enaR: An R package for Ecological Network Analysis

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Abstract

1 Introduction

Network Ecology – the study of ecological systems using network models and analysis to characterize their structure, function, and evolution – is a large and rapidly growing area of ecology. Borrett et al. (submitted) found that more than 5% of the ecology and evolutionary biology papers published in 2012 and indexed by Web of Science could be classified as Network Ecology. Likewise, Ings et al. (2009) showed that a sizable fraction of 2008 publications in 11 select journals were related to food webs (≈2.4%), mututalitsic networks (≈0.9%), and host-parasitoid networks (≈0.055%). Network ecology is growing in part because network models are are inherently a relational model, which is useful for disciplines like ecology that are fundamentally relational. In addition, this rise of network ecology contributes to, mirrors, and builds on the more general development of network sciences (Barabási, 2002; Barabási, 2012; Borgatti and Foster, 2003; Freeman, 2004; Newman, 2003; Wasserman and Faust, 1994)

Ecological Network Analysis (ENA) is a branch of network ecology that is rooted in ecosystem ecology (Borrett et al., 2012). It works like a "macroscope" to investigate (1) whole system organization, (2) the direct and indirect effects among system components, and (3) the processes that create and sustain ecological systems. More specifically, ENA is a family of algorithms that are an ecological application and extension of Leontief's (1966) economic Input-Output Analysis. These algorithms are applied to network models of energy and matter exchange among ecosystem components (Fath and Patten, 1999; Patten et al., 1976; Ulanowicz, 1986).

The development of ENA has contributed to a new theoretical understanding of ecosystems (Belgrano et al., 2005; Higashi and Burns, 1991; Jørgensen et al., 2007; Ulanowicz, 1986) and the techniques have been applied in a multiple ways. For example, Patten (1982) used a storage analysis to identify two nearly separate hydrologic subsystems in the Okefenokee Swamp, USA. Bondavalli and Ulanowicz (1999) showed that in the Florida Everglades the American alligator is an indirect mutualist with several of its prey items, including frogs. Hines et al. (2012) used ENA to study the Cape Fear River estuary sediment nitrogen cycle, and applied the tools to quantify the coupling between biogeochemical processes (e.g., nitrification + anammox). Subsequent work showed the potential impact of sea water intrusion on the N cycle (Hines et al., in press). Furthermore, several scientists have used ENA to investigate urban sustainability (Bodini and Bondavalli, 2002; Bodini et al., 2012; Chen and Chen, 2012; Zhang et al., 2010). Collectively, this work consistently shows the power of the interaction network to transform relationships among system components in non-obvious ways that require whole-systems analysis to elucidate (Fath et al., 2007; Patten, 1991; Ulanowicz and Puccia, 1990).

While many influences combined to create what we now call ENA (e.g., Golley, 1993; Hannon, 1973; Margalef, 1963; Patten, 1959; Pimm, 1982), since the 1970s two primary schools of thought have developed (Scharler and Fath, 2009). The first is based on the work of Dr. Robert E. Ulanowicz, which was centered at the University of Maryland (Ulanowicz, 1986, 1997, 2009). The Ulanowicz school of ENA is primarily focused on trophic ecology, and its starting point is a phenomenological map of the energy–matter exchanges among ecosystem components. A key contribution of this work is the use of information theory and the development of the ascendecy concept that Ulanowicz (1986, 1997) used to characterize ecosystem growth and development. The second school is based on the work of Dr. Bernard C. Patten at the University of Georgia (Fath and Patten, 1999; Matis and Patten, 1981; Patten, 1982; Patten et al., 1976). Its initial perspective was steeped in dynamic equations, simulations, and systems analysis, with a distinct network flavor. A key contribution of this work is the environ concept that formalizes the concept of environment for study inside the network models (Patten, 1978). The Patten School of work has often been referred to as "Network Environ Analysis". The Ulanowicz and Patten School's of ENA represent two distinct but interwoven developments. Together, they join information theory, environmental concepts, and network science to study ecosystems.

Several software tools have been created to enable scientists to more easily apply ENA. The first widely distributed tool was NETWRK (Ulanowicz and Kay, 1991). This program is a collection of analyses from the Ulanowicz School that is programmed in Fortran and distributed as a DOS executable file. Version 4.2 is available from (http://www.cbl.umces.edu/ ulan/ntwk/network.html). WAND is a Microsoft Excel based re-implementation of many but not all of the algorithms in NETWRK (Allesina and Bondavalli, 2004). An explicit goal of WAND was to be more accessible for ecologists, who have tended to be more familiar with Excel than DOS. Fath and Borrett (2006) introduced a Matlab function, NEA.m, that assembled the primary algorithms from the Patten School. One advantage of NEA.m is that the algorithms are transparent to the user and available for modification. While the NEA.m function is freely available (http://www.mathworks.com/matlabcentral/fileexchange/526 nea-m) it requires Matlab, which is a powerful but expensive program. With modification, the function can be run in Octave, an open source clone of Matlab, but it executes more slowly. EcoNet is a web-based tool that lets users apply ENA primarily from the Patten School, but with some computational enhancements (Kazanci, 2007; Schramski et al., 2011). Ecopath with Ecosim (Christensen and Pauly, 1992; Christensen and Walters, 2004) is used primarily for model construction and simulation, but it also includes a network analysis plug-in that implements several ENA algorithms mostly from the Ulanowicz School. Other tools have been created, but do not appear to have a large user base (Kones et al., 2009; Latham II, 2006). A challenge for ENA users has been that no existing software covers both schools of analysis, and the tools vary widely in their availability, usability, and extensibility.

To address the limitations of the existing tools, we created `enaR`, which is a professional grade set of R tools for Ecological Network Analysis. Here, we introduce version 2.0 of this package. For this software, we had three specific design objectives. The first objective was to collect the algorithms from both the Ulanowicz and Patten schools of ENA to enable users to implement both approaches. The second objective was to increase both the availability and extensibility of the software. Users can freely download the code from the CRAN website, access the original code, make modifications, and add new functionality as techniques develop. The third design objective was to let users connect to other existing network science tools. To enable this, `enaR` was built on top of two existing R packages: `network` (Butts, 2008a) and `sna` (Butts, 2008b). In summary, the `enaR` package should make the ENA tools more available and easier to use and adapt by ecologists.

2 Overview of `enaR`

ENA is applied to network models of energy or matter flow and storage in an ecosystem. After describing the data required as input to ENA, we highlight the primary ENA algorithms currently included in `enaR` and illustrate an application of the Flow analysis to an example model.

2.1 Data Requirements and Input

For ENA, the system is modeled as a set of n compartments or nodes that represent species, species-complexes (i.e., trophic guilds or functional groups), or non-living components of the system in which energy or matter is stored. These nodes are connected by L observed fluxes, termed directed edges or links. The estimates of the internal system energy–matter flow from i to j are notated as $\mathbf{F}_{n\times n} = [f_{ij}]$, $i, j = 1, 2, \ldots, n$. These models also have energy–matter inputs into the system $\mathbf{z}_{1\times n} = [z_i]$, and output losses from the system $\mathbf{y}_{1\times n} = [y_i]$. While the Patten School treats all outputs the same, the Ulanowicz School partitions outputs into respiration $\mathbf{r}_{1\times n} = [r_i]$ and export $\mathbf{e}_{1\times n} = [e_i]$ to account for differences in energetic quality. Note that $y_i = r_i + e_i$ for all i. Some analyses also need the amount of energy–matter stored in each node (e.g., biomass), $\mathbf{X}_{1\times n} = [x_i]$. The final required information is a categorization of each node as living or not, which is essential for algorithms from the Ulanowicz School. We specified this node attribute by creating a logical vector $\mathbf{Living}_{1\times n}$ that indicates whether the i^{th} node is living (TRUE) or not (FALSE). Together, the model data can be summarized as $\{\mathbf{F}, \mathbf{z}, \mathbf{e}, \mathbf{r}, \mathbf{X}, \mathbf{Living}\}$.

Most analytical functions in `enaR` assume the model data is presented as an R network data object defined in the `network` package. Given the data elements, the *pack* function can be used to manually combine the data elements to create the necessary R network data object. While there is no standard data format for an ENA model, there are two commonly used formats. First, there is the Scientific Committee for Ocean Research (SCOR) format that is the required input to NETWRK (Ulanowicz and Kay, 1991), and the second format is the Excel sheet formatted data that is the input to WAND (Allesina and Bondavalli, 2004). The `enaR` package includes a *read.scor* and a *read.wand* function to read in these common data formats.

2.2 Included Algorithms

While the long-term goal is for the `enaR` package to be comprehensive, this initial release is more limited. It does include many of the most commonly used algorithms (Table 1), along with a number of work flow tools (e.g., the read.x functions). `enaR` captures all of the Patten School algorithms previously implemented in NEA.m, along with some recent developments. Ulanowicz School algorithms are more limited, including the ascendency calculations (Ulanowicz, 1997) and mixed trophic impacts analyses (Ulanowicz and Puccia, 1990). We expect to grow the package in time and through collaboration with users.

2.3 Example Application

Given a network model, applying ENA algorithms with `enaR` is straight forward. Table **??** illustrates applying the ENA Flow analysis to the six compartment model of energy flow in a South Carolina oyster reef (Dame and Patten, 1981). After loading the `enaR` package, the first step is to enter the model data. In this example, we use the *read.scor* function to read the SCOR formatted data from a text file. We can then apply the AVG2 algorithm (Allesina and Bondavalli, 2003) to ensure that the model is at steady-state — one of the assumptions of the flow analysis. We then applied the *enaFlow* function to the model to perform the desired ENA flow analysis. This analysis returns 4 matrices ($\mathbf{G}$, $\mathbf{GP}$, $\mathbf{N}$, $\mathbf{NP}$) and two vectors (throughflow T, and a vector of 20 whole-network statistics ns). Guidance for how to interpret these results can be found in previously published literature (Fath and Borrett, 2006; Schramski et al., 2011).

3 Value Added Features

Beyond the basic functionality of the `enaR` package, there are several features that add substantive value for users. We highlight four of these features here: visualization, model library, batch analysis, and connections to other network analysis tools.

3.1 Visualization

Visualization of network models can be an essential analytical tool (Lima, 2011; Moody et al., 2005). Because `enaR` is built on top of the `network` package and data type, it is possible to quickly create network plots of the model internal structure. Fig. 1a shows an example of the Oyster Reef ecosystem model.

3.2 Model Library

To facilitate new systems ecology and network science, we included a library of 100 previously published ecosystem network models with the `enaR` package. These models each trace a thermodynamically conserved unit (e.g., C, N, P) through a particular ecosystem. The models in this set are empirically-based in that the authors attempted to model a specific system and parameterized the model to some degree with empirical estimates. The library includes models used previously to test several systems ecology hypotheses (Borrett, 2013; Borrett and Salas, 2010; Borrett et al., 2010; Salas and Borrett, 2011) and the set overlaps 47% with the set of models made available by Dr. Ulanowicz (http://www.cbl.umces.edu/ ulan/ntwk/network.html)

We have tentatively split these models into two classes. The most abundant class is the trophic network models. These models tend to have a food web at their core, but also include fluxes generated by processes like death and excretion. The annual carbon flux model for the mesohaline region of the Chesapeake Bay is a typical example (Baird and Ulanowicz, 1989). The second class of models focuses on biogeochemical cycling. In contrast to the trophic networks, the biogeochemical cycling models tend to have more highly aggregated nodes (more species grouped into a compartment), include more abiotic nodes that could represent chemical species (e.g., ammonia in a nitrogen cycle), have a lower dissipation rate, and therefore they tend to have more recycling (Borrett et al., 2010; Christian et al., 1996). Christian and Thomas's (2003) models of nitrogen cycling in the Neuse River Estuary are good examples of the class. The package vignette has a full listing of the models included along with references to their original publications (Lau et al., 2013)

3.3 Batch Analysis

Given a list of models like the model library, it is possible to efficiently batch apply one or more analyses to the models. This facilitates the kind of comparative network analysis often of interests to ecologists (Christian et al., 2005; Monaco and Ulanowicz, 1997). For example, van Oevelen et al. (2011) compared the food webs and their organic matter processing in three sections of the Nazaré submarine canyon, and Hines et al. (in press) used a comparative approach to investigate the impact of sea level rise on process coupling in the estuarine nitrogen cycle. The `enaR` tool simplifies the work flow for these types of comparison.

This batch analysis can be used in several additional ways. One application is for meta-analyses, such as tests of the generality of hypothesized ecosystem properties like network non-locality (Salas and Borrett, 2011) and network homogenization (Borrett and Salas, 2010), or to investigate how physical features might influence ENA results (Niquil et al., 2012). Fig. 1b illustrates the rank-ordered network homogenization statistic for the 56 trophic-based ecosystem models in the library, which extends previous results to include several new models (Borrett and Salas, 2010). A second kind of application is the exploration of new ENA relationships. Given the collection of the Patten and Ulanowicz school algorithms and the library of models, the ENA community can investigate possible statistical relationships among the ENA indicators from different schools (Fig. 1c). A third application of batch analysis is to investigate the previously unknown empirical ranges of ENA whole-network statistics, which is useful for interpreting results from specific applications. Fig. 2 shows the observed distribution of values for selected network statistics from the 100 models in the library.

The `enaR` package enables and simplifies these types of analysis.

3.4 New Connections

A fourth key feature of the `enaR` package design is that it enables network ecologists easier access to other network tools and analyses that might be useful. The `enaR` package uses the R network data structure defined in the `network` package (Butts, 2008a). This means that network ecologists using R can also use the network manipulation functions and visualization features of the `network` package. Further, the R Social Network Analysis (SNA) package (Butts, 2008b) also uses this network data object. This means that network ecologists can apply many of the SNA algorithms directly to their ecological network models. Fig. 1d illustrates applying the betweenness centrality function to the Chesapeake Bay trophic model (Baird and Ulanowicz, 1989) and visualizing the results using the target centrality plot (Brandes et al., 2003). This analysis highlights the central role of Sedimentary Particulate Carbon and bacteria in the Sediment Particulate Organic Carbon (POC) in the carbon flux of the estuary.

In addition, `enaR` can be a starting point for ecosystem network ecologists to use other R network tools. For example, the `iGraph` package provides functions to apply classic graph theory (Csardi and Nepusz, 2006). The `limSolve` package provides capabilities to infer network model fluxes from empirical data by linear inverse modeling (Soetaert et al., 2009), which can also be used for sensitivity analysis of ENA (Hines et al., in press; Kones et al., 2009). *MENTION/CITE recent packages published in MEE.*

4 Conclusion and Future Development

The enaR package provides a set of functions to perform Ecological Network Analysis. The library joins analyses from both the Patten and Ulanowicz Schools of ENA into a single software package. The library is built in R so that the functions are transparent and adaptable by the community of users. It also lets users have access to other network and statistical analysis tools that are already part of R.

In the future, we anticipate two initial lines of continued development for the enaR package. The first is to extend the package's capability. While it currently contains most of the most commonly used ENA algorithms used by ecologists, it does not yet meet our comprehensive ideal. For example, Ulanowicz's (1983) decomposition of cycles nor is his construction for the Lindeman trophic spine (Ulanowicz and Kemp, 1979). The package could also include network model construction tools, such as least-inference methods for building models from empirical data (Ulanowicz and Scharler, 2008) and Fath's (2004) algorithm for constructing plausible ecosystems models. The second line of development is to increase the connections between the enaR package and other modeling and analytical tools. For example, we are currently working with colleagues to enable users of Ecopath with Ecosim (Christensen and Walters, 2004) to apply the enaR tools in a seamless way. We are also developing functions to connect between enaRand the R limSolve package (Soetaert et al., 2009) for creating models using Linear Inverse Modelling and to enable network sensitivity analysis (Hines et al., in press; Kones et al., 2009).

A major reason behind our decision to use an open source software tool is that we want to foster user development and extension of the package's functionality. It is our hope that enaR can serve as an organizing point for ENA computational methods and in doing so can facilitate the merger and growth of both theory and applications. We look forward to working with the community of ecological software developers to move this software forward.

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Table 1: Primary Ecological Network Analysis algorithms in `enaR`.

Analysis	**Function Name**	**School**
Structure	*enaStructure*	foundational, Patten
Flow	*enaFlow*	foundational, Patten
Ascendency	*enaAscendency*	Ulanowicz
Storage	*enaStorage*	Patten
Utility	*enaUtility*	Patten
Mixed Trophic Impacts	*enaMTI*	Ulanowicz
Control	*enaControl*	Patten
Environ	*enaEnviron*	Patten

Table 2: Example code for applying enaR Flow analysis to Dame and Patten's (1981) oyster reef model.

```
> library(enaR)                   # load package
> m <- read.scor("oyster.dat")  # read model data from SCOR formatted file
> m <- balance(m)                 # balance model using AVG2 algorithm
[1] BALANCED
> u <- unpack(m)                  # unpack model data to illustrate components
> attributes(u)
$names
[1] "F"      "z"      "r"      "e"      "y"      "X"      "Living"

> F <- enaFlow(m)                 # perform ENA flow analysis
> attributes(F)                    # show analysis objects created
$names
[1] "T"  "G"  "GP" "N"  "NP" "ns"

> F$ns                            # show flow analysis network statistics
     Boundary     TST     TSTp      APL       FCI       BFI       DFI       IFI
[1,]    41.47 83.5833 125.0533 2.015512 0.1101686 0.4961517 0.1950689 0.3087794
         ID.F   ID.F.I   ID.F.O    HMG.I    HMG.O AMP.I AMP.O mode0.F  mode1.F
[1,] 1.582925 1.716607 1.534181 2.051826 1.891638     3     1   41.47 32.90504
      mode2.F  mode3.F mode4.F
[1,] 9.208256 32.90504   41.47
>
```

8 Figures

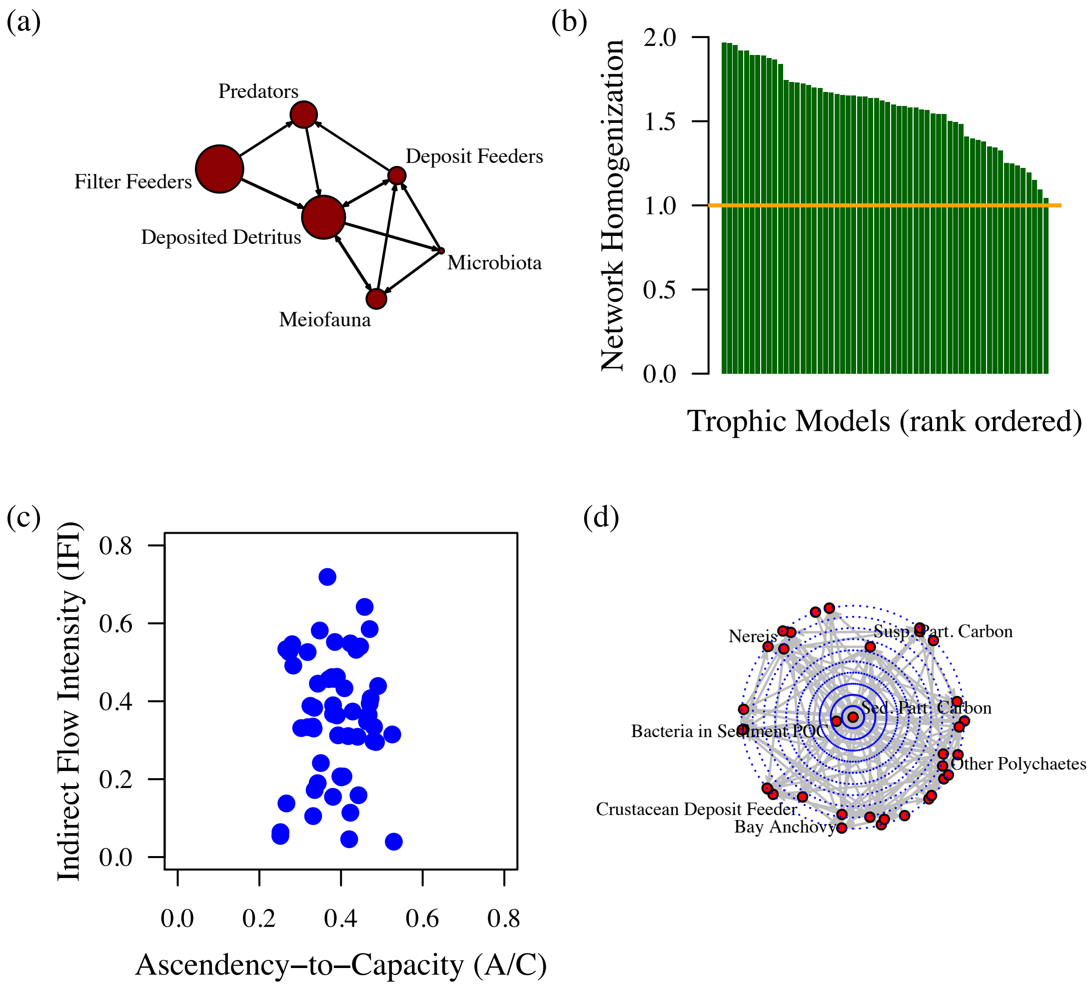

Figure 1: Example of analysis and visualizations created with `enaR` (a) network digraph of the internal flows of an oyster reef ecosystem model (Dame and Patten, 1981), (b) network homogenization statistic for 56 trophic ecosystem models (rank-ordered), (c) scatter plot showing the relationship between the ascendency-to-capacity ratio and the indirect flow index for the 56 trophic ecosystem models (Table xx), and (d) target plot of the betweenness centrality from social network analysis calculated for the xx nodes of the Chesapeake Bay ecosystem model (Baird and Ulanowicz, 1989).

Statistic	Min	Distribution	Max	Median	Mean	CV
n	4		125	15	26.66	1.02
C	0.05		0.45	0.22	0.25	0.51
LD	1		16.91	3.14	4.58	0.89
lam1A	0		14.17	3.27	4.27	0.76
FCI	0		0.98	0.26	0.38	0.86
APL	1.37		186.25	3.67	20	1.91
IFI	0.04		0.99	0.53	0.56	0.52
HMG.O	1.04		13.07	1.78	2.3	0.83
AMP.O	0		323	6.5	19.77	1.91
AMI	1		2.25	1.57	1.58	0.21
ASC.CAP	0.25		0.75	0.39	0.42	0.28
synergism.F	2.41		60.51	3.95	5.69	1.1
mutualism.F	0.6		4	1.16	1.43	0.5

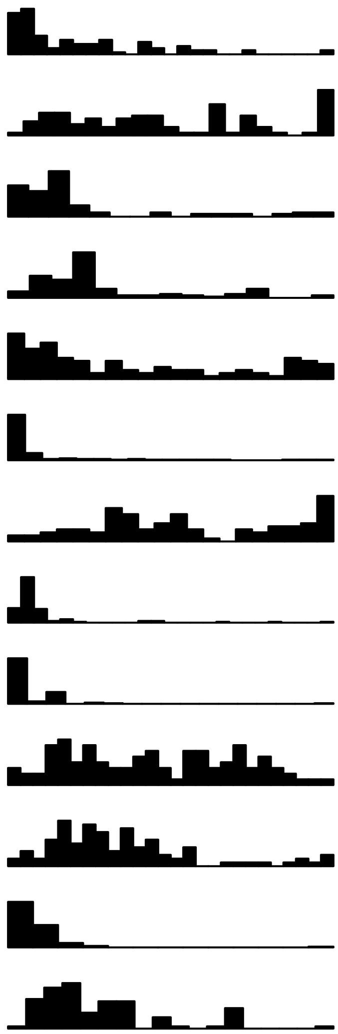

Figure 2: Distributions of selected ENA network statistics from to the 100 empircially-based ecosystem models included in `enaR` 2.0. The results are summarized using a histogram showing the distribution of the values of each network statistic between the observed minimum and maximum values. The median, mean, and coefficient of variation (ratio of standard deviation and mean) values are also reported. The network statistics are the number of nodes (n), the connectance ($C = L/n^2$), link density ($LD = L/n$), pathway proliferation rate (lam1A), Finn cycling index (FCI), average path length (APL), indirect flow intensity (IFI), output oriented network homogenization ratio (HMG.O), output-oriented network amplification ratio (AMP.O), average mutual information (AMI), the ascendency-to-capacity ratio (ASC.CAP), flow-based network synergism (synergism.F) and mutualism (mutualism.F).