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# Weak indirect effects inherent to nitrogen biogeochemical cycling within anthropogenic ecosystems: A network environ analysis

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ABSTRACT

Indirect effects are assumed to be the major causes of the complexity and stability of ecological networks. The complexity of urban–rural complexes (URCs) could also be attributed to the indirect effects associated with human activities. No studies, however, have quantified the strength of indirect effects in relation to urban biogeochemistry. A network environ analysis (NEA) was used for this study to investigate and compare indirect effects in relation to the nitrogen (N) cycling networks of 22 natural ecosystems and five URCs. Results show that indirect effects were proven to be weak for URC N cycling networks (accounting for only ∼2% of the overall effects measured in natural ecosystems). The weak indirect effects found provide a counterexample for the hypothesis that indirect effects are in fact the dominant components of biogeochemical networks. It also implies that human activity in itself does not always raise the complexity of ecological processes as previously suggested. Weak indirect effects also lead to perturbation fragility for URC N cycles (where the decay rate is greater in comparison to natural ecosystems by a factor of 13). In order to improve the robustness and efficiency of URC biogeochemical cycling, a knockout analysis was carried out. By comparing results after removing single interactions between natural ecosystems and URCs it was found that the loss of indirect effects require cooperative strategies to optimize N cycling networks within URCs.



## 1. Introduction

Organisms and their abiotic environments are linked through an intricate network of energy, matter, and nutritional exchanges. When the impact of one species on another requires the presence of a third species, indirect effects occur (Wootton, 1994, 2002). According to the definition by Wootton (1994), there are two major types of indirect effects within ecological networks: interaction chains and interaction modifications. Interaction chains occur by linking two or more direct interactions together. For example, in the chain A → B → C, A indirectly influences C by directly influencing B. Interaction modifications occur when a species modifies the interaction between two other species. There are two types of interaction modifications: "trait-mediated" and "environment-mediated" modifications. Trait-mediated modifications occur when one species changes traits or behaviors of a second that, in turn, alters its interactions with a third (Werner and Peacor, 2003; Schmitz et al., 2004). Environment-mediated modifications occur when one species changes the environmental context in which two species interact (Jones et al., 1997). In sum, multiple types of indirect effects lead to the emergence of complexity within an ecosystem. Recently, indirect effects have been recognized as a fundamental cause of ecosystem complexity (Wootton, 2002).

Urban–rural complex (URC) is a new emerging concept in ecology that integrates a city core and its periphery ecosystems and couples human activity and nature as a system (Liu et al., 2007; Gu et al., 2009). Biogeochemical cycles within URCs have been considered to be deeply affected by the indirect effects of human activity (Collins et al., 2000; Alberti et al., 2003; Kaye et al., 2006; Grimm et al., 2008). First, anthropogenic inputs, such as fertilizers, fossil fuels, and chemicals containing N or C, could be dispersed into the environment by way of interaction chains (Schlesinger, 2009). Second, human activity will always modify species traits, soils, or water bodies. For example, the capacity of riparian areas to convert soil nitrate to nitrogenous gases (denitrification) can be reduced

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in humid urban areas (Kaye et al., 2006). Third, environment-mediated modifications also occur in URCs. For instance, increased temperatures in and around cities (heat island effect) enhance ozone formation that will subsequently alter the type, development, behavior, and spatial extent of plants within URCs (Gregg et al., 2003). Although indirect effects play a critical role in URC biogeochemical cycling, no studies have actually attempted to quantify indirect effects within URCs and compare them to natural conditions within the same context (Bodini and Bondavalli, 2002; Bailey et al., 2004a,b; Zhang et al., 2009). This gap is largely due to the lack of appropriate models and datasets to study biogeochemical cycles in urban areas (Kaye et al., 2006; Min et al., 2011a).

Network Environ Analysis (NEA) is one type of ecological network analysis that can be used to study the transaction network variable in ecology (including trophic and biogeochemical networks) (Patten, 1978; Fath and Patten, 1999; Ulanowicz, 2004). NEA can assess interaction chains and their indirect effects at the system level and can also quantify details of indirect effects, including pathway length as well as recycling and decay rates (Fath and Patten, 1999). While observation and analysis of ecological transaction networks cannot identify specific mechanisms or depict all types of indirect interactions in trophic dynamics and biogeochemistry, NEA could shed light on the consequences of particular system organizations, especially indirect effects mediated by these transaction networks (Borrett et al., 2006). Additionally, NEA requires only network topology and steady state flow distribution; hence, it could provide a platform to study indirect effects in relation to URC biogeochemical cycles.

For this study, two specific hypotheses taken from current biogeochemical studies were tested. First, the hypothesis that indirect effects are the dominant components of biogeochemical networks was examined. This hypothesis has been confirmed in many natural ecosystems (Montoya et al., 2009; Borrett et al., 2010) but remains unclear in URCs. Second, N biogeochemical cycling was hypothesized to be more complex in URCs than in natural ecosystems. Many studies support this hypothesis from the standpoint of different points of view (Alberti et al., 2003; Kaye et al., 2006). The two hypotheses are potentially related to each other. Since indirect effects are a fundamental cause of ecosystem complexity (Wootton, 2002), the dominance of indirect effects could correspond to the high complexity found in ecological systems. The two hypotheses were ascertained by performing throughflow NEA analysis based on 27 natural or URC nitrogen (N) biogeochemical network models. In accordance with the results obtained from NEA, knockout analysis (Min et al., 2011b) was also imported to determine effective strategies to improve robustness and efficiency of N cycling within URCs.

## 2. Materials and methods

Based on NEA, 27 N biogeochemical network models were characterized by four common parameters, including the ratio of indirect-to-direct flow intensity (*I*/*D*) (Fath and Patten, 1999), the decay rate ($\lambda_1$) (Borrett et al., 2010), the average path length (i.e., network aggradation, *AGG*) (Fath and Borrett, 2006), and Finn's cycling index (*FCI*) (Finn, 1976).

### 2.1. Selected ecological networks

For this study, natural ecosystem N biogeochemical network models were selected from published literature. The selection of these models was based on the following two objectives. First, all models must have been widely used to study indirect effects in natural ecosystems. They were consequently suitable for use as a URC comparison (control group). Second, the models must have been well established and also have been used in multiple studies for different purposes (Borrett et al., 2006; Gattie et al., 2006; Schramski et al., 2006, 2007; Whipple et al., 2007). These models include (1) the Neuse River Estuary (16 seasons) (Christian and Thomas, 2003), (2) the Baltic Sea (Hinrichsen and Wulff, 1998), (3) the Sylt-Romo Bight (Baird et al., 2008), (4) the mesohaline region of Chesapeake Bay (Baird et al., 1995), and (5) three networks taken from the published dataset of the website established by *Robert E. Ulanowicz* (http://www.cbl.umces.edu/~ulan/).

URC N biogeochemical network models have been rarely used in studies. Five models were collected from literature as well as from the unpublished data from the authors of this study. These models include: (1) an 18-node model created for the Central Arizona-Phoenix ecosystem, United States of America (Baker et al., 2001); (2) a 15-node model created for the Greater Hangzhou Area, developed by Gu et al. (2009); and (3) three unpublished 15-node models established by the authors of this study following the methodology of Gu et al. (2009) (Appendix A). The topology and flow distribution of the four Chinese models are provided in Table 1 and Fig. 1.

**Table 1**
Inputs and outputs of the four urban–rural complexes in China (Gg N yr$^{-1}$): Greater Hangzhou Area (GHA), Greater Shenzhen Area (GSZA), Greater Shanghai Area (GSA), and Greater Guangzhou Area (GGA).

| Type | Name | GHA | GSZA | GSA | GGA |
|---|---|---|---|---|---|
| Input | Cropland | 69.71 | 2.34 | 90.14 | 61.10 |
| | Aquiculture | 32.64 | 3.71 | 28.76 | 28.78 |
| | Livestock | 32.78 | 4.03 | 49.00 | 60.12 |
| | Human | 39.04 | 86.28 | 164.73 | 109.85 |
| | Pet | 4.16 | 0.74 | 5.50 | 1.12 |
| | Lawn | 9.80 | 6.42 | 2.47 | 6.72 |
| | Fixation | 23.15 | 4.75 | 13.60 | 13.66 |
| | Outer-atmosphere | 29.76 | 1.30 | 46.10 | 21.28 |
| Output | Human | 6.61 | 0.00 | 0.00 | 0.00 |
| | Forest | 26.33 | 2.54 | 5.56 | 11.32 |
| | Near-atmosphere | 76.75 | 52.47 | 155.48 | 116.05 |
| | Surface-water | 26.60 | 21.77 | 53.05 | 78.61 |
| | Subsurface | 9.67 | 0.64 | 11.08 | 9.44 |
| | Denitrification | 86.78 | 26.40 | 162.38 | 80.96 |
| | Landfill | 8.30 | 5.75 | 12.75 | 6.25 |

### 2.2. Network environ analysis

NEA is a family of input–output methods that mathematically trace matter through systems (Fath and Patten, 1999). It is applied to ecosystem models to investigate the organization of their internal structure and flow distribution. The methodology includes analyses of structure, throughflow, storage, utility, and control within systems (Fath and Patten, 1999; Fath and Borrett, 2006). The relevant definitions of throughflow analysis have been described in detail in previous studies. Therefore, the parameters used in this study are only briefly introduced. Modifications, however, are carefully presented.

In an *n* node network, $F_{nxn} = (f_{ij})$ represents the observed flow from ecosystem compartment *j* to ecosystem compartment *i*. $Z_{nx1}$ is the inputs to the compartments, and $Y_{nx1}$ is the boundary losses from the compartments. At a steady-state, the amount of matter that flows through each node is equated as:

$$T_{nx1} = \sum_{j=1}^{n} f_{ij} + z_i = \sum_{i=1}^{n} f_{ij} + y_j \quad (1)$$

The matrix of the output oriented direct flow intensity can be calculated as: $G_{nxn} = (g_{ij}) = f_{ij}/T_j$. With this information in hand, the integral flow intensity, that is, the flow intensity over all pathways for all lengths between each model node (i.e., boundary + direct + indirect) can be determined. This is accomplished by

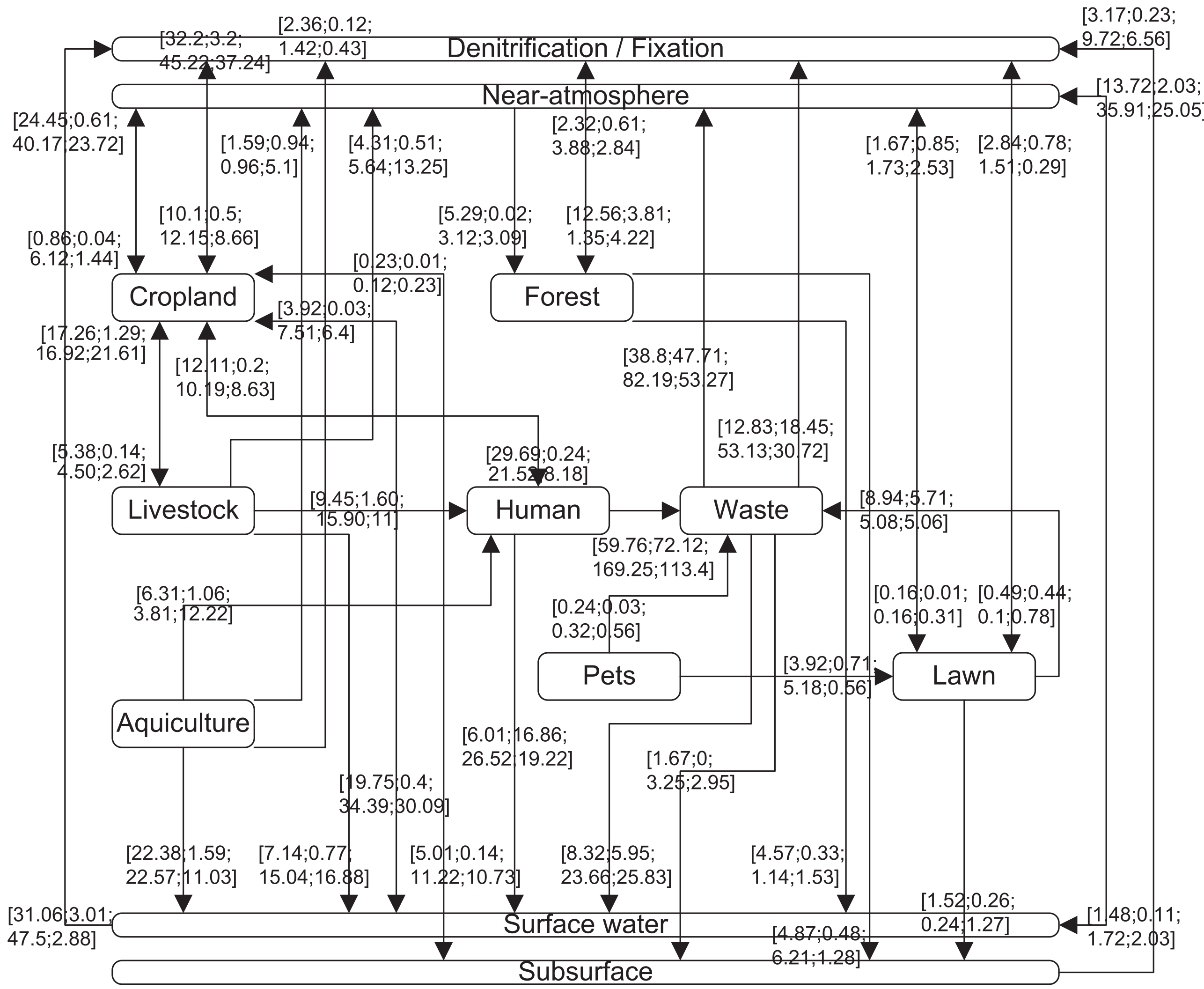


**Fig. 1.** 15-node network model that describes nitrogen cycles of the four URCs in China. The outer atmosphere and the placement of landfills are not provided since they are simple input or output nodes. Life-supporters are shown as flat nodes at the top and bottom. The flow of each interaction is labeled within arrows as a 2 × 2 matrix. The order of the four flow values within a matrix is: Greater Hangzhou Area (upper-left of the matrix), Greater Shenzhen Area (upper-right), Greater Shanghai Area (bottom-left), and Greater Guangzhou Area (bottom-right).

implicitly applying the following equation:

$$N_{nxn} = \sum_{m=0}^{\infty} G^m = E + G^1 + G^2 + \cdots + G^m + \cdots \qquad (2)$$

where $E=(i_{ij})=G^0$ is the boundary intensity; $I=G^1$ is the direct intensity; $D = \sum_{m=2}^{\infty} G^m$ is the indirect intensity of the interaction chain. Ecosystems are open thermodynamic systems (Borrett et al., 2010). The exact value of $N$ can therefore be explicitly calculated as $m \to \infty$ using the following identity:

$$N = (E - G)^{-1} \qquad (3)$$

If $G$ is an irreducible non-negative matrix, then the dominant eigenvalue of $G(\lambda_1)$ is the asymptotic decay rate (Borrett et al., 2010). If $\lambda_1 > 1$, the system is gaining more energy or matter than it is dissipating, but if $0 < \lambda_1 < 1$, energy or matter is dissipating from the system without gain (open thermodynamic system). As $\lambda_1$ approaches zero the decay rate increases and the system becomes more dissipative.

Finn's cycling index (Finn, 1976) is defined as: $FCI = \sum_{i=1}^{n}((n_{ii} - 1)Z_i)/TST$ where $TST = \left\|NZ\right\|$ is the total system throughflow ($0 \le FCI \le 1$). $FCI = 1$ indicates that all matter-energy recycles into the system and no dissipation takes place.

The weight matrix $W=(w_{ij})$ was developed to calculate $I/D$ where $w_{ii}=T_i$ and $w_{ij}=0$ if $i \neq j$. $W$ is essential for two reasons. First, using flow intensity matrixes ($G$ and $N$) alone could lead to flow heterogeneity error since $G$ only reflects the proportion of $f_{ij}$ to $T_j$. However, URC N cycling is typically heterogeneous. For example, N flow that occurs within a lawn ecosystem is less intense than N flow that occurs in a cropland ecosystem. The two simple models provided in Fig. 2 have the same $I/D$ (=1) without weights, but the reuse proportion is higher in the model shown in Fig. 2b than in the model shown in Fig. 2a. The existence of $W$ could indicate such differences ($I/D = 1.315$ and 0.881, respectively). Moreover, $Z$ inputs typically take on the role of $W$ in traditional research approaches. The utilization of $Z$, however, will lead to the retrenchment of direct effects (the direct interaction between any pair of nodes is considered a direct effect in this study) for large networks. For example, direct interactions between nodes $N_2$ or $N_4$ and $N_5$ in Fig. 2 will be treated as indirect interactions when weighted by $Z$. Therefore, the $I/D$ equation that points to the role of indirect effects within a system is:

$$\frac{I}{D} = \frac{\left\|W \times (N - I - G)\right\|}{\left\|W \times G\right\|} \qquad (4)$$

If $I/D > 1$ it is assumed that indirect effects are dominant.

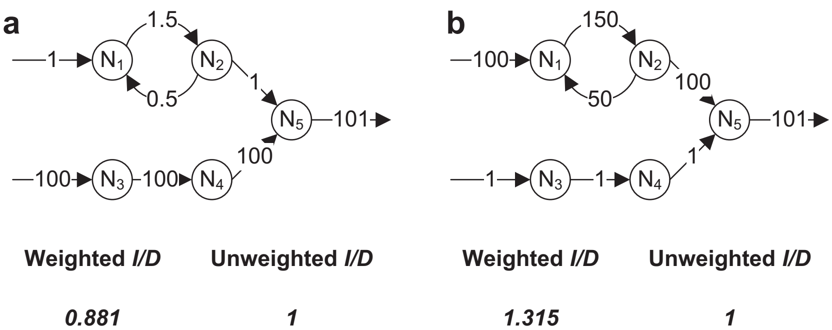


**Fig. 2.** Comparison between weighted and unweighted calculations of the indirect/direct ratio for different flow distributions. (a) Flow concentrates in a linear pathway; and (b) flow concentrates in a circular pathway.

*AGG* is the average length of the N pathway in a given system.

$$AGG = \frac{TST}{\sum_{i=1}^{n} Z_i} \quad (5)$$

A small *AGG* indicates that N travels quickly through a system (from input to output) without sufficient reuse and recycling.

### 2.3. Knockout analysis

Knockout analysis was used to discover the role of single interactions in maintaining or preventing indirect effects taking place within the URC models for the benefit of management and optimization (Min et al., 2011b). A simple knockout was carried out in which an interaction was first chosen and removed. The flow intensity was then redistributed among the remaining interactions (from the same compartment) while maintaining the original proportions (Fig. 3). The redistribution was carried out on the matrix of flow intensity ($G_{nxn}$), which is only related to the proportion of flow distribution. Therefore, the knockout analysis carried out did not interfere with steady-state conditions. The *I/D* value ratio $\gamma$ between the knocked and original system was used to measure the influence of the interaction.

$$\gamma = \frac{I/D_{knocked}}{I/D_{original}} \quad (6)$$

If $\gamma > 1$, the interaction will suppress indirect effects. Conversely, $\gamma < 1$ indicates that the interaction will benefit indirect effects. $\gamma$ can be calculated by knocking out every single interaction and evaluating the overall proportion of interactions that suppress or benefit the indirect effects.

## 3. Results

### 3.1. The ratio of indirect to direct flow

For 19 out of the 22 natural models used for this study, indirect flow was larger than direct flow by a factor of 10 ($I/D > 10$), and

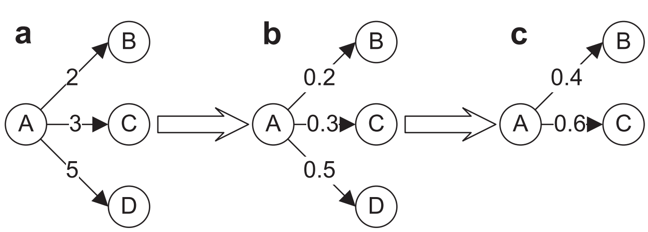


**Fig. 3.** The knockout analysis process. (a) Original network with flow occurring between different compartments; (b) the flow intensity of three interactions ($r_{AB}$, $r_{AC}$, and $r_{AD}$); and (c) the knockout of $r_{AD}$, $h(r_{AB}) = 0.4$, and $h(r_{AC}) = 0.6$ as a result of the redistribution in flow intensity.

the maximal *I/D* value was greater than 160 (Table 2). Although three exceptions to this pattern were observed, indirect flow still exceeded direct flow by three fold. In contrast, $I/D < 1$ in four out of the five URC models tested. The only exception was the Central Arizona-Phoenix model where $I/D = 1.75$ (Fig. 4a), which was also lower than natural conditions.

### 3.2. Flow intensity decay rates

A clear difference in decay rates was apparent between the natural and URC models (Fig. 4b). Decay rates ($\lambda_1$) ranged from 0.99 to 0.12 in all models with an average value of 0.95 for natural ecosystems and 0.33 for URCs. In general, N loss occurred more rapidly in the URC models (Fig. 5), and, hence, N activity within the URCs depended heavily upon external inputs that drive them rather than internal dynamics.

### 3.3. Conversion times and cycling index

Fig. 4c shows that *AGG* (average path length) for natural ecosystems (57.48 on average) was notably larger compared to the five URCs (3.20 on average). The natural model with the largest *AGG* was the Neuse River Estuary model during the spring of 1987 ($AGG = 173.50$). In this case, recycling was also observed to be the highest ($FCI = 0.96$). Most N flowed from natural models via long pathways and was then reused multiple times (Fig. 4d). In contrast, the largest *AGG* of the four Chinese URC models was only 3.04, which was less than the natural model with the least *AGG* (=3.65). In addition, the average *FCI* for the natural and URC models was 0.79 and 0.03, respectively, and the lowest *FCI* observed in the URC models was only 0.0005 (Table 2).

### 3.4. I/D change rate in knockout analysis

The curve shape in Fig. 6a shows three distinct regions: (1) an initial steep portion of the curve ($\gamma > 1$) representing few interactions (~8%) that suppress indirect effects where the maximal $\gamma$ is less than 1.2; (2) a flat region ($\gamma \approx 1$) where most interactions (~86%) have no clear influence on indirect effects (<5%); and (3) a final region containing atypical interactions (~6%) that are highly favorable in maintaining and promoting indirect effects. Natural ecosystems behaved differently. The overall shape of knockout curves (not shown in this paper) for the Neuse River Estuary models were similar to the URC models; however, 36% of all interactions had a clear influence on indirect effects. Curve shape was completely different for the Baltic Sea models (Fig. 6b). In this case, a small number of interactions (~4%) were critical to greatly improving indirect effects ($\gamma > 16$), but the removal of a single interaction does not obviously lead to a decrease in indirect effects.

**Table 2**
Indirect effects and related network indicators.

| Model | *n* | *C* | *I/D* | $\lambda_1$ | *FCI* | *AGG* |
|---|---|---|---|---|---|---|
| Natural ecosystems | | | | | | |
| Neuse Estuary[a] | | | | | | |
| SP 1985 | 7 | 0.45 | 64.49 | 0.98 | 0.91 | 68.58 |
| SP 1986 | 7 | 0.45 | 95.30 | 0.99 | 0.93 | 100.88 |
| SP 1987 | 7 | 0.45 | 34.68 | 0.97 | 0.84 | 34.54 |
| SP 1988 | 7 | 0.45 | 37.77 | 0.97 | 0.85 | 39.21 |
| Sum 1985 | 7 | 0.45 | 159.18 | 0.99 | 0.96 | 169.62 |
| Sum 1986 | 7 | 0.45 | 69.05 | 0.99 | 0.91 | 72.61 |
| Sum 1987 | 7 | 0.45 | 161.32 | 0.99 | 0.96 | 173.50 |
| Sum 1988 | 7 | 0.45 | 126.62 | 0.99 | 0.95 | 127.36 |
| F 1985 | 7 | 0.45 | 47.48 | 0.98 | 0.88 | 48.55 |
| F 1986 | 7 | 0.45 | 95.79 | 0.99 | 0.93 | 98.69 |
| F 1987 | 7 | 0.45 | 85.24 | 0.99 | 0.93 | 86.20 |
| F 1988 | 7 | 0.45 | 42.88 | 0.98 | 0.86 | 44.74 |
| W 1986 | 7 | 0.43 | 36.53 | 0.97 | 0.85 | 36.79 |
| W 1987 | 7 | 0.45 | 10.10 | 0.91 | 0.62 | 11.44 |
| W 1988 | 7 | 0.45 | 51.26 | 0.98 | 0.89 | 50.74 |
| W 1989 | 7 | 0.45 | 18.66 | 0.95 | 0.75 | 19.73 |
| Baltic Sea long-term | 16 | 0.15 | 15.57 | 0.94 | 0.67 | 18.95 |
| Chesapeake Bay | 36 | 0.12 | 5.36 | 0.84 | 0.32 | 6.55 |
| Sylt-Romo Bight | 59 | 0.09 | 3.76 | 0.78 | 0.23 | 3.65 |
| Tropical rain forest[b] | 5 | 0.24 | 6.07 | 0.86 | 0.48 | 7.04 |
| Southeastern pine forest[c] | 6 | 0.31 | 25.77 | 0.96 | 0.80 | 24.26 |
| Ocean euphotic zone[d] | 7 | 0.39 | 19.77 | 0.95 | 0.75 | 20.94 |
| Urban–rural complex systems | | | | | | |
| Central Arizona-Phoenix | 18 | 0.13 | 1.75 | 0.62 | 0.11 | 4.28 |
| Great Hangzhou | 15 | 0.21 | 0.79 | 0.34 | 0.02 | 2.99 |
| Great Shenzhen | 15 | 0.20 | 0.48 | 0.12 | 0.00 | 2.83 |
| Great Shanghai | 15 | 0.21 | 0.71 | 0.31 | 0.01 | 3.04 |
| Great Guangzhou | 15 | 0.21 | 0.62 | 0.27 | 0.01 | 2.86 |

*Notes*: *n* is the number of nodes or compartments within the network model; $C = L/n^2$ is the connectance of the mode; *I/D* is the ratio of indirect-to-direct flow intensity; $\lambda_1$ is the decay rate; *FCI* is Finn's cycling index; and *AGG* is the average conversion time per unit of nitrogen.

[a] The data of Neuse River Estuary contain 5 years (1895–1989) and 16 seasons (SP for spring, Sum for summer, F for fall, and W for winter).
[b] Located in Puerto Rico.
[c] Located in Aiken, South Carolina.
[d] Composite from literature data without explicit units.

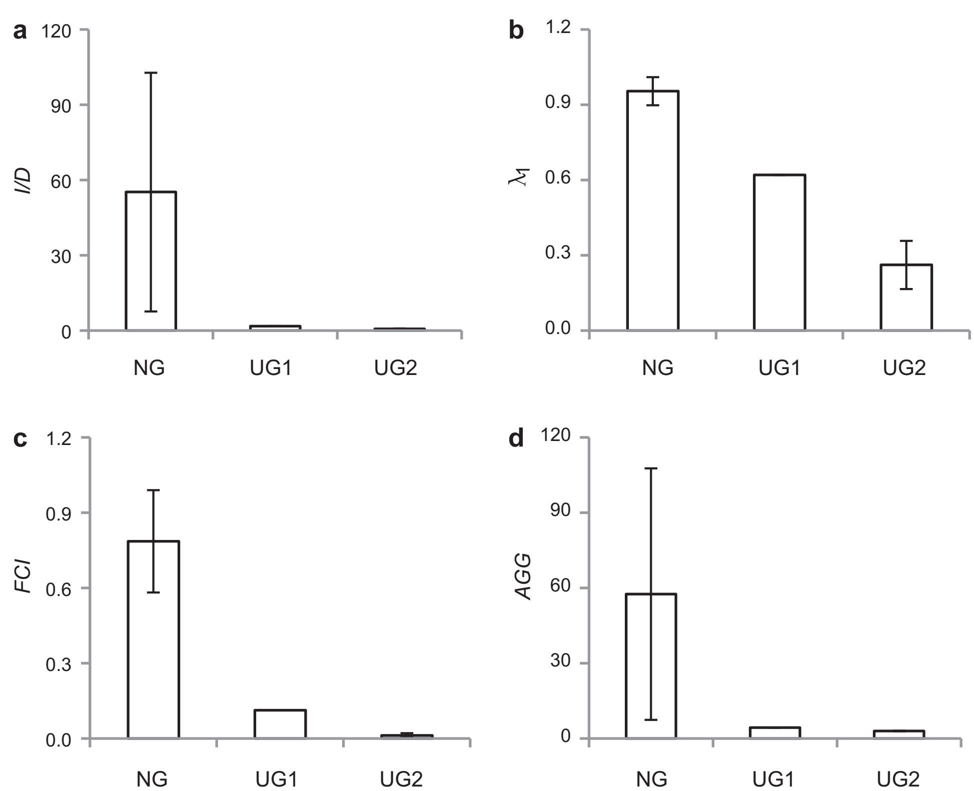


**Fig. 4.** Parameter comparison between natural ecosystems and URCs. (a) indirect/direct ratio (*I/D*); (b) decay rate ($\lambda_1$); (c) Finn's cycling index (*FCI*); and (d) average pathway length (*AGG*). A comparison of the mean value and standard deviation of the four indictors among three groups: the natural group (NG) contains 22 models; the URC group one (UG1) contains only one model in the United States ($I/D > 1$); and the URC group two (UG2) contains four models in China ($I/D < 1$).

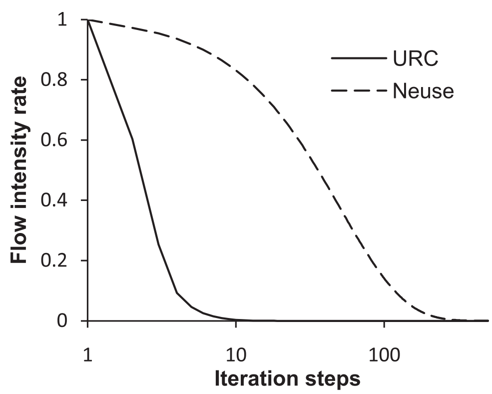


**Fig. 5.** Comparison of decay lines between natural ecosystems and URCs. The average flow intensity decay lines within the five URC models (solid lines) and 16 Neuse models (dash lines).

The parameter $I/D$ for the 22 models were divided into two groups, natural and URC (Table 2), and the difference between the two groups was checked by the Kolomogoroy–Smimov test. The result showed that natural and URC models were significantly different from each other because for $I/D$ ($p < 0.001$). The other three parameters, *FCI*, *AGG* and $\lambda_1$, were also divided into the two groups (Table 2) and checked using the same method. The test of *FCI* ($p < 0.001$), *AGG* ($p < 0.001$), and $\lambda_1$ ($p < 0.001$) also proved the significantly different between natural and URC models. The $I/D$, *FCI*, and *AGG* of the URC models were two orders of magnitude lower (only 1%, 3%, and 3%, respectively) than those of the natural models, and $\lambda_1$ was only 35%. Although different treatments of detritus could alter decay rates in ecological webs (Fath and Halnes, 2007), decay rates were also higher in the URC models in comparison to the natural models. Therefore, indirect effects were weak within the URC N cycling networks.

## 4. Discussion

Weak indirect effects that occur within a URC may be due to two possible structural anomalies, the first by way of a lack of cascading effects (Schmitz et al., 2004). A conclusive URC N cycle trophic cascade should flow from producers to consumers (humans) and finally transmute to decomposers (Fath et al., 2007; Gu et al., 2009). However, a large amount of bypass flow exists in the form of food waste and agricultural N runoff (Gu et al., 2009). Due to the existence of bypass, only marginal cascading effects actually occur within URC N cycling. Small amounts of *AGG* will quantify cascading effects, and it was discovered that 85% of total system throughflow experienced no more than a two-step conversion within the URCs investigated. Second, the recycling that took place within the URCs was minimal (*FCI* < 1%). Infrequent recycling could also lead to a loss of indirect effects due to the positive correlation between the recycling rate and indirect effects (Borrett et al., 2006). Moreover, large amounts of N are reused within natural ecosystems (*FCI* > 20%) that benefit indirect effects (Borrett et al., 2010). The lack of cascading effects and the low recycling rates together suppress indirect effects with respect to URC N cycling. According to the relationship between indirect effects and ecological complexity, the absence of indirect effects implies that URC N cycling is, in fact, less complex than postulated by urban ecologists (Alberti et al., 2003; Grimm et al., 2008). Results partly support Kaye et al. (2006) who states that URCs possess a distinct biogeochemistry compared to natural or agricultural ecosystems. However, the distinction is due to the absence of indirect effects rather than greater complexity as previously postulated.

The simplification of URC N cycling caused by the absence of indirect effects leads to fragility in perturbation resistance (Kitano, 2004; Ulanowicz et al., 2009). Fast decay rates address the problem of fragility (i.e. high sensitive to the perturbation of environment) within URC N cycles. Theoretically, decay rates are linked to ecosystem growth and stability (Fath et al., 2004). A feature of a well-organized ecosystem exhibiting a low decay rate is its tendency to internalize activity and become relatively indifferent to the external supplies and demands of matter (Fath et al., 2004). This suggests that URC conditions are far below those of a well-organized state ($\lambda_1 < 0.5$). They remain in a fragile infancy state for which internal processes are heavily dependent upon inputs (between growth form zero and growth form I in connection with Fath et al. (2004)). Numbers of iterations ($G^m$) were therefore used to represent specific times of decay (Borrett et al., 2010). With respect to the Neuse River Estuary models ($\lambda_1 > 0.97$), flow intensity could be maintained within a level of 50% without the introduction of inputs to iteration cycles for up to 50 repetitions. In all five URCs, however, flow intensity decayed to less than 10% after only two iteration cycles on average. During periods of rapid urbanization, humans depend heavily on large import quantities of N (food, fertilizer, and fossil fuel) to support a growing population (Vitousek et al., 1997; Gu et al., 2009). Meanwhile, the establishment of recycling mechanisms often lags behind the development of URCs (Gu et al., 2009). In biological systems, an appropriate level of complexity is indispensible to maintain stability (Ulanowicz, 2004; Kitano, 2004). Moreover, the knockout analysis clearly shows that the URC models have more key interactions, which maintain indirect effects, than natural models (Fig. 6); hence URCs are less redundant than natural models. Although human activity leads to a sharp increase in components and altered pathways, weak indirect effects suggest

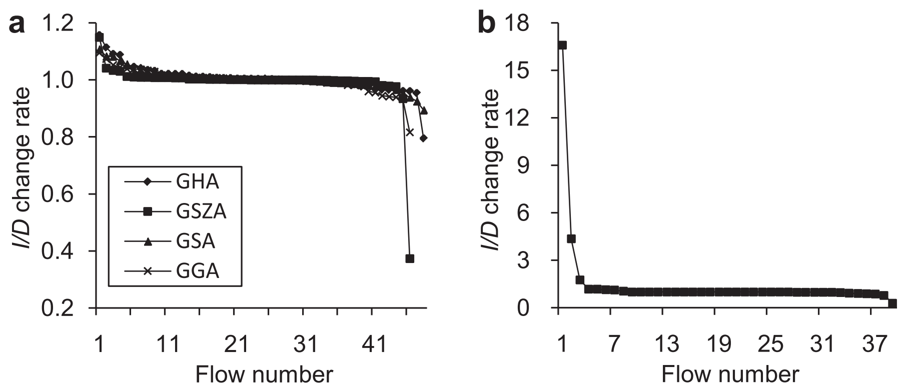


**Fig. 6.** Response of natural ecosystems and URCs to a single interaction knockout. (a) The four URCs in China and (b) the Baltic Sea long-term models. Note that the interaction number was sorted in descending order. This was done so that the interaction number in each model corresponded to a different interaction.

that URC N cycles are simpler and more fragile than those in natural ecosystems.

In order to improve the robustness and efficiency of URC N cycling, knockout analysis was carried out to discover the influence of single interaction to maintain indirect effects for both the Baltic Sea long-term models and the four Chinese URC models ($I/D < 1$). This was done to evaluate the result of removing a single interaction. It was found that the removal of a single interaction in the Baltic Sea long-term models could increase indirect effects by a factor of 17 (Fig. 5b). However, the maximal enhancement achieved by removing a single interaction was only 14% with respect to the URCs (Fig. 5a). Simple blocking strategies are therefore powerless to improve indirect effects. Although wetlands, for example, could prevent agricultural pollution from seeping into water bodies (Liu et al., 2009), they cannot improve URC recycling rates since knockout interactions that occur between cropland and surface water only improves indirect effects by 3%. The recovery of indirect effects is a difficult process. Establishing proper indirect effects in natural ecosystems is the result of long-term evolutional processes incorporating self-adaptive mechanisms. Therefore, cooperative strategies, which can be inspired by natural ecosystems, are necessary to regulate current urban N cycles (Tero et al., 2010) instead of the traditional "trial and error" method (Kitano, 2002).

As a complementary point of view to current hypotheses on N cycling (Wootton, 2002; Borrett et al., 2010), results from the URCs investigated for this study show that indirect effects are weak and lead to rapid decay and inherent fragility for environmental perturbation (Ulanowicz et al., 2009). The hypothesis that states that human activity raises complexity in ecological processes (Alberti et al., 2003; Kaye et al., 2006; Grimm et al., 2008) was found to be debatable after testing direct and indirect effects that occur within URCs. Moreover, knockout analysis suggests that cooperative regulation is a crucial step for URCs in reestablishing robustness despite the inherent weakness of indirect effects.

In sum, this study offered an initial step to quantitatively understand indirect effects that occur within anthropogenic ecosystems. In the future, this study should be developed further via several directions. First, mechanisms and types of indirect effects must be carefully identified in URC N biogeochemistry since NEA only provides a general quantification of indirect effects from interaction chains. Second, the influence of structural features, e.g. network size and degree distribution, on indirect effects should be studied in order to improve the quality of comparison between URC and natural models. Third, the results could be tested with more samples, including terrestrial natural systems, URCs in other countries with different levels of development, and other material or energy networks. Fourth, new optimization algorithms should be developed to clearly interpret network properties and to discover how to modify and introduce interactions to improve indirect effects that occur in human dominated ecosystems. Moreover, the relationship between indirect effects and complexity should be further discussed in depth.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2011.06.013.

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