



Mathematical Modeling for Studying the Sustainability of Plants Subject to the Stress of Two Distinct Herbivores

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Received: July 3, 2019; Accepted: January 27, 2020

Abstract

Viability of plants, especially endangered species, are usually affected by multiple stressors, including insects, herbivores, environmental factors and other plant species. We present new mathematical models, based on systems of ordinary differential equations, of two distinct herbivore species feeding (two stressors) on the same plant species. The new feature is the explicit functional form modeling the simultaneous feedback interactions (synergistic or additive or antagonistic) between the three species in the ecosystem. The goal is to investigate whether the coexistence of the plant and both herbivore species is possible (a sustainable system) and under which conditions sustainability is feasible. Our theoretical analysis of the novel model without including competitions among the two herbivores reveals that the number of equilibrium states and their local stability depends on the type of interaction between the stressors: synergistic or additive or antagonistic. Our numerical results, based on value of parameters available, suggest that a sustainable system requires significant herbivore inter- or intra-species competition or both types. Additionally, our numerical findings indicate that competition and interaction of additive type promotes coexistence equilibrium states with the highest plant biomass. Furthermore, the system can exhibit periodic behavior and show the potential for multi-stability.

Keywords: Plant multiple stressors; Herbivores-plant mathematical models; Herbivores-plant preference; Intra and inter-competition

MSC 2010 No.: 92D40, 65L05

1. Introduction

Today there is a widespread scientific consensus that interactions between multiple ecosystem stressors are expected to jeopardize biological processes, functions and biodiversity and the scientific community has declared interactions among stressors a key issue for conservation and management (e.g., Aber et al. (2001), Blackwood et al. (2011), Côté et al. (2016), Dávalos et al. (2014), Fuller et al. (2015), Goussen et al. (2016), Liu et al. (2013), Preisler et al. (2010), Rodriguez-Saona et al. (2005), Van der Putten et al. (2001)). We define stressor as in Côté et al. (2016), that is, any natural or anthropogenic pressure that causes a quantifiable change, whether positive or negative, in biological response. In the literature, the interaction between ecological stressors is divided into synergetic, antagonistic and additive Côté et al. (2016), Darling and Côté (2008), Folt et al. (1999). The effect of several stressors is additive if the total effect is the sum of the individual effects; the effect is synergistic if the total effect is larger than the sum of the individual effects; and the effect is antagonistic if the total effect is less than the sum of the individual effects. References to experimental studies testing types of interactions among stressors are given, for example, in Coors and De Meester (2008), Côté et al. (2016), Piggott et al. (2015).

The review by Côté et al. (2016) highlights the theoretical and empirical evidence as to how, why, and when the interactions of multiple stressors occur and discusses their importance and implications within ecological scenarios. Other studies discussing these matters are, for example, Coors and De Meester (2008), Côté et al. (2016), Folt et al. (1999), Rodriguez-Saona et al. (2010)). Côté et al. (2016) pointed out that identifying stressor interactions is important because it can inform which stressors are critical to act on, and what is the most appropriate timing and location to intervene. On the other hand, in real systems some stressors are inextricably linked and understand these links can reduce the number of variables required to quantify the benefits of managing interactive disturbances. Despite of four decades of research in the field of interactions among ecosystem stressors and the advances brought to the community, there is still a significant number of uncertainties in defining and predicting the types of ecological interactions (synergetic, additive, antagonistic). Furthermore, the understanding of their effects on ecosystems and implications for conservation measures remains elusive Coors and De Meester (2008), Côté et al. (2016), Côté and Darling (2010), Rodriguez-Saona et al. (2010).

Thus, in this work we build and study novel process-based mathematical models of plants subject to two stressors, which are two distinct herbivore species. We consider population of grasses, shrubs, trees and other plants because they form the matrix on which communities and ecosystems are embedded and on which food webs are shaped Franklin et al. (2016), Maron and Crone (2006). Thus, understanding how plant dynamics are affected by stressors is crucial for gaining insights on the survival and abundance of species in any ecosystem Franklin et al. (2016), Goussen et al.

(2016).

Plants are subject to many stressors such as climate variabilities (e.g., drought, frost, floods, extreme heat and cold), diseases, herbivores, fire and harvesting. In the case of plants under the influence of only one stressor there have been many empirical and theoretical studies. In particular, mathematical models have been developed for studying the effect of a single stressor on plant dynamics (e.g., Beckage et al. (2011), Berryman (1979), Castillo-Chavez et al. (2012), Edelstein-Keshet (1986), Gaoue et al. (2016), Kato et al. (2007), Saha and Bandyopadhyay (2005), Shi et al. (2014), Whitfield et al. (2015)). But plants can be affected by two stressors at the same time and there are some mathematical models addressing this situation (e.g., Blackwood et al. (2011), Chen-Charpentier and Leite (2014), Collins et al. (2011), Fuller et al. (2015), Leite et al. (2018), Lynch (2006), Preisler et al. (2010), Nakazawa et al. (2012), Ramegowda and Senthil-Kumar (2015), Rodriguez-Saona et al. (2010), Stam et al. (2014), Svirezhev (2000), Vergés et al. (2007)).

Herbivores are common stressors of plants and several works investigate how herbivory translates to meaningful impacts on abundance, distribution or dynamics of plant populations (e.g., Choh et al. (2017), Feng et al (2009), Feng et al. (2011), Maron and Crone (2006), Pan et al. (2016), Rodriguez-Saona et al. (2010), Stam et al. (2014), Vergés et al. (2007)). Additionally, it has been shown that competition (intra and/or inter) among herbivores influences the plant population dynamics Maron and Crone (2006), Pan et al. (2016). In this context, a question of great importance for conservation and management of resources is whether the coexistence of the plant species and all herbivore species is possible (e.g., Aiello and Venci (2007), Shinya et al. (2016), Stam et al. (2014), Van der Putten et al. (2001)). Moreover, it is critical to investigate the role of competition among herbivores and the type of interactions among stressors in promoting such coexistence.

In this paper we build and study novel process-based mathematical models of plant dynamics subject to the stress of two herbivore species (two stressors) instead of one (Sections 2.2 and 2.3). The novel feature of our models is the explicit integration of a functional form representing the simultaneous interactions between the three species: plant / shrub and the two distinct herbivores. This feedback interaction between the two stressors is not fixed *a priori* but it is introduced in the model as parameters. The desired type of interaction (synergetic, additive, or antagonistic) is selected by choosing the value of the parameters. In the models, we also incorporate different assumptions of competition among the herbivore species: intra- and inter-competition.

To the best of our knowledge, this is the first work using this model framework. Therefore we do not aim to present a thorough theoretical analysis of the dynamics exhibited by the models, which may prove to be challenging due to their considerable nonlinear nature. Instead we analyze some dynamical properties of the models focused on equilibrium states, which corresponds to the simplest asymptotically temporal dynamical behavior of the models (Section 3). In Section 4 we explore “if-then” scenarios aiming to investigate the following questions: (1) In the absence of inter- and intra-species competition between the herbivore species, is it possible for the three species to coexist under each of the stressor interaction types? (2) How do the answers to question (1) change with the addition of inter- and intra-species competition between the herbivore species? (3) Given the variability in the values of the parameters, what is the effect of varying the type and

strength of the competition as well as of varying the type and strength of the interactions between the two stressors. We explore these questions by varying the parameters that give the interactions between the three species and find that there are changes in the number and stability of solutions. Section 5 summarizes and discusses the results and Section 6 gives some conclusions of the study.

2. Modeling dynamics of one plant species subject to herbivores stressors

In this section we introduce the novel process-based mathematical models incorporating two stressors (two herbivores) interactions (Section 2.2) and two stressors interactions with intra- and inter-herbivores competition (Section 2.3). For completeness, in Section 2.1 we present two classical predator-prey Lotka-Volterra models giving the population dynamics of one plant and one herbivore. These two classical models are the foundation on which the models in Section 2.2 and Section 2.3 are built.

2.1. One plant and one herbivore Lotka-Volterra model

The basic mathematical model of one plant species and one herbivore species, based on the predator-prey model given by Lotka and Volterra, is a classical model and is in most mathematical biology textbooks, for example, it is in Edelstein-Keshet (1986), Saha and Bandyopadhyay (2005). The model reads:

$$\frac{dP}{dt} = rP - d_1 h_1 P, \quad (1a)$$

$$\frac{dh_1}{dt} = \beta_1 d_1 h_1 P - m_1 h_1, \quad (1b)$$

where P is the plant species biomass, h_1 is the herbivore species, r is the growth rate of the plant, d_1 is the death rate of the plant caused by the herbivore, β_1 is the growth rate of the herbivore due to the ingestion of plant and m_1 is the death rate of the herbivore. The terms $d_1 h_1 P$ and $\beta_1 d_1 h_1 P$ model the herbivore-plant interactions and, thus, are called *the interaction terms*. All parameters are positive because they represent physical quantities. Their description as well as their units are summarized in Table 1.

A standard way of extending model (1) is to add limiting functions both in the growth rate of the plant and in the interaction terms. An example of such extension is the model (2) given below that can be found in Edelstein-Keshet (1986). In the extended model (2) the growth rate for the plant is logistic and the interaction terms are modeled by a Holling type II (also called Michaelis-Menten) functional response Holling (1959a). A functional response in ecology is the intake rate of a consumer as a function of the amount of food available. The Holling Type II functional response is commonly used as the simplest functions that models a decreasing intake rate as food availability increases Edelstein-Keshet (1986), Holling (1959a,b). This functional type is based on the assumptions that 1) the consumer is limited by its capacity to process food and 2) processing and searching

for food are mutually exclusive behaviors. It is a widely used functional response and this is the reason we adopt it here. The equations describing the dynamics are:

$$\frac{dP}{dt} = rP \left(1 - \frac{P}{K} \right) - \frac{d_1 h_1 P}{1 + \sigma_1 P}, \quad (2a)$$

$$\frac{dh_1}{dt} = \beta_1 \frac{d_1 h_1 P}{1 + \sigma_1 P} - m_1 h_1, \quad (2b)$$

where K is the carrying capacity of the plants and σ_1 is the functional response constant. The meaning of the remaining parameters are as described for model (1). The units of each parameter are given in Table 1. All parameters are assumed to be positive so they are biologically meaningful.

2.2. Two non competing herbivores and one plant model

Drawing on the ideas introduced in models (1) and (2) we now present the model (3) concerning the effect of two distinct herbivores feeding in one plant species. That is, the two distinct herbivores species play the role of two different stressors on the plant system. A model for the related problem of two predators and one prey is presented in Hsu et al. (2001), where the functional response for consumption of the prey by one predator is of Holling type. The effect of the second predator is added by a term in the denominator of the functional response, which is distinct from the approach we use in this work. We incorporate the same effect by adding a term proportional to the amount of the second herbivore species in accordance with the law of mass action Edelman-Keshet (1986).

The one plant species and two herbivores (two stressors) dynamics is modeled as follows:

$$\frac{dP}{dt} = rP \left(1 - \frac{P}{K} \right) - (d_1 - k_1 h_2) h_1 P - (d_2 - k_2 h_1) h_2 P, \quad (3a)$$

$$\frac{dh_1}{dt} = \beta_1 (d_1 - k_1 h_2) h_1 P - m_1 h_1, \quad (3b)$$

$$\frac{dh_2}{dt} = \beta_2 (d_2 - k_2 h_1) h_2 P - m_2 h_2, \quad (3c)$$

where P is the plant species biomass and h_1 , h_2 represent two distinct herbivore species. The description and units of the other parameters in the model are given in Table 1.

The model (3) incorporates the logistic growth rate introduced in model (2) and the interaction terms similar to those modeled as in (1). Additionally, we incorporate new interaction terms $k_1 h_1 h_2 P$ and $k_2 h_1 h_2 P$ that appear in the last two terms in (3a) and the first term in (3b),(3c). These functionals model the feedback interactions among the three species. These terms constitute, to the best of our knowledge, a novel feature modeling the fact that the presence of a herbivore may affect the feeding behavior of the other herbivore that is not a result of competition for resources. They can be viewed, for example, as a result of plant's defense mechanisms adaptation (e.g., Rodriguez-Saona et al. (2010)). The coefficient k_1 measures the preference of herbivore 1 for the plant in the

presence of herbivore 2. Similarly, k_2 is the preference of herbivore 2 for the plant in the presence of herbivore 1 (see Table 1). Thus, in the classical sense there is no intra- or inter-species competition between the herbivore species in (3). Those factors will be included in the model (4) given in Section 2.3.

We assume that all parameters, except k_1, k_2 , are positive as they are physical quantities. The interaction coefficients k_1 and k_2 are positive if their effect is antagonistic (see model (3)). That is, one species is less likely to eat a plant that has been eaten by the other species. But both coefficients are negative if the effect is synergistic meaning that one species is more likely to feed on a plant that has already been eaten by the other species. The coefficients can be $k_1 = k_2 = 0$ modeling additive effects.

An example of an effect which is synergistic is given in Aiello and Vencel (2007) where the chemical cues produced by a plant in defense to one insect herbivore also protects it against the second one. In Van der Putten et al. (2001) the authors mention that a herbivore eating the roots of a plant may either increase or inhibit the production of defense compounds above ground. Also see, for example, Coors and De Meester (2008), Côté et al. (2016), Piggott et al. (2015), Rodriguez-Saona et al. (2005, 2010) for other specific contexts where different interaction types are studied.

Table 1. Description of the parameters in the models and the values used in the numerical simulations. The values of parameters are based on Feng et al (2009) and Feng et al. (2011)

Par.	Value	Unit	Description
d_1	0.1	$1/(\#herb. \cdot day)$	Death rate of plant cause by herbivore-1
d_2	$d_1/2 = 0.05$	$1/(\#herb. \cdot day)$	Death rate of plant caused by herbivore-2
K	7×10^5	Kg	Plant-based carrying capacity of the ecosystem
k_1	-0.007 to 0.007	$1/((\#herb.)^2 \cdot day)$	Preference of herbivore-1 for the plant in the presence of herbivore-2
k_2	-0.007 to 0.007	$1/((\#herb.)^2 \cdot day)$	Preference of herbivore-2 for the plant in the presence of herbivore-1
m_1	0.00125	$1/day$	Death rate of the herbivore-1
m_2	$m_1/2$	$1/day$	Death rate of the herbivore-2
m_{11}	0 to 0.005	$1/(\#herb. \cdot day)$	Herbivore-1 intra-species competition coefficient
m_{22}	$m_2 = m_1/2$	$1/(\#herb. \cdot day)$	Herbivore-2 intra-species competition coefficient
r	0.01	$1/day$	Growth rate of the plant
β_1	0.01	$\#herb./Kg$	Growth rate of herbivore-1 due to the ingestion of plant
β_2	0.01	$\#herb./Kg$	Growth rate of herbivore-2 due to the ingestion of plant
β_{12}	$m_2/2 = m_1/4$	$1/(\#herb. \cdot day)$	Herbivore-1 removal coefficient due to inter-species competition
β_{21}	$\beta_{12}/2 = m_1/8$	$1/(\#herb. \cdot day)$	Herbivore-2 removal coefficient due to inter-species competition
σ_1	0.001	$1/Kg$	Herbivore-1 Holling type II functional response constant
σ_2	$2\sigma_1 = 0.002$	$1/Kg$	Herbivore-2 Holling type II functional response constant

As we will see in Section 4 for sets of reasonable values of the parameters, the coexistence equilibrium points of model (3) where the three species are non zero are unstable. Since our aim is to build a simple mathematical model that exhibits locally asymptotically stable equilibrium states with the presence of the three species (i.e., coexistence states), we next introduce a model with one more layer of complexity - both intra- and inter-herbivores competition.

2.3. Two competing herbivores and one plant model

A more realistic novel model that includes competition, both intra- and inter-species (in the classic sense), between the two herbivore species is given below. The model (4) also includes Holling type II interaction between the herbivores and the plants:

$$\frac{dP}{dt} = rP \left(1 - \frac{P}{K} \right) - \frac{(d_1 - k_1 h_2) h_1 P}{1 + \sigma_1 P} - \frac{(d_2 - k_2 h_1) h_2 P}{1 + \sigma_2 P}, \quad (4a)$$

$$\frac{dh_1}{dt} = \beta_1 (d_1 - k_1 h_2) h_1 \frac{P}{1 + \sigma_1 P} - m_1 h_1 - m_{11} h_1^2 - \beta_{12} h_1 h_2, \quad (4b)$$

$$\frac{dh_2}{dt} = \beta_2 (d_2 - k_2 h_1) h_2 \frac{P}{1 + \sigma_2 P} - m_2 h_2 - m_{22} h_2^2 - \beta_{21} h_1 h_2. \quad (4c)$$

We assume that all parameters have positive values to guarantee their biological meaning, with the exception of k_1 and k_2 , which may be positive, negative or zero as discussed in Section 2.2. Note that when $m_{11} = 0, m_{22} = 0, \beta_{12} = 0, \beta_{21} = 0$ the model includes Holling type II interaction between the herbivores and the plant but no inter- or intra-species competition between two distinct herbivore species.

3. Analysis of the dynamics

To the best of our knowledge, this is the first work using this model framework to study dynamics of plants subject to herbivory of two distinct interacting herbivores (two coupled stressors). Thus, our aim is not to perform a thorough theoretical analysis of the dynamics exhibited by the models, which may be challenging to accomplish since they exhibit a significant nonlinear structure. Instead we focus on equilibrium states, which corresponds to the simplest asymptotically temporal dynamical behavior of the models (3) and (4).

The numerical study of the bifurcations near equilibrium states described in Section 4 shows that periodic solutions occurring via Hopf bifurcations can arise when equilibrium solutions destabilize. This finding is in agreement with the literature and theoretical evidence (e.g., Hastings and Gross (2012)) showing that many ecological systems support this type of temporal dynamical behavior. Literature also indicates that even more complex temporal dynamics such as heteroclinic cycles (e.g., Hastings and Gross (2012), pages 528–529, Tachikawa (2007)) and chaos (e.g., Hastings and Gross (2012), pages 528–529) occur. However, we do not include in this work the study of these complex dynamics (e.g, periodic solutions, chaos).

We denote by *coexistence or interior equilibrium* points the equilibrium states for which the plant / shrub / tree species and the two herbivore species are simultaneously present. The steady-states with all species absent are called *trivial equilibrium* solutions. The equilibrium solutions that are neither *trivial equilibrium* nor *coexistence equilibrium* are denoted by *boundary equilibrium*

points. The set of parameters, assumed to have positive values, except k_1, k_2 that are assumed to be any real number, is referred as *the set of admissible parameters*.

3.1. Existence and stability of equilibrium states of the model (3)

The equilibrium states are found by setting the left-hand side in (3) equal to zero and simultaneously solving the three resulting equations. The results on existence of steady state solutions are consolidated in Table 2 (trivial and boundary equilibrium points) and Table 3 (coexistence equilibrium points). The proof of these results is given in Appendix A.

We investigate the local stability (l.s.) of equilibrium solutions. An equilibrium solution is said to be linearized or local stable if, when solving a differential equations system with an initial value close to the equilibrium solution, the solutions at all time stay close to the equilibrium solution. A solution that doesn't satisfy this property is said to be unstable. A solution that is unstable is also unstable for any size perturbation of the equilibrium solution while a solution that is locally stable is stable for small perturbations of the equilibrium solution.

To establish the linearized stability of an equilibrium state, the Jacobian matrix of the right hand side of the differential equation systems (3) is evaluated at the desirable equilibrium state. If the real part of any eigenvalue of this Jacobian matrix is positive the equilibrium state is linearly unstable and if all eigenvalues have negative real part the equilibrium is locally asymptotically stable (l.a.s.), see, for example, Coddington and Levinson (1955). In the case that an eigenvalue has a zero real part, it is possible that the system have periodic solutions.

The stability of the equilibrium solutions of the model (3) is summarized in Tables 2 and 3. The proof of these results is given in Appendix B. For simplicity of presentation we introduce the following quantities:

$$\begin{aligned}
 Q &= \beta_1 d_1 m_2 - \beta_2 d_2 m_1; & R_1 &= \frac{r k_2 \beta_2 m_1}{d_1} \left(1 - \frac{m_1}{K \beta_1 d_1} \right); \\
 R_2 &= \frac{r k_1 \beta_1 m_2}{d_2} \left(1 - \frac{m_2}{K \beta_2 d_2} \right); & S_1 &= \frac{K \beta_1 d_1^2}{m_1 r \beta_2 k_2} (\beta_2 d_2 m_1 - \beta_1 d_1 m_2), \quad k_2 \neq 0; \\
 S_2 &= \frac{K \beta_2 d_2^2}{m_2 r \beta_1 k_1} (\beta_1 d_1 m_2 - \beta_2 d_2 m_1), \quad k_1 \neq 0; & A_1 &= \frac{\beta_2 d_2 m_1 k_1 + \beta_1 d_1 k_2 m_2}{r K \beta_1 \beta_2 k_1 k_2}, \quad k_1, k_2 \neq 0; \\
 A_2 &= \frac{m_1 m_2 (k_1 + k_2)}{r K^2 \beta_1 \beta_2 k_1 k_2}, \quad k_1, k_2 \neq 0; & a_1 &= r K A_1; & a_0 &= -A_2 r K^2; \\
 \Delta &= q^2 + p^3; & p &= -\frac{1}{27} + \frac{A_1}{6} - \frac{A_2}{2}; & q &= \frac{3A_1 - 1}{9}.
 \end{aligned}$$

Result:

Trivial and boundary equilibrium states and their stability. Consider the model (3) in the region

of admissible parameters. Then,

- (a) there exists one trivial equilibrium and three boundary equilibrium points. These solutions and their corresponding conditions for existence as well as for their l.a.s, if it exists, are listed in Table 2.
- (b) The coexistence equilibrium solutions as well as the conditions on parameters for their stability depend on the sign of the values of k_1, k_2 . That is, they depend on the type of interaction between herbivore 1 and 2 on the effect of the herbivory: antagonistic ($k_1 > 0$), or synergetic ($k_i > 0$), or additive ($k_i = 0$) and they are listed in Table 3. Namely, if $k_1 = 0$ and $k_2 = 0$ simultaneously, the system has no coexistence equilibrium. If either $k_1 = 0$ or $k_2 = 0$, the system exhibits a unique coexistence equilibrium but the conditions for locally asymptotically stability changes with the signs of k_1 , in the case $k_2 = 0$ or k_2 , in the case $k_1 = 0$. However, if $k_1, k_2 > 0$, the system has 1 or 3 steady states; if both k_1 and $k_2 < 0$, or if $sign(k_1) \neq sign(k_2)$, the system has either 0, or 1 or 2 equilibrium solutions.

Table 2. Trivial and boundary equilibrium states of the model 3 and their stability

Equilibrium	Conditions for existence	Case	Condition for l.a.s
$E^0 = (0, 0, 0)$	none		unstable
$E^P = (K, 0, 0)$	none		$K\beta_2d_2 - m_2 < 0$ and $K\beta_1d_1 - m_1 < 0$
$E^{h_1} = (\frac{m_1}{\beta_1d_1}, h_1, 0)$	$K\beta_1d_1 - m_1 > 0$	$k_2 = 0$	$0 < m_1 < \min\{K\beta_1d_1, \frac{\beta_1d_1m_2}{\beta_2d_2}\}$
$h_1 = \frac{r}{K\beta_1d_1^2}(K\beta_1d_1 - m_1)$		$k_2 > 0$	$K\beta_1d_1 - m_1 > \max\{0, S_1\}$
		$k_2 < 0$	$0 < K\beta_1d_1 - m_1 < S_1$ and $Q > 0$
$E^{h_2} = (\frac{m_1}{\beta_1d_1}, 0, h_2)$	$K\beta_2d_2 - m_2 > 0$	$k_1 = 0$	$0 < m_2 < \min\{K\beta_2d_2, \frac{\beta_2d_2m_1}{\beta_1d_1}\}$
$h_2 = \frac{r}{K\beta_2d_2^2}(K\beta_2d_2 - m_2)$		$k_1 > 0$	$K\beta_2d_2 - m_2 > \max\{0, S_2\}$
		$k_1 > 0$	$0 < K\beta_2d_2 - m_2 < S_2$ and $Q < 0$

Remark 3.1.

Observe that from the Table 2, rows corresponding to E^P, E^{h_1}, E^{h_2} it follows that if the herbivore death rates are sufficiently small, the herbivores can establish themselves in the system. Our theoretical analysis in Appendix B reveals that periodic solutions arising from Hopf bifurcations as the system goes through the boundary equilibrium states is not possible since the eigenvalues of the associated Jacobian matrices are real for all values of the admissible parameters.

Remark 3.2.

From Table 3, we conclude that when either $k_1 = 0$ or $k_2 = 0$ there is a unique coexistence equilibrium state. However, when these coefficients are not simultaneously zero, the system can exhibit multiple steady states and they can be locally asymptotically stable. Thus, multi-stability is possible. For cases satisfying simultaneously $k_1, k_2 \neq 0$, we only provide the number of possible interior equilibrium states (or coexistence equilibrium states). Their expressions were computed using software packages (e.g., Mathematica, Maple) but they were too complex which impaired us from giving their closed forms. However, we calculate them numerically using selected values of parameters (Section 4). The expressions b_0, b_1, b_2 are expressed as a function of parameters and an interior equilibrium. They are long, therefore, for readability of this paper we do not include

Table 3. Coexistence equilibrium states of the model 3 and their stability

Equilibrium	Case	Conditions for existence	Condition for l.a.s
none	$k_1 = 0 = k_2$		
$P = \frac{m_1}{\beta_1 d_1}$ $h_1 = \frac{-Q}{\beta_2 k_2 m_1}$ $h_2 = \frac{rk_2 \beta_2 m_1 (K \beta_1 d_1 - m_1) - K \beta_1 d_1^2 Q}{K \beta_1^2 d_1^2 k_2 m_2}$	$k_1 = 0, k_2 > 0$	$k\beta_1 d_1 - m_1 > 0$ $0 < -Q < R_1$	$b_0, b_2 > 0$ $b_2 b_1 > b_0$
	$k_1 = 0, k_2 < 0$	$k\beta_1 d_1 - m_1 > 0$ $R_1 < -Q < 0$	
$P = \frac{m_2}{\beta_2 d_2}$ $h_1 = \frac{rk_1 \beta_1 m_2 (K \beta_2 d_2 - m_2) + K \beta_2 d_2^2 Q}{K \beta_2^2 d_2^2 k_1 m_1}$ $h_2 = \frac{Q}{\beta_1 k_1 m_2}$	$k_1 > 0, k_2 = 0$	$k\beta_2 d_2 - m_2 > 0$ $0 < Q < R_2$	
	$k_1 < 0, k_2 = 0$	$k\beta_2 d_2 - m_2 > 0$ $R_2 < Q < 0$	
3 1 1	$k_1, k_2 > 0$	$\Delta < 0$	
2 1 0		$\Delta = 0$	
1 2 0	$k_1, k_2 < 0$	$\Delta > 0$	
1 2 0		$\Delta < 0$	
1 2 0	$sign(k_1) \neq sign(k_2)$	$\Delta = 0$	
1		$\Delta > 0$	
1	$sign(k_1) \neq sign(k_2)$	$a_1, a_0 > 0; \Delta < 0$	
		$a_1, a_0 < 0; \Delta < 0$	
		$a_1, a_0 < 0; \Delta > 0$	

them in the main text. However, they can be found in Appendix B, Section B.3.

3.2. Existence and stability of equilibrium states of the model (4)

In this section we discuss existence and stability of equilibrium states for model (4), which includes competition, both intra- and inter-species, between the two herbivore species. The study is presented in Results 2–4 given next and summarized in Table 4. The proof of some analytical results concerning both existence and stability of some equilibrium states are given at the end of this section.

Result:

Existence of trivial and boundary equilibrium states. Consider the model (4) with

- (a) Competition and Holling type II, that is, all parameters in the model have positive values,

except k_1, k_2 that can be any real number. Then, the model have a trivial equilibrium point $E^0 = (P, h_1, h_2) = (0, 0, 0)$ and seven boundary equilibrium points: one with herbivores absent $E^P = (K, 0, 0)$, three with only herbivore 1 present, and three with only herbivore 2 present in the system.

- (b) No competition but with Holling type II, that is, $m_{11} = m_{22} = \beta_{12} = \beta_{21} = 0$ and the remaining parameters having positive values, except k_1, k_2 , which can take any real value. Then, the system has the trivial state E^0 and three boundary equilibrium points: one with no herbivores present in the system, $E^P = (K, 0, 0)$; one with herbivore 1 absent, E^{h_1} ; and one with only herbivore 1 present, E^{h_2} . The equilibrium E^{h_1} exists if $\beta_1 d_1 - m_1 \sigma_1 > \frac{m_1}{K}$ while the equilibrium E^{h_2} exists if $\beta_2 d_2 - m_2 \sigma_2 > \frac{m_2}{K}$.

Result:

Existence of coexistence equilibrium points. Consider the model (4), with and without competition as well as both without (not given in this paper) and with Holling type II interaction, there are equilibrium points for which the three species coexist (see Remark 3).

Remark 3.3.

For all equilibrium states listed in Result 2 and Result 3, including the coexistence equilibrium states in which we are most interested, the expressions can be computed analytically with the aid of software (such as Maple or Mathematica) but for most of them the formulas are not given in this paper because they were very complicated and long. This impaired the determination of which equilibrium states, if any, could have real and positive values in admissible region of parameters. This equilibrium solutions are the ones that have meaning within ecological context.

Linearized stability of the equilibrium states. For model (4), the eigenvalues of the Jacobian matrix of the linearized system can be calculated analytically for arbitrary values of the parameters, but for most of the equilibrium states the expressions are very complicated and it is very hard or even impossible to determine the sign of the real part of the eigenvalues. Only the expressions of the eigenvalues corresponding to the Jacobian matrix evaluated at the solutions with no herbivores revealed to be simple. Thus, we only present analytical results on linearized stability for those equilibrium solutions (Result 4). For all other equilibrium solutions the eigenvalues were calculated numerically for specific values of the parameters and are presented in Section 4.

Result:

Stability of the trivial state and the boundary equilibrium point with $h_1 = 0 = h_2$. Consider the trivial steady-state E^0 and the boundary equilibrium point E^P of the system (4) given in Result 2. Then the trivial state is unstable and the boundary equilibrium point is locally asymptotically stable (l.a.s.) if

$$\beta_1 d_1 - m_1 \sigma_1 < \frac{m_1}{K} \quad \text{and} \quad \beta_2 d_2 - m_2 \sigma_2 < \frac{m_2}{K}. \quad (5)$$

Proof of Result 2:

The equilibrium points are found by setting the right-hand side of the differential equations in (4) equal to zero. The equilibrium points E^0 and E^P exist for all values of admissible parameters. The conditions for existence of equilibrium states E^{h_1} , E^{h_2} given in Result 2, Part (b) are derived as follow. Consider the equilibrium E^{h_1} as given in Table 4. Observe that

$$P = \frac{m_1}{\beta_1 d_1 - m_1 \sigma_1} \quad \text{and} \quad h_1 = \frac{\beta_1 r (\beta_1 d_1 - m_1 (1 + K \sigma_1))}{K (\beta_1 d_1 - m_1 \sigma_1)^2}.$$

Hence, in order for P and h_1 to be positive the following two conditions need to be simultaneously satisfied:

$$\beta_1 d_1 - m_1 \sigma_1 > 0 \quad \text{and} \quad \beta_1 d_1 - m_1 (1 + K \sigma_1) > 0. \quad (6)$$

These conditions yield the desire result. The condition for existence of E^{h_2} , by symmetry of the system, is derived in a similar fashion. ■

Proof of Result 4:

Consider the trivial equilibrium given in Result 2. The Jacobian matrix evaluated at this state has eigenvalues $-m_1, -m_2, r$. Since m_1, m_2, r are assumed to be positive we have that $r > 0$. Therefore the equilibrium point is unstable.

When consider the boundary equilibrium, E^P , the eigenvalues of the Jacobian matrix at this point are $(\beta_1 d_1 K)/(1 + K \sigma_1) - m_1$ and $(\beta_2 d_2 K)/(1 + K \sigma_2) - m_2, -r$. Hence, the point is unstable if $(\beta_1 d_1 K)/(1 + K \sigma_1) - m_1 > 0$ or $(\beta_2 d_2 K)/(1 + K \sigma_2) - m_2 > 0$, which is equivalent to the condition given in Result 5 for l.a.s. ■

4. Numerical simulation results

We present a numerical study to determine the equilibrium points corresponding to the coexistence of the three species. We also study their local stability. In addition, to better understand the dynamics near the equilibrium states, we perform a numeric bifurcation study. That is, we calculate the branches of steady solutions and bifurcation points. In this work we do not aim to give an exhaustive classification of the dynamics. Instead we explore a few scenarios. Thus, we use as a bifurcation parameter m_{11} (herbivore 1 intra-competition coefficient) or k_1 (coefficient measuring how the presence of herbivore 2 affects the preference of herbivore 1 for the plant). Note that by varying k_1 different types (additive or synergetic or antagonistic) of interactions between the two herbivores can be chosen. Due to the symmetry of the model similar results hold for the bifurcation study when choosing bifurcation parameter m_{22} (intra-herbivore 2 competition coefficient) or k_2 (coefficient measuring how the presence of herbivore 2 affects preference of herbivore 1 for the plant). The choice of of using as bifurcation parameters those parameters determining the type of interaction allows us to establish the possibility of coexistence under synergistic, additive or antagonistic interaction.

We restrict the presentation of the results to the coexistence equilibrium points. These are scenarios in which all three species are present in the ecosystem. We searched for regions in the parameter

Table 4. Equilibrium states of the model (4) and their stability. The results are valid for (4) with and without competition unless stated otherwise

Model	Equilibrium	Conditions for existence	Condition for l.a.s
(4)	$\mathbf{E}^0 = (\mathbf{0}, \mathbf{0}, \mathbf{0})$	No restriction	unstable
(4)	$\mathbf{E}^P = (\mathbf{K}, \mathbf{0}, \mathbf{0})$	No restriction	$\beta_1 d_1 - m_1 \sigma_1 < m_1 / K$ and $\beta_2 d_2 - m_2 \sigma_2 < m_2 / K$
(4) with competition	3 possible distinct states with with $P \neq 0, h_1 = 0, h_2 \neq 0$	Not determined analytically (see Remark 3.3)	Not determined analytically (see Remark 3.3)
(4) with competition	3 possible distinct states with with $P \neq 0, h_1 \neq 0, h_2 = 0$	Determined only numerically (see Remark 3.3)	Determined only numerically (see Remark 3.3)
(4) with competition	Coexistence Equilibria $P \neq 0, h_1 \neq 0, h_2 \neq 0$	Determined only numerically (see Remark 3.3)	Determined only numerically (see Remark 3.3)
(4) with no competition but Holling Type II $m_{11} = m_{22} = \beta_{12} = \beta_{21} = 0$	$\mathbf{E}^{h1} = (\mathbf{P}, \mathbf{h}_1, \mathbf{0})$ $P = \frac{m_1}{\beta_1 d_1 - m_1 \sigma_1}$ $h_1 = \frac{\beta_1 r (\beta_1 d_1 - m_1 (1 + K \sigma_1))}{K (\beta_1 d_1 - m_1 \sigma_1)^2}$	$\beta_1 d_1 - m_1 \sigma_1 > m_1 / K$	Determined only numerically (see Remark 3.3)
(4) with no competition but Holling Type II	$\mathbf{E}^{h2} = (\mathbf{P}, \mathbf{0}, \mathbf{h}_2)$ $P = \frac{m_2}{\beta_2 d_2 - m_2 \sigma_2}$ $h_2 = \frac{\beta_2 r (\beta_2 d_2 - m_2 (1 + K \sigma_2))}{K (\beta_2 d_2 - m_2 \sigma_2)^2}$	$\beta_2 d_2 - m_2 \sigma_2 > m_2 / K$	Determined only numerically (see Remark 3.3)
(4) with no competition but Holling Type II	Coexistence Equilibria with $P \neq 0, h_1 \neq 0, h_2 = 0$	Determined only numerically (see Remark 3.3)	Determined only numerically (see Remark 3.3)

space in which, together with initial conditions, lead the three species to a locally asymptotic stable nonzero state. Although the models can sustain periodic solutions via Hopf bifurcation as shown in the bifurcation diagrams, we do not address neither this type of dynamics nor more complex ones.

Our numerical study for model (3), which does not include competition, show that coexistence equilibrium states are unstable for value of parameters found in the literature (presented in Table 1). This study is not presented here. Instead we consider model (4) with $m_{11} = 0 = m_{22}, \beta_{12} = 0 = \beta_{21}$, which models the system of interest with no inter- or intra-species competition between the herbivore species. Therefore, studying model (4) includes the exploration of stable steady state solutions for a model with no herbivores competition but with a Holling type II saturation term.

In summary, we give the numerical solutions for the model (4) with no competition assuming that the interaction between a herbivore and the plant species is of Holling type II (Section 4.1). We present numerical solutions and bifurcation study for model (4) when there is only intra-species competition (Sections 4.2) and when both intra- and inter-species are present (Section 4.3). In the last two cases we did simulations varying the type of effect caused by the presence of the two herbivore species, from additive to synergistic to antagonistic effects (i.e, distinct types of feedback interactions between the stressors). We did not performed an exhaustive study but choose a few scenarios to illustrate the dynamics for the cases above mentioned.

We use three numerical tools, namely *Mathematica*, *Octave*, and *Xppaut*. *Mathematica* was selected to find the equilibrium points and their linearized stability, both analytically and numerically. *Octave* was the main numerical tool to solve numerically the system of differential equations

for given values of the parameters and *Xppaut* was used to calculate the branches of equilibrium solutions and bifurcation points as functions of a parameter (m_{11} or k_1).

The values of the parameters, their units and description used for the numerical simulations are indicated in Table 1. They are based on the values given in Feng et al (2009) and Feng et al. (2011). In these papers, the values of the parameters are presented in the context of mathematical modeling of effects of interspecies competition, herbivory and plant's toxic defense against herbivores on vegetation dynamics. Additionally, we are assuming that $k_2 = k_1$ in all simulations, except when perform bifurcation studies. The units used for the state variable biomass is kg and time is in days.

4.1. Model (4) with no competition but with Holling type II

The simplest case is when the model includes Holling type II interaction between the herbivores and the plants but no inter- or intra-species competition between the herbivore species. So we take $m_{11} = 0$, $m_{22} = 0$, $\beta_{12} = 0$, and $\beta_{21} = 0$. Numerical calculations show that there exist coexistence points for $k_1 = -0.007$ to 0.007 (values of some equilibrium points are given in Appendix C) but they are unstable. We note that our numerical calculations for $k_1 = 0 = k_2$ show that the model does not support coexistence equilibrium states, which is analogous to the findings of the theoretical analysis of model (3).

4.2. Model (4) with only intra-species competition and Holling type II

Next we add intra-species competition to the model. The competition parameters used are: $\beta_{12} = 0$, $\beta_{21} = 0$, $m_{11} = 0.00125$. The results of the simulations of the model are given in Figure 1 for different values of k_1 (parameter that measures the preference of herbivore 1 for the plant in the presence of herbivore 2). Note that if $k_1 > 0$ the preference effect is antagonistic, if $k_1 = 0$ the effect is additive and if $k_1 < 0$ the effect of the preference is synergistic.

Figure 3(a) shows the bifurcation diagram for branch continuation using $-0.008 \leq k_1 \leq 0.006$ and a summary of results is provided in Table 5. We recall that by symmetry of the model similar results hold when we use k_2 (parameter that measures the preference of herbivore 2 for the plant in the presence of herbivore 1) as the bifurcation parameter.

Figure 1, depicts biomass of plant as well as number of herbivores 1 and 2 as a function of time. The plotted variable P is the calculated plant biomass divided by 10. Panels (a), (b) show simulations for two negative values of k_1 , that is, the effects are synergistic, Figure 1 panel (c) is for $k_1 = 0$, which gives additive effects, and Figure 1 panel (d) for $k_1 > 0$, that is, the effects are antagonistic.

In the bifurcation diagram (see Figure 3(a)), two solution branches are shown with the value of $P/10$ plotted against k_1 . The solution branches that are stable are depicted with dashed red line and those that are unstable with solid black line. The horizontal branch have solutions with $h_1 = 0$, that is, the herbivore 1 is absent and is independent of the value of k_1 . In the second branch, the

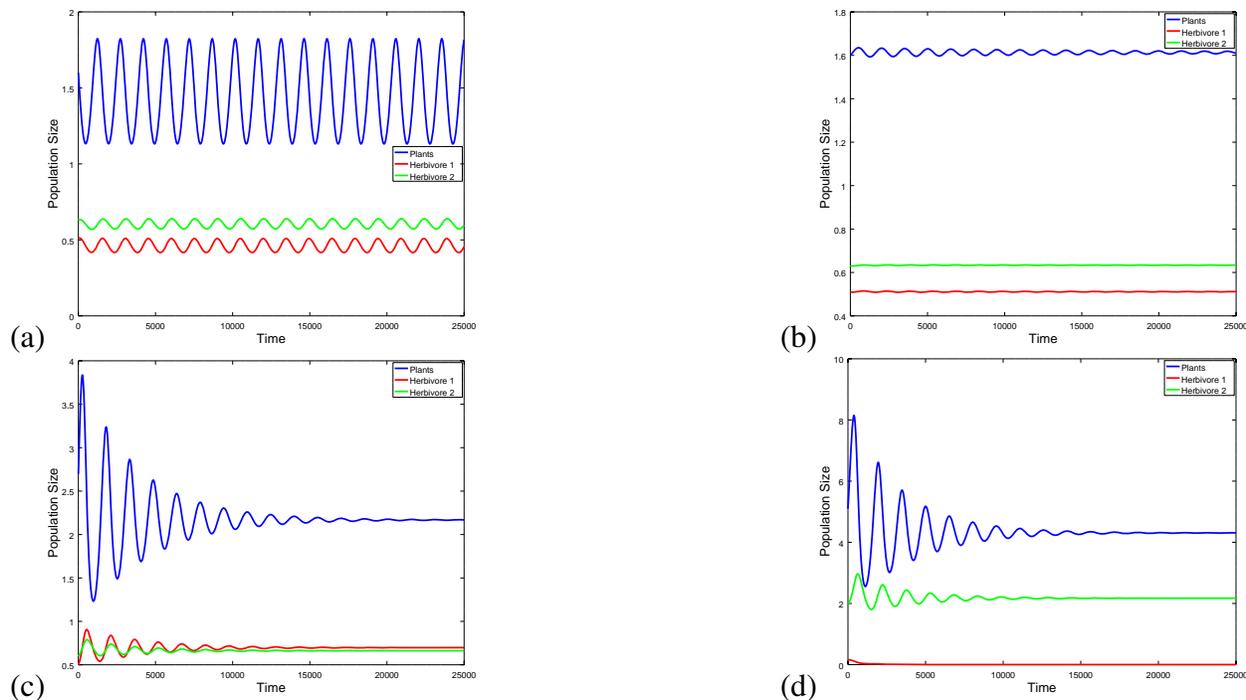


Figure 1. Integration of the model (4) when considering only intra-species competitions and Holling type II. With $k_1 = -0.0046$ in panel (a), $k_1 = -0.003$ in panel (b), $k_1 = 0$ in panel (c), and $k_1 = 0.003$ in panel (d). The plotted variable P is the calculated plant population divided by 10 and the time is expressed in days. The panel (a) solution is oscillatory and comes from a Hopf bifurcation. The panel (b) solution is asymptotically tending to a steady solution with synergistic interaction. In panels (c) and (d) both solutions tend asymptotically to a steady solution, but the graph on the panel (c) satisfies $k_1 = 0$, meaning that the effect of the interaction herbivore 2-herbivore 1-plant is additive and the graph on the panel (d) satisfies $k_1 > 0$, that is, the effect of the interaction is antagonistic. In addition, in the former all species coexist while in the latter the herbivore 1 goes to extinction (h_1 tends to zero)

two herbivores and the plant species coexist. For the coexistence branch, the solution is unstable from the starting point $k_1 = -0.008$ to $k_1 = -0.004596$ where there is a Hopf bifurcation point. The oscillatory solutions are stable for $k_1 < -0.004596$ and at that value of k_1 merge with the steady coexistence branch. Figure 1 left panel shows this oscillatory branch. Following the steady coexistence branch by increasing k_1 there is a branch point at $k_1 = 0.002407$ where the solution has $h_1 = 0$. Increasing k_1 further on this branch gives unstable solutions with negative h_1 and, therefore, the equilibrium solutions along the coexistence branch are not biologically meaningful. The horizontal steady solution branch with $h_1 = 0$ is unstable for $k_1 < 0.002407$ and stable for $k_1 > 0.002407$. There is a second value of k_1 where the two branches apparently cross but at that point the value of h_1 in the two branches is different.

4.3. Model (4) with intra- and inter-species competition with Holling type II

We consider the model (4) with Holling II type interactions between herbivores and plants and both inter- and intra-species competition between the herbivores. For the simulations of this model we use the following values for the competition parameters: $m_{11} = 0.00125$, $\beta_{12} = m_{11}/2$, $\beta_{21} = \beta_{12}$. The values of the remaining parameters are as given in Table 1. The results of some simulations

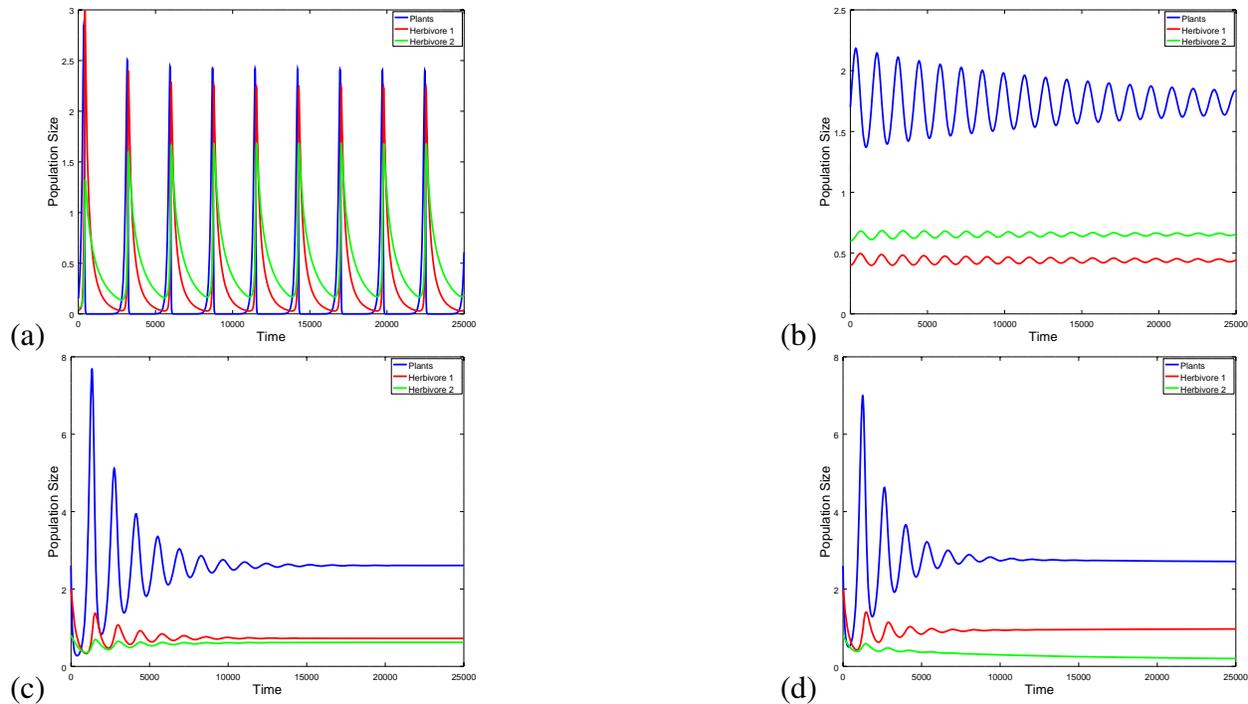


Figure 2. Simulations of the model (4) when considering intra- and inter-species competitions and Holling type II. With $k_1 = -0.0062$ panel (a), $k_1 = -0.0045$ panel (b), that is, the interaction effects are synergistic in both cases. Simulations for which the interaction effect is additive $k_1 = 0$ on panel (c), and for which the interaction effect is antagonistic $k_1 = 0.001$ on panel (d). The plotted variable P is the calculated plant population divided by 10 and the time scale is given in days. The graph in (a) gives the oscillatory coexistence solution near the Hopf bifurcation point. In (a) shows a solution that tends asymptotically to the coexistence steady solution. In panels (c) and (d) both solutions tend asymptotically to an equilibrium solution. The panel (c) depicts a coexistence solution and the panel (d) depicts a solution on which the herbivore 2 approaches extinction, that is, the solution approaches $h_2 = 0$

are presented in Figure 2 where the plant’s biomass and the number of herbivores is plotted against time.

The bifurcation plot in Figure 3(b) shows the results of varying k_1 from -0.008 to 0.006 . Table 5 summarizes these results. Two steady solution branches are plotted in the figure. The vertical variable corresponds to $P/10$ and the horizontal to k_1 . The horizontal branch is independent of k_1 and has $h_2 = 0$. The other branch is the steady branch of coexistence solutions. The parts of the branches that are stable are plotted using a dashed line and the unstable ones using a solid black line. The coexistence steady branch is unstable from $k_1 = -0.008$ to $k_1 = -0.006589$, where there is a Hopf bifurcation point and the steady coexistence branch turns stable. The oscillatory branch is stable for $k_1 < -0.006589$ and merger with the steady coexistence branch at the Hopf bifurcation point. For k_1 between -0.006589 and 0.001141 , the steady coexistence solution is stable and changes to unstable for $k_1 > 0.001141$, where the branch crosses with the horizontal branch satisfying $h_2 = 0$. After this value of k_1 , h_2 on the coexistence branch turns negative and thus it is non-physical. But the horizontal branch, which is unstable for $k_1 < 0.001141$, turns stable for larger values of k_1 . Note that there is an apparent branch point to the left of $k_1 = 0.001141$ but here the values of h_2 on both branches are not the same.

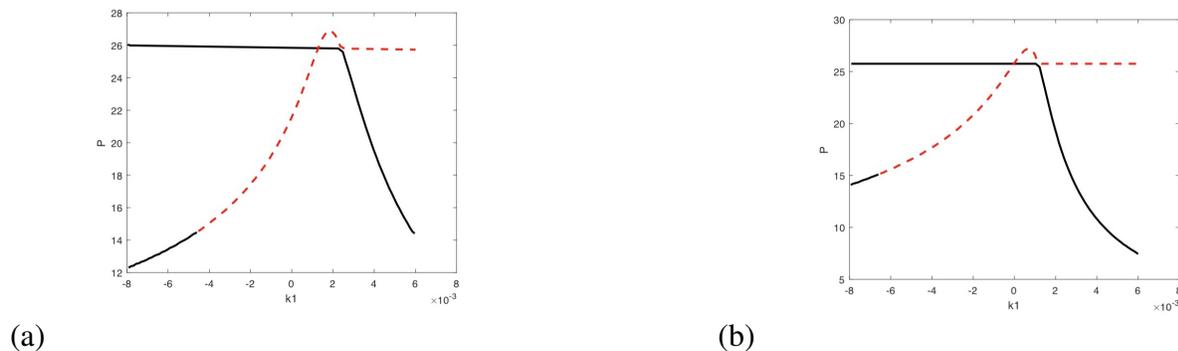


Figure 3. Bifurcation diagram with continuation on k_1 when considering model (4). The steady part of the branches is in dashed red line while the unstable is in solid black line. (a) Model including only intra-species competition. The horizontal branch corresponds to solutions with $h_1 = 0$ that are independent of k_1 . The other branch corresponds to coexistence solutions and at $k_1 = 0.002407$ it has a branching point with $h_1 = 0$ as well as a change of stability. Increasing k_1 on this branch beyond the branching point gives unstable solutions with negative h_1 . Furthermore, there is a Hopf bifurcation point at $k_1 = -0.004596$, also with a change of stability, stable solutions for values of $k_1 > -0.004596$ and unstable for $k_1 < -0.004596$. (b) Model including intra- and inter-species competition. There is a branching point at $k_1 = 0.001141$ where $h_2 = 0$. Increasing k_1 on this branch gives solutions with negative h_2 . There is Hopf bifurcation point at $k_1 = -0.006589$. Decreasing k_1 further gives unstable solutions. The horizontal branch corresponds to solutions with $h_2 = 0$ that are independent of k_1

Table 5. Summary of bifurcation study varying the coefficient measuring how the presence of herbivore 2 affects the preference of herbivore 1 for the plant, parameter k_1 . “SS” stands for steady-state branch while “OS” represents branch of oscillatory solutions. The symbols “u” and “s” indicates unstable and stable solutions, respectively

Case	$-0.008 < k_1 < 0.006$				
	$k_1 \in [-8, -4.596] * 10^{-3}$	$k_1 = -4.596 * 10^{-3}$	$k_1 \in (-4.596, 2.407) * 10^{-3}$	$k_1 = 2.407 * 10^{-3}$	$k_1 \in (2.407, 6] * 10^{-3}$
(4) Only intra-species competition	1 SS: $h_1, h_2, P > 0$; u 1 OS: $h_1, h_2, P > 0$; s 1 SS: $h_2, P > 0, h_1 = 0$; u	Hopf Bif. Point OS merges with SS	1 SS: $h_1, h_2, P > 0$; s 1 SS: $h_2, P > 0, h_1 = 0$; u	Branch point 1 SS: $h_1 = 0$	1 SS: $h_2, P > 0, h_1 < 0$; u 1 SS: $h_2, P > 0, h_1 = 0$; s
(4) Intra- and inter-species competition	$k_1 \in [-8, -6.589] * 10^{-3}$ 1 SS: $h_1, h_2, P > 0$; u 1 OS: $h_1, h_2, P > 0$; s 1 SS: $h_2, P > 0, h_1 = 0$; u	$k_1 = -6.589 * 10^{-3}$ Hopf Bif. Point OS merges with SS	$k_1 \in (-6.589, 1.141) * 10^{-3}$ 1 SS: $h_1, h_2, P > 0$; s 1 SS: $h_2, P > 0, h_1 = 0$; u	$k_1 = 1.141 * 10^{-3}$ Branch Point 1 SS: $h_2 = 0$	$k_1 \in (1.141, 6] * 10^{-3}$ 1 SS: $h_1, P > 0, h_2 < 0$; u 1 SS: $h_1, P > 0, h_2 = 0$; s

We also studied the effect of varying m_{11} , which is the intra-species competition coefficient for herbivore species 1, for fixed values of k_1 . The parameter m_{11} varies from 0 to 0.004. The values of the other competition parameters are $\beta_{12} = m_{11}/2$, $\beta_{21} = \beta_{12}$. The results for this continuation in terms of the coexistence solution branch are presented in Figure 4(a)–(b) and summarized in Table 6. First we took $k_1 = -0.001$ which corresponds to synergistic effects (see Figure 4(a)). In the interval $0 < m_{11} < 0.0004664$ there is a branch of unstable coexistence equilibrium solutions ($h_2, h_1, P > 0$). There is Hopf bifurcation point at $m_{11} = 0.0004664$ where there is an exchange of stability and a branch of limit cycles emanates. There one eigenvalue has negative real part and two eigenvalues have positive real part.

We also did another continuation in $0 < m_{11} < 0.004$ but now with $k_1 = 0$, which means that the interaction effects are additive. The results are presented in Figure 4(b) and the summary is in Table 6. In the range $0 < m_{11} < 0.00003206$ there is a non-physical branch of coexistence equilibrium solutions with $h_2 < 0$. The point $m_{11} = 0.00003206$ is a branch point. For $0 <$

$m_{11} < 0.00000832$ two of the eigenvalues have negative real part and one positive. At $m_{11} = 0.00000832$ there is a Hopf bifurcation point, where the two eigenvalues with negative real part start having positive real part. At the $m_{11} = 0.00003206$ branch point, the value of h_2 is zero and the coexistence branch intersects with a branch having only the h_1 herbivore. For $0.00003206 < m_{11} < 0.00021934$ the coexistence branch satisfies $h_2 > 0$ has two eigenvalues with positive real parts and one with negative real part. Thus, the branch is unstable although $h_2 > 0$. At $m_{11} = 0.00021934$ there is a second Hopf bifurcation point. There the three eigenvalues start having negative real parts and the coexistence branch is stable for, at least, until $m_{11} = 0.004$ where we stopped the calculation. Both branches emanating from the branch bifurcation point at $m_{11} = 0.00003206$ are very close together and in order to avoid superimposition only the coexistence branch is shown in the figure.

Finally, we did a third continuation in m_{11} , but now with $k_1 = 0.001$, which corresponds to antagonistic effects. The bifurcation diagram is given in Figure 4(c) and the summary of dynamics observed are presented in Table 6. For $0.00003206 < m_{11} < 0.0009527$ there is one branch of unstable non-physical coexistence equilibrium solutions with $h_2 < 0$. For $0.0009527 < m_{11} < 0.004$ there is one branch of locally asymptotically stable coexistence equilibrium solutions with $h_1, h_2, P > 0$. The point $m_{11} = 0.0009527$ is a branch bifurcation point. The second branch has $h_2 = 0$ and is stable for $m_{11} < 0.0009527$ and unstable for larger values of m_{11} . This branch corresponds to solutions with only one herbivore and was not followed for all the values of m_{11} given since we are interested in the coexistence of the three species. There is a Hopf bifurcation point on the second branch at $m_{11} = 0.0001367$.

Table 6. Summary of bifurcation study varying the intra-species competition associated with herbivore 1, parameter m_{11} for three distinct values of $k_1 : -0.01, 0, 0.01$. “SS” stands for steady-state branch while “OS” represents branch of oscillatory solutions. The symbols “u” and “s” indicates unstable and stable solutions, respectively. When not stated, the branch indicated corresponds to the coexistence solutions, that is, $h_1, h_2, P \neq 0$

$0 < m_{11} < 0.004, k_1 = -0.01$							
m_{11}	$(0, 4.664) * 10^{-4}$		$4.664 * 10^{-4}$			$(4.664, 40) * 10^{-4}$	
	1 SS: $h_1, h_2, P > 0; u$		Hopf Bif. Point			1 SS: $h_1, h_2, P > 0; s$	1 OS, u
$0 < m_{11} < 0.004, k_1 = 0$							
m_{11}	$(0, 8.32) * 10^{-6}$	$8.32 * 10^{-6}$	$(8.32, 32.06) * 10^{-6}$	$3.206 * 10^{-5}$	$(3.206, 21.934) * 10^{-5}$	$2.1934 * 10^{-4}$	$(2.1934, 40) * 10^{-4}$
	1 SS; u $h_2 < 0$ on 1 SS	Hopf Bif. Point	1 SS; u $h_2 < 0$ on 1 SS	Branch Point $h_2 = 0$ 1 SS	1 SS; u	Hopf Bif.	1 SS; s
$0 < m_{11} < 0.004, k_1 = 0.01$							
m_{11}	$(3.206, 13.67) * 10^{-5}$	$1.367 * 10^{-4}$	$(1.367, 9.527) * 10^{-4}$		$9.527 * 10^{-4}$		$(9.527, 40) * 10^{-4}$
	1 SS; u; $h_2 < 0$ 1 SS; s; $h_2 = 0$	1 SS; u; $h_2 < 0$ Hopf Bif. Point	1 SS; s; $h_2 < 0$ 1 SS; s; $h_2 = 0$		Branch Point		1 SS; s; $P, h_1, h_2 > 0$ 1 SS; u; $h_2 = 0$

5. Summary of results and discussion

In this paper we propose and discuss process-based mathematical models describing the dynamics of a plant under the influence of two distinct stressors (two herbivore species). The feedback interactions between the stressors is incorporated in the models via two parameters: k_1 and k_2 measuring herbivory behavior of a herbivore species in the presence of a different herbivore species.

Concerning dynamics of the model, our focus was mostly in characterizing the simplest temporal dynamics a system can exhibit: equilibrium points and, in particular, we characterize conditions for linearized stability of the equilibrium solutions where all three species coexist - coexistence or

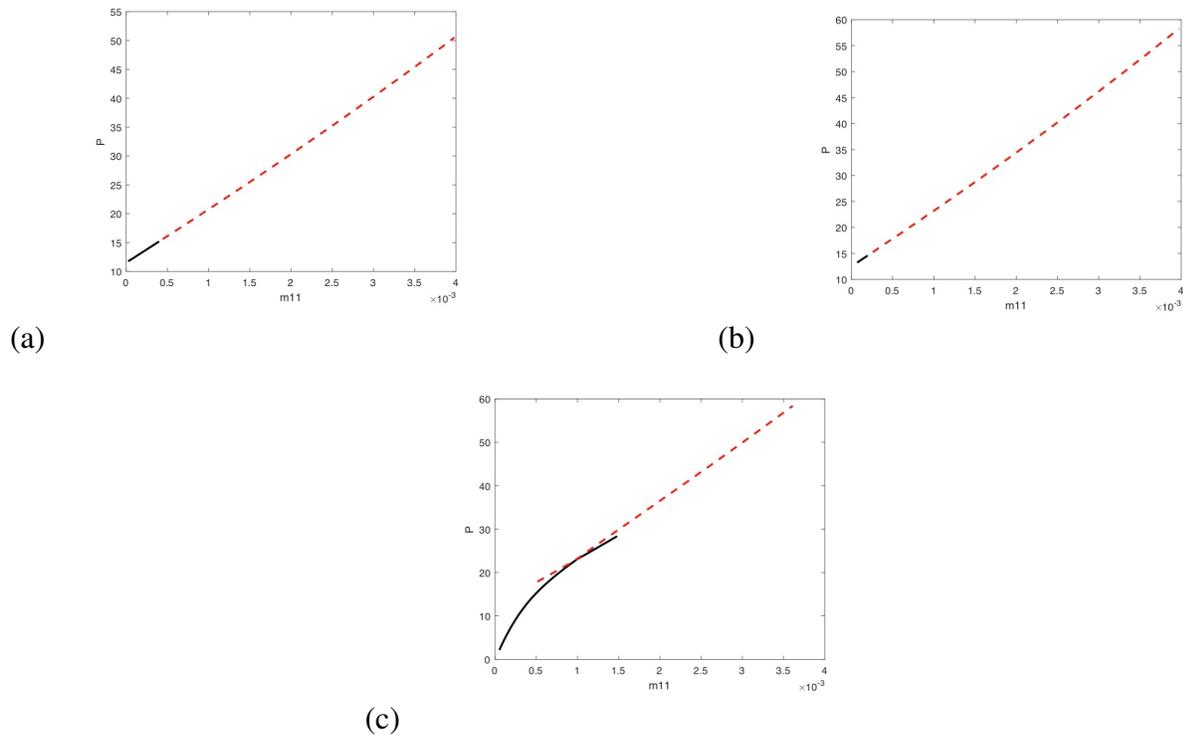


Figure 4. Bifurcation diagram of the coexistence branch for model (4) with continuation on m_{11} . The vertical axis is P and the dashed red line part of the branches represents stable solutions while the solid black line denotes unstable solutions. (a) $k_1 = -0.001$. The figure only shows the coexistence branch. There is Hopf bifurcation point at $m_{11} = 0.0004664$, where there is an exchange of stability, with two of the eigenvalues now having a positive real part. (b) $k_1 = 0$. There is Hopf bifurcation point at $m_{11} = 0.0000832$, a branch point at $m_{11} = 0.00003206$ where $h_2 = 0$ and a second Hopf bifurcation point at $m_{11} = 0.00021934$. (c) $k_1 = 0.001$. The coexistence branch and a branch with $h_2 = 0$ are plotted. There is a branching point at $m_{11} = .0009527$ where the coexistence branch goes through $h_2 = 0$. Decreasing in m_{11} from this branching point we obtain unstable solutions with h_2 negative on the coexistence branch and the solutions on the second branch are stable. The coexistence branch is stable for $m_{11} > 0.0009527$ while the branch with $h_2 = 0$ is unstable

interior equilibrium points. This is one important case since the system is sustainable supporting simultaneously plants and both species of herbivores. We did not give an exhaustive theoretical analysis of the temporal dynamics of the models, which may be challenging due to their nonlinear structure. But our numerical results and bifurcation study demonstrate that periodic solutions via Hopf bifurcations can arise in the system when changes in the stability of equilibrium points occur.

Our theoretical analysis of the model without competition and no Holling type II functional response (model (3)) shows that the number of the equilibrium states and the conditions for their local stability depend on the type of interactions between the stressors, represented in the model by the parameter k_1, k_2 . That is, the dynamics of the model depend on the herbivory behavior of a herbivore species in the presence of other herbivore species.

When considering the boundary steady-state solution with the plant and only herbivore 1 present, the stability analysis reveal that the conditions for its stability depends on the sign of the coefficient k_2 , which indicates weather the preference of herbivore 2 for the plant in the presence of herbivore 1

is not influenced (additive type: $k = 0$), is synergetic ($k_2 < 0$) or is antagonistic ($k_2 > 0$). Likewise, the stability of the boundary steady-state solution with only herbivore 2 depends on the sign of the coefficient k_1 . Additionally, our study reveals that periodic solutions via Hopf bifurcation through either the trivial equilibrium or boundary equilibrium points cannot occur in the system.

Concerning coexistence equilibrium points, when the interaction among the herbivores (stressors) is additive they cannot occur in the system. When one of the two herbivores feeds on the plant as it was the only herbivore in the system, that is, either $k_1 \neq 0, k_2 = 0$ or $k_1 = 0, k_2 \neq 0$, there is a unique coexistence equilibrium solution. However, the local asymptotically stability conditions on the set of admissible parameters depends on how the feeding behavior of the other herbivore is affected by the presence of the first herbivore. For example, if $k_1 = 0$, then the stability of the coexistence equilibrium changes as the value of k_2 changes from negative (herbivore 2 is synergistically affected by herbivore 1), to zero (interaction is additive), to positive (herbivory on the plant by herbivore 2 experience an antagonistic effect in the presence of herbivores of the other species). On the other hand, when the interaction among herbivores is not two-ways additive (that is, both $k_1 \neq 0$ and $k_2 \neq 0$), the number of coexistence equilibrium states range from zero to one to three. The number of equilibrium states depends on the type of interaction among stressors as well as on additional restriction involving the remaining parameters of the model. It is interesting to note that, within the last scenario, the antagonistic case (k_1 and k_2 simultaneously positive) leads to a higher number of possible coexistence equilibrium states than the other other cases. Namely, in the former case there exists either a unique equilibrium or three equilibrium states while in the latter cases the system may support zero, or one, or two equilibrium solutions. Our stability analysis show that the coexistence equilibrium points, when both k_1, k_2 are simultaneously nonzero, exhibit local asymptotically stability in certain regions of the admissible values of the parameters. Therefore, multi-stability can occur in the system. Since the expressions resulting from calculations were very long, in this study we did not verify if the conditions for existence and stability associated to each coexistence equilibrium state could be simultaneously satisfied for some region of parameters. This will be consider as a future work.

Our finding, when $k_1 = 0 = k_2$ (two-way additive interactions), show that there is no coexistence equilibrium points, which conforms with the known results for the standard consumer-resource model (e.g., Feng et al (2009)). In our novel model the interactions among the herbivores can be chosen to be different from zero and we observe that this leads to the existence of locally asymptotically stable coexistence equilibrium points when the other parameters of the model satisfy certain relations. Thus, our model indicates that introducing terms modeling the feedback interactions between the herbivory behavior of each herbivore (interactions between stressors) changes the traditional consumer-resource dynamics. Similar result was obtained numerically for our model that includes Holling type II functional response but no competition (model (4), with $m_{11} = 0 = m_{22}$, and $\beta_{12} = 0 = \beta_{21}$). However, our numerical simulations using the parameter values found in the literature, show that these equilibrium states are unstable, that is, the instability is a result of the parameters chosen.

When considering model with Holling type functional response and competition, most of the results obtained were obtained numerically because of the complexity of the formulas for the equilib-

rium points and for the corresponding eigenvalues of the linearized system about these points. We did not investigate all possible cases due to the number of parameters involved in models. These parameters have a large variability due to different species, intra-species differences and variations in environmental conditions. There is also variability due to the way the parameters are determined which, of course, includes measurement errors. We could only find a few bibliographic reference for their values. Hence, we concentrated on a few scenarios using the parameter values found in the literature Feng et al (2009), Feng et al. (2011) and assumed the parameters are in viable intervals.

For these parameter values, our simulations show that the differential equations of the model with no inter- and intra-species competition have coexistence equilibrium points but they are unstable. The results also show that, for the parameter values used, adding intra-species competition stabilizes those equilibrium points but the competition term cannot be very small. The same is true with both inter- and intra-species competition. From the bifurcation diagrams we found Hopf bifurcations and periodic solutions. We also found ranges of the herbivore intra-competition coefficient and the coefficient measuring the stressors interaction effect for which the coexistence equilibrium points are local asymptotically stable.

For intra-species competition only and for the parameter values explored, when the effect is antagonistic, one herbivore species goes extinct. But all species survive for the additive and synergistic effects.

When all species co-exist, the highest plant biomass occurs when the effect is additive. That is, additive interactions lead to sustainability of the three species and higher plant biomass. However, the antagonistic effect leads to higher biomass when one of the herbivores go extinct (see Figure 1). If we add inter-species competition, for the parameter values used, the results show that for the synergistic and additive effects all three species survive and one herbivore goes extinct for the antagonistic effect. Interactions of synergistic type induce the lowest plant biomass equilibrium state and the antagonistic effects lead to the largest amount of plant biomass but with only one herbivore surviving (see Figure 2). These results are in agreement with the theoretical evidence (e.g., Côté et al. (2016) and references therein). We point out that the antagonistic interactions resulting in one herbivore going extinct (Figures 1 and 2) is a result of numerical values chosen, as we can see from Figure 4(c) and Table 6.

From the simulations presented (Figures 1 and 2), it appears that herbivore 2 is the better competitor (higher number of individual of species 2 in the system) except when the effects are additive. However, with the exception of the additive case listed above, we observe from Figures 1 and 2 that the better competitor in the first case, that is, when there is only intra-species competition, remains the better competitor as k increases. Meanwhile, there is a change in the dominant competitor in the second case, i.e, when there is both types of competition. Due to the symmetry of the model, similar results are obtained if k_2 is the parameter varied but with role of herbivores reversed. That is an interesting difference but it can be a result of the parameter values used in the simulations. Further investigations are needed to assist determining how general is this result.

6. Conclusions

In this paper we propose and discuss new process-based mathematical models describing the dynamics of a plant under the influence of two distinct stressors (two herbivore species). The herbivores feeding on the plant may experience intra-species, or inter-species, or both. The new process included in the model framework is the preference of a herbivore for the plant is influenced, either positively or negatively, by the presence of a second herbivore. This model feature is materialized by including a functional modeling the simultaneous interactions among the three species: plant and the two distinct herbivores. The feedback interactions between stressors can be of additive, synergistic and antagonistic type and they are not fixed *a priori*. Instead they are introduced in the models as a parameter that can be tuned to obtain the desired type.

Thus, the models can be tools for either investigating “if-then” scenarios where distinct values of the interaction coefficients are chosen or for identifying the type of interaction in specific ecosystems when data is available. Therefore, the mathematical framework can increase the understanding of the interactions between two distinct herbivores and their impact on the dynamics of plants. It can be employed by scientists and resource managers, in real ecosystems that satisfy the models’ assumptions, to obtain insights into the best management strategies to be implemented.

For example, the model with only intra-herbivore species competition of Holling type II can be used when there is one above and one under ground herbivore species (Kutyniok and Muller (2012)), or when one of the herbivore species is a mammal and the other an insect (Ritchie and Olff (1999)). On the other hand, the model incorporating intra- and inter-species competition with Holling type II can be applied, for example, when there are two rodent herbivore species feeding on the same plant species (Latorre et al. (2013)).

To the best of our knowledge, there is no data available for two interacting herbivores stressors acting on one plant species. So we did not focus on specific ecological examples. We introduce the framework and characterize the simplest temporal dynamics of the mathematical process-based models. Our main interest in this study is the case when the three species (two herbivores and plant) coexist, i.e, when the system is sustainable.

Our theoretical analysis of the model without competition and no Holling type II functional response shows that the dynamics of the model depend on the type (synergetic, additive, or antagonistic) of feedback interactions between herbivory behavior of the two distinct herbivore species. Our finding conforms with the known results for the standard consumer-resource model. For that model there is no coexistence equilibrium (e.g., Feng et al (2009)). However, in our novel model with distinct interactions among the herbivores (stressors) we observe that there exists coexistence equilibrium points. Thus, predicting that the feedback interactions between the herbivory behavior of each herbivore changes the traditional consumer-resource dynamics.

The analysis show that multi-stability may occur in the system but we did not investigate if the conditions for existence and stability, associated to each coexistence equilibrium state, are compatible. This will be addressed in future work. However, our numerical simulations using the parameter

values found in the literature, show that these equilibrium states are unstable. Similar result was obtained numerically for the model that includes Holling type II functional response but no competition. We hope this work motivates more studies to determine if stability of interior steady states and multi-stability is only a mathematical result or an ecological reality.

For the parameter values used, the numerical results show that adding intra-species competition promotes sustainability of the system (stabilizes the coexistence equilibrium points) but the competition term cannot be very small. The same is true when introduce both inter- and intra-species competition. Furthermore, the simulations show that, as long as at least one type of competition is present, the synergistic and additive effects lead to the survival of all three species while one herbivore goes extinct for the antagonistic effect. The numerical findings also show that interactions of synergistic type induce the lowest plant biomass equilibrium state and the antagonistic effects lead to the largest amount of plant biomass but with only one herbivore surviving. When the system is sustainable, the highest biomass is achieved when the interaction is additive. These results do not contradict the theoretical evidence (e.g., Côté et al. (2016) and references therein). However, our bifurcation study indicates that the antagonistic interactions resulting in one herbivore going extinct is a result of numerical values chosen.

We do not give a thorough theoretical analysis of the temporal dynamics of the models, which may be challenging due to their nonlinear structure. But our numerical results show that periodic solutions via Hopf bifurcations can arise when coexistence equilibrium points destabilize. It is sometimes argued that cyclic behavior provides less "stable" coexistence since perturbations to cycles that bring a population to low levels may cause the population to go extinct. Nonetheless it may be important to establish coexistence of the species with other dynamics and it will be a goal of future work.

The review by Côté et al. (2016) emphasizes the need of more experimental studies, use of meta-analysis and process-based mathematical models to increase the understanding in the field of multi-stressors interactions in ecological systems. In this work we build novel process-based mathematical models that may be used to increase the understanding in the field. We hope this paper will encourage research, both theoretical and experimental, on the effects of interactions among multiple stressors on ecological systems.

Acknowledgment:

The authors thanks the referees for useful comments that assist improving this paper.

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Appendices

A. Proof of Result 1: Existence of equilibrium solutions of model (3)

The equilibrium solutions of the model (3) in the main text are found by solving simultaneously the following system:

$$\begin{aligned} rP(1 - P/K) - (d_1 - k_1h_2)h_1P - (d_2 - k_2h_1)h_2P &= 0; \\ \beta_1(d_1 - k_1h_2)h_1P - m_1h_1 &= 0; \\ \beta_2(d_2 - k_2h_1)h_2P - m_2h_2 &= 0. \end{aligned} \tag{A.1}$$

We recall that the parameters of the model are all positive real numbers except the parameters k_1, k_2 that are real numbers. This is sometimes referred in this paper as the set of *admissible parameters*.

A.1. Existence of trivial and boundary equilibrium states

Straightforward calculations lead to the following trivial and boundary equilibrium solutions:

- (1) Trivial equilibrium $E^0 = (0, 0, 0)$;
- (2) Boundary equilibrium $E^P = (K, 0, 0)$;
- (3) Boundary equilibrium $E^{h_1} = (P, h_1, 0)$ with $h_1 = r \frac{\beta_1 d_1 K - m_1}{\beta_1 d_1^2 K}$, $P = \frac{m_1}{\beta_1 d_1}$;
- (4) Boundary equilibrium $E^{h_2} = (P, 0, h_2)$ with $h_2 = r \frac{\beta_2 d_2 K - m_2}{\beta_2 d_2^2 K}$, $P = \frac{m_2}{\beta_2 d_2}$.

Observe that the equilibrium solutions need to be positive so to have physical meaning. Thus, E^{h_1} and E^{h_2} have biological meaning if the following conditions hold:

$$K\beta_1 d_1 - m_1 > 0, \tag{A.2}$$

$$K\beta_2 d_2 - m_2 > 0. \tag{A.3}$$

Hence, (A.2) and (A.3) are the conditions for existence of steady state solutions of E^{h_1} and E^{h_2} , respectively.

A.2. Existence of interior (coexistence) equilibrium states

We look for additional positive equilibrium states of the system (3) for which all three species are present - *interior equilibrium states* or *coexistence equilibrium states*. To com-

pute the coexistence equilibrium states we solve simultaneously three equations that remain after solving for trivial and boundary equilibrium states for the model (3). Thus, these three equations satisfy $h_1 \neq 0$, $h_2 \neq 0$, $P \neq 0$.

We proceed with proof by dividing it into four cases: Case I, when $k_1, k_2 = 0$, Case II, when $k_1 = 0, k_2 \neq 0$, Case III, when $k_1 \neq 0, k_2 = 0$, and Case IV, when $k_1, k_2 \neq 0$.

A.2.1. Case I: $k_1, k_2 = 0$

For this values of parameters, the coexistence equilibrium states of (A.1) are found by solving the following system

$$\begin{aligned} r(1 - P/K) - d_1h_1 - d_2h_2 &= 0; \\ \beta_1d_1P - m_1 &= 0; \\ \beta_2d_2P - m_2 &= 0. \end{aligned} \tag{A.4}$$

From the last two equations of (A.4) it follows that $P = \frac{m_1}{\beta_1d_1} = \frac{m_2}{\beta_2d_2}$, which implies that herbivore 1 is the same as herbivore 2, that is, there is only one herbivore in the system. This is a contradiction with the initial assumption of having two distinct predators. Thus, there are no interior equilibrium states when $k_1 = 0 = k_2$.

A.2.2. Case II: $k_1 = 0, k_2 \neq 0$

The system (A.1), when $P, h_1, h_2 \neq 0$ and $k_1 = 0$, reduces to

$$\begin{aligned} r(1 - P/K) - d_1h_1 - (d_2 - k_2h_1)h_2 &= 0; \\ \beta_1d_1P - m_1 &= 0; \\ \beta_2(d_2 - k_2h_1)P - m_2 &= 0. \end{aligned} \tag{A.5}$$

Solving this systems leads to a unique equilibrium point with coordinates:

$$P = \frac{m_1}{\beta_1d_1}; \tag{A.6}$$

$$h_1 = \frac{\beta_2d_2m_1 - \beta_1d_1m_2}{\beta_2k_2m_1}; \tag{A.7}$$

$$h_2 = \frac{rk_2\beta_2m_1(K\beta_1d_1 - m_1) + K\beta_1d_1^2(\beta_1d_1m_2 - \beta_2d_2m_1)}{K\beta_1^2d_1^2k_2m_2}. \tag{A.8}$$

Conditions for existence. Since h_1, h_2, P are physical quantities they must have positive values. The study of the conditions on parameters that satisfy such restrictions is divided into two cases: Case II.a, when $k_2 > 0$ and Case II.b, when $k_2 < 0$.

Case II.a: $k_1 = 0, k_2 > 0$. From (A.7) it follows that $h_1 > 0$ if

$$\beta_2 d_2 m_1 - \beta_1 d_1 m_2 > 0. \tag{A.9}$$

Straightforward calculations show that in order to guarantee that the right hand-side of (A.8) is greater than zero (that is, $h_2 > 0$) the following condition

$$0 < m_1 < K\beta_1 d_1 - T_1, \quad T_1 = \frac{K\beta_1 d_1^2}{rk_2\beta_2 m_1} (\beta_2 d_2 m_1 - \beta_1 d_1 m_2) > 0 \tag{A.10}$$

must hold.

Observe that $T_1 > 0$ since all parameter values are positive and condition (A.9) holds. The first inequality in (A.10) implies that $K\beta_1 d_1 - T_1 > 0$. Manipulation of this inequality yields

$$\beta_2 d_2 m_1 - \beta_1 d_1 m_2 < \frac{rk_2\beta_2 m_1}{d_1} > 0. \tag{A.11}$$

Condition $m_1 < K\beta_1 d_1 - T_1$ can be re-written as

$$\beta_2 d_2 m_1 - \beta_1 d_1 m_2 < \frac{rk_2\beta_2 m_1}{d_1} \left(1 - \frac{m_1}{K\beta_1 d_1}\right) > 0, \tag{A.12}$$

with the last inequality following from the fact that that $K\beta_1 d_1 - m_1 > 0$. Combining conditions (A.9), (A.11) and (A.12), the unique interior equilibrium exists if

$$0 < \beta_2 d_2 m_1 - \beta_1 d_1 m_2 < \frac{rk_2\beta_2 m_1}{d_1} \left(1 - \frac{m_1}{K\beta_1 d_1}\right) \quad \text{and} \quad K\beta_1 d_1 - m_1 > 0. \tag{A.13}$$

Case II.b: $k_1 = 0, k_2 < 0$. From (A.7) it follows that, when $k_2 < 0, h_1 > 0$ if

$$\beta_2 d_2 m_1 - \beta_1 d_1 m_2 < 0. \tag{A.14}$$

Observe that, in the expression for h_2 in (A.8), the denominator is negative because $k_2 < 0$ and all other parameters are positive. Additionally, the second term in the numerator is positive by (A.14). Thus, in order for h_2 to be positive the following condition must hold:

$$K\beta_1 d_1 - m_1 > 0. \tag{A.15}$$

Additionally, the numerator of (A.8) has to be negative, which leads to the condition:

$$K\beta_1 d_1 - T_1 > m_1 > 0 \tag{A.16}$$

that implies $K\beta_1 d_1 - T_1 > 0$. Manipulation of the latter inequality yields:

$$\beta_2 d_2 m_1 - \beta_1 d_1 m_2 > \frac{rk_2\beta_2 m_1}{d_1} < 0. \tag{A.17}$$

Similarly to the Case II.a, the first inequality in (A.16) can be re-arranged to yield:

$$\beta_2 d_2 m_1 - \beta_1 d_1 m_2 > \frac{rk_2\beta_2 m_1}{d_1} \left(1 - \frac{m_1}{K\beta_1 d_1}\right) < 0, \tag{A.18}$$

where the last inequality follows from the fact that $k_2 < 0$ and (A.15) holds true. The conditions (A.14), (A.15), (A.17), and (A.18) reduces to the following equivalent restriction on the parameters

$$\frac{rk_2\beta_2m_1}{d_1} \left(1 - \frac{m_1}{K\beta_1d_1}\right) < \beta_2d_2m_1 - \beta_1d_1m_2 < 0 \quad \text{and} \quad K\beta_1d_1 - m_1 > 0, \quad (\text{A.19})$$

which is the condition for the existence of the unique interior equilibrium when $k_1 = 0$, $k_2 < 0$.

A.2.3. Case III: $k_1 \neq 0$, $k_2 = 0$.

Due to the symmetric nature of the system with respect to permutation of h_1, h_2 , it follows that the model (3), for these set of parameters, has a unique equilibrium solution satisfying:

$$P = \frac{m_2}{\beta_2d_2}; \quad (\text{A.20})$$

$$h_1 = \frac{rk_1\beta_1m_2(K\beta_2d_2 - m_2) - K\beta_2d_2^2(\beta_1d_1m_2 - \beta_2d_2m_1)}{K\beta_2^2d_2^2k_1m_1}; \quad (\text{A.21})$$

$$h_2 = \frac{\beta_1d_1m_2 - \beta_2d_2m_1}{\beta_1k_1m_2}. \quad (\text{A.22})$$

Conditions for existence. Using arguments and calculations similar to the ones presented in Section A.2.2 the conditions for existence of this unique coexistence equilibrium state are as follow:

Case III.a: $k_1 > 0$, $k_2 = 0$.

$$0 < \beta_1d_1m_2 - \beta_2d_2m_1 < \frac{rk_1\beta_1m_2}{d_2} \left(1 - \frac{m_2}{K\beta_2d_2}\right) \quad \text{and} \quad K\beta_2d_2 - m_2 > 0. \quad (\text{A.23})$$

Case III.b: $K_1 < 0$, $k_2 = 0$.

$$\frac{rk_1\beta_1m_2}{d_2} \left(1 - \frac{m_2}{K\beta_2d_2}\right) < \beta_1d_1m_2 - \beta_2d_2m_1 < 0 \quad \text{and} \quad K\beta_2d_2 - m_2 > 0. \quad (\text{A.24})$$

A.2.4. Case IV: $k_1, k_2 \neq 0$

The interior equilibrium states of the system satisfy the following cubic equation:

$$F(P) = a_3P^3 + a_2P^2 + a_1P + a_0 = 0, \quad (\text{A.25})$$

where

$$a_3 = \frac{r}{K} > 0, \quad a_2 = -r < 0,$$

$$a_1 = \frac{d_1 m_2}{\beta_2 k_1} + \frac{d_2 m_1}{\beta_1 k_2}, \quad a_0 = -\frac{m_1 m_2}{\beta_1 \beta_2 k_1 k_2} (k_1 + k_2),$$

and

$$\Delta = q^2 + p^3, \quad p = -\frac{1}{27} + \frac{A_1}{6} - \frac{A_2}{2}, \quad q = \frac{3A_1 - 1}{9},$$

$$A_1 = \frac{\beta_2 d_2 m_1 k_1 + \beta_1 d_1 k_2 m_2}{r K \beta_1 \beta_2 k_1 k_2}, \quad A_2 = \frac{m_1 m_2 (k_1 + k_2)}{r K^2 \beta_1 \beta_2 k_1 k_2}.$$

Based on the cubic equation (A.25) (sign of Δ) the following three situations are possible:

- (1) If $\Delta > 0$ there are a real and two complex coexistence equilibrium states,
- (2) If $\Delta < 0$ there are three real coexistence equilibrium states,
- (3) If $\Delta = 0$ there are one real or two real multiple coexistence equilibrium states.

We next combine this information with the application of Descartes' rule of signs to determine the number of positive real equilibrium states. These are the ones that have biological meaning. Observe that if $k_1, k_2 < 0$ then $a_1 < 0$ and $a_0 > 0$ (Case IV.a) while if $k_1, k_2 > 0$ we have $a_1 > 0$ and $a_0 < 0$ (Case IV.b). If the signs of k_1 and k_2 are different, then we have two additional cases: $a_1, a_0 < 0$ (Case IV.c) or $a_1, a_0 > 0$ (Case IV.d). Therefore, the Descartes' rule of signs has to be applied to these four cases separately to prove the results. We first consider the case $k_1, k_2 > 0$ and the analysis is given in Tables 7. Similar arguments yields the results for the remaining cases and the summary is given in Table 8.

Table 7. Number of positive real roots of the cubic equation $F(P)$ when $k_1, k_2 > 0$ (Case IV.b)

Cases	a_3	a_2	a_1	a_0	Δ	Number of sign changes in $F(P)$	Number of sign changes in $F(-P)$	Number of positive real roots (steady-state equilibrium)
1	+	-	+	-	> 0	3	0	1
2	+	-	+	-	< 0	3	0	3
3	+	-	+	-	$= 0$	3	0	2 (1 simple; 1 multiple)

This concludes the proof of Result 1, part existence of equilibrium solutions given in the main text.

Table 8. Summary of the number of positive real roots of the cubic equation $F(P)$, which is the number of coexistence equilibrium states

Condition on k_1, k_2	Δ Case	$\Delta > 0$	$\Delta < 0$	$\Delta = 0$
$k_1, k_2 > 0$	Case IV.a	1	3	1 simple
$k_1, k_2 < 0$	Case IV.b	0	2	1 multiple
$sign(k_1) \neq sign(k_2)$	Case IV.c	1	1	1
	Case IV.d	0	2	1 multiple

B. Linearized stability of the equilibrium states

The Jacobian matrix associated with the model (3) is:

$$J = \begin{pmatrix} (1 - \frac{P}{K})r - \frac{Pr}{K} + h_2(h_1k_2 - d_2) - h_1(d_1 - h_2k_1) & Ph_2k_2 - P(d_1 - h_2k_1) & P(h_1k_2 - d_2) + Ph_1k_1 \\ \beta_1h_1(d_1 - h_2k_1) & P\beta_1(d_1 - h_2k_1) - m_1 & -P\beta_1h_1k_1 \\ \beta_2h_2(d_2 - h_1k_2) & -P\beta_2h_2k_2 & P\beta_2(d_2 - h_1k_2) - m_2 \end{pmatrix} \tag{B.1}$$

B.1. Local stability of the trivial equilibrium $E^0 = (0, 0, 0)$

The Jacobian matrix evaluated at E^0 is

$$J_0 = \begin{pmatrix} r & 0 & 0 \\ 0 & -m_1 & 0 \\ 0 & 0 & -m_2 \end{pmatrix} \tag{B.2}$$

and the eigenvalues can be read-off the diagonal: $r > 0, -m_1, m_2$. Since one of the eigenvalues is positive the equilibrium E^0 is unstable.

B.2. Local stability of boundary equilibrium states: E^P, E^{h_1}, E^{h_2}

We next study the stability of the trivial and boundary equilibrium states by evaluating J at each equilibrium and computing the associated eigenvalues.

B.2.1. Stability of $E^P = (K, 0, 0)$

The Jacobian and eigenvalues associated with equilibrium state E^P can be calculated as in Section B.1 yield the eigenvalues:

$$-r, \quad K\beta_2d_2 - m_2, \quad K\beta_1d_1 - m_1.$$

Thus, the equilibrium state E^P is locally asymptotically stable (l.a.s.) if

$$K\beta_2d_2 - m_2 < 0 \quad \text{and} \quad K\beta_1d_1 - m_1 < 0.$$

This results indicates that if the herbivore death rates are sufficiently small the herbivores can establish themselves in the system.

B.2.2. *Stability of $E^{h_1} = (P, h_1, 0)$*

Evaluate J at this state yields

$$J_1 = \begin{pmatrix} \left(1 - \frac{m_1}{K\beta_1 d_1}\right)r - \frac{m_1 r}{K\beta_1 d_1} - \frac{(K\beta_1 d_1 - m_1)r}{K\beta_1 d_1} - \frac{m_1}{\beta_1} \frac{m_1 \left(\frac{k_2(K\beta_1 d_1 - m_1)r - d_2}{K\beta_1 d_1^2} + \frac{k_1(K\beta_1 d_1 - m_1)m_1 r}{K\beta_1^2 d_1^3}\right)}{\beta_1 d_1} & 0 & -\frac{k_1(K\beta_1 d_1 - m_1)m_1 r}{K\beta_1 d_1^3} \\ \frac{(K\beta_1 d_1 - m_1)r}{K\beta_1 d_1} & 0 & \frac{\beta_2 m_1 \left(d_2 - \frac{k_2(K\beta_1 d_1 - m_1)r}{K\beta_1 d_1^2}\right)}{\beta_1 d_1} - m_2 \\ 0 & 0 & 0 \end{pmatrix}.$$

The eigenvalues of J_1 are

$$\lambda_1 = \frac{1}{K\beta_1^2 d_1^3} [rm_1\beta_2 k_2(m_1 - K\beta_1 d_1) + K\beta_1 d_1^2(\beta_2 d_2 m_1 - \beta_1 d_1 m_2)] \tag{B.3}$$

and λ_2, λ_3 that are the roots of the characteristic equation of the 2×2 matrix J_2 formed by eliminated the third row and third column of J_1 . This equations reads:

$$P(\lambda) = \lambda^2 - tr J_2 + \det J_2 = \lambda^2 + \frac{m_1 r}{K\beta_1 d_1} \lambda + \frac{m_1 r}{K\beta_1 d_1} (K\beta_1 d_1 - m_1) = 0$$

Observe that $tr J_2 = \lambda_2 + \lambda_3 = -\frac{m_1 r}{K\beta_1 d_1} < 0$ since all parameters are positive. Also $\det J_2 = \lambda_2 \lambda_3 = \frac{m_1 r}{K\beta_1 d_1} (K\beta_1 d_1 - m_1) > 0$ whenever E^{h_1} exists (see (A.2)). Thus, λ_2, λ_3 are negative real numbers whenever the equilibrium solution exists and the stability of E^{h_1} is determined by the sign of λ_1 .

Next we determine the conditions for $\lambda_1 < 0$ by dividing the study into three cases: Case 1 with $k_2 = 0$ and $k_1 \in \mathbf{R}$; Case 2 with $k_2 > 0, k_1 \in \mathbf{R}$; and Case 3 with $k_2 < 0, k_1 \in \mathbf{R}$.

Case 1: $k_1 \in \mathbf{R}, k_2 = 0$. Observe that λ_1 only depends on k_2 . Thus, when this parameter is zero, (B.3) reduces to

$$\lambda_1 = \frac{1}{\beta_1 d_1} (\beta_2 d_2 m_1 - \beta_1 d_1 m_2).$$

It is easy to check that $\lambda_1 < 0$ if

$$0 < m_1 < \frac{\beta_1 d_1 m_2}{\beta_2 d_2}. \tag{B.4}$$

Observe that the equilibrium exists if (A.2) is satisfied, which is equivalent to

$$0 < m_1 < K\beta_1 d_1. \tag{B.5}$$

Combing conditions (B.4) and (B.5) yields that E^{h_1} is l.a.s if

$$0 < m_1 < \min \left\{ K\beta_1 d_1, \frac{\beta_1 d_1 m_2}{\beta_2 d_2} \right\}.$$

Case 2: $k_1 \in \mathbf{R}, k_2 > 0$. In this case, it follow from (B.3) that $\lambda_1 < 0$ if

$$rm_1\beta_2k_2(m_1 - K\beta_1d_1) + K\beta_1d_1^2(\beta_2d_2m_1 - \beta_1d_1m_2) < 0. \quad (\text{B.6})$$

Mathematical manipulations of this inequality yields:

$$K\beta_1d_1 - m_1 > \frac{K\beta_1d_1^2}{rm_1\beta_2k_2}(\beta_2d_2m_1 - \beta_1d_1m_2) = S_1. \quad (\text{B.7})$$

Thus combining condition (B.5) (condition for existence of E^{h_1}) and (B.7), the equilibrium state E^{h_1} is l.a.s. if

$$K\beta_1d_1 - m_1 > \max\{0, S_1\}.$$

Case 3: $k_1 \in \mathbf{R}, k_2 < 0$. As in Case 3, $\lambda_1 < 0$ if (B.6) holds true. Since $k_2 < 0$ this condition reduces to

$$K\beta_1d_1 - m_1 < \frac{K\beta_1d_1^2}{rm_1\beta_2k_2}(\beta_2d_2m_1 - \beta_1d_1m_2) = S_1. \quad (\text{B.8})$$

Observe that $K\beta_1d_1 - m_1 > 0$ (inequality (B.5)) is required for existence of the equilibrium E^{h_1} . So $S_1 > 0$ must hold true. Since $k_2 < 0$ and all other parameters in S_1 are positive we have that $S_1 > 0$ if

$$\beta_2d_2m_1 - \beta_1d_1m_2 < 0. \quad (\text{B.9})$$

Conditions (B.8) and (B.9) show that E^{h_1} , when $k_1 \in \mathbf{R}$ and $k_2 < 0$, is locally asymptotically stable (l.a.s) when

$$0 < K\beta_1d_1 - m_1 < S_1, \quad \text{and} \quad \beta_2d_2m_1 - \beta_1d_1m_2 < 0$$

as desired.

B.2.3. Stability of $E^{h_2} = (P, 0, h_2)$

Note that the system (A.1) is symmetric with respect to h_1, h_2 . Thus, similar to the strategy to investigate the stability of h_1 , the study is divided into Case 1, Case 2 and Case 3. The results for the three cases are given next.

Case 1: $k_1 = 0, k_2 \in \mathbf{R}$. It follows that E^{h_2} is l.a.s if

$$0 < m_2 < \min \left\{ K\beta_2d_2, \frac{\beta_2d_2m_1}{\beta_1d_1} \right\}.$$

Case 2: $k_1 > 0, k_2 \in \mathbf{R}$. The l.a.s of E^{h_2} is observed if

$$K\beta_2d_2 - m_2 > \max\{0, S_2\}; \quad S_2 = \frac{K\beta_2d_2^2}{rm_2\beta_1k_1}(\beta_1d_1m_2 - \beta_2d_2m_1).$$

Case 3: $k_1 < 0$, $k_2 \in \mathbf{R}$. The condition on the admissible parameters for l.a.s of boundary equilibrium state E^{h_2} is now

$$0 < K\beta_2d_2 - m_2 < S_2, \quad \text{and} \quad \beta_1d_1m_2 - \beta_2d_2m_1 < 0.$$

This completes the proof of local asymptotical stability of trivial and boundary equilibrium points for model (3) in the main text.

Remark B.1:

The eigenvalues corresponding to Jacobian matrices evaluated at any of the equilibrium states E^0 , E^P , E^{h_1} , E^{h_2} are real. Thus, periodic solutions arising through Hopf Bifurcation are not possible nearby any of such equilibria.

B.3. Local stability of interior equilibrium points

To complete the proof of Result 1 in the main text we next address the stability of the interior equilibrium states. In Appendix A it was found that interior equilibrium states only exist if k_1 and k_2 are not simultaneously zero. For each interior equilibrium point computed in Case II: $k_1 = 0, k_2 \neq 0$ and Case III: $k_1 \neq 0, k_2 = 0$ it is possible to compute the eigenvalues of the Jacobian matrix. However, the expressions are very long. In Case IV, the coexistence equilibria are not given in closed form. Thus, we will use the Routh–Hurwitz stability criterion Allen (2007) to give conditions for local asymptotical stability of all coexistence equilibrium points, which apply to Case II - Case IV. Note that the Jacobian matrix of the model (3) evaluated at an equilibrium satisfying $P \neq 0, h_1 \neq 0, h_2 \neq 0$ is given by (B.1). The characteristic equation is given by

$$P(\gamma) = \gamma^3 + b_2\gamma^2 + b_1\gamma + b_0. \tag{B.10}$$

By Routh–Hurwitz stability criterion the equilibrium state is locally asymptotically stable (l.a.s) if

$$b_2 > 0, \quad b_0 > 0, \quad b_2b_1 > b_0,$$

where

$$b_2 = \frac{2Pr}{K} - r + m_2 + m_1 - h_1h_2k_2 + P\beta_2h_1k_2 - h_1h_2k_1 + P\beta_1h_2k_1 + d_2h_2 + d_1h_1 - P\beta_2d_2 - P\beta_1d_1;$$

$$\begin{aligned} b_1 = & \frac{2Pm_2r}{K} - m_2r + \frac{2Pm_1r}{K} - m_1r + \frac{2P^2\beta_2h_1k_2r}{K} - P\beta_2h_1k_2r + \frac{2P^2\beta_1h_2k_1r}{K} - P\beta_1h_2k_1r \\ & - \frac{2P^2\beta_2d_2r}{K} + P\beta_2d_2r - \frac{2P^2\beta_1d_1r}{K} + P\beta_1d_1r + m_1m_2 - h_1h_2k_2m_2 - h_1h_2k_1m_2 \\ & + P\beta_1h_2k_1m_2 + d_2h_2m_2 + d_1h_1m_2 - P\beta_1d_1m_2 - h_1h_2k_2m_1 + P\beta_2h_1k_2m_1 \\ & - h_1h_2k_1m_1 + d_2h_2m_1 + d_1h_1m_1 - P\beta_2d_2m_1 + P\beta_2d_1h_1^2k_2 - P^2\beta_1\beta_2d_1h_1k_2 \\ & + P\beta_1d_2h_2^2k_1 - P^2\beta_1\beta_2d_2h_2k_1 - P\beta_1d_1d_2h_2 - P\beta_2d_1d_2h_1 + P^2\beta_1\beta_2d_1d_2; \end{aligned}$$

$$\begin{aligned} b_0 = & \frac{1}{K} \{ ((2P - K)m_1 \\ & + (2P^2 - KP)\beta_1h_2k_1 + (KP - 2P^2)\beta_1d_1) m_2 \\ & + ((2P^2 - KP)\beta_2h_1k_2 + (KP - 2P^2)\beta_2d_2) m_1 \\ & + (KP^2 - 2P^3)\beta_1\beta_2d_1h_1k_2 + (KP^2 - 2P^3)\beta_1\beta_2d_2h_2k_1 + (2P^3 - KP^2)\beta_1\beta_2d_1d_2 \} r \\ & + [(-Kh_1h_2k_2 - Kh_1h_2k_1 + Kd_2h_2 + Kd_1h_1) m_1 + KP\beta_1d_2h_2^2k_1 - KP\beta_1d_1d_2h_2] m_2 \\ & + (P\beta_2d_1h_1^2k_2 - KP\beta_2d_1d_2h_1) m_1 \}. \end{aligned}$$

Remark B.1.

Observe that some terms in the expressions of b_0, b_1, b_2 will vanish when either $k_1 = 0, k_2 \neq 0$ (Case II) or $k_1 \neq 0, k_2 = 0$ (Case III).

C. Coexistence equilibrium solutions for model (4) with no competition but with Holling type II

The simplest case is when the model includes Holling type II interaction between the herbivores and the plants but no inter- or intra-species competition between the herbivore species. So we take $m_{11} = 0, m_{22} = 0, \beta_{12} = 0,$ and $\beta_{21} = 0$. In the cases presented below, we are assuming $k_1 = k_2$. Numerical calculations show that there exist coexistence points for $k_1 = -0.007$ to 0.007 but they are locally unstable. Below we give, for some values of k_1 within the range $[-0.007, 0.007]$, the number of interior equilibrium points and the values of the corresponding state variables when applicable.

$$(1) k_1 = -0.004 : \quad P = 9.6819, \quad h_1 = 0.3951, \quad h_2 = 0.7589.$$

(2) $k_1 = -0.001$: $P = 11.6352$, $h_1 = 0.4966$, $h_2 = 0.8682$.

(3) $k_1 = 0$: No coexistence equilibrium points.

(4) $k_1 = 0.001$: Three positive coexistence equilibrium points.

(i) $P = 14.4384$, $h_1 = 0.5462$, $h_2 = 1.2176$.

(ii) $P = 108.237$, $h_1 = 4.2976$, $h_2 = 8.7201$.

(iii) $P = 6999877$, $h_1 = 4.87491$, $h_2 = 9.8748$.

(5) $k_1 = 0.004$: $P = 699969$, $h_1 = 1.2187$, $h_2 = 2.4687$.