An almost periodic dynamic model for some mutualistic systems between two species

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Abstract. In this work, we propose an almost periodic model to describe mutualistic relationships. We prove that when some conditions on the parameters of the model are satisfied, then there exists a global almost periodic attractor. Numerical simulations show that if seasonal effects are modeled by periodic rates rather than by almost periodic ones, then predictions may either underestimate or overestimate the real number of individuals in each species. This miscalculation could be catastrophic from a biodiversity conservation perspective.

Key-words: *almost periodic model; almost periodic rates; mutualism; phenological match.*

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1. Introduction

In nature, species interact in different ecological relationships such as prey-predator, victim-exploiter, competition and mutualism, among others. These ecological relationships have been analyzed from a biological and also from mathematical perspective. However, mutualism has been studied in a rather less depth compared to all other relationships mentioned before; see Hale and Valdovinos (2021).

In a mutualistic interaction, species receive benefits from the interaction with the partner species, which can affect fitness either directly or indirectly. For instance, mutualism can increase the intrinsic growth rates and/or the carrying capacities of the species; see Addicott (1981); Wolin and Lawlor (1984). Mutualism is generally divided into facultative or obligate.

In the first attempts to model mutualistic interactions, we could mention Lotka-Volterra systems were parameters are considered as constant. This type of models yield two qualitatively distinct predictions depending on the parameters. On type of predictions yield a unique nontrivial equilibrium where, each species reaches a population density which is bigger than if it had grown alone. In other non-realistic predictions population densities grow up unboundedly. This unboundedness phenomenon is explained by the fact that the benefits received from the interaction is bigger than the cost imposed by the intraspecific competition; see Moore et al. (2018). In other words, the benefits received increase without considering mechanisms of population regulation. In conclusion, conditioned interactions need to be implemented in mathematical ecology. Specifically, in mutualistic models with conditioned interactions both species are mutualistic at low population densities, while becoming competitors at high population densities. Thus, coexistence is an effect not only of a mutualistic interaction but also of competition or victim-exploiter relationships. Moreover, mutualistic species with conditioned interaction might lead to exclusion of the partner species, Hernandez and Barradas (2003). Similar results have been obtained when mutualistic relationships are analyzed using resources-consumer models, Holland et al. (2013).

Besides using differential equations, mutualism can also be analyzed with delay differential equations, discrete equations, integrodifferential equations and stochastic differential equations, see for instance Li and Xu (2001); Ding and Guo (2012); Yang and Li (2007); Liu et al. (2008); Li et al. (2016); Xie et al. (2015); Xue et al. (2015). In this direction, Hale and Valdovinos (2021)

show a semi-chronological list of differential models describing historically the development of autonomous mutualistic models. On the other hand, the study of non-autonomous mutualistic models is rather scarce. Nonetheless, we could mention some works under time-dependence assumption such as Li (2001); Liu et al. (2019); Xia et al. (2013).

Amon time-dependent models, seasonal effects are modeled through periodic functions such as $\sin(t)$ and $\cos(t)$ or by trigonometric polynomials, see Dembele and Yakubu (2009); Korman (2016). However, seasonal rates that are affected by seasonal drivers might be non periodic. A wider family of models is possible by using almost periodic functions Wang et al. (2019); Dumont and Thulliez (2016).

In this work, we propose an almost periodic model to describe mutualism between two species. We prove that a unique global almost periodic attractor exists when some conditions on the parameters are satisfied. In Section 2, we present the almost periodic model. In Section 3, we give some preliminary results about almost periodic functions and some results about cooperative systems. In Section 4, we write down our main result of existence and uniqueness of almost periodic solutions, giving the corresponding proof. In Section 5, we show numerical simulations of solutions. Finally, in Section 6, we discuss some conclusion about the results we have obtained.

2. The model

In this section, we show an almost periodic model to describe seasonal effects in mutualism. To describe seasonal effects in a mutualistic relationship, we use as a baseline the model proposed in Gopalsamy (1992), p. 191. In contrast with Gopalsamy's model, we assume that rates $r_i(t), \alpha_i(t), \beta_i(t), k_i(t) \geq 0$ and $a_i(t) \geq 0$ are continuous almost periodic functions. Additionally, we suppose that $\alpha_i(t) - k_i(t)\beta_i(t) \geq 0$. The proposed model is

$$
\begin{aligned}
\frac{dN_1}{dt} &= r_1(t)N_1\left(\frac{k_1(t) + \alpha_1(t)N_2}{1 + \beta_1(t)N_2} - a_1(t)N_1\right), \\
\frac{dN_2}{dt} &= r_2(t)N_2\left(\frac{k_2(t) + \alpha_2(t)N_1}{1 + \beta_2(t)N_1} - a_2(t)N_2\right).
\end{aligned}
\tag{2.1}
$$

The system (2.1) describes a facultative mutualism since the dynamics of each population is described by a logistic model when species are not interact-

ing. For $i = 1, 2$, the rates $r_i(t)$ describe the intrinsic growth rate for species i, while the rates $a_i(t)$ describes the intraspecific competition among individuals of the species i. The term $\alpha_i(t)$ describe the benefits received by species i by the interaction with the species j. A factor of regulation of benefits is given by $1 + \beta_i(t)N_j$, where $\beta_i(t)$ is the seasonal mutualistic per capita effect of N_j on N_i, $j \neq i$.

In the following section, we give some results about almost periodic functions and cooperative systems.

3. Almost periodic functions and cooperative systems

In this first part we summarize some well known basic facts about the almost periodic functions and cooperative systems. Almost periodic functions are nowadays a very active theme. We give here only a very basic introduction to the topic and refer the reader to Bohr (1947); Corduneanu (1989) for much more details.

Definition 1 *A function $\phi \in \mathrm{C}^0(\mathbb{R})$ is* almost periodic *if, for all $\epsilon > 0$ there exist a set of real numbers $T(\epsilon) \subseteq \mathbb{R}$ altogether with a length $l(\epsilon) > 0$ such that for any interval of length $l(\epsilon)$, there is at least one point $\tau \in T(\epsilon)$ contained in that interval such that*

$$|\phi(x + \tau) - \phi(x)| < \epsilon$$

for each $x \in \mathbb{R}$.

The above collection of all almost periodic functions, which is a Banach space endowed with the usual $\sup -$norm, will be denoted by $AP(\mathbb{R})$. Note that a periodic function is a special case of an almost periodic function.

For any almost periodic function φ, it is possible to associate a unique Fourier series:

$$\varphi \sim \sum_{n \in \mathbb{N}} a(\lambda_n) e^{i \lambda_n x}. \tag{3.2}$$

The exponents λ_n are called the frequencies of ϕ. Another well-known result in this area is that, for every almost periodic function there exists the *mean value*

$$M(\phi) := \lim_{T \to \infty} \frac{1}{T} \int_0^T \phi(x)dx,$$

which defgines a bounded linear function $M : AP(\mathbb{R}) \to \mathbb{R}$ having the following features Corduneanu (1989).

Properties 1 *1. $\phi \geq 0$ implies $M[\phi] \geq 0$.*

2. The Parseval equality holds:

$$M[|\phi|^2] = \sum_{n \in \mathbb{N}} |a(\lambda_n)|^2. \tag{3.3}$$

3. Given ϕ_1, ϕ_2 almost periodic functions with $\phi_2(t) \geq \phi_1(t) \geq 0$, $M[\phi_1] = M[\phi_2]$, then $\phi_1(t) = \phi_2(t)$, $\forall t \in \mathbb{R}$.

Now we review some aspects about cooperative systems, for a brief introduction to cooperative systems see Smith (1995). For two points $x, y \in \mathbb{R}^2$ denote the partial order $u \leq v$ if $u_i \leq v_i$ for each i, also denote $u < v$ if $u \leq v$ and $u \neq v$. Let $f, g : \mathbb{R} \times D \subseteq \mathbb{R}^3 \to \mathbb{R}$ be a couple of differentiable and almost periodic functions on the first variable. We consider the system:

$$\begin{aligned} x'(t) &= f(t, x(t), y(t)) \\ y'(t) &= g(t, x(t), y(t)), \end{aligned} \tag{3.4}$$

where we suppose that $f(t, x, y), g(t, x, y)$ are both *uniformly almost periodic with respect to* $(x, y) \in C$ for every compact $C \subseteq D$, i.e., the set of translation numbers, $\tau(\epsilon)$, is independent of $(x, y) \in C$.

More specifically, if f have generalized Fourier expansions,

$$f(t, x, y) \sim \overline{f}(x, y) + \sum_{n=0}^{\infty} a(f, \lambda_n) \cos(\lambda_n t) + b(f, \lambda_n) \sin(\lambda_n t),$$

f is uniformly almost periodic, whenever the frequencies λ_n do not depend on (x, y), see Corduneanu (1989) Chapter VI.

Definition 2 *System* (3.4) *is said to be of* cooperative type *if for all $t \in \mathbb{R}$, $x \in (a(t), A(t))$, $y \in (b(t), B(t))$ we have*

$$f_y(t, x, y) \geq 0, \ g_x(t, x, y) \geq 0.$$

We will say that $(a(t), b(t))$ are a sub-solution pair *if*

$$\begin{aligned} a'(t) &\leq f(t, a(t), b(t)) & (3.5) \\ b'(t) &\leq g(t, a(t), b(t)), & (3.6) \end{aligned}$$

For every $t \in \mathbb{R}$. A super-solution $(A(t), B(t))$ *is defined similarly with the reversing inequalities. We will say that a sub-solution $(a(t), b(t))$ and a supersolution $(A(t), B(t))$ are* ordered *if $a(t) \leq A(t)$ and $b(t) \leq B(t)$ for all $t \in \mathbb{R}$.*

An important feature for cooperative system (3.4) related to almost-periodic orbits was established in Díaz-Marín et al. (2022), Theorem 2. Explicitly the following result holds.

Theorem 1 *Consider an ordered pair of a sub-solution pair $(a(t), b(t))$ and a super-solution pair $(A(t), B(t))$ of the system (3.4) such that $a(t) < A(t)$, and $b(t) < B(t)$. Suppose that there is no equilibrium point (x_0, y_0) such that $a(t) \leq x_0 \leq A(t)$ and $b(t) \leq y_0 \leq B(t)$. If the system is of cooperative type, then it has an almost periodic solution satisfying $a(t) \leq x(t) \leq A(t)$ and $b(t) \leq x(t) \leq B(t)$ for all $t \in \mathbb{R}$. Furthermore, if $(\underline{x}(t), \underline{y}(t)), (\overline{x}(t), \overline{y}(t))$, denote the minimal and maximal almost periodic solutions having initial data satisfying $a(0) < x(0) < A(0)$ and $b(0) < y(0) < B(0)$. Then any solution of (3.4), having such initial condition, converges to the product of strips $(\underline{x}(t), \overline{x}(t)) \times (\underline{y}(t), \overline{y}(t))$.*

In the case where there is an equilibrium point we could have a stable equilibrium, instead of a genuine almost periodic orbit.

4. Results

Given an almost periodic function $u : \mathbb{R} \to \mathbb{R}$, we denote

$$u_* := \inf_{t \in \mathbb{R}} u(t) \text{ and } u^* := \sup_{t \in \mathbb{R}} u(t).$$

Now we state our main result

Theorem 2 *Assume $r_i(t), \alpha_i(t), \beta_i(t), k_i(t) \geq 0$ and $a_i(t) \geq 0$ are continuous almost periodic functions (not all constant) with $a_{i*} > 0, \beta_{i*} > 0, k_{i*} > 0$ and that there is no equilibrium point of (2.1) with positive coordinates. Suppose that $\alpha_i(t) - k_i(t)\beta_i(t) \geq 0$, then*

  i) There exists at least one almost periodic solution (N_1, N_2) of (2.1) whose components are positive.

ii) If $(r_1\alpha_1)^*(r_2\alpha_2)^* < (r_1a_1)_*(r_2a_2)_*$, then there exists a unique almost periodic solution in $\mathbb{R}^2_{>0}$ which attracts any other positive solution of (2.1) as $t \to \infty$.

Proof 1 *Firstly we prove the existence claim stated in i). Since $\alpha_i(t) - k_i(t)\beta_i(t) \geq 0$ it is straightforward to verify that the system (2.1) is cooperative. We construct sub- and super-solution pairs. For a super-solution pair; we take*

$$(A(t), B(t)) = (N, N), \ N > 0,$$

and require that these functions satisfy the following inequalities,

$$
\begin{aligned}
A'(t) = 0 \ &\geq \ r_1(t)\left(\frac{k_1^* + \alpha_1^* N}{1 + \beta_{1*}N} - a_{1*}N\right)N \\
&\geq \ r_1(t)\left(\frac{k_1(t) + \alpha_1(t)N}{1 + \beta_1(t)N} - a_1(t)N\right)N, \\
B'(t) = 0 \ &\geq \ r_2(t)\left(\frac{k_2^* + \alpha_2^* N}{1 + \beta_{2*}N} - a_{2*}N\right)N \\
&\geq \ r_2(t)\left(\frac{k_2(t) + \alpha_2(t)N}{1 + \beta_2(t)N} - a_2(t)N\right)N.
\end{aligned}
$$

Since $a_{i*} > 0$, then by taking N big enough the right side is effectively negative. Therefore, they constitute a super-solution pair.

For constructing a sub-solution pair, we consider

$$(a(t), b(t)) = (\epsilon, \ \epsilon), \ \epsilon > 0,$$

demanding that these functions satisfy the inequalities stated in (3.5),

$$
\begin{aligned}
a'(t) = 0 \ &\leq \ r_1(t)\left(\frac{k_{1*} + \alpha_1(t)\epsilon}{1 + \beta_1(t)\epsilon} - a_1^*\epsilon\right)\epsilon \\
&\leq \ r_1(t)\left(\frac{k_1(t) + \alpha_1(t)\epsilon}{1 + \beta_1(t)\epsilon} - a_1(t)\epsilon\right)\epsilon, \\
b'(t) = 0 \ &\leq \ r_2(t)\left(\frac{k_{2*} + \alpha_2(t)\epsilon}{1 + \beta_2(t)\epsilon} - a_2^*\epsilon\right)\epsilon \\
&\leq \ r_2(t)\left(\frac{k_2(t) + \alpha_2(t)\epsilon}{1 + \beta_2(t)\epsilon} - a_2(t)\epsilon\right)\epsilon.
\end{aligned}
$$

Since $k_{i*} > 0$ and any almost periodic function is bounded, then the right side is not negative for $\epsilon > 0$ small enough. Thus, we have a sub-solution pair. Therefore, by Theorem 1 there exists at least one almost periodic solution for

system (2.1). *This finishes the proof of the existence of an almost periodic solution.*

We now prove the uniqueness statement. We consider a maximal pair $(\hat{N}_1, \hat{N}_2)$ and minimal pair $(\check{N}_1, \check{N}_2)$ of almost periodic solutions. If we recall $M[(\ln \hat{N}_i)'] = 0$, then

$$M\left[r_i\left(\frac{k_i(t) + \alpha_i(t)\hat{N}_j}{1 + \beta_i(t)\hat{N}_j}\right)\right] = M\left[r_i a_i \hat{N}_i\right], \ i \neq j, \qquad (4.7)$$

and

$$M\left[r_i\left(\frac{k_i(t) + \alpha_i(t)\check{N}_j}{1 + \beta_i(t)\check{N}_j}\right)\right] = M\left[r_i a_i \check{N}_i\right] \ i \neq j. \qquad (4.8)$$

Thus,

$$M\left[r_i\left(\frac{k_i(t) + \alpha_i(t)\hat{N}_j}{1 + \beta_i(t)\hat{N}_j} - \frac{k_i(t) + \alpha_i(t)\check{N}_j}{1 + \beta_i(t)\check{N}_j}\right)\right] = M\left[r_i a_i \left(\hat{N}_i - \check{N}_i\right)\right] \ i \neq j. \qquad (4.9)$$

A straightforward calculation yields

$$\frac{k_i(t) + \alpha_i(t)\hat{N}_j}{1 + \beta_i(t)\hat{N}_j} - \frac{k_i(t) + \alpha_i(t)\check{N}_j}{1 + \beta_i(t)\check{N}_j} \leq \alpha_i(t)(\hat{N}_j - \check{N}_j).$$

Therefore, from this inequality and from (4.9), we conclude that

$$M\left[r_i a_i \left(\hat{N}_i - \check{N}_i\right)\right] \leq M\left[r_i \alpha_i \left(\hat{N}_j - \check{N}_j\right)\right]. \qquad (4.10)$$

Hence

$$(r_1 a_1)_* M\left[\hat{N}_1 - \check{N}_1\right] \leq (r_1 \alpha_1)^* M\left[\hat{N}_2 - \check{N}_2\right] \leq \frac{(r_1 \alpha_1)^* (r_2 \alpha_2)^*}{(r_2 a_2)_*} M\left[\hat{N}_1 - \check{N}_1\right].$$

If $M\left[\hat{N}_1 - \check{N}_1\right] > 0$ the we reach a contradiction with respect to condition ii). Therefore, $M\left[\hat{N}_1\right] = M\left[\check{N}_1\right]$, whence $\hat{N}_1 = \check{N}_1$ by 3) in Properties 1. To see this argument in detail see Díaz-Marín et al. (2022). By the equation (4.10) we also get $\hat{N}_2 = \check{N}_2$. Finally, with our construction, we can make the supersolutions arbitrarily large, and the sub-solutions arbitrarily small. Therefore, we have a single attractor consisting of an almost periodic orbit in the whole set $\mathbb{R}^2_{>0}$. This concludes ii) and therefore ends the proof of Theorem 2.

5. Numerical examples

In this section, we show the behavior of the solutions of model (2.1) for some values of the parameters of the model. To do this, we use the almost periodic functions given in (5.11) with $r_1 = 0.4, r_2 = 0.2, k_1 = 0.02, k_2 = 0.01, \alpha_1 = 0.05, \alpha_2 = 0.02, \beta_1 = 0.00004, \beta_2 = 0.00002, a_1 = 0.095, a_2 = 0.09, c_1 = 5, c_2 = 3, c_3 = 1, c_4 = 0.66, c_5 = 1, c_6 = 0.65, \eta_1 = \sqrt{7}, s_1 = 0.01, s_2 = 0.1$. These parameter values guarantee that conditions of Theorem 2 are satisfies, since $\alpha_i(t) - k_i(t)\beta_i(t) \geq 0$ and $(r_1\alpha_1)^*(r_2\alpha_2)^* = 0.00084093 < (r_1a_1)_*(r_2a_2)_* = 0.0054487$. With In Figure 1, it is shown that solutions go to a global almost periodic attractor. Figure 1 (a) shows simultaneously both mutualistic population densities. Figure 1 (b) shows that, for different initial conditions, N_1 converges to a global almost periodic attractor. In Figure 1 (c), it is shown that N_2 converges to a global almost periodic attractor.

$$
\begin{aligned}
r_1(t) &= r_1 \left(c_1 + 0.18 \cos\left(s_1 2\pi t \right) + 0.46 \cos\left(s_1 2\pi \eta_1 t \right) \right), \\
k_1(t) &= k_1 \left(c_1 + 0.18 \cos\left(s_1 2\pi t \right) + 0.46 \cos\left(s_1 2\pi \eta_1 t \right) \right), \\
\alpha_1(t) &= \alpha_1 \left(c_3 + 0.18 \cos\left(s_1 2\pi t \right) + 0.46 \cos\left(s_1 2\pi \eta_1 t \right) \right), \\
\beta_1(t) &= \beta_1 \left(c_1 + 0.18 \cos\left(s_1 2\pi t \right) + 0.46 \cos\left(s_1 2\pi \eta_1 t \right) \right), \\
a_1(t) &= a_1 \left(c_4 + 0.18 \cos\left(s_1 2\pi t \right) + 0.46 \cos\left(s_1 2\pi \eta_1 t \right) \right), \\
r_2(t) &= r_2 \left(c_2 + 0.18 \cos\left(s_1 2\pi t \right) + 0.46 \cos\left(s_1 2\pi \eta_1 t \right) \right), \\
k_2(t) &= k_2 \left(c_2 + 0.18 \cos\left(s_1 2\pi t \right) + 0.46 \cos\left(s_1 2\pi \eta_1 t \right) \right), \\
\alpha_2(t) &= \alpha_2 \left(c_5 + 0.18 \cos\left(s_1 2\pi t \right) + 0.46 \cos\left(s_1 2\pi \eta_1 t \right) \right), \\
\beta_2(t) &= \beta_2 \left(c_2 + 0.18 \cos\left(s_1 2\pi t \right) + 0.46 \cos\left(s_1 2\pi \eta_1 t \right) \right), \\
a_2(t) &= a_2 \left(c_6 + 0.18 \cos\left(s_1 2\pi t \right) + 0.46 \cos\left(s_1 2\pi \eta_1 t \right) \right).
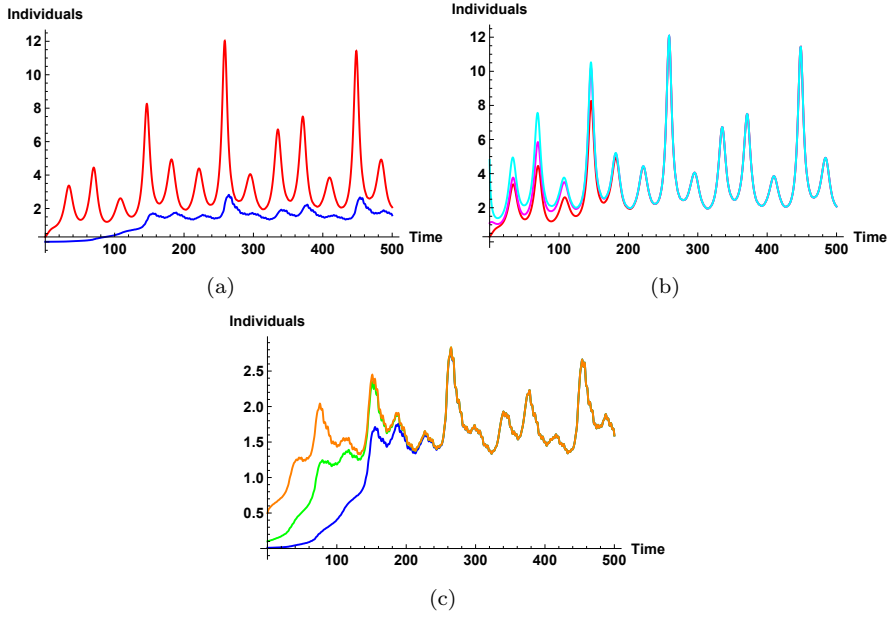\end{aligned}
\tag{5.11}
$$

Figure 1: Behavior of the solutions of model (2.1). In case (a), species N_1 is shown in red color and N_2 is shown in blue color. Case (b) and (c) show that solutions with different initial conditions converge to an almost periodic solutions. For case (a) $N_1(0) = 0.3, 1.1, 4.8$ and for case (b) $N_2(0) = 0.01, 0.1, 0.5$.

In figure 2, we compare the behavior of the solutions of the almost periodic model with the behavior of the solutions of the periodic model. To do this, in the functions given by (5.11), we use $\eta_1 = \sqrt{7}$ for the almost periodic case while we use $\eta_1 = 2$ for the periodic case. All the parameter values are the same as those used in figure 1.
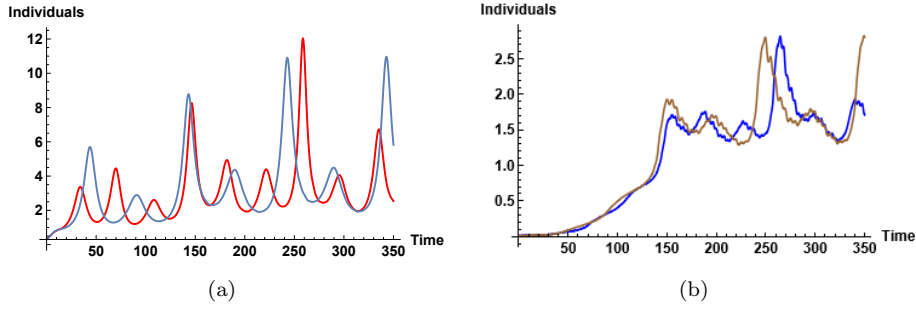
(a)

(b)

Figure 2: Figure (a) shows the behavior of N_1 in two scenarios: almost periodic scenario and periodic scenario. In a similar way, figure (b) shows the behavior of N_2 in both scenarios: the almost periodic and the periodic one. For the numerical simulations $N_1(0) = 0.3$ and $N_2(0) = 0.01$. In the almost periodic case (periodic case), N_1 and N_2 are shown in color red and blue (violet and brown), respectively.

Finally, figure 3 shows that phenological match/mismatch might be obtained by varying the values of the intrinsic growth rates. In figure 3 (a) we use the values $r_1 = 0.4$ and $r_2 = 0.8$ while in figure 3 (b) we use $r_1 = 0.4$ and $r_2 = 1.8$. All other parameter values remain the same as those used in Figure 2.
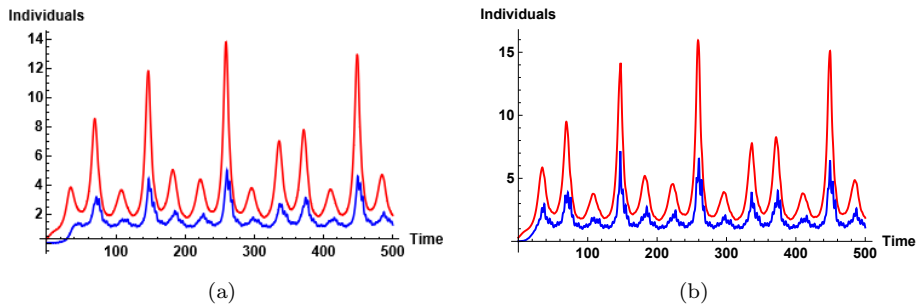

(a)

(b)

Figure 3: Figure shows the effects due to mutualistic interaction. Notice that, when r_2 increases, the abundance peak of both species increases.

6. Conclusions

In this work, we propose an almost periodic model to describe a mutualistic interaction between two species. We proved that solutions converge to a global almost periodic attractor when some conditions over the parameters of the model are satisfied. By comparing the almost periodic case with the periodic one, we show that even though the solutions are similar while time remains small, they separate as time increases. Thus, modeling seasonal effects with periodic rates can lead either to an underestimation or to an overestimation of population densities. This miscalculation might lead to wrong conservation strategies, with catastrophic consequences for sustainability. Therefore, the analysis of almost periodic mutualistic models can help to decision makers to design helpful interventions in the maintenance of biodiversity.

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