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## Gause's exclusion principle revisited: artificial modified species and competition

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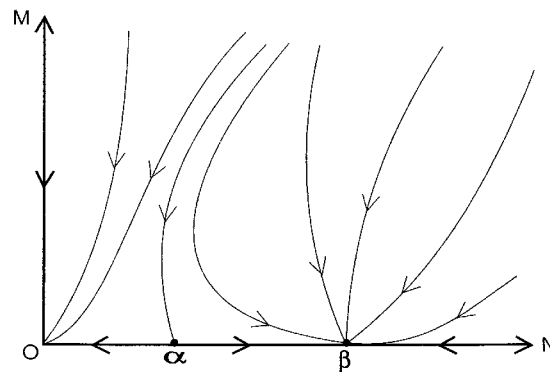
**Abstract.** Gause's principle of competition between two species is studied when one of them is sterile. We study the condition for total extinction in the niche, namely, when the sterile population exterminates the native one by an optimal use of resources. A mathematical Lotka–Volterra nonlinear model of interaction between a native and sterile species is proposed. The condition for total extinction is related to the initial number  $M_0$  of sterile individuals released in the niche. In fact, the existence of a critical sterile-population value  $M_c$  is conjectured from numerical analysis and an analytical estimation is found. When spatial diffusion (migration) is considered a critical size territory is found and, for small territory, total extinction exist in any case. This work is motivated by the extermination agriculture problem of fruit flies in our region.

In ecological systems Gause's exclusion principle is widely accepted [1–5]. Originally it was deduced from competition between *Paramecium caudatum* and *Paramecium aurelia* [1–3]. Nevertheless, it applies to many other situations. For instance, in [6] it was conjectured that Neanderthal extinction in Europe was a consequence of Gause's principle. From a formal point of view, it states that *two competing species cannot coexist in the same ecological niche*. Within this framework, it is assumed that the strong species completely fills the niche and the weak one disappears (exclusion). We remark that this principle is limited in the sense that it applies when re-adaptation, migration or genetic changes does not exist. This principle seems very intuitive in a natural environment or for species in laboratories; but what is the situation with genetically prepared sterile populations? To be more explicit, consider the well known problem related to extermination of native fruit flies by genetically sterilized fruit flies [7, 8]. The two species exist in the same ecological niche when the sterile population is released. Before the interaction, we assume that the native species fills the niche in a stable way. In some geographic regions and for optimal initial conditions, native fruit flies can be exterminated by the sterile population. Namely, in this case both species disappear and the principle must be reformulated as:

*Gause's principle.* Two competing species cannot coexist in the same ecological niche and at least one of the species will disappear.

Namely, it contains explicitly the possibility of total extinction (of both species). This formulation of the principle includes all strategies of extermination with genetically altered species [7, 8].

In this paper we consider a mathematical nonlinear model of competition between a native species with a number of individuals  $N(t)$ , and another sterile one with a number of individuals



**Figure 1.** A sketch of the critical points associated with equations (1) and (2). Note that no equilibrium point exists on the  $M$ -axis because this population is sterile. When  $(0, 0)$  is stable, we obtain total extinction in accord with Gause's principle.

given by  $M(t)$ . Explicitly, we are interested in the mathematical conditions for total extinction in the ecological niche. This paper is organized as follows. First, we present a predator–predator nonlinear model for variables  $N$  and  $M$  (equations (1)–(3)), and a stability analysis. Numerical simulation confirms the stability analysis and the existence of a threshold  $M_c$  where total extinction exist. We give an analytical estimation of this threshold value (equation (5)). Near to the critical value, the behaviour of the extinction time  $\tau_{ext}$  is studied. This extinction time is, after our numerical calculation, related to a critical exponent  $\nu$  (equation (6)). Finally, the case including diffusion is considered, here we found the existence of a critical size territory  $L_c$  where total extinction holds (for any initial condition of the species  $M$ ). Some possible generalizations are stressed at the end of the paper.

To be explicit, consider the Lotka–Volterra-type evolution equations with the interaction

$$\frac{dM}{dt} = -\alpha' M - \delta N M \quad (1)$$

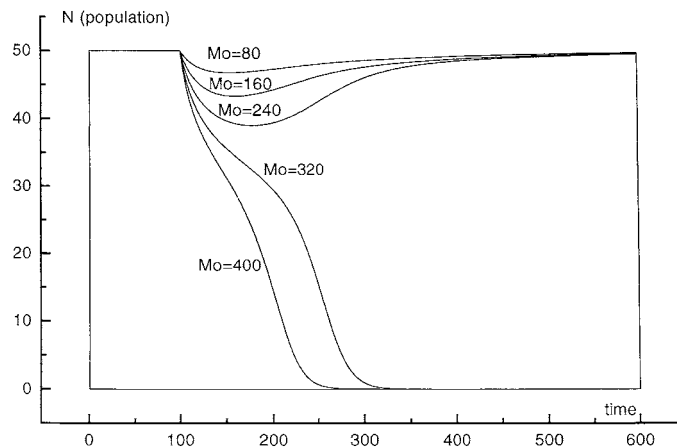
$$\frac{dN}{dt} = N F(N) - \delta N M \quad (2)$$

where  $\alpha'$  is the death rate of the sterile population,  $\delta$  is the interaction parameter and the function  $F(N)$  describes the population growing of the native species when interaction does not exist. For instance, when  $F(N) = \alpha - N$  ( $\alpha$  is a constant) we obtain the usual Verlhust, or logistic, equation. Note that the stability of the point  $(N = 0, M = 0)$  depends on the sign of  $F(0)$ . In fact, when  $F(0) < 0$  this point becomes stable and the possibility of total extinction exists in accordance with Gause's principle. Moreover, this condition of stability of  $(0, 0)$  seems reasonable if we think that species needs a minimal social structure, or genetic diversity, to survive (i.e. a minimal number of individuals). We stress that the dynamical systems (1)–(3) is irreversible, for instance, a Lyapounov function  $L$  associated with the systems is just  $L = M(t)$ .

To carry out explicit calculations we consider the model where

$$F(N) = (\alpha - N)(N - \beta) \quad (3)$$

with  $\alpha$  and  $\beta$  positive parameters ( $\alpha < \beta$ ). Since  $F(0) < 0$ , the point  $(N = 0, M = 0)$  is stable and total extinction would be expected. The linear analysis of (1)–(3) shows that the point  $(N = \alpha, M = 0)$  is unstable (saddle) and  $(N = \beta, M = 0)$  is a stable focus. Figure 1



**Figure 2.** A numerical simulation of equations (1)–(3). The native population  $N(t)$  can be exterminated by an appropriate choice of the initial-value population  $M_o$  for the sterile population. In the figure we have five initial value for  $M_o$ . The critical value to complete extinction is  $M_o \sim 270$  in good accord with our conjecture (4). The parameters are  $\alpha = 30$ ,  $\beta = 50$ ,  $\delta = 1$  and  $\alpha' = 35$ . The sterile population  $M$  is released at  $t_o = 100$  (arbitrary units).

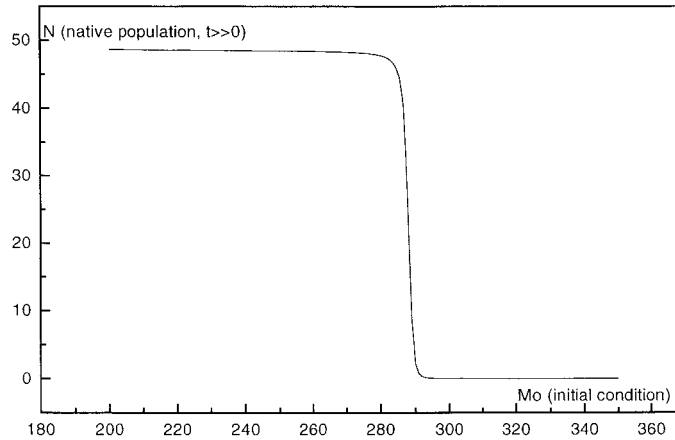
shows the stability diagram for our equations. So, the sterile population  $M$  disappears and, depending on the initial conditions, total extinction would exist in the niche. Namely, the systems has two attractors, the first  $(0, 0)$  related to total extinction and the other  $(\beta, 0)$  related to survival of species  $N$ .

The explicit question that we are concerned with here is as follows. If initially the native species number is  $N = \beta$  (a stable point without interaction) then, after  $M_o$  sterile individuals have been released, when do we have total extinction? Namely, before the interaction, the native species is in the niche in a stable way. After,  $M_o$  sterile individuals are released and the interaction process produces a competitive struggle. Here we ask about the minimal population  $M_o$  of sterile individuals producing total extinction in the niche. In fact, if the sterile population is not enough then they die and total extermination does not occur.

Numerical calculations confirm the existence of a critical value  $M_c$  and when  $M_o > M_c$  total extinction exists in the niche. Figure 2 shows the time behaviour of  $N(t)$  for different initial value  $M_o$ , of the sterile species released in the niche. There is a critical value for the initial condition  $M_o$  related to total extinction. A criterion for total extinction is dependent on the initial number in the sterile population  $M_o$  and is given by

$$M_o > 2.7 \frac{(\alpha - \beta)^2}{4\delta}. \quad (4)$$

This criterion is established as follows: from (1) and (3), we have that  $M(t) = \exp(-\alpha' - \delta \langle N \rangle_t) t$ , where  $\langle N \rangle_t = (1/t) \int^t N(\tau) d\tau$ . When  $T \rightarrow \infty$ , i.e. small  $t$ , and assuming total extinction, we expect an exponential decaying behaviour for  $M$ . So, an important fraction of the decaying process, assumed to be slow, is reached when  $M \sim M_o e^{-1}$ . If now we stress that no other stationary point (excepting  $(0, 0)$ ) exists in (2), we obtain the criterion (4). We have used the maximum value of the function  $F(N)$  given by (3). We remark that this is a coarse criterion, nevertheless, it works in accord with our numerical simulations. For instance, figure 2 describes extinction when  $M_o > 270$  in accordance with (4). This is also true for other parameter values. The criterion (4) can be generalized easily to a system with



**Figure 3.** The final distribution of the native population  $N$  for different initial conditions  $M_o$  of the sterile population. The existence of a critical value  $M_c$ , separating survival and extinction, is clearly shown. The parameters are the same as in figure 2.

arbitrary distribution  $F(N)$  in (1) and (2). Namely, by imposing the inequality  $F_{\max} < \delta M_o e^{-1}$  (with  $e \sim 2.7$ ).

Figure 3 shows a simulation of the final native population  $N(t = \infty)$  for different initial conditions  $M_o$  of the sterile population. Clearly there is a critical value  $M_c$  which separates the survival and extermination regime. From equation (4), a first approximation for this critical value is

$$M_c \sim 2.7 \frac{(\alpha - \beta)^2}{4\delta}. \tag{5}$$

Moreover, figure 2 suggests that near to this critical value the extinction time  $\tau_{ext}$  depends on  $(M_o - M_c)$ . This is so because when  $M_o \rightarrow M_c^+$  the extinction time must be infinity. Explicitly we expect a behaviour like

$$\tau_{ext} \sim \frac{1}{(M_o - M_c)^\nu} \quad M_o > M_c \tag{6}$$

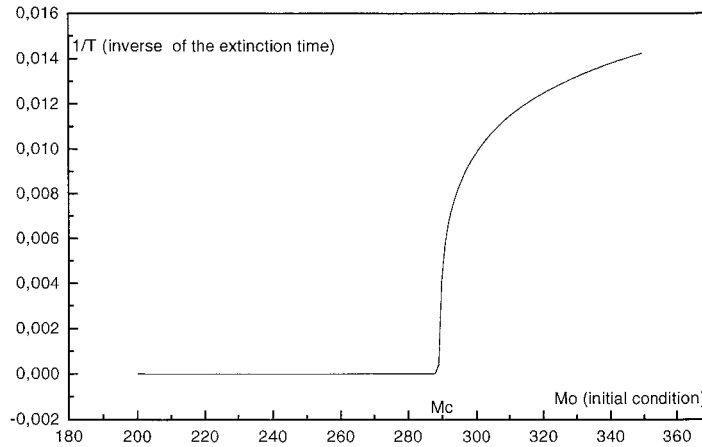
where  $\nu$  is an unknown parameter. The evaluation of this critical exponent requires computational work which is beyond of the scope of this paper. It will be done elsewhere. The conjecture (6) is reinforced by numerical calculation. In fact, using the same parameter values as in figure 2, and the definition

$$\tau_{ext}^{-1} = -\frac{1}{t} \lim_{t \rightarrow \infty} \ln(N(t)/\beta) \tag{7}$$

we see that the existence of the critical exponent  $\nu$  is confirmed numerically (figure 4).

Now we discuss briefly the incorporation of migration into the set of evolution equations (1) and (2). In fact, total extermination could also be carried out by a diffusion process. In some cases unstable points become stable by diffusion in limited territories. Thus in a model where  $(0, 0)$  is unstable, i.e. only one species survives, diffusion would change this instability and total extinction takes place. We add the diffusion terms  $D_M \frac{\partial^2 M}{\partial x^2}$  and  $D_N \frac{\partial^2 N}{\partial x^2}$  to (1) and (2), respectively. Namely, consider the pair of reaction–diffusion evolution equations

$$\frac{dM}{dt} = -\alpha' M - \delta N M + D_M \frac{\partial^2 M}{\partial x^2} \tag{8}$$



**Figure 4.** The extinction time  $\tau_{ext}$ , for different initial conditions  $M_o$ , showing the transition. This numerical result seems to be in accord with our hypothesis (6) and is related to the existence of a critical exponent  $\nu$ .

$$\frac{dN}{dt} = NF(N) - \delta NM + D_N \frac{\partial^2 N}{\partial x^2}. \tag{9}$$

The linear analysis of stability for the stationary point (0, 0) can be done in the usual way, namely, consider the small perturbation

$$M = 0 + \eta \tag{10}$$

$$N = 0 + \varepsilon \tag{11}$$

where the variables  $\eta$  and  $\varepsilon$  are assumed to be small. Equations (8) and (9), give the first-order linear equations

$$\frac{\partial \eta}{\partial t} = -\alpha' M \eta + D_M \frac{\partial^2 \eta}{\partial x^2} \tag{12}$$

$$\frac{\partial \varepsilon}{\partial t} = F(0)\varepsilon + D_N \frac{\partial^2 \varepsilon}{\partial x^2} \tag{13}$$

where we assume  $F(0) > 0$ , corresponding to the unstable case when migration is not present. For a finite territory, solutions such as  $\varepsilon \sim e^{\omega t} \sin kx$  can be visualized. The relationship between the stability parameter  $\omega$  and the wavenumber  $k$  is given by

$$\omega = F(0) - k^2 D_N \tag{14}$$

and clearly for  $k > \sqrt{F(0)/D_N}$  the point (0, 0) becomes stable and total extinction in the niche exists. Since  $k \sim \frac{1}{L}$ , with  $L$  the territory size, equation (14) defines a critical size territory  $L_c \sim \sqrt{D_N/F(0)}$  where total extinction holds. Namely, for any sized territory with  $L < L_c$  total extinction exists.

In conclusion, Gause's principle was generalized to consider the case of the biological struggle when one competing species is sterile. In fact, under appropriate conditions, total extinction could occur in the niche. Most agricultural competitive extermination methods are carried out assuming this principle. For instance, this is the case of the extermination programme of fruit flies with sterile flies irradiated in laboratories [9, 10]. We have presented

a simple model which has total extinction in the niche in some cases. Conjectures related to a critical sterile population (number of individuals) producing total extinction were pointed out with a coarse criterion (4). This conjecture is based on our numerical simulation of the model. The role of migration was briefly discussed and the possibility of total extinction from diffusion was also explored for small territories.

To end, we note that our model can be extended to incorporate some modifications. Particularly we are thinking about generalizations such as:

- (a) Periodic variation of coefficients. In fact, in the extinction fruit flies programmes, daily, seasonal or El Niño (ENSO) oscillations must be considered.
- (b) Sexual selection. Many extermination programs are based on sexual selection, namely, a sterile male released in a given niche. It creates interaction between the sterile male and fertile female which becomes directly related to the evolution of the native male. Such models require a phase-space which is greater than two.
- (c) Many random factors are present in a real niche; for instance, humidity, temperature, wind, etc. These factors can be incorporated into our model by introducing adequate stochastic process for the parameter ( $\alpha$ ,  $\beta$  or  $\delta$ ).

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