Lotka–Volterra competition models with small or intermediate diffusions (Y. Lou/Ohio State, July 1st & 2nd, Summer School on analysis, Zhejiang University)

1. Lotka–Volterra competition model (without diffusion) i.e. ODE

$$(1)\quad \begin{cases} \dfrac{du}{dt} = u\,(a_1 - b_1 u - c_1 v), & t>0, \\ \dfrac{dv}{dt} = v\,(a_2 - b_2 u - c_2 v), & t>0, \\ u(0) > 0, \quad v(0) > 0 \end{cases}$$

$u(t)$, $v(t)$: population density of two competing species

a_i, b_i, and c_i are all positive constants, and

a_1, a_2 : intrinsic growth rates

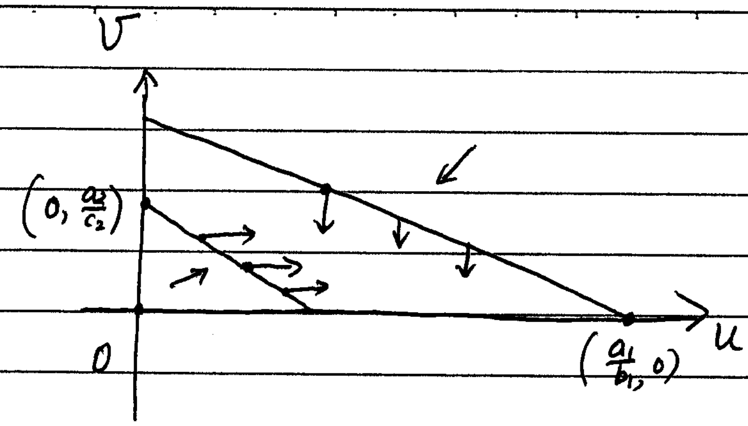
b_1, c_2 : competition coefficients (among same species)

b_2, c_1 : competition coefficients (between different species)

Question 1. Given $u(0)$ and $v(0)$, what is $\lim_{t\to\infty} u(t)$ and $\lim_{t\to\infty} v(t)$? (so called asymptotic behavior of solutions)

It turns out (essentially) that there are four different cases:

Case A. $\dfrac{a_1}{a_2} > \dfrac{b_1}{b_2}$ and $\dfrac{a_1}{a_2} > \dfrac{c_1}{c_2}$



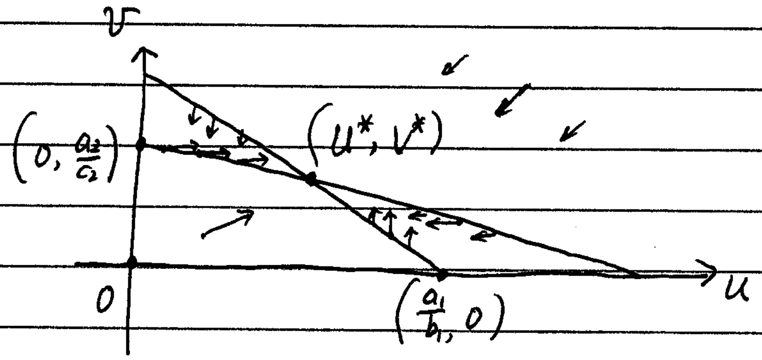
Th'm 2. As $t \to +\infty$, $u(t) \to \frac{a_1}{b_1}$ and $v(t) \to 0$.

Biologically, this means that species u wins the competition, and species 2 becomes extinct.

Case B. $\frac{a_1}{a_2} < \frac{b_1}{b_2}$ and $\frac{a_1}{a_2} < \frac{c_1}{c_2}$.

For this case, $u(t) \to 0$ and $v(t) \to \frac{a_2}{c_2}$ as $t \to +\infty$.

Case C. $\frac{b_1}{b_2} > \frac{a_1}{a_2} > \frac{c_1}{c_2}$



Th'm 3. As $t \to +\infty$, $u(t) \to u^* = \dfrac{a_1 c_2 - a_2 c_1}{b_1 c_2 - b_2 c_1} > 0$,
$v(t) \to \dfrac{a_1 b_2 - a_2 b_1}{c_1 b_2 - c_2 b_1} > 0$. From biological point of view, these two competing species will coexist in a unique way, regardless of

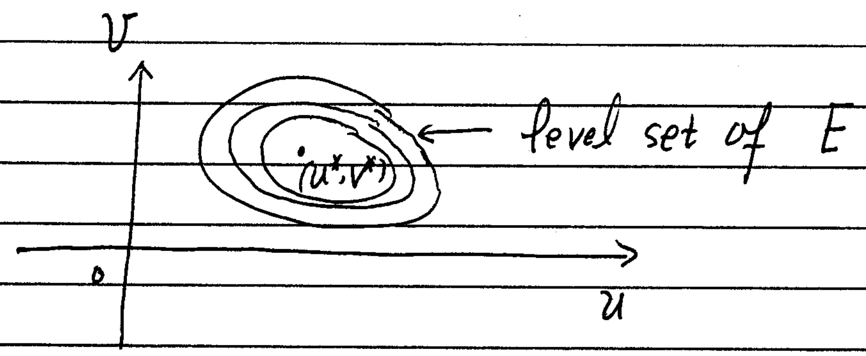
the initial data.

Key ingredient in the proof: Construct some Lyapunov functional

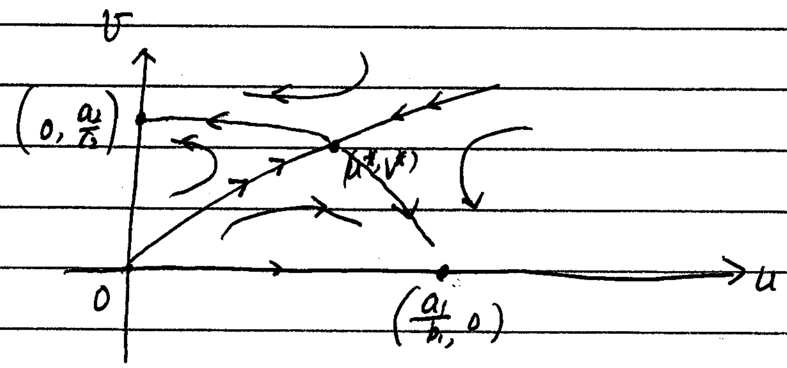
$$(2) \quad E(t) = b_2\left(u - u^* - u^* \ln \frac{u}{u^*}\right) + c_1\left(v - v^* - v^* \ln \frac{v}{v^*}\right).$$

Claim. $\frac{dE}{dt} \leq 0$ for all $t > 0$, and $\frac{dE}{dt}(\tilde{t}) = 0$ if and only if $u(\tilde{t}) = u^*$ and $v(\tilde{t}) = v^*$.

Proof.
$$(3) \quad \frac{dE}{dt} = -\left[b_1 b_2 (u-u^*)^2 + 2 b_2 c_1 (u-u^*)(v-v^*) + c_1 c_2 (v-v^*)^2 \right], \quad \forall t > 0.$$



Case D. $\frac{b_1}{b_2} < \frac{a_1}{a_2} < \frac{c_1}{c_2}$



Th'm 4. There exists a function $u = h(v)$ with $h(0)=0$, h monotone increasing, $\lim_{v\to+\infty} h(v) = +\infty$ such that

i) If $u(0) > h(v(0))$, $u(t) \to \frac{a_1}{b_1}$ and $v(t) \to 0$ as $t\to\infty$;

ii) If $u(0) = h(v(0))$, $u(t) \to u^*$ and $v(t) \to v^*$ as $t\to\infty$;

iii) If $u(0) < h(v(0))$, $u(t) \to 0$ and $v(t) \to \frac{a_2}{c_2}$ as $t\to\infty$.

In this talk, for the sake of clarity, we'll discuss a special subcase of Case C:

$$
(4)\quad \begin{cases} \dfrac{du}{dt} = u(a - u - bv) & t>0, \\ \dfrac{dv}{dt} = v(a - cu - v) & t>0, \\ u(0)>0, \quad v(0)>0, \end{cases}
$$

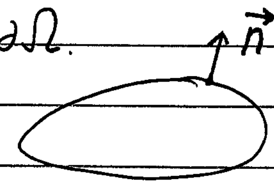
where $a>0$, $0<b<1$, $0<c<1$ are all constants. By Theorem 3 we have $u(t) \to \frac{a(1-b)}{1-bc}$ and $v(t) \to \frac{a(1-c)}{1-bc}$ as $t \to +\infty$.

2. Lotka–Volterra competition model with diffusion (PDE)

Biologically, it's interesting to know what happens if the two competing species diffuse (migrate), say, randomly (this is probably the simplest case).

$$(5)\quad \begin{cases} \dfrac{\partial u}{\partial t} = d_1 \Delta u + u(a-u-bv) & t>0,\ x\in\Omega, \\ \dfrac{\partial v}{\partial t} = d_2 \Delta v + v(a-cu-v) & t>0,\ x\in\Omega, \\ \nabla u\cdot\vec{n} = \nabla v\cdot\vec{n} = 0 & t>0,\ x\in\partial\Omega, \\ u(x,0) \geqq\not\equiv 0, \quad v(x,0)\geqq\not\equiv 0, \end{cases}$$

Where Ω (habitat) is a bounded domain in R^N with smooth boundary $\partial\Omega$. $\vec{n}$ is the unit normal vector on $\partial\Omega$.



$\Delta = \sum_{i=1}^{N} \frac{\partial^2}{\partial x_i^2}$ is the Laplace operator $\longrightarrow$ random diffusion of species; the boundary condition $\nabla \vec{u}\cdot\vec{n} = \nabla v\cdot\vec{n} = 0$ is referred as no-flux condition, i.e., the boundary $\partial\Omega$ acts as a reflecting barrier.

Th'm 5. Suppose that $a>0$, $0<b<1$, $0<c<1$ are all constants. Then $\lim_{t\to\infty} u(x,t) = u^*$ and $\lim_{t\to\infty} v(x,t) = v^*$ uniformly for $x\in\bar{\Omega}$.

Th'm 5 implies that the diffusion terms have essentially no other effects than "smoothing" and "averaging": (a) $u(x,t)$ and $v(x,t)$ are smooth in x and t; (b) no matter how inhomogeneous $u(x,0)$, $v(x,0)$ are, the solutions $u(x,t)$ and $v(x,t)$ are close to constant for large t.

Proof of Thm 5 (main ingredient) By the strong maximum principle, $u(x,t)>0$ and $v(x,t)>0$ for $x\in\bar{\Omega}$ and $t>0$. So without loss of generality we may assume that $u(x,0)>0$ and $v(x,0)$ in $\bar{\Omega}$.

Let $\bar{u}(t)$ and $\underline{v}(t)$ be the solution of

$$(6)\quad \begin{cases} \dfrac{d\bar{u}}{dt} = \bar{u}(a-\bar{u}-b\underline{v}) & t>0 \\ \dfrac{d\underline{v}}{dt} = \underline{v}(a-c\bar{u}-\underline{v}) & t>0 \\ \bar{u}(0) = \max\limits_{x\in\bar{\Omega}} u(x,0), \quad \underline{v}(0) = \min\limits_{x\in\bar{\Omega}} v(x,0)>0. \end{cases}$$

It's easy to see that $\bar{u}$, $\underline{v}$ satisfy the following differential inequality (compare with (5))

$$(7)\quad \begin{cases} \dfrac{\partial\bar{u}}{\partial t} \geqslant d_1\Delta\bar{u} + \bar{u}(a-\bar{u}-b\underline{v}) & t>0,\ x\in\Omega, \\ \dfrac{\partial\underline{v}}{\partial t} \leqslant d_2\Delta\underline{v} + \underline{v}(a-c\bar{u}-\underline{v}) & t>0,\ x\in\Omega, \\ \nabla\bar{u}\cdot\vec{n} = \nabla\underline{v}\cdot\vec{n} = 0 & t>0,\ x\in\partial\Omega, \\ \bar{u}(0) \geqslant u(x,0), \quad \underline{v}(0)\leqslant v(x,0), & \forall x\in\bar{\Omega}. \end{cases}$$

By the comparison principle, we have

$$(8)\qquad \bar{u}(t)\geqslant u(x,t), \qquad \underline{v}(t)\leqslant v(x,t), \qquad \forall x\in\bar{\Omega},\ \forall t>0.$$

Similarly, let $\underline{u}(t)$ and $\bar{v}(t)$ be the solution of

$$(9)\quad \begin{cases} \dfrac{d\underline{u}}{dt} = \underline{u}\,(a - \underline{u} - b\overline{v}) & t>0 \\ \dfrac{d\overline{v}}{dt} = \overline{v}\,(a - c\underline{u} - \overline{v}) & t>0 \\ \underline{u}(0) = \min\limits_{x\in\overline{\Omega}} u(x,0), \quad \overline{v}(0) = \max\limits_{x\in\overline{\Omega}} v(x,0). \end{cases}$$

Similarly we find

$$(10)\qquad u(x,t) \geqslant \underline{u}(t), \qquad \overline{v}(t) \geqslant v(x,t), \quad \forall x\in\overline{\Omega},\ \forall t>0.$$

By Thm 3, $\lim\limits_{t\to\infty} \overline{u}(t) = \lim\limits_{t\to\infty} \underline{u}(t) = u^*$ and $\lim\limits_{t\to\infty} \overline{v}(t) = \lim\limits_{t\to\infty} \underline{v}(t) = v^*$. Therefore, by (10) we have $u(x,t) \to u^*$ and $v(x,t) \to v^*$ in $L^\infty(\Omega)$ as $t\to\infty$. ■

Since environment and resources (food, water etc) are spatially inhomogeneous, d_i, a, b and c in general are functions of x and t. For the rest of discussions we'll consider the following "slight" generalization of (5)

$$(11)\quad \begin{cases} \dfrac{\partial u}{\partial t} = d_1 \Delta u + u\,[a(x) - u - bv] & t>0,\ x\in\Omega, \\ \dfrac{\partial v}{\partial t} = d_2 \Delta v + v\,[a(x) - cu - v] & t>0,\ x\in\Omega, \\ \nabla u\cdot\vec{n} = \nabla v\cdot\vec{n} = 0 & t>0,\ x\in\partial\Omega, \\ u(x,0) \geqslant\not\equiv 0, \quad v(x,0) \geqslant\not\equiv 0, \end{cases}$$

where $d_1>0$, $d_2>0$, $0<b<1$, $0<c<1$ are constants, $a(x)>0$ and $a(x) \not\equiv$ constant. In particular, we are interested in the question

on whether something similar to Thm 5 still holds: e.g.,
(11) has a unique positive steady state solution, denoted by $(\hat{u}(x), \hat{v}(x))$ such that $\lim_{t\to+\infty} u(x,t) = \hat{u}(x)$ and $\lim_{t\to+\infty} v(x,t) = \hat{v}(x)$ in $L^\infty(\Omega)$ norm?

3. Lotka–Volterra competition model with diffusion ($a(x)$ nonconstant case)

For every $x\in\bar{\Omega}$, $a(x)-u-bv = a(x)-cu-v=0$ has a unique positive solution $\left(\frac{a(x)(1-b)}{1-bc}, \frac{a(x)(1-c)}{1-bc}\right) := (u^*(x), v^*(x))$. However, in constrast to the case when a is a positive constant, $(u^*(x), v^*(x))$ is NOT a steady state solution of (11) since $\Delta a(x)=0$ in Ω, $\nabla a\cdot\vec{n}=0$ on $\partial\Omega$ can not hold simultaneously. As we'll see later, finding conditions (for which positive steady state solution exists) is non-trivial. We thus consider three different situations.

3a. Large diffusion

When both d_1 and d_2 are sufficiently large, solutions of (11) behave like that of the following ODE system

$$(12)\quad \begin{cases} \dfrac{dU}{dt} = U\left[⨍ a(x)dx - U - bV\right] & t>0, \\ \dfrac{dV}{dt} = V\left[⨍ a(x)dx - cU - V\right] & t>0, \\ U(0) = ⨍ u(x,0)dx, \quad V(0) = ⨍ v(x,0)dx, \end{cases}$$

where $⨍ f(x)dx = \frac{1}{|\Omega|}\int f(x)dx$. Roughly speaking, if $d_1 \gg 1$ and $d_2 \gg 1$, solutions of (11) behave like

$$u(x,t) \to ⨍ u, \quad v(x,t) \to ⨍ v$$

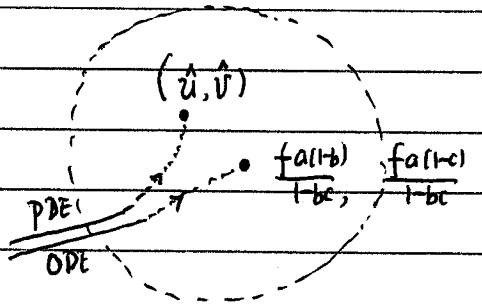
in some short time

$$\downarrow$$

$$⨍ u \approx U(t), \quad ⨍ v \approx V(t)$$

for some large time period

$$\downarrow$$



PDE vs. ODE as $t \to +\infty$

More precisely, the following result holds:

<u>Thm 6</u>. There exists some large constant $D>0$ such that if $d_1 \geq D$ and $d_2 \geq D$, (11) has a unique positive steady state solution, denoted by $(\hat{u}(x;d_1,d_2), \hat{v}(x;d_1,d_2))$, which is globally asymptotically stable (i.e stable, $u(x,t) \to \hat{u}(x)$ and $v(x,t) \to \hat{v}(x)$ as $t \to +\infty$, regardless of the initial data). Moreover, as $d_1 \to +\infty$ and $d_2 \to +\infty$, $\hat{u} \to \frac{fa(1-b)}{1-bc}$, $\hat{v} \to \frac{fa(1-c)}{1-bc}$, where $\left(\frac{fa(1-b)}{1-bc}, \frac{fa(1-c)}{1-bc}\right)$ is the unique positive steady state solution of (12).

3b. Small diffusion

When both d_1 and d_2 are both sufficiently small, solution of (11) somewhat behave like the following "pointwise" ODE

$$
(13)\quad \begin{cases} \dfrac{dU}{dt} = U\left[a(x) - U - bV\right] & t>0, \\ \dfrac{dV}{dt} = V\left[a(x) - cU - V\right] & t>0, \\ U(0) = u(x,0), \quad V(0) = v(x,0) \end{cases}
$$

More precisely, as a corollary of some general results of V. Hutson, K. Mischaikow and Y.L. (2003), we have

Thm 7. If d_1 and d_2 are sufficiently small, (11) has a unique positive steady state solution, denoted by $\left(\hat{u}(x;d_1,d_2), \hat{v}(x;d_1,d_2)\right)$, which is globally asymptotically stable. Moreover, as $d_1 \to 0$ and $d_2 \to 0$, $\hat{u}(x;d_1,d_2) \to \frac{a(x)(1-b)}{1-bc}$, $\hat{v}(x;d_1,d_2) \to \frac{a(x)(1-c)}{1-bc}$.

The proof of Thm 7 turns out to be much harder than that of Thm 6. It consists of two main steps:

Step 1. Show that for any positive steady state solution, say $\left(\tilde{u}(x), \tilde{v}(x)\right)$, we have $\left(\tilde{u}(x), \tilde{v}(x)\right) \longrightarrow \left(\frac{a(x)(1-b)}{1-bc}, \frac{a(x)(1-c)}{1-bc}\right)$ uniformly as $d_1 \to 0$ and $d_2 \to 0$. Here the main method is "iteration method", and we omit the proof here. One of the sub-steps uses the following

<u>Calculus Lemma</u>. Let $\{f_i(x)\}$ be a sequence of continuous functions defined on some compact set K, and $f_1(x) \geq f_2(x) \geq \cdots \geq f_k(x) \geq f_{k+1}(x) \geq \cdots$. Suppose that $f_i(x) \to f(x)$ pointwisely as $i \to +\infty$ and $f \in C(K)$. Then $f_i(x) \rightrightarrows f(x)$ uniformly as $i \to +\infty$.

<u>Step 2</u>. Show that every positive steady-state (if exists) is linearly stable (if d_1, d_2 ...).

The proof here relies on "blow-up" argument — again, some standard method in study of PDEs.

<u>3C</u>. Intermediate diffusion (one or two of the diffusion rates is/are not small or large)

Note that (11) always has two special steady state solutions, i.e., $(\tilde{u}(x), 0)$ and $(0, \tilde{v}(x))$, where $\tilde{u}$ and $\tilde{v}$ are solutions of

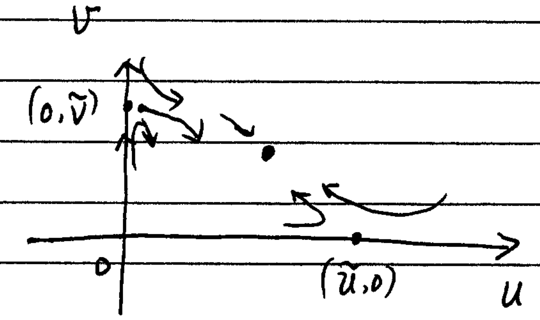
(14) $$d_1 \Delta \tilde{u} + \tilde{u}[a(x) - \tilde{u}] = 0 \text{ in } \Omega, \quad \tilde{u} > 0 \text{ in } \Omega, \quad \nabla \tilde{u} \cdot \vec{n}|_{\partial\Omega} = 0$$

and

(15) $$d_2 \Delta \tilde{v} + \tilde{v}[a(x) - \tilde{v}] = 0 \text{ in } \Omega, \quad \tilde{v} > 0 \text{ in } \Omega, \quad \nabla \tilde{v} \cdot \vec{n}|_{\partial\Omega} = 0,$$

respectively. In view of Thms 6 and 7 we see that if d_1 and d_2 are both sufficiently large, or both sufficiently small, then $(\tilde{u}, 0)$ and

$(0, \tilde{v})$ are unstable.



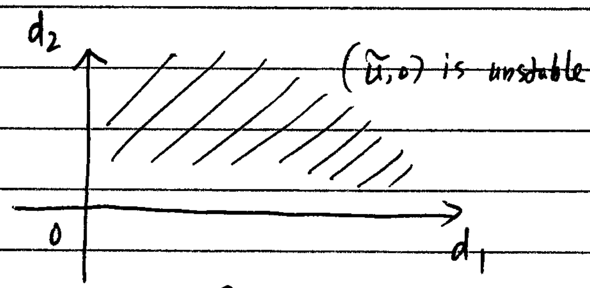
<u>Question</u>. Is it always true that (11) has a positive steady-state such that it is globally asymptotically stable?

From our previous discussions, the answer is affirmative if $a(x) \equiv$ constant, or $a(x) \not\equiv$ constant, $d_1 \gg 1$ and $d_2 \gg 1$ or $d_1 \ll 1$ and $d_2 \ll 1$. However, for other ranges of d_1, d_2, we have

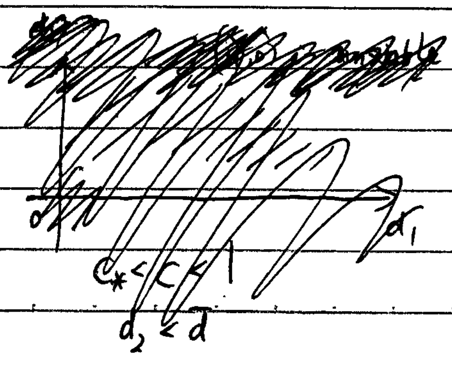
<u>Thm 8</u>. (Stability of $(\tilde{u}, 0)$) $\exists\, C_* \in (0, 1)$ such that

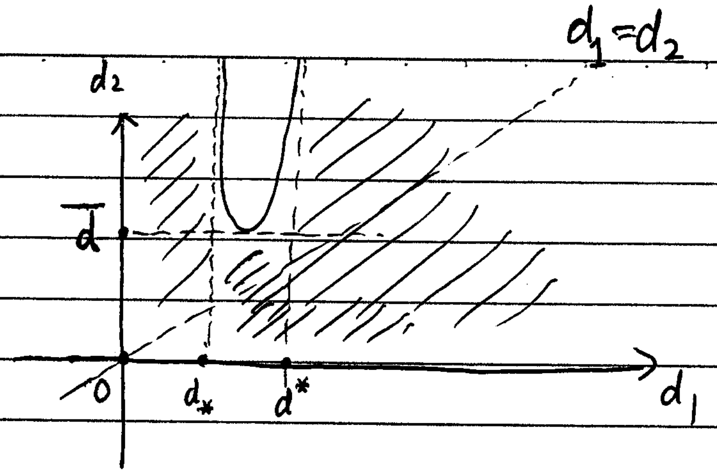
a) for every $c \in (0, C_*)$, $(\tilde{u}, 0)$ is unstable, $\forall d_1 > 0$, $\forall d_2 > 0$;

b) for every $c \in (C_*, 1)$, $\exists!\, \bar{d} > 0$ such that $(\tilde{u}, 0)$ is unstable when $d_1 > 0$ and $d_2 < \bar{d}$; for every $d_2 > \bar{d}$, $(\tilde{u}, 0)$ changes stability at least twice as d_1 varies from 0 to ∞.



$c < C_*$

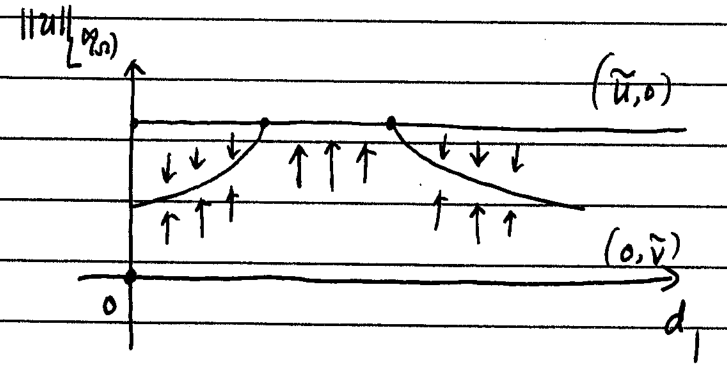




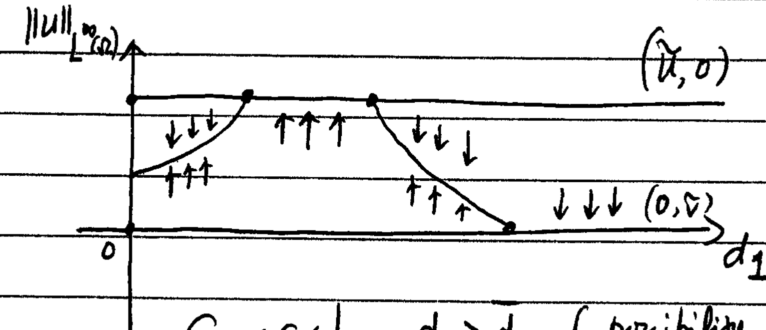
$C_* < C < 1$: $(\tilde{u}, 0)$ is stable in the unshaded region.

Conjecture. For every $C_* < C < 1$, there exist $d_* < d^*$ and some function $d_2 = h(d_1)$ ~~such that $(\tilde{u}, 0)$ is globally asymptotically stable for $d_2 > h(d_1)$ and $d_1 \in (d_*, d^*)$.~~

Intuitively, the dynamics of (11) may look like



$C_* < C < 1$, $d_2 > \bar{d}$ (possibility one)



$C_* < C < 1$, $d_2 > \bar{d}$ (possibility two)

Both cases are possible, and which one occurs is dependent on the value of $\underline{\underline{b}}$.

<u>Proof of Th'm 8 (sketch)</u>. One of the key ingredients is to understand the shape of $\int_\Omega \tilde{u}(x;d_1)\,dx$, as a function of d_1. This kind of problem seems rather unconventional and is of independent interest.

First we illustrate the connection between the stability of $(\tilde{u},0)$ and $\int_\Omega \tilde{u}(x;d_1)\,dx$ — can be thought as the total population of species. The stability of $(\tilde{u},0)$ is determined by the sign of the smallest eigenvalue of the problem

(16) $$d_2\Delta\varphi + [a(x) - c\tilde{u}]\varphi = -\lambda\varphi \text{ in } \Omega, \quad \nabla\varphi\cdot\vec{n}\big|_{\partial\Omega} = 0.$$

To be more precise, $(\tilde{u},0)$ is stable if $\lambda>0$, $(\tilde{u},0)$ is unstable if $\lambda<0$. Roughly speaking, $\lambda=0 \iff d_2 = h(d_1)$.

Note that λ is a monotone increasing function of d_2, and the following estimates hold:

(17) $$\lim_{d_2\to 0}\lambda = \min_{x\in\bar{\Omega}}\left[c\tilde{u}(x) - a(x)\right] < 0;$$

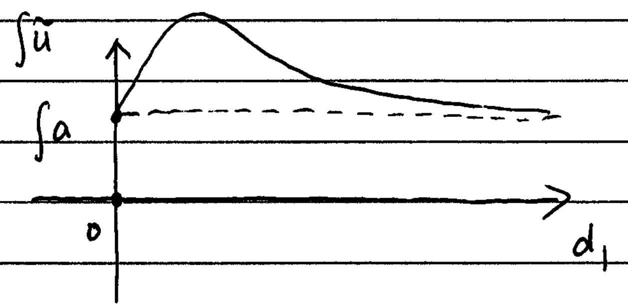
(18) $$\lim_{d_2\to+\infty}\lambda = c\int_\Omega \tilde{u}(x;d_1)\,dx - \int_\Omega a(x)\,dx.$$

The first equality of (17) is a corollary of some fairly general result: the smallest eigenvalue of the operator $-\varepsilon\Delta + m(x)$, subject to no-flux boundary condition, converge to $\min_{\bar{\Omega}} m$ as $\varepsilon \to 0+$.

The second inequality in (17) follows from $c<1$ and $a-\tilde{u}$ is positive somewhere in $\bar{\Omega}$ (since $\int_\Omega \tilde{u}(a-\tilde{u})=0$).

By (18) we see that the shape of $\int_\Omega \tilde{u}(x;d_1)dx$ is crucial:

Th'm 9. Suppose that $a \geq 0$, $a \not\equiv$ constant. Then $\lim_{d_1\to 0}\int_\Omega \tilde{u}(x;d_1)dx$
$= \lim_{d_1\to+\infty}\int_\Omega \tilde{u}(x;d_1)dx = \int_\Omega a(x)dx < \int_\Omega \tilde{u}(x;d_1)dx$.

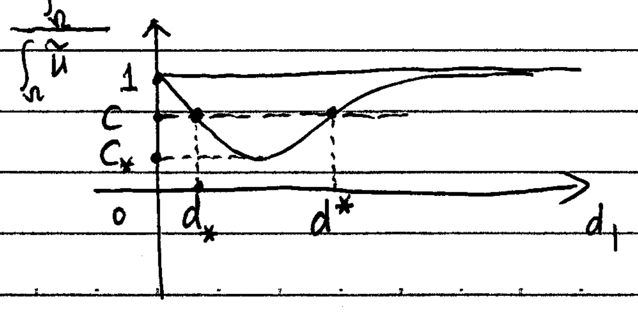


How to prove $\int_\Omega a(x)dx < \int_\Omega \tilde{u}(x;d_1)dx$:

$$d_1\frac{\Delta\tilde{u}}{\tilde{u}} + a(x) - \tilde{u} = 0$$

$$\Rightarrow \int_\Omega \tilde{u}(x;d_1)dx - \int_\Omega a(x)dx = d_1\int_\Omega \frac{\Delta\tilde{u}}{\tilde{u}} = d_1\int_\Omega \frac{|\nabla\tilde{u}|^2}{\tilde{u}^2} > 0$$

$$C_* := \frac{\int_\Omega a(x)dx}{\sup_{0<d_1<\infty}\int_\Omega \tilde{u}(x;d_1)dx} \in (0,1), \text{ by Th'm 9.}$$



$\Rightarrow$ $(\tilde{u},0)$ is stable if $C_* < c < 1$, $d_* < d_1 < d^*$ and $d_2 > h(d_1)$.

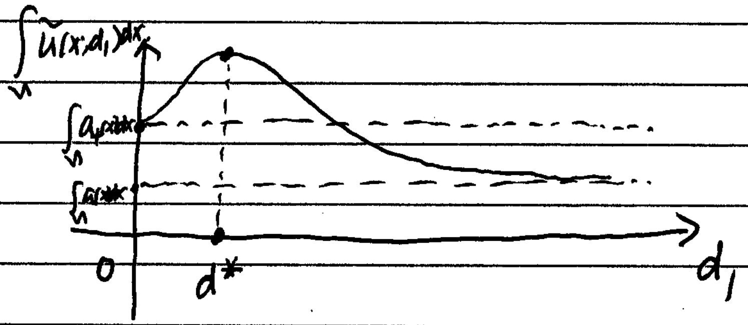
• Shape of $\int_\Omega \tilde{u}(x;d_1)\,dx$ as a function of d_1.

(*) $\quad d_1 \Delta \tilde{u} + \tilde{u}\,[a(x) - \tilde{u}] = 0$ in Ω, $\quad \nabla \tilde{u} \cdot \vec{n}\big|_{\partial\Omega} = 0$.

If $\int_\Omega a(x)\,dx > 0$, (*) has a unique positive solution for every $d_1 > 0$.

<u>Conjecture</u>. $\exists\, d^* > 0$ such that $\int_\Omega \tilde{u}(x;d_1)\,dx$ is an increasing function of d_1 in $(0, d^*)$ and $\int_\Omega \tilde{u}(x;d_1)\,dx$ is decreasing for $d_1 > d^*$.

That is, $\int_\Omega \tilde{u}(x;d_1)\,dx$ has a unique critical point in $(0,\infty)$.



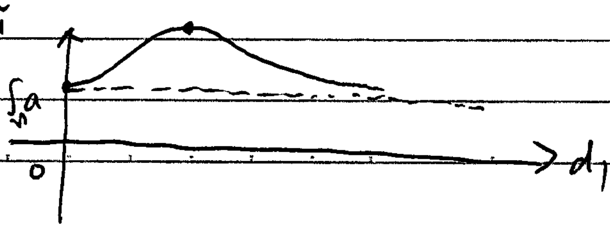
We have some partial results:

<u>Th'm</u> (Y.L. 2004)

a) Suppose that $a \geq 0$, $a \not\equiv$ constant. Then

This is the same as Th'm 9.

$$\lim_{d_1 \to 0} \int_\Omega \tilde{u} = \lim_{d_1 \to \infty} \int_\Omega \tilde{u} = \int_\Omega a(x)\,dx < \int_\Omega \tilde{u}(x;d_1)\,dx, \quad \forall d_1$$



<u>Note.</u> For this case, we do not know whether $\int_\Omega \tilde{u}$ has a unique critical point in $(0, +\infty)$.

<u>b)</u> Suppose that $\int_\Omega a(x)dx > 0$, $a \not\equiv$ constant, $(N=1)$ a changes sign and has only finite simple roots. Then

$$(19) \quad \lim_{d_1 \to \infty} \int_\Omega \tilde{u} < \lim_{d_1 \to 0} \int_\Omega \tilde{u} < \sup_{0<d_1<\infty} \int_\Omega \tilde{u}(x; d_1)dx.$$

<u>Note.</u> We do not (even) know whether (19) holds under the assumption $\int_\Omega a(x)dx > 0$ and $a \not\equiv$ constant. The proof of (b) follows from the following estimate: (Suppose that) $\Omega =$ interval, $a \in C^2[0, 1]$ and $a(x) = 0$ has finite number of roots in $[0, 1]$, none of them is degenerate. Then $\exists$ two positive constants C_0 and C_1 such that

$$(20) \quad \int_\Omega \tilde{u}(x; d_1)dx \geqslant \int_\Omega a_+(x)dx + C_0\, d_1^{\frac{2}{3}}$$

for every $d_1 \in (0, C_1)$.