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Note: The following was prepared as a part of referee's report on a journal submission.

No ecologist will knowingly choose the Malthusian exponential growth model for population dynamics, yet we use it unknowingly all the time. Take the following Rosenzweig-MacArthur model as an example

$$\begin{cases} \dfrac{dX}{dt} = rX\left(1 - \dfrac{X}{K}\right) - \dfrac{aX}{1+ahX}Y \\[2ex] \dfrac{dY}{dt} = b\dfrac{aX}{1+ahX}Y - dY \end{cases}$$

which is used by the authors and many others in the literature. It is haunted by the Malthusian ghost. To see it, a thought experiment will do. Assume we are able to fix the prey population throughout an experiment. Then the predator population will grow exponentially, which cannot be right especially in laboratory settings which are always confined to limited spaces. The exponential growth in turn induce artificial instability which underlies all the "paradoxes" in theoretical ecology: the Enrichment Paradox, the Biological Control Paradox, the Competition Exclusion Principle, etc. They are all Malthusian artifacts.

The simplest way to exorcize the Malthusian ill-effect is to include this intraspecific competition term, $-mY^2$, to the predator ([4, 5]). The simplest, comprehensive competition model is the following

$$\text{(1)} \qquad \begin{cases} \dfrac{dX}{dt} = rX\left(1 - \dfrac{X}{K}\right) - \dfrac{a_1X}{1+a_1h_1X}Y - \dfrac{a_2X}{1+a_2h_2X}Z := XF(X,Y,Z) \\[2ex] \dfrac{dY}{dt} = b_1\dfrac{a_1X}{1+a_1h_1X}Y - d_1Y - m_1Y^2 := YG(X,Y) \\[2ex] \dfrac{dZ}{dt} = b_2\dfrac{a_2X}{1+a_2h_2X}Z - d_2Z - m_2Z^2 := ZH(X,Z) \end{cases}$$

Parameter m_1, m_2 are referred to as the *intracompetition parameter*. The corresponding terms do not have to mean additional death rate as a particular interpretation. It can alternatively mean a reduced birth rate due to energy lost to competition, or other particular narratives. None of the paradoxes persists in the invariant XY and XZ subsystems ([4]). Competition exclusion is not always the case for the full system.

Regarding competition, one must define the concept of competitiveness of the predators, and do it in a way which makes sense both biologically and mathematically. Here is my take. We note first that the invariant subsystem XY and XZ can either have an equilibrium point or a limit cycle as a global attractor. Call them XY and XZ global attractor respectively.

> **Definition:** Predator Y is *competitive* if its average per-capita growth rate $G(X,Y)$ is positive along the XZ global attractor. Symmetrical definition applies to predator Z.

For the equilibrium point case, let (X_e, Z_e) be the XZ attractor, then Y is competitive if and only if $G(X_e, 0) > 0$. That is, Y can grow and pull away from the XZ-subsystem's attractor. For the limit cycle case, we only need to replace the criterion by the average value

$$\frac{1}{T}\int_0^T G(X(t), 0)dt$$

with T the period and $(X(t), Z(t))$ the limit cycle attractor. It is a simple exercise in both cases to show that the definition is equivalent to the statement that the global XZ attractor is not attracting with respect to the full XYZ system. In other words, the linearization of the full system along the attractors has a positive eigenvalue in the direction normal to attractor.

Given the definition, a result, similarly to what the authors wanted to prove, can be stated as follows:

> **Theorem:** *For a system of 2 specialist predators competing for one common prey, stable co-existence steady state occurs if both predators are competitive. Moreover, the stable co-existence steady state is an equilibrium point if the competition-free subsystems each contains a capacity equilibrium.*

(The definition of *capacity equilibrium* is given in the Appendix.)

Esoterical mathematics is of little interest and usefulness. One extreme example is ref[3] of the manuscript. The mathematical catalogues of the 2-d system from ref[3] are completely detached from biology, so is the manuscript, although to a lesser extend. One should let biology drive the categorization. Case in point, the phenomena of multiple equilibrium states, heteroclinic orbits, etc. of the 2-d system enumerated in ref[3] only occupy a marginal parameter region of the system, and thus command the least prioritized biological importance. The Routh-Hurwitz conditions (i,ii) of page 7 of the manuscript wrap up many *distinct* biological scenarios, one of which — the capacity equilibrium case —is extracted in the Appendix.

Last, it would be interesting if the authors can explain what does the Liapunov function (2.10) stand for. For example, in the analogy of physics, does it mean some type of energy function? Otherwise, it remains completely mysterious to mathematicians, and clueless to everyone else.

Appendix

For the full model (1), the XYZ-equilibrium lies on the nontrivial nullcline surfaces

$$F(X, Y, Z) = G(X, Y) = H(X, Z) = 0,$$

which in practical terms define the *per-capita growth equilibrium* for individual species. With $m_1 = m_2 = 0$, one finds immediately that $G = 0$ gives rise to $X = X_1 := d_1/[a_1(b_1 - d_1h_1)]$ while $H = 0$ gives rise to $X = X_2 := d_2/[a_2(b_2 - d_2h_2)]$. Hence, XYZ-equilibrium exclusion occurs if $X_1 \neq X_2$. The meaning of X_1, X_2 are given later.

Here, an XYZ-equilibrium always means to have all positive components. In contrast, an XY-equilibrium has positive X, Y value for the competition-free XY-subsystem with $Z = 0$. XZ-equilibrium point is similarly defined. Thus, the X-equilibrium is the predator-free prey capacity $(K, 0, 0)$ for the X-equation with $Y = Z = 0$.

Predator-Mediated Prey Capacity. The predator-free capacity K must continue with the induction of predators. For example, fix $Z = 0$ and treat the X-equation as parameterized by its predator Y. Then increasing Y from $Y = 0$ decreases the X-capacity equilibrium $(K(Y, 0), Y, 0)$ with $K(Y, 0) < K(0, 0) = K$ for $Y > 0$. Increasing Y until a value, denoted by $Y_{max} > 0$, the X-capacity fails to exist. This results in a branch of the X-nullcline $F(X, Y, 0) = 0$ which we call *predator* Y *mediated carrying capacity*. It is given by the curve $K(Y, 0)$ defined for $0 < Y < Y_{max}$, satisfying the property that $X = K(Y, 0)$ decreases as Y increases.

Exactly the same definition for *predator* Z *mediated prey capacity* $X = K(0, Z)$, as well as for the joint YZ *predator-mediated prey capacity* surface $X = K(Y, Z)$ for which $F(K(Y, Z), Y, Z) \equiv 0$ in a YZ region, denoted by Δ, in the YZ-plane. See Fig.1.

The region Δ is bounded by the Y-axis interval $Z = 0, 0 < Y < Y_{max}$, symmetrically the Z-axis interval $Y = 0, 0 < Z < Z_{max}$, and a boundary curve $(YZ)_{max}$, see illustration. This curve, like many others, is of reciprocal relation between Y and Z. To explain, look first the simple case without predator $Z = 0$. As we already know the termination of the Y-mediated X capacity takes place at $(Y_{max}, 0) \in (YZ)_{max}$. Introducing predator $Z > 0$ leads to a smaller Y_{max} density required to terminate the predator-mediated capacity. That is, increasing either of the two predators on the curve $(YZ)_{max}$ decreases the other.

Analytically, the predator-mediated prey capacity is defined by the equation

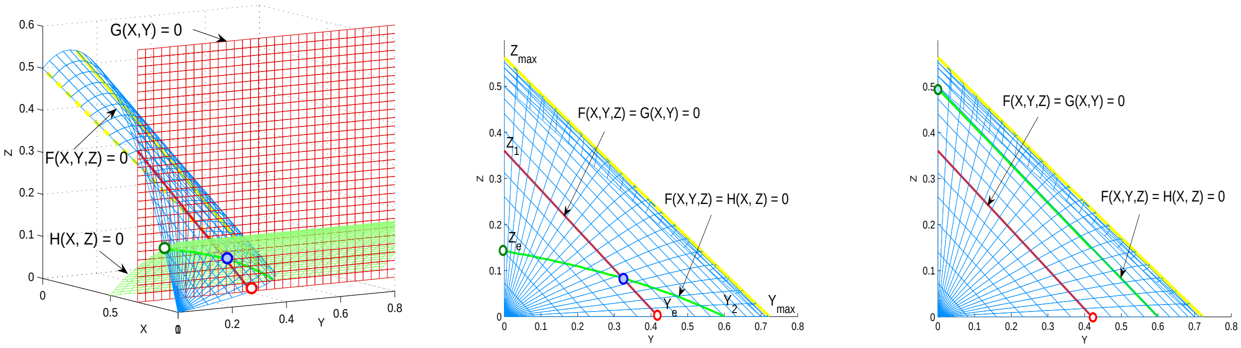
$$F(X, Y, Z) = 0, \ \frac{\partial F}{\partial X}(X, Y, Z) < 0.$$

This completes the preparation for the X-nullcline $F = 0$.

Prey-Supported Predator Capacity. The predator nullclines can be analyzed similarly. First of all, $G(X, Y) = 0$ is a surface in the XYZ-space. It divides the space into two parts: the per-capita decay region $G < 0$ and the per-capita growth region $G > 0$. The origin $X = 0, Y = 0$ is in $G < 0$, and the predator-free prey capacity $(K, 0)$ is assumed in the per-capita grow region $G > 0$. (The case that $G(K, 0) < 0$ is a trivial case for which there does not exist an XYZ-equilibrium point.) The predator-free, per-capita equilibrium state is $G(X, 0) = 0$ whose solution is X_1 introduced earlier for XYZ-equilibrium exclusion. It is predator Y's *survival threshold*: For $X < X_1$, predator Y always declines to extinction $Y = 0$. If $m_1 = 0$ and $X > X_1$ is fixed, then predator Y grows exponentially without bound. In contrast, if $m_1 > 0$ and for fixed $X > X_1$, then predator Y is governed by a logistic growth, and every nontrivial initial density converges to its *prey-supported capacity* $G(X, Y) = 0$. That is, the Y-capacity curve $G(X, Y) = 0$ is defined for $X > X_1$, and on it Y increases as X increases. Solve $G(X, Y) = 0$ to get

$$Y = \frac{1}{m_1}\left[b_1 \frac{a_1 X}{1 + a_1 h_1 X} - d_1\right], \text{ if } m_1 > 0 \ ,$$

and $X = X_1$ if $m_1 = 0$. Clearly, for the case $m_1 > 0$, it saturates at $Y_{cap} = [b_1/h_1 - d_1]/m_1$ as $X \to \infty$. As a result, for sufficiently large $m_1 > 0$, the predator-mediated X-capacity and the prey-supported Y-capacity must intersect to create an XY-equilibrium point. For example, this is the case if the Y-capacity saturation Y_{cap} amount is smaller than the amount Y_{max} to terminate the predator-mediated X-capacity. Such an XY equilibrium point is called *the capacity*



(a) (b) (c)

FIGURE 1. (a) Nullcline surfaces. (b) The projection of (a) to the YZ-plane. (a,b) is for the case of coexistence. Notice that the XY capacity equilibrium is in Z's per-capita growing region $H > 0$ and the XZ capacity equilibrium is in Y's per-capita growing region $G > 0$, hence both are competitive. (c) Coexisting equilibrium exclusion in which only Z is competitive. The 3-d surfaces are not shown for this case. Open circles are capacity equilibrium points of the invariant subsystems. Filled circle is the capacity equilibrium of the full system.

equilibrium. It is unique because of the opposite incline of the two capacity branches. It is always locally stable because its linearization takes the following form:

$$\begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} = \begin{bmatrix} - & - \\ + & - \end{bmatrix}$$

That the diagonal entries are negative is because the equilibrium lies on the X-capacity branch and the Y-capacity branch for which both $\partial F/\partial X < 0$ and $\partial G/\partial Y < 0$. The signs of other entries are fixed by the predator-prey nature of the problem. For example, that $a_{12} < 0$ is because the per-capita growth rate F is negatively suppressed by predation.

We consider next the competition interplay from predator Z to the XY-system. The XY-nullcline $F = G = 0$ is a curve in the full space. The same reciprocal relation applies. More precisely, the *competition-mediated* XY-equilibrium branch continues with nonvanishing competitor Z, and increasing Z decreases the corresponding Y value of the XY-equilibrium. On the YZ-plane, the projection of this competition-mediated XY-equilibrium branch is a curve of negative slope with two end points: $(Y_e, 0), (0, Z_1)$. Here $(X_e, Y_e, 0)$ is the competition-free XY-equilibrium: $F(X_e, Y_e, 0) = G(X_e, Y_e) = 0$; and $(X_1, 0, Z_1)$ corresponds to predator Y's survival threshold: $F(X_1, 0, Z_1) = G(X_1, 0) = 0$. For large X_1 close to K, the competition-mediated XY-equilibrium branch must lie on the predator-mediated X-capacity. That is, the projection in the YZ-plane lies in the X-capacity region Δ. It is important to note that values X_1, Z_1 associated with predator Y's survival threshold do not depend on Y's intraspecific competition parameter m_1, but the XY capacity equilibrium point does. In particular, the greater the m_1 value, the smaller the equilibrium value Y_e becomes because of the intraspecific competition.

Exactly the same analysis applies to the competition-mediated XZ-equilibrium branch. With the symmetrical conditions, we add the YZ-projection of the competition-mediated XZ-equilibrium branch to the region Δ. It is of capacity-capacity type if X_2 is close enough to K.

Existence and Stability of Co-Existing Equilibrium Point. By definition, Y is competitive if it can grow per-capita at the XZ capacity equilibrium state. That is

$$\frac{1}{Y}\frac{dY}{dt} = G(X,Y)\Big|_{(X,Y,Z)=XZ\text{ capacity equilibrium}} > 0$$

That is, the XZ capacity equilibrium is a saddle in the full XYZ-system. Fig.1(a,b) is for a case when both predators are competitive, and Fig.1(c) is for a case when Z is competitive, but Y is not. (For the case where the subsystems have a stable limit cycle, see [6, 2].)

Now, the existence of the XYZ-equilibrium point depends on whether or not the XY-equilibrium curve and the XZ-equilibrium curve intersect. For the Malthusian case $m_1 = m_2 = 0$, they do not in general. For m_1, m_2 small, they do not intersect neither, see Fig.1(c). In such cases, the following order relation on the end points of the curves are typical:

$$Y_e < Y_2 \text{ and } Z_1 < Z_e,$$

where $F(X_1, 0, Z_1) = G(X_1, 0) = 0$ is associated with Y's survival threshold and $F(X_2, Y_2, 0) = H(X_2, 0) = 0$ is associated with Z's survival threshold. In such cases, only one predator is competitive. For the configuration above, it can be easily shown that the XY-equilibrium point is in Z's per-capita growing region $H > 0$ and the XZ-equilibrium point is in Y's per-capita decay region $G > 0$, implying Z is competitive and Y is not.

Assuming that this is the configuration when we start to increase predator Z's intracompetition parameter m_2. The change does not move the XY-equilibrium curve, nor the end point $(0, Y_2)$ of the XZ-curve. However, it decreases Z's capacity equilibrium value Z_e and increase its corresponding $X_e \le 1$ value. Since $Z_e = [b_2X_e/(1 + a_2h_2X_e) - d_2]/m_2 \to 0$ as $m_2 \to \infty$, for large enough m_2, Z_e must lie below Z_1, i.e., the second order relation above is reversed to

$$Y_e < Y_2 \text{ and } Z_e < Z_1.$$

Biologically, Z's intensive intraspecific competition allows an otherwise noncompetitive Y to become competitive. As a result of a variant Intermediate Value Theorem, the two curve must intersect to give an XYZ-equilibrium point because of these curves relative position switching, Fig.1(a,b). This proves the existence. In this case, both predators are competitive.

As for the local stability, the linearization must take the following form

$$J = \begin{bmatrix} - & - & - \\ + & - & 0 \\ + & 0 & - \end{bmatrix}.$$

That the diagonal entries are all negative is because the equilibrium point lies on the predator-mediated prey capacity surface and the prey-supported predator capacity surfaces. That is, it is a capacity equilibrium point. That all other entries have the denoted fixed signs is due to the competitive and predatory nature of the system. Without the need of explicitly finding the expressions of all entries, a simple exercise using the Routh-Hurwitz criterion shows that all eigenvalues of this class of such matrixes have a negative real part, hence the local stability of the co-existing XYZ-equilibrium point.

Further Comments. The system can have non-capacity equilibrium point, which is typically unstable. It can be stabilized for large birth-to-consumption ratio b_1, b_2, which corresponds to the case when both predators are reproductive efficient. A proof will take us too far from our purpose above to demonstrate the co-existence of a stable equilibrium.

The only question left is whether or not this capacity equilibrium is a global attractor for the full system. I believe it is without any additional condition. The Lyapunov method can be used by the authors to this end.

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