Environ Indicator Sensitivity to Flux Uncertainty in a Phosphorus Model of Lake Sidney Lanier, USA

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Abstract

Effective environmental impact assessment and management requires improved understanding of the organization and transformation of ecosystems in which independent agents are linked through an intricate network of energy, matter, and informational interactions. While advances have been made, we still lack a complete understanding of the processes that create, constrain, and sustain ecosystems. Network Environ Analysis (NEA) provides one approach for building novel ecosystem insights, but it is model dependent. As ecological modeling is an imprecise art, often complicated by inadequate empirical data, the utility of NEA may be limited by model uncertainty. Here, we investigate the sensitivity of NEA indicators of ecosystem growth and development to flow and storage uncertainty in a phosphorus model of Lake Sidney Lanier, USA. The indicators are total system throughflow (TST), total system storage (TSS), total boundary input ($Boundary$), Finn cycling index (FCI), ratio of indirect-to-direct flows ($Indirect/Direct$), indirect flow index (IFI), network aggradation (AGG), network homogenization (HMG), and network amplification (AMP). Our results make two primary contributions. First, they demonstrate that five of the indicators—FCI, $Indirect/Direct$, IFI, AGG and HMG—are relatively robust to the flow and storage uncertainty in the Lake Lanier model. This stability lets us draw robust conclusions about the Lake Lanier ecosystem organization (e.g., phosphorus flux in the lake is dominated by internal processes) in spite of uncertainties in the model. Second, we show that the majority of the indicators co-vary and that most of their common variation could be mapped onto two latent factors, which we interpret as (1) system integration and (2) boundary influences.

Key words: aquatic ecosystem, environ analysis, flow analysis, indirect effects, network analysis, uncertainty

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> “The desire for simplification is justified, but the same does not always apply to simplification itself, which is a working hypothesis, useful as long as it is recognized as such and not mistaken for reality. The greater part of historical and natural phenomena are [sic] not simple, or not simple in the way that we would like.” (Levi, 1988)

1 Introduction and Motivation

Ecosystems are open, non-equilibrium, thermodynamic systems that are knit together by an intricate network of energy, matter, and information exchanges among biological organisms and their environments (Capra, 1996; Higashi and Burns, 1991; Jørgensen, 2002; Ulanowicz, 1986). Like other types of complex adaptive hierarchical systems, ecosystems appear to self-organize in response to thermodynamic gradients (Levin, 1998; Müller, 1996; Schneider and Kay, 1994). However, a clear understanding of ecosystem organization and transformation has yet to crystalize, despite several empirical and theoretical attempts (e.g., Gunderson and Holling, 2002; Jørgensen, 2002; Odum, 1969; Ulanowicz, 1986). This understanding is critical because ecosystems provide the natural capital and services that support human endeavors (Costanza et al., 1997; Daily, 1997), and this knowledge is essential for effective ecosystem assessment and management (Christensen et al., 1996; Reichman and Pulliam, 1996).

Ecosystem science has a long history of characterizing patterns of organization and development (e.g., Lindeman, 1942; Margalef, 1963; Odum, 1969; Teal,

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1962). Numerous measures of ecosystem organization have been proposed including gross production-to-biomass ratio, species diversity, flow diversity, cycling (Odum, 1969), power (Lotka, 1922), and ascendency (Ulanowicz, 1986, 1997). As systems develop, several of these measures appear to consistently increase or decrease, suggesting possible orienting forces or constraints on self-organization (Fath et al., 2001; Müller and Leupelt, 1998; Odum, 1969; Patten, 1998; Schneider and Kay, 1994; Ulanowicz, 1986).

In Jørgensen's (2002) efforts to weave together multiple ecosystem theories into a coherent whole, he acknowledged that a plurality of approaches remains necessary. Holoecology (Patten, in prep.) offers one distinct approach. The overarching goals of the Holoecology Research Program are (1) to understand the lawful processes that create, constrain, and sustain ecological systems and (2) to create a formal theory of environment. Network Environ Analysis (NEA) is the primary methodology of Holoecology (Fath and Patten, 1999b; Matis and Patten, 1981; Patten, in prep.; Patten et al., 1976), and it is fundamentally an environmental application and extension of economic Input–Output Analysis (Leontief, 1966). Although it has elements in common with other forms of ecosystem network analysis such as Input–Output Analysis as implemented in Ecopath (Christensen and Pauly, 1992; Christensen and Walters, 2004) or Acendency Theory (Allesina and Bondavalli, 2004; Ulanowicz, 1986, 1997), NEA is distinguished by its explicit environment focus. It is used in the holistic study of ecological networks to describe and quantify component-level, bounded environments within systems, termed environs (Patten, 1978, 1981, 1982).

A strength of NEA is its inclusion of several indicators that summarize whole-system organization including total system storage (TSS), total boundary input or output ($Boundary$), total system throughflow (TST), Finn cycling index (FCI), average path length or network aggradation (AGG), ratio of indirect-to-direct flows ($Indirect/Direct$), indirect flow index (IFI), network homogenization (HMG), and network amplification (AMP). TSS, $Boundary$, TST, FCI, and AGG are commonly used in other forms of ecosystem network analysis, while $Indirect/Direct$, IFI, HMG, and AMP are unique to NEA (Fath and Patten, 1999b; Patten, 1998). Collectively, these indicators provide insight into the flow and storage organization of ecosystem models. Based on these indicators, Patten (1998, in prep.) argues that ecological systems are integrated by indirect effects.

The Achilles heel of these indicators, NEA, and ecosystem network analyses in general is that they are based on models of real ecosystems. Ecological modeling remains a challenging endeavor with no consensus on the best approach or evaluation procedures (e.g., Ginzburg and Jensen, 2003; Jakeman et al., 2006; Oreskes et al., 1994). In truth, an infinite number of models fit a given data set, and choosing among them remains difficult. As the opening quote from Levi states, natural phenomena are not always simple in the way we wish.

Previous research found that ecosystem indicators can be highly dependent upon the model form, especially the model aggregation (e.g., Abarca-Arenas and Ulanowicz, 2002; Cale and Odell, 1979; Cale and O'Neill, 1988; Gardner et al., 1982; Pahl-Wostl, 1992; Sugihara et al., 1997). Less research has explored the sensitivity of these indicators to uncertainty in the magnitude of flows and storages (but see Allesina and Bondavalli, 2003; Bosserman, 1983; Fath, 2004), which can arise from both incomplete or unknown data for model calibration and from evaluation or empirical measurement error.

In this work, we determined the sensitivity and interrelations of the indicators of ecosystem organization listed above to flux and storage uncertainty in a phosphorus-based ecosystem model of Lake Sidney Lanier, USA. Specifically, we investigated two hypotheses. First, we conjectured that six of the focal system indicators (FCI, $Indirect/Direct$, IFI, AGG, AMP, and HMG) would be robust to model flux uncertainty. Quantitatively we expected each of these indicators to be less variable than TST and TSS; qualitatively we expected their interpretations to be consistent. Support for this hypothesis lets us draw more robust conclusions about Lake Lanier despite uncertainty in the model uncertainty. Second, we anticipated that these six indicators would characterize different aspects of the same latent factor, which we tentatively term *system integration*. This hypothesis implies that the indicators will be highly correlated. We also expected that they would largely map into one principle latent factor. Support for this hypothesis would let us reduce the number of NEA indicators required to characterize the degree of system integration by indirect effects.

2 Materials and Methods

2.1 Study System

Lake Sydney Lanier is a large reservoir in the headwaters of the Chattahoochee River in Georgia, USA that drains a 2704 km^2 watershed, and at the conservation pool elevation of 326 m it covers 150 km^2 with 869 km of shoreline (Fath and Beck, 2005; Guan, 1993). Constructed in the 1950s by the U.S. Army Corp of Engineers, the reservoir was initially to provide flood control, hydroelectric power, and downstream navigation regulation (U.S. Army Corps of Engineers, 2005). However, the reservoir lies just northeast of downtown Atlanta, one of the fastest growing metropolitan areas in the United States for the past two decades (Metro Atlanta Chamber of Commerce, 2000), and it has become an increasingly important source of drinking water, wastewater dilution, and recreation for the region. Lake Lanier is a key resource supporting the expansion of Atlanta and the rapid urbanization of its own watershed (Fath and Beck, 2005).

2.2 Model Construction

To address our hypotheses, we required a model of phosphorus flux in the Lake Lanier ecosystem that was valid given our knowledge of the system, but that let us investigate the space of plausible variability. We constructed this model in two steps. We first built a conceptual model modified from on an existing model of the system. We then identified a set of plausible parameterizations for this model whose generated behavior matched the empirically observed summer behavior of the ecosystem.

For our model, we modified the thirteen compartment Lanier ecosystem model introduced by (Osidele and Beck, 2004). We converted the original model to a consistent currency (phosphorus) and replaced the nonlinear mechanistic functions with phenomenological donor controlled functions, which we modeled with first-order differential equations of the generic form

$$\frac{dX}{dt} = -\lambda_X \cdot X, \tag{1}$$

where X is a generic compartmental state variable, λ_X is a rate constant, and t is continuous time. Since the function is donor controlled, the negative sign indicates a loss or transfer from the donor compartment. We made these model changes so that the output would readily meet the assumptions of NEA described in Section 2.3.

The modified model shown in Figure 1 has eleven state variables or storage compartments (mg P m^{-2}), twenty six within-system flows (mg P m^{-2} d^{-1}), five boundary inputs, and 4 boundary losses. The compartments represent (1) epilimnion soluble reactive phosphorus (SRP), (2) hypolimnion SRP, (3) phytoplankton, (4) microbes (bacteria, etc.), (5) microzooplankton, (6) macrozooplankton, (7) macroinvertebrates (insect larvae, etc.), (8) larval–juvenile fish, (9) suspended detritus, (10) sediment detritus, and (11) sediment pore space phosphorus. Phosphorus enters the model via fluxes into compartments 1, 2, 8, 9 and 11, and exits from compartments 1, 3, 7, and 8.

Given this system conceptualization, we then used Monte Carlo simulations (Manly, 1991) and regionalized sensitivity analysis (Osidele and Beck, 2001; Spear and Hornberger, 1980) to identify parameterizations whose summer behavior of epilimnion phosphorus, phytoplankton, and fish fell within their empirically known variability. We defined the behavior targets as a range of values to account for uncertainty and spatial variability in the observational data, which we obtained from the literature for phosphorus and phytoplankton (Hatcher et al., 1994), and fish (Weaver, 2000). These records indicate that the average annual phosphorus concentration in the photic zone ranges from 2 to 4 μg L^{-1}, with no distinct spatial pattern of variation across the reservoir. Phytoplankton chlorophyll concentrations range from 7 μg L^{-1} at the tributary inlets to 2 μg L^{-1} at the dam site, and larval–juvenile fish average 20 to 50 kg ha^{-1} lake wide. We then translated these observations into the model currency to prescribe the following summer behavior definition:

- epilimnion SRP concentration should be between 58 and 70 mg P m^{-2};
- phytoplankton concentration should be between 13 and 52 mg P m^{-2};
- larval–juvenile fish concentration should be between 100 and 250 mg P m^{-2}.

The regionalized sensitivity analysis considered 30 parameters (i.e., the mass transfer rate constants λ_X in equation 1). The program sampled each parameter from a uniform distribution over the interval [0.0, 0.5], i.e., 0% to 50% rate of loss from each donor compartment. We considered parameterizations that satisfied the summer behavior definition to be plausible representations given our knowledge of the system. Furthermore, all successful parameterizations generated static, steady-state behavior. To insure that the sample of parameterizations represented the larger population, we compared the mean and variance of the ecosystem indicators in successful samples from trial runs of 500, 1000, and 5000 realizations. We used a Welsh t-test to compare the means as it does not assume identical variance (Dalgaard, 2002).

2.3 Network Environ Analysis—Throughflow

NEA is a family of input–output methods that analytically decompose observed flows and storages to identify their origins and fates within a system of interest (Fath and Patten, 1999b; Patten et al., 1976). This methodology includes analyses of structure, throughflow, storage, utility, and control within systems, and is extensively described in the literature (e.g., Borrett and Patten, 2003; Fath and Borrett, 2006; Fath and Patten, 1999b; Gattie et al., 2006; Matis and Patten, 1981; Patten et al., 1976). Hence, we only briefly summarize the input and output variables of the output-oriented throughflow analysis and the calculations for the indicators of interest.

NEA requires four input variables: (1) the observed flows from compartment j to i ($\mathbf{F} = (f_{ij})$), (2) the boundary inputs (z_i), (3) the boundary outputs (y_i), and (4) the storage values (x_i) of an n compartment system. This methodology assumes that all variables have a consistent currency (i.e., carbon or phosphorus) and that the system they describe is in a static steady-state (i.e., the inflows equal the outflows for each compartment). The static steady-state assumption is required for the current methods to partition the integral flows into categories based on pathway types (e.g., direct, indirect). As ecologists are often interested in ecosystem dynamics, this assumption limits the use of NEA (see discussion in Borrett et al., 2006; Fath and Patten, 1999b). However, investigation of the static, steady-state case provides a snapshot of the system organization that is otherwise unavailable. This assumption influences the whole-system indicators because they depend on the throughflow decomposition, but we expect their qualitative interpretations to remain valid.

Given these variables, the output-oriented throughflow analysis characterizes the fate of material flowing into the system, which is accomplished with three analytical steps. First, we calculate the total material flowing through each node, which at steady-state is

$$\begin{aligned} \mathbf{T} = T_k^{(in)} &= \sum_{j(\neq k)1}^{n} f_{kj} + z_k \\ = T_k^{(out)} &= \sum_{i(\neq k)1}^{n} f_{ik} + y_k. \end{aligned} \tag{2}$$

Second, we determine the dimensionless direct flow intensities from j to i as

$$\mathbf{G} = (g_{ij}) = f_{ij}/T_j. \tag{3}$$

Third, we find the dimensionless integral (boundary + direct + indirect) flow intensities

$$\mathbf{N} = \underbrace{\mathbf{I}}_{\text{Boundary}} + \underbrace{\mathbf{G}^1}_{\text{Direct}} + \underbrace{\mathbf{G}^2 + \ldots + \mathbf{G}^m + \ldots}_{\text{Indirect}} = (\mathbf{I} - \mathbf{G})^{-1}, \tag{4}$$

where $\mathbf{I} = \mathbf{G}^0$ is the matrix multiplicative identity and the elements of $\mathbf{G}^m$ are the flow intensities from j to i over all pathways of length m. We can then verify that equation 2 is a true partition of the input flows across the many pathways by ensuring that $\mathbf{T} = \mathbf{Nz}$. From these initial calculations, we then derive the indicators of whole-system organization shown in Table 1.

2.4 Data Analysis

Our data analysis involved several steps. First, we calculated the whole-system indicators for each plausible model parameterization using a modified version of the MATLAB function NEA.m (Fath and Borrett, 2006). We then compared the coefficient of variation for each indicator to evaluate robustness with the assumption that more robust indicators are less variable. We chose to use the dimensionless coefficient of variation because the indicator's absolute values are measured on different scales. For example, TST has units of mg P m^{-2}, and $Indirect/Direct$ is a dimensionless ratio where $0 < Indirect/Direct < \infty$. The variability of TST, TSS, and *Boundary* provided a baseline indication of the flow and storage variability in the alternative parameterizations.

We used two statistical approaches to determine whether the indicators characterized different aspects of any underlying factors. We initially evaluated the correlation strength of the indicators using ordinary least-squares regression. Then, we detected latent or underlying variables with principle components factor analysis (Grimm and Yarnold, 1995; Johnson, 1998), using the Kaiser criterion to select the number of relevant factors. These statistical methods assume that the variable distributions are normal and that the relationships are linear. To meet these assumptions, we used the natural log transformation of TST, TSS, $Indirect/Direct$, and AGG. We used a combination of MATLAB (version 6.5, The Mathworks, Inc.) and R (R Development Core Team, 2005) for our calculations.

3 Results

There are three aspects to our results. We first show results of our model identification and illustrate why the sample used for subsequent analysis is representative of the space of valid flow–storage models. We then present the ecosystem indicator variability within this sample of model parameterizations. Finally, we describe relationships among the indicators.

3.1 Model Identification

With the methodology described in Section 2.2, we identified multiple model parameterizations whose generated behavior satisfied our empirically derived criteria for epilimnion phosphorus, phytoplankton, and fish storage (Figure 2). Monte Carlo simulations with sample sizes of 500, 1000, and 5000 produced 14, 18, and 90 plausible parameterizations, respectively. To determine if these samples represent the population of valid parameterizations, we compared the mean and variability of the ecosystem indicators among the samples, shown in Figure 3, and found no statistically significant differences between the samples for TST, TSS, FCI, $Indirect/Direct$, IFI, AGG, and AMP. However, sample variance of the total boundary inputs ($Boundary$) is significantly different, increasing with sample size, and the mean and variability of HMG is statistically different between the 500 and 5000 trials. While a larger sample size might have stabilized results for total boundary flow and homogenization, we concluded that, for our purposes, the 90 plausible parameterizations provide a large enough sample size to address our hypotheses. Therefore, all subsequent analysis is of the 90 plausible parameterizations.

While each of the 90 parameterizations generates a valid model because they satisfy the behavior criteria in Section 2.2, Table 2 shows that there remains substantial uncertainty in the phosphorus flow and storage values. For example, phosphorus in the sediment pore space had a mean of 341.3 (±588.7). Boundary flows were less variable with a maximum standard deviation of 21.5 associated with the largest mean boundary from the larval–juvenile fish compartment. Internal system flows ranged from a minimum of 4.3 (±2.7) from phytoplankton to epilimnion P to a maximum of 55.8 (±47.2) from the hypolimnion to the microbial compartment. Notice that phosphorus stored in the epilimnion, phytoplankton, and larval–juvenile fish varies the least because these compartments are constrained by the empirical observations.

3.2 Indicator Variability

Table 3 reports the mean and variability of the NEA ecosystem indicators from the 90 model parameterizations. The mean and standard deviation of TST, $Boundary$, and TSS are 749 (±303), 96 (±20) and 1634 (±985), respectively. The mean FCI indicates that recycling contributed on average 39% of phosphorus TST in Lake Lanier. We expected a large degree of recycling because we are analyzing an ecosystem model of phosphorus cycling. Furthermore, the values of IFI and the $Indirect/Direct$ suggest that a large fraction of TST comes from indirect flows. The degrees of AGG, HMG, and AMP imply that (1) an average input passes through an average of 7.84 nodes before exiting the system, (2) the off-diagonal integral flow probabilities were 3 times more evenly distributed than the direct flow probabilities, and (3) on average 22% of the integral flow probabilities exceeded unity. This degree of amplification indicates that generally two compartments received more than a unit input, probably due to recycling.

To compare the relative variability of the ecosystem indicators, we calculated their coefficients of variation (CV; Table 1). The CV of TST (0.40) and TSS (0.60) reflect the whole system flow and storage variability due to model uncertainty, so we used these values as benchmarks to compare the other seven indicators. IFI and HMG have the lowest CVs at 0.10, while AMP varies the most at 0.59. AMP is the only indicator to have a CV larger than TST, close to TSS. The CV of AGG and $Indirect/Direct$ are similar at 0.34 and 0.38 respectively, which is close to that of TST. FCI is less variable at 0.28, and *Boundary* is 0.21. Given these quantitative results, the relative variability and hence the robustness of the indicators is not uniform.

Despite their quantitative variability derived from model uncertainty, the qualitative interpretations of the indicators are robust. In all 90 parameterizations we conclude that recycling was a large if not dominant source of phosphorus flux. $Indirect/Direct$ always surpassed unity implying that indirect flows were dominant, and network homogenization, amplification, and aggradation always occurred.

3.3 Indicator Relations

Analysis of the statistical relationships among the ecosystem indicators revealed several interesting patterns. We first describe the correlations among the variables, and then explain the results of our factor analysis.

The pairwise scatter plots of the indicator combinations shown in Figure 4 reveal several close associations. In 27 of 36 cases there is a statistically significant positive association between the variables (Table 4). For example, strong positive associations exist between FCI, $\ln(Indirect/Direct)$, IFI, $\ln(AGG)$, and AMP, whose correlation coefficients ranged from 0.89 to 0.98. Both the scatter plots and correlation coefficients suggest that several of these indicators may be influenced by the same underlying factor, lending support to our second hypothesis. However, in some cases a linear model may not be the most appropriate (e.g., between $\ln(Indirect/Direct)$ and IFI). *Boundary* and HMG provide exceptions to the trend. Although *Boundary* does increase with $\ln(TST)$ and $\ln(TSS)$, it is not significantly correlated with the other variables. HMG shows relatively weak correlations with the other indicators, three of which are not statistically significant.

We used a principle component factor analysis to further evaluate these associations. After examining several alternatives (not shown) we decided that two factors are appropriate for the data, which is supported by the Kaiser criterion. Only two correlation matrix eigenvalues are larger than unity ($\lambda_1 = 5.94$ and $\lambda_2 = 1.46$), which implies that only the first two factors account for more variability than any single variable. Furthermore, the first factor captures 65% of the variance and the cumulative variance accounted for by the two factors was 80%. Including a third factor only increased this to 85%. The factor loadings shown in Table 5 indicate the correlation of each NEA indicator with the two factors. Factor 1 is highly associated with the variability in $\ln(TST)$, FCI, $\ln(Indirect/Direct)$, IFI, $\ln(AGG)$ and AMP. HMG, $\ln(TSS)$, and *Boundary* appear to have a small role in Factor 1. *Boundary* dominates Factor 2, with minor contributions from $\ln(TST)$ and $\ln(TSS)$.

In contrast to principal components analysis, factor analysis only examines the common variation of the variables (Tabachnick and Fidell, 1983). Indicator uniqueness indicates the proportion of variation not in common with the other variables (Table 5). HMG has the highest uniqueness factor, followed by $\ln(TSS)$, and then AMP. The remaining variables had a uniqueness factor below 0.10.

Figure 5 illustrates these results with a plot of the factor loadings. In this plot, an indicator's distance from the origin indicates its strength of association with the factor represented by the axis. As $\ln(AGG)$ is the furthest distance from the origin of the x-axis, it is the most highly associated with Factor 1. This plot emphasizes the clustering of the variability of $\ln(AGG)$, IFI, $\ln(Indirect/Direct)$, FCI, and AMP, and their distance from variation in total boundary flux (*Boundary*). Three factors do not fall along an axis—HMG, $\ln(TSS)$, and $\ln(TST)$—which could make interpretation of the factors difficult. However, the uniqueness vector indicates that variation in HMG and $\ln(TSS)$ is largely independent of the other indicators, and $\ln(TST)$ is a special case that we address in the discussion.

4 Discussion

The results reported here generally support our hypotheses regarding indicator robustness and their interrelationships, but they also suggest a more complicated story than we initially expected. In this Section, we discuss the evidence for each hypothesis, offer additional explanations for these results, and interpret their significance for the growth and development of ecological systems in general and Lake Lanier in particular.

4.1 Indicator Robustness

The NEA indicators of ecosystem organization are qualitatively consistent and quantitatively differentially robust, lending support to our first hypothesis. Qualitatively the index interpretations did not change. Indirect flows consistently dominate direct, both indirect and cycled flows consistently comprise a large proportion of TST, and some degree of network aggradation, network homogenization and network amplification occur. Quantitatively, the indicators have differing degrees of robustness, decreasing in variability as $AMP > Indirect/Direct > AGG > FCI > HMG = IFI$. Given the Lake Lanier model structure and the relatively large flow and storage uncertainty, the magnitudes of network homogenization and indirect flow index are remarkably consistent.

We claim that the small variability in the ecosystem indicators lets us circumvent part of the modeling and data uncertainty to draw more robust conclusions regarding the condition of the Lake Lanier ecosystem. Although we lack certainty about the true summer flux and storage of phosphorus for some of the model compartments, we expect the values to occur within our model parameterizations. Thus, the more constrained ecosystem indicators should be informative of the real system organization. An alternative interpretation is that an indicator's consistency implies that it is uninformative because it lacks the necessary sensitivity. We doubt this is the case as previous applications of these indices demonstrate a wide range of values for these indices (e.g., Borrett et al., 2006; Fath, 2004; Finn, 1980).

From this study, we draw two primary conclusions about the Lake Lanier ecosystem organization. First, internal processes heavily influence phosphorus flow and storage. This is evident in the consistently high indirect flow index, indirect-to-direct ratio, and degree of recycling. This result suggests a relatively well developed ecosystem as the system gains high utility from the phosphorus inputs. Second, based on the robust measure of network homogenization we conclude that even though phosphorus storage is heterogeneous, phosphorus in the flows is well mixed.

4.2 Indicator Interrelations

Our second hypothesis anticipated that the NEA indicators were different measures of the same underlying factor, which we expected to be a form of functional connectivity we termed *system integration*. The results revealed many associations among the indicators and that their common variance could be largely partitioned into two latent factors. We can chiefly attribute common variance in six of the nine measures (TST, FCI, $Indirect/Direct$, IFI, AGG, and AMP) to one latent factor, which suggests that they capture different aspects of a common unmeasured system variable. In addition, we ascribe total boundary flows ($Boundary$) and a portion of TST is attributed to a second factor. Together these latent factors account for about 80% of the total variance. These results support our hypothesis with one major exception: the variation of HMG has a high uniqueness factor.

Further consideration of these indicators explains why the relationships exist among the variables in Factor 1. From a given network topology there are two ways of increasing TST. The first is to increase energy–matter input into the system. This action increases TST, but in this case the organization of the system remains constant. The second approach is to increase the system recycling by reapportioning the flux distribution, which necessarily increases IFI because by definition all cyclic flows are indirect[1] . In addition, this recycling likely increases *Indirect/Direct* (see Higashi and Patten, 1989; Patten, 1991, for additional detail). Another consequence is that the proportion of TST derived from *Boundary* will decline and its inverse, AGG, will increase. Likewise AMP should increase because the proportion of compartments receiving more flow than they contribute depends directly dependent upon recycling (Patten et al., 1990). Thus, cycling plays a central role in each of these six indicators.

Our discovery that the nine ecosystem indicators cluster around two latent factors denotes that they contain some redundancy, but we wonder if the factors might have additional import. Grimm and Yarnold (1995) advise that caution is wise when interpreting factor analysis, but our findings suggest that we can link the two emergent factors to the conceptual model of ecosystem growth introduced by Jørgensen et al. (2000) and extended by Fath et al. (2004). These authors describe four forms of growth:

Form 0—Boundary growth. A constant source of low-entropy material sustains open thermodynamic systems and fundamentally limits the work a system can perform. This growth Form 0 represents the increase in boundary input.

Form I—Structural growth. This growth type corresponds to increasing biomass caused by component growth in number, size, and types.

Form II—Network growth. This form of growth captures shifts in the in-

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[1] The converse is not necessarily true: all indirect flows are are not cyclic. This implies that $IFI \geq FCI$ and that the values will converge as cycling increases.

ternal organization of the system, which includes an increase in connectivity and recycling of energy and matter.

Form III—Informational growth This type of growth augments the internal order of the informational content of the system, and includes behavioral changes from a more exploitative to a more conservative system as well as possible increases in genetic information of component organisms.

As cycling is the essential element linking TST, FCI, $Indirect/Direct$, IFI, AGG, and AMP in Factor 1, we suspect that this Factor represents Growth Form II. We also expect HMG to be associated with this growth type even though its variability is largely independent. Furthermore, energy–matter cycles are fundamental to system growth and development because they establish routes of cybernetic feedback (DeAngelis et al., 1986; Patten and Odum, 1981), and provide a means of integrating ecosystem flows and storage (Patten et al., 1990; Ulanowicz, 1983). Therefore, we tentatively suggest that this factor is Patten's hypothesized system integration through indirect effects.

Factor 2 captures both the variability of boundary flows and a portion of the variability of TST and expresses the effects of environmental variability. Therefore, this factor relates to Growth Form 0. Notice that TST is a component of this factor as well as the first because boundary flows and internal flows are combined in its calculation.

Variation in TSS has a large uniqueness factor, so it was only weakly associated with Factor 1 and Factor 2. By definition, TSS is an indicator of Growth Form I.

5 Related Work

The work reported here builds upon previous developments in ecological network analysis. In this section, we briefly describe related work that established or suggested indicator interrelationships as well as one study that anticipated the indicator robustness. We conclude by highlighting the unique contribution of our work.

Several studies laid the foundations for the indicator interrelationship hypothesis. Higashi (Higashi and Patten, 1986; Patten, 1991; Patten et al., 1990) showed algebraically that increasing the number of nodes, connectance, storage, strength of direct flows, or the amount of recycling tends to increase $Indirect/Direct$. Hence, the positive association of this ratio with TSS, TST and FCI is not surprising. Further, Christensen (1995) compared several proposed network indicators of ecosystem maturity in a study of 41 aquatic ecosystem models, which had a consistent currency but varied in the number of nodes and connectance. He found a strong correlation between FCI and AGG, but they were not well correlated with TST. In his principle components analysis, FCI and AGG were closely associated with his first component, while TST was more closely associated with the second. This finding agrees with our results, but ours shows a stronger relationship between TST and FCI and AGG. The different model currencies likely drive this incongruity. With a more analytical approach, Fath et al. (2001) used a five mode pathway decomposition to show how simultaneous increases in TST, TSS, $Boundary$ and FCI were reconcilable. In their discussion of AMP and HMG, Patten et al. (1990) illustrated how recycling influence both of these indicators. When Fath and Patten (1999a) introduced the quantitative measure for HMG, they confirmed that it tended to increase with cycling in a twenty node model. Later, Fath (2004) used large ($n > 100$) cyber-ecosystem models to show that both $Indirect/Direct$ and HMG tended to increase with FCI. However, network amplification never occurred in these models, which may be attributed to the restricted cycling range in the cyber-ecosystem models ($0.14 < FCI < 0.26$). Borrett et al. (2006) observed a strong association between $Indirect/Direct$ and AGG in sixteen nitrogen network models of the Neuse River Estuary. These networks were highly retentive and exhibited a large degree of cycling. The first characteristic caused $Direct$ to be nearly equivalent to $Boundary$ and the second characteristic made $Indirect$ and TST to converge such that $TST/Boundary \sim Indirect/Direct$.

Allesina and Bondavalli's (2004) study of the effects of alternative flow balancing procedures is the most closely related work to our investigation of the indicator's robustness to uncertainty. They found that altering model coefficients ±10% led to small changes in the balanced system's TST[2], such that 50% of the resultant TST values were less than 2.5% of their original value. Thus, TST appears to be robust to these flow perturbations. Significantly, the authors compared the TST of a flow model that is slightly out of steady-state to a balanced one. In contrast, all 90 model parameterizations used in our study generated steady-state behavior. Furthermore, our investigation covers a wider range of network indicators whereas Allesina and Bondavalli (2003) restrict their investigation to TST and Ascendency, which is not in our study.

We conclude that several of the relationships among the NEA indicators were known or anticipated from independent investigations. Our work brings these indicators together into one quantitative study and begins to describe the quantitative forms of these relationships. In addition, our data support the

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[2] These authors calculate TST by summing both inputs and outputs in their calculation, whereas we include only one direction of these boundary flows because total inputs equal total outputs in a steady-state system.

hypotheses that many of these indicators are characterizing similar aspects of ecosystem organization and are robust under flow and storage uncertainty.

6 Future Work

This research is a step toward understanding the effect of system uncertainty on the NEA ecosystem indicators, but additional work is necessary to evaluate the generality of the results and to determine their significance for environmental impact assessment and management. We must be careful not to overgeneralize from this case study. Our approach reveals the influence of flow and storage uncertainty on the NEA indictors in Lake Lanier given the initial conceptual model. An important next step is to investigate the effect of uncertainty in the model structure (e.g., conceptual model, flow formulation). Further, we require additional case studies for two reasons. First, our analysis of indicator relationships is limited by their small range, which results from their robustness. Second, we ultimately want to use these indicators to characterize the Lake Lanier ecosystem's healthy, maturity, or integrity. These classifications are relative and require meaningful comparisons that do not yet exist. More case studies will let us develop a meaningful scale to evaluate ecosystem condition in the future.

7 Concluding Remarks

The results of this study make two primary contributions to ecosystem network analysis. First, they demonstrate that five of the ecosystem network analysis indicators—FCI, $Indirect/Direct$, IFI, AGG and HMG—are robust to the flow and storage uncertainty in the Lake Lanier phosphorus model. This finding lets us bypass the modeling problem and conclude that internal processes heavily influence phosphorus flux in the Lake Lanier ecosystem. Second, the results show that the majority of the nine ecosystem indicators investigated co-varied and that their common variation could largely be mapped into two latent factors, which we have tentatively interpreted as (1) system integration (Growth Form II) and (2) boundary (Growth Form 0). This case study provides a window into the workings of network environ analysis and the Lake Lanier ecosystem. Continued research into ecological network analysis sensitivity to model uncertainty will lead to a better understanding of when our model simplifications are justified, and when we must alter our simplifications to better match natural phenomena.

8 ACKNOWLEDGEMENTS

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gia Department of Natural Resources, Fisheries Section of the Wildlife Resources Division.

List of Figures

9 Tables

Table 1. Network Environ Analysis indicators of whole-system organization.

Indicator	Symbol	Description	Formula
Total System Throughflow	TST	Sum of total flow into or out of nodes	$\sum_{k=1}^{n} T_k = \sum_{k=1}^{n}\sum_{k=1}^{n}(f_{kj} + z_k) = \sum_{k=1}^{n}\sum_{k=1}^{n}(f_{ik} + y_k)$
Total System Storage	TSS	Total amount of model currency stored in nodes	$\sum_{k=1}^{n} x_k$
Total Boundary Flow	$Boundary$	Total amount of boundary input or output	$\sum_{i=1}^{n} z_i = \sum_{j=1}^{n} y_j$
Finn Cycling Index	FCI	Cyclic portion of TST	$\sum_{i=1}^{n}((n_{ii} - 1)z_i)$
Indirect/Direct	$Indirect/Direct$	Ratio of indirect to direct flow	$\frac{\sum(\mathbf{N} - \mathbf{I} - \mathbf{G})\mathbf{z}}{\sum \mathbf{Gz}}$
Indirect Flow Index	IFI	Proportion of TST derived from indirect flows	$\frac{\sum(\mathbf{N} - \mathbf{I} - \mathbf{G})\mathbf{z}}{TST}$
Homogenization	HMG	Tendency to uniformly distribute causality across the network	$\frac{\mathrm{CV}(\mathbf{G})}{\mathrm{CV}(\mathbf{N})}$
Amplification	AMP	Proportion of flows obtaining more than face value	$\frac{\# n_{ij} > 1 \quad (i \neq j)}{n(n-1)}$
Aggradation[a]	AGG	Average number of times an average input passes through the system	$\frac{TST}{Boundary}$

[a] Aggradation is also known as average path length (Finn, 1976), flow multiplying ability (Han, 1997), and multiplier effect (Samuelson, 1948).

Table 2. Average (±SD) inter-compartment flows ($\mathbf{F}$) oriented from column to row, inputs ($\mathbf{z}$), outputs ($\mathbf{y}$) in mg P m^{-2} d^{-1}, and storage ($\mathbf{x}$, mg P m^{-2}) for 90 plausible models of phosphorus flow and storage in Lake Lanier. Compartment labels are in the vector Names.

$$\mathbf{F} = \begin{bmatrix} 0 & 33.6\ (10.1) & 4.3\ (2.7) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 28.3\ (29.6) & 0 & 0 & 0 & 0 & 0 & 0 & 39.9\ (25.8) \\ 25.3\ (5.3) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 55.8\ (47.2) & 0 & 0 & 0 & 0 & 0 & 0 & 33.9\ (28.4) & 0 & 0 \\ 0 & 0 & 5.2\ (3.1) & 29.6\ (25.2) & 0 & 0 & 0 & 0 & 38.2\ (32.4) & 0 & 0 \\ 0 & 0 & 5.1\ (3.3) & 0 & 16.8\ (15.1) & 0 & 0 & 0 & 35.7\ (24.0) & 0 & 0 \\ 0 & 0 & 0 & 0 & 18.8\ (16.7) & 0 & 0 & 0 & 38.3\ (25.4) & 0 & 0 \\ 0 & 0 & 0 & 0 & 18.1\ (13.9) & 28.4\ (17.2) & 18.8\ (16.0) & 0 & 0 & 0 & 0 \\ 0 & 0 & 5.4\ (3.2) & 31.7\ (29.1) & 19.3\ (18.1) & 29.1\ (25.6) & 19.2\ (16.9) & 39.8\ (25.7) & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 26.2\ (23.3) & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 26.2\ (23.3) & 0 \end{bmatrix}$$

$$\text{Names} = \begin{bmatrix} \text{Epilimnion P} \\ \text{Hypolimnion P} \\ \text{Phytoplankton} \\ \text{Microbes} \\ \text{Microzooplankton} \\ \text{Macrozooplankton} \\ \text{Macroinverts} \\ \text{Larval/Juvenile fish} \\ \text{Suspended detritus} \\ \text{Sediment detritus} \\ \text{Pore Space P} \end{bmatrix} \quad \mathbf{z} = \begin{bmatrix} 6.9 & (5.3) \\ 21.1 & (9.9) \\ 0 & \\ 0 & \\ 0 & \\ 0 & \\ 0 & \\ 27.5 & (12.6) \\ 27.6 & (11.2) \\ 0 & \\ 13.8 & (8.6) \end{bmatrix} \quad \mathbf{y^T} = \begin{bmatrix} 19.4 & (9.1) \\ 0.0 & \\ 5.3 & (2.9) \\ 0.0 & \\ 0.0 & \\ 0.0 & \\ 19.1 & (16.0) \\ 53.0 & (21.5) \\ 0.0 & \\ 0.0 & \\ 0.0 & \end{bmatrix} \quad \mathbf{x} = \begin{bmatrix} 64.4 & (3.5) \\ 228.5 & (208.7) \\ 22.3 & (7.0) \\ 129.9 & (106.7) \\ 77.6 & (50.1) \\ 154.0 & (223.0) \\ 81.4 & (55.8) \\ 171.1 & (42.5) \\ 152.6 & (83.5) \\ 240.0 & (398.4) \\ 341.3 & (588.7) \end{bmatrix}$$

Table 3
Mean, standard deviation (SD), and coefficient of variation (CV) of Network Environ Analysis ecosystem indicators to flow and storage uncertainty in a phosphorus model of Lake Lanier. They are ordered by decreasing variability described by CV

Indicator	Mean	SD	CV
TSS	1634	985	0.60
AMP	0.21	0.12	0.59
TST	749	303	0.40
$Indirect/Direct$	7.45	2.83	0.38
AGG	7.84	2.69	0.34
FCI	0.39	0.11	0.28
$Boundary$	96	20	0.21
HMG	3.10	0.31	0.10
IFI	0.75	0.07	0.10

Table 4
Pairwise linear ordinary least-squares regression coefficients ($Y = b + mX$).

Y	X	b	m	$Pr(> F)$
$\ln(TST)$	$\ln(TSS)$	2.94 *	0.50 *	0.00 *
$\ln(TST)$	$Boundary$	5.78 *	0.01 *	0.00 *
$\ln(TST)$	FCI	5.53 *	2.63 *	0.00 *
$\ln(TST)$	$\ln(Indirect/Direct)$	5.01 *	0.80 *	0.00 *
$\ln(TST)$	IFI	3.62 *	3.94 *	0.00 *
$\ln(TST)$	$\ln(AGG)$	4.75 *	0.90 *	0.00 *
$\ln(TST)$	HMG	5.88 *	0.23	0.07
$\ln(TST)$	AMP	6.09 *	2.22 *	0.00 *
$\ln(TSS)$	$Boundary$	6.75 *	0.01 *	0.03 *
$\ln(TSS)$	FCI	6.41 *	2.20 *	0.00 *
$\ln(TSS)$	$\ln(Indirect/Direct)$	5.87 *	0.72 *	0.00 *
$\ln(TSS)$	IFI	4.44 *	3.78 *	0.00 *
$\ln(TSS)$	$\ln(AGG)$	5.48 *	0.89 *	0.00 *
$\ln(TSS)$	HMG	5.64 *	0.54 *	0.00 *
$\ln(TSS)$	AMP	6.92 *	1.66 *	0.00 *
$Boundary$	FCI	105.76 *	-22.67	0.26
$Boundary$	$\ln(Indirect/Direct)$	108.03 *	-5.75	0.33
$Boundary$	IFI	132.44 *	-47.43	0.11
$Boundary$	$\ln(AGG)$	116.34 *	-9.66	0.14
$Boundary$	HMG	140.14 *	-14.09 *	0.04 *
$Boundary$	AMP	99.95 *	-14.55	0.40
FCI	$\ln(Indirect/Direct)$	-0.16 *	0.28 *	0.00 *
FCI	IFI	-0.68 *	1.43 *	0.00 *
FCI	$\ln(AGG)$	-0.24 *	0.31 *	0.00 *
FCI	HMG	0.17	0.07 *	0.05
FCI	AMP	0.22 *	0.81 *	0.00 *
$\ln(Indirect/Direct)$	IFI	-1.74 *	4.92 *	0.00 *
$\ln(Indirect/Direct)$	$\ln(AGG)$	-0.21 *	1.07 *	0.00 *
$\ln(Indirect/Direct)$	HMG	0.64	0.43 *	0.00 *
$\ln(Indirect/Direct)$	AMP	1.36 *	2.73 *	0.00 *
IFI	$\ln(AGG)$	0.31 *	0.22 *	0.00 *
IFI	HMG	0.47 *	0.09 *	0.00 *
IFI	AMP	0.64 *	0.52 *	0.00 *
$\ln(AGG)$	HMG	0.91 *	0.36 *	0.00 *
$\ln(AGG)$	AMP	1.51 *	2.37 *	0.00 *
HMG	AMP	2.98 *	0.45	0.08

* indicates significant at $\alpha = 0.05$

Table 5
Principle components factor analysis.

Variable	Factor 1	Factor 2	Uniqueness
$ln(TST)$	0.84	0.53	0.01
$\ln(TSS)$	0.61	0.28	0.55
$Boundary$	-0.09	0.99	0.01
FCI	0.95	-0.04	0.09
$\ln(Indirect/Direct)$	0.96	-0.02	0.07
IFI	0.98	-0.09	0.04
$\ln(AGG)$	1.00	-0.07	0.01
HMG	0.34	-0.18	0.85
AMP	0.91	-0.01	0.17
Loading Sums of Squares	5.81	1.40	
Proportion of Variance	0.65	0.16	
Cumulative Variance	0.65	0.80	

10 Figures

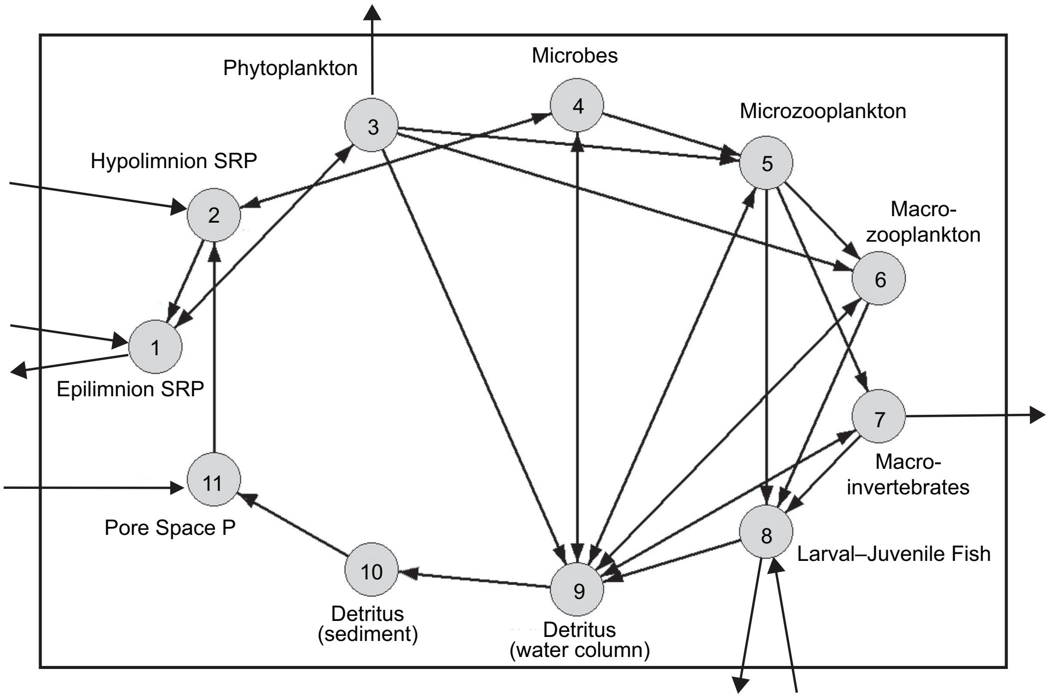

Fig. 1. Eleven compartment model of phosphorus flux in Lake Sidney Lanier, Georgia, USA.

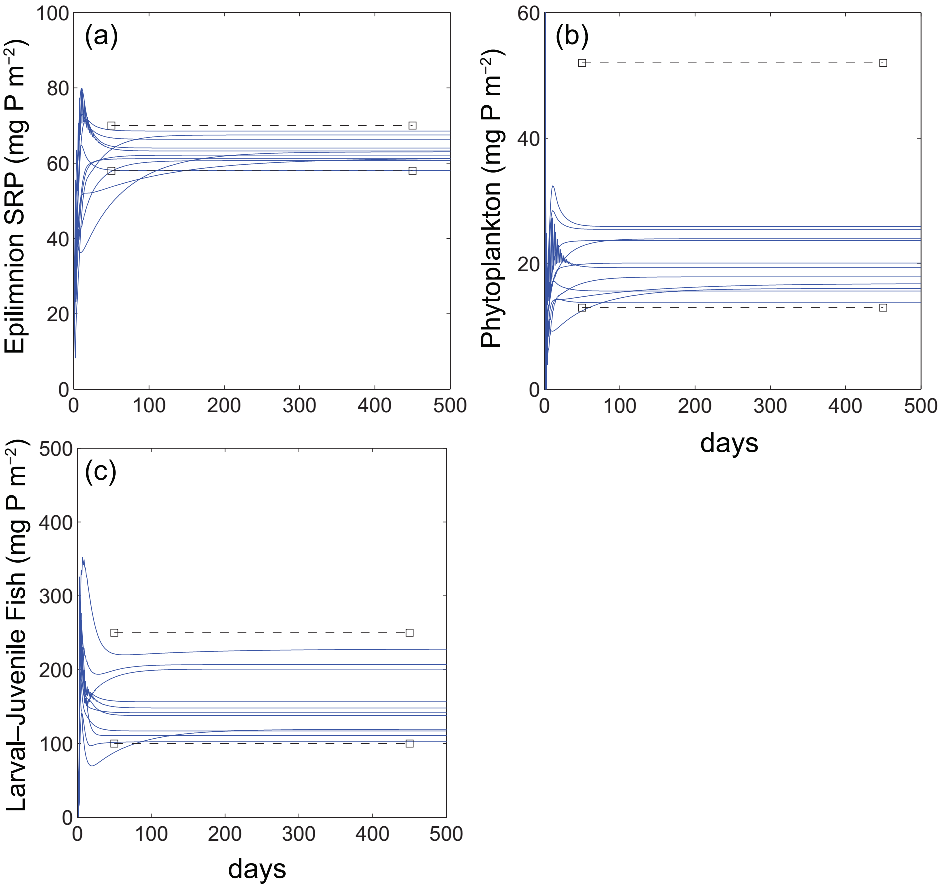

Fig. 2. Example of eleven successful model outputs for (a) epilimnion soluble reactive phosphorus, (b) phytoplankton, and (c) larval–juvenile fish. Dashed lines and square markers represent the constraints for the behavior definitions.

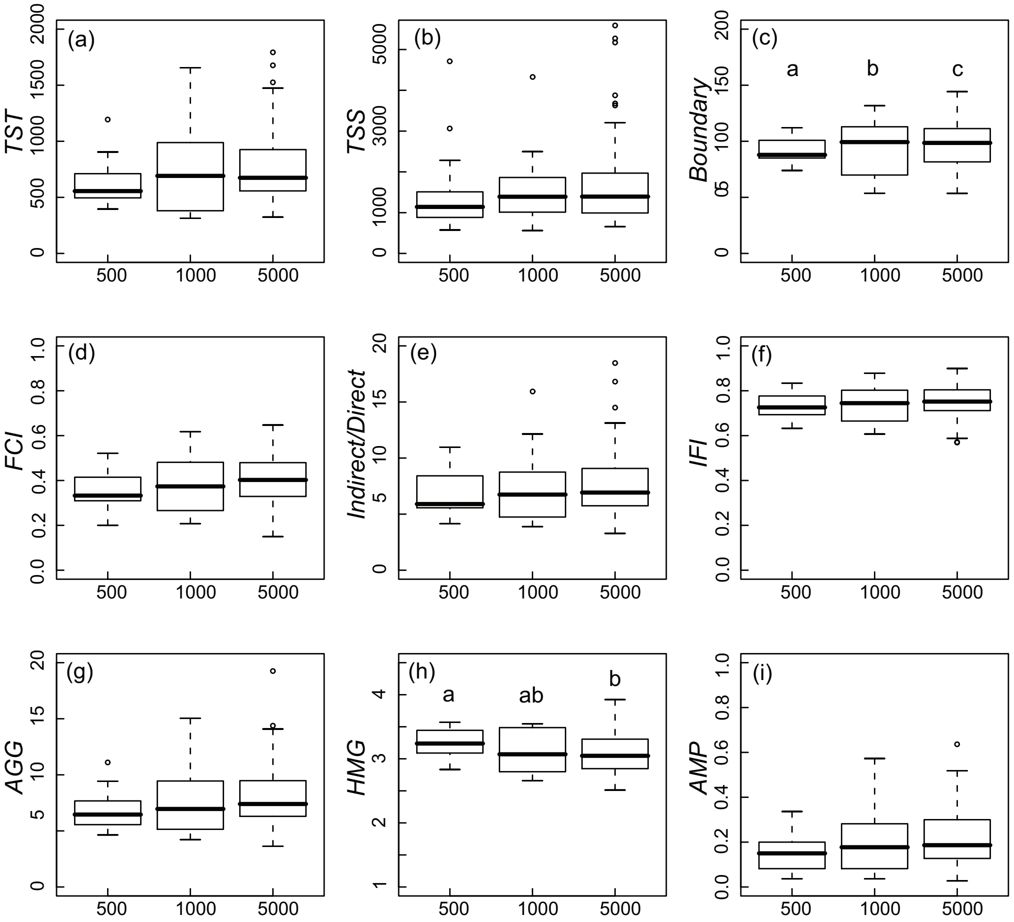

Fig. 3. Sample distributions of nine Network Environ Analysis indicators in plausible parameterizations of the Lake Lanier phosphorus model from simulations with 500, 1000, and 5000 trials. The trials generated 14, 18, and 90 plausible model parameterizations respectfully. The indicators are (a) Total System Throughflow (TST), (b) Total System Storage (TSS), (c) Total Boundary Input ($Boundary$), (d) Finn cycling index (FCI), (e) ratio of indirect-to-direct flows ($Indirect/Direct$), (f) indirect flow index (IFI), (g) network aggradation (AGG), (h) network homogenization (HMG), and (i) network amplification (AMP).

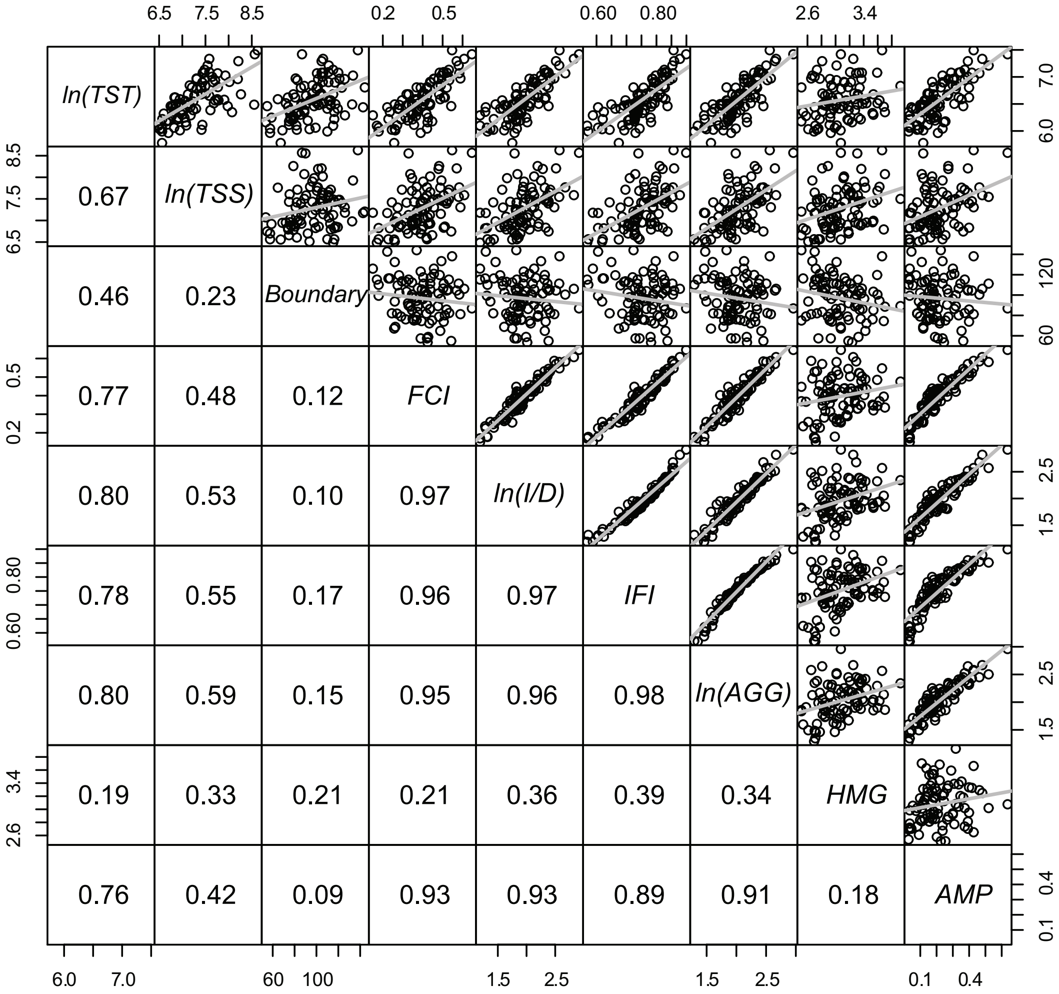

Fig. 4. Pairwise scatter plots of nine Network Environ Analysis indicators of ecosystem organization in 90 plausible parameterizations of the Lake Lanier phosphorus model. Scatter plots and ordinary least-squares regression lines are plotted above the principle diagonal and corresponding Pearson correlation coefficients are positioned below. Notice that we transformed TST, TSS, $Indirect/Direct$ (symbolized here as I/D), and AGG by the natural logarithm.

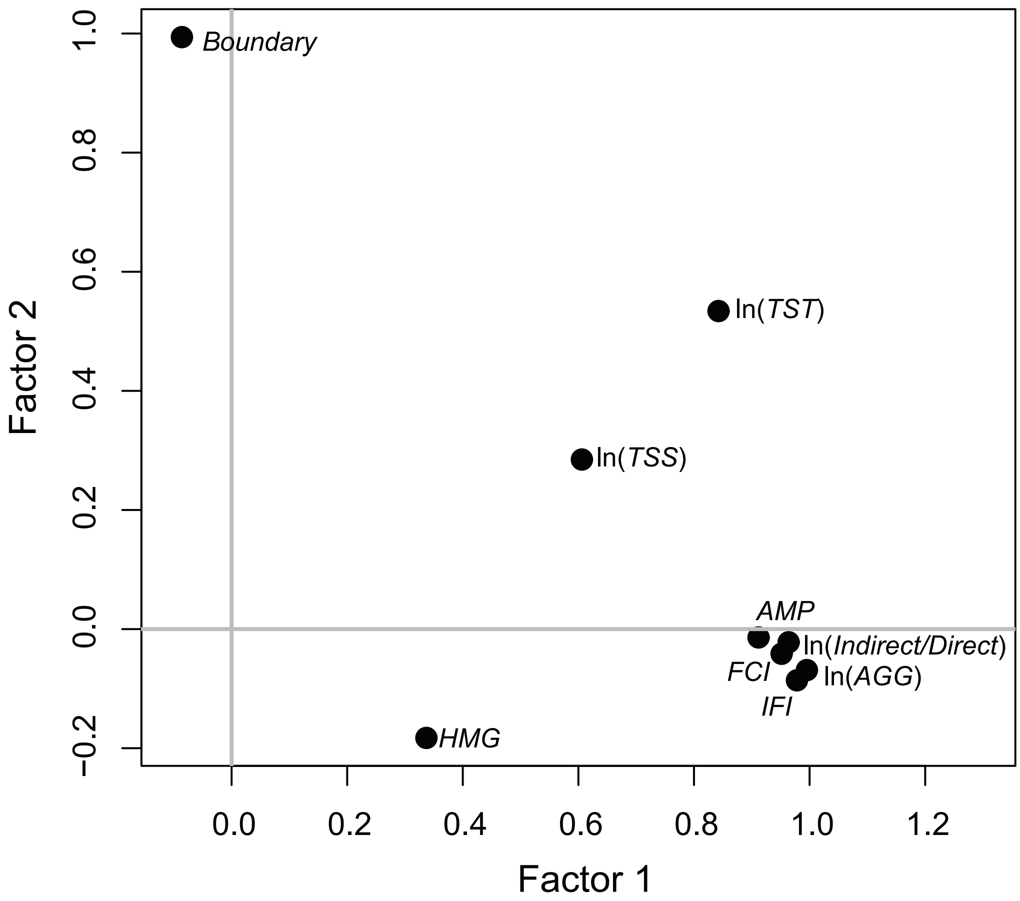

Fig. 5. Factor analysis loadings plot. Distance from the origin to an indicator implies the strength of its association with a factor. For example, *Boundary* is highly associated with Factor 2 and has little common variation with Factor 1.