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Research article

A heterogeneous parasitic-mutualistic model of mistletoes and birds on a periodically evolving domain

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Abstract: In this paper, a parasitic-mutualistic model of mistletoes and birds defined in a heterogeneous and periodically evolving domain is comprehensively investigated to reveal some new dynamical phenomena caused by the domain evolution. By establishing the core spatial-temporal risk index R_0^B and R_0^M for birds population and mistletoes-birds population, respectively, the fundamental extinction, persistence and coexistence behaviors are studied, and distinguished by such indexes. Moreover, the impact of domain evolution on the viability of mistletoes is examined as well, and it is concluded that the average expansion of the domain can enhance mistletoes' transmission capability, therefore, promote the viability of mistletoes, and vice versa. Finally, numerical simulations are also exhibited for some specific cases to verify the theoretical conclusions.

Keywords: Parasitic-mutualistic model of mistletoes and birds; heterogeneous environment; periodically evolving domain; nonlinear reaction-diffusion equation

1. Introduction and model formulation

As a unique vector-borne parasite, mistletoe is not only parasitic and commensal, but also mutulistic with its vectors, that is, the avian seed-dispersers. In fact, Mistletoes always infect vascular plants ranging from cacti to pines, and prevail in many areas [1]. Although mistletoes are always thought as pests that kill trees and depreciate natural habitats, more and more recent investigators have gradually recognized them as an indispensable ecological keystone species, which contribute greatly to biodiversity by providing high quality food and habitat for a broad range of animals living in woodlands and forests worldwide [2].

Due to so special nature of the interaction between mistletoes and their bird vectors, the model of mistletoes and birds has received impressive attention from researchers in many disciplines. In particular, in the earlier study of Liu et al. [3], they first proposed a single species model to investigate the dynamics of mistletoes, in which the population of the birds was assumed to be constant, and lived in a common isolated and fixed habitat with mistletoes. Different from [3], recently, Wang et al. [4] built a more complex model to incorporate the spatial dispersal, the maturation delay of mistletoes and homogeneous spatial-temporal interaction between mistletoes and birds in a fixed spatial domain. By the different choices of the dispersal fashion of mistletoe fruits by birds, Wang et al. [4] obtained some detailed information about the spatial patterns of mistletoes and birds, which are extremely beneficial for people to understand the long time dynamics of mistletoes and birds world. Following this pioneering work, Wang et al. [5] still explored the spatial spreading behaviors of the same model with some simpler assumptions, and derived the existences of asymptotic spreading speed and traveling waves by monotone semiflow theory.

Although all aforementioned studies are developed on time-independent domains with homogeneous hypothesis on the spatial-temporal environment, one must note that in reality, either the habit that the creature living in or the environment they undergo always keeps changing as time evolving. For example, many birds periodically migrate between different latitudes, where both the food resource and the mortality vary obviously. In fact, there were more and more literatures concerning the asymptotic behaviors of the solutions to the reaction-diffusion systems on some changing domains, and we refer to [6, 7] for the pattern formation on a growing domain, [8, 9] for the species model on finite or infinite growing domains, respectively, [10] for the logistic equation on a periodically evolving domain, and [11, 12] for the epidemic systems on a periodically evolving domain.

Motivated by aforementioned studies and the periodicity of birds' territory, we will investigate a heterogeneous parasitic-mutualistic model of mistletoes and birds in a periodically evolving domain, and reveal some new phenomena caused by the domain evolution in the model.

For such aims, we start with some fundamental assumptions for our model. In accordance to [10], let $\Omega(t) \subset \mathbb{R}^n$ be a bounded and simply connected domain that periodically evolves over time $t \ge 0$ with smooth boundary $\partial \Omega(t)$. Denote B(t, X(t)) and M(t, X(t)), respectively, be the population densities of birds and mistletoes at time *t* and spatial position $X(t) \in \Omega(t)$. In the light of [4, 5] and Reynolds transport theorem [13], we will focus on the following dimensionless reaction-diffusion equation

$$\begin{cases} M_t - d_M \Delta M + \vec{v} \cdot \nabla M + M(\nabla \cdot \vec{v}) = \bar{\alpha}(t, X) \frac{MB}{M+B} - \bar{\delta}(t, X)M, & t > 0, X \in \Omega(t), \\ B_t - d_B \Delta B + \vec{v} \cdot \nabla B + B(\nabla \cdot \vec{v}) = B(\bar{r}(t, X) - B) + \bar{\beta}(t, X) \frac{MB}{M+B}, & t > 0, X \in \Omega(t), \\ M(t, X(t)) = B(t, X(t)) = 0, & t > 0, X \in \partial\Omega(t) \end{cases}$$
(1.1)

with the initial functions defined on the initial domain $\Omega_0 := \Omega(0)$. In the mistletoes and birds world, $\bar{\alpha}(t, X)$ is the rate of successfully attaching the mistletoe seeds to birds, which is equivalent to the rate of parasites transmission, while $\bar{\delta}(t, X)$ is the mortality rate of the mistletoes. Meanwhile, $\bar{\beta}(t, X)$ is the conversion rate, at which energy is transformed from mistletoes fruits birds eaten into birds population, and $\bar{r}(t, X)$ is the abundance of the food resources other than mistletoes fruits. Moreover, d_M and d_B represent the random diffusivity of mistletoes and birds, respectively, which satisfy $0 < d_M \ll d_B$ attributed to the tremendous scale difference between their territories. On the other hand, \vec{v} is the flow velocity yielded by the domain evolving, the advection terms $\vec{v} \cdot \nabla M$ and $\vec{v} \cdot \nabla B$ represent the transport of populations determined by \vec{v} , and $M(\nabla \cdot \vec{v})$ and $B(\nabla \cdot \vec{v})$ are the annihilation term due to local volume changes [6, 7, 14].

To circumvent the complexities due to the terms of dilution and advection, we adopt the transformation between Eulerian coordinate and Lagrangian coordinate in fluid mechanics to modify problem (1.1) from the evolving domain into the fixed domain. Therefore, we first suppose that domain evolves periodically and isotropically, that is,

$$X(t) = \kappa(t)x \text{ for all } X(t) \in \Omega(t) \text{ and } (t, x) \in [0, \infty) \times \Omega_0, \tag{1.2}$$

where x and X are the spatial coordinates of the initial domain Ω_0 and evolving domain $\Omega(t)$, respectively; the evolving ratio $\kappa(t) \in C^1([0, T], (0, \infty))$ is a T-periodic function, i.e., $\kappa(t) = \kappa(t + T)$, and satisfies $\kappa(0) = 1$ and $0 < \kappa(t) \le \kappa^*$ for all $t \ge 0$, where κ^* is a positive constant. Moreover, without loss of generality, we also assume that the flow velocity is equivalent to the changing velocity of the domain, i.e., $\vec{v} = \dot{X}(t)$. As a result, we have

$$\vec{v} = \dot{X}(t) = \dot{\kappa}(t)x = \frac{\dot{\kappa}(t)}{\kappa(t)}X(t).$$

Hence, redefine

$$M(t, X(t)) := m(t, x), \quad B(t, X(t)) := b(t, x), \tag{1.3}$$

then problem (1.2) and (1.3) yield that

$$\begin{split} M_t + \vec{v} \cdot \nabla M &= m_t, \quad B_t + \vec{v} \cdot \nabla B = b_t, \\ M(\nabla \cdot \vec{v}) &= n \frac{\dot{\kappa}(t)}{\kappa(t)} m, \quad B(\nabla \cdot \vec{v}) = n \frac{\dot{\kappa}(t)}{\kappa(t)} b, \\ \Delta M &= \frac{1}{\kappa^2(t)} \Delta m, \quad \Delta B = \frac{1}{\kappa^2(t)} \Delta b. \end{split}$$

Meanwhile, redefining

$$\bar{\alpha}(t, X(t)) = \alpha(t, x), \quad \delta(t, X(t)) = \delta(t, x),$$

$$\bar{r}(t, X(t)) = r(t, x), \quad \bar{\beta}(t, X(t)) = \beta(t, x)$$

as well, problem (1.1) is thus transformed into

$$\begin{cases} m_t - \frac{d_M}{\kappa^2(t)} \Delta m = \alpha(t, x) \frac{mb}{m+b} - \delta(t, x)m - n\frac{\dot{\kappa}(t)}{\kappa(t)}m, & t > 0, x \in \Omega_0, \\ b_t - \frac{d_B}{\kappa^2(t)} \Delta b = b(r(t, x) - b) + \beta(t, x) \frac{mb}{m+b} - n\frac{\dot{\kappa}(t)}{\kappa(t)}b, & t > 0, x \in \Omega_0, \\ m(t, x) = b(t, x) = 0, & t > 0, x \in \partial\Omega_0 \end{cases}$$
(1.4)

with the nontrivial, bounded and continuous initial conditions

$$m(0, x) := m_0(x) \ge 0, \ b(0, x) := b_0(x) \ge 0, \quad x \in \Omega_0.$$
(1.5)

Here, we still suppose that $\alpha(t, x)$, $\delta(t, x)$, r(t, x), and $\beta(t, x) \in C^{\frac{\theta}{2}, \theta}([0, \infty) \times \overline{\Omega_0})(\theta \in (0, 1))$ are positive and T-periodic with respect to *t*. Meanwhile, suppose that

$$0 < z_* \le z(t, x) \le z^*,$$

on $[0, \infty) \times \overline{\Omega_0}$, where $z = \alpha, \delta, r, \beta$; z_* and z^* are constants.

Additionally, by extending the definition to be zero either m = 0 or b = 0, we can reconstruct the reaction function $\frac{MB}{M+B}$ as a locally Lipschitz continuous one in the entire first quadrant. Hence, in view

Mathematical Biosciences and Engineering

of all the assumptions above and the uniform estimates in Lemma 3.4, the standard regularity theory [15, 16] indicates that problem (1.4)–(1.5) have a unique global solution $(m, b) \in [C^{1+\frac{\theta}{2},2+\theta}([0,\infty) \times \overline{\Omega_0})]^2$. Hence, the primary objective of the current article is to investigate the persistence, extinction and coexistence of the birds and mistletoes populations in problem (1.4)–(1.5), and to reveal the important influence and new phenomena caused by the domain evolution. The key technique we adopt here is the spatial-temporal risk index that is similar to the basic reproduction number in epidemiology, which will be established by the principal eigenvalue theory of periodic reaction-diffusion equations.

The remainder of our article is arranged in the following way. In Section 2, we first limit ourself to examine the diffusive dynamics in birds world without mistletoes, and present a fundamental extinction-persistence dichotomy distinguished by the associated spatial-temporal risk index R_0^B . Section 3 is devoted to comprehensively investigating the dynamics behaviors in the mistletoes-birds world, in which we establish the core spatial-temporal risk index R_0^M , then obtain the extinctioncoexistence dichotomy distinguished by R_0^M , and explore the impact of evolving domain on the viability of mistletoes. Finally, numerical simulations are also exhibited for some specific cases in Section 4 to illustrate our theoretical conclusions.

2. The diffusive dynamics in birds world

In this section, we first explore the diffusive dynamics in birds world without mistletoes, and present a fundamental extinction-persistence dichotomy distinguished by the spatial-temporal risk index R_0^B , which plays a role being similar to the basic reproduction number in epidemiology.

In fact, provided $m \equiv 0$, problem (1.4)–(1.5) become

$$\begin{cases} b_t - \frac{d_B}{\kappa^2(t)} \Delta b = b(r(t, x) - b) - n \frac{\dot{\kappa}(t)}{\kappa(t)} b, & t > 0, x \in \Omega_0, \\ b(t, x) = 0, & t > 0, x \in \partial \Omega_0, \\ b(0, x) := b_0(x) \ge 0, & x \in \Omega_0. \end{cases}$$
(2.1)

To further analyze the asymptotic behavior of the solution of problem (2.1), we focus on the periodic parabolic eigenvalue problem

$$\begin{cases} \phi_t - \frac{d_B}{\kappa^2(t)} \Delta \phi = \frac{r(t, x)}{\mu} \phi - n \frac{\dot{\kappa}(t)}{\kappa(t)} \phi, & t > 0, x \in \Omega_0, \\ \phi(t, x) = 0, & t > 0, x \in \partial \Omega_0, \\ \phi(0, x) = \phi(T, x), & x \in \Omega_0. \end{cases}$$
(2.2)

Denote $R_0^B(\kappa) := \mu_0$, where μ_0 is the principal eigenvalue of problem (2.2). We have the following key results.

Lemma 2.1. $sign(1 - R_0^B(\kappa)) = sign\lambda_0$, where λ_0 is the principal eigenvalue of the following eigenvalue problem

$$\begin{cases} \phi_t - \frac{d_B}{\kappa^2(t)} \Delta \phi = r(t, x)\phi - n \frac{\dot{\kappa}(t)}{\kappa(t)} \phi + \lambda \phi, & t > 0, x \in \Omega_0, \\ \phi(t, x) = 0, & t > 0, x \in \partial \Omega_0, \\ \phi(0, x) = \phi(T, x), & x \in \Omega_0. \end{cases}$$
(2.3)

Mathematical Biosciences and Engineering

Proof. For any fixed $\mu > 0$, consider the eigenvalue problem

$$\begin{cases} \phi_t - \frac{d_B}{\kappa^2(t)} \Delta \phi = \frac{r(t, x)}{\mu} \phi - n \frac{\dot{\kappa}(t)}{\kappa(t)} \phi + \Lambda \phi, & t > 0, x \in \Omega_0, \\ \phi(t, x) = 0, & t > 0, x \in \partial \Omega_0, \\ \phi(0, x) = \phi(T, x), & x \in \Omega_0, \end{cases}$$

and denote its principal eigenvalue as $\Lambda_0(\mu)$. It is well-known [17] that $\Lambda_0(\mu)$ is continuous and strictly increasing with respect to μ . Moreover, the uniqueness of principal eigenvalue implies that $\lambda_0 = \Lambda_0(1)$ and $\Lambda_0(\mu_0) = 0$.

On the other hand, since $\Lambda_0(\mu)$ satisfies $\lim_{\mu\to 0^+} \Lambda_0(\mu) < 0$ and $\lim_{\mu\to\infty} \Lambda_0(\mu) > 0$ [17], one can deduce from the monotonicity of $\Lambda_0(\mu)$ that $R_0^B(\kappa) = \mu_0$ is the unique positive solution for the equation $\Lambda_0(\mu) = 0$. Due to

$$\lambda_0 = \Lambda_0(1) - \Lambda_0(\mu_0) = \Lambda_0(1) - \Lambda_0(R_0^B(\kappa)),$$

the monotonicity also yields that $sign(1 - R_0^B(\kappa)) = sign\lambda_0$, and the proof is completed.

Therefore, completely identical to [10], we obtain the following existence and attractivity results of the periodic solutions of problem (2.1) in the evolving domain.

Theorem 2.2. Let $b(t, x; b_0)$ be the solution of problem (2.1) with nonnegative, bounded and continuous initial conditions $b_0(x) \ge 0$ on $\overline{\Omega_0}$.

(i) If $R_0^B(\kappa) \leq 1$, then the trivial solution $b(t, x) \equiv 0$ is globally asymptotically stable in the sense that

$$\lim_{i \to \infty} b(t + iT, x; b_0) = 0$$

holds uniformly on $[0, T] \times \overline{\Omega_0}$;

(ii) If $R_0^B(\kappa) > 1$, then problem (2.1) has a positive and T-periodic solution $b^*(t, x)$, which is globally asymptotically stable for all nontrivial b_0 in the sense that

$$\lim_{i \to \infty} b(t + iT, x; b_0) = b^*(t, x)$$

holds uniformly on $[0, T] \times \overline{\Omega_0}$ *.*

3. The diffusive dynamics in the mistletoes-birds world

Since the case that $R_0^B(\kappa) \le 1$ could lead to some trivial extinction for small invasion populations, throughout this section, we focus on discussing the diffusive dynamics of mistletoes under the influence of birds for the case $R_0^B(\kappa) > 1$.

3.1. The spatial-temporal risk index R_0^M

We will introduce the spatial-temporal risk index $R_0^M(\kappa)$ associated with the problem (1.4)–(1.5), which is a similar role as index $R_0^B(\kappa)$, while it will be constructed by a more epidemic fashion. The readers are also referred to the similar conception defined by Lin et al. [18, 19] for the free boundary problems.

For such aim, we first consider the linearized equation for problem (1.4)–(1.5) at point $(m, b) = (0, b^*)$ as follows

$$\begin{cases} m_t - \frac{d_M}{\kappa^2(t)} \Delta m = \alpha(t, x)m - \delta(t, x)m - n\frac{\dot{\kappa}(t)}{\kappa(t)}m, & t > 0, x \in \Omega_0, \\ b_t - \frac{d_B}{\kappa^2(t)} \Delta b = \beta(t, x)m + (r - 2b^*)b - n\frac{\dot{\kappa}(t)}{\kappa(t)}b, & t > 0, x \in \Omega_0, \\ m(t, x) = b(t, x) = 0, & t > 0, x \in \partial\Omega_0. \end{cases}$$
(3.1)

Let $d(t) = \frac{d_M}{\kappa^2(t)}$ and $\eta(t, x) = \delta(t, x) + n\frac{k(t)}{\kappa(t)}$, then the first equation of problem (3.1) yields

$$\begin{cases} m_t - d(t)\Delta m = \alpha(t, x)m - \eta(t, x)m, & t > 0, x \in \Omega_0, \\ m(t, x) = 0, & t > 0, x \in \Omega_0. \end{cases}$$
(3.2)

We first consider the case that $\eta(t, x) \ge 0$ for any $t \ge 0$ and $x \in \overline{\Omega_0}$.

Let C_T be all the continuous and T-periodic functions from \mathbb{R} to $C(\Omega_0, \mathbb{R})$, which is equipped with the positive cone $C_T^+ := \{\zeta \in C_T : \zeta(t)(x) \ge 0, \forall t \in \mathbb{R}, x \in \overline{\Omega_0}\}$ and maximum norm $\|\cdot\|$. It is easy to see that C_T is an ordered Banach space. We denote $\zeta(t, x) := \zeta(t)(x)$ for any $\zeta \in C_T$.

Besides, let $A(t, \tau)$ be the evolution operator of problem

$$\begin{cases} m_t - d(t)\Delta m = -\eta(t, x)m, & t > 0, x \in \Omega_0, \\ m(t, x) = 0, & t > 0, x \in \partial \Omega_0. \end{cases}$$
(3.3)

Due to the standard semigroup theory, we know that there exist positive constants K and c_0 such that

$$||A(t,\tau)|| \le K e^{-c_0(t-\tau)}, \quad \forall t \ge \tau, t, \tau \in \mathbb{R}.$$

Now, assume that $\zeta \in C_T$, and let $\zeta(\tau, x)$ be the density distribution of mistletoes individuals at the time τ and spatial location $x \in \overline{\Omega_0}$. Then the term $\alpha(\tau, x)\zeta(t, x)$ is just the density distribution of the new individuals engendered by the old individuals introduced at time τ . Thus, for any $t \ge \tau$, we let $A(t, \tau)\alpha(\tau, x)\zeta(\tau, x)$ be the density distribution at location x of the individuals, who are newly introduced at time τ and still are survival at time t. Therefore, the following expression

$$\int_{-\infty}^{t} A(t,\tau)\alpha(\tau,\cdot)\zeta(\tau,\cdot)\mathrm{d}\tau = \int_{0}^{\infty} A(t,t-a)\alpha(t-a,\cdot)\zeta(t-a,\cdot)\mathrm{d}a$$

is called the accumulative density distribution of the new mistletoes individuals at time *t* and location *x*, and they are engendered by those individuals $\zeta(\tau, x)$ introduced at all the time before *t*.

According to the statements in [20] and [21], we are going to define the operator $\mathfrak{L} : C_T \to C_T$ as the next generation operator, where

$$\mathfrak{L}(\zeta,t) := \int_{-\infty}^{t} A(t,\tau)\alpha(\tau,\cdot)\zeta(\tau,\cdot)\mathrm{d}\tau = \int_{0}^{\infty} A(t,t-a)\alpha(t-a,\cdot)\zeta(t-a,\cdot)\mathrm{d}a.$$

It is clear that \mathfrak{L} is continuous, positive and compact on C_T . Hence, similar as in [21], we choose the spectral radius $r(\mathfrak{L})$ to be defined as the basic reproduction number to problem (1.4)–(1.5), i.e., $R_0 := r(\mathfrak{L})$.

Furthermore, we have the following significant conclusions.

Mathematical Biosciences and Engineering

Lemma 3.1. (i) $R_0^M = \mu_0^M$ and where μ_0^M is the principal eigenvalue of the following periodic parabolic eigenvalue problem

$$\begin{cases} \psi_t - \frac{d_M}{\kappa^2(t)} \Delta \psi = \frac{\alpha(t, x)}{\mu_0^M} \psi - \delta(t, x) \psi - n \frac{\dot{\kappa}(t)}{\kappa(t)} \psi, & t > 0, x \in \Omega_0, \\ \psi(t, x) = 0, & t > 0, x \in \partial \Omega_0, \\ \psi(0, x) = \psi(T, x), & x \in \Omega_0; \end{cases}$$
(3.4)

(ii) $sign(1 - R_0^M) = sign\lambda_0^M$, where λ_0^M is the principal eigenvalue of the following eigenvalue problem

$$\begin{cases} \psi_t - \frac{d_M}{\kappa^2(t)} \Delta \psi = \alpha(t, x) \psi - \delta(t, x) \psi - n \frac{\dot{\kappa}(t)}{\kappa(t)} \psi + \lambda_0^M \psi, & t > 0, x \in \Omega_0, \\ \psi(t, x) = 0, & t > 0, x \in \partial \Omega_0, \\ \psi(0, x) = \psi(T, x), & x \in \Omega_0. \end{cases}$$
(3.5)

On the other hand, for the case that $\eta(t, x) < 0$ for any $t \ge 0$ and $x \in \overline{\Omega_0}$, we can still adopt the completely identical method used by Lemma 2.1 in Section 2 to obtain Lemma 3.1, and we omit the details for simplicity.

Remark 3.2. To better explore the association between $\kappa(t)$ and R_0^M , we denote $R_0^M = R_0^M(\kappa)$ and let $\overline{\kappa^{-2}} = \frac{1}{T} \int_0^T \frac{1}{\kappa^2(t)} dt$ hereafter.

By Lemma 3.1, we have the following results.

Theorem 3.3. (*i*) If $\alpha(t, x) \equiv \alpha(t)$, and $\delta(t, x) \equiv \delta(t)$ for all $t \in [0, T]$, then

$$R_0^M(\kappa) = \frac{\int_0^T \alpha(t) dt}{\int_0^T (\delta(t) + \frac{d_M}{\kappa^2(t)} \lambda_0^M) dt};$$

(*ii*) If $\alpha(t, x) \equiv \alpha > 0$ and $\delta(t, x) \equiv \delta > 0$ are both constants, then

$$R_0^M(\kappa) = \frac{\alpha}{\delta + d_M \lambda_0^M \overline{\kappa^{-2}}},$$

where λ_0^M is the principal eigenvalue of the following problem

$$\begin{cases} -\Delta \varphi = \lambda_0^M \varphi, & x \in \Omega_0, \\ \varphi = 0, & x \in \partial \Omega_0 \end{cases}$$

Proof. (i) Let $\psi_0(t, x) = p(t)\varphi(x) > 0$ for $(t, x) \in (0, \infty) \times \Omega_0$ be the eigenfunction associating with $R_0^M(\kappa)$. Consequently, problem (3.4) sees

$$\dot{p}(t)\varphi(x) + \frac{d_M\lambda_0^M}{\kappa^2(t)}p(t)\varphi(x) + \delta(t)p(t)\varphi(x) + n\frac{\dot{\kappa}(t)}{\kappa(t)}p(t)\varphi(x) = \frac{\alpha(t)}{R_0^M(\kappa)}p(t)\varphi(x),$$

Mathematical Biosciences and Engineering

which deduces to

$$\frac{\dot{p}(t)}{p(t)} + \frac{d_M \lambda_0^M}{\kappa^2(t)} + \delta(t) + n \frac{\dot{\kappa}(t)}{\kappa(t)} - \frac{\alpha(t)}{R_0^M(\kappa)} = 0.$$
(3.6)

Integrating (3.6) from 0 to *t* gives

$$\int_0^t \left(\frac{\alpha(t)}{R_0^M(\kappa)} - n \frac{\dot{\kappa}(t)}{\kappa(t)} - \delta(t) - \frac{d_M \lambda_0^M}{\kappa^2(t)} \right) \mathrm{d}t = 0.$$

It follows from $\psi(t + T, x) = \psi(t, x)$ that one has p(T) = p(0). Thus, we have

$$R_0^M(\kappa) = \frac{\int_0^T \alpha(t) dt}{\int_0^T (\delta(t) + \frac{d_M}{\kappa^2(t)} \lambda_0^M) dt}$$

(ii)Due to $\overline{\kappa^{-2}} = \frac{1}{T} \int_0^T \frac{1}{\kappa^2(t)} dt$, it is clear that we have

$$R_0^M(\kappa) = \frac{\alpha}{\delta + d_M \lambda_0^M \overline{\kappa^{-2}}}.$$

The proof is completed.

3.2. The extinction and coexistence dynamics of mistletoes-birds populations

We first make some preliminaries for the proof of the existence of periodic solution.

Lemma 3.4. There exist positive constants C_m and C_b such that the solution (m, b)(t, x) of problem (1.4)–(1.5) satisfying

$$(0,0) < (m,b)(t,x) \le (C_m, C_b)$$
(3.7)

holds uniformly on $[0, \infty) \times \overline{\Omega_0}$, provided that $(0, 0) \not\equiv (m_0, b_0)(x) \leq (C_m, C_b)$ on $\overline{\Omega_0}$.

Proof. First, the maximum principle confirms the strict positivity, and we will prove the right side of (3.7).

In fact, by the second equation of (1.4), we deduce that

$$b_t - \frac{d_B}{\kappa^2(t)} \Delta b = b(r(t, x) - b) + \beta(t, x) \frac{mb}{m+b} - n \frac{\dot{\kappa}(t)}{\kappa(t)} b$$

$$\leq b \left[r(t, x) + \beta(t, x) - n \frac{\dot{\kappa}(t)}{\kappa(t)} - b \right]$$

$$\leq b(r^* + \beta^* - c_\kappa - b).$$

Consequently, we obtain

 $b(t, x) \le \max\{r^* + \beta^* - c_{\kappa}, \|b_0\|_{\infty}\}$

uniformly on $[0, \infty) \times \overline{\Omega_0}$, where $c_{\kappa} := \min_{t \in [0,T]} \left\{ n_{\kappa(t)}^{\underline{\kappa}(t)} \right\} < 0$. Denote $C_b := r^* + \beta^* - c_{\kappa}$. Then we obtain

$$b(t, x) \le C_{l}$$

uniformly on $[0, \infty) \times \overline{\Omega_0}$ if $||b_0||_{\infty} \le C_b$.

Mathematical Biosciences and Engineering

Volume 17, Issue 6, 6678-6698.

Similarly, after assuming that $\delta_* + c_{\kappa} > 0$, we still have

$$m(t, x) \leq C_m$$

uniformly on $[0, \infty) \times \overline{\Omega_0}$ if $||m_0||_{\infty} \le C_m$ where $C_m := \frac{\alpha^* C_b}{\delta_* + c_\kappa}$

In brief, we have

$$(0,0) < (m,b)(t,x) \le (C_m,C_b)$$

uniformly on $[0, \infty) \times \overline{\Omega_0}$, provided that $(0, 0) \neq \le (m_0, b_0)(x) \le (C_m, C_b)$ on $\overline{\Omega_0}$. The proof is finished.

Theorem 3.5. Let $(m, b)(t, x; m_0, b_0)$ be the solution of problem (1.4)-(1.5) with nonnegative, bounded and continuous initial conditions $m_0(x) \ge 0$ and $b_0(x) \ge \neq 0$ on $\overline{\Omega_0}$. If $R_0^M(\kappa) \le 1$, then the solution $(0, b^*)$ is globally asymptotically stable in the sense that

$$\lim_{i \to \infty} (m, b)(t + iT, x; m_0, b_0) = (0, b^*)(t, x)$$

holds uniformly on $[0, T] \times \overline{\Omega_0}$.

Proof. For $(t, x) \in [0, T) \times \overline{\Omega_0}$, selecting $m^u(t, x) = Ce^{-\sigma t}\psi(t, x)$, where $\psi(t, x)$ satisfying $||\psi||_{\infty} = 1$ is the normalized eigenfunction associated with $R_0^M(\kappa)$, $0 \le \sigma \le \alpha(t, x)(\frac{1}{R_0^M} - 1)$, and C > 0 is a sufficiently large constant. It follows that

$$\begin{split} m_t^u &- \frac{d_M}{\kappa^2(t)} \Delta m^u - \alpha(t, x) \frac{b}{m^u + b} m^u + \delta(t, x) m^u + n \frac{\dot{\kappa}(t)}{\kappa(t)} m^u \\ \geq m_t^u &- \frac{d_M}{\kappa^2(t)} \Delta m^u - \alpha(t, x) m^u + \delta(t, x) m^u + n \frac{\dot{\kappa}(t)}{\kappa(t)} m^u \\ = C e^{-\sigma t} \psi_t - \sigma C e^{-\sigma t} \psi - C e^{-\sigma t} \frac{d_M}{\kappa^2(t)} \Delta \psi - \alpha(t, x) C e^{-\sigma t} \psi \\ &+ \delta(t, x) C e^{-\sigma t} \psi + n \frac{\dot{\kappa}(t)}{\kappa(t)} C e^{-\sigma t} \psi \\ = m^u (-\sigma + \frac{\alpha(t, x)}{R_0^M} - \alpha(t, x)) \\ > 0. \end{split}$$

Then, m^{μ} is the upper solution of the following problem

$$\begin{cases} m_t - \frac{d_M}{\kappa^2(t)} \Delta m = \alpha(t, x) \frac{b}{m+b} m - \delta(t, x) m - n \frac{\dot{\kappa}(t)}{\kappa(t)} m, & t > 0, x \in \Omega_0, \\ m(t, x) = 0, & t > 0, x \in \partial \Omega_0, \\ m(0, x) = m_0(x) \ge 0, & x \in \Omega_0. \end{cases}$$

Hence, the uniform limit $\lim_{t\to\infty} m(t, x) = 0$ is derived from the fact that $\lim_{t\to\infty} m^u(t, x) = 0$ uniformly for $x \in \overline{\Omega_0}$. Furthermore, by the almost parallel method adopted in [22], we also can show that $\lim_{t\to\infty} b(t + iT, x) = b^*(t, x)$ holds uniformly on $[0, T] \times \overline{\Omega_0}$. The proof is completed.

6687

Next, we combine the related eigenvalue problem and ordered upper and lower solutions to explore the periodic steady state coexistence solutions of problem (1.4)–(1.5) and their attractivity. Concretely speaking, we will focus on the following problem

$$\begin{cases} m_{t} - \frac{d_{M}}{\kappa^{2}(t)} \Delta m = \alpha(t, x) \frac{b}{m+b} m - \delta(t, x) m - n \frac{\dot{\kappa}(t)}{\kappa(t)} m, & t > 0, x \in \Omega_{0}, \\ b_{t} - \frac{d_{B}}{\kappa^{2}(t)} \Delta b = b(r(t, x) - b) + \beta(t, x) \frac{m}{m+b} b - n \frac{\dot{\kappa}(t)}{\kappa(t)} b, & t > 0, x \in \Omega_{0}, \\ m(t, x) = b(t, x) = 0, & t > 0, x \in \partial \Omega_{0}, \\ m(0, x) = m(T, x), & b(0, x) = b(T, x), & x \in \Omega_{0}. \end{cases}$$
(3.8)

The following definition of upper and lower solutions is fundamental.

Definition 3.6. $(\widetilde{m}, \widetilde{b})(t, x)$ and $(\widehat{m}, \widehat{b})(t, x)$ are called upper and lower solutions to problem (3.8) if

$$\begin{cases} \widetilde{m}_{t} - \frac{d_{M}}{\kappa^{2}(t)} \Delta \widetilde{m} \geq \alpha(t, x) \frac{\widetilde{b}}{\widetilde{m} + \widetilde{b}} \widetilde{m} - \delta(t, x) \widetilde{m} - n \frac{\dot{\kappa}(t)}{\kappa(t)} \widetilde{m}, & t > 0, x \in \Omega_{0}, \\ \widetilde{b}_{t} - \frac{d_{B}}{\kappa^{2}(t)} \Delta \widetilde{b} \geq \widetilde{b}(r(t, x) - \widetilde{b}) + \beta(t, x) \frac{\widetilde{m}}{\widetilde{m} + \widetilde{b}} \widetilde{b} - n \frac{\dot{\kappa}(t)}{\kappa(t)} \widetilde{b}, & t > 0, x \in \Omega_{0}, \\ \widetilde{m}_{t} - \frac{d_{M}}{\kappa^{2}(t)} \Delta \widetilde{m} \leq \alpha(t, x) \frac{\widetilde{b}}{\widetilde{m} + \widetilde{b}} \widetilde{m} - \delta(t, x) \widehat{m} - n \frac{\dot{\kappa}(t)}{\kappa(t)} \widetilde{m}, & t > 0, x \in \Omega_{0}, \\ \widetilde{b}_{t} - \frac{d_{B}}{\kappa^{2}(t)} \Delta \widetilde{b} \leq \widetilde{b}(r(t, x) - \widetilde{b}) + \beta(t, x) \frac{\widetilde{m}}{\widetilde{m} + \widetilde{b}} \widetilde{b} - n \frac{\dot{\kappa}(t)}{\kappa(t)} \widetilde{b}, & t > 0, x \in \Omega_{0}, \\ \widetilde{m}(t, x) = 0 \leq \widetilde{m}(t, x), \quad \widetilde{b}(t, x) = 0 \leq \widetilde{b}(t, x), & t > 0, x \in \partial\Omega_{0}, \\ \widetilde{m}(0, x) \leq \widetilde{m}(T, x), \quad \widetilde{b}(0, x) \leq \widetilde{b}(T, x), & x \in \Omega_{0}, \\ \widetilde{m}(0, x) \geq \widetilde{m}(T, x), \quad \widetilde{b}(0, x) \geq \widetilde{b}(T, x), & x \in \Omega_{0}. \end{cases}$$

Moreover, $(\widetilde{m}, \widetilde{b})(t, x)$ and $(\widehat{m}, \widehat{b})(t, x)$ are called a pair of ordered upper and lower solutions if they satisfy $(0, 0) \leq (\widetilde{m}, \widetilde{b}) \leq (\widetilde{m}, \widetilde{b}) \leq (C_m, C_b)$.

The parallel definition to problem (1.4)–(1.5) could be obtained by similar fashion as well. For further analysis, we also set

$$\begin{cases} K_1 := \max_{[0,T] \times \Omega_0} \left(\delta(t, x) + n \frac{\dot{\kappa}(t)}{\kappa(t)} \right), \\ K_2 := \max_{[0,T]} \left(n \frac{\dot{\kappa}(t)}{\kappa(t)} \right) + C_b \end{cases}$$

and

$$\begin{cases} F(m,b) := \alpha(t,x)\frac{b}{m+b}m - \delta(t,x)m - n\frac{\dot{\kappa}(t)}{\kappa(t)}m + K_1m, & t > 0, x \in \Omega_0, \\ G(m,b) := b(r(t,x)-b) + \beta(t,x)\frac{m}{m+b}b - n\frac{\dot{\kappa}(t)}{\kappa(t)}b + K_2b, & t > 0, x \in \Omega_0, \end{cases}$$

Mathematical Biosciences and Engineering

where F and G are clearly nondecreasing about m and b. Then problem (3.8) can be rewritten as

$$\begin{cases} m_t - \frac{d_M}{\kappa^2(t)} \Delta m + K_1 m = F(m, b), & t > 0, x \in \Omega_0, \\ b_t - \frac{d_B}{\kappa^2(t)} \Delta b + K_2 b = G(m, b), & t > 0, x \in \Omega_0, \\ m(t, x) = b(t, x) = 0, & t > 0, x \in \partial \Omega_0, \\ m(0, x) = m(T, x), & b(0, x) = b(T, x), & x \in \Omega_0. \end{cases}$$
(3.10)

We now select $(\overline{m}^{(0)}, \overline{b}^{(0)}) = (\widetilde{m}, \widetilde{b})$ and $(\underline{m}^{(0)}, \underline{b}^{(0)}) = (\widehat{m}, \widehat{b})$ as initial functions and construct sequences $\{(\overline{m}^{(i)}, \overline{b}^{(i)})\}$ and $\{(\underline{m}^{(i)}, \underline{b}^{(i)})\}$ (i = 1, 2, ...,) by the following iteration procedure

$$\begin{cases} \overline{m}_{t}^{(i)} - \frac{d_{M}}{\kappa^{2}(t)} \Delta \overline{m}^{(i)} + K_{1} \overline{m}^{(i)} = F(\overline{m}^{(i-1)}, \overline{b}^{(i-1)}), & t > 0, x \in \Omega_{0}, \\ \overline{b}_{t}^{(i)} - \frac{d_{B}}{\kappa^{2}(t)} \Delta \overline{b}^{(i)} + K_{2} \overline{b}^{(i)} = G(\overline{m}^{(i-1)}, \overline{b}^{(i-1)}), & t > 0, x \in \Omega_{0}, \\ \underline{m}_{t}^{(i)} - \frac{d_{M}}{\kappa^{2}(t)} \Delta \underline{m}^{(i)} + K_{1} \underline{m}^{(i)} = F(\underline{m}^{(i-1)}, \underline{b}^{(i-1)}), & t > 0, x \in \Omega_{0}, \\ \underline{b}_{t}^{(i)} - \frac{d_{B}}{\kappa^{2}(t)} \Delta \underline{b}^{(i)} + K_{2} \underline{b}^{(i)} = G(\underline{m}^{(i-1)}, \underline{b}^{(i-1)}), & t > 0, x \in \Omega_{0}, \\ \overline{m}^{(i)}(t, x) = \underline{m}^{(i)}(t, x) = \overline{b}^{(i)}(t, x) = \underline{b}^{(i)}(t, x) = 0, & t > 0, x \in \partial\Omega_{0}, \\ \overline{m}^{(i)}(0, x) = \overline{m}^{(i-1)}(T, x), & \overline{b}^{(i)}(0, x) = \overline{b}^{(i-1)}(T, x), & x \in \Omega_{0}, \\ \underline{m}^{(i)}(0, x) = \underline{m}^{(i-1)}(T, x), & \underline{b}^{(i)}(0, x) = \underline{b}^{(i-1)}(T, x), & x \in \Omega_{0}. \end{cases}$$

We first derive the following fundamental properties of the two sequences above.

Lemma 3.7. Assume that $(\overline{m}^{(i)}, \overline{b}^{(i)})$ and $(\underline{m}^{(i')}, \underline{b}^{(i')})$ are ordered upper and lower solutions of problem (3.8) for any *i* and *i'*. If there exist

$$(\underline{m}^{(i')}, \underline{b}^{(i')})(0, x) \le (m_0(x), b_0(x)) \le (\overline{m}^{(i)}, \overline{b}^{(i)})(0, x)$$

in Ω_0 , then $(\overline{m}^{(i)}, \overline{b}^{(i)})$ and $(\underline{m}^{(i')}, \underline{b}^{(i')})$ are also ordered upper and lower solutions of problem (1.4)–(1.5).

If we still denote the two sequences generated by (3.11) as $\{(\overline{m}^{(i)}, \overline{b}^{(i)})\}$ and $\{(\underline{m}^{(i)}, \underline{b}^{(i)})\}$ with

$$(\overline{m}^{(i)}, \overline{b}^{(i)})(0, x) = (\underline{m}^{(i)}, \underline{b}^{(i)})(0, x) = (m_0(x), b_0(x)), \ x \in \Omega_0,$$
(3.12)

and $(\widehat{m}, \widehat{b}) \leq (m_0(x), b_0(x)) \leq (\widetilde{m}, \widetilde{b})$ in Ω_0 , then the following result holds.

Lemma 3.8. The two sequences $\{(\overline{m}^{(i)}, \overline{b}^{(i)})\}$ and $\{(\underline{m}^{(i)}, \underline{b}^{(i)})\}$ converge monotonically to a unique solution (m, b)(t, x) of problem (1.4)–(1.5). Moreover,

$$(\widehat{m},\widehat{b}) \leq (\underline{m}^{(i-1)},\underline{b}^{(i-1)}) \leq (\underline{m}^{(i)},\underline{b}^{(i)}) \leq (m,b) \leq (\overline{m}^{(i)},\overline{b}^{(i)}) \leq (\overline{m}^{(i-1)},\overline{b}^{(i-1)}) \leq (\widetilde{m},\widetilde{b})$$

holds on $[0, \infty) \times \overline{\Omega_0}$.

Mathematical Biosciences and Engineering

All the proofs of the lemmas above are routine, so we omit them and refer the details to [23, Theorem B, Lemmas 3.1-3.2].

To present our coexistence results, we need the following key lemma.

Lemma 3.9. The principal eigenvalue λ_0^M of problem (3.5) is also an eigenvalue for the following eigenvalue problem with some strict positive eigenfunctions (Ψ_0, Φ_0)

$$\begin{cases} \Psi_t - \frac{d_M}{\kappa^2(t)} \Delta \Psi = \alpha(t, x) \Psi - \delta(t, x) \Psi - n \frac{\dot{\kappa}(t)}{\kappa(t)} \Psi + \Lambda \Psi, & t > 0, x \in \Omega_0, \\ \Phi_t - \frac{d_B}{\kappa^2(t)} \Delta \Phi = \beta(t, x) \Psi + (r(t, x) - 2b^*) \Phi - n \frac{\dot{\kappa}(t)}{\kappa(t)} \Phi + \Lambda \Phi, & t > 0, x \in \Omega_0, \\ \Psi(t, x) = \Phi(t, x) = 0, & t > 0, x \in \partial \Omega_0, \\ \Psi(0, x) = \Psi(T, x), & \Phi(0, x) = \Phi(T, x), & x \in \Omega_0, \end{cases}$$
(3.13)

provided that $\lambda_0^M < 0$.

Proof. Let (λ_0^M, ψ_0) be the eigenpair of problem (3.5) with $\lambda_0^M < 0$ and $\psi_0 > 0$. Then, (λ_0^M, ψ_0) satisfies

$$\begin{cases} \Psi_t - \frac{d_M}{\kappa^2(t)} \Delta \Psi = \alpha(t, x) \Psi - \delta(t, x) \Psi - n \frac{\dot{\kappa}(t)}{\kappa(t)} \Psi + \Lambda \Psi, & t > 0, x \in \Omega_0, \\ \Psi(t, x) = 0, & t > 0, x \in \partial \Omega_0, \\ \Psi(0, x) = \Psi(T, x), & x \in \Omega_0. \end{cases}$$
(3.14)

We then consider the following inhomogeneous problem of $\Phi = \Phi(t, x)$

$$\begin{cases} \Phi_t - \frac{d_B}{\kappa^2(t)} \Delta \Phi = (r(t, x) - 2b^*) \Phi - n \frac{\dot{\kappa}(t)}{\kappa(t)} \Phi + \lambda_0^M \Phi + \beta(t, x) \psi_0, & t > 0, x \in \Omega_0, \\ \Phi(t, x) = 0, & t > 0, x \in \partial \Omega_0, \\ \Phi(0, x) = \Phi(T, x), & x \in \Omega_0. \end{cases}$$
(3.15)

Since $b^*(t, x)$ solves

$$\begin{cases} b_t^* - \frac{d_B}{\kappa^2(t)} \Delta b^* = (r(t, x) - b^*) b^* - n \frac{\dot{\kappa}(t)}{\kappa(t)} b^*, & t > 0, x \in \Omega_0, \\ b^*(t, x) = 0, & t > 0, x \in \partial \Omega_0, \\ b^*(0, x) = b^*(T, x), & x \in \Omega_0, \end{cases}$$

the monotonicity of the principal eigenvalue implies that the following problem

$$\begin{cases} \Phi_t - \frac{d_B}{\kappa^2(t)} \Delta \Phi = (r(t, x) - 2b^*) \Phi - n \frac{\dot{\kappa}(t)}{\kappa(t)} \Phi + \Lambda \Phi & t > 0, x \in \Omega_0, \\ \Phi(t, x) = 0, & t > 0, x \in \partial \Omega_0, \\ \Phi(0, x) = \Phi(T, x), & x \in \Omega_0 \end{cases}$$

. . .

has a positive principal eigenvalue $\Lambda_0 > 0$.

Thus, utilizing the positivity of β and ψ_0 together with [16, Theorem 16.6], we derive that problem (3.15) has a unique solution $\Phi_0(t, x)$ satisfying $\Phi_0(t, x) > 0$ for all $(t, x) \in [0, T] \times \Omega_0$. To sum up, if the principal eigenvalue $\lambda_0^M < 0$, then it is still an eigenvalue of the eigenvalue problem (3.13) with strict positive eigenfunctions $(\Psi_0, \Phi_0) = (\psi_0, \Phi_0)$. The lemma is proved. Now, it is the turn to present our main theorem as following.

Theorem 3.10. If $R_0^M(\kappa) > 1$, then the following conclusions hold:

- (i) There are a pair of minimal and maximal positive T-periodic solutions $(\underline{m}, \underline{b}) \leq (\overline{m}, \overline{b})$ of problem (3.8) over $(0, b^*)$, moreover, if $(\underline{m}, \underline{b})(0, x) = (\overline{m}, \overline{b})(0, x)$, then $(\overline{m}, \overline{b}) = (\underline{m}, \underline{b}) := (m^{\diamond}, b^{\diamond})$ is the unique positive T-periodic solution to problem (3.8);
- (ii) Let $(m, b)(t, x; m_0, b_0)$ be the solution of problem (1.4)–(1.5) with bounded and continuous initial conditions $(0, 0) \not\equiv d \leq (m_0, b_0)(x) \leq (C_m, C_b)$ on $\overline{\Omega_0}$, then $(\underline{m}, \underline{b}) \leq (\overline{m}, \overline{b})$ is attractive in the sense that

$$(\underline{m}, \underline{b})(t, x) \leq \liminf_{i \to \infty} (m, b)(t + iT, x; m_0, b_0)$$

$$\leq \limsup_{i \to \infty} (m, b)(t + iT, x; m_0, b_0) \leq (\overline{m}, \overline{b})(t, x)$$
(3.16)

holds uniformly on $[0, T] \times \overline{\Omega_0}$.

Proof. (i) It is clear that (C_m, C_b) and $(0, b^*)$ are ordered upper and lower solutions of problem (3.8). We select the $(\overline{m}^{(0)}, \overline{b}^{(0)}) = (\widetilde{m}, \widetilde{b}) = (C_m, C_b)$ and $(\underline{m}^{(0)}, \underline{b}^{(0)}) = (\widehat{m}, \widehat{b}) = (\gamma \Psi, b^* + \gamma \Phi)$ as initial iteration, where (Ψ, Φ) is the positive eigenfunction of eigenvalue problem (3.13) associated with $\lambda_0^M < 0$ given by Lemma 3.9, and γ is sufficiently small positive number.

[23, Lemma 3.1] ensures that the sequences $\{(\overline{m}^{(i)}, \overline{b}^{(i)})\}$ and $\{(\underline{m}^{(i)}, \underline{b}^{(i)})\}$ defined by (3.11) have the monotonicity

$$\underbrace{(\underline{m}^{(0)}, \underline{b}^{(0)}) \leq (\underline{m}^{(i-1)}, \underline{b}^{(i-1)}) \leq (\underline{m}^{(i)}, \underline{b}^{(i)})}_{\leq (\overline{m}^{(i)}, \overline{b}^{(i)}) \leq (\overline{m}^{(i-1)}, \overline{b}^{(i-1)}) \leq (\overline{m}^{(0)}, \overline{b}^{(0)}).$$
(3.17)

Therefore, the the monotone convergence theorem [23, Theorem A] implies that there exist a pair of $(\overline{m}, \overline{b})$ and $(\underline{m}, \underline{b})$ satisfying

$$\lim_{i \to \infty} (\overline{m}^{(i)}, \overline{b}^{(i)}) = (\overline{m}, \overline{b}), \quad \lim_{i \to \infty} (\underline{m}^{(i)}, \underline{b}^{(i)}) = (\underline{m}, \underline{b}),$$

$$(\underline{m}^{(0)}, \underline{b}^{(0)}) \leq (\underline{m}^{(i-1)}, \underline{b}^{(i-1)}) \leq (\underline{m}^{(i)}, \underline{b}^{(i)}) \leq (\underline{m}, \underline{b})$$

$$\leq (\overline{m}, \overline{b}) \leq (\overline{m}^{(i)}, \overline{b}^{(i)}) \leq (\overline{m}^{(i-1)}, \overline{b}^{(i-1)}) \leq (\overline{m}^{(0)}, \overline{b}^{(0)}),$$
(3.18)

and

$$\begin{cases} \overline{m}_{t} - \frac{d_{M}}{\kappa^{2}(t)} \Delta \overline{m} = \alpha(t, x) \frac{\overline{b}}{\overline{m} + \overline{b}} \overline{m} - \delta(t, x) \overline{m} - n \frac{\dot{k}(t)}{\kappa(t)} \overline{m}, & t > 0, x \in \Omega_{0}, \\ \overline{b}_{t} - \frac{d_{B}}{\kappa^{2}(t)} \Delta \overline{b} = \overline{b}(r(t, x) - \overline{b}) + \beta(t, x) \frac{\overline{m}}{\overline{m} + \overline{b}} \overline{b} - n \frac{\dot{k}(t)}{\kappa(t)} \overline{b}, & t > 0, x \in \Omega_{0}, \\ \underline{m}_{t} - \frac{d_{M}}{\kappa^{2}(t)} \Delta \underline{m} = \alpha(t, x) \frac{\underline{b}}{\underline{m} + \underline{b}} \underline{m} - \delta(t, x) \underline{m} - n \frac{\dot{k}(t)}{\kappa(t)} \underline{m}, & t > 0, x \in \Omega_{0}, \\ \underline{b}_{t} - \frac{d_{B}}{\kappa^{2}(t)} \Delta \underline{b} = \underline{b}(r(t, x) - \underline{b}) + \beta(t, x) \frac{\underline{m}}{\underline{m} + \underline{b}} \underline{b} - n \frac{\dot{k}(t)}{\kappa(t)} \underline{b}, & t > 0, x \in \Omega_{0}, \\ \overline{m}(t, x) = \underline{m}(t, x) = \overline{b}(t, x) = \underline{b}(t, x) = 0, & t > 0, x \in \partial\Omega_{0}, \\ \overline{m}(0, x) = \overline{m}(T, x), & \overline{b}(0, x) = \overline{b}(T, x), & x \in \Omega_{0}, \\ \underline{m}(0, x) = \underline{m}(T, x), & \underline{b}(0, x) = \underline{b}(T, x), & x \in \Omega_{0}. \end{cases}$$

Mathematical Biosciences and Engineering

Clearly, $(\underline{m}, \underline{b})$ and $(\overline{m}, \overline{b})$ are T-periodic solutions of problem (3.8) satisfying $(0, b^*) \le (\underline{m}, \underline{b}) \le (\overline{m}, \overline{b})$. Next, we claim that $(\underline{m}, \underline{b})$ and $(\overline{m}, \overline{b})$ are minimal and maximal, respectively.

In fact, any T-periodic solution (m^{**}, b^{**}) over $(0, b^*)$ satisfies $(\widehat{m}, \widehat{b}) \le (m^{**}, b^{**}) \le (\widetilde{m}, \widetilde{b})$ on $[0, T] \times \overline{\Omega_0}$ if $\gamma > 0$ is sufficiently small. Hence, after choosing $(\widetilde{m}, \widetilde{b})$ and (m^{**}, b^{**}) as the initial data for iteration, and operate iteration like problem (3.11), it follows that

$$(m^{**}, b^{**}) \le (\overline{m}, \overline{b})$$
 on $[0, T] \times \overline{\Omega_0}$

that is, $(\overline{m}, \overline{b})$ is the maximal T-periodic solution of problem (3.8). Similarly, we also have

$$(m, b) \le (m^{**}, b^{**})$$
 on $[0, T] \times \overline{\Omega_0}$,

which indicates that (m, b) is the minimal T-periodic solution of problem (3.8) over $(0, b^*)$.

Lastly, the conclusion $(\overline{m}, \overline{b}) = (\underline{m}, \underline{b}) = (m^{\circ}, b^{\circ})$ can be derived by the standard existenceuniqueness theorem on the initial-boundary parabolic equations, provided that $(\overline{m}, \overline{b})(0, x) = (m, b)(0, x)$.

(ii) Due to the comparison principle, we first have $b(t, x) \ge \widetilde{b}(t, x)$ on $[0, \infty) \times \overline{\Omega_0}$ for the same initial data, where $\widetilde{b}(t, x)$ is the solution of problem (2.1). Since $R_0^B(\kappa) > 1$, Theorem 2.2 yields that $\lim_{i\to\infty} \widetilde{b}(t+iT, x) = b^*(t, x)$ holds uniformly on $[0, T] \times \overline{\Omega_0}$. Thus, $\liminf_{i\to\infty} b(t+iT, x) \ge b^*(t, x)$ holds uniformly on $[0, T] \times \overline{\Omega_0}$. Thus, $\liminf_{i\to\infty} b(t+iT, x) \ge b^*(t, x)$ holds uniformly on $[0, T] \times \overline{\Omega_0}$ for any $i \ge i_{\varepsilon}^*$.

Set

$$(m_i, b_i)(t, x) := (m, b)(t + iT, x; m_0, b_0)$$

for any positive integer $i \ge 1$. Since

$$(0,0) < (\widehat{m}, \widehat{b} - \frac{\varepsilon}{2})(0,x) \le (m_{i_{\varepsilon}^*}, b_{i_{\varepsilon}^*})(0,x) \le (\widetilde{m}, \widetilde{b})(0,x)$$

uniformly in Ω_0 for sufficiently small $\varepsilon, \gamma > 0$, Lemma 3.8 implies

$$(\widehat{m},\widehat{b}-\frac{\varepsilon}{2})(t+iT,x) \le (m_{i_{\varepsilon}^*+i},b_{i_{\varepsilon}^*+i})(t,x) \le (\widetilde{m},\widetilde{b})(t+iT,x)$$

on $[0, \infty) \times \overline{\Omega_0}$. In particular,

$$(\widehat{m},\widehat{b}-\frac{\varepsilon}{2})(t+T,x) \le (m_{i^*+1},b_{i^*+1})(t,x) \le (\widetilde{m},\widetilde{b})(t+T,x)$$

on $[0, \infty) \times \overline{\Omega_0}$.

Therefore, by choosing $(\widehat{m}, \widehat{b} - \frac{\varepsilon}{2})$ as new initial data $(\underline{m}_{\varepsilon}^{(0)}, \underline{b}_{\varepsilon}^{(0)})$, we still obtain a similar monotone sequences $(\underline{m}_{\varepsilon}^{(i)}, \underline{b}_{\varepsilon}^{(i)})(i = 1, 2, \cdots)$ from (3.11). Moreover, the monotone convergence theorem [23, Theorem A] still yields that $(\underline{m}_{\varepsilon}^{(i)}, \underline{b}_{\varepsilon}^{(i)})$ converge uniformly to a T-periodic solution $(\underline{m}_{\varepsilon}, \underline{b}_{\varepsilon})$ of problem (3.8) as $i \to \infty$, and the later converge uniformly to $(\underline{m}, \underline{b})$ as $\varepsilon \to 0$.

By the periodic condition in problem (3.11), we derive

$$\begin{cases} (\widetilde{m}, \widetilde{b})(t+T, x) = (\overline{m}^{(0)}, \overline{b}^{(0)})(t+T, x) = (\overline{m}^{(1)}, \overline{b}^{(1)})(t, x), & \text{in } \Omega_0, \\ (\widehat{m}, \widehat{b} - \frac{\varepsilon}{2})(t+T, x) = (\underline{m}^{(0)}_{\varepsilon}, \underline{b}^{(0)}_{\varepsilon})(t+T, x) = (\underline{m}^{(1)}_{\varepsilon}, \underline{b}^{(1)}_{\varepsilon})(t, x), & \text{in } \Omega_0, \end{cases}$$

Mathematical Biosciences and Engineering

which implies that

$$(\underline{m}_{\varepsilon}^{(1)}, \underline{b}_{\varepsilon}^{(1)})(0, x) \le (m_{i^*+1}, b_{i^*+1})(0, x) \le (\overline{m}^{(1)}, \overline{b}^{(1)})(0, x)$$

in Ω_0 . Therefore, we know $(\overline{m}^{(1)}, \overline{b}^{(1)})$ and $(\underline{m}^{(1)}_{\varepsilon}, \underline{b}^{(1)}_{\varepsilon})$ are a pair of order upper and lower solutions to problem (3.8) with initial data $(m_{i^*+1}, b_{i^*+1})(0, x)$ due to Lemma 3.7. By Lemma 3.8 again, the unique solution $(m_{i^*+1}, b_{i^*+1})(t, x)$ of problem (3.8) satisfies

$$(\underline{m}_{\varepsilon}^{(1)}, \underline{b}_{\varepsilon}^{(1)})(t, x) \le (m_{i^*+1}, b_{i^*+1})(t, x) \le (\overline{m}^{(1)}, \overline{b}^{(1)})(t, x)$$

on $[0, \infty) \times \overline{\Omega_0}$. We obtain from the induction principle that for $i \ge 1$,

$$(\underline{m}_{\varepsilon}^{(i)}, \underline{b}_{\varepsilon}^{(i)})(t, x) \le (m_{i^*+i}, b_{i^*+i})(t, x) \le (\overline{m}^{(i)}, \overline{b}^{(i)})(t, x)$$

holds on $[0, \infty) \times \overline{\Omega_0}$. Consequently, we have

$$\begin{split} (\underline{m}_{\varepsilon}, \underline{b}_{\varepsilon})(t, x) &\leq \liminf_{i \to \infty} (m, b)(t + iT, x; m_0, b_0) \\ &\leq \limsup_{i \to \infty} (m, b)(t + iT, x; m_0, b_0) \leq (\overline{m}, \overline{b})(t, x) \end{split}$$

holds uniformly on $[0, T] \times \overline{\Omega_0}$, and the desired result follows from passing to the limits as $\varepsilon \to 0$. The proof is finished.

3.3. The impact of domain evolution on the viability of mistletoes

The discussion in section 3.2 is fulfilled on the evolving domain, and we will explore the asymptotic behaviors of the related solution on the fixed domain in the sequel. In fact, if $\kappa(t) \equiv 1$ and $\Omega(t) = \Omega(0)$, then the underlying domain is constant, and problem (1.4) is transformed to

$$\begin{cases} u_t - d_M \Delta u = \alpha(t, x) \frac{v}{u + v} u - \delta(t, x) u, & t > 0, x \in \Omega(0), \\ v_t - d_B \Delta v = v(r(t, x) - v) + \beta(t, x) \frac{u}{u + v} v, & t > 0, x \in \Omega(0), \\ u(t, x) = v(t, x) = 0, & t > 0, x \in \partial\Omega(0) \end{cases}$$
(3.20)

with the similar nontrivial, nonnegative and continuous initial conditions

$$u(0, x) = u_0(x), v(0, x) = v_0(x), \quad x \in \Omega(0).$$
 (3.21)

(1)

The associated periodic steady state coexistence problem is defined by

$$\begin{cases} u_t - d_M \Delta u = \alpha(t, x) \frac{v}{u + v} u - \delta(t, x) u, & t > 0, x \in \Omega(0), \\ v_t - d_B \Delta v = v(r(t, x) - v) + \beta(t, x) \frac{u}{u + v} v, & t > 0, x \in \Omega(0), \\ u(t, x) = v(t, x) = 0, & t > 0, x \in \partial\Omega(0), \\ u(0, x) = u(T, x), v(0, x) = v(T, x), & x \in \Omega(0). \end{cases}$$
(3.22)

We still denote the spatia-temporal risk index of problem (3.20)–(3.21) as

$$\mathfrak{R}_0^M = R_0^M(1)$$

by the identical arguments with Lemma 3.1, and we have the following threshold results completely similar to Theorems 3.5 and 3.10.

Mathematical Biosciences and Engineering

Theorem 3.11. Let $(u, v)(t, x; m_0, b_0)$ be the solution of problem (3.20)–(3.21) with nonnegative, bounded and continuous initial conditions $u_0(x) \ge 0$ and $v_0(x) \ge \neq 0$ on $\overline{\Omega}(0)$, then the following conclusions hold:

(i) If $\mathfrak{R}_0^M \leq 1$, then the solution $(0, v^*)$ of problem (3.22) is globally asymptotically stable in the sense that

$$\lim_{i \to \infty} (u, v)(t + iT, x; u_0, v_0) = (0, v^*)(t, x)$$
(3.23)

holds uniformly on $[0, T] \times \overline{\Omega}(0)$, where $v^*(t, x)$ is the unique solution of the periodic parabolic problem

$$\begin{cases} v_t - \frac{d_B}{\kappa^2(t)} \Delta v = v(r(t, x) - v), & t > 0, x \in \Omega(0), \\ v(t, x) = 0, & t > 0, x \in \partial \Omega(0), \\ v(0, y) = b_0(x), & x \in \Omega(0); \end{cases}$$

(ii) If $\mathfrak{R}_0^M > 1$, then problem (3.22) has a pair of maximal and minimal positive positive T-periodic solution $(\underline{u}, \underline{v}) \leq (\overline{u}, \overline{v})$ over than $(0, b^*)$; moreover, if $(\underline{u}, \underline{v})(0, x) = (\overline{u}, \overline{v})(0, x)$, then $(\overline{u}, \overline{v}) =$ $(\underline{u}, \underline{v}) := (u^\circ, v^\circ)$ is the unique positive T-periodic solution to problem (3.22). Lastly, $(\underline{u}, \underline{v})$ and $(\overline{u}, \overline{v})$ are also attractive in the sense that

$$(\underline{u}, \underline{v})(t, x) \leq \liminf_{i \to \infty} (u, v)(t + iT, x; u_0, v_0)$$

$$\leq \limsup_{i \to \infty} (u, v)(t + iT, x; u_0, v_0) \leq (\overline{u}, \overline{v})(t, x)$$
(3.24)

holds uniformly on $[0, T] \times \overline{\Omega}(0)$ for any initial conditions $(u_0(x), v_0(x)) \ge \neq (0, 0)$ on $\overline{\Omega}(0)$.

At the last, in order to evaluate the effect of the periodically evolving domain on the viability of mistletoes, we present the following investigation, which results directly from Theorem 3.3 (i).

Theorem 3.12. If $\alpha(t, x) \equiv \alpha(t)$, $\delta(t, x) \equiv \delta(t)$ for all $t \in [0, T]$, then the following statements hold:

- (i) if $\overline{\kappa^{-2}} = 1$, then we have $R_0^M = \mathfrak{R}_0^M$; (ii) if $\overline{\kappa^{-2}} > 1$, then we have $R_0^M < \mathfrak{R}_0^M$;
- (iii) if $\overline{\kappa^{-2}} < 1$, then we have $R_0^M > \mathfrak{R}_0^M$,

where $\overline{\kappa^{-2}} = \frac{1}{T} \int_0^T \frac{1}{\kappa^2(t)} \mathrm{d}t.$

In fact, Theorem 3.12 reveals that $\overline{\kappa^{-2}}$ can be deemed to an index to forecast the impact of the periodic evolution of domain on the viability of mistletoes. If $\overline{\kappa^{-2}} = 1$, then the periodical domain evolution has no effect on the viability of mistletoes. However, if $\overline{\kappa^{-2}} > 1$, we guess that the domain evolution caused by the diffusion of mistletoes is not conducive to their survival and transmission. Lastly, if $\overline{\kappa^{-2}} < 1$, we find that mistletoes can survive well on the fixed and evolving domains, what is more, the domain evolution can promote diffusion of mistletoes and thus give mistletoes more space for transmission. In brief, the average expansion of the domain can enhance the viability of mistletoes, and vice versa.

4. Numerical simulations and conclusions

In this section, we will implement some numerical simulations to test the previous theoretical results. In addition, to put more emphasis on the diffusive dynamics of mistletoes under the influence of birds, we give the following assumptions about the some coefficients.

$$d_M = 0.0001, \quad d_B = 0.5, \quad r = 0.2, \quad \beta = 0.1, \quad \lambda_0^M = \pi^2,$$

 $m_0(x) = 2\sin(\pi x), \quad b_0(x) = 0.2\sin(\pi x) + 0.1\sin(3\pi x).$

To better survey the asymptotic behaviors of the solution of problem (1.4)–(1.5), we select different α , δ and $\kappa(t)$.

Example 4.1. Fix $\alpha = 0.1$ and $\delta = 0.09905$. Choose different $\kappa(t)$:

(*i*) Let $\kappa(t) = 1$, then

$$R_0^M(1) = \frac{\alpha}{\delta + d_M \lambda_0^M} = 0.9996 < 1.$$

It is easy to know from Figure 1 that m rapidly decreases to 0, which agrees with Theorem 3.11 (i) that at length mistletoes on a fixed domain will go to extinction;



Figure 1. $\alpha = 0.1$, $\delta = 0.09905$ and $\kappa(t) = 1$. Graph (a) is a three-dimensional space of density *m* varying with time *t* and space *x*. Graph (b) is the contour map. Graph (c) is the cross-sectional view.

(*ii*) Set $\kappa(t) = e^{0.1(1-\cos(4t))}$, calculation obtains

$$\overline{\kappa^{-2}} = \frac{2}{\pi} \int_0^{\frac{\pi}{2}} \frac{1}{\kappa^2(t)} dt = 0.8269 < 1$$

and

$$R_0^M(\kappa) = \frac{\alpha}{\delta + d_M \lambda_0^M \overline{\kappa^{-2}}} = 1.0013 > 1.$$

It is shown in Figure 2 (a) that m tends to a positive steady state. (b)–(c) implies that domain is periodically evolving. And it is line with Theorem 3.10 that mistletoes can coexist with birds on a periodically evolving domain, which also consists with Theorem 3.12 (iii).

Mathematical Biosciences and Engineering



Figure 2. $\alpha = 0.1$, $\delta = 0.09905$ and $\kappa(t) = e^{0.1(1-\cos(4t))}$. Graph (a) is a three-dimensional space of density *m* varying with time *t* and space *x*. Graph (b) is the contour map. Graph (c) is the cross-sectional view.

Example 4.2. Fix $\alpha = 0.0845$ and $\delta = \frac{1}{12}$. Choose different $\kappa(t)$:

(*i*) Let $\kappa(t) = 1$, then

$$R_0^M(1) = \frac{\alpha}{\delta + d_M \lambda_0^M} = 1.0021 > 1.$$

Observing Figure 3, we easily find that m stabilizes a positive steady state, which is consistent with Theorem 3.11 (ii) that mistletoes and birds can coexist in a fixed domain;



Figure 3. $\alpha = 0.0845$, $\delta = \frac{1}{12}$ and $\kappa(t) = 1$. Graph (a) is a three-dimensional space of density *m* varying with time *t* and space *x*. Graph (b) is the contour map. Graph (c) is the cross-sectional view.

(*ii*) Set $\kappa(t) = e^{0.1(\cos(4t)-1)}$, result is

$$\overline{\kappa^{-2}} = \frac{2}{\pi} \int_0^{\frac{\pi}{2}} \frac{1}{\kappa^2(t)} dt = 1.2336 > 1$$

and

$$R_0^M(\kappa) = \frac{\alpha}{\delta + d_M \lambda_0^M \overline{\kappa^{-2}}} = 0.9994 < 1.$$

Mathematical Biosciences and Engineering

Figure 4 (a) shows that m decays to 0 eventually. (b)–(c) tells us that domain evolves periodically. And it agrees to Theorem 3.10 that mistletoes will be eradicated in a periodically evolving domain, which also consists with Theorem 3.12 (ii).



Figure 4. $\alpha = 0.0845$, $\delta = \frac{1}{12}$ and $\kappa(t) = e^{0.1(\cos(4t)-1)}$. Graph (a) is a three-dimensional space of density *m* varying with time *t* and space *x*. Graph (b) is the contour map. Graph (c) is the cross-sectional view.

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Conflict of interest

The authors declare there is no conflict of interest.

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