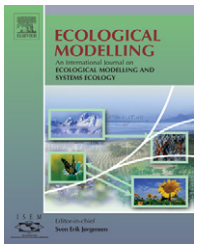
ECOLOGICAL MODELLING 208 (2007) 49–55

available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/ecolmodel



Ecological network analysis: network construction

Brian D. Fath[a,*], *Ursula M. Scharler*[b,c], *Robert E. Ulanowicz*[d], *Bruce Hannon*[e]

[a] *Biology Department, Towson University, Towson, MD 21252, USA*
[b] *School of Biological and Conservation Sciences, University of KwaZulu-Natal, Howard College Campus, George Campbell Building, 4041 Durban, South Africa*
[c] *Department of Aquatic Ecology and Water Quality Management (AEW), Wageningen University and Research Centre, Ritzema Bosweg 32-A, 6703 AZ Wageningen, The Netherlands*
[d] *Chesapeake Biological Laboratory, University of Maryland, Solomons, MD 20688, USA*
[e] *Department of Geography, University of Illinois, Urbana, IL 61801, USA*

ARTICLE INFO

Article history:
Accepted 27 April 2007
Published on line 18 June 2007

Keywords:
Ascendency
Ecological network analysis
Food webs
Systems analysis

ABSTRACT

Ecological network analysis (ENA) is a systems-oriented methodology to analyze within system interactions used to identify holistic properties that are otherwise not evident from the direct observations. Like any analysis technique, the accuracy of the results is as good as the data available, but the additional challenge is that the data need to characterize an entire ecosystem's flows and storages. Thus, data requirements are substantial. As a result, there have, in fact, not been a significant number of network models constructed and development of the network analysis methodology has progressed largely within the purview of a few established models. In this paper, we outline the steps for one approach to construct network models. Lastly, we also provide a brief overview of the algorithmic methods used to construct food web typologies when empirical data are not available. It is our aim that such an effort aids other researchers to consider the construction of such models as well as encourages further refinement of this procedure.

1. Introduction

Ecological network analysis (ENA) is a methodology to holistically analyze environmental interactions (see e.g., Hannon, 1973, 1985a,b, 1986, 1991, 2001; Hannon et al., 1986, 1991; Hannon and Joiris, 1989; Finn, 1976; Patten, 1978, 1981, 1982, 1985; Higashi and Patten, 1989; Fath and Patten, 1999; Ulanowicz, 1980, 1983, 1986, 1997, 2004; Ulanowicz and Kemp, 1979). As such, it is necessary that the network model be a partition of the environment being studied, i.e., be mutually exclusive and exhaustive. The latter criterion in particular is difficult to realize and most models such as Lotka–Volterra predator–prey or competition models represent only a small subset of the interactions occurring in the ecosystem, excluding both the majority of other species in the community and all abiotic processes. As a result of this limited perspective, it is impossible for such approaches to quantify the wholeness and consequent indirectness in the system, but this has been the trend of reductionist science for over a century. The reductionistic approach results in a self-fulfilling realization in that only the few species or processes in the model have influence and significance in the final interpretation, without considering the embedded nature of these activities within the larger ecological context. Ecosystems comprise a rich web of many interactions and it would be remiss to exclude, *a priori*, most of them or to rely on analysis techniques that do so. ENA, on the other hand, is capable of analyzing the structural and functional properties of this web of interactions without reducing the model to its presumed minimal constituents. Therefore, network models aim to include all ecological com-

* *Corresponding author*. Tel.: +1 410 704 2535; fax: +1 410 704 2405.
E-mail address: bfath@towson.edu (B.D. Fath).
0304-3800/$ – see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.ecolmodel.2007.04.029

partments and interactions and the analysis determines the overall relationships and significance of each. The difficulty of course lies in obtaining the data necessary to quantify all the ecological compartments and interactions. When sufficient data sets are not available, simple algorithms, called community assembly rules, have been employed to construct realistic food webs to test various food web theories. Once the network is constructed, via data or algorithms, the ENA is quite straightforward and software is available to assist in this (Allesina and Bondavalli, 2004; Fath and Borrett, 2006). This paper outlines a possible scenario for developing network models.

2. Data requirements and acquisition for developing network models

A network flow model is essentially an ecological food web (energy–matter flow of who eats whom), which also includes non-feeding pathways such as dissipative export out of the system and pathways to detritus. The first step is to identify the system of interest and place a boundary (real or conceptual) around it. Energy–matter transfers within the system boundary comprise the network; transfers crossing the boundary are either input or output to the network, and all transactions starting and ending outside the boundary without crossing it are external to the system and are not considered. Once the system boundary has been established, it is necessary to compartmentalize the system into the major groupings. The most aggregated model would have three compartments: producers, decomposers/detritus, and consumers; a slightly more disaggregated model could have producers, herbivores, carnivores, omnivores, decomposers, and detritivores (Fath, 2004); and the most disaggregated a different compartment for each species. Most models use some aggregation based on the functional groups of the ecosystem such that network models in the literature typically have between 6 and 60 compartments. However, this does not completely resolve the aggregation issue. It is likely that one is interested in greater detail for one group, but it is not entirely clear how disaggregation of one functional group and not others affects the analysis results. Identifying the major species or functional groups should be done by those knowledgeable about the system.

Once the compartments have been chosen, an energy–matter flow currency must be selected. Typically, the currency is biomass (e.g., grams of carbon) or energy (e.g., kilojoules) per area for terrestrial and aquatic ecosystems or volume for aquatic ecosystems per time. The flow dimensions then would be $ML^{-2}T^{-1}$ or $ML^{-3}T^{-1}$ where M = mass, L = length, and T = time. There is flexibility however in the biomass units chosen, which could also be grams of nitrogen, phosphorus, other nutrients, or even water per space dimension per time. Multiple currency network models using a combination of C, N, or P, etc. can also be constructed (Ulanowicz and Baird, 1999). In addition to the input, output, and within systems flow transfer values, it is also necessary to measure empirically as best as possible the mass density (biomass/area) of each compartment. Storage dimensions are ML^{-2} or ML^{-3}, since they are not rates. Together the transfers and storages comprise the data requirements for ecological network analysis.

Once the currency has been chosen, we would arrange them in the columns and rows of an adjacency matrix to determine whether or not a resource flow of that currency occurs from each compartment to each other one. An adjacency matrix, **A**, is a representation of the graph structure such that $a_{ij} = 1$ if there is a flow from j to i, else $a_{ij} = 0$, using a column to rows orientation (note that although we use a column to row orientation here, a row to column orientation is also used in the literature). This procedure forces one to ascertain the possible connectivity of each pair of compartments in the network, thus reducing the chances of over-looking certain connections. This exercise might also illuminate compartments that were excluded initially, thereby providing an iterative feedback in the network development.

The data required for ecological network analysis are as follows: For each compartment in the network, the biomass and physiological parameters, such as consumption (C), production (P), respiration (R) and egestion (E) must be quantified. It is possible to lump respiration and egestion into one outflow if necessary. Furthermore, the diet of each compartment must be apportioned amongst the inputs from other compartments (consumption) in the network. This apportionment of "who eats whom and by how much" can be depicted in a dietary matrix, where material flows from compartment j to compartment i. For all compartments, inputs should balance outputs ($C = P + R + E$), in accordance with the conservation of matter and the laws of thermodynamics.

To quantify the network, flows of the chosen currency into and out of each compartment should be determined. Some of the flows could also be empirically gathered from primary field research regarding primary production, respiration, and feeding, but others could be assembled from various sources such as literature sources and simulation model results. Furthermore, two recently developed methods of assigning a flow value between compartments can be employed to estimate transfers (Ulanowicz and Scharler, in preparation). The first method, MATBLD, assigns the transfers according to the joint proportion of predator demand and prey availability. The second method, MATLOD, begins with assigning a very small flow to all designated links and keeps on doing so until either the demand is met or the source exhausted. The input data for both methods are the biomasses, consumption, production, respiration, egestion, imports and exports of all compartments, and the topology of the networks (i.e., who eats whom). The networks originating from both methods are balanced using the algorithm developed by Allesina and Bondavalli (2003). A comparison of the two methods to networks constructed "by hand" revealed no statistical difference between the magnitudes of the compartmental transfers.

In most cases, field data, literature sources, or results from simulation models do not supply all the system-specific data necessary for the network construction. In those cases, it is recommended to perform a sensitivity analysis to assess a variation of the most inaccurate input data on network analysis results.

Table 1 provides a step-by-step procedure for constructing ecological networks.