Link tracking: Quantifying network flows from qualitative node–link digraphs

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ABSTRACT

This paper gives a possible explanation for how changes in holistic network organization can come to be reflected in changes in mechanistic processes thought to be under local control by organisms and abiota. Most point-contact, or node($\bullet$)-link ($-,\rightarrow$), networks in science are qualitative. Their complexity is great and quantification is difficult. Networks depict wholeness and are models for holism. Mathematically, they are graphs, unweighted when unquantified, and either undirected ($\bullet-\bullet$; most social networks) or directed ($\bullet\rightarrow\bullet$; most ecological food webs). Directed graphs are digraphs. The question of this paper is, can unweighted digraphs be used to quantify mass–energy link flows? A methodology, *link tracking*, is developed to achieve this. Simple paths (no repeated nodes) and cycles in the network are identified. Links for different node pairs are tallied along these pathways, and used to calculate transition probabilities. These are extended to all pathways (direct + indirect) by matrix inversion; the resultant coefficients are used in conjunction with boundary inputs to generate flows. Applied to an ecological stock-and-flow model, empirical measurements lay within ± 2 times the corresponding link tracking values. This reinforces the intuition that digraph structure and flow function are intimately related, which is the principal general finding of the paper. However, only one "structure-based" parameterization is calculable per digraph by link tracking, whereas many "functional" empirical flows are possible. The meaning of the link tracking values is therefore to be resolved. In discussion, it is hypothesized that link tracking structural flows are basins of attraction – centrally tending mean flows around which realizable empirical flows are constrained by structure to be distributed. The methodology sheds light on previously unexplained results from an early radiotracer study of experimental ecological networks. Uses of link tracking to expand existing knowledge of food webs and other kinds of qualitative networks are considered.

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1. Introduction

1.1. Background

In controlled laboratory radiotracer experiments with terrestrial microcosms conducted to determine patterns and rates of ^{134}Cs transfers between compartments, Patten and Witkamp (1967) showed that flow rates varied with different compartment combinations. The compartments were leaf litter, soil, microflora, millipedes, and aqueous leachate in different amounts and combinations. Microecosystems of increasing complexity were synthesized by adding one compartment at a time, and under constant experimental conditions the radioactivity in each was assayed periodically over time. It was found that the radiocesium

transfer kinetics (turnover rates, concentration factors, total-system flux, and other properties), determined by fitting analog computer models to the data, changed with the pattern of network interconnection. The processes involved were physiological – uptake, ingestion, assimilation, excretion, and decomposition – all thought to be under local mechanistic control by organisms, not holistic influences transmitted by network organization. The authors concluded (p. 824):

> These results focus attention on the exceeding importance in natural complex ecosystems of the organizational networks which define compartment interactions. . . . The multiplicity of material transfers and interactions conceivable in macro-ecosystems, together with the effects of intrasystem coupling as revealed in this investigation, make it apparent that to understand ecosystems ultimately will be to understand networks.

These words were written at the beginning of what for me became a career-long quest to understand "the network variable in

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ecology." Change the network, change the system, including its putatively local mechanistic processes; it made no sense under reductionism. Witkamp and I had no explanation for the results we got, but for me they were seminal and remained a subconscious driver of all my subsequent research directions. This paper contains the first hint of a possible explanation for what we found at Oak Ridge.

2. Systems: parts and wholes

In ecology, now a century and a half old, a fundamental whole/part schism persists in the form of "Gleasonian" (individualistic) vs. "Clementsian" (holistic) perspectives on how nature works. Physics and engineering have long integrated this same scale-crossing dualism in a wide variety of quantitative methodologies, categorized as Lagrangian (in the small) and Eulerian (in the large). Ecology's resistance to such integration has left it with a scattershot body of theory derived not from first principles, but from a reductive empiricism that continues describing minutiae it cannot put into a unified, coherent scientific framework. It is widely understood that ecological problems of the day are systemic; they involve wholes not parts – overpopulation, overexploitation, extinction and biodiversity loss, global change, sustainable development, ecosystem management, etc. There is little progress to be made on these kinds of problems by focusing on the small. But the field persists in doing so with its established reductive empiricism rather than embracing the holism the problems imply, requiring attention by whole-systems approaches.

The stubbornness of the reductive method in the face of a widespread need for its opposite is, quite frankly, puzzling. It is as if an archaic enterprise just clings to what it knows because it is untutored in what is required. The mismatch between old and new, the progressive dressing of old-paradigm thinking in new garb and jargon, does not make a new or ample science. The resistance must find its source in the empirical intractability of wholes since the majority of ecology embraces either theory-free empiricism (Peters, 1991), or grudgingly, empirically-based naive theory with special, and many venerable (and colorful), names like "founder effects" (for initial conditions), "succession" (transient dynamics), "climax" (steady-state dynamics), "resistance" (bounded input/output stability), "resilience" (Liapunov stability), "disturbance" (trajectory deflection), "keystone species" (high-degree nodes in networks), "regimes" (basins of attraction), "tipping points" (singularities), "regime shift" (attractor change, catastrophe), and "creative destruction" (senescent dynamics). These and other empirically-generated, concepts appear to lay claim to primary discovery when in fact the phenomena they mainly represent are already old, well-established, and previously brought to the point of formalization in other disciplines.

Systems science teaches that whole-part determination is mutual, that interior states and exterior environments combine always to drive open systems (which all systems of ecology are) into determinate future dynamics. No nature–nurture, or other similarly uncertain dichotomies here; system theory asserts from first principles that both the insides and outsides of systems are implicated, in different weighted combinations, in moving from here to there.

3. Purpose

Parts determine wholes, and wholes determine parts; this is elementary, and unequivocal. The latter – holistic determination – is the background investigation in this paper. The foreground, which it is the purpose of this paper to pursue, concerns the measurement from wholes of interchange between parts. Specifically, this paper focuses on the quantification of substance (energy and matter) flows (digraph links) from purely qualitative, unweighted digraphs.

4. Methods

4.1. Example system: a compartment model

Fig. 1a shows a directed graph (digraph) depiction of an ecological food web – a simple one, but sufficient for present purposes. It is self evident that the quantitative compartment model on the right (Fig. 1b) is sufficient ($\leftarrow$s) to determine the qualitative digraph on the left, which is necessary (n$\rightarrow$) for the system on the right. And it seems also equally certain that the unweighted digraph (Fig. 1a) contains insufficient information to determine the quantified model (Fig. 1b). Being counterintuitive is
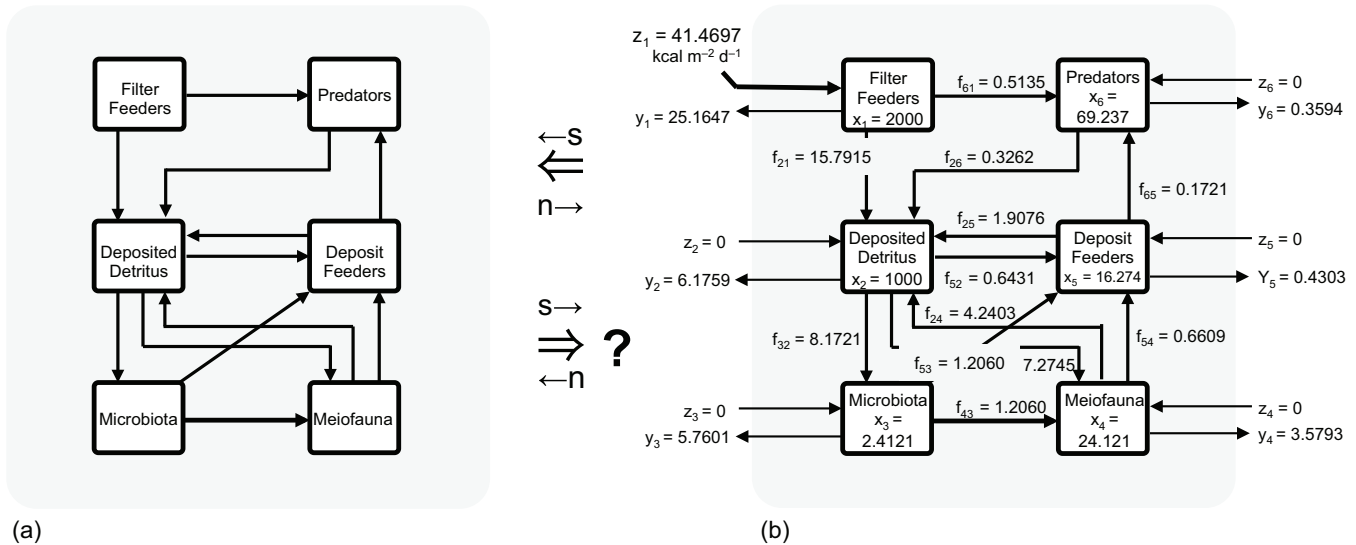
Fig. 1. (a) Qualitative node–link digraph corresponding to the compartment model of energy stocks and flows in the intertidal oyster-reef ecosystem shown in (b) (Dame and Patten, 1981). The hypothesis of this paper ("?") is that the food web network on the left (a) contains both sufficient (s$\rightarrow$) and necessary (n$\rightarrow$) system-wide (holistic) stock-and-flow information to constrain, limit, serve as an attractor for, or otherwise determine the set of possible local (mechanistic) parameterizations, of which the empirical system (b) is one example.