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Implications of network particle tracking (NPT) for ecological model interpretation

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ABSTRACT

Network particle tracking (NPT), building on the foundation of network environ analysis (NEA), is a new development in the definition of coherence relations within and between connected systems. This paper evaluates three ecosystem models in a comparison of throughflow- and storage-based NEA and NPT. Compartments in models with high indirect effects and Finn cycling showed low correlation of NEA storage and throughflow with particle repeat visits and numbers of particles in compartments at steady state. Conversely, the correlation between NEA and NPT results was high with two models having lower indirect effects and Finn cycling. Analysis of ecological orientors associated with NEA showed NPT to fully support conventional NEA results when the common conditions of donor control and steady state are satisfied. Particle trajectories are recorded in the new concept of a particle "passport". Ability to track and record particle in-system histories enables views of multiple scales and opens the possibility of making pathway-dependent modeling decisions. NPT may also enable modeling of time, allowing integration of Newtonian, organismal and stochastic modeling perspectives in a single comprehensive analysis.

1. Background

Definitions of ecosystems forming distinct subsections of the biosphere are a common feature of many ecosystem models (Barkmann et al., 1998). These authors acknowledged that delineated ecosystems have a subjective quality but nevertheless exist as units that, in principle, can be described empirically as open systems. These systems exhibit developmental trends abstracted from observational data (e.g., Fath et al., 2004). Following classical enlightenment era approaches, Newtonian determinism prevailed in ecological modeling efforts beginning with linear tropic models, thoroughly western and mechanistic in orientation (e.g., Matis et al., 1979). Dynamical models may be classified into two types, *Eulerian* and *Lagrangian*. The former gives a macroscopic perspective on system dynamics, and the latter a microscopic perspective. Both aspects of this duality are valid.

Patten and colleagues developed an Eulerian methodology, *network environ analysis* (NEA), to analyze the within-system environments of subsystem-level components, or *compartments*, defined within a system's mathematical description (Patten, 1978, 1982; Matis and Patten, 1981; Patten and Matis, 1982; Barber et al., 1979; Fath and Patten, 1999; Fath and Borrett, 2006; Schramski, 2006). NEA is a variant of general *ecological network analysis* (ENA), which analyzes boundary contributions to and consequences of interior storages and flows of conservative energy or matter. NEA and ENA both are built upon a deterministic premise and reflect the organic holism often seen for ecological systems. A number of thermodynamic goal functions, or orientors, reflecting such holism have been investigated with NEA and other approaches to heuristically describe developmental trends in ecosystems (Patten, 1995; Jorgensen and Nielsen, 1998; Fath et al., 2001; Jørgensen and Fath, 2004).

Motivated by information theory and statistical thermodynamics, Tollner and Kazanci (2007) presented a Lagrangian extension of ENA they called *network particle tracking* (NPT). NPT maintains a systems perspective while enabling explicit attention to the movement of individual particles that underly real-time change within and between compartments. The NPT algorithm discretizes mass or energy flows and storages into a set of *particles* or *quanta* that track through the system from their points of entry to those of exit. For example, in the three-compartment model of Fig. 1, a particle entering phytoplankton as boundary input (the only such input) will track through the system following the connecting links until it exits from one of the three compartments. Knowledge of particle routing probabilities provides interpretive insight as to how particular particles move through a system before exiting. An improved version of Gillespie's algorithm (1977) for solving stochastic differential equations has greatly extended the tracking capability of the

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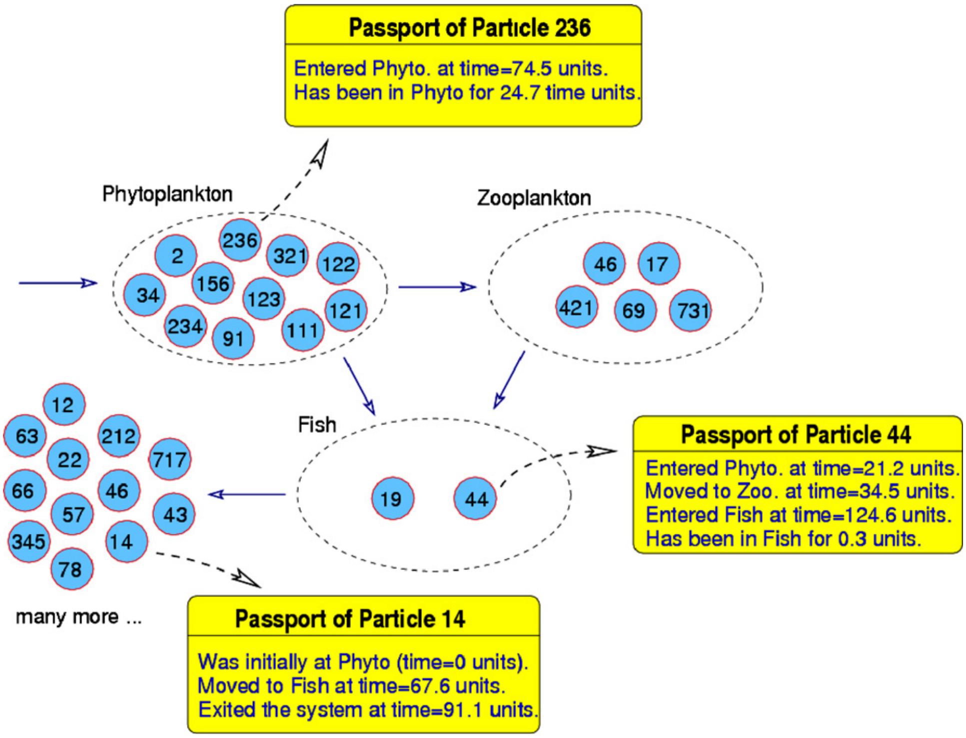


Fig. 1. Three-compartment model depicting particles and their transport information. A record of the trajectory and timing of each particle from its point and time of entry to (potentially) its point and time of exit is given in the particle "passports".

Tollner and Kazanci (2007) approach, enabling feasible solutions to problems at ecological scales.

Kazanci and Tollner (in preparation) used Gillespie's algorithm to mark and follow each discrete element. They attached various identifying attributes to each particle as it passed through compartments, and maintained a historical record of compartment contacts. NPT is essentially an individual-based (or agent-based) method that deduces its rules on how an individual particle moves directly from the differential equation representation of the network model. This eliminates the need for extra parameters or decisions required to build an individual-based model. Therefore, causality is preserved. NPT is a stochastic method compatible with Gillespie's (1977, 1992, 2000) "master equation". In other words, the mean of many Lagrangian NPT simulations agrees with the Eulerian differential equation solution. This property enables accurate comparison of NPT results with conventional simulation and analysis, including ENA and NEA.

Each particle's identity and routing history, similar to an international traveler's passport data (Fig. 1), can be further augmented with additional information documenting all desired aspects or properties of travel through the network. The travel history could also be used to gather additional routing information or as insight for other decisions. For example, chemical energy changes can be logged to calculate exergy content variations, or steady-state models can be inspected to determine a distribution of system and compartment residence times. NPT weaves a stochastic nominalism into the organic holism and Newtonian determinism of ecological network modeling. Patten (1998) articulated a series of orientor statements to describe the basic principles that define the tendencies of directional development, self-organization and autoevolution. NPT provides an approach for mimicking and modeling some of these principles.

The purpose of this study is to advance the further development of NPT by analyzing three compartment models and comparing selected NPT versus NEA results. We also review the philosophic underpinnings of modeling in general, and NEA in particular, to examine logical extensions of particle tracking from its NEA foundations.

2. Network particle tracking and network environ analysis

For comparative purposes, we will investigate three different small ecosystem models using NEA and NPT. These are shown in Fig. 2a–c; two are mass-based and one energy-based. First, NPT will describe how particles are distributed within these systems and shared by their coupled compartments. To quantify this, we focus on particles stored in the compartments at a given time. As illustrated in Fig. 1, NPT provides the pathway history of each particle; therefore, it indicates how many compartments a particle has previously visited. Networks with cycles can generate very high repetitive visitations. NPT, as a Lagrangian approach, implies that each particle in a system represents a mass volume that retains its identity during its passage within the system. Referring to Fig. 1, when the mass arrives at a compartment it figuratively accepts a tag representing that event. We refer to the accumulated history of such events as the compartment's "passport". For each compartment a histogram of visitation locations is constructed from the history of all the particles in that compartment (Fig. 3a–c). For example, a value like $(x,y) = (12,71)$ in the red-circled zone on the histogram for the Detritus compartment in Fig. 3a indicates that 71 of the particles residing in Detritus at any given moment previously entered other compartments 12 times. This number 12 includes repeated compartments, including Detritus. One concern is that NPT is developed from a dynamic simulation; therefore the histograms shown in Fig. 3 will evolve over time. However, given enough simulation time, the dynamics converge to steady-state distributions, which are the focus of this paper.

Using EcoNet (Kazanci, 2007) and PTA-generated statistical histograms of particles' compartmental visits, we focus on the Finn cycling index (FCI) (Finn, 1976), indirect/direct effects (I/D) ratio

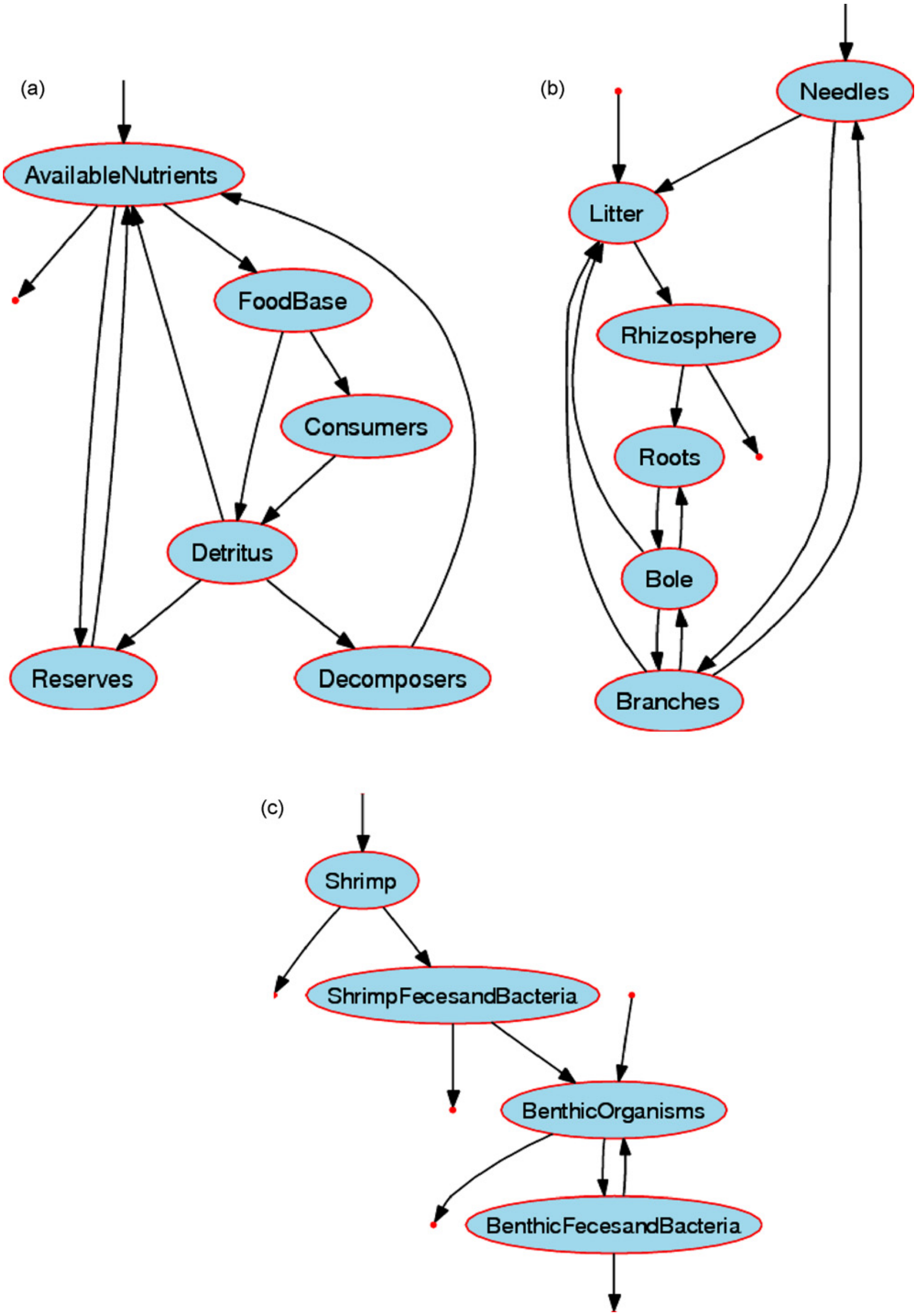


Fig. 2. (a) EcoNet generated compartment model of mineral flows in a generic temperate forest ecosystem (Webster et al., 1975). (b) EcoNet generated compartment model of flows in a nitrogen model, USA (McLeod and Running, 1988). (c) EcoNet generated compartment model of energy flows in Coprophagic web, Chesapeake Oyster community, VA, USA (Haven and Morales-Alamo, 1966).

(Higashi and Patten, 1989), and storage and throughflow analyses in our NEA and NPT comparisons of Fig. 2 models. Tables 1a–1c summarize selected NEA and NPT results for these models. FCIs range from 0.97 to 0.12, and I/D ratios, which directly correlate with degree of cycling, range from 211 to 0.61. Low cycling in the marine model (Table 1c) lessens the accumulation of particle statistics. Histograms of contact visits versus frequency generated by NPT for one compartment of the tropical forest system of Webster et al. (1975) are given in Fig. 3a. Of the several statistical distributions investigated with each model—compartment combination, the cumulative exponential distribution best describes the number of compartments visited by a typical particle, particularly where the number of visits is low. The lognormal distribution provided the best to the high compartmental visit frequencies in several cases. With the models and compartments investigated in this study, these observations are consistent for the near steady-state condition.

Table 1 shows NEA storage and throughflow data for each of the three models. The mean number of compartmental visits is the average number of compartments visited by particles in each compartment since their entry into the model. The particle content numbers represent the number of particles in the

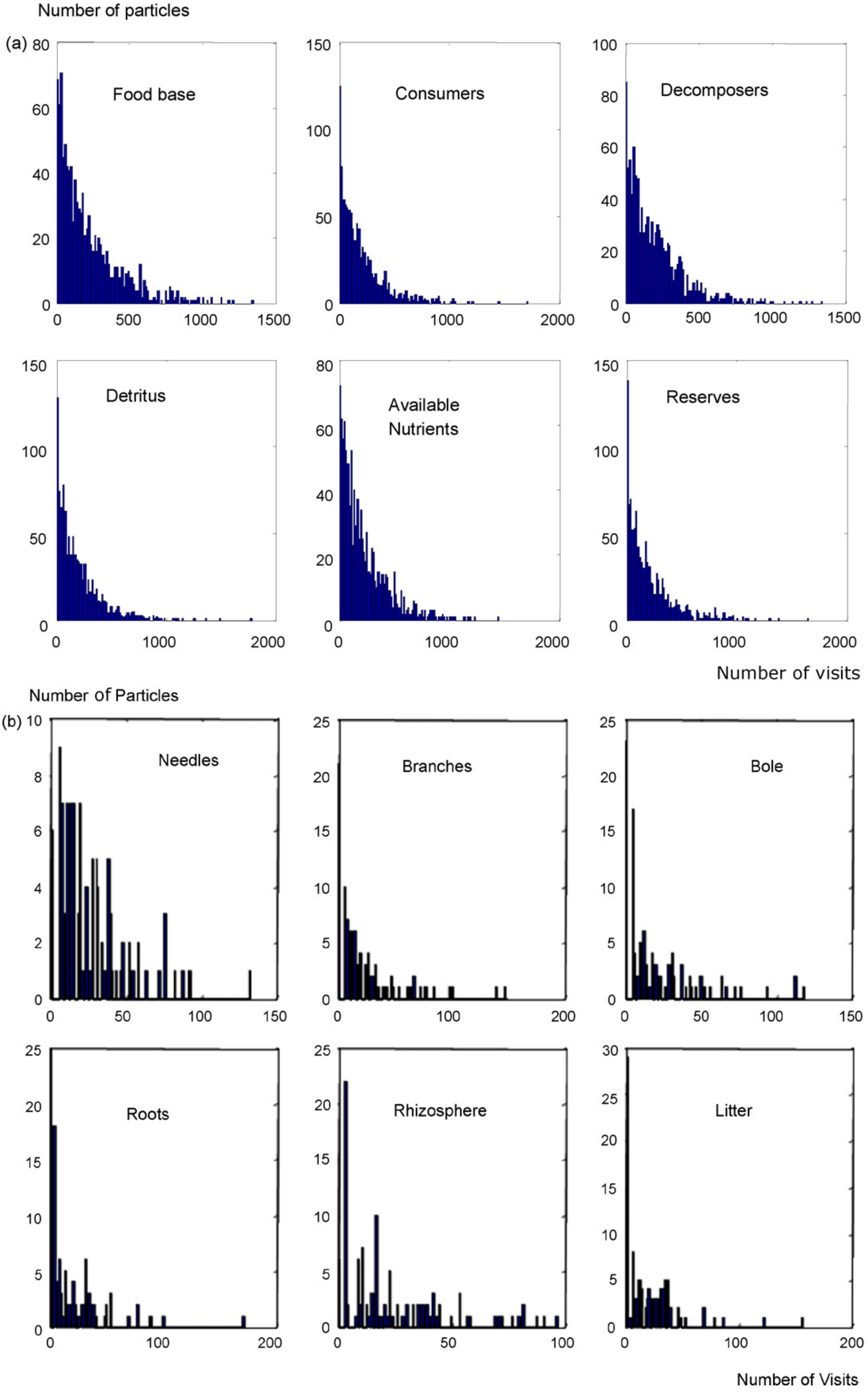


Fig. 3. (a) Histograms of particle visits at steady-state by compartments in Webster et al. (1975) tropical forest mineral model. (b) Histograms of particle visits at steady state by compartments in McLeod and Running (1988) forest model. (c) Histograms of particle visits at steady state by compartments in Haven and Morales-Alamo (1966) Marine model.

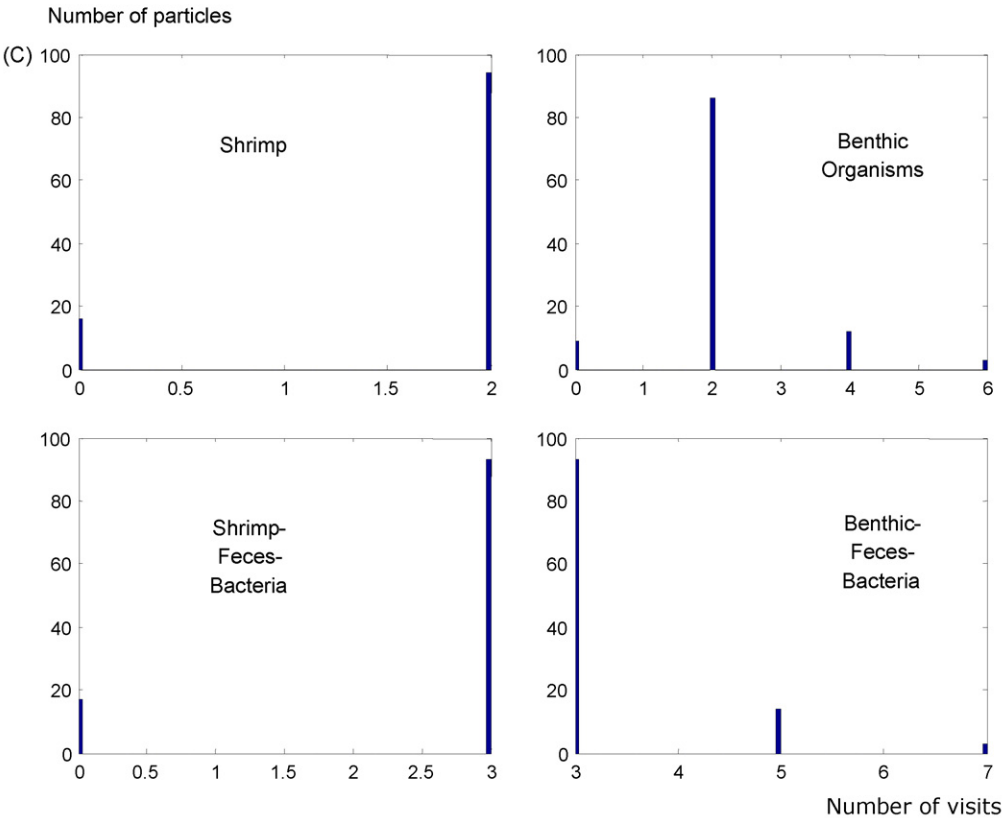


Fig. 3. (*Continued*).

Table 1a
NEA compartment storage (kg/Ha), throughflow (kg/(Ha year)), and NPT mean, and mean particle numbers for Webster et al. (1975) tropical forest model of mineral nitrogen flow. Finn cycling index = 0.97. Indirect to direct effects ratio = 211.

Compartment	NPT mean compartmental visits and (content number)	NEA storage	NEA throughflow
Food base	220 (21)	6.01	307
Consumers	199 (45)	6.30	31.1
Decomposers	205 (30)	6.24	303
Detritus	200 (10)	6.31	309
Available nutrients	224 (20)	6.00	318
Reserves	203 (40)	6.91	7.60

compartment at any given time. Total storage and throughflow were computed as column sums of the NEA storage and throughflow matrices, respectively. For all three models, NEA storage (Figs. 4a and 5a) and throughflow (Figs. 4b and 5b), as assessed from these matrices, were plotted versus the mean number of compartmental visits. Fig. 1a model (with highest FCI, 0.97, and *I*/*D*, 211) shows considerable variation in particle contents and mean compartment visits versus both NEA storage (Figs. 4a and 5a) and throughflow (Figs. 4b and 5b) values, whereas other models were more homogenous across compartments. As FCI and *I*/*D* increase, the correlation between NEA statistics and NPT outputs tends to diverge.

3. NPT and NEA orientors

Patten (1998) articulated 20 organizational properties considered relevant to a cosmography of all ecosystems. The microscale resolution afforded by NPT can reinforce, or perhaps falsify, the orig-

Table 1b
NEA compartment storage (kg N/Ha), throughflow (kg N/(Ha year)), and NPT mean, and mean particle content numbers for McLeod and Running (1988) forest model. Finn cycling index = 0.79. Indirect to direct effects ratio = 25.7.

Compartment	Particle tracking mean compartmental visits and (content number)	NEA storage	NEA throughflow
Needles	27.8 (4)	0.376	25.68
Branches	24.01 (3)	0.372	32.9
Bole	20.87 (2)	0.354	31.9
Roots	20.1 (3)	0.339	23.8
Rhizosphere	24.38 (2)	0.315	23.0
Litter	22.44 (3)	0.302	22.1

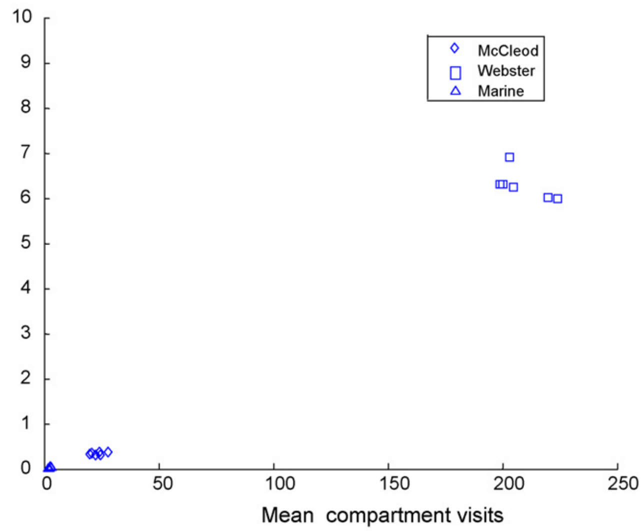
Table 1c
NEA compartment storage (kcal/M^2), throughflow (kcal/(M^2 year)), and NPT mean, and particle content numbers for Haven and Morales-Alamo (1966) model of energy flow. Finn cycling index = 0.12. Indirect to direct effects ratio = 0.61.

Compartment	Particle tracking mean compartmental visits and (content number)	NEA storage	NEA throughflow
Shrimp	18 (2)	0.0081	1
Benthics	40 (2)	0.009	2.96
Shrimp, feces, bacteria complex	40 (3)	0.05	1.17
Benthic, feces, bacteria complex	10 (3)	0.02	1.72

inal orientor statements based on macroscale NEA methods. We consider a number of Patten's properties.

3.1. Property 8—network homogenization

The significance of cycling in generating long food chains contrasts with the classical Lindeman (1942) acyclic paradigm in ecosystem ecology, which promotes short food chains. This is ironic because Lindeman's conceptual model was food cycles. The mathematics of cycles eluded implementation at the time, with the result


(a) NEA storage

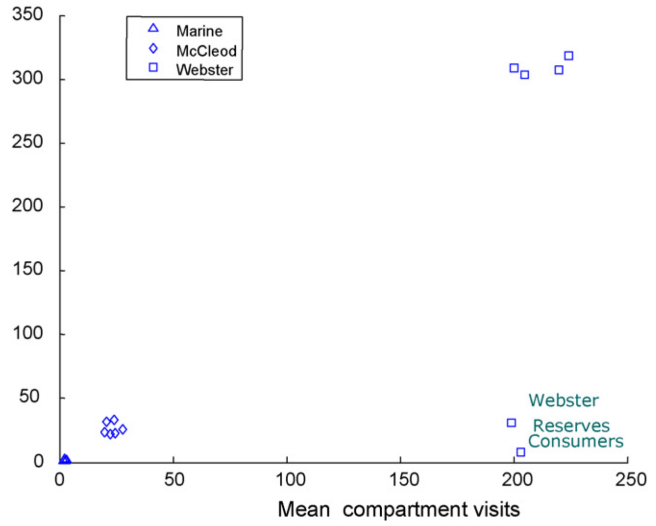
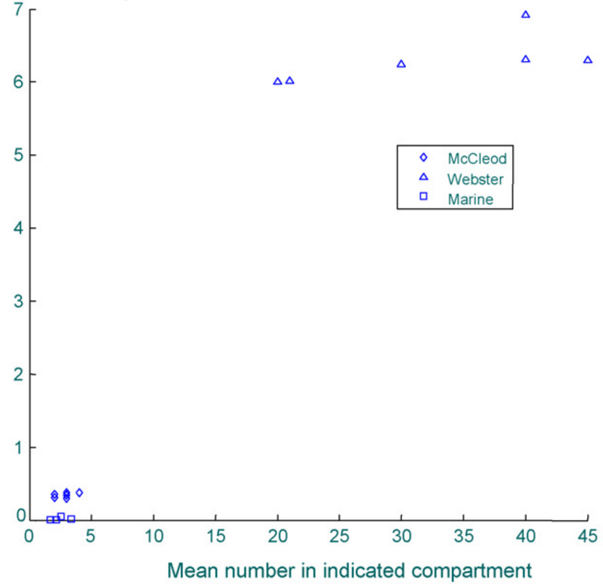

(b) NEA Throughflow

Fig. 4. (a) NEA storage per unit time versus mean particle compartment visits for each compartment in the indicated model. (b) NEA throughflow versus the mean particle compartmental visits in respective compartments for the indicated models.


(a) NEA Storage

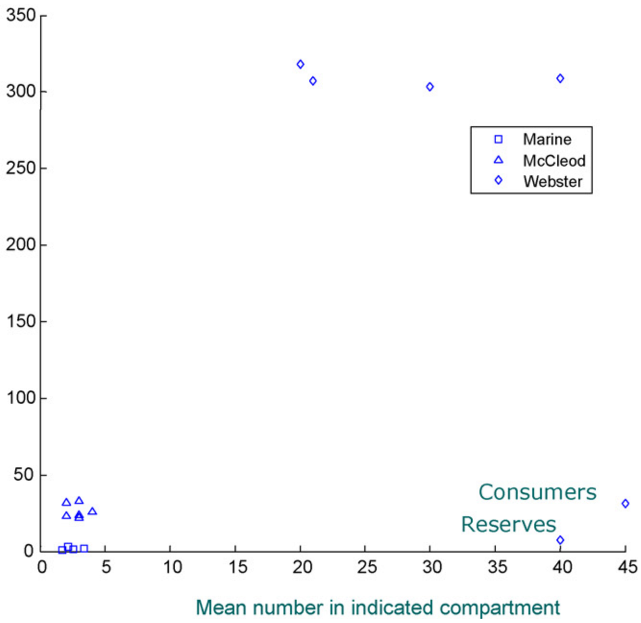

(b) NEA Throughflow

Fig. 5. (a) NEA storage versus mean particle compartment contents for respective compartments in the indicated models. (b) NEA throughflow versus mean repeat visits for each compartment in the indicated model.

that the food-chain concept ascended to paradigm status. Cycling tends to distribute heterogeneous incoming energy and matter uniformly over increasing numbers of indirect pathways. This leads to the notion that most compartments have nearly equal access to both energy and matter. This is *network homogenization*; the property is promulgated by both cycling and its correlate, dominant indirect effects. It suggests that ecosystem networks tend to equalize energy–matter flows between their constituents. NPT enables explicit visualization of network homogenization, as the particles in Fig. 1 tagged with a variety of complicated routes through the system illustrate.

As an example, in the low FCI and I/D marine model of Fig. 2c, energy may enter the system as carbonaceous materials digestible by shrimp, be excreted as shrimp feces to bacteria in the same compartment, then be consumed by benthic organisms, excreted to benthic feces and their bacteria, and cycle back (within the same compartment) to benthic organisms. Each energy particle is physically manifested as an organic substrate unique to each compartment. Thus, going back to primary producers not in the model, if a quantum of energy enters these as radiation, it may leave as a protein or carbohydrate, or as dissipated heat following the performance of work. The particular form of the outflow is mechanistically determined, but in NPT has a high stochastic component. NPT demonstrates that matter or energy distribution within the network becomes both more complex and more homogeneous as respective particles flow. NPT enables the investigator to track and more clearly visualize the development of this homogenization (per Figs. 1 and 3a–c). Cycling in the marine model is very low, so any homogenization would have to be due to the single cycle between benthis organisms and benthic feces and bacteria. Compartments not touched by the cycle would not experience network homogenization.

The situation is different in the highly cyclic forest model of Figs. 2a and 3a. In this system, nitrogen is fixed into the Available Nutrients compartment and then distributed as a variety of nitrogen forms to the food base compartment. The consumers utilize the available food base, transforming this into detritus. Material may also pass from the food base directly to detritus. NPT-defined particles bearing the physical nitrogen particles generally have different chemical compositions. The possibility of compositional complexity increases with cycling of the nitrogen particles within the system.

3.2. *Property 9—network amplification*

Ecosystems derive more than face value from their inputs (Patten, 1998). The fact that one unit of input can lead to more than one unit of throughflow (at steady state) is a frequent occurrence in network models. This is referred to as *network amplification*, and Patten's instinct about it derived from NEA is readily verified by NPT. The latter unambiguously demonstrates that one particle introduced into a system can reappear many times in the throughflow of a particular compartment. NPT, in other words, makes the visualization of network amplification explicit.

3.3. *Property 10—network aggradation*

Ecosystems, as growing biological systems, move away from thermodynamic equilibrium and thereby increase their distance from thermodynamic ground. NPT provides an approach for visualizing this increasing distance as ecosystem growth and development proceed. If one were to follow the prescription of Jorgensen and Ulanowicz (2008) and cast model currency in terms of "eco-exergy", the passport of each particle in a system could be incremented with the eco-exergy of the compartment just visited. The passport, in other words, would record the accumulation of distance from equilibrium—network aggradation. The same would hold as well for other less general currencies.

3.4. *Property 16—niche proliferation*

Ecosystems create and proliferate new niches indefinitely as a manifestation of their growth and development and resultant network aggradation. Long range increases in distance from thermodynamic ground are associated with evolving niche development and associated changes in network connectivity. Although NPT as currently implemented does not contain inherent mechanisms for niche proliferation, it could potentially be used to construct logic for switching connectivity as a function of pathway use, and this might imply ongoing niche development.

3.5. *Property 19—ecosystem coevolution*

Ecosystems can be considered units of co-evolution of their biotic and abiotic entities taken all together. NPT does not provide for inherent coevolution as it does not in its present form contain any representation of agency or life force. Ideas discussed in conjunction with properties 10 and 16 may, however, provide some basis for simulation of externally hypothesized directions of coevolution.

3.6. *Property 20—network virtualization*

Patten (1998) observed that ecosystems expand what he called the inner space of reality. Physical energy–matter flow and storage networks based on conservation of mass and energy give rise secondarily to relational networks in which the conservation principles are left behind. Patten (1991) demonstarted this is an NEA-based "utility" analysis. Thus, aphysical virtual networks can always be taken to arise in parallel with physical networks, and are probably the seat of many obscure phenomena (including the occult) in human experience. The encoding of covert properties in an NEA model might be visualized by a form of NPT. Particle tracking presently does not include any endowments of life forces or agency, or embody in itself particular goals, but it may provide modeling degrees of freedom to enable the "visualization" of networks and their finer-grained temporal and spatial behavior that are not really there and therefore not really visualizable in a physical sense (Small et al., in press). The intuition that ecosystems expand an inner, virtual space of reality as a concomitant of their physical growth and development will require some special methodologies to enable exposure of the relational phenomena that may be involved. PTA, in its ability to track and codify the movements of physical particles, may also offer some potential to track and codify relational quanta as well, as these arise from physical manifestations.

4. Implications of network particle tracking

Residence time of a particle in a compartment may be related to likelihood of that particle to trigger emergent behavior in a given compartment (e.g., connection to other compartments, failure of an existing connection, or change of behavior of the compartment). Compartments having concentrations of particles with high system resident times are thought most likely to exhibit emergent behavior in terms of new compartmental behavior and/or new network connections. From a statistical thermodynamics viewpoint, the exponential distribution, which appears to be the best fitting distribution with the three models evaluated, is also at the heart of the Maxwell speed distribution function (Zemansky and Dittman, 1997). This opens the possibility of numbers of resident particles being analogous to velocity of gas molecules. Thus, NPT with its underlying Gillespie algorithm has a stochastic flavor. Just as statistical thermodynamics of gas systems enables an assessment of the arrow of time, to a certain extent NPT may enable the modeling of ecological time.

A shortcoming of NPT and NEA is the current lack of an inherent way to simulate niche development. The ubiquitous Holling figure-eight model encompassing exploitation, conservation, creative destruction, and renewal (see Bass, 1998; Patten, 1981; Patten and Auble, 1981) is not inherent in current approaches to NPT or NEA. NPT approaches may enable modeling for systems susceptible to environmental impacts. Connection viability is likely a part of niche development and decay over time. NPT approaches could enable simulation of connection viability as a function of particles traveling over the connection, which could also provide a modeling foothold on modeling connection viability.

NPT analyses performed thus far have implicitly assumed that compartmental contacts in models have equal effects. However, modeling schemes could weight particle contacts, for example, with compartmental eco-exergy (Jorgensen and Ulanowicz, 2008) or other weighting attributes such as emergy. Weighting the quality of external energy or mass may be the basis of a strategy to transfer environmental information into the system. Much remains to be explored with respect to weighting factors and how they might be used to model compartmental connectivity changes, choice of pathways a given particle travels and types of attributes assigned to specific particles.

While exploring conditional probabilities attributed to Popper, Ulanowicz (1998) advanced the notion of conditional probabilities not simply to cover the ignorance of the observer but also to pertain to a degree of indeterminacy inherent in the situation being modeled. Although this propensity is a generalized force, Ulanowicz further drew from Popper the notion that propensities, unlike forces, cannot exist divorced from their surroundings. Context is essential, and circularity can be built into the conditional probabilities. Since NPT is stochastic by nature, the "memory" that may be acquired by particular particles is based on chance, yet trends become apparent when viewing large numbers of particles, which in turn may provide additional insights into Popper's conditional calculus. Ulanowicz, through the notions of propensity, autocatalysis, conditional probability, and statistical thermodynamics arrived at "ascendancy" to articulate his view of ecosystem emergence. Ascendency of an ecosystem is defined as the flow-averaged system level propensity for activity, and represents a measure of distance from thermodynamic ground. Ulanowicz (2000) presents computational details for his *ascendency analysis* wherein future intersection with NPT appear promising.

Ulanowicz (1998) summarized three disparate metaphors that have dominated discourse on ecosystem dynamics: (1) the Newtonian machine, (2) the organism and (3) stochastic or chance assembly. The observed propensity for ascendency was stated to become, over time, the probabilistic counterpart for living systems to Newton's second law in mechanics. A Venn diagram illustrating a proposed relationship between the three metaphors is shown in Fig. 6. This figure shows how intersections of two of the three metaphorical descriptions highlight contemporary trends in biological research, with the intersection zone of all three metaphorical descriptions being illusive. NPT has Newtonian overtones, tries to maintain an organic holism and is stochastic in nature. Each of the three areas representing intersections of two primary areas in Fig. 6 is reaching developmental maturity. Ecosystem succession and evolutionary modeling are increasingly being thought of together in systems ecology. The same can be said of the other areas. NPT may enable insights leading to penetration of the intersection of all three metaphors in Fig. 6. Again, it is understood that the NPT approach does not account for the agency or life force that distinguishes living organisms from other materials.

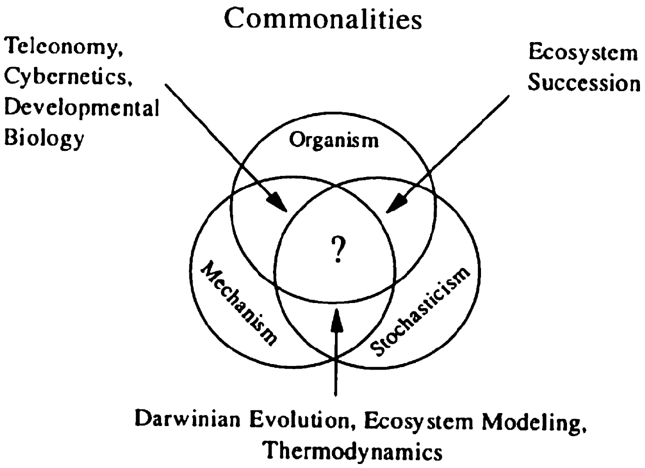


Fig. 6. Venn diagram showing ecological system modeling metaphors (Ulanowicz, 1998).

In general, there are many kinds of mathematical analyses originally developed and used for engineering purposes that are now available for application to the growing set of complex systems problems represented by human interactions with environment. Potential benefits from such knowledge may extend to risk assessment applications, or to knowing where collections of specific compounds may most likely concentrate to cause new network connections or emergence of new states. For example, NPT may enable following a contaminant particle through a system wherein it could be tagged with accumulative information based on compartmental visits and residence times. A critical value of these indices could trigger an adverse or beneficial symptom leading to a system change. The original goal of using NPT for further developing thermodynamic concepts of eco-exergy (Jorgensen and Svirezhev, 2004) and analogues to conventional measures of temperature, pressure and energy measures continues to be pursued.

Ecological modeling has developed from what philosophers of science label 'soft realism', which is characterized as a limited, metaphoric and approximate view of reality (Ratzsch, 1986). NEA and NPT appreciate that just as electrical, magnetic and gravitational fields function in accordance with the laws of their respective natures, biological systems possess fields that include degrees of autonomy. This has been labeled 'emergentism' (Hasker, 1983) in recognition of the emergence of fields, or if focused, environs, associated with compartments within modeled biological systems. NPT takes an atomistic approach to ecosystem function, just as process philosophy characterizes human existence as an atomistic movement of discrete events from future 'pretension', present to past (Whitehead, 1933). Particularly as scales become smaller and we attempt to comprehend developments in quantum physics, an anti-realist thread begins to appear in which a phenomena takes on a type of reality only when described linguistically or mathematically with appropriate instrumental means. NPT will not in itself convert 'soft reality' into a more firm reality. Likewise, NPT will probably not shed much light on how emergent fields appear and relate to their modeled compartment.

5. Summary and salient implications

NEA is a continuous, steady-state, input–output analysis based on conserved currency (energy, mass) movement through compartments (described by states), each with input and output environs defining closed fields of influence. NPT discretizes the transported currency in the NEA model into particles or quanta that may acquire various designated histories as they move through the system prior to dissipation or exit. NPT offers avenues and suggests strategies for modeling dynamic and structural changes. NPT does not confer any agency or life force in itself and does not suggest at this time any inherent structural change relations. Following are several of the salient implications we see for NPT at the present time:

- NPT outputs related to contact history of particles in compartments seem to parallel NEA storage and throughflow analyses for systems with low indirect effects and cycling. At higher indirect effects and cycling, the correlation breaks down, perhaps due to increased diversity in compartmental types and turnover times in more complex systems.
- Particle movement represents a type of internal time, enabling future thermodynamic analyses. NPT creates an inherent system memory and thus history development. Work to date has assumed uniform effects of all compartments and uniform external input effects. There is no reason to assume that all compartments should be equally weighted in terms of particle interactions. Weighting factors related to exergy or emergy may be useful. As a means of communication with the environment, particles also may bring history into the system from the environment.
- NEA analysis and current implementations of NPT do not allow for structural changes; however, NPT offers avenues for modeling structural change based on a “demand function” potentially defined using the attributes of particles passing through the system.
- NPT, inherently Newtonian and stochastic, attempts to take an organismal view. NPT may be a step toward the development of an integrated modeling paradigm based on the historically used Newtonian, organismal and stochastic paradigms in ecosystem modeling.

In conclusion, NPT may help probe the intricacies of ecosystem organization by providing a platform for elucidating aspects of Popperian calculus, and implementing the mechanical, organismal and stochastic metaphors that have served as the backdrop to modeling ecosystems.

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