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# An ecogenetic model

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ABSTRACT

A model for the effects of a predator on a genetically distinguished prey population is formulated and investigated. The predator-free system settles at an equilibrium which can be destabilized by the predators if a suitably defined parameter, the predator invasion number, exceeds a threshold. The system can then coexist at a stable equilibrium or via persistent oscillations.



## 1. The model

Ecoepidemiology (see Chapter 7 of [1] and its references) studies interacting populations among which diseases spread. In this study, we extend the idea to a population containing genetically different characteristics and investigate the influence of another population on its evolution.

In fact, we consider a genetically differentiated prey population, in which $x$ and $y$ represent the two genotypes, subject to the interference of natural predators $z$. Let $R$ denote the reproduction rate and $p$ and $q = 1 - p$ denote the fractions of the newborns being of genotypes $x$ and $y$ respectively. Assuming that the two subpopulations live in the same environment, let $a$ denote the population pressure felt by genotype $x$ and $b$ the same pressure experienced by the genotype $y$, taking possibly $a \neq b$ to allow for more generality. Let $m$ denote the mortality rate of the predators, let $h$ and $g$ be the possibly different rates at which the two genotypes are hunted and let $e < 1$ represent the conversion factor of prey into predators' newborns. All the model parameters are assumed to be nonnegative. The model then can be written as follows:

$$\frac{dx}{d\tau} = [Rp - ax](x + y) - hxz, \qquad (1)$$
$$\frac{dy}{d\tau} = [Rq - by](x + y) - gyz,$$
$$\frac{dz}{d\tau} = z[e(hx + gy) - m].$$

The first two equations then describe prey reproduction, intraspecies competition and predator hunting. The last equation contains the predator dynamics, regulated by the return obtained from successful prey hunting and natural mortality.

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The system trajectories are bounded. Letting $W = x+y+z$ be the total environmental population and taking an arbitrary $m > \eta > 0$, we find

$$\frac{dW}{d\tau} + \eta W = (x+y)(R+\eta-ax-by) + (e-1)(hxz+gyz) + (\eta-m)z$$
$$\leq x(R+\eta-ax) + y(R+\eta-by) + (\eta-m)z \leq \frac{(R+\eta)^2}{4ab}(a+b) \equiv V,$$

so integrating for all $\tau$, we have $W(\tau) \leq \max\{V\eta^{-1}+\epsilon, W(0)\}$, for any arbitrary $\epsilon > 0$.

Note that in the case of the absence of predators the above result is immediate on taking a box in the phase plane, bounded by the coordinate axes and the horizontal and vertical lines $y = y_h > Rqb^{-1}$, $x = x_v > Rpa^{-1}$, as trajectories on these lines are seen to enter into the box.

We now adimensionalize (1). Let $X(t) = \alpha x(\tau)$, $Y(t) = \beta y(\tau)$, $Z(t) = \zeta z(\tau)$, and $t = \gamma\tau$. Taking then $\gamma = m$, $\alpha = \beta = a^{-1}Rp$, $\zeta = g^{-1}m$, and defining the new parameters $c = hg^{-1}$, $r = Rpm^{-1}$, $s = ba^{-1}$, and $w = qp^{-1}$, $v = egpR(am)^{-1} = egra^{-1}$, the model (1) becomes

$$\frac{dX}{dt} = r(X+Y)(1-X) - cXZ, \tag{2}$$
$$\frac{dY}{dt} = r(X+Y)(w-sY) - YZ,$$
$$\frac{dZ}{dt} = Z[v(cX+Y)-1].$$

## 2. Analysis

### 2.1. Equilibria

The system (2) has the following equilibria: the origin $E_0$, the predator-free equilibrium $E^\dagger = (E_0^\dagger, 0)$, with $E_0^\dagger = (X^\dagger, Y^\dagger)$ being the equilibrium of the predator-free subsystem, and the coexistence equilibrium $E^* = (X^*, Y^*, Z^*)$. Explicitly, for the second one, $X^\dagger = 1$, $Y^\dagger = ws^{-1}$, while for the third one we have

$$X^* = \frac{1}{c}\left(\frac{1}{v} - Y^*\right), \qquad Z^* = \frac{r}{Y}^*(X^*+Y^*)(w-sY^*) = \frac{r}{cX^*}(X^*+Y^*)(1-X^*) \tag{3}$$

and $Y^*$ solves the quadratic

$$v(cs-1)Y^2 - Y(cvw+cs+cv-1) + cw = 0. \tag{4}$$

We denote its roots by $Y^\pm$, with $Y^- < Y^+$. For $cs < 1$, by Descartes' rule of signs there is one positive root $Y^* = Y^+$; for $cs > 1$, the discriminant can be restated as follows: $\Delta = [cvw-(cs-1)]^2 + c^2v^2(1+2w) + 2cv(cs-1)$ and then, again using Descartes' rule, if also $cvw+sc+cv > 1$ there are two real positive roots $0 < Y_1^*(\equiv Y^-) < Y_2^*(\equiv Y^+)$.

$E_0$, $E_0^\dagger$ and $E^\dagger$ are always feasible; for $E^*$ we must instead require

$$X^\pm \leq 1, \qquad Y^\pm \leq \min\left\{\frac{1}{v}, \frac{w}{s}\right\}. \tag{5}$$

**Remark 1.** The expression for $Y^\pm$ can be explicitly evaluated, which we omit, but it is important to note that it is independent of $r$ and consequently also $X^*$ is independent of the adimensionalized reproduction rate, $r$.

### 2.2. Stability

The Jacobian $J$ of (2) is

$$\begin{pmatrix} r(1-2X-Y)-cZ & r(1-X) & -cX \\ r(w-sY) & r(w-sX-2sY)-Z & -Y \\ cvZ & vZ & v(cX+Y)-1. \end{pmatrix}. \tag{6}$$

At the origin, since the characteristic equation factors, the eigenvalues are $-1$, and in addition those of the predator-free subsystem 0 and $r(1+w)$. This result indicates that the origin for the predator-free subsystem is unstable and this characteristic remains unaltered also in the larger system, on the introduction of the predators. This is a result with the good outcome that the ecosystem will never completely disappear.

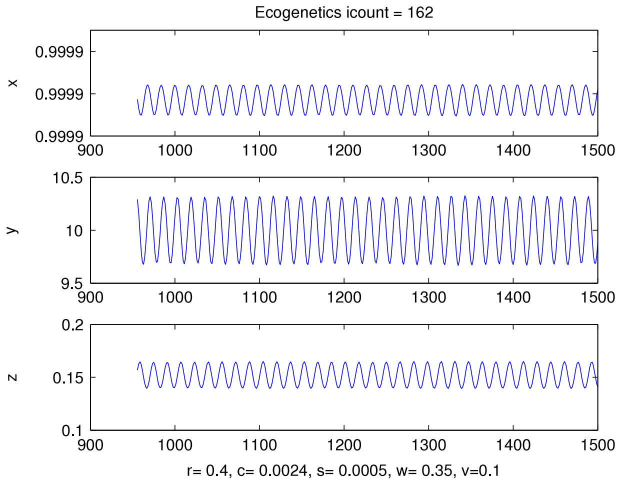


**Fig. 1.** Persistent oscillations obtained for the parameter values $r = 0.4$, $c = 0.0024$, $s = 0.0005$, $w = 0.35$, $v = 0.1$; note that the oscillation for the $x$ variable is extremely small.

At $E^{\dagger}$ the Jacobian becomes a diagonal matrix with eigenvalues

$$\lambda_1 = -r\left(1+\frac{w}{s}\right), \qquad \lambda_2 = -rs\left(1+\frac{w}{s}\right), \qquad \lambda_3 = v\left(c+\frac{w}{s}\right) - 1 \tag{7}$$

where $\lambda_1$ and $\lambda_2$ are the eigenvalues of the equilibrium $E_0^{\dagger}$ in the predator-free subsystem. The latter is therefore always locally asymptotically stable and no Hopf bifurcations are possible. We can also introduce the predator invasion number as

$$R_Z = v\left(c+\frac{w}{s}\right). \tag{8}$$

Depending on whether $R_Z > 1$, the predators establish themselves permanently in the ecosystem.

For the coexistence equilibrium the Jacobian evaluated at the equilibrium, $J^* = J(E^*)$, simplifies somewhat; using (3) we find $J_{33}^* = 0$ and

$$J_{11}^* = -\frac{r}{X^*}[(X^*)^2 + Y^*] < 0, \qquad J_{22}^* = -\frac{r}{Y^*}[s(Y^*)^2 + wX^*] < 0. \tag{9}$$

The characteristic equation is the cubic $\lambda^3 - \mathrm{tr} J^* \lambda^2 + M_2^* \lambda - \det J^* = 0$, where the coefficients are evaluated at the equilibrium $E^*$, and $M_2$ represents the sum of the principal minors of order 2 of (6). The first Routh–Hurwitz condition for stability from (9) is then clearly satisfied, $-\mathrm{tr} J^* > 0$; for the second one, observe that

$$\det J^* = vZ^*\{-cr[(1-X^*)Y^* + X^*(w-sY^*)] + c^2 X^* J_{22}^* + Y^* J_{11}^*\} < 0$$

since all the terms are negative in view of (5), so it is also satisfied: $-\det J^* > 0$. For the third one, let us define $Q^* = \mathrm{tr} J^* M_2^* - \det J^*$. We need to show it to be negative. Performing the expansions and using (5), and using the simplification $J_{33}^* = 0$, the inequality $Q^* < 0$ becomes

$$|J_{11}^* + J_{22}^*|(|J_{11}^* J_{22}^*| - J_{12}^* - J_{21}^*) > J_{32}^* J_{21}^* |J_{13}^*| + J_{31}^* J_{12}^* |J_{23}^*| + |J_{13}^* |J_{31}^* |J_{22}^*| + |J_{23}^* |J_{32}^* |J_{11}^*|. \tag{10}$$

We substitute the relevant quantities into (10) and letting $A^* = v(X^* + Y^*)(w - sY^*)L$ and $B^* = ((X^*)^2 Y^*)^{-1} M$ with

$$L = cwX^* + cs(Y^*)^2 + (X^*)^2 + Y^* + cwX^* - csX^*Y^* + cY^* - cX^*Y^*,$$
$$M = s(X^*Y^*)^2 + w(X^*)^3 + s(Y^*)^3 + sX^*(Y^*)^2 + w(X^*)^2 Y^* - sw(X^*Y^*)^2$$

we introduce $r^+ \equiv AB^{-1}$. Here it is relevant to observe that, in view of Remark 1, all the quantities appearing on the right hand side of this equation do not depend on $r$. Stability is then attained for

$$r > r^+. \tag{11}$$

Further, $r$ can be taken as a bifurcation parameter. When $r = r^+$ then, we have equality in the third Routh–Hurwitz condition, so purely imaginary roots arise. Hence at $r^+$ the equilibrium $E^*$ bifurcates. In Fig. 1 we show the limit cycles obtained for the parameter values $r = 0.4$, $c = 0.0024$, $s = 0.0005$, $w = 0.35$, $v = 0.1$. Observe that in them, the value of the $x$ subpopulation is however essentially constant.

### 2.3. Persistence

For this task, we must destabilize all boundary equilibria at the same time. For the predator-free subsystem the result holds, since the origin is unconditionally unstable. For system (2), the origin remains unstable. Further, $E^{\dagger}$ can be destabilized by imposing $\lambda_3 > 0$, since $\lambda_1 < 0$, $\lambda_2 < 0$; see (7). Thus

$$R_Z > 1 \tag{12}$$

ensures not only that the presence of the predators in the environment becomes permanent, but also the persistence of the system (2).

From the main theorem of [2] the system (2) is therefore permanent for $\lambda_3 > 0$, since it is uniformly persistent and uniformly bounded.

### 2.4. Global stability for the prey subsystem

For the system (2) without predators, the origin is always unstable, while at $E_0^{\dagger}$ the eigenvalues are still $\lambda_1$ and $\lambda_2$ of (7). The equilibrium is then always locally asymptotically stable and no bifurcations are possible. Further, on letting $\mathbf{u} = (X, Y)^T$, taking $G(X, Y) = (X + Y)^{-1}$ and evaluating $\nabla \cdot (G\dot{\mathbf{u}}) = -r(1 + s) < 0$, by Dulac's criterion we can exclude the possibility that there are limit cycles.

Consider then the set $\Omega = \{0 \leq X \leq H, 0 \leq Y \leq K\}$ in the phase space, with $H > 1$, $K > ws^{-1}$. On its sides we find

$$\left.\frac{dX}{dt}\right|_{X=H} = r(H + Y)(1 - H) < 0, \qquad \left.\frac{dY}{dt}\right|_{Y=K} = r(X + K)(w - sK) < 0,$$

which implies that all the trajectories enter into $\Omega$ through its sides in the first quadrant. The other sides on the coordinate axes cannot be crossed by the system's trajectories in view of the existence and uniqueness theorem, since the system is homogeneous. Thus $\Omega$ is a positively invariant set. Since in it the equilibrium $E_0^{\dagger}$ is the only one that is locally asymptotically stable, and no cycles exist, its global stability then follows.

## 3. Discussion and conclusion

The proposed model shows that the predator population can destabilize the equilibrium between the two genetically different strains of prey. Not only can the predators establish themselves permanently in the system if (12) holds, but also they can destabilize the equilibrium giving rise to limit cycles, when the reproduction rate $r$ falls below the threshold $r^+$ given by (11).

The subsystem without predators attains instead always the globally asymptotically stable equilibrium $E_0^{\dagger}$.

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