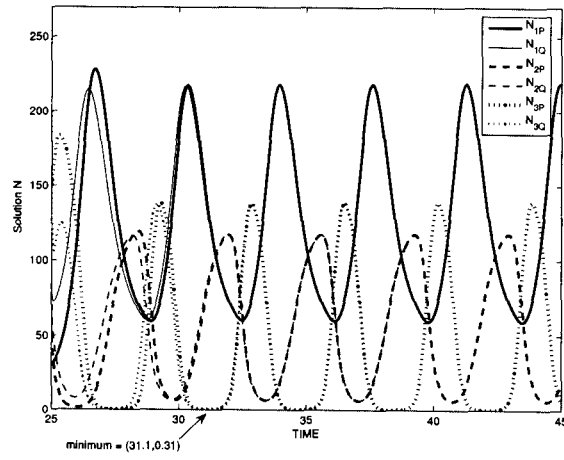


Figure 5.15: A two (identical) patch model in which 3 species disperse with small travel delay. Numerical data set used is: $D_1 = 0.3$, $D_2 = 0.4$, $D_3 = 0.1$, $M_1 = 0.5$, $M_2 = 0.4$, $M_3 = 0.6$, $\mathcal{T} = 0.01$, $r_1 = 25$, $r_2 = 16$, $r_3 = 60$, $K_1 = 250$, $K_2 = 160$, $K_3 = 240$, $\alpha_{12} = 1.5$, $\alpha_{21} = 0.5$, $\alpha_{13} = 1$, $\alpha_{31} = 1.1$, $\alpha_{23} = 1$ and $\alpha_{32} = 1.1$.

interpretation in the classical case with no dispersal ($h_1, h_2 = 1$). For the two patch models, both patches are assumed to be identical. The analytical results hold for arbitrary distributions of dispersal times, whereas the numerical simulations in Section 4.1 are for the case of constant dispersal time.

First we consider the case in which only one species disperses. Boxes *I* through *IV* in Tables 2.1 and 3.2 summarize the stability results for some fixed interspecific competition parameters a_{12} and a_{21} . Note that going from Box *I* to Box *IV* via either Box *II* or Box *III*, the parameter h_1 decreases implying an increase in the dispersal rate of species 1.

Box *I* is the case where the dispersal rate of species 1 is low. The result is competitive exclusion of species 2, since the stronger interspecific competition of species 1 dominates. This shifts the local stability to the steady states $(h_1, 0)$ and $(h_1, h_1, 0, 0)$.

In Box *II*, species 1 disperses at a rate higher than that in Box *I* and the equilibrium points $(h_1, 0)$ and $(h_1, h_1, 0, 0)$ are destabilized. In terms of the original parameters,

$$\frac{\alpha_{12}K_2}{K_1} < h_1 < \frac{K_2}{\alpha_{21}K_1}.$$

Thus for example, if K_1 is approximately equal to K_2 , then the effect of the interspecific competition parameters (measured by α_{12} and α_{21}) is not too strong ($\alpha_{12}\alpha_{21} < 1$), and as a result the two species adjust to a lower population size than if there were no competition or dispersal. The coexistence steady state (i.e., (u_1^*, u_2^*) in the one patch model and $(u_{1P}^*, u_{1P}^*, u_{2P}^*, u_{2P}^*)$ in the two patch model) is now locally asymptotically stable.

The conditions in Box *III* result in competitive exclusion that is initial

condition dependent. There is a curve, behaving as a separatrix which divides the positive quadrant into two non-overlapping regions. The curve passes through the coexistence steady states (u_1^*, u_2^*) in the one patch model and $(u_{1P}^*, u_{1P}^*, u_{2P}^*, u_{2P}^*)$ in the two patch model, and is one of the saddle point-like trajectories. This is a clear example of competitive exclusion, and the initial values determine which species outcompetes the other. In terms of the original parameters,

$$\frac{K_2}{\alpha_{21}K_1} < h_1 < \frac{\alpha_{12}K_2}{K_1}.$$

Therefore for increased dispersal rates of species 1, if K_1 is again approximately equal to K_2 , then the effect of the interspecific competition parameters is stronger ($\alpha_{12}\alpha_{21} > 1$). Analysis shows that competition is such that only $(h_1, 0)$ and $(0, 1)$ are locally stable in the one patch case while $(h_1, h_1, 0, 0)$ and $(0, 0, 1, 1)$ are locally asymptotically stable in the two patch case, so one species is eliminated. In fact, extinction of one species is expected even if the initial populations are close to the separatrix-like curve, and in the rare cases where the initial densities lie exactly on the curve, any perturbations in the system will inevitably cause one of the species to tend to zero, thus becoming extinct.

In Box IV, the dispersal rate of species 1 is very high and the effect of the interspecific competition parameter for species 2, i.e., α_{12} , is much higher than that of species 1, i.e., α_{21} . In the one patch case, the local stability shifts to the steady state $(0, 1)$, while the steady state $(0, 0, 1, 1)$ is stable in the two patch case. This results in competitive exclusion, in which species 2 is favoured by the competition and reaches its environmental carrying capacity, while species 1 tends to extinction. This is also the case for very high

dispersal rates, i.e., $h_1 < 0$, for then species 1 disperses out of the patch at a very high rate and is therefore not available to compete for resources effectively.

Comparing the above results with those of the classical case of competition between two species (with no dispersal; thus $h_1 = 1$), yields the following conclusions, provided that $0 < h_1 < 1$.

1. Replacing a_{21} by $a_{21}h_1$ implies that dispersal of species 1 reduces the competition of species 1 on species 2.
2. Replacing a_{12} by $\frac{a_{12}}{h_1}$ implies that dispersal of species 1 increases the competition of species 2 on species 1.

Therefore in both cases, dispersal seems to be a disadvantage to the dispersing species, and species 2 will eventually dominate and win the competition as the dispersal rate for species 1 increases.

Next we consider the case where both species disperse. Tables 2.2 and 3.1 summarizes the outcome of the competition with dispersal in the one patch and the two patch models, respectively. The table is set up such that Box $I \rightarrow$ Box II /Box $III \rightarrow$ Box IV implies an increase in the dispersal rate of species 1 and a decrease in the dispersal rate of species 2. The stability of the system in this case depends on $\frac{h_1}{h_2}$ which is the ratio of the difference between growth and dispersal for species 1 and 2. The effect of the interspecific competition parameters on the overall outcome of the competition is not as strong as in the previous case of one species dispersing. Assuming that both

species have similar carrying capacities, the first box is the case in which

$$\frac{\alpha_{12}h_2}{h_1} < 1 < \frac{\alpha_{21}h_1}{h_2}$$

and thus for approximately equal interspecific competition parameters, $h_1 > h_2$ and so the dispersal rate of species 1 is much lower than that of species 2. The result is competitive exclusion of species 2 and the steady states $(h_1, 0)$ or $(h_1, h_1, 0, 0)$ are locally asymptotically stable. This is also the case for very high dispersal rates of species 2, i.e., $h_2 < 0$ and $h_1 > 0$, since clearly $\alpha_{21}h_1 > h_2$ and $\alpha_{12}h_2 < h_1$.

In Box *II*, the ratio $\frac{h_1}{h_2}$ is lower and therefore u_1 disperses at a rate higher than that of Box *I*, which in turn destabilizes the equilibrium points $(h_1, 0)$ and $(h_1, h_1, 0, 0)$. In terms of the original parameters,

$$\alpha_{12}h_2 < h_1 < \frac{h_2}{\alpha_{21}} \quad \Rightarrow \quad \alpha_{12} < \frac{h_1}{h_2} < \frac{1}{\alpha_{21}} \quad \text{for } K_1 \approx K_2.$$

This implies that the interspecific competition parameters (measured by α_{12} and α_{21}) are not too strong. As in the 1-species dispersal case, both species adjust to a lower population size than if there were no competition or dispersal, and so the coexistence steady states (u_1^*, u_2^*) and $(u_{1P}^*, u_{1P}^*, u_{2P}^*, u_{2P}^*)$ are locally asymptotically stable.

As before, Box *III* represents the case of initial condition dependent competitive exclusion. Again, the separatrix-like curve passes through the coexistence steady states mentioned above and divides the positive quadrant into two non-overlapping regions. In this case

$$\frac{h_2}{\alpha_{21}} < h_1 < \alpha_{12}h_2 \quad \Rightarrow \quad \frac{1}{\alpha_{21}} < \frac{h_1}{h_2} < \alpha_{12} \quad \text{for } K_1 \approx K_2.$$

The ratio of h_1 to h_2 in this box is lower than that in Box *II*, this implies that either the dispersal rate of species 1 has increased or that of species

2 has decreased. The result is competitive exclusion and the initial values determine which species outcompetes the other.

Finally, in Box *IV* the ratio between h_1 and h_2 is small and therefore the dispersal rate of species 1 is much higher than that of species 2 (for similar interspecific competition parameters), since

$$\frac{\alpha_{21}h_1}{h_2} < 1 < \frac{\alpha_{12}h_2}{h_1} \quad \text{for } K_1 \approx K_2.$$

The local stability shifts to the steady state $(0, h_2)$ in the one patch model and $(0, 0, h_2, h_2)$ in the two patch model, resulting in competitive exclusion and again species 2 is favoured by the competition, while species 1 tends to extinction. Identical results are obtained for the case in which species 1 disperses at a very high rate, i.e., $h_1 < 0$ and $h_2 > 0$, since $\alpha_{21}h_1 < h_2$ and $\alpha_{12}h_2 > h_1$ are clearly true.

When both species disperse out of the patch at a very high rate, i.e., when $h_1, h_2 < 0$, all non-trivial steady states cease to exist or are unstable and the equilibrium points $(0, 0)$ and $(0, 0, 0, 0)$ are linearly asymptotically stable. This outcome is not possible in the absence of dispersal.

The results above can be related to the classical case of competition between two species (with no dispersal; i.e., $h_1 = h_2 = 1$) as in (1.3). Assume that $0 < h_1 < 1$ and $0 < h_2 < 1$. Thus from the results of the dimensionless system in Table 2.2, a_{21} is replaced by $\frac{a_{21}h_1}{h_2}$, while a_{12} is replaced by $\frac{a_{12}h_2}{h_1}$. This implies that as the dispersal rate of species 1 increases, the dispersal ratio $\frac{h_1}{h_2}$ becomes smaller and the competition of species 1 on species 2 is reduced, while the competition of species 2 on species 1 is increased, and vice versa. Therefore, again in both cases, dispersal seems to be a disadvantage

to the dispersing species.

Note that in the two patch model with both species dispersing, if the two competing species have identical dispersal rates and the same dispersal distribution, (i.e., $h_1 = h_2 > 0$), then the stability conditions summarized in Theorem 3.1.1 and Table 3.1 are now identical to those required in the classical case of competition, even though the two systems are different due to dispersal. In this case, stability of all steady states depends solely on the interspecific competition parameters (a_{12} and a_{21}).

In the special case in which the two patches are identical, the two competing species have identical local dynamics, $d_1 = d_2$, $\tilde{g}_1(m_1) = \tilde{g}_2(\rho m_2)$ with $\rho = 1$ and $a_{12}, a_{21} > 1$, spatially inhomogeneous coexistence is possible with small dispersal rates and travel delay (for some carefully chosen initial conditions). Thus in contrast with the classical case of competition, starting with competitive exclusion then introducing small dispersal rates along with a small travel delay can be an advantage (under the restrictions above) in that it results in coexistence as a possible outcome.

Chapter 6

Conclusions and Open Problems

6.1 Conclusions

Homogeneous patchy environments with two competitors yield non-oscillatory systems with solutions that always approach a non-negative steady state (i.e., no limit cycles are found). For the general two patch model (Section 3.1), there are four possible outcomes: competitive exclusion of one species, coexistence, initial condition dependent competitive exclusion, and extinction of both species. The dynamics of the system depends on the ratio $\frac{h_1}{h_2}$. For most parameter values, a dispersing species is at a disadvantage (i.e., a situation in which species 2 is extinct may be turned into a coexistence situation if species 1 disperses). As dispersal rates of one species increase, the other species eventually wins the competition. Extinction results when both species disperse at a very high rate ($h_1, h_2 < 0$). For a small range of parameter values, equal

small dispersal rates can be an advantage to one of the species as exclusion is turned into coexistence.

For non-identical patches, even though coexistence is possible, yet one species usually dominates in each patch. This is dictated by the local dynamics of the species on each patch; i.e., growth rates, carrying capacities and interspecific competition.

Increasing the number of competitors to three, changes the dynamics of the system for then oscillatory coexistence is a possible outcome.

6.2 Open Problems

Global asymptotic stability of steady states for the models discussed in this thesis still remains an open problem. One approach to solving this, is to find a suitable Liapunov functional or Razumikhin function; see [9, Sections 2.5 and 2.6].

Another open question not addressed in this thesis, is whether intraspecific competition between patches (during dispersal) affects the overall outcome of the system. Some patchy environments are connected via a corridor in which the dispersing species compete for resources. In these and similar situations, competition during dispersal should be accounted for in the models as this could change the overall outcome. Now the question arises: Is dispersal still a disadvantage?

The general case of an arbitrary number of dispersing competitors (with travel delay) on n patches, is also an open problem. As indicated by the case of 2 competitors on three patches (Chapter 4 with $n = 3$), the qualitative behaviour may become difficult to analyze.

The two competitor ODE model for non-identical patches is analyzed by Takeuchi [14]. For the case with dispersal and travel delay, some numerical simulations are presented in Chapter 5 (Figure 5.14). However, local and global stability analyses have not been considered.

For all numerical simulations in this thesis, a delta function is used as a specific example of a probability density function. Trying other dispersal distributions (e.g, uniform) is interesting and should yield the same qualitative outcome.

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Appendix A

MatLab Program

The MatLab code shown in this section is used for numerical simulations of the two patch model with both species dispersing (see Section 3.1 and Figure 5.2). There are two files needed: *dde-competition.m* and *test-competition.m*. In running the program, the MatLab command *run test-competition* is used. In the first file, *dde-competition.m*, $y(1)$, $y(2)$, $y(3)$ and $y(4)$ are used to denote u_{1P} , u_{1Q} , u_{2P} and u_{2Q} , respectively.

File Name: dde-competition.m

```
function dydt = dde-competition(t,y,z,p);
```

```
ylag1 = z(:,1);
```

```
dydt=[y(1)*(1-y(1)-p.a12*y(3)) + p.d1*(exp(-p.m1*p.tau)*ylag1(2)-y(1))  
y(2)*(1-y(2)-p.a12*y(4)) + p.d1*(exp(-p.m1*p.tau)*ylag1(1)-y(2))
```

```

y(3)*(1-y(3)-p.a21*y(1)) + p.d2*(exp(-p.m2*p.tau)*ylag1(4)-y(3))
y(4)*(1-y(4)-p.a21*y(2)) + p.d2*(exp(-p.m2*p.tau)*ylag1(3)-y(4));

```

File Name: test-competition.m

```

t-start = 0;
t-stop = 14;
p.d1 = 0.3;
p.d2 = 1.6;
p.m1 = 1.5;
p.m2 = 1.3;
p.tau = 0.3;
p.h1 = 1 - p.d1*(1 - exp(-p.m1*p.tau));
p.h2 = 1 - p.d2*(1 - exp(-p.m2*p.tau));
p.a12 = 0.5;
p.a21 = 1.2;

ic = [0.4 0.8 0.1 0.7];

sol = dde23(@dde-competition, p.tau,ic,[t-start, t-stop],[],p);

figure;
plot(sol.x,sol.y);

```

```
legend('u1P','u1Q','u2P','u2Q');  
xlabel('TIME')  
ylabel('Solution u')  
axis([t-start t-stop 0 1]);  
title('Two Patch 2-Species Model, (h1,h1,0,0) STABLE');
```