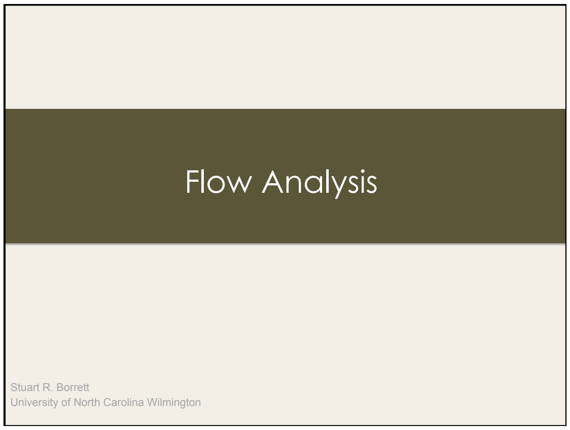
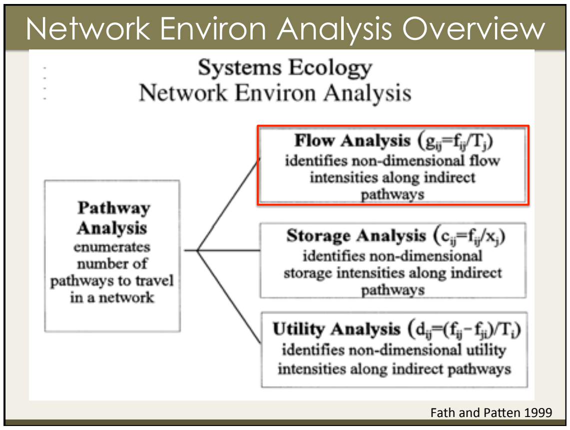


Flow Analysis

Stuart R. Borrett
University of North Carolina Wilmington



Network Environ Analysis Overview

Systems Ecology
Network Environ Analysis

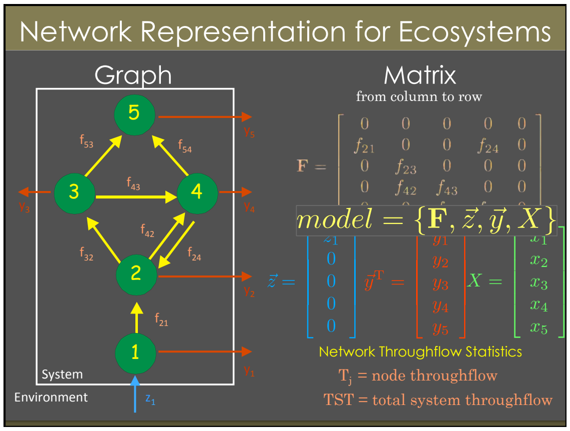
Pathway Analysis enumerates number of pathways to travel in a network

Flow Analysis ($g_{ij}=f_{ij}/T_j$) identifies non-dimensional flow intensities along indirect pathways

Storage Analysis ($c_{ij}=f_{ij}/x_j$) identifies non-dimensional storage intensities along indirect pathways

Utility Analysis ($d_{ij}=(f_{ij}-f_{ji})/T_i$) identifies non-dimensional utility intensities along indirect pathways

Fath and Patten 1999



Network Representation for Ecosystems

Matrix
from column to row

$$\mathbf{F} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ f_{21} & 0 & 0 & f_{24} & 0 \\ 0 & f_{23} & 0 & 0 & 0 \\ 0 & f_{42} & f_{43} & 0 & 0 \end{bmatrix}$$

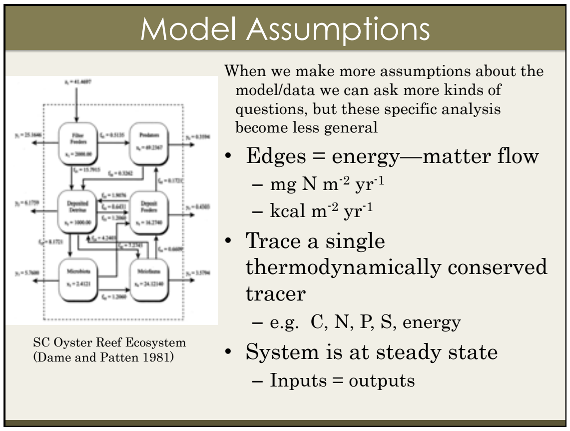
$$model = \{\mathbf{F}, \vec{z}, \vec{y}, X\}$$

$$\vec{z} = \begin{bmatrix} z_1 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} \quad \vec{y}^{\mathrm{T}} = \begin{bmatrix} y_1 \\ y_2 \\ y_3 \\ y_4 \\ y_5 \end{bmatrix} \quad X = \begin{bmatrix} x_1 \\ x_2 \\ x_3 \\ x_4 \\ x_5 \end{bmatrix}$$

Network Throughflow Statistics

T_j = node throughflow

TST = total system throughflow

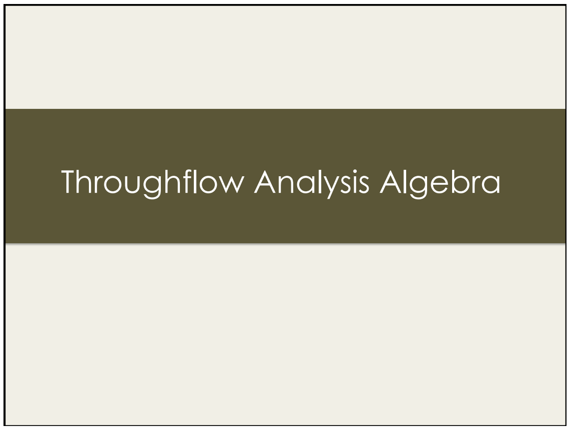


Model Assumptions

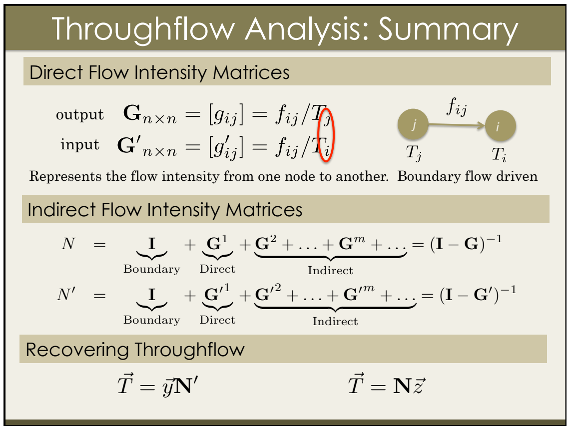
SC Oyster Reef Ecosystem
(Dame and Patten 1981)

When we make more assumptions about the model/data we can ask more kinds of questions, but these specific analysis become less general

- Edges = energy—matter flow
  - mg N m^{-2} yr^{-1}
  - kcal m^{-2} yr^{-1}
- Trace a single thermodynamically conserved tracer
  - e.g. C, N, P, S, energy
- System is at steady state
  - Inputs = outputs



Throughflow Analysis Algebra



Throughflow Analysis: Summary

Direct Flow Intensity Matrices

$$\text{output} \quad \mathbf{G}_{n\times n} = [g_{ij}] = f_{ij}/T_j$$

$$\text{input} \quad \mathbf{G'}_{n\times n} = [g'_{ij}] = f_{ij}/T_i$$

Represents the flow intensity from one node to another. Boundary flow driven

Indirect Flow Intensity Matrices

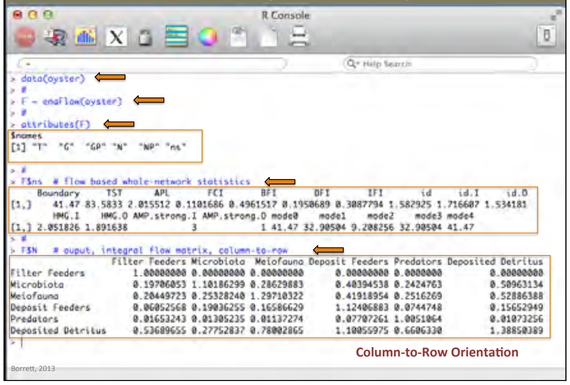
$$N = \underbrace{\mathbf{I}}_{\text{Boundary}} + \underbrace{\mathbf{G}^1}_{\text{Direct}} + \underbrace{\mathbf{G}^2 + \ldots + \mathbf{G}^m + \ldots}_{\text{Indirect}} = (\mathbf{I}-\mathbf{G})^{-1}$$

$$N' = \underbrace{\mathbf{I}}_{\text{Boundary}} + \underbrace{\mathbf{G}'^1}_{\text{Direct}} + \underbrace{\mathbf{G}'^2 + \ldots + \mathbf{G}'^m + \ldots}_{\text{Indirect}} = (\mathbf{I}-\mathbf{G}')^{-1}$$

Recovering Throughflow

$$\vec{T} = \vec{y}\mathbf{N}' \qquad \vec{T} = \mathbf{N}\vec{z}$$

Flow Analysis Example



```
> data(oyster)
> #
> F = enaFlow(oyster)
> #
> attributes(F)
$names
[1] "T"   "G"   "GP"  "N"   "NP"  "ns"

> #
> F$ns  # flow based whole-network statistics
      Boundary     TST      APL       FCI       BFI       DFI       IFI       id      id.I      id.O
[1,]     41.47 83.5833 2.015512 0.1101686 0.4961517 0.1950689 0.3087794 1.582925 1.716607 1.534181
        HMG.I     HMG.O AMP.strong.I AMP.strong.O mode0    mode1    mode2    mode3 mode4
[1,] 2.051826 1.891638            3            1 41.47 32.90504 9.208256 32.90504 41.47
> #
> F$N   # ouput, integral flow matrix, column-to-row
                  Filter Feeders Microbiota  Meiofauna Deposit Feeders Predators Deposited Detritus
Filter Feeders        1.00000000 0.00000000 0.00000000      0.00000000 0.0000000         0.00000000
Microbiota            0.19706053 1.10186299 0.28629883      0.40394538 0.2424763         0.50963134
Meiofauna             0.20449723 0.25328240 1.29710322      0.41918954 0.2516269         0.52886388
Deposit Feeders       0.06052568 0.19036255 0.16586629      1.12406883 0.0744748         0.15652949
Predators             0.01653243 0.01305235 0.01137274      0.07707261 1.0051064         0.01073256
Deposited Detritus    0.53689655 0.27752837 0.78002865      1.10055975 0.6606330         1.38850389
> |
```

Column-to-Row Orientation

Borrett, 2013

Cone Springs Model

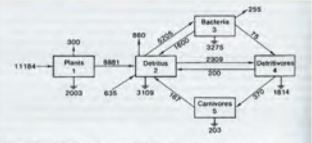


Figure B4.1 Schematic of the network of energy exchanges (kcal/m²/year) in the Cone Spring ecosystem (Tilly, 1968). Arrows not originating from a box represent inputs from outside the system. Arrows not terminating in a compartment represent exports of useable energy out of the system. Ground symbols represent dissipations.

F = internal flows
z = inputs
y = outputs (respiration + exports)
x = storages

Unit: kcal m^{-2} yr^{-1}

$$F = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 8881 & 0 & 1600 & 200 & 167 \\ 0 & 5205 & 0 & 0 & 0 \\ 0 & 2309 & 75 & 0 & 0 \\ 0 & 0 & 0 & 370 & 0 \end{bmatrix} \quad z = \begin{bmatrix} 11184 \\ 635 \\ 0 \\ 0 \\ 0 \end{bmatrix} \quad x = \begin{bmatrix} 285 \\ 3579.4 \\ 116.6 \\ 60 \\ 17 \end{bmatrix}$$

$$y = \begin{bmatrix} 2302 & 3970.9 & 3529.2 & 1814 & 203 \end{bmatrix}$$

$$S = \begin{bmatrix} F_{n\times n} & z_{n\times 1} & x_{n\times 1} \\ y_{1\times n} & 0 & 0 \end{bmatrix}_{(n+1)\times(n+2)}$$

Output Oriented Throughflow Analysis

$$N \;=\; \underbrace{\mathbf{I}}_{\text{Boundary}} + \underbrace{\mathbf{G}^1}_{\text{Direct}} + \underbrace{\mathbf{G}^2 + \ldots + \mathbf{G}^m + \ldots}_{\text{Indirect}} = (\mathbf{I}-\mathbf{G})^{-1}$$

Direct Flow Intensities

$$G = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0.7942 & 0 & 0.3075 & 0.0839 & 0.4514 \\ 0 & 0.4532 & 0 & 0 & 0 \\ 0 & 0.2011 & 0.0144 & 0 & 0 \\ 0 & 0 & 0 & 0.1552 & 0 \end{bmatrix}$$

Local

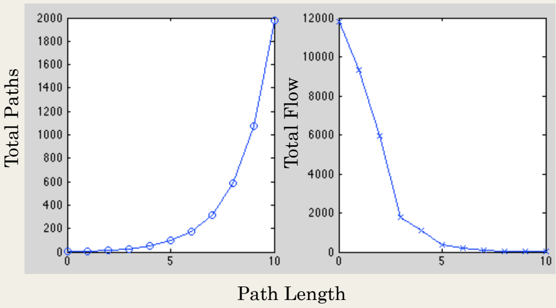
Indirect Flow Intensities

$$N = \begin{bmatrix} 1.0000 & 0 & 0 & 0 & 0 \\ 0.9583 & 1.2067 & 0.3737 & 0.1858 & 0.5446 \\ 0.4343 & 0.5468 & 1.1694 & 0.0842 & 0.2468 \\ 0.1989 & 0.2505 & 0.0920 & 1.0386 & 0.1131 \\ 0.0309 & 0.0389 & 0.0143 & 0.1612 & 1.0175 \end{bmatrix}$$

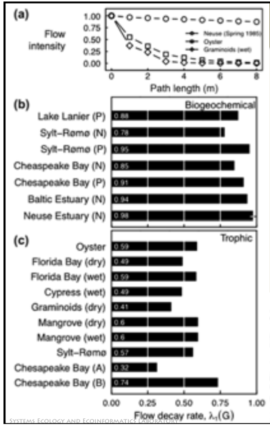
Global

Paths and Flow vs. Path length

Cone Springs Model

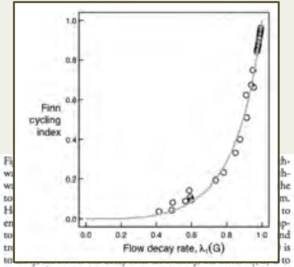


Variable Flow Decay Rates



$\lambda_1(G)$ = dominant eigenvalue of G, exponential flow decay rate

As $\lambda_1(G) \rightarrow 1$ flow decay slows, higher ecosystem efficiency



zero, the faster the decay rate.

Borrett et al. 2010. Oikos

Network Statistics

Selected Throughflow Statistics

T_j – total amount of stuff flowing into (out of) a node

TST – sum of T_j

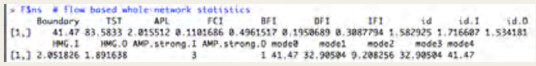
Indirect/Direct – indicator of importance of indirect flows (effects) [Network non-locality]

- Multiple ways of calculating – [id, id.i, id.o]

Borrett and Freeze (2011) Ecological Modelling DOI: 10.1016/j.ecolmodel.2010.10.015

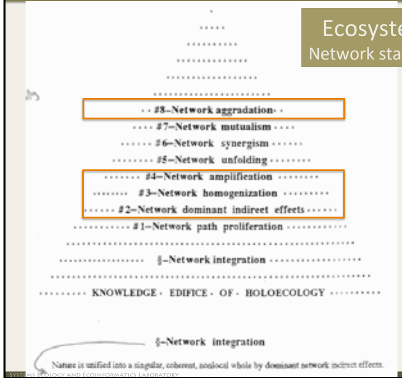
TST/Input – network aggradation, average path length, multiplier effect

Homogenization – a comparison of the evenness of the distribution of flows between a local and a global neighborhood.



```
> F$ns  # flow based whole-network statistics
     Boundary     TST      APL       FCI       BFI       DFI       IFI       id     id.I     id.O
[1,]    41.47 83.5833 2.015512 0.1101686 0.4961517 0.1950689 0.3087794 1.582925 1.716607 1.534181
        HMG.I    HMG.O AMP.strong.I AMP.strong.O mode0    mode1    mode2    mode3 mode4
[1,] 2.051826 1.891638            3            1 41.47 32.90504 9.208256 32.90504 41.47
```

NEA Hypotheses: Holoecology



· · #8–Network aggradation · ·
· · · · #7–Network mutualism · · · ·
· · · · · · #6–Network synergism · · · · · ·
· · · · · · · · #5–Network unfolding · · · · · · · ·
· · · · · · · #4–Network amplification · · · · · · · ·
· · · · · · · · #3–Network homogenization · · · · · · · · ·
· · · · · · #2–Network dominant indirect effects · · · · · ·
· · · · · · · · · · · #1–Network path proliferation · · · · · · · · · · · ·
· · · · · · · · · · · · · · · · · · §–Network integration · · · · · · · · · · · · · · · · · ·
· · · · · · · · · KNOWLEDGE · EDIFICE · OF · HOLOECOLOGY · · · · · · · · · ·

§–Network integration

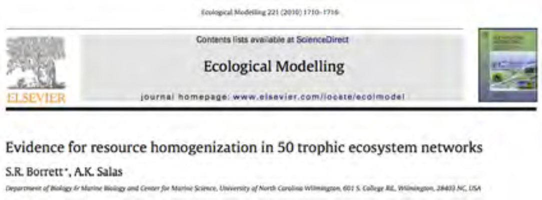
Nature is unified into a singular, coherent, nonlocal whole by dominant network indirect effects.

Ecosystem Properties
Network statistics are indicators

…now up to 13
See Jorgensen 2012 Ch 12

Patten, unpublished

Network Homogenization



Ecological Modelling 221 (2010) 1710–1716

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Evidence for resource homogenization in 50 trophic ecosystem networks

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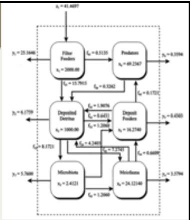
Network Homogenization

Oyster Reef Model



Dame & Patten 1981

Direct Flow Intensities

$$\mathbf{G} = (g_{ij}) = f_{ij}/T_j$$

$$\mathbf{G} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.37 \\ 0 & 0.15 & 0 & 0 & 0 & 0.33 \\ 0 & 0.15 & 0.078 & 0 & 0 & 0.029 \\ 0.012 & 0 & 0 & 0.069 & 0 & 0 \\ 0.38 & 0 & 0.50 & 0.76 & 0.48 & 0 \end{bmatrix}$$

Integral Flow Intensities

$$\mathbf{N} = (\mathbf{I} - \mathbf{G})^{-1}$$

$$\mathbf{N} = \begin{bmatrix} 1.0 & 0 & 0 & 0 & 0 & 0 \\ 0.20 & 1.1 & 0.29 & 0.40 & 0.24 & 0.51 \\ 0.20 & 0.25 & 1.3 & 0.42 & 0.25 & 0.53 \\ 0.061 & 0.19 & 0.17 & 1.1 & 0.074 & 0.16 \\ 0.017 & 0.013 & 0.011 & 0.077 & 1.0 & 0.011 \\ 0.54 & 0.28 & 0.78 & \boxed{1.1} & 0.66 & 1.4 \end{bmatrix}$$

$$\mathbf{HMG} = \frac{CV(\mathbf{G})}{CV(\mathbf{N})} = \frac{2.0195}{1.0676} = 1.8916$$

HMG > 1 implies network homogenization

Model Database

Trophically-based Ecosystem Networks

50 models

35 distinct systems

$4 \leq n \leq 125$

$0.05 \leq C \leq 0.33$

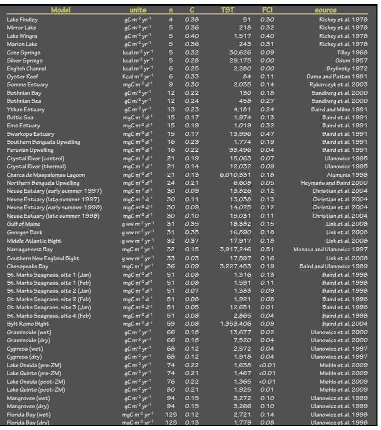
$0 \leq FCI \leq 0.51$

Uncertainty Analysis

10,000 perturbed models
+/- 5% of orig. flows

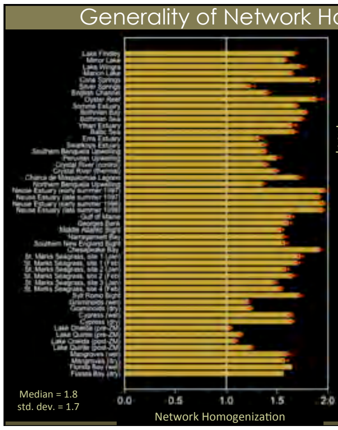
See Borrett and Salas 2010
For details

DOI: 10.1016/j.ecolmodel.2010.12.002

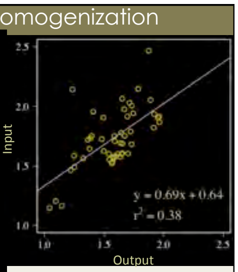


Model	units	n	C	TST	FCI	source
Lake Findley	$gC\ m^{-2}\ yr^{-1}$	4	0.38	51	0.30	Richey et al. 1978
Mirror Lake	$gC\ m^{-2}\ yr^{-1}$	5	0.36	218	0.32	Richey et al. 1978
Lake Wingra	$gC\ m^{-2}\ yr^{-1}$	5	0.40	1,517	0.40	Richey et al. 1978
Marion Lake	$gC\ m^{-2}\ yr^{-1}$	5	0.36	243	0.31	Richey et al. 1978
Cone Springs	$kcal\ m^{-2}\ yr^{-1}$	5	0.32	30,626	0.09	Tilley 1968
Silver Springs	$kcal\ m^{-2}\ yr^{-1}$	5	0.28	29,175	0.00	Odum 1957
English Channel	$kcal\ m^{-2}\ yr^{-1}$	6	0.25	2,280	0.00	Brylinsky 1972
Oyster Reef	$Kcal\ m^{-2}\ yr^{-1}$	6	0.33	84	0.11	Dame and Patten 1981
Somme Estuary	$mgC\ m^{-2}\ d^{-1}$	9	0.30	2,035	0.14	Rybarczyk et al. 2003
Bothnian Bay	$gC\ m^{-2}\ yr^{-1}$	12	0.22	130	0.18	Sandberg et al. 2000
Bothnian Sea	$gC\ m^{-2}\ yr^{-1}$	12	0.24	458	0.27	Sandberg et al. 2000
Ythan Estuary	$gC\ m^{-2}\ yr^{-1}$	13	0.23	4,181	0.24	Baird and Milne 1981
Baltic Sea	$mgC\ m^{-2}\ d^{-1}$	15	0.17	1,974	0.13	Baird et al. 1991
Ems Estuary	$mgC\ m^{-2}\ d^{-1}$	15	0.19	1,019	0.32	Baird et al. 1991
Swarkops Estuary	$mgC\ m^{-2}\ d^{-1}$	15	0.17	13,996	0.47	Baird et al. 1991
Southern Benguela Upwelling	$mgC\ m^{-2}\ d^{-1}$	16	0.23	1,774	0.19	Baird et al. 1991
Peruvian Upwelling	$mgC\ m^{-2}\ d^{-1}$	16	0.22	33,496	0.04	Baird et al. 1991
Crystal River (control)	$mgC\ m^{-2}\ d^{-1}$	21	0.19	15,063	0.07	Ulanowicz 1995
Crystal River (thermal)	$mgC\ m^{-2}\ d^{-1}$	21	0.14	12,032	0.09	Ulanowicz 1995
Charca de Maspalomas Lagoon	$mgC\ m^{-2}\ d^{-1}$	21	0.13	6,010,331	0.18	Alumunia 1998
Northern Benguela Upwelling	$mgC\ m^{-2}\ d^{-1}$	24	0.21	6,608	0.05	Heymans and Baird 2000
Neuse Estuary (early summer 1997)	$mgC\ m^{-2}\ d^{-1}$	30	0.09	13,826	0.12	Christian et al. 2004
Neuse Estuary (late summer 1997)	$mgC\ m^{-2}\ d^{-1}$	30	0.11	13,038	0.13	Christian et al. 2004
Neuse Estuary (early summer 1998)	$mgC\ m^{-2}\ d^{-1}$	30	0.09	14,025	0.12	Christian et al. 2004
Neuse Estuary (late summer 1998)	$mgC\ m^{-2}\ d^{-1}$	30	0.10	15,031	0.11	Christian et al. 2004
Gulf of Maine	$g\ ww\ m^{-2}\ yr^{-1}$	31	0.35	18,382	0.15	Link et al. 2008
Georges Bank	$g\ ww\ m^{-2}\ yr^{-1}$	31	0.35	16,890	0.18	Link et al. 2008
Middle Atlantic Bight	$g\ ww\ m^{-2}\ yr^{-1}$	32	0.37	17,917	0.18	Link et al. 2008
Narragansett Bay	$mgC\ m^{-2}\ yr^{-1}$	32	0.15	3,917,246	0.51	Monaco and Ulanowicz 1997
Southern New England Bight	$g\ ww\ m^{-2}\ yr^{-1}$	33	0.03	17,597	0.16	Link et al. 2008
Chesapeake Bay	$mgC\ m^{-2}\ yr^{-1}$	36	0.09	3,227,453	0.19	Baird and Ulanowicz 1989
St. Marks Seagrass, site 1 (Jan)	$mgC\ m^{-2}\ d^{-1}$	51	0.08	1,316	0.13	Baird et al. 1998
St. Marks Seagrass, site 1 (Feb)	$mgC\ m^{-2}\ d^{-1}$	51	0.08	1,591	0.11	Baird et al. 1998
St. Marks Seagrass, site 2 (Jan)	$mgC\ m^{-2}\ d^{-1}$	51	0.07	1,383	0.09	Baird et al. 1998
St. Marks Seagrass, site 2 (Feb)	$mgC\ m^{-2}\ d^{-1}$	51	0.08	1,921	0.08	Baird et al. 1998
St. Marks Seagrass, site 3 (Jan)	$mgC\ m^{-2}\ d^{-1}$	51	0.05	12,651	0.01	Baird et al. 1998
St. Marks Seagrass, site 4 (Feb)	$mgC\ m^{-2}\ d^{-1}$	51	0.08	2,865	0.04	Baird et al. 1998
Sylt Romo Bight	$mgC\ m^{-2}\ d^{-1}$	59	0.08	1,353,406	0.09	Baird et al. 2004
Graminoids (wet)	$gC\ m^{-2}\ yr^{-1}$	66	0.18	13,677	0.02	Ulanowicz et al. 2000
Graminoids (dry)	$gC\ m^{-2}\ yr^{-1}$	66	0.18	7,520	0.04	Ulanowicz et al. 2000
Cypress (wet)	$gC\ m^{-2}\ yr^{-1}$	68	0.12	2,572	0.04	Ulanowicz et al. 1997
Cypress (dry)	$gC\ m^{-2}\ yr^{-1}$	68	0.12	1,918	0.04	Ulanowicz et al. 1997
Lake Oneida (pre-ZM)	$gC\ m^{-2}\ yr^{-1}$	74	0.22	1,638	<0.01	Miehls et al. 2009
Lake Quinte (pre-ZM)	$gC\ m^{-2}\ yr^{-1}$	74	0.21	1,467	<0.01	Miehls et al. 2009
Lake Oneida (post-ZM)	$gC\ m^{-2}\ yr^{-1}$	76	0.22	1,365	<0.01	Miehls et al. 2009
Lake Quinte (post-ZM)	$gC\ m^{-2}\ yr^{-1}$	80	0.21	1,925	0.01	Miehls et al. 2009
Mangroves (wet)	$gC\ m^{-2}\ yr^{-1}$	94	0.15	3,272	0.10	Ulanowicz et al. 1999
Mangroves (dry)	$gC\ m^{-2}\ yr^{-1}$	94	0.15	3,266	0.10	Ulanowicz et al. 1999
Florida Bay (wet)	$mgC\ m^{-2}\ yr^{-1}$	125	0.12	2,721	0.14	Ulanowicz et al. 1998
Florida Bay (dry)	$mgC\ m^{-2}\ yr^{-1}$	125	0.13	1,779	0.08	Ulanowicz et al. 1998

Generality of Network Homogenization



Median = 1.8
std. dev. = 1.7

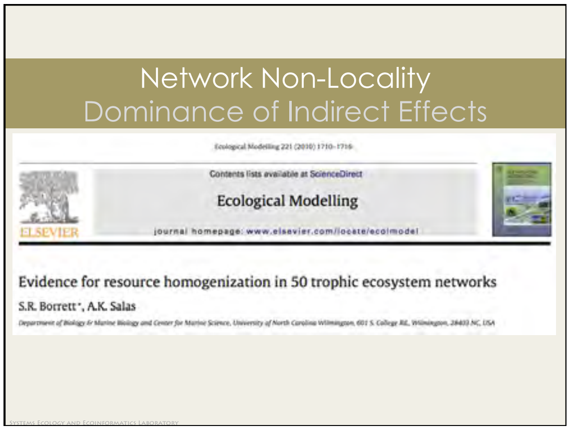


HMG occurs in all 50 models

HMG is robust to uncertainty

Orientation does not change qualitative results

Borrett and Salas 2010



Network Non-Locality
Dominance of Indirect Effects

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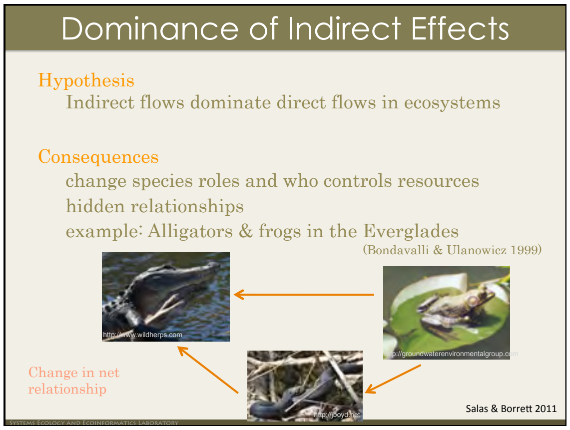

Dominance of Indirect Effects

Hypothesis
  Indirect flows dominate direct flows in ecosystems

Consequences
  change species roles and who controls resources
  hidden relationships
  example: Alligators & frogs in the Everglades
(Bondavalli & Ulanowicz 1999)

Change in net relationship

Salas & Borrett 2011

Dominance of Indirect Effects

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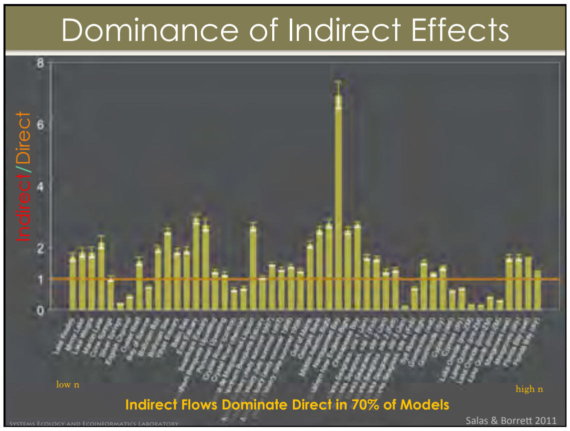
  example: Alligators & frogs in the Everglades
(Bondavalli & Ulanowicz 1999)

Existing Evidence
  Oyster Model (Patten 1985)
  Algebraic Arguments (Patten and Higashi 1989)
  Cyber-Models (Fath 2004)

What about empirically based ecosystem networks?

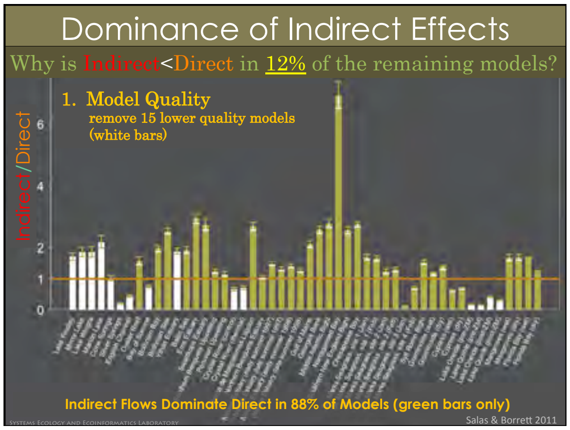
Salas & Borrett 2011



Dominance of Indirect Effects

Indirect Flows Dominate Direct in 70% of Models

Salas & Borrett 2011



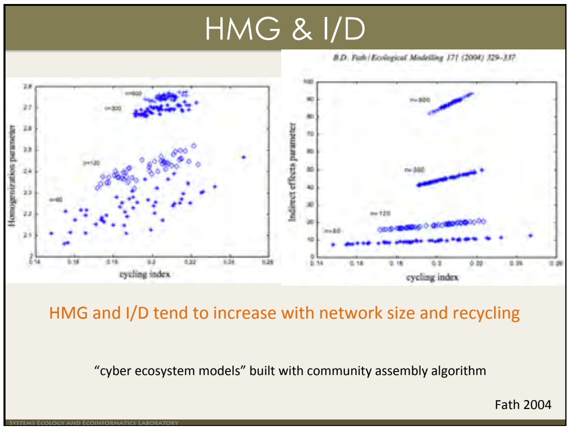
Dominance of Indirect Effects

Why is Indirect<Direct in <u>12%</u> of the remaining models?

1. Model Quality
   remove 15 lower quality models
   (white bars)

Indirect Flows Dominate Direct in 88% of Models (green bars only)

Salas & Borrett 2011



HMG & I/D

B.D. Fath / Ecological Modelling 171 (2004) 329–337

HMG and I/D tend to increase with network size and recycling

"cyber ecosystem models" built with community assembly algorithm

Fath 2004

Other Properties

- Recycling – Finn Cycling Index
- Network Amplification
  - Number of $n_{ij} > 1$ where $i \neq j$
- Network Aggradation
  - TST/sum(z_i)
  - a.k.a. average path length, multiplier effect
  - Consequence of system formation

Throughflow Centrality

Ecological Indicators 32 (2013) 182–196

Contents lists available at SciVerse ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

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Throughflow centrality is a global indicator of the functional importance of species in ecosystems

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Borrett, S.R. 2013. *Throughflow centrality is a global indicator of the functional importance of species in ecosystems.* Ecological Indicators 32:182-196
doi:10.1016/j.ecolind.2013.03.014

What do species do in ecosystems?

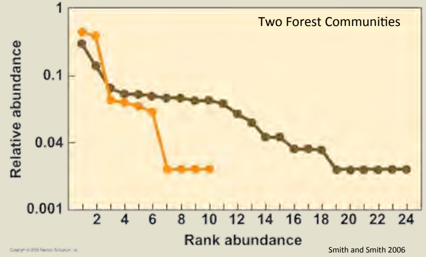
John H. Lawton OIKOS 71: 367–374. Copenhagen 1994

- What are the relative roles of species/groups in ecosystems and communities?
- Are some species more or differently important than another? When? Why? How?
- Describe the functional roles

Significance

- Conservation biology and ecosystem management
- Understand biodiversity loss

Rank-Abundance Curves



Smith and Smith 2006

Dominant Species

Assume species importance is proportional to its abundance or biomass

Communities tend to have few dominants and a long tail of rare species

Whitaker 1965

Diversity of Ecological Importance Concepts

Keystone Species

Ecological Engineers

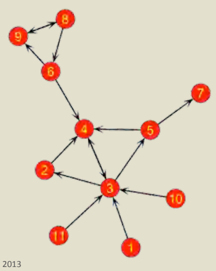
Foundational Species

Whole Ecosystem Functioning?

Centrality (Social Science)

The relative importance of a node in a network

- Many measures with nuanced interpretations
- Often correlated



Importance of indirect flows

(Borgatti 2005, Scotti et al. 2007)

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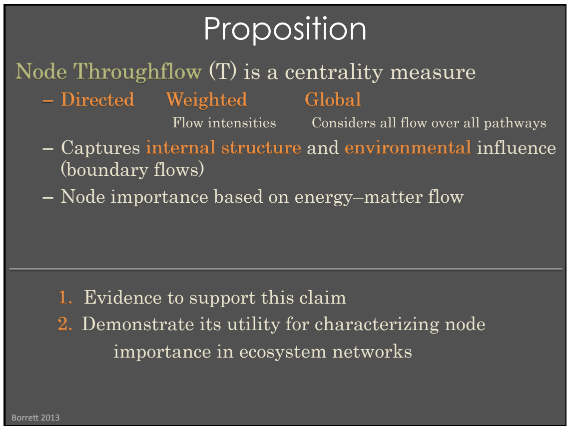

Proposition

Node Throughflow (T) is a centrality measure

- Directed Weighted Global
  - Flow intensities
  - Considers all flow over all pathways
- Captures internal structure and environmental influence (boundary flows)
- Node importance based on energy–matter flow

1. Evidence to support this claim
2. Demonstrate its utility for characterizing node importance in ecosystem networks

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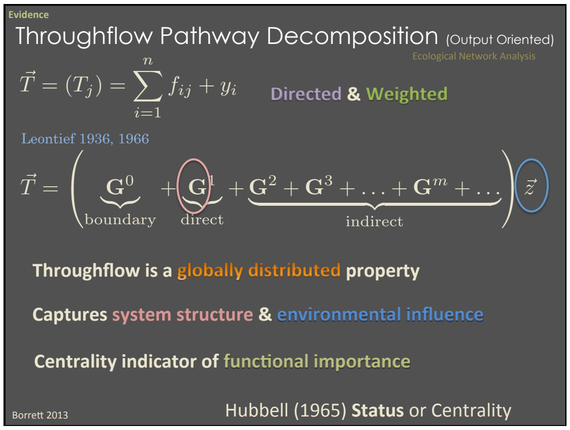

Evidence

Throughflow Pathway Decomposition (Output Oriented)

Ecological Network Analysis

$$\vec{T} = (T_j) = \sum_{i=1}^{n} f_{ij} + y_i$$

Directed & Weighted

Leontief 1936, 1966

$$\vec{T} = \left(\underbrace{\mathbf{G}^0}_{\text{boundary}} + \underbrace{\mathbf{G}^1}_{\text{direct}} + \underbrace{\mathbf{G}^2 + \mathbf{G}^3 + \ldots + \mathbf{G}^m + \ldots}_{\text{indirect}} \right) \vec{z}$$

Throughflow is a globally distributed property

Captures system structure & environmental influence

Centrality indicator of functional importance

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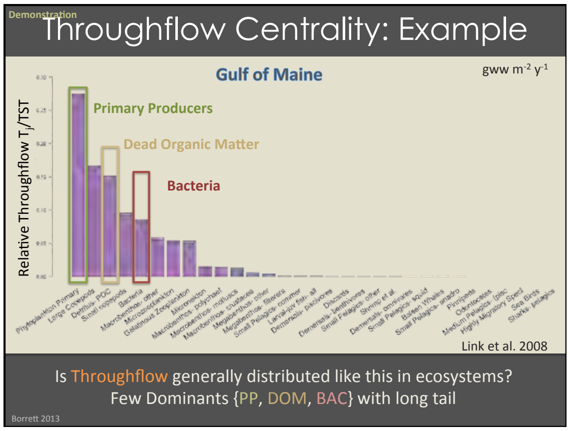
Hubbell (1965) **Status** or Centrality



Demonstration

Throughflow Centrality: Example

Link et al. 2008

Is Throughflow generally distributed like this in ecosystems?
Few Dominants {PP, DOM, BAC} with long tail

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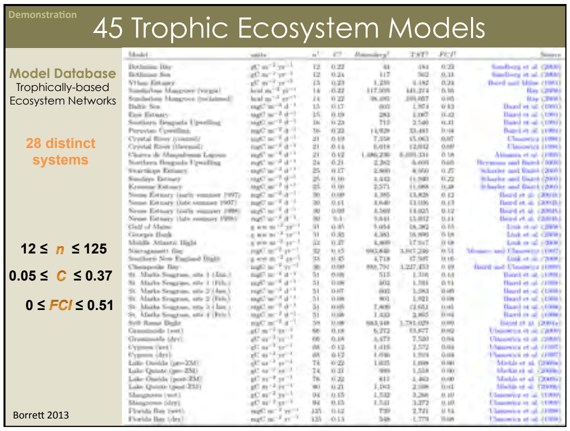

Demonstration

45 Trophic Ecosystem Models

Model Database
Trophically-based Ecosystem Networks

28 distinct systems

$12 \le n \le 125$

$0.05 \le C \le 0.37$

$0 \le FCI \le 0.51$

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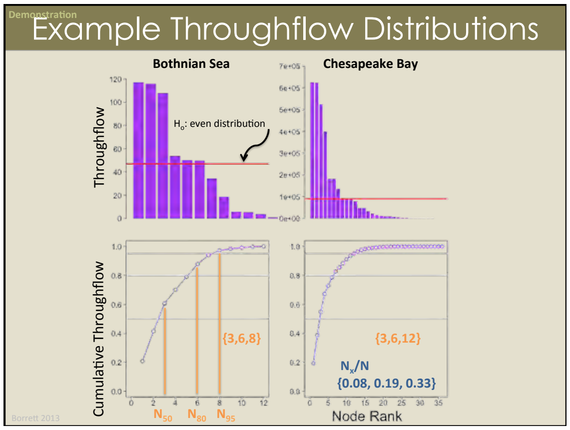

Demonstration

Example Throughflow Distributions

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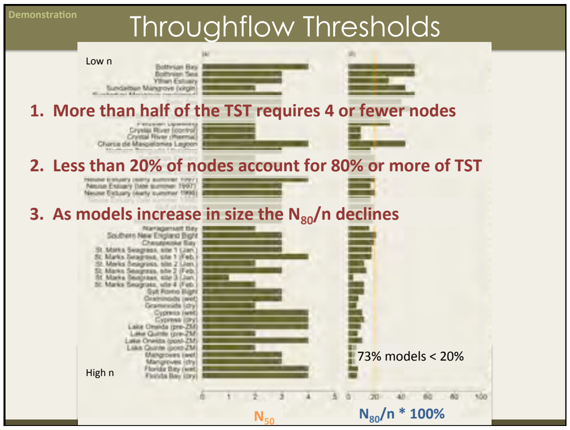

Demonstration

Throughflow Thresholds

1. More than half of the TST requires 4 or fewer nodes
2. Less than 20% of nodes account for 80% or more of TST
3. As models increase in size the N_{80}/n declines

Demonstration

N_{50} Dominant Species

Model	T_1	T_2	T_3	T_4
Bothnian Bay	DOM	Bacteria	Sediment C	Pelagic Producers
Bothnian Sea	Macrofauna	Sediment C	Pelagic Producers	
Ythan Estuary	Nutrient Pool	Suspended POC	Benthic Macrophytes	
Sundarban Mangrove (virgin)	Detritus	Macrophytes		
Sundarban Mangrove (reclaimed)	Detritus	Macrophytes	Benthic algae	
Baltic Sea	Pelagic Production	Mesozooplankton	Suspended POC	
Ems Estuary	Sediment POC	Pelagic Producers	Benthic Producers	
Southern Benguela Upwelling	Suspended POC	Phytoplankton		
Peruvian Upwelling	Pelagic Producers	Mesozooplankton		
Crystal River (control)	Macrophytes	Detritus		
Crystal River (thermal)	Macrophytes	Detritus		
Charca de Maspalomas Lagoon	Sedimented POC	Mesozooplankton	Benthic Deposit Feeders	Cyanobacteria
Northern Benguela Upwelling	POC	DOC	Bacteria	
Swartkops Estuary	Sediment POC	Sediment Bacteria		
Sundays Estuary	Sediment POC	Sediment Bacteria	Phytoplankton	
Kromme Estuary	Sediment POC	Sediment Bacteria		
Neuse Estuary (early summer 1997)	Free living bacteria	DOC	Sediment POC	Sediment Bacteria
Neuse Estuary (late summer 1997)	DOC	Free living bacteria	Sediment POC	
Neuse Estuary (early summer 1998)	Free living bacteria	DOC	Sediment POC	
Neuse Estuary (late summer 1998)	DOC	Free living bacteria	Phytoplankton	
Gulf of Maine	Phytoplankton- Primary	Large Copepods	Detritus POC	
Georges Bank	Phytoplankton- Primary	Detritus POC	Bacteria	
Middle Atlantic Bight	Phytoplankton- Primary	Detritus POC	Bacteria	
Narragansett Bay	Detritus	SedPOC Bacteria		
Southern New England Bight	Phytoplankton- Primary	Detritus POC	Bacteria	
Chesapeake Bay	Sediment Particulate Carbon	Bacteria in Sediment POC	Phytoplankton	
St. Marks Seagrass, site 1 (Jan.)	Benthic Bacteria	Micro-epiphytes	Sediment POC	
St. Marks Seagrass, site 1 (Feb.)	Benthic Bacteria	Sediment POC	Benthic algae	Meiofauna
St. Marks Seagrass, site 2 (Jan.)	Micro-epiphytes	Sediment POC		
St. Marks Seagrass, site 2 (Feb.)	Sediment POC	Benthic algae	Benthic Bacteria	
St. Marks Seagrass, site 3 (Jan.)	Micro-epiphytes			
St. Marks Seagrass, site 4 (Feb.)	Pinfish	Sediment POC		
Sylt Romo Bight	Sediment POC	Microphytobenthos	Phytoplankton	
Graminoids (wet)	Sediment Carbon	Periphyton	Refractory Detritus	
Graminoids (dry)	Periphyton	Sediment Carbon		
Cypress (wet)	Refractory Det.	Cypress	Living Sediment	Liable Detritus
Cypress (dry)	Refractory Det.	Living sediment	Understory	Liable Detritus
Lake Oneida (pre-ZM)	Pelagic Detritus	Diatoms	Blue-green Algae	Epiphytes
Lake Quinte (pre-ZM)	Pelagic Detritus	Diatoms		
Lake Oneida (post-ZM)	Diatoms	Epiphytes	Pelagic Detritus	Blue-green Algae
Lake Quinte (post-ZM)	Zebra Mussels	Diatoms		
Mangroves (wet)	C in Sediment	Leaf	Other Primary Producers	
Mangroves (dry)	C in Sediment	Leaf	Other Primary Producers	
Florida Bay (wet)	Benthic POC	Water POC	Water Flagellates	Thalassia
Florida Bay (dry)	Benthic POC	Water POC	Thalassia	DOC

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Demonstration

N_{50} Dominant Species

Primary Producers

Dead Organic Matter

Bacteria

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Discussion – Ecosystem Organization and Development

- TST → Power (Patten 1991)
  - Operationalized Maximum Power principle (Lotka 1922)
- T_j is partial power
  - Each node is a subsystem, so maximum power should apply to each node
  - Why is throughflow not evenly distributed?
  - restrained by
    - evolutionary constraints of the individual organisms
    - embedded within the existing ecosystem – autocatalysis & centripitality

Throughflow Centrality Summary

- Characterizes the relative importance of nodes in an ecosystem network – with respect to flow generation

- Weighted degree type centrality
- Special case of Hubbell Centrality (SNA)

- In ecosystems, TC tends to be concentrated in a few nodes (<4) with a longer tail of less central nodes
- Important nodes tend to be primary producers, detritus, and bacteria

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Ecological Network Analysis: Flow Analysis

Flow Analysis Summary

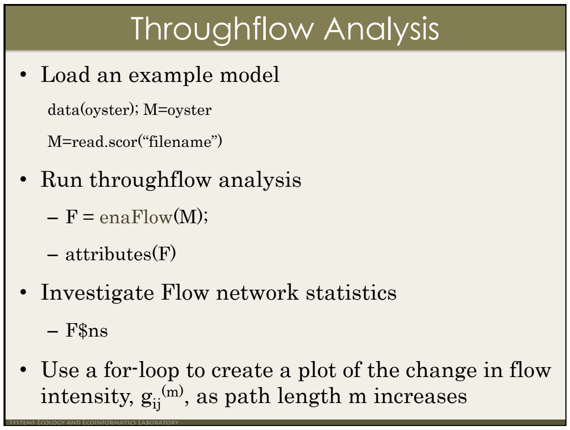
- Introduction to Flow Analysis
- Flow Analysis Algebra

  main results {T, G, GP, N, NP, ns}
- Network Statistics & Ecosystem Properties
  - Network Homogenization
  - Network Non-locality (dominance of indirect effects)
- Throughflow Centrality
- Ecosystem Impacts of Shrimp Trawling

Suggested Activities

Each Person/Team Should Select a Model

Use enaR to complete the activities



Throughflow Analysis

- Load an example model
  - data(oyster); M=oyster
  - M=read.scor("filename")
- Run throughflow analysis
  - F = enaFlow(M);
  - attributes(F)
- Investigate Flow network statistics
  - F$ns
- Use a for-loop to create a plot of the change in flow intensity, $g_{ij}^{(m)}$, as path length m increases