

Research Article

Modelling the Effects of Pollution on a Population and a Resource in a Polluted Environment

Victoria Maystruk¹ and Kenzu Abdella^{1,2}

¹ *Department of Mathematics, Trent University, Peterborough, ON, Canada K9J 7B8*

² *Department of Mathematics, Statistics and Physics, Qatar University, P.O. Box 2713, Doha, Qatar*

Correspondence should be addressed to Kenzu Abdella, kabdella@trentu.ca

Received 18 July 2011; Accepted 23 August 2011

Academic Editors: X. Meng and E. Skubalska-Rafajlowicz

Copyright © 2011 V. Maystruk and K. Abdella. This is an open access article distributed under the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

A model for the effect of pollution on an animal population partially dependent on a plant resource is examined. Using a system of ordinary differential equations, the model tracks and relates changes in an animal population and its internal pollution levels, a plant population and its internal pollution levels, and the overall environmental pollution level. The model system is analysed using standard mathematical techniques, including the direct Lyapunov method and numerical simulations. Criteria for the stability of the system are found and numerically tested. Three inequalities are sufficient to establish global stability, and a parameter range exists in which these criteria are satisfied. The stability criteria dictate that the system will be globally stable provided that the removal rate of the pollution from the environment, the intrinsic growth rate of the plant population, and the rate the animal population relieves itself of its pollution are all sufficiently large.

1. Introduction

Industrial production does not currently occur without emitting waste and byproducts. The industrial emissions enter the environment surrounding the industrial site and affect the local ecosystem. It has been shown that industrial wastes can decrease the birth rates, increase the death rates, and reduce the carrying capacity of flora and fauna proximal to the source of the industrialization [1]. Moreover, the local species can also affect the concentration of pollution in the environment; the species may absorb, digest, and eventually metabolize the pollution.

Modeling how pollution emitted into an ecosystem travels through that environment as well as modeling the subsequent effects of the pollution on the surrounding populations is an important step toward the conservation and preservation of populations living near industrial sites. Accurate simulation of the pollution-population system is crucial to mitigating

the potential loss of biodiversity. The majority of previous research endeavours that have mathematically modelled the effects of industrial pollution on species surrounding the industrial site have used the rate of uptake of pollution by the species as one of the variables in the model [2–9]. In these instances, the rate of uptake has been modeled as a linear process. While this approach simplifies some of the mathematical analysis, it does not track the movement of pollution through the ecosystem.

Recently, research modelling the movement of pollution through an ecosystem using a mass-balance approach for the pollution level was published [10]. This paper only deals with a single species living in a polluted environment; however, a similar approach can be used for a multi species model.

This paper draws on the multi species models previously developed by Dubey, Shukla, and their collaborators, while implementing a mass-balance approach for the pollution levels in the system presented by He and Wang to produce a new population-pollution model which is analysed using classical stability techniques.

We begin by proposing a new model to study the effects of a pollutant on local animal and plant biomass. We conduct local and global stability analysis on the nontrivial equilibrium solution of the model using the direct Lyapunov method. And finally, we conduct numerical simulations in order to compare the analytical results with numerical computations, in order to confirm that there is a parameter range for which the results are relevant.

2. Mathematical Model

Consider an ecosystem in which there are two principal biological species—a plant species and an animal species. The animal species consumes and is partially dependent on the plant species. Pollution is also being inputted into the ecosystem. We assume that the ecosystem is a spatially homogeneous environment and also that there is no migration to or emigration from the ecosystem. Additionally, we assume that all of the individuals within either species population are identical.

To model this system we will use five state variables— $N(t)$, $B(t)$, $C_N(t)$, $C_B(t)$, and $C_E(t)$. $N(t)$ represents the animal species density at time t , $B(t)$ represents the plant species density at time t , $C_N(t)$ represents the concentration of the toxicant in an individual animal at time t , $C_B(t)$ represents the concentration of the toxicant in an individual plant at time t , and $C_E(t)$ represents the concentration of the toxicant in the environment at time t .

We assume that the growth dynamics of the animal species and the plant species can be described using a modified version of the logistic growth equations.

When discussing the dynamics of population growth it can be useful to discuss the dynamics in terms of the birth rate, $b(t)$, and death rate, $d(t)$, of the populations. In general, we can think of population growth as

$$\frac{dN}{dt} = (b(t) - d(t))N, \quad (2.1)$$

If we let $r_0 = b_0 - d_0$ where b_0 is the intrinsic birth rate and d_0 is the intrinsic death rate of the population, then we can think of the general birth rate of a population growing according to a logistic growth model as

$$b(t) = b_0 - \frac{r_0 N}{K}. \quad (2.2)$$

Similarly, the general death rate can be thought of as

$$d(t) = d_0. \quad (2.3)$$

In the development of our model, we will first consider the population dynamics.

2.1. Population Dynamics

When developing an equation for the carrying capacity of the plant population, we assume that the carrying capacity of the plant species decreases due to the presence of pollution in the environment. Additionally, we assume that this change is proportional to the concentration of pollution in the environment. Let b_{B0} denote the intrinsic birth rate of the plant species, r_{B0} the intrinsic growth rate of the plant species, K_{B0} the intrinsic carrying capacity of the plant species, and K_{BC_E} the rate the carrying capacity decreases relative to the concentration of pollution in the environment. The birth rate of the plant species can be written as

$$b_B(B, C_E) = b_{B0} - \frac{r_{B0}B}{K_{B0} - K_{BC_E}C_E}. \quad (2.4)$$

For the death rate of the plant population, we assume that the death rate increases proportional to the animal species population and proportional to the concentration of toxicant present within the plant. These dynamics are akin to the animal population eating and the pollution poisoning the plant population. If d_{B0} is the intrinsic death rate of the plant species, let d_{BN} and d_{BC_B} denote the rates the death rate of the plant species increases relative to biomass of the animal species and the concentration of pollution in the plant species, respectively. Then, we describe the death rate of the plant population as

$$d_B(N, C_B) = d_{B0} + d_{BN}N + d_{BC_B}C_B. \quad (2.5)$$

Using $r_{B0} = b_{B0} - d_{B0}$, the equation governing the plant population is

$$\frac{dB}{dt} = (b_B(B, C_E) - d_B(N, C_B))B, \quad (2.6)$$

$$\frac{dB}{dt} = \left(r_{B0} - \frac{r_{B0}B}{K_{B0} - K_{BC_E}C_E} - d_{BN}N - d_{BC_B}C_B \right) B. \quad (2.7)$$

Now, consider the animal population dynamics.

Similar to the plant population, we assume that the animal species carrying capacity decreases in proportion to the quantity of pollution in the environment. Additionally, for the animal population, we assume that the carrying capacity increases in proportion to the population of the plant species. This increase is due to our assumption that the animals are partially dependent on the plants. Let b_{N0} , r_{N0} , and K_{B0} represent the intrinsic birth rate, growth rate, and carrying capacity of the animal species, respectively. Additionally, let K_{NB} denote the rate the carrying capacity increases relative to the plant biomass and K_{NC_E} the rate

the carrying capacity decreases relative to the concentration of pollution in the environment. Then, we can write the birth rate of the animal species as

$$b_N(N, B, C_E) = b_{N0} - \frac{r_{N0}N}{K_{N0} + K_{NB}B - K_{NC_E}C_E}. \quad (2.8)$$

To formulate the death rate of the animal species, we assume that the death rate decreases in proportion to the quantity of plant biomass and increases in proportion to the concentration of pollution present within the animal itself. We let d_{N0} represent the intrinsic death rate of the animal species, d_{NB} the rate the animals death rate decreases relative to the biomass of the plant, and d_{NC_N} the rate the animals death rate increases relative to the concentration of pollution present within the animal. We can write the animal death rate as

$$d_N(B, C_N) = d_{N0} - d_{NB}B + d_{NC_N}C_N. \quad (2.9)$$

Clearly, using $r_{N0} = b_{N0} - d_{N0}$, we can describe the dynamics of the animal population as

$$\frac{dN}{dt} = (b_N(N, B, C_E) - d_N(B, C_N))N, \quad (2.10)$$

$$\frac{dN}{dt} = \left(r_{N0} - \frac{r_{N0}N}{K_{N0} + K_{NB}B - K_{NC_E}C_E} + d_{NB}B - d_{NC_N}C_N \right) N. \quad (2.11)$$

Continuing the derivation of our model, we next develop the equations for the concentration of pollution dynamics via balance arguments.

2.2. Pollution Dynamics

The use of balance equations to model movements within a system is based upon the first law of thermodynamics [11–13].

We use m_n and m_b to represent the average per capita mass of the animal and plant populations, respectively, and we use m_e to represent the mass of the environment. Then m_bBC_B represents the total mass of toxicant in the plant population, m_nNC_N represents the total mass of toxicant in the animal population, and m_eC_E represents the total quantity of toxicant free in the environment. m_e is assumed to be sufficiently large and near constant, and hence variations in m_e do not need to be modeled. The flow of pollution in the system can be visualized in Figure 1 and is described next.

We assume that pollution first enters the environment at a rate $U(t)$. This pollution naturally dissipates at a rate relative to the amount of pollution present in the environment hm_eC_E . The environmental pollution level decreases due to absorption into both the plant and animal populations. The loss of environmental pollution due to absorption to the plant population is given as $g_1m_bC_EB$. The loss of environmental pollution due to absorption into the animal population is given as $k_2m_nC_EN$. Pollution reenters the environment, as part of the pollution cycle as it is egested by the animal population. The egestion occurs at the rate $k_3m_nC_NN$. Pollution also reenters the general environment as it is released from dead animals and plants. The pollution is released from dead animals at the rate

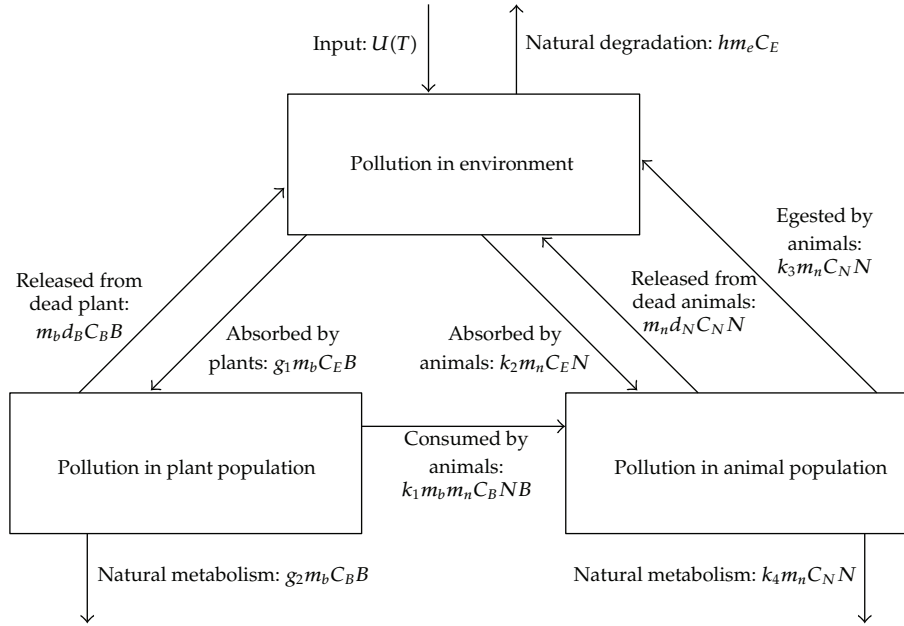


Figure 1: Flowchart of the pollution movement through the ecosystem.

$m_n d_N(B, C_N) C_N N$ and from dead plants at the rate $m_b d_B(N, C_B) C_B B$. Using these rates pertaining to the amount of pollution in the environment, we get

$$\begin{aligned} \frac{dm_e C_E}{dt} = & U(t) - hm_e C_E - g_1 m_b C_E B - k_2 m_n C_E N + k_3 m_n C_N N \\ & + m_n d_N(B, C_N) C_N N + m_b d_B(N, C_B) C_B B; \end{aligned} \quad (2.12)$$

then, dividing by m_e and using the notation $u(t) = U(t)/m_e$, we have

$$\begin{aligned} \frac{dC_E}{dt} = & u(t) - hC_E - \frac{g_1 m_b}{m_e} C_E B - \frac{k_2 m_n}{m_e} C_E N \\ & + \frac{k_3 m_n}{m_e} C_N N + \frac{m_n}{m_e} (d_{N0} - d_{NB} B + d_{NC_N} C_N) C_N N \\ & + \frac{m_b}{m_e} \left(b_{N0} - \frac{r_{N0} N}{K_{N0} + K_{NB} B - K_{NC_E} C_E} \right) C_B B. \end{aligned} \quad (2.13)$$

Next, we consider the quantity of toxicant in the plant biomass.

We have already established that the plant biomass absorbs pollutant from the environment, increasing the plant toxicant at a rate $g_1 m_b C_E B$. Pollution inside the plant biomass is naturally metabolized, leaving the system at a rate $g_2 m_b C_B B$. Pollution returns to the environment due to dead biomass at a rate $d_B(N, C_B) m_b C_B B$. Finally, pollution from

the plant population is transferred to the animal population due to ingestion of plant matter by the animal population at a rate $k_1 m_b m_n C_B B N$. So we get

$$\frac{dC_B m_b B}{dt} = g_1 m_b C_E B - g_2 m_b C_B B - d_B(N, C_B) m_b C_B B - k_1 m_b m_n C_B B N; \quad (2.14)$$

dividing by m_b , we have

$$\frac{dC_B B}{dt} = g_1 C_E B - g_2 C_B B - k_1 m_n C_B B N - d_B(N, C_B) C_B B, \quad (2.15)$$

but clearly

$$\frac{dC_B B}{dt} = C_B \frac{dB}{dt} + B \frac{dC_B}{dt}. \quad (2.16)$$

Substituting in (2.6) and (2.15), using

$$b_B(B, C_E) = b_{B0} + \frac{r_{B0} B}{K_{B0} - K_{BC_E} C_E}, \quad (2.17)$$

and factoring, we have

$$\frac{dC_B}{dt} = g_1 C_E - k_1 m_n C_B N - \left(g_2 + b_{B0} - \frac{r_{B0} B}{K_{B0} - K_{BC_E} C_E} \right) C_B. \quad (2.18)$$

We now consider the quantity of toxicant in the animal biomass.

Pollution enters the animal population via two routes—by the absorption of pollution from the environment at a rate $k_2 m_n C_E N$ and by the ingestion of plant biomass containing pollution at a rate $k_1 m_n m_b C_B B N$. Pollution is released from the animal population as a result of being egested, which occurs at a loss rate of $k_3 m_n C_N N$, metabolized, which occurs at a loss rate of $k_4 m_n C_N N$, and released from dead animals, which occurs at a rate of $d_N(B, C_N) m_n C_N N$. Hence, we obtain

$$\begin{aligned} \frac{dC_N m_n N}{dt} &= k_1 m_n m_b C_B B N + k_2 m_n C_E N - k_3 m_n C_N N \\ &\quad - k_4 m_n C_N N - d_N(B, C_N) m_n C_N N. \end{aligned} \quad (2.19)$$

First, we divide by m_n to get

$$\begin{aligned} \frac{dC_N N}{dt} &= k_1 m_b C_B B N + k_2 C_E N - k_3 C_N N \\ &\quad - k_4 C_N N - d_N(B, C_N) C_N N. \end{aligned} \quad (2.20)$$

Then, we use the fact that

$$\frac{dC_N N}{dt} = C_N \frac{dN}{dt} + N \frac{dC_N}{dt}. \quad (2.21)$$

Substituting in (2.10) and (2.20), using $b_N(N, B, C_E) = b_{N0} + r_{N0}N/(K_{N0} + K_{NB}B - K_{NC_E}C_E)$, and factoring we determine that

$$\frac{dC_N}{dt} = k_1 m_b C_B B + k_2 C_E - \left(k_3 + k_4 + b_{N0} - \frac{r_{N0}N}{K_{N0} + K_{NB}B - K_{NC_E}C_E} \right) C_N. \quad (2.22)$$

After the previous assumptions and derivations we can combine (2.7), (2.11), (2.13), (2.18), and (2.22) and arrive at our completed model:

$$\begin{aligned} \frac{dN}{dt} &= \left(r_{N0} - \frac{r_{N0}N}{K_{N0} + K_{NB}B - K_{NC_E}C_E} + d_{NB}B - d_{NC_N}C_N \right) N, \\ \frac{dB}{dt} &= \left(r_{B0} - \frac{r_{B0}B}{K_{B0} - K_{BC_E}C_E} - d_{BN}N - d_{BC_B}C_B \right) B, \\ \frac{dC_N}{dt} &= k_1 m_b C_B B + k_2 C_E \\ &\quad - \left(k_3 + k_4 + b_{N0} - \frac{r_{N0}N}{K_{N0} + K_{NB}B - K_{NC_E}C_E} \right) C_N, \\ \frac{dC_B}{dt} &= g_1 C_E - k_1 m_n C_B N - \left(g_2 + b_{B0} - \frac{r_{B0}B}{K_{B0} - K_{BC_E}C_E} \right) C_B, \\ \frac{dC_E}{dt} &= u(t) + \frac{m_b}{m_e} (d_{B0} + d_{BN}N + d_{BC_B}C_B) C_B B \\ &\quad + \frac{m_n}{m_e} (k_3 + d_{N0} - d_{NB}B + d_{NC_N}C_N) C_N N \\ &\quad - \frac{m_b}{m_e} g_1 C_E B - \frac{m_n}{m_e} k_2 C_E N - h C_E. \end{aligned} \quad (2.23)$$

3. Equilibrium Analysis

Our model has four nonnegative equilibria:

$$\begin{aligned} E_0 &= (0, 0, C_{N0}, C_{B0}, C_{E0}), \\ E_1 &= (0, B_1, C_{N1}, C_{B1}, C_{E1}), \\ E_2 &= (N_2, 0, C_{N2}, C_{B2}, C_{E2}), \\ E^* &= (N^*, B^*, C_N^*, C_B^*, C_E^*). \end{aligned} \quad (3.1)$$

Since we derived the equations for dC_B/dt and dC_N/dt under the assumption that both N and B are nonzero, then the solution we are chiefly concerned with is E^* .

3.1. Existence of $E^* = (N^*, B^*, C_N^*, C_B^*, C_E^*)$

For $E^* = (N^*, B^*, C_N^*, C_B^*, C_E^*)$, N^*, B^*, C_N^*, C_B^* , and C_E^* are the positive solutions of,

$$0 = r_{N0} - \frac{r_{N0}N^*}{K_{N0} + K_{NB}B^* - K_{NC_E}C_E^*} + d_{NB}B^* - d_{NC_N}C_N^*, \quad (3.2)$$

$$0 = r_{B0} - \frac{r_{B0}B^*}{K_{B0} - K_{BC_E}C_E^*} - d_{BN}N^* - d_{BC_B}C_B^*, \quad (3.3)$$

$$0 = k_1m_bC_B^*B^* + k_2C_E^* - \left(k_3 + k_4 + b_{N0} - \frac{r_{N0}N^*}{K_{N0} + K_{NB}B^* - K_{NC_E}C_E^*} \right) C_N^*, \quad (3.4)$$

$$0 = g_1C_E^* - k_1m_nC_B^*N^* - \left(g_2 + b_{B0} - \frac{r_{B0}B^*}{K_{B0} - K_{BC_E}C_E^*} \right) C_B^* - \frac{m_b}{m_e}g_1C_E^*B^*, \quad (3.5)$$

$$\begin{aligned} 0 = u(t) + \frac{m_b}{m_e}(d_{B0} + d_{BN}N^* + d_{BC_B}C_B^*)C_B^*B^* - \frac{m_b}{m_e}g_1C_E^*B^* \\ + \frac{m_n}{m_e}(k_3 + d_{N0} - d_{NB}B^* + d_{NC_N}C_N^*)C_NN^* - \frac{m_n}{m_e}k_2C_E^*N^* - hC_E^*. \end{aligned} \quad (3.6)$$

Recall that $r_{B0} = b_{B0} - d_{B0}$, and so, by (3.3),

$$b_{B0} - \frac{r_{B0}B^*}{K_{B0} - K_{BC_E}C_E^*} = d_{b0} + d_{BN}N^* + d_{BC_B}C_B^*. \quad (3.7)$$

Substituting this into (3.5), we have

$$0 = d_{BC_B}(C_B^*)^2 + (k_1m_nN^* + g_2 + d_{b0} + d_{BN}N^*)C_B^* - g_1C_E^*. \quad (3.8)$$

Hence,

$$C_B^* = \frac{-\beta_1(N^*) + \sqrt{\beta_1(N^*)^2 + 4g_1d_{BC_B}C_E^*}}{2d_{BC_B}}, \quad (3.9)$$

where,

$$\beta_1(N^*) = k_1m_nN^* + d_{BN}N^* + g_2 + d_{b0}. \quad (3.10)$$

Let

$$f_1(N^*, C_E^*) = \frac{-\beta_1(N^*) + \sqrt{\beta_1(N^*)^2 + 4g_1d_{BC_B}C_E^*}}{2d_{BC_B}}. \quad (3.11)$$

Consider (3.3). Since $C_B = f_1(N^*, C_E^*)$,

$$B^* = \frac{(K_{B0} - K_{BC_E} C_E^*)(r_{B0} - d_{BN} N^* - d_{BC_B} f_1(N^*, C_E^*))}{r_{B0}}. \quad (3.12)$$

Let

$$f_2(N^*, C_E^*) = \frac{(K_{B0} - K_{BC_E} C_E^*)(r_{B0} - d_{BN} N^* - d_{BC_B} f_1(N^*, C_E^*))}{r_{B0}}. \quad (3.13)$$

Next, recall that $r_{N0} = b_{N0} - d_{N0}$, and so, by (3.2),

$$b_{N0} - \frac{r_{N0} N^*}{K_{N0} + K_{NB} B^* - K_{NC_E} C_E^*} = d_{N0} - d_{NB} B^* + d_{NC_N} C_N^*. \quad (3.14)$$

Substituting this into (3.4), we have

$$0 = d_{NC_N} (C_N^*)^2 + (k_3 + k_4 + d_{N0} - d_{NB} B^*) C_N^* - (k_1 m_b C_B^* B^* + k_2 C_E^*). \quad (3.15)$$

Using $C_B^* = f_1(N^*, C_E^*)$ and $B^* = f_1(N^*, C_E^*)$, we find

$$C_N^* = \frac{-\beta_2(N^*, C_E^*) + \sqrt{\beta_2(N^*, C_E^*)^2 + \beta_3(N^*, C_E^*)}}{2d_{NC_N}}, \quad (3.16)$$

where

$$\begin{aligned} \beta_2(N^*, C_E^*) &= k_3 + k_4 + d_{N0} - d_{NB} f_2(N^*, C_E^*), \\ \beta_3(N^*, C_E^*) &= 4d_{NC_N} (k_1 m_b f_1(N^*, C_E^*) f_2(N^*, C_E^*) + k_2 C_E^*). \end{aligned} \quad (3.17)$$

Let

$$f_3(N^*, C_E^*) = \frac{-\beta_2(N^*, C_E^*) + \sqrt{\beta_2(N^*, C_E^*)^2 + \beta_3(N^*, C_E^*)}}{2d_{NC_N}}. \quad (3.18)$$

Next, if we consider (3.2), we have

$$0 = r_{N0} - \frac{r_{N0} N^*}{K_{N0} + K_{NB} B^* - K_{NC_E} C_E^*} + d_{NB} B^* - d_{NC_N} C_N^*. \quad (3.19)$$

Using $B^* = f_2(N^*, C_E^*)$ and $C_N^* = f_3(N^*, C_E^*)$, we find

$$N^* = \frac{\beta_4(N^*, C_E^*)(r_{N0} + d_{NB} f_2(N^*, C_E^*) - d_{NC_N} f_3(N^*, C_E^*))}{r_{N0}}, \quad (3.20)$$

where

$$\beta_4(N^*, C_E^*) = K_{N0} + K_{NB}f_2(N^*, C_E^*) - K_{NC_E}C_E^*. \quad (3.21)$$

Finally, we consider (3.6) and

$$\begin{aligned} 0 = u(t) + \frac{m_b}{m_e}(d_{B0} + d_{BN}N^* + d_{BC_B}C_B^*)C_B^*B^* - \frac{m_b}{m_e}g_1C_E^*B^* \\ + \frac{m_n}{m_e}(k_3 + d_{N0} - d_{NB}B^* + d_{NC_N}C_N^*)C_NN^* - \frac{m_n}{m_e}k_2C_E^*N^* - hC_E^*. \end{aligned} \quad (3.22)$$

Substituting in $C_B^* = f_1(N^*, C_E^*)$, $B^* = f_2(N^*, C_E^*)$, and $C_N^* = f_3(N^*, C_E^*)$, we find

$$\begin{aligned} C_E^* = \frac{m_e u + m_b(d_{B0} + d_{BN}N^* + d_{BC_B}f_1)f_1f_2}{m_b g_1 f_2 + m_n k_2 N^* + m_e h} \\ + \frac{m_n(k_3 + d_{N0} - d_{NB}f_2 + d_{NC_N}f_3)f_3N^*}{m_b g_1 f_2 + m_n k_2 N^* + m_e h}. \end{aligned} \quad (3.23)$$

Thus, the nontrivial solution to the system is given by

$$\begin{aligned} N^* &= \frac{\beta_4(N^*, C_E^*)(r_{N0} - d_{NC_N}f_3(N^*, C_E^*) + d_{NB}f_2(N^*, C_E^*))}{r_{N0}}, \\ B^* &= f_2(N^*, C_E^*), \\ C_N^* &= f_3(N^*, C_E^*), \\ C_B^* &= f_1(N^*, C_E^*), \\ C_E^* &= \frac{m_e u + m_b \beta_6(N^*, C_E^*)f_1(N^*, C_E^*)f_2(N^*, C_E^*)}{\beta_5(N^*, C_E^*)} \\ &\quad + \frac{m_n \beta_7(N^*, C_E^*)f_3(N^*, C_E^*)N^*}{\beta_5(N^*, C_E^*)}, \end{aligned} \quad (3.24)$$

where

$$\begin{aligned} f_1(N^*, C_E^*) &= \frac{-\beta_1(N^*) + \sqrt{\beta_1(N^*)^2 + 4g_1d_{BC_B}C_E^*}}{2d_{BC_B}}, \\ f_2(N^*, C_E^*) &= \frac{(K_{B0} - K_{BC_E}C_E^*)(r_{B0} - d_{BN}N^* + d_{BC_B}f_1(N^*, C_E^*))}{r_{B0}}, \\ f_3(N^*, C_E^*) &= \frac{-\beta_2(N^*, C_E^*) + \sqrt{\beta_2(N^*, C_E^*)^2 + \beta_3(N^*, C_E^*)}}{2d_{NC_N}}, \end{aligned} \quad (3.25)$$

where

$$\begin{aligned}
\beta_1(N^*) &= k_1 m_n N^* + d_{BN} N^* + g_2 + d_{B0}, \\
\beta_2(N^*, C_E^*) &= k_3 + k_4 + d_{N0} - d_{NB} f_2(N^*, CE^*), \\
\beta_3(N^*, C_E^*) &= 4d_{NC_N} (k_1 m_b f_1(N^*, CE^*) f_2(N^*, CE^*) + k_2 C_E^*), \\
\beta_4(N^*, C_E^*) &= K_{N0} + K_{NB} f_2(N^*, C_E^*) - K_{NC_E} C_E^*, \\
\beta_5(N^*, C_E^*) &= m_b g_1 f_2(N^*, C_E^*) + m_n k_2 N^* + m_e h, \\
\beta_6(N^*, C_E^*) &= d_{B0} + d_{BN} N^* + d_{BC_B} f_1(N^*, C_E^*), \\
\beta_7(N^*, C_E^*) &= k_3 + d_{N0} - d_{NB} f_2(N^*, C_E^*) + d_{NC_N} f_3(N^*, C_E^*).
\end{aligned} \tag{3.26}$$

Provided that N^* and C_E^* exist, we can find the corresponding C_B^* , B^* , and C_N^* .

4. Stability Analysis

Theorem 4.1 (conditions for local stability). *Given*

$$\begin{aligned}
c_3 &< \frac{1}{4} \frac{r_{N0} (g_2 + k_1 m_n N^* + b_B (B^*, C_E^*))}{K_N (B^*, C_E^*) (k_1 m_n C_B^*)^2}, \\
c_1 &= c_3 \frac{r_{B0} C_B^*}{d_{BC_B} K_B (C_E^*)}, \\
c_2 &< \frac{c_3}{4} (k_3 + k_4 + b_N (N^*, B^*, C_E^*)) \Omega(N^*, B^*, C_N^*, C_B^*, C_E^*),
\end{aligned} \tag{4.1}$$

where

$$\begin{aligned}
&\Omega(N^*, B^*, C_N^*, C_B^*, C_E^*) \\
&= \min \left(\frac{C_B^*}{d_{BC_B}} \left(\frac{r_{B0}}{K_B (C_E^*) \delta(N^*, B^*, C_N^*, C_B^*, C_E^*)} \right)^2, \frac{k_1 m_n N^* + g_2 + b_B (B^*, C_E^*)}{(k_1 m_b B^*)^2} \right),
\end{aligned} \tag{4.2}$$

where

$$\delta(N^*, B^*, C_N^*, C_B^*, C_E^*) = k_1 m_b C_B^* - \frac{K_{NB} r_{N0} N^* C_N^*}{K_N (B^*, C_E^*)^2}. \tag{4.3}$$

if the following inequalities hold:

(1)

$$\left(d_{NC_N} - \frac{c_2 r_{N0} C_N^*}{K_N(B^*, C_E^*)} \right)^2 < \frac{c_2}{4} \frac{r_{N0}(k_3 + k_4 + b_N(N^*, B^*, C_E^*))}{K_N(B^*, C_E^*)}, \quad (4.4)$$

(2)

$$\begin{aligned} & \frac{3c_1}{4} \frac{r_{B0}}{K_B(C_E^*)} \\ & > \frac{\left(d_{NB} + K_{NB} r_{N0} N^* / K_N(B^*, C_E^*)^2 - c_1 d_{BN} \right)^2}{r_{N0} / K_N(B^*, C_E^*)} \\ & + \frac{\left(c_1 m_e K_{BC_E} r_{B0} B^* / K_B(C_E^*)^2 - m_b d_B(N^*, C_B^*) C_B^* + m_n d_{NB} C_N^* N^* + m_b g_1 C_E^* \right)^2}{m_e (m_b g_1 B^* + m_n k_2 N^* + h m_e)}, \end{aligned} \quad (4.5)$$

(3)

$$\begin{aligned} & \frac{3m_e}{4} (m_b g_1 B^* + m_n k_2 N^* + m_e h) \\ & > \frac{\left(m_e K_{NC_E} r_{N0} N^* / K_N(B^*, C_E^*)^2 - m_b d_{BN} C_B^* B^* - m_n (k_3 + d_N(B^*, C_N^*)) C_N^* + m_n k_2 C_E^* \right)^2}{r_{N0} / K_N(B^*, C_E^*)} \\ & + \frac{\left(c_2 m_e (k_2 + K_{NC_E} r_{N0} N^* C_N^* / K_N(B^*, C_E^*)^2) + m_n N^* (k_3 + d_N(B^*, C_N^*) + d_{NC_N} C_N^*) \right)^2}{c_2 (k_3 + k_4 + b_N(N^*, B^*, C_E^*))} \\ & + \frac{\left(c_3 m_e (g_1 + K_{BC_E} r_{B0} B^* C_B^* / K_B(C_E^*)^2) + m_b B^* (d_B(N^*, C_B^*) + d_{BC_B} C_B^*) \right)^2}{c_3 (k_1 m_n N^* + g_2 + b_B(B^*, C_E^*))}, \end{aligned} \quad (4.6)$$

then E^* is a locally stable equilibrium of system (2.23).

Theorem 4.2 (conditions for global stability). *Using the notation*

$$\begin{aligned} K_N(B, C_E) &= K_{N0} + K_{NB} B - K_{NC_E} C_E, \\ K_B(C_E) &= K_{B0} - K_{BC_E} C_E, \\ D_N(B, C_N) &= d_{N0} - d_{NB} B + d_{NC_N} C_N, \\ D_B(N, C_B) &= d_{B0} + d_{BN} N + d_{BC_B} C_B, \end{aligned} \quad (4.7)$$

let $K_N(B, C_E), K_B(C_E), D_N(B, C_N)$, and $D_B(N, C_B)$ be such that

$$\begin{aligned}\underline{K_N} &= K_{N0} - K_{NC_E} \leq K_N(B, C_E) \leq K_{N0} + K_{NB}K_{B0} = \overline{K_N}, \\ \underline{K_B} &= K_{B0} - K_{BC_E} \leq K_B(C_E) \leq K_{B0} = \overline{K_B}, \\ |D_N(B, C_N)| &\leq d_{N0} + d_{NC_N} = \overline{D_N}, \\ |D_B(N, C_B)| &\leq d_{B0} + d_{BN}N_M + d_{BC_B} = \overline{D_B}.\end{aligned}\tag{4.8}$$

Then, given

$$\begin{aligned}0 < c_2 &< \frac{r_{N0}(g_2 + k_1 m_n N^*)}{4(k_1 m_n)^2 \overline{K_N}}, \\ 0 < c_1 &< \frac{k_3 + k_4}{4} \max \left(\frac{r_{B0}}{\overline{K_B}(k_1 m_b + r_{N0} N^* C_N^* \overline{\eta_1})^2} \frac{c_2(g_2 + k_1 m_n N^*)}{(k_1 m_b B^*)^2} \right),\end{aligned}\tag{4.9}$$

where

$$\begin{aligned}\overline{\eta_1} &= \frac{K_{NB}}{(K_{N0} + B^* K_{NB} - K_{NC_E})^2}, \\ \overline{\eta_2} &= \frac{K_{NC_E}}{(K_{N0} + B^* K_{NB} - K_{NC_E} C_E^*)^2}, \\ \overline{\mu} &= \frac{K_{BC_E}}{(K_{B0} - K_{BC_E} C_E^*)^2},\end{aligned}\tag{4.10}$$

if the following inequalities hold:

(1)

$$\frac{c_1}{4} \frac{r_{N0}(k_3 + k_4)}{\overline{K_N}} > \left(d_{NC_N} + \frac{c_1 r_{N0}}{\underline{K_N}} \right)^2,\tag{4.11}$$

(2)

$$\begin{aligned}\frac{3}{4} \frac{r_{B0}}{\overline{K_B}} &> \frac{(d_{NB} + N^* r_{N0} \overline{\eta_1} + d_{BN})^2 \overline{K_N}}{r_{N0}} + \frac{(d_{BC_B} + c_2 r_{B0} / \underline{K_B})^2}{c_2(g_2 + k_1 m_n N^*)} \\ &+ \frac{(B^* r_{B0} \overline{\mu} m_e + m_b g_1 + m_b \overline{D_B} + m_n N^* C_N^* d_{NB})^2}{m_e(m_e h + m_b g_1 B^* + m_n k_2 N^*)},\end{aligned}\tag{4.12}$$

Table 1

Population parameters		
$b_{n0} = 3$	$d_{n0} = 2$	$k_{n0} = .5$
$b_{b0} = 80$	$d_{b0} = 3$	$k_{b0} = .5$
$k_{nb} = 1$	$k_{nce} = 0.1667$	$d_{nb} = 0$
$d_{ncn} = 0.01$	$k_{bce} = 0.0125$	$d_{bn} = 1$
$d_{bcb} = 1$		
Mass parameters		
$m_n = 1$	$m_b = 1$	$m_e = 1$
Pollution parameters		
$k_1 = 3.01$	$k_2 = 1$	$k_3 = 1$
$k_4 = 52.01$	$g_1 = 5.5$	$g_2 = 100$
$U = 1$	$h = 100$	

(3)

$$\begin{aligned}
& \frac{3m_e}{4} (m_e h + m_b g_1 B^* + m_n k_2 N^*) \\
& > \frac{\overline{K_N} \left(m_e N^* r_{N0} \overline{\eta_2} + m_n k_3 + m_n k_2 + m_n \overline{D_N} + m_b B^* C_B^* d_{BN} \right)^2}{r_{N0}} \\
& + \frac{\left(c_1 m_e (k_2 + r_{N0} N^* C_N^* \overline{\eta_2}) + N^* m_n (k_3 + \overline{D_N} + C_N^* d_{NCN}) \right)^2}{c_1 (k_3 + k_4)} \\
& + \frac{\left(c_2 m_e (g_1 + r_{B0} B^* C_B^* \overline{\mu}) + m_b B^* (\overline{D_B} + C_B^* d_{BCB}) \right)^2}{c_2 (g_2 + k_1 m_n N^*)}, \tag{4.13}
\end{aligned}$$

then E^* is a globally stable equilibrium of system (2.23).

5. Numerical Simulation

To study the applicability of the model we need to test a range of parameter values for which E^* exists and is stable.

Example 5.1. Consider the set of parameter values for our numerical calculations in Table 1.

With these parameter values, the nontrivial equilibrium, E^* , of the model exists and is

$$N^* \approx .9919, \quad B^* \approx 0.4934, \quad C_N^* \approx 0.0007, \quad C_B^* \approx 0.0003, \quad C_E^* \approx 0.0095. \tag{5.1}$$

Using $c_1 = 0.0751$, $c_2 = 1$, and $c_3 = 1$, it can be verified that the conditions given by (4.4)–(4.6) for Theorem 4.1 are satisfied. Hence, E^* is locally asymptotically stable.

Moreover, using $c_1 = 1$ and $c_2 = 1$, it can also be verified that the conditions given by (4.11)–(4.13) for Theorem 4.2 are satisfied. Hence, E^* is globally asymptotically stable.

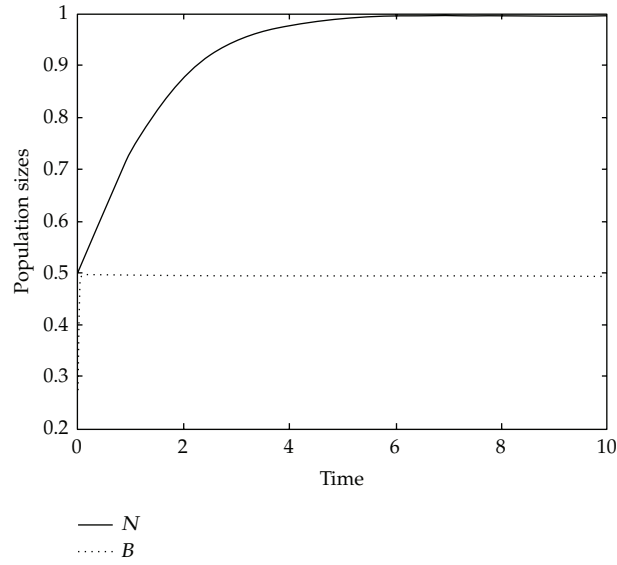
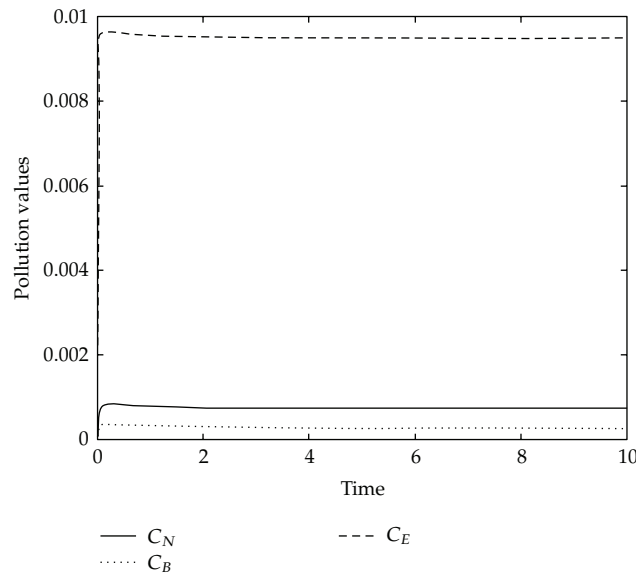
(a) Numerical approximation of N and B (b) Numerical approximation of C_N , C_B and C_E

Figure 2: Numerical approximation to the time series solutions for the system of differential equations (2.23). The parameter values used were $b_{n0} = d_{b0} = 3$, $d_{n0} = 2$, $k_{n0} = k_{b0} = .5$, $b_{b0} = 80$, $d_{ncn} = 0.01$, $k_1 = g_2 = h = 100$, $k_{nce} = 0.1667$, $k_{bce} = 0.0125$, $k_2 = 3.01$, $d_{nb} = 0$, $k_4 = 52.01$, $g_1 = 5.5$, and $k_{nb} = d_{bn} = d_{bcb} = m_n = m_b = m_e = k_3 = U = 1$. The initial condition used was $(N_0, B_0, C_{N0}, C_{B0}, C_{E0}) = (0.5, 0.25, 0, 0, 0)$.

Figure 2(a) depicts the numerical approximation to the time series for the populations, and Figure 2(b) depicts the numerical approximation to the time series for the pollution levels. An initial condition of $(N_0, B_0, C_{N0}, C_{B0}, C_{E0}) = (0.5, 0.25, 0, 0, 0)$ was used for the simulation. Both time series were achieved using the MATLAB solver ode15s.

Table 2

Population parameters		
$b_{n0} = 3$	$d_{n0} = 2$	$k_{n0} = .5$
$b_{b0} = 9$	$d_{b0} = 3$	$k_{b0} = .5$
$k_{nb} = 1$	$k_{nce} = 0.1667$	$d_{nb} = 0$
$d_{ncn} = 0.01$	$k_{bce} = 0.0125$	$d_{bn} = 1$
$d_{bcb} = 1$		
Mass parameters		
$m_n = 1$	$m_b = 1$	$m_e = 1$
Pollution parameters		
$k_1 = 3.01$	$k_2 = 1$	$k_3 = 1$
$k_4 = 52.01$	$g_1 = 5.5$	$g_2 = 100$
$U = 100$	$h = 100$	

Example 5.2. If we increase the amount of pollution being input to the system, reduce the birthrate of the plant population, and rerun the simulations using the set of parameter values in Table 2.

The nontrivial equilibrium, E^* , of the model exists and is

$$N^* \approx .7634, \quad B^* \approx 0.4236, \quad C_N^* \approx 0.0749, \quad C_B^* \approx 0.02925, \quad C_E^* \approx 0.9795. \quad (5.2)$$

Using $c_1 = 0.6104$, $c_2 = 1$, and $c_3 = 1$, the conditions given by (4.4)–(4.6) for Theorem 4.1 are satisfied, and therefore E^* is proven to be locally asymptotically stable.

Similarly, using $c_1 = 1$ and $c_2 = 1$, the conditions given by (4.11)–(4.13) for Theorem 4.2 are satisfied and E^* is globally asymptotically stable.

Figure 3(a) depicts the numerical approximation to the time series for the populations, and Figure 3(b) depicts the numerical approximation to the time series for the pollution levels. An initial condition of $(N_0, B_0, C_{N0}, C_{B0}, C_{E0}) = (0.5, 0.25, 0, 0, 0)$ was used for the simulation. Both time series were achieved using the MATLAB solver ode15s. Notice that the plant population approaches the equilibrium much slower in Example 5.2 than in Example 5.1. Also, it appears as though with the parameter settings used in Example 5.2 that the pollution has a greater impact on the animal population than the plant population; the magnitude of the decrease in size of the animal population at the equilibrium between the two examples is greater than the decrease seen in the plant population. It is also interesting to note that the pollution values are two degrees of magnitude larger in the second example than in the first example. The increase in the concentration of the pollution levels is of the same level of magnitude as the increase in the rate of pollution input into the system. It was found that if the simulation is rerun with $b_{B0} = 8$, then the second global stability criterion given in (4.12) fails; however, numerical solution remains similar to that computed in Example 5.2. This implies that the stability criteria are sufficient but not necessary.

6. Conclusions

In this paper a new system of differential equations designed to study the effects of pollution on two species—one plant and one animal—in a closed environment was developed. The model was analysed using standard methods for nonlinear systems of differential

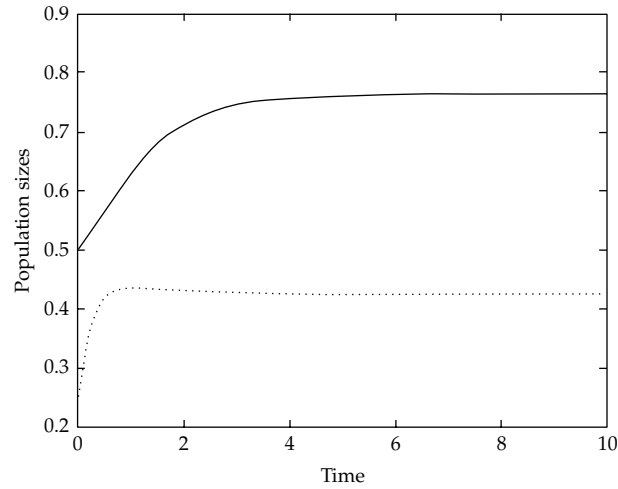
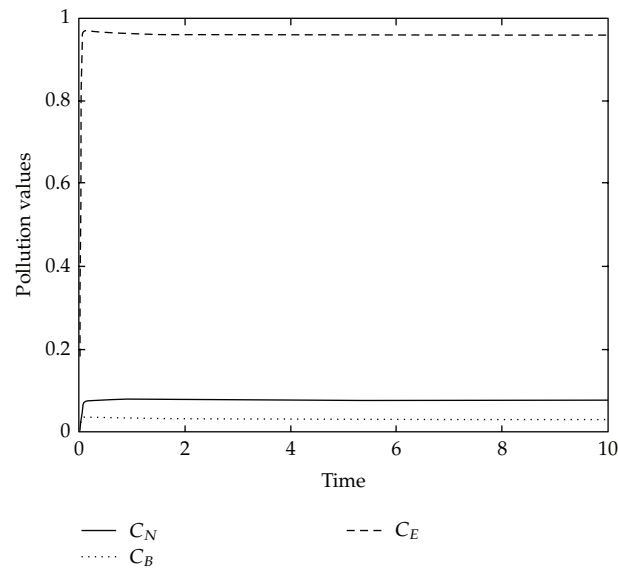
(a) Numerical approximation of N and B (b) Numerical approximation of C_N , C_B and C_E

Figure 3: Numerical approximation to the time series solutions for the system of differential equations (2.23). The parameter values used were $b_{n0} = d_{b0} = 3$, $d_{n0} = 2$, $k_{n0} = k_{b0} = .5$, $b_{b0} = 9$, $d_{ncn} = 0.01$, $k_1 = g_2 = h = U = 100$, $k_{nce} = 0.1667$, $k_{bce} = 0.0125$, $k_2 = 3.01$, $d_{nb} = 0$, $k_4 = 52.01$, $g_1 = 5.5$, and $k_{nb} = d_{bn} = d_{bcb} = m_n = m_b = m_e = k_3 = 1$. The initial condition used was $(N_0, B_0, C_{N0}, C_{B0}, C_{E0}) = (0.5, 0.25, 0, 0, 0)$.

equations. The problem was chosen as much work in the field has been done in the past; however, simplifications have always been introduced in order to help make the problem mathematically tractable. Our work strives to incorporate another level of biological realism to the model by fully accounting for the movement of pollution in the system using a mass-balance approach. In addition, the work was designed to include practical parameters that would be measurable in a real-world context.

It is clear from Examples 5.1 and 5.2 that the nontrivial solution for our system is stable for at least some range of parameter values and there is also a parameter range in which the stability criteria are satisfied. By analysing the model using the Lyapunov direct method we were able to derive criteria for the stability of the system. For both the local and global stability, three sufficient conditions for stability were determined. For local stability, these are given in (4.4), (4.5), and (4.6). The three criteria sufficient for establishing global stability are given in (4.11), (4.12), and (4.13). We can interpret the biological meaning of these criteria to gain further insight into our model.

Upon analysing the parameters included in stability criteria it was found that the system is locally stable provided that

- (1) pollution degrades or is removed from the environment at a fast enough rate,
- (2) the plant population experiences net growth at a fast enough rate,
- (3) (a) the animal population relieves itself of pollution at a fast enough rate
(b) the animal carrying capacity is large enough,
(c) the animal population births at a fast enough rate.

The system is globally stable provided that

- (1) pollution degrades or is removed from the environment at a fast enough rate,
- (2) the plant population experiences net growth at a fast enough rate,
- (3) the animal population is able to relieve itself of its pollution burden at a great enough.

Further work that could be done with the model includes parameterizing the model using parameters for a known situation and comparing the predictions of the model to the real-world phenomena.

Further extension that could be made based upon the model includes incorporating features such as age structure, delay, or diffusion.

Appendices

A. Proof of Theorem 4.1

We will work with the linearized form of the model, which can be written as

$$\begin{aligned}
 \frac{d\widehat{N}}{dt} &= -j_{11}\widehat{N} + j_{12}\widehat{B} - j_{13}\widehat{C}_N - j_{15}\widehat{C}_E, \\
 \frac{d\widehat{B}}{dt} &= -j_{21}\widehat{N} - j_{22}\widehat{B} - j_{24}B^*\widehat{C}_B - j_{25}\widehat{C}_E, \\
 \frac{d\widehat{C}_N}{dt} &= j_{31}\widehat{N} + j_{32}\widehat{B} - j_{33}\widehat{C}_N + j_{34}\widehat{C}_B + j_{35}\widehat{C}_E, \\
 \frac{d\widehat{C}_B}{dt} &= -j_{41}\widehat{N} + j_{42}\widehat{B} - j_{44}\widehat{C}_B + j_{45}\widehat{C}_E, \\
 \frac{d\widehat{C}_E}{dt} &= j_{51}\widehat{N} + j_{52}\widehat{B} + j_{53}\widehat{C}_N + j_{54}\widehat{C}_B - j_{55}\widehat{C}_E,
 \end{aligned} \tag{A.1}$$

where j_{ij} represents the absolute value from the i th row and j th column of the Jacobian matrix evaluated at $E^* = (N^*, B^*, C_N^*, C_B^*, C_E^*)$.

Consider the positive definite function

$$V(\widehat{N}, \widehat{B}, \widehat{C}_N, \widehat{C}_B, \widehat{C}_E) = \frac{1}{2} \left[\frac{1}{N^*} (\widehat{N} - N^*)^2 + \frac{c_1}{B^*} (\widehat{B} - B^*)^2 + c_2 (\widehat{C}_N - C_N^*)^2 + c_3 (\widehat{C}_B - C_B^*)^2 + (\widehat{C}_E - C_E^*)^2 \right]. \quad (\text{A.2})$$

Differentiating V with respect to t , we get

$$\begin{aligned} \frac{dV}{dt} &= \frac{1}{N^*} (\widehat{N} - N^*) \frac{d\widehat{N}}{dt} + \frac{c_1}{B^*} (\widehat{B} - B^*) \frac{d\widehat{B}}{dt} + c_2 (\widehat{C}_N - C_N^*) \frac{d\widehat{C}_N}{dt} \\ &\quad + c_3 (\widehat{C}_B - C_B^*) \frac{d\widehat{C}_B}{dt} + (\widehat{C}_E - C_E^*) \frac{d\widehat{C}_E}{dt}. \end{aligned} \quad (\text{A.3})$$

Using the notation

$$\begin{aligned} 2a_{11} &= j_{11} = \frac{r_{N0}}{K_N(B^*, C_E^*)}, \\ 2a_{22} &= c_1 j_{22} = c_1 \frac{r_{B0}}{K_B(C_E^*)}, \\ 2a_{33} &= c_2 j_{33} = c_2 (k_3 + k_4 + b_N(N^*, B^*, C_E^*)), \\ 2a_{44} &= c_3 j_{44} = c_3 (k_1 m_n N^* + g_2 + b_B(B^*, C_E^*)), \\ 2a_{55} &= j_{55} = \frac{m_b}{m_e} g_1 B^* + \frac{m_n}{m_e} k_2 N^* + h, \\ a_{12} &= \frac{j_{12}}{N^*} - c_1 \frac{j_{21}}{B^*} = d_{NB} + \frac{K_{NB} r_{N0} N^*}{K_N(B^*, C_E^*)^2} - c_1 d_{BN}, \\ a_{13} &= \frac{j_{13}}{N^*} - c_2 j_{31} = d_{NC_N} - c_2 \frac{r_{N0} C_N^*}{K_N(B^*, C_E^*)}, \\ a_{14} &= c_3 j_{14} = c_3 k_1 C_B^*, \\ a_{15} &= \frac{j_{15}}{N^*} - j_{51} = \frac{K_{NCE} r_{N0} N^*}{K_N(B^*, C_E^*)^2} - \frac{m_b}{m_e} d_{BN} C_B^* B^* \\ &\quad - \frac{m_n}{m_e} (k_3 + d_N(B^*, C_N^*)) C_N^* + \frac{m_n}{m_e} k_2 C_E^*, \\ a_{23} &= c_2 j_{32} = c_2 \left(k_1 m_b C_B^* - \frac{K_{NB} r_{N0} N^* C_N^*}{K_N(B^*, C_E^*)^2} \right), \end{aligned}$$

$$\begin{aligned}
a_{24} &= c_1 \frac{j_{24}}{B^*} - c_3 j_{42} = c_1 d_{BC_B} - c_3 \frac{r_{B0} C_B^*}{K_B (C_E^*)}, \\
a_{25} &= c_1 \frac{j_{25}}{B^*} - j_{52} = c_1 \frac{K_{BC_E} r_{B0} B^*}{K_B (C_E^*)^2} \\
&\quad - \frac{m_b}{m_e} d_B(N^*, C_B^*) C_B^* + \frac{m_n}{m_e} d_{NB} C_N^* N^* + \frac{m_b}{m_e} g_1 C_E^*, \\
a_{34} &= c_2 j_{34} = c_2 k_1 m_b B^*, \\
a_{35} &= c_2 j_{35} + j_{53} = c_2 \left(k_2 + \frac{K_{NC_E} r_{N0} N^* C_N^*}{K_N (B^*, C_E^*)^2} \right), \\
&\quad + \frac{m_n}{m_e} N^* (k_3 + d_N(B^*, C_N^*) + d_{NC_N} C_N^*), \\
a_{45} &= c_3 j_{45} + j_{54} = c_3 \left(g_1 + \frac{K_{BC_E} r_{B0} B^* C_B^*}{K_B (C_E^*)^2} \right), \\
&\quad + \frac{m_b}{m_e} B^* (d_B(N^*, C_B^*) + d_{BC_B} C_B^*).
\end{aligned} \tag{A.4}$$

and some algebraic manipulation, we can rewrite the system as

$$\begin{aligned}
\frac{dV}{dt} &= -\frac{a_{11}}{2} (\widehat{N} - N^*)^2 + a_{12} (\widehat{N} - N^*) (\widehat{B} - B^*) - \frac{a_{22}}{2} (\widehat{B} - B^*)^2 \\
&\quad - \frac{a_{11}}{2} (\widehat{N} - N^*)^2 - a_{13} (\widehat{N} - N^*) (\widehat{C}_N - C_N^*) - \frac{a_{33}}{2} (\widehat{C}_N - C_N^*)^2 \\
&\quad - \frac{a_{11}}{2} (\widehat{N} - N^*)^2 - a_{14} (\widehat{N} - N^*) (\widehat{C}_B - C_B^*) - \frac{a_{44}}{2} (\widehat{C}_B - C_B^*)^2 \\
&\quad - \frac{a_{11}}{2} (\widehat{N} - N^*)^2 - a_{15} (\widehat{N} - N^*) (\widehat{C}_E - C_E^*) - \frac{a_{55}}{2} (\widehat{C}_E - C_E^*)^2 \\
&\quad - \frac{a_{22}}{2} (\widehat{B} - B^*)^2 + a_{23} (\widehat{B} - B^*) (\widehat{C}_N - C_N^*) - \frac{a_{33}}{2} (\widehat{C}_N - C_N^*)^2 \\
&\quad - \frac{a_{22}}{2} (\widehat{B} - B^*)^2 - a_{24} (\widehat{B} - B^*) (\widehat{C}_B - C_B^*) - \frac{a_{44}}{2} (\widehat{C}_B - C_B^*)^2 \\
&\quad - \frac{a_{22}}{2} (\widehat{B} - B^*)^2 - a_{25} (\widehat{B} - B^*) (\widehat{C}_E - C_E^*) - \frac{a_{55}}{2} (\widehat{C}_E - C_E^*)^2 \\
&\quad - \frac{a_{33}}{2} (\widehat{C}_N - C_N^*)^2 + a_{34} (\widehat{C}_N - C_N^*) (\widehat{C}_B - C_B^*) - \frac{a_{44}}{2} (\widehat{C}_B - C_B^*)^2 \\
&\quad - \frac{a_{33}}{2} (\widehat{C}_N - C_N^*)^2 + a_{35} (\widehat{C}_N - C_N^*) (\widehat{C}_E - C_E^*) - \frac{a_{55}}{2} (\widehat{C}_E - C_E^*)^2 \\
&\quad - \frac{a_{44}}{2} (\widehat{C}_B - C_B^*)^2 + a_{45} (\widehat{C}_B - C_B^*) (\widehat{C}_E - C_E^*) - \frac{a_{55}}{2} (\widehat{C}_E - C_E^*)^2.
\end{aligned} \tag{A.5}$$

Then, factoring the equations, we obtain

$$\begin{aligned}
 \frac{dV}{dt} = & -\frac{1}{2}a_{11}\left(\left(\widehat{N}-N^*\right)-\frac{a_{12}}{a_{11}}\left(\widehat{B}-B^*\right)\right)^2-\frac{1}{2}\left(a_{22}-\frac{a_{12}^2}{a_{11}}\right)\left(\widehat{B}-B^*\right)^2 \\
 & -\frac{1}{2}a_{11}\left(\left(\widehat{N}-N^*\right)+\frac{a_{13}}{a_{11}}\left(\widehat{C}_N-C_N^*\right)\right)^2-\frac{1}{2}\left(a_{33}-\frac{a_{13}^2}{a_{11}}\right)\left(\widehat{C}_N-C_N^*\right)^2 \\
 & -\frac{1}{2}a_{11}\left(\left(\widehat{N}-N^*\right)+\frac{a_{14}}{a_{11}}\left(\widehat{C}_B-C_B^*\right)\right)^2-\frac{1}{2}\left(a_{44}-\frac{a_{14}^2}{a_{11}}\right)\left(\widehat{C}_B-C_B^*\right)^2 \\
 & -\frac{1}{2}a_{11}\left(\left(\widehat{N}-N^*\right)+\frac{a_{15}}{a_{11}}\left(\widehat{C}_E-C_E^*\right)\right)^2-\frac{1}{2}\left(a_{55}-\frac{a_{15}^2}{a_{11}}\right)\left(\widehat{C}_E-C_E^*\right)^2 \\
 & -\frac{1}{2}a_{22}\left(\left(\widehat{B}-B^*\right)-\frac{a_{23}}{a_{22}}\left(\widehat{C}_N-C_N^*\right)\right)^2-\frac{1}{2}\left(a_{33}-\frac{a_{23}^2}{a_{22}}\right)\left(\widehat{C}_N-C_N^*\right)^2 \\
 & -\frac{1}{2}a_{44}\left(\left(\widehat{C}_B-C_B^*\right)+\frac{a_{24}}{a_{44}}\left(\widehat{B}-B^*\right)\right)^2-\frac{1}{2}\left(a_{22}-\frac{a_{24}^2}{a_{44}}\right)\left(\widehat{B}-B^*\right)^2 \\
 & -\frac{1}{2}a_{55}\left(\left(\widehat{C}_E-C_E^*\right)+\frac{a_{25}}{a_{55}}\left(\widehat{B}-B^*\right)\right)^2-\frac{1}{2}\left(a_{22}-\frac{a_{25}^2}{a_{55}}\right)\left(\widehat{B}-B^*\right)^2 \\
 & -\frac{1}{2}a_{33}\left(\left(\widehat{C}_N-C_N^*\right)-\frac{a_{34}}{a_{33}}\left(\widehat{C}_B-C_B^*\right)\right)^2-\frac{1}{2}\left(a_{44}-\frac{a_{34}^2}{a_{33}}\right)\left(\widehat{C}_B-C_B^*\right)^2 \\
 & -\frac{1}{2}a_{33}\left(\left(\widehat{C}_N-C_N^*\right)-\frac{a_{35}}{a_{33}}\left(\widehat{C}_E-C_E^*\right)\right)^2-\frac{1}{2}\left(a_{55}-\frac{a_{35}^2}{a_{33}}\right)\left(\widehat{C}_E-C_E^*\right)^2 \\
 & -\frac{1}{2}a_{44}\left(\left(\widehat{C}_B-C_B^*\right)-\frac{a_{45}}{a_{44}}\left(\widehat{C}_E-C_E^*\right)\right)^2-\frac{1}{2}\left(a_{55}-\frac{a_{45}^2}{a_{44}}\right)\left(\widehat{C}_E-C_E^*\right)^2.
 \end{aligned} \tag{A.6}$$

Sufficient conditions for dV/dt to be negative definite are

$$a_{14}^2 < a_{11}a_{44}, \tag{A.7}$$

$$a_{23}^2 < a_{22}a_{33}, \tag{A.8}$$

$$a_{34}^2 < a_{33}a_{44}, \tag{A.9}$$

$$a_{13}^2 < a_{11}a_{33}, \tag{A.10}$$

$$\frac{a_{12}^2}{a_{11}} + \frac{a_{24}^2}{a_{44}} + \frac{a_{25}^2}{a_{55}} < 3a_{22}, \tag{A.11}$$

$$\frac{a_{15}^2}{a_{11}} + \frac{a_{35}^2}{a_{33}} + \frac{a_{45}^2}{a_{44}} < 3a_{55}. \tag{A.12}$$

Examining (A.7), we find

$$\begin{aligned} a_{14}^2 &< a_{11}a_{44}, \\ c_3 &< \frac{1}{4} \frac{r_{N0}(g_2 + k_1N^* + b_B(B^*, C_E^*))}{K_N(B^*, C_E^*)(k_1m_nC_B^*)^2}. \end{aligned} \quad (\text{A.13})$$

Considering (A.8), we find:

$$\begin{aligned} a_{23}^2 &< a_{22}a_{33}, \\ c_2 &< \frac{c_1}{4} \frac{r_{B0}(k_3 + k_4 + b_N(N^*, B^*, C_E^*))}{K_B(C_E^*)(k_1m_bC_B^* - K_{NB}r_{N0}N^*C_N^*/K_N(B^*, C_E^*)^2)^2}. \end{aligned} \quad (\text{A.14})$$

Considering (A.9), we find an additional condition for choosing our coefficient c_2 :

$$\begin{aligned} a_{34}^2 &< a_{33}a_{44}, \\ c_2 &< \frac{c_3}{4} \frac{(k_3 + k_4 + b_N(N^*, B^*, C_E^*))(k_1m_nN^* + g_2 + b_B(B^*, C_E^*))}{(k_1m_bB^*)^2}. \end{aligned} \quad (\text{A.15})$$

Note that, if both of the conditions relating to c_2 are satisfied, then

$$\begin{aligned} c_2 &< \min \left(\frac{c_3}{4} \frac{(k_3 + k_4 + b_N(N^*, B^*, C_E^*))(k_1m_nN^* + g_2 + b_B(B^*, C_E^*))}{(k_1m_bB^*)^2}, \right. \\ &\quad \left. \frac{c_1}{4} \frac{r_{B0}(k_3 + k_4 + b_N(N^*, B^*, C_E^*))}{K_B(C_E^*)(k_1m_bC_B^* - (K_{NB}r_{N0}N^*C_N^*/K_N(B^*, C_E^*)^2))^2} \right). \end{aligned} \quad (\text{A.16})$$

Looking at (A.10), we find the first general condition for local stability:

$$\begin{aligned} a_{13}^2 &< a_{11}a_{33}, \\ \left(d_{NC_N} - c_2 \frac{r_{N0}C_N^*}{K_N(B^*, C_E^*)} \right)^2 &< \frac{c_2}{4} \frac{r_{N0}(k_3 + k_4 + b_N(N^*, B^*, C_E^*))}{K_N(B^*, C_E^*)}. \end{aligned} \quad (\text{A.17})$$

Equation (A.11) gives the second condition for stability:

$$\begin{aligned}
 3a_{22} &> \frac{a_{12}^2}{a_{11}} + \frac{a_{24}^2}{a_{44}} + \frac{a_{25}^2}{a_{55}}, \\
 \frac{3c_1}{4} \frac{r_{B0}}{K_B(C_E^*)} &> \frac{\left(d_{NB} + \left(K_{NB}r_{N0}N^*/K_N(B^*, C_E^*)^2\right) - c_1d_{BN}\right)^2}{r_{N0}/K_N(B^*, C_E^*)} \\
 &+ \frac{(c_1d_{BC_B} - c_3(r_{B0}C_B^*/K_B(C_E^*)))^2}{c_3(k_1m_nN^* + g_2 + b_B(B^*, C_E^*))} \\
 &+ \frac{\left(c_1m_e\left(K_{BC_E}r_{B0}B^*/K_B(C_E^*)^2\right) - m_b d_B(N^*, C_B^*)C_B^* + m_n d_{NB}C_N^*N^* + m_b g_1 C_E^*\right)^2}{m_e(m_b g_1 B^* + m_n k_2 N^* + h m_e)}.
 \end{aligned} \tag{A.18}$$

If we let $c_1 = c_3(r_{B0}C_B^*/d_{BC_B}K_B(C_E^*))$, this reduces to

$$\begin{aligned}
 \frac{3c_1}{4} \frac{r_{B0}}{K_B(C_E^*)} &> \frac{\left(d_{NB} + \left(K_{NB}r_{N0}N^*/K_N(B^*, C_E^*)^2\right) - c_1d_{BN}\right)^2}{r_{N0}/K_N(B^*, C_E^*)} \\
 &+ \frac{\left(c_1m_e\left(K_{BC_E}r_{B0}B^*/K_B(C_E^*)^2\right) - m_b d_B(N^*, C_B^*)C_B^* + m_n d_{NB}C_N^*N^* + m_b g_1 C_E^*\right)^2}{m_e(m_b g_1 B^* + m_n k_2 N^* + h m_e)}.
 \end{aligned} \tag{A.19}$$

Finally, (A.12) gives the third and final condition for local stability:

$$\begin{aligned}
 3a_{55} &> \frac{a_{15}^2}{a_{11}} + \frac{a_{35}^2}{a_{33}} + \frac{a_{45}^2}{a_{44}}, \\
 \frac{3m_e}{4} (m_b g_1 B^* + m_n k_2 N^* + m_e h) &> \frac{\left(m_e K_{NC_E} r_{N0} N^*/K_N(B^*, C_E^*)^2 - m_b d_{BN} C_B^* B^* - m_n (k_3 + d_N(B^*, C_N^*)) C_N^* + m_n k_2 C_E^*\right)^2}{r_{N0}/(K_N(B^*, C_E^*))}
 \end{aligned}$$

$$\begin{aligned}
& + \frac{\left(c_2 m_e \left(k_2 + K_{NC_E} r_{N0} N^* C_N^* / K_N (B^*, C_E^*)^2\right) + m_n N^* (k_3 + d_N(B^*, C_N^*) + d_{NC_N} C_N^*)\right)^2}{c_2 (k_3 + k_4 + b_N(N^*, B^*, C_E^*))} \\
& + \frac{\left(c_3 m_e \left(g_1 + K_{BC_E} r_{B0} B^* C_B^* / K_B (C_E^*)^2\right) + m_b B^* (d_B(N^*, C_B^*) + d_{BC_B} C_B^*)\right)^2}{c_3 (k_1 m_n N^* + g_2 + b_B(B^*, C_E^*))}.
\end{aligned} \tag{A.20}$$

These conditions are equivalent to those given in (4.1)–(4.6).

B. Proof of Theorem 4.2

Consider the positive definite function

$$\begin{aligned}
V_1(N, B, C_N, C_B, C_E) &= N - N^* - N^* \ln\left(\frac{N}{N^*}\right) + B - B^* - B^* \ln\left(\frac{B}{B^*}\right) \\
&+ \frac{c_1}{2} (C_N - C_N^*)^2 + \frac{c_2}{2} (C_B - C_B^*)^2 + \frac{1}{2} (C_E - C_E^*)^2.
\end{aligned} \tag{B.1}$$

Then, differentiating V_1 with respect to t , we get

$$\begin{aligned}
\frac{dV_1}{dt} &= \frac{(N - N^*)}{N} \frac{dN}{dt} + \frac{(B - B^*)}{B} \frac{dB}{dt} + c_1 (C_N - C_N^*) \frac{dC_N}{dt} \\
&+ c_2 (C_B - C_B^*) \frac{dC_B}{dt} + (C_E - C_E^*) \frac{dC_E}{dt}.
\end{aligned} \tag{B.2}$$

Using (2.23), we find

$$\begin{aligned}
\frac{dV_1}{dt} &= (N - N^*) \left(b_{N0} - \frac{r_{N0} N}{K_N(B, C_E)} - D_N(B, C_N) \right) \\
&+ (B - B^*) \left(b_{B0} - \frac{r_{B0} B}{K_B(C_E)} - D_B(N, C_B) \right) \\
&+ c_1 (C_N - C_N^*) \left(k_1 m_b C_B B + k_2 C_E - (k_3 + k_4 + b_{N0}) C_N + \frac{r_{N0} N C_N}{K_N(B, C_E)} \right) \\
&+ c_2 (C_B - C_B^*) \left(g_1 C_E - k_1 m_N C_B N - (g_2 + b_{B0}) C_B + \frac{r_{B0} B C_B}{K_B(C_E)} \right) \\
&+ (C_E - C_E^*) \left(u + \frac{m_b}{m_e} D_B(N, C_B) C_B B \right. \\
&\quad \left. + \frac{m_n}{m_e} (k_3 + D_N(B, C_N)) C_N N - \frac{m_b}{m_e} g_1 C_E B - \frac{m_n}{m_e} k_2 C_E N - h C_E \right).
\end{aligned} \tag{B.3}$$

Using the notation

$$\begin{aligned}
 \eta_1(B, C_E) &= \begin{cases} \left(\frac{1}{K_N(B, C_E)} - \frac{1}{K_N(B^*, C_E)} \right) / (B - B^*), & B \neq B^*, \\ \frac{-1}{K_N^2(B^*, C_E)} \frac{\partial K_N(B^*, C_E)}{\partial B}, & B = B^*, \end{cases} \\
 \eta_2(B^*, C_E) &= \begin{cases} \left(\frac{1}{K_N(B^*, C_E)} - \frac{1}{K_N(B^*, C_E^*)} \right) / (C_E - C_E^*), & C_E \neq C_E^*, \\ \frac{-1}{K_N^2(B^*, C_E^*)} \frac{\partial K_N(B^*, C_E^*)}{\partial C_E}, & C_E = C_E^*, \end{cases} \\
 \mu(C_E) &= \begin{cases} \left(\frac{1}{K_B(C_E)} - \frac{1}{K_B(C_E^*)} \right) / (C_E - C_E^*), & C_E \neq C_E^*, \\ \frac{-1}{K_B^2(C_E^*)} \frac{\partial K_B(C_E^*)}{\partial C_E}, & C_E = C_E^*, \end{cases} \\
 \psi_1(B, C_N) &= \begin{cases} \frac{D_N(B, C_N) - D_N(B^*, C_N)}{B - B^*}, & B \neq B^*, \\ \frac{\partial D_N(B, C_N)}{\partial B}, & B = B^*, \end{cases} \\
 \psi_2(B^*, C_N) &= \begin{cases} \frac{D_N(B^*, C_N) - D_N(B^*, C_N^*)}{C_N - C_N^*}, & C_N \neq C_N^*, \\ \frac{\partial D_N(B^*, C_N)}{\partial C_N}, & C_N = C_N^*, \end{cases} \\
 \zeta_1(N, C_B) &= \begin{cases} \frac{D_B(N, C_B) - D_B(N^*, C_B)}{N - N^*}, & N \neq N^*, \\ \frac{\partial D_B(N, C_B)}{\partial N}, & N = N^*, \end{cases} \\
 \zeta_2(N^*, C_B) &= \begin{cases} \frac{D_B(N^*, C_B) - D_B(N^*, C_B^*)}{C_B - C_B^*}, & C_B \neq C_B^*, \\ \frac{\partial D_B(N^*, C_B)}{\partial C_B}, & C_B = C_B^* \end{cases}
 \end{aligned} \tag{B.4}$$

and some algebraic manipulation, we can rewrite the systems as

$$\begin{aligned}
 \frac{dV_1}{dt} &= -\frac{1}{2}a_{11}(N - N^*)^2 + a_{12}(N - N^*)(B - B^*) - \frac{1}{2}a_{22}(B - B^*)^2 \\
 &\quad - \frac{1}{2}a_{11}(N - N^*)^2 + a_{13}(N - N^*)(C_N - C_N^*) - \frac{1}{2}a_{33}(C_N - C_N^*)^2 \\
 &\quad - \frac{1}{2}a_{11}(N - N^*)^2 + a_{14}(N - N^*)(C_B - C_B^*) - \frac{1}{2}a_{44}(C_B - C_B^*)^2
 \end{aligned}$$

$$\begin{aligned}
& -\frac{1}{2}a_{11}(N - N^*)^2 + a_{15}(N - N^*)(C_E - C_E^*) - \frac{1}{2}a_{55}(C_E - C_E^*)^2 \\
& -\frac{1}{2}a_{22}(B - B^*)^2 + a_{23}(B - B^*)(C_N - C_N^*) - \frac{1}{2}a_{33}(C_N - C_N^*)^2 \\
& -\frac{1}{2}a_{22}(B - B^*)^2 + a_{24}(B - B^*)(C_B - C_B^*) - \frac{1}{2}a_{44}(C_B - C_B^*)^2 \\
& -\frac{1}{2}a_{22}(B - B^*)^2 + a_{25}(B - B^*)(C_E - C_E^*) - \frac{1}{2}a_{55}(C_E - C_E^*)^2 \\
& -\frac{1}{2}a_{33}(C_N - C_N^*)^2 + a_{34}(C_N - C_N^*)(C_B - C_B^*) - \frac{1}{2}a_{44}(C_B - C_B^*)^2 \\
& -\frac{1}{2}a_{33}(C_N - C_N^*)^2 + a_{35}(C_N - C_N^*)(C_E - C_E^*) - \frac{1}{2}a_{55}(C_E - C_E^*)^2 \\
& -\frac{1}{2}a_{44}(C_B - C_B^*)^2 + a_{45}(C_B - C_B^*)(C_E - C_E^*) - \frac{1}{2}a_{55}(C_E - C_E^*)^2,
\end{aligned} \tag{B.5}$$

where

$$\begin{aligned}
a_{11} &= \frac{r_{N0}}{2K_N(B, C_E)}, \\
a_{22} &= \frac{r_{B0}}{2K_B(C_E)}, \\
a_{33} &= \frac{c_1}{2} \left(k_3 + k_4 + b_{N0} - \frac{r_{N0}N^*}{K_N(B, C_E)} \right), \\
a_{44} &= \frac{c_2}{2} \left(g_2 + k_1 m_n N^* + b_{B0} - \frac{r_{B0}B^*}{K_B(C_E)} \right), \\
a_{55} &= \frac{1}{2} \left(h + \frac{m_b}{m_e} g_1 B^* + \frac{m_n}{m_e} k_2 N^* \right), \\
a_{12} &= -\psi_1(B, C_N) - N^* r_{N0} \eta_1(B, C_E) - \zeta_1(N, C_B), \\
a_{13} &= -\psi_2(B^*, C_N) + \frac{c_1 r_{N0} C_N}{K_N(B, C_E)}, \\
a_{14} &= -c_2 k_1 m_n C_B, \\
a_{15} &= -N^* r_{N0} \eta_2(B^*, C_E) + \left(\frac{mn}{me} (k_3 + D_N(B, C_N)) C_N \right. \\
& \quad \left. - \frac{mn}{me} k_2 C_E + \frac{mb}{me} B^* C_B^* \zeta_1(N, C_B) \right), \\
a_{23} &= c_1 (k_1 m_b C_B + r_{N0} N^* C_N^* \eta_1(B, C_E)), \\
a_{24} &= -\zeta_2(N^*, C_B) + \frac{c_2 r_{B0} C_B}{K_B(C_E)},
\end{aligned}$$

$$\begin{aligned}
a_{25} &= -B^* r_{B0} \mu(C_E) + \left(\frac{m_b}{m_e} D_B(N, C_B) C_B \right. \\
&\quad \left. - \frac{m_b}{m_e} g_1 C_E + \frac{m_n}{m_e} N^* C_N^* \psi_1(B, C_N) \right), \\
a_{34} &= c_1 k_1 m_b B^*, \\
a_{35} &= c_1 (k_2 + r_{N0} N^* C_N^* \eta_2(B^*, C_E)) \\
&\quad + \frac{m_n}{m_e} N^* (k_3 + D_N(B, C_N) + C_N^* \psi_2(B^*, C_N)), \\
a_{45} &= c_2 (g_1 + r_{b0} B^* C_B^* \mu(C_E)) \\
&\quad + \frac{m_b}{m_e} B^* (D_B(N, C_N) + C_B^* \zeta_2(N^*, C_B)).
\end{aligned} \tag{B.6}$$

Note that

$$\begin{aligned}
\left| \frac{\partial K_N(B, C_E)}{\partial B} \right| &= K_{NB}, & \left| \frac{\partial K_N(B, C_E)}{\partial C_E} \right| &= K_{NC_E}, \\
\left| \frac{\partial K_B(C_E)}{\partial C_E} \right| &= K_{BC_E}, & \left| \frac{\partial D_N(B, C_N)}{\partial B} \right| &= d_{NB}, \\
\left| \frac{\partial D_N(B, C_N)}{\partial C_N} \right| &= d_{NC_N}, & \left| \frac{\partial D_B(N, C_B)}{\partial N} \right| &= d_{BN}, \\
\left| \frac{\partial D_B(N, C_B)}{\partial C_B} \right| &= d_{BC_B}.
\end{aligned} \tag{B.7}$$

Additionally, note that, by mean value theorem and the previous definitions,

$$\begin{aligned}
|\eta_1| &\leq \frac{K_{NB}}{(K_{N0} + B^* K_{NB} - K_{NC_E})^2} = \overline{\eta}_1, \\
|\eta_2| &\leq \frac{K_{NC_E}}{(K_{N0} + B^* K_{NB} - K_{NC_E} C_E^*)^2} = \overline{\eta}_2, \\
|\mu| &\leq \frac{K_{BC_E}}{(K_{B0} - K_{BC_E} C_E^*)^2} = \overline{\mu}, \\
|\psi_1| &\leq d_{NB}, \\
|\psi_2| &\leq d_{NC_N}, \\
|\zeta_1| &\leq d_{BN}, \\
|\zeta_2| &\leq d_{BC_B}.
\end{aligned} \tag{B.8}$$

Factoring dV_1/dt as

$$\begin{aligned}
 \frac{dV_1}{dt} = & -\frac{1}{2}a_{11}\left((N - N^*) - \frac{a_{12}}{a_{11}}(B - B^*)\right)^2 - \frac{1}{2}\left(a_{22} - \frac{a_{12}^2}{a_{11}}\right)(B - B^*)^2 \\
 & - \frac{1}{2}a_{11}\left((N - N^*) - \frac{a_{13}}{a_{11}}(C_N - C_N^*)\right)^2 - \frac{1}{2}\left(a_{33} - \frac{a_{13}^2}{a_{11}}\right)(C_N - C_N^*)^2 \\
 & - \frac{1}{2}a_{11}\left((N - N^*) - \frac{a_{14}}{a_{11}}(C_B - C_B^*)\right)^2 - \frac{1}{2}\left(a_{44} - \frac{a_{14}^2}{a_{11}}\right)(C_B - C_B^*)^2 \\
 & - \frac{1}{2}a_{11}\left((N - N^*) - \frac{a_{15}}{a_{11}}(C_E - C_E^*)\right)^2 - \frac{1}{2}\left(a_{55} - \frac{a_{15}^2}{a_{11}}\right)(C_E - C_E^*)^2 \\
 & - \frac{1}{2}a_{22}\left((B - B^*) - \frac{a_{23}}{a_{22}}(C_N - C_N^*)\right)^2 - \frac{1}{2}\left(a_{33} - \frac{a_{23}^2}{a_{22}}\right)(C_N - C_N^*)^2 \\
 & - \frac{1}{2}a_{44}\left((C_B - C_B^*) - \frac{a_{24}}{a_{44}}(B - B^*)\right)^2 - \frac{1}{2}\left(a_{22} - \frac{a_{24}^2}{a_{44}}\right)(B - B^*)^2 \\
 & - \frac{1}{2}a_{55}\left((C_E - C_E^*) - \frac{a_{25}}{a_{55}}(B - B^*)\right)^2 - \frac{1}{2}\left(a_{22} - \frac{a_{25}^2}{a_{55}}\right)(B - B^*)^2 \\
 & - \frac{1}{2}a_{33}\left((C_N - C_N^*) - \frac{a_{34}}{a_{33}}(C_B - C_B^*)\right)^2 - \frac{1}{2}\left(a_{44} - \frac{a_{34}^2}{a_{33}}\right)(C_B - C_B^*)^2 \\
 & - \frac{1}{2}a_{33}\left((C_N - C_N^*) - \frac{a_{35}}{a_{33}}(C_E - C_E^*)\right)^2 - \frac{1}{2}\left(a_{55} - \frac{a_{35}^2}{a_{33}}\right)(C_E - C_E^*)^2 \\
 & - \frac{1}{2}a_{44}\left((C_B - C_B^*) - \frac{a_{45}}{a_{44}}(C_E - C_E^*)\right)^2 - \frac{1}{2}\left(a_{55} - \frac{a_{45}^2}{a_{44}}\right)(C_E - C_E^*)^2,
 \end{aligned} \tag{B.9}$$

we see that sufficient conditions for dV_1/dt to be negative definite are:

$$a_{14}^2 < a_{11}a_{44}, \tag{B.10}$$

$$a_{23}^2 < a_{22}a_{33}, \tag{B.11}$$

$$a_{34}^2 < a_{33}a_{44}, \tag{B.12}$$

$$a_{13}^2 < a_{11}a_{33}, \tag{B.13}$$

$$\frac{a_{12}^2}{a_{11}} + \frac{a_{24}^2}{a_{44}} + \frac{a_{25}^2}{a_{55}} < 3a_{22}, \tag{B.14}$$

$$\frac{a_{15}^2}{a_{11}} + \frac{a_{35}^2}{a_{33}} + \frac{a_{45}^2}{a_{44}} < 3a_{55}. \tag{B.15}$$

To simplify the conditions, we can find an upper bound for the left-hand sides of the inequalities and lower bounds for the right-hand sides of the inequalities.

First consider (B.10). This can be used to place a restriction on c_2 :

$$\begin{aligned} a_{14}^2 &< a_{11}a_{44}, \\ c_2 &< \frac{r_{N0}(g_2 + k_1m_nN^*)}{4\overline{K_N}(k_1m_n)^2}. \end{aligned} \quad (\text{B.16})$$

Equation (B.11) can be used to place a restriction on c_1 :

$$\begin{aligned} a_{23}^2 &< a_{22}a_{33}, \\ c_1 &< \frac{r_{B0}(k_3 + k_4)}{4\overline{K_B}(k_1m_b + r_{N0}N^*C_N^*\overline{\eta_1})^2}. \end{aligned} \quad (\text{B.17})$$

Considering (B.12), an additional restriction can be placed on c_1 :

$$\begin{aligned} a_{34}^2 &< a_{33}a_{44}, \\ c_1 &< \frac{c_2(k_3 + k_4)(g_2 + k_1m_nN^*)}{4(k_1m_bB^*)^2}. \end{aligned} \quad (\text{B.18})$$

Since we have established

$$\begin{aligned} c_1 &< \frac{r_{B0}(k_3 + k_4)}{4\overline{K_B}(k_1m_b + r_{N0}N^*C_N^*\overline{\eta_1})^2}, \\ c_1 &< \frac{c_2(k_3 + k_4)(g_2 + k_1m_nN^*)}{4(k_1m_bB^*)^2}, \end{aligned} \quad (\text{B.19})$$

both conditions will be satisfied if

$$c_1 < \min\left(\frac{r_{B0}(k_3 + k_4)}{4\overline{K_B}(k_1m_b + r_{N0}N^*C_N^*\overline{\eta_1})^2}, \frac{c_2(k_3 + k_4)(g_2 + k_1m_nN^*)}{4(k_1m_bB^*)^2}\right). \quad (\text{B.20})$$

Next consider (B.13) to establish the first condition for global stability:

$$\begin{aligned} a_{13}^2 &< a_{11}a_{33}, \\ \left(d_{NC_N} + \frac{c_1r_{N0}}{\overline{K_N}}\right)^2 &< \frac{c_1r_{N0}(k_3 + k_4)}{4\overline{K_N}}. \end{aligned} \quad (\text{B.21})$$

Considering (B.14), we develop the second sufficient condition for global stability:

$$\begin{aligned}
 3a_{22} &> \frac{a_{12}^2}{a_{11}} + \frac{a_{24}^2}{a_{44}} + \frac{a_{25}^2}{a_{55}} \\
 \frac{3}{4} \frac{r_{B0}}{\overline{K}_B} &> \frac{\overline{K}_N (d_{NB} + N^* r_{N0} \overline{\eta}_1 + d_{BN})^2}{r_{N0}} + \frac{(d_{BC_B} + c_2 r_{B0} / \overline{K}_B)^2}{c_2 (g_2 + k_1 m_n N^*)} \\
 &\quad + \frac{(m_e B^* r_{B0} \overline{\mu} + m_b \overline{D}_B + m_b g_1 + m_n N^* C_N^* d_{NB})^2}{m_e (m_e h + m_b g_1 B^* + m_n k_2 N^*)}.
 \end{aligned} \tag{B.22}$$

Finally, considering (B.15),

$$\begin{aligned}
 3a_{55} &> \frac{a_{15}^2}{a_{11}} + \frac{a_{35}^2}{a_{33}} + \frac{a_{45}^2}{a_{44}}, \\
 \frac{3m_e}{4} (m_e h + m_b g_1 B^* + m_n k_2 N^*) &> \frac{\overline{K}_N (m_e N^* r_{N0} \overline{\eta}_2 + m_n k_3 + m_n \overline{D}_N + m_n k_2 + m_b d_{BN} B^* C_B^*)^2}{r_{N0}} \\
 &\quad + \frac{(c_1 m_e (k_2 + r_{N0} N^* C_N^* \overline{\eta}_2) + m_n N^* (k_3 + \overline{D}_N + d_{NC_N} C_N^*))^2}{c_1 (k_3 + k_4)} \\
 &\quad + \frac{(c_2 m_e (g_1 + r_{B0} B^* C_B^* \overline{\mu}) + m_b B^* (\overline{D}_B + d_{BC_B} C_B^*))^2}{c_2 (g_2 + k_1 m_n N^*)}.
 \end{aligned} \tag{B.23}$$

These conditions are equivalent to the conditions for global stability given in Theorem 4.2.

Acknowledgment

This work was supported by the National Science and Engineering Research Council of Canada.

References

- [1] R. E. Munn and V. Fedorov, *An Assessment of Environmental Impacts of Industrial Development : With Special Reference to the Doon Valley, India*, International Institute of Applied Systems Analysis, Laxenburg, Austria, 1986.
- [2] B. Dubey, "A model for the effect of time delay on the dynamics of a population living in a polluted environment," *Journal of Biological Systems*, vol. 12, no. 1, pp. 35–43, 2004.
- [3] B. Dubey and J. Hussain, "A model for the allelopathic effect on two competing species," *Ecological Modelling*, vol. 129, no. 2-3, pp. 195–207, 2000.
- [4] B. Dubey and J. Hussain, "Modelling the interaction of two biological species in a polluted environment," *Journal of Mathematical Analysis and Applications*, vol. 246, no. 1, pp. 58–79, 2000.

- [5] B. Dubey and J. Hussain, "Models for the effect of environmental pollution on forestry resources with time delay," *Nonlinear Analysis: Real World Applications*, vol. 5, no. 3, pp. 549–570, 2004.
- [6] B. Dubey and J. Hussain, "Modelling the survival of species dependent on a resource in a polluted environment," *Nonlinear Analysis: Real World Applications*, vol. 7, no. 2, pp. 187–210, 2006.
- [7] B. Dubey, R. K. Upadhyay, and J. Hussain, "Effects of industrialization and pollution on resource biomass: a mathematical model," *Ecological Modelling*, vol. 167, no. 1-2, pp. 83–95, 2003.
- [8] J. B. Shukla, A. K. Agrawal, B. Dubey, and P. Sinha, "Existence and survival of two competing species in a polluted environment: a mathematical model," *Journal of Biological Systems*, vol. 9, no. 2, pp. 89–103, 2001.
- [9] J. B. Shukla and B. Dubey, "Modelling the depletion and conservation of forestry resources: effects of population and pollution," *Journal of Mathematical Biology*, vol. 36, no. 1, pp. 71–94, 1997.
- [10] J. He and K. Wang, "The survival analysis for a single-species population model in a polluted environment," *Applied Mathematical Modelling*, vol. 31, no. 10, pp. 2227–2238, 2007.
- [11] S. A. L. M. Kooijman, *Dynamic Energy and Mass Budgets in Biological Systems*, Cambridge University Press, Cambridge, UK, 2000.
- [12] J. R. von Mayer, "Über die Kräfte der unbelebten Natur," *Annalen der Chemie und Pharmacie*, vol. 42, p. 233, 1842.
- [13] H. B. Callen, *Thermodynamics*, John Wiley & Sons, Chichester, UK, 1960.

