Model analyses show how biodiversity conservation could reduce infectious diseases in an ecosystem

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Abstract
Biodiversity conservation benefits the sustainability of the environment and also the well-being of humanity. Here we consider the possible importance of biodiversity of resources in limiting disease. With this aim we formulate a dynamical system model for a terrestrial ecosystem that takes into account, biodiversity of resources together with competition among species. The dynamics of the model are explored using appropriate dynamical system analyses. The effects of the competition terms and carrying capacity on the dynamics of the model are considered in terms of which ranges allow sustainability of the system. Simulations illustrate how biodiversity conservation can of itself lead to reduction in infectious diseases in an ecosystem.

Recommendations for Resource Managers:

- The sustainability of the environment is generally improved by robust biodiversity and important for human welfare.
- Diseases and their control are also important in natural and human systems.
- Here we use models to establish to what extent natural resource biodiversity can reduce the extent of infected resources.
Our results show that biodiversity conservation is a possible control mechanism for reducing infectious diseases in an ecosystem.

These results can help natural resource managers concentrate time and money on biodiversity conservation over and above the already obvious need for such efforts.

**KEYWORDS**

bifurcation analysis, biodiversity conservation, consumer–resource model, ecosystem dynamics, epidemiology, stability analysis

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### 1 | INTRODUCTION

Environmental biodiversity benefits the sustainability of the environment but also the well-being of humanity through the protection of water, soil, and nutrient resources, as well as breaking down pollution and contributing to climate stability (Shah, 2014). Ultimately, humans depend on biodiversity conservation in meeting their needs in several areas of life. Human health depends on ecosystem products and services, such as freshwater, food, and fuel resources and it has been shown that biodiversity conservation enhances overall human health and productive livelihoods (Naeem, 2009; Pimentel et al., 1997). Many pharmacological and medical discoveries are made possible through an understanding of the earth’s biodiversity. Several economic and environmental benefits of biodiversity can be found in Ostfeld and Keesing (2012) and Naeem (2009). Conservation of biodiversity using natural processes enhances ecosystem reliability, where reliability refers to consistent performance over time (Naeem & Li, 1997). Also, biodiversity has been shown to improve resistance to changes in productivity during, and resilience after, a broad range of climate events, including moderate or extreme events (Isbell et al., 2015). Biodiversity is considered a major factor that regulates the transmission of many infectious diseases (Patz et al., 2005, Chap. 14). The significance of biodiversity conservation to humanity cannot be overemphasized. In this study, our interest is in the effects of biodiversity conservation on infectious diseases in a terrestrial ecosystem.

Infectious diseases have been shown to affect biodiversity (Daszak et al., 2000). The nature of the interactions between consumers and infected resources has either a positive or negative effect in the system depending on the behavior of the consumers (Duffy et al., 2011; Hethcote et al., 2004; Holt & Roy, 2007; Packer et al., 2003). A positive effect is when consumers help eliminate infectious resources, thereby decreasing infections (Hethcote et al., 2004; Packer et al., 2003), while a negative effect is when consumers enhance the spread of disease (Duffy et al., 2011; Holt & Roy, 2007).

Preserving biodiversity has been shown to have positive effects on infectious disease transmission (Ezenwa et al., 2006; Haas et al., 2011; Johnson et al., 2013; Keesing et al., 2010; Ostfeld & Keesing, 2012). Specifically, reduction of the risk of forest diseases (Haas et al., 2011), a decrease in amphibian diseases (Johnson et al., 2013), reduction in Lyme disease infections (LoGiudice
et al., 2003), reduction in the prevalence of diseases in vertebrate habitats (Ostfeld & Keesing, 2012) and reductions in infectious disease prevalence in general (Keesing et al., 2010).

It has been shown theoretically that sustainable consumer and resource coexistence can benefit disease limitation (Duffy & Collins, 2019) and how increasing biodiversity could reduce infectious diseases as well (Collins & Duffy, 2018). However, these studies ignored competition between resources. Thus, using a similar modeling approach we test the following questions:

1. Does increasing resource biodiversity, where there is competition between resources, reduce disease in those resources?
2. Does the degree of competition positively affect any reduction in disease?

We consider biomass values of the population models. Thus, comparisons are made in terms of these biomass estimates.

2 | MODEL FORMULATION

A dynamical system model that takes into account species diversity in resources, such as plants, with competition among those resources is developed. The model is made up of multiple resources. Each species of resource ($N_i$) comprises two classes: a susceptible class $S_i$ and an infected class $I_i$. The parameter $\delta_{ij}$ denotes the competition between any two resources $i$ and $j$. The density of pathogen denoted by $P$ grows, through feeding on the various resources, at rates $\nu_i$ and each decay with time at a rate $\xi$. Direct transmission of infection from $I_i$ to $S_i$ is not assumed possible (e.g., when both $I_i$ and $S_i$ are plants) and so the introduction of $P$ in the model generates infections. A logistic growth is used to model the growth of resource while a linear interaction is used to model the nature of interaction between susceptible resources and pathogen (Tien & Earn, 2010; Turchin, 2003; Collins & Duffy, 2016b). From the above assumptions, the model is

$$
\frac{dS_1}{dt} = N_1 r_1 \left( 1 - \frac{N_1 + \sum_{i=1}^{m} \delta_{ij} N_j}{K_1} \right) - \alpha_1 S_1 P + \gamma_1 I_1,
$$

$$
\frac{dI_1}{dt} = \alpha_1 S_1 P - (\gamma_1 + \mu_1) I_1,
$$

$$
\frac{dS_2}{dt} = N_2 r_2 \left( 1 - \frac{N_2 + \sum_{i=1}^{m} \delta_{ij} N_j}{K_2} \right) - \alpha_2 S_2 P + \gamma_2 I_2,
$$

$$
\frac{dS_m}{dt} = N_m r_m \left( 1 - \frac{N_m + \sum_{i=1}^{m} \delta_{ij} N_j}{K_m} \right) - \alpha_m S_m P + \gamma_m I_m,
$$

$$
\frac{dI_m}{dt} = \alpha_m S_m P - (\gamma_m + \mu_m) I_m,
$$

$$
\frac{dP}{dt} = \sum_{i=1}^{m} \gamma_i I_i - \xi P.
$$

\[1\]
Note that \( N_i = S_i + I_i, \sum_{i=1}^{m} S_i = S, \) and \( \sum_{i=1}^{m} I_i = I. \) Refer to Table 1 for the meaning of variables and parameters. From the above formulation, species biodiversity can be increased or decreased in this model by increasing or decreasing \( m \) accordingly.

3 | ANALYSIS OF MODEL (1) FOR \( m = 1 \)

A special case of model \((1)\) \((m = 1)\) when there is only one species of resource in the ecosystem is considered first.

For this special case, the essential ecological and epidemiological features of the model \((1)\) \((m = 1)\), which follow those given in Collins and Duffy (2018) and Duffy and Collins (2019) but are different in the details, are presented here.

Using the next-generation matrix method of Van den Driessche and Watmough (2002) the basic reproduction number \((R_0)\) for model \((1)\) \((m = 1)\) is determined as follows. The next-generation matrix for model \((1)\) \((m = 1)\) is

\[
FV^{-1} = \begin{pmatrix}
\frac{\alpha K \nu}{\xi (\gamma + \mu)} & \frac{\alpha K}{\xi} \\
0 & 0
\end{pmatrix},
\]

where \( F = \begin{pmatrix} 0 & \alpha K \\ 0 & 0 \end{pmatrix} \) and \( V^{-1} \) is the inverse of the matrix \( V = \begin{pmatrix} \gamma + \mu & 0 \\ -\nu & \xi \end{pmatrix} \). The basic reproduction number \( R_0 \) becomes the dominant positive eigenvalue of the next-generation matrix \( FV^{-1} \) and is

\[
R_0 = \frac{\alpha \nu K}{\xi (\gamma + \mu)}. \tag{2}
\]

Epidemiologically, the value of \( R_0 \) is an indication of whether an outbreak can persist in a system or not (Castillo-Chavez et al., 2002; Tien & Earn, 2010; Van den Driessche & Watmough, 2002). Thus, the value of \( R_0 \) is very useful for analyzing models of infectious

| Variables/parameters | Meaning | Unit |
|----------------------|---------|------|
| \( S_i \) | Density of susceptible resources \( i \) | g/m² |
| \( I_i \) | Density of infected resources \( i \) | g/m² |
| \( p \) | Measure of foliar diseases pathogen | g/m² |
| \( \eta \) | Growth rate of resources \( i \) | /year |
| \( K_i \) | Carrying capacity of resources \( i \) | g/m² |
| \( \delta_{ij} \) | Competition effect \( N_j \) has on \( N_i \) | Dimensionless |
| \( \alpha_i \) | Exposure of \( S_i \) to \( p \), /year |
| \( \mu_i \) | Death rate of \( I_i \) | /year |
| \( \gamma_i \) | Recovery rate of \( I_i \) | /year |
| \( \nu_i \) | Shedding rate of \( I_i \) in \( p \) | /year |
| \( \xi \) | Net decay rate of \( p \) | /year |
disease dynamics. In the subsequent sections, this quantity will be used to analyze model (1) ($m = 1$).

The possible equilibrium states of model (1) ($m = 1$) are

\begin{align*}
E_1 &= (S^*, I^*, P^*) = (0, 0, 0), \\
E_2 &= (S^*, I^*, P^*) = (K, 0, 0), \\
E_3 &= (S^*, I^*, P^*) = \left( \frac{K}{R_0}, \frac{\mu N^*}{\mu - \frac{N^*}{K}}, \frac{\mu^*}{\xi} \right) \quad \text{if } R_0 \geq 1,
\end{align*}

where $N^* = \frac{-K(\mu - r) + \sqrt{K^2(\mu - r)^2 + 4\mu K\xi S^*}}{2r}$. Note that $E_2 = E_2$ if $R_0 = 1$. This suggests that $R_0$ is a bifurcation quantity. The short-term (and long-term) dynamics of model (1) ($m = 1$) can be determined by the stability about the equilibrium states (Liao & Wang, 2011). Thus, a summary of the stability results of model (1) ($m = 1$) is presented in the following theorem.

Theorem 1.

(i) The trivial equilibrium state $E_1$ is unstable.

(ii) The equilibrium state $E_2$ is stable if $R_0 < 1$.

(iii) For $R_0 > 1$, the equilibrium state $E_3$ is stable.

The proof of Theorem 1 is given in Appendix A. The ecological implications of Theorem 1 are: (i) It will be difficult for all the resources and pathogens in the ecosystem to vanish such that nothing is left in the ecosystem. (ii) It is possible for the infected resource and pathogen to die out while only uninfected resource remains and increases over time to carrying capacity provided $R_0 < 1$. (iii) For $R_0 > 1$ resources (susceptible and infected) together with pathogens remain (coexistence) over a long period in the ecosystem.

4 | ANALYSIS OF MODEL (1) WITH INCREASED BIODIVERSITY

The dynamical system analysis of model (1) with increased biodiversity is presented here.

4.1 | Analysis of model (1) for $m = 2$

Another special case of model (1) which is obtained by increasing the resource biodiversity (i.e., $m = 2$) is considered here. In this scenario there are two distinct species of resources. The basic dynamical features of the model (1) ($m = 2$) which is an extension of model (1) ($m = 1$) will be presented here. Model (1) ($m = 2$) has many equilibrium states, however we consider only the simple ones denoting disease eradication and they are

\begin{align*}
E_1 &= \left( S_1^*, I_1^*, S_2^*, I_2^*, P^* \right) = (0, 0, 0, 0, 0), \\
E_2 &= \left( S_1^*, I_1^*, S_2^*, I_2^*, P^* \right) = \left( \frac{K_1 - K_2 \delta_{12}}{1 - \delta_{12} \delta_{21}}, 0, \frac{K_2 - K_1 \delta_{21}}{1 - \delta_{12} \delta_{21}}, 0, 0 \right).
\end{align*}
Using a similar method (next-generation matrix method; Van den Driessche & Watmough, 2002) the basic reproduction number of model (1) \((m = 2)\) is computed as follows. The next-generation matrix for model (1) \((m = 2)\) is

\[
FV^{-1} = \begin{pmatrix}
\frac{\alpha_1 K_1 v_1}{\xi (y_1 + \mu_1)} & \frac{\alpha_1 K_1 v_2}{\xi (y_2 + \mu_2)} & \frac{\alpha_1 K_1}{\xi} \\
\frac{\alpha_2 K_2 v_1}{\xi (y_1 + \mu_1)} & \frac{\alpha_2 K_2 v_2}{\xi (y_2 + \mu_2)} & \frac{\alpha_2 K_2}{\xi} \\
0 & 0 & 0
\end{pmatrix},
\]

where \(F = \begin{pmatrix} 0 & \alpha_1 K_1 \\
0 & \alpha_2 K_2 \\
0 & 0 \end{pmatrix}\) and \(V^{-1}\) is the inverse of the matrix \(V = \begin{pmatrix} y_1 + \mu_1 & 0 & 0 \\
0 & y_2 + \mu_2 & 0 \\
-\nu_1 & -\nu_2 & \xi \end{pmatrix}\). The basic reproduction number \(R_0\) becomes the dominant positive eigenvalue of the next-generation matrix \(FV^{-1}\) and is

\[
R_0 = \frac{R_{11} + R_{22} + \sqrt{(R_{11} + R_{22})^2 + 4(R_{12}R_{21} - R_{11}R_{22})}}{2},
\]

where \(R_{11} = \frac{\alpha_1 K_1 v_1}{\xi (y_1 + \mu_1)}\), \(R_{12} = \frac{\alpha_1 K_1 v_2}{\xi (y_2 + \mu_2)}\), \(R_{21} = \frac{\alpha_2 K_2 v_1}{\xi (y_1 + \mu_1)}\), and \(R_{22} = \frac{\alpha_2 K_2 v_2}{\xi (y_2 + \mu_2)}\). By simplifying the above equation and taking into account that \(R_{12}R_{21} = R_{11}R_{22}\), the basic reproduction number \(R_0\) of model (1) \((m = 2)\) becomes

\[
R_0 = R_1 + R_2,
\]

where \(R_1 = R_{11} = \frac{\alpha_1 v_1 K_1}{\xi (y_1 + \mu_1)}\) and \(R_2 = R_{22} = \frac{\alpha_2 v_2 K_2}{\xi (y_2 + \mu_2)}\). The quantities \(R_1\) and \(R_2\) represent the generation of secondary infections in the ecosystem that results from each of species 1 and 2, respectively.

Determining the dynamics of model (1) \((m = 2)\) analytically is generally complex so we report some of the results analytically and the remaining results numerically (Section 5). Part of the dynamics of model (1) \((m = 2)\) is summarized in the following stability results.

**Theorem 2.**

(i) The trivial equilibrium state \(E_1\) is unstable.

(ii) The equilibrium state \(E_2\) is stable if \(R_0 < 1\).

The proof of Theorem 2(i) and (ii) can be established using the same approach used in the proof of Theorem 1. The epidemiological and ecological implications of these results are similar to the case when \(m = 1\) except that biodiversity has been increased. Similar to model (1) \((m = 1)\), the dynamics of model (1) \((m = 2)\) is also governed by \(R_0\). Analytically, the dynamics of model (1) \((m = 2)\) are unknown, when \(R_0 > 1\). To determine these dynamics, we consider numerical simulations also given in Section 5.

### 4.2 Analysis of the general case of model (1)

Here we present some preliminary analyses of the general case of model (1). Using a similar method, the \(R_0\) of the general consumer–resource model (1) is
\[ R_0 = \sum_{i=1}^{m} R_i, \quad (4) \]

where \( R_i = \frac{\alpha_i \eta_i K_i}{\xi (\gamma_i + \mu_i)} \). It is expected that the \( R_0 \) for this general case governs the model dynamics as illustrated in the special cases of the model. This possibility requires further analyses and will be put into consideration in future work.

The \( R_0 \) in this general model comprises of \( m \) parts, respectively, where each part emanates from a separate species. Thus, without any restrictions on the parameters, it is expected that as the number of species increases (an increase in biodiversity), the value of \( R_0 \) will increase accordingly. This result is also true for the different models proposed by Collins and Duffy (2018) and Duffy and Collins (2019).

5 | NUMERICAL SIMULATIONS

Numerical simulations are used here to explore the dynamics of model (1) for \( m = 1, 2, \) and 3, in particular to investigate the effects of biodiversity on infected resources dynamics. The values of the parameters used are given in Table 2. For uniformity, we make the following assumptions: \( \eta = r, \alpha = \alpha, K = K/n, \mu = \mu, \gamma = \gamma, \nu = \nu, \delta_{ij} = \delta \) for \( i, j = 1, 2, 3 \). Using these assumptions, the \( R_0 \) for each scenario of \( m = 1, 2, \) and 3 coincides. Therefore, using the model (1), changes in infectious disease dynamics can be compared for these various levels of biodiversity (\( m = 1, 2, \) and 3).

5.1 | Effects of biodiversity on the dynamics model (1) for \( m = 1, 2, \) and 3

The dynamics of model (1) for different levels of biodiversity (i.e., \( m = 1, 2, \) and 3) are compared in Figure 1. The figure shows that increasing diversity results in less infectious disease density and less pathogen when they are present. This result suggests that biodiversity conservation could be a possible control measure for reducing infectious diseases in an ecosystem. For all these simulations the parameters for competition between resources are set at \( \delta_{ij} = 0.25 \).

| Parameters | Value | Unit | Source |
|------------|-------|------|--------|
| \( r_i \)  | 0.014 | /day | Duffy (2001) |
| \( K \)    | 500.00| g/m² | Owen-Smith (2004) and Duffy (2001) |
| \( \alpha_i \) | 0.100—0.750 | /year | Estimated |
| \( \delta_{ij} \) | 0.250 | Dimensionless | Estimated |
| \( \gamma \) | 0.800 | /year | Estimated |
| \( \mu_i \) | 0.002 | /year | Estimated |
| \( \nu_i \) | 0.00275 | /year | Estimated |
| \( \xi \) | 0.333 | /year | Estimated |
5.2 | Effects of competition terms on the dynamics model (1) for \( m = 2 \) and 3

In a terrestrial ecosystem, resources can compete for space and food. This competition among resources has been shown to be a sensitive parameter for the dynamics in a consumer–resource model (Abrams et al., 2008). The effects of the competition terms on the dynamics of model (1) for the different levels of biodiversity (i.e., \( m = 2 \) and 3) are presented in Figure 2. Increasing competition among resources (increasing \( \delta_{ij} \)) results in less disease density and less pathogen irrespective of the level of biodiversity.

5.3 | Effects of the carrying capacity \( K \) on the dynamics of model (1)

To complement existing literature on the importance of carrying capacity (Seidl & Tisdell, 1999), we explore the effects of the carrying capacity \( K_i \) on the dynamics of our model (1) with increasing biodiversity, that is, \( m = 1, 2, \) and 3 (Figure 3). Considering model (1) \((m = 2)\), the carrying capacity \( K_i \) is one of three parameters for which \( \mathcal{R}_0 \) is an increasing function. To avoid repetition, the analyses are in terms of \( K \) and we assumed that \( K_i = K_1 = K_2 \) and \( K_m = \frac{K}{m} \).

In Figure 3, focusing primarily on the infected resources, the dynamics change in the region \( K = 150 - 200 \) which corresponds to a basic reproduction number around \( \mathcal{R}_0 = 1 \). From the figure, below this region infected resources die out while above this region the infected resources persist. This agrees with fundamental results in epidemiology (Liao & Wang, 2011; Tien & Earn, 2010; Van den Driessche & Watmough, 2002). Again increasing biodiversity results in less disease in the system.
Conserving biodiversity has many economic, social, environmental, and geographical benefits (see, e.g., Pimentel et al., 1997). Thus, optimal preservation of biodiversity is necessary to maximize these benefits. Furthermore, new discoveries of the impacts of biodiversity on the dynamics of natural systems can assist in the understanding and management of conservation areas. This study uses a mathematical model to illustrate how biodiversity might reduce infectious diseases in a terrestrial ecosystem. A dynamical system model with diversity in resource species is formulated. This model is an extension of other consumer–resource models in the literature (Collins & Duffy, 2016a, 2018; Duffy & Collins, 2019). Resources can compete for space and food and so the model used here includes competition between resources. This addition is also important because consumer–resource model dynamics have been shown to be sensitive to competition parameters (Abrams et al., 2008). Species diversity in resources is considered using the model to address the questions posed in Section 1.

The fundamental dynamics of the system are first explored analytically using the special case when there is only one resource. For this case, the basic reproduction number ($R_0$) is determined and used to analyze the dynamics. These analyses show that infectious diseases can be eradicated when $R_0$ is below unity in agreement with results in the literature (Collins & Duffy, 2016a, 2018; Duffy & Collins, 2019). In the absence of infected resources and pathogens, susceptible resources remain and increase to the carrying capacity when $R_0 < 1$. When $R_0 > 1$, the disease can persist in the system and remain endemic. This result also agrees with previous results (Collins & Duffy, 2018).

For the model simulations, different values of $R_0$ are compared by adjusting $\nu$, the rate at which infected resources shed pathogens into the ecosystem. Increasing resource biodiversity (increasing the number of species) introduces the possibility of competition between species.
which is introduced into the model as $\delta_{ij}$. As biodiversity is increased the dynamics have basic similarities with the special case of a single species of resources. In particular, with increased species, infectious diseases and pathogens are eradicated for $R_0 < \text{critical value}$ and not eradicated for $R_0 > \text{critical value}$ and this value increases with increasing species (Figure 1). Also, where disease is present the disease is reduced for increasing diversity in terms of both pathogen biomass and infected resource biomass values. This fact is especially relevant for $R_0 > 1.5$ where the same amounts of susceptible resources are present regardless of the degree of diversity. Thus, with regard to our model, the answer to Question 1 is

- Increasing resource biodiversity, where there is competition between resources, reduces disease in those resources.

The degree of competition between resource species improves this effect. Again, the critical value of $R_0$ at which pathogen persists increases with an increasing competition effect (Figure 2). Also, where disease is present the disease is reduced for increasing competition in terms of both pathogen biomass and infected resource biomass values. Thus, with regard to our model, the answer to Question 2 is

- The degree of resource competition positively affects the reduction in resource disease.

Thus, increasing resource diversity, and furthermore the extent of competition between resources, decreases the amounts of infected resources when those infections are present highlighting the dynamic role diversity can take in limiting diseases.

Another parameter whose effects on the dynamics are investigated is the carrying capacity $K_i$. This parameter is one of the parameters in our model that is positively sensitive for $R_0$. Again, the effects are explored using numerical simulations. For low values of $K$ there are susceptible resources and no infected resources. This result agrees with other findings in the literature for $R_0$ below unity (Castillo-Chavez et al., 2002; Tien & Earn, 2010; Van den Driessche & Watmough, 2002). With an
increase in $K$ beyond a threshold, infected resource increases in agreement with epidemiological and ecological results as $R_0 > 1$ (Collins & Duffy, 2016a, 2018; Duffy & Collins, 2019). These results stress further the importance of carrying capacity in wildlife systems.

In summary, the results agree with previous work where an increase in resource biodiversity can reduce infected resources (Collins & Duffy, 2018; Duffy & Collins, 2019). This shows that biodiversity conservation is a possible control mechanism for reducing infectious diseases in an ecosystem irrespective of the level of infections. How might this be possible? One aspect is an increase in the appreciation of biodiversity as a public good and of its economic value which can improve effective conservation (Rands et al., 2010). Persons, especially decision makers, knowing that conservation of biodiversity can limit disease might be inclined to greater conservation efforts. This fact is particularly important in the tropics that contain the majority of our terrestrial biodiversity (Barlow et al., 2018).

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AUTHOR CONTRIBUTIONS
Both authors contributed substantially to the conception of this study, the analyses and the write up. They also both approved the final version of the manuscript.

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APPENDIX A

Theorem 3.

(i) The trivial equilibrium state $E_1$ is unstable.
(ii) The equilibrium state $E_2$ is stable if $\mathcal{R}_0 < 1$.
(iii) For $\mathcal{R}_0 > 1$, the equilibrium state $E_3$ is stable.

Proof. The proof of Theorem 1 is given as follows:

(i) The Jacobian of model (1) ($m = 1$) evaluated at the trivial equilibrium point $E_1$ has the following eigenvalues:

$$\lambda_1 = r > 0, \quad \lambda_2 = -(\gamma + \mu), \quad \lambda_3 = -\xi.$$ 

Thus, $E_1$ is unstable since $\lambda_1 = r > 0$.

(ii) The Jacobian of model (1) ($m = 1$) evaluated at the equilibrium point $E_2$ has the following eigenvalues:

$$\lambda_1 = -r < 0, \quad \lambda_{2,3} = \frac{-\vartheta \pm \sqrt{\vartheta^2 + 4\xi(\gamma + \mu)(\mathcal{R}_0 - 1)}}{2},$$

where $\vartheta = \gamma + \mu + \xi$. Clearly, $\lambda_{2,3} < 0 \iff \mathcal{R}_0 < 1$. Thus, the equilibrium point $E_2$ is stable if $\mathcal{R}_0 < 1$.

(iii) Here we show that the Jacobian of model (1) ($m = 1$) evaluated at the equilibrium point $E_3$ satisfies the Ruth–Hurwize criterion for local stability. To simplify our analysis, we make the following assumptions: $r = \mu, \nu = \xi$, and $aK = 4(\gamma + \mu)$. On the basis of these assumptions, the characteristic polynomial of the Jacobian of model (1) ($m = 1$) evaluated at the equilibrium point $E_3$ becomes

$$a_3\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0 = 0,$$

where $a_3 = 1, a_2 = \gamma + \mu + \alpha S^*, a_1 = \xi(\gamma + \mu) + \alpha S^*,$ and $a_0 = \xi\mu\alpha S^*$. Clearly, these conditions $a_3 > 0, a_2 > 0, a_1 > 0, a_0 > 0,$ and $a_2a_1 - a_3a_0 = a_1\xi(\gamma + \mu) + \alpha S^*(\gamma + \mu + \alpha S^*) > 0$ are satisfied. Thus, for $\mathcal{R}_0 > 1$, the equilibrium state $E_3$ is stable. □