



# Evaluating control of nutrient flow in an estuarine nitrogen cycle through comparative network analysis



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## ABSTRACT

Ecologists, ecosystem managers and ecological engineers often seek to identify which components of an ecosystem are most important to its functioning. Ecosystem Network Analyses (ENA) can be used as a tool to address this challenge while taking into consideration the complex direct and indirect interactions that occur in natural systems. One way that ENA can inform researchers and policy makers is through a broad array of centrality metrics, which quantitatively describe the relative importance of each ecosystem component. Control analysis, a type of ENA, identifies which ecosystem members regulate the organization and distribution of energy matter once it enters the ecosystem. We applied two subroutines of control analysis, system control and control difference, to two nitrogen cycling models constructed at sites with different salinity regimes (one oligohaline and one polyhaline) in the Cape Fear River Estuary, NC, USA. We compared the analysis results for these two models to infer how salinity and seawater intrusion might change the control relationships, and therefore functional importance, of nitrogen cycling components. We assert that system control analysis can be used as a centrality metric for evaluating the relative function of ecosystem components, and we compared the system control results to three centrality measures that are established in the literature. Spearman's  $\rho$  tests for correlation indicated no significant relationship between the system control results and selected centrality measures, highlighting the ability of this tool to provide novel information. The system control results indicated that sedimentary nitrate and nitrite were most important for regulating the distribution of nitrogen at both sites, highlighting the centrality of nitrate and nitrite in estuarine nitrogen cycling. However, the control difference analysis, which has finer resolution than system control, indicated that the ammonium pool regulated the movement of nitrogen through the nitrate and nitrite pools at the oligohaline site, while the opposite was observed at the polyhaline site. This reversal of control relationship suggests that seawater intrusion may alter which ecosystem components regulate the distribution of energy matter for reactive nitrogen species in estuaries. This work identifies the utility and uniqueness of system control as a centrality measure, provides an example of an application of control analysis to identify key ecosystem components, and identifies a potentially important difference in the roles of nitrogen cycling components at two sites.

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## 1. Introduction

Ecologists, policy makers, and ecological engineers are interested in the management, maintenance, and restoration of estuaries because of the economic and environmental services

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that these ecosystems provide (Costanza et al., 1997; Thom, 1997; Zedler and Kercher, 2005; Boesch, 2006; Paerl, 2006). In estuarine ecosystems, nitrogen (N) availability often limits primary production (Ryther and Dunstan, 1971; Howarth and Marino, 2006) and an excess of N containing compounds can lead to eutrophication that can result in algal blooms, hypoxia, and fish kills (Burkholder et al., 1997; Anderson et al., 2002). The negative effect that eutrophication can have on estuarine ecosystem services has contributed to sustained interest in quantifying, understanding, and ultimately managing the role of nutrients in these environments (Nixon, 1995; Seitzinger and Sanders, 1997; Cloern, 2001; Whittall et al., 2004;

Kemp et al., 2005). Furthermore, concern over health risks from cyanobacterial toxins that are sometimes produced in eutrophication events has fueled interest in management strategies for N in estuaries (Codd, 2000).

Despite the need for well informed management policies in estuarine ecosystems, the majority of studies evaluating the estuarine N cycle incorporate only a fraction of the ecosystem's functioning because the complexity of the interactions among different N species makes a whole-ecosystem approach difficult to achieve (Boynton et al., 2008). N is present in estuaries as dissolved and particulate organic matter, as well as in inorganic forms including ammonium ( $\text{NH}_4^+$ ), nitrite ( $\text{NO}_2^-$ ), nitrate ( $\text{NO}_3^-$ ), and di-nitrogen gas ( $\text{N}_2$ ). The abundance of these different forms of inorganic N can have important implications for primary production in these ecosystems (Fisher et al., 1988; Anderson et al., 2002). For example, Paerl (2006) found that both the quantity and form of N compounds were closely linked to duration and species composition of phytoplankton blooms in the Neuse River Estuary, NC.

The diversity of N forms present in estuaries, along with the implications of these substrates for biological activity, make achieving a whole-ecosystem analysis of the estuarine N cycle an essential step for informing management policies for estuaries (Boynton et al., 2008). The N species in estuaries are influenced by allochthonous N inputs from outside of the ecosystem, chemical factors such as ion content, physical factors such as flushing time, and the biological communities that rely on these nutrients (Rudek et al., 1991; Caraco et al., 1998; Cabrita et al., 1999). Microbial organisms in estuaries convert N between different forms as part of metabolic redox reactions, creating a complex biogeochemical cycle that regulates the flow of N through these ecosystems. For example, the process of nitrification oxidizes  $\text{NH}_4^+$  to  $\text{NO}_3^-$  to provide electrons for organic carbon fixation, while dissimilatory nitrate reduction to ammonium (DNRA) reduces  $\text{NO}_3^-$  to  $\text{NH}_4^+$  to oxidate organic carbon under anaerobic conditions (Canfield et al., 2010). These processes recycle N within an estuary by converting it from one biologically available form to another, while other microbial processes such as denitrification (conversion of  $\text{NO}_3^-$  to  $\text{N}_2$ ) and anaerobic ammonium oxidation (anammox; combination of  $\text{NH}_4^+$  and  $\text{NO}_2^-$  to produce  $\text{N}_2$ ) effectively remove N from estuaries. The  $\text{N}_2$  gas produced by these processes is relatively bio-unavailable due to low N fixation rates in these ecosystems, and therefore is removed to the atmosphere (Howarth et al., 1988; Boynton and Kemp, 2008). Detailed reviews of the estuarine N cycle can be found in Boynton and Kemp (2008), Joye and Anderson (2008), and Canfield et al. (2010).

The microbial communities that conduct these N transformation processes are susceptible to changes in environmental conditions. For example, seawater intrusion, which can occur gradually as a result of climate change (Day et al., 2005) or more rapidly as a result of engineering projects including dredging (Jang et al., 2012), may alter which organisms and processes are dominant in an estuarine N cycle. Bernhard et al. (2005, 2007) found that diversity and functionality of ammonia-oxidizing bacteria differed along an estuarine salinity gradient. Furthermore, some N cycling reactions, such as nitrification, are inhibited by high levels of salinity (Joye and Hollibaugh, 1995), while other reactions, such as DNRA, can be enhanced by the same conditions (Giblin et al., 2010, 2013). As seawater intrusion from dredging and climate change progresses (Hackney and Yelverton, 1990; Zhang et al., 2012), it is unclear how these changes in water chemistry will effect the microbial communities involved in the N cycle or the interactions among N cycling processes (Santoro, 2010). Therefore, understanding how these projected environmental changes will alter the estuarine N cycle from a whole-ecosystem perspective is a crucial goal for managers and policy makers.

As a step toward managing ecosystems, it is useful to identify which components of an ecosystem are most important to

its functioning (Mills et al., 1993; Jordán et al., 2006; Sutherland et al., 2006; Crowder and Norse, 2008). Identifying the components, both biotic and abiotic, that regulate ecosystem functioning provides information on how to appropriately apply ecological data to implement management policies and monitor environmental responses (Ehrlich and Mooney, 1983; Christensen et al., 1996; Kremen, 2005). For example, Bengtsson (1998) found that understanding which members and relationships in an ecosystem contribute to its function can be more useful to managers than measures focused on community diversity. However, identifying which components are most important from a whole-ecosystem perspective can be a difficult task because of the complex nature of the interactions among ecosystem members (Walker, 1992; Hooper et al., 2005; Levin and Lubchenco, 2008).

As one tool to evaluate ecosystems from a whole-ecosystem perspective, ecologists have developed a set of computational algorithms called Ecosystem Network Analysis (ENA; Fath and Patten, 1999; Ulanowicz, 2004; Schramski et al., 2011). ENA, part of the rapidly growing field of network ecology (Borrett et al., 2014), traces the movement of energy-matter through network models that explicitly include both the direct and indirect interactions among all ecosystem components (Fath et al., 2007; Schramski et al., 2011). These networks represent steady-state budgets of thermodynamically conserved material as it moves through the different biotic and abiotic resource pools within an ecosystem, enabling ENA techniques to provide the whole-system measures of ecosystem relationships and functioning that are commonly lacking in studies of complex systems (Boynton et al., 2008; Patten, 2013).

Several ENA tools, which are often adapted from the social and economic sciences (Hannon, 1973; Wasserman and Faust, 1994; Borgatti, 2005; Estrada, 2010), have been used to define and identify key components in ecosystems (Jordán et al., 2007; Estrada and Bodin, 2008; Borrett, 2013). These algorithms compute measures of centrality for each component in an ecosystem network. Centrality metrics provide information on the ability of each component of an ecosystem network to influence the other network components, and thus quantify the importance of each piece of an ecosystem network to the overall functioning of the system (Estrada, 2007). Some centrality metrics consider only which connections are present between network components, while others take into account the magnitudes of these network connections (Borgatti and Everett, 2006).

ENA produces centrality metrics that range from local to global in scope (Estrada, 2010; Borrett, 2013). For example, one type of centrality called degree centrality provides a local measure of importance by quantifying the number of direct relationships each ecosystem member has with other ecosystem components (Freeman, 1979; Wasserman and Faust, 1994). Another type of centrality called eigenvector centrality, however, provides a global measure of importance by quantifying the equilibrium number of pathways for material moving through each component in an ecosystem network, considering all direct and indirect interaction (Bonacich, 1972, 1987, 2007). Global centrality measures can be particularly useful for understanding the roles of different components in ecosystem networks.

Another global analysis in ENA called control analysis identifies the relative influence of each network component on the movement of energy-matter through a network (Patten and Auble, 1981; Fath, 2004; Schramski et al., 2006). This tool can be useful to ecosystem managers because it identifies which components regulate the flow of energy-matter through an ecosystem network, but is rarely used because of heavy data requirements and difficulty interpreting the degree of uncertainty in the results of steady-state models. More specifically, this analysis allows researchers to quantify the ability of each network component to regulate flow in the context of

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