Ecological Dynamics

Ecological networks (1 / 2)
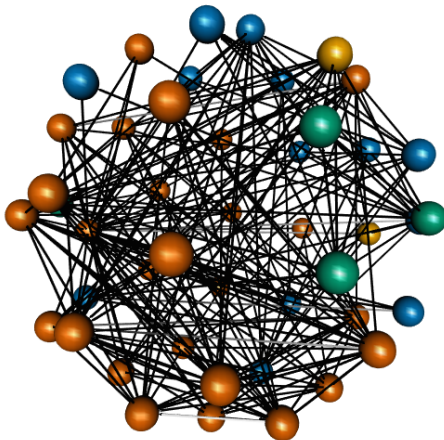
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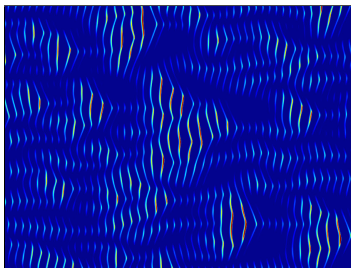
# Most ecosystems are complex and species-rich ...

... But theory suggests that complexity begets instability

- May (1972) showed that the stability of randomly assembled food webs depends on the following relationship: $\alpha < \dfrac{1}{\sqrt{nC}}$

- Where α is the mean interaction strength, C is the connectance or proportion of all possible interactions that are realized, and n is the number of species

- This result suggests that increasing complexity by either increasing n or C will reduce stability by making the inequality less likely to be true

- Similarly, increasing the average interaction strength α would also destabilize randomly assembled food webs

- Hence, why are complex food webs so frequently found in nature and could it have something to do with their non-random structure?

Natural complexity has mostly been ignored

Analysis of all papers published in Ecology from 1981 to 1990
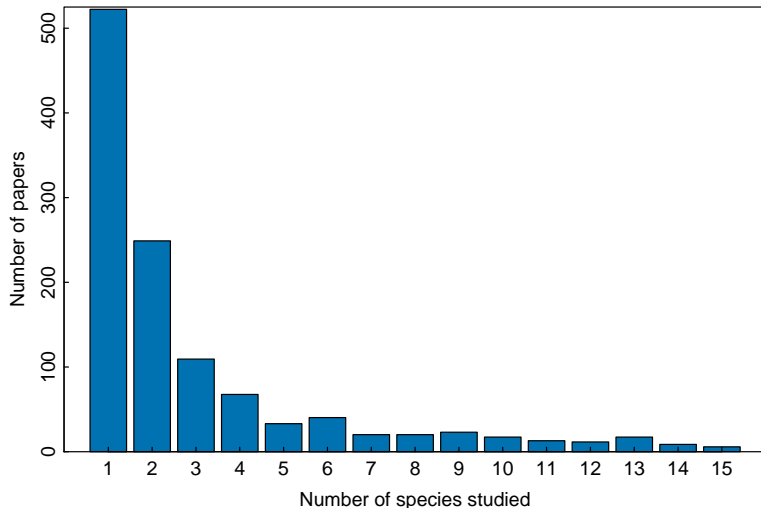
Strategies for reducing natural complexity

Foundational — Corals

Keystone — Sea stars

Cornerstone — Macroalgae

Dominant — Mussels

Focusing on foundational (Dayton, 1971), keystone (Paine, 1969), cornerstone (Bracken and Low, 2012) and dominant species.

Dealing with natural complexity

Methodology	Ontology (nature of world)	Epistemology (knowledge of world)
Reductionism	Properties of the whole can be derived from parts	Knowledge of parts necessary and sufficient to understand whole
Emergentism	Some properties of whole cannot be derived from parts	Knowledge of parts necessary but not sufficient to understand whole
Organicism	Parts cannot exist independently of whole	Knowledge of whole necessary to understand parts and vice versa
Holism	Basic unit is the whole Parts cannot be used to understand whole	Knowledge of parts is neither necessary nor sufficient to understand whole

Using graph theory to represent ecological networks
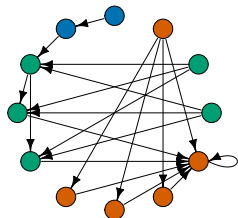
**Chesapeake Bay
food web**
Cohen (1978)

Graphs consist of:

- Nodes or vertices representing species
- Links or edges representing species interactions

Graphs can be:

- Undirected or directed: (un)directed means that the edges are (bi)directional
- Unweighted or weighted: (un)weighted means that the edges contain (no) information about the strength of the interaction

Graphs can represent:

- Predator-prey interactions in food webs
- Dependencies in mutualistic networks

Using ecological data to create graphs

The adjacency matrix $\mathbf{A}$ is a square $S \times S$ matrix that can be used to represent ecological networks as graphs.

$\mathbf{A}(i,j) = 0$ indicates no interaction between the species in row i and the species in column j.
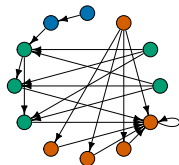
$\mathbf{A}(i,j) = 1$ indicates an interaction between the species in row i and the species in column j.

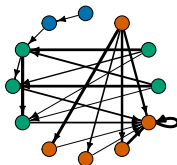Example of an adjacency matrix $\mathbf{A}$ for $S = 5$ species:

	Species j				
	0	1	0	1	1
	1	1	0	1	1
Species i	0	0	0	1	0
	0	1	0	0	0
	0	1	0	1	1

Different perspectives on ecological networks

Descriptive webs:

Describe presence or
abscence of species
interactions
(Elton, 1958)

Bioenergetic webs:

Describe amount of
energy flowing from
prey to predator
(Lindeman, 1942)

Interaction webs:

Describe strength of
interaction between
prey and predator
(Paine, 1980)

Topological features of food web networks

Metric	Description	Computation
Size	Total number of species	S
Degree	Number of links for vertex v	$\deg(v)$
$d(v_i, v_j)$	Distance between vertices i and j	Dijkstra's algorithm
Char. path length	Mean distance between species	$\frac{2}{S(S-2)} \sum_{i \neq j} d(v_i, v_j)$
Connectance	Proportion of realized links	$C = L/S^2$
Link density	Number of links per species	$l_D = L/S$
Trophic level	Number of links + 1	$T = L + 1$
Chain length	Number of species - 1	$l_C = S - 1$

Ecological features of food web networks

Metric	Description
B, I, T	Proportion of basal, intermediate and top species
Omnivory	Feeding on prey at multiple trophic levels
Cycles	Reciprocal feeding relationships between pairs of species
Loops	Three species feed on each other ($A \rightarrow B \rightarrow C \rightarrow A$)

Reverse engineering food webs

Current models take empirical parameters such as S and C and use specific algorithms to generate food webs.

The characteristics of the generated food webs can be compared to those observed in nature in order to infer the generating processes.

The most popular approaches to date are the **random**, **cascade** (Cohen and Newman, 1985) and **niche** (Williams and Martinez, 2000) models.

Slight deviations of the niche model have also been introduced more recently (Allesina et al., 2008; Cattin et al., 2004).

Reverse engineering food webs: the random model

Each interaction between all pairs of S species occurs at the same probability $P = C$, with C corresponding to the connectance observed in the empirical food web.

This algorithm is often used as a **null model** that is free of all biology against which to compare the performance of more realistic models.

```
# Random food web model
random <- function(S, C) {
    adj <- matrix(nrow = S, ncol = S, 0)
    rand <- matrix(nrow = S, ncol = S, runif(S * S))
    adj[rand < C] <- 1
    return(adj)
}
```
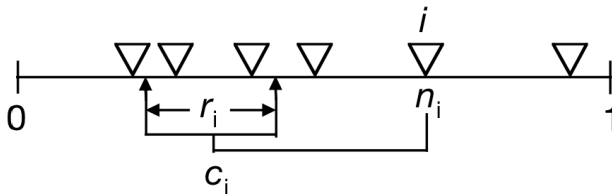
Reverse engineering food webs: the cascade model
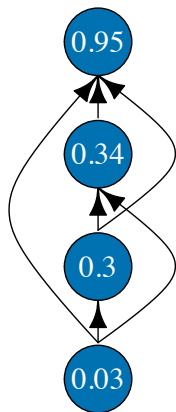
- Cohen and Newman (1985) developed a simple model to build realistic food webs based on only two parameters: number of species S and connectance C

- Each species i is given a random position n_i along a single niche axis using a uniform distribution between 0 and 1

- Species i consumes all species that have a lower niche position

Reverse engineering food webs: the cascade model

```r
# Cascade food web model
cascade <- function(S, C = NULL) {
    adj <- matrix(nrow = S, ncol = S, 0)
    niches <- runif(S)  # Random niches n
    if (is.null(C)) {
        prob <- 1
    } else {
        prob <- 2 * C * S/(S - 1)
    }
    for (i in 1:S) {
        consumed <- which(niches < niches[i] & runif(1) <
            prob)
        adj[consumed, i] <- 1
    }
    return(adj)
}
```

Reverse engineering food webs: niche model

- Williams and Martinez (2000) developed a simple model that allowed them to build realistic food webs based on only two parameters: the number of species S and connectance C
- Each species i is given a random position n_i along a single niche axis using a uniform distribution between 0 and 1
- Species i consumes all species falling in a range r_i that is placed by drawing the center of the range c_i randomly in the interval $[r_i/2, n_i]$ according to a beta distribution

# Reverse engineering food webs: the niche model

```r
# Niche food web model
niche <- function(S, C) {
    adj <- matrix(nrow = S, ncol = S, 0)
    niches <- runif(S)  # Random niches n
    radius <- rbeta(S, 1, 1/(2 * C) - 1) * niches  # Random radii r
    # Feed between [r/2, n)
    center <- runif(S, min = radius/2, max = niches)
    for (i in 1:S) {
        consumed <- which(niches > (center[i] - radius[i]/2) &
            niches < (center[i] + radius[i]/2))
        adj[consumed, i] <- 1
    }
    return(adj)
}
```

# Comparing these theoretical food web models
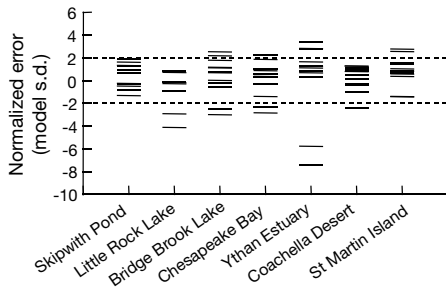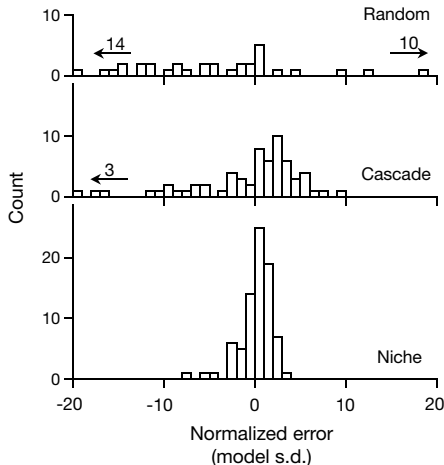
The niche model is better able to reproduce charactersitics of natural food webs than the random or cascade models (Williams and Martinez, 2000).

Topology of natural food webs networks
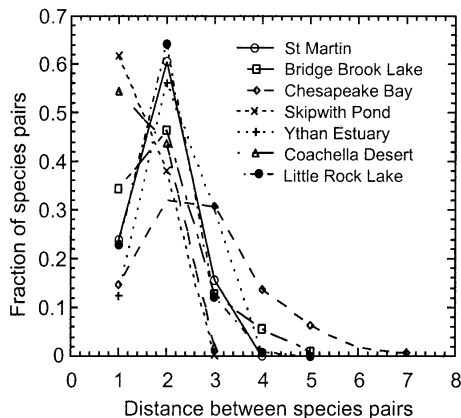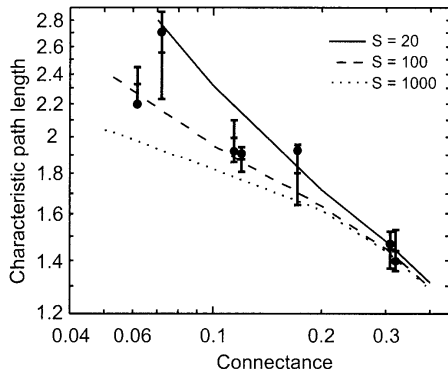
Natural food webs with higher connectance have lower characteristic path lengths, with species being separated from each other by an average of two species (Williams et al., 2002).

Structural resilience of natural food web networks
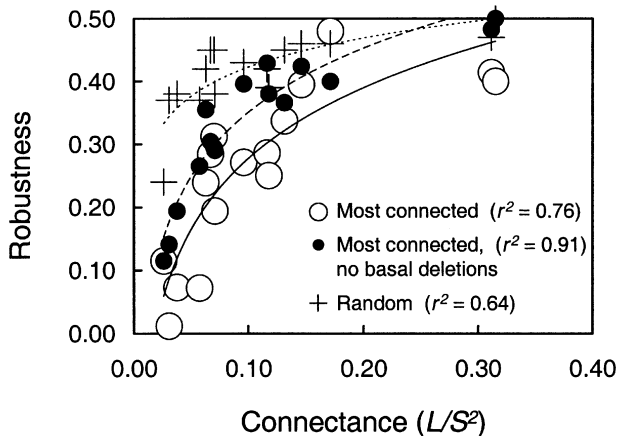
Species deletion experiments show that removing the most connected species leads to the greatest number of secondary extinctions and the lowest levels of food web robustness (Dunne et al., 2002).

Conclusions

We can build realistic food web networks by following a few simple rules (Stouffer et al., 2005):

- Niche values assigned to each species must be strictly ordered (i.e., creating a trophic hierarchy)
- Each species must have an exponentially decaying probability of preying on a fraction of the species having lower niche values

This means that biology is not needed to recover the structure of natural food web networks.

Hence, need to move beyond these simple topological characteristics in order to understand how biological processes affect the assembly of food webs.

This is a great example of theory both explaining natural patterns and suggesting a new empirical research agenda.

References

Allesina, S., D. Alonso, and M. Pascual. 2008. A general model for food web structure. Science, **320**:658–661.

Bracken, M. E. S. and N. H. N. Low. 2012. Realistic losses of rare species disproportionately impact higher trophic levels. Ecology Letters, **15**:461–467.

Cattin, M.-F., L.-F. Bersier, C. Banasek-Richter, R. Baltensperger, and J.-P. Gabriel. 2004. Phylogenetic constraints and adaptation explain food-web structure. Nature, **427**:835–839.

Cohen, J. E. 1978. Food webs and niche space. Number 11, Princeton University Press, Princeton, New Jersey.

Cohen, J. E. and C. M. Newman. 1985. A stochastic theory of community food webs: I. models and aggregated data. Proceedings of the Royal Society of London B: Biological Sciences, **224**:421–448.

References

Dayton, P. K. 1971. Competition, disturbance, and community organization - provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs, **41**:351–389.

Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecology Letters, **5**:558–567.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, London.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology, **23**:399–417.

May, R. M. 1972. Will a large complex system be stable? Nature, **238**:413–414.

Paine, R. T. 1969. Pisaster-tegula interaction - prey patches, predator food preference, and intertidal community structure. Ecology, **50**:950–961.

References

Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. The Journal of Animal Ecology, **49**:666–685.

Stouffer, D. B., J. Camacho, R. Guimera, C. A. Ng, and L. A. N. Amaral. 2005. Quantitative patterns in the structure of model and empirical food webs. Ecology, **86**:1301–1311.

Williams, R. J., E. L. Berlow, J. A. Dunne, A.-L. Barabasi, and N. D. Martinez. 2002. Two degrees of separation in complex food webs. Proceedings of the National Academy of Sciences, **99**:12913–12916.

Williams, R. J. and N. D. Martinez. 2000. Simple rules yield complex food webs. Nature, **404**:180–183.