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An almost periodic θ-logistic model to describe climate-mediated shifts in mutualistic species with K strategies

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ABSTRACT: Mutualism relationships have a great impact in biodiversity. From an ecological perspective, modeling the dynamics of large long-lived mutualistic species when their phenology changes can be useful. In this work, we propose an almost periodic θ-logistic model to describe changes in the phenology of species that have concave (linear) decreasing per capita growth rates (species with a K strategy). We prove that a single global almost periodic attractor exists when some conditions over the parameters of the model are satisfied. Numerical solutions show sustained oscillations on the population which tend to a unique globally stable almost periodic orbit. Modeling seasonal drivers through periodic functions can lead to underestimate or to overestimate population densities with respect to almost periodic functions (synchronous mismatch).This misleading estimation can lead to the design of erroneous conservation strategies, which could have a great impact on biodiversity management.

Key Words: θ-logistic model, mutualism, almost periodic model, K strategy.

Contents

1. Introduction

Forecasting the population dynamics of mutualistic species is of paramount importance from an ecological perspective. However, predicting the evolution of interacting species is difficult mainly because of the change on population densities due to the alteration of both exogenous (e.g., climate) and endogenous (e.g., predation, competition, mutualism) processes.

Among the ecological relationships, mutualism (facultative or obligated) is ubiquitous in nature and it has profoundly molded biodiversity as we know it nowadays. Interacting species in a mutualistic relationship receive benefits in their fitness due to the interaction among their individuals. Whence, they can increase their equilibrium densities, their intrinsic growth rates, or both [37]. A mutualistic individual receives benefits from its partner species either directly or indirectly. For example, plants get a direct benefit when their zygotes and gametes are dispersed by their pollinators. In contrast, plants obtain an indirect benefit from ants by obtaining protection against herbivory [37,1]. It has been documented that when climate-mediated factors shift, the force of the mutualistic interaction can change. For example, during the dry season plant nectar is scarce. Hence, the ants feed on the honeydew produced by insects. Thus, the protection that ants give to plants is weakened due to much less presence of ants [20].

Mutualistic interactions have been analyzed using differential equation models. Most of these models are constructed assuming constant interaction coefficients and decreasing linear per capita growth rates [3,30,25,31,32,33,35,36]. However, models constructed under these assumptions present some limitations

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such as: 1) Assuming constant coefficients, they describe a static interaction between species and they do not capture changes in exogenous and in endogenous factors. 2) Assuming decreasing linear per capita growth rates, the models neglect two main phenomena. Some populations experience strong density-dependent regulation at low population numbers, therefore the population growth is constrained well in advance of reaching a stable equilibrium (carrying capacity). Whereas, in other populations, the full effects of density dependence are not manifest until the population is resource-limited and closer to its carrying capacity [26,27]. Borlestean et al., (2015) show that the two effects mentioned before are possible, even for the same species, when the density of the nutrient is varied [5]. To analyze a mutualistic relationship with density dependence, the per capita growth rate of each population is modeled by a θ-logistic equation. However, even in such scenarios the interaction coefficient is considered as a constant [19].

On the other hand, we must mention that there are ecological models that incorporate seasonal effects in the demographic and the ecological parameters [21,7,2,9,10]. Most of these models use functions such as $\sin(t)$ or $\cos(t)$ to describe periodic mechanisms. However, the seasonal shifts are far from having a pattern as simple as that. Moreover, it could be assumed that seasonality involves both exogenous and endogenous processes, appearing in the model as a linear combination of trigonometric functions, which are not necessarily synchronized [34,21,8].

We are interested in studying the temporal coincidence of species in a mutualistic relationship when the parameters are oscillating time-dependent and the intrinsic per capita growth rates are density dependent functions. Specifically, we propose an almost periodically forced model to describe scenarios for mutualistic populations in which the population growth rates are relatively unaffected until populations are nearing carrying capacity. We use the theory of almost periodic functions [4] to showing the results.

2. The model

In this section, we present an almost periodic model wit density-dependence to describe the effect of seasonality in mutualistic large long-live species.

We consider that the per capita growth rate for each species changes as a function of its density as follows

$$\frac{1}{N_i}\frac{dN_i}{dt} = r_i(t) - \alpha_i(t) g_i(N_i), \qquad \text{with } i = 1, 2. \tag{2.1}$$

The parameters $r_i(t)$ and $\alpha_i(t)$ denote the population growth rate and the intraspecific competition rate, for the species i, respectively.

To model the density effects, we consider that the decline of the per capita growth rate of the species N is commonly modeled by the θ-logistic equation

$$\frac{1}{N}\frac{dN}{dt} = r - \alpha N^{\theta}, \tag{2.2}$$

with r, α, and θ positive constant parameters.

According to Sibly and coworkers, from the analysis of 1780 time series of different populations, there are far more cases in which the per capita growth rate in (2.2) is related to $0 < \theta < 1$ than cases in which $\theta > 1$; see [26]. It has been suggested that the geometrical behavior of the per capita growth rate depends on the a species' life history [26,24,12]. In [26], it is mentioned that large long-live species live close to the carrying capacity of their environments. These species are limited mainly by resources. Therefore, the per capita growth rate of large long-lived species remain unaffected until populations are attaining their carrying capacity (species with a K strategy). This behavior is described by a per capita growth rate with a value of $\theta > 1$. Sibly et al., (2005) analyze 1780 time series of mammals, birds, fish, and insects and they show that 32 species that represent the major taxonomic groups have associated values of $\theta > 1$ [26,27,28]. In contrast, the per capita growth rates of insects and some fish are related to values of $0 < \theta < 1$ (species with a r strategy).

Therefore, to model the density dependence in (2.1), we use

$$g(N_i) = N_i^{\theta_i}, \qquad \text{with } \theta_i > 1, \text{and } i = 1, 2. \tag{2.3}$$

The interaction between the mutualistic species is modeled by a term of the type mass action law given by $\beta_i(t)N_iN_j$. The term $\beta_i(t)N_iN_j$ describes the benefit received for individuals in the species i from interaction with the individuals of the species j, with $i \neq j$.

Since we are interested in analyzing the behavior of mutualistic species with a seasonal phenology, we assume that $r_i(t)$, $\alpha_i(t)$ and $\beta_i(t)$ are non negative almost periodic functions.

Therefore, the almost periodic model proposed is given by

$$\begin{aligned} \frac{dN_1}{dt} &= \Big(r_1(t) - \alpha_1(t)N_1^{\theta_1} + \beta_1(t)N_2\Big)\,N_1, \\ \frac{dN_2}{dt} &= \Big(r_2(t) - \alpha_2(t)N_2^{\theta_2} + \beta_2(t)N_1\Big)\,N_2. \end{aligned} \tag{2.4}$$

In [19], model (2.4) is analyzed when all rates are constant. They showed that when $\theta_i > 1$, for $i = 1, 2$, the model has a single attractor interior equilibrium, for all values of the parameters of the model. The authors proved that an accelerating density dependence of each species, ($\theta_i > 1$), has a stabilizing effect in the mutualistic relationship. In contrast, when $0 < \theta_i < 1$, for $i = 1, 2$, the model presents two scenarios. In a first case, the model has no interior equilibrium points. In such a scenario, the model presents unbounded solutions. In the second case, the model has two interior equilibrium points for some values of their parameters. In such a scenario, there is a stable and a saddle equilibrium point. In a first case, the model does not present interior equilibrium points. In such a scenario, the model presents unbounded solutions. In a second case, the model can present two interior equilibrium points. In such a scenario, there is a stable and a saddle equilibrium point.

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 [4,6] for much more details.

Definition 3.1 *A function $\phi \in \mathrm{C}^0(\mathbb{R})$ is almost periodic if, for all $\epsilon > 0$ there exists 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 $x \in \mathbb{R}$. We will call numbers in $T(\epsilon)$ translation numbers and while $l(\epsilon)$ will be called a length for $T(\epsilon)$.

The collection of all almost periodic functions is a Banach space endowed with the usual sup $-$norm and will be denoted as $AP(\mathbb{R})$. To an almost periodic function φ, it is possible to associate its unique Fourier series:

$$\phi \sim \sum_{n\in\mathbb{N}} a(\lambda_n)e^{i\lambda_n x}. \tag{3.1}$$

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

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

This is a bounded linear function, $M : AP(\mathbb{R}) \to \mathbb{R}$, with the following properties:

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

2. The Parseval equality holds:

$$M[|\phi|^2] = \sum_{n\in\mathbb{N}} |a(\lambda_n)|^2. \tag{3.2}$$

The following result is well known; we include a full proof for completeness.

Lemma 3.1 *Let $\hat{\phi}, \check{\phi}$ be almost periodic functions such that*

$$\hat{\phi}(t) \geq \check{\phi}(t) \geq 0, \qquad M\left[\hat{\phi}\right] = M\left[\check{\phi}\right]. \tag{3.3}$$

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

Proof: Since $\hat{\phi}(t), \check{\phi}(t)$ are almost periodic, then they are bounded. Hence,

$$\begin{aligned} 0 \leq M\left[\hat{\phi}^2 - \check{\phi}^2\right] &\leq M\left[(\hat{\phi} - \check{\phi})(\hat{\phi} + \check{\phi})\right] \\ &\leq (2\sup\{\hat{\phi}(t)\}) \cdot M\left[\hat{\phi} - \check{\phi}\right] = 0. \end{aligned}$$

Therefore, $M\left[\hat{\phi}^2\right] = M\left[\check{\phi}^2\right]$. Thus,

$$0 \leq M\left[(\hat{\phi} - \check{\phi})^2\right] \leq 2\left(M\left[\hat{\phi}^2\right] - M\left[\hat{\phi}\check{\phi}\right]\right) \leq 2\left(M\left[\hat{\phi}^2\right] - M\left[\check{\phi}^2\right]\right) = 0.$$

If we apply Parseval's Theorem on the sum of the squares of the Fourier coefficients of $\hat{\phi} - \check{\phi}$ we get $\hat{\phi} \equiv \check{\phi}$. □

Now we review some aspects about cooperative systems, for a brief introduction to cooperative systems see [29]. 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 has 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 $(x, y) \in C$, see [6] Chapter VI.

Definition 3.2 *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 subsolution pair if

$$a'(t) \leq f(t, a(t), b(t)), \tag{3.5}$$

$$b'(t) \leq g(t, a(t), b(t)), \tag{3.6}$$

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 systems (3.4) related to almost-periodic orbits was established in [8], Theorem 2. Explicitly, the following result holds.

Theorem 3.1 *Consider an ordered pair of a subsolution pair* $(a(t), b(t))$ *and a supersolution 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* $a(t) \le x_0 \le A(t)$ *and* $b(t) \le y_0 \le B(t)$. *If the system is cooperative type, then it has an almost periodic solution satisfying* $a(t) \le x(t) \le A(t)$ *and* $b(t) \le x(t) \le B(t)$ *for all* $t \in \mathbb{R}$. *Furthermore, if* $(\underline{x}(t), \underline{y}(t)), (\overline{x}(t), \overline{y}(t))$, *denotes 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), *converges to the product of strips* $(\underline{x}(t), \overline{x}(t)) \times (\underline{y}(t), \overline{y}(t))$.

4. Results

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

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

Now we state our main result

Theorem 4.1 *Assume* $\alpha_i(t), \beta_i(t) \ge 0$ *and* $r_i(t) \ge 0$ *are continuous almost periodic functions (not all of them constant) with* $r_{i*} > 0, \alpha_{i*} > 0$, $\theta_i \ge 1$. *Suppose at least one of the following conditions holds true:*

a) Either $\theta_i > 1$ *for* $i = 1, 2$,

b) or $\alpha_{i*} > \beta_i^*$ *when* $\theta_i = 1$ *for some* i.

Then there exists at least one almost periodic solution (N_1, N_2) *of* (2.4) *whose components are strictly positive.*
In addition, assuming that $\theta_i \in \mathbb{N}$, *if at least one of the following assertions holds true*

i) $\theta_1 \ne \theta_2$ *or*

ii) $\alpha_{i*} > \beta_i^*$ *when* $\theta_1 = \theta_2$.

Then there exists a unique almost periodic solution in $\mathbb{R}^2_{>0}$ *attracting all other positive solutions of* (2.4), *when* $t \to \infty$.

Proof: For existence, we verify straightforward that the system (2.4) is cooperative. Then, we construct sub- and super-solution pairs. For a super-solution pair; we have

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

these functions satisfy the inequalities.

$$\begin{aligned} A'(t) = 0 \quad &\ge \quad \left(r_1^* - \alpha_{1*} N^{\theta_1} + \beta_1^* N\right) N \\ &\ge \quad \left(r_1(t) - \alpha_1(t) N^{\theta_1} + \beta_1(t) N\right) N, \\ B'(t) = 0 \quad &\ge \quad \left(r_2^* - \alpha_{2*} N^{\theta_2} + \beta_2^* N\right) N \\ &\ge \quad \left(r_2(t) - \alpha_2(t) N^{\theta_2} + \beta_2(t) N\right) N. \end{aligned}$$

By taking N big enough and using the conditions $a)$ and $b)$, the right side is negative. Then they constitute a super-solution pair.

In order to construct a sub-solution, we take

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

where, in order to satisfy the inequalities in (3.5)

$$\begin{aligned} a'(t) = 0 \quad &\le \quad \left(r_{1*} - \alpha_1^* \epsilon^{\theta_1} + \beta_{1*}\epsilon\right)\epsilon \le \left(r_1(t) - \alpha_1(t)\epsilon^{\theta_1} + \beta_1(t)\epsilon\right)\epsilon, \\ b'(t) = 0 \quad &\le \quad \left(r_{2*} - \alpha_2^* \epsilon^{\theta_2} + \beta_{2*}\epsilon\right)\epsilon \le \left(r_2(t) - \alpha_2(t)\epsilon^{\theta_2} + \beta_2(t)\epsilon\right)\epsilon, \end{aligned}$$

we take $\epsilon > 0$ in the right side small enough. Thus, we have a sub-solution pair. Therefore, by Theorem 3.1, there exists at least one almost periodic solution for system (2.4). This finishes the proof of the existence of an almost periodic solution.

For uniqueness, by the symmetry of the equations, without loss of generality we can assume $\theta_1 \leq \theta_2$. 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 that the mean $M[(\ln \hat{N}_i)'] = 0$, then

$$\begin{aligned} M[r_1] &= M\left[\alpha_1 \hat{N}_1^{\theta_1}\right] - M[\beta_1 \hat{N}_2] \\ &= M\left[\alpha_1 \check{N}_1^{\theta_1}\right] - M[\beta_1 \check{N}_2], \end{aligned}$$

Thus,

$$M\left[\alpha_1\left(\hat{N}_1^{\theta_1} - \check{N}_1^{\theta_1}\right)\right] = M\left[\beta_1\left(\hat{N}_2 - \check{N}_2\right)\right], \tag{4.1}$$

Similarly

$$M\left[\alpha_2\left(\hat{N}_2^{\theta_2} - \check{N}_2^{\theta_2}\right)\right] = M\left[\beta_2\left(\hat{N}_1 - \check{N}_1\right)\right].$$

From the well known identity

$$b^n - a^n = \left(\sum_{i=0}^{n-1} b^{n-1-i} a^i\right)(b-a), \ n \in \mathbb{N},$$

applying this inequality with $b = \hat{N}_i, a = \check{N}_i$ and $n = \theta_i$; using that $\epsilon \leq \check{N}_i \leq \hat{N}_i$ for some $\epsilon > 0$ as in the first part, we obtain

$$\theta_i \epsilon^{\theta_i - 1}(\hat{N}_i - \check{N}_i) \leq \left(\hat{N}_i^{\theta_i} - \check{N}_i^{\theta_i}\right).$$

From (4.1), we get

$$\begin{aligned} \alpha_{1*}\theta_1\epsilon^{\theta_1-1} M\left[\hat{N}_1 - \check{N}_1\right] &\leq M\left[\alpha_1\left(\hat{N}_1^{\theta_1} - \check{N}_1^{\theta_1}\right)\right] \leq \beta_1^* M\left[\hat{N}_2 - \check{N}_2\right] \\ &\leq \alpha_{2*} M\left[\hat{N}_2 - \check{N}_2\right] \leq \frac{\beta_1^*}{\alpha_{2*}}\theta_2\epsilon^{\theta_2-1}\beta_2^* M\left[\hat{N}_1 - \check{N}_1\right]. \end{aligned}$$

Therefore,

$$0 \leq \frac{\alpha_{1*}\alpha_{2*}\theta_1}{\beta_1^*\beta_2^*\theta_2\epsilon^{\theta_2-\theta_1}} M\left[\hat{N}_1 - \check{N}_1\right] \leq M\left[\hat{N}_1 - \check{N}_1\right].$$

If $M\left[\hat{N}_1 - \check{N}_1\right] > 0$, this leads to a contradiction $\alpha_{i*} > \beta_i^*$ when $\theta_1 = \theta_2$. If $\theta_2 > \theta_1$, then we obtain a contradiction making $\epsilon > 0$ small enough. Therefore, $M\left[\hat{N}_1\right] = M\left[\check{N}_1\right]$, whence $\hat{N}_1 = \check{N}_1$ by Lemma 3.1. By the equation (4.1) we get $\hat{N}_2 = \check{N}_2$.

Finally, with our construction, we can make the super-solutions arbitrarily large, and the sub-solutions arbitrarily small. Thus, we conclude that there exists just one single almost periodic attractor in the set $\mathbb{R}^2_{>0}$. This concludes *ii*) and therefore ends the proof of Theorem 4.1.

□

5. Numerical examples

In this section, we show different scenarios for the solutions of model (2.4). We consider arbitrary values of the parameters to show scenarios given by Theorem 4.1.

To model seasonal drivers in the mutualistic interaction, we consider that all rates in model (2.4) are a linear combination of two trigonometric functions such that each term is associated to abiotic and biotic factors that can be altered by climate-mediated factors. Then, we define the following functions

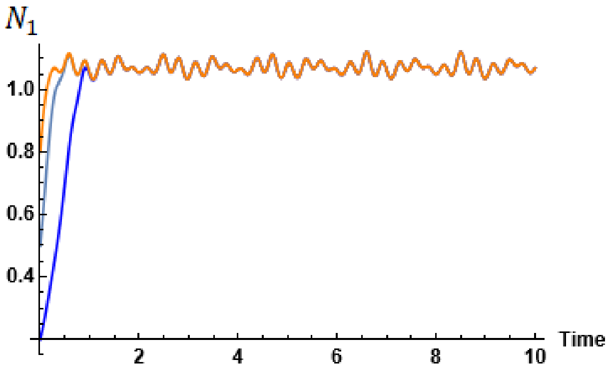
$$\begin{aligned} r_i(t) &= r_i^p(t) + r_i^q(t), \\ \alpha_i(t) &= \alpha_i^p(t) + \alpha_i^q(t), \\ \beta_i(t) &= \beta_i^p(t) + \beta_i^q(t), \end{aligned} \tag{5.1}$$

with $r_i^p(t) = \gamma_i\,(\delta_i + \varepsilon_i \cos(2\pi t))$, $\alpha_i^p(t) = \vartheta_i\,(\iota_i + \kappa_i \cos(2\pi t))$, $\beta_i^p(t) = \xi_i\,(\pi_i + \rho_i \cos(2\pi t))$, $r_i^q(t) = \gamma_i\,(\zeta_i \sin(2\pi\eta_i t))$, and $\alpha_i^q(t) = \vartheta_i\,(\lambda_i \sin(2\pi\mu_i t))$, $\beta_i^q(t) = \xi_i\,(\sigma_i \sin(2\pi\tau_i t))$.

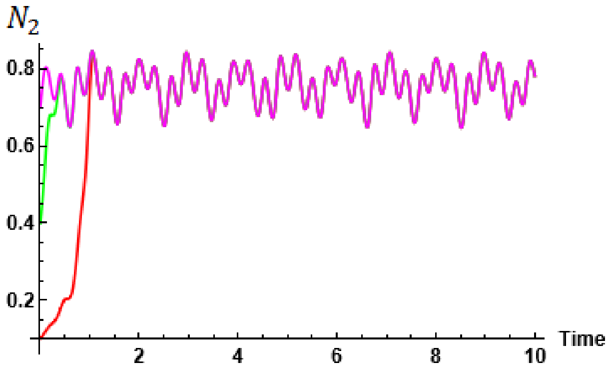
In a first scenario, we assume that $r_i^p(t)$, $\alpha_i^p(t)$ and $\beta_i^p(t)$ are periodic functions. That is, they do not loss their periodicity by changes in environmental drivers. In contrast, we assume that $r_i^q(t)$, $\alpha_i^q(t)$ and $\beta_i^q(t)$ are almost periodic functions since they loss their synchronicity due to changes in environmental factors.

In such a scenario, for the numerical simulations, we use the following values of the parameters. $\gamma_i = 0.7, 0.09$, $\delta_i = 3.5, 2.1$, $\varepsilon_i = 0.7, 0.54$, $\zeta_i = 0.3, 0.38$, $\eta_i = \sqrt{7}, \sqrt{10}$, $\vartheta_i = 0.9, 5.2$, $\iota_i = 2.2, 3.1$, $\kappa_i = 0.6, 0.52$, $\lambda_i = 0.35, 0.33$, $\mu_i = \sqrt{10}, \sqrt{7}$, $\xi_i = 0.11, 4.85$, $\phi_i = 3.7, 0.6$, $\rho_i = 0.8, 0.3$, $\sigma_i = 0.45, 0.35$, $\tau_i = \sqrt{7}, \sqrt{10}$ and $\theta_i = 5.0, 6.0$, for $i = 1, 2$, respectively. With these values of the parameters of model (2.4), the functions $r_i(t)$, $\alpha_i(t)$ and $\beta_i(t)$ are almost periodic functions and the conditions a) and i) of Theorem 4.1 are satisfied.

Figure 1 shows the behavior of the numerical solutions of model (2.4) for different initial conditions. When the conditions a) and i) of Theorem 4.1 hold, solutions of model (2.4) with different initial conditions converge to a single attractor almost periodic orbit in the set $\mathbb{R}^2_{>0}$.



(a)

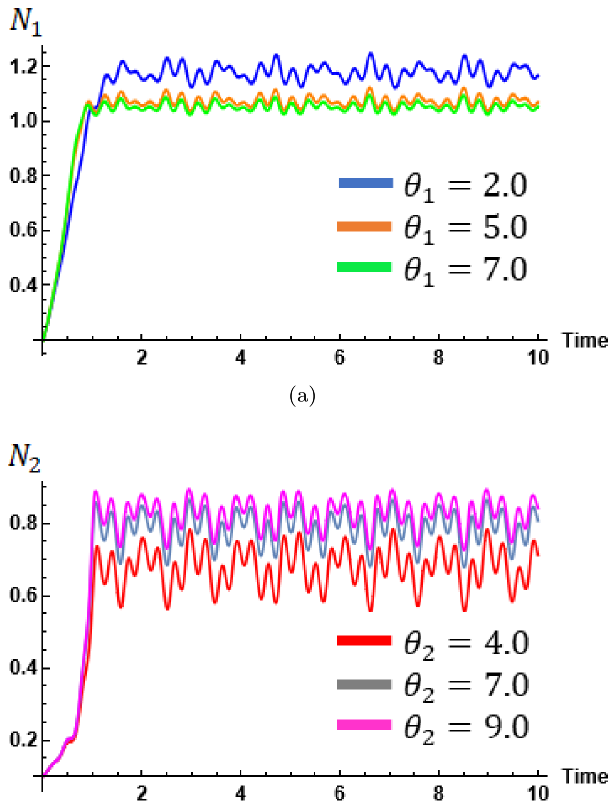


(b)

Figure 1: Solutions of model (2.4) converge to a unique globally stable almost periodic solution for different initial conditions. Case (a) shows the behavior of $N_1(t)$ for $N_1(0) = 0.2, 0.5, 0.8$ while case (b) shows the behavior of $N_2(t)$ with $N_2(0) = 0.1, 0.4, 0.7$.

Figure 2 shows numerical solutions of model (2.4) when the parameters θ_1 and θ_2 are simultaneously varied and all other parameters of the model are the same used in the previous example. Notice that, the species $N_1(t)$ reaches bigger population densities when θ_1 and θ_2 are smaller; see Figure 2 (a). In contrast, the species $N_2(t)$ reaches bigger population densities when θ_1 and θ_2 are bigger; see Figure 2 (b).

Observe that, the results shown in Theorem 4.1 include the periodic case when $r_i(t)$, $\alpha_i(t)$ and $\beta_i(t)$



(a)

(b)

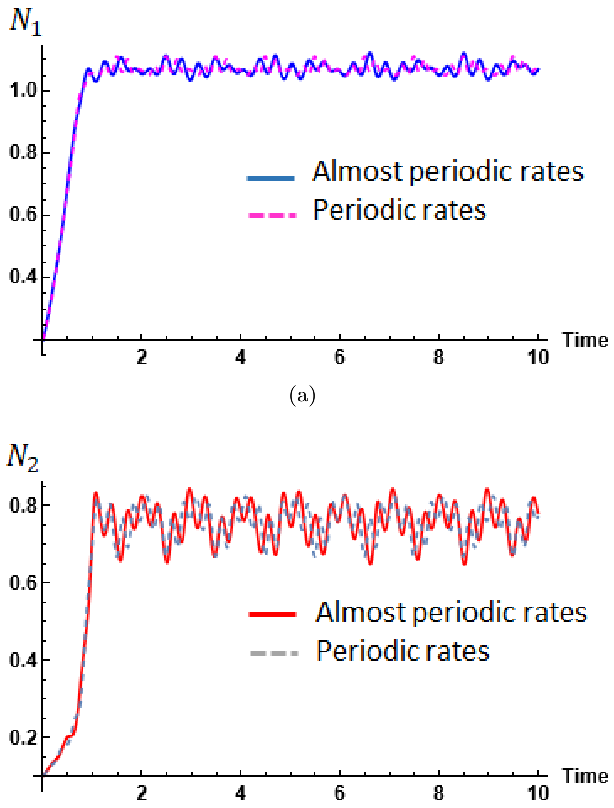
Figure 2: By varying the values of θ_1 and θ_2, the population densities are affected in different proportions which oscillate around a global attractor almost periodic.

are periodic functions. To compare a periodic case with an almost periodic one, we change some values of the parameters of the functions $r_i^q(t)$, $\alpha_i^q(t)$ and $\beta_i^q(t)$ in (5.1) such that they are periodic functions. To do this we use $\eta_1 = \mu_1 = \tau_1 = 5$ and $\eta_2 = \mu_2 = \tau_2 = 4$ and all other values of the parameters are the same used in Figure 1. For the almost periodic case, we use the scenario shown in Figure 1. Figure 3 shows the behavior of the solutions of model (2.4) when the rates are modeled by almost periodic (continuous lines) or periodic functions (dashed lines). Notice that, both solutions are similar at the beginning of the time. However, for future times, the solutions might be separated.

6. Discussion

Climate-mediated changes can alter the phenology of species, which could negatively affect their population densities. Unfortunately, it has been recorded that global climate change has affected the phenology of some tightly interacting species in such a way that a phenological mismatch occurs between them [16,22]. A phenological mismatch in mutualistic species can have catastrophic consequences for the biodiversity of species since mutualism plays indispensable roles in the ecosystem function. In this direction, according to Hale and Valdovinos, nearly all species on Earth participate in at least one of the following mutualistic functions: pollination, seed dispersal, protection, and resource exchange [13].

Knowing the effects that climate change produces in mutualistic species has been of great interest from an economical and biological perspective. It has been described that plants and pollinators have suffered a phenology mismatch due to changes in abiotic factors such as temperature and weather [14,18,11,23,16,17]. However, mutualism has been subjected to less experimental or theoretical study than other ecological relationships, for example, prey-predator and competition relationship between species [13].



(a)

(b)

Figure 3: Solutions of model (2.4) when $r_i(t)$, $\alpha_i(t)$ and $\beta_i(t)$ are either almost periodic functions (continuous lines) or periodic functions (dashed lines).

Even though phenological changes in species are occurring with increasing frequency, seasonal mutualism trough mathematical models has been little studied. Mutualistic models with non constant parameters are scarce in mathematical ecology. To with, there are few ecological mutualistic models either with density-dependent rates or with time-dependent rates in comparison with models with constant rates. Usually, mutualistic models with density-dependent rates describe scenarios in which the net rates of benefits-costs change as a function of the population densities. In such a scenario, the type of interaction ecological between two species can change from a mutualism to a competition scenario, among other ecological relationships, when the parameters of the model change [15]. On the other hand, ecological non-autonomous models can be used to understand population dynamics of mutualistic species when their dynamics are governed by seasonal drivers. Since modeling mutualistic interactions using constant rates can be very restrictive in a scenario of global climate change, it is a priority to model seasonal mutualisms with rates that capture these seasonal changes and the population density dependence.

In this work, we combine seasonal drivers and density-dependence to construct an almost periodic mutualism model. In the construction of the model proposed, it is assumed the following: a) the population dynamics of each species, when the partner species is absent, is modeled by a θ-logistic model. b) the demographic and ecological rates are given by almost periodic functions. The assumption a) models large long-lived species which are related to per capita growth rates that are being limited mainly by resources, that is, species with a K strategy ($\theta_i > 1$, for $i = 1, 2$). These species are rarely subject to natural selection for increased performance at a low population density. The assumption b) models that changes in environmental drivers cause demographic and ecological rates to loss periodicity. The analysis of the model shows that if environmental drivers affect the demographic and ecological rates of large long-lived species, then the populations show sustained oscillations converging to a single almost periodic global attractor.

Figure 1 shows that the numerical solutions of model (2.4) tend to a single stable almost periodic solution for different initial conditions. Therefore, even though the phenology of each species has asynchronous behavior both species can coexist when some conditions on the values of the parameters are satisfied. In such a scenario, the number of individuals in each species will tend to an almost periodic orbit.

Figure 2 shows how the population densities of mutualistic species are affected when the density dependence of the mutualistic species is varied. Note that, when the parameters θ_1 and θ_2 increase simultaneously, the population density of the species N_1 is negatively affected; see Figure 2 case (a). In contrast, the population density of the species N_2 is positively affected; Figure 2 case (b). It is important to point out that varying the parameters θ_1 and θ_2 has a direct effect on the seasonal dynamics by reducing the amplitude of the oscillations in the population density of both species.

For comparison purposes, Figure 3 shows the behavior of the solutions of model (2.4) under two scenarios: a periodic scenario and an almost periodic scenario. Notice that, the solutions of the periodic model and the almost periodic model remain close to each other at the beginning of the interaction. Later, the solutions separate from each other. Therefore, if a periodic model is used to describe mutualism when the mutualistic dynamics is almost periodic, the overlapping intervals and the population densities can be underestimated or overestimated. In such a scenario, modeling asynchronous behavior with periodic rates can lead to misleading forecasts. This misleading estimation can lead to the design of inaccurate conservation strategies, which can be catastrophic from an ecological perspective.

We also prove that when the per capita growth rate is a decreasing linear function, ($\theta = 1$), for N_1 or N_2 or both, a global attractor almost periodic for model (2.4) exists when $\alpha_{i*} > \beta_i^*$. A similar result is obtained when $\theta_i \in \mathbb{N}$ and $\theta_1 = \theta_2$; see Theorem 4.1 cases *b*) and *ii*). Numerical simulations for these cases are similar to cases shown in Figures 1-3.

In summary, we show that density-dependent mutualistic species can coexist at population densities that oscillate around a single stable almost periodic solution when seasonal factors affect the growth rate and/or the carrying capacity of the species. The model can be useful to describe scenarios in which the phenology of large long-lived mutualistic species is seasonally almost periodic. In such a scenario, to model the population dynamics with a periodic model can lead to misleading prediction. The results can be a useful tool to explain or forecast possible synchronous mismatch that could result in changes in species richness and biodiversity in a region.

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