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Multi-stage Vector-Borne Zoonoses Models: A Global Analysis

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Abstract A class of models that describes the interactions between multiple host species and an arthropod vector is formulated and its dynamics investigated. A host-vector disease model where the host's infection is structured into n stages is formulated and a complete global dynamics analysis is provided. The basic reproduction number acts as a sharp threshold, that is, the disease-free equilibrium is globally asymptotically stable (GAS) whenever $\mathcal{R}_0^2 \leq 1$ and that a unique interior endemic equilibrium exists and is GAS if $\mathcal{R}_0^2 > 1$. We proceed to extend this model with m host species, capturing a class of zoonoses where the cross-species bridge is an arthropod vector. The basic reproduction number of the multi-host-vector, $\mathcal{R}_0^2(m)$, is derived and shown to be the sum of basic reproduction numbers of the model when each host is isolated with an arthropod vector. It is shown that the disease will persist in all hosts as long as it persists in one host. Moreover, the overall basic reproduction number increases with respect to the host and that bringing the basic reproduction number of each isolated host below unity in each host is not sufficient to eradicate the disease in all hosts. This is a type of "amplification effect," that is, for the considered vector-borne zoonoses, the increase in host diversity increases the basic reproduction number and therefore the disease burden.

Keywords Vector-borne zoonoses · Stage progression · Multi-host · One health · Amplification effect · Global stability · Nonlinear dynamical systems

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1 Introduction

Zoonoses, infectious diseases caused by pathogens transmissible under natural conditions from vertebrate animals to humans, account for 75% of emerging infectious diseases (Taylor et al. 2001), with wildlife being an important source. Zoonotic pathogens represent 61% of all known human pathogens (Taylor et al. 2001). These zoonoses are responsible for over one billion cases of human morbidity, millions of human mortality each year, and over $80 billion USD of global economic burden, including public and animal health and livestock, from 1997 to 2009 (World Bank 2010). Therefore, understanding the dynamics of the underlying mechanisms that drive the inter-host, between hosts, and/or vectors interactions to formulate better control strategies should be a worldwide priority.
Zoonoses are transmitted through four majors transmission routes (Centers for Disease Control and Prevention 2015c):

(i) *Vector-borne* class that includes diseases such as Lyme disease, tick-borne relapsing fever (TBRF), West Nile virus (WNV), Chagas disease. They are transmitted by the bite of arthropod vectors;
(ii) *Direct transmission* including Brucellosis, hantavirus, influenza, rabies, these zoonoses are due to a close contact with bodily fluids of an infected host, including contacts with fomites;
(iii) *Indirect transmission* (e.g., Anthrax, Echinococcosis, Leptospirosis) that are transmitted through the air by droplet transfer from an infected host to susceptible host; and
(iv) *Food-borne or oral transmission* class that includes Toxoplasmosis, Trichinellosis, Salmonellosis. that are caused by ingesting food or water contaminated with a pathogen.

However, according to Johnson et al. (2015), arthropod vectors transmit 40% of zoonoses involving wild animals and 20% of zoonoses involving domestic animals, making vector-borne zoonoses (VBZ) arguably the most important class of zoonoses (see Lloyd-Smith et al. (2009) for an excellent review on VBZ). The understanding and control of zoonoses have been hampered because of the complexities of interactions of zoonoses at the interface of humans, animals, vectors, and the ecosystem. Mathematical models have long been used to gain insights of key components of the disease in consideration, although most have dealt with only one host and a pathogen (Anderson and May 1991; Kermack and McKendrick 1927) or along with a vector (Ross 1911, 1916; Ross and Hudson 1917a, b).

While dynamical models capturing directly transmitted zoonoses, including food-borne and free-living pathogens, have received substantial, yet insufficient, attention (Begon and Bowers 1994; Begon et al. 1992; Bowers and Begon 1991; Greenman and Hudson 2000; Holt and Pickering 1985; Lloyd-Smith et al. 2009) (and the references therein), the literature on the dynamics of multi-host zoonoses is sparse when transmission involves an arthropod vector (mosquitoes, flies, fleas, ticks, etc.) (Bowman et al. 2005; Cruz-Pacheco et al. 2012a, b; Johnson et al. 2016; Simpson et al. 2011), most of

which are focused on WNV and with at most two hosts. Indeed, even among papers that claim to model a zoonosis, authors usually disregard the multi-host component.

The main goal of this paper is to formulate and investigate the global asymptotic behavior of systems describing the interactions between multiple hosts and vectors that capture the evolution of a class of vector-borne zoonoses. The outline of this endeavor is based on the following steps:

- We begin by formulating a single host-vector model with an arbitrary number of stages (or relapses) during the host's infectiosity. The proposed model revisits the models in Johnson et al. (2016), Palmer et al. (2016) and generalizes them in order to incorporate the heterogeneity of the vector's infection with respect to the host's stage of infection (Sect. 2).
- We then derive the basic reproduction number and provide a complete investigation of the global stability of equilibria, which surprisingly has not been done (Sects. 2.2 and 2.3).
- We formulate a multi-host-vector model where each host's infection dynamics have an arbitrary number of stages (or relapses). The proposed model allows also that some of the hosts are dead-end hosts, that is, they carry the pathogen but are not infectious. This feature of the model allows for inspecting whether host diversity (with respect to the number of different host species) increases or mitigates the overall infection.
- We complete the global stability of equilibria of the model with m host species on which a common arthropod vector is feeding. These results are new (Sect. 3).

The basic reproduction number of the multi-host-vector system is $\mathcal{R}_0^2(m) = \sum_{j=1}^{m} \mathcal{R}_{0,j}^2$, where $\mathcal{R}_{0,j}^2$, for $j = 1, 2, \ldots, m$, is the basic reproduction number of a single host-vector system, when taken in isolation. We prove that the disease-free equilibrium (DFE) is globally asymptotically stable if $\mathcal{R}_0^2(m) \leq 1$. That is, in this case, the disease dies out in all hosts and in the vector populations. If $\mathcal{R}_0^2(m) > 1$, a unique interior endemic equilibrium exists and is shown to be globally asymptotically stable. Given the expression of $\mathcal{R}_0^2(m)$ in terms of $\mathcal{R}_{0,j}^2$, for $j = 1, 2, \ldots, m$, this implies that controlling vector-borne zoonoses requires a coordinated effort in controlling the disease in all hosts. This result echoes the One Health concept (Centers for Disease Control and Prevention 2017), which advocates for optimal health for all species and the environment (One Health 2017). Moreover, the basic reproduction number $\mathcal{R}_0^2(m)$ increases with respect to the number of hosts, although the increase in dead-hosts does not affect $\mathcal{R}_0^2(m)$. This is a type of "amplification effect."

2 Single Host-Vector with Stage Progression

In this section, we derive an SEIR-SEI vector-borne disease for a single host-vector and study its asymptotic properties. We later extend to the multi-host case in Sect. 3.

2.1 Formulation of the Model

We consider a host population, denoted by N_h, that interacts with a population of vectors, denoted by N_v. This host-vector interaction leads to a transmission of pathogens from host to vector and conversely. We suppose that the host population is subdivided into susceptible hosts, denoted by S_h, latent hosts (infected but not infectious) E_h, hosts in a successive chain of infected classes I_i, for $i = 1, 2, \ldots, n$ that represents the different stages of the disease progression, and a class of recovered hosts, denoted by R_h. The total host population is therefore, $N_\mathrm{h} = S_\mathrm{h} + E_\mathrm{h} + \sum_{i=1}^{n} I_i + R_\mathrm{h}$. A host's infection thus follows an SEIR type of framework. The vectors' population is composed of susceptible, latent, and infected vectors, denoted, respectively, by S_v, E_v, and I_v, and their infection follows an SEI model type of structure. The hosts' susceptible population is generated via a constant recruitment Λ_h and reduced by a per capita mortality rate of μ_h and through an infectious vector bite. The dynamics of the susceptible host is therefore given by:

$$\dot{S}_\mathrm{h} = \Lambda_\mathrm{h} - b(N_\mathrm{h}, N_\mathrm{v})\beta_\mathrm{vh} S_\mathrm{h} \frac{I_\mathrm{v}}{N_\mathrm{v}} - \mu_\mathrm{h} S_\mathrm{h}, \tag{1}$$

where $b(N_\mathrm{h}, N_\mathrm{v})$ is the number of mosquito bites per human per unit of time. The new infected hosts become latent and leave this stage either by natural death or entering the infectious stage after an incubation period of $1/\nu_\mathrm{h}$. Hence, the dynamics of latent host is given by:

$$\dot{E}_\mathrm{h} = b(N_\mathrm{h}, N_\mathrm{v})\beta_\mathrm{vh} S_\mathrm{h} \frac{I_\mathrm{v}}{N_\mathrm{v}} - (\mu_\mathrm{h} + \nu_\mathrm{h}) E_\mathrm{h}. \tag{2}$$

The hosts' incubation period is important for vector-borne diseases in general and vector-borne zoonoses in particular. For instance, the latency period for the Japanese Encephalitis Virus is 10 days in pigs (Khan et al. 2014) and 5–15 days (Centers for Disease Control and Prevention 2015b) for humans. Humans are dead-end hosts, that is, although deadly, the parasitaemia is insufficient to infect biting mosquitoes. Similarly, the incubation period of TBRF is 7 days (Dworkin et al. 2008; Southern and Sanford 1969). For other tick-borne diseases, the incubation period varies from more than 2 weeks and up to 9 weeks (see Centers for Disease Control and Prevention (2015a) for an overview of the incubation period of tick-borne diseases). The long incubation period of some zoonoses (for instance, in Chagas's disease case, human host may stay asymptomatic his/her whole life), compared to their infectiosity period, make it indispensable to incorporate a latent class in the dynamics of zoonoses.

After the incubation period, the latent host enters the first stage of infectiousness, namely I_1. The evolution of the latter follows,

$$\dot{I}_1 = \nu_\mathrm{h} E_\mathrm{h} - (\mu_\mathrm{h} + \eta_1 + \gamma_1) I_1.$$

The infected hosts I_1 leave this stage either by natural death at a rate μ_h, through recovery at a per capita rate η_1, or by progressing to the second stage of infectiousness at a per capita rate of γ_1. Hence,

$$\dot{I}_2 = \gamma_1 I_1 - (\mu_h + \eta_2 + \gamma_2) I_2.$$

Similarly, for $i = 3, 4, \ldots, n-1$, the dynamics of the infected at stage i is captured by:

$$\dot{I}_i = \gamma_{i-1} I_{i-1} - (\mu_h + \eta_i + \gamma_i) I_i,$$

and

$$\dot{I}_n = \gamma_{n-1} I_{n-1} - (\mu_h + \eta_n) I_n.$$

Hosts' stage-structured infectiousness in vector-borne zoonoses have long been recognized in the literature (Cruz-Pacheco et al. 2012a; Homer et al. 2000; Velascohernandez 1994). Although a review of the epidemiology of VBZ is beyond the scope of this paper, we present in the following a list of some known VB zoonoses to justify the rationale behind incorporating an stage-structure host infectiosity in the host's dynamics.

- Tick-borne relapsing fever (TBRF): Caused by *Borrelia* spirochetes and transmitted by ticks of genus *Ornithodoros*, the infection has two main stages after the latency period: the febrile and afebrile stages that last on average 3.1 and 9.25 days, respectively (Southern and Sanford 1969). Moreover, according to Southern and Sanford (1969), although there is an average of 3 stages (or relapses), up to 13 relapses could be observed in TBRF. It is worthwhile to note that different nomenclatures have been used to describe different infectious stages during an infection. The terminology of stage progression is used in mathematical modeling (Guo and Li 2006a; Guo et al. 2012; Iggidr et al. 2007), whereas the relapses is used more in ecology (Johnson et al. 2016; Palmer et al. 2016; Southern and Sanford 1969).
- American Trypanosomiasis: After an incubation period of 1–2 weeks, the infection, also known as Chagas disease (caused by the parasite *Trypanosoma cruzi* and transmitted by the vector *kissing* bug), has three main infectious stages: acute (lasts 4–8 weeks), indeterminate, and chronic. In the first two stages, symptoms might be absent, mild or unspecific. Similarly, for the African Trypanosomiasis, also known as *sleeping sickness*, there are two main infectious stages (Franco et al. 2014) after a 7-year incubation period (Wengert et al. 2014). In the first stage, the parasitaemia is in the peripheral bloodstream, whereas in the later stage, the parasites enter the nervous system. However, during this long latency period, the parasitaemia in the bloodstream is considered to be sufficient to maintain the transmission cycle (Wengert et al. 2014).
- West Nile Virus: Transmitted to different species mainly by *Culex* mosquitoes, WNV has different pathogenicity depending on the host species under consideration. For humans, there is an asymptomatic stage of 3–14 days and two main

infectious stages, namely West Nile Fever, and West Nile neuroinvasive disease (WNND).

The recovered hosts are replenished by the sum of the infected of all stages who recovered from the disease and are reduced by the natural death rate. As the recovery rate of infectious hosts at stage i is η_i, the dynamics of the recovered are given by:

$$\dot{R}_\mathrm{h} = \sum_{i=1}^{n} \eta_i I_i - \mu_\mathrm{h} R_\mathrm{h}.$$

The susceptible vectors are recruited via a constant recruitment Λ_v and die at natural death rate of μ_v or via control measures at a rate of δ_v. The infection of susceptible vectors occurs after biting an infectious host. The total number of infectious hosts is $\sum_{i=1}^{n} I_i$. However, for many vector-borne zoonoses, it is reasonable to assume that the vector's infectiousness to hosts' early stages of the infection differs from that of later stages as the parasite load in infectious individuals increases with respect to the duration of infection. Therefore, by denoting β_i as the infectiousness of the host at stage i to vectors per bite and a as the biting rate, we incorporate the differential infectiousness of vectors to the stage-structured infection of the host. Hence, the dynamics of the susceptible and infected vectors are, respectively, given by:

$$\dot{S}_\mathrm{v} = \Lambda_\mathrm{v} - a S_\mathrm{v} \sum_{i=1}^{n} \frac{\beta_i I_i}{N_\mathrm{h}} - (\mu_\mathrm{v} + \delta_\mathrm{v}) S_\mathrm{v},$$

$$\dot{E}_\mathrm{v} = a S_\mathrm{v} \sum_{i=1}^{n} \frac{\beta_i I_i}{N_\mathrm{h}} - (\mu_\mathrm{v} + \nu_\mathrm{v} + \delta_\mathrm{v}) E_\mathrm{v},$$

and

$$\dot{I}_\mathrm{v} = \nu_\mathrm{v} E_\mathrm{v} - (\mu_\mathrm{v} + \delta_\mathrm{v}) I_\mathrm{v}.$$

By the conservation law, the total number of bites on the host by mosquitoes (aN_v) should equal the total number of bites received by host ($b(N_\mathrm{h}, N_\mathrm{v})N_\mathrm{h}$). Therefore,

$$b(N_\mathrm{h}, N_\mathrm{v}) N_\mathrm{h} = a N_\mathrm{v},$$

or equivalently,

$$b(N_\mathrm{h}, N_\mathrm{v}) = \frac{a N_\mathrm{v}}{N_\mathrm{h}}. \tag{3}$$

By plugging (3) into (1) and (2), the overall dynamics of the host-vector interaction are given by the following system:

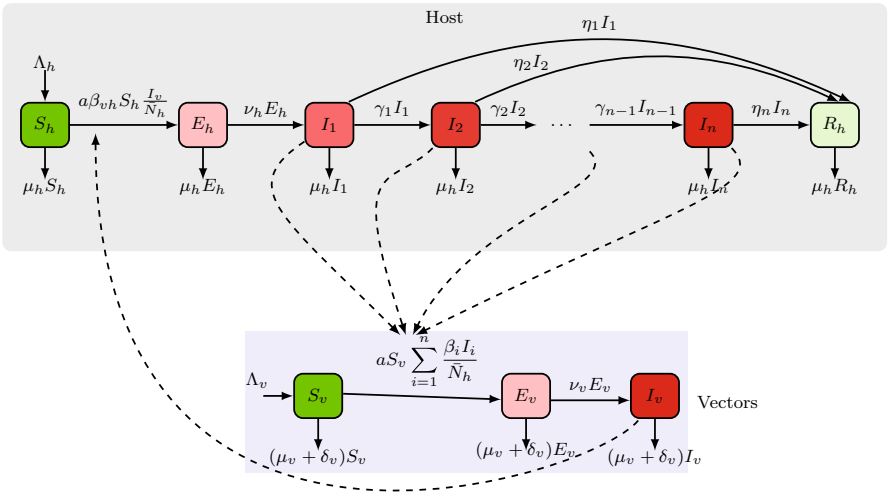

Fig. 1 Flow diagram of Model 4

$$
\begin{cases}
\dot{S}_{\mathrm{h}} = \Lambda_{\mathrm{h}} - a\,\beta_{\mathrm{vh}}\,S_{\mathrm{h}}\,\dfrac{I_{\mathrm{v}}}{N_{\mathrm{h}}} - \mu_{\mathrm{h}} S_{\mathrm{h}} \\
\dot{E}_{\mathrm{h}} = a\,\beta_{\mathrm{vh}}\,S_{\mathrm{h}}\,\dfrac{I_{\mathrm{v}}}{N_{\mathrm{h}}} - (\mu_{\mathrm{h}} + \nu_{\mathrm{h}}) E_{\mathrm{h}} \\
\dot{I}_1 = \nu_{\mathrm{h}} E_{\mathrm{h}} - (\mu_{\mathrm{h}} + \eta_1 + \gamma_1) I_1 \\
\dot{I}_2 = \gamma_1 I_1 - (\mu_{\mathrm{h}} + \eta_2 + \gamma_2) I_2 \\
\vdots \\
\dot{I}_{n-1} = \gamma_{n-2} I_{n-2} - (\mu_{\mathrm{h}} + \eta_{n-1} + \gamma_{n-1}) I_{n-1} \\
\dot{I}_n = \gamma_{n-1} I_{n-1} - (\mu_{\mathrm{h}} + \eta_n) I_n \\
\dot{R}_{\mathrm{h}} = \sum_{i=1}^{n} \eta_i I_i - \mu_{\mathrm{h}} R_{\mathrm{h}} \\
\dot{S}_{\mathrm{v}} = \Lambda_{\mathrm{v}} - a S_{\mathrm{v}} \sum_{i=1}^{n} \dfrac{\beta_i I_i}{N_{\mathrm{h}}} - (\mu_{\mathrm{v}} + \delta_{\mathrm{v}}) S_{\mathrm{v}} \\
\dot{E}_{\mathrm{v}} = a S_{\mathrm{v}} \sum_{i=1}^{n} \dfrac{\beta_i I_i}{N_{\mathrm{h}}} - (\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}}) E_{\mathrm{v}} \\
\dot{I}_{\mathrm{v}} = \nu_{\mathrm{v}} E_{\mathrm{v}} - (\mu_{\mathrm{v}} + \delta_{\mathrm{v}}) I_{\mathrm{v}}
\end{cases}
\tag{4}
$$

The flow diagram of System (4) is represented in Fig. 1, and the parameters are described in Table 1.

The subsystem describing the dynamics of the host is triangular, and hence we can disregard the dynamics of the recovered host R_{h}. Moreover, the dynamics of the total host and vector populations are given by $\dot{N}_{\mathrm{h}} = \Lambda_{\mathrm{h}} - \mu_{\mathrm{h}} N_{\mathrm{h}}$ and $\dot{N}_{\mathrm{v}} = \Lambda_{\mathrm{v}} - (\mu_{\mathrm{h}} + \delta_{\mathrm{v}}) N_{\mathrm{h}}$. Hence, we can deduce that:

$$
\lim_{t \to \infty} N_{\mathrm{h}} = \frac{\Lambda_{\mathrm{h}}}{\mu_{\mathrm{h}}} := \bar{N}_{\mathrm{h}} \quad \text{and} \quad \lim_{t \to \infty} N_{\mathrm{v}} = \frac{\Lambda_{\mathrm{v}}}{\mu_{\mathrm{v}} + \delta_{\mathrm{v}}} := \bar{N}_{\mathrm{v}}.
$$

Table 1 Description of the parameters used in System (4)

Parameters	Description
Λ_{h}	Recruitment of the host
Λ_{v}	Recruitment of vectors
a	Biting rate
μ_{h}	Host's death rate
$\beta_{\mathrm{v,h}}$	Vector's infectiousness to the host per biting
β_i	Infectiousness of the host at stage i to vectors per biting
ν_{h}	Host's rate at which the exposed individuals become infected
η_i	Per capita recovery rate of an infected host at stage i
γ_i	Host's per capita progression rate from stage i to $i+1$
μ_{v}	Vectors' natural mortality rate
ν_{v}	Vectors' incubation rate
δ_{v}	Vectors' control-induced mortality rate

By using the theory of asymptotically autonomous systems for triangular systems (Castillo-Chavez and Thieme 1995; Vidyasagar 1980), we can say that System (4) is asymptotically equivalent to:

$$\begin{cases} \dot{S}_{\mathrm{h}} = \Lambda_{\mathrm{h}} - a\,\beta_{\mathrm{vh}}\,S_{\mathrm{h}}\,\dfrac{I_{\mathrm{v}}}{\bar{N}_{\mathrm{h}}} - \mu_{\mathrm{h}}S_{\mathrm{h}} \\ \dot{E}_{\mathrm{h}} = a\,\beta_{\mathrm{vh}}\,S_{\mathrm{h}}\,\dfrac{I_{\mathrm{v}}}{\bar{N}_{\mathrm{h}}} - (\mu_{\mathrm{h}}+\nu_{\mathrm{h}})E_{\mathrm{h}} \\ \dot{I}_1 = \nu_{\mathrm{h}}E_{\mathrm{h}} - (\mu_{\mathrm{h}}+\eta_1+\gamma_1)I_1 \\ \dot{I}_2 = \gamma_1 I_1 - (\mu_{\mathrm{h}}+\eta_2+\gamma_2)I_2 \\ \vdots \\ \dot{I}_{n-1} = \gamma_{n-2}I_{n-2} - (\mu_{\mathrm{h}}+\eta_{n-1}+\gamma_{n-1})I_{n-1} \\ \dot{I}_n = \gamma_{n-1}I_{n-1} - (\mu_{\mathrm{h}}+\eta_n)I_n \\ \dot{E}_{\mathrm{v}} = a(\bar{N}_{\mathrm{v}} - E_{\mathrm{v}} - I_{\mathrm{v}})\sum_{i=1}^{n}\dfrac{\beta_i I_i}{\bar{N}_{\mathrm{h}}} - (\mu_{\mathrm{v}}+\nu_{\mathrm{v}}+\delta_{\mathrm{v}})E_{\mathrm{v}} \\ \dot{I}_{\mathrm{v}} = \nu_{\mathrm{v}}E_{\mathrm{v}} - (\mu_{\mathrm{v}}+\delta_{\mathrm{v}})I_{\mathrm{v}} \end{cases} \tag{5}$$

Variations of this model have been considered in the literature. Indeed in modeling tick-borne relapsing fever (TBRF), in Johnson et al. (2016) and Palmer et al. (2016) considered an SIR-SI model where the dynamics of the infected host is structured into n stages. However, these authors assume that the transmission from vector to host is homogeneous with respect to the host's stage of infection. Authors in Guo and Li (2006b), Guo et al. (2012) have investigated SIR and SEIR multi-stages models, respectively, although their systems describe infections that are directly transmitted, that is, not coupled with an arthropod vector. Model (5) is an SEIR-SEI type with heterogeneous infectiousness of vectors. When $\dfrac{1}{\nu_{\mathrm{h}}}, \dfrac{1}{\nu_{\mathrm{v}}} \to 0$, that is, when the mean

latency period is 0, Model (5) is the limit of an SIR-SI model proposed in Johnson et al. (2016) and Palmer et al. (2016). In many vector-borne diseases, zoonotic or otherwise, the incubation period of the vector is relatively short compared to the length of infection, as most arthropod vectors die while infected. However, mosquito-borne diseases have a characteristic that differ from latter. Indeed, mosquitoes live for only a couple weeks and the incubation period is often nearly 2 weeks, which means the incubation period is on the same scale as the vector lifespan and most vectors die before they become infectious. Moreover, most mosquito-borne disease models show a high sensitivity to this incubation period. Therefore, for the sake of generality, we assume that the dynamics of the vector is captured by an SEI structure. Also, Park (2004) has proposed an SEIR-SEI stage progression model. In the abovementioned papers, the authors derived the explicit expression of the equilibria and studied their local stability. However, the global analysis of the asymptotic behavior of these models is lacking.

Remark 2.1 In Johnson et al. (2016), the authors assume different natural death rates in each of the infected classes but assume that $\mu_i = \dfrac{0.01}{i+2}$ for all i. In Model (4), we assumed that all death rates are equal. However, it is not difficult to transform System (4) into a system with different death rates in each class. Indeed, by choosing $\Lambda_\mathrm{h} = \mu_S S_\mathrm{h} + \mu_E E_\mathrm{h} + \sum_{i=1}^{n} \mu_{h,i} I_i + \mu_R R$, the total population will be constant, and by converting the variables into proportions, we obtain exactly System (5). This mechanism of making the recruitment density dependent to stabilize the total population is called "density-dependence compensation" and has been identified in the literature (McDonald et al. 2016) [but see also Anderson and May (1981), Thrall et al. (1993)]. However, in cases in which there is no dependent compensation and that the vital dynamics is captured by a constant recruitment and a disease-induced mortality, the total host population will no longer be asymptotically constant and the results obtained in this paper may not hold.

System (5) could be written in a more compact form as follows:

$$\begin{cases} \dot{S}_\mathrm{h} = \Lambda_\mathrm{h} e_1 - a\,\beta_\mathrm{vh}\, S_\mathrm{h}\, \dfrac{I_\mathrm{v}}{\bar{N}_\mathrm{h}} - \mu_\mathrm{h} S_\mathrm{h} \\ \dot{\mathbf{I}}_\mathrm{h} = a\,\beta_\mathrm{vh}\, S_\mathrm{h}\, \dfrac{I_\mathrm{v}}{\bar{N}_\mathrm{h}} e_1 + A\,\mathbf{I}_\mathrm{h} \\ \dot{E}_\mathrm{v} = a\, \dfrac{\bar{N}_\mathrm{v} - E_\mathrm{v} - I_\mathrm{v}}{N_\mathrm{h}} \left\langle \begin{pmatrix} 0 \\ \boldsymbol{\beta} \end{pmatrix} \,\middle|\, \mathbf{I}_\mathrm{h} \right\rangle - (\mu_\mathrm{v} + \nu_\mathrm{v} + \delta_\mathrm{v}) E_\mathrm{v} \\ \dot{I}_\mathrm{v} = \nu_\mathrm{v} E_\mathrm{v} - (\mu_\mathrm{v} + \delta_\mathrm{v}) I_\mathrm{v} \end{cases} \tag{6}$$

where $\mathbf{I}_\mathrm{h} = (E_\mathrm{h}, I_1, \ldots, I_n)^\mathrm{T}$, $e_1 = (1, 0, \ldots, 0)^\mathrm{T} \in \mathbb{R}^{n+1}$, $\boldsymbol{\beta} = (\beta_1, \beta_2, \ldots, \beta_n)^\mathrm{T}$, $\langle x \,|\, y \rangle$ is the canonical scalar product (here in $\mathbb{R}^{n+1}$), and A is given by:

$$A = \begin{pmatrix} -(\nu + \mu_{\mathrm{h}}) & 0 & \dots & \dots & 0 \\ \nu & -\alpha_1 & \dots & \dots & 0 \\ 0 & \gamma_1 & -\alpha_2 & \dots & 0 \\ \vdots & \ddots & \ddots & \vdots & \vdots \\ 0 & \dots & \ddots & \gamma_{n-1} & -\alpha_n \end{pmatrix},$$

where $\alpha_i = \gamma_i + \eta_i + \mu_{\mathrm{h}}$, for $i = 1, 2, \dots, n-1$ and $\alpha_n = \eta_n + \mu_{\mathrm{h}}$.

In the following lemma, we prove that the solutions of Model (6) remain positive and bounded, that is, the solutions are biologically substantiated.

Lemma 2.1 *The region defined by*

$$\Omega = \left\{ (S_{\mathrm{h}}, E_{\mathrm{h}}, I_i, E_{\mathrm{v}}, I_{\mathrm{v}}) \in \mathbb{R}_+^{n+4} \;\middle|\; S_{\mathrm{h}} + E_{\mathrm{h}} + \sum_{i=1}^{n} I_i \le \bar{N}_{\mathrm{h}}, \quad E_{\mathrm{v}} + I_{\mathrm{v}} \le \bar{N}_{\mathrm{v}} \right\}$$

is a compact attracting positively invariant set for system (6)*.*

The disease-free equilibrium is $E_0 = (\bar{S}_{\mathrm{h}}, 0_{\mathbb{R}^{n+3}})$, where $\bar{S}_{\mathrm{h}} = \dfrac{\Lambda_{\mathrm{h}}}{\mu_{\mathrm{h}}}$. This equilibrium always exists and it belongs to Ω.

The infected compartments of System (6) are the sum of $\mathcal{F}$ and $\mathcal{V}$ where

$$\mathcal{F}(\mathbf{I}_{\mathrm{h}}, E_{\mathrm{v}}, I_{\mathrm{v}}) = \begin{pmatrix} a\,\beta_{\mathrm{vh}}\, S_{\mathrm{h}}\, \dfrac{I_{\mathrm{v}}}{\bar{N}_{\mathrm{h}}} e_1 \\ a \dfrac{\bar{N}_{\mathrm{v}} - E_{\mathrm{v}} - I_{\mathrm{v}}}{N_{\mathrm{h}}} \left\langle \begin{pmatrix} 0 \\ \boldsymbol{\beta} \end{pmatrix} \;\middle|\; \mathbf{I}_{\mathrm{h}} \right\rangle \\ 0 \end{pmatrix} \text{ and}$$

$$\mathcal{V}(\mathbf{I}_{\mathrm{h}}, E_{\mathrm{v}}, I_{\mathrm{v}}) = \begin{pmatrix} A\,\mathbf{I}_{\mathrm{h}} \\ -(\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}}) E_{\mathrm{v}} \\ \nu_{\mathrm{v}} E_{\mathrm{v}} - (\mu_{\mathrm{v}} + \delta_{\mathrm{v}}) I_{\mathrm{v}} \end{pmatrix}.$$

Let $F = D\mathcal{F}(\mathbf{I}_{\mathrm{h}}, E_{\mathrm{v}}, I_{\mathrm{v}})$ and $V = D\mathcal{V}(\mathbf{I}_{\mathrm{h}}, E_{\mathrm{v}}, I_{\mathrm{v}})$ be function-valued matrices evaluated at the DFE. We obtain:

$$F = \begin{pmatrix} \mathbf{0}_{n+1,n+1} & 0 & a\beta_{\mathrm{vh}} e_1 \\ a \dfrac{\bar{N}_{\mathrm{v}}}{\bar{N}_{\mathrm{h}}} (0, \boldsymbol{\beta})^{\mathrm{T}} & 0 & 0 \\ \mathbf{0}_{1,n+1} & 0 & 0 \end{pmatrix} \text{ and}$$

$$V = \begin{pmatrix} A & 0 & 0 \\ \mathbf{0}_{1,n+1} & -(\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}}) & 0 \\ \mathbf{0}_{1,n+1} & \nu_{\mathrm{v}} & -(\mu_{\mathrm{v}} + \delta_{\mathrm{v}}) \end{pmatrix}.$$

Given the particular form of A, it is not difficult to verify that:

$$-A^{-1} = \begin{pmatrix} \frac{1}{\nu+\mu_h} & 0 & \dots & \dots & 0 \\ \frac{\nu}{\alpha_1(\nu+\mu_h)} & \frac{1}{\alpha_1} & \dots & \dots & 0 \\ \frac{\gamma_1\nu}{\alpha_1\alpha_2(\nu+\mu_h)} & \frac{\gamma_1}{\alpha_1\alpha_2} & \frac{1}{\alpha_2} & \dots & 0 \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ \frac{\gamma_1\dots\gamma_{n-1}\nu}{\alpha_1\dots\alpha_n(\nu+\mu_h)} & \dots & \dots & \frac{\gamma_{n-1}}{\alpha_{n-1}\alpha_n} & \frac{1}{\alpha_n} \end{pmatrix}. \tag{7}$$

Hence, the next-generation matrix is given by:

$$-FV^{-1} = \begin{pmatrix} \mathbf{0}_{n+1,n+1} & \frac{a\,\beta_{vh}\nu_v}{(\mu_v+\nu_v+\delta)(\mu_v+\delta)}\,e_1 & \frac{a\,\beta_{vh}}{\mu_v+\delta}\,e_1 \\ -a\,\frac{\bar{N}_v}{\bar{N}_h}(0,\boldsymbol{\beta})^T A^{-1} & 0 & 0 \\ \mathbf{0}_{1,n+1} & 0 & 0 \end{pmatrix}.$$

The basic reproduction number, defined as the average number of secondary cases produced by an infected host during its infectious period while interacting with a completely susceptible population, is computed using the next-generation method (Diekmann and Heesterbeek 2000; van den Driessche and Watmough 2002). Denoted by $\mathcal{R}_0$, it is the spectral radius of the next-generation matrix $-FV^{-1}$. Therefore, for Model (6), the basic reproduction number is,

$$\begin{aligned} \mathcal{R}_0^2 &= \frac{a^2\,\beta_{vh}\nu_v}{(\mu_v+\nu_v+\delta_v)(\mu_v+\delta_v)}\,\frac{\bar{N}_v}{\bar{N}_h}(0,\boldsymbol{\beta})^T(-A^{-1})e_1 \\ &:= \frac{a^2\beta_{vh}\bar{N}_v\nu_v\nu_h}{\bar{N}_h(\mu_v+\nu_v+\delta_v)(\mu_v+\delta_v)(\nu_h+\mu_h)}\sum_{i=1}^{n}\frac{\gamma_1\gamma_2\dots\gamma_{i-1}}{\alpha_1\alpha_2\dots\alpha_i}\,\beta_i \quad \text{with } \gamma_0=1. \end{aligned}$$

This quantity is intrinsically tied to the dynamics of the disease as we will discuss in the next subsection.

2.2 Global Stability of the DFE

By the derivation of the basic reproduction number, the DFE is locally asymptotically stable if $\mathcal{R}_0^2 < 1$ and unstable if $\mathcal{R}_0^2 > 1$ (Diekmann and Heesterbeek 2000; van den Driessche and Watmough 2002). The following theorem provides a global result.

Theorem 2.1 *The DFE is globally asymptotically stable if* $\mathcal{R}_0^2 \le 1$.

Proof The instability of the DFE when $\mathcal{R}_0^2 > 1$ follows (van den Driessche and Watmough 2002). As for the global stability of the DFE when $\mathcal{R}_0^2 < 1$, let us consider

the candidate Lyapunov function:

$$\mathcal{V}(\mathbf{I}_\mathrm{h}, I_\mathrm{v}) = \mathcal{L}(\mathbf{I}_\mathrm{h}) + c_{\mathrm{v},1}\dot{E}_\mathrm{v} + c_{\mathrm{v},2}\dot{I}_\mathrm{v}$$

where

$$\mathcal{L}(\mathbf{I}_\mathrm{h}) = c_0 E_\mathrm{h} + \sum_{i=1}^{n} c_i I_i,$$

with $c_{\mathrm{v},1} = \dfrac{\bar{N}_\mathrm{h}}{a\bar{N}_\mathrm{v}}$, $c_{\mathrm{v},2} = \dfrac{\mu_\mathrm{v} + \nu_\mathrm{v} + \delta_\mathrm{v}}{\nu_\mathrm{v}} c_{\mathrm{v},1}$ and the coefficients c_i for $i = 1, 2, \ldots, n-1$ are given by the following induction relationship:

$$\begin{cases} c_0 = \dfrac{\nu}{\nu + \mu_\mathrm{h}}\, c_1 \\ c_1 = \dfrac{\beta_1}{\alpha_1} + \dfrac{\gamma_1}{\alpha_1\alpha_2}\beta_2 + \cdots + \dfrac{\gamma_1 \ldots \gamma_{n-1}}{\alpha_1\alpha_2 \ldots \alpha_n}\beta_n, \\ c_{i+1} = \dfrac{1}{\gamma_i}\left(\alpha_i c_i - \beta_i\right), \quad \text{for} \quad i = 1, 2, \ldots, n-2, \\ c_n = \dfrac{\beta_n}{\alpha_n}. \end{cases} \tag{8}$$

The derivative along the trajectories of the system is:

$$\begin{aligned} \dot{\mathcal{V}}(\mathbf{I}_\mathrm{h}, E_\mathrm{v}, I_\mathrm{v}) &= \dot{\mathcal{L}}(\mathbf{I}_\mathrm{h}) + c_{\mathrm{v},1}\dot{E}_\mathrm{v} + c_{\mathrm{v},2}\dot{I}_\mathrm{v} \\ &= c_0\dot{E}_\mathrm{h} + \sum_{i=1}^{n} c_i\dot{I}_i + c_{\mathrm{v},1}\dot{E}_\mathrm{v} + c_{\mathrm{v},2}\dot{I}_\mathrm{v} \\ &= c_0\left(a\,\beta_\mathrm{vh}\,S_\mathrm{h}\,\frac{I_\mathrm{v}}{\bar{N}_\mathrm{h}} - (\mu_\mathrm{h} + \nu_\mathrm{h})E_\mathrm{h}\right) + c_1\left(\nu_\mathrm{h}E_\mathrm{h} - \alpha_1 I_1\right) \\ &\quad + \sum_{i=2}^{n} c_i\dot{I}_i + c_{\mathrm{v},1}\dot{E}_\mathrm{v} + c_{\mathrm{v},2}\dot{I}_\mathrm{v} \\ &= c_0 a\,\beta_\mathrm{vh}\,S_\mathrm{h}\,\frac{I_\mathrm{v}}{\bar{N}_\mathrm{h}} - c_1\alpha_1 I_1 + c_2\left(\gamma_1 I_1 - \alpha_2 I_2\right) \\ &\quad + \sum_{i=3}^{n} c_i\dot{I}_i + c_{\mathrm{v},1}\dot{E}_\mathrm{v} + c_{\mathrm{v},2}\dot{I}_\mathrm{v} \\ &= c_0 a\,\beta_\mathrm{vh}\,S_\mathrm{h}\,\frac{I_\mathrm{v}}{\bar{N}_\mathrm{h}} - c_1\alpha_1 I_1 + (c_1\alpha_1 - \beta_1)I_1 - c_2\alpha_2 I_2 \\ &\quad + \sum_{i=3}^{n} c_i\dot{I}_i + c_{\mathrm{v},1}\dot{E}_\mathrm{v} + c_{\mathrm{v},2}\dot{I}_\mathrm{v}, \end{aligned}$$

since $c_2\gamma_1 = \alpha_1 c_1 - 1$. Therefore,

$$\dot{\mathcal{V}}(\mathbf{I}_\mathrm{h}, E_\mathrm{v}, I_\mathrm{v}) = c_0 a\, \beta_{\mathrm{vh}}\, S_\mathrm{h}\, \frac{I_\mathrm{v}}{\bar{N}_\mathrm{h}} - \beta_1 I_1 - c_2\alpha_2 I_2 + \sum_{i=3}^{n} c_i \dot{I}_i + c_{\mathrm{v},1}\dot{E}_\mathrm{v} + c_{\mathrm{v},2}\dot{I}_\mathrm{v}.$$

Similarly, by using successively the induction relationship (8), we obtain,

$$\begin{aligned}\dot{\mathcal{V}}(\mathbf{I}_\mathrm{h}, E_\mathrm{v}, I_\mathrm{v}) = {} & c_0 a\, \beta_{\mathrm{vh}}\, S_\mathrm{h}\, \frac{I_\mathrm{v}}{\bar{N}_\mathrm{h}} - \sum_{i=1}^{n} \beta_i I_i \\ & + c_{\mathrm{v},1}\left(a(N_\mathrm{v} - E_\mathrm{v} - I_\mathrm{v}) \sum_{i=1}^{n} \frac{\beta_i I_i}{\bar{N}_\mathrm{h}} - (\mu_\mathrm{v} + \nu_\mathrm{v} + \delta_\mathrm{v})E_\mathrm{v}\right) \\ & + c_{\mathrm{v},2}\left(\nu_\mathrm{v} E_\mathrm{v} - (\mu_\mathrm{v} + \delta_\mathrm{v})I_\mathrm{v}\right). \end{aligned} \tag{9}$$

Considering the expression of $c_{\mathrm{v},1}$ and $c_{\mathrm{v},2}$ along with the inequality $S_\mathrm{h} \leq \bar{N}_\mathrm{h}$, Equality (9) leads to:

$$\begin{aligned}\dot{\mathcal{V}}(\mathbf{I}_\mathrm{h}, E_\mathrm{v}, I_\mathrm{v}) &= c_0 a\beta_{\mathrm{vh}} \frac{S_\mathrm{h}}{\bar{N}_\mathrm{h}} I_\mathrm{v} - (E_\mathrm{v} + I_\mathrm{v}) \sum_{i=1}^{n} \beta_i I_i - \frac{\bar{N}_\mathrm{h}(\mu_\mathrm{v} + \nu_\mathrm{v} + \delta_\mathrm{v})(\mu_\mathrm{v} + \delta_\mathrm{v})}{a\bar{N}_\mathrm{v}\nu_\mathrm{v}} I_\mathrm{v} \\ &= c_0 a\beta_{\mathrm{vh}} \frac{S_\mathrm{h}}{\bar{N}_\mathrm{h}} I_\mathrm{v} - (E_\mathrm{v} + I_\mathrm{v}) \sum_{i=1}^{n} \beta_i I_i - \frac{\bar{N}_\mathrm{h}(\mu_\mathrm{v} + \nu_\mathrm{v} + \delta_\mathrm{v})(\mu_\mathrm{v} + \delta_\mathrm{v})}{a\bar{N}_\mathrm{v}\nu_\mathrm{v}} I_\mathrm{v} \\ &= \left(c_0 a\beta_{\mathrm{vh}} \frac{S_\mathrm{h}}{\bar{N}_\mathrm{h}} - \frac{\bar{N}_\mathrm{h}(\mu_\mathrm{v} + \nu_\mathrm{v} + \delta_\mathrm{v})(\mu_\mathrm{v} + \delta_\mathrm{v})}{a\bar{N}_\mathrm{v}\nu_\mathrm{v}}\right) I_\mathrm{v} - (E_\mathrm{v} + I_\mathrm{v}) \sum_{i=1}^{n} \beta_i I_i \\ &= \frac{\bar{N}_\mathrm{h}(\mu_\mathrm{v} + \nu_\mathrm{v} + \delta_\mathrm{v})}{a\bar{N}_\mathrm{v}\nu_\mathrm{v}} \left(c_0 a^2 \beta_{\mathrm{vh}} \frac{\bar{N}_\mathrm{v}\nu_\mathrm{v}}{\bar{N}_\mathrm{h}(\mu_\mathrm{v} + \nu_\mathrm{v} + \delta_\mathrm{v})(\mu_\mathrm{v} + \delta_\mathrm{v})} \frac{S_\mathrm{h}}{\bar{N}_\mathrm{h}} - 1\right) I_\mathrm{v} \\ &\quad - I_\mathrm{v} \sum_{i=1}^{n} \beta_i I_i \\ &= \frac{\bar{N}_\mathrm{h}(\mu_\mathrm{v} + \nu_\mathrm{v} + \delta_\mathrm{v})(\mu_\mathrm{v} + \delta_\mathrm{v})}{a\bar{N}_\mathrm{v}\nu_\mathrm{v}} \left(\mathcal{R}_0^2 \frac{S_\mathrm{h}}{\bar{N}_\mathrm{h}} - 1\right) I_\mathrm{v} - I_\mathrm{v} \sum_{i=1}^{n} \beta_i I_i, \end{aligned}$$

since $c_0 = \dfrac{\nu}{\nu + \mu_\mathrm{h}} \displaystyle\sum_{i=1}^{n} \frac{\gamma_1\gamma_2\ldots\gamma_{i-1}}{\alpha_1\alpha_2\ldots\alpha_i}\, \beta_i$. Thus, we conclude that

$$\dot{\mathcal{V}}(\mathbf{I}_\mathrm{h}, E_\mathrm{v}, I_\mathrm{v}) \leq 0,$$

whenever $\mathcal{R}_0^2 \leq 1$ as $S_\mathrm{h} \leq \bar{N}_\mathrm{h}$. Moreover, $\dot{\mathcal{V}}(\mathbf{I}_\mathrm{h}, E_\mathrm{v}, I_\mathrm{v}) = 0$ if $I_\mathrm{v} = 0$ or if $\mathcal{R}_0^2 = 1$, $S_\mathrm{h} = \bar{N}_\mathrm{h}$ and $\sum_{i=1}^{n} \beta_i I_i = 0$. Hence, we deduce that the largest set contained in $\{(\mathbf{I}_\mathrm{h}, E_\mathrm{v}, I_\mathrm{v}) \in \Omega \mid \dot{\mathcal{V}}(\mathbf{I}_\mathrm{h}, E_\mathrm{v}, I_\mathrm{v}) = 0\}$ is reduced to the DFE. Since the set Ω is compact and positively invariant, by LaSalle's invariance principle (Bhatia and Szegö

1970; LaSalle and Lefschetz 1961), the DFE is globally asymptotically stable on Ω. The attractiveness of Ω makes the DFE globally asymptotically stable on $\mathbb{R}^{n+4}$. □

2.3 Endemic Equilibria

In this section, we discuss the existence conditions for the endemic equilibrium and investigate its global stability whenever it exists.

Let $(S_{\mathrm{h}}^*, \mathbf{I}_{\mathrm{h}}^*, E_{\mathrm{v}}^*, I_{\mathrm{v}}^*)^{\mathrm{T}} \gg 0$ be an endemic equilibrium for Model (6). Therefore $(S_{\mathrm{h}}^*, \mathbf{I}_{\mathrm{h}}^*, E_{\mathrm{v}}^*, I_{\mathrm{v}}^*)^{\mathrm{T}}$ satisfies the endemic relations:

$$\begin{cases} 0 = \Lambda_{\mathrm{h}} - a\,\beta_{\mathrm{vh}}\, S_{\mathrm{h}}^* \dfrac{I_{\mathrm{v}}^*}{\bar{N}_{\mathrm{h}}} - \mu_{\mathrm{h}} S_{\mathrm{h}}^* \\ 0 = a\,\beta_{\mathrm{vh}}\, S_{\mathrm{h}}^* \dfrac{I_{\mathrm{v}}^*}{\bar{N}_{\mathrm{h}}} - (\mu_{\mathrm{h}} + \nu_{\mathrm{h}}) E_{\mathrm{h}}^* \\ E_{\mathrm{h}}^* = \dfrac{\alpha_1}{\nu_{\mathrm{h}}} I_1^* \\ I_2^* = \dfrac{\gamma_1}{\alpha_2} I_1^* \\ I_3^* = \dfrac{\gamma_2}{\alpha_3} I_2^* = \dfrac{\gamma_1\gamma_2}{\alpha_2\alpha_3} I_1^* \\ \vdots \\ I_{n-1}^* = \dfrac{\gamma_{n-2}}{\alpha_{n-1}} I_{n-2}^* = \dfrac{\gamma_1\gamma_2\cdots\gamma_{n-2}}{\alpha_2\alpha_3\ldots\alpha_{n-1}} I_1^* \\ I_n^* = \dfrac{\gamma_{n-1}}{\alpha_n} I_{n-1}^* = \dfrac{\gamma_1\gamma_2\cdots\gamma_{n-1}}{\alpha_2\alpha_3\ldots\alpha_n} I_1^* \\ 0 = a(\bar{N}_{\mathrm{v}} - E_{\mathrm{v}}^* - I_{\mathrm{v}}^*) \sum_{i=1}^{n} \dfrac{\beta_i I_i^*}{\bar{N}_{\mathrm{h}}} - (\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}}) E_{\mathrm{v}}^* \\ 0 = \nu_{\mathrm{v}} E_{\mathrm{v}}^* - (\mu_{\mathrm{v}} + \delta_{\mathrm{v}}) I_{\mathrm{v}}^* \end{cases} \tag{10}$$

where $\alpha_i = \mu_i + \eta_i + \gamma_i$. It follows from (10) that there is an interior endemic equilibrium if $I_1^* > 0$. Moreover, we can deduce that:

$$\begin{aligned} \sum_{i=1}^{n} \beta_i I_i^* &= I_1^* \left(\beta_1 + \frac{\gamma_1}{\alpha_2}\beta_2 + \cdots + \frac{\gamma_1\gamma_2\cdots\gamma_{n-1}}{\alpha_2\ldots\alpha_n}\beta_n \right) \\ &= \alpha_1 c_1 I_1^*. \end{aligned} \tag{11}$$

The first equation of (10) implies that:

$$S_{\mathrm{h}}^* = \frac{\mu_{\mathrm{h}}\bar{N}_{\mathrm{h}}}{\mu_{\mathrm{h}} + a\beta_{\mathrm{vh}}\dfrac{I_{\mathrm{v}}^*}{\bar{N}_{\mathrm{h}}}} \quad \text{and} \quad E_{\mathrm{h}}^* = \frac{a\beta_{\mathrm{vh}}}{\mu_{\mathrm{h}} + \nu_{\mathrm{h}}} \frac{\mu_{\mathrm{h}} I_{\mathrm{v}}^*}{\mu_{\mathrm{h}} + a\beta_{\mathrm{vh}}\dfrac{I_{\mathrm{v}}^*}{\bar{N}_{\mathrm{h}}}}.$$

After some algebraic operations, we successively obtain,

$$I_{\mathrm{v}}^* = \frac{(\mu_{\mathrm{h}} + \nu_{\mathrm{h}})(\mu_{\mathrm{v}} + \delta_{\mathrm{v}})\mu_{\mathrm{h}}\bar{N}_{\mathrm{h}}(\mathcal{R}_0^2 - 1)}{(\mu_{\mathrm{h}} + \nu_{\mathrm{h}})(\mu_{\mathrm{v}} + \delta_{\mathrm{v}})a\beta_{\mathrm{vh}} + a^2\beta_{\mathrm{vh}}c_1\nu_{\mathrm{h}}\mu_{\mathrm{h}}},$$

$$E_{\mathrm{h}}^{*}=\frac{\mu_{\mathrm{h}}(\mu_{\mathrm{v}}+\delta_{\mathrm{v}})\bar{N}_{\mathrm{h}}(\mathcal{R}_0^2-1)}{ac_1\nu_{\mathrm{h}}\mu_{\mathrm{h}}+(\mu_{\mathrm{v}}+\delta_{\mathrm{v}})(\mu_{\mathrm{h}}+\nu_{\mathrm{h}})\mathcal{R}_0^2},$$

and

$$I_1^{*}=\frac{\mu_{\mathrm{h}}\nu_{\mathrm{h}}(\mu_{\mathrm{v}}+\delta_{\mathrm{v}})\bar{N}_{\mathrm{h}}(\mathcal{R}_0^2-1)}{a\alpha_1c_1\nu_{\mathrm{h}}\mu_{\mathrm{h}}+\alpha_1(\mu_{\mathrm{v}}+\delta_{\mathrm{v}})(\mu_{\mathrm{h}}+\nu_{\mathrm{h}})\mathcal{R}_0^2},\tag{12}$$

where c_1 is defined by the relations (8). Hence, relations (11–12) and the endemic relations imply that $(S_{\mathrm{h}}^{*},\mathbf{I}_{\mathrm{h}}^{*},E_{\mathrm{v}}^{*},I_{\mathrm{v}}^{*})^{\mathrm{T}}\gg 0$ if and only if $\mathcal{R}_0^2>1$. The next theorem gives the asymptotic behavior of this equilibrium whenever it exists.

Theorem 2.2 *The endemic equilibrium for the multi-host Model (6) is globally asymptotically stable whenever* $\mathcal{R}_0^2>1$.

Proof Let us consider the Lyapunov function

$$\begin{aligned}\mathcal{W}=\;&b_0\left(S_{\mathrm{h}}-S_{\mathrm{h}}^{*}\log S_{\mathrm{h}}+E_{\mathrm{h}}-E_{\mathrm{h}}^{*}\log E_{\mathrm{h}}\right)+\sum_{i=1}^{n}b_i\left(I_i-I_i^{*}\log I_i\right)\\&+v_1\left(S_{\mathrm{v}}-S_{\mathrm{v}}^{*}\log S_{\mathrm{v}}+E_{\mathrm{v}}-E_{\mathrm{v}}^{*}\log E_{\mathrm{v}}\right)\\&+v_2\left(I_{\mathrm{v}}-I_{\mathrm{v}}^{*}\log I_{\mathrm{v}}\right)+K\end{aligned}$$

where

$$\begin{aligned}K=\;&v_1\left(S_{\mathrm{v}}^{*}-S_{\mathrm{v}}^{*}\log S_{\mathrm{v}}^{*}+E_{\mathrm{v}}^{*}-E_{\mathrm{v}}^{*}\log E_{\mathrm{v}}^{*}\right)+v_2\left(I_{\mathrm{v}}^{*}-I_{\mathrm{v}}^{*}\log I_{\mathrm{v}}^{*}\right)\\&+b_0\left(S_{\mathrm{h}}^{*}-S_{\mathrm{h}}^{*}\log S_{\mathrm{h}}^{*}+E_{\mathrm{h}}^{*}-E_{\mathrm{h}}^{*}\log E_{\mathrm{h}}^{*}\right)\\&+\sum_{i=1}^{n}b_i\left(I_i^{*}-I_i^{*}\log I_i^{*}\right)\end{aligned}$$

and b_i, for $i=0,1,\ldots,n$, and v_1,v_2 are positive constants. The function $\mathcal{W}$ is therefore positive-definite with respect to the endemic equilibrium. The challenge is how to choose these coefficients to make the derivative of $\mathcal{W}$ along the trajectories of (6) negative-definite. To ease the notations and WLOG, we denote

$$\bar{\beta}_i=a\beta_i\frac{1}{\bar{N}_{\mathrm{h}}},\quad \bar{\boldsymbol{\beta}}_{\mathrm{h}}=(\bar{\beta}_1,\ldots,\bar{\beta}_n)^{\mathrm{T}}\quad\text{and}\quad \bar{\beta}_{\mathrm{v}}=a\beta_{\mathrm{vh}}\frac{1}{\bar{N}_{\mathrm{h}}}.$$

The derivation of $\mathcal{W}$ along the trajectories of (6) is as follows:

$$\begin{aligned}\dot{\mathcal{W}}=\;&b_0\left(1-\frac{S_{\mathrm{h}}^{*}}{S_{\mathrm{h}}}\right)\left(\Lambda_{\mathrm{h}}-\bar{\beta}_{\mathrm{v}}S_{\mathrm{h}}I_{\mathrm{v}}-\mu_{\mathrm{h}}S_{\mathrm{h}}\right)\\&+b_0\left(1-\frac{E_{\mathrm{h}}^{*}}{E_{\mathrm{h}}}\right)\left(\bar{\beta}_{\mathrm{v}}S_{\mathrm{h}}I_{\mathrm{v}}-(\mu_{\mathrm{h}}+\nu_{\mathrm{h}})E_{\mathrm{h}}\right)\\&+b_1\left(1-\frac{I_1^{*}}{I_1}\right)(\nu_{\mathrm{h}}E_{\mathrm{h}}-\alpha_1I_1)+\sum_{i=2}^{n}b_i\left(1-\frac{I_i^{*}}{I_i}\right)(\gamma_{i-1}I_{i-1}-\alpha_iI_i)\end{aligned}$$

$$
\begin{aligned}
&+ v_1 \left(1 - \frac{S_{\mathrm{v}}^*}{S_{\mathrm{v}}}\right) \left(\Lambda_{\mathrm{v}} - S_{\mathrm{v}} \sum_{i=1}^{n} \bar{\beta}_i I_i - (\mu_{\mathrm{v}} + \delta_{\mathrm{v}}) S_{\mathrm{v}}\right) \\
&+ v_1 \left(1 - \frac{E_{\mathrm{v}}^*}{E_{\mathrm{v}}}\right) \left(S_{\mathrm{v}} \sum_{i=1}^{n} \bar{\beta}_i I_i - (\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}}) E_{\mathrm{v}}\right) \\
&+ v_2 \left(1 - \frac{I_{\mathrm{v}}^*}{I_{\mathrm{v}}}\right) (\nu_{\mathrm{v}} E_{\mathrm{v}} - (\mu_{\mathrm{v}} + \delta_{\mathrm{v}}) I_{\mathrm{v}}) \,. \qquad (13)
\end{aligned}
$$

By grouping all linear terms of (13) in E_{h}, I_i, for $i = 1, 2, \ldots, n$ and I_{v}, and denoting it by L, we obtain after lengthy computations and arrangements:

$$
\begin{aligned}
L = &\left(b^{\mathrm{T}} \tilde{A} + v_1 S_{\mathrm{v}}^* \bar{\boldsymbol{\beta}}_{\mathrm{h}}^{\mathrm{T}}\right) \mathbf{I}_{\mathrm{h}} + (b_1 \nu_{\mathrm{h}} - b_0(\mu_{\mathrm{h}} + \nu_{\mathrm{h}})) E_{\mathrm{h}} \\
&+ (v_2 \nu_{\mathrm{v}} - v_1(\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}}))\, E_{\mathrm{v}} \\
&+ \left(b_0 \bar{\beta}_{\mathrm{v}} S_{\mathrm{h}}^* - v_1(\mu_{\mathrm{v}} + \delta_{\mathrm{v}})\right) I_{\mathrm{v}} \qquad (14)
\end{aligned}
$$

where $b^{\mathrm{T}} = (b_1, b_2, \ldots, b_n)$ and $\tilde{A}$ is the submatrix A obtained by removing the first row and first column. We choose b, b_0 and v_2 that cancel the coefficients of $\mathbf{I}_{\mathrm{h}}$, E_{h} and E_{v}, respectively. That is,

$$
\tilde{b} = -v_1 S_{\mathrm{v}}^* \tilde{A}^{-T} \bar{\boldsymbol{\beta}}_{\mathrm{h}}, \quad b_0 = \frac{\nu_{\mathrm{h}}}{\mu_{\mathrm{h}} + \nu_{\mathrm{h}}} b_1 \quad \text{and} \quad v_2 = \frac{\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}}}{\nu_{\mathrm{v}}} v_1.
$$

More precisely, from the expression of b and using endemic relations (10), the first component of b could take the following different forms:

$$
\begin{aligned}
b_1 &= v_1 S_{\mathrm{v}}^* \sum_{i=1}^{n} \frac{\gamma_1 \cdots \gamma_{i-1}}{\alpha_1 \ldots \alpha_i} \bar{\beta}_i \\
&= v_1 S_{\mathrm{v}}^* \left(\frac{1}{\alpha_1} \bar{\beta}_1 + \frac{\gamma_1}{\alpha_1 \alpha_2} \bar{\beta}_2 + \cdots + \frac{\gamma_1 \cdots \gamma_{n-1}}{\alpha_1 \alpha_2 \ldots \alpha_n} \bar{\beta}_n\right) \\
&= v_1 S_{\mathrm{v}}^* \frac{1}{\alpha_1} \left(\bar{\beta}_1 + \frac{\gamma_1}{\alpha_2} \bar{\beta}_2 + \cdots + \frac{\gamma_1 \cdots \gamma_{n-1}}{\alpha_2 \ldots \alpha_n} \bar{\beta}_n\right) \\
&= v_1 S_{\mathrm{v}}^* \frac{1}{\alpha_1} \frac{\sum_{i=1}^{n} \bar{\beta}_i I_i^*}{I_1^*}. \qquad (15)
\end{aligned}
$$

Also, b_0 could clearly be expressed as

$$
\begin{aligned}
b_0 &= \frac{\nu_{\mathrm{h}}}{\mu_{\mathrm{h}} + \nu_{\mathrm{h}}} b_1 \\
&= \frac{\nu_{\mathrm{h}}}{\mu_{\mathrm{h}} + \nu_{\mathrm{h}}} v_1 S_{\mathrm{v}}^* \frac{1}{\alpha_1} \frac{\sum_{i=1}^{n} \bar{\beta}_i I_i^*}{I_1^*}. \qquad (16)
\end{aligned}
$$

The use of (16) cancels the coefficient of I_v in (14). Indeed,

$$\begin{aligned}
b_0\bar{\beta}_\mathrm{v}S_\mathrm{h}^* - v_2(\mu_\mathrm{v}+\delta_\mathrm{v}) &= \frac{\nu_\mathrm{h}}{\mu_\mathrm{h}+\nu_\mathrm{h}}v_1 S_\mathrm{v}^*\frac{1}{\alpha_1}\frac{\sum_{i=1}^n \bar{\beta}_i I_i^*}{I_1^*}\bar{\beta}_\mathrm{v}S_\mathrm{h}^* - v_2(\mu_\mathrm{v}+\delta_\mathrm{v})\\
&= v_1\frac{\nu_\mathrm{h}}{(\mu_\mathrm{h}+\nu_\mathrm{h})\alpha_1 I_1^*}S_\mathrm{v}^*\sum_{i=1}^n \bar{\beta}_i I_i^*\,\bar{\beta}_\mathrm{v}S_\mathrm{h}^* - v_2(\mu_\mathrm{v}+\delta_\mathrm{v})\\
&= v_1\frac{1}{(\mu_\mathrm{h}+\nu_\mathrm{h})E_n^*}(\mu_\mathrm{v}+\nu_\mathrm{v}+\delta_\mathrm{v})\,E_\mathrm{v}^*\,\bar{\beta}_\mathrm{v}S_\mathrm{h}^* - v_2(\mu_\mathrm{v}+\delta_\mathrm{v})\\
&= v_1(\mu_\mathrm{v}+\nu_\mathrm{v}+\delta_\mathrm{v})\,E_\mathrm{v}^* - v_2(\mu_\mathrm{v}+\delta_\mathrm{v})\\
&= v_1\frac{1}{\bar{\beta}_\mathrm{v}S_\mathrm{h}^*I_\mathrm{v}^*}(\mu_\mathrm{v}+\nu_\mathrm{v}+\delta_\mathrm{v})\,E_\mathrm{v}^*\,\bar{\beta}_\mathrm{v}S_\mathrm{h}^* - v_2(\mu_\mathrm{v}+\delta_\mathrm{v})\\
&= v_1(\mu_\mathrm{v}+\nu_\mathrm{v}+\delta_\mathrm{v})\,\frac{E_\mathrm{v}^*}{I_\mathrm{v}^*} - v_2(\mu_\mathrm{v}+\delta_\mathrm{v})\\
&= v_1(\mu_\mathrm{v}+\nu_\mathrm{v}+\delta_\mathrm{v})\,\frac{\mu_\mathrm{v}+\delta_\mathrm{v}}{\nu_\mathrm{v}} - v_2(\mu_\mathrm{v}+\delta_\mathrm{v})\\
&= 0.
\end{aligned}$$

Therefore, with this choice for b, b_0 and v_2, all linear terms in (13) cancel. The remaining terms in $\dot{\mathcal{W}}$ are:

$$\begin{aligned}
\dot{\mathcal{W}} &= v_1\left(1-\frac{S_\mathrm{v}^*}{S_\mathrm{v}}\right)(\Lambda_\mathrm{v}-(\mu_\mathrm{v}+\delta_\mathrm{v})S_\mathrm{v}) + v_1(\mu_\mathrm{v}+\nu_\mathrm{v}+\delta_\mathrm{v})E_\mathrm{v}^* - v_1\frac{E_\mathrm{v}^*}{E_\mathrm{v}}S_\mathrm{v}\sum_{i=1}^n\bar{\beta}_i I_i\\
&\quad - v_2\nu_\mathrm{v}E_\mathrm{v}\frac{I_\mathrm{v}^*}{I_\mathrm{v}} + v_2(\mu_\mathrm{v}+\delta_\mathrm{v})I_\mathrm{v}^* + b_0\left(1-\frac{S_\mathrm{h}^*}{S_\mathrm{h}}\right)(\Lambda_\mathrm{h}-\mu_\mathrm{h}S_\mathrm{h})\\
&\quad + b_0\left((\mu_\mathrm{h}+\nu_\mathrm{h})E_\mathrm{h}^* - \bar{\beta}_\mathrm{v}S_\mathrm{h}I_\mathrm{v}\frac{E_\mathrm{h}^*}{E_\mathrm{h}}\right) + b_1(\mu_\mathrm{h}+\eta_1+\gamma_1)I_1^* - b_1\nu_\mathrm{h}\frac{I_1^*E_\mathrm{h}}{I_1}\\
&\quad + \sum_{i=2}^{n-1}\left(b_i(\mu_\mathrm{h}+\eta_i+\gamma_i)I_i^* - b_i\gamma_{i-1}\frac{I_i^*\,I_{i-1}}{I_i}\right)\\
&\quad + b_n(\mu_\mathrm{h}+\eta_n)I_n^* - b_n\gamma_{n-1}\frac{I_n^*\,I_{n-1}}{I_n}\\
&= \underbrace{v_1\,(\mu_\mathrm{v}+\delta_\mathrm{v})S_\mathrm{v}^*\left(2-\frac{S_\mathrm{v}^*}{S_\mathrm{v}}-\frac{S_\mathrm{v}}{S_\mathrm{v}^*}\right)}_{\mathcal{A}_\mathrm{v}} + 2v_1(\mu_\mathrm{v}+\nu_\mathrm{v}+\delta_\mathrm{v})E_\mathrm{v}^*\\
&\quad - v_1(\mu_\mathrm{v}+\nu_\mathrm{v}+\delta_\mathrm{v})E_\mathrm{v}^*\frac{S_\mathrm{v}^*}{S_\mathrm{v}}\\
&\quad - v_1\frac{E_\mathrm{v}^*}{E_\mathrm{v}}S_\mathrm{v}\sum_{i=1}^n\bar{\beta}_i I_i - v_2\nu_\mathrm{v}E_\mathrm{v}\frac{I_\mathrm{v}^*}{I_\mathrm{v}} + v_2(\mu_\mathrm{v}+\delta_\mathrm{v})I_\mathrm{v}^*
\end{aligned}$$

$$
\begin{aligned}
&+ b_0 \underbrace{\mu_h S_h^* \left(2 - \frac{S_h^*}{S_h} - \frac{S_h}{S_h^*}\right)}_{\mathcal{A}_h} + 2b_0(\mu_h + \nu_h)E_h^* \\
&- b_0(\mu_h + \nu_h)E_h^* \frac{S_h^*}{S_h} + b_0\left(-\bar{\beta}_v S_h I_v \frac{E_h^*}{E_h}\right) \\
&+ b_1(\mu_h + \eta_1 + \gamma_1)I_1^* - b_1 \nu_h E_h \frac{I_1^*}{I_1} \\
&+ \sum_{i=2}^{n-1}\left(b_i(\mu_h + \eta_i + \gamma_i)I_i^* - b_i \gamma_{i-1}\frac{I_i^* I_{i-1}}{I_i}\right) \\
&+ b_n(\mu_h + \eta_n)I_n^* - b_n \gamma_{n-1}\frac{I_n^* I_{n-1}}{I_n}.
\end{aligned}
$$

By using the endemic relations and (15–16), b_0 and b_1 could be written as:

$$
\begin{aligned}
b_0 &= \frac{\nu_h}{\mu_h + \nu_h} b_1 \\
&= \frac{\nu_h}{\mu_h + \nu_h} v_1 S_v^* \frac{1}{\alpha_1} \frac{\sum_{i=1}^n \bar{\beta}_i I_i^*}{I_1^*} \\
&= \frac{v_1}{\mu_h + \nu_h} S_v^* \frac{\sum_{i=1}^n \bar{\beta}_i I_i^*}{E_h^*} \\
&= \frac{v_1}{\bar{\beta}_v} S_v^* \frac{\sum_{i=1}^n \bar{\beta}_i I_i^*}{S_h^* I_v^*}.
\end{aligned}
$$

Hence,

$$
\begin{aligned}
\dot{\mathcal{W}} = {} & v_1 \mathcal{A}_v + 2v_1(\mu_v + \nu_v + \delta_v)E_v^* - v_1(\mu_v + \nu_v + \delta_v)E_v^* \frac{S_v^*}{S_v} \\
& - v_1 \frac{E_v^*}{E_v} S_v \sum_{i=1}^n \bar{\beta}_i I_i - v_2 \nu_v E_v \frac{I_v^*}{I_v} + v_2(\mu_v + \delta_v)I_v^* \\
& + b_0 \mathcal{A}_h + 2b_0(\mu_h + \nu_h)E_h^* - b_0(\mu_h + \nu_h)E_h^* \frac{S_h^*}{S_h} + b_0\left(-\bar{\beta}_v S_h I_v \frac{E_h^*}{E_h}\right) \\
& + b_1(\mu_h + \eta_1 + \gamma_1)I_1^* - b_1 \nu_h E_h \frac{I_1^*}{I_1} \\
& + \sum_{i=2}^{n-1}\left(b_i(\mu_h + \eta_i + \gamma_i)I_i^* - b_i \gamma_{i-1}\frac{I_i^* I_{i-1}}{I_i}\right) \\
& + b_n(\mu_h + \eta_n)I_n^* - b_n \gamma_{n-1}\frac{I_n^* I_{n-1}}{I_n}.
\end{aligned}
$$

Taking into account the construction of b_i, we have

$$2b_0(\mu_{\rm h}+\nu_{\rm h})E_{\rm h}^* = 2v_1(\mu_{\rm v}+\delta_{\rm v})I_{\rm v}^* = 2v_1 S_{\rm v}^* \sum_{i=1}^{n} \bar{\beta}_i I_i^*,$$

$$\begin{aligned} b_i &= v_1 S_{\rm v}^* \frac{\sum_{j=i}^{n} \bar{\beta}_j I_j^*}{(\mu_{\rm h}+\eta_i+\gamma_i)I_i^*} \\ &= v_1 S_{\rm v}^* \frac{\sum_{j=i}^{n} \bar{\beta}_j I_j^*}{\alpha_i I_i^*}, \quad \forall i = 1, 2, \ldots, n-1, \end{aligned}$$

and,

$$b_n = v_1 \frac{\bar{\beta}_n S_{\rm v}^*}{\alpha_n}.$$

It follows that:

$$\begin{aligned} \frac{\dot{\mathcal{W}}}{v_1} = {} & \mathcal{A}_{\rm v} + b_0 \frac{\mathcal{A}_{\rm h}}{v_1} + 2S_{\rm v}^* \sum_{i=1}^{n} \bar{\beta}_i I_i^* - S_{\rm v}^* \sum_{i=1}^{n} \bar{\beta}_i I_i^* \frac{S_{\rm v}^*}{S_{\rm v}} - \frac{E_{\rm v}^*}{E_{\rm v}} S_{\rm v} \sum_{i=1}^{n} \bar{\beta}_i I_i \\ & - \frac{E_{\rm v}}{E_{\rm v}^*} \frac{I_{\rm v}^*}{I_{\rm v}} S_{\rm v}^* \sum_{i=1}^{n} \bar{\beta}_i I_i^* + 4S_{\rm v}^* \sum_{i=1}^{n} \bar{\beta}_i I_i^* - S_{\rm v}^* \sum_{i=1}^{n} \bar{\beta}_i I_i^* \frac{S_{\rm h}^*}{S_{\rm h}} \\ & - S_{\rm v}^* \sum_{i=1}^{n} \bar{\beta}_i I_i^* \frac{S_{\rm h}}{S_{\rm h}^*} \frac{E_{\rm h}^*}{E_{\rm h}} \frac{I_{\rm v}}{I_{\rm v}^*} - S_{\rm v}^* \sum_{i=1}^{n} \bar{\beta}_i I_i^* \frac{I_1^*}{I_1} \frac{E_{\rm h}}{E_{\rm h}^*} \\ & + \sum_{i=2}^{n-1} \left(S_{\rm v}^* \sum_{j=i}^{n} \bar{\beta}_j I_j^* - S_{\rm v}^* \sum_{j=i}^{n} \bar{\beta}_j I_j^* \frac{I_i^*}{I_i} \frac{I_{i-1}}{I_{i-1}^*} \right) \\ & + \bar{\beta}_n S_{\rm v}^* I_n^* - \bar{\beta}_n S_{\rm v}^* I_n^* \frac{I_n^*}{I_n} \frac{I_{n-1}}{I_{n-1}^*}. \end{aligned}$$

By separating the first index from the sum, we obtain:

$$\begin{aligned} \frac{\dot{\mathcal{W}}}{v_1} = {} & \mathcal{A}_{\rm v} + b_0 \frac{\mathcal{A}_{\rm h}}{v_1} + 6S_{\rm v}^* \bar{\beta}_1 I_1^* + 6S_{\rm v}^* \sum_{i=2}^{n} \bar{\beta}_i I_i^* - S_{\rm v}^* \bar{\beta}_1 I_1^* \frac{S_{\rm v}^*}{S_{\rm v}} - S_{\rm v}^* \sum_{i=2}^{n} \bar{\beta}_i I_i^* \frac{S_{\rm v}^*}{S_{\rm v}} \\ & - \frac{E_{\rm v}^*}{E_{\rm v}} S_{\rm v} \bar{\beta}_1 I_1 - \frac{E_{\rm v}^*}{E_{\rm v}} S_{\rm v} \sum_{i=2}^{n} \bar{\beta}_i I_i - \frac{E_{\rm v}}{E_{\rm v}^*} \frac{I_{\rm v}^*}{I_{\rm v}} S_{\rm v}^* \bar{\beta}_1 I_1^* - \frac{E_{\rm v}}{E_{\rm v}^*} \frac{I_{\rm v}^*}{I_{\rm v}} S_{\rm v}^* \sum_{i=2}^{n} \bar{\beta}_i I_i^* \\ & - S_{\rm v}^* \bar{\beta}_1 I_1^* \frac{S_{\rm h}^*}{S_{\rm h}} - S_{\rm v}^* \sum_{i=2}^{n} \bar{\beta}_i I_i^* \frac{S_{\rm h}^*}{S_{\rm h}} - S_{\rm v}^* \bar{\beta}_1 I_1^* \frac{S_{\rm h}}{S_{\rm h}^*} \frac{E_{\rm h}^*}{E_{\rm h}} \frac{I_{\rm v}}{I_{\rm v}^*} \\ & - S_{\rm v}^* \sum_{i=2}^{n} \bar{\beta}_i I_i^* \frac{S_{\rm h}}{S_{\rm h}^*} \frac{E_{\rm h}^*}{E_{\rm h}} \frac{I_{\rm v}}{I_{\rm v}^*} - S_{\rm v}^* \bar{\beta}_1 I_1^* \frac{I_1^*}{I_1} \frac{E_{\rm h}}{E_{\rm h}^*} - S_{\rm v}^* \sum_{i=2}^{n} \bar{\beta}_i I_i^* \frac{I_1^*}{I_1} \frac{E_{\rm h}}{E_{\rm h}^*} \\ & + \sum_{i=2}^{n} \left(S_{\rm v}^* \sum_{j=i}^{n} \bar{\beta}_j I_j^* - S_{\rm v}^* \sum_{j=i}^{n} \bar{\beta}_j I_j^* \frac{I_i^*}{I_i} \frac{I_{i-1}}{I_{i-1}^*} \right). \end{aligned}$$

Therefore,

$$\begin{aligned}\frac{\dot{\mathcal{W}}}{v_1} &= \mathcal{A}_{\mathrm{v}} + b_0\frac{\mathcal{A}_{\mathrm{h}}}{v_1}\\ &+ S_{\mathrm{v}}^*\bar{\beta}_1 I_1^*\left(6 - \frac{S_{\mathrm{v}}^*}{S_{\mathrm{v}}} - \frac{S_{\mathrm{v}}}{S_{\mathrm{v}}^*}\frac{I_1}{I_1^*}\frac{E_{\mathrm{v}}^*}{E_{\mathrm{v}}} - \frac{E_{\mathrm{v}}}{E_{\mathrm{v}}^*}\frac{I_{\mathrm{v}}^*}{I_{\mathrm{v}}} - \frac{S_{\mathrm{h}}^*}{S_{\mathrm{h}}} - \frac{S_{\mathrm{h}}I_{\mathrm{v}}E_{\mathrm{h}}^*}{S_{\mathrm{h}}^*I_{\mathrm{v}}^*E_{\mathrm{h}}} - \frac{E_{\mathrm{h}}I_1^*}{E_{\mathrm{h}}^*I_1}\right)\\ &+ S_{\mathrm{v}}^*\sum_{i=2}^{n}\bar{\beta}_i I_i^*\left(6 - \frac{S_{\mathrm{v}}^*}{S_{\mathrm{v}}} - \frac{S_{\mathrm{v}}I_i E_{\mathrm{v}}^*}{S_{\mathrm{v}}^*I_i^*E_{\mathrm{v}}} - \frac{E_{\mathrm{v}}I_{\mathrm{v}}^*}{E_{\mathrm{v}}^*I_{\mathrm{v}}} - \frac{S_{\mathrm{h}}^*}{S_{\mathrm{h}}} - \frac{S_{\mathrm{h}}I_{\mathrm{v}}E_{\mathrm{h}}^*}{S_{\mathrm{h}}^*I_{\mathrm{v}}^*E_{\mathrm{h}}} - \frac{E_{\mathrm{h}}I_1^*}{E_{\mathrm{h}}^*I_1}\right)\\ &+ \sum_{i=2}^{n}\left(S_{\mathrm{v}}^*\sum_{j=i}^{n}\bar{\beta}_j I_j^* - S_{\mathrm{v}}^*\sum_{j=i}^{n}\bar{\beta}_j I_j^*\frac{I_i^*}{I_i}\frac{I_{i-1}}{I_{i-1}^*}\right).\end{aligned}$$

By using the properties of nested sums, $\sum_{i=2}^{n}\left(\sum_{j=i}^{n}u_j w_i\right) = \sum_{i=2}^{n}u_i\sum_{j=2}^{i}w_j$, we obtain,

$$\sum_{i=2}^{n}\left(\sum_{j=i}^{n}\bar{\beta}_j I_j^*\right) = \sum_{i=2}^{n}\bar{\beta}_i I_i^*(i-1),$$

and

$$\sum_{i=2}^{n}\left(\sum_{j=i}^{n}\bar{\beta}_j I_j^*\frac{I_i^*}{I_i}\frac{I_{i-1}}{I_{i-1}^*}\right) = \sum_{i=2}^{n}\bar{\beta}_i I_i^*\left(\sum_{j=2}^{i}\frac{I_j^*}{I_j}\frac{I_{j-1}}{I_{j-1}^*}\right).$$

Finally,

$$\begin{aligned}\frac{\dot{\mathcal{W}}}{v_1} &= \mathcal{A}_{\mathrm{v}} + b_0\frac{\mathcal{A}_{\mathrm{h}}}{v_1} + S_{\mathrm{v}}^*\bar{\beta}_1 I_1^*\left(6 - \frac{S_{\mathrm{v}}^*}{S_{\mathrm{v}}} - \frac{S_{\mathrm{v}}}{S_{\mathrm{v}}^*}\frac{I_1}{I_1^*}\frac{E_{\mathrm{v}}^*}{E_{\mathrm{v}}} - \frac{E_{\mathrm{v}}}{E_{\mathrm{v}}^*}\frac{I_{\mathrm{v}}^*}{I_{\mathrm{v}}} - \frac{S_{\mathrm{h}}^*}{S_{\mathrm{h}}}\right.\\ &\left. - \frac{S_{\mathrm{h}}I_{\mathrm{v}}E_{\mathrm{h}}^*}{S_{\mathrm{h}}^*I_{\mathrm{v}}^*E_{\mathrm{h}}} - \frac{E_{\mathrm{h}}I_1^*}{E_{\mathrm{h}}^*I_1}\right) + S_{\mathrm{v}}^*\sum_{i=2}^{n}\bar{\beta}_i I_i^*\left(5 + i - \frac{S_{\mathrm{v}}^*}{S_{\mathrm{v}}} - \frac{S_{\mathrm{v}}I_i E_{\mathrm{v}}^*}{S_{\mathrm{v}}^*I_i^*E_{\mathrm{v}}}\right.\\ &\left. - \frac{E_{\mathrm{v}}I_{\mathrm{v}}^*}{E_{\mathrm{v}}^*I_{\mathrm{v}}} - \frac{S_{\mathrm{h}}^*}{S_{\mathrm{h}}} - \frac{S_{\mathrm{h}}I_{\mathrm{v}}E_{\mathrm{h}}^*}{S_{\mathrm{h}}^*I_{\mathrm{v}}^*E_{\mathrm{h}}} - \frac{E_{\mathrm{h}}I_1^*}{E_{\mathrm{h}}^*I_1} - \sum_{j=2}^{i}\frac{I_j^*}{I_j}\frac{I_{j-1}}{I_{j-1}^*}\right).\end{aligned}$$

By setting $v_1 = 1$ and replacing $\mathcal{A}_{\mathrm{v}}$ and $\mathcal{A}_{\mathrm{h}}$ by their respective values, the final expression of $\dot{\mathcal{W}}$ is:

$$\begin{aligned}\dot{\mathcal{W}} = {} & (\mu_{\mathrm{v}}+\delta_{\mathrm{v}})S_{\mathrm{v}}^*\left(2-\frac{S_{\mathrm{v}}^*}{S_{\mathrm{v}}}-\frac{S_{\mathrm{v}}}{S_{\mathrm{v}}^*}\right)+b_0\mu_{\mathrm{h}}S_{\mathrm{h}}^*\left(2-\frac{S_{\mathrm{h}}^*}{S_{\mathrm{h}}}-\frac{S_{\mathrm{h}}}{S_{\mathrm{h}}^*}\right)\\ & +S_{\mathrm{v}}^*\bar{\beta}_1 I_1^*\left(6-\frac{S_{\mathrm{v}}^*}{S_{\mathrm{v}}}-\frac{S_{\mathrm{v}}}{S_{\mathrm{v}}^*}\frac{I_1}{I_1^*}\frac{E_{\mathrm{v}}^*}{E_{\mathrm{v}}}-\frac{E_{\mathrm{v}}}{E_{\mathrm{v}}^*}\frac{I_{\mathrm{v}}^*}{I_{\mathrm{v}}}-\frac{S_{\mathrm{h}}^*}{S_{\mathrm{h}}}-\frac{S_{\mathrm{h}}I_{\mathrm{v}}E_{\mathrm{h}}^*}{S_{\mathrm{h}}^*I_{\mathrm{v}}^*E_{\mathrm{h}}}-\frac{E_{\mathrm{h}}I_1^*}{E_{\mathrm{h}}^*I_1}\right)\\ & +S_{\mathrm{v}}^*\sum_{i=2}^{n}\bar{\beta}_i I_i^*\left(5+i-\frac{S_{\mathrm{v}}^*}{S_{\mathrm{v}}}-\frac{S_{\mathrm{v}}I_iE_{\mathrm{v}}^*}{S_{\mathrm{v}}^*I_i^*E_{\mathrm{v}}}-\frac{E_{\mathrm{v}}I_{\mathrm{v}}^*}{E_{\mathrm{v}}^*I_{\mathrm{v}}}-\frac{S_{\mathrm{h}}^*}{S_{\mathrm{h}}}\right.\\ & \left.-\frac{S_{\mathrm{h}}I_{\mathrm{v}}E_{\mathrm{h}}^*}{S_{\mathrm{h}}^*I_{\mathrm{v}}^*E_{\mathrm{h}}}-\frac{E_{\mathrm{h}}I_1^*}{E_{\mathrm{h}}^*I_1}-\sum_{j=2}^{i}\frac{I_j^*I_{j-1}}{I_jI_{j-1}^*}\right),\end{aligned} \tag{17}$$

with $b_0 = S_{\mathrm{v}}^*\dfrac{\sum_{i=1}^{n}\bar{\beta}_i I_i^*}{(\mu_{\mathrm{h}}+\nu_{\mathrm{h}})E_{\mathrm{h}}^*}$. By using the geometric-arithmetic mean inequality, we conclude that $\dot{\mathcal{W}}$ is negative-definite, which proves the global asymptotic stability of the endemic equilibrium. □

This result of global stability of the endemic equilibrium is new and extend the results of Palmer et al. (2016) in which the endemic equilibrium is proven to be locally asymptotically stable if $\mathcal{R}_0^2 > 1$ and $\mathcal{R}_0^2$ is close to one. Theorems 2.1 and 2.2 solve completely the global dynamics of the vector-borne staged progression model (6). The basic reproduction number $\mathcal{R}_0^2$ acts as a sharp threshold for the disease in the sense that the latter dies out if $\mathcal{R}_0^2 \leq 1$ and persists whenever $\mathcal{R}_0^2 > 1$.

Now that the dynamics of the single host-vector staged progression is solved, we tackle the dynamics of multi-host vector-borne zoonoses in the next section.

3 Multi-host Vector-Borne Models

Vector-borne zoonoses are central in understanding the dynamics of zoonoses in general as vectors play the bridging role in transporting the infection from one species to another. Many zoonotic pathogens are shared in multiple hosts. For instance, for West Nile virus, the pathogen has been found in more 300 bird species as well as in other mammals such as horses, bats, and squirrels, among others (Marfin et al. 2001). Therefore, it is important to investigate a general model that captures the dynamics of an arbitrary number of host species interacting with an arthropod vector that bridges the infection among hosts. In Cruz-Pacheco et al. (2012a, b), the authors investigated the dynamics of Chagas' disease and WNV, respectively, with two host species. In modeling TBRF, Johnson et al. (2016) proposed a two hosts and one vector model, namely pine squirrels and deer mice. These two hosts are bitten by the same vector (ticks).

Building upon the same scheme as in Model (4), we derive a multi-host vector-borne zoonoses model with m hosts and n stages of infection. However, the infection terms in the multi-host necessitates a detailed formulation as it differs from the one host scenario. For instance, the equation of susceptible of Host j is given by

$$\dot{S}_j = \Lambda_j - b_j(N_j, N_{\mathrm{v}})\beta_{\mathrm{vh}}S_j\frac{I_{\mathrm{v}}}{N_{\mathrm{v}}} - \mu_{\mathrm{h}}S_{\mathrm{h}}, \tag{18}$$

where $b_j(N_j, N_v)$ is the number of bites per Host j per unit of time. Hence, the total number of bites on Host j is $b_j(N_j, N_v)N_j$.

The equation of susceptible vectors is given by:

$$\dot{S}_v = \Lambda_v - \sum_{j=1}^{m} a_j \beta_{hv} S_v \frac{\sum_{i=1}^{n} \beta_{j,i} I_{j,i}}{N_j} - (\mu_v + \delta_v) S_v$$

where a_j is the number of bites per mosquito per unit of time on Host j.

By the conservation law, the total number of bites on Host j by mosquitoes ($a_j N_v$) should equal the total number of bites received by Host j ($b_j(N_j, N_v)N_j$). Therefore,

$$b_j(N_j, N_v)N_j = a_j N_v,$$

or equivalently,

$$b_j(N_j, N_v) = \frac{a_j N_v}{N_j}.$$

Hence, for $j = 1, 2, \ldots, m$, Eq. (18) leads to,

$$\dot{S}_j = \Lambda_j - a_j \beta_{vh} S_j \frac{I_v}{N_j} - \mu_j S_j.$$

Therefore, the dynamics of a model that captures the interactions between m host species and an arthropod vector is given by:

$$\begin{cases} \text{For } j = 1, 2 \ldots, m: \\ \dot{S}_j = \Lambda_j - a_j \beta_{v,j} S_j \frac{I_v}{\bar{N}_j} - \mu_j S_j \\ \dot{E}_j = a_j \beta_{v,j} S_j \frac{I_v}{\bar{N}_j} - (\mu_j + \nu_j) E_{h,j} \\ \dot{I}_{j,1} = \nu_j E_{h,j} - (\mu_j + \eta_{j,1} + \gamma_{j,1}) I_{j,1} \\ \dot{I}_{j,2} = \gamma_{j,1} I_{j,1} - (\mu_j + \eta_{j,2} + \gamma_{j,2}) I_{j,2} \\ \vdots \\ \dot{I}_{j,n-1} = \gamma_{j,n-2} I_{j,n-2} - (\mu_j + \eta_{j,n-1} + \gamma_{j,n-1}) I_{j,n-1} \\ \dot{I}_{j,n} = \gamma_{j,n-1} I_{j,n-1} - (\mu_j + \eta_{j,n} + \gamma_{j,n}) I_{j,n} \\ \dot{S}_v = \Lambda_v - \sum_{j=1}^{m} a_j S_v \frac{\sum_{i=1}^{n} \beta_{j,i} I_{j,i}}{\bar{N}_j} - (\mu_v + \delta_v) S_v \\ \dot{E}_v = \sum_{j=1}^{m} a_j S_v \frac{\sum_{i=1}^{n} \beta_{j,i} I_{j,i}}{\bar{N}_j} - (\mu_v + \nu_v + \delta_v) E_v. \\ \dot{I}_v = \nu_v E_v - (\mu_v + \delta_v) I_v. \end{cases} \tag{19}$$

Parameters in System (19) are described in Table 2.

Table 2 Description of the parameters used in System (19)

Parameters	Description
Λ_j	Recruitment of Host j
Λ_{v}	Recruitment of vectors
a_j	Biting rate on Host j
μ_j	Host j's death rate
$\beta_{\mathrm{v},j}$	Vector's infectiousness to Host j per biting
$\beta_{j,i}$	Infectiousness of Host j at stage i to vectors per biting
ν_j	Host j's rate at which the exposed individuals become infected
ν_{v}	Vector's rate at which the exposed individuals become infected
μ_{v}	Vector's natural death rate.
$\eta_{j,i}$	Per capita recovery rate for Host j at stage i
$\gamma_{j,i}$	Host j's per capita progression rate from stage i to $i+1$

Remark 3.1 Some authors Bowman et al. (2005), Dobson (2004) and Simpson et al. (2011) assumed that the vectors' biting rate is constant on all hosts (that is, vectors bite a certain fixed number of bites a day regardless of hosts) and denoted by a. By the conservation law,

$$b_j(N_j, N_{\mathrm{v}}) = \frac{aN_{\mathrm{v}}}{\sum_{j=1}^{m} N_j}.$$

Our approach assumes that a_j represents the biting rate of vector on Host j. This differential vector biting rates on hosts embodies also the well-documented biting/feeding preference of vectors with respect to the hosts (Johnson et al. 2016; Simpson et al. 2011). However, the two approaches are mathematically equivalent if the host populations are asymptotically constant.

System (19) models a range of modeling scenarios in vector-borne zoonoses. For instance, if a subset K of the considered hosts carries the pathogen but are dead-end hosts, that is, they do not spread the infection, it is sufficient to let $\beta_{k,i} = 0$ for all $k \in K$ and $i = 1, 2, \ldots, n$. It also captures the case where different hosts have different epidemiological responses to the infection. That is, by appropriately choosing the parameters in System (19), the model could describe the case the infection follows an SIR-type of structure for a collection of hosts and SEIR-type or SI-type with multiple stage of infections for other hosts.

With $\boldsymbol{\beta_j} = (\beta_{j,1}, \ldots, \beta_{j,m})^{\mathrm{T}}$, System (19) could be written in a more compact vectorial form as:

$$\begin{cases} \dot{S}_1 = \Lambda_1 e_1 - a_1 \beta_{\mathrm{v},1} S_1 \dfrac{I_{\mathrm{v}}}{\bar{N}_1} - \mu_1 S_1 \\ \dot{S}_2 = \Lambda_2 e_1 - a_2 \beta_{\mathrm{v},2} S_2 \dfrac{I_{\mathrm{v}}}{\bar{N}_2} - \mu_2 S_2 \\ \vdots \\ \dot{S}_m = \Lambda_m e_1 - a_m \beta_{\mathrm{v},m} S_m \dfrac{I_{\mathrm{v}}}{\bar{N}_m} - \mu_m S_m \\ \dot{\mathbf{I}}_1 = a_1 \beta_{\mathrm{v},1} S_1 \dfrac{I_{\mathrm{v}}}{\bar{N}_1} e_1 + A_1 \mathbf{I}_1 \\ \dot{\mathbf{I}}_2 = a_2 \beta_{\mathrm{v},2} S_2 \dfrac{I_{\mathrm{v}}}{\bar{N}_2} e_1 + A_2 \mathbf{I}_2 \\ \vdots \\ \dot{\mathbf{I}}_m = a_m \beta_{\mathrm{v},m} S_m \dfrac{I_{\mathrm{v}}}{\bar{N}_m} e_1 + A_m \mathbf{I}_m \\ \dot{E}_{\mathrm{v}} = \displaystyle\sum_{j=1}^{m} a_j \frac{\bar{N}_{\mathrm{v}} - I_{\mathrm{v}}}{\bar{N}_{h,j}} \left\langle \begin{pmatrix} 0 \\ \boldsymbol{\beta_j} \end{pmatrix} \,\middle|\, \mathbf{I}_j \right\rangle - (\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}}) E_{\mathrm{v}}, \\ \dot{I}_{\mathrm{v}} = \nu_{\mathrm{v}} E_{\mathrm{v}} - (\mu_{\mathrm{v}} + \delta_{\mathrm{v}}) I_{\mathrm{v}}. \end{cases} \tag{20}$$

where $\mathbf{I}_j = (E_j, I_{j,1}, I_{j,2} \ldots, I_{j,n})^{\mathrm{T}}$ is the vector of infected of Host j ($j = 1, 2, \ldots, m$) and

$$A_j = \begin{pmatrix} -(\nu_j + \mu_j) & 0 & \ldots & \ldots & 0 \\ \nu_j & -\alpha_{j,1} & \ldots & \ldots & 0 \\ 0 & \gamma_{j,1} & -\alpha_{j,2} & \ldots & 0 \\ \vdots & \ddots & \ddots & \vdots & \vdots \\ 0 & \ldots & \ddots & \gamma_{j,n-1} & -\alpha_{j,n} \end{pmatrix}$$

where $\alpha_{j,i} = \gamma_{j,i} + \eta_{j,i} + \mu_j$, for $j = 1, \ldots, m$ and $i = 1, 2, \ldots, n$. The term $\alpha_{j,i}$ represents the mean period for which infected population of Host j in stage i leave this stage.

3.1 Basic Reproduction Number and Basic Properties

In this subsection, we derive the basic reproduction number of the multi-host system. First of all, the solutions of Model (20) are bounded as a result of the following Lemma, whose proof is straightforward.

Lemma 3.1 *The region defined by*

$$\Omega = \left\{ (S_j, E_j, I_{j,i}, E_{\mathrm{v}}, I_{\mathrm{v}}) \in \mathbb{R}_+^{m(n+2)+2} \;\middle|\; S_j + E_j + \sum_{i=1}^{n} I_{j,i} \leq \frac{\Lambda_j}{\mu_j}, \text{ for } j = 1, \dots m, \; E_{\mathrm{v}} + I_{\mathrm{v}} \leq \frac{\Lambda_{\mathrm{v}}}{\mu_{\mathrm{v}}} \right\}$$

is a compact attracting positively invariant set for system (20).

The disease-free equilibrium of Model (20) is $(S^*, 0_{\mathbb{R}^{(n+1)m+2}})$ with $S^* = [S_1^*, S_2^*, \dots, S_m^*] = \left[\frac{\Lambda_1}{\mu_1}, \frac{\Lambda_2}{\mu_2}, \dots, \frac{\Lambda_m}{\mu_m}\right]$. The vector field of Model (20) could be subdivided into new infections vector $\mathcal{F}$ and transition vector $\mathcal{V}$ where

$$\mathcal{F}(\mathbf{I}_1, \dots, \mathbf{I}_m, E_{\mathrm{v}}, I_{\mathrm{v}}) = \begin{pmatrix} a_1 \beta_{\mathrm{v},1} S_1 \frac{I_{\mathrm{v}}}{\bar{N}_1} e_1 \\ a_2 \beta_{\mathrm{v},2} S_2 \frac{I_{\mathrm{v}}}{\bar{N}_2} e_1 \\ \cdots \\ a_m \beta_{\mathrm{v},m} S_m \frac{I_{\mathrm{v}}}{\bar{N}_m} e_1 \\ \sum_{j=1}^{m} a_j \frac{\bar{N}_{\mathrm{v}} - I_{\mathrm{v}}}{\bar{N}_{h,j}} \left\langle \begin{pmatrix} 0 \\ \boldsymbol{\beta_j} \end{pmatrix} \middle| \mathbf{I}_j \right\rangle \\ 0 \end{pmatrix},$$

and

$$\mathcal{V}(\mathbf{I}_1, \dots, \mathbf{I}_m, E_{\mathrm{v}}, I_{\mathrm{v}}) = \begin{pmatrix} A_1 \mathbf{I}_1 \\ A_2 \mathbf{I}_2 \\ \vdots \\ A_m \mathbf{I}_m \\ -(\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}}) E_{\mathrm{v}} \\ \nu_{\mathrm{v}} E_{\mathrm{v}} - (\mu_{\mathrm{v}} + \delta_{\mathrm{v}}) I_{\mathrm{v}} \end{pmatrix}.$$

The Jacobian matrices at the DFE of $\mathcal{F}$ and $\mathcal{V}$ are $F = D\mathcal{F}(\mathbf{I}_1, \mathbf{I}_2, \dots, \mathbf{I}_m, I_{\mathrm{v}})\big|_{\mathrm{DFE}}$ and $V = D\mathcal{V}(\mathbf{I}_1, \mathbf{I}_2, \dots, \mathbf{I}_m, E_{\mathrm{v}}, I_{\mathrm{v}})\big|_{\mathrm{DFE}}$ and are given by:

$$F = \begin{pmatrix} \mathbf{0}_{n+1,n+1} & \mathbf{0}_{n+1,n+1} & \cdots & \cdots & \mathbf{0}_{n+1,1} & a_1 \beta_{\mathrm{v},1} e_1 \\ \mathbf{0}_{n+1,n+1} & \mathbf{0}_{n+1,n+1} & \cdots & \cdots & \mathbf{0}_{n+1,1} & a_2 \beta_{\mathrm{v},2} e_1 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ \mathbf{0}_{n+1,n+1} & \mathbf{0}_{n+1,n+1} & \cdots & \cdots & \mathbf{0}_{n+1,1} & a_m \beta_{\mathrm{v},m} e_1 \\ a_1 \frac{\bar{N}_{\mathrm{v}}}{\bar{N}_1} (0, \boldsymbol{\beta_1})^{\mathrm{T}} & a_2 \frac{\bar{N}_{\mathrm{v}}}{\bar{N}_2} (0, \boldsymbol{\beta_2})^{\mathrm{T}} & \cdots & a_m \frac{\bar{N}_{\mathrm{v}}}{\bar{N}_m} (0, \boldsymbol{\beta_m})^{\mathrm{T}} & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 & 0 \end{pmatrix},$$

and

$$V = \text{diag}(A_1, A_2, \ldots, A_m, A_{\text{v}}),$$

where

$$A_{\text{v}} = \begin{pmatrix} -(\mu_{\text{v}} + \nu_{\text{v}} + \delta_{\text{v}}) & 0 \\ \nu_{\text{v}} & -(\mu_{\text{v}} + \delta_{\text{v}}) \end{pmatrix}.$$

It follows that

$$-V^{-1} = \text{diag}\left(-A_1^{-1}, -A_2^{-1}, \ldots, -A_m^{-1}, -A_{\text{v}}^{-1}\right).$$

Thus, the next-generation matrix is:

$$-FV^{-1} = \begin{pmatrix} \mathbf{0}_{n+1,n+1} & \cdots & \cdots & (\mathbf{0}_{n+1,1}, a_1\beta_{\text{v},1}e_1)(-A_{\text{v}}^{-1}) \\ \mathbf{0}_{n+1,n+1} & \cdots & \cdots & (\mathbf{0}_{n+1,1}, a_2\beta_{\text{v},2}e_1)(-A_{\text{v}}^{-1}) \\ \vdots & \vdots & \vdots & \vdots \\ \mathbf{0}_{n+1,n+1} & \cdots & \cdots & (\mathbf{0}_{n+1,1}, a_m\beta_{\text{v},m}e_1)(-A_{\text{v}}^{-1}) \\ a_1\frac{\bar{N}_{\text{v}}}{\bar{N}_1}(0, \boldsymbol{\beta_1})^{\text{T}}(-A_1^{-1}) & \cdots & a_m\frac{\bar{N}_{\text{v}}}{\bar{N}_m}(0, \boldsymbol{\beta_m})^{\text{T}}(-A_m^{-1}) & \mathbf{0}_{1,2} \\ \mathbf{0}_{1,n+1} & \cdots & \mathbf{0}_{1,n+1} & \mathbf{0}_{1,2} \end{pmatrix}.$$

The matrix $(-FV^{-1})^2$ is of rank one, and its largest eigenvalue is:

$$\begin{aligned} \mathcal{R}_0^2(m) &= \sum_{j=1}^{m} \frac{a_j^2\beta_{\text{v},j}\nu_{\text{v}}}{(\mu_{\text{v}} + \nu_{\text{v}} + \delta_{\text{v}})(\mu_{\text{v}} + \delta_{\text{v}})} \frac{\bar{N}_{\text{v}}}{\bar{N}_{h,j}}(0, \boldsymbol{\beta}_j)^{\text{T}}\left(-A_j^{-1}\right)e_1 \\ &:= \sum_{j=1}^{m} \mathcal{R}_{0,j}^2, \end{aligned}$$

where $\mathcal{R}_{0,j}^2$ is the basic reproduction number when Host j is the only coupled host to the vector. A more explicit expression of $\mathcal{R}_0^2$ could be obtained by computing A_j^{-1}. Indeed,

$$-A_j^{-1} = \begin{pmatrix} \frac{1}{\nu_j + \mu_j} & 0 & \cdots & \cdots & 0 \\ \frac{\nu_j}{\alpha_{j,1}(\nu_j + \mu_j)} & \frac{1}{\alpha_{j,1}} & \cdots & \cdots & 0 \\ \frac{\gamma_{j,1}\nu}{\alpha_{j,1}\alpha_{j,2}(\nu_j + \mu_j)} & \frac{\gamma_{j,1}}{\alpha_{j,1}\alpha_{j,2}} & \frac{1}{\alpha_{j,2}} & \cdots & 0 \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ \frac{\gamma_{j,1}\ldots\gamma_{j,n-1}\nu_j}{\alpha_{j,1}\alpha_{j,2}\ldots\alpha_{j,n}(\nu_j + \mu_j)} & \cdots & \cdots & \frac{\gamma_{j,n-1}}{\alpha_{j,n-1}\alpha_{j,n}} & \frac{1}{\alpha_{j,n}} \end{pmatrix}. \quad (21)$$

Hence, we deduce that,

$$\begin{aligned}(0,\boldsymbol{\beta_j})^{\mathrm{T}}(-A_j^{-1})e_1 &= \beta_{j,1}\frac{\nu_j}{\alpha_{j,1}(\nu_j+\mu_j)}+\beta_{j,2}\frac{\gamma_{j,1}\nu_j}{\alpha_{j,1}\alpha_{j,2}(\nu_j+\mu_j)}+\cdots\\ &\quad+\beta_{j,n}\frac{\gamma_{j,1}\cdots\gamma_{j,n-1}\nu_j}{\alpha_{j,1}\alpha_{j,2}\ldots\alpha_{j,n}(\nu_j+\mu_j)}\\ &= \frac{\nu_j}{\nu_j+\mu_j}\left(\frac{\beta_{j,1}}{\alpha_{j,1}}+\frac{\beta_{j,2}\gamma_{j,1}}{\alpha_{j,1}\alpha_{j,2}}+\cdots+\frac{\beta_{j,n}\gamma_{j,1}\cdots\gamma_{j,n-1}}{\alpha_{j,1}\alpha_{j,2}\ldots\alpha_{j,n}}\right)\\ &= \frac{\nu_j}{\nu_j+\mu_j}\sum_{i=1}^{n}\frac{\gamma_{j,1}\gamma_{j,2}\cdots\gamma_{j,i-1}}{\alpha_{j,1}\alpha_{j,2}\ldots\alpha_{j,i}}\beta_{j,i}\quad\text{with}\quad\gamma_{j,0}=1.\end{aligned}$$

Finally, the basic reproduction number of a multi-host-vector model with n stages is given by

$$\mathcal{R}_0^2(m)=\sum_{j=1}^{m}\mathcal{R}_{0,j}^2,$$

where

$$\mathcal{R}_{0,j}^2=\frac{a_j^2\beta_{\mathrm{v},j}\nu_{\mathrm{v}}}{(\mu_{\mathrm{v}}+\nu_{\mathrm{v}}+\delta_{\mathrm{v}})(\mu_{\mathrm{v}}+\delta_{\mathrm{v}})}\frac{\bar{N}_{\mathrm{v}}}{\bar{N}_{h,j}}\frac{\nu_j}{\nu_j+\mu_j}\sum_{i=1}^{n}\frac{\gamma_{j,1}\gamma_{j,2}\cdots\gamma_{j,i-1}}{\alpha_{j,1}\alpha_{j,2}\ldots\alpha_{j,i}}\beta_{j,i}.$$

This result generalizes the results of Cruz-Pacheco et al. (2012a, b), Johnson et al. (2016), for which $j=2$, and Palmer et al. (2016) for which $j=1$. Similar remarks hold for Bowman et al. (2005).

The overall basic reproduction number increases with respect to the number of host species. Indeed, since the reproduction number for m host species interacting with an arthropod vector is $\mathcal{R}_0^2(m)=\sum_{j=1}^{m}\mathcal{R}_{0,j}^2$, by adding an additional new host species, say $m+1$, the new global basic reproduction number will be

$$\begin{aligned}\mathcal{R}_0^2(m+1) &= \sum_{j=1}^{m+1}\mathcal{R}_{0,j}^2\\ &= \mathcal{R}_0^2(m)+\mathcal{R}_{0,m+1}^2\\ &\geq \mathcal{R}_0^2(m).\end{aligned}$$

Moreover, this implies that the addition of dead-end hosts, for which the basic reproduction number is zero in isolation, keeps the overall basic reproduction number steady. However, it is worthwhile noting that an underlying assumption to this is that the addition of the new host did not affect the biting or the transmissibility for the vectors to the previous m hosts and vice versa. If this hypothesis is not satisfied, the monotonicity of $\mathcal{R}_0^2(m)$ with respect to host species may not hold. A similar, yet contrasting, result has been obtained in Dobson (2004). Indeed, in Dobson (2004) the authors found that the basic reproduction number in multi-host models, when not

coupled with an arthropod vector, increases with host diversity for density-dependent transmission and decreases for frequency-dependent transmission. Our model consists of frequency-dependent transmission, but $\mathcal{R}_0^2(m)$ increases with host diversity. This contrast from Dobson (2004) stems from our modeling approach, particularly the total number of vector bites on hosts. Indeed, as pointed out in Remark 3.1, we consider a frequency-dependent infection process but in which the arthropod vector has a fixed number of bites on each Host j, that is $b_j(N_j, N_\mathrm{v})$. In Bowman et al. (2005), Dobson (2004) and Simpson et al. (2011), the authors define $b(\sum_{j=1}^m N_j, N_\mathrm{v})$ as the number of bites on all hosts. The latter will lead to a factor of $\sum_{j=1}^m N_j$ in the denominator of the infection term. Thus, increasing host diversity decreases the infection force and therefore the basic reproduction number. In spite of this difference on the overall basic reproduction numbers, the systems are mathematically asymptotically equivalent if the host populations are either constant or asymptotically constant. Moreover, since the hosts' populations are asymptotically constant, our transmission term could be seen as density-dependent, for which the monotonicity of $\mathcal{R}_0^2(m)$ coincides with that of Dobson (2004).

3.2 Global Stability of Equilibria

In this subsection, we study the global behavior of the steady states of models describing VBZ, that is Model (20), with respect to the overall basic reproduction number $\mathcal{R}_0^2(m)$.

Theorem 3.1 *The DFE is globally asymptotically stable for the multi-host Model* (20) *whenever* $\mathcal{R}_0^2(m) \leq 1$.

Proof We consider a barycentric-type Lyapunov function, a weighted sum of Lyapunov functions of the one host case:

$$\mathcal{V} = \sum_{j=1}^{m} p_j \mathcal{L}_j + E_\mathrm{v} + \frac{\mu_\mathrm{v} + \nu_\mathrm{v} + \delta_\mathrm{v}}{\nu_\mathrm{v}} I_\mathrm{v}$$

where $\mathcal{L}_j = c_{j,0}E_j + c_{j,1}I_{j,1} + c_{j,2}I_{j,2} + \cdots + c_{j,n}I_{j,n}$ and $p_j = a_j\beta_{j,v}\dfrac{\bar{N}_\mathrm{v}}{\bar{N}_{h,j}}$. The coefficients $c_{j,i}$ for $i = 1, 2, \ldots, n$ are similar to those chosen in the proof of Theorem 2.1. They are defined recursively as follows:

$$\begin{cases} c_{j,0} = \dfrac{\nu_j}{\nu_j + \mu_j} c_{j,1} \\ c_{j,1} = \left(\dfrac{\beta_{j,1}}{\alpha_{j,1}} + \dfrac{\gamma_{j,1}}{\alpha_{j,1}\alpha_{j,2}}\beta_{j,2} + \cdots + \dfrac{\gamma_{j,1}\cdots\gamma_{j,n-1}}{\alpha_{j,1}\alpha_{j,2}\ldots\alpha_{j,n}}\beta_{j,n} \right) \\ c_{j,i+1} = \dfrac{1}{\gamma_{j,i}} \left(\alpha_{j,i}c_{j,i} - \beta_{j,i} \right), \quad \forall i = 1, \ldots, n-2 \\ c_{j,n} = \dfrac{\beta_n}{\alpha_{j,n}}. \end{cases} \tag{22}$$

The derivative of $\mathcal{V}$ along the solutions of System (20) is:

$$\dot{\mathcal{V}} = \sum_{j=1}^{m} p_j \dot{\mathcal{L}}_j + \dot{E}_{\mathrm{v}} + \frac{\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}}}{\nu_{\mathrm{v}}} \dot{I}_{\mathrm{v}},$$

where:

$$\dot{\mathcal{L}}_j = c_{j,0} \dot{E}_j + \sum_{i=1}^{n} c_{j,i} \dot{I}_{j,i}.$$

By using the induction relationship (22) and as in the proof of Theorem 2.1, we obtain

$$\dot{\mathcal{L}}_j = c_{j,0} a_j \beta_{\mathrm{v},j} S_j \frac{I_{\mathrm{v}}}{\bar{N}_j} - \sum_{i=1}^{n} \beta_{j,i} I_{j,i}. \tag{23}$$

Thus, the derivative of the function $\mathcal{V}$ becomes:

$$\begin{aligned}
\dot{\mathcal{V}} &= \sum_{j=1}^{m} p_j \left(c_{j,0} a_j \beta_{\mathrm{v},j} S_j \frac{I_{\mathrm{v}}}{\bar{N}_j} - \sum_{i=1}^{n} \beta_{j,i} I_{j,i} \right) \\
&\quad + \left(\sum_{j=1}^{m} a_j (\bar{N}_{\mathrm{v}} - E_{\mathrm{v}} - I_{\mathrm{v}}) \frac{\sum_{i=1}^{n} \beta_{j,i} I_{j,i}}{\bar{N}_j} - (\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}}) E_{\mathrm{v}} \right) \\
&\quad + \frac{\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}}}{\nu_{\mathrm{v}}} (\nu_{\mathrm{v}} E_{\mathrm{v}} - (\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}}) I_{\mathrm{v}}) \\
&= \sum_{j=1}^{m} \left(a_j \frac{\bar{N}_{\mathrm{v}}}{\bar{N}_j} - p_j \right) \sum_{i=1}^{n} \beta_{j,i} I_{j,i} - \sum_{j=1}^{m} a_j (E_{\mathrm{v}} + I_{\mathrm{v}}) \frac{\sum_{i=1}^{n} \beta_{j,i} I_{j,i}}{\bar{N}_j} \\
&\quad + \left(\sum_{j=1}^{m} p_j c_{j,0} a_j \beta_{\mathrm{v},j} \frac{S_j}{\bar{N}_j} - \frac{(\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}})(\mu_{\mathrm{v}} + \delta_{\mathrm{v}})}{\nu_{\mathrm{v}}} \right) I_{\mathrm{v}} \\
&= - \sum_{j=1}^{m} a_j (E_{\mathrm{v}} + I_{\mathrm{v}}) \frac{\sum_{i=1}^{n} \beta_{j,i} I_{j,i}}{\bar{N}_j} \\
&\quad + \left(\sum_{j=1}^{m} c_{j,0} a_j^2 \beta_{\mathrm{v},j} \frac{\bar{N}_{\mathrm{v}}}{\bar{N}_j} \frac{S_j}{\bar{N}_j} - \frac{(\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}})(\mu_{\mathrm{v}} + \delta_{\mathrm{v}})}{\nu_{\mathrm{v}}} \right) I_{\mathrm{v}},
\end{aligned}$$

since $p_j = a_j \dfrac{\bar{N}_{\mathrm{v}}}{\bar{N}_j}$. Hence, we obtain,

$$\begin{aligned}
\dot{\mathcal{V}} &= - \sum_{j=1}^{m} a_j (E_{\mathrm{v}} + I_{\mathrm{v}}) \frac{\sum_{i=1}^{n} \beta_{j,i} I_{j,i}}{\bar{N}_j} \\
&\quad + \frac{(\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}})(\mu_{\mathrm{v}} + \delta_{\mathrm{v}})}{\nu_{\mathrm{v}}} \left(\sum_{j=1}^{m} \mathcal{R}_{0,j}^2 \frac{S_j}{\bar{N}_j} - 1 \right) I_{\mathrm{v}}
\end{aligned}$$

$$\leq -\sum_{j=1}^{m} a_j (E_{\mathrm{v}} + I_{\mathrm{v}}) \frac{\sum_{i=1}^{n} \beta_{j,i} I_{j,i}}{\bar{N}_j}$$
$$+ \frac{(\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}})(\mu_{\mathrm{v}} + \delta_{\mathrm{v}})}{\nu_{\mathrm{v}}} \left(\mathcal{R}_0^2(m) - 1 \right) I_{\mathrm{v}}, \quad \text{since} \quad S_j \leq \bar{N}_j, \quad \forall j.$$
$$\leq 0 \quad \text{whenever} \quad \mathcal{R}_0^2(m) \leq 1. \tag{24}$$

It is not difficult to see that the largest invariant set within $\{\dot{\mathcal{V}} = 0\}$ is reduced to the DFE, which is therefore globally asymptotically stable in the compact set Ω thanks to (Bhatia and Szegö 1967, Theorem 3.7.11, p. 346; LaSalle 1968, Theorem 3). Since Ω is an attractive set, it follows that the DFE is globally asymptotically stable in $\mathbb{R}^{m(n+2)+2}$. □

Theorem 3.2 *A unique endemic equilibrium exists for the multi-host Model* (20) *whenever* $\mathcal{R}_0^2(m) > 1$.

Proof The endemic relations of (20) are as follows, for $j = 1, 2, \ldots, m$:

$$E_j = \frac{\alpha_{j,1}}{\nu_j} I_{j,1}^*, \quad I_{j,1}^* = \frac{\alpha_{j,2}}{\gamma_{j,1}} I_{j,2}^*,$$

and for $i = 2, \ldots, n$,

$$I_{j,i-1}^* = \frac{\alpha_{j,i}}{\gamma_{j,i-1}} I_{j,i}^*.$$

Hence, as in (11) for the one host case, we can show that:

$$\sum_{i=1}^{n} \beta_{j,i} I_{j,i}^* = \alpha_{j,1} c_{j,1} I_{j,1}^*. \tag{25}$$

Indeed, the relationship (25) could be shown by expressing all components of the endemic equilibrium in terms of I_{v}^*. From the first equation of (19), taken at the equilibrium, we obtain:

$$S_j^* = \frac{\mu_j \bar{N}_j^2}{\mu_j \bar{N}_j + a_j \beta_{\mathrm{v},j} I_{\mathrm{v}}^*}$$
$$E_j^* = \frac{a_j \beta_{\mathrm{v},j}}{\mu_j + \nu_j} \frac{\mu_j \bar{N}_j^2}{\mu_j \bar{N}_j + a_j \beta_{\mathrm{v},j} I_{\mathrm{v}}^*} \frac{I_{\mathrm{v}}^*}{\bar{N}_j}$$
$$= \frac{a_j \beta_{\mathrm{v},j}}{\mu_j + \nu_j} \frac{\mu_j \bar{N}_j I_{\mathrm{v}}^*}{\mu_j \bar{N}_j + a_j \beta_{\mathrm{v},j} I_{\mathrm{v}}^*}$$
$$I_{j,1}^* = \frac{\nu_j}{\alpha_{j,1}} E_j^*$$
$$= \frac{\nu_j}{\alpha_{j,1}} \frac{a_j \beta_{\mathrm{v},j}}{\mu_j + \nu_j} \frac{\mu_j \bar{N}_j I_{\mathrm{v}}^*}{\mu_j \bar{N}_j + a_j \beta_{\mathrm{v},j} I_{\mathrm{v}}^*}.$$

We can express, similarly, the expressions of $I^*_{j,i}$ in term of I^*_{v} and by summing them up, we obtain (25).

From the equation of vectors in (19) at the equilibrium, we obtain

$$\begin{aligned}
0 &= \left(\bar{N}_{\mathrm{v}} - E^*_{\mathrm{v}} - I^*_{\mathrm{v}}\right)\sum_{j=1}^{m} a_j \frac{\sum_{i=1}^{n}\beta_{j,i} I^*_{j,i}}{\bar{N}_j} - (\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}})E^*_{\mathrm{v}} \\
&= \left(\bar{N}_{\mathrm{v}} - E^*_{\mathrm{v}} - I^*_{\mathrm{v}}\right)\sum_{j=1}^{m} a_j \frac{\alpha_{j,1} c_{j,1} I^*_{j,1}}{\bar{N}_j} - (\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}})E^*_{\mathrm{v}} \\
&= \left(\bar{N}_{\mathrm{v}} - \frac{\mu_{\mathrm{v}} + \delta_{\mathrm{v}}}{\nu_{\mathrm{v}}} I^*_{\mathrm{v}} - I^*_{\mathrm{v}}\right)\sum_{j=1}^{m} a_j \frac{\alpha_{j,1} c_{j,1}}{\bar{N}_j}\frac{\nu_j}{\alpha_{j,1}}\frac{a_j\beta_{\mathrm{v},j}}{\mu_j + \nu_j}\frac{\mu_j \bar{N}_j I^*_{\mathrm{v}}}{\mu_j \bar{N}_j + a_j\beta_{\mathrm{v},j} I^*_{\mathrm{v}}} \\
&\quad - \frac{(\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}})(\mu_{\mathrm{v}} + \delta_{\mathrm{v}})}{\nu_{\mathrm{v}}} I^*_{\mathrm{v}} \\
&= \left(\bar{N}_{\mathrm{v}} - \frac{\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}}}{\nu_{\mathrm{v}}} I^*_{\mathrm{v}}\right)\sum_{j=1}^{m} a_j c_{j,1}\frac{\nu_j a_j \beta_{\mathrm{v},j}}{\mu_j + \nu_j}\frac{\mu_j I^*_{\mathrm{v}}}{\mu_j \bar{N}_j + a_j\beta_{\mathrm{v},j} I^*_{\mathrm{v}}} \\
&\quad - \frac{(\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}})(\mu_{\mathrm{v}} + \delta_{\mathrm{v}})}{\nu_{\mathrm{v}}} I^*_{\mathrm{v}}.
\end{aligned} \tag{26}$$

Since the equilibrium is endemic $I^*_{\mathrm{v}} > 0$, Eq. (26) is satisfied if, and only if:

$$\begin{aligned}
0 &= \left(\bar{N}_{\mathrm{v}} - \frac{\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}}}{\nu_{\mathrm{v}}} I^*_{\mathrm{v}}\right)\sum_{j=1}^{m} c_{j,1}\frac{a_j^2\beta_{\mathrm{v},j}}{\mu_j + \nu_j}\frac{\nu_j \nu_{\mathrm{v}}}{(\mu_{\mathrm{v}} + \nu_{\mathrm{v}} + \delta_{\mathrm{v}})(\mu_{\mathrm{v}} + \delta_{\mathrm{v}})} \\
&\quad \frac{\mu_j}{\mu_j \bar{N}_j + a_j\beta_{\mathrm{v},j} I^*_{\mathrm{v}}} - 1 \\
&:= f\left(I^*_{\mathrm{v}}\right).
\end{aligned} \tag{27}$$

The function $f(I^*_{\mathrm{v}})$ is decreasing and $f(0) = \mathcal{R}_0^2(m) - 1$. Moreover, $f(\frac{\nu_{\mathrm{v}}\bar{N}_{\mathrm{v}}}{\mu_{\mathrm{v}}+\nu_{\mathrm{v}}+\delta_{\mathrm{v}}}) = -1 < 0$. Hence, the equation $f(I^*_{\mathrm{v}})$ has a unique positive root in $(0, \bar{N}_{\mathrm{v}})$ if, and only if $f(0) > 0$, that is, whenever $\mathcal{R}_0^2(m) > 1$.

Since the other components S^*_j, E^*_j, $I^*_{i,j}$, for $j = 1, 2, \ldots, m$ and $i = 1, 2, \ldots, n$, are uniquely expressed in terms of I^*_{v}, we conclude that there is a unique endemic equilibrium in $\mathrm{Int}(\Omega)$ whenever $\mathcal{R}_0^2(m) > 1$. □

Theorem 3.3 *The endemic equilibrium is globally asymptotically stable on* $\mathbb{R}^{m(n+2)+2}$.

Proof We consider the following Lyapunov function

$$\begin{aligned}
\mathcal{V} = &\sum_{j=1}^{m} A_{j0}\left(S_j - S^*_j \log S_j + E_j - E^*_j \log E_j\right) \\
&+ \sum_{j=1}^{m}\left(\sum_{i=1}^{n} A_{j,i}\left(I_{j,i} - I^*_{j,i}\log I_{j,i}\right)\right)
\end{aligned}$$

$$+ V_1\left(S_\mathrm{v} - S_\mathrm{v}^* \log S_\mathrm{v}\right) + V_1\left(E_\mathrm{v} - E_\mathrm{v}^* \log E_\mathrm{v}\right)$$
$$+ V_2\left(I_\mathrm{v} - I_\mathrm{v}^* \log I_\mathrm{v}\right) \tag{28}$$

where the coefficients V_1, V_2, A_{j0}, A_{ji}, for $i = 1, 2, \ldots, n$ and $j = 1, 2, \ldots, m$ are positive to be determined later. The function $\mathcal{V}$ is thus positive-definite.

The derivative of $\mathcal{V}$ along trajectories is:

$$\begin{aligned}
\dot{\mathcal{V}} = {} & V_1 \sum_{j=1}^{m} \left(a_j \frac{S_\mathrm{v}^*}{\bar{N}_j} \sum_{i=1}^{n} \beta_{j,i} I_{j,i}^* \left(2 - \frac{S_\mathrm{v}^*}{S_\mathrm{v}} - \frac{S_\mathrm{v}}{S_\mathrm{v}^*} \frac{I_{j,i}}{I_{j,i}^*} \frac{E_\mathrm{v}^*}{E_\mathrm{v}} \right) + a_j S_\mathrm{v}^* \frac{\sum_{i=1}^{n} \beta_{j,i} I_{j,i}}{\bar{N}_j} \right) \\
& + V_1 \mathcal{A}_\mathrm{v} - \left(V_1(\mu_\mathrm{v} + \nu_\mathrm{v} + \delta_\mathrm{v}) - V_2 \nu_\mathrm{v} \right) E_\mathrm{v} - V_2(\mu_\mathrm{v} + \delta_\mathrm{v}) I_\mathrm{v} + V_2 \nu_\mathrm{v} E_\mathrm{v}^* \\
& - V_2 \nu_\mathrm{v} E_\mathrm{v}^* \frac{E_\mathrm{v}}{E_\mathrm{v}^*} \frac{I_\mathrm{v}^*}{I_\mathrm{v}} + \sum_{j=1}^{m} \left(A_{j0} \mathcal{A}_{hj} + A_{j0} a_j \beta_{\mathrm{v},j} S_j^* \frac{I_\mathrm{v}^*}{\bar{N}_j} \left(2 - \frac{S_j^*}{S_j} - \frac{S_j}{S_j^*} \frac{I_\mathrm{v}}{I_\mathrm{v}^*} \frac{E_j^*}{E_j} \right) \right. \\
& \left. + A_{j0} \left(a_j \beta_{\mathrm{v},j} S_j^* \frac{I_\mathrm{v}}{\bar{N}_j} \right) - A_{j0}(\mu_j + \nu_j) E_j + A_{j1} \left(\nu_j E_j - \alpha_{j,1} I_{j,1} \right) \right. \\
& \left. - A_{j1} \nu_j E_j \left(\frac{I_{j,1}^*}{I_{j,1}} \right) + A_{j1} \alpha_{j,1} I_{j,1}^* + \sum_{i=2}^{n} \left(A_{ji} \left(\gamma_{j,i-1} I_{j,i-1} - \alpha_{j,i} I_{j,i} \right) \right. \right. \\
& \left. \left. - A_{ji} \gamma_{j,i-1} I_{j,i-1} \left(\frac{I_{j,i}^*}{I_{j,i}} \right) + A_{ji} \alpha_{j,i} I_{j,i}^* \right) \right),
\end{aligned} \tag{29}$$

where $\mathcal{A}_\mathrm{v} = (\mu_\mathrm{v} + \delta_\mathrm{v}) S_\mathrm{v}^* \left(2 - \frac{S_\mathrm{v}^*}{S_\mathrm{v}} - \frac{S_\mathrm{v}}{S_\mathrm{v}^*} \right)$ and $\mathcal{A}_{hj} = \mu_\mathrm{h} S_j^* \left(2 - \frac{S_j^*}{S_j} - \frac{S_j}{S_j^*} \right)$.

We choose the coefficients A_{ji} and V_2 in a similar fashion as in the one host case, that is,

$$\begin{aligned}
V_2 &= \frac{\mu_\mathrm{v} + \nu_\mathrm{v} + \delta_\mathrm{v}}{\nu_\mathrm{v}} V_1 \\
A_{j0}(\mu_j + \nu_j) E_j^* &= A_{j0} a_j \beta_{\mathrm{v},j} S_j^* \frac{I_\mathrm{v}^*}{N_j} \\
&= V_1 a_j \frac{S_\mathrm{v}^*}{\bar{N}_j} \left(\sum_{i=1}^{n} \beta_{j,i} I_{j,i}^* \right) \quad \text{for all} \quad j = 1, 2, \ldots, m,
\end{aligned} \tag{30}$$

and

$$A_{j1} = \frac{1}{\nu_j E_j^*} V_1 a_j \frac{S_\mathrm{v}^*}{\bar{N}_j} \left(\sum_{i=1}^{n} \beta_{j,i} I_{j,i}^* \right) \quad \text{for all} \quad j = 1, 2, \ldots, m.$$

Also,

$$A_{ji} = \frac{\sum_{k=i}^{n} \beta_{j,k} I_{j,k}^*}{\alpha_{j,i} I_{j,i}^*} V_1 a_j \beta_{j,v} \frac{S_\mathrm{v}^*}{\bar{N}_j} \quad \text{for all} \quad 2 \le i \le n-1, 1 \le j \le m,$$

and

$$\alpha_{j,n}A_{jn} = V_1 a_j \beta_{j,v}\frac{S_{\mathrm{v}}^*}{\bar{N}_j} \quad \text{for all} \quad 1 \le j \le m.$$

We obtain

$$\begin{aligned}\dot{\mathcal{V}} = V_1 \sum_{j=1}^{m} a_j \beta_{j,1} \frac{S_{\mathrm{v}}^*}{\bar{N}_j} I_{j,1}^* \left(6 - \frac{S_{\mathrm{v}}^*}{S_{\mathrm{v}}} - \frac{S_{\mathrm{v}}}{S_{\mathrm{v}}^*}\frac{I_{j,1}}{I_{j,1}^*}\frac{E_{\mathrm{v}}^*}{E_{\mathrm{v}}} - \frac{E_{\mathrm{v}}}{E_{\mathrm{v}}^*}\frac{I_{\mathrm{v}}^*}{I_{\mathrm{v}}} - \frac{S_j^*}{S_j}\right.\\ \left. - \frac{S_j}{S_j^*}\frac{I_{\mathrm{v}}}{I_{\mathrm{v}}^*}\frac{E_j^*}{E_j} - \frac{E_j}{E_j^*}\frac{I_{j,1}^*}{I_{j,1}}\right) + V_1 \sum_{j=1}^{m} a_j \frac{S_{\mathrm{v}}^*}{\bar{N}_j} \sum_{i=2}^{n} \beta_{j,i} I_{j,i}^*\\ \left(5 + i - \frac{S_{\mathrm{v}}^*}{S_{\mathrm{v}}} - \frac{S_{\mathrm{v}}}{S_{\mathrm{v}}^*}\frac{I_{j,i}}{I_{j,i}^*}\frac{E_{\mathrm{v}}^*}{E_{\mathrm{v}}} - \frac{E_{\mathrm{v}}}{E_{\mathrm{v}}^*}\frac{I_{\mathrm{v}}^*}{I_{\mathrm{v}}} - \frac{S_j^*}{S_j} - \frac{S_j}{S_j^*}\frac{I_{\mathrm{v}}}{I_{\mathrm{v}}^*}\frac{E_j^*}{E_j}\right.\\ \left. - \frac{E_j}{E_j^*}\frac{I_{j,1}^*}{I_{j,1}} - \sum_{k=2}^{i} \frac{I_{j,k-1}}{I_{j,k-1}^*}\frac{I_{j,k}^*}{I_{j,k}}\right) + \mathcal{A}_{\mathrm{v}} + V_1 \sum_{j=1}^{m} \mathcal{A}_{hj}.\end{aligned}$$

The function $\dot{\mathcal{V}}$ is therefore negative-definite for any positive value of V_1, particularly for $V_1 = 1$. Since $\mathcal{V}$ is positive-definite, the global stability of the interior endemic equilibrium on $\mathbb{R}^{m(n+2)+2}$ follows from the Lyapunov stability theorem. □

The result of global stability of the endemic equilibrium generalizes (Cruz-Pacheco et al. 2012a, b) for an arbitrary number of hosts. Indeed, in Cruz-Pacheco et al. (2012a), Cruz-Pacheco et al. considered and SIR-SI with two hosts in their model capturing Chagas' disease. The authors also considered the case where one host (humans) has two stages of infections, namely acute and chronic. Our model considers an arbitrary number of hosts and hosts' infectious stages. Similarly, Cruz-Pacheco et al. (2012b) considered a model describing NWV dynamics with an arbitrary number of hosts, but the result of global stability has been done only for the two hosts case.

Remark 3.2 We have proved that the multi-host model (20) satisfies the sharp-threshold property, that is, the disease dies out if $\mathcal{R}_0^2(m) \le 1$ and persists otherwise. However, $\mathcal{R}_0^2(m) = \sum_{j=1}^{m} \mathcal{R}_{0,j}^2$, where $\mathcal{R}_{0,j}^2$ is the basic reproduction number in the presence of Host j only. Hence, $\mathcal{R}_0^2(m) \le 1 \Longrightarrow \mathcal{R}_{0,j}^2 \le 1$ for all $j = 1, 2, \ldots, m$. Thus, the eradication of the multi-host disease in one host is subject to the eradication of the disease from all hosts. However, the multi-host system could have a basic reproduction number greater than one even though the reproduction number of each isolated host-vector is less than one (see Figs. 2, 3). This phenomenon has been observed in childhood diseases in a metapopulation setting where the disease could persist globally even if the disease dies out locally (at patch level) (Lloyd and May 1996). For zoonoses, this phenomenon could be seen as follows: even if the infectious hosts and/or vectors in a single host-vector system are small enough to prevent persistence of the disease (that is $\mathcal{R}_{0,j}^2 \le 1$), the connection of a new host species may lead to a new infectious transmission route, which in turn could trigger new infectious

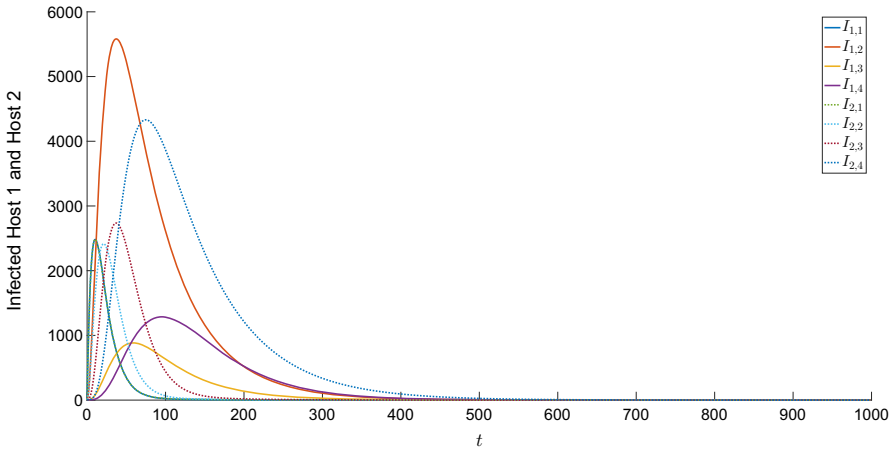

Fig. 2 (Color figure online) Simulation of two separate systems with one host each and four stages of infection. The $\mathcal{R}^2_{0,j}$ values are 0.52 for the host 1 population and 0.66 for the host 2 population. As expected, the infected populations go to zero

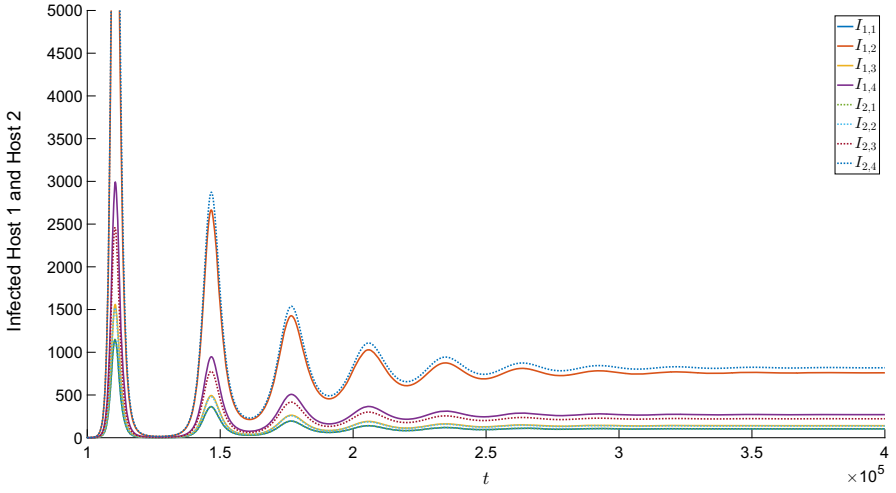

Fig. 3 (Color figure online) Simulation of a two host system where there are four stages of infection for each host. The $\mathcal{R}^2_{0,j}$ values are 0.52 for the host 1 population and 0.66 for the host 2 population, giving a combined system $\mathcal{R}^2_0(2) = 1.18$. The infected populations eventually go to the nonzero endemic equilibrium

hosts or vectors. This, therefore, may make $\mathcal{R}^2_0(m) > 1$, and thus the disease will persist for the two host-vector system.

In the next subsection, we provide a set of simulations that illustrate our analytical results and showcase that control strategies that target host-vector system in isolation may not be sufficient to eradicate VBZ.

3.3 Simulations

To illustrate the previous theoretical results, we run a set of simulations of a two host system with four stages of infection, that is $m = 2$ and $n = 4$. Unless otherwise stated, the baseline parameters for the simulations are those given in Table 3. For these values, the overall basic reproduction number is $\mathcal{R}_0^2(2) = 1.18$. Figure 3 shows that the trajectories of the solutions representing the infected populations for all stages for both hosts tend to a nonzero endemic equilibrium as predicted by Theorems 3.2 and 3.3. However, if the two hosts are considered separately, the system behaves as two isolated host-vector systems, with the same parameter values, the corresponding basic reproduction numbers are $\mathcal{R}_{0,1}^2 = 0.52$ and $\mathcal{R}_{0,2}^2 = 0.66$ and therefore the disease dies out from both hosts and the vector population as portrayed in Fig. 2 and stated in Theorem 2.1. Figures 2 and 3 exemplify also Remark 3.2, in which it is noted that controlling VBZ in each species in isolation, does not lead necessarily a complete control of VBZ. A coordinated effort in all host species and vector population is needed to steer the overall basic reproduction number below unity, and therefore eliminating the disease in all host species and vectors. Also, the simulations capture that host

Table 3 Parameters used in the simulations

Parameter	Host 1	Host 2
Λ_j	100	100
$\beta_{\mathrm{v},j}$	0.2	0.2
μ_j	1/28,875	1/28,875
ν_j	1/15	1/15
a_j	0.37	0.37
$\beta_{j,1}$	0.2	0.2
$\beta_{j,2}$	0.3	0.3
$\beta_{j,3}$	0.4	0.4
$\beta_{j,4}$	0.5	0.5
$\eta_{j,1}$	0.01	0.01
$\eta_{j,2}$	0.007	0.007
$\eta_{j,3}$	0.004	0.004
$\eta_{j,4}$	0.001	0.001
$\gamma_{j,1}$	0.125	0.125
$\gamma_{j,2}$	0.01	0.0875
$\gamma_{j,3}$	0.05	0.05
$\gamma_{j,4}$	0.025	0.0125
Λ_{v}	10,000	
μ_{v}	1/15	
δ_{v}	0.001	
ν_{v}	0.25	
$\mathcal{R}_{0,j}^2$	0.52	0.66
$\mathcal{R}_0^2(2)$	1.18	

diversity increases the prevalence of the disease, leading to the "amplification effect." By choosing the values of βs lower than those given in Table 3 will lead to the overall basic reproduction number $\mathcal{R}_0^2(2) \leq 1$ and the simulations show that all infected population tend to zero as proved in Theorem 3.1. Alternatively, if the parameters are chosen such that $\mathcal{R}_{0,1}^2 > 1$ and $\mathcal{R}_{0,2}^2 > 1$, the trajectories of the isolated host-vector systems converge to an endemic equilibria as expected (Theorem 2.2). We decided not to displays the figures of these cases.

4 Conclusion and Discussions

Mathematical models of zoonoses have often been investigated when the transmission is direct, in which case, these models could be seen as multi-group models that well investigated in the literature. However, most zoonotic pathogens are spread through arthropod vectors such as mosquitoes, flies, fleas, ticks that transmit pathogens across species.

We considered a general host-vector SEIR-SEI model where a host's infectious state is subdivided into n classes, each of which has a different infectiosity to the vector. We derived the basic reproduction number $\mathcal{R}_0^2$. Our results show that the dynamics of the model is robust and is tied to $\mathcal{R}_0^2$. The disease-free equilibrium is globally asymptotically stable (GAS) if $\mathcal{R}_0^2 \leq 1$ and unstable otherwise (Theorem 2.1). A unique endemic equilibrium exists and is GAS whenever $\mathcal{R}_0^2 > 1$ (Theorem 2.2).

We extended the host-vector-staged progression model to m host species interacting with an arthropod vector to obtain a general framework in modeling a class of zoonoses. The basic reproduction number $\mathcal{R}_0^2(m)$ for the system with m hosts is derived and happened to be the sum of basic reproduction number of the host-vector systems when a unique host is interacting with the arthropod vector, that is, $\mathcal{R}_{0,j}^2$, for $j = 1, 2, \ldots, m$. We proved that the system with m hosts remains robust as its asymptotic behavior is solely determined by $\mathcal{R}_0^2(m)$. The disease dies out from all hosts if $\mathcal{R}_0^2(m) \leq 1$ (Theorem 3.1) and persists in all hosts if $\mathcal{R}_0^2(m) > 1$. Moreover, we proved that a unique endemic equilibrium exists and is globally asymptotically stable if $\mathcal{R}_0^2(m)$ is above unity (Theorems 3.2 and 3.3).

However, the disease might persist in all hosts, that is, the global $\mathcal{R}_0^2(m)$ could be greater than unity even if $\mathcal{R}_{0,j}^2 < 1$ for $j = 1, 2 \ldots, m$, that is, for all hosts. Therefore, host heterogeneity favors the spread of the infection, and thus causes the so-called "amplification effect" (Miller and Huppert 2013) as opposed to the "dilution effect" (Miller and Huppert 2013; Ostfeld and Keesing 2012; Salkeld et al. 2013), for which the increase in host diversity could potentially decrease or drive out the pathogens (Ostfeld and Keesing 2012). As $\mathcal{R}_0^2(m) = \sum_{j=1}^{m} \mathcal{R}_{0,j}^2$ and considering the GAS of the unique endemic equilibrium, we deduced that the persistence of the disease in one host-vector system is sufficient to ensure persistence in all hosts. The overall mitigation or elimination of vector-borne zoonoses requires control strategies that bring the basic reproduction numbers in all hosts significantly below unity, and therefore reduces the disease burden in all hosts. Hence, this paper encompasses and reinforces the One Health (Centers for Disease Control and Prevention 2017) concept,

for which human, animal and ecosystem health are ecologically interconnected (One Health 2017).

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