Network Construction

for Ecological Network Analysis

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ENA Tutorial, ISEM, May 2023, Toronto, Canada

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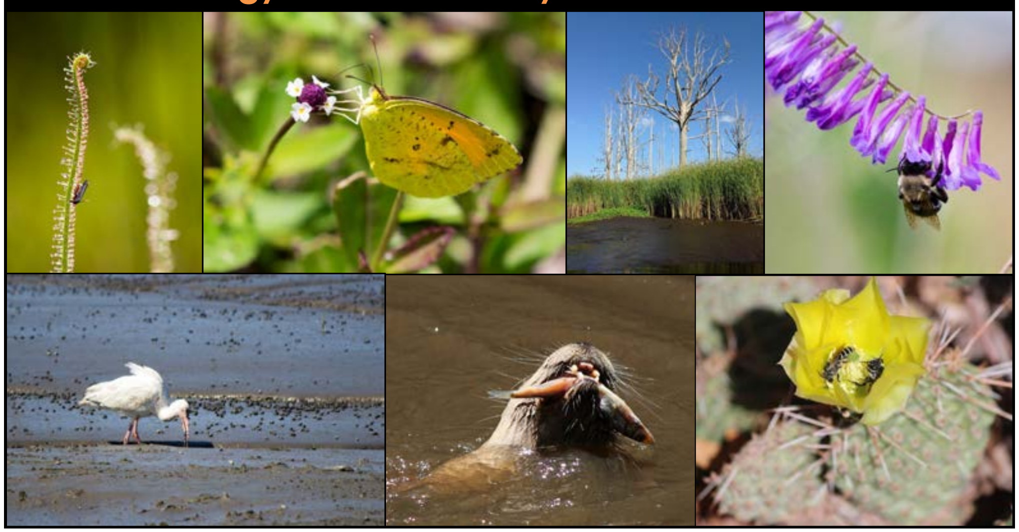
Ecology is fundamentally about Interactions



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1

Modeling Fundamentals

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Network are one type of model

What is a model?

Model

A model is an abstract (perhaps idealized), non-unique, description of a natural system that captures its features essential for addressing the modeling objectives.

Patten, pers. Com.

Ahl & Allen 1996

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Formal Modeling Relation: Mapping

Q: What does the model tell you about the natural system?

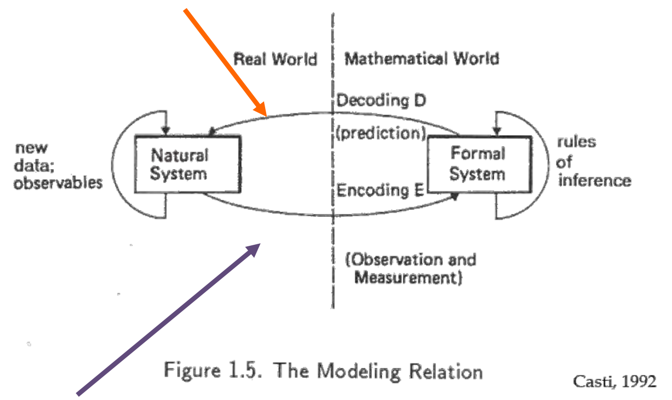

Figure 1.5. The Modeling Relation

Casti, 1992

This abstraction process is key to model making.

Q: What do you include in the model and how do you formally represent it?

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All Models are wrong, some are useful

George Box, 1979

How do we know if our model is sufficient?

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Classic Modeling Process

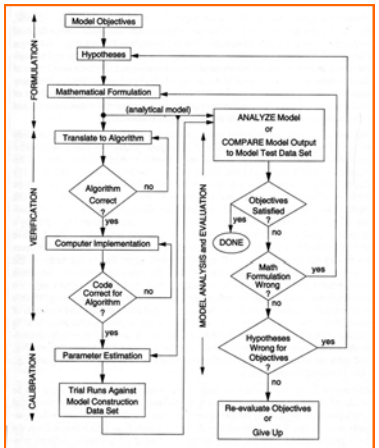

Figure 2.1: The classical approach to the modeling process, showing the four basic stages. In this approach, alternative models are developed sequentially, conditional on the failure of a previous model.

Haefner 2005

Also See Figure 1 in Jackson et al. 2000

- State project objectives
- Obtain background information
- System conceptualization
  - Specify model components, connections, and controls
  - Specify model boundaries
- Represent formally (Math)
  - Construct diagram
  - Write equations or algorithms
- Est. parameters, Init. Cond.'s and calibrate equations with data
- Implement model (encoding), simulate, and analyze
- Evaluate model (verify, validate)
- Sensitivity/Uncertainty analysis
- Use and Revise.

Recursive!

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Mathematical Model Anatomy

Bound the system of interest

(scale, level, space, time)

Identify & categorize

Components, Connections, & Controls – 3 C's of modeling

State Variables – describe the "state" of the system component, change in time

- Storages (M L^{-2} or M L^{-3})
- currency (energy or matter)
- Aggregation problem – how to lump or split components

Driving Variables – force the system behavior, outside of system boundary

Auxiliary Variables – other variables of interest in the system (eg, growth rate)

Parameters – constant within a model, but may vary between systems

Constants – universal – don't vary across systems (eg Avogadro's number)

Flows (M L^{-2} T^{-1} or M L^{-3} T^{-1})

- processes that generate fluxes

Information Connections & Controls

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Alternative Models

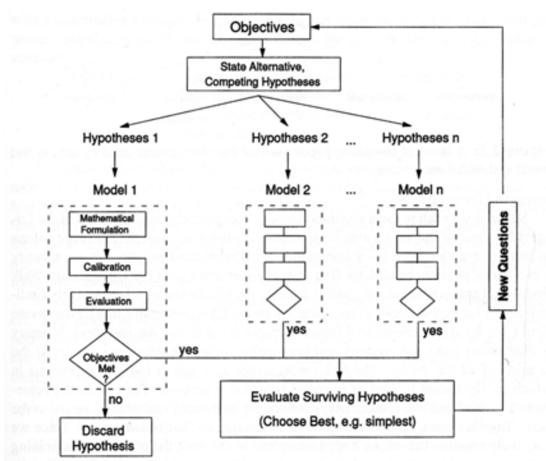

Figure 2.2: Another view of the modeling process, in which alternative hypotheses and models are developed and tested independently.

Haefner 2005

Modeling as Search

through the space of possible models

guided by

theory and data

Model = Hypothesis?

Hypothetico-deductive science

Null model

Neutral model

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Example: Conceptual Model Iteration

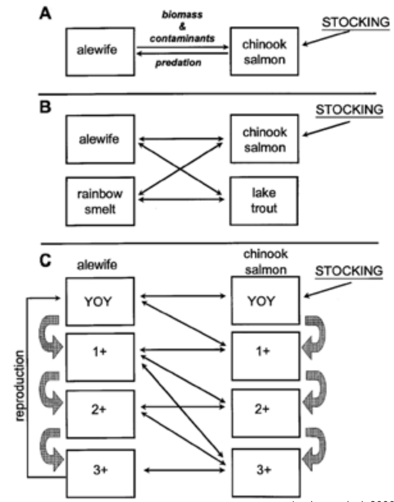
Objective

determine the relationship between different strategies for stocking exotic salmon in the Great Lakes and the concentrations of potentially toxic contaminants in the salmon and their alewife prey.

Consider

A. Simple model
B. Food web is key
C. Population structure matters

What **conceptual structure** is most *useful* to address the research question?



Jackson et al. 2000

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Modeling Questions

- How do we *use* models in ecological science?
- What features characterize "good" models?
- How can we **represent a natural process** N in a formal system M?
- How can we **compare** two models of the same natural process?
- How can we **identify key features** of a natural system?
- **How complex** should a model be?

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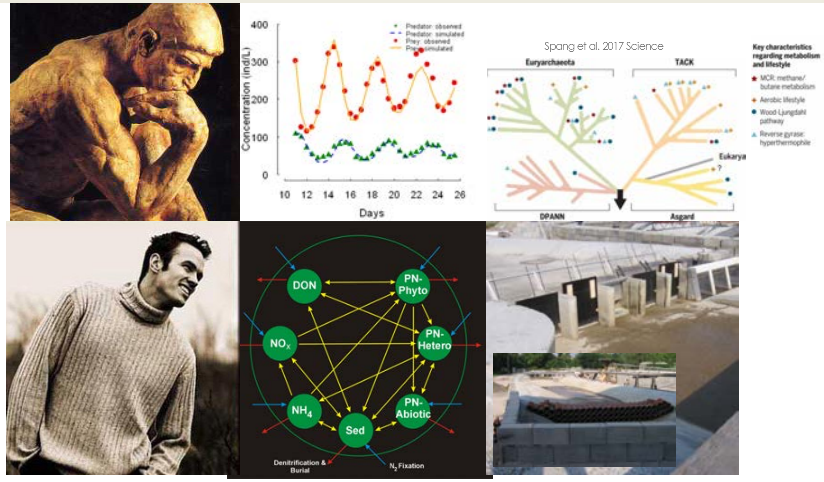
What do these have in common?



How are they different?

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Network Elements

a Relational Model

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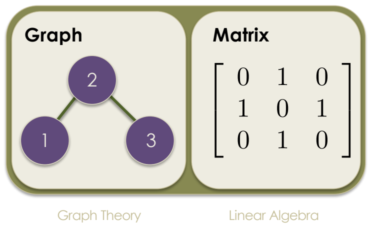
Network Models

Network models map relationships between objects

Networks are Graphs

G = {N, E}

- N = nodes→ objects
- E = edges → relationship



Adjacency

Two nodes (i, j) are adjacent if there is an edge between them

Adjacency Matrix

$$A = (a_{ij}) = \begin{cases} a_{ij} = 1 & \text{if i, j adjacent,} \\ a_{ij} = 0 & \text{otherwise} \end{cases}$$

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Network Models

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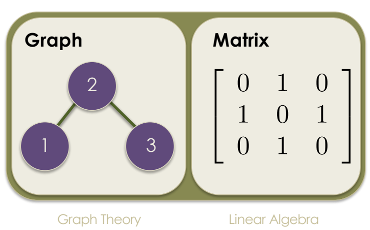
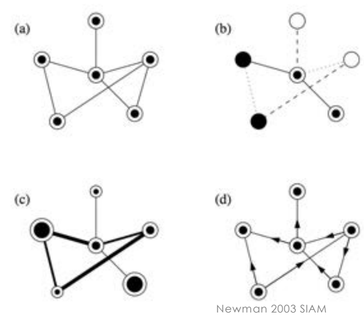


Graph Variations



Typically Simple Graphs

One edge to/from each node, no loops

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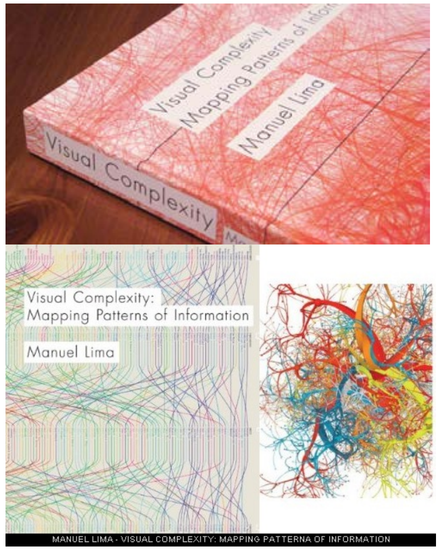

Networks are Everywhere

Manuel Lima
2011

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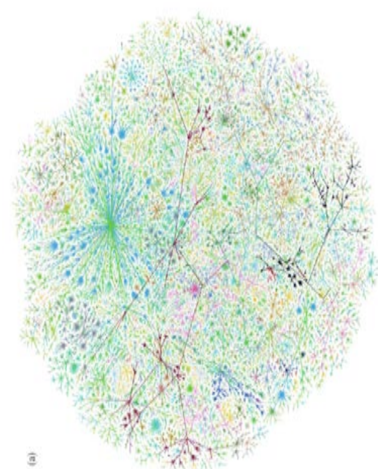
Internet



G = {N, E}

Nodes

Autonomous systems (computer groups)

Edges

Physical Internet connection

"…at the level of "autonomous systems"—local groups of computers each representing hundreds or thousands of machines. Picture by Hal Burch and Bill Cheswick, courtesy of Lumeta Corporation. " Newman 2003

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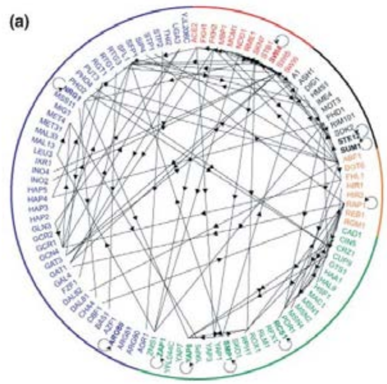
Gene Regulatory Network



G = {N, E}

Nodes

Genes

Edges

Directed regulation of transcription of other genes

As in Proloux et al. 2005. Network thinking in ecology and evolution

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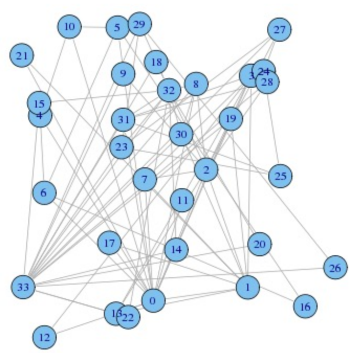
Zachary's Karate Club



Zachary 1977

G = {N, E}

Nodes

Individual people

Edges

Friendships

(note as drawn its undirected and thus assumes friendships are necessarily reciprocal)

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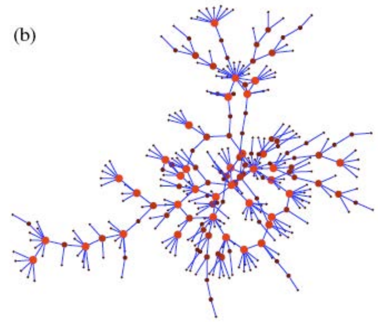
Sexual Contacts - HIV

(b)



Potterat et al. 2002, as in Newman 2003

G = {N, E}

Nodes

Individual people

Edges

Sexual Intercourse

How do the scientists get the data for this kind of model? How reliable is the data?

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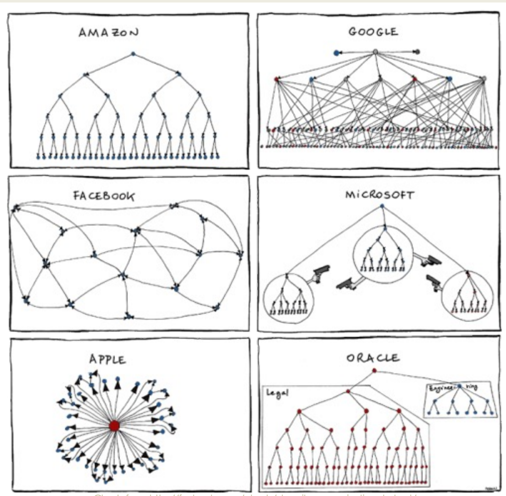
Organization Charts: *Comparison* of Tech Companies



Charts from http://foxhugh.com/charts/describe-organizational-chart/

G = {N, E}

Nodes

People

Edges

Reporting relationships (control)

What does the modeler (cartoonist) want you to know about each company?

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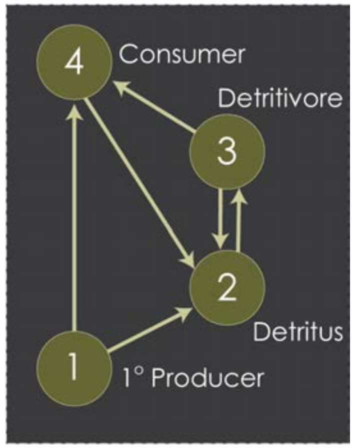
Describing a Network



$G = \{N, E\}$ N = ???; E = ????

Type of Graph → Simple, Directed

Number of Nodes (Vertices) $n = 4$

Number of Edges (Links) $L = 6$

Connectance or Density

$$C = \frac{L}{n^2} = \frac{6}{16} = 0.375$$ With loops

$$C = \frac{L}{n(n-1)} = \frac{6}{12} = 0.5$$ No loops

Loop (aka self loop)
Edge from a node to itself

Have not described patterns of connections

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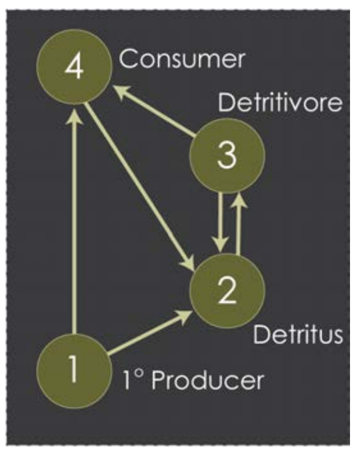
Describing a Network: Pathways



Walk: a sequence of edges

1 → 2 → 3 → 4 → 2 → 3

Walk length: the number of edges in the sequence (5 in example)

Distance (Geodesic): the minimum path length required to get from one node to another.

$$\mathbf{D} = \begin{bmatrix} 0 & 1 & 2 & 1 \\ \infty & 0 & 1 & 2 \\ \infty & 1 & 0 & 1 \\ \infty & 1 & 2 & 0 \end{bmatrix}$$

Row-to-Col

Reachability

Diameter: the *mean* or *__maximum__* distance

Cycle: pathway that starts and stops at the same node

2→3 → 2 *or* 2 → 3 → 4 → 2

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Network Ecology

Study of ecological systems using network models

Borrett, Christian, Ulanowicz 2012
Encyclopedia of Environmetrics

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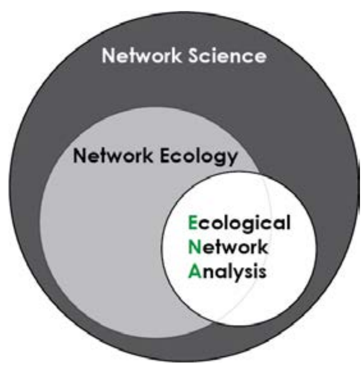
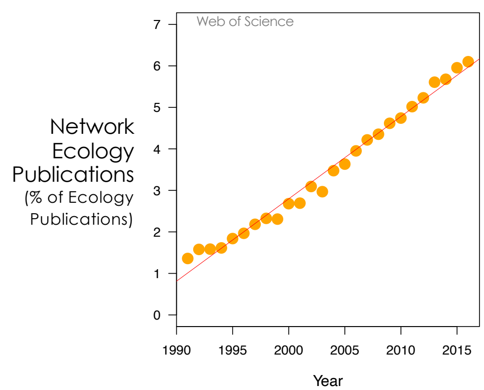
Network Ecology

Study of ecological systems using network models and analysis to characterize their structure, function, and evolution



Scharler & Borrett 2021



Extended from Borrett et al. 2014 in Lau et al. 2017

Network Ecology is a large, and rapidly growing domain

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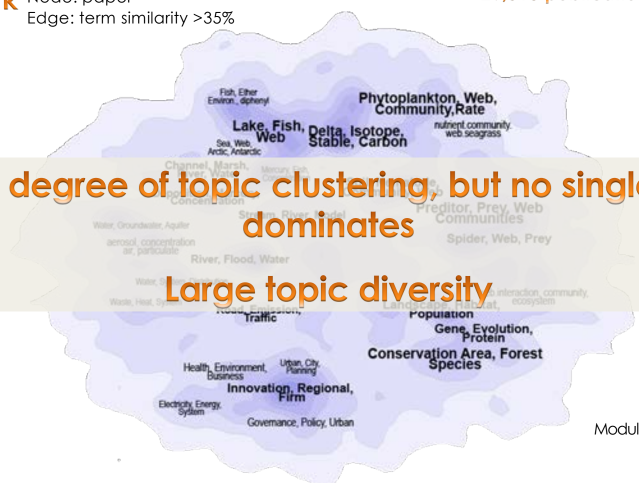
Diverse Topics

Topic Network Node: paper
Edge: term similarity >35%

29,513 publications (1900-2012) WOS



Large degree of topic clustering, but no single topic dominates

Large topic diversity

Modularity Score = 0.927

Borrett et al. 2014

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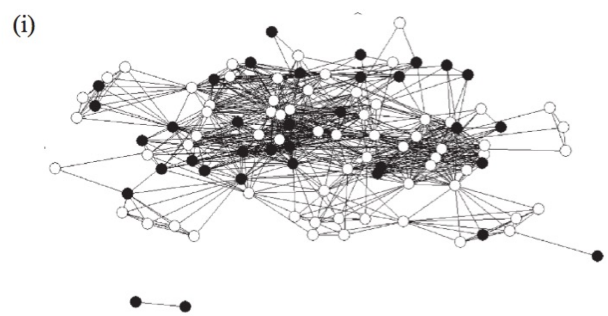
Animal Behavioral Network

Population

Social Network of Guppy Fish



Node = individual Guppy Fish *Poecilia reticulata* (male, filled; female, open)
Edge = individual co-occurance in shoal

Conclude: Highly structured social system

Croft et al. 2004

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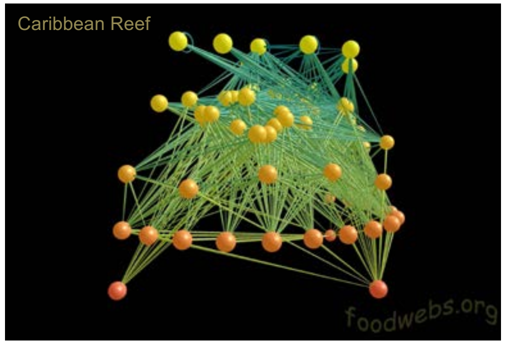
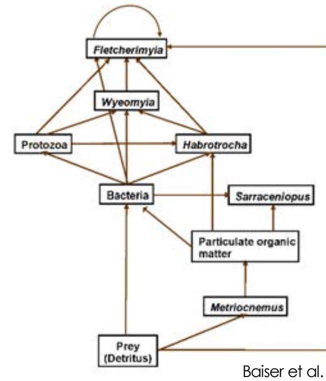
Food Webs

Community



http://foodwebs.org



Baiser et al. 2011

Nodes: Species, Trophospecies, Functional Group, or NL Resource

Edges: classically who **eats** whom

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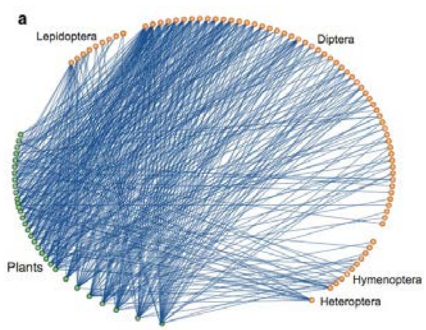
Mutualistic Networks

Community

Plant-Animal Interactions



G = {N, E}

Nodes

(a) Plant species

(b) Animal species

Edges

Pollination visit

Bipartite Graph

Bascompte & Jordano 2007

Discovered re-occurring **nested** pattern
What causes this pattern? Consequences?

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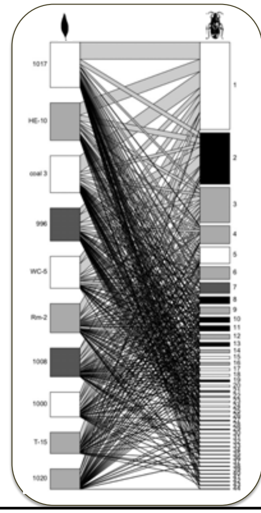
Genotype-Community



G = {N, E}

Nodes – Two Types

A: Tree Genotypes

B: Insect Species

Edges

Co-occurrence

Bipartite Graph

Clear effect of tree *genotype* on insect community composition

Lau et al. 2016

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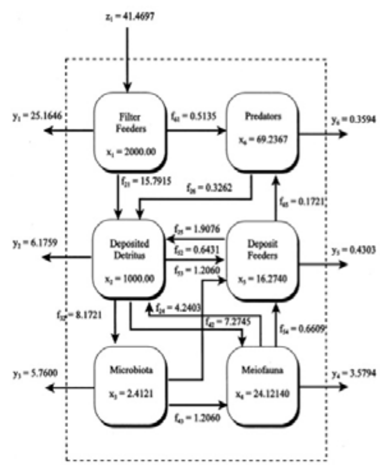
Trophic Ecosystem Model

Ecosystem

SC Oyster Reef Ecosystem (Dame and Patten 1981)

"Compartment Models"



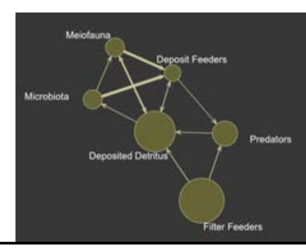
G = {N, E}

Nodes

Species, Functional Groups

Edges

Flux of energy kcal m^{-2} yr^{-1}



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Urban Water Metabolism

Ecosystem

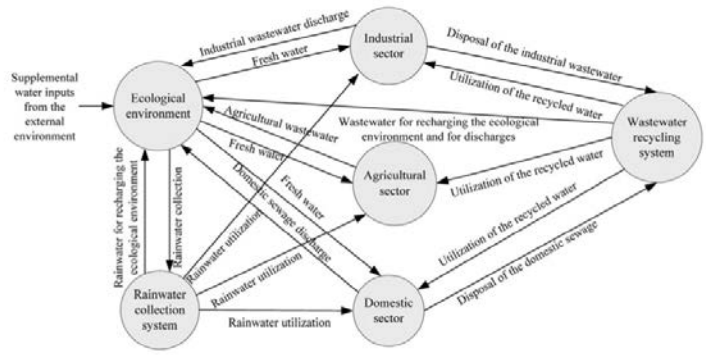

Fig. 1. A conceptual model of the water flows in the urban water metabolism.

G = {N, E}

Nodes: Economic Sector

Edges: Flux of water $m^3\ yr^{-1}$ (not certain of time unit)

Zhang et al. 2010

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Habitat Networks

Landscape

Animal movement across the landscape

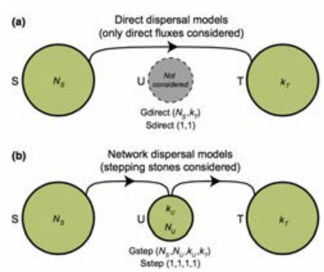
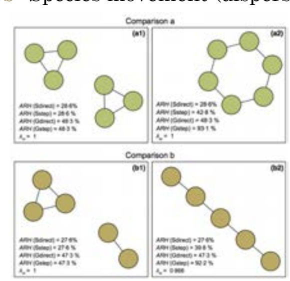


Fig. 1. Illustration of the assumptions and implications of the different connectivity models in a three-patch system. The system consists of a source patch S, a destination (target) patch T and a patch U that may act as a stepping stone facilitating dispersal from S to T. Patch S is fully occupied up to its carrying capacity by the focal species (with N_S individuals dispersing from S), whereas U and T are initially vacant. The species may get established in U or T if at least k_U or k_T individuals are able to colonize the patch, respectively. Many connectivity models (Sdirect, Gdirect) do not consider the potential role of U in facilitating the colonization of T (a), which is accounted for in models Sstep and Gstep through network analysis (b).

G = {N, E}

Nodes: Habitat Patches

Edges: Species movement (dispersal)



Spatial arrangement, patch quality

"Stepping Stones"

Saura et al. 2014

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Trophic Cascades & Pollination

Combination

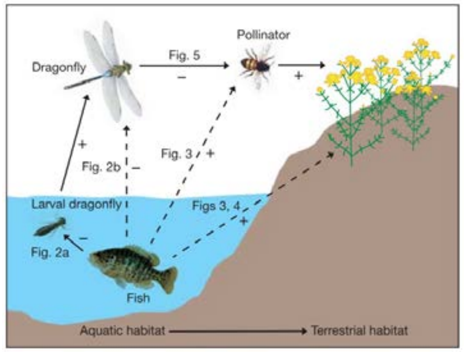

Figure 1 | Interaction web showing the pathway by which fish facilitate plant reproduction. Solid arrows indicate direct interactions; dashed arrows denote indirect interactions. The sign refers to the expected direction of the direct or indirect effect (see the text). Figure numbers indicate which figure presents data supporting each of the predicted effects. (Figure created by S. White and C. Stierwalt.)

Presence of **fish** in ponds decreases the **fitness** of nearby **plants**

Linked food web and pollination network

Knight et al. 2005

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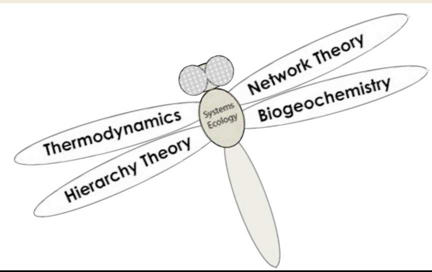
Ecosystem Networks for ENA



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to understand ecosystems…
will be to understand networks
Patten & Witcamp 1967 Ecology
J. theor. Biol. (1973) 41, 535–546
1973
The Structure of Ecosystems
Bruce Hannon
Energy Research Group, Center for Advanced Computation, University of Illinois, Urbana, Illinois 61801, U.S.A.
Application of Input-Output Economics
55+ years of Development
Systems Analysis and Simulation in Ecology
1975
1981
1984
Growth and Development
1986
Network Analysis in Marine Ecology
1989
Ecological Network Analysis

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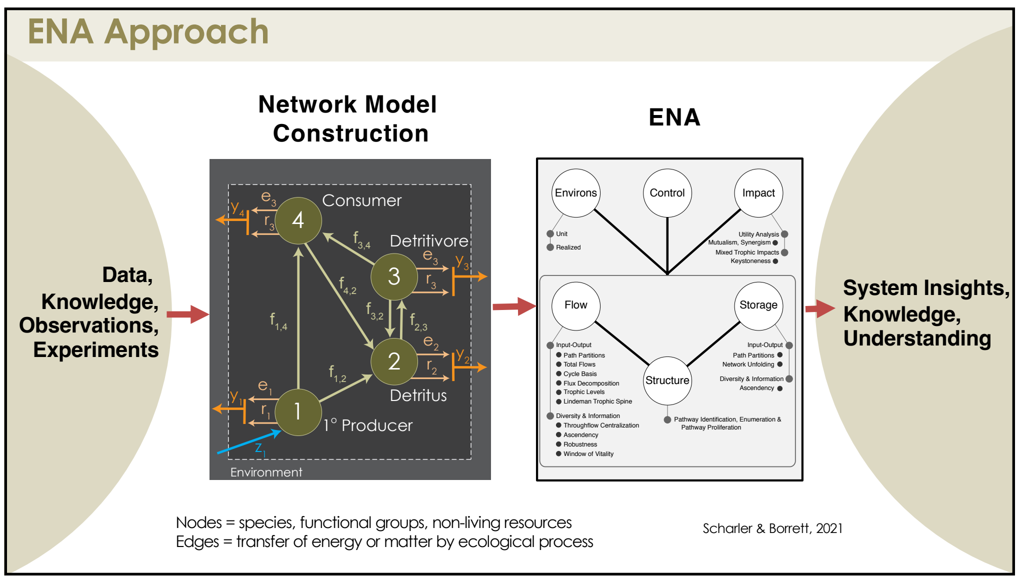
ENA Approach
Data, Knowledge, Observations, Experiments
Network Model Construction
Consumer
Detritivore
Detritus
1° Producer
Environment
ENA
Environs
Control
Impact
Flow
Storage
Structure
System Insights, Knowledge, Understanding
Nodes = species, functional groups, non-living resources
Edges = transfer of energy or matter by ecological process
Scharler & Borrett, 2021

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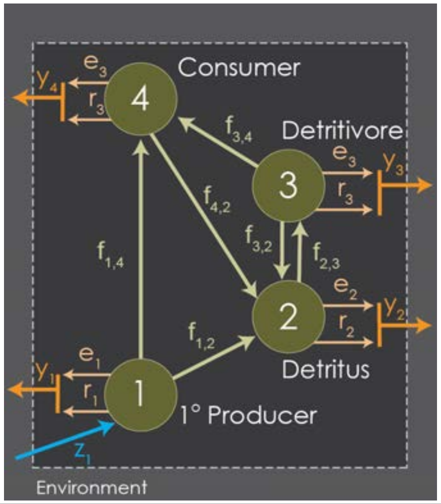
Model Details



G = {N, E}

Nodes

Species,

Functional Groups,

Non-living resources

Edges

Flux of energy (e.g., kcal m^{-2} yr^{-1})

or matter (M $L^{-2 \text{ or } -3}$ T^{-1})

Thermodynamically conserved tracer
process agnostic

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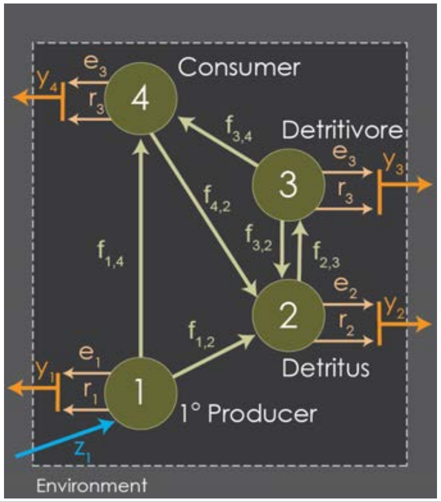
Model Details



Node Names

F: Flows from *i* to *j*

z: Inputs

e: Exports

r: Respirations

y: Outputs (e + r)

X: storage or biomass

Living: logical (T or F)

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Modeling Approaches

- Phenomenological
- Budget
- Simulation
- Linear Inverse Modelling

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Consider

What **system** do you want to model?

Why? **Objective**?

System Boundary?

What **Nodes**? What **Edges**? What to include?

Units? **Currency**? How to parameterize?

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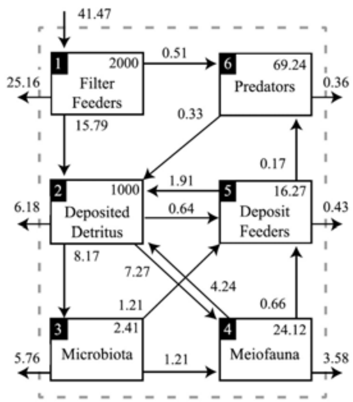
Oyster Reef Ecosystem Model

(a) Graph Representation



(b) Matrix Representation

$$\mathbf{F} = \begin{bmatrix} 0 & 15.79 & 0 & 0 & 0 & 0.51 \\ 0 & 0 & 8.17 & 7.27 & 0.64 & 0 \\ 0 & 0 & 0 & 1.21 & 1.21 & 0 \\ 0 & 4.24 & 0 & 0 & 0.66 & 0 \\ 0 & 1.91 & 0 & 0 & 0 & 0.17 \\ 0 & 0.33 & 0 & 0 & 0 & 0 \end{bmatrix}$$

Inputs

$$\mathbf{z} = \begin{bmatrix} 41.47 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}$$

Outputs

$$\mathbf{r} = \begin{bmatrix} 25.16 \\ 6.18 \\ 5.76 \\ 3.58 \\ 0.43 \\ 0.36 \end{bmatrix} \quad \mathbf{e} = \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}$$

$$\mathbf{X} = \begin{bmatrix} 2000.00 \\ 1000.00 \\ 2.41 \\ 24.12 \\ 16.27 \\ 69.24 \end{bmatrix} \quad \mathbf{Living} = \begin{bmatrix} \text{TRUE} \\ \text{FALSE} \\ \text{TRUE} \\ \text{TRUE} \\ \text{TRUE} \\ \text{TRUE} \end{bmatrix}$$

G = {N, E}

Nodes

Species,
Functional Groups

Edges

Flux of energy kcal m^{-2} yr^{-1}

Scharler & Borrett, 2021

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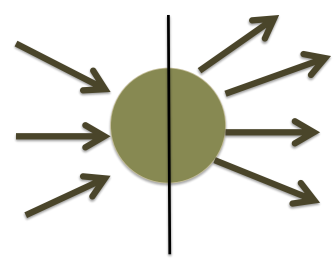
Steady State Assumption

Throughflow (T_j)

Total energy–matter entering or exiting a node

Significance & Interpretation

Node Activity
Node Power
GPP



Input $\overset{\text{@ steady-state}}{=}$ Output

Storage or biomass is ***NOT*** changing

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Network Documentation

- List ***methodologies for measured data*** used in the construction phase
- Identify all ***literature sources*** and those from ***expert opinion*** used in the calculations.
- List ***pre-and/or post-balance diagnostics***, and ***adjustments*** that were necessary to balance the network. This can include a measure of divergence of the balanced model from the nominal model, which flows adjustments were made, and how the remaining discrepancy is justified.
- ***Publish*** final model flow information, for example include flow matrices and vectors in appendices.

Scharler & Borrett, 2021

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Network Software/Tools

Box 6
Summary of ENA software tools and model databases:

Software	Source	Reference
Netwrk 4.2	Available from RE Ulanowicz	Ulanowicz and Kay (1991)
WAND	No longer available	Allesina and Bondavalli (2004)
EcoNet	http://eco.engr.uga.edu	Kazanci (2007), Schramski et al. (2011)
Ecopath with Ecosim	http://ecopath.org	Christensen and Pauly (1992)
MATLOD	Available from RE Ulanowicz	Ulanowicz and Scharler (2008)
Rpath	https://github.com/NOAA-EDAB/Rpath	Lucey et al. (2020)
LIM	https://cran.r-project.org/web/packages/LIM/index.html	Soetart and van (2015)
NEA.m	https://github.com/SEELab/NEA	Fath and Borrett (2006)
enaR	https://github.com/SEELab/enaR	Borrett and Lau (2014)
enaUncertainty	Part of enaR, https://github.com/SEELab/enaR	Hines et al. (2018)
FlowCAr	https://zenodo.org/record/1408672	Waspe et al. (2018)
LINX	https://www.mathworks.com/matlabcentral/fileexchange/72143-linx/	Kazanci et al. (2020)
Model Database	**Source**	**Reference**
>100 ecosystem models distributed with enaR	https://github.com/SEELab/enaR	Borrett and Lau (2014)
Ecobase	http://sirs.agrocampus-ouest.fr/EcoBase/	

Scharler & Borrett, 2021

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1. Modeling Fundamentals
2. Network Elements
3. Network Ecology
4. Ecosystem Networks for ENA

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Assemble the Pieces


Things Come Apart, Todd McLellan

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Connectivity is Transformative

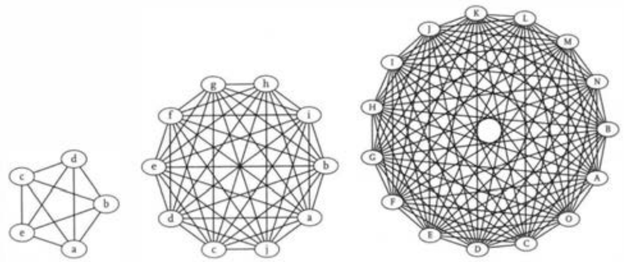

Figure 2-1: Three clusters, with all connections drawn. The small cluster has 5 members and 10 connections; the middle one has 10 members and 45 connections; and the large one has 15 and 105. A group's complexity grows faster than its size.

Shirkey 2008

In these "complete" graphs, the **number of connections increases much faster than the number of** nodes

Constraint of transaction costs

How to lower the transaction cost?

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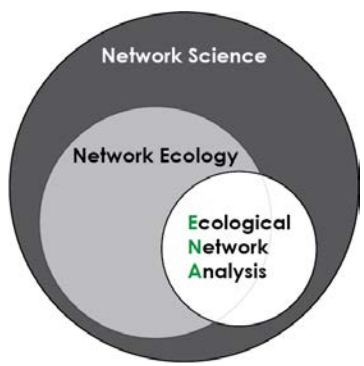
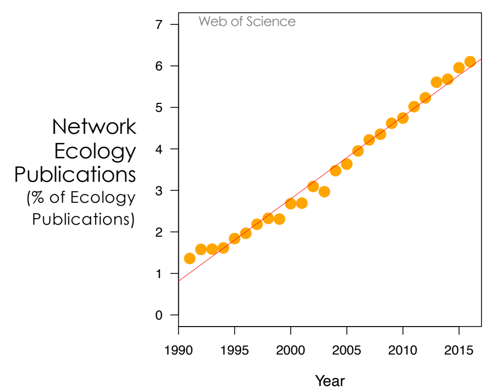
Network Ecology

Study of ecological systems using network models and analysis to characterize their structure, function, and evolution



Scharler & Borrett 2021



Extended from Borrett et al. 2014 in Lau et al. 2017

Network Ecology is a large, and rapidly growing domain

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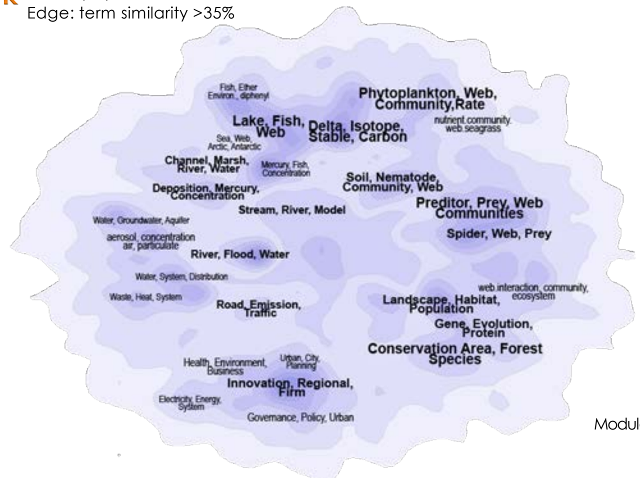
Diverse Topics

Topic Network Node: paper
Edge: term similarity >35%

29,513 publications (1900-2012) WOS



Modularity Score = 0.927

Borrett et al. 2014

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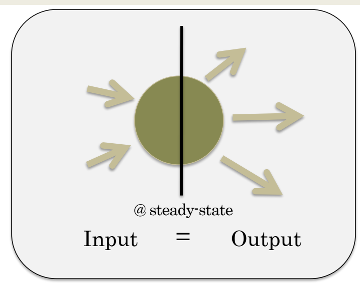
ENA Flow: Key Concepts & Metrics

Throughflow

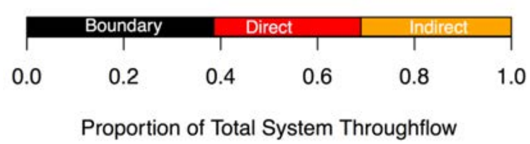
Total amount of energy–matter entering or exiting a node, T_j

Interpretation
Node Activity, Node Power, Centrality (Borrett 2013)

Total System Throughflow = **TST** = $\Sigma\ T_j$



Input–Output Analysis



Indirect / Direct

Indirect / TST

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ENA Applications

How and to what degree do species **indirectly influence** each other through the food web?

1999 Trophic Ecology

ECOSYSTEMS

Unexpected Effects of Predators Upon Their Prey: The Case of the American Alligator

Cristina Bondavalli* and Robert E. Ulanowicz

2015 Biogeochemistry

Vol. 526: 137–156, 2015 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published March 30

Estimating the effects of seawater intrusion on an estuarine nitrogen cycle by comparative network analysis

David E. Hines[1,2,*], Jessica A. Lisa[3], Bongkeun Song[3], Craig R. Tobias[4], Stuart R. Borrett[1,2,5]

How important is **process coupling** in biogeochemical cycles?

Impact of **sea water intrusion** on ecosystem services

Urban Metabolism 2012

Environmental Science & Technology

Network Environ Perspective for Urban Metabolism and Carbon Emissions: A Case Study of Vienna, Austria

Shaoqing Chen[1] and Bin Chen*[1]

How **sustainable** are **cities** (materials & energy) and **economies**?

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Ecosystem Management

Ocean & Coastal Management 68 (2012) 169–188

Contents lists available at SciVerse ScienceDirect

Ocean & Coastal Management

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

ELSEVIER

Integrating ecological, economic and social aspects to generate useful management information under the EU Directives' 'ecosystem approach'

Victor N. de Jonge[a,b,*], Rute Pinto[c], R. Kerry Turner[d]

Vol. 538: 257–272, 2015 doi: 10.3354/meps11502 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published October 28

REVIEW

Role of trophic models and indicators in current marine fisheries management

C. Longo[1,8,*], S. Hornborg[2], V. Bartolino[3], M. T. Tomczak[4], L. Ciannelli[5], S. Libralato[6], A. Belgrano[3,7]

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Dominance of Indirect Effects

Hypothesis

Indirect flows dominate direct flows in ecosystems

Indirect > Direct   Indirect / Direct > 1   Higashi & Patten 1989

Consequences

Alter species roles and who controls resources

Hidden relationships

Impact assessment and management implications

Conservation

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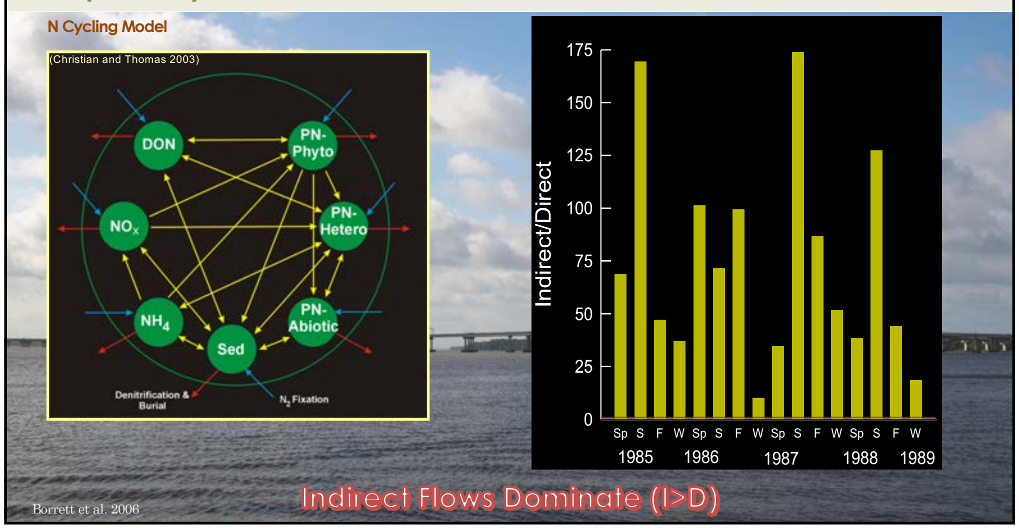
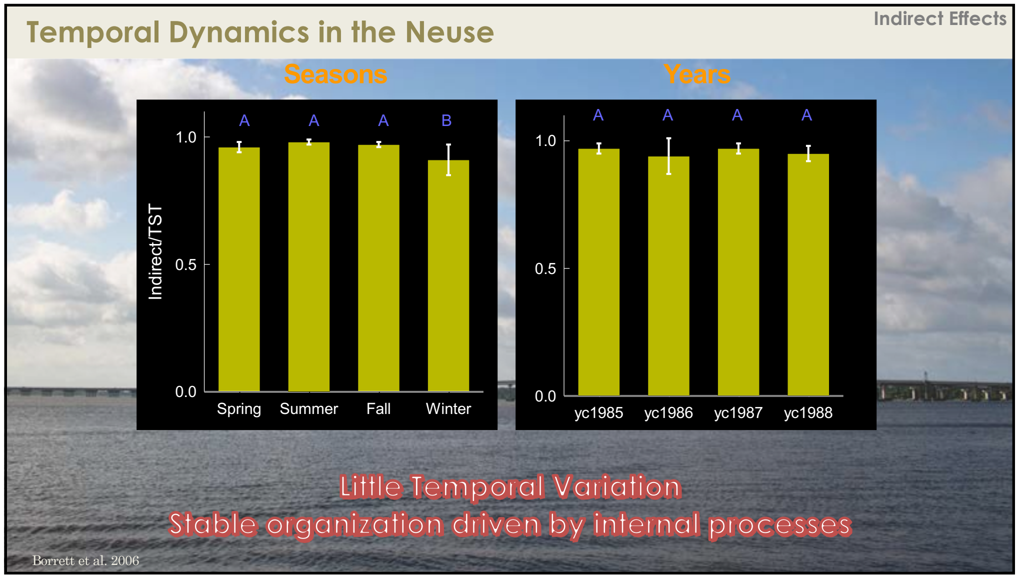
Indirect Effects

Temporal Dynamics in the Neuse



58


Temporal Dynamics in the Neuse
Indirect Effects
Seasons
Years
Indirect/TST
1.0
0.5
0.0
A A A B
Spring Summer Fall Winter
A A A A
yc1985 yc1986 yc1987 yc1988
Little Temporal Variation
Stable organization driven by internal processes
Borrett et al. 2006

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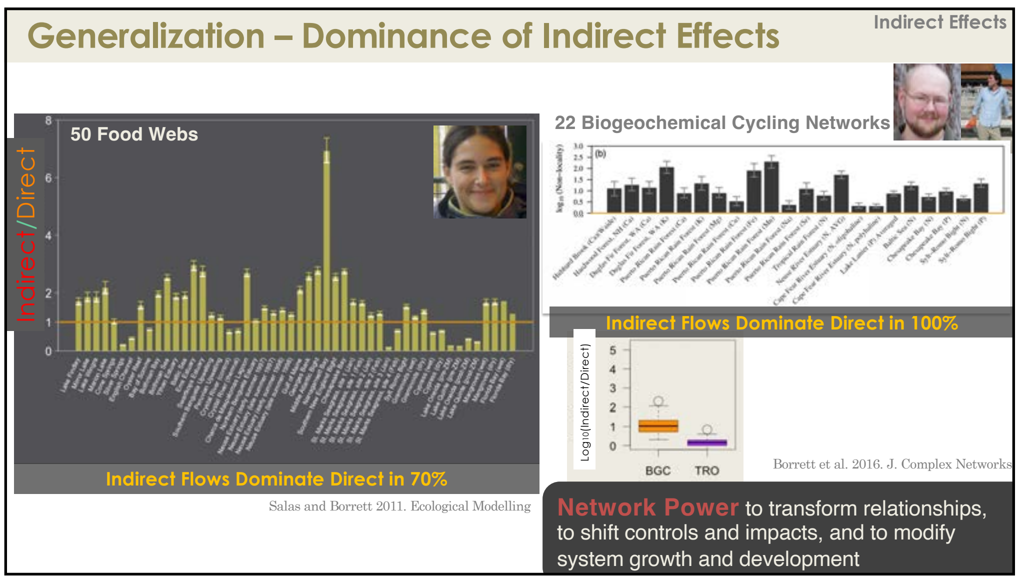
Generalization – Dominance of Indirect Effects
Indirect Effects
50 Food Webs
Indirect/Direct
Indirect Flows Dominate Direct in 70%
Salas and Borrett 2011. Ecological Modelling
22 Biogeochemical Cycling Networks
Indirect Flows Dominate Direct in 100%
Log10(Indirect/Direct)
BGC TRO
Borrett et al. 2016. J. Complex Networks
Network Power to transform relationships, to shift controls and impacts, and to modify system growth and development

60

Indirect Effects

Evidence supports the
Dominance of Indirect Effects hypothesis

Temporal stability of organization (Neuse)

General ecosystem property
- trophic < biogeochemical cycles
(perspective matters)

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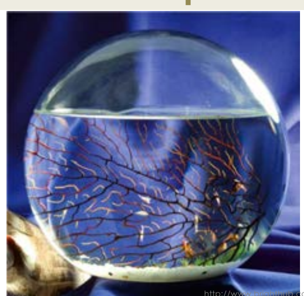
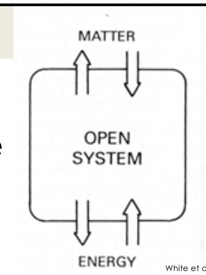
Network Imperative



Living Systems are

Open



White et al. 1992

Exchange energy & matter

Schrodinger 1946; Jorgensen et al. 1999

Claim

Living Systems must form exchange networks

A fundamental feature of life

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