

UNDERSTANDING MULTIPLE SPECIES ECOSYSTEM DYNAMICS USING A CONSUMER RESOURCE MODEL

OBIORA C. COLLINS

Institute of Systems Science, Durban University of Technology, Durban 4000, South Africa
E-mail: obiora.c.collins@gmail.com

KEVIN J. DUFFY*

Institute of Systems Science, Durban University of Technology, Durban 4000, South Africa
E-mail: kevind@dut.ac.za

ABSTRACT. Most ecological systems comprise multiple species coexisting and the dynamics of these multiple species can be important for understanding, management, and conservation. One method to study such ecological system dynamics is the use of heterogeneous models. Here we formulate and analyze a multiple species (n patches or groups) consumer resource model. Initial insights are gained by analyzing the special cases $n = 1$ and $n = 2$. A threshold consumption number C_0 is used to investigate system stability and hence the long-term dynamics of the system. It is shown how this threshold consumption number can measure the effects and extent of multiple species coexistence in the system.

KEY WORDS: Differential equations, multiple species coexistence, stability analysis, heterogeneity.

1. Introduction. Most ecological systems are made up of multiple species of resources and consumers living together in close proximity and understanding how these species coexist is a major challenge in ecology (Chesson, [1991]; Taper, [1993]; Young et al., [1997]; Siepielski and McPeck, [2010]). For systems where species differ in resource use, partitioning of resources is often thought to reflect the primary role of competition in determining coexistence of species (Martin, [1988]). In reality, the nature of interactions among these species vary, hence leading to heterogeneity in the dynamics of the ecological system.

Many theoretical studies of ecological dynamics focus on homogeneous (single) consumer and resource populations (Lotka, [1925]; Volterra, [1926]; Rosenzweig and MacArthur, [1963]; Owen-Smith, [2004]; Duffy, [2010]) and do not take multiple species coexistence (MSC) into account. Interactions among species can affect the population dynamics of each (Kinzey, [2008]). Thus, considering the effects of heterogeneities introduced by MSC, as in this paper, should be important to a fuller understanding of the dynamics of most ecosystems. To investigate this idea we develop a mathematical model incorporating MSC in the form of ordinary differential equations. A threshold quantity, the consumption number C_0 , defined by

*Corresponding author. K.J. Duffy; Institute of Systems Science, Durban University of Technology, Durban 4000, South Africa, e-mail: kevind@dut.ac.za

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TABLE 1. Variables and parameters for model (1).

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
δ_{ij}	The effect X_j has on X_i	Dimensionless
α_i	X_i removal by Y_i	/year
β_i	X_i when α_i is half	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

us to quantify resource consumption per equivalent of consumer biomass, is used to highlight multiple species effects on population dynamics (Collins and Duffy, [2016]).

1.1. Consumer resource model for a multiple species coexistence ecosystem. To account for MSC in a consumer resource model, we assume that consumers are made up of n patches or groups ($X_i, i = 1, 2, \dots, n$) while resources are also partitioned in the same way ($Y_i, i = 1, 2, \dots, n$). To simplify the analyses we assume that each consumer uses a unique resource. However, similar results are indicated when consumers use more than one resource (Collins and Duffy, [2016]). We introduce competition terms δ_{ij} that describe how the resources compete for space. Based on the above assumptions, the consumer resource population model that incorporates MSC is

$$(1) \quad \begin{aligned} \frac{dX_i}{dt} &= X_i r_i \left(1 - \frac{X_i + \sum_{j=1}^n (\delta_{ij} X_j)}{K_i} \right) - \frac{\alpha_i X_i Y_i}{\beta_i + X_i}, \\ \frac{dY_i}{dt} &= \frac{c_i \alpha_i X_i Y_i}{\beta_i + X_i} - \tau_i Y_i, \end{aligned}$$

with subscript i denoting variables or parameters for patch i . The meaning of variables and parameters, with their units, are presented in Table 1.

2. Consumer resource multiple species coexistence model (1) for $n = 2$. In this section, we consider the case where there are only two resources and two consumers in the system. Analyses of this special case give insights into the dynamics of the general n -groups MSC model (1). When $n = 2$, model (1) reduces to

$$(2) \quad \begin{aligned} \frac{dX_1}{dt} &= X_1 r_1 \left(1 - \frac{X_1 + \delta_{12} X_2}{K_1} \right) - \frac{\alpha_1 X_1 Y_1}{\beta_1 + X_1}, \\ \frac{dX_2}{dt} &= X_2 r_2 \left(1 - \frac{X_2 + \delta_{21} X_1}{K_2} \right) - \frac{\alpha_2 X_2 Y_2}{\beta_2 + X_2}, \\ \frac{dY_1}{dt} &= \frac{c_1 \alpha_1 X_1 Y_1}{\beta_1 + X_1} - \tau_1 Y_1, \\ \frac{dY_2}{dt} &= \frac{c_2 \alpha_2 X_2 Y_2}{\beta_2 + X_2} - \tau_2 Y_2. \end{aligned}$$

For example, this could represent the most common resources in a savanna: trees (X_1) and grasses (X_2) together with their respective consumers browsers (Y_1) and grazers (Y_2).

2.1. Basic analyses of model (2). The system (2) has the following equilibrium points:

$$\begin{aligned} E_1 &= (X_1^1, X_2^1, Y_1^1, Y_2^1) = (0, 0, 0, 0), \\ E_2 &= (X_1^2, X_2^2, Y_1^2, Y_2^2) = (K_1, 0, 0, 0), \\ E_3 &= (X_1^3, X_2^3, Y_1^3, Y_2^3) = (0, K_2, 0, 0), \\ E_4 &= (X_1^4, X_2^4, Y_1^4, Y_2^4) = \left(\frac{K_1 - \delta_{12} K_2}{1 - \delta_{12} \delta_{21}}, \frac{K_2 - \delta_{21} K_1}{1 - \delta_{12} \delta_{21}}, 0, 0 \right), \\ E_5 &= (X_1^5, X_2^5, Y_1^5, Y_2^5) = \left(\frac{\tau_1 \beta_1}{c_1 \alpha_1 - \tau_1}, 0, \frac{r_1}{\alpha_1} \left(1 - \frac{X_1^5}{K_1} \right) (\beta_1 + X_1^5), 0 \right), \\ E_6 &= (X_1^6, X_2^6, Y_1^6, Y_2^6) = \left(0, \frac{\tau_2 \beta_2}{c_2 \alpha_2 - \tau_2}, 0, \frac{r_2}{\alpha_2} \left(1 - \frac{X_2^6}{K_2} \right) (\beta_2 + X_2^6) \right), \\ E_7 &= (X_1^7, X_2^7, Y_1^7, Y_2^7) \\ &= \left(K_1 - \delta_{12} X_2^7, \frac{\tau_2 \beta_2}{c_2 \alpha_2 - \tau_2}, 0, \frac{r_2}{\alpha_2} \left(1 - \frac{X_2^7 + \delta_{21} X_1^7}{K_2} \right) (\beta_2 + X_2^7) \right), \\ E_8 &= (X_1^8, X_2^8, Y_1^8, Y_2^8) \\ &= \left(\frac{\tau_1 \beta_1}{c_1 \alpha_1 - \tau_1}, K_2 - \delta_{21} X_1^8, \frac{r_x}{\alpha_1} \left(1 - \frac{X_1^8 + \delta_{12} X_2^8}{K_1} \right) (\beta_1 + X_1^8), 0 \right), \end{aligned}$$

$$E_9 = (X_1^9, X_2^9, Y_1^9, Y_2^9) = \left(\frac{\tau_1 \beta_1}{c_1 \alpha_1 - \tau_1}, \frac{\tau_2 \beta_2}{c_2 \alpha_2 - \tau_2}, Y_1^9, Y_2^9 \right),$$

where $Y_1^9 = \frac{r_1}{\alpha_1} \left(1 - \frac{X_1^9 + \delta_{12} X_2^9}{K_1}\right) (\beta_1 + X_1^9)$ and $Y_2^9 = \frac{r_2}{\alpha_2} \left(1 - \frac{X_2^9 + \delta_{21} X_1^9}{K_2}\right) (\beta_2 + X_2^9)$. Note that for each of the equilibrium points E_i (for $i = 1, 2, 3, \dots, 9$) to exist, they must each satisfy the inequalities: $0 \leq X_i^0 \leq K_1$, $0 \leq Y_i^0 \leq K_2$. Based on this, we can easily see that for E_4 to exist, the following inequalities must hold: $K_1 - \delta_{12} K_2 \geq 0$, $K_2 - \delta_{21} K_1 \geq 0$, $1 - \delta_{12} \delta_{21} > 0$. It then follows that the competition terms δ_{12} and δ_{21} must satisfy the inequalities $0 \leq \delta_{12}, \delta_{21} \leq 1$. If both competitors are such that $\delta_{12} = \delta_{21} = 0$, neither resource is dominating. Mathematically, we can show that it is not possible to have $\delta_{12} = \delta_{21} = 1$. This makes sense since no two competitors can be in total domination of each other at the same time. There is always one superior competitor at each point in time. Also, $c_1 \alpha_1 - \tau_1 > 0$ and $c_2 \alpha_2 - \tau_2 > 0$ for E_5, E_6, E_7, E_8, E_9 to exist.

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 \mathcal{R}_0 (van den Driessche and Watmough, [2002]) in epidemiological models and C_0 is calculated in the same way using the next generation matrix approach (Collins and Duffy, [2016]):

$$(3) \quad C_0 = \max\{C_1, C_2\},$$

where $C_1 = \frac{c_1 \alpha_1 X_1^4}{\tau_1 (\beta_1 + X_1^4)}$, $C_2 = \frac{c_2 \alpha_2 X_2^4}{\tau_2 (\beta_2 + X_2^4)}$. Note that in the absence of competition between grass and trees (i.e., $\delta_{12} = \delta_{21} = 0$), then $C_1 = \frac{c_1 \alpha_1 K_1}{\tau_1 (\beta_1 + K_1)}$, $C_2 = \frac{c_2 \alpha_2 K_2}{\tau_2 (\beta_2 + K_2)}$ since $X_1^4 = K_1$ and $X_2^4 = K_2$.

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). Stability analysis of models such as this can help describe the short-term and long-term dynamics of the system. Before investigating the stability of model (2) we first present the relationship between the equilibrium points at $C_0 = 1$.

- (i) $E_2 = E_5$ if $C_0 = C_1 = 1$ (i.e., C_1 when $\delta_{12} = \delta_{21} = 0$).
- (ii) $E_3 = E_6$ if $C_0 = C_2 = 1$ (i.e., C_2 when $\delta_{12} = \delta_{21} = 0$).
- (iii) $E_4 = E_7$ if $C_0 = C_2 = 1$.
- (iv) $E_4 = E_8$ if $C_0 = C_1 = 1$.
- (v) $E_4 = E_9$ if $C_0 = C_1 = C_2 = 1$.

Note that E_5, E_6, E_7, E_8, E_9 do not exist when $C_0 < 1$. Therefore, their stability will only be investigated for $C_1 \geq 1$ and $C_2 \geq 1$.

Theorem 1. *The equilibrium points E_1, E_2, E_3 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 model (2), evaluated at the equilibrium point, has a positive real part. The eigenvalues of (2) at the trivial equilibrium point E_1 are $\lambda_1 = r_1, \lambda_2 = r_2, \lambda_3 = -\tau_1, \lambda_4 = -\tau_2$. Thus, E_1 is unstable irrespective of the value of C_0 . The eigenvalues of (2) evaluated at the equilibrium point E_2 are $\lambda_1 = r_1, \lambda_2 = \frac{r_2}{K_2}(K_2 - \delta_{21}K_1), \lambda_3 = \alpha c_1 K_1 / (K_1 + \beta_1) - \tau_1, \lambda_4 = -\tau_2$. Clearly $\lambda_2 > 0$. Thus, E_2 is unstable irrespective of the value of C_0 . Similarly, we can also show that E_3 is unstable irrespective of the value of C_0 . \square

Theorem 2. *The equilibrium point E_4 is stable if $C_0 \leq 1$ and unstable otherwise.*

Proof. The eigenvalues of (2) evaluated at E_4 are

$$\begin{aligned} \lambda_1 &= \tau_1 \left(\frac{c_1 \alpha_1 X_1^4}{\tau_1 (\beta_1 + X_1^4)} - 1 \right), \\ \lambda_2 &= \tau_2 \left(\frac{c_2 \alpha_2 X_2^4}{\tau_2 (\beta_2 + X_2^4)} - 1 \right), \\ \lambda_3 &= -\frac{1}{2} \left(\left(\frac{r_1 X_1^4}{K_1} + \frac{r_2 X_2^4}{K_2} \right) + \sqrt{\left(\frac{r_1 X_1^4}{K_1} + \frac{r_2 X_2^4}{K_2} \right)^2 - \frac{4r_1 r_2 X_1^4 X_2^4}{K_1 K_2} (1 - \delta_{12} \delta_{21})} \right), \\ \lambda_4 &= -\frac{1}{2} \left(\left(\frac{r_1 X_1^4}{K_1} + \frac{r_2 X_2^4}{K_2} \right) - \sqrt{\left(\frac{r_1 X_1^4}{K_1} + \frac{r_2 X_2^4}{K_2} \right)^2 - \frac{4r_1 r_2 X_1^4 X_2^4}{K_1 K_2} (1 - \delta_{12} \delta_{21})} \right). \end{aligned}$$

Clearly λ_3 and λ_4 are negative real numbers irrespective of the value of C_0 . We can also see that if $C_0 < 1$ then λ_1 and λ_2 become negative. This shows that E_4 is stable when $C_0 < 1$. Next, if $C_0 = 1$, then $\lambda_1 \leq 0$ or $\lambda_2 \leq 0$. This shows that E_4 is also stable when $C_0 = 1$. However, if $C_0 > 1$ we have $\lambda_1 > 0$ or $\lambda_2 > 0$. This confirms that E_4 is unstable when $C_0 > 1$. Thus, for $C_0 \leq 1$ all the eigenvalues of the Jacobian of model (2) evaluated at E_4 have negative real part and the proof is complete. \square

Theorem 3. *The equilibrium points E_5 and E_6 are unstable if $C_1 \geq 1$ and $C_2 \geq 1$.*

Proof. At $C_0 = C_1 = 1, E_2 = E_5$. So E_5 is unstable at $C_0 = 1$ since E_2 is unstable (see Theorem 1). When $C_1 > 1$ and $C_2 > 1$ one of the eigenvalues of the Jacobian of model (2) evaluated at E_5 is $\frac{r_2}{K_2}(K_2 - \delta_{21}X_5^0)$. Clearly, $K_2 - \delta_{21}X_5^0 > 0$ since,

$K_2 - \delta_{21}K_1 > 0$. Thus $\overline{E_5}$ is unstable. By a similar argument we can also show that E_6 is unstable when $C_1 \geq 1$ and $C_2 \geq 1$.

Theorem 4. *The equilibrium points E_7 and E_8 are stable if $C_0 = 1$ and unstable if $C_1 > 1$ and $C_2 > 1$.*

Proof. Having shown that $E_4 = E_7$ when $C_0 = C_1 = 1$, then E_7 is automatically stable at $C_0 = C_1 = 1$ since E_4 is stable when $C_0 = 1$ (see Theorem 2). On the other hand, when $C_1 > 1$ and $C_2 > 1$, one of the eigenvalues of the Jacobian of model (2) evaluated at E_7 is $\frac{1}{\tau_1} \left(\frac{\alpha_1 c_1 X_1^7}{\tau_1 (X_1^7 + \beta_1)} - 1 \right)$. This eigenvalue is positive since $X_1^7 > X_1^4$ when $C_1 > 1$ and $C_2 > 1$. Thus E_7 is unstable if $C_1 > 1$ and $C_2 > 1$. Similarly, E_8 is stable when $C_0 = 1$ and unstable if $C_1 > 1$ and $C_2 > 1$. \square

Theorem 5. *The equilibrium point E_9 is stable when $C_1 \geq 1$ and $C_2 \geq 1$.*

The overall proof of this theorem is analytically complex and so here we illustrate the proof by making the simplification that $\delta_{12} = 0$ and $\delta_{21} = 0$. The more general case is then investigated numerically below.

Proof. For $C_1 = C_2 = 1$, $E_9 = E_4$, so the stability of E_7 follows from the stability of E_4 . Next, when $C_1 > 1$ and $C_2 > 1$, the eigenvalues of the Jacobian of model (2) evaluated at E_9 for $\delta_{12} = \delta_{21} = 0$ are given by

$$\lambda_1 = \frac{1}{2} \left(a_{11} - \sqrt{a_{11}^2 + 4a_{13}a_{31}} \right), \lambda_2 = \frac{1}{2} \left(a_{11} + \sqrt{a_{11}^2 + 4a_{13}a_{31}} \right)$$

$$\lambda_3 = \frac{1}{2} \left(a_{22} - \sqrt{a_{22}^2 + 4a_{24}a_{42}} \right), \lambda_4 = \frac{1}{2} \left(a_{22} + \sqrt{a_{22}^2 + 4a_{24}a_{42}} \right)$$

where $a_{11} = -\frac{\alpha_1 Y_1^9}{X_1^9 + \beta_1} \left(1 - \frac{X_1^9}{X_1^9 + \beta_1} \right) - r_1 \left(\frac{2X_1^9}{K_1} - 1 \right)$, $a_{13} = -\frac{\alpha_1 X_1^9}{X_1^9 + \beta_1}$, $a_{31} = -\frac{\alpha_1 c_1 Y_1^9}{X_1^9 + \beta_1} \left(1 - \frac{X_1^9}{X_1^9 + \beta_1} \right)$, $a_{22} = -\frac{\alpha_2 Y_2^9}{X_2^9 + \beta_2} \left(1 - \frac{X_2^9}{X_2^9 + \beta_2} \right) - r_2 \left(\frac{2X_2^9}{K_2} - 1 \right)$, $a_{24} = -\frac{\alpha_2 X_2^9}{X_2^9 + \beta_2}$, $a_{42} = -\frac{c_2 \alpha_2 Y_2^9}{X_2^9 + \beta_2} \left(1 - \frac{X_2^9}{X_2^9 + \beta_2} \right)$. Obviously, $a_{13} < 0$, $a_{31} > 0$, $a_{24} < 0$, $a_{42} > 0$. Also, $a_{11} < 0$ and $a_{22} < 0$ provided that $K_1 \leq \frac{2\tau_1 \beta_1}{\alpha_1 c_1 - \tau_1}$ and $K_2 \leq \frac{2\tau_2 \beta_2}{\alpha_2 c_2 - \tau_2}$. Based on this, the eigenvalues $\lambda_1, \lambda_2, \lambda_3, \lambda_4$ have negative real parts. \square

The more general case, $\delta_{12} \neq 0$ and $\delta_{21} \neq 0$, is investigated numerically using the parameter values in Table 2 such that $C_1 > 1$ and $C_2 > 1$. Stable cyclic dynamics are obtained for the system as shown in Figure 1(c). Thus, for the more general case, these results suggest that E_9 will be stable when $C_1 > 1$ and $C_2 > 1$.

From these results, of all nine points, E_4 and E_9 are the only stable equilibrium points when $C_0 \neq 1$ and their stability is governed by C_0 . Also, our stability analyses have shown that the consumption number partitions the dynamics of the

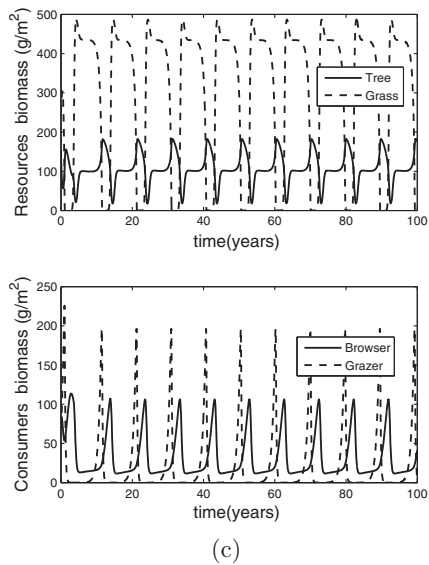
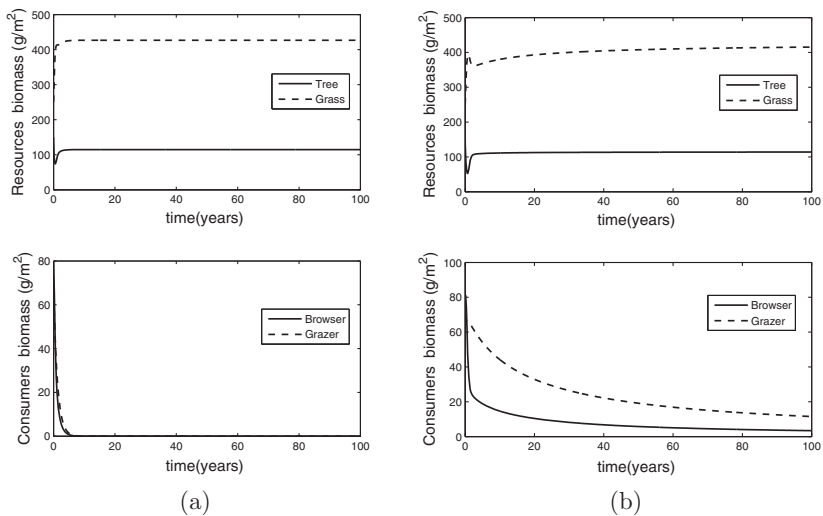


FIGURE 1. Plots illustrating the long-term dynamics of the MSC model (2) for various values of consumption number: (a) $C_1 < 1, C_2 < 1$, (b) $C_1 = C_2 = 1$, (c) $C_1 > 1, C_2 > 1$ (see text for details).

TABLE 2. Parameters values used for model simulations with their reference source.

Parameters	Value	Unit	Source
r_1	0.20	/week	Owen-Smith, [2004]
r_2	0.25	/week	Owen-Smith, [2004]
K_1	200	g/m^2	Owen-Smith, [2004]
K_2	500	g/m^2	Owen-Smith, [2004]; Duffy, [2010]
δ_{12}	0.1–0.3	Dimensionless	estimate
δ_{21}	0.64	Dimensionless	estimate
α_1	0.175	/week	Owen-Smith, [2004]
α_2	$0.025 * 7$	/week	Duffy, [2010]
β_1	50	g/m^2	Owen-Smith, [2004]
β_2	20	g/m^2	Owen-Smith, [2004]
c_1	0.73	Dimensionless	Owen-Smith, [2004]
c_2	0.75	Dimensionless	Owen-Smith, [2004]; Duffy, [2010]
τ_1	0.012–0.01485	/day	estimate
τ_2	0.014–0.02	/day	estimate

system into three parts: $C_0 < 1$, $C_0 = 1$ and $C_0 > 1$. 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 and varying τ_1 and τ_2 (Figures 1a–c). τ_1 and τ_2 are varied because they are more sensitive in terms of affecting the consumption number. For Figure 1(a), $\tau_1 = 0.0148$, $\tau_2 = 0.0200$ results in $C_1 = 0.8564$, $C_2 = 0.8955$ ($C_1 < 1$, $C_2 < 1$). For Figure 1(b), $\tau_1 = \frac{c_1 \alpha_1 X_1^4}{\beta_1 + X_1^4}$, $\tau_2 = \frac{c_2 \alpha_2 X_2^4}{\beta_2 + X_2^4}$ results in $C_1 = C_2 = 1$. For Figure 1(c), $\tau_1 = 0.0120$, $\tau_2 = 0.014$ results in $C_1 = 1.0562$, $C_2 = 1.2793$ ($C_1 > 1$, $C_2 > 1$). From Figures 1(a) and 1(b) the trajectories for both resources and consumers converge to the equilibrium point E_4 supporting Theorem 2. So at infinite time, the dynamics for resources and consumers can be estimated from the equilibrium point. On the other hand, when consumption numbers are greater than one, the trajectories for both resources and consumers become periodic or cyclic (Figure 1c). For all these cases, grass and grazer biomasses mostly dominate tree and browser biomasses.

3. Homogeneous version of model (1). To determine the influence of MSC, the homogeneous version of model (1) is used as reference. With one group of resources and one group of consumers the model (1) is reduced to the homogeneous version

$$(4) \quad \frac{dX}{dt} = Xr \left(1 - \frac{X}{K} \right) - \frac{\alpha XY}{\beta + X},$$

$$\frac{dY}{dt} = \frac{c\alpha XY}{\beta + X} - \tau Y,$$

where

$$(5) \quad r = \sum_{i=1}^n r_i/n, K = \sum_{i=1}^n K_i/n, \alpha = \sum_{i=1}^n \alpha_i/n, \beta = \sum_{i=1}^n \beta_i/n, c = \sum_{i=1}^n c_i/n, \tau = \sum_{i=1}^n \tau_i/n.$$

The consumption number for model (4) is given by

$$(6) \quad C_0^* = \frac{\alpha c K}{\tau(\beta + K)}.$$

The system (4) has the following equilibrium points:

$$\begin{aligned} P_1 &= (X_0^1, Y_0^1) = (0, 0), \\ P_2 &= (X_0^2, Y_0^2) = (K, 0), \\ P_3 &= (X_0^3, Y_0^3) = \left(\frac{\tau\beta}{\alpha c - \tau}, \frac{r}{\alpha} \left(1 - \frac{X_0^3}{K} \right) (\beta + X_0^3) \right). \end{aligned}$$

Note that $P_2 = P_3$ when $C_0^* = 1$.

3.1. Stability analyses of model (4). Using similar reasoning to that used for model (2) one can easily establish the following:

- (i) P_1 is unstable.
- (ii) P_2 is stable (locally and globally) when $C_0^* \leq 1$.
- (iii) P_3 is stable when $C_0^* \geq 1$.

These results also show that only two equilibrium points P_2 and P_3 of the homogeneous model (4) are stable and their stability is also governed by the consumption number C_0^* . The MSC model analogs to P_2 and P_3 are E_4 and E_9 , respectively.

4. Effects of multiple species coexistence. From our formulation, the parameters in the homogeneous model (4) are defined as averages of the associated parameters of the MSC model (1). Intuitively, the homogeneous model (4) might be expected to feature the average characteristic dynamics of the MSC model (1). If this were true, the homogeneous model results would average the corresponding MSC model results. However, this is not true. In particular, the average consumption numbers for the MSC model are not equal to the consumption numbers of the homogeneous model (which can be confirmed analytically by simple algebraic

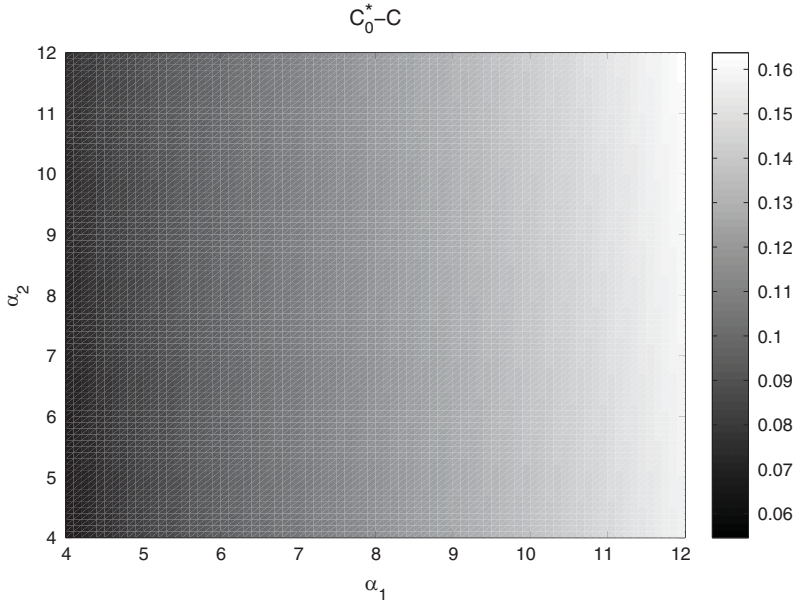


FIGURE 2. Plot illustrating the difference between C and C_0^* for various values of α_1 and α_2 .

manipulation). Thus, differences in the dynamics for various resource and consumer MSC models arise not only from parameters but also from the model structure.

4.1. The extent of multiple species coexistence effects on population dynamics. Here we investigate the extent of MSC effects on the consumer resource model dynamics by considering these effects on the consumption number and then on the actual dynamics.

4.1.1. Extent of multiple species coexistence effects on the consumption number.

The null hypothesis assumed here is that the homogeneous model (2) will average the MSC model (1). To test this hypothesis we consider the difference between the consumption number C_0^* and the average of the consumption numbers for the corresponding MSC model, denoted by $C = \sum_{j=1}^n C_j/n$. Differences between C ($n=2$) and C_0^* for various values of α_1 and α_2 are given in Figure 2. α_1 and α_2 are varied because they are also more sensitive in terms of affecting the consumption number. From the figure, $C_0^* > C$ for all values of α_1 and α_2 , so in this case if the MSC model is more representative of the real system using C_0^* would lead to overestimation of the consumption number. Note that C_0^* will not always be necessarily greater than C . Our example is dependent on the parameters we obtained from

research on particular African savannas but other situations might give different results.

4.1.2. *Extent of multiple species coexistence effects on long-term dynamics.* To assess the effect of MSC, we compare this model to a homogeneous version where the resource and consumer biomasses are averaged ($\sum_{j=1}^n X_j/n$ and $\sum_{j=1}^n Y_j/n$). Since the consumption number was already found to partition the dynamics into three parts: $C_0, C_0^* < 1$, $C_0 = C_0^* = 1$, and $C_0, C_0^* > 1$, we compare the models (with $n=2$) for these cases. For Figure 3(a), $C_1 = 0.8535, C_2 = 0.8955, C_0^* = 0.9639$ ($C_1 < 1, C_2 < 1, C_0^* < 1$). For Figure 3(b), $C_1 = C_2 = C_0^* = 1$. For Figure 3(c), $C_1 = 1.0562, C_2 = 1.2793, C_0^* = 1.2919$ ($C_1 > 1, C_2 > 1, C_0^* > 1$). Thus, when consumption numbers are less than or equal to one, the biomass dynamics of both models are still stable equilibria and in this example the homogeneous dynamics are larger for both resources and consumers (Figures 3a and b). When consumption numbers are greater than one, the cyclical dynamics of biomasses over time have larger amplitudes but smaller periods for the homogeneous model as compared to the dynamics for the MSC model (Figure 3c).

5. Analyses of the general MSC model (1). In this section, we extend several results obtained for the MSC model (2) $n = 2$ to the more general n MSC model (1). For the case $n = 2$, of the nine equilibrium points, only two equilibrium points are important for stability analyses (E_4 , the equilibrium in the absence of consumers, and E_9 , the positive equilibrium of consumers and resources). For the homogeneous model, there are also two important equilibrium points: P_2 and P_3 . Thus, to simplify our analyses for the general case we consider the analogs for these equilibrium pairs.

The first of these points is the equilibrium in the absence of consumers given by

$$(7) \quad \overline{E}_p = (X_1^p, X_2^p, \dots, X_n^p, Y_1^p, Y_2^p, \dots, Y_n^p),$$

where $X_i^p = K_p - \sum_{j=1}^n \delta_{pj} X_j^p$ and $Y_i^p = 0$ for $i = 1, 2, \dots, n$. In the absence of competition, the terms $\delta_{pj} = 0$ and then $X_i^p = K_p$, the carrying capacity.

The second equilibrium point is the positive equilibrium point and is given by

$$(8) \quad \overline{E}_q = (X_1^q, X_2^q, \dots, X_n^q, Y_1^q, Y_2^q, \dots, Y_n^q),$$

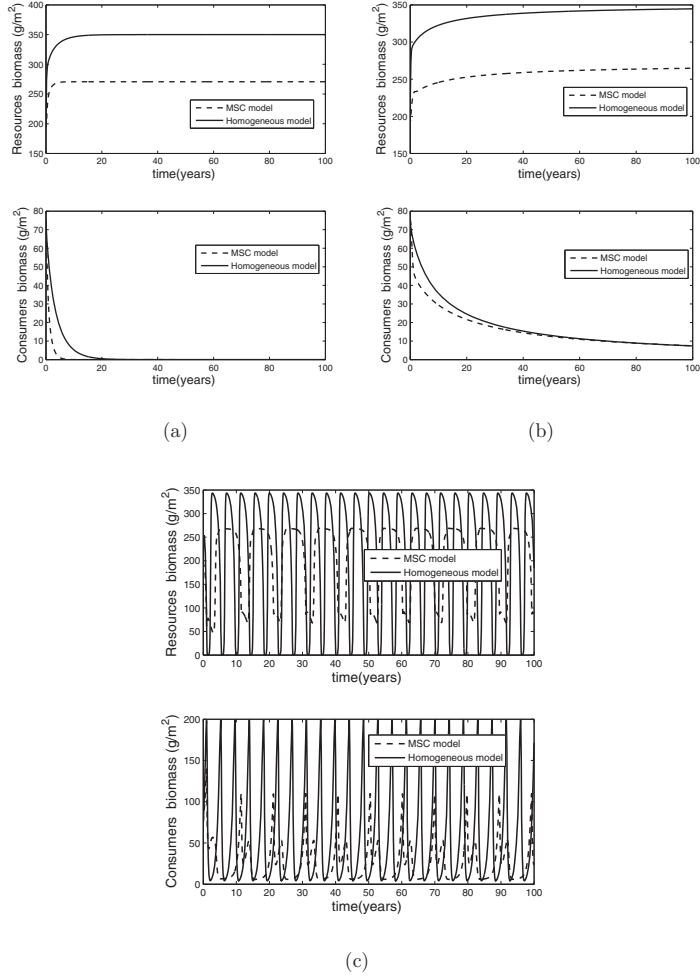


FIGURE 3. Plots comparing the long-term dynamics from the MSC model (averaged) and the homogeneous model for various values of consumption number: (a) $C_1 < 1, C_2 < 1, C_0^* < 1$, (b) $C_1 = C_2 = C_0^* = 1$, (c) $C_1 > 1, C_2 > 1, C_0^* > 1$ (see text for details).

where $X_i^q = \frac{\tau_q \beta_q}{\alpha_q c_q - \tau_q}$ and $Y_i^q = \frac{r_q}{\alpha_q} \left(1 - \frac{X_i^q + \sum_{j=1}^n \delta_{qj} X_j^q}{K_q}\right) (\beta_q + X_i^q)$ for $q = 1, 2, \dots, n$. In the absence of competition terms ($\delta_{qj} = 0$), the X_i^q remain the same while $Y_i^q = \frac{r_q}{\alpha_q} \left(1 - \frac{X_i^q}{K_q}\right) (\beta_q + X_i^q)$.

The consumption number for this general case is

$$(9) \quad C_0 = \max\{C_1, C_2, \dots, C_n\},$$

where $C_p = \frac{c_p \alpha_p X_i^p}{\tau_p (\beta_p + X_i^p)}$, for $p = 1, 2, \dots, n$. Also, in the absence of competition terms $C_p = \frac{c_p \alpha_p K_p}{\tau_p (\beta_p + K_p)}$. Note that when $C_0 = 1$, the equilibrium points $\overline{E}_p = \overline{E}_q$. In the absence of competition the following results hold:

- (i) \overline{E}_p is stable (locally and globally) when $C_0 \leq 1$.
- (ii) \overline{E}_q is stable when $C_0 \geq 1$.

The above results can be established using reasoning similar to that used for model (2). These results also suggest that the long-term dynamics of this general MSC model (1) are also governed by the consumption number C_0 . Thus, the effects of multiple species on the consumption numbers, and thus on resource and consumer dynamics, should be important for the general case as reasoned for $n = 2$.

6. Discussion. Most ecological systems are made up of multiple species coexisting in their natural habitat. Understanding the dynamics of such ecosystems is important for their management and preservation. To study these dynamics we formulated an n -patch consumer resource mathematical model for multiple species coexisting.

Initial insights for MSC dynamics were gained by analyzing the special case when $n = 2$. For the purpose of illustration, resources X_1 and X_2 could be trees and grass, respectively, while their associated consumers would be browsers and grazers denoted by Y_1 and Y_2 , respectively. A threshold consumption number C_0 , which summarizes most of the parameters, is computed and used to identify system stability. The homogeneous version of the model is similar to consumer resource models found in the literature (Rosenzweig and MacArthur, [1963]; Turchin, [2003]; Owen-Smith, [2004]; Duffy, [2010]). Interestingly, while the MSC model is preferable because it should provide more information, we show that the long-term dynamics of this extended model is also governed by a similarly defined consumption number C_0 . This allows us to investigate the effects of MSC using C_0 . We find that increasing the number of species can change the stability dynamics. For example, parameter combinations that would eventually result in stable foci or cyclical dynamics can change. We show in Section 5 how these results should extend to more complex multiple consumer and resource models.

A criticism could be that our simplifying assumptions are restrictive and that real ecosystems are never close to equilibrium. However, theoretical studies using simple models are designed to highlight fundamental effects. If multiple species complexity can have an effect on understanding these simple stable dynamics a similar effect on the actual dynamics of more complex formulations is likely. Also, these effects can be tested by further theoretical and practical research.

Another important perspective here is that, as might be expected, the structure of the model apart from the parameter values has an effect on population dynamics as one increases species complexity. Increasing the complexity of the model results in averages of resource and consumer biomasses different to a system where parameters are averaged. We present an example where with increasing complexity biomasses are reduced when the dynamics are stable foci or become tighter in amplitude when the dynamics are cyclical. In as much as the model structure corresponds to real systems these results show how the extent of multiplicity could have a population dynamic consequence in and of itself and how this could be measured. In our example, the tighter amplitudes shown indicate a possible benefit for long-term survival as external impacts (biotic or abiotic) could have less chance of crashing the dynamics. Thus, it appears that when dynamics are cyclical there is a trade-off between biomass levels in the system and stability. This possibility would agree with other ecosystem simulations where increased heterogeneity changed dynamics to tighter, perhaps less vulnerable, solutions (Duffy, [2010]). Regardless of whether these speculations are true, the importance of taking multiple species dynamics into account is emphasized by those results and our results here.

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