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Consumption threshold used to investigate stability and ecological dominance in consumer-resource dynamics

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ABSTRACT

Understanding consumer resource population dynamics can be important to an understanding of the overall ecology of systems. For example, the tree-grass continuum dynamics of savannas, an important ecological biome, is influenced by the population dynamics. Here we investigate herbivory driven population dynamics of a savanna using a simple model of the interactions of the dominant players, namely: trees, grasses, browsers, grazers and mixed browsers-grazers. We introduce a consumption threshold that summarises some of the parameters and this is used as a guide to understanding the dynamics. This number is used in investigating system stability and sensitivity to parameter fluctuations. It is also used to identify degrees of ecological dominance.

1. Introduction

Savannas are an important ecological biome, economically and geographically (Sankaran et al., 2005). Grass-tree co-existence is of interest as it defines a savanna. In particular, understanding this co-existence is important as it affects plant and livestock production, and the overall functioning of the ecosystem (Sankaran et al., 2005). Most savannas have browsers, grazers and mixed feeders that influence the dynamics of the system. Here we are interested in the degree to which these consumers can affect the state of the system through grazing and browsing alone, in other words affecting the population dynamics of the entire system. For this reason we use a simple consumer resource equation model that focuses on herbivory to understand the propensity of a savanna system to produce stable population dynamics and investigate for which situations these dynamics are cyclical. For this we use biomass in g/m^2 as our units. This is convenient as it allows further simplification in terms of combining growth and reproduction into single parameters (Getz, 2012).

Any model is a simplification of the real system. For example, the actual dynamics are dependent on rainfall and fire events. However, of interest here is the effect of population cycles independent of fire and rain and this is how our model is formulated. On the other hand, fire and rainfall can be taken into account by investigating ranges in parameter values as provided by data (for example by (Dye and Spear, 1982)).

For our model, the consumers increase their biomass through eating resource biomass (i.e. both increasing biomass and birth). As the resource diminishes its effect on increasing consumer biomass reduces. Consumer biomass also reduces by a mortality type factor (death and weight loss) due to factors other than resource. The resource grows by a factor towards a carrying capacity and is also limited by competition with other resources. The consumers remove resources proportional to their own and the resource biomass. This effect also diminishes as the resource reduces. The model describing these dynamics is a system of differential equations presented below in Eq. (1).

We introduce a threshold quantity (consumption number denoted by C_0) similar to the basic reproduction $\mathcal{R}_0$ in epidemiological models (van den Driessche and Watmough, 2002). Ecologically, C_0 can be understood as the expected quantity of resources consumed per equivalent of consumer biomass for the duration of consumption. So, $C_0 = 1$ signifies that each unit of consumer biomass consumes an equivalent biomass of resource. For $C_0 < 1$ less resource is consumed per unit of consumer and for $C_0 > 1$ more resource is consumed per unit of consumer. C_0 is defined below in Eq. (2).

The type of model described here could be used to investigate a particular situation of a consumer resource system. Here, however, the primary aim is to describe theoretically how this type of system can benefit from the perspective of this consumption threshold

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Table 1
Variables for model (1).

Variables	Meaning	Unit
X	Tree density	g/m^2
Y	Grass density	g/m^2
U	Browser density	g/m^2
V	Grazer density	g/m^2
W	Mixed feeders density	g/m^2

quantity. Shown is the possible use of this threshold to investigate system stability and sensitivity to parameter fluctuations. It is also used to identify degrees of ecological dominance.

2. The model

Since the time of Lotka (1925) and Volterra (1926) ordinary differential equations have been used in consumer resource population models. Interesting dynamical behaviours have been discovered for these types of models and links to real systems established (Kooi et al., 2011; Fussmann et al., 2000; Turchin, 2003). In this paper we are interested in the possibility of cyclical population dynamics and the standard Rosenzweig and MacArthur (1963) model is a good starting place because it can result in either cyclical or equilibrium conditions. We have developed this basic model into a model that describes grazer and browser dynamics with their respective resources (1). Also, these resources compete for space. The final model is given by

$$\begin{aligned}
\frac{dX}{dt} &= Xr_x(1-X/K_x) - \alpha_u XU/(\alpha_{1/2}+X) - \alpha_w XW/(\alpha_{1/2}+X),\\
\frac{dY}{dt} &= Yr_y(1-Y/K_y) - \beta_v YV/(\beta_{1/2}+Y) - \beta_w YW/(\beta_{1/2}+Y),\\
\frac{dU}{dt} &= c_x\alpha_u XU/(\alpha_{1/2}+X) - U\tau_u,\\
\frac{dV}{dt} &= c_y\beta_v YV/(\beta_{1/2}+Y) - V\tau_v,\\
\frac{dW}{dt} &= c_x\alpha_w XW/(\alpha_{1/2}+X) + c_y\beta_w YW/(\beta_{1/2}+Y) - W\tau_w.
\end{aligned} \tag{1}$$

The meaning of variables and parameters used in the model with their various units are presented in Tables 1 and 2 respectively.

Table 2
Parameters with their units for model (1).

Parameters	Meaning	Unit
r_x	Tree density growth rate	/year
r_y	Grass density growth rate	/year
K_x	Tree density carrying capacity	g/m^2
K_y	Grass density carrying capacity	g/m^2
α_u	Tree removal by browser	/year
α_w	Grass removal by mixed feeders	/year
β_v	Grass removal by grazer	/year
β_w	Tree removal by mixed feeders	/year
$\alpha_{1/2}$	Tree density when removal by browser and mixed feeders is half	g/m^2
$\beta_{1/2}$	grass density when removal by grazer and mixed feeders is half	g/m^2
c_x	Conversion of tree biomass into browser/mixed feeders biomass	Dimensionless
c_y	Conversion of grass biomass into grazer/mixed feeders biomass	Dimensionless
τ_u	Reduction of browsers due to other factors	/year
τ_v	Reduction of grazers due to other factors	/year
τ_w	Reduction of mixed feeders due to other factors	/year

Introduced and defined here is a threshold quantity (consumption number denoted by C_0), and this quantity is used to show conditions under which the equilibrium points of the system are stable. This number is similar to the basic reproduction number $\mathcal{R}_0$ in epidemiological models and C_0 is calculated in the same way using the next generation matrix approach (van den Driessche and Watmough, 2002):

$$C_0 = \max\{C_1, C_2, C_3\}, \tag{2}$$

where

$$\begin{aligned}
C_1 &= \frac{c_x\alpha_u K_x}{\tau_u(\alpha_{1/2}+K_x)},\ C_2 = \frac{c_y\beta_v K_y}{\tau_v(\beta_{1/2}+K_y)},\\
C_3 &= \frac{c_x\alpha_w K_x}{\tau_w(\alpha_{1/2}+K_x)} + \frac{c_y\beta_w K_y}{\tau_w(\beta_{1/2}+K_y)}.
\end{aligned}$$

C_3 can be rewritten as $C_3 = \frac{\alpha_w\tau_u C_1}{\tau_w\alpha_u} + \frac{\beta_w\tau_v C_2}{\tau_w\beta_v}$. Note that C_1, C_2 and C_3 denote consumption numbers induced by browsers, grazers and mixed feeders respectively.

3. Results

Model (1) has infinitely many equilibrium points given by

$$\begin{aligned}
E_1 &= (X_1^0, Y_1^0, U_1^0, V_1^0, W_1^0) = (0,0,0,0,0),\\
E_2 &= (X_2^0, Y_2^0, U_2^0, V_2^0, W_2^0) = (K_x,0,0,0,0),\\
E_3 &= (X_3^0, Y_3^0, U_3^0, V_3^0, W_3^0) = (0,K_y,0,0,0),\\
E_4 &= (X_4^0, Y_4^0, U_4^0, V_4^0, W_4^0) = (K_x,K_y,0,0,0),\\
E_5 &= (X_5^0, Y_5^0, U_5^0, V_5^0, W_5^0)\\
&= \left(\frac{\tau_u\alpha_{1/2}}{c_x\alpha_u-\tau_u}, 0, \frac{r_x}{\alpha_u}\left(1-X_5^0/K_x\right)(\alpha_{1/2}+X_5^0), 0, 0\right),\\
E_6 &= (X_6^0, Y_6^0, U_6^0, V_6^0, W_6^0)\\
&= \left(0, \frac{\tau_v\beta_{1/2}}{c_y\beta_v-\tau_v}, 0, \frac{r_y}{\beta_v}\left(1-Y_6^0/K_y\right)(\beta_{1/2}+Y_6^0), 0\right),\\
E_7 &= (X_7^0, Y_7^0, U_7^0, V_7^0, W_7^0) = \left(X_5^0, K_y, U_5^0, 0, 0\right),\\
E_8 &= (X_8^0, Y_8^0, U_8^0, V_8^0, W_8^0) = \left(K_x, Y_6^0, 0, V_6^0, 0\right),\\
E_9 &= (X_9^0, Y_9^0, U_9^0, V_9^0, W_9^0) = \left(X_5^0, Y_6^0, U_5^0, V_6^0, 0\right),\\
E_{10} &= (X_{10}^0, Y_{10}^0, U_{10}^0, V_{10}^0, W_{10}^0)\\
&= \left(X_5^0, Y_6^0, U_5^0 - \alpha_w W^*/\alpha_u, V_6^0 - \beta_w W^*/\beta_u, W^*\right),
\end{aligned}$$

where W^* is any fixed value. Note, for existence of the equilibrium points E_i (for i = 1, 2, 3, ..., 10) the inequalities $0 \le X_i^0 \le K_x$, $0 \le Y_i^0 \le K_y$ must hold. Before investigating the stability of the above equilibrium points we will first discuss the relationship between the equilibrium points at $C_0 = 1$.

(i) $E_2 = E_5$, if $C_0 = C_1 = 1$.
(ii) $E_3 = E_6$, if $C_0 = C_2 = 1$.
(iii) $E_4 = E_7$, if $C_0 = C_1 = 1$.
(iv) $E_4 = E_8$, if $C_0 = C_2 = 1$.
(v) $E_4 = E_9$, if $C_0 = C_1 = C_2 = 1$.

The above relationships suggest that C_0 is a bifurcation parameter. This will be confirmed later using mathematical analyses. Note that $E_5, E_6, \ldots, E_{10}$ do not exist when $C_0 < 1$ and so their stability will be investigated for $C_0 \ge 1$.