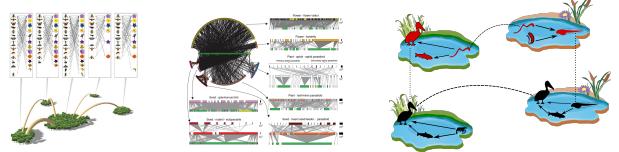
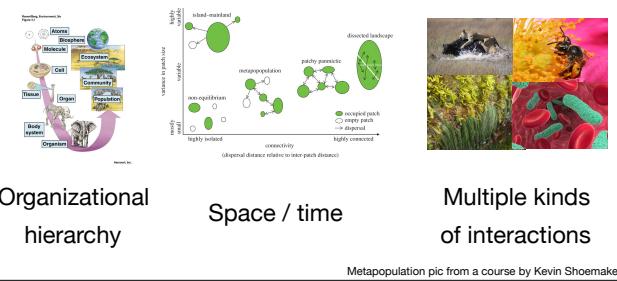


Week 6: Ecological Multilayer Networks

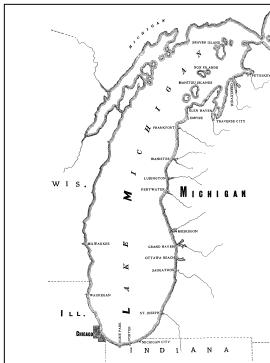


Higher dimensionality in ecology



« It is interesting to contemplate an **entangled bank**, clothed with plants of many kinds, with birds singing... so dependent on each other in so complex a manner... »

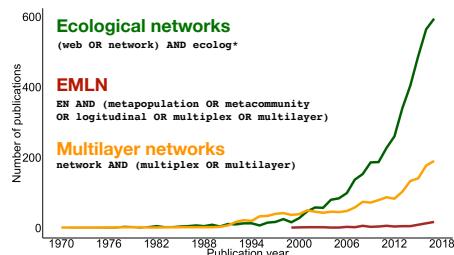
Charles Darwin, 1859



“...so ecologists seek to study those plant structures which are changing at the present time, and thus to throw light on the origin of plant structures themselves.”

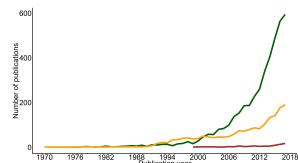
Cowles HC. Botanical Gazette, 1899

Ecological networks are usually studied in “isolation” or aggregated



Ecological networks are usually studied in “isolation” or aggregated

- Data
- Methodology
- Immature field



First explorations of (modern) ecological multilayer networks

Ecological Monographs, 60(3), 1990, pp. 331-347
© 1990 by the Ecological Society of America

Ecological Monographs, 55(3), 1991, pp. 267-298
© 1991 by the Ecological Society of America

Spatial and temporal variation in tropical fish trophic networks¹

KIRK O. WINEMILLER
Department of Zoology and Texas Memorial Museum,
The University of Texas at Austin, Austin 78712 USA

Temporal variation in food web structure: 16 empirical cases²

KENNETH SCHONIUS AND JOEL E. COHEN
Rockefeller University, 1230 York Avenue, Box 20, New York, NY 10021-6399 USA

OIKOS 40: 289-306, Copenhagen 1987

OIKOS 55: 299-311, Copenhagen 1990

Spatial and temporal variation in food webs in water-filled treeholes

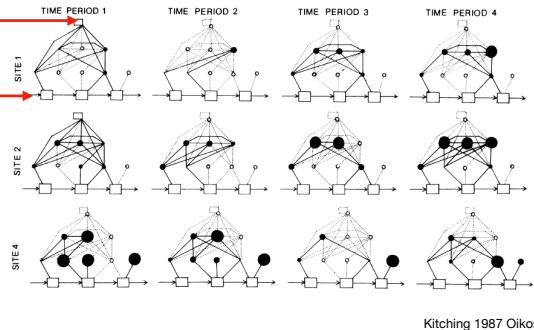
R. L. Kitching

Spatial and temporal variation in the structure of a freshwater food web

Philip H. Warren

Frog

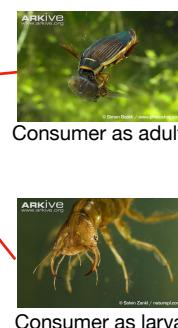
Detritus



Kitching 1987 Oikos

Resource (species number)	Consumer (species number)
0	1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30
1	1 1 2 1 2 1
2	2 2
3	3 2
4	4 2
5	5 2
6	6 2
7	7 2
8	8 2
9	9 2
10	10 2
11	11 2
12	12 2
13	13 2
14	14 2
15	15 2
16	16 2
17	17 2
18	18 2
19	19 2
20	20 2
21	21 2
22	22 2
23	23 2
24	24 2
25	25 2
26	26 2
27	27 2
28	28 2
29	29 2
30	30 2

Warren 1989 Oikos



Consumer as adult
Consumer as larva

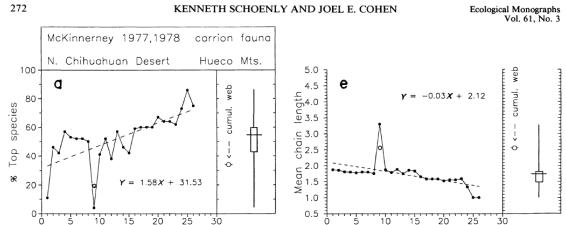


TEMPORAL VARIATION IN FOOD WEB STRUCTURE:
16 EMPIRICAL CASES¹

KENNETH SCHOENLY AND JOEL E. COHEN
Rockefeller University, 1230 York Avenue, Box 20, New York, New York 10021-6399 USA

Used 16 webs from **published** data

1. Quantify 9 properties.
2. Compare aggregated to time-specific.
3. Remove rare species to detect their effects on aggregation.

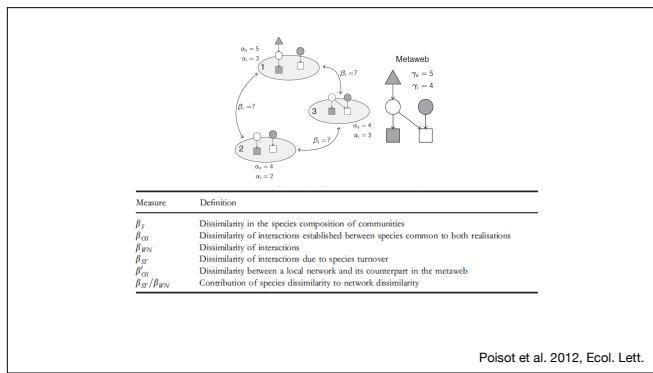
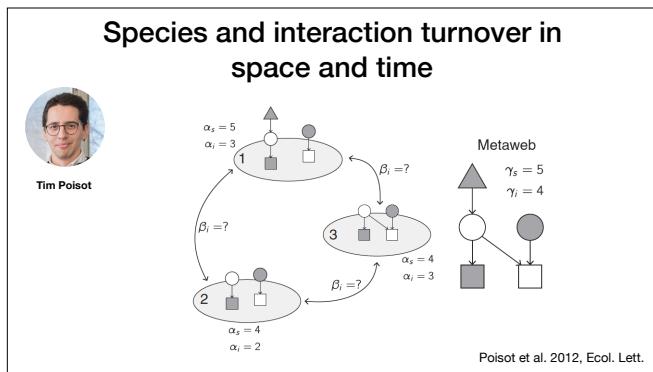
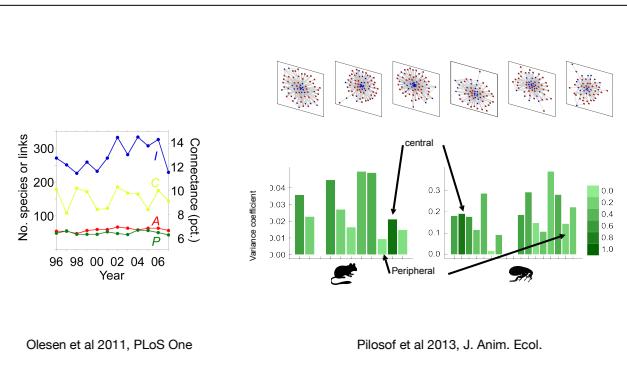


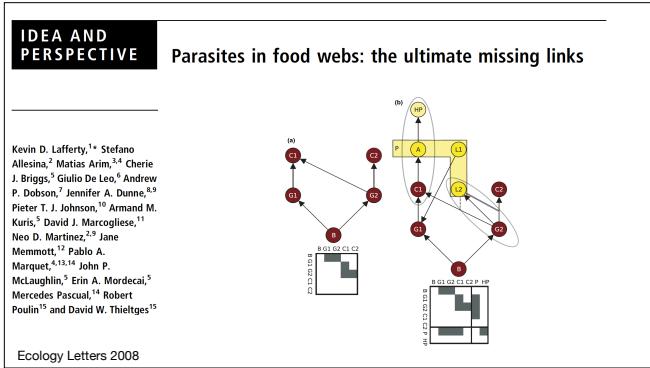
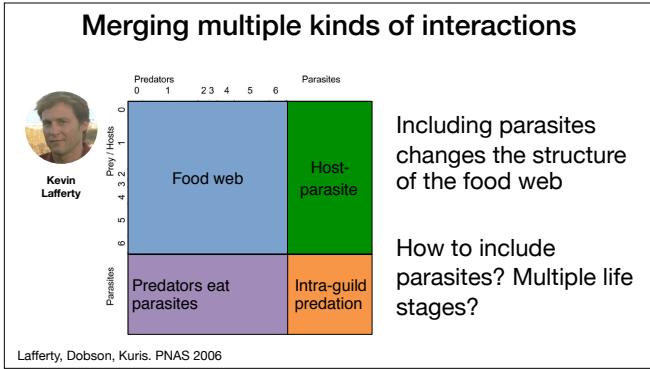
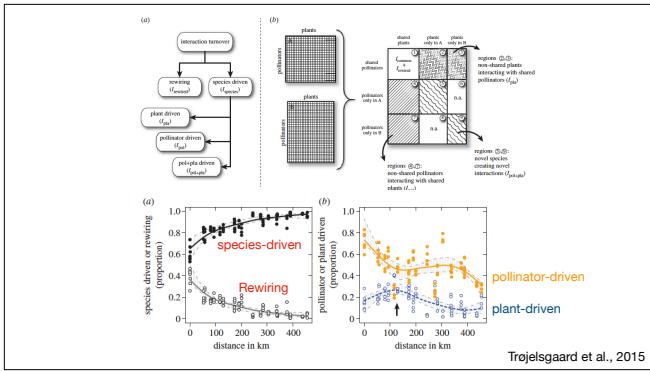
Temporal fluctuations in some properties but not others

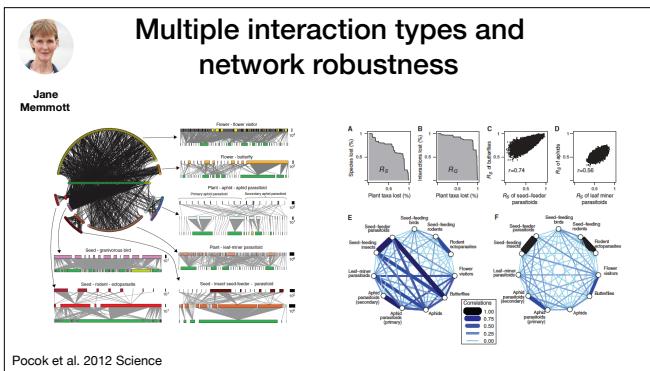
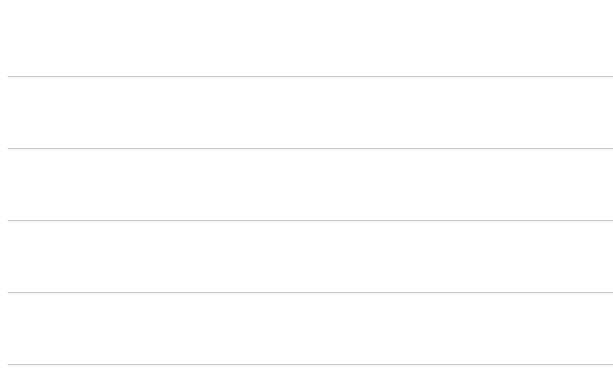
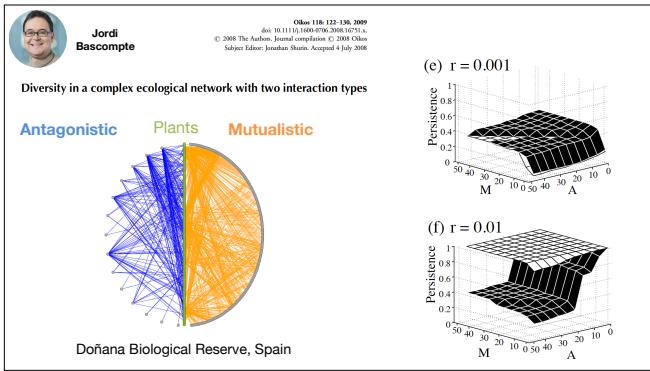
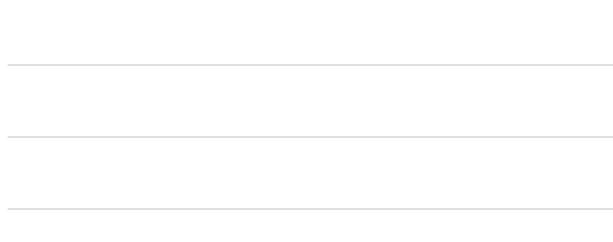
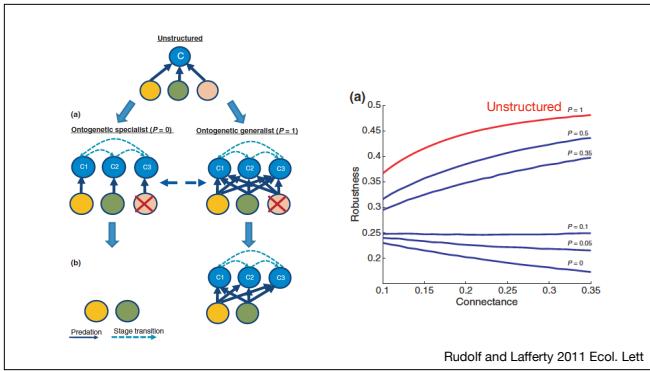
$S \times C \parallel = 2L/(S - 1)$					
No. links (L)			$(S - 1)$		
Range	Med.	Cum.	Range	Med.	Cum.
3-92	36	195	2.0-8.06	4.4	8.48
2-39	22	50	2.0-4.22	2.62	4.17
3-9	7	11	2.0-3.0	2.8	3.14
47-156	75	192	2.57-3.67	2.82	3.46
70-117	116	199	2.69-2.99	2.90	2.88

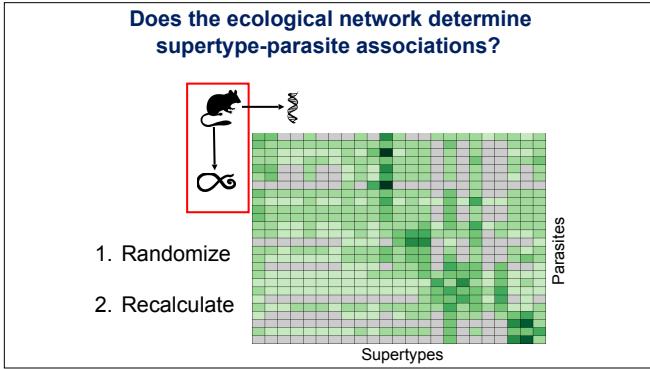
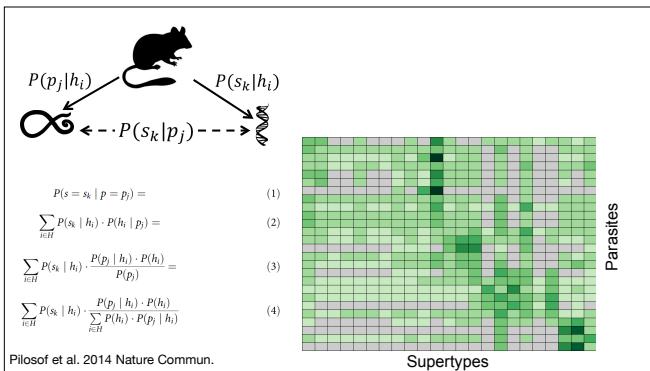
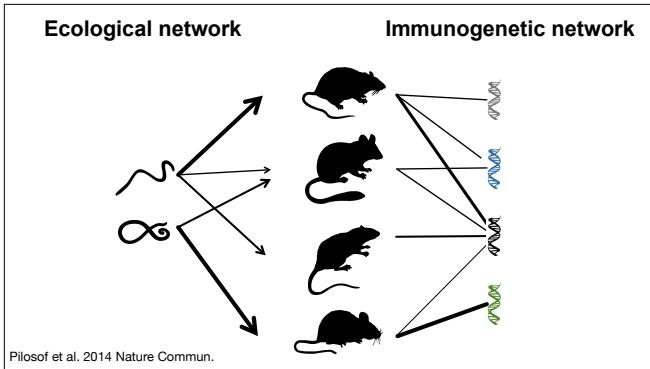
The aggregated network consistently:

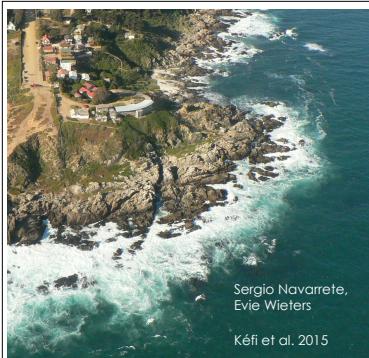
- overestimates the number of species, edges and $S \times C$
- underestimates %B











Sergio Navarrete,
Evie Wieters
Kéfi et al. 2015



Trophic interactions

Negative non-trophic
interactions

Positive non-trophic
interactions

Slide courtesy Sonia Kéfi
Kéfi et al. 2015

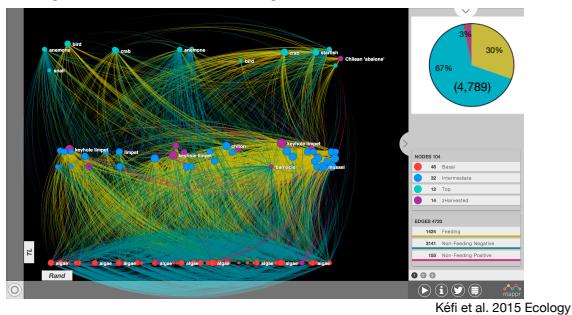


Positive non-trophic
interactions

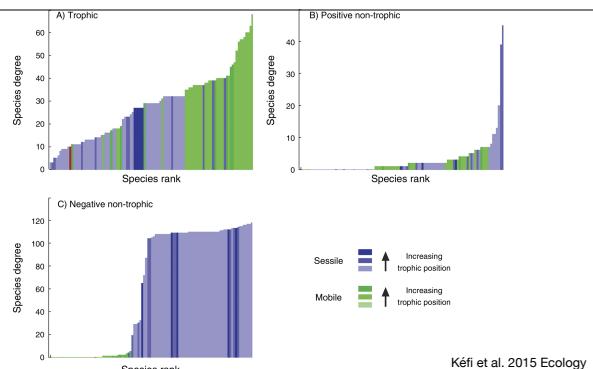
Trophic and non-trophic interactions



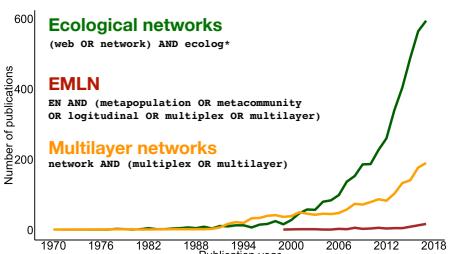
Sonia
Kéfi



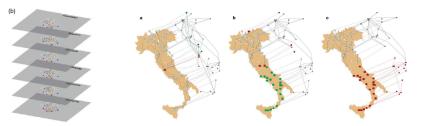
Kéfi et al. 2015 Ecology



Kéfi et al. 2015 Ecology



Multilayer networks in the broader network science



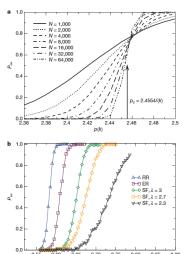
Roethlisberger & Dickson (1939)

Buldyrev et al. (Nature, 2010)

Cardillo et al. (2013)

Catastrophic cascade of failures in interdependent networks

Sergey V. Buldyrev^{1,2}, Roni Poshart¹, Gerald Paul², H. Eugene Stanley² & Shlomo Havlin³

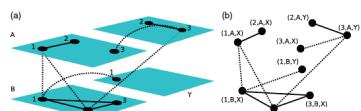


- Couple ER networks.
- Randomly remove nodes.
- Obtain giant mutually connected component.

Buldyrev et al. (Nature, 2010)



Mason
Porter



General definitions for
multilayer networks

Kivelä et al. (2014)

Development of new
metrics

So so many...

An example for a generalization to a multilayer metric: multilayer modularity function

$$Q_B = \frac{1}{2\mu} \sum_{ijsr} \left[\left(A_{ijs} - \gamma_s \frac{k_{is}d_{js}}{m_s} \right) \delta_{sr} + \delta_{ij} \omega_{jsr} \right] \delta(g_{is}, g_{jr})$$

within-layer between-layer

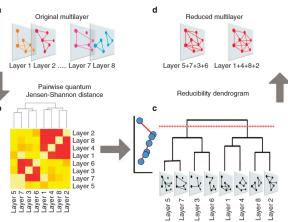
Mucha et al. 2010 Science

An example for a novel development of a multilayer metric: network reducibility

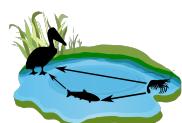


Manlio De Domenico

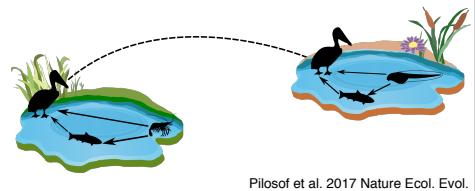
Alex Arenas



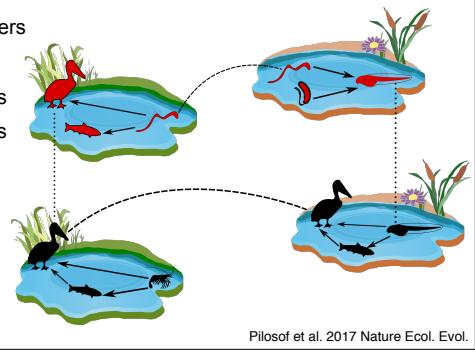
De Domenico et al. 2015 Nature Commun.



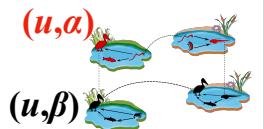
Pilosof et al. 2017 Nature Ecol. Evol.



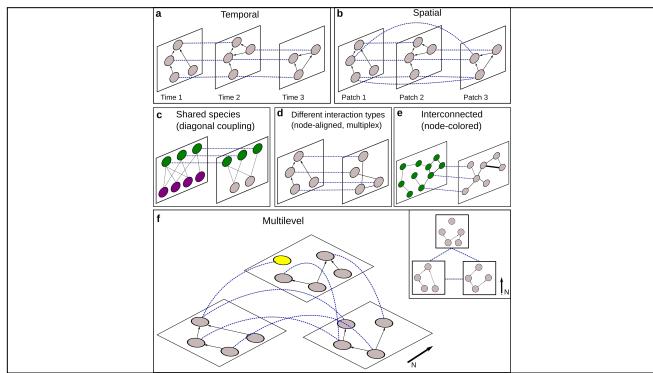
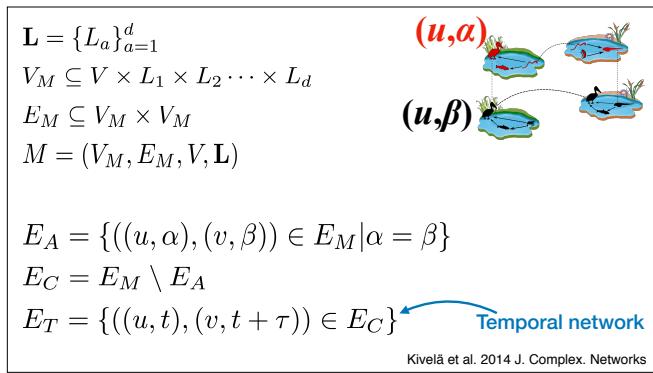
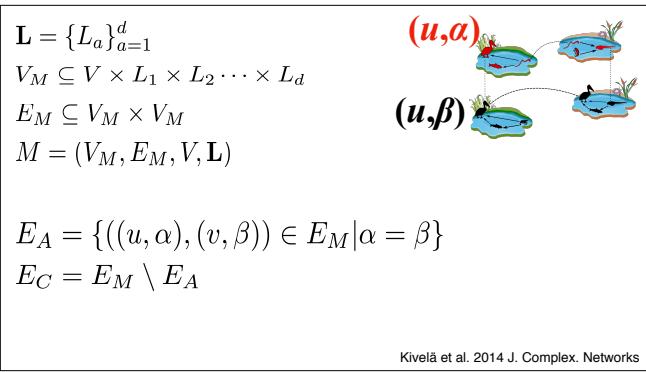
- Dimensions, layers
- State nodes
- Intra-layer edges
- Inter-layer edges

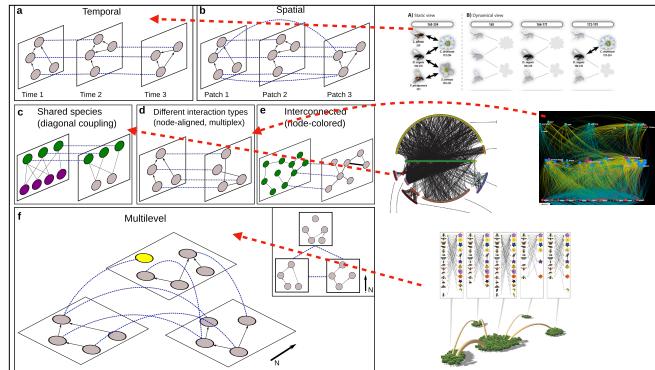


$$\begin{aligned}\mathbf{L} &= \{L_a\}_{a=1}^d \\ V_M &\subseteq V \times L_1 \times L_2 \cdots \times L_d \\ E_M &\subseteq V_M \times V_M \\ M &= (V_M, E_M, V, \mathbf{L})\end{aligned}$$

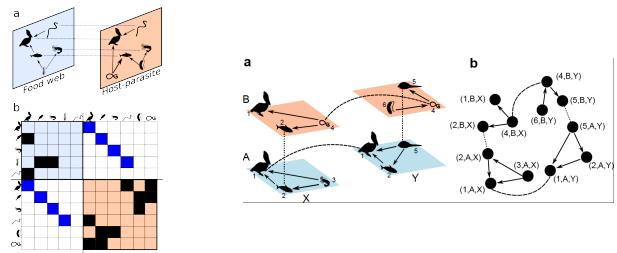


Kivelä et al. 2014 J. Complex. Networks



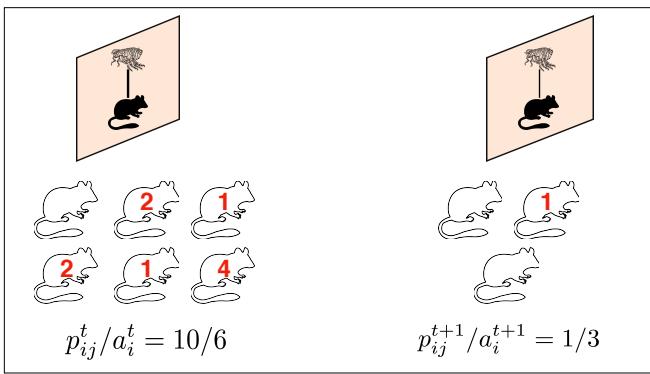
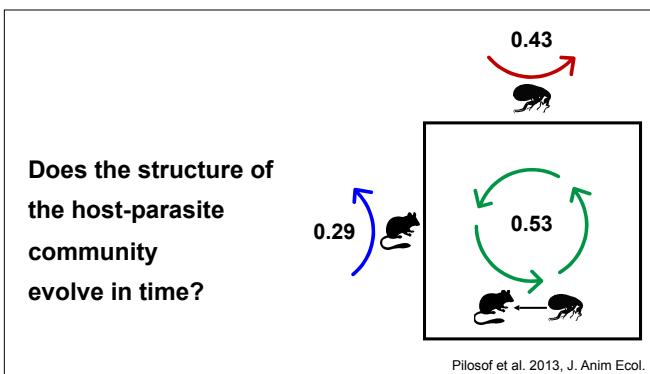
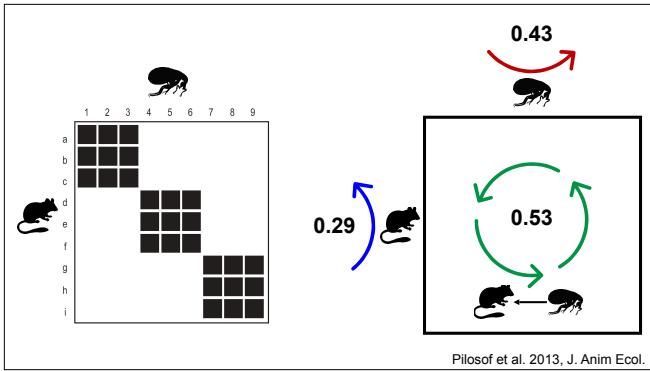


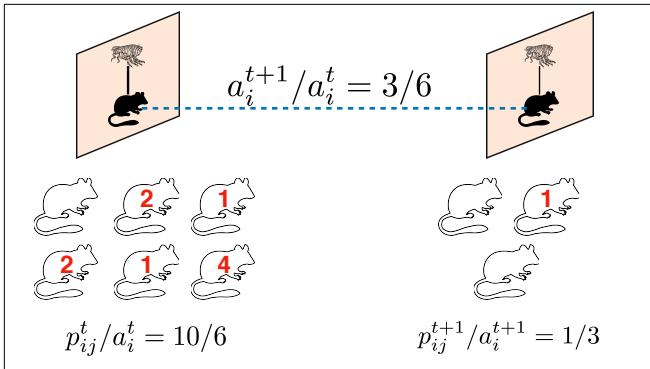
Multilayer networks can be represented as tensors (or supra-adjacency matrices)



- 6 consecutive summers (1982-1987).
- 22 mammalian hosts.
- 56 ectoparasites (fleas and mites).







- **Intra-layer edges:** Incidence of parasite species in a host species.

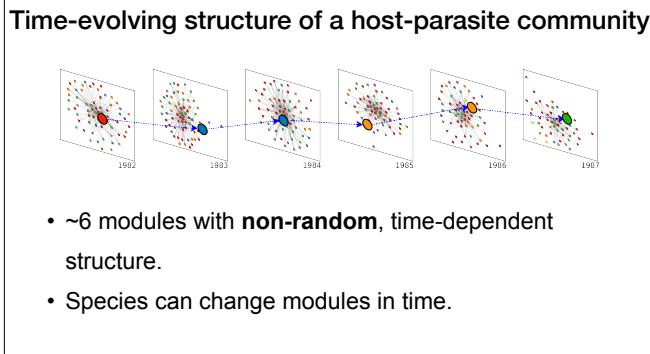
$$m_{ij}^t = p_{ij}^t/a_i^t$$

- **Inter-layer edges:** Relative change in abundance.

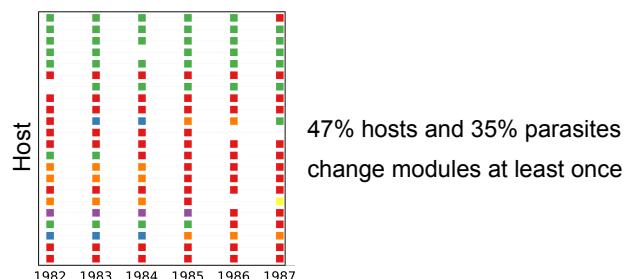
$$n_i^{t \rightarrow t+1} = a_i^{t+1}/a_i^t$$

- The future infection of a host i with parasite j :

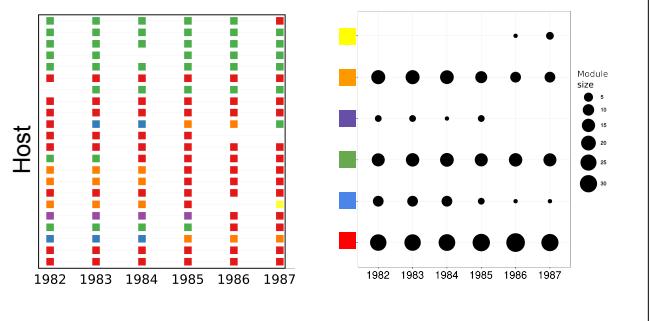
$$m_{ij}^{t \rightarrow t+1} = \frac{p_{ij}^{t+1}}{a_i^{t+1}} = \frac{p_{ij}^{t+1}}{n_i^{t \rightarrow t+1} a_i^t} = \frac{n_j^{t \rightarrow t+1} p_j^t}{n_i^{t \rightarrow t+1} a_i^t}$$



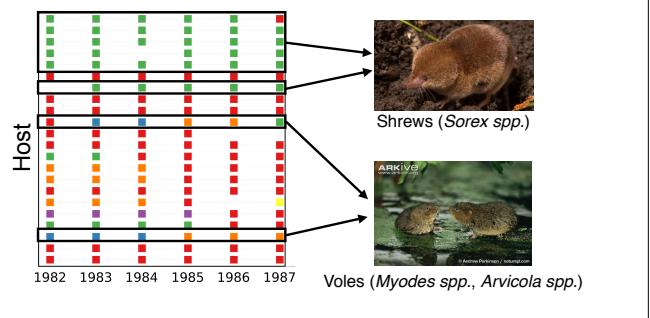
Network flexibility -- community structure evolves in time



Network flexibility -- community structure evolves in time



Network flexibility -- community structure evolves in time





Non-flexible

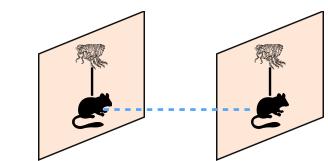


Flexible

- Support consistent parasite assemblages.

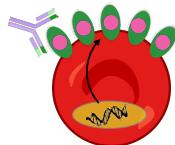
- Support variable parasite assemblages.
- Bridge infections between species and in time.

- Time-dependent distribution of parasites in hosts.



State nodes!

Revealing ecological niches using community detection



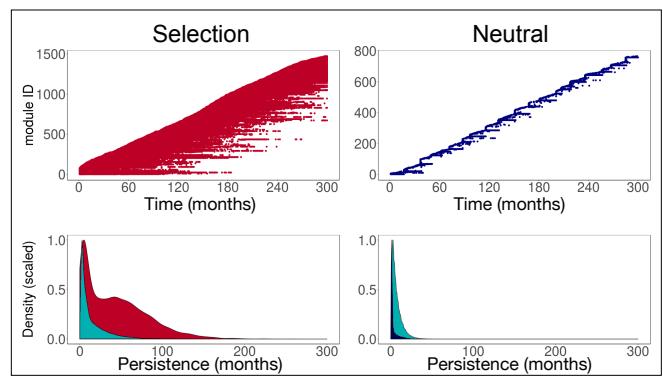
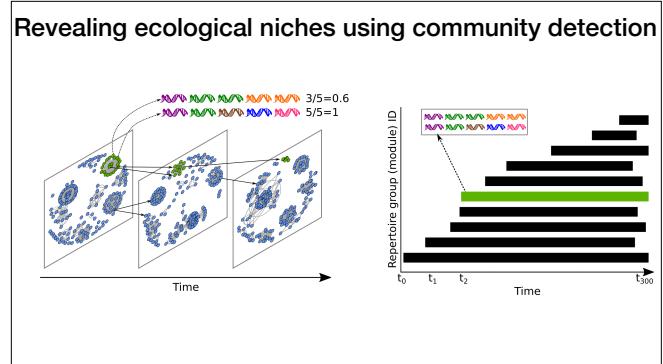
1

2

3

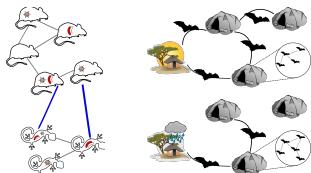
...

60



Applications

- Community ecology
- Biogeography
- Disease ecology
- Movement ecology
- Conservation biology



Key questions

- How do multiple interaction types affect the stability of communities?
- Will a multilayer approach change understanding of ecological concepts (e.g., “key-stone species”)?

Multilayer networks and global change ecology

- How does a focus on whole communities shift our understanding of ecosystem dynamics?
- How do interaction networks change across land-use gradients?
- How do dynamic processes spread across layers?
 - Disease
 - Extinctions and invasions

Hutchinson et al. (in prep)

Challenges

- Quantification of both intra- and inter-layer edges.
 - Common currency for multiple interactions/ processes.
- Large-scale data collection and curation.