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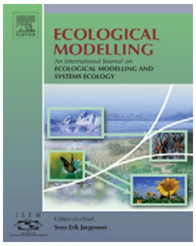

Indirect effects and distributed control in ecosystems: Distributed control in the environ networks of a seven-compartment model of nitrogen flow in the Neuse River Estuary, USA—Time series analysis

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ABSTRACT

The methods of network environ analysis (NEA) currently apply to steady-state models. Networks of real ecosystems are near steady-state in long-term mean characteristics, but are dynamic in short-term responses. A formal mathematical approach to dynamic NEA analysis has never been fully developed, though Hippe [Hippe, P.W., 1983. Environ analysis of linear compartmental systems: the dynamic, time-invariant case. Ecol. Model. 19, 1–26] offers one approach. Another potential approach to addressing this limitation is to analyze a discrete-time series of steady-state models, each a snapshot for the time period it represents. Using concepts from open-loop control theory, four throughflow-based ecological control terms (control ratio, CR; control difference, CD; system control, sc_j; and total system control, TC) as developed using an environ framework are evaluated for 16 consecutive seasons of nitrogen cycling in the Neuse River Estuary, North Carolina, USA. Results of this assessment offer a quantitative measure of the quasi-dynamic distributed control in this network. The NO_x and Sediment components assume opposing but dominant roles (high sc_j magnitudes) in all 16 seasons. Low total compartmental throughflow (T_i) to respective boundary inflow (z_i) or outflow (y_j) ratios are shown to be indicators of component control dominance, suggesting a role for boundary flows in the consideration of a system component's dominance. This conclusion may also be a property of the high cycling nature of this nitrogen model (average Finn cycling index of 89% for all 16 seasons). TC appears to be correlated with total system throughflow (TST), suggesting that TST may indicate a system's distributed control patterns. This correlation may likewise be fruitful if TST proves to be an indicator for system stability, an important and logical consideration in the notion of control.

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1. Introduction

> Taken overall, any reaction in the nitrogen cycle may act as a rate-limiting step and hence control the overall process.
> Janet I. Sprent (1987)

An ecological neologism for the expression *stuff happens* could simply be *nitrogen cycles*. It is a fact of life, literally. Patten's original distributed control methodology was built from an energetics perspective where all of the initial presentations (Patten, 1978b; Patten and Auble, 1981; Dame and Patten, 1981) involved energy models. While individual and ecosystem energetics have been widely studied (Pandian and Vernberg, 1987; Wiegert, 1988; Wright et al., 1994; Brown, 1995), alternatives to energy as a primary currency have developed. Mansson and McGlade (1993) scrutinized energy-based approaches to ecosystem dynamics and evolutionary biology. Redfield et al. (1963) hypothesized from their ocean studies that deep water ratios of C:N:P at 100:16:1 represented the relative requirements of living matter. Recently, others present elementary stoichiometry (typically focused on the varying combinations of the C:N:P ratios) as a causal mechanism linking cellular, ecosystemic, and evolutionary processes (Reiners, 1986; Sterner et al., 1992; Elser and Dobberfuhl, 1996; Elser et al., 2000; Sterner and Elser, 2002). Schlesinger (1997) suggests theoretically that since N-fixing organisms have a high demand for P (linking the global cycles of N and P) that P could possibly be the ultimate limit on nitrogen availability and net primary production. Levin (1989), however, demonstrates that net primary production in most terrestrial and marine ecosystems usually shows an immediate response to additions of N. Additionally, White (1993) articulates that, due to disparate nitrogen compositions between consumers and their foods, energy availability [less than 10% of the sun's energy is captured by the ecosystems of the world (Radmer and Kok, 1977)] is less important than nitrogen in the reproductive success of animals and their subsequent population dynamics. White posits that nitrogen plays one of the pivotal roles in ecosystem functionality. Boyer et al. (1994) identify the literature confirming N (and in particular, not P) as the critical limiting factor in both coastal marine waters in general and in the Neuse River Estuary in particular.

Assuming the environment for all organisms is inadequate at some point in time, populations continue to grow until the limit of a minimum resource is reached. *Survival of the fittest* is a contrapositive expression inherently describing those individuals or species that cannot cope with the specific limiting resource and as a result change their requirements, move, or die. Following an abbreviated form of White's (1993) argument, assume that the supply of life's basic chemicals is finite. Although carbon, oxygen, hydrogen, and nitrogen are all in great abundance, nitrogen is calculated as the only chemical not readily available. In fact, 99.95% of the total nitrogen in the biosphere is in the form of the inert gas, N_2 which comprises over 80% of the earth's atmosphere. Only 0.5% of the world's supply of nitrogen is ever fixed, however, and combined with other chemicals. Only half of this small quantity is organic ($0.5 \times 0.005 = 0.0025 = 0.25\%$ organic), and 95% of this is trapped in abiotic litter, soil, or particulate and dissolved matter in the oceans ($0.95 \times 0.0025 = 0.00238 = 0.238\%$ abiotic material). Hence, of the essential chemicals necessary for biotic processes, nitrogen is considered the least available and most limiting (Delwiche, 1970; Rosswall, 1983; Stewart et al., 1983), yet it is second, only to carbon, with regard to quantities required to sustain life's processes.

The entire nitrogen cycle is an incomprehensibly broad network of complex abiotic and biotic interactions. Absent a thermostat-like controller regulating these nitrogen related interactions, the multitude of independent variables (e.g., temperature, pressure, pH, salinity, humidity, and space) continue to impact the system's time-forward progress as a mosaic of intractable distributed controllers manages the process. Whereas empirical, mechanistic, or hybrid modeling is usually concerned with the fate of nitrogen in an ecological process (Tonitto and Powell, 2006; Lee et al., 2006; Corbeels et al., 2005) or the effect of a nitrogen cycle step or deficiency on an ecological process (Biber et al., 2004; Schulte et al., 2003), this methodology considers nitrogen as a potential rate limiting or dominating currency. This perspective on the nitrogen cycle in the Neuse River Estuary provides a novel and unique look into the controlling actions of nitrogen in an ecosystem. As such, the Neuse River Estuary nitrogen model (Christian and Thomas, 2000, 2003) continues to present an opportunity to not only augment additional development of a distributed control theory for ecology, but to also provide a contrasting view to energy as the primary regulatory currency.

One insight attributed to network environ analysis (NEA) is its ability to quantify the integral (direct, indirect, and boundary) relationships between compartments. NEA, although offering a holistic perspective, is currently a steady-state analysis methodology. The original conservation equations assume the rate of mass or energy accumulation to be zero ($dx/dt = 0$), significantly simplifying subsequent equation development (Barber et al., 1979). Networks of real ecosystems are not steady-state and change over time. Although advanced dynamic simulation software exists, the mathematics required for true theoretical dynamic NEA are daunting and have yet to be fully developed. The non-steady-state case is discussed by Patten et al. (1976). Hippe (1983) explored a very specific time-dependent input function which yielded time dependent results. Hannon (1986) and Levine (1988) pursue dynamic-linear, but nevertheless time-invariant, studies of input–output network analysis.

One approach to overcoming this limitation is to analyze a discrete-time series of steady-state models, each a fixed snapshot for the period it represents (Leontief, 1970). The NEA control metrics generated for each steady-state network can then be contrasted to determine how they change over time to generate a quasi-dynamic perspective. Some network measures (e.g., compartmental throughflow, T_j, and total system throughflow, TST) are sensitive to the number of components in the model. In this work, we circumvent this issue by comparing NEA control measures in a time sequence of models with fixed structure. This paper represents a continuation of the ongoing series exploring indirect effects and distributed control in the nitrogen cycles of the Neuse River Estuary, North Carolina, USA (Borrett et al., 2006; Gattie et al., 2006; Schramski et al., 2006; and Whipple et al., 2007).