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Corrigendum to "Pathogen evolution in switching environments: a hybrid dynamical system approach"

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Abstract

We provide a corrected proof of Theorems 3.3 and 3.6 in the paper "Pathogen evolution in switching environments: a hybrid dynamical system approach", *Mathematical Biosciences* **240** (2012), p. 70-75.

In the proofs of Theorems 3.3 and 3.6 of our paper we cannot assume a special structure for the generator matrix Q with nearly identical rows (this would mean that the infinitesimal probability to jump into a new environment is independent of the current environment). Nevertheless, the idea of the proof, namely that the Lyapunov function can be written as a sum of functions, is correct.

To fix notation, we consider the switching differential equation

$$\frac{dP_i(t)}{dt} = P_i(t)\left(w_i^k - \sum_{j=1}^{m} w_j^k P_j(t)\right), \tag{1}$$

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where $w_i^k > 0$ is the fitness value of genotype i in environment (host species) k and

$$\sum_{j=1}^{m} P_j(t) = 1. \tag{2}$$

The switching process $k = \alpha(t)$ is a Markov process with generator matrix $Q(P)$ whose entries $q_{kl}(P)$ are defined by

$$\mathbf{P}\{\alpha(t+\Delta t) = l \,|\, \alpha(t) = k,\, (P(s), \alpha(s)),\, s \leq t\} = q_{kl}(P(t))\Delta t + o(\Delta t). \tag{3}$$

The elements q_{kl} of the generator matrix Q satisfy $q_{kl} \geq 0$ for all $k \neq l$ and $\sum_{l \in \mathcal{M}} q_{kl} = 0$ for every $k \in \mathcal{M}$.

Theorem 1. *Assume that the generator matrix $Q = (q_{kl})_{k,l=1}^{n}$ is irreducible and let π be its unique stationary distribution. Let P_1 be the genotype with the highest mean fitness, that is*

$$\pi \cdot \mathbf{w}_1 > \pi \cdot \mathbf{w}_i \quad \textit{for all } i = 2, \ldots, m \tag{4}$$

Then the equilibrium e_1 is asymptotically stable in probability and all other equilibria are unstable in probability.

Proof. For $i = 2, \ldots, m$ we set $a_{i,1}^k = w_i^k - w_1^k$ for the difference of fitness values with respect to genotype 1 and $\mathbf{a}_{i,1} = (a_{i,1}^1, \ldots, a_{i,1}^n)$. Using the constraint (2), we eliminate P_1 and obtain the *reduced systems*

$$\frac{dP_i(t)}{dt} = a_{i,1}^k P_i(1 - P_i) - P_i \sum_{j=2,\, j \neq i}^{m} a_{i,1}^k P_j, \tag{5}$$

for $i = 2, \ldots, m$ and $k = 1, \ldots, n$. Notice that for fixed environment k the linear part of this system has a diagonal structure. We define

$$\beta_i := -\pi \cdot \mathbf{a}_{i,1} > 0,$$

with the last inequality holding true since genotype 1 has the higher mean fitness compared to every other genotype. For $i = 2, \ldots, m$ we solve the systems of equations

$$Q\mathbf{c}_i = \mathbf{a}_{i,1} + \beta_i \mathbf{1}$$

for the vector $\mathbf{c}_i = (c_i^1, \ldots, c_i^n)$ where $\mathbf{1}$ is the column vector with n entries 1. The right hand sides of these equation are orthogonal to the kernel of Q which is spanned by $\mathbf{1}$, hence there exist solutions. For $i = 2, \ldots, m$ and $k = 1, \ldots, n$, we define

$$V_i(P_i, k) = (1 - \gamma c_i^k) P_i^\gamma, \quad P_i > 0,$$

with $0 < \gamma < 1$ yet to be selected, in such a way that all coefficients are positive. We have

$$\begin{aligned}
\mathcal{L}V_i(P_i, k) &= \gamma(1 - \gamma c_i^k) P_i^{\gamma-1}(a_{i,1}^k P_i + o(1)) + \sum_{j=1}^n q_{kj}(1 - \gamma c_i^j) P_i^\gamma \\
&= \gamma P_i^\gamma \left((1 - \gamma c_i^k) a_{i,1}^k - \sum_{j=1}^n q_{kj} c_i^j + o(1) \right) \qquad (6) \\
&= \gamma P_i^\gamma \left((1 - \gamma c_i^k) a_{i,1}^k - (a_{i,1}^k + \beta_i) + o(1) \right) \\
&= \gamma P_i^\gamma \left(-\gamma c_i^k a_{i,1}^k + \pi \cdot \mathbf{a}_{i,1} + o(1) \right),
\end{aligned}$$

where we have made use of the fact that the row sums of Q are zero. In order to make all the factors in parentheses negative, we have to choose $0 < \gamma < 1$ such that the inequality

$$\pi \cdot \mathbf{a}_{i,1} < \gamma c_i^k a_i^k \qquad (7)$$

holds. By assumption (4), the left hand side of inequality (7) is negative. Therefore, for those indices i and k for which $c_i^k a_{i,1}^k \geq 0$, no condition arises for γ. If on the other hand $c_i^k a_{i,1}^k < 0$, then we can select

$$0 < \gamma < \min_{\substack{i=2,\ldots m \\ k=1,\ldots,n}} \left\{ \frac{\pi \cdot \mathbf{a}_{i,1}}{c_i^k a_{i,1}^k} \ : \ c_i^k a_{i,1}^k < 0 \right\}.$$

Although the c_i^k are not explicitly known, this is a minimum of finitely many positive numbers. The Lyapunov function is the sum of functions of a single variable

$$V(P_2, \ldots, P_m, k) = \sum_{i=2}^m V_i(P_i, k)$$

and the condition of Proposition 8.6 in [1] follows from the linearity of the operator $\mathcal{L}$ and the choice of γ.

To prove the unstability in probability of equilibrium e_i for $i > 1$, we use the constraint (2) to eliminate P_i. This results in the reduced systems

$$\frac{dP_i(t)}{dt} = a^k_{l,i} P_l(1 - P_l) - P_l \sum_{j \neq i,l}^{m} a^k_{j,i} P_j, \tag{8}$$

for $l \neq i$ and $a^k_{l,i} = w^k_l - w^k_i$. For $i = 2, \ldots, m$ let $\mathbf{c}_i = (c^1_i, \ldots, c^n_i)$ be the solution of

$$Q\mathbf{c}_i = \mathbf{a}_{1,i} - \beta_i \mathbf{1}.$$

We set

$$V(P_1, \ldots, P_{i-1}, P_{i+1}, \ldots, P_m, k) = V(P_1, k) = (1 - \gamma c^k_i) P^\gamma_1, \quad P_1 > 0,$$

where $0 > \gamma > -1$ has yet to be selected, small enough that all coefficients are positive. With a calculation similar to (6) we obtain

$$\begin{aligned}
\mathcal{L}V(P_1, k) &= \gamma(1 - \gamma c^k_i) P^{\gamma-1}_1 (a^k_{1,i} P_1 + o(1)) + \sum_{j=1}^{n} q_{kj} (1 - \gamma c^j_i) P^\gamma_1 \\
&= \gamma P^\gamma_1 \left((1 - \gamma c^k_i) a^k_{1,i} - \sum_{j=1}^{n} q_{kj} c^j_i + o(1) \right) \\
&= \gamma P^\gamma_1 \left((1 - \gamma c^k_i) a^k_{1,i} - (a^k_{1,i} - \beta_i) + o(1) \right) \\
&= \gamma P^\gamma_1 \left(-\gamma c^k_i a^k_{1,i} + \pi \cdot \mathbf{a}_{1,i} + o(1) \right).
\end{aligned}$$

In order to make all the factors in parentheses positive (so that the entire expression becomes negative), we need to have

$$0 > \gamma > \max_{\substack{i=2,\ldots m \\ k=1,\ldots,n}} \left\{ \frac{\pi \cdot \mathbf{a}_{1,i}}{c^k_i a^k_{1,i}} \ : \ c^k_i a^k_{1,i} < 0 \right\}.$$

The expressions whose maximum is taken are all negative since $\pi \cdot \mathbf{a}_{1,i} > 0$ by assumption (4). The condition of Proposition 8.7 in [1] is thereby verified. □

References

[1] G. G. Yin and C. Zhu, *Hybrid Switching Diffusions*, Springer, New York (2010)