



# Marker Transport Through Ecosystem Energy Flow

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Markers are substances which are artificially introduced into ecosystems in small quantities and which have no acute effects on energy flow. A marker might be a pollutant which affects life significantly only over long time frames. Alternatively, a marker might be a benign substance easily detected in small amounts and introduced in order to trace energy flow and so evaluate energy flow models. The flow of markers can be modeled in parallel to energy flow by assuming that energy flowing out of a compartment carries with it a proportional mass of marker. The purpose of this paper is to derive qualitative conditions on the food-web structure and the consumption functions of a model which guarantee stability of energy and marker flows. We will show that many consumption functions used in mathematical ecology lead to sign-stable models of energy flow and furthermore that such models enjoy inherent stability of associated marker flows.

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## 1. Introduction

The purpose of this paper is to model and characterize the flow of a marker in ecosystems. A marker is defined to be a substance which is carried by ecosystem energy flows but which does not acutely affect those flows. For our purposes, the energy content of an ecosystem compartment means its mass of fixed carbon. A marker is also measured as mass in each compartment. The foundation of our effort is the physical notion of conservation of mass of biologically indivisible entities, among which is assumed to be the marker.

A marker is herein also assumed to be neither preferentially excreted nor retained by any compartment, so the mechanism of bioaccumulation is absent. Certain radionuclide tracers may be examples of markers (Odum, 1971), as would be, therefore, certain types of radioactive pollutants. If an ecosystem model has  $n$  energy compartments, the same compartments also contain amounts of marker, leading in a natural way to a  $2n$ -dimensional dynamical system.

To illustrate the parallelism between energy and

marker flows, let us start with an example of the familiar Lotka–Volterra model

$$\begin{aligned} dx_1/dt &= x_1(A - Bx_1 - Cx_2) \\ dx_2/dt &= x_2(Dx_1 - Ex_2 - F) \\ dx_3/dt &= Fx_2 - Gx_3x_4 \\ dx_4/dt &= x_4(Hx_3 - Ix_4) \end{aligned} \quad (1)$$

where  $x_1$  = autotroph,  $x_2$  = herbivore,  $x_3$  = detritus generated by the herbivore and  $x_4$  = detritivore. The variables  $\{x_i\}$  are the amounts of energy (as fixed carbon) in ecosystem compartments. The coefficients  $A$  through  $I$  are positive constants. The terms  $A - Bx_1 - Cx_2$  and  $Dx_1 - Ex_2 - F$  are in units: [mass per time]/mass. Coefficient  $A$  arises from photosynthesis, coefficients  $C$  and  $D$  correspond to energy transfer through consumption, and coefficients  $B$  and  $E$  are intracompartmental energy loss effects (excretion, heat loss, or autolysis). Here compartments  $x_1$  and  $x_2$  comprise a two-dimensional “consumption community”, a subsystem with dynamics independent of the downstream detritus compartment  $x_3$  and detritivore compartment  $x_4$ . Coefficient  $F$  corresponds to “detritus donation” from the herbivore compartment  $x_2$  to the detritus compartment  $x_3$ . A second

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consumption community with compartments  $x_3$  and  $x_4$  is built upon detritus. The coefficient  $G$  corresponds to consumption of detritus energy and the coefficient  $H$  corresponds to energy arrival in a detritivore. Finally, coefficient  $I$  is another intracompartamental energy loss term.

$$L = \begin{pmatrix} -B_{x_1} & -C_{x_1} & 0 & 0 & 0 & 0 & 0 & 0 \\ D_{x_2} & -E_{x_2} & 0 & 0 & 0 & 0 & 0 & 0 \\ * & * & -G_{x_4} & -G_{x_3} & 0 & 0 & 0 & 0 \\ * & * & H_{x_4} & -I_{x_4} & 0 & 0 & 0 & 0 \\ * & * & * & * & -K_1 - A & 0 & 0 & 0 \\ * & * & * & * & * & -K_2 - E_{x_2} - F & 0 & 0 \\ * & * & * & * & * & * & -K_3 - G_{x_4} & 0 \\ * & * & * & * & * & * & * & -K_4 - I_{x_4} \end{pmatrix} \quad (4)$$

Provided  $F$  is sufficiently small, this energy flow model (1) has a unique constant trajectory in which all components are positive (as well as other constant trajectories). The constant trajectory with positive components is

$$\begin{aligned} \bar{x}_1 &= (AE + FC)/(BE + CD) \\ \bar{x}_2 &= (D\bar{x}_1 - F)/E \\ \bar{x}_3 &= [F\bar{x}_2/(GH)]^{1/2} \\ \bar{x}_4 &= H\bar{x}_3/I \end{aligned} \quad (2)$$

Now let  $u_1, u_2, u_3, u_4$  represent the amounts of a marker in the same compartments. Thus each  $u_i$  is in units of mass. Suppose by virtue of excretion, metabolic consumption, or autolysis, the concentration of marker in compartment  $i$  exponentially decays at the rate  $-K_i$  times concentration. We allow the possibility that some or all  $K_i = 0$ . Such first-order kinetics are sometimes assumed in mathematical biology in lieu of details of biochemical mechanisms. For example, excretion of an element in an aquatic plant-herbivore system has been so modeled by Nisbet *et al.* (1991). The coefficients  $K_i$  are also in units [mass per time]/mass. Mass conservation and the assumption of proportional transport of energy and marker imply that the associated equations for marker rates of change are

$$\begin{aligned} du_1/dt &= -K_1u_1 + u_1(-Bx_1 - Cx_2) \\ du_2/dt &= -K_2u_2 + u_1Dx_2 - u_2Ex_2 - Fu_2 \\ du_3/dt &= -K_3u_3 + Fu_2 - u_3Gx_4 \\ du_4/dt &= -K_4u_4 + u_3Hx_4 - u_4Ix_4 \end{aligned} \quad (3)$$

Together (1) and (3) constitute an eight-dimensional dynamical system.

The trajectory trapping theorem (Jeffries, 1989)

shows that if all eight state variables in  $(x, u)$  are initially positive, then no state variable can reach zero in finite time.

The linear approximation matrix  $L$  for the full, eight-dimensional system at the constant trajectory  $(\bar{x}_1, \bar{x}_2, \bar{x}_3, \bar{x}_4, 0, 0, 0, 0)$  is

The first and second consumption communities correspond to the two 2-by-2 blocks in the upper left corner. The \* entries are unimportant in the sense that regardless of their values, this matrix is sign-stable (Jeffries, 1989, pp. 108–113). That is, just the sign pattern of the displayed entries in this matrix guarantees that the real parts of all eigenvalues of the matrix are negative. Thus every trajectory starting sufficiently close to the constant trajectory must asymptotically approach it.

The significance of sign-stability lies in the fact that the qualitative pattern of interactions insures stability, provided that no parameters change sign. Precise values of ecosystem flow parameters are generally difficult if not impossible to obtain. Thus sign-stable systems not only can be relied upon to exhibit stability as models but also can be argued to capture the general nature of organization at the ecosystem level. Systems with linear approximations which are not sign-stable will be unstable or topologically the same as unstable systems.

## 2. General Stability Criteria

A dynamical system with a constant trajectory  $\bar{x}$  is

$$dx_i/dt = \sum_{j=1 \dots n} L_{ij}(x_j - \bar{x}_j) + \text{higher order terms in } (x_j - \bar{x}_j) \quad (4a)$$

The linear approximation matrix of this system at  $\bar{x}$  is, of course,  $L$  itself. This system (4a) is stable at  $\bar{x}$  provided the real part of every eigenvalue of  $L$  is negative (Brauer & Nohel, 1989). In turn, this eigenvalue condition is satisfied provided  $L$  meets the following qualitative-quantitative conditions (Jeffries, 1979, 1989):

- (a) every diagonal entry of **L** is negative;
- (b) matrix **L** is in block form (possibly after relabeling the system variables) in which all blocks above and right of main diagonal blocks are all zero; the diagonal blocks are either submatrices (corresponding to subsystems called consumption communities) with positive and negative off-diagonal pairs of entries, or lower triangular blocks; in every consumption community submatrix (diagonal block),  $i \neq j$  and  $L_{ij} \neq 0$  imply  $L_{ij}L_{ji} < 0$ ;
- (c) in every consumption community, no loops exist, that is, every cyclic product of  $p \geq 3$  terms in a consumption community is zero; thus, for example,  $L_{12}L_{23} \dots L_{p1} = 0$ .

A more complicated but less restrictive condition can replace (c): all loops in consumption communities

### 3. Some Consumption Functions Appearing in the Literature

The survey by DeAngelis (1992 p. 83) lists a variety of two-compartment predation models of the form

$$\begin{aligned} dx/dt &= G(x) - F(x, y) = G(x) - xy\Phi_i(x) \\ dy/dt &= \eta F(x, y) - H(y) = \eta xy\Phi_i(x) - \tilde{H}(y) \end{aligned} \quad (5)$$

Here and throughout our analysis, only positive values of energy densities (such as  $x$  and  $y$ ) are considered. Here  $\eta$  is an efficiency constant and  $\Phi_i(x)$  is one of the first six functions in (6). For purposes to be explained below, we also list  $\Phi_i + x d\Phi_i/dx$  for each  $\Phi_i$ .

$\Phi_i$	$\Phi_i + x d\Phi_i/dx$
$\Phi_1 = 1/(b + x)$	$b/(b + x)^2$
$\Phi_2 = [1 - \exp(-kx)]/x$	$k \exp(-kx)$
$\Phi_3 = x/(b^2 + x^2)$	$2xb^2/(b^2 + x^2)^2$
$\Phi_4 = x/[(b_1 + x)(b_2 + x)]$	$x(2b_1b_2 + b_1x + b_2x)/[(b_1 + x)^2(b_2 + x)^2]$
$\Phi_5 = (x - x_0)/[x(b + x)]$	$(b + x_0)/(b + x)^2$
$\Phi_6 = 1/[x^{1/2}(b + x^{1/2})]$	$b/[2x^{1/2}(b + x)^{1/2}]$

are "balanced" in the sense of equality of magnitudes of products of factors in the two directions around each loop (Jeffries, 1979). Thus, for example,  $|L_{12}L_{23} \dots L_{p1}| = |L_{1p}L_{p,p-1} \dots L_{21}|$ . The ecological interpretation of "balanced loops" is equality of products of efficiencies  $|L_{ij}/L_{ji}|$  of different paths in a consumption community from a compartment in a low trophic level to a top consumer compartment.

Sign-stability can replace lengthy algebra arguments to establish stability of or point to specific destabilizing entries in some linear approximation matrices appearing in the mathematical ecology literature. For example, many of the 3-by-3 matrices in Schmitz (1992) can be so treated.

A constant trajectory  $\underline{x}$  for a nonlinear dynamical system is called locally stable if all trajectories starting sufficiently close to  $\underline{x}$  must stay arbitrarily close to  $\underline{x}$  and must asymptotically approach  $\underline{x}$ . If the linear approximation at  $\underline{x}$  of the nonlinear system (4a) is stable (all eigenvalues of the linear approximation matrix **L** have negative real parts), then the full nonlinear system is locally stable (Brauer & Nohel, 1989). In particular, the linear approximation matrix **L** in (4) fulfills the above four conditions. Note that **L** has two 2-by-2 consumption community blocks and a 4-by-4 lower triangular diagonal block.

The parameters  $b, k, b_1, b_2, x_0$  are all positive constants.

The linear approximation matrix **L** of (5) at a constant trajectory  $(\underline{x}, \underline{y})$  using  $\Phi_i$  from (6) has off-diagonal entries

$$\begin{aligned} L_{12} &= -\underline{x}\Phi_i(\underline{x}) \\ L_{21} &= \eta \underline{y}(\Phi_i + \underline{x} d\Phi_i/dx) \end{aligned} \quad (7)$$

Thus a constant trajectory meets conditions (b) and (c) of the general stability criteria only if

$$\Phi_i(\underline{x}) + \underline{x}\Phi_i'(\underline{x}) > 0 \quad (8)$$

where ' is the derivative of  $\Phi_i(x)$  with respect to  $x$ . Remarkably enough, for all  $(x, y)$  in the positive orthant, not just for a constant trajectory  $(\underline{x}, \underline{y})$ , each of the functions  $\Phi_i$  in (6) fulfills (8). The biological interpretation of (8) is this: near  $(\underline{x}, \underline{y})$  the full consumption term  $xy\Phi(x)$  must increase if biomass available for consumption  $x$  increases. This condition is related to but not the same as one of Kolmogorov's criteria for existence of a constant attractor trajectory or limit cycle in two-dimensional systems (Yodzis, 1989).

The diagonal entries in **L** at  $(\underline{x}, \underline{y})$  are

$$\begin{aligned} L_{11} &= dG/dx - \underline{y}[\Phi_i(\underline{x}) + \underline{x} d\Phi_i/dx] \\ L_{22} &= \eta \underline{x}\Phi_i(\underline{x}) - dH/dy \end{aligned} \quad (9)$$

Condition (a) of the general stability criteria requires at a constant trajectory  $(\bar{x}, \bar{y})$ —but not necessarily at all  $(x, y)$  in the positive orthant—that

$$dG/dx - \bar{y}[\Phi_i(\bar{x}) + \bar{x}d\Phi_i/dx] < 0 \quad (10)$$

$$\eta\bar{x}\Phi_i(\bar{x}) - dH/dy < 0$$

Thus if  $dG/dx$  is non-positive at  $(\bar{x}, \bar{y})$  and  $dH/dy$  is greater than  $\eta\bar{x}\Phi_i(\bar{x})$ , then all of (10) is fulfilled. The requirement  $dH/dy > \eta\bar{x}\Phi_i(\bar{x})$  might be referred to as the dominance of auto-regulation in the dynamics of the predator population near the constant trajectory  $(\bar{x}, \bar{y})$ .

It is natural to consider models in which  $\Phi_i + x\Phi_i'$  is not positive. As described in Jeffries (1989) and the several primary references therein, the northern prairie of western Canada is characterized by long, cold winters followed each spring by a tremendous burst of productivity. Rather than settling on a constant trajectory, such an ecosystem goes between extremes of compartment dynamics, extremes represented by arrival in spring of migratory birds and emergence of adult grasshoppers. Insectivorous birds find themselves in an ocean of food. In such a case, the rate of energy taken up by birds such as clay-colored sparrows (*Spizella pallida*) depends upon the bird population but not upon the superabundant grasshopper population. That is,  $\eta xy\Phi(x, y)$  in (5) must be replaced by some  $\eta\Psi(y)$  so  $\partial\Psi/\partial x = 0$  in  $L_{21}$  becomes zero.

#### 4. A General Model for Energy and Marker Flows

The main point of this paper is to develop implications of the general stability criteria for  $n$ -dimensional energy (fixed carbon mass) flow systems as well as analogous criteria for marker transport systems.

The basis of energy and marker flow modeling is consistent accounting of introduction, transport and removal effects. We assume the compartments of the model are partitioned into predation communities connected by detritus donation. Every compartment must generate energy (as do autotrophs), consume the energy from some other compartments or receive detritus from some other compartments. The general energy flow model is

$$dx_i/dt = x_i I_i(x_i) - x_i L_i(x_i) - \sum_{i < j} x_i G_{ij}(x_i) x_j + \sum_{i > j} \eta_{ij} x_i G_{ij}(x_j) x_j + \sum_{k < i} D_{ik}(x) x_k \quad (11)$$

The terms on the right side of (11) are respectively self-mediated input (such as photosynthesis), self-mediated loss (heat, detritus), consumption loss, consumption gain, and detritus gain from other compartments in other upstream consumption communities. The system functions  $I$ ,  $L$ ,  $G$  and  $D$  are all assumed to be piecewise smooth; predation efficiency  $\eta_{ij}$  (energy gain to  $i$  per energy loss to  $j$ ) is assumed constant between 0 and 1.

The partition of compartments means that as a matrix of functions,  $D_{ik}$  is zero unless compartments  $i$  and  $k$  are in different consumption communities. Detritus donation functions  $D_{ik}(x)x_k$  depend only upon components of  $x$  in upstream consumption communities; the numbering of components reflects this in that  $D_{ik} \neq 0$  implies:  $i > k$ ;  $D_{ik} > 0$ ;  $D_{ki} = 0$ ; and  $\partial D_{ik}/\partial x_j = 0$  unless  $i > j$ . Regarding the matrix  $G$  of consumption functions, if  $G_{ij} \neq 0$ , then compartments  $i$  and  $j$  are in the same predation community and  $G_{ij}G_{ji} < 0$ . Moreover,  $G_{ij}$  depends only upon the consumed compartment level (the lesser of  $i$  and  $j$ ); this is shown in (11) by the  $G_{ij}(x_i)x_j$  terms for  $i < j$  and the  $x_i G_{ij}(x_j)$  terms for  $i > j$ . The partition assumption implies indices can be chosen so that  $G_{ij} > 0$  implies  $i > j$ .

The model (1) is an example of (11). It should be appreciated, however, that (11) allows for consumption communities of arbitrary size (not just two-dimensional) and number (not just two). Furthermore, (11) allows for non-constant coefficients  $I$ ,  $L$ ,  $G$ ,  $D$ —in contrast to the simple constant coefficients of (1).

In parallel to (11) we define the general marker flow model by

$$du_i/dt = -K_i u_i - u_i L_i(x_i) - \sum_{i < j} u_i G_{ij}(x_i) x_j + \sum_{i > j} \eta_{ij} x_i G_{ij}(x_j) u_j + \sum_{k < i} D_{ik}(x) u_k. \quad (12)$$

Here  $K_i$  is a decay constant (possibly zero). This model could be modified by adding a term  $u_i I_i(x_i)$  to represent incorporation of a marker from the environment, for example, a soil contaminant. This system is readily derived from the assumption that the marker per energy ratio  $u_i/x_i$  multiplied by the rate at which energy moves to or from compartment  $i$  is the rate at which marker arrives in or departs from that compartment. Together (11) and (12) comprise a  $2n$ -dimensional dynamical system.

The model (1), (3) from the first section can be seen to be an example of (11) and (12). Again, the full energy-marker model offers much more generality

than that low-dimensional, constant coefficient example.

**5. Implications of General Stability Criteria for Energy and Marker Flows**

The energy flow model (11) and marker flow model (12) combine to yield a  $2n$ -dimensional dynamical system. If a constant trajectory  $(\underline{x}, \underline{u})$  exists for the full model, the linear approximation matrix  $L$  of partial derivatives at  $(\underline{x}, \underline{u})$  has the following form. For all  $i$  and  $j$  in the same consumption community,

- (a)  $\partial[dx_i/dt]/\partial x_i = I_i - L_i - \sum_{i < j} G_{ij}(\underline{x}_i)\underline{x}_j$   
 $+ \sum_{i > j} \eta_{ij}G_{ij}(\underline{x}_j)\underline{x}_j + \underline{x}_i[I_i' - L_i'] - \sum_{i < j} \underline{x}_i\underline{x}_jG_{ij}(\underline{x}_i)'$
- (b)  $\partial[dx_i/dt]/\partial x_j = -\underline{x}_jG_{ij}(\underline{x}_i)$  if  $i < j$
- (c)  $\partial[dx_i/dt]/\partial x_j = \eta_{ij}\underline{x}_i[G_{ij}(\underline{x}_j) + \underline{x}_jG_{ij}(\underline{x}_j)']$  if  $i > j$
- (d)  $\partial[du_i/dt]/\partial u_i = -k - L_i - \sum_{i < j} G_{ij}(\underline{x}_i)\underline{x}_j$
- (e)  $\partial[du_i/dt]/\partial u_j = 0$  if  $i < j$

We want to show that certain restrictions imply the form of  $L$  is consistent with the general stability conditions.

*Theorem.* Suppose  $(\underline{x}, \underline{u})$  is a constant trajectory for the energy-marker model. If an ecosystem model can be partitioned into consumption communities as in Section 2; if no loops exist in any consumption community (or if all loops are balanced); if for all  $i$ ,  $I_i' - L_i' - \sum_{i < j} \underline{x}_jG_{ij}(\underline{x}_i)' < 0$ ; and if for all  $i > j$  with  $G_{ij} \neq 0$ ,  $G_{ij}(\underline{x}_i) + \underline{x}_jG_{ij}(\underline{x}_i)' > 0$ ; then the energy-marker model is stable at  $(\underline{x}, \underline{u})$ .

*Proof.* The typical form of the linear approximation matrix  $L$  of (11), (12) at a constant trajectory  $(\underline{x}, \underline{u})$  is as follows.

$$L = \begin{pmatrix} \mathbf{A} & 0 & 0 & \dots & 0 & 0 & 0 & 0 \\ * & \mathbf{A} & 0 & \dots & 0 & 0 & 0 & 0 \\ * & * & \mathbf{A} & \dots & 0 & 0 & 0 & 0 \\ * & * & * & \dots & 0 & 0 & 0 & 0 \\ * & * & * & \dots & \mathbf{T} & 0 & 0 & 0 \\ * & * & * & \dots & * & \mathbf{T} & 0 & 0 \\ * & * & * & \dots & * & * & \mathbf{T} & 0 \\ * & * & * & \dots & * & * & * & \dots \end{pmatrix} \quad (14)$$

The  $A$  blocks represent  $q$ -by- $q$  consumption communities,  $1 \leq q \leq n$ . Concerning diagonal entries in  $A$ , we note that at a constant trajectory the first four terms of the right side of (13a) add to  $-(1/\underline{x}_i)\sum_{k < i} D_{ik}(\underline{x})\underline{x}_k$ , which is non-positive. Hence the assumption  $I_i' - L_i' - \sum_{i < j} \underline{x}_jG_{ij}(\underline{x}_i)' < 0$  implies the diagonal entries in each  $A$  are negative. Furthermore, the sum of the last two terms of the right side of (13) must be negative, for otherwise compartment  $i$  is not an autotroph, does not consume any other compartment and does not receive detritus from any other compartment. Thus each  $T$  has negative diagonal entries. The condition  $G_{ij}(\underline{x}_i) + \underline{x}_jG_{ij}(\underline{x}_i)' > 0$  implies the symmetric pairs of off-diagonal entries in each  $A$  are of opposite sign. Since condition (c) is assumed, each  $A$ , in itself, meets the general stability criteria. Each matrix  $*$  is of arbitrary form;  $0$  represents the zero matrix. Thus the upper left  $n$ -by- $n$  block in (14)—corresponding to the energy flow subsystem—meets the general stability criteria and so insures the stability of the energy flow part of (11).

Each marker compartment in each consumption community is paired with an energy compartment. Thus each marker submatrix  $T$  in (14) is of the same size as its corresponding consumption community matrix  $A$ . Considering (13d), we see each  $T$  has negative diagonal entries. By the choice of indices in Section 4,  $T$  is in lower triangular form (reflected in equation (13e)). Again  $*$  blocks among  $T$  blocks and  $*$  blocks corresponding to detritus donation are essential to the existence and values of the constant trajectory, but do not influence the eigenvalues of  $L$ . Note that the form of the lower right block is quite different from the upper left block; the full energy-marker system is not a trivial doubling of the energy system.

The above sign-pattern analysis shows that  $L$  meets the general stability criteria and that the real part of every eigenvalue of  $L$  is negative. By the linear approximation theorem of dynamical systems theory, the full energy-marker system is locally stable at the constant trajectory  $(\underline{x}, \underline{u})$ .

For a given matrix of the form of  $L$  in (14), sufficiently small additional terms in any positions (arising from partial derivatives of more general coefficients) would not change the fact that the linear approximation (and so the full system) is locally stable at  $(\underline{x}, \underline{u})$ .

**6. Conclusion**

We have modeled the flow of markers as part of an energy flow model by assuming that energy flowing out of a compartment carries with it a certain

proportional mass of marker. In describing sufficient qualitative conditions for stability, the condition (8) on consumption functions  $\Phi_i + x\Phi'_i > 0$  repeatedly presents itself. Here the rate of energy loss due to consumption is  $xy\Phi_i$ , so this condition is equivalent to requiring that the partial derivative of  $xy\Phi_i$  with respect to the consumed variable  $x$  be positive. This condition turns out to be met by several rates (6) studied by populations dynamicists. Given this condition and some additional flow conditions (including the absence or balancing of loops within consumption communities), the stability of an energy-marker model can be guaranteed. The flow conditions are largely qualitative, pointing to a model class with very desirable mathematical characteristics and arguably many reflections in nature.

In some special cases of (11) the general stability criteria assure not merely local stability near a constant trajectory, but also global asymptotic stability for all non-zero initial conditions (Cohen *et al.*, 1990). For example, consider the Lotka-Volterra equations with constant coefficients  $I_i$  and  $G_{ij}$ ,

$$dx_i/dt = x_i \left( I_i + \sum_{j=1 \dots n} G_{ij} x_j \right) \quad i = 1, \dots, n \quad (15)$$

Suppose each  $x_i(0) > 0$ , there is a constant trajectory (with positive components), each  $G_{ii} < 0$ , and every eigenvalue of  $G$  has non-positive real part. It can be shown then that every trajectory of (15) is bounded, has a limit as  $t \rightarrow \infty$ , and that the limit is independent of the initial conditions (Redheffer & Zhou, 1989; Cohen *et al.*, 1990, p. 611). The strength of (11) compared to (15) lies in the non-constancy of  $I_i$  and  $G_{ij}$ , but the conclusion of our present theorem is limited to local (not global) stability, as we next elucidate.

Global stability is not a hidden general feature of (11) or even its special case (5). For example, the abstract model

$$\begin{aligned} dx/dt &= \frac{1}{3}x + \frac{1}{6}x^2 - \frac{1}{2\pi} \sin(2\pi x) - xy/(1+x) \\ dy/dt &= \frac{1}{10}xy/(1+x) - \frac{1}{12}y + \frac{1}{30} \end{aligned} \quad (16)$$

satisfies the conditions of the theorem at two stable constant trajectories (1, 1) and (2, 2). Thus the theorem of the previous section gives only sufficient conditions for local stability of a constant trajectory. This example shows the mathematical possibility that such local attractors are not global attractors.

The model (11), (12) of marker transport has potential applications as a null model for comparison with the observed transport of a suspected toxin with decay. If a credible model of the form (11) can be constructed for energy flow and if the corresponding marker flow model (12) clearly fails to describe the trajectory of the suspected substance, then bioaccumulation, intoxication, selective sequestration, selective excretion, selective degradation, or some other deviation from passive neutral transport may be suspected.

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