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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

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

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

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

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

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

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*

$$\pi \cdot \mathbf{w}_1 > \pi \cdot \mathbf{w}_i \quad \text{for all } i = 2, \dots, m \quad (4)$$

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

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

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

for $i = 2, \dots, m$ and $k = 1, \dots, n$. 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 $i = 2, \dots, m$ we solve the systems of equations

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

for the vector $\mathbf{c}_i = (c_i^1, \dots, c_i^n)$ 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 $i = 2, \dots, m$ and $k = 1, \dots, n$, 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

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

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

$$\pi \cdot \mathbf{a}_{i,1} < \gamma c_i^k a_{i,1}^k \tag{7}$$

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

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

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

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

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

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

for $l \neq i$ and $a_{l,i}^k = w_l^k - w_i^k$. For $i = 2, \dots, m$ let $\mathbf{c}_i = (c_i^1, \dots, c_i^n)$ be the solution of

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

We set

$$V(P_1, \dots, P_{i-1}, P_{i+1}, \dots, P_m, k) = V(P_1, k) = (1 - \gamma c_i^k) P_1^\gamma, \quad P_1 > 0,$$

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

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

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

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

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. \square

References

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