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Modeling exploitation and interference competition: The impact of almost periodic dynamics on species coexistence

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Abstract. An almost periodic competition model, in which the population growth of two species depends on shared and/or exclusive resources, shows scenarios of coexistence or exclusion. We prove the existence and uniqueness of a global almost periodic attractor for the model when certain conditions on the parameters are satisfied. In contrast, if such conditions do not hold, the model presents either two simultaneous coexistence scenarios, or the exclusion of one species. We also analyze simplified versions of the proposed model that show a wide variety of ecologically relevant scenarios. Furthermore, a global sensitivity analysis using Sobol indices reveals that the model is highly additive, implying that the parameter variances propagate linearly. The threshold condition is strongly governed by the parameters associated with resource exploitation and intraspecific regulation rates. Through numerical simulations, we show that modeling almost periodic competition dynamics with periodic models can lead to misleading scenarios of long-term population sizes. This is concluded because the solutions in the almost periodic case and the periodic one present significant differences. Forecasting the possible scenarios that occur when asynchronous competition interactions are modeled can be a useful tool for the conservation decision-makers.

Key Words and Phrases: Exploitation competition, interference competition, almost periodic function, cooperative systems.

2020 Mathematics Subject Classifications: 34C12, 34C27, 94D25

1. Introduction

Climate-mediated shifts are altering relevant seasonal variables whose changes negatively impacting the interactions among predators and their prey, mutualistic partners and competing species. These perturbations in environmental drivers can change some ecological interactions. For example, deer adjust their behavior to manage predation risk, prioritizing evasion and foraging based on factors like forest cover, snow and plant phenology. During milder times, deer have more freedom to counter predators, but in winter, their responsiveness is reduced due to food scarcity and other factors. This suggests that predator-prey interactions vary seasonally in seasonal environments [8]. In plants, phenological traits such as flowering time and emergence can exhibit temperature sensitivity, leading to disruptions in seasonally-timed species interactions [16]. For example, climate-driven changes in flowering phenology can result in temporal mismatches between mutualistic species such as plants and their pollinators [31]. A classic example of seasonal competition is provided by squirrels competing for nuts. In this case, the fitness of squirrels depends largely on the quantity of nuts. However, if a large squirrel hoards most of the nuts, adding more nuts will provide little benefit to other squirrels because it will result in greater hoarding by the large squirrel [57].

Changes in environmental factors can alter the population densities or affect competitive abilities of species. In particular, interspecific competition is a force that structures

communities (e.g., in carnivores, [37, 4]). Wherever ecologically similar species are sympatric, competition can occur over shared limited resources with varying levels of intensity, depending on the similarity of ecological niches [55, 39, 6], which poses a risk to biodiversity. Temperature fluctuations can exert a profound impact on the biology and behavior of living organisms. For instance, temperature can modulate the metabolic rates of ectothermic species and the energetic requirements of endothermic organisms, thereby influencing activity patterns, survival rates, individual growth, and reproductive success [20, 42]. This, in turn, can alter species encounter rates, potentially due to individuals avoiding thermal stress or increasing foraging efforts to meet their metabolic demands. Notably, each species possesses a unique physiological optimum and responds differently to abiotic conditions, which can yield disparate effects on species within a community [23]. Furthermore, temperature-mediated changes can influence the outcome of interspecific interactions by modifying body size and other biological traits [56].

An example of how asynchronous environmental fluctuations shape species interactions is observed in the competition for nest sites between the resident great tit (*Parus major*) and the migratory pied flycatcher (*Ficedula hypoleuca*). Because climate warming desynchronizes their phenologies, the arrival of the migratory bird critically coincides with the resident's peak laying period, whose territorial aggressiveness and winter abundance increase, significantly elevating mortality due to within-guild competition [43].

This loss of synchrony and its ecological consequences have been extensively documented across various types of species interactions. For instance, in [26], it is analyzed the phenological response to climate change in 54 pairwise trophic interactions, demonstrating widespread shifts between consumers and their respective food species. Beyond antagonistic interactions, climate-mediated mismatches also threaten mutualistic species, hosts and parasitoids and prey and predators [36, 40, 10].

Classically, two forms of competition have been described [6, 49]. Exploitation competition is an indirect form of competition where competitors negatively affect each other by depleting a shared resource, with its strength determined by spatiotemporal patterns of resource abundance [24, 35, 34, 49, 53, 25]. Interference competition, on the other hand, is a direct form of competition where individuals prevent others from accessing resources, ranging from passive blocking to interspecific killing [2, 48]. This type of competition can occur aggressively (e.g., hoarding, defense) or passively (e.g., collisions), and its strength increases with competitor density, potentially independent of resource availability [47, 7, 24, 1].

A fundamental question that remains unanswered is whether the relative strength of interference competition remains fixed for a given population at a specific time and place or whether it varies with population density [11]. There is little consensus in the literature on the nature of the relationship between the relative strength of interference competition and consumer density. Some studies suggest that interference competition is only significant at unusually high consumer densities [18], while others find significant effects across a wide range of densities, including low densities. In [12], it is shown that the strength of interference competition and exploitation competition had an inverse relationship in populations of *Didinium* feeding on *Paramecium* but did not propose any mechanism to explain why this might be the case. In this context, models of exploitation competition assume that consumers encounter resources randomly at a rate proportional to resource density [28, 54]. An increase in resources will result in an increase in encounter rates. However, interference competition becomes more important when consumer behavior affects encounter rates regardless of resource availability [24, 1].

Competition between species has been analyzed through systems of differential equations. From the model proposed independently by Lotka (1924) and Volterra (1931) [3], there are models that describe the population dynamics using constant rates, density-dependent rates, periodic rates, and almost periodic rates [47, 45, 46, 44, 41, 17, 63, 59, 60, 29, 30, 33, 21, 22, 61, 62, 52]. However, in order to overcome the limitations of Lotka-Volterra type models, the

works of Schoener [44, 46, 45, 47] introduce new mathematical formulations. These models make it possible to explore four key aspects: the consequences of competing for resources of the same nature, the role of mutual interference, the impact of increasing the abundance of a common resource in systems dominated by interference, and the patterns that give rise to multiple equilibria. Each one of these models might capture ecological, demographic, or environmental mechanisms that are relevant for the decision makers on biodiversity and conservation issues.

From a modeling perspective, seasonal population dynamics are described by periodic or almost periodic models. However, modeling seasonal dynamics of interacting species with periodic models is very restrictive because changes in environmental factors can disturb the periodic rates in a way that each of them is given by periodic functions that do not have a common period. In such a case, almost periodic models are preferred. In particular, simplified versions of Schoener's model have been proposed to analyze seasonal effects on the coexistence of competing species [60, 29, 19, 61, 32, 38]. To do this, the authors use periodic or almost periodic rates. In these works, the models consider intra-and interspecific competition, maintenance and replacement costs, and assume that each species has an exclusive resource. These models generalize, in a sense, Schoener's model since they consider discrete, time-varying delays, as well as impulsive effects, and harvesting. The authors show results concerning the existence and uniqueness of almost periodic solutions, but they do not analyze their results from an ecological perspective. In particular, these works do not analyze the consequences of resource sharing among the species.

In this work, we propose a two-species model that accounts for both exclusive and shared resources, as well as intra- and interspecific competition, and maintenance and replacement costs. In the modeling process, we assume that all ecological and demographic rates involved in the model are given by almost periodic functions that describe environmental factors. The method used in this paper to establish uniqueness and attractivity, based on sub- and super-solutions and involving almost periodic functions, has been previously applied by some of the authors, although only for simpler systems [15, 13]. The main difficulty in applying this method lies in formulating the necessary conditions according to the specific features of this more intricate model. In this paper, we derive such conditions for the proposed model, which incorporates the relevant parameters needed to make the simulations more effective. Through a parameter sensitivity analysis, we show which parameters the model solutions are most sensitive to. Furthermore, we quantitatively show that describing almost periodic dynamics with periodic models can lead to population estimation errors. Through numerical simulations, we show different scenarios of coexistence or exclusion of species associated with the almost periodic model. In particular, we present population scenarios related to the model when certain ecological characteristics are not considered. The results obtained could be used to design public conservation strategies.

2. The Almost Periodic Model

In this section we propose an almost periodic model to describe the population dynamics of competing species, which are denoted by N_1 and N_2. In our proposal, all ecological and demographic rates are considered almost periodic functions, unlike in Schoener's proposal, where rates are considered constant [47]. We consider almost periodic rates to model that climate-mediated shifts affect the population dynamics since the use of almost periodic rates allows for modeling a loss of synchronicity in the ecological interaction due to environmental perturbations.

In the modeling process, we assume that the per capita growth rate of each species is affected by:

- The availability of share and exclusive resources for both species.

- The intraspecific and interspecific competition.

- Maintenance and replacement costs.

- Seasonal effects.

To model how these factors alter the per capita growth rate of each species, we use the terms show in Table 1.

Term	Shared resources **I**	Exclusive resources **II**	Intraspecific competition **III**	Interspecific competition **IV**	Maintenance and replacement costs **V**
Species 1	$\frac{I_{01}(t)}{N_1+\beta(t)N_2}$	$\frac{I_{E_1}(t)}{N_1}$	$\gamma_{11}(t)N_1$	$\gamma_{12}(t)N_2$	$C_1(t)$
Species 2	$\frac{\beta(t)I_{02}(t)}{N_1+\beta(t)N_2}$	$\frac{I_{E_2}(t)}{N_2}$	$\gamma_{22}(t)N_2$	$\gamma_{21}(t)N_1$	$C_2(t)$

Table 1: Terms used in model (1) to describe shared and exclusive resources, as well as inter-and intraspecific competition and metabolic costs.

The seasonal competition model is given by the following coupled system of almost periodic ordinary differential equations:

$$\begin{aligned}\frac{dN_1}{dt} &= N_1\left[\frac{I_{01}(t)}{N_1+\beta(t)N_2}+\frac{I_{E_1}(t)}{N_1}-\gamma_{11}(t)N_1-\gamma_{12}(t)N_2-C_1(t)\right],\\ \frac{dN_2}{dt} &= N_2\left[\frac{\beta(t)I_{02}(t)}{N_1+\beta(t)N_2}+\frac{I_{E_2}(t)}{N_2}-\gamma_{22}(t)N_2-\gamma_{21}(t)N_1-C_2(t)\right].\end{aligned} \tag{1}$$

In model (1), the terms that describe competition for collectively available resources model that each individual of the species N_1 gets a fraction $\frac{1}{N_1+\beta(t)N_2}$ of the overlapping resources, I_{01}, while each individual of the species N_2 gets a fraction $\frac{\beta(t)}{N_1+\beta(t)N_2}$ of the overlapping resources, I_{02}. The function $\beta(t)$ is the per capita effect of N_2 on the per capita growth rate of the species N_1. This function also models the inherent propensity of an individual of the species N_2 to consume the overlapping resources. Both terms $\frac{I_{01}(t)}{N_1+\beta(t)N_2}$ and $\frac{\beta(t)I_{02}(t)}{N_1+\beta(t)N_2}$ are used to model exploitation competition. Notice that, the parameter $\beta(t)$ relates the individual biological mechanism and the population level competitive outcome. In the numerator, $\beta(t)$ acts as resource-use efficiency parameter, where a value of $\beta(t) > 1$ indicates that an individual of species N_2 is more efficient at capturing or harvesting the available resource than an individual of species N_1. In the denominator, this trait translates into a per capita competitive asymmetry. When $\beta(t) > 1$, each individual of species N_2 exerts a consumption and depletion pressure on the system equivalent to more than one individual of species N_1, it is an adaptive advantage of species N_2 that dampens the growth of species N_1. Conversely, when $\beta(t) < 1$, an individual of species N_2 exerts less pressure than an individual of species N_1, effectively favoring the first species. Finally, if $\beta(t) = 1$ at any given time, the system momentarily reduces to a case where both species share identical resource-exploitation efficiencies.

The terms $\frac{I_{E_1}}{N_1}$ and $\frac{I_{E_2}}{N_2}$ describe the effects of exclusive resources on the per capita growth rate of the species N_1 and N_2, respectively. Notice that the larger the population, the less exclusive resources are available to each individual with the addition of another. The terms $\gamma_{ij}(t)N_i$, for $i, j = 1, 2$, describe a density-dependent linear effect on the per capita growth rate of the species i due to intraspecific and interspecific interference. Then, in model (1),

the functions $\gamma_{11}(t)$ and $\gamma_{22}(t)$ are the intraspecific competition rates while $\gamma_{12}(t)$ and $\gamma_{21}(t)$ are the interspecific competition rates. These rates are associated with the interference competition between species. Finally, the terms $C_i(t)$, for $i = 1, 2$, model the effects of the maintenance and replacement costs of an individual of the species i, which are independent of its population density.

3. Almost periodic functions in competitive systems

In this section, we show results on the application of almost periodic functions in competitive systems. We refer the reader to [5, 9] and [50, 51] for a detailed description about almost periodic functions and competitive systems, respectively.

Definition 1. *We say that a continuous function $\phi \in C^0(\mathbb{R})$ is* almost periodic *if every sequence $\{\phi(t + \alpha_n)\}$ of translations of ϕ has a subsequence that converges uniformly in $\mathbb{R}$.*

We denote by $AP(\mathbb{R})$ this set; it is well known that for every $\phi \in AP(\mathbb{R})$, we can associate its Fourier series:

$$\phi \sim \sum_{n\in\mathbb{N}} c(\phi, \lambda_n)e^{i\lambda_n t}$$

as well as a *mean*

$$\mathcal{M}[\phi] := \lim_{T\to\infty} \frac{1}{T}\int_0^T \phi(t)\, dt,$$

which is a linear bounded functional, $\mathcal{M} : AP(\mathbb{R}) \to \mathbb{R}$. The corresponding Parseval's Theorem for almost periodic functions says

$$\mathcal{M}\left[|\phi|^2\right] = \sum_{n\in\mathbb{N}} |c(\phi, \lambda_n)|^2.$$

Define the (IV)-partial order as follows: For every $u = (u_1, u_2), w = (w_1, w_2) \in \mathbb{R}^2$, we say that $u \leq_{IV} w$, if $u_1 \leq w_1$ and $u_2 \geq w_2$. Observe that the condition $u \leq w$ is equivalent to $w - u$ belonging to the IV quadrant of the plane $\mathbb{R}^2$; for example $(3, 5) \leq_{IV} (4, 2)$. If $u_1 < w_1$ and $u_2 > w_2$, then we write $u \ll_{IV} w$. This partial order is explicitly defined in [51].

Consider a system

$$\begin{aligned} \dot{x} &= f_1(t, x(t), y(t)),\\ \dot{y} &= f_2(t, x(t), y(t)), \end{aligned} \tag{2}$$

where f_i are C^1 in an open $D \subset \mathbb{R}^2$ and continuous functions on t. Recall that (2) is said to be a *competitive system* in $\mathbb{R} \times D$ if

$$f_{1y}(t, x, y) \leq 0, \text{ and } f_{2x}(t, x, y) \leq 0, \text{ for all } t \in \mathbb{R}, (x, y) \in D. \tag{3}$$

We say that a pair of differentiable functions $(r(t), s(t))$ is a (IV)-*sub-solution pair* of (2) if

$$\begin{aligned} \dot{r} &\leq f_1(t, r(t), s(t)),\\ \dot{s} &\geq f_2(t, r(t), s(t)), \text{ for all } t. \end{aligned} \tag{4}$$

Similarly the differentiable functions $(R(t), S(t))$ are a (IV)-*super-solution pair* if

$$\begin{aligned} \dot{R} &\geq f_1(t, R(t), S(t)),\\ \dot{S} &\leq f_2(t, R(t), S(t)), \text{ for all } t. \end{aligned} \tag{5}$$

We say that sub- and super-solution pairs are ordered if for all t we have $r(t) < R(t)$ and $s(t) > S(t)$, i.e. if $(r(t), s(t)) \ll_{IV} (R(t), S(t))$.

An important feature for the competitive system (2) related to almost periodic orbits was established in [14], Theorem 3.2. Explicitly, the following result holds.

Theorem 1. *Assume that the system* (2) *has components* f_i, *that are uniformly almost periodic with respect to* $(x, y) \in D$ *of class* C^1 *in* (x, y). *Suppose that it is competitive and has* (IV)*-ordered sub- and super-solution pairs* $(r(t), s(t)) \ll_{IV} (R(t), S(t))$. *If there is no equilibrium point* (x_0, y_0) *such that* $r(t) \leq x_0 \leq R(t)$ *and* $S(t) \leq y_0 \leq s(t)$. *Then the system has an almost periodic solution* $(x(t), y(t))$, *satisfying*

$$r(t) \leq x(t) \leq R(t),\ s(t) \geq y(t) \geq S(t), \quad \text{for all } t \geq 0, \tag{6}$$

such that for every sub- super-solution pair we have

$$r(t) \leq x_0 \leq R(t), \qquad S(t) \leq y_0 \leq s(t).$$

Furthermore, any solution of (2), *with initial condition* $(x(0), y(0))$ *satisfying* $r(0) < x(0) < R(0)$ *and* $s(0) > y(0) > S(0)$, *converges to the product of the strips*

$$(\check{x}(t), \hat{x}(t)) \times (\hat{y}(t), \check{y}(t)),$$

where $(\check{x}(t), \check{y}(t)) \leq_{IV} (\hat{x}(t), \hat{y}(t))$ *are* (IV)*-minimal, maximal almost periodic solutions, respectively.*

4. Results

For an almost periodic function $\phi : \mathbb{R} \to \mathbb{R}$, we denote

$$\phi^- := \inf_{t\in\mathbb{R}} \phi(t) \ \text{ and } \ \phi^+ := \sup_{t\in\mathbb{R}} \phi(t).$$

We recall the following lemma, whose proof can be found in [14].

Lemma 1. *Given two almost periodic functions* ϕ, ψ *such that*

$$\phi(t) \geq \psi(t) \geq 0, \qquad \mathcal{M}[\phi] = \mathcal{M}[\psi].$$

Then $\phi(t) = \psi(t)$ *for every* $t \in \mathbb{R}$.

The following result establishes the existence of almost periodic solutions for (1).

Proposition 1. *Suppose* $I_{0i}(t), I_{E_i}(t), \gamma_{ij}(t), \beta(t), C_i(t) \geq 0$ *are continuous almost periodic functions (not all constant) with* $\gamma_{ij}^-, \beta^-, I_{E_i}^- > 0$ *Then, there exists at least one almost periodic solution* (N_1, N_2) *of* (1) *whose components are positive.*

Proof. A direct computation shows us that system (1) is competitive in $\mathbb{R}^2_{\geq 0}$. We need to prescribe suitable sub- and super-solution pairs. To construct a sub-solution pair, we consider

$$(r(t), s(t)) = \left(\frac{1}{N^2},\ N\right),\ N > 0.$$

These functions satisfy the inequalities in (4), indeed

$$\begin{aligned} \dot{r}(t) = 0 \ &\leq \ \frac{1}{N^2}\left[\frac{I_{01}}{\frac{1}{N^2} + \beta(t)N} + I_{E_1}^- N^2 - \frac{\gamma_{11}(t)}{N^2} - \gamma_{12}(t)N - C_1(t)\right] \qquad (7)\\ &\leq \ \frac{1}{N^2}\left[\frac{I_{01}}{\frac{1}{N^2} + \beta(t)N} + I_{E_1}(t)N^2 - \frac{\gamma_{11}(t)}{N^2} - \gamma_{12}(t)N - C_1(t)\right]. \\ \dot{s}(t) = 0 \ &\geq \ N\left[\frac{\beta(t)I_{02}}{\frac{1}{N^2} + \beta(t)N} + \frac{I_{E_2}(t)}{N} - \gamma_{22}^- N - \frac{\gamma_{21}(t)}{N^2} - C_2(t)\right] \qquad (8) \end{aligned}$$

$$\geq \quad N\left[\frac{\beta(t)I_{02}}{\frac{1}{N^2}+\beta(t)N}+\frac{I_{E_2}(t)}{N}-\gamma_{22}(t)N-\frac{\gamma_{21}(t)}{N^2}-C_2(t)\right].$$

Taking N big enough, then the right side of the first equation in (7) is positive and the right side of the second equation in (7) is negative, thus $(r(t), s(t))$ is a sub-solution pair.

For a super-solution pair, we take

$$(R(t), S(t)) = \left(N,\ \frac{1}{N^2}\right),\ N > 0.$$

These functions verify:

$$\begin{aligned}
\dot{R}(t) = 0 \quad &\geq \quad N\left[\frac{I_{01}(t)}{\frac{1}{N^2}+\beta(t)N}+\frac{I_{E_1}(t)}{N}-\gamma_{11}^{-}N-\frac{\gamma_{12}(t)}{N^2}-C_1(t)\right] \qquad (9)\\
&\geq \quad N\left[\frac{I_{01}(t)}{\frac{1}{N^2}+\beta(t)N}+\frac{I_{E_1}(t)}{N}-\gamma_{11}(t)N-\frac{\gamma_{12}(t)}{N^2}-C_1(t)\right].\\
\dot{S}(t) = 0 \quad &\leq \quad \frac{1}{N^2}\left[\frac{\beta(t)I_{02}(t)}{\frac{1}{N^2}+\beta(t)N}+I_{E_2}^{-}N^2-\frac{\gamma_{22}(t)}{N^2}-\gamma_{21}(t)N-C_2(t)\right] \qquad (10)\\
&\leq \quad \frac{1}{N^2}\left[\frac{\beta(t)I_{02}(t)}{\frac{1}{N^2}+\beta(t)N}+I_{E_2}(t)N^2-\frac{\gamma_{22}(t)}{N^2}-\gamma_{21}(t)N-C_2(t)\right].
\end{aligned}$$

Taking N big enough, they constitute a super-solution pair. Therefore, by Theorem 1 there exists at least one almost periodic solution of the system (1). This concludes the proof of the proposition.

Consider the number

$$\mu := \max\left\{1, \frac{\gamma_{11}^{+}+\gamma_{12}^{+}/\beta^{-}+C_1^{+}}{I_{E_1}^{-}}, \frac{\gamma_{21}^{+}+\gamma_{22}^{+}/\beta^{-}+C_2^{+}}{\beta^{-}I_{E_2}^{-}}\right\}. \qquad (11)$$

Lemma 2. *Suppose $I_{0i}(t), I_{E_i}(t), \gamma_{ij}(t), \beta(t), C_i(t) \geq 0$ are continuous almost periodic functions (not all constant) with $\gamma_{ij}^{-}, \beta^{-}, I_{E_i}^{-} > 0$. Then the set*

$$\Omega := \{(N_1, N_2) \in \mathbb{R}^2_{>0} \ : \frac{1}{N_1+\beta^{-}N_2} \leq \mu\}$$

is positively invariant and a global attractor of system (1) *in $\mathbb{R}^2_{>0}$.*

Proof. For any solution $(N_1(t), N_2(t)) \in \mathbb{R}^2_{>0}$ of (1), we consider the real set

$$A := \left\{t \in \mathbb{R} : \frac{1}{N_1(t)+\beta^{-}N_2(t)} \leq \mu\right\}.$$

We will show that the following statements hold.

1. If $a \in A$, then $[a, \infty) \subset A$.
2. The set A is nonempty.

Let

$$\nu = \frac{\beta^{-}\min\{I_{01}^{-}, (\beta I_{02})^{-}\}}{\beta^{+}}.$$

First, we will prove that

$$\dot{N}_1(t) + \beta^- \dot{N}_2(t) > \nu \tag{12}$$

for each $t \in \mathbb{R} \setminus A$. Indeed, given $t \in \mathbb{R} \setminus A$, we must have

$$\frac{1}{N_1(t) + \beta^- N_2(t)} > \mu = \max\left\{1, \frac{\gamma_{11}^+ + \gamma_{12}^+/\beta^- + C_1^+}{I_{E_1}^-}, \frac{\gamma_{21}^+ + \gamma_{22}^+/\beta^- + C_2^+}{\beta^- I_{E_2}^-}\right\}.$$

Consequently

$$\frac{1}{N_1(t)} > \frac{1}{N_1(t) + \beta^- N_2(t)} \geq \frac{\gamma_{11}^+ + \gamma_{12}^+/\beta^- + C_1^+}{I_{E_1}^-};$$
$$\frac{1}{N_2(t)} > \frac{\beta^-}{N_1(t) + \beta^- N_2(t)} \geq \frac{\gamma_{21}^+ + \gamma_{22}^+/\beta^- + C_2^+}{I_{E_2}^-}.$$

It follows that

$$\frac{I_{E_1}^-}{N_1(t)} - \gamma_{11}^+ - \gamma_{12}^+/\beta^- - C_1^+ > 0 \quad \text{and} \quad \frac{I_{E_2}^-}{N_2(t)} - \gamma_{21}^+ - \gamma_{22}^+/\beta^- - C_2^+ > 0. \tag{13}$$

By replacing (13) in (1), we obtain that

$$\begin{aligned}
\dot{N}_1(t) + \beta^- \dot{N}_2(t) &\geq N_1(t)\left[\frac{I_{01}^-}{N_1(t) + \beta^+ N_2(t)} + \frac{I_{E_1}^-}{N_1(t)} - \gamma_{11}^+ - \gamma_{12}^+/\beta^- - C_1^+\right] \\
&\quad + \beta^- N_2(t)\left[\frac{(\beta I_{02})^-}{N_1(t) + \beta^+ N_2(t)} + \frac{I_{E_2}^-}{N_2(t)} - \gamma_{21}^+ - \gamma_{22}^+/\beta^- - C_2^+\right] \\
&> N_1(t)\left[\frac{I_{01}^-}{N_1(t) + \beta^+ N_2(t)}\right] + \beta^- N_2(t)\left[\frac{(\beta I_{02})^-}{N_1(t) + \beta^+ N_2(t)}\right] \\
&\geq N_1(t)\left[\frac{\beta^+ \nu}{\beta^-(N_1(t) + \beta^+ N_2(t))}\right] + \beta^- N_2(t)\left[\frac{\beta^+ \nu}{\beta^-(N_1(t) + \beta^+ N_2(t))}\right] \\
&= \frac{\beta^+ \nu (N_1(t) + \beta^- N_2(t))}{\beta^-(N_1(t) + \beta^+ N_2(t))} \\
&= \nu \frac{\beta^+ N_1(t)/\beta^- + \beta^+ N_2(t)}{N_1(t) + \beta^+ N_2(t)} \\
&\geq \nu \frac{N_1(t) + \beta^+ N_2(t)}{N_1(t) + \beta^+ N_2(t)} \\
&= \nu.
\end{aligned}$$

To prove case (1), we assume on the contrary that $(a, \infty) \setminus A$ is nonempty. Fix $t \in (a, \infty) \setminus A$ and let $s = \sup((a, t] \cap A)$. It follows that $N_1(s) + \beta^- N_2(s) \geq 1/\mu > N_1(t) + \beta^- N_2(t)$ and by the Mean Value Theorem, $\dot{N}_1(r) + \beta^- \dot{N}_2(r) < 0$ for some $r \in (s, t) \subset \mathbb{R} \setminus A$, contradicting (12). So our initial assumption is false, and this proves (1).

To establish case (2), we proceed by contradiction and assume that A is empty. It follows from (12) that $\dot{N}_1(t) + \beta^- \dot{N}_2(t) > \nu$ for each $t \in \mathbb{R}$. It follows that

$$\frac{d}{dt}\left(\frac{1}{N_1(t) + \beta^- N_2(t)}\right) = -\frac{\dot{N}_1(t) + \beta^- \dot{N}_2(t)}{(N_1(t) + \beta^- N_2(t))^2} < -\mu^2 \nu.$$

for each $t \in \mathbb{R}$. By taking $b = 1/(N_1(0) + \beta^- N_2(0))$ we observe that this last inequality implies that the graph of $1/(N_1(t) + \beta^- N_2(t))$ lies below the graph of the line $l(t) = b - \mu^2 \nu t$, which contradicts our assumption that $(N_1(t), N_2(t)) \in \mathbb{R}^2_{>0}$. This proves case (2).

We are now ready to establish our main result

Theorem 2. *Suppose $I_{0i}(t), I_{E_i}(t), \gamma_{ij}(t) \geq 0$ and $C_i(t) \geq 0$ are continuous almost periodic functions (not all constant) with $\gamma_{ij}^- > 0, \beta^- > 0$ and $I_{E_i}^- > 0$. If*

$$\frac{[\beta^+ I_{01}^+ \mu^2 + \gamma_{12}^-][\beta^+ I_{02}^+ \mu^2 + \gamma_{21}^-]}{\gamma_{11}^- \gamma_{22}^-} < 1, \tag{14}$$

Then, there exists a unique almost periodic solution of (1) in $\mathbb{R}^2_{>0}$ and any other solution with positive initial conditions converges to this almost periodic solution, when $t \to \infty$.

Proof. Proposition 1 implies that the competitive system (1) has at least one almost periodic solution pair (N_1, N_2) whose components are positive. Since the set Ω in Lemma 2 is positively invariant and a global attractor of system (1), the recurrence of any almost periodic solutions implies that $(\hat{N}_1(t), \hat{N}_2(t)) \in \Omega$ for every almost periodic solution (N_1, N_2). Consider a maximal pair $(\hat{N}_1, \hat{N}_2)$ and a minimal pair $(\check{N}_1, \check{N}_2)$ of almost periodic solutions. If we prove that $\hat{N}_1(t) = \check{N}_1(t)$ and $\hat{N}_2(t) = \check{N}_2(t)$, then Theorem 1 implies the uniqueness of an almost periodic solution and that any other solution with positive initial conditions converges to this almost periodic solution, when $t \to \infty$. To prove that $\hat{N}_1(t) = \check{N}_1(t)$ and $\hat{N}_2(t) = \check{N}_2(t)$ we will apply Lemma 1. Note that by the Fundamental Theorem of Calculus, the mean satisfies $\mathcal{M}[\frac{d}{dt}\ln(\hat{N}_i)] = \mathcal{M}\left[\frac{d}{dt}\ln(\check{N}_i)\right] = 0$. Dividing the first equation of the system (1) by N_1 and replacing in the maximal and minimal solutions in the resulting expressions, we obtain the following chain of direct inequalities.

$$\begin{aligned}
& \frac{d}{dt}\ln(\hat{N}_1) - \frac{d}{dt}\ln(\check{N}_1) \\
= & \left[\frac{I_{01}(t)}{\hat{N}_1 + \beta(t)\hat{N}_2} + \frac{I_{E_1}(t)}{\hat{N}_1} - \gamma_{11}(t)\hat{N}_1 - \gamma_{12}(t)\hat{N}_2 - C_1(t)\right] \\
& - \left[\frac{I_{01}(t)}{\check{N}_1 + \beta(t)\check{N}_2} + \frac{I_{E_1}(t)}{\check{N}_1} - \gamma_{11}(t)\check{N}_1 - \gamma_{12}(t)\check{N}_2 - C_1(t)\right] \\
\leq & \frac{I_{01}(t)}{\hat{N}_1 + \beta(t)\hat{N}_2} - \frac{I_{01}(t)}{\check{N}_1 + \beta(t)\check{N}_2} - \gamma_{11}(t)(\hat{N}_1 - \check{N}_1) - \gamma_{12}(t)(\hat{N}_2 - \check{N}_2) \\
= & \frac{I_{01}(t)}{\hat{N}_1 + \beta(t)\hat{N}_2} - \frac{I_{01}(t)}{\hat{N}_1 + \beta(t)\check{N}_2} + \frac{I_{01}(t)}{\hat{N}_1 + \beta(t)\check{N}_2} - \frac{I_{01}(t)}{\check{N}_1 + \beta(t)\check{N}_2} \\
& -\gamma_{11}(t)(\hat{N}_1 - \check{N}_1) - \gamma_{12}(t)(\hat{N}_2 - \check{N}_2) \\
\leq & \frac{I_{01}(t)}{\hat{N}_1 + \beta(t)\hat{N}_2} - \frac{I_{01}(t)}{\hat{N}_1 + \beta(t)\check{N}_2} - \gamma_{11}(t)(\hat{N}_1 - \check{N}_1) - \gamma_{12}(t)(\hat{N}_2 - \check{N}_2) \\
= & \frac{I_{01}(t)\beta(t)(\check{N}_2 - \hat{N}_2)}{(\hat{N}_1 + \beta(t)\hat{N}_2)(\hat{N}_1 + \beta(t)\check{N}_2)} - \gamma_{11}(t)(\hat{N}_1 - \check{N}_1) - \gamma_{12}(t)(\hat{N}_2 - \check{N}_2) \\
\leq & \frac{I_{01}(t)\beta(t)(\check{N}_2 - \hat{N}_2)}{(\hat{N}_1 + \beta(t)\hat{N}_2)^2} - \gamma_{11}(t)(\hat{N}_1 - \check{N}_1) - \gamma_{12}(t)(\hat{N}_2 - \check{N}_2) \\
\leq & I_{01}^+\beta^+\mu^2(\check{N}_2 - \hat{N}_2) - \gamma_{11}^-(\hat{N}_1 - \check{N}_1) - \gamma_{12}^-(\hat{N}_2 - \check{N}_2), \big(\text{since } (\hat{N}_1(t), \hat{N}_2(t)) \in \Omega\big) \\
= & [I_{01}^+\beta^+\mu^2 + \gamma_{12}^-](\check{N}_2 - \hat{N}_2) - \gamma_{11}^-(\hat{N}_1 - \check{N}_1).
\end{aligned}$$

And this inequality implies that

$$\begin{aligned}
0 &\leq \mathcal{M}\left[[I_{01}^+\beta^+\mu^2 + \gamma_{12}^-](\check{N}_2 - \hat{N}_2) - \gamma_{11}^-(\hat{N}_1 - \check{N}_1)\right] \\
\mathcal{M}[\hat{N}_1 - \check{N}_1] &\leq \frac{I_{01}^+\beta^+\mu^2 + \gamma_{12}^-}{\gamma_{11}^-}\mathcal{M}[\check{N}_2 - \hat{N}_2].
\end{aligned} \tag{15}$$

Similarly, we consider the following series of inequalities.

$$\frac{d}{dt}\ln(\check{N}_2) - \frac{d}{dt}\ln(\hat{N}_2)$$

$$
\begin{aligned}
&= \left[\frac{\beta(t)I_{02}(t)}{\check{N}_1+\beta(t)\check{N}_2}+\frac{I_{E_2}(t)}{\check{N}_2}-\gamma_{21}(t)\check{N}_1-\gamma_{22}(t)\check{N}_2-C_2(t)\right]\\
&\quad-\left[\frac{\beta(t)I_{02}(t)}{\hat{N}_1+\beta(t)\hat{N}_2}+\frac{I_{E_2}(t)}{\hat{N}_2}-\gamma_{21}(t)\hat{N}_1-\gamma_{22}(t)\hat{N}_2-C_2(t)\right]\\
&\leq \frac{\beta(t)I_{02}(t)}{\check{N}_1+\beta(t)\check{N}_2}-\frac{\beta(t)I_{02}(t)}{\hat{N}_1+\beta(t)\hat{N}_2}-\gamma_{21}(t)(\check{N}_1-\hat{N}_1)-\gamma_{22}(t)(\check{N}_2-\hat{N}_2)\\
&= \frac{\beta(t)I_{02}(t)}{\check{N}_1+\beta(t)\check{N}_2}-\frac{\beta(t)I_{02}(t)}{\hat{N}_1+\beta(t)\check{N}_2}+\frac{\beta(t)I_{02}(t)}{\hat{N}_1+\beta(t)\check{N}_2}-\frac{\beta(t)I_{02}(t)}{\hat{N}_1+\beta(t)\hat{N}_2}\\
&\quad-\gamma_{21}(t)(\check{N}_1-\hat{N}_1)-\gamma_{22}(t)(\check{N}_2-\hat{N}_2)\\
&\leq \frac{\beta(t)I_{02}(t)}{\check{N}_1+\beta(t)\check{N}_2}-\frac{\beta(t)I_{02}(t)}{\hat{N}_1+\beta(t)\check{N}_2}-\gamma_{21}(t)(\check{N}_1-\hat{N}_1)-\gamma_{22}(t)(\check{N}_2-\hat{N}_2)\\
&= \frac{\beta(t)I_{02}(t)(\hat{N}_1-\check{N}_1)}{(\check{N}_1+\beta(t)\check{N}_2)(\hat{N}_1+\beta(t)\check{N}_2)}-\gamma_{21}(t)(\check{N}_1-\hat{N}_1)-\gamma_{22}(t)(\check{N}_2-\hat{N}_2)\\
&\leq \frac{\beta(t)I_{02}(t)(\hat{N}_1-\check{N}_1)}{(\check{N}_1+\beta(t)\check{N}_2)^2}-\gamma_{21}(t)(\check{N}_1-\hat{N}_1)-\gamma_{22}(t)(\check{N}_2-\hat{N}_2)\\
&\leq \beta^+I_{02}^+\mu^2(\hat{N}_1-\check{N}_1)-\gamma_{21}^-(\check{N}_1-\hat{N}_1)-\gamma_{22}^-(\check{N}_2-\hat{N}_2),\ \big(\text{since } (\check{N}_1(t),\check{N}_2(t))\in\Omega\big)\\
&= [\beta^+I_{02}^+\mu^2+\gamma_{21}^-](\hat{N}_1-\check{N}_1)-\gamma_{22}^-(\check{N}_2-\hat{N}_2).
\end{aligned}
$$

This time we get

$$
\begin{aligned}
0 &\leq \mathcal{M}\left[[\beta^+I_{02}^+\mu^2+\gamma_{21}^-](\hat{N}_1-\check{N}_1)-\gamma_{22}^-(\check{N}_2-\hat{N}_2)\right]\\
\mathcal{M}[\check{N}_2-\hat{N}_2)] &\leq \frac{\beta^+I_{02}^+\mu^2+\gamma_{21}^-}{\gamma_{22}^-}\mathcal{M}[\hat{N}_1-\check{N}_1]. \qquad (16)
\end{aligned}
$$

By combining (15) and (16) we obtain

$$
\mathcal{M}[\hat{N}_1-\check{N}_1]\leq\frac{[\beta^+I_{01}^+\mu^2+\gamma_{12}^-][\beta^+I_{02}^+\mu^2+\gamma_{21}^-]}{\gamma_{11}^-\gamma_{22}^-}\mathcal{M}[\hat{N}_1-\check{N}_1]. \qquad (17)
$$

By the last inequality and condition (14) we must have that $\mathcal{M}[\hat{N}_1]=\mathcal{M}[\check{N}_1]$, therefore by Lemma 1, we obtain $\hat{N}_1=\check{N}_1$, which via equation (16) implies that $\hat{N}_2=\check{N}_2$.

From a biological perspective, the threshold condition (14) can be rigorously interpreted as a requirement for sufficiently strong intraspecific self-regulation relative to interspecific coupling effects. The denominator $\gamma_{11}^-\gamma_{22}^-$ explicitly represents the strength of the self-regulation for each species. Conversely, the numerator captures the effects driven by interspecific interactions (γ_{12}^- and γ_{21}^-), amplified by the exclusive resources and by the parameter μ, which is a critical value highly sensitive to changes in sharing resources.

The following result gives conditions of uniqueness and global stability in a specific case of the system (1). In this case, we have the following.

Theorem 3. *Suppose $I_{0i}(t), I_{E_i}(t), \gamma_{ij}(t), C_i(t)\geq 0$ are continuous almost periodic functions (not all constant) with $\gamma_{ij}^-, I_{E_i}^->0$. If $\beta>0$ is constant, $I_{02}=\alpha I_{01}$ for some constant $\alpha>0$, $\frac{\gamma_{22}(t)}{\alpha\beta}-\gamma_{12}(t)>0$ and $\frac{\gamma_{21}(t)}{\alpha\beta}-\gamma_{11}(t)<0$, then there exists a unique almost periodic solution of (1) in $\mathbb{R}^2_{>0}$, and any other solution with positive initial conditions converges to this almost periodic solution, when $t\to\infty$.*

Proof. For uniqueness, we follow the same reasoning as in Theorem 2, thus we consider a maximal pair $(\hat{N}_1,\hat{N}_2)$ and minimal pair $(\check{N}_1,\check{N}_2)$ of almost periodic solutions. Using that

the mean satisfies $\mathcal{M}[\frac{d}{dt}(\ln(\hat{N}_i))] = \mathcal{M}\left[\frac{d}{dt}(\ln(\check{N}_i))\right] = 0$ together with the assumptions β constant and $I_{02} = \alpha I_{01}$ for some α, then for the minimal pair $(\check{N}_1, \check{N}_2)$, we have

$$\mathcal{M}[C_1(t)] = \mathcal{M}\left[\frac{I_{01}(t)}{\check{N}_1 + \beta\check{N}_2}\right] + \mathcal{M}\left[\frac{I_{E_1}(t)}{\check{N}_1}\right] - \mathcal{M}\left[\gamma_{11}(t)\check{N}_1\right] - \mathcal{M}\left[\gamma_{12}(t)\check{N}_2\right], \tag{18}$$

$$\mathcal{M}\left[\frac{C_2(t)}{\alpha\beta}\right] = \mathcal{M}\left[\frac{I_{01}(t)}{\check{N}_1 + \beta\check{N}_2}\right] + \mathcal{M}\left[\frac{I_{E_2}(t)}{\alpha\beta\check{N}_2}\right] - \mathcal{M}\left[\frac{\gamma_{22}(t)\check{N}_2}{\alpha\beta}\right] - \mathcal{M}\left[\frac{\gamma_{21}(t)\check{N}_1}{\alpha\beta}\right]. \tag{19}$$

Similarly for the maximal pair $(\hat{N}_1, \hat{N}_2)$

$$\mathcal{M}[C_1(t)] = \mathcal{M}\left[\frac{I_{01}(t)}{\hat{N}_1 + \beta\hat{N}_2}\right] + \mathcal{M}\left[\frac{I_{E_1}(t)}{\hat{N}_1}\right] - \mathcal{M}\left[\gamma_{11}(t)\hat{N}_1\right] - \mathcal{M}\left[\gamma_{12}(t)\hat{N}_2\right], \tag{20}$$

$$\mathcal{M}\left[\frac{C_2(t)}{\alpha\beta}\right] = \mathcal{M}\left[\frac{I_{01}(t)}{\hat{N}_1 + \beta\hat{N}_2}\right] + \mathcal{M}\left[\frac{I_{E_2}(t)}{\alpha\beta\hat{N}_2}\right] - \mathcal{M}\left[\frac{\gamma_{22}(t)\hat{N}_2}{\alpha\beta}\right] - \mathcal{M}\left[\frac{\gamma_{21}(t)\hat{N}_1}{\alpha\beta}\right]. \tag{21}$$

Subtracting equation (18) from (20), we have

$$\begin{aligned}\mathcal{M}\left[\frac{I_{01}(t)}{\hat{N}_1 + \beta\hat{N}_2} - \frac{I_{01}(t)}{\check{N}_1 + \beta\check{N}_2}\right] &+ \mathcal{M}\left[\frac{I_{E_1}(t)}{\hat{N}_1} - \frac{I_{E_1}(t)}{\check{N}_1}\right] = \mathcal{M}\left[\gamma_{11}(t)\left(\hat{N}_1 - \check{N}_1\right)\right] \\ &+ \mathcal{M}\left[\gamma_{12}(t)\left(\hat{N}_2 - \check{N}_2\right)\right].\end{aligned} \tag{22}$$

Also subtracting equation (19) from (21), we get

$$\begin{aligned}\mathcal{M}\left[\frac{I_{01}(t)}{\hat{N}_1 + \beta\hat{N}_2} - \frac{I_{01}(t)}{\check{N}_1 + \beta\check{N}_2}\right] &+ \mathcal{M}\left[\frac{I_{E_2}(t)}{\alpha\beta\hat{N}_2} - \frac{I_{E_2}(t)}{\alpha\beta\check{N}_2}\right] = \mathcal{M}\left[\frac{\gamma_{22}(t)}{\alpha\beta}\left(\hat{N}_2 - \check{N}_2\right)\right] \\ &+ \mathcal{M}\left[\frac{\gamma_{21}(t)}{\alpha\beta}\left(\hat{N}_1 - \check{N}_1\right)\right].\end{aligned} \tag{23}$$

Now subtracting (22) from (23), we obtain

$$\begin{aligned}\mathcal{M}\left[\frac{I_{E_2}(t)}{\alpha\beta\hat{N}_2} - \frac{I_{E_2}(t)}{\alpha\beta\check{N}_2}\right] &+ \mathcal{M}\left[\frac{I_{E_1}(t)}{\check{N}_1} - \frac{I_{E_1}(t)}{\hat{N}_1}\right] + \mathcal{M}\left[\left(\frac{\gamma_{22}(t)}{\alpha\beta} - \gamma_{12}(t)\right)\left(\check{N}_2 - \hat{N}_2\right)\right] \\ &= \mathcal{M}\left[\left(\frac{\gamma_{21}(t)}{\alpha\beta} - \gamma_{11}(t)\right)\left(\hat{N}_1 - \check{N}_1\right)\right].\end{aligned} \tag{24}$$

Since $\hat{N}_2 \leq \check{N}_2$ and $\check{N}_1 \leq \hat{N}_1$ then $\mathcal{M}\left[\frac{I_{E_2}(t)}{\alpha\beta\hat{N}_2} - \frac{I_{E_2}(t)}{\alpha\beta\check{N}_2}\right] + \mathcal{M}\left[\frac{I_{E_1}(t)}{\check{N}_1} - \frac{I_{E_1}(t)}{\hat{N}_1}\right] \geq 0$, thus

$$\mathcal{M}\left[\left(\frac{\gamma_{22}(t)}{\alpha\beta} - \gamma_{12}(t)\right)\left(\check{N}_2 - \hat{N}_2\right)\right] \leq \mathcal{M}\left[\left(\frac{\gamma_{21}(t)}{\alpha\beta} - \gamma_{11}(t)\right)\left(\hat{N}_1 - \check{N}_1\right)\right]. \tag{25}$$

If $\mathcal{M}[\hat{N}_1 - \check{N}_1] > 0$, the above inequality contradicts the hypotheses in the theorem. Therefore $\mathcal{M}[\hat{N}_1] = \mathcal{M}[\check{N}_1]$, whence $\hat{N}_1 = \check{N}_1$ by Lemma 1. This in turn implies that $\hat{N}_2 = \check{N}_2$ via (25).

Now, from Proposition 1 we can take an arbitrarily large super-solutions and also arbitrarily small sub-solutions. Thus, we have a single almost periodic orbit which is an attractor in an arbitrarily large compact set inside $\mathbb{R}^2_{>0}$. Then the almost periodic orbit is attractor at the entire set $\mathbb{R}^2_{>0}$. This concludes the proof of Theorem 3.

5. Numerical examples

In this section, we show the population dynamics of competing species described by model (1). We also show some scenarios associated with simplified versions of the model. There are obtained by removing certain terms listed in Table 1, while retaining the maintenance and replacement costs are considered. Through numerical simulations of the solutions of the model, we show scenarios of coexistence which are represented by a positive almost periodic attractor or exclusion of species which are represented by a non-negative almost periodic attractor.

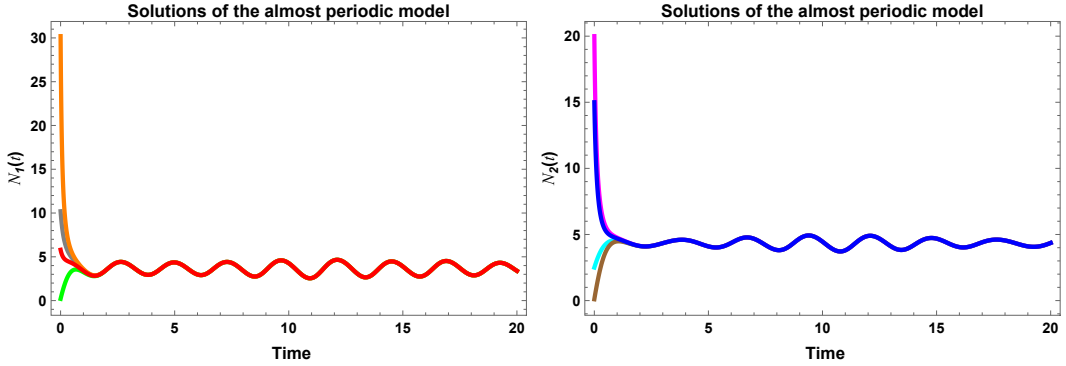
5.1. Exclusive and overlapping resources as well as intra- and interspecific interference, terms I-V

To show the principal result of this work, we use the following almost periodic functions

$$\begin{aligned}
I_{E_1}(t) &= 7.5 + 0.75\sin(\sqrt{5}t) + 3.75\cos(\sqrt{7}t),\\
I_{E_2}(t) &= 10.0 + 2.0\,\sin\left(\sqrt{5}t\right) + 1.0\,\cos\left(\sqrt{7}t\right),\\
\beta(t) &= 0.7 + 0.014\,\sin\left(\sqrt{3}t\right) + 0.007\,\cos\left(\sqrt{7}t\right),\\
I_{01}(t) &= 0.50 + 0.100\,\sin\left(\sqrt{5}t\right) + 0.150\,\cos\left(\sqrt{7}t\right),\\
I_{02}(t) &= 0.10 + 0.040\,\sin\left(\sqrt{5}t\right) + 0.010\,\cos\left(\sqrt{7}t\right),\\
\gamma_{11}(t) &= 0.40 + 0.0080\,\sin\left(\sqrt{2}t\right) + 0.0120\,\cos\left(\sqrt{3}t\right),\\
\gamma_{22}(t) &= 0.40 + 0.0040\,\sin\left(\sqrt{7}t\right) + 0.0080\,\cos\left(\sqrt{3}t\right),\\
\gamma_{12}(t) &= 0.1 + 0.001\,\sin\left(\sqrt{11}t\right) + 0.003\,\cos\left(\sqrt{3}t\right),\\
\gamma_{21}(t) &= 0.1 + 0.002\,\sin\left(\sqrt{2}t\right) + 0.0001\,\cos\left(\sqrt{3}t\right),\\
c_1(t) &= 0.2 + 0.0004\,\sin\left(\sqrt{5}t\right) + 0.004\,\sin\left(\sqrt{7}t\right),\\
c_2(t) &= 0.2 + 0.0008\,\sin\left(\sqrt{5}t\right) + 0.002\,\sin\left(\sqrt{7}t\right).
\end{aligned} \tag{26}$$

Functions in (26) are continuous almost periodic functions, including the function $\beta(t)$. Therefore, by Proposition 1, there is at least one almost periodic solution.

With these functions, $\frac{[\beta^+ I_{01}^+\mu^2+\gamma_{12}^-][\beta^+ I_{02}^+\mu^2+\gamma_{21}^-]}{\gamma_{11}^-\gamma_{22}^-} = 0.8812 < 1$ with $\mu = 1$. To calculate this specific value of μ, we used the expression in (11). For this example, $\mu := \max\left\{1, \frac{\gamma_{11}^+ + \gamma_{12}^+/\beta^- + C_1^+}{I_{E_1}^-}, \frac{\gamma_{21}^+ + \gamma_{22}^+/\beta^- + C_2^+}{\beta^- I_{E_2}^-}\right\} = \max\{1, 0.1246, 0.0476\}$. Then, the conditions in Theorem 2 are satisfied. Therefore, we conclude that model admits a unique positive almost periodic attractor. In Figure 1, we show that solutions of the model with different initial conditions converge to a unique scenario of coexistence.



(a) (b)

Figure 1: For different initial conditions, the solutions converge to a unique almost periodic solution. Therefore, both competing species coexist and their population dynamics have an almost periodic behavior.

Modeling almost periodic dynamics through periodic models can lead to misleading scenarios in the long term; see Figure 2. To show the scenario, without loss of generality, we

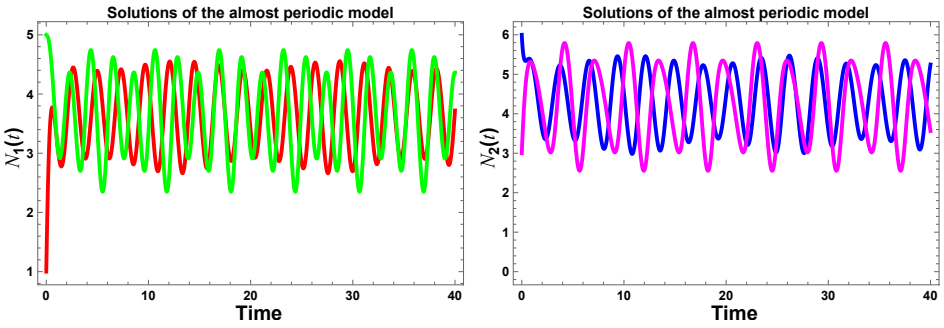
assume that the exclusive resource has either an almost periodic or periodic behavior which are given by

$$\begin{aligned} I_{E_1}(t) &= 7.5 + 0.1\sin(\sqrt{5}t) + 0.5\cos(\sqrt{7}t), \\ I_{E_2}(t) &= 10.0 + 0.5\,\sin\left(\sqrt{5}t\right) + 0.1\,\cos\left(\sqrt{7}t\right), \end{aligned} \tag{27}$$

in the almost periodic case and

$$\begin{aligned} I_{E_1}(t) &= 7.5 + 0.2\sin(2t) + 0.6\cos(3t), \\ I_{E_2}(t) &= 10.0 + 0.6\,\sin\left(2t\right) + 0.2\,\cos\left(3t\right), \end{aligned} \tag{28}$$

in the periodic case. All other values of the parameters of the model are considered constant, which are given by the independent term of the other functions in (26).



(a) (b)

Figure 2: The population sizes of both competing species are similar at the beginning, close to the initial condition. However, these population densities behave differently in their future evolution.

Uniqueness of the solutions of the model, as shown in Figure 1, is a desirable characteristic from an ecological perspective since it allows for a reliable forecasting of the population dynamics even though the environmental setting is disturbed. However, model (1) can admit simultaneously two positive almost periodic attractors. This occurs when the conditions in Proposition 1 are satisfied while the condition (14) in Theorem 2 do not hold. To show this scenario, all the functions are the same as those used in the scenario given in Figure 1, but the functions $\gamma_{11}(t)$, $\gamma_{22}(t)$, $I_{E_2}(t)$, and $I_{01}(t)$ are multiplied by $\frac{1}{20}$ while the functions $I_{E_1}(t)$ and $I_{02}(t)$ are multiplied by $\frac{1}{15}$ and $\frac{1}{100}$, respectively. In this case, $\frac{[\beta^+ I_{01}^+\mu^2+\gamma_{12}^-][\beta^+ I_{02}^+\mu^2+\gamma_{21}^-]}{\gamma_{11}^-\gamma_{22}^-} = 3.8\times 10^6 > 1$ with $\mu = \max\{1, 1.8697, 0.9515\}$. In Figure 3, we show the simultaneous existence of two scenarios of coexistence of competing species. Therefore, which species has a larger number of individuals in the coexistence scenario is a function of the initial population sizes. So, the outcome of the interaction can change depending on the initial size of the populations.

In the following, we show other ecologically relevant scenarios obtained by using only some of the terms from Table 1 in the modeling process.

5.2. Exclusive resources only, intra- and interspecific interference, terms II, III, IV, V

Here, we show a scenario in which the species do not share resources, but instead, each species has only exclusive resources. Also, all other factors in Table 1 are considered. To show this scenario, we use $I_{01}(t) = I_{02}(t) = 0$ and the functions $\beta(t)$, $I_{E_1}(t)$, $I_{E_2}(t)$, $\gamma_{11}(t)$, $\gamma_{22}(t)$ and $\gamma_{12}(t)$ are multiplied by 0.14, 0.06, 5, 2.5, 10 and 0.5, respectively. Other values of the parameters are the same as those used in the scenario given in Figure 1. With these values of the parameters, the conditions in Theorem 2 are satisfied. Therefore, a unique positive almost periodic attractor exists. This scenario of coexistence is shown in Figure 4

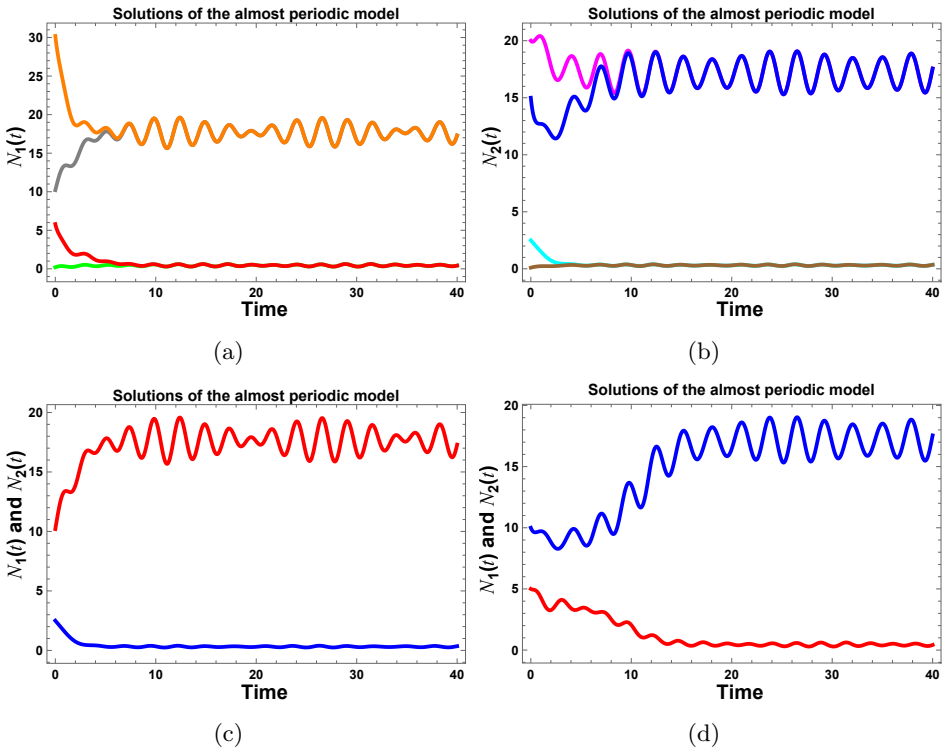


Figure 3: A bistability phenomenon occurs when the uniqueness condition of the solution is not satisfied. In this scenario, the competing species converge to different population sizes depending on the initial conditions (cases (a)-(b)). In cases (c)-(d), we show that one species can reach a larger population size than the other depending on the initial conditions.

cases (a)-(b). Also, the model associated with this case admits two non-negative attractors, which describe exclusion scenarios, when the condition (14) in the theorem does not hold. In particular, these cases occur when the intraspecific competition is small enough. In Figure 4 cases (c)-(d), we show that one species goes to extinct while the other persists, depending on the initial population size of each species.

5.3. Completely overlapping resources, intra- and interspecific interference only, terms I, III, IV, V

In this case, we show a scenario in which both species do not have exclusive resources but they share resources. All other terms of the model are considered. To do this, unlike the scenario shown in Figure 1, in Figure 5 cases (a)-(b), we consider $I_{E_1}(t) = I_{E_2}(t) = 0$. Notice that, the model admits a positive almost periodic attractor when the share resources are big enough even though the conditions $I_{E_i}^- > 0$, for $i = 1, 2$, in proposition 1 do not hold. In Figure 5 cases (c)-(d), we also show that two non-negative attractors occur when the intraspecific competition rates are small enough. Therefore, depending on the initial population sizes, one species excludes the other. Finally, with the values $I_{E_1}(t) = I_{E_2}(t) = 0, I_{01}(t) = 12(1+0.001\sin(\sqrt{5}t)+0.003\sin(\sqrt{7}t)), I_{02}(t) = 10(1+0.005\sin(\sqrt{5}t)+0.007\sin(\sqrt{7}t)), \beta(t) = 0.93, \gamma_{11}(t) = 0.05, \gamma_{12}(t) = 73.5, \gamma_{22}(t) = 57.05, \gamma_{21}(t) = 0.014, C_1(t) = 0.2$, and $C_2(t) = 0.2$, two almost periodic attractor exist; however one attractor is positive while the other is non-negative; see Figure 5 cases (e)-(f).

5.4. Completely overlapping resources, intraspecific interference only, terms I, III, V

Now, we show the behavior of the solutions of the model when the terms modeling the interspecific competition and the exclusive resources are not considered. In this case, even

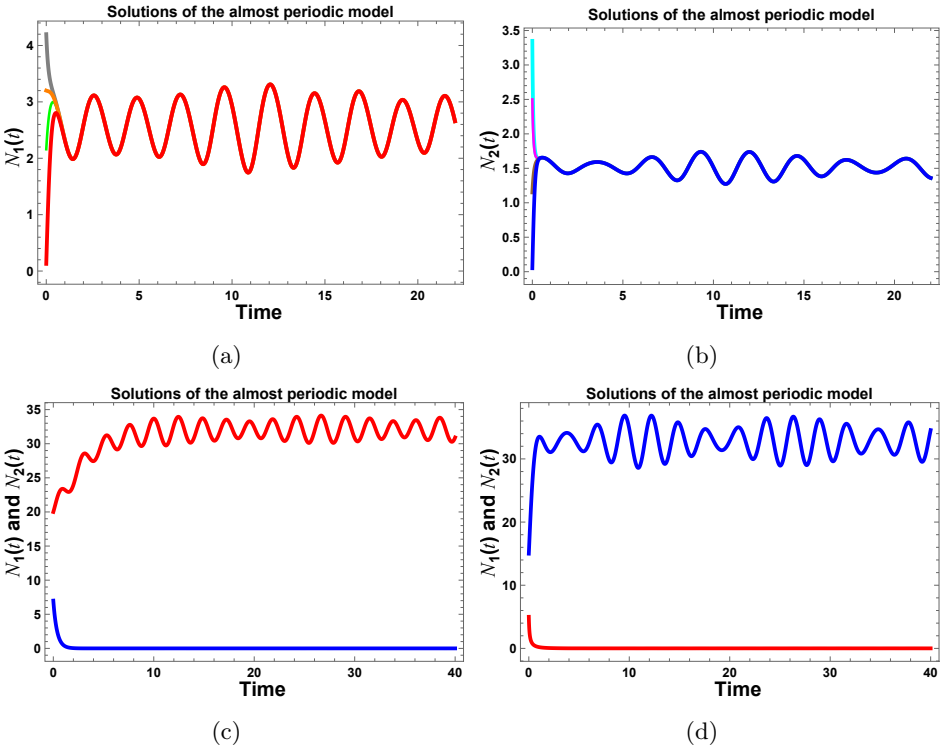


Figure 4: Coexistence of both competing species occurs when each species has exclusive resources, even though the species do not share resources: cases (a)-(b). However, although exclusive resources exist, exclusion scenarios occur when intraspecific competition is low in any competing species: cases (c)-(d).

though the conditions in Proposition 1 and Theorem 2 do not hold, a positive almost periodic attractor can exist. Also, in this case, a unique non-negative almost periodic attractor can occur. Therefore, the same species persists while the other perishes, regardless of their population sizes. What species wins depends on the values of the parameters and not on the population sizes. Both cases are shown in Figure 6.

5.5. Completely overlapping resources, interspecific interference only, terms I, IV, V

Finally, we show the solution of the model associated with the case in which intraspecific competition and exclusive resources are not considered. Notice that, the conditions in Proposition 1 and Theorem 2 are not satisfied. Unlike the last case, in this case there are no almost periodic attractors. However, two non-negative almost periodic attractors always exist. Therefore, one species is excluded while the other persist. What species wins depends on its initial condition. In Figure 7 we show this scenario.

By calculating the Sobol indices on the uniqueness and stability condition, given by (14), of the solutions of the model, it is revealed that the parameter μ constitutes the critical sensitivity node, accounting by itself for a first order effect of $S_1 = 0.5829$ and a total order effect of $S_T = 0.5951$, followed secondarily by the parameter β^+ with $S_1 = 0.1476$ and $S_T = 0.1547$. Since changes in this macro condition depend mainly on μ, it becomes essential to inspect the underlying sources of variation through its functional components. This analysis shows that the behavior of the component $\frac{\gamma_{11}^+ + \gamma_{12}^+/\beta^- + C_1^+}{I_{E_1}^-}$ is strongly dominated by the parameter $I_{E_1}^-$ with $S_1 = 0.6961$ and $S_T = 0.6972$ and the parameter γ_{11}^+ with $S_1 = 0.2007$ and $S_T = 0.2014$. In contrast, the variance in the component $\frac{\gamma_{21}^+ + \gamma_{22}^+/\beta^- + C_2^+}{\beta^- I_{E_2}^-}$ is mainly governed by β^- for which $S_1 = 0.6469$ and $S_T = 0.6505$, $I_{E_2}^-$ with $S_1 = 0.2324$ and $S_T = 0.2350$, and γ_{22}^+ with $S_1 = 0.1026$ and $S_T = 0.1043$. In conclusion, the total variability

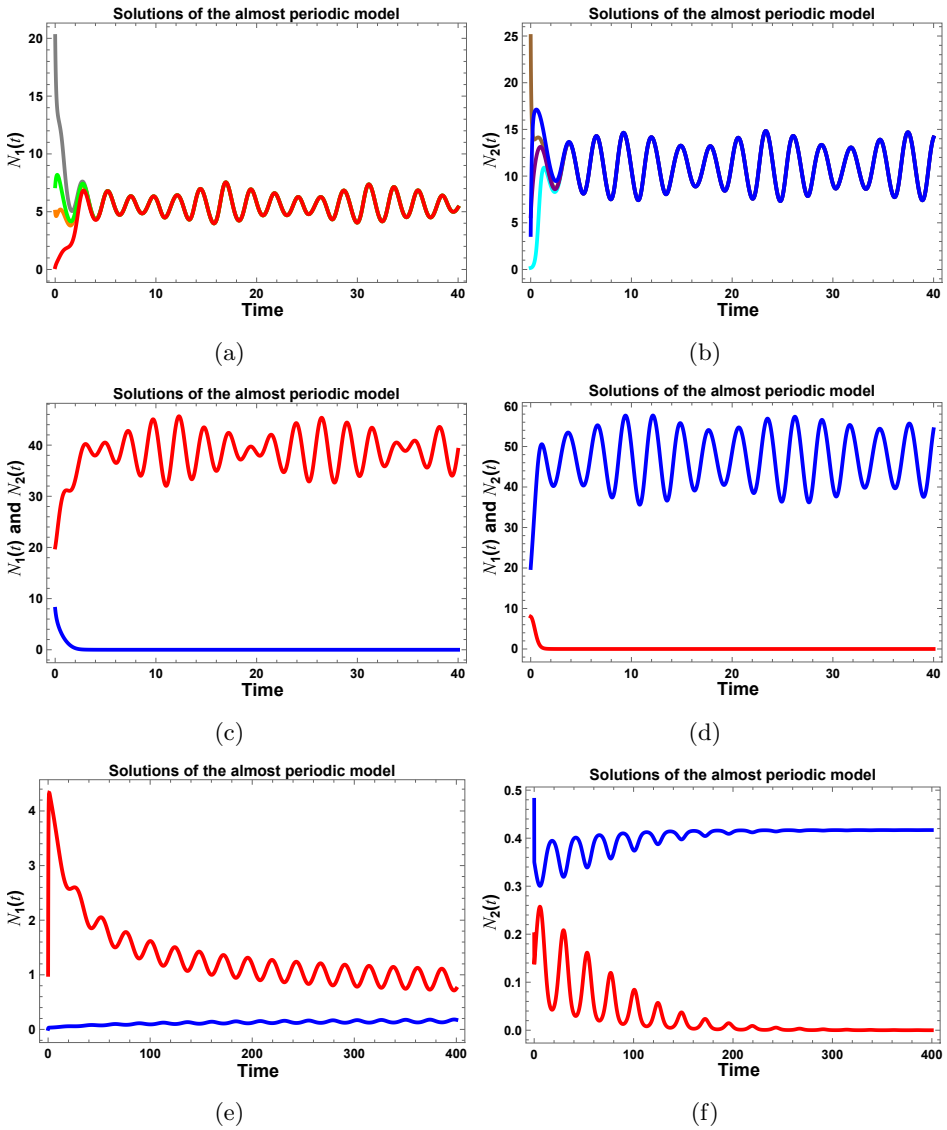


Figure 5: Competing species without exclusive resources but sharing resources can reach a scenario of coexistence (cases (a)-(b)). However, scenarios of competitive exclusion occur when intraspecific competition rates are sufficiently small (cases (c)-(d)). Finally, a bistability scenario emerges under low intraspecific and high interspecific competition for species N_1, and the opposite pattern for species N_2: cases (e)-(f).

of the system is determined in a concentrated manner by a critical set of physical parameters $I_{E_1}^-$, β^-, $I_{E_2}^-$, γ_{11}^+, and γ_{22}^+ that dictate the behavior through μ. Furthermore, the fact that the sum of all first order indices accounts for 98.47% of the total variance shows that the model is highly close to being additive. Therefore, individual parameter uncertainties propagate and accumulate cleanly and linearly toward the condition $\frac{[\beta^+ I_{01}^+ \mu^2 + \gamma_{12}^-][\beta^+ I_{02}^+ \mu^2 + \gamma_{21}^-]}{\gamma_{11}^- \gamma_{22}^-} < 1$; see Figure 8. Therefore, the transition toward the threshold boundary occurs in a smooth manner.

To provide a rigorous quantitative calculation of the dynamical discrepancies between the solutions of the periodic and almost periodic model, the Root Mean Square Error (RMSE) and the maximum absolute divergence (L_∞ norm) were calculated over three disjoint time intervals, with the complete metrics synthesized in Table 2. In the early transient phase ($t \in [0, 2]$), both solutions exhibit a high level of proximity, yield low discrepancy metrics ($RMSE_{N_1} = 0.2473$, $\|N_1\|_{L_\infty} = 0.5797$ and $RMSE_{N_2} = 0.2639$, $\|N_2\|_{L_\infty} = 0.5088$). During the intermediate interval ($t \in [10, 20]$), solutions show a progressive desynchronization, driving the point-to-point error to its peak values ($RMSE_{N_1} = 0.8338$, $\|N_1\|_{L_\infty} = 2.0464$ and $RMSE_{N_2} = 1.6649$, $\|N_2\|_{L_\infty} = 2.8498$). Finally, in the third interval ($t \in [35, 40]$), the solutions show the metrics ($RMSE_{N_1} = 0.4541$, $\|N_1\|_{L_\infty} = 1.0018$ and $RMSE_{N_2} = 1.5176$,

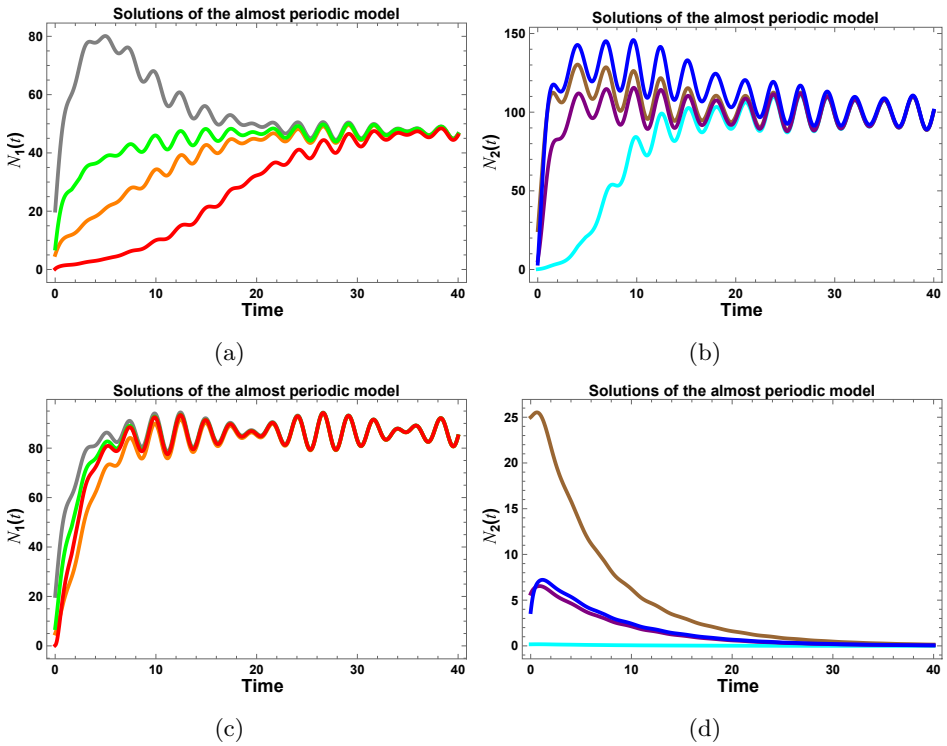


Figure 6: Coexistence between competing species occurs when exclusive resources and the interspecific competition rate are not considered: cases (a)-(b). Scenarios of exclusion emerge when intraspecific competition increases: cases (c)-(d).

$\|N_2\|_{L_\infty} = 2.4968$). These results show a permanent dynamical asynchronicity between the periodic and almost periodic solutions.

	State $N_1(t)$		State $N_2(t)$	
Time Interval	**RMSE**	**Max Dist (L_∞)**	**RMSE**	**Max Dist (L_∞)**
Transient $[0, 2]$	0.2473	0.5797	0.2639	0.5088
Intermediate $[10, 20]$	0.8338	2.0464	1.6649	2.8498
Asymptotic $[35, 40]$	0.4541	1.0018	1.5176	2.4968

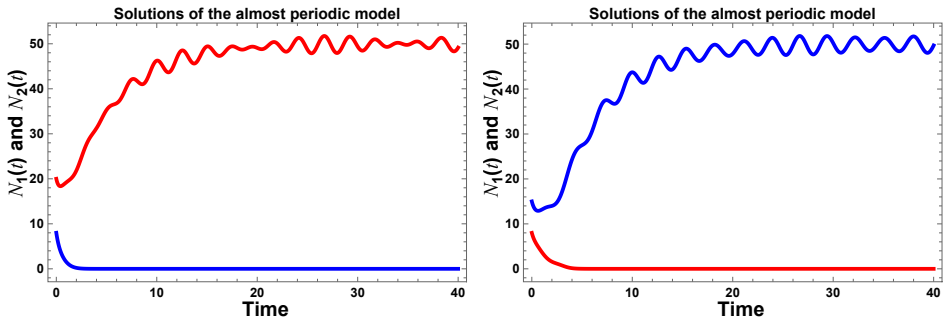
Table 2: Quantitative discrepancy analysis between periodic and almost periodic configurations for states $N_1(t)$ and $N_2(t)$ across distinct time windows.

6. Discussion

The influence of seasonality in ecological relationships has lagged behind other mechanisms driving the population dynamics due to two main reasons. First, the empirical study of seasonality requires that data to be collected over multiples time points or occasions, which presents problems of diverse kinds. And second, the theoretical study of seasonality through mathematical models presents a great challenge due to the complexity of the underlying theories [58].

Recognizing the relevance that seasonality has over competing species, we propose an almost periodic model to analyze the existence of a global almost periodic attractor, the transients and variability of the almost periodic solutions of the system rather than analyzing it in terms of equilibrium point dynamics. We chose to model the effects of seasonality on competing species using almost periodic rates because assuming that climate-mediated shifts do not affect the periodicity of the ecological and demographic rates is very restrictive.

From an analysis of model (1), we show that diverse scenarios of coexistence and exclusion of species are possible for some values of the parameters of the model. Each of them



(a) (b)

Figure 7: Competitive exclusion always occur when intraspecific competition and exclusive resources are not considered.

represents relevant ecological scenarios which are described as follows.

Model (1) which describes competing species with overlapping and exclusive resources as well as intraspecific and interspecific competition, and maintenance and replacement costs (modeled by terms I-V) admits a unique almost periodic globally stable attractor if the condition in Theorem 2 given by $\frac{[\beta^+ I_{01}^+ \mu^2 + \gamma_{12}^-][\beta^+ I_{02}^+ \mu^2 + \gamma_{21}^-]}{\gamma_{11}^- \gamma_{22}^-} < 1$ is satisfied, with $\mu := \max\left\{1, \frac{\gamma_{11}^+ + \gamma_{12}^+/\beta^- + C_1^+}{I_{E_1}^-}, \frac{\gamma_{21}^+ + \gamma_{22}^+/\beta^- + C_2^+}{\beta^- I_{E_2}^-}\right\}$. Therefore, in this scenario, the competing species coexist for all initial population sizes; see Figure 1. From the analysis of these expressions, we conclude that the larger $I_{E_1}^-$ and $I_{E_2}^-$ are, the easier the condition of uniqueness of the coexistence scenario is satisfied. In contrast, the smaller I_{01}^+ and I_{02}^+ are, the easier the condition holds. Observe that for the condition relating the shared resources to be satisfied, if the resource shared by one species is abundant, the resource shared by the other competing species must be scarce. Therefore, an increase of the amount of exclusive resources available for each species promotes uniqueness of the scenario of coexistence while a decrease of the amount of overlapping resources of both species leads to this uniqueness. Similar conclusions can be obtained when in these expressions, the intraspecific and interspecific rates are analyzed. So, the larger the intraspecific competition rates given by γ_{11}^- and γ_{22}^- are, the easier the condition of uniqueness is satisfied. In contrast, the smaller the interspecific competition rates γ_{12}^- and γ_{21}^- are, the easier the condition of uniqueness of the scenario of coexistence holds. Notice that the larger $\beta(t)$, the inherent propensity of an individual of the species N_2 to consumer the overlapping resources, is, the harder the condition of uniqueness of the scenario of coexistence is satisfied. A similar result is obtained for the maintenance and replacement costs.

Although the uniqueness of a scenario of coexistence is desirable, it can occur that this is not reached for diverse situations. In such scenarios, diverse ecological scenarios occurs.

Model (1) admits two positive attractors when the condition in Theorem 2 is not satisfied. In this case, two scenarios of coexistence arise and the outcome of the interaction between competing species depends on the initial population size of them. According to Figure 3, one species reaches a larger population level while the other reaches a very smaller population level. Therefore, in this case, there is a priority effect.

In the following, we show results associated with simplified versions of model (1).

The dynamics of the competing species, when considering only exclusive resources, intra- and interspecific competition, and maintenance and replacement costs (modeled by terms II-V), admit a unique scenario of coexistence when the conditions in Theorem 2 are satisfied; however, when the condition of uniqueness in Theorem 2 does not hold, two non-negative almost periodic attractor exist simultaneously. Therefore, one species persists while the other is excluded depending on their population sizes. To show this case, we use small values of the intraspecific competition rates; see Figure 4.

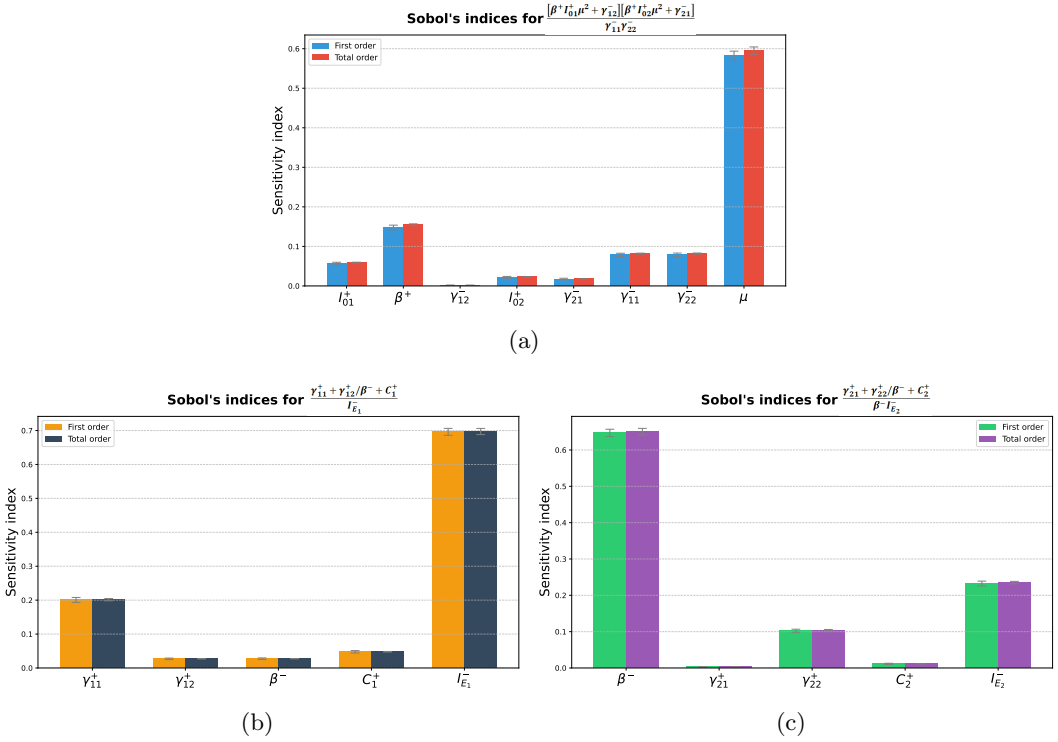


Figure 8: Case (a) shows the Sobol's indices for $\frac{[\beta^+ I_{01}^+ \mu^2+\gamma_{12}^-][\beta^+ I_{02}^+ \mu^2+\gamma_{21}^-]}{\gamma_{11}^- \gamma_{22}^-}$ associated with Theorem 2. Cases (b) and (c) show the Sobol's indices for $\frac{\gamma_{11}^+ + \gamma_{12}^+/\beta^- + C_1^+}{I_{E_1}^-}$ and $\frac{\gamma_{21}^+ + \gamma_{22}^+/\beta^- + C_2^+}{\beta^- I_{E_2}^-}$ given in (11), respectively.

The population dynamics of the competing species when it is considered overlapping resources only, intra- and interspecific competition, and the maintenance and replacement costs (modeled by terms I, III-V) admits the following scenarios. First, we want to underline that in this case the conditions in Proposition 1 are not satisfied since $I_{E_1}^- = I_{E_2}^- = 0$. Notice that, Proposition 1 is a result of sufficiency. Therefore, although the conditions are not satisfied, for some values of the parameters a positive attractor exists. Also, changing the values of the parameters two non-negative attractor also exist. Finally, when the values of the parameters are varied, one positive and one non-negative attractor exist simultaneously. Therefore, the scenario described here includes the results mentioned in the last case and it also shows a new scenario in which coexistence and exclusion of species can occur simultaneously; see Figure 5. Then, the outcome of the interaction between the species depends on their initial population sizes.

In the case where completely overlapping resources, intraspecific interference only and the maintenance and replacement costs are considered (modeled by terms I, III, V), the model admits a positive attractor even though the conditions in Proposition 1 and Theorem 2 are not satisfied since it is considered $I_{E_1}^- = I_{E_2}^- = \gamma_{11}^- = \gamma_{22}^- = 0$. Also, by varying the values of the parameters one non-negative attractor exists. Therefore, in this case, both coexistence or species exclusion scenarios can occur; however, unlike some cases described above, one species always wins while the other becomes extinct. This outcome can be reversed for other values of the parameters; see Figure 6.

The dynamics of the competing species when it is considered completely overlapping resources only, interspecific competition, and the maintenance and replacement costs (modeled by terms I, IV, V) shows only two non-negative attractors which exist simultaneously. Therefore, one species can be excluded, and the outcome (i.e., which species persists) depends on the initial population sizes; see Figure 7.

Sobol sensitivity analysis reveals that condition (14) is primarily governed by $I_{E_1}^-$, β^-, $I_{E_2}^-$, γ_{11}^+, and γ_{22}^+; see Figure 8. The high additivity of the model (98.47%) guarantees that the

parameter variances propagate linearly. In particular, the transition toward the boundary condition given by (14) occurs in a predictable manner.

Finally, numerical simulations show that modelling almost-periodic dynamics with periodic models induces a permanent asynchrony, leading to critical miscalculations in population sizes; see Figure 2. To quantify these discrepancies, the Root Mean Square Error and maximum divergence were evaluated across three disjoint intervals. The systems show tight proximity during the early transient phase, and a desynchronization occurs during the subsequent intervals: See Table 2. Therefore, analyzing the interaction of competing species when environmental drivers change using almost periodic models can be a useful tool for the decision makers since the results obtained can be used in the design of conservation strategies.

In summary, we proved the existence and uniqueness of solutions to the model. Furthermore, a sensitivity analysis using Sobol indices was applied to the threshold condition (14), which biologically represents the requirement for strong intraspecific self-regulation against the pressures of sharing resources. Our findings reveal that the system is highly additive (98.47%), implying that parameter variances propagate linearly and the transition toward the threshold boundary occurs in a smooth, predictable manner. This variability is heavily dominated by the parameters $I_{E_1}^-$, β^-, $I_{E_2}^-$, γ_{11}^+, and γ_{22}^+. Through numerical simulations, we show that when different phenomenological mechanisms are considered, the model shows scenarios of coexistence that can be given by the existence of a unique attractor or by the existence of two attractors associated with a bistability phenomenon. Also, we show that different configurations of scenarios of exclusion can occur. Finally, we show that modeling almost periodic dynamics with periodic models can lead to misleading scenarios of the population sizes. Therefore, we show that a persistent dynamical asynchrony exists between the periodic and almost periodic cases. This mismatch can result in either the underestimation or overestimation of population densities, leading to potentially catastrophic ecological consequences. Analyzing the interaction of competing species when environmental drivers change using almost periodic models can be a useful tool for the decision makers since the results obtained can be used in the design of conservation strategies.

Data Availability

The authors confirm that the data supporting the findings of this study are available within the article [and/or] its supplementary materials.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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