

Supplementary Information: A Paradoxical Evolutionary Mechanism in Stochastically Switching Environments

Kang Hao Cheong^{1,*}, Zong Xuan Tan², Neng-gang Xie³, and Michael C. Jones⁴

¹Engineering Cluster, Singapore Institute of Technology, 10 Dover Drive, Singapore 138683, Singapore

²Yale University, New Haven, CT 06520, United States

³Department of Mechanical Engineering, Anhui University of Technology, Anhui Ma'anshan 243002, China

⁴Columbia, Missouri, United States

*To whom correspondence should be addressed. E-mail: Kanghao.Cheong@SingaporeTech.edu.sg

The results in this paper are corroborated by both numerical simulations and analytical derivations. Detailed analytical derivations are given below for completeness.

Proof A

Let $\tilde{\mathbf{X}}_n$ be the random variable that represents the population vector after n generations. $\tilde{\mathbf{X}}_n$ can be expressed as

$$\tilde{\mathbf{X}}_n = \mathbf{X}_0 \prod_{i=1}^n (\mathbf{M}\tilde{\mathbf{S}}_i\mathbf{G}) \quad (\text{S1})$$

where each $\tilde{\mathbf{S}}_i$ is an independent random variable representing the switching matrix for generation i :

$$\tilde{\mathbf{S}}_i = \begin{cases} \mathbf{S}_0 & \text{with probability } 1 - p, \\ \mathbf{S}_1 & \text{with probability } p. \end{cases} \quad (\text{S2})$$

We can express $\tilde{\mathbf{X}}_n$ recursively in terms of $\tilde{\mathbf{X}}_{n-1}$ as

$$\tilde{\mathbf{X}}_n = \tilde{\mathbf{X}}_{n-1} \mathbf{M}\tilde{\mathbf{S}}_n\mathbf{G}. \quad (\text{S3})$$

Since $\tilde{\mathbf{X}}_{n-1}$ and $\tilde{\mathbf{S}}_n$ are independent random variables, it follows that:

$$\begin{aligned} \mathbb{E}[\tilde{\mathbf{X}}_n] &= \mathbb{E}[\tilde{\mathbf{X}}_{n-1}] \mathbb{E}[\tilde{\mathbf{S}}_n] \mathbf{G} \\ &= \mathbb{E}[\tilde{\mathbf{X}}_{n-1}] \mathbf{M}\mathbf{S}\mathbf{G} \end{aligned}$$

where $\mathbf{S}$ is the expected switching matrix, as defined in Equation 20.

We proceed by induction on n and Equation 21 follows (restated here):

$$\mathbb{E}[\tilde{\mathbf{X}}_n] = \mathbf{X}_0 (\mathbf{M}\mathbf{S}\mathbf{G})^n.$$

Proof B

For the following analysis, we define for convenience the overall growth matrix for a single generation, $\mathbf{T} = \mathbf{M}\mathbf{S}\mathbf{G}$, as well as the complementary probabilities $q = 1 - p$ and $t_i = 1 - s_i$.

$\mathbf{T}$ can be expressed in terms of $\mathbf{A}$ and $\mathbf{B}$ from Equation 6 and $\mathbf{G}_1$ and $\mathbf{G}_2$ from Equation 15:

$$\mathbf{T} = \begin{pmatrix} \mathbf{C} & \mathbf{D} \\ \mathbf{C} & \mathbf{D} \end{pmatrix} \quad \text{where} \quad \mathbf{C} = (q\mathbf{A} + p\mathbf{B})\mathbf{G}_1 \quad \text{and} \quad \mathbf{D} = (p\mathbf{A} + q\mathbf{B})\mathbf{G}_2. \quad (\text{S4})$$

Proof.

$$\begin{aligned} \mathbf{T} = \mathbf{M}\mathbf{S}\mathbf{G} &= \begin{pmatrix} \mathbf{A} & \mathbf{B} \\ \mathbf{A} & \mathbf{B} \end{pmatrix} \begin{pmatrix} q\mathbf{I}_L & p\mathbf{I}_L \\ p\mathbf{I}_L & q\mathbf{I}_L \end{pmatrix} \begin{pmatrix} \mathbf{G}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{G}_2 \end{pmatrix} \\ &= \begin{pmatrix} q\mathbf{A} + p\mathbf{B} & p\mathbf{A} + q\mathbf{B} \\ q\mathbf{A} + p\mathbf{B} & p\mathbf{A} + q\mathbf{B} \end{pmatrix} \begin{pmatrix} \mathbf{G}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{G}_2 \end{pmatrix} = \begin{pmatrix} \mathbf{C} & \mathbf{D} \\ \mathbf{C} & \mathbf{D} \end{pmatrix} \end{aligned}$$

□

From this, we can derive Equation 29, restated here:

$$\mathbf{E}[\tilde{\mathbf{Y}}_{\mathbf{n}}] = \mathbf{Y}_0 \mathbf{K}^n$$

where $\mathbf{K}$ can be expressed as

$$\mathbf{K} = \mathbf{C} + \mathbf{D}. \quad (\text{S5})$$

Proof.

$$\begin{aligned} \mathbf{E}[\tilde{\mathbf{Y}}_{\mathbf{n}}] &= \mathbf{X}_0 \mathbf{T}^n \begin{pmatrix} \mathbf{I}_L \\ \mathbf{I}_L \end{pmatrix} = \mathbf{X}_0 \begin{pmatrix} \mathbf{C} & \mathbf{D} \\ \mathbf{C} & \mathbf{D} \end{pmatrix}^n \begin{pmatrix} \mathbf{I}_L \\ \mathbf{I}_L \end{pmatrix} \\ &= \mathbf{X}_0 \begin{pmatrix} (\mathbf{C} + \mathbf{D})^n \\ (\mathbf{C} + \mathbf{D})^n \end{pmatrix} = \mathbf{X}_0 \begin{pmatrix} \mathbf{I}_L \\ \mathbf{I}_L \end{pmatrix} (\mathbf{C} + \mathbf{D})^n = \mathbf{Y}_0 \mathbf{K}^n \end{aligned}$$

□

When mutation is absent, we have $\mathbf{G}_1 = E_1 \mathbf{I}_L$ and $\mathbf{G}_2 = E_2 \mathbf{I}_L$. Given this, we can derive Equations 30 and 31:

$$\mathbf{K} = \begin{pmatrix} \kappa_1 & 0 & \cdots & 0 \\ 0 & \kappa_2 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & \kappa_L \end{pmatrix} \quad (\text{without mutation})$$

$$\kappa_j = 1 - \delta(2p - 1)(2s_j - 1)$$

Proof. Since $\mathbf{A}$, $\mathbf{B}$, $\mathbf{G}_1$ and $\mathbf{G}_2$ are all diagonal matrices when mutation is absent, so are $\mathbf{C}$, $\mathbf{D}$, and $\mathbf{K} = \mathbf{C} + \mathbf{D}$. Recall that the i th diagonal entries of $\mathbf{A}$ and $\mathbf{B}$ respectively are s_i and $t_i = 1 - s_i$. Computing the i th diagonal entry of $\mathbf{K}$, $\kappa_i = C_{ii} + D_{ii}$, we have

$$\begin{aligned} \kappa_i &= (qs_i + pt_i)E_1 + (ps_i + qt_i)E_2 \\ &= (qs_i + pt_i)(1 + \delta) + (ps_i + qt_i)(1 - \delta) \\ &= qs_i + pt_i + ps_i + qt_i + \delta(qs_i + pt_i - ps_i - qt_i) \\ &= (q + p)(s_i + t_i) + \delta(q - p)(s_i - t_i) \\ &= 1 - \delta(2p - 1)(2s_i - 1) \end{aligned}$$

□

When mutation is present and the number of sensor levels $L = 3$, $\mathbf{K}$ can be expressed as

$$\mathbf{K} = \begin{pmatrix} \kappa_1 & \alpha_1^* & \beta_1^* \\ \alpha_2^* & \kappa_2 & \alpha_2^* \\ \beta_3^* & \alpha_3^* & \kappa_3 \end{pmatrix} \quad (\text{with mutation}) \quad (\text{S6})$$

where we define the overall growth and mutation rates

$$\kappa_i = 1 - \delta(2p - 1)(2s_i - 1) \quad (\text{S7})$$

$$\alpha_i^* = \bar{\alpha} - \sigma_\alpha(2p - 1)(2s_i - 1) \quad (\text{S8})$$

$$\beta_i^* = \bar{\beta} - \sigma_\beta(2p - 1)(2s_i - 1) \quad (\text{S9})$$

and where α_i^* are β_i^* are defined using the averages and the standard deviations of the mutation rates

$$\bar{\alpha} = \frac{\alpha_1 + \alpha_2}{2} \quad \sigma_\alpha = \frac{\alpha_1 - \alpha_2}{2}, \quad (\text{S10})$$

$$\bar{\beta} = \frac{\beta_1 + \beta_2}{2} \quad \sigma_\beta = \frac{\beta_1 - \beta_2}{2}. \quad (\text{S11})$$

Proof. We define the matrices $\bar{\mathbf{G}}$ and $\mathbf{G}_\sigma$ as:

$$\bar{\mathbf{G}} = \frac{1}{2}(\mathbf{G}_1 + \mathbf{G}_2) = \begin{pmatrix} 1 & \bar{\alpha} & \bar{\beta} \\ \bar{\alpha} & 1 & \bar{\alpha} \\ \bar{\beta} & \bar{\alpha} & 1 \end{pmatrix} \quad \mathbf{G}_\sigma = \frac{1}{2}(\mathbf{G}_1 - \mathbf{G}_2) = \begin{pmatrix} \delta & \sigma_\alpha & \sigma_\beta \\ \sigma_\alpha & \delta & \sigma_\alpha \\ \sigma_\beta & \sigma_\alpha & \delta \end{pmatrix}. \quad (\text{S12})$$

We can thus write $\mathbf{G}_1$ as $\bar{\mathbf{G}} + \mathbf{G}_\sigma$ and $\mathbf{G}_2$ as $\bar{\mathbf{G}} - \mathbf{G}_\sigma$. It follows from $\mathbf{K} = \mathbf{C} + \mathbf{D}$ that

$$\begin{aligned} \mathbf{K} &= (q\mathbf{A} + p\mathbf{B})(\bar{\mathbf{G}} + \mathbf{G}_\sigma) + (p\mathbf{A} + q\mathbf{B})(\bar{\mathbf{G}} - \mathbf{G}_\sigma) \\ &= (q\mathbf{A} + p\mathbf{B} + p\mathbf{A} + q\mathbf{B})\bar{\mathbf{G}} + (q\mathbf{A} + p\mathbf{B} - p\mathbf{A} - q\mathbf{B})\mathbf{G}_\sigma \\ &= \bar{\mathbf{G}} - (p - q)(\mathbf{A} - \mathbf{B})\mathbf{G}_\sigma \\ &= \begin{pmatrix} 1 & \bar{\alpha} & \bar{\beta} \\ \bar{\alpha} & 1 & \bar{\alpha} \\ \bar{\beta} & \bar{\alpha} & 1 \end{pmatrix} + (2p - 1) \begin{pmatrix} 2s_1 - 1 & 0 & 0 \\ 0 & 2s_2 - 1 & 0 \\ 0 & 0 & 2s_3 - 1 \end{pmatrix} \begin{pmatrix} \delta & \sigma_\alpha & \sigma_\beta \\ \sigma_\alpha & \delta & \sigma_\alpha \\ \sigma_\beta & \sigma_\alpha & \delta \end{pmatrix} \\ &= \begin{pmatrix} \kappa_1 & \alpha_1^* & \beta_1^* \\ \alpha_2^* & \kappa_2 & \alpha_2^* \\ \beta_3^* & \alpha_3^* & \kappa_3 \end{pmatrix}. \end{aligned}$$

□

Proof C

Substituting $p = 0.5$ into the general expression for $\mathbf{K}$ gives us Equation 33. As shown earlier, when $p = 0.5$, the sub-populations y_1 and y_3 grow at equal rates. We can now also see why y_1 grows more slowly than y_3 if $p < 0.5$ and why y_1 grows more quickly than y_3 if $p > 0.5$, even if $y_1 = y_3$ initially. Expanding the matrix notation in Equation 29 using $\mathbf{K}$ from Equation S6 gives us the following recurrence relations:

$$\mathbb{E}[(\tilde{\mathbf{Y}}_n)_1] = \kappa_1 \mathbb{E}[(\tilde{\mathbf{Y}}_{n-1})_1] + \alpha_1^* \mathbb{E}[(\tilde{\mathbf{Y}}_{n-1})_2] + \beta_1^* \mathbb{E}[(\tilde{\mathbf{Y}}_{n-1})_3], \quad (\text{S13})$$

$$\mathbb{E}[(\tilde{\mathbf{Y}}_n)_3] = \kappa_1 \mathbb{E}[(\tilde{\mathbf{Y}}_{n-1})_3] + \alpha_1^* \mathbb{E}[(\tilde{\mathbf{Y}}_{n-1})_2] + \beta_1^* \mathbb{E}[(\tilde{\mathbf{Y}}_{n-1})_1]. \quad (\text{S14})$$

From Equations S7 to S9, it is clear that when $p < 0.5$, κ_i , α_i^* and β_i^* all increase with increasing s_i , whereas when $p > 0.5$, κ_i , α_i^* and β_i^* decrease with increasing s_i . Since $s_3 > s_1$, it follows from the recurrence relations that even if y_3 and y_1 start off being equal, y_3 will be greater than y_1 in the next generation if $p < 0.5$, whereas the opposite will occur if $p > 0.5$.