Ecological Modelling 220 (2009) 3219–3224

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Dynamic environ analysis of compartmental systems: A computational approach

Jane Shevtsov[a,*], Caner Kazanci[b,c], Bernard C. Patten[a,c]

[a] Odum School of Ecology, University of Georgia, Athens, GA 30602, USA
[b] Department of Mathematics, University of Georgia, Athens, GA 30602, USA
[c] Faculty of Engineering, University of Georgia, Athens, GA 30602, USA

ARTICLE INFO

Article history:
Available online 23 September 2009

Keywords:
Environ analysis
Dynamic environ approximation
Ecosystem models
Compartment models
Food webs

ABSTRACT

Ecosystems are often modeled as stocks of matter or energy connected by flows. Network environ analysis (NEA) is a set of mathematical methods for using powers of matrices to trace energy and material flows through such models. NEA has revealed several interesting properties of flow–storage networks, including dominance of indirect effects and the tendency for networks to create mutually positive interactions between species. However, the applicability of NEA is greatly limited by the fact that it can only be applied to models at constant steady states. In this paper, we present a new, computationally oriented approach to environ analysis called dynamic environ approximation (DEA). As a test of DEA, we use it to compute compartment throughflow in two implementations of a model of energy flow through an oyster reef ecosystem. We use a newly derived equation to compute model throughflow and compare its output to that of DEA. We find that DEA approximates the exact results given by this equation quite closely – in this particular case, with a mean Euclidean error ranging between 0.0008 and 0.21 – which gives a sense of how closely it reproduces other NEA-related quantities that cannot be exactly computed and discuss how to reduce this error. An application to calculating indirect flows in ecosystems is also discussed and dominance of indirect effects in a nonlinear model is demonstrated.

1. Introduction

Compartment models (Matis et al., 1979) are widely used to represent ecological networks of *stocks*, x_i ($i = 1, 2, \ldots, n$), and *flows*, f_{ij} ($i, j = 1, 2, \ldots, n$), of conserved substances (energy or matter). The flows are generated by boundary *inputs*, z_j, and they terminate in boundary *outputs*, y_i. *Throughflows* are the sums of inflows, T_i^{in}, and outflows, T_i^{out}, to and from each stock. Within-model environments of the compartments are *environs* (Patten, 1978). These may be found using the system's mathematical description by *network environ analysis* (NEA), a set of methods derived from Leontief (1936, 1966) input–output analysis. NEA has revealed several interesting properties of flow–storage networks, including dominance of indirect effects (Patten, 1984; Higashi and Patten, 1989) and the tendency for networks to create mutually positive interactions between species (Patten, 1991).

At least three aspects of dynamical behavior limit the applicability of present NEA methods. (1) The methodology can only be applied to models at constant steady states where inputs balance outputs. This greatly limits the range of applicability because (2) not all models reach constant steady states, and (3) those that do may also have significant, but unanalyzable, transient behavior. Previous attempts to respond to these limitations and develop methods for non-steady-state linear (Hippe, 1983) as well as nonlinear (Hallam and Antonios, 1985) systems have not found use, in part because of their mathematical difficulty.

This paper describes a computational approach to dynamic environ analysis. Like NEA, the dynamic methodology can be applied to any compartment model that satisfies two properties. First, either all compartments that have an input must have a boundary output or, failing that, every block of compartments that receives an input must have a boundary output (Fadeev and Fadeeva, 1963). Second, at least one compartment must receive input from outside the system to prevent system descent to the zero state (although zero-input transient dynamics from a nonzero initial state may be of interest, and could be analyzed using DEA).

2. The method

2.1. Overview of standard environ analysis

For a compartmental system, let $\mathbf{x}_{n\times 1} = (x_i)$, $\mathbf{z}_{n\times 1} = (z_j)$, and $\mathbf{y}_{n\times 1} = (y_i)$ be stock, input, and output vectors, respectively; let $\mathbf{1}_{n\times 1}$ be a vector of ones, and $\mathbf{F}^{\text{T}}$ the transpose of the matrix of flows, $\mathbf{F}_{n\times n} = (f_{ij})$. We define $\bar{\mathbf{F}}$ as the flow matrix $\mathbf{F}$ with negative throughflows on the diagonal, so $\bar{f}_{ij} = f_{ij}$ for $i \neq j$ and $\bar{f}_{ii} = -T_i$. Then, for a

* Corresponding author. Tel.: +1 706 542 2968; fax: +1 706 542 4819.
E-mail address: jaia@uga.edu (J. Shevtsov).

0304-3800/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.ecolmodel.2009.07.022

system at steady state, input- and output-driven ordinary differential equation descriptions of model dynamics, in matrix notation, are

$$\frac{d\boldsymbol{x}}{dt} = 0 = \bar{\mathbf{F}} \cdot \mathbf{1} + \mathbf{z} \tag{1a}$$

$$0 = -\bar{\mathbf{F}}^{\mathrm{T}} \cdot \mathbf{1} - \mathbf{y} \tag{1b}$$

The first equation represents time-forward dynamics generated by input, **z**. The second denotes reverse-time trace-back dynamics beginning at output, **y**, which serves as the forcing condition. (The flows **z** and **y** may be termed boundary flows.) In Eq. (1b), taking the transpose of $\bar{\boldsymbol{F}}$ orients it to backward movement of time, signified by the negative signs of both terms.

Standard NEA converts boundary inputs (in output-environ analysis) and outputs (in input-environ analysis) into steady-state throughflows, $\mathbf{T}_{n\times 1} = (T_i^{\mathrm{in}}) = (T_i^{\mathrm{out}})$, and storages (stocks), $\mathbf{x}_{n\times 1} = (x_i)$, employing flow intensity matrices, $\mathbf{N}_{n\times n}$ and $\mathbf{N}'_{n\times n}$ for throughflow analysis, and $\mathbf{S}_{n\times n}$ and $\mathbf{S}'_{n\times n}$ for storage analysis:

$$\boldsymbol{T} = \boldsymbol{N}\boldsymbol{z} = \boldsymbol{N}'\boldsymbol{y} \tag{2a}$$

$$\boldsymbol{x} = \boldsymbol{S}\boldsymbol{z} = \boldsymbol{S}'\boldsymbol{y}. \tag{2b}$$

Here, $\mathbf{N} = (\mathbf{I} - \mathbf{G}_{n\times n})^{-1}$, $\mathbf{N}' = (\mathbf{I} - \mathbf{G}'_{n\times n})^{-1}$, $\mathbf{S} = -\mathbf{C}_{n\times n}{}^{-1}$, and $\mathbf{S}' = -\mathbf{C}'_{n\times n}{}^{-1}$, where $\mathbf{I}_{n\times n}$ is the multiplicative identity matrix, and the elements of **G** and **C** are $g_{ij} = f_{ij}/T_j$ and $c_{ij} = f_{ij}/x_j$, and those of **G**′ and **C**′ are, $g_{ij}' = f_{ij}/T_i$ and $c_{ij}' = f_{ij}/x_i$. Both **G** and **G**′ are dimensionless, while **C** and **C**′ have the dimensions of reciprocal time; note that **C** is the familiar “community matrix” used in population and community ecology.

Inputs, **z**, outputs, **y**, and throughflows, **T**, have the same dimensions, therefore **N** and **N**′, Eq. (2a), are dimensionless transformations from boundary flows, **z** and **y**, to interior throughflows, **T**. Both Eqs. (2a) and (2b) have infinite power series equivalents that reflect trajectories of the boundary flows over all interior pathways of all lengths traveled in reaching the points where the steady-state throughflows, **T**, are registered. For Eq. (2a), these series are

$$\boldsymbol{T} = [\boldsymbol{I} + \boldsymbol{G} + \boldsymbol{G}^2 + \cdots + \boldsymbol{G}^k + \cdots]\boldsymbol{z} \tag{3a}$$

$$= [\boldsymbol{I} + \boldsymbol{G}' + \boldsymbol{G}'^2 + \cdots + \boldsymbol{G}'^k + \cdots]\boldsymbol{y} \tag{3b}$$

2.2. *The dynamic case*

The equation that governs the dynamics of a single compartment k is

$$\frac{dx_k}{dt} = T_k^{\mathrm{in}}(t) - T_k^{\mathrm{out}}(t) \tag{4}$$

where $T_k^{\mathrm{in}}(t)$ and $T_k^{\mathrm{out}}(t)$ are functions that represent rates of input to and output from compartment k at time t. Note that $T_k^{\mathrm{in}}(t)$ is a combinations of environmental and inter-compartmental flows:

$$T_k^{\mathrm{in}} = \sum_{i=1}^{n} f_{ki}(t) + z_k(t) \tag{5}$$

Combining Eqs. (4) and (5), we get, for $i \neq k$,

$$\sum_{i=1}^{n} f_{ki} + z_k = T_k^{\mathrm{out}} + \frac{dx_k}{dt} \tag{6}$$

As before, we define **G**, the flow matrix normalized with respect to throughflows (T_k^{out}), as $g_{ik} = f_{ik}/T_k^{\mathrm{out}}$. Replacing **F** with **G** in Eq. (6), we get

$$z_k - \frac{dx_k}{dt} = T_k^{\mathrm{out}} - \sum_{i=1}^{n} g_{ki} T_i^{\mathrm{out}} \tag{7}$$

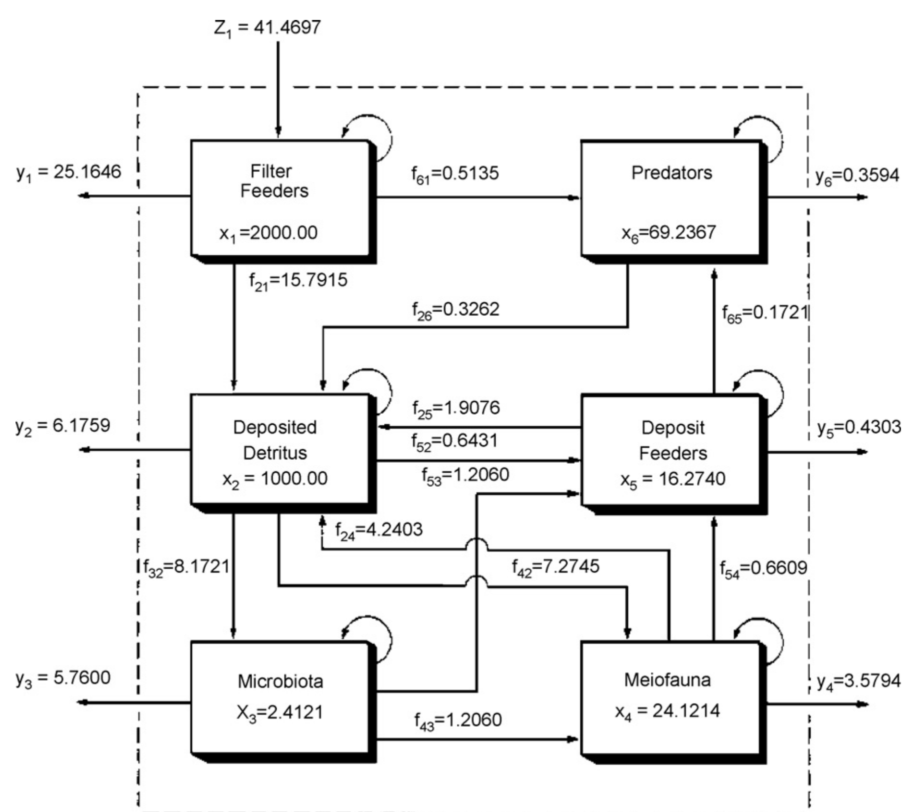

Fig. 1. Energy flows in an oyster reef ecosystem. The stock and flow values are for a constant steady state. Note that only Compartment 1 receives direct boundary inflow. From Patten (1985).

Table 1
Steps of dynamic environ approximation and illustration using oyster reef model.

Step	Description	Implementation in oyster reef model analysis
1	Numerically simulate the system using discrete time steps, δt, to obtain stocks, $\mathbf{x}(t_m)$	$\delta t = 0.025$ day
2	At time steps $\Delta t \geq \delta t$, compute inputs $\mathbf{z}(t_m)$, outputs $\mathbf{y}(t_m)$, interior flows $\mathbf{F}(t_m)$ and throughflows $\mathbf{T}(t_m)$	$\Delta t = 0.25$ day (one time unit in the empirical model)
3	Letting $\mathbf{V}_{\mathrm{NEA}}$ denote any of Eq. (2) transformation matrices ($\mathbf{N}$, $\mathbf{N}'$, $\mathbf{S}$, or $\mathbf{S}'$) relating these quantities, derive corresponding DEA versions, $\mathbf{V}_{\mathrm{DEA}}$	The $\mathbf{N}_{\mathrm{DEA}}$ matrix was calculated using a moving window of length 20
4	Perform any of the customary NEA computations using $\mathbf{V}_{\mathrm{DEA}}$ instead of $\mathbf{V}_{\mathrm{NEA}}$ matrices	As a test of the method, $\mathbf{T}$ was calculated using the equation $\mathbf{T} = \mathbf{N}_{\mathrm{DEA}}\mathbf{z}$. Indirect flows were calculated as $\mathbf{N}_{\mathrm{DEA}}$-$\mathbf{I}$-$\mathbf{G}$.

Using matrix notation, the equation above can be expressed as follows:

$$\boldsymbol{z} - \frac{d\boldsymbol{x}}{dt} = (\boldsymbol{I} - \boldsymbol{G})\boldsymbol{T}^{\mathrm{out}} \tag{8}$$

Assuming that the matrix $\mathbf{I} - \mathbf{G}$ is invertible and $\mathbf{N} = (\mathbf{I} - \mathbf{G})^{-1}$ as before, we get

$$\boldsymbol{N}\left(\boldsymbol{z} - \frac{d\boldsymbol{x}}{dt}\right) = \boldsymbol{T}^{\mathrm{out}} \tag{9}$$

Note that at steady state, $d\mathbf{x}/dt = 0$ and the above equation reduces to Eq. (2a).

We will now show how $\mathbf{N}$ is obtained in the dynamic case, where $d\mathbf{x}/dt \neq 0$.

2.3. Dynamic environ approximation

The constant matrices $\mathbf{G}$ and $\mathbf{G}'$ of static NEA do not reflect the reality that systems and their flow coefficients change over time, including the (infinite) time required for the power series in Eq. (3) to become equal to the transformation matrices $(\mathbf{I} - \mathbf{G})^{-1}$ and $(\mathbf{I} - \mathbf{G}')^{-1}$ of Eq. (2). In NEA, the matrix powers in (3) are interpreted as corresponding to pathway lengths, implying that (as $k \to \infty$) all pathways of all lengths are utilized in the limit in bringing $\mathbf{T}$ ((3a), (3b)) to its measured or modeled value. In throughflow analysis, *paths* are pathways lacking self-loop subsequences, $\ldots i \to i \to \ldots \to i \ldots$. If each adjacent link, denoting a pathway of length 1, is associated with a discrete time of passage, $\Delta t = t_{m+1} - t_m$, then the time required to traverse pathways of lengths $m = 0, 1, 2, \ldots, \infty$ is $m\Delta t$. Therefore, matrix powers may also be viewed as representing numbers of time steps (Patten, 1985; Patten et al., 1990). This interpretation is helpful in understanding dynamic environ approximation.

DEA involves four computational steps:

Step 1. Generate a numerical solution of the system differential equations (Eq. (1)) using discrete computational time steps, δt, to obtain stocks, $\mathbf{x}(t_m)$. This computational interval may be constant or time-varying; in the latter case, it will be necessary to interpolate $\mathbf{x}(t_m)$ for all integer values of m until the end of the time series.
Step 2. At sampling times $\Delta t = n\delta t$, where n is an integer, compute from the simulated values at times t_m the NEA quantities indicated in Eqs. (1) and (2): inputs $\mathbf{z}(t_m)$, outputs $\mathbf{y}(t_m)$, interior flows $\mathbf{F}(t_m)$ and throughflows $\mathbf{T}(t_m)$.
Step 3. Letting $\mathbf{V}_{\mathrm{NEA}}$ denote any of the Eq. (2) transformation matrices ($\mathbf{N}$, $\mathbf{N}'$, $\mathbf{S}$, or $\mathbf{S}'$) relating these quantities, derive corresponding DEA versions, $\mathbf{V}_{\mathrm{DEA}}$.
Step 4. Perform any of the customary NEA computations using $\mathbf{V}_{\mathrm{DEA}}$ instead of $\mathbf{V}_{\mathrm{NEA}}$ matrices.

Integer powers, m, of any scalar or matrix quantity, say $\mathbf{W}$, correspond to $m - 1$ repeated multiplications of that quantity: $\mathbf{W}^m = \mathbf{W}\cdot\mathbf{W}\cdot \ \ldots \ \cdot\mathbf{W}$ (m terms). The innovation behind DEA is the recognition that this makes it possible to substitute a non-constant, time- and pathway-varying product series for each constant-generated time- and pathway-varying term of the NEA power series. Thus, if the generalized NEA form of the power series in Eq. (3) is

$$\boldsymbol{V}_{\mathrm{NEA}} = \boldsymbol{W}^0 + \boldsymbol{W}^1 + \boldsymbol{W}^2 + \boldsymbol{W}^3 + \cdots + \boldsymbol{W}^m + \ldots \tag{10a}$$

$$= \boldsymbol{I} + \boldsymbol{W} + \boldsymbol{W}\cdot\boldsymbol{W} + \boldsymbol{W}\cdot\boldsymbol{W}\cdot\boldsymbol{W} + \cdots + [\boldsymbol{W}\cdot\boldsymbol{W}\cdot\ldots(m \text{ terms})\ldots\boldsymbol{W}] + \ldots, \tag{10b}$$

then the corresponding DEA form can be written as:

$$\boldsymbol{V}_{\mathrm{DEA}}(t_0) = \boldsymbol{V}_0 + \boldsymbol{V}_1 + \boldsymbol{V}_2 + \boldsymbol{V}_3 + \cdots + \boldsymbol{V}_m + \ldots \tag{11a}$$

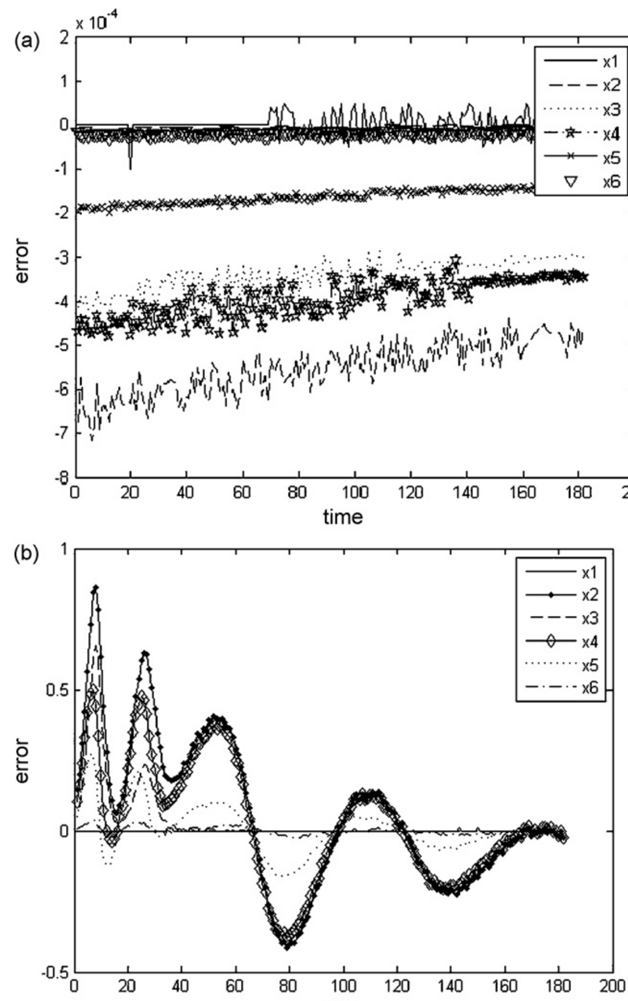

Fig. 2. Difference, in kcal/day/m^2, between actual and calculated throughflows in linear (a) and nonlinear (b) simulations of the oyster reef model. Error is the Euclidean distance between a throughflow vector computed with the $\mathbf{N}_{\mathrm{DEA}}$ matrix (Eq. (9)) and one computed as the sum of outflows in the dynamic simulation. Compartment names ($x_1 \ldots x_6$) are explained in Fig. 1.

This expression can be expanded to get:

$$\boldsymbol{V}_{\mathrm{DEA}}(t_0) = \boldsymbol{W}_0 + [\boldsymbol{W}_0 \cdot \boldsymbol{W}_1] + [\boldsymbol{W}_0 \cdot \boldsymbol{W}_1 \cdot \boldsymbol{W}_2] + \cdots + [\boldsymbol{W}_0 \cdot \boldsymbol{W}_1 \cdot \boldsymbol{W}_2 \cdot \ldots \cdot \boldsymbol{W}_m] + \ldots, \tag{11b}$$

where $\mathbf{W}_0 = \mathbf{I}$. Truncation after $m + 1$ terms gives the approximation:

$$\boldsymbol{V}_{\mathrm{DEA}}(t_0) \approx \boldsymbol{W}_0 + [\boldsymbol{W}_0 \cdot \boldsymbol{W}_1] + [\boldsymbol{W}_0 \cdot \boldsymbol{W}_1 \cdot \boldsymbol{W}_2] + \cdots + [\boldsymbol{W}_0 \cdot \boldsymbol{W}_1 \cdot \boldsymbol{W}_2 \cdot \ldots \cdot \boldsymbol{W}_m] \tag{11c}$$

where **V** and **W** represent any appropriately related pair of NEA matrices. Here, $m + 1$ is the length of the longest product in the series as well as the number of terms in the sum. In general,

$$\boldsymbol{V}_{\mathrm{DEA}}(t_k) = \boldsymbol{W}(t_k) + [\boldsymbol{W}(t_k) * \boldsymbol{W}(t_{k+1})] + [\boldsymbol{W}(t_k) * \boldsymbol{W}(t_{k+1}) * \boldsymbol{W}(t_{k+2})] + \cdots + [\boldsymbol{W}(t_k) * \boldsymbol{W}(t_{k+1}) * \ldots * \boldsymbol{W}(t_{k+m})] \tag{11d}$$

These calculations can be thought of as stepping a moving window of fixed length m along the simulated dynamics at a fixed sampling interval, Δt, which must be at least as large as the numerical integration step size. At each sampling step, a value for $\mathbf{V}_{\mathrm{DEA}}(t_k)$ is calculated. The interpretation of $\mathbf{V}_{\mathrm{DEA}}$ is simplest when $\Delta t = 1$.

The forms for $\mathbf{V}_{\mathrm{DEA}} = \mathbf{N}$ and $\mathbf{V}_{\mathrm{DEA}} = \mathbf{N}'$ (with $\mathbf{W}_0 = \mathbf{G}_0 = \mathbf{G}'_0 = \mathbf{I}$ omitted from the $m > 1$ terms, as multiplication by **I** does not affect the results) are as follows:

$$\boldsymbol{N}_{\mathrm{DEA}}(t_k) = \boldsymbol{I} + \boldsymbol{G}(t_1) + \boldsymbol{G}(t_1) \cdot \boldsymbol{G}(t_2) + \boldsymbol{G}(t_1) \cdot \boldsymbol{G}(t_2) \cdot \boldsymbol{G}(t_3) + \ldots \tag{12a}$$

$$\boldsymbol{N}'_{\mathrm{DEA}}(t_k) = \boldsymbol{I} + \boldsymbol{G}'(t_1) + \boldsymbol{G}'(t_1) \cdot \boldsymbol{G}'(t_2) + \boldsymbol{G}'(t_1) \cdot \boldsymbol{G}'(t_2) \cdot \boldsymbol{G}'(t_3) + \ldots \tag{12b}$$

where **G** is the matrix of flows normalized by donor throughflows and **G**′ is the matrix of flows normalized by recipient throughflows. Using this methodology, non-steady- or steady-state analyses can be performed, and a dynamic analysis applicable to nonlinear as well as linear systems becomes possible. Standard NEA becomes a special case of the more general DEA approach, which, in principle, becomes arbitrarily exact as $\Delta t \to \delta t$ and $\delta t \to 0$. That is, the approximations of Eq. (11) can be improved by re-simulating the dynamical model with coefficients re-calculated using a smaller time unit (e.g. hours instead of days). This is particularly important for systems that exhibit high-frequency dynamics.

There is a trade-off involved in increasing window size (m). Notice that $\mathbf{V}(t)$ is defined at a particular time, t, but computed using $\mathbf{W}(t + 1)$, $\mathbf{W}(t + 2)$ and other future values. This creates an unavoidable error, and introducing more distant time points will increase this error, while decreasing the error due to truncation of the infinite series defining $\mathbf{V}(t)$. Note that terms added to the end of Eq. (11d) will be very small. In general, there is little gain from using a window size larger than about 20.

2.4. Numerical test of DEA methodology

Dame and Patten (1981) modeled energy flow in an intertidal oyster reef in South Carolina, USA (Fig. 1). This model has one nonzero boundary input, z_1, six compartments (x_1 to x_6) each dissipating energy to nonzero outputs (y_1 to y_6), and twelve empirically

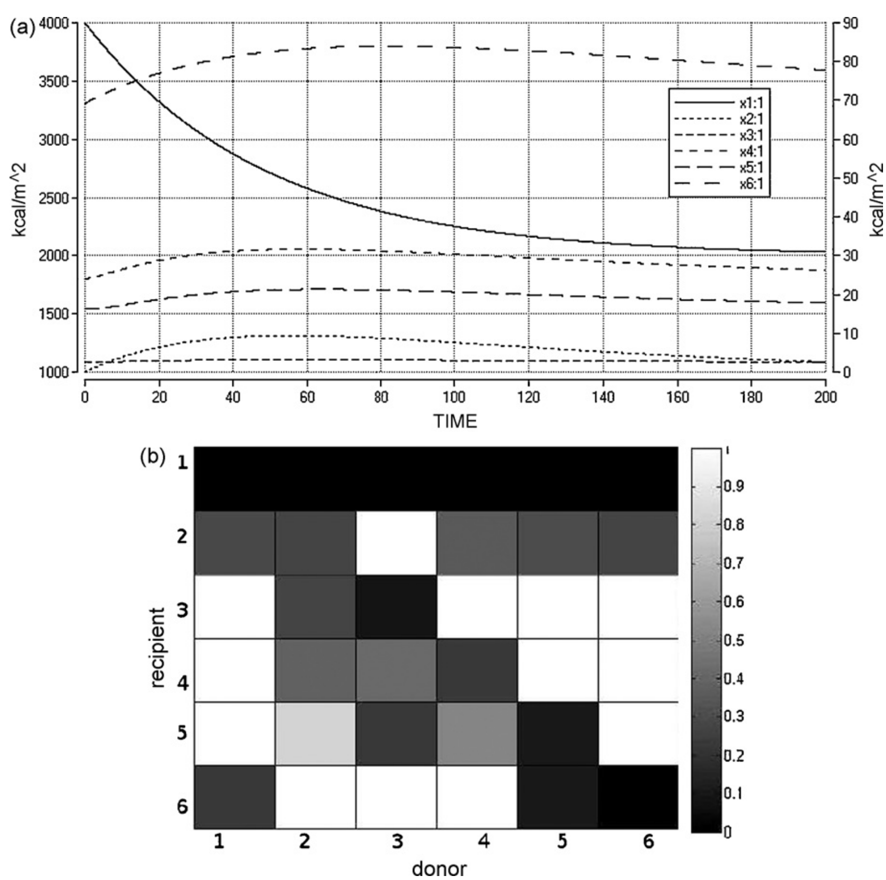

Fig. 3. Evolution of stock values (a) and direct to indirect flow ratios (b) in the oyster model after the oyster compartment was doubled. x_1 and x_2 are on the left scale; all other stocks are on the right scale. Compartment abbreviations ($x_1 \ldots x_6$) are explained in Fig. 1.

measured internal flows (f_{ij}, i, $j = 1, 2, \ldots, 6$). The flow units are kcal/(m^2 day) and the stocks kcal/m^2. Two implementations of this model, described below, were used to test dynamic environ approximation methods. Table 1 gives a summary of the analysis.

A linear time-forward model (Eq. (1a)) was formulated by defining interior flows as scalar multiples of the donor compartments, $f_{ij} = c_{ij}x_j$. In Step 1 the model was simulated using EcoNet (Kazancı, 2007). A 200-time unit (50 day) run with the initial filter feeder stock, $x_1(t_0)$, displaced from 2000 to 4000 kcal/m^2 is shown in Fig. 2a. In Step 2, stock vectors, $\mathbf{x}(t)$, and community matrices, $\mathbf{C}(t)$, were assembled for each sample time step of $\delta t = 0.1$ day. Using the $\mathbf{C}$ matrices, $\mathbf{F}(t)$ (Eq. (1a)), and $\mathbf{G}(t)$ matrices were computed for each sampling time in Step 3, then used to compute $\mathbf{N}_{\mathrm{DEA}}$ (Eq. (12a)) with a window size of 20.

A nonlinear, mass-action version of the Fig. 1 model was formulated by making flows functions of the product of the donor and recipient stocks, $f_{ij} = a_{ij}x_ix_j$. Flows to Detritus (x_2) remained donor-dependent, as in the linear model. The same computations as described for the linear model above were performed.

For both models, the $\mathbf{N}_{\mathrm{DEA}}$ matrix was used to calculate the throughflow vector, $\mathbf{T}$ (Eq. (9)). Throughflow for each compartment was also computed directly as the sum of outflows in the dynamic simulation program Berkeley Madonna 8.0.1 (www.berkeleymadonna.com). Since the analysis presented here is forward-looking (i.e., Eq. (12a)), T_i was defined as the sum of outflows from compartment i; a backward-looking analysis (i.e., Eq. (12b)) would have used the sum of inflows to compartment i. Error was calculated using the Euclidean norm:

$$\mathrm{Error} = \sqrt{(T_1^{\mathrm{calc}} - T_1^{\mathrm{actual}})^2 + \cdots + (T_n^{\mathrm{calc}} - T_n^{\mathrm{actual}})^2} \qquad (13)$$

(Here, n is the number of compartments in the model.) The error thus defined was calculated for ten randomly selected time points in both model implementations. The mean error in the linear model was 0.0008 with a standard deviation of 0.0004; that of the nonlinear model was 0.2171 with a standard deviation of 0.11. Differences between actual and calculated throughflows are displayed in Fig. 2.

3. Application to indirect effects

Output from the linear and nonlinear dynamic oyster reef model implementations was analyzed to compute the fraction of flow between pairs of compartments that traveled over pathways of lengths greater than one (indirect flow fraction). This quantity was calculated by dividing entries in $\mathbf{N_{DEA}}$-$\mathbf{I}$-$\mathbf{G}$, which isolates indirect flows, by the corresponding entries in $\mathbf{N}$, which represents total flows. If there is no directed path of any length between two compartments, the ratio is undefined; in this case, it was arbitrarily set

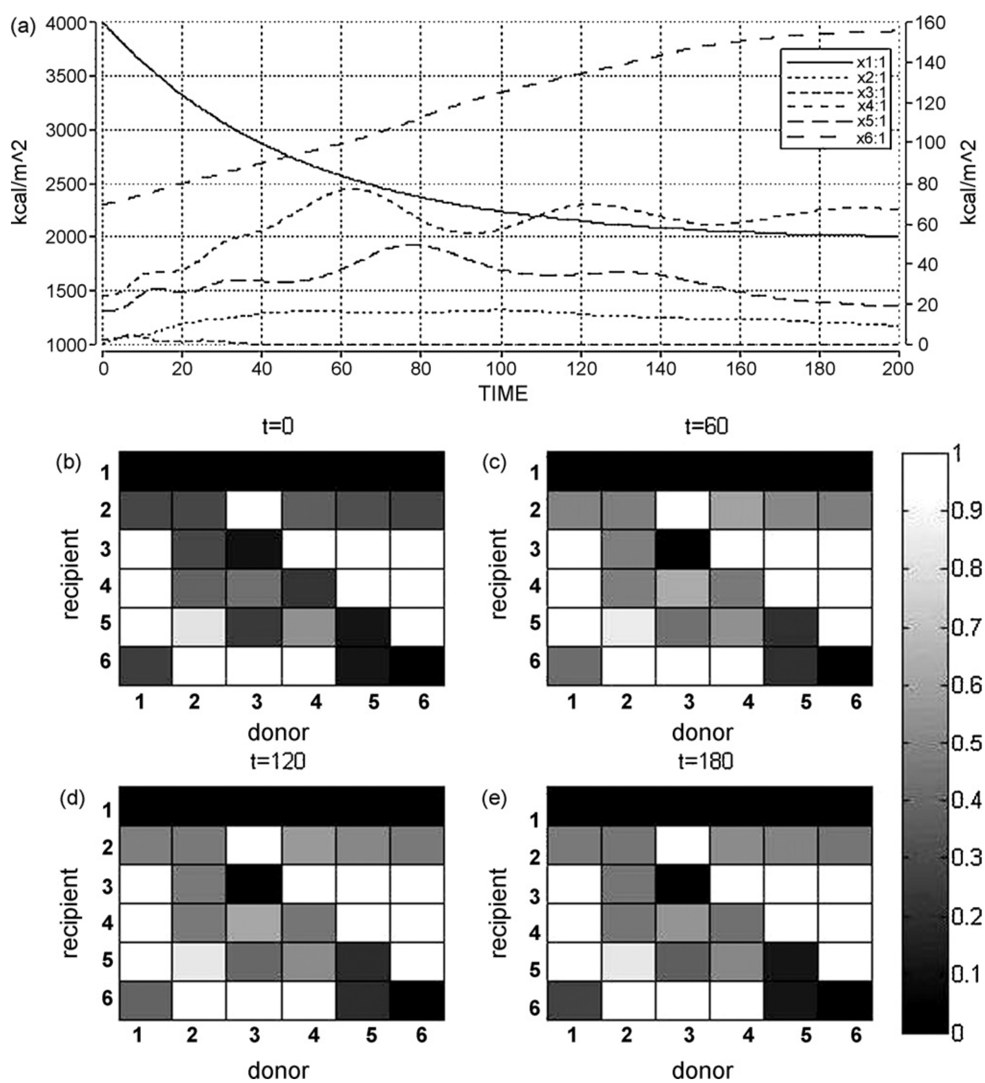

Fig. 4. Evolution of stock values (a) and direct to indirect flow ratios (b–e) in a nonlinear version of the oyster reef model (explained in text) after the oyster compartment was doubled. x_1 and x_2 are on the left scale; all other stocks are on the right scale. Compartment abbreviations ($x_1 \ldots x_6$) are explained in Fig. 1.

equal to zero. The results of this calculation for the linear model are shown in Fig. 3b; those for the nonlinear model appear in Fig. 4b–e. The Matlab function used to do these calculations is given in Appendix 1.

In the linear model, direct to indirect flow ratios remained constant as the system evolved; in the nonlinear model, they varied with time. The mean and median values for the two models were similar: between 0.45 and 0.6. Typically, direct to indirect flow ratios in the nonlinear model changed gradually and, over the 45 days simulated, underwent proportionately much less change than stock values (Fig. 4b–e). This relationship should be explored in future research, as should the constancy of indirect flow fractions in linear models.

4. Discussion

The dynamic environ approximation approach described in this paper potentially has a broad range of applications. Here, we have described the approach and given an example of its accuracy.

Previous attempts to develop a dynamic environ analysis were primarily analytical. (Hippe, 1983; Hallam and Antonios, 1985) (Hippe's approach appears related to the dynamic inverse in input–output analysis (Leontief, 1970; Kendrick, 1972; Johnson, 1985; ten Raa, 2005) and deeper exploration of the relationship between the two methodologies may prove worthwhile.) The strength of DEA lies in the fact that, like NEA, it makes no assumptions about the underlying dynamics of the model being analyzed. Although two simulation models were used in the present instance to produce the background data for DEA, the analysis could also proceed based on purely empirical time series data gathered in context of a defined network model. Only output is used; what happens in the equations stays in the equations. This lets DEA sidestep the mathematical difficulties associated with prior methods.

Borrett et al. (in review) have found that, in empirically based trophic and biogeochemical models at a constant steady state, indirect effects become dominant after only a few terms of the infinite series expansion of the **N** matrix. These results are consistent with our finding that a window size of about 20 is sufficient to closely approximate **N**.

We note that there might be better approximations than our method. However, the value of DEA methodology is in its intuitive definition. Eqs. (4) and (7) imply that any network characteristic investigated by NEA can also be studied with DEA, provided that the measure in question makes sense for a system away from steady state. It should be possible to investigate energy cycling (Patten, 1985) and system properties such as dominance of indirect effects (Patten, 1984), as well as the defined network properties of environs (e.g. Patten, 1995; Fath and Patten, 1999). Other promising areas of application for dynamic environ approximation include the analysis of bioenergetic food web models, the study of system-level properties of individual-based models, including those incorporating evolution, and investigation of exactstochastic simulations of trophic dynamics. Applications such as these could provide a much-needed link between conventional and systems ecology.

Acknowledgments

JS thanks Rick Vance and Kristin McCully. Although none of us knew it at the time, their help and encouragement opened the door to the work described in this paper.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2009.07.022.

References

Borrett, S.R., Whipple, S.J., Patten, B.C., in review. Rapid development of indirect effects in ecological networks.
Dame, R.F., Patten, B.C., 1981. Analysis of energy flows in an intertidal oyster reef. Mar. Ecol. Prog. Ser. 5 (2), 115–124.
Fadeev, D.K., Fadeeva, V.N., 1963. Computational Methods of Linear Algebra. (R. C. Williams, transl.). Freeman, San Francisco.
Fath, B.D., Patten, B.C., 1999. Review of the foundations of network environ analysis. Ecosystems 2 (2), 167–179.
Hallam, T.G., Antonios, M.N., 1985. An environ analysis for nonlinear compartment models. Bull. Math. Biol. 47 (6), 739–748.
Higashi, M., Patten, B.C., 1989. Dominance of indirect causality in ecosystems. Am. Nat. 133, 288–302.
Hippe, P.W., 1983. Environ analysis of linear compartmental systems: the dynamic, time-invariant case. Ecol. Model. 19 (1), 1–26.
Johnson, T., 1985. A continuous Leontief dynamic input–output model. Pap. Reg. Sci. 56 (1), 177–188.
Kazancı, C., 2007. EcoNet: a new software for ecological modeling, simulation and network analysis. Ecol. Model. 208 (1), 3–8.
Kendrick, D., 1972. On the Leontief dynamic inverse. Q. Jon. Econ. 86 (4), 693–696.
Leontief, W.W., 1936. Quantitative input–output relations in the economic system of the United States. Rev. Econ. Stat. 18, 105–125.
Leontief, W.W., 1966. Input–Output Economics. Oxford University Press, London and New York.
Leontief, W.W., 1970. The dynamic inverse. In: Proceedings of the Fourth International Conference on Input–Output Techniques, Geneva, 8–12 January 1968: Published in Honor of Wassily Leontief.
Matis, J.H., Patten, B.C., White, G.C. (Eds.), 1979. Compartmental Analysis of Ecosystem Models. International Cooperative Publishing House, Fairland, Maryland.
Patten, B.C., 1978. Systems approach to the concept of environment. Ohio J. Sci. 78, 206–222.
Patten, B.C., 1984. Toward a theory of the quantitative dominance of indirect effects in ecosystems. Verhalt Gesellschaft für Ökologie 13, 271–284.
Patten, B.C., 1985. Energy cycling in the ecosystem. Ecol. Model. 28, 1–71.
Patten, B.C., 1991. Network ecology: indirect determination of the life–environment relationship in ecosystems. In: Higashi, M., Burns, T.P. (Eds.), Theoretical Ecosystem Ecology: The Network Perspective. Cambridge University Press, London, pp. 288–351.
Patten, B.C., 1995. Network integration of ecological extremal principles: exergy, emergy, power, ascendency, and indirect effects. Ecol. Model. 79, 75–84.
Patten, B.C., Higashi, M., Burns, T.P., 1990. Trophic dynamics in ecosystem networks: significance of cycles and storage. Ecol. Model. 51, 1–28.
ten Raa, T., 2005. The Economics of Input–Output Analysis. Cambridge University Press, New York.