Dynamic Ecological System Measures

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A Holistic Analysis of Compartmental Systems

Abstract. A new mathematical method for the dynamic analysis of nonlinear ecological systems has recently been developed by the author and was presented in a separate article. Based on this methodology, multiple new dynamic ecological system measures and indices of matrix, vector, and scalar types are systematically introduced in the present paper. These mathematical system analysis tools are quantitative ecological indicators that monitor the flow distribution and storage organization, quantify the effect and utility of one compartment directly or indirectly on another, identify the system efficiency and stress, measure the compartmental exposure to system flows, determine the residence time and compartmental activity levels, and ascertain the restoration time and resilience in the case of disturbances. Major flow- and stock-related concepts and quantities of the current static network analyses are also extended to nonlinear dynamic settings and integrated with the proposed dynamic measures and indices within this novel and unifying mathematical framework. In particular, the dynamic versions of the static indirect effect and celebrated cycling indices are formulated integrally. This unifying comprehensive framework enables a holistic view and analysis of ecological systems. The proposed dynamic system measures and indices, thus, extract detailed information about ecosystems’ characteristics, as well as their functions, properties, behaviors, and various other system attributes that are potentially hidden in and even obscured by data.

Key words. dynamic ecological network analysis, nonlinear dynamic compartmental systems, dynamic system and subsystem partitioning, diact flows and storages, diact effect measures and indices, system efficiency and stress, diact utility measures and indices, diact exposure, residence time, resilience, dynamic cycling index

AMS subject classifications. 34A34, 70G60, 37N25, 92C42, 92D40

1. Introduction. Environmental problems have been a common topic of scholarly conversation for decades. As environmental issues persist and proliferate, the language and methods through which these problems are examined also evolve. Although traditional ecology has been used effectively in dealing with a variety of complex environmental problems, the field remains largely descriptive in nature. It has yet to arrive at a formal theory and methodology for analyzing the complex relationships between organisms and their environment or man and nature.

Ecosystems are natural systems made up of living and non-living components. Ecosystem ecology deals with interactions between species and their physical environment. More specifically, this interdisciplinary science studies the flows of energy and matter between the biotic and abiotic components of ecosystems based on conservation principles. Ecosystem ecology plays an important role in understanding current global environmental problems and determining how local mechanisms interact with these problems. Enhancements in dealing with environmental issues will ultimately depend on advances in such basic sciences. Mathematical theories and modeling are at the forefront of continued endeavors leading to a more formalistic and theoretical ecological science devoted to the discovery of basic scientific laws. Compartmental models are generally used for mathematical abstractions of ecological systems where the compartments represent ecosystem components. Within this mathematical framework, system measures and indices are then formulated to serve as quantitative ecological indicators.

Ecological models are widely analyzed in literature, but current methodologies
are developed for special cases, such as linear systems and static models. Ecological networks and complexity in living systems are analyzed, for example, at steady state in the context of information theory and thermodynamics [35, 22, 36, 37] as well as the hierarchy theory [1]. Along parallel research lines, building on economic input-output analysis [24, 25] introduced into ecology by [18], another static approach called the environ theory has also been developed over recent decades based on conservation principles [30, 28]. Several software developments computerize these static methods [38, 7, 13, 23, 34, 5].

Despite the fact that major environmental problems of the day involve change, dynamic analysis of nonlinear systems has remained a long-standing, open problem. Finn’s cycling index (FCI), defined for static ecological network analysis over four decades ago, for example, has still not been made applicable to dynamic ecosystem models [15]. Similarly, the current ecosystem measures and indices are all formulated for static systems. Therefore, there is an urgent need for analytical methods and dynamic measures for nonlinear system analysis [6, 19].

A mathematical theory and method recently developed by [9, 10] potentially addresses the mismatch between current static and computational methods and applied ecological needs. This comprehensive mathematical method is introduced for the dynamic analysis of nonlinear dynamic ecological systems. The proposed method is based on the novel analytical and explicit, mutually exclusive and exhaustive system and subsystem partitioning methodologies. As the proposed dynamic system partitioning yields the subthroughflow and substorage functions to determine the distribution of environmental inputs and the organization of associated storages individually and separately within the system, the subsystem partitioning yields the transient and the dynamic direct, indirect, acyclic, cycling, and transfer (diact) flow and storage functions to determine the distribution of intercompartmental flows and the organization of associated storages within the subsystems. Consequently, the evolution of environmental inputs and arbitrary intercompartmental system flows as well as the associated storages generated by these inputs and flows can be tracked individually and separately within the system. In effect, the proposed methodology brings a novel, formal, deterministic, complex system theory to the service of urgent environmental problems of the day.

The proposed methodology constructs a base for the development of mathematical system analysis tools as quantitative ecosystem indicators. Based on this methodology, multiple measures and indices of matrix, vector, and scalar type for the dynamic diact effect, utility, exposure, and residence time as well as the corresponding system efficiencies, stress, and resilience are introduced systematically in the present paper for the first time in literature. In particular, dynamic versions of the existing static indirect effect and celebrated cycling indices, developed about four decades ago for static ecological network analysis, are formulated in the present paper with a different derivation rationale. The proposed dynamic system measures and indices monitor the flow distribution and storage organization, quantify the effect and utility of one compartment directly or indirectly on another, identify the system efficiency and stress, measure the compartmental exposure to system flows, determine the residence time and compartmental activity levels, and ascertain the restoration time and resilience in the case of disturbances. As a result, these measures dynamically quantify ecosystems’ characteristics, including their functions, features, properties, and various other system attributes that are potentially hidden in and even obscured by data. They ultimately enable the characterization and classification of ecosystems, precise analyses of system structure and behavior, as well as a detailed understanding of the dynam-
ics of individual system compartments. The proposed methodology, therefore, leads to a holistic analysis of ecosystems and serves as a quantitative platform for testing empirical hypotheses, ecological inferences, and, potentially, theoretical developments.

The proposed methodology is applicable to any compartmental system regardless of its nature, whether naturogenic or anthropogenic. It can be used, for example, to analyze mass or energy transfers between species of different tropic levels in a complex network or along a given food chain of a food web [3]. The proposed method can also be used for the analysis of models designed for material flows in industry or the dynamics of the terrestrial carbon cycle [2, 33]. Although the motivating applications for this paper are ecological and environmental, the applicability of the proposed method extends to other realms such as economics, pharmacology, epidemiology, chemical reaction kinetics, biomedical systems, neural networks, and information science—in fact, wherever dynamical compartmental models of conserved quantities can be constructed.

The proposed methodology is applied to several ecosystem models in Section 3 to illustrate the efficiency and wide applicability of the proposed measures and indices. These models have recently been analyzed for their flow and storage distributions and intercompartmental dynamics through the substorage, subthroughflow, and \textit{diact} transaction matrices by [9, 11]. In the present manuscript, the measures and indices for the dynamic \textit{diact} effect, utility, exposure, and residence time as well as the system efficiencies, stress, and resilience are presented for these ecosystem models. The dynamic \textit{diact} effect measures and indices quantify the direct, indirect, acyclic, cycling, and total (\textit{diact}) influence of system compartments, in terms of energy or nitrogen transfer, on the other compartments or themselves within these ecosystems. The dynamic \textit{diact} utility measures and indices determine the relative \textit{diact} effects of the compartments on each other. The residence time functions ascertain the compartmental activity levels. The time dependent nature of these dynamic measures and indices also allows their time derivatives and integrals to be formulated as novel system measures. The time derivatives of the proposed \textit{diact} measures and indices quantify system efficiency, stress, and resilience as presented in Section 3.

The paper is organized as follows: the mathematical formulations of the ecological system measures and indices are introduced in Sec. 2, results and examples are provided in Sec. 3, and discussion and conclusions follow in Sec. 4 and 5. The dynamic subsystem methodology and the \textit{diact} flow and storage formulations introduced by [9] is summarized in Appendices.

2. Methods. A new mathematical theory and method has been recently developed for the dynamic analysis of nonlinear compartmental systems by [9, 10]. The proposed theory is based on the dynamic system and subsystem partitioning methodologies that formulate the distribution of environmental inputs and intercompartmental flows and the organization of the associated storages generated by the inputs and flows individually and separately within the systems. The proposed methodology, therefore, as a whole, yields the decomposition of all system flows and storages to the utmost level. This methodology is summarized below.

Based on the proposed methodology, multiple measures and indices of matrix, vector, and scalar type for the dynamic \textit{diact} effect, utility, exposure, and residence time as well as the corresponding system efficiencies, stress, and resilience are introduced systematically as quantitative ecosystem indicators further below in this section. The terminology and notations used in this paper are adopted from [10, 9].
The standard governing equations for compartmental dynamics are

\[
\dot{x}_i(t) = \left( z_i(t,x) + \sum_{j=1}^{n} f_{ij}(t,x) \right) - \left( y_i(t,x) + \sum_{j=1}^{n} f_{ji}(t,x) \right) \tag{2.1}
\]

with the initial conditions \( x_i(t_0) = x_{i,0} \), for \( i = 1, \ldots, n \). The concepts and notations employed in this formulation are as follows:

- \( n \) number of compartments
- \( t \) time [t]
- \( x_i(t) \) total material (mass) [m] (or energy, currency) stored in compartment \( i \), \( i = 1, \ldots, n \), at time \( t \)
- \( f_{ij}(t,x) \) non-negative flow from compartment \( j \) to \( i \), at time \( t \) [m/t]
- \( z_i(t,x) = f_{i0}(t,x) \) environmental \((j = 0)\) input into compartment \( i \) at time \( t \)
- \( y_i(t,x) = f_{0i}(t,x) \) environmental output from compartment \( i \) at time \( t \)

For notational convenience, we define a direct flow matrix function \( F \) of size \( n \times n \) as

\[
F(t,x) = (f_{ij}(t,x))
\]

and the inward and outward throughput vector functions as

\[
\hat{\tau}(t,x) = [\hat{\tau}_1(t,x), \ldots, \hat{\tau}_n(t,x)]^T = z(t,x) + F(t,x)1 \quad \text{and} \quad \hat{\tau}(t,x) = [\hat{\tau}_1(t,x), \ldots, \hat{\tau}_n(t,x)]^T = y(t,x) + F^T(t,x)1
\]

where \( z(t,x) = [z_1(t,x), \ldots, z_n(t,x)]^T \) is the input, \( y(t,x) = [y_1(t,x), \ldots, y_n(t,x)]^T \) is the output vector functions, and \( 1 \) denotes the column vector of size \( n \) whose entries are one.

The system partitioning methodology yields the governing equations for subcompartmental dynamics as follows (see Figs. 1 and 2):

\[
\dot{x}_{ik}(t) = \left( z_{ik}(t,x) + \sum_{j=1}^{n} f_{ikj}(t,x) \right) - \left( y_{ik}(t,x) + \sum_{j=1}^{n} f_{jk i}(t,x) \right) \tag{2.3}
\]

for \( i = 1, \ldots, n, k = 0, \ldots, n \), with the initial conditions

\[
x_{ik}(t_0) = \begin{cases}
  x_{i,0}, & k = 0 \\
  0, & k \neq 0
\end{cases}
\]

where

\[
x(t) = [x_{01}(t), \ldots, x_{0n}(t), x_{11}(t), \ldots, x_{1n}(t), \ldots, x_{n1}(t), \ldots, x_{nn}(t)]^T.
\]

The relationship between the compartmental and subcompartmental flows and storages can be stated as

\[
x_i(t) = \sum_{k=0}^{n} x_{ik}(t) \quad \text{and} \quad f_{ij}(t,x) = \sum_{k=0}^{n} f_{ijk}(t,x) \tag{2.4}
\]

where

\[
f_{ijk}(t,x) = x_{jk}(t) \frac{f_{ijk}(t,x)}{x_j(t)} = d_{jk}(x) f_{ij}(t,x), \tag{2.5}
\]
and the decomposition factor is defined as \( d_{jk}(x) = x_{jk}(t)/x_j(t) \).

The concepts and notations used in the system partitioning methodology are summarized below:

- \( x_{ik}(t) \): storage generated by environmental input \( z_k(t, x) \) during \([t_0, t]\) and stored in subcompartment \( k \) of compartment \( i \), that is, in subcompartment \( i_k \), \( k = 0, \ldots, n \), at time \( t \)
- \( f_{ik,jk}(t, x) \): non-negative flow from subcompartment \( j_k \) to \( i_k \) at time \( t \)
- \( y_{ik}(t, x) = f_{0ik}(t, x) \): environmental \((j = 0)\) output from subcompartment \( i_k \) at time \( t \)
- \( z_{ik}(t, x) = \delta_{ik} z_i(t, x) \): environmental input into subcompartment \( i_k \) at time \( t \), where \( \delta_{ik} \) is the discrete delta function

Total subcompartimental inflows and outflows at each compartment \( i \) at time \( t \) generated by the environmental input into compartment \( k \) during \([t_0, t]\) can then be defined, respectively, as

\[
\bar{\tau}_{ik}(t, x) = z_{ik}(t, x) + \sum_{j=1}^{n} f_{ik,jk}(t, x) \quad \text{and} \quad \bar{\tau}_{ik}(t, x) = y_{ik}(t, x) + \sum_{j=1}^{n} f_{jk,ik}(t, x)
\]

for \( k = 0, 1, \ldots, n \). Therefore, \( \bar{\tau}_{ik}(t, x) \) and \( \bar{\tau}_{ik}(t, x) \) will respectively be called inward and outward subthroughflow at subcompartment \( i_k \) at time \( t \).

The \( n \times n \) inward and outward subthroughflow and substorage matrix functions, \( T(t, x), \hat{T}(t, x), \) and \( X(t) \), whose entries represent the inward and outward subthroughflows and associated substorages are defined, respectively, as follows:

\[
X_{ik}(t) = x_{ik}(t), \quad T_{ik}(t, x) = \bar{\tau}_{ik}(t, x), \quad \text{and} \quad \hat{T}_{ik}(t, x) = \bar{\tau}_{ik}(t, x)
\]

for \( i, k = 1, \ldots, n \). The inward and outward subthroughflow and associated substorage vector functions of size \( n \) for the initial subsystem, \( \hat{\tau}_0(t, x), \bar{\tau}_0(t, x), \) and \( x_0(t) \), are also
defined as \( \hat{\tau}_0(t, x) = [\hat{\tau}_{10}(t, x), \ldots, \hat{\tau}_{n0}(t, x)]^T \), \( \hat{\tau}_0(t, x) = [\hat{\tau}_{10}(t, x), \ldots, \hat{\tau}_{n0}(t, x)]^T \), and \( x_0(t) = [x_{10}(t), \ldots, x_{n0}(t)]^T \), respectively. The governing equation, Eq. 2.3, can then be expressed as a matrix-vector equation in terms of the matrix and vector functions as follows:

\[
\begin{align*}
\dot{X}(t) &= \hat{T}(t, x) - \tilde{T}(t, x), \\
\dot{x}(t) &= \hat{\tau}_0(t, x) - \tilde{\tau}_0(t, x),
\end{align*}
\]

where \( \mathbf{0} \) is used for both \( n \times n \) zero matrix and the zero vector of size \( n \).

Let the notation \( \text{diag}(x(t)) \) represent the diagonal matrix whose diagonal elements are the elements of vector \( x(t) \) and \( \text{diag}(X(t)) \) represent the diagonal matrix whose diagonal elements are the same as the diagonal elements of matrix \( X(t) \). The \( n \times n \) diagonal storage, output, and input matrix functions, \( \mathcal{X}(t), \mathcal{Y}(t, x), \) and \( \mathcal{Z}(t, x) \) will be defined, respectively, as

\[
\mathcal{X}(t) = \text{diag}(x(t)), \quad \mathcal{Y}(t, x) = \text{diag}(y(t, x)), \quad \text{and} \quad \mathcal{Z}(t, x) = \text{diag}(z(t, x)).
\]

Using Eq. 2.5, the subthroughflow matrices can then be formulated as follows:

\[
\begin{align*}
\hat{T}(t, x) &= \mathcal{T}(t, x) + F(t, x) \mathcal{X}^{-1}(t) X(t) \\
\tilde{T}(t, x) &= \left( \mathcal{Y}(t, x) + \text{diag} \left( F^T(t, x) \mathbf{1} \right) \right) \mathcal{X}^{-1}(t) X(t) \\
&= \mathcal{T}(t, x) \mathcal{X}^{-1}(t) X(t)
\end{align*}
\]

where \( \mathcal{T}(t, x) = \text{diag} \left( \tilde{\tau}(t, x) \right) = \mathcal{Y}(t, x) + \text{diag} \left( F^T(t, x) \mathbf{1} \right) \).

We also define an \( n \times n \) matrix function \( A(t, x) \) as

\[
A(t, x) = \left( F(t, x) - \mathcal{Y}(t, x) - \text{diag} \left( F^T(t, x) \mathbf{1} \right) \right) \mathcal{X}^{-1}(t)
\]

\[
= \left( F(t, x) - \mathcal{T}(t, x) \right) \mathcal{X}^{-1}(t)
\]

\[
= Q(t, x) - \mathcal{R}^{-1}(t, x)
\]

where \( Q(t, x) = F(t, x) \mathcal{X}^{-1}(t) \) and \( \mathcal{R}^{-1}(t, x) = \mathcal{T}(t, x) \mathcal{X}^{-1}(t) \). Note that the first term in the definition of \( A(t, x) \), \( Q(t, x) \), represents the intercompartmental flow intensity, and the second term, \( \mathcal{R}^{-1}(t, x) \), represents the outward throughflow intensity. Consequently, we call \( A(t, x) \) the flow intensity matrix. It is sometimes called the compartmental matrix. The \( n \times n \) diagonal matrix \( \mathcal{R}(t, x) \) will be called the residence matrix.
time matrix and will be discussed further below in Sec. 2.4. The governing equations, Eq. 2.8, can then be expressed in the following form

\begin{align}
\dot{X}(t) &= Z(t, x) + A(t, x) X(t), \quad X(t_0) = 0,
\dot{x}_0(t) &= A(t, x) x_0(t), \quad x_0(t_0) = x_0,
\end{align}

as formulated in [9].

The proposed methodology constructs a base for the development of new mathematical system analysis tools. Multiple dynamic measures and indices of matrix, vector, and scalar type are developed as quantitative ecological indicators in the present paper. Since the dynamic measures are functions of time, their time derivatives and integrals can also be used for further analysis of various system attributes as formulated in what follows.

We will start with a brief summary of the measures developed in this section and in Appendix B, such as the substorage and subthroughflow matrices and diact flows and storages. The introduction of new dynamic system analysis tools will follow that discussion. The static versions of these measures and indices are formulated in [12].

2.1. Subthroughflows, Substorages, and the diact Transactions. The dynamic system partitioning methodology yields the subthroughflow and substorage matrices that measure the environmental influence on system compartments in terms of the flow and storage generation. For the quantification of intercompartmental flow and storage dynamics, the dynamic subsystem partitioning methodology then formulates the transient and dynamic diact flows and associated storages.

The elements of the net subthroughflow and substorage matrices, $T(t, x)$ and $X(t)$, represent the distribution of environmental inputs and the organization of the associated storages generated by the inputs within the system. More precisely, $\tau_{ik}(t, x)$ and $x_{ik}(t)$ represent the net subthroughflow and substorage in compartment $i$ at time $t$ generated by the environmental input into compartment $k$, $z_k(t)$, during $[t_0, t]$ (see Fig. 2). In other words, the proposed methodology can dynamically partition composite compartmental throughflows and associated storages into subcompartmental segments based on their constituent environmental inputs of the same conserved quantity. This partitioning enables tracking the evolution of environmental inputs and the associated storages generated by the inputs individually and separately within the system. Note that the composite compartmental net throughflows and storages, $\tau_i(t, x)$ and $x_i(t)$, cannot be used to distinguish the portions of these throughflows and storages derived from individual environmental inputs separately. Therefore, the solution to the decomposed system brings out inferences that cannot be obtained through the analysis of the original system by the state of the art techniques. The arguments presented for the net throughflow functions above are also valid individually for the inward and outward throughflow functions, $\bar{\tau}_{ik}(t, x)$ and $\bar{\tau}_{ik}(t, x)$, as well.

The transient flows and associated storages transmitted along a given subflow path are also formulated through the dynamic subsystem partitioning methodology. Therefore, the dynamic subsystem partitioning determines the distribution of arbitrary intercompartmental flows and the organization of the associated storages generated by these flows along given subflow paths within the subsystems. Consequently, arbitrary composite intercompartmental flows and storages are dynamically decomposed into the constituent transient subflow and substorage segments along a given set of subflow paths. In other words, the subsystem decomposition enables dynamically tracking the fate of arbitrary intercompartmental flows and associated storages within the subsystems. Based on the concept of transient flow and storage, the dynamic di-
rect, indirect, acyclic, cycling, transfer (diact) flows and storages transmitted from one compartment, directly or indirectly, to any other—including itself—within the system are also systematically formulated.

2.2. The diact Effect Measures and Indices. The effect of one compartment on another through direct transactions is relatively easier to analyze, even in complex networks. The proposed subsystem partitioning methodology enables also the determination of the indirect effect of one compartment indirectly through other compartments on another or itself within the system. In fact, parallel to the definitions of diact flows and storages, we systematically introduce all the other diact effect measures and indices in this section.

Based on the transfer flow definition presented in Appendix B, the transfer effect measures and indices and the corresponding system efficiencies and stress are introduced below at the compartmental level. The subcompartmental level formulations in parallel are straightforward, using the transfer subflows and substorages instead of the transfer flows and storages.

The flow-based transfer effect index will be defined as the transfer flow normalized by total system throughput. The flow-based system transfer efficiency will then be defined as the time derivative of the effect index, and, so, it measures the rate of change of the dynamic index. The storage-based transfer effect index and system efficiency can be defined similarly, using the transfer storages instead of the flows and total system storage for normalization. Therefore, the flow- and storage-based effect indices are fractions of total system throughput and storage, respectively. Both flow- and storage-based effect indices quantify the influence of system compartments on the others.

The flow- and storage-based transfer effect indices, \( t_{IK}^T(t) \) and \( t_{IK}^S(t) \), of a set of compartments, \( K \), on another set, \( I \), can be formulated as the fraction of total system throughput that is initiated at compartments \( K \) during \([t_0, t]\) and transmitted directly or indirectly to \( I \) at time \( t \), and as the fraction of total system storage generated by these transfer flows, respectively. That is,

\[
(2.12) \quad t_{IK}^T(t) = \frac{\sum_{i \in I} \sum_{k \in K} \tau_{ik}^T(t)}{\sum_{i=1}^n x_i(t)} \quad \text{and} \quad t_{IK}^S(t) = \frac{\sum_{i \in I} \sum_{k \in K} x_{ik}^S(t)}{\sum_{i=1}^n x_i(t)}
\]

where \( I, K \subseteq \{1, \ldots, n\} \). If the sets \( I \) and \( K \) have one element, that is, \( I = \{i\} \) and \( K = \{k\} \), transfer effect indices will be denoted by \( t_{ik}^T(t) \) and \( t_{ik}^S(t) \). Note that the transfer effect indices are dimensionless.

The flow- and storage-based transfer effect matrix functions are denoted by \( T^\tau(t) = (t_{ik}^\tau(t)) \) and \( T^S(t) = (t_{ik}^S(t)) \) and formulated in matrix form as

\[
(2.13) \quad T^\tau(t) = \frac{T^\tau(t)}{\sigma^\tau(t)} \quad \text{and} \quad T^S(t) = \frac{X^\tau(t)}{\sigma^S(t)}
\]

where the scalar functions \( \sigma^\tau(t) = \mathbf{1}^T \tau(t) \) and \( \sigma^S(t) = \mathbf{1}^T x(t) \) are the total inward system throughput and system storage, respectively. The flow-based transfer effect of the system on the compartments, \( T^\tau(t) \), and those of the compartments on the system, \( T^\tau(t) \), will be defined as vector measures:

\[
(2.14) \quad \dot{T}^\tau(t) = T^\tau(t) \mathbf{1} \quad \text{and} \quad \dot{T}^S(t) = \mathbf{1}^T T^S(t).
\]

The storage-based transfer effect vector functions can be defined similarly.
We will use the notations $\tau^s(t)$ and $\tau^x(t)$ for the sum of the transfer effects of the entire system on all compartments, that is, for $I = K = \{1, \ldots, n\}$. They can be formulated as

$$\tau^s(t) = \int_1^T T^s(t) \frac{1}{\sigma^s(t)} \, ds = 1^T T^s(t) \mathbf{1} \quad \text{and} \quad \tau^x(t) = \int_1^T X^x(t) \frac{1}{\sigma^x(t)} \, ds = 1^T X^x(t) \mathbf{1}.$$  

These scalar functions will be called the flow- and storage-based transfer effect indices for the system.

The dynamic measures are functions of time, and their time derivatives and integrals also represent various system attributes. In addition to the local-in-time indices introduced above, the average or non-local transfer effect indices over time interval $[t_1, t]$, $t_1 \geq t_0$, can be defined by integrating both the numerator and denominator of $\tau^s(t)$ and $\tau^x(t)$ separately over the interval. That is,

$$\tau^s(t_1, t) = \int_{t_1}^t \frac{1^T T^s(s)}{1^T \sigma^s(s)} \, ds \quad \text{and} \quad \tau^x(t_1, t) = \int_{t_1}^t \frac{1^T X^x(s)}{1^T \sigma^x(s)} \, ds.$$  

The integrals of the transfer flows and associated storages involved componentwise in the formulations above, $\int_{t_1}^t \tau_{ij}^s(s) \, ds$ and $\int_{t_1}^t x_{ij}^x(s) \, ds$, measure the total transfer flows and associated storages transmitted during $[t_1, t]$. Similarly, $\int_{t_1}^t \sigma^x(s) \, ds$ and $\int_{t_1}^t \sigma^x(s) \, ds$ are the cumulative total system throughflow and storage during the same time period.

The time derivatives of transfer effect indices, $\dot{\tau}^s(t)$ and $\dot{\tau}^x(t)$, will be called the system flow and storage transfer efficiencies, respectively, as the higher rates indicate increasing transfer effects and, consequently, more efficient compartmental transactions. They are formulated as,

$$\dot{\tau}^s(t) = \frac{d}{dt} \left( \frac{1^T T^s(t)}{\sigma^s(t)} \right) \quad \text{and} \quad \dot{\tau}^x(t) = \frac{d}{dt} \left( \frac{1^T X^x(t)}{\sigma^x(t)} \right).$$  

The time derivatives of the transfer flows and associated storages involved componentwise in the formulations above, $\dot{\tau}_{ij}^s(t)$ and $\dot{x}_{ij}^x(t)$, measure the rate of change at which the flows and associated storages are transferred at time $t$. Similarly, $\dot{\sigma}^s(t)$ and $\dot{\sigma}^x(t)$ are the rate of change of the total system throughflow and storage at time $t$, respectively.

These novel system efficiencies have the potential to play a similar role to heart rate graphs in examining the human body for ecological systems, as they can detect system disturbances and abnormalities. The rapid unusual fluctuations in the graphs of these functions indicate an excess amount of input into the system as presented in Examples 3.1 and 3.3.

The flow- and storage-based diact effect measures and indices for all diact transaction types can be formulated similar to the transfer effect measures and indices introduced in this section. More specifically, the local and average diac effect indices and system efficiencies can be formulated for the other transaction types by substituting the corresponding diact flows and storages for their transfer counterparts in Eqs. 2.15, 2.16, and 2.17. As examples, the flow-based cycling and indirect effect indices at the compartmental level become

$$c^s(t) = \frac{1^T T^c(t)}{\sigma^s(t)} \quad \text{and} \quad \dot{c}^s(t) = \frac{d}{dt} \left( \frac{1^T T^c(t)}{\sigma^s(t)} \right).$$
The direct, indirect, acyclic, and transfer effect indices can be interpreted as respective direct, indirect, through (non-cycling), and total influence of one system compartment on another. However, due to reflexive nature of the cycling flow and storage, the cycling effect index can be interpreted as the influence of a compartment indirectly on itself. More specifically, the flow-based direct, indirect, and transfer effect indices, $d_{ik}(t)$, $i_{ik}(t)$, and $t_{ik}(t)$, can be interpreted as the direct, indirect, and total influence of compartment $k$ on $i$ at time $t$, induced by all environmental inputs during $[t_0, t]$. Equivalently, they can be interpreted as respective direct, indirect, and total influence of environment on compartment $i$ via $k$ at time $t$. The acyclic and cycling effect indices, $a_{ik}(t)$ and $c_{ik}(t)$, can then be interpreted as the through influence of compartment $k$ on $i$ and the indirect influence of subcompartment $i_k$ on itself, respectively, at time $t$, induced by the single environmental input $z_k(t)$ during $[t_0, t]$. Equivalently, they can be interpreted as the respective through and cycling influence of the single environmental input $z_k(t)$ on compartment $i$ via $k$ at time $t$. The storage-based diact effect indices can be interpreted similarly.

The diac effect vectors can be formulated as their transfer counterparts given in Eq. 2.14 by the corresponding substitutions. The diac effect vectors, $\hat{d}(t)$ and $\hat{i}(t)$, can be interpreted as the direct and indirect effects of the system (or environment) on the compartments and, $\hat{d}(t)$ and $\hat{i}(t)$, as those of the compartments on the system at time $t$. The ac effect vectors, $\hat{a}(t)$ and $\hat{c}(t)$, can then be interpreted as the through and cycling effects of the system (or environment) on the compartments and, $\hat{a}(t)$ and $\hat{c}(t)$, as those effects on the subsystems at time $t$. The scalar diac system effect indices can also be formulated as their transfer counterparts given in Eq. 2.15 by the corresponding substitutions. They can be interpreted as the diac effects of the system on itself.

In static ecological network analyses, Finn’s Cycling Index (FCI) is the standard flow-based measure that quantifies cycling system flows [16]. A storage-based cycling index is also formulated in the literature [27]. A dynamic measure for flow or storage cycling has not been proposed yet. The proposed methodology formulates the dynamic local and average, flow- and storage-based cycling indices as well as the corresponding system efficiencies explicitly at both compartmental and subcompartmental levels for the first time. It is also shown by [11] that, at steady-state, the proposed dynamic flow- and storage-based cycling effect indices at the compartmental level are equivalent to the FCI and SCI, respectively. Static cycling index is sometimes associated with ecosystem stress [39]. The cycling flow efficiency will alternatively be called system stress, accordingly.

In the environment theory, the indirect effects are considered to be flow contributions carried by subsequent steps after the first entrance into a compartment. Even the direct transactions, after the first step, are considered as indirect contribution in various formulations proposed in the literature [29, 31, 20, 4, 26]. They are, therefore, microscopic quantities. These static indirect effect indices are formulated without actually defining the indirect flow between two system compartments. The proposed dynamic indirect effect indices have different derivation rationale than these current static indices, as the proposed indices are based on the indirect flows and storages introduced in Appendix A and are measurable physical quantities. The proposed indices capture experimental system behavior more accurately than the previous formulations, as shown in [12].

### 2.3. The diact Utility Measures and Indices

A direct utility index was introduced in the literature for static systems [32, 14]. The local, compartmental
normalization in this formulation makes the physical interpretation of the utility index harder as a system measure. In this section, a dynamic direct utility index will be introduced following the same rationale. The proposed index is different from the authors’ static formulation, due to its global normalization procedure in accordance with the diact effect index formulations introduced in Sec. 2.2. This procedure allows for local interpretations of intercompartmental dynamics relative to the entire system.

All the other novel diact utility measures and indices and the corresponding efficiencies are also systematically introduced in this section. In general terms, the dynamic diact utility measure will be defined as the relative diact effect of one compartment on another. The subcompartmental level formulations in parallel are straightforward, using subflows and associated substorages instead of flows and storages.

We will first define the dynamic transfer utility measures and indices. The flow- and storage-based transfer utility indices of a set of compartments $K$ to another set $I$, $\dot{t}_{IK}^I(t)$ and $\dot{t}_{IK}^I(t)$, quantify the relative flow- and storage-based transfer effects of $K$ on $I$ at time $t$. They measure the normalized relative net benefit ($\dot{t}_{IK}^I(t) > 0$ and $\dot{t}_{IK}^I(t) > 0$) or harm ($\dot{t}_{IK}^I(t) < 0$ and $\dot{t}_{IK}^I(t) < 0$), that is transmitted from the set of compartments $K$ to $I$ at time $t$ based on their respective net gains (inflows and associated storages) or losses (outflows and associated storages). The transfer utility indices are formulated as

$$
\dot{t}_{IK}^I(t) = \dot{t}_{IK}^I(t) - \dot{t}_{KI}^I(t) \quad \text{and} \quad \dot{t}_{IK}^I(t) = \dot{t}_{IK}^I(t) - \dot{t}_{KI}^I(t)
$$

where $I, K \subseteq \{1, \ldots, n\}$. If the sets $I$ and $K$ have one element, that is, $I = \{i\}$ and $K = \{k\}$, these indices will be denoted by $\dot{t}_{ik}^I(t)$ and $\dot{t}_{ik}^I(t)$. Note that since the transfer effect indices are dimensionless, the transfer utility indices are also dimensionless.

The flow- and storage-based transfer utility matrix measures are denoted by $\breve{T}^\tau(t) = (\dot{t}_{ik}^I(t))$ and $\breve{T}^\sigma(t) = (\dot{t}_{ik}^I(t))$ and formulated in matrix form as

$$
\breve{T}^\tau(t) = \frac{1}{\tau^\tau(t)} \left( T^\tau(t) - T^\tau(t) \right) \quad \text{and} \quad \breve{T}^\sigma(t) = \frac{1}{\tau^\sigma(t)} \left( X^\tau(t) - X^\tau(t) \right)
$$

where the superscript $(T)$ stands for the matrix transpose. The flow-based transfer utility of the system on the compartments, $\breve{x}^\tau(t)$, and that of the compartments on the system, $\breve{x}^\tau(t)$, at time $t$ will be defined as vector measures:

$$
\breve{x}^\tau(t) = \breve{T}^\tau(t) \mathbf{1} \quad \text{and} \quad \breve{x}^\sigma(t) = \mathbf{1}^T \breve{T}^\sigma(t) \quad \text{with} \quad \breve{x}^\tau(t) = -(\breve{x}^\tau(t))^T.
$$

The storage-based transfer utility vectors can be defined similarly. Note that, since $\breve{T}^\tau(t)$ and $\breve{T}^\sigma(t)$ are skew-symmetric matrices, the flow- and storage-based transfer utility indices for the system are zero:

$$
\breve{t}^\tau(t) = \mathbf{1}^T \breve{T}^\tau(t) \mathbf{1} = 0 \quad \text{and} \quad \breve{t}^\sigma(t) = \mathbf{1}^T \breve{T}^\sigma(t) \mathbf{1} = 0.
$$

These relationships are true for all diact utility matrix measures. For the same reason, the average transfer utility indices, which can be formulated similar to the average effect indices defined in Sec. 2.2, are also zero. That is,

$$
\breve{t}^\tau(t_1, t) = 0 \quad \text{and} \quad \breve{t}^\sigma(t_1, t) = 0.
$$

The system flow- and storage-based transfer utility efficiencies are then defined as the time derivatives of the flow and storage-based utility indices, respectively:

$$
\dot{\breve{t}}^\tau_{IK}(t) = \dot{t}^\tau_{IK}(t) - \dot{t}^\tau_{KI}(t) \quad \text{and} \quad \dot{\breve{t}}^\sigma_{IK}(t) = \dot{t}^\sigma_{IK}(t) - \dot{t}^\sigma_{KI}(t).
$$
The flow- and storage-based dynamic \textbf{diac} utility measures and indices for all \textbf{diac} transaction types can be formulated, similar to the transfer utility measures and indices introduced in this section, by substituting the corresponding \textbf{diac} flows and storages for their transfer counterparts in Eq. 2.19 and 2.23.

The \textbf{diac} utility indices can be interpreted as the relative \textbf{diac} influence of system compartments on each other. More specifically, the direct, indirect, and transfer utility indices, $d_{ik}(t)$, $i_{ik}(t)$, and $t_{ik}(t)$, can be interpreted as the direct, indirect, and total relative influence of compartment $k$ on $i$ at time $t$ induced by all environmental inputs during $[t_0, t]$. The acyclic and cycling utility indices, $a_{ik}(t)$ and $c_{ik}(t)$, however, can be interpreted as the relative through and cycling influence of compartment $k$ on $i$ at time $t$ induced only by the corresponding two environmental inputs, $z_k(t)$ and $z_i(t)$, during $[t_0, t]$.

The \textbf{diac} utility vectors can be formulated as their transfer counterparts given in Eq. 2.21 by the corresponding substitutions. The utility vectors $\mathbf{d}(t)$, $\mathbf{i}(t)$, $\mathbf{a}(t)$, and $\mathbf{c}(t)$ can be interpreted as the relative \textbf{diac} effects of a system (or environment) on its compartments and $\mathbf{d}(t)$, $\mathbf{i}(t)$, $\mathbf{a}(t)$, and $\mathbf{c}(t)$ as those effects of the compartments on the system at time $t$.

2.4. The \textbf{diac} Exposure and Residence Time. The impact of environment on the system compartments can also be evaluated directly by their exposure to environmental input. The exposure to ionizing radiation, poisons, and other bioactive chemical agents are important topics of concern for human health and welfare. In this section, we introduce the dynamic exposure and residence time measures and indices. These novel quantitative system analysis tools can find use in radiobiology, toxicology, pharmacokinetics, and other applied environmental and medical fields.

The exposure of compartment $i$ during $[t_1, t]$ ($t_1 \geq t_0$) to the environmental input into component $k$, $z_k(t)$, over time period $[t_0, t]$, can be defined component-wise as

$$e_{ik}(t_1, t) = \int_{t_1}^{t} x_{ik}(s) \, ds$$

for $i = 1, \ldots, n$, and $k = 0, \ldots, n$. Note that, the unit of exposure is mass $\times$ time, $[m \, \tau]$. Depending on the conserved quantity in question, the unit of storage can be changed from mass to the unit of that quantity of interest, such as energy or currency. Excluding exposure of the initial subsystem ($k = 0$), the $n \times n$ exposure matrix, $E_{ik}(t_1, t) = (e_{ik}(t_1, t))$, can be expressed in matrix form as

$$E(t_1, t) = \int_{t_1}^{t} X(s) \, ds.$$

The exposure of compartments, $\mathbf{e}(t)$, and subsystems, $\mathbf{e}(t)$, to all environmental inputs during $[t_1, t]$ can then be formulated as vector functions:

$$\mathbf{e}(t) = E(t_1, t) \mathbf{1} \quad \text{and} \quad \mathbf{e}(t) = \mathbf{1}^T E(t_1, t).$$

The scalar system exposure index to environmental inputs during $[t_1, t]$ can also be formulated as

$$e(t_1, t) = \mathbf{1}^T E(t_1, t) \mathbf{1}.$$

We also define the exposure time or residence time of the storage in compartment $i$ at time $t$ as

$$r_i(t) = \frac{x_i(t)}{\tau_i(t, x)} = \frac{x_i(t)}{\tau_i(t, x)} = \frac{x_{ik}(t)}{\tau_{ik}(t, x)}$$
for \( i = 1, \ldots, n \). Note that the unit of the residence time is time, \([t]\). The residence time of substorage in subcompartment \( \hat{r}_{ik}(t, x) \) at time \( t \) is also the same for any \( k = 0, \ldots, n \), as indicated in Eq. 2.27, when \( \hat{r}_{ik}(t, x) \neq 0 \). Therefore, the residence time matrix, \( \mathcal{R}(t) \), is an \( n \times n \) diagonal matrix function. Excluding the initial subsystem, \( \mathcal{R}(t) = \text{diag}([\hat{r}_{1}(t), \ldots, \hat{r}_{n}(t)]) \) can be expressed in the following matrix forms:

\[
\mathcal{R}(t) = \mathcal{X}_{k}(t, x) \mathcal{T}_{k}^{-1}(t, x) = \mathcal{X}(t) \mathcal{T}(t, x)^{-1} = X(t) \hat{T}(t, x)^{-1},
\]

as formulated in Eq. 2.10. The diagonal \( k \)th substorage, inward and outward sub-throughflow matrices are defined as \( \mathcal{X}_{k}(t) = \text{diag}([x_{1k}(t), \ldots, x_{nk}(t)]) \), \( \mathcal{T}_{k}(t, x) = \text{diag}([\tau_{1k}(t, x), \ldots, \tau_{nk}(t, x)]) \), and \( \mathcal{R}_{k}(t, x) = \text{diag}([\tau_{1k}(t, x), \ldots, \tau_{nk}(t, x)]) \), respectively, for the \( k \)th subsystem. The \( i \)th diagonal entry of \( \mathcal{R}(t) \) at time \( t_1 \), \( r_{i}(t_1) \), can be interpreted as time required for outward throughflow, at the constant rate of \( \hat{r}_{i}(t_1) \), to completely empty compartment \( i \) with initial storage \( x_{i}(t_1) \). The diagonal structure of the residence time matrix indicates that all subcompartment of compartment \( i \) vanish simultaneously. Ecologically, \( \mathcal{R}(t) \) can be used as a dynamic indicator for compartmental activity levels in ecological networks; the smaller the residence time, the more active the compartments.

The exposure of compartments to the transient and diact flows can be formulated by substituting the corresponding transient and diact storages for substorage, \( \hat{x}_{ik}(t) \), in Eq. 2.24. The exposure of compartments to the transient and diact flows will be called the transient and diact exposures, respectively, and be denoted by \( e^{w} \) and diact symbols. For a given subflow path \( p_{n_{j}k}^{w} = i_{k} \rightarrow j_{k} \rightarrow \ell_{k} \rightarrow n_{k} \), for example, the transient exposure of subcompartment \( \ell_{k} \) at time \( t \) to transient inflow \( f_{n_{j}k}^{w} \) along path \( p_{n_{j}k}^{w} \) during \([t_1, t]\) can be formulated as

\[
(2.29) \quad e^{w}_{\ell_{k}}(t_1, t) = \int_{t_1}^{t} \frac{x^{w}_{n_{j}k, j_{k}k}(s)}{x^{w}_{n_{j}k, j_{k}k}(s)} ds.
\]

Note that the residence time of the transient and diact storages in subcompartment \( \ell_{k} \) are also equal to \( r_{k}(t) \), due to the equivalence of the outward flow and throughflow intensities [10]. For example, the transient residence time is \( r_{k}(t) = x^{w}_{n_{j}k, j_{k}k}(t)/\hat{x}^{w}_{\ell_{k}}(t) \), where the transient throughflow \( \hat{x}^{w}_{\ell_{k}}(t) \) is defined by Eq. A.4.

It is also worth noting that the diact exposures can be interpreted as unnormalized, storage-based, average diact effect indices. The indirect exposure of compartment \( i \) at time \( t \) to the storage transmitted indirectly through other compartments from \( k \) during \([t_1, t]\), for example, can be formulated as

\[
(2.30) \quad q_{ik}(t_1, t) = \int_{t_1}^{t} x^{k}_{ik}(s) ds = i_{ik}(t_1, t) \int_{t_1}^{t} \sigma^{w}(s) ds.
\]

Illustrative examples for the system measures and indices introduced in this section are presented in the next section.

3. Results. The proposed dynamic methodology is applied to various discrete and continuous ecological models from the literature. The dynamic measures and indices formulated above for diact effect, utility, exposure, and residence time as well as the corresponding system efficiencies, stress, and resilience together with their ecological implications are presented for these models in this section.

The results indicate that the proposed methodology precisely quantifies dynamic system functions, properties, and behaviors, effectively determine the environmental
influence on system compartments and intercompartmental dynamics, is sensitive to
perturbations due to even a brief unit impulse, and, thus, can be used for rigorous
dynamic analysis of nonlinear ecological systems. It is worth noting, however, that
this present work proposes a mathematical method—a systematic technique designed
for analyzing dynamic nonlinear ecosystem models using the proposed measures and
indices as ecosystem indicators—and it is not a model. Therefore, we focus more on
demonstrating the efficiency and wide applicability of the quantitative system analysis
tools introduced as ecological indicators in the present paper. It is expected that once
the method is accessible to a broader community of environmental ecologists, it can
be used for ecological inferences and detailed analyses of specific models of interest.

3.1. Case study. A nonlinear model proposed by [17] has recently been ana-
yzed through the proposed methodology by [9]. In particular, the substorage and
subthroughflow matrix measures and transient flows and storages as well as their eco-
logical interpretations are provided. In this section, the dynamic measures and indices
introduced in the present manuscript are presented for this ecosystem model together
with their ecological interpretations.

The resource-producer-consumer model by [17] consists of the dynamics for three
components: resource, \( x_1(t) = r(t) \), which is the nutrient storage (such as phosphorus
or nitrogen) present at time \( t \); producer, \( x_2(t) = s(t) \), which denotes the nutrient stor-
age in the producer (such as phytoplankton) population; and consumer, \( x_3(t) = c(t) \),
which denotes the nutrient storage in the consumer (such as zooplankton) popula-
tion. The conservation of nutrient is the basic model assumption. The system flows
are described as follows:

\[
F(t, x) = \begin{bmatrix}
0 & \frac{d_1}{\alpha_1} s(t) & d_2 c(t) \\
\frac{\alpha_1}{\alpha_2 + r(t)} & 0 & 0 \\
0 & \frac{d_1}{\beta_1} s(t) & 0 \\
\end{bmatrix}, \quad z(t) = \begin{bmatrix} z_1(t) \\
z_2(t) \\
z_3(t) \\
\end{bmatrix}, \quad y(t) = \begin{bmatrix} r(t) \\
s(t) \\
c(t) \\
\end{bmatrix}
\]

where the constant input is \( z(t) = [1, 1, 1]^T \), and the parameters are given as
\[
d_1 = 2.7, \quad d_2 = 2.025, \quad \alpha_2 = 0.098, \quad \beta_1 = 2, \quad \beta_2 = 20, \quad \text{and} \quad \alpha_1 = 1.
\]

The system of governing equations then takes the following form:

\[
\begin{align*}
\dot{r}(t) &= -r(t) + d_1 s(t) + d_2 c(t) - \frac{\alpha_1 s(t) r(t)}{\alpha_2 + r(t)} + z_1(t) \\
\dot{s}(t) &= -(1 + d_1) s(t) + \frac{\alpha_1 s(t) r(t)}{\alpha_2 + r(t)} - \frac{\beta_1 c(t) s(t)}{\beta_2 + s(t)} + z_2(t) \\
\dot{c}(t) &= -(1 + d_2) c(t) + \frac{\beta_1 c(t) s(t)}{\beta_2 + s(t)} + z_3(t)
\end{align*}
\]

with the initial conditions of \( [r_0, s_0, c_0] = [1, 1, 1] \).

Let the subcompartmentalization become

\[
x_{1k}(t) = r_k(t), \quad x_{2k}(t) = s_k(t), \quad \text{and} \quad x_{3k}(t) = c_k(t), \quad k = 0, \ldots, 3.
\]

The flow partitioning yields

\[
F_k(t, x) = \begin{bmatrix}
0 & \frac{d_1}{\alpha_2 + r} & d_2 c \\
\frac{\alpha_1}{\alpha_2 + r} & 0 & 0 \\
0 & \frac{\beta_1}{\beta_2 + s} & 0 \\
\end{bmatrix}, \quad \hat{z}_k(t, x) = \begin{bmatrix} \delta_{1k} z_1 \\
\delta_{2k} z_2 \\
\delta_{3k} z_3 \\
\end{bmatrix}, \quad \hat{y}_k(t, x) = \begin{bmatrix} d_{1k} r \\
d_{2k} s \\
d_{3k} c \\
\end{bmatrix}
\]
where \( F_k, \hat{z}_k, \) and \( \hat{y}_k \) describe the \( k^{th} \) direct flow matrix, input, and output vectors for the \( k^{th} \) subsystem, and the decomposition factors \( d_{i_k}(x) \) are defined by Eq. 2.5. Therefore, the dynamic system partitioning methodology yields

\[
\begin{align*}
\dot{r}_k(t) &= \delta_{1k} z_1(t) + d_1 s_k(t) + d_2 c_k(t) - r_k(t) - \frac{\alpha_1 s(t) r_k(t)}{\alpha_2 + r(t)} \\
\dot{s}_k(t) &= \delta_{2k} z_2(t) + \frac{\alpha_1 s(t) r_k(t)}{\alpha_2 + r(t)} - s_k(t) - d_1 s_k(t) - \frac{\beta_1 c(t) s_k(t)}{\beta_2 + s(t)} \\
\dot{c}_k(t) &= \delta_{3k} z_3(t) + \frac{\beta_1 c(t) s_k(t)}{\beta_2 + s(t)} - c_k(t) - d_2 c_k(t)
\end{align*}
\]

with the initial conditions

\[
x_{i_k}(t_0) = \begin{cases} 
1, & k = 0 \\
0, & k \neq 0
\end{cases}
\]

for \( i = 1, \ldots, 3 \). There are \( n \times (n + 1) = 3 \times 4 = 12 \) equations in this system.

The system is solved numerically, and the graphs for selected elements of the substorage and the subthroughflow matrices are depicted in Fig. 3. As seen from the graphs, the system converges to a steady-state quickly at about \( t \approx 6 \) units. The results show, for example, that the nutrient storage in the resource compartment \((i = 1)\) derived from nutrient input into the consumers compartment \((3)\), \( x_{13}(t) \), increases from 0 to 0.62 units until the system reaches the steady state, while the initial nutrient storage in the resource compartment, \( x_{11} \), first increases from 1 to 1.36 units and then vanishes. The throughflow into the resource compartment generated by nutrient input into the producers compartment \((2)\), \( \tau_{12}(t, x) \), increases until about \( t \approx 2 \). The outward throughflow at the same subcompartment, \( \tau_{12}(t, x) \), is slightly smaller than inward throughflow, \( \tau_{12}(t, x) \), but has a similar behavior. As seen from these results, the distribution of environmental nutrient inputs and the organization of the associated nutrient storages generated by the inputs can be analyzed individually and separately within the system.

To demonstrate the capability of the proposed method to analyze time dependent inputs, the system is also perturbed with a Gaussian input \( z_2(t) = e^{-\frac{(t-15)^2}{2}} + 0.1 \),
which represents a brief, unit local impulse about \( t = 15 \). The other two environmental nutrient inputs are kept constant as before for a comparison, that is, \( z_1(t) = z_2(t) = 1 \). The graphical representation for the selected elements of the substorage and subthroughflow matrices are given in Fig. 4. Clearly, the substorage and the subthroughflow matrix elements reflect the impact of the unit impulse about \( t = 15 \). Note that, the system completely recovers after the disturbance in about 10 time units. This time interval can be taken as a quantitative measure for the restoration time and system resilience. Therefore, the proposed measures can also be used as quantitative ecological indicators for various ecosystem characteristics and behaviors.

For the system perturbed with the Gaussian input, the exposure function \( e_{12}(5, 10) \) defined in Sec. 2.4, which measures the exposure of the resource compartment during time interval \([5, 10]\) to the nutrient input entering the system at the producers compartment, can be obtained as follows:

\[
e_{12}(5, 10) = \int_{5}^{10} x_{12}(s) \, ds = 25 \times 10^{-3}.
\]

In Fig. 5, a (scaled) graphical representation of \( e_{12}(t) \) is presented together with the corresponding input, \( z_2(t) \). The graph shows the exposure of the resource compartment to \( z_2(t) \) during time interval \([0, 25]\). There is clearly a sudden increase in \( e_{12}(t) \) at about \( t = 15 \) due to the disturbance, as expected.

The same brief impulse is detected as rapid fluctuations around the stimulus time in the graphs of the subcompartmental indirect and cycling effect indices, \( \tau_{23,31}^\tau(t) = \tau_{23,31}(t)/\sigma^\tau(t) \) and \( c_{31}^\tau(t) = \tau_{31}^\tau(t)/\sigma^\tau(t) \), and the corresponding system efficiency and stress as presented in Fig. 5. The indirect and cycling nutrient subflows are obtained by using the formulations in Eqs. B.5 and B.7. Although they have different values, both indices have the same behavior due to their complementary nature (see Fig. 12). The system stress and efficiencies have the potential to play a similar role as heart rate graphs in examining the human body for ecological systems, because they can detect system disturbances and abnormalities. The unusual rapid fluctuations in the corresponding graphs of these functions presented in Fig. 5 indicate an excess amount of nutrient input into the system. Therefore, they can be used to quantify the system resilience and resistance to disturbances similar to the subthroughflow and substorage
matrices as discussed above. Consequently, the system efficiency and stress can be used as ecological indicators to monitor ecosystems for possible environmental effects.

When the system is perturbed with the same Gaussian impulse, now centered at $t = 50$ instead of $t = 15$, the residence time, formulated in Sec. 2.4, stays the same at its steady-state value before and after the disturbance, at $t = 40$ and $t = 60$, that is $R(40) = R(60) = \text{diag}([0.98, 0.27, 0.33])$. At the maximum stimulus time $t = 50$, however, it becomes $R(50) = \text{diag}([0.85, 0.27, 0.33])$. Surprisingly, the Gaussian impulse $z_2(t)$ at the producers compartment decreases the residence time of the nutrient storage in and, therefore, increases the activity level of the resource compartment (and all of its subcompartments) only.

![Fig. 5. The numerical results for the indirect effect index of subcompartment $3_3$ on $2_3$ and the corresponding system efficiency, $\tau_{3_3}^{2_3}$ and $\tau_{3_3}^{2_3,3_3}(t)$, the cycling effect index at subcompartment $3_3$ and the corresponding system stress, $e_{3_3}(t)$ and $e_{3_3}^{2_3}(t)$, and exposure function $e_{3_3}(t)$ (scaled up by a factor of 30 for clarity) and the corresponding time dependent Gaussian impulse $z_2(t) = e^{-\frac{(t-15)^2}{2}} + 0.1$ (Case Study 3.1).]

The dynamic diact effect and utility measures and indices are introduced in Sec. 2.2 and 2.3. The diact effect formulations can be simplified in a way that the diact effect of compartment $k$ on $i$ induced by a single environmental input can be determined. This modification allows for restricting the effect and utility analyses to specific environmental inputs. The flow-based transfer effect index of compartment $k$ on $i$ induced only by $z_k(t)$ can be formulated as $\tau_{ik}^{jk}(t) = \tau_{ik,k}(t)/\sigma^2(t)$. The corresponding flow-based transfer utility index induced only by inputs $z_k(t)$ and $z_i(t)$ reads: $\tau_{ik}^{ij}(t) = \tau_{ik}^{ji} - \tau_{ki}^{ij}$. For notational simplicity, we used the same notations of Secs. 2.2 and 2.3 for these restricted effect and utility functions.

The flow-based direct and indirect utilities transmitted from the producers to the consumers induced only by the corresponding nutrient inputs, $z_2(t)$ and $z_3(t)$, can then be formulated as

$$d_{32}^*(t) = d_{32}^*(t) - d_{33}^*(t) = \frac{\tau_{3_2}^{4_2} - \tau_{3_3}^{4_3}(t)}{\sigma^*(t)},$$

$$i_{32}^*(t) = i_{32}^*(t) - i_{33}^*(t) = \frac{\tau_{3_2}^{4_2} - \tau_{3_3}^{4_3}(t)}{\sigma^*(t)}.$$

The direct and indirect subflows in the expressions above are computed as formulated in Eqs. B.4 and B.5. For the perturbed system, the graphical representation of these functions are given in Fig. 6. Both graphs have fluctuations due to the Gaussian impulse at about $t = 15$. Interestingly, while the direct utility function is always positive, $d_{32}^*(t) > 0$, the indirect utility function is negative, $i_{32}^*(t) < 0$, during $t \in [0, 25]$. That is, considering the effects induced only by nutrient inputs $z_2(t)$ and $z_3(t)$,
although the consumers have relative net nutrient gain (benefit) from the producers through direct interactions, they have relative net nutrient loss (harm from) the producers indirectly through the resource compartment.

![Graph](image)

**Fig. 6.** The numerical results for the flow-based direct and the indirect utility indices of compartment 2 to 3, $d_{23}(t)$ and $i_{23}(t)$, induced by inputs $z_2(t)$ and $z_3(t)$, for the system perturbed with time dependent Gaussian impulse $z_2(t) = e^{-\frac{(t-15)^2}{2}} + 0.1$. In the figure legends, $d$ and $i$ notations are used for $d$ and $i$ due to the limited font library of Matlab software (Case Study 3.1).

### 3.2. Case study.

The linear model introduced by [21] was recently solved analytically through the proposed methodology by [9]. In particular, the substorage and subthroughflow matrix measures as well as the transient and diact flows and storages were presented.

This linear dynamic ecosystem model has two compartments, $x_1(t)$ and $x_2(t)$ (see Fig. 7). The flows regime is described as

$$F(t, x) = \begin{bmatrix} 0 & 2x_2(t) \\ \frac{2}{3}x_1(t) & 0 \end{bmatrix}, \quad z(t, x) = \begin{bmatrix} z_1(t) \\ z_2(t) \end{bmatrix}, \quad y(t, x) = \begin{bmatrix} \frac{1}{3}x_1(t) \\ \frac{2}{3}x_2(t) \end{bmatrix}. $$

The governing equations take the following form:

$$\begin{align*}
\dot{x}_1(t) &= z_1(t) + \frac{2}{3}x_2(t) - \left(\frac{4}{3} + \frac{1}{3}\right)x_1(t) \\
\dot{x}_2(t) &= z_2(t) + \frac{4}{3}x_1(t) - \left(\frac{2}{3} + \frac{5}{3}\right)x_2(t)
\end{align*}$$

with the initial conditions $[x_{1,0}, x_{2,0}]^T = [3, 3]^T$.

Let the subcompartmentalization become

$$x_{1k}(t) \quad \text{and} \quad x_{2k}(t), \quad k = 0, 1, 2.$$ 

The flow partitioning then yields

$$F_k(t, x) = \begin{bmatrix} 0 & \frac{2}{3}d_{2k}x_2(t) \\ \frac{2}{3}d_{1k}x_1(t) & 0 \end{bmatrix}, \quad z_k(t, x) = \begin{bmatrix} \delta_{1k}z_1(t) \\ \delta_{2k}z_2(t) \end{bmatrix}, \quad y_k(t, x) = \begin{bmatrix} \frac{1}{3}d_{1k}x_1(t) \\ \frac{2}{3}d_{2k}x_2(t) \end{bmatrix}$$

where the decomposition factors, $d_{ik}(x)$, are defined by Eq. 2.5. Consequently, the
The cycling flows and the associated storages generated by these flows are calculated below along the corresponding closed subflow paths. The sets of mutually exclusive and exhaustive subflow paths from subcompartment $1_k$ to itself, $P^2_{1_k}$, are given as $P^1_{1_0} = \{p^1_{1_0}, p^2_{1_0}\}$, $P^1_{1_1} = \{p^1_{1_1}\}$, $P^2_{1_2} = \{p^2_{1_2}\}$ where $p^1_{1_0} = 1_0 \rightarrow 1_0 \rightarrow 2_0 \rightarrow 1_0$, $p^2_{1_0} = 2_0 \rightarrow 2_0 \rightarrow 1_0 \rightarrow 2_0 \rightarrow 1_0$, $p^1_{1_1} = 1_1 \rightarrow 1_1 \rightarrow 2_1 \rightarrow 1_1$, and $p^2_{1_2} = 2_2 \rightarrow 2_2 \rightarrow 2_2 \rightarrow 1_2 \rightarrow 1_2$ (see Fig. 7). The links that do not contribute to the cycling subflows are represented by $\rightarrow$ symbol. The closed subflow path sets from subcompartment $2_k$ to itself, $P^2_{2_k}$, $k = 0, 1, 2$, can similarly be defined in parallel.

The cycling subflow at subcompartment $1_2$ along the only ($w_2 = 1$) subflow path $p^1_{1_2} \in P^1_{1_2}$, and the associated substorage are

$$\gamma^1_{1_2}(t) = \sum_{w=1}^{1} \sum_{t=1}^{2} f^w_{1_2}(t) = f^1_{1_2}(t) \quad \text{and} \quad x^w_{1_2}(t) = \sum_{w=1}^{1} x^w_{1_2}(t) = x^1_{1_2}(t),$$

as given in Eq. B.1. The links that contribute to the cycling flow along the path, $p^1_{1_2}$, are numbered with the red cycle numbers, $m$, in the extended subflow path diagram below:

$$p^1_{1_2} = 0_2 \rightarrow 2_2 \rightarrow 1_2 \rightarrow 2_2 \rightarrow 1_2 \rightarrow 2_2 \rightarrow 1_2 \rightarrow \cdots$$
The cumulative transient inflow $f_{12}^1(t)$ and the substorage $x_{12}^1(t)$ can be approximated by two terms ($m_1 = 2$) using Eq. A.3:

$$x_{12}^1(t) \approx \sum_{m=1}^{2} x_{2122}^{1m}(t) = x_{2122}^{11}(t) + x_{2122}^{22}(t),$$

$$f_{12}^1(t) \approx \sum_{m=1}^{2} f_{1221}^{1m}(t) = f_{1221}^{11}(t) + f_{1221}^{12}(t).$$

The transient subflows and associated substorages, $f_{12}^{w,m}(t)$ and $x_{12}^{w,m}(t)$, and the other transient subflows and substorages involved in Eq. 3.1, as formulated in Eqs. A.1 and A.2, are solved simultaneously together with the decomposed system in Eq. 2.3. Numerical results for the cycling flows and associated storages

$$\tau_i^c(t) = \sum_{k=0}^{2} \tau_{ik}(t) \quad \text{and} \quad x_i^c(t) = \sum_{k=0}^{2} x_{ik}(t)$$

for $i = 1, 2$ are presented in Fig. 8.

The dynamic flow- and storage-based cycling effect indices defined in Eq. 2.18 can be expressed for this system as

$$c^\tau(t) = \frac{\tau_1^c(t) + \tau_2^c(t)}{\tau_1(t) + \tau_2(t)} \quad \text{and} \quad c^x(t) = \frac{x_1^c(t) + x_2^c(t)}{x_1(t) + x_2(t)}.$$

Their graphs are presented in Fig. 8. As seen from the graphs, the flow- and storage-based cycling effect indices have similar behaviors.

### 3.3 Case Study

The Neuse River Estuary is a drowned river valley located at the transition from the Neuse River to Pamlico Sound in North Carolina. In 1997, the State of North Carolina legislated a reduction in nitrogen loading to the estuary. As part of the monitoring program to study the estuary’s response to new environmental management, nitrogen loading data is constructed for 16 seasons starting from Spring 1985 to Winter 1989 [8].

This ecosystem is modeled with seven compartments: phytoplankton particulate nitrogen, 1−PN-phyto; heterotroph particulate nitrogen, 2−PN-hetero; sediment particulate nitrogen, 3−N-sed; dissolved organic nitrogen, 4−DON; nitrate and nitrites,
5–NOx; ammonium, 6–NH4; and abiotic particulate nitrogen, 7–PN-abiotic. The compartments are indexed in the given order; for example, $x_1$ is the storage value of PN-phyto. The units for nitrogen storage and flow are (mmol m$^{-2}$) and (mmol m$^{-2}$ season$^{-1}$), respectively. The conserved quantity of interest in this case is nitrogen. Each season is considered to be a discrete time step. That is, $t = 1$ corresponds to Spring 1985 and $t = 16$ to Winter 1989. At each time step, the system is at steady state.

The Neuse River Estuary ecosystem were recently analyzed through the proposed system and subsystem partitioning methodologies by [11, 12]. The subthroughflow and substorage matrix measures, the transient and diact flows and storages, the measures and indices for the diact effect, utility, and residence time were presented for this ecosystem model in these papers. It was demonstrated that the proposed method can effectively detect and quantify system properties, such as the seasonality, dominance of indirect effects, and high phytoplankton production that the Neuse River and its estuary were experiencing, from the experimental data. The discrete model is studied extensively in the literature, but some of these important results obtained through the proposed methodology have not been observed in these analyses or could not be demonstrated, although anticipated [11, 12].

The diact system efficiencies and exposure measures are introduced in the present paper as the time derivative and integral of the effect indices and substorage functions, respectively. A discrete version of these measures and indices are presented for this ecosystem model in Fig. 9. The system efficiency graphs have rapid fluctuations at about $t = 7, 8, 9$, just as the impact of the Gaussian impulse in Case Study 3.1 (cf. Fig. 5 and Fig. 9). The unusual rapid fluctuations in the graphs of these functions indicate an excess amount of nitrogen input into the system. Indeed, the excess nitrogen input during this time period [8, 9] at compartments 4 (DON) and 5 (NOx), that is, $z_4(t)$ and $z_5(t)$, seems to be responsible for the fluctuations [11]. The exposure of compartment 1 (PN-phyto) to the nitrogen input into the system at compartment 2 (PN-hetero) during [0, 16], $e_{12}(0, t)$, is also presented in Fig. 9 with the corresponding environmental nitrogen input, $z_2(t)$.

4. Discussion. Nature is always on the move, and its systems are constantly changing to meet ever-renewing circumstances. Therefore, environment is not an easy concept to define and analyze mathematically. Although sound rationales have been offered in literature for considering natural system dynamics under special cases, such as linear models and steady state conditions, the need for mathematically dynamic...
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and nonlinear formulations has always been present.

There have been several attempts in recent decades to analyze dynamic ecological systems, but all of them have disadvantages as identified and comprehensively addressed by [9]. The mathematical theory and method proposed by [10, 9] are based on the analytical and explicit, mutually exclusive and exhaustive, novel system and subsystem partitioning methodologies. The system partitioning refines system analysis from the current static, linear, compartmental level to the dynamic, nonlinear, subcompartmental level. As the system partitioning determines the distribution of environmental inputs and the organization of the associated storages generated by the inputs within the system, the subsystem partitioning ascertains the distribution of intercompartmental flows and the organization of associated storages within the subsystems. The mathematical method then, as a whole, decomposes the system to the utmost level. The substorage and subthroughflow matrices as well as the transient and dynamic diact flows and storages are formulated based on these methodologies [9].

Considering a hypothetical ecosystem modeling a food web with several interacting species for which the effect of a specific poison needs to be investigated, one of the most critical inquiries would be about the influence of the toxin in one species on any other in the system. Assuming that the interspecific interactions are formulated deterministically, current mathematical methods can analyze only the direct effect of the toxin through direct transactions. On the other hand, the dynamic indirect effect of the toxin in one species, indirectly through other species, on another, for example, has never been formulated before. The proposed methodology enables monitoring how an arbitrary amount of the toxin would spread and travel throughout the food web and, therefore, ascertaining the effect of the toxin in one species, directly or indirectly, on any other in the ecosystem. The dynamic indirect effect measure is one of the multiple quantitative system analysis tools introduced in the present manuscript.

The current measures and indices have significant shortcomings as well. For example, Finn’s flow-based cycling index, $FCI$, developed four decades ago, has been an essential measure for ecosystem analysis but only for systems at steady state [15, 16]. The storage-based cycling effect index, $SCI$, was recently introduced by [27], also for static systems. A dynamic measure for flow or storage cycling has not yet been proposed. Moreover, various versions of the static flow-based indirect effect indices have been formulated by several groups, but none of these seem to be precisely identifying the indirect effect behavior, as discussed in Section 2.2 [29, 31, 4, 26]. The dynamic versions of these static indices are also formulated integrally in the present manuscript. It is worth noting that, although derived with a different rationale, the static version of the proposed flow- and storage-based, compartmental, dynamic cycling indices are equivalent to the $FCI$ and $SCI$, respectively [12]. The proposed static indirect effect indices ascertain the corresponding phenomena more precisely than the previous static formulations in the literature, as shown by [12].

The dynamic methodology proposed by [9] constructs a base for the development of new mathematical system analysis tools as quantitative ecological indicators. The time dependent nature of these dynamic measures also enables their time derivatives and integrals to be formulated as novel system measures. The dynamic subthroughflow and substorage matrix measures, for example, monitor the distribution of each environmental input and the organization of the associated storages generated by the input individually and separately, as introduced by [9]. The transient and dynamic diact transaction types introduced in the same article enable the determination of the flows and storages transmitted along a given flow path or from one compartment,
directly or indirectly, to any other within the system. In the present paper, multiple dynamic measures and indices of matrix, vector, and scalar type are systematically formulated for the analysis of various attributes and characteristics of ecosystems. More specifically, the flow- and storage-based, local-in-time and average *diact* effect, utility, exposure, and residence time functions as well as the corresponding system efficiencies, stress, and resilience are formulated systematically at both compartmental and subcompartmental levels. All of these dynamic measures and indices are introduced analytically and explicitly as quantitative ecosystem indicators in the present paper for the first time in literature.

The *diact* effect measures and indices quantify the influence of compartments directly or indirectly on the others, and the *diact* effect efficiencies and stress determine the efficiency of these influences. Besides the intercompartmental interactions, they can also measure the influence of environment on system compartments. The *diact* utility measures and indices then quantify the relative influence of compartments on each other, and the *diact* utility efficiencies ascertain the efficiency of these relative influences. The *diact* exposure and residence time are two other novel system measures proposed in the present manuscript which unravel the compartmental exposures to system flows and compartmental activity levels, respectively. The time derivatives of all these measures can detect disturbances and, therefore, dynamically quantify restoration time and system resilience.

The proposed methodology is applied to several ecosystem models to illustrate the efficiency and wide applicability of the proposed dynamic measures and indices in Section 3. The case studies demonstrate that these mathematical system analysis tools can be used for rigorous analysis of ecosystems as quantitative ecological indicators.

5. Conclusions. In the present manuscript, we systematically introduced multiple dynamic measures and indices of matrix, vector, and scalar type for the nonlinear ecological system analysis. These dynamic measures and indices for the *diact* effect, utility, exposure, and residence time, as well as the corresponding system efficiencies, stress, and resilience are novel mathematical system analysis tools that serve as quantitative ecological indicators. In particular, the indirect effect and celebrated cycling effect index are formulated for dynamic nonlinear systems about four decades after the formulation of their static counterparts.

The proposed dynamic system measures and indices extract detailed information about ecosystems’ characteristics, functions, and behaviors. As quantitative system analysis tools, they monitor the flow distribution and storage organization, quantify the effect and utility of one compartment directly or indirectly on another, identify the system efficiency and stress, measure the compartmental exposure to system flows, determine the residence time and compartmental activity levels, and ascertain the restoration time and resilience in the case of disturbances. Several case studies from ecosystem ecology are presented to demonstrate the efficiency and wide applicability of the proposed measures and indices.

The proposed dynamic methodology extends the strength and applicability of the state of the art techniques and provides significant advancements in theory, methodology, and practicality. It serves, therefore, as a quantitative platform for testing empirical hypotheses, ecological inferences, and, potentially, theoretical developments.

Appendices. The dynamic subsystem partitioning methodology decomposes subsystems along a set of mutually exclusive and exhaustive subflow paths. This methodology yields the *diact* flows and storages that represent intercompartmental flow and storage dynamics. The subsystem partitioning and the *diact* flows and
storphes are summarized in this section.

Appendix A. Dynamic Subsystem Partitioning.

The dynamic system partitioning methodology is summarized at the beginning of Section 2. The dynamic subsystem partitioning methodology has been recently introduced by [9, 10]. As the dynamic system partitioning methodology formulates the distribution of environmental inputs and the organization of associated storages within the system, the subsystem partitioning methodology formulates the distribution of intercompartmental subflows and the organization of associated substorages within the subsystems. The dynamic subsystem partitioning methodology is summarized in this section.

The transient and cumulative transient subflows along a subflow path between two subcompartments will be defined as follows. Along a given subflow path \( p_{n_k}^{w_{i_k}} = i_k \rightarrow j_k \rightarrow \ell_k \rightarrow n_k \), the transient inflow at subcompartment \( \ell_k \), \( f_{
 k \rightarrow j_k \rightarrow \ell_k \rightarrow n_k}^{w_{i_k}}(t) \), is the subflow segment transmitted to \( \ell_k \) at time \( t \), which is generated by the local input from subcompartment \( i_k \) (local source) into the first subcompartment of the path, \( j_k \), (connection) during \([t_1, t], t_1 \geq t_0 \). Similarly, the transient outflow at subcompartment \( \ell_k \), \( f_{n_k \rightarrow \ell_k \rightarrow j_k}^{w_{i_k}}(t) \), is the subflow segment transmitted from \( \ell_k \) to the next subcompartment, \( n_k \), along the path at time \( t \), which is generated by the transient inflow into \( \ell_k \) during \([t_1, t]\). The associated transient substorage, \( x_{n_k \rightarrow \ell_k \rightarrow j_k}^{w_{i_k}}(t) \), is then the substorage segment in subcompartment \( \ell_k \) at time \( t \), which is derived from the transient inflow and governed by the transient inflow and outflow balance during \([t_1, t]\).

The transient outflow at subcompartment \( \ell_k \) at time \( t \), from \( j_k \) to \( n_k \) along subflow path \( p_{n_k}^{w_{i_k}} \), is formulated as

\[
(A.1) \quad f_{n_k \rightarrow \ell_k \rightarrow j_k}^{w_{i_k}}(t) = \frac{x_{n_k \rightarrow \ell_k \rightarrow j_k}^{w_{i_k}}(t)}{x_{\ell_k}(t)} \cdot f_{n_k \rightarrow \ell_k}(t, x)
\]

where the transient substorage \( x_{n_k \rightarrow \ell_k \rightarrow j_k}^{w_{i_k}}(t) \) is determined by the governing equation

\[
(A.2) \quad \tau_{\ell_k}(t, x) = f_{n_k \rightarrow \ell_k \rightarrow j_k}^{w_{i_k}}(t) - \frac{\tau_{\ell_k}(t, x)}{x_{\ell_k}(t)} \cdot x_{n_k \rightarrow \ell_k \rightarrow j_k}^{w_{i_k}}(t), \quad x_{n_k \rightarrow \ell_k \rightarrow j_k}^{w_{i_k}}(t_1) = 0.
\]

The governing Eqs. A.1 and A.2 establish the foundation of the dynamic subsystem partitioning (see Fig. 10). These equations for each subcompartment along a given flow path of interest will then be coupled with the decomposed system, Eq. 2.3, or the original system, Eq. 2.1, and be solved simultaneously.

The transient subflows and substorages are defined for linear subflow paths above. The sum of the transient inflows from subcompartment \( j_k \) to \( \ell_k \) and outflows from
\[ \ell_k \] to \( n_k \) at subcompartment \( \ell_k \) along a given self-intersecting path \( p_{n_k, i_k}^w \) is called the cumulative transient inflow, \( f_{\ell_k, i_k}^w (t) \), and outflow, \( f_{n_k, \ell_k}^w (t) \), respectively, and the associated total substorage is called the cumulative transient substorage, \( x_{\ell_k}^w (t) \). They can be formulated as

\[
(A.3) \quad x_{\ell_k}^w (t) = \sum_{m=1}^{m_w} x_{n_k, \ell_k, j_k}^{w,m} (t), \quad f_{\ell_k, i_k}^w (t) = \sum_{m=1}^{m_w} f_{\ell_k, j_k, i_k}^{w,m} (t), \quad f_{n_k, \ell_k}^w (t) = \sum_{m=1}^{m_w} f_{n_k, \ell_k, j_k}^{w,m} (t)
\]

where the superscript \( m \) represents the cycle number, and \( m_w \) is the number of cycles, that is, the number of times the path \( p_{n_k, i_k}^w \) intersects itself.

The sum of the cumulative transient inflows from and outflows to all subcomponents generated at subcompartment \( \ell_k \) at time \( t \) by local input into the connection of a given subflow path \( p_{n_k, i_k}^w \) during \([t_1, t]\) is then defined as

\[
(A.4) \quad \tilde{\tau}_{i_k}^w (t) = \sum_{j=1}^{n} f_{i_k, j_k}^w (t) \quad \text{and} \quad \tilde{\tau}_{j_k}^w (t) = \sum_{j=1}^{n} f_{j_k, \ell_k}^w (t),
\]

for \( k = 0, 1, \ldots, n \). Therefore, \( \tilde{\tau}_{i_k}^w (t) \) and \( \tilde{\tau}_{j_k}^w (t) \) will be called the respective inward and outward transient subthroughflow at subcompartment \( \ell_k \) at time \( t \) along subflow path \( p_{n_k, i_k}^w \) in subsystem \( k \).

**Appendix B. The diact Flows and Storages.**

In this section, we present five important transaction types for ecological systems which have been recently introduced by [10, 9] for dynamic compartmental systems: the diact flows and associated storages. The transfer flows (denoted by \( t \)) and the associated storages generated by these flows are summarized below, and parallel derivations for direct (d), indirect (i), cycling (c), and acyclic (a) flows and associated storages are straightforward.

The transfer flow will be defined as the total intercompartmental transient flow from one compartment, directly or indirectly through other compartments, to another. The direct and indirect flow will be defined as the transfer flows from one compartment to another directly and indirectly through other compartments, respectively. The cycling flow will be defined as the transfer flow from a compartment, indirectly through other compartments, back into itself. Lastly, the acyclic flow at a compartment will be defined as the non-cyclic segment of the compartmental throughflow at that compartment. The diact storage will then be defined as the storage generated by the corresponding diact flow.
The transfer subflow is defined as the total intercompartmental flow from one subcompartment, directly or indirectly through other subcompartments, to another in the same subsystem. Let $P^T_{i_k,j_k}$ be the set of mutually exclusive and exhaustive subflow paths $p^w_{i_k,j_k}$ from subcompartment $j_k$ directly or indirectly to $i_k$ in subsystem $k$. The transfer inflow and substorage are formulated as

$$
\tau^t_{i_k,j_k}(t) = \sum_{w=1}^{n} \sum_{\ell=1}^{n} f^w_{i_k,\ell_k}(t) \quad \text{and} \quad x^t_{i_k,j_k}(t) = \sum_{w=1}^{n} x^w_{i_k}(t)
$$

where $w_k$ is the number of subflow paths $p^w_{i_k,j_k} \in P^T_{i_k,j_k}$. The sum of all the transfer subflows and associated storages from subcompartment $j_k$ to $i_k$ for each subsystem $k$ is called the transfer flow and storage, $\tau^t_{ij}(t)$ and $x^t_{ij}(t)$, from compartment $j$ to $i$:

$$
\tau^t_{ij}(t) = \sum_{k=0}^{n} \tau^t_{i_k,j_k}(t) \quad \text{and} \quad x^t_{ij}(t) = \sum_{k=0}^{n} x^t_{i_k,j_k}(t).
$$

For notational convenience, we define $n \times n$ matrix functions $T^T_k(t)$ and $X^T_k(t)$, whose $(i,j)$-elements are $\tau^t_{i_k,j_k}(t)$ and $x^t_{i_k,j_k}(t)$, respectively, as

$$
T^T_k(t) = \left(\tau^t_{i_k,j_k}(t)\right) \quad \text{and} \quad X^T_k(t) = \left(x^t_{i_k,j_k}(t)\right).
$$

These matrix measures $T^T_k(t)$ and $X^T_k(t)$ are called the $k^{th}$ transfer subflow and associated substorage matrix functions. The corresponding transfer flow and associated storage matrix measures are $T^t(t) = \left(\tau^t_{ij}(t)\right)$ and $X^t(t) = \left(x^t_{ij}(t)\right)$, respectively.

Let $P^d_{i_k,j_k}$ and $P^i_{i_\ell,j_k}$ be defined as the sets of subflow paths $p^w_{i_\ell,j_k}$ from subcompartment $j_k$, directly and indirectly, to $i_k$; $P^c_{i_k}$ be the set of subflow paths $p^w_{i_k}$ from subcompartment $i_k$ indirectly back to itself; and $P^a_{i_k}$ be the set of linear subflow paths $p^w_{i_k}$ from subcompartment $k_k$ directly or indirectly, to $i_k$ in subsystem $k$. All these diact subflow sets are assumed to be mutually exclusive and exhaustive. The transfer flows, associated storages, and corresponding matrix functions are formulated in Eqs. B.1, B.2, and B.3 using the subflow set $P^c_{i_k,j_k}$. The other diact flows, associated storages, and matrix functions can then be formulated similarly by substituting the corresponding diact flow and storage for their transfer counterparts in these equations and using the corresponding diact subflow sets. Figure 12 depicts the relationships among direct, indirect and cycling flows.

![Fig. 12](image)

**Fig. 12.** Schematic representation of direct and indirect subflows in the $k^{th}$ subsystem. The direct subflow, $f_{i_k,j_k}(t,x)$, is represented by solid arrow. This subflow also contributes to the cycling subflow at subcompartment $k_k$. The indirect subflow, $\tau^d_{i_k,j_k}(t)$, through other compartments (not shown) is represented by dashed arrows.

Note that the direct subflow from a subcompartment $j_k$ to $i_k$ is

$$
\tau^d_{i_k,j_k}(t) = f_{i_k,j_k}(t,x)
$$
and the indirect subflow from an input-receiving subcompartment \( k \) to \( i \) can, alternatively, be expressed as

\[
\tau_{ik,k}^i(t) = \sum_{\substack{j=1 \atop j \neq k}}^{n} f_{ik,jk}(t, x) = \hat{\tau}_{ik}(t, x) - f_{ik,kk}(t, x) - z_{ik}(t, x)
\]

for \( i, k = 1, \ldots, n \) \cite{9}. Similarly, the transfer subflow from \( k \) to \( i \) can be formulated as

\[
\tau_{ik,k}^t(t) = \sum_{j=1}^{n} f_{ik,jk}(t, x) = \hat{\tau}_{ik}(t, x) - z_{ik}(t, x).
\]

The cycling subflow from an input-receiving subcompartment \( i \) to itself, \( \tau_{ii}^c(t) \), can, alternatively, be defined in terms of the indirect or transfer subflows as

\[
\tau_{ii}^c(t) = \tau_{ii}^t(t) = \tau_{ii}^i(t) = \sum_{j=1}^{n} f_{ii,j}(t, x) = \hat{\tau}_{ii}(t, x) - z_{ii}(t, x).
\]

Consequently, the acyclic subflow can be written as

\[
\tau_{ii}^a(t) = \hat{\tau}_{ii}(t, x) - \tau_{ii}^c(t) = z_{ii}(t, x).
\]

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