Biodiversity through high intensity competition

Emerging Challenges at the Interface of Maths.,
Environmental Science and Spatial Ecology

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Structure of the talk:

1. Opening a debate.

2. Classic competing species models.

3. Incorporating territorial refuges.

4. The underlying mathematical tools.

5. References

1. OPENING A DEBATE

- Basically, the **Competitive Exclusion Principle** (CEP) establishes that two species cannot coexist when they have identical needs of a limited resource; the key being that the more similar the needs share are, the more intense the competition is (Oosting 1956).

- Rather paradoxically, in investigating the validity of the CEP it seems that competitive tendencies overlap with environmental heterogeneities and hidden predating and facilitative mechanisms which give rise to very complex process that make it extremely difficult to isolate the CEP in the laboratories experiments carried out to confirm its validity (Begon, Harper and Townsend 1996, Quinlan 2004).

- Actually, in many circumstances, as in the Park's pioneering experiments with flour beetles (Park 1954, Edmunds, Cushing et. al. 2003), the outcome of competition is extremely sensitive to environmental conditions, such as humidity.

- Most strikingly, in some laboratories experiments involving a high number of species it has been observed that many more populations than expected persisted for many generations (Belovsky et al. 1999), though in others one species is driven to extinction by the competitors in a rather robust fashion (Tilman, Matsson and Langer 1981).

- Nevertheless, the CEP does not appear to occur in nature, where high biodiversity is commonly observed even in seemingly homogeneous habitats (Loladze et al. 2001, Cushing et al. 2004, Cheeson and Huntly 1997, Li and Smith 2001).

- These and other paradoxical situations have originated an important controversy concerning the validity and the precise meaning of the CEP.

- As a consequence from this debate, May 1981 defined the CEP as the instance where two species make their livings in identical ways being unable to coexist in a stable fashion, as a result of which they cannot occupy the same niche and, consequently, must segregate to avoid extinction.

- Other experts, as Crawley 1986, go further defending that the CEP simply *does not work*, that being logically impeccable its assumptions are wrong. As a matter of fact, the nature of the environments where most of the validating experiments for the CEP have been carried out was not neither spatially nor temporally heterogeneous (Tilman 1982).

- Strongly supporting the serious concerns of May 1981 and Crawley 1986 about the validity of the CEP, are the so called ‘Lazaro’ species in zoo-paleontology (Kauffman and Harries 1996); those disappearing from fossil registers and suddenly appearing after many million years.

- The well documented existence of Lazaro species strongly supports the theory that the existence of refuge areas (islands, caves, deep see waters, etc.) is a crucial mechanism to avoid extinction when an ‘apparent’ mass extinction occurs.

- It is commonly agreed that the standard concept of competition is consistent with the general assumptions of the Lotka-Volterra assumptions, which still conforms the basis of the mathematical theory of competition.

2. CLASSIC COMPETING SPECIES MODELS

2.1. The non-spatial model of Lotka and Volterra

$$\boxed{\begin{cases} \dfrac{dN_1}{dt} = \dfrac{\lambda}{K_1} N_1 \left(K_1 - N_1 - \alpha_{12} N_2\right) \\[2ex] \dfrac{dN_2}{dt} = \dfrac{\mu}{K_2} N_2 \left(K_2 - N_2 - \alpha_{21} N_1\right) \\[2ex] N_1(0) = N_1^0 > 0, \quad N_2(0) = N_2^0 > 0, \end{cases}}$$

(Volterra 1931, Lotka 1932)

- N_1 and N_2 measure the abundance of the species at time t, (N_1^0 and N_2^0 are the abundances at $t = 0$).
- λ and μ are their intrinsic growth rates.
- K_1 and K_2 are their carrying capacities.
- α_{12} and α_{21} are their competition coefficients; they measure the strength of the inhibitory effects between the species.

By setting

$$b := \frac{\lambda K_2}{\mu K_1}\,\alpha_{12}, \qquad c := \frac{\mu K_1}{\lambda K_2}\,\alpha_{21},$$

$$u := \frac{\lambda}{K_1}\,N_1, \qquad v := \frac{\mu}{K_2}\,N_2,$$

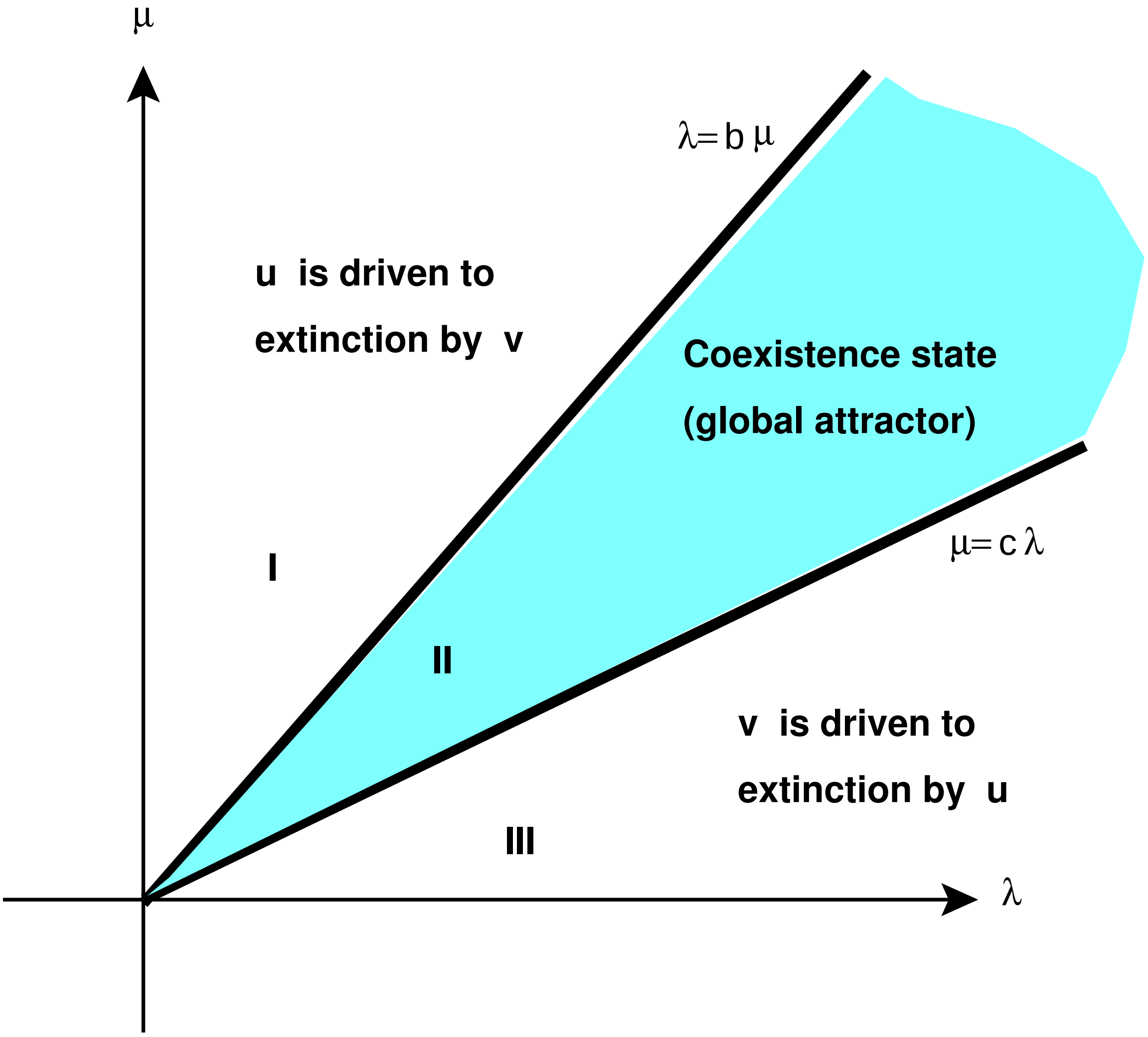
$$u_0 := \frac{\lambda}{K_1}\,N_1^0, \qquad v_0 := \frac{\mu}{K_2}\,N_2^0,$$

the model can be equivalently written as

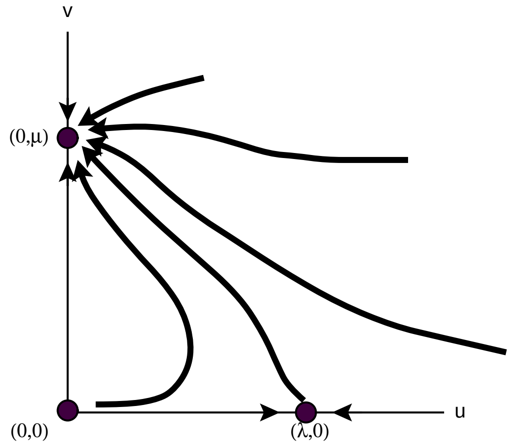
$$\boxed{\begin{cases} \dfrac{du}{dt} = \lambda u - u^2 - buv, \\[2ex] \dfrac{dv}{dt} = \mu v - v^2 - cuv, \\[2ex] u(0) = u_0 > 0, \quad v(0) = v_0 > 0. \end{cases}}$$

$$\boxed{bc = \alpha_{12}\alpha_{21} \begin{cases} < 1 \text{ (low intensity competition)} \\[2ex] > 1 \text{ (high intensity competition)} \end{cases}}$$

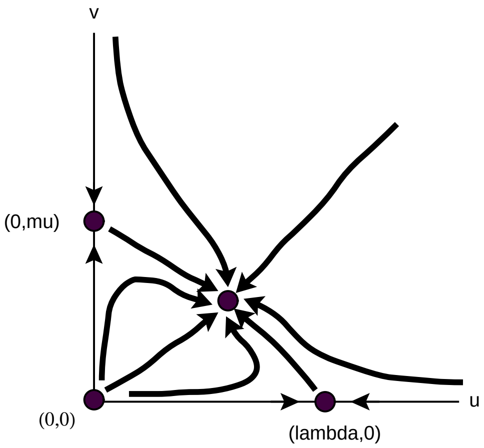
Low intensity competition ($bc < 1$)



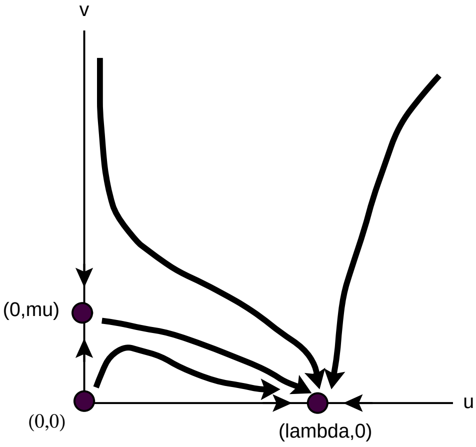
- Region I: $c < \frac{1}{b} < \frac{\mu}{\lambda} \quad [\lambda < b\mu;\ \mu > c\lambda]$
- Region II: $c < \frac{\mu}{\lambda} < \frac{1}{b} \quad [\lambda > b\mu;\ \mu > c\lambda]$
- Region III: $\frac{\mu}{\lambda} < c < \frac{1}{b} \quad [\lambda > b\mu;\ \mu < c\lambda]$



Region I:

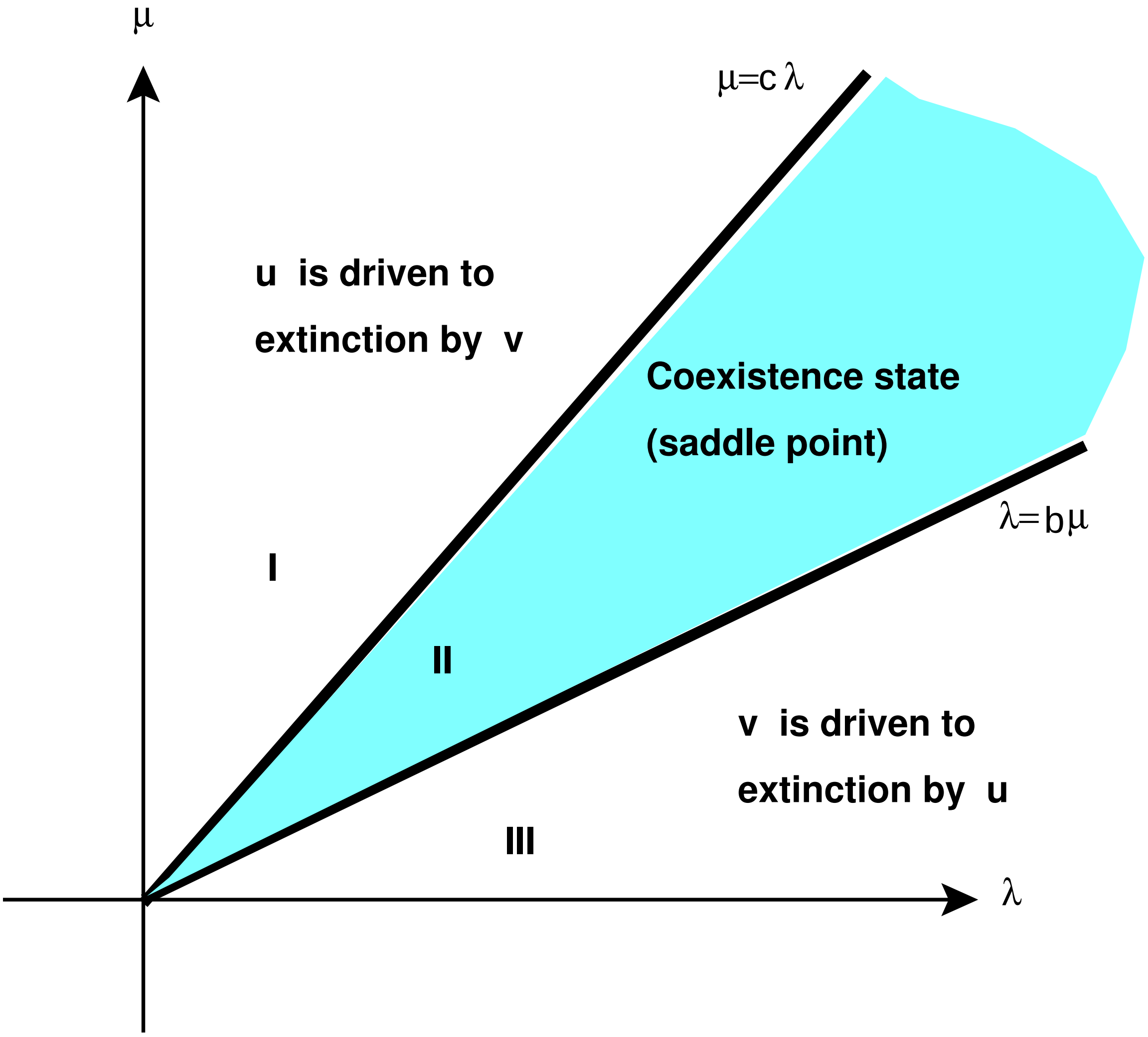


Region II:



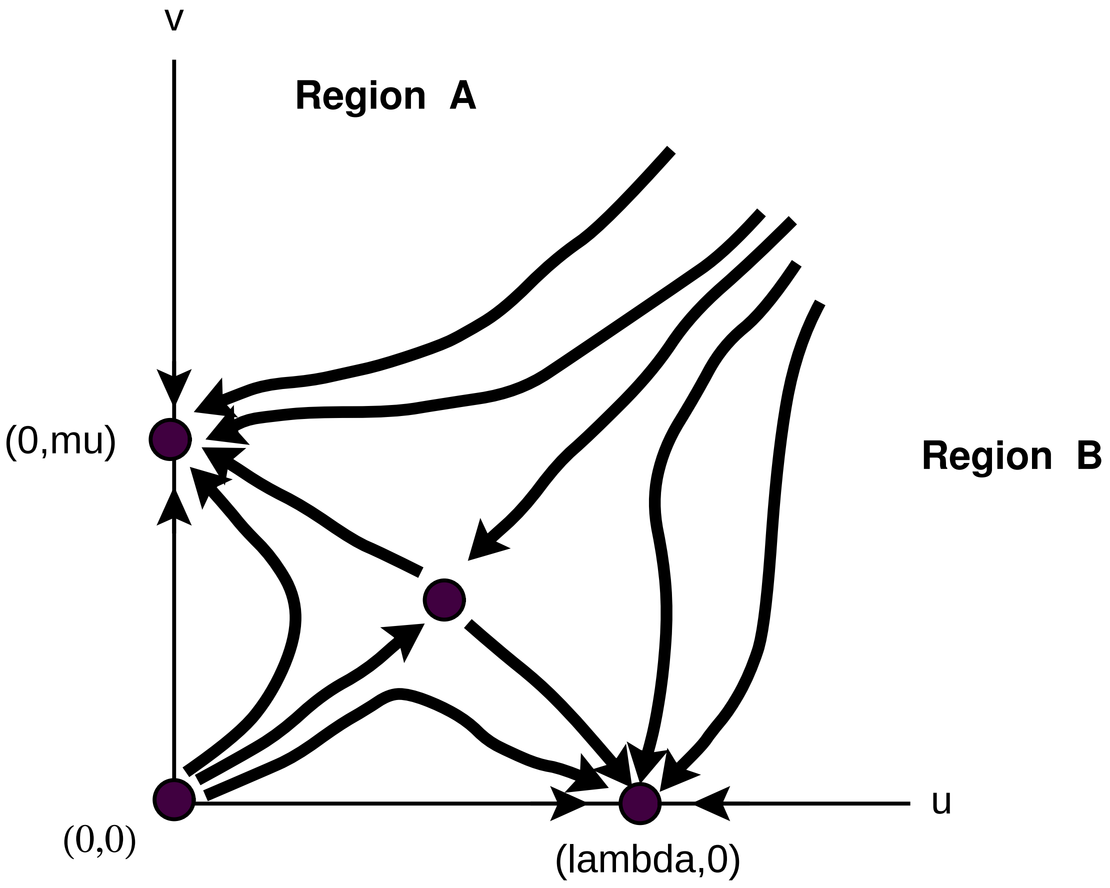
Region III:

High intensity competition ($bc > 1$)



- Region I: $\frac{1}{b} < c < \frac{\mu}{\lambda}$ $[\lambda < b\mu;\ \mu > c\lambda]$
- Region II: $\frac{1}{b} < \frac{\mu}{\lambda} < c$ $[\lambda < b\mu;\ \mu < c\lambda]$
- Region III: $\frac{\mu}{\lambda} < \frac{1}{b} < c$ $[\lambda > b\mu;\ \mu < c\lambda]$

Dynamics in Region II:

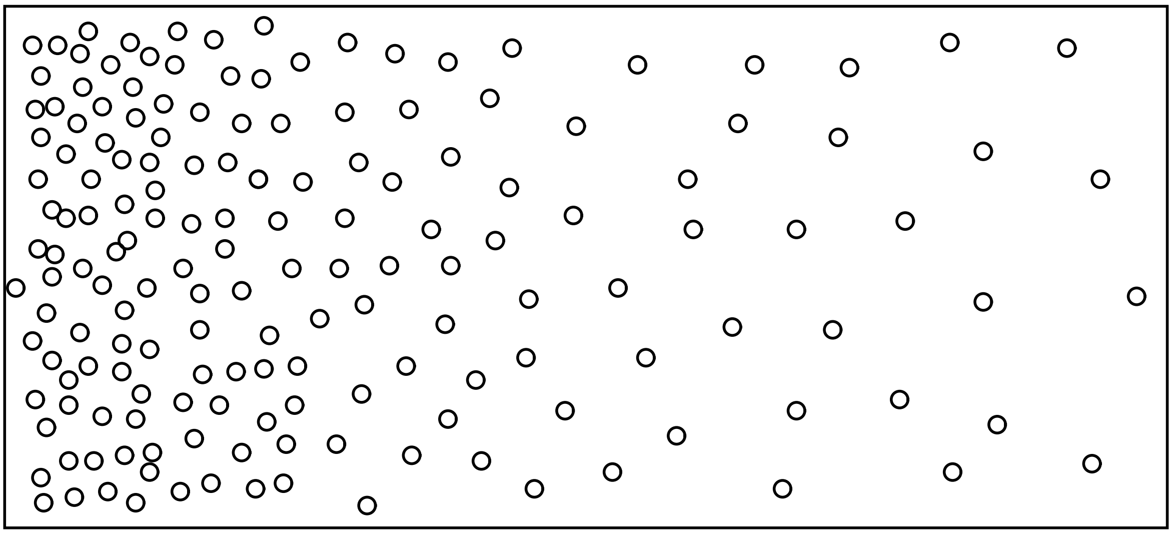


BI-STABILITY
Founder control competition

- v wins if $(u_0, v_0) \in A$.
- u wins if $(u_0, v_0) \in B$.

2.2. The Lotka-Volterra spatial model

It is assumed that each individual moves around randomly, with no preference for a particular direction, much like in Brownian motion.



This provokes a regular migration from highly populated areas to less populated areas according to the Fourier-Fick law.

$$\boxed{\mathbf{J_u} := -d_1 \nabla u, \qquad \mathbf{J_v} = -d_2 \nabla v.}$$

where $d_1 > 0$, $d_2 > 0$, are the diffusivities of u and v.

The resulting spatial model is

$$\boxed{\begin{cases} \dfrac{\partial u}{\partial t} - d_1 \Delta u = \lambda u - u^2 - buv, \\[2ex] \dfrac{\partial v}{\partial t} - d_2 \Delta v = \mu v - v^2 - cuv, \end{cases}}$$

for every $x = (x_1, x_2, x_3) \in \Omega$ and $t > 0$,
where Ω is the inhabiting area, and

$$\Delta = \frac{\partial^2}{\partial x_1^2} + \frac{\partial^2}{\partial x_2^2} + \frac{\partial^2}{\partial x_3^2} = \nabla^2$$

is the Laplace operator.

The spatial model has to be completed with:

- Boundary conditions along the habitat edges, e.g.,

$$\boxed{u = v = 0 \text{ on } \partial\Omega \text{ for all } t > 0.}$$

- Initial conditions

$$\boxed{u(x,0) = u_0(x), \quad v(x,0) = v_0(x),\ x \in \Omega.}$$

Here, we are assuming that the region outside the habitat is immediately lethal. In other words, the habitat is surrounded by an absorbing boundary, though most of our findings are still valid if other boundary conditions are imposed.

Terrestrial-aquatic edges are absorbing boundaries for seeds of plant species incapable of surviving in both habitats (Fagan, Cantrell and Cosner 1999), as it was in the legislative boundary of Yellowstone National Park for bison dispersing into Montana, where they were shot to control the spread of brucellosis (Dobson and Meagher 1996).

2.3. A crucial feature of the spatial model

The fact that individuals cannot choose to migrate, or not, with full freedom, for as the migration occurs from densely populated areas to sparse areas, is a pivotal mechanism for permanence.

Ecological Principle 1:

Independently of the geometry of the habitat Ω, *if*

$$(1-b)(1-c)<0$$

and

$$bc-1>0$$

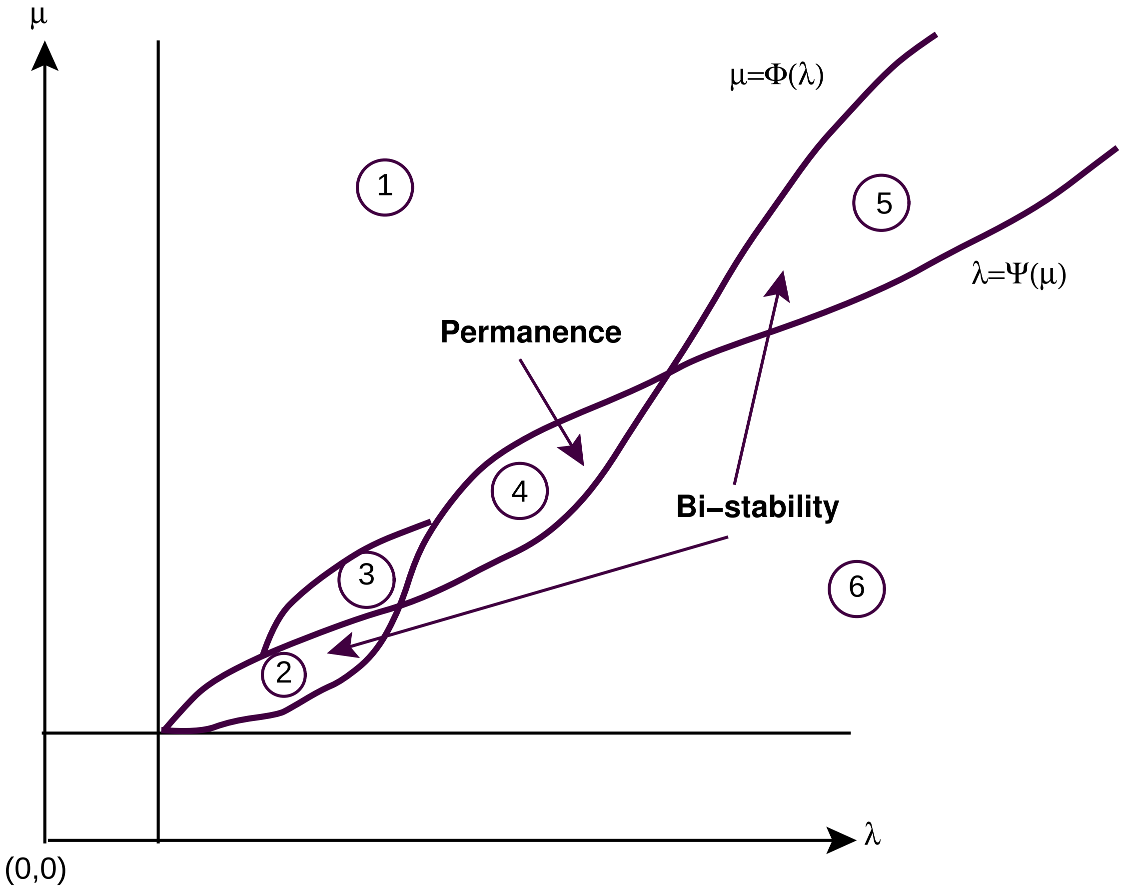
is sufficiently small, then there is a range of values of λ *and* μ *for which the species are permanent.*

So, the spatial model can be permanent even when the non-spatial model is bi-stable.

(Eilbeck, Furter and López-Gómez 1994).

Utterly attributable to dispersal!

Sketch of the proof:



$$\Phi(\lambda) = \sigma[-d_2\Delta + c\theta_\lambda],$$

$$\Psi(\mu) = \sigma[-d_1\Delta + b\theta_\mu],$$

where $(\theta_\lambda, 0)$ and $(0, \theta_\mu)$ stand for the semi-trivial solutions of the problem. They are defined iff

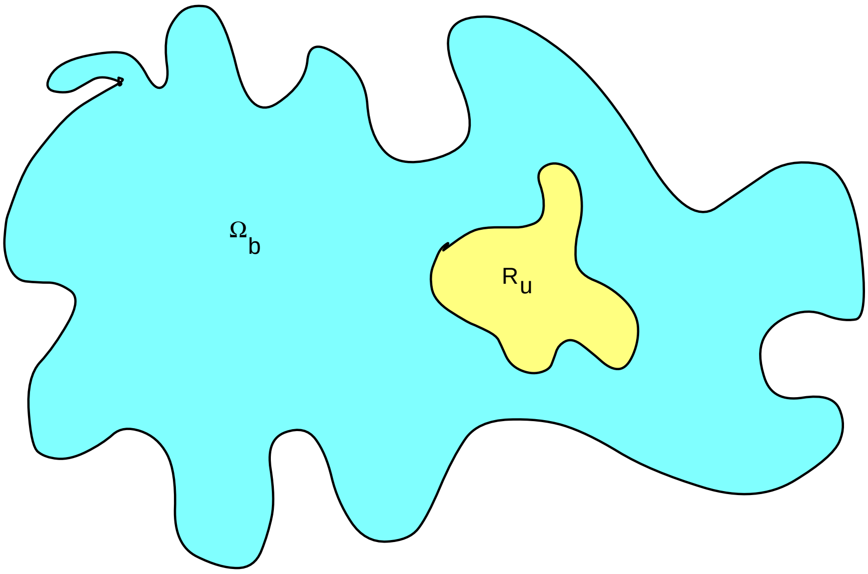
$$\lambda > d_1\sigma_0, \quad \mu > d_2\sigma_0, \quad \sigma_0 := \sigma[-\Delta; \Omega].$$

3. INCORPORATING TERRITORIAL REFUGES

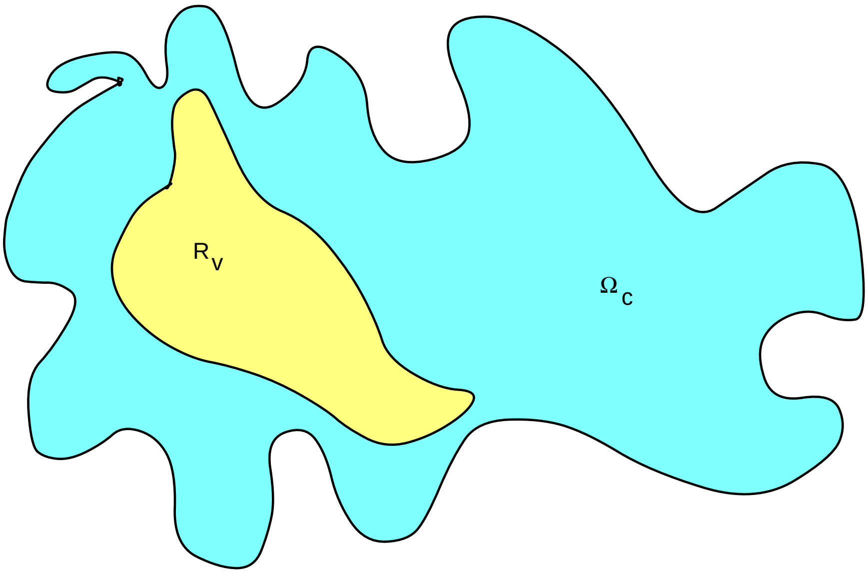
More generally, we can assume that

$$b = B \cdot b(x), \qquad c = C \cdot c(x),$$

depend upon the location $x \in \Omega$.



Nodal behaviour of b(x)



Nodal behaviour of

- Ω_b is the region where $b(x) > 0$ (u receives aggressions from v).
- R_u is the region where $b = 0$ (u is free from v), i.e., the refuge of u.
- Ω_c is the region where $c(x) > 0$ (v receives aggressions from u).
- R_v is the region where $c = 0$ (v is free from u), i.e., the refuge of v.
- B and C measure the intensity of the aggressions between the species u and v.

Ecological Principle 2:

The model is permanent if $(\theta_\lambda, 0)$ *and* $(0, \theta_\mu)$ *are linearly unstable. In other words, if*

$$\lambda > \sigma[-d_1\Delta + B\,b(x)\theta_\mu],$$

$$\mu > \sigma[-d_2\Delta + C\,c(x)\theta_\lambda].$$

Moreover,

$$\lim_{B\uparrow\infty} \sigma[-d_1\Delta + B\,b(x)\theta_\mu] = \sigma[-d_1\Delta; R_u],$$

$$\lim_{C\uparrow\infty} \sigma[-d_2\Delta + C\,c(x)\theta_\lambda] = \sigma[-d_2\Delta; R_v].$$

Consequently, if R_u *can support to* u *and* R_v *can support to* v*, i.e., if*

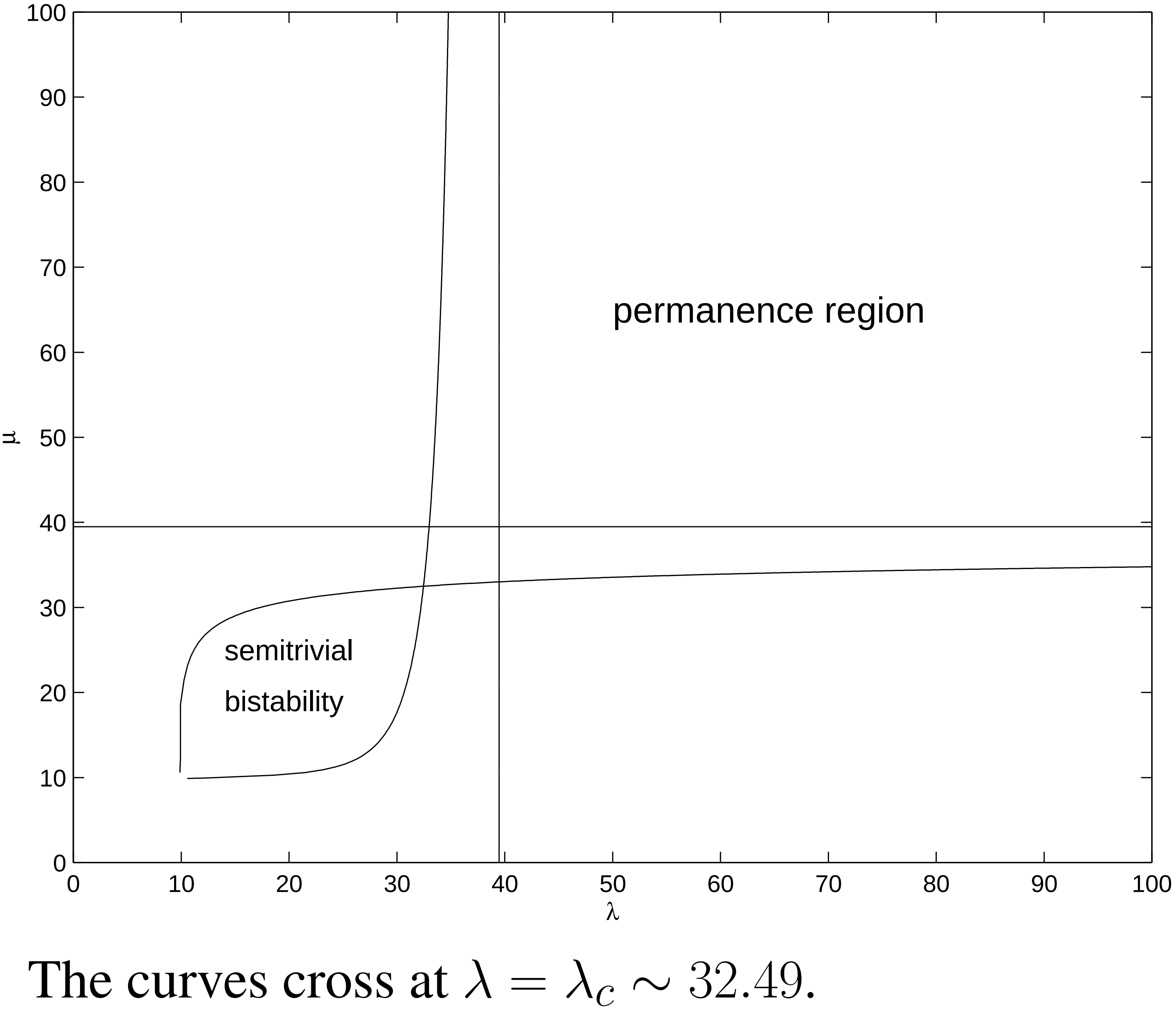
$$\lambda > \sigma[-d_1\Delta; R_u] \quad \textit{and} \quad \mu > \sigma[-d_2\Delta; R_v],$$

then, the species persist for all $B > 0$ *and* $C > 0$*.*

So, the CEP is false in the presence of refuges.

(López-Gómez 1994, L-G and Molina-Meyer 2006)

The next plot shows the curves of change of stability of the semi-trivial states for a simple one-dimensional model with sufficiently large B and C.



The curves cross at $\lambda = \lambda_c \sim 32.49$.

These curves were computed in the special case when

$$\Omega = (0,1), \qquad d_1 = d_2 = 1,$$

$$b(x) = \begin{cases} \sin(2\pi x) & \textbf{if } 0 \le x \le 0.5, \\ 0 & \textbf{if } 0.5 \le x \le 1, \end{cases}$$

$$c(x) = \begin{cases} 0 & \textbf{if } 0 \le x \le 0.5, \\ \sin(2\pi x) & \textbf{if } 0.5 \le x \le 1, \end{cases}$$

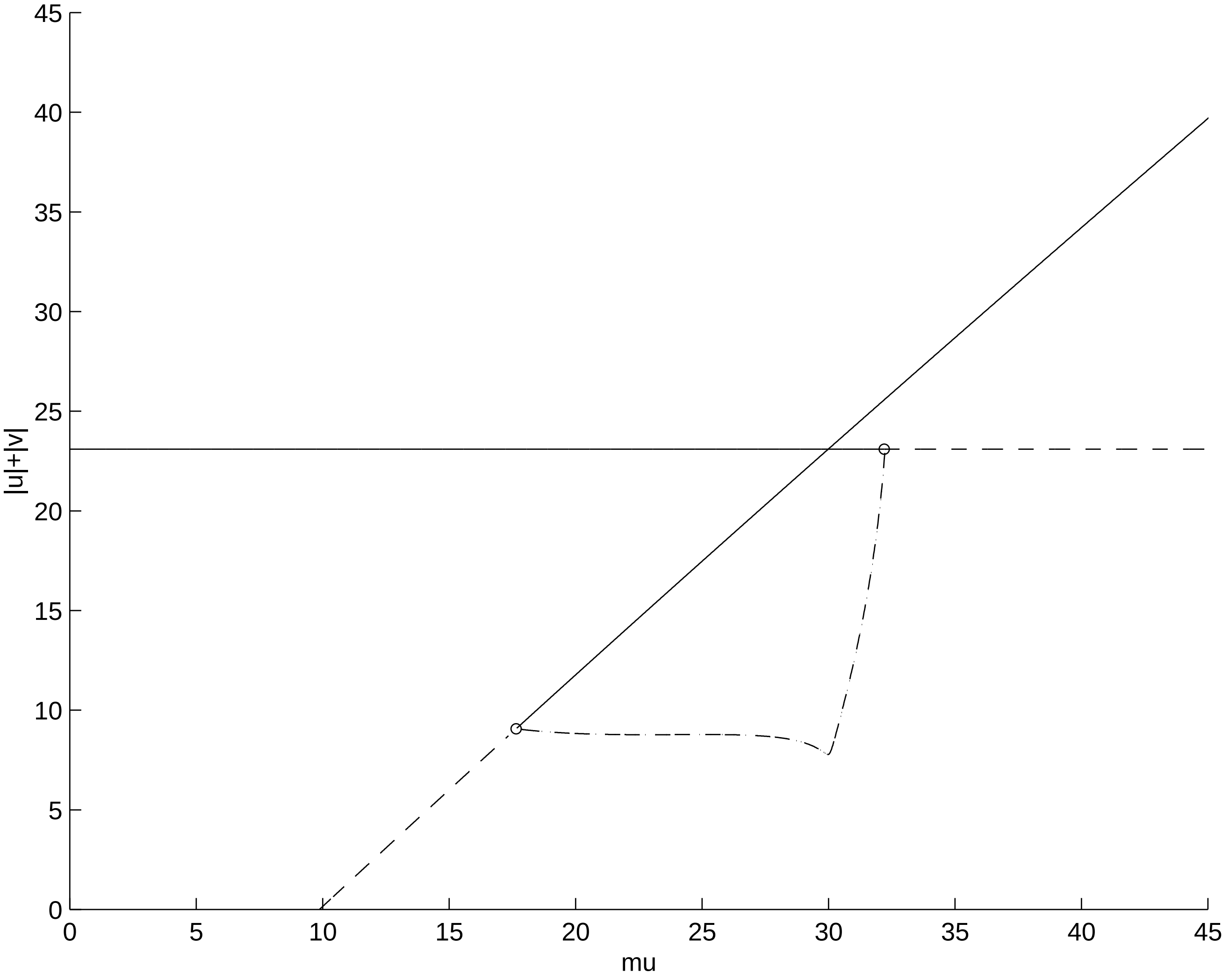
and

$$B = C = 120.$$

(López-Gómez and Molina-Meyer 2006)

In this example, $R_u = (0.5, 1)$ and $R_v = (0, 0.5)$. Consequently, the model is permanent for all $B > 0$ and $C > 0$ if

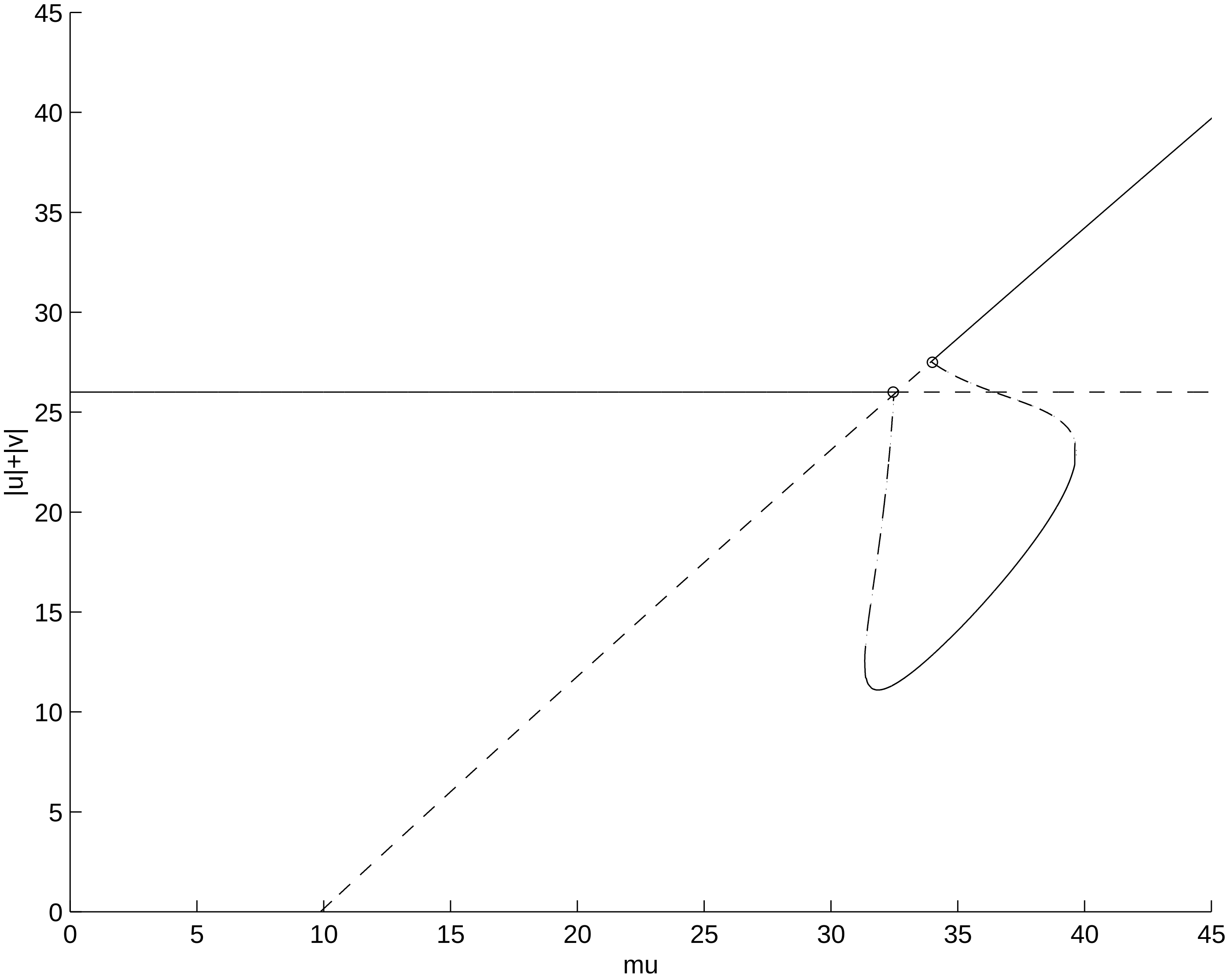
$$\lambda, \mu > \sigma[-\Delta; (0, 0.5)] = 4\pi^2 \sim 39.4784.$$



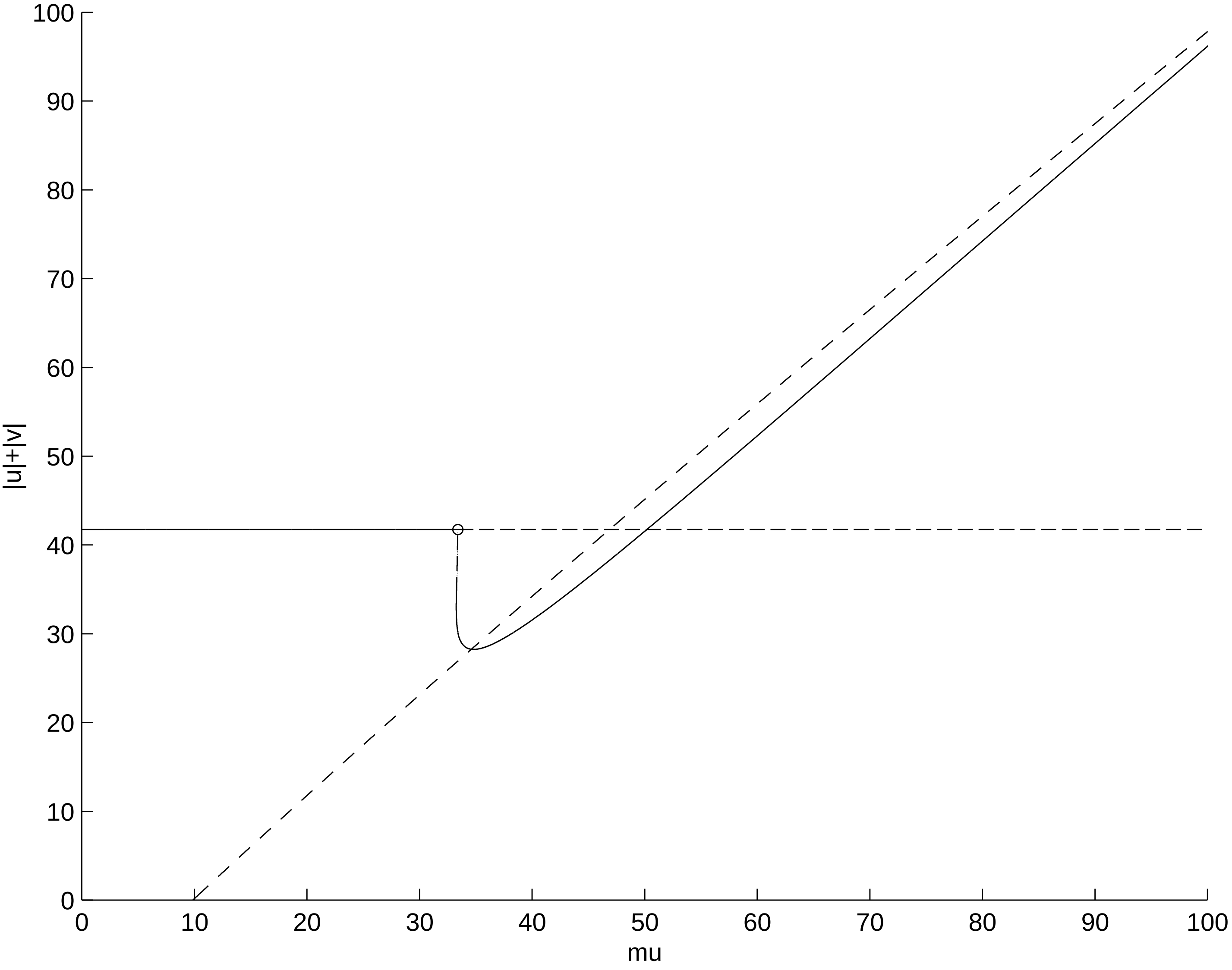
A plot of the bifurcation diagram of non-negative solutions fixing

$$\lambda = 30 < \lambda_c = 32.49$$

and using μ as the main continuation parameter. Each point on each of the plotted curves represents a non-negative steady-state pair of the model.



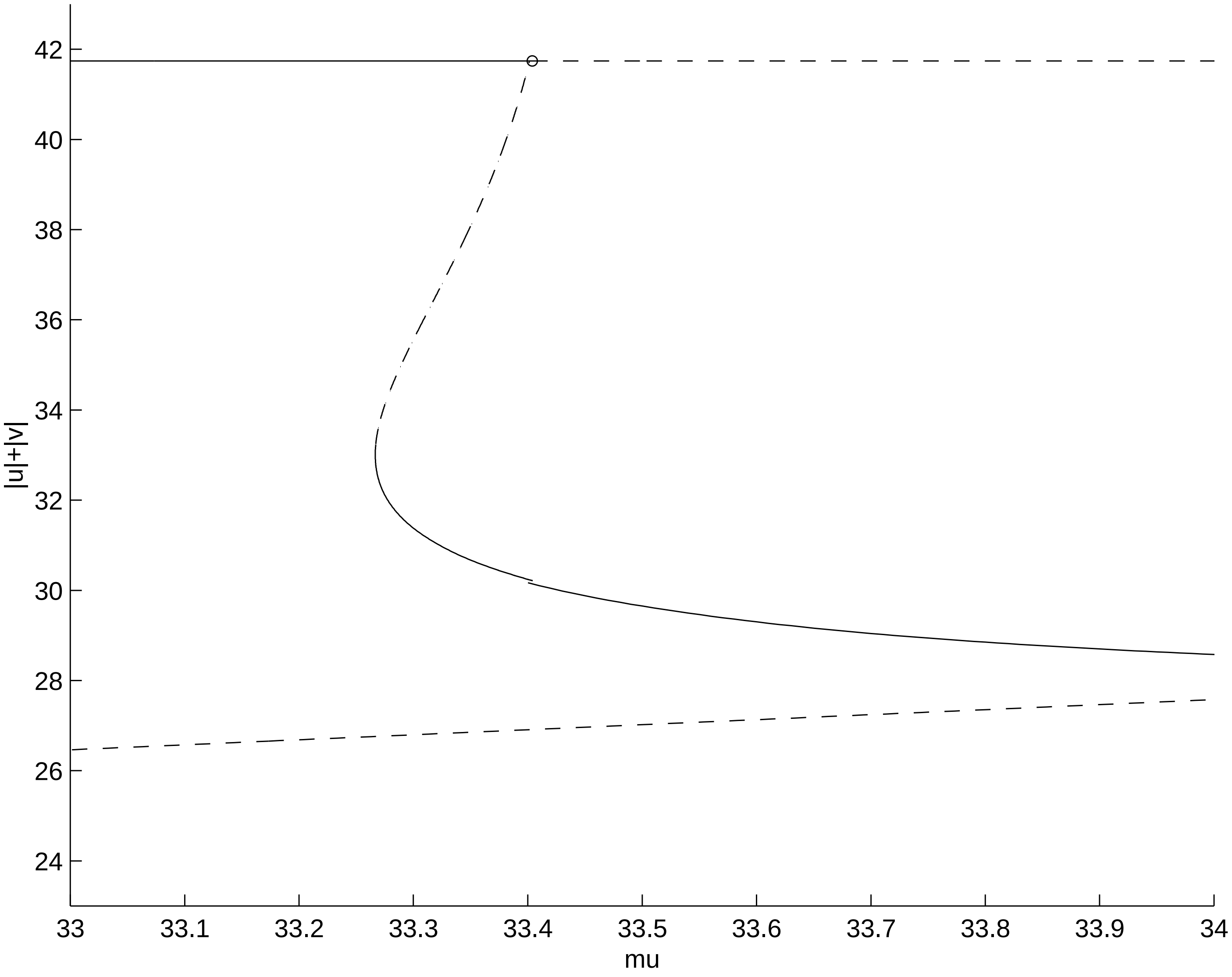
A plot of the bifurcation diagram of non-negative solutions fixing $\lambda = 32.6 > \lambda_c$ and using μ as the main continuation parameter.



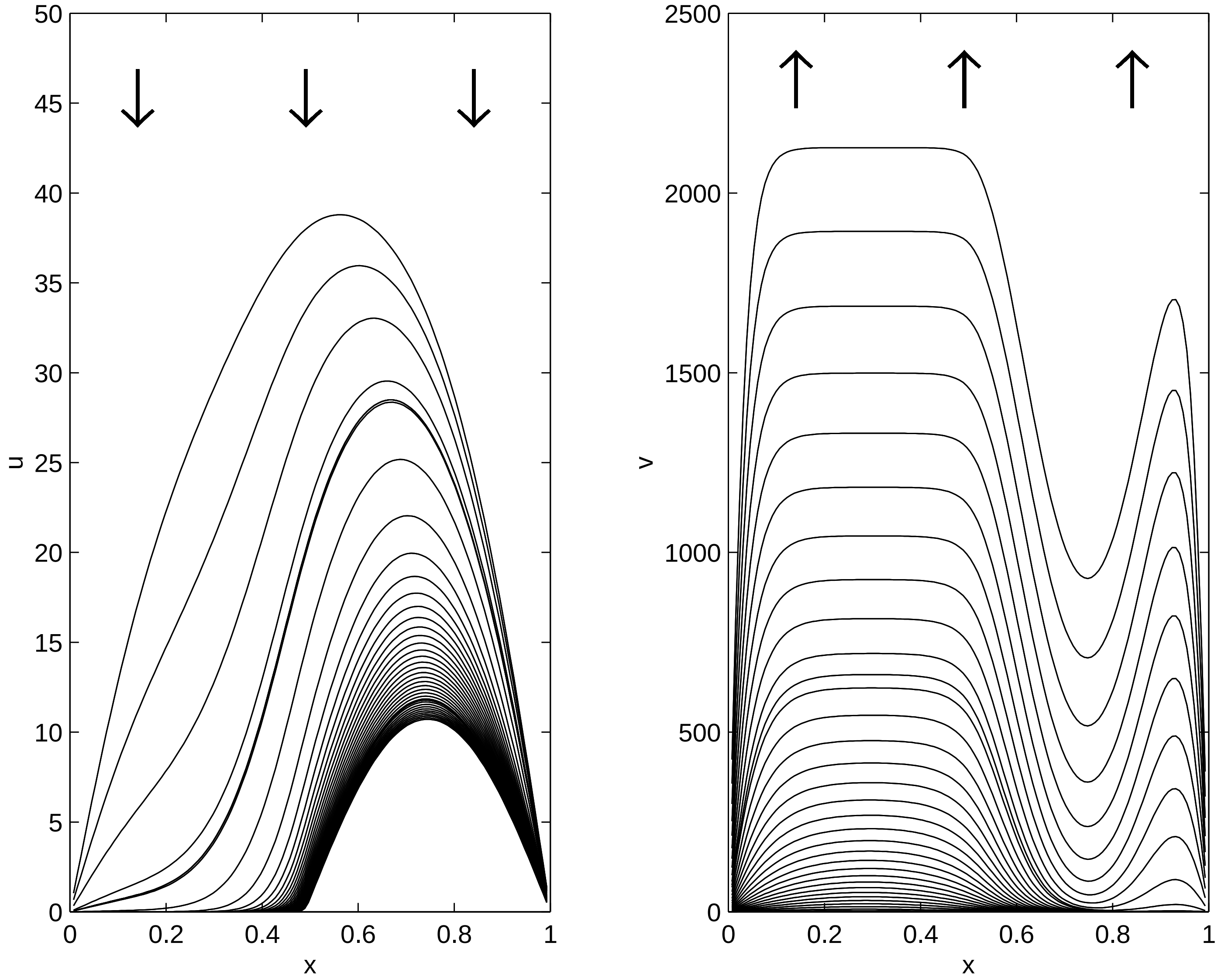
A plot of the bifurcation diagram of non-negative solutions fixing

$$\lambda = 46.88 > 4\pi^2 \sim 39.47$$

and using μ as the main continuation parameter.



A magnification of the previous plot around the bifurcation point from the semi-trivial state



A series of (linearly stable) coexistence states along the curve of coexistence states of the previous bifurcation diagram. As μ grows, the species v grows everywhere in Ω, while u segregates into R_u.

Ecological Principle 3:

Suppose $\lambda > \sigma[-d_1\Delta; R_u]$ *and let*

$$(\mu_n, u_n, v_n), \qquad n \geq 1,$$

be a sequence of coexistence states such that

$$\lim_{n\uparrow\infty} \mu_n = \infty.$$

Then,

$$\boxed{\lim_{n\uparrow\infty} v_n(x) = \infty \qquad \text{for all } \; x \in \Omega,}$$

while

$$\boxed{\lim_{n\uparrow\infty} u_n = \begin{cases} 0 & \text{in } \; \Omega_b, \\ \theta_\lambda[R_u] & \text{in } \; R_u, \end{cases}}$$

where $\theta_\lambda[R_u]$ *is the density of the* u*-population supported by* R_u*.*

Consequently, in the presence of refuges, the species segregate into them as the intensity of the competition grows.
(López-Gómez 1994, L-G and Molina-Meyer 2006)

These segregation mechanisms, as a result from severe competition, combined with some subsequent species differentiation, enhanced by spatial and temporal heterogeneities, after the appropriate number of generations, might explain the Earth bio-diversity, which seems to be confirmed by the available fossil registers.
(López-Gómez and Molina-Meyer 2006)

The mathematical result are valid for any number of species under rather general conditions on the habitat edges. (López-Gómez 1997).

4. THE UNDERLYING MATHEMATICAL TOOLS

The main technical tool is the next characterization of the maximum principle, attributable to López-Gómez and Molina-Meyer 1994 (for cooperative systems under Dirichlet boundary conditions), and to Amann and López-Gómez 1998 for general boundary operators $\mathfrak{B}$ of mixed non-classical type.

THEOREM 1: *Let* $(\mathfrak{L}, \mathfrak{B}, \Omega)$ *a linear elliptic b.v.p. in* Ω. *Then, the following three conditions are equivalent:*

(a) $\sigma[\mathfrak{L}, \mathfrak{B}, \Omega] > 0$.

(b) $(\mathfrak{L}, \mathfrak{B}, \Omega)$ *admits a positive strict supersolution.*

(c) $(\mathfrak{L}, \mathfrak{B}, \Omega)$ *satisfies the strong maximum principle.*

Simultaneously, Berestycki, Nirenberg and Varadhan 1994 got the equivalence of (a) and (c) for the single equation under Dirichlet boundary conditions with no regularity constraints on the boundary.

Theorem 1 provides with the next fundamental result

THEOREM 2: *Let* $\mathfrak{L}$ *a second order elliptic operator in* Ω *and* $V > 0$ *a continuous potential such that*

$$\Omega_0 := \{\, x \in \Omega \;\; : \; V(x) = 0 \,\}$$

is a nice sub-domain of Ω*. Then,*

$$\boxed{\lim_{\lambda \uparrow \infty} \sigma[\mathfrak{L} + \lambda V; \Omega] = \sigma[\mathfrak{L}; \Omega_0].}$$

Proof: By the monotonicity of the principal eigenvalue with respect to the domain,

$$\sigma[\mathfrak{L} + \lambda V; \Omega] \leq \sigma[\mathfrak{L}; \Omega_0]$$

for all $\lambda \in \mathbb{R}$. It remains to show that, for any given $\varepsilon > 0$, there exists $\lambda_0 = \lambda_0(\varepsilon) > 0$ such that

$$\sigma[\mathfrak{L} + \lambda V; \Omega] \geq \sigma[\mathfrak{L}; \Omega_0] - \varepsilon$$

for all $\lambda \geq \lambda_0$.

Now, for sufficiently small $\delta > 0$, we consider the δ-neighborhood of Ω_0

$$\Omega_\delta := \Omega_0 + B_\delta.$$

By the continuous dependence of the principal eigenvalue with respect to the domain (López-Gómez 1996),

$$\lim_{\delta \downarrow 0} \sigma[\mathfrak{L}; \Omega_\delta] = \sigma[\mathfrak{L}; \Omega_0].$$

Consequently,

$$\sigma[\mathfrak{L}; \Omega_0] - \varepsilon < \sigma[\mathfrak{L}; \Omega_\delta] < \sigma[\mathfrak{L}; \Omega_0]$$

for sufficiently small $\delta > 0$. Choose one of those δ's. Then, it suffices to show that

$$\sigma[\mathfrak{L} + \lambda V; \Omega] > \sigma[\mathfrak{L}; \Omega_\delta]$$

for sufficiently large λ, or, equivalently,

$$\sigma[\mathfrak{L} + \lambda V - \sigma[\mathfrak{L}; \Omega_\delta]; \Omega] > 0.$$

According to Theorem 1, this occurs if the operator

$$L_{\lambda,\delta} := \mathfrak{L} + \lambda V - \sigma[\mathfrak{L}; \Omega_\delta]$$

admits a positive strict supersolution in Ω for large λ.

Let $\varphi_\delta > 0$ denote the principal eigenfunction associated to $\sigma[\mathfrak{L}; \Omega_\delta]$, and consider any function of the form

$$\Phi := \begin{cases} \varphi_\delta & \text{in } \; \Omega_{\delta/2} \\ \\ \psi_\delta & \text{in } \; \Omega \setminus \Omega_{\delta/2} \end{cases}$$

where ψ_δ is any smooth extension separated away from zero. A simple calculation shows that

$$h := \kappa\Phi$$

provides us with a positive strict supersolution of $L_{\lambda,\delta}$ in Ω provided $\kappa > 1$ is sufficiently large.

Adapting these argument to a nonlinear context, one can easily complete the proofs of the Principles 2,3.

5. REFERENCES

- Amann, H., López-Gómez, J., 1998. A priori bounds and multiple solutions for superlinear indefinite elliptic problems. J. Diff. Eqns. 146, 336-374.
- Begon, M., Harper, J. L., Townsend, C. R., 1996. Ecology, Blackwell Science, Oxford.
- Belovsky, G. E., Mellison, C., larson, C., Zandt, P. A., 1999. Experimental studies of extinction dynamics. Science 286, 1175-1177.
- Berestycki, H., Nirenberg, L., Varadhan, S. R. S., 1994. The principal eigenvalue and maximum principle for second order elliptic operators in general domains. Comm. in Pure and Appl. Maths. XLVII (1), 47-92.
- Cheeson, P., Huntly, N., 1997. The roles of harsh and fluctuating in the dynamics of ecological communities, Amer. Nat. 150, 519-553.
- Crawley, M. J., (Ed.) 1986. Plant Ecology. Blackwell Scientific Publications. Oxford.
- Cushing, J. M., Levarge, S., Chitnis, N., Henson, S. M., 2004. Some discrete competition models and the competitive exclusion principle. J. Diff. Eqns. Appns. 10, 1139-1151.
- Dobson, A., Meagher, M., 1996, The population dynamics of brucellosis in Yellowstone National Park. Ecology 177, 1026-1036.
- Edmunds, J., Cushing, J. M., Constantino, R. F., Shandelle, M. H., Dennis, B., Desharnais, R. A., 2003. Park's Tribolium competition experiments: a non-equilibrium species coexistence hypothesis. J. Anim. Ecol. 72, 703-712.
- Eilbeck, J. C., Furter, J. E., López-Gómez, J., 1994. Coexistence in the competition model with diffusion. J. Diff. Eqns. 107, 96-139.
- Fagan, W. F., Cantrell, R. S., Cosner, C., 1999. How habitat edges change species interactions. Amer. Nat. 153, 165-182.
- Li, B. T., Smith, H., 2001. How many species can two resources support? SIAM J. Appl. Maths. 62, 336-366.
- Loladze, I., Kuang, Y., Else, J. J., Fagan, W. F. 2004. Competition and Stoichiometry: coexistence of two predators on a prey. Theoretical Population Biology 65, 1-15.
- López-Gómez, J., 1995. Permanence under strong competition. WSSIAA 4, 473-488, World Scientific Company, Singapore.
- López-Gómez, J., 1996. The maximum principle and the existence of principal eigenvalues for some linear weighted b.v.p.'s. J. Diff. Eqns. 127, 263-294.
- López-Gómez, J., 1997. Strong competition with refuges. Nonl. Anal. TMA 30, 5167-5178.

- López-Gómez, J., Molina-Meyer, 1994. The maximum principle for cooperative weakly coupled elliptic systems and some applications, Diff. Int. Eqns. 7, 383-398.
- López-Gómez, J., Molina-Meyer, 2006. The competitive exclusion principle versus bio-diversity through competitive segregation and further adaptation to spatial heterogeneities. Theoretical Population Biology 69, 94-109.
- Lotka, A. J., 1932. The growth of mixed populations: two species competing for a common food supply. J. Washington Acad. Sci. 22, 461-469.
- Kauffman, E. G., Harries, P. J., 1996. The consequence of mass extinctions. The logic of extinctions. In Agustí, J., (Ed.) Metatemas vol. 42. Tusquets, Barcelona 1996.
- May, R. M., (Ed.) 1981. Theoretical Ecology. Principles and Applications. Sinauer Associates. Oxford.
- Oosting, H. J., 1956. The study of plant communities. Freeman and Company, San Francisco.
- Park, T., 1954. Experimental studies of interspecific competition II. Temperature, humidity and competition in two species of Tribolium. Physiol. Zool. 27, 177-238.
- Quinlan, R., 2004. The competitive exclusion principle. http://www.headwaterstreams.com
- Tilman, D., Mattson, M., Langer, S., 1981. Competition and nutrient kinetics along a temperature gradient: an experimental test of a mechanistic approach to niche theory. Limneology Oceanography 26, 1020-1033.
- Volterra, V., 1931. Leçons sur la théorie mathématique de la lute pour la vie. Gauthier Villars, Paris.