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enaR: An R package for Ecological Network Analysis

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Abstract

- Network analysis is a useful approach for complex, relational datasets in many biological fields, including ecology and molecular and evolutionary biology.
- Here, we introduce `enaR`, an R package for conducting Ecological Network Analysis (ENA), an analytical tool set rooted in ecosystem ecology with over 30 years of development, which examines the structure and dynamics of matter and energy movement between discrete ecological compartments (e.g., a food web).
- In addition to describing the primary functionality of the package, we also highlight several value added features, including a library of 100 empirical ecosystem models, the ability to analyze and compare multiple models simultaneously, and connections to useful ecological network analysis tools in R.

KEYWORDS: network analysis, ecosystem, open-source software, network environ analysis, ascendency, input–output analysis, food web, urban metabolism, Ecopath, WAND

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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, the 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 examines the flows of matter and energy in an ecosystem. Rooted in ecosystem ecology (Borrett *et al.*, 2012), it functions as 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 the economic Input-Output Analysis developed by Leontief (1966). These algorithms are applied to network models of energy and matter exchange among ecosystem components with the iconic example of this being the food-web (Fath & Patten, 1999; Hannon, 1973; Patten *et al.*, 1976; Ulanowicz, 1986). Here are some examples of how ecologists have applied ENA. 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). Recently, scientists have begun to use ENA to analyze models in urban metabolism models (Bodini & Bondavalli, 2002; Bodini *et al.*, 2012; Chen & Chen, 2012; Zhang *et al.*, 2010). Collectively, this work consistently shows the power of a network approach to reveal patterns that are only evident at the scale of entire systems (Fath *et al.*, 2007; Patten, 1991; Ulanowicz & Puccia, 1990).

We have created `enaR` to provide open-source access to ENA tools with three specific software design objectives. The first objective was to collect the major ENA functions into a single software package, which we describe below. The second was to increase both the availability and extensibility of the software. We chose to implement the software in R because of its increasing popularity as an analytical tool in the biological sciences (e.g., Dixon, 2003; Metcalf *et al.*, 2012; Revell, 2012). Users can freely download a stable version of the package from the CRAN website (http://cran.r-project.org/web/packages/enaR/), and development is being conducted via GitHub (https://github.com/TheSeeLab/enaR). The third design objective was to let users connect to other analytical tools. To enable this, `enaR` was built specifically to connect to two existing R network analysis 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 present `enaR` with a brief illustration of its functionality. For a more detailed user introduction, please refer to the package vignette: http://cran.r-project.org/web/packages/enaR/vignettes/enaR.pdf.

2 Overview of enaR

ENA was devleoped to analyze network models of energy or matter flow and storage in an ecosystem. More generally, the analyses could be used to analyze any system in which some physically conserved unit moves among compartments. After describing the data required as input to ENA, we highlight the primary ENA algorithms currently included in `enaR` . We then walk through an application of the `enaR` Flow analysis to an example ecosystem 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. 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.

As ENA is an agglomeration of tools developed by multiple perspectives (e.g., Golley, 1993; Hannon, 1973; Margalef, 1963; Patten, 1959; Pimm, 1982), the data requirements vary from function to function. The main differences arise from two distinct schools of thought that have driven the development of ENA since the 1970s (Scharler & Fath, 2009). The first school is based on the work of Dr. Robert E. Ulanowicz and colleagues at the University of Maryland (Ulanowicz, 1986, 1997, 2009). Primarily focused on trophic ecology, this approach uses information theory and the ascendency concept that characterizes ecosystem growth and development Ulanowicz (1986, 1997). The second school is based on the work of Dr. Bernard C. Patten at the University of Georgia (Fath & Patten, 1999; Matis & Patten, 1981; Patten, 1982; Patten *et al.*, 1976). Steeped in dynamic equations, simulations, and systems analysis, this work developed the environ concept that formalizes the concept of environment (Patten, 1978) and has often been referred to as "Network Environ Analysis."

The primary difference in data requirements among ENA functions is that the Patten School treats all outputs the same, while the Ulanowicz School partitions outputs into respiration and export to account for differences in energetic quality between these two types of ecosystem output. Note that the more generic outputs can be the sum of the respiration and export values. 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). Some analyses also need the amount of energy–matter stored in each node (e.g., biomass).

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

The package is built hierarchically with primary functions that employ "lower level" support functions that implement the algorithms relevant to a major category of analysis. 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" functions mentioned above). `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). It is our hope that user participation will develop the the package further through the inclusion of more algorithms. Although described more comprehensively in the package's vignette, here is a brief description of the primary functions:

`enaStructure`: analyzes how nodes are connected together.

`enaFlow`: quantifies the amount of matter or energy moving among nodes.

`enaAscendency`: analyzes the developmental status of a network by comparing the observed network to a theoretical network structure based on information theory.

`enaStorage`: quantifies the amount of matter or energy that is held within nodes.

`enaUtility`: estimates the importance of nodes in the network in terms of the relative quantities of matter or energy that passes through each node.

`enaMTI`: assesses the effect changing a given node will have on the rest of the network.

`enaControl`: quantifies the degree to which nodes influence the dynamics across the network.

`enaEnviron`: analyzes the quantities of mattern and energy that are traveling to and from each node across all pathways in the network

2.3 Example Application

Given a network model, applying ENA algorithms with `enaR` is straight forward. Although the functions vary in their specifications and the results that are returned to the user, all `enaR` functions follow a similar argument structure. All analytical functions begin with the prefix 'ena' followed by the specific analysis name (see Table 1). For simplicity's sake, we demonstrate how to use the package with an example that conducts Flow analysis on a published ecosystem model. Table 2 shows an example script for applying the ENA Flow analysis to the six compartment model of energy flow in the South Carolina oyster reef ecosystem (Dame & Patten, 1981). Briefly, the analysis invovles: (1) loading the model data, (2) checking and balancing the model if necessary, and (3) inputing the balanced model into the analysis function.

After loading the `enaR` package, the first step is to enter the model data. In this example, we use the `read.scor` function to import 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 apply 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 & Borrett, 2006; Schramski *et al.*, 2011).

2.4 Visualization

Visualization of network models can be an essential analytical tool (Lima, 2011; Moody *et al.*, 2005). Because `enaR` uses the the `network` package data class, it is possible to quickly create network plots of the model's 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 Value Added Features

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

3.1 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).

3.2 Batch Analysis

Major advancements in ecosystem ecology have been made through an approach that examines network metric for multiple ecosystem models. 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. Given a list of models like the model library, it is possible to quickly analyze multiple models using R's `lapply` function (see `help`("lapply")). This facilitates the kind of comparative network analysis often of interest to ecologists (Christian *et al.*, 2005; Monaco & Ulanowicz, 1997).

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), (Borrett & 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. 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 easily analyzed using `lapply` and the associated `enaR` functions.

3.3 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

Although software has existed previously that enables scientists to apply ENA, `enaR` provides greater accessibility, breadth of available algorithms and potential for development. The first widely distributed tool for ENA was NETWRK (Ulanowicz & Kay, 1991), 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) with the explicit goal of increasing access 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 algorithm software is open 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). The `enaR` package addresses many of the limitations of the previously published set of ENA tools. The library joins analyses from both the currently separate 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 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). The second line of development is to extend the package's capabilities. While it currently contains most of the many commonly used ENA algorithms used by ecologists, it is far from complete. 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. Looking to the future of ENA, we hope to facilitate the rapid developemnt of accessible network analysis tools for the ecological community. A major reason for our use of open source software is that we want to foster user driven development and extension of the package's functionality. Although the network approach promotes innovation and collaboration across fields, network ecology has developed along multiple, largely separate lines (Allesina , 2012; Scharler & Fath, 2009). It is our hope that enaR can serve as an organizing point for ENA and other ecological network methods with the hope that doing so will not only produce relevant software, but also promote feedback bewteen theory and applications. Toward this end, we have created a GitHub development repository (https://github.com/MKLau/enaR_development) and project page (http://theseelab.github.io/enaR/), where researchers can find more information on how to contribute software. 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 dynamic community of peoople interested in network analyses to promote the use and development of network tools in ecology.

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6 Tables

Table 1: Primary Ecological Network Analysis (ENA) 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 applying ENA Flow Analysis to Dame & Patten's (1981) oyster reef model. This illustrates the main steps that would be conducted for analyses using the primary functions, including: 1) loading the model, 2) balancing, 3) examining the model's attraibutes, 4) running the analysis, and 5) checking the output.

```
> library(enaR)                  # load package
> data(troModels)                # load the model library
> m <- troModels$"Oyster Reef"  # isolate the Oyster Reef model
> 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

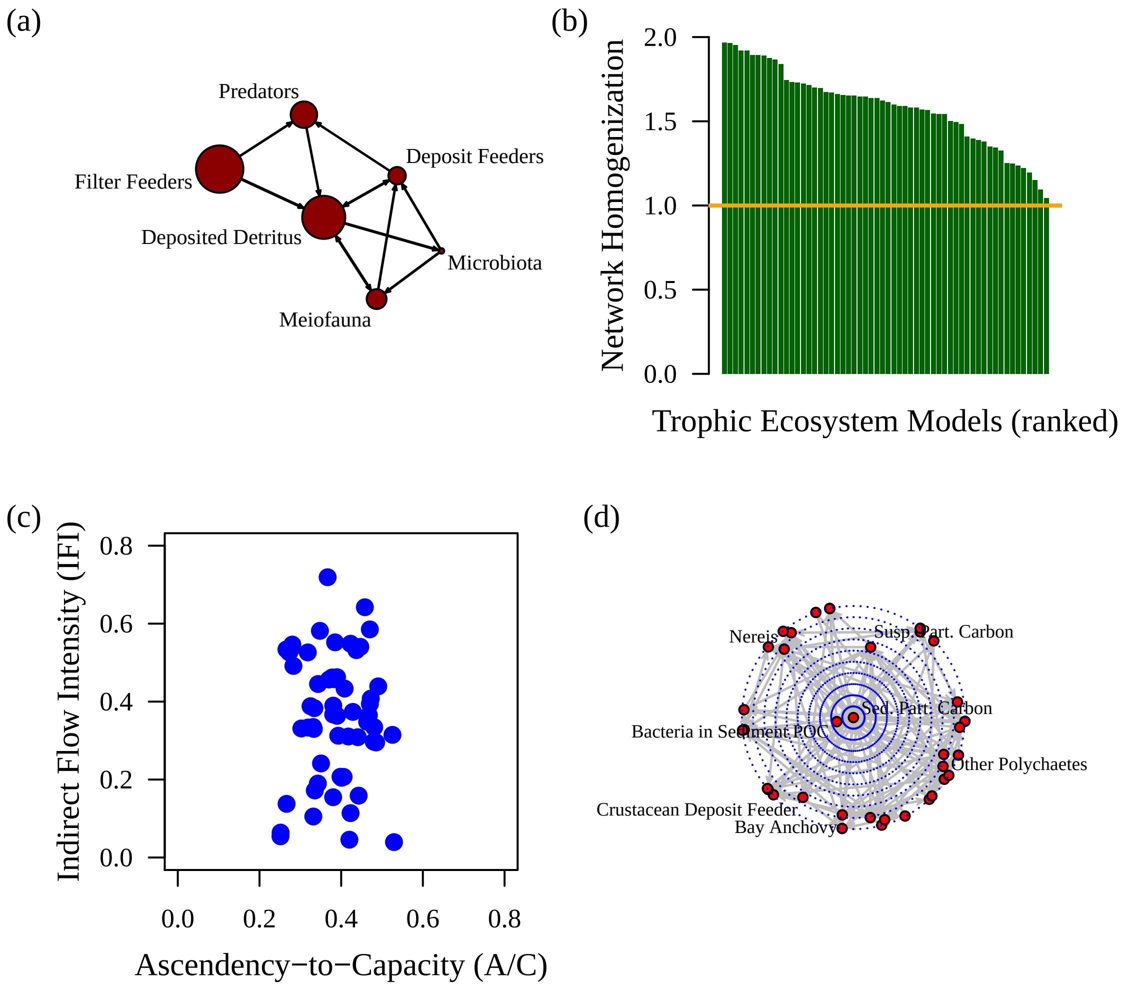
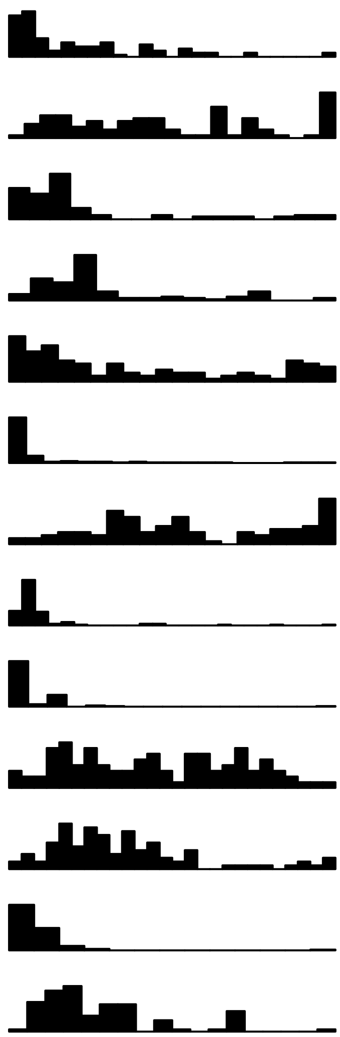


Figure 1: Example of analysis and visualizations created with `enaR` (a) network digraph of the internal flows of an oyster reef ecosystem model (Dame & Patten, 1981), (b) network homogenization statistic for 56 trophic ecosystem models (rank-ordered), (c) scatter plot showing the relationship between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