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PROGRAMA DE MAESTRÍA Y DOCTORADO EN CIENCIAS MATEMÁTICAS Y
DE LA ESPECIALIZACIÓN EN ESTADÍSTICA APLICADA

# DYNAMIC MODELS IN MACROPARASITE COMMUNITIES AND THEIR HOSTS

TESIS
QUE PARA OPTAR POR EL GRADO DE:
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# Contents

# Introduction

Currently, there are different types of host-parasite models, this is because many important diseases for both humans and animals that affect the abundance of individuals in the population arise from parasitism, which makes parasitism a fundamental characteristic of life. Diseases caused by the presence of parasites in an organism are infections that can be caused by intragenomic parasites or genetic parasites, microparasites, macroparasites or metazoans organism [1–3]. In this thesis we focus on studying macroparasites, of which, a majority of them belong to the helminth and arthropod groups, that include flukes, tapeworms, nematodes, lice, fleas and ticks. Table 1 shows some examples of helminthic macroparasites that can be studied with the models presented in this thesis.

| Class | Parasite | Infection |
|---|---|---|
| Filarial nematodes | *Brugia malayi* | Lymphatic filariasis |
| | *Dracunculus medinensis* | Dracunculiasis |
| | *Onchocerca volvulus* | Onchocerciasis |
| | *Wuchereria bancrofti* | Lymphatic filariasis |
| Flukes | *Fasciola hepatica* | Fascioliasis |
| | *Opisthorchis sinensis* | Clonorchiasis |
| | *Paragonimus westermani* | Paragonimiasis |
| | *Schistosoma haematobium* | Urogenital schistosomiasis |
| | *Schistosoma japonicum* | Intestinal schistosomiasis |
| Intestinal nematodes | *Ancylostoma duodenale* | Ancylostomiasis |
| | *Ascaris lumbricoides* | Ascariasis |
| | *Enterobius vermicularis* | Enterobiasis |
| | *Necator americanus* | Necatoriasis |
| | *Trichuris trichiura* | Trichuriasis |
| Tapeworms | *Echinococcus granulosus* | Cystic echinococcosis |
| | *Taenia saginata* | Taeniasis |
| | *Taenia solium* | Cysticercosis |

TABLE 1: The major helminth infections of humans (see [3]).

An important characteristic of macroparasites is that these types of organisms tend to have much longer generation times than microparasites, and usually have complex life cycles that may involve more than one host species. This because macroparasites undergo different metamorphosis during its life cycle. Each of these metamorphosis occur within individuals of at least one specific host species, which they colonize after spending a period in free life or, alternatively, by the trophic or non-trophic interaction of an individual of this host species with a host of another species infected with the parasite in its previous life-stage, until reaching its adult stage where typically a macroparasite is able to reproduce. Also, even if reproduction of parasites occurs within the definitive or final host, the eggs produced by the adult parasites are expelled from the hosts, so the larvae are born in free life, and may undergo different metamorphoses before colonizing a host for the first time. Figure 1 shows an example of a macroparasite life cycle with these characteristics.

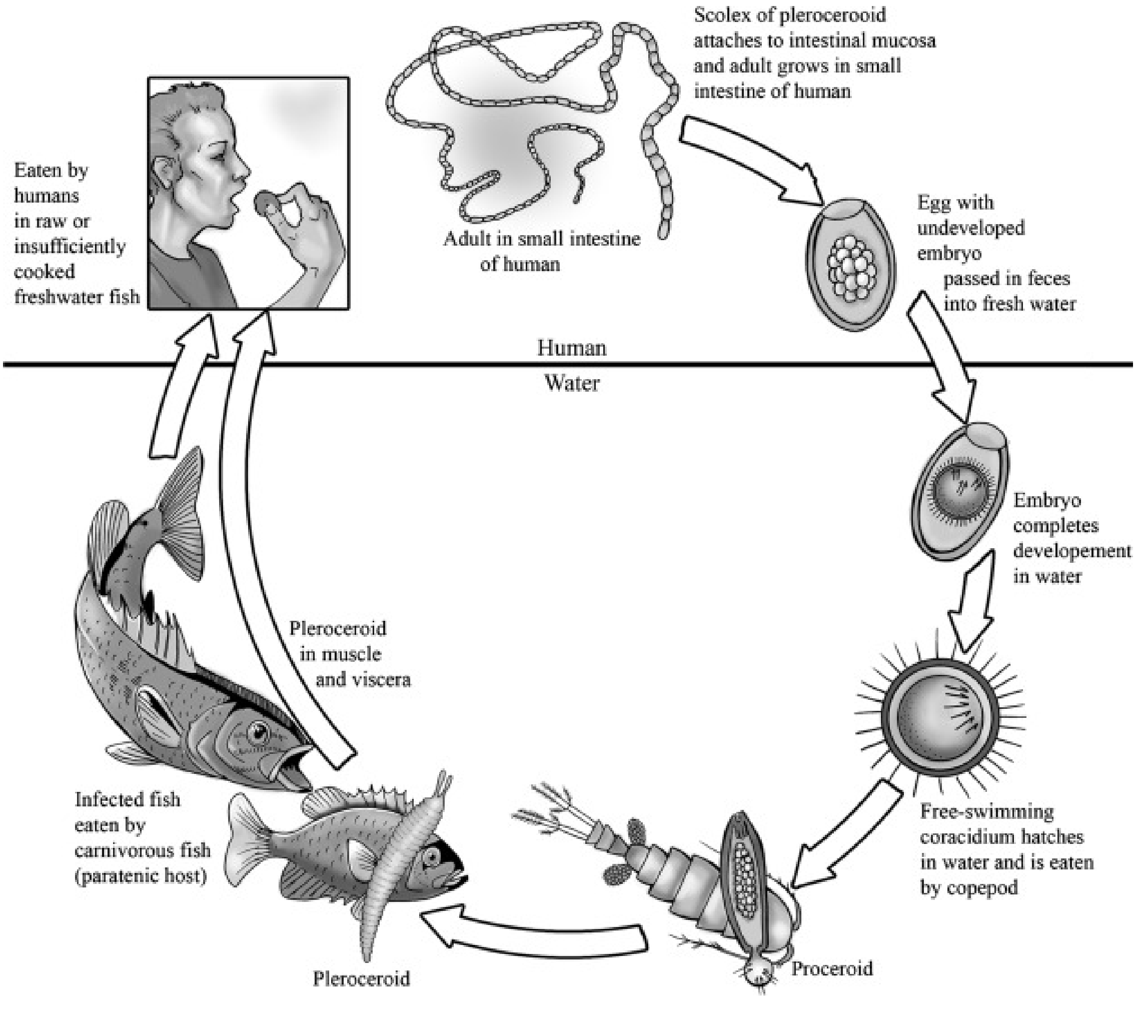


FIGURE 1: *Diphyllobothrium latum* life cycle. Credit: Image by Gino Barzizza [4].

Since the parasite larvae are born in free life, and the parasitic transmission does not necessarily occur by the direct contact between hosts, there are free-living stages in the life cycle of any macroparasite species. However, for the stages that occur within a host, we define the parasite at each stage as a specialist if it can inhabit individuals of a single host species during that stage, and generalist if that metamorphosis occurs within individuals of at least two different host species.

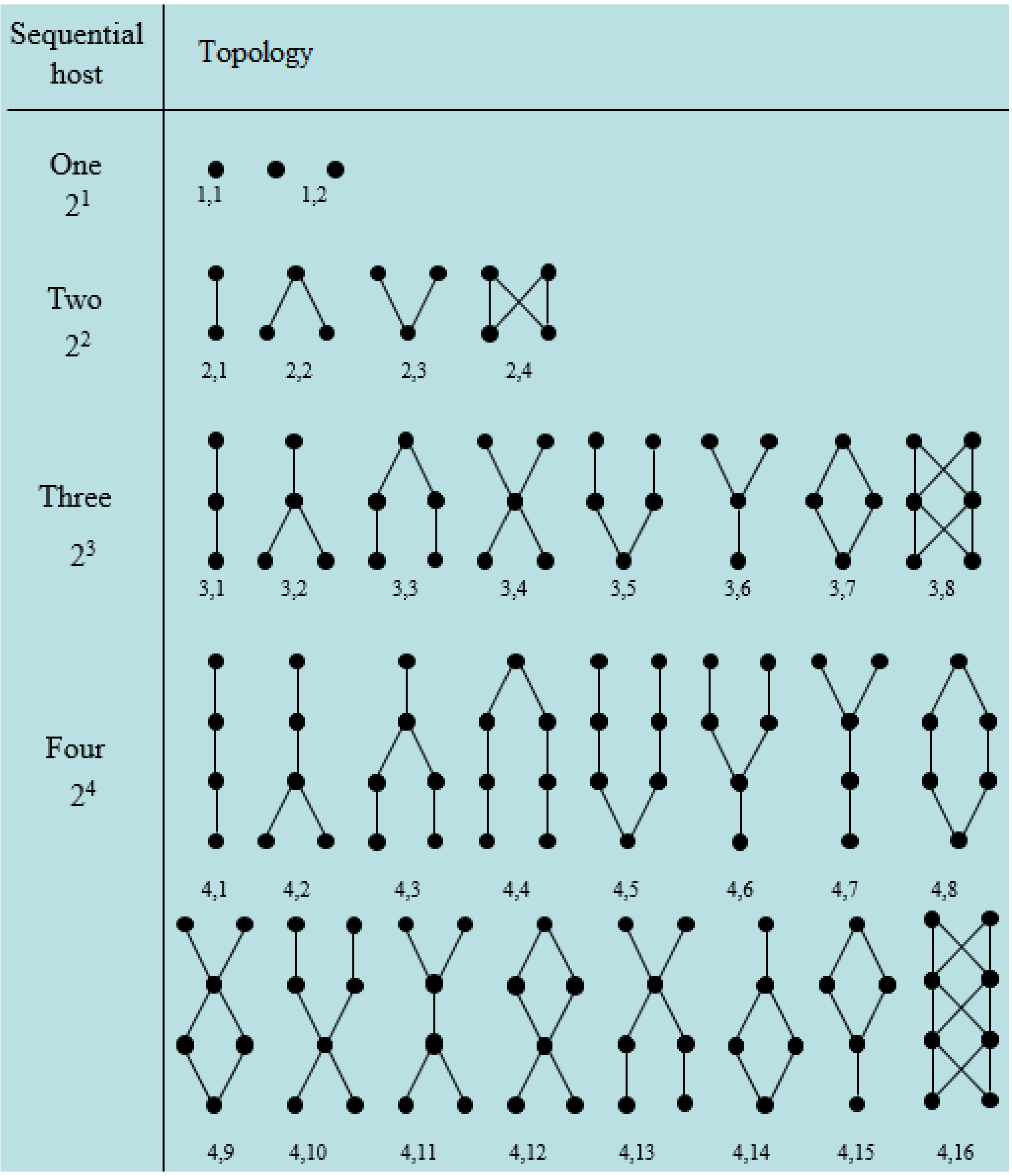


FIGURE 2: Representation of the topologies of macroparasite's transmission networks. The number of sequential hosts is indicated with the number of levels, and at each level there are two conditions; be a specialist parasite (one node) or generalist parasite (two nodes). Credit: Image courtesy of Dr. Pablo A. Marquet (personal communication).

Figure 2 shows a representation of all possible topologies of the transmission networks generated when considering the host species and the different parasitic stages that occur within these communities. These topologies can also be viewed as the food webs of a macroparasite species [5], since the food web of a parasite is formed by all the hosts in which it enters, where the parasite feeds on the nutrients provided by each host.

As we mentioned before, many macroparasite species colonize more than one host species during its life cycle, as in the example shown in Figure 1, however, many of the host-parasite models are limited to studying communities with a single host species that do not allow analyzing communities with parasite species that have a complex life cycle. Therefore, throughout this thesis, we study host-parasite models based on the interactions of host and parasite populations structured by its transmission networks, this because the objectives of this thesis are: develop a general model that allows studying the population dynamics of a community with multiple host species that may or may not interact with each other, and a parasite species that passes different stages of its life cycle in individuals of the different host species in the system, by considering the possible parasitic transmission networks in the system. We also want to give concepts or results that allow the study of this model, in order to determine sufficient conditions for an equilibrium point with a biological meaning to exist, where none of the populations becomes extinct. In particular, we want to give generalizations of the concepts of basic reproductive number and threshold host density for multi-host-parasite models, based on the topology of the parasite transmission network in the system. Finally, we want to see if it is possible to mathematically determine the possible topologies of the transmission network of a parasite species if initially only the number of host species in the system and the number of stages of the parasite life cycle that occur within the hosts are known.

To study the interactions of host and macroparasite populations, it is important to clarify that many of the host-parasite models are epidemiological models, focused on how the infection spreads over the individuals of the host population and determine the necessary conditions for the infection to disappear or persist without extinguishing the community of hosts. However, macroparasites are parasites visible to the naked eye, allowing counting the number of macroparasites on a single host, so we can study the spread of these parasites in a host community instead of the spread of infection caused by these organisms, in order to determine under what conditions the host and parasitic populations remain in the environment. This because, unlike what happens with other types of parasites, the infectivity of the hosts depends on the number of macroparasites it contains. The models addressed in this dissertation allow simulating the dynamics of a community of hosts, assuming that in the absence of parasitism might grow in an uncontrolled way in the environment in which they are found, that is, these models are used to determine the necessary conditions to regulate the growth of populations of different host species through an infection caused by a parasite species.

One of the first population models for the dynamics between a host community and a parasite population was studied and formulated in 1978 by Robert M. May and Roy M. Anderson in their work *Regulation and Stability of Host-Parasite Population Interactions* [6, 7]. This model is introduced in the first chapter of this thesis, and is used as a reference for the analysis of different models generated from it, developed and studied by Andrew P. Dobson, M. G. Roberts and Peter J. Hudson during the years 1992-1995 (see [8–10]).

From the previous models, in Chapter 2 we propose a new model for a multi-host system by considering different types of parasitic transmission between the host species and the topologies of the possible parasitic transmission networks in the system.

In the third chapter, we also define the basic reproductive number for population models of multi-host-parasite systems [11], and present a way to calculate its value, in particular, we determined an expression for the value of $R_0$ in the multi-host model we proposed. Additionally, we present a definition of the threshold host density for host-parasite models with a single host species previously considered [11], similar to the definition of this concept in epidemiological models, and give a generalization of this concept that we use in the multi-host model proposed in this thesis.

The last chapter shows an analysis of the models corresponding to the possible transmission networks for macroparasitic organisms in a community with a fixed number of host species, generated by taking particular conditions for the parameters in the multi-host model that we study in this thesis. We also present some simulation for the host and parasitic populations in these systems, to show how the growth of the host populations is regulated and, at the same time, how it regulates the growth of the parasitic population.

Finally, we present some conclusions of the results obtained from this study, and we add appendices with the necessary concepts to justify some of the hypotheses and results used in the development and study of the models presented.

# Chapter 1

# Single Host Macroparasite Models

This thesis comprises the situation in which there is a community of $m$ host species that would grow exponentially in the absence of parasitism, and a parasite species, with $n$ stages in its life cycle, that may regulate the growth of each host species. This chapter presents models showing the basic components of macroparasite systems that we will use as a basis to develop a more sophisticated model for a multi-host community system.

We will first introduce the model for the interactions between a single host and parasite species developed by Anderson and May in 1978 [6, 7], that has been taken as a starting point for the study and development of models for the interactions between a host species and a community of parasitic species. Later, we will present a model for the population dynamics of a host species that interacts with a community of parasitic species, published by Dobson and Roberts in 1995 [8]. This model will help us to introduce a model for the interactions between a host species and a stage-structured parasite species with two stages in its life cycle, developed by Dobson and Hudson in 1992 [9, 10].

## 1.1 Anderson and May Model

This section presents a model for the host-macroparasite interactions developed and studied by Anderson and May [6, 7], and its generalization published by Dobson and Roberts [8].

### 1.1.1 Basic Model

Anderson and May demonstrated with the aid of a simple differential equation model that a parasite species could regulate the size of a host population that would otherwise grow exponentially. To introduce this model, it is necessary to make some additional biological assumptions. The first is that the basic model is for a parasite species that may or may not reproduce directly within its definitive or final host, however, the parasite begins its life cycle in free life, possibly after offspring were expelled from the host where they were produced. This implies that the parasite has transmission stages such as eggs, spores or cysts that, as a developmental necessity, leave the host, that is, it has a free-living stage in its life cycle, before entering a host and reach its adult stage. This type of parasite life cycle is shown by helminth and arthropod species. The second is that the parasites present an aggregated distribution among the individuals of the host population, best described by the negative binomial distribution [12, 13]. Finally, we assume that parasite load induce an increase in the mortality rate of the host species and thus may regulate its growth. Figure 1.1 shows a schematic representation of the interaction between the host and the parasite, based on these biological assumptions.

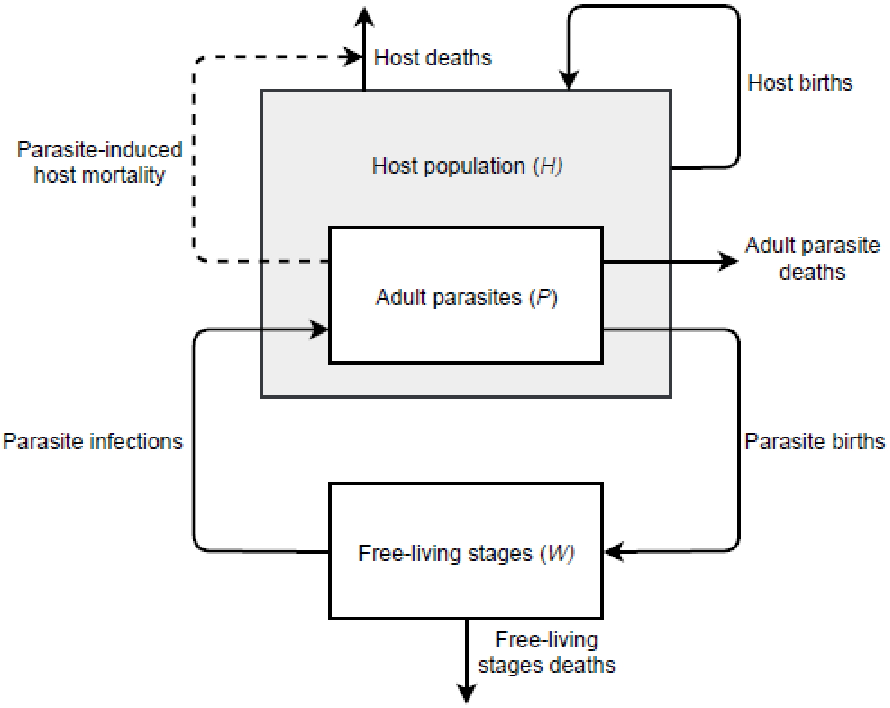


Figure 1.1: Schematic representation of a direct one-host, one-parasite life-cycle, illustrating the different birth, death and transmission rates [14].

To develop the equations, we define $H(t)$, $P(t)$ and $W(t)$ as the size of the host, adult parasite within the host and free-living larvae populations, respectively, at time $t$. In addition, we use the parameters shown in Table 1.1.

| Parameter | Description |
|---|---|
| $a$ | Instantaneous birth rate of host. |
| $b$ | Instantaneous intrinsic death rate of host due to natural causes. |
| $\alpha$ | Instantaneous additional death rate of host induced by the parasite load. |
| $\lambda$ | Instantaneous hatching rate of parasite eggs. |
| $\mu$ | Instantaneous death rate of adult parasites within the hosts. |
| $\gamma$ | Instantaneous death rate of parasite eggs and larvae in free life. |
| $\beta$ | Instantaneous rate of ingestion of parasite infective stages. |

Table 1.1: Description of the population parameters used in the A&M model.

**Host population dynamics**

We assume that the net growth of the host population is determined by the natural intrinsic rate of increase in the absence of parasitism minus the host death rate induced by parasites.

Based on the previous assumption, and considering that the host population would grow exponentially in the absence of parasitism, it follows that if we exclude the limitations to the growth of the host population imposed by the environment, the natural intrinsic rate of increase in the absence of parasites depends only on the difference between the host reproductive rate $a$ and the natural host mortality rate $b$ (deaths due to all causes except the parasite). Therefore, the natural intrinsic rate of increase in the absence of parasites is given by $(a - b)H(t)$.

On the other hand, this model assumes that the parasites have a negative binomial distribution within the host population, so if we define $p(i)$ as the probability that a given host contains $i$ parasites, then the probability generating function for this distribution is given by

$$G(m, k, z) = \left[1 + \frac{m}{k}(1 - z)\right]^{-k},$$

were $m$ and $k$ are the mean of the distribution and a parameter that varies inversely with the the degree of aggregation of parasites within the host population respectively (see Appendix A). So, assuming that the increase in the host death rate induced by the parasites is linearly proportional to the number of parasites that a host harbors, the total rate of loss of hosts at time $t$ induced by the parasites is

$$\alpha H(t)\sum_{i=0}^{\infty} ip(i) = \alpha H(t)m = \alpha H(t)\frac{P(t)}{H(t)} = \alpha P(t),$$

this because, the mean of a probability distribution is $\sum_{i=0}^{\infty} ip(i) = m$, that in this model is the expected number of parasites per host, given by $P(t)/H(t)$.

**Free-living parasite population dynamics**

Next, we analyze the growth of the number of individuals in free life, that will help us to develop an equation for the dynamics of the population size of adult parasites. Let $W(t)$ be the number of larvae in free life at time $t$. Note that because parasite offspring leave the host, parasite reproduction does not increase its density within the host. Therefore, all newborn parasites, given by $\lambda P(t)$, belong to the free-living stage. Now, the number of larvae in free life is reduced by the number of individuals who die in free life $\gamma W(t)$, further, free-living parasites are removed by attaching to a host, given by $\beta W(t)H(t)$. Therefore, the growth of the population in the free-living stage is:

$$\frac{dW}{dt} = \lambda P - \gamma W - \beta W H$$

(for parameters definitions see Table 1.1).

**Adult parasite population dynamics**

To develop the equation of the adult parasite population size it is necessary to consider the proportion of free-living parasites that reach the adult stage, the intrinsic natural mortality of the parasites within the host, the number of adult parasite deaths due to death of the host they are attached to, both natural and parasite-induced.

Based on the previous discussion of the larvae population in free life $W(t)$, and assuming that every parasite ingested by a host reaches its adult stage, the number of free-living parasites that reach the adult stage is given by $\beta W(t)H(t)$. Moreover, we can approximate the number of new adult parasites by the product of the number of new individuals in the free-living stage $\lambda P(t)$ and the transmission factor (see [15]), given by the ratio of the rate of free-living parasites ingested by the host $\beta H(t)$ and the rate of decrease in the population of parasites in free life $\gamma + \beta H(t)$, that is, $\beta\lambda P(t)H(t)/(\gamma + \beta H)$. This approximation can also be obtained from the value of $\beta W(t)H(t)$ if we consider $W(t)$ as the expected value of the proportion of parasites in free life that survives the necessary time to enter a host, given by the product of the number of offspring $\lambda P(t)$ and its life expectancy outside a host $1/(\gamma + \beta H(t))$.

The above implies that only the equations for $dP/dt$ and $dH/dt$ are needed to model the dynamics of the size of the host and parasite total populations.

The intrinsic natural mortality of the parasites within the host is $\mu P(t)$, whereas the number of deaths of adult parasites due to the natural death of the hosts is

$$bH(t)\sum_{i=0}^{\infty} ip(i) = bH(t)m = bH(t)\frac{P(t)}{H(t)} = bP(t).$$

Finally, the number of adult parasite deaths due to the death of hosts induced by parasites is given by

$$\begin{aligned}\alpha H(t)\sum_{i=0}^{\infty} i^2p(i) &= \alpha H(t)\mathrm{E}\left(i^2\right) = \alpha H(t)\left[\mathrm{E}\left(i^2\right) - m^2 + m^2\right]\\ &= \alpha H(t)\left(\sigma^2 + m^2\right) = \alpha H(t)\left(\frac{k+1}{k}m^2 + m\right)\\ &= \alpha H(t)\left[\frac{k+1}{k}\left(\frac{P(t)}{H(t)}\right)^2 + \frac{P(t)}{H(t)}\right]\\ &= \alpha\frac{k+1}{k}\frac{P(t)^2}{H(t)} + \alpha P(t),\end{aligned}$$

since the per capita host loss rate induced by the parasites is $\alpha i$, and, by definition, the second moment of the distribution is

$$\mathrm{E}\left(i^2\right) = \sum_{i=0}^{\infty} i^2p(i).$$

This expression may be estimated as $\sigma^2 + m^2$, with $m = P(t)/H(t)$ and $\sigma^2 = (k+1)m^2/k + m - m^2$ (see Appendix A), implying that

$$\mathrm{E}\left(i^2\right) = \frac{k+1}{k}m^2 + m = \frac{k+1}{k}\left(\frac{P(t)}{H(t)}\right)^2 + \frac{P(t)}{H(t)}.$$

With the previous analysis Anderson and May showed that it is possible to model the dynamics of the host population size $H(t)$ and the total population size of the parasite within the hosts $P(t)$ using the differential equations

$$\begin{aligned}\frac{dH}{dt} &= (a-b)H - \alpha P,\\ \frac{dP}{dt} &= \frac{\lambda PH}{H+H_0} - (b+\mu+\alpha)P - \frac{\alpha(1+k)}{k}\frac{P^2}{H}.\end{aligned} \tag{1.1}$$

### 1.1.2 Multi-Parasite Model

A generalized version of the A&M model (1.1), that considers a host species that would grow exponentially in the absence of parasitism, and a community of $n$ parasite species that may regulate this growth, was developed by Dobson and Roberts [8]. Those authors assume that the distribution of the individuals of the $n$ species of parasites among the host population is described by a negative multinomial distribution [16], and thus each parasitic species is distributed in the host population through a negative binomial distribution. Also, it is necessary to assume that adult parasites of each species may induce an increase in the mortality rate of the host species to regulate their growth, and each parasite species has a free-living stage in its life cycle.

To develop the equations that model the dynamics in this system, define $H(t)$, $P_j(t)$ and $W_j(t)$ as the sizes of the host, $j$-th parasite species within the host and the $j$-th free-living parasite species populations, respectively, at time $t$. In this case it is not necessary to specify the generating function for the negative multinomial distribution of the parasites since we only need to assume that if the mean of the negative binomial distribution of each parasite species $P_j$ is $m_j$, then the variances of each parasitic species $P_j$ is given by $m_j(1 + m_j/k_j)$, and the covariance between the species $P_i$ and $P_j$ is given as $m_i m_j/l_{ij}$, for all $i, j = 1, \ldots, n$, $i \neq j$.

The parameters for the model are presented in Table 1.2.

| Parameter | Description |
|---|---|
| $a$ | Instantaneous birth rate of host. |
| $b$ | Instantaneous intrinsic death rate of host due to natural causes. |
| $\alpha_j$ | Instantaneous additional death rate of host due to parasite load of the $P_j$ population. |
| $\lambda_j$ | Instantaneous birth rate of the $j$-th parasite species eggs. |
| $\mu_i$ | Death rate of the $j$-th parasites species within the hosts. |
| $\gamma_j$ | Instantaneous death rate of the $j$-th free-living parasites. |
| $\beta_j$ | Instantaneous rate of ingestion of the $W_j$ population. |
| $k_j$ | Parameter of the negative binomial distribution of the adult parasite population $P_j$. |
| $l_{ij}$ | Parameter of the negative multinomial distribution of all the parasite species related to the covariance of $P_i$ and $P_j$. |

TABLE 1.2: Description of the parameters used in the Dobson and Roberts model.

As in the previous model, the dynamics of the size of the host population is determined by the natural rate of increase in the absence of parasitism minus the host death rate induced by each of the parasitic species:

$$\sum_{j=1}^{n}\left(\alpha_j H(t)\sum_{i=0}^{\infty} i p_j(i)\right) = \sum_{j=1}^{n}\alpha_j H(t) m_j = \sum_{j=1}^{n}\alpha_j H(t)\frac{P_j(t)}{H(t)} = \sum_{j=1}^{n}\alpha_j P_j(t),$$

where $p_j(i)$ is the probability that a given host contains $i$ parasites of the $j$-th parasitic species and no parasites of any other species.

To develop the equations to model the dynamics of the population of the each parasite species in its free-living stage we follow the analysis conducted for the previous model. Therefore, the growth of the population $W_j$ is

$$\frac{dW_j}{dt} = \lambda_j P_j - \gamma_j W_j - \beta_j W_j H,$$

for each parasite species $j = 1, \ldots, n$.

From the above, we have that the number of new individuals in each population $P_j$ is given by $\lambda_j P_j H/(H + H_{0j})$, with $H_{0j} = \gamma_j/\beta_j$. To further simplify the model, Dobson and Roberts assumed that $H_{0i} = H_{0j} = H_0$ for all $1 \le i, j \le n$.

Similarly, it can be shown that the intrinsic natural mortality of the parasites species within the host are $\mu_j P_j(t)$, and the number of deaths of the individuals of $P_j$ due to the natural death of the hosts is given by $bP_j(t)$, for each $j = 1, \ldots, n$.

Finally, we must consider the number of adult parasite deaths of the $j$-th parasitic species induced by host deaths from infection. To do this, we will separately analyze the deaths of individuals in the adult parasite population of a focal species $j$, due to its own the effect on the host they are attached to, and the effect of other parasite species $i$ within the same host.

of the $j$-th species due to the death of hosts induced by parasites of the same species, and the deaths of individuals in the $P_j$ population due to the death of the hosts induced by the parasites of the $P_i$ population.

As in the previous model, the number of parasite deaths in the $P_j$ population due to the death of hosts induced by parasites of the same species is given by

$$\alpha_j H(t)\sum_{i=0}^{\infty} i^2 p_j(i) = \alpha_j H(t)\left(\frac{k+1}{k} m_j^2 + m_j\right) = \frac{\alpha_j (k_j+1)}{k_j}\frac{P_j(t)^2}{H(t)} + \alpha_j P_j(t).$$

Now, if we define $p_{i,j}(k,r)$ as the probability that a given host contains $k$ parasites of the $i$-th parasitic species, $r$ parasites of the $j$-th parasitic species, the number of parasite deaths of species $i$ due to host deaths induced by parasites of species $j$, can be calculated as

$$\begin{aligned}
\alpha_i H(t) \sum_{k,r=0}^{\infty} k r p_{i,j}(k,r) &= \alpha_i H(t) \left( \sum_{k,r=0}^{\infty} k r p_{i,j}(k,r) - m_i m_j + m_i m_j \right) \\
&= \alpha_i H(t) \left[ \mathrm{E}(P_i P_j) - \mathrm{E}(P_i)\mathrm{E}(P_j) + m_i m_j \right] \\
&= \alpha_i H(t) \left[ \mathrm{Cov}(P_i, P_j) + m_i m_j \right] \\
&= \frac{\alpha_i (l_{ij}+1)}{l_{ij}} H(t) m_i m_j \\
&= \frac{\alpha_i (l_{ij}+1)}{l_{ij}} \frac{P_i(t) P_j(t)}{H(t)}.
\end{aligned}$$

As conclusion, Dobson and Roberts showed that the following system of ordinary differential equations models the dynamics of the host population and $n$ populations of different parasitic species

$$\begin{aligned}
\frac{dH}{dt} &= (a-b)H - \sum_{i=1}^{n} \alpha_i P_i, \\
\frac{dP_j}{dt} &= \frac{\lambda_j P_j H}{H + H_0} - (b + \mu_j + \alpha_j) P_j - \frac{\alpha_j (1 + k_j)}{k_j} \frac{P_j^2}{H} - \sum_{\substack{i=1 \\ i \neq j}}^{n} \frac{\alpha_i (1 + l_{ij})}{l_{ij}} \frac{P_i P_j}{H}.
\end{aligned} \tag{1.2}$$

## 1.2 Dobson and Hudson Model

In 1992, Andrew P. Dobson and Peter J. Hudson developed and studied a model for the dynamics of a community of *Trichostrongylus tenuis* in a red grouse population [9, 10], that turned out to be a modification of the $n$-dimensional version of the Anderson and May model (1.2) published a couple of years later, described in the previous section. The purpose of this model was to simulate the dynamics of a host population that would grow exponentially in the absence of parasitism, and a parasitic population that has three stages in its life cycle, the first in free life, by the hypothesis that offspring does not remain within the host, while the second and third stage of its life cycle occur within a single individual of the host population, first as a larva and then as an adult parasite.

Another biological assumption here is that, unlike in the previous models, parasites, in addition to inducing an increase in the mortality rate of individuals in the host population, also reduce the fertility rate of hosts, thus regulating its growth. In addition, typically the arrested larvae (parasites in its pre-adult stage inside the hosts) have a significantly lower effect on the growth rate of hosts than adult parasites, so, to simplify the model, we assume that the parasite larvae inside the hosts does not have a perceptible effect on the survival or fertility of the host and that its intrinsic mortality rate is extremely low. Finally, we assume that the distribution of the individuals of each stage of the parasite life cycle among the individuals of the host population is described by a negative multinomial distribution.

Figure 1.2 shows a schematic representation of the interactions between the host species and parasites at each stage of its life cycle, based on previous biological assumptions.

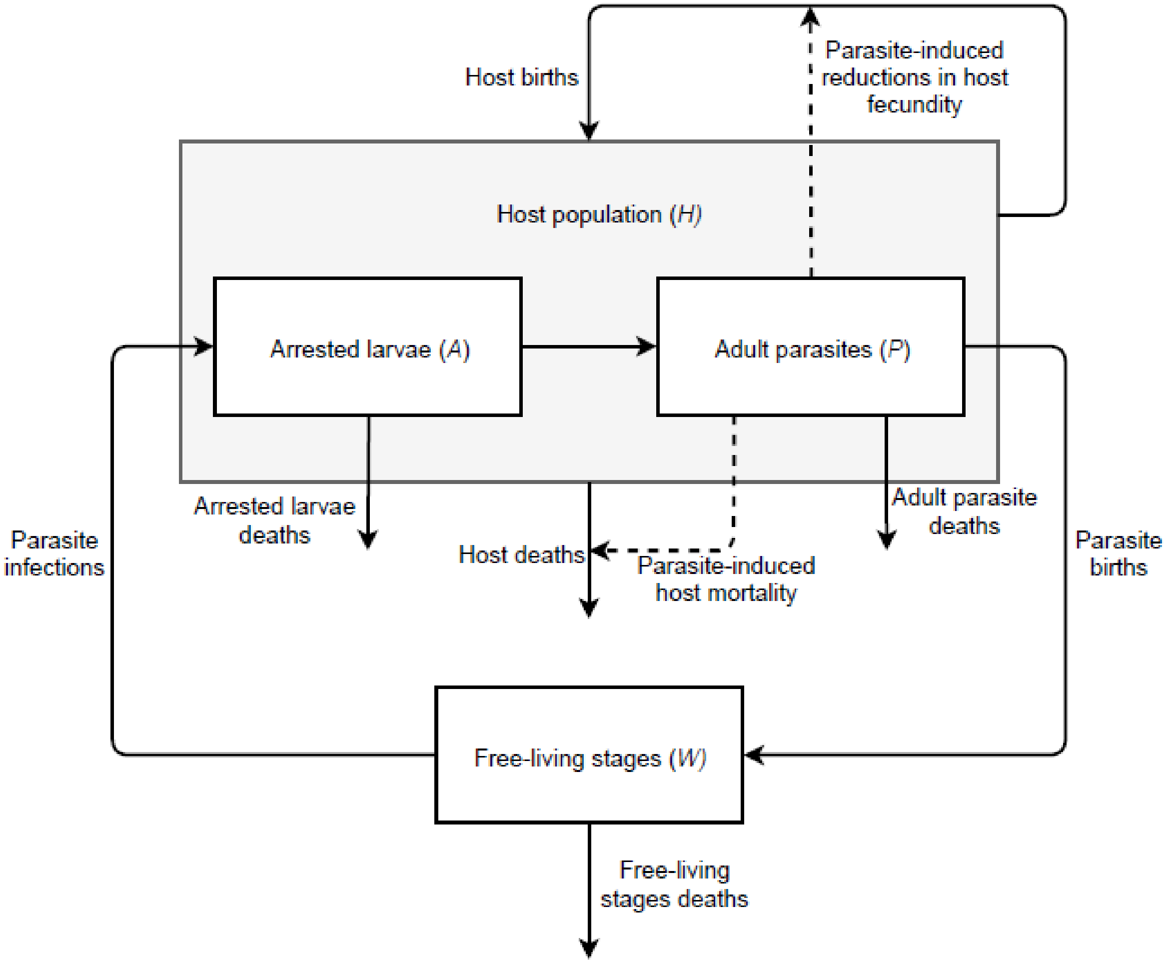


FIGURE 1.2: Schematic representation of the life cycle of the parasite illustrating the different birth, death and transmission rates occurring in the life cycle [10].

From the above it follows that this system of equations can be obtained from (1.2), used by Dobson and Roberts for the multi-parasite version of the Anderson and May model, studying the parasite populations at different stages of its life cycle similarly to the populations of different parasitic species in (1.2), and modifying the equations of each of these based on their relations with the populations of the other stages. To start doing this, we define $H(t)$, $A(t)$, $P(t)$ and $W(t)$ as the size of the host, arrested larvae within the host, adult parasite within the host, and free-living parasite (eggs and larvae) populations, respectively, at time $t$.

The parameters used in this models are shown in Table 1.3.

| Parameter | Description |
|---|---|
| $a$ | Instantaneous birth rate of host. |
| $b$ | Instantaneous intrinsic death rate of host due to natural causes. |
| $\alpha$ | Instantaneous death rate of host induced by adult parasite load. |
| $\delta$ | Instantaneous reduction in host fertility due to adult parasite load. |
| $\lambda$ | Instantaneous birth rate of parasite eggs. |
| $\mu_A$ | Instantaneous death rate of arrested parasite. |
| $\mu_P$ | Instantaneous death rate of adult parasite. |
| $\gamma$ | Instantaneous death rate of eggs and larvae in free life. |
| $\beta$ | Instantaneous rate of ingestion of parasite infective stages. |
| $\theta$ | Rate at wich arrested larvae develop into adult parasite. |
| $k$ | Parameter of the negative binomial distribution of the adult parasite population within the hosts. |

TABLE 1.3: Description of the parameters used in the Dobson and Hudson model.

From the equation for the dynamics of the host population (1.2), and considering the hypothesis that the population of arrested larvae does not affect the mortality and fertility rates of the hosts, while adult parasites do affect both rates, the dynamics of the host population is governed by the equation

$$\frac{dH}{dt} = (a-b)H - (\alpha+\delta)\,P,$$

because the dynamics of the host population can be determined by subtracting the total decrease in the number of newborn hosts induced by adult parasites to the dynamics of the host population used in the model (1.2), given by

$$\delta H(t)\sum_{i=0}^{\infty} i p_2(i) = \delta H(t) m_P = \delta H(t)\frac{P(t)}{H(t)} = \delta P(t),$$

with $p_2(i)$ define as the probability that a given host contains $i$ adult parasites and $m_2$ as the expected value of $p_2(i)$, which is $P(t)/H(t)$.

Before analyzing the population dynamics of the different stages of the parasite's life cycle, it is important to clarify that one assumption in this model is that there is no intraspecific competition in the system, that is, parasites of the same species does not attack each other. Thus, the competition between parasites at different stages of its life cycle occurs indirectly, by exploiting the resources that the individuals at each parasitic stage need to survive within the same host [17, 18]. Since competition occurs indirectly, there is no correlation between the populations of the different stages of the parasite's life cycle within the hosts, implying that the covariance between the variables corresponding to these populations is zero [19]. Therefore, assuming that the covariance between $A(t)$ and $P(t)$ is given by $m_A m_P / l_{AP}$, with $m_A m_P > 0$, we pose that, necessarily, $l_{AP} \to \infty$, so $(1 + l_{AP})/l_{AP} = 1$.

For the dynamics of parasite larvae within the host, in addition to the terms related to the number of new larvae arrested and the number of natural and induced deaths of individuals in this population, it is necessary to consider the number of larvae that become adult parasites within the same host, which can be calculated as

$$\theta H(t) \sum_{i=0}^{\infty} i p_1(i) = \theta H(t) m_A = \theta H(t) \frac{A(t)}{H(t)} = \theta A(t),$$

considering $p_1(i)$ to be the probability that a given host contains $i$ parasite larvae, and $m_A$ as the expected value of $p_1(i)$, given by $A(t)/H(t)$.

From the above, and based on the hypothesis that only adult parasites affect the number of host deaths, the equation that models the dynamics of the arrested larvae population is

$$\frac{dA}{dt} = \frac{\lambda P H}{H + H_0} - (\mu_A + b + \theta)\, A - \alpha \frac{PA}{H}.$$

Finally, the dynamics of the adult parasites population can be modeled by modifying the equation for the population of parasitic species used in (1.2). One hypothesis in this model is that the hosts ingest only larvae that enter in the arrested larvae population $A(t)$, implying that the number of new adult parasites is given only by the number of arrested larvae that become adult parasites, given by $\theta A(t)$. Thus, the growth in the number of individuals in the population of adult parasites is governed by the equation

$$\frac{dP}{dt} = \theta A - (\mu_P + b + \alpha)\, P - \alpha \left(\frac{k+1}{k}\right) \frac{P^2}{H}.$$

The previous analysis is a way to justify the model published by Dobson and Hudson, which consists of the following system of ordinary differential equations

$$\begin{aligned} \frac{dH}{dt} &= (a-b)H - (\alpha+\delta)\, P, \\ \frac{dA}{dt} &= \frac{\lambda P H}{H + H_0} - (\mu_A + b + \theta)\, A - \alpha \frac{PA}{H}, \\ \frac{dP}{dt} &= \theta A - (\mu_P + b + \alpha)\, P - \alpha \left(\frac{k+1}{k}\right) \frac{P^2}{H}, \end{aligned} \tag{1.3}$$

where $H(t)$, $A(t)$ and $P(t)$ are the number of the hosts, arrested larvae and adult parasites in the system at time $t$, respectively, used to model the dynamics of a host population and the population of a single parasite species that undergoes two transformations within the same host after a period of free life.

# Chapter 2

# Modeling Multi-Host Communities

This chapter introduces a model for the population dynamics of a community with $m$ host species that interacts with a single parasite that undergoes $n$ different stages within different hosts.

We consider several biological assumptions for this system. The first is that, as in the previous models, there is a host population that would grow exponentially in the absence of parasitism (there is no carrying capacity in the system), and the distribution of the parasites at different stages of its life cycle within the individuals of a host population is described by a negative multinomial distribution, for each host species. We also assume that individuals of any parasitic stage can affect the mortality and fertility rates of host populations, and, as in the previous models, the parasitic species produce offspring in its definitive or final host, but the offspring is released into the environment, so there is at least one free-living stage in the life cycle of the parasite.

Before continuing, it is necessary to determine the type of parasitic transmission that may occur between different hosts in relation to the developmental stages experienced by parasites. For this, we consider only the transmission where the parasite advances to the next developmental stage when passing from one host to another, that is, we ignore transmission events occurring at the same stage of the parasite's life cycle. This is because transmissions at the same stage of the parasite's life cycle can be considered as transmissions at different parasitic stages through a vector, possibly transport hosts (hosts that carries parasites between successive hosts; while in the transport host, the parasite does not develop further [20]). Another reason to ignore these types of transmissions is that one of the objectives in developing this model is to analyze the population dynamics of the system in relation to the parasitic transmission network, which does not relate hosts at the same level of the parasite's life cycle.

We consider that vector transmission between two hosts can be modeled similarly to the transmission given by the direct interaction of both hosts. Therefore, we consider three types of parasitic transmission: the first is by predation, if the hosts are trophically related. The second occurs when two hosts of different species, not trophically related, have contact, either physical (direct) or indirect through a vector, this is because, it is not necessary to consider contact transmissions between hosts of the same species, since we can simply assume that the parasite metamorphosis occurs within the same host. The last type of parasitic transmission occurs when a parasite leaves a host and remains for a period of time in free life until it colonizes another host. However, the transmission of parasites in the $j$-th stage of its life cycle can be by physical interaction between hosts (direct) or transmissions that depend on a period of free life (indirect), but not both, this for all $j = 1, \dots, n$.

Next, to introduce the equations of this model for a parasite with $n$ stages in its life cycle within the individuals of a community with $m$ host species, we define $H_i(t)$ as the number of hosts of the $i$-th species at time $t$, $W_{j-1}(t)$ as the number of parasites in free life that will reach the $j$-th stage of their life cycle when introduced into a host at time $t$, and $P_{ij}(t)$ as the size of the parasite population at the $j$-th stage of its life cycle within the hosts of the $i$-th species at time $t$, for all $i = 1, \dots, m$ and $j = 1, \dots, n$. With this notation, the transition of parasites between the different stages of its life cycle is given as in Figure 2.1.

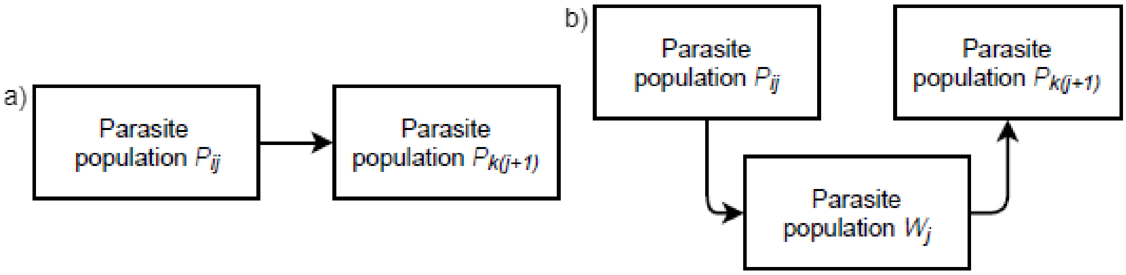


FIGURE 2.1: Schematic representation of the possible types of transmission of parasite in the $j$-th stage of its life cycle, direct (a) and indirect (b), from an individual of the $i$-th host species to an individual of the $k$-th host species, that allow transmitted parasites to reach the next departmental stage of its life cycle.

Parameters needed to model the dynamics of this system are presented in Table 2.1.

| Parameter | Description |
|---|---|
| $a_i$ | Instantaneous birth rate of individuals of the $i$-th species of hosts. |
| $b_i$ | Instantaneous intrinsic death rate of individuals of the $i$-th species of hosts due to natural causes. |
| $\alpha_{ij}$ | Instantaneous death rate of the individuals of the $i$-th species of hosts due to $j$-th stage parasite load. |
| $\delta_{ij}$ | Instantaneous reduction in the fecundity of the individuals in the $i$-th host population due to $j$-th stage parasite load. |
| $\eta_{ir}$ | Increase in the growth of the individuals of the $r$-th host species due predation upon individuals of the $i$-th host species. |
| $\omega_{ir}$ | Instantaneous death rate of the individuals of the $i$-th host species due to predation by a single individual of the $r$-th host species. |
| $\lambda$ | Instantaneous birth rate of parasite eggs. |
| $\epsilon_{ij}$ | Rate at which the parasites in the $j$-th stage of their life cycle leave a host of the $i$-th species. |
| $\gamma_j$ | Instantaneous death rate of the free-living parasites in the $W_j$ population. |
| $\beta_{ij}$ | Instantaneous rate of ingestion of free-living parasites parasites of population $W_j$ by an individual from the host population belonging to the $i$-th species. |
| $\mu_{ij}$ | Instantaneous death rate of parasites in the $j$-th stage of their life cycle within a host of the population $H_i$. |
| $\theta_{ir}^{j}$ | Rate at which the parasites in $j$-th stage of its life cycle reach the stage $j+1$ when transmitted directly from population $H_i$ to population $H_r$. |
| $k_{ij}$ | Parameter of the negative binomial distribution of the parasite population $P_{ij}$ within the individuals of the host population $H_i$. |

Table 2.1: Description of the parameters used in this model.

Regarding Table 2.1, it is important to clarify that $\omega_{ir} \neq 0$ implies $\eta_{ri} = 0$, because there is no increase in the growth rate of the prey population. Also, $\eta_{ii} = \omega_{ii} = 0$ for all $i = 1, \ldots, m$, because, although it is possible that some host species, not all, may be regulated by another host species in the absence of parasitism, we assume that there is not predation among individuals of the same host species. In addition, since not all host species can be regulated by another host species in the absence of parasitism, there are $i, r \in \{1, \ldots, m\}$ such that $\eta_{ir} = \omega_{ri} = 0$, that is, $H_i$ and $H_r$ are not trophically related.

Since the parasitic transmission in the system is caused by predation, non-trophic interaction of hosts or due to the ingestion of a parasite in free life, to simplify the model we assume that if there are $i \in \{1, \dots, m\}$, $j \in \{1, \dots, n\}$ such that $\epsilon_{ij} > 0$, then $\theta^j_{rs} = \omega_{ir} = 0$ for all $r, s \in \{1, \dots, m\}$. Also, if there are $r, s \in \{1, \dots, m\}$, $j \in \{1, \dots, n\}$ such that $\theta^j_{rs} > 0$, then $\omega_{sr} = \epsilon_{ij} = 0$ for all $i = 1, \dots, m$. Finally, if there are $r, s \in \{1, \dots, m\}$ such that $\omega_{rs} > 0$, then $\omega_{sr} = \theta^j_{sr} = \beta_{sj} = 0$ for all $j = 1, \dots, n$. In other words, to simplify the model we consider that all parasitic transmission between two consecutive parasite stages are restricted to one and only one type of parasitic transmission (direct or indirect, see Figure 2.1), and if the $s$-th host species preys on the $r$-th host species, then there is no parasitic transmission from individuals in $H_s$ to individuals in $H_r$ at any parasitic stage.

The last assumption in this model related to the parameters in Table 2.1 is that if there are $r, s \in \{1, \dots, m\}$ such that $\beta_{r(j-1)} \neq 0$ or $\theta^j_{sr} \neq 0$, then $\epsilon_{rj} \neq 0$ or $\theta^{j+1}_{ri} \neq 0$ for some $1 \leq i \leq m$, respectively, for all $j = 1, \dots, n-1$. This because the parasites should be able to leave any intermediate host (hosts that supports the immature or non-reproductive forms of a parasite [20]) in order to colonize another host species where can be further developed.

Through a similar analysis to that of Dobson and Hudson, and since the effect in the growth rate of the $H_i$ population caused by trophic interaction with individuals of the $H_r$ population is given by $(\eta_{ri} - \omega_{ir})H_iH_r$ for all $i, r \in \{1, \dots, m\}$ [21], we have that the equation that reflects the population size dynamics of each host species is

$$\frac{dH_i}{dt} = (a_i - b_i)H_i + \sum_{\substack{r=1 \\ r \neq i}}^{m} (\eta_{ri} - \omega_{ir})H_iH_r - \sum_{l=1}^{n} (\alpha_{il} + \delta_{il})\, P_{il},$$

for all $i = 1, \dots, m$. Note that the dynamics of each host population is given by the increase in the absence of parasitism minus the decrease in the fecundity of each host and the deaths induced by the parasites in any of its stages.

The dynamics of the population of newborn parasites in free life can be determined in a similar way to the previous models, because the increase in the number of individuals in this population depends on the number of newly born larvae minus the total amount of larvae that enter a host or die in free life. Thus, the dynamics of the $W_0(t)$ population is described by

$$\frac{dW_0}{dt} = \lambda \sum_{r=1}^{m} P_{rn} - \gamma_0 W_0 - \sum_{r=1}^{m} \beta_{r0} H_r W_0. \tag{2.1}$$

Similarly, we can determine the equation for the growth of the population size of free-living parasites in the $j$-th stage of their life cycle as the difference between the number of parasites in this stage that leave a host and the total number of individuals in this population who die in free life or enter a host, given by the following equation:

$$\frac{dW_j}{dt} = \sum_{r=1}^{m} \epsilon_{rj} P_{rj} - \gamma_j W_j - \sum_{r=1}^{m} \beta_{rj} H_r W_j, \tag{2.2}$$

for all $j = 1, \ldots, n$ such that the transmission of parasites in stage $j$ does not occur due to the interaction between hosts.

Since the entry and exit of individuals to the different parasitic stages within the hosts does not occur in the same way, we proceed to analyze these populations separately. First, the increase in the number of newly born larvae or free-living larvae that are introduced for the first time into a host in population $H_i$ is given by the proportion of the transmission factor (see [15]) that considers only the introduction of parasites to the population $H_i$, which, by the same analysis performed in Anderson and May (1.1), can be estimated as $\beta_{i0} H_i W_0^*$, where $W_0^*$ is the equilibrium point of the equation (2.1). Therefore, the number of new individuals in the $P_{i1}$ population is given by

$$\frac{\lambda \beta_{i0} H_i \sum_{r=1}^{m} P_{rn}}{\gamma_0 + \sum_{r=1}^{m} \beta_{r0} H_r},$$

for all $i = 1, \ldots, m$.

On the other hand, the factors that influence the decrease of this population are the parasitic transmission that furthers a developmental stage in the parasites and the death of individuals within the hosts, either by the intrinsic mortality rate of the parasite due to the host or by the deaths of hosts in this population, natural or induced by individuals of the different parasitic stages.

Since there is more than one way in which a parasite can be transmitted between two hosts, although no all types of parasitic transmission can occur, we consider that the parasites can leave this population through any type of parasitic transmission. The restrictions about what types of transmissions can occur in a row, given by the relationships between $\epsilon_{ij}$, $\theta_{rs}^{j}$ and $\omega_{rs}$, will determine the real loss of individuals in the population.

The first transmission that we analyze is when the parasites enter in a free-living stage before colonizing another host. The parasites that leave the $P_{i1}$ population can be modeled with the term

$$\epsilon_{i1} H_i \sum_{k=0}^{\infty} k p_{i1}(k) = \epsilon_{i1} H_i \frac{P_{i1}}{H_i} = \epsilon_{i1} P_{i1},$$

where $p_{i1}(k)$ is the probability that a host in the population $H_i$ contains $k$ parasites in the first stage of their life cycle within a host, and $P_{i1}/H_i$ as the expected value of this probability function.

For the parasitic transmission by any type interaction between hosts (trophic or non-trophic, direct or indirect through a vector), it is necessary to analyze separately the case in which the parasite undergoes a transformation within the same type of host and the case where this transformation occurs when passing to a host of different species. In the same way as was done in Dobson and Hudson (1.3), we can model the case where the parasite does not need to change of host species to reach the next stage of its life cycle with the term

$$\theta_{ii}^{1} H_i \sum_{k=0}^{\infty} k p_{i1}(k) = \theta_{ii}^{1} H_i \frac{P_{i1}}{H_i} = \theta_{ii}^{1} P_{i1},$$

while the case in which parasitic metamorphosis depends on switching to a different species of hosts is modeled using the next term:

$$\theta_{ir}^{1} H_i H_r \sum_{k=0}^{\infty} k p_{i1}(k) = \theta_{ir}^{1} H_i H_r \frac{P_{i1}}{H_i} = \theta_{ir}^{1} H_r P_{i1},$$

for all $r \in \{1, \ldots, m\}$, $r \neq i$.

To model parasite deaths, either intrinsic, within a given host, or extrinsic, that is caused by host death (natural or parasite-induced), it is sufficient to note that it is possible to calculate the number of dead individuals in the parasitic population in the same way as in the Dobson and Roberts model (1.2), assuming that the type of competition between parasites within the same host is by exploitation, as in the Dobson and Hudson model (1.3), since all the parasites in the model are individuals of the same parasitic species. Therefore, deaths in this population are given by

$$\left(\mu_{i1} + b_i + \alpha_{i1}\right) P_{i1} + \frac{\alpha_{i1}\left(1 + k_{i1}\right)}{k_{i1}} \frac{P_{i1}^2}{H_i} + \sum_{l=2}^{n} \alpha_{il} \frac{P_{i1} P_{il}}{H_i},$$

and then, the dynamics of the population $P_{i1}$ is governed by the equation

$$\begin{aligned}\frac{dP_{i1}}{dt} &= \frac{\lambda\beta_{i0}H_i\sum_{r=1}^{m}P_{rn}}{\gamma_0+\sum_{r=1}^{m}\beta_{r0}H_r} - \left(\mu_{i1}+b_i+\epsilon_{i1}+\alpha_{i1}+\theta_{ii}^{1}+\sum_{\substack{r=1\\r\neq i}}^{m}\theta_{ir}^{1}H_r\right)P_{i1}\\ &\quad - \frac{\alpha_{i1}\left(1+k_{i1}\right)}{k_{i1}}\frac{P_{i1}^{2}}{H_i} - \sum_{l=2}^{n}\alpha_{il}\frac{P_{i1}P_{il}}{H_i},\end{aligned}$$

for all $i=1,\ldots,m$.

Given the hypotheses of this system, the dynamics of the parasite populations at a more developed stage of its life cycle within the same host species is similar to the dynamics of the first stages, except for the number of new parasites in the population. This is because the number of new individuals in the $P_{ij}$ population, with $j>1$, depends on the number of parasites that were at the stage $j-1$ of its life cycle and advanced to the next developmental stage, that could happen either within the same host type in which they were or in a different host species to which they were introduced by any type of parasitic transmissions considered in this model. The number of parasites transmitted when leaving a host and entering another after spending a period of time in free life is given by $\beta_{i(j-1)}H_iW_{j-1}^{*}$, where $W_{j-1}^{*}$ is the equilibrium point of the equation (2.2). Thus, the number of parasites that enter the population $P_{ij}$ due to this type of transmission is

$$\frac{\beta_{i(j-1)}H_i\sum_{r=1}^{m}\epsilon_{r(j-1)}P_{r(j-1)}}{\gamma_{j-1}+\sum_{r=1}^{m}\beta_{r(j-1)}H_r}.$$

On the other hand, the number of new parasites in $P_{ij}$ given by the interaction (trophic or non-trophic) of the $H_i$ population with other host species populations is

$$\sum_{\substack{r=1\\r\neq i}}^{m}\theta_{ri}^{j-1}H_rH_i\sum_{k=0}^{\infty}kp_{r(j-1)}(k)=\sum_{\substack{r=1\\r\neq i}}^{m}\theta_{ri}^{j-1}H_rH_i\frac{P_{r(j-1)}}{H_r}=\sum_{\substack{r=1\\r\neq i}}^{m}\theta_{ri}^{j-1}H_iP_{r(j-1)},$$

while the number of parasites that reach the $j$-th stage of its life cycle while remaining at the same host species is

$$\theta_{ii}^{j-1}H_i\sum_{k=0}^{\infty}kp_{i(j-1)}(k)=\theta_{ii}^{j-1}H_i\frac{P_{i(j-1)}}{H_i}=\theta_{ii}^{j-1}P_{i(j-1)}.$$

Therefore, the number of new individuals in the $P_{ij}$ population is given by

$$\frac{\beta_{i(j-1)} H_i \sum_{r=1}^{m} \epsilon_{r(j-1)} P_{r(j-1)}}{\gamma_{j-1} + \sum_{r=1}^{m} \beta_{r(j-1)} H_r} + \theta_{ii}^{j-1} P_{i(j-1)} + \sum_{\substack{r=1\\ r\neq i}}^{m} \theta_{ri}^{j-1} H_r P_{r(j-1)},$$

for all $j = 2, \ldots, n$.

Since the number of parasites that leave the $P_{ij}$ population is similarly found for all $j = 1, \ldots, n-1$, using the same analysis done to determine how many parasites leave the $P_{i1}$ population, and changing the parameters to those corresponding to stages $j = 2, \ldots, n-1$ of the parasite's life cycle, the dynamics of the $P_{ij}$ population is given by the equation

$$\begin{aligned} \frac{dP_{ij}}{dt} = {} & \frac{\beta_{i(j-1)} H_i \sum_{r=1}^{m} \epsilon_{r(j-1)} P_{r(j-1)}}{\gamma_{j-1} + \sum_{r=1}^{m} \beta_{r(j-1)} H_r} + \theta_{ii}^{j-1} P_{i(j-1)} + \sum_{\substack{r=1\\ r\neq i}}^{m} \theta_{ri}^{j-1} H_i P_{r(j-1)} \\ & - \left( \mu_{ij} + b_i + \epsilon_{ij} + \alpha_{ij} + \theta_{ii}^{j} + \sum_{\substack{r=1\\ r\neq i}}^{m} \theta_{ir}^{j} H_r \right) P_{ij} - \frac{\alpha_{ij}\left(1 + k_{ij}\right)}{k_{ij}} \frac{P_{ij}^2}{H_i} \\ & - \sum_{\substack{l=1\\ l\neq j}}^{n} \alpha_{il} \frac{P_{ij} P_{il}}{H_i}, \end{aligned}$$

for all $i = 1, \ldots, m$.

Finally, since adult parasites do not leave their final host, the equations of the $P_{in}$ populations do not show loss of individuals due to parasitic transmissions. Only the number adult parasites deaths

$$\left(\mu_{in} + b_i + \alpha_{in}\right) P_{in}$$

decreases the size of the $P_{in}$ population. Thus, the equation that reflects the dynamics of the adult parasites population $P_{in}$ is

$$\begin{aligned} \frac{dP_{in}}{dt} = {} & \frac{\beta_{i(n-1)} H_i \sum_{r=1}^{m} \epsilon_{r(n-1)} P_{r(n-1)}}{\gamma_{n-1} + \sum_{r=1}^{m} \beta_{r(n-1)} H_r} + \theta_{ii}^{n-1} P_{i(n-1)} + \sum_{\substack{r=1\\ r\neq i}}^{m} \theta_{ri}^{n-1} H_i P_{r(n-1)} \\ & - \left(\mu_{in} + b_i + \alpha_{in}\right) P_{in} - \frac{\alpha_{in}\left(1 + k_{in}\right)}{k_{in}} \frac{P_{in}^2}{H_i} - \sum_{l=1}^{n-1} \alpha_{il} \frac{P_{in} P_{il}}{H_i}, \end{aligned}$$

for all $i = 1, \ldots, m$.

Based on the previous analysis, it is possible to model the dynamics of the host populations and the populations of the different parasitic stages inside individuals of each host species with the following system of ordinary differential equations:

$$
\begin{aligned}
\frac{dH_i}{dt} &= (a_i - b_i)H_i + \sum_{\substack{r=1\\ r\neq i}}^{m}(\eta_{ri} - \omega_{ir})H_iH_r - \sum_{l=1}^{n}\left(\alpha_{il} + \delta_{il}\right)P_{il},\\
\frac{dP_{i1}}{dt} &= \frac{\lambda\beta_{i0}H_i\sum_{r=1}^{m}P_{rn}}{\gamma_0 + \sum_{r=1}^{m}\beta_{r0}H_r} - \left(\mu_{i1} + b_i + \epsilon_{i1} + \alpha_{i1} + \theta_{ii}^{1} + \sum_{\substack{r=1\\ r\neq i}}^{m}\theta_{ir}^{1}H_r\right)P_{i1}\\
&\quad - \frac{\alpha_{i1}\left(1+k_{i1}\right)}{k_{i1}}\frac{P_{i1}^2}{H_i} - \sum_{l=2}^{n}\alpha_{il}\frac{P_{i1}P_{il}}{H_i},\\
\frac{dP_{ij}}{dt} &= \frac{\beta_{i(j-1)}H_i\sum_{r=1}^{m}\epsilon_{r(j-1)}P_{r(j-1)}}{\gamma_{j-1} + \sum_{r=1}^{m}\beta_{r(j-1)}H_r} + \theta_{ii}^{j-1}P_{i(j-1)} + \sum_{\substack{r=1\\ r\neq i}}^{m}\theta_{ri}^{j-1}H_iP_{r(j-1)}\\
&\quad - \left(\mu_{ij} + b_i + \epsilon_{ij} + \alpha_{ij} + \theta_{ii}^{j} + \sum_{\substack{r=1\\ r\neq i}}^{m}\theta_{ir}^{j}H_r\right)P_{ij} - \frac{\alpha_{ij}\left(1+k_{ij}\right)}{k_{ij}}\frac{P_{ij}^2}{H_i}\\
&\quad - \sum_{\substack{l=1\\ l\neq j}}^{n}\alpha_{il}\frac{P_{ij}P_{il}}{H_i},\\
\frac{dP_{in}}{dt} &= \frac{\beta_{i(n-1)}H_i\sum_{r=1}^{m}\epsilon_{r(n-1)}P_{r(n-1)}}{\gamma_{n-1} + \sum_{r=1}^{m}\beta_{r(n-1)}H_r} + \theta_{ii}^{n-1}P_{i(n-1)} + \sum_{\substack{r=1\\ r\neq i}}^{m}\theta_{ri}^{n-1}H_iP_{r(n-1)}\\
&\quad - \left(\mu_{in} + b_i + \alpha_{in}\right)P_{in} - \frac{\alpha_{in}\left(1+k_{in}\right)}{k_{in}}\frac{P_{in}^2}{H_i} - \sum_{l=1}^{n-1}\alpha_{il}\frac{P_{in}P_{il}}{H_i},
\end{aligned}
\tag{2.3}
$$

for all $i = 1,\dots,m,\ j = 2,\dots,n.$

# Chapter 3

# Basic Reproductive Number

One of the main challenges of studying models of macroparasitic populations in communities with multiple host species, either with an epidemiological approach focuses on modeling the infection or with an eco-epidemiological approach focused on the size of the populations involved, is to determine the necessary conditions that guarantee the persistence of the parasites and host populations [22]. Typically, in parasitic models with a single host species these conditions are defined by determining the basic reproductive number and threshold host density of the system.

In this chapter we define the concepts of basic reproductive number and host threshold density for macroparasitic populations. We also determine and analyze an explicit expression of these concepts for the models presented in the previous chapters, particularly for the model proposed in (2.3).

## 3.1 Definition

In epidemiology, the basic reproductive number, denoted by $R_0$, is a threshold quantity that determines under what conditions there is an epidemic or not [23], more precisely, for compartmental models $R_0$ represents the average number of secondary infections produced when a single infected individual is introduced into a population full of susceptible individuals during his infectious period [24, 25]. This definition of $R_0$ is applicable for those models used to simulate the presence of an infection in a susceptible population, as in the case of host-microparasite models.

For host-macroparasite models the idea of the basic reproductive number is analogous. In these models, $R_0$ it is a threshold parameter that determines under what conditions a macro-parasitic species might persist in a host community [23], but its formal definition and how it is calculated are different.

The reason that $R_0$ is defined differently is that in the case of epidemiological models, particularly microparasite models, the basic reproductive number allows characterizing the ability of a microparasitory species to invade individuals from a susceptible host population in which it was not present before, however, in the macroparasite population models, the actual number of parasites per host is of interest, rather than hosting parasites or not. Therefore, for macroparasitic populations $R_0$ is defined as the average number of established, reproductively mature offspring produced by a mature parasite throughout its life in a population of uninfected hosts [28].

## 3.2 Computation of the Basic Reproductive Number

The basic reproductive number is one of the most important concepts in many epidemiological studies because it allows to determine under what conditions the infectious disease persists. This is because if $R_0 < 1$, then, on average, an infected individual produces less than one new infected individual during its infectious period, implying that infection cannot grow. On the other hand, if $R_0 > 1$, each infected individual, on average, infects more than one susceptible individual, so that the disease can invade the population [25].

The same is true for macroparasite populations, if $R_0 < 1$, then, on average, less than one new adult parasite is produced from a mature parasite during its period of reproductive life, implying that new generations of mature parasites cannot be bigger than their predecessors, so the parasite population cannot grow when it is first introduced into the host population. Conversely, if $R_0 > 1$, each adult parasite produces, on average, more than one new adult parasite over the course of its reproductive life, therefore, the parasite population can increase in its next generations.

For each model, $R_0$ can be obtained by calculating the average number of offspring (or female offspring in the case of a dioecious species) produced during the reproductive life of a mature parasite (or mature female parasite), and determining how much of the offspring is established in the host population, reaching reproductive maturity as an adult parasite. Since the basic reproductive number is defined in a population of uninfected hosts, $R_0$ is calculated when the parasite species is first introduced into host populations; at this time pathogenicity and other density-dependent constraints are effectively trivial.

In order to find an expression of $R_0$ for the model we proposed in (2.3), we first consider the case where there is only one host species and only the adult stage of the parasite enters the hosts, that is, the Anderson and May model (1.1). For this model, the number of offspring produced by an adult parasite, in the absence of density-dependent constraints acting anywhere in the life cycle of the parasite, is given by the product of the per capita reproduction rate of the parasite and the life expectancy of the parasite in its adult stage, since only adult parasites are able to reproduce [26]. Thus, since the per capita reproduction rate of the parasite is $\lambda$ and the life expectancy of an adult parasite in the absence of density-dependent restrictions is $1/(b+\mu+\alpha)$, the number of offspring produced by an adult parasite in this model is given by

$$\frac{\lambda}{b+\mu+\alpha}. \tag{3.1}$$

This expression accounts only for new individuals in the $W$ population. However, since not all parasites at this stage reach their adult stage, and $\lambda PH/(H+H_0)$ models the number of parasites in free life that become adults when entering a host, the $R_0$ of (1.1) that incorporates the dynamics of all stages of the life cycle of the parasite population can be calculated as the product of the rate at which new adult parasites are generated from an adult parasite $\lambda H/(H+H_0)$ and the life expectancy of an adult parasite $1/(b+\mu+\alpha)$, that is,

$$R_0 = \frac{\lambda H}{(H+H_0)(b+\mu+\alpha)} \tag{3.2}$$

(see [10]).

Something important about the value of $R_0$ given by (3.2) is that if $R_0 > 1$, then the value of (3.1) is greater than one, and particularly $R_0 \to \lambda/(b+\mu+\alpha)$ when $\gamma \to 0$, implying that, the greater the life expectancy of parasites in free life, given by $1/\gamma$, a greater number of parasites reach reproductive maturity when colonizing a host. Figure 3.1 shows how the value of $R_0$, given by (3.2), is affected by the life expectancy of the free-living larvae.

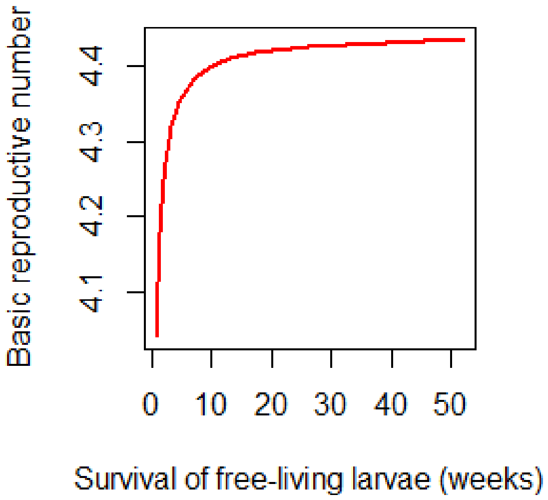


Figure 3.1: Effect of changes in life expectancy of larvae in free life on the basic reproductive number of the A&M model with parameter values $b = 1.05$, $\alpha = 3 \times 10^{-4}$, $\beta = 0.1$, $\mu = 1.2$, $k = 0.1$, $\lambda = 10$.

Now, in the Dobson and Hudson model (1.3) with a single host species and two stages of the parasite's life cycle within the hosts, the number of offspring produced by an adult parasite when there are no density-dependent constraints acting anywhere in the life cycle of the parasite can also be calculated as (3.1). However, as in the previous case, this expression does not consider the number of parasites that do not reach its adult stage. Therefore, taking into account the number of parasites that pass through each stage of its life cycle until become adult parasites, an expression for $R_0$ that incorporates the dynamics of the parasitic population at any stage of its life cycle is given by the product of the transition rates between the different stages of the parasite's life cycle and the life expectancy of a parasite in each of these stages [10], that is,

$$R_0 = \frac{\theta \lambda H}{(\mu_P + b + \alpha)(H + H_0)(\mu_A + b + \theta)}. \tag{3.3}$$

Figure 3.2 shows the changes generated in the value of $R_0$ of this model by varying the life expectancy of the free-living larvae. We can also analyze the effect of adding a second parasitic stage in the hosts on the value of $R_0$ when comparing with the values in Figure 3.1, since the parametric values are the same.

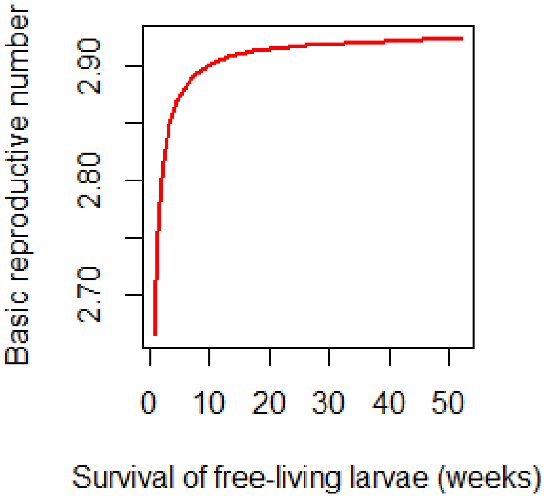


FIGURE 3.2: Effect of changes in life expectancy of larvae in free life on the basic reproductive number of the D&H model with parameter values $b = 1.05$, $\alpha = 3 \times 10^{-4}$, $\beta = 0.1$, $\theta = 3$, $\mu_A = 0.5$, $\mu_P = 1.2$, $k = 0.1$, $\lambda = 10$.

From the above, it follows that the $R_0$ for model (2.3) when there is a single host species and $n$ parasitic stages, using the corresponding notation, is given by

$$R_0 = \frac{\lambda \beta_{10} H_1}{(\mu_{1n} + b_1 + \alpha_{1n})(\beta_{10} H_1 + \gamma_0)} \prod_{j=1}^{n-1} \frac{\theta_{11}^j}{(\mu_{1j} + b_1 + \alpha_{1j} + \theta_{11}^j)}. \tag{3.4}$$

For multi-host models, finding the expression for the reproductive number is not simple. In these models we can calculate a threshold quantity equivalent to a partial basic reproductive number for parasites within the same host species, denoted $R_{0,i}$ for each host species $H_i$, and the total basic reproductive number of the parasite within all host species, denoted $R_0$ (or $R_{0,tot}$) [29, 30]. As in models with a single host species, we define $R_{0,i}$ as the average number of parasite offspring that reach its adult stage in a host of the population $H_i$, and $R_0$ as the average number of offspring that reach the adult stage in any host. Therefore, $R_0 = \sum_{i=1}^{m} R_{0,i}$.

From the definition of $R_{0,i}$ it follows that if $R_{0,i} > 1$ then the number of parasites with a definitive host in the population $H_i$ increases after parasites are introduced into the host community, implying that it is possible that the parasitic population can be maintained in each host species $H_i$ such that $R_{0,i} > 1$. The same is true for the basic reproductive number over all host species, $R_0 > 1$ implies that it is possible that the parasite population remains in the host community. Since $R_0 = \sum_{i=1}^{m} R_{0,i}$, if $R_{0,i} > 1$ for some $1 \leq i \leq m$, then $R_0 > 1$, but the reciprocal is not necessarily true, that is, it is possible that $R_0 > 1$ and $R_{0,i} < 1$ for all $1 \leq i \leq m$, this case implies that the parasite population needs all the host species to survive. Since we are interested in determine the necessary conditions for the parasite population to remain in the different host species, we focus on studying $R_0$.

As in the previous models, to determine $R_0$ we need to determine the number of parasites that pass from one stage of its life cycle to the next. To do this, it is necessary to calculate the average number of parasites in the $j$-th stage of its life cycle that are within a host of the $i$-th species and, after spending a period of time in that host, reach the next stage of its life cycle, not necessarily in the same host, for all $1 \leq i \leq m$, $1 \leq j \leq n$.

Since the number of parasites entering and leaving different populations $P_{ij}$ changes according to the stage of the life cycle that corresponds to the value of $j$, we first analyze the dynamics of the populations $P_{i1}$. In the absence of density-dependent constraints acting anywhere in the parasite's life cycle, we can estimate the number of parasites that survive in $P_{i1}$ until reaching the next stage of its life cycle as the quotient of the number of parasites that enter $P_{i1}$ and the number of parasites that leave $P_{i1}$, given by

$$\frac{\lambda \beta_{i0} H_i \sum_{r=1}^{m} P_{rn}}{\left(\gamma_0 + \sum_{r=1}^{m} \beta_{r0} H_r\right) \left(\mu_{i1} + b_i + \epsilon_{i1} + \alpha_{i1} + \theta_{ii}^{1} + \sum_{\substack{r=1 \\ r \neq i}}^{m} \theta_{ir}^{1} H_r\right) P_{i1}}$$

for all $i = 1, \ldots, m$. Therefore, the average number of parasite offspring produced by a mature parasite, with a definitive host in the $H_q$ population, that colonize the $P_{i1}$ population and reach the second stage of its life cycle is given by

$$\frac{\lambda \beta_{i0} H_i P_{qn}}{\left(\gamma_0 + \sum_{r=1}^{m} \beta_{r0} H_r\right) \left(\mu_{i1} + b_i + \epsilon_{i1} + \alpha_{i1} + \theta_{ii}^{1} + \sum_{\substack{r=1 \\ r \neq i}}^{m} \theta_{ir}^{1} H_r\right) P_{i1}}.$$

Now, for the $P_{ij}$ population, the number of parasites that enter and leave this population is given in a similar way for all $1 < j < n$. Thus, using the same analysis we performed previously, the number of parasites within a host in the $H_i$ population that pass from the $j$-th stage of its life cycle to the next is

$$\frac{\dfrac{\beta_{i(j-1)} H_i \sum_{r=1}^{m} \epsilon_{r(j-1)} P_{r(j-1)}}{\gamma_{j-1} + \sum_{r=1}^{m} \beta_{r(j-1)} H_r} + \theta_{ii}^{j-1} P_{i(j-1)} + \sum_{\substack{r=1 \\ r \neq i}}^{m} \theta_{ri}^{j-1} H_i P_{r(j-1)}}{\left(\mu_{ij} + b_i + \epsilon_{ij} + \alpha_{ij} + \theta_{ii}^{j} + \sum_{\substack{r=1 \\ r \neq i}}^{m} \theta_{ir}^{j} H_r\right) P_{ij}}$$

for all $j = 2, \ldots, n-1$, implying that the average number of parasites that leave the hosts in $H_q$ to enter the $P_{ij}$ population, and after spending time in the $P_{ij}$ population passes to the next stage of its life cycle, is given by

$$\frac{\dfrac{\beta_{i(j-1)}H_i\epsilon_{q(j-1)}P_{q(j-1)}}{\gamma_{j-1}+\sum_{r=1}^{m}\beta_{r(j-1)}H_r}+\theta_{qi}^{j-1}P_{q(j-1)}}{\left(\mu_{ij}+b_i+\epsilon_{ij}+\alpha_{ij}+\theta_{ii}^{j}+\sum_{\substack{r=1\\r\neq i}}^{m}\theta_{ir}^{j}H_r\right)P_{ij}}$$

if $q = i$, and

$$\frac{\dfrac{\beta_{i(j-1)}H_i\epsilon_{q(j-1)}P_{q(j-1)}}{\gamma_{j-1}+\sum_{r=1}^{m}\beta_{r(j-1)}H_r}+\theta_{qi}^{j-1}H_iP_{q(j-1)}}{\left(\mu_{ij}+b_i+\epsilon_{ij}+\alpha_{ij}+\theta_{ii}^{j}+\sum_{\substack{r=1\\r\neq i}}^{m}\theta_{ir}^{j}H_r\right)P_{ij}}$$

if $q \neq i$.

Finally, since at the last level of the parasite's life cycle parasites cannot leave the population, the total number of parasites that reach its adult stage in a host in $H_i$, and from which new offspring will be produced, can be calculated as

$$\frac{\dfrac{\beta_{i(n-1)}H_i\sum_{r=1}^{m}\epsilon_{r(n-1)}P_{r(n-1)}}{\gamma_{n-1}+\sum_{r=1}^{m}\beta_{r(n-1)}H_r}+\theta_{ii}^{n-1}P_{i(n-1)}+\sum_{\substack{r=1\\r\neq i}}^{m}\theta_{ri}^{n-1}H_iP_{r(n-1)}}{\left(\mu_{in}+b_i+\alpha_{in}\right)P_{in}}.$$

Therefore, the average number of adult parasites in a host in population $H_i$ that came from a host in population $H_q$, that will produce offspring by staying in these hosts during the rest of its life, is given by

$$\frac{\dfrac{\beta_{i(n-1)}H_i\epsilon_{r(n-1)}P_{q(n-1)}}{\gamma_{n-1}+\sum_{r=1}^{m}\beta_{r(n-1)}H_r}+\theta_{qi}^{n-1}P_{q(n-1)}}{\left(\mu_{in}+b_i+\alpha_{in}\right)P_{in}},$$

if $q = i$, and

$$\frac{\dfrac{\beta_{i(n-1)}H_i\epsilon_{r(n-1)}P_{q(n-1)}}{\gamma_{n-1}+\sum_{r=1}^{m}\beta_{r(n-1)}H_r}+\theta_{qi}^{n-1}H_iP_{q(n-1)}}{\left(\mu_{in}+b_i+\alpha_{in}\right)P_{in}},$$

if $q \neq i$.

For the above, denoting by $H$ the set $\{H_i\}_{i=1}^{m}$, and considering $F_{i,j-1,q}$ and $G_{i,j}$ functions of $H$ that represent the rate of parasite entry to the $P_{ij}$ population from the $P_{q(j-1)}$ population if $j > 1$ or $P_{qn}$ population if $j = 1$, and the rate of exit of parasites from the $P_{ij}$ population in absence of density-dependent constraints, respectively, given by

$$F_{i,j-1,q}(H) = \begin{cases} \dfrac{\lambda\beta_{i0}H_i}{\gamma_0 + \sum_{r=1}^{m}\beta_{r0}H_r} & \text{if } j = 1, \\ \dfrac{\beta_{i(j-1)}H_i\epsilon_{q(j-1)}}{\gamma_{j-1} + \sum_{r=1}^{m}\beta_{r(j-1)}H_r} + \theta_{qi}^{j-1} & \text{if } j > 1 \text{ and } i = q, \\ \dfrac{\beta_{i(j-1)}H_i\epsilon_{q(j-1)}}{\gamma_{j-1} + \sum_{r=1}^{m}\beta_{r(j-1)}H_r} + \theta_{qi}^{j-1}H_i & \text{if } j > 1 \text{ and } i \neq q, \end{cases} \tag{3.5}$$

and

$$G_{i,j}(H) = \begin{cases} \mu_{in} + b_i + \alpha_{in} & \text{if } j = n, \\ \mu_{ij} + b_i + \epsilon_{ij} + \alpha_{ij} + \theta_{ii}^{j} + \sum_{\substack{r=1 \\ r\neq i}}^{m}\theta_{ir}^{j}H_r & \text{otherwise,} \end{cases} \tag{3.6}$$

for all $1 \leq i \leq m$ and $1 \leq j \leq n$, we can express the average number of parasites that enter the $P_{ij}$ population when leaving the $P_{q(j-1)}$ population if $j > 1$ or $P_{qn}$ population if $j = 1$, that remain in these populations during the life expectancy of individuals in the $j$-th stage of the parasite's life cycle, as

$$\frac{F_{i,j-1,q}(H)P_{q(j-1)}}{G_{i,j}(H)P_{ij}}. \tag{3.7}$$

Before determining the value of $R_0$ for the general model (2.3), it is important to note that, if $F_{i,j-1,q}(H) \neq 0$ for all $i, q = 1, \dots, m$ and $j = 1, \dots, n$, then this model simulates a system where the parasite's transmission network covers the $m$ different host species at each parasitic stage. This transmission network can be represented by a digraph whose nodes represent the $P_{ij}$ populations, connected by arcs that represent the parasitic transmission between these populations. From the digraph that represents the parasite's transmission network, it follows that, to calculate $R_0$ it is necessary to consider only the product of the number of parasites that pass through the $P_{ij}$ populations that are on the same directed path that begins at the node of a $P_{i1}$ population and ends at the node a $P_{rn}$ population, with $i, r \in \{1, \dots, m\}$. Therefore, since (3.7) is the number of parasites that pass through the $P_{ij}$ populations, the total reproduction number is given by

$$\begin{aligned} R_0 &= \sum_{(i_1,\dots,i_n,i_{n+1})\in\{1,\dots,m\}^{n+1}} \left[ \frac{F_{i_1,0,i_{n+1}}(H)P_{i_{n+1}n}}{G_{i_1,1}(H)P_{i_1 1}} \prod_{j=2}^{n} \frac{F_{i_j,j-1,i_{j-1}}(H)P_{i_{j-1}(j-1)}}{G_{i_j,j}(H)P_{i_j j}} \right] \\ &= \sum_{(i_1,\dots,i_n,i_{n+1})\in\{1,\dots,m\}^{n+1}} \left[ \frac{F_{i_1,0,i_{n+1}}(H)P_{i_{n+1}n}}{G_{i_n,n}(H)P_{i_n n}} \prod_{j=2}^{n} \frac{F_{i_j,j-1,i_{j-1}}(H)}{G_{i_{j-1},j-1}(H)} \right]. \end{aligned} \tag{3.8}$$

Figure 3.3 shows an example of the digraph that represent the transmission network of a parasite that has three stages in its life cycle within individuals of three host species, and whose $R_0$ is given by (3.8).

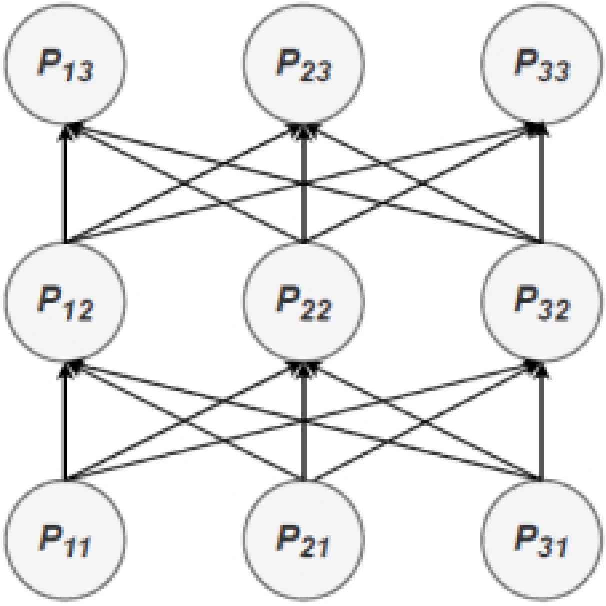


FIGURE 3.3: Complete transmission network of a system with 3 host species and 3 stages in the parasite's life cycle, where $P_{ij}$ are the parasites in the $j$-th stage of its life cycle within a host of $H_i$.

## 3.3 Threshold Host Density

We previously defined the concept of basic reproductive number for host-parasite models as the average number of offspring produced by an adult parasite, this in order to obtain an estimate of the rate of parasite transmission in a host community that allows determining under what conditions the parasitic population persists. The threshold host density, denoted $H_T$, is a quantity related to the basic reproductive number that requires that the host population density is large enough to accommodate a persisting parasite population [10, 11], that is, $H_T$ is a quantity related to the parasitic transmission rate of the system.

For host-parasite models with a single host species the value of $R_0$ is given as a function of $H$, therefore, since the threshold host density is the value of $H$ such that the parasitic population persist, $H_T$ is the size of the host population that satisfies $R_0 = 1$.

With the above definition, we can determine the value of $H_T$ for the Anderson and May model (1.1) considering $R_0 = 1$, with $R_0$ given by (3.2). Thus, the threshold host density for this model is

$$H_T = \frac{H_0(b+\mu+\alpha)}{\lambda-(b+\mu+\alpha)},$$

if $\lambda > b+\mu+\alpha$, otherwise, the parasitic population goes to extinction.

Since the life expectancy of larvae in free life affect the value of $R_0$, Figure 3.4 shows how the value of the threshold host density varies in relation to life expectancy of the free-living larvae in the Anderson and May model.

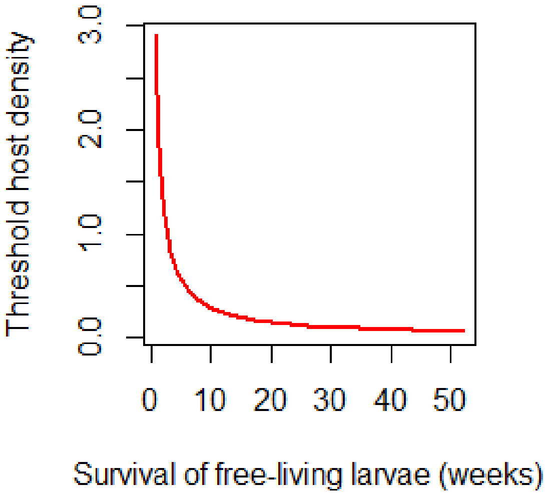


FIGURE 3.4: Effect of changes in life expectancy of larvae in free life on the threshold host density in the A&M model with parameter values $b = 1.05$, $\alpha = 3 \times 10^{-4}$, $\beta = 0.1$, $\mu = 1.2$, $k = 0.1$, $\lambda = 10$.

In this model, an initial value of $H$ greater than $H_T$ guarantees $R_0 > 1$, and thus, in addition to proving that the population persists, it can be proved that there is a stable equilibrium point in the system where the parasite population prevails over the host population (see Section 4.1).

Following a similar analysis, we can calculate $H_T$ for the Dobson and Hudson model (1.3), where $R_0$ is given by (3.3). In this model, the threshold host density is given by

$$H_T = \frac{H_0(\mu_P+b+\alpha)(\mu_A+b+\theta)}{\theta\lambda-(\mu_P+b+\alpha)(\mu_A+b+\theta)},$$

when $\theta\lambda > (\mu_P+b+\alpha)(\mu_A+b+\theta)$.

As with the basic reproductive numbers of the A&M and G&H models, we can compare the changes in threshold host density of both models with the results shown in Figure 3.4 and Figure 3.5, resulting from considering a second parasitic stage within the hosts .

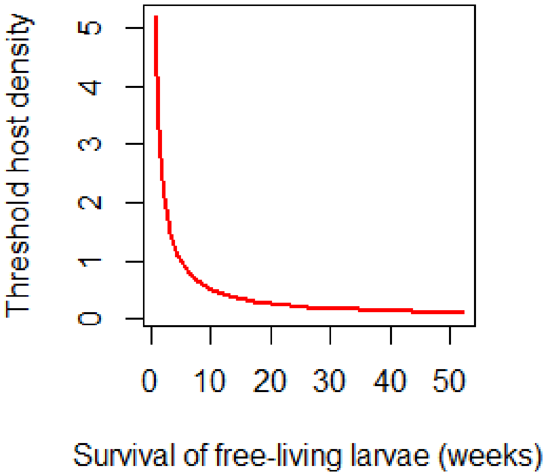


FIGURE 3.5: Effect of changes in life expectancy of larvae in free life on the threshold host density in the D&H model with parameter values $b = 1.05$, $\alpha = 3 \times 10^{-4}$, $\beta = 0.1$, $\theta = 3$, $\mu_A = 0.5$, $\mu_P = 1.2$, $k = 0.1$, $\lambda = 10$.

The two previous models are particular cases of model (2.3) whose most obvious generalization is to have $n$ stages in the parasite's life cycle and a single host species. The basic reproductive number for this particular case is (3.4), so, regardless of the value of $n$, and using the corresponding notation, we can calculate $H_T$ for this model as

$$H_T = \frac{\frac{\gamma_0}{\beta_{10}}(\mu_{1n} + b_1 + \alpha_{1n}) \prod_{j=1}^{n-1}(\mu_{1j} + b_1 + \alpha_{1j} + \theta_{11}^j)}{\lambda \prod_{j=1}^{n-1} \theta_{11}^j - (\mu_{1n} + b_1 + \alpha_{1n}) \prod_{j=1}^{n-1}(\mu_{1j} + b_1 + \alpha_{1j} + \theta_{11}^j)}. \tag{3.9}$$

Now, since it is possible to determine the basic reproductive number for host-parasite models with more than one host species, given as a function of the densities of the different host species, we can define the threshold host density in these models as a configuration of values of the different host densities such that $R_0 = 1$.

For model (2.3) with more than one host species, the basic reproductive number, given by (3.8), it is a function not only of the densities of the host populations, it also depends on the size of the parasitic populations in its first and last stage, so, instead of calculating the threshold host density in terms of parasitic populations, we can find a lower bound for $R_0$ that depends only on the values of $H_i$, so we can find sizes for host populations such that $R_0 \geq 1$, guaranteeing that the parasite population is able to subsist.

From the definition of $R_0$ for this model, given by (3.8), it follows that

$$\begin{aligned}
R_0 &= \sum_{(i_1,\ldots,i_n,i_{n+1})\in\{1,\ldots,m\}^{n+1}} \left[ \frac{F_{i_1,0,i_{n+1}}(H)P_{i_{n+1}n}}{G_{i_n,n}(H)P_{i_n n}} \prod_{j=2}^{n} \frac{F_{i_j,j-1,i_{j-1}}(H)}{G_{i_{j-1},j-1}(H)} \right] \\
&= \sum_{(i_1,\ldots,i_n)\in\{1,\ldots,m\}^{n}} \left[ \frac{F_{i_1,0,i_n}(H)}{G_{i_1,1}(H)} \prod_{j=2}^{n} \frac{F_{i_j,j-1,i_{j-1}}(H)}{G_{i_j,j}(H)} \right] + \\
&\quad \sum_{\substack{(i_1,\ldots,i_n)\in\{1,\ldots,m\}^{n} \\ i_{n+1}\in\{1,\ldots,m\}\setminus\{i_n\}}} \left[ \frac{F_{i_1,0,i_{n+1}}(H)P_{i_{n+1}n}}{G_{i_n,n}(H)P_{i_n n}} \prod_{j=2}^{n} \frac{F_{i_j,j-1,i_{j-1}}(H)}{G_{i_{j-1},j-1}(H)} \right] \\
&\geq \sum_{(i_1,\ldots,i_n)\in\{1,\ldots,m\}^{n}} \left[ \frac{F_{i_1,0,i_n}(H)}{G_{i_1,1}(H)} \prod_{j=2}^{n} \frac{F_{i_j,j-1,i_{j-1}}(H)}{G_{i_j,j}(H)} \right].
\end{aligned} \tag{3.10}$$

The problem of calculating $H_T$ as a configuration of values of $H_i$ such that $R_0 = 1$, is that $R_0$ consists of the sum of $m^{n+1}$ terms that may depend on the product of the quotient of different $P_{ij}$ populations. For this reason, in this model we define an auxiliary value $H_T'$ as any configuration of values of $\{H_i\}_{i=1}^{m}$ such that

$$\sum_{(i_1,\ldots,i_n)\in\{1,\ldots,m\}^{n}} \left[ \frac{F_{i_1,0,i_n}\left(H_T'\right)}{G_{i_1,1}\left(H_T'\right)} \prod_{j=2}^{n} \frac{F_{i_j,j-1,i_{j-1}}\left(H_T'\right)}{G_{i_j,j}\left(H_T'\right)} \right] = 1. \tag{3.11}$$

Note that (3.11) consists of the sum $m^n$ terms that depend only on the host populations, and any $H_T'$ that satisfies the equation (3.11) gives $R_0 \geq 1$. In particular, $H_T' = H_T$ when equality is satisfied in (3.10).

## 3.4 Some Conclusions on the Basic Reproductive Number

Unlike the results on $R_0$ in epidemiological models, the basic reproductive number and the threshold host density in the type of host-parasite models only allow to determine under what conditions it is possible that the parasite density increases, or at least persist, in the host community when the parasite is first introduced into the population, implying that it is possible that the parasite population persists as long as the host population does not become extinct. Therefore, for models where it is not possible to determine analytically the existence of a non-trivial equilibrium point, the fact that the parasite population is maintained when it is just introduced in the hosts does not imply that the parasite population persists for all time $t$, or does not even guarantee that the host community persists. Even if the parasites persist in the host community for all time $t$, this does not imply that the host and parasite populations are regulated.

An example of a model in which $R_0 > 1$ and none of the host or parasite populations persists is shown in Figure 3.6, where $R_0 \approx 2.73$. This happens when the growth rates of the parasitic populations are higher than the growth rates of the host populations, causing both populations to grow until the induced mortality on the hosts exceeds the natural birth rate, and thus, the host populations tend to become extinct, implying that parasites also disappear from the system.

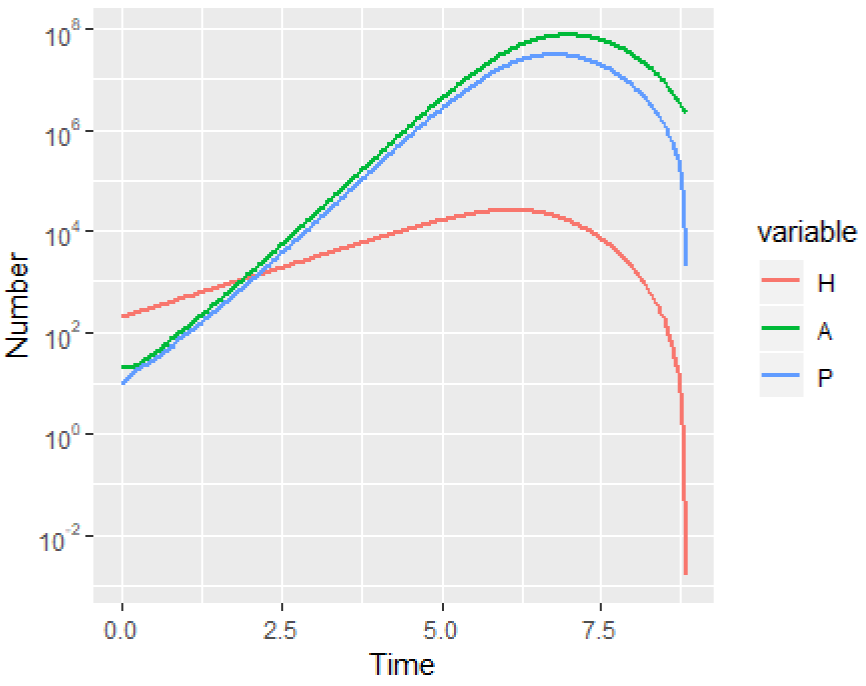


FIGURE 3.6: Population dynamics in the D&H model with parameter values and initial conditions $a = 1.95$, $b = 1.05$, $\alpha = 3 \times 10^{-4}$, $\delta = 8 \times 10^{-4}$, $\beta = 0.1$, $\theta = 3$, $\mu_A = 0.3$, $\mu_P = 0.8$, $k = 0.1$, $\lambda = 11$, $\gamma = 10$, $H = 200$, $A = 20$, $P = 10$.

When $R_0 > 1$, another possibility is that the parasite population persists in the host community, but does not regulate its growth, that is, the host and parasite populations grow without bounds, under the assumption that there is no carrying capacity in the system for the host community, as in Figure 3.7, where $R_0 \approx 2.06$.

This occurs when the growth rates of the host populations are higher than the growth rates of the parasitic populations for all time $t$, and the parasites are unable to decrease the growth of host populations enough to cause all populations in the system to stabilize.

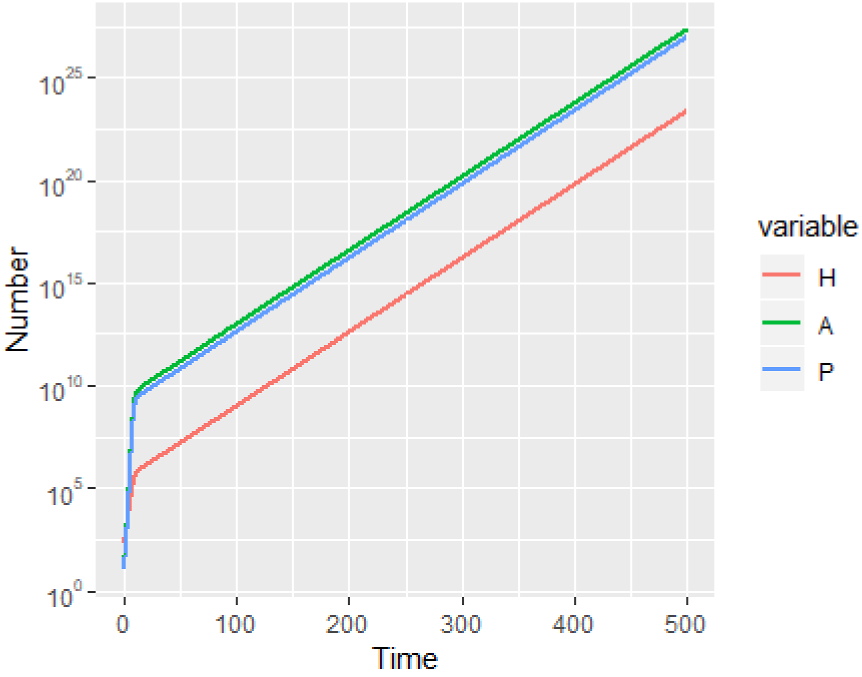


FIGURE 3.7: Population dynamics in the D&H model with parameter values and initial conditions $a = 1.95$, $b = 1.05$, $\alpha = 1 \times 10^{-4}$, $\delta = 1 \times 10^{-4}$, $\beta = 0.1$, $\theta = 3$, $\mu_A = 0.7$, $\mu_P = 1.2$, $k = 0.1$, $\lambda = 11$, $\gamma = 10$, $H = 200$, $A = 20$, $P = 10$.

Finally, it is possible that the introduction of the parasitic species into the host community regulates the host populations, but not stabilize them to a non-trivial equilibrium in the system. This is possible when all the populations in the system oscillate with some period of time $T$.

Something important about $R_0$ is that it is possible to slightly modify the conditions in a model, so that even the value of $R_0$ can be preserved, but that it changes if the populations stabilize or not. Figure 3.8 shows an example of this, stabilizing the populations in the model of Figure 3.7, and maintaining the value of $R_0$, by adding the induced mortality rates and the decrease in the fertility rate over the hosts due to arrested larvae, with values at least thirty times lower than those of adult parasites, and maintaining the same value for the rest of the parameters and initial conditions in the system. This particular example occurs when the parasite populations are big enough so that the overall effect of all parasites that have not reached reproductive maturity reduce the growth of host and parasitic populations until they tend to stabilize.

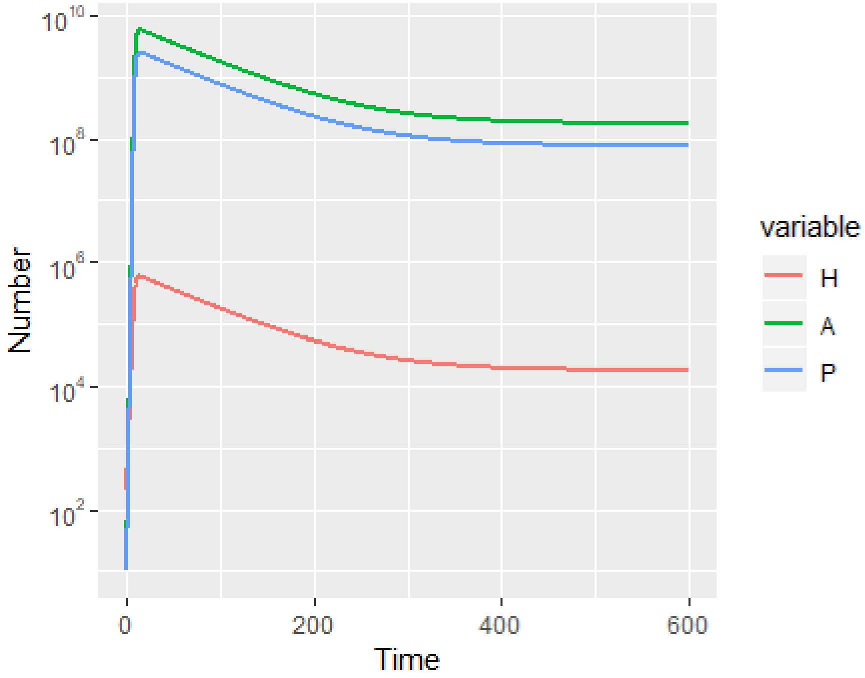


FIGURE 3.8: Population dynamics in the D&H model with parameter values and initial conditions $a = 1.95$, $b = 1.05$, $\alpha_A = 3\times10^{-6}$, $\alpha_P = 1\times10^{-4}$, $\delta_A = 3\times10^{-6}$, $\delta_P = 1\times10^{-4}$, $\beta = 0.1$, $\theta = 3$, $\mu_A = 0.7$, $\mu_P = 1.2$, $k_A = 0.1$, $k_P = 0.1$, $\lambda = 11$, $\gamma = 10$, $H = 200$, $A = 20$, $P = 10$.

In addition to the above, in the model with a single host species and $n$ parasitic stages the value of $R_0$, given by (3.4), decreases for all $t > 0$ as the value of $n$ increases if the parameter values used in the equations are equal, as in the examples in Figure 3.1 and Figure 3.2. This because increasing the value of $n$ decreases the value of $\prod_{j=1}^{n-1}\left[\theta_{11}^j/(\mu_{1j}+b_1+\alpha_{1j}+\theta_{11}^j)\right]$, since $\theta_{11}^j/(\mu_{1j}+b_1+\alpha_{1j}+\theta_{11}^j) < 1$ for all $j = 1,\ldots,n-1$. This result reflects the additional mortality added by each parasitic stage in the model, since $R_0$ represents the average number of parasite offspring that reach reproductive maturity in its adult stage. This is also true for the general case in (2.3) with basic reproductive number (3.8). Since

$$R_0 = \sum_{(i_1,\ldots,i_n,i_{n+1})\in\{1,\ldots,m\}^{n+1}} \left[\frac{F_{i_1,0,i_{n+1}}(H)P_{i_{n+1}n}}{G_{i_n,n}(H)P_{i_nn}} \prod_{j=2}^{n} \frac{F_{i_j,j-1,i_{j-1}}(H)}{G_{i_{j-1},j-1}(H)}\right],$$

so, from the definition of $F_{i_j,j-1,i_{j-1}}(H)$ and $G_{i_{j-1},j-1}(H)$, given by (3.5) and (3.6) respectively, it follows that

$$\frac{F_{i_j,j-1,i_{j-1}}(H)}{G_{i_{j-1},j-1}(H)} < 1$$

for all $i_{j-1}$, with $j = 2, \ldots n$. Thus,

$$\prod_{j=2}^{n_1} \frac{F_{i_j,j-1,i_{j-1}}(H)}{G_{i_{j-1},j-1}(H)} > \prod_{j=2}^{n_2} \frac{F_{i_j,j-1,i_{j-1}}(H)}{G_{i_{j-1},j-1}(H)}$$

if $n_1 < n_2$, proving that the value of $R_0$ in these models, decreases for all $t > 0$ as the value of $n$ increases if the parametric values used in the equations are equal.

An opposite result is true for threshold host density in communities with a single host species. The value of $H_T$, given by (3.9), increases as the value of $n$ increases if the parameter values used in the equations are equal, as in the examples in Figure 3.4 and Figure 3.5. This because,

$$H_T = \frac{\frac{\gamma_0}{\beta_{10}}(\mu_{1n} + b_1 + \alpha_{1n}) \prod_{j=1}^{n-1}(\mu_{1j} + b_1 + \alpha_{1j} + \theta_{11}^j)}{\lambda \prod_{j=1}^{n-1} \theta_{11}^j - (\mu_{1n} + b_1 + \alpha_{1n}) \prod_{j=1}^{n-1}(\mu_{1j} + b_1 + \alpha_{1j} + \theta_{11}^j)},$$

so, if $n_1 < n_2$, then

$$\lambda \prod_{j=1}^{n_2-1} \theta_{11}^j < \lambda \left( \prod_{j=1}^{n_1-1} \theta_{11}^j \right) \prod_{j=n_1}^{n_2-1} (\mu_{1j} + b_1 + \alpha_{1j} + \theta_{11}^j),$$

implying that

$$\lambda \prod_{j=1}^{n_2-1} \theta_{11}^j - (\mu_{1n} + b_1 + \alpha_{1n}) \prod_{j=1}^{n_2-1} (\mu_{1j} + b_1 + \alpha_{1j} + \theta_{11}^j)$$

is smaller than

$$\left[ \lambda \prod_{j=1}^{n_1-1} \theta_{11}^j - (\mu_{1n} + b_1 + \alpha_{1n}) \prod_{j=1}^{n_1-1} (\mu_{1j} + b_1 + \alpha_{1j} + \theta_{11}^j) \right] \prod_{j=n_1}^{n_2-1} (\mu_{1j} + b_1 + \alpha_{1j} + \theta_{11}^j),$$

and hence

$$\frac{\frac{\gamma_0}{\beta_{10}}(\mu_{1n} + b_1 + \alpha_{1n}) \prod_{j=1}^{n_1-1}(\mu_{1j} + b_1 + \alpha_{1j} + \theta_{11}^j)}{\lambda \prod_{j=1}^{n_1-1} \theta_{11}^j - (\mu_{1n} + b_1 + \alpha_{1n}) \prod_{j=1}^{n_1-1}(\mu_{1j} + b_1 + \alpha_{1j} + \theta_{11}^j)},$$

that can be written as

$$\frac{\frac{\gamma_0}{\beta_{10}}(\mu_{1n}+b_1+\alpha_{1n})\prod_{j=1}^{n_1-1}(\mu_{1j}+b_1+\alpha_{1j}+\theta_{11}^j)}{\lambda\prod_{j=1}^{n_1-1}\theta_{11}^j-(\mu_{1n}+b_1+\alpha_{1n})\prod_{j=1}^{n_1-1}(\mu_{1j}+b_1+\alpha_{1j}+\theta_{11}^j)}\prod_{j=n_1}^{n_2-1}\frac{\mu_{1j}+b_1+\alpha_{1j}+\theta_{11}^j}{\mu_{1j}+b_1+\alpha_{1j}+\theta_{11}^j},$$

is bigger than

$$\frac{\frac{\gamma_0}{\beta_{10}}(\mu_{1n}+b_1+\alpha_{1n})\prod_{j=1}^{n_2-1}(\mu_{1j}+b_1+\alpha_{1j}+\theta_{11}^j)}{\lambda\prod_{j=1}^{n_2-1}\theta_{11}^j-(\mu_{1n}+b_1+\alpha_{1n})\prod_{j=1}^{n_2-1}(\mu_{1j}+b_1+\alpha_{1j}+\theta_{11}^j)}.$$

This result shows that to compensate for the decrease in the average number of parasite offspring that reach its adult stage, that is, the decrease of $R_0$, it is necessary to increase the number of hosts in the system so that the parasite population can persist.

# Chapter 4

# Model Analysis

In the previous chapter we concluded that the basic reproductive number and the threshold host density allow us to determine under what conditions the parasitic population is able to maintain or increase in the host community, however, these conditions do not necessarily guarantee that there is a non-trivial equilibrium point where the host and parasite populations are regulated. For this reason, when it is possible, the equilibrium point of the system of equations is calculated for each host-parasite model, if it exists.

Before attempting to calculate the equilibrium points of the system (2.3) it is necessary to remember that we model a system where there is a community of $m$ different host species and a parasite species with $n$ stages in its life cycle, whose transmission network can be represented with a digraph as explained in Section 3.2. However, most parasite's transmission networks do not satisfy that all the parasitic stages are present in each host species as in Figure 3.3, so, one of the problems is that it is necessary to elucidate the parasitic transmission network.

The life cycle of many parasitic species has been studied, and their the transmission network determined. An example of these studies is shown in the representation of the Carpinteria database, presented in Appendix C. This database shows that most parasite species satisfy that the stages of its life cycle occur within different communities of host species, implying that $m \geq n$, and more important, without loss of generality, the equations of (2.3) in these cases can be written as

$$
\begin{aligned}
\frac{dH_i}{dt} &= (a_i - b_i)H_i - \left(\alpha_{iL(i)} + \delta_{iL(i)}\right) P_{iL(i)} + \sum_{\{r \,|\, \eta_{ri} - \omega_{ir} \neq 0\}} (\eta_{ri} - \omega_{ir}) H_i H_r, \\
\frac{dP_{i1}}{dt} &= \frac{\lambda \beta_{i0} H_i \sum_{\{r \,|\, L(r)=n\}} P_{rn}}{\gamma_0 + \sum_{\{r \,|\, L(r)=1\}} \beta_{r0} H_r} - \left( \mu_{i1} + b_i + \epsilon_{i1} + \alpha_{i1} + \sum_{\{r \,|\, L(r)=2\}} \theta^1_{ir} H_r \right) P_{i1} \\
&\quad - \frac{\alpha_{i1}\left(1 + k_{i1}\right)}{k_{i1}} \frac{P_{i1}^2}{H_i} \quad \forall i \in \{L(i) = 1\}, \\
\frac{dP_{ij}}{dt} &= \frac{\beta_{i(j-1)} H_i \sum_{\{r \,|\, L(r)=j-1\}} \epsilon_{r(j-1)} P_{r(j-1)}}{\gamma_{j-1} + \sum_{\{r \,|\, L(r)=j\}} \beta_{r(j-1)} H_r} + \sum_{\{r \,|\, L(r)=j-1\}}^{m} \theta^{j-1}_{ri} H_i P_{r(j-1)} \\
&\quad - \left( \mu_{ij} + b_i + \epsilon_{ij} + \alpha_{ij} + \sum_{\{r \,|\, L(r)=j+1\}}^{m} \theta^j_{ir} H_r \right) P_{ij} - \frac{\alpha_{ij}\left(1 + k_{ij}\right)}{k_{ij}} \frac{P_{ij}^2}{H_i} \\
&\quad \forall i \in \{L(i) = j,\ 1 < j < n\}, \\
\frac{dP_{in}}{dt} &= \frac{\beta_{i(n-1)} H_i \sum_{\{r \,|\, L(r)=n-1\}} \epsilon_{r(n-1)} P_{r(n-1)}}{\gamma_{n-1} + \sum_{\{r \,|\, L(r)=n\}} \beta_{r(n-1)} H_r} + \sum_{\{r \,|\, L(r)=n-1\}} \theta^{n-1}_{ri} H_i P_{r(n-1)} \\
&\quad - \left(\mu_{in} + b_i + \alpha_{in}\right) P_{in} - \frac{\alpha_{in}\left(1 + k_{in}\right)}{k_{in}} \frac{P_{in}^2}{H_i} \quad \forall i \in \{L(i) = n\},
\end{aligned}
\tag{4.1}
$$

where $L(r)$ is given by

$$
L(r) = \begin{cases} j & \text{if there is } i \in \{1, \dots, m\} \text{ such that } \max\left\{\beta_{r(j-1)}, \theta^{j-1}_{ir}\right\} \neq 0, \\ 0 & \text{otherwise.} \end{cases}
$$

Therefore, in systems without predation, the equilibrium point in these cases satisfies

$$
P^*_{iL(i)} = \frac{a_i - b_i}{\alpha_{iL(i)} + \delta_{iL(i)}} H^*_i, \tag{4.2}
$$

Thus, defining $A_{iL(i)} = (a_i - b_i)/(\alpha_{iL(i)} + \delta_{iL(i)})$ and

$$
B_{iL(i)} = \begin{cases} A_{iL(i)} \left[ \mu_{iL(i)} + b_i + \epsilon_{iL(i)} + \alpha_{iL(i)} + \dfrac{\alpha_{iL(i)}\left(1 + k_{iL(i)}\right)}{k_{iL(i)}} A_{iL(i)} \right] & \text{if } L(i) < n, \\ A_{in} \left[ \mu_{in} + b_i + \alpha_{in} + \dfrac{\alpha_{iL(i)}\left(1 + k_{in}\right)}{k_{in}} A_{in} \right] & \text{if } L(i) = n, \end{cases} \tag{4.3}
$$

since $H^*_i \neq 0$ for all $1 \leq i \leq m$, replacing $P^*_{iL(i)}$ in $dP^*_{iL(i)} = 0$ we obtain the following equations

$$B_{i1} = \frac{\sum_{\{r \,|\, L(r)=n\}} \lambda \beta_{i0} A_{rn} H_r^*}{\gamma_0 + \sum_{\{r \,|\, L(r)=1\}} \beta_{r0} H_r^*} - \sum_{\{r \,|\, L(r)=2\}} A_{i1} \theta_{ir}^1 H_r^* \tag{4.4}$$

for all $i \in \{i \mid L(i) = 1\}$,

$$\begin{aligned} B_{ij} =& \frac{\sum_{\{r \,|\, L(r)=j-1\}} \beta_{i(j-1)} \epsilon_{r(j-1)} A_{r(j-1)} H_r^*}{\gamma_{j-1} + \sum_{\{r \,|\, L(r)=j\}} \beta_{r(j-1)} H_r^*} + \sum_{\{r \,|\, L(r)=j-1\}}^{m} \theta_{ri}^{j-1} A_{r(j-1)} H_r^* \\ & - \sum_{\{r \,|\, L(r)=j+1\}} A_{ij} \theta_{ir}^1 H_r^* \end{aligned} \tag{4.5}$$

for all $i$ such that $L(i) = j$, with $1 < j < n$, and

$$B_{in} = \frac{\sum_{\{r \,|\, L(r)=n-1\}} \beta_{i(n-1)} \epsilon_{r(n-1)} A_{r(n-1)} H_r^*}{\gamma_{j-1} + \sum_{\{r \,|\, L(r)=n\}} \beta_{r(n-1)} H_r^*} + \sum_{\{r \,|\, L(r)=n-1\}}^{m} \theta_{ri}^{n-1} A_{r(n-1)} H_r^* \tag{4.6}$$

for all $i$ that satisfies $L(i) = n$. Hence, to calculate the equilibrium point, if it exists, it is only necessary to solve (4.2), (4.4), (4.5) and (4.6), for all $i = 1, \ldots, m$, $j = 1, \ldots, n$.

We can not follow a similar method to try to determine the equilibrium point when there are trophic interactions between the hosts, because the equilibrium point in these systems must satisfy

$$P_{iL(i)}^* = \frac{a_i - b_i}{\alpha_{iL(i)} + \delta_{iL(i)}} H_i^* + \sum_{\{r \,|\, \eta_{ri} - \omega_{ir} \neq 0\}} \frac{\eta_{ri} - \omega_{ir}}{\alpha_{iL(i)} + \delta_{iL(i)}} H_i^* H_r^*,$$

if $\alpha_{iL(i)} + \delta_{iL(i)} \neq 0$, and

$$\sum_{\{r \,|\, \eta_{ri} - \omega_{ir} \neq 0\}} (\eta_{ri} - \omega_{ir}) H_r^* = b_i - a_i,$$

when $\alpha_{iL(i)} + \delta_{iL(i)} \neq 0$. In these cases it is not possible to give a method to determine the equilibrium point.

In cases where there are parasite species that remain in the same host species for more than one stage of its life cycle, it is also not possible to give a general method to calculate its equilibrium points, since in these cases the model cannot be written as in (4.1).

For a better understanding of the above, we analyze some particular cases of the model when initially we only know the values of $m$ and $n$.

## 4.1 Case $m$=1, $n$=1

This case coincides with the Anderson and May model when $\delta_{11} = 0$. Thus, to simplify the notation in this particular case, and in order to show a complete analysis of the Anderson and May model, we use the same notation as in (1.1). Since $\delta$ does not directly affect the dynamics of the parasitic population, and since the effect of this parameter on the growth rate of the host population is relatively small, we only consider the case where $\delta = 0$. Hence, the model in this case is exactly the same as in (1.1):

$$\begin{aligned}\frac{dH}{dt} &= (a-b)H - \alpha P,\\ \frac{dP}{dt} &= \frac{\lambda PH}{H+H_0} - (b+\mu+\alpha)\,P - \frac{\alpha(1+k)}{k}\frac{P^2}{H}.\end{aligned}$$

Since the model has the form (4.1), without predation between hosts, from (4.4) it follows that the equilibrium point satisfies

$$\frac{\lambda(a-b)H^*}{\alpha(H^*+H_0)} = B$$

with $B$ defined as in (4.3):

$$B = \left(\frac{a-b}{\alpha}\right)\left[b+\mu+\alpha+\frac{(1+k)}{k}(a-b)\right].$$

Therefore,

$$H^* = \frac{\alpha B H_0}{\lambda(a-b)-\alpha B},$$

and from (4.2)

$$P^* = \frac{B(a-b)H_0}{\lambda(a-b)-\alpha B}.$$

Thus, for the equilibrium point to exist and make biological sense, it is necessary that $\lambda > \alpha B/(a-b)$, that is, $\lambda > b+\mu+\alpha+(1+k)(a-b)/k$.

To determine the stability of the equilibrium point $(H^*, P^*)$ we analyze the eigenvalues of the linearized system $H(t) = H^* + x(t)$, $P(t) = P^* + y(t)$, calculated using the characteristic polynomial of the Jacobian matrix of the system (1.1) at $(H^*, P^*)$, that is

$$\begin{aligned}
P(c) &= \det\begin{pmatrix} a-b-c & -\alpha \\ \frac{\lambda P^* H_0}{(H^*+H_0)^2} + \frac{\alpha(1+k)}{k}\frac{(P^*)^2}{(H^*)^2} & \frac{\lambda H^*}{H^*+H_0} - (b+\mu+\alpha) - 2\frac{\alpha(1+k)}{k}\frac{P^*}{H^*} - c \end{pmatrix} \\
&= c^2 + \left[(b+\mu+\alpha) + 2\frac{\alpha(1+k)}{k}\frac{P^*}{H^*} - \frac{\lambda H^*}{H^*+H_0} - (a-b)\right] c \\
&\quad + (a-b)\left[\frac{\lambda H^*}{H^*+H_0} - (b+\mu+\alpha) - 2\frac{\alpha(1+k)}{k}\frac{P^*}{H^*}\right] \\
&\quad + \alpha\left[\frac{\lambda P^* H_0}{(H^*+H_0)^2} + \frac{\alpha(1+k)}{k}\frac{(P^*)^2}{(H^*)^2}\right] \\
&= c^2 + \frac{a-b}{k}c + B\left(\lambda - \frac{\alpha}{a-b}B\right),
\end{aligned}$$

and since $(a-b)/(k) > 0$ and $B[\lambda - \alpha B/(a-b)] > 0$ as long as $H^* > 0$ and $P^* > 0$, the eigenvalues of the linearized system have a negative real part (see Appendix B), so $(H^*, P^*)$ is locally stable.

This model can be applied to all parasitic species that enter a single host species during its adult stage, for example, *Nerocila californica, Baylisascaris procyonis*, *Eugregarine*, etc. Figure 4.1 shows a simulation of the system where the conditions for the existence and stability of the equilibrium point are satisfied.

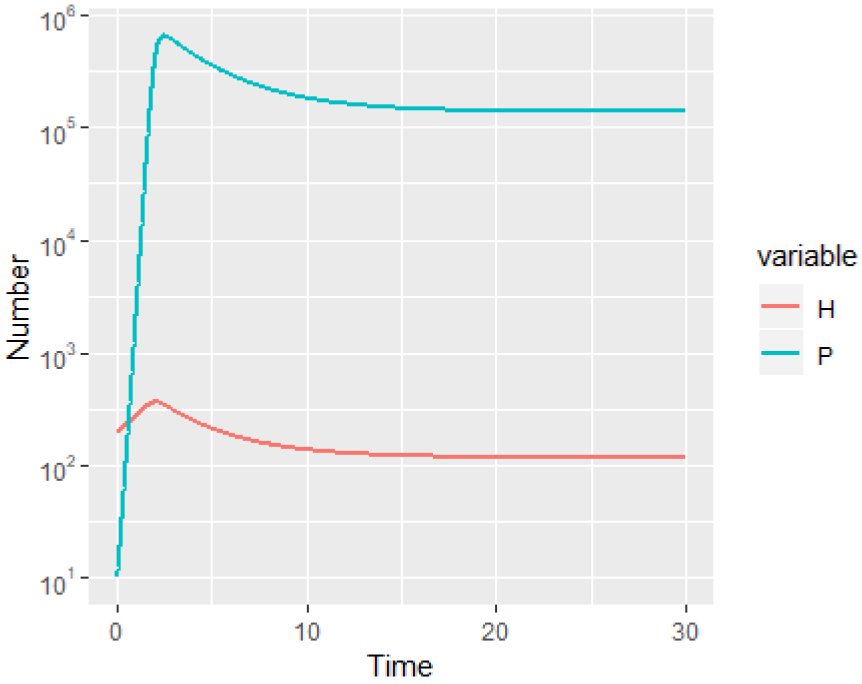


Figure 4.1: Population dynamics in the A&M model with parameter values $a = 1.4$, $b = 1.05$, $\alpha = 3 \times 10^{-4}$, $\beta = 0.1$, $\mu = 0.5$, $k = 0.1$, $\lambda = 10$, $\gamma = 10$, and initial conditions $H = 200$, $P = 10$.

## 4.2 Case $m$=2, $n$=1

Given the structure of the model, in this case we consider a community with two host species, that the parasite only colonizes them during its adult stage. The equations for population dynamics in this case are given by

$$\begin{aligned}
\frac{dH_1}{dt} &= (a_1 - b_1)H_1 - (\alpha_{11} + \delta_{11})P_{11},\\
\frac{dH_2}{dt} &= (a_2 - b_2)H_2 - (\alpha_{21} + \delta_{21})P_{21},\\
\frac{dP_{11}}{dt} &= \frac{\lambda\beta_{10}H_1(P_{11}+P_{21})}{\gamma_0 + \beta_{10}H_1 + \beta_{20}H_2} - (\mu_{11} + b_1 + \alpha_{11})P_{11} - \alpha_{11}\frac{1+k_{11}}{k_{11}}\frac{P_{11}^2}{H_1},\\
\frac{dP_{21}}{dt} &= \frac{\lambda\beta_{20}H_2(P_{11}+P_{21})}{\gamma_0 + \beta_{10}H_1 + \beta_{20}H_2} - (\mu_{21} + b_2 + \alpha_{21})P_{21} - \alpha_{21}\frac{1+k_{21}}{k_{21}}\frac{P_{21}^2}{H_2}.
\end{aligned} \tag{4.7}$$

As in the previous case, this system is also a particular case of (4.1) where there are no trophic interactions between the hosts, so, from (4.4) it follows that

$$\frac{\lambda\beta_{i0}\left(\dfrac{a_1-b_1}{\alpha_{11}+\delta_{11}}H_1^* + \dfrac{a_2-b_2}{\alpha_{21}+\delta_{21}}H_2^*\right)}{\gamma_0 + \beta_{10}H_1^* + \beta_{20}H_2^*} = B_i \tag{4.8}$$

where $B_i$, defined as in (4.3), is

$$B_i = \frac{a_i - b_i}{\alpha_{i1}+\delta_{i1}}\left[\mu_{i1} + b_i + \alpha_{i1} - \alpha_{i1}\frac{1+k_{i1}}{k_{i1}}\left(\frac{a_i-b_i}{\alpha_{i1}+\delta_{i1}}\right)\right], \tag{4.9}$$

for $i = 1, 2$. Thus, the equations in (4.8) imply that

$$\left(\lambda\beta_{i0}\frac{a_1-b_1}{\alpha_{11}+\delta_{11}} - \beta_{10}B_i\right)H_1^* + \left(\lambda\beta_{i0}\frac{a_2-b_2}{\alpha_{21}+\delta_{21}} - \beta_{20}B_i\right)H_2^* = B_i\gamma_0, \tag{4.10}$$

for $i = 1, 2$. Assuming that $(a_1 - b_1)/(\alpha_{11} + \delta_{11}) \neq (a_2 - b_2)/(\alpha_{21} + \delta_{21})$, $\beta_{10} \neq \beta_{20}$ and $B_1 \neq B_2$, the solution of (4.10) is given by

$$\begin{aligned}
H_1^* &= \frac{\gamma_0\dfrac{a_2-b_2}{\alpha_{21}+\delta_{21}}}{\beta_{20}\dfrac{a_1-b_1}{\alpha_{11}+\delta_{11}} - \beta_{10}\dfrac{a_2-b_2}{\alpha_{21}+\delta_{21}}},\\
H_2^* &= \frac{\gamma_0\dfrac{a_1-b_1}{\alpha_{11}+\delta_{11}}}{\beta_{10}\dfrac{a_2-b_2}{\alpha_{21}+\delta_{21}} - \beta_{20}\dfrac{a_1-b_1}{\alpha_{11}+\delta_{11}}}.
\end{aligned}$$

Since $\beta_{20}(a_1 - b_1)/(\alpha_{11} + \delta_{11}) \neq \beta_{10}(a_2 - b_2)/(\alpha_{21} + \delta_{21})$, the above implies that there is no biologically feasible equilibrium point in the system, because either $H_1^* < 0$ or $H_2^* < 0$ depending on whether $\beta_{20}(a_1 - b_1)/(\alpha_{11} + \delta_{11}) - \beta_{10}(a_2 - b_2)/(\alpha_{21} + \delta_{21})$ is negative or positive. Hence, a parasitic species cannot regulate the growth of two distinct host species if the intrinsic growth rates of each species and the effect of the parasites on both are not equal. In these systems one of the host populations tends to become extinct, allowing the other population to be regulated if it satisfies the conditions established in the Anderson and May model, as in Figure 4.2, assuming that parasitism regulates at least one of the host populations.

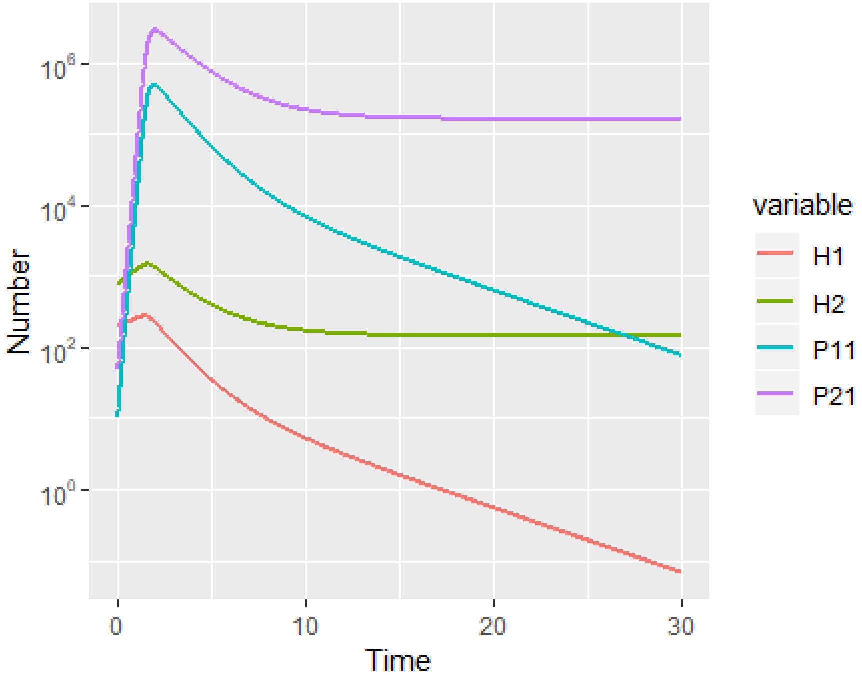


FIGURE 4.2: Population dynamics of the model (2.3) with $m = 2$, $n = 1$, parameter values $a_1 = 1.4$, $a_2 = 1.6$, $b_1 = b_2 = 1.05$, $\alpha_{11} = \alpha_{21} = 3 \times 10^{-4}$, $\delta_{11} = \delta_{21} = 1 \times 10^{-4}$, $\beta_{10} = \beta_{20} = 0.1$, $\mu_{11} = \mu_{21} = 1.2$, $k_{11} = k_{21} = 0.1$, $\lambda = 10$, $\gamma_0 = 10$, and initial conditions $H_1 = 200$, $H_2 = 800$, $P_{11} = 10$, $P_{21} = 50$.

Now, we need to analyze the case where the two host species in the system have the same growth rate in the absence of parasitism and the parameters corresponding to the interaction of parasites with both host species are equal. Under these conditions, system (4.7) can be written as

$$\begin{aligned}
\frac{dH_1}{dt} &= (a-b)H_1 - (\alpha+\delta)P_{11},\\
\frac{dH_2}{dt} &= (a-b)H_2 - (\alpha+\delta)P_{21},\\
\frac{dP_{11}}{dt} &= \frac{\lambda\beta H_1(P_{11}+P_{21})}{\gamma+\beta(H_1+H_2)} - (\mu+b+\alpha)P_{11} - \alpha\frac{1+k}{k}\frac{P_{11}^2}{H_1},\\
\frac{dP_{21}}{dt} &= \frac{\lambda\beta H_2(P_{11}+P_{21})}{\gamma+\beta(H_1+H_2)} - (\mu+b+\alpha)P_{21} - \alpha\frac{1+k}{k}\frac{P_{21}^2}{H_2}.
\end{aligned} \tag{4.11}$$

Following the same analysis, the equations (4.10) are expressed by the equation

$$\left(\lambda\beta\frac{a-b}{\alpha+\delta} - \beta B\right)H_1^* + \left(\lambda\beta\frac{a-b}{\alpha+\delta} - \beta B\right)H_2^* = B\gamma, \tag{4.12}$$

where $B = B_1 = B_2$ defined in (4.9), that is,

$$B = \frac{a-b}{\alpha+\delta}\left[\mu+b+\alpha-\alpha\frac{1+k}{k}\left(\frac{a-b}{\alpha+\delta}\right)\right].$$

Since we look for positive values of $H_1^*$ and $H_2^*$, there is $c>0$ such that $H_2^* = cH_1^*$. Thus, the equation (4.12) allows to determine the value of $H_1^*$, given by

$$H_1^* = \frac{B\gamma}{(1+c)\left(\lambda\beta\frac{a-b}{\alpha+\delta} - \beta B\right)},$$

and, from (4.2) it follows that the values $H_2^*$, $P_{11}^*$ and $P_{21}^*$ are

$$\begin{aligned}
H_2^* &= \frac{cB\gamma}{(1+c)\left(\lambda\beta\frac{a-b}{\alpha+\delta} - \beta B\right)},\\
P_{11}^* &= \frac{(a-b)B\gamma}{(\alpha+\delta)(1+c)\left(\lambda\beta\frac{a-b}{\alpha+\delta} - \beta B\right)},\\
P_{21}^* &= \frac{c(a-b)B\gamma}{(\alpha+\delta)(1+c)\left(\lambda\beta\frac{a-b}{\alpha+\delta} - \beta B\right)}.
\end{aligned}$$

Therefore, for the existence of a biologically acceptable equilibrium point is necessary that the intrinsic growth rates for both host species are equal, just as it is necessary that the parasitic species have the same effect on both host species.

Since in a neighborhood of $(H_1^*, H_2^*, P_{11}^*, P_{21}^*)$ it is satisfied that $H_2 \approx cH_1$ and $P_{21} \approx cP_{11}$, we have that

$$\begin{aligned}\frac{dH_1}{dt} &= (a-b)H_1 - (\alpha+\delta)P_{11},\\ \frac{dP_{11}}{dt} &= \frac{\lambda\beta' H_1 P_{11}}{\gamma+\beta' H_1} - (\mu+b+\alpha)P_{11} - \alpha\frac{1+k}{k}\frac{P_{11}^2}{H_1},\end{aligned}$$

where $\beta' = \beta(1+c)$, so, from the previous section it follows that $(H_1^*, P_{11}^*)$ is locally stable whenever $H_1^* > 0$ and $P_{11}^* > 0$, what happens if and only if $\lambda > b + \mu + \alpha + (1+k)(a-b)/k$. The same is true for $(H_2^*, P_{21}^*)$ in the system $dH_2 \approx d(cH_1)$, $dP_{21} \approx d(cP_{11})$. Therefore, in a neighborhood of $(H_1^*, H_2^*, P_{11}^*, P_{21}^*)$ the system (4.11) is stable, and the value of $c$ is given by $c = H_2(0)/H_1(0)$.

From the above we conclude that it is possible to mathematically determine if a parasite can colonize two different host species, depending on the intrinsic growth rates of both species and the effect that the parasite would have on the hosts. Figure 4.3 shows a simulation of the system (4.11) where the conditions for the existence and stability of the equilibrium point are satisfied.

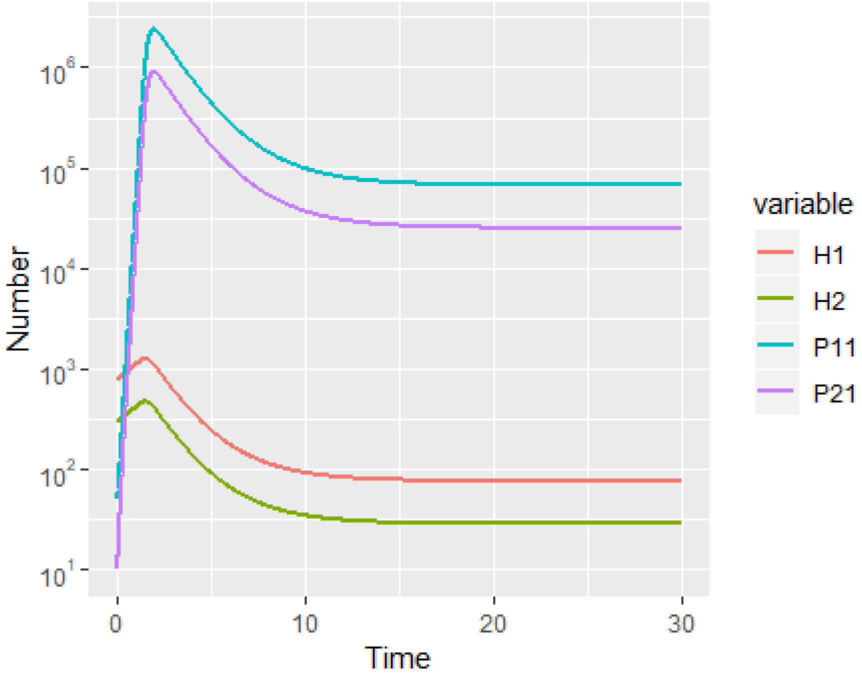


FIGURE 4.3: Population dynamics of the model (2.3) with $m = 2$, $n = 1$, parameter values $a = 1.4$, $b = 1.05$, $\alpha = 3\times10^{-4}$, $\delta = 1\times10^{-4}$, $\beta = 0.1$, $\mu = 1.2$, $k = 0.1$, $\lambda = 10$, $\gamma = 10$, and initial conditions $H_1 = 800$, $H_2 = 300$, $P_{11} = 50$, $P_{21} = 10$.

Following the same analysis, we obtain the same results for the generalization of this case where only adult parasites can colonize individuals from a community with $m$ host species where there is no predation, for any $m \geq 2$. This because, an equilibrium point of the system

$$\begin{aligned} \frac{dH_i}{dt} &= (a_i - b_i)H_i - (\alpha_{i1} + \delta_{i1})P_{i1}, \\ \frac{dP_{i1}}{dt} &= \frac{\lambda\beta_{i0}H_i \sum_{r=1}^{m} P_{r1}}{\gamma_0 + \sum_{r=1}^{m}\beta_{r0}H_r} - (\mu_{i1} + b_i + \alpha_{i1})P_{i1} - \alpha_{i1}\frac{1+k_{i1}}{k_{i1}}\frac{P_{i1}^2}{H_i}, \end{aligned} \tag{4.13}$$

must satisfy (4.4)

$$\frac{\lambda\beta_{i0}\sum_{r=1}^{m}\dfrac{a_r - b_r}{\alpha_{r1} + \delta_{r1}}H_r^*}{\gamma_0 + \sum_{r=1}^{m}\beta_{r0}H_r^*} = B_i,$$

where $B_i$, defined as (4.3), are

$$B_i = \frac{a_i - b_i}{\alpha_{i1} + \delta_{i1}}\left[\mu_{i1} + b_i + \alpha_{i1} - \alpha_{i1}\frac{1+k_{i1}}{k_{i1}}\left(\frac{a_i - b_i}{\alpha_{i1} + \delta_{i1}}\right)\right]$$

for all $i = 1, \ldots, m$, from what follows

$$\frac{\lambda\beta_{i0}}{B_i}\sum_{r=1}^{m}\frac{a_r - b_r}{\alpha_{r1} + \delta_{r1}}H_r^* = \gamma_0 + \sum_{r=1}^{m}\beta_{r0}H_r^*,$$

for all $i = 1, \ldots, m$. Hence, if $\beta_{i_1 0}/B_{i_1} \neq \beta_{i_2 0}/B_{i_2}$ for any $i_1, i_2 \in \{1, \ldots, m\}$, then

$$\left(\frac{\lambda\beta_{i_1 0}}{B_{i_1}} - \frac{\lambda\beta_{i_2 0}}{B_{i_2}}\right)\sum_{r=1}^{m}\frac{a_r - b_r}{\alpha_{r1} + \delta_{r1}}H_r^* = 0$$

implies that

$$\sum_{r=1}^{m}\frac{a_r - b_r}{\alpha_{r1} + \delta_{r1}}H_r^* = 0,$$

and, since $(a_r - b_r)/(\alpha_{r1} + \delta_{r1})$ is positive for all $r = 1, \ldots, m$, then $H_r^* < 0$ for some $1 \leq r \leq m$. For the above, a necessary condition for a biologically acceptable equilibrium point to exist is that the intrinsic growth rates of all host species are equal and that the parasites have the same effect on all host species.

Now, if we define $c_1, \ldots, c_{m-1}$ such that $H_i^* = c_{i-1}H_1^*$ for all $i = 2, \ldots, m$, where $(H_1^*, \ldots, H_m^*)$ are the sizes of the host populations at the equilibrium point of (4.13),if it exists, then, from (4.4), it follows

$$\gamma B = \left(\lambda\beta\frac{a-b}{\alpha+\delta} - \beta B\right)\sum_{r=1}^{m}H_r^* = \left(1 + \sum_{r=2}^{m}c_{r-1}\right)\left(\lambda\beta\frac{a-b}{\alpha+\delta} - \beta B\right)H_1^*,$$

where $B$, defined as (4.3), is

$$B = \frac{a-b}{\alpha+\delta}\left[\mu + b + \alpha - \alpha\frac{1+k}{k}\left(\frac{a-b}{\alpha+\delta}\right)\right]$$

for all $i = 1, \ldots, m$. Therefore, the equilibrium point is given by

$$H_1^* = \frac{\gamma B}{\left(1+\sum_{r=2}^{m} c_{r-1}\right)\left(\lambda\beta\frac{a-b}{\alpha+\delta} - \beta B\right)}, \quad H_r^* = c_{r-1}H_1^* \text{ and } P_{i1} = \frac{a-b}{\alpha+\delta}H_i^*,$$

for all $r = 2, \ldots, m$. Thus, for the equilibrium point to exist, it is necessary that $\lambda > b + \mu + \alpha + (1+k)(a-b)/k$. This condition, as in the A&M model, also guarantees the local stability of the system.

Figure 4.4 shows a simulation of a system with five host species that satisfy the conditions for existence and stability of the equilibrium point.

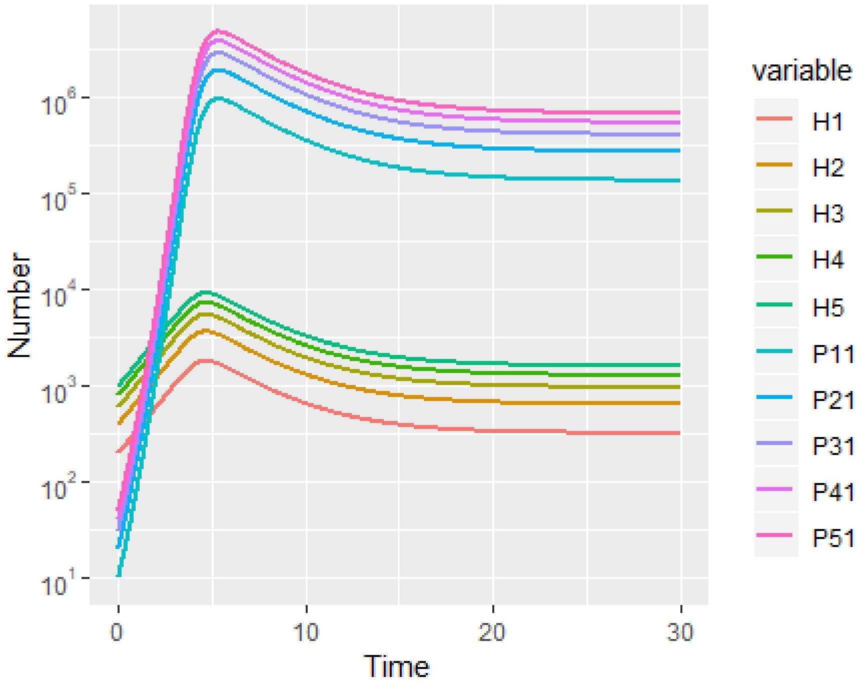


FIGURE 4.4: Population dynamics of the model (2.3) with $m = 5$, $n = 1$, parameter values $a = 1.6$, $b = 1.05$, $\alpha = 5 \times 10^{-4}$, $\delta = 8 \times 10^{-4}$, $\beta = 0.01$, $\mu = 1.6$, $k = 0.1$, $\lambda = 6$, $\gamma = 10$, and initial conditions $H_1 = 200$, $H_2 = 400$, $H_3 = 600$, $H_4 = 800$, $H_5 = 1000$, $P_{11} = 10$, $P_{21} = 20$, $P_{31} = 30$, $P_{41} = 40$, $P_{51} = 50$.

## 4.3 Case $m$=1, $n$=2

When there is a single host species in the system, biologically it makes sense to assume that the parasite reaches its reproductive maturity within the same host colonized in the first stage of its life cycle when it undergoes a metamorphosis, instead of changing the stage of its life cycle leaving one host and colonizing another.

To simplify the model, we only consider the effect of adult parasites on the fertility and mortality of the hosts, this under the assumption that individuals of the parasitic stages that occur before reproductive maturity have a significantly lower effect on the hosts than the effect of adult parasites, so this consideration does not really affect the model most of the time. Only in cases where the host and parasite populations grow without regulation is it necessary to consider the effect of all parasitic stages on each host species. Similarly, in multi-host models we consider only the effect of the most developed parasitic population within the same host species. With this assumption, the model coincides with the Dobson and Hudson model, so, using the same notation as in (1.3), we have

$$\begin{aligned}
\frac{dH}{dt} &= (a-b)H - (\alpha+\delta)\,P,\\
\frac{dA}{dt} &= \frac{\lambda PH}{H+H_0} - (\mu_A + b + \theta)\,A - \alpha\frac{PA}{H},\\
\frac{dP}{dt} &= \theta A - (\mu_P + b + \alpha)\,P - \alpha\left(\frac{k+1}{k}\right)\frac{P^2}{H}.
\end{aligned}$$

Taking $H' = A' = P' = 0$ we obtain that the equilibrium point must satisfy

$$\begin{aligned}
P^* = \frac{(a-b)H^*}{\alpha+\delta} \;\Rightarrow\; & \theta A^* - \left(\mu_P + b + \alpha + \frac{\alpha(a-b)(k+1)}{(\alpha+\delta)k}\right)P^* = 0\\
\Rightarrow\; & \theta A^* - B_1 P^* = 0\\
\Rightarrow\; & A^* = \frac{B_1 P^*}{\theta} = \frac{B_1(a-b)H^*}{\theta(\alpha+\delta)}\\
\Rightarrow\; & \frac{\lambda\theta H^*}{B_1(H^*+H_0)} - (\mu_A + b + \theta) - \frac{\alpha(a-b)}{\alpha+\delta} = 0\\
\Rightarrow\; & H^* = \frac{B_1 B_2 H_0}{\lambda\theta - B_1 B_2},\\
& A^* = \frac{(a-b)B_1^2 B_2 H_0}{\theta(\alpha+\delta)(\lambda\theta - B_1 B_2)},\\
& P^* = \frac{(a-b)B_1 B_2 H_0}{(\alpha+\delta)(\lambda\theta - B_1 B_2)},
\end{aligned} \tag{4.14}$$

where

$$B_1 = \mu_P + b + \alpha + \frac{\alpha(a-b)(k+1)}{(\alpha+\delta)k} \quad \text{and} \quad B_2 = \mu_A + b + \theta + \frac{\alpha(a-b)}{\alpha+\delta}.$$

Therefore, the necessary condition for a non-trivial equilibrium point with positive population sizes to exist is $\lambda\theta > B_1 B_2$.

As with the Anderson and May model we analyzed in the case $m = n = 1$, we consider the eigenvalues of the linearized system to determine if $(H^*, A^*, P^*)$ is a stable equilibrium point. For this, we calculate the characteristic polynomial $P(c)$ as follows

$$\det\begin{pmatrix} a-b-c & 0 & -(\alpha+\delta) \\ \frac{\lambda P^* H_0}{(H^*+H_0)^2} + \frac{\alpha A^* P^*}{(H^*)^2} & -(\mu_A + b + \theta) - \frac{\alpha P^*}{H^*} - c & \frac{\lambda H^*}{H^*+H_0} - \frac{\alpha A^*}{H^*} \\ \alpha\frac{k+1}{k}\frac{(P^*)^2}{(H^*)^2} & \theta & -(\mu_P + b + \alpha) - 2\alpha\frac{k+1}{k}\frac{P^*}{H^*} - c \end{pmatrix}$$

what is equal to

$$\det\begin{pmatrix} a-b-c & 0 & -(\alpha+\delta) \\ \frac{(a-b)B_1B_2(\lambda\theta-B_1B_2)}{(\alpha+\delta)\lambda\theta^2} + \frac{\alpha(a-b)^2B_1}{(\alpha+\delta)^2\theta} & -B_2 - c & \frac{B_1B_2}{\theta} - \frac{\alpha B_1(a-b)}{\theta(\alpha+\delta)} \\ \frac{\alpha(k+1)(a-b)^2}{k(\alpha+\delta)^2} & \theta & -B_1 - \frac{\alpha(k+1)(a-b)}{k(\alpha+\delta)} - c \end{pmatrix},$$

so

$$\begin{aligned} P(c) = &- c^3 - \left[B_1 + B_2 + \frac{(\alpha-\delta k)(a-b)}{k(\alpha+\delta)}\right]c^2 - \frac{(a-b)[(\alpha-\delta k)B_2 - \delta k B_1]}{(\alpha+\delta)k}c \\ &- \frac{(a-b)B_1B_2(\lambda\theta - B_1B_2)}{\lambda\theta}A_0. \end{aligned}$$

Considering $-P(c)$ instead of $P(c)$, the Routh-Hurwitz stability criterion require

$$\begin{gathered} \frac{(a-b)B_1B_2(\lambda\theta-B_1B_2)}{\lambda\theta} > 0, \\ B_1 + B_2 + \frac{(\alpha-\delta k)(a-b)}{k(\alpha+\delta)} > 0, \\ \left[B_1 + B_2 + \frac{(\alpha-\delta k)(a-b)}{k(\alpha+\delta)}\right]\frac{(a-b)[(\alpha-\delta k)B_2 - \delta k B_1]}{(\alpha+\delta)k} > \frac{(a-b)B_1B_2(\lambda\theta-B_1B_2)}{\lambda\theta}, \end{gathered} \tag{4.15}$$

so that the eigenvalues of the linearized system have a negative real part, implying that $(H^*, A^*, P^*)$ is locally stable.

A sufficient condition for inequality $B_1 + B_2 + (\alpha - \delta k)(a - b)/k(\alpha + \delta) > 0$ to be true is that $\alpha > \delta k$.

Now, since $\lambda\theta > B_1 B_2$ is a necessary condition for the equilibrium point to exist, the inequality $(a - b)B_1 B_2(\lambda\theta - B_1 B_2)/\lambda\theta > 0$ is always true.

Finally, a necessary condition for the third inequality in (4.15) to be true is that $(\alpha - \delta k)B_2 > \delta k B_1$. However, this inequality cannot be easily simplified, so we consider that the conditions for the existence of a stable equilibrium point in the system are $\alpha > \delta k$, $\lambda\theta > B_1 B_2$ and

$$\left[B_1 + B_2 + \frac{(\alpha - \delta k)(a - b)}{k(\alpha + \delta)}\right] \frac{(\alpha - \delta k)B_2 - \delta k B_1}{(\alpha + \delta)k} > \frac{B_1 B_2(\lambda\theta - B_1 B_2)}{\lambda\theta}.$$

Figure 4.5 shows the dynamics of the host and parasite populations in a system where the conditions for the existence and stability of the equilibrium point are satisfied, using parameter values within the ranges established in [6, 10, 31] for the *Trichostrongylus tenuis* and red grouse populations, and initial conditions $H = 200$, $A = 30$, $P = 10$.

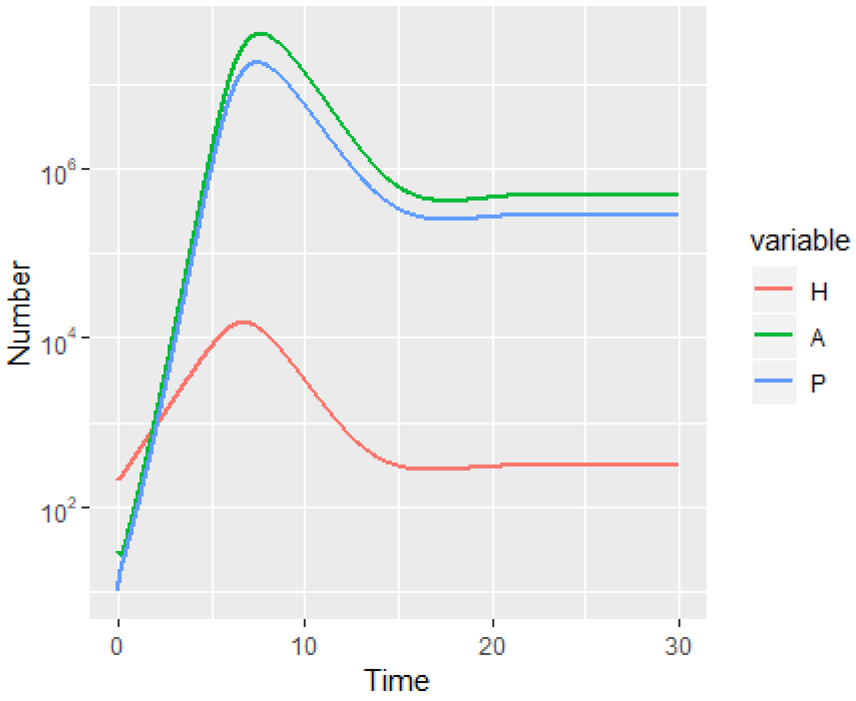


FIGURE 4.5: Population dynamics of the D&H model with parameter values $a = 1.8$, $b = 1.05$, $\alpha = 3 \times 10^{-4}$, $\delta = 5 \times 10^{-4}$, $\beta = 0.1$, $\theta = 3$, $\mu_A = 0.5$, $\mu_P = 1$, $k = 0.1$, $\lambda = 11$, $\gamma = 10$, and initial conditions $H = 200$, $A = 30$, $P = 10$.

Following the same analysis performed previously, we can determine the equilibrium point of the generalization of this case, with a single host species and $n$ parasitic stages within the hosts, obtained by taking $m = 1$ in (2.3), and assuming the same hypothesis formulated in the Dobson and Hudson model that only the population of adult parasites affects guests, since the populations of parasites that do not yet reach its reproductive maturity have a very small effect on guests compared to the effect caused by adult parasites.

Simplifying the notation, the equilibrium point $(H^*, P_1^*, \dots, P_n^*)$ satisfies

$$\begin{aligned}
0 &= (a-b)H^* - (\alpha+\delta)\,P_n^*,\\
0 &= \frac{\lambda H^* P_n^*}{H^*+H_0} - (\mu_1+b+\theta_1)\,P_1^* - \alpha\frac{P_1^* P_n^*}{H^*},\\
0 &= \theta_{j-1}P_{j-1}^* - (\mu_j+b+\theta_j)\,P_j^* - \alpha\frac{P_j^* P_n^*}{H^*},\\
0 &= \theta_{n-1}P_{n-1}^* - (\mu_n+b+\alpha)\,P_n^* - \frac{\alpha\,(1+k)}{k}\frac{(P_n^*)^2}{H^*},
\end{aligned}$$

and in consequence

$$P_n^* = \frac{(a-b)H^*}{\alpha+\delta} \;\Rightarrow\; P_{j-1}^* = \frac{B_j}{\theta_{j-1}}P_j^*,\; j = 2\dots,n,$$

where $B_j$ is defined as

$$B_j = \begin{cases} \mu_j + b + \theta_j + \dfrac{\alpha(a-b)}{\alpha+\delta} & \text{if } 1 \le j \le n-1,\\[2ex] \mu_j + b + \alpha + \dfrac{\alpha(a-b)(1+k)}{(\alpha+\delta)k} & \text{if } j = n. \end{cases}$$

Therefore,

$$\begin{aligned}
P_n^* = \prod_{j=2}^{n}\frac{\theta_{j-1}}{B_j}P_1^* \;&\Rightarrow\; \frac{\lambda H^*\prod_{j=1}^{n-1}\theta_j}{(H^*+H_0)\prod_{j=2}^{n}B_j} - B_1 = 0\\
&\Rightarrow\; H^* = \frac{H_0\prod_{j=1}^{n}B_j}{\lambda\prod_{j=1}^{n-1}\theta_j - \prod_{j=1}^{n}B_j},\\
&\qquad P_j^* = \frac{(a-b)H_0\left(\prod_{j=1}^{n}B_j\right)\left(\prod_{l=j}^{n-1}B_l\right)}{\left(\prod_{l=j}^{n-1}\theta_l\right)(\alpha+\delta)\left(\lambda\prod_{j=1}^{n-1}\theta_j - \prod_{j=1}^{n}B_j\right)}.
\end{aligned}$$

Hence, it is necessary that $\lambda\prod_{j=1}^{n-1}\theta_j > \prod_{j=1}^{n}B_j$ for the non-trivial equilibrium point to exist.

We can determine the conditions for the equilibrium point to be stable using the Routh-Hurwitz stability criterion (see Appendix B) in the characteristic polynomial of the Jacobian matrix of the system at the equilibrium point, denoted $J$, given by

$$J = \begin{pmatrix} a-b & 0 & 0 & 0 & \dots & 0 & -(\alpha+\delta) \\ \frac{\lambda H_0 P_n^*}{(H^*+H_0)^2} + \frac{\alpha P_1^* P_n^*}{(H^*)^2} & -B_1 & 0 & 0 & \dots & 0 & -\frac{\alpha P_1^*}{H^*} \\ \frac{\alpha P_2^* P_n^*}{(H^*)^2} & \theta_1 & -B_2 & 0 & \dots & 0 & -\frac{\alpha P_2^*}{H^*} \\ \frac{\alpha P_3^* P_n^*}{(H^*)^2} & 0 & \theta_2 & -B_3 & \dots & 0 & -\frac{\alpha P_3^*}{H^*} \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \frac{\alpha P_{n-1}^* P_n^*}{(H^*)^2} & 0 & 0 & 0 & \dots & -B_{n-1} & -\frac{\alpha P_{n-1}^*}{H^*} \\ \frac{\alpha(1+k)(P_n^*)^2}{k(H^*)^2} & 0 & 0 & 0 & \dots & \theta_{n-1} & -B_n - \frac{\alpha(1+k)P_n^*}{kH^*} \end{pmatrix}$$

The above allows to study any system where a parasite colonizes individuals from a community with a single host species. Figure 4.6 shows an example of a stable system where there is a parasitic species with more than two stages of its life cycle within the same host.

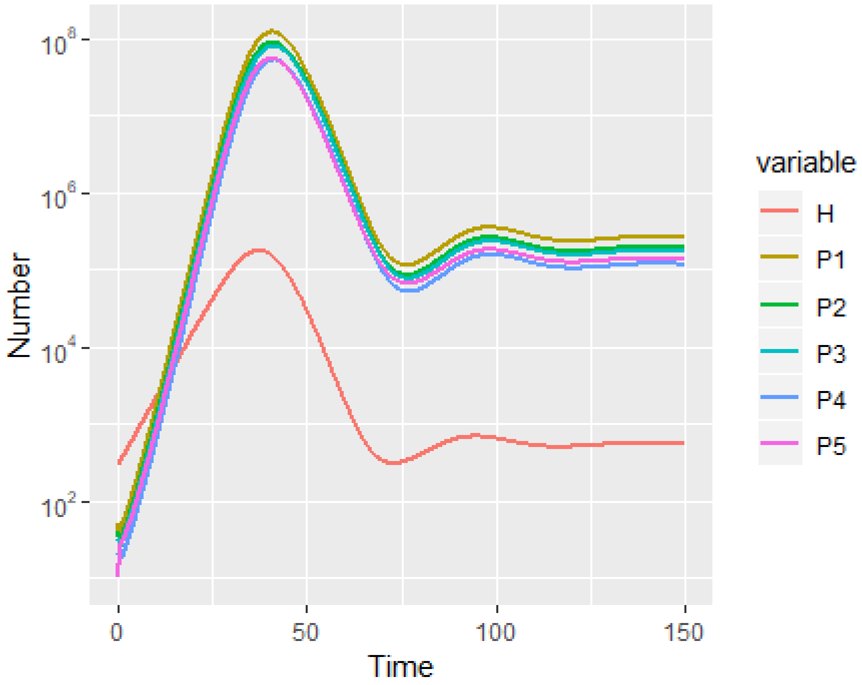


FIGURE 4.6: Population dynamics of the model (2.3) with $m = 1$, $n = 5$, parameter values $a = 1.3$, $b = 1.1$, $\alpha = 3 \times 10^{-4}$, $\delta = 5 \times 10^{-4}$, $\beta = 0.1$, $\theta_1 = 4$, $\theta_2 = 4$, $\theta_3 = 3$, $\theta_4 = 3$, $\mu_1 = 0.2$, $\mu_2 = 0.2$, $\mu_3 = 0.3$, $\mu_1 = 0.3$, $\mu_5 = 0.6$, $k = 0.1$, $\lambda = 12$, $\gamma = 10$, and initial conditions $H = 300$, $P_1 = 50$, $P_2 = 40$, $P_3 = 30$, $P_4 = 20$, $P_5 = 10$.

## 4.4 Case $m$=2, $n$=2

In the previous models there was a single possible parasitic transmission network, however, for cases where there are $m > 1$ different host species in the system and the parasite life cycle consists of more than one stage within the hosts, it is necessary to analyze the possible transmission networks with different topologies in order to determine the model that best fits to the conditions of the system.

Figure 4.7 shows the possible topologically distinct parasitic transmission networks in a system with $m = 2$, $n = 2$, assuming that there must be individuals of at least one parasitic stage in the population of each host species.

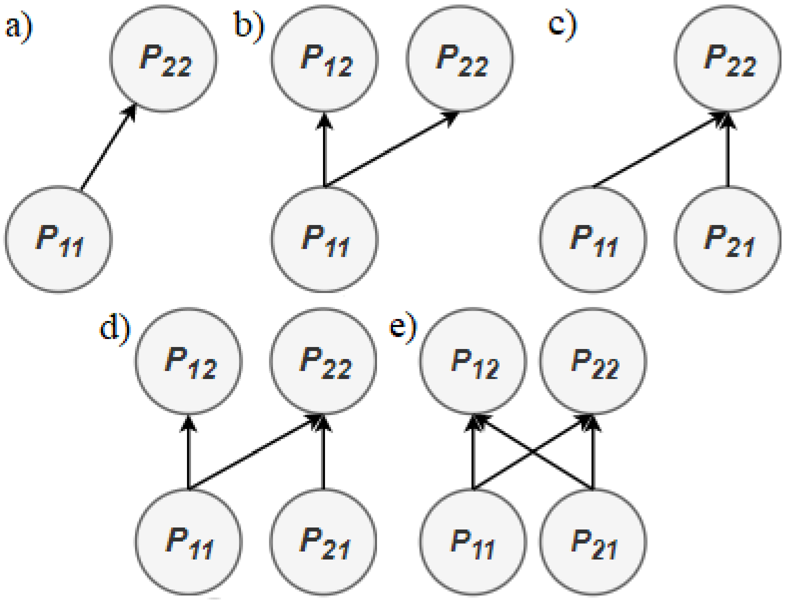


FIGURE 4.7: Topologically distinct parasitic transmission networks in (2.3) with $m = n = 2$.

Since there are only two host species, given the hypothesis that at least one host species grows exponentially in the absence of parasitism, we consider that there are no trophic interactions in any of the transmission networks shown in Figure 4.7.

### Case a)

There are two different models for the case where the stages of the parasite's life cycle occur within individuals of different host species: one considering that parasitic transmission between hosts occurs by non-trophic contact and the other when the parasite remains in free life between both stages of its life cycle. When parasites are transmitted directly between non-trophic related hosts, model (2.3) looks like

$$\begin{aligned}
\frac{dH_1}{dt} &= (a_1 - b_1)H_1 - (\alpha_{11} + \delta_{11})P_{11},\\
\frac{dH_2}{dt} &= (a_2 - b_2)H_2 - (\alpha_{22} + \delta_{22})P_{22},\\
\frac{dP_{11}}{dt} &= \frac{\lambda\beta_{10}H_1P_{22}}{\gamma_0 + \beta_{10}H_1} - \left(\mu_{11} + b_1 + \alpha_{11} + \theta_{12}^1 H_2\right) P_{11} - \alpha_{11}\frac{1 + k_{11}}{k_{11}}\frac{P_{11}^2}{H_1},\\
\frac{dP_{22}}{dt} &= \theta_{12}^1 H_2 P_{11} - (\mu_{22} + b_2 + \alpha_{22})P_{22} - \alpha_{22}\frac{1 + k_{22}}{k_{22}}\frac{P_{22}^2}{H_2},
\end{aligned} \tag{4.16}$$

while, for the case where the parasite remains in free life between one parasitic stage and the next, the system of equations is

$$\begin{aligned}
\frac{dH_1}{dt} &= (a_1 - b_1)H_1 - (\alpha_{11} + \delta_{11})P_{11},\\
\frac{dH_2}{dt} &= (a_2 - b_2)H_2 - (\alpha_{22} + \delta_{22})P_{22},\\
\frac{dP_{11}}{dt} &= \frac{\lambda\beta_{10}H_1P_{22}}{\gamma_0 + \beta_{10}H_1} - \left(\mu_{11} + b_1 + \alpha_{11} + \epsilon_{11}\right) P_{11} - \alpha_{11}\frac{1 + k_{11}}{k_{11}}\frac{P_{11}^2}{H_1},\\
\frac{dP_{22}}{dt} &= \frac{\epsilon_{11}\beta_{21}H_2P_{11}}{\gamma_1 + \beta_{21}H_2} - (\mu_{22} + b_2 + \alpha_{22})P_{22} - \alpha_{22}\frac{1 + k_{22}}{k_{22}}\frac{P_{22}^2}{H_2}.
\end{aligned} \tag{4.17}$$

These systems have the form (4.1), so, (4.4) and (4.6) imply that an equilibrium point of (4.16) must satisfy

$$\begin{aligned}
B_{11} &= \frac{\lambda\beta_{10}}{\gamma_0 + \beta_{10}H_1^*}\left(\frac{a_2 - b_2}{\alpha_{22} + \delta_{22}}\right) H_2^* - \theta_{12}^1 H_2^* \frac{a_1 - b_1}{\alpha_{11} + \delta_{11}},\\
B_{22} &= \theta_{12}^1 H_1^* \frac{a_1 - b_1}{\alpha_{11} + \delta_{11}},
\end{aligned}$$

where

$$B_{ii} = \frac{a_i - b_i}{\alpha_{ii} + \delta_{ii}}\left[\mu_{ii} + b_i + \alpha_{ii} + \alpha_{ii}\frac{1 + k_{ii}}{k_{ii}}\left(\frac{a_i - b_i}{\alpha_{ii} + \delta_{ii}}\right)\right],$$

for $i = 1, 2$. Since $H_1^* \neq 0$ and $H_2^* \neq 0$, the above implies that

$$\begin{aligned}
H_1^* &= \frac{B_{22}(\alpha_{11} + \delta_{11})}{\theta_{12}^1(a_1 - b_1)},\\
H_2^* &= \frac{B_{11}}{\dfrac{\lambda\beta_{10}\theta_{12}^1(a_1 - b_1)}{\gamma_0\theta_{12}^1(a_1 - b_1) + \beta_{10}B_{22}(\alpha_{11} + \delta_{11})}\left(\dfrac{a_2 - b_2}{\alpha_{22} + \delta_{22}}\right) - \theta_{12}^1\left(\dfrac{a_1 - b_1}{\alpha_{11} + \delta_{11}}\right)},
\end{aligned}$$

and then

$$P_{11}^* = \frac{B_{22}}{\theta_{12}^1},$$

$$P_{22}^{*} = \frac{B_{11}\left(\dfrac{a_2 - b_2}{\alpha_{22} + \delta_{22}}\right)}{\dfrac{\lambda\beta_{10}\theta_{12}^{1}(a_1 - b_1)}{\gamma_0\theta_{12}^{1}(a_1 - b_1) + \beta_{10}B_{22}(\alpha_{11} + \delta_{11})}\left(\dfrac{a_2 - b_2}{\alpha_{22} + \delta_{22}}\right) - \theta_{12}^{1}\left(\dfrac{a_1 - b_1}{\alpha_{11} + \delta_{11}}\right)}.$$

Therefore, for there to be a biological acceptable equilibrium point in (4.16), it is necessary that

$$\lambda\beta_{10}\left(\frac{a_2 - b_2}{\alpha_{22} + \delta_{22}}\right) > \gamma_0\theta_{12}^{1}\left(\frac{a_1 - b_1}{\alpha_{11} + \delta_{11}}\right) + \beta_{10}B_{22}.$$

As in the previous cases, we analyze the eigenvalues of the linearized system to determine the stability of the equilibrium point. We first calculate the characteristic polynomial $P(c)$ of the Jacobian matrix of the system at the point $(H_1^*, H_2^*, P_{11}^*, P_{22}^*)$, given by

$$P(c) = \det\begin{pmatrix} J_{11} - c & 0 & J_{13} & 0 \\ 0 & J_{22} - c & 0 & J_{24} \\ J_{31} & J_{32} & J_{33} - c & J_{34} \\ 0 & J_{42} & J_{43} & J_{44} - c \end{pmatrix}$$

with

$$\begin{aligned}
J_{11} &= a_1 - b_1, \\
J_{22} &= a_2 - b_2, \\
J_{13} &= -(\alpha_{11} + \delta_{11}), \\
J_{24} &= -(\alpha_{22} + \delta_{22}), \\
J_{31} &= \frac{\lambda\beta_{10}\gamma_0 P_{22}^*}{(\gamma_0 + \beta_{10}H_1^*)^2} + \alpha_{11}\frac{1 + k_{11}}{k_{11}}\frac{(P_{11}^*)^2}{(H_1^*)^2} \\
J_{32} &= -\theta_{12}^{1}P_{11}^*, \\
J_{33} &= -\left(\mu_{11} + b_1 + \alpha_{11} + \theta_{12}^{1}H_2^* + 2\alpha_{11}\frac{1 + k_{11}}{k_{11}}\frac{P_{11}^*}{H_1^*}\right), \\
J_{34} &= \frac{\lambda\beta_{10}H_1^*}{\gamma_0 + \beta_{10}H_1^*}, \\
J_{42} &= \theta_{12}^{1}P_{11}^* + \alpha_{22}\frac{1 + k_{22}}{k_{22}}\frac{(P_{22}^*)^2}{(H_2^*)^2}, \\
J_{43} &= \theta_{12}^{1}H_2^*, \\
J_{44} &= -\left(\mu_{22} + b_2 + \alpha_{22} + 2\alpha_{22}\frac{1 + k_{22}}{k_{22}}\frac{P_{22}^*}{H_2^*}\right),
\end{aligned}$$

so, calculating the determinant, we have that $P(c) = c^4 + A_3c^3 + A_2c^2 + A_1c + A_0$, where

$$\begin{aligned}
A_0 =& J_{11}J_{22}J_{33}J_{44} + J_{13}J_{31}J_{24}J_{42} + J_{11}J_{24}J_{32}J_{43} - J_{11}J_{22}J_{34}J_{43} - J_{22}J_{44}J_{13}J_{31} \\
&- J_{11}J_{33}J_{24}J_{42}, \\
A_1 =& J_{11}J_{24}J_{42} + J_{33}J_{24}J_{42} + J_{22}J_{13}J_{31} + J_{22}J_{34}J_{43} + J_{11}J_{34}J_{43} + J_{44}J_{13}J_{31} \\
&- J_{11}J_{22}J_{33} - J_{24}J_{32}J_{43} - J_{11}J_{22}J_{44} - J_{22}J_{33}J_{44} - J_{11}J_{33}J_{44}, \\
A_2 =& J_{11}J_{22} + J_{11}J_{33} + J_{11}J_{44} + J_{22}J_{33} + J_{22}J_{44} + J_{33}J_{44} - J_{13}J_{31} - J_{24}J_{42} - J_{34}J_{43}, \\
A_3 =& - J_{11} - J_{22} - J_{33} - J_{44}.
\end{aligned}$$

Using the Routh-Hurwitz stability criterion presented in Appendix B we have that the necessary conditions for $(H_1^*, H_2^*, P_{11}^*, P_{22}^*)$ to be stable are $A_0 > 0$, $A_3 > 0$, $A_2A_3 - A_1 > 0$ and $(A_2A_3 - A_1)A_1 - A_0A_3^2 > 0$.

On the other hand, using (4.4) and (4.6) in the system (4.17) we obtain the following equations

$$\begin{aligned}
\frac{\lambda\beta_{10}}{\gamma_0 + \beta_{10}H_1^*}\left(\frac{a_2 - b_2}{\alpha_{22} + \delta_{22}}\right)H_2^* &= B_{11}, \\
\frac{\epsilon_{11}\beta_{21}}{\gamma_1 + \beta_{21}H_2^*}\left(\frac{a_1 - b_1}{\alpha_{11} + \delta_{11}}\right)H_1^* &= B_{22}
\end{aligned}$$

with $B_{11}$ and $B_{22}$ defined as in (4.3), that is,

$$\begin{aligned}
B_{11} &= \frac{a_1 - b_1}{\alpha_{11} + \delta_{11}}\left[\mu_{11} + b_1 + \alpha_{11} + \epsilon_{11} + \alpha_{11}\frac{1 + k_{11}}{k_{11}}\left(\frac{a_1 - b_1}{\alpha_{11} + \delta_{11}}\right)\right], \\
B_{22} &= \frac{a_2 - b_2}{\alpha_{22} + \delta_{22}}\left[\mu_{22} + b_2 + \alpha_{22} + \alpha_{22}\frac{1 + k_{22}}{k_{22}}\left(\frac{a_2 - b_2}{\alpha_{22} + \delta_{22}}\right)\right].
\end{aligned}$$

Therefore,

$$\begin{aligned}
H_1^* &= \frac{\lambda}{B_{11}}\left(\frac{a_2 - b_2}{\alpha_{22} + \delta_{22}}\right)H_2^* - \frac{\gamma_0}{\beta_{10}}, \\
H_2^* &= \frac{\epsilon_{11}}{B_{22}}\left(\frac{a_1 - b_1}{\alpha_{11} + \delta_{11}}\right)H_1^* - \frac{\gamma_1}{\beta_{21}},
\end{aligned}$$

from what follows that the equilibrium point is given by

$$
\begin{aligned}
H_1^* &= \frac{\dfrac{\lambda\gamma_1}{B_{11}\beta_{21}}\left(\dfrac{a_2-b_2}{\alpha_{22}+\delta_{22}}\right)+\dfrac{\gamma_0}{\beta_{10}}}{\dfrac{\lambda\epsilon_{11}}{B_{11}B_{22}}\left(\dfrac{a_1-b_1}{\alpha_{11}+\delta_{11}}\right)\left(\dfrac{a_2-b_2}{\alpha_{22}+\delta_{22}}\right)-1},\\
H_2^* &= \frac{\dfrac{\epsilon_{11}\gamma_0}{B_{22}\beta_{10}}\left(\dfrac{a_1-b_1}{\alpha_{11}+\delta_{11}}\right)+\dfrac{\gamma_1}{\beta_{21}}}{\dfrac{\lambda\epsilon_{11}}{B_{11}B_{22}}\left(\dfrac{a_1-b_1}{\alpha_{11}+\delta_{11}}\right)\left(\dfrac{a_2-b_2}{\alpha_{22}+\delta_{22}}\right)-1},\\
P_{11}^* &= \frac{\dfrac{a_1-b_1}{\alpha_{11}+\delta_{11}}\left[\dfrac{\lambda\gamma_1}{B_{11}\beta_{21}}\left(\dfrac{a_2-b_2}{\alpha_{22}+\delta_{22}}\right)+\dfrac{\gamma_0}{\beta_{10}}\right]}{\dfrac{\lambda\epsilon_{11}}{B_{11}B_{22}}\left(\dfrac{a_1-b_1}{\alpha_{11}+\delta_{11}}\right)\left(\dfrac{a_2-b_2}{\alpha_{22}+\delta_{22}}\right)-1},\\
P_{22}^* &= \frac{\dfrac{a_2-b_2}{\alpha_{22}+\delta_{22}}\left[\dfrac{\epsilon_{11}\gamma_0}{B_{22}\beta_{10}}\left(\dfrac{a_1-b_1}{\alpha_{11}+\delta_{11}}\right)+\dfrac{\gamma_1}{\beta_{21}}\right]}{\dfrac{\lambda\epsilon_{11}}{B_{11}B_{22}}\left(\dfrac{a_1-b_1}{\alpha_{11}+\delta_{11}}\right)\left(\dfrac{a_2-b_2}{\alpha_{22}+\delta_{22}}\right)-1}.
\end{aligned}
$$

Therefore, the necessary condition for a biologically acceptable equilibrium point of (4.17) to exist is

$$
\lambda\epsilon_{11}\left(\frac{a_1-b_1}{\alpha_{11}+\delta_{11}}\right)\left(\frac{a_2-b_2}{\alpha_{22}+\delta_{22}}\right) > B_{11}B_{22}.
$$

The stability conditions for this case are obtained by analyzing the eigenvalues of the characteristic polynomial $P(c)$, given by

$$
P(c) = \det\begin{pmatrix} J_{11}-c & 0 & J_{13} & 0\\ 0 & J_{22}-c & 0 & J_{24}\\ J_{31} & 0 & J_{33}-c & J_{34}\\ 0 & J_{42} & J_{43} & J_{44}-c \end{pmatrix}
$$

where

$$
\begin{aligned}
J_{11} &= a_1-b_1,\\
J_{22} &= a_2-b_2,\\
J_{13} &= -(\alpha_{11}+\delta_{11}),\\
J_{24} &= -(\alpha_{22}+\delta_{22}),\\
J_{31} &= \frac{\lambda\beta_{10}\gamma_0P_{22}^*}{(\gamma_0+\beta_{10}H_1^*)^2}+\alpha_{11}\frac{1+k_{11}}{k_{11}}\frac{(P_{11}^*)^2}{(H_1^*)^2},
\end{aligned}
$$

$$\begin{aligned}
J_{33} &= -\left(\mu_{11} + b_1 + \alpha_{11} + \epsilon_{11} + 2\alpha_{11}\frac{1+k_{11}}{k_{11}}\frac{P_{11}^*}{H_1^*}\right),\\
J_{34} &= \frac{\lambda\beta_{10}H_1^*}{\gamma_0 + \beta_{10}H_1^*},\\
J_{42} &= \frac{\epsilon_{11}\beta_{21}\gamma_1 P_{11}^*}{(\gamma_1 + \beta_{21}H_2^*)^2} + \alpha_{22}\frac{1+k_{22}}{k_{22}}\frac{(P_{22}^*)^2}{(H_2^*)^2},\\
J_{43} &= \frac{\epsilon_{11}\beta_{21}H_2^*}{\gamma_1 + \beta_{21}H_2^*},\\
J_{44} &= -\left(\mu_{22} + b_2 + \alpha_{22} + 2\alpha_{22}\frac{1+k_{22}}{k_{22}}\frac{P_{22}^*}{H_2^*}\right).
\end{aligned}$$

Calculating the determinant, we have that $P(c) = c^4 + A_3c^3 + A_2c^2 + A_1c + A_0$ where $A_0$, $A_1$, $A_2$ and $A_3$ are

$$\begin{aligned}
A_0 =& J_{11}J_{22}J_{33}J_{44} + J_{13}J_{31}J_{24}J_{42} + -J_{11}J_{22}J_{34}J_{43} - J_{22}J_{44}J_{13}J_{31} - J_{11}J_{33}J_{24}J_{42},\\
A_1 =& J_{11}J_{24}J_{42} + J_{33}J_{24}J_{42} + J_{22}J_{13}J_{31} + J_{22}J_{34}J_{43} + J_{11}J_{34}J_{43} + J_{44}J_{13}J_{31}\\
&- J_{11}J_{22}J_{33} - J_{11}J_{22}J_{44} - J_{22}J_{33}J_{44} - J_{11}J_{33}J_{44},\\
A_2 =& J_{11}J_{22} + J_{11}J_{33} + J_{11}J_{44} + J_{22}J_{33} + J_{22}J_{44} + J_{33}J_{44} - J_{13}J_{31} - J_{24}J_{42} - J_{34}J_{43},\\
A_3 =& -J_{11} - J_{22} - J_{33} - J_{44}.
\end{aligned}$$

Therefore, from the Routh-Hurwitz stability criterion presented in Appendix B it follows that the necessary conditions for the equilibrium point $(H_1^*, H_2^*, P_{11}^*, P_{22}^*)$ to be locally stable are $A_0 > 0$, $A_3 > 0$, $A_2A_3 - A_1 > 0$ and $(A_2A_3 - A_1)A_1 - A_0A_3^2 > 0$.

A numerical analysis of the conditions of existence and stability of the equilibrium point in the two possible systems of equations with this parasitic transmission network, suggests that for any combination of biologically feasible parameter values (non-negative or positive values, depending on the biological interpretation of each parameter) the equilibrium points of both systems are unstable or not biologically acceptable. However, it is possible to find parametric values such that the size of each of the populations at the equilibrium point is a number greater than one, and that satisfies that the host and parasitic populations are regulated for a relatively large period of time.

Figure 4.8 shows the simulation in different time periods of the populations in (4.17), with theoretical parametric values and initial conditions, found using the Tabu search algorithm (see [32, 33]) and the threshold host density of the system, which satisfy that host populations, that in the absence of parasitism would grow exponentially, are regulated for a period of time due to the introduction of a parasitic species into the system, even more, for a period of time the host species remains almost stable due to the presence of parasites.

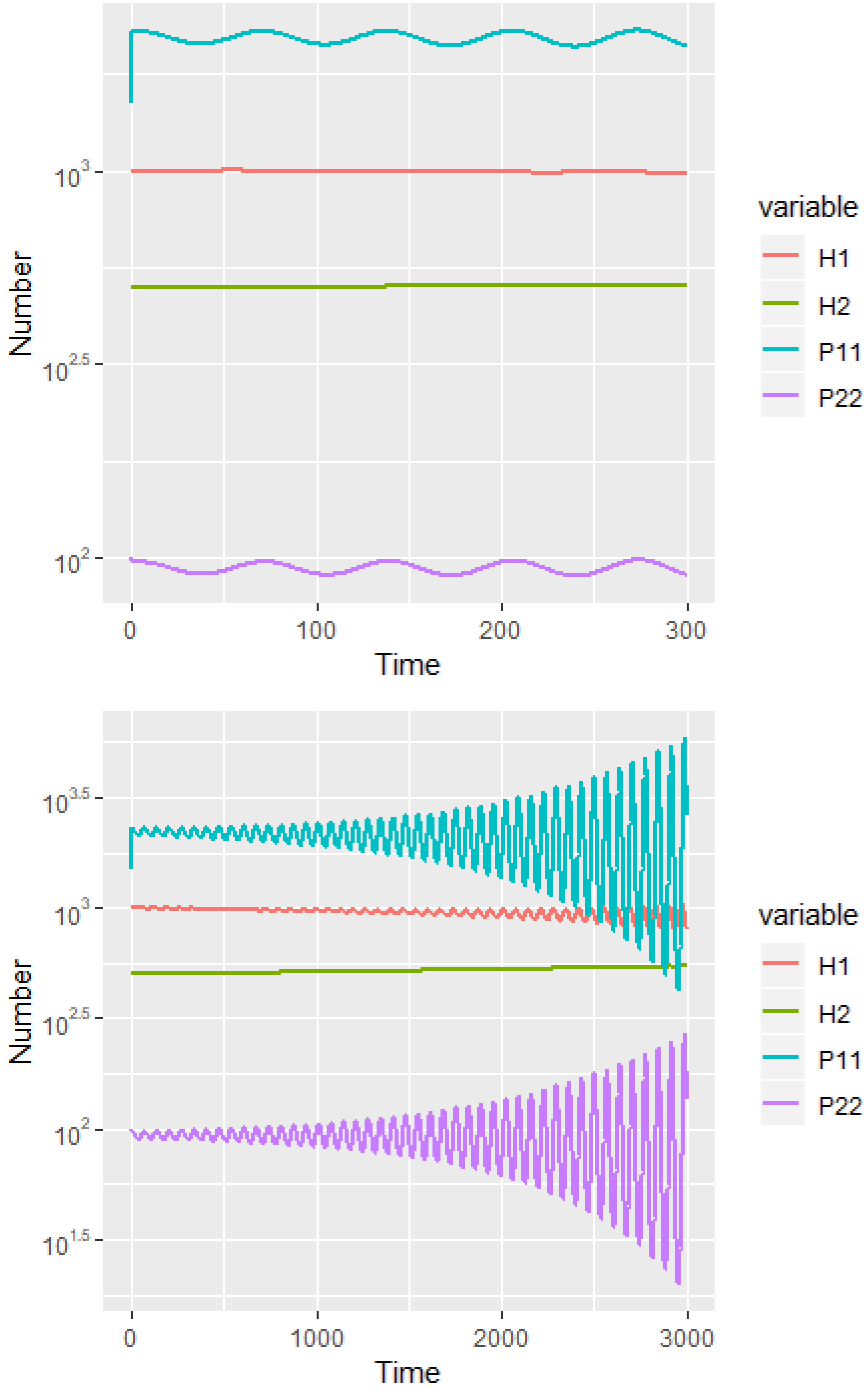


FIGURE 4.8: Population dynamics of the model (4.17) with parameter values $a_1 = 1.41$, $a_2 = 1.05018$, $b_1 = 1.4$, $b_2 = 1.05006$, $\alpha_{11} = 3 \times 10^{-5}$, $\alpha_{22} = 1 \times 10^{-5}$, $\delta_{11} = 4.5 \times 10^{-3}$, $\delta_{22} = 5 \times 10^{-4}$, $\beta_{10} = 1.211 \times 10^{-2}$, $\beta_{21} = 9 \times 10^{-5}$, $\mu_{11} = 1 \times 10^{-1}$, $\mu_{22} = 1 \times 10^{-5}$, $k_{11} = 1 \times 10^{-1}$, $k_{22} = 1$, $\lambda = 2.5 \times 10^2$, $\gamma_0 = 10^2$, $\gamma_1 = 10$, and initial conditions $H_1 = 1000$, $H_2 = 500$, $P_{11} = 1500$, $P_{21} = 100$.

**Case b)**

As in the previous section, we assume that, in the models where more than one parasitic stage occurs within the same host species, the parasitic transmission is given by contact between hosts. We make this assumption for all models with the same conditions. With this assumption, in the case where there are two host species that do not interact trophically, and the parasite can only enter one host species before reaching its adult stage in both host species, the model (2.3) has the form

$$\begin{aligned}
\frac{dH_1}{dt} &= (a_1-b_1)H_1-(\alpha_{12}+\delta_{12})P_{12},\\
\frac{dH_2}{dt} &= (a_2-b_2)H_2-(\alpha_{22}+\delta_{22})P_{22},\\
\frac{dP_{11}}{dt} &= \frac{\lambda\beta_{10}H_1(P_{12}+P_{22})}{\gamma_0+\beta_{10}H_1}-\left(\mu_{11}+b_1+\theta_{11}^1+\theta_{12}^1H_2\right)P_{11}-\alpha_{12}\frac{P_{11}P_{12}}{H_1},\\
\frac{dP_{12}}{dt} &= \theta_{11}^1P_{11}-\left(\mu_{12}+b_1+\alpha_{12}\right)P_{12}-\alpha_{12}\frac{1+k_{12}}{k_{12}}\frac{P_{12}^2}{H_1},\\
\frac{dP_{22}}{dt} &= \theta_{12}^1H_2P_{11}-(\mu_{22}+b_2+\alpha_{22})P_{22}-\alpha_{22}\frac{1+k_{22}}{k_{22}}\frac{P_{22}^2}{H_2}.
\end{aligned} \tag{4.18}$$

If there is an equilibrium point in (4.18), then

$$P_{i2}^*=\frac{a_i-b_i}{\alpha_{i2}+\delta_{i2}}H_i^*$$

for $i=1,2$. Replacing $P_{12}^*$ and $P_{22}^*$ in $dP_{12}=dP_{22}=0$ we obtain that

$$\begin{aligned}
0&=\left(\theta_{11}^1P_{11}^*-B_{12}H_1^*\right)H_1^*,\\
0&=\left(\theta_{12}^1P_{11}^*-B_{22}\right)H_2^*,
\end{aligned}$$

where

$$B_{i2}=\frac{a_i-b_i}{\alpha_{i2}+\delta_{i2}}\left[\mu_{i2}+b_i+\alpha_{i2}+\alpha_{i2}\frac{1+k_{i2}}{k_{i2}}\left(\frac{a_i-b_i}{\alpha_{i2}+\delta_{i2}}\right)\right]$$

for $i=1,2$. Therefore, $H_1^*$, $P_{11}^*$ and $P_{12}^*$ are given by

$$H_1^*=\frac{\theta_{11}^1B_{22}}{\theta_{12}^1B_{12}},\quad P_{11}^*=\frac{B_{22}}{\theta_{12}^1}\quad\text{and}\quad P_{12}^*=\frac{\theta_{11}^1B_{22}(a_1-b_1)}{\theta_{12}^1B_{12}(\alpha_{12}+\delta_{12})}.$$

Replacing $H_1^*$, $P_{11}^*$, $P_{12}^*$ and $P_{22}^*=(a_2-b_2)H_2^*/(\alpha_{22}+\delta_{22})$ in $dH_1=0$ it turns out that

$$\frac{\lambda\beta_{10}\frac{\theta_{11}^1 B_{22}}{\theta_{12}^1 B_{12}}\left(\frac{\theta_{11}^1 B_{22}(a_1-b_1)}{\theta_{12}^1 B_{12}(\alpha_{12}+\delta_{12})}+\frac{a_2-b_2}{\alpha_{22}+\delta_{22}}H_2^*\right)}{\gamma_0+\beta_{10}\frac{\theta_{11}^1 B_{22}}{\theta_{12}^1 B_{12}}}-B_{22}H_2^*-B_{11}=0,$$

where $B_{11}$ is defined as follows

$$B_{11}=\frac{B_{22}}{\theta_{12}^1}\left[\mu_{11}+b_1+\theta_{11}^1+\alpha_{12}\frac{a_1-b_1}{\alpha_{12}+\delta_{12}}\right],$$

so, the values of $H_2^*$ and $P_{22}^*$ are

$$H_2^*=\frac{\lambda\beta_{10}\frac{a_1-b_1}{\alpha_{12}+\delta_{12}}\left(\frac{\theta_{11}^1 B_{22}}{\theta_{12}^1 B_{12}}\right)^2-B_{11}\left(\gamma_0+\beta_{10}\frac{\theta_{11}^1 B_{22}}{\theta_{12}^1 B_{12}}\right)}{B_{22}\left(\gamma_0+\beta_{10}\frac{\theta_{11}^1 B_{22}}{\theta_{12}^1 B_{12}}\right)-\lambda\beta_{10}\frac{\theta_{11}^1 B_{22}}{\theta_{12}^1 B_{12}}\left(\frac{a_2-b_2}{\alpha_{22}+\delta_{22}}\right)},$$

$$P_{22}^*=\frac{\frac{a_2-b_2}{\alpha_{22}+\delta_{22}}\left[\lambda\beta_{10}\frac{a_1-b_1}{\alpha_{12}+\delta_{12}}\left(\frac{\theta_{11}^1 B_{22}}{\theta_{12}^1 B_{12}}\right)^2-B_{11}\left(\gamma_0+\beta_{10}\frac{\theta_{11}^1 B_{22}}{\theta_{12}^1 B_{12}}\right)\right]}{B_{22}\left(\gamma_0+\beta_{10}\frac{\theta_{11}^1 B_{22}}{\theta_{12}^1 B_{12}}\right)-\lambda\beta_{10}\frac{\theta_{11}^1 B_{22}}{\theta_{12}^1 B_{12}}\left(\frac{a_2-b_2}{\alpha_{22}+\delta_{22}}\right)}.$$

Thus, the necessary conditions for the existence of a biologically acceptable equilibrium point are

$$\frac{\lambda\beta_{10}}{B_{11}}\left(\frac{a_1-b_1}{\alpha_{12}+\delta_{12}}\right)\left(\frac{\theta_{11}^1 B_{22}}{\theta_{12}^1 B_{12}}\right)^2>\gamma_0+\beta_{10}\frac{\theta_{11}^1 B_{22}}{\theta_{12}^1 B_{12}}>\lambda\beta_{10}\frac{\theta_{11}^1}{\theta_{12}^1 B_{12}}\left(\frac{a_2-b_2}{\alpha_{22}+\delta_{22}}\right)$$

or

$$\frac{\lambda\beta_{10}}{B_{11}}\left(\frac{a_1-b_1}{\alpha_{12}+\delta_{12}}\right)\left(\frac{\theta_{11}^1 B_{22}}{\theta_{12}^1 B_{12}}\right)^2<\gamma_0+\beta_{10}\frac{\theta_{11}^1 B_{22}}{\theta_{12}^1 B_{12}}<\lambda\beta_{10}\frac{\theta_{11}^1}{\theta_{12}^1 B_{12}}\left(\frac{a_2-b_2}{\alpha_{22}+\delta_{22}}\right).$$

In this case the characteristic polynomial of the linearized system around the equilibrium of the system is given by

$$P(c)=\det\begin{pmatrix} J_{11}-c & 0 & 0 & J_{14} & 0 \\ 0 & J_{22}-c & 0 & 0 & J_{25} \\ J_{31} & J_{32} & J_{33}-c & J_{34} & J_{35} \\ J_{41} & 0 & J_{43} & J_{44}-c & 0 \\ 0 & J_{52} & J_{53} & 0 & J_{55}-c \end{pmatrix}$$

with

$$
\begin{aligned}
J_{11} &= a_1 - b_1,\\
J_{14} &= -(\alpha_{12} + \delta_{12}),\\
J_{22} &= a_2 - b_2,\\
J_{25} &= -(\alpha_{22} + \delta_{22}),\\
J_{31} &= \frac{\lambda\beta_{10}\gamma_0(P_{12}^* + P_{22}^*)}{(\gamma_0 + \beta_{10}H_1^*)^2} + \alpha_{12}\frac{P_{11}^*P_{12}^*}{(H_1^*)^2},\\
J_{32} &= -\theta_{12}^1 P_{11}^*,\\
J_{33} &= -\left(\mu_{11} + b_1 + \alpha_{11} + \theta_{12}^1 H_2^* + \alpha_{12}\frac{P_{12}^*}{H_1^*}\right),\\
J_{34} &= \frac{\lambda\beta_{10}H_1^*}{\gamma_0 + \beta_{10}H_1^*} - \alpha_{12}\frac{P_{11}^*}{H_1^*},\\
J_{35} &= \frac{\lambda\beta_{10}H_1^*}{\gamma_0 + \beta_{10}H_1^*},\\
J_{41} &= \alpha_{12}\frac{1 + k_{12}}{k_{12}}\frac{(P_{12}^*)^2}{(H_1^*)^2},\\
J_{43} &= \theta_{11}^1,\\
J_{44} &= -\left(\mu_{12} + b_1 + \alpha_{12} + 2\alpha_{12}\frac{1 + k_{12}}{k_{12}}\frac{P_{12}^*}{H_1^*}\right),\\
J_{52} &= \theta_{12}^1 P_{11}^* + \alpha_{22}\frac{1 + k_{22}}{k_{22}}\frac{(P_{22}^*)^2}{(H_2^*)^2},\\
J_{53} &= \theta_{12}^1 H_2^*,\\
J_{55} &= -\left(\mu_{22} + b_2 + \alpha_{22} + 2\alpha_{22}\frac{1 + k_{22}}{k_{22}}\frac{P_{22}^*}{H_2^*}\right).
\end{aligned}
$$

Therefore, the coefficients of $P(c) = -c^5 + A_4c^4 + A_3c^3 + A_2c^2 + A_1c + A_0$ are given by

$$
\begin{aligned}
A_0 =& J_{11}J_{22}J_{33}J_{44}J_{55} + J_{11}J_{25}J_{32}J_{44}J_{53} + J_{11}J_{25}J_{34}J_{43}J_{52} + J_{14}J_{22}J_{31}J_{43}J_{55}\\
&+ J_{14}J_{25}J_{33}J_{41}J_{52} + J_{14}J_{22}J_{35}J_{41}J_{53} - J_{11}J_{22}J_{35}J_{44}J_{53} - J_{11}J_{25}J_{33}J_{44}J_{52}\\
&- J_{11}J_{22}J_{34}J_{43}J_{55} - J_{14}J_{25}J_{31}J_{43}J_{52} - J_{14}J_{25}J_{32}J_{41}J_{53} - J_{14}J_{22}J_{33}J_{41}J_{55},\\
A_1 =& J_{11}J_{35}J_{44}J_{53} + J_{11}J_{35}J_{43}J_{55} + J_{14}J_{33}J_{41}J_{55} + J_{22}J_{35}J_{44}J_{53} + J_{22}J_{34}J_{43}J_{55}\\
&+ J_{11}J_{25}J_{44}J_{52} + J_{25}J_{33}J_{44}J_{52} + J_{14}J_{22}J_{41}J_{55} + J_{11}J_{25}J_{33}J_{52} + J_{11}J_{22}J_{35}J_{53}\\
&+ J_{14}J_{22}J_{33}J_{41} + J_{11}J_{22}J_{34}J_{43} - J_{25}J_{34}J_{43}J_{52} - J_{25}J_{32}J_{44}J_{53} - J_{11}J_{33}J_{44}J_{55}\\
&- J_{14}J_{35}J_{41}J_{53} - J_{11}J_{22}J_{44}J_{55} - J_{22}J_{33}J_{44}J_{55} - J_{14}J_{31}J_{43}J_{55} - J_{11}J_{25}J_{32}J_{53}\\
&- J_{14}J_{22}J_{31}J_{43} - J_{11}J_{22}J_{33}J_{44},
\end{aligned}
$$

$$\begin{aligned}
A_2 =& J_{11}J_{22}J_{33} + J_{11}J_{22}J_{44} + J_{11}J_{33}J_{44} + J_{11}J_{22}J_{55} + J_{11}J_{33}J_{55} + J_{11}J_{44}J_{55} \\
&+ J_{22}J_{33}J_{44} + J_{22}J_{33}J_{55} + J_{22}J_{44}J_{55} + J_{33}J_{44}J_{55} + J_{25}J_{32}J_{53} + J_{14}J_{31}J_{43} \\
&- J_{34}J_{43}J_{55} - J_{11}J_{35}J_{53} - J_{14}J_{41}J_{55} - J_{22}J_{34}J_{43} - J_{11}J_{34}J_{43} - J_{14}J_{33}J_{41} \\
&- J_{25}J_{33}J_{52} - J_{11}J_{25}J_{52} - J_{22}J_{35}J_{53} - J_{25}J_{44}J_{52} - J_{14}J_{22}J_{41} - J_{35}J_{44}J_{53}, \\
A_3 =& J_{14}J_{41} + J_{34}J_{43} + J_{25}J_{52} + J_{35}J_{53} - J_{11}J_{22} - J_{11}J_{33} - J_{11}J_{44} - J_{11}J_{55} \\
&- J_{22}J_{33} - J_{22}J_{44} - J_{22}J_{55} - J_{33}J_{44} - J_{33}J_{55} - J_{44}J_{55}, \\
A_4 =& J_{11} + J_{22} + J_{33} + J_{44} + J_{55}.
\end{aligned}$$

Using the Routh-Hurwitz stability criterion we have that all the roots of $P(c)$ have a negative real part if and only if $A_0$, $A_4$, $(A_3A_4 - A_2)A_2 - (A_1A_4 - A_0)A_4$ and $[(A_3A_4 - A_2)A_2 - (A_1A_4 - A_0)A_4](A_1A_4 - A_0) - (A_3A_4 - A_2)A_0$ are negative, while $A_3A_4 - A_2$ is positive. These conditions also imply that the equilibrium point $(H_1^*, H_2^*, P_{11}^*, P_{12}^*, P_{22}^*)$ is stable.

**Case c)**

When the second stage of the parasite's life cycle occurs within hosts of one of the two species in which its first parasitic stage occurs, the equations for the growth of host and parasitic populations look like

$$\begin{aligned}
\frac{dH_1}{dt} &= (a_1 - b_1)H_1 - (\alpha_{11} + \delta_{11})P_{11}, \\
\frac{dH_2}{dt} &= (a_2 - b_2)H_2 - (\alpha_{22} + \delta_{22})P_{22}, \\
\frac{dP_{11}}{dt} &= \frac{\lambda\beta_{10}H_1P_{22}}{\gamma_0 + \beta_{10}H_1 + \beta_{20}H_2} - \left(\mu_{11} + b_1 + \alpha_{11} + \theta_{12}^1H_2\right)P_{11} - \alpha_{11}\frac{1 + k_{11}}{k_{11}}\frac{P_{11}^2}{H_1}, \\
\frac{dP_{21}}{dt} &= \frac{\lambda\beta_{20}H_2P_{22}}{\gamma_0 + \beta_{10}H_1 + \beta_{20}H_2} - \left(\mu_{21} + b_2 + \theta_{22}^1\right)P_{21} - \alpha_{22}\frac{P_{21}P_{22}}{H_2}, \\
\frac{dP_{22}}{dt} &= \theta_{12}^1H_2P_{11} + \theta_{22}^1P_{21} - (\mu_{22} + b_2 + \alpha_{22})P_{22} - \alpha_{22}\frac{1 + k_{22}}{k_{22}}\frac{P_{22}^2}{H_2}.
\end{aligned}$$

From taking $dH_1^* = dH_2^* = 0$ it turns out that

$$\begin{aligned}
P_{11}^* &= \frac{a_1 - b_1}{\alpha_{11} + \delta_{11}}H_1^* \quad \text{and} \\
P_{22}^* &= \frac{a_2 - b_2}{\alpha_{22} + \delta_{22}}H_2^*.
\end{aligned}$$

Thus, defining $B_{11}$, $B_{21}$ and $B_{22}$ as follows

$$\begin{aligned}
B_{11} &= (\mu_{11} + b_1 + \alpha_{11}) \left( \frac{a_1 - b_1}{\alpha_{11} + \delta_{11}} \right) + \alpha_{11} \frac{1 + k_{11}}{k_{11}} \left( \frac{a_1 - b_1}{\alpha_{11} + \delta_{11}} \right)^2, \\
B_{21} &= \mu_{21} + b_2 + \theta_{22}^1 + \alpha_{22} \left( \frac{a_2 - b_2}{\alpha_{22} + \delta_{22}} \right), \\
B_{22} &= (\mu_{22} + b_2 + \alpha_{22}) \left( \frac{a_2 - b_2}{\alpha_{22} + \delta_{22}} \right) + \alpha_{22} \frac{1 + k_{22}}{k_{22}} \left( \frac{a_2 - b_2}{\alpha_{22} + \delta_{22}} \right)^2,
\end{aligned}$$

we conclude that

$$P_{21}^* = \left[ \frac{B_{22}}{\theta_{22}^1} - \frac{\theta_{12}^1}{\theta_{22}^1} \left( \frac{a_1 - b_1}{\alpha_{11} + \delta_{11}} \right) H_1^* \right] H_2^*,$$

and consequently

$$\begin{aligned}
0 &= \left[ \frac{\lambda \beta_{10}}{\gamma_0 + \beta_{10} H_1^* + \beta_{20} H_2^*} \left( \frac{a_2 - b_2}{\alpha_{22} + \delta_{22}} \right) H_2^* - \theta_{12}^1 \left( \frac{a_1 - b_1}{\alpha_{11} + \delta_{11}} \right) H_2^* - B_{11} \right] H_1^*, \\
0 &= \left[ \frac{\lambda \beta_{20}}{\gamma_0 + \beta_{10} H_1^* + \beta_{20} H_2^*} \left( \frac{a_2 - b_2}{\alpha_{22} + \delta_{22}} \right) H_2^* + \frac{B_{21} \theta_{12}^1}{\theta_{22}^1} \left( \frac{a_1 - b_1}{\alpha_{11} + \delta_{11}} \right) H_1^* - \frac{B_{21} B_{22}}{\theta_{22}^1} \right] H_2^*.
\end{aligned}$$

Therefore,

$$-\beta_{20} \theta_{12}^1 \left( \frac{a_1 - b_1}{\alpha_{11} + \delta_{11}} \right) H_2^* - \beta_{20} B_{11} = \frac{\beta_{10} B_{21} \theta_{12}^1}{\theta_{22}^1} \left( \frac{a_1 - b_1}{\alpha_{11} + \delta_{11}} \right) H_1^* - \frac{\beta_{10} B_{21} B_{22}}{\theta_{22}^1},$$

so $H_2^*$ is given by

$$H_2^* = \frac{\dfrac{\beta_{10} B_{21} B_{22}}{\theta_{22}^1} - \dfrac{\beta_{10} B_{21} \theta_{12}^1}{\theta_{22}^1} \left( \dfrac{a_1 - b_1}{\alpha_{11} + \delta_{11}} \right) H_1^* - \beta_{20} B_{11}}{\beta_{20} \theta_{12}^1 \left( \dfrac{a_1 - b_1}{\alpha_{11} + \delta_{11}} \right)},$$

and then

$$C_2 (H_1^*)^2 + C_1 H_1^* + C_0 = 0, \tag{4.19}$$

where

$$\begin{aligned}
C_0 &= \lambda \theta_{22}^1 \beta_{20} B_{11} + \gamma_0 \theta_{12}^1 B_{21} B_{22} \left( \frac{a_1 - b_1}{\alpha_{11} + \delta_{11}} \right) + \frac{\beta_{10} B_{12} B_{21} B_{22}^2}{\theta_{22}^1} + \beta_{20} B_{11} B_{21} B_{22} \\
&\quad - \lambda \beta_{10} B_{21} B_{22}, \\
C_1 &= \Bigg[ \beta_{20} \theta_{12}^1 B_{11} B_{21} + \lambda \beta_{10} B_{21} \theta_{12}^1 + \beta_{10} \theta_{12}^1 B_{21} B_{22} - \gamma_0 B_{21} (\theta_{12}^1)^2 \left( \frac{a_1 - b_1}{\alpha_{11} + \delta_{11}} \right) \\
&\quad -2 \frac{\beta_{10} \theta_{12}^1 B_{12}^2 B_{22}}{\theta_{22}^1} \Bigg] \left( \frac{a_1 - b_1}{\alpha_{11} + \delta_{11}} \right), \\
C_2 &= \frac{\beta_{10} B_{21}^2 (\theta_{12}^1)^2 - \beta_{10} \theta_{22}^1 B_{21} (\theta_{12}^1)^2}{\theta_{22}^1} \left( \frac{a_1 - b_1}{\alpha_{11} + \delta_{11}} \right)^2.
\end{aligned}$$

Since $B_{21} > \theta_{22}^1$, we have that $C_2 > 0$, so it is necessary that $C_1^2 - 4 C_2 C_0 > 0$ for

$H_1^*$ not to be a complex number, and $\min\{C_0, C_1\} < 0$ so that there is at least one positive value of $H_1^*$.

Therefore, the necessary conditions for there to be at least one biologically acceptable equilibrium point $(H_1^*, H_2^*, P_{11}^*, P_{21}^*, P_{22}^*)$ are $C_1^2 - 4C_2C_0 > 0$, $\min\{C_0, C_1\} < 0$ and

$$\left(\frac{a_1 - b_1}{\alpha_{11} + \delta_{11}}\right) H_1^* < \min\left\{\frac{B_{22}}{\theta_{12}^1}, \frac{\beta_{10}B_{21}B_{22} - \beta_{20}\theta_{22}^1 B_{11}}{\beta_{10}\theta_{12}^1 B_{21}}\right\},$$

considering $H_1^*$ as the lowest positive root of (4.19).

Now, as in the previous cases, to analyze the stability of the equilibrium point, we need to calculate characteristic polynomial of the linearized system around the equilibrium point, given by

$$P(c) = \det\begin{pmatrix} J_{11} - c & 0 & J_{13} & 0 & 0 \\ 0 & J_{22} - c & 0 & 0 & J_{25} \\ J_{31} & J_{32} & J_{33} - c & 0 & J_{35} \\ J_{41} & J_{42} & 0 & J_{44} - c & J_{45} \\ 0 & J_{52} & J_{53} & J_{54} & J_{55} - c \end{pmatrix}$$

where

$$\begin{aligned}
J_{11} &= a_1 - b_1, \\
J_{22} &= a_2 - b_2, \\
J_{13} &= -(\alpha_{11} + \delta_{11}), \\
J_{25} &= -(\alpha_{22} + \delta_{22}), \\
J_{31} &= \frac{\lambda\beta_{10}(\gamma_0 + \beta_{20}H_2^*)P_{22}^*}{(\gamma_0 + \beta_{10}H_1^* + \beta_{20}H_2^*)^2} + \alpha_{11}\frac{1 + k_{11}}{k_{11}}\frac{(P_{11}^*)^2}{(H_1^*)^2}, \\
J_{32} &= -\frac{\lambda\beta_{10}\beta_{20}H_1^*P_{22}^*}{(\gamma_0 + \beta_{10}H_1^* + \beta_{20}H_2^*)^2} - \theta_{12}^1 P_{11}^*, \\
J_{33} &= -\left(\mu_{11} + b_1 + \alpha_{11} + \theta_{12}^1 H_2^* + 2\alpha_{11}\frac{1 + k_{11}}{k_{11}}\frac{P_{11}^*}{H_1^*}\right), \\
J_{35} &= \frac{\lambda\beta_{10}H_1^*}{\gamma_0 + \beta_{10}H_1^* + \beta_{20}H_2^*}, \\
J_{41} &= -\frac{\lambda\beta_{10}\beta_{20}H_2^*P_{22}^*}{(\gamma_0 + \beta_{10}H_1^* + \beta_{20}H_2^*)^2}, \\
J_{42} &= \frac{\lambda\beta_{20}(\gamma_0 + \beta_{10}H_1^*)P_{22}^*}{(\gamma_0 + \beta_{10}H_1^* + \beta_{20}H_2^*)^2},
\end{aligned}$$

$$
\begin{aligned}
J_{44} &= -\left(\mu_{21} + b_2 + \theta_{22}^1 + \alpha_{22}\frac{P_{22}^*}{H_2^*}\right),\\
J_{45} &= \frac{\lambda\beta_{20}H_2^*}{\gamma_0 + \beta_{10}H_1^* + \beta_{20}H_2^*} - \alpha_{22}\frac{P_{21}^*}{H_2^*},\\
J_{52} &= \theta_{12}^1 P_{11}^* + \alpha_{22}\frac{1+k_{22}}{k_{22}}\frac{(P_{22}^*)^2}{(H_2^*)^2},\\
J_{53} &= \theta_{12}^1 H_2^*,\\
J_{54} &= \theta_{22}^1,\\
J_{55} &= -\left(\mu_{22} + b_2 + \alpha_{22} + 2\alpha_{22}\frac{1+k_{22}}{k_{22}}\frac{P_{22}^*}{H_2^*}\right).
\end{aligned}
$$

Therefore, we have that $P(c) = -c^5 + A_4c^4 + A_3c^3 + A_2c^2 + A_1c + A_0$, where the coefficients $A_k$ are given by

$$
\begin{aligned}
A_0 =& J_{11}J_{22}J_{33}J_{44}J_{55} + J_{11}J_{25}J_{33}J_{42}J_{54} + J_{11}J_{25}J_{32}J_{44}J_{53} + J_{13}J_{25}J_{31}J_{44}J_{52}\\
&+ J_{13}J_{25}J_{32}J_{41}J_{54} + J_{13}J_{22}J_{31}J_{45}J_{54} - J_{11}J_{22}J_{33}J_{45}J_{54} - J_{11}J_{25}J_{33}J_{44}J_{52}\\
&- J_{13}J_{25}J_{31}J_{42}J_{54} - J_{13}J_{22}J_{31}J_{44}J_{55} - J_{11}J_{22}J_{35}J_{44}J_{53} - J_{13}J_{22}J_{35}J_{41}J_{54},\\
A_1 =& J_{11}J_{22}J_{35}J_{53} + J_{11}J_{22}J_{45}J_{54} + J_{11}J_{25}J_{44}J_{52} + J_{11}J_{33}J_{45}J_{54} + J_{11}J_{35}J_{44}J_{53}\\
&+ J_{22}J_{33}J_{45}J_{54} + J_{13}J_{22}J_{31}J_{55} + J_{11}J_{25}J_{33}J_{52} + J_{25}J_{33}J_{44}J_{52} + J_{22}J_{35}J_{44}J_{53}\\
&+ J_{13}J_{22}J_{33}J_{44} + J_{13}J_{35}J_{41}J_{54} + J_{13}J_{31}J_{44}J_{55} - J_{25}J_{33}J_{42}J_{54} - J_{25}J_{32}J_{44}J_{53}\\
&- J_{13}J_{31}J_{45}J_{54} - J_{11}J_{25}J_{42}J_{54} - J_{11}J_{22}J_{44}J_{55} - J_{22}J_{33}J_{44}J_{55} - J_{13}J_{25}J_{31}J_{52}\\
&- J_{11}J_{33}J_{44}J_{55} - J_{11}J_{25}J_{32}J_{53} - J_{11}J_{22}J_{33}J_{55} - J_{11}J_{22}J_{33}J_{44},\\
A_2 =& J_{11}J_{22}J_{33} + J_{11}J_{22}J_{44} + J_{11}J_{22}J_{55} + J_{11}J_{33}J_{44} + J_{11}J_{33}J_{55} + J_{11}J_{44}J_{55}\\
&+ J_{22}J_{33}J_{44} + J_{22}J_{33}J_{55} + J_{22}J_{44}J_{55} + J_{33}J_{44}J_{55} + J_{25}J_{42}J_{54} + J_{25}J_{32}J_{53}\\
&- J_{22}J_{45}J_{54} - J_{25}J_{33}J_{52} - J_{11}J_{45}J_{54} - J_{22}J_{35}J_{53} - J_{11}J_{35}J_{53} - J_{13}J_{31}J_{44}\\
&- J_{13}J_{31}J_{55} - J_{35}J_{44}J_{53} - J_{11}J_{25}J_{52} - J_{25}J_{44}J_{52} - J_{13}J_{22}J_{31} - J_{33}J_{45}J_{54},\\
A_3 =& J_{13}J_{31} + J_{45}J_{54} + J_{25}J_{52} + J_{35}J_{53} - J_{11}J_{22} - J_{11}J_{33} - J_{11}J_{44} - J_{11}J_{55}\\
&- J_{22}J_{33} - J_{22}J_{44} - J_{22}J_{55} - J_{33}J_{44} - J_{33}J_{55} - J_{44}J_{55},\\
A_4 =& J_{11} + J_{22} + J_{33} + J_{44} + J_{55},
\end{aligned}
$$

The Routh-Hurwitz stability criterion implies that for the equilibrium point to be locally stable it is necessary that $A_4 < 0$, $(A_3A_4 - A_2)A_2 - (A_1A_4 - A_0)A_4 < 0$, $A_0 < 0$, $[(A_3A_4 - A_2)A_2 - (A_1A_4 - A_0)A_4](A_1A_4 - A_0) - (A_3A_4 - A_2)A_0 < 0$ and $A_3A_4 - A_2 > 0$.

**Case d)**

Since there is no predation between hosts, systems with this transmission network are particular cases of system (4.20), considering $\theta^1_{21}$, that we analyze next.

**Case e)**

Finally, when all host species contain parasites at each stage of their life cycle, the assumption that only adult stages actually affect host species makes the system of equations (2.3) looks like

$$\begin{aligned}
\frac{dH_1}{dt} &= (a_1 - b_1)H_1 - (\alpha_{12} + \delta_{12})P_{12},\\
\frac{dH_2}{dt} &= (a_2 - b_2)H_2 - (\alpha_{22} + \delta_{22})P_{22},\\
\frac{dP_{11}}{dt} &= \frac{\lambda\beta_{10}H_1(P_{12} + P_{22})}{\gamma_0 + \beta_{10}H_1 + \beta_{20}H_2} - \left(\mu_{11} + b_1 + \theta^1_{11} + \theta^1_{12}H_2\right)P_{11} - \alpha_{12}\frac{P_{11}P_{12}}{H_1},\\
\frac{dP_{21}}{dt} &= \frac{\lambda\beta_{20}H_2(P_{12} + P_{22})}{\gamma_0 + \beta_{10}H_1 + \beta_{20}H_2} - \left(\mu_{21} + b_2 + \theta^1_{21}H_1 + \theta^1_{22}\right)P_{21} - \alpha_{22}\frac{P_{21}P_{22}}{H_2},\\
\frac{dP_{12}}{dt} &= \theta^1_{11}P_{11} + \theta^1_{21}H_1P_{21} - \left(\mu_{12} + b_1 + \alpha_{12}\right)P_{12} - \alpha_{12}\frac{1 + k_{12}}{k_{12}}\frac{P^2_{12}}{H_1},\\
\frac{dP_{22}}{dt} &= \theta^1_{12}H_2P_{11} + \theta^1_{22}P_{21} - (\mu_{22} + b_2 + \alpha_{22})P_{22} - \alpha_{22}\frac{1 + k_{22}}{k_{22}}\frac{P^2_{22}}{H_2}.
\end{aligned} \tag{4.20}$$

$dH_1$ and $dH_2$ are the same as in case b), so in this case it is also true that

$$P^*_{12} = \frac{a_1 - b_1}{\alpha_{12} + \delta_{12}}H^*_1 \quad \text{and} \quad P^*_{22} = \frac{a_2 - b_2}{\alpha_{22} + \delta_{22}}H^*_2,$$

which allows to rewrite the equations $dP_{ij} = 0$ as follows

$$\begin{aligned}
0 &= \frac{\lambda\beta_{10}H^*_1\left(\frac{a_1 - b_1}{\alpha_{12} + \delta_{12}}H^*_1 + \frac{a_2 - b_2}{\alpha_{22} + \delta_{22}}H^*_2\right)}{\gamma_0 + \beta_{10}H_1 + \beta_{20}H_2} - (B_{11} + \theta^1_{12}H_2)P^*_{11},\\
0 &= \frac{\lambda\beta_{20}H^*_2\left(\frac{a_1 - b_1}{\alpha_{12} + \delta_{12}}H^*_1 + \frac{a_2 - b_2}{\alpha_{22} + \delta_{22}}H^*_2\right)}{\gamma_0 + \beta_{10}H_1 + \beta_{20}H_2} - (B_{21} + \theta^1_{21}H_1)P^*_{21},\\
0 &= \theta^1_{11}P^*_{11} + \theta^1_{21}H^*_1P^*_{21} - B_{12}H^*_1,\\
0 &= \theta^1_{12}H^*_2P^*_{11} + \theta^1_{22}P^*_{21} - B_{22}H^*_2,
\end{aligned}$$

where

$$\begin{aligned}
B_{i1} &= \mu_{i1} + b_i + \theta^1_{i1} + \alpha_{i2}\frac{a_i - b_i}{\alpha_{i2} - \delta_{i2}},\\
B_{i2} &= \frac{a_i - b_i}{\alpha_{i2} + \delta_{i2}}\left[\mu_{i2} + b_i + \alpha_{i2} + \alpha_{i2}\frac{1 + k_{i2}}{k_{i2}}\left(\frac{a_i - b_i}{\alpha_{i2} + \delta_{i2}}\right)\right],
\end{aligned}$$

for $i = 1, 2$. Therefore,

$$P_{11}^* = \frac{B_{12} - \theta_{21}^1 P_{21}^*}{\theta_{11}^1} H_1^* \quad \text{and} \quad P_{21}^* = \frac{B_{22} - \theta_{12}^1 P_{11}^*}{\theta_{22}^1} H_2^*,$$

what is satisfied if and only if

$$P_{11}^* = \frac{\theta_{22}^1 B_{12} - \theta_{21}^1 B_{22} H_2^*}{\theta_{11}^1 \theta_{22}^1 - \theta_{12}^1 \theta_{21}^1} H_1^* \quad \text{and} \quad P_{21}^* = \frac{\theta_{11}^1 B_{22} - \theta_{12}^1 B_{12} H_1^*}{\theta_{11}^1 \theta_{22}^1 - \theta_{12}^1 \theta_{21}^1} H_2^*.$$

Thus, using this expression for $P_{11}^*$ in $dP_{11} = 0$, we obtain the following equations

$$0 = \frac{\lambda \beta_{10} \left( \frac{a_1 - b_1}{\alpha_{12} + \delta_{12}} H_1^* + \frac{a_2 - b_2}{\alpha_{22} + \delta_{22}} H_2^* \right)}{\gamma_0 + \beta_{10} H_1^* + \beta_{20} H_2^*} - (B_{11} + \theta_{12}^1 H_2^*) \frac{\theta_{22}^1 B_{12} - \theta_{21}^1 B_{22} H_2^*}{\theta_{11}^1 \theta_{22}^1 - \theta_{12}^1 \theta_{21}^1},$$

so we can express $H_1^*$ as a function of $H_2^*$ as follows

$$H_1^* = \frac{(\gamma_0 + \beta_{20} H_2^*)(B_{11} + \theta_{12}^1 H_2^*) \frac{\theta_{22}^1 B_{12} - \theta_{21}^1 B_{22} H_2^*}{\theta_{11}^1 \theta_{22}^1 - \theta_{12}^1 \theta_{21}^1} - \lambda \beta_{10} \frac{a_2 - b_2}{\alpha_{22} + \delta_{22}} H_2^*}{\beta_{10} \left[ \lambda \frac{a_1 - b_1}{\alpha_{12} + \delta_{12}} - (B_{11} + \theta_{12}^1 H_2^*) \frac{\theta_{22}^1 B_{12} - \theta_{21}^1 B_{22} H_2^*}{\theta_{11}^1 \theta_{22}^1 - \theta_{12}^1 \theta_{21}^1} \right]}, \tag{4.21}$$

and substituting $P_{21}^*$ in $dP_{21}^*$ it turns out that $H_2^*$ must be the solution of the following equation

$$0 = \frac{\lambda \beta_{20} \left( \frac{a_1 - b_1}{\alpha_{12} + \delta_{12}} H_1^* + \frac{a_2 - b_2}{\alpha_{22} + \delta_{22}} H_2^* \right)}{\gamma_0 + \beta_{10} H_1^* + \beta_{20} H_2^*} - (B_{21} + \theta_{21}^1 H_1^*) \frac{\theta_{11}^1 B_{22} - \theta_{12}^1 B_{12} H_1^*}{\theta_{11}^1 \theta_{22}^1 - \theta_{12}^1 \theta_{21}^1} \tag{4.22}$$

with $H_1^*$ given by (4.21). However, solving (4.22) is equivalent to solving a fifth-degree polynomial whose coefficients are not easy to simplify, so we do not calculate the explicit value of $H_2^*$.

The characteristic polynomial of the linearized system around the non-trivial equilibrium point is given by

$$P(c) = \begin{pmatrix} J_{11} - c & 0 & 0 & 0 & J_{15} & 0 \\ 0 & J_{22} - c & 0 & 0 & 0 & J_{26} \\ J_{31} & J_{32} & J_{22} - c & 0 & J_{35} & J_{36} \\ J_{41} & J_{42} & 0 & J_{44} - c & J_{45} & J_{46} \\ J_{51} & 0 & J_{53} & J_{54} & J_{55} - c & 0 \\ 0 & J_{62} & J_{63} & J_{64} & 0 & J_{66} - c \end{pmatrix}$$

where

$$
\begin{aligned}
J_{11} &= a_1 - b_1,\\
J_{15} &= -(\alpha_{12} + \delta_{12}),\\
J_{22} &= a_2 - b_2,\\
J_{26} &= -(\alpha_{22} + \delta_{22}),\\
J_{31} &= \frac{\lambda\beta_{10}(\gamma_0 + \beta_{20}H_2^*)(P_{12}^* + P_{22}^*)}{(\gamma_0 + \beta_{10}H_1^* + \beta_{20}H_2^*)^2} + \alpha_{12}\frac{P_{11}^*P_{12}^*}{(H_1^*)^2},\\
J_{32} &= -\frac{\lambda\beta_{10}\beta_{20}H_1^*(P_{12}^* + P_{22}^*)}{(\gamma_0 + \beta_{10}H_1^* + \beta_{20}H_2^*)^2},\\
J_{33} &= -\left(\mu_{11} + b_1 + \theta_{11}^1 + \theta_{12}^1 H_2^* + \alpha_{12}\frac{P_{12}^*}{H_1^*}\right),\\
J_{35} &= \frac{\lambda\beta_{10}H_1^*}{\gamma_0 + \beta_{10}H_1^* + \beta_{20}H_2^*} - \alpha_{12}\frac{P_{11}^*}{H_1^*},\\
J_{36} &= \frac{\lambda\beta_{10}H_1^*}{\gamma_0 + \beta_{10}H_1^* + \beta_{20}H_2^*},\\
J_{41} &= -\frac{\lambda\beta_{10}\beta_{20}H_2^*(P_{12}^* + P_{22}^*)}{(\gamma_0 + \beta_{10}H_1^* + \beta_{20}H_2^*)^2},\\
J_{42} &= \frac{\lambda\beta_{10}(\gamma_0 + \beta_{10}H_1^*)(P_{12}^* + P_{22}^*)}{(\gamma_0 + \beta_{10}H_1^* + \beta_{20}H_2^*)^2} + \alpha_{22}\frac{P_{21}^*P_{22}^*}{(H_2^*)^2},\\
J_{44} &= -\left(\mu_{21} + b_2 + \theta_{21}^1 H_1^* + \theta_{22}^1 + \alpha_{22}\frac{P_{22}^*}{H_2^*}\right),\\
J_{45} &= \frac{\lambda\beta_{20}H_2^*}{\gamma_0 + \beta_{10}H_1^* + \beta_{20}H_2^*},\\
J_{46} &= \frac{\lambda\beta_{20}H_2^*}{\gamma_0 + \beta_{10}H_1^* + \beta_{20}H_2^*} - \alpha_{22}\frac{P_{21}^*}{H_2^*},\\
J_{51} &= \theta_{21}^1 P_{21}^* + \alpha_{12}\frac{1 + k_{12}}{k_{12}}\frac{(P_{12}^*)^2}{(H_1^*)^2},\\
J_{53} &= \theta_{11}^1,\\
J_{54} &= \theta_{21}^1 H_1^*,\\
J_{55} &= -\left(\mu_{12} + b_1 + \alpha_{12} + 2\alpha_{12}\frac{1 + k_{12}}{k_{12}}\frac{P_{12}^*}{H_1^*}\right),\\
J_{62} &= \theta_{12}^1 P_{11}^* + \alpha_{22}\frac{1 + k_{22}}{k_{22}}\frac{(P_{22}^*)^2}{(H_2^*)^2},\\
J_{63} &= \theta_{12}^1 H_2^*,\\
J_{64} &= \theta_{22}^1,\\
J_{66} &= -\left(\mu_{22} + b_2 + \alpha_{22} + 2\alpha_{22}\frac{1 + k_{22}}{k_{22}}\frac{P_{22}^*}{H_2^*}\right).
\end{aligned}
$$

Therefore, $P(c) = c^6 + A_5c^5 + A_4c^4 + A_3c^3 + A_2c^2 + A_1c + A_0$, with $A_i$ given by

$$
\begin{aligned}
A_0 = {} & J_{11}J_{22}J_{33}J_{44}J_{55}J_{66} - J_{11}J_{22}J_{33}J_{45}J_{54}J_{66} + J_{15}J_{22}J_{33}J_{41}J_{54}J_{66} \\
& + J_{15}J_{22}J_{31}J_{44}J_{53}J_{66} - J_{15}J_{22}J_{33}J_{44}J_{51}J_{66} - J_{11}J_{22}J_{33}J_{46}J_{55}J_{64} \\
& + J_{11}J_{26}J_{33}J_{42}J_{55}J_{64} - J_{15}J_{22}J_{31}J_{46}J_{53}J_{64} - J_{11}J_{22}J_{36}J_{45}J_{53}J_{64} \\
& + J_{11}J_{26}J_{32}J_{45}J_{53}J_{64} + J_{15}J_{26}J_{31}J_{42}J_{53}J_{64} + J_{15}J_{22}J_{36}J_{41}J_{53}J_{64} \\
& - J_{15}J_{26}J_{32}J_{41}J_{53}J_{64} + J_{15}J_{22}J_{33}J_{46}J_{51}J_{64} - J_{15}J_{26}J_{33}J_{42}J_{51}J_{64} \\
& - J_{11}J_{22}J_{36}J_{44}J_{55}J_{63} + J_{11}J_{26}J_{32}J_{44}J_{55}J_{63} + J_{15}J_{22}J_{31}J_{46}J_{54}J_{63} \\
& + J_{11}J_{22}J_{36}J_{45}J_{54}J_{63} - J_{11}J_{26}J_{32}J_{45}J_{54}J_{63} - J_{15}J_{26}J_{31}J_{42}J_{54}J_{63} \\
& - J_{15}J_{22}J_{36}J_{41}J_{54}J_{63} + J_{15}J_{26}J_{32}J_{41}J_{54}J_{63} + J_{15}J_{22}J_{36}J_{44}J_{51}J_{63} \\
& - J_{15}J_{26}J_{32}J_{44}J_{51}J_{63} - J_{11}J_{26}J_{33}J_{44}J_{55}J_{62} + J_{11}J_{26}J_{33}J_{45}J_{54}J_{62} \\
& - J_{15}J_{26}J_{33}J_{41}J_{54}J_{62} - J_{15}J_{26}J_{31}J_{44}J_{53}J_{62} + J_{15}J_{26}J_{33}J_{44}J_{51}J_{62}, \\
A_1 = {} & J_{22}J_{44}J_{53}J_{66}J_{35} + J_{11}J_{44}J_{53}J_{66}J_{35} + J_{11}J_{22}J_{53}J_{66}J_{35} - J_{22}J_{46}J_{53}J_{64}J_{35} \\
& - J_{11}J_{46}J_{53}J_{64}J_{35} + J_{26}J_{42}J_{53}J_{64}J_{35} + J_{22}J_{46}J_{54}J_{63}J_{35} + J_{11}J_{46}J_{54}J_{63}J_{35} \\
& - J_{26}J_{42}J_{54}J_{63}J_{35} - J_{26}J_{44}J_{53}J_{62}J_{35} - J_{11}J_{26}J_{53}J_{62}J_{35} + J_{11}J_{22}J_{44}J_{53}J_{35} \\
& - J_{22}J_{33}J_{44}J_{55}J_{66} - J_{11}J_{33}J_{44}J_{55}J_{66} - J_{11}J_{22}J_{44}J_{55}J_{66} - J_{11}J_{22}J_{33}J_{55}J_{66} \\
& + J_{22}J_{33}J_{45}J_{54}J_{66} + J_{11}J_{33}J_{45}J_{54}J_{66} + J_{11}J_{22}J_{45}J_{54}J_{66} - J_{15}J_{33}J_{41}J_{54}J_{66} \\
& - J_{15}J_{22}J_{41}J_{54}J_{66} - J_{15}J_{31}J_{44}J_{53}J_{66} - J_{15}J_{22}J_{31}J_{53}J_{66} + J_{15}J_{33}J_{44}J_{51}J_{66} \\
& + J_{15}J_{22}J_{44}J_{51}J_{66} + J_{15}J_{22}J_{33}J_{51}J_{66} - J_{11}J_{22}J_{33}J_{44}J_{66} + J_{22}J_{33}J_{46}J_{55}J_{64} \\
& + J_{11}J_{33}J_{46}J_{55}J_{64} + J_{11}J_{22}J_{46}J_{55}J_{64} - J_{26}J_{33}J_{42}J_{55}J_{64} - J_{11}J_{26}J_{42}J_{55}J_{64} \\
& + J_{15}J_{31}J_{46}J_{53}J_{64} + J_{22}J_{36}J_{45}J_{53}J_{64} + J_{11}J_{36}J_{45}J_{53}J_{64} - J_{26}J_{32}J_{45}J_{53}J_{64} \\
& - J_{15}J_{36}J_{41}J_{53}J_{64} - J_{15}J_{33}J_{46}J_{51}J_{64} - J_{15}J_{22}J_{46}J_{51}J_{64} + J_{15}J_{26}J_{42}J_{51}J_{64} \\
& + J_{11}J_{22}J_{33}J_{46}J_{64} - J_{11}J_{26}J_{33}J_{42}J_{64} + J_{22}J_{36}J_{44}J_{55}J_{63} + J_{11}J_{36}J_{44}J_{55}J_{63} \\
& - J_{26}J_{32}J_{44}J_{55}J_{63} + J_{11}J_{22}J_{36}J_{55}J_{63} - J_{11}J_{26}J_{32}J_{55}J_{63} - J_{15}J_{31}J_{46}J_{54}J_{63} \\
& - J_{22}J_{36}J_{45}J_{54}J_{63} - J_{11}J_{36}J_{45}J_{54}J_{63} + J_{26}J_{32}J_{45}J_{54}J_{63} + J_{15}J_{36}J_{41}J_{54}J_{63} \\
& - J_{15}J_{36}J_{44}J_{51}J_{63} - J_{15}J_{22}J_{36}J_{51}J_{63} + J_{15}J_{26}J_{32}J_{51}J_{63} + J_{11}J_{22}J_{36}J_{44}J_{63} \\
& - J_{11}J_{26}J_{32}J_{44}J_{63} + J_{26}J_{33}J_{44}J_{55}J_{62} + J_{11}J_{26}J_{44}J_{55}J_{62} + J_{11}J_{26}J_{33}J_{55}J_{62} \\
& - J_{26}J_{33}J_{45}J_{54}J_{62} - J_{11}J_{26}J_{45}J_{54}J_{62} + J_{15}J_{26}J_{41}J_{54}J_{62} + J_{15}J_{26}J_{31}J_{53}J_{62} \\
& - J_{15}J_{26}J_{44}J_{51}J_{62} - J_{15}J_{26}J_{33}J_{51}J_{62} + J_{11}J_{26}J_{33}J_{44}J_{62} - J_{11}J_{22}J_{33}J_{44}J_{55} \\
& + J_{11}J_{22}J_{33}J_{45}J_{54} - J_{15}J_{22}J_{33}J_{41}J_{54} - J_{15}J_{22}J_{31}J_{44}J_{53} + J_{15}J_{22}J_{33}J_{44}J_{51},
\end{aligned}
$$

$$\begin{aligned}
A_2 = {} & -J_{44}J_{53}J_{66}J_{35} - J_{22}J_{53}J_{66}J_{35} - J_{11}J_{53}J_{66}J_{35} + J_{46}J_{53}J_{64}J_{35} - J_{46}J_{54}J_{63}J_{35} \\
& + J_{26}J_{53}J_{62}J_{35} - J_{22}J_{44}J_{53}J_{35} - J_{11}J_{44}J_{53}J_{35} - J_{11}J_{22}J_{53}J_{35} + J_{33}J_{44}J_{55}J_{66} \\
& + J_{22}J_{44}J_{55}J_{66} + J_{11}J_{44}J_{55}J_{66} + J_{22}J_{33}J_{55}J_{66} + J_{11}J_{33}J_{55}J_{66} + J_{11}J_{22}J_{55}J_{66} \\
& - J_{33}J_{45}J_{54}J_{66} - J_{22}J_{45}J_{54}J_{66} - J_{11}J_{45}J_{54}J_{66} + J_{15}J_{41}J_{54}J_{66} + J_{15}J_{31}J_{53}J_{66} \\
& - J_{15}J_{44}J_{51}J_{66} - J_{15}J_{33}J_{51}J_{66} - J_{15}J_{22}J_{51}J_{66} + J_{22}J_{33}J_{44}J_{66} + J_{11}J_{33}J_{44}J_{66} \\
& + J_{11}J_{22}J_{44}J_{66} + J_{11}J_{22}J_{33}J_{66} - J_{33}J_{46}J_{55}J_{64} - J_{22}J_{46}J_{55}J_{64} - J_{11}J_{46}J_{55}J_{64} \\
& + J_{26}J_{42}J_{55}J_{64} - J_{36}J_{45}J_{53}J_{64} + J_{15}J_{46}J_{51}J_{64} - J_{22}J_{33}J_{46}J_{64} - J_{11}J_{33}J_{46}J_{64} \\
& - J_{11}J_{22}J_{46}J_{64} + J_{26}J_{33}J_{42}J_{64} + J_{11}J_{26}J_{42}J_{64} - J_{36}J_{44}J_{55}J_{63} - J_{22}J_{36}J_{55}J_{63} \\
& - J_{11}J_{36}J_{55}J_{63} + J_{26}J_{32}J_{55}J_{63} + J_{36}J_{45}J_{54}J_{63} + J_{15}J_{36}J_{51}J_{63} - J_{22}J_{36}J_{44}J_{63} \\
& - J_{11}J_{36}J_{44}J_{63} + J_{26}J_{32}J_{44}J_{63} - J_{11}J_{22}J_{36}J_{63} + J_{11}J_{26}J_{32}J_{63} - J_{26}J_{44}J_{55}J_{62} \\
& - J_{26}J_{33}J_{55}J_{62} - J_{11}J_{26}J_{55}J_{62} + J_{26}J_{45}J_{54}J_{62} + J_{15}J_{26}J_{51}J_{62} - J_{26}J_{33}J_{44}J_{62} \\
& - J_{11}J_{26}J_{44}J_{62} - J_{11}J_{26}J_{33}J_{62} + J_{22}J_{33}J_{44}J_{55} + J_{11}J_{33}J_{44}J_{55} + J_{11}J_{22}J_{44}J_{55} \\
& + J_{11}J_{22}J_{33}J_{55} - J_{22}J_{33}J_{45}J_{54} - J_{11}J_{33}J_{45}J_{54} - J_{11}J_{22}J_{45}J_{54} + J_{15}J_{33}J_{41}J_{54} \\
& + J_{15}J_{22}J_{41}J_{54} + J_{15}J_{31}J_{44}J_{53} + J_{15}J_{22}J_{31}J_{53} - J_{15}J_{33}J_{44}J_{51} - J_{15}J_{22}J_{44}J_{51} \\
& - J_{15}J_{22}J_{33}J_{51} + J_{11}J_{22}J_{33}J_{44}, \\
A_3 = {} & J_{53}J_{66}J_{35} + J_{44}J_{53}J_{35} + J_{22}J_{53}J_{35} + J_{11}J_{53}J_{35} - J_{44}J_{55}J_{66} - J_{33}J_{55}J_{66} \\
& - J_{22}J_{55}J_{66} - J_{11}J_{55}J_{66} + J_{45}J_{54}J_{66} + J_{15}J_{51}J_{66} - J_{33}J_{44}J_{66} - J_{22}J_{44}J_{66} \\
& - J_{11}J_{44}J_{66} - J_{22}J_{33}J_{66} - J_{11}J_{33}J_{66} - J_{11}J_{22}J_{66} + J_{46}J_{55}J_{64} + J_{33}J_{46}J_{64} \\
& + J_{22}J_{46}J_{64} + J_{11}J_{46}J_{64} - J_{26}J_{42}J_{64} + J_{36}J_{55}J_{63} + J_{36}J_{44}J_{63} + J_{22}J_{36}J_{63} \\
& + J_{11}J_{36}J_{63} - J_{26}J_{32}J_{63} + J_{26}J_{55}J_{62} + J_{26}J_{44}J_{62} + J_{26}J_{33}J_{62} + J_{11}J_{26}J_{62} \\
& - J_{33}J_{44}J_{55} - J_{22}J_{44}J_{55} - J_{11}J_{44}J_{55} - J_{22}J_{33}J_{55} - J_{11}J_{33}J_{55} - J_{11}J_{22}J_{55} \\
& + J_{33}J_{45}J_{54} + J_{22}J_{45}J_{54} + J_{11}J_{45}J_{54} - J_{15}J_{41}J_{54} - J_{15}J_{31}J_{53} + J_{15}J_{44}J_{51} \\
& + J_{15}J_{33}J_{51} + J_{15}J_{22}J_{51} - J_{22}J_{33}J_{44} - J_{11}J_{33}J_{44} - J_{11}J_{22}J_{44} - J_{11}J_{22}J_{33}, \\
A_4 = {} & J_{55}J_{66} - J_{53}J_{35} + J_{44}J_{66} + J_{33}J_{66} + J_{22}J_{66} + J_{11}J_{66} - J_{46}J_{64} - J_{36}J_{63} \\
& - J_{26}J_{62} + J_{44}J_{55} + J_{33}J_{55} + J_{22}J_{55} + J_{11}J_{55} - J_{45}J_{54} - J_{15}J_{51} + J_{33}J_{44} \\
& + J_{22}J_{44} + J_{11}J_{44} + J_{22}J_{33} + J_{11}J_{33} + J_{11}J_{22}, \\
A_5 = {} & -J_{66} - J_{55} - J_{44} - J_{33} - J_{22} - J_{11}.
\end{aligned}$$

Thus, knowing the size of the populations at the non-trivial equilibrium point, the Routh-Hurwitz stability criterion implies that the equilibrium point is locally stable if $A_0$, $A_5$, $A_4A_5 - A_3$, $(A_4A_5 - A_3)A_3 - (A_2A_5 - A_1)A_5$, $D_1$ and $E_1$ are positive, with

$$\begin{aligned}
D_1 &= [(A_4A_5 - A_3)A_3 - (A_2A_5 - A_1)A_5](A_2A_5 - A_1) \\
&\quad - [(A_4A_5 - A_3)A_1 - A_0A_5^2](A_4A_5 - A_3), \\
E_1 &= [(A_4A_5 - A_3)A_3 - (A_2A_5 - A_1)A_5][(A_4A_5 - A_3)A_1 - A_0A_5^2](A_2A_5 - A_1) \\
&\quad - [(A_4A_5 - A_3)A_1 - A_0A_5^2][(A_4A_5 - A_3)A_1 - A_0A_5^2](A_4A_5 - A_3) \\
&\quad - [(A_4A_5 - A_3)A_3 - (A_2A_5 - A_1)A_5]A_0
\end{aligned}$$

(see Appendix B).

# Conclusions

From the work done in this thesis we can conclude that model (2.3) is a reasonable generalization of pre-existing models for the interaction of host and parasitic populations presented in Chapter 1, since it allows studying the dynamics between the parasite population and a host community during each of the stages of the parasite's life cycle, in addition to allowing an intuitive generalization for multi-host models of the basic reproductive number and threshold host density, based on the transmission network of the parasite population.

We also present a reasonable generalization of the basic reproductive number and threshold host density for models with more than a single host species, that allows to find under what conditions a parasitic population that is introduced to a community of host species is able to persist, and as we mentioned in the conclusions of Chapter 3, this does not guarantee that the populations are regulated, but it allows to start analyzing the dynamics of populations in systems where it is not possible to determine analytically if there is a biologically acceptable equilibrium point.

In Chapter 3 we also show that the effect of non-adult parasites on the growth rates of the host populations, however small it is, and even if this does not affect the values of the basic reproductive number or the threshold host density, can regulate the growth of a host population, as shown in the simulations shown in Figure 3.7 and Figure 3.8. This supports that it is not necessary that a host population, that would grow exponentially in the absence of parasitism, needs to be colonized by adult individuals of a parasitic species to regulate its growth. Therefore, given a community with different host species, it is reasonable to study the systems of equations that model all possible topologically distinct parasitic transmission networks, as in the examples presented in Chapter 4.

One of the conclusions reached is that it is possible to mathematically determine the possible transmission networks of a parasitic species in a host community, as in the example analyzed in Section 4.2. This also allows to determine the different numbers of host species that are needed in the system so that a parasitic species has a specific transmission network.

As we can see in the representation of the Carpinteria database shown in Appendix C, many parasitic species pass each stage of their life cycle in hosts of different species, so in those cases the equations in (2.3) looks like (4.1), and this system, as we can see in the examples analyzed in Chapter 4, it is the easiest to determine the conditions of existence and stability of the equilibrium point. Therefore, given a community of $m$ host species and a parasitic species with $n$ stages of its life cycle, if we do not know exactly what the parasite's transmission network is, before considering the complete system (2.3), we can try model the dynamics of populations with systems of form (4.1).

One of the purposes of the model is to regulate the growth of a host community through the introduction of a parasitic species. To guarantee that at least one host species grows exponentially in the absence of parasitism, one hypothesis of the model is that at least one host species is not trophically related to the other host species of the system, however, this is not entirely necessary. With the equations for the dynamics of the host and parasitic populations, presented in (2.3), we can also analyze the effect of a parasitic species in a community where all host species regulate their growth due to trophic interaction with other hosts, or the effect of introducing parasites into a community where there is predation among all the host species of the system, and at least one host species grows exponentially or becomes extinct in the absence of parasitism.

Although in this thesis we focus on analyzing sufficient conditions for there to be coexistence between the species parasites and a host community, when studying parasites whose hosts are human, usually it is desired to determine conditions for the extinction of the parasite species. In particular, this case can also be analyzed with the model (2.3), if we assume that host populations regulate their growth in the absence of parasitism.

Finally, one hypothesis of this model is that the potency between parasites of the same species is by exploitation, however, this is not the case for all parasite species. For parasite species where there is intraspecific competition, further analysis is necessary, similar to the analysis done in (1.2), since the covariances between the populations $P_{ij}$ and $P_{ir}$ are not necessarily trivial and finding the probability generating function for the distribution of parasites in host populations in these cases is more complicated.

Since it is possible to study the previous all the previous cases with small modifications in the growth rates of the host populations, and therefore in the mortality of the parasitic stages related to the natural mortality of the hosts, or by taking particular values for the parameters in (2.3), this is one reason why model (2.3) is a reasonable model for multi-host-parasite systems.

# Appendix A

# Probability Generating Function

This appendix shows the results related to the probability generating functions of the negative binomial distribution and the negative multinomial distribution obtained from [8, 16, 34], used in the development of the models in Chapter 1 and Chapter 2.

By definition, the probability generating function of a discrete random variable $X$ that takes values in the set of non-negative integers, with probability mass function $p(x)$, is given by

$$G(z) = \mathrm{E}\left(z^X\right) = \sum_{x=0}^{\infty} p(x) z^x,$$

so, the mean and the variance of $p(x)$ are given by

$$\mu = \mathrm{E}(X) = \sum_{x=0}^{\infty} x p(x) = \lim_{z \to 1} \sum_{x=0}^{\infty} x p(x)(1-z)^{x-1} = \frac{d}{dz}\left(\sum_{x=0}^{\infty} p(x) z^x\right)\Bigg|_{z=1} = G'(1),$$

and

$$\begin{aligned}
\sigma^2 &= \mathrm{E}\left(X^2\right) - \mathrm{E}(X)^2 = \sum_{x=0}^{\infty} x^2 p(x) - \left[G'(1)\right]^2 \\
&= \lim_{z \to 1}\left[\sum_{x=0}^{\infty} x(x-1)p(x)(1-z)^{x-2} + \lim_{z \to 1} \sum_{x=0}^{\infty} x p(x)(1-z)^{x-2}\right] - \left[G'(1)\right]^2 \\
&= \frac{d^2}{dz^2}\left(\sum_{x=0}^{\infty} p(x) z^x\right)\Bigg|_{z=1} + \frac{d}{dz}\left(\sum_{x=0}^{\infty} p(x) z^x\right)\Bigg|_{z=1} - \left[G'(1)\right]^2 \\
&= G''(1) + G'(1) - \left[G'(1)\right]^2.
\end{aligned}$$

From the above, and given that the negative binomial distribution can be characterized through its probability generating function by two parameters, referred to as $m$ and $k$ in this thesis, where $m$ is the mean of this probability distribution, that in the models considered in this thesis is the average number of parasites per host for each time $t$, and $k$ is a parameter that varies inversely with the the degree of aggregation of parasites within the host population, we can calculate the variance and the second moment of this distribution if we know the values of $m$ and $k$. This characterization is given by the probability generating function:

$$G(m,k,z) = \left[1 + \frac{m}{k}(1-z)\right]^{-k}. \tag{A.1}$$

If we know the total number of hosts $H$ and parasites $P$ in the system, and the value of $k$, we are able to calculate the average number of parasites per host for each time $t$ as follows

$$m = \sum_{i=0}^{\infty} ip(i) = \frac{P(t)}{H(t)}.$$

The variance is given by

$$\begin{aligned}\sigma^2 &= G''(m,k,1) + G'(m,k,1) - \left[G'(m,k,1)\right]^2 \\ &= \frac{k+1}{k}m^2 + m - m^2 = m\left(1 + \frac{m}{k}\right) = \frac{P(t)}{H(t)}\left(1 + \frac{P(t)}{kH(t)}\right),\end{aligned}$$

and the second moment, defined as $\mathrm{E}(P^2) = \sigma^2 + m^2$, is

$$\sum_{i=0}^{\infty} i^2 p(i) = \frac{k+1}{k}m^2 + m = \frac{k+1}{k}\frac{P^2(t)}{H^2(t)} + \frac{P(t)}{H(t)}.$$

The definition of probability generating function is not restricted to the univariate case, for the multivariate case where $X = (X_1, \ldots, X_n)$ is a discrete random variable that takes values in the set of non-negative integers, with probability mass function $p(x_1, \ldots, x_n)$, the probability generating function of $X$ is defined as

$$G(z) = G(z_1, \ldots, z_n) = \mathrm{E}\left(\prod_{i=1}^{n} z_i^{X_i}\right) = \sum_{x_1,\ldots,x_n=0}^{\infty}\left(p(x_1,\ldots,x_n)\prod_{i=1}^{n} z_i^{x_i}\right).$$

From the previous definition, and since a distribution of $n$ variables is a negative binomial distribution if and only if the univariate marginals are negative binomials distribution, a candidate for the probability generation function for the negative multinomial distribution, also called multivariate negative binomial distribution, used in models with more than one parasite species, is the function $G_n(m, k, l, z)$, given by

$$G_n(m, k, l, z) = \prod_{i=1}^{n} G(m_i, k_i, z_i) + \sum_{j=2}^{n} \sum_{i=1}^{j} \frac{[1 - G(m_i, k_i, z_i)][1 - G(m_j, k_j, z_j)]}{l_{ij}}, \tag{A.2}$$

where $G(m_i, k_i, z_i)$ is define as the probability generating function of the negative binomial distribution of the $i$-th parasitic species, given by (A.1), $m = (m_1, \ldots, m_n)$ with $m_i$ defined as the expected value of the probability distribution of $i$-th parasitic species population for all $i = 1, \ldots, n$, $k = (k_1, \ldots, k_n)$ with $k_1, \ldots, k_n$ parameters of the negative binomial distributions of the population of each parasitic species, $l = (l_{12}, \ldots, l_{1n}, l_{23}, \ldots, l_{2n}, \ldots, l_{(n-1)n})$, and $z = (z_1, \ldots, z_n)$.

For $G_n$ to be a probability generating function it is necessary that $G_n = 1$ when $z_i = 1$, for all $i = 1, \ldots, n$, and that the coefficients of the Taylor expansion of $G_n$ in $z$ are positive. The first condition is satisfied because $G(m_i, k_i, z_i)$ is a probability generating function, implying that $G(m_i, k_i, 1) = 1$, for all $i = 1, \ldots, n$. The second condition is not satisfied for all values of $l_{ij}$, it is necessary to determine the values of $l_{ij}$ that do satisfy this condition for each vector pair $m$ and $k$. However, if $1/l_{ij} = 0$ for all $1 \leq i < j \leq n$, it can be verified that $G_n = \prod_{i=1}^{n} G(m_i, k_i, z_i)$ satisfies this condition since each function $G(m_i, k_i, 1)$ satisfies it.

For the values of $m_i$, $k_i$ and $l_{ij}$ that satisfy that the function $G_n$ is a probability generating function of a negative multinomial distribution, the mean and variance of the univariate marginal distribution $P_i$ are $m_i$ and $m_i(1 + m_i/k_i)$, respectively, for all $i = 1, \ldots, n$, and the covariance between $P_i$ and $P_j$, that can be calculated as

$$\begin{aligned}
\mathrm{Cov}(P_i, P_j) &= \mathrm{E}([P_i - \mathrm{E}(P_i)][P_j - \mathrm{E}(P_j)]) \\
&= \mathrm{E}(P_i P_j - P_i \mathrm{E}(P_j) - \mathrm{E}(P_i) P_j + \mathrm{E}(P_i)\mathrm{E}(P_j)) \\
&= \mathrm{E}(P_i P_j) - \mathrm{E}(P_i)\mathrm{E}(P_j)) - \mathrm{E}(P_i)\mathrm{E}(P_j)) + \mathrm{E}(P_i)\mathrm{E}(P_j)) \\
&= \mathrm{E}(P_i P_j) - \mathrm{E}(P_i)\mathrm{E}(P_j)),
\end{aligned}$$

for all $i, j = 1, \ldots, n$, is given by $m_i m_j / l_{ij}$.

The model of interest in this thesis satisfies that competition between individuals at different stages of the parasite's life cycle is by exploitation, implying that

$1/l_{ij} = 0$, so the probability generating function used in this thesis is the function (A.2) without the term corresponding to the correlation of the different stages, i.e., the product of the probability generating functions of the negative binomial distributions of the population corresponding to each stage of the parasite's life cycle.

# Appendix B

# Routh-Hurwitz Stability Criterion

The Routh-Hurwitz stability criterion is a mathematical proof that provides a necessary and sufficient condition for the stability of an equilibrium point in a system of linear equations, based on the characteristic polynomial of the system and the Routh-Hurwitz theorem [35]. Given a linear system of form

$$\frac{d\mathbf{x}}{dt} = A\mathbf{x}, \tag{B.1}$$

where $\mathbf{x} \in \mathbb{R}^n$ and $A \in M_{n\times n}(\mathbb{R})$ is the matrix of the linearized nonlinear interaction terms in a not necessarily linear system, that is, $A$ is the Jacobian matrix at the equilibrium point of the original system. The solutions the system (B.1) have the form

$$\mathbf{x} = \mathbf{x}_0 e^{\lambda t},$$

where $\mathbf{x}_0$ is a constant vector in $\mathbb{R}^n$ and $\lambda$ is an eigenvalue of $A$, i.e., $\lambda$ is a root of the characteristic polynomial of $A$, denoted $P(\lambda) = \det|A - \lambda I|$, with $I$ the identity matrix in $M_{n\times n}(\mathbb{R})$. Thus, considering

$$P(\lambda) = \lambda^n + a_{n-1}\lambda^{n-1} + \ldots + a_1\lambda + a_0, \tag{B.2}$$

the solution $\mathbf{x} = 0$ is stable if all roots $\lambda$ of the characteristic polynomial $P(\lambda)$ lie in the left side of the complex plane, that is, if $\mathrm{Re}(\lambda) < 0$ for all $\lambda$ such that $P(\lambda) = 0$.

To determine if all roots of $P(\lambda)$ have a negative real part, we first consider when $P(\lambda)$ is a second or third degree polynomial.

If $P(\lambda)$ is a second degree polynomial, then $P(\lambda) = \lambda^2 + a_1\lambda + a_0$ has both roots on the left half of the complex plane if and only if $a_1$ and $a_2$ are positive.

On the other hand, if $P(\lambda)$ is a third degree polynomial, then all the roots of $P(\lambda) = \lambda^3 + a_2\lambda^2 + a_1\lambda + a_0$ lie in the left-hand complex plane if and only if $a_0$ and $a_2$ are positive, and $a_1a_2 > a_0$.

When $P(\lambda)$ is a characteristic polynomial of a higher order, a tabular method can be used to determine the stability when the roots of $P(\lambda)$ are difficult to obtain. This method is given for polynomials with the form

$$P(\lambda) = \sum_{k=0}^{n} a_k\lambda^k.$$

First we consider the following table:

| | | | | |
|---|---|---|---|---|
| $a_n$ | $a_{n-2}$ | $a_{n-4}$ | $a_{n-6}$ | $\dots$ |
| $a_{n-1}$ | $a_{n-3}$ | $a_{n-5}$ | $a_{n-7}$ | $\dots$ |
| $b_1$ | $b_2$ | $b_3$ | $b_4$ | $\dots$ |
| $c_1$ | $c_2$ | $c_3$ | $c_4$ | $\dots$ |
| $d_1$ | $d_2$ | $d_3$ | $d_4$ | $\dots$ |
| $\vdots$ | $\vdots$ | $\vdots$ | $\vdots$ | $\ddots$ |

Table B.1: Coefficients used in the Routh-Hurwitz stability criterion.

where $b_k$ and $c_k$ can be computed as follows:

$$\begin{aligned} b_k &= \frac{a_{n-1}a_{n-2k} - a_n a_{n-(2k+1)}}{a_{n-1}}, \\ c_k &= \frac{b_1 a_{n-(2k+1)} - a_{n-1}b_{k+1}}{b_1}, \\ d_k &= \frac{c_1 b_{k+1} - b_1 c_{k+1}}{c_1}. \end{aligned}$$

When completed, the number of sign changes in the first column is the number roots of $P(\lambda)$ with non-negative real part.

Therefore, since $a_n = (-1)^n$ in the characteristic polynomial $P(\lambda)$, to guarantee the stability of the equilibrium point of a linearized system with characteristic polynomial of degree greater than three, it is necessary that all the coefficients of the first column in Table B.1 be positive if $n$ is even or negative if $n$ is odd.

For example, for $P(\lambda) = \lambda^4 + a_3\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0$ the Table B.1 is given by

| $1$ | $a_2$ | $a_0$ |
|---|---|---|
| $a_3$ | $a_1$ | $0$ |
| $\dfrac{a_2a_3-a_1}{a_3}$ | $a_0$ | $0$ |
| $\dfrac{(a_2a_3-a_1)a_1-a_0a_3^2}{a_2a_3-a_1}$ | $0$ | $0$ |
| $a_0$ | $0$ | $0$ |

Therefore, for the roots of $P(\lambda)$ to have a negative real part, it is necessary that $a_3 > 0$, $a_2a_3 - a_1 > 0$, $(a_2a_3 - a_1)a_1 - a_0a_3^2 > 0$ and $a_0 > 0$.

On the other hand, for $P(\lambda) = \lambda^5 + a_4\lambda^4 + a_3\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0$ the Table B.1 looks like

| $1$ | $a_3$ | $a_1$ |
|---|---|---|
| $a_4$ | $a_2$ | $a_0$ |
| $\dfrac{a_3a_4-a_2}{a_4}$ | $\dfrac{a_1a_4-a_0}{a_4}$ | $0$ |
| $\dfrac{(a_3a_4-a_2)a_2-(a_1a_4-a_0)a_4}{a_3a_4-a_2}$ | $a_0$ | $0$ |
| $\dfrac{[(a_3a_4-a_2)a_2-(a_1a_4-a_0)a_4](a_1a_4-a_0)-(a_3a_4-a_2)a_0}{[(a_3a_4-a_2)a_2-(a_1a_4-a_0)a_4]a_4}$ | $0$ | $0$ |
| $a_0$ | $0$ | $0$ |

Hence, the roots of $P(\lambda)$ have negative real part if $(a_3a_4 - a_2)a_2 - (a_1a_4 - a_0)a_4$, $[(a_3a_4 - a_2)a_2 - (a_1a_4 - a_0)a_4](a_1a_4 - a_0) - (a_3a_4 - a_2)a_0$, $a_3a_4 - a_2$, $a_4$ and $a_0$ are positive.

For $P(\lambda) = \lambda^6 + a_5\lambda^5 + a_4\lambda^4 + a_3\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0$ the Table B.1 is

| $1$ | $a_4$ | $a_2$ | $a_0$ |
|---|---|---|---|
| $a_5$ | $a_3$ | $a_1$ | $0$ |
| $b_1$ | $b_2$ | $b_3$ | $0$ |
| $c_1$ | $c_2$ | $0$ | $0$ |
| $d_1$ | $d_2$ | $0$ | $0$ |
| $e_1$ | $0$ | $0$ | $0$ |
| $f_1$ | $0$ | $0$ | $0$ |

where

$$b_1 = \frac{a_4a_5 - a_3}{a_5},$$
$$b_2 = \frac{a_2a_5 - a_1}{a_5},$$

$$
\begin{aligned}
b_3 &= a_0,\\
c_1 &= \frac{(a_4a_5 - a_3)a_3 - (a_2a_5 - a_1)a_5}{a_4a_5 - a_3},\\
c_2 &= \frac{(a_4a_5 - a_3)a_1 - a_0a_5^2}{a_4a_5 - a_3},\\
d_1 &= \frac{[(a_4a_5 - a_3)a_3 - (a_2a_5 - a_1)a_5](a_2a_5 - a_1) - [(a_4a_5 - a_3)a_1 - a_0a_5^2](a_4a_5 - a_3)}{[(a_4a_5 - a_3)a_3 - (a_2a_5 - a_1)a_5]a_5},\\
d_2 &= a_0,\\
e_1 &= [[(a_4a_5 - a_3)a_3 - (a_2a_5 - a_1)a_5](a_2a_5 - a_1) - [(a_4a_5 - a_3)a_1 - a_0a_5^2](a_4a_5 - a_3)]\times\\
&\quad \frac{[(a_4a_5 - a_3)a_1 - a_0a_5^2] - [(a_4a_5 - a_3)a_3 - (a_2a_5 - a_1)a_5]a_0}{[(a_4a_5 - a_3)a_3 - (a_2a_5 - a_1)a_5](a_2a_5 - a_1) - [(a_4a_5 - a_3)a_1 - a_0a_5^2](a_4a_5 - a_3)\times},\\
&\quad (a_4a_5 - a_3)\\
f_1 &= a_0.
\end{aligned}
$$

Therefore, the roots of $P(\lambda)$ have negative real part if $a_0$, $a_5$, $b_1$, $c_1$, $d_1$ and $e_1$ are positive.

# Appendix C

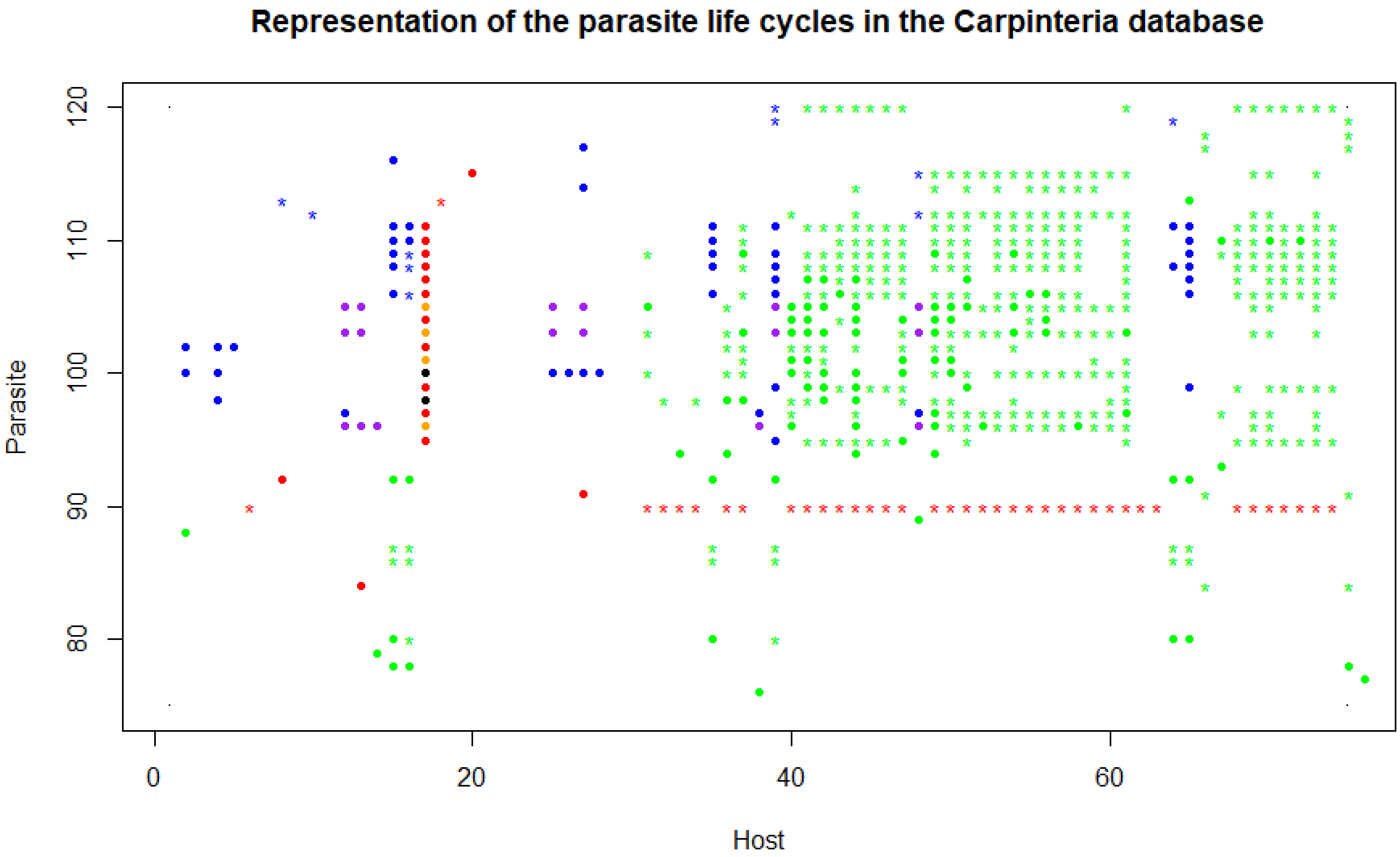
# Carpinteria Data from NCEAS

The Carpinteria database obtained in a study conducted at Carpinteria Salt Marsh Reserve, Carpinteria, Santa Barbara County, California, consists of four subnets given by predator-prey, parasite-host, predator-parasite and parasite-parasite interactions. The complete database contains 128 animal species classified as predatory, host and parasite species, of which, 120 correspond to host or parasitic species.

This appendix shows a representation of the life cycles of the parasite species found in the host species, considering only the parasite-host relationships between the 75 host species and 45 parasitic species in the database. The following table shows a description of the symbols used in the representation of the parasitic stages of each parasite species found in the host species, and the symbols used to represent the possible host species in which a parasitic species could enter during some stage of its life cycle, but nevertheless, were not found during the study.

| Symbol | Description |
|---|---|
| ● | First intermediate host. |
| ● | First and second intermediate host. |
| ● | First and second intermediate host, excysts outside second intermediate host. |
| ● | Second intermediate host. |
| ● | Second intermediate host external (non-trophic) cyst. |
| ● | Final host |
| ★ | Proposed/presumed first intermediate host. |
| ★ | Proposed/presumed second intermediate host. |
| ★ | Proposed/presumed final host. |

Table C.1: Description of the symbols used in the life cycles representation.


Representation of the parasite life cycles in the Carpinteria database
Parasite
120
110
100
90
80
0
20
40
60
Host

The complete list of animal species studied in this database is given in two parts, the first part consists of the 75 host species in the system, and the second part contains the 45 parasitic species observed. The first part of the list, with all the host species, is as follows:

| No. | Species |
|---|---|
| 1 | Oligochaete. |
| 2 | Capitella capitata. |
| 3 | Phoronid. |
| 4 | Spionidae. |
| 5 | Eteone lightii. |
| 6 | Turkey vulture. |
| 7 | Corophium sp. |
| 8 | Harpacticoid. |
| 9 | Ostracods. |
| 10 | Anisogammarus confervicolus. |
| 11 | Traskorchestia. |
| 12 | Uca crenulata. |
| 13 | Neotrypaea. |
| 14 | Upogebia. |
| 15 | Atherinops affinis. |
| 16 | Mugil cephalus. |
| 17 | Cerithidea californica. |
| 18 | Acteocina inculcata. |
| 19 | Melampus. |
| 20 | Assiminea. |
| 21 | Trichocorixia. |
| 22 | Ephydra larva. |
| 23 | Mosquito larva. |
| 24 | Ephydra adult. |
| 25 | Macoma nasuta. |
| 26 | Protothaca. |
| 27 | Tagelus spp. |
| 28 | Cryptomya. |
| 29 | Mytilus galloprovincialis. |
| 30 | Geonemertes. |
| 31 | American coot. |
| 32 | Mallard. |
| 33 | Killdeer. |
| 34 | Green-winged teal. |
| 35 | Cleavlandia ios. |
| 36 | Semipalmated plover. |
| 37 | Greater Yellowlegs. |
| 38 | Hemigrapsus oregonensis. |
| 39 | Fundulus parvipinnis. |
| 40 | Western sandpiper. |
| 41 | Dunlin. |
| 42 | Least sandpiper. |
| 43 | Forster's tern. |
| 44 | Dowitcher. |
| 45 | Green heron. |
| 46 | Belted kingfisher. |
| 47 | American avocet. |
| 48 | Pachygrapsus crassipes. |
| 49 | Willet. |
| 50 | Black-bellied plover. |
| 51 | California gull. |
| 52 | Whimbrel. |
| 53 | Mew gull. |
| 54 | Marbled godwit. |
| 55 | Ring-billed gull. |
| 56 | Western gull. |
| 57 | Bonaparte's gull. |
| 58 | Long-billed curlew. |
| 59 | Surf scoter. |
| 60 | Bufflehead. |
| 61 | Clapper rail. |
| 62 | Cooper's hawk. |
| 63 | Northern harrier. |
| 64 | Leptocottus armatus. |
| 65 | Gillycthys mirabilis. |
| 66 | Urolophus halleri. |
| 67 | Procyon locator. |
| 68 | Great blue heron. |
| 69 | Snowy egret. |
| 70 | Black-crowned night heron. |
| 71 | Double crested cormorant. |
| 72 | Great egret. |
| 73 | Pied billed grebe. |
| 74 | Osprey. |
| 75 | Triakis semifasciata. |

On the other hand, the rest of the list, with all parasitic species, is given by

| No. | Species |
|---|---|
| 76 | Portunion conformis. |
| 77 | Picornavirus. |
| 78 | Nerocila californica. |
| 79 | Orthione. |
| 80 | Ergasilus auritious. |
| 81 | Aedes taeniorhynchus. |
| 82 | Culex tarsalis. |
| 83 | Leech (glossiphonidae). |
| 84 | Proleptus. |
| 85 | Carcinonemertes. |
| 86 | Gyrodactylus. |
| 87 | Trichodina. |
| 88 | Eugregarine. |
| 89 | Eugregarine. |
| 90 | Plasmodium. |
| 91 | Nematode in tagelus. |
| 92 | Spirocamellanus perarai. |
| 93 | Baylisascaris procyonis. |
| 94 | Acanthocephalan in gillichthys. |
| 95 | Euhaplorchis californiensis. |
| 96 | Himasthla rhigedana. |
| 97 | Probolocoryphe uca. |
| 98 | Himasthla species B. |
| 99 | Renicola buchanani. |
| 100 | Acanthoparyphium sp. |
| 101 | Catatropis johnstoni. |
| 102 | Large xiphideocercaria. |
| 103 | Parorchis acanthus. |
| 104 | Austrobiharzia. |
| 105 | Cloacitrema michiganensis. |
| 106 | Phocitremoides ovale. |
| 107 | Renicola cerithidicola. |
| 108 | Small cyathocotylid. |
| 109 | Stictodora hancocki. |
| 110 | Mesostephanus appendiculatoides. |
| 111 | Pygidiopsoides spindalis. |
| 112 | Microphallid 1. |
| 113 | Hysterolecitha. |
| 114 | Parvatrema. |
| 115 | Microphallid 2. |
| 116 | Galactosomum. |
| 117 | Tetraphyllidean. |
| 118 | Tetraphyllid fish. |
| 119 | Trypanorynch. |
| 120 | Dilepidid. |

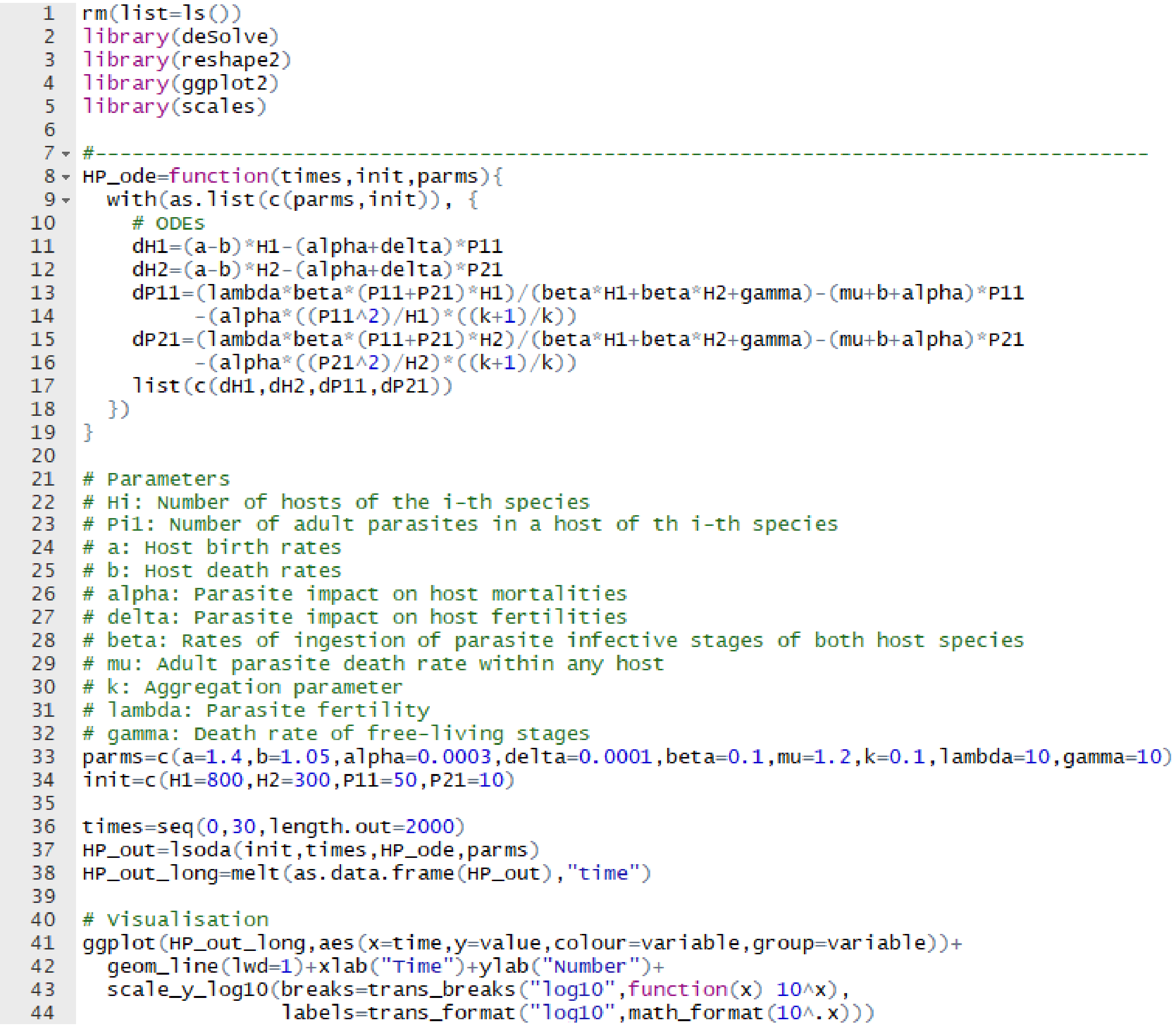
# Appendix D

# R Codes

This appendix contains the R codes used to perform the simulations present in this thesis. The first code presented here was used to simulate population dynamics in the Anderson and May model (1.1) presented in Figure 4.1.

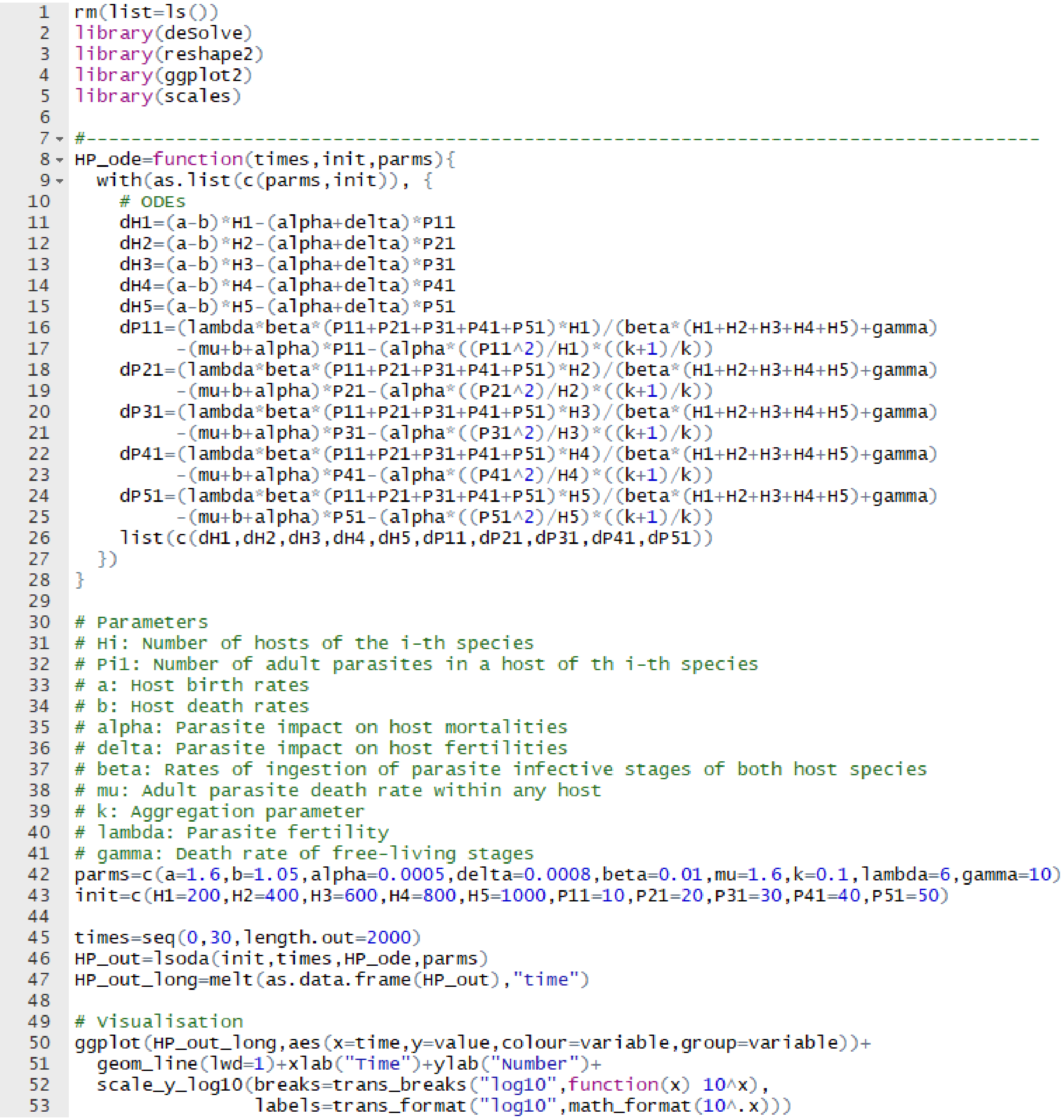
```r
rm(list=ls())
library(deSolve)
library(reshape2)
library(ggplot2)
library(scales)

#------------------------------ Anderson and May Model ------------------------------
HP_ode=function(times,init,parms){
  with(as.list(c(parms,init)), {
    # ODEs
    dH=(a-b)*H-(alpha)*P
    dP=(lambda*P*H)/(H+gamma/beta)-(mu+alpha+b)*P-(alpha*((P^2)/H)*((k+1)/k))
    list(c(dH,dP))
  })
}

# Parameters
# H: Number of hosts
# P: Number of parasites
# a: Host birth rate
# b: Host death rate
# alpha: Parasite impact on host mortality
# beta: Rate of ingestion of parasite infective stages
# mu: Parasite death rate
# k: Aggregation parameter
# lambda: Parasite fertility
# gamma: Death rate of free-living stages
parms=c(a=1.4,b=1.05,alpha=0.0003,beta=0.1,mu=0.5,k=0.1,lambda=10,gamma=10)
init=c(H=200,P=10)

times=seq(0,30,length.out=3000)
HP_out=lsoda(init,times,HP_ode,parms)
HP_out_long=melt(as.data.frame(HP_out),"time")

# Visualisation
ggplot(HP_out_long,aes(x=time,y=value,colour=variable,group=variable))+
  geom_line(lwd=1)+xlab("Time")+ylab("Number")+
  scale_y_log10(breaks=trans_breaks("log10",function(x) 10^x),
                labels=trans_format("log10",math_format(10^.x)))
```

The next code was used for the simulation of the model (2.3) shown in Figure 4.3, where there are two host species and only the adult parasites enter in the individuals of any host species.



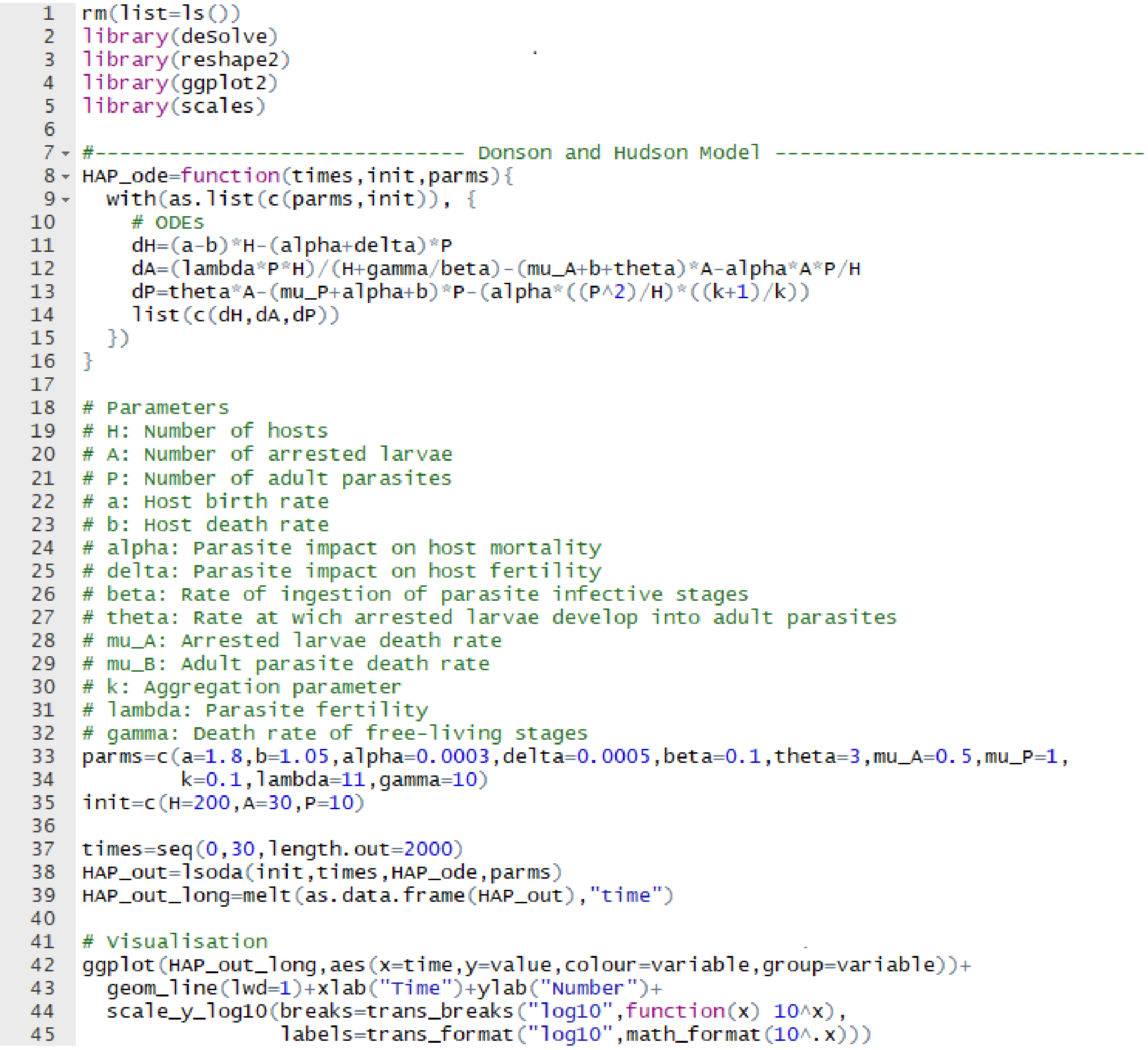
```
rm(list=ls())
library(deSolve)
library(reshape2)
library(ggplot2)
library(scales)

#-------------------------------------------------------------------------------------
HP_ode=function(times,init,parms){
  with(as.list(c(parms,init)), {
    # ODEs
    dH1=(a-b)*H1-(alpha+delta)*P11
    dH2=(a-b)*H2-(alpha+delta)*P21
    dP11=(lambda*beta*(P11+P21)*H1)/(beta*H1+beta*H2+gamma)-(mu+b+alpha)*P11
         -(alpha*((P11^2)/H1)*((k+1)/k))
    dP21=(lambda*beta*(P11+P21)*H2)/(beta*H1+beta*H2+gamma)-(mu+b+alpha)*P21
         -(alpha*((P21^2)/H2)*((k+1)/k))
    list(c(dH1,dH2,dP11,dP21))
  })
}

# Parameters
# Hi: Number of hosts of the i-th species
# Pi1: Number of adult parasites in a host of th i-th species
# a: Host birth rates
# b: Host death rates
# alpha: Parasite impact on host mortalities
# delta: Parasite impact on host fertilities
# beta: Rates of ingestion of parasite infective stages of both host species
# mu: Adult parasite death rate within any host
# k: Aggregation parameter
# lambda: Parasite fertility
# gamma: Death rate of free-living stages
parms=c(a=1.4,b=1.05,alpha=0.0003,delta=0.0001,beta=0.1,mu=1.2,k=0.1,lambda=10,gamma=10)
init=c(H1=800,H2=300,P11=50,P21=10)

times=seq(0,30,length.out=2000)
HP_out=lsoda(init,times,HP_ode,parms)
HP_out_long=melt(as.data.frame(HP_out),"time")

# Visualisation
ggplot(HP_out_long,aes(x=time,y=value,colour=variable,group=variable))+
  geom_line(lwd=1)+xlab("Time")+ylab("Number")+
  scale_y_log10(breaks=trans_breaks("log10",function(x) 10^x),
                labels=trans_format("log10",math_format(10^.x)))
```

This is the code used to simulate population dynamics in a system with five host species that only adult parasites can colonize, presented in Figure 4.4.



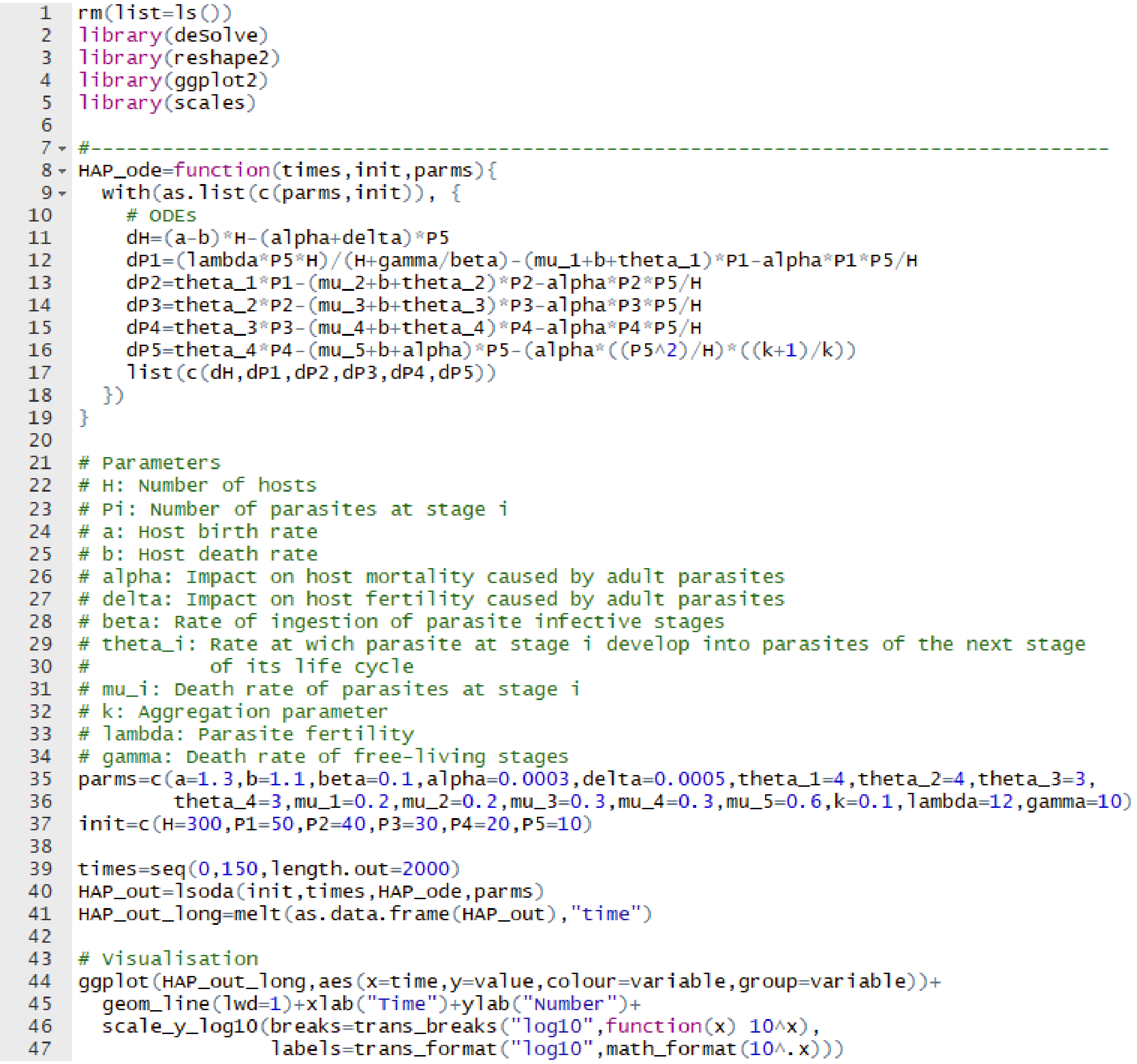
```
rm(list=ls())
library(deSolve)
library(reshape2)
library(ggplot2)
library(scales)

#-------------------------------------------------------------------------------------
HP_ode=function(times,init,parms){
  with(as.list(c(parms,init)), {
    # ODEs
    dH1=(a-b)*H1-(alpha+delta)*P11
    dH2=(a-b)*H2-(alpha+delta)*P21
    dH3=(a-b)*H3-(alpha+delta)*P31
    dH4=(a-b)*H4-(alpha+delta)*P41
    dH5=(a-b)*H5-(alpha+delta)*P51
    dP11=(lambda*beta*(P11+P21+P31+P41+P51)*H1)/(beta*(H1+H2+H3+H4+H5)+gamma)
         -(mu+b+alpha)*P11-(alpha*((P11^2)/H1)*((k+1)/k))
    dP21=(lambda*beta*(P11+P21+P31+P41+P51)*H2)/(beta*(H1+H2+H3+H4+H5)+gamma)
         -(mu+b+alpha)*P21-(alpha*((P21^2)/H2)*((k+1)/k))
    dP31=(lambda*beta*(P11+P21+P31+P41+P51)*H3)/(beta*(H1+H2+H3+H4+H5)+gamma)
         -(mu+b+alpha)*P31-(alpha*((P31^2)/H3)*((k+1)/k))
    dP41=(lambda*beta*(P11+P21+P31+P41+P51)*H4)/(beta*(H1+H2+H3+H4+H5)+gamma)
         -(mu+b+alpha)*P41-(alpha*((P41^2)/H4)*((k+1)/k))
    dP51=(lambda*beta*(P11+P21+P31+P41+P51)*H5)/(beta*(H1+H2+H3+H4+H5)+gamma)
         -(mu+b+alpha)*P51-(alpha*((P51^2)/H5)*((k+1)/k))
    list(c(dH1,dH2,dH3,dH4,dH5,dP11,dP21,dP31,dP41,dP51))
  })
}

# Parameters
# Hi: Number of hosts of the i-th species
# Pi1: Number of adult parasites in a host of th i-th species
# a: Host birth rates
# b: Host death rates
# alpha: Parasite impact on host mortalities
# delta: Parasite impact on host fertilities
# beta: Rates of ingestion of parasite infective stages of both host species
# mu: Adult parasite death rate within any host
# k: Aggregation parameter
# lambda: Parasite fertility
# gamma: Death rate of free-living stages
parms=c(a=1.6,b=1.05,alpha=0.0005,delta=0.0008,beta=0.01,mu=1.6,k=0.1,lambda=6,gamma=10)
init=c(H1=200,H2=400,H3=600,H4=800,H5=1000,P11=10,P21=20,P31=30,P41=40,P51=50)

times=seq(0,30,length.out=2000)
HP_out=lsoda(init,times,HP_ode,parms)
HP_out_long=melt(as.data.frame(HP_out),"time")

# Visualisation
ggplot(HP_out_long,aes(x=time,y=value,colour=variable,group=variable))+
  geom_line(lwd=1)+xlab("Time")+ylab("Number")+
  scale_y_log10(breaks=trans_breaks("log10",function(x) 10^x),
                labels=trans_format("log10",math_format(10^.x)))
```

The following code was used to simulate population dynamics in the Dobson and Hudson model (1.3) in the Figure 4.5.



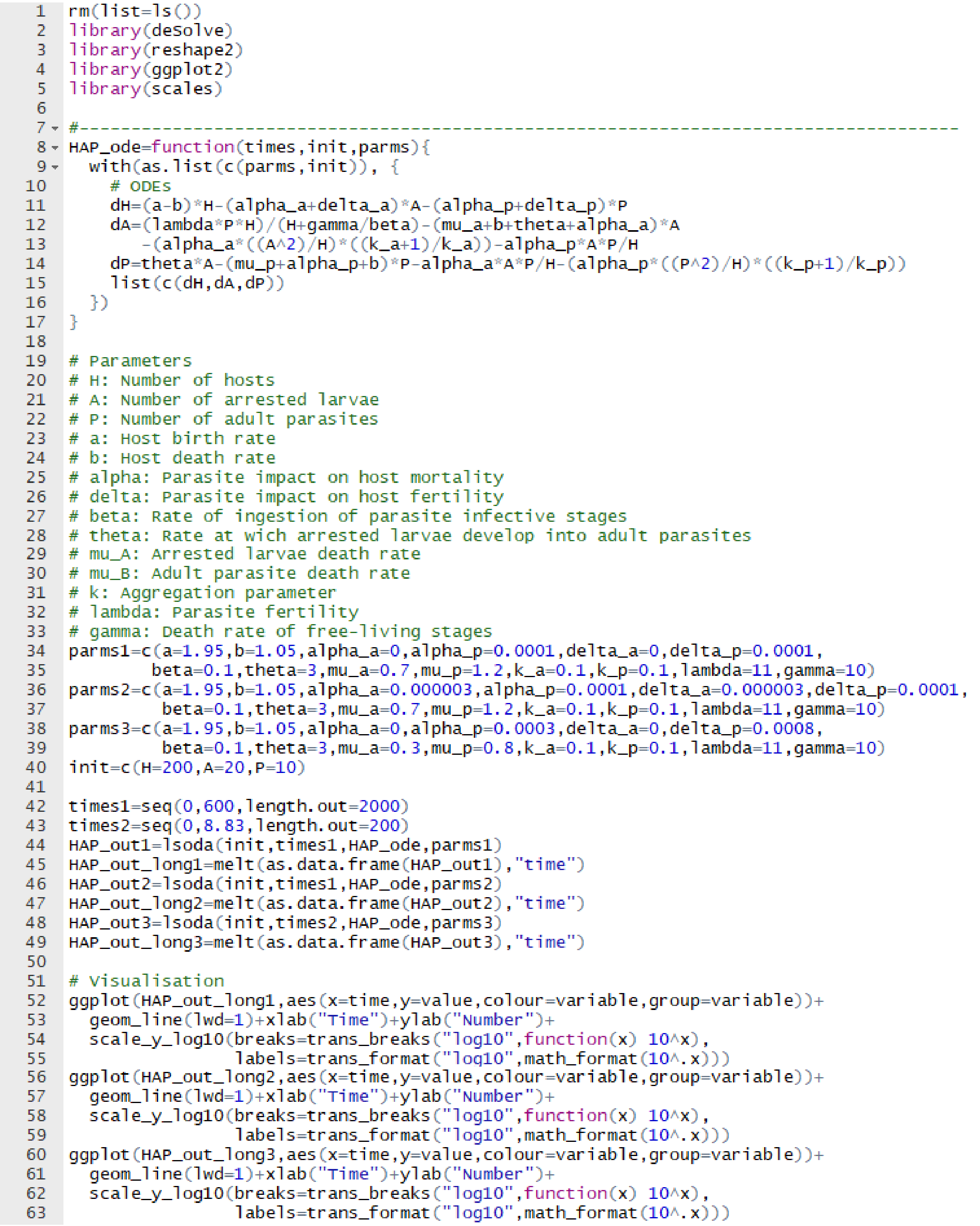
```r
rm(list=ls())
library(desolve)
library(reshape2)
library(ggplot2)
library(scales)

#------------------------------ Donson and Hudson Model -------------------------------
HAP_ode=function(times,init,parms){
  with(as.list(c(parms,init)), {
    # ODEs
    dH=(a-b)*H-(alpha+delta)*P
    dA=(lambda*P*H)/(H+gamma/beta)-(mu_A+b+theta)*A-alpha*A*P/H
    dP=theta*A-(mu_P+alpha+b)*P-(alpha*((P^2)/H)*((k+1)/k))
    list(c(dH,dA,dP))
  })
}

# Parameters
# H: Number of hosts
# A: Number of arrested larvae
# P: Number of adult parasites
# a: Host birth rate
# b: Host death rate
# alpha: Parasite impact on host mortality
# delta: Parasite impact on host fertility
# beta: Rate of ingestion of parasite infective stages
# theta: Rate at wich arrested larvae develop into adult parasites
# mu_A: Arrested larvae death rate
# mu_B: Adult parasite death rate
# k: Aggregation parameter
# lambda: Parasite fertility
# gamma: Death rate of free-living stages
parms=c(a=1.8,b=1.05,alpha=0.0003,delta=0.0005,beta=0.1,theta=3,mu_A=0.5,mu_P=1,
        k=0.1,lambda=11,gamma=10)
init=c(H=200,A=30,P=10)

times=seq(0,30,length.out=2000)
HAP_out=lsoda(init,times,HAP_ode,parms)
HAP_out_long=melt(as.data.frame(HAP_out),"time")

# Visualisation
ggplot(HAP_out_long,aes(x=time,y=value,colour=variable,group=variable))+
  geom_line(lwd=1)+xlab("Time")+ylab("Number")+
  scale_y_log10(breaks=trans_breaks("log10",function(x) 10^x),
                labels=trans_format("log10",math_format(10^.x)))
```

Below is the code used for the simulations in Figure 4.6.

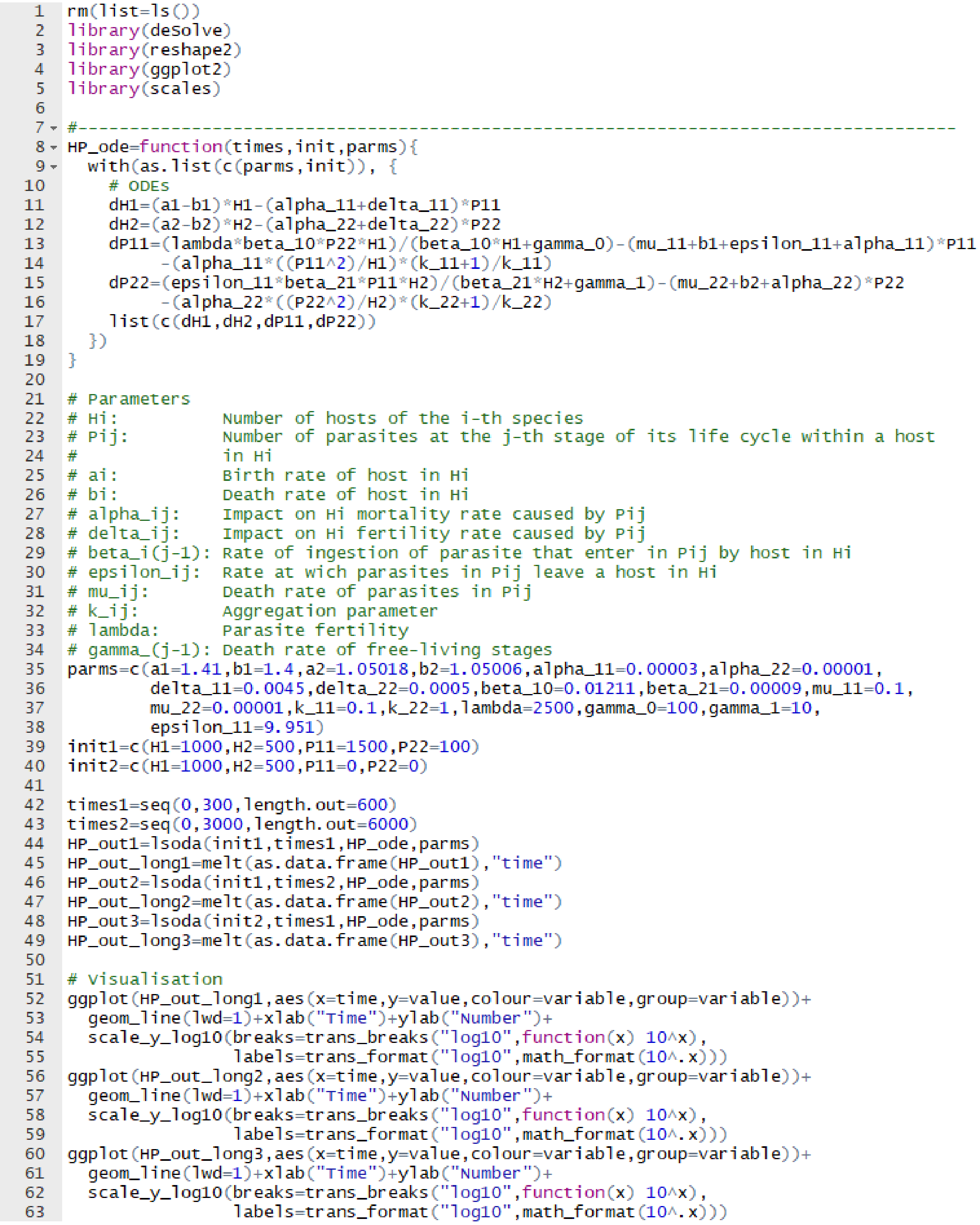


```r
rm(list=ls())
library(deSolve)
library(reshape2)
library(ggplot2)
library(scales)

#--------------------------------------------------------------------------------------
HAP_ode=function(times,init,parms){
  with(as.list(c(parms,init)), {
    # ODEs
    dH=(a-b)*H-(alpha+delta)*P5
    dP1=(lambda*P5*H)/(H+gamma/beta)-(mu_1+b+theta_1)*P1-alpha*P1*P5/H
    dP2=theta_1*P1-(mu_2+b+theta_2)*P2-alpha*P2*P5/H
    dP3=theta_2*P2-(mu_3+b+theta_3)*P3-alpha*P3*P5/H
    dP4=theta_3*P3-(mu_4+b+theta_4)*P4-alpha*P4*P5/H
    dP5=theta_4*P4-(mu_5+b+alpha)*P5-(alpha*((P5^2)/H)*((k+1)/k))
    list(c(dH,dP1,dP2,dP3,dP4,dP5))
  })
}

# Parameters
# H: Number of hosts
# Pi: Number of parasites at stage i
# a: Host birth rate
# b: Host death rate
# alpha: Impact on host mortality caused by adult parasites
# delta: Impact on host fertility caused by adult parasites
# beta: Rate of ingestion of parasite infective stages
# theta_i: Rate at wich parasite at stage i develop into parasites of the next stage
#          of its life cycle
# mu_i: Death rate of parasites at stage i
# k: Aggregation parameter
# lambda: Parasite fertility
# gamma: Death rate of free-living stages
parms=c(a=1.3,b=1.1,beta=0.1,alpha=0.0003,delta=0.0005,theta_1=4,theta_2=4,theta_3=3,
        theta_4=3,mu_1=0.2,mu_2=0.2,mu_3=0.3,mu_4=0.3,mu_5=0.6,k=0.1,lambda=12,gamma=10)
init=c(H=300,P1=50,P2=40,P3=30,P4=20,P5=10)

times=seq(0,150,length.out=2000)
HAP_out=lsoda(init,times,HAP_ode,parms)
HAP_out_long=melt(as.data.frame(HAP_out),"time")

# Visualisation
ggplot(HAP_out_long,aes(x=time,y=value,colour=variable,group=variable))+
  geom_line(lwd=1)+xlab("Time")+ylab("Number")+
  scale_y_log10(breaks=trans_breaks("log10",function(x) 10^x),
                labels=trans_format("log10",math_format(10^.x)))
```

The next code was used for the simulations presented in Figure 3.6, Figure 3.7 and Figure 3.8.

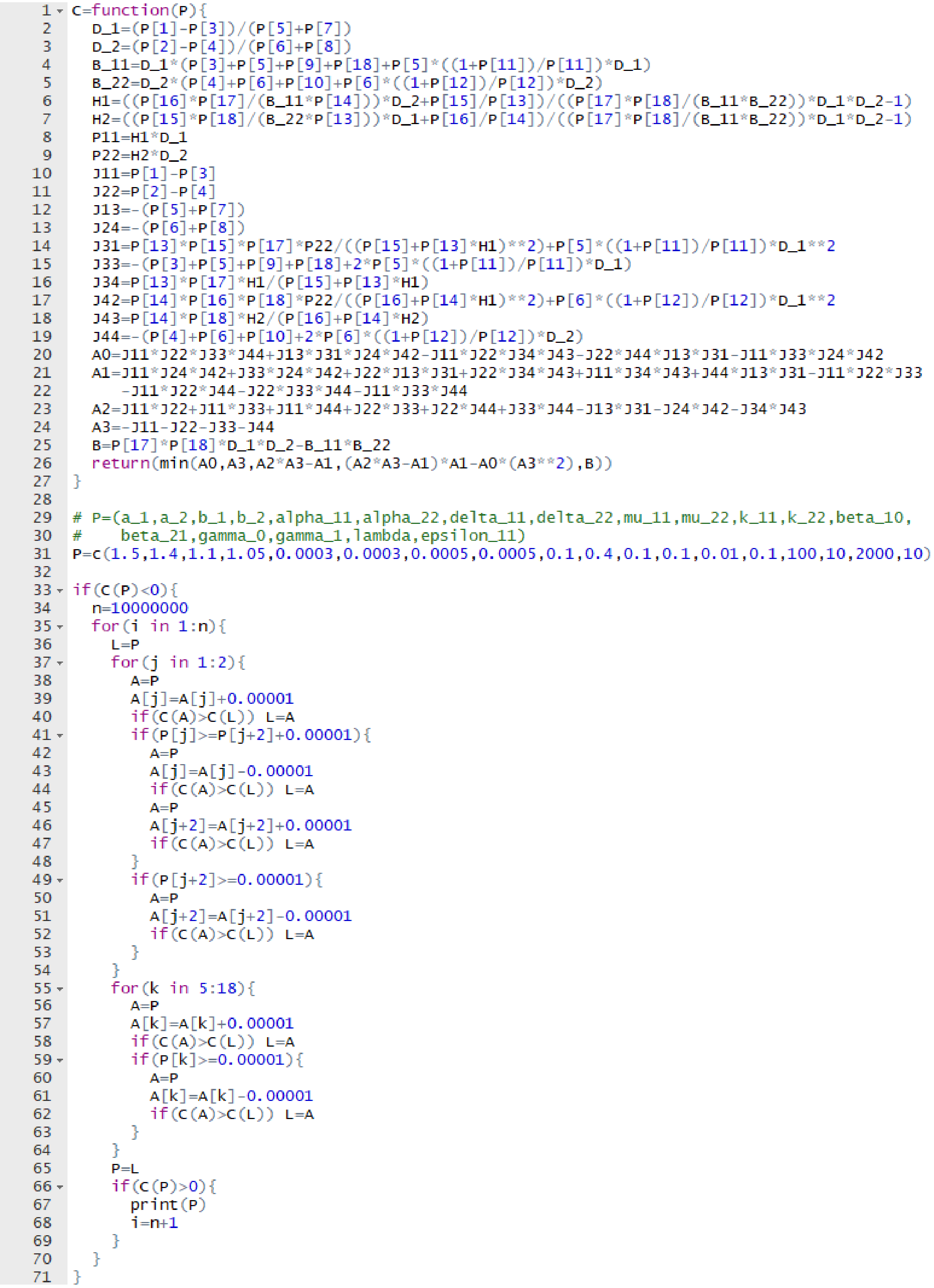


```r
rm(list=ls())
library(deSolve)
library(reshape2)
library(ggplot2)
library(scales)

#-------------------------------------------------------------------------------------
HAP_ode=function(times,init,parms){
  with(as.list(c(parms,init)), {
    # ODEs
    dH=(a-b)*H-(alpha_a+delta_a)*A-(alpha_p+delta_p)*P
    dA=(lambda*P*H)/(H+gamma/beta)-(mu_a+b+theta+alpha_a)*A
       -(alpha_a*((A^2)/H)*((k_a+1)/k_a))-alpha_p*A*P/H
    dP=theta*A-(mu_p+alpha_p+b)*P-alpha_a*A*P/H-(alpha_p*((P^2)/H)*((k_p+1)/k_p))
    list(c(dH,dA,dP))
  })
}

# Parameters
# H: Number of hosts
# A: Number of arrested larvae
# P: Number of adult parasites
# a: Host birth rate
# b: Host death rate
# alpha: Parasite impact on host mortality
# delta: Parasite impact on host fertility
# beta: Rate of ingestion of parasite infective stages
# theta: Rate at wich arrested larvae develop into adult parasites
# mu_A: Arrested larvae death rate
# mu_B: Adult parasite death rate
# k: Aggregation parameter
# lambda: Parasite fertility
# gamma: Death rate of free-living stages
parms1=c(a=1.95,b=1.05,alpha_a=0,alpha_p=0.0001,delta_a=0,delta_p=0.0001,
        beta=0.1,theta=3,mu_a=0.7,mu_p=1.2,k_a=0.1,k_p=0.1,lambda=11,gamma=10)
parms2=c(a=1.95,b=1.05,alpha_a=0.000003,alpha_p=0.0001,delta_a=0.000003,delta_p=0.0001,
         beta=0.1,theta=3,mu_a=0.7,mu_p=1.2,k_a=0.1,k_p=0.1,lambda=11,gamma=10)
parms3=c(a=1.95,b=1.05,alpha_a=0,alpha_p=0.0003,delta_a=0,delta_p=0.0008,
         beta=0.1,theta=3,mu_a=0.3,mu_p=0.8,k_a=0.1,k_p=0.1,lambda=11,gamma=10)
init=c(H=200,A=20,P=10)

times1=seq(0,600,length.out=2000)
times2=seq(0,8.83,length.out=200)
HAP_out1=lsoda(init,times1,HAP_ode,parms1)
HAP_out_long1=melt(as.data.frame(HAP_out1),"time")
HAP_out2=lsoda(init,times1,HAP_ode,parms2)
HAP_out_long2=melt(as.data.frame(HAP_out2),"time")
HAP_out3=lsoda(init,times2,HAP_ode,parms3)
HAP_out_long3=melt(as.data.frame(HAP_out3),"time")

# Visualisation
ggplot(HAP_out_long1,aes(x=time,y=value,colour=variable,group=variable))+
  geom_line(lwd=1)+xlab("Time")+ylab("Number")+
  scale_y_log10(breaks=trans_breaks("log10",function(x) 10^x),
                labels=trans_format("log10",math_format(10^.x)))
ggplot(HAP_out_long2,aes(x=time,y=value,colour=variable,group=variable))+
  geom_line(lwd=1)+xlab("Time")+ylab("Number")+
  scale_y_log10(breaks=trans_breaks("log10",function(x) 10^x),
                labels=trans_format("log10",math_format(10^.x)))
ggplot(HAP_out_long3,aes(x=time,y=value,colour=variable,group=variable))+
  geom_line(lwd=1)+xlab("Time")+ylab("Number")+
  scale_y_log10(breaks=trans_breaks("log10",function(x) 10^x),
                labels=trans_format("log10",math_format(10^.x)))
```



```r
rm(list=ls())
library(deSolve)
library(reshape2)
library(ggplot2)
library(scales)

#------------------------------------------------------------------------------------
HP_ode=function(times,init,parms){
  with(as.list(c(parms,init)), {
    # ODEs
    dH1=(a1-b1)*H1-(alpha_11+delta_11)*P11
    dH2=(a2-b2)*H2-(alpha_22+delta_22)*P22
    dP11=(lambda*beta_10*P22*H1)/(beta_10*H1+gamma_0)-(mu_11+b1+epsilon_11+alpha_11)*P11
         -(alpha_11*((P11^2)/H1)*(k_11+1)/k_11)
    dP22=(epsilon_11*beta_21*P11*H2)/(beta_21*H2+gamma_1)-(mu_22+b2+alpha_22)*P22
         -(alpha_22*((P22^2)/H2)*(k_22+1)/k_22)
    list(c(dH1,dH2,dP11,dP22))
  })
}

# Parameters
# Hi:          Number of hosts of the i-th species
# Pij:         Number of parasites at the j-th stage of its life cycle within a host
#              in Hi
# ai:          Birth rate of host in Hi
# bi:          Death rate of host in Hi
# alpha_ij:    Impact on Hi mortality rate caused by Pij
# delta_ij:    Impact on Hi fertility rate caused by Pij
# beta_i(j-1): Rate of ingestion of parasite that enter in Pij by host in Hi
# epsilon_ij:  Rate at wich parasites in Pij leave a host in Hi
# mu_ij:       Death rate of parasites in Pij
# k_ij:        Aggregation parameter
# lambda:      Parasite fertility
# gamma_(j-1): Death rate of free-living stages
parms=c(a1=1.41,b1=1.4,a2=1.05018,b2=1.05006,alpha_11=0.00003,alpha_22=0.00001,
        delta_11=0.0045,delta_22=0.0005,beta_10=0.01211,beta_21=0.00009,mu_11=0.1,
        mu_22=0.00001,k_11=0.1,k_22=1,lambda=2500,gamma_0=100,gamma_1=10,
        epsilon_11=9.951)
init1=c(H1=1000,H2=500,P11=1500,P22=100)
init2=c(H1=1000,H2=500,P11=0,P22=0)

times1=seq(0,300,length.out=600)
times2=seq(0,3000,length.out=6000)
HP_out1=lsoda(init1,times1,HP_ode,parms)
HP_out_long1=melt(as.data.frame(HP_out1),"time")
HP_out2=lsoda(init1,times2,HP_ode,parms)
HP_out_long2=melt(as.data.frame(HP_out2),"time")
HP_out3=lsoda(init2,times1,HP_ode,parms)
HP_out_long3=melt(as.data.frame(HP_out3),"time")

# Visualisation
ggplot(HP_out_long1,aes(x=time,y=value,colour=variable,group=variable))+
  geom_line(lwd=1)+xlab("Time")+ylab("Number")+
  scale_y_log10(breaks=trans_breaks("log10",function(x) 10^x),
                labels=trans_format("log10",math_format(10^.x)))
ggplot(HP_out_long2,aes(x=time,y=value,colour=variable,group=variable))+
  geom_line(lwd=1)+xlab("Time")+ylab("Number")+
  scale_y_log10(breaks=trans_breaks("log10",function(x) 10^x),
                labels=trans_format("log10",math_format(10^.x)))
ggplot(HP_out_long3,aes(x=time,y=value,colour=variable,group=variable))+
  geom_line(lwd=1)+xlab("Time")+ylab("Number")+
  scale_y_log10(breaks=trans_breaks("log10",function(x) 10^x),
                labels=trans_format("log10",math_format(10^.x)))
```

Tabu search algorithm [32, 33] used to find feasible parametric values in (4.17).



```r
C=function(P){
  D_1=(P[1]-P[3])/(P[5]+P[7])
  D_2=(P[2]-P[4])/(P[6]+P[8])
  B_11=D_1*(P[3]+P[5]+P[9]+P[18]+P[5]*((1+P[11])/P[11])*D_1)
  B_22=D_2*(P[4]+P[6]+P[10]+P[6]*((1+P[12])/P[12])*D_2)
  H1=((P[16]*P[17]/(B_11*P[14]))*D_2+P[15]/P[13])/((P[17]*P[18]/(B_11*B_22))*D_1*D_2-1)
  H2=((P[15]*P[18]/(B_22*P[13]))*D_1+P[16]/P[14])/((P[17]*P[18]/(B_11*B_22))*D_1*D_2-1)
  P11=H1*D_1
  P22=H2*D_2
  J11=P[1]-P[3]
  J22=P[2]-P[4]
  J13=-(P[5]+P[7])
  J24=-(P[6]+P[8])
  J31=P[13]*P[15]*P[17]*P22/((P[15]+P[13]*H1)**2)+P[5]*((1+P[11])/P[11])*D_1**2
  J33=-(P[3]+P[5]+P[9]+P[18]+2*P[5]*((1+P[11])/P[11])*D_1)
  J34=P[13]*P[17]*H1/(P[15]+P[13]*H1)
  J42=P[14]*P[16]*P[18]*P22/((P[16]+P[14]*H1)**2)+P[6]*((1+P[12])/P[12])*D_1**2
  J43=P[14]*P[18]*H2/(P[16]+P[14]*H2)
  J44=-(P[4]+P[6]+P[10]+2*P[6]*((1+P[12])/P[12])*D_2)
  A0=J11*J22*J33*J44+J13*J31*J24*J42-J11*J22*J34*J43-J22*J44*J13*J31-J11*J33*J24*J42
  A1=J11*J24*J42+J33*J24*J42+J22*J13*J31+J22*J34*J43+J11*J34*J43+J44*J13*J31-J11*J22*J33
     -J11*J22*J44-J22*J33*J44-J11*J33*J44
  A2=J11*J22+J11*J33+J11*J44+J22*J33+J22*J44+J33*J44-J13*J31-J24*J42-J34*J43
  A3=-J11-J22-J33-J44
  B=P[17]*P[18]*D_1*D_2-B_11*B_22
  return(min(A0,A3,A2*A3-A1,(A2*A3-A1)*A1-A0*(A3**2),B))
}

# P=(a_1,a_2,b_1,b_2,alpha_11,alpha_22,delta_11,delta_22,mu_11,mu_22,k_11,k_22,beta_10,
#     beta_21,gamma_0,gamma_1,lambda,epsilon_11)
P=c(1.5,1.4,1.1,1.05,0.0003,0.0003,0.0005,0.0005,0.1,0.4,0.1,0.1,0.01,0.1,100,10,2000,10)

if(C(P)<0){
  n=10000000
  for(i in 1:n){
    L=P
    for(j in 1:2){
      A=P
      A[j]=A[j]+0.00001
      if(C(A)>C(L)) L=A
      if(P[j]>=P[j+2]+0.00001){
        A=P
        A[j]=A[j]-0.00001
        if(C(A)>C(L)) L=A
        A=P
        A[j+2]=A[j+2]+0.00001
        if(C(A)>C(L)) L=A
      }
      if(P[j+2]>=0.00001){
        A=P
        A[j+2]=A[j+2]-0.00001
        if(C(A)>C(L)) L=A
      }
    }
    for(k in 5:18){
      A=P
      A[k]=A[k]+0.00001
      if(C(A)>C(L)) L=A
      if(P[k]>=0.00001){
        A=P
        A[k]=A[k]-0.00001
        if(C(A)>C(L)) L=A
      }
    }
    P=L
    if(C(P)>0){
      print(P)
      i=n+1
    }
  }
}
```

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