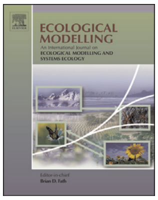
Ecological Modelling 293 (2014) 161–186

Contents lists available at ScienceDirect

Ecological Modelling

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



Indirect effects and distributed control in ecosystems Comparative network environ analysis of a seven-compartment model of nitrogen storage in the Neuse River Estuary, USA: Time series analysis

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ARTICLE INFO

Article history:
Received 23 July 2013
Received in revised form 19 August 2014
Accepted 21 August 2014
Available online 13 October 2014

Keywords:
Network environ analysis
Biogeochemical model
Estuary
Extensive/intensive environs
Nitrogen cycling
Time-series/seasonal analysis
Systems ecology

ABSTRACT

Compartmental, or "stock-and-flow", models describe the storage and transfer of conservative energy or matter entering and leaving open systems. The storages are the standing "stocks", and the intra-system and boundary transfers are transactional "flows". Network environ analysis (NEA) provides network methods and perspectives for the quantitative analysis of compartment models. These emphasize the distinction between direct and indirect relationships between the compartments, and also with their environments. In NEA, each compartment in a system has an incoming network that brings energy or matter to it from the system's boundary inputs, and an outgoing network that takes substance from it to boundary outputs. These networks are, respectively, input and output environs. Individual pathways in environs have an identity not unlike spaghetti in a bowl, each strand of which originates at some boundary input and terminates at some boundary output. All strands originating at the *j*'th input collectively comprise, no matter where they terminate, the *j*'th output environ; similarly, all strands terminating at the *i*'th output comprise, no matter where they originate, the *i*'th input environ. Thus, any substance freely mixing in the system as a whole runs in pathways consigned to one and only one output environ traced forward from its compartment of entry, and also one and only one input environ traced backward from its compartment of exit. The environs are partition elements – they decompose the interior stocks and flow according to their input origins and output destinations. Moreover, each environ's dynamics and other systems and network properties are unique, and sum over all the environs to give the aggregate dynamics and properties of the whole. It is this composite, aggregate whole that empirical methods measure; empiricism unaided by theoretical analysis is blind to the environ pathways that actually compose the wholes.

A previous study of nitrogen dynamics in the Neuse River Estuary (NRE), North Carolina, USA (Whipple et al., 2007) described within-environ transfers using a throughflow-based network analysis, NEA-T. Throughflow (T_{in}, T_{out}) is the sum of flows into or out of each compartment. This paper extends this work using a companion storage-based methodology, NEA-S, re-notated from its antecedent and originating contributions (Barber, 1978a,b, 1979; Matis and Patten, 1981). Time-series data implementing 16 seasonal steady-state network models of nitrogen (N) storage and flow in the Neuse system were constructed for spring 1985 through winter 1989 by Christian and Thomas (2000, 2003). Network topology was constant over time, but the storage and transfer quantities changed. Environ analysis of this model showed that nitrogen storage and residence times differ within the different environs composing the compartments, and moreover, that these differences originate in the system's interconnecting network as a whole. Thus, environs function within themselves as autonomous flow–storage units, but this individuality derives from, and at the same time contributes to the entire system's properties. Environ autonomy is reflected in unique standing stocks and residence times, and whole empirical systems are formed as additive compositions of these. Because storage is durable and transfers ephemeral, storage environs revealed by NEA-S have more autonomy than flow environs computed using NEA-T. We quantified this autonomy by comparing the heterogeneity of extensive environs in models driven by actual inputs with intensive environs normalized to unit inputs. The former is more storage-heterogeneous than their unit reference

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http://dx.doi.org/10.1016/j.ecolmodel.2014.08.025

counterparts, with dissolved nutrients NO_x, DON, and NH_4 exhibiting greatest heterogeneity. A previous NEA study of distributed control in this same model by Schramski et al. (2007) showed that NO_x controls the system whereas sediment is controlled by the system. In the present study, NO_x dominates storage in extensive environs, and therefore, is controlling in actuality. However, in the intensive unit, environs sediment accounted for most of the storage, reflecting greater control potential. This potential is expressed by the sediment acting like a capacitor for N, seasonally sequestering and releasing this element in the role of a biogeochemical regulator.

1. Introduction

Network environ analysis (NEA) is a family of mathematical input–output methods descended from (Leontief, 1936, 1951, 1966) and applied to analyze open compartmental systems (Matis et al., 1979). Compartmental "stock-and-flow" models describe such systems in terms of the storage and transfer of conservative energy or matter entering and leaving. The storages are flow impedances – standing stocks, and the within-system and boundary transfers are transactions – the flows. NEA provides network methods and perspectives for the quantitative analysis of such models. The distinction between direct and indirect inter-compartmental and boundary transfers is emphasized. Each compartment has an incoming network that directly or indirectly brings energy or matter to it from the system's boundary inputs, and an outgoing network that takes substance from it to the boundary outputs. These networks are, respectively, input and output environs (Patten, 1978a, 1982).

Environs have an identity that can be likened to spaghetti in a bowl. Each strand (a pathway) originates at some boundary input and terminates at some boundary output. All the strands originating at the *j*'th input collectively comprise, no matter where they terminate, the *j*'th output environ, and all the strands terminating at the *i*'th output collectively comprise, no matter where they originate, the *i*'th input environ. Any substance freely mixing in the system runs in one and only one output environ traced forward from its compartment of entry, and also one and only one input environ traced backward from its compartment of exit. The *n* environs of either orientation account for the entire system's (modeled) energy or matter storage and flow (exhaustive property), and no environ with the same orientation shares the material of another (mutually exclusive property). Thus, environs are partition elements in providing discrete, non-intersecting channels to and from the stocks and flows according to their input origins and output destinations. No two environs are alike, quantitatively and often also qualitatively (Patten, 2001). Each one's distinctive characteristics reflect an autonomy expressing unique dynamics and other properties that, summed over all the environs, give aggregate dynamics and properties to the whole. It is the composite, aggregate whole that becomes accessible to empirical observation and measurement. Underlying relationships can only be revealed through model analyses.

Environs are a modern implementation of the two-environment conception of von Uexküll (1926). He argued that the organism in and of itself is not the fundamental unit of organic nature, but that such units had to include also the organisms' incoming and outgoing environments, "Merkwelt" and "Wirkwelt", respectively. The latter wrapped around to the former via function circles ("Funktionskries") to close and form the canonical organism–environment whole (Patten, 2001). Environs can be likened to ecological niches in being environmental places within systems defined after-the-fact by organism occupancy (Patten and Auble, 1980, 1981; Patten, 1981). They are extended niches, and niches are in fact the proximate leading and trailing "edges" of environs. Input environs conclude at output compartments as habitat niches (Grinnell, 1917), and output environs begin at input compartments as role niches (Elton, 1927). Like niches, once established, environs can be thought of as before-the-fact, more or less permanent, albeit virtual, "infrastructure" fixed in place and exhibiting structural and functional integrity and whole-environ autonomy. Fig. 1 shows the decomposition of a hypothetical 3-compartment system into its $2n = 6$ environs.

Throughflow is the summation of incoming or outgoing transfers (flows) at each compartment. Storage or standing stock is the accumulation of substance within compartments. Whipple et al. (2007) described a throughflow-based comparative network environ analysis (CNEA-T) for a 4-year, 16-season time series of steady-state nitrogen models for the Neuse River Estuary (NRE), North Carolina, USA. The present paper describes a comparable storage-based analysis (CNEA-S) of this same model, in which the compartments and flow structure remain constant while the quantities change seasonally. Nitrogen turnover rates, expected residence times, and standing stocks are all shown to vary seasonally, and this is reflected in environ differences also. Patten and Matis (1982) found large differences in these variables between the environs of a steady-state water budget model for Okefenokee Swamp. Here, the differences are analyzed for both the Neuse model whole networks and the output environs of selected compartments into which the wholes are decomposed. Input environs will not be discussed in this paper to spare unnecessary complications.

Two previous Neuse River results from CNEA-T justify applying CNEA-S to the same 16-season time series. First is a strong conclusion that these model systems have a remarkably invariant internal organization (Borrett et al., 2006). Second is the finding that throughflow indirect effects become dominant over direct effects within very short pathway lengths; the vast majority of throughflow is generated by indirect paths of small lengths (Borrett et al., 2010). Patten (1985) showed that time delay in storage not only extends the time and increases the number of pathways over which indirect effects develop, but it also amplifies the magnitudes of these effects. The latter is verified here, in relation to throughflow indirect effects, for the Neuss River model. Our objectives are twofold: (1) present CNEA-S results for the Neuse River system and (2) compare these with those obtained from CNEA-T. Questions to be addressed include: Do expected nitrogen storages and residence times differ in the same compartments of different environs? Do these differ in different seasons? What are the main differences compared to prior CNEA-T results (Whipple et al., 2007)? And how does environ autonomy as given by CNEA-S compare with that from CNEA-T?

The concept of environ autonomy brings a new perspective to the study of ecosystem biogeochemistry and also energetics. These fields are ready to take the next step beyond quantitative description into more theoretical domains of analysis. In this paper, this next step will be to show that substance dynamics are co-determined by both parts and the whole. The parts are the compartments that provide needs, processes, standing stocks, and interchange. The whole is the collective environs referenced to specific boundary points of introduction (for output environs) and