Dynamics of Interacting Species for a Consumer Resource System

Praise-God Madueme, Godwin C. E. Mbah

Abstract— The nature of interaction in a consumer resource system is very complex and has been studied extensively using different types of functional response. In this study, we consider the hyperbolic functional response to study a consumer resource model with alternative food source. In particular, we were able to investigate the coexistence of interacting species with the presence of unique alternative resources and also look at variations in resources and consumer biomass as a function of their interactions. The model was generated using a set of five ordinary differential equations. In the analysis of the study, it was discovered that our model shows that in order to promote long term coexistence, consumers must depend on unique alternative resources.

Index Terms— Alternative resources, competition, functional response, specie coexistence, threshold quantity.

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1. INTRODUCTION

Many ecological systems consists of multiple species of consumers and resources and understanding how these species coexist is a big challenge in ecology [1], [8], [10], [7]. Understanding consumer resource population dynamics is important to understanding of the overall ecology of systems [2]. A lot of studies on dynamics of ecological systems focus on single resource and consumer populations [6], [5], [4] and did not consider multiple species coexistence (MSC).However, in reality, the nature of interactions among these species vary significantly, and thus will not be simple (homogeneous). The effect of heterogeneity helps in understanding the dynamics of most ecosystems [2]. A threshold quantity, the consumption number C_0 is used to quantify resource consumption per equivalent of consumer biomass and used to highlight multiple species effects on population dynamics [3]. In this paper, we will extend [3] by introducing an alternative resource (that is, n = 3 for the resources) in addition to gaining a fuller understanding of the dynamics of most ecosystems to where coexistence of species is promoted. We will investigate the impact of the presence of unique resources to the two consumers in order to promote coexistence and discuss the long-term dynamics.

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1.1 Consumer resource model for a multiple species coexistence ecosystem.

In order to incorporate MSC in a consumer resource model, we assume that consumers are made up of n patches or groups (X_i, $i = 1, 2, \ldots, n$) while resources are also partitioned in the same way (Y_i, $i = 1, 2, \ldots, n$). In simplicity, each consumer has a unique resource while they both feed on a particular resource. We also note the fact that the two consumers move in the time of scarcity of the common resource to resort to their unique alternatives. Based on these assumptions, the consumer resource population model is

$$\frac{dX_i}{dt} = X_i r_i \left(1 - \frac{\sum_{j=1}^{n} (X_j)}{K_i} \right) - \frac{\alpha_i X_i Y_i}{\beta_i + X_i}$$

$$\frac{dY_i}{dt} = \frac{c_i \alpha_i X_i Y_i}{\beta_i + X_i} - \tau_i Y_i$$

(1)

with subscript i denoting variables or parameters for patch i. Table 1 describes the meaning and units of the variables and parameters.

2 Consumer resource multiple species coexistence model (1) for n=3.

Our interest in this section is to consider the case where there are three resources and two consumers in the system. When we analyze this special case, we gain insight into the dynamics of the general n-groups MSC model (1). When n = 3 for X_i and n = 2 for Y_i, model (1) reduces to

$$\frac{dX_1}{dt} = X_1 r_1 \left(1 - \frac{X_1}{K_1} \right) - \frac{\alpha_1 X_1 Y_1}{\beta_1 + X_1}$$

$$\frac{dX_2}{dt} = X_2 r_2 \left(1 - \frac{X_2}{K_2} \right) - \frac{\alpha_2 X_2 Y_2}{\beta_2 + X_2}$$

$$\frac{dX_3}{dt} = X_3 r_3 \left(1 - \frac{X_3}{K_3} \right) - \frac{\alpha_3 X_3 Y_1}{\beta_3 + X_3} - \frac{\alpha_3 X_3 Y_2}{\beta_3 + X_3}$$

$$\frac{dY_1}{dt} = \frac{c_1 \alpha_1 X_1 Y_1}{\beta_1 + X_1} + \frac{c_1 \alpha_3 X_3 Y_1}{\beta_3 + X_3} - \tau_1 Y_1$$

$$\frac{dY_2}{dt} = \frac{c_2 \alpha_2 X_2 Y_2}{\beta_2 + X_2} + \frac{c_2 \alpha_3 X_3 Y_2}{\beta_3 + X_3} - \tau_2 Y_2$$

(2)

A possible real life example can be a savanna where grazers (Y_1) feed on grass (X_1), browser (Y_2) feed on trees (X_2), both grazers (Y_1) and browser(Y_2) have a common food (X_3) that both can feed on.

Variables/Parameters	Meaning	Unit
X_i	Density of resources i	g/m^2
Y_i	Density of consumers i	g/m^2
r_i	Growth rate of X_i	/year
K_i	Carrying capacity of X_i	g/m^2
α_i	Xi removal by Y_i	/year
β_i	X_i when α_i is half (half saturation constant)	g/m^2
c_i	Conversion of X_i biomass into Y_i biomass	Dimensionless
τ_i	Reduction of Y_i due to other factors	/year

Table 1: Variables and Parameters for model (1).

2.1 Basic analyses of model (2).

The system (2) has the following equilibrium points:

$$\frac{dX_2}{dt} = \frac{dX_3}{dt} = \frac{dY_1}{dt} = \frac{dY_2}{dt} = 0$$

$$E_1 : (X_1^1, X_2^1, X_3^1, Y_1^1, Y_2^1) = (0,0,0,0,0)$$

$$E_2 : (X_1^2, X_2^2, X_3^2, Y_1^2, Y_2^2) = (K_1,0,0,0,0)$$

$$E_3 : (X_1^3, X_2^3, X_3^3, Y_1^3, Y_2^3) = (0, K_2,0,0,0)$$

$$E_4 : (X_1^4, X_2^4, X_3^4, Y_1^4, Y_2^4) = (0,0, K_3,0,0)$$

$$E_5 : (X_1^5, X_2^5, X_3^5, Y_1^5, Y_2^5) = (K_1, K_2, K_3,0,0)$$

$$E_6 : (X_1^6, X_2^6, X_3^6, Y_1^6, Y_2^6) = (0,0,\frac{\beta_3\tau_1}{c_1\alpha_3 - \tau_1}, Y_1, Y_2)$$

$$where Y_1 = \frac{r_3(K_3 - X_3)(\beta_3 + X_3)}{\alpha_3 K_3} - Y_2$$

$$E_7 : (X_1^7, X_2^7, X_3^7, Y_1^7, Y_2^7) = (\frac{\beta_1\tau_1}{c_1\alpha_1 - \tau_1}, \frac{\beta_2\tau_2}{c_2\alpha_2 - \tau_2},0, Y_1, Y_2)$$

$$where \ Y_1 = \frac{r_1(K_1 - X_1)(\beta_1 + X_1)}{\alpha_1 K_1}, \ Y_2 = \frac{r_2(K_2 - X_2)(\beta_2 + X_2)}{\alpha_2 K_2},$$

$$E_8 : (X_1^8, X_2^8, X_3^8, Y_1^8, Y_2^8) = (\frac{c_2\beta_2\tau_2 - c_1\beta_1\tau_2}{c_1c_2\alpha_1 + c_1\tau_2 - c_2\tau_1},0,\frac{\beta_3\tau_2}{c_2\alpha_3 - \tau_2}, Y_1, Y_2)$$

$$where \ Y_1 = \frac{r_1(K_1 - X_1)(\beta_1 + X_1)}{\alpha_1 K_1}, \ Y_2 = \frac{r_3(K_3 - X_3)(\beta_3 + X_3)}{\alpha_3 K_3} - Y_1$$

$$E_9 : (X_1^9, X_2^9, X_3^9, Y_1^9, Y_2^9) = (0, \frac{c_1\beta_2\tau_2 - c_2\beta_2\tau_1}{c_1c_2\alpha_2 + c_2\tau_1 - c_1\tau_2}, \frac{\beta_3\tau_2}{c_2\alpha_3 - \tau_2}, Y_1, Y_2)$$

where $Y_2 = \dfrac{r_2(K_2 - X_2)(\beta_2 + X_2)}{\alpha_2 K_2}$, $Y_1 = \dfrac{r_3(K_3 - X_3)(\beta_3 + X_3)}{\alpha_3 K_3} - Y_2$

$$E_{10} : (X_1^{10}, X_2^{10}, X_3^{10}, Y_1^{10}, Y_2^{10}) = (X_1, X_2, X_3, Y_1, Y_2)$$

Where $Y_2 = \dfrac{r_2(K_2 - X_2)(\beta_2 + X_2)}{\alpha_2 K_2}$, $X_1 = \dfrac{[\tau_1(\beta_3 + X_3) - c_1\alpha_3 X_3](\beta_1 + X_1)}{c_1\alpha_1(\beta_3 + X_3)}$,

$X_2 = \dfrac{[\tau_2(\beta_3 + X_3) - c_2\alpha_3 X_3](\beta_2 + X_2)}{c_2\alpha_2(\beta_3 + X_3)}$, $X_3 = K_3 - \dfrac{\alpha_3 K_3(Y_1 + Y_2)}{r_3\beta_3 + X_3}$,

$Y_1 = \dfrac{r_1(K_1 - X_1)(\beta_1 + X_1)}{\alpha_1 K_1}$,

We remark that for each of the equilibrium points E_i (for i = 1, 2, . . . , 10) to exist, the inequalities $0 \leq X_i \leq K_i$ must be satisfied by each of them. Furthermore, for each of the equilibrium points E_6, E_7, E_8, E_9, E_{10} to exist, they must each satisfy the inequalities:

$$c_1\alpha_3 - \tau_1 > 0, \ c_1\alpha_1 - \tau_1 > 0, \ c_2\alpha_2 - \tau_2 > 0, \ c_2\alpha_3 - \tau_2 > 0.$$

We use a threshold quantity (consumption number denoted by C_0) that gives a condition under which the equilibrium points of the system are stable. This quantity is similar to the basic reproduction number R_0 [9] in epidemiological models and C_0 is calculated in the same way using the next generation matrix approach [3]:

$$C_0 = \max\{C_1, C_2\} \tag{3}$$

where $C_1 = \dfrac{c_1\alpha_1 K_1}{\tau_1(\beta_1 + K_1)} + \dfrac{c_1\alpha_3 K_3}{\tau_1(\beta_3 + K_3)}$ and $C_2 = \dfrac{c_2\alpha_2 K_2}{\tau_2(\beta_2 + K_2)} + \dfrac{c_2\alpha_3 K_3}{\tau_2(\beta_3 + K_3)}$

Ecologically, C_0 can be understood as the parameter combination ensuring the resource consumption required for survival. So, C_0 = 1 signifies that the consumer utilizes resource biomass at a rate almost equivalent to their own biomass loss. For $C_0 < 1$ less resource is consumed per unit of consumer biomass loss. For $C_0 > 1$ more resource is consumed per unit of consumer biomass loss.

2.2 Stability analyses of model (2).
The stability analysis of this model is a tool that will help us to describe the short-term and long-term dynamics of the system. We will investigate the stability using the threshold quantity C_0.

Theorem 1. *The equilibrium points E_1, E_2, E_3, E_4 are unstable irrespective of the value of C_0.*
Proof. We show that for each of these equilibrium points at least one of the eigenvalues of the Jacobian of the model (2), evaluated at the equilibrium points, has a positive real part. The eigenvalues of (2) at the trivial equilibrium point E_1 are $\lambda_2 = r_2$, $\lambda_3 = r_3$, $\lambda_4 = -\tau_1$, $\lambda_4 = -\tau_2$.

Hence, E_1 is unstable despite the value of C_0. The eigenvalues of (2) at the equilibrium point E_2 are

$$\lambda_1 = \frac{\alpha_1 c_1 K_1}{\beta_1 + K_1} - \tau_1, \ \lambda_2 = r_2, \ \lambda_3 = r_3, \ \lambda_4 = -r_1, \ \lambda_5 = -\tau_2.$$

Hence, E_2 is unstable despite the value of C_0. Similarly, we can show that E_3, E_4 are unstable despite the value of C_0.

Theorem 2. *The equilibrium point E_5 is stable if $C_0 \leq 1$ and unstable otherwise.*

Proof. When we evaluate the eigenvalues of (2) at E_5 we obtain

$$\lambda_1 = \tau_1 \left(\frac{\alpha_1 c_1 K_1}{\beta_1 + K_1} + \frac{\alpha_3 c_1 K_3}{\beta_3 + K_3} - 1 \right),$$

$$\lambda_2 = \tau_2 \left(\frac{\alpha_2 c_2 K_2}{\beta_2 + K_2} + \frac{\alpha_3 c_2 K_3}{\beta_3 + K_3} - 1 \right),$$

$$\lambda_3 = -r_1, \ \lambda_4 = -r_2, \ \lambda_5 = -r_3.$$

We can see that λ_3, λ_4 and λ_5 are negative real numbers despite the value of C_0. We can also see that λ_1 and λ_2 will be negative if $C_0 < 1$. This shows that E_5 is stable when $C_0 < 1$.

Furthermore, $\lambda_1 \leq 0$ and $\lambda_2 \leq 0$ when $C_0 = 1$. This shows that E_5 is stable when $C_0 = 1$. But $\lambda_1 > 0$ and $\lambda_2 > 0$ when $C_0 > 1$. Hence, E_5 is unstable when $C_0 > 1$. So, all the eigenvalues of the Jacobian model of (2) evaluated at E_5 have negative real part when $C_0 \leq 1$.

Theorem 3. *The equilibrium point E_6 is unstable if $C_1 > 1$ and $C_2 > 1$.*

Proof. When $C_1 > 1$ and $C_2 > 1$, E_6 has at least one eigenvalue with a positive real part ($\lambda_4 = r_2$).

Theorem 4. *The equilibrium points E_7, E_8, E_9, E_{10} are also unstable.*

Proof. The overall proof of this claim is analytically complex. Hence, we investigated this numerically using parameter values in **Table 2**. We obtain eigenvalues occurring as complex conjugate pairs. For each of the eigenvalues, there is at least one positive real part. Hence, E_7, E_8, E_9, E_{10} are unstable irrespective of the value of C_0.

Parameters	Value	Unit	Source
r_1	0.20	/week	[5]
r_2	0.25	/week	[5]
r_3	0.30	/week	[3]
K_1	200	g/m²	[5]
K_2	500	g/m²	[5], [4]
K_3	800	g/m²	[3]
α_1	0.175	/week	[5]
α_2	0.175	/week	[4]
α_3	0.18	/week	[3]
β_1	50	g/m²	[5]
β_2	20	g/m²	[5]

β_3	80	g/m²	[3]
c_1	0.73	Dimensionless	[5]
c_2	0.75	Dimensionless	[5], [4]
τ_1	0.012	/day	[3]
τ_2	0.014	/day	[3]

Table 2: Parameter values used for model simulations with their reference sources.
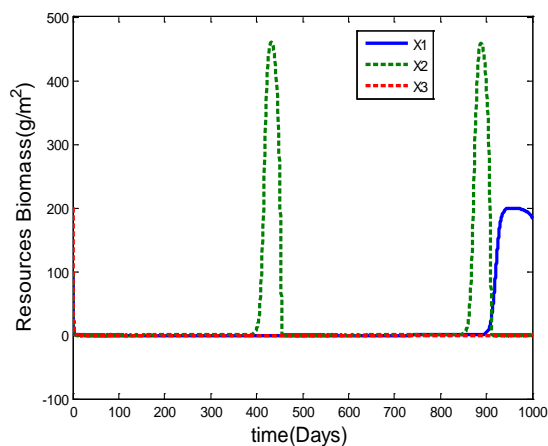
To support these analytical results, we investigate the long-term dynamics of the model by performing numerical simulations using the parameter values given in Table 2.
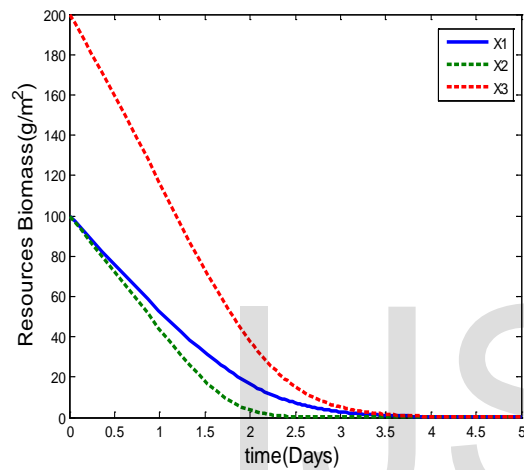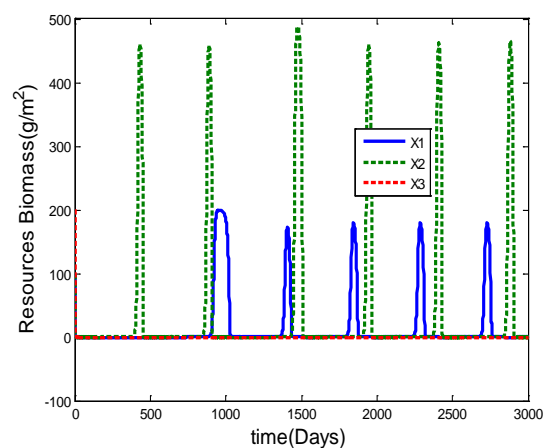

Figure (a)
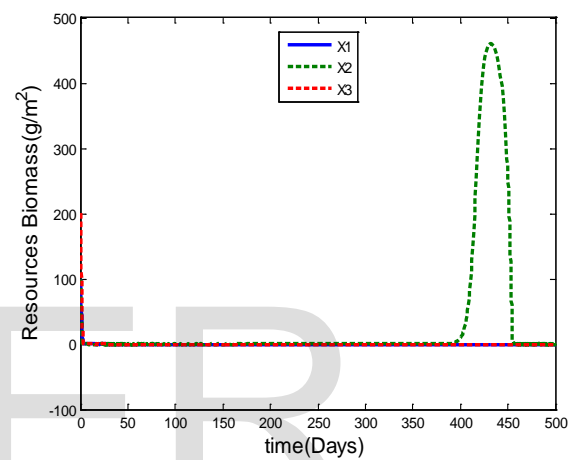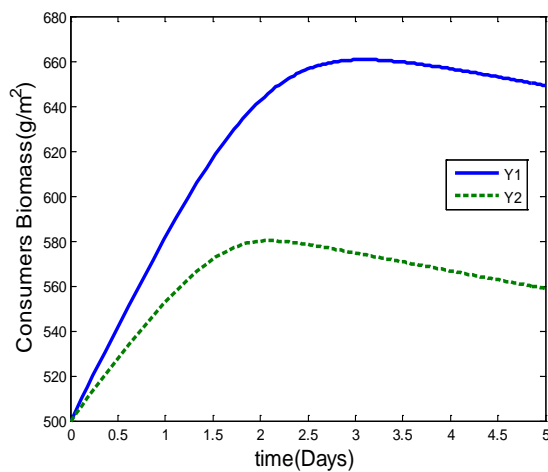

Figure (b)

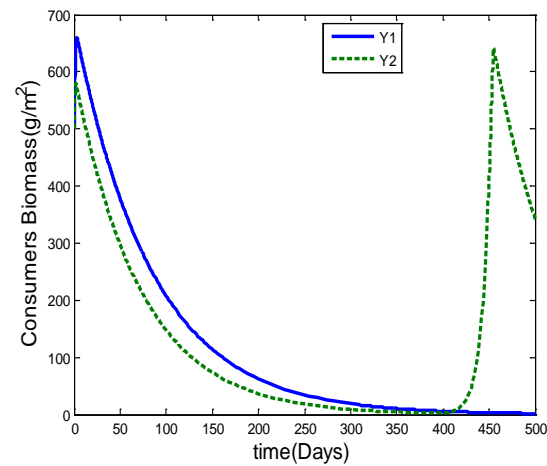**Figure (c)**

Figure (d)
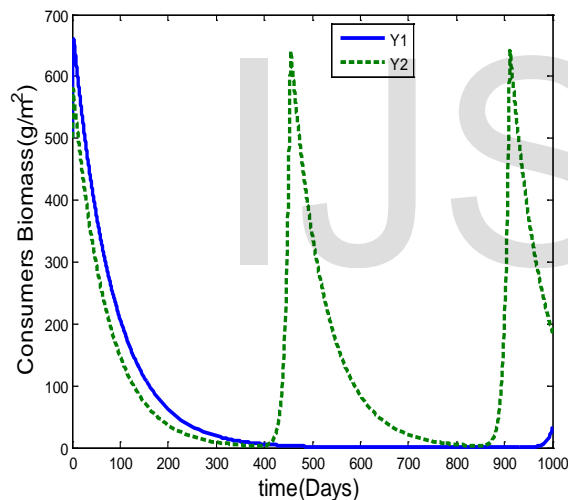
Figure (e)

Figure (f)

Figure (g)

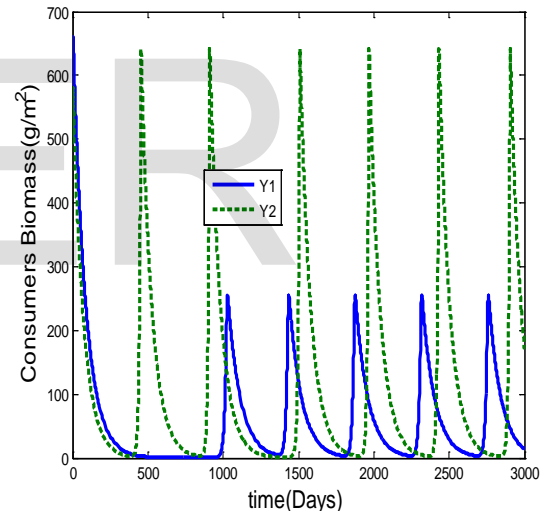**Figure (h)**

3 DISCUSSION AND CONCLUSION

Ecologically, from the stability analysis of E_1, E_2, E_3, E_4, we see that it is not possible for any or all of the resources and consumers to go into extinction. From the analysis of E_5, we see that in the absence of consumers, the resources will simply grow to their carrying capacity. From E_6, we observe that in the absence of the alternative resources (X_1 and X_2), the biomass of the consumers will be strongly affected due to intense competition. From E_7, we see that in the absence of the common resource (X_3), the consumers rely solely on their unique alternatives resources. This is not also feasible in a long term since they lack their main resource. From E_8 and E_9, we observe in the absence of any alternative resource (X_1 or X_2), it will force the particular consumer (Y_1 or Y_2) to rely solely on the main resource (X_3). This will grossly affect the biomass of the main resource. From E_{10}, we can see that over a long term it may be difficult to maintain the biomass of both

consumers and resources. In this work, our model shows that in order to promote long term coexistence, it is not possible for a consumer to completely depend on a particular resource.

From Figure (a) and (e), we see that the increase in the biomass of the consumers shows the depletion of the resources. From figure (b) and (f), we see that in the absence of the alternative resources, there is intense competition on the common resource such that it is intensively depleted and this in turn affects the biomass of the consumers. From figures (c) and (d), (g) and (h), in the long run, the alternative resources begin to grow and so affects the biomass of the consumers. We also see that since X3 is the common resource, its increase in biomass is almost negligible since at any slightest growth, the consumers return back to feed on it again. When either of X_1 or X_2 is not available, it forces the particular Y_1 and Y_2 without this alternative to intensely compete for the main resource X_3 thereby forcing either Y_1 or Y_2 to seek for the particular alternative easily enough. Hence, both X_1 or X_2 and the main resource X_3 will be intensively depleted.

Furthermore, we can see from Figures (a) to (h) above that at infinite time, the trajectories for both resources and consumers become cyclic or periodic. Hence the resources (X_1 and X_2) cannot be completely depleted as long as they are in the same ecological niche with X_3. Their biomass can decrease depending on the consumption rate of the consumers, but as the consumers feed on X_3, they have the opportunity to grow back again.

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