THE COMPETITIVE EXCLUSION PRINCIPLE IN STOCHASTIC ENVIRONMENTS

ALEXANDRU HENING AND DANG H. NGUYEN

ABSTRACT. The competitive exclusion principle states that a number of species competing for a smaller number of resources cannot coexist. Even though this is a fundamental principle in ecology, it has been observed empirically that in some settings it will fail. One example is Hutchinson’s ‘paradox of the plankton’. This is an instance where a large number of phytoplankton species coexist while competing for a very limited number of resources. Both experimental and theoretical studies have shown that in some instances (deterministic) temporal fluctuations of the environment can facilitate coexistence for competing species. Hutchinson conjectured that one can get coexistence because nonequilibrium conditions would make it possible for different species to be favored by the environment at different times.

In this paper we look at how environmental noise interacts with competitive exclusion. If the environmental stochasticity is modeled by white noise, and the per-capita growth rates of the competitors depend linearly on the resources, we prove that the competitive exclusion principle has to hold. However, if either the dependence between the growth rates and the resources is not linear or the white noise term is nonlinear, the competitive exclusion principle can be violated. Maybe even more surprisingly, if the noise comes from switching the environment at random times between a finite number of possible states it is possible for all species to coexist even if the growth rates depend linearly on the resources. Moreover, we show in an example that, contrary to Hutchinson’s explanation, one can switch between two environments in which the same species is favored and still get coexistence.

1. Introduction

The competitive exclusion principle \cite{Vol28, Gan32, Har60} says that when multiple species compete with each other for the same resource, one competitor will win and drive all the others to extinction. In contrast to this principle, it has been observed in nature that multiple species can coexist despite limited resources. For example, phytoplankton species can coexist even though they all compete for a small number of resources. This apparent violation of the competitive exclusion principle has been called by Hutchinson ‘the paradox of the plankton’ \cite{Hut61}. Hutchinson gave a possible explanation by arguing that variations of the environment can keep species away from the deterministic equilibria that are forecasted by the competitive exclusion principle.

There has been continued debate regarding the competitive exclusion principle. Some have argued that the principle is a tautology or that since all species have finite population sizes they will eventually go extinct, therefore questioning the value of the principle. Analysing the competitive exclusion principle mathematically for a large class of models can guide us in this debate. Even though from a mathematical point of view, coexistence means that
no species goes extinct in finite time, we will interpret this as providing evidence that no species will go extinct for a long period of time. The first general deterministic framework for examining problems of competitive exclusion appeared in [AM80]. This paper and the beautiful proofs from [HS98] inspired us to look into extending competitive exclusion to a more realistic setting that includes environmental stochasticity.

It is well documented that one has to look carefully at both the biotic interactions and the environmental fluctuations when trying to determine criteria for the coexistence or extinction of species. Sometimes biotic effects can result in species going extinct. However, if one adds the effects of the environment, extinction might be reversed into coexistence. These phenomena have been seen in competitive settings as well as in settings where prey share common predators - see [CW81, AHR98, Hol77]. In other instances, deterministic systems that coexist become extinct once one takes into account environmental fluctuations - see for example [HGT94]. One successful way of analyzing the interplay between biotic interactions and environmental noise is by modelling the populations as discrete or continuous-time Markov processes. The problem of coexistence or extinction then becomes equivalent to studying the asymptotic behaviour of these Markov processes. There are many different ways of modeling the environmental noise. One way that is widely used is adding white noise to the system and transforming differential equations into stochastic differential equations (SDE). However, for many systems, the randomness might not be best modelled by SDE [Tur77b]. Because of this, it is relevant to see how the long term fate of ecosystems is changed by different types of noise. The idea that extinction can be reversed, due to (deterministic) environmental variations, into coexistence has been revisited many times since Hutchinson’s explanation [CW81, Che00]. However, to our knowledge, our paper is the first analysing how different types of environmental stochasticity interact with competitive exclusion.

2. THE DETERMINISTIC MODEL

Volterra’s original model [Vol28] assumed that the dynamics of $n$ competing species can be described using a system of ordinary differential equations (ODE). Most people who have studied the competitive exclusion principle mathematically have used ODE models. This is a key assumption and we will adhere to it in the current paper. Suppose we have $n$ species $x_i, i = 1, \ldots, n$ and denote the density of species $i$ at time $t \geq 0$ by $x_i(t)$. Each species uses $m$ possible resources whose abundances are $R_j, j = 1, \ldots, m$. The resources themselves depend on the species densities, i.e. $R_j = R_j(x)$ is a function of the densities of the species $x(t) = (x_1(t), \ldots, x_n(t))$. We assume that the per-capita growth rate of each species increases linearly with the amount of resources present. Based on the above, the dynamics of the $n$ species is given by

$$dx_i(t) = x_i(t) \left(-\alpha_i + \sum_{j=1}^{m} b_{ij} R_j(x(t))\right) dt, \ i = 1, \ldots, n$$

where $-\alpha_i \leq 0$ is the rate of death in the absence of any resource, $R_k \geq 0$ is the abundance of the $k$th resource, and the coefficients $b_{ik}$ describe the efficiency of the $i$th species in using the $k$th resource. A key requirement is that the resources $R_k$ all eventually get exhausted. In mathematical terms this means that

$$R_k(x) = \overline{R}_k - F_k(x)$$
where the $F_k$'s are unbounded positive functions of the population densities $x_i$ with $F_k(0, \ldots, 0) = 0$. This will make it impossible for the densities $x_i$ to grow indefinitely, and will be a standing assumption throughout the paper.

In the special case when the resources depend linearly on the densities, so that $F_k(x) = \sum_{i=1}^{n} x_i a_{ki}$ for constants $a_{ki} \geq 0$, equation (2.2) becomes

$$(2.3) \quad R_k(x) = R_k - \sum_{i=1}^{n} x_i a_{ki}$$

and the system (2.1) is of Lotka–Volterra type. The model given by (2.1) and (2.2) is called by [AM80] a linear abiotic resource model. The linearity comes from (2.1) which intrinsically assumes that the per capita growth rates of the competing species are linear functions of the resource densities. The resources are abiotic because they regenerate according to the algebraic equation (2.2), in contrast to being biotic and following systems of differential equations themselves.

The following result is a version of the competitive exclusion principle - see [HS98] for an elegant proof.

**Theorem 2.1.** Suppose $n > m$, the dynamics is given by (2.1), and the resources eventually get exhausted. Then at least one species will go extinct.

**Assumption 2.1.** It is common to make the following assumptions when studying the competitive exclusion principle [AM80].

(i) The populations are unstructured and as such the system can be fully described by the densities of the species.

(ii) The $n$ species interact with each other only through the resources. This way the growth rates of the species only depend on the resources $R_k, k = 1, \ldots, m$ and not directly on the densities $x_i, i = 1, \ldots, n$.

(iii) The resources all eventually get exhausted.

(iv) The growth rates of the species depend linearly on the resources that are available. Note that this is implicit in (2.1).

(v) The system is homogenous in space and the resources are uniform in quality.

(vi) There is no explicit time dependence in the interactions.

(vii) There is no environmental noise that can affect the resources and species.

When one or more of the assumptions (i)-(vi) are violated competitive exclusion can fail and the coexistence of all species is possible. For example, if assumption (i) is violated it has been shown in [HS72] that two predators can coexist competing for the same prey if they eat different life stages (larval vs adult) of the prey. Similarly, two herbivores eating one plant can survive if they eat different parts of the plant. If (vi) is violated and the environment is time-varying it has been showcased in [SL73, Koc74a, Cus80, DMS81] that multiple species can coexist using a single resource. If the linear dependence on the resources (iv) does not hold several authors [Koc74b, Zic75, AM76b, AM76a, KY77, MA77, AM80] have shown that the coexistence of $n$ species competing for $m < n$ resources is possible.

**2.1. Competitive exclusion without Assumption 2.1 (iv).** Some authors [AM80] have relaxed the linearity constraint from Assumption 2.1 (iv) and studied general systems of $n$
species competing for \( m \) abiotic resources. The dynamics is then given by

\[
\frac{dx_i(t)}{dt} = x_i u_i(R_1, \ldots, R_m), \ i = 1, \ldots, m,
\]

\[
R_j = \overline{R}_j - F_j(x_1, \ldots, x_n), \ j = 1, \ldots, m.
\]

The \( R_j \)'s are considered resources, so it is assumed that species growth rates will increase with resource availability, while resource densities will decrease with species densities. These conditions can be written as

\[
\frac{\partial u_i}{\partial R_j} \geq 0 \text{ and } \frac{\partial F_j}{\partial x_i} \geq 0, \ i = 1, \ldots, n, \ j = 1, \ldots, m
\]

where the equalities hold if any only if species \( i \) does not use resource \( j \).

Volterra [Vol28] proved that \( n > 1 \) species cannot coexist if they compete for one abiotic resource. However, Volterra assumed as many others, that the \( u_i \)'s from (2.4) are linear, i.e. the growth rates depend linearly on the resources. If one assumes there is only one resource, surprisingly, the linearity assumption is not necessary. The conditions from (2.5) are enough to force all but one species to go extinct. Only the species which can exist at the lowest level of available resource will persist and the following version of the competitive exclusion principle (see [AMS80]) holds.

**Theorem 2.2.** Suppose there are \( n > 1 \) species competing for one abiotic resource \( R \). If the dynamics is given by (2.4) and the monotonicity conditions (2.5) are satisfied then one species persists and all the others go extinct.

We will study what happens when assumptions (i)-(vi) hold and assumption (vii) does not as well as how white noise interacts with the system when assumption (iv) fails.

### 3. Stochastic Coexistence Theory

We start by defining what we mean by extinction and coexistence in the stochastic setting. Assume \((\Omega, \mathcal{F}, \mathbb{P})\) is a probability space and let \((X(t)) = (X_1(t), \ldots, X_n(t))\) denote the densities of the \( n \) species at time \( t \geq 0 \). We will assume that \((\Omega, \mathcal{F}, \mathbb{P})\) satisfies all the natural assumptions and that \( X \) is a Markov process. We will denote by \( \mathbb{P}_y(\cdot) = \mathbb{P}( \cdot | X(0) = y) \) and \( \mathbb{E}_y[\cdot] = \mathbb{E}[ \cdot | X(0) = y] \) the probability and expected value given that the process starts at \( X(0) = y \). Let \( \partial \mathbb{R}_n^+ = [0, \infty)^n \setminus (0, \infty)^n \) be the boundary of the positive orthant.

**Definition 3.1.** Species \( X_i \) goes **extinct** if for any initial species densities \( X(0) \in (0, \infty)^n \) we have with probability 1 that

\[
\lim_{t \to \infty} X_i(t) = 0.
\]

We say that **at least one species goes extinct** if the process \( X(t) \) converges to the boundary \( \partial \mathbb{R}_n^+ \) in the following sense: there exists \( \alpha > 0 \) such that for any initial densities \( X(0) \in (0, \infty)^n \) with probability 1

\[
\limsup_{t \to \infty} \frac{\ln \left( d \left( X(t), \partial \mathbb{R}_n^+ \right) \right)}{t} \leq -\alpha,
\]

where \( d(y, \partial \mathbb{R}_n^+) = \min \{y_1, \ldots, y_n\} \) is the distance from \( y \) to the boundary \( \partial \mathbb{R}_n^+ \).
**Definition 3.2.** The species $X_j$ is **persistent in probability** if for any $\varepsilon > 0$, there exists $\delta > 0$ such that for any $X(0) = y \in (0, \infty)^n$ we have with probability 1 that
\[
\liminf_{t \to \infty} P_y \{X_j(t) > \delta\} \geq 1 - \varepsilon.
\]
If all species $X_j$ for $j = 1, \ldots, n$ persist in probability we say the species **coexist**.

There is a general theory of coexistence for deterministic models [Hof81, Hut84, HS89, HS98, ST11]. It can be shown that a sufficient condition for coexistence is the existence of a fixed set of weights associated with the interacting populations, such that this weighted combination of the populations’s invasion rates is positive for any invariant measure supported by the boundary (i.e. associated to a sub-collection of populations) – see [Hof81]. This coexistence theory has been generalized to stochastic difference equations in a compact state space [SBA11], stochastic differential equations [SBA11, HN18a], and recently to general Markov processes [Ben18].

The intuition behind the stochastic coexistence results is as follows. Let $\mu$ be an invariant probability measure of the process $X$ that is supported on the boundary $\partial \mathbb{R}_+^n$. Loosely speaking $\mu$ describes the coexistence of a sub-community of species, where at least one of the initial $n$ species is absent. If the process $X$ spends a lot of time close to (the support of) $\mu$ then it will get attracted or repelled in the $i$th direction according to the invasion rate $\Lambda_i(\mu)$. This quantity can usually be computed by averaging some growth rates according to the measure $\mu$. The invasion rate $\Lambda_i(\mu)$ quantifies how the $i$th species behaves when introduced at a low density into the sub-community supported by the measure $\mu$. If the invasion rate is positive, then the $i$th species tends to increase when rare, while if it is negative, the species tends to decrease when rare. We will use the following stochastic coexistence criterion for $n = 2$ species.

**Theorem 3.3.** Suppose species $X_1$ survives on its own and has the unique invariant measure $\mu_1$ on $(0, \infty)$. Similarly, assume species $X_2$ survives in the absence of $X_1$ and has the unique invariant measure $\mu_2$ on $(0, \infty)$. Assume furthermore that the invasion rates of the two species are strictly positive, i.e. $\Lambda_{x_1} := \Lambda_1(\mu_2) > 0$ and $\Lambda_{x_2} := \Lambda_2(\mu_1) > 0$. Then the two species coexist.

Various forms of this result have appeared for two species in [TG80, KO81, EHS15] and for the general multi-species setting in [SBA11, HN18a, Ben18].

### 4. Stochastic differential equations

#### 4.1. Growth rates depend linearly on resources.

One way of adding stochasticity to a deterministic system is based on the assumption that the environment mainly affects the growth/death rates of the populations. This way, the growth/death rates in an ODE (ordinary differential equation) model are replaced by their average values to which one adds a white noise fluctuation term; see [Tur77a, Bra02, Gar88, ERSS13, SBA11, Gar84] for more details. We will first assume that the growth rates of the species depend linearly on the resources. In this setting the system (2.1) becomes

\[
\text{(4.1)} \quad dx_i(t) = x_i(t) \left( -\alpha_i + \sum_{j=1}^m b_{ij} R_j(x(t)) \right) dt + x_i(t) g_i(x(t)) dE_i(t), \quad i = 1, \ldots, n
\]

where $E(t) = (E_1(t), \ldots, E_n(t))^T = \Gamma^T B(t)$ for an $n \times n$ matrix $\Gamma$ such that $\Gamma^T \Gamma = \Sigma = (\sigma_{ij})_{n \times n}$, $B(t) = (B_1(t), \ldots, B_n(t))$ is a vector of independent standard Brownian motions,
and $g_i : [0, \infty)^n \to \mathbb{R}$ are continuous functions that are continuously differentiable on $(0, \infty)^n$. Under appropriate smoothness and growth conditions, this system has unique solutions and $(0, \infty)^n$ is an invariant set for the dynamics, i.e. if the process starts in $(0, \infty)^n$ it will stay there forever.

The following stochastic version of the competitive exclusion principle holds.

**Theorem 4.1.** Suppose $n$ species compete with each other according to (4.1); the number of species is greater than the number of resources $n > m$, the resources depend on the species densities according to (2.2) so that they eventually get exhausted and the noise is linear, i.e. $g_i(x) = 1$ for all $x \in [0, \infty)^n$ and all $i = 1, \ldots, n$. Then for any initial species densities $x(0) \in (0, \infty)^n$ with probability one at least one species will go extinct.

We note that even though according to Theorem 4.1 white noise terms that are linear cannot facilitate coexistence, they can change which species go extinct and which persist as the next two-species example shows.

**Example 4.1 (Two dimensional Lotka–Volterra SDE).** Assume for simplicity we have two species $x_1, x_2$ competing for one resource $R$. Then if we assume the resource depends linearly on the species densities (2.3) and we set $b_i := b_{i1}, \mu_i = -\alpha_i + b_1R, \beta_{ij} = b_ia_j$, and $g_i(\cdot) = 1$ then the system (4.1) becomes

\begin{equation}
\begin{align*}
    dx_1(t) &= x_1(t)(\mu_1 - \beta_{11}x_1(t) - \beta_{12}x_2(t)) \, dt + x_1(t)dE_1(t) \\
    dx_2(t) &= x_2(t)(\mu_2 - \beta_{21}x_1(t) - \beta_{22}x_2(t)) \, dt + x_2(t)dE_2(t).
\end{align*}
\end{equation}

Suppose $\Sigma = \text{diag}(\sigma_1^2, \sigma_2^2)$, $\mu_2 - \frac{\sigma_2^2}{2} > 0$, and $\mu_1 - \frac{\sigma_1^2}{2} > 0$ so that none of the species go extinct on their own, as well as $\frac{b_1}{\mu_1} < \frac{b_2}{\mu_2}$ such that in the absence of noise species $x_1$ dominates species $x_2$, i.e. $x_1$ persists while $x_2$ goes extinct. The following scenarios are possible (see [HN18a, EHS15, HN18b] for proofs of these results)

- If $\frac{b_1}{\mu_1} < \frac{b_2}{\mu_2} \frac{1 - \frac{\sigma_1^2}{2\mu_1}}{1 - \frac{\sigma_2^2}{2\mu_2}}$ then with probability one $x_1$ persists and $x_2$ goes extinct.
- If $\frac{b_1}{\mu_1} > \frac{b_2}{\mu_2} \frac{1 - \frac{\sigma_1^2}{2\mu_1}}{1 - \frac{\sigma_2^2}{2\mu_2}}$ then with probability one $x_2$ persists and $x_1$ goes extinct.

The noise acts on the dominance criteria according to the term $\frac{1 - \frac{\sigma_1^2}{2\mu_1}}{1 - \frac{\sigma_2^2}{2\mu_2}}$. As a result, we can get reversal in certain situations. Nevertheless, just as predicted by Theorem 4.1 one species will always go extinct and the competitive exclusion principle holds.

This shows the competitive exclusion principle will hold when one models the environmental stochasticity by a white noise term of the form $x_i(t)dE_i(t)$ and if one assumes the growth rates of the species depend linearly on the resources. The linear noise increases the expected resource level for each isolated species. The problem is that it also increases the death rates from $\alpha_i$ to $\alpha_i + \frac{\sigma_i^2}{2}$, therefore making coexistence impossible.

However, if the noise term is not linear, the next result shows this need not be the case anymore.

**Theorem 4.2.** Suppose all assumptions, other than the linearity of the noise term, of Theorem 4.1 hold. More particularly, assume that two species interact according to

\begin{equation}
    dx_i(t) = x_i(t)(-\alpha_i + b_iR(x(t))) \, dt + x_i(t)\sqrt{\beta_i}x_i(t) dB_i(t), \ i = 1, 2
\end{equation}


and the resource $R$ depends linearly on the species densities, i.e. \((2.3)\) holds. There exist $\beta_1, \beta_2 > 0$ such that $\Lambda_{x_2} > 0$ and $\Lambda_{x_1} > 0$ and the two species coexist.

The nonlinear noise terms create a nonlinearity when computing the expected values of the resource when each species is on its own. This breaks the symmetry when computing the invasion rates and allows to have both invasion rates be strictly positive. One example of parameters for which we get coexistence is presented in Figure 1.

![Figure 1](image)

**Figure 1.** Example showing the coexistence of the species $x_1$ and $x_2$ in the SDE setting from Theorem B.2. The parameters are $\alpha_1 = 0.5, \beta_1 = 4, \alpha_2 = 0.6, \beta_2 = 4, R = 3, a_1 = a_2 = 1$, and the invasion rates $\Lambda_{x_2} = 1.9, \Lambda_{x_1} = 2.02$.

### 4.2. Non-linear dependence on the resources.

If the assumption that the dependence of the per-capita growth rates on the resources is linear is dropped like in Theorem 2.2 and the noise is modeled by linear white noise the competitive exclusion principle will be violated. Specifically, assume the dynamics is modeled by

\[
\begin{align*}
    dx_i(t) &= x_i u_i(R) dt + x_i g_i(x) dE_i(t), \ i = 1, \ldots, m, \\
    R &= \overline{R} - F(x_1, \ldots, x_n).
\end{align*}
\]

(4.4)

**Theorem 4.3.** It is possible for $n > 1$ species to compete for one abiotic resource according to (4.4), satisfy the monotonicity conditions (2.5) and coexist.

We prove this is true in Appendix C. An example of two-species dynamics which satisfies this, is

\[
\begin{align*}
    dx_1(t) &= x_1(t) \left(-\alpha_1 + f(\overline{R} - a_1 x_1(t) - a_2 x_2(t))\right) dt + \sigma_1 x_1 dB_1(t) \\
    dx_2(t) &= x_2(t) \left(-\alpha_2 + (\overline{R} - a_1 x_1(t) - a_2 x_2(t))\right) dt
\end{align*}
\]

(4.5)

where $\overline{R} = 5, a_1 = a_2 = 2; \sigma_1 = 1, \alpha_1 = 0.5, \alpha_2 = 0.4$ and the function $f = f^*$ for

\[
f^*(x) = \begin{cases} 
\ln(x + 3) & x \geq -2 \\
    x + 2 & x \leq -2.
\end{cases}
\]
The intuition is as follows: Consider (4.5) for an arbitrary function $f$. One can show that if one considers the species $x_1$ in the absence of species $x_2$, i.e.

$$dx(t) = x(t)(-\alpha_1 + f(R - a_1 x(t))) dt + \sigma_1 x dB_1(t).$$

then, under certain conditions, the process $(x(t))$ has a unique stationary distribution $\mu$ on $(0, \infty)$. Ergodic theory then implies $\alpha_1 + \frac{\sigma_1^2}{2} = \int_0^\infty f(R - a_1 x) \mu(dx)$. If the function $f$ is concave then by Jensen’s inequality and taking inverses

$$\int_0^\infty (R - a_1 x) \mu(dx) > f^{-1}\left( \alpha_1 + \frac{\sigma_1^2}{2} \right).$$

The concavity of $f$ increases the expected value of the resource $R$. However, in the deterministic setting or if $f$ is linear and there is no noise, one would have equality

$$\int_0^\infty (R - a_1 x) \mu(dx) = f^{-1}\left( \alpha_1 + \frac{\sigma_1^2}{2} \right).$$

This is the main intuition behind the counterexample (4.5). Because $f^*$ is concave, we can see that there will be by (4.6) an increase in the expected value of the resource. This will in turn make coexistence possible. If $f$ is linear or $\sigma_1 = 0$, i.e. the system is deterministic, this cannot happen, and we always have competitive exclusion by Theorems 2.2 or 4.1.

5. Piecewise deterministic Markov processes

The basic intuition behind piecewise deterministic Markov processes (PDMP) is that due to different environmental conditions, the way species interact changes. For example, in [TL16], it has been showcased that the predation behavior can vary with the environmental conditions and therefore change predator-prey cycles. Since the environment is random, its changes (or switches) cannot be predicted in a deterministic way. For a PDMP, the process follows a deterministic system of differential equations for a random time, after which the
environment changes, and the process switches to a different set of ordinary differential equations (ODE), follows the dynamics given by this ODE for a random time and then the procedure gets repeated. This class of Markov processes was first introduced in the seminal paper of Davis \[\text{Dav84}\] and has been used in various biological settings \[\text{CDG}^{+17}\], from population dynamics \[\text{BL16, HS17, Ben18, DDTI1, DD14}\] to studies of the cell cycle \[\text{LM99}\], neurobiology \[\text{DL17}\], cell population models \[\text{BDMTI1}\], gene expression \[\text{YZLM14}\] and multiscale chemical reaction network models \[\text{HCKT15}\].

Suppose \((r(t))\) is a process taking values in the finite state space \(\mathcal{N} = \{1, \ldots, N\}\). This process keeps track of the environment, so if \(r(t) = i \in \mathcal{N}\) this means that at time \(t\) the dynamics takes place in environment \(i\). Once one knows in which environment the system is, the dynamics are given by a system of ODE. The PDMP version of \((2.1)\) therefore is

\[
(5.1) \quad dx_i(t) = x_i(t) \left(-\alpha_i(r(t)) + \sum_{j=1}^{m} b_{ij}(r(t)) R_j(x(t), r(t))\right) dt.
\]

In order to have a well-defined system one has to specify the switching-mechanism, e.g. the dynamics of the process \((r(t))\). Suppose that the switching intensity of \(r(t)\) is given as follows

\[
(5.2) \quad \mathbb{P}\{r(t + \Delta) = j \mid r(t) = i, x(s), r(s), s \leq t\} = q_{ij} \Delta + o(\Delta) \text{ if } i \neq j \quad \text{and} \quad \mathbb{P}\{r(t + \Delta) = i \mid r(t) = i, x(s), r(s), s \leq t\} = 1 + q_{ii} \Delta + o(\Delta)
\]

where \(q_{ii} := -\sum_{j \neq i} q_{ij}\). Here, we assume that the the matrix \(Q = (q_{ij})_{n \times n}\) is irreducible. It is well-known that a process \((X(t), r(t))\) satisfying \((5.1)\) and \((5.2)\) is a strong Markov process \[\text{Dav84}\] while \((r(t))\) is a continuous-time Markov chain that has a unique invariant probability measure \(\nu\) on \(\mathcal{N}\).

We define for \(u \in \mathcal{N}\) the \(u\)th environment, \(\mathcal{E}_u\). This is the deterministic setting where we follow \((5.1)\) with \(r(t) = u\) for all \(t \geq 0\), i.e.

\[
(5.3) \quad dx_i^u(t) = x_i^u(t) \left(-\alpha_i(u) + \sum_{j=1}^{m} b_{ij}(u) R_j(x^u(t), u)\right) dt.
\]

The dynamics of the switched system can be constructed as follows: We follow the dynamics of \(\mathcal{E}_u\) and switch between environments \(\mathcal{E}_u\) and \(\mathcal{E}_v\) at the rate \(q_{uv}\). It is interesting to note that in the limit case where the switching between the different states is fast, the dynamics can be approximated by the ‘mixed’ deterministic dynamics

\[
(5.4) \quad d\bar{x}_i(t) = \bar{x}_i(t) \sum_{u \in \mathcal{N}} \nu_u \left(-\alpha_i(u) + \sum_{j=1}^{m} b_{ij}(u) R_j(\bar{x}(t), u)\right) dt.
\]

If the number of species is strictly greater than the number of resources, \(n > m\), for any \(u \in \{1, \ldots, N\}\) the system

\[
(5.5) \quad \sum_{j=1}^{m} c_i(u) b_{ij}(u), \quad j = 1, \ldots, m
\]

admits a nontrivial solution \((c_1(u), \ldots, c_n(u))\). We can prove the following PDMP version of the competitive exclusion principle.
Theorem 5.1. Assume the dynamics of $n$ competing species is given by (5.1) and (5.2) and all resources eventually get exhausted. Suppose that there exists a non-zero vector $(c_1, \ldots, c_n)$ that is simultaneously a solution to systems (5.5) for all $u \in \{1, \ldots, N\}$. Then, with probability 1, at least one species goes extinct.

This shows that competitive exclusion holds if there is some kind of ‘uniformity’ of solutions of (5.5) in all the different environments. However, the next example shows that competitive exclusion can fail for PDMP.

Suppose we have two species, two environments, one resource and the dependence of the resource on the population densities is linear, i.e. (2.3) holds. In environment $E_u, u \in \{1, 2\}$ the system is modelled by the ODE

$$dx_i(t) = x_i(t)\left(-\alpha_i(u) + b_i(u)\left[\overline{R}(u) - \sum_{i=1}^{2} x_i(t)a_i(u)\right]\right) dt,$$

and therefore the switched system is given by

$$dx(t) = x(t)\left(-\alpha_i(r(t)) + b_i(r(t))\left[\overline{R}(r(t)) - \sum_{i=1}^{2} x(t)a_i(r(t))\right]\right) dt.$$

If we define $\mu_i(u) = -\alpha_i(u) + b_i(u)\overline{R}(u), \beta_{ij}(u) = b_i(u)a_j(u)$ we get the well known two-dimensional competitive Lotka–Volterra system

$$dx_1(t) = x_1(t)\mu_1(r(t))\left(1 - \frac{\beta_{11}(r(t))}{\mu_1(r(t))}x_1(t) - \frac{\beta_{12}(r(t))}{\mu_1(r(t))}x_2(t)\right),$$

$$dx_2(t) = x_2(t)\mu_2(r(t))\left(1 - \frac{\beta_{21}(r(t))}{\mu_2(r(t))}x_1(t) - \frac{\beta_{22}(r(t))}{\mu_2(r(t))}x_2(t)\right).$$

By the deterministic competitive exclusion principle from Theorem 2.1 we know that in each environment $E_u, u \in \{1, 2\}$ one species is dominant and drives the other one extinct.

Theorem 5.2. Suppose two species compete according to (5.6). There exist environments $E_1, E_2$ for which the maximal resource is equal $\overline{R}(1) = \overline{R}(2)$ such that

1. in both environments $E_1, E_2$ species $x_1$ persists and species $x_2$ goes extinct, or
2. in environment $E_1$ species $x_1$ persists and species $x_2$ goes extinct while in environment $E_2$ the reverse happens and $x_1$ goes extinct while $x_2$ persists,

and rates $q_{12}, q_{21} > 0$ such that the process $x(t)$ modelled by (5.6) converges to a unique invariant measure supported on a compact subset $K$ of the positive orthant $(0, \infty)^2$. In particular, with probability 1 the two species coexist, and the competitive exclusion principle does not hold.

We emphasize that the resource does not have to change with the environment - in the above example the maximal resources in the two environments $E_1$ and $E_2$ are equal. Two examples of systems satisfying Theorem 5.2 are given in Figures 3 and 4. For the environments given by the coefficients from Figure 3 one notes that species $x_1$ persists and $x_2$ goes extinct in $E_1$ while the reverse happens in environment $E_2$. Even more surprisingly, for the environments given by the coefficients from Figure 4 species $x_1$ persists and $x_2$ goes extinct in both environments. By spending time in both environments there is a rescue effect which forces both species to persist.
Figure 3. Example showing the coexistence of the species $x_1$ and $x_2$ when one switches between two environments. The constants are $\alpha_1(1) = \alpha_1(2) = 0.66, \alpha_2(1) = \alpha_2(2) = 1, R(1) = R(2) = 2, a_1 = 1, a_2 = 1, b_1(1) = b_1(2) = 1, b_2(1) = 1, b_2(2) = 5, q_{12} = 1, q_{21} = 5$. The invasion rates of the two species are $\Lambda_{x_1} \approx 0.137, \Lambda_{x_2} \approx 0.1$

Figure 4. Example showing the coexistence of the species $x_1$ and $x_2$ when one switches between two environments in both of which species $x_1$ dominates and drives species $x_2$ extinct. The constants are $\alpha_1(1) = 3, \alpha_1(2) = 0.2, \alpha_2(1) = 3.5, \alpha_2(2) = 0.8, R(1) = R(2) = 4, a_1 = 1, a_2 = 0.2, b_1(1) = 1, b_1(2) = 2, b_2(1) = 1, b_2(2) = 4, q_{12} = 1, q_{21} = 5$. The invasion rates of the two species are $\Lambda_{x_1} \approx 0.00531, \Lambda_{x_2} \approx 0.00519$
6. Discussion

We have analyzed how environmental stochasticity influences the competitive exclusion principle for \( n \) species competing for \( m < n \) abiotic resources. The assumptions we make are the ones that have been made before throughout the literature: the populations are unstructured, the species compete through the resources which eventually get exhausted, and there is no explicit time dependence in the interactions. Another common assumption is that the per-capita growth rates of the species depend linearly on the resources.

We are able to show that for stochastic differential equations, if we assume that the per-capita growth rates of the species depend linearly on the resources and the white noise term is linear, the stochastic analogue of the competitive exclusion principle holds: for any initial starting densities, at least one species will go extinct with probability 1. The noise can change which species persist and which go extinct as well as drive more species towards extinction. This is in line with [HN18c, HN18b] where we show that white noise of the form \( x_i(t) \, dE_i(t) \) makes the coexistence of species in a Lotka–Volterra food chain less likely. In a sense, this type of white noise is on average detrimental to the ecosystem if the interaction between the species is linear enough.

However, if one drops the assumption that the per-capita growth rates of the species depend linearly on the resources, then competitive exclusion can fail. We exhibit an example of two species competing for one resource where the species coexist because of the linear white noise. The combination of noise and non-linear dependence on the resources make it possible for one species to get an increased expected value of the resource. This will in turn make it possible for the two species to coexist.

If instead, we drop the condition that the noise term is linear, we construct an example of two species where the noise looks like \( x_i(t)^{3/2} \, dE_i(t) \) and the per-capita growth rates of the species depend linearly on the resources in which the competitive exclusion principle fails and the two species coexist.

The above two examples show that in order to have competitive exclusion it is key to assume both that the growth rates depend linearly on the resources and that the white noise term is linear. If either one of these assumptions is violated we are able to give examples of two species that compete for one resource and coexist, therefore violating the competitive exclusion principle. Nonlinear terms facilitate the coexistence of species. Since there is no reason one should assume the interactions or the noise terms in nature are linear, this can possibly explain why the competitive exclusion has been violated in empirical settings.

The second type of noise we analyze is coming from switching the environment between a finite number of states at random times, and following a system of ODE while being in a fixed environment. We prove that if the different environments are uniform, in the sense that there exists a solution \((c_1, \ldots, c_n)\) that solves the system

\[
\sum_{i=1}^{n} c_i b_{ij}(u), \quad j = 1, \ldots, m,
\]

simultaneously in all environments then the competitive exclusion principle holds. If this condition does not hold, we construct an example with two species \( x_1, x_2 \) competing for one resource, and two environments \( E_1 \) and \( E_2 \) such that in the switched system the two species coexist. We note that in this setting we do have that the growth rates of the species depend linearly on the resource. This example is interesting as it relates to Hutchinson’s explanation of why environmental fluctuations can favor different species at different times and thus
facilitate coexistence [Hut61, LC16]. We are able to find environments $E_1$ and $E_2$ such that without the switching species $x_1$ persists and species $x_2$ goes extinct in both environments. However, once we switch randomly between the environments we get coexistence (see Figure 1). This implies the surprising result that species can coexist even if one species is unfavored at all times, in all environments.

Our analysis shows that different types of noise interact differently with competitive exclusion according to whether the growth rates depend linearly on the resources or not. As long as the noise is ‘smooth’ and ‘linear’ and changes the dynamics in a continuous way and the growth rates are linear in the resources, the competitive exclusion principle cannot be violated. One needs nonlinear continuous noise, ‘discontinuous’ noise that abruptly changes the dynamics of the system, or a nonlinearity in the dependence of the per-capita growth rates on the resources in order to disrupt this fundamental principle.

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Appendix A. Proof of Theorems [4.1]

If the number of species is strictly greater than the number of resources, \( n > m \), the system

\[
\sum_{i=1}^{n} c_i b_{ij} = 0, \ j = 1, \ldots, m
\]

admits a nontrivial solution \((c_1, \ldots, c_n)\).

**Theorem A.1.** Assume that \( \lim_{\|x\| \to \infty} R_j(x) = 0, j = 1, \ldots, m \). Suppose further that \( n \) species interact according to (4.1), the number of species is greater than the number of resources \( n > m \) and the resources depend on the species densities according to (2.2) so that they eventually get exhausted. Suppose further that \( g_i(x) = 1 \). Let \((c_1, \ldots, c_n)\) be a non-trivial solution to (A.1) and assume that \( \sum_{i=1}^{n} c_i \left( \alpha_i + \frac{\sigma_{ii}}{2} \right) \neq 0 \). Then, for any starting densities \( x(0) \in (0, \infty)^n \) with probability 1

\[
\limsup_{t \to 0} \frac{\ln \min \{x_1(t), \ldots, x_n(t)\}}{t} < 0.
\]

**Proof of Theorem 4.1.** Suppose \( g_i(x) = 1, \ i = 1, \ldots, n \). Since \( \lim_{\|x\| \to \infty} R_j(x) = 0, j = 1, \ldots, m \), [HN18a, Assumptions 1.1 & 1.5] are satisfied. As a result for any starting point
\( \mathbf{x}(0) \in (0, \infty)^n \) the SDE (4.1) has a unique positive solution. Moreover,

\[
(A.2) \quad \limsup_{t \to \infty} \frac{\ln \| \mathbf{x} \|}{t} \leq 0, \text{ a.s.}
\]

By possibly replacing all \( c_i \) by \( -c_i \) we can assume that \( \sum_{i=1}^{n} c_i \left( \alpha_i + \frac{\sigma_{ii}}{2} \right) > 0 \). Using this in conjunction with (4.1), (A.1) and Ito’s Lemma yields

\[
\sum_{i=1}^{n} c_i \ln x_i(t) \int_{t}^{\infty} E_i(s) \, ds = -\sum_{i=1}^{n} c_i \left( \alpha_i + \frac{\sigma_{ii}}{2} \right) + \frac{1}{t} \sum_{i=1}^{n} c_i \int_{0}^{t} E_i(s) \, ds
\]

Letting \( t \to \infty \) and using that \( \lim_{t \to \infty} \sum_{i=1}^{n} c_i E_i(t) / t = 0 \) with probability 1, we obtain that with probability 1

\[
\sum_{i=1}^{n} c_i \ln x_i(t) / t = -\sum_{i=1}^{n} c_i \left( \alpha_i + \frac{\sigma_{ii}}{2} \right) < 0,
\]

In view of (A.2) this implies that with probability 1

\[
\limsup_{t \to \infty} \frac{\ln \min\{x_1(t), \ldots, x_n(t)\}}{t} < 0.
\]

\[\square\]

**Appendix B. Proof of Theorem 4.2**

**Theorem B.1.** Assume two species interact according to

\[
(B.1) \quad dx_i(t) = x_i(t) \left( -\alpha_i + b_i R(x(t)) \right) \, dt + x_i(t) \sqrt{\beta_i x_i(t)} \, dB_i(t), \quad i = 1, 2,
\]

the resource \( R \) depends linearly on the species densities

\[ R(x) = \overline{R} - a_1 x_1(t) - a_2 x_2(t) \]

and \( b_i \overline{R} > \alpha_i, i = 1, 2 \). Then there exist \( \beta_1, \beta_2 > 0 \) such that the two species coexist.

**Proof.** Consider

\[
(B.2) \quad dx_i(t) = x_i(t) \left( -\alpha_i + b_i R(x(t)) \right) \, dt + x_i(t) \sqrt{\beta_i x_i(t)} \, dB_i(t), \quad i = 1, 2.
\]

If the species \( x_2 \) is absent species \( x_1 \) has the one-dimensional dynamics

\[ dx(t) = x(t) \left( -\alpha_1 + dt + b_1 (\overline{R} - a_1 x(t)) \right) \, dt + x(t) \sqrt{\beta_1 x(t)} \, dB_1(t). \]

If \( b_1 \overline{R} > \alpha_1 \), we can use [HN18a] to show that the process \( x(t) \) has a unique invariant measure on \((0, \infty)\), say \( \mu_1 \). Moreover, [HN18a, Lemma 2.1] shows that

\[
\int_{0}^{\infty} (-\alpha_1 + b_1 (\overline{R} - a_1 x) - \beta_1 x) \, x \mu_1(dx) = 0
\]

or

\[
\int_{0}^{\infty} x \mu_1(dx) = \frac{b_1 \overline{R} - \alpha_1}{b_1 a_1 + \beta_1}.
\]

The invasion rate of \( x_2 \) with respect to \( x_1 \) can be computed as

\[
\Lambda_{x_2} = \int_{0}^{\infty} (-\alpha_2 + b_2 (\overline{R} - a_1 x)) \, x \mu_1(dx) = (b_2 \overline{R} - \alpha_2) - b_2 a_1 \frac{b_1 \overline{R} - \alpha_1}{b_1 a_1 + \beta_1}.
\]
Similarly, one can compute the invasion rate of \( x_1 \) with respect to \( x_2 \) as

\[
\Lambda_{x_1} = (b_1 R - \alpha_1) - b_1 a_2 \frac{b_2 R - \alpha_2}{b_2 a_2 + \beta_2}.
\]

Since \( b_1 R - \alpha_1 > 0 \), one can easily see that \( \Lambda_{x_2} > 0 \), and \( \Lambda_{x_1} > 0 \) if \( \beta_1 > \frac{b_2 a_1 (b_1 R - \alpha_1)}{b_2 R - \alpha_2} - b_1 a_1 \).

and \( \beta_2 > \frac{b_1 a_2 (b_2 R - \alpha_2)}{b_1 R - \alpha_1} - b_2 a_2 \). If both invasion rates are positive we get by [HN18a] that the species coexist.

\[ \square \]

**Appendix C. Proof of Theorem 4.3**

We construct an SDE example of two species competing for one abiotic resource and coexisting. We remark that this happens solely because of the noise term.

**Theorem C.1.** Suppose the dynamics of the two species is given by

\[
\begin{align*}
\frac{dx_1}{dt} &= x_1(t)(-\alpha_1 + f(R - a_1 x_1(t) - a_2 x_2(t))) dt + \sigma_1 x_1 dB_1(t) \\
\frac{dx_2}{dt} &= x_2(t)(-\alpha_2 + (R - a_1 x_1(t) - a_2 x_2(t))) dt
\end{align*}
\]

where \( f \) is a continuously differentiable Lipschitz function satisfying \( \lim_{x \to -\infty} f(x) = -\infty \), \( \frac{df(x)}{dx} > 0 \), \( \frac{d^2 f(x)}{dx^2} \leq 0 \) for all \( x \in \mathbb{R} \) and \( \frac{d^2 f(x)}{dx^2} < 0 \) for \( x \) in some subinterval of \( (-\infty, \frac{R}{a_1}) \).

Let \( a_1, a_2, \sigma_1, \alpha_1, \sigma_1, R \) be any fixed positive constants satisfying \( f(R) > \alpha_1 + \frac{\sigma_1^2}{2} \). Then there exists an interval \( (c_0, c_1) \subset (0, \infty) \) such that the two species coexist for all \( \alpha_2 \in (c_0, c_1) \).

**Proof.** The dynamics of species \( x_1 \) in the absence of species \( x_2 \) is given by the one-dimensional SDE

\[
\frac{dx}{dt} = x(t)(-\alpha_1 + f(R - a_1 x(t))) dt + \sigma_1 x dB_1(t).
\]

Since \( \lim_{x \to -\infty} f(R - a_1 x) = -\infty \), and \( f(R) > \alpha_1 + \frac{\sigma_1^2}{2} \), this diffusion has a unique invariant probability measure \( \mu \) on \( (0, \infty) \) whose density is strictly positive on \( (0, \infty) \) (see [BS16] or [Mao97]). Moreover, by noting that \( \lim_{t \to \infty} \frac{x(t)}{t} = 0 \) with probability 1 (see [HN18a]) and using Ito’s formula one sees that

\[
\int_0^\infty f(R - a_1 x)\mu(dx) = \alpha_1 + \frac{\sigma_1^2}{2}.
\]

Since \( f \) is a concave function and \( \frac{d^2 f(x)}{dx^2} > 0 \) for all \( x \) in some subinterval of \( (-\infty, \frac{R}{a_1}) \) we must have by Jensen’s inequality that

\[
\int_0^\infty f(R - a_1 x)\mu(dx) < f \left( \int_0^\infty (R - a_1 x)\mu(dx) \right).
\]

The fact that the function \( f \) is strictly increasing together with (C.2) and (C.3) forces

\[
\varepsilon_0 := \int_0^\infty (R - a_1 x)\mu(dx) - f^{-1} \left( \alpha_1 + \frac{\sigma_1^2}{2} \right) > 0,
\]
where \( f^{-1} \) is the inverse of \( f \) – it exists because \( f \) is strictly increasing. As a result, the invasion rate of species \( x_2 \) with respect to \( x_1 \), or the Lyapunov exponent \( \lambda_2(\mu) \) of the invariant probability measure \( \mu \) (see [HN18a]), can be computed as

\[
\Lambda_{x_2} = -\alpha_2 + \int_0^\infty (R - a_1 x) \mu(dx) = \varepsilon_0 + f^{-1} \left( \alpha_1 + \frac{\sigma_1^2}{2} \right) - \alpha_2.
\]

This implies that \( \Lambda_{x_2} > 0 \) if and only if

\[
(\text{C.5}) \quad \alpha_2 < \varepsilon_0 + f^{-1} \left( \alpha_1 + \frac{\sigma_1^2}{2} \right).
\]

The dynamics of species \( x_2 \) in the absence of species \( x_1 \) is

\[
dy(t) = y(t)(R - \alpha_2 - a_2 y(t))dt.
\]

The positive solutions of this equation converge to the point \( y^* = \frac{R - \alpha_2}{a_2} \) if and only if

\[
(\text{C.6}) \quad R > \alpha_2.
\]

The invasion rate of \( x_1 \) with respect to \( x_2 \) will be

\[
\Lambda_{x_1} = -\alpha_1 - \frac{\sigma_1^2}{2} + f(\alpha_2).
\]

Note that since the function \( f \) is increasing we get \( \Lambda_{x_1} > 0 \) if and only if

\[
(\text{C.7}) \quad \alpha_2 > f^{-1} \left( \alpha_1 + \frac{\sigma_1^2}{2} \right).
\]

Note that \( f^{-1} \left( \alpha_1 + \frac{\sigma_1^2}{2} \right) < R \) since by assumption \( f(R) > \alpha_1 + \frac{\sigma_1^2}{2} \). As a result, making use of the inequalities (C.5), (D.3) and (C.7) we get that \( \Lambda_{x_2} > 0, \Lambda_{x_1} > 0 \) if and only if

\[
\alpha_2 \in \left( f^{-1} \left( \alpha_1 + \frac{\sigma_1^2}{2} \right), R \right) \cup \left( f^{-1} \left( \alpha_1 + \frac{\sigma_1^2}{2} \right) + \varepsilon_0 \right).
\]

This implies by Theorem 3.3 that the two species coexist. \( \square \)

**Appendix D. Proof of Theorem 5.1**

**Theorem D.1.** Assume that

\[
(\text{D.1}) \quad \lim_{\|x\| \to \infty} \left( -\alpha_i(u) + \sum_{j=1}^m b_{ij}(u) R_j(x, u) \right) < 0, \quad i = 1, \ldots, n, \quad u = 1, \ldots, N.
\]

Suppose further that there exists a vector \( (c_1, \ldots, c_n) \) that is simultaneously a solution to the systems (5.5) for all \( u \in \{1, \ldots, N\} \). Then, with probability 1,

\[
\lim\sup_{t \to 0} \frac{\ln \min\{x_1(t), \ldots, x_n(t)\}}{t} < 0
\]

except possibly for the critical case when

\[
(\text{D.2}) \quad \sum_{i=1}^n c_i \sum_{k=1}^N \alpha_i(k) \nu_k = 0,
\]

where \( (\nu_k)_{k \in \mathcal{N}} \) is the invariant probability measure of the Markov chain \( (r(t)) \).
Proof. Under the condition (D.1), there exists an $M > 0$ such that the set $K_M := \{ x \in \mathbb{R}^n : \| x \| \leq M \}$ is a global attractor of (5.4). As a result, the solution to (5.4) is eventually enters and never leaves the compact set $K_M$. In particular, this shows that the process $x(t)$ is bounded. Next, note that we can assume that

\begin{equation}
(D.3) \sum_{i=1}^{n} c_i \sum_{k=1}^{N} \alpha_i(k) \pi_k > 0.
\end{equation}

Otherwise, if $\sum_{i=1}^{n} c_i \sum_{k=1}^{N} \alpha_i(k) \pi_k < 0$, we can replace $c_i$ by $-c_i$, $i = 1, \ldots, n$ and then get (D.3). Using (5.1) and the fact that that $c_i$’s solve (5.5) simultaneously we get

$$\sum_{i=1}^{n} c_i \ln x_i(t) = -\frac{1}{t} \int_{0}^{t} \sum_{i=1}^{n} c_i \alpha_i(r(s)) ds$$

Letting $t \to \infty$ and using the ergodicity of the Markov chain $(r(t))$ we obtain that with probability 1

$$\limsup_{t \to \infty} \frac{\sum_{i=1}^{n} c_i \ln x_i(t)}{t} = \liminf_{t \to \infty} \frac{1}{t} \int_{0}^{t} \sum_{i=1}^{n} c_i \alpha_i(r(s)) ds = -\sum_{i=1}^{n} c_i \sum_{k=1}^{N} \alpha_i(k) \pi_k < 0 \text{ a.s.}$$

Since $x(t)$ is bounded, this implies that with probability 1

$$\limsup_{t \to \infty} \frac{\ln \min\{x_1(t), \ldots, x_n(t)\}}{t} < 0.$$

\[\Box\]

Appendix E. Proof of Theorem 5.2

According to [BL16, MZ17, MP16] it is enough to find an example for which the invasion rates $\Lambda_{x_1}, \Lambda_{x_2}$ are positive. We will follow [BL16] in order to compute the invasion rates of the two species. Set for $u = 1, 2$ $\mu_u = -\alpha_1(u) + b_1(u) \bar{R}, \nu_u = -\alpha_2(u) + b_2(u) \bar{R} \bar{a}_u = \frac{b_1(u) a_1(u)}{\mu_u}, \bar{b}_u = \frac{b_1(u) a_2(u)}{\mu_u}, \bar{c}_u = \frac{b_2(u) a_1(u)}{\nu_u}, \bar{d}(u) = \frac{b_2(u) a_2(u)}{\nu_u}$, $p_u = \frac{1}{\bar{a}_u}, q_u = \frac{1}{\bar{d}_u}, \gamma_1 = \frac{q_{12}}{\mu_u}, \gamma_2 = \frac{q_{21}}{\nu_u}$. If $p_1 \neq p_2$, suppose without loss of generality that $p_1 < p_2$. Define the functions

$$\theta(x) = \frac{|x - p_1|^{\gamma_1-1}|p_2 - x|^{\gamma_2-1}}{x^{1+\gamma_1+\gamma_2}}$$

and

$$P(x) = \frac{\bar{a}_2 - \bar{a}_1}{\bar{a}_2 - \bar{a}_1} \left[ \frac{\nu_u}{\mu_u} (1 - \bar{c}_2 x)(1 - \bar{a}_1 x) - \frac{\nu_u}{\mu_1} (1 - \bar{c}_1 x)(1 - \bar{a}_2 x) \right].$$

By [BL16] we have

\begin{equation}
(E.1) \Lambda_{x_2} = \begin{cases} 
\frac{1}{p_1 p_2} \int_{p_1}^{p_2} \theta(x) P(x) dx & \text{if } p_1 = p_2 = p \\
\left( \frac{q_{12} \nu_1 (1 - \bar{c}_1 p) + q_{12} \nu_2 (1 - \bar{c}_2 p)}{p_1 p_2} \int_{p_1}^{p_2} \theta(x) P(x) dx \right) & \text{if } p_1 < p_2
\end{cases}
\end{equation}

The expression for $\Lambda_{x_1}$ can be obtained by swapping $\mu_i$ and $\nu_i$, $(\pi_i, \tau_i)$ with $(\bar{a}_i, \bar{b}_i)$, and $p_i$ with $q_i$. 

\[\Box\]
For the example from Figures 3 and 4 we have used the integral equation from (E.1) together with the numerical integration package of Mathematica in order to find \( \Lambda_{x_1} > 0 \) and \( \Lambda_{x_2} > 0 \). This implies by Theorem 3.3 that the two species coexist.

Department of Mathematics, Tufts University, Bromfield-Pearson Hall, 503 Boston Avenue, Medford, MA 02155, United States

E-mail address: alexandru.hening@tufts.edu

Department of Mathematics, University of Alabama, 345 Gordon Palmer Hall, Box 870350, Tuscaloosa, AL 35487-0350, United States

E-mail address: dangnh.maths@gmail.com