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On a discrete selection–mutation model

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A discrete-time population model in which individuals are distributed over a discrete phenotypic trait-space is studied. It is shown that, for an irreducible mutation matrix Γ , if mutation is small, then an interior equilibrium exists, that is globally asymptotically stable in $\mathbb{R}_+^n \setminus \{0\}$, while for arbitrary large mutation, each trait persists uniformly. For the model reduced to only two traits, conditions for the global stability of the interior equilibrium are provided. When structure is introduced in the model, namely when mutation matrix Γ has block-diagonal form, with each diagonal block being irreducible, competitive exclusion among traits is analysed and sufficient conditions are given for one trait to drive all the other traits to extinction.

Keywords: selection–mutation; robust uniform persistence; coexistence; competitive exclusion

1. Introduction

In recent years, researchers have focused their attention on studying selection–mutation models, also referred to as replicator-mutator equations or distributed rate population models [2–5,8–10,12–14,17–20]. These are equations in which individuals are distributed according to a (discrete [3,5,17] or continuous [2,4,9,10,14,19]) phenotypic trait space. Here, selection means that individuals with a particular trait produce individuals of that trait only (faithful reproduction). While mutation means that individuals carrying a particular trait are able to produce individuals with other traits (unfaithful reproduction).

In [4], the following pure selection model was considered

$$\frac{dx(t, q)}{dt} = x(t, q) \left[q_1 - q_2 \int_Q x(t, q) dq \right], \quad (1.1)$$

where individuals are distributed over the continuous 2D compact trait space $Q = \{(q_1, q_2) \in \text{int}(\mathbb{R}_+^2) : \underline{q}_1 \leq q_1 \leq \overline{q}_1, \underline{q}_2 \leq q_2 \leq \overline{q}_2\}$ with q_1 and q_2 describing the growth rate and the mortality rate of individuals carrying trait q , respectively (as usual, we denote by \mathbb{R} the set of real numbers, by \mathbb{R}^n the set $\{(x_1, \dots, x_n) \mid x_i \in \mathbb{R} \text{ for all } i = 1, \dots, n\}$, by \mathbb{R}_+^n the non-negative cone in \mathbb{R}^n , namely the set $\{x = (x_1, \dots, x_n) \in \mathbb{R}^n \mid x_i \geq 0 \text{ for all } i = 1, \dots, n\}$ and by $\text{int}(\mathbb{R}_+^n)$ the interior of \mathbb{R}_+^n , namely the set $\{x = (x_1, \dots, x_n) \in \mathbb{R}^n \mid x_i > 0 \text{ for all } i = 1, \dots, n\}$). Therein, the authors prove that the density $x(t, q)$ converges (in the weak-star topology) to a weighted Dirac measure centred at the point of highest growth to mortality ratio given by $q^* = \overline{q}_1 / \underline{q}_2$ (i.e.,

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$x(t, q) \rightarrow c\delta_{q^*}$ in weak-star topology as $t \rightarrow \infty$). This result can be described in the context of competitive exclusion where the individuals carrying the fittest trait q^* win the competition and all other traits go to extinction. In [2], the authors formulated a general selection model on the space of measures (appropriate for such models) and extended the competitive exclusion result in [4] to this model. In [9,10], the authors consider selection–mutation models with continuous trait space (albeit 1D) and establish similar competitive exclusion result when the probability of mutation becomes extremely small.

In [3], a selection–mutation model was formulated on a discrete trait space. An equivalent formulation to the discrete selection–mutation model in [3] takes the form

$$\frac{dx_i}{dt} = \sum_{j=1}^n \gamma_{ij} a_j x_j - b_i x_i \sum_{j=1}^n x_j, \quad i = 1, 2, \dots, n. \quad (1.2)$$

Here, the total population is given by $\sum_{j=1}^n x_j$, and the i th subpopulation is identified by the two-dimensional discrete trait $(a_i, b_i) \in \mathbb{R}_+^2$, where a_i is the per-capita growth rate and b_i is the per-capita mortality rate. The parameter γ_{ij} denotes the fraction of offspring of an individual in the j th subpopulation which belongs to the i th subpopulation, $0 \leq \gamma_{ij} \leq 1$ and $\sum_{i=1}^n \gamma_{ij} = 1$. For convenience, we will denote by $\Gamma = (\gamma_{ij})$ the selection–mutation matrix whose (i, j) entry is given by γ_{ij} . Clearly Γ is a column stochastic matrix since each of the column sums of Γ is equal to one. Note that if Γ is the identity matrix then the model (1.2) reduces to the following pure selection model which is the discrete trait space analogue of the model (1.1):

$$\frac{dx_i}{dt} = x_i \left[a_i - b_i \sum_{j=1}^n x_j \right], \quad i = 1, 2, \dots, n. \quad (1.3)$$

The goal of this article is to develop and study a selection–mutation model which is discrete not only in the trait space but in time as well. To our knowledge, this is the first study of a selection–mutation model which is discrete in trait space and time. We mention that discrete time selection-only models (that is, without mutation) have been used to describe the dynamics of multiple pathogen strains [7]. Accounting for mutation allows us to accurately model the dynamics of many pathogens including the flu virus. The model studied here generalizes the pure selection model studied in [1]. Therein, the authors used a non-standard finite difference approximation [15] to develop the following discrete time analogue of the selection model (1.3):

$$x_i(t+1) = \frac{(a_i + 1)x_i(t)}{1 + b_i \sum_{j=1}^n x_j(t)}, \quad i = 1, \dots, n. \quad (1.4)$$

In [1], the authors show that, provided there is a unique trait with maximum carrying capacity a_i/b_i , the equilibrium $(0, \dots, 0, a_i/b_i, 0, \dots, 0)$ describing the competitive exclusion between the n traits, with i being the fittest trait, is locally asymptotically stable. For the special case $n = 2$, they were able to prove that this equilibrium is globally asymptotically stable. Recently, in [11] the authors were able to extend the results in [1] and prove that $(0, \dots, 0, a_i/b_i, 0, \dots, 0)$ is globally asymptotically stable for a general n provided there is a unique species having a maximum carrying capacity a_i/b_i . They also show that if more than one trait have the same (maximum) carrying capacity then all subpopulations with the largest carrying capacity coexist and in this case, the system has a linear stable manifold.

In this work, we present a more general model which allows for selection and mutation. For completeness, we include the competitive exclusion result obtained in [11] for the model without mutation, but we offer a new (and much shorter) proof. For the model with mutation, which represents the focus of our analysis, we investigate both possibilities of coexistence and competitive exclusion. In regard to coexistence, we show that when the mutation matrix Γ is irreducible, then the model is (robustly) uniformly persistent, that is, roughly speaking, all traits survive above a certain threshold that is independent of the non-zero initial conditions (and of small changes in parameters). If, in addition to being irreducible, Γ is also ‘small’, then there is a globally asymptotically stable interior equilibrium. For Γ that is not necessarily small, but satisfying some additional conditions, we show that all interior solutions are attracted to a (possibly degenerated) ‘box’ with ‘faces’ parallel to the boundary hyperplanes and which intersects every nullcline only at points situated on its boundary. Using these properties of the attracting box, we give a set of explicit conditions under which we have a globally asymptotically stable interior equilibrium for the case when $n = 2$. In regard to competitive exclusion, we show that if there is a trait i such that all the other traits have negative relative exponential rate of increase (negative fitness) with respect to trait i (see Section 2.2 for a precise definition of this concept), then trait i drives all the other traits to extinction.

The article is organized as follows. In Section 2, we present the general model. In Section 3, we study the model in the pure selection case (no mutation is assumed). In Section 4, we study the model with mutation. Concluding remarks are made in Section 5. Section 6 contains some preliminary material that we use to establish needed persistence results.

2. The model

Consider the following selection–mutation model:

$$x_i(t+1) = \frac{(\gamma_{ii}a_i + 1)x_i(t) + \sum_{j \neq i} \gamma_{ij}a_jx_j(t)}{1 + b_i \sum_j x_j(t)}, \quad i = 1, \dots, n, \quad (2.1)$$

where $a_i > 0$, $b_i > 0$ and $\Gamma = (\gamma_{ij})_{1 \leq i, j \leq n}$ is a non-negative matrix.

This model accounts for competition among individuals having one of n possible traits. Here, x_i is the number of individuals carrying trait i with per-capita birth and mortality rates given by a_i and b_i , respectively. The parameter γ_{ij} represents the fraction of offspring of an individual with trait j that belongs to trait i .

The assumption that $\sum_{i=1}^n \gamma_{ij} = 1$, $j = 1, \dots, n$ (made in [3]) is not needed for establishing the mathematical results, yet we make it in here due to biological reasons, as the fractions of all newborns that belong to one individual is equal to 1. Note that when Γ is the identity matrix, model (2.1) reduces to the selection model (1.4).

For convenience, for an $x = (x_1, \dots, x_n) \in \mathbb{R}_+^n$, we will hereafter denote $x_1 + \dots + x_n$ by $|x|$.

PROPOSITION 2.1. *The system (2.1) is dissipative:*

$$\frac{|x(t)|}{b} \leq (a\gamma + 1), \quad \forall t \geq 1, \quad (2.2)$$

where $a = \max_i \{a_i\}$, $b = \min_i \{b_i\}$ and $\gamma = \max_{i,j} \gamma_{ij}$.

The proof of Proposition 2.1 is straightforward; thus, we omit it.

2.1 The model without mutation

In this section, we study the pure selection case in which the matrix Γ is the identity. Here, the model (2.1) reduces to

$$x_i(t+1) = \frac{(a_i+1)x_i(t)}{1 + b_i \sum_j x_j(t)} \doteq f_i(x_i(t)), \quad i = 1, \dots, n. \quad (2.3)$$

We first show that for the model (2.3) there are either isolated fixed points on the bounding hyperplanes of the positive cone \mathbb{R}_+^n , or a continuum of fixed points.

THEOREM 2.2. *If $\hat{x} = (\hat{x}_1, \hat{x}_2, \dots, \hat{x}_n)$ is a fixed point of (2.3), then*

$$\frac{a_{i_1}}{b_{i_1}} = \frac{a_{i_2}}{b_{i_2}} = \dots = \frac{a_{i_m}}{b_{i_m}} = \sum_j \hat{x}_j \doteq k, \quad (2.4)$$

for all i_s such that $\hat{x}_{i_s} \neq 0$. Conversely, if

$$\frac{a_{i_1}}{b_{i_1}} = \frac{a_{i_2}}{b_{i_2}} = \dots = \frac{a_{i_m}}{b_{i_m}} \doteq k, \quad (2.5)$$

for a subset $S \doteq \{i_1, i_2, \dots, i_m\} \subset \{1, 2, \dots, n\}$ that is maximal with respect to (2.5), then all $\hat{x} = (\hat{x}_1, \hat{x}_2, \dots, \hat{x}_n)$ satisfying $\sum_j \hat{x}_j = k$ and $\hat{x}_j = 0$ for $j \notin S$ are fixed points of (2.3).

Proof. Let \hat{x} be a fixed point, define $S = \{i | \hat{x}_i \neq 0\}$ and let k be defined as in (2.4). Then, for each $i \in S$

$$\hat{x}_i = \frac{(a_i+1)\hat{x}_i}{1 + b_i \sum_j \hat{x}_j} \Rightarrow k = \frac{a_i}{b_i}.$$

To prove the converse, let (2.5) hold where k is defined to be the common value of the ratios. Define the simplex

$$\mathcal{H}_k \doteq \{x = (x_1, x_2, \dots, x_n) \in \mathbb{R}_+^n \mid |x| = k\}, \quad (2.6)$$

where, as before, we use the notation $|x| = x_1 + \dots + x_n$. Then, for all $x(t) \in \mathcal{H}_k$, (2.3) takes the form

$$x_i(t+1) = \frac{(a_i+1)x_i(t)}{1 + (a_i/k) \sum_j x_j(t)} = x_i(t).$$

□

Remark 2.3. Note that if $r_j \doteq a_j/b_j$ constitute n distinct numbers, then applying the converse assertion serially for $j = 1, 2, \dots, n$, we find that the only fixed points that exist are on the coordinate axes with $x_j = r_j$.

The following result states that the species that is capable of living alone (in the absence of all the other species) at a carrying capacity that is the largest, compared to the carrying capacities of all the other species, wins the competition by driving all the other

species to extinction. The same result can be found in [11] (but the proof is tedious and requires many preliminary lemmas).

THEOREM 2.4. *Assume that $a_1/b_1 = a_2/b_2 = \dots = a_k/b_k > a_{k+1}/b_{k+1} \geq \dots \geq a_n/b_n$, for some $k \in \{1, \dots, n\}$. Then, $x(t) \rightarrow \bar{x}$ and $x_i(t) \rightarrow 0$ as $t \rightarrow \infty$, for all $i = k + 1, \dots, n$, for every solution $x(t) = (x_1(t), \dots, x_n(t))$ of (2.3) with $x_1(0) + \dots + x_k(0) > 0$, where $\bar{x} = \bar{x}(x(0))$ is an equilibrium with $|\bar{x}| = a_1/b_1$.*

Proof. Let $f = (f_1, \dots, f_n)$, where each f_i is as in (2.3). Let $\mathcal{H}_c = \{x \in \mathbb{R}_+^n \mid |x| = c > 0\}$ and assume $c \leq a_1/b_1$. Then, for $x \in \mathcal{H}_c$, we have

$$|f(x)| = \sum_{i=1}^n \frac{a_i + 1}{1 + b_i c} x_i. \tag{2.7}$$

Hence, the maximum of $|f(x)|$, for $x \in \mathcal{H}_c$, is attained at a point $x = (0, \dots, 0, c, 0, \dots, 0)$:

$$\max_{x \in \mathcal{H}_c} |f(x)| = \frac{a_i + 1}{1 + b_i c} c, \text{ for some } i \in \{1, \dots, n\}. \tag{2.8}$$

But

$$\frac{a_i + 1}{1 + b_i c} c > \frac{a_1}{b_1} \Leftrightarrow c(a_i b_1 - a_1 b_i + b_1) > a_1. \tag{2.9}$$

If $c(a_i b_1 - a_1 b_i + b_1) > a_1$ is true then, since $a_1/b_1 \geq a_i/b_i$, we have $c b_1 > a_1$, which represents a contradiction. Hence, $c(a_i b_1 - a_1 b_i + b_1) \leq a_1$ and, from (2.9), $c(a_i + 1)/(1 + b_i c) \leq a_1/b_1$. This implies that $\mathcal{S} := \{x \in \mathbb{R}_+^n \mid |x| \leq a_1/b_1\}$ is positively invariant for (2.3).

Now, let $\tilde{x} \in \mathbb{R}_+^n$ such that $\tilde{x}_1 + \dots + \tilde{x}_k > 0$ and consider the solution $x(t)$ of (2.3) with $x(0) = \tilde{x}$. Without loss of generality, we consider $\tilde{x}_i > 0$ for all $i = 1, \dots, k$.

Case 1: $\tilde{x} \in \mathcal{S}$. Then, $x(t) \in \mathcal{S}$ for all $t \geq 0$, which implies that $x_i(t+1) \geq x_i(t)$, $i = 1, \dots, k$, for all $t \geq 0$. Hence $x_i(t)$ is convergent to an $\bar{x}_i > 0$, $i = 1, \dots, k$, as $t \rightarrow \infty$. Then, from the equation for x_1 in (2.3), it follows that $|x(t)| \rightarrow a_1/b_1$. This implies that $\lim_{t \rightarrow \infty} x_i(t+1)/x_i(t) = (a_i + 1)/(1 + a_1 b_i/b_1) < 1$, for all $i = k + 1, \dots, n$, hence $x_i(t) \rightarrow 0$, $i = k + 1, \dots, n$. Thus, $x(t) \rightarrow \bar{x} = (\bar{x}_1, \dots, \bar{x}_k, 0, \dots, 0)$, where \bar{x} must be an equilibrium with $|\bar{x}| = a_1/b_1$.

Case 2: $\tilde{x} \notin \mathcal{S}$. If $x(t) \notin \mathcal{S}$ for all $t \geq 0$ then

$$x_i(t+1) < \frac{a_i + 1}{1 + b_i(a_1/b_1)} x_i(t), \quad \forall t \geq 0, \quad i = 1, \dots, n. \tag{2.10}$$

If $i \notin \{1, \dots, k\}$, then (2.10) implies that $x_i(t) \rightarrow 0$ as $t \rightarrow \infty$, because $a_1/b_1 > a_i/b_i$. If $i \in \{1, \dots, k\}$, then (2.10) implies that $x_i(t+1) < x_i(t)$ for all $t \geq 0$, hence $x_i(t)$ converges to some \bar{x}_i , as $t \rightarrow \infty$. Then, from the equation for x_1 in (2.3), it follows that $|x(t)| \rightarrow a_1/b_1$. So again, $x(t) \rightarrow \bar{x} = (\bar{x}_1, \dots, \bar{x}_k, 0, \dots, 0)$, where \bar{x} must be an equilibrium with $|\bar{x}| = a_1/b_1$. If $x(t) \in \mathcal{S}$ for some $t > 0$, then, without loss of generality we can consider that we are in Case 1 above. \square

COROLLARY 2.5. When $a_1/b_1 > a_i/b_i$ for all $i = 2, \dots, n$, the equilibrium $(a_1/b_1, 0, \dots, 0)$ is asymptotically stable and attracts all solutions $x(t)$ of (2.3) with $x_1(0) > 0$.

The proof of this corollary follows in a straightforward manner from the proof of Theorem 2.4 and we omit it.

2.2 The full model with mutation

2.2.1 Coexistence and global convergence

In this section, we re-consider model (2.1) with $\Gamma \neq I$, with I denoting the $n \times n$ identity matrix. For $i_1, \dots, i_k \in \{1, \dots, n\}$, $i_1 < i_2 < \dots < i_k$, let Γ_{i_1, \dots, i_k} be the matrix $\tilde{\Gamma} = (\tilde{\gamma}_{lm})_{1 \leq l, m \leq k}$ defined by $\tilde{\gamma}_{lm} = \gamma_{i_l i_m}$.

THEOREM 2.6. Assume that there exist $1 \leq k \leq n$ and $i_1, \dots, i_k \in \{1, \dots, n\}$ with $i_1 < i_2 < \dots < i_k$, such that Γ_{i_1, \dots, i_k} is irreducible. Then, there exists $\varepsilon = \varepsilon(\Gamma) > 0$ such that

$$\liminf_{t \rightarrow \infty} |x(t)| > \varepsilon, \quad (2.11)$$

for every non-zero solution of (2.1).

Proof. Without loss of generality assume $i_j = j$ for all $j = 1, \dots, k$. Let $x^{(1)}(t) = (x_1(t), \dots, x_k(t))$, for all $t \geq 0$. Let $A_{\Gamma_{1, \dots, k}}(x) = (a_{ij}(x))_{1 \leq i, j \leq k}$, where $a_{ij}(x) = \gamma_{ij} a_j / (1 + b_j |x|)$ if $i \neq j$, and $a_{ii}(x) = (\gamma_{ii} a_i + 1) / (1 + b_i |x|)$. Then, $x^{(1)}(t+1) \geq A_{\Gamma_{1, \dots, k}}(x(t)) x^{(1)}(t)$ for all $t \geq 0$. Let

$$P(t, x_0) := A_{\Gamma_{1, \dots, k}}(x(t-1)) \cdots A_{\Gamma_{1, \dots, k}}(x(0)), \quad (2.12)$$

where $x(0) = x_0$. $\Gamma_{1, \dots, k}$ being irreducible, for all $j = 1, \dots, k$ there exists $i = 1, \dots, k$ such that $\gamma_{ij} > 0$. Hence, $\sum_{i=1}^k a_{ij}(0) > 1$ for all $j = 1, \dots, k$. This implies that the spectral radius of $A_{\Gamma_{1, \dots, k}}(0)$ is greater than 1. Also, $P(1, 0)$ is primitive, because it is irreducible (since $\Gamma_{1, \dots, k}$ is irreducible) and all the entries on its main diagonal are positive. It is straightforward to check that (H1) and (H2) from Section 4 hold with $B = \{x \in \mathbb{R}_+^n \mid |x(t)| \leq (a\gamma + 1)/b\}$ (see Proposition 2.1) and $X = \{0\}$. Also, regarding the origin as a periodic orbit with period $T = 1$, Corollary 4.7 in [21] implies (via Proposition 4.1 in [21]) that (A.7) holds. Thus, Theorem 4.1 in the Appendix implies (2.11). \square

Thus, in ‘biological terms’, Theorem 2.6 says that if there is a subpopulation consisting only of certain infection traits, such that individuals belonging to a certain trait in that subpopulation are capable of producing (not necessarily directly) individuals belonging to all the traits in the subpopulation, then the total population is guaranteed to survive above a certain level that is independent of the initial, non-zero total population. When the total population has the above mentioned property, the result can be improved (as we show later) in that all traits survive above such a fixed, positive level.

LEMMA 2.7. (UNIFORM PERSISTENCE). If Γ is irreducible then there exists $\varepsilon = \varepsilon(\Gamma) > 0$ such that

$$\liminf_{t \rightarrow \infty} \min_i \{x_i(t)\} > \varepsilon, \quad (2.13)$$

for every non-zero solution of (2.1). In particular, there exists a unique interior equilibrium (that is, an equilibrium with all coordinates positive). Moreover, when $b_1 = \dots = b_n$, all non-zero solutions are attracted to this interior equilibrium.

Proof. The model (2.1) can be written in the form

$$x(t + 1) = A_\Gamma(x(t))x(t), \tag{2.14}$$

where $A_\Gamma(x) = (a_{ij}(x))_{1 \leq i, j \leq n}$, $a_{ij}(x) = \gamma_{ij}a_j / (1 + b_i|x|)$ if $i \neq j$ and $a_{ii}(x) = (\gamma_{ii}a_i + 1) / (1 + b_i|x|)$.

Γ being irreducible, for all $j = 1, \dots, n$ there exists $i \neq j$ such that $\gamma_{ij} > 0$. Hence, $\sum_{i=1}^n a_{ij}(0) > 1$ for all $j = 1, \dots, n$. This implies that the spectral radius of $A_{\Gamma_{1, \dots, k}}(0)$ is greater than one.

Since $A_\Gamma(0)$ is irreducible and $a_{ii}(0) > 0$ for all $i = 1, \dots, n$, $A_\Gamma(0)$ is also primitive. Now again, as explained in the proof of Theorem 2.6, from Corollary 4.7 in [21] and Theorem 4.1, it follows that there exists $\varepsilon_1 > 0$ such that

$$\liminf_{t \rightarrow \infty} |x(t)| > \varepsilon_1, \tag{2.15}$$

for every non-zero solution of (2.1).

Proposition 2.1 together with (2.15) implies that there exists a compact set $B \subset \mathbb{R}_+^n \setminus \{0\}$ that attracts all initial data in $\mathbb{R}_+^n \setminus \{0\}$.

Again, since Γ is irreducible, we have that $A_\Gamma(x)$ is irreducible for all x in \mathbb{R}_+^n . And, since $a_{ii}(x) > 0$, we have that $A_\Gamma(x)$ is primitive. In fact, $A_\Gamma(x)$ has the same primitive incidence matrix for all $x \in \mathbb{R}_+^n$. Hence, there exists a positive integer p such that $A(y_1) \cdots A(y_p) \gg 0$, for all $y_1, \dots, y_p \in \mathbb{R}_+^n$ (see the Appendix for notation). Define $\tilde{A}(x) = A(x(n+p-1)) \cdots A(x(n))$, when $x(n) = x$. Therefore, $\tilde{A}(x)x \gg 0$ for all $x \in B$. Now, (2.13) follows from Proposition 3.4 in [21].

Now, we prove the existence of a unique interior equilibrium. First, the existence part comes from (2.13), by applying ([27], Theorem 1.3.6.). Let $\bar{x} \gg 0$ be an equilibrium. Then, \bar{x} is an eigenvector of $A(\bar{x})$ corresponding to the eigenvalue $\lambda = 1$. Since $A(\bar{x})$ is irreducible (because Γ is so), again from Theorem A.4 in [25] we have that the spectral radius of $A(\bar{x})$, $r(A(\bar{x}))$, is equal to one. If $\hat{x} \gg 0$ is another equilibrium, then again \hat{x} is an eigenvector of $A(\hat{x})$ corresponding to $r(A(\hat{x})) = 1$. Hence, $r(A(\bar{x})) = r(A(\hat{x}))$ which again, by applying [25], Theorem A.4, implies $|\bar{x}| = |\hat{x}|$. Therefore, $A(\bar{x}) = A(\hat{x})$. Also, from the same theorem, \hat{x} must be a positive multiple of \bar{x} , hence $\hat{x} = \alpha\bar{x}$, for some $\alpha > 0$. However, since $|\bar{x}| = |\hat{x}|$, α must equal one, and so $\hat{x} = \bar{x}$.

For the last assertion, it suffices to show that every non-zero solution converges to an equilibrium. Thus, assume that $b_1 = \dots = b_n = b > 0$. Then, (2.14) becomes

$$x(t + 1) = \frac{1}{1 + b|x(t)|} Ax(t), \tag{2.16}$$

where $A = A_\Gamma(0)$. It is known (see, for example, [26], Theorem A.49.) that $r^{-t}A^t x_0$ tends to a constant vector $u(x_0) \gg 0$, where $r = r(A)$ and $x_0 = x(0) \neq 0$. From (2.16) we obtain

$$x(t) = \frac{1}{1 + b|x(t-1)|} \cdots \frac{1}{1 + b|x(0)|} A^t x(0). \tag{2.17}$$

Let $g(t, x_0) = r^t / ((1 + b|x(t-1)|) \cdots (1 + b|x_0|))$. Then, (2.17) becomes

$$x(t) = g(t, x_0) r^{-t} A^t x_0. \quad (2.18)$$

Substituting $x(t)$ from (2.18) into (2.16), we obtain

$$g(t+1, x_0) r^{-1} A(r^{-t} A^t x_0) = \frac{g(t, x_0)}{1 + b g(t, x_0) |r^{-t} A^t x_0|} A(r^{-t} A^t x_0). \quad (2.19)$$

Regarding (2.19) as an equation for the scalar function $g(t, x_0)$, the corresponding ‘limiting equation’ is

$$\tilde{g}(t+1, x_0) r^{-1} A u(x_0) = \frac{\tilde{g}(t, x_0)}{1 + b \tilde{g}(t, x_0) |u(x_0)|} A u(x_0). \quad (2.20)$$

Since $A u(x_0) > 0$, (2.20) implies that

$$\tilde{g}(t+1, x_0) = \frac{r \tilde{g}(t, x_0)}{1 + b \tilde{g}(t, x_0) |u(x_0)|}. \quad (2.21)$$

The above represents the well-known Beverton–Holt equation, hence $\tilde{x} := r - 1 / (b|u(x_0)|)$ is asymptotically stable and

$$\tilde{g}(t, x_0) \rightarrow \tilde{x}, \text{ as } t \rightarrow \infty. \quad (2.22)$$

From the theory of asymptotically autonomous systems (see, for example, Theorem 1.8 in [16]), it follows then that (2.22) holds also for g . Hence, from (2.18) we have that $x(t) \rightarrow \tilde{x} u(x_0)$ as $t \rightarrow \infty$. This means that $\tilde{x} u(x_0)$ is an equilibrium point, which completes the proof. \square

Remark 2.8. Based on (2.2), it is a simple exercise to verify that assumptions (H3) and (H4) in Section 4 are satisfied in regard to our model (2.1). Thus, the persistence results given in Theorem 2.6 and Lemma 2.7 are, in fact, robust.

As shown in Theorem 2.4 (see also [11]), when $a_1/b_1 > a_i/b_i$ for all $i = 2, \dots, n$, and $\Gamma = I$, all initial data in $\{x \in \mathbb{R}_+^n \mid x_1 > 0\}$ are attracted to $E_1 = (a_1/b_1, 0, \dots, 0)$, which is also locally asymptotically stable (see [1]). Then, as our next result shows, when small mutations take place, the model exhibits an interior equilibrium (in some neighbourhood of E_1) that attracts all initial data in $\mathbb{R}_+^n \setminus \{0\}$.

THEOREM 2.9. *Assume that $a_1/b_1 > a_i/b_i$ for all $i = 2, \dots, n$. Then, for every $\varepsilon > 0$ there exists $\delta > 0$ such that, for every Γ irreducible and satisfying $\|\Gamma - I\| < \delta$, there exists an equilibrium E^Γ with all coordinates positive, satisfying $\|E^\Gamma - a_1/b_1\| < \varepsilon$, that attracts all solutions of (2.1) that start in $\mathbb{R}_+^n \setminus \{0\}$.*

Proof. We apply Theorem 2.1 in [24]. For this, we first show that the species x_1 is robustly uniformly persistent for (2.3): there exist $\tilde{\delta}, \tilde{\varepsilon} > 0$ such that $\liminf_{t \rightarrow \infty} x_1(t) > \tilde{\varepsilon}$, for all solutions of (2.1) with $x_1(0) > 0$ that correspond to Γ satisfying $\|\Gamma - I\| < \tilde{\delta}$. Thus, let $X = \{x \in \mathbb{R}_+^n \mid x_1 = 0\}$ (note that both X and $\mathbb{R}_+^n \setminus X$ are positively invariant for (2.3)). From Theorem 2.4, any solution of (2.3) with $x(0) \in X \setminus \{0\}$ converges to an equilibrium $\bar{x} = \bar{x}(x(0))$ such that $|\bar{x}| \in \{a_2/b_2, \dots, a_n/b_n\}$.

Let $P(t, x_0)$ be defined as in (2.12) where we take $i = 1$ and $\gamma_{11} = 1$. Then, for every \bar{x} as above, $P(1, \bar{x}) > 1$. Also, $P(1, 0) = a_1 + 1 > 1$. Then, from Theorem 3.2 (via Proposition 4.1 and Corollary 4.7) in [21], we have that x_1 is robustly uniformly persistent for (2.3).

We have that the Jacobian of (2.3) evaluated at $E_1 = (a_1/b_1, 0, \dots, 0)$ has all eigenvalues smaller than one (see [1]). Then, using Theorem 2.4, we can apply Theorem 2.1 in [24] (with $\Lambda = \{\Gamma \mid \|\Gamma - I\| < \delta\}$, $U := \{x \in \mathbb{R}_+^n \mid x_1 > 0\}$ and $B_\lambda = U \cap \{x \in \mathbb{R}_+^n \mid |x| \leq (a + 1)/b\}$, where a and b are as in Proposition 2.1), to obtain that for every $\varepsilon > 0$ there exists $\delta > 0$ such that for every Γ satisfying $\|\Gamma - I\| < \delta$ there exist an equilibrium E^Γ satisfying $\|E^\Gamma - a_1/b_1\| < \varepsilon$, that attracts all solutions of (2.1) that start in U . Now Γ being irreducible, every non-zero solution of (2.1) corresponding to such a Γ , including E^Γ , has eventually all coordinates positive, hence it enters U . \square

If we allow for arbitrary mutations, then the interior attractor might not consist just of the interior equilibrium. Let l_i be the curve defined by the equation

$$x_i = h_i(x_1, \dots, x_{i-1}, x_{i+1}, \dots, x_n) = \frac{-\left(\sum_{j \neq i} b_j x_j - \gamma_{ii} a_i\right) + \sqrt{\left(\sum_{j \neq i} b_j x_j - \gamma_{ii} a_i\right)^2 + 4b_i \sum_{j \neq i} \gamma_{ij} a_j x_j}}{2b_i} \tag{2.23}$$

That is, $l_i = \{x = (x_1, \dots, x_n) \in \mathbb{R}_+^n \mid x_i = h_i(x_1, \dots, x_{i-1}, x_{i+1}, \dots, x_n)\}$.

THEOREM 2.10. *Assume the following*

- (i) $\gamma_{ii} a_i + 1 \geq \gamma_{ij} a_j$, for all $j \neq i$ and every $i \in \{1, \dots, n\}$;
- (ii) $\forall i \in \{1, \dots, n\} \exists j$ such that $\gamma_{ij} a_j \neq \gamma_{ii} a_i$.

Then, every solution of (2.1) originating in the interior of \mathbb{R}_+^n is attracted to a positively invariant box $\mathcal{B} = \cap_{i=1}^n \mathcal{B}_i$, where $\mathcal{B}_i = \{x \in \mathbb{R}_+^n \mid m_i \leq x_i \leq M_i\}$, for some $m_i, M_i \geq 0\}$, having the property that $(l_i \cap f_i^m) \subset \{x \in \mathbb{R}_+^n \mid x_j = m_j\}$, for some $j \neq i\}$, $(l_i \cap f_i^M) \subset \{x \in \mathbb{R}_+^n \mid x_j = M_j\}$, for some $j \neq i\}$ and both $l_i \cap f_i^m$ and $l_i \cap f_i^M$ contain at least one vertex of \mathcal{B} , where $f_i^m = \{x \in \mathcal{B} \mid x_i = m_i\}$ and $f_i^M = \{x \in \mathcal{B} \mid x_i = M_i\}$.

Proof. First, we prove the theorem assuming that $\gamma_{ij} > 0$, for all $i, j = 1, \dots, n$. To this end, denote the right hand side of (2.1) by $f = (f_1, \dots, f_n)$. Then $\gamma_{ii} a_i + 1 \geq \gamma_{ij} a_j$, for $j \neq i$, implies that $\partial f_i / \partial x_i > 0$, hence each f_i is increasing in x_i .

Now let $x(t) = (x_1(t), \dots, x_n(t))$ be a non-zero solution and denote the vector $(x_1, \dots, x_{i-1}, x_{i+1}, \dots, x_n)$ by x_i^c . Then, f_i being increasing in x_i , we have that

$$\begin{aligned} x_i(t) < h_i(x_i^c(t)) &\Rightarrow x_i(t+1) = f_i(x_1(t), \dots, x_n(t)) \\ &< f_i(x_1(t), \dots, x_{i-1}(t), h_i(x_i^c(t)), x_{i+1}(t), \dots, x_n(t)) \\ &= h_i(x_i^c(t)). \end{aligned} \tag{2.24}$$

Similarly,

$$x_i(t) > h_i(x_i^c(t)) \Rightarrow x_i(t+1) > h_i(x_i^c(t)). \tag{2.25}$$

Also, from (2.23), it follows that points are mapped towards the nullclines. That is,

$$0 < x_i(t) < h_i(x_i^c(t)) \Rightarrow x_i(t+1) > x_i(t), \quad (2.26)$$

and

$$x_i(t) > h_i(x_i^c(t)) \Rightarrow x_i(t+1) < x_i(t). \quad (2.27)$$

Next, we claim that h_i does not have critical points in $\text{int}(\mathbb{R}_+^{n-1})$. Since the equations for h_i 's are symmetric, we prove this only for h_1 . Thus, suppose h_1 has a critical point x in $\text{int}(\mathbb{R}_+^{n-1})$. Then,

$$\frac{\partial h_1}{\partial x_j}(x) = 0, \quad \text{for all } j = 2, \dots, n. \quad (2.28)$$

Let $k \in \{1, \dots, n\}$ such that $\gamma_{1k}a_k \leq \gamma_{1j}a_j$ for all $j = 1, \dots, n$.

Case 1: $k \neq 1$. We have

$$\frac{\partial h_1}{\partial x_k}(x) = 0 \Leftrightarrow \gamma_{1k}a_k(\gamma_{1k}a_k - \gamma_{11}a_1) + \sum_{j \neq 1, k} b_1 x_j (\gamma_{1k}a_k - \gamma_{1j}a_j) = 0. \quad (2.29)$$

Hence, since $\gamma_{1k} > 0$, $\partial h_1 / \partial x_k(x) = 0$ if and only if $\gamma_{1k}a_k = \gamma_{1j}a_j$ for all $j = 1, \dots, n$. However, this contradicts (ii).

Case 2: $k = 1$. Let $l \in \{2, \dots, n\}$ such that $\gamma_{1j}a_j \leq \gamma_{1l}a_l$ for all $j = 2, \dots, n$. We have

$$\frac{\partial h_1}{\partial x_l}(x) = 0 \Leftrightarrow \gamma_{1l}a_l(\gamma_{1l}a_l - \gamma_{11}a_1) + \sum_{j \neq 1, l} b_1 x_j (\gamma_{1l}a_l - \gamma_{1j}a_j) = 0. \quad (2.30)$$

Hence, since $\gamma_{1l} > 0$, $\partial h_1 / \partial x_l = 0$ if and only if $\gamma_{1l}a_l = \gamma_{1j}a_j$ for all $j = 1, \dots, n$. But again, this contradicts (ii). Hence, the claim holds.

From (2.23) it follows that each h_i is bounded above on \mathbb{R}_+^{n-1} . Thus, for each $i \in \{1, \dots, n\}$ there exist numbers $r_i^{m_0} = 0$ and $r_i^{M_0} > 0$ such that $l_i \subset B_i^0 := \{x \in \mathbb{R}_+^n \mid r_i^{m_0} \leq x_i \leq r_i^{M_0}\}$, where $r_i^{M_0} > 0$ are such that $r_i^{M_0}/2 \geq x_i$ for all $x \in l_i$. Let $B^0 = \bigcap_{i=1}^n B_i^0$. Note that B^0 is compact. Also, from (2.24)–(2.27), B^0 is positively invariant and attracts all orbits of (2.1). Now for each $i \in \{1, \dots, n\}$, $r_i^{m_1} := \min\{x_i \mid x \in l_i \cap B^0\}$ and $r_i^{M_1} := \max\{x_i \mid x \in l_i \cap B^0\}$ satisfy

$$r_i^{m_0} < r_i^{m_1} < r_i^{M_1} < r_i^{M_0}. \quad (2.31)$$

We briefly argue in support of (2.31). Notice that weak inequalities hold by definition. If $0 = r_i^{m_0} = r_i^{m_1}$, then there exists $x \in B^0$ such that $0 = h_i(x_i^c)$. By direct calculation, this implies that $\sum_{j \neq i} b_j x_j - \gamma_{ij}a_i \geq 0$ and $\sum_{j \neq i} \gamma_{ij}a_j x_j = 0$, which represents a contradiction, since $\gamma_{ij}, a_j > 0$, for all j . If $r_i^{m_1} = r_i^{M_1}$ then $h_i(x_i^c)$ is constant. Then again, by direct calculation it follows that $\gamma_{i1}a_1 = \dots = \gamma_{in}a_n$, which contradicts (ii). Finally, using that $r_i^{M_0}/2 \geq x_i$ for all $x \in l_i \cap B^0$, we obtain that $r_i^{M_0} \geq 2r_i^{M_1} \geq r_i^{M_1}$. Thus, if $r_i^{M_1} = r_i^{M_0}$, then $r_i^{M_1} = 0$, which implies that $h_i(x_i^c) = 0$ for all $x \in l_i \cap B^0$, which again represents a contradiction.

Now, define $B_i^1 := \{x \in \mathbb{R}_+^n \mid r_i^{m_1} \leq x_i \leq r_i^{M_1}\}$ and $B^1 = \bigcap_{i=1}^n B_i^1$. Then, B^1 is strictly contained in B^0 (\star), in the sense that $B^1 \subset B^0$ and $\partial B^1 \cap \partial B^0 = \emptyset$. Similarly, let now $r_i^{m_2} := \min\{x_i \mid x \in l_i \cap B^1\}$ and $r_i^{M_2} := \max\{x_i \mid x \in l_i \cap B^1\}$. Using the claim from

above, we have that both $r_i^{m_2}$ and $r_i^{M_2}$ are attained at points only on ∂B^1 . Also, since $B^1 \subset B^0$, we have $r_i^{m_1} \leq r_i^{m_2}$ and $r_i^{M_2} \leq r_i^{M_1}$. If $r_i^{m_1} = r_i^{m_2}$, then from (★) we would have that there would be a point y on ∂B^1 such that $r_i^{m_1} = y_i = h_i(y_i^c)$. Then, y_i^c would be a local minimum point of h_i . Hence, again from (★), $y_i^c \in \text{int}(\mathbb{R}_+^{n-1})$ would be a critical point of h_i , which would contradict the claim. Hence, $r_i^{m_1} < r_i^{m_2}$. By similar arguments, we obtain that $r_i^{M_2} < r_i^{M_1}$. Thus, defining the box B^2 in an analogous manner to B^1 , we have that $B^2 \subset B^1$ and $\partial B^1 \cap \partial B^2 = \emptyset$. By repeating this algorithm we obtain a sequence $(B^k)_{k \geq 1}$ of compact boxes, $B^{k+1} \subset B^k$ for all $k \geq 1$, and $\partial B^k \cap \partial B^{k+1} = \emptyset$. Also, based on (2.24)–(2.27), each B^k (P1): is positively invariant and (P2): it attracts all orbits of (2.1). Now suppose there exists $\bar{x} \in \text{int}(f_i^{m_k}) \cap l_i$, where $f_i^{m_k} := \{x \in B^k \mid x_i = r_i^{m_k}\}$. That is $\bar{x} \in f_i^{m_k} \cap l_i$ and $\bar{x}_j \in (r_j^{m_k}, r_j^{M_k})$ for all $j \neq i$. Then, this means that h_i has a local minimum point at $\bar{x}_i^c \in \text{int}(\mathbb{R}_+^{n-1})$, which contradicts our previous claim. Thus, we obtained that (P3): each l_i intersects $f_i^{m_k}$ ($i = 1, \dots, n, k \geq 1$) only at points situated on the boundary of $f_i^{m_k}$. Let $\tilde{x} \in f_i^{m_k} \cap l_i$. Then, we have that $\tilde{x}_i = r_i^{m_k} = h_i(\tilde{x}_i^c)$, which is equivalent to

$$\sum_{j \neq i} (b_i r_i^{m_k} - \gamma_{ij} a_j) \tilde{x}_j = r_i^{m_k} (\gamma_{ii} a_i - b_i r_i^{m_k}). \tag{2.32}$$

Now, suppose there are two disjoint sets S_1 and S_2 such that $S_1 \cup S_2 = \{1, \dots, i-1, i+1, \dots, n\}$ and $j \in S_2$ if and only if $\tilde{x}_j \in (r_j^{m_k}, r_j^{M_k})$. If $S_2 = \emptyset$ then \tilde{x} is a vertex of B^k . If $S_2 \neq \emptyset$ and $b_i r_i^{m_k} - \gamma_{ij} a_j = 0$ for all $j \in S_2$, then Equation (2.32) is also satisfied by a vertex of B^k . If $S_2 \neq \emptyset$ and $b_i r_i^{m_k} - \gamma_{ij} a_j \neq 0$ for some $j = p \in S_2$ then we can write (2.32) in the form

$$\sum_{j \in S_1} (b_i r_i^{m_k} - \gamma_{ij} a_j) \tilde{x}_j + \sum_{j \in S_2 \setminus \{p\}} (b_i r_i^{m_k} - \gamma_{ij} a_j) \tilde{x}_j + (b_i r_i^{m_k} - \gamma_{ip} a_p) \tilde{x}_p = r_i^{m_k} (\gamma_{ii} a_i - b_i r_i^{m_k}). \tag{2.33}$$

$$\begin{aligned} & \sum_{j \in S_1} (b_i r_i^{m_k} - \gamma_{ij} a_j) (\tilde{x}_j + s_j \delta) + \sum_{j \in S_2 \setminus \{p\}} (b_i r_i^{m_k} - \gamma_{ij} a_j) \tilde{x}_j + (b_i r_i^{m_k} - \gamma_{ip} a_p) \left(\frac{\tilde{x}_p + u(\delta)}{b_i r_i^{m_k} - \gamma_{ip} a_p} \right) \\ & = r_i^{m_k} (\gamma_{ii} a_i - b_i r_i^{m_k}), \end{aligned} \tag{2.34}$$

where $u(\delta) = \sum_{j \in S_1} (b_i r_i^{m_k} - \gamma_{ij} a_j) s_j \delta$ and, for all $j \in S_1$, $s_j = 1$ if $x_j = r_i^{m_k}$, while $s_j = -1$ if $x_j = r_i^{M_k}$. Let $\bar{x}_j = \tilde{x}_j + s_j \delta$ for $j \in S_1$, $\bar{x}_j = \tilde{x}_j$ for $j \in S_2$, $\bar{x}_i = r_i^{m_k}$, and let $\bar{x}(\delta) = (\bar{x}_1, \dots, \bar{x}_n)$. Then, from (2.34), it follows that there exists $\delta > 0$ such that $\bar{x}(\delta) \in \text{int}(f_i^{m_k}) \cap l_i$ which, as shown earlier, represents a contradiction. We can repeat the reasoning above with $f_i^{m_k}$ replaced by $f_i^{M_k} := \{x \in B^k \mid x_i = r_i^{M_k}\}$. Hence we established that (P4): for every $i = 1, \dots, n$ and every $k \geq 1$, both $f_i^{m_k} \cap l_i$ and $f_i^{M_k} \cap l_i$ contain at least one vertex of B^k .

The sequence $(B^k)_{k \geq 1}$ converges to a box B (that is, $r_i^{m_k} \rightarrow r_i^m, r_i^{M_k} \rightarrow r_i^M$, as $k \rightarrow \infty$, for all $i = 1, \dots, n$). Then, B has also the properties (P1)–(P4) above, where f_i^m and f_i^M are defined analogously to $f_i^{m_k}$ and $f_i^{M_k}$, namely $f_i^m := \{x \in B \mid x_i = r_i^m\}$ and $f_i^M := \{x \in B \mid x_i = r_i^M\}$.

Now for Γ not necessarily having all entries positive, let Γ_ε be the matrix obtained from Γ by replacing all off-diagonal zero entries of Γ (if any) by ε . Let B_ε be the box corresponding to Γ_ε (for each ε we will assume the notation defined above). Hence each B_ε has the properties (P1)–(P4). Next, we show that $r_i^p(\varepsilon) \rightarrow r_i^p(0)$ as $\varepsilon \rightarrow 0, p = m, M$, from which it should be clear that $\mathcal{B} := B_0$ has the claimed properties. Thus, let $i \in \{1, \dots, n\}$

be fixed and suppose that $r_i^p(\varepsilon) \rightarrow r_i^p(0)$ as $\varepsilon \rightarrow 0$. Then

$$\exists \delta_1 > 0, \quad \forall \delta_2 > 0, \quad \exists \varepsilon \in (0, \delta_2) \text{ such that } |r_i^p(\varepsilon) - r_i^p(0)| \geq \delta_1. \quad (2.35)$$

Since $r_i^{pk}(\varepsilon) \rightarrow r_i^p(\varepsilon)$ and $r_i^{pk}(0) \rightarrow r_i^p(0)$ as $k \rightarrow \infty$, from the triangle inequality we have that, for every ε as in (2.35),

$$\exists N = N(\varepsilon) \geq 0 \text{ such that } |r_i^{pk}(\varepsilon) - r_i^{pk}(0)| \geq \delta_1/2, \quad \forall k \geq N. \quad (2.36)$$

In addition, from the definitions of r_i^{pk} and the fact that h_i is continuous at $\varepsilon = 0$, uniformly in x belonging to a compact set, it should be clear that

$$\exists \delta_3 > 0 \text{ such that } |r_i^{pk}(\varepsilon) - r_i^{pk}(0)| < \delta_1/2, \quad \forall \varepsilon \in (0, \delta_3), \quad (2.37)$$

which contradicts (2.36). Hence $r_i^p(\varepsilon) \rightarrow r_i^p(0)$ as $\varepsilon \rightarrow 0$. \square

Thus, according to the above-mentioned theorem, if we are able to prove that such a box (as in the statement of the theorem) cannot exist, unless it is a point (that is, a degenerate box with each side being reduced to a point), then that point must be a globally asymptotically stable equilibrium. For the planar version of (2.1), we discuss this scenario in the following corollary, although we do not consider the pure selection case (that is, $\gamma_{12} = \gamma_{21}$), as this case was covered in Theorem 2.4.

COROLLARY 2.11. *Assume $n = 2$ in (2.1) and the hypotheses of Theorem 2.10 are satisfied. Then, the following hold:*

- (a) *if there exists an interior equilibrium $\bar{x} = (\bar{x}_1, \bar{x}_2)$ of (2.1), and $(h_2 \circ h_1)^2$ has no fixed points different from \bar{x}_2 , then \bar{x} is globally asymptotically stable in $\text{int}(\mathbb{R}_+^2)$;*
- (b) *if (2.1) does not have an interior equilibrium and $\gamma_{12} = 0 < \gamma_{21}$, then $(0, \gamma_{22}/b_2)$ is globally asymptotically stable in $\mathbb{R}_+^2 \setminus \{0\}$, while if $\gamma_{21} = 0 < \gamma_{12}$ then $(\gamma_{11}/b_1, 0)$ is globally asymptotically stable in $\mathbb{R}_+^2 \setminus \{0\}$.*

Proof. Let \mathcal{B} be a box as in Theorem 2.10. There exist numbers $\tilde{x}_1, \tilde{x}_2, \hat{x}_1, \hat{x}_2$ such that $(\tilde{x}_1, \hat{x}_2), (\hat{x}_1, \tilde{x}_2) \in l_1 \cap \mathcal{B}$ and $(\tilde{x}_1, \tilde{x}_2), (\hat{x}_1, \hat{x}_2) \in l_2 \cap \mathcal{B}$ and $\tilde{x}_1 = h_1(\hat{x}_2)$, $\hat{x}_1 = h_1(\tilde{x}_2)$, $\tilde{x}_2 = h_2(\tilde{x}_1)$ and $\hat{x}_2 = h_2(\hat{x}_1)$. This implies that $(h_2 \circ h_1)^2(\tilde{x}_2) = \tilde{x}_2$ and $(h_2 \circ h_1)^2(\hat{x}_2) = \hat{x}_2$; so \tilde{x}_2 and \hat{x}_2 are fixed points of $(h_2 \circ h_1)^2$. Therefore, we have $\tilde{x}_2 = \hat{x}_2 = \bar{x}_2$. This further implies $\tilde{x}_1 = \hat{x}_1 = \bar{x}_1$. Hence, $\mathcal{B} = (\bar{x}_1, \bar{x}_2)$, which, by Theorem 2.10, means that \bar{x} is globally asymptotically stable in $\text{int}(\mathbb{R}_+^2)$.

- (a) In this case, since \bar{x}_2 is a fixed point of $(h_2 \circ h_1)^2$, we have that $\tilde{x}_2 = \bar{x}_2$. If \bar{x}_2 is also a fixed point of $(h_2 \circ h_1)$, then $E = (\hat{x}_1, \bar{x}_2)$ is an equilibrium point of (2.1), which further implies that $\mathcal{B} = \{E\}$. Thus, by Theorem 2.10, E attracts all solutions with $x_1(0), x_2(0) > 0$. Also, from the proof of Theorem 2.10 it follows that E is asymptotically stable.
- (b) We just treat the case when $\gamma_{21} = 0 < \gamma_{12}$, as the other case is analogous. Suppose \mathcal{B} is a non-degenerate box (that is, not a point). Then, every nullcline l_i ($i = 1, 2$) must contain two diagonal opposite vertices of \mathcal{B} (this follows using that l_i represents the graph of h_i and $h_i(x) \neq 0$ for all $x > 0$). But then \mathcal{B} contains the intersection point of l_1 and l_2 in its interior, which means that (2.1) has an interior equilibrium, a contradiction. Hence, \mathcal{B} is a point, which must belong to $l_1 \cap l_2$.

However, $l_1 \cap l_2 = \{(\gamma_{11}/b_1, 0)\}$. Then, by Theorem 2.10, $(\gamma_{11}/b_1, 0)$ is globally asymptotically stable in $\mathbb{R}_+^2 \setminus \{0\}$. \square

Note from the above corollary that competitive exclusion between two traits can occur even for an upper or lower diagonal mutation matrix Γ , case not covered by Theorem 2.4.

In the following corollary, we elaborate more on the possibility of existence of a globally asymptotically stable interior equilibrium.

COROLLARY 2.12. *Assume $n = 2$ in (2.1) and the hypotheses of Theorem 2.10 are satisfied. In any of the following cases:*

- (i) $\gamma_{11}a_1 > \gamma_{12}a_2 > 0$ and $\gamma_{22}a_2 > \gamma_{21}a_1 > 0$;
 - (ii) $\gamma_{11}a_1 > \gamma_{12}a_2 > 0$ and $\gamma_{21}a_1/2 < \gamma_{22}a_2 < \gamma_{21}a_1$;
 - (iii) $\gamma_{22}a_2 > \gamma_{21}a_1 > 0$ and $\gamma_{12}a_2/2 < \gamma_{11}a_1 < \gamma_{12}a_2$;
 - (iv) $\gamma_{12} = 0, \gamma_{22}a_2 > \gamma_{21}a_1 > 0$ and $\gamma_{11}a_1/b_1 > \gamma_{22}a_2/b_2$;
 - (v) $\gamma_{21} = 0, \gamma_{11}a_1 > \gamma_{12}a_2 > 0$ and $\gamma_{22}a_2/b_2 > \gamma_{11}a_1/b_1$;
 - (vi) $\gamma_{12} = 0, \gamma_{21}a_1/2 < \gamma_{22}a_2 < \gamma_{21}a_1$ and $\gamma_{11}a_1/b_1 > \gamma_{22}a_2/b_2$;
 - (vii) $\gamma_{21} = 0, \gamma_{12}a_2/2 < \gamma_{11}a_1 < \gamma_{12}a_2$ and $\gamma_{22}a_2/b_2 > \gamma_{11}a_1/b_1$,
- there exists an interior equilibrium that is asymptotically stable and attracts all solutions with $x_1(0), x_2(0) > 0$.

Proof. In cases (i) – (iii), there exists a unique interior equilibrium (Lemma 2.7). Let \mathcal{B} be a box as given by Theorem 2.10.

- (i) Direct calculation shows that $h'_1(x) < 0$ and $h'_2(x) < 0$ for all $x > 0$, hence both h_1 and h_2 are decreasing. Then, clearly \mathcal{B} must be the interior equilibrium, which also must be asymptotically stable.
- (ii) Using that $\gamma_{11}a_1 > \gamma_{12}a_2 > 0$, by straightforward calculation we obtain that

$$-1 < h'_1(x) < 0, \quad \forall x > 0. \tag{2.38}$$

$\gamma_{22}a_2 < \gamma_{21}a_1$ implies that $h'_2(x) > 0$ for all $x > 0$. Next, we show that $h'_2(x) < 1$ for all $x > 0$. This is equivalent to

$$Q(x) := 2b_2^2x^2 + 4b_2(2\gamma_{21}a_1 - \gamma_{22}a_2)x + (2\gamma_{22}^2a_2^2 + \gamma_{21}a_1\gamma_{22}a_2 - \gamma_{21}^2a_1^2) > 0, \quad \forall x > 0. \tag{2.39}$$

$Q(x)$ has discriminant

$$\Delta = 8b_2^2(9\gamma_{21}^2a_1^2 - 9\gamma_{21}a_1\gamma_{22}a_2) > 0. \tag{2.40}$$

Thus, $Q(x)$ has two real roots $u_1 < u_2$. If $u_2 < 0$ then again (2.39) holds. However, $u_2 < 0$ is equivalent to

$$2\gamma_{22}^2a_2^2 + \gamma_{21}a_1\gamma_{22}a_2 - \gamma_{21}^2a_1^2 > 0,$$

which holds, because $\gamma_{21}a_1/2 < \gamma_{22}a_2$. Therefore,

$$0 < h'_2(x) < 1, \quad \forall x > 0. \tag{2.41}$$

Now, let $g(x) = (h_2 \circ h_1)^2(x) - x$. Then from (2.38) and (2.41), we have $g'(x) < 0$

for all $x > 0$. Hence, $(h_2 \circ h_1)^2$ has at most one fixed point in $[0, \infty)$ (note that $x = 0$ is not a fixed point of g). Thus, the conclusion follows from Corollary 2.11 part (a).

- (iii) Analogous to (ii).
- (iv) The conditions $\gamma_{22}a_2 > \gamma_{21}a_1 > 0$ and $\gamma_{11}a_1/b_1 > \gamma_{22}a_2/b_2$ guarantee the existence of an interior equilibrium. Again, both h_1 and h_2 are decreasing, hence \mathcal{B} must be the interior equilibrium, which also must be asymptotically stable.
- (v) Analogous to (iv).
- (vi) In this case, $\gamma_{22} > 0$ and so $0 < \gamma_{22}a_2 < \gamma_{21}a_1$ and $\gamma_{11}a_1/b_1 > \gamma_{22}a_2/b_2$ imply the existence of a unique interior equilibrium. First, we show that x_1 is uniformly persistent:

$$\exists \varepsilon > 0 \text{ such that } \liminf_{t \rightarrow \infty} x_1(t) > \varepsilon, \text{ whenever } x_1(0) > 0. \tag{2.42}$$

Thus, let $X = \{x = (x_1, x_2) \in \mathbb{R}_+^2 \mid x_1 = 0\}$. Notice that all non-zero solutions with initial condition in X converge to $\{(0, \gamma_{22}/b_2)\}$. Then, $P(1, (0, 0)) = \gamma_{11} + 1 > 0$ and $P(1, (0, \gamma_{22}/b_2)) = (\gamma_{11} + 1)/(1 + b_1 \gamma_{22}a_2/b_2) > 0$, where $P(t, x)$ is as in (2.12), with $k = 1$. Then, from Theorem 2.3 and Corollary 1 in [22] we obtain (2.42).

From here, we can use the same reasoning as in (ii), but restricted to $\{x \in \mathbb{R}_+^2 \mid x_1 > \varepsilon\}$, and using that l_1 restricted to this set is $\{x \in \mathbb{R}_+^2 \mid x_2 \in [0, \gamma_{11}a_1/b_1 - \varepsilon) \text{ and } x_1 = h_1(x_2) = -x_2 + \gamma_{11}a_1/b_1\}$, hence $h'_1(x) = -1$.

- (vii) Analogous to (vi). □

Notice that (see case (iv) – (vii) in Corollary 2.12) the irreducibility of the mutation matrix is not a necessary condition for coexistence of both traits. Thus, as long as the ‘stronger trait’ (that is, the trait with the larger per-capita birth rate versus death rate ratio $\gamma_{ii}a_i/b_i$) mutates, through newborns, into the other trait, then both traits can coexist at an interior equilibrium.

2.2.2 Competitive exclusion with block-diagonal mutation matrix

In this section, we look at the case when Γ is reducible, but of the form

$$\Gamma = \begin{pmatrix} \Gamma_1 & 0 & 0 & 0 & 0 \\ 0 & \Gamma_2 & 0 & 0 & 0 \\ & & \ddots & & \\ \vdots & \vdots & \dots & \ddots & 0 \\ 0 & 0 & 0 & 0 & \Gamma_l \end{pmatrix} \tag{2.43}$$

where each $\Gamma_i = (\gamma_{ij}^{(i)})_{1 \leq i, j \leq n_i}$ is an irreducible matrix ($n_1 + \dots + n_l = n$). Then $A(x)$ has an analogous form, and (2.1) can be written as

$$x^{(i)}(t + 1) = A_i(x(t))x^{(i)}(t), \quad i = 1, \dots, l, \tag{2.44}$$

where

$$A_i(x) = \begin{pmatrix} \frac{\gamma_{11}^{(i)} a_1^{(i)} + 1}{1 + b_1^{(i)} |x|} & \frac{\gamma_{12}^{(i)} a_2^{(i)}}{1 + b_1^{(i)} |x|} & \cdots & \frac{\gamma_{1n_i}^{(i)} a_{n_i}^{(i)}}{1 + b_1^{(i)} |x|} \\ \vdots & \vdots & \dots & \vdots \\ \frac{\gamma_{n_i 1}^{(i)} a_1^{(i)}}{1 + b_{n_i}^{(i)} |x|} & \frac{\gamma_{n_i 2}^{(i)} a_2^{(i)}}{1 + b_{n_i}^{(i)} |x|} & \cdots & \frac{\gamma_{n_i n_i}^{(i)} a_{n_i}^{(i)}}{1 + b_{n_i}^{(i)} |x|} \end{pmatrix}, \tag{2.45}$$

and $x = (x^{(1)}, \dots, x^{(l)})$, $a = (a^{(1)}, \dots, a^{(l)})$, $b = (b^{(1)}, \dots, b^{(l)})$, with $x^{(i)}$, $a^{(i)}$, $b^{(i)} \in \mathbb{R}^{n_i}$.

Let B be a compact and positively invariant set for (2.1) that absorbs all solutions. For all $i = 1, \dots, l$ define $U_i := \{\eta \in \mathbb{R}_+^{n_i} \mid |\eta| = 1\}$. Let

$$P_i(t, x) = A_i(x(t - 1, x)) \cdot A_i(x(t - 2, x)) \cdots A_i(x), \text{ for } t \geq 1, \tag{2.46}$$

where $P_i(0, x)$ is the identity $n_i \times n_i$ matrix, and $x(t, x)$ is a solution of (2.44), with $x(0) = x$. For every $x \in \mathbb{R}_+^n$, $\eta_1 \in U_1$ and $\eta_i \in U_i$, we define the relative exponential rate of increase of species i with respect to species 1 as

$$\chi_i(x, \eta_1, \eta_i) = \liminf_{t \rightarrow \infty} \frac{1}{t} \ln \frac{|P_i(t, x) \eta_i|}{|P_1(t, x) \eta_1|}, \quad i = 2, \dots, n. \tag{2.47}$$

Note that χ_i is well defined.

LEMMA 2.13.

$$\chi_i(x, \eta_1, \eta_i) = \liminf_{t \rightarrow \infty} \frac{1}{t} \ln \frac{\|P_i(t, x)\|}{\|P_1(t, x)\|}, \quad i = 2, \dots, n. \tag{2.48}$$

Proof. Without loss of generality assume $i = 2$. We follow an idea similar to that in the proof of Lemma 8.46 in [23]. We first show that, if there exist constants $a, b, c, d > 0$ such that $a\eta_1 \leq \tilde{\eta}_1 \leq b\eta_1$ and $c\eta_2 \leq \tilde{\eta}_2 \leq d\eta_2$, then

$$\chi_2(x, \tilde{\eta}_1, \tilde{\eta}_2) = \chi_2(x, \eta_1, \eta_2). \tag{2.49}$$

Note that, for $j = 1, 2$,

$$\theta_j, v_j \in \mathbb{R}_+^{n_j} \text{ and } \theta_j \leq v_j \Rightarrow P_j(t, x) \theta_j \leq P_j(t, x) v_j, \quad \forall t \geq 0, x \in \mathbb{R}_+^n. \tag{2.50}$$

Thus, we have

$$\begin{aligned} \chi_2(x, \tilde{\eta}_1, \tilde{\eta}_2) &= \liminf_{t \rightarrow \infty} \frac{1}{t} \ln \frac{|P_2(t, x) \tilde{\eta}_2|}{|P_1(t, x) \tilde{\eta}_1|} \leq \liminf_{t \rightarrow \infty} \frac{1}{t} \ln \frac{|P_2(t, x)(d\eta_2)|}{|P_1(t, x)(a\eta_1)|} \\ &= \liminf_{t \rightarrow \infty} \frac{1}{t} \left(\ln \frac{|P_2(t, x) \eta_2|}{|P_1(t, x) \eta_1|} + \ln \frac{d}{a} \right) \\ &= \liminf_{t \rightarrow \infty} \frac{1}{t} \ln \frac{|P_2(t, x) \eta_2|}{|P_1(t, x) \eta_1|} = \chi_2(x, \eta_1, \eta_2). \end{aligned} \tag{2.51}$$

The other inequality can be proved analogously. Thus, (2.49) holds.

Now Γ_1 and Γ_2 being irreducible, $A_1(x)$ and $A_2(x)$ have the same primitive incidence matrix for all $x \in \mathbb{R}_+^n$ (see (2.45)). Hence, there exists $T \geq 0$ such that $P_i(T, x) \gg 0$ and $P_1(T, x) \gg 0$. Let $\hat{1}_{n_j} = (1, 1, \dots, 1) \in \mathbb{R}_+^{n_j}$, $j = 1, 2$. For a matrix A , denote by $\|A\|_1 = \sum_{ij} |a_{ij}|$. Then, using (2.51), we have that for any $\eta_1 \in U_1$ and $\eta_2 \in U_2$,

$$\begin{aligned} \chi_2(x, \eta_1, \eta_2) &= \liminf_{t \rightarrow \infty} \frac{1}{t} \ln \frac{|P_2(t, x)\eta_2|}{|P_1(t, x)\eta_1|} \\ &= \liminf_{t \rightarrow \infty} \frac{1}{t} \ln \frac{|P_2(t-T, x(T, x))P_2(T, x)\eta_2|}{|P_1(t-T, x(T, x))P_1(T, x)\eta_1|} \\ &= \liminf_{t \rightarrow \infty} \frac{1}{t} \ln \frac{|P_2(t-T, x(T, x))P_2(T, x)\hat{1}_{n_2}|}{|P_1(t-T, x(T, x))P_1(T, x)\hat{1}_{n_1}|} \\ &= \liminf_{t \rightarrow \infty} \frac{1}{t} \ln \frac{|P_2(t, x)\hat{1}_{n_2}|}{|P_1(t, x)\hat{1}_{n_1}|} \\ &= \liminf_{t \rightarrow \infty} \frac{1}{t} \ln \frac{\|P_2(t, x)\|_1}{\|P_1(t, x)\|_1} \\ &= \liminf_{t \rightarrow \infty} \frac{1}{t} \ln \frac{\|P_2(t, x)\|}{\|P_1(t, x)\|}, \end{aligned} \tag{2.52}$$

since all matrix norms are equivalent. \square

Thus, we denote $\chi_i(x, \eta_1, \eta_i)$, in short, by $\chi_i(x)$.

LEMMA 2.14. *Let $i \in \{2, \dots, n\}$. The following statements are equivalent.*

- (i) $\chi_i(x) < 0$ for all $x \in B$.
- (ii) $\exists c \in (0, 1)$, $T \geq 1$, $\forall x \in B$, $\eta_i \in U_i$, $\eta_1 \in U_1$, $\exists 1 \leq t \leq T$ such that $|P_i(t, x)\eta_i|/|P_1(t, x)\eta_1| < c$.

Proof. (i) \Rightarrow (ii). First, we show

$$\forall x \in B, \eta_i \in U_i, \eta_1 \in U_1 \exists 0 < c < 1, T \geq 1 \text{ such that } \frac{|P_i(T, x)\eta_i|}{|P_1(T, x)\eta_1|} < c. \tag{2.53}$$

Let $x \in B$. Then, from (i), there exists $\bar{c} > 0$ such that

$$\liminf_{t \rightarrow \infty} \frac{1}{t} \ln \frac{|P_i(t, x)\eta_i|}{|P_1(t, x)\eta_1|} < -2\bar{c}. \tag{2.54}$$

Furthermore, (2.54) implies that there exists $T \geq 1$ such that

$$\frac{\|P_i(T, x)\|}{\|P_1(T, x)\|} < c := \exp(-\bar{c}T). \tag{2.55}$$

Hence, (2.53) holds. Then (ii) follows using a standard compactness argument (as, for example, in the proofs of Lemma 4.1 in [22], or Lemma 3.1 in [21]).

(ii) \Rightarrow (i). Let $x \in B$, $\eta_1 \in U_1$ and $\eta_i \in U_i$. Then, there exists $1 \leq t_1 \leq T$ such that

$$\frac{|P_i(t_1, x)\eta_i|}{|P_1(t_1, x)\eta_1|} < c. \tag{2.56}$$

Now, let $\eta_i^1 := P_i(t_1, x)\eta_i/|P_i(t_1, x)\eta_i|$ and $\eta_1^1 := P_1(t_1, x)\eta_1/|P_1(t_1, x)\eta_1|$. Then again, there exists $1 \leq t_2 \leq T$ such that

$$\frac{|P_i(t_2, x(t_1, x))\eta_i^1|}{|P_1(t_1, x(t_1, x))\eta_1^1|} < c. \tag{2.57}$$

From (2.57) and (2.57), we obtain

$$\frac{|P_i(t_1 + t_2, x)\eta_i|}{|P_1(t_1 + t_2, x)\eta_1|} = \frac{|P_i(t_2, x(t_1, x))P_i(t_1, x)\eta_i|}{|P_1(t_1, x(t_1, x))P_1(t_1, x)\eta_1|} < c \frac{|P_i(t_1, x)\eta_i|}{|P_1(t_1, x)\eta_1|} < c^2. \tag{2.58}$$

Thus, inductively we find that there exists a sequence $\tau_n \geq n$ ($\tau_n = t_1 + \dots + t_n$) such that

$$\frac{|P_i(\tau_n, x)\eta_i|}{|P_1(\tau_n, x)\eta_1|} < c^n. \tag{2.59}$$

This implies

$$\frac{1}{\tau_n} \ln \frac{|P_i(\tau_n, x)\eta_i|}{|P_1(\tau_n, x)\eta_1|} < \frac{n}{\tau_n} \ln c \leq \ln c < 0. \tag{2.60}$$

Now, (i) follows from (2.60). □

We now have the following competitive exclusion result.

THEOREM 2.15. *If $\chi_i(x) < 0$ for all $x \in B$, $i = 2, \dots, n$, then $x^{(i)}(t) \rightarrow 0$ as $t \rightarrow \infty$, for all $i = 2, \dots, l$, for all solutions $x(t)$ of (2.44) with $x^{(1)} > 0$.*

Proof. Let $x \in B$ such that $x^{(1)} > 0$. Assume also, without loss of generality, that $x^{(i)} > 0$. Then, from (2.59), applied with $\eta_i = x^{(i)}/|x^{(i)}|$ and $\eta_1 = x^{(1)}/|x^{(1)}|$, we obtain that $|x^{(i)}(\tau_n, x)|/|x^{(1)}(\tau_n, x)| < c^n|x^{(i)}/x^{(1)}|$. Hence, $|x^{(i)}(\tau_n, x)| \rightarrow 0$ as $n \rightarrow \infty$. Then, $\tau_{n+1} - \tau_n \leq T$ and continuity of $x(t, x)$ in x further imply that $|x^{(i)}(t, x)| \rightarrow 0$ as $t \rightarrow \infty$. □

Let $b_1^M = \max_{j=1}^{n_1} b_j^{(1)}$ and $b_i^m = \min_{j=1}^{n_i} b_j^{(i)}$, $i = 2, \dots, l$. Let \tilde{A}_j , $j = 1, \dots, n$, be the (constant) matrix obtained by multiplying row k of $A_j(x)$ by $1 + b_k|x|$. Denote the spectral radius of \tilde{A}_j by r_j .

COROLLARY 2.16. *Assume that Γ is of the form (2.43), and that $(r_i/r_1)\max\{1, b_1^M/b_i^m\} < 1$ for all $i = 2, \dots, l$. Then, $x^{(i)}(t) \rightarrow 0$, as $t \rightarrow \infty$, for all $i = 2, \dots, n$, for all solutions $x(t)$ of (2.44) with $x^{(1)} > 0$.*

Proof. We have that $\|P_i(t, x)\| \leq (\prod_{k=0}^{t-1} (1/(1 + b_i^m|x(k, x))))\tilde{A}_i$, for all $i = 2, \dots, n$, and $\|P_1(t, x)\| \geq (\prod_{k=0}^{t-1} (1/(1 + b_1^M|x(k, x))))\tilde{A}_1$. Hence,

$$\begin{aligned} \chi_i(x) &= \liminf_{t \rightarrow \infty} \frac{1}{t} \ln \frac{\|P_i(t, x)\|}{\|P_1(t, x)\|} \leq \liminf_{t \rightarrow \infty} \frac{1}{t} \ln \left(\prod_{k=0}^{t-1} \frac{1 + b_1^M|x(k, x)|}{1 + b_i^m|x(k, x)|} \right) \frac{\|\tilde{A}_i\|}{\|\tilde{A}_1\|} \\ &= \liminf_{t \rightarrow \infty} \frac{1}{t} \ln \prod_{k=0}^{t-1} \frac{r_i}{r_1} \frac{1 + b_1^M|x(k, x)|}{1 + b_i^m|x(k, x)|} \end{aligned} \tag{2.61}$$

But

$$\frac{r_i}{r_1} \frac{1 + b_1^M |x|}{1 + b_i^m |x|} \leq \frac{r_i}{r_1} \max \left\{ 1, \frac{b_1^M}{b_i^m} \right\}, \quad \forall x \geq 0. \quad (2.62)$$

Hence, from (2.61) and (2.61), we have

$$\chi_i(x) \leq \ln \frac{r_i}{r_1} \max \left\{ 1, \frac{b_1^M}{b_i^m} \right\} < 0, \quad (2.63)$$

and further we can apply Theorem 2.15. \square

Remark 2.17. With respect to the model without mutation (2.3), competitive exclusion can also be obtained from Theorem 2.15, applied with the positively invariant set $B = \{x \in \mathbb{R}_+^n \mid a_k/b_k \leq |x| \leq a_1/b_1\}$, where $a_k/b_k = \min\{a_i/b_i \mid i = 2, \dots, n\}$, assuming that $a_1/b_1 > a_i/b_i, i = 2, \dots, n$.

3. Conclusion

In this paper, we studied a discrete competition model among n species, where individuals from species j could give birth, by mutation, to individuals belonging to another species i . The model is an extension of the pure selection model considered in [1,11]. The dynamics of the model is strongly related to the form of the mutation matrix Γ . Thus, for the model without mutation, we proved that the species having the largest birth versus death ratio survives at a positive equilibrium and drives all the other species to extinction; hence the pure selection model predicts competitive exclusion. The proof is different from that in [11], and it is much shorter. Based on this, and using a theorem from [24], we proved that, when small mutation occurs, such that Γ is irreducible, then there is an interior equilibrium that is globally asymptotically stable in $\mathbb{R}_+^n \setminus \{0\}$ (Theorem 2.4). For arbitrarily large mutations, in Theorem 2.10, we obtained a specific form of a positively invariant set that attracts all non-zero solutions. With the help of this result, we were able to provide explicit sufficient conditions for the existence of an interior globally asymptotically stable equilibrium for the case when $n = 2$. It is worth noting that, in the case of reducible Γ , the interior dynamics can exhibit both coexistence, in the form of a globally asymptotically stable equilibrium, and competitive exclusion, as shown in Corollaries 2.11 and 2.12. Also for arbitrary mutation, we provided sufficient condition for uniform persistence of both total population and of each individual trait. Finally, for a block-diagonal form of the mutation matrix Γ , with each block consisting of an irreducible matrix, we provided a sufficient condition for the relative exponential rates of increase of species i with respect to species 1 to be negative, which leads to the exclusion of species i from the competition. The approach developed in this regard can also be applied to other discrete-time competition models.

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Appendix

In this section, we present a generalization of Theorem 3.2 in [21], for the purpose of applying it to our model (2.1), to obtain sufficient conditions for the total population to persist uniformly and robustly.

Consider the following partial order relations on \mathbb{R}^n :

$$\begin{aligned} a \geq b &\Leftrightarrow a_i \geq b_i, \quad \forall i = 1, \dots, n; \\ a > b &\Leftrightarrow a_i \geq b_i, \quad \forall i = 1, \dots, n, \text{ and } a \neq b; \\ a \gg b &\Leftrightarrow a_i > b_i, \quad \forall i = 1, \dots, n. \end{aligned} \tag{A.1}$$

Partial order relations for matrices can be defined in an analogous manner.

Consider the following system

$$\begin{aligned} x(t+1) &= f(x(t), y(t), \xi) \\ y(t+1) &= g(x(t), y(t), \xi), \end{aligned} \tag{A.2}$$

with $z(t) = (x(t), y(t)) \in \mathbb{R}_+^p \times \mathbb{R}_+^q$ for all $t \in \mathbb{Z}_+$ (where \mathbb{Z}_+ denotes the set of non-negative integers), $\xi \in \Xi \subseteq \mathbb{R}^l$, where Ξ is an open set. The maps $f, g : \mathbb{R}_+^p \times \mathbb{R}_+^q \times \mathbb{R}^l$ are assumed to be continuous. Writing $y(t) = (y_1(t), y_2(t)) \in \mathbb{R}^{q_1} \times \mathbb{R}^{q_2}$, assume that

$$y_2(t+1) \geq A(z(t), \xi)y_2(t), \quad \forall t \geq 0, \tag{A.3}$$

where $A(z, \xi)$ is a non-negative continuous matrix for $z \in \mathbb{R}_+^{p+q}$, $\xi \in \mathbb{R}^l$. Furthermore, let ξ_0 be a fixed parameter and assume that the set $X = \{z = (x, y) \in \mathbb{R}_+^p \times \mathbb{R}_+^q \mid y = 0\}$ is positively invariant (with respect to ξ_0), while

$$\mathbb{R}_+^{p+q} \setminus \{z = (x, y_1, y_2) \mid x \in \mathbb{R}_+, (y_1, y_2) \in \mathbb{R}_+^{q_1} \times \mathbb{R}_+^{q_2} \text{ and } y_2 = 0\}$$

is positively invariant for all ξ .

Now, let $P(t, z, \xi)$, $P(0, z, \xi) = I$, be the fundamental matrix solution for the (non-autonomous) equation

$$u(n+1) = A(z(t), \xi)u(n), \tag{A.4}$$

where $z(t) = z(t, z, \xi)$ satisfies (A.2), with $z(0) = z = (x, y_1, y_2)$. Therefore,

$$P(t, z, \xi) = A(z(t-1), \xi) \cdot A(z(t-2), \xi) \cdots A(z(0), \xi). \tag{A.5}$$

Then, from (A.3) and (A.5) we have

$$y_2(t+1) \geq P(t, z, \xi)y_2, \quad \forall t \geq 0. \tag{A.6}$$

Abusing notation, denote the norm $|v|$ of a vector $v = (v_1, \dots, v_k)$ by $|v_1| + \dots + |v_k|$, where $|v_i|$ is the absolute value of v_i , for all $i = 1, \dots, k$. Furthermore, we make the following assumptions, among which the first two are in regard to the fixed parameter ξ_0 .

- (H1): There exists a closed set $B \subset \mathbb{R}_+^p \times \mathbb{R}_+^q$ such that for every $z_0 \in \mathbb{R}_+^p \times \mathbb{R}_+^q$ there exists $t_0 = t_0(z_0)$ such that $z(t) \in B$ for all $t \geq t_0$, where $z(0) = z_0$ (that is, B is an absorbing set for (A.2)).
- (H2): There exists $\rho > 0$ such that the set $\{z = (x, y) \in B \mid |y| \leq \rho\}$ is bounded (hence compact).

(H3): For every V_0 a neighbourhood of B there exists Ξ_0 a bounded neighborhood of ξ_0 such that

$$\forall z \in \mathbb{R}_+^p \times \mathbb{R}_+^q, \xi \in \Xi_0, \exists t(z, \xi) \in \mathbb{Z}_+ \text{ such that } z(t, z, \xi) \in V_0, \\ \forall t \geq t(z, \xi).$$

(H4): For every $\delta > 0$ there exist V_0 a neighbourhood of B and Ξ_0 a bounded neighbourhood of ξ_0 such that

$$\inf_{z \in V_0^\delta, \xi \in \Xi_0} |g(z, \xi)| > 0,$$

where $V_0^\delta = \{z = (x, y) \in V_0 \mid |y| \geq \delta\}$.

Now, let B be as in (H1) and $M = X \cap B$. Let $U = \{\eta \in \mathbb{R}_+^q \mid |\eta| = 1\}$. Then, in an analogous manner, as compared to [21] (see also [22]), the above lead to the following persistence result involving the y_2 subvector of y .

THEOREM 4.1. Assume that (H1)–(H4) hold and

$$\forall (z, \eta) \in M \times U, \exists \tau = \tau(z, \eta) \in \mathbb{Z}_+ \setminus \{0\} \text{ such that } |P(\tau, z, \xi_0)\eta| > 1. \tag{A.7}$$

Then, there exists $\varepsilon > 0$ such that

$$\liminf_{t \rightarrow \infty} |y(t, z, \xi)| > \varepsilon, \quad \forall z \in Z \setminus X, \quad \xi \in \Xi. \tag{A.8}$$

Remark 4.2. Similar considerations apply to the continuous time version of (A.2) (and, for that matter, to its non-autonomous counterparts, both in continuous and discrete time; see also [6], Remark 3.3). Although in the continuous time case (H4) is not needed, additional assumptions need to be made in order to ensure that (A.6) holds (for example, if the matrix $A(z, \xi)$ has all off diagonal entries non-negative; see [25]).

Assumptions (H3) and (H4) are used for the robustness of the persistence. If we remove them, then Theorem 4.1 gives us only uniform persistence (that is, (A.8) without the parameter ξ).