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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 investigating complex and relational datasets in  
3     many fields including ecology, molecular, and evolutionary biology.
- 4     • Here, we introduce **enaR**, an R package for Ecosystem Network Analysis (ENA). ENA is an  
5     analytical tool set rooted in ecosystem ecology with over 30 years of development that exam-  
6     ines the structure and dynamics of matter and energy movement between discrete ecological  
7     compartments (e.g., a food web).
- 8     • In addition to describing the primary functionality of the package, we highlight several features  
9     including a library of 100 empirical ecosystem models, the ability to analyze and compare  
10    multiple models simultaneously, and connections to other ecological network analysis tools in  
11    R.

12    KEYWORDS: network analysis, ecosystem, open-source software, network environ analysis,  
13    ascendency, input–output analysis, food web, urban metabolism, Ecopath, NETWRK, 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 (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 led 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 pack-

38 ages (Allesina & Bondavalli, 2004; Christensen & Walters, 2004; Fath & Borrett, 2006; Kazanci,  
39 2007; Ulanowicz & Kay, 1991) each have critical limitations, which led us to three primary design  
40 objectives for `enaR`. The first objective was to collect the major ENA functions into a single software  
41 package. While multiple investigators have contributed to algorithmic development (e.g., Allesina  
42 & Bondavalli, 2003; Fath & Patten, 1999; Finn, 1976; Ulanowicz, 1986; Ulanowicz & Kay, 1991), the  
43 broad set of tools is not available in a single existing software. The second objective was to increase  
44 the availability and extensibility of the software. We chose to use R in part because of its increasing  
45 popularity as an analytical tool in the biological sciences (e.g., Dixon, 2003; Metcalf *et al.*, 2012;  
46 Revell, 2012). Further, users can freely download a stable version of the package from the CRAN  
47 website (<http://cran.r-project.org/web/packages/enaR>), and the code for every function in  
48 R 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, 1997).  
58 For a more comprehensive description on how to use the `enaR` package, please refer to the package  
59 vignette: <http://cran.r-project.org/web/packages/enaR/vignettes/enaR-vignette.pdf>.

## 60 2 Overview of enaR

61 ENA is an agglomeration of algorithms developed to analyze network models of energy or matter  
62 movement in ecosystems (e.g., [Fath & Patten, 1999](#); [Hannon, 1973](#); [Ulanowicz, 1986](#)), but it can  
63 generally be applied to any Input-Output system that follows a thermodynamically conserved  
64 unit among the compartments. Thus, it is a family of related algorithms to analyze the ecosystem  
65 from several perspectives including its structure, flow, storage, and utility. Together, these analyses  
66 function as a “macroscope” to investigate (1) whole system organization, (2) the direct and indirect  
67 effects among system components, and (3) the processes that create and sustain ecological systems.  
68 In this section we provide an overview of the algorithms and tools included in the `enaR` software.  
69 After describing the required model information, we highlight the primary ENA algorithms included  
70 in `enaR`. We then walk through an example application of the `enaR` Flow analysis.

### 71 2.1 Data Requirements and Input

72 ENA is a data-intensive methodology. The system is modeled as a set of compartments or network  
73 nodes that represent species, species-complexes (i.e., trophic guilds or functional groups), or non-  
74 living components of the system in which energy or matter is stored. These nodes are connected  
75 by a set of direct energy or matter transactions among the nodes, termed directed edges or links.  
76 These models also have energy–matter inputs into the system and output losses from the system.  
77 In summary, the full set of data required includes: (1) internal flows, (2) boundary inputs, (3)  
78 boundary exports, (4) boundary respiration, (5) boundary outputs, which may be the sum of  
79 exports and respiration, (6) biomass or storage values, and (7) designation of living status of each  
80 node. While all seven elements are required for a full analysis, the specific data requirements varies  
81 among the ENA algorithms.

82 The primary ENA algorithms in `enaR` assume the model data is presented as an R network data

83 object defined in the `network` package. Given the data elements, users can use the `pack` function  
84 to combine the data elements into the R network data object. While a standard data format for an  
85 ENA model does not yet exist, there are two commonly used formats. First, there is the Scientific  
86 Committee for Ocean Research (SCOR) format that is the required input to NETWRK (Ulanowicz  
87 & Kay, 1991), and the second format is the Excel sheet formatted data that is the input to WAND  
88 (Allesina & Bondavalli, 2004). The `enaR` package includes a `read.scor` and a `read.wand` function  
89 to read in these common data formats (Table 1).

## 90 2.2 Visualization

91 Visualization of network models can be an essential analytical tool (Lima, 2011; Moody *et al.*,  
92 2005). Because `enaR` is built specifically to use the `network` package and data type, it is possible to  
93 quickly create network plots of the model internal structure. Fig. 1a shows an example visualization  
94 of Dame & Patten's (1981) Oyster Reef ecosystem model. The `network` package includes three  
95 network layout algorithms: circle, Fruchterman-Reingold, and Kamada-Kawai. The Fruchterman-  
96 Reingold algorithm used here is the default. The R script to generate this visualization is included  
97 in the online supplementary information (Item S1).

## 98 2.3 Algorithm Overview

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

105 [Scharler & Fath \(2009\)](#) identify two schools of ENA. The first school is based on the work of  
106 Robert Ulanowicz and colleagues at the University of Maryland ([Ulanowicz, 1986, 1997, 2009](#)).  
107 Primarily focused on trophic ecology, this approach uses information theory and the ascendancy  
108 concept to characterize ecosystem growth and development ([Ulanowicz, 1986, 1997](#)). This work  
109 is often referred to as “Ecological Network Analysis” as it predates many other types of network  
110 ecology. The second school is based on the work of Bernard Patten at the University of Georgia  
111 ([Fath & Patten, 1999; Matis & Patten, 1981; Patten, 1982; Patten \*et al.\*, 1976](#)). Steeped in dynamic  
112 equations, simulations, and systems analysis, this approach developed around the environ concept  
113 that formalizes the concept of environment ([Patten, 1978](#)), and has often been referred to as “Net-  
114 work Environ Analysis.” `enaR` currently captures all of the Patten School algorithms previously  
115 implemented in `NEA.m` ([Fath & Borrett, 2006](#)). Presently, the Ulanowicz School algorithms are  
116 more limited, including the ascendancy calculations ([Ulanowicz, 1997](#)) and mixed trophic impacts  
117 analyses ([Ulanowicz & Puccia, 1990](#)); however, we expect the package capabilities to continue to  
118 grow, especially with the assistance of new users. This combination of the Patten and Ulanowicz  
119 schools of analyses is rare in existing software.

## 120 **2.4 Example Application**

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

127 After loading the `enaR` package, the next step is to enter the model data. Here, we extract the

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

138 Interpreting the ENA results is the final challenge. Here, we provide a few illustrative interpre-  
139 tations of the Flow analysis. Starting with the whole-network flow statistics, we see that the total  
140 system throughflow (TST) of the oyster reef model is  $83.6 \text{ Kcal m}^{-2} \text{ d}^{-1}$ . TST is a measure of  
141 the total activity of the system, which is often referred to as the size or power of the system. The  
142 Finn Cycling Index (FCI) indicates that 11% of this activity was generated by recycling. Further,  
143 the average path length (APL = 2.02) shows that an average input passes over two paths before  
144 exiting the system, and the ratio of indirect to direct flows (ID.F = 1.58) indicates that the indirect  
145 flow exceeds the direct flow in this system. Together, these whole network indicators show the  
146 importance of indirect interactions in the system. A next analytical step might be to apply the  
147 Utility or Mixed Trophic Impacts analyses to determine the net relationships among the ecosystem  
148 components when we consider the direct and indirect interactions, but this is beyond our analysis  
149 here. More detailed guidance for how to interpret ENA results can be found in previously published  
150 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

174 recycling (Borrett *et al.*, 2010; Christian *et al.*, 1996). Christian & Thomas’s (2003) models of  
175 nitrogen cycling in the Neuse River Estuary are good examples of the class. The package vignette  
176 has a full listing of the models included along with references to their original publications (Lau  
177 *et al.*, 2013).

### 178 3.2 Batch Analysis

179 Advances in ecosystem ecology have been made by comparing network metrics across multiple  
180 ecosystem models. For example, Christensen (1995) applied ENA to identify and compare the  
181 maturity of 41 ecosystem models, and van Oevelen *et al.* (2011) compared the organic matter  
182 processing of food webs in three sections of the Nazaré submarine canyon. The `enaR` tool simplifies  
183 the work flow for these types of comparison. Given a list of models like the model library, it is  
184 possible to quickly analyze multiple models using R’s `lapply` function (see `help(“lapply”)`). This  
185 facilitates the kind of comparative network analysis often of interest to ecologists (Christian *et al.*,  
186 2005; Monaco & Ulanowicz, 1997; Whipple *et al.*, 2007).

187 Batch analysis can be used in several additional ways. One application is for meta-analyses,  
188 such as tests of the generality of hypothesized ecosystem properties like network non-locality (Salas  
189 & Borrett, 2011), or to investigate how physical features might influence ENA results (Niquil *et al.*,  
190 2012). Fig. 1b illustrates the rank-ordered network homogenization statistic for the 56 trophic-  
191 based ecosystem models in the library. The homogenization statistic is greater than one in all of  
192 these models indicating that the network of indirect interactions tend to more uniformly distribute  
193 the resources than is obvious from the direct interactions, which extends previous results of Borrett  
194 & Salas (2010) to include several new models. A second kind of application is the exploration of  
195 new ENA inter-relationships. With the collection of algorithms and the library of models, we can  
196 now investigate possible relationships among ENA indicators from different schools (Fig. 1c). The

197 R script to generate Fig. 1 is available as an online enhancement (Item S1). A third application  
198 of batch analysis is to investigate the previously unknown empirical ranges of ENA whole-network  
199 statistics, which may be useful for interpreting results from specific applications. Fig. 3 shows the  
200 observed distribution of values for selected network statistics from the 100 models in the library  
201 easily analyzed using `lapply` and the associated `enaR` functions.

### 202 3.3 New Connections

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

214 In addition, `enaR` can be a starting point for ecosystem network ecologists to use other R  
215 network tools. For example, the `iGraph` package provides functions to apply classic graph theory  
216 (Csardi & Nepusz, 2006). The `limSolve` package provides capabilities to infer network model fluxes  
217 from empirical data by linear inverse modeling (Soetaert *et al.*, 2009), which can also be used for  
218 uncertainty analyses of ENA (Kones *et al.*, 2009). There are a wealth of additional R package that  
219 network ecologists may find useful including `bipartite` (Dormann *et al.*, 2008), `vegan` (Dixon,

220 2003), Cheddar (Hudson *et al.*, 2013), and packages in the `statnet` family (Handcock *et al.*, 2008).

## 221 4 Conclusion and Future Development

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

232 In the near future, we anticipate two initial lines of continued development for the `enaR` package.  
233 The first is to increase the connections between the `enaR` package and other modeling and analytical  
234 tools. For example, we are currently working with colleagues to enable users of Ecopath with Ecosim  
235 (Christensen & Walters, 2004) to apply the `enaR` tools in a seamless way. We are also developing  
236 functions to connect between `enaR` and the R `limSolve` package (Soetaert *et al.*, 2009) for creating  
237 models using Linear Inverse Modeling and to enable uncertainty analysis (Kones *et al.*, 2009). The  
238 second line of development is to extend the package’s capabilities. While it currently contains  
239 most of the many commonly used ENA algorithms used by ecologists, it is far from complete. For  
240 example, Ulanowicz’s (1983) decomposition of cycles is not yet included nor is his construction  
241 for the Lindeman trophic spine (Ulanowicz & Kemp, 1979). Network model construction tools,  
242 such as least-inference methods for building models from empirical data (Ulanowicz & Scharler,

243 2008) and Fath's (2004) algorithm for constructing plausible ecosystems models are also possible  
244 enhancements.

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

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## 6 Tables

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

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

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

Function	Description	Example Reference
<code>enaStructure</code>	ENA Structural analysis returns the adjacency matrix and multiple common descriptive statistics (e.g., number of nodes, connectance, pathway proliferation rate).	<a href="#">Borrett <i>et al.</i> (2007)</a>
<code>enaFlow</code>	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.	<a href="#">Finn (1976)</a>
<code>enaAscendency</code>	Performs ascendency analysis on the model flows and returns whole-network statistics including the average mutual information, Ascendency, Capacity, and Overhead.	<a href="#">Ulanowicz (1997)</a>
<code>enaStorage</code>	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.	<a href="#">Matis &amp; Patten (1981)</a>
<code>enaUtility</code>	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.	<a href="#">Patten (1991)</a>
<code>enaMTI</code>	Mixed Trophic Impacts assesses the net relationships among species in a food web.	<a href="#">Ulanowicz &amp; Puccia (1990)</a>
<code>enaControl</code>	Control analysis determines the relative control one node exerts on another through the transaction network.	<a href="#">Dame &amp; Patten (1981)</a>
<code>enaEnviron</code>	Returns the $n$ unit and $n$ realized input and output environs of the model.	<a href="#">Patten (1978)</a>

Table 3: Selected `enaR` auxiliary functions and analyses.

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

## 7 Figures

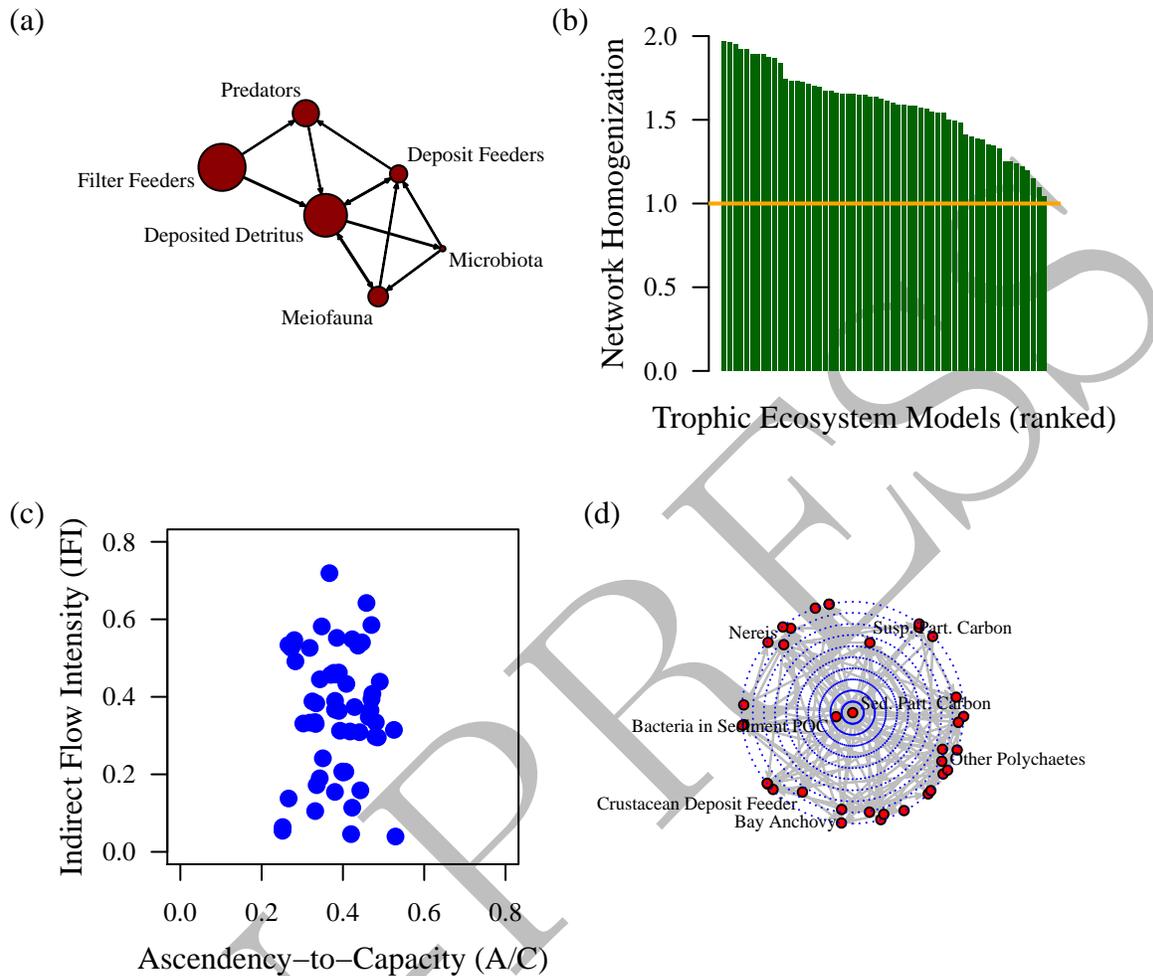


Figure 1: Example of analysis and visualizations created with `enaR` (a) network digraph of the internal flows of an oyster reef ecosystem model (Dame & Patten, 1981), (b) network homogenization statistic for 56 trophic ecosystem models (rank-ordered), (c) scatter plot showing the relationship between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

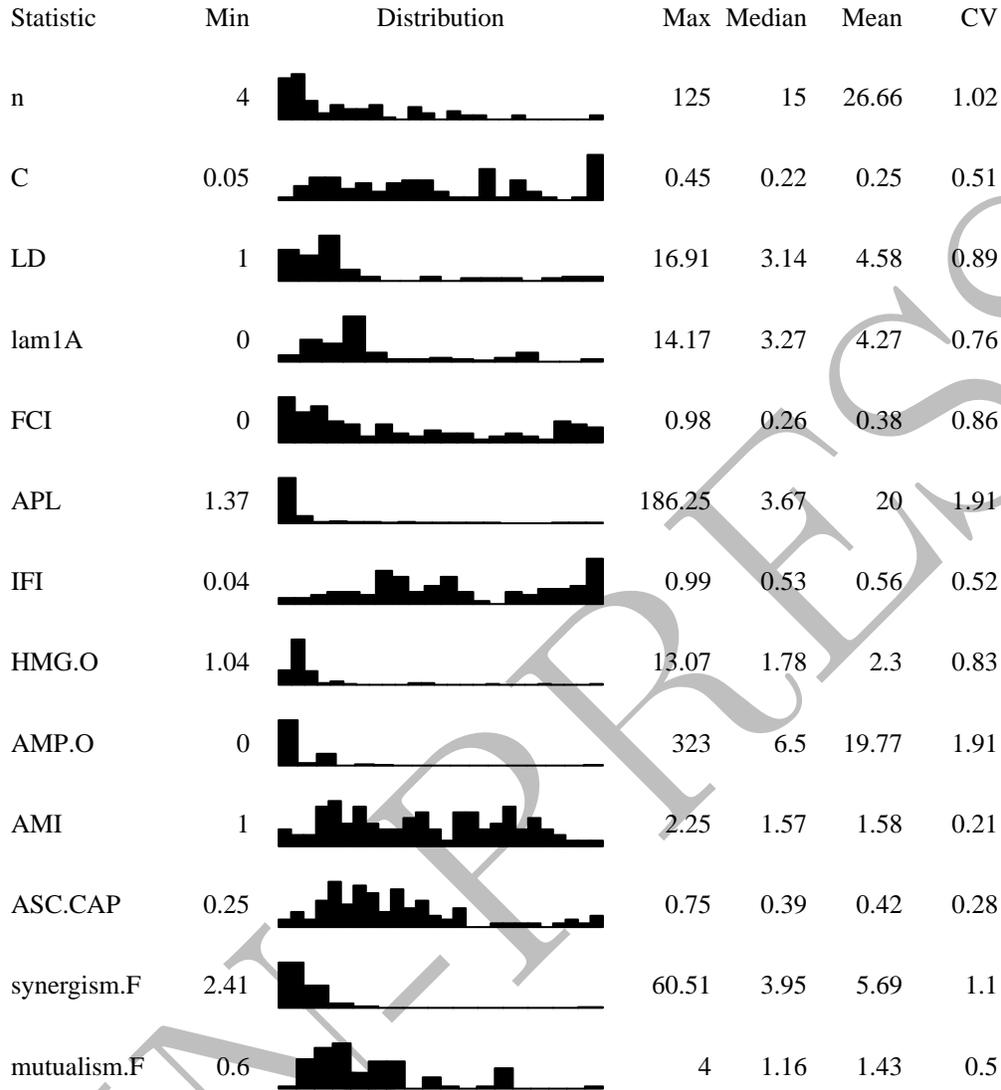


Figure 3: Distributions of selected ENA network statistics from the u 100 empirically-based ecosystem models included in `enaR`. The results are summarized using a histogram showing the distribution of the values of each network statistic between the observed minimum and maximum values. The median, mean, 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 ( $\text{lam1A}$ ), 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 ascendancy-to-capacity ratio ( $ASC.CAP$ ), flow-based network synergism ( $\text{synergism.F}$ ) and mutualism ( $\text{mutualism.F}$ ).