Integrating Natural and Computer Sciences to Explore the Structure and Dynamics of Complex Ecological Networks

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Lake Tahoe food web
Food web graphics by Web3D © Rich Williams
Early paradigm: complex communities are more stable than simple ones (Odum 1953, MacArthur 1955, Elton 1958)

Less invasions, less species turnover, less calamities,...
Mathematically, stability decreases with system diversity (species) and complexity (interactions)


Change of paradigm: Unstable complex systems

Fig. 1. Variation of stability with connectance.
3 “niche model” food webs with $S = 50$ and empirically observed range of connectance ($C = \text{Links}/\text{Species}^2$)

- $C = 0.03$ (75 links)
- $C = 0.10$ (250 links)
- $C = 0.30$ (750 links)
Low Connectance Webs, $C < 0.10$

- **UK Grassland**
  - $C = 0.03$, $S = 61$, $L/S = 1.6$
  - Martinez et al. 1999

- **Scotch Broom**
  - $C = 0.03$, $S = 85$, $L/S = 2.6$
  - Memmott et al. 2000

- **Ythan Estuary**
  - $C = 0.04$, $S = 124$, $L/S = 4.7$
  - Huxham et al. 1996

- **Ythan Estuary, no parasites**
  - $C = 0.06$, $S = 83$, $L/S = 4.8$
  - Hall & Raffaelli 1991

- **El Verde Rainforest**
  - $C = 0.06$, $S = 155$, $L/S = 9.7$
  - Waide & Reagan 1996

- **Canton Creek**
  - $C = 0.07$, $S = 102$, $L/S = 6.8$
  - Townsend et al. 1998

- **Stony Stream**
  - $C = 0.07$, $S = 109$, $L/S = 7.6$
  - Townsend et al. 1998

- **Chesapeake Bay**
  - $C = 0.07$, $S = 31$, $L/S = 2.2$
  - Baird & Ulanowicz 1989
Middle and High Connectance Webs, $C < 0.10$

- **St. Marks Seagrass**
  - $C = 0.10$, $S = 48$, $L/S = 4.6$
  - Christian & Luczkovich 1999

- **St. Martin Island**
  - $C = 0.12$, $S = 42$, $L/S = 4.9$
  - Goldwasser & Roughgarden 1993

- **Little Rock Lake**
  - $C = 0.12$, $S = 92$, $L/S = 10.8$
  - Martinez 1991

- **Lake Tahoe**
  - $C = 0.13$, $S = 172$, $L/S = 22.6$
  - Vaccaro and Martinez unpbl.

- **Mirror Lake**
  - $C = 0.15$, $S = 172$, $L/S = 25.1$
  - Puleston and Martinez unpbl.

- **East River**
  - $C = 0.15$, $S = 104$, $L/S = 15$
  - Harvey and Martinez unpbl.

- **Coachella Valley**
  - $C = 0.31$, $S = 29$, $L/S = 9.0$
  - Polis 1991

- **Skipwith Pond**
  - $C = 0.32$, $S = 25$, $L/S = 7.9$
  - Warren 1989
Are food webs scale-free? Not really…

• Most food webs display single-scale (exponential or uniform) distributions. -i.e., no structurally ‘over-dominant’ taxa in food webs.

• The relatively high $C$ and low $S$ of food webs limits potential heterogeneity of feeding link distribution.

Dunne, Williams and Martinez
2002 PNAS 99:12917
Constant Connectance \((L/S^2)\): 
\(S\) is orthogonal to \(L/S^2\)

- **Taxonomic webs**
  - Slope = 2.01
  - \(R^2 = 93\%\)

- **Trophic webs**
  - Slope = 2.07
  - \(R^2 = 97\%\)

2 Versions of Havens’
50 Pelagic Food Webs
Martinez Science 1993
Challenge

Which structural properties enable network persistence

Analyses by an ecoinformatics approach that synthesizes
(1) structural models of food webs and
(2) allometrically scaling population dynamics
Structural models of complex food webs

Cascade model
Cohen et al. 1990
Strong trophic hierarchy

Niche model
Williams & Martinez 2000 Nature
Looping allowed, contiguity required

Nested-hierarchy model
Cattin et al. 2004 Nature
Phylogenetic grouping and adaptation
Niche Model: Simple Rules

- Inputs: Diversity and Complexity (S & C)
  - Ecological contingency

- 3 Simple Rules
Niche Model Rule 1

- Fixed one-dimensional community niche space
- Each species given a fixed location or “niche value”

- Rule 1: Assign each of S species a uniformly random number \([0, 1]\) so that the “niche value” of \(S_i\) is \(n_i\)
Niche Model

Rule 2

- Rule 1: Each species gets uniform random $n_i$

- Rule 2: Each species gets assigned a random “feeding range” ($r_i$) $0 \leq r_i \leq 1$
  - chosen from a beta function (mean of $2C$) multiplied by the species niche value ($n_i$).

- Stochastically distributes generality among species while ensuring web has comparable $C$
Niche Model
Final Step 3

- Step 1: Each species gets uniform random $n_i$
- Step 2: Each species gets beta random $r_i$

- Step 3: Each niche range is placed by uniformly choosing a random range center $(c_i)$ so that $r_i/2 < c_i < n_i$

- Establishes relaxed trophic hierarchy while allowing cannibalism and looping
Niche Model: Mechanics

- Randomly assign “j” species a niche value (n_j)
- Randomly assign species a niche range (r_j)
- Randomly assign the center of the range (c_j)
- Repeat 1000 times with observed S and C
Nested Hierarchy Model

- Inputs: Diversity and Complexity (S & C)
  - Ecological contingency

- Phylogenetic Adaptation
  - Species get beta-distributed diets
  - Starting with lowest ranked species, Species join feeding guilds that consume lower ranked species
  - If needed, more prey are randomly added
Bioenergetic Nonlinear Population Dynamics

Biomass change \sim \text{growth} - \text{metabolism} + \text{consumption} - \text{being consumed}

\[ B_i'(t) = r_i G_i(\bar{B}) - x_i B_i(t) + \sum_{j=1}^{n} \left( x_i y_{ij} F_{ij}(\bar{B}) B_i(t) - x_j y_{ji} F_{ji}(\bar{B}) B_j(t) / e_{ji} \right) \]

- Growth rate
- Metabolic rate
- Maximum consumption rate
- Functional response
Gradation from Type II to Type III Functional Response

\[ F_{ij}(B) = \frac{B_j(t)^{1+q_{ij}}}{\sum_{k=1}^{n} \alpha_{ik} B_k(t)^{1+q_{ij}}} + B_{0,ji}^{1+q_{ij}} \]

\( \alpha \): relative prey preference of predator species
\( B \): biomass
\( B_0 \): half saturation density of prey species when consumed by predator species
\( q \): controls form of functional response
  - \( q = 0 \) (Type II)
  - \( q = 1 \) (Type III)

Addition of Predator Interference to Type II Functional Response:

\[ F_{ij}(B) = \frac{B_j(t)}{\sum_{k=1}^{n} \alpha_{ik} B_k(t) + (1 + c_{ij} B_i(t)) B_{0,ji}} \]
Bioenergetic Nonlinear Population Dynamics

Biomass change ~ growth – metabolism + consumption – being consumed

\[ B_i'(t) = r_i G_i(B) - x_i B_i(t) + \sum_{j=1}^{n} \left( x_{ij} y_{ij} F_{ij}(B) B_i(t) - x_{ji} y_{ji} F_{ji}(B) B_j(t) / e_{ji} \right) \]

Growth rate  Metabolic rate  Maximum consumption rate  Functional response

Power law allometric scaling relationships

Different metabolic types of species:
- same negative quarter exponent
- different allometric constants

From: Yodzis & Innes
Generate binary network with structural network model

Scale biological rates with negative quarter power-law

Parameterize network model of population dynamics

Simulate nonlinear population dynamics

Measure stability as probability of species persistence
c) Metabolic types:
- Invertebrates
- Ectotherm vertebrates

Community stability vs. \( \log_{10} \) consumer resource body size ratio
Global data base on natural body size ratios

Data for 3887 invertebrate predators and 1501 ectotherm vertebrate predators

Geometric mean body size ratios are above break points
Negative diversity stability relationships under uniform body size distributions

Positive diversity stability relationships under natural body size distributions
a) Functional responses: log₁₀ consumer resource body size ratio

Community stability

-2 0 2 4

Results qualitatively robust to variation in Functional Responses
Results generally robust to limited variation in Network Structure.
Conclusions - Part I

• Instability under abstract (random) dynamics on abstract (random) networks

• Stability under realistic (allometrically scaled) dynamics on realistic (non-random) networks

• Natural ecosystems are stabilized by their body size structure

• Including empirical realism allows simulation of complex ecological network dynamics – So where do we get the data? How can more scientists contribute to and conduct such simulations?

• INFORMATICS!
Conclusions Part II & Future Directions

• Ecoinformatics are Key to Computational and Basic Ecology

• Improve empirical estimates of maximum consumption rates, especially for invertebrates

• Empirically explore functional responses, especially variability within food webs

• *In Silico* explorations of network structure
• Improve and implement “data forever” ecoinformatics
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→ Scaling of Network Complexity with Diversity in Food Webs
→ Webs on the Web: Internet Database, Analysis and Visualization of Ecological Networks
→ Science on the Semantic Web: Prototypes in Bioinformatics


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The Niche model recovers the negative complexity-stability relationship effect in adaptive food webs.
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*American Naturalist* 163: 458-468

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