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enaR: An R package for Ecological Network Analysis

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Abstract

- Network ecologists apply network models and analyses to investigate the structure, function, and evolution of ecological systems. Ecological Network Analysis (ENA) is an approach rooted in ecosystem ecology with over 30 years of development. While some software tools exist to assist ecologists with the application of ENA, they vary in their comprehensiveness, availability, usability, transparency, and extensibility.

- Here, we introduce enaR, a set of R tools that enables ecologists to perform a broad set of ENA algorithms to analyze ecosystem models.

- In addition to the basic functionality of the package, we highlight several value added features including the ability to visualize the networks, the inclusion of a library of 100 empirically-based ecosystem models, the ability to conduct analyses for many models simultaneously, and connects to other network and ecological analysis tools in R.

- We expect this package to enable more ecologists to apply ecological analyses and contribute to ENA software development.

KEYWORDS: network analysis, ecosystem, social network analysis, software, network environ

analysis, ascendency, input–output analysis, food web, Ecopath, WAND

1 Introduction

Network Ecology – the study of ecological systems using network models and analyses 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 notable fraction of 2008 publications in 11 select journals were related to food webs (≈2.4%), mutualistic networks (≈0.9%), and host-parasitoid networks (≈0.055%). Network ecology is growing in part because ecology is fundamentally a relational science and network models are excellent tools for relational analyses. In addition, this rise of network ecology contributes to, mirrors, and builds on the more general development of network sciences (Barabási, 2012; Borgatti & Foster, 2003; Freeman, 2004; Newman, 2003; Wasserman & 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 economic Input-Output Analysis developed by Leontief (1966) . These algorithms are applied to network models of energy and matter exchange among ecosystem components (Fath & Patten, 1999; Hannon, 1973; Patten *et al.*, 1976; Ulanowicz, 1986), the iconic example of this being the food-web.

The development of ENA has contributed to a new theoretical understanding of ecosystems (Belgrano *et al.*, 2005; Higashi & 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 & Ulanowicz (1999) showed that in the Florida Everglades the American alligator is an indirect mutualist with several of its prey, 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). Furthermore, several scientists have used ENA to investigate urban sustainability (Bodini & Bondavalli, 2002; Bodini *et al.*, 2012; Chen & 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 & Puccia, 1990).

Several software tools have been created to enable scientists to more easily apply ENA. The first widely distributed tool was NETWRK (Ulanowicz & Kay, 1991). This program is a collection of analyses 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 & 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 & Borrett (2006) introduced a Matlab function, NEA.m, which collected algorithms largely developed for network environ analysis, hence NEA (Patten, 1991). One advantage of NEA.m is that the algorithms are transparent to the user and accessible for modification. While the NEA.m function is freely available (`http://www.mathworks.com/matlabcentral/fileexchange/5261-nea-m`) it requires Matlab, which is powerful but expensive proprietary software. With modification, the function can be run in Octave, an open source clone of Matlab, but it executes more slowly and doesn't have the same level of support provided by Matlab. EcoNet is a web-based tool that lets users apply ENA analyses similar to to NEA.m, but with some computational enhancements (Kazanci, 2007; Schramski *et al.*, 2011). Ecopath with Ecosim (Christensen & Pauly, 1992; Christensen & Walters, 2004) is used primarily for model construction and simulation, but it also includes a network analysis plug-in that implements several other ENA algorithms. 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 all of the major analyses, which has lead to separate, over-lapping approaches to ENA and high variation in software availability, usability, and extensibility.

To address the limitations of the existing tools, we created `enaR`, which is a set of R tools for Ecological Network Analysis. We had three specific design objectives for this software. The first objective was to collect the major ENA analyses. 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. We selected to implement the software in R in part because of its increasing popularity as an analytical tool in the biology and ecology communities (e.g., Dixon, 2003; Metcalf *et al.*, 2012; Revell, 2012). The third design objective was to let users connect to other analytical tools. To enable this, `enaR` was built on top of two existing R packages: `network` (Butts, 2008a) and `sna` (Butts, 2008b). In summary, the aim of the `enaR` package is to make ENA tools more available and easier to use, adapt, and extend. In this paper, we briefly present `enaR`version 2.5. For a more detailed introduction, please see the package vignette: i.e., `vignette`('enaR').

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 compartments or network 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 a set of observed fluxes, termed directed edges or links. These models also have energy–matter inputs into the system and output losses from the system. While the Patten School treats all outputs the same, the Ulanowicz School partitions outputs into respiration and export to account for differences in energetic quality. Note that the more generic outputs can be the sum of the respiration and export values. Some analyses also need the amount of energy–matter stored in each node (e.g., biomass). 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 that indicates whether the node is living (TRUE) or not (FALSE). In summary, the full set of data required to perform ENA includes (1) internal flows, (2) boundary inputs, (3) boundary exports, (4) boundary respiration, (5) boundary outputs, which may be the sum of exports and respiration, (6) biomass or storage values, and (7) designation of living status of each node.

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 & Kay, 1991), and the second format is the Excel sheet formatted data that is the input to WAND (Allesina & 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, but provides a foundation for future expansion. The package currently includes 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 & 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 2 illustrates applying the ENA Flow analysis to the six compartment model of energy flow in a South Carolina oyster reef (Dame & 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 one of four automated balancing algorithms introduced by Allesina & Bondavalli (AVG, Input-Output, Output-Input, AVG2, 2003) to ensure that the model is at steady-state — one of the assumptions of the flow analysis. In this example we used the default AVG2 algorithm, which tends to cause the least distortion of flows while balancing the network (Allesina & Bondavalli, 2003). We then applied the `enaFlow` function to the model to perform the desired ENA flow analysis. This analysis returns 4 matrices (**G**, **GP**, **N**, **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 & 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. The network package includes three network layout algorithms: circle, Fruchterman-Reingold, and Kamada-Kawai. The Fruchterman-Reingold algorithm used here is the default.

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 & Salas, 2010; Borrett *et al.*, 2010; Salas & Borrett, 2011). This set has a 47% overlap with the set of models previously collected 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 non-trophic 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 & 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 & 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 interest to ecologists (Christian *et al.*, 2005; Monaco & Ulanowicz, 1997). For example, Christensen (1995) applied ENA to identify and compare the maturity of 41 ecosystem models, Baird *et al.* (2008) compared different nutrient dynamics in the Sylt-Rømø Bight ecosystem, and van Oevelen *et al.* (2011) compared the food webs and their organic matter processing in three sections of the Nazaré submarine canyon. 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 & Borrett, 2011), 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. Notice that the homogenization statistic is greater than one in all of these models indicating that the network of indirect interactions tend to more uniformly distribute the resources than is obvious from the direct interactions, which extends previous results of Borrett & Salas (2010) to include several new models. A second kind of application is the exploration of new ENA inter-relationships. Given the collection of the Patten and Ulanowicz school algorithms and the library of models, the ENA community can investigate possible 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 may be 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 `enaR` can also use the network manipulation functions and visualization features of the `network` package. Further, the R Social Network Analysis (SNA) package, `sna`, (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. For example, Fig. 1d illustrates applying the betweenness centrality function to the Chesapeake Bay trophic model (Baird & 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 & 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 uncertainty analyses of ENA (Kones *et al.*, 2009). There are a wealth of additional R package that network ecologists may find useful including `bipartite` (Dormann *et al.*, 2008), `vegan` (Dixon, 2003), `bioconductor` (Gentleman *et al.*, 2004), `Cheddar` (Hudson *et al.*, 2013), `Diversitree` (FitzJohn, 2012), and packages in the `statnet` family (Handcock *et al.*, 2008) beyond `network` and `sna`.

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 many commonly used ENA algorithms used by ecologists, it does not yet meet our comprehensive ideal. For example, Ulanowicz's (1983) decomposition of cycles is not yet included nor is his construction for the Lindeman trophic spine (Ulanowicz & Kemp, 1979). The package could also include network model construction tools, such as least-inference methods for building models from empirical data (Ulanowicz & 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 & Walters, 2004) to apply the `enaR` tools in a seamless way. We are also developing functions to connect between `enaR` and the R limSolve package (Soetaert *et al.*, 2009) for creating models using Linear Inverse Modeling and to enable uncertainty analysis (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. Toward this same end, we are developing a Git repository (Open-Source Freedom Conservancy) and a GitHub (https://github.com/) project page. Together, the open-source tools for version control and project management provided by Git and GitHub will increase the potential for collaborative software development. We look forward to working with the community of ecological software developers to move this software forward.

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6 Tables

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 & 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
>
```

7 Figures

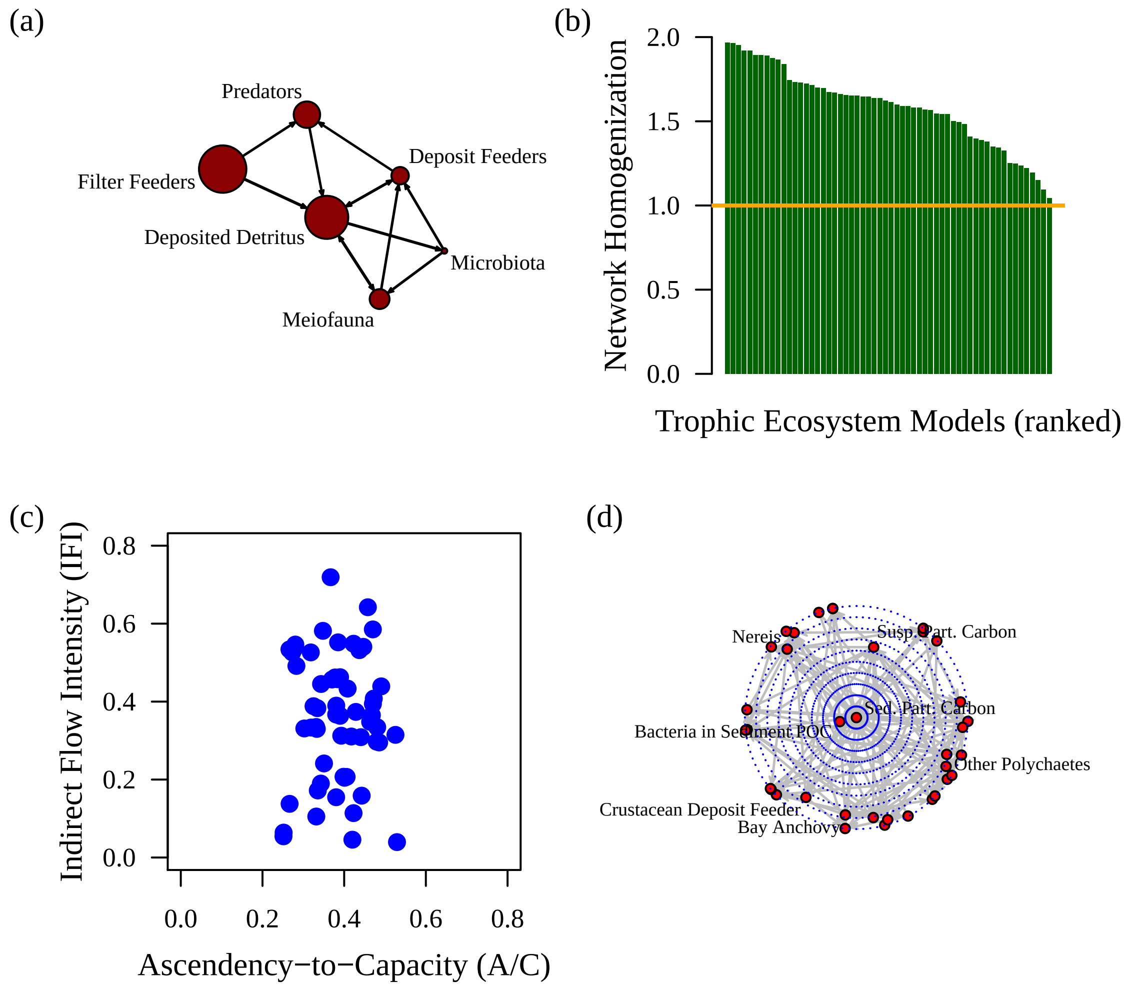

Figure 1: Example of analysis and visualizations created with `enaR` (a) network digraph of the internal flows of an oyster reef ecosystem model (Dame & Patten, 1981), (b) network homogenization statistic for 56 trophic ecosystem models (rank-ordered), (c) scatter plot showing the relationship between 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 & 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 empirically-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).