

LETTER TO THE EDITOR

Global Stability of Two-level Detritus Decomposer Food Chains

Decomposition of dead organic material provides a major pathway of energy transport in ecosystems. Trophic interactions in which detritus is involved play an important role in ecosystem structure and function (DeAngelis *et al.*, 1989; McNaughton *et al.*, 1989; Hairston & Hairston, 1993; Moore *et al.*, 1993). The stability of ecosystems is usually studied by analysing the dynamics of the interacting populations, represented by Lotka–Volterra type equations (May, 1973; Pimm, 1982; Moore *et al.*, 1993). For food chains of arbitrary length, Harrison (1979) showed that these kinds of models are globally asymptotically stable, provided that there is intraspecific competition at the primary producer level. Lotka–Volterra equations, however, do not model detritus. Here we show that detritus-decomposer chains, as modelled by Moore *et al.* (1993), can also be globally asymptotically stable.

Let the dynamics of detritus (X_1) in a system of n “species” be represented by the following differential equation (Moore *et al.*, 1993; *sensu* DeAngelis *et al.*, 1989; for similar equations see also Hofbauer & Sigmund, 1988: 64 and Logofet, 1993: 192):

$$\frac{dX_1}{dt} = R + \sum_{i=2}^n d_i X_i + \sum_{i=1}^{n-1} \sum_{j=2}^n (1 - a_j) c_{ij} X_i X_j - \sum_{i=2}^n c_{1i} X_1 X_i, \quad (1)$$

where X_i is the density of species i , R is the input of allochthonous material, a_j is the assimilation efficiency of group j ($0 < a_j < 1$), c_{ij} is the coefficient of predation on group i by group j , d_i is the specific death rate of group i , and all parameters are defined to be positive. This equation describes the rate of change in detritus formed by an increase resulting from external inputs, other species’ deaths and uneaten meals, and a decrease due to decomposition (or grazing by detritivores). The equation contains terms that do not depend on the density

† In which case $e_{ij} = 0$ unless $|j - i| = 1$ or $j = i$; $e_{i,i-1} > 0$ and $e_{i,i+1} < 0$.

of detritus itself, which distinguishes a detrital model from a standard Lotka–Volterra model, the latter having the general form:

$$\frac{dX_i}{dt} = X_i \left(b_i + \sum_{j=1}^n e_{ij} X_j \right), \quad i = 1, \dots, n, \quad (2)$$

where b_i is the specific growth rate of species i , and e_{ij} is either a predation, consumption or self-limiting coefficient; b_i and e_{ij} can be positive or negative.

To prove global stability of a Lotka–Volterra system described by eqn (2), with a non-trivial equilibrium $X^* = (X_1^*, X_2^*, \dots, X_n^*)$, the energy function V can be used (Goh, 1977):

$$V(X) = \sum_{i=1}^n l_i \left[X_i - X_i^* - X_i^* \ln \frac{X_i}{X_i^*} \right]. \quad (3)$$

Writing the parameters b_i in terms of equilibrium values X_i^* , the time derivative of V can be written as follows:

$$\begin{aligned} \frac{dV}{dt} &= \sum_{i=1}^n l_i (X_i - X_i^*) \frac{1}{X_i} \frac{dX_i}{dt} \\ &= \sum_{i=1}^n l_i (X_i - X_i^*) \sum_{j=1}^n e_{ij} (X_j - X_j^*). \end{aligned} \quad (4)$$

If $dV/dt \leq 0$, V is called a Lyapunov function and the system is globally stable, provided all solutions are bounded for $t \geq 0$, which is the case since $V(X) \rightarrow \infty$ as $\|X\| \rightarrow \infty$ (La Salle & Lefschetz, 1961). For food chains†, Harrison (1979) elegantly showed how to construct a Lyapunov function, choosing positive numbers l_i such that $l_i e_{i,i+1} = l_{i+1} e_{i+1,i}$, which cancels out the terms in eqn (4) referring to a predator–prey interaction. Thus, the time derivative of V could be written in terms of only intraspecific parameters:

$$\frac{dV}{dt} = \sum_{i=1}^n l_i e_{ii} (X_i - X_i^*)^2. \quad (5)$$

Since $e_{ii} \leq 0$, $dV/dt \leq 0$. For chains of arbitrary length, Harrison (1979) proved inductively that intraspecific competition at the basic (primary producer) level is a sufficient condition for global asymptotic stability.

Now, consider a detritus-decomposer model using eqn (1):

$$\frac{dX_1}{dt} = R + d_2X_2 - a_2c_{12}X_1X_2 \quad (6)$$

$$\frac{dX_2}{dt} = X_2(-d_2 + a_2p_2c_{12}X_1), \quad (7)$$

where p_2 is the production efficiency of the decomposer ($0 < p_2 < 1$) and all parameters are defined to be positive.

To evaluate whether V as defined in eqn (3) could serve as a Lyapunov function, the same method, as was used for the Lotka-Volterra models, could not be applied directly, because writing the parameters d_2 and R in terms of the equilibrium values, $d_2 = a_2p_2c_{12}X_1^*$ and $R = (1 - p_2)a_2c_{12}X_1^*X_2^*$, gives:

$$\frac{dX_1}{dt} = (X_2 - X_2^*)a_2p_2c_{12}X_1^* - (X_1X_2 - X_1^*X_2^*)a_2c_{12} \quad (8)$$

$$\frac{dX_2}{dt} = X_2(X_1 - X_1^*)a_2p_2c_{12}, \quad (9)$$

and there is no straightforward way to choose values l_i in eqn (3) such that $dV/dt \leq 0$ for all states. However, if we express the first two terms of eqn (6) as functions of X_1 :

$$R + d_2X_2 = \frac{X_1}{X_1^*}(R + d_2X_2) - \frac{(X_1 - X_1^*)}{X_1^*}(R + d_2X_2), \quad (10)$$

and use $d_2 = a_2p_2c_{12}X_1^*$ and $R = (1 - p_2)a_2c_{12}X_1^*X_2^*$, the system can be rewritten:

$$\frac{dX_1}{dt} = -X_1(X_2 - X_2^*)(1 - p_2)a_2c_{12} - \frac{(X_1 - X_1^*)}{X_1^*}(R + d_2X_2) \quad (11)$$

$$\frac{dX_2}{dt} = X_2(X_1 - X_1^*)a_2p_2c_{12}, \quad (12)$$

and the time derivative of V becomes

$$\begin{aligned} \frac{dV}{dt} &= \sum_{i=1,2} l_i(X_i - X_i^*) \frac{1}{X_i} \frac{dX_i}{dt} \\ &= (X_1 - X_1^*)(X_2 - X_2^*)a_2c_{12}(-l_1(1 - p_2) \\ &\quad + l_2p_2) - l_1 \frac{(X_1 - X_1^*)^2}{X_1X_1^*}(R + d_2X_2). \end{aligned} \quad (13)$$

If we choose positive numbers l_i such that $l_1(1 - p_2) = l_2p_2$, V is a Lyapunov function because its time derivative is

$$\frac{dV}{dt} = -l_1 \frac{(X_1 - X_1^*)^2}{X_1X_1^*}(R + d_2X_2) \leq 0. \quad (14)$$

Hence, the equilibrium is globally stable. It is also globally asymptotically stable because the system never remains on a "ledge". If there is a trajectory for which $dV/dt = 0$ for all t , $X_1 = X_1^*$ for all t and consequently $dX_1/dt = 0$. But also $dX_2/dt = 0$, as can be concluded from eqn (12). The only solution that satisfies these conditions is the equilibrium solution. All other trajectories approach X^* as $t \rightarrow \infty$.

The present analysis shows that food chains can be asymptotically stable without intraspecific competition through the input of detritus from outside the system (R) and the recycling of material (d_2X_2). For primary producer food chains each link could be analysed in the same way as the two-species interaction (see Harrison, 1979). If we add trophic levels to the detritus chain, however, we do not obtain a chain in the strict sense because all levels are connected with detritus through the feedbacks from natural death rates and unassimilated fractions of consumption [see eqn (1)]. Although the results have only been demonstrated to hold for two-level chains, they furthermore support the idea that a greater role of detritus in material fluxes in ecosystems is associated with greater stability (Odum, 1966).

The authors thank John Moore and Franjo Weissing for advice and comments on the manuscript.

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(Received on 19 January 1994, Accepted in revised form on 1 July 1994)

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