MEMOIRS
of the
American Mathematical Society

Number 740

Mutual Invadability Implies Coexistence in Spatial Models

Rick Durrett

March 2002 • Volume 156 • Number 740 (first of 5 numbers) • ISSN 0065-9266

American Mathematical Society

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American Mathematical Society
Providence, Rhode Island

2000 *Mathematics Subject Classification.*
Primary 60K35; Secondary 34-xx, 35-xx.

Library of Congress Cataloging-in-Publication Data

Durrett, Richard, 1951–
Mutual invadability implies coexistence in spatial models / Rick Durrett.
p. cm. — (Memoirs of the American Mathematical Society, ISSN 0065-9266 ; no. 740)
"March 2002, vol. 156, number 740 (first of 5 numbers)."
Includes bibliographical references.
ISBN 0-8218-2768-5 (alk. paper)
1. Stochastic processes. 2. Reaction-diffusion equations. 3. Biology—Mathematical models. I. Title. II. Series.

QA3 .A57 no. 740
[QA274.3]
510 s—dc21
[519.2] 2001056086

Memoirs of the American Mathematical Society

This journal is devoted entirely to research in pure and applied mathematics.

Subscription information. The 2002 subscription begins with volume 155 and consists of six mailings, each containing one or more numbers. Subscription prices for 2002 are $524 list, $419 institutional member. A late charge of 10% of the subscription price will be imposed on orders received from nonmembers after January 1 of the subscription year. Subscribers outside the United States and India must pay a postage surcharge of $31; subscribers in India must pay a postage surcharge of $43. Expedited delivery to destinations in North America $35; elsewhere $130. Each number may be ordered separately; *please specify number* when ordering an individual number. For prices and titles of recently released numbers, see the New Publications sections of the *Notices of the American Mathematical Society.*

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Memoirs of the American Mathematical Society is published bimonthly (each volume consisting usually of more than one number) by the American Mathematical Society at 201 Charles Street, Providence, RI 02904-2294. Periodicals postage paid at Providence, RI. Postmaster: Send address changes to Memoirs, American Mathematical Society, P. O. Box 6248, Providence, RI 02940-6248.

This publication is indexed in *Science Citation Index®*, *SciSearch®*, *Research Alert®*, *CompuMath Citation Index®*, *Current Contents®/Physical, Chemical & Earth Sciences.*
Printed in the United States of America.

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10 9 8 7 6 5 4 3 2 1 07 06 05 04 03 02

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ABSTRACT

In (1994) Durrett and Levin proposed that the equilibrium behavior of stochastic spatial models could be determined from properties of the solution of the mean field ordinary differential equation (ODE) that is obtained by pretending that all sites are always independent. Here we prove a general result in support of that picture. We give a condition on an ordinary differential equation which implies that densities stay bounded away from 0 in the associated reaction-diffusion equation, and that coexistence occurs in the stochastic spatial model with fast stirring. Then using biologists' notion of invadability as a guide, we show how this condition can be checked in a wide variety of examples that involve two or three species: epidemics, diploid genetics models, predator-prey systems, and various competition models.

Received by the editor July 2, 1999; and in revised form June 23, 2000

Key words and phrases: stochastic spatial models, predator-prey systems, competition models, epidemics, ecology, genetics

AMS Subject Classifications. Primary: 60K35, 92B05. Secondary: 34C60, 35K57

Introduction. In the stochastic spatial models we consider, space is represented by a grid of sites, $\mathbf{Z}^d$, the d-dimensional integer lattice, each site can be in one of a finite set of states $\mathcal{S}$ and each site changes its state at a rate that depends on its state and the states of a few nearby sites. In the jargon of probability theory these models are interacting particle systems. See Liggett (1985,1999), Durrett (1995,1999). As the reader will soon see, these models which arose from physics, are very useful for studying a variety of systems in ecology and genetics.

The goal of this paper is to develop a methodology for proving coexistence of species in the presence of fast stirring, i.e., when the values at adjacent sites are exchanged at a large rate ν. Here, coexistence means that there is a stationary distribution that concentrates on configurations that have infinitely many sites in each state $s \in S$. The assumption of fast stirring greatly simplifies proofs since, as we will explain in more detail later, systems with stirring at rate ν on rescaled lattices $\nu^{-1/2}\mathbf{Z}^d$ in the limit as $\nu \to \infty$ become deterministic and approximate solutions of partial differential equations.

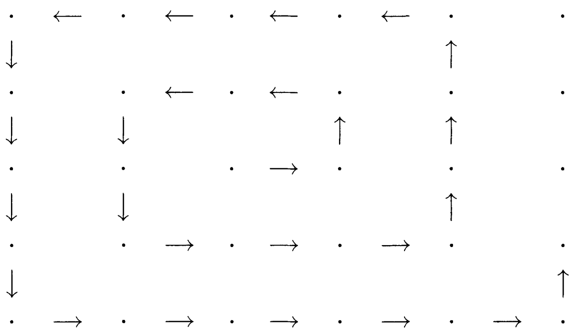
We will eventually apply our method to to more than ten families of examples. To explain have in mind, we will first consider one example in detail.

Example 1. A Predator-Prey System. The states of the system are $0 =$ vacant site, $1 =$ fish (prey), $2 =$ shark (predator). For simplicity, restrict our attention to two dimensional space. Inspired by Durrett and Levin (2000), we define the system in continuous time as follows.

(a) Fish die at rate δ_1. Sharks die at rate δ_2.

(b) Fish are born at vacant sites at rate $\beta_1 f_1$, where f_1 is the fraction of adjacent sites in state 1.

(c) Each shark get hungry at rate 1. When hungry it inspects a random number Q of neighboring sites moving outward in a spiral pattern from its current location. To describe the pattern in symbols, let $\|z\|_\infty = \max\{|z_1|, |z_2|\}$. Start at $(1, 0)$ and search the eight points with $\|z\|_\infty = 1$ in counterclockwise order ending at $(1, -1)$. Move to $(2, -1)$ and search the 16 points with $\|z\|_\infty = 2$, again in counterclockwise order ending at $(2, -2)$. Move to $(3, -2)$, etc. In a picture the pattern is



(d) The shark stops at the first fish it finds and eats it. A shark that has just eaten gives birth with probability β_2 to a new shark that is placed on the starting square. A shark that finds no fish returns to its starting square. These conventions about shark placement are needed to guarantee there is never more than one shark per site.

Before moving on the the analysis, we will make an assumption that will be the default condition throughout the paper.

Generic Parameters. If no assumptions are stated, then all transition rates referred to in the definition of the model are positive.

In some cases, we will want to set parameters to 0 in order to include some of the examples which were discussed earlier in the literature that had fewer parameters, and we will explicitly say so. In general, we can treat approximations of these by replacing the 0 parameters by a very small positive values.

We will begin our analysis with the special case of the predator-prey model in which $Q = q$ is constant, a case that was considered by Durrett and Levin (2000). The first step in their analysis, and in ours, is to look at the *mean field ODE* which is obtained by pretending that the states of all sites are always indepedent. In this case the mean field ODE is:

$$\begin{aligned} \frac{du_1}{dt} &= \beta_1 u_1(1-u_1-u_2) - \delta_1 u_1 - u_2\{1-(1-u_1)^q\} \\ \frac{du_2}{dt} &= \beta_2 u_2\{1-(1-u_1)^q\} - \delta_2 u_2 \end{aligned} \tag{1}$$

The first term on the right represents the birth of fish onto vacant sites, the second death of fish. The last term on the second line refers to death of sharks. To explain the remaining terms, we note that $u_2\{1-(1-u_1)^q\}$ gives the fraction of sites occupied by sharks times the probability a given shark will find at least one fish when it inspects q neighbors, so β_2 times this gives the rate at which new sharks are produced.

The generalization to a random Q is straightforward. If we let $g(u) = 1 - E(1-u)^Q$ be the probability a fish is found during the search then the mean field ODE becomes

$$\begin{aligned} \frac{du_1}{dt} &= \beta_1 u_1(1-u_1-u_2) - \delta u_1 - u_2\, g(u_1) \\ \frac{du_2}{dt} &= \beta_2 u_2\, g(u_1) - \delta_2 u_2 \end{aligned} \tag{2}$$

The reason for interest in the general form is that by choosing suitable distributions we can generate other functional forms considered in ecology. It is interesting to note that two of the most commonly used examples in ecology come from two of the most commonly used examples in probability.

I. *Q has a geometric distribution:* $P(Q=n) = p(1-p)^{n-1}$ for $n \geq 1$. In this case

$$\begin{aligned} g(u) = 1 - \sum_{q=1}^{\infty} p(1-p)^{q-1}(1-u)^q &= 1 - \frac{p(1-u)}{1-(1-p)(1-u)} \\ &= \frac{u}{p+(1-p)u} = \frac{Bu}{A+u} \end{aligned}$$

where $B = 1/(1-p)$ and $A = p/(1-p)$. This is a Holling Type 2 functional response, see Holling (1959), or Chapter 3 of Hassell (1978).

II. *Q has a Poisson distribution:* $P(Q=n) = e^{-\lambda}\lambda^n/n!$, for $n \geq 0$. In this case

$$g(u) = 1 - \sum_{q=0}^{\infty} e^{-\lambda}\frac{\lambda^n}{n!}(1-u)^q = 1 - e^{-\lambda}e^{\lambda(1-u)} = 1 - e^{-\lambda u}$$

which is the form introduced by Nicholson and Bailey (1935).

The most important feature of the nonlinear terms in I and II is that the per capita birth rate for the predator tends to a positive limit as the density of prey $u_1 \to \infty$, rather than increasing without bound as in the linear case.

To prove coexistence for the linear case $q = 1$ of the predator prey model, Durrett (1992) used a Lyapunov function for the mean field ODE, i.e., a function that is decreasing along solutions. However, in order to keep densities from hitting zero this is overkill. One only needs to know that solutions stay away from the boundary. To introduce the relevant generalization of Lyapunov function, consider the ODE

$$\frac{du_i}{dt} = f_i(u)$$

defined for $u \in \Gamma = \{u \in \mathbf{R}^n : u_i \geq 0, u_1 + \cdots + u_n \leq 1\}$, and to have a unique solution suppose that the f_i are Lipshitz continuous. A continuous function $\phi : \Gamma \to [0, \infty]$ is said to be a *repelling function for the closed set G in the ODE* if

(i) $G = \{u \in \Gamma : \phi(u) = \infty\}$

(ii) for each $\delta > 0$ there is a $c_\delta > 0$ so that

$$d\phi(u(t))/dt \leq -c_\delta \quad \text{when} \quad M + \delta < \phi < \infty$$

Note that the constant in (ii) is uniform over $(M + \delta, \infty)$. At first this may seem stronger than

(ii′) for each $0 < \delta < K < \infty$ there is a $c_{\delta,K} > 0$ so that

$$d\phi(u(t))/dt \leq -c_{\delta,K} \quad \text{when} \quad M + \delta < \phi < M + K$$

However, if we consider $\psi(\phi(u))$ where ψ increases rapidly then the conclusion (ii′) can be improved to (ii).

It should be clear from (i) and (ii) that we can replace ϕ by $\max\{\phi, M\}$ and assume without loss of generality that $\phi \geq M$. With a little undergraduate analysis, see Section 9, one can show that

Proposition 0. *Suppose (i) and (ii) hold. If $\phi(u(0)) < \infty$ then*

$$\limsup_{t \to \infty} \phi(u_i(t)) \leq M$$

In view of (i) this implies that at large times $u_i(t)$ stays bounded away from G. Let

$$\Gamma^+ = \{u \in \Gamma : u_i > 0 \text{ for all } i\} \quad \text{and} \quad \Gamma^0 = \Gamma - \Gamma^+$$

be the points in Γ where at least one coordinate is equal to 0. When the conclusion of Proposition 0 holds for $G = \Gamma^0$, the ODE is said to be *uniformly persistent* or *permanent.* Hofbauer (1988) used repelling functions and a weaker concept called *average Lyapunov functions* to prove permanence for ODE in general and for Lotka-Volterra systems in particular. See Hofbauer and Sigmund (1998) for an account of this method and its application to a number of concrete examples. The reader will see this book cited numerous times in Section 2. We would like to thank Odo Diekmann for bringing Hofbauer's results to our attention.

In order to prove coexistence of species in the stochastic spatial model using the methods of Durrett and Neuhauser (1994), we must prove a persistence results for the corresponding RDE (reaction diffusion equation),

$$\frac{du_i}{dt} = \Delta u_i + f_i(u)$$

where $\Delta = \partial^2 u/\partial x_1^2 + \cdots + \partial^2 u/\partial x_k^2$. To do this, we let $\log^- z = \max\{0, -\log z\}$ be the negative part of $\log z$ and add three more conditions:

(iii) $\phi(u)$ is convex

(iv) $\phi(u) \le C\left(1 + \sum_{i=1}^k \log^- u_i\right)$

(v) $f_i(u) \ge -\alpha_i u_i$

A function satisfying (i)–(iv) is said to be a *repelling function for G in the reaction diffusion equation (RDE).* The last condition, (v), is a technicality concerning the ODE. In most examples, the rate at which the process can leave state i is bounded so (v) holds. Note that we did not assume $f_i(u) \le C_i u_i$, since this would for example rule out epidemic models where removed individuals arise only from infected individuals.

Proposition 1. *Suppose a repelling function exists for the RDE, (v) holds, the initial condition $u(0,x) \in \Gamma$ is continuous, and has*

$$u_i(0,x) \ge \eta_i > 0 \quad \textit{when} \quad x \in [-\delta,\delta]^2$$

There are constants $\kappa > 0$ and $t_0 < \infty$, which only depend on η_i, δ, and ϵ so that

$$\phi(u(t,x)) \le M + \epsilon \quad \text{when} \quad |x| \le \kappa t, \quad t \ge t_0$$

In words $u(t, x)$ stays bounded away from G on a linearly growing set. Proposition 1 is essentially due to Durrett (1992). However, since the proof was given there only for a special case, and we will need its sharper conclusion in our more general setting, we will give a complete proof in Section 8. The proof for the new general result is shorter than the previous one for the special case.

The conclusion of Proposition 1 is most informative when $G = \Gamma^0$, in which case it implies that probabilities are bounded away from 0 on a linearly growing set. However we will also use this result several times for smaller $G \subset \partial\Gamma$ (see Examples 2.2, 2.3, and 2.5). The uniformity in Proposition 1 is needed so that we can use the methods of Durrett and Neuhauser (1994) in the form explained in Section 9 of Durrett's (1995) St. Flour notes. If we make the assumption:

($\star$) There are constants $A_i < a_i < b_i < B_i$, L, and T so that if $u_i(0, x) \in (A_i, B_i)$ when $x \in [-L, L]^d$ then $u_i(T, x) \in (a_i, b_i)$ when $x \in [-3L, 3L]^d$.

then we can state Theorem 9.1 of Durrett (1995) as:

Proposition 2. *If ($\star$) holds then there is coexistence for the stochastic spatial model with fast stirring.*

Combining Propositions 1 and 2, gives

Proposition 3. *If (i)–(v) hold then there is coexistence for the stochastic spatial model with fast stirring.*

As the reader can see from the citations, all of this was known in 1995. What is the new here, is the realization that the biologists notion of invadability leads to a systematic procedure for constructing such functions. To explain this type of reasoning, we will apply it to our predator prey model. To begin, we note that if $u_1 = 0$ (no fish) then sharks cannot give birth so $u_2(t) \downarrow 0$. On the other hand, if $u_2 = 0$ (no sharks) then

$$\frac{du_1}{dt} = \beta_1 u_1(1 - u_1) - \delta u_1 = \beta_1 u_1 \left(\frac{\beta_1 - \delta_1}{\beta_1} - u_1 \right)$$

so if $\beta_1 > \delta_1$, and $u_1(0) > 0$ then $u_1(t) \to (\beta_1 - \delta_1)/\beta_1$.

The last observation implies that if u_2 is small then u_1 will equilibrate to a density $\sigma_1 = (\beta_1 - \delta_1)/\beta_1$. When the 1's are in equilibrium, the 2's satisfy

$$\frac{du_2}{dt} = u_2(\beta_2 g(\sigma_1) - \delta_2)$$

and so they will increase if

$$\beta_2 g(\sigma_1) > \delta_2 \tag{3}$$

Abstracting from these observations we make the following definitions.

Definition 1. *We say that 2's die out, and write* $2 \downarrow 0$, *if*

$$du_2/dt < 0 \quad \text{when } u_1 = 0 \text{ and } u_2 > 0$$

Definition 2. *We say that 1's equilibrate at density* σ_1, *and write* $1 \to \sigma_1$, *if*

$$u_1(t) \to \sigma_1 \quad \text{as } t \to \infty \text{ when } u_2 = 0 \text{ and } u_1(0) > 0.$$

Definition 3. *We say that species 2 can invade species 1 in equilibrium, and write* $2 \succ 1$, *if as* $u \to (\sigma_1, 0)$ *through* Γ^+ *we have*

$$\liminf \frac{1}{u_2}\frac{du_2}{dt} > 0$$

To help the reader remember the notation, we remark that the TeX name for the symbol we have just defined is \succ which is short for "successor." In words, we could say 2 succeeds 1, but we will usually read this as 2 invades 1.

For the sake of symmetry, it is natural to write "technical conditions" $\beta_1 > \delta_1$ for the equilibrium distribution $\sigma_1 > 0$ in invadability language as:

Definition 4. *We say that* $i \succ 0$ *if as* $u \to 0$ *inside* Γ_+ *we have*

$$\liminf \frac{1}{u_i}\frac{du_i}{dt} > 0$$

As the example $du_1/dt = u_1^2(\sigma_1 - u_1)$ shows $1 \to \sigma_1$ does not imply $1 \succ 0$. Having introduced these definitions we can state our predator-prey result abstractly as

Theorem 1. *If* $2 \downarrow 0$, $1 \succ 0$, $1 \to \sigma_1$, *and* $2 \succ 1$ *in the mean field ODE then there is coexistence in the stochastic spatial model with fast stirring.*

Proof. See Figure 1. We begin with the edge $\Gamma_1^0 = \{u \in \Gamma : u_1 = 0\}$. A little calculus (see Proposition 1.2) shows that if we suppose (a) $2 \downarrow 0$ and (b) $1 \succ 0$, and positive constants λ_1, ν_1, and η_1 are chosen appropriately, then $h_1(u_1, u_2) = u_2 - \lambda_1 \log u_1$ has

$$(5) \qquad dh_1/dt \le -\nu_1 < 0 \quad \text{when } 0 < u_1 \le \eta_1 \text{ (and } u \in \Gamma)$$

In words, h_1 is a repelling function for Γ_1^0. To prepare for the next step of the construction we have to *tighten* h_1 so that it is strictly decreasing in a strip near Γ_1^0. To do this, we first pick M_1 large enough then the function $\bar{h}_1 = h_1 \vee M_1$ is only nontrivial when $0 \le u_1 \le \eta_1$, then we take $\bar{\eta}_1 \le \eta_1$ so that $h_1 > M_1$ when $0 \le u_1 \le \bar{\eta}_1$.

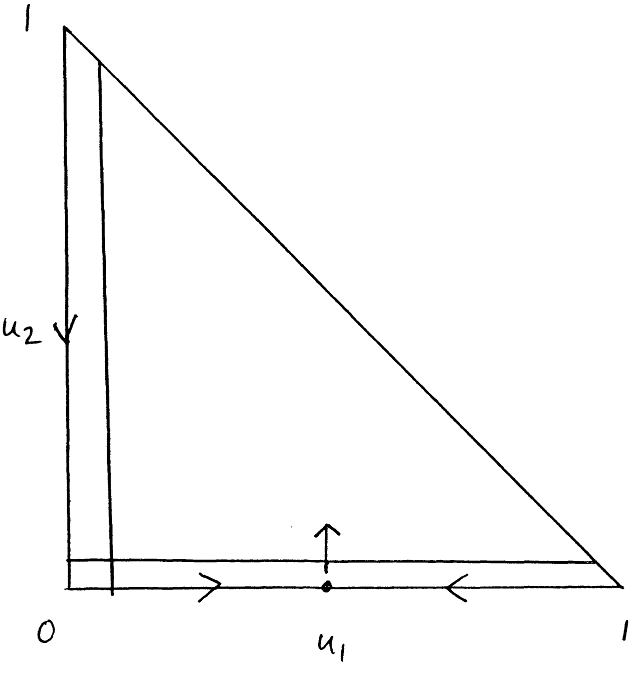


Figure 1

Moving to the other edge $\Gamma_2^0 = \{u \in \Gamma : u_2 = 0\}$, we let $\sigma_1 = (\beta_1 - \delta_1)/\beta_1$ be the equilibrium and $g(u) = u - \sigma_1 \log u$. Since $g'(u) = 1 - \sigma_1/u$ and $g''(u) = \sigma_1/u^2$, $g(u)$ is convex and has a minimum at σ_1. Since we have assumed $1 \to \sigma_1$, g is a convex Lyapunov function for the ODE on Γ_2^0. Let and $\psi_2(u) = (\epsilon_2 - u)^{+2}$. A little more calculus (see Proposition 1.1) shows that if (a) $1 \to \sigma_1$ and (b) $2 \succ 1$, and positive constants θ_2, λ_2, $\eta_2 \le \epsilon_2$, $\nu_2 \le \nu_1$, and B_2 are chosen appropriately, then

$$h_2(u_1,u_2) = g_1(u_1 + \theta_2\psi_2(u_1)u_2) - \lambda_2 \log u_2 \tag{6}$$

has (i) $dh_2/dt \le -\nu_2 < 0$ when $\epsilon_2 \le u_1 \le 1$ and $0 < u_2 \le \eta_2$

and (ii) $dh_1/dt \le B_2$ when $0 \le u_1 \le \epsilon_2$ and $0 < u_2 \le \eta_1$.

To see the reason for the form of $\psi_2(u)$, note that when $u_1 \ge \epsilon_2$ then $h_2(u) = g_1(u_1) - \lambda_2 \log u_2$. In words h_2 is a repelling function for $\{u \in \Gamma : u_2 = 0, u_1 \ge \epsilon_2\}$ and does only a bounded amount of damage near the corner $(0,0)$. The region in (ii) is not a problem because of (5). To finish up now, we *truncate* h_2, that is, we pick M_2 large enough so that the function $\bar{h}_2 = h_2 \vee M_2$ is only nontrivial when $0 \le u_2 \le \eta_2$. Finally we pick $K \ge 1$ large enough so that $K\bar{h}_1 + \bar{h}_2$ is a repelling function for Γ^0, and the desired result then follows from Proposition 3. □

The details of the proof may seem mysterious now, but as the reader will see through a dozen examples below, all proofs follow the same simple pattern. The construction is arranged so that when each stage is complete we have a repelling function for some set $G \subset \Gamma_0$. Here, $\bar{h}_1$ is a repelling function for Γ_1^0 and then $K\bar{h}_1 + \bar{h}_2$ is a repelling function for Γ^0. This proceduce dictates we start with the side Γ_1^0 where the perturbation result (Proposition 3.2) has no exceptional set, rather that with Γ_2^0 where the fixed point at $(0,0)$ causes trouble for the perturbation in Proposition 3.1. We then use the good properties of the first function to cancel the trouble with the second one.

One of the advantages of this style of argument is that it uses only qualitative features of the ODE and hence generalizes easily to other systems. For example from our analysis of the predator prey system, we can immediately get a result for

Example 2. Epidemic models. Following Mollison (1972), (1977) we formulate a continuous time model on an infinite grid with three states, 0 = susceptible, 1 = infected, and 2 = removed. The word "removed" will mean dead in the case of a fatal disease like rabies, or in the case of measles, that the individual has had the disease once and is immune to having it again.

Letting f_i be the fraction of neighbors in state i, we can write down the transition rates for our model as follows.

$$1 \to 2 \quad \beta_2 f_2 \qquad\qquad 2 \to 0 \quad \delta_2 \qquad\qquad 0 \to 1 \quad \beta_0 + \beta_1 f_1$$

In words, susceptibles become infected a rate proportional to the number of infected neighbors. Infecteds die after an exponential amount of time with mean $1/\delta_2$, leaving an empty space which is colonized by nearby occupied sites at rate $\beta_1 f_1$ or filled by an immigrant from outside the system at rate β_0.

The mean field differential equations in this case are simple:

$$\begin{aligned} \frac{du_1}{dt} &= u_0(\beta_0 + \beta_1 u_1) - \beta_2 u_1 u_2 \\ \frac{du_2}{dt} &= \beta_2 u_1 u_2 - \delta_2 u_2 \end{aligned} \tag{7}$$

From the equations and Definitions 1–4, it is easy to see that

(8) If $\delta_2 > 0$ then $2 \downarrow 0$.

(9) If $\beta_0 + \beta_1 > 0$ then $1 \succ 0$ and $1 \to \sigma_1$ where $\sigma_1 = 1$.

(10) If $\beta_2 > \delta_2$ then $2 \succ 1$.

Combining the last three conditions we have:

Theorem 2. *If $\delta_2 > 0$, $\beta_0 + \beta_1 > 0$, and $\beta_2 > \delta_2$ then there is coexistence for the epidemic with fast stirring.*

Proof. The conditions imply $2 \downarrow 0$, $1 \succ 0$, $1 \to \sigma_1 = 1$, and $2 \succ 1$ so the result follows from Theorem 1. □

For the nearest neighbor model with no stirring and spontaneous regrowth (i.e., $\beta_0 > 0$, $\beta_1 = 0$) Durrett and Neuhauser (1991) showed in two dimensions that if the epidemic without regrowth (i.e., $\beta_0 + \beta_1 = 0$) is supercritical, then the system with spontaneous regrowth has a nontrivial stationary distribution. By using results of Zhang (1990) instead of those in Cox and Durrett (1988) one should be able to extend Durrett and Neuhauser's result to finite range models with no stirring and spontaneous regrowth in dimensions $d \geq 2$.

The result given in Theorem 2 is the first that we know of for epidemic models with contact regrowth ($\beta_0 = 0$, $\beta_1 > 0$.) For more on spatial epidemic models, see Mollison and Kuulasmaa (1985), Bak, Chen, and Tang (1990), Drossel and Schwabl (1992), Henley (1993), Durrett (1995b), Durrett and Levin (1996), Holmes (1997) or the conference proceedings edited by Mollison (1995), and by Grenfell and Dobson (1995). Closely related to epidemic models are host-pathogen systems. See Rand, Keeling, and Wilson (1995), and Thrall and Burton (1997) for spatial models in this context.

Overview of the rest of the paper. In Section 1 we will prove Propostions 1.1 and 1.2 which we have used in the proof of Theorem 1. In Section 2 we will state our results for the five two-species examples we will consider. In a few cases we emerge with something less than a repelling function (e.g., we can conclude only that $u_1 + u_2$ stays bounded away from 0 on a linearly growing set) so to complete the proof we need an auxillary argument to conclude that the individual u_i stay bounded away from 0 in the RDE. This is done in Section 3 with the help of the Feynman-Kac formula.

In Section 4, we prove perturbation results for three dimensional systems that generalize those for the two dimensional case given in Section 1. In Section 5, we introduce the raw material that feeds into the machinery of the Section 4: Lyapunov functions for the two dimensional boundary systems, which we assume to be of the Lotka-Volterra form. In Section 6 and 7, we combine the results from Sections 4 and 5 to prove coexistence results for linear competition models and for three species predator-prey systems. Section 8 ties up loose ends giving the proofs of Propositions 0 and 1, and Theorem 6.3

Acknowledgements. The research reported on here was partially supported by grants through the program in Statistics and Probability at the National Science Foundation. The author would like to express his appreciation to Janet Best and to an anonymous referee for their comments which have led to many improvements in the paper.

1. Perturbation of one-dimensional systems.

In this section we will prove Propositions 1.1 and 1.2 that were used in the proof of Theorem 1. More generally, we will prove a result that allows us to extend a Lyapunov function defined on a one-dimensional face $F_1 = \{u \in \Gamma : u_2 = 0, \dots u_n = 0\}$ to be a repelling function in a neighborhood of that face (in Γ). The reader should feel free to just read the statements of Propositions 1.1 and 1.2 (along with the relevant definitions) before moving on to the examples.

We reduce the number of perturbation variables from $n-1$ to 1 by looking at a positive linear combination of the last $n-1$ coordinates. Let

$$z = \sum_{k=2}^{n} \omega_k u_k \qquad \text{where each of the } \omega_k > 0$$

let $\|\omega\| = \sup_{2 \le k \le n} \omega_k$, and note that $z \le \|\omega\|$ for all $u \in \Gamma$. In the other direction to extend vectors from 1 to n dimensions let $0_{n-1} \in \mathbf{R}^{n-1}$ be a vector of all 0's, and for real numbers x we define $(x, 0_{n-1}) \in \mathbf{R}^n$ to be the vector with x in the first coordinate and then all 0's.

Proposition 1.1. *Let* $\sigma > 0$ *and* $g(u) = u - \sigma \log u$. *Suppose*

(a) σ *is an attracting fixed point on* $F_1^+ = \{u \in F_1 : u_1 > 0\}$

(b) If $u \to (\sigma, 0_{n-1})$ *from inside* Γ^+, *then* $\liminf \frac{1}{z}\frac{dz}{dt} \ge 3\alpha_0 > 0$.

(c) $dz/dt \ge -C_c z$ *and* $du_1/dt \ge -C_c u_1$

Let $0 < \epsilon < \sigma/(1 + \|\omega\|)$ *and let* $\psi(u) = (\epsilon - u)^{+2}$, *i.e., the square of the positive part of* $\epsilon - u$. *If positive constants* θ, λ, η, ν, *and* B *are chosen appropriately with* $\theta \le 1$ *and* $\eta \le \epsilon$ *then*

$$h(u) = g(u_1 + \theta\psi(u_1)z) - \lambda \log z$$

satisfies: (i) $dh/dt \le -\nu < 0$ *when* $\epsilon \le u_1$ *and* $0 < z \le \eta$.

and (ii) $dh/dt \le B$ *when* $0 \le u_1 \le \epsilon$ *and* $0 < z \le \eta$.

Remark. The conditions in (c) are implied by (v). The first condition is what we have called $1 \to \sigma_1$ in the introduction. The second is more general than $2 \succ 1$ so we need a new definition.

Definition 5. *We say that $2, \dots n$ can invade 1 and write $2, \dots n \succ 1$ if (b) holds.*

Proof of Proposition 1.1. Calculus tells us that

$$\frac{dh}{dt} = g'(u_1 + \theta\psi(u_1)z)\left(\{1 + \theta\psi'(u_1)z\}\frac{du_1}{dt} + \theta\psi(u_1)\frac{dz}{dt}\right) - \frac{\lambda}{z}\frac{dz}{dt} \tag{1.1}$$

We begin by checking (ii) since it is only a few lines. Differentiating we find

$$g'(u) = 1 - \frac{\sigma}{u} \qquad \text{so} \qquad |g'(u)| \le \frac{C_d}{u} \quad \text{for } 0 < u \le 1 \tag{1.2}$$

When $u_1 \le \epsilon$ and $\theta \le 1$, $g'(u_1 + \theta\psi(u_1)z) < 0$, so using (1.2) and assumption (c) with the trivial bounds that hold for $0 \le u \le 1$: $\psi(u) \le 1$, $\psi'(u) \le 2\epsilon$:

$$\begin{aligned} &g'(u_1 + \theta\psi(u_1)z)\left(\{1 + \theta\psi'(u)z\}\frac{du_1}{dt} + \theta\psi(u_1)\frac{dz}{dt}\right) \\ &\le \left(\frac{C_d}{u_1 + \theta\psi(u_1)z}\right) \cdot C_c\{(1 + 2\epsilon\|\omega\|)u_1 + \theta z\} \le C_e \end{aligned} \tag{1.3}$$

for some $C_e < \infty$. Using (c) again we have

$$-\lambda\frac{dz}{dt} \le \lambda C_c z \tag{1.4}$$

Combining (1.1), (1.3) and (1.4) proves (ii) with $B = C_e + \lambda C_c$.

Proof of (i). To begin, we note that (b) implies we can pick $\eta_1 < \sigma/2$ so that if $|u_1 - \sigma| \le \eta_1$, and $0 < z \le \eta_1$ then

$$\frac{\lambda}{z}\frac{dz}{dt} \ge 2\alpha_0\lambda > 0 \tag{1.5}$$

Our first goal is the control the derivative dh/dt away from the fixed point.

Lemma 1.1. *Given ϵ and η_1, there are $\alpha_1, \eta_2, \lambda_0 > 0$ so that if $\lambda \le \lambda_0$ then*

$$\frac{dh}{dt} \le -\alpha_1 < 0$$

when $u_1 \geq \epsilon$, $|u_1 - \sigma| \geq \eta_1$, *and* $0 < z \leq \eta_2$.

Proof of Lemma 1.1. When $u_1 \geq \epsilon$, we have $\psi(u) = 0$, so $h(u) = g(u_1) - \lambda \log z$ and

$$\frac{dh}{dt} = g'(u_1)\frac{du_1}{dt} - \frac{\lambda}{z}\frac{dz}{dt} \tag{1.6}$$

Property (a), implies that there is a constant $\alpha_1 > 0$ so that

$$g'(u_1)\,\frac{du_i}{dt}(u_1, 0_{n-1}) \leq -3\alpha_1 \tag{1.7}$$

when $u_1 \geq \epsilon$ and $|u_1 - \sigma| \geq \eta_1$. Using the boundedness of $g'(u_1)$ for $u_1 \geq \epsilon$ which comes from (1.2), and the continuity of du_i/dt it follows that if η_2 is small then

$$g'(u_1)\,\frac{du_i}{dt}(u) \leq -2\alpha_1 \tag{1.8}$$

when $u_1 \geq \epsilon$, $|u_1 - \sigma| \geq \eta_1$, and $0 < z \leq \eta_2$. To bound the second term in (1.6), we use (1.4). Combining this with (1.8), it follows that

$$\frac{dh}{dt} \leq -2\alpha_1 + C_c\lambda_0 \leq -\alpha_1$$

if η_2 and λ_0 are chosen small enough. □

To complete the proof of (i) in Proposition 1.1, we have to consider the region near the fixed point. To do this, we will prove

Lemma 1.2. *Given* η_1 *and* η_2, *if* $\eta_3 \leq \eta_2$ *is chosen small enough*

$$\sup\left\{\frac{dh}{dt} : |u_1 - \sigma| \leq \eta_1,\ 0 < z \leq \eta_3\right\} \leq -\lambda\alpha_0$$

Proof of Lemma 1.2. Again we use (1.6). By (a), the first term has

$$g'(u_1)\,\frac{du_1}{dt}(u_1, 0_{n-1}) \leq 0 \tag{1.9}$$

for all $0 < u_1 \leq 1$. Using the boundedness of g' near the fixed point (which follows from (1.2)) and the continuity of du_i/dt, it follows that if $\eta_3 \leq \eta_2$ is small then

$$g'(u_1)\,\frac{du_1}{dt}(u) \leq \lambda\alpha_0 \tag{1.10}$$

when $|u_1 - \sigma| \leq \eta_1$ and $z \leq \eta_3$. Combining (1.10) with (1.6), and (1.5), we have

$$\frac{dh}{dt} \leq \lambda\alpha_0 - 2\lambda\alpha_0 < 0$$

when $|u_1 - \sigma| \leq \eta_1$, $0 < z \leq \eta_3$. From this the desired result follows. □

In Proposition 1.1 we considered the case of a fixed point $\sigma_1 > 0$. The next case covers the case in which the fixed point on the edge is at 0. The new result is an improvement over Proposition 1.1 in that there is no need to exclude small values of u_1, so the conclusion holds all the way along the edge. Here, again $z = \omega_2 u_2 + \cdots + \omega_n u_n$ with $\omega_k > 0$ for $2 \leq k \leq n$.

Proposition 1.2. *Suppose that (a) 0 is an attracting fixed point on the edge* F_1, *i.e.,* $du_1/dt < 0$ *when* $u_1 > 0, u_2 = 0, \dots u_n = 0$

(b) *If* $u \to 0_n$ *from inside* Γ_+, *then* $\liminf \frac{1}{z}\frac{dz}{dt} \geq 3\alpha_0 > 0$.

(c) $dz/dt \geq -C_c z$.

If positive constants λ, ν *and* η *are chosen appropriately then* $h(u) = u_1 - \lambda \log z$ *has* $dh/dt \leq -\nu < 0$ *for* $0 \leq u_1 \leq 1$ *and* $0 < z \leq \eta$.

Proof. Calculus tells us

$$\frac{dh}{dt} = \frac{du_1}{dt} - \frac{\lambda}{z}\frac{dz}{dt} \tag{1.11}$$

which is a special case of (1.6). It follows from (b) that if we pick η_1 small then

$$\frac{1}{z} \cdot \frac{dz}{dt} \geq 2\alpha_0 \tag{1.12}$$

when $0 < u_1, z \leq \eta_1$. Continuity of the right-hand side of the ODE allows us to extend the result to the points with $u_1 = 0$, $0 < z \leq \eta_1$. Continuity also implies that if $0 \leq u_1, z \leq \eta_2$ and η_2 is small

$$\frac{du_1}{dt} \leq \lambda_0 \tag{1.13}$$

Combining (1.11)–(1.13), we have shown that

$$dh/dt \leq -\lambda\alpha_0 \quad \text{when } 0 < u_1 \leq \eta_2 \text{ and } 0 \leq z \leq \eta_2$$

To complete the proof, we need an upper bound on dh/dt when $\eta_2 \leq u_1 \leq 1$ and $0 \leq z \leq \eta_3$ for some $0 < \eta_3 \leq \eta_2$. To begin, note that (a) and continuity of the right-hand side of the ODE imply that there is are $\eta_3, \alpha_1 > 0$ so that

$$\frac{du_1}{dt} \leq -2\alpha_1 < 0 \tag{1.14}$$

when $\eta_2 \leq u_1 \leq 1$ and $0 < z \leq \eta_3$. Using (1.11) and the inequality in (c), gives

$$\frac{dh}{dt} = \frac{du_1}{dt} - \frac{\lambda}{z}\frac{dz}{dt} \leq -2\alpha_1 + \lambda C_c \leq -\alpha_1 \tag{1.15}$$

if λ is small, and the proof of the lemma is complete. □

2. Two-Species Examples. In this section we will describe our coexistence results for our two-species examples. By Proposition 3 it is enough to check (i)–(v). All of our processes have bounded rates and hence satisfy (v), so it is sufficient to prove the existence of a repelling function for Γ^0. We begin with a fairly general competition model.

Example 2.1. Linear competition with exclusion. In this model each site can be in state 0, 1, or 2, where 0 is vacant while $i = 1, 2$ indicate sites occupied by types 1 or 2 respectively. The word "exclusion" here refers to the fact that the two types cannot occupy the same site at the same time. To formulate the dynamics of this and of many of our other models we will let $p_i(z)$ be a probability distribution on $\mathbf{Z}^d$ that represents the interaction kernel for species i, and let

$$f_i = \sum_y p_i(y - x) 1_{\{\xi_t(y)=i\}} \tag{2.1.1}$$

be the "fraction of neighbors in state i." For simplicity we will suppose that $\{z : p_i(z) > 0\}$ is finite and $p_i(z) = p_i(-z)$. It is a strength (and weakness) of our approach that it does not depend on the interaction kernels p_i. Indeed, one could even use different kernels for each of the local densities f_i in the table below.

Writing $i \to j$ for state i changes to j, we can now describe the jump rates for the model as follows:

$0 \to 1$	$\beta_1 f_1$	$1 \to 2$	$\beta_{12} f_2$
$0 \to 2$	$\beta_2 f_2$	$2 \to 1$	$\beta_{21} f_1$
$1 \to 0$	$\delta_1 + \gamma_{11} f_1 + \gamma_{12} f_2$		
$2 \to 0$	$\delta_2 + \gamma_{21} f_1 + \gamma_{22} f_2$		

In words, individuals of type i's give birth at rate β_i onto vacant sites, at rate $\beta_{i,3-i}$ onto sites of the opposite type, and die at a rate that is a linear function of the number of 1's and 2's in their neighborhood.

This model contains as a special case several others in the literature. In the category of processes that cannot give birth onto occupied sites, i.e., $\beta_{12} = \beta_{21} = 0$, Neuhauser (1992) studied the situation in which all $\gamma_{ij} = 0$, while Durrett and Levin (1997) used a model with $\gamma_{21} > 0$ and all of the other $\gamma_{ij} = 0$ in their study of allelopathy. To describe the second system in words, species 1 is a type of *E. coli* that produces colicin, a chemical that increases the death rate of species

2. More recently Neuhauser and Pacala (1999) have considered this model with general competition coefficients to study the effect of local competitive interactions between species on the outcome of competition.

If we set $\beta_{12} = \beta_2$, $\beta_{21} = 0$, and all the $\gamma_{ij} = 0$ then we get a process studied by Crawley and May (1987), Durrett and Swindle (1991), Durrett and Schinazi (1993), and in an n-species form by Tilman (1994). In Tilman's generalization type i is allowed to give birth onto sites occupied by types $j < i$. Silvertown et al. (1992) and Durrett and Levin (1998) generalized Tilman's strictly hierarchical model by setting $\beta_{ij} = \beta_i c_{ij}$. In words, species i gives birth at rate β_i and successfully displaces j with probability c_{ij}.

If we let u_i denote the fraction of sites in state i then the mean field ODE for the linear competition with exclusion can be written as:

$$\begin{aligned}\frac{du_1}{dt} &= \beta_1 u_1 u_0 - u_1(\delta_1 + \gamma_{11}u_1 + \gamma_{12}u_2) - \beta_{12}u_1u_2 + \beta_{21}u_1u_2\\ \frac{du_2}{dt} &= \beta_2 u_2 u_0 - u_2(\delta_2 + \gamma_{21}u_1 + \gamma_{22}u_2) - \beta_{21}u_1u_2 + \beta_{12}u_1u_2\end{aligned}$$

The first term in the first equation comes from sites changing from 0 to 1 at rate $\beta_1 f_1$, which if we assume adjacent sites are independent, results in new 1's being produced at rate $u_0 \cdot \beta_1 u_1$. The second term comes from the death mechanism in a similar way. The third and fourth terms arise from 1's turning into 2's and from 2's turning into 1's, respectively.

To begin to analyze the mean field ODE, we let $u_0 = 1 - u_1 - u_2$ and rearrange to get

$$\begin{aligned}\frac{du_1}{dt} &= u_1\{(\beta_1 - \delta_1) - (\beta_1 + \gamma_{11})u_1\\ &\qquad - (\beta_1 + \gamma_{12} + \beta_{12} - \beta_{21})u_2\}\\ \frac{du_2}{dt} &= u_2\{(\beta_2 - \delta_2) - (\beta_2 + \gamma_{22})u_2\\ &\qquad - (\beta_2 + \gamma_{21} + \beta_{21} - \beta_{12})u_1\}\end{aligned} \tag{2.1.2}$$

This differential equation has the *Lotka-Volterra form*

$$\frac{du_i}{dt} = u_i\left(r_i - \sum_j a_{ij}u_j\right) \tag{2.1.3}$$

In ecological terms, r_i is the intrinsic growth rate of species i, a_{ii} measures intraspecific competition for species i, and when $j \neq i$, a_{ij} measures interspecific competition between species i and j.

In the case of two species, one can easily solve for the coordinates of the only possible equilibrium state (ρ_1, ρ_2) with both components non-zero:

$$\rho_1 = \frac{a_{22}r_1 - a_{12}r_2}{a_{22}a_{11} - a_{12}a_{21}} \qquad \rho_2 = \frac{a_{11}r_2 - a_{21}r_1}{a_{22}a_{11} - a_{12}a_{21}} \tag{2.1.4}$$

Plugging in the values for r_i and a_{ij} we have

$$\begin{aligned} \rho_1 &= \frac{(\beta_2 + \gamma_{22})(\beta_1 - \delta_1) - (\beta_1 + \gamma_{12} + \beta_{12} - \beta_{21})(\beta_2 - \delta_2)}{D} \\ \rho_2 &= \frac{(\beta_1 + \gamma_{11})(\beta_2 - \delta_2) - (\beta_2 + \gamma_{21} + \beta_{21} - \beta_{12})(\beta_1 - \delta_1)}{D} \end{aligned} \tag{2.1.5}$$

where $D = (\beta_1 + \gamma_{11})(\beta_2 + \gamma_{22}) - (\beta_2 + \gamma_{21} + \beta_{21} - \beta_{12})(\beta_1 + \gamma_{12} + \beta_{12} - \beta_{21})$.

With the brute force approach of solving the equations for the equilibrium distribution, it is hard to understand what the conditions $\rho_i > 0$ mean, or what is more important, how to use them in a proof. As we will now show the condition becomes transparent and useful for proofs if we approach the question from the viewpoint of mutual invadability. To show the generality of the calculation, and to have simpler notation, we will carry it out for the Lotka-Volterra system in (2.1.3) assuming only that all of the constants r_i and a_{ij} are positive.

The first step is to note that if $r_i > 0$ then species i in the absence of the other, will have equilibrium densities given by

$$\sigma_i = r_i / a_{ii} \tag{2.1.6}$$

Using Definitions 2 and 4 from the introduction we can say that if $r_i > 0$ then $1 \succ 0$ and $1 \to \sigma_1$. From equation (2.1.3) and Definition 3, it is easy to see that

$$\begin{aligned} 1 \succ 2 \quad &\text{if} \quad r_1 - a_{12}\sigma_2 > 0 \\ 2 \succ 1 \quad &\text{if} \quad r_2 - a_{21}\sigma_1 > 0 \end{aligned} \tag{2.1.7}$$

In the concrete situation of Example 2.1,

$$r_i = \beta_i - \delta_i \qquad \sigma_i = \frac{\beta_i - \delta_i}{\beta_i + \gamma_{ii}} \tag{2.1.8}$$

so recalling the definition of the a_{ij} we have

$$
\begin{aligned}
&1 \succ 2 \quad \text{if} \quad \beta_1 - \delta_1 - (\beta_1 + \gamma_{12} + \beta_{12} - \beta_{21}) \frac{\beta_2 - \delta_2}{\beta_2 + \gamma_{22}} > 0 \\
&2 \succ 1 \quad \text{if} \quad \beta_2 - \delta_2 - (\beta_2 + \gamma_{21} + \beta_{21} - \beta_{12}) \frac{\beta_1 - \delta_1}{\beta_1 + \gamma_{11}} > 0
\end{aligned}
\tag{2.1.9}
$$

To make the connection between the last two conditions and the existence of an interior fixed point, note that (2.1.9) clearly implies that the numerators of the ρ_i given in (2.1.5) are positive. To see that the denominator D will also be positive, note that the two conditions in (2.1.9) imply

$$\frac{\beta_1 + \gamma_{12} + \beta_{12} - \beta_{21}}{\beta_2 + \gamma_{22}} < \frac{\beta_1 - \delta_1}{\beta_2 - \delta_2} < \frac{\beta_1 + \gamma_{11}}{\beta_2 + \gamma_{21} + \beta_{21} - \beta_{12}}$$

Combining the calculations above, we expect coexistence in a Lotka-Volterra system if $r_1 > 0$, $r_2 > 0$, $r_2 - a_{21}\sigma_1 > 0$, and $r_1 - a_{12}\sigma_2 > 0$. The next result confirms this.

Theorem 2.1. *Suppose that (a)* $1 \succ 0$, $2 \succ 0$*; (b)* $1 \to \sigma_1$, $2 \succ 1$*; and (c)* $2 \to \sigma_2$ *and* $1 \succ 2$ *in the mean field ODE. Then there is coexistence in the stochastic spatial model with fast stirring.*

Proof of Theorem 2.1. For a picture see Figure 2.1. The three sets of assumptions correspond to the three steps in the proof. We start at the corner and work our way out. Since we have assumed $1 \succ 0$ and $2 \succ 0$, we can pick $\alpha, \eta_0 > 0$ so that if $u_1 + u_2 < 3\eta_0$ then

$$\frac{d(u_1 + u_2)}{dt} \geq \alpha(u_1 + u_2)$$

Letting $h_0(u_1, u_2) = \log^-((u_1 + u_2)/3\eta_0)$ and using calculus we have

$$\frac{dh_0}{dt} = \frac{-1}{u_1 + u_2} \cdot \frac{d(u_1 + u_2)}{dt} \leq -\alpha \quad \text{when } u_1 + u_2 < 3\eta_0 \tag{2.1.10}$$

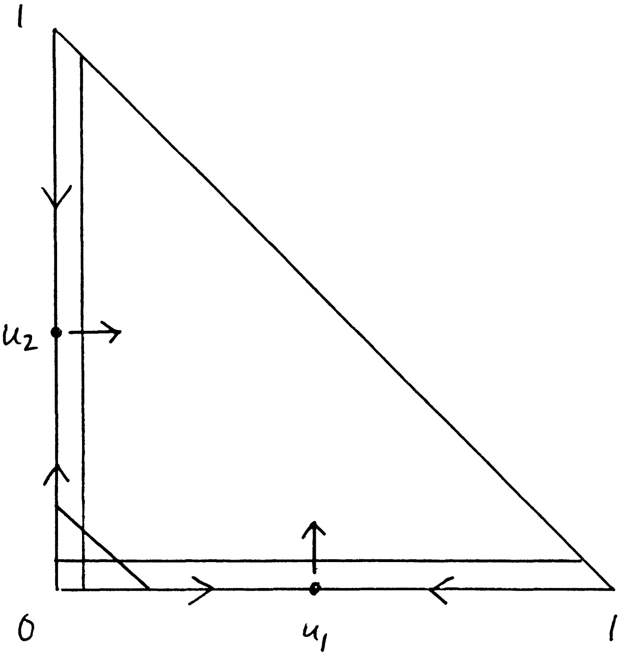


Figure 2.1.

Edge Γ_2^0. Let $\sigma_i = (\beta_i - \delta_i)/(\beta_i + \gamma_{ii})$ be the equilibrium density of type i in the absence of its competitor, and let $g_i(u) = u - \sigma_i \log u$. σ_i is an attracting point for u with $u_i > 0$ and $u_j = 0$, $j \neq i$ so (a) of Proposition 1.1 is satisfied. The invadability condition $2 \succ 1$ implies that (b) holds. Applying Proposition 1.1 now, with $\epsilon_1 \leq \eta_0$, it follows that if θ_1, λ_1, $\eta_1 \leq \epsilon_1$, ν_1 and B_1 are chosen appropriately, and $\psi_1(u) = (\epsilon_1 - u)^{+2}$ then

$$h_1(u_1, u_2) = g_1(u_1 + \theta_1 \psi_1(u_1) u_2) - \lambda_1 \log u_2 \tag{2.1.11}$$

has (i) $dh_1/dt \leq -\nu_1 < 0$ when $\epsilon_1 \leq u_1 \leq 1$ and $0 < u_2 \leq \eta_1$ and (ii) $dh_1/dt \leq B_1$ when $0 \leq u_1 \leq \epsilon_1$ and $0 < u_2 \leq \eta_1$. If we pick M_1 large enough then the function $\bar{h}_1 = h_1 \vee M_1$ is only nontrivial when $0 < u_2 < \eta_1$.

Edge Γ_1^0. Interchanging the roles of the axes and applying Proposition 1.1 now, with $\epsilon_2 \leq \eta_1$, it follows that if θ_2, λ_2, $\eta_2 \leq \epsilon_2$, ν_2 and B_2 are chosen appropriately, and $\psi_2(u) = (\epsilon_2 - u)^{+2}$ then

$$h_2(u_1, u_2) = g_2(u_2 + \theta_2 \psi_2(u_2) u_1) - \lambda_2 \log u_1 \tag{2.1.12}$$

with (i) $dh_2/dt \le -\nu_2 < 0$ when $\epsilon_2 \le u_2 \le 1$ and $0 < u_1 \le \eta_2$ and (ii) $dh_2/dt \le B_2$ when $0 \le u_2 \le \epsilon_2$ and $0 < u_1 \le \eta_2$. Again if we pick M_2 large enough then the function $\bar{h}_2 = h_2 \vee M_2$ is only nontrivial when $0 < u_1 < \eta_2$. In each case (ii) is not a problem because of (2.1.10). Adding our three functions, we see that if $K \ge 1$ is chosen large enough then $K\bar{h}_0 + \bar{h}_1 + \bar{h}_2$ is a repelling function for Γ_0, completing the proof of Theorem 2.1. □

In Example 2.1 there is a positive fixed point on each boundary edge. In Examples 1 and 2 in the introduction, there is a positive fixed point on Γ_1^0 but not on Γ_2^0. Somewhat surprisingly two species can coexist when there is no positive fixed point on either boundary segment Γ_i^0.

Example 2.2. Two stage contact process. Following Krone (1999) we consider a variation of the contact process in which individuals have two life stages, 1 = young and 2 = adult. In keeping with this interpretation, we declare that only adults can give birth and each new offspring is young. Taking 0 = vacant and letting f_i be the fraction of neighbors in state i we can write the transition rates for our model as follows.

$$0 \to 1 \quad \beta f_2 \qquad\qquad 1 \to 2 \quad \gamma \qquad\qquad i \to 0 \quad \delta_i$$

Recall that under our generic paremeters assumption, we are assuming that all four parameters β, γ, δ_1, $\delta_2 > 0$.

In this case the mean field differential equation is

$$\begin{aligned} \frac{du_1}{dt} &= -(\gamma + \delta_1)u_1 + \beta u_2(1 - u_1 - u_2) \\ \frac{du_2}{dt} &= \gamma u_1 - \delta_2 u_2 \end{aligned} \tag{2.2.1}$$

From the ODE it is clear that $du_2/dt > 0$ when $u_1 > (\delta_2/\gamma)u_2$, while $du_1/dt > 0$ when

$$u_1 < c(u_2)u_2 \quad \text{where} \quad c(u_2) = \frac{\beta(1 - u_2)}{\gamma + \delta_1 + \beta u_2}$$

The coefficient $c(u_2)$ decreases as u_2 increases, so drawing a picture (Figure 2.2) we see that there will be an intersection (and hence a nontrivial fixed point) if and only if

$$c(0) = \frac{\beta}{\gamma + \delta_1} > \frac{\delta_2}{\gamma} \tag{2.2.2}$$

Near the equilibrium (0,0) we can ignore $\beta u_2(-u_1 - u_2)$ so

$$\frac{du_1}{dt} \approx -(\gamma + \delta_1)u_1 + \beta u_2 \qquad \frac{du_2}{dt} \approx \gamma u_1 - \delta_2 u_2 \tag{2.2.3}$$

so $d(au_1 + u_2)/dt \approx (\gamma - a(\gamma + \delta_1))u_1 + (a\beta - \delta_2)u_2$. Both coefficients will be positive if we choose

$$\frac{\delta_2}{\beta} < a < \frac{\gamma}{\gamma + \delta_1}$$

This is possible if (2.2.2) holds. A little calculus shows that if

$$h_0(u_1, u_2) = \log^-((au_1 + u_2)/\eta) \tag{2.2.4}$$

$au_1 + u_2 < \eta$ then

$$\frac{dh_0}{dt} = \frac{-1}{au_1 + u_2}\left(a\frac{du_1}{dt} + \frac{du_2}{dt}\right) \leq -\alpha_0 < 0$$

if η is small enough. In words h_0 is a repelling function for $(0, 0)$.

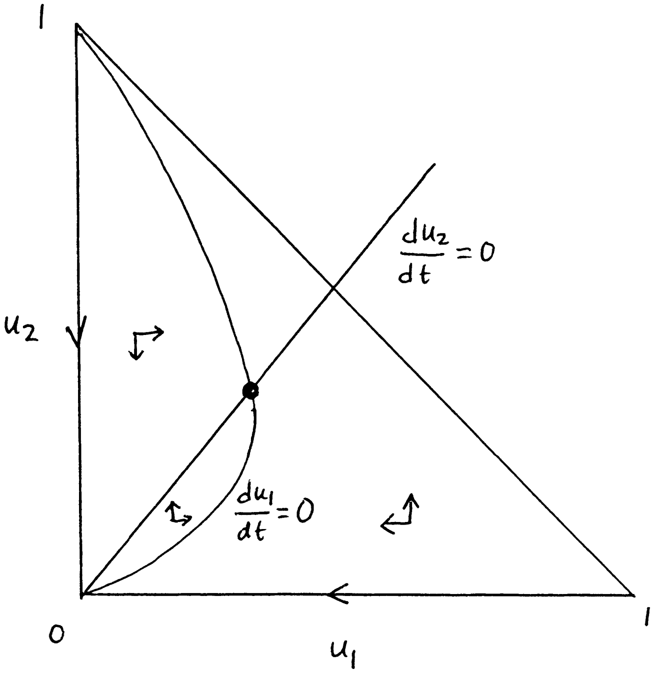


Figure 2.2.

Theorem 2.2. *If (2.2.2) holds then there is coexistence in the two stage contact process with fast stirring.*

Proof of Theorem 2.2. Applying Proposition 1 to $\phi = h_0$ shows that if $u(0,x) \in \Gamma$ is continuous, and has $u_i(0,x) \geq \eta_i > 0$ when $x \in [-\delta, \delta]^2$, there are constants $\kappa > 0$, $\gamma > 0$, and $t_0 < \infty$, which only depend on η_i and δ, so that

$$au_1(t,x) + u_2(t,x) \geq \gamma > 0 \quad \text{when } |x| \leq \kappa t \text{ and } t \geq t_0 \tag{2.2.5}$$

Using the dynamics of the model, it is not hard to improve the last conclusion to: there are constants $\epsilon_i > 0$ so that

$$u_i(t,x) \geq \epsilon_i \quad \text{when } |x| \leq \kappa(t-3) - 1 \text{ and } t \geq t_0 + 3 \tag{2.2.6}$$

Once (2.2.6) is established, the result follows from Proposition 2. Examples 2.3 and 2.5 will require similar patches, so we delay the proof of (2.2.6) to Section 3, where it will be Lemma 3.1. □

In the previous example we wanted (u_1, u_2) to avoid $(0,0)$. In the next we have two points $(1,0)$ and $(0,1)$ to stay away from.

Example 2.3. Diploid genetics. Our next model is a slight generalization of one in Cox and Durrett (1995) and Durrett, Buttel, and Harrison (1999). It is a spatial version of the Moran model for diploid individuals with one locus having two alleles that are under selection. Each site can have state AA, Aa, or aa. To formulate the dynamics, we let μ_{AA}, μ_{Aa}, $\mu_{aa} \in [0,1]$ be the relative fitnesses of the three genotypes. At times of a rate 1 Poisson process, the individual at x is subject to replacement by a new individual. To make the proposed new individual, we choose two parents $y_1 \neq y_2$ according to a joint distribution $q(y_1 - x, y_2 - x)$. Then one letter is selected at random from each parent to produce the proposed new type ij. With probability μ_{ij}, the new individual is accepted and replaces the one currently at x. With probability $1 - \mu_{ij}$, the new individual is rejected and no change occurs.

To calculate the mean-field ODE, we observe that if all sites are independent and are type ij with probability u_{ij} then the probability of picking an A allele is $v_A = u_{AA} + u_{Aa}/2$ and the probability of picking an a allele is $v_a = 1 - v_A$, so the rate at which new individuals are born is given by

$$\begin{aligned}
\beta_{AA}(u) &= \mu_{AA} \cdot v_A^2 &&= \mu_{AA} \cdot (u_{AA} + u_{Aa}/2)^2 \\
\beta_{Aa}(u) &= \mu_{Aa} \cdot 2v_A v_a &&= \mu_{Aa} \cdot 2(u_{AA} + u_{Aa}/2)(u_{aa} + u_{Aa}/2) \\
\beta_{aa}(u) &= \mu_{aa} \cdot v_a^2 &&= \mu_{aa} \cdot (u_{aa} + u_{Aa}/2)^2
\end{aligned}$$

The total rate at which replacements occur is $\delta(u) = \beta_{AA}(u) + \beta_{Aa}(u) + \beta_{aa}(u)$, so

$$\frac{du_{ij}}{dt} = \beta_{ij}(u) - \delta(u)u_{ij} \quad \text{for } ij = AA, Aa, aa \tag{2.3.1}$$

Since $u_{AA} + u_{Aa} + u_{aa} = 1$, we can reduce to two variables, which for maximum symmetry we choose to be $u_1 = u_{AA}$ and $u_2 = u_{aa}$. In contrast to previous examples, we don't have to worry about the equilibrium point $u_1 = 0$, $u_2 = 0$, since a population consisting entirely of Aa's immediately starts to generate AA's and aa's. Thus our main concern is to keep the ODE away from the all A state (1,0) and the all a state (0,1). To do this we will generalize the approach in the previous example and use two corner functions. To study the ODE near (1,0) we begin by noting that when (u_{AA}, u_{aa}) is near $(1,0)$, $v_{AA} \approx 1$ and v_a is small, we have

$$\begin{aligned} \beta_{AA}(u) &\approx \mu_{AA} \cdot 1 \\ \beta_{Aa}(u) &\approx \mu_{Aa} \cdot 2v_a \\ \beta_{aa}(u) &\approx \mu_{aa} \cdot v_a^2 \approx 0 \end{aligned} \tag{2.3.2}$$

and hence $\delta(u) \approx \mu_{AA}$. Using this with (2.3.2) we can write

$$\begin{aligned} \frac{dv_a}{dt} &= \frac{1}{2} \cdot \frac{du_{Aa}}{dt} + \frac{du_{aa}}{dt} = \frac{1}{2} \cdot \beta_{Aa}(u) + \beta_{aa}(u) - \delta(u)v_a \\ &\approx \frac{1}{2} \cdot \mu_{Aa} \cdot 2v_a - \mu_{AA}v_a \end{aligned}$$

so a's can invade the all AA state if $\mu_{Aa} > \mu_{AA}$. By symmetry A's can invade aa if $\mu_{Aa} > \mu_{aa}$. Combining the last two inequalities we see that coexistence should occur when heterozygotes have an advantage:

$$\mu_{Aa} > \mu_{aa}, \mu_{AA} \tag{2.3.3}$$

Theorem 2.3. *If* (2.3.3) *holds then there is coexistence in the diploid genetics model with fast stirring.*

Proof. It follows from our calculations that if (2.3.3) holds and η is small and

$$h_0(u_{AA}, u_{aa}) = \log^-(v_a/\eta) + \log^-(v_A/\eta) \tag{2.3.4}$$

then h_0 is repelling function for $\{(1,0),(0,1)\}$. Writing $u_1 = u_{AA}$, $u_2 = u_{aa}$ and applying Proposition 1 to $\phi = h_0$ shows that if $u(0,x) \in \Gamma$ is continuous, and has $u_i(0,x) \geq \eta_i > 0$ when $x \in [-\delta,\delta]^2$, there are constants $\kappa > 0$, $\gamma_i > 0$, and $t_0 < \infty$, which only depend on η_i and δ, so that if $u_0 = 1 - u_1 - u_2 = u_{Aa}$ then

$$u_i(t,x) + u_0(t,x)/2 \geq \gamma_i > 0 \quad \text{when } |x| \leq \kappa t \text{ and } t \geq t_0 \tag{2.3.5}$$

Using the dynamics of the model, it is not hard to improve the last conclusion to: there are constants $\epsilon_i > 0$ so that

$$u_i(t,x) \geq \epsilon_i \quad \text{when } |x| \leq \kappa(t-3) - 1 \text{ and } t \geq t_0 + 3 \tag{2.3.6}$$

Once (2.3.6) is established, which will be done in Lemma 3.2, the result follows from Proposition 2. □

Example 2.4. One-dimensional systems. Cox and Schinazi (1998) examined a special case of the diploid genetics model in which $\mu_{aa} = 0$. Their motivation came from sickle cell anemia where *aa*'s have sickle cell anemia but *Aa*'s have no disease and increased immunity to malaria (see Haldane 1949). They used a slightly different reproduction scheme, which I call

Good News/Bad News Mating. At times of a rate 1 Poisson process the individual gets the good news that he has been chosen to mate with a randomly chosen neighbor, but also the bad news that if the offspring is viable it will replace him.

Introducing states $0 = AA$ and $1 = Aa$, setting relative fitnesses $\mu_{Aa} = 1$, $\mu_{aa} = \kappa < 1$, and introducing a fudge factor q that we will explain in a minute, we can write jump rates as:

$$\begin{array}{lll} 0 \to 1 & \text{at rate} & f_1/2 \\ 1 \to 0 & \text{at rate} & \kappa(f_0/2 + qf_1) \end{array}$$

To explain the rates, note that when 0 picks a neighbor, it will pick a 1 with probability f_1 and in this case will only make a new 1 with probability 1/2. Since *Aa* has higher fitness the new 1 is always accepted. In the second situation, we have generalized the genetics to allow the mating of two 1's to produce a 0 with probability q. Due to selection the 0 will only be accepted with probability κ. Our motivation for this is that in some situations (e.g., t-haplotypes in mice) the distribution of genotypes produced is far from a random combination.

A second reason for introducing q is that it allowed Cox and Schinazi (1998) to prove that for any $\kappa < 1$ there is a q_c so that if $q < q_c$ then the 1's survive. To convert our model into the one given in Cox and Schinazi (1998), multiply the rates above by $\lambda = 1/\kappa$, and set $q = p\lambda$. An alternative approach to proving persistence is to introduce fast stirring. The mean field ODE for the density of 1's is

$$\frac{du_1}{dt} = u_0 u_1/2 - \kappa u_1(u_0/2 + q u_1) \tag{2.4.1}$$

Using $u_0 = 1 - u_1$ and rearranging we have

$$\frac{du_1}{dt} = \frac{u_1}{2}\{(1-u_1)(1-\kappa) - 2q\kappa u_1\} = \frac{\beta u_1}{2}(\sigma_1 - u_1) \tag{2.4.2}$$

where $\beta = [(1-\kappa) + 2q\kappa]$ and $\sigma = (1-\kappa)/\beta$. From this it follows easily that we have

Theorem 2.4. *If $\kappa < 1$ and $0 < q < \infty$ there is coexistence in the Cox-Schinazi model with fast stirring.*

Proof. $g(u_1) = u_1 - \sigma_1 \log u_1$ is a repelling function for $\{0\}$ and (v) holds, so the result follows from Proposition 3. □

Of course this reasoning applies in general to one species systems in which the mean field ODE has an attractive positive fixed point. For example we could consider the one species linear competition model (a generalized contact process) in which

$$0 \to 1 \quad \text{at rate } \beta f_1 \qquad 1 \to 0 \quad \text{at rate } \delta + \gamma f_1$$

In this case the mean field ODE is

$$\frac{du}{dt} = \beta u(1-u) - u(\delta + \gamma u) = (\beta+\gamma)u\left(\frac{\beta - \delta}{\beta+\gamma} - u\right)$$

so we will have survival under fast stirring if $\beta > \delta$.

Our next example leads to a three-dimensional ODE. However, as the proof will make clear, this example is better classified with the two-species systems considered in this section rather than with the three-species systems considered in Sections 6 and 7.

Example 2.5. Linear competition without exclusion. In this model, each site can be in a state 0, 1, 2, or 3 where 0 is vacant, $i = 1, 2$ indicate sites occupied by types 1 or 2, and $3 = 1 + 2$ indicates a site occupied by both types. To have a general but manageable model we will have proportional birth rates, but restrict our attention to constant death rates. Letting f_i be the fraction of neighbors in state i, we can write the transition rates of the model as follows:

$$\begin{array}{llll}
0 \to 1 & \beta_{11} f_1 + \beta_{13} f_3 & 1 \to 0 & \delta_1 \\
0 \to 2 & \beta_{22} f_2 + \beta_{23} f_3 & 2 \to 0 & \delta_2 \\
2 \to 3 & \beta_{31} f_1 + \beta_{33} f_3 & 3 \to 2 & \delta_3 \\
1 \to 3 & \beta_{42} f_2 + \beta_{43} f_3 & 3 \to 1 & \delta_4
\end{array}$$

Apart from a change of notation this is the general model introduced on page 12 of Durrett and Neuhauser (1997) for the competition of two strains of the barley yellow dwarf virus. Caswell and Etter (1992) have earlier formulated a similar model in discrete time.

Schinazi (1996) and (1998) has considered special cases of our model in which the presence of the other type on the source or target site does not change the birth rate of the species. In symbols:

$$\beta_{11} = \beta_{13} = \beta_{31} = \beta_{33} = \beta_1, \qquad \beta_{22} = \beta_{23} = \beta_{42} = \beta_{43} = \beta_2$$

In his (1996) predator-prey paper, the death rates are

$$\delta_1 = 0, \quad \delta_2 = \delta_2, \quad \delta_3 = \phi, \quad \delta_4 = 0$$

In words, a predator on a site not occupied by a prey dies at rate δ_2, while a prey is eaten by a predator on the same site at rate ϕ. In his (1998) competition model

$$\delta_1 = \delta_1, \quad \delta_2 = \delta_2, \quad \delta_3 = p\phi, \quad \delta_4 = (1-p)\phi$$

In words, at each doubly occupied site a competition occurs which lasts an exponential amount of time with mean $1/\phi$. At the end of the fight, 2 is the victor with probability p and 1 wins with probability $1 - p$.

Returning to the general model, we can write the mean field ODE as

$$(2.5.1)\qquad \begin{aligned} \frac{du_1}{dt} &= \beta_{11}u_0u_1 + \beta_{13}u_0u_3 - \beta_{42}u_1u_2 - \beta_{43}u_1u_3 \\ &\quad - u_1\delta_1 + u_3\delta_4 \\ \frac{du_2}{dt} &= \beta_{22}u_0u_2 + \beta_{23}u_0u_3 - \beta_{31}u_2u_1 - \beta_{33}u_2u_3 \\ &\quad - u_2\delta_2 + u_3\delta_3 \\ \frac{du_3}{dt} &= \beta_{31}u_2u_1 + \beta_{33}u_2u_3 + \beta_{42}u_1u_2 + \beta_{43}u_1u_3 \\ &\quad - u_3(\delta_3 + \delta_4) \end{aligned}$$

To help check this note that a term $\beta_{kj}u_iu_j$ corresponds to sites of type j giving birth onto those of type i resulting in a site with state $k \wedge 3$. Note that we cannot factor u_i out of the equation for du_i/dt so this does not have the Lotka-Volterra form.

To begin to analyze this system we look at the invadability conditions. If $\beta_{11} > \delta_1$ then in the absence of individuals of type 2, there are no sites in states 2 or 3 and the 1's reach an equilibrium density of

$$\sigma_1 = \frac{\beta_{11} - \delta_1}{\beta_{11}}$$

Using Definitions 4 and 2 we can write this conclusion as $1 \succ 0$ and $1 \to \sigma_1$. To investigate the stability of this fixed point we note that if $u_1 = \sigma_1$ and $0 \le u_2, u_3 \le \epsilon$ then $u_0 \approx 1 - \sigma_1$ so dropping $u_2u_3 \approx \epsilon^2$ gives

$$(2.5.2)\qquad \begin{aligned} \frac{du_2}{dt} &\approx \beta_{22}(1-\sigma_1)u_2 + \beta_{23}(1-\sigma_1)u_3 - \beta_{31}\sigma_1u_2 \\ &\qquad - u_2\delta_2 + u_3\delta_3 \\ \frac{du_3}{dt} &\approx \beta_{31}\sigma_1u_2 + \beta_{42}\sigma_1u_2 + \beta_{43}\sigma_1u_3 - u_3(\delta_3 + \delta_4) \end{aligned}$$

This is a linear system of the form

$$(2.5.3)\qquad \frac{du_j}{dt} = \sum_{k=2}^{3} b_{jk}u_k \quad j = 2,3$$

with matrix b_{ij} given by:

$$\begin{array}{ll} b_{22} = \beta_{22}(1-\sigma_1) - \beta_{31}\sigma_1 - \delta_2 & b_{23} = \beta_{23}(1-\sigma_1) + \delta_3 > 0 \\ b_{32} = \beta_{31}\sigma_1 + \beta_{42}\sigma_1 > 0 & b_{33} = \beta_{43}\sigma_1 - \delta_3 - \delta_4 \end{array}$$

Using Definition 5 from Section 1, we say that species 2 and 3 can invade species 1 in equilibrium, and write $2, 3 \succ 1$ if there is a linear combination $z = \omega_2 u_2 + \omega_3 u_3$ with $\omega_i > 0$ so that if $u \to (\sigma_1, 0, 0)$ through Γ^+ then

$$\liminf \frac{1}{z}\frac{dz}{dt} > 0$$

To see what the definition says in this problem, we note that by scaling one can without loss of generality consider $\omega_2 = \theta$, $\omega_3 = (1-\theta)$ where $\theta \in (0,1)$. From the form of the differential equation in (2.5.3) we have

$$\frac{d(\theta u_2 + (1-\theta)u_3)}{dt} = \{\theta b_{22} + (1-\theta)b_{32}\}\, u_2 + \{\theta b_{23} + (1-\theta)b_{33}\}\, u_3 \tag{2.5.4}$$

The off-diagonal entries b_{23} and b_{32} are strictly positive, so if $b_{22} \geq 0$ then we can pick θ close to 1 and have the coefficients of u_2 and u_3 on the right-hand side of (2.5.4) both positive, thus ensuring that $\theta u_2 + (1-\theta)u_3$ is increasing in the original system (2.5.1) when $0 \leq u_2, u_3 \leq \epsilon$ and $|u_1 - \sigma_1| \leq \epsilon$. If $b_{33} \geq 0$ then we can do this by picking θ close to 0. To deal with the case in which $b_{22}, b_{33} < 0$ we note that

$$(1-\theta)b_{32} + \theta b_{22} \text{ goes from } + \text{ to } - \text{ at } \theta_1 = b_{32}/(b_{32} - b_{22})$$

$$(1-\theta)b_{33} + \theta b_{23} \text{ goes from } - \text{ to } + \text{ at } \theta_2 = -b_{33}/(b_{23} - b_{33})$$

Thus we can pick θ to make both coefficients positive if and only if $\theta_1 > \theta_2$. Cross multiplying we see that this is equivalent to

$$b_{32}(b_{23} - b_{33}) > -b_{33}(b_{32} - b_{22})$$

or that the determinant, $b_{33}b_{22} - b_{32}b_{23} < 0$.

Combining the results in the previous paragraph, we see that for $2, 3 \succ 1$ it is sufficient that

$$b_{22} \geq 0, \quad \text{or} \quad b_{33} \geq 0, \quad \text{or} \quad b_{33}b_{22} - b_{32}b_{23} < 0 \tag{2.5.5}$$

To see that this is also necessary, recall that the trace of b is the sum of the eigenvalues, $\lambda_1 + \lambda_2$ while the determinant is the product $\lambda_1\lambda_2$.

From this we see that if $b_{22} < 0$, $b_{33} < 0$, and $b_{33}b_{22} - b_{32}b_{23} > 0$, then the real parts of the two eigenvalues are negative, so the origin is attracting and hence $\omega_2 u_2 + \omega_3 u_3$ cannot be increasing.

To get a mental picture of the linearization when invadability occurs, note that the invariance of Γ implies that the eigenvalues will be real. Consider the case in which the trace and the determinant are both negative. In this case there is one positive eigenvalue and one negative eigenvalue, so (0,0) is a saddle point with the unstable direction pointing into the positive quadrant and the stable direction (which is perpendicular) having exactly one negative component. On the other hand if b_{22} and b_{33} are both large enough then the trace and determinant will both be positive, so both eigenvalues will be positive.

Interchanging the roles of 2's and 1's we see that if there are no individuals of type 1, then there are no sites in states 1 and 3, so the equilibrium density of type 2 is

$$\sigma_2 = \frac{\beta_{22} - \delta_2}{\beta_{22}}$$

assuming, of course, that $\beta_{22} > \delta_2$. Repeating the calculations from the first case we can derive conditions for $1, 3 \succ 2$ from (2.5.5).

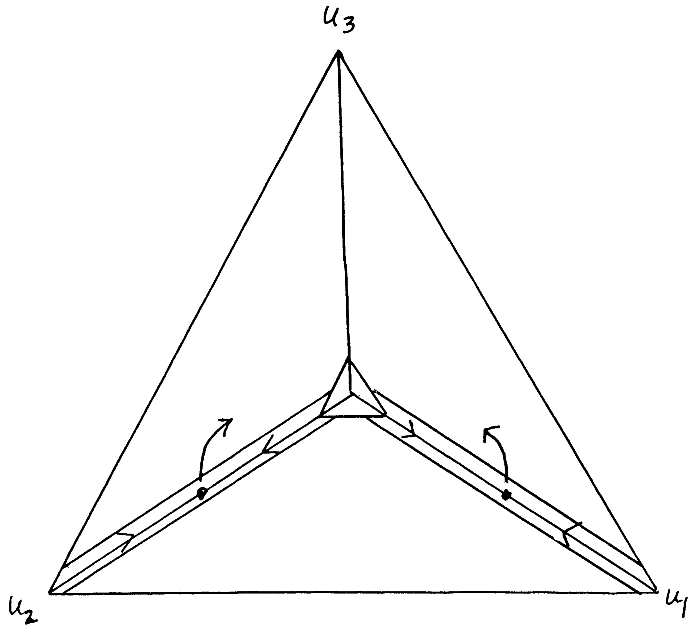


Figure 2.3.

Theorem 2.5. *Suppose that* $\beta_{11} > \delta_1$, $\beta_{22} > \delta_2$, $2,3 \succ 1$, *and* $1,3 \succ 2$. *Then with fast stirring there is coexistence for linear competition without exclusion.*

Proof of Theorem 2.5. The details of the proof are very similar to those for Theorem 1.1. We begin at the origin and work our way out. See Figure 2.3. To handle this region near (0,0,0) we look at the linearization which results from ignoring all terms of the form $u_i u_j$ with $i, j \geq 1$ in (2.5.1)

$$\begin{aligned} \frac{du_1}{dt} &\approx (\beta_{11} - \delta_1)u_1 + (\beta_{13} + \delta_4)u_3 \\ \frac{du_2}{dt} &\approx (\beta_{22} - \delta_2)u_2 + (\beta_{23} + \delta_3)u_3 \\ \frac{du_3}{dt} &\approx -u_3(\delta_3 + \delta_4) \end{aligned}$$

Summing the three equations gets rid of the negative term in the third one producing

$$\frac{d}{dt}(u_1 + u_2 + u_3) \approx (\beta_{11} - \delta_1)u_1 + (\beta_{22} - \delta_2)u_2 + (\beta_{13} + \beta_{23})u_3$$

which has all coefficients positive on the right-hand side. Let

$$h_0(u_1, u_2, u_3) = \log^-\{(u_1 + u_2 + u_3)/4\eta_0\}$$

If $\alpha = \min\{\beta_{11} - \delta_1, \beta_{22} - \delta_2, \beta_{13} + \beta_{23}\}$ and η_0 is chosen small enough

$$\frac{dh_0}{dt} = \frac{-1}{u_1 + u_2 + u_3} \cdot \frac{d(u_1 + u_2 + u_3)}{dt} \leq -\frac{\alpha}{2} \quad \text{when } v < 4\eta_0 \tag{2.5.6}$$

i.e., h_0 is a repelling function for $\{(0, 0, 0)\}$.

Having covered the corner, we move to

Edge $\Gamma^0_{2,3}$. In the absence of other species 1's reach an equilibrium density of σ_1, so (a) of Proposition 1.1 holds. The invadability condition $2, 3 \succ 1$ furnishes us with constants ω^1_2 and ω^1_3 which we can use to define $z_1 = \omega^1_2 u_2 + \omega^1_3 u_3$ so that (b) holds. Applying Proposition 1.1 now with $\epsilon_1 \leq \eta_0$, and letting $g_1(u) = u - \sigma_1 \log u$, we see that if $\theta_1 \leq 1$, λ_1, $\eta_1 \leq \epsilon_1$, ν_1 and B_1 are chosen appropriately and $\psi_1(u) = (\epsilon_1 - u)^{+2}$ then

$$h_1(u_1, u_2, u_3) = g_1(u_1 + \theta_1 \psi_1(u_1) z_1) - \lambda_1 \log z_1$$

has (i) $dh_1/dt \le -\nu_1 < 0$ when $\epsilon_1 \le u_1 \le 1$ and $0 < z_1 \le \eta_1$, and (ii) $dh_1/dt \le B_1$ when $0 \le u_1 \le \epsilon_1$ and $0 < z_1 \le \eta_1$. If we pick M_1 large enough then $\bar{h}_1 = h_1 \vee M_1$ is only nontrivial when $0 < z_1 \le \eta_1$.

A similar construction can be done on the

Edge $\Gamma^0_{1,3}$. In the absence of other species 2's reach an equilibrium density of σ_2, so (a) of Proposition 1.1 holds. The invadability condition $1,3 \succ 2$ furnishes us with constants ω^2_1 and ω^2_3, which we can use to define $z_2 = \omega^2_1 u_1 + \omega^2_3 u_3$ so that (b) holds. Applying Proposition 1.1 again and letting $g_2(u) = u - \sigma_2 \log u$, we see that if $\theta_2 \le 1$, λ_2, $\eta_2 \le \epsilon_2$, ν_2 and B_2 are chosen appropriately and $\psi_2(u) = (\epsilon_2 - u)^{+2}$ then

$$h_2(u_1, u_2, u_3) = g_2(u_2 + \theta_2 \psi(u_2) z_2) - \lambda_2 \log z_2$$

has (i) $dh_2/dt \le -\nu_2 < 0$ when $\epsilon_2 \le u_2 \le 1$ and $0 < z_2 \le \eta_2$, and (ii) $dh_2/dt \le B_2$ when $0 \le u_2 \le \epsilon_2$ and $0 < z_2 \le \eta_2$. If we pick M_2 large enough then the function $\bar{h}_2 = h_2 \vee M_2$ is only nontrivial when $0 < z_2 < \eta_2$.

Denouement. (ii) is not a problem in either case because of (2.5.6). Thus if $K_1 \ge 1$ is chosen large $\phi = K_1 h_0 + \bar{h}_1 + \bar{h}_2$ is a repelling function for two edges $\Gamma^0_{2,3} \cup \Gamma^0_{1,3}$. Applying Proposition 1 to ϕ shows that if the initial condition $u(0,x) \in \Gamma$ is continuous, and has $u_i(0,x) \ge \eta_i > 0$ when $x \in [-\delta,\delta]^2$. There are constants $\kappa > 0$, $\gamma_i > 0$, and $t_0 < \infty$, which only depend on η_i and δ, so that

(2.5.7)
$$\omega^1_2 u_2(t,x) + \omega^1_3 u_3(t,x) \ge \gamma_1 > 0 \quad \omega^2_1 u_1(t,x) + \omega^2_3 u_3(t,x) \ge \gamma_2 > 0$$

when $|x| \le \kappa t$ and $t \ge t_0$. Using the dynamics of the model, it is not hard to improve the last conclusion to: there are constants $\epsilon_i > 0$ so that

$$u_i(t,x) \ge \epsilon_i \quad \text{when } |x| \le \kappa(t-3) - 1 \text{ and } t \ge t_0 + 3 \tag{2.5.8}$$

Once (2.5.8) is established, which will be done in Lemma 3.3, the result follows from Proposition 2. □

3. Lower bounding lemmas for PDE. Here we will be concerned with completing the three unfinished proofs from Section 2. This will be done with the help of Lemmas 3.1–3.4. In this section we will often be working with cubes, so we will use the "box" norm $\|x\| = \max_i |x_i|$ for $x \in \mathbf{R}^d$. Referring to (2.2.5) and (2.2.6) we see that to finish the proof of Theorem 2.2 it is enough to show

Lemma 3.1. *Given* $a, \gamma > 0$ *there are constants* $\epsilon_i > 0$ *so that if*

$$au_1(0,y) + u_2(0,y) \geq \gamma \quad \textit{for } y \in [-1,1]^d$$

then for $i = 1, 2$, $u_i(t,x) \geq \epsilon_i$ *for* $x \in [1,1]^d$ *and* $3 \leq t \leq 4$.

Proof. Since (v) holds, each coordinate has a lower bound of the form

$$\frac{\partial u_i}{\partial t} \geq \Delta u_i - \alpha_i u_i \tag{3.1.1}$$

From (3.1.1) we see that if $p_t(x,y)$ is the transition probability for Brownian motion (run at rate 2 since we have Δ instead of $\Delta/2$) then

$$u_i(t,x) \geq e^{-\alpha_i t} \int p_t(x,y)\, u_i(0,y)\, dy \tag{3.1.2}$$

Since $p_t(x,t) = (4\pi t)^{-d/2} \exp(-|y-x|^2/4t)$ it is easy to see that there is a constant $c_{1,4}$ so that

$$p_t(x,y) \geq c_{1,4} \tag{3.1.3}$$

if $\|x\|, \|y\| \leq 1$ and $1 \leq t \leq 4$. From this follows that if $\|x\| \leq 1$ and $1 \leq t \leq 4$ then

$$u_i(t,x) \geq e^{-4\alpha_i} \int_{[-1,1]^d} c_{1,4}\, u_i(0,y)\, dy \tag{3.1.4}$$

If $au_1(0,y) + u_2(0,y) \geq \eta$ whenever $\|y\| \leq 1$ then either

$$A. \int_{[-1,1]^d} u_1(0,y)\, dy \geq 2^d \eta/2a \quad \text{or} \quad B. \int_{[-1,1]^d} u_2(0,y)\, dy \geq 2^d\eta/2$$

for otherwise, we would have a contradiction. In Case A, (3.1.4) implies that for all $1 \leq t \leq 4$ and $\|x\| \leq 1$,

$$u_1(t,x) \geq \epsilon_1 \equiv e^{-3\alpha_i} c_{1,4} \cdot 2^d \eta/2a \tag{3.1.5}$$

which is more than we promised to show for the first coordinate. To get a lower bound for u_2 we will use the second equation from (2.2.1)

$$du_2/dt = \Delta u_2 - \delta_2 u_2 + \gamma u_1 \tag{3.1.6}$$

and its probabilistic solution:

Lemma 3.1.1. *The equation* $du/dt = \Delta u(t,x) - c(t,x)u(t,x) + g(t,x)$ *is solved by*

$$u(t,x) = E_x\left(\exp(-c_t^t)u(0,B_t) + \int_0^t \exp(-c_r^t) g(t-r,B_r)\,ds\right)$$

where B_s *is Brownian motion run at rate 2,* E_x *denotes expected value starting from* $B_0 = x$*, and* $c_r^t = \int_0^r c(t-s,B_s)\,ds$*.*

Proof. This is a straightforward combination of the ideas in Sections 4.2 and 4.3 of Durrett (1996). It suffices to show that if u satisfies the PDE then

$$(\star) \qquad M_s = \exp(-c_s^t)u(t-s,B_s) + \int_0^s \exp(c_r^t) g(t-r,B_r)\,dr$$

is a martingale. For then taking $E_x M_t$ gives the desired formula. To prove $(\star)$ we let $X_s = c_s^t$, $Y_t = t-s$, $Z_s = B_s$ and use Ito's formula on $e^{-X_s}u(Y_s,Z_s)$ to conclude that

$$\begin{aligned} &\exp(-c_s^t)u(t-s,B_s) - u(t,B_0) \\ &\qquad = \int_0^s \exp(-c_r^t)u(t-r,B_r)\cdot(-c(t-r,B_r))\,dr \\ &\qquad + \int_0^s \exp(-c_r^t)u_t(t-r,B_r)\cdot(-1)\,dr \\ &\qquad + \textit{martingale} + \int_0^s \exp(-c_r^t)\Delta u(t-r,B_r)\,dr \end{aligned}$$

The PDE implies that $-c(t-r,B_r)u(t-r,B_r) - u_t(t-r,B_r) + \Delta u(t-r,B_r) = g(t-r,B_r)$, from which the desired result follows. □

Our main interest in Lemma 3.1.1 is to prove the next comparison theorem, which is an immediate consequence.

Lemma 3.1.2. *Suppose* $du/dt = \Delta u - \delta(t,x)u(t,x) + g(t,x)$ *where* $\delta(t,x) \le \hat\delta$ *and* $0 \le \hat g(t,x) \le g(t,x)$ *then*

$$u(t,x) \ge E_x\left(e^{-\hat\delta t}u(0,B_t) + \int_0^t e^{-\hat\delta s}\hat g(t-s,B_s)\,ds\right)$$

Proof of Lemma 3.1. Using Lemma 3.1.2 on (3.1.6) and with the lower bounds in (3.1.5), we have that for $3 \le t \le 4$ and $\|x\| \le 1$.

$$\begin{aligned} u_2(t,x) &\ge E_x \int_1^2 e^{-\delta(t-r)} \cdot \gamma\epsilon_1 \cdot 1\{B_{t-r} \in [-1,1]^d\}\,dr \\ &\ge e^{-3\delta} \cdot \gamma\epsilon_1 \cdot 2^d c_{1,4} \ge \epsilon_2 \end{aligned}$$

Combining this inequality with (3.1.5) gives the result in case A. In Case B, (3.1.4) implies that

$$u_2(t,x) \ge \hat\epsilon_2 \equiv e^{-4\alpha_i} c_{1,4} \cdot 2^d \eta/2 \tag{3.1.7}$$

for all $1 \le t \le 4$ and $\|x\| \le 1$. To get a lower bound for u_1 we rewrite the first equation in (1.2.1) and then use the inequality

$$\begin{aligned} du_1/dt &= \Delta u_1 + \beta u_2(1-u_2) - (\gamma + \delta_1 + \beta u_2)u_1 \\ &\ge \Delta u_1 + \beta u_2(1-u_2) - \kappa u_1 \end{aligned} \tag{3.1.8}$$

where $\kappa = \gamma + \delta_1 + \beta$. To make this useful we have to have an upper bound on u_2. Using the inequality

$$\frac{du_2(t,x)}{dt} \le \Delta u_2 + \gamma(1-u_2) - \delta u_2$$

and comparing with the solution of the ODE:

$$dv_2(t)/dt = \gamma(1-u_2) - \delta u_2 \qquad v_2(0) = 1$$

which is decreasing in t, we conclude that $u_2(t,x) \le v_2(t)$ and hence that if $t \ge 1$ then

$$u_2(t,x) \le v_2(1) \tag{3.1.9}$$

Using Lemma 3.1.2 on (3.1.8), with the bounds in (3.1.9) and (3.1.7) now we have that when $3 \le t \le 4$ and $\|x\| \le 1$.

$$u_1(t,x) \ge E_x \int_1^2 e^{-\kappa(t-r)} \cdot \beta_2 \hat\epsilon_2 (1 - v_2(1)) \cdot 1\{B_{t-r} \in [-2,2]^d\}\,dr \ge \hat\epsilon_1$$

This completes case B and hence the proof of Lemma 3.1. □

To complete the proof of Theorem 2.3, we let

$$v_A(t,x) = u_{AA}(0,x) + u_{Aa}(0,x)/2$$
$$v_A(t,x) = u_{aa}(0,x) + u_{Aa}(0,x)/2$$

By (2.3.5) and (2.3.6) it is enough to show

Lemma 3.2. *Given $\gamma_i > 0$ there are constants $\epsilon_i > 0$ so that if $v_A(0,x) \geq \gamma_1$ and $v_a(0,x) \geq \gamma_2$ for $x \in [-1,1]^d$ and $0 \leq t \leq 1$ then $u_i(t,x) \geq \epsilon_i$ for $x \in [1,1]^d$ and $2 \leq t \leq 3$.*

Remark. The result is different here and the proof simpler than for Lemma 3.1. The quantities bounded in Proposition 1 can be used to give lower bounds on the right hand side of the ODE, so we do not need the initial bootstrapping or a division into cases.

Proof. We begin by recalling the mean-field ODE given in (4.3.1):

$$\begin{aligned}\frac{du_{AA}}{dt} &= \mu_{AA} \cdot v_A^2 - \psi(u)u_{AA} \\ \frac{du_{Aa}}{dt} &= \mu_{Aa} \cdot 2v_A v_a - \psi(u)u_{Aa} \\ \frac{du_{aa}}{dt} &= \mu_{aa} \cdot v_a^2 - \psi(u)u_{aa}\end{aligned} \tag{3.2.1}$$

where $\psi(u) = \sum_{ij} \beta_{ij}(u) \leq \mu_{Aa} \leq 1$. If we let

$$\alpha = \min\{\mu_{AA}\gamma_1^2,\ 2\mu_{Aa}\gamma_1\gamma_2,\ \mu_{aa}\gamma_2^2\}$$

then each coordinate has a lower bound of the form

$$\frac{\partial u_{ij}}{\partial t} \geq \Delta u_{ij} + g(t,x) - u_{ij} \tag{3.2.2}$$

where $g(t,x) = \alpha$ if $0 \leq t \leq 1$ and $x \in [-1,1]^d$. Using Lemma 3.1.2 now, we have

$$\begin{aligned}u_{ij}(t,x) &\geq E_x \int_0^1 e^{-(t-r)} g(r, B_{t-r})\, dr \\ &\geq \alpha e^{-3} \int_0^1 P_x(B_{t-r} \in [-1,1]^d)\, dr \geq \alpha e^{-3} \cdot 2^d c_{14}\end{aligned}$$

for $2 \le t \le 3$ and $\|x\| \le 1$, which proves the desired conclusion. $\square$

In view of (2.5.7) and (2.5.8) we can complete the proof of Theorem 2.5 by showing

Lemma 3.3. *Given $\omega_j^i, \gamma_i > 0$ there are constants $\epsilon_i > 0$ so that if*

$$\omega_2^1 u_2(0,x) + \omega_3^1 u_3(0,x) \ge \gamma_1 \quad \textit{and} \quad \omega_1^2 u_1(0,x) + \omega_3^2 u_3(0,x) \ge \gamma_2$$

for $x \in [-1,1]^d$ then for $i = 1,2,3$, $u_i(t,x) \ge \epsilon_i$ for $x \in [1,1]^d$ and $3 \le t \le 4$.

Proof. Condition (v) implies that each coordinate has a lower bound of the form

$$\frac{\partial u_i}{\partial t} \ge \Delta u_i - \alpha_i u_i \tag{3.3.1}$$

Using (3.1.2) and (3.1.3), we see that if $\|x\| \le 1$ and $1 \le t \le 4$ then

$$u_i(t,x) \ge e^{-4\alpha_i} \int_{[-1,1]^d} c_{1,4} u_i(0,y)\, dy \tag{3.3.2}$$

Pick ν small enough so that $\gamma_1 - \omega_3^1 \nu > 0$ and $\gamma_2 - \omega_3^2 \nu > 0$. Either

$$A. \int_{[-1,1]^d} u_3(0,y)\, dy \ge 2^d \nu \quad \text{or} \quad B. \int_{[-1,1]^d} u_3(0,y)\, dy < 2^d \nu$$

In Case A, (3.3.2) implies that

$$u_3(t,x) \ge \epsilon_3 \equiv c_{1,4} e^{-4\alpha_i} \cdot 2^d \nu \tag{3.3.3}$$

for all $1 \le t \le 4$ and $\|x\| \le 1$. To get a lower bound for u_1 and u_2 we will use the inequalities

$$\begin{aligned} du_1/dt &\ge \Delta u_1 - \alpha_1 u_1 + \delta_4 u_3 \\ du_2/dt &\ge \Delta u_2 - \alpha_2 u_2 + \delta_3 u_3 \end{aligned} \tag{3.3.4}$$

which improve (3.3.1) by keeping one positive term. Using Lemma 3.1.2 on (3.3.4) with the bound in (3.3.3) we have that when $\|x\| \le 1$, $3 \le t \le 4$, and $i = 1,2$

$$u_i(t,x) \ge E_x \int_1^2 e^{-\alpha_i(t-r)} \cdot \delta_{5-i} \epsilon_3 \cdot 1\{B_{t-r} \in [-1,1]^d\}\, dr \ge \epsilon_i$$

In Case B, by our assumption and choice of ν we have

$$\begin{aligned} &\int_{[-1,1]^d} u_2(0,y)\,dy \geq 2^d(\gamma_1 - \omega_3^1\nu)/\omega_2^1 > 0 \\ &\int_{[-1,1]^d} u_1(0,y)\,dy \geq 2^d(\gamma_2 - \omega_3^2\nu)/\omega_1^2 > 0 \end{aligned} \tag{3.3.5}$$

Using (3.3.2) now gives lower bounds for $i = 1, 2$

$$u_i(t,x) \geq \hat{\epsilon}_i \quad \text{for } \|x\| \leq 1 \text{ and } 1 \leq t \leq 4 \tag{3.3.6}$$

To get a lower bound for u_3 we will use the inequality

$$du_3/dt \geq \Delta u_3 - \alpha_3 u_3 + (\beta_{31} + \beta_{42})u_1 u_2 \tag{3.3.7}$$

which again comes from improving (3.3.1) by keeping positive terms. Using Lemma 3.1.2 on (3.3.7) with the lower bound in (3.3.6), we see that or $\|x\| \leq 1$ and $3 \leq t \leq 4$,

$$u_3(t,x) \geq E_x \int_1^2 e^{-\alpha_3(t-r)} \cdot (\beta_{31} + \beta_{42})\hat{\epsilon}_1\hat{\epsilon}_2 \cdot 1\{B_{t-r} \in [-1,1]^d\}\,dr \geq \hat{\epsilon}_3$$

This completes case B and hence the proof of Lemma 3.3. □

4. Perturbation of higher dimensional systems. In order to prove results for three-species we need perturbation results that generalize those in Section 1. In this section we will prove three results that allows us to extend a Lyapunov function g defined on an m dimensional face

$$F_m = \{u \in \Gamma : u_{m+1} = 0, \dots u_n = 0\}$$

to be a repelling function in a neighborhood of that face (in Γ). We need three results because in the case $m = 2$, the boundary fixed point may have 2, 1, or 0 positive components.

To set up for our first theorem we need some notation. It is natural to separate the variables in the face F_m from those in the perturbation. Let $w = (u_1, \dots, u_m)$ be the first m coordinates. As in Section 1, the perturbation will involve a positive linear combination of the last $n - m$ coordinates

$$z = \sum_{k=m+1}^{n} \omega_k u_k \qquad \text{where each of the } \omega_k > 0$$

In our new setting, z is a number while w is a vector in $\mathbf{R}^m$ with $m > 1$. To bridge this gap let 1_k be the vector in $\mathbf{R}^k$ with all components equal to 1 and let 0_k be the vector of k 0's. We will use the norm $\|z\| = \sup_i |z_i|$ throughout and in particular, when we define Lipschitz continuity.

In dimension $m = 1$ we can always take $g(u) = u - \sigma_1 \log u$ when $\sigma_1 > 0$ and $g(u) = u$ when $\sigma_1 = 0$. In dimensions $m > 1$ we cannot always use simple explicit Lyapunov functions, so we need to introduce assumptions (a), (d), and (e) to control their behavior. Assumption (b) gives the invadability condition as it did in Section 1. Finally, in (c) we take the luxury of imposing bounds on the absolute value of the derivatives, since they will be satisfied in all of the examples we consider. In dimension $m = 1$ the problem region was only near $0 \le u_1 \le \epsilon$. Here, it is much larger, $0 < \min w_i \le \epsilon$, and there are more derivatives $\partial g / \partial w_m$ to worry about.

Proposition 4.1. *Suppose that (a) $g(w)$ is decreasing on the face F_m and strictly decreasing for w with strictly positive coordinates and $w \neq \sigma$.*

(b) If $u \to (\sigma, 0_{n-m})$ from inside Γ_+, then $\liminf \frac{1}{z}\frac{dz}{dt} \ge 3\alpha_0 > 0$.

(c) $|dz/dt| \le C_c z$ *and for each* $1 \le i \le m$, $|du_i/dt| \le C_c u_i$

(d) *For each* $1 \le i \le m$, $|\partial g/\partial w_i| \le C_d/w_i$

(e) $\partial g/\partial w_i$ *is Lipschitz continuous on* $\{w \in \Gamma_m : \min_i w_i \ge \epsilon\}$ *with constant* $C_{L,\epsilon}$

Let $0 < \epsilon < \min_i \sigma_i/2$. *If positive constants* θ, λ, η, ν, *and* B *are chosen appropriately with* $\theta \le 1$ *and* $\eta \le \epsilon$ *then*

$$h(u) = g(w + \theta z 1_m) - \lambda \log z$$

satisfies: (i) $dh/dt \le -\nu < 0$ *when* $\epsilon \le \min_i w_i$ *and* $0 < z \le \eta$.

and (ii) $dh/dt \le B$ *when* $0 \le \min_i w_i \le \epsilon$ *and* $0 < z \le \eta$.

Proof of Proposition 4.1. Calculus tells us that

$$\frac{dh}{dt} = \sum_{i=1}^{m} \frac{\partial g}{\partial x_i}(w + \theta z 1_m)\left(\frac{du_i}{dt} + \theta \frac{dz}{dt}\right) - \frac{\lambda}{z}\frac{dz}{dt} \tag{4.1}$$

We begin by checking (ii) since it is only two lines. Using assumptions (d) and (c), it follows that if $1 \le i \le m$ then

$$\left|\frac{\partial g}{\partial x_i}(u + \theta z 1_m)\left(\frac{du_i}{dt} + \theta \frac{dz}{dt}\right)\right| \le C_d C_c \tag{4.2}$$

Using (c) again we have

$$\left|\frac{dz}{dt}\right| \le C_c z \tag{4.3}$$

Combining (4.1)–(4.3) proves (ii) with $B = C_d C_c + \lambda C_c$. □

Proof of (i). To begin, we note that (b) implies we can pick $\eta_1 < \min_i \sigma_i/2$ so that if $\|u - \sigma\| \le \eta_1$, and $0 < z \le \eta_1$ then

$$\frac{\lambda}{z}\frac{dz}{dt} \ge 2\alpha_0 \lambda > 0 \tag{4.4}$$

Our first goal is the control the derivative dh/dt away from the fixed point.

Lemma 4.1.1. *Given* ϵ *and* η_1, *there are* $\alpha_1, \eta_2, \lambda_0 > 0$ *so that if* $0 \le \theta \le 1$ *and* $\lambda \le \lambda_0$ *then*

$$\frac{dh}{dt} \le -\alpha_1 < 0$$

when $\min w_i \ge \epsilon$, $\|w - \sigma\| \ge \eta_1$, *and* $0 < z \le \eta_2$.

Proof of Lemma 4.1.1. We begin by writing the term inside the sum in (4.1) as

$$\begin{aligned} \frac{\partial g}{\partial x_i}(w)\,\frac{du_i}{dt} &+ \left\{\frac{\partial g}{\partial x_i}(w+\theta z 1_m) - \frac{\partial g}{\partial x_i}(w)\right\}\frac{du_i}{dt} \\ &+ \frac{\partial g}{\partial x_i}(w+\theta z 1_m)\cdot\theta\,\frac{dz}{dt} \end{aligned} \tag{4.5}$$

By the strict decreasing property in (a) we can define a constant α_1 so that

$$\sum_{i=1}^{m} \frac{\partial g}{\partial x_i}(w)\,\frac{du_i}{dt}(w, 0_{n-m}) \le -3\alpha_1 \tag{4.6}$$

when $\min_i w_i \ge \epsilon$ and $\|w-\sigma\| \ge \eta_1$. Using the boundedness of $\partial g/\partial x_i$ when $\min_i w_i \ge \epsilon$, which comes from (d), and the continuity of du_i/dt it follows that if η_2 is small then

$$\sum_{i=1}^{m} \frac{\partial g}{\partial x_i}(w)\,\frac{du_i}{dt}(u) \le -2\alpha_1 \tag{4.7}$$

when $\min_i w_i \ge \epsilon$, $\|w - \sigma\| \ge \eta_1$, and $0 < u_3 \le \eta_2$.

Using the Lipschitz continuity assumed in (e) it follows that if $\min_i w_i \ge \epsilon$, and $0 < z \le \eta_2$, then

$$\left|\left\{\frac{\partial g}{\partial x_i}(w+\theta z 1_m) - \frac{\partial g}{\partial x_i}(w)\right\}\frac{du_i}{dt}\right| \le C_{L,\epsilon} C_c \theta \eta_2 \tag{4.8}$$

With the proof of Lemma 4.2 in mind, note that for (4.8) (and for (4.9) below) we do not need to exclude the region near the fixed point.

For the last term in (4.5) we note that using (d) and (4.3) it follows that when $\min_i w_i \ge \epsilon$ and $0 < z \le \eta_2$ we have that

$$\left|\frac{\partial g}{\partial x_i}(w+\theta z 1_m)\cdot\theta\frac{dz}{dt}\right| \le \frac{C_d}{\epsilon}\cdot C_c\theta z \le \frac{C_d C_c}{\epsilon}\theta\eta_2 \tag{4.9}$$

Combining (4.7)–(4.9) with (4.5) and (4.4) we see that if $\theta \le 1$ then the right hand side of (4.1) is

$$\le -2\alpha_1 + m\left(C_{L,\epsilon}C_c + \frac{C_d C_c}{\epsilon}\right)\eta_2 + C_c\lambda_0 \le -\alpha_1$$

when $0 < z \le \eta_2$ if η_2 and λ_0 are chosen small enough. □

To complete the proof of (i) in Proposition 4.1, we have to consider the region near the fixed point. To do this, we will prove

Lemma 4.1.2. *Given η_1 and η_2, if $\eta_3 \le \eta_2$ is chosen small enough*

$$\lim_{\theta\to 0}\left(\sup\left\{\frac{dh}{dt} : \|w-\sigma\| \le \eta_1, 0 < z \le \eta_3\right\}\right) \le -\lambda\alpha_0$$

Proof of Lemma 4.1.2. Again we use (4.5). By (a), the first term has

$$\sum_{i=1}^{m} \frac{\partial g}{\partial x_i}(w)\,\frac{du_i}{dt}(w, 0_{n-m}) \le 0 \tag{4.10}$$

for all $w \in \Delta_m^+$. Using the boundedness of $\partial g/\partial x_i$ near the fixed point (which follows from (d)) and continuity of du_i/dt it follows that if $\eta_3 \le \eta_2$ is small then

$$\sum_{i=1}^{m} \frac{\partial g}{\partial x_i}(w)\,\frac{du_i}{dt}(u) \le \lambda\alpha_0 \tag{4.11}$$

when $\|w-\sigma\| \le \eta_1$ and $z \le \eta_3$. Combining (4.11) with (4.8) and (4.9), then using (4.5), and (4.4), we have the right hand side of (4.1) is

$$\le \lambda\alpha_0 + m\left(C_{L,\epsilon}C_c + \frac{C_d C_c}{\epsilon}\right)\theta\eta_3 - 2\lambda\alpha_0$$

when $\|u-\sigma\| \le \eta_1$, $0 < z \le \eta_3$ and the desired result follows. □

For some our examples we will need extensions of Proposition 4.1 where one or both of the coordinates of our boundary equilibrium are 0. For simplicity we restrict our attention to $m = 2$. Note that the conditions on the derivatives in (d) and (e) have gotten stronger but the conclusion in (i) requires only that $w_1 \ge \epsilon$ not $w_1 \wedge w_2 \ge \epsilon$

Proposition 4.2. *Suppose that* $m = 2$ *with* $\sigma_1 > 0$ *and* $\sigma_2 = 0$.

(a) $g(w)$ *is decreasing on the face* F_m, *strictly decreasing when* $w_1 > 0$, $w \neq \sigma$.

(b) *If* $u \to (\sigma_1, 0_{n-1})$ *from inside* Γ_+, *then* $\liminf \frac{1}{z}\frac{dz}{dt} \geq 3\alpha_0 > 0$.

(c) $|dz/dt| \leq C_c z$ *and for each* $1 \leq i \leq m$, $|du_i/dt| \leq C_c\, u_i$

(d) $|\partial g_1/\partial w_i| \leq C_d/w_1$ *and* $|\partial g_2/\partial w_i| \leq C_d/(w_1 + w_2)$

(e) $\partial g/\partial w_i$ *is Lipschitz continuous on* $\{w \in \Gamma_m : w_1 \geq \epsilon\}$ *with constant* $C_{L,\epsilon}$

Let $0 < \epsilon < \sigma_1/2$. *If positive constants* θ, λ, η, ν, *and* B *are chosen appropriately with* $\theta \leq 1$ *and* $\eta \leq \epsilon$ *then*

$$h(u) = g(w + \theta z 1_m) - \lambda \log z$$

satisfies: (i) $dh/dt \leq -\nu < 0$ *when* $w_1 \geq \epsilon$ *and* $0 < z \leq \eta$.

and (ii) $dh/dt \leq B$ *when* $w_1 \leq \epsilon$ *and* $0 < z \leq \eta$.

Proof. We will follow the outline of Proposition 4.1. (c) is the same as in Proposition 4.1 but (d) is stronger, so repeating (4.1)–(4.3) proves (ii). (4.4) works as before and brings us to the proof of

Lemma 4.2.1. *Given* ϵ *and* η_1, *there are* $\alpha_1, \eta_2, \lambda_0 > 0$ *so that if* $0 \leq \theta \leq 1$ *and* $\lambda \leq \lambda_0$ *then*

$$\frac{dh}{dt} \leq -\alpha_1 < 0$$

when $w_1 \geq \epsilon$, $\|w - \sigma\| \geq \eta_1$, *and* $0 < z \leq \eta_2$.

Proof. (4.5) is as before, but using the new condition (a) in (4.6) gives a constant α_1 so that

$$\sum_{i=1}^{2} \frac{\partial g}{\partial x_i}(w)\, \frac{du_i}{dt}(w, 0_{n-m}) \leq -3\alpha_1 \tag{4.6$'$}$$

when $w_1 \geq \epsilon$ and $\|w - \sigma\| \geq \eta_1$. Using the boundedness of $\partial g / \partial x_i$ when $w_1 \geq \epsilon$, which comes from (d), and the continuity of du_i/dt it follows that if η_2 is small then

$$\sum_{i=1}^{m} \frac{\partial g}{\partial x_i}(w) \, \frac{du_i}{dt}(u) \leq -2\alpha_1 \tag{4.7$'$}$$

when $w_1 \geq \epsilon$, $\|w - \sigma\| \geq \eta_1$, and $0 < z \leq \eta_2$.

At this point we have proved the conclusion of (4.7) for $w_1 \geq \epsilon$ rather than $\min_i w_i > \epsilon$. Thanks to our new assumptions, this pattern continues throughout the rest of the proof of Lemma 4.2.1. Using the Lipschitz continuity assumed in (e) it follows that if $w_1 \geq \epsilon$, and $0 < z \leq \eta_2$, then

$$\left| \left\{ \frac{\partial g}{\partial x_i}(w + \theta z 1_m) - \frac{\partial g}{\partial x_i}(w) \right\} \frac{du_i}{dt} \right| \leq C_{L,\epsilon} C_c \theta \eta_2 \tag{4.8$'$}$$

Again for (4.8′) (and for (4.9′) below) we do not need to exclude the region near the fixed point. For the last term in (4.5) we note that using (d) and (4.3) it follows that when $w_1 \geq \epsilon$ and $0 < z \leq \eta_2$ we have that

$$\left| \frac{\partial g}{\partial x_i}(w + \theta z 1_m) \cdot \theta \frac{dz}{dt} \right| \leq \frac{C_d C_c}{\epsilon} \theta \eta_2 \tag{4.9$'$}$$

Combining (4.7′)–(4.9′) with (4.5) and (4.4) we can complete the proof as before. □

To complete the proof of (i) of Proposition 4.2, we have to consider the region near the fixed point. Our new (a) and the boundedness of $\partial g / \partial x_i$ near the fixed point allows us to conclude (4.11) holds when $\|w - \sigma\| \leq \eta$ and $z \leq \eta_3$, and the rest of the proof is the same as before. □

For Example 2.3 we will need the special case when the fixed point is at the origin. The assumptions in (d) and (e) get stronger once again, but now there is no exceptional set in the conclusion.

Proposition 4.3. *Suppose that $m = 2$ and $\sigma_1 = \sigma_2 = 0$.*

(a) $g(w)$ is decreasing on the face F_m and strictly decreasing when $w_1 + w_2 > 0$

(b) *If* $u \to 0_n$ *from inside* Γ_+, *then* $\liminf \frac{1}{z}\frac{dz}{dt} \geq 3\alpha_0 > 0$

(c) $|dz/dt| \leq C_c z$ *and for each* $1 \leq i \leq m$, $|du_i/dt| \leq C_c u_i$

(d) *For each* $1 \leq i \leq m$, $|\partial g/\partial w_i| \leq C_d$

(e) $\partial g/\partial w_i$ *is Lipschitz continuous with constant* C_L

Let $0 < \epsilon < \sigma_1/2$. *If positive constants* θ, λ, η, ν, *and* B *are chosen appropriately with* $\theta \leq 1$ *and* $\eta \leq \epsilon$ *then*

$$h(u) = g(w + \theta z 1_m) - \lambda \log z$$

satisfies $dh/dt \leq -\nu < 0$ *when* $0 < z \leq \eta$.

Proof. We will follow the proof of Proposition 4.2, but the strong assumptions in (d) and (e) will make things easier. (4.2′) becomes

$$(4.2'') \qquad \left| \frac{\partial g}{\partial x_i}(u + \theta z 1_m)\left(\frac{du_i}{dt} + \theta \frac{dz}{dt}\right)\right| \leq C_d \cdot C_c(u_i + \theta z) \leq C_d C_c$$

Turning to the proof of

Lemma 4.3.1. *Given* ϵ *and* η_1, *there are* $\alpha_1, \eta_2, \lambda_0 > 0$ *so that if* $0 \leq \theta \leq 1$ *and* $\lambda \leq \lambda_0$ *then*

$$\frac{dh}{dt} \leq -\alpha_1 < 0$$

when $\|w - \sigma\| \geq \eta_1$, *and* $0 < z \leq \eta_2$.

Proof. (4.5) is as before, but using the new condition (a) in (4.6) gives a constant α_1 so that

$$(4.6'') \qquad \sum_{i=1}^{2} \frac{\partial g}{\partial x_i}(w)\,\frac{du_i}{dt}(w, 0_{n-m}) \leq -3\alpha_1$$

when $\|w - \sigma\| \geq \eta_1$. Using the boundedness of $\partial g/\partial x_i$ from (d), and the continuity of du_i/dt it follows that if η_2 is small then

$$(4.7'') \qquad \sum_{i=1}^{m} \frac{\partial g}{\partial x_i}(w)\,\frac{du_i}{dt}(u) \leq -2\alpha_1$$

when, $\|w - \sigma\| \geq \eta_1$, and $0 < z \leq \eta_2$.

At this point we have proved the conclusion of (4.7) for all w rather than $w_1 > \epsilon$. Thanks to our assumptions this pattern will continue throughout the rest of the proof. Using the Lipschitz continuity assumed in (e) it follows that if $0 < z \leq \eta_2$, then

$$\left| \left\{ \frac{\partial g}{\partial x_i}(w + \theta z 1_m) - \frac{\partial g}{\partial x_i}(w) \right\} \frac{du_i}{dt} \right| \leq C_{L,\epsilon} C_c \theta \eta_2 \tag{4.8''}$$

For the last term in (4.5) we note that using (d) and (4.3) it follows that when $0 < z \leq \eta_2$ we have that

$$\left| \frac{\partial g}{\partial x_i}(w + \theta z 1_m) \cdot \theta \frac{dz}{dt} \right| \leq C_d C_c \theta \eta_2 \tag{4.9''}$$

Combining (4.7″)–(4.9″) together give Lemma 4.3.1. □

It remains to consider the region near the fixed point. Our new (a) and the boundedness of $\partial g / \partial x_i$ allows us to conclude (4.11) holds when $\|w - \sigma\| \leq \eta$ and $z \leq \eta_3$ and the rest of the proof of Lemma 4.2 goes as before. □

5. Lyapunov functions for Lotka-Volterra systems.

In order to use the results in Section 4 to construct repelling functions for three-species systems, we need convex Lyapunov functions for each of the three two-dimensional systems on the faces that make up Γ^0. In this section we study the question when the mean field ODE has the Lotka-Volterra form

$$\frac{du_j}{dt} = u_j \left(r_j - \sum_k a_{jk} u_k \right) \qquad j = 1, 2 \tag{5.1}$$

For our needs, it is sufficient to consider two cases.

I. *competition.* all $a_{ij} > 0$.

II. *exploiter-victim.* $a_{21} < 0$, the other $a_{ij} > 0$.

Case II is simpler so we consider it first.

Lemma 5.0. *In Case II if the Lotka-Volterra system* (5.1) *has a fixed point* (ρ_1, ρ_2) *with each component* $\rho_i > 0$ *then*

$$h(u_1, u_2) = -a_{21}\{u_1 - \rho_1 \log u_1\} + a_{12}\{u_2 - \rho_2 \log u_2\} \tag{5.2}$$

is a convex Lyapunov function.

Proof. Since the $\rho_i > 0$, $a_{21} < 0$ and $a_{12} > 0$, h is convex. A little calculus shows that

$$\begin{aligned} \frac{dh}{dt} = &- a_{21}(u_1 - \rho_1)\{r_1 - a_{11}u_1 - a_{12}u_2\} \\ &+ a_{12}(u_2 - \rho_2)\{r_2 - a_{21}u_1 - a_{22}u_2\} \end{aligned}$$

Using the fact that the ρ_i are equilibrium probabilities and hence $r_i = a_{i1}\rho_1 + a_{i2}\rho_2$ we can rewrite this as

$$\frac{dh}{dt} = a_{11}a_{21}(u_1 - \rho_1)^2 - a_{12}a_{22}(u_2 - \rho_2)^2 < 0.$$

For the last step, note that the cross terms $(u_1 - \rho_1)(u_2 - \rho_2)$ cancel due to our choice of constants in the definition of h, while the assumed signs of the a_{ij} make each coefficient negative. □

We turn now to case I. In order for both species to have a possibility to survive we must have $r_1, r_2 > 0$. In the absence of the other species, type i will reach an equilibrium level $\sigma_i = r_i/a_{ii}$. In the (u_1, u_2) plane the derivative $du_i/dt = 0$ when $a_{i1}u_1 + a_{i2}u_2 = r_i$, i.e., on a straight line connecting $(r_i/a_{i1}, 0)$ to $(0, r_i/a_{i2})$. There are several situations to consider.

Case 1. $r_1/a_{11} > r_2/a_{21}$ and $r_2/a_{22} > r_1/a_{12}$.

These inequalities guarantee the lines $du_i/dt = 0$ intersect at a point (ρ_1, ρ_2) in the first quadrant. Rearranged they say $r_2 < a_{21}\sigma_1$ and $r_1 < a_{12}\sigma_2$ or using (2.1.7), they become $2 \not> 1$ and $1 \not> 2$. In words, neither species can invade the other.

To argue geometrically, note that the boundary fixed point $(\sigma_1, 0)$ is above the line $du_2/dt = 0$, see Figure 5.1, so u_2 will be decreasing in a neighborhood and $(\sigma_1, 0)$ will be locally attracting. Reversing roles, the boundary fixed point $(0, \sigma_2)$ is above the line $du_1/dt = 0$, so again $(0, \sigma_2)$ will be locally attracting. Once there are two locally attracting fixed points, there can be no convex Lyapunov function. This disappointing fact kills our interest in this case, so we leave it as an exercise to the reader to show that the interior fixed point (ρ_1, ρ_2) is always a saddle point.

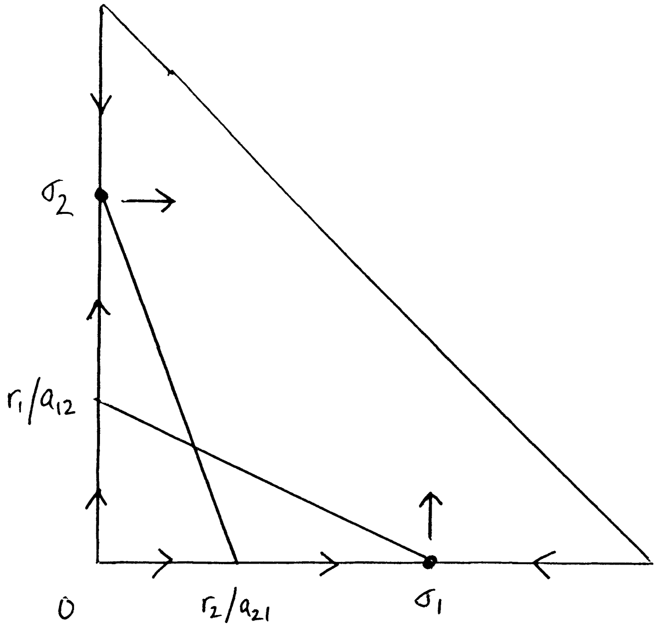


Figure 5.1.

Case 2. $r_1/a_{11} < r_2/a_{21}$ and $r_2/a_{22} < r_1/a_{12}$.

These inequalities also guarantee the lines $du_i/dt = 0$ intersect at a point (ρ_1, ρ_2) in the first quadrant. Rearranged they say $r_2 > a_{21}\sigma_1$ and $r_1 > a_{12}\sigma_2$ or using (2.1.7), $2 \succ 1$ and $1 \succ 2$. In words, each species can invade the other.

To argue geometrically, note that the boundary fixed point $(\sigma_1, 0)$ is below the line $du_2/dt = 0$, see Figure 5.2, so u_2 will be increasing in a neighborhood of the fixed point and 2 will be able to invade 1. Reversing roles, the boundary fixed point $(0, \sigma_2)$ is below the line $du_1/dt = 0$ so 1 will be able to invade 2.

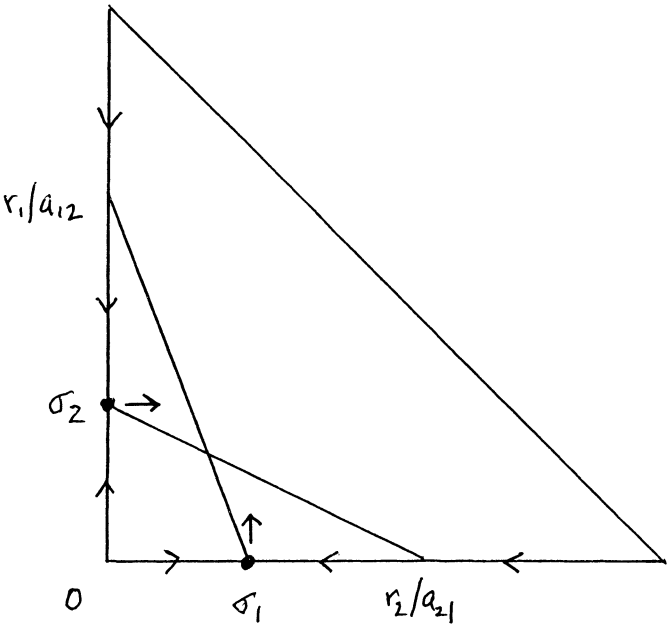


Figure 5.2.

Our goal is to prove that the interior fixed point (ρ_1, ρ_2) is attracting by showing

Lemma 5.1. *Let* $\kappa = a_{12}/a_{21}$. *In Case 2*

$$h(u_1, u_2) = (u_1 - \rho_1 \log u_1) + \kappa\,(u_2 - \rho_2 \log u_2) \tag{5.3}$$

is a convex Lyapunov function.

Remarks. (5.3) bears a striking similarity to the Lyapunov function for the predator-prey case given in (5.2). However this time all the

$a_{ij} > 0$, so we can't hope to cancel the off diagonal terms. In order to use this function with the result in Proposition 4.1, we will need bounds on the derivatives, so we note that

$$\left|\frac{\partial h}{\partial u_i}\right| = |c(1-\rho_i/u_i)| \le \frac{C_c}{u_i}$$

for $u \in \Gamma_+$ and $\partial h/\partial u_i$ is Lipschitz continuous on $\{u \in \Gamma_+ : u_1 \wedge u_2 \ge \epsilon\}$.

Proof. Since $\kappa > 0$, h is convex. A little calculus shows that

$$\begin{aligned}\frac{dh}{dt} =& (u_1-\rho_1)\{r_1 - a_{11}u_1 - a_{12}u_2\}\\ &+ \kappa(u_2-\rho_2)\{r_2 - a_{21}u_1 - a_{22}u_2\}\end{aligned}$$

Using the fact that the ρ_i are equilibrium probabilities and hence $r_i = a_{i1}\rho_1 + a_{i2}\rho_2$ we can rewrite this as

$$\begin{aligned}\frac{dh}{dt} =& - a_{11}(u_1-\rho_1)^2 - a_{12}(u_1-\rho_1)(u_2-\rho_2)\\ &- \kappa a_{21}(u_2-\rho_2)(u_1-\rho_1) - \kappa a_{22}(u_2-\rho_2)^2\end{aligned} \tag{5.4}$$

To check that the right-hand side is < 0 except at the fixed point we want to prove that the matrix

$$\begin{pmatrix} a_{11} & a_{12} \\ \kappa a_{21} & \kappa a_{22} \end{pmatrix}$$

is positive definite. Multiplying the matrix by the vector $(\theta, 1)$ on each side, what we want to establish is

$$a_{11}\theta^2 + (a_{12} + \kappa a_{21})\theta + \kappa a_{22} > 0 \tag{5.5}$$

Since $a_{11} > 0$ this will be true if and only if there are no real roots for this quadratic equation, i.e.,

$$(a_{12} + \kappa a_{21})^2 - 4a_{11}a_{22}\kappa < 0 \tag{5.6}$$

Taking $\kappa = a_{12}/a_{21}$ to simplify the square converts the last condition into

$$4a_{12}^2 - 4a_{11}a_{22} \cdot \frac{a_{12}}{a_{21}} < 0$$

or simply that the determinant $a_{11}a_{22} - a_{12}a_{21} > 0$. To check this, we have to use the inequalities that define case 2. Rearranged they say

$$\frac{a_{11}}{a_{21}} > \frac{r_1}{r_2} \quad \text{and} \quad \frac{r_1}{r_2} > \frac{a_{12}}{a_{22}}$$

Combining the two inequalities and cross multiplying shows $a_{11}a_{22} - a_{12}a_{21} > 0$, completing the proof of Lemma 5.1. □

Our first two cases for the competition model have considered the two possible ways that the lines $du_i/dt = 0$ can intersect in the positive quadrant. There are also two ways that the lines can fail to intersect there. We will consider here "Case 3a" in which $du_1/dt = 0$ lies above $du_2/dt = 0$ inside Γ. Since $(\sigma_1, 0)$ lies above $du_2/dt = 0$, it is locally attracting. Conversely, $(0, \sigma_2)$ lies below $du_1/dt = 0$, so 1's can invade the 2's. In this case we expect that the 1's will drive the 2's to extinction. The next result constructs a Lyapunov function to prove this for the ODE.

Lemma 5.2. *In Case 3a, if $0 < \epsilon, \kappa, K < \infty$ are chosen appropriately, and we define $v_i = a_{i1}u_1 + a_{i2}u_2$ then*

$$h(u_1, u_2) = u_1 - \sigma_1 \log u_1 + \kappa u_2 + K \log^-(v_2/(r_2 + \epsilon))$$

is a convex Lyapunov function. In the degenerate case $\sigma_2 = 0$, it is possible to take

$$h(u_1, u_2) = u_1 - \sigma_1 \log u_1 + \kappa u_2$$

Remark. In order to use these functions with the results in Proposition 4.2, we need bounds on the derivatives. Consulting (d) and (e) of that result, the desired bounds are

$$\left|\frac{\partial h}{\partial u_1}\right| \leq \frac{C_d}{u_1} \qquad \left|\frac{\partial h}{\partial u_2}\right| \leq \frac{C_d}{(u_1 + u_2)}$$

for $u \in \Gamma_+$ and $\partial h/\partial u_i$ is Lipschitz continuous on $\{u \in \Gamma_+ : u_1 \geq \epsilon\}$. It is easy to see that these conditions are satisfied by the functions in Lemma 5.2.

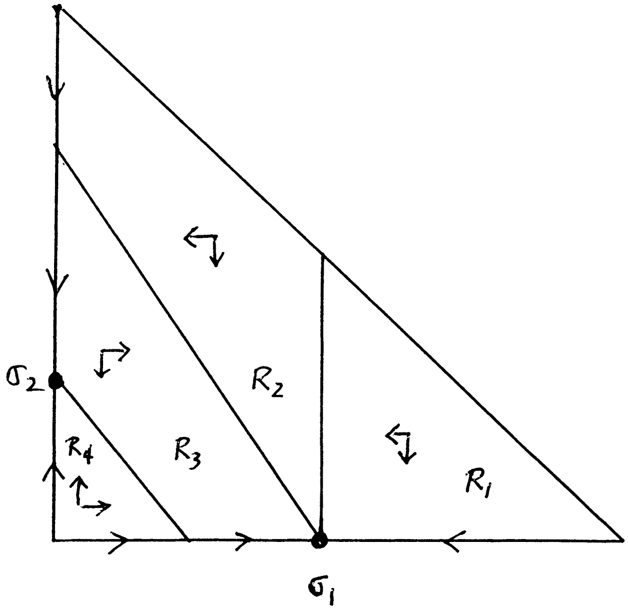


Figure 5.3

Proof. It is clear that h is convex. Letting $h_1 = u_1 - \sigma_1 \log u_1$ and $h_2 = u_2$,

$$\begin{aligned} \frac{dh_1}{dt} &= (u_1 - \sigma_1)\{r_1 - a_{11}u_1 - a_{12}u_2\} \\ \frac{dh_2}{dt} &= u_2\{r_2 - a_{21}u_1 - a_{22}u_2\} \end{aligned} \tag{5.7}$$

Now $dh_2/dt < 0$ when $v_2 > r_2$ i.e., above $du_2/dt = 0$. On the other hand, using $r_1 = a_{11}\sigma_1$

$$\frac{dh_1}{dt} = -a_{11}(u_1 - \sigma_1)^2 - (u_1 - \sigma_1)a_{12}u_2 \tag{5.8}$$

From this formula we can see that $dh_1/dt < 0$ if $u_1 > \sigma_1$. Using (5.7), we see that $dh_1/dt < 0$ if $u_1 < \sigma_1$ and $r_1 > v_1$. Combining the two results gives us four regions to look at. See Figure 5.3. Here and in what follows all points we consider are assumed to lie in Γ.

R_1. $u_1 > \sigma_1$: $dh_1/dt < 0$, $dh_2/dt < 0$

R_2. $u_1 \leq \sigma_1$, $v_1 \geq r_1$: $dh_1/dt \geq 0$, $dh_2/dt < 0$

R_3. $r_1 > v_1$, $v_2 > r_2$: $dh_1/dt < 0$, $dh_2/dt < 0$

R_4. $v_2 \le r_2$: $dh_1/dt < 0$, $dh_2/dt \ge 0$.

In regions R_1 and R_3 we have $dh/dt < 0$. To deal with R_2, we will choose κ large. To see that this will succeed despite the fact that dh_2/dt vanishes when $u_2 = 0$, note that (i) the only point on the boundary of R_2 with $u_2 = 0$ is $(\sigma_1, 0)$, and (ii) if we near that point inside R_2 we have $|u_1 - \sigma_1| \le Cu_2$, so $dh_1/dt = O(u_2^2)$ versus $dh_2/dt \sim cu_2$.

When $\sigma_2 = 0$, $R_4 = \emptyset$ and we are done with the proof. To control the behavior in R_4 when $\sigma_2 > 0$, we will add a corner function. To do this, we observe that $dv_2/dt > 0$ on $R_4 = \{v_2 \le r_2\}$, so we can find an $\epsilon > 0$ so that this this holds for $v_2 \le r_2 + \epsilon$. Letting

$$h_3(u_1, u_2) = \log^- \left(\frac{v_2}{r_2 + \epsilon} \right)$$

calculus tells us that

$$\frac{dh_3}{dt} = \frac{-1}{v_2} \cdot \frac{dv_2}{dt} < 0$$

when $v_2 \le r_2 + \epsilon$. As $v_2 \to 0$,

$$\frac{1}{v_2} \frac{dv_2}{dt} \to a_{21} r_1 + a_{22} r_2 > 0$$

so dh_3/dt is bounded away from 0 on R_4. Since dh_2/dt is bounded there, if K is chosen large enough, $h_1 + \kappa h_2 + h_3$ is a Lyapunov function. □

The previous result takes care of the competition case when the fixed point has one positive component, so we turn now to this case for the exploiter-victim system. The set $\{du_2/dt = 0\}$ is a line with positive slope

$$u_2 = \frac{r_2}{a_{22}} - \frac{a_{21}}{a_{22}} u_1$$

There are two ways this can fail to intersect the line $\{du_1/dt = 0\}$ inside the positive quadrant: (a) 2's are a predator ($r_2 < 0$) but the prey are not nutritious enough to sustain the predator:

$$r_2 - a_{21}\sigma_1 < 0 \quad \text{where } \sigma_1 = r_1/a_{11} \tag{5.9}$$

or (b) 2's can survive on their own ($r_2 > 0$) and cannot be invaded by the 1's

$$r_1 - a_{12}\sigma_2 < 0 \quad \text{where } \sigma_2 = r_2/a_{22} \tag{5.10}$$

Lemma 5.3. *Consider case (a) described in (5.9). If* $0 < \alpha, \kappa, K < \infty$ *are chosen appropriately, and* y^{+2} *denotes the square of the positive part of* y *then*

$$h(u_1,u_2) = u_1 - \sigma_1 \log u_1 + \kappa u_2 + K(u_1-\alpha)^{+2}$$

is a convex Lyapunov function. In the degenerate case $\sigma_1 = 0$, *we can take*

$$h(u_1,u_2) = u_1 + \kappa u_2 + K(u_1-\alpha)^{+2}$$

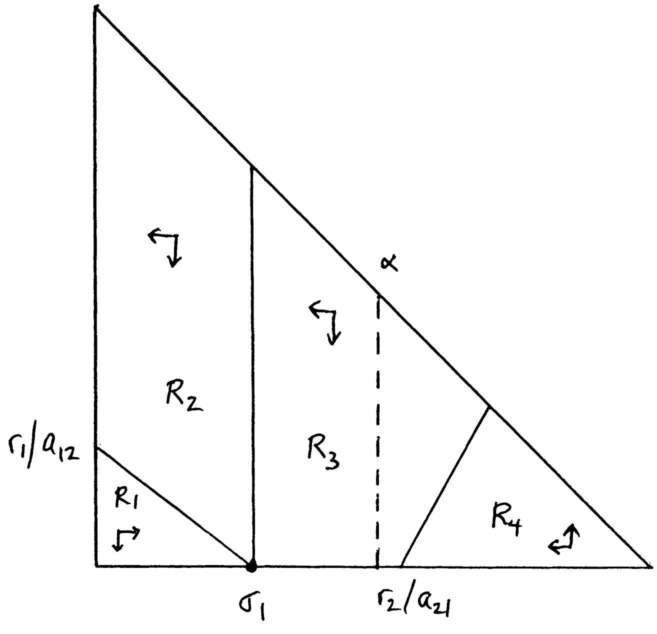


Figure 5.4.

Remark. In order to use these functions with the results in Proposition 4.2 and 4.3. we need bounds on the derivatives. In the first case the boundary equilibirum is $(\sigma_1, 0)$, so the desired bounds (which are satisfied here) are

$$\left|\frac{\partial h}{\partial u_1}\right| \le \frac{C_d}{u_1} \qquad \left|\frac{\partial h}{\partial u_2}\right| \le \frac{C_d}{u_1+u_2}$$

for $u \in \Gamma_+$ and $\partial h/\partial u_i$ is Lipschitz continuous on $\{u \in \Gamma_+ : u_1 \geq \epsilon\}$. In the second case the boundary equilibirum is $(0,0)$, so the desired bounds from (d) and (e) of Proposition 4.3 (which are satisfied here) are $|\partial h/\partial u_i| \leq C_d$ for $u \in \Gamma_+$ and $\partial h/\partial u_i$ is Lipschitz continuous on Γ_+.

Proof. It is clear that h is convex. Letting $h_1 = u_1 - \sigma_1 \log u_1$ and $h_2 = u_2$, (5.7) implies that $dh/dt = dh_1/dt + \kappa\, dh_2/dt$ where

$$\begin{aligned} \frac{dh_1}{dt} &= (u_1 - \sigma_1)\{r_1 - a_{11}u_1 - a_{12}u_2\} \\ \frac{dh_2}{dt} &= u_2\{r_2 - a_{21}u_1 - a_{22}u_2\} \end{aligned} \tag{5.11}$$

Now $dh_2/dt < 0$ when $a_{22}u_2 > r_2 - a_{21}u_1$ i.e., above the line $du_2/dt = 0$, which now has positive slope and by (5.9) crosses the x-axis at $r_2/a_{21} > \sigma_1$. On the other hand, using $r_1 = a_{11}\sigma_1$

$$\frac{dh_1}{dt} = -a_{11}(u_1 - \sigma_1)^2 - (u_1 - \sigma_1)a_{12}u_2 \tag{5.12}$$

In this form we can see that $dh_1/dt < 0$ if $u_1 > \sigma_1$. Using (5.11), we see that $dh_1/dt < 0$ if $u_1 < \sigma_1$ and $r_1 > v_1$. Combining the two results gives us four regions to look at. See Figure 5.4. Here, and in what follows, all points we consider are assumed to lie in Γ.

R_1. $r_1 > v_1$: $dh_1/dt < 0$, $dh_2/dt < 0$

R_2. $u_1 \leq \sigma_1$, $v_1 \geq r_1$: $dh_1/dt \geq 0$, $dh_2/dt < 0$

R_3. $a_{22}u_2 > r_2 - a_{21}u_1$, $u_1 > \sigma_1$: $dh_1/dt < 0$, $dh_2/dt < 0$

R_4. $a_{22}u_2 \leq r_2 - a_{21}u_1$: $dh_1/dt < 0$, $dh_2/dt \geq 0$.

Note that the regions have been numbered in parallel to those in Lemma 5.3. In R_1 and R_3 we have $dh/dt < 0$. To deal with R_2, we will choose κ large. To see that this will succeed despite the fact that dh_2/dt vanishes when $u_2 = 0$, note that (i) the only point on the boundary of R_3 with $u_2 = 0$ is $(\sigma_1, 0)$, and (ii) if we near that point inside R_2 we have $|u_1 - \sigma_1| \leq Cu_2$, so $dh_1/dt = O(u_2^2)$ versus $dh_2/dt \sim cu_2$.

To control the behavior in R_4, we will add a corner function. Pick $\alpha \in (\sigma_1, r_2/a_{21})$ and let $h_3(u_1, u_2) = (u_1 - \alpha)^+2$. Calculus tells us that when $u_1 > \alpha$

$$\frac{dh_3}{dt} = \frac{du_1}{dt} < 0$$

since $\alpha > \sigma_1$. Our other choice $\alpha < r_2/a_{21}$ implies that dh_3/dt is bounded away from 0 on R_4. Since dh_2/dt is bounded there, if K is chosen large enough, $h_1 + \kappa h_2 + K h_3$ is a Lyapunov function.

This proves the result when $\sigma_1 > 0$. If $\sigma_1 = 0$ (i.e., $r_1 = 0$) there are only regions R_1 and R_2. Changing now to $h_1(u_1) = u_1$ we still have $dh_1/dt < 0$ in R_1 and R_2. To control the behavior in R_1, we add the corner function h_3 as before. □

We now consider the case in which $r_2 > 0$ and the boundary equilibrium is $(0, \sigma_2)$ cannot be invaded by 1's.

Lemma 5.4. *Consider case (b) described in* (5.10). *If* $0 < \alpha, \kappa, K < \infty$ *are chosen appropriately, and we let* y^{+2} *indicate the square of the positive part of* y *then*

$$h(u_1, u_2) = u_2 - \sigma_2 \log u_2 + \kappa u_1 + K(\alpha - u_2)^{+2}$$

is a convex Lyapunov function. In the degenerate case $\sigma_1 = 0$ *we can take*

$$h(u_1, u_2) = u_2 - \sigma_2 \log u_2 + \kappa u_1$$

Remark. In order to use these functions with the results in Proposition 4.2 we need bounds on the derivatives. In each case the boundary equilibirum is $(0, \sigma_2)$, so interchanging the roles of the coordinates the desired bounds (which are satisfied here) are

$$\left|\frac{\partial h}{\partial u_2}\right| \le \frac{C_d}{u_2} \qquad \left|\frac{\partial h}{\partial u_1}\right| \le \frac{C_d}{u_1 + u_2}$$

for $u \in \Gamma_+$ and $\partial h/\partial u_i$ is Lipschitz continuous on $\{u \in \Gamma_+ : u_1 \ge \epsilon\}$.

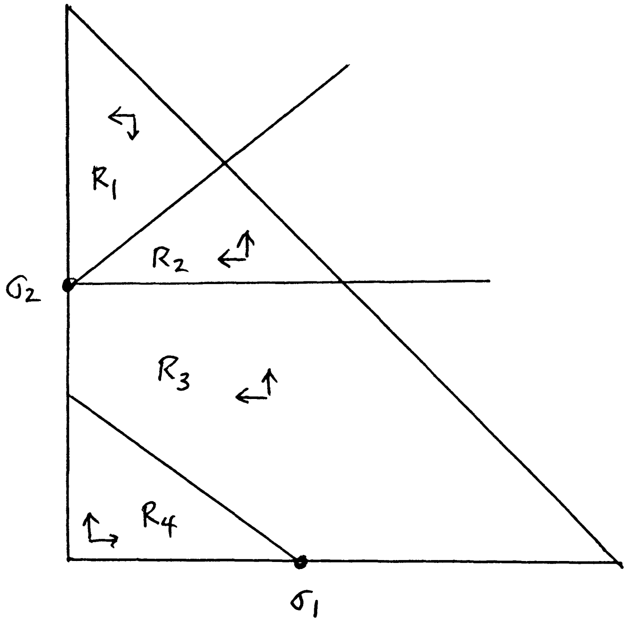


Figure 5.5.

Proof. As you can see by comparing the conclusions with those of the two previous lemmas, this proof is very similar to the proof of Lemma 5.2, but now the fixed point is on the other axis. It is clear that h is convex. Letting $h_2 = u_2 - \sigma_2 \log u_2$ and $h_1 = u_1$, (5.7) implies that $dh/dt = dh_2/dt + \kappa\, dh_1/dt$ where

$$\begin{aligned} \frac{dh_2}{dt} &= (u_2 - \sigma_2)\{r_2 - a_{21}u_1 - a_{22}u_2\} \\ \frac{dh_1}{dt} &= u_1\{r_1 - a_{11}u_1 - a_{12}u_2\} \end{aligned} \tag{5.13}$$

Now $dh_1/dt < 0$ when $a_{12}u_2 > r_1 - a_{11}u_1$ i.e., above the line $du_1/dt = 0$. On the other hand, using $r_2 = a_{22}\sigma_2$

$$\frac{dh_2}{dt} = -a_{22}(u_2 - \sigma_2)^2 - (u_2 - \sigma_2)a_{21}u_1 \tag{5.14}$$

In this form we can see that $dh_2/dt < 0$ if $u_2 < \sigma_2$. Using (5.13), we see that $dh_2/dt < 0$ if $u_2 > \sigma_2$ and $r_2 < v_2$. Combining the two results gives us four regions to look at. See Figure 5.5. Here, and in what follows, all points we consider are assumed to lie in Γ.

R_1. $r_2 < v_2$: $dh_2/dt < 0$, $dh_1/dt \le 0$.

R_2. $r_2 \le v_2$, $u_2 \ge \sigma_2$: $dh_2/dt \ge 0$, $dh_1/dt < 0$

R_3. $u_2 < \sigma_1$, $v_1 \ge r_1$: $dh_2/dt < 0$, $dh_1/dt \le 0$

R_4. $r_1 > v_1$: $dh_2/dt < 0$, $dh_1/dt \ge 0$

The numbering of the regions parallels that in Lemmas 5.3 and 5.4. In regions R_1 and R_3 we have $dh/dt < 0$. To deal with R_2, we will choose κ large. To see that this will succeed despite the fact that dh_1/dt vanishes when $u_1 = 0$, note that (i) the only point on the boundary of R_3 with $u_1 = 0$ is $(0, \sigma_2)$, and (ii) if we near that point inside R_2 we have $|u_2 - \sigma_2| \le Cu_1$, so $dh_2/dt = O(u_1^2)$ versus $dh_1/dt \sim cu_1$.

When $\sigma_1 = 0$, $R_4 = \emptyset$ and we are done with the proof. To control the behavior in R_4 when $\sigma_1 > 0$, we will add a corner function. Pick $\alpha \in (\sigma_2, r_1/a_{12})$ and let $h_3(u_1, u_2) = (\alpha - u_2)^+2$. Calculus tells us that when $u_1 > \alpha$ $dh_3/dt = du_1/dt < 0$ since $\alpha > \sigma_1$. Our other choice $\alpha < r_2/a_{21}$ implies that dh_3/dt is bounded away from 0 on R_4. Since dh_2/dt is bounded there, if K is chosen large enough, $h_1 + \kappa h_2 + K h_3$ is a Lyapunov function. □

The final degenerate case to consider is when the origin is an attracting fixed point. The exploiter victim special case is covered by Lemma 5.3. This leaves us with only the competition case where the result is trivial.

Lemma 5.5. *Suppose* $r_i < 0$ *and* $a_{ij} > 0$. *In this case* $u_1 + u_2$ *is a convex Lyapunov function.*

Proof. Clearly $d(u_1+u_2)/dt = \sum_i u_i(r_i - \sum_j a_{ij}u_j) < 0$ when $u_i \ge 0$, $u_1 + u_2 > 0$. □

6. Three species linear competition models.

In this section, we will consider the following generalization of Example 2.1 to three species. Each site can be in state 0, 1, 2, or 3, where 0 is vacant, while $i = 1, 2, 3$ indicate sites occupied by type i. Letting f_i be the fraction of neighbors in state i, we can write the transition rates of the model as follows:

$$\begin{aligned} i \to j &\quad \text{at rate} \quad \beta_{ij} f_j \\ j \to 0 &\quad \text{at rate} \quad \delta_j + \sum_k \gamma_{jk} f_k \end{aligned}$$

The mean field ODE for this system is:

$$\frac{du_j}{dt} = \sum_i (\beta_{ij} - \beta_{ji}) u_i u_j - u_j \left(\delta_j + \sum_k \gamma_{jk} u_k \right)$$

Letting $\beta_j = \beta_{0j}$, noting $\beta_{j0} = 0$, and substituting $u_0 = 1 - u_1 - u_2 - u_3$, the equations above can be rewritten as

$$\frac{du_j}{dt} = (\beta_j - \delta_j)\, u_j - u_j \sum_{k=1}^{3} (\beta_j + \gamma_{jk} + \beta_{jk} - \beta_{kj}) u_k \tag{6.1}$$

which has the Lotka-Volterra form

$$\frac{du_j}{dt} = u_j \left(r_j - \sum_k a_{jk} u_k \right) \tag{6.2}$$

It follows from the definition of the a_{jk} and our generic parameters assumption that (i) $a_{jj} = \beta_j + \gamma_{jj} > 0$ and (ii) if $a_{jk} < 0$ $\beta_{kj} > \beta_{jk}$ and hence $a_{kj} > 0$.

We begin with the special case in which each species can survive on its own. That is, we will suppose that

$$r_i = \beta_i - \delta_i > 0 \quad \text{for } i = 1, 2, 3 \tag{6.3}$$

conditions that we can write in invadability notation as $i \succ 0$ using Definition 4. If we let

$$\sigma_i = \frac{\beta_i - \delta_i}{\beta_i + \gamma_{ii}}$$

and define the two indices $j < k$ complementary to i by the requirement $\{1, 2, 3\} = \{i, j, k\}$ then the point $u_i = \sigma_i$, $u_j = u_k = 0$ is an attracting fixed point on the edge $\Gamma^0_{j,k} = \{u : u_j = u_k = 0\}$. In the notation of Definition 2 we have $i \to \sigma_i$. From Definition 3, we see that i can invade j in equilibrium, or $i \succ j$, if

$$r_i - a_{ij}\sigma_j > 0 \tag{6.4}$$

Since we have supposed that $r_i > 0$, this will always hold when $a_{ij} < 0$. Results in Example 1.1 imply that if $i \succ j$ and $j \succ i$ and $k = \{1,2,3\} - \{i,j\}$ then there is a fixed point $u_i = \sigma_i^k$, $u_j = \sigma_j^k$, $u_k = 0$. To treat this fixed point we need

(6.5) **Definition 6.** *We say that k can invade i, j in equilibrium and write $k \succ i, j$ if as $u \to \sigma^k$ inside Γ_+*

$$\liminf \frac{1}{u_k}\frac{du_k}{dt} > 0$$

In the current situation it is easy to see that this holds if

$$r_k - a_{ki}\sigma_i^k - a_{kj}\sigma_j^k > 0 \tag{6.6}$$

The simplest possible situation occurs when all of the invadability conditions hold.

Theorem 6.1. *Suppose that for all distinct i, j, k we have (a) $i \succ 0$, (b) $i \succ j$, and (c) $k \succ i, j$. Then there is coexistence in the three species linear competition model with fast stirring.*

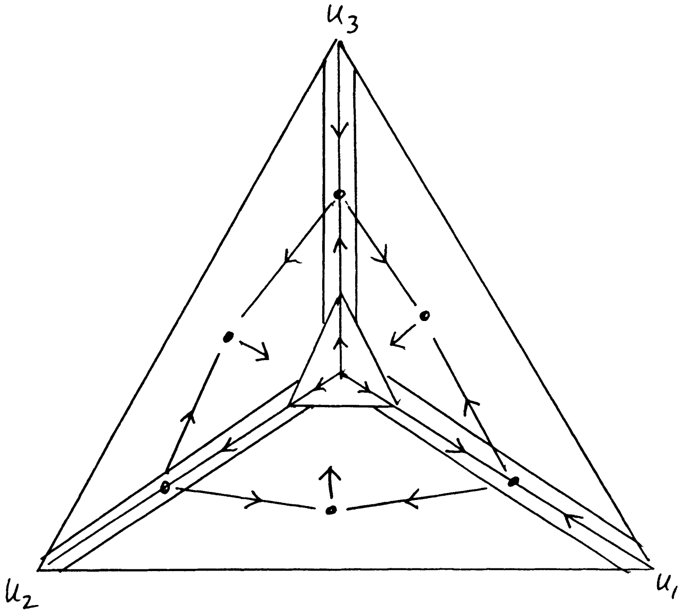


Figure 6.1.

Proof. See Figure 6.1 for a picture. Since $1 \succ 0$, $2 \succ 0$, and $3 \succ 0$ we can pick positive η_0 and ν_0, so that $h_0 = \log^-((u_1+u_2+u_3)/4\eta_0)$ has

$$dh_0/dt \le -\nu_0 \quad \text{when } 0 \le (u_1+u_2+u_3) < 4\eta_0 \tag{6.7}$$

From the corner we move to the

Edges $\Gamma^0_{j,k}$. Let $\sigma_i = r_i/a_{ii}$ be the equilibrium density of type i in the absence of competitors, and let $g_i(u) = u - \sigma_i \log u$. Each σ_i is an attracting fixed point, so (a) of Proposition 1.1 is satisfied. Let $z_i = u_j + u_k$ where $j < k$ are the elements of $\{1,2,3\} - \{i\}$. Since $j \succ i$ and $k \succ i$, (b) holds. Applying Proposition 1.1, with $\epsilon_i \le \eta_0$, we see that if $\theta_i \le 1$, λ_i, $\eta_i \le \eta_{i-1}$, $\nu_i \le \nu_{i-1}$, and B_i are chosen appropriately for $i = 1,2,3$ and $\psi_i(u) = (\epsilon_i - u)^{+2}$ then

$$h_i(u) = g_i(u_i + \theta_i\psi_i(u_i)z_i) - \lambda_i \log z_i$$

has (i) $dh_i/dt \le -\nu_i$ when $u_i \ge \epsilon_i$ and $0 < z_i \le \eta_i$ and (ii) $dh_i/dt \le B_i$ when $0 \le u_i \le \epsilon_i$ and $0 < z_i \le \eta_i$. If we pick M_i large enough then the function $\bar{h}_i = h_i \wedge M_i$ is only nontrivial when $0 < z_i \le \eta_i$. If we take $\bar{\eta}_3 < \eta_3$ small enough then we will have $h_i > M_i$ when $0 < z_i \le \bar{\eta}_3$. Region (ii) is not a problem because of (6.7), so if we pick $K_1 \ge 1$ large then

$$\frac{dK_1h_0 + \bar{h}_1 + \bar{h}_2 + \bar{h}_3}{dt} \le -\nu_3 \tag{6.8}$$

when $0 < z_i \le \bar{\eta}_3$ for some $1 \le i \le 3$. In words, $j_1 = K_1h_0 + \bar{h}_1 + \bar{h}_2 + \bar{h}_3$ is a repelling function for $Y = \Gamma^0_{2,3} \cup \Gamma^0_{1,3} \cup \Gamma^0_{1,2}$. We can now add the Lyapunov functions for the

Faces Γ^0_i. Here we have competitive systems that fall into Case 2 of Section 5, so Lemma 5.1 implies the existence of a Lyapunov function f_i that satisfies (a), (d), and (e) of Proposition 4.1. The condition $i \succ j,k$ implies that (b) holds. Applying Proposition 4.1, with $\epsilon \le \bar{\eta}_3$, we see that if $\theta_{3+i} \le 1$, λ_{3+i}, $\eta_{3+i} \le \eta_{2+i}$, $\nu_{3+i} \le \nu_{2+i}$, and B_{3+i} are chosen appropriately for $i = 1,2,3$ then

$$h_{3+i}(u) = f_i(u_j + \theta_{3+i}u_i, u_k + \theta_{3+i}u_3) - \lambda_{3+i}\log z_i$$

has (i) $dh_{3+i}/dt \le -\nu_{3+i}$ when $u_j \wedge u_k \ge \epsilon$ and $0 < u_i \le \eta_{3+i}$ and (ii) $dh_{3+i}/dt \le B_{3+i}$ when $0 \le u_j \wedge u_k \le \epsilon$ and $0 < u_i \le \eta_{3+i}$. If we pick M_{3+i} large enough then the function $\bar{h}_{3+i} = h_{3+i} \wedge M_{3+i}$ is only nontrivial when $0 < u_i \le \eta_{3+i}$. Region (ii) is not a problem because of (6.8). Thus if we pick $K_2 \ge 1$ large then $K_2 j_1 + h_4 + h_5 + h_6$ is a repelling function for Γ^0 and the proof of Theorem 6.1 is complete. $\square$

Concrete Example. To show that it is possible to satisfy all of the conditions in Theorem 2.1, we consider the following numerical example:

$$\begin{aligned} du_1/dt &= u_1\{1 - 8u_1 - 2u_2 - 2u_3\} \\ du_2/dt &= u_2\{1 - 2u_1 - 8u_2 - 2u_3\} \\ du_3/dt &= u_3\{1 - 2u_1 - 2u_2 - 8u_3\} \end{aligned}$$

which corresponds to the system with $\beta_i = 2$, $\delta_i = 1$, $\gamma_{ii} = 6$, the other γ_{ij} and β_{ij} are equal to 0. In this case, $\sigma_i = 1/8$ so $r_i - a_{ij}\sigma_j = 3/4 > 0$ and $i \succ j$. When $u_k = 0$ the boundary equilibrium, is $\sigma_i^k = \sigma_j^k = 1/10$. To check $k \succ i, j$, we note that $r_k - a_{ki}\sigma_i^k - a_{kj}\sigma_j^k = 1 - 4/10 > 0$ $\square$

It is natural to ask if all three species can coexist when some pair cannot. There are six invadability conditions in (b) of Theorem 2.1. We will break things down according to the number of these conditions that fail, starting with the situation in which there is only one. The reader who tires of the large number of cases can skip ahead to Section 7 where we consider three-species predator-prey examples.

ONE. Without loss of generality we can suppose that $3 \not\succ 2$. In this case Lemma 5.2 implies that $2 \gg 3$ where

(6.9) **Definition 7.** $2 \gg 3$ *means there is a convex Lyapunov function on the face* Γ_1^0 *that is decreasing whenever* $u_2 > 0$.

Note that in general (a) $2 \gg 3$ is stronger than the pair of conditions (b) $2 \succ 3$ and $3 \not\succ 2$, however, our calculations in Section 5 show that for Lotka-Volterra systems (a) and (b) are equivalent.

Theorem 6.2. *Suppose that* (*a*) $1 \succ 0$, $2 \succ 0$, $3 \succ 0$,

(*b*) $2 \succ 1$, $1 \succ 2$, $3 \succ 1$, $1 \succ 3$, $2 \gg 3$

(*c*) $3 \succ 1, 2$, *and* $2 \succ 1, 3$.

Then there is coexistence in the three species linear competition model with fast stirring.

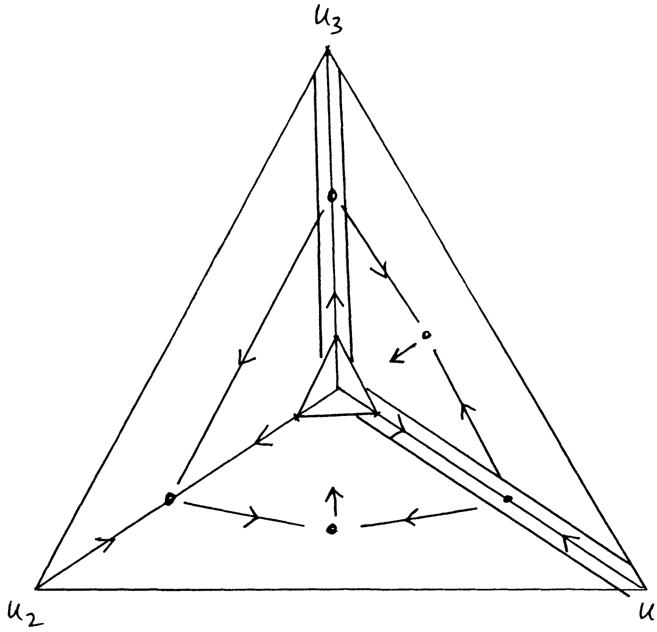


Figure 6.2

Proof. Again we start at the corner and work our way out. See Figure 6.2. The structure of the proof is dictated by our greedy algorithm: at each step we extend the domain of our repelling function by as much as possible. Schematically the proof is

$$\{(0,0,0)\} \to \Gamma^0_{2,3} \cup \Gamma^0_{1,2} \to \Gamma^0_1 \cup \Gamma^0_2 \to \Gamma^0$$

Since $1 \succ 0$, $2 \succ 0$, and $3 \succ 0$ we can pick positive η_0 and ν_0, so that $h_0 = \log^-((u_1 + u_2 + u_3)/4\eta_0)$ has

$$dh_0/dt \le -\nu_0 \quad \text{when } 0 \le (u_1 + u_2 + u_3) < 4\eta_0 \tag{6.10}$$

From the corner we move to the

Edges $\Gamma^0_{2,3}$ *and* $\Gamma^0_{1,2}$. We must leave out $\Gamma^0_{1,3}$ since $3 \not\succ 2$. Let $\sigma_i = r_i/a_{ii}$ be the equilibrium density of type i in the absence of competitors, and let $g_i(u) = u - \sigma_i \log u$. Each σ_i is an attracting fixed point, so (a) of Proposition 1.1 is satisfied. Let $z_i = u_j + u_k$ where $j < k$ are the elements of $\{1,2,3\} - \{i\}$. When $i = 1$ and $i = 3$

(but not when $i = 2$), we have $j \succ i$ and $k \succ i$, so (b) holds. Applying Proposition 1.1, with $\epsilon_1 \leq \eta_0$, we see that if $\theta_1 \leq 1$, λ_1, $\eta_1 \leq \epsilon$, $\nu_1 \leq \nu_0$, and B_1 are chosen appropriately and $\psi_1(u) = (\epsilon_1 - u)^{+2}$ then

$$h_1(u) = g_1(u_1 + \theta_1\psi_1(u_1)z_1) - \lambda_1 \log z_1$$

has (i) $dh_1/dt \leq -\nu_1$ when $u_1 \geq \epsilon_1$ and $0 < z_1 \leq \eta_i$ and (ii) $dh_1/dt \leq B_1$ when $0 \leq u_1 \leq \epsilon_1$ and $0 < z_1 \leq \eta_1$. If we pick M_1 large enough then the function $\bar{h}_1 = h_1 \wedge M_1$ is only nontrivial when $0 < z_1 \leq \eta_1$. If we take $\bar{\eta}_1 < \eta_1$ then we will have $h_1 > M_1$ when $0 < z_1 \leq \bar{\eta}_1$.

Applying Proposition 1.1 again, with $\epsilon_2 \leq \bar{\eta}_1$, we see that if $\theta_2 \leq 1$, λ_2, $\eta_2 \leq \epsilon$, $\nu_2 \leq \nu_1$, and B_2 are chosen appropriately and $\psi_2(u) = (\epsilon_2 - u)^{+2}$then

$$h_2(u) = g_3(u_3 + \theta_2\psi_2(u_3)z_3) - \lambda_2 \log z_3$$

has (i) $dh_2/dt \leq -\nu_2$ when $u_3 \geq \epsilon_2$ and $0 < z_3 \leq \eta_2$ and (ii) $dh_2/dt \leq B_3$ when $0 \leq u_3 \leq \epsilon_2$ and $0 < z_3 \leq \eta_2$. If we pick M_2 large enough then the function $\bar{h}_2 = h_2 \wedge M_2$ is only nontrivial when $0 < z_3 \leq \eta_2$. If we take $\bar{\eta}_2 < \eta_2$ then we will have $h_2 > M_2$ when $0 < z_3 \leq \bar{\eta}_2$. Region (ii) is not a problem in either case because of (6.10), so if we pick $K_1 \geq 1$ large then

$$\frac{dK_1h_0 + \bar{h}_1 + \bar{h}_2}{dt} \leq -\nu_2 \tag{6.11}$$

when $0 < z_1 \leq \bar{\eta}_2$ or $0 < z_3 \leq \bar{\eta}_2$. In words, $j_1 = K_1h_0 + \bar{h}_1 + \bar{h}_2$ is a repelling function for $\Gamma^0_{2,3} \cup \Gamma^0_{1,2}$. We are now ready to add

Faces Γ^0_2 *and* Γ^0_1. On the face Γ^0_2, the fixed point has both components positive, so Lemma 5.1 implies the existence of a Lyapunov function f_2 that satisfies (a), (d), and (e) of Proposition 4.1. The condition $2 \succ 1, 3$ implies that (b) holds. Applying Proposition 4.1, with $\epsilon \leq \bar{\eta}_2$, we see that if $\theta_3 \leq 1$, λ_3, $\eta_3 \leq \eta_2$, $\nu_3 \leq \nu_2$, and B_3 are chosen appropriately then

$$h_3(u) = f_2(u_1 + \theta_3u_2, u_3 + \theta_3u_2) - \lambda_3 \log u_2$$

has (i) $dh_3/dt \leq -\nu_3$ when $u_1 \wedge u_3 \geq \epsilon$ and $0 < u_2 \leq \eta_3$ and (ii) $dh_3/dt \leq B_3$ when $0 \leq u_1 \wedge u_3 \leq \epsilon$ and $0 < u_2 \leq \eta_3$. Region (ii) is not a problem because of (6.11). If we pick M_3 large enough then the function $\bar{h}_3 = h_3 \wedge M_3$ is only nontrivial when $0 < u_2 \leq \eta_3$. If we take $\bar{\eta}_3 < \eta_3$ then we will have $h_3 > M_3$ when $0 < u_2 \leq \bar{\eta}_3$.

On the face Γ_1^0, the fixed point has $\sigma_2^1 > 0$ and $\sigma_3^1 = 0$, so Lemma 5.2 implies the existence of a Lyapunov function f_1 that satisfies (a), (d), and (e) of Proposition 4.2. The condition $1 \succ 2$ implies that (b) holds. Applying Proposition 4.2, with $\epsilon \le \bar{\eta}_3$, we see that if $\theta_4 \le 1$, λ_4, $\eta_4 \le \epsilon$, $\nu_4 \le \nu_3$, and B_4 are chosen appropriately then

$$h_4(u) = f_1(u_2 + \theta_4 u_1, u_3 + \theta_4 u_1) - \lambda_4 \log u_1$$

has (i) $dh_4/dt \le -\nu_4$ when $u_2 \ge \epsilon$ and $0 < u_1 \le \eta_4$ and (ii) $dh_4/dt \le B_4$ when $0 \le u_2 \le \epsilon$ and $0 < u_1 \le \eta_4$. Region (ii) is not a problem because of (6.11). If we pick M_4 large enough then the function $\bar{h}_4 = h_4 \wedge M_4$ is only nontrivial when $0 < u_1 \le \eta_4$. If we take $\bar{\eta}_4 < \eta_4$ then we will have $h_4 > M_4$ when $0 < u_1 \le \bar{\eta}_4$. If we pick $K_2 \ge 1$ large then

$$\frac{dK_2 j_1 + \bar{h}_3 + \bar{h}_4}{dt} \le -\nu_4 \tag{6.12}$$

when $0 < u_2 \le \bar{\eta}_4$ or $0 < u_1 \le \bar{\eta}_4$. In words, $j_2 = K_2 j_1 + \bar{h}_3 + \bar{h}_4$ is a repelling function for $\Gamma_2^0 \cup \Gamma_1^0$. We are now ready to finish with the

Face Γ_3^0. Here, the fixed point has both components positive, so Lemma 5.1 implies the existence of a Lyapunov function f_3 that satisfies (a), (d), and (e) of Proposition 4.1. The condition $3 \succ 1, 2$ implies that (b) holds. Applying the Proposition 4.1, with $\epsilon \le \bar{\eta}_4$, we see that if $\theta_5 \le 1$, λ_5, $\eta_5 \le \epsilon$, $\nu_5 \le \nu_4$, and B_4 are chosen appropriately then

$$h_5(u) = f_3(u_1 + \theta_5 u_3, u_2 + \theta_5 u_3) - \lambda_5 \log u_3$$

has (i) $dh_5/dt \le -\nu_5$ when $u_1 \wedge u_2 \ge \epsilon$ and $0 < u_3 \le \eta_5$ and (ii) $dh_5/dt \le B_5$ when $0 \le u_1 \wedge u_2 \le \epsilon$ and $0 < u_3 \le \eta_5$. If we pick M_5 large enough then the function $\bar{h}_5 = h_5 \wedge M_3$ is only nontrivial when $0 < u_3 \le \eta_5$. It follows from (6.12) that if we pick $K_3 \ge 1$ large then $K_3 j_2 + h_5$ is a repelling function for Γ_0 and the proof of Theorem 6.2 is complete. □

Remark. Mimura and Fife (1986) considered a three species Lotka-Volterra system satisfying the conditions of Theorem 6.2 and showed that if the diffusion rates for the 2's and 3's are small then the reaction-diffusion equation has non-constant equilibrium state.

Tilman's (1994) Model. To illustrate that the situation in Theorem 6.2 can occur we will consider a special case of (6.1) that is of considerable interest in its own right. We set $\beta_{ij} = \beta_j$ if $i < j$, $\beta_{ij} = 0$ otherwise, and for simplicity take $\gamma_{ij} = 0$. The mean field ODE for the three species system is

$$\begin{aligned}
\frac{du_1}{dt} &= \beta_1 u_1(1-u_1) - \delta_1 u_1 \\
\frac{du_2}{dt} &= \beta_2 u_2(1-u_1-u_2) - \delta_2 u_2 - u_2\beta_1 u_1 \\
\frac{du_3}{dt} &= \beta_3 u_3(1-u_1-u_2-u_3) - \delta_3 u_3 - u_3(\beta_1 u_1 + \beta_2 u_2)
\end{aligned}$$

which has the Lotka-Volterra form with a lower-triangular matrix a_{ij}:

$$\begin{aligned}
\frac{du_1}{dt} &= u_1\{(\beta_1-\delta_1) - \beta_1 u_1\} \\
\frac{du_2}{dt} &= u_2\{(\beta_2-\delta_2) - (\beta_1+\beta_2)u_1 - \beta_2 u_2\} \\
\frac{du_3}{dt} &= u_3\{(\beta_3-\delta_3) - (\beta_1+\beta_3)u_1 - (\beta_2+\beta_3)u_2 - \beta_3 u_3\}
\end{aligned} \tag{6.13}$$

It is clear that $1 \succ 0$ (and $1 \succ 2$ and $1 \succ 3$) if $\beta_1 > \delta_1$. Letting $\sigma_i = (\beta_i - \delta_i)/\beta_i$ we will have $2 \succ 1$ if

$$\beta_2 - \delta_2 - (\beta_1 + \beta_2)\sigma_1 > 0$$

and in this case there will be an equilibrium with

$$\sigma_1^3 = \sigma_1 \qquad \sigma_2^3 = \frac{\beta_2 - \delta_2 - (\beta_1+\beta_2)\sigma_1}{\beta_2}$$

We will have $3 \succ 1,2$ if $\beta_3 - \delta_3 - (\beta_1+\beta_3)\sigma_1^3 - (\beta_2+\beta_3)\sigma_2^3 > 0$. In contrast we have $3 \succ 2$ if

$$\beta_3 - \delta_3 - (\beta_2 + \beta_3)\sigma_2 > 0$$

To give a numerical example we set $\beta_i = 1$ for all i. In this case $\sigma_i = 1 - \delta_i$ and $\sigma_2^3 = \sigma_2 - 2\sigma_1$ so the invadability conditions are

$1 \succ 0$	$\sigma_1 > 0$
$2 \succ 1$	$\sigma_2 > 2\sigma_1$
$3 \succ 1,2$	$\sigma_3 > 2\sigma_1 + 2(\sigma_2 - 2\sigma_1) = 2(\sigma_2 - \sigma_1)$
$3 \succ 2$	$\sigma_3 > 2\sigma_2$

It should be clear from this that in the special case $\beta_i \equiv 1$, $3 \succ 2$ implies $3 \succ 1,2$ but not conversely. To better understand the invadability conditions $2 \succ 1$ and $3 \succ 1,2$, we consider $\delta_3 < \delta_2 < \delta_1$ as points in $(0,1)$ and rewrite the two desired conditions as

$$(6.14) \qquad \delta_2 < \delta_1 - \sigma_1 \qquad \delta_3 < \delta_2 - (\sigma_2 - 2\sigma_1)$$

In words, species 1 casts a shadow of length equal to its frequency in equilibrium $\rho_1 = \sigma_1$, where species 2 is not allowed to fall. Similarly, species 2 casts a shadow of length equal to its frequency in equilibrium $\rho_2 = \sigma_2 - 2\sigma_1$ where species 3 is not allowed to fall. This observation leads to a simple algorithm for computing the equilibrium. Start with your pen at (1,0). Go to the left and up at a 45 degree angle until you reach the first species at δ_1. The height on the y axis (in this case $1-\delta_1$) is its equilibrium density. Continue to the left but now down at a 45 degree angle until you hit x axis. Any species passed over in the phase will have density 0 in equilibrium. Now go up at a 45 degree angle until you hit the next species and repeat the procedure. For more about this procedure, and properties that can be derived from it see May and Nowak (1994). Having determined the conditions for a positive equilibrium to exist, the rest is easy.

Theorem 6.3. *Consider the n species Tilman model. If there is a fixed point with all components positive then coexistence of all species occurs for fast stirring.*

Sketch of Proof. A convergence theorem for the mean field ODE for the Tilman model is trivial. Clearly, $u_1(t) \to \rho_1$. Once u_1 is close to ρ_1, du_2/dt is almost a function of u_2 alone and has an attracting fixed point at ρ_2, so $u_2(t) \to \rho_2$, etc. One way of proving the second conclusion is to let $g_i(u) = u - \rho_i \log u$ and to introduce the convex function $[g_2(u) - g_2(\rho_2) - \epsilon_2]^+$ which is decreasing along solutions when $u_1(t)$ is close enough to ρ_1. Using Proposition 1 on this function we can show that on a linearly growing set $u_2(t,x)$ is close to ρ_2. This observation and induction allows us to check the assumption $(\star)$ in Proposition 2 and the desired result follows. Details are given in Section 8. $\square$

TWO. Suppose now that two of the invadability conditions fail. There are several cases to consider. If we have $i \not\succ j$ and $j \not\succ i$ then we have two locally attracting equilibria on Γ_k^0 (where k is the remaining index $\neq i,j$) and our methods cannot work. Thus we can assume without loss of generality the index 1 appears in each of the failed conditions while 2 and 3 appear once. This gives us three possibilities:

(i) $1 \gg 2$, $1 \gg 3$. In this case the boundary equilibrium $(\sigma_1, 0, 0)$ is locally attracting so our methods fail and we expect the 1's to take over.

(ii) $2 \gg 1$, $1 \gg 3$. We will now show that coexistence is possible in this case.

Theorem 6.4. *Suppose that* (*a*) $1 \succ 0$, $2 \succ 0$, $3 \succ 0$,

(*b*) $2 \gg 1$, $1 \gg 3$, $3 \succ 2$, $2 \succ 3$, *and* (*c*) $1 \succ 2, 3$.

Then there is coexistence in the three species linear competition model with fast stirring.

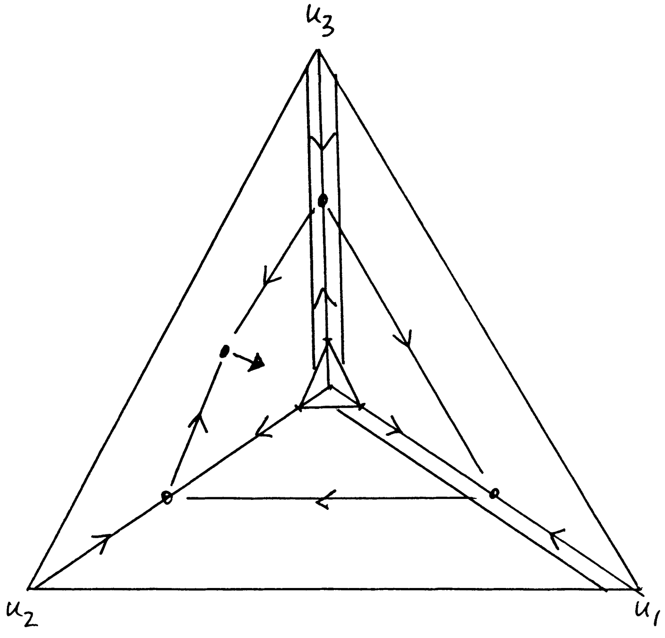


Figure 6.3

Proof of Theorem 6.4. We begin in the corner and work our way out. See Figure 6.3. The schematic of the proof is

$$\{(0,0,0)\} \to \Gamma^0_{1,2} \to \Gamma^0_2 \to \Gamma^0_2 \cup \Gamma^0_3 \to \Gamma^0$$

As in the two previous cases, since $1 \succ 0$, $2 \succ 0$ and $3 \succ 0$, we can pick positive η_0 and ν_0, so that $h_0 = \log^-((u_1 + u_2 + u_3)/4\eta_0)$ has

$$dh_0/dt \le -\nu_0 \quad \text{when } 0 \le (u_1 + u_2 + u_3) < 4\eta_0 \tag{6.15}$$

Edge $\Gamma^0_{1,2}$. This time there is only one edge with a nonsaddle point so we start with it. Let $\sigma_i = r_i/a_{ii}$ be the equilibrium density of type i in the absence of competitors, and let $g_i(u) = u - \sigma_i \log u$. Each σ_i is an attracting fixed point, so (a) of Proposition 1.1 is satisfied. Let $z_i = u_j + u_k$ where $j < k$ are the elements of $\{1, 2, 3\} - \{i\}$. When $i = 3$ (but not when $i = 1$ or $i = 2$), we have $j \succ i$ and $k \succ i$, so (b) holds. Applying Proposition 3.1, with $\epsilon_1 \le \eta_0$, we see that if $\theta_1 \le 1$, λ_1, $\eta_1 \le \epsilon_1$, $\nu_1 \le \nu_0$, and B_1 are chosen appropriately and $\psi_1(u) = (\epsilon_1 - u)^{+2}$ then

$$h_1(u) = g_1(u_3 + \theta_1\psi_1(u_3)z_3) - \lambda_1 \log z_3$$

has (i) $dh_1/dt \le -\nu_1$ when $u_1 \ge \epsilon_1$ and $0 < z_3 \le \eta_i$ and (ii) $dh_1/dt \le B_1$ when $0 \le u_1 \le \epsilon_1$ and $0 < z_3 \le \eta_1$. If we pick M_1 large enough then the function $\bar{h}_1 = h_1 \wedge M_1$ is only nontrivial when $0 < z_3 \le \eta_1$. If we take $\bar{\eta}_1 < \eta_1$ then we will have $h_1 > M_1$ when $0 < z_3 \le \bar{\eta}_1$. Region (ii) is not a problem because of (6.15), so if we pick $K_1 \ge 1$ large then

$$\frac{dK_1 h_0 + \bar{h}_1}{dt} \le -\nu_1 \tag{6.16}$$

when $0 < z_3 \le \bar{\eta}_1$. In words, $j_1 = K_1 h_0 + \bar{h}_1$ is a repelling function for the edge $\Gamma^0_{1,2}$. We are now ready to add the

Face Γ^0_2. Here the boundary fixed point has $\sigma^2_1 > 0$ and $\sigma^2_3 = 0$, so Lemma 5.2 implies the existence of a Lyapunov function f_1 that satisfies (a), (d), and (e) of Proposition 4.2. The condition $2 \succ 1$ implies that (b) holds. Applying Proposition 4.2, with $\epsilon \le \bar{\eta}_1$, we see that if $\theta_2 \le 1$, λ_2, $\eta_2 \le \epsilon$, $\nu_2 \le \nu_1$, and B_2 are chosen appropriately then

$$h_2(u) = f_2(u_1 + \theta_2 u_2, u_3 + \theta_2 u_2) - \lambda_2 \log u_2$$

has (i) $dh_2/dt \le -\nu_2$ when $u_1 \ge \epsilon$ and $0 < u_2 \le \eta_2$ and (ii) $dh_2/dt \le B_2$ when $0 \le u_1 \le \epsilon$ and $0 < u_2 \le \eta_2$. If we pick M_2 large enough then the function $\bar{h}_2 = h_2 \wedge M_2$ is only nontrivial when $0 < u_1 \le \eta_2$. If we take $\bar{\eta}_2 < \eta_2$ then we will have $h_2 > M_2$ when $0 < u_2 \le \bar{\eta}_2$.

Region (ii) is not a problem because of (6.16), so if we pick $K_2 \geq 1$ large then

$$\frac{dK_2 j_1 + \bar{h}_2}{dt} \leq -\nu_2 \tag{6.17}$$

when $0 < u_2 \leq \bar{\eta}_2$. In words, $j_2 = K_2 j_1 + \bar{h}_2$ is a repelling function for the face Γ_2^0. We are now ready to add the

Face Γ_3^0. Here the boundary fixed point has $\sigma_2^3 > 0$ and $\sigma_1^3 = 0$, so Lemma 5.2 implies the existence of a Lyapunov function f_3 that satisfies (a), (d), and (e) of Proposition 4.2. The condition $3 \succ 2$ implies that (b) holds. Applying Proposition 4.2, with $\epsilon \leq \bar{\eta}_2$, we see that if $\theta_3 \leq 1$, λ_3, $\eta_3 \leq \epsilon$, $\nu_3 \leq \nu_2$, and B_2 are chosen appropriately then

$$h_3(u) = f_3(u_1 + \theta_3 u_3, u_2 + \theta_3 u_3) - \lambda_3 \log u_3$$

has (i) $dh_3/dt \leq -\nu_3$ when $u_2 \geq \epsilon$ and $0 < u_3 \leq \eta_3$ and (ii) $dh_3/dt \leq B_3$ when $0 \leq u_2 \leq \epsilon$ and $0 < u_3 \leq \eta_3$. If we pick M_3 large enough then the function $\bar{h}_3 = h_3 \wedge M_3$ is only nontrivial when $0 < u_3 \leq \eta_3$. If we take $\bar{\eta}_3 < \eta_3$ then we will have $h_3 > M_3$ when $0 < u_3 \leq \bar{\eta}_3$. Region (ii) is not a problem because of (6.17), so if we pick $K_3 \geq 1$ large then

$$\frac{dK_3 j_2 + \bar{h}_3}{dt} \leq -\nu_3 \tag{6.18}$$

when $0 < u_3 \leq \bar{\eta}_3$ or $0 < u_2 \leq \bar{\eta}_3$. In words, $j_3 = K_3 j_2 + \bar{h}_3$ is a repelling function for two faces, $\Gamma_3^0 \cup \Gamma_2^0$. We are now ready to add the final

Face Γ_1^0. Here, the fixed point has both components positive, so Lemma 5.1 implies the existence of a Lyapunov function f_1 that satisfies (a), (d), and (e) of Proposition 4.1. The condition $1 \succ 2, 3$ implies that (b) holds. Applying Proposition 4.1, with $\epsilon \leq \bar{\eta}_3$, we see that if $\theta_4 \leq 1$, λ_4, $\eta_4 \leq \eta_3$, $\nu_4 \leq \nu_3$, and B_4 are chosen appropriately then

$$h_4(u) = f_1(u_2 + \theta_4 u_1, u_3 + \theta_4 u_1) - \lambda_4 \log u_1$$

has (i) $dh_4/dt \leq -\nu_4$ when $u_2 \wedge u_3 \geq \epsilon$ and $0 < u_1 \leq \eta_4$ and (ii) $dh_4/dt \leq B_4$ when $0 \leq u_2 \wedge u_3 \leq \epsilon$ and $0 < u_1 \leq \eta_4$. If we pick M_4 large enough then the function $\bar{h}_4 = h_4 \wedge M_4$ is only nontrivial when $0 < u_3 \leq \eta_4$. It follows from (6.17) that if we pick $K_4 \geq 1$ large then

$K_4 j_3 + \bar{h}_4$ is a repelling function for Γ_0 and the proof of Theorem 6.4 is complete. □

(iii) $2 \gg 1$, $3 \gg 1$. One can easily generalize the proof of Theorem 6.4 to get a coexistence result. Unfortunately, the conditions in the resulting theorem are mutually contradictory! The conditions $2 \gg 1$ and $3 \gg 1$ imply that the fixed points $(0, \sigma_2, 0)$ and $(0, 0, \sigma_3)$ are in $H_1^- = \{du_1/dt < 0\}$. If $2 \succ 3$ and $3 \succ 2$ then the fixed point $(0, \sigma_2^1, \sigma_3^1)$ will be above the line segment from $(0, \sigma_2, 0)$ to $(0, 0, \sigma_3)$ and hence lie in $H_1^- = \{du_1/dt < 0\}$. Thus we cannot have $1 \succ 2, 3$.

THREE. Finally, we have the case in which three of the invadability conditions fail. To avoid bistability on the faces exactly one of each pair $i \succ j$, $j \succ i$ must fail. Then to avoid one species dominating the other two we must have a cyclic relationship between competitors, which without loss of generality we can take to be $1 \ll 2 \ll 3 \ll 1$. Figure 6.4 shows that this case can happen. Unfortunately, each of the three fixed points on the edges is a saddle point, so we have no place to start our construction.

There is a good reason we cannot construct a Lyapunov function in general for this case. By results in Section 16.1 of Hofbauer and Sigmund (1998) if we write the mean field ODE as

$$\frac{du_i}{dt} = r_i u_i \left(1 - \sum_{j=1}^{3} c_{ij} u_j \right) \tag{6.19}$$

then the case under consideration corresponds to

$$c_{31} > c_{11} > c_{21} \quad c_{12} > c_{22} > c_{32} \quad c_{23} > c_{33} > c_{13}$$

The three boundary fixed points and their saddle connections, orbits having one saddle as α-limit set (time → $-\infty$) and one as ω-limit set (time → $+\infty$), form what is called a *heteroclinic cycle.* If we let

$$\alpha_i = \frac{c_{i-1,i}}{c_{ii}} > 1 > \frac{c_{i+1,i}}{c_{ii}} = \beta_i$$

where the arithmetic in the subscript is done modulo 3, then Theorem 16.1.1 in Hofbauer and Sigmund (1998) implies that the heteroclinic cycle is an attractor if

$$\prod_{i=1}^{3} (\alpha_i - 1) > \prod_{i=1}^{3} (1 - \beta_i) \tag{6.20}$$

while the system is persistent if $\det C > 0$ and

$$\prod_{i=1}^{3}(\alpha_i - 1) < \prod_{i=1}^{3}(1 - \beta_i) \tag{6.21}$$

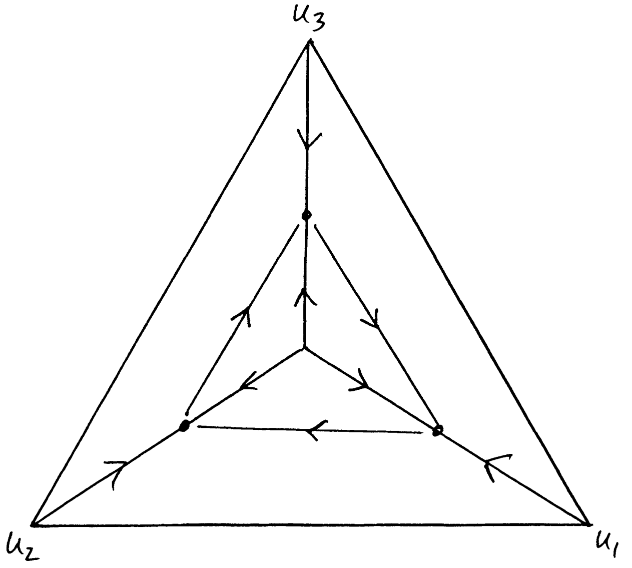


Figure 6.4

A concrete example of this situation occurs in Section 6 of Durrett and Levin (1998). They consider a competitive cycle in which $1 \gg 2 \gg 3 \gg 1$. In their model,

(a) Vacant sites become occupied by type i at rate f_i

(b) Occupied sites x at rate $\beta - 1$ attack a randomly chosen neighbor y.

(c) If y is occupied by the type which can be outcompeted by the one at x the individual at y is killed. It is replaced by the type at x with probability $(1 - \alpha)/(\beta - 1)$

The rather strange choice of constants is motivated by the fact that if this is done then the mean field ODE will be an equation studied by May and Leonard (1975).

$$\begin{aligned}\frac{dN_1}{dt} &= N_1\{1 - N_1 - \alpha N_2 - \beta N_3\} \\ \frac{dN_2}{dt} &= N_2\{1 - \beta N_1 - N_2 - \alpha N_3\} \\ \frac{dN_3}{dt} &= N_3\{1 - \alpha N_1 - \beta N_2 - N_3\}\end{aligned} \tag{6.22}$$

When $\alpha + \beta > 2$ and $\alpha < 1$, orbits of the ODE spiral outward to the hetroclinic cycle. See Figure 6 on page 39 in Durrett and Levin (1998).

7. Three species predator-prey models. In this section we consider three species Lotka-Volterra systems in which $a_{ij} < 0$ for some $i \neq j$.

Example 7.1. Two-prey, one-predator model. Following the set-up of Example 1 in the Introduction, we say that each site can be in a state $0 =$ vacant, $i = 1, 2$ to indicate sites occupied by prey species i, or 3 to indicate a predator. Letting f_i be the fraction of neighbors in state i, we can write the transition rates of the model as follows:

$0 \to 1$	$\beta_1 f_1$	$1 \to 0$	δ_1
$0 \to 2$	$\beta_2 f_2$	$2 \to 0$	δ_2
$1 \to 3$	$\beta_3 f_3$	$3 \to 0$	$\delta_3 + \gamma f_3$
$2 \to 3$	$\beta_4 f_3$		

In words, individuals of species i dies at rate δ_i; those of type $i = 1, 2$ give birth at rate β_i, successfully colonizing only vacant squares. Last but not least, prey sites are taken over by predators at rates that depend upon the species being attacked.

Results of Neuhauser (1992) show that if $\delta_1 = \delta_2$ and there is no predator then two species competing will in general lead to one type competitively excluding the other. In view of this, it is somewhat suprising that the presence of a predator can stabilize the competition of two prey species, leading to coexistence of all three species. One of the first experiments suggesting that this could occur was conducted by Paine (1966). He showed in a marine system that predator removal could lead to the extinction of previously coexisting species. Parrish and Saila (1970) conjectured and Cramer and May (1972) later proved the possibility of predator mediated coexistence in the ODE:

$$\begin{aligned}
\frac{dN_1}{dt} &= N_1\{\epsilon_1 - \alpha_{11}N_1 - \alpha_{12}N_2 - \alpha_{13}N_3\} \\
\frac{dN_2}{dt} &= N_2\{\epsilon_2 - \alpha_{21}N_1 - \alpha_{22}N_2 - \alpha_{23}N_3\} \\
\frac{dN_3}{dt} &= N_3\{-\epsilon_3 + \alpha_{31}N_1 + \alpha_{32}N_2\}
\end{aligned}$$

Further work on the ODE, see Vance (1978), Fujii (1978), Hsu (1981), Huston and Vickers (1983), Takeuchi and Adachi (1983), has led to a complete understanding of when two-prey and a predator can permanently coexist, that is,

$$\liminf_{t \to \infty} N_i(t) \geq \epsilon_i > 0$$

In a different direction, Caswell (1978) and Crowley (1979) considered metapopulation models, i.e., systems that consist of a large number of patches each of which is equally accessible to all the others. Mimura and Kan-on (1996) studied predator-mediated coexistence in reaction-diffusion equations and showed the existence of periodic and chaotic spatio-temporal structures in these models. Shah (1997) was the first to demonstrate predator-mediated coexistence could occur in a stochastic spatial model. In the terminology of this paper, he used a collection of repelling functions to confine the PDE in smaller and smaller regions of Γ, until he could conclude that the densities $u_i(t,x)$ in the PDE stay bounded away from 0 on a linearly growing set. Here, we show that his result can be proved with a single repelling function.

To begin our analysis, we note that the mean field ODE for this model is

$$\begin{aligned}\frac{du_1}{dt} &= \beta_1 u_1 u_0 - \delta_1 u_1 - \beta_3 u_1 u_3\\ \frac{du_2}{dt} &= \beta_2 u_2 u_0 - \delta_2 u_2 - \beta_4 u_2 u_3\\ \frac{du_3}{dt} &= \beta_3 u_1 u_3 + \beta_4 u_2 u_3 - \delta_3 (u_3 + \gamma u_3)\end{aligned}$$

which can be rearranged to give

$$\begin{aligned}\frac{du_1}{dt} &= u_1\{(\beta_1 - \delta_1) - \beta_1 u_1 - \beta_1 u_2 - (\beta_1 + \beta_3) u_3\}\\ \frac{du_2}{dt} &= u_2\{(\beta_2 - \delta_2) - \beta_2 u_1 - \beta_2 u_2 - (\beta_2 + \beta_4) u_3\}\\ \frac{du_3}{dt} &= u_3\{-\delta_3 + \beta_3 u_1 + \beta_4 u_2 - \gamma u_3\}\end{aligned} \tag{7.1.1}$$

To begin to analyze this system, we start with the behavior of each species in the absence of the others. If we suppose

$$\beta_1 > \delta_1 \tag{7.1.2}$$

and let $\sigma_1 = (\beta_1 - \delta_1)/\beta_1$ then on the edge Γ^0_{23}, $(\sigma_1, 0, 0)$ is an attracting fixed point. Similarly, if we suppose

$$\beta_2 > \delta_2 \tag{7.1.3}$$

and let $\sigma_2 = (\beta_2 - \delta_2)/\beta_2$ then on the edge Γ^0_{13}, $(0, \sigma_2, 0)$ is an attracting fixed point. To bring out the connection with the other conditions we will write the assumptions (7.1.2) and (7.1.3) in invadability notation using Definition 4 as $1 \succ 0$ and $2 \succ 0$ respectively. In the absence of prey

$$du_3/dt < 0 \quad \text{on } \Gamma_{12}^0 \tag{7.1.4}$$

a condition that using Definition 1 we write as $3 \downarrow 0$.

On the face Γ_3^0 we have a competition between two species so if we assume

$$\beta_1/\delta_1 > \beta_2/\delta_2 \tag{7.1.5}$$

then Lemma 5.2 implies there is a convex Lyapunov function which is decreasing whenever $u_3 = 0$ and $u_1 > 0$, a conclusion that we have defined in (6.9) as $1 \gg 2$. On the faces Γ_1^0 and Γ_2^0 the ODE is of the predator-prey type. From (7.1.3) we see that 1's and 3's can coexist if $3 \succ 1$ or

$$\frac{\beta_1 - \delta_1}{\beta_1} > \frac{\delta_3}{\beta_3} \tag{7.1.6}$$

and using (2.1.4) that in this case there is an attracting fixed point on the face Γ_2^0 with coordinates

$$\sigma_1^2 = \frac{\gamma(\beta_1 - \delta_1) + (\beta_1 + \beta_3)\delta_3}{\beta_1\gamma + \beta_3(\beta_1 + \beta_3)} \qquad \sigma_3^2 = \frac{-\beta_1\delta_3 + \beta_3(\beta_1 - \delta_1)}{\beta_1\gamma + \beta_3(\beta_1 + \beta_3)}$$

Similarly, we conclude that 2's and 3's can coexist if $3 \succ 2$ or

$$\frac{\beta_2 - \delta_2}{\beta_2} > \frac{\delta_3}{\beta_4} \tag{7.1.7}$$

and in this case there is an attracting fixed point on the face Γ_1^0 with coordinates

$$\sigma_2^1 = \frac{\gamma(\beta_2 - \delta_2) + (\beta_2 + \beta_4)\delta_3}{\beta_2\gamma + \beta_4(\beta_2 + \beta_4)} \qquad \sigma_3^1 = \frac{-\beta_2\delta_3 + \beta_4(\beta_2 - \delta_2)}{\beta_2\gamma + \beta_4(\beta_2 + \beta_4)}$$

From (7.1.1) we see that 2's can invade the 1,3 equilibrium (or $2 \succ 1, 3$) if

$$\beta_2 - \delta_2 - \beta_2\sigma_1^2 - (\beta_2 + \beta_4)\sigma_3^2 > 0 \tag{7.1.8}$$

while 1's can invade the 2,3 equilibrium (or $1 \succ 2,3$) if

$$\beta_1 - \delta_1 - \beta_1\sigma_2^1 - (\beta_1 + \beta_3)\sigma_3^1 > 0 \tag{7.1.9}$$

Theorem 7.1. *Suppose that (a)* $1 \succ 0$, $2 \succ 0$, $0 \succ 3$,

(b) $1 \gg 2$, $3 \succ 1$, $3 \succ 2$, *and (c)* $2 \succ 1,3$ *and* $1 \succ 2,3$.

Then coexistence occurs in the two-prey, one-predator model with fast stirring.

Remark. To be precise, the assumptions of the theorem are that (7.1.2)–(7.1.9) hold.

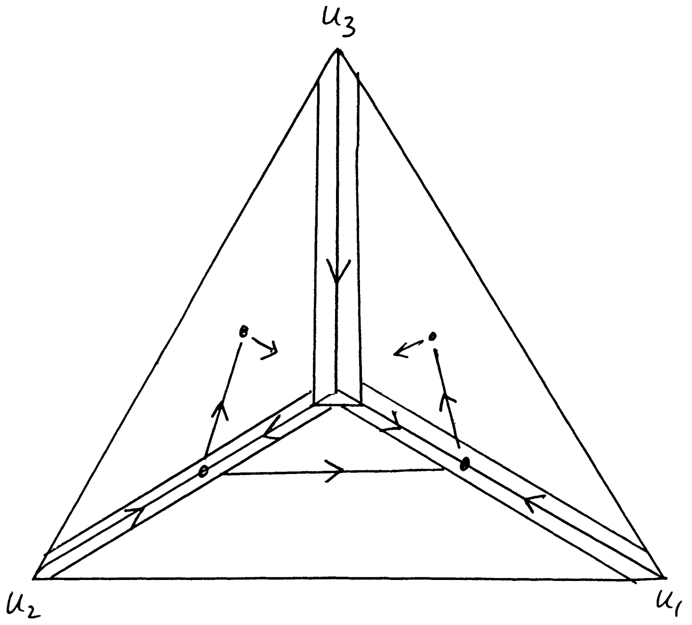


Figure 7.1

Sketch of Proof. See Figure 7.1. This time we cannot begin with the corner function so we instead let $z_3 = u_1 + u_2$ and

$$h_1 = \max\{u_3 - \lambda_1 \log z_3, M_1\}$$

Proposition 1.2 implies that if the parameters are chosen appropriately h_1 is a repelling function for the edge $\Gamma^0_{1,2}$. There is no exceptional set since the fixed point is at 0. The fixed point on $\Gamma^0_{2,3}$ is a saddle point so we ignore it and use Proposition 1.1 to extend to $\Gamma^0_{1,2} \cup \Gamma^0_{1,3}$. On the face Γ^0_3 we have $\sigma^3_1 > 0$, $\sigma^3_2 = 0$, so using Proposition 4.2, we can extend to $\Gamma^0_3 \cup \Gamma^0_{1,2}$. This covers the problem regions for the other two faces, so two uses of Porposition 4.1, gives a repelling function for Γ^0. □

Proof of Theorem 7.1. Following the outline just given, the first step is:

Edge $\Gamma^0_{1,2}$. In the absence of prey, the predators die out, so (a) of Proposition 1.2 holds. Let $z_3 = u_1 + u_2$. Since $1, 2 \succ 0$, (b) holds. Applying Proposition 1.2, we see that if λ_1, ν_1, and η_1 are chosen appropriately then $h_1(u) = u_3 - \lambda_1 \log z_3$ has

$$dh_1/dt \le -\nu_1 \quad \text{when } 0 < z_3 \le \eta_1 \tag{7.1.10}$$

If we pick M_1 large enough then the function $\bar{h}_1 = h_1 \wedge M_1$ is only nontrivial when $0 < z_3 \le \eta_1$. If we now take $\bar{\eta}_1 < \eta_1$ then we will have $h_1 > M_1$ when $0 < z_3 \le \bar{\eta}_1$.

Edge $\Gamma^0_{1,3}$. Let $\sigma_2 = (\beta_2 - \delta_2)/\beta_2$ be the equilibrium density of type 2 in the absence of competitors, and let $g_2(u_2) = u_2 - \sigma_2 \log u_2$. Since σ_2 is an attracting fixed point, (a) of Proposition 1.1 is satisfied. Let $z_2 = u_1 + u_3$. Since $1 \succ 2$ and $3 \succ 2$, (b) holds. Applying Proposition 1.1, with $\epsilon_2 \le \bar{\eta}_1$, we see that if $\theta_2 \le 1$, λ_2, $\eta_2 \le \epsilon$, $\nu_2 \le \nu_1$, and B_2 are chosen appropriately and $\psi(u) = (\epsilon_2 - u)^{+2}$ then

$$h_2(u) = g_2(u_2 + \theta_2 \psi_2(u_2) z_2) - \lambda_2 \log z_2$$

has (i) $dh_2/dt \le -\nu_2$ when $u_2 \ge \epsilon_2$ and $0 < z_2 \le \eta_2$ and (ii) $dh_2/dt \le B_2$ when $0 \le u_2 \le \epsilon_2$ and $0 < z_2 \le \eta_2$. If we pick M_2 large enough then the function $\bar{h}_2 = h_2 \wedge M_2$ is only nontrivial when $0 < z_2 \le \eta_2$. If we take $\bar{\eta}_2 < \eta_2$, then we will have $h_2 > M_2$ when $0 < z_2 \le \bar{\eta}_2$. Region (ii) is not a problem because of (7.1.10), so if we pick $K_1 \ge 1$ large then

$$\frac{d(K_1 \bar{h}_1 + \bar{h}_2)}{dt} \le -\nu_2 \tag{7.1.11}$$

when $0 < z_2 \le \eta_2$ or $0 < z_1 \le \eta_2$. In words, $j_1 = K_1 \bar{h}_1 + \bar{h}_2$ is a repelling function for two edges $\Gamma^0_{1,2} \cup \Gamma^0_{1,3}$. The arguments in this paragraph fail for the edge $\Gamma^0_{2,3}$, since $2 \not\succ 1$, so we turn now to the

Face Γ_3^0. Here the fixed point has $\sigma_1^3 > 0$ and $\sigma_2^3 = 0$, so Lemma 5.2 gives a Lyapunov function f_3 that satisfies (a), (d), and (e) of Proposition 4.2. The condition $3 \succ 1$ implies that (b) holds. Applying Proposition 4.2, with $\epsilon \le \bar\eta_2$, we see that if $\theta_3 \le 1$, λ_3, $\eta_3 \le \epsilon$, $\nu_3 \le \nu_2$, and B_3 are chosen appropriately then

$$h_3(u) = f_3(u_1 + \theta_3 u_3, u_2 + \theta_3 u_3) - \lambda_3 \log u_3$$

has (i) $dh_3/dt \le -\nu_3$ when $u_1 \ge \epsilon$ and $0 < u_3 \le \eta_3$ and (ii) $dh_3/dt \le B_3$ when $0 \le u_1 \le \epsilon$ and $0 < u_3 \le \eta_2$. If we pick M_3 large enough then the function $\bar h_3 = h_3 \wedge M_3$ is only nontrivial when $0 < u_3 \le \eta_3$. If we now take $\bar\eta_3 < \eta_3$ then we will have $h_3 > M_3$ when $0 < u_3 \le \bar\eta_3$. Region (ii) is not a problem because of (7.1.11), so if we pick $K_2 \ge 1$ large then

$$\frac{dK_2 j_1 + h_3}{dt} \le -\nu_3 \tag{7.1.12}$$

when $u_3 \le \eta_3$ or $z_3 \le \bar\eta_3$. In words, $j_2 = K_2 j_1 + h_2$ is a repelling function for a face and an edge: $\Gamma_3^0 \cup \Gamma_{1,2}^0$. We are now ready to add the Lyapunov functions on the

Faces Γ_1^0 *and* Γ_2^0. Here we have supercrtical predator-prey interactions, so Lemma 5.0 gives us Lyapunov functions f_1 and f_2 for these faces that satisfy (a), (d), and (e) of Proposition 4.1. The invadability conditions $2 \succ 1,3$ and $1 \succ 2,3$ imply that (b) holds. Applying Proposition 4.1 now, with $\epsilon \le \bar\eta_3$, we see that if $\theta_4 \le 1$, λ_4, $\eta_4 \le \epsilon$, $\nu_4 \le \nu_3$, and B_4 are chosen appropriately then

$$h_4(u) = f_1(u_2 + \theta_4 u_1, u_3 + \theta_4 u_1) - \lambda_4 \log u_1 \tag{7.1.13}$$

has (i) $dh_4/dt \le -\nu_4$ when $u_2 \wedge u_3 \ge \epsilon$ and $0 < u_1 \le \eta_4$ and (ii) $dh_4/dt \le B_4$ when $u_2 \wedge u_3 \le \epsilon$ and $0 < u_1 \le \eta_4$. If we pick M_4 large enough then the function $\bar h_4 = h_4 \wedge M_4$ is only nontrivial when $0 < u_1 \le \eta_4$. Another application of Proposition 4.1, gives a function

$$h_5(u) = f_2(u_1 + \theta_5 u_2, u_3 + \theta_5 u_2) - \lambda_5 \log u_2 \tag{7.1.14}$$

has (i) $dh_5/dt \le -\nu_5$ when $u_2 \wedge u_3 \ge \epsilon$ and $0 < u_1 \le \eta_4$ and (ii) $dh_5/dt \le B_5$ when $u_1 \wedge u_3 \le \epsilon$ and $0 < u_2 \le \eta_5$. If we pick M_5 large enough then the function $\bar h_5 = h_5 \wedge M_5$ is only nontrivial when $0 < u_2 \le \eta_5$. Combining (7.1.12)–(7.1.14), we see that if K_3 is chosen large enough then $K_3 j_2 + \bar{h}_4 + \bar{h}_5$ is a repelling function for Γ_0 and the proof of Theorem 7.1 is complete. □

Concrete Example. To get a feel for what the conditions in Theorem 7.1 mean and to demonstrate that they can all hold simultaneously, we will investigate what happens when we take $\gamma = 0$ to simplify the formulas, fix $\delta_1 = \delta_2 = 1$, assign values to δ_3, and to $\beta_3 < \beta_4$, then look at the behavior as a function of the birth rates β_1 and β_2. Letting $D = 1 - \delta_3/\beta_4$, $F = 1 - \delta_3/\beta_3$, we can write the conditions in (7.1.8) and (7.1.9) as

$$\begin{gathered}(\beta_1 + \beta_3)(F\beta_2 - 1) - (\beta_2 + \beta_4)(F\beta_1 - 1) > 0 \\ (\beta_2 + \beta_4)(D\beta_1 - 1) - (\beta_1 + \beta_3)(D\beta_2 - 1) > 0\end{gathered}$$

Expanding out and canceling $\pm F\beta_1\beta_2$ in the first line and $\pm D\beta_1\beta_2$ in the second we have two linear inequalities

$$\begin{aligned}-(F\beta_4 + 1)\beta_1 + (F\beta_3 + 1)\beta_2 &> \beta_3 - \beta_4 \\ (D\beta_4 + 1)\beta_1 - (D\beta_3 + 1)\beta_2 &> \beta_4 - \beta_3\end{aligned}$$

Rearranging these equations leads to

$$\begin{aligned}\beta_2 &> \frac{\beta_4 F + 1}{\beta_3 F + 1} \cdot \beta_1 + \frac{\beta_3 - \beta_4}{\beta_3 F + 1} \\ \beta_2 &< \frac{\beta_4 D + 1}{\beta_3 D + 1} \cdot \beta_1 + \frac{\beta_3 - \beta_4}{\beta_3 D + 1}\end{aligned} \tag{7.1.15}$$

At this point the reader may be wondering: How do these conditions compare to the existence of a fixed point with all coordinates positive? Some tedious algebra left as an exercise for the reader shows that yet again the invadability conditions in (7.1.15) are equivalent to the existence of a fixed point with all components positive. Half of this is a general result. Theorem 5.2.1 of Hofbauer and Sigmund (1998) shows that for a Lotka-Volterra system, the interior of $\mathbf{R}_n^+$ contains α or ω limit points if and only if the system has an interior fixed point. The invadability condition gives a nontrivial ω-limit set by Proposition 0, so there must be a fixed point. We know of no general result in the other direction, but we have been able to check this equivalence algebraically in most of our examples.

The existence of an interior fixed point does not mean that it will be attracting. See Figure 7.2 for an example due to Gilpin (1975):

$r_1 = r_2 = 1$, $r_3 = -1$,

$$a_{ij} = \begin{pmatrix} .001 & .001 & .01 \\ .0015 & .001 & .001 \\ -.005 & -.0005 & 0 \end{pmatrix}$$

One does not have to be be this extreme with the matrix a_{ij}. According to Exercise 16.2.9 of Hofbauer and Sigmund (1998), we will also get chaos if we multiply a_{ij} by 1000 (which is the same as suitably changing time and units of measurement of u_i) and then change a_{33} to .01 (to be 100% sure that the 3's remain bounded).

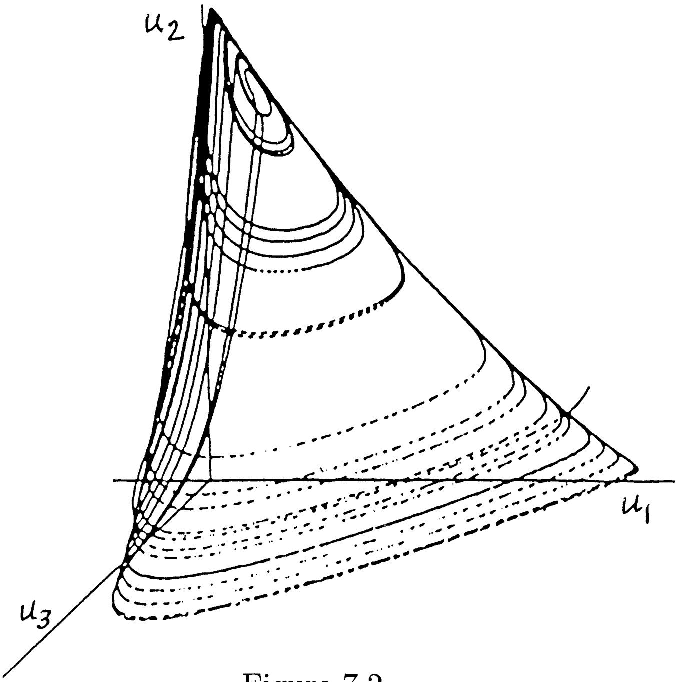


Figure 7.2

To have a numerical example to plug into (7.1.15) we set $\beta_3 = 3$, $\beta_4 = 2$, $\delta_1 = \delta_2 = \delta_3 = 1$, in which case $D = 1 - 1/2 = 1/2$, $F = 1 - 1/3 = 2/3$ and the equations say

$$\frac{7}{9}\beta_1 + \frac{1}{3} < \beta_2 < \frac{4}{5}\beta_1 + \frac{2}{5} \tag{7.1.16}$$

Keeping in mind the fact that we have imposed the condition $\beta_1 > \beta_2$ and noting that

(i) the lower bound in (7.1.16) is β_1 when $(2/9)\beta_1 = 1/3$ or $\beta_1 = 3/2$,

(ii) the upper bound in (7.1.16) is β_1 when $(1/5)\beta_1 = 2/5$ or $\beta_2 = 2$.

(iii) the upper bound has slope .8 versus the .777... slope of the lower bound.

it follows that the region in (7.1.16) is an infinite three sided polygonal region, the interior of which we will call $\mathcal{C}$ for coexistence region. See Figure 7.3.

To apply Theorem 7.1 and conclude coexistence we must also have (7.1.6) and (7.1.7), which in the current notation would be written as

$$\beta_1 > 1/F = 3/2, \qquad \beta_2 > 1/D = 2$$

It is interesting here that each of the corresponding constraint lines goes through one of the corners of the polygon $\mathcal{C}$. To prove that this always happens we note that taking $\beta_1 = 1/F$ in the first equation of (7.1.15) gives a lower bound of $1/F$ while taking $\beta_2 = 1/D$ in the second gives an upper bound of $1/D$.

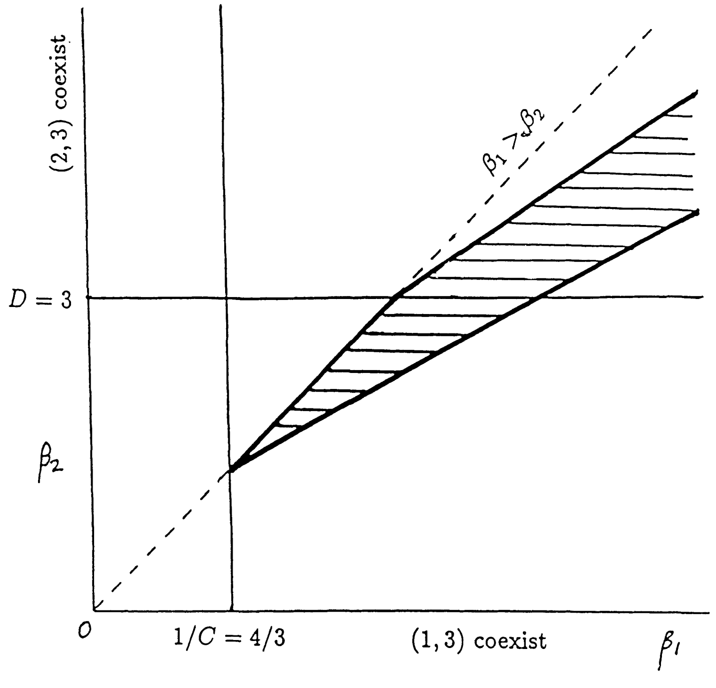


Figure 7.3

When $\beta_3 > \beta_4$, $1/F < 1/D$, so Theorem 7.1 applies only to the parameter values in $\mathcal{C} \cap \{\beta_2 > 1/D\}$. When $\beta_2 \le 1/D$, the second prey species is not nutritious enough to sustain the predator by itself but this does not rule out the possibility of the three species coexisting. Based on the existence of a fixed point, one might conjecture that there is coexistence in $\mathcal{C} \cap \{\beta_2 \le 1/D\}$. To do this when $\beta_2 < 1/D$, we return to the general set-up at the beginning of the example and note that if $3 \succ 1$ and $2 \succ 1,3$ then the fixed point $(\sigma_1^2, 0, \sigma_3^2)$ exists and 2's can invade it. When $3 \succ 2$ fails the predator-prey system on the face Γ_1^0 only has the boundary equilibrium

$$\sigma_2^2 = \frac{\beta_2 - \delta_2}{\beta_2} \qquad \sigma_3^2 = 0$$

We have assumed that $\beta_1/\delta_1 > \beta_2/\delta_2$ so in the plane Γ_0^3, $(0, \sigma_2^2, 0)$ is unstable, i.e., 1's can invade this degenerate 1,3 equilibrium. Combining the conditions and writing $3 \not\succ 2$ for

$$\frac{\beta_2 - \delta_2}{\beta_2} < \frac{\delta_3}{\beta_4} \tag{7.1.17}$$

we can state our result as

Theorem 7.2. *Suppose (a)* $1 \succ 0$, $2 \succ 0$, $0 \succ 3$,

(b) $1 \gg 2$, $3 \succ 1$, $3 \not\succ 2$ *and (c)* $2 \succ 1, 3$.

Then with fast stirring there is coexistence in the two-prey, one-predator model.

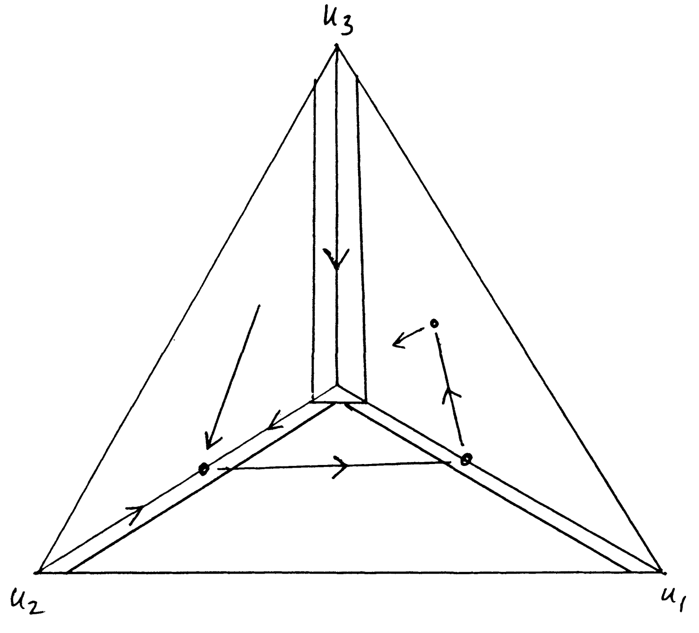


Figure 7.4

Sketch of Proof. See Figure 7.4. As in the previous result, we let $z_3 = u_1 + u_2$ and

$$h_1 = \max\{u_3 - \lambda_1 \log z_3, M_1\}$$

which is a repelling function for Γ^0_{12}. On the face Γ^0_2 the fixed point has $\sigma^2_2 > 0$ and $\sigma^2_3 = 0$, so Proposition 4.2 allows us to extend to Γ^0_1. On the face Γ^0_3 the fixed point has $\sigma^3_1 > 0$ and $\sigma^3_2 = 0$, so another use of Proposition 4.2 extends to $\Gamma^0_1 \cup \Gamma^0_3$. This covers the problem region for the face Γ^0_2, so using Proposition 4.1 now gives a repelling function for Γ^0. □

Proof of Theorem 7.2. The first step, as in the proof of Theorem 7.1, is the

Edge $\Gamma^0_{1,2}$. If λ_1, ν_1, and η_1 are chosen appropriately and $z_3 = u_1 + u_2$ then $h_1(u) = u_3 - \lambda_1 \log z_3$ has

$$dh_1/dt \le -\nu_1 \quad \text{for } 0 < z_3 \le \eta_1 \tag{7.1.18}$$

If we pick M_1 large enough then the function $\bar{h}_1 = h_1 \wedge M_1$ is only nontrivial when $0 < z_3 \le \eta_1$. If we take $\bar{\eta}_1 < \eta_1$ then we will have $h_1 > M_1$ when $0 < z_3 \le \bar{\eta}_1$. Since $3 \not\succ 2$, the next step in the proof is different from that of Theorem 7.1. This time we next look to the face where the predators cannot invade.

Face Γ^0_1. On this face, the ODE is a subcritical predator-prey system with a fixed point that has $\sigma^1_2 > 0$ and $\sigma^1_3 = 0$, so Lemma 5.3 gives a Lyapunov function f_1 that satisfies (a), (d), and (e) of Proposition 4.2. Since $1 \succ 2$, (b) holds. Applying Proposition 4.2, with $\epsilon \le \bar{\eta}_1$, we see that if $\theta_2 \le 1$, λ_2, $\eta_2 \le \epsilon$, $\nu_2 \le \nu_1$, and B_2 are chosen appropriately then

$$h_2(u) = f_1(u_2 + \theta_2 u_1, u_3 + \theta_2 u_1) - \lambda_2 \log u_1$$

has (i) $dh_2/dt \le -\nu_2$ when $u_2 \ge \epsilon$ and $0 < u_1 \le \eta_2$ and (ii) $dh_2/dt \le B_2$ when $0 \le u_2 \le \epsilon$ and $0 < u_1 \le \eta_2$. If we pick M_2 large enough then the function $\bar{h}_2 = h_2 \wedge M_2$ is only nontrivial when $0 < u_1 \le \eta_2$. If we take $\bar{\eta}_2 < \eta_2$ then we will have $h_2 > M_2$ when $0 < u_1 \le \bar{\eta}_2$. Region (ii) is not a problem because of (7.1.18). Thus, if we pick $K_1 \ge 1$ large then

$$\frac{d(K_1\bar{h}_1 + \bar{h}_2)}{dt} \le -\nu_2 \tag{7.1.19}$$

when $u_1 \le \epsilon$. In words $j_1 = K_1\bar{h}_1 + \bar{h}_2$ is a repelling function for the face Γ_1^0. We move on now to the

Face Γ_3^0. On this face, the fixed point has $\sigma_1^3 > 0$ and $\sigma_2^3 = 0$, so the ODE is in Case 3a of the linear competition model, and Lemma 5.2 gives a Lyapunov function f_3 that satisfies (a), (d), and (e) of Proposition 4.2. Since $3 \succ 1$, (b) holds. Applying Proposition 4.2, with $\epsilon \le \bar{\eta}_2$, we see that if $\theta_3 \le 1$, λ_3, $\eta_3 \le \epsilon$, $\nu_3 \le \nu_2$, and B_3 are chosen appropriately then

$$h_3(u) = f_3(u_1 + \theta_3 u_3, u_2 + \theta_3 u_3) - \lambda_3 \log u_3$$

has (i) $dh_3/dt \le -\nu_3$ when $u_1 \ge \epsilon$ and $0 < u_3 \le \eta_3$ and (ii) $dh_2/dt \le B_3$ when $0 \le u_1 \le \epsilon$ and $0 < u_3 \le \eta_3$. If we pick M_3 large enough then the function $\bar{h}_3 = h_3 \wedge M_3$ is only nontrivial when $0 < u_3 \le \eta_3$. If we take $\bar{\eta}_3 < \eta_3$ then we will have $h_3 > M_3$ when $0 < u_3 \le \bar{\eta}_3$. Region (ii) is not a problem because of (7.1.19). Thus, if we pick $K_2 \ge 1$ large then

$$\frac{dK_2 j_1 + \bar{h}_3}{dt} \le -\nu_3 \tag{7.1.20}$$

when $u_1 \le \eta_3$ or $u_3 \le \eta_3$. In words, $j_2 = K_2 j_1 + \bar{h}_3$ is a repelling function for two faces: $\Gamma_1^0 \cup \Gamma_3^0$. It remains to cover the

Face Γ_2^0. The first step is to note that on this face, the ODE is a supercritcal predator-prey model, so Lemma 5.0 gives a Lyapunov function f_2 that satisfies (a), (d), and (e) of Proposition 4.1. Since $2 \succ 1, 3$, (b) holds. Applying Proposition 4.1, with $\epsilon \le \eta_3$, we see that if $\theta_4 \le 1$, λ_4, $\eta_4 \le \epsilon$, $\nu_4 \le \nu_3$, and B_4 are chosen appropriately then

$$h_4(u) = f_2(u_1 + \theta_4 u_2, u_3 + \theta_4 u_2) - \lambda_4 \log u_2$$

has (i) $dh_4/dt \le -\nu_4$ when $u_1 \wedge u_3 \ge \epsilon$ and $0 < u_2 \le \eta_4$ and (ii) $dh_4/dt \le B_3$ when $0 \le u_1 \wedge u_3 \le \epsilon$ and $0 < u_2 \le \eta_4$. Region (ii) is not a problem because of (7.1.20). If we pick M_4 large enough then the function $\bar{h}_4 = h_4 \wedge M_4$ is only nontrivial when $0 < u_2 \le \eta_4$. Thus if we pick $K_3 \ge 1$ large then $K_3 j_2 + \bar{h}_4$ is a repelling function for Γ_0 and the proof of Theorem 7.2 is complete. □

Example 7.2. Three species food chain. As the name might suggest, in this system 0 = vacant, 1 = prey, 2 = a predator that feeds on 1's, while 3 = a predator that feeds on 2's. Using our traditional notation the rates may be written as follows:

$0 \to 1$	$\beta_1 f_1$	$1 \to 0$	δ_1
$1 \to 2$	$\beta_2 f_2$	$2 \to 0$	$\delta_2 + \gamma_2 f_2$
$2 \to 3$	$\beta_3 f_3$	$3 \to 0$	$\delta_3 + \gamma_3 f_3$

One can write the mean field ODE for this model as

$$\begin{aligned}
\frac{du_1}{dt} &= \beta_1 u_1 u_0 - \delta_1 u_1 - \beta_2 u_2 u_1 \\
\frac{du_2}{dt} &= \beta_2 u_2 u_1 - u_2(\delta_2 + \gamma_2 u_2) - \beta_3 u_2 u_3 \\
\frac{du_3}{dt} &= \beta_3 u_3 u_2 - u_3(\delta_3 + \gamma_3 u_3)
\end{aligned}$$

and rearrange to write the system in Lotka-Volterra form:

$$\begin{aligned}
\frac{du_1}{dt} &= u_1\{\beta_1 - \delta_1 - \beta_1 u_1 - (\beta_1 + \beta_2)u_2 - \beta_1 u_3\} \\
\frac{du_2}{dt} &= u_2\{-\delta_2 + \beta_2 u_1 - \gamma_2 u_2 - \beta_3 u_3\} \\
\frac{du_3}{dt} &= u_3\{-\delta_3 \qquad\qquad + \beta_3 u_2 - \gamma_3 u_3\}
\end{aligned} \tag{7.2.1}$$

To begin to analyze this system, we note that all species will die out unless

$$\beta_1 > \delta_1 \tag{7.2.2}$$

On the face Γ^0_3 the ODE is of the predator-prey type. From (2.1.7) we see that 1's and 2's can coexist if $2 \succ 1$ or

$$\frac{\beta_1 - \delta_1}{\beta_1} > \frac{\delta_2}{\beta_2} \tag{7.2.3}$$

and using (2.1.4) that in this case there is an attracting fixed point on the face Γ^3_0 with coordinates

(7.2.4)

$$\sigma_1^3 = \frac{\gamma_2(\beta_1 - \delta_1) + (\beta_1 + \beta_2)\delta_2}{\beta_1\gamma_2 + \beta_2(\beta_1 + \beta_2)} \qquad \sigma_2^3 = \frac{-\beta_1\delta_2 + \beta_2(\beta_1 - \delta_2)}{\beta_1\gamma_2 + \beta_2(\beta_1 + \beta_2)}$$

The next step is to ask if the 3's can invade the 1,2 equilibrium. This will occur if

$$\beta_3\sigma_2^3 - \delta_3 > 0 \quad \text{or} \quad \sigma_2^3 > \frac{\delta_3}{\beta_3} \tag{7.2.5}$$

Plugging (7.2.4) into (7.2.5), the condition becomes

$$\frac{-\beta_1\delta_2 + \beta_2(\beta_1 - \delta_1)}{\beta_1\gamma_2 + \beta_2(\beta_1 + \beta_2)} > \frac{\delta_3}{\beta_3} \tag{7.2.6}$$

Clearly this can hold only if $\beta_1 > \delta_1$, which is (7.2.2), and if $\beta_2(\beta_1 - \delta_1) > \beta_1\delta_2$, which implies (7.2.3). Though in this case (7.2.6) implies the other two conditions, we will write all three in the theorem in their invadability form.

Theorem 7.3. *Suppose* (*a*) $1 \succ 0$, $2 \downarrow 0$, $3 \downarrow 0$, (*b*) $2 \succ 1$, *and* (*c*) $3 \succ 1, 2$. *Then with fast stirring, coexistence occurs in the three species food chain.*

Remark. Here, $2 \downarrow 0$ and $3 \downarrow 0$ simply indicate that 2's and 3's are predators, while $1 \succ 0$, $2 \succ 1$, and $3 \succ 1, 2$ are our three conditions (7.2.2), (7.2.3), (7.2.6).

Sketch of proof. On the face Γ_1^0 the fixed point is at (0,0), so by Proposition 4.3, there is no exceptional set and we have a repelling function for Γ_1^0. On the face Γ_2^0 the fixed point has $\sigma_1^2 > 0$ and $\sigma_2^2 = 0$, so Proposition 4.2 allows us to extend to $\Gamma_1^0 \cup \Gamma_2^0$. This covers the problem region for the final extension, so Proposition 4.1 gives us a repelling function for Γ^0. □

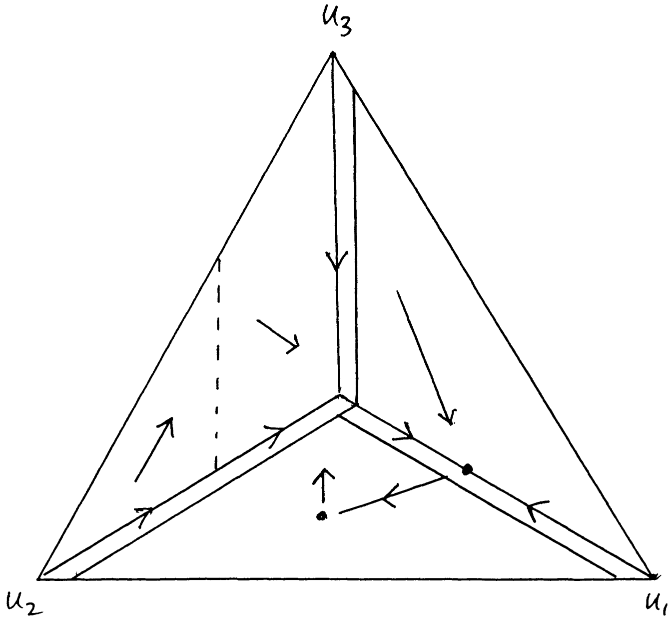


Figure 7.5

Proof of Theorem 7.3. Following the outline in the sketch, we begin with the

Face Γ_1^0. Here, we have a predator-prey system in which the prey die out, so Lemma 5.3 gives us a Lyapunov function f_1 which satisfies (a), (d), and (e) of Proposition 4.3. Since $1 \succ 0$, (b) holds. Using Proposition 4.3 now, we see that if constants θ_1, λ_1, η_1, ν_1, and B_1 are chosen correctly $h_1 = f_1(u_2 + \theta_1 u_1, u_3 + \theta_1 u_1) - \lambda_1 \log u_1$ has

$$dh_1/dt \le -\nu_1 < 0 \quad \text{when } 0 < u_1 \le \eta_1 \tag{7.2.7}$$

There is no exceptional set since the fixed point is at $(0,0)$. If we pick M_1 large enough then the function $\bar{h}_1 = h_1 \wedge M_1$ is only nontrivial when $0 < z_1 \le \eta_1$. If we take $\bar{\eta}_1 < \eta_1$ then we will have $h_1 > M_1$ when $0 < z_1 \le \bar{\eta}_1$. We move now to the

Face Γ_2^0. Here the ODE is a degenerate linear competition model with $\sigma_1^2 > 0$ and $\sigma_3^2 = 0$, so Lemma 5.2 gives us a Lyapunov function f_2 that satisfies (a), (d), and (e) of Proposition 4.2. The condition $2 \succ 1$ implies that (b) holds. Using Proposition 4.2 now with $\epsilon \le \bar{\eta}_1$, we see that if constants $\theta_2 \le 1$, λ_2, $\eta_2 \le \epsilon$, $\nu_2 \le \nu_1$, and B_2 are chosen correctly

$$h_2 = f_2(u_1 + \theta_2 u_2, u_3 + \theta_2 u_2) - \lambda_2 \log u_2$$

has (i) $dh_2/dt \le -\nu_2 < 0$ when $u_1 \ge \epsilon$, $0 < u_2 \le \eta_2$ and (ii) $dh_2/dt \le B_2$ when $0 \le u_1 \le \epsilon$, $0 < u_2 \le \eta_2$. If we pick M_2 large enough then the function $\bar{h}_2 = h_2 \wedge M_2$ is only nontrivial when $0 < u_2 \le \eta_2$. If we now take $\bar{\eta}_2 < \eta_2$ then we will have $h_2 > M_2$ when $0 < u_2 \le \bar{\eta}_2$. Region (ii) is not a problem because of (7.2.7). Thus if we pick $K_1 \ge 1$ large then

$$\frac{d(K_1 \bar{h}_1 + \bar{h}_2)}{dt} \le -\nu_2 \tag{7.2.8}$$

when $u_1 \le \bar{\eta}_2$ or $u_2 \le \bar{\eta}_2$. In words, $j_1 = K_1 \bar{h}_1 + \bar{h}_2$ is a repelling function for two faces: $\Gamma_1^0 \cup \Gamma_2^0$. We are now ready for the final

Face Γ_3^0. Here, the system is a supercritical predator-prey system, so Lemma 5.0 provides us with a Lyapunov function, f_3 which satisfies (a), (d), and (e) of Proposition 4.1. The condition $3 \succ 1, 2$ implies that (b) holds. Using Proposition 4.1 now with $\epsilon \le \bar{\eta}_2$, we see that if constants $\theta_3 \le 1$, λ_3, $\eta_3 \le \epsilon$, $\nu_3 \le \nu_2$, and B_3 are chosen correctly

$$h_3 = f_3(u_1 + \theta_3 u_3, u_2 + \theta_3 u_3) - \lambda_3 \log u_3$$

has (i) $dh_3/dt \le -\nu_3 < 0$ when $u_1 \wedge u_2 \ge \epsilon$, $0 < u_3 \le \eta_3$ and (ii) $dh_3/dt \le B_3$ when $0 \le u_1 \wedge u_2 \le \epsilon$, $0 < u_3 \le \eta_3$. If we pick M_3 large enough then the function $\bar{h}_3 = h_3 \wedge M_3$ is only nontrivial when $0 < u_3 \le \eta_3$. Region (ii) is not a problem because of (7.2.8). Thus if we pick $K_2 \ge 1$ large then $K_2 j_1 + \bar{h}_3$ defines a repelling function for Γ_0 completing the proof of Theorem 7.3. □

Remark. It would be interesting to be able to analyze the three species food chain with type 2 predators since Hastings and Powell (1991) have shown that in this case the ODE can be chaotic. However to do this with our methods, we would need a convex Lyapunov function for each face.

Continuing our fascination with the relationship between invadability conditions and the existence of an interior fixed point we note that if $\rho_3 = c$ then the third and second equations in (7.2.1) imply

$$\rho_2 = \frac{\gamma_3 c + \delta_3}{\beta_3} \qquad \rho_1 = \frac{1}{\beta_2}\{\gamma_2 \rho_2 + \beta_3 c + \delta_2\}$$

The ρ_i increase with c, so we will have $\beta_1\rho_1 + (\beta_1 + \beta_2)\rho_2 + \beta_1\rho_3 = \beta_1 - \delta_1$ for some $c > 0$ if and only if when we set $c = 0$

$$\beta_1 \cdot \frac{1}{\beta_2}\left\{\gamma_2 \frac{\delta_3}{\beta_3} + \delta_2\right\} + (\beta_1 + \beta_2)\frac{\delta_3}{\beta_3} < \beta_1 - \delta_1$$

Multiplying each side by β_2 and rearranging this becomes

$$[\beta_1\gamma_2 + \beta_2(\beta_1 + \beta_2)]\frac{\delta_3}{\beta_3} < -\beta_1\delta_2 + (\beta_1 - \delta_1)\beta_2 \tag{7.2.9}$$

which is clearly equivalent to to (7.2.6).

Remark. Hofbauer and Sigmund (1998) have considered a closely related ODE:

$$\begin{aligned} \frac{du_1}{dt} &= u_1\{q_1 - b_{11}u_1 - b_{12}u_2\} \\ \frac{du_2}{dt} &= u_2\{-q_2 + b_{21}u_1 - b_{22}u_2 - b_{23}u_3\} \\ \frac{du_3}{dt} &= u_3\{-q_3 + b_{32}u_2 - b_{33}u_3\} \end{aligned} \tag{7.2.10}$$

where we have departed from our usual notation to have all the $q_i > 0$ and $b_{ij} > 0$. As the reader will see in a moment, the absence of the $-b_{13}u_3$ term makes life considerably easier. Theorem 5.3.1 in Hofbauer and Sigmund (1998) shows that, in contrast to the chaotic two-prey one-predator example,

Theorem 7.4. *If* (7.2.10) *has an interior fixed point* ρ *then* ρ *is the limit from any starting point in* Γ^+.

Proof. If we pick c_i so that $c_1 a_{12} = c_2 a_{21}$ and $c_2 a_{23} = c_3 a_{32}$ then repeating the proof of Lemma 5.0 shows $\sum_i c_i(u_i - \rho_i \log u_i)$ is a convex Lyapunov function. We leave it to the reader to see if this reasoning can be extended to our case which has $a_{13} \neq 0$. See the proof of Lemma 5.1 for some tips about how to proceed. □

Having considered predator-prey systems of types 1–2, and 1–1–1, it is natural to also consider 2–1:

Example 7.3. Two-predator one-prey model. In this case we do not expect to be successful in getting coexistence. The *exclusion principle* states that if n populations depend linearly on m resources with $m < n$, then at least one of the populations will vanish. To be precise, we state

(7.3.1) *Suppose that for* $1 \le i \le n$

$$\frac{1}{u_i}\frac{du_i}{dt} = -\alpha_i + \sum_{j=1}^{m} b_{ij} R_j(u_1, \dots u_n)$$

and the $u_i(t)$ *stay bounded as* $t \to \infty$. *Then* $\lim_{t\to\infty} \inf_i u_i(t) = 0$.

Proof. This result is given on pages 47–48 of Hofbauer and Sigmund (1998). Since the proof is short and closely related to our methods we give it. Since $n > m$ there is a nontrival vector c so that $\sum_i c_i b_{ij} = 0$ for all j. Let $h(u) = \sum_i c_i \log u_i$. Calculus shows that

$$\frac{dh}{dt} = -\sum_i c_i \alpha_i \equiv -\alpha \tag{7.3.2}$$

We will only consider the generic case in which $\alpha \neq 0$. In this case we can suppose that $\alpha > 0$. Integrating (7.3.2) gives $h(u(t)) = h(u(0)) - \alpha t$ so

$$\prod_{i=1}^{n} u_i(t)^{c_i} = e^{h(u(0))} e^{-\alpha t} \to 0$$

as $t \to \infty$. By assumption we cannot have $\limsup u_i(t) = \infty$ so this must be caused by the convergence of $\inf_i u_i(t) \to 0$. $\square$

Despite the bad news in (7.3.1), we will proceed to formulate our two-predator, one prey model. Part of the reason for our perseverance is that our results will show that changing the death term $-\alpha_i$ in (7.3.1) to $-\alpha_i - \gamma_i u_i$ will allow coexistence to occur in some cases. The states of our model are $0 =$ vacant, $1 =$ sites occupied by prey, $2, 3 =$ predators 1 and 2. The transition rates of the model as follows:

$0 \to 1$	$\beta_1 f_1$	$1 \to 0$	δ_1
$1 \to 2$	$\beta_2 f_2$	$2 \to 0$	$\delta_2 + \gamma_{22} f_2 + \gamma_{23} f_3$
$1 \to 3$	$\beta_3 f_3$	$3 \to 0$	$\delta_3 + \gamma_{32} f_2 + \gamma_{33} f_3$

Remark. Even though formulated as a two-predator one-prey model, one can think of the intertidal region and rename the states $0 =$ bare rock, $1 =$ barnacles, and $2, 3 =$ occupancy by two different types of mussels, which need the presence of barnacles to be able to attach to the rock. In this interpretation, it would be natural to have rates δ_{21} and δ_{31} for $2 \to 1$ and $3 \to 1$. However, even without this generalization, the analogy suggests that we should be able to get coexistence of the two predators when the diagonal terms γ_{ii} are large.

The mean field ODE for our two-predator one-prey model is

$$\begin{aligned}
\frac{du_1}{dt} &= \beta_1 u_1 u_0 - \delta_1 u_1 - \beta_2 u_1 u_2 - \beta_3 u_1 u_3 \\
\frac{du_2}{dt} &= \beta_2 u_2 u_1 - u_2(\delta_2 + \gamma_{22} u_2 + \gamma_{23} u_3) \\
\frac{du_3}{dt} &= \beta_3 u_3 u_1 - u_3(\delta_3 + \gamma_{32} u_2 + \gamma_{33} u_3)
\end{aligned}$$

which has the Lotka-Volterra form

$$\begin{aligned}
\frac{du_1}{dt} &= u_1 \{\beta_1 - \delta_1 - \beta_1 u_1 - (\beta_1 + \beta_2) u_2 - (\beta_1 + \beta_2) u_3\} \\
\frac{du_2}{dt} &= u_2 \{-\delta_2 + \beta_2 u_1 - \gamma_{22} u_2 - \gamma_{23} u_3\} \qquad (7.3.3) \\
\frac{du_3}{dt} &= u_3 \{-\delta_3 + \beta_3 u_1 - \gamma_{32} u_2 - \gamma_{33} u_3\}
\end{aligned}$$

To begin to analyze this system we note that if the 1's die out then all the other species will as well, so we must have

$$\beta_1 > \delta_1 \qquad (7.3.4)$$

On the faces Γ_3^0 and Γ_2^0 the ODE is of the predator-prey type. From (2.1.7) we see that 1's and 2's can coexist if

$$\frac{\beta_1 - \delta_1}{\beta_1} > \frac{\delta_2}{\beta_2} \tag{7.3.5}$$

and using (2.1.4) that in this case there is an attracting fixed point with coordinates

$$\begin{aligned} \sigma_1^3 &= \frac{\gamma_{22}(\beta_1 - \delta_1) + (\beta_1 + \beta_2)\delta_2}{\gamma_{22}\beta_1 + (\beta_1 + \beta_2)\beta_2} \\ \sigma_2^3 &= \frac{-\beta_1\delta_2 + (\beta_1 - \delta_1)\beta_2}{\gamma_{22}\beta_1 + (\beta_1 + \beta_2)\beta_2} \end{aligned} \tag{7.3.6}$$

Replacing all of the subscript 2's by 3's in the last two formulas, we see that 1's and 2's can coexist if

$$\frac{\beta_1 - \delta_1}{\beta_1} > \frac{\delta_3}{\beta_3} \tag{7.3.7}$$

and in this case there is an attracting fixed point with coordinates

$$\begin{aligned} \sigma_1^2 &= \frac{\gamma_{33}(\beta_1 - \delta_1) + (\beta_1 + \beta_3)\delta_3}{\gamma_{33}\beta_1 + (\beta_1 + \beta_3)\beta_3} \\ \sigma_3^2 &= \frac{-\beta_1\delta_3 + (\beta_1 - \delta_1)\beta_3}{\gamma_{33}\beta_1 + (\beta_1 + \beta_3)\beta_3} \end{aligned} \tag{7.3.8}$$

Turning to the next level of competition, 3's can invade the 1,2 equilibrium if

$$-\delta_3 + \beta_3\sigma_1^3 - \gamma_{32}\sigma_2^3 > 0 \tag{7.3.9}$$

while 2's can invade the 1,3 equilibrium if

$$-\delta_2 + \beta_2\sigma_1^2 - \gamma_{23}\sigma_3^2 > 0 \tag{7.3.10}$$

In view of the result in (7.3.2) it is natural to ask if the conditions we have just introduced can all be satisfied simultaneously. To see that the answer is yes, consider the special case in which $\gamma_{23} = 0$ and $\gamma_{32} = 0$ then plug the equations for the densities given in (7.3.6) and (7.3.8) into the invadability conditions (7.3.9) and (7.3.10) to get

$$-\delta_3 + \beta_3 \cdot \frac{\gamma_{22}(\beta_1 - \delta_1) + (\beta_1 + \beta_2)\delta_2}{\gamma_{22}\beta_1 + (\beta_1 + \beta_2)\beta_2} > 0$$

$$-\delta_2 + \beta_2 \cdot \frac{\gamma_{33}(\beta_1 - \delta_1) + (\beta_1 + \beta_3)\delta_3}{\gamma_{33}\beta_1 + (\beta_1 + \beta_3)\beta_3} > 0$$

If $\gamma_{22} = \gamma_{33} = 0$ then these inequalities reduce to the mutually contradictory: $\delta_2/\beta_2 > \delta_3/\beta_3$ and $\delta_2/\beta_2 < \delta_3/\beta_3$. If γ_{22} and γ_{33} are large then two fractions are each close to $(\beta_1 - \delta_1)/\beta_1$, so it is clear that the two conditions can be satisfied simultaneously. Having shown that there is a nonempty set of examples we can now in good conscience state our result.

Theorem 7.5. *Suppose (a)* $1 \succ 0$, $2 \downarrow 0$, $3 \downarrow 0$,

(b) $2 \succ 1$, $3 \succ 1$, *and (c)* $3 \succ 1, 2$, *and* $3 \succ 1, 2$.

Then with fast stirring, we have coexistence in the one-prey, two-predator model.

Remark. Again $2 \downarrow 0$ and $3 \downarrow 0$ simply say that 2's and 3's are predators, while the other five conditions correspond to (7.3.4), (7.3.5), (7.3.7), (7.3.9), and (7.3.10)

Sketch of Proof. On the face Γ_1^0 the fixed point is $(0,0)$ so we can use Proposition 4.3 to construct a repelling function for that face. Using Proposition 1.1 now we can extend to $\Gamma_1^0 \cup \Gamma_{23}^0$. This covers the problem regions for the other two faces so two uses of Proposition 4.1, give a repelling function for Γ^0. □

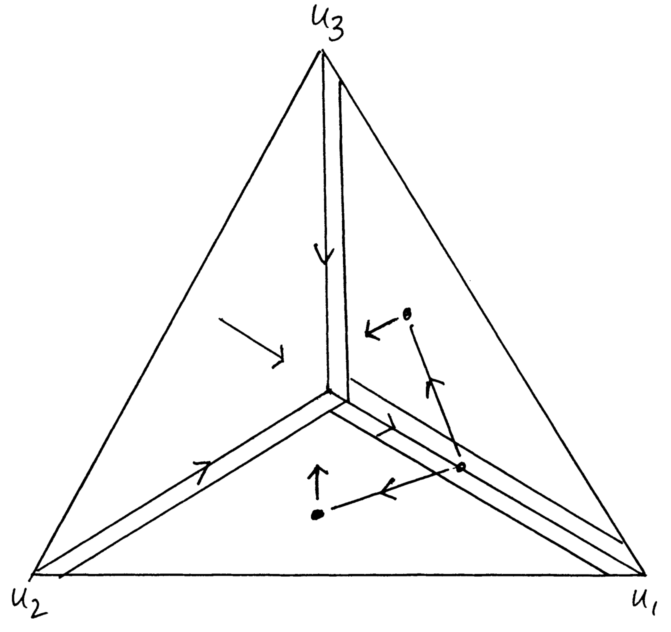


Figure 7.6

Proof of Theorem 7.5. Following the outline in the sketch, the first step is:

Face Γ^0_1. In the absence of prey both predators have $du_i/dt < 0$ for $u_i > 0$, so $f_1(u_1, u_2) = u_1 + u_2$ is a Lyapunov function which satisfies (a), (d), and (e) of Proposition 4.3. Since $1 \succ 0$, (b) holds. Using Proposition 4.3 now, we see that if constants θ_1, λ_1, η_1, ν_1, and B_1 are chosen correctly $h_1 = f_1(u_2 + \theta_1 u_1, u_3 + \theta_1 u_1) - \lambda_1 \log u_1$ has

$$dh_1/dt \le -\nu_1 < 0 \quad \text{when } 0 < u_1 \le \eta_1 \tag{7.3.11}$$

If we pick M_1 large enough then the function $\bar{h}_1 = h_1 \wedge M_1$ is only nontrivial when $0 < z_1 \le \eta_1$. If we take $\bar{\eta}_1 < \eta_1$ then we will have $h_1 > M_1$ when $0 < z_1 \le \bar{\eta}_1$. We move now to the

Edge $\Gamma^0_{2,3}$. $\sigma_1 = (\beta_1 - \delta_1)/\beta_1$ is an attracting fixed point, so if we let $g_1(u) = u - \sigma_1 \log u$ then (a) of Proposition 1.1 holds. Invadability conditions $2 \succ 1$ and $3 \succ 1$ imply that (b) holds when $z_1 = u_2 + u_3$. Using Proposition 1.1 now with $\epsilon_2 \le \bar{\eta}_1$, we see that if constants $\theta_2 \le 1$, λ_2, $\eta_2 \le \epsilon_2$, $\nu_2 \le \nu_1$, and B_2 are chosen appropriately and $\psi_2(u) = (\epsilon_2 - u)^+$ then

$$h_2 = g_1(u_1 + \theta_2 \psi_2(u_1) z_1) - \lambda_2 \log z_1$$

has (i) $dh_2/dt \le -\nu_2 < 0$ when $u_1 \ge \epsilon_2$, $0 < z_1 \le \eta_2$ and (ii) $dh_2/dt \le B_2$ when $0 \le u_1 \le \epsilon_2$, $0 < z_1 \le \eta_2$. If we pick M_2 large enough then the function $\bar{h}_2 = h_2 \wedge M_2$ is only nontrivial when $0 < u_2 + u_3 \le \eta_2$. If we now take $\bar{\eta}_2 < \eta_2$ then we will have $h_2 > M_2$ when $0 < u_2 + u_3 \le \bar{\eta}_2$. Region (ii) is not a problem because of (7.3.11). Thus if we pick $K_1 \ge 1$ large then

$$\frac{d(K_1 \bar{h}_1 + \bar{h}_2)}{dt} \le -\nu_2 \tag{7.3.12}$$

when $u_1 \le \eta_2$ or $u_2 + u_3 \le \eta_2$. In words, $j_1 = K_1 \bar{h}_1 + \bar{h}_2$ is a repelling function for a face and an edge: $\Gamma^0_1 \cup \Gamma^0_{2,3}$. We are now ready for the

Faces Γ^0_3 *and* Γ^0_2. Here we have supercritical predator-prey systems, so Lemma 5.0 gives us Lyapunov functions f_3 and f_2 for these faces that satisfy (a), (d), and (e) of Proposition 4.1. The invadability conditions $3 \succ 1, 2$ and $2 \succ 1, 3$ imply that (b) holds. Applying Proposition 4.1

now, with $\epsilon \le \bar\eta_2$, we see that if $\theta_3 \le 1$, λ_3, $\eta_3 \le \epsilon$, $\nu_3 \le \nu_2$, and B_3 are chosen appropriately then

$$h_3(u) = f_3(u_1 + \theta_3 u_3, u_2 + \theta_3 u_3) - \lambda_3 \log u_3 \tag{7.3.13}$$

has (i) $dh_3/dt \le -\nu_3$ when $u_1 \wedge u_2 \ge \epsilon$ and $0 < u_3 \le \eta_3$ and (ii) $dh_3/dt \le B_3$ when $u_1 \wedge u_2 \le \epsilon$ and $0 < u_3 \le \eta_3$. If we pick M_3 large enough then the function $\bar h_3 = h_3 \wedge M_3$ is only nontrivial when $0 < u_1 \le \eta_3$. Another application of Proposition of 4.1, gives a function

$$h_4(u) = f_2(u_1 + \theta_4 u_2, u_3 + \theta_4 u_2) - \lambda_4 \log u_2 \tag{7.3.14}$$

has (i) $dh_4/dt \le -\nu_4$ when $u_1 \wedge u_3 \ge \epsilon$ and $0 < u_2 \le \eta_4$ and (ii) $dh_4/dt \le B_4$ when $u_1 \wedge u_3 \le \epsilon$ and $0 < u_2 \le \eta_4$. If we pick M_4 large enough then the function $\bar h_4 = h_4 \wedge M_4$ is only nontrivial when $0 < u_2 \le \eta_4$. Combining (7.3.12)–(7.3.14), we see that if K_3 is chosen large enough then $K_2 j_1 + \bar h_3 + \bar h_4$ is a repelling function for Γ_0 and the proof of Theorem 7.5 is complete. □

From 2-predator and 1-prey we move now to:

Example 7.4. Two-infection model. The case in which susceptibles can be doubly infected is covered by Example 2.5. Indeed the original motivation for Durrett and Neuhauser (1997) was to study the competition of different strains of the barley yellow dwarf virus. Thus, we will concentrate on the situation where individuals can have at most one type of infection. That is, our states are 0 = removed, 1 = susceptible, and 2 = infected with strain 1, and 3 = infected with strain 2. Generalizing from Example 2 in the Introduction, but changing notation, we take the rates of the form

$0 \to 1$	$\beta_1 f_1$	$1 \to 0$	δ_1
$1 \to 2$	$\gamma_2 f_2$	$2 \to 0$	δ_2
$1 \to 3$	$\gamma_3 f_3$	$3 \to 0$	δ_3

Note that we have removed the spontaneous birth term, but now the 1's can die from other causes. The mean field ODE for this model is

$$\begin{aligned} \frac{du_1}{dt} &= \beta_1 u_1 u_0 - u_1(\delta_1 + \gamma_2 u_2 + \gamma_3 u_3) \\ \frac{du_2}{dt} &= \gamma_2 u_2 u_1 - u_2 \delta_2 \\ \frac{du_3}{dt} &= \gamma_3 u_3 u_1 - u_3 \delta_3 \end{aligned} \tag{7.4.1}$$

The second and third equations have the form of two types feeding on the same resource, so adapting the proof of (7.3.2) gives.

(7.4.2) *Suppose* $\gamma_2/\delta_2 > \gamma_3/\delta_3$. *Then for any starting point in* Γ_+ *we have* $u_3(t) \to 0$.

Remark. In words, if we assume that the two strains are equally transmissible, i.e., $\gamma_2 = \gamma_3$, this says that the less virulent strain, i.e., the one with the smaller δ_i, wins the competition.

Proof. A little calculus shows

$$\frac{d}{dt}(-\gamma_3 \log u_2 + \gamma_2 \log u_3) = \delta_2\gamma_3 - \delta_3\gamma_2 < 0$$

Integrating, letting $-\alpha = \delta_2\gamma_3 - \delta_3\gamma_2$ and then exponentiating we have

$$u_2(t)^{-\gamma_3} u_3(t)^{\gamma_2} = u_2(0)^{-\gamma_3} u_3(0)^{\gamma_2} e^{-\alpha t}$$

Since $u_2(t) \le 1$, it follows that $u_3(t) \le Ce^{-\alpha t/\gamma_2} \to 0$. □

In order to allow for the possibility of coexistence, we will now generalize the model. Following Section 16.5 of Hofbauer and Sigmund (1998), we note that many parasites can be transmitted horizontally (through infection) and vertically (i.e., from parent to offspring). With this in mind we use the states introduced before but now take the rates of the form

$0 \to 1$	$\beta_1 f_1$	$1 \to 0$	δ_1
$0 \to 2$	$\beta_2 f_2$	$2 \to 0$	δ_2
$0 \to 3$	$\beta_3 f_3$	$3 \to 0$	δ_3
$1 \to 2$	$\gamma_2 f_2$	$1 \to 3$	$\gamma_3 f_3$

The mean field ODE for this model is

$$\begin{aligned}
\frac{du_1}{dt} &= \beta_1 u_1 u_0 - u_1(\delta_1 + \gamma_2 u_2 + \gamma_3 u_3) \\
\frac{du_2}{dt} &= \beta_2 u_2 u_0 + \gamma_2 u_2 u_1 - u_2\delta_2 \\
\frac{du_3}{dt} &= \beta_3 u_3 u_0 + \gamma_3 u_3 u_1 - u_3\delta_3
\end{aligned}$$

which has the Lotka-Volterra form

$$\begin{aligned}
\frac{du_1}{dt} &= u_1\left\{(\beta_1-\delta_1)-\beta_1 u_1-(\beta_1+\gamma_2)u_2-(\beta_1+\gamma_3)u_3\right\}\\
\frac{du_2}{dt} &= u_2\left\{(\beta_2-\delta_2)+(\gamma_2-\beta_2)u_1-\beta_2 u_2-\beta_2 u_3\right\} \qquad (7.4.3)\\
\frac{du_3}{dt} &= u_3\left\{(\beta_3-\delta_3)+(\gamma_3-\beta_3)u_1-\beta_3 u_2-\beta_3 u_3\right\}
\end{aligned}$$

To begin to analyze this system we note that unless

$$\beta_1 > \delta_1 \tag{7.4.4}$$

the whole system will collapse, while if (7.4.4) holds then in the absence of the two infections the susceptibles will reach a density $\sigma_1 = (\beta_1-\delta_1)/\beta_1$. Infection 2 can invade this equilibrium if

$$\beta_2-\delta_2+(\gamma_2-\beta_2)\sigma_1 > 0 \tag{7.4.5}$$

Likewise infection 3 can invade the 1's equilibrium if

$$\beta_3-\delta_3+(\gamma_3-\beta_3)\sigma_1 > 0 \tag{7.4.6}$$

At this point there are several cases to consider. We expect to have the best success with coexistence when one epidemic survives by horizontal transmission and the other by vertical transmission since this corresponds to two ecologicial 'niches.' Thus we will suppose

$$\beta_2-\delta_2 > 0 \quad \text{and} \quad \beta_3-\delta_3 < 0 \tag{7.4.7}$$

or invadability language that $2 \succ 0$ while $0 \succ 3$. When $\beta_2 > \delta_2$, the 2's reach a density $\sigma_2 = (\beta_2-\delta_2)/\beta_2$ which can be invaded by the 1's if

$$\beta_1-\delta_1-(\beta_1+\gamma_2)\sigma_2 > 0 \tag{7.4.8}$$

If, in addition, (7.4.5) holds then (2.1.4) implies there is an equilibrium with

$$\begin{aligned}
\sigma_1^3 &= \frac{\beta_2(\beta_1-\delta_1)-(\beta_1+\gamma_2)(\beta_2-\delta_2)}{\beta_1\beta_2+(\beta_1+\gamma_2)(\gamma_2-\beta_2)}\\
\sigma_2^3 &= \frac{\beta_1(\beta_2-\delta_2)+(\gamma_2-\beta_2)(\beta_1-\delta_1)}{\beta_1\beta_2+(\beta_1+\gamma_2)(\gamma_2-\beta_2)}
\end{aligned}$$

On the face Γ_2^0, the system is of the predator-prey type, so using (2.1.4) again or more simply changing all the 2's to 3's in the previous formula

$$\sigma_1^2 = \frac{\beta_3(\beta_1 - \delta_1) - (\beta_1 + \beta_3)(\beta_3 - \delta_3)}{\beta_1\beta_3 + (\beta_1 + \beta_3)(\gamma_3 - \beta_3)}$$

$$\sigma_3^2 = \frac{\beta_1(\beta_3 - \delta_3) + (\gamma_3 - \beta_3)(\beta_1 - \delta_1)}{\beta_1\beta_3 + (\beta_1 + \gamma_3)(\gamma_3 - \beta_3)}$$

On the face Γ_0^1, we have a competition model in which the 3's lose to the 1's. Turning now to the higher order competitions, 3's can invade the 1,2 equilibrium if

$$\beta_3 - \delta_3 + (\gamma_3 - \beta_3)\sigma_1^3 - \beta_3\sigma_2^3 > 0 \tag{7.4.9}$$

and 2's can invade the 1,3 equilibrium if

$$\beta_2 - \delta_2 + (\gamma_2 - \beta_2)\sigma_1^2 - \beta_2\sigma_2^3 > 0 \tag{7.4.10}$$

Combining our calculations we have

Theorem 7.6. *Suppose (a)* $1 \succ 0$, $2 \succ 0$, $3 \downarrow 0$,

(b) $2 \succ 1$, $1 \succ 2$, $3 \succ 1$, $2 \gg 3$, *and (c)* $2 \succ 1,3$ *and* $3 \succ 1,2$.

Then there is coexistence for the two infection model with fast stirring.

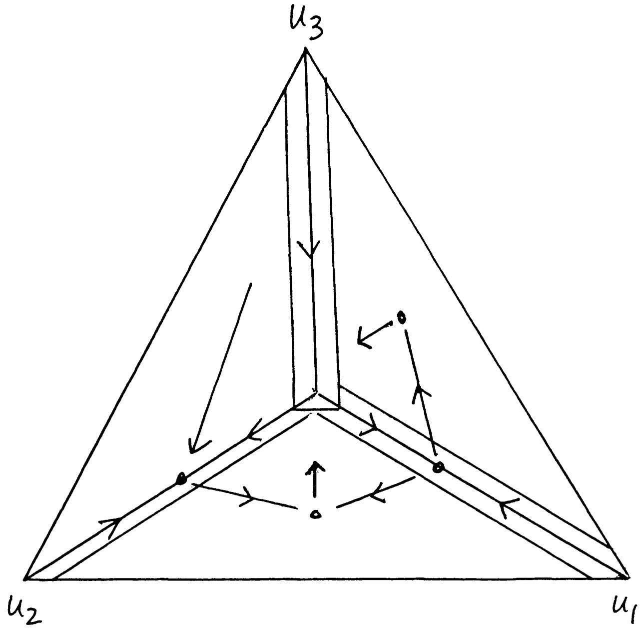


Figure 7.7

Sketch of Proof. See Figure 7.7. As in the proof of Theorem 7.1, we let $z_3 = u_1 + u_2$ and

$$h_1 = \max\{u_3 - \lambda_1 \log z_3, M_1\}$$

On the face Γ_1^0 the fixed point has $\sigma_2^1 > 0$ and $\sigma_3^1 = 0$, so Proposition 4.2, allows us to extend to $\Gamma_1^0 \cup \Gamma_{2,3}^0$. This covers the problem regions for the remaining two faces, so two uses of Proposition 4.1 give a repelling function for Γ^0. □

Proof of Theorem 7.6. Following the outline in the sketch, we begin with the

Edge Γ_{12}^0. In the absence of prey, the predators die out, so (a) of Proposition 1.2 holds. Let $z_1 = u_1 + u_2$. Since $1, 2 \succ 0$, (b) holds. Applying Proposition 1.2, we see that if λ_1, ν_1, and η_1 are chosen appropriately then $h_1(u) = u_3 - \lambda_1 \log z_1$ has

$$dh_1/dt \le -\nu_1 \quad \text{for } 0 < z_1 \le \eta_1 \tag{7.4.11}$$

If we pick M_1 large enough then the function $\bar{h}_1 = h_1 \wedge M_1$ is only nontrivial when $0 < z_1 \le \eta_1$. If we now take $\bar{\eta}_1 < \eta_1$ then we will have $h_1 > M_1$ when $0 < z_1 \le \bar{\eta}_1$. We move now to the

Face Γ_1^0. Here the ODE is a degenerate linear competition model with $\sigma_2^1 > 0$ and $\sigma_3^1 = 0$, so Lemma 5.2, gives us a Lyapunov function f_1 that satisfies (a), (d), and (e) of Proposition 4.2. The condition $1 \succ 2$ implies that (b) holds. Using Proposition 4.2 now with $\epsilon \le \bar{\eta}_1$, we see that if constants $\theta_2 \le 1$, λ_2, $\eta_2 \le \epsilon$, $\nu_2 \le \nu_1$, and B_2 are chosen correctly

$$h_2 = f_1(u_2 + \theta_2 u_1, u_3 + \theta_2 u_1) - \lambda_2 \log u_1$$

has (i) $dh_2/dt \le -\nu_2 < 0$ when $u_2 \ge \epsilon$, $0 < u_1 \le \eta_2$ and (ii) $dh_2/dt \le B_2$ when $0 \le u_2 \le \epsilon$, $0 < u_1 \le \eta_2$. If we pick M_2 large enough then the function $\bar{h}_2 = h_2 \wedge M_2$ is only nontrivial when $0 < u_1 \le \eta_2$. If we now take $\bar{\eta}_2 < \eta_2$ then we will have $h_2 > M_2$ when $0 < u_2 \le \bar{\eta}_2$. Region (ii) is not a problem because of (7.4.11). At this point we can also add the

Edge $\Gamma_{2,3}^0$. $\sigma_1 = (\beta_1 - \delta_1)/\beta_1$ is an attracting fixed point, so if we let $g_1(u) = u - \sigma_1 \log u$ then (a) of Proposition 1.1 holds. Let $z_3 = u_2 + u_3$. The invadability conditions $2 \succ 1$ and $3 \succ 1$ imply that (b) holds.

Using Proposition 1.1 now with $\epsilon_3 \le \bar{\eta}_2$, we see that if constants $\theta_3 \le 1$, λ_3, $\eta_3 \le \epsilon_3$, $\nu_3 \le \nu_2$, and B_3 are chosen appropriately and $\psi_3(u) = (\eta_3 - u)^{+2}$ then

$$h_3(u) = g_1(u_1 + \theta_3\psi_3(u_1)z_2) - \lambda_3 \log z_3$$

has (i) $dh_3/dt \le -\nu_3 < 0$ when $u_1 \ge \epsilon_3$, $0 < z_3 \le \eta_3$ and (ii) $dh_3/dt \le B_3$ when $0 \le u_1 \le \epsilon_3$, $0 < z_3 \le \eta_3$. If we pick M_3 large enough then the function $\bar{h}_3 = h_3 \wedge M_3$ is only nontrivial when $0 < u_2 + u_3 \le \eta_3$. If we now take $\bar{\eta}_3 < \eta_3$ then we will have $h_2 > M_2$ when $0 < u_2 + u_3 \le \bar{\eta}_3$. Region (ii) is not a problem because of (7.4.11). Thus if we pick $K_1 \ge 1$ large then

$$\frac{d(K_1\bar{h}_1 + \bar{h}_2 + \bar{h}_3)}{dt} \le -\nu_3 \tag{7.4.12}$$

when $u_1 \le \eta_3$ or $u_2 + u_3 \le \eta_3$. In words, $j_1 = K_2\bar{h}_1 + \bar{h}_2 + \bar{h}_3$ is a repelling function for a face and an edge: $\Gamma_1^0 \cup \Gamma_{2,3}^0$. With this, we can complete the proof by adding the

Faces Γ_2^0 *and* Γ_3^0. On the face Γ_2^0 we have a supercritical predator-prey system, while on the face Γ_3^0 we have a Case 2 competitive system. Thus, Lemmas 5.0 and 5.1 give us Lyapunov functions f_2 and f_3 for these faces that satisfy (a), (d), and (e) of Proposition 4.1. The invadability conditions $3 \succ 1,2$ and $2 \succ 1,3$ imply that (b) holds. Applying Proposition 4.1 now, with $\epsilon \le \bar{\eta}_3$, we see that if $\theta_4 \le 1$, λ_4, $\eta_4 \le \epsilon$, $\nu_4 \le \nu_3$, and B_4 are chosen appropriately then

$$h_4(u) = f_3(u_1 + \theta_4 u_3, u_2 + \theta_4 u_3) - \lambda_4 \log u_3 \tag{7.4.13}$$

has (i) $dh_4/dt \le -\nu_4$ when $u_1 \wedge u_2 \ge \epsilon$ and $0 < u_3 \le \eta_4$ and (ii) $dh_4/dt \le B_4$ when $u_1 \wedge u_2 \le \epsilon$ and $0 < u_3 \le \eta_4$. If we pick M_4 large enough then the function $\bar{h}_4 = h_4 \wedge M_4$ is only nontrivial when $0 < u_1 \le \eta_4$.

Another application of Proposition of 4.1, gives a function

$$h_5(u) = f_2(u_1 + \theta_5 u_2, u_3 + \theta_5 u_2) - \lambda_5 \log u_2 \tag{7.4.14}$$

has (i) $dh_5/dt \le -\nu_5$ when $u_1 \wedge u_3 \ge \epsilon$ and $0 < u_2 \le \eta_5$ and (ii) $dh_5/dt \le B_5$ when $u_1 \wedge u_3 \le \epsilon$ and $0 < u_2 \le \eta_5$. If we pick M_5 large enough then the function $\bar{h}_5 = h_5 \wedge M_5$ is only nontrivial when $0 < u_2 \le \eta_5$. Combining (7.4.12)–(7.4.14), we see that if K_2 is chosen large enough then $K_2 j_1 + \bar{h}_4 + \bar{h}_5$ is a repelling function for Γ_0 and the proof of Theorem 7.6 is complete. □

8. Some asymptotic results for our ODE and PDE.

In this section we will give the proofs of Propositions 0 and 1, and Theorem 6.3.

Proof of Proposition 0. Let $\epsilon > \delta$, let $Q = \inf\{t : \phi(u(t)) \leq M+\delta\}$ be the quitting time from $\phi > M+\delta$, $R = \inf\{t \geq Q : \phi(u(t)) > M+\epsilon\}$ be the time of the first return to $\phi > M + \epsilon$, and $T = \sup\{s \leq R : \phi(u(t)) \leq M + \delta\}$. On $(T, R]$ we have $\phi(u(t)) > M + \delta$, so $d\phi/dt < 0$ leading to a contradiction

$$0 < \epsilon - \delta = \phi(u(R)) - \phi(u(T)) = \int_T^R \frac{d\phi}{dt}(u(s))\,ds < 0$$

Thus, once $u(t)$ leaves $\{\phi > M+\delta\}$ it can never re-enter $\{\phi > M+\epsilon\}$ with $\epsilon > \delta$. To see that the ODE must leave $\{\phi > M + \delta\}$ in finite time note that by (ii) we have $d\phi(u(t))/dt \leq -c_\delta < 0$ while $\phi(u(t)) > M + \delta$, so we must have

$$Q_\delta \leq \{\phi(u(0)) - (M + \delta)\}/c_\delta \qquad \square$$

To prove the second result, we use the obvious generalization of the previous idea: put the reaction-diffusion equation inside the repelling function. This time, however, it is useful to introduce a smooth enough truncation. Let $\psi(z) = 0$ for $z \leq 0$, and let

$$\psi(z) = \int_0^z \frac{y}{y+1}\,dy \quad \text{for } z \geq 0$$

It is immediate from the definition that ψ' is increasing so ψ is convex and satisfies

$$\frac{z^2}{2} \leq \psi(z) \leq z \tag{8.1}$$

Let $\hat{\phi}(u) = \psi(\phi(u) - (M + \epsilon))$ be the truncated version of ϕ.

Proof of Proposition 1. Let $h(t, x) = \hat{\phi}(u(t, x))$, where u is a solution of

$$\frac{\partial u_i}{\partial t} = \Delta u_i + f_i(u) \quad \text{for } 1 \leq i \leq k \tag{8.2}$$

In what follows the indices i and j are in $[1,k]$, while the index $m \in [1,d]$. Differentiating and using the equation in (8.2) gives

$$\frac{\partial h}{\partial t} = \sum_i \frac{\partial \hat{\phi}}{\partial u_i} \cdot \frac{\partial u_i}{\partial t} = \sum_i \frac{\partial \hat{\phi}}{\partial u_i} \cdot (\Delta u_i + f_i(u))$$

$$\frac{\partial h}{\partial x_m} = \sum_i \frac{\partial \hat{\phi}}{\partial u_i} \cdot \frac{\partial u_i}{\partial x_m}$$

$$\frac{\partial^2 h}{\partial x_m^2} = \sum_i \frac{\partial \hat{\phi}}{\partial u_i} \cdot \frac{\partial^2 u_i}{\partial x_m^2} + \sum_{i,j} \frac{\partial u_i}{\partial x_m} \cdot \frac{\partial^2 \hat{\phi}}{\partial u_i \partial u_j} \cdot \frac{\partial u_j}{\partial x_m}$$

Summing the last equation for $1 \le m \le d$ and using $\hat{\phi}_t = \sum_i \frac{\partial \hat{\phi}}{\partial u_i} f_i(u)$ to denote the time derivative of $\hat{\phi}$ along solutions of the ODE gives

$$\frac{\partial h}{\partial t} = \Delta h + \hat{\phi}_t - \sum_{m,i,j} \frac{\partial u_i}{\partial x_m} \cdot \frac{\partial^2 \hat{\phi}}{\partial u_i \partial u_j} \cdot \frac{\partial u_j}{\partial x_m}$$

Being the composition of two convex functions $\hat{\phi}(u) = \psi(\phi(u) - (M + \epsilon))$ is convex, so the last term (including the minus sign) is nonpositive and we have

$$\frac{\partial h}{\partial t} \le \Delta h + \hat{\phi}_t \tag{8.3}$$

Remark. The calculation leading to (8.3) is simple but also very fragile. It breaks down for example if we consider unequal diffusion rates, since in that case

$$\frac{\partial h}{\partial t} = \sum_i \frac{\partial \hat{\phi}}{\partial u_i} \cdot (\sigma_i^2 \Delta u_i + f_i(u))$$

and we have no way to get σ_i^2 into the expression

$$\frac{\partial^2 h}{\partial x_m^2} = \sum_i \frac{\partial \hat{\phi}}{\partial u_i} \cdot \frac{\partial^2 u_i}{\partial x_m^2} + \sum_{i,j} \cdots \qquad \square$$

To prove Proposition 1 we need to show that if the initial condition $u(0,x) \in \Gamma$ is continuous, and has

$$u_i(0,x) \ge \eta_i > 0 \quad \text{when} \quad x \in [-\delta, \delta]^2 \tag{8.4}$$

There are constants $\kappa > 0$ and $t_0 < \infty$, which only depend on η_i, δ, and γ so that

$$h(t,x) \le \gamma \quad \text{when} \quad |x| \le \kappa t, \quad t \ge t_0$$

To get upper bounds on $h(t,x)$, we note that the definition of ψ and (ii) imply that when $\phi(u) > M + \epsilon$

$$\begin{aligned} \hat{\phi}_t &= \psi'(\phi(u) - (M+\epsilon)) \cdot \phi_t \\ &\le -c_\epsilon \frac{\phi(u) - (M+\epsilon)}{1 + \phi(u) - (M+\epsilon)} \le -c_\epsilon \frac{\hat{\phi}(u)}{1+\hat{\phi}(u)} \end{aligned} \tag{8.5}$$

since $\psi(u) \le u$ and $z/(z+1)$ is increasing for $z \in [0,\infty)$. Our initial condition may have $h(0,x) = \infty$. To get things started we show

Lemma 8.1. *There is a constant K which only depends on the constants η_i and δ in (8.4), so that if $t \ge 1$ and $|x| \le t$ then $h(t,x) \le Kt$.*

Proof: Assumption (v) implies that $\frac{\partial u_i}{\partial t} \ge \Delta u_i - \alpha_i u_i$. Using Lemma 5.1.2 and the assumptions in (8.4) gives

$$\begin{aligned} u_i(t,x) &\ge e^{-\alpha_i t}\eta_i \int_{y\in[-\delta,\delta]^d} (4\pi t)^{-d/2} e^{-|x-y|^2/4t}\, dy \\ &\ge e^{-\alpha_i t}\eta_i \cdot (2\delta)^d (4\pi t)^{-d/2} \exp(-(|x|+\delta)^2/4t) \end{aligned}$$

We have $\phi(u) \le C(1 + \sum_{i=1}^k \log^-(u_i))$ by (iv), and the desired result follows. □

Remark. If we instead use the bound $\phi(u) \le C(1+\sum_{i=1}^k u_i^{-\rho})$ where $\rho > 0$ we end up with $h(t,x) \le Ke^{\gamma t}$ which is not good enough to satisfy the demands of Lemma 8.4.

Our SECOND STEP in the proof of Proposition 1 is to let $D_r = \{y : |y| < r\}$ and define $h_1^t(t,x)$ to be the function with $h(s,x) = Ks$ if $s = at$, or $x \in \partial D_{at}$ and

$$\frac{\partial h}{\partial t} = \Delta h - c_\epsilon \frac{h}{1+h} \quad \text{in } \mathcal{D}_t \equiv [at,t] \times D_{at}$$

Using Lemma 8.1 we see that $h(s,x) \le h_1^t(s,x)$ when $s = at$ or $x \in \partial D_{at}$, so taking into account the inequality in (8.5) we should expect to find that

$$h(s,x) \le h_1^t(s,x) \quad \text{for } (s,x) \in \mathcal{D}_t \tag{8.6}$$

To prove this we use the following comparison result:

Lemma 8.2. *Suppose $f_1(h) \ge f_2(h)$ and the h_i solve*

$$\frac{\partial h_i}{\partial t} = \Delta h_i - f_i(h_i) \quad \textit{in } \mathcal{D}_t$$

with $h_1(s,x) \le h_2(s,x)$ if $s = at$, or $x \in \partial D_{at}$ then

$$h_1(s,x) \le h_2(s,x) \quad \text{in } \mathcal{D}_t$$

Proof. This type of conclusion usually goes under the name of the "maximum principle." However, the version we need is easier to prove than to find in the library. Suppose first that $f_1(h) > f_2(h)$ and $h_1(s,x) < h_2(s,x)$ if $s = at$, or $x \in \partial D_{at}$. Let s_0 be the smallest value of s for which there is an x with $h_1(s,x) \ge h_2(s,x)$. Continuity of the h_i implies that we can find an x_0 so that $h_1(s_0,x_0) = h_2(s_0,x_0)$. The strict inequality between the h_i on the boundary implies $x_0 \in D_{at}$ and $s_0 > 0$. The definition of s_0 implies that $h_1(s_0,x) \le h_2(s_0,x)$ for all x. Since $h_1(s_0,x_0) = h_2(s_0,x_0)$, we must have $\nabla h_1(s_0,x_0) = \nabla h_2(s_0,x_0)$ and $\Delta h_1(s_0,x_0) \le \Delta h_2(s_0,x_0)$. Using the last fact and $f_1(h) > f_2(h)$ it follows that at (s_0,x_0)

$$\frac{\partial h_1}{\partial t} = \Delta h_1 - f_1(h_1) < \Delta h_2 - f_2(h_2) = \frac{\partial h_2}{\partial t}$$

However this implies that $h_1(s_0-\epsilon,x) > h_2(s_0-\epsilon,x_0)$ for small ϵ contradicting the definition of s_0, so we must have $h_1(s,x) < h_2(s,x)$ for all $(s,x) \in \mathcal{D}_{at}$. To prove the result in (2.4) now let $f_0(h) = f_1(h) + \epsilon$ and change the boundary values to $h_1(s,x) - \epsilon$. The new solution $h_0^\epsilon(s,x) < h_2(s,x)$ and converges pointwise to $h_1(s,x)$ as $\epsilon \to 0$. □

Our THIRD STEP is to bound $h_1^t(s,x)$ by $h_2^t(s,x) = w_{Kat}(s-at)$ where $w_q(r)$ is the solution of

$$w'(t) = -c_\epsilon \cdot \frac{w}{1+w} \quad \text{with} \quad w(0) = q$$

Lemma 8.3. *If* $|x| \le at/2$ *then we have*

$$0 \le h_1^t(t,x) - h_2^t(t,x) \le (K+\alpha)t \cdot Ce^{-\delta t} \tag{8.7}$$

Proof. For the left-hand inequality we note that Lemma 8.2 implies $h_1^t(s,x) \ge h_2^t(s,x)$ in $\mathcal{D}_t$. To estimate the difference we let $\bar g(x) = c_\epsilon x/(1+x)$ and observe that Itô's formula (see e.g., Section 4.2 of Durrett (1996)) implies that if $\tau = \inf\{s : B_s \notin D_{at}\}$ then

$$h_i^t(t - s\wedge\tau, B_{s\wedge\tau}) - \int_0^{s\wedge\tau} \bar g(h_i^t(t-r,B_r))\,dr \qquad s \le (1-a)t$$

is a bounded martingale. Using the martingale property at time $s = (1-a)t$ gives that

$$\begin{aligned} h_i^t(t,x) = E_x\Bigg(& h_i^t(at, B_{(1-a)t}) \\ & - \int_0^{s\wedge\tau} \bar g(h_i^t(t-r,B_r))\,dr; \tau > (1-a)t\Bigg) \\ + E_x\Bigg(& h_i^t(t-\tau, B_\tau) \\ & - \int_0^{s\wedge\tau} \bar g(h_i^t(t-r,B_r))\,dr; \tau \le (1-a)t\Bigg) \end{aligned} \tag{8.8}$$

Since $h_1^t(at,x) = h_2^t(at,x)$ and $0 \le h_2^t(t-r,B_r) \le h_1^t(t-r,B_r)$ for $\tau > r$ we have

$$\begin{aligned} h_1^t(at, B_{(1-a)t}) &- \int_0^{s\wedge\tau} \bar g(h_1^t(t-r,B_r))\,dr \\ &\le h_2^t(at, B_{(1-a)t}) - \int_0^{s\wedge\tau} \bar g(h_2^t(t-r,B_r))\,dr \end{aligned}$$

on $\{\tau > (1-a)t\}$. Subtracting the two expressions for $h_i^t(t,x)$ in (8.7) and recalling that $h_i^t \ge 0$ gives

$$\begin{aligned} h_1^t(t,x) - h_2^t(t,x) &\le 0 + E_x(h_1^t(t-\tau,B_\tau) \\ &\qquad + \int_0^\tau \bar g(h_2^t(t-r,B_r))\,dr; \tau \le (1-a)t) \\ &\le (K+\alpha)t\, P_x(\tau \le (1-a)t) \end{aligned}$$

since $h_1^t(s,x) = Ks$ when $x \in \partial D_{at}$ and $0 \le \bar{g} \le \alpha$. Standard large deviations estimates for Brownian motion imply that for $|x| \le at/2$, $P_x(\tau < (1-a)t) \le C\exp(-\delta t)$, which completes the proof. □

Our FOURTH STEP is to investigate $w_{Kat}((1-a)t)$. Abstracting a little to simplify notation, we begin by considering the behavior of solutions of

$$w' = -\beta \cdot \frac{w}{1+w} \quad \text{with} \quad w(0) = W$$

Lemma 8.4. *Let $T_\gamma = \inf\{t : w(t) \le \gamma\}$. There is a constant C so that given $w \ge 2$ and $\gamma < 1$ we have*

$$\frac{(W-\gamma)}{\beta} \le T_\gamma \le \frac{W}{\beta} + CW^{1/2}(\log W^{1/2} - \log \gamma) \tag{8.9}$$

Proof of Proposition 1. From (8.9), we see that for fixed γ as $W \to \infty$ the time to go from W to γ is $\sim W/\beta$. Thus if we pick a so that $Ka/\beta < 1-a$ then for $t \ge t_0$ we will have $w_{Kat}((1-a)t) \le \gamma$ and the proof of Proposition 1 is complete. □

Proof of Lemma 8.4. Since $w'(t) \ge -\beta$ we have $w(t) \ge W - \beta t$ and $T_\gamma \ge (W-\gamma)/\beta$. To prove the other bound, we observe that while $w(t) \ge W^{1/2}$,

$$w' \le -\beta\frac{W^{1/2}}{1+W^{1/2}} \le -\beta(1 - W^{-1/2})$$

so $w(t)$ reaches level $W^{1/2}$ at a time

$$\le \frac{W}{\beta(1-W^{-1/2})} \le \frac{W}{\beta} + CW^{1/2} \tag{8.10}$$

where C is independent of $W \ge 2$. When $w(t) \le W^{1/2}$ we have $w' \le -\beta w/\{1 + W^{1/2}\}$ or integrating that

$$w(t) \le w(0)\exp(-\beta t/\{1 + W^{1/2}\})$$

This implies that the time to go from level $W^{1/2}$ to γ is

$$\le \frac{1+W^{1/2}}{\beta} \cdot (\log W^{1/2} - \log \gamma) \tag{8.11}$$

Adding this to (8.10) gives the desired estimate. This completes the proof of Lemma 8.4 and hence the proof of Proposition 1. □

Proof of Theorem 6.3. For simplicity, we will do the proof only for the two species Tilman model. The general case can be done with the same idea but with n steps in the proof instead of 2. We begin by recalling the mean field ODE given in (2.1.5):

$$\begin{aligned}\frac{du_1}{dt} &= \Delta u_1 + u_1\left\{(\beta_1-\delta_1)-\beta_1 u_1\right\}\\ \frac{du_2}{dt} &= \Delta u_2 + u_2\left\{(\beta_2-\delta_2)-(\beta_1+\beta_2)u_1-\beta_2 u_2\right\}\end{aligned}$$

Let $\rho_1 = (\beta_1-\delta_1)/\beta_1$ and $\phi_1(u_1) = u_1 - \rho_1\log u_1$. ϕ_1 is a convex Lyapunov function, so Proposition 1 implies that given ϵ_1, η_1, and δ there are constants κ_1 and t_1 so that if $u_1(0,x)\ge\eta_1>0$ when $x\in[-\delta,\delta]^d$ then

$$|u_1(t,x)-\rho_1|\le\epsilon_1 \quad\text{when}\quad |x|\le\kappa_1 t,\quad t\ge t_1 \tag{8.12}$$

Let $\rho_2 = \{(\beta_2-\delta_2)-(\beta_1+\beta_2)\sigma_1\}/\beta_2$ be the equilibrium density of 2's, let $\phi_2(u_2)=u_2-\sigma_2\log u_2$, and introduce the truncated version

$$\zeta_2(u_2) = (\phi_2(u_2)-\phi_2(\sigma_2)-\epsilon_2)^+ \tag{8.13}$$

that is flat near the fixed point. If the constant ϵ_1 in the first step was chosen small enough, ζ_2 will be a repelling function with $M=0$ when $|u_1(t,x)-\sigma_1|\le\epsilon_1$. If we pick $a>0$ small enough then the region $\mathcal{D}_t=[at,t]\times\{y:|y|<at\}$ will for large t lie inside the good region for (8.12): $\{(t,x):|x|\le\kappa t, t\ge t_0\}$.

Introducing the smoothly truncated version $\hat{\zeta}_2=\psi(\zeta_2(u)-\epsilon_3)$, we have the differential inequality (8.3) and the estimate (8.5) from the proof of Proposition 1. The proofs of Lemmas 8.1–8.4 go through as before and we conclude that given ϵ_2, η_2 and δ there are constants $\kappa_2\le\kappa_1$ and $t_2\ge t_1$ so that if $u_2(0,x)\ge\eta_2>0$ when $x\in[-\delta,\delta]^d$ then

$$|u_2(t,x)-\rho_2|\le\epsilon_2 \quad\text{when}\quad |x|\le\kappa_2 t,\quad t\ge t_2$$

Combined with (8.12) this implies that $(\star)$ holds, so the desired result now follows from Proposition 2. □

A List of the Invadability Conditions

The first three definitions are for two dimensional systems only.

Definition 1. *We say that 2's die out, and write* $2 \downarrow 0$, *if*

$$du_2/dt < 0 \quad \textit{when } u_1 = 0 \textit{ and } u_2 > 0.$$

Definition 2. *We say that 1's equilibrate at density* σ_1, *and write* $1 \to \sigma_1$, *if*

$$u_1(t) \to \sigma_1 \quad \textit{as } t \to \infty \textit{ when } u_2 = 0 \textit{ and } u_1(0) > 0.$$

Definition 3. *We say that species 2 can invade species 1 in equilibrium, and write* $2 \succ 1$, *if as* $u \to (\sigma_1, 0)$ *inside* Γ^+, *we have*

$$\liminf \frac{1}{u_2} \frac{du_2}{dt} > 0.$$

Definition 4. *We say that* $i \succ 0$ *if as* $u \to 0$ *inside* Γ_+, *we have*

$$\liminf \frac{1}{u_i} \frac{du_i}{dt} > 0.$$

Definition 5. *We say that* $2, \dots n$ *can invade 1 and write* $2, \dots n \succ 1$ *if there is a positive linear combination* $z = \omega_2^1 u_2 + \cdots + \omega_n^1 u_n$ *so that as* $u \to (\sigma, 0_{n-1})$ *from inside* Γ^+, *we have*

$$\liminf \frac{1}{z} \frac{dz}{dt} > 0.$$

The last two definitions are for three dimensional systems. Here $\{i, j, k\} = \{1, 2, 3\}$.

Definition 6. *We say that* k *can invade* i, j *in equilibrium and write* $k \succ i, j$ *if as* $u \to \sigma^k$ *(the fixed point on the boundary* Γ_k^0*) inside* Γ_+, *we have*

$$\liminf \frac{1}{u_k} \frac{du_k}{dt} > 0.$$

Definition 7. $2 \gg 3$ *means there is a convex Lyapunov function on the face* Γ_1^0 *that is decreasing whenever* $u_2 > 0$.

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