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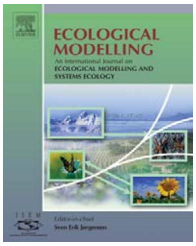

Indirect effects and distributed control in ecosystems Network environ analysis of a seven-compartment model of nitrogen flow in the Neuse River Estuary, USA—Steady-state analysis

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ARTICLE INFO

Article history:
Available online 29 November 2005

Keywords:
Environs
Network analysis
Indirect effects
Throughflow
Nitrogen

ABSTRACT

Network environ analysis (NEA) was used to analyze a seven-compartment, steady-state model of nitrogen flow in the Neuse River Estuary, North Carolina, USA. Four perspectives for analyzing network properties emerge: (1) throughflow-specific oriented to output environs; (2) throughflow-specific oriented to input environs; (2) storage-specific oriented to output environs; (4) storage-specific oriented to input environs.

Analysis of the model is based on a decomposition of total system throughflow, TST, into total environ throughflow, TET, for each of the seven compartments, and a further decomposition of total environ throughflow into compartmental boundary exchanges and environ flows generated by boundary inputs and outputs at individual compartments. The analysis provided a quantitative basis for the development of indirect effects between compartments and is the basis for analyzing the fate of nitrogen entering the system and the origin of nitrogen leaving the system. The decomposition of TST is also the basis for analyzing four network properties: pathway proliferation, ratio of indirect effects to direct effects, homogenization and amplification. Results indicate dominance of indirect effects within the model due to cycling. Moreover, insight about the interrelationship of all model compartments is developed quantitatively based on the NEA methodology.

1. Introduction

Ecosystems are structural, functional study units that import, process and export energy, material and information among its system compartments. The linking of everything to everything else in an ecosystem and the concepts of self-organization are semantic constructs for describing the subtle yet complex nature of ecosystems. Pioneering systems ecologists perceived ecosystems as partially interconnected sets of biotic and abiotic components functioning as a whole to process and transport energy, material and information, and developed fundamental contributions in mathematical syntax to describe the complex processes and relationships that are established among all ecosystem compartments (Patten et

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doi:10.1016/j.ecolmodel.2005.10.017

al., 1976; Ulanowicz, 1980). Information theory, input–output analysis of economic systems, general systems theory and state–space theory provided foundations for constructing ecosystems as networks of thermodynamically conservative flows and storages, to which mature mathematics could be applied in analyzing complex network properties (Shannon, 1948; Leontief, 1936; Zadeh and Desoer, 1963; Klir, 1969).

Theoretical developments in the propagation of cause and effects within ecosystems, and the conceptualization of ecosystems as networks of flows and storages led Patten and co-workers (1976, 1978, 1982) to propose *environs* as relativistic "particles" of nature. Conceived as dualistic entities, ecosystem compartments are considered as having input and output environs, where input environs are described as the network of material, energy and potentially information flows into a compartment required to generate outputs, and output environs are described as the network of material, energy and potentially information flows out of a compartment required to sustain compartmental inputs. Central to environ theory is the concept of network indirect effects whereby flows and storages along extended network pathways of path length $m > 1$ establish distal, indirect relationships between ecosystem compartments, which can dominate ecosystem function (Patten, 1985, 1991; Wootton, 1994). Environ theory is a mathematical theory of environment and is distinct from traditional constructs of environment primarily because the environ construct quantifies effects between ecosystem compartments over direct and indirect pathways of energy and material flow. The emphasis on analyzing distal (indirect) intercompartmental effects as well as proximal (local, direct) effects separates environ analysis from traditional analyses of environmental systems where conclusions are often based on multivariate statistical correlations among biotic and abiotic compartments. While a conceptual feel for indirect effects can perhaps be attained through careful semantics, quantifying them is an analytical challenge. The environ construct and network environ analysis (NEA) provide the basis for building insight into the holistic network-like properties of ecosystems, and quantifying the direct and indirect intercompartmental relationships.

Network environ analysis is a flow-based, environmental extension of input–output analysis that traces the movement of conservative substances in an ecosystem's interconnected, extended flow network (Fath and Patten, 1999). It utilizes network structure and function to decompose empirically observed flows into boundary inputs, boundary outputs, direct flows (path length $m = 1$) between compartments, and indirect flows ($m > 1$) over extended pathways, providing a quantitative analysis of the relationships between all compartments within a system, including those not related by empirically observed flows.

The objective of this paper is to use NEA in the analysis of a steady-state model of nitrogen flow in the Neuse River Estuary, North Carolina, USA, developed by Christian and Thomas (2000). The emphasis will be on analyzing the partial contributions of all compartmental boundary inputs z_k to all observed, intercompartmental nitrogen flows, f_{ij} (denoting flow from j to i), and the partition of all f'_{ij}s required to sustain all boundary outputs y_k. In essence, this is a decomposition of total system throughflow (TST) into system-level boundary exchanges (z_k and y_k), environ flows ($e_{ij,k}$ and $e'_{ij,k}$) and compartmental storages (x_k). This provides the basis for determining the fate of nitrogen entering the network at each compartment, the origin of nitrogen leaving the network at each compartment and the relative contributions of boundary exchanges to the internal dynamics of the system. Only the average data model of Christian and Thomas (2000) is used here, therefore temporal effects associated with seasonal changes are not considered. Results from four analyses are presented: (1) throughflow-specific, output environ analysis; (2) throughflow-specific, input environ analysis; (3) storage-specific, output environ analysis; (4) storage-specific, input environ analysis. Four system-level properties are also presented:

1. network pathway proliferation—pathway numbers increase with length;
2. network non-locality—dominance of indirect over direct effects;
3. network homogenisation—tendency to uniformly distribute material throughout the network;
4. network amplification—obtaining more than face value from system-level inputs.

The paper presents a full application of throughflow- and storage-specific network environ analysis of nitrogen flow in the steady-state Neuse River model, which represents only the second such application of NEA; the first being the water environs of Okefenokee Swamp, Georgia, USA (Patten and Matis, 1982). Moreover, new terminology and mathematical developments will be introduced for describing the decomposition of total system throughflow, TST, into total environ throughflow, TET and environ flows ($e_{ij,k}$ and $e'_{ij,k}$).

2. Network model description

A seven-compartment, steady-state network model of the Neuse River Estuary developed by Christian and Thomas (2000) represents average nitrogen flows and storages quantified for 16 seasons during the period spring 1985–winter 1989 (Fig. 1).

Intercompartmental flows, f_{ij}, represent flows from j to i, and compartmental storages are represented as x_k. Compartments and associated abbreviations are: phytoplankton (PN-Phyto), heterotrophs (PN-Hetero), Sediment, dissolved organic nitrogen (DON), nitrate–nitrites (NO_x), ammonium (NH_4) and detritus (PN-Abiotic). Processes include inorganic N uptake, ammonification, nitrification, N_2 fixation and denitrification. Trophic transfers include planktonic herbivory and detritivory, and benthic/water column interactions including suspension-feeding and bottom-feeding. The estuary feeds into Pamlico Sound so nitrogen retention in the water column ultimately results in transport to the Sound, represented in the model as export of particulates and dissolved organics. The network has 22 intercompartmental transfers, and all compartments have boundary inputs and outputs. Data sources to estimate standing stocks and flows, from most to least reliable, were: (1) direct measurements in the Neuse Estuary; (2) interpolations or extrapolations from Neuse River or