



Corrigendum

Corrigendum to “Pathogen evolution in switching environments: A hybrid dynamical system approach” [Math. Biosci. 240 (2012) 70–75]

József Z. Farkas<sup>a</sup>, Peter Hinow<sup>b,\*</sup>, Jan Engelstädter<sup>c</sup>

<sup>a</sup> Division of Computing Science and Mathematics, University of Stirling, Stirling FK9 4LA, United Kingdom

<sup>b</sup> Department of Mathematical Sciences, University of Wisconsin – Milwaukee, P.O. Box 413, Milwaukee, WI 53201, USA

<sup>c</sup> Institute of Integrative Biology, Swiss Federal Institute of Technology, Universitätsstrasse 16, 8092 Zürich, Switzerland

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

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

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

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

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  $\pi$  be its unique stationary distribution. Let  $P_1$  be the genotype with the highest mean fitness, that is

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

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

**Proof.** For  $i = 2, \dots, m$  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

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

for  $i = 2, \dots, m$  and  $k = 1, \dots, n$ . Note 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 equations 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  $\gamma$ . If on the other hand  $c_i^k a_{i,1}^k < 0$ , then we can select

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 \* Corresponding author. Current address: School of Biological Sciences, University of Queensland, Brisbane, Qld 4072, Australia.  
 E-mail addresses: [jzf@maths.stir.ac.uk](mailto:jzf@maths.stir.ac.uk) (J.Z. Farkas), [hinow@uwm.edu](mailto:hinow@uwm.edu) (P. Hinow), [jengelstaedter@uq.edu.au](mailto:jengelstaedter@uq.edu.au) (J. Engelstädter).

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

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  $\gamma$ .

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

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

for  $l \neq i$  and  $a_{i,i}^k = w_l^k - w_i^k$ . 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

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

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.  $\square$

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**Reference**

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