enaR: Ecological Network Analysis with R

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Abstract

Ecological Network Analysis (ENA) provides a framework for investigating the structure, function and dynamics of ecological systems. This is used primarily for ecosystem models focused on food webs or biogeochemical cycling, but the methods can be applied more broadly to any flow model that traces a thermodynamically conserved unit. This paper documents the *enaR* package, which collects and synthesizes the core ENA functions, including those developed by the Ulanowicz and Patten schools. Further, the package connects users to additional network analysis tools available in **R** and beyond. This document details how to use the primary functions for the analysis of single models. In addition, we demonstrate a key strength of this package, which is that it enables a user to perform simultaneous, synthetic analysis of multiple ecosystem models.

Introduction

Network models have provided insights into a variety of complex systems (Watts and Strogatz 1998; Newman 2001; Barabási 2012; Newman, Barabási, and Watts 2006; Wasserman and Faust 1994). Although the network approach has deep roots (Newman, Barabási, and Watts 2006), its use has been expanding rapidly in a variety of disciplines including ecology (Borrett, Moody, and Edelmann 2014; Ings et al. 2009). Investigators are building a science of networks (National Research Council, Committee on Network Science for Army Applications 2006; Brandes et al. 2013). This is due in part to the flexibility of the core representation, its utility in answering relational questions, and its applicability to "Big Data" problems.

Ecosystem ecologists developed and have been using network modeling and analysis for several decades (Hannon 1973; Ulanowicz 1986; Fath and Patten 1999). The core network model maps transfers of thermodynamically conserved energy or matter (represented by weighted, directed graph edges) between nodes that represent species, groups of species, or non-living components (e.g., dead organic matter) of the ecosystem. These analyses, collectively known as Ecosystem Network Analysis (ENA), have been used in a variety of ways including to reveal the relative importance of indirect effects in ecosystems (Patten 1983; Higashi and Patten 1989; Salas and Borrett 2011) and their capacity to effectively transform the relations among organisms (Ulanowicz and Puccia 1990; Patten 1991; Fath and Patten 1998; Bondavalli and Ulanowicz 1999; Borrett, Hines, and Carter 2016). From these applications a new theoretical understanding of ecosystems has emerged (Higashi and Burns 1991; Belgrano et al. 2005; Jørgensen et al. 2007). Recently, scientists have applied these methods to understand trophic dynamics in the Sylt-Romo Bight (Baird, Asmus, and Asmus 2004; Baird, Asmus, and Asmus 2008), biogeochemical cycling in lakes and estuaries (Christian and Thomas 2003; Small, Sterner, and Finlay 2014; Hines et al. 2015), the impacts of human activities on ecosystems (Tecchio et al. 2016), and urban sustainability (Zhang, Yang, and Fath 2010; Chen and Chen 2012; Xia et al. 2016).

Two major schools of ENA have developed (Scharler and Fath 2009). The first is based on Dr. Robert E. Ulanowicz's work with a strong focus on trophic dynamics and a use of information theory (Ulanowicz 1986 Ulanowicz (1997); Ulanowicz 2004). The second school has an environment focus and is built on the environ

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concept introduced by Dr. Bernard C. Patten (Patten et al. 1976; Patten 1978; Fath and Patten 1999). Patten's approach has been collectively referred to separately as *Network Environ Analysis*. At the core the two approaches are very similar; however, they make some different starting assumptions and follow independent yet braided development tracks.

Disparate software packages have been created to support ENA. Initially algorithms were developed and distributed as the DOS based NETWRK4 (Ulanowicz and Kay 1991), which is still available from www.cbl.umces.edu/~ulan/ntwk/network.html. Some of these algorithms were re-implemented in a Microsoft Excel based toolbox, WAND (Allesina and Bondavalli 2004). The popular Ecopath with Ecosim software that assists with model construction (Christensen and Walters 2004) also provides multiple ENA algorithms. The algorithms for flow analysis – one component of ENA – were collected into a stand-alone software tool (Latham II 2006). Fath and Borrett (2006) published NEA.m that collects most of the Patten School ENA algorithms together in a single **MATLAB** function. Similarly, the online tool EcoNet (Kazanci 2007) has made many of the ENA algorithms available in an easy access framework. The NetIndicies is an alternative **R** package that returns an impressive subset of the whole network metrics derived from ENA (Kones et al. 2009). Although these packages collectively provide access to a large set of powerful analytic tools, the fragmented distribution of the key algorithms among the software tools has inhibited the development of theory and the further implementation of important algorithms.

The *enaR* package brings together the ENA algorithms into one common software framework that is readily available and extensible. The package is written in the **R** language, which is free and open-source. Due largely to this, **R** is now one of the most widely used analytic programming languages in the biological sciences. *enaR* builds on existing **R** packages for network analysis. For example, it uses the *network* data structure developed by (Butts 2008a) and the network analysis tools built into the *network*, *sna* (social network analysis) (Butts 2008b), and *statnet* (Handcock et al. 2008) packages. While Borrett and Lau (2014) introduced the *enaR* package, this document provides a richer documentation of the software and illustrate its use.

New in version 2.10

Version 2.10 of *enaR* contains a number of new features, extensions, and software fixes. Here we highlight some of the key substantive changes.

- enaFlow
  - Added calculations for Total Dependency Coefficients (TDC) and Total Contribution Coefficients (TCC) (Szyrmer and Ulanowicz 1987, Kay1991).
  - The flow diversity metrics including the Ascendency family of metrics are now included in the the enaFlow vector of network statistics.
- The enaAscendency function has been extended to return additional metrics including
  - The Shannon Diversity of the extended flow matrix (H) following (MacArthur 1955).
  - The tetra-partite division of the Capacity, Ascendency, and Overhead metrics into the component parts for input, internal, export, and respiration.
- We added a *Relations.Table* to both enaUtility and enaMTI that summarizes the direct and integral (net) qualitative pairwise relationships among the model nodes determined by these analyses.
- enaStorage; we added calculations for variance in expected input- and output-oriented residence times (Barber 1979)
- enaControl; This function was updated to include the Control Allocation Matrix and Control Dependency Matrix (Chen, Fath, and Chen 2011)
- Bug fixed in the findPathLength function for identifying the path (walk) length at which indirect flow exceeds direct flow.

- New function ShannonDiveristy that calculates a set of metrics based on Shannon's diversity (entropy) functions for any vector. For example, this can be applied to the system biomasses or the system throughflows.
- New function signs that evaluates and returns a number of qualitative evaluations on a given matrix. This function is useful on its own, but it is also used by enaUtility and enaMTI to generate the Relations.Table
- This release changes the way that *enaR* builds its NAMESPACE and documentation. This is now managed with *roxygen2*. Function imports from other packages and exports from *enaR* are now more selective to reduce the time to load and conflicts in the names space. Most of the changes are positive for the package management, but one consequence is that some dependent packages that were previously loaded with *enaR* are not completely loaded. Thus, a user may need to load packages like *network* or *sna* to access the full breadth of their functionality.

Getting Started

In this section we describe the data necessary for Ecological Network Analysis and show how to build the central network data object in **R** that contains the model data for subsequent analysis. To start, the current stable version can be installed from CRAN:

```
install.packages('enaR')
```

The development version can be installed from GitHub:

```
require(devtools)
install_github('SEELab/enaR',ref='develop')
```

You can now load the package:

```
require(enaR)
```

Ecosystem Network Model

ENA is applied to a network model of energy–matter exchanges among system components. The system is modeled as a set of n compartments or nodes that represent species, species-complexes (i.e., trophic guilds or functional groups), or non-living components of the system in which energy–matter is stored. Nodes are connected by L observed fluxes, termed directed edges or links. This analysis requires an estimate of the energy–matter flowing from node i to j over a given period, $\mathbf{F}_{n\times n} = [f_{ij}]$, $i, j = 1, 2, \ldots, n$. These fluxes can be generated by any process such as feeding (like a food web), excretion, and death. As ecosystems are thermodynamically open, there must also be energy or matter inputs into the system $\mathbf{z}_{1\times n} = [z_i]$, and output losses from the system $\mathbf{y}_{1\times n} = [y_i]$. While the Patten School treats all outputs the same, the Ulanowicz School typically partitions outputs into respiration $\mathbf{r}_{1\times n} = [r_i]$ and export $\mathbf{e}_{1\times n} = [e_i]$ to account for differences in energetic quality. Note that $y_i = r_i + e_i, \forall i$. Some analyses also require the amount of energy–matter stored in each node (e.g., biomass), $\mathbf{X}_{1\times n} = [x_i]$. The final required information is a categorization of each node as living or not, which is essential for algorithms from the Ulanowicz School. For our implementation, we have created a logical vector $\mathbf{Living}_{1\times n}$ that indicates whether the i^{th} node is living (TRUE) or not (FALSE). This obviates the need to order the nodes in a specific way (i.e., living before non-living). Together, the model data $\mathcal{M}$ can be summarized as $\mathcal{M} = \{\mathbf{F}, \mathbf{z}, \mathbf{e}, \mathbf{r}, \mathbf{X}, \mathbf{Living}\}$.

Notice the row-to-column orientation of the flow matrix: $\mathbf{F}$. This is consistent with the Ulanowicz School of network analysis, as well as the orientation commonly used in Social Network Analysis and used in the *statnet* packages. However, this is the opposite orientation typically used in the Patten School of analysis

that conceptually builds from a system of differential equations and thus uses the column-to-row orientation common in this area of mathematics. Even though the difference is only a matrix transpose, this single difference may be the source of much confusion in the literature and frustration on the part of users. We have selected to use row-to-column orientation for our primary data structure, as it is the dominant form across network analytics as evidenced by it use in the *statnet* packages. The package algorithms also return the results in the row-to-column orientation by default; however, we have built in functionality with get.orient and set.orient that allows users to return output in the Patten School row-to-column orientation (see the Orientation Section for details).

Model Construction

There are multiple methods for constructing ecosystem network models and tools for assisting with this process (Fath et al. 2007). One approach is to construct a dynamic, processes-based, mathematical model of the system typically using ordinary differential equations. For example, the EcoPath with EcoSim (Christensen and Pauly 1992; Christensen 1995) software assists scientists with constructing food-web focused ecosystem models using an underlying bioenergetic approach. Alternatively, Ulanowicz (1986) has called for a more phenomenological approach to the model construction. This modeling process starts with a conceptual network model of the system and then the node and edge weights are estimated directly from observations. Its phenomenological in the sense that it focuses on what the flows are, rather than the forms of the mechanistic processes that generate the flows. As this approach is essentially an inverse problem, some have developed inverse linear modeling methods to assist with inferring the network weights from data (Vézina and Platt 1988; Oevelen et al. 2010). The *limSolve* **R** package can assist with this modeling approach (Soetaert, Van den Meersche, and Oevelen 2009). Ulanowicz and Scharler (2008) also introduced two least-inference algorithms to assist with this kind of model construction. These methods focus on constructing models to represent specific empirical systems. Algorithms also exist for constructing simulated ecosystems, including the Cyber Model algorithm that use a community assembly type approach (Fath 2004). Currently, the *enaR* software focuses on the analysis of network models and assumes that the user has a network model to be analyzed.

Network Data Class

The *enaR* package stores the model data in the **network** class defined in the *network* package (Butts 2008a). In this software, a complete ecosystem network model description includes:

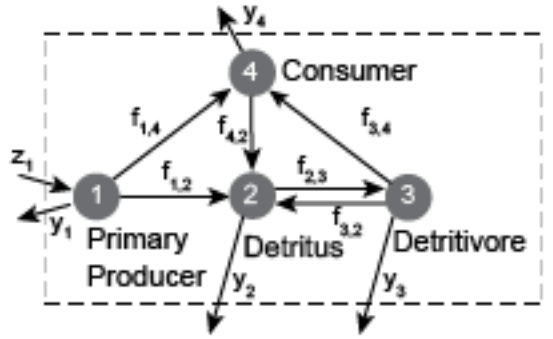
- **F** is the $n \times n$ flow matrix, oriented row-to-column
- **z** a vector of inputs
- **r** a vector of respirations
- **e** a vector of exports
- **y** a vector of outputs, which are respirations plus exports
- **X** a vector of biomass or storage values
- **Living** = logical vector indicating if the node is living (TRUE) or non-living (FALSE)

Building a Network Object

At present, *enaR* assumes that the user has a model constructed. Thus, the first task is to get the model into the software. One way to to this is to assemble the necessary data elements and then use the pack function to create the network data object. Here is an example of doing this for the generic hypothetical ecosystem model shown in the following Figure (modified from Borrett, Whipple, and Patten (2010)).

```
## Generate the flow matrix
flow.mat <- matrix( c(0,0,0,0,
                      10,0,2.026,1.4805,
```

(a)



(b)

$$\mathbf{F} = \begin{bmatrix} 0 & 10 & 0 & 1 \\ 0 & 0 & 6.7532 & 0 \\ 0 & 2.026 & 0 & 2.7013 \\ 0 & 1.4805 & 0 & 0 \end{bmatrix}$$

$$\vec{z} = \begin{bmatrix} 100 & 0 & 0 & 0 \end{bmatrix}$$

$$\vec{y}^{\mathrm{T}} = \begin{bmatrix} 89 & 6.7532 & 2.026 & 2.2208 \end{bmatrix}$$

Figure 1:

```
                    0,6.7532,0,
                    0,1,0,2.7013,0), ncol = 4)

## Name the nodes
rownames(flow.mat) <- colnames(flow.mat) <- c("Primary Producer", "Detritus",
                                              "Detritivore", "Consumer")

## Generate the inputs
inputs <- c(100, 0, 0, 0)
## Generate the exports
exports <- c(89, 6.7532, 2.026, 2.2208)
## "Pack" the model into a network object
fake.model <- pack(flow = flow.mat,
                   input = inputs,
                   export = exports,
                   living = c(TRUE,FALSE,TRUE,TRUE))
```

```
## [1] "respiration" "storage"
```

```
## Warning in pack(flow = flow.mat, input = inputs, export = exports, living =
## c(TRUE, : Missing model components: respiration, storage
```

When we pack this model, we receive a *warning* that reminds us that the model we have specified is missing the respiration and storage components. This is not an error, as we did not specify these components. With the information we have, we can still complete many of the analyses collected in *enaR*; however, some of them

will not work without the required information (i.e., enaStorage returns the storage information). Individual *enaR* functions check to ensure the required information is present in the model before they are applied.

We can take a closer look at the network data object as follows:

```
## The model network object contents
fake.model
```

```
##  Network attributes:
##   vertices = 4
##   directed = TRUE
##   hyper = FALSE
##   loops = TRUE
##   multiple = FALSE
##   bipartite = FALSE
##   balanced = TRUE
##   total edges= 6
##     missing edges= 0
##     non-missing edges= 6
##
##  Vertex attribute names:
##     export input living output respiration storage vertex.names
##
##  Edge attribute names:
##     flow
```

These results tell the user what the software has already inferred about the network from the initial data. The network data object divides these initial properties into whole network attributes, vertex attributes, and edge attributes. At the network level, the network has 4 vertices, it is a directed network, it is not a hypergraph, it can contain self-loops (set by the pack function), it is not a bipartite matrix, it is balanced (inputs = outputs), and it has 6 edges. The Vertices (nodes) have a set of attributes including the values for export, input, living, output, respiration, storage, and vertex.names. Finally, the edge attributes are currently limited to the flow weights.

The individual components can be extracted from the data object using the form specified in the *network* package (network vignette).

For example, we can extract specific network attributes as follows:

```
# is the network directed?
fake.model%n%"directed"
```

```
## [1] TRUE
```

```
# how many nodes are in the network?
fake.model%n%"n"
```

```
## [1] 4
```

```
# alternatively, we can use a different network package function to find the number of nodes
network.size(fake.model)
```

```
## [1] 4
```

Similarly, we can pull out "vertex" (i.e. node) attributes as follows:

```
fake.model%v%'output'
```

```
## [1] 89.0000  6.7532  2.0260  2.2208
```

```
fake.model%v%'input'
```

```
## [1] 100   0   0   0
```

```
fake.model%v%'living'
```

```
## [1]  TRUE FALSE  TRUE  TRUE
```

The network flows are stored as edge weights in the network object, which lets users fully manipulate the network object with the network functions. The flow matrix can be extracted from the object with:

```
as.matrix(fake.model, attrname="flow")
```

```
##                   Primary Producer Detritus Detritivore Consumer
## Primary Producer                 0  10.0000      0.0000   1.0000
## Detritus                         0   0.0000      6.7532   0.0000
## Detritivore                      0   2.0260      0.0000   2.7013
## Consumer                         0   1.4805      0.0000   0.0000
```

There are times that it is useful to extract all of the ecosystem model data elements from the network data object. This can be accomplished using the unpack function. The unpack output is as follows:

```
unpack(fake.model)
```

```
## $F
##                   Primary Producer Detritus Detritivore Consumer
## Primary Producer                 0  10.0000      0.0000   1.0000
## Detritus                         0   0.0000      6.7532   0.0000
## Detritivore                      0   2.0260      0.0000   2.7013
## Consumer                         0   1.4805      0.0000   0.0000
##
## $z
## [1] 100   0   0   0
##
## $r
## [1] 0 0 0 0
##
## $e
## [1] 89.0000  6.7532  2.0260  2.2208
##
## $y
## [1] 89.0000  6.7532  2.0260  2.2208
##
## $X
```

```
## [1] NA NA NA NA
##
## $living
## [1]  TRUE FALSE  TRUE  TRUE
```

Since we did not specify the storage values when we used pack, the storage values were set to NA values. In contrast, pack generated zero values for the respiration values. The function assumes that if you don't specify respiration (or export) then the values must be zero. The output values are generated by adding the respiration and export values together. Although the package is designed to help users navigate missing data issues, you should check that you are providing the appropriate input for a given function.

Model Library

enaR includes a library of 104 empirically-based, previously published ecosystem models that can be categorized into three general classes: trophic, biogeochemical cycling, and urban metabolism (Christian et al. 1996; Baird, Asmus, and Asmus 2008; Borrett, Whipple, and Patten 2010; Borrett, Hines, and Carter 2016). First, 59 of the models are trophically-based models with food webs at their core and 43 models focused on biogeochemical cycling in ecosystems (Network Model Information Table). These models were originally published for a number of different types of ecosystems, though predominantly aquatic, by a number of author teams. Models in the library range in size from 4 nodes to 125 nodes with connectance values ranging from 7% to 45%.

This collection of models overlaps with other extant data sets. For example, twenty-four of the models are included in the set of forty-eight models compiled and distributed by Dr. Ulanowicz (http://www.cbl.umces.edu/~ulan/ntwk/network.html). All 50 of the models analyzed by (Borrett and Salas 2010) and (Salas and Borrett 2011) and the 45 models analyzed in (Borrett 2013) are included in this model library.

The full set of models are collected into the enaModels object, and a list of information about the models is stored as enaModelInfo. Further, the trophic models are grouped as the troModels object and the biogeochemically-based models are available as the bgcModels object. Both data objects return a list of the model network objects. To use these models simply use the **R** *base* data function. This will load the models into the working memory as a named list of network objects:

```
## Import the model sets
data(enaModels)
data(bgcModels)
data(troModels)
## Find the names of the first few models
head(names(bgcModels))
```

```
## [1] "Hubbard Brook (Ca)(Waide)"     "Hardwood Forest, NH (Ca)"
## [3] "Duglas Fir Forest, WA (Ca)"    "Duglas Fir Forest, WA (K)"
## [5] "Puerto Rican Rain Forest (Ca)" "Puerto Rican Rain Forest (K)"
```

```
head(names(troModels))
```

```
## [1] "Marine Coprophagy (oyster)" "Lake Findley "
## [3] "Mirror Lake"                "Lake Wingra"
## [5] "Marion Lake"                "Cone Springs"
```

```r
## Isolate a single model
x <- troModels[[1]]
x <- troModels$"Marine Coprophagy (oyster)"
## Check out the model
summary(x)
```

```
## Network attributes:
##   vertices = 4
##   directed = TRUE
##   hyper = FALSE
##   loops = TRUE
##   multiple = FALSE
##   bipartite = FALSE
##   balanced = TRUE
##  total edges = 4
##    missing edges = 0
##    non-missing edges = 4
##  density = 0.25
##
## Vertex attributes:
##
##  export:
##    logical valued attribute
##    attribute summary:
##    Mode    NA's
## logical       4
##
##  input:
##    numeric valued attribute
##    attribute summary:
##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##    0.00    0.00   62.05   94.90  157.00  255.50
##
##  living:
##    logical valued attribute
##    attribute summary:
##    Mode   FALSE    TRUE    NA's
## logical       2       2       0
##
##  output:
##    numeric valued attribute
##    attribute summary:
##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##    6.60   21.67   64.45   94.90  137.70  244.10
##
##  respiration:
##    numeric valued attribute
##    attribute summary:
##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##    6.60   21.67   64.45   94.90  137.70  244.10
##
##  storage:
##    numeric valued attribute
```

```
##    attribute summary:
##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##       1       1       1       1       1       1
##   vertex.names:
##    character valued attribute
##    4 valid vertex names
##
## Edge attributes:
##
##  flow:
##    numeric valued attribute
##    attribute summary:
##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##   15.30   20.25   37.40   42.42   59.58   79.60
##
## Network adjacency matrix:
##                           SHRIMP BENTHIC ORGANISMS SHRIMP FECES & BACTERIA
## SHRIMP                         0                 0                       1
## BENTHIC ORGANISMS              0                 0                       0
## SHRIMP FECES & BACTERIA        0                 1                       0
## BENTHIC FECES & BACTERIA       0                 1                       0
##                           BENTHIC FECES & BACTERIA
## SHRIMP                                           0
## BENTHIC ORGANISMS                                1
## SHRIMP FECES & BACTERIA                          0
## BENTHIC FECES & BACTERIA                         0
```

Network Model Information

Table 1: Trophic ecosystem (n = 59), biogeochemical ecosystem (n = 43), and Urban metabolism networks (n=2) included in the *enaR* model library. n is the number of nodes in the network model.

Model	Type	Units	n	Reference
Marine Coprophagy (oyster)	Tro	kcal m^{-2} yr^{-1}	4	Haven and Morales-Alamo (1966)
Lake Fndley	Tro	gC m^{-2} yr^{-1}	4	Richey et al. (1978)
Mirror Lake	Tro	gC m^{-2} yr^{-1}	5	Richey et al. (1978)
Lake Wngra	Tro	gC m^{-2} yr^{-1}	5	Richey et al. (1978)
MarionLake	Tro	gC m^{-2} yr^{-1}	5	Richey et al. (1978)
Cone Srings	Tro	kcal m^{-2} yr^{-1}	5	Tilly (1968)
SilverSprings	Tro	kcal m^{-2} yr^{-1}	5	Odum (1957)
Englis Channel	Tro	kcal m^{-2} yr^{-1}	6	Brylinsky (1972)
OysterReef	Tro	kcal m^{-2} yr^{-1}	6	Dame and Patten (1981)
Baie de Somme	Tro	mgC m^{-2} d^{-1}	9	Rybarczyk et al. (2003)
Bothnin Bay	Tro	gC m^{-2} yr^{-1}	12	Sandberg, Elmgren, and Wulff (2000)
Bothnin Sea	Tro	gC m^{-2} yr^{-1}	12	Sandberg, Elmgren, and Wulff (2000)
Ythan Estuary	Tro	gC m^{-2} yr^{-1}	13	Baird and Milne (1981)
Sundarban Mangrove (virgin)	Tro	kcal m^{-2} yr^{-1}	14	Ray (2008)

Model	Type	Units	n	Reference
Sundarban Mangrove (reclaimed)	Tro	kcal m^{-2} yr^{-1}	14	Ray (2008)
Baltic Sea	Tro	mg C m^{-2} d^{-1}	15	Baird, McGlade, and Ulanowicz (1991)
Ems Estuary	Tro	mg C m^{-2} d^{-1}	15	Baird, McGlade, and Ulanowicz (1991)
Swartkops Estuary 15	Tro	mg C m^{-2} d^{-1}	15	Baird, McGlade, and Ulanowicz (1991)
Southern Benguela Upwelling	Tro	mg C m^{-2} d^{-1}	16	Baird, McGlade, and Ulanowicz (1991)
Peruvian Upwelling	Tro	mg C m^{-2} d^{-1}	16	Baird, McGlade, and Ulanowicz (1991)
Crystal River (control)	Tro	mg C m^{-2} d^{-1}	21	Ulanowicz (1986)
Crystal River (thermal)	Tro	mg C m^{-2} d^{-1}	21	Ulanowicz (1986)
Charca de Maspalomas Lagoon	Tro	mg C m^{-2} d^{-1}	21	Almunia et al. (1999)
Northern Benguela Upwelling	Tro	mg C m^{-2} d^{-1}	24	Heymans and Baird (2000)
Swartkops Estuary	Tro	mg C m^{-2} d^{-1}	25	Scharler and Baird (2005)
Sunday Estuary	Tro	mg C mˆ-2 d^{-1}	25	Scharler and Baird (2005)
Kromme Estuary	Tro	mg C m^{-2} d^{-1}	25	Scharler and Baird (2005)
Okefenokee Swamp	Tro	g dw m^{-2} y^{-1}	26	Whipple and Patten (1993)
Neuse Estuary (early summer 1997)	Tro	mg C m^{-2} d^{-1}	30	Baird et al. (2004)
Neuse Estuary (late summer 1997)	Tro	mg C m^{-2} d^{-1}	30	Baird et al. (2004)
Neuse Estuary (early summer 1998)	Tro	mg C m^{-2} d^{-1}	30	Baird et al. (2004)
Neuse Estuary (late summer 1998)	Tro	mg C m^{-2} d^{-1}	30	Baird et al. (2004)
Gulf of Maine	Tro	g ww m^{-2} yr^{-1}	31	Link et al. (2008)
Georges Bank	Tro	g ww m^{-2} yr^{-1}	31	Link et al. (2008)
Middle Atlantic Bight	Tro	g ww m^{-2} yr^{-1}	32	Link et al. (2008)
Narragansett Bay	Tro	mgC m^{-2} yr^{-1}	32	Monaco and Ulanowicz (1997)
Southern New England Bight	Tro	g ww m^{-2} yr^{-1}	33	Link et al. (2008)
Chesapeake Bay	Tro	mg C m^{-2} yr^{-1}	36	Baird and Ulanowicz (1989)
Mondego Estuary (Zostera Meadows)	Tro	g AFDW mˆ2 yr^{-1}	43	Patrício and Marques (2006)
St. Marks Seagrass site 1 (Jan.)	Tro	mg C m^{-2} d^{-1}	51	Baird, Luczkovich, and Christian (1998)
St. Marks Seagrass site 1 (Feb.)	Tro	mg C m^{-2} d^{-1}	51	Baird, Luczkovich, and Christian (1998)
St. Marks Seagrass site 2 (Jan.)	Tro	mg C m^{-2} d^{-1}	51	Baird, Luczkovich, and Christian (1998)
St. Marks Seagrass site 2 (Feb.)	Tro	mg C m^{-2} d^{-1}	51	Baird, Luczkovich, and Christian (1998)
St. Marks Seagrass site 3 (Jan.)	Tro	mg C m^{-2} d^{-1}	51	Baird, Luczkovich, and Christian (1998)

Model	Type	Units	n	Reference
St. Marks Seagrass site 4 (Feb.)	Tro	mg C m^{-2} d^{-1}	51	Baird, Luczkovich, and Christian (1998)
Sylt-Romo Bight	Tro	mg C m^{-2} d^{-1}	59	Baird, Asmus, and Asmus (2004)
Graminoids (wet)	Tro	g C m^{-2} yr^{-1}	66	Ulanowicz et al. (2000)
Graminoids (dry)	Tro	g C m^{-2} yr^{-1}	66	Ulanowicz et al. (2000)
Cypress (wet)	Tro	g C m^{-2} yr^{-1}	68	Ulanowicz, Bondavalli, and Egnotovich (1997)
Cypress (dry)	Tro	g C m^{-2} yr^{-1}	68	Ulanowicz, Bondavalli, and Egnotovich (1997)
Lake Oneida (pre-ZM)	Tro	g C m^{-2} yr^{-1}	74	Miehls, Mason, et al. (2009b)
Lake Oneida (post-ZM)	Tro	g C m^{-2} yr^{-1}	76	Miehls, Mason, et al. (2009b)
Bay of Quinte (pre-ZM)	Tro	g C m^{-2} yr^{-1}	74	Miehls, Mason, et al. (2009a)
Bay of Quinte (post-ZM)	Tro	g C m^{-2} yr^{-1}	80	Miehls, Mason, et al. (2009a)
Mangroves (wet)	Tro	g C m^{-2} yr^{-1}	94	Ulanowicz et al. (1999)
Mangroves (dry)	Tro	g C m^{-2} yr^{-1}	94	Ulanowicz et al. (1999)
Florida Bay (wet)	Tro	mg C m^{-2} yr^{-1}	125	Ulanowicz, Bondavalli, and Egnotovich (1998)
Florida Bay (dry)	Tro	mg C m^{-2} yr^{-1}	125	Ulanowicz, Bondavalli, and Egnotovich (1998)
Hubbard Brook (Waide)	BGC	kg Ca Ha^{-1} yr^{-1}	4	Waide et al. (1974)
Hardwood Forest NH	BGC	kg Ca Ha^{-1} yr^{-1}	4	Jordan, Kline, and Sasscer (1972)
Douglas Fir Forest WA	BGC	kg Ca Ha^{-1} yr^{-1}	4	Jordan, Kline, and Sasscer (1972)
Douglas Fir Forest WA	BGC	kg K Ha^{-1} yr^{-1}	4	Jordan, Kline, and Sasscer (1972)
Puerto Rican Rain Forest	BGC	kg Ca Ha^{-1} yr^{-1}	4	Jordan, Kline, and Sasscer (1972)
Puerto Rican Rain Forest	BGC	kg K Ha^{-1} yr^{-1}	4	Jordan, Kline, and Sasscer (1972)
Puerto Rican Rain Forest	BGC	kg Mg Ha^{-1} yr^{-1}	4	Jordan, Kline, and Sasscer (1972)
Puerto Rican Rain Forest	BGC	kg Cu Ha^{-1} yr^{-1}	4	Jordan, Kline, and Sasscer (1972)
Puerto Rican Rain Forest	BGC	kg Fe Ha^{-1} yr^{-1}	4	Jordan, Kline, and Sasscer (1972)
Puerto Rican Rain Forest	BGC	kg Mn Ha^{-1} yr^{-1}	4	Jordan, Kline, and Sasscer (1972)
Puerto Rican Rain Forest	BGC	kg Na Ha^{-1} yr^{-1}	4	Jordan, Kline, and Sasscer (1972)
Puerto Rican Rain Forest	BGC	kg Sr Ha^{-1} yr^{-1}	4	Jordan, Kline, and Sasscer (1972)
Tropical Rain Forest	BGC	g N m^{-2} d^{-1}	5	Edmisten (1970)
Neuse River Estuary (AVG)	BGC	mmol N m^{-2} $season^{-1}$	7	Christian and Thomas (2003)
Neuse River Estuary (Spring 1985)	BGC	mmol N m^{-2} $season^{-1}$	7	Christian and Thomas (2003)

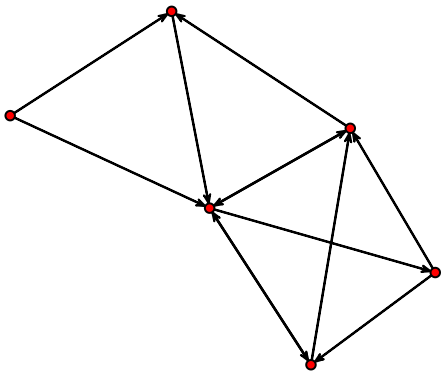
Model	Type	Units	n	Reference
Neuse River Estuary (Summer 1985)	BGC	mmol N m^{-2} $season^{-1}$	7	Christian and Thomas (2003)
Neuse River Estuary Fall 1985)	BGC	mmol N m^{-2} $season^{-1}$	7	Christian and Thomas (2003)
Neuse River Estuary Winter 1986)	BGC	mmol N m^{-2} $season^{-1}$	7	Christian and Thomas (2003)
Neuse River Estuary (Spring 1986)	BGC	mmol N m^{-2} $season^{-1}$	7	Christian and Thomas (2003)
Neuse River Estuary (Summer 1986)	BGC	mmol N m^{-2} $season^{-1}$	7	Christian and Thomas (2003)
Neuse River Estuary (Fall 1986)	BGC	mmol N m^{-2} $season^{-1}$	7	Christian and Thomas (2003)
Neuse River Estuary (Winter 1987)	BGC	mmol N m^{-2} $season^{-1}$	7	Christian and Thomas (2003)
Neuse River Estuary (Spring 1987)	BGC	mmol N m^{-2} $season^{-1}$	7	Christian and Thomas (2003)
Neuse River Estuary (Summer 1987)	BGC	mmol N m^{-2} $season^{-1}$	7	Christian and Thomas (2003)
Neuse River Estuary (Fall 1987)	BGC	mmol N m^{-2} $season^{-1}$	7	Christian and Thomas (2003)
Neuse River Estuary (Winter 1988)	BGC	mmol N m^{-2} $season^{-1}$	7	Christian and Thomas (2003)
Neuse River Estuary (Spring 1988)	BGC	mmol N m^{-2} $season^{-1}$	7	Christian and Thomas (2003)
Neuse River Estuary (Summer 1988)	BGC	mmol N m^{-2} $season^{-1}$	7	Christian and Thomas (2003)
Neuse River Estuary (Fall 1988)	BGC	mmol N m^{-2} $season^{-1}$	7	Christian and Thomas (2003)
Neuse River Estuary (Winter 1989)	BGC	mmol N m^{-2} $season^{-1}$	7	Christian and Thomas (2003)
Cape Fear River Estuary (Oligohaline)	BGC	nmol N cmˆ-3 d^{-1}	8	Hines et al. (2012)
Cape Fear River Estuary (Polyhaline)	BGC	nmol N cmˆ-3 d^{-1}	8	Hines et al. (2015)
Lake Lanier (AVG)	BGC	mg P m^{-2} day^{-1}	11	Borrett and Osidele (2007)
Baltic Sea	BGC	mg N mˆ-3 day^{-1}	16	Hinrichsen and Wulff (1998)
Chesapeake Bay	BGC	mg N m^{-2} yr^{-1}	36	Baird, Ulanowicz, and Boynton (1995)
Chesapeake Bay	BGC	mg P m^{-2} yr^{-1}	36	Ulanowicz and Baird (1999)
Chesapeake Bay (Winter)	BGC	mg P m^{-2} $season^{-1}$	36	Ulanowicz and Baird (1999)
Chesapeake Bay (Spring)	BGC	mg P m^{-2} $season^{-1}$	36	Ulanowicz and Baird (1999)
Chesapeake Bay (Summer)	BGC	mg P m^{-2} $season^{-1}$	36	Ulanowicz and Baird (1999)
Chesapeake Bay (Fall)	BGC	mg P m^{-2} $season^{-1}$	36	Ulanowicz and Baird (1999)
Sylt-Romo Bight	BGC	mg N m^{-2} yr^{-1}	59	Baird, Asmus, and Asmus (2008)

Model	Type	Units	n	Reference
Sylt-Romo Bight	BGC	mg P m^{-2} yr^{-1}	59	Baird, Asmus, and Asmus (2008)

Network Visualization

Network plots are a useful tool to visualize patterns in complex datasets. Here, we present one example of how to plot a network model using the plot tools in the *network* package. The figure scaling may need to be adjusted depending on computer and the graphics devices. Also, note that the graph only shows internal system flows.

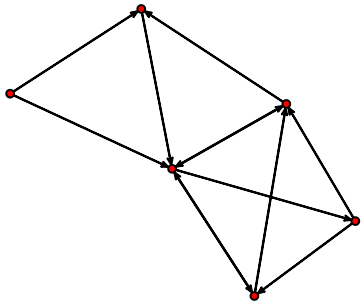
```
## Load data
data(oyster)
m <- oyster
## Set the random seed to control plot output
set.seed(2)
## Plot network data object (uses plot.network)
plot(m)
```

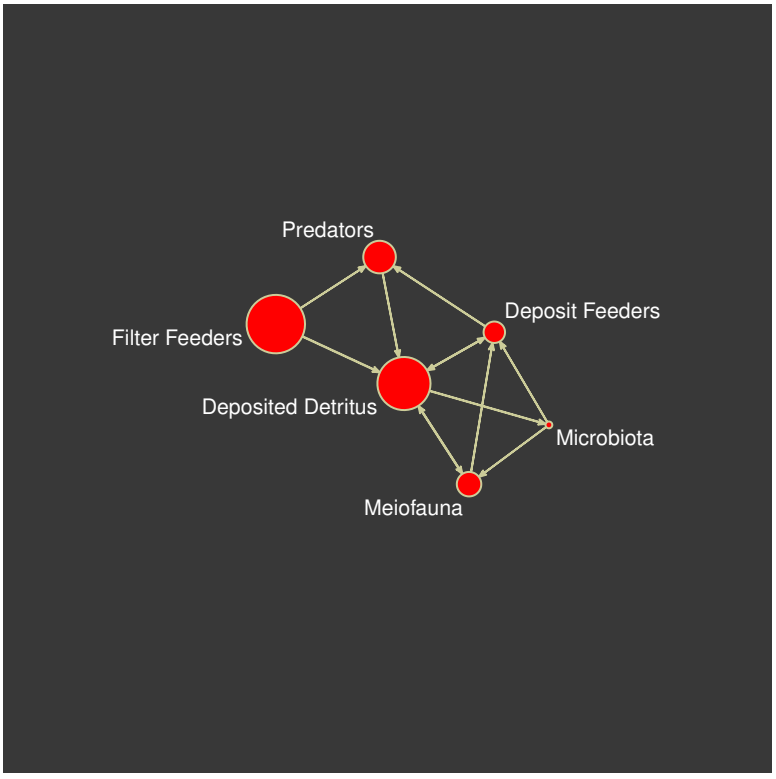


We can use the powerful graphics capabilities of **R** to make a fancier plot of the same data.

```
## Set colors to use
my.col <- c('red','yellow',rgb(204,204,153,maxColorValue=255),'grey22')
## Extract flow information for later use.
F <- as.matrix(m,attrname='flow')
## Get indices of positive flows
f <- which(F!=0, arr.ind=T)
opar <- par(las=1,bg=my.col[4],xpd=TRUE,mai=c(1.02, 0.62, 0.82, 0.42))
## Set the random seed to control plot output
set.seed(2)
plot(m,
## Scale nodes with storage
     vertex.cex=log(m%v%'storage'),
## Add node labels
     label= m%v%'vertex.names',
     boxed.labels=FALSE,
     label.cex=0.65,
## Make rounded nodes
     vertex.sides=45,
```

```
## Scale arrows to flow magnitude
     edge.lwd=log10(abs(F[f])),
     edge.col=my.col[3],
     vertex.col=my.col[1],
     label.col='white',
     vertex.border = my.col[3],
     vertex.lty = 1,
     xlim=c(-4,1),ylim=c(-2,-2))
## Lastly, remove changes to the plotting parameters
rm(opar)
```





Two networks for the Oyster Reef model (Dame and Patten 1981) showing a simple (left) and more elaborate (right) implementation of the network plotting function.

Model Input/Output: Common Data File Formats

Several software packages exist in the literature for running ENA. We have written functions to read in a few of the more common data formats used by them to help *enaR* users to import models formatted for these

other packages. Example data files can be found in the data folder here: https://github.com/SEELab/enaR_development.

SCOR

The read.scor function reads in data stored in the Scientific Committee on Oceanic Research (SCOR) format specified by (Ulanowicz and Kay 1991) that is the input to the NETWRK4 programs. This function can be run as follows.

```
scor.model <- readLines('../../data/oyster.dat')  # input is path to file
m <- read.scor(scor.model,from.file=FALSE)
```

This constructs the network data object from the SCOR file that stores the ecosystem model data for an oyster reef model (Dame and Patten 1981). The individual model elements are

```
unpack(m)
```

```
## $F
##                    Filter Feeders Microbiota Meiofauna Deposit Feeders
## Filter Feeders                  0     0.0000    0.0000          0.0000
## Microbiota                      0     0.0000    1.2060          1.2060
## Meiofauna                       0     0.0000    0.0000          0.6609
## Deposit Feeders                 0     0.0000    0.0000          0.0000
## Predators                       0     0.0000    0.0000          0.0000
## Deposited Detritus              0     8.1721    7.2745          0.6431
##                    Predators Deposited Detritus
## Filter Feeders        0.5135            15.7910
## Microbiota            0.0000             0.0000
## Meiofauna             0.0000             4.2403
## Deposit Feeders       0.1721             1.9076
## Predators             0.0000             0.3262
## Deposited Detritus    0.0000             0.0000
##
## $z
## [1] 41.47  0.00  0.00  0.00  0.00  0.00
##
## $r
## [1] 25.1650  5.7600  3.5794  0.4303  0.3594  6.1759
##
## $e
## [1] 0 0 0 0 0 0
##
## $y
## [1] 25.1650  5.7600  3.5794  0.4303  0.3594  6.1759
##
## $X
## [1] 2000.0000    2.4121   24.1210   16.2740   69.2370 1000.0000
##
## $living
## [1]  TRUE  TRUE  TRUE  TRUE  TRUE FALSE
```

This same data is stored as a network data object that is distributed with this package, which can be accessed as:

```
data(oyster)
m <- oyster
```

WAND

In part to make ENA more accessible to biologists, Allesina and Bondavalli (2004) recoded some of Ulanowicz's NETWRK4 algorithms into a Microsoft Excel based tool called WAND. For this tool, the model data is stored as a separate Excel file with two worksheets. The first contains many of the node attributes and the second contains the flow matrix. The read.wand function will create an **R** network data object from a WAND model file.

```
m <- read.wand('../../data/MDmar02_WAND.xls')
network.size(m)  # check number of nodes in the model to check that the read worked
```

```
## [1] 49
```

This code creates a network data object for *enaR* from the WAND formatted Mdloti ecosystem model data (Scharler 2012). This data is courtesy of U.M. Scharler.

NEA

For their MATLAB function to perform network environ analysis (Patten School), Fath and Borrett (2006) packaged the model flows, inputs, outputs, and storage values into what they called a system matrix

$$\mathbf{S} = \left[\begin{array}{ccc} \mathbf{F} & \vec{z} & \vec{X} \\ \vec{y} & 0 & 0 \end{array} \right]_{(n+1)\times(n+2)}. \tag{1}$$

Flows in the system matrix are oriented from column to row.

The *enaR* function read.nea reads in data with this format stored as a comma separated value file (CSV). The function write.nea() will write any network model to a CSV file with this format.

While convenient, this data format does not enable inclusion of the full range of model information included in the *enaR* network data object. This format does not partition outputs into exports and respiration values, nor does it identify the node labels or their living status. This missing information will prevent the use of some *enaR* functions.

Here is an example of using these functions:

```
data(oyster)

## Write oyster reef model to a CSV file
write.nea(oyster, file.name="oyster.csv")
```

```
##         [,1]  [,2]   [,3]   [,4]   [,5]   [,6]  [,7]      [,8]
## [1,]  0.0000 0.000 0.0000 0.0000 0.0000 0.0000 41.47 2000.0000
## [2,]  0.0000 0.000 0.0000 0.0000 0.0000 8.1721  0.00    2.4121
## [3,]  0.0000 1.206 0.0000 0.0000 0.0000 7.2745  0.00   24.1210
## [4,]  0.0000 1.206 0.6609 0.0000 0.0000 0.6431  0.00   16.2740
## [5,]  0.5135 0.000 0.0000 0.1721 0.0000 0.0000  0.00   69.2370
## [6,] 15.7910 0.000 4.2403 1.9076 0.3262 0.0000  0.00 1000.0000
## [7,] 25.1650 5.760 3.5794 0.4303 0.3594 6.1759  0.00    0.0000
```

```
## Read in oyster reef model data from NEA.m formatted CSV file
m <- read.nea("oyster.csv")
```

```
## [1] "export" "living"
```

```
## Warning in pack(flow = Flow, input = z, respiration = y, storage = X):
## Missing model components: export, living
```

```
## Again, this model object does NOT contain all
## of the information in the "oyster" data object.
```

ENAM

Another commonly used data format stores the necessary model data in a CSV or Excel formatted file. We include an example Excel file of the Mdloti estuary (Scharler 2012) stored in this format ("MDMAR02.xlsx", courtesy of U. M. Scharler). This format has not been described technically in the literature nor has it been named. We refer to it as ENAM as it is the ENA model data stored primarily as a square matrix with several preliminary rows that include meta-data, the number of nodes, and number of living nodes (similar to SCOR). The data format is generally similar in concept, if not exact form, to the data system matrix used as the input to the NEA.m function (Fath and Borrett 2006). However, the ENAM format includes information on whether nodes are living and partitions output into respiration and exports.

Using an example data file, MDMAR02.xlsx, this data format can be read into the *enaR* package as:

```
m <- read.enam('../../data/MDMAR02.xlsx')
network.size(m)  # check the model size (number of nodes) to determine if the load worked.
```

```
## [1] 49
```

The current read.enam function assumes the data are stored on the first worksheet of an Excel file. In the future, we expect to expand this function's capabilities to read the data from a CSV file.

EcoNet

The read.EcoNet lets users read in models that were originally formatted for the EcoNet software. For example, the following model for a food web in a Purple Pitcher Plant is formatted for EcoNet

```
m <- read.EcoNet('../../data/pitcherCN.eco')
```

```
## [1] "export"      "respiration" "living"
```

```
m%v%'vertex.names'  # check the model node names to determine if the load worked.
```

```
## [1] "Pitcher"   "Ants"      "BacteriaC" "BacteriaN" "MosquitoC" "MosquitoN"
```

enaR also has a function to write out existing models input the EcoNet format. This function writes the output to a separate plain text file.

```
#Mixed-Model of C and N for pitcher plant

Pitcher -> Ants          c=.5
Ants -> BacteriaN        c=.5
Ants -> BacteriaC        c=.5
BacteriaC -> MosquitoC   c=.1
BacteriaN -> MosquitoN   c=.1
BacteriaN -> Pitcher     c=.7
* -> Pitcher             c=.5 # inputs
MosquitoC -> *           c=.5 # outputs
MosquitoN -> *           c=.75


Pitcher=10, Ants=10, BacteriaC=5, MosquitoC=1, BacteriaN=5,
MosquitoN=1 #initial stock values
```

Figure 2:

```
m <- write.EcoNet(oyster, filename = "oyster.eco")
```

Analyzing an Ecosystem Model

ENA is often applied to investigate the structure and function of a single ecosystem model. Here, we walk through an example of applying multiple ENA algorithms to the South Carolina oyster reef model (Dame and Patten 1981). The table below summarizes the main ENA algorithms encoded in *enaR*.

Table 2: Primary Ecosystem Network Analysis algorithms in *enaR*.

Analysis	Function.Name	School
Structure	enaStructure	foundational/Patten
Flow	enaFlow	foundational/Patten
Ascendency	enaAscendency	Ulanowicz
Storage	enaStorage	Patten
Utility	enaUtility	Patten
Mixed Trophic Impacts	enaMTI	Ulanowicz
Control	enaControl	Patten
Environ	enaEnviron	Patten
Cycle Basis	enaCycle	Ulanowicz
Canonical Trophic Aggregation	enaTroAgg	Ulanowicz

Again, in this package results are reported in the row-to-column orientation by default – including the algorithms from the Patten school. Please see Orientation Section for how to change this default if needed.

Balancing to Steady-State

Many of the ENA functions assume that the network model is at steady-state (node inputs equal node outputs). Thus, this package has functions for (1) checking to see if the assumption is met and (2) automatically balancing the model so that input equal outputs.

To determine if the model is balanced and then balance it if necessary:

```
## Check to see if the model is balanced
```

```
## To FORCE BALANCE a model if needed
oyster <- force.balance(oyster)
```

Caution is warranted when using these techniques, as they tend to alter all of the model flows. A more nuanced approach may be desired when the uncertainty in estimates of model fluxes are known.

Structural Network Analysis

Structural network analysis is common to many types of network analysis. The structural analyses applied here are largely based on those presented in *NEA.m* (Fath and Borrett 2006) following the Patten School. Output of the enaStructure function is summarized in following table.

Table 3: Resultant matrices and network statistics returned by the enaStructure function in *enaR*.

Code.Label	Description
	Matrices
A	$n \times n$ binary adjacency matrix
	Network Metrics
n	number of nodes
L	number of directed edges
C	connectance ($C = L/n^2$); the proportion of possible directed edges connected. The network science literature often refers to this as network density.
LD	Link Density (L/n); average number of edges per nodes
ppr	estimated rate of pathway proliferation (Borrett and Patten 2003)
lam1A	dominant eigenvalue of A ($\lambda_1(\mathbf{A})$) (i.e. the asymptotic rate of pathway proliferation) (Borrett, Fath, and Patten 2007)
mlam1A	multiplicity of the dominant eigenvalue (number of times repeated)
rho	damping ratio (how quickly $[a_{ij}]^{(m)}/[a_{ij}]^{(m-1)}$ goes to $\lambda_1(\mathbf{A})$) (Caswell 2001)
R	distance of $\lambda_1(\mathbf{A})$ from the bulk of the eigen spectrum (Farkas et al. 2001)
d	difference between dominant eigenvalue and link density (expected value for random graph)
no.scc	number of strongly connected components (SCC)
no.scc.big	number of SCC with more than one node
pscc	fraction of network nodes included in a big SCC

```
# data(oyster)
St <- enaStructure(oyster)
attributes(St)
```

```
## $names
## [1] "A"  "ns"
```

```
St$ns
```

```
##      n  L         C LD      ppr    lam1A mlam1A      rho         R
## [1,] 6 12 0.3333333  2 2.147899 2.147899      1 2.147899 0.4655712
##             d no.scc no.scc.big      pscc
## [1,] 0.147899      2          1 0.8333333
```

The number of nodes, number of links, link density, and connectance (density) are common statistics used to describe networks like food webs (Martinez 1992; Dunne, Williams, and Martinez 2002; Eklöf and Ebenman 2006; Estrada 2007; Brandes and Erlebach 2005). The pathway proliferation rate quantifies if and how fast the number of pathways increases with path length in the network (Borrett and Patten 2003; Borrett, Fath, and Patten 2007). This rate is equivalent to the dominant eigenvalue of the adjacency matrix ($\lambda_1(A)$) if the network is comprised of a single strongly connected component (Borrett, Fath, and Patten 2007).

The structural network statistics for the oyster reef model shows that it has 6 nodes, a pathway proliferation rate of 2.14 (ppr), and that the model is comprised of two strongly connected components (no.scc) but that only one has more than one node (no.scc.big). Thus, 83% of the nodes are participating in a strongly connected component (pscc).

Flow Analysis

Flow analysis is one of the core ENA analyses for both the Ulanowicz and Patten Schools (Fath and Patten 1999; Latham II 2006; Fath and Borrett 2006; Schramski, Kazanci, and Tollner 2011). The *enaR* implementation enaFlow mostly follows the NEA.m function, with small updates (Borrett and Freeze 2011; Borrett, Freeze, and Salas 2011). The function also returns matrices for what Szyrmer and Ulanowicz (1987) refers to as the total contribution coefficients and total dependency coefficients (Kay, Graham, and Ulanowicz 1989). Results returned by enaFlow are summarized in following table.

To validly apply flow analysis, the network model must meet two analytical assumptions. First, the model must trace a single, thermodynamically conserved currency, such as energy, carbon, or nitrogen. Second, the model must be at steady-state for many of the analyses.

Flow analysis has been used in a variety of ways. For example, Finn (1980) used ENA flow analysis to compare the cycling of multiple nutrients through the Hubbard Brook Ecosystem, New Hampshire, USA, and Oevelen et al. (2009) used the technique to show how different marine canyon conditions change the flow of carbon through the food webs in Nazaré Canyon. Gattie et al. (2006) applied the analysis to characterize N cycling in the Neuse River Estuary (North Carolina, USA), and Zhang, Yang, and Fath (2010) used flow analysis to help assess the sustainability of the urban water metabolism of Beijing, China. Borrett (2013) showed that the throughflow vector T can be considered as a type of centrality measure that indicates the relative importance of each node to the generation of the total system throughflow or activity.

Table 4: Matrices and network statistics returned by the enaFlow function in *enaR*.

Code.Label	Description	Common.Symbols
Vectors & Matrices		
T	$n \times 1$ vector of node throughflows (M L^{-2} or $^{-3}$ T^{-1})	T
G	output-oriented direct throughflow intensity matrix	**G** or **B**

Code.Label	Description	Common.Symbols
GP	input-oriented direct throughflow intensity matrix	$\mathbf{G}'$ or $\mathbf{B}'$
N	output-oriented integral throughflow intensity matrix	$\mathbf{N}$
NP	input-oriented integral throughflow intensity matrix	$\mathbf{N}'$
TCC	$n \times n$ matrix of total contribution coefficients (Szyrmer and Ulanowicz 1987)	
TDC	$n \times n$ matrix of total dependency coefficients total diet (Szyrmer and Ulanowicz 1987)	
Network Metrics		
Input	Total input boundary flow	$Input$ or $Boundary$ or $z_\bullet$
TST	Total System ThroughFLOW	TST
TSTp	Total System ThroughPUT	TST or $TSTp$
APL	Average Path Length (Finn 1976)	APL or AGG
FCI	Finn Cycling Index (Finn 1980)	FCI
BFI	Boundary Flow Intensity (Borrett et al. 2006)	$Boundary/TST$ or BFI
DFI	Direct Flow Intensity (Borrett et al. 2006)	$Direct/TST$ or DFI
IFI	Indirect Flow Intensity (Borrett et al. 2006)	$Indirect/TST$ or IFI
ID.F	Ratio of Indirect to Direct Flow (Borrett and Freeze 2011; Borrett, Freeze, and Salas 2011)	$Indirect/Direct$ or I/D_F
ID.F.I	Input oriented ratio of indirect to direct flow intensity (Fath and Patten 1999)	$I/D_F^{[\text{unit input}]}$ or i/d
IF.F.O	output oriented ratio of indirect to direct flow intensity (Fath and Patten 1999)	$I/D_F^{[\text{unit output}]}$ or I/D or i/d
HMG.F.I	input oriented network homogenization to direct flow intensity	$HMG_F^{[\text{input}]}$
HMG.F.O	output oriented network homogenization to direct flow intensity	$HMG_F^{[\text{output}]}$
AMP.F.I	input oriented network amplification	$AMP_F^{[\text{input}]}$
AMP.F.O	output oriented network amplification	$AMP_F^{[\text{output}]}$
mode0.F	Boundary Flow (Higashi, Patten, and Burns 1993; Fath, Patten, and Choi 2001)	$Mode_{0F}$
mode1.F	Internal First Passage Flow (Higashi, Patten, and Burns 1993; Fath, Patten, and Choi 2001)	$Mode_{1F}$
mode2.F	Cycled Flow (Higashi, Patten, and Burns 1993; Fath, Patten, and Choi 2001)	$Mode_{2F}$
mode3.F	Dissipative Equivalent to mode1.F (Fath, Patten, and Choi 2001)	$Mode_{3F}$
mode4.F	Dissipative Equivalent to mode0.F (Fath, Patten, and Choi 2001)	$Mode_{4F}$

Here, we extract the flow statistics and then isolate and remove the output-oriented direct flow intensity ($\mathbf{G}$) matrix. Recall that ENA is partially derived from Input–Output analysis; the input and output orientations provide different information about the system. We also show the input-oriented integral flow matrix $\mathbf{N}'$.

```
F <- enaFlow(oyster)
attributes(F)
```

```
## $names
## [1] "T"   "G"   "GP"  "N"   "NP"  "TCC" "TDC" "ns"
```

```
F$ns
```

```
##      Boundary     TST     TSTp      APL       FCI       BFI       DFI
## [1,]    41.47 83.5833 125.0533 2.015512 0.1101686 0.4961517 0.1950689
##            IFI     ID.F   ID.F.I   ID.F.O    HMG.I    HMG.O AMP.I AMP.O
## [1,] 0.3087794 1.582925 1.716607 1.534181 2.051826 1.891638     3     1
##      mode0.F  mode1.F  mode2.F  mode3.F mode4.F        H      AMI       Hr
## [1,]   41.47 32.90504 9.208256 32.90504   41.47 3.018275 1.330211 1.688063
##           CAP      ASC       OH   ASC.CAP    OH.CAP robustness     ELD
## [1,] 377.4452 166.3473 211.0979 0.4407191 0.5592809  0.3611021 1.79506
##            TD  A.input A.internal A.export A.respiration OH.input
## [1,] 2.514395 66.03696   72.62476        0      27.68558        0
##      OH.internal OH.export OH.respiration CAP.input CAP.internal
## [1,]    103.2914         0       107.8065  66.03696     175.9162
##      CAP.export CAP.respiration
## [1,]          0         135.492
```

```
## Output-oriented direct flow matrix
F$G
```

```
##                    Filter Feeders Microbiota Meiofauna Deposit Feeders
## Filter Feeders                  0  0.0000000 0.0000000      0.00000000
## Microbiota                      0  0.0000000 0.1475753      0.14757529
## Meiofauna                       0  0.0000000 0.0000000      0.07793173
## Deposit Feeders                 0  0.0000000 0.0000000      0.00000000
## Predators                       0  0.0000000 0.0000000      0.00000000
## Deposited Detritus              0  0.3670363 0.3267221      0.02888377
##                     Predators Deposited Detritus
## Filter Feeders     0.01238245          0.3807813
## Microbiota         0.00000000          0.0000000
## Meiofauna          0.00000000          0.5000059
## Deposit Feeders    0.06856574          0.7600000
## Predators          0.00000000          0.4757876
## Deposited Detritus 0.00000000          0.0000000
```

```
## Input-oriented integral flow matrix
F$NP
```

```
##                    Filter Feeders Microbiota Meiofauna Deposit Feeders
## Filter Feeders                  1  1.0000000 1.0000000       1.0000000
## Microbiota                      0  1.1018630 0.2440716       0.6197856
## Meiofauna                       0  0.2971032 1.2971032       0.5604100
## Deposit Feeders                 0  0.1240688 0.1240688       1.1240688
## Predators                       0  0.0203426 0.0203426       0.0203426
## Deposited Detritus              0  1.3885039 1.3885039       1.3885039
```

```
##                    Predators Deposited Detritus
## Filter Feeders     1.0000000          1.0000000
## Microbiota         0.1555792          0.1018630
## Meiofauna          0.1406747          0.2971032
## Deposit Feeders    0.2821649          0.1240688
## Predators          1.0051064          0.0203426
## Deposited Detritus 0.3485436          1.3885039
```

Ascendency

A key contribution of the Ulanowicz School to ENA is the Ascendency concept and the development of several information based network-level statistics (Ulanowicz 1986; Ulanowicz 1997). This analysis is based on all of the flows in the system and does not assume the modeled system is at steady-state. The enaAscendency function returns several of these information based measures. The function also returns the tetra-partite division of the Ascendency metrics into the components for the inputs, internal flows, exports, and respirations (Ulanowicz and Norden 1990). This is run as follows:

```
enaAscendency(oyster)
```

```
##             H      AMI       Hr      CAP      ASC       OH   ASC.CAP
## [1,] 3.018275 1.330211 1.688063 377.4452 166.3473 211.0979 0.4407191
##         OH.CAP robustness     ELD       TD  A.input A.internal A.export
## [1,] 0.5592809  0.3611021 1.79506 2.514395 66.03696   72.62476        0
##      A.respiration OH.input OH.internal OH.export OH.respiration CAP.input
## [1,]      27.68558        0    103.2914         0       107.8065  66.03696
##      CAP.internal CAP.export CAP.respiration
## [1,]     175.9162          0         135.492
```

Table 5: Graph-level network statistics returned by the *enaR* interpretations (Ulanowicz 1986; Ulanowicz 1997).

Label	Description	Common.Symbols
H	total flow diversity (Shannon Diversity or entropy) where H = AMI + Hr	H
AMI	average mutual information	AMI
Hr	residual mutual information	H_r
CAP	Capacity (CAP = H × TSTp and CAP = ASC + OH)	C
ACS	ascendency (AMI × TSTp)	A or ASC
OH	overhead (Hr × TSTp)	Φ or OH
ASC.CAP	relative ascendency (dimensionless)	A/C
OH.CAP	relative overhead (dimensionless)	Φ/C
Robustness	robustness of the network (Goerner, Lietaer, and Ulanowicz 2009; Fath 2014)	
ELD	effective link density of the network (Ulanowicz, Holt, and Barfield 2014)	
TD	trophic depth of the network (Ulanowicz, Holt, and Barfield 2014)	
	Tetrapartite Partition of Ascendency Metrics	
A.input	Ascendency of just the imports	A_{import}

Label	Description	Common.Symbols
A.internal	Ascendnecy of just the internal flows	A_i
A.export	Ascendnecy of just the export flows	A_e
A.respiration	Ascendnecy of just the respiration flows	A_r
OH.input	Overhead of the imports alone	O_{import} or Φ_{input}
OH.internal	Overhead of the internal flows	Φ_i
OH.export	Overhead of the exports alone	Φ_e
OH.respiration	Respiration portion of system overhead	Φ_r
CAP.input	Input portion of system capacity	C_{input}
CAP.internal	Internal portion of system capacity	C_i
CAP.export	Export portion of system capacity	C_e
CAP.respiration	Respiration portion of system capacity	C_r

Storage Analysis

Storage ENA was developed in the Patten School (Barber 1978a; Barber 1978b; Barber 1979). It is similar to flow ENA, but divides the flows by storage (e.g., biomass) instead of throughflow. Several papers provide an overview of this methodology (Kay, Graham, and Ulanowicz 1989; Fath and Patten 1999; Gattie et al. 2006; Schramski, Kazanci, and Tollner 2011). Output of this function is summarized in Table~(tab:storage). What follows is an example of applying the storage analysis to the oyster reef model.

```
S <- enaStorage(oyster)
attributes(S)
```

```
## $names
##  [1] "X"   "C"   "P"   "S"   "VS"  "Q"   "CP"  "PP"  "SP"  "VSP" "QP"
## [12] "dt"  "ns"
```

```
S$ns
```

```
##           TSS       CIS         BSI         DSI       ISI     ID.S  ID.S.I
## [1,] 3112.044 0.9940252 0.003331412 0.003320932 0.9933477 299.1171 454.227
##        ID.S.O  HMG.S.O  HMG.S.I NAS NASP mode0.S  mode1.S mode2.S  mode3.S
## [1,] 294.1527 1.115985 1.464503  20   21 10.3675 8.226261 3093.45 8.226261
##      mode4.S
## [1,] 10.3675
```

Table 6: Matrices and graph-level network statistics returned by the *enaR* enaStorage function.

Label	Description	Common.Symbols
	Matrices	
X	$n \times 1$ vector of storage values [M L^{-2}]; storage is commonly referred to as biomss in ecosystems	X or B
C	$n \times n$ donor-storage normalized output-oriented direct flow intensity matrix (T^{-1})	$\mathbf{C}$
P	$n \times n$ storage-normalized output-oriented direct flow matrix (dimensionless)	$\mathbf{P}$ or $\mathbf{P}''$

Label	Description	Common.Symbols
S	$n \times n$ donor-storage normalized output-oriented integralflow intensity matrix (T^{-1})	
VS	variance in expected output-oriented residance times (Barber 1979)	$\mathbf{VS}$ or $\mathbf{VS}''$
Q	$n \times n$ output-oriented integral flow intensity matrix (dimensionless)	$\mathbf{Q}$ or $\mathbf{Q}''$
CP	$n \times n$ recipient-storage normalized input-oriented direct flow intensity matrix (T^{-1})	$\mathbf{C}'$
PP	$n \times n$ storage-normalized input-oriented direct flow matrix (dimensionless)	$\mathbf{P}'$
SP	$n \times n$ donor-storage normalized input-oriented integral flow intensity matrix (T^{-1})	$\mathbf{S}'$
VSP	variance in expected input-oriented residance times (Barber 1979)	$\mathbf{VS}'$
QP	$n \times n$ input-oriented integral flow intensity matrix (dimensionless)	$\mathbf{Q}'$
dt	discrete time step	
	Network Statistics	
TSS	Total System Storage	TSS or $X_{\bullet}$
CIS	Storage Cycling Index	CIS
BSI	Boundary Storage Intensity	BSI
DSI	Direct Storage Intensity	DSI
ISI	Indirect Storage Intensity	ISI
ID.S	Ratio of Indirect-to-Direct storage (realized)	I/D_s or $Indirect/Direct_s$
ID.S.I	storage-based input-oriented indirect-to-direct ratio (Fath and Borrett 2006)	$I/D_S^{[\text{unit input}]}$ or I/D or i/d
ID.S.O	storage-based input-oriented indirect-to-direct ratio (Fath and Borrett 2006)	$I/D_S^{[\text{unit output}]}$
HMG.S.I	input-oriented storage network homogenization	$HMG_S^{[\text{input}]}$
HMG.S.O	output-oriented storage network homogenization	$HMG_S^{[\text{output}]}$
AMP.S.I	input-oriented storage network amplification	$AMP_S^{[\text{input}]}$
AMP.S.O	output-oriented storage network amplification	$AMP_S^{[\text{output}]}$
mode0.S	Storage from Boundary Flow	$Mode_{0S}$
mode1.S	Storage from Internal First Passage Flow	$Mode_{1S}$
mode2.S	Storage from Cycled Flow	$Mode_{2S}$
mode3.S	Dissipative Equivalent to mode1.S	$Mode_{3S}$
mode4.S	Dissipative Equivalent to mode0.S	$Mode_{4S}$

This storage analysis of the oyster reef model indicates that the total energy stored in the system on an average day is 3,112 kcal m^{-2}, and that 99.3% of this storage is generated by energy flowing over indirect pathways (ISI).

Whipple, Patten, and Borrett (2014) provides a detailed example of applying storage analysis to characterize the dynamic organization of an ecosystem. They investigated how the storage analysis properties changed across sixteen consecutive seasonal N cycling models of the Neuse River Estuary. They found that from this storage perspective NO_x was the dominant compartment, and thus a primary controller of the system dynamics. Note that this work provides an example of applying this analysis at multiple levels of analysis (Hines and Borrett 2014).

Environ Analysis

Environ Analysis finds the n unit input and output environs for the model (Patten 1978; Fath and Patten 1999). These unit environs are returned by the *environ* function as in NEA.m. They indicate the flow activity in each subnetwork generated by pulling a unit out of a node (input environs) or pushing a unit into a node (output environ). These unit environs can be converted into "realized" environs by multiplying each by the relevant observed input or output (Borrett and Freeze 2011; Whipple et al. 2007; Whipple, Patten, and Borrett 2014).

```
E <- enaEnviron(oyster)
attributes(E)
```

```
## $names
## [1] "input"  "output"
```

```
E$output[1]
```

```
## $`Filter Feeders`
##                     Filter Feeders Microbiota   Meiofauna Deposit Feeders
## Filter Feeders                  -1  0.0000000  0.00000000      0.00000000
## Microbiota                       0 -0.1970605  0.02908126      0.02908126
## Meiofauna                        0  0.0000000 -0.20449723      0.01593682
## Deposit Feeders                  0  0.0000000  0.00000000     -0.06052568
## Predators                        0  0.0000000  0.00000000      0.00000000
## Deposited Detritus               0  0.1970605  0.17541596      0.01550760
## z                                1  0.0000000  0.00000000      0.00000000
##                       Predators Deposited Detritus           y
## Filter Feeders      0.012382445        0.380781288 0.606836267
## Microbiota          0.000000000        0.000000000 0.138897999
## Meiofauna           0.000000000        0.102249819 0.086310586
## Deposit Feeders     0.004149988        0.045999518 0.010376176
## Predators          -0.016532433        0.007865927 0.008666506
## Deposited Detritus  0.000000000       -0.536896552 0.148912467
## z                   0.000000000        0.000000000 0.000000000
```

The TET function returns vectors of the unit and realized input and output total environ throughflow. The realized total environ throughflow is an environ based partition of the total system throughflow (Whipple et al. 2007).

```
tet <- TET(oyster)
show(tet)
```

```
## $realized.input
## [1] 25.165000 22.647638 14.582798  2.028052  1.053786 18.107007
```

```
##
## $realized.output
## [1] 83.5833  0.0000  0.0000  0.0000  0.0000  0.0000
##
## $unit.input
## [1] 1.000000 3.931882 4.074090 4.713111 2.932069 2.931882
##
## $unit.output
## [1] 2.015512 1.836089 2.540670 3.124836 2.234317 2.594261
```

The TES functions returns the both the realized and unit total environ storage for the input and output environs. Again, the realized TES is a partition of the total system storage (TSS).

```
tes <- TES(oyster)
show(tes)
```

```
## $realized.input
##     Filter Feeders         Microbiota          Meiofauna
##         2000.00000            2.41209           24.12171
##    Deposit Feeders          Predators Deposited Detritus
##           16.27440           69.23803         1000.03118
##
## $realized.output
## [1] 3112.044    0.000    0.000    0.000    0.000    0.000
##
## $unit.input
##     Filter Feeders         Microbiota          Meiofauna
##        289.3658066          0.6561948          7.3735209
##    Deposit Feeders          Predators Deposited Detritus
##         11.5308112        109.7205293        265.1036470
##
## $unit.output
##     Filter Feeders         Microbiota          Meiofauna
##           75.04326           16.06273           41.03146
##    Deposit Feeders          Predators Deposited Detritus
##           65.81279          132.44451           66.11575
```

Realized TET and TES might be considered network centrality measures that indicate the relative importance of the environs in generating the observed flow or storage, respectively.

Utility Analysis

Utility analysis describes the relationship between node pairs in the ecosystem model when considering both direct and indirect interactions. It developed in the Patten School (Patten 1991; Fath and Patten 1999) and is similar to yet distinct from the Ulanowicz School mixed trophic impacts analysis (Ulanowicz and Puccia 1990). Utility analysis can be conducted from both the flow and storage perspectives, so the "type" argument needs to be set to suit the user's needs. This is again implemented as in *NEA.m*. The following table summarizes the function output for the flow and storage versions. These analyses are executed as:

```
UF <- enaUtility(oyster, eigen.check=TRUE,type="flow")
US <- enaUtility(oyster, eigen.check=TRUE,type="storage")
attributes(UF)
```

```
## $names
## [1] "D"              "SD"              "U"               "Y"
## [5] "SY"             "Relations.Table" "ns"
```

Table 7: Matrices and graph-level network statistics returned by the *enaR* enaUtility function.

Label	Description	Common.Symbols
Matrices		
$D_{n \times n}$	throughflow-normalized direct utility intensity (dimensionless)	$\mathbf{D}$
$U_{n \times n}$	integral flow utility (dimensionless)	$\mathbf{U}$
$Y_{n \times n}$	integral flow utility scaled by original throughflow (M $L^{-2 \text{ or } -3}$ T^{-1})	$\mathbf{Y}$
$DS_{n \times n}$	storage-normalized direct utility intensity (dimensionless)	$\mathbf{D_S}$
$US_{n \times n}$	integral storage utility (dimensionless)	$\mathbf{U_S}$
$YS_{n \times n}$	integral storage utility scaled by original throughflow (M $L^{-2 \text{ or } -3}$ T^{-1})	$\mathbf{Y_S}$
Other Objects		
Relations.Table	a table listing the pairwise relationships derived from both the direct and integral perspective.	
Network Statistics		
lam1D	dominant eigenvalue of D; must be <1 for $\mathbf{D}$ power series to converge	$\lambda_1(\mathbf{D})$
relation.change.F	Percent of relatinoships that changed between the direct and integral flow utility analysis	
synergism.F	benefit-cost ratio or network synergism (flow)	SYN_F
mutualism.F	positive to negative interaction ratio or network mutualism (flow)	MUT_F
lam1DS	dominant eigenvalue of DS; must be <1 for the $\mathbf{D}_S$ power series to converge	$\lambda_1(\mathbf{D}_S)$
relation.change.S	Percent of relatinoships that changed between the direct and integral storage utility analysis	
synergism.S	benefit-cost ratio or network synergism (storage)	SYN_S
mutualism.S	positive to negative interaction ratio or network mutualism (storage)	MUT_S

Please note the function argument *eigen.check = TRUE*. For this analysis to work, the power series of the direct utility matrices must converge, which is only TRUE if the dominant eigenvalue of the direct utility matrix is less than 1. The function default prevents the analysis from being performed if this condition is not met. Users that wish to perform the analysis anyway can set "eigen.check=FALSE". Care should be used when doing this, as the meaning of the underlying mathematics is uncertain.

While this function returns a number of results, the *Relations.Table* summarizes a number of the critical results. It shows the character of the pairwise relationships between each node combination when considering the direct and the integral relations. Thus, it shows the power of the network to transform the nature of

the ecological relationships among the system components. This change is reflected in the synergism and mutualism whole-network metrics.

```
UF$Relations.Table
```

From	To	Direct	Integral	changed
Filter Feeders	Filter Feeders	(0,0)	(+,+)	*
Filter Feeders	Microbiota	(0,0)	(+,+)	*
Filter Feeders	Meiofauna	(0,0)	(+,+)	*
Filter Feeders	Deposit Feeders	(0,0)	(+,-)	*
Filter Feeders	Predators	(+,-)	(+,-)	-
Filter Feeders	Deposited Detritus	(+,-)	(+,-)	-
Microbiota	Microbiota	(0,0)	(+,+)	*
Microbiota	Meiofauna	(+,-)	(+,-)	-
Microbiota	Deposit Feeders	(+,-)	(+,-)	-
Microbiota	Predators	(0,0)	(+,+)	*
Microbiota	Deposited Detritus	(-,+)	(-,+)	-
Meiofauna	Meiofauna	(0,0)	(+,+)	*
Meiofauna	Deposit Feeders	(+,-)	(+,-)	-
Meiofauna	Predators	(0,0)	(+,+)	*
Meiofauna	Deposited Detritus	(-,+)	(-,+)	-
Deposit Feeders	Deposit Feeders	(0,0)	(+,+)	*
Deposit Feeders	Predators	(+,-)	(+,-)	-
Deposit Feeders	Deposited Detritus	(+,-)	(+,+)	*
Predators	Predators	(0,0)	(+,+)	*
Predators	Deposited Detritus	(+,-)	(-,-)	*
Deposited Detritus	Deposited Detritus	(0,0)	(+,+)	*

```
UF$ns
```

```
##              lam1D relation.change.F synergism.F mutualism.F
## r.change 0.8991676              61.9    4.915298    2.272727
```

Mixed Trophic Impacts

Mixed Trophic Impacts is a popular analysis from the Ulanowicz School of ENA (Ulanowicz and Puccia 1990). The enaMTI function generates comparable results to the calculations in (Ulanowicz and Puccia 1990). These are implemented as follows:

```
mti <- enaMTI(oyster)
attributes(mti)
```

```
## $names
## [1] "G"               "FP"              "Q"               "M"
## [5] "Relations.Table"
```

```
mti$M
```

```
## [1] NA
```

In this case, the power series of the direct trophic impacts matrix does not converge (dominant eigenvalue is greater than one). Thus, the function returns NA. Like with Utility analysis, however, we can use the eigen.check argument to do the calculation despite the mathematical problem.

```
mti <- enaMTI(oyster,eigen.check=FALSE)
attributes(mti)
```

```
## $names
## [1] "G"               "FP"              "Q"               "M"
## [5] "Relations.Table"
```

```
mti$M
```

```
##                    Filter Feeders  Microbiota    Meiofauna Deposit Feeders
## Filter Feeders      -0.0250635283  0.16956382  0.431493557      0.26144106
## Microbiota          -0.0015848556 -0.30675078 -0.182458391      0.20520368
## Meiofauna           -0.0001241781 -0.47413204 -0.070959618      0.01607831
## Deposit Feeders     -0.0069255188 -0.26769125 -0.007062628     -0.10329881
## Predators           -0.0301817448  0.02000515 -0.004028911     -0.07586335
## Deposited Detritus  -0.0034657973  0.21795628  0.612654910      0.44874394
##                      Predators Deposited Detritus
## Filter Feeders      0.795834137        0.516016759
## Microbiota          0.050323410       -0.295378609
## Meiofauna           0.003942987       -0.001592286
## Deposit Feeders     0.219903765        0.177109591
## Predators          -0.041648786       -0.019939324
## Deposited Detritus  0.110048344       -0.251366300
```

Table 9: Matrices returned by the *enaR* enaMTI function, which are based on Ulanowicz and Puccia (1990).

Label	Description	Common.Symbols
Matrices		
$G_{n\times n}$	positive effect of prey on its predator; identical to the input-oriented direct flow matrix	$\mathbf{G}'$ or $\mathbf{B}'$
$FP_{n\times n}$	negative impact of the predator on its prey	$\mathbf{F}'$ or $\check{\mathbf{B}}$
$Q_{n\times n}$	direct net impact of one node on another	$\mathbf{Q}$ or $\check{\mathbf{D}}$
$M_{n\times n}$	total impact of i on j (direct and indirect)	$\mathbf{M}$ or $\check{\mathbf{U}}$

The mixed trophic impacts analysis has been usefully applied to discover interesting and sometimes unexpected ecological relationships. For example, although alligators directly eat frogs in the Florida Everglades (USA), it appears that their net relationship when considering the whole food web is actually mutualistic (Bondavalli and Ulanowicz 1999). This is in part because the alligators also eat other key predators of the frogs such as snakes.

As with enaUtility, enaMTI returns a summary table of the pairwise relationships between each node pair (*Relations.Table*). This table includes the relationship when only the direct connection are considered, and the relationships when the mixed or integral connections are considered.

```
mti$Relations.Table
```

From	To	Net (direct)	Mixed (integral)	changed
Filter Feeders	Filter Feeders	(0,0)	(-,-)	*
Filter Feeders	Microbiota	(0,0)	(-,+)	*
Filter Feeders	Meiofauna	(0,0)	(-,+)	*
Filter Feeders	Deposit Feeders	(0,0)	(-,+)	*
Filter Feeders	Predators	(-,+)	(-,+)	-
Filter Feeders	Deposited Detritus	(0,+)	(-,+)	*
Microbiota	Microbiota	(0,0)	(-,-)	*
Microbiota	Meiofauna	(-,+)	(-,-)	*
Microbiota	Deposit Feeders	(-,+)	(-,+)	-
Microbiota	Predators	(0,0)	(+,+)	*
Microbiota	Deposited Detritus	(+,-)	(+,-)	-
Meiofauna	Meiofauna	(0,0)	(-,-)	*
Meiofauna	Deposit Feeders	(-,+)	(-,+)	-
Meiofauna	Predators	(0,0)	(-,+)	*
Meiofauna	Deposited Detritus	(+,-)	(+,-)	-
Deposit Feeders	Deposit Feeders	(0,0)	(-,-)	*
Deposit Feeders	Predators	(-,+)	(-,+)	-
Deposit Feeders	Deposited Detritus	(+,+)	(+,+)	-
Predators	Predators	(0,0)	(-,-)	*
Predators	Deposited Detritus	(0,+)	(+,-)	*
Deposited Detritus	Deposited Detritus	(0,0)	(-,-)	*

In the exemplar Oyster Reef model, we see that the *Filter Feeder* compartment has no direct relationship with the *Microbiota*. However, when the Mixed or integral relationships are considered in the MTI framework, the relationship changes such that the *Microbiota* appear to be functionally predators of the *Filter Feeders*.

Control Analysis

Control analysis was implemented as in the NEA.m function, but we also include recent updates to control analysis (Schramski et al. 2006; Schramski et al. 2007). In general, these analyses determine the pairwise control relationships between the nodes in the network.

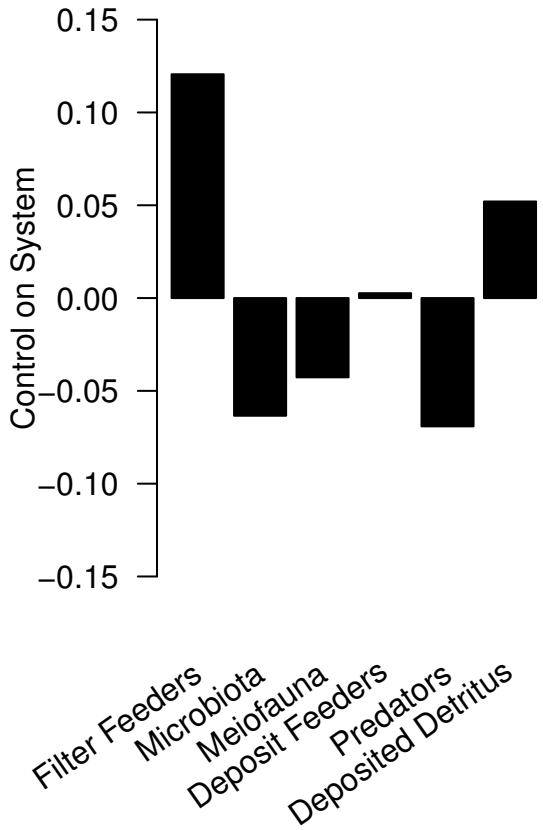
```
C <- enaControl(oyster)
attributes(C)
```

```
## $names
## [1] "CN"   "CQ"   "CD"   "CR"   "CA"   "CDep" "sc"   "psc"  "ns"
```

```
C$sc
```

```
##     Filter Feeders         Microbiota          Meiofauna
##        0.120569086       -0.063400232       -0.042706068
##    Deposit Feeders          Predators Deposited Detritus
##        0.002634493       -0.069125297        0.052028018
```

```r
# plot system control vector
opar <- par(las = 1, mfrow = c(1,2), mar = c(7,5,1,1),
            xpd = TRUE, bg = "white")
bp = barplot(C$sc,
    names.arg = NA, # turn off label names
    col = "black",
    ylab = "Control on System", xlab = "",
    ylim = c(-0.15, 0.15))
## Adding labels
text(bp,-0.2,
     labels=names(C$sc),
     srt = 35, adj = 1, cex = 1)
```



The elements of the sc vector indicate the relative control exerted by each node on the system functioning.

Table 11: Matrices returned by the *enaR* enaControl function, which are based on (Dame and Patten 1981; Patten and Auble 1981; Schramski et al. 2006; Schramski et al. 2007).

Label	Description
Matrices	
$CN_{n\times n}$	Control matrix using flow values
$CQ_{n\times n}$	Control matrix using storage values
$CR_{n\times n}$	Schramski's Control Ratio Matrix
$CD_{n\times n}$	Schramski's Control Difference Matrix
$CA_{n\times n}$	Control Allocation Matrix (Chen, Fath, and Chen 2011)

Label	Description
$\text{CDep}_{n\times n}$	Control Dependency Matrix (Chen, Fath, and Chen 2011)
$\text{sc}_{n\times 1}$	Schramski's System Control vector
$\text{psc}_{n\times 1}$	Schramski's system control vector as percent of total control
ns	*Network Statistics*
TSC	total system control

Cycle Analysis

The Cycle Analysis provides the detailed account of the cycling present in the network. It follows the algorithm by the DOS-based NETWRK 4.2b software by Ulanowicz (Ulanowicz and Kay 1991; Ulanowicz 1983) and provides results similar to NETWRK's 'Full Cycle Analysis'. Cycles in a network are grouped together into disjoint nexuses and each nexus is characterized by a weak arc. This function gives details of the individual cycles along with the disjoint nexuses present in the network. Note that this analysis does not require the

```
  cyc <- enaCycle(oyster)
attributes(cyc)
```

```
## $names
## [1] "Table.cycle"      "Table.nexus"      "CycleDist"
## [4] "NormDist"         "ResidualFlows"    "AggregatedCycles"
## [7] "ns"
```

```
## The individual cycles
names(cyc$Table.cycle)
```

```
## [1] "CYCLE" "NEXUS" "NODES"
```

```
## The disjoint nexuses
names(cyc$Table.nexus)
```

```
## [1] "NEXUS"      "CYCLES"     "W.arc.From" "W.arc.To"   "W.arc.Flow"
```

[1] "1" "2" "3" "4" "5" "6" "7" "8" "9" "10" "11" "12"

Table 12: Data frames, matrices and graph-level network statistics returned by the *enaR* enaCycle function, which is based on Ulanowicz (1983).

Label	Description
Data frames	
Table.cycle	Data frame of cycles in the network. Up to 50 cycles are returned per nexus
Table.nexus	Data frame with details of the disjoint nexuses present in the network
Matrices	

Label	Description
$\text{CycleDist}_{n\times 1}$	Vector of flows cycling in loops of increasing length
$\text{NormDist}_{n\times 1}$	Vector of Cycle Distributions normalized by the total system throughput
$\text{ResidualFlows}_{n\times n}$	Matrix of straight-through flows or the underlying acyclic graph
$\text{AggregatedCycles}_{n\times n}$	Matrix of all the cycled flows or the underlying cyclic graph
Network Statistics	
NCYCS	Number of cycles detected in the network
NNEX	Number of disjoint nexuses detected in the network
CI	Cycling index of the network based on flow matrix

Trophic Analysis

The Trophic Aggregation algorithm (enaTroAgg) assumes that the network being analyzed is a food web and performs a number of trophic-based analyses. Specifically, it identifies the trophic structure of the given network based on the Lindeman's trophic concepts (Lindeman 1942). This includes identifying the effective trophic level of each network node, and building the 'Lindeman Trophic Spine'.

The algorithm is implemented as in NETWRK 4.2b by Ulanowicz (Ulanowicz and Kemp 1979) and provides similar results as NETWRK's 'Lindeman Trophic Aggregations' (Ulanowicz and Kay 1991). It apportions the nodes into integer trophic levels and estimates the corresponding inputs, exports, respirations and the grazing chain and trophic spine which represent the transfers between integer trophic levels.

It is crucial for this algorithm that the cycles among the living nodes of the network (Feeding Cycles) be removed beforehand to assign trophic levels to nodes. Thus, the output for this function contains the Cycle Analysis for the Feeding Cycles in the network.

Following (Ulanowicz and Kay 1991), the non-living nodes are grouped together for this analysis and referred to as the detrital pool.

The following table summarizes the function output except the outputs for the feeding cycles which are similar to the enaCycle outputs.

```
trop <- enaTroAgg(oyster)
attributes(trop)
```

```
## $names
##  [1] "Feeding_Cycles" "A"              "ETL"            "CE"
##  [5] "CR"             "GC"             "RDP"            "LS"
##  [9] "TE"             "ns"
```

```
## Cycle analysis output for Feeding Cycles
trop$Feeding_Cycles
```

```
## $ResidualFlows
##                 Filter Feeders Microbiota Meiofauna Deposit Feeders
## Filter Feeders               0          0     0.000          0.0000
## Microbiota                   0          0     1.206          1.2060
```

```
## Meiofauna                   0          0     0.000          0.6609
## Deposit Feeders             0          0     0.000          0.0000
## Predators                   0          0     0.000          0.0000
##                 Predators
## Filter Feeders     0.5135
## Microbiota         0.0000
## Meiofauna          0.0000
## Deposit Feeders    0.1721
## Predators          0.0000
```

[1] “1” “2” “3” “4” “5” “6” “7” “8” “9” “10” “11” “12” “13” “14” [15] “15” “16” “17” “18”

Table 13: Matrices and graph-level network statistics returned by the *enaR* enaTroAgg function, which are based on Ulanowicz and Kemp (1979).

Label	Description
Matrices	
$A_{nl \times nl}$	Lindeman transformation matrix that apportions nodes to integer trophic levels
$ETL_{n \times 1}$	Vector of the effective trophic levels of different nodes
$M.Flow_{nl \times 1}$	Migratory flows in living nodes (if present)
$CI_{n \times 1}$	Vector of canonical inputs to integer trophic levels (if migratory flows present)
$CE_{n \times 1}$	Canonical Exports. Vector of exports from Integer trophic levels
$CR_{n \times 1}$	Canonical Respirations. Vector of respiration from Integer trophic levels
$GC_{nl \times 1}$	Grazing Chain. Vector of inputs to Integer trophic levels from preceding level
$RDP_{nl \times 1}$	Vector of returns from each level to the detrital pool
$LS_{nl \times 1}$	Vector representing the Lindeman Spine
$TE_{nl \times 1}$	Vector of the trophic efficiencies for integer trophic levels
Network Statistics	
Detritivory	Flow from the detrital pool (non-living nodes) to the second trophic level
DetritalInput	Exogenous inputs to the detrital pool
DetritalCirc	internal circulation within the detrital pool
NCYCS	number of feeding cycles removed from the network
NNEX	number of disjoint nexuses detected for the feeding cycles
CI	cycling index of the living component of the network based on flow matrix

Additional Analyses

There are a number of additional analyses available in the package. These additions extended the *enaR* functionality.

Centrality

Centrality analysis is a large topic in network science (Brandes and Erlebach 2005; Wasserman and Faust 1994). In general the goal is to describe the relative importance of parts of the networks (nodes, edges, environs). Many different types of centrality measures exist in network science (Freeman 1979; Freeman, Borgatti, and White 1991; Borgatti and Everett 2006; Brandes and Erlebach 2005). Environ centrality is unique to ENA (Fann and Borrett 2012), but like eigenvector centrality, it is a degree-based centrality measure that considers the equilibrium effect of all pathways of all lengths in the system and as such can be classified as a global centrality measure. Both of these centralities can be calculated in *enaR* as follows:

```
F <- enaFlow(oyster)

ec <- environCentrality(F$N)
show(ec)
```

```
## $ECin
##     Filter Feeders         Microbiota          Meiofauna
##          0.1404961          0.1279889          0.1771034
##    Deposit Feeders          Predators Deposited Detritus
##          0.2178241          0.1557484          0.1808391
##
## $ECout
##     Filter Feeders         Microbiota          Meiofauna
##         0.06970737         0.19108709         0.20595483
##    Deposit Feeders          Predators Deposited Detritus
##         0.12350944         0.07903903         0.33070223
##
## $AEC
##     Filter Feeders         Microbiota          Meiofauna
##          0.1051017          0.1595380          0.1915291
##    Deposit Feeders          Predators Deposited Detritus
##          0.1706668          0.1173937          0.2557707
```

```
eigenCentrality(F$G)
```

```
## $EVCin
## [1] 0.1207568 0.1093625 0.1876329 0.2518905 0.1470501 0.1833072
##
## $EVCout
## [1] 0.00000000 0.23325048 0.26566843 0.11130122 0.01286707 0.37691280
##
## $AEVC
## [1] 0.06037842 0.17130647 0.22665067 0.18159586 0.07995858 0.28011000
```

These centrality values have been normalized to sum to one. In addition, the throughflow vector from flow analysis (Borrett 2013), the total environ throughflow, and total environ storage vectors might also be considered centrality metrics (Whipple et al. 2007; Whipple, Patten, and Borrett 2014). The following code and figure demonstrates how the Average Environ Centrality can be quantified and visualized.

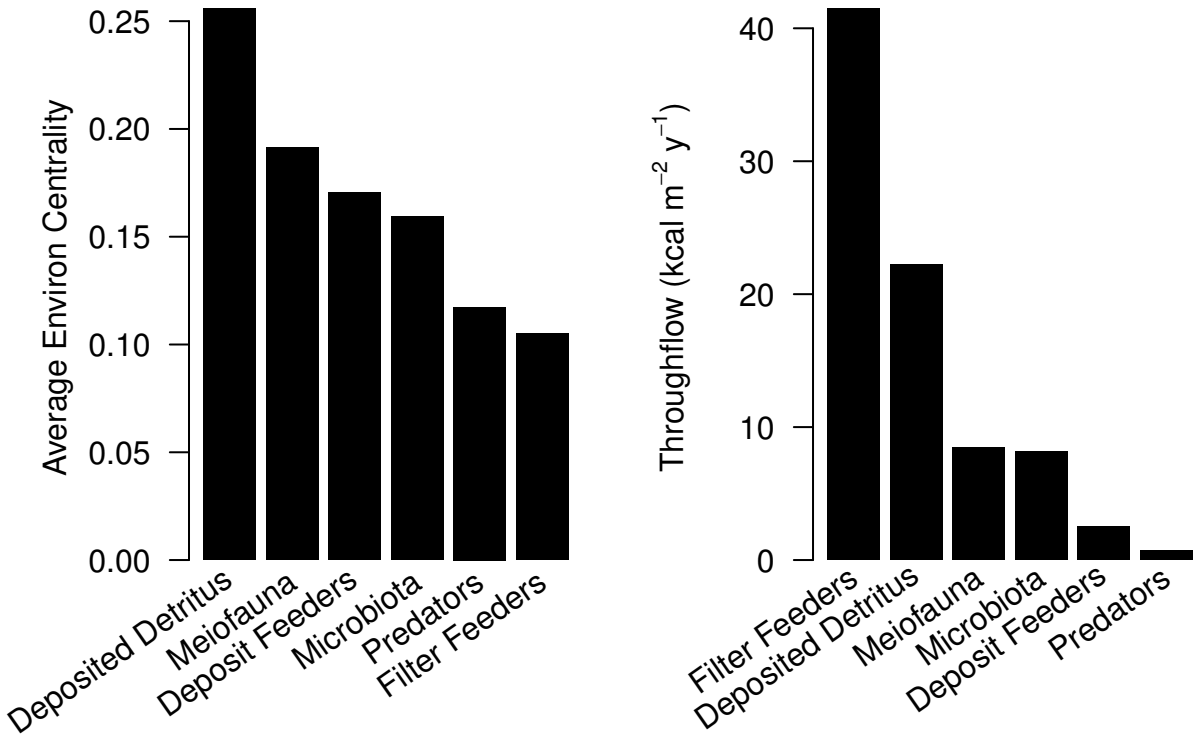
```
## Set plotting parameters
opar <- par(las=1,mfrow=c(1,2),mar=c(7,5,1,1),xpd=TRUE,bg="white")
## Find centrality order
o <- order(ec$AEC,decreasing=TRUE)

## Creating a barplot
bp <- barplot(ec$AEC[o],
              names.arg=NA,
              ylab="Average Environ Centrality",
              col="black",border=NA)
## Adding labels
text(bp,-0.008,
     labels=names(ec$AEC)[o],
     srt=35,adj=1,cex=1)

# throughflow centrality
T <- enaFlow(oyster)$T
```

```
## Warning in enaAscendency(x): Export data is absent from the model.
```

```
o <- order(T,decreasing=TRUE)
bp2 <- barplot(T[o],
               names.arg=NA,
               ylab=expression(paste("Throughflow (kcal m"^-2, " y"^-1,")")),
               col="black", border=NA)
text(bp2,-1,
     labels=names(T)[o],
     srt=35,adj=1,cex=1)
```



```
## Remove the plotting parameters
 rm(opar)
```

Shannon Diversity

Biodiversity is a critical concept in ecology and conservation biology. For example, it is hypothesized to contribute to the stability, productivity, and broad ecosystem functioning of these complex dynamic systems (Tilman, Wedin, and Knops 1996; Hooper et al. 2005). Ecologists often use Shannon's measure of information entropy (H) as an indicator of biodiversity because it captures the effects of richness (number of species) and the evenness of the distribution of individuals among the species (Shannon and Weaver 1949).

Shannon's entropy based metric of diversity is

$$H = -1 \sum_{i=1}^{n} p_i \log(p_i) \tag{2}$$

where p_i is the relative abundance or quantity and n is the number of species (nodes in this context).

This metrics can be applied in a number of ways within the context of ENA. For example, we can find the diversity of storage (biomass) by letting $p_i = X_i/X_\bullet = X_i/\sum X_i$, or we can find the throughflow diversity by letting $p_i = T_i/T_\bullet$. In fact, this can be applied to nearly any node Centrality metrics.

For any given input vector, the maximum possible value of H is $H_{max} = \log(n)$. Thus, we can focus on the evenness component of biodiversity by calculating the relative entropy $0 \leq (H_r = H/H_{max}) \leq 1$. The closer H_r gets to 1, the more evenly distributed the stuff is among the n nodes. From this we can derive a metric of *centralization* ($H_{centralization} = 1 - H_r$ or how concentrated the elements are in a smaller number of nodes. This is a useful metric because it ties back to concepts in Social Network Analysis (Wasserman and Faust 1994). We can recover the effective number of nodes based on the evenness as $s = e^H$ (Ulanowicz, Holt, and Barfield 2014).

The ShannonDiversity function in *enaR* returns each of these metrics for any vector input. For example,

```
ShannonDiversity(F$T)  # throughflow diversity
```

```
##           H        Hmax          Hr    Hcentral           n effective.n
##   1.3042705   1.7917595   0.7279272   0.2720728   6.0000000   3.6849998
```

```
ShannonDiversity(S$X)  # storage (biomass) diversity
```

```
##           H        Hmax          Hr    Hcentral           n effective.n
##   0.8043025   1.7917595   0.4488898   0.5511102   6.0000000   2.2351370
```

The results for the Oyster Reef model indicate that throughflow diversity is greater than the diversity from the storage perspective. This is because the throughflow values are more evenly distributed (less centralized) than the storage values. This is perhaps most clear when we determine the effective richness in the system. From the throughflow perspective there are 3.7 nodes acting, while from the storage perspective the effective number of nodes is estimated to be 2.2.

Quickly Return Multiple Analyses

There are two functions that aggregate multiple analyses and report selected results. A quick way to get a list of the global network statistics reported in Structure, Flow, Ascendency, Storage, and Utility analysis is to use the get.ns function.

```
ns <- get.ns(oyster)
## Examine the whole-network statistics (metrics)
show(ns)
```

```
##  n  L         C LD      ppr    lam1A mlam1A      rho         R        d
##  6 12 0.3333333  2 2.147899 2.147899      1 2.147899 0.4655712 0.147899
##  no.scc no.scc.big      pscc Boundary     TST     TSTp      APL       FCI
##       2          1 0.8333333    41.47 83.5833 125.0533 2.015512 0.1101686
##        BFI       DFI       IFI     ID.F   ID.F.I   ID.F.O    HMG.I
##  0.4961517 0.1950689 0.3087794 1.582925 1.716607 1.534181 2.051826
##     HMG.O AMP.I AMP.O mode0.F  mode1.F  mode2.F  mode3.F mode4.F        H
##  1.891638     3     1   41.47 32.90504 9.208256 32.90504   41.47 3.018275
##       AMI       Hr      CAP      ASC       OH   ASC.CAP    OH.CAP
##  1.330211 1.688063 377.4452 166.3473 211.0979 0.4407191 0.5592809
##  robustness     ELD       TD  A.input A.internal A.export A.respiration
##   0.3611021 1.79506 2.514395 66.03696   72.62476        0      27.68558
##  OH.input OH.internal OH.export OH.respiration CAP.input CAP.internal
##         0    103.2914         0       107.8065  66.03696     175.9162
##  CAP.export CAP.respiration      TSS       CIS         BSI         DSI
##           0         135.492 3112.044 0.9940252 0.003331412 0.003320932
##        ISI     ID.S  ID.S.I   ID.S.O  HMG.S.O  HMG.S.I NAS NASP mode0.S
##  0.9933477 299.1171 454.227 294.1527 1.115985 1.464503  20   21 10.3675
##   mode1.S mode2.S  mode3.S mode4.S     lam1D relation.change.F synergism.F
##  8.226261 3093.45 8.226261 10.3675 0.8991676              61.9    4.915298
##  mutualism.F    lam1DS relation.change.S synergism.S mutualism.S
##     2.272727 0.3022958              61.9    13.08994         2.6
```

It is also possible to instantly return most of the main ENA output with enaAll:

```
oyster.ena <- enaAll(oyster)
```

```
## Warning in enaAscendency(x): Export data is absent from the model.

## Warning in enaAscendency(x): Export data is absent from the model.

## Warning in enaAscendency(x): Export data is absent from the model.

## Warning in enaAscendency(x): Export data is absent from the model.

## Node 1, Reach 1, Total 1
## Node 2, Reach 6, Total 7
## Node 3, Reach 6, Total 13
## Node 4, Reach 6, Total 19
## Node 5, Reach 6, Total 25
## Node 6, Reach 6, Total 31
```

```
names(oyster.ena)
```

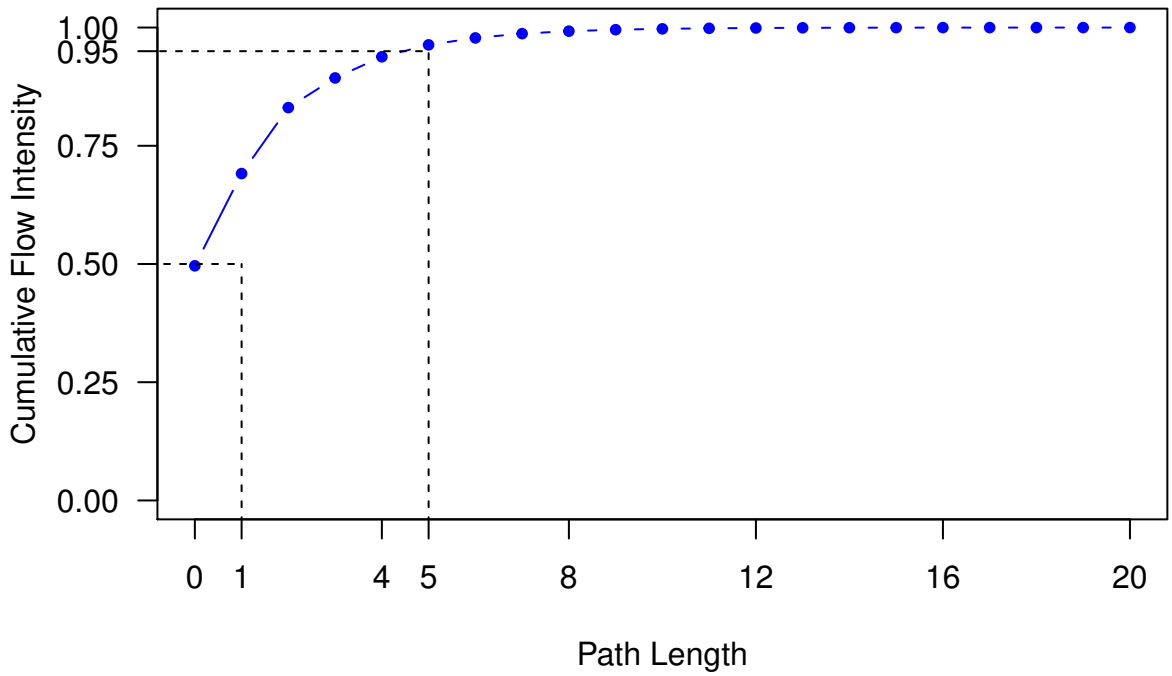
```
## [1] "ascendency" "control"    "environ"    "flow"       "mti"
## [6] "storage"    "structure"  "utility"
```

The *enaCycle* and *enaTroAgg* analyses are not yet included in this function because they can be computationally intensive for large models.

findPathLength

The findPathLength function builds on Flow Analyses and explores how the proportion of throughflow is generated as walk length increases. Specifically, it finds the walk lengths by which 50%, 80%, 90%, and 95% of the total system throughflow is recovered, as well as the walk length at which indirect flow exceeds direct flows (if $I/D_F > 1$). It also returns vectors of the total flow generated by all the pathways of each length and a vector of the proportion of total cumulative flow. This is the basis for the analyses presented in Borrett (2013).

```
p <- findPathLength(oyster, maxPath = 20, plot.sw = TRUE)
```




```
attributes(p)
```

```
## $names
## [1] "thresholds" "tf"         "ctf"
```

```
p$thresholds
```

```
## mID m50 m80 m95
##   3   1   2   5
```

Utility Functions

The *enaR* library contains several utility functions that designed to help the user and other functions with common actions.

ssCheck

The ssCheck function is applied to an ecological network model to determine if the model is at steady state. Specifically, it compares T_i^{input} to T_i^{output} for all i. For practical reasons, this function returns the logical value *TRUE* if

$$(|T_i^{input} - T_j^{output}|)/T_i^{output} * 100 \leq 5\%, \quad \forall i. \tag{3}$$

This effectively lets each node throughflow to be off by 5% .

```
ssCheck(oyster)
```

```
## [1] TRUE
```

```
data(enaModels)
ssCheck(enaModels[[11]])
```

```
## [1] FALSE
```

While users and other *enaR* functions most often simply need to know if the system is at steady state, the function can also return the input and output throughflow vectors and a vector of the percent differences.

```
ssCheck(enaModels[[11]], more = TRUE)
```

```
## $ss
## [1] FALSE
##
## $Tin
## Pelagic Producers          Bacteria   Microzooplakton    Mesozooplakton
##             27.90              8.00              6.00             12.00
##   Inv. Carnivores      Pelagic Fish Benthis Producers         Dem. Fish
##              1.70              1.57              3.90              0.22
##        Macrofauna         Meiofauna          Sedim. C               DOM
##              2.02              4.32             14.57             31.35
##
## $Tout
## Pelagic Producers          Bacteria   Microzooplakton    Mesozooplakton
##             24.90              8.00              6.00             12.00
##   Inv. Carnivores      Pelagic Fish Benthis Producers         Dem. Fish
##              1.70              1.57              3.90              0.21
##        Macrofauna         Meiofauna          Sedim. C               DOM
##              2.02              4.32              5.47              9.05
##
## $perror
## Pelagic Producers          Bacteria   Microzooplakton    Mesozooplakton
##         12.048193          0.000000          0.000000          0.000000
```

```
##   Inv. Carnivores      Pelagic Fish Benthis Producers         Dem. Fish
##          0.000000          0.000000          0.000000          4.761905
##        Macrofauna         Meiofauna          Sedim. C               DOM
##          0.000000          0.000000        166.361974        246.408840
```

Knowing which nodes are not at steady state and how far off they are can help model construction and manual balancing steps. It is also a handy tool to ensure that models are imported correctly into the package.

Output Orientation

To facilitate package use by the existing ENA community, some of which use the column-to-row orientation (e.g. the Patten School), we have created orientation functions that enable the user to set the expected output orientation for functions written in a particular "school" of analysis. Thus, functions from either school will receive network models with the standard row-to-column, but will return output with flow matrices oriented in the column-to-row orientation when appropriate (i.e. Patten school functions) and return them in that same orientation.

Here is an example of how to use the model orientation functions to re-orient the output from enaFlow:

```
## Check the current orientation
get.orient()
```

```
## [1] "rc"
```

```
## enaFlow output in row-column
flow.rc <- enaFlow(oyster)$G
## Set the global orientation to school
set.orient('school')
## Check that it worked
get.orient()
```

```
## [1] "school"
```

```
## enaFlow output in column-row
flow.cr <- enaFlow(oyster)$G
## Check. Outputs should be transposed from each other.
all(flow.rc == flow.cr)
```

```
## [1] FALSE
```

```
all(flow.rc == t(flow.cr))
```

```
## [1] TRUE
```

```
## Now change back to the default orientation ('rc')
set.orient('rc')
```

Matrix Exponentiation

Matrix powers – raising a matrix to a power is not a native operation in **R**. Thus, the *enaR* package includes a function mExp to facilitate this matrix operation commonly used in ENA. Here we illustrate raising the oyster reef output-oriented direct flow intensity matrix to the power 2, $\mathbf{G}^2$:

```
mExp(F$G,2)
```

```
##                    Filter Feeders Microbiota  Meiofauna Deposit Feeders
## Filter Feeders                  0  0.1397606 0.12440966      0.01099840
## Microbiota                      0  0.0000000 0.00000000      0.01150080
## Meiofauna                       0  0.1835203 0.16336297      0.01444205
## Deposit Feeders                 0  0.2789476 0.24830879      0.02195166
## Predators                       0  0.1746313 0.15545033      0.01374254
## Deposited Detritus              0  0.0000000 0.05416549      0.07962750
##                       Predators Deposited Detritus
## Filter Feeders     0.000000000        0.005891414
## Microbiota         0.010118608        0.185945731
## Meiofauna          0.005343446        0.059228112
## Deposit Feeders    0.000000000        0.032622730
## Predators          0.000000000        0.000000000
## Deposited Detritus 0.001980437        0.185314635
```

netOrder

Sometimes it is helpful to reorder the nodes in a network. While a simple re-ordering should not change the linear algebra based *enaR* results, it can be helpful to present results or for the construction of some algorithms. Thus, the netOrder function lets the user reorder the nodes in a network to any specified vector.

```
troModels[[6]]%v%'vertex.names' # original node name order
```

```
## [1] "PLANTS"           "BACTERIA"         "DETRITUS FEEDERS"
## [4] "CARNIVORES"       "DETRITUS"
```

```
new.network <- netOrder(troModels[[6]], c(1, 3, 2, 5, 4))
# new.network is the rearranged network with nodes in the desired order.

new.network%v%'vertex.names' # new node name order
```

```
## [1] "PLANTS"           "DETRITUS FEEDERS" "BACTERIA"
## [4] "DETRITUS"         "CARNIVORES"
```

```
as.matrix(new.network, attr="flow")
```

```
##                   PLANTS DETRITUS FEEDERS BACTERIA DETRITUS CARNIVORES
## PLANTS                 0                0        0      200          0
## DETRITUS FEEDERS       0                0        0      167       8881
## BACTERIA               0             2309        0     1600          0
## DETRITUS               0             5205       75        0          0
## CARNIVORES             0                0        0      370          0
```

Note that this will also change the order for the model flows, as the whole network data object has been reordered.

as.extended

The as.extended function returns the extended flow matrix. This matrix builds a composite matrix for the internal flows and the boundary fluxes. Ulanowicz's often denotes this as the $T_{(n+3)\times(n+3)}$ matrix, though it has also been called the fat flow matrix and denoted as $\hat{\mathbf{F}}_{(n+3)\times(n+3)}$. This is defined as follows.

$$\hat{\mathbf{F}} = \begin{bmatrix} \mathbf{F} & export & respiration & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ imports & 0 & 0 & 0 \end{bmatrix} \tag{4}$$

For example, we can get the $\hat{\mathbf{F}}$ for the oyster model as

```
fat <- as.extended(oyster)
fat
```

```
##                     Filter Feeders Microbiota Meiofauna Deposit Feeders
## Filter Feeders                0.00     0.0000    0.0000          0.0000
## Microbiota                    0.00     0.0000    1.2060          1.2060
## Meiofauna                     0.00     0.0000    0.0000          0.6609
## Deposit Feeders               0.00     0.0000    0.0000          0.0000
## Predators                     0.00     0.0000    0.0000          0.0000
## Deposited Detritus            0.00     8.1721    7.2745          0.6431
##                               0.00     0.0000    0.0000          0.0000
##                               0.00     0.0000    0.0000          0.0000
## import                       41.47     0.0000    0.0000          0.0000
##                     Predators Deposited Detritus export respiration
## Filter Feeders         0.5135            15.7910      0     25.1650 0
## Microbiota             0.0000             0.0000      0      5.7600 0
## Meiofauna              0.0000             4.2403      0      3.5794 0
## Deposit Feeders        0.1721             1.9076      0      0.4303 0
## Predators              0.0000             0.3262      0      0.3594 0
## Deposited Detritus     0.0000             0.0000      0      6.1759 0
##                        0.0000             0.0000      0      0.0000 0
##                        0.0000             0.0000      0      0.0000 0
## import                 0.0000             0.0000      0      0.0000 0
```

```
dim(fat)
```

```
## [1] 9 9
```

```
network.size(oyster)
```

```
## [1] 6
```

signs

The signs function can be applied to any square matrix to determine a number qualitative features. The function returns:

- a *sign* matrix in which the elements indicate whether the elements were positive (+), negative (-), or neutral (0).

- a *relations* matrix showing the pairwise qualitative relationships among the matrix elements.
- the *rs.tab* that summarizes the pairwise relationships in tabular form. This also provides the common ecological interpretation of the relationship (e.g., (+,+) is a mutualism).
- *relationships.counts* summarizes the number of the different qualitative relationships found in the matrix.

```
mti <- enaMTI(oyster, eigen.check = FALSE) # calculate Mixed Trophic Impacts
signs(mti$M)  # find the signs for the integral utility matrix
```

```
## $sign
##                    Filter Feeders Microbiota Meiofauna Deposit Feeders
## Filter Feeders     "-"            "+"        "+"       "+"
## Microbiota         "-"            "-"        "-"       "+"
## Meiofauna          "-"            "-"        "-"       "+"
## Deposit Feeders    "-"            "-"        "-"       "-"
## Predators          "-"            "+"        "-"       "-"
## Deposited Detritus "-"            "+"        "+"       "+"
##                    Predators Deposited Detritus
## Filter Feeders     "+"       "+"
## Microbiota         "+"       "-"
## Meiofauna          "+"       "-"
## Deposit Feeders    "+"       "+"
## Predators          "-"       "-"
## Deposited Detritus "+"       "-"
##
## $relations
##                    Filter Feeders Microbiota Meiofauna Deposit Feeders
## Filter Feeders     "(-,-)"        "(-,+)"    "(-,+)"   "(-,+)"
## Microbiota         "0"            "(-,-)"    "(-,-)"   "(-,+)"
## Meiofauna          "0"            "0"        "(-,-)"   "(-,+)"
## Deposit Feeders    "0"            "0"        "0"       "(-,-)"
## Predators          "0"            "0"        "0"       "0"
## Deposited Detritus "0"            "0"        "0"       "0"
##                    Predators Deposited Detritus
## Filter Feeders     "(-,+)"   "(-,+)"
## Microbiota         "(+,+)"   "(+,-)"
## Meiofauna          "(-,+)"   "(+,-)"
## Deposit Feeders    "(-,+)"   "(+,+)"
## Predators          "(-,-)"   "(+,-)"
## Deposited Detritus "0"       "(-,-)"
##
## $rs.tab
##                  From                 To Relationship      R.name
## 1      Filter Feeders     Filter Feeders        (-,-) competition
## 2      Filter Feeders         Microbiota        (-,+)   predation
## 3      Filter Feeders          Meiofauna        (-,+)   predation
## 4      Filter Feeders    Deposit Feeders        (-,+)   predation
## 5      Filter Feeders          Predators        (-,+)   predation
## 6      Filter Feeders Deposited Detritus        (-,+)   predation
## 7          Microbiota         Microbiota        (-,-) competition
## 8          Microbiota          Meiofauna        (-,-) competition
## 9          Microbiota    Deposit Feeders        (-,+)   predation
## 10         Microbiota          Predators        (+,+)   mutualism
```

```
## 11         Microbiota Deposited Detritus        (+,-)    altruism
## 12          Meiofauna          Meiofauna        (-,-) competition
## 13          Meiofauna    Deposit Feeders        (-,+)   predation
## 14          Meiofauna          Predators        (-,+)   predation
## 15          Meiofauna Deposited Detritus        (+,-)    altruism
## 16    Deposit Feeders    Deposit Feeders        (-,-) competition
## 17    Deposit Feeders          Predators        (-,+)   predation
## 18    Deposit Feeders Deposited Detritus        (+,+)   mutualism
## 19          Predators          Predators        (-,-) competition
## 20          Predators Deposited Detritus        (+,-)    altruism
## 21 Deposited Detritus Deposited Detritus        (-,-) competition
##
## $relationship.counts
##
## (-,-) (-,+) (+,-) (+,+)
##     7     9     3     2
```

Multi-Model Analyses (Batch Processing)

While many investigators analyze single models, much of ENA is used to compare ecosystem models (Baird, McGlade, and Ulanowicz 1991; Oevelen et al. 2006; Christian and Thomas 2003; Niquil et al. 2012; Hines et al. 2015). Investigators have also analyzed large sets of models to determine the generality of hypothesized ecosystem properties (Christensen 1995; Borrett and Salas 2010; Salas and Borrett 2011). For both of these applications, investigators need to analyze multiple models. One advantage of the *enaR* **R** package is that it simplifies this batch processing. Here we illustrate how to batch analyze a selection of models.

Our first step is to build an **R** list data object with ecosystem network models to batch analyze as the elements of the list. To illustrate batch processing, we will use a subset of the trophic models distributed with *enaR*, which are already stored as a list.

```
data(troModels)
```

Now that we have the models loaded, we can start to manipulate them. Once we have balanced the models, we can run the flow analysis on them. We are using the lapply function to iterate the analysis across the list of models stored in model.list. This approach is more compact and computationally efficient than a using for-loop.

```
# balance models as necessary
m.list <- lapply(troModels[1:10],balance)  # selected first 10 models in the list
```

```
## [1] BALANCED
## [1] BALANCED
## [1] BALANCED
## [1] BALANCED
## [1] BALANCED
## [1] BALANCED
## [1] BALANCED
## [1] BALANCED
## [1] BALANCED
## [1] BALANCED
```

```
# check that models are balanced
unlist(lapply(m.list,ssCheck))
```

```
## Marine Coprophagy (oyster)              Lake Findley
##                       TRUE                      TRUE
##                Mirror Lake                Lake Wingra
##                       TRUE                      TRUE
##                Marion Lake               Cone Springs
##                       TRUE                      TRUE
##             Silver Springs            English Channel
##                       TRUE                      TRUE
##               Oyster Reef               Baie de Somme
##                       TRUE                      TRUE
```

```
## If balancing fails, you can use force.balance
## to repeatedly apply the balancing procedure
## although this is not the case with our model set

m.list <- lapply(m.list,force.balance)
## Check that all the models are balanced
all(unlist(lapply(m.list,ssCheck)))
```

```
## [1] TRUE
```

```
## Example Flow Analysis
F.list <- lapply(m.list, enaFlow)

## The full results of the flow analysis is now stored in the elements
## of the F.list.  To get the results for just the first model:
F.list[[1]]
```

```
## $T
##                    SHRIMP        BENTHIC ORGANISMS  SHRIMP FECES & BACTERIA
##                     124.1                    323.7                      21.9
## BENTHIC FECES & BACTERIA
##                      79.6
##
## $G
##                            SHRIMP BENTHIC ORGANISMS SHRIMP FECES & BACTERIA
## SHRIMP                          0         0.0000000               0.1764706
## BENTHIC ORGANISMS               0         0.0000000               0.0000000
## SHRIMP FECES & BACTERIA         0         0.6986301               0.0000000
## BENTHIC FECES & BACTERIA        0         0.6645729               0.0000000
##                            BENTHIC FECES & BACTERIA
## SHRIMP                                    0.0000000
## BENTHIC ORGANISMS                         0.2459067
## SHRIMP FECES & BACTERIA                   0.0000000
## BENTHIC FECES & BACTERIA                  0.0000000
##
## $GP
##                            SHRIMP BENTHIC ORGANISMS SHRIMP FECES & BACTERIA
## SHRIMP                          0        0.00000000                       1
```

```
## BENTHIC ORGANISMS             0        0.00000000                       0
## SHRIMP FECES & BACTERIA       0        0.04726599                       0
## BENTHIC FECES & BACTERIA      0        0.16342292                       0
##                           BENTHIC FECES & BACTERIA
## SHRIMP                                           0
## BENTHIC ORGANISMS                                1
## SHRIMP FECES & BACTERIA                          0
## BENTHIC FECES & BACTERIA                         0
##
## $N
##                           SHRIMP BENTHIC ORGANISMS SHRIMP FECES & BACTERIA
## SHRIMP                         1         0.1473716               0.1764706
## BENTHIC ORGANISMS              0         1.1953471               0.0000000
## SHRIMP FECES & BACTERIA        0         0.8351055               1.0000000
## BENTHIC FECES & BACTERIA       0         0.7943953               0.0000000
##                           BENTHIC FECES & BACTERIA
## SHRIMP                                  0.03623966
## BENTHIC ORGANISMS                       0.29394387
## SHRIMP FECES & BACTERIA                 0.20535805
## BENTHIC FECES & BACTERIA                1.19534712
##
## $NP
##                           SHRIMP BENTHIC ORGANISMS SHRIMP FECES & BACTERIA
## SHRIMP                         1        0.05649926                       1
## BENTHIC ORGANISMS              0        1.19534712                       0
## SHRIMP FECES & BACTERIA        0        0.05649926                       1
## BENTHIC FECES & BACTERIA       0        0.19534712                       0
##                           BENTHIC FECES & BACTERIA
## SHRIMP                                 0.05649926
## BENTHIC ORGANISMS                      1.19534712
## SHRIMP FECES & BACTERIA                0.05649926
## BENTHIC FECES & BACTERIA               1.19534712
##
## $TCC
##      [,1]      [,2]      [,3]       [,4]
## [1,]    0 0.1232877 0.1764706 0.03031726
## [2,]    0 0.1634229 0.0000000 0.24590670
## [3,]    0 0.6986301 0.0000000 0.17179783
## [4,]    0 0.6645729 0.0000000 0.16342292
##
## $TDC
##      [,1]       [,2] [,3]       [,4]
## [1,]    0 0.05649926    1 0.05649926
## [2,]    0 0.16342292    0 1.00000000
## [3,]    0 0.05649926    0 0.05649926
## [4,]    0 0.16342292    0 0.16342292
##
## $ns
##      Boundary   TST  TSTp     APL       FCI       BFI       DFI       IFI
## [1,]    379.6 549.3 928.9 1.44705 0.1199863 0.6910614 0.1542493 0.1546893
##          ID.F    ID.F.I    ID.F.O    HMG.I    HMG.O AMP.I AMP.O mode0.F
## [1,] 1.002852 0.3603839 0.6126851 2.014161 1.891504     1     0   379.6
##       mode1.F  mode2.F  mode3.F mode4.F        H      AMI       Hr
## [1,] 103.7915 65.90846 103.7915   379.6 2.719296 1.034247 1.685049
```

```
##           CAP      ASC       OH   ASC.CAP    OH.CAP robustness      ELD
## [1,] 2525.954 960.7117 1565.242 0.3803362 0.6196638  0.3676709 1.793185
##            TD  A.input A.internal A.export A.respiration OH.input
## [1,] 2.048044 402.8692   249.2812        0      308.5612 433.3118
##      OH.internal OH.export OH.respiration CAP.input CAP.internal
## [1,]    460.6126         0       671.3179   836.181     709.8939
##      CAP.export CAP.respiration
## [1,]          0        979.8791
```

We can use the same technique to extract specific information, like just the ratio of Indirect-to-Direct flow for each model.

```
## Example of extracting just specific information - Indirect Effects Ratio
IDs <- unlist(lapply(m.list, function(x) enaFlow(x)$ns[9]))
## Look at the first few ID's
head(IDs)
```

```
## Marine Coprophagy (oyster)              Lake Findley
##                   1.002852                   1.723221
##                Mirror Lake                Lake Wingra
##                   1.861121                   1.861719
##                Marion Lake               Cone Springs
##                   2.175878                   1.023016
```

We can also collect the set of output-oriented integral flow matrices.

```
## Here is a list containing only the
## output-oriented integral flow matrices
N.list <- lapply(m.list,function(x) enaFlow(x)$N)
```

We can also apply the get.ns function to extract all of the network statistics for each model. We then use the do.call function to reshape the network statistics into a single data frame.

```
## Collecting and combining all network statistics
ns.list <- lapply(m.list,get.ns) # returns as list
ns <- do.call(rbind,ns.list)  # ns as a data.frame
## Let's take a quick look at some of the output
colnames(ns)    # return network statistic names.
```

```
##  [1] "n"                "L"                "C"
##  [4] "LD"               "ppr"              "lam1A"
##  [7] "mlam1A"           "rho"              "R"
## [10] "d"                "no.scc"           "no.scc.big"
## [13] "pscc"             "Boundary"         "TST"
## [16] "TSTp"             "APL"              "FCI"
## [19] "BFI"              "DFI"              "IFI"
## [22] "ID.F"             "ID.F.I"           "ID.F.O"
## [25] "HMG.I"            "HMG.O"            "AMP.I"
## [28] "AMP.O"            "mode0.F"          "mode1.F"
## [31] "mode2.F"          "mode3.F"          "mode4.F"
## [34] "H"                "AMI"              "Hr"
## [37] "CAP"              "ASC"              "OH"
```

```
## [40] "ASC.CAP"           "OH.CAP"            "robustness"
## [43] "ELD"               "TD"                "A.input"
## [46] "A.internal"        "A.export"          "A.respiration"
## [49] "OH.input"          "OH.internal"       "OH.export"
## [52] "OH.respiration"    "CAP.input"         "CAP.internal"
## [55] "CAP.export"        "CAP.respiration"   "TSS"
## [58] "CIS"               "BSI"               "DSI"
## [61] "ISI"               "ID.S"              "ID.S.I"
## [64] "ID.S.O"            "HMG.S.O"           "HMG.S.I"
## [67] "NAS"               "NASP"              "mode0.S"
## [70] "mode1.S"           "mode2.S"           "mode3.S"
## [73] "mode4.S"           "lam1D"             "relation.change.F"
## [76] "synergism.F"       "mutualism.F"       "lam1DS"
## [79] "relation.change.S" "synergism.S"       "mutualism.S"
```

```
dim(ns)          # show dimensions of ns matrix
```

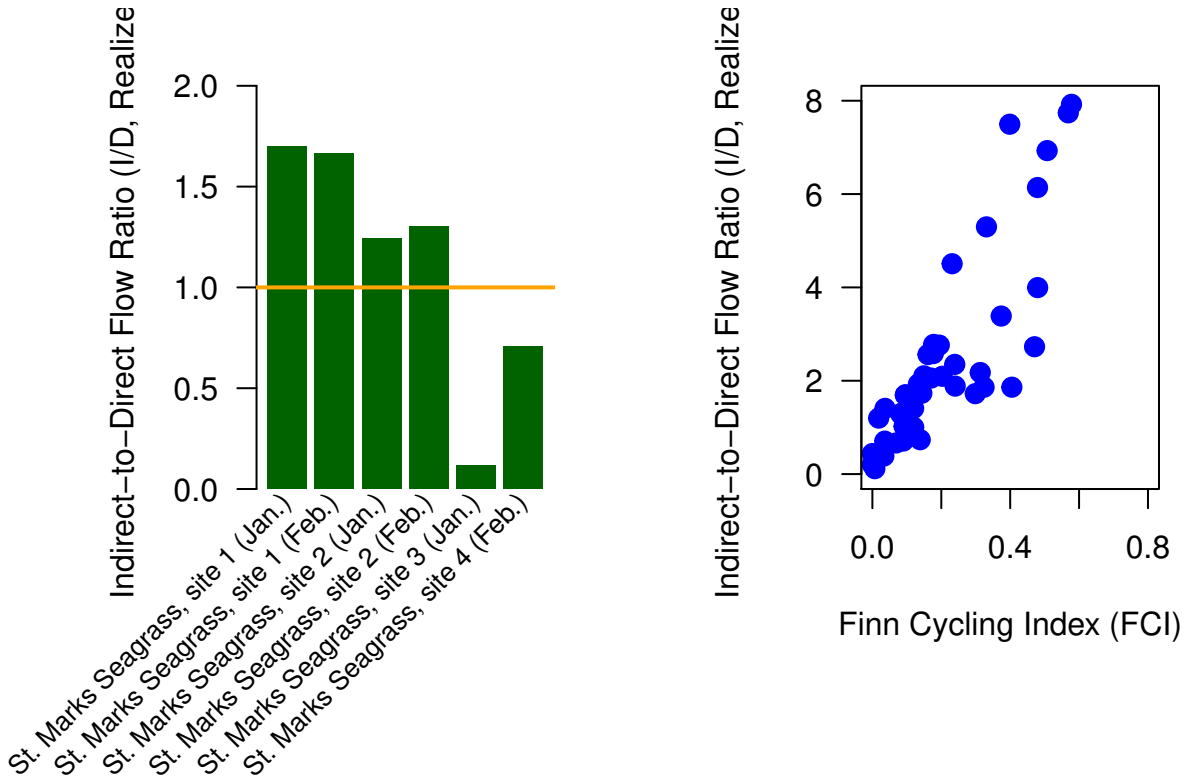
```
## [1] 74 81
```

```
ns[1:5,1:5]      # show selected results
```

	n	L	C	LD	ppr
Marine Coprophagy (oyster)	4	4	0.250	1.0	1.000000
Lake Findley	4	6	0.375	1.5	1.004975
Mirror Lake	5	9	0.360	1.8	1.324718
Lake Wingra	5	10	0.400	2.0	2.000000
Marion Lake	5	9	0.360	1.8	1.324718

Given this data frame of network statistics, we can construct interesting plots for further analysis. Here we focus on results of the St. Marks Seagrass ecosystem (Baird, Luczkovich, and Christian 1998).

```
opar <- par(las=1,mar=c(9,7,2,1),xpd=TRUE,mfrow=c(1,2),oma=c(1,1,0,0))
## Number of models
x=dim(ns)[1]
m.select <- 26:31
bp=barplot(ns$ID.F[m.select],ylab="Indirect-to-Direct Flow Ratio (I/D, Realized)",
        col="darkgreen",border=NA,ylim=c(0,2))
## Add labels
text(bp,-0.05,
     labels=rownames(ns)[m.select],
       srt=45,adj=1,cex=0.85)
opar <- par(xpd=FALSE)
abline(h=1,col="orange",lwd=2)
#
plot(ns$FCI,ns$ID.F,pch=20,col="blue",cex=2,
     ylab="Indirect-to-Direct Flow Ratio (I/D, Realized)",
     xlab="Finn Cycling Index (FCI)",
     xlim=c(0,0.8),ylim=c(0,8))
```




```
## Remove the plotting parameters
rm(opar)
```

A strength of this software is the ease with which users can apply ENA to multiple models. We expect that this will simplify users' analytic workflows and reduce the time required to conduct the work.

Connecting to Other Useful Software

Another advantage of building the *enaR* package in **R** is that it lets ecologists take advantage of other types of network analysis and statistical tools that already exist in **R**. We highlight three examples here.

network

enaR uses the network data object introduced in the *network* package (Butts 2008a). One advantage of using this data object is that analysts can then use the tools for network construction and manipulation that are part of the *network* package. For example, *network* can import network models from Pajek project files, which is another widely used network modeling and analysis software (Batagelj and Mrvar 2007). The package also includes functions to seamlessly add and delete nodes (edges). It also provides the capability to visualize the network shown previously.

sna: Social Network Analysis

The *sna* package for Social Network Analysis is bundled in the *statnet* package and uses the same network data object defined in *network*. Thus, the design decision to use the network data object gives users direct access to *sna* tools.

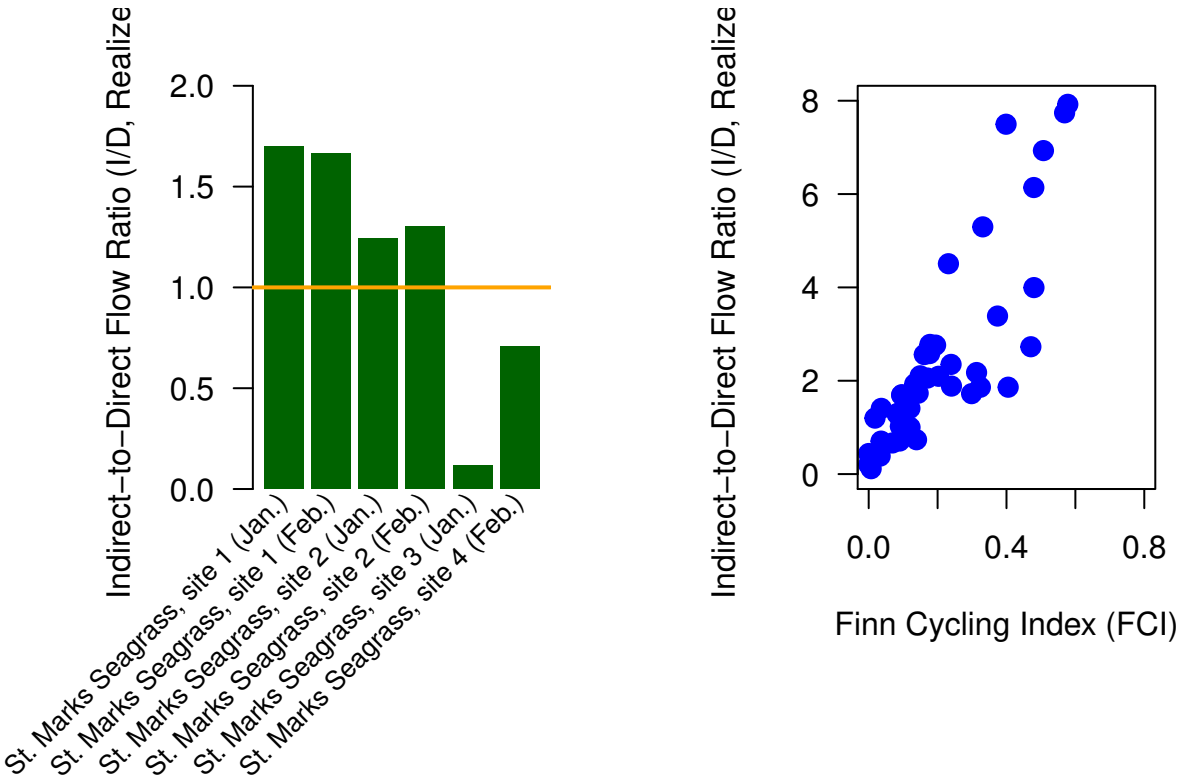


Figure 3: Ratio of Indirect-to-Direct Flow for six ecosystem models (left) and relationship between the Finn Cycling Index and the ratio of Indirect-to-Direct flow in the 74 ecosystem models.

As an example, the *sna* package provides a way of calculating several common centrality measures. Thus, ecologists can now use the *sna* algorithms to determine different types of centrality for their models. This includes betweenness and closeness centrality as follows:

```
sna::betweenness(oyster)
```

```
## [1] 0.0 0.0 0.5 3.5 0.0 9.0
```

```
sna::closeness(oyster)
```

```
## [1] 0.625 0.000 0.000 0.000 0.000 0.000
```

The *sna* package introduced new graphical capabilities as well. For example, it will create a target diagram to visualize the centralities.

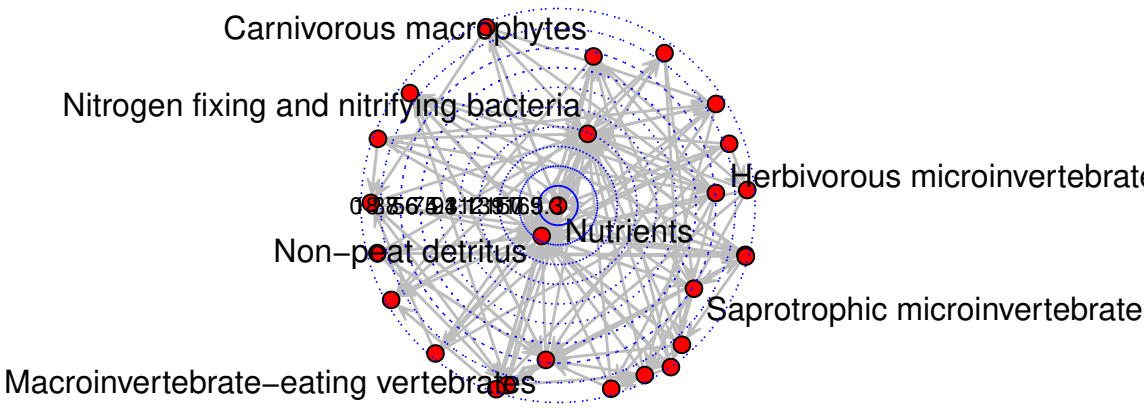
```
m <- m.list[[17]]  # Okefenokee Food Web
## Calculate betweenness centrality
b <- sna::betweenness(m)
## Get vertex names
nms <- m%v%'vertex.names'
show(nms)
```

```
##  [1] "Peat decomposers"
```

```
##  [2] "Detritus decomposers"
##  [3] "Nitrogen fixing and nitrifying bacteria"
##  [4] "Autotrophic macrophytes"
##  [5] "Carnivorous macrophytes"
##  [6] "Phytoplankton"
##  [7] "Periphyton"
##  [8] "Filamentous algae"
##  [9] "Herbivorous microinvertebrates"
## [10] "Predaceaous microinvertebrates"
## [11] "Saprotrophic microinvertebrates"
## [12] "Algae-eating macroinvertebrates"
## [13] "Macrophyte-eating macroinvertebrates"
## [14] "Microinvertebrate-eating macroinvertebrates"
## [15] "Macroinvertebrate-eating macroinvertebrates"
## [16] "Vertebrate-eating macroinvertebrates"
## [17] "Saprotrophic macroinvertebrates"
## [18] "Algae-eating vertebrates"
## [19] "Macrophyte-eating vertebrates"
## [20] "Microinvertebrate-eating vertebrates"
## [21] "Macroinvertebrate-eating vertebrates"
## [22] "Vertebrate-eating vertebrates"
## [23] "Saprotrophic vertebrates"
## [24] "Superficial peat"
## [25] "Non-peat detritus"
## [26] "Nutrients"
```

```
## Exclude less central node names
nms[b<=(0.1*max(b))] <- NA

set.seed(2)
opar <- par(xpd=TRUE,mfrow=c(1,1))
## Create target plot showing only
## labels of most central nodes
sna::gplot.target(m,b,
             edge.col="grey",
             label=nms)
```




```
## Remove plot settings
rm(opar)
```

```
{r, fig=TRUE,echo=FALSE,eval=TRUE,fig.cap="Target plot of node   betweenness centrality
for the Okefenokee Swamp trophic model."} <<target>>
```

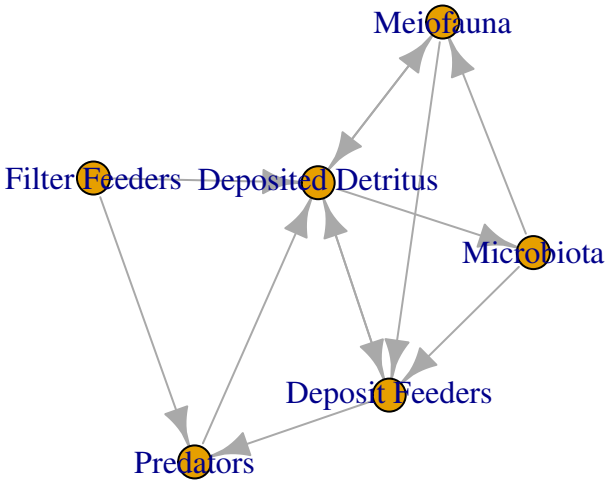
In addition to the node-level measures, *sna* includes graph-level indices.

iGraph

The *iGraph* package can also be useful for analyzing network data. Here are a few examples of using the package. Note that some functions in *iGraph* conflict with other functions already defined, so care is required when using *iGraph*.

```
## The adjacency matrix
A <- St$A

## Creating an iGraph graph
g <- igraph::graph.adjacency(A)
plot(g)
```



iGraph has a different set of visualization tools and generates a different looking plot.

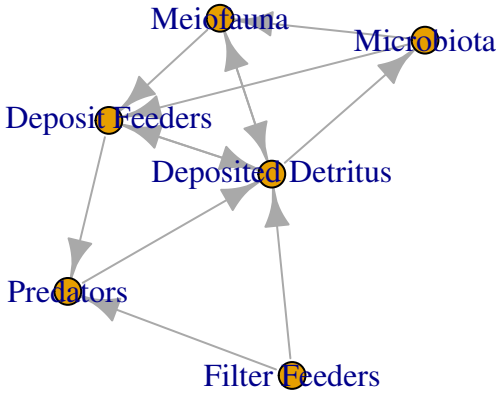


Figure 4: Plot of Oyster reef model using iGraph

```
## Betweenness centrality (calculated by iGraph and sna)
igraph::betweenness(g)
```

```
##     Filter Feeders         Microbiota          Meiofauna
##                0.0                0.0                0.5
##    Deposit Feeders          Predators Deposited Detritus
##                3.5                0.0                9.0
```

```
## Shortest path between any two nodes
igraph::shortest.paths(g)
```

```
##                     Filter Feeders Microbiota Meiofauna Deposit Feeders
## Filter Feeders                   0          2         2                2
## Microbiota                       2          0         1                1
## Meiofauna                        2          1         0                1
## Deposit Feeders                  2          1         1                0
## Predators                        1          2         2                1
## Deposited Detritus               1          1         1                1
##                     Predators Deposited Detritus
## Filter Feeders              1                  1
## Microbiota                  2                  1
## Meiofauna                   2                  1
## Deposit Feeders             1                  1
## Predators                   0                  1
## Deposited Detritus          1                  0
```

```
## Average path length in the network (graph theory sense)
igraph::average.path.length(g,directed=TRUE)
```

```
## [1] 1.52
```

```
## Diameter of the graph
igraph::diameter(g)
```

```
## [1] 2
```

```
## Connectivity of the group and sub-components
igraph::vertex.connectivity(g)  # connectivity of a graph (group cohesion)
```

```
## [1] 0
```

```
igraph::subcomponent(g,1,'in')  # subcomponent reachable from 1 along inputs
```

```
## + 1/6 vertex, named:
## [1] Filter Feeders
```

```
igraph::subcomponent(g,2,'in')  # subcomponent reachable from 2 along inputs
```

```
## + 6/6 vertices, named:
## [1] Microbiota         Deposited Detritus Filter Feeders
## [4] Meiofauna          Deposit Feeders    Predators
```

```
igraph::subcomponent(g,1,'out') # subcomponent reachable from 1 along outputs
```

```
## + 6/6 vertices, named:
## [1] Filter Feeders     Predators          Deposited Detritus
## [4] Microbiota         Meiofauna          Deposit Feeders
```

```
igraph::subcomponent(g,2,'out') # subcomponent reachable from 2 along output
```

```
## + 5/6 vertices, named:
## [1] Microbiota         Meiofauna          Deposit Feeders
## [4] Deposited Detritus Predators
```

```
igraph::edge.connectivity(g)
```

```
## [1] 0
```

bipartite

The bipartite package provides as set of functions largely developed directly from community ecology for the analysis of two-mode networks (e.g. plant-pollinator, plant-disperser, predator-prey). To facilitate analysis of ecosystem networks using the bipartite toolbox, we created a simple function for converting ecosystem models in the network format to a bipartite matrix. Here's a quick example using the Oyster Reef model (Dame and Patten 1981) where we create a vector of "membership" to divide the ecosystem compartments to create a bipartite network.

```
as.bipartite(x = oyster, y = gl(2, 3))
```

```
##                Deposit Feeders Predators Deposited Detritus
## Filter Feeders          0.0000    0.5135            15.7910
## Microbiota              1.2060    0.0000             0.0000
## Meiofauna               0.6609    0.0000             4.2403
```

EcoNet

The *EcoNet* software is an online, web-interface that provides a tool box for dynamic modeling and ENA analytics (Kazanci 2007). We have provided a write function that enables *enaR* users to output models for easy input into the *EcoNet* interface. The *EcoNet* package and details on the model input syntax can be found at http://eco.engr.uga.edu. Here is an example of how to use the write.EcoNet function in *enaR* in your current working directory:

```
data(oyster)
write.EcoNet(oyster, file = 'oyster.txt', mn = 'oyster_model')
oyster <- read.EcoNet(file = 'oyster.txt')
```

Models can also be read from the set hosted on the *EcoNet* website. If you know the name of the model that you want, you can request it directly. If not, you can leave the input empty to receive a prompt detailing the list of models:

```
EcoNetWeb(model.name = "Intertidal Oyster Reef Ecosystem Model")
EcoNetWeb()
```

Conclusion

These examples show how to use the key features of the *enaR* package that enables scientists to perform Ecosystem Network Analysis in **R**. The vision for this package is that it provides access to ENA algorithms from both the Ulanowicz and Patten Schools to facilitate theoretical synthesis and broader application. In its current form it replicates, updates, and extends the functionality of the *NEA.m* function (Fath and Borrett 2006) and replicates much of the main analyses in *NETWRK* (Ulanowicz and Kay 1991). Through the connections that *enaR* provides to other **R** packages users can connect to other network analyses provided by packages, such as *sna* and *iGraph*. There are other **R** packages that have graph and network analysis tools, like *Bioconductor*, *WGCNA*, *tnet* and *rmangal*, that might also be useful for ecologists. Our aim is for *enaR* to serve as a nexus for the introduction of analyses from the broader field of network theory into ecology. In addition, we would like to invite users to connect, collaborate and contribute to development of ENA theory and *enaR*. Programmers that are interested can visit https://github.com/SEELab/enaR_development for more information on how to contribute to development of the *enaR* package.

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