REFERENCE

INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS

A PHASE–TRANSITION INDUCED BY THE STRUGGLE FOR LIFE IN A COMPETITIVE COEXISTENCE MODEL IN ECOLOGY

Horacio S. Wio

and

M.N. Kuperman

INTERNATIONAL ATOMIC ENERGY AGENCY

UNITED NATIONS EDUCATIONAL, SCIENTIFIC AND CULTURAL ORGANIZATION

MIRAMARE-TRIESTE

International Atomic Energy Agency
and
United Nations Educational Scientific and Cultural Organization
INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS

A PHASE–TRANSITION INDUCED BY THE STRUGGLE FOR LIFE IN A COMPETITIVE COEXISTENCE MODEL IN ECOLOGY

Horacio S. Wio[1]
International Centre for Theoretical Physics, Trieste, Italy

and

M.N. Kuperman[2]
Centro Atómico Bariloche (CNEA) and Instituto Balseiro (UNC),
8400 Bariloche, Río Negro, Argentina.

ABSTRACT

We have studied a spatially homogeneous model of an ecological system consisting of two species: a *strong* and a *weak* one, competing for a single food resource. The inclusion of a term corresponding to intraspecies competition, in particular for the *strong* species, shows that, if a certain threshold value is overcome, the classical result on extinction and coexistence of Lotka–Volterra type equations can drastically change yielding a kind of phase-transition to a coexistence phase.

MIRAMARE –TRIESTE

July 1994

[1]Member Carrera del Investigador CONICET, Argentina.
Permanent Address: Centro Atómico Bariloche (CNEA) and Instituto Balseiro (UNC), 8400 Bariloche, Río Negro, Argentina.
[2]Fellow CONICET, Argentina.

The origin of the mathematical theory of competition can be traced back, among other works to Volterra's 1927 paper [1]. Since then, it has became one of the most important problems among those discussed by Mathematical Ecology. Those first results showed that the coexistence of two or more species of predators limited to only one species of prey is impossible. Volterra's results have been generalized, and today are included within the *Competitive Exclusion Principle* (or *ecological theorem*), that states: *N species that compete for n(< N) food resources, cannot coexist* [2,3]. Several aspects of this problem have been analized by different authors, emphasizing, for instance, the conflict between the need to forage and the need to avoid competition; effects of diffusion-mediated persistence; global effects associated with the possibility of refuges [4,5,6,7]; etc.

In this work we study the possibility of coexistence in a simplified situation: two species competing for a unique food resource. The model to be discussed here is similar to the one used by Eigen [8] in relation with problems of prebiological evolution, by Mikhailov [9] in order to describe a noise–induced transition in a biological system with diffusion, and also to show the possibility of coexistence in the form of wave–like solutions [10,11].

We analyze here the case where, within each species, we take into account the existence of the *carrying capacity* of the enviroment [12]. That means, to consider the effect of *intracompetition* or *struggle for life* within each species. As a matter of fact, such a contribution produces a qualitative dramatic difference particularly coming from its inclusion into the *strong* species.

The model, as indicated above, consists of two species competing for the same food resource. We indicate with the N the population density of the *strong* species, with n the population density of the *weak* species, and with M the food density. The set of differential equations that describes the behaviour of such a system for the spatially homogeneous case is:

$$\partial_t n(t) = [b\,M(t) - a]\,n(t)$$
$$\partial_t N(t) = [B\,M(t) - A]\,N(t)$$
$$\partial_t M(t) = Q(t) - [G + c\,n(t) + C\,N(t)]\,M(t), \tag{1}$$

that are Malthusian–like *birth–death* equations [13] for each species where $b\,M(t)$ and $B\,M(t)$ indicate the growth rate while a and A indicate the death rate (assumed constant) of the species $n(t)$ and $N(t)$ respectively. For the food $M(t)$ the production

is given by $Q(t)$, that is assumed to be independent of the population densities, while the decay is due not only to the natural degradation (rotting) with a rate G, but to the consumption by both predator species with rates $c\, n(t)$ and $C\, N(t)$.

As in Ref.[11], and in order to simplify the algebra we rewrite Eqs.(1) assuming that $c = b$ and $C = B$. We also scale the variables n, N, M, Q, (multipliying each one by b/a), and call : $G = g/a$, $\beta = B/b$, $\alpha = A/a$ and $q = bQ/a^2$. Finally we change the temporal coordinate according to $t \rightarrow \tau = at$. After these changes, Eq.(1) adopts the simplified form

$$
\begin{aligned}
\partial_\tau n(\tau) &= [M(\tau) - 1]\, n(\tau) \\
\partial_\tau N(\tau) &= [\beta M(\tau) - \alpha]\, N(\tau) \\
\partial_\tau M(\tau) &= q(\tau) - [g + n(\tau) + \beta N(\tau)]\, M(\tau)
\end{aligned}
\tag{2}
$$

Asymptotically ($\tau \rightarrow \infty$), we have the following stationary solutions (or fixed points) for these equations:

$$
\begin{aligned}
M_n &= 1, & n_n &= q - g, & N_n &= 0 \\
M_N &= \frac{\alpha}{\beta}, & N_N &= \frac{q}{\alpha} - \frac{q}{\beta}, & n_N &= 0
\end{aligned}
\tag{3}
$$

Under the assumption of the condition

$$
\alpha < \beta
\tag{4}
$$

the threshold for the survival of the species N is lower than the threshold needed for the survival of the species n and after a linear stability analysis it can be shown that the first solution is unstable while the second one is stable. This corresponds to the initial assumption that N will have the characteristics of the *strong* species, the one that survives, while n will be the *weak* species, the one that becomes extinct. Hence, an arbitrary initial condition will move towards the attractor corresponding to the second of the indicated stationary solutions.

If we consider the stationary solutions of this system, and eliminate (in an *adiabatic-like* form) the food, we reduce our system to a two variable system. The nullclines in the (n, N) plane have the usual form [2], as is shown in Figure 1.

We consider now the effect of including the *carrying capacity* of the environment that, of course, must be a function of the resources (food in the present case). The terms describing the *intracompetition* or *struggle for life* we are going to consider have the form

$$
\gamma_N \frac{N(\tau)^2}{M(\tau)}, \qquad \gamma_n \frac{n(\tau)^2}{M(\tau)}
\tag{5}
$$

2

for the *strong* and *weak* species respectively. It clearly includes the effect of the environment as it depends (inversely) on the amount of the resource $M(\tau)$ [14]. Taking into account such terms, Eq.(2) changes to

$$
\begin{aligned}
\partial_\tau n(\tau) &= [M(\tau) - 1]\, n(\tau) - \gamma_n \frac{n(\tau)^2}{M(\tau)} \\
\partial_\tau N(\tau) &= [\beta M(\tau) - \alpha]\, N(\tau) - \gamma_N \frac{N(\tau)^2}{M(\tau)} \\
\partial_\tau M(\tau) &= q - [g + n(\tau) + \beta N(\tau)]\, M(\tau)
\end{aligned}
\tag{6}
$$

Clearly, the enviroment's *carrying capacity* must be considered within both species. However, the analysis of the system indicates that it is its inclusion within the *strong* species that produces the qualitatively dramatic changes on the above indicated situation. For this reason, in what follows we will restrict ourselves to such a case and assume $\gamma_n = 0$ and $\gamma_N = \gamma$.

As far as $\gamma < \gamma_t$ (to be defined latter), we found similar stationary solutions as before. That means, we get (as n, N, M are population densities, only solutions in the $(n > 0, N > 0, M > 0)$ quadrant are physically relevant):

$$
M_u = 1, \qquad\qquad n_u = q - g, \qquad N_u = 0
$$

$$
M_s = \tfrac{\alpha}{2\beta}(1 + \sqrt{1 + 4\gamma\beta N_s/\alpha^2}), \quad N_s = \tfrac{1}{\beta}(\tfrac{q}{M_s} - g), \quad n_s = 0
\tag{7}
$$

Again the first one is linearly unstable, while the second is stable.

When $\gamma = \gamma_t = \beta\frac{\beta - \alpha}{q - g}$, this fixed point coincides with the intersection of the other nullcline with the vertical ($n = 0$) axis. The stability analysis indicates that this solution is now only *marginally stable*.

When $\gamma > \gamma_t$, as is indicated in Figure 1, we found a new stationary or fixed point at the intersection of both nullclines. The position of this point is given by

$$
M_\nu = 1, \quad n_\nu = q - g - (\beta - \alpha)\tfrac{\beta}{\gamma}, \quad N_\nu = \frac{(\beta - \alpha)}{\gamma}
\tag{8}
$$

Again, performing a linear stability analysis of this fixed point and of those indicated in Eqs.(7), we find that the last two are unstable while the new one becomes stable. Clearly this point corresponds to a coexisting (stable) solution in our model.

Hence, we have that the stable branch ($n = 0$) for $\gamma < \gamma_t$ becomes unstable and there is a bifurcation to a new stable branch when $\gamma > \gamma_t$. This result corresponds to a *phase-transition* like phenomena induced by the variation of the *carrying capacity* parameter γ from a *phase* without coexistence to a *phase* where coexistence

3

is allowed. In Figure 2, we depicted the projection on the (n, N) plane of this new stable fixed point corresponding to the cross between both nullclines, for different values of the parameter γ. The bifurcation of the new stable branch is clearly seen.

The above indicated result shows how the study of simplified models could help in the understanding of the role played by some *environmental* parameters in situations where the complexity of the ecological reality makes its complete modelization very hard. In our case, the model so far studied could give some hints on the behavior of systems of species in competence and the possibility of coexistence. Here we have analyzed the effect of explicitly including the *carrying capacity* of the enviroment within our *toy* model for describing the coexistence of species in competence. The analysis of such situation, particularly when we took it into account within the *strong* species, shows that, if the parameter γ, measuring the magnitude of this contribution, superates some threshold value γ_t, there is a dramatic change in the qualitative behavior of the system. This is indicated by a kind of *phase transition* to a new solution (attractor) corresponding to a coexistence phase. We have performed a linear stability analysis of this new solution indicating that it is the only stable one.

A more detailed analysis of this problem will be given elsewhere [17]. We are also analyzing the effect of this contribution together with the possibility of diffusion of both species [10,11,15,16]. Such a situation can be, for instance, studied numerically [18]. The study of such a case, as well as other possible extensions of the present model will be discussed elsewhere [17].

Г

References

[1] Volterra, V., R. Comitato Talassografico Italiano, Memoria **131**, pp 1–142 (1927).

[2] Murray, J. D., *Mathematical biology*, Springer–Verlag, 1989.

[3] Levin, S.A.; Amer.Nat.**104**, 413 (1970).

[4] Gopalsamy, K.; Math.Biosciences **33**, 25 (1977);
Gopalsamy, K.; Math.Biosciences **36**, 229 (1977).

[5] Takeuchi, Yasuhiro, Math. Biosciences **99**, 181 (1990).

Takeuchi, Yasuhiro, Math. Biosciences **106**, 111 (1991).

Takeuchi, Yasuhiro, WSSIA A **1**, 531, (1992).

[6] Muratori, S. and Rinaldi, S., SIAM J. Appl. Math. **49**, 1462 (1989).

[7] Mimura, M. and Fife, P. C., Hiroshima Math. J. **16**, 189 (1986).

[8] Eigen, M., Naturwissenschaften **58**, 465 (1971).

[9] Mikhailov, A. S., Phys. Lett. **73A**, 143 (1979).

Mikhailov, A. S., Z. Physik B **41**, 277 (1981).

Mikhailov, A. S., Phys. Rep. **184**, 308 (1989).

[10] Schat, Carlos L., *Nonequilibrium Dynamics in Reaction–Diffusion Systems*, M.Sc.Thesis in Physics, Instituto Balseiro, 1991.

Schat, C. and Wio, H.S., *An Exact Analytic Solution of a Three Component Model for Competitive Coexistence*, Submitted to Math. Biosciences (1993).

[11] Kuperman, M., von Haeften, B. and Wio, H.S., *Quantum Mechanical Analogy for Solving a Competitive Coexistence Model in Ecology*, submitted to Phys. Rev. E (1994).

[12] Freedman, H.I.; *Deterministic Mathematical Models in Population Ecology*, (M.Dekker, N.Y., 1980); chapters 7 and 8.

[13] Malthus, T. R., *An essay on the principle of population, 1798*, Penguin Books, 1970.

[14] van Kampen, N.G.; *Stochastic Processes in Physics and Chemistry*, (North–Holland, 1981), p.320.

[15] Fife, Paul C., *Mathematical aspects of reacting and diffusing systems*, Springer–Verlag, 1979.

[16] Okubo, A.; *Diffusion and ecological problems: Mathematical models*, Biomathematical Series Vol.10, Springer–Verlag, 1980.

[17] Kuperman, M. and Wio, H.S., *Influence of the carrying capacity of the enviroment on the exact wave–like solutions of a competitive coexistence model in ecology*, in preparation.

Kuperman, M., Wio, H.S. and Rodriguez, M.A., *Influence of chemotactic like behavior on competitive coexistence*, in preparation.

[18] Hassan, S. A., Kuperman, M. N., Wio, H. S., Zanette, D. H., Physica A **206**, 380 (1994).

FIGURE CAPTIONS

FIGURE 1 : Nullclines in the (n, N) plane. Lines labeled as (1) and (2) corresponds to the case $\gamma = 0$. The attractors found in Eqs.(3), are indicated in the figure as N_N and n_n respectively. The rest of the lines indicates the changes in the nullcline due to variations of γ. The parameters we have used are: $\alpha = .13, \beta = .14, g = 1., q = 1.3\frac{\alpha}{\beta}$ and $.1 < \gamma < 1$. The insert shows an enlargement of the same situation.

FIGURE 2 : Projection of the crossing point of the nullclines on the scaled $(x = n/(q - g), y = N/(q - g))$ plane for different values of the parameter γ), and for the same set of values of Figure 1. The regions where $\gamma < \gamma_t$ and $\gamma > \gamma_t$ as well as the point where $\gamma = \gamma_t$ are indicated.
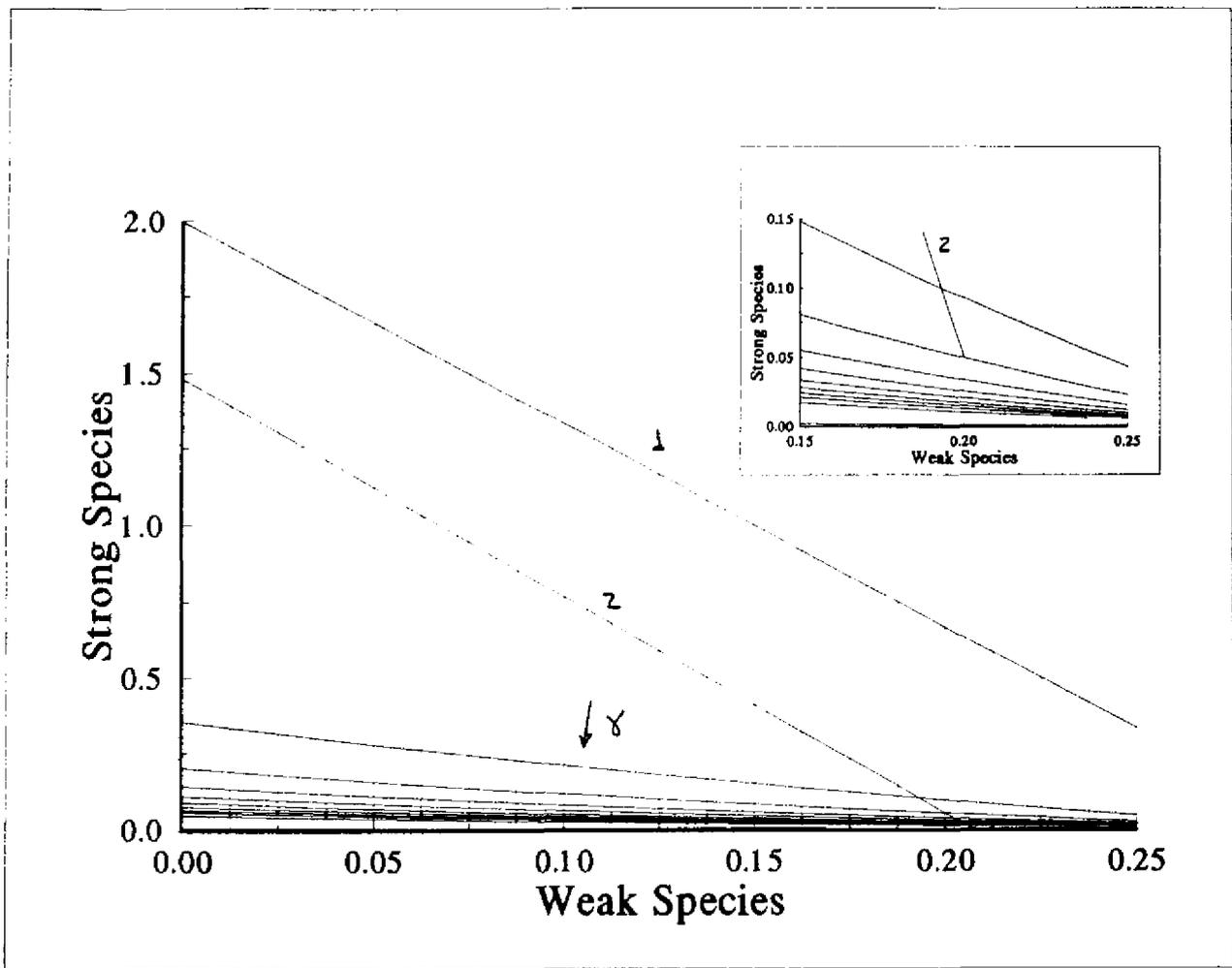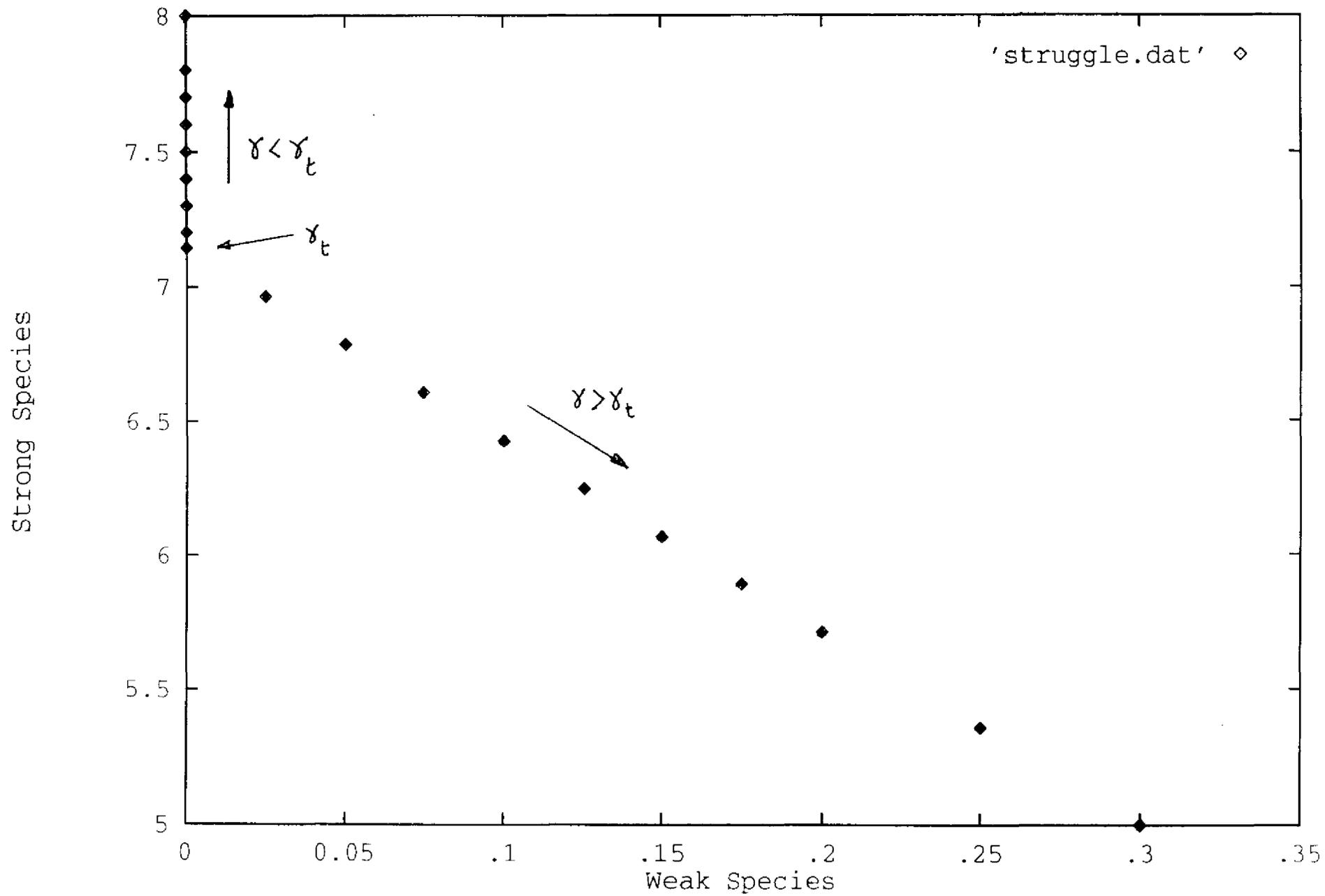
Fig.1

Fig.2