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enaR: An R package for Ecosystem 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 Ecosystem 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, NETWRK, 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 (Proulx *et al.*, 2005). For example, Ings *et al.* (2009) discovered 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 (≈0.06%). Likewise, Borrett *et al.* (2014) found that the percent of ecology and evolutionary biology papers indexed by Web of Science that could be classified as network ecology increased from 1.3% in 1991 to more than 5% in 2012. This rise of network ecology contributes to, mirrors, and builds on the more general growth of network sciences (Barabási, 2012; Borgatti & Foster, 2003; Freeman, 2004; Newman, 2003; Wasserman & Faust, 1994).

Ecosystem Network Analysis (ENA) is a branch of network ecology that has been used to address a range of key ecosystem questions (Borrett *et al.*, 2012; Fath & Patten, 1999; Ulanowicz, 1986). For example, in the food web of Big Cypress National Preserve (Florida, USA) Bondavalli & Ulanowicz (1999) found evidence of an indirect mutualism between the American alligator and some of its prey items. Applications of ENA have also lead to new insights into the classic trophic questions of "What limits food-chain length?" (Ulanowicz *et al.*, 2014) and "Are food webs modular?" (Allesina *et al.*, 2005; Borrett *et al.*, 2007; Krause, 2004). Hines *et al.* (2012) used ENA to quantify the relative importance of coupling between biogeochemical processes (e.g., nitrification) in the Cape Fear River estuary sedimentary nitrogen cycle. Further, scientists have used ENA to investigate differences in urban sustainability (Bodini & Bondavalli, 2002; Bodini *et al.*, 2012; Chen & Chen, 2012; Zhang *et al.*, 2010). Collectively, this work consistently shows the power of a transactional network to generate unexpected ecological relationships that then influence the system function and evolution (Jørgensen *et al.*, 2007; Patten, 1991; Ulanowicz, 1997).

`enaR` is an open-source software to facilitate ENA. The currently available ENA software packages (Allesina & Bondavalli, 2004; Christensen & Walters, 2004; Fath & Borrett, 2006; Kazanci, 2007; Ulanowicz & Kay, 1991) each have critical limitations, which led us to three primary design objectives for `enaR`. The first objective was to collect the major ENA functions into a single software package. While multiple investigators have contributed to algorithmic development (e.g., Allesina & Bondavalli, 2003; Fath & Patten, 1999; Finn, 1976; Ulanowicz, 1986; Ulanowicz & Kay, 1991), the broad set of tools is not available in a single existing software. The second objective was to increase the availability and extensibility of the software. We chose to use R in part because of its increasing popularity as an analytical tool in the biological sciences (e.g., Dixon, 2003; Metcalf *et al.*, 2012; Revell, 2012). Further, users can freely download a stable version of the package from the CRAN website (http://cran.r-project.org/web/packages/enaR), and the code for every function in R is available from within R (e.g., `edit(`*function_name*`)`). In addition, `enaR` development is being managed via GitHub (https://github.com/TheSeeLab/enaR) to encourage collaborative development. The third design objective was to enable `enaR` users access to network analysis tools from other disciplines. To enable this, `enaR` was designed to work directly with 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 an overview of `enaR` and highlight some of its functionality. A full description of the ENA algorithms and their use and interpretation is beyond the scope of this short paper, but we refer interested readers to a selection of reviews as an entry point to ENA (Fath & Borrett, 2006; Fath & Patten, 1999; Jørgensen *et al.*, 2007; Schramski *et al.*, 2011; Ulanowicz, 1997). For a more comprehensive description on how to use the `enaR` package, please refer to the package vignette: http://cran.r-project.org/web/packages/enaR/vignettes/enaR-vignette.pdf.

2 Overview of `enaR`

ENA is an agglomeration of algorithms developed to analyze network models of energy or matter movement in ecosystems (e.g., Fath & Patten, 1999; Hannon, 1973; Ulanowicz, 1986), but it can generally be applied to any Input-Output system that follows a thermodynamically conserved unit among the compartments. Thus, it is a family of related algorithms to analyze the ecosystem from several perspectives including its structure, flow, storage, and utility. Together, these analyses function 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. In this section we provide an overview of the algorithms and tools included in the `enaR` software. After describing the required model information, we highlight the primary ENA algorithms included in `enaR`. We then walk through an example application of the `enaR` Flow analysis.

2.1 Data Requirements and Input

ENA is a data-intensive methodology. 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 direct energy or matter transactions among the nodes, termed directed edges or links. These models also have energy–matter inputs into the system and output losses from the system. In summary, the full set of data required 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. While all seven elements are required for a full analysis, the specific data requirements varies among the ENA algorithms.

The primary ENA algorithms in `enaR` assume the model data is presented as an R network data object defined in the `network` package. Given the data elements, users can use the `pack` function to combine the data elements into the R network data object. While a standard data format for an ENA model does not yet exist, 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 (Table 1).

2.2 Visualization

Visualization of network models can be an essential analytical tool (Lima, 2011; Moody *et al.*, 2005). Because `enaR` is built specifically to use the `network` package and data type, it is possible to quickly create network plots of the model internal structure. Fig. 1a shows an example visualization of Dame & Patten's (1981) 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. The R script to generate this visualization is included in the online supplementary information (Item S1).

2.3 Algorithm Overview

`enaR` includes many of the most commonly used ENA algorithms (Table 2), along with a number of work flow tools and specialty analyses (Tables 1 and 3). The nine primary ENA functions begin with the prefix 'ena' followed by the specific analysis name (see Table 2). There are a total of 34 functions in the `enaR` package. Comparison of the `enaR` package to previous implementations of ENA algorithms (i.e., NETWRK, NEA.m, EcoNet) shows high agreement in function output and significant expansion of the available ENA algorithms (Table S1 online).

Scharler & Fath (2009) identify two schools of ENA. The first school is based on the work of Robert 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 to characterize ecosystem growth and development (Ulanowicz, 1986, 1997). This work is often referred to as "Ecological Network Analysis" as it predates many other types of network ecology. The second school is based on the work of Bernard 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 approach developed around the environ concept that formalizes the concept of environment (Patten, 1978), and has often been referred to as "Network Environ Analysis." `enaR` currently captures all of the Patten School algorithms previously implemented in NEA.m (Fath & Borrett, 2006). Presently, the Ulanowicz School algorithms are more limited, including the ascendency calculations (Ulanowicz, 1997) and mixed trophic impacts analyses (Ulanowicz & Puccia, 1990); however, we expect the package capabilities to continue to grow, especially with the assistance of new users. This combination of the Patten and Ulanowicz schools of analyses is rare in existing software.

2.4 Example Application

Given a network model, applying ENA algorithms with `enaR` is straightforward. We demonstrate how to use the package with an example Flow analysis on Dame & Patten's (1981) model of energy flow in an Oyster Reef ecosystem. Figure 2 shows the example script. The analysis involves: (1) loading the model data, (2) checking and balancing the model if necessary, and (3) inputting the balanced model into the analysis function. The final step is interpreting the analytical output. This is a typical workflow for ENA.

After loading the `enaR` package, the next step is to enter the model data. Here, we extract the model information from the paper and create a vector of node names, the flow matrix (F), inputs (z), outputs (y), and the logical vector indicating whether or not the nodes are living (Fig. 2). We then use the `pack` function to create the required network data object. The next step is to apply the `ssCheck` function ensure that the model is at steady-state, which is one of the assumptions of the flow analysis (Fath & Borrett, 2006; Finn, 1976). If the model had not been at steady-state, we could have then applied one of four automated balancing algorithms (AVG, Input-Output, Output-Input, AVG2; Allesina & Bondavalli, 2003) to force the model into a steady-state. We then apply the `enaFlow` function to the model to perform the desired ENA flow analysis. As shown with the `attributes` function, this analysis returns 4 matrices (**G**, **GP**, **N**, **NP**) and two vectors (throughflow, T, and a vector of 20 whole-network statistics, ns).

Interpreting the ENA results is the final challenge. Here, we provide a few illustrative interpretations of the Flow analysis. Starting with the whole-network flow statistics, we see that the total system throughflow (TST) of the oyster reef model is 83.6 Kcal m^{-2} d^{-1}. TST is a measure of the total activity of the system, which is often referred to as the size or power of the system. The Finn Cycling Index (FCI) indicates that 11% of this activity was generated by recycling. Further, the average path length (APL = 2.02) shows that an average input passes over two paths before exiting the system, and the ratio of indirect to direct flows (ID.F = 1.58) indicates that the indirect flow exceeds the direct flow in this system. Together, these whole network indicators show the importance of indirect interactions in the system. A next analytical step might be to apply the Utility or Mixed Trophic Impacts analyses to determine the net relationships among the ecosystem components when we consider the direct and indirect interactions, but this is beyond our analysis here. More detailed guidance for how to interpret ENA results can be found in previously published literature (Fath & Borrett, 2006; Jørgensen *et al.*, 2007; Schramski *et al.*, 2011).

3 Value Added Features

There are several features of the enaR package beyond the core analyses that add substantive value for users. In this section we highlight several of these features including a library of 100 ecosystem network models, methods for conducting batch analysis (i.e., simultaneous analysis of multiple models), and connections to other analytical software.

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. While the library includes models used previously to test several systems ecology hypotheses (Borrett, 2013; Borrett & Salas, 2010; Borrett *et al.*, 2010; Salas & Borrett, 2011), and the set has a 47% overlap with the set of models previously collected by Dr. Ulanowicz (http://www.cbl.umces.edu/~ulan/ntwk/network.html), the full set has not previously been collected and distributed together.

We 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

Advances in ecosystem ecology have been made by comparing network metrics across multiple ecosystem models. For example, Christensen (1995) applied ENA to identify and compare the maturity of 41 ecosystem models, and van Oevelen *et al.* (2011) compared the organic matter processing of food webs 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; Whipple *et al.*, 2007).

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. 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. With the collection of algorithms and the library of models, we can now investigate possible relationships among ENA indicators from different schools (Fig. 1c). The

R script to generate Fig. 1 is available as an online enhancement (Item S1). 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. 3 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 third advantage 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. Fig. 1d illustrates applying the betweenness centrality function to the Chesapeake Bay trophic model (Baird & Ulanowicz, 1989) and visualizing the results using a 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), `Cheddar` (Hudson *et al.*, 2013), and packages in the `statnet` family (Handcock *et al.*, 2008).

4 Conclusion and Future Development

The `enaR` package encodes exiting ENA algorithms, and is designed to address limitations of current ENA software and facilitate wider use and development. It does this by (1) providing greater accessibility to the code (e.g., free and open source software available on multiple OS), (2) collecting a broad set of available ENA algorithms and workflow management functions, and (3) creating the potential for collaborative development (via GitHub and CRAN). Further, the software is extensible for individual needs and it lets users integrate ENA into a broader workflow in R in a way that is more challenging when using web based tools like EcoNet (Kazanci, 2007; Schramski *et al.*, 2011). Finally, it lets users have access to other network and statistical analysis tools (e.g., social network analysis) that are already part of R. These benefits come at the cost of having a steeper learning curve (e.g., users must know R), which may make `enaR` more suited to advanced practitioners.

In the near 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). 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 are also possible enhancements.

In conclusion, `enaR` is an R package intended to facilitate the use and the collaborative development of Ecosystem Network Analysis, a branch of network ecology. This domain is rapidly growing in part because the tools and techniques let ecologists address a wide range of relational questions at the core of ecology. We look forward to seeing new ecological discoveries made through the use of `enaR`.

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6 Tables

Table 1: Selected data input, management, and export functions in `enaR`.

Function	Description	Example Reference
pack	This function lets users combine model elements into a network data object.	None
unpack	Extracts the individual model elements (e.g., flows, inputs, outputs) from the network data object.	None
read.scor	Creates a network data object from a SCOR formatted data file.	Ulanowicz & Kay (1991)
read.wand	Creates a network data object from a WAND formatted data file.	Allesina & Bondavalli (2004)
ssCheck	Checks to see if the model is at steady-state.	None
balance	Applies one of four balancing algorithms to a model not at steady-state.	Allesina & Bondavalli (2003)
force.balance	Runs balancing algorithm as many times as necessary to balance the model.	None
write.nea	Writes the model data to the file format used as input for NEA.m.	Fath & Borrett (2006)

Table 2: Ecosystem Network Analysis functions in `enaR`.

Function	Description	Example Reference
`enaStructure`	ENA Structural analysis returns the adjacency matrix and multiple common descriptive statistics (e.g., number of nodes, connectance, pathway proliferation rate).	Borrett *et al.* (2007)
`enaFlow`	Calculates node throughflow and input and output oriented direct and integral flow intensity matrices. It also returns multiple whole network descriptive statistics including Total System Throughflow, Finn Cycling Index, and Average Path Length.	Finn (1976)
`enaAscendency`	Performs ascendency analysis on the model flows and returns whole-network statistics including the average mutual information, Ascendency, Capacity, and Overhead.	Ulanowicz (1997)
`enaStorage`	ENA Storage analysis considers how the model fluxes generate the node storage (e.g., biomass) in the system. This function returns the input and output oriented direct and integral storage matrices.	Matis & Patten (1981)
`enaUtility`	ENA Utility analysis investigates the direct relationships among the network nodes as well as the integral relationships when all of the indirect interactions are also considered.	Patten (1991)
`enaMTI`	Mixed Trophic Impacts assesses the net relationships among species in a food web.	Ulanowicz & Puccia (1990)
`enaControl`	Control analysis determines the relative control one node exerts on another through the transaction network.	Dame & Patten (1981)
`enaEnviron`	Returns the n unit and n realized input and output environs of the model.	Patten (1978)

Table 3: Selected enaRauxiliary functions and analyses.

Function	Description	Example Reference
Specialty Analyses		
enaAll	Runs all of the primary ENA algorithms.	None
get.ns	Returns the whole-network statistics from enaStructure, enaFlow, enaAscendency, enaStorage, and enaUtility.	None
eigenCentrality	Calculates the average eigenvalue centrality for any input matrix.	Fann & Borrett (2012)
environCentrality	Returns the input, output, and average environ centralities for a matrix.	Fann & Borrett (2012)
TET	Returns the total environ throughflows.	Whipple *et al.* (2007)
TES	Returns the total environ storages.	Matis & Patten (1981)
Auxiliary Functions		
get.orient	Determine the orientation of the results (row-to-column vs. School).	None
set.orient	Set the orientation of the results (row-to-column vs. School).	None
mExp	This function lets users calculate matrix exponents.	None

7 Figures

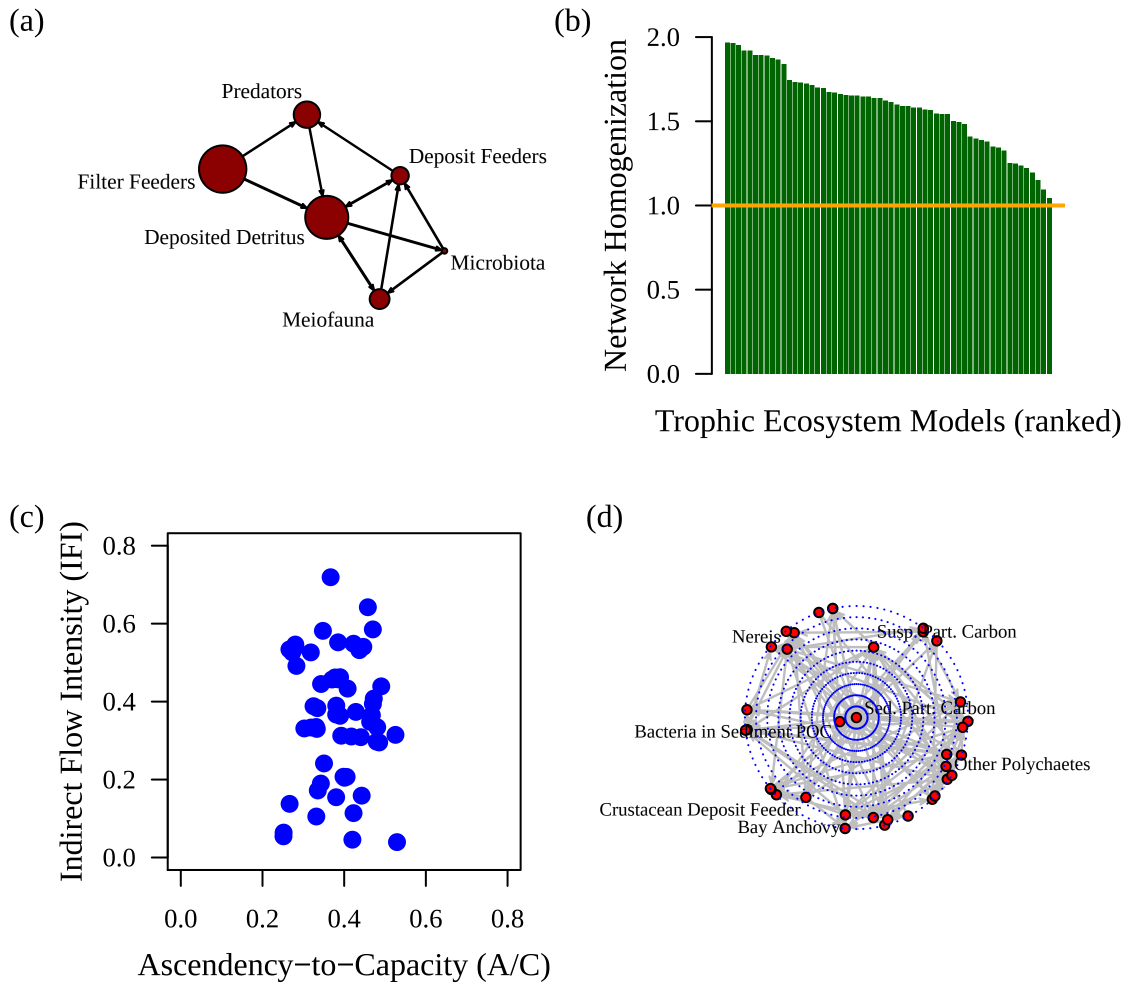

Figure 1: Example of analysis and visualizations created with `enaR` (a) network digraph of the internal flows of an oyster reef ecosystem model (Dame & Patten, 1981), (b) network homogenization statistic for 56 trophic ecosystem models (rank-ordered), (c) scatter plot showing the relationship between the ascendency-to-capacity ratio and the indirect flow index for the 56 trophic ecosystem models included in the package, and (d) target plot of the betweenness centrality from social network analysis calculated for the 36 nodes of the Chesapeake Bay ecosystem model (Baird & Ulanowicz, 1989).

```
library(enaR)   # load enaR package
> # -- ENTER MODEL DATA -- from Dame and Patten (1981)
> # node names
> names <- c("Filter Feeders","Microbiota","Meiofauna",
+                       "Deposit Feeders","Predators","Deposited Detritus")
> # Internal Flows of model, as matrix (oriented row to column)
> F <- matrix(c(0, 0, 0, 0, 0, 0, 0, 0, 0,
+                 0, 0, 8.1721, 0, 1.2060, 0, 0, 0, 7.2745,
+                 0, 1.2060, 0.6609, 0, 0, 0.6431, 0.5135, 0, 0,
+                 0.1721, 0, 0, 15.7910, 0, 4.2403, 1.9076, 0.3262, 0),
+              ncol=6)
> rownames(F) <- names  # add node names to rows
> colnames(F) <- names  # add node names to cols
> # boundary flows
> inputs <- c(41.47,0, 0, 0, 0, 0)
> outputs <- c(25.1650, 5.76, 3.5794, 0.4303, 0.3594, 6.1759)
> # Living
> Living <- c(TRUE,TRUE,TRUE,TRUE,TRUE,FALSE)
> # pack the model data into the R network data object
> m <- pack(flow=F,input=inputs, respiration=outputs, outputs=outputs, living=Living)
>
> ssCheck(m)               # check to see if the model is at steady-state
[1] TRUE
> # perform flow analysis
> F <- enaFlow(m)              # perform ENA flow analysis
> attributes(F)                 # show analysis objects created
$names
[1] "T"  "G"  "GP" "N"  "NP" "ns"

> F$ns                          # show flow analysis network statistics
     Boundary     TST TSTp      APL       FCI       BFI       DFI       IFI
[1,]    41.47 83.5833   NA 2.015512 0.1101686 0.4961517 0.1950689 0.3087794
         ID.F   ID.F.I   ID.F.O    HMG.I    HMG.O AMP.I AMP.O mode0.F  mode1.F
[1,] 1.582925 1.716607 1.534181 2.051826 1.891638     3     1   41.47 32.90504
      mode2.F  mode3.F mode4.F
[1,] 9.208256 32.90504   41.47
> F$T
    Filter Feeders         Microbiota          Meiofauna    Deposit Feeders
           41.4700             8.1721             8.4805             2.5100
         Predators Deposited Detritus
            0.6856            22.2651
```

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

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 3: Distributions of selected ENA network statistics from the u 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).