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enaR: An R package for Ecosystem Network Analysis

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1 Abstract

2 • Network analysis is a useful approach for complex, relational datasets in many biological

3   fields, including ecology and molecular and evolutionary biology.

4 • Here, we introduce enaR, an R package for conducting Ecosystem Network Analysis (ENA),

5   an analytical tool set rooted in ecosystem ecology with over 30 years of development, which

6   examines the structure and dynamics of matter and energy movement between discrete eco-

7   logical compartments (e.g., a food web).

8 • In addition to describing the primary functionality of the package, we also highlight several

9   value added features, including a library of 100 empirical ecosystem models, the ability to

10 analyze and compare multiple models simultaneously, and connections to useful ecological

11 network analysis tools in R.

12   KEYWORDS: network analysis, ecosystem, open-source software, network environ analysis,

13 ascendency, input–output analysis, food web, urban metabolism, 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 (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 ($\approx$2.4%), mutualistic networks ($\approx$0.9%), and host-parasitoid networks ($\approx$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. Extant ENA software (Allesina & Bondavalli,

38 2004; Christensen & Walters, 2004; Fath & Borrett, 2006; Kazanci, 2007; Ulanowicz & Kay, 1991)

39 each have critical limitations, which led us to three primary design objectives for enaR. The first

40 objective was to collect the major ENA functions into a single software package. While multiple

41 investigators have contributed to algorithmic development (e.g., Allesina & Bondavalli, 2003; Fath

42 & Patten, 1999; Finn, 1976; Ulanowicz, 1986; Ulanowicz & Kay, 1991), the broad set of tools is

43 not available in a single existing software. The second objective was to increase the availability

44 and extensibility of the software. We chose to use R in part because of its increasing popular-

45 ity as an analytical tool in the biological sciences (e.g., Dixon, 2003; Metcalf *et al.*, 2012; Revell,

46 2012). Further, users can freely download a stable version of the package from the CRAN web-

47 site (http://cran.r-project.org/web/packages/enaR/), and the code for every function in R

48 is available from within R (e.g., edit(*function_name*)). In addition, enaR development is being

49 managed via GitHub (https://github.com/TheSeeLab/enaR) to encourage collaborative devel-

50 opment. The third design objective was to enable enaR users access to network analysis tools from

51 other disciplines. To enable this, enaR was designed to work directly with two existing R network

52 analysis packages: network (Butts, 2008a) and sna (Butts, 2008b). In summary, the aim of the

53 enaR package is to make ENA tools more available and easier to use, adapt, and extend.

54   In this paper, we present an overview of enaR and highlight some of its functionality. A full

55 description of the ENA algorithms and their use and interpretation is beyond the scope of this short

56 paper, but we refer interested readers to a selection of reviews as an entry point to ENA (Fath

57 & Borrett, 2006; Fath & Patten, 1999; Jørgensen *et al.*, 2007; Schramski *et al.*, 2011; Ulanowicz,

58 1997). For a more comprehensive description on how to use the enaR package, please refer to the

59 package vignette: http://cran.r-project.org/web/packages/enaR/vignettes/enaR.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 these algorithms and tools include 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.

2.3 Algorithm Overview

enaR includes many of the most commonly used ENA algorithms (Table 2), along with a number of work flow and specialty analyses (Tables 1 and 3). Note that 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.

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 that characterizes 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), along with some recent developments. 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 extant software.

2.4 Example Application

Given a network model, applying ENA algorithms with enaR is straight forward. 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. Table 4 shows the example script. The analysis involves: (1) loading the model data, (2) checking and balancing the model if necessary, and (3) inputing 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 have extracted the model information from the paper and created a vector of node names, the flow matrix (F), inputs (z), outputs (y), and the logical vector indicating whether or not the nodes

128 are living (Table 4). We then use the `pack` function to create the required network data object.

129 The next step is to apply the `ssCheck` function ensure that the model is at steady-state, which is

130 one of the assumptions of the flow analysis (Fath & Borrett, 2006; Finn, 1976). If the model had

131 not been at steady-state, we could have then applied one of four automated balancing algorithms

132 (AVG, Input-Output, Output-Input, AVG2; Allesina & Bondavalli, 2003) to force the model into a

133 steady-state. We then apply the `enaFlow` function to the model to perform the desired ENA flow

134 analysis. As shown with the `attributes` function, this analysis returns 4 matrices (**G**, **GP**, **N**,

135 **NP**) and two vectors (throughflow, T, and a vector of 20 whole-network statistics, ns).

136   Interpreting the ENA results is the final challenge. Here, we provide a few illustrative interpre-

137 tations of the Flow analysis. Starting with the whole-network flow statistics, we see that the total

138 system throughflow (TST) of the oyster reef model is 83.6 Kcal m^{-2} d^{-1}. TST is a measure of

139 the total activity of the system, which is often referred to as the size or power of the system. The

140 Finn Cycling Index (FCI) indicates that 11% of this activity was generated by recycling. Further,

141 the average path length (APL = 2.02) shows that an average input passes over two paths before

142 exiting the system, and the ratio of indirect to direct flows (ID.F = 1.58) indicates that the indirect

143 flow exceeds the direct flow in this system. Together, these whole network indicators show the

144 importance of indirect interactions in the system. A next analytical step might be to apply the

145 Utility or Mixed Trophic Impacts analyses to determine the net relationships among the ecosystem

146 components when we consider the direct and indirect interactions, but this is beyond our analysis

147 here. More detailed guidance for how to interpret ENA results can be found in previously published

148 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 value added 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 thermo-dynamically 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 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 meso-haline region of the Chesapeake Bay is a typical example (Baird & Ulanowicz, 199). The second class of models focuses on biogeochemical cycling. In contrast to the trophic networks, the bio-geochemical 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

9

(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 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. 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. 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 enhancment. 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 third added benefit 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, 199) 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 wide development and use. 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 not possible in 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), and 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.

In conclusion, enaR is an R package intended to facilitate the use and the collaborative devel-

12

opment of Ecosystem Network Analysis, a branch of field of Network Ecology, which 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`.

5   Acknowledgments

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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 the user combine model elements into a network data object	none
unpack	Extracts the invidual 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	
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	
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 **enaR** auxiliary functions and analyses.

Function	Description	Example Reference
Specialty Analyses		
enaAll	Runs all of the primary ENA algorithms	
get.ns	Returns the whole-network statistics from enaStructure, enaFlow, enaAscendency, enaStorage, and enaUtility	
eigenCentrality	Calculates the average eigenvalue centrality for any input matrix	
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 enivron storages	Matis & Patten (1981)
Auxiliary Functions		
get.orient	Determine the orientation of the results (row-to-column vs. School)	
set.orient	Set the orientation of the results (row-to-column vs. School)	
mExp	This function les users calculate matrix exponents.	

Table 4: Example code for applying enaR Flow analysis to Dame & Patten's (1981) oyster reef model.

```
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
```
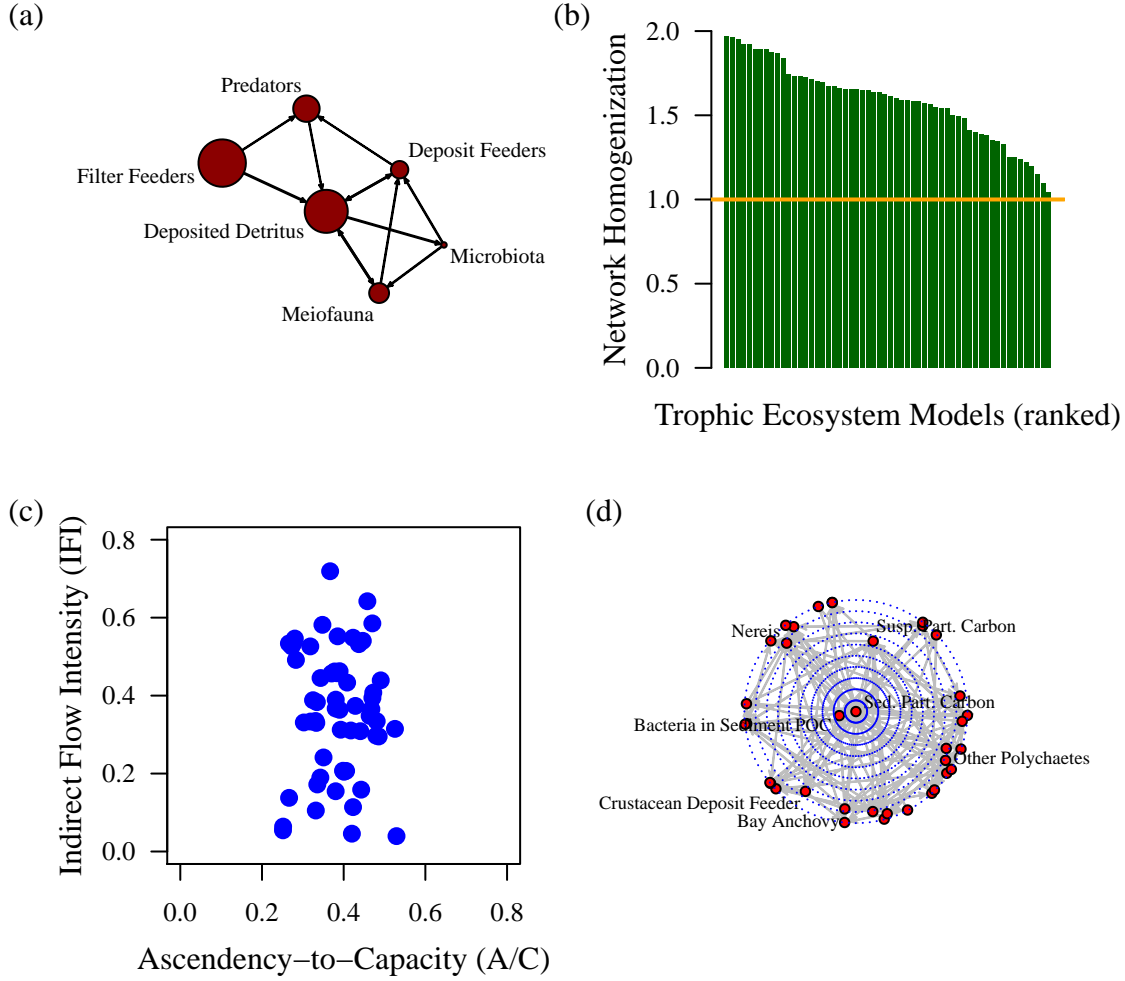
7 Figures

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 xx nodes of the Chesapeake Bay ecosystem model (Baird & Ulanowicz, 199).

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 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).