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Research article

A periodic model for biotic interactions of many species with a continuous spectrum of outcomes

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Abstract: In this paper, we study an n-species population model with periodically varying biotic interactions that can continuously span mutualism, competition, and consumer–resource outcomes, as a natural extension of a previous two-species framework. Each pairwise interaction is modulated by a periodic function representing the time-dependent fraction of events with positive effects, thus capturing ecologically realistic scenarios where the sign and strength of interactions fluctuate seasonally. Under mild assumptions on the model parameters, we prove that there exists an explicit threshold for the intraspecific competition coefficients above which the system admits a unique positive T-periodic coexistence state that is asymptotically stable. Some illustrative numerical examples are included. The results support the ecological principle that sufficiently strong intraspecific regulation is the key mechanism ensuring long-term coexistence in communities with temporally variable interaction outcomes.

Keywords: Population dynamics; periodic solutions; coexistence state; biotic interactions; multispecies systems

1. Introduction

A central question in both ecology and the mathematical analysis of dynamical systems is how multiple interacting species can stably coexist. While much of the classical models has focused on the interaction between two species, natural ecosystems are primarily multispecies: each population may experience positive and negative influences from many others, thereby forming complex interaction networks [1–5]. In this context, coexistence depends both on intraspecific interactions that modulate

the growth of each population as well as on the strength of interactions established between all populations that co-occur in the community [6].

In our previous work [7], we proposed a periodic two-species model which incorporated the idea of a temporally variable proportion of positive and negative interactions through periodic functions $P_i(t) \in [0, 1]$. There, we showed that if the intraspecific competition coefficients exceed a certain explicit threshold, then the system admits a unique positive periodic solution (a coexistence state) that is asymptotically stable. This result provided a mathematical foundation for the widely accepted ecological principle that stable coexistence requires the internal regulation of a given species to be stronger than interspecific interactions [8, 9].

The main objective of the present article is to extend this theoretical framework to the case of n species, generalizing both the model formulation and the stability conditions obtained in the two-species case. In the new version, each species i interacts with all others through periodic functions $P_{ij}(t)$, representing the temporal change in the proportion of events with positive effects resulting from the interaction between species i and j. This approach allows us to capture a broad range of ecological configurations in which a species simultaneously maintains mutualistic, antagonistic, competitive, or commensalistic interactions with different members of the community [10, 11].

A paradigmatic example of this situation can be found in oak forests (*Quercus* spp.) and their interacting communities (see Figure 1 in [12]). Oak trees interact with a wide and diverse range of animal species that consume their fruits and seeds (acorns), from beetles and moths to rodents and corvids, as well as cranes, pigeons, ungulates, and monkeys. Each of these animals can have both positive and negative effects. Negative effects occur when animals ingest and digest acorns, thus killing the seed embryo, while positive effects occur when these same animals, instead of ingesting the entire acorns and killing the embryo, sometimes transport them away from the mother plant and bury them with the aim of consuming them later, or activate the embryo and cause excessive compensatory growth later in the life cycle [13, 14]. Similarly, in plant and pollinator communities, many species of floral visitors can sometimes act as legitimate pollinators, thereby depositing compatible pollen grains that increase the reproductive success of flowers, or as mere nectar robbers that consume this product but do not deposit pollen, and the proportions between these two roles also fluctuate periodically [15–17]. Both examples illustrate the need for a general framework to study coexistence and stability in communities where the signs and magnitudes of interactions change periodically.

From a mathematical perspective, the extension to n species introduces new analytical challenges: the phase space becomes higher-dimensional, interactions couple nonlinearly, and global stability requires additional tools. In this work, we prove that under reasonable assumptions on the periodic functions $P_{ij}(t)$ and the model parameters, there exists an explicit threshold a^* such that if the intraspecific competition parameters satisfy $a_i > a^*$ for all i, then the system admits a unique positive periodic solution which is asymptotically stable. This result extends [7] to the multispecies setting and provides an explicit condition guaranteeing stability.

This article is organized as follows. First, we present the model in Section 2. In Section 3, we establish general conditions of stability and instability for periodic linear systems, including sufficient criteria based on positive definite symmetric matrices and their application to linearized multispecies systems. Section 4 focuses on obtaining a priori bounds for periodic coexistence solutions of the multispecies model. In Section 5, we prove the existence and uniqueness of an asymptotically stable periodic coexistence state for sufficiently large intraspecific competition values, using the classical

perturbation theory. Section 6 provides an explicit quantitative condition to guarantee the stability of this coexistence state, deriving a computable threshold for the system parameters. Then, in Section 7, we analyze particular cases for $n = 2$ and $n = 3$, illustrating how the stability conditions apply and providing numerical examples. Finally, in Section 8, we discuss the ecological and mathematical implications of the results, as well as possible extensions of the model and future research perspectives.

Overall, the results show that the stability of the coexistence state is a robust property of the model, maintained when moving from two to many species, provided that the intraspecific competition is sufficiently strong. This confirms, from a mathematical viewpoint, the idea that self-regulation of each population is the essential mechanism sustaining stable coexistence in ecological communities with temporally variable interactions.

We conclude this Introduction by fixing the terminology used throughout the paper: any solution with strictly positive components will be referred to as a coexistence state or, equivalently, a coexistence solution.

2. The model

In the present paper, the model under study is the following:

$$x_i' = x_i\,(r_i - a_i x_i) + \sum_{\substack{j=1\\ j\neq i}}^{n} \left(x_i \frac{\varepsilon_{ij} x_j}{h_j + x_j} P_{ij}(t) - x_i \frac{\alpha_{ij} x_j}{e_i + x_i}(1 - P_{ij}(t)) \right), \tag{2.1}$$

where the coefficients $r_i, a_i, \varepsilon_{ij}, h_j, \alpha_{ij}$ and e_i are positive constants, and $P_{ij} : \mathbb{R} \to [0, 1]$ are T-periodic and continuous functions for $i, j = 1, 2, \ldots, n \in \mathbb{N}$, that is,

$$P_{ij}(t + T) = P_{ij}(t) \qquad \text{for every } t.$$

This is the natural extension of the model proposed in [6, 7] to an arbitrary number of species. The meaning of the parameters involved is as follows. The term $x_i(r_i - a_i x_i)$ represents the intrinsic logistic growth of species i, where r_i is the maximum per-capita growth rate and a_i is the coefficient of intraspecific competition. The interaction between species i and j is described by the two terms inside the summation. The coefficient $\varepsilon_{ij} > 0$ represents the maximum positive effect of species j on species i, while $h_j > 0$ is a half-saturation constant regulating the dependence of this effect on the abundance of species j. Similarly, $\alpha_{ij} > 0$ denotes the maximum negative effect of species j on species i, and $e_i > 0$ is a saturation constant associated with the density of species i. The function $P_{ij}(t) \in [0, 1]$ represents the proportion of interaction events between species i and j that have a positive outcome for species i at time t, while $1 - P_{ij}(t)$ corresponds to the proportion of events with negative outcomes. In this way, System (2.1) incorporates both positive and negative interaction effects for each pair of species, weighted by time-periodic functions, and extends the two-species framework to a general multispecies setting.

We emphasize that the proposed model encompasses several classical interaction types as particular limiting cases. In particular,

- $P_{ij}(t) = 1$ and $P_{ji}(t) = 1$: mutualistic interaction between species i and j;
- $P_{ij}(t) = 0$ and $P_{ji}(t) = 0$: competitive interaction between species i and j;

- $P_{ij}(t) = 1$ and $P_{ji}(t) = 0$: consumer–resource interaction, where species i acts as the consumer and species j as the resource.

More generally, the model allows for a continuous transition between these interaction types, thereby capturing the context-dependent nature of many ecological relationships.

3. A stability and instability condition for linear systems

Let us consider a linear system

$$\dot{\mathbf{z}} = B(t)\mathbf{z} \tag{3.1}$$

where $B(t) = \left[b_{ij}(t)\right]$ is a matrix of $n \times n$ with continuous and T-periodic entries.

Proposition 3.1. *Assume that for all $t \in \mathbb{R}$ and the matrix $B(t)$ in* (3.1)*, there exists a symmetric positive definite matrix $M \in \mathbb{R}^n$ such that for all t, $(B^T M + MB)$ is negative definite. Then, System* (3.1) *is asymptotically stable.*

Proof. Consider the function $V(z) : \mathbb{R}^n \to \mathbb{R}$ defined as the inner product

$$z \cdot z = V(z) = z^T M z,$$

for some symmetric positive definite matrix $M = \left[m_{ij}\right]$. The function $V(z)$ is positive definite since M is positive definite. Now, compute the time derivative of $V(z)$ along the trajectories of System (3.1) as follows:

$$\dot{V}(z) = \frac{d}{dt}(z^T M z). \tag{3.2}$$

Differentiation yields the following:

$$\dot{V}(z) = \left(\frac{d}{dt}z\right)^T Mz + z^T M \frac{d}{dt}z.$$

The derivative of z satisfies the system $\dot{z} = B(t)z$, so we can substitute $\dot{z}$ into the equation as follows:

$$\dot{V}(z) = (\dot{z})^T Mz + z^T M(\dot{z}) = z^T B(t)^T Mz + z^T MB(t)z.$$

Simplifying leads to the following:

$$\dot{V}(z) = z^T(B(t)^T M + MB(t))z.$$

Consider the matrix $B(t)^T M + MB(t)$. If $B(t)^T M + MB(t)$ is negative definite, then $\dot{V}(z) < 0$ for all nonzero z, implying that $V(z)$ is a Lyapunov function that decreases along the trajectories of the system, guaranteeing asymptotic stability by the direct Lyapunov method. This completes the proof. □

Corollary 3.2. *Let M be a symmetric positive definite matrix in Proposition 3.1. Assume that*

$$\sum_{k=1}^{n} b_{ki}(t)m_{ki} < 0, \tag{3.3}$$

and that the inequality below holds

$$-2\sum_{k=1}^{n} b_{ki}(t)m_{ki} > \sum_{\substack{j=1\\ j\neq i}}^{n} \left| \sum_{k=1}^{n} \left(b_{kj}(t)m_{ik} + b_{ki}(t)m_{kj} \right) \right| \tag{3.4}$$

for all $t \in \mathbb{R}$ and for each $i = 1, 2, \ldots, n$. Then, System (3.1) *is asymptotically stable.*

Proof. By Proposition 3.1, System (3.1) is asymptotically stable if there exists a symmetric positive definite matrix M such that $B^T M + MB$ is negative definite.

A sufficient condition for this is to show that $-(B^T M + MB)$ is positive definite. For $-(B^T M + MB)$ to be positive definite, it must have a strictly dominant diagonal with positive diagonal entries.

The entries of $B^T M + MB$ are given by the following:

$$(B^T M + MB)_{ij} = \sum_{k=1}^{n} \left(b_{kj}(t)m_{ik} + b_{ki}(t)m_{kj} \right).$$

Now, consider the diagonal entries of $-(B^T M + MB)$:

$$-(B^T M + MB)_{ii} = -2\sum_{k=1}^{n} b_{ki}(t)m_{ki}.$$

By the hypothesis, we assume that (3.3) holds, which ensures that the diagonal elements of $-(B^T M + MB)$ are positive.

Furthermore, imposing the strict diagonal dominance condition

$$-2\sum_{k=1}^{n} b_{ki}(t)m_{ki} > \sum_{\substack{j=1\\ j\neq i}}^{n} \left| \sum_{k=1}^{n} \left(b_{kj}(t)m_{ik} + b_{ki}(t)m_{kj} \right) \right|, \tag{3.5}$$

for all i, ensures that $-(B^T M + MB)$ is strictly diagonally dominant.

Since $-(B^T M + MB)$ is a symmetric matrix with a positive diagonal and is strictly diagonally dominant, it follows that it is positive definite. Consequently, $B^T M + MB$ is negative definite, which implies that System (3.1) is asymptotically stable by Proposition 3.1. □

Corollary 3.3. *A particular case of Corollary 3.2 occurs when $M = I$, namely the identity matrix. In this case, conditions* (3.3) *and* (3.4) *simplify to*

$$b_{ii}(t) < 0, \tag{3.6}$$

and

$$-2b_{ii}(t) > \sum_{\substack{j=1\\ j\neq i}}^{n} |b_{ij}(t) + b_{ji}(t)|, \tag{3.7}$$

for all $t \in \mathbb{R}$ and for each $i = 1, 2, \ldots, n$. Thus, if $B(t)$ satisfies (3.6) *and* (3.7)*, then System* (3.1) *is asymptotically stable.*

4. A priori bounds for periodic coexistence solutions

In this section, a priori bounds for periodic coexistence states of System (2.1) are derived. In the space C_T of the continuous and T-periodic functions, we denote the usual uniform norm by $\|\cdot\|_\infty$, i.e.,

$$\|g\|_\infty = \max_{t\in[0,T]} |g(t)|$$

for any $g \in C_T$.

Proposition 4.1. *Any potential periodic coexistence state* $(x_1, \dots, x_n)$ *in system* (2.1) *satisfies the a priori bounds*

$$\frac{r_i}{a_i} - \sum_{\substack{j=1\\ j\neq i}}^{n} \left[\frac{\alpha_{ij}}{a_i a_j e_i} \left(r_j + \sum_{\substack{k=1\\ k\neq j}}^{n} \varepsilon_{jk} \left\| P_{jk} \right\|_\infty \right) (1 - \min_{t\in[0,T]} P_{ij}(t)) \right] \leq x_i(t) \leq \frac{1}{a_i} \left(r_i + \sum_{\substack{j=1\\ j\neq i}}^{n} \varepsilon_{ij} \left\| P_{ij} \right\|_\infty \right), \tag{4.1}$$

for every t.

Proof. Let $x_i(t)$ be a given component of a periodic coexistence state of (2.1). Since it is a periodic function, $x_i(t)$ achieves its absolute extremes (maximum and minimum) in the period interval $[0, T]$, and since it is a regular function, such absolute extremes must be attained in a critical point. Let us assume that $x_i(t^*)$ is a critical point, that is, $\dot{x}_i(t^*) = 0$. Then, from the system, we obtain the following:

$$a_i x_i(t^*) = r_i + \sum_{\substack{j=1\\ j\neq i}}^{n} \left(\frac{\varepsilon_{ij} x_j(t^*)}{h_j + x_j(t^*)} P_{ij}(t^*) - \frac{\alpha_{ij} x_j(t^*)}{e_i + x_i(t^*)} (1 - P_{ij}(t^*)) \right) \leq r_i + \sum_{\substack{j=1\\ j\neq i}}^{n} \varepsilon_{ij} P_{ij}(t^*).$$

Then, the upper bound

$$x_i(t^*) \leq \frac{1}{a_i} \left(r_i + \sum_{\substack{j=1\\ j\neq i}}^{n} \varepsilon_{ij} \left\| P_{ij}(t^*) \right\|_\infty \right) \tag{4.2}$$

is obtained, and in consequence,

$$\|x_i\|_\infty \leq \frac{1}{a_i} \left(r_i + \sum_{\substack{j=1\\ j\neq i}}^{n} \varepsilon_{ij} \left\| P_{ij} \right\|_\infty \right). \tag{4.3}$$

To derive the lower bound, observe that

$$a_i x_i(t^*) = r_i + \sum_{\substack{j=1\\ j\neq i}}^{n} \left(\frac{\varepsilon_{ij} x_j(t^*)}{h_j + x_j(t^*)} P_{ij}(t^*) - \frac{\alpha_{ij} x_j(t^*)}{e_i + x_i(t^*)} (1 - P_{ij}(t^*)) \right) \geq r_i - \sum_{\substack{j=1\\ j\neq i}}^{n} \left[\frac{\alpha_{ij}}{e_i} x_j(t^*) (1 - \min_{t\in[0,T]} P_{ij}(t)) \right],$$

and using the upper bound derived in (4.2) for $x_j(t^*)$,

$$x_i(t^*) \geq \frac{r_i}{a_i} - \sum_{\substack{j=1\\ j\neq i}}^{n} \left[\frac{\alpha_{ij}}{a_i a_j e_i} \left(r_j + \sum_{\substack{k=1\\ k\neq j}}^{n} \varepsilon_{jk} \left\| P_{jk} \right\|_\infty \right) (1 - \min_{t\in[0,T]} P_{ij}(t)) \right]. \tag{4.4}$$

This inequality, together with (4.2), proves the result. □

Remark 4.2. To be biologically meaningful in our model, the lower bound in (4.1) must be a positive number. Observe that it is indeed positive if and only if

$$r_i > \sum_{\substack{j=1\\ j\neq i}}^{n} \left[\frac{\alpha_{ij}}{a_j e_i} \left(r_j + \sum_{\substack{k=1\\ k\neq j}}^{n} \varepsilon_{jk} \left\| P_{jk} \right\|_{\infty} \right) (1 - \min_{t\in[0,T]} P_{ij}(t)) \right].$$

A way to read this inequality is that it is valid whenever the values of the intraspecific competition parameters a_j are large enough in comparison to the rest of parameters. Still, we have not proved that such a coexistence state exists, only that, if it exists, it satisfies the obtained a priori bounds.

5. Stable coexistence state for high values of a_i

This section establishes the existence and asymptotic stability of a unique T-periodic coexistence state for sufficiently large intraspecific competition coefficients. The proof is based on a classical perturbation argument [18] after a convenient re-parametrization. A suitable rescaling is introduced, transforming the model into a perturbation of a decoupled logistic system.

Theorem 5.1. *There exists $a_* > 0$ such that if $a_i > a_*$, $i = 1, 2, \ldots, n$, then System* (2.1) *has a unique asymptotically stable T-periodic coexistence solution.*

Proof. Writing $\lambda_i = \dfrac{1}{a_i}$ and defining $x_i = \lambda_i X_i$ for $i = 1, 2, \ldots, n$ in (2.1), we find the equivalent system

$$X_i'(t, \lambda_i) = X_i (r_i - X_i) + \sum_{\substack{j=1\\ j\neq i}}^{n} \lambda_j \left(\frac{\varepsilon_{ij} X_i X_j}{h_j + \lambda_j X_j} P_{ij}(t) - \frac{\alpha_{ij} X_i X_j}{e_i + \lambda_i X_i} (1 - P_{ij}(t)) \right). \tag{5.1}$$

The Jacobian matrix $J_{\lambda_i}(X_i) = \left[J_{ij} \right]$ of System (5.1) is given by the following components:

$$J_{ii} = r_i - 2X_i + \sum_{\substack{j=1\\ j\neq i}}^{n} \left(\frac{\lambda_j \varepsilon_{ij} P_{ij}(t) X_j}{h_j + \lambda_j X_j} - \frac{\lambda_j e_i \alpha_{ij} (1 - P_{ij}(t)) X_j}{(e_i + \lambda_i X_i)^2} \right),$$

$$J_{ij} = \frac{\lambda_j \varepsilon_{ij} P_{ij}(t) h_j X_i}{(h_j + \lambda_j X_j)^2} - \frac{\lambda_j \alpha_{ij} (1 - P_{ij}(t)) X_i}{e_i + \lambda_i X_i} \quad (j \neq i). \tag{5.2}$$

Observe that for $\lambda_i = 0$, $i = 1, \ldots, n$, the Jacobian matrix is as follows:

$$J_0(X_i) = [J_{ii}] = \operatorname{diag}[r_i - 2X_i]. \tag{5.3}$$

Evaluating (5.3) at the point $r = (r_1, \ldots, r_n)$ yields the following:

$$J_0(r_i) = [J_{ii}] = \operatorname{diag}[-r_i]. \tag{5.4}$$

Thus, the unperturbed part ($\lambda_i = 0$) of System (5.1) has a hyperbolic equilibrium in $r = (r_1, \ldots, r_n)$, which is globally asymptotically stable. By a classical perturbation result (see Theorems 1.1 and 1.2

in [18, Chapter 14]), this means that there exists $\lambda_* > 0$ such that for $\lambda_i < \lambda_*$, System (5.1) possesses a periodic solution with the same stability properties as the equilibrium of the unperturbed system. Such solutions form a continuous branch of asymptotically stable periodic coexistence states in the vector parameter $\lambda = (\lambda_1, \ldots, \lambda_n)$ bifurcating from the equilibrium $r = (r_1, \ldots, r_n)$, and this branch is unique in a neighborhood of $r = (r_1, \ldots, r_n)$.

Uniqueness is established by contradiction. Suppose there exists a sequence $\lambda_m \to (\mathbf{0})$ with $m \to \infty$, and corresponding solutions $(X_i(t, \lambda_m))$, other than the solution mentioned above. Note that the bounds (4.1) in the new variables X_i read as follows:

$$r_i - \sum_{\substack{j=1 \\ j\neq i}}^{n} \left[\frac{\lambda_j \alpha_{ij}}{e_i} \left(r_j + \sum_{\substack{k=1 \\ k\neq j}}^{n} \varepsilon_{jk} \left\| P_{jk}(t) \right\|_\infty \right) (1 - \min P_{ij}(t)) \right] \leq X_i(t) \leq \left(r_i + \sum_{\substack{j=1 \\ j\neq i}}^{n} \varepsilon_{ij} \left\| P_{ij}(t) \right\|_\infty \right). \tag{5.5}$$

Using these uniform bounds in the system, one can prove that the sequence of derivatives $(X_i'(t, \lambda_m))$ is also uniformly bounded, so in consequence $(X_i(t, \lambda_m))$ is equicontinuous. By the Ascoli-Arzelà Theorem, these solutions, being uniformly bounded and equicontinuous, admit a convergent subsequence $\sigma(m)$ as $m \to \infty$. Since $\lambda_{\sigma(m)} \to (\mathbf{0})$, the subsequence tends to a periodic solution of the unperturbed system $(X_i(t, \mathbf{0}))$, i.e., the system with $\lambda_i = 0$. However, the only periodic solution of this unperturbed system is the equilibrium point $r = (r_1, \ldots, r_n)$. Therefore, the subsequence $(X_i(t, \lambda_m))$ must converge to the equilibrium point $r = (r_1, \ldots, r_n)$ as $m \to \infty$. Since it is known that the branch of periodic solutions bifurcating from $(r_1, \ldots, r_n)$ is unique in a neighborhood of this equilibrium, this leads to a contradiction. The existence of another branch of periodic solutions would imply that there is a second, distinct periodic solution in this neighborhood, which is not possible. Consequently, the coexistence state is unique. □

6. A quantitative stability condition for the coexistence state for high values of the intraspecific competition coefficients

Theorem 5.1 establishes the existence of a threshold a_*, but does not provide an explicit estimate of its magnitude. The purpose of this section is to derive an explicit quantitative estimate for a_* to ensure asymptotic stability.

6.1. Mutual invasibility

The Jacobian matrix associated with System (2.1) is

$$J(x) = \left[J_{ij} \right],$$

whose entries are given by the following components:

$$J_{ii} = r_i - 2a_i x_i + \sum_{\substack{j=1 \\ j\neq i}}^{n} \left(\frac{\varepsilon_{ij} P_{ij}(t) x_j}{h_j + x_j} - \frac{e_i \alpha_{ij} (1 - P_{ij}(t)) x_j}{(e_i + x_i)^2} \right),$$

$$J_{ij} = \frac{\varepsilon_{ij} P_{ij}(t) h_j x_i}{(h_j + x_j)^2} - \frac{\alpha_{ij} (1 - P_{ij}(t)) x_i}{e_i + x_i} \qquad (j \neq i). \tag{6.1}$$

In addition to the trivial equilibrium $E_0 = (0, 0, \ldots, 0)$, System (2.1) possesses n semi-trivial equilibria. Note that since the intrinsic growth rates r_i are strictly positive for all species, the trivial equilibrium E_0 acts as a source (fully unstable repeller) in the positive orthant.

Proposition 6.1 (Stability of semi-trivial equilibria for n species)**.** *Consider the semi-trivial equilibrium*

$$E_j = (0, \ldots, 0, x_j^*, 0, \ldots, 0)$$

of System (2.1)*, with* $x_j^* = r_j/a_j$ *and* $j = 1, 2, \ldots, n$*. For each* $i \neq j$*, define the threshold*

$$P_{ij}^* = \frac{\dfrac{\alpha_{ij} r_j}{a_j e_i} - r_i}{\dfrac{\varepsilon_{ij} r_j}{a_j h_j + r_j} + \dfrac{\alpha_{ij} r_j}{a_j e_i}}, \qquad \overline{P}_{ij} = \frac{1}{T}\int_0^T P_{ij}(t)\, dt. \tag{6.2}$$

Then, E_j *is a local attractor in the* x_i*-direction if* $\overline{P}_{ij} < P_{ij}^*$*, and unstable (saddle point) in the* x_i*-direction if* $\overline{P}_{ij} > P_{ij}^*$*.*

Proof. Without loss of generality, we consider the semi-trivial equilibrium $E_j = (0, \ldots, 0, x_j^*, 0, \ldots, 0)$, where only the j-th species persists with density $x_j^* = r_j/a_j$, while all other $n-1$ species are absent. E_j has the same stability character as the origin of the linearized system

$$\dot{z} = A(t)z, \tag{6.3}$$

where $z = (\tilde{z}_1, \ldots, \tilde{z}_n)^T$, and $A(t) = J(E_j)$ represents the Jacobian matrix (6.1) evaluated at E_j.

Let us examine the structure of the coefficients of the matrix $A(t) = [a_{kh}(t)]$. For any absent species $k \neq j$, the corresponding vector field in the multi-species system (2.1) contains the population density x_k as a factoring multiplier. Consequently, the partial derivative of the k-th equation with respect to any other absent species $h \neq j$ (with $h \neq k$) evaluated at the boundary where $x_k = 0$ vanishes identically. This means that $a_{kh}(t) = 0$ for all $k \neq j$ and $h \neq j$ whenever $k \neq h$.

Since the coefficient matrix $A(t)$ displays this decoupled block structure for the sub-community of the $n-1$ absent species, the first-order linear equations for each absent species completely separate from one another and read as follows:

$$\dot{\tilde{z}}_i = a_{ii}(t)\tilde{z}_i, \qquad \text{for } i \neq j. \tag{6.4}$$

By evaluating the diagonal entries J_{ii} from the Jacobian matrix (6.1) at the semi-trivial state E_j, we substitute $x_j = x_j^* = r_j/a_j$ and $x_m = 0$ for all $m \neq j$. Since the absent species i satisfies $x_i = 0$ at E_j, the summation reduces to the single interaction with species j, yielding the following:

$$a_{ii}(t) = r_i + \frac{\varepsilon_{ij} P_{ij}(t)\left(\dfrac{r_j}{a_j}\right)}{h_j + \dfrac{r_j}{a_j}} - \frac{\alpha_{ij}(1 - P_{ij}(t))\left(\dfrac{r_j}{a_j}\right)}{e_i}.$$

Clearing the complex fractions by multiplying the numerator and denominator of the positive interaction term by a_j, and algebraic rearrangement of the negative interaction term leads to the following:

$$a_{ii}(t) = r_i + \frac{r_j \varepsilon_{ij} P_{ij}(t)}{a_j h_j + r_j} - \frac{r_j \alpha_{ij}(1 - P_{ij}(t))}{a_j e_i}. \tag{6.5}$$

It is known that the solution of this first-order equation is given by

$$\tilde{z}_i(t) = \tilde{z}_i(0)e^{\int_0^t a_{ii}(s)ds},$$

which tends to 0 (resp. ∞) as $t \to \infty$ if and only if $\overline{a_{ii}} < 0$ (resp. $\overline{a_{ii}} > 0$). To determine the stability conditions in the x_i-direction, we compute the average of $a_{ii}(t)$ over one period by integrating (6.5) and using $\overline{P}_{ij} = \frac{1}{T}\int_0^T P_{ij}(t)dt$:

$$\overline{a_{ii}} = r_i + \frac{r_j\varepsilon_{ij}\overline{P}_{ij}}{a_jh_j + r_j} - \frac{r_j\alpha_{ij}(1-\overline{P}_{ij})}{a_je_i}.$$

Setting $\overline{a_{ii}} = 0$ and solving for $\overline{P}_{ij}$, the critical threshold value exactly matches P^*_{ij} as defined in (6.2):

$$P^*_{ij} = \frac{\dfrac{\alpha_{ij}r_j}{a_je_i} - r_i}{\dfrac{\varepsilon_{ij}r_j}{a_jh_j + r_j} + \dfrac{\alpha_{ij}r_j}{a_je_i}}. \tag{6.6}$$

Thus, if $\overline{P}_{ij} > P^*_{ij}$, then $\overline{a_{ii}} > 0$, which implies that $\tilde{z}_i(t) \to \infty$. By the linear approximation of Lyapunov, the equilibrium point E_j is a saddle point (with the stable manifold containing the sub-community axes).

Conversely, if $\overline{P}_{ij} < P^*_{ij}$ for all $i \neq j$, then $\overline{a_{ii}} < 0$, and $\tilde{z}_i(t) \to 0$ exponentially for each absent species. Next, consider the remaining equation for species j in the linearized system (6.3), which reads as follows:

$$\dot{\tilde{z}}_j = -r_j\tilde{z}_j + \sum_{\substack{i=1\\ i\neq j}}^{n} a_{ji}(t)\tilde{z}_i, \tag{6.7}$$

Since the off-diagonal coupling coefficients $a_{ji}(t)$ are continuous and periodic (hence bounded on $\mathbb{R}$), $r_j > 0$, and $\tilde{z}_i(t) \to 0$ as $t \to \infty$ for all $i \neq j$, an application of Gronwall's inequality to the non-homogeneous expression (6.7) shows that any solution $\tilde{z}_j(t)$ tends to 0 as $t \to \infty$. All of the above assures us that the origin of the linearized system is asymptotically stable. Therefore, by the application of the standard Lyapunov stability results for periodic systems, the point E_j acts as a local attractor, and the proof is done. □

Remark 6.2. The above proposition characterizes the stability of the semi-trivial equilibria in terms of the thresholds P^*_{ij} and the mean values $\overline{P}_{ij}$ of the switching functions. In particular, if $\overline{P}_{ij} > P^*_{ij}$ for all $i, j = 1, \ldots, n$, then each species can invade any semi-trivial equilibrium where it is absent. This condition, known as **mutual invasibility**, is a well-known ecological notion (see for instance [9, 19, 20]). The mutual invasibility condition $\overline{P}_{ij} > P^*_{ij}$ suggests that the boundary dynamics are repelling and therefore provides evidence for persistence. Rigorously establishing persistence would require verification of the hypotheses of an appropriate persistence theorem for periodic Kolmogorov systems, which lies beyond the scope of the present work.

6.2. Quantitative existence of a coexistence state

In the previous subsection, conditions for mutual invasibility are derived. However, mutual invasibility is generally necessary but not sufficient for coexistence in multispecies communities [21]. The

objective of this subsection is to present an alternative proof for the existence of at least one T-periodic coexistence solution.

For convenience, let us call

$$m_i = \frac{r_i}{a_i} - \sum_{\substack{j=1 \\ j\neq i}}^{n} \left[\frac{\alpha_{ij}}{a_i a_j e_i} \left(r_j + \sum_{\substack{k=1 \\ k\neq j}}^{n} \varepsilon_{jk} \left\| P_{jk} \right\|_\infty \right) (1 - \min_{t\in[0,T]} P_{ij}(t)) \right]$$

and

$$M_i = \frac{1}{a_i} \left(r_i + \sum_{\substack{j=1 \\ j\neq i}}^{n} \varepsilon_{ij} \left\| P_{ij} \right\|_\infty \right)$$

the lower and upper bounds, respectively, derived in Proposition 4.1 for any eventual periodic coexistence state.

Proposition 6.3. *Assume that $m_i > 0$ for any $i = 1, \dots, n$. Then, System* (2.1) *has at least one T-periodic coexistence solution.*

Proof. The method of proof relies on a classical continuation theorem for periodic perturbations of autonomous systems [22, Theorem 2]. First, System (2.1) is embedded into the homotopic system

$$x_i' = x_i (r_i - a_i x_i) + \lambda \sum_{\substack{j=1 \\ j\neq i}}^{n} \left(x_i \frac{\varepsilon_{ij} x_j}{h_j + x_j} P_{ij}(t) - x_i \frac{\alpha_{ij} x_j}{e_i + x_i} (1 - P_{ij}(t)) \right), \tag{6.8}$$

where $\lambda \in [0, 1]$ is a deformation parameter that drives the original system (for $\lambda = 1$) into the system of decoupled logistic equations (for $\lambda = 0$). We can write this system as follows:

$$x' = f(t, x, \lambda), \tag{6.9}$$

where

$$f(t, x, 0) = f_0(x) = (x_1 (r_1 - a_1 x_1), \dots, x_n (r_n - a_n x_n)).$$

Define the set:

$$\Omega = \{x = (x_1, \dots, x_n) \in C_T^n \ : \ m_i < x_i(t) < M_i \text{ for every } t \in [0, T]\}.$$

The set Ω is open and bounded in the Banach space C_T^n endowed with the uniform norm. Using Proposition 4.1, any eventual T-periodic solution of the homotopic system (6.9) verifies the uniform bounds $m_i < x_i(t) < M_i$ for every $t \in [0, T]$ and $i = 1, \dots, n$. It is important to remark that the bounds obtained do not explicitly depend on the parameter λ. Thus, Ω does not contain T-periodic solutions of (6.9) in its frontier, and the homotophy is said to be admissible. Then, [22, Theorem 2] establishes that a sufficient condition for the existence of at least one T-periodic solution of (2.1) belonging to $\overline{\Omega}$ is

$$d_B(f_0, \Omega \cap \mathbb{R}^n, 0) \neq 0,$$

where d_B denotes the Brouwer degree. Notice the only zero of the function f_0 belonging to $\Omega \cap \mathbb{R}^n$ is $\xi = (r_1/a_1, \dots, r_n/a_n)$. Then, an elementary computation gives

$$d_B(f_0, \Omega \cap \mathbb{R}^n, 0) = sgn \det J f_0(\xi) = (-1)^n,$$

and the result is proven. □

6.3. Quantitative condition for stability of the coexistence state

From now on, we consider conditions that ensure the existence of a coexistence periodic solution. For the main result of this section, we define the following quantities;

$$L_i = \frac{2r_i}{S_i + 2C_i}, \quad \text{for } i = 1, 2, \ldots, n, \tag{6.10}$$

where S_i, C_i are given by

$$\begin{aligned} S_i &= \sum_{\substack{j=1 \\ j\neq i}}^{n} \left|F_{ij}\right|, \\ C_i &= \sum_{\substack{j=1 \\ j\neq i}}^{n} \left(r_j + \sum_{\substack{k=1 \\ k\neq j}}^{n} \varepsilon_{jk}\|P_{jk}\|_\infty \right) \left[\frac{2\alpha_{ij}}{e_i} + \frac{\varepsilon_{ij}\|P_{ij}\|_\infty}{h_j} \right], \end{aligned} \tag{6.11}$$

and

$$F_{ij} = \frac{\varepsilon_{ij}\|P_{ij}\|_\infty}{h_j} \left(r_i + \sum_{\substack{k=1 \\ k\neq i}}^{n} \varepsilon_{ik}\|P_{ik}\|_\infty \right) + \frac{\varepsilon_{ji}\|P_{ji}\|_\infty}{h_i} \left(r_j + \sum_{\substack{k=1 \\ k\neq j}}^{n} \varepsilon_{jk}\|P_{jk}\|_\infty \right). \tag{6.12}$$

Theorem 6.4. *Let us assume that the constant*

$$a_* = \max\left\{\frac{1}{L_i}\right\} \tag{6.13}$$

is well-defined and positive. If $a_i > a_*$, $i = 1, 2, \ldots, n$, then System (2.1) *has a unique asymptotically stable positive coexistence state.*

Proof. As in Section 5, we introduce the reparametrization and change of variables $\lambda_i = \frac{1}{a_i}$, $x_i = \lambda_i X_i$ in (2.1) and consider the equivalent system (5.1). Such system has a coexistence state (X_i) and the linearized system is of the following form:

$$\dot{\mathbf{z}} = B_{\lambda_i}(t)\mathbf{z} \tag{6.14}$$

where $B_{\lambda_i}(t) = J_{\lambda_i}(X_i) = \left[b_{ij}(t, \lambda_i)\right]$ is the Jacobian matrix described in (5.2). The objective is to prove that there exists a computable λ_* such that (6.14) verifies conditions (3.6) and (3.7) of Corollary 3.3 for any $0 < \lambda_i < \lambda_*$.

First, observe that

$$\begin{aligned} b_{ii} &= r_i - 2X_i + \sum_{\substack{j=1\\ j\neq i}}^{n}\left(\frac{\lambda_j\varepsilon_{ij}P_{ij}(t)X_j}{h_j+\lambda_jX_j} - \frac{\lambda_j e_i\alpha_{ij}(1-P_{ij}(t))X_j}{(e_i+\lambda_iX_i)^2}\right)\\ &< r_i - 2X_i + \sum_{\substack{j=1\\ j\neq i}}^{n}\frac{\lambda_j\varepsilon_{ij}P_{ij}(t)X_j}{h_j+\lambda_jX_j}\\ &< r_i - 2X_i + \sum_{\substack{j=1\\ j\neq i}}^{n}\frac{\lambda_j\varepsilon_{ij}\|P_{ij}(t)\|_\infty X_j}{h_j}\\ &< r_i - 2\left(r_i - \sum_{\substack{j=1\\ j\neq i}}^{n}\left[\frac{\lambda_j\alpha_{ij}}{e_i}\left(r_j+\sum_{\substack{k=1\\ k\neq j}}^{n}\varepsilon_{jk}\|P_{jk}\|_\infty\right)(1-\min P_{ij}(t))\right]\right) +\\ &+ \sum_{\substack{j=1\\ j\neq i}}^{n}\frac{\lambda_j\varepsilon_{ij}\|P_{ij}\|_\infty}{h_j}\left(r_j+\sum_{\substack{k=1\\ k\neq j}}^{n}\varepsilon_{jk}\|P_{jk}\|_\infty\right), \end{aligned}$$

where the last inequality was obtained using the derived bounds in (5.5). Then, the upper bound for the diagonal elements b_{ii} is as follows:

$$b_{ii} < -r_i + \sum_{\substack{j=1\\ j\neq i}}^{n}\lambda_j\left(r_j+\sum_{\substack{k=1\\ k\neq j}}^{n}\varepsilon_{jk}\|P_{jk}(t)\|_\infty\right)\left[\frac{2\alpha_{ij}}{e_i}+\frac{\varepsilon_{ij}\|P_{ij}(t)\|_\infty}{h_j}\right]. \tag{6.15}$$

Now, we derive upper bounds for $|b_{ij}+b_{ji}|$, with $j\neq i$, as follows:

$$\begin{aligned} |b_{ij}+b_{ji}| &= \left|\frac{\lambda_j\varepsilon_{ij}P_{ij}(t)h_jX_i}{(h_j+\lambda_jX_j)^2} - \frac{\lambda_j\alpha_{ij}(1-P_{ij}(t))X_i}{e_i+\lambda_iX_i} + \frac{\lambda_i\varepsilon_{ji}P_{ji}(t)h_iX_j}{(h_i+\lambda_iX_i)^2} - \frac{\lambda_i\alpha_{ji}(1-P_{ji}(t))X_j}{e_j+\lambda_jX_j}\right|\\ &< \left|\frac{\lambda_j\varepsilon_{ij}P_{ij}(t)h_jX_i}{(h_j+\lambda_jX_j)^2} + \frac{\lambda_i\varepsilon_{ji}P_{ji}(t)h_iX_j}{(h_i+\lambda_iX_i)^2}\right|\\ &< \frac{\lambda_j\varepsilon_{ij}P_{ij}(t)h_jX_i}{(h_j+\lambda_jX_j)^2} + \frac{\lambda_i\varepsilon_{ji}P_{ji}(t)h_iX_j}{(h_i+\lambda_iX_i)^2}\\ &< \frac{\lambda_j\varepsilon_{ij}\|P_{ij}(t)\|_\infty X_i}{h_j} + \frac{\lambda_i\varepsilon_{ji}\|P_{ji}(t)\|_\infty X_j}{h_i}\\ &< \lambda_j\frac{\varepsilon_{ij}\|P_{ij}(t)\|_\infty}{h_j}\left(r_i+\sum_{\substack{k=1\\ k\neq i}}^{n}\varepsilon_{ik}\|P_{ik}(t)\|_\infty\right) + \lambda_i\frac{\varepsilon_{ji}\|P_{ji}(t)\|_\infty}{h_i}\left(r_j+\sum_{\substack{k=1\\ k\neq j}}^{n}\varepsilon_{jk}\|P_{jk}(t)\|_\infty\right), \end{aligned} \tag{6.16}$$

where (5.5) has been used once more.

It remains to verify conditions (3.6) and (3.7) of Corollary 3.3. In particular, we will use the upper bounds from (6.15) to guarantee that $b_{ii} < 0$, or equivalently, that $-b_{ii} > 0$. Additionally, we apply the upper bounds derived in (6.16). Thus,

$$-b_{ii} > r_i - \sum_{\substack{j=1 \\ j\neq i}}^{n} \lambda_j \left(r_j + \sum_{\substack{k=1 \\ k\neq j}}^{n} \varepsilon_{jk} \|P_{jk}(t)\|_\infty \right) \left[\frac{2\alpha_{ij}}{e_i} + \frac{\varepsilon_{ij}\|P_{ij}(t)\|_\infty}{h_j} \right]. \tag{6.17}$$

If $\lambda_i, \lambda_j < A$ (to be defined later) for all $i, j = 1, 2, 3, \ldots, n$ with C_i, F_{ij}, S_i defined in (6.11) and (6.12), then $-b_{ii} > r_i - AC_i$ and $|b_{ij} + b_{ji}| < AF_{ij}$. Consequently,

$$\begin{aligned} -2b_{ii}(t) &> \sum_{\substack{j=1 \\ j\neq i}}^{n} |b_{ij}(t) + b_{ji}(t)|, \\ 2(r_i - AC_i) &> \sum_{\substack{j=1 \\ j\neq i}}^{n} AF_{ij}, \\ 2r_i - 2AC_i &> AS_i, \\ A &< \frac{2r_i}{S_i + 2C_i} = L_i. \end{aligned} \tag{6.18}$$

Combining the previous estimates, Theorem 6.4 holds for

$$\lambda_i < \lambda_* = \min\{L_i\}$$

which is the same as saying, if

$$a_i > a_* = \max\left\{\frac{1}{L_i}\right\}.$$

□

7. Particular cases

In this section, we derive explicit expressions for the stability threshold in the cases $n = 2$ and $n = 3$, and illustrate the results with numerical examples.

7.1. Case n = 2

For $n = 2$, the stability condition given in Theorem 6.4 can be explicitly computed. Using (6.10) and (6.13), we obtain that

$$L_1 = \frac{2r_1}{S_1 + 2C_1}, \quad L_2 = \frac{2r_2}{S_2 + 2C_2}, \tag{7.1}$$

where

$$S_1 = |F_{12}|, \quad S_2 = |F_{21}|, \tag{7.2}$$

and

$$F_{12} = \frac{\varepsilon_{12}\|P_{12}\|_\infty}{h_2}(r_1 + \varepsilon_{12}\|P_{12}\|_\infty) + \frac{\varepsilon_{21}\|P_{21}\|_\infty}{h_1}(r_2 + \varepsilon_{21}\|P_{21}\|_\infty), \tag{7.3}$$

$$F_{21} = \frac{\varepsilon_{21}\|P_{21}\|_\infty}{h_1}(r_2 + \varepsilon_{21}\|P_{21}\|_\infty) + \frac{\varepsilon_{12}\|P_{12}\|_\infty}{h_2}(r_1 + \varepsilon_{12}\|P_{12}\|_\infty), \tag{7.4}$$

$$C_1 = (r_2 + \varepsilon_{21}\|P_{21}\|_\infty)\left[\frac{2\alpha_{12}}{e_1} + \frac{\varepsilon_{12}\|P_{12}\|_\infty}{h_2}\right], \tag{7.5}$$

$$C_2 = (r_1 + \varepsilon_{12}\|P_{12}\|_\infty)\left[\frac{2\alpha_{21}}{e_2} + \frac{\varepsilon_{21}\|P_{21}\|_\infty}{h_1}\right]. \tag{7.6}$$

Thus, the threshold value a_* is

$$a_* = \max\left\{\frac{1}{L_1}, \frac{1}{L_2}\right\}. \tag{7.7}$$

The following parameter values are considered for illustration. The values $r_1 = r_2 = 1$, $e_1 = e_2 = h_1 = h_2 = 50$ were used in numerical simulations shown in [6]. Additionally, we consider $\|P_{12}\|_\infty = \|P_{21}\|_\infty = 1$. Using these values into (6.13), the resulting values of a_* are reported in the following table.

Table 1. Values of parameters and resulting a_*.

α_{12}	α_{21}	ε_{12}	ε_{21}	a_*
0.1	0.1	0.1	0.1	0.0088
0.1	0.1	0.9	0.9	0.076
0.1	0.1	0.9	0.1	0.0424
0.9	0.1	0.9	0.1	0.0776
0.9	0.9	0.9	0.9	0.1368

The table shows that, to stabilize two interacting species, strong interspecific interactions, particularly negative ones (i.e., α_{ij} close to 1), require higher intraspecific competition coefficients (i.e., larger values of a_*). From an ecological perspective, this reflects the fact that strong interactions between species must be counterbalanced by sufficiently strong self-regulation mechanisms to ensure a stable coexistence.

To validate the theoretical results, we performed a numerical integration of the system for the parameter values given above. The numerical results are fully consistent with the theoretical predictions (Figure 1).

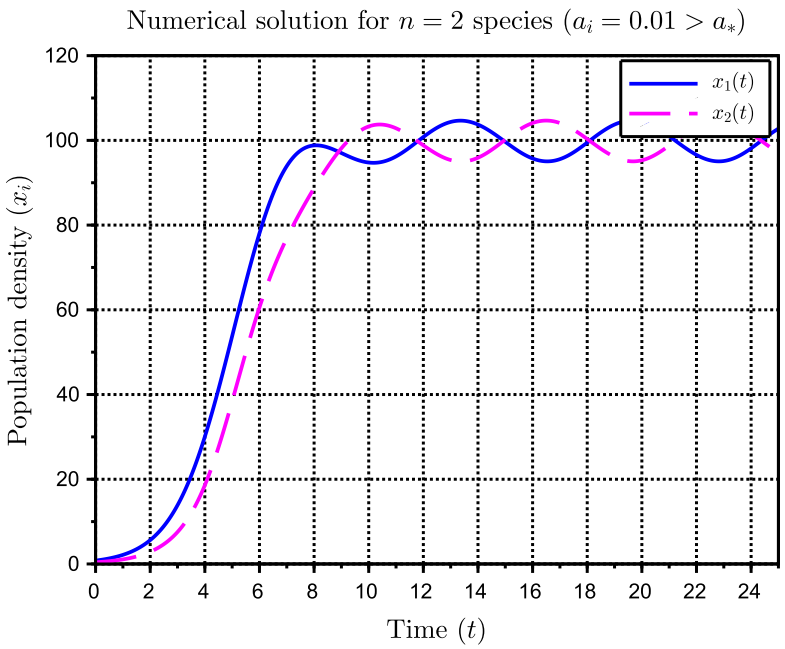

Figure 1. Numerical time series for the two-species scenario ($n = 2$) computed using the parameter values from the first row of Table 1, illustrating the rapid stabilization toward the stable positive periodic orbit. Periodic functions are chosen with distinct phase profiles as $P_{12}(t) = \frac{1}{2}(1 + \cos(t))$ and $P_{21}(t) = \frac{1}{2}(1 - \cos(t))$, with a uniform time average $\overline{P}_{ij} = 0.5$. The intraspecific competition coefficients are fixed at $a_1 = a_2 = 0.01$, satisfying the theoretical stabilization barrier $a_i > a_* = 0.0088$. Trajectories are integrated under the positive initial vector $x(0) = (0.8, 0.4)$

7.2. Case $n = 3$

For $n = 3$, we extend the stability condition from Theorem 6.4. Using the definitions of L_i, S_i, C_i, and F_{ij} given in (6.10), (6.11), and (6.12), we obtain the following:

$$L_1 = \frac{2r_1}{S_1 + 2C_1}, \quad L_2 = \frac{2r_2}{S_2 + 2C_2}, \quad L_3 = \frac{2r_3}{S_3 + 2C_3}, \tag{7.8}$$

where

$$S_1 = |F_{12}| + |F_{13}|, \quad S_2 = |F_{21}| + |F_{23}|, \quad S_3 = |F_{31}| + |F_{32}|, \tag{7.9}$$

and

$$\begin{aligned}
C_1 &= (r_2 + \varepsilon_{21}\|P_{21}\|_\infty + \varepsilon_{23}\|P_{23}\|_\infty)\left(\frac{2\alpha_{12}}{e_1} + \frac{\varepsilon_{12}\|P_{12}\|_\infty}{h_2}\right) \\
&\quad + (r_3 + \varepsilon_{31}\|P_{31}\|_\infty + \varepsilon_{32}\|P_{32}\|_\infty)\left(\frac{2\alpha_{13}}{e_1} + \frac{\varepsilon_{13}\|P_{13}\|_\infty}{h_3}\right), \\
C_2 &= (r_1 + \varepsilon_{12}\|P_{12}\|_\infty + \varepsilon_{13}\|P_{13}\|_\infty)\left(\frac{2\alpha_{21}}{e_2} + \frac{\varepsilon_{21}\|P_{21}\|_\infty}{h_1}\right) \\
&\quad + (r_3 + \varepsilon_{31}\|P_{31}\|_\infty + \varepsilon_{32}\|P_{32}\|_\infty)\left(\frac{2\alpha_{23}}{e_2} + \frac{\varepsilon_{23}\|P_{23}\|_\infty}{h_3}\right), \\
C_3 &= (r_1 + \varepsilon_{13}\|P_{13}\|_\infty + \varepsilon_{12}\|P_{12}\|_\infty)\left(\frac{2\alpha_{31}}{e_3} + \frac{\varepsilon_{31}\|P_{31}\|_\infty}{h_1}\right) \\
&\quad + (r_2 + \varepsilon_{23}\|P_{23}\|_\infty + \varepsilon_{21}\|P_{21}\|_\infty)\left(\frac{2\alpha_{32}}{e_3} + \frac{\varepsilon_{32}\|P_{32}\|_\infty}{h_2}\right);
\end{aligned} \tag{7.10}$$

furthermore,

$$\begin{aligned}
F_{12} &= \frac{\varepsilon_{12}\|P_{12}\|_\infty}{h_2}(r_1 + \varepsilon_{13}\|P_{13}\|_\infty + \varepsilon_{12}\|P_{12}\|_\infty) + \frac{\varepsilon_{21}\|P_{21}\|_\infty}{h_1}(r_2 + \varepsilon_{23}\|P_{23}\|_\infty + \varepsilon_{21}\|P_{21}\|_\infty) = F_{21}, \\
F_{13} &= \frac{\varepsilon_{13}\|P_{13}\|_\infty}{h_3}(r_1 + \varepsilon_{12}\|P_{12}\|_\infty + \varepsilon_{13}\|P_{13}\|_\infty) + \frac{\varepsilon_{31}\|P_{31}\|_\infty}{h_1}(r_3 + \varepsilon_{32}\|P_{32}\|_\infty + \varepsilon_{31}\|P_{31}\|_\infty) = F_{31}, \\
F_{23} &= \frac{\varepsilon_{23}\|P_{23}\|_\infty}{h_3}(r_2 + \varepsilon_{21}\|P_{21}\|_\infty + \varepsilon_{23}\|P_{23}\|_\infty) + \frac{\varepsilon_{32}\|P_{32}\|_\infty}{h_2}(r_3 + \varepsilon_{31}\|P_{31}\|_\infty + \varepsilon_{32}\|P_{32}\|_\infty) = F_{32}.
\end{aligned} \tag{7.11}$$

Thus, the threshold value a_* is

$$a_* = \max\left\{\frac{1}{L_1}, \frac{1}{L_2}, \frac{1}{L_3}\right\}. \tag{7.12}$$

To illustrate this case, we consider specific numerical values. For instance, we fix the values $r_1 = r_2 = r_3 = 1$, $e_1 = e_2 = e_3 = h_1 = h_2 = h_3 = 50$. Then, for $\|P_{12}\|_\infty = \|P_{21}\|_\infty = \|P_{13}\|_\infty = \|P_{31}\|_\infty = \|P_{23}\|_\infty = \|P_{32}\|_\infty = 1$, we can generate the following table

Table 2. Values of parameters and resulting a_* for the case $n = 3$.

α_{12}	α_{21}	α_{13}	α_{31}	α_{23}	α_{32}	ε_{12}	ε_{21}	ε_{13}	ε_{31}	ε_{23}	ε_{32}	a_*
0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.0192
0.1	0.1	0.1	0.1	0.1	0.1	0.9	0.9	0.9	0.9	0.9	0.9	0.224
0.1	0.9	0.1	0.9	0.1	0.9	0.9	0.1	0.9	0.1	0.9	0.1	0.2176
0.9	0.1	0.9	0.1	0.9	0.1	0.9	0.1	0.9	0.1	0.9	0.1	0.2264
0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.4032

This table shows that for $n = 3$, the threshold a_* increases as the intensity of interspecific interactions grows. It is interesting to compare with Table 1 for two species. Even a few strong interactions are enough to raise a_*, and when all interactions are strong, the system requires very high intraspecific competition to stabilize. Ecologically, this reflects that in multispecies communities, the combined effect of multiple interactions amplifies the pressure on populations, so stronger self-regulation is needed for stable coexistence.

As in the case of $n = 2$, it is easy to implement a numerical integration of the system (Figure 2).

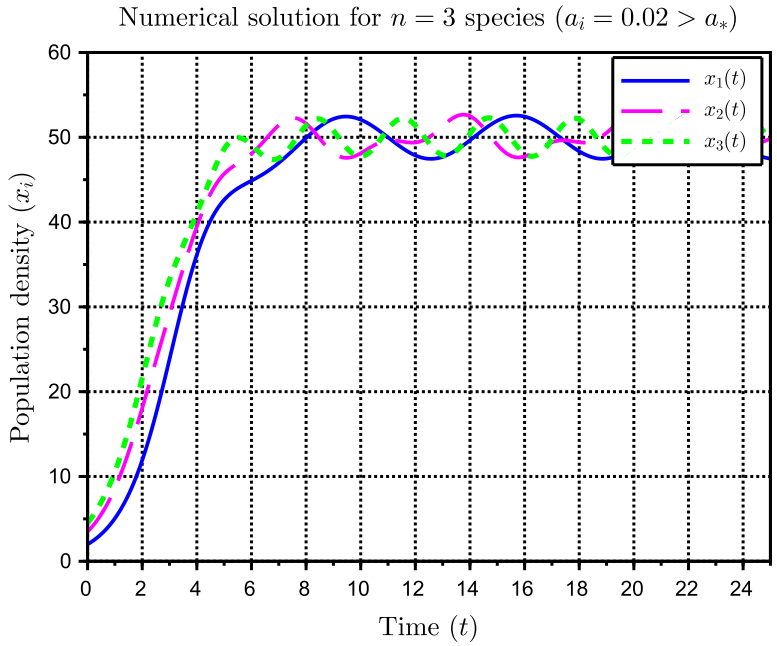

Figure 2. Numerical time series for the three-species community ($n = 3$) computed using the parameter values from the first row of Table 2. The periodic functions are as follows: $P_{12}(t) = \frac{1}{2}(1 + \sin(t))$, $P_{21}(t) = \frac{1}{2}(1 + \cos(t))$, $P_{13}(t) = \frac{1}{2}(1 - \cos(t))$, $P_{23}(t) = \frac{1}{2}(1 + \sin(2t))$, and $P_{31}(t) = P_{32}(t) = \frac{1}{2}(1 - \cos(2t))$. Intraspecific competition coefficients are set above the analytical threshold to $a_1 = a_2 = a_3 = 0.02 > a_* = 0.0192$. Solutions are computed starting from the positive initial distribution $x(0) = (2.0, 3.5, 4.5)$

8. Conclusions

The main result of this paper, stated in Theorem 5.1, establishes that a broad class class of periodic multispecies systems with a continuous spectrum of interaction outcomes admits a simple and robust mechanism for stable coexistence. If the intraspecific self-regulation coefficients exceed a computable bound a_*, then there exists a unique T-periodic coexistence state that is asymptotically stable. This result rigorously extends previous knowledge on the two-species theory and confirms the central role of intraspecific regulation in sustaining coexistence under temporally variable interactions.

The numerical examples presented for $n = 2$ and $n = 3$ illustrate that the threshold a_* increases with the strength of negative interactions and the number of interacting species. Ecologically, this highlights that multispecies communities are inherently more sensitive to strong antagonistic interactions, and that the combined effect of multiple interactions amplifies the requirement for self-regulation. In other words, the larger the community or the stronger the interspecific effects, the more robust the intraspecific density dependence must be to maintain a stable coexistence.

From a theoretical perspective, the framework developed here provides a quantitative tool to predict coexistence in complex ecological networks with temporally varying interaction outcomes. Overall, the results reinforce the ecological principle that self-regulation is a key driver of stability, and show that this principle remains valid and quantitatively tractable when moving from two-species to multispecies communities with interactions that periodically vary in their outcomes.

Use of AI tools declaration

The authors declare they have not used Artificial Intelligence (AI) tools in the creation of this article.

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Conflict of interest

The authors declare there is no conflict of interest.

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