

# Spatiotemporal Variation of Mistletoes: a Dynamic Modeling Approach

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**Abstract** Mistletoes are common aerial stem-parasites and their seeds are dispersed by fruit-eating birds. In the mutually beneficial relationships between mistletoes and bird species that disperse mistletoes' seeds, the preference of birds for infected trees influences the spread of mistletoes and the spatiotemporal pattern formation of mistletoes. We formulate a deterministic model to describe the dynamics of mistletoes in an isolated patch containing an arbitrary number of trees. We establish concrete criteria, expressed in terms of the model parameters, for mistletoes establishing in this area. We conduct numerical simulations based on a field study to reinforce and expand our results.

**Keywords** Mistletoes · Spatiotemporal · Age-structured population dynamics

## 1 Introduction

Mistletoes are common aerial stem-parasites that infect vascular plants ranging from pines to cacti. Mistletoes produce flowers and fruits. With a few notable exceptions, mistletoe seeds are dispersed by fruit-eating birds, many of which are highly specialized to consume their berries. After being deposited by a bird onto an appropriate

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host, a seed germinates and forms a haustorium that taps into the xylem of the host plant to absorb water, minerals and, in some cases, sugars and amino acids (Aukema and del Rio 2002). Mistletoes range from extremely host specific (e.g. *Arceuthobium apachecum*) to host generalist (e.g. *Den—drophthoe falcata*) (Reid et al. 1995; Norton and Carpenter 1998). Often, the prevalence and intensity of mistletoe infections differ among host species. The differential use of hosts by mistletoes within a site has been explained by three processes. First, because birds may perch and defecate mistletoe seeds more frequently on some hosts than on others, seed rain may differ among hosts (Reid 1989). Second, mistletoe seedlings may become established more successfully on some host species than others (Reid et al. 1995). Third, adult mistletoes may differ in persistence among host species (Hoffmann et al. 1986). Because mistletoes form mutually beneficial relationships with the bird species that disperse their seeds, the birds' preferences can influence the mistletoes spread (Aukema 2003; Silva et al. 1996; Martinez del Rio et al. 1996; Aukema et al. 2002).

Mistletoes have no seed bank and must arrive on branches with well-defined characteristics to have a chance of survival. In the case of *Amyema preissi*, these must be small branches of *Acacia victoriae* or of some other functionally similar minor host. Seedlings establish successfully or die within 3 months. Survivors normally grow rapidly and flower 18 months later, producing fruit at 3 years old. Thereafter, they fruit annually until death. Life span is a maximum of about 17 years. Age-specific survival rates, growth, and fecundity have been quantified (Lavorel et al. 1999).

The aim of this paper is to formulate a deterministic model to describe the dynamics of mistletoes in an isolated patch containing  $n$  trees, with  $n$  being an arbitrary integer. These  $n$  trees are different in terms of mistletoe seed deposition rate, and hence establishment, as well as in supporting nutrition for the parasites. Seed dispersal by fruit-eating birds is a critically important component of mistletoe life history. Mistletoe seeds are often coated with a sticky substance called viscin that fastens them to the host branches after being defecated by birds (Aukema 2003). We use a Holling type II functional response to model fruit removal by birds. We then assume that either the birds remove fruits from trees without any bias or with preference for certain types of trees. After a bird removes seeds from a mistletoe, we assume that the bird distributes the seeds randomly among trees.

The model for adult mistletoes then becomes a system of delay differential equations with the delay corresponding to the maturation time of the mistletoes. Our model derivation is described in detail in Sect. 2, where we also provide detailed biological explanations of all the terms involved. We consider the qualitative behaviors of the model and its reduced system in Sect. 3 for two cases, one is when birds uniformly take the fruit, the other one is when birds take the fruits with preference. In the case of uniform fruit-taking by birds, we establish a threshold value expressed in terms of model parameters, which can be interpreted as the reproduction number in the entire patchy environment, and we use this value to determine whether mistletoes can establish in the patch under consideration. In the case where birds take fruits with preference, we show the system may exhibit coexistence of a stable positive equilibrium and a stable trivial equilibrium, and the long-term asymptotic behavior (namely, survival or extinction of mistletoes) of a particular solution depends on the initial level of mistletoe infection in the patch. We show theoretically that the long-

term spatial distribution of mistletoes is given by a stable equilibrium, the structure of equilibria can be described by solving a scalar algebraic equation, and there is a simple set of relationships that describe the spatial distribution at a given equilibrium explicitly in terms of tree specific parameters.

## 2 Model Formulation

We consider an environment consisting of  $n$  trees, denoted by  $T_1, \dots, T_n$ , respectively. We are interested in the long-term spatiotemporal spread patterns of mistletoes in such an environment. We describe our model formulation in several steps, following the mistletoe life cycle depicted in Fig. 1.

### 2.1 Age structure

Many of the dynamic processes that contribute to mistletoe spread, including fruit removal, seedling maturation, and reproduction are age-dependent. Therefore, incorporating age structure of mistletoes in our model is important. For the sake of simplicity, we only consider two stages: immature and mature mistletoes, and we assume that only mature individuals produce fruit. We refer to Metz and Diekmann (1983) and Smith (1993, 1994) for general discussions how structure population models can be developed from simple first order hyperbolic partial differential equations and how such partial differential equation models can be reduced to systems of delay differential equations. We also assume that immature mistletoes mature when they reach age  $\tau$ . We use  $\tau$  to denote the average maturation time, stochastic perturbations around this average can be described by some distributed delays rather than a discrete delay, as we use in this paper.

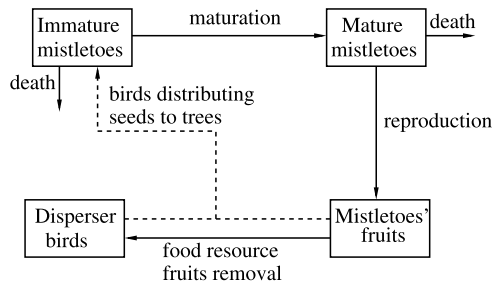
In what follows, we assume the mortality rate is different for mistletoes at different stages, and we denote this stage-dependent tree-specific mortality rate by positive constants  $d_{mi}$  and  $d_i$  for the matured and the immature, respectively, in the  $i$ th tree. We will denote by  $M_i(t)$  the total number of adult mistletoes at time  $t$  in the  $i$ th tree.

### 2.2 Fruit Production

We use  $r_i(M_i(t))$  to denote the total number of fruits produced by the adult mistletoes in the  $i$ th tree at time  $t$ . Here  $r_i : R \rightarrow R$  is a continuous function such that

$$r_i(0) = 0, \quad r_i(M_i) \geq 0 \quad \text{for } M_i \geq 0.$$

**Fig. 1** A schematic illustration of the life cycle of mistletoes



A simple fruit production function is

$$r_i(M_i) = s_i M_i \tag{1}$$

with a constant  $s_i > 0$ . In this study, we use the above function.

### 2.3 Fruit-Removal

To describe fruit removal, we use Holling type II functional response (Holling 1959a, 1959b). As noted above, the total number of available fruits at time  $t$  in the  $i$ th tree is  $r_i(M_i)$ . Let  $S_T$  denote the searching time a bird spends when it is in a tree and  $a$  the encounter rate per fruit. Let  $\sigma$  be a choice coefficient that indicates whether the bird ingests or not a fruit after it encounters it. Then the total number of fruits a bird eats in the  $i$ th tree is  $S_T \times a \times \sigma \times r_i(M_i)$ . If  $h$  denotes the handling time the bird spends on one fruit, then the total handling time is given by  $h \times S_T \times a \times \sigma \times r_i(M_i)$ . The Holling type II functional response gives the fruit-removal rate defined as the total number of fruits removed by birds divided by the total amount of time they spend (searching time and handling time combined). Therefore, we have the removal rate as

$$f_i(M_i) = \frac{S_T a \sigma r_i(M_i)}{S_T + h S_T a \sigma r_i(M_i)} = \frac{a \sigma r_i(M_i)}{1 + h a \sigma r_i(M_i)}. \tag{2}$$

Consequently, at time  $t$ , the number of fruits removed from the  $i$ th tree is  $f_i(M_i) \times B_i$ , where  $B_i$  is the number of birds at the  $i$ th tree that will be described in the next subsection. So, the total number of fruits removed in the environment for the purpose of seeding is

$$\sum_{i=1}^n f_i(M_i) B_i.$$

### 2.4 Birds Preferential or Uniform Dispersal

We now proceed to model the dispersal by birds of mistletoe seeds which are excreted in the droppings of birds after they ate the fruits, and stick to twigs. In this study, we focus on mistletoe spread at a local scale within an isolated environment, and we assume birds can arrive at every tree with equal probability after they eat the fruit. As mentioned earlier, the birds' preference for infected trees has been observed (Aukema 2003; Silva et al. 1996; Martinez del Rio et al. 1996; Aukema et al. 2002). We therefore start with a general case where the total number of birds in the environment is a fixed constant  $B$  but its distribution  $(B_1, \dots, B_n)$  to each tree at any given time may not be uniform and may vary in time. Note that  $B = \sum_{i=1}^n B_i(t)$  for all  $t \geq 0$ .

The time dependence  $B_i$  can result from the time dependence of bird populations in different trees. In this study, we focus on two special cases.

**[BP1]:** Birds are uniformly distributed among these  $n$  trees. In this case, we have

$$B_i := B_i(M_1, \dots, M_n) = \frac{B}{n + w} \quad \text{for each } i \in \{1, \dots, n\}. \tag{3}$$

The constant  $w$  quantifies the observation that birds sometimes perch on non-host trees or other features of the environment.

**[BP2]:** Birds tend to visit trees that are heavily parasitized preferentially, so that

$$B_i := B_i(M_1, \dots, M_n) = B \frac{r_i(M_i)}{\sum_{j=1}^n r_j(M_j) + w}, \tag{4}$$

again, the constant  $w$  is used to reflect the fact that birds may stop in other trees and structures irrelevant to the dynamic process of mistletoes.

### 2.5 Seeding and Maturation

Summarizing the above discussions, we obtain the total amount of seeds produced in the entire environment as

$$S = \sum_{i=1}^n f_i(M_i(t)) B_i(t), \tag{5}$$

and the total amount of seeds which are successfully attached to the  $i$ th tree as

$$\alpha_i \frac{1}{n} \sum_{j=1}^n f_j(M_j(t)) B_j(t), \tag{6}$$

where  $\alpha_i$  is the possibility that a seed is successfully attached to the  $i$ th tree.

Therefore, we end up with the following model for the dynamics of the matured mistletoes:

$$\begin{aligned} \frac{dM_i(t)}{dt} &= e^{-d_i \tau} b_i(M_1(t - \tau), \dots, M_n(t - \tau)) - d_{mi} M_i \quad \text{for } t > 0, \\ M_i(t) &= M_{i0}(t), \quad i = 1, 2, \dots, n, \quad \text{for } t \in [-\tau, 0], \end{aligned} \tag{7}$$

where  $M_{i0}(t)$ ,  $t \in [-\tau, 0]$ , represents prescribed initial data, and

$$b_i(M_1, \dots, M_n) = \alpha_i \frac{1}{n} \sum_{j=1}^n f_j(M_j) B_j(M_1, \dots, M_n).$$

The terms in this model can now be interpreted ecologically. The rate at which new adults arise at time  $t$  is the rate at which the immature become matured at time  $t$ . Considering the maturation age  $\tau$ , the rate at which adult mistletoes originate at time  $t$  is the rate at which immature individuals reach reproductive age after  $t$  units of time. This rate equals the “birth” (or seed establishment) rate at time  $t - \tau$  scaled by the fraction of these mistletoes that survived to maturity, which is  $e^{-d_i \tau}$ . In addition, adults are lost due to mortality which is quantified by the mortality rate  $d_{mi}$ . Defini-

**Table 1** Definition of parameters and their assumed values in the simulation, where sub-index  $i$  refers to the  $i$ th tree. The values are referenced from Aukema (2003), Silva et al. (1996), Martinez del Rio et al. (1996), and Aukema et al. (2002)

Parameter	Definition	Values
$n$	number of trees in an isolated patch	variable
$d_i$	mortality rate of immature mistletoes	$1/(365 * 3)$
$d_{mi}$	mortality rate of adult mistletoes	$1/(365 * 10)$
$\tau$	maturation time for mistletoes	$365 * 3$
$a$	encounter rate of a bird to the fruit	0.01
$h$	handling time	0.01
$\sigma$	consumption choice coefficient	1
$s_i$	the reproduction rate of adult mistletoes	variable
$\alpha_i$	the establishment rate in the $i$ th tree <sup>1</sup>	variable
$B$	the total number of birds in the environment	variable
$w$	quantification that birds sometimes perch on non-host trees or other features	variable

tions of model parameters are given in Table 1, where values of these parameters in our later simulations are also given.

### 3 Global Dynamics and Threshold Phenomena

To describe the global dynamics and threshold behaviors of model (7), we note that the equilibrium of the model (7) can be found by solving the ‘‘algebraic’’ equations:

$$e^{-d_i \tau} \alpha_i \frac{1}{n} \sum_{j=1}^n f_j(M_j^*) B_j(M_1^*, \dots, M_n^*) - d_{mi} M_i^* = 0 \quad \text{for } i = 1, 2, \dots, n. \quad (8)$$

From the above equations, we have

$$\frac{e^{d_i \tau} d_{mi} M_i^*}{\alpha_i} = \frac{1}{n} \sum_{j=1}^n f_j(M_j^*) B_j(M_1^*, \dots, M_n^*) \quad \text{for } i = 1, 2, \dots, n.$$

Because the right-hand side of the above equation is independent of  $i$ , we have

$$\frac{e^{d_1 \tau} d_{m1}}{\alpha_1} M_1^* = \frac{e^{d_i \tau} d_{mi}}{\alpha_i} M_i^* \quad \text{for } i = 2, 3, \dots, n.$$

Letting

$$p_i = \alpha_i e^{-d_i \tau} d_{mi}^{-1}, \quad (9)$$

<sup>1</sup>This parameter may depend on the number of existing mistletoes in this tree.

we obtain

$$M_i^* = p_i p_1^{-1} M_1^*, \quad i = 1, 2, \dots, n. \tag{10}$$

Substituting (10) into the first equation of (8), we have

$$p_1 \frac{1}{n} \sum_{j=1}^n f_j(p_j p_1^{-1} M_1^*) B_j(p_1 p_1^{-1} M_1^*, \dots, p_n p_1^{-1} M_1^*) - M_1^* = 0. \tag{11}$$

The above scalar algebraic equation determines the size of the first component of an equilibrium, and the relations expressed in (10) describe the spatial distributions at a given equilibrium. Note that the spatial distributions are fully determined by tree specific parameters  $p_i$  with  $1 \leq i \leq n$ .

### 3.1 Birds Uniformly Distributed

If we assume birds are uniformly distributed among all trees, we obtain

$$B_i(M_1, \dots, M_n) = \frac{B}{n + w} \quad \text{for each } i \in \{1, \dots, n\}. \tag{12}$$

The model equation takes on the form

$$\frac{dM_i(t)}{dt} = e^{-d_i \tau} \alpha_i \frac{1}{n} \sum_{j=1}^n \frac{a \sigma s_j M_j(t - \tau)}{1 + h a \sigma s_j M_j(t - \tau)} \frac{B}{n + w} - d_{mi} M_i(t). \tag{13}$$

Note that the partial derivative of each component of the right-hand side of the model with respect to all terms with delay is positive. Therefore, the solutions generate a strongly monotone semi-flow on the phase space  $X^+$  that consists of non-negative elements of the Banach space  $X := C \in [-\tau, 0]; R^n$  of continuous mappings from  $[-\tau, 0]$  to  $R^n$ , equipped with the sup-norm.

**Theorem 1** *For the model (7) where  $B_i$  takes the form (12), we define*

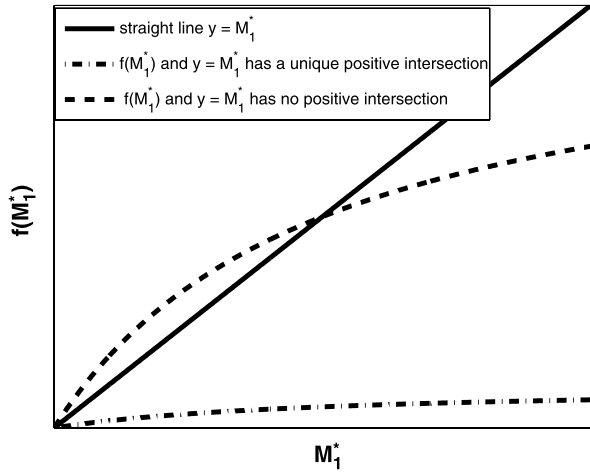
$$R_u = \frac{1}{n} \frac{B}{n + w} \sum_{j=1}^n a \sigma s_j \alpha_j e^{-d_j \tau} d_{mj}^{-1}.$$

*If  $R_u < 1$ ,  $M^0 = (0, 0, \dots, 0)$  is the only equilibrium in  $X^+$  and it is globally asymptotically stable. Otherwise, if  $R_u > 1$ ,  $M^0$  is unstable and there exists a positive equilibrium  $M^+ = (M_1^+, M_2^+, \dots, M_n^+)$ , where  $M_i^+ = p_i p_1^{-1} M_1^+$  for  $i = 2, 3, \dots, n$ , and where  $M_1^+$  is the positive intersection of the curve*

$$f(M_1^*) := p_1 \frac{1}{n} \frac{B}{n + w} \sum_{j=1}^n \frac{a \sigma s_j p_j p_1^{-1} M_1^*}{1 + h a \sigma s_j p_j p_1^{-1} M_1^*} \tag{14}$$

*with the straight line  $M_1^*$ . In this case, every solution of the model system starting from non-trivial initial data in  $X^+$  is convergent to this positive equilibrium as  $t \rightarrow \infty$ .*

**Fig. 2** A graphic illustration of the result in Theorem 1. If  $R_u < 1$ , the curve  $f(M_1^*)$  and straight line  $y = M_1^*$  have no positive intersection in  $X^+$ ; if  $R_u > 1$ , the curve  $f(M_1^*)$  and straight line  $y = M_1^*$  have a unique positive intersection in  $X^+$



*Remark 1*  $R_u$  is a threshold which indicates whether mistletoes can persist in this environment consisting of  $n$  trees. The product  $\alpha_j$  and  $e^{-d_j\tau}$  is the probability of survival from establishment to the onset of adulthood. The sum in  $R_u$  represents the net production of a single seed introduced to the entire environment consisting of the  $n$  trees. If  $R_u < 1$ , mistletoes cannot persist whereas if  $R_u > 1$ , mistletoes persist and reach an equilibrium given by (14).

*Remark 2* Figure 2 presents a graphic illustration of the result in Theorem 1.

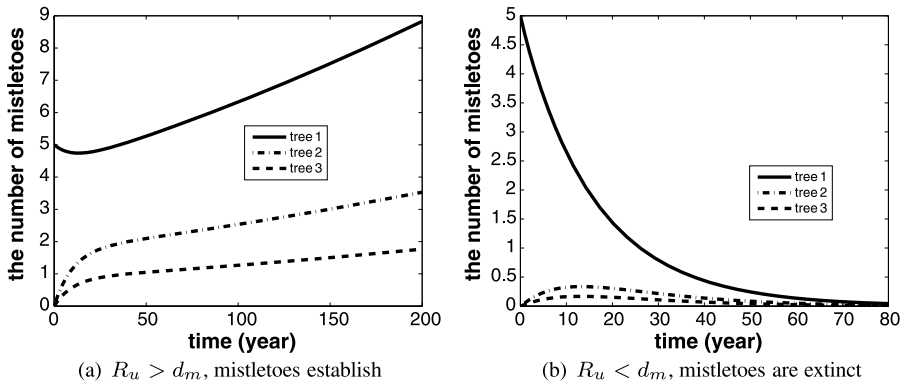
*Remark 3* We have conducted some numerical simulations to reinforce and illustrate the above theoretical result. In the simulations, we assume there are 3 trees in an isolated environment. We fix all the parameters except the establishment rate  $\alpha_i$  and reproduction rate  $s_i, i = 1, 2, 3$ . The parameter values are given in Table 1. In Fig. 3(a), we assume the establishment rates are 0.0028, 0.0011, and 0.0006, respectively, the reproduction rates are 30, 10, and 3, respectively. In this case, we can calculate that  $R_u > d_m$  and the mistletoes will establish in this area. Due to the different establishment rates and reproduction rates, the numbers of mistletoes in three trees are different. The first tree has the largest number of mistletoes. In Fig. 3(b), we decrease the reproduction rate in the first tree to  $s_1 = 10$  while keeping all other parameters unchanged from the values used for Fig. 3(a). Under this set of parameters,  $R_u < d_m$  and the mistletoes die out in this area.

*Proof of Theorem 1* First, we look at the equilibrium of the model (13). Substituting  $r_j$  defined in (2) and  $B_j$  defined in (12) into (11), we have

$$p_1 \frac{1}{n} \sum_{j=1}^n \frac{a\sigma s_j p_j p_1^{-1} M_1^*}{1 + ha\sigma s_j p_j p_1^{-1} M_1^*} \frac{B}{n + w} - d_m M_1^* = 0. \tag{15}$$

We can observe that the equilibrium is the intersection of the curve  $f(M_1^*)$  defined in (14) and the straight line  $M_1^*$ . Obviously, the origin is always an intersection.  $f(M_1^*)$





**Fig. 3** Number of mistletoes in the three trees. We assume birds are uniformly distributed in this environment

is a concave down, monotonically increasing function. The curve  $f(M_1^*)$  and the line  $M_1^*$  have either no positive intersection or a single positive intersection  $M_1^+$  if  $f'(0) < 1$  or if  $f'(0) > 1$ . Note that  $R_u = f'(0)$ .

Let  $M^* = (M_1^*, \dots, M_n^*)$  be a given equilibrium. The linearization of the model at the equilibrium  $M^*$  is given by

$$\frac{dM_i(t)}{dt} = e^{-d_i\tau} \alpha_i \frac{1}{n} \sum_{j=1}^n \frac{a\sigma s_j}{[1 + ha\sigma s_j M_j^*]^2} \frac{B}{n+w} M_j(t-\tau) - d_{mi} M_i(t). \tag{16}$$

According to (Smith 1987), the stability of the above system is the same as the following system of ordinary differential equations

$$\frac{dM_i(t)}{dt} = e^{-d_i\tau} \alpha_i \frac{1}{n} \sum_{j=1}^n \frac{a\sigma s_j}{[1 + ha\sigma s_j M_j^*]^2} \frac{B}{n+w} M_j(t) - d_{mi} M_i(t), \tag{17}$$

or equivalently

$$\frac{d\chi_i(t)}{dt} = d_{mi} \frac{1}{n} \sum_{j=1}^n \frac{a\sigma s_j \alpha_j e^{-d_j\tau} d_{mj}^{-1}}{[1 + ha\sigma s_j M_j^*]^2} \frac{B}{n+w} \chi_j(t) - d_{mi} \chi_i(t), \tag{18}$$

with  $\chi_i(t) = \alpha_i^{-1} e^{d_i\tau} d_{mi} M_i(t)$ .

Moreover, the stability of (18) is determined by the real eigenvalue of the matrix  $A = [a_{ij}]$  of the above linear system, with

$$a_{ii} = -d_{mi} + d_{mi} \frac{1}{n} \frac{a\sigma s_i \alpha_i e^{-d_i\tau} d_{mi}^{-1}}{[1 + ha\sigma s_i M_i^*]^2} \frac{B}{n+w}, \quad 1 \leq i \leq n,$$

$$a_{ij} = d_{mi} \frac{1}{n} \frac{a\sigma s_j \alpha_j e^{-d_j\tau} d_{mj}^{-1}}{[1 + ha\sigma s_j M_j^*]^2} \frac{B}{n+w}, \quad 1 \leq i \neq j \leq n.$$

The Gerschgorin Disc Covering theorem (Gerschgorin 1932; Varga 2004) then implies that every real eigenvalue  $\lambda$  of  $A$  satisfies

$$\lambda \leq -d_{mi} + d_{mi} \frac{1}{n} \sum_{j=1}^n \frac{a\sigma s_j \alpha_j e^{-d_j \tau} d_{mj}^{-1}}{[1 + ha\sigma s_j M_j^*]^2} \frac{B}{n + w}. \tag{19}$$

In the case where  $M_j^* = 0$  for  $1 \leq j \leq n$ , we have

$$\begin{aligned} \lambda &\leq -d_{mi} \left[ 1 - \frac{1}{n} \sum_{j=1}^n a\sigma s_j \alpha_j e^{-d_j \tau} d_{mj}^{-1} \frac{B}{n + w} \right] \\ &= -d_{mi} (1 - R_u), \quad 1 \leq i \leq n. \end{aligned}$$

Therefore, if  $R_u < 1$ , then  $\lambda < 0$  and hence the zero solution  $M^* = 0$  is asymptotically stable.

In the case where  $R_u > 1$ , the positive equilibrium  $M^+$  is obtained by having  $M_j^+ = p_j p_1^{-1} M_1^+$  for  $1 \leq j \leq n$  and  $M_1^+$  being the positive intersection of the concave down curve  $f(M_1^*)$  given in (14) with the straight line  $M_1^*$ . This gives

$$f'(M_1^*) = \alpha_1 e^{-d_1 \tau} d_{m1}^{-1} \frac{1}{n} \frac{B}{n + w} \sum_{j=1}^n \frac{a\sigma s_j p_j p_1^{-1}}{(1 + ha\sigma s_j p_j p_1^{-1} M_1^*)^2} < 1.$$

That is, as  $p_j = \alpha_j e^{-d_j \tau} d_{mj}^{-1}$  for  $1 \leq j \leq n$ , we have

$$\frac{1}{n} \frac{B}{n + w} \sum_{j=1}^n \frac{a\sigma s_j p_j p_1^{-1}}{(1 + ha\sigma s_j p_j p_1^{-1} M_1^*)^2} < 1.$$

Therefore, at  $M^+$ , the inequality (19) implies

$$\lambda \leq -d_{mi} \left[ 1 - \frac{1}{n} \sum_{j=1}^n \frac{a\sigma s_j \alpha_j e^{-d_j \tau} d_{mj}^{-1}}{(1 + ha\sigma s_j M_j^+)^2} \frac{B}{n + w} < 0 \right] < 0.$$

So, if  $R_u > 1$ , then  $M^+$  is asymptotically stable.

To describe the global dynamics of (13), we note that

$$\frac{a\sigma s_j M_j(t - \tau)}{1 + ha\sigma s_j M_j(t - \tau)} \leq \frac{1}{h}, \quad 1 \leq j \leq n.$$

Therefore,

$$\frac{dM_i(t)}{dt} \leq -d_{mi} M_i(t) + e^{-d_i \tau} \alpha_i \frac{B}{n + w} h^{-1},$$

from which it follows that

$$\limsup_{t \rightarrow \infty} M_i(t) \leq e^{-d_i \tau} \alpha_i d_{mi}^{-1} h^{-1} \frac{B}{n + w}. \tag{20}$$

This shows the monotone semi-flow defined by the system (13) on the phase space  $X^+$  has a global attractor which is bounded above by  $e^{-d_i\tau}\alpha_i d_{mi}^{-1} h^{-1} \frac{B}{n+w}$  for  $1 \leq i \leq n$ .

In the case where  $R_u < 1$ , this global attractor contains only one equilibrium, namely  $M^* = (0, 0, \dots, 0)$ , which is asymptotically stable. Therefore, every solution of (13) with initial data in  $X^+$  converges to zero equilibrium as  $t \rightarrow \infty$ .

In the case where  $R_u > 1$ , the global attractor has two equilibria  $M^* = (0, 0, \dots, 0)$  and  $M^+ = (M_1^+, M_2^+, \dots, M_n^+)$  and  $M^+$  is asymptotically stable. Therefore, every non-trivial solution of (13) with initial data in  $X^+$  is converge to  $M^+$  as  $t \rightarrow \infty$ . This completes the proof.  $\square$

### 3.2 Birds with Fruit-Preference

In the case of [BP2], birds tend to visit trees that are heavily parasitized preferentially. We have the model

$$\frac{dM_i(t)}{dt} = e^{-d_i\tau} \alpha_i \frac{1}{n} \sum_{j=1}^n \frac{a\sigma s_j M_j(t-\tau)}{1 + ha\sigma s_j M_j(t-\tau)} B \frac{s_j M_j(t-\tau)}{\sum_{k=1}^n s_k M_k(t-\tau) + w} - d_m M_i, \tag{21}$$

for  $i = 1, 2, \dots, n$ .

We consider the case where  $d_{mi} = d_m$  for  $1 \leq i \leq n$ . Under this assumption, we have

$$\frac{dM_i(t)}{dt} + d_m M_i(t) = (\alpha_i e^{-d_i\tau})(\alpha_j e^{-d_j\tau})^{-1} \left( \frac{dM_j(t)}{dt} + d_m M_j(t) \right), \quad 1 \leq i, j \leq n, \tag{22}$$

or equivalently,

$$\frac{d}{dt} [e^{d_m t} M_i(t)] = (\alpha_i e^{-d_i\tau})(\alpha_j e^{-d_j\tau})^{-1} \frac{d}{dt} [e^{d_m t} M_j(t)], \quad 1 \leq i, j \leq n.$$

From this, it follows that

$$M_i(t) = \alpha_i e^{-d_i\tau} (\alpha_j e^{-d_j\tau})^{-1} M_j(t) + e^{-d_m t} [M_i(0) - \alpha_i e^{-d_i\tau} (\alpha_j e^{-d_j\tau})^{-1} M_j(0)], \quad 1 \leq i, j \leq n.$$

In particular,

$$M_i(t) - \alpha_i e^{-d_i\tau} (\alpha_1 e^{-d_1\tau})^{-1} M_1(t) \rightarrow 0 \quad \text{as } t \rightarrow \infty, \quad 1 \leq i, j \leq n.$$

Consequently, as an application of the asymptotically autonomous system theory in (Mischaikow et al. 1995), the dynamics of the full system (21) is determined by the dynamics of the following scalar equation (for  $M_1(t)$ ):

$$\frac{d}{dt} x(t) = -d_m x(t) + e^{-d_1\tau} \alpha_1 \frac{B}{n} \sum_{j=1}^n \frac{a\sigma s_j q_j x(t-\tau)}{1 + ha\sigma s_j q_j x(t-\tau)} \frac{s_j q_j x(t-\tau)}{\sum_{k=1}^n s_k q_k x(t-\tau) + w} \tag{23}$$

with

$$q_j = \alpha_j e^{-d_j \tau} (\alpha_1 e^{-d_1 \tau})^{-1}, \quad 1 \leq j \leq n.$$

$x^* = 0$  is clearly an equilibrium of (23). If positive solutions exist, they are given by

$$d_m = \alpha_1 e^{-d_1 \tau} \frac{B}{n} \sum_{j=1}^n \frac{a \sigma (s_j q_j)^2}{(1 + ha \sigma s_j q_j x) ((\sum_{k=1}^n s_k q_k)x + w)} x := G(x). \quad (24)$$

Note that  $G(0) = G(\infty) = 0$  and

$$G'(x) = \alpha_1 e^{-d_1 \tau} \frac{B}{n} a \sigma \frac{1}{((\sum_{k=1}^n s_k q_k)x + w)^2} H(x)$$

with

$$H(x) = \sum_{j=1}^n (s_j q_j)^2 \frac{w - ha \sigma (\sum_{k=1}^n s_k q_k) s_j q_j x^2}{(1 + ha \sigma s_j q_j x)^2}. \quad (25)$$

Straightforward calculations show that

$$H'(x) = -2 \sum_{j=1}^n \frac{(s_j q_j)^3 ha \sigma ((\sum_{k=1}^n s_k q_k)x + w)}{(1 + ha \sigma s_j q_j x)^3} < 0.$$

Therefore,  $H$  is a decreasing function with  $H(0) > 0 > H(\infty)$ . Consequently, there exists  $x_c$  such that  $H(x_c) = 0$ ,  $H(x) > 0$  for  $0 < x < x_c$  and  $H(x) < 0$  for  $x > x_c$ . This implies that  $G(x)$  is increasing for  $(0, x_c)$  and then decreasing for  $x \in (x_c, \infty)$ . So  $G(x)$  reaches its maximum at  $x = x_c$ . This implies that if  $d_m > G(x_c)$  then (24) has no positive solution, but if  $d_m < G(x_c)$ , (24) has two positive solutions, denoted by  $M_{11}^+$  and  $M_{12}^+$  with

$$M_{11}^+ < x_c < M_{12}^+.$$

$d_m = G(x_c)$  is a critical value where (24) has a double zero at  $x_c$ . In conclusion, we have shown that system (23) has a unique equilibrium  $x = 0$  when  $d_m > G(x_c)$ , and has three equilibria  $0 < M_{11}^+ < M_{12}^+$  if  $d_m < G(x_c)$ .

To describe the stability of these equilibria, we note that, if  $d_m < G(x_c)$  then

$$G'(M_{11}^+) > 0 > G'(M_{12}^+). \quad (26)$$

Equation (23) can be written as

$$\frac{d}{dt} x(t) = -d_m x(t) + x(t - \tau) G(x(t - \tau)).$$

Linearizing (23) at a given equilibrium  $x^*$ , we have

$$\frac{d}{dt} x(t) = -d_m x(t) + x^* G'(x^*) x(t - \tau) + G(x^*) x(t - \tau). \quad (27)$$

If  $x^* = 0$ , we have  $G(x^*) = 0$ , and hence (27) becomes

$$\frac{d}{dt}x(t) = -d_m x(t).$$

So,  $x^* = 0$  is always asymptotically stable.

If  $x^* > 0$ , then we have  $G(x^*) = d_m$ , and hence (27) becomes

$$\frac{d}{dt}x(t) = -d_m x(t) + d_m x(t - \tau) + x^* G'(x^*) x(t - \tau).$$

As the non-linearity  $xG(x)$  in the delayed term of (23) is strictly monotonic, the stability of  $x^*$  is determined by a real eigenvalue of the corresponding ordinary differential equation

$$x'(t) = -d_m x(t) + d_m x(t) + x^* G'(x^*) x(t) = x^* G'(x^*) x(t).$$

Using inequality (26), we then conclude that if  $d_m < G(x_c)$ ,  $M_{11}^+$  is unstable and  $M_{12}^+$  is asymptotically stable.

Again, (23) generates a monotone semi-flow with a global attractor. This attractor contains a unique equilibrium  $x^* = 0$  when  $d_m > G(x_c)$ , and hence  $x^* = 0$  is the global attractor. When  $d_m < G(x_c)$ , (23) generates a monotone semi-flow with a global attractor. This attractor contains three equilibria  $0 < M_{11}^* < M_{12}^*$ . It follows that solutions of (23) are generically convergent to either 0 or  $M_{12}^*$ . In particular, if  $x(\theta) \geq M_{11}^+$  for  $\theta \in [-\tau, 0]$  and  $x$  is not identical to  $M_{11}^+$  on  $[-\tau, 0]$ , then the solution converges to  $M_{12}^+$ . If  $x(\theta) \leq M_{11}^+$  for  $\theta \in [-\tau, 0]$  and  $x$  is not identical to  $M_{11}^+$  on  $[-\tau, 0]$ , then the solution converges to 0 as  $t \rightarrow \infty$ .

Summarizing up the above discussion, we have the following theorem.

**Theorem 2** *Let  $G(x)$  be defined in (24) and let  $x_c$  denote the unique zero of  $H(x)$  given by (25). Then we have*

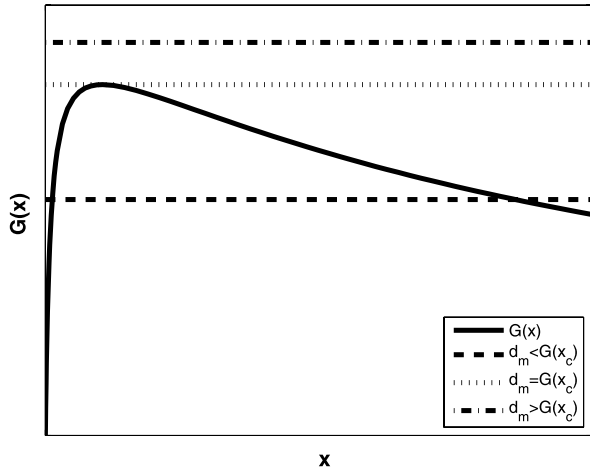
- (i) *if  $d_m > G(x_c)$ , model (21) has a unique non-negative equilibrium  $M^* = 0$  which is globally asymptotically stable;*
- (ii) *if  $d_m < G(x_c)$ , model (21) has three non-negative equilibria  $M^0 < M_1^+ < M_2^+$  with  $M_0 = (0, 0, \dots, 0)$ ,  $M_1^+ = (M_{11}^+, M_{21}^+, \dots, M_{n1}^+)$ , and  $M_2^+ = (M_{12}^+, M_{22}^+, \dots, M_{n2}^+)$  such that  $M_{jh}^+ = (\alpha_j e^{-d_j \tau})(\alpha_1 e^{-d_1 \tau})^{-1} M_{1h}^+$  for  $1 \leq j \leq n$ ,  $h = 1, 2$ . The equilibria  $M^0$  and  $M_2^+$  are asymptotically stable and  $M_1^+$  is unstable. Solutions of (21) with initial data in  $X^+$  are generically convergent to either  $M^0$  or  $M_2^+$ .*

Figure 4 gives the graphic illustration of the result in Theorem 2, and Fig. 5 illustrates the bifurcation process from a single globally asymptotically stable trivial equilibrium to bi-stability.

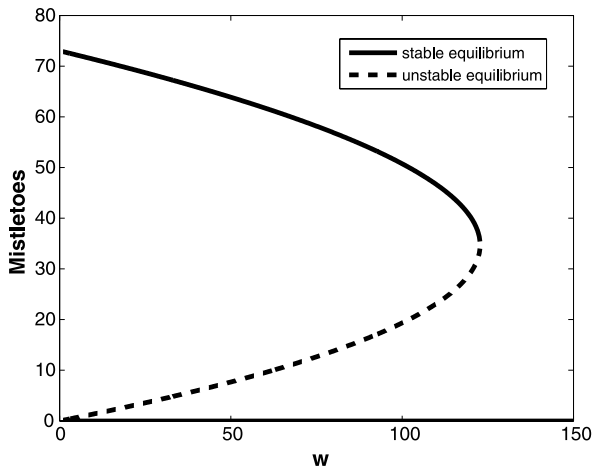
**Remark 4** System (23), i.e., the scalar delay differential equation

$$x'(t) = -d_m x(t) + x(t - \tau)G(x(t - \tau)),$$

**Fig. 4** A graphic illustration of the result in Theorem 2. If  $d_m > G(x_c)$ , model (21) has a unique nonnegative equilibrium; if  $d_m < G(x_c)$ , model (21) has two interior equilibria besides the origin

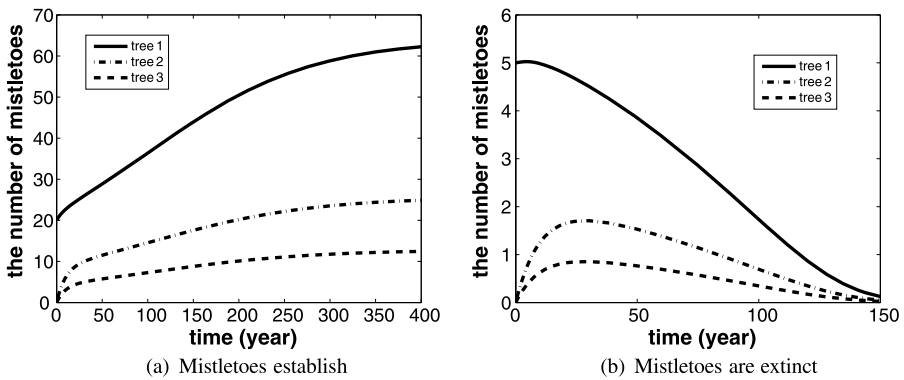


**Fig. 5** The number of equilibria of model (21) changes with respect to parameter  $w$ . If  $w$  is increased, the number of nonnegative equilibria changes from two to zero



represents a system with instantaneous decay and a delayed feedback with strictly positive  $(xG(x))' > 0$  feedback. The structure of the global attractor, in addition to the generic convergence to  $\{M^0, M_2^+\}$ , was described by Mallet-Paret and Sell (1996) and Krisztin et al. (1999) in great detail. In particular, this global attractor contains the closure of the global forward extension of the unstable manifold of the equilibrium  $M_{11}^+$ . In the case where the unstable manifold of  $M_{11}^+$  is one dimensional, this closure is just a union of  $M^0, M_1^+, M_2^+$  and the two connecting orbits from  $M_2^+$  to  $M^0$  and from  $M_1^+$  to  $M_2^+$ .

*Remark 5* Figure 6 provides some numerical simulation results for an environment of three trees where birds have their preference for infected trees. We observe a bi-stable situation where whether mistletoes can establish (see Fig. 6(a)) or die out (see Fig. 6(b)) depends on the initial conditions.



**Fig. 6** In the above simulations, we have  $w = 50$  and other parameters' value are fixed and the same as Fig. 5. In this case, we have a bi-stable case: two stable equilibria. In the *left panel*, we assume the first tree has 20 mistletoes and we notice that eventually mistletoes establish in these three trees. In the *right panel*, we assume the first tree has 5 mistletoes and the mistletoes die out eventually

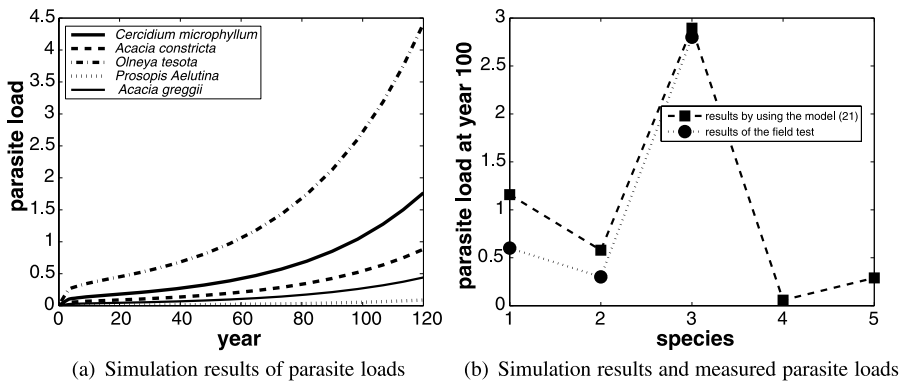
### 4 Discussion

Aukema and del Rio (2002) conducted a field study to investigate differences in host infection by a desert mistletoe, *Phoradendron californicum*. They examined one of the processes contributing to these differences: variation in seed deposition among host individuals and species. Their database contains five different host trees, *Acacia constricta*, *Acacia greggii*, *Cercidium microphyllum*, *Olneya tesota*, and *Prosopis Aelutina*. Table 2 gives relative abundance, number infected, and number of individuals receiving seeds among the hosts of *P. californicum*. They found significant difference in mistletoe prevalence and intensity among both individual hosts as well as among species.

We used our model and Aukema and Martinez del Rio's data to simulate the spread of mistletoes. We assumed a site with 168 individuals divided into 5 species as described in Table 2. Because Aukema and Martinez del Rio (2002) found that seed

**Table 2** Data are based on  $23.50 \times 8$  m transects that included 168 host trees. Values in parentheses are expected values, assuming that numbers of individuals that were parasitized and that received seeds were independent of species. The overall frequency of parasitism was 24.4% and the overall frequency of individuals that received seeds was 32.7%

Species	Number of individuals	Parasitized	Receiving seeds	$i$	$\alpha_i$	$s_i$
<i>Cercidium microphyllum</i>	93	21	21	1	0.0004	15
<i>Acacia constricta</i>	37	5	6	2	0.0002	10
<i>Olneya tesota</i>	21	15	16	3	0.001	30.5
<i>Prosopis Aelutina</i>	14	0	12	4	0.000205	3
<i>Acacia greggii</i>	3	0	0	5	0.00001	3
Total	168	41	55			



**Fig. 7** In this figure, the panel (a) gives the parasite load of five trees belonging to five different species by numerically solving the model (21), assuming that birds distribute mistletoes' seeds with the fruit-preference. The panel (b) shows the average parasite load of different species of model results, *black square*, and field test result, *black circle*, assuming that in this area the mistletoes had established for about 100 years when the test was conducted

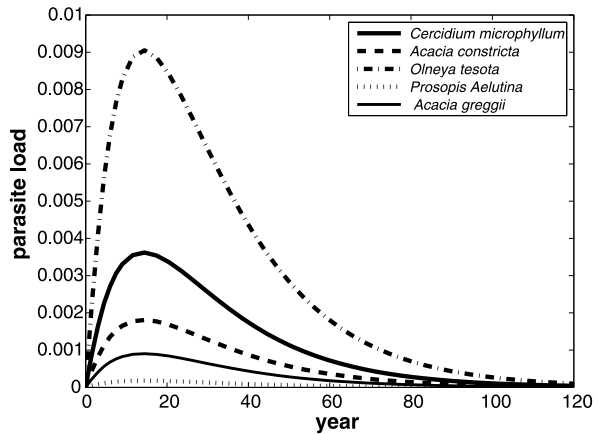
deposition was higher in infected than in non-infected host trees, we used the model in which birds have preferences. We ignored the heterogeneity of tree height within the same species, although the study indicates dependence of seed deposition on the tree height for some species of trees. All other simulation parameters values are found in Table 1, except that  $s_i$  and  $\alpha_i$  which are host-species specific and are given in Table 2. The parameter  $i$  represents species number. We assumed that there were 924 birds dispersing seeds and they were equally distributed in each tree so that on average there were 5.5 birds per tree. Initially, we assumed only two infected individual tree hosts: *Cercidium microphyllum* and *Olneya tesota*. Each one of these trees had a single parasite. Figure 7(a) plots the time course of the changes in parasite load of five trees belonging to these five species, respectively, by numerically solving the model (21), assuming that birds distribute mistletoes' seeds with the fruit-preference. We see that the parasite load of the tree belonging to *Olneya tesota* has the fastest increasing rate. This is due to the assumption that the mistletoes in this kind of species trees have a higher fruit production rate. Note that we assume the linear fruit production rate in our models, in reality, the fruit production rate is limited by available resources. We will study this factor in the future.

Figure 8 shows the parasite load of five trees belonging to five different species by numerically solving the model (7), and under the assumption that birds uniformly distribute mistletoes' seeds to trees. Since the parameter values and initial values are exactly the same for Figs. 7 and 8, we can see the pattern of seed distribution by birds plays a big role for the establishment of mistletoes. If we assume birds uniformly distribute mistletoes' seeds among trees, mistletoes cannot invade the trees in this area, while if birds have preference among trees, mistletoes can establish in this area.

Aukema and Martinez del Rio, in 2002, found that the number of mistletoes per host individual, the parasite load, differed significantly among species. *Olneya tesota* had the highest mean parasite load 2.8. *Cercidium microphyllum* and *Acacia constricta* had much lower parasite loads 0.6 and 0.3, respectively. Figure 7(b) gives



**Fig. 8** The parasite load of five trees belonging to five different species by numerically solving the model (7), under the assumption that birds uniformly distribute mistletoes' seeds to trees. The parameter values and the initial value are the same as Fig. 7



the average parasite loads of the five species at year 100 (the black square) and the measured parasite loads of three species in 1998. Figure 7(a) shows one possible trajectory that was initiated 100 years at our specified initial condition of this area. Since only one year field data was collected, the model prediction could only be verified using a future field data. Figure 7(a) indicates that with the parameters listed, host trees tend to accumulate parasites at a rate largely determined by the interaction between  $\alpha_i$  (establishment rate) and  $s_i$  (the reproduction rate of mistletoes). The values that we used lead to monotonically increasing infection intensities, once an individual becomes infected. Because the parameters of our model can be readily measured, we believe that our model can be used as a framework in the design and interpretation of field studies on the spread and distribution of mistletoes.

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