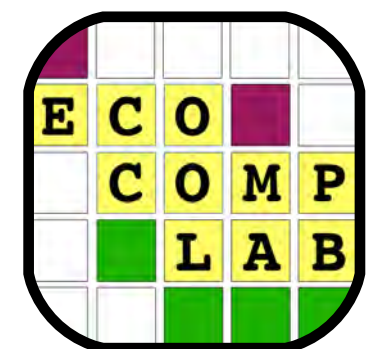
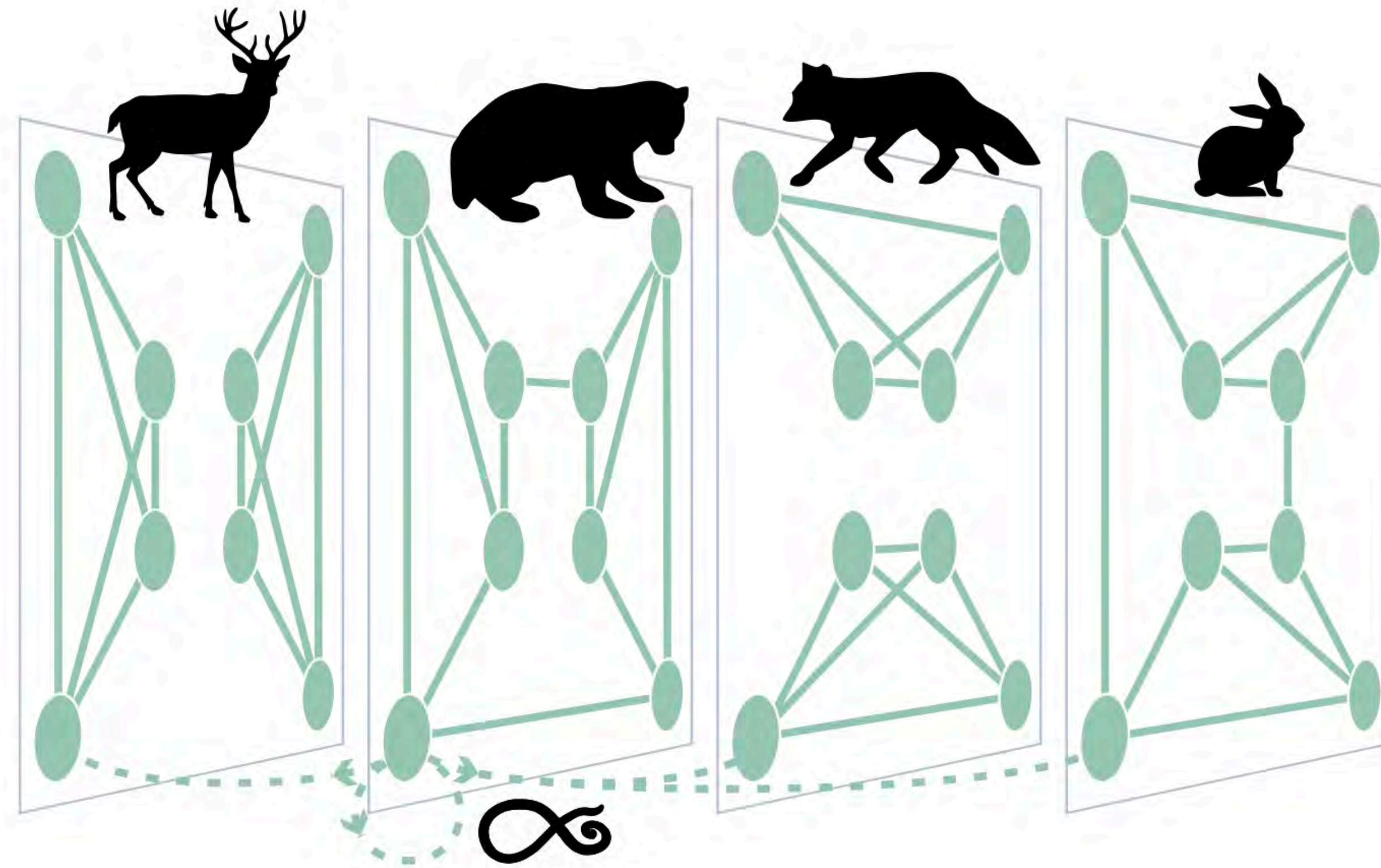


Multilayer networks

Analysis of Ecological - Biological Networks

Prof. Shai Pilosof



ecomplab.com

pilos@post.bgu.ac.il



Ben-Gurion University
of the Negev

Class goals

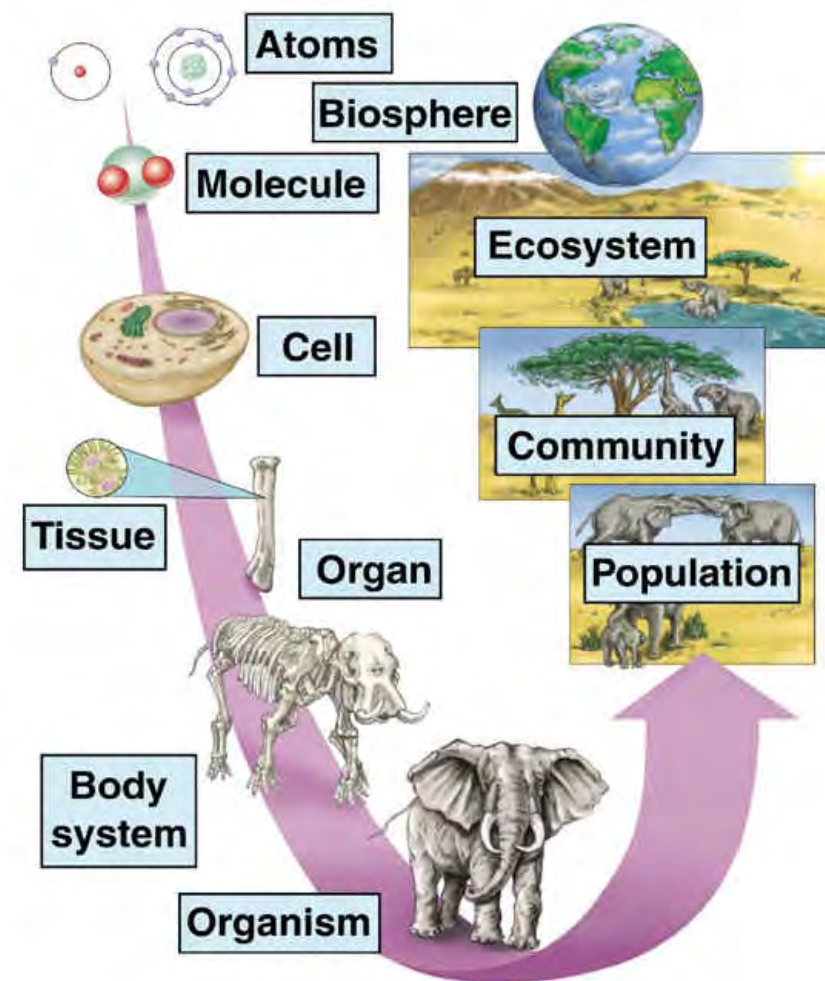
1. Introduce multilayer networks.
2. Emphasize the role of interlayer edges.
3. Provide examples for research questions.

Outline

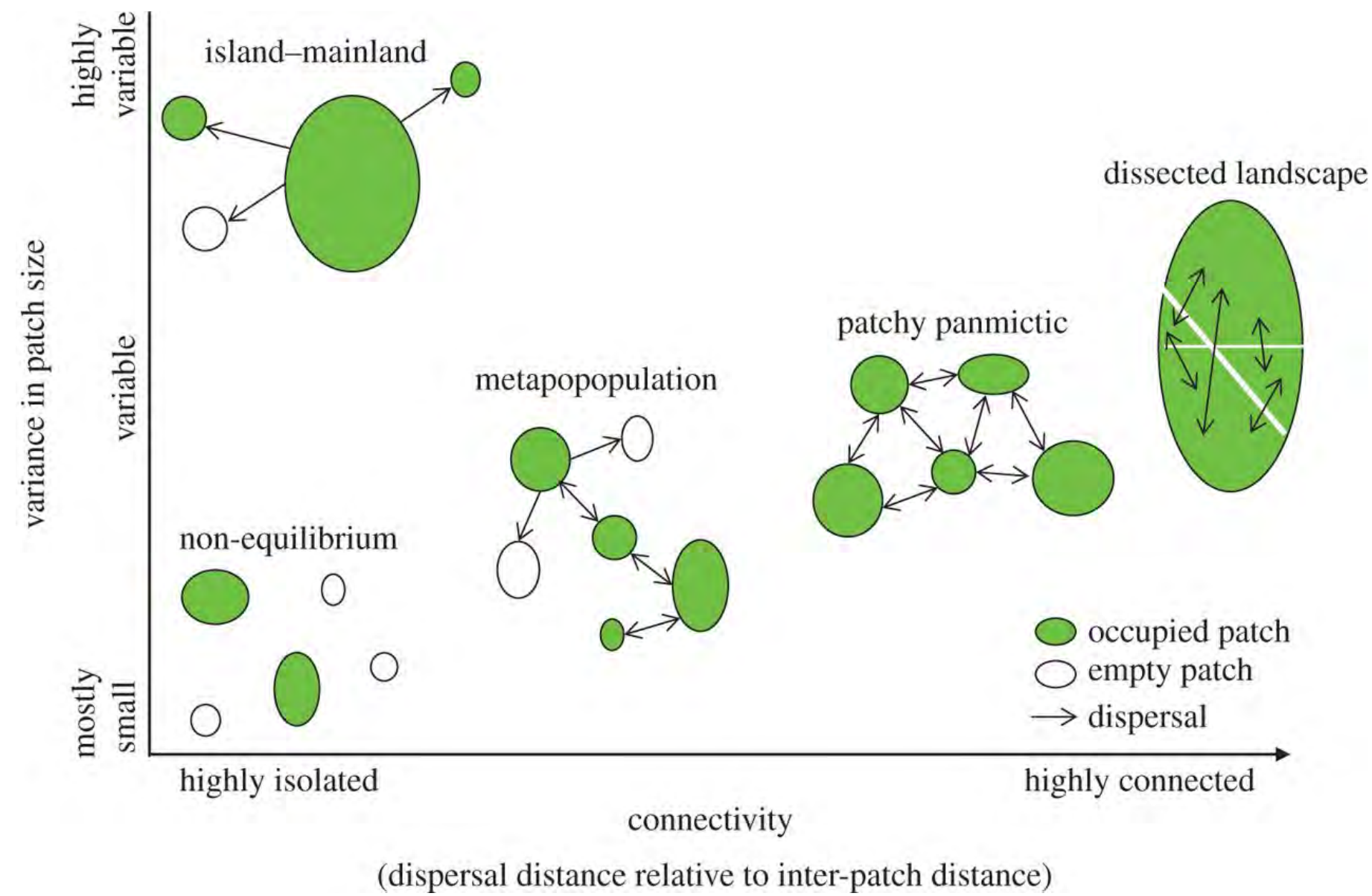
- History of multilayer networks in ecology.
- Definitions and tools.
- Interlayer links.
- Research directions (what can we study?)

Higher dimensionality in ecology

Raven/Berg, Environment, 3/e
Figure 4.1



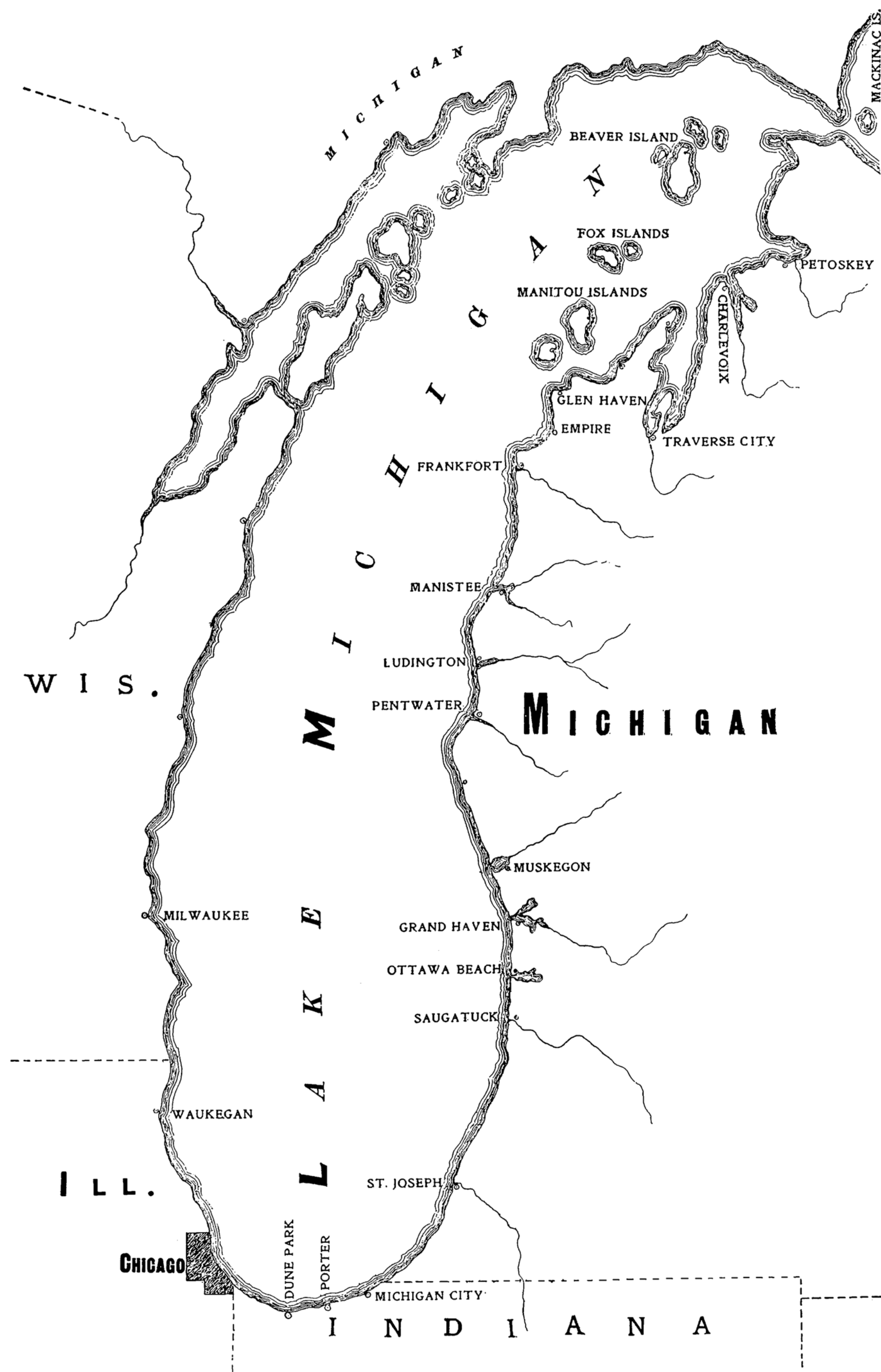
Harcourt, Inc.



Organizational
hierarchy

Space / time

Multiple kinds
of interactions



“...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.**”

Data

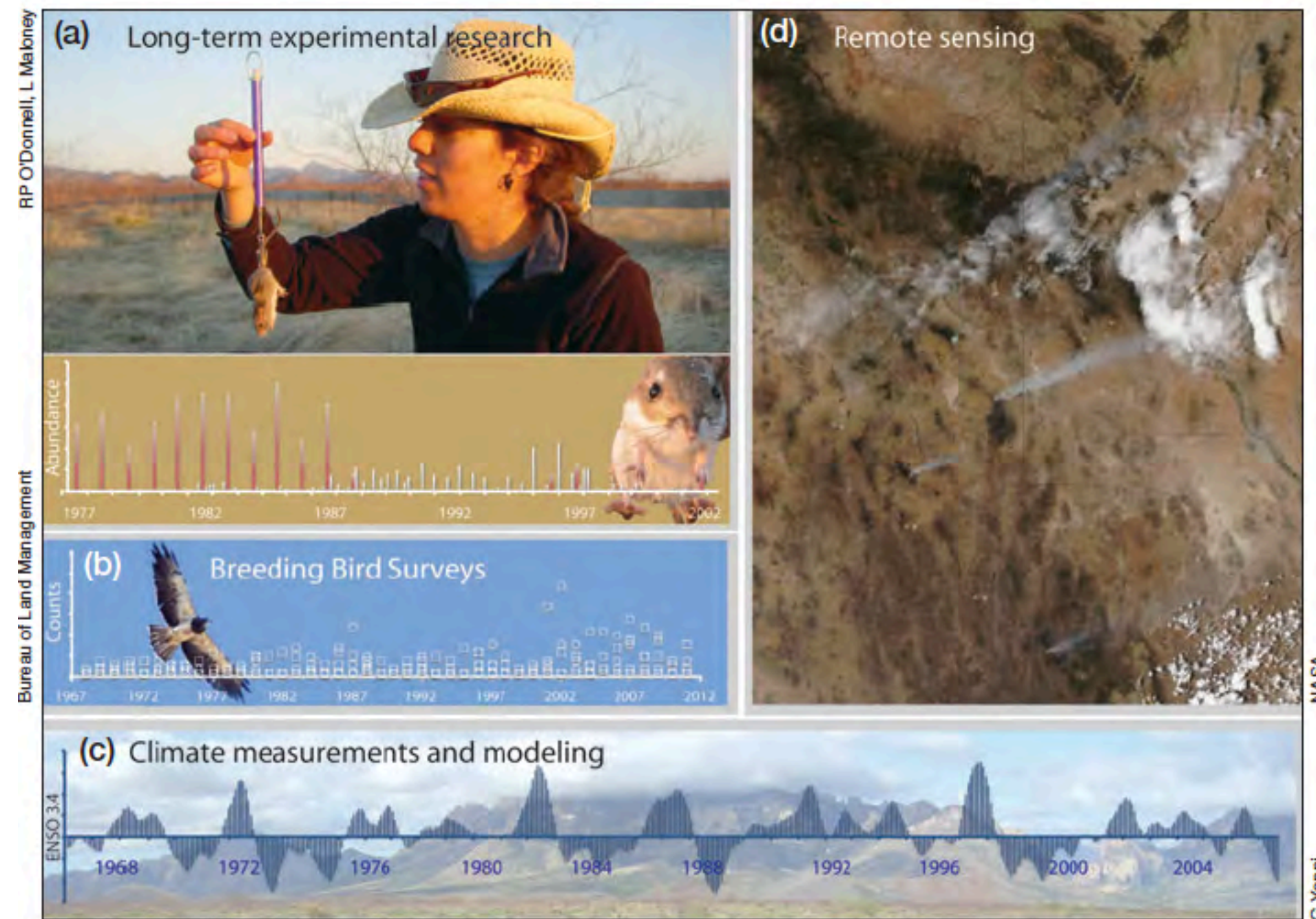


Figure from Hampton et al. 2013

Tools

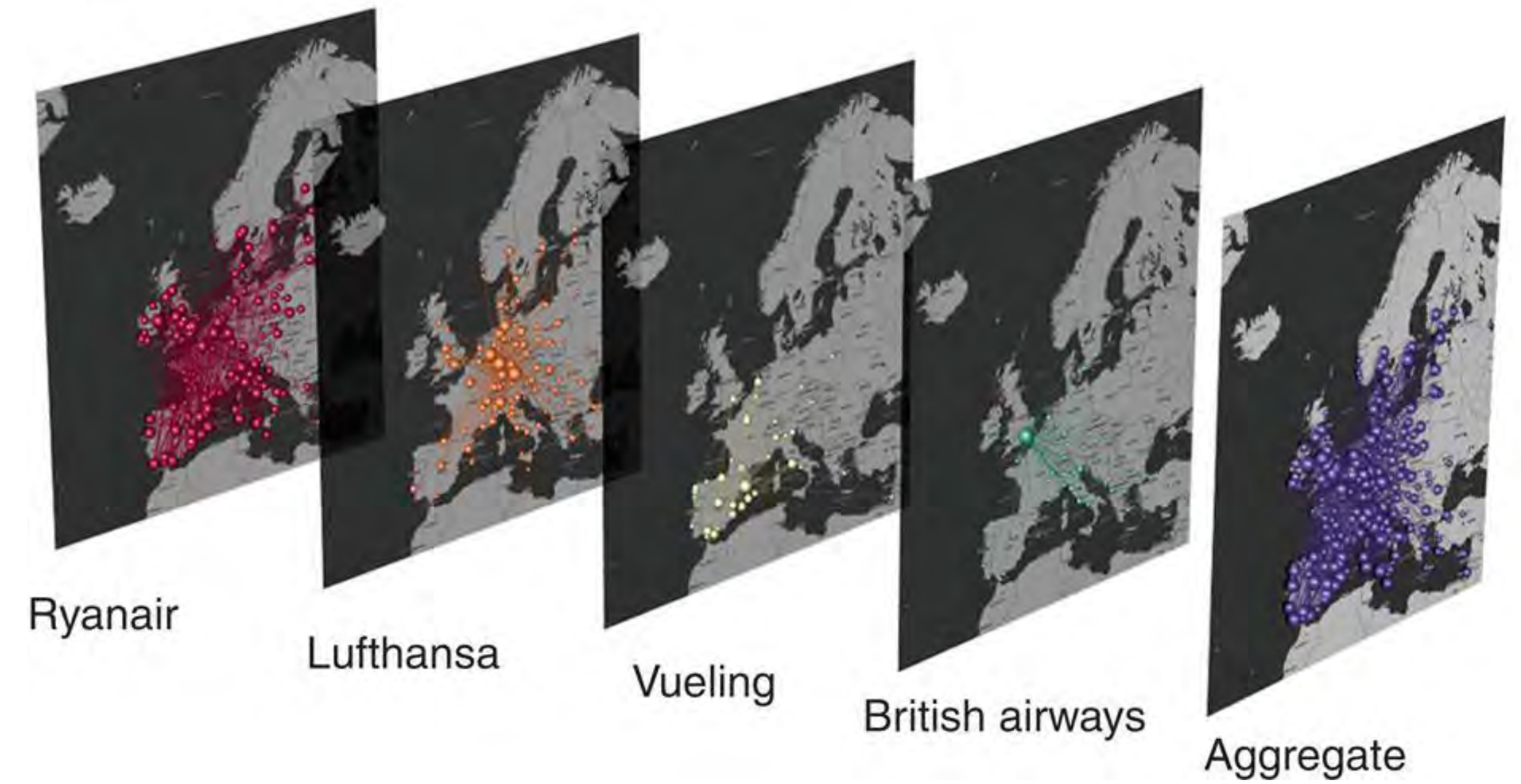


Figure from Cardillo et al. 2014

First explorations of (modern) ecological multilayer networks

Ecological Monographs, 60(3), 1990, pp. 331–367
© 1990 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, Austin, Texas 78712 USA*

OIKOS 48: 280–288. Copenhagen 1987

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

R. L. Kitching

Ecological Monographs, 61(3), 1991, pp. 267–298
© 1991 by the Ecological Society of America

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

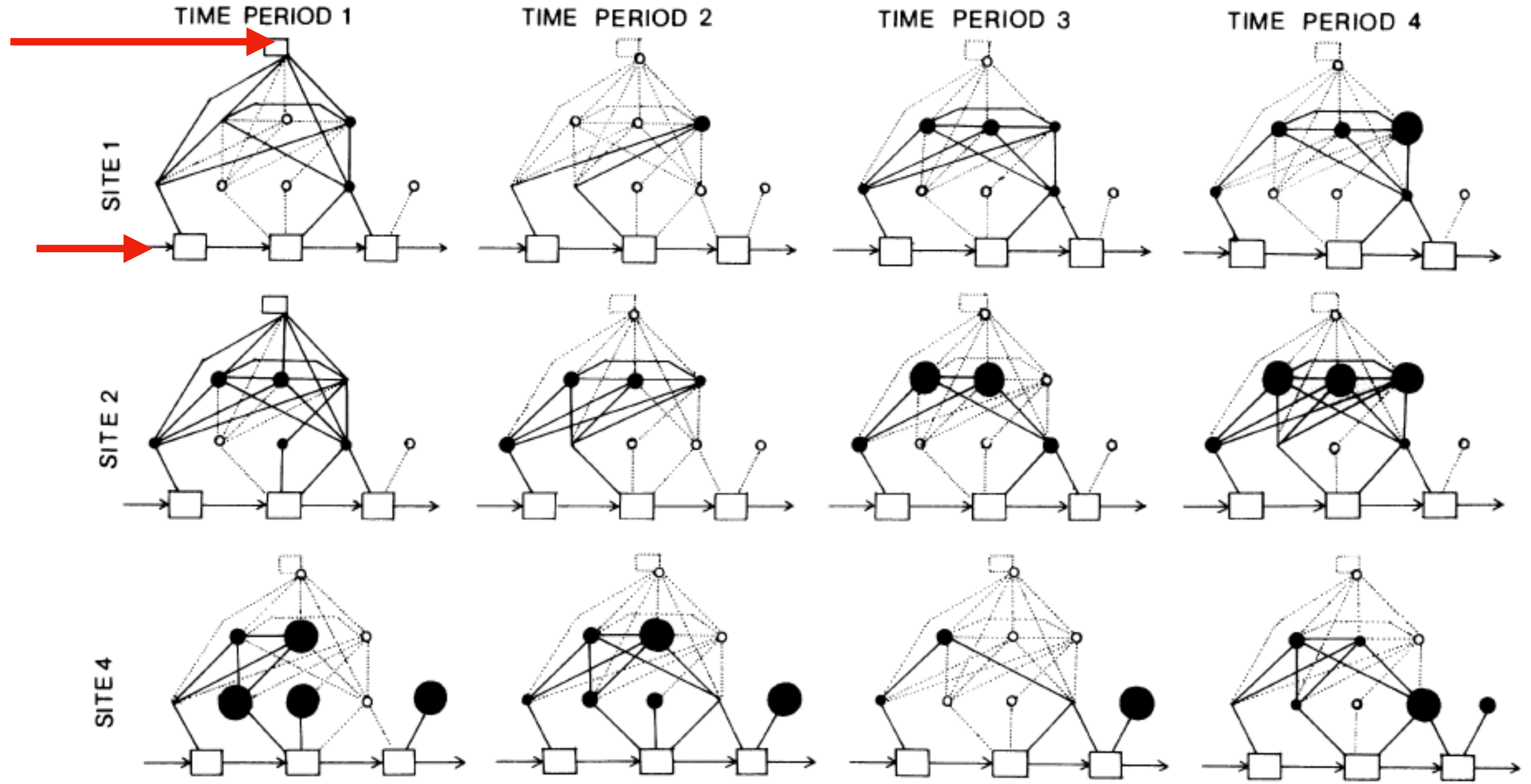
OIKOS 55: 299–311. Copenhagen 1989

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

Philip H. Warren

Frog

Detritus



Consumer (species number)

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



Consumer as adult



Consumer as larva

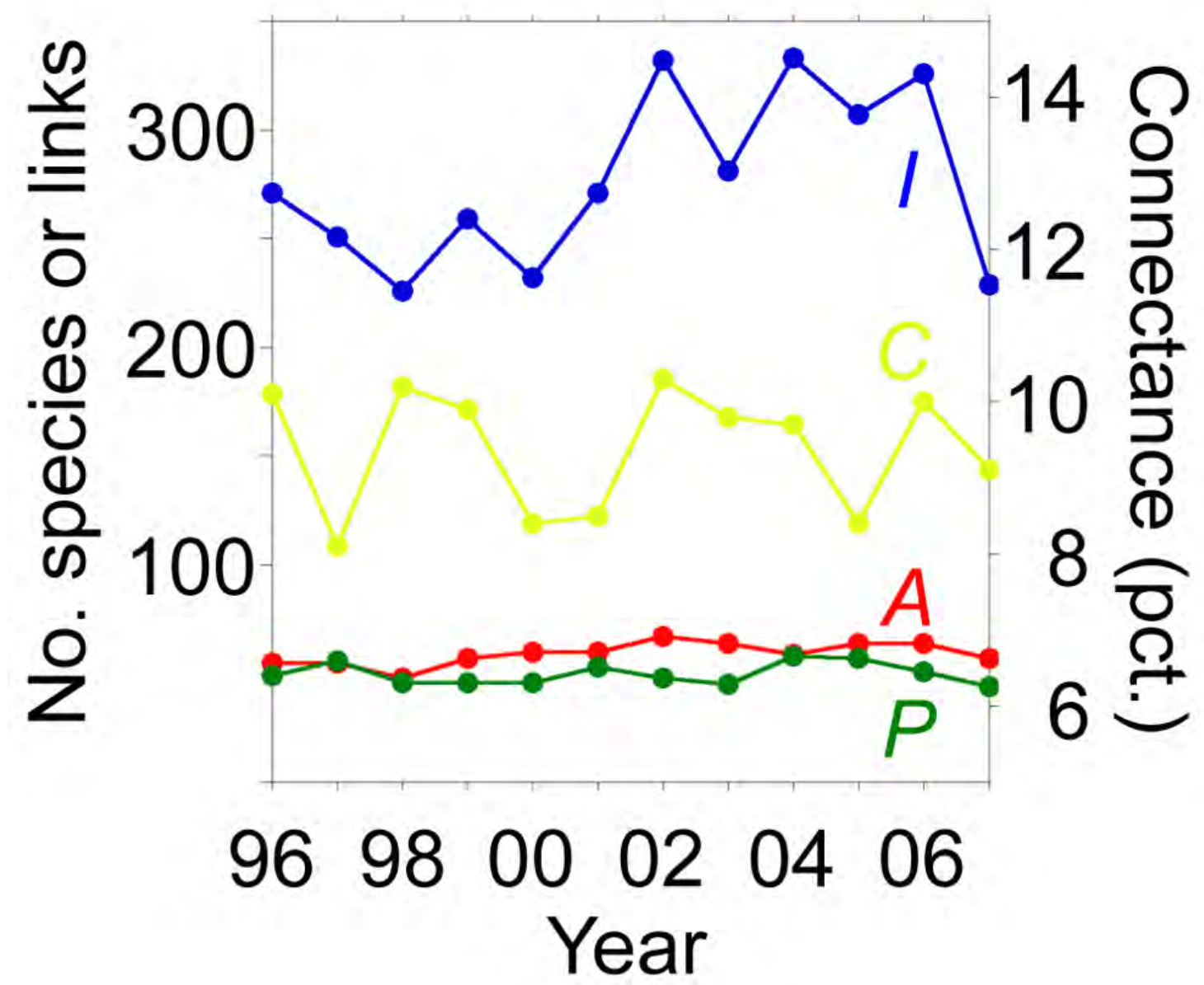
TEMPORAL VARIATION IN FOOD WEB STRUCTURE: 16 EMPIRICAL CASES¹

KENNETH SCHOENLY AND JOEL E. COHEN

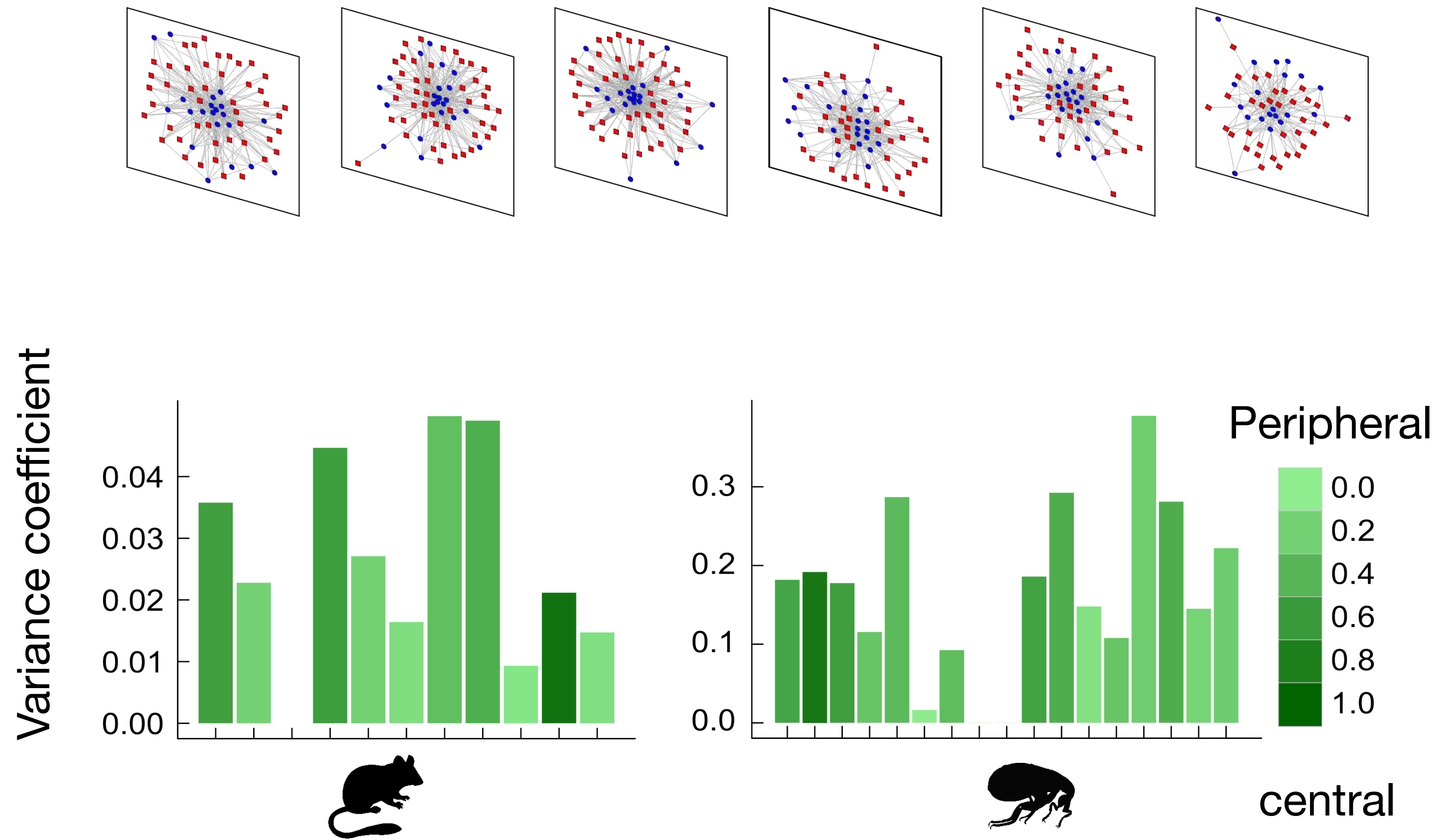
Rockefeller University, 1230 York Avenue, Box 20, New York, New York 10021-6399 USA

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.

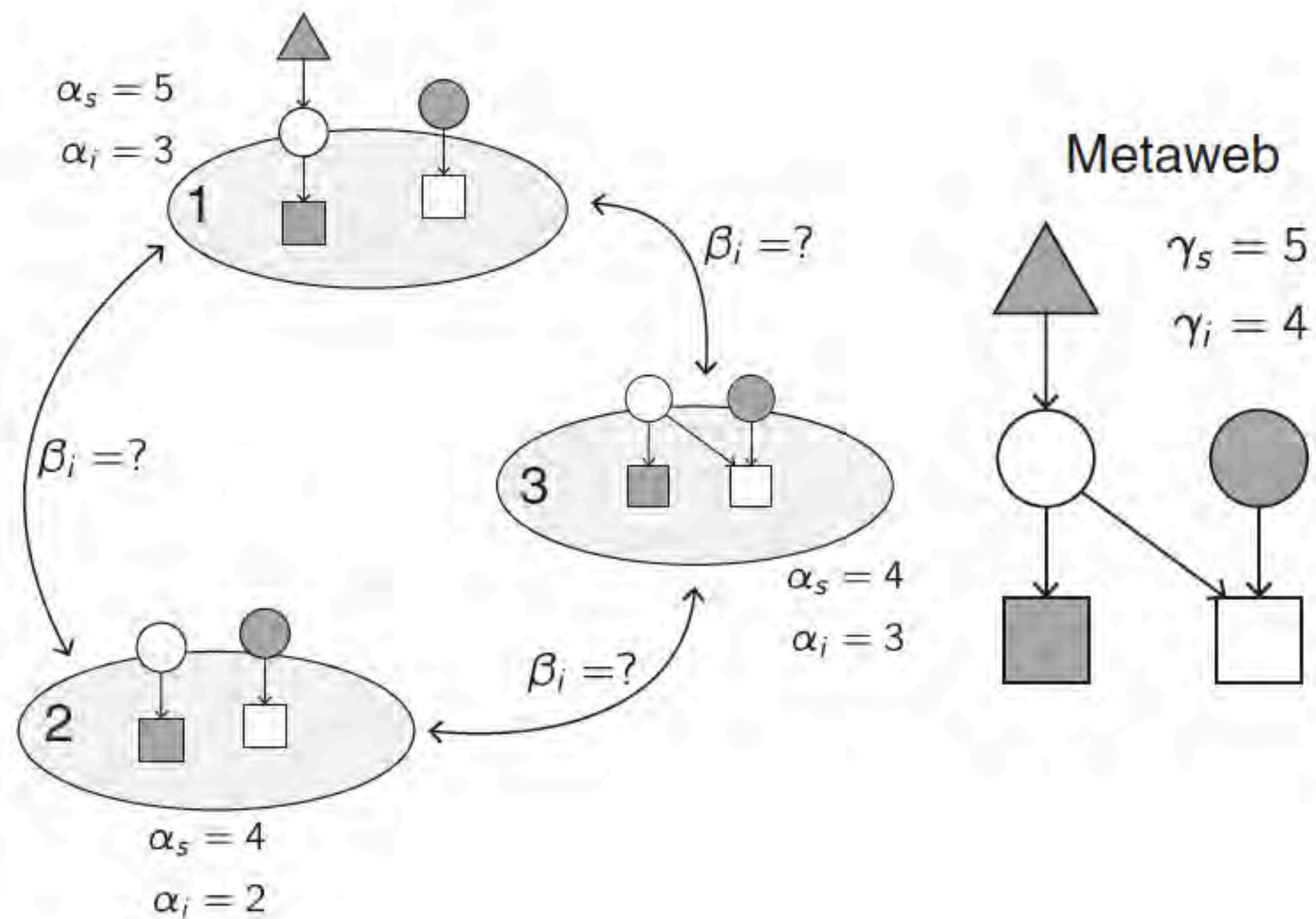


Olesen et al 2011, PLoS One

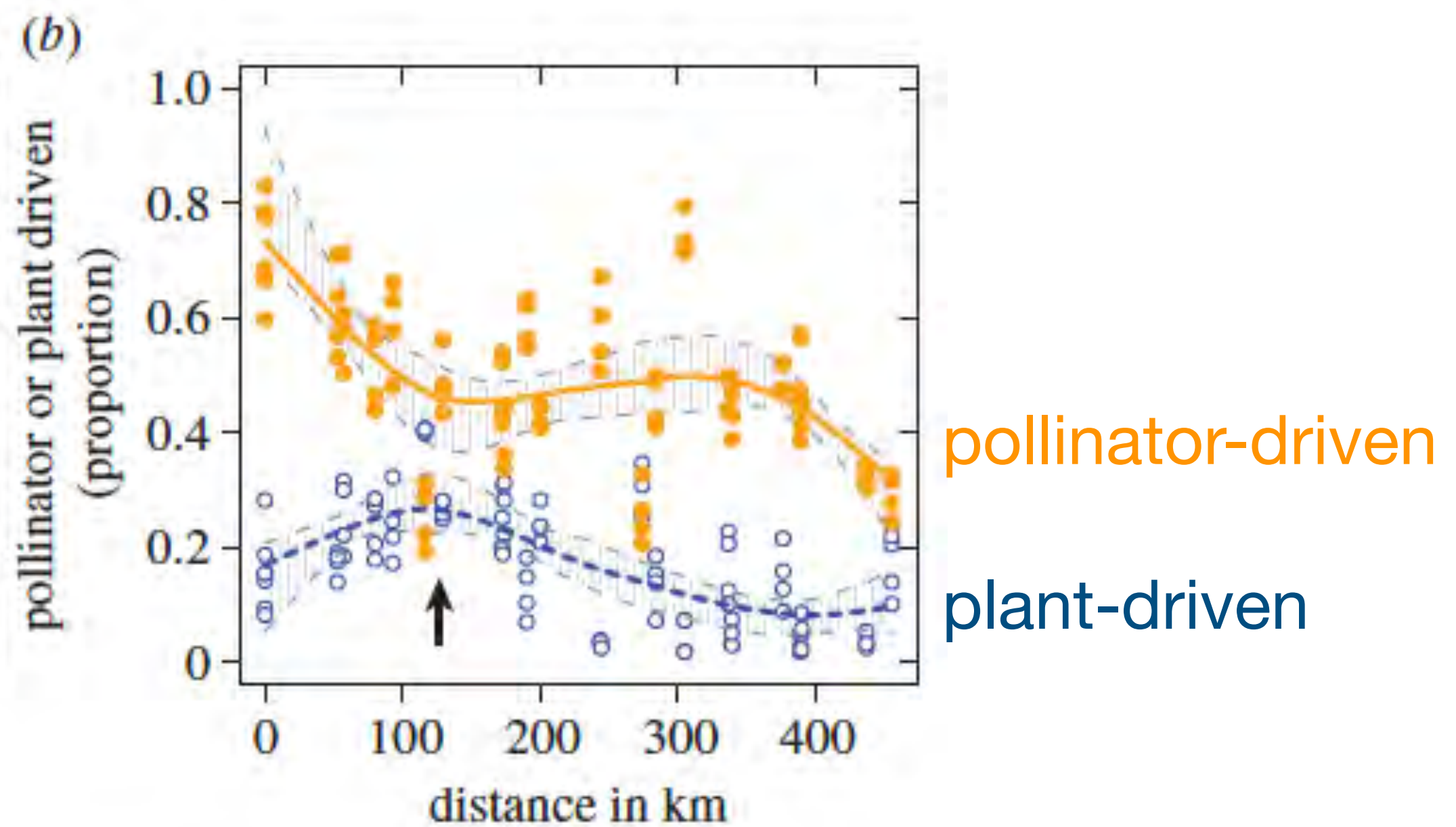
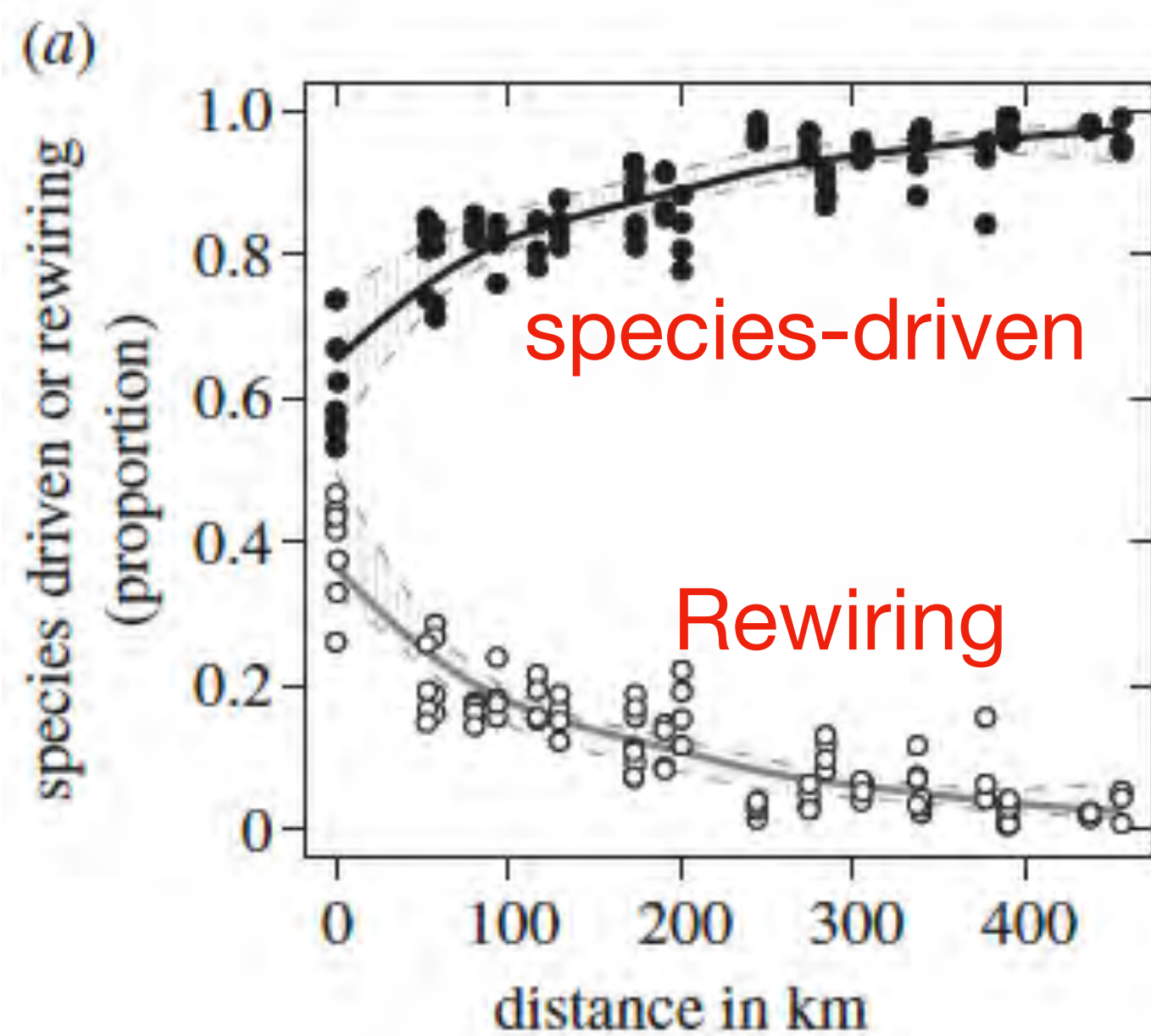
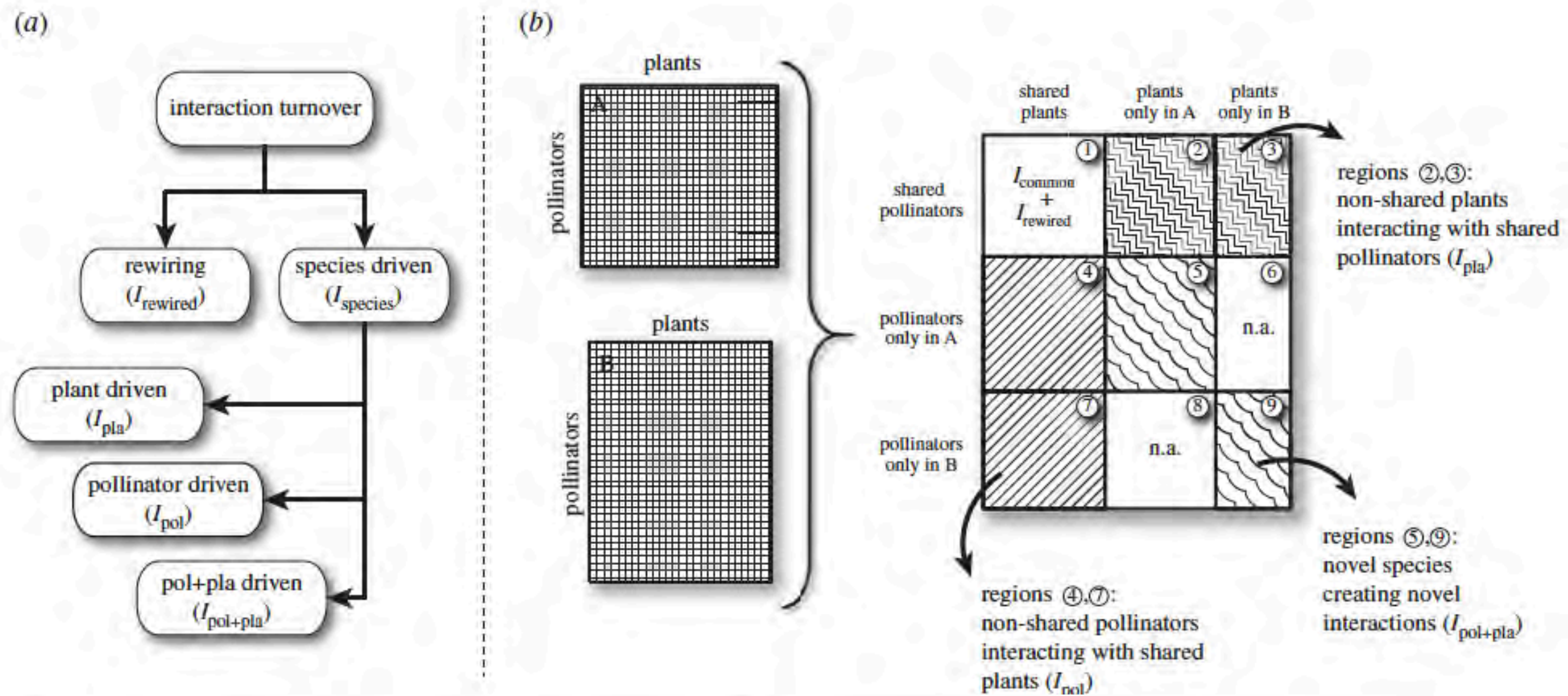


Pilosof et al 2013, J. Anim. Ecol.

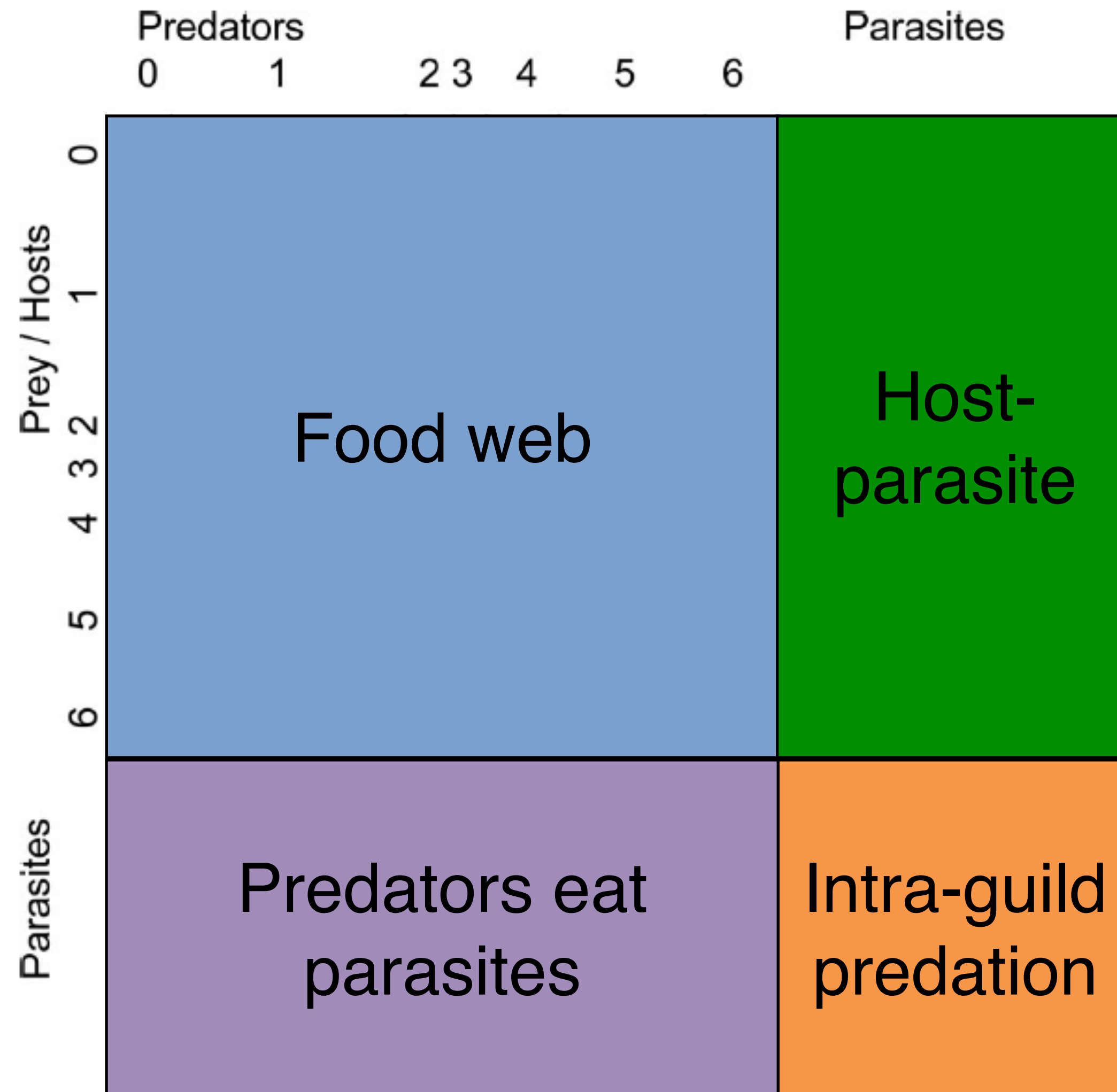
Species and interaction turnover in space and time



Measure	Definition
β_S	Dissimilarity in the species composition of communities
β_{OS}	Dissimilarity of interactions established between species common to both realisations
β_{WN}	Dissimilarity of interactions
β_{ST}	Dissimilarity of interactions due to species turnover
β'_{OS}	Dissimilarity between a local network and its counterpart in the metaweb
β_{ST}/β_{WN}	Contribution of species dissimilarity to network dissimilarity



Merging multiple kinds of interactions



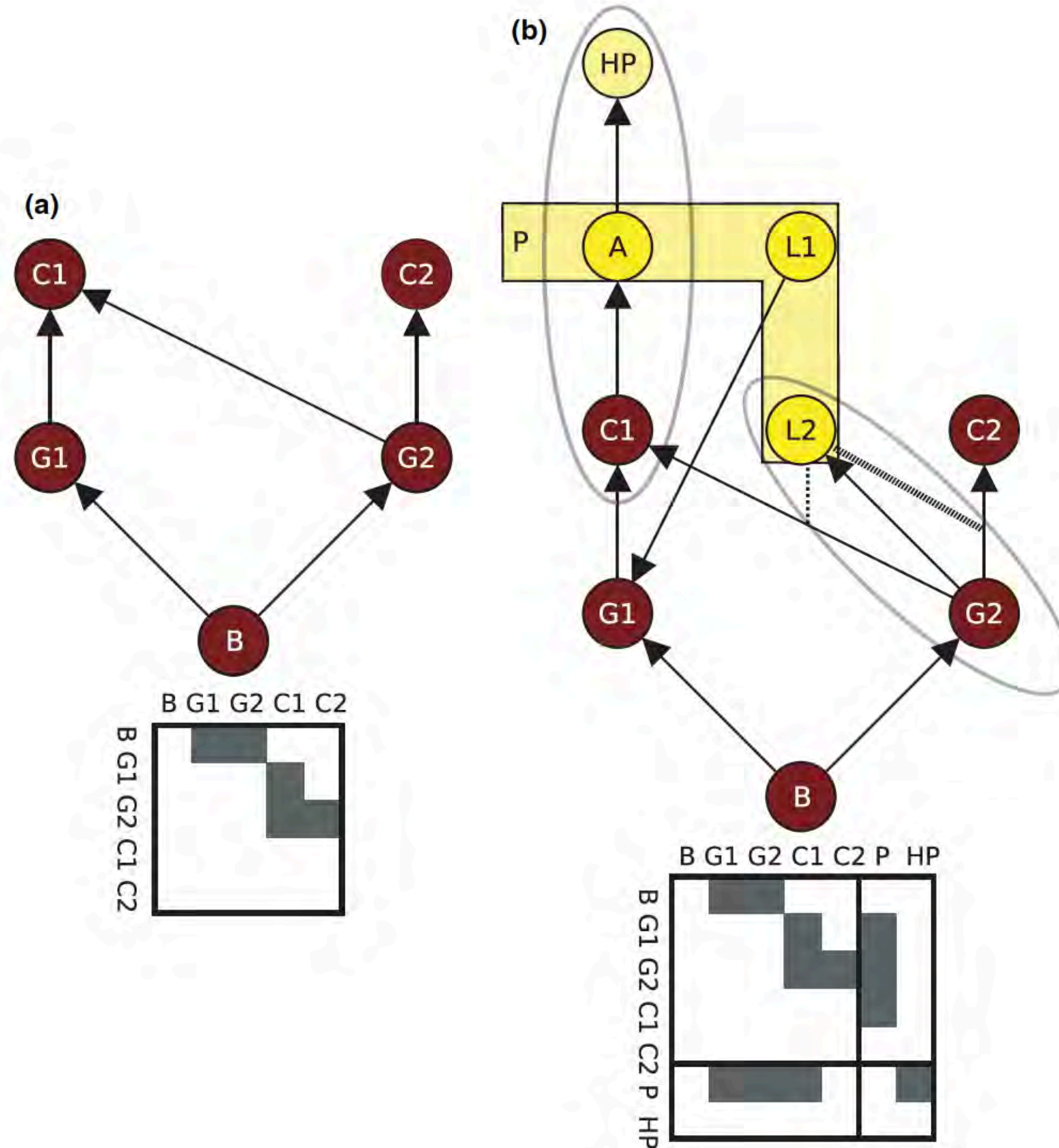
Including parasites changes the structure of the food web

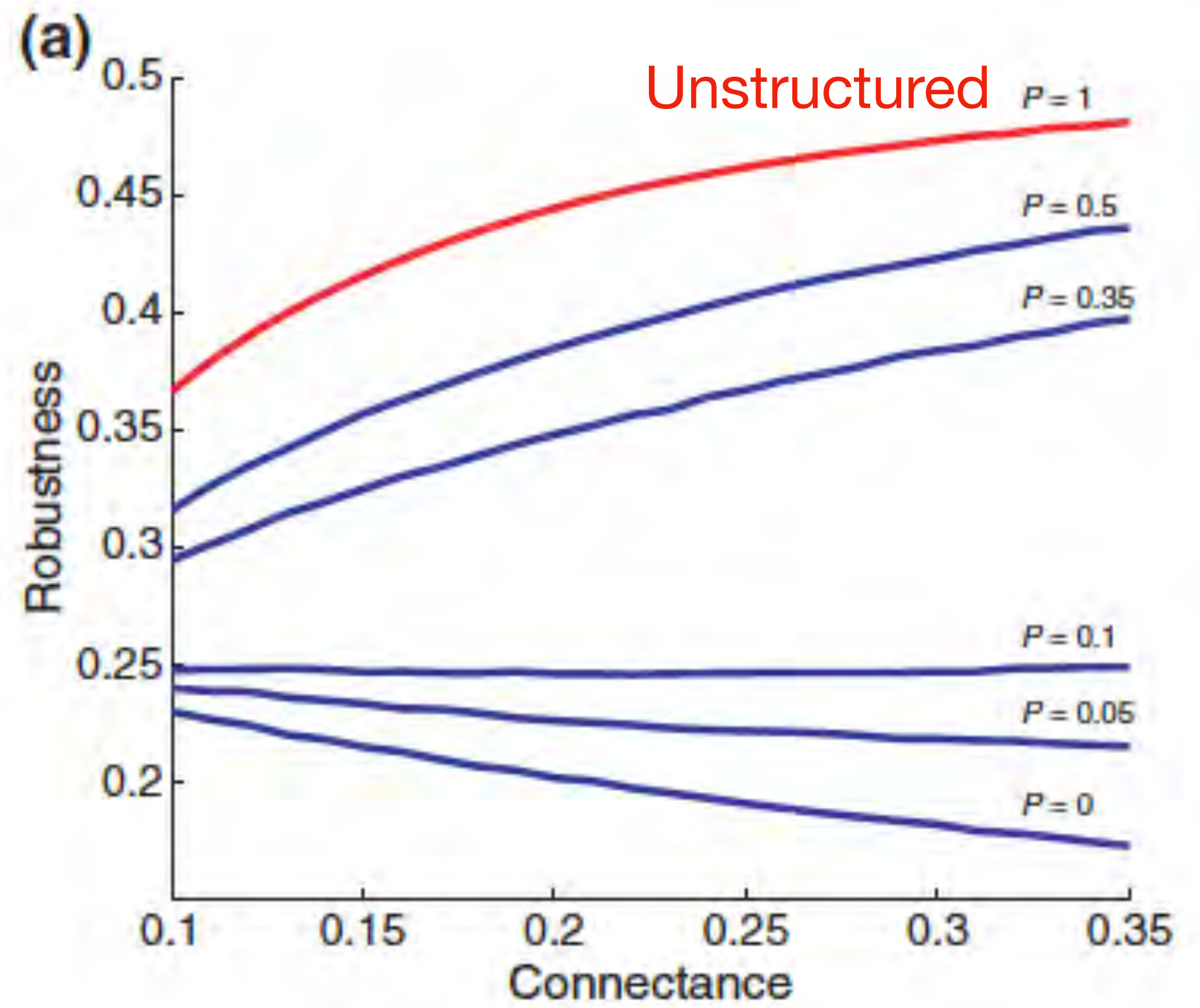
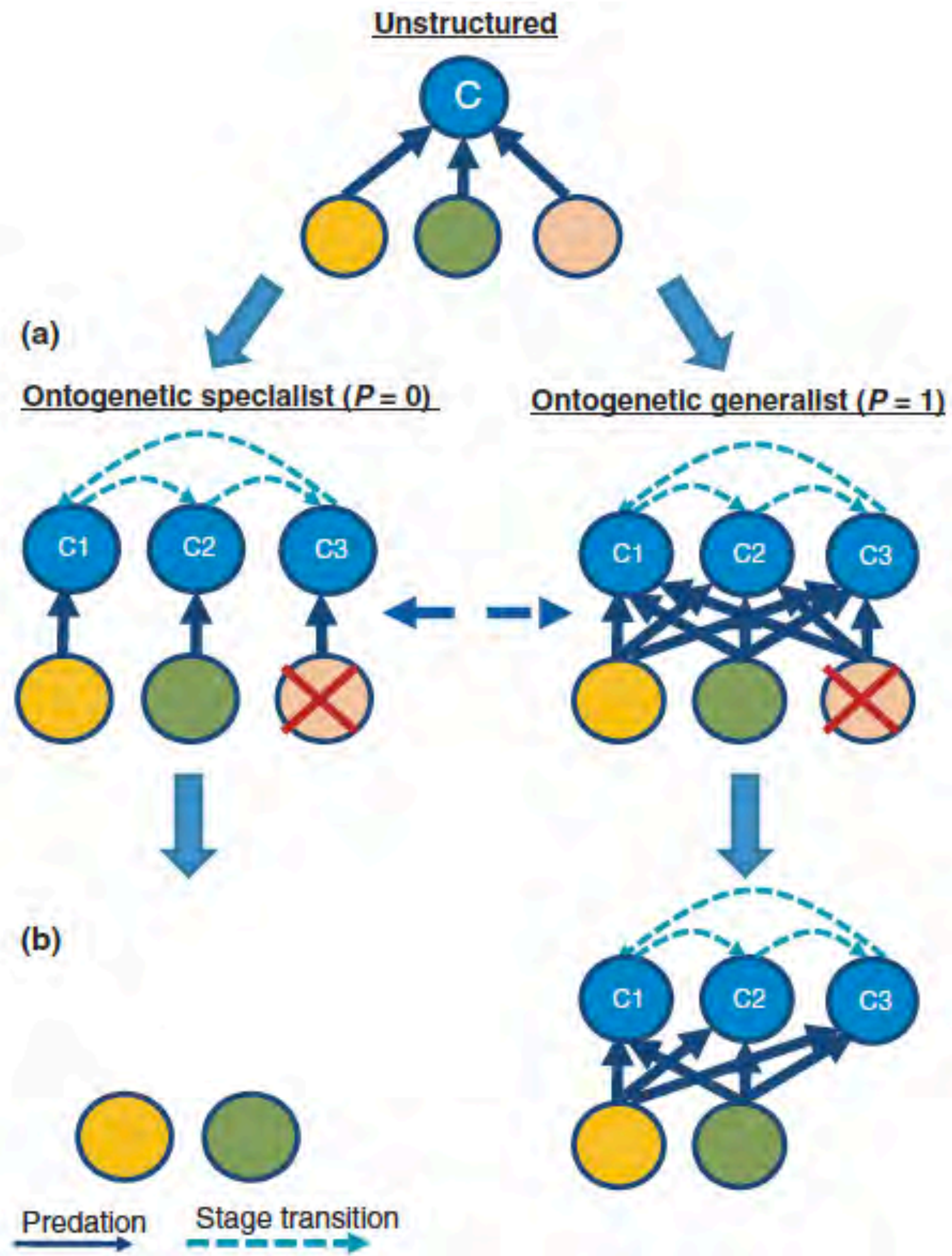
How to include parasites?
Multiple life stages?

IDEA AND PERSPECTIVE

Parasites in food webs: the ultimate missing links

Kevin D. Lafferty,^{1*} Stefano Allesina,² Matias Arim,^{3,4} Cherie J. Briggs,⁵ Giulio De Leo,⁶ Andrew P. Dobson,⁷ Jennifer A. Dunne,^{8,9} Pieter T. J. Johnson,¹⁰ Armand M. Kuris,⁵ David J. Marcogliese,¹¹ Neo D. Martinez,^{2,9} Jane Memmott,¹² Pablo A. Marquet,^{4,13,14} John P. McLaughlin,⁵ Erin A. Mordecai,⁵ Mercedes Pascual,¹⁴ Robert Poulin¹⁵ and David W. Thieltges¹⁵





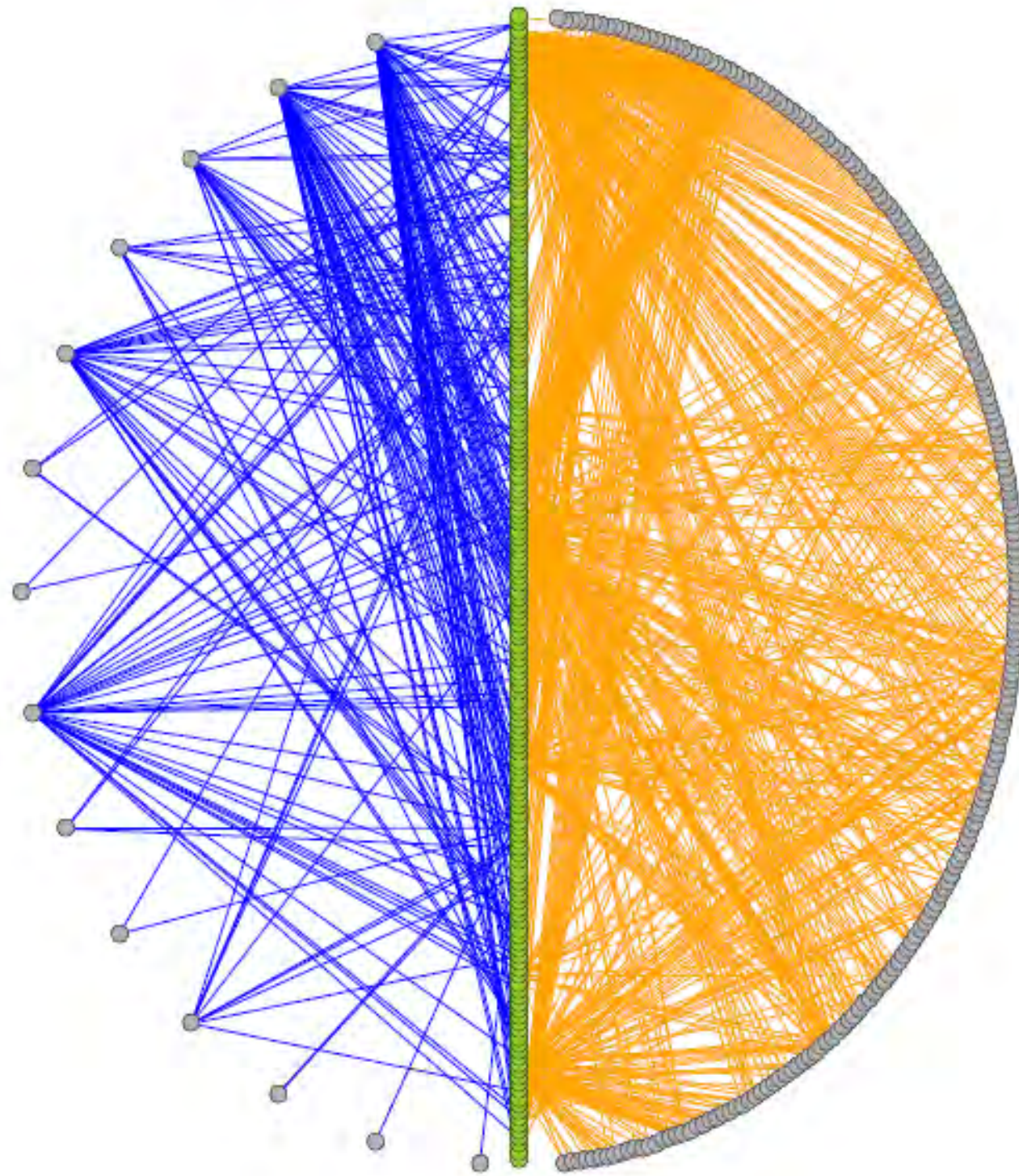


Diversity in a complex ecological network with two interaction types

Antagonistic

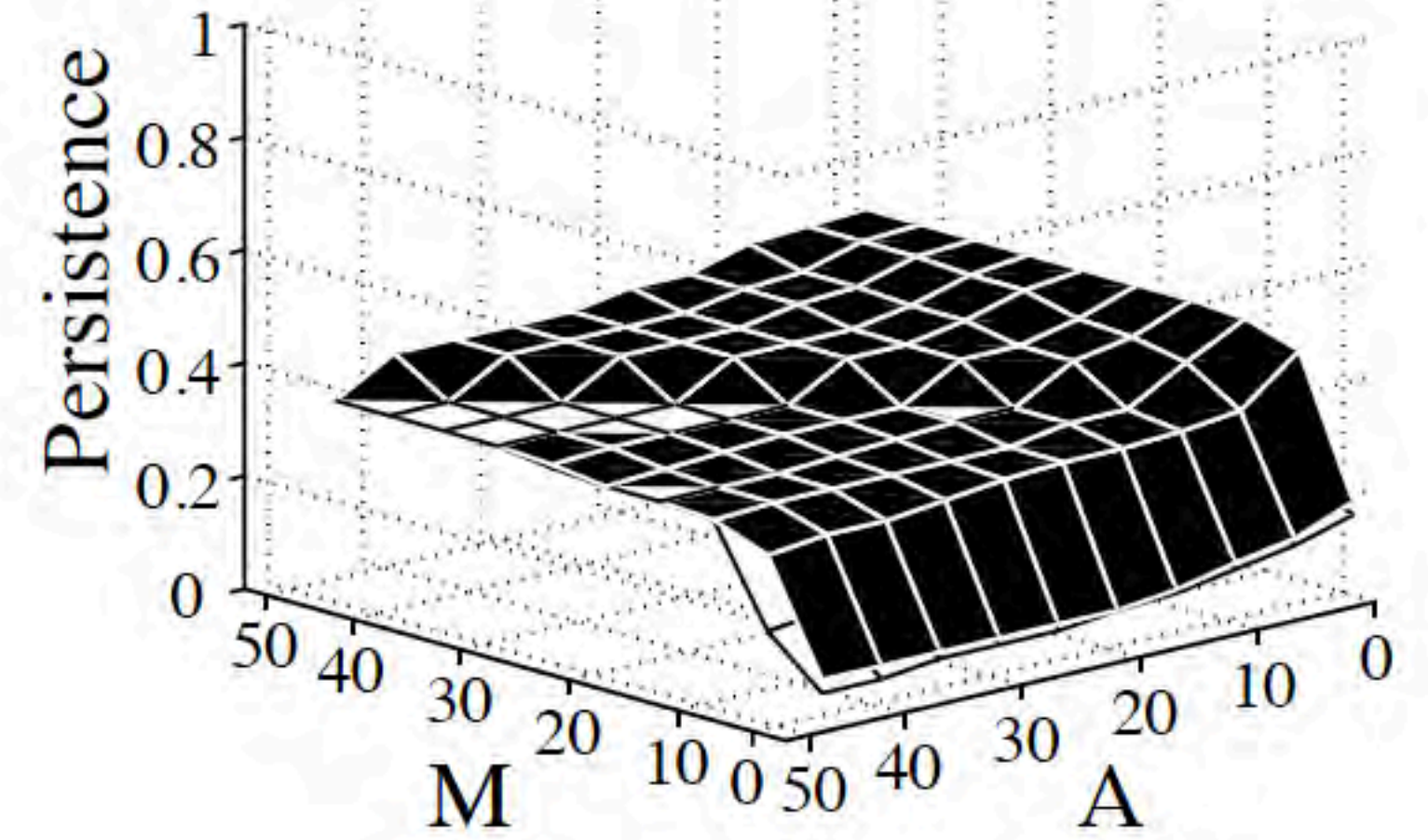
Plants

Mutualistic

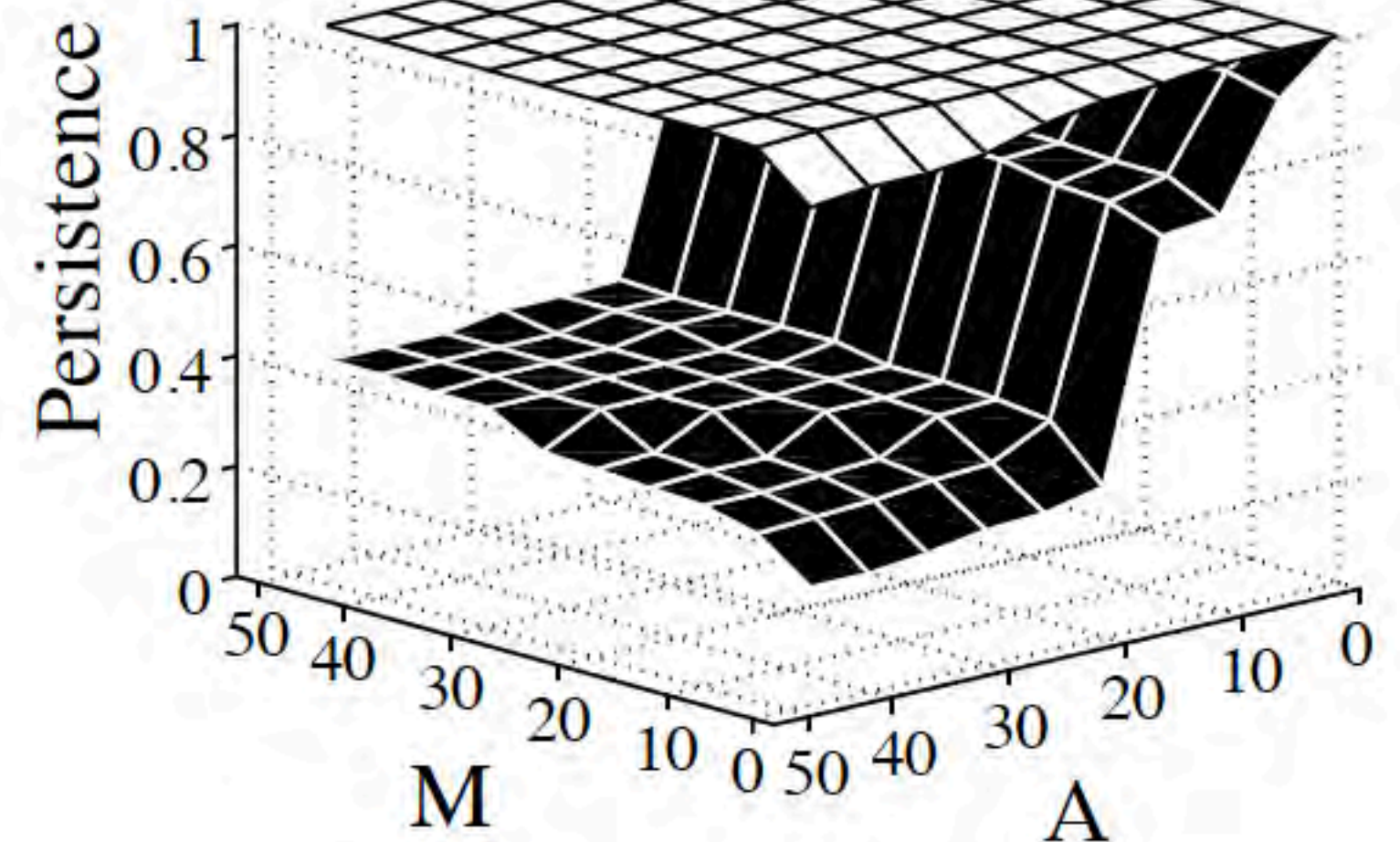


Doñana Biological Reserve, Spain

(e) $r = 0.001$



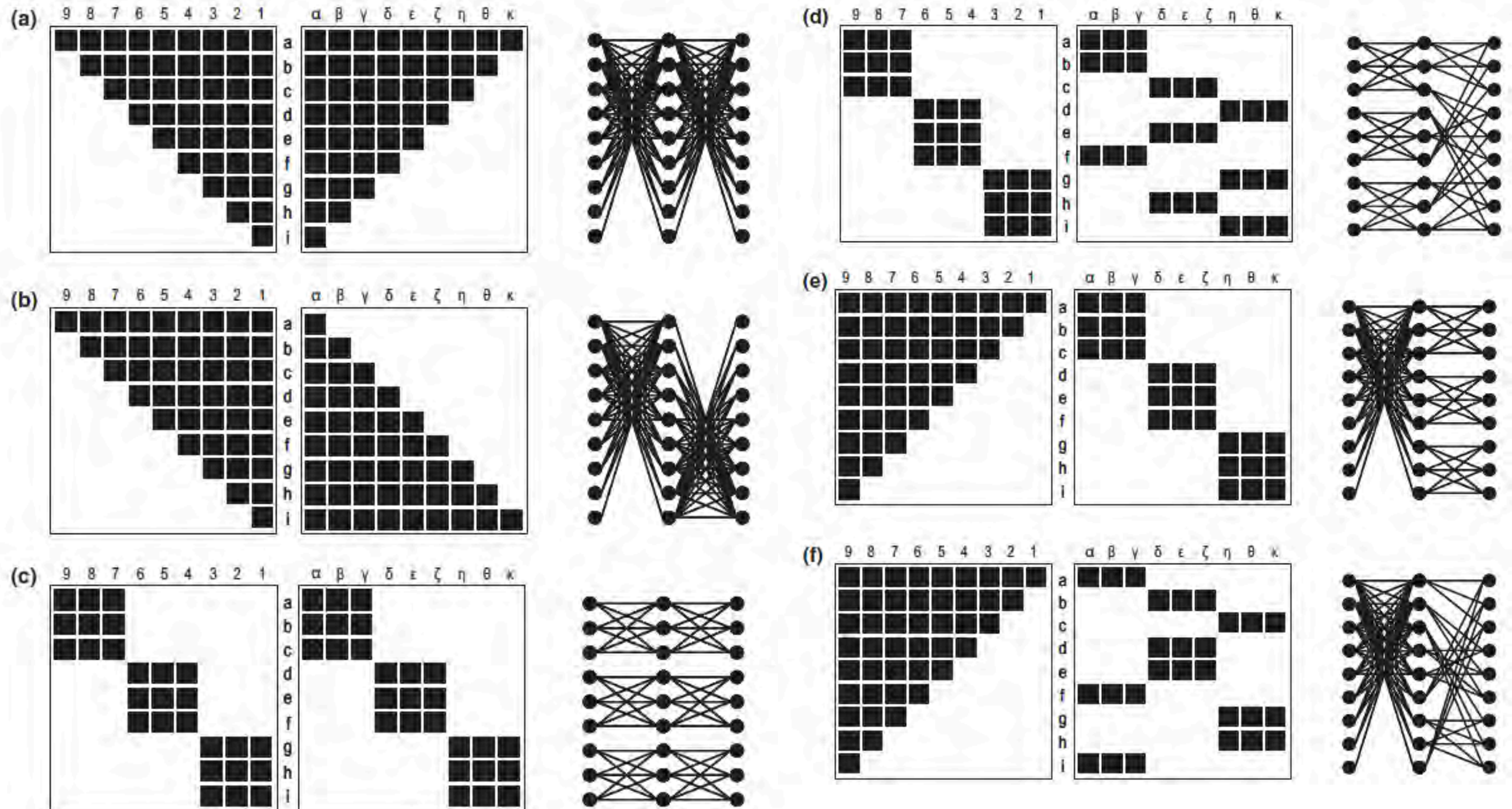
(f) $r = 0.01$



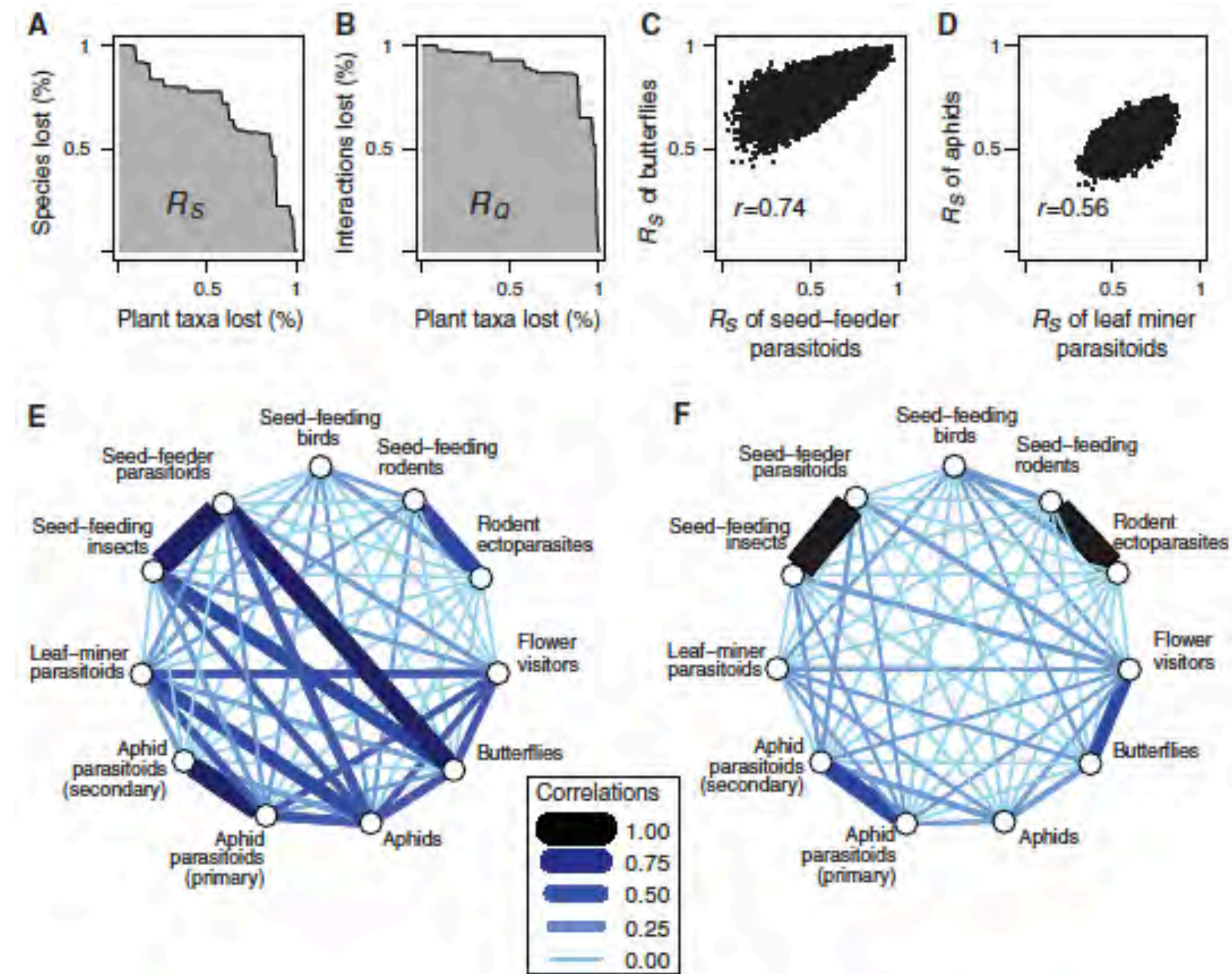
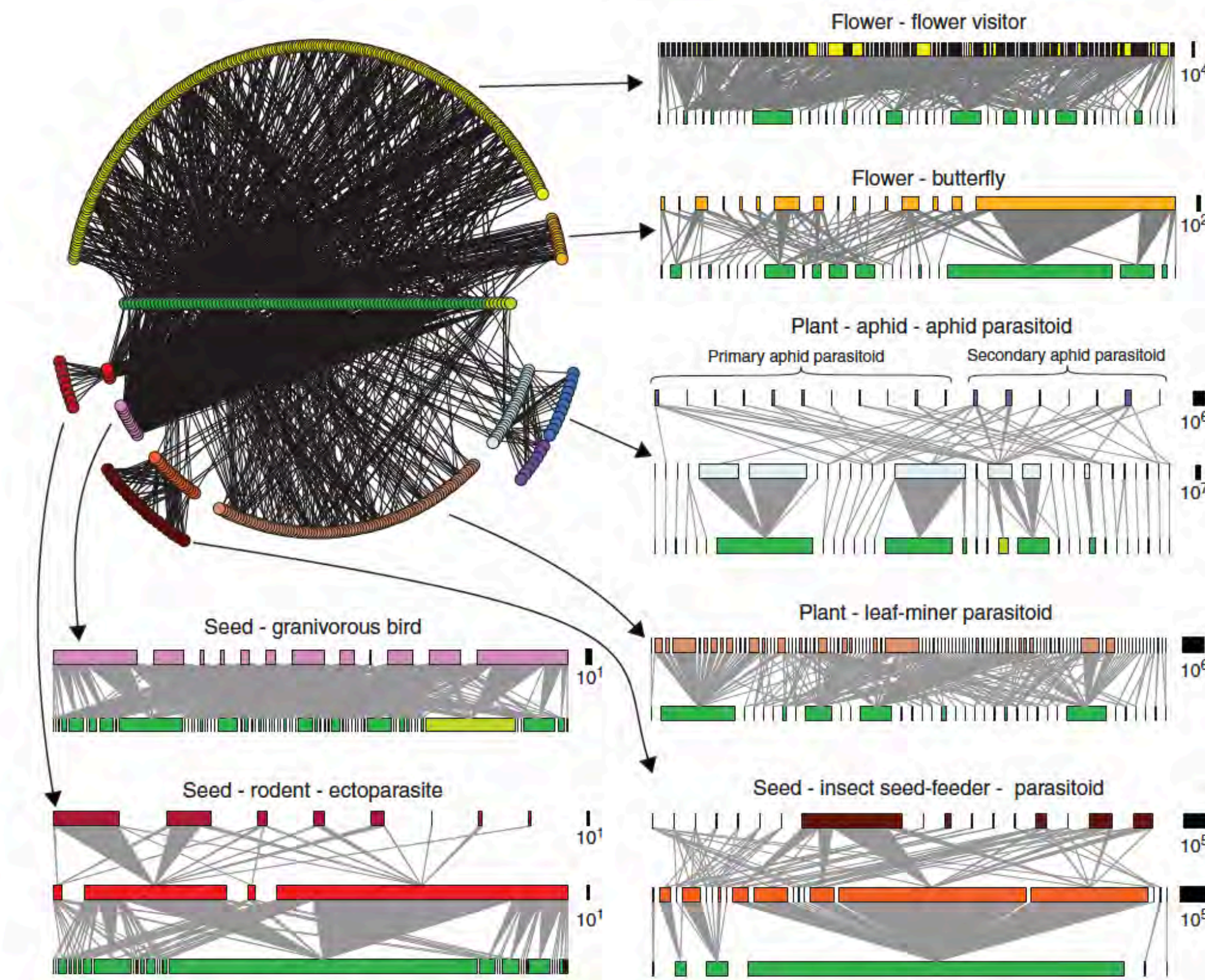
REVIEW AND SYNTHESIS

The ecological and evolutionary implications of merging different types of networks

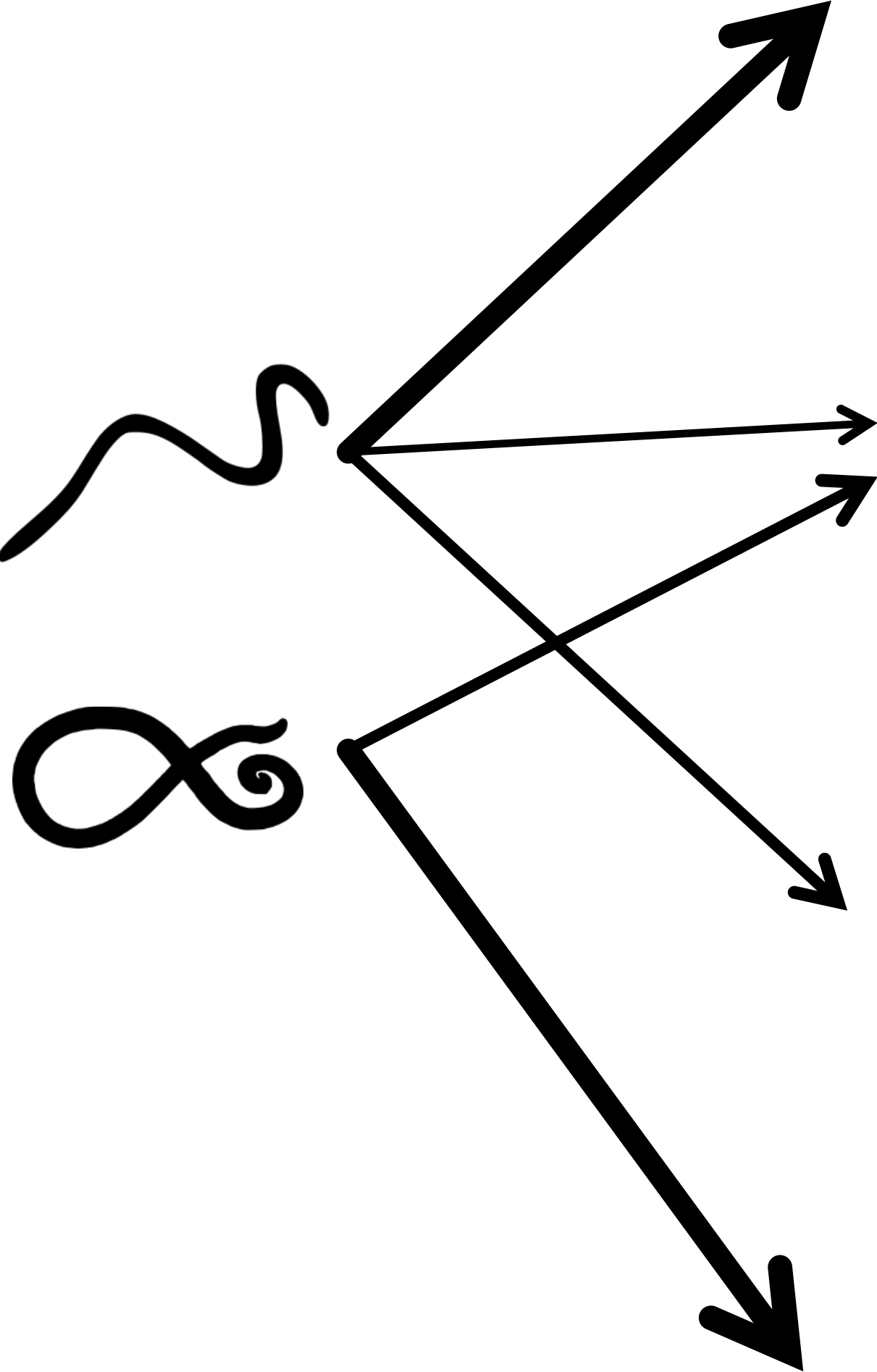
Colin Fontaine,^{1*} Paulo R. Guimarães Jr.,² Sonia Kéfi,³ Nicolas Loeuille,^{4,5} Jane Memmott,⁶ Wim H van der Putten,^{7,8} Frank J. F. van Veen⁹ and Elisa Thébault¹⁰



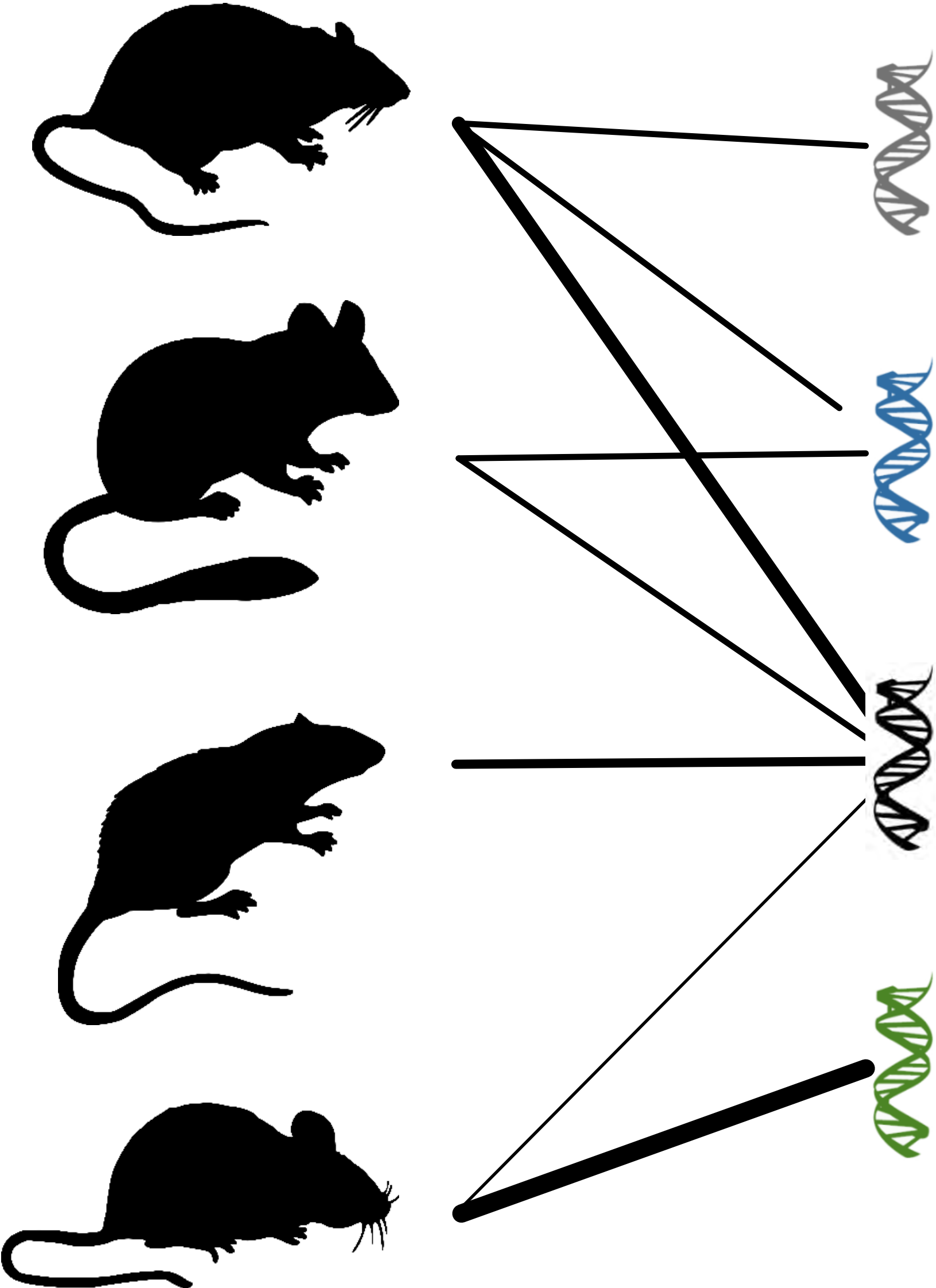
Multiple interaction types and network robustness

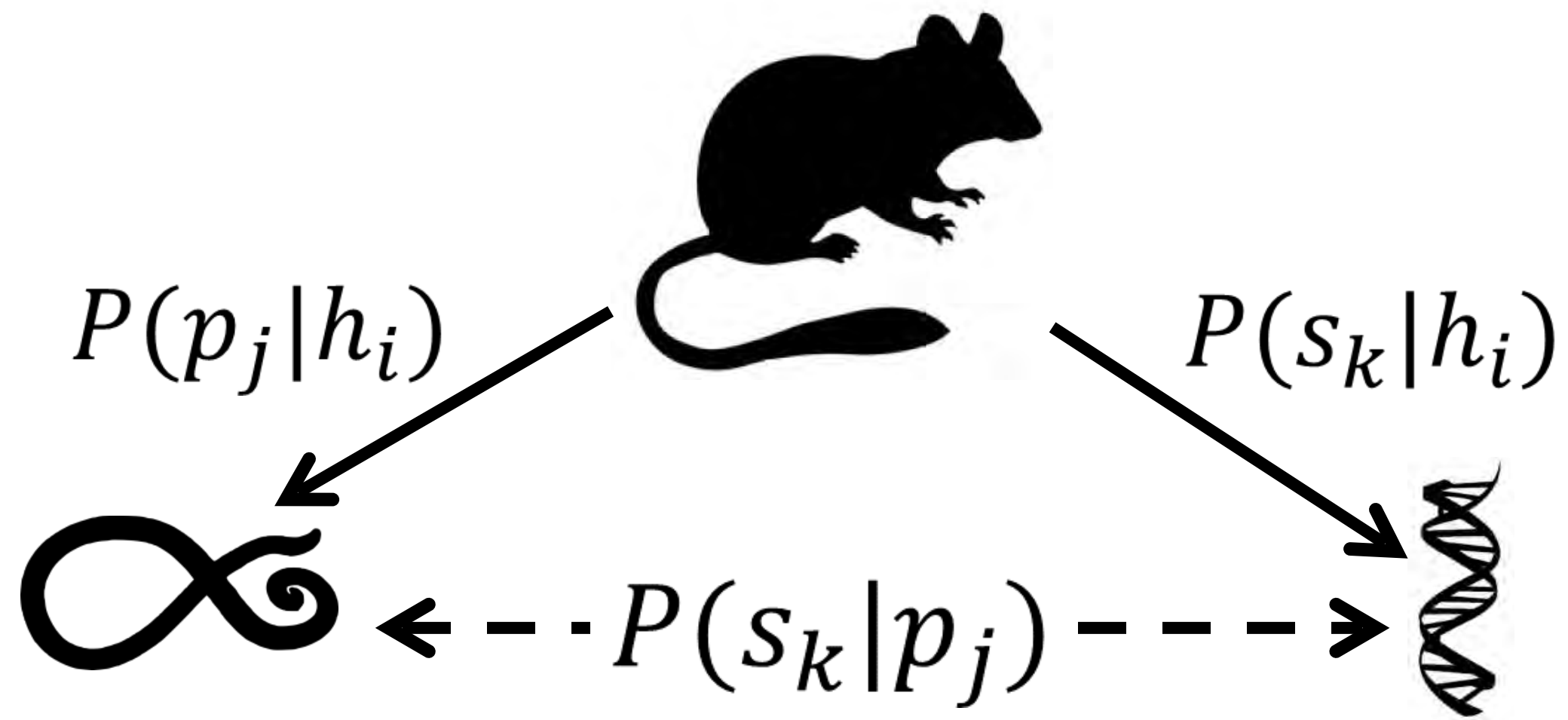


Ecological network



Immunogenetic network



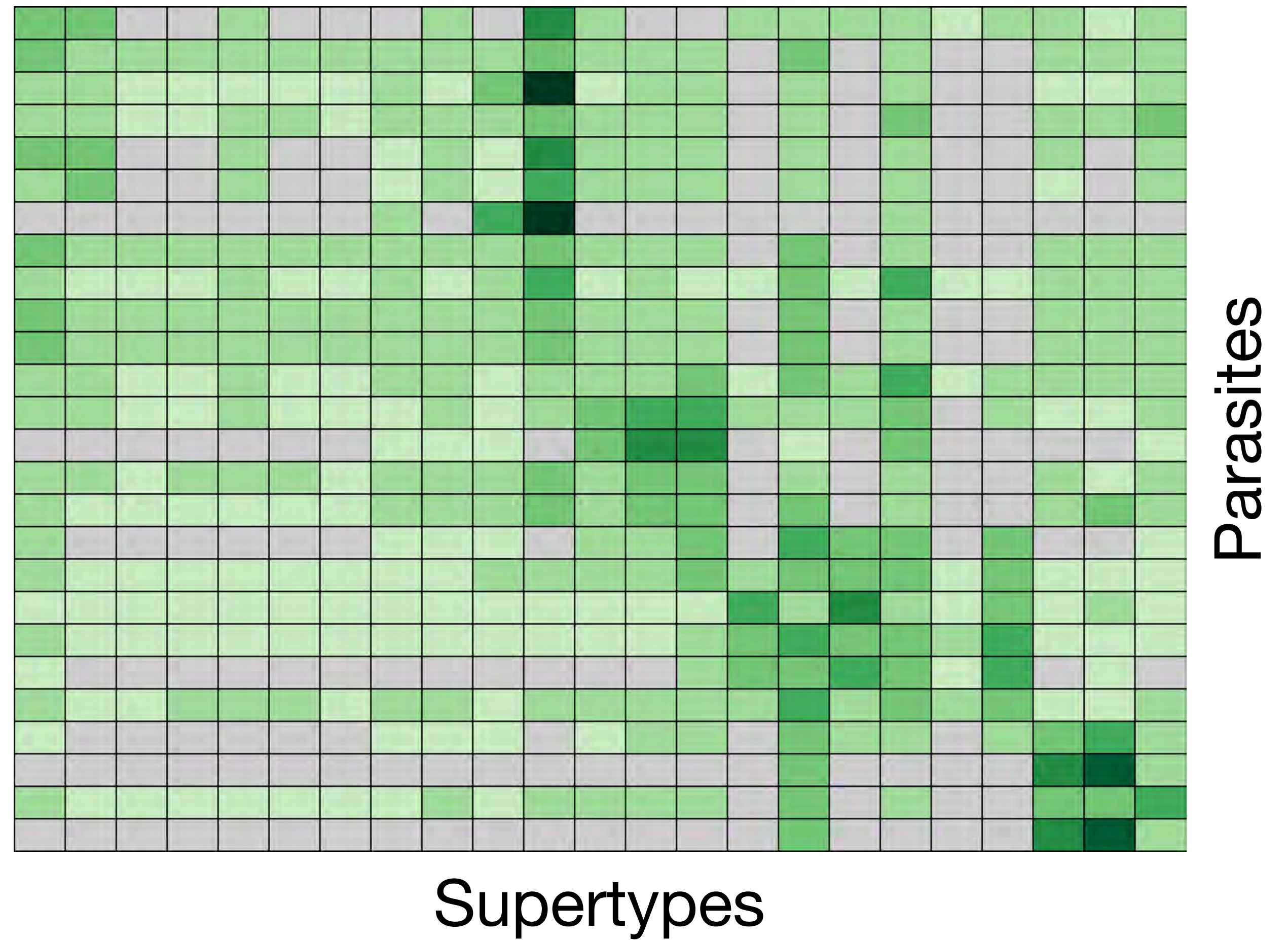


$$P(s = s_k | p = p_j) = \quad (1)$$

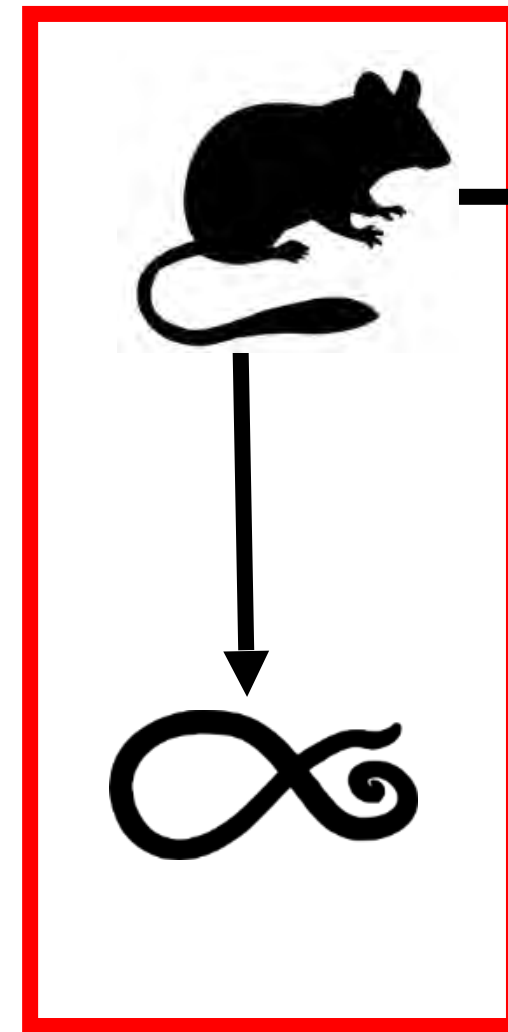
$$\sum_{i \in H} P(s_k | h_i) \cdot P(h_i | p_j) = \quad (2)$$

$$\sum_{i \in H} P(s_k | h_i) \cdot \frac{P(p_j | h_i) \cdot P(h_i)}{P(p_j)} = \quad (3)$$

$$\sum_{i \in H} P(s_k | h_i) \cdot \frac{P(p_j | h_i) \cdot P(h_i)}{\sum_{i \in H} P(h_i) \cdot P(p_j | h_i)} = \quad (4)$$

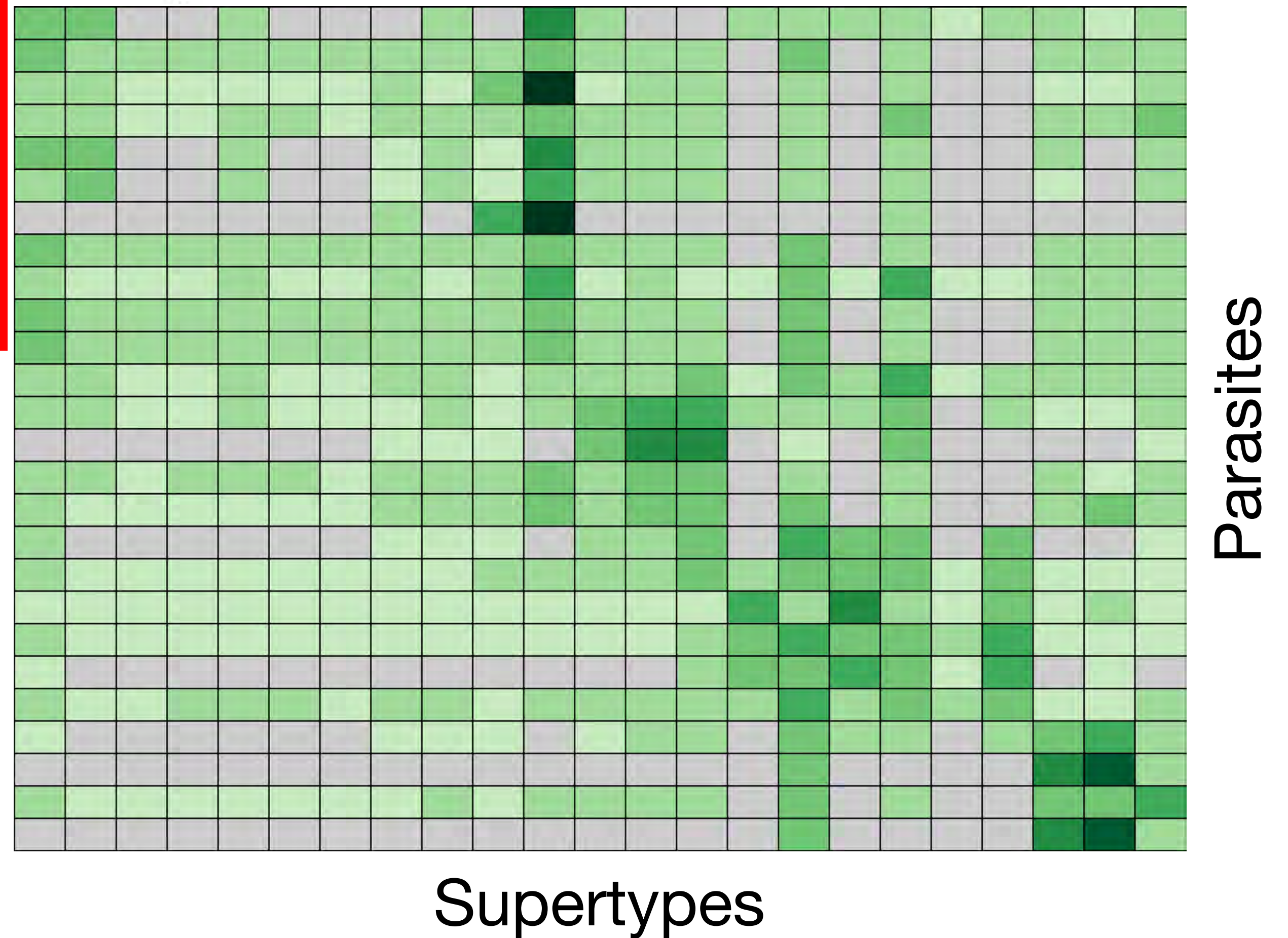


Does the ecological network determine supertype-parasite associations?



1. Randomize
2. Recalculate

Over 50% of associations are non-random

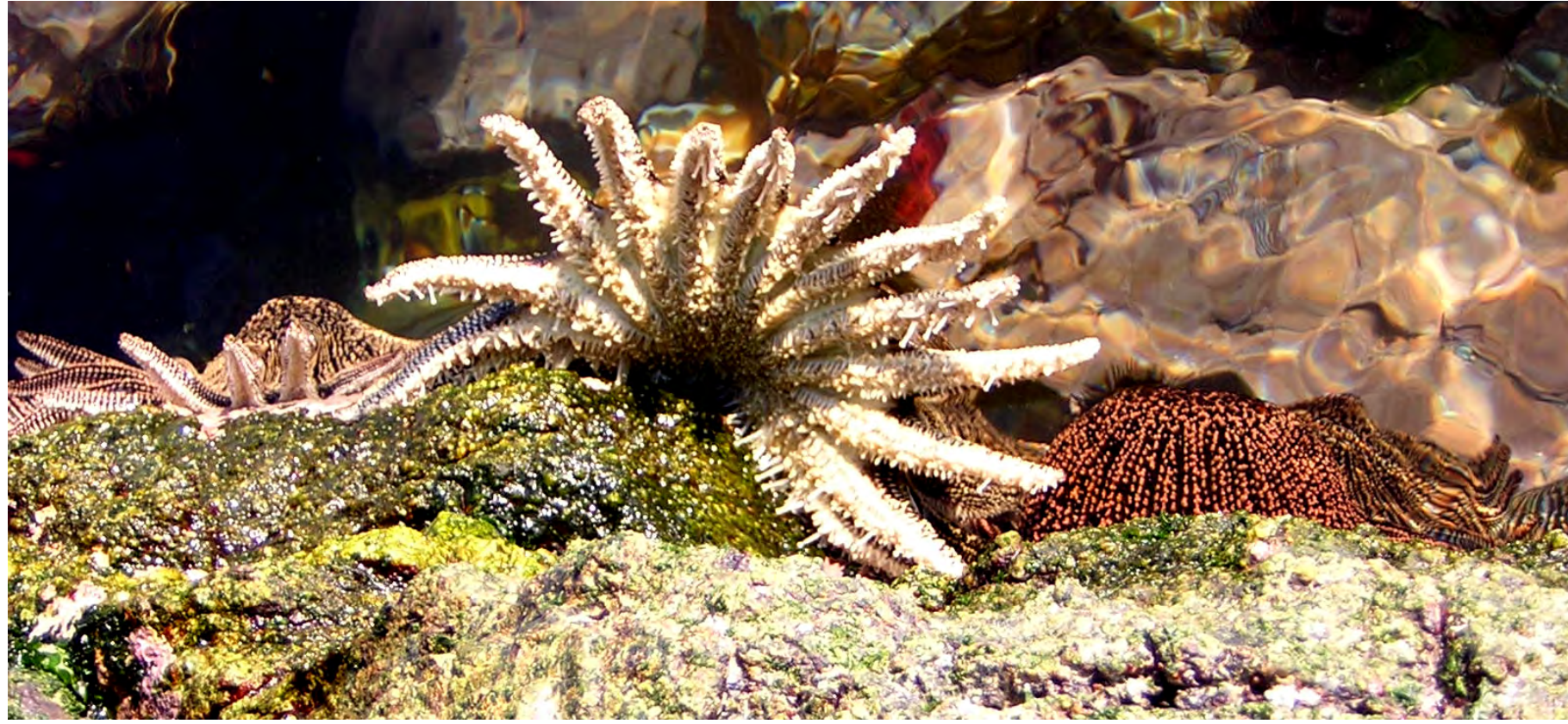




Sergio Navarrete,
Evie Wieters

Kéfi et al. 2015





Trophic interactions



Negative non-trophic interactions



Positive non-trophic interactions

*Slide courtesy Sonia Kéfi
Kéfi et al. 2015*

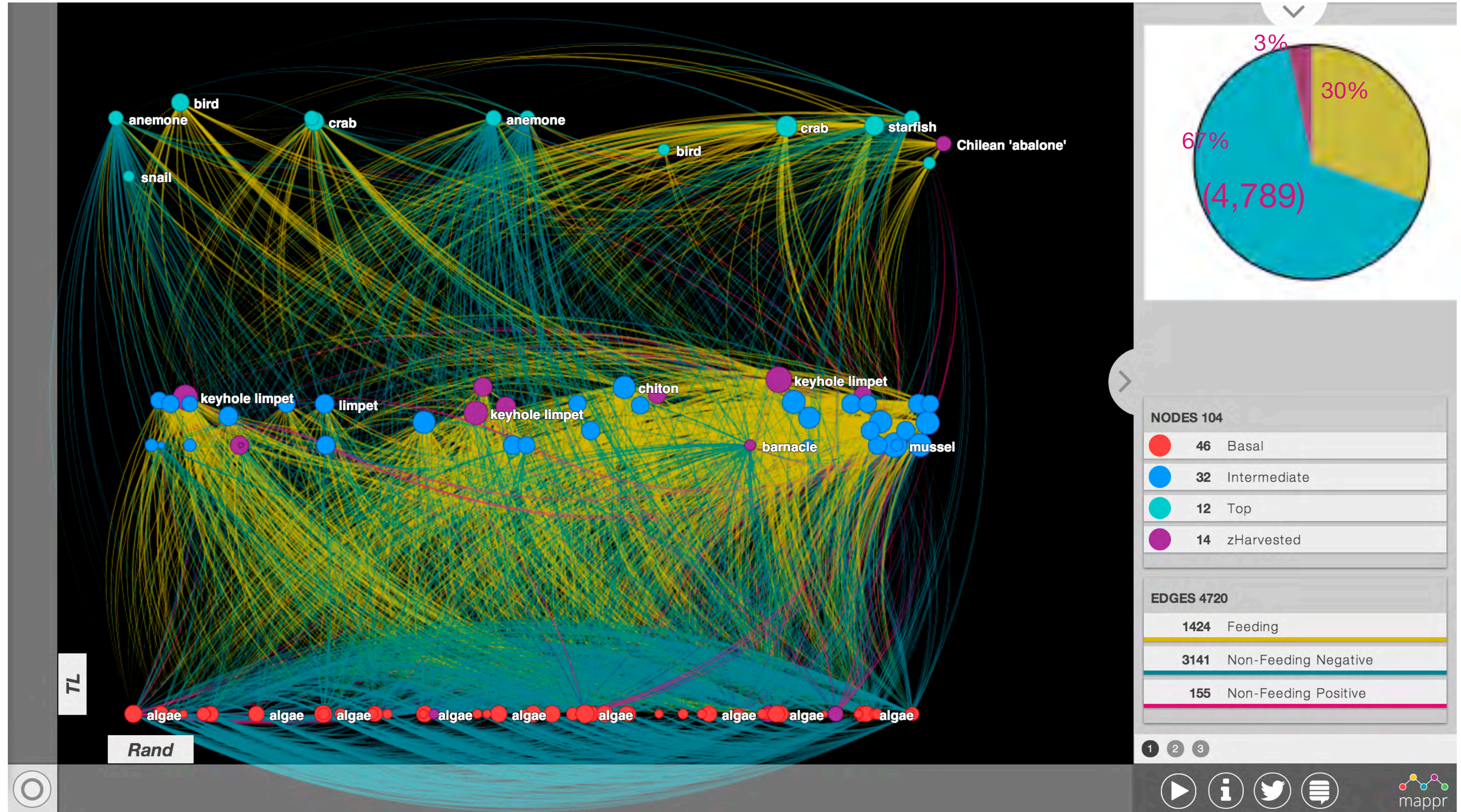


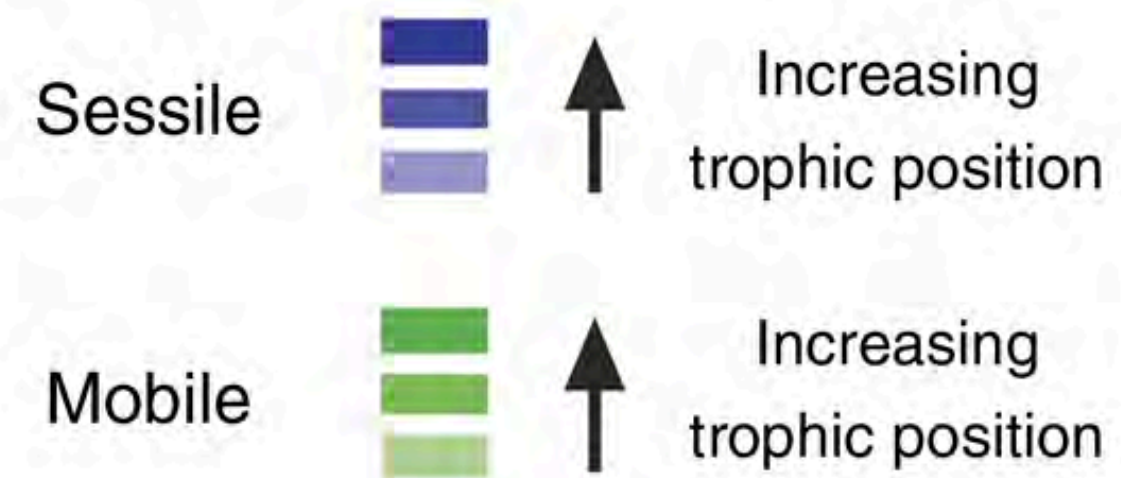
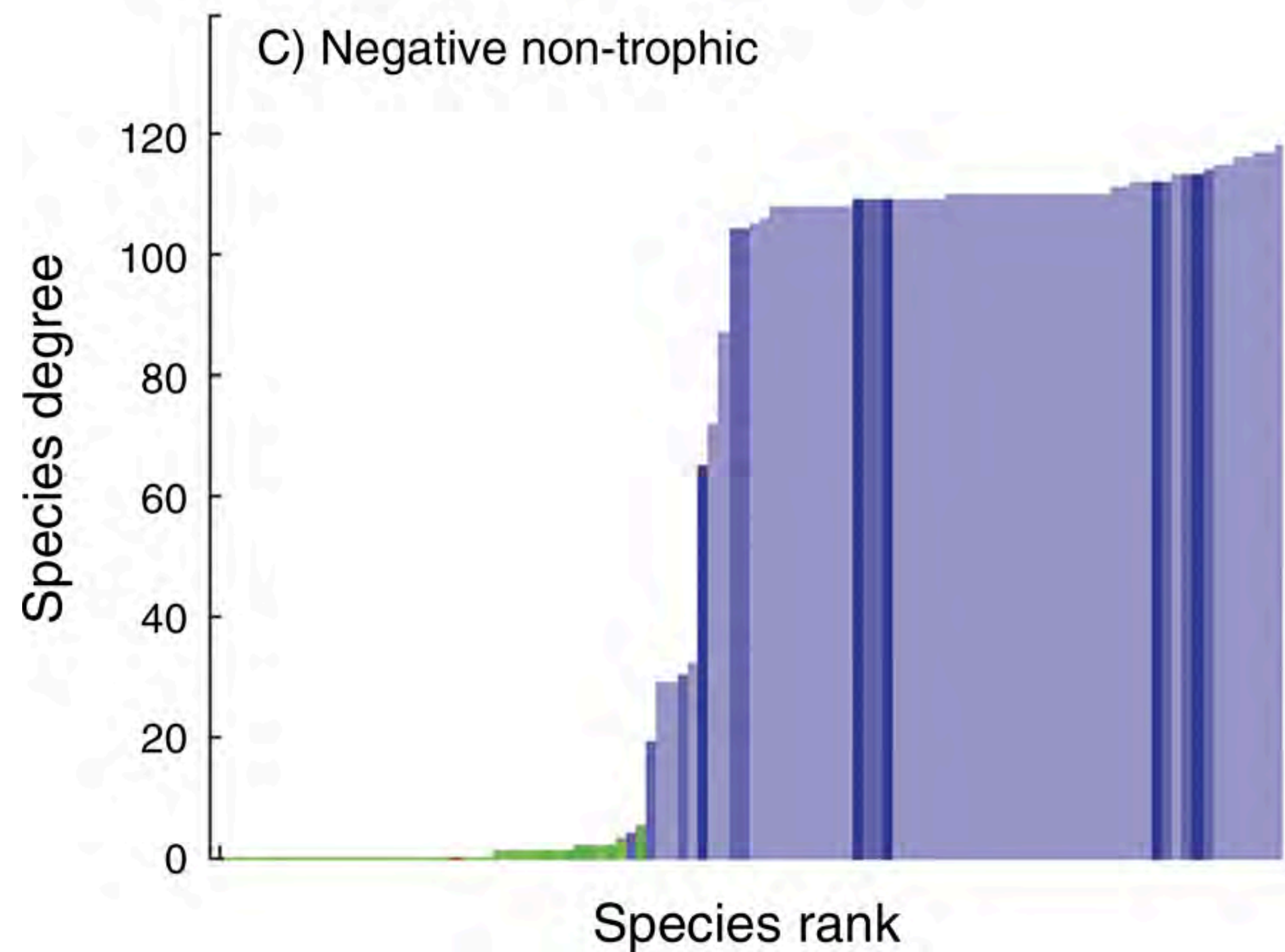
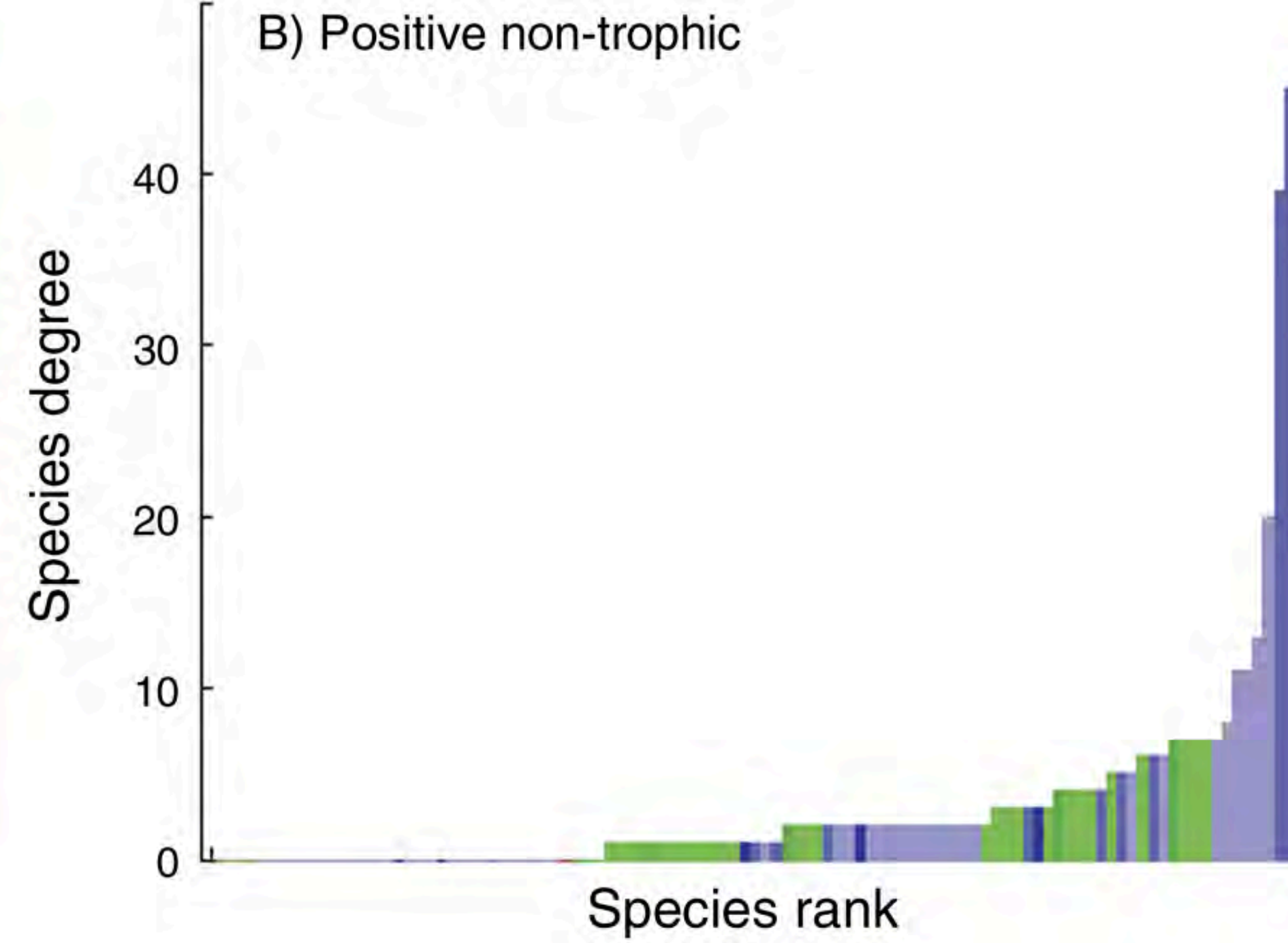
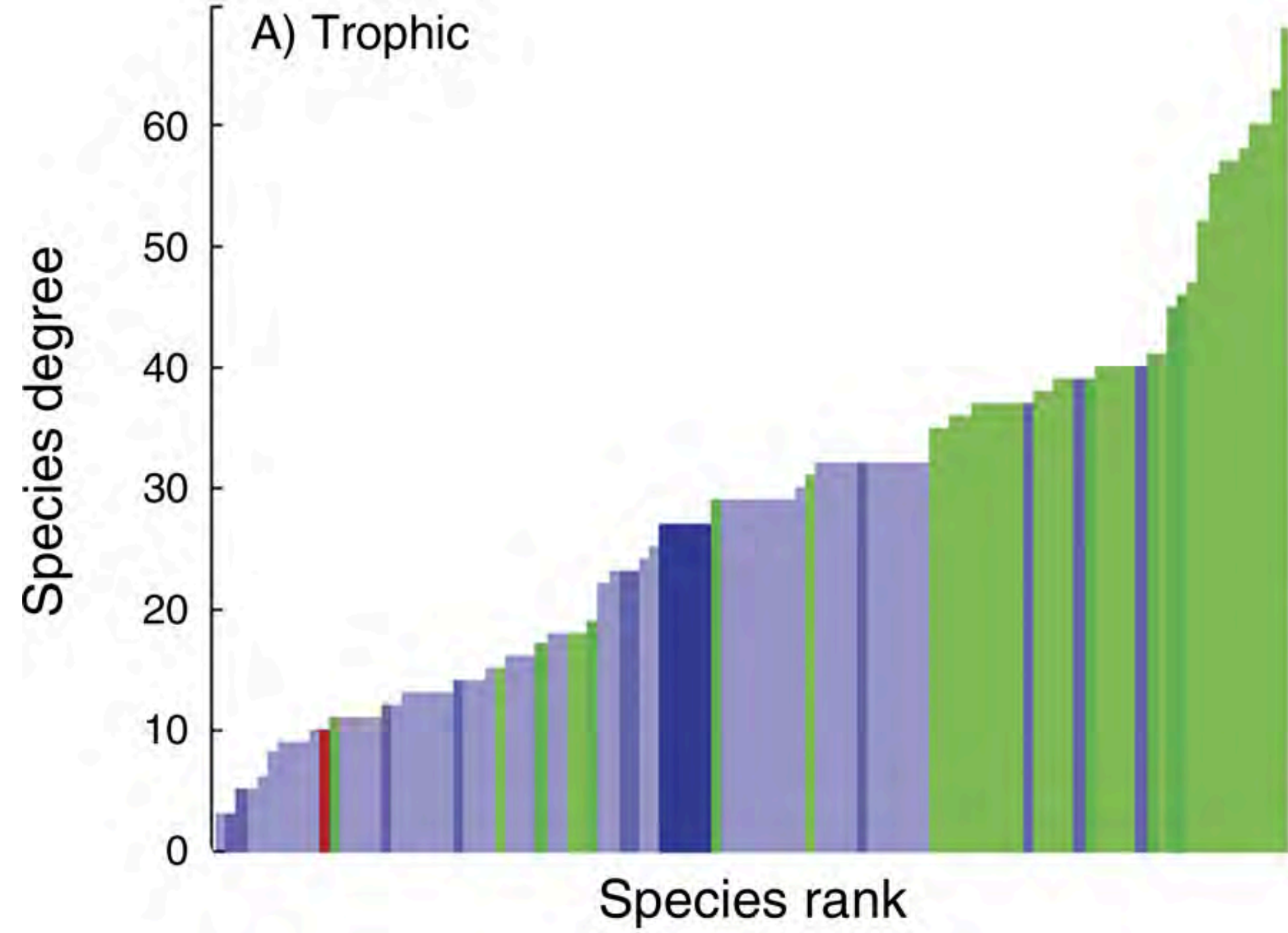
Positive non-trophic interactions

Trophic and non-trophic interactions

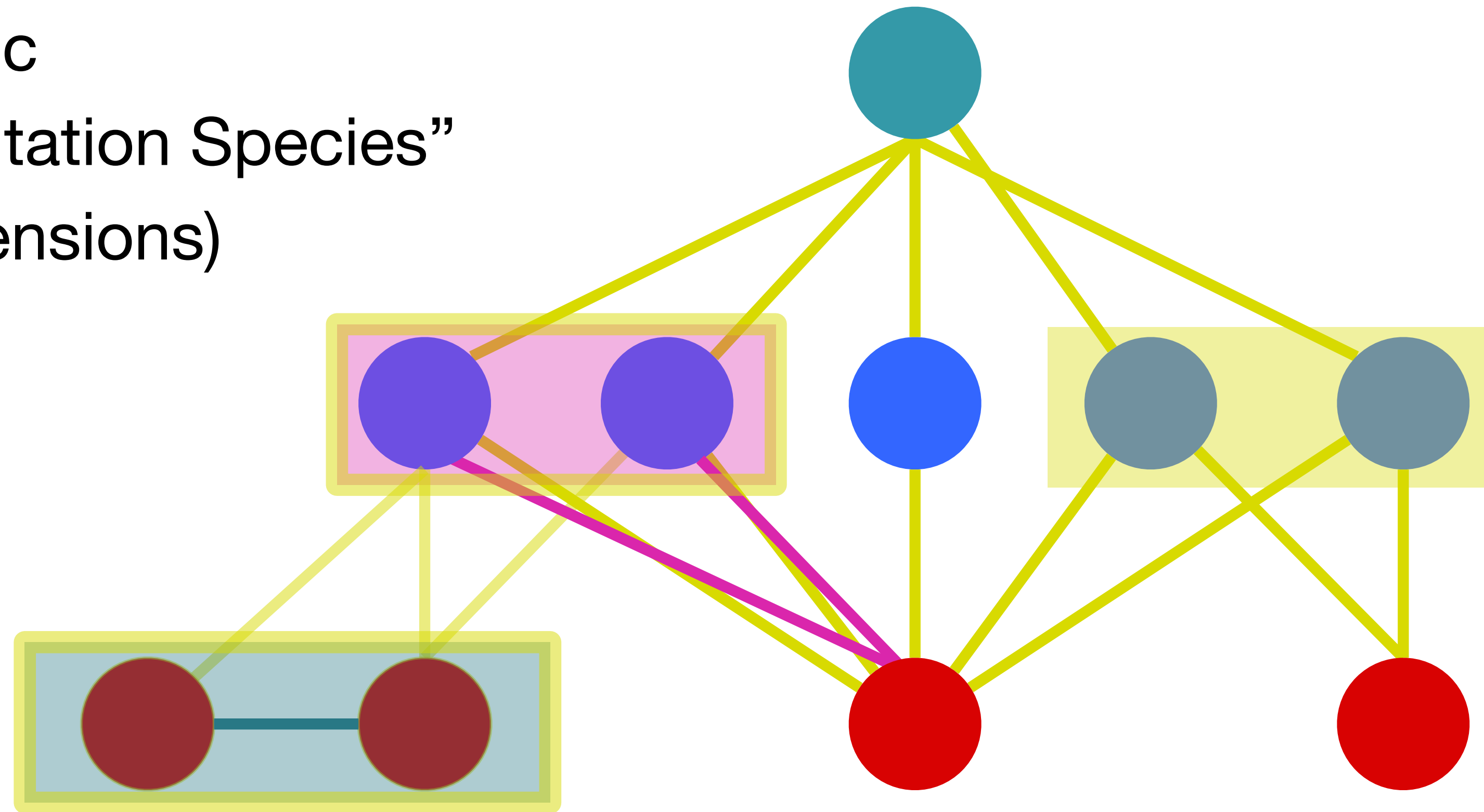


Sonia Kéfi





“Trophic
+ Facilitation Species”
(2 dimensions)

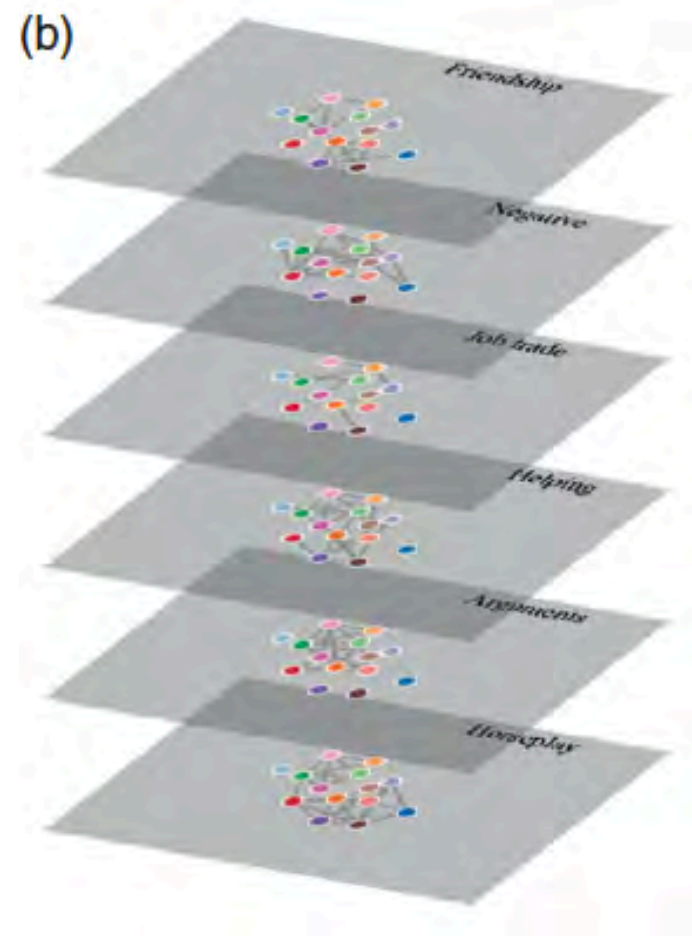


— feeding
— facilitation
— competition

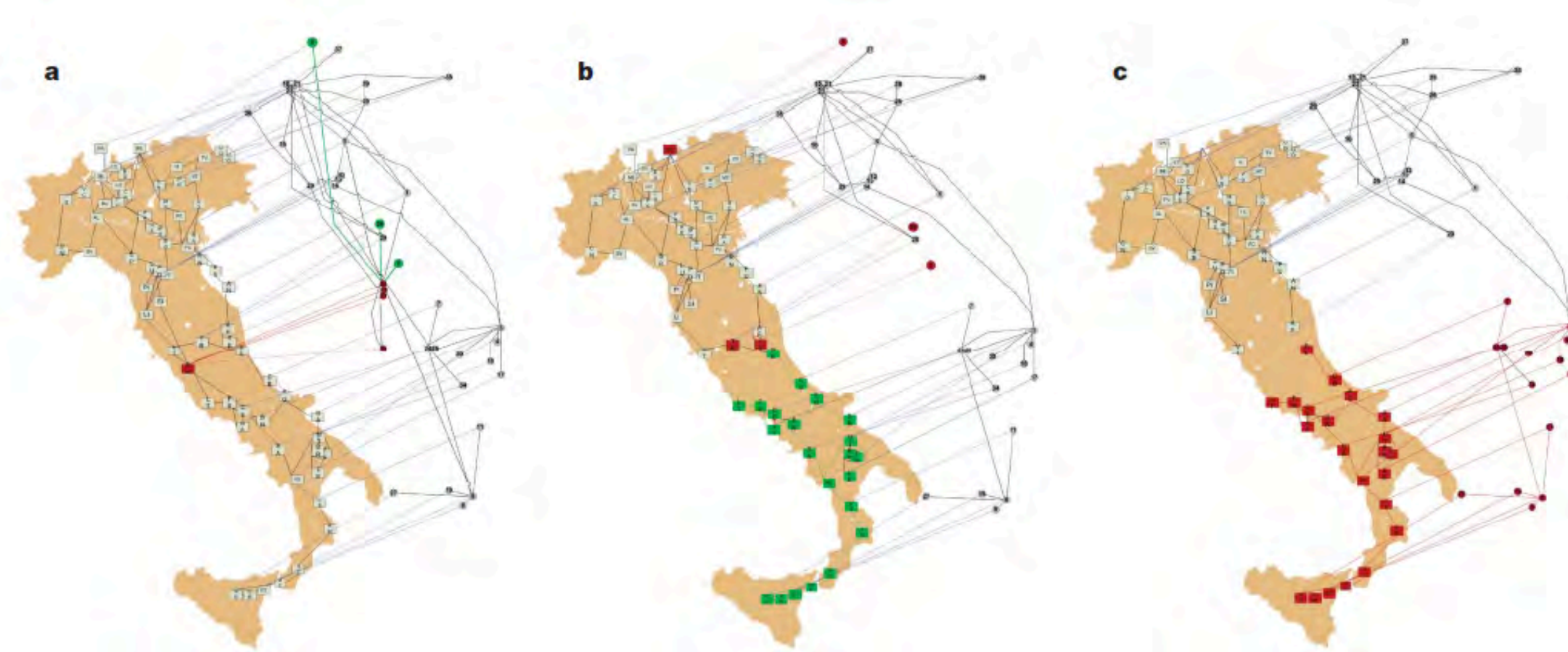
“Trophic Species”
(1 dimension)

“Trophic
+ Competition Species”
(2 dimensions)

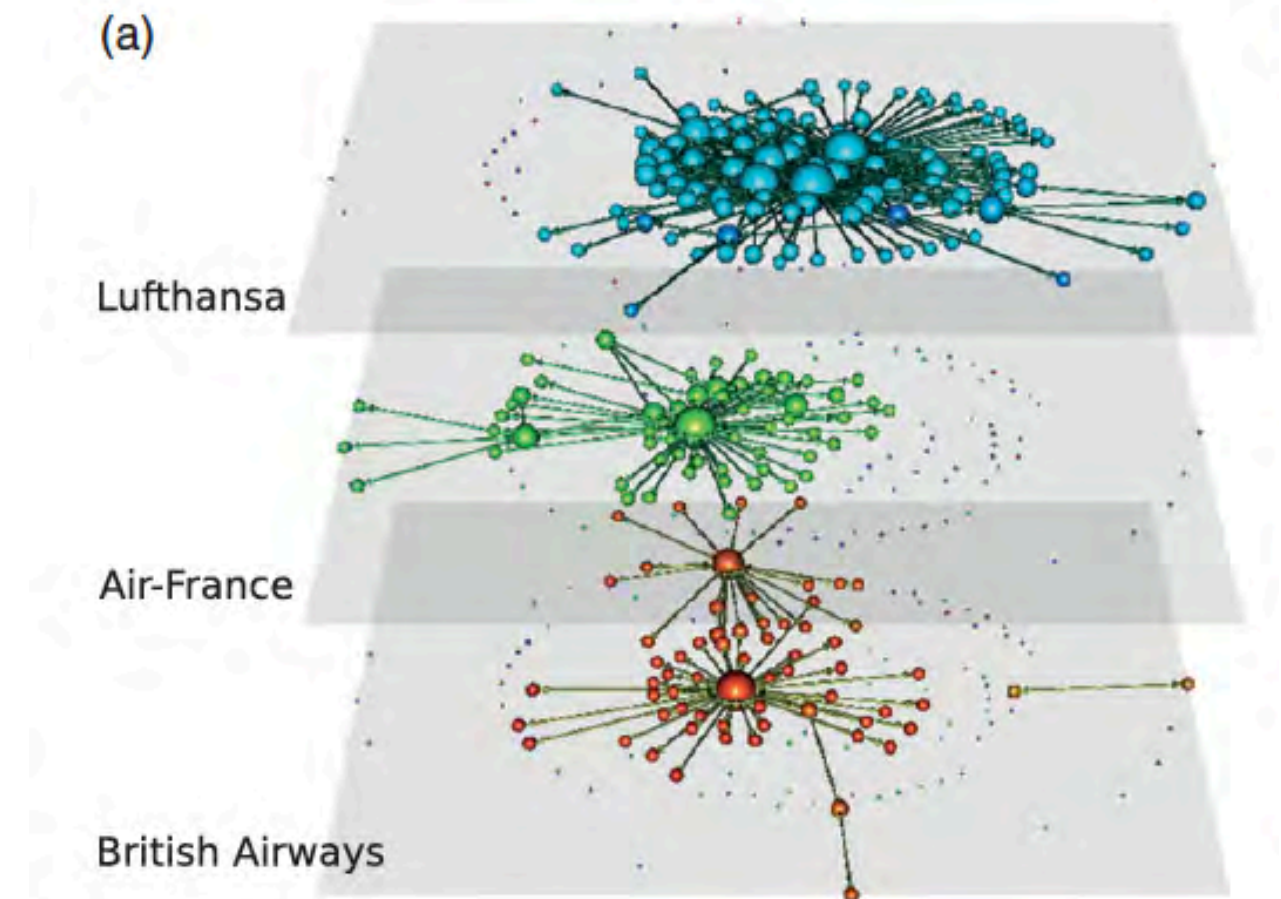
Multilayer networks in the broader network science



Roethlisberger &
Dickson (1939)



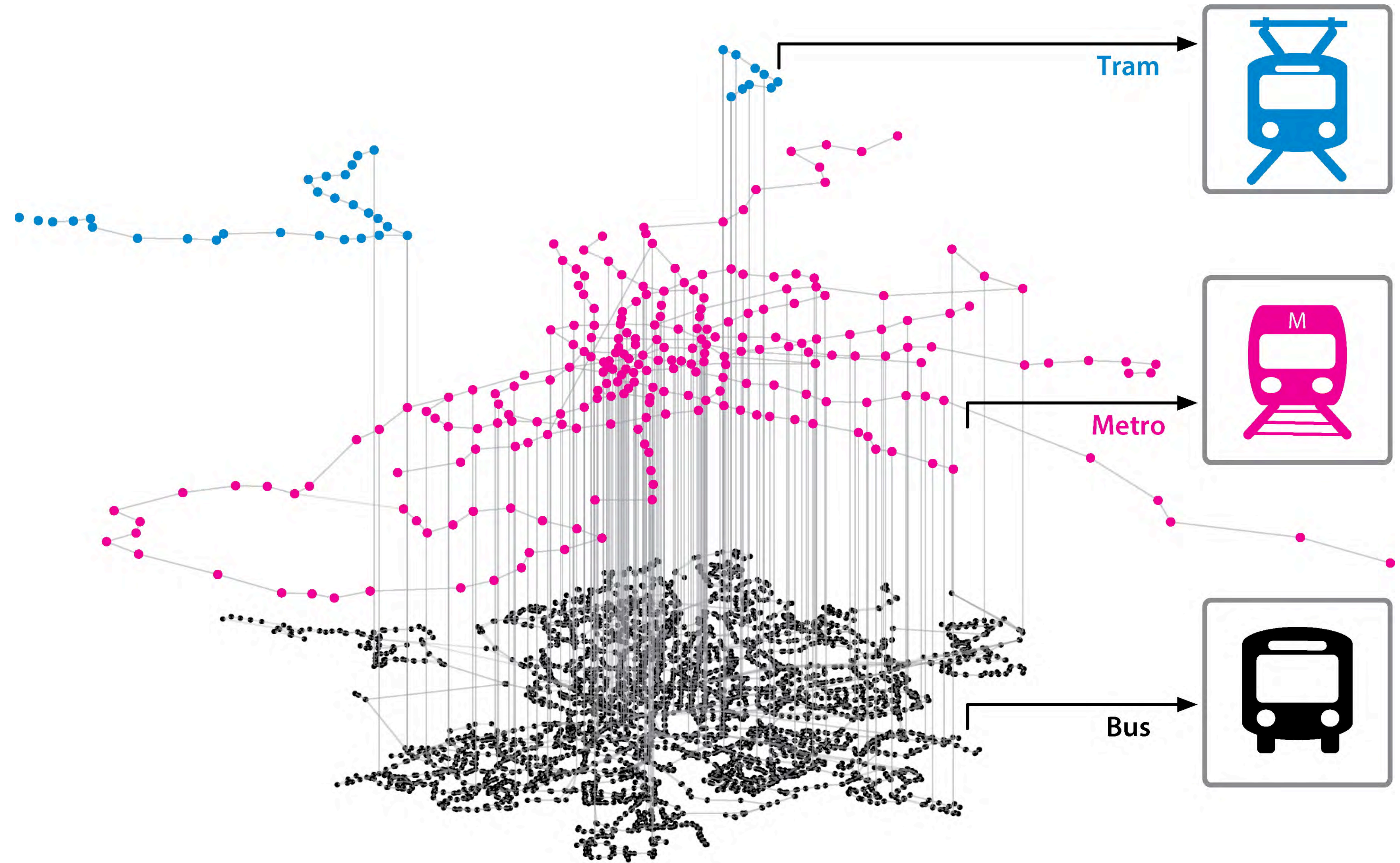
Buldyrev et al. (Nature, 2010)



Cardillo et al. (2013)

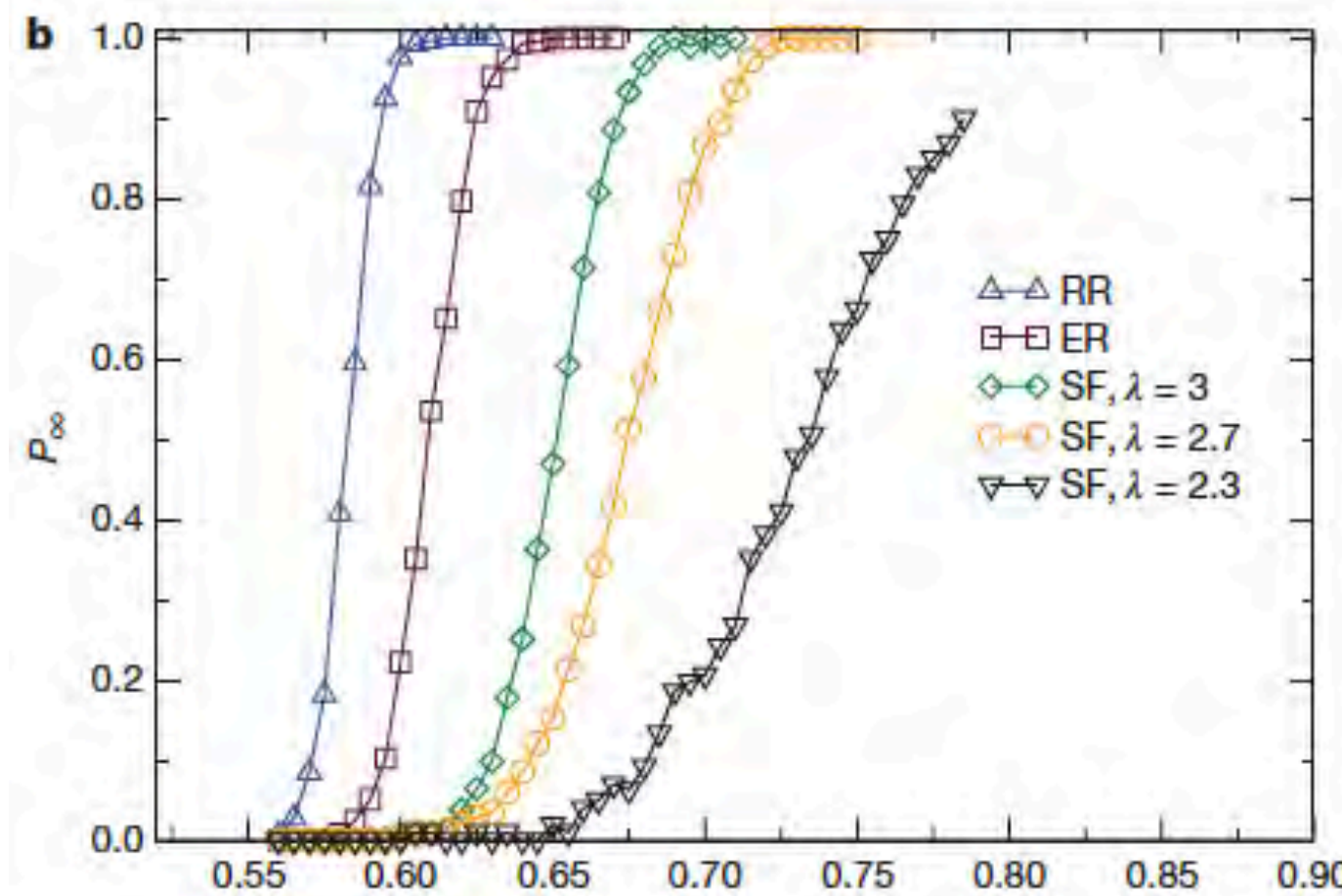
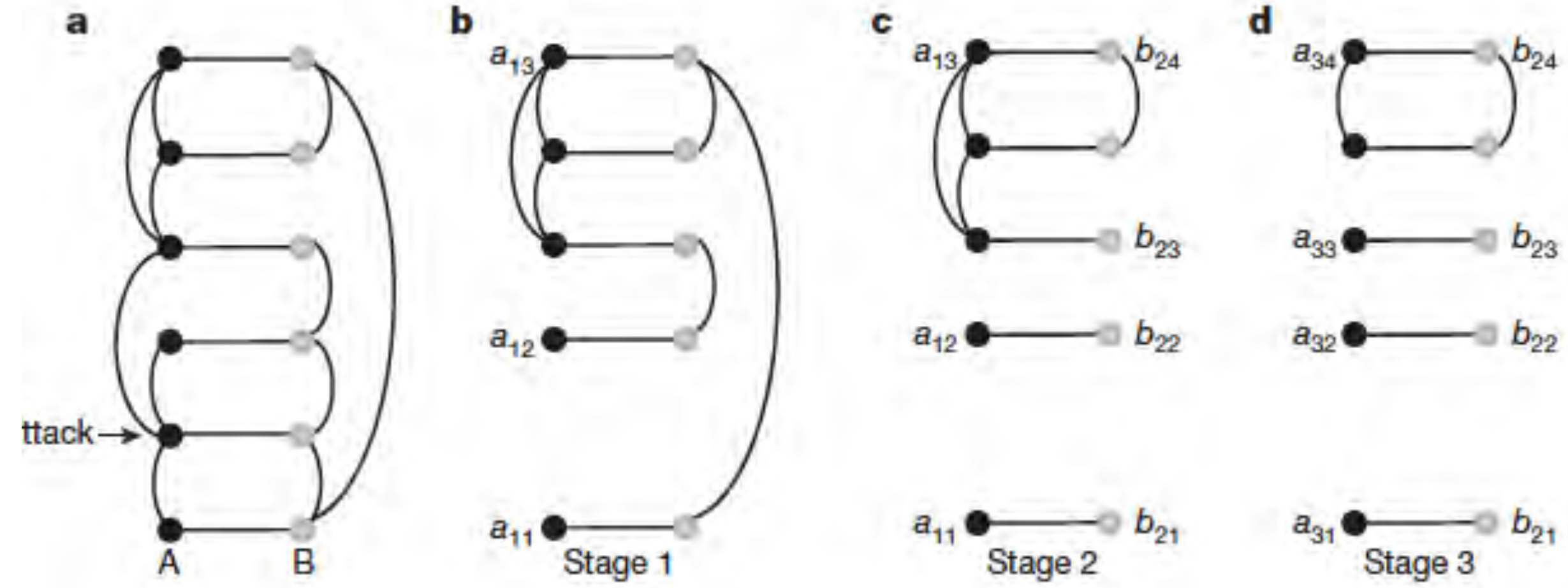
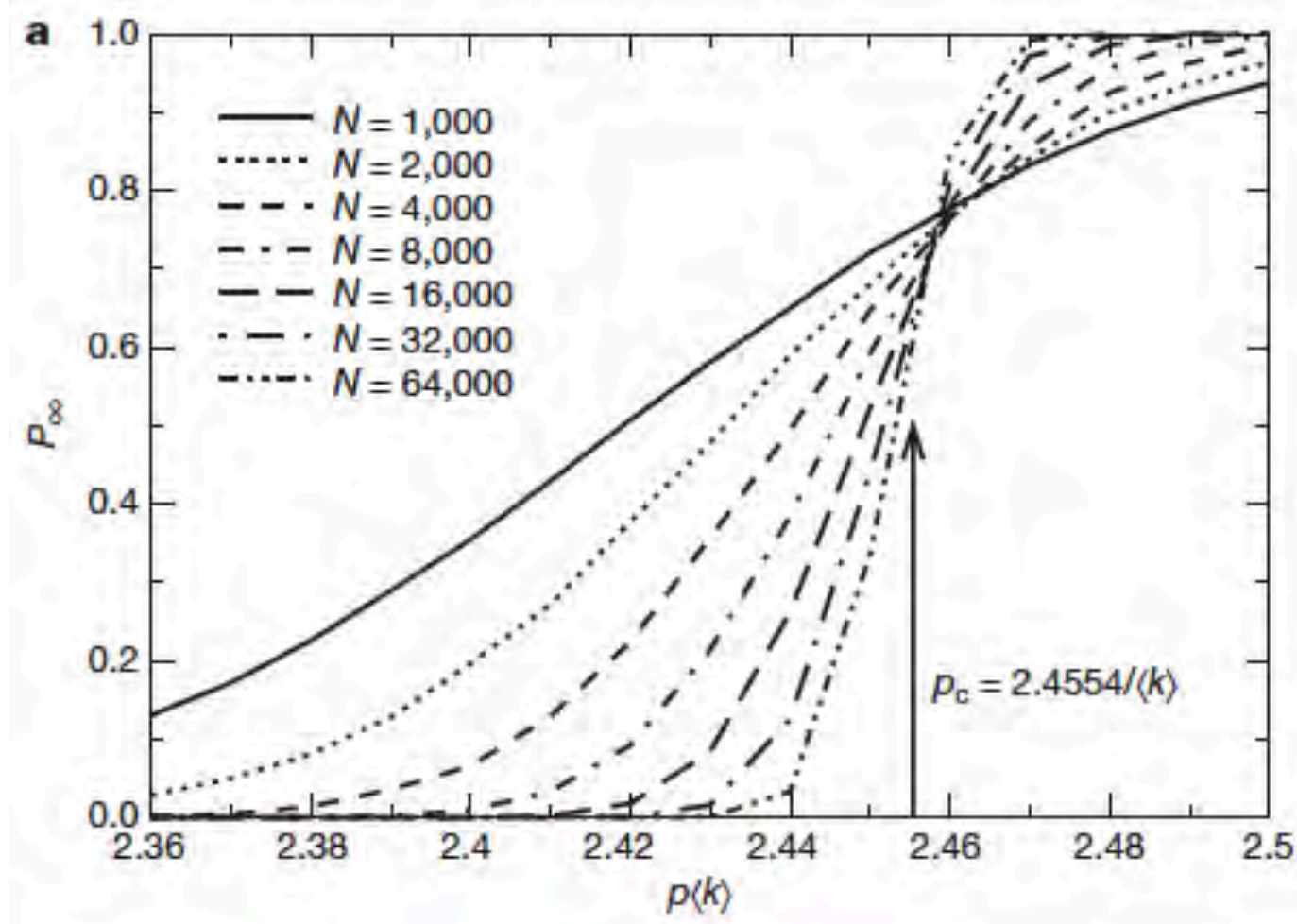
Intra-layer links: connected stops of a transport system.

Inter-layer links: connect stops of different transport modes that are within a 150-m radius.

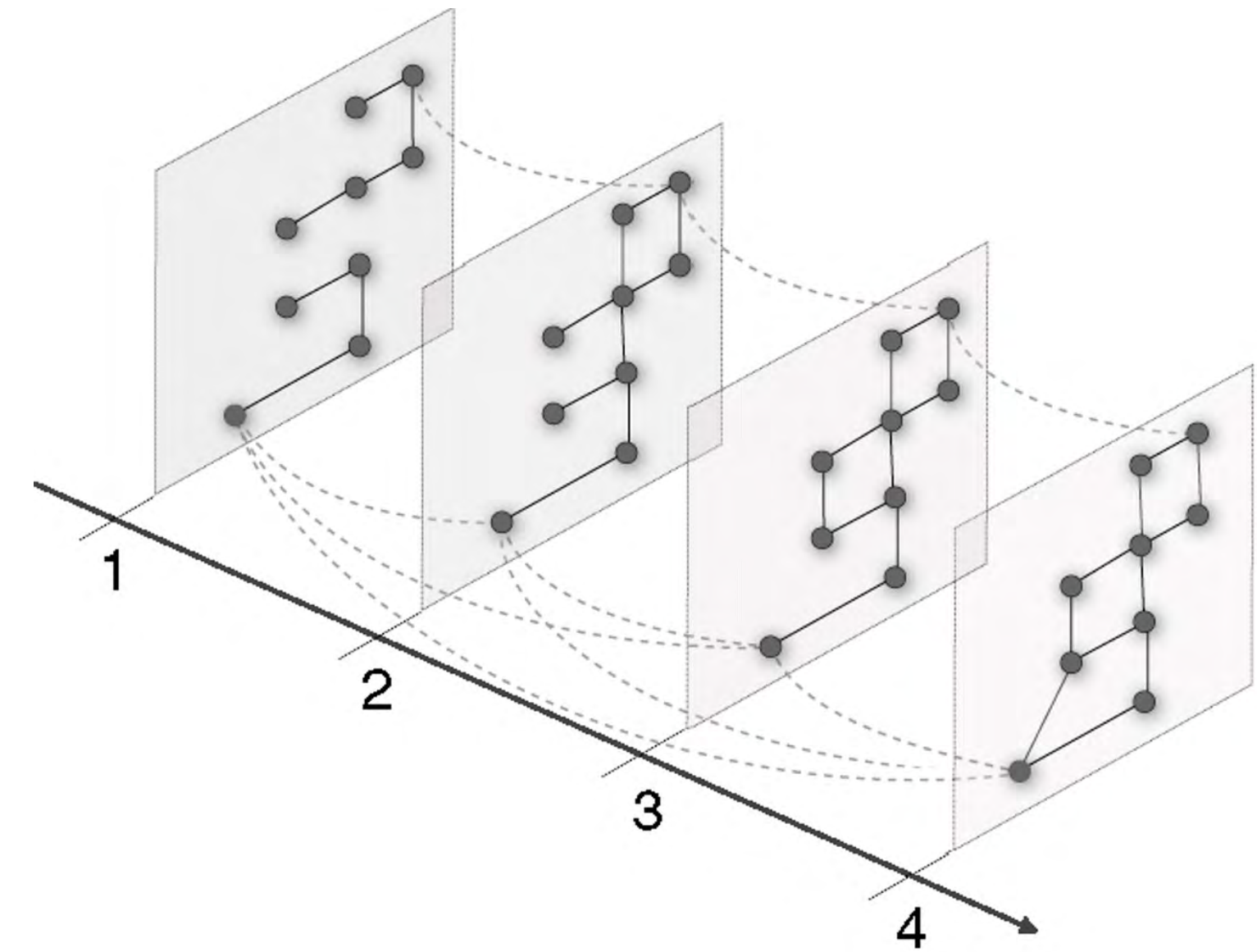
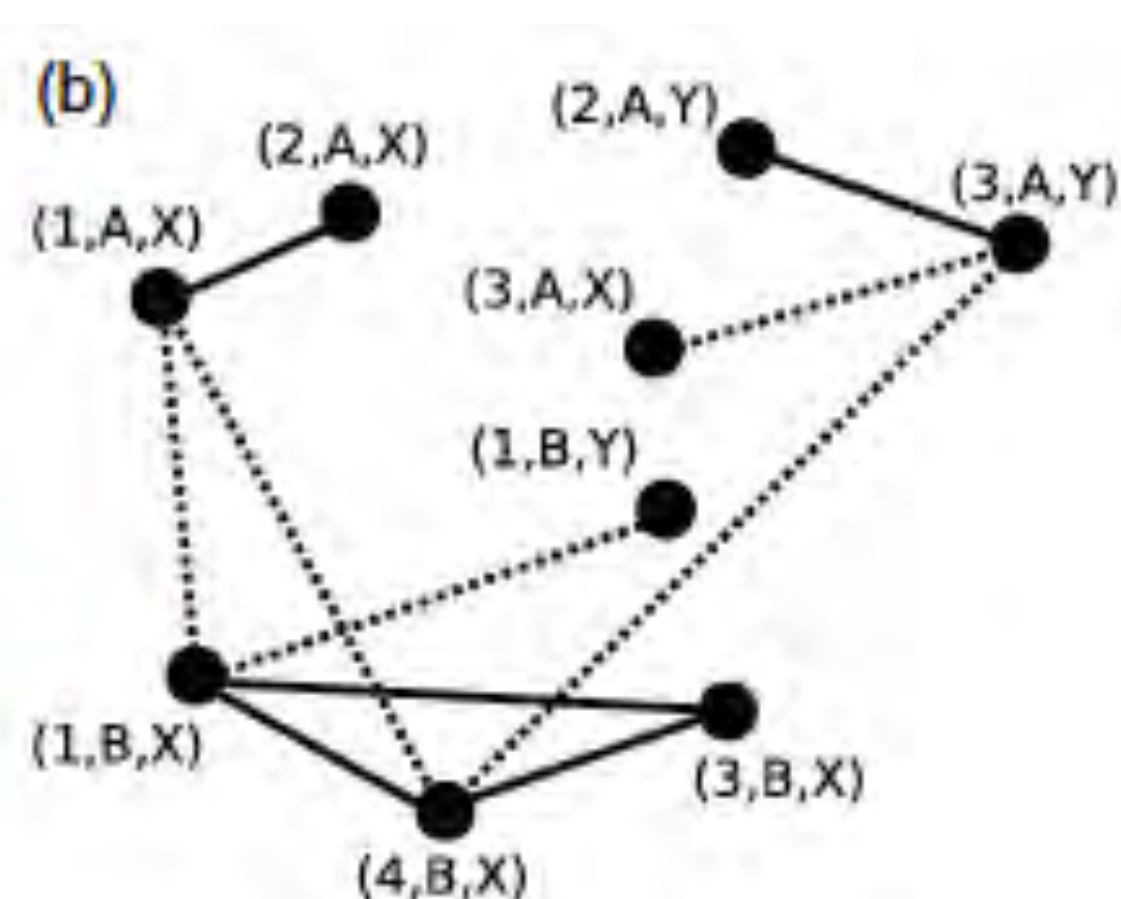
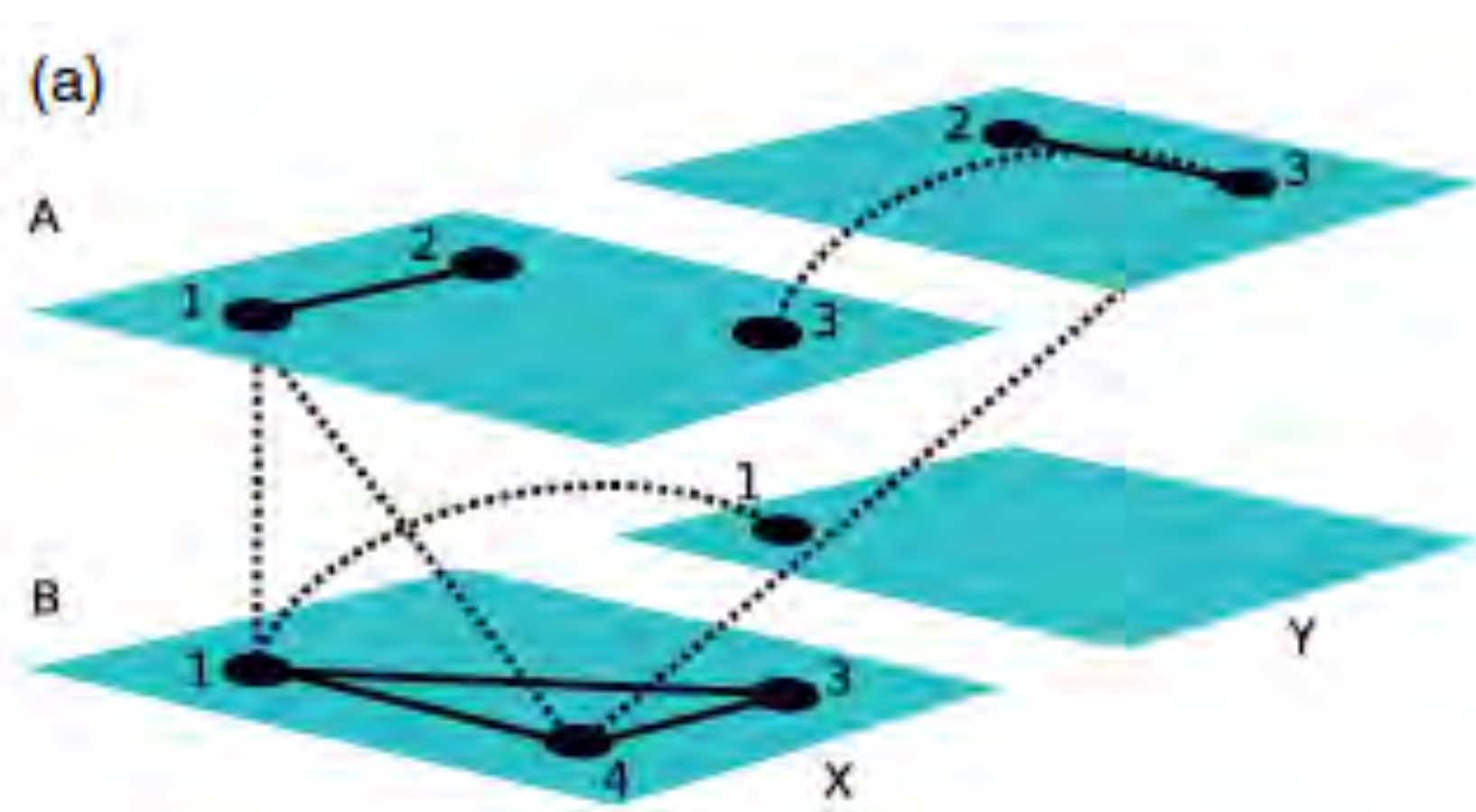


Catastrophic cascade of failures in interdependent networks

Sergey V. Buldyrev^{1,2}, Roni Parshani³, Gerald Paul², H. Eugene Stanley² & Shlomo Havlin³



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



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

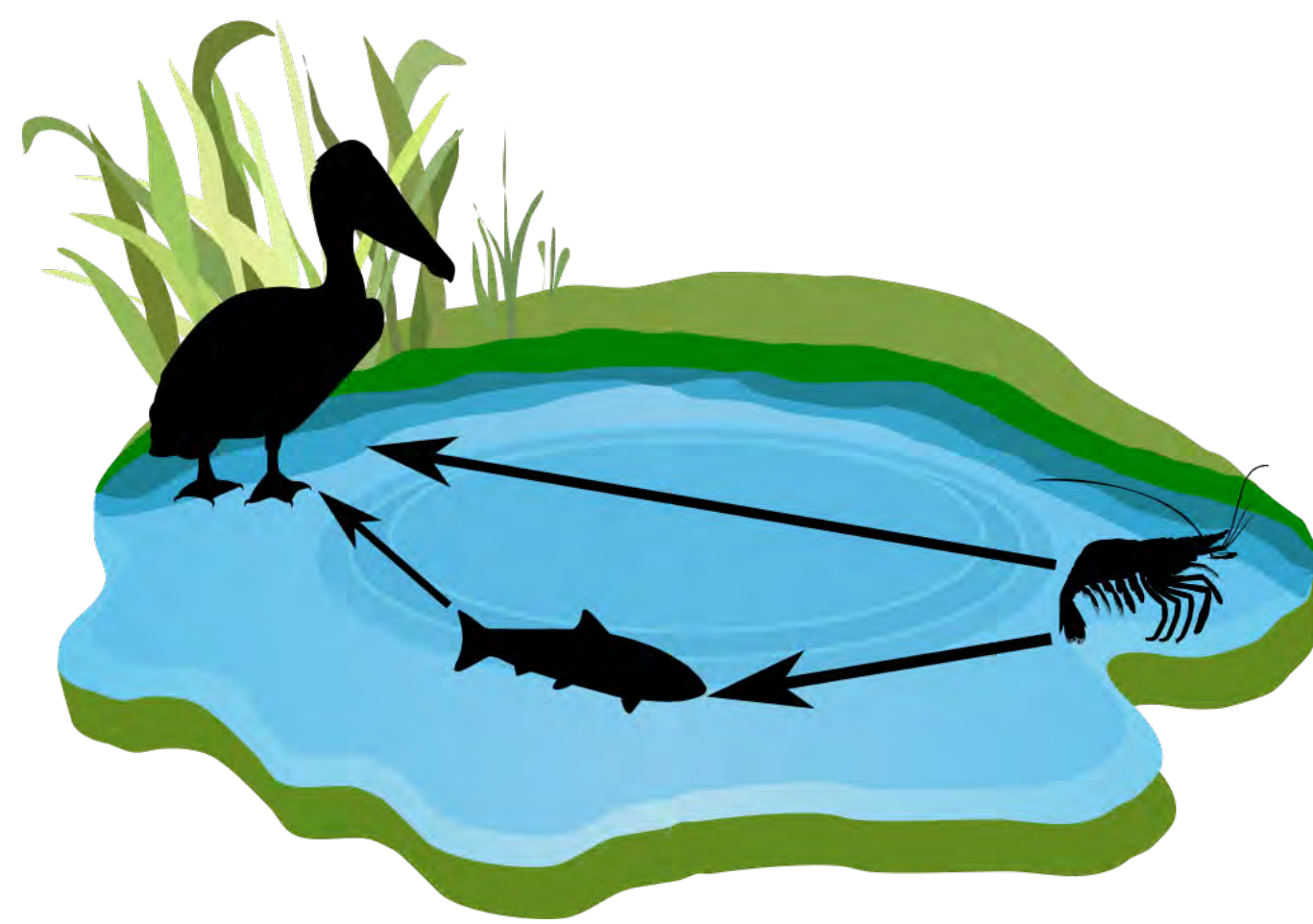
$$Q_{\text{multislice}} = \frac{1}{2\mu} \sum_{ijsr} \left[\left(A_{ijs} - \gamma_s \frac{k_{is}k_{js}}{2m_s} \right) \delta_{sr} + \delta_{ij} \omega_{jsr} \right] \delta(g_{is}, g_{jr})$$

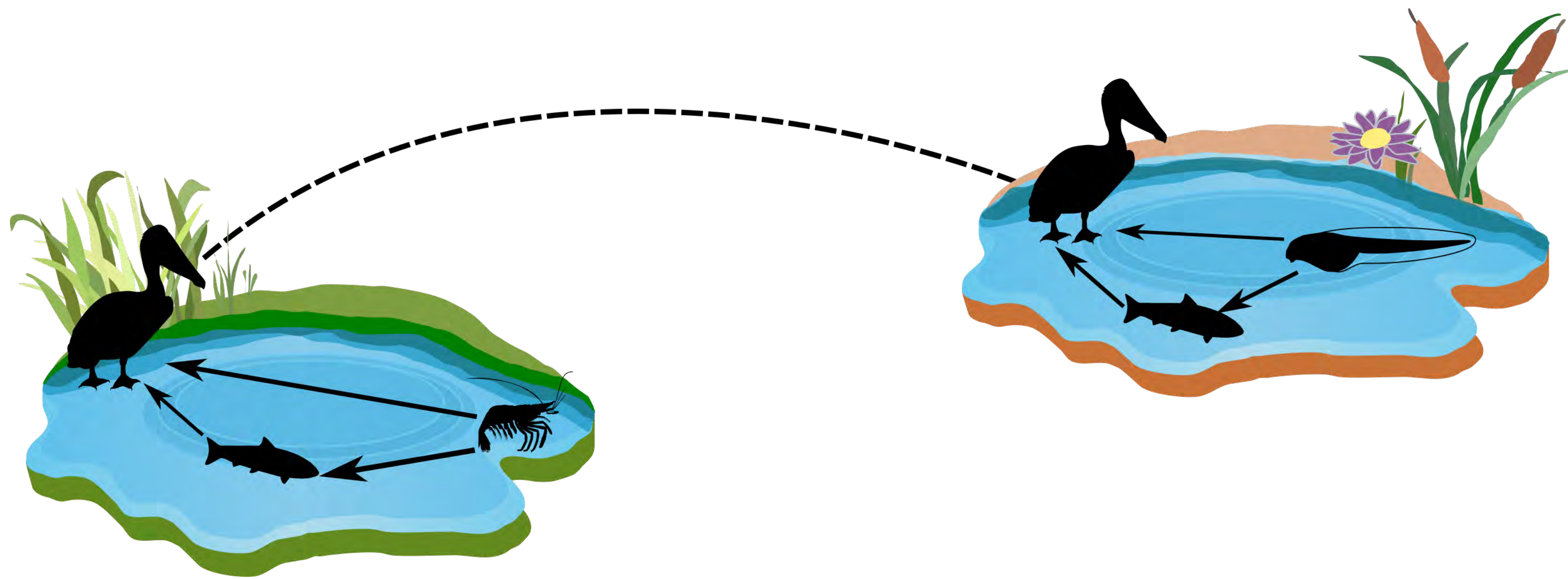
within-layer between-layer

The multilayer nature of ecological networks

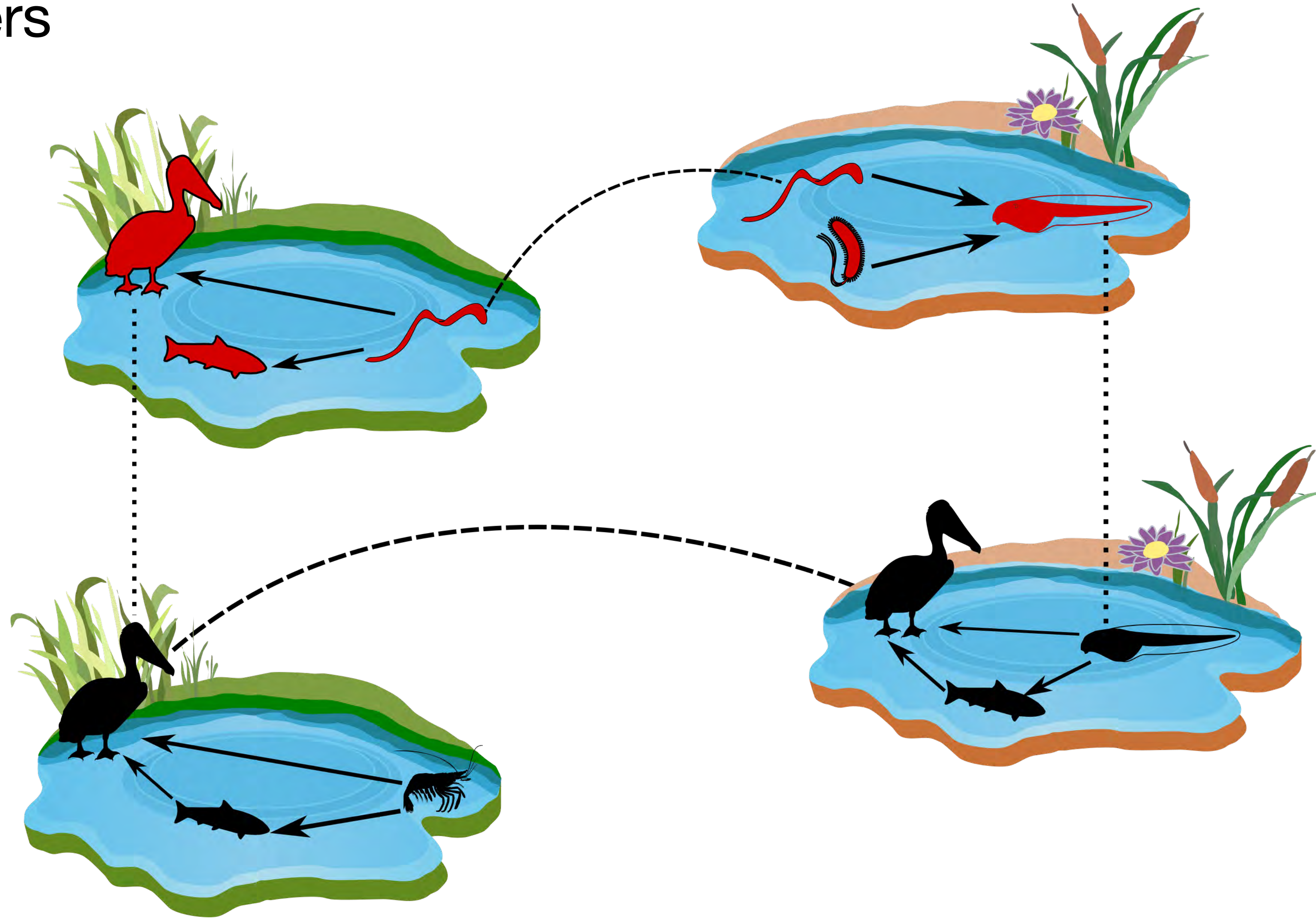
Shai Pilosof^{1*}, Mason A. Porter^{2,3,4}, Mercedes Pascual^{1,5} and Sonia Kéfi⁶







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

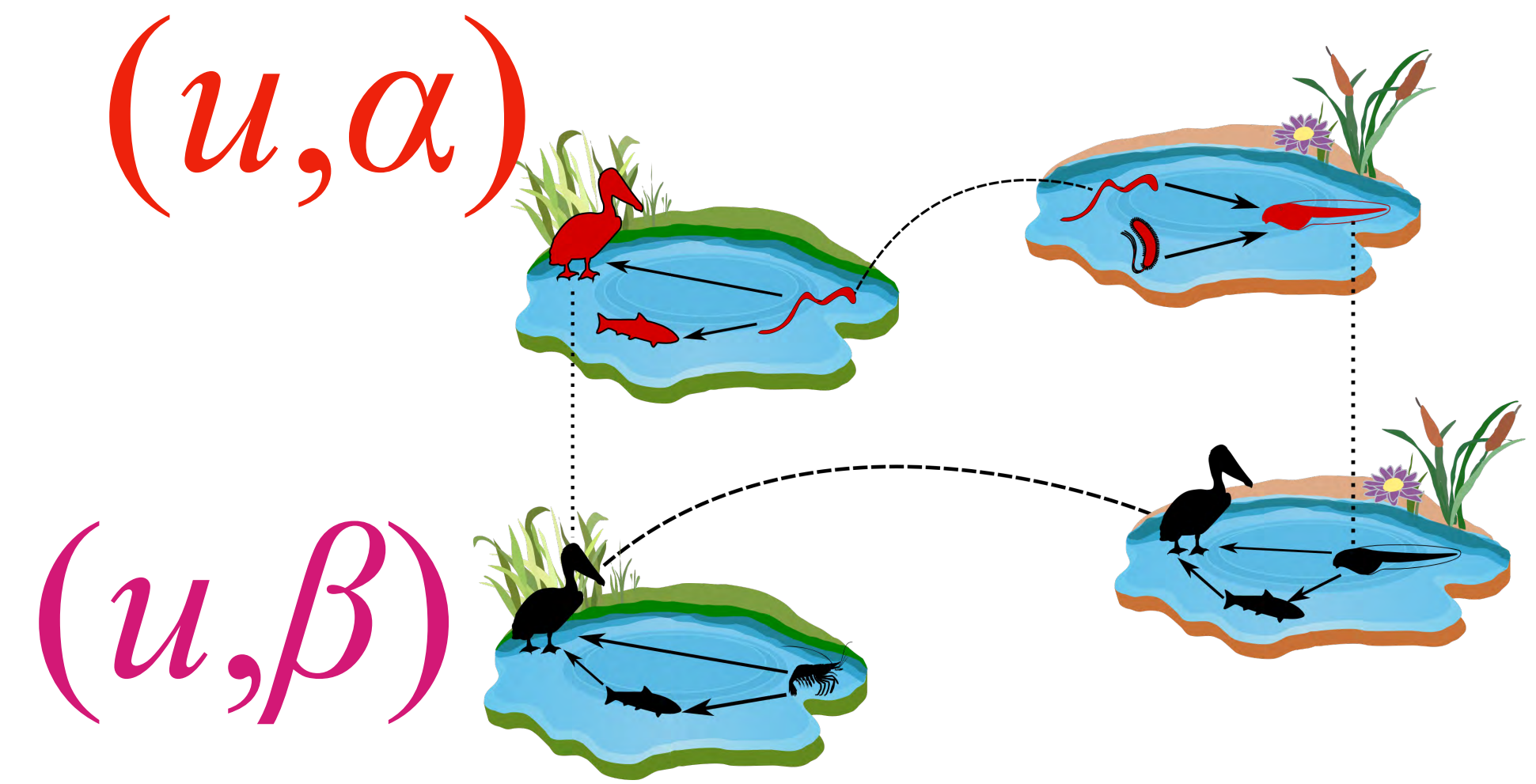


$$\mathbf{L} = \{L_a\}_{a=1}^d$$

$$V_M \subseteq V \times L_1 \times L_2 \cdots \times L_d$$

$$E_M \subseteq V_M \times V_M$$

$$M = (V_M, E_M, V, \mathbf{L})$$



$$\mathbf{L} = \{L_a\}_{a=1}^d$$

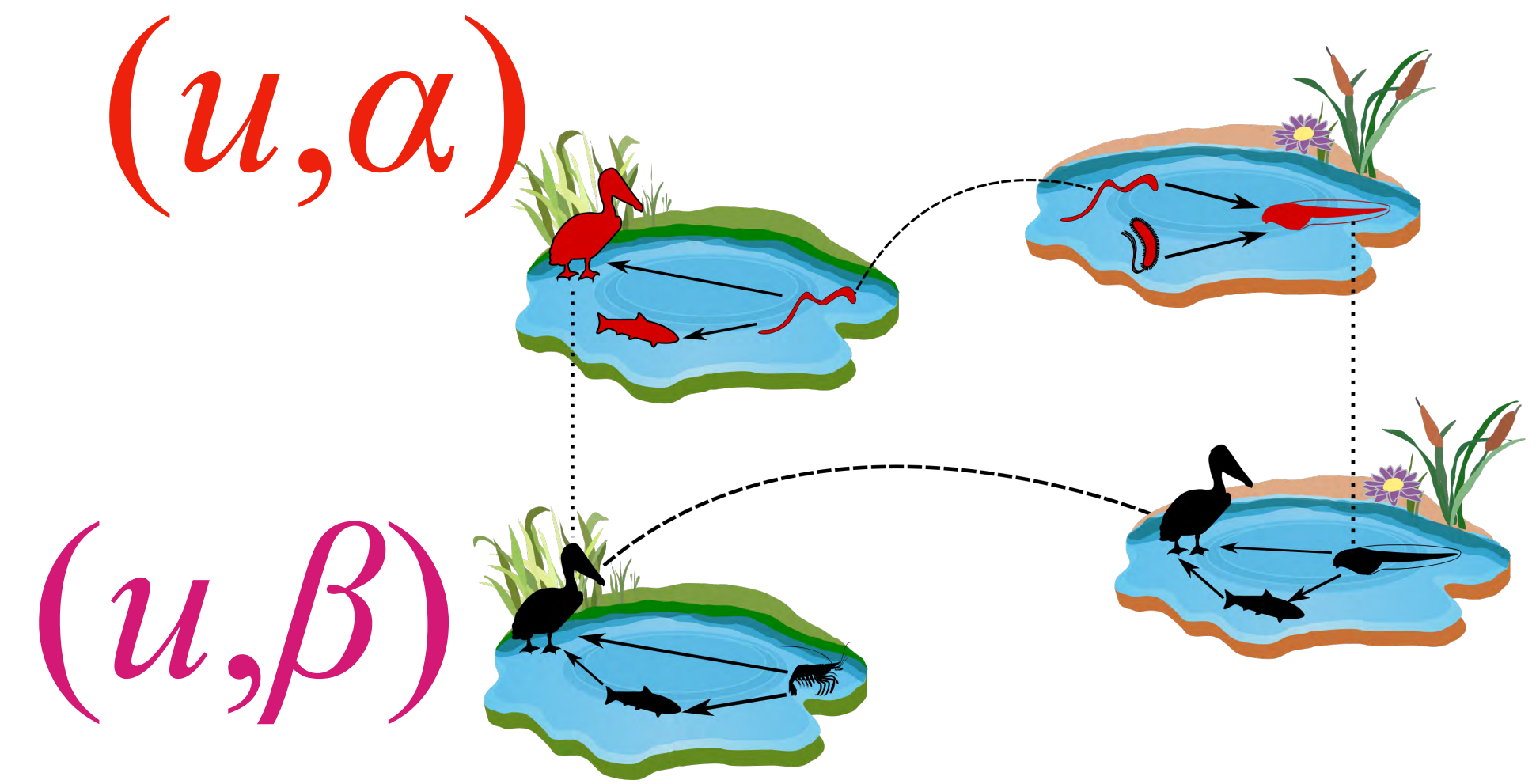
$$V_M \subseteq V \times L_1 \times L_2 \cdots \times L_d$$

$$E_M \subseteq V_M \times V_M$$

$$M = (V_M, E_M, V, \mathbf{L})$$

$$E_A = \{((u, \alpha), (v, \beta)) \in E_M \mid \alpha = \beta\}$$

$$E_C = E_M \setminus E_A$$

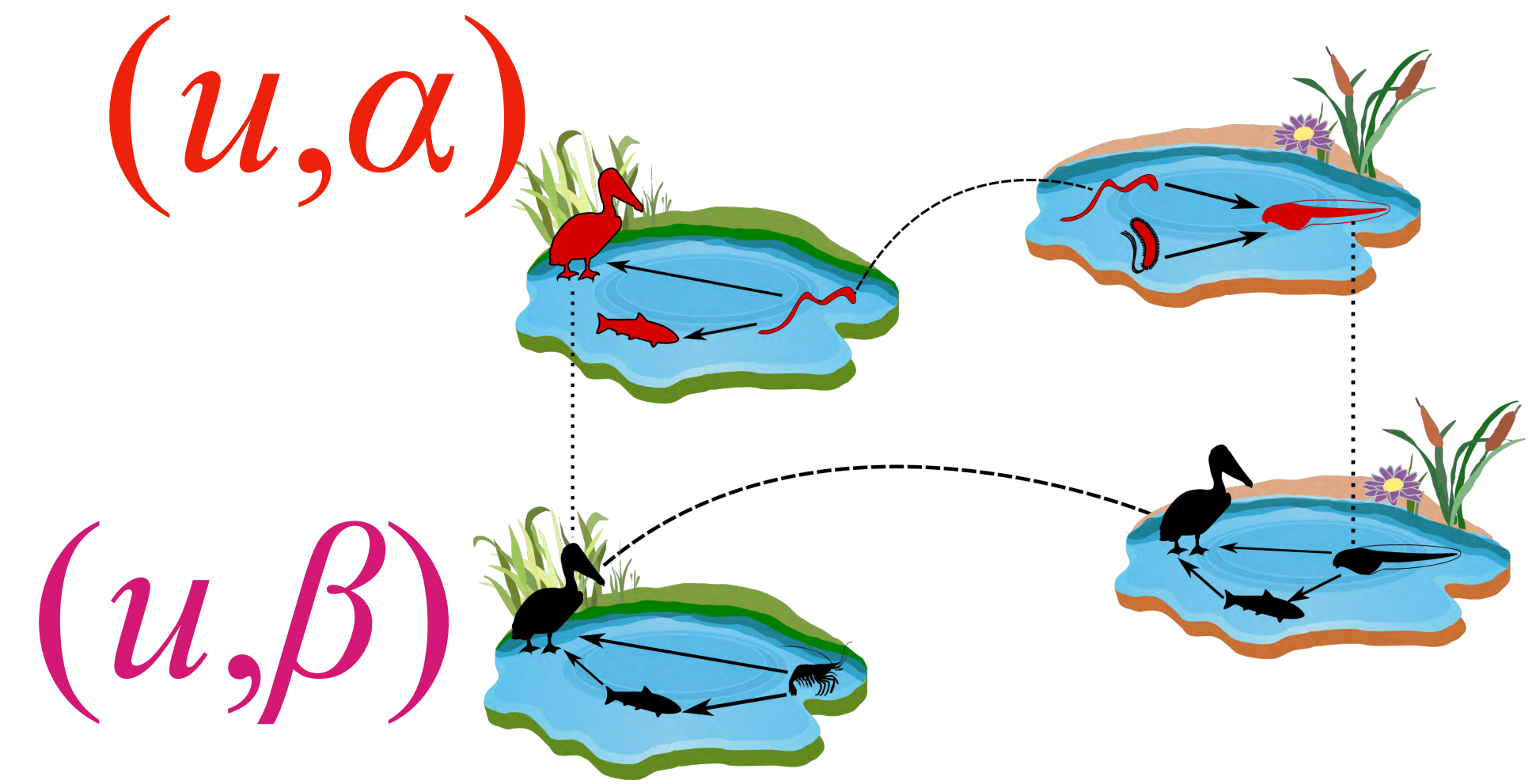


$$\mathbf{L} = \{L_a\}_{a=1}^d$$

$$V_M \subseteq V \times L_1 \times L_2 \cdots \times L_d$$

$$E_M \subseteq V_M \times V_M$$

$$M = (V_M, E_M, V, \mathbf{L})$$



$$E_A = \{((u, \alpha), (v, \beta)) \in E_M \mid \alpha = \beta\}$$

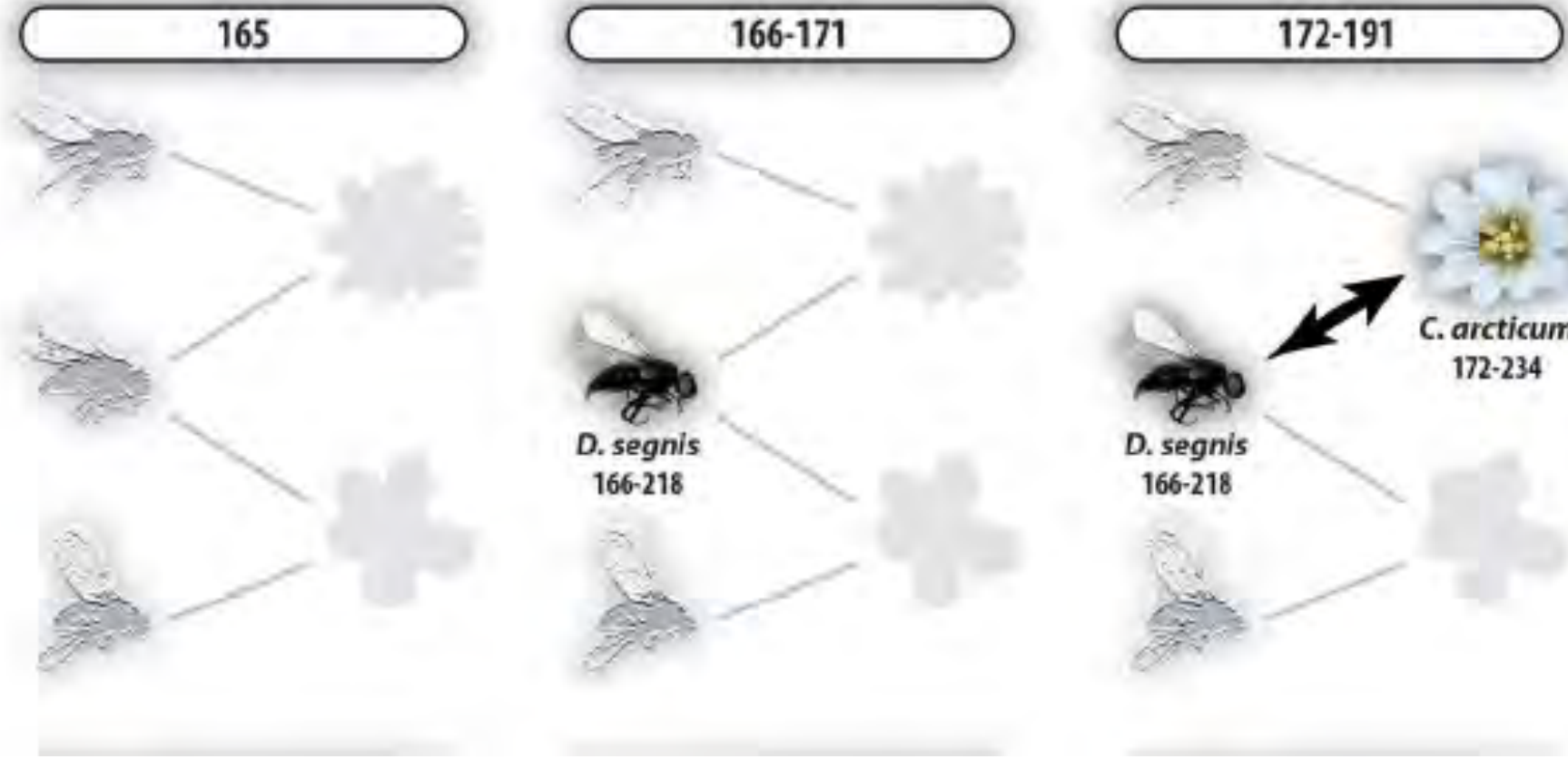
$$E_C = E_M \setminus E_A$$

$$E_T = \{((u, t), (v, t + \tau)) \in E_C\}$$

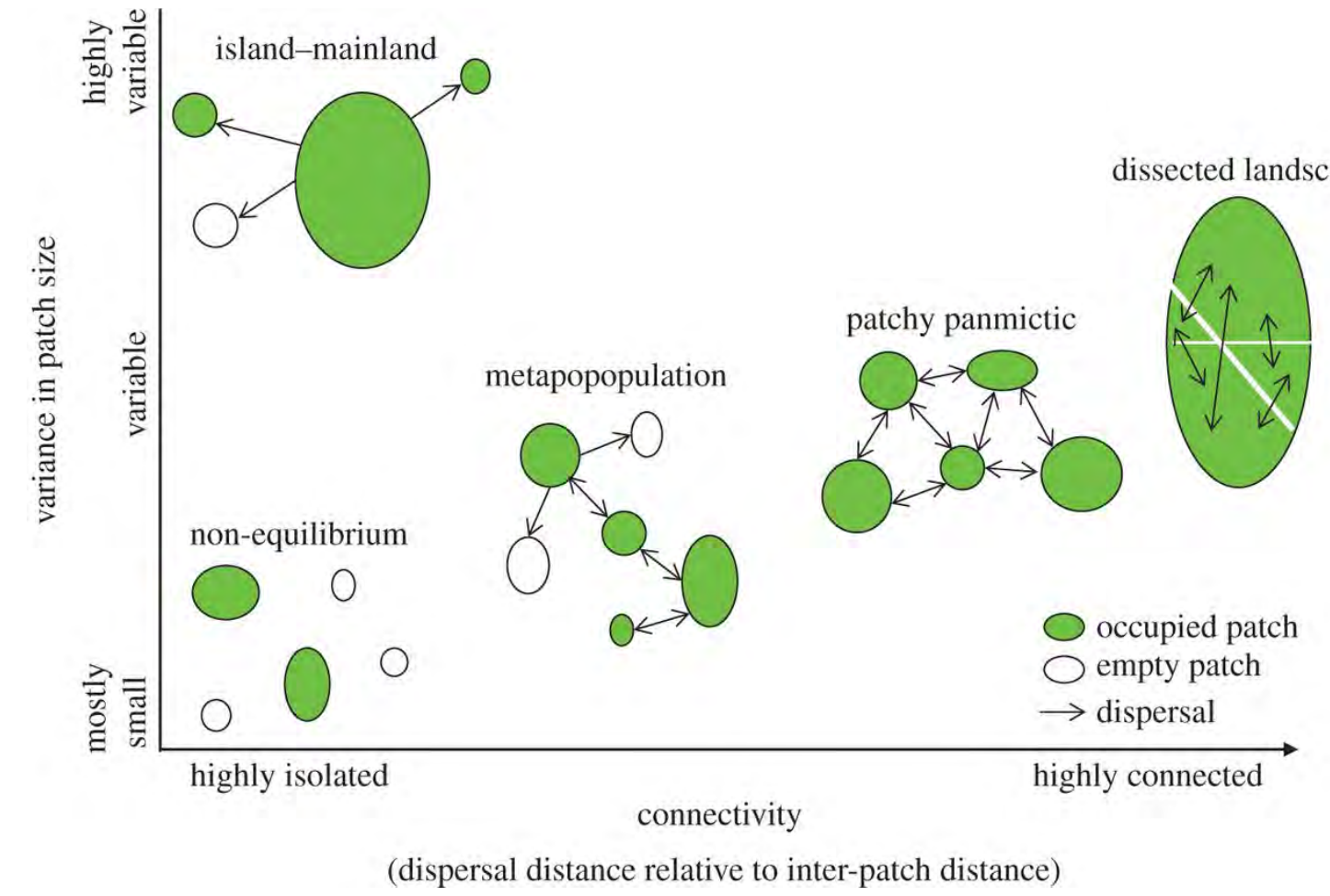
Temporal network

Categories of Ecological Multilayer networks

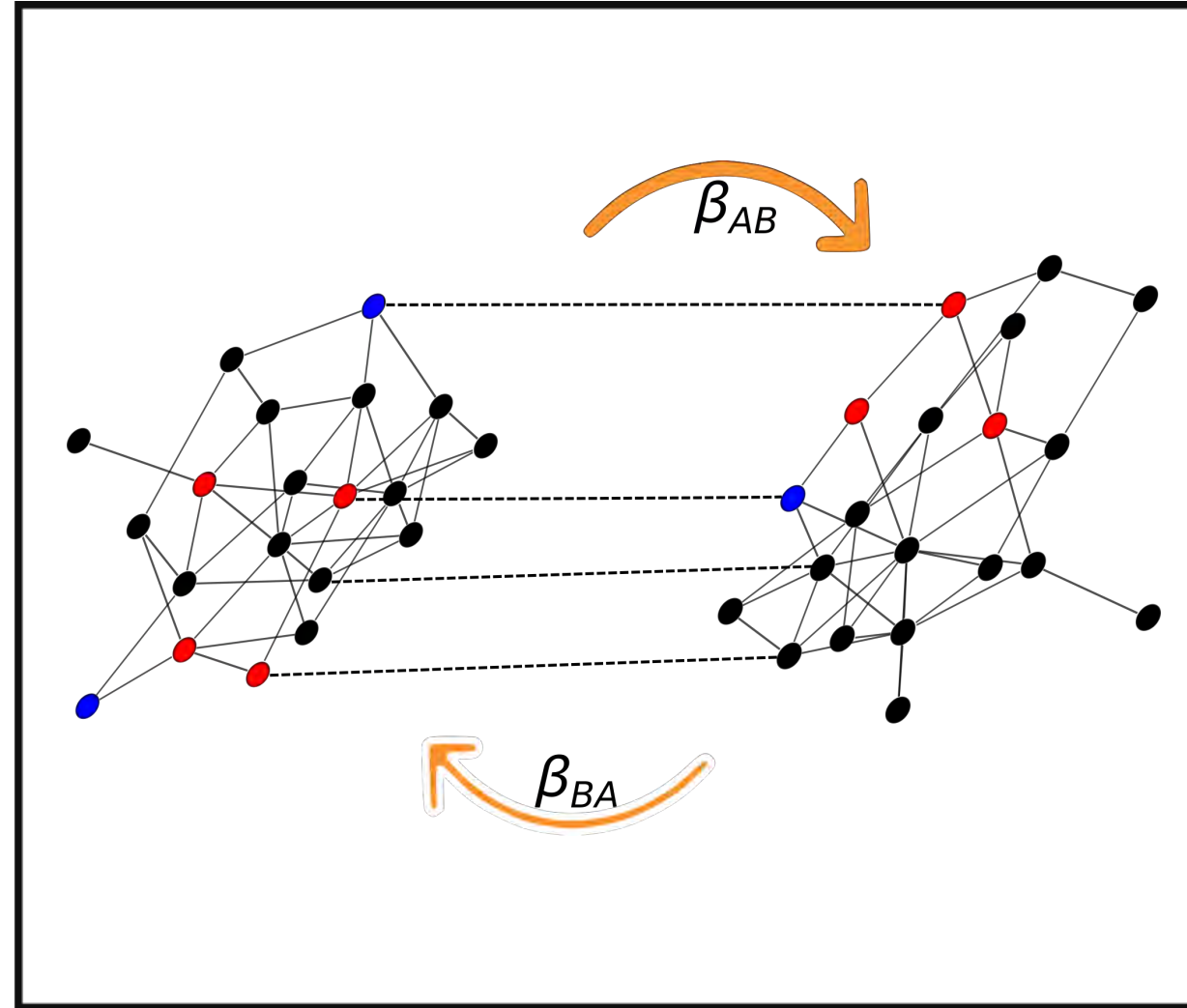
B) Dynamical view



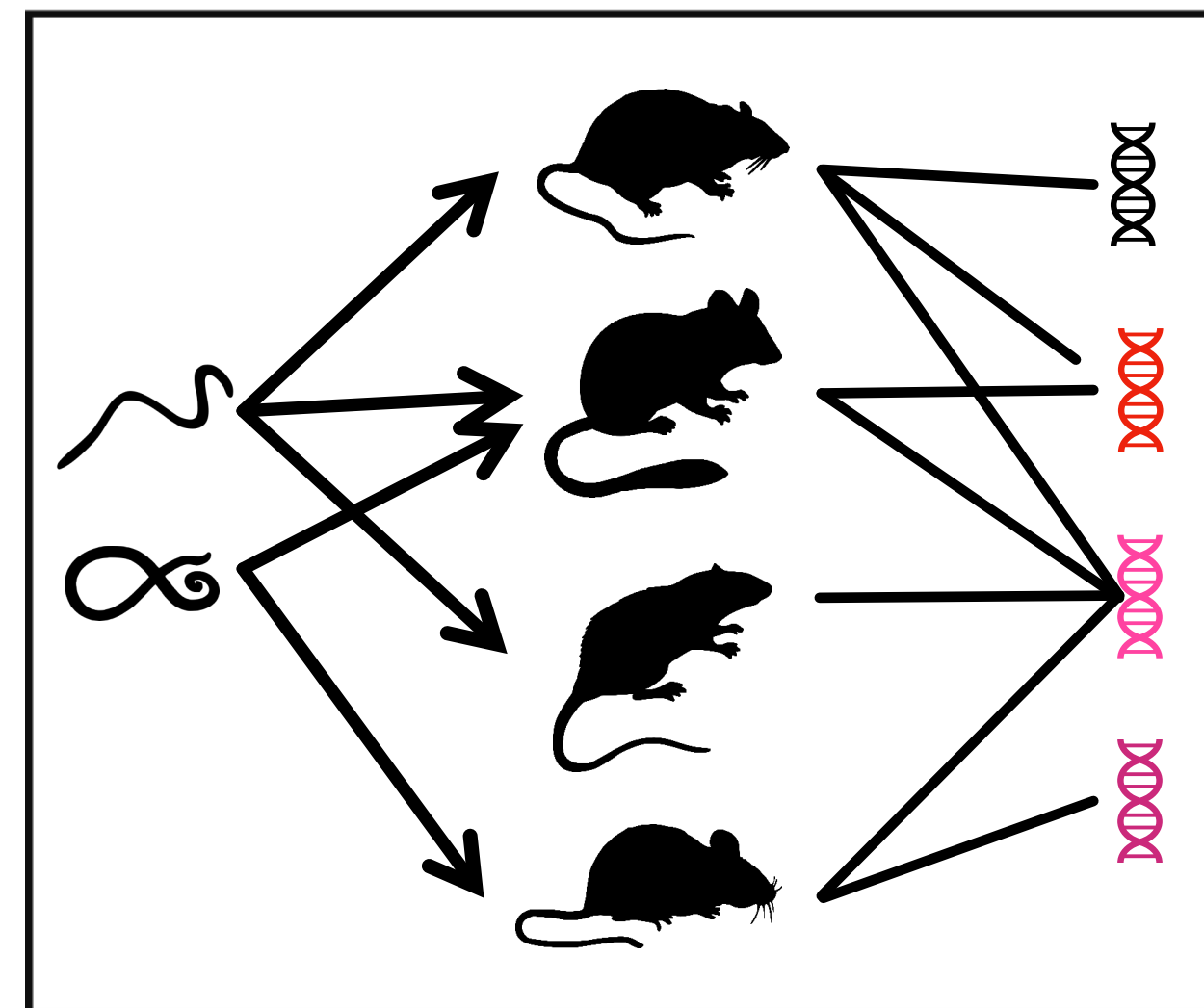
Rasmussen et al. 2013



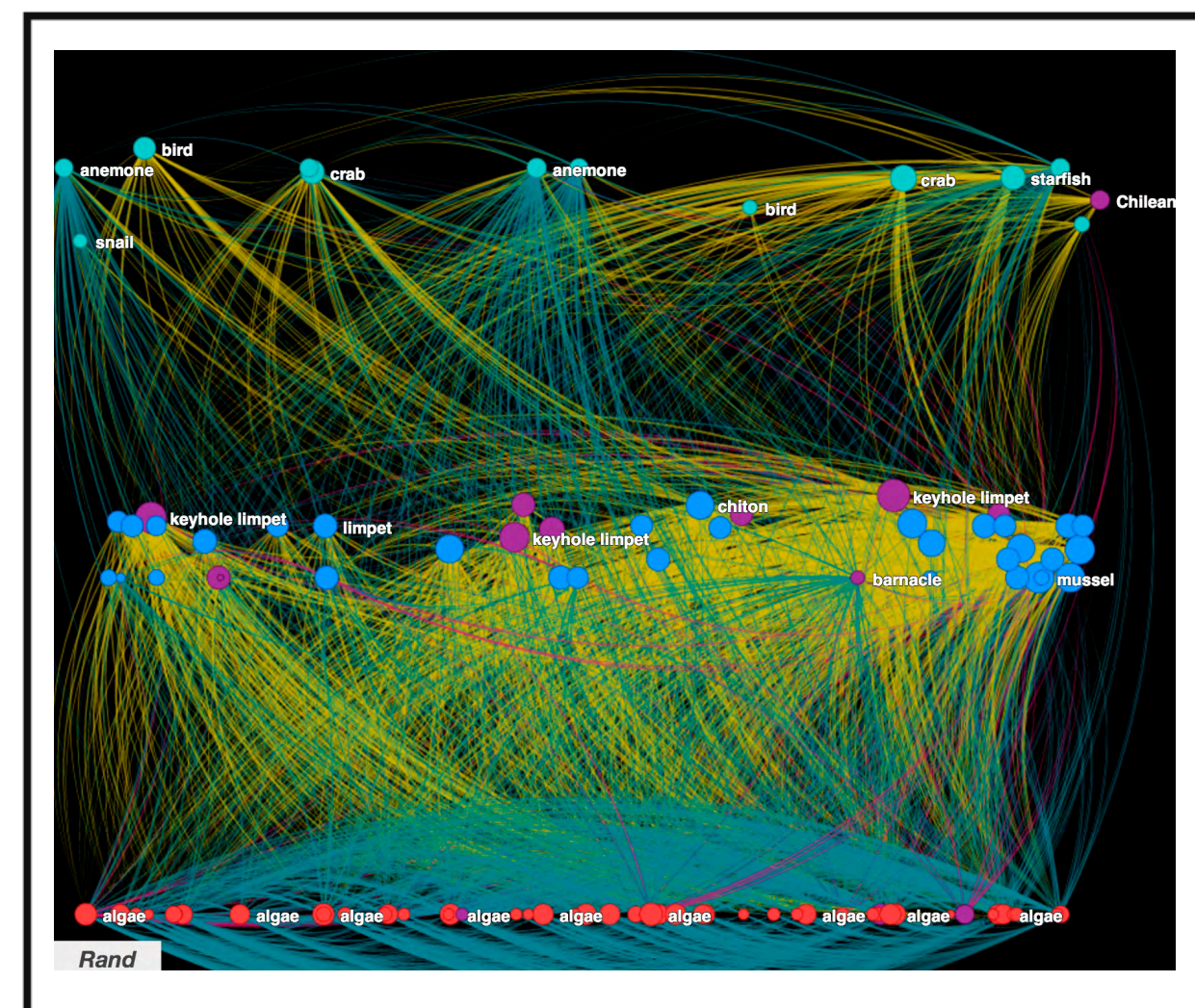
Cheptou et al., 2014



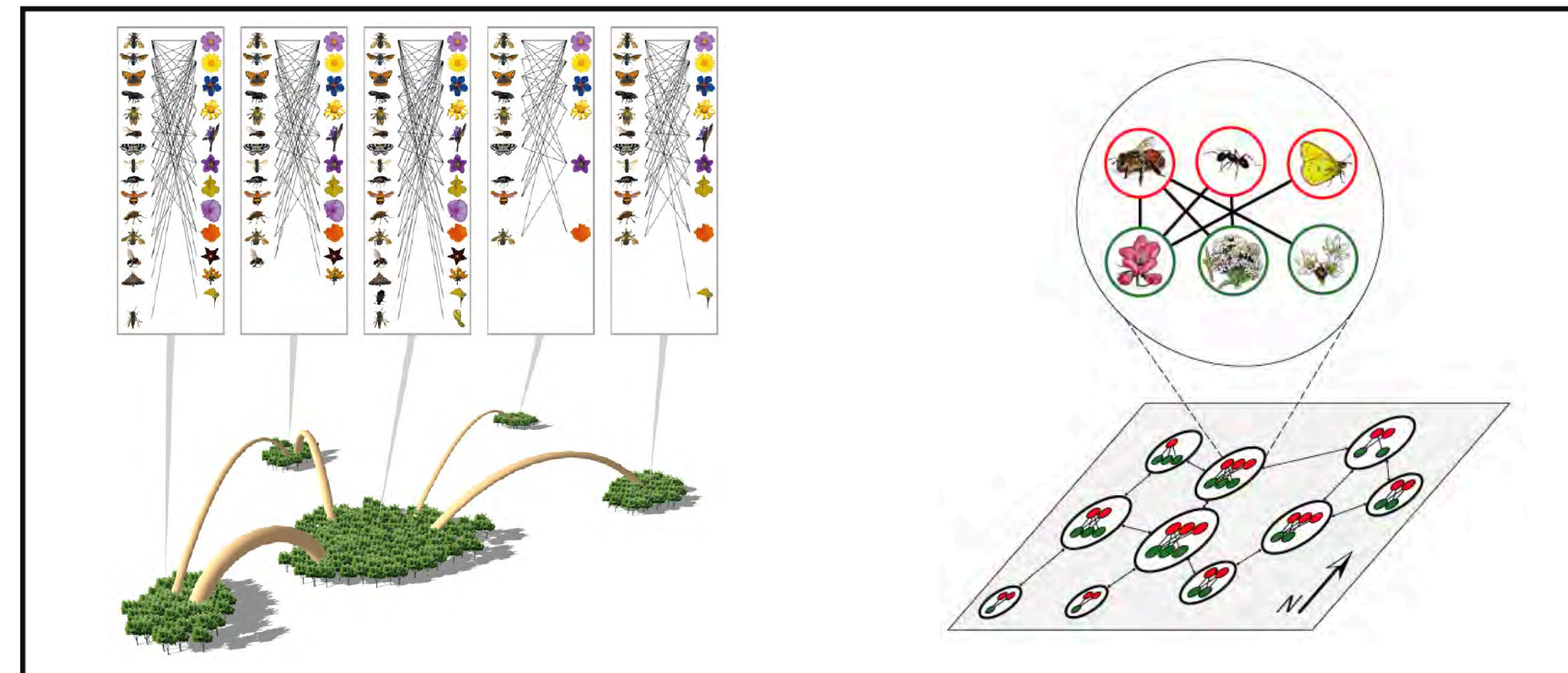
Pilosof et al., 2017



Pilosof et al. 2014



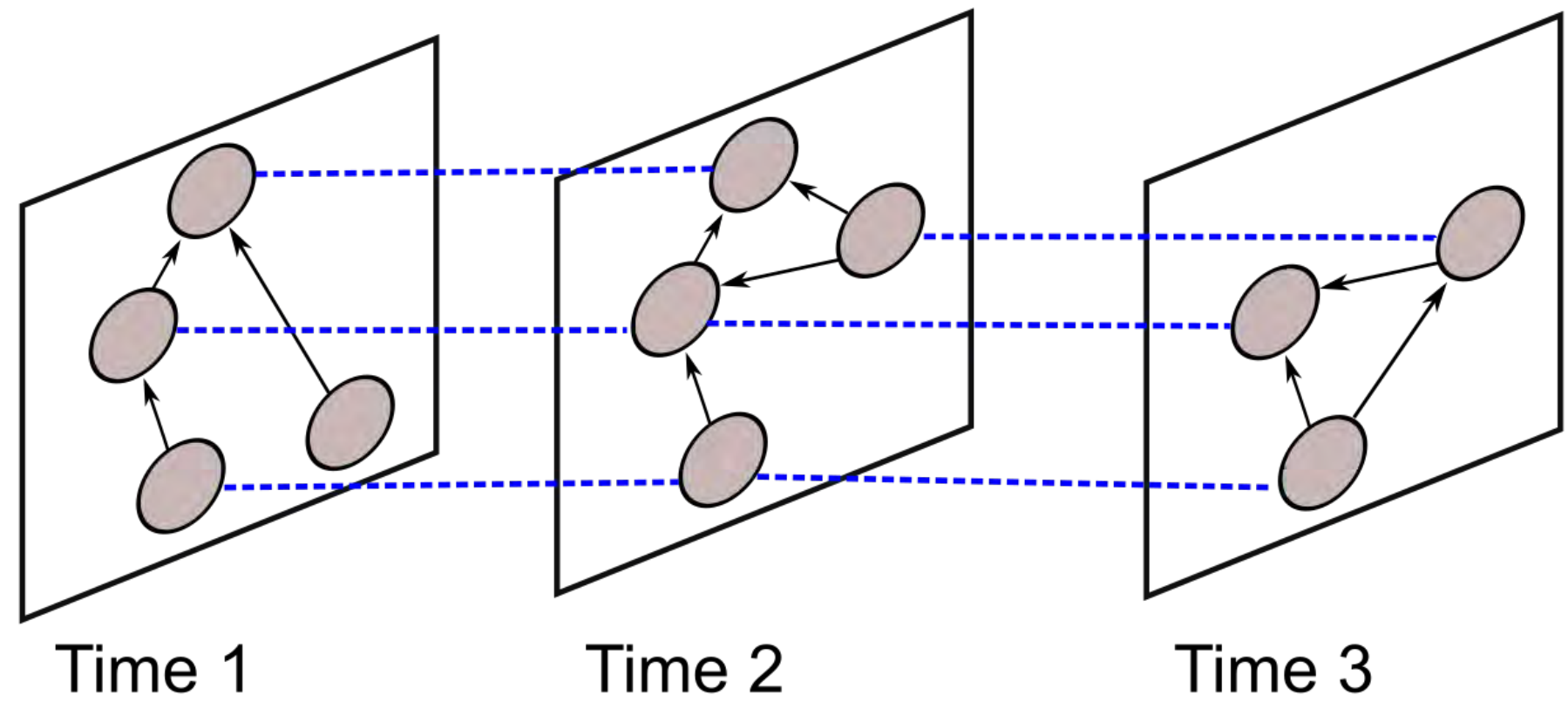
Kéfi et al. 2016



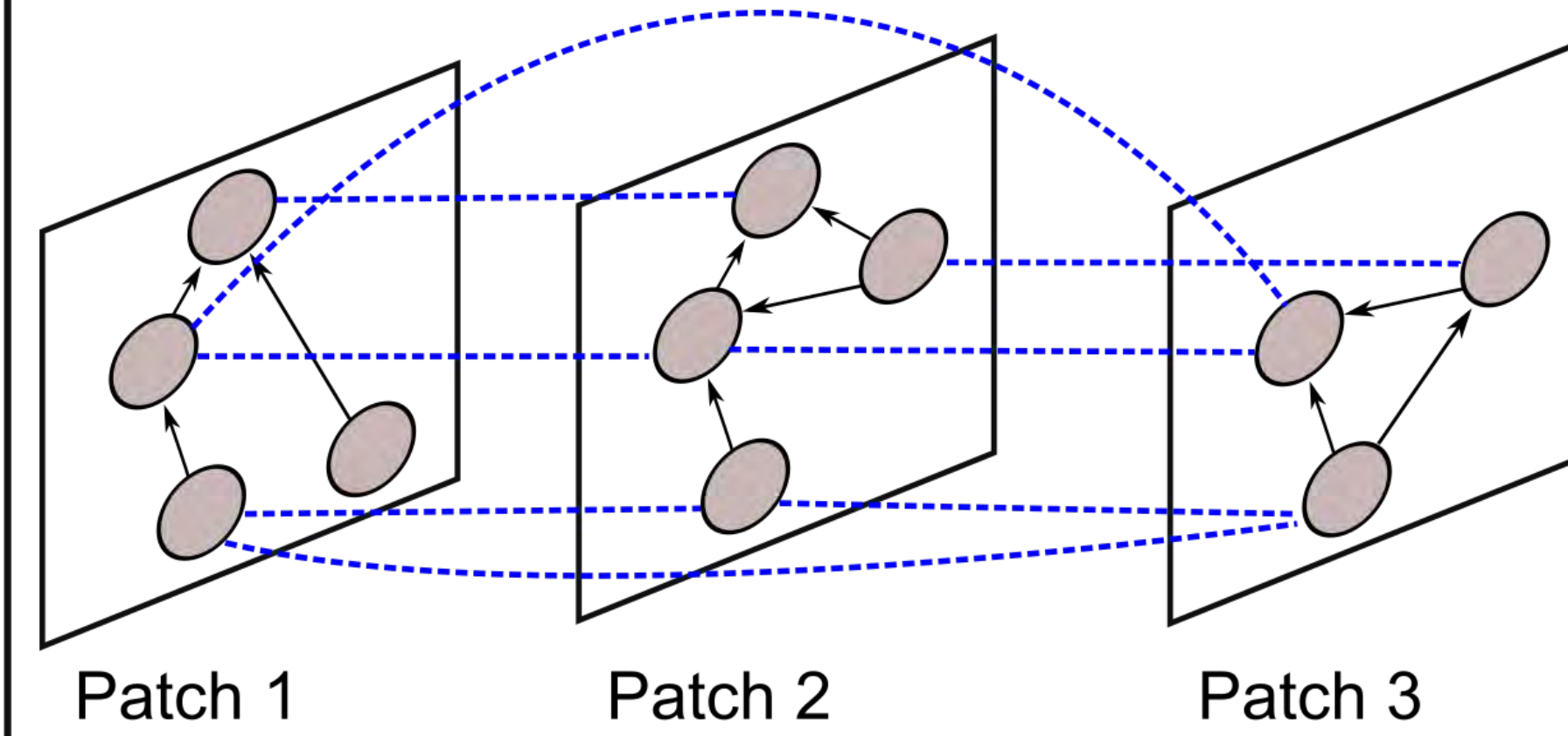
Hagen et al. 2012, Gilarranz et al. 2014

Categories of Ecological Multilayer networks

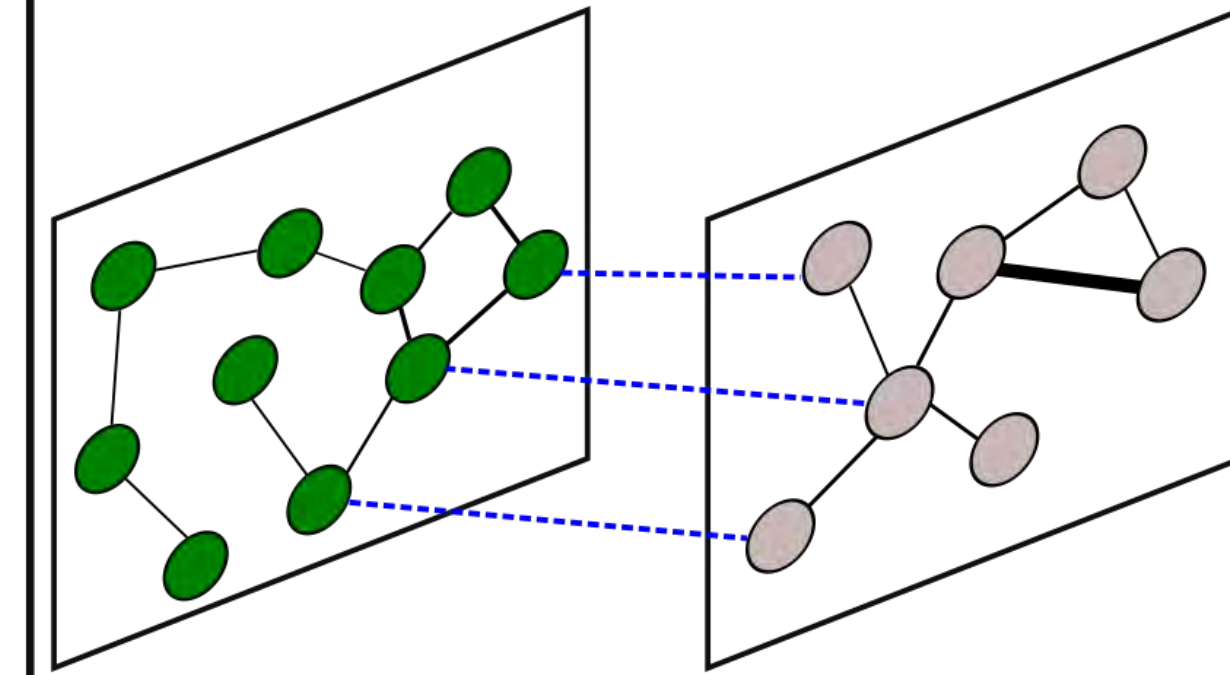
Temporal



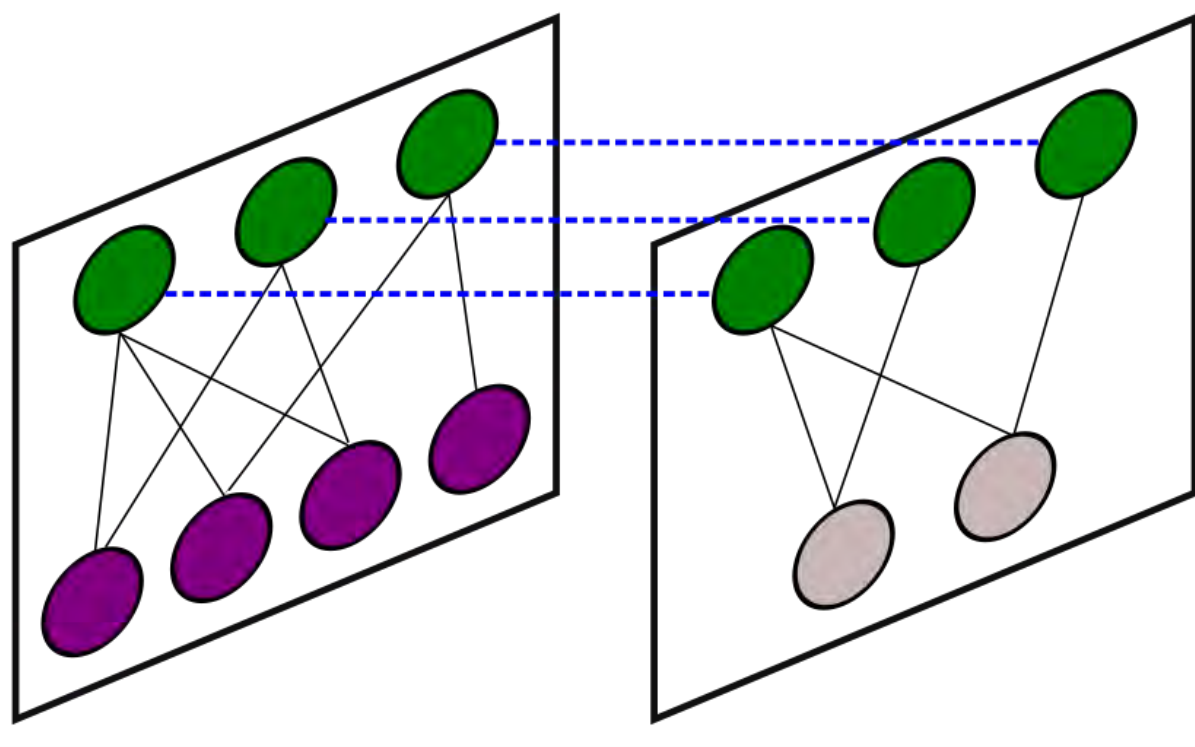
Spatial



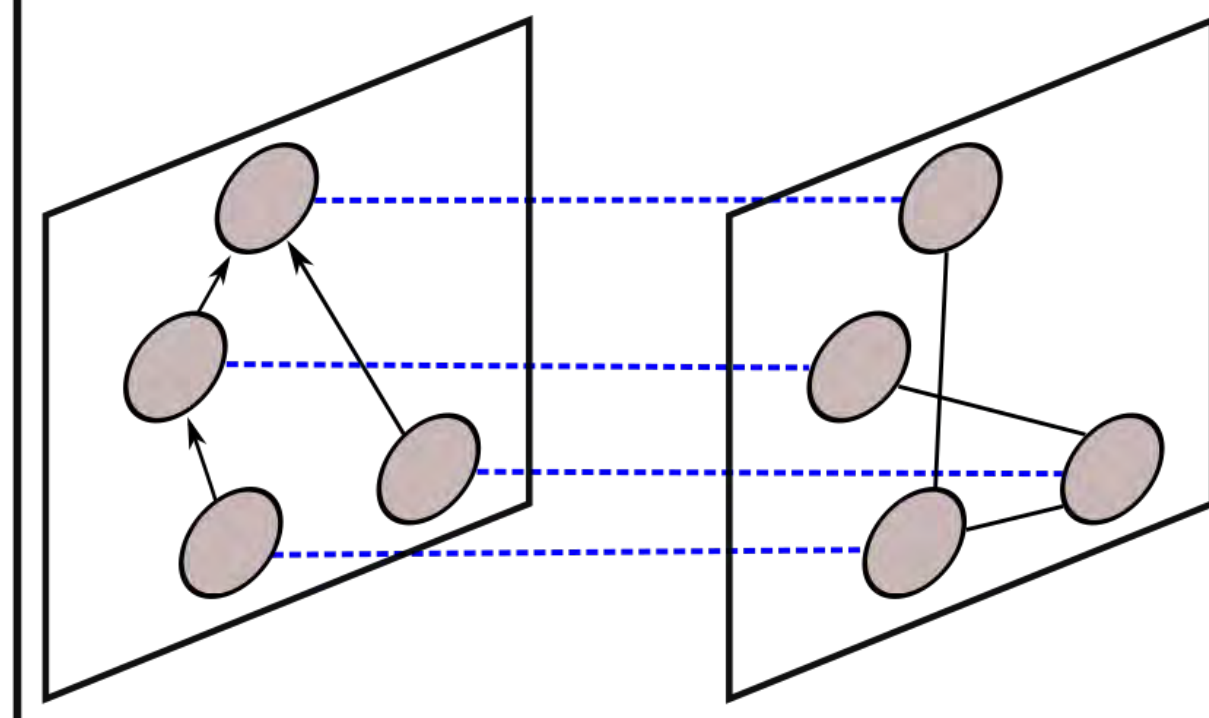
Interconnected



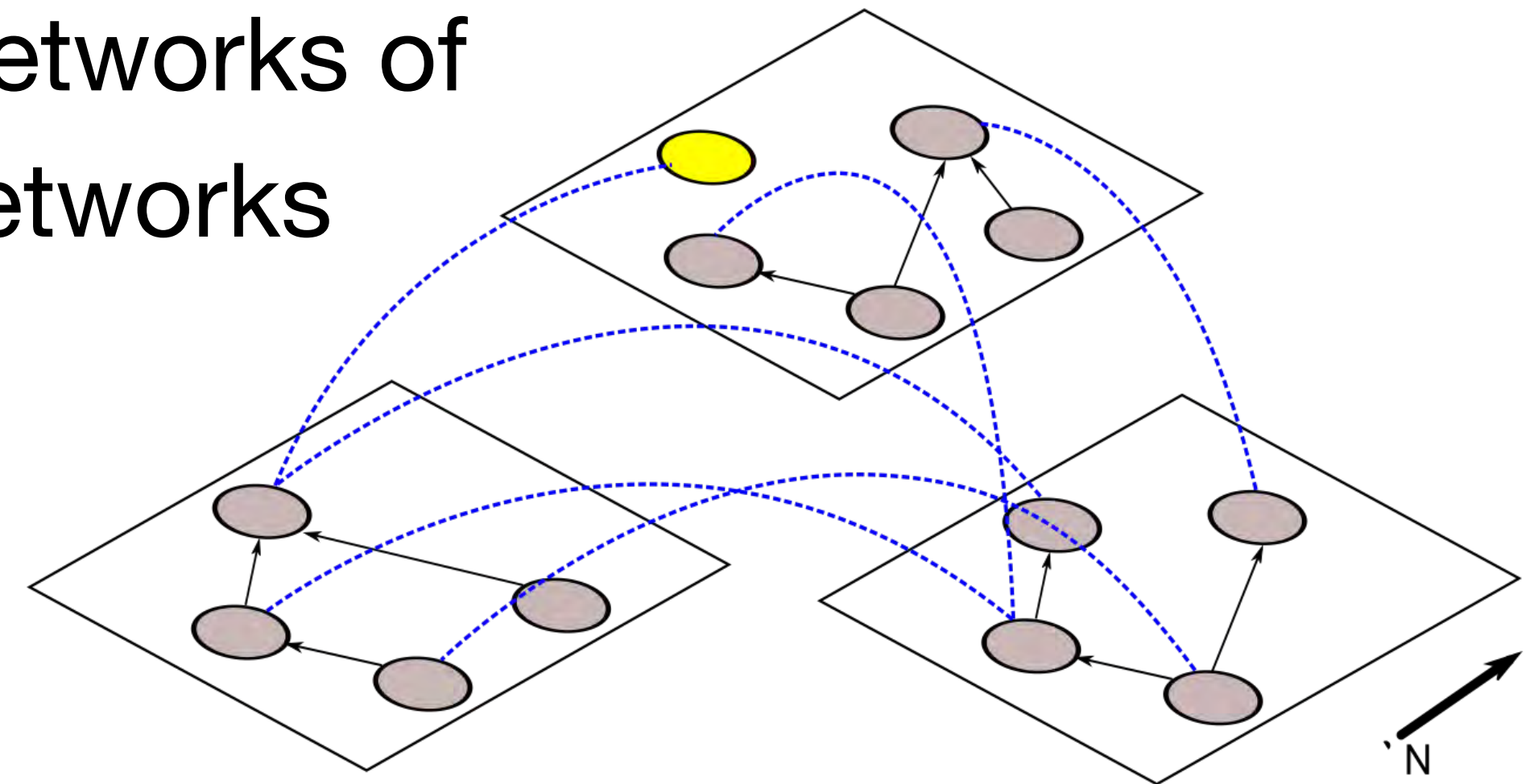
Diagonally-coupled



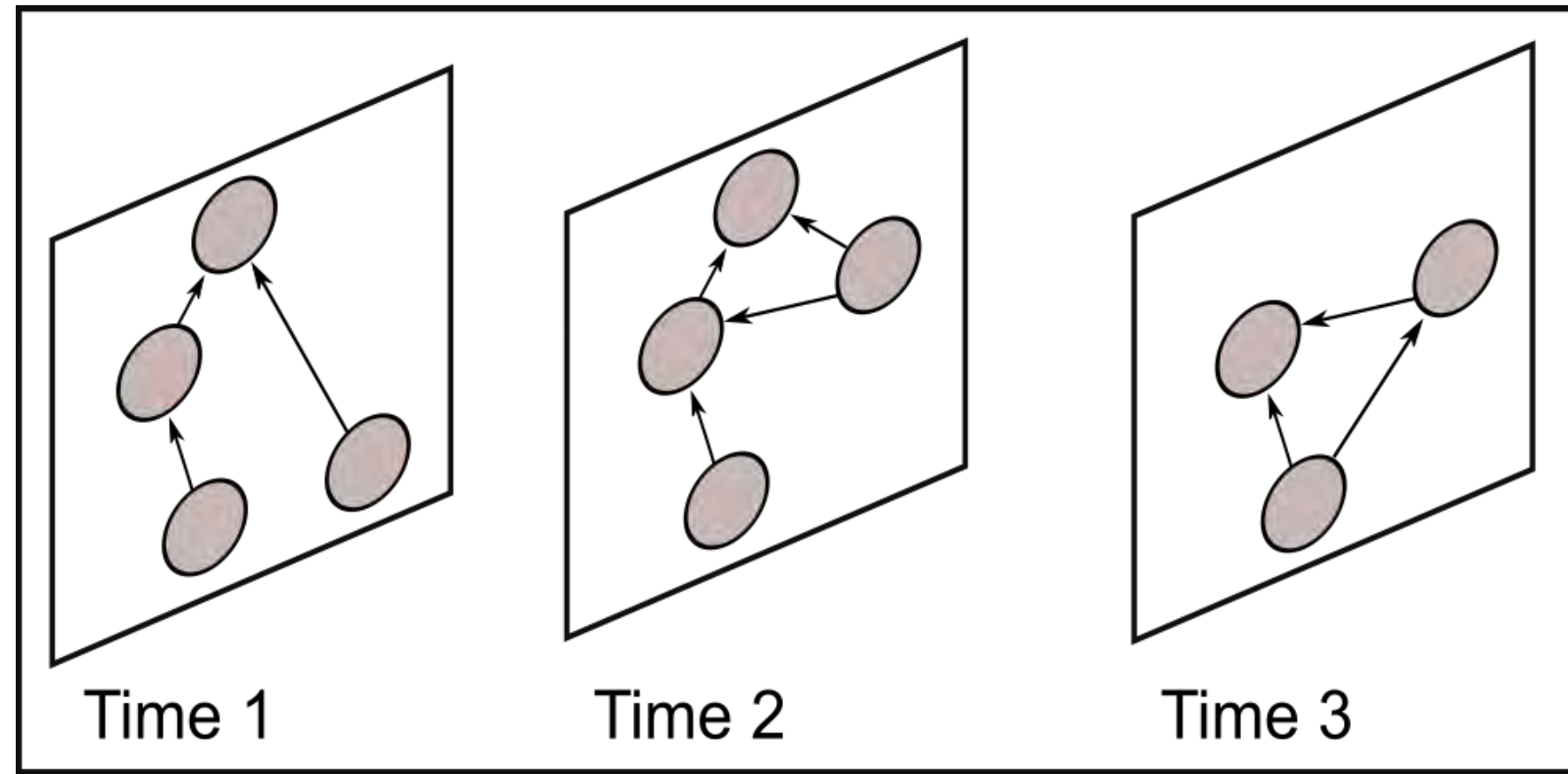
Node-aligned



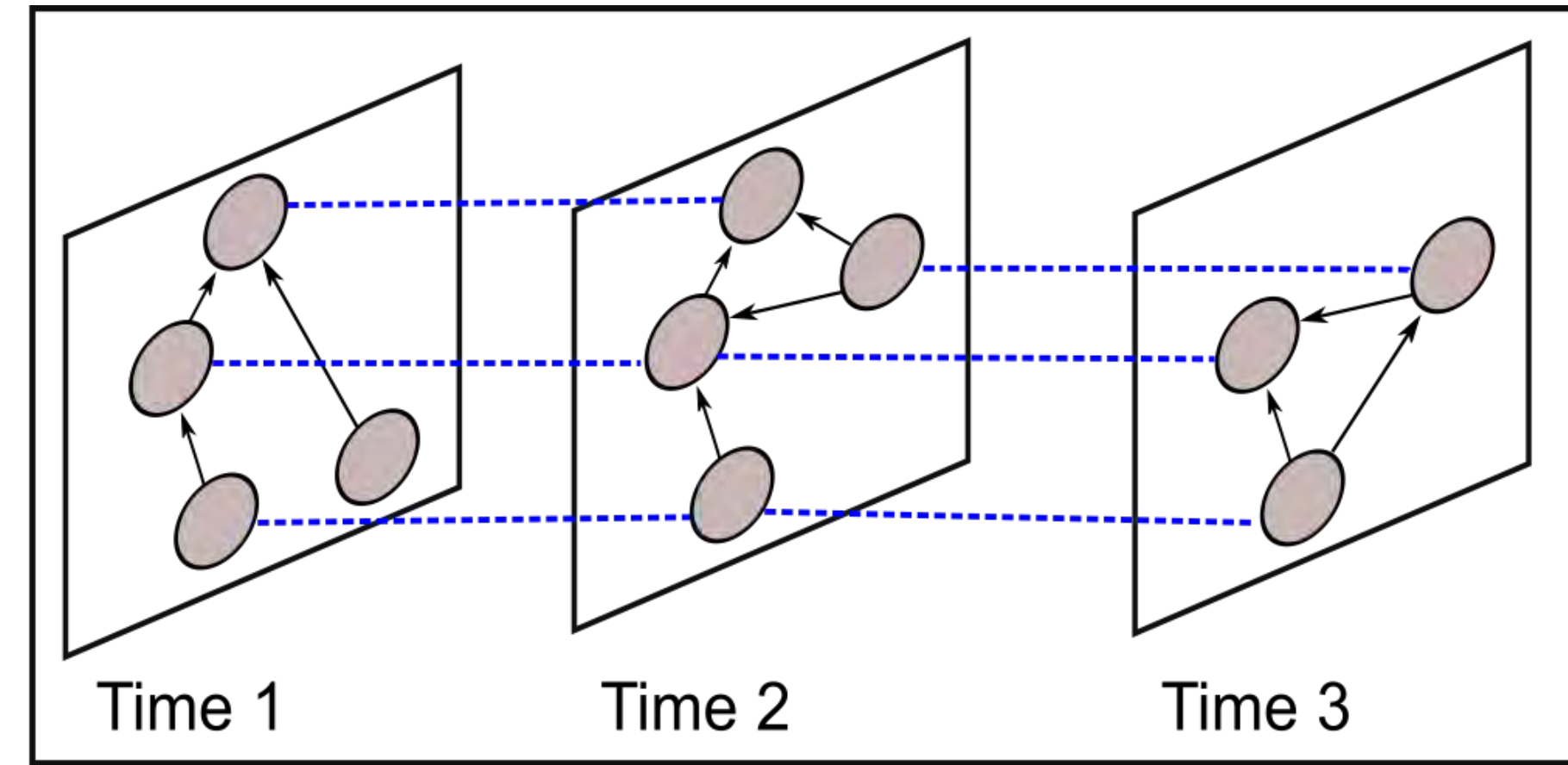
Networks of networks



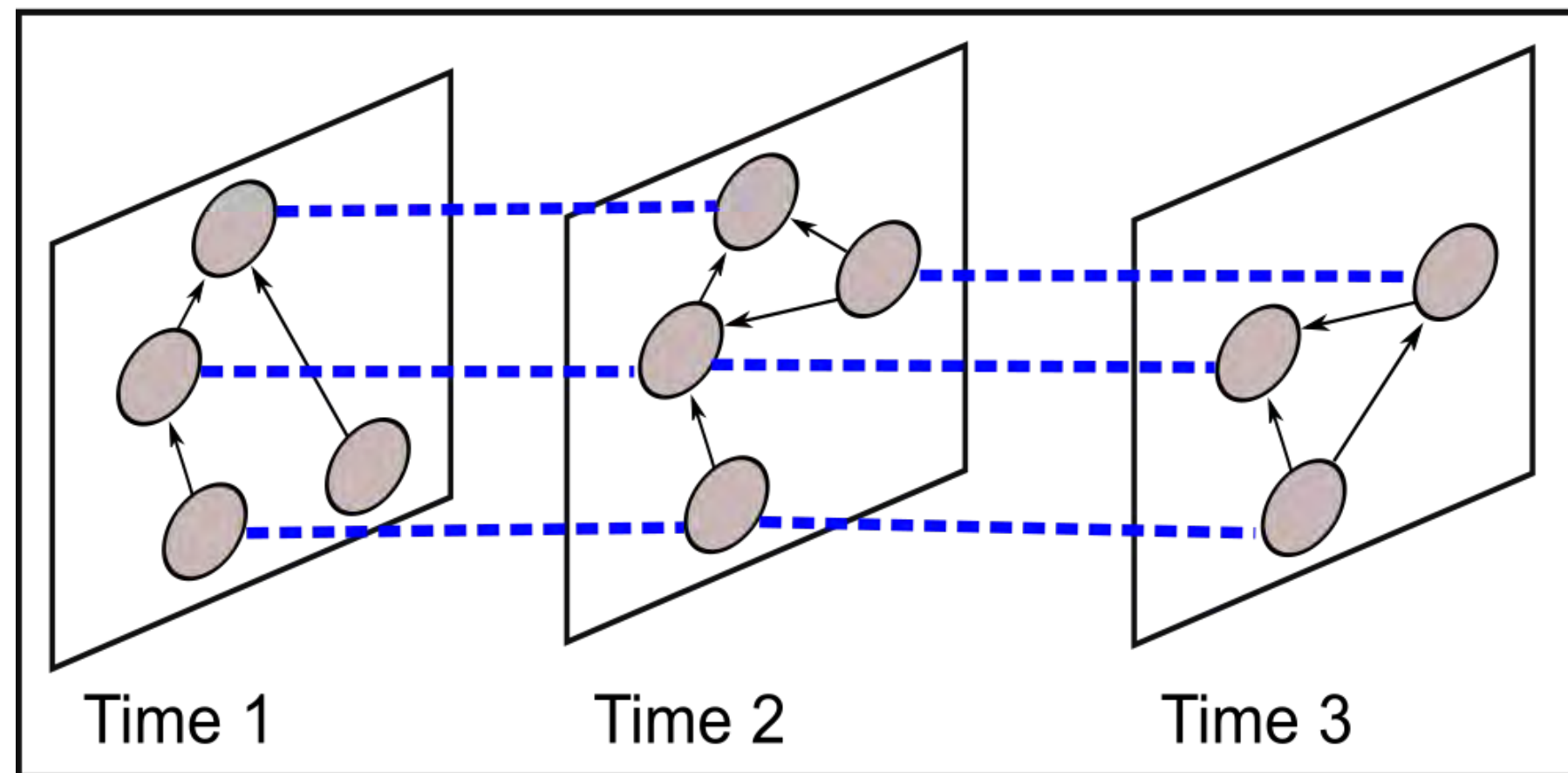
Interlayer edges are the key component



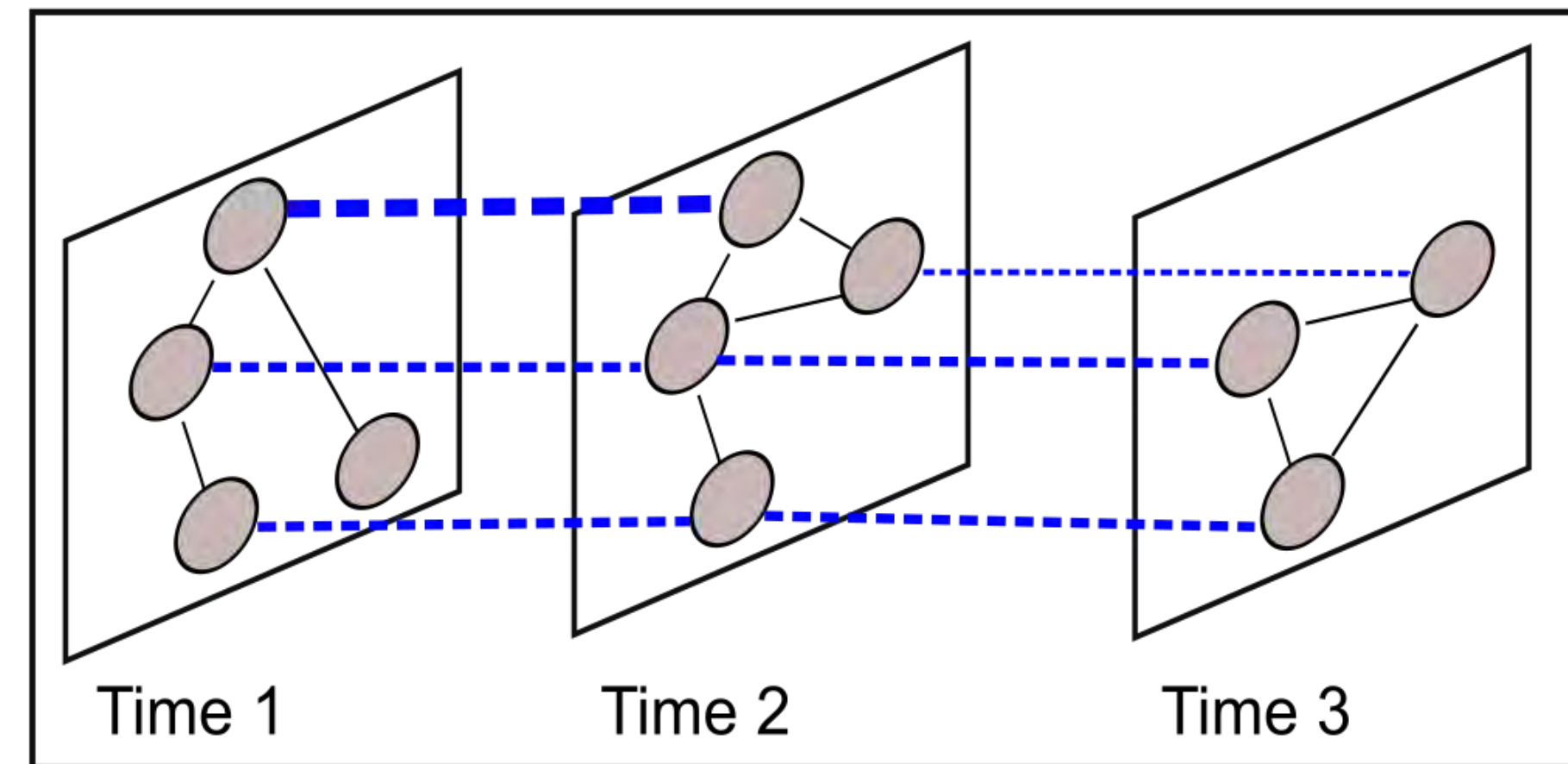
None



Uniform — scale 1

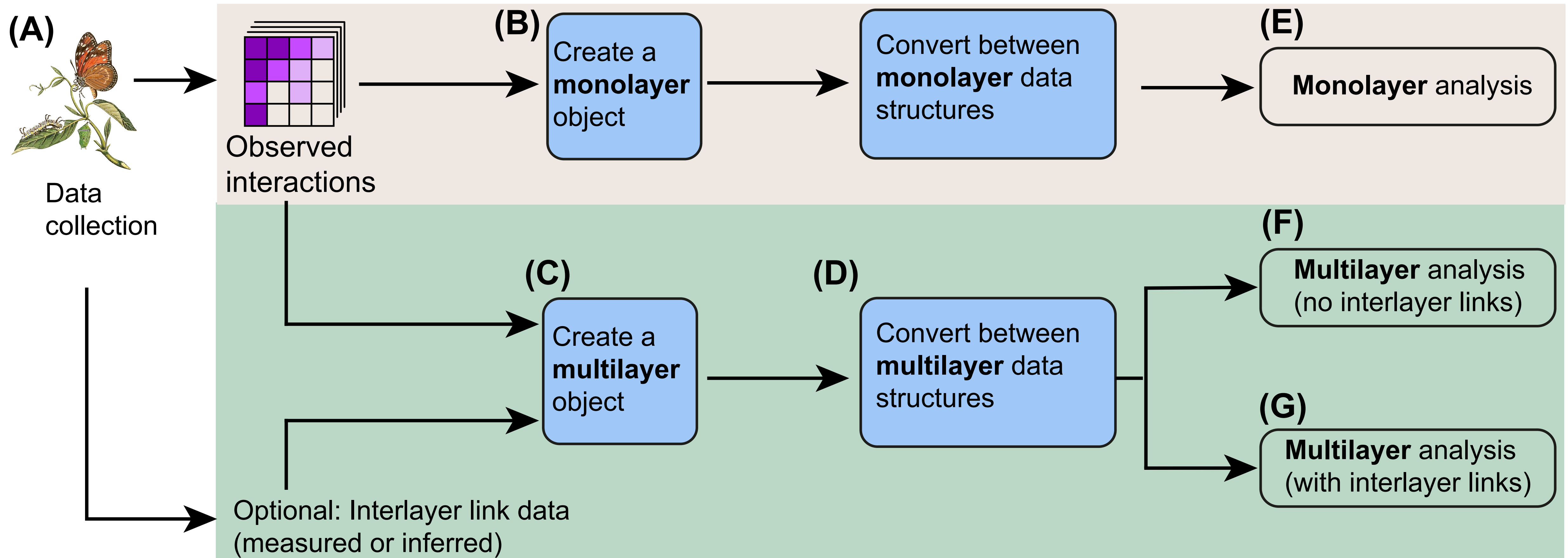


Uniform — scale 2









Non-uniform

Workflow and data organization



Identifying flow modules in ecological networks using Infomap

Carmel Farage¹  | Daniel Edler^{2,3,4}  | Anna Eklöf⁵  | Martin Rosvall²  |
Shai Pilosof¹ 

-  Community detection
-  Organize and analyze EMLNs



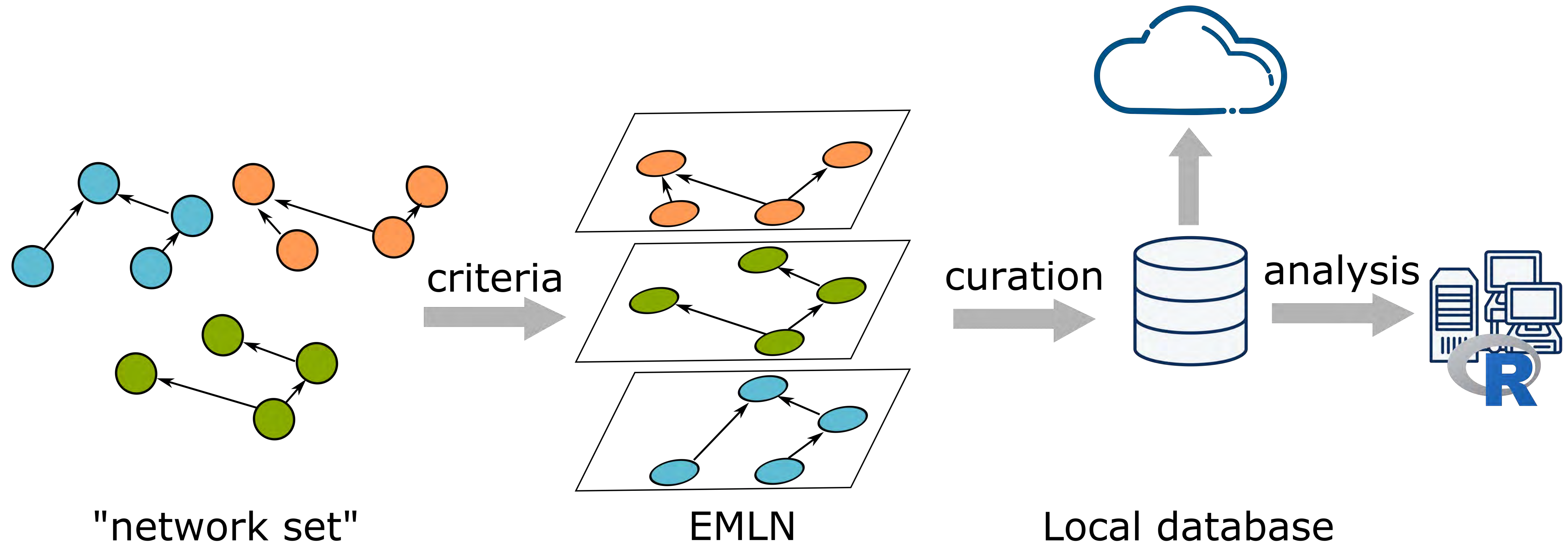
Martin Rosvall



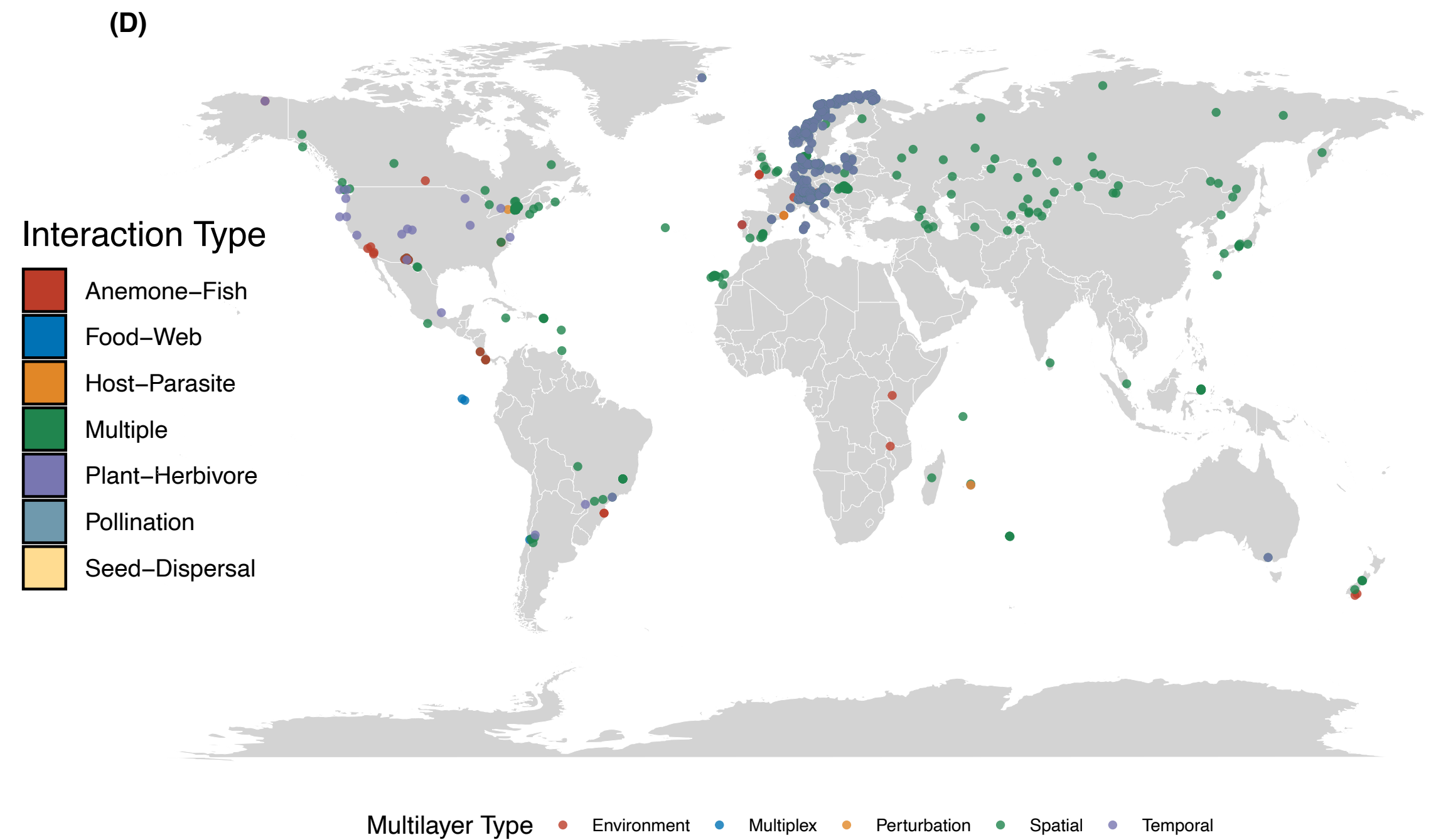
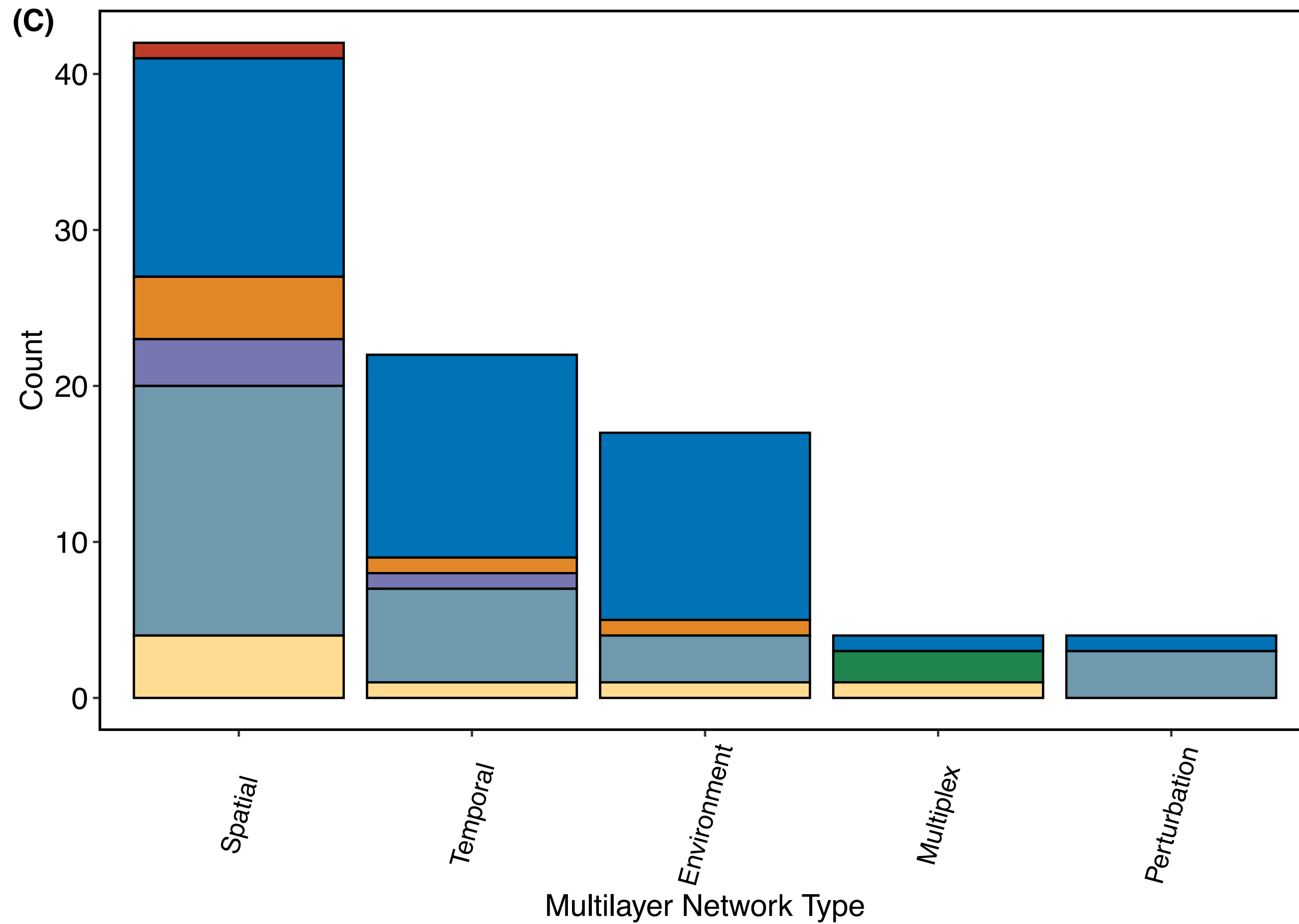
Anna Eklöf



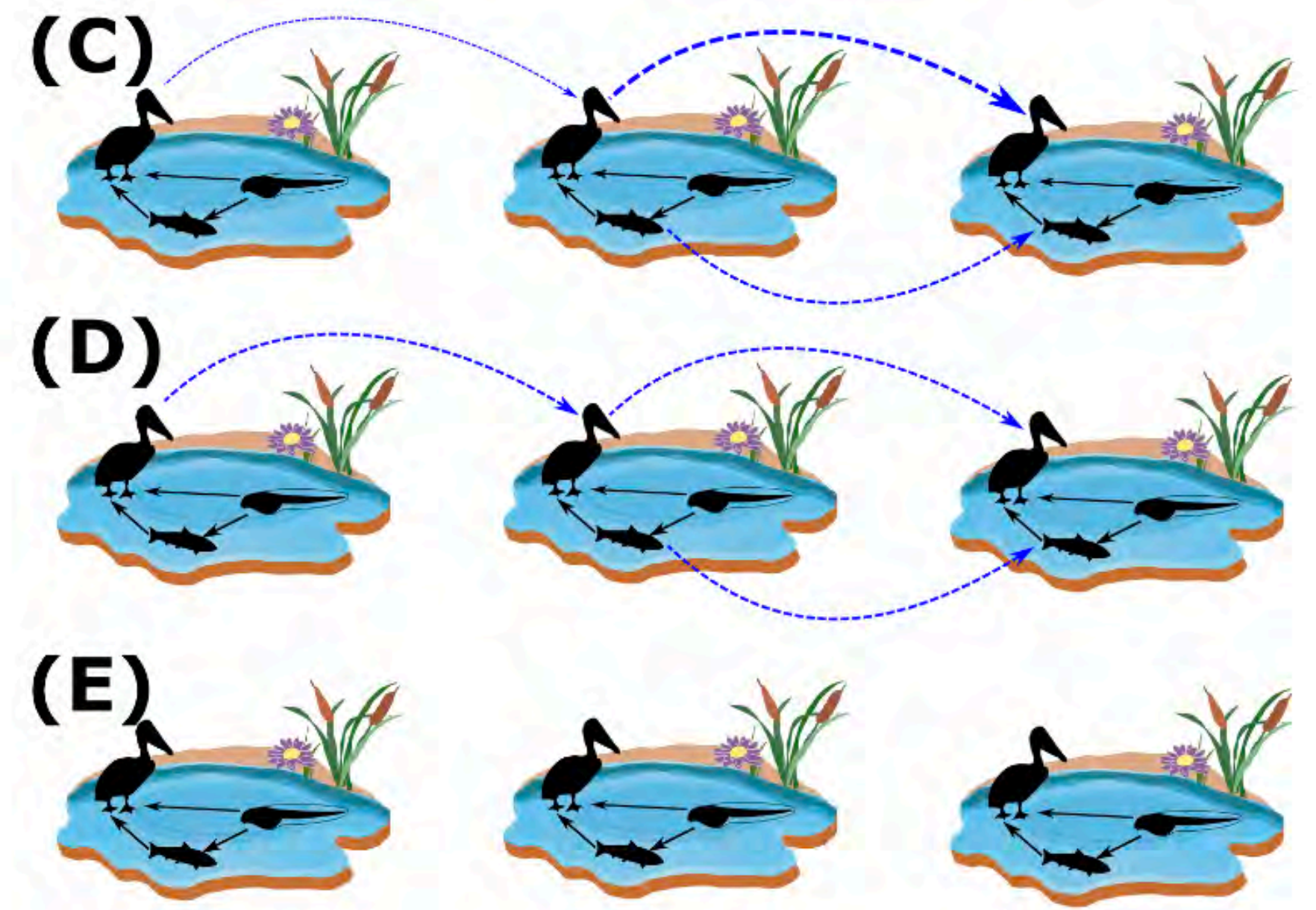
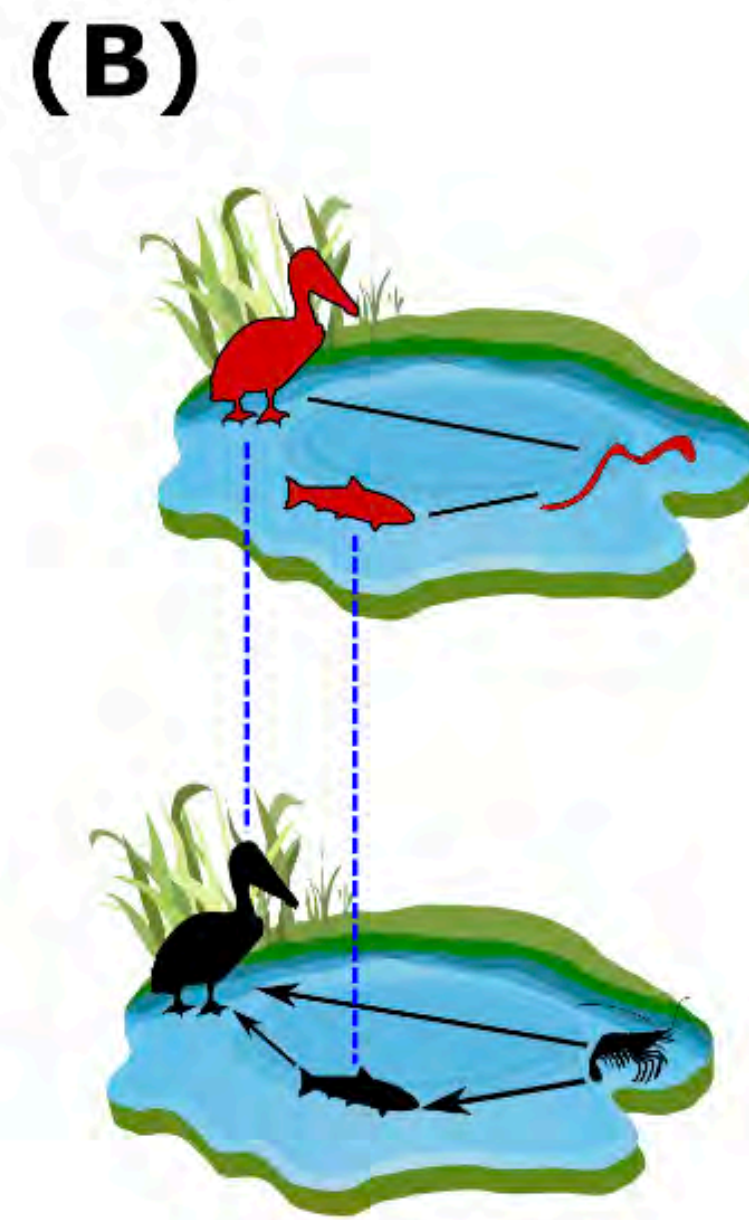
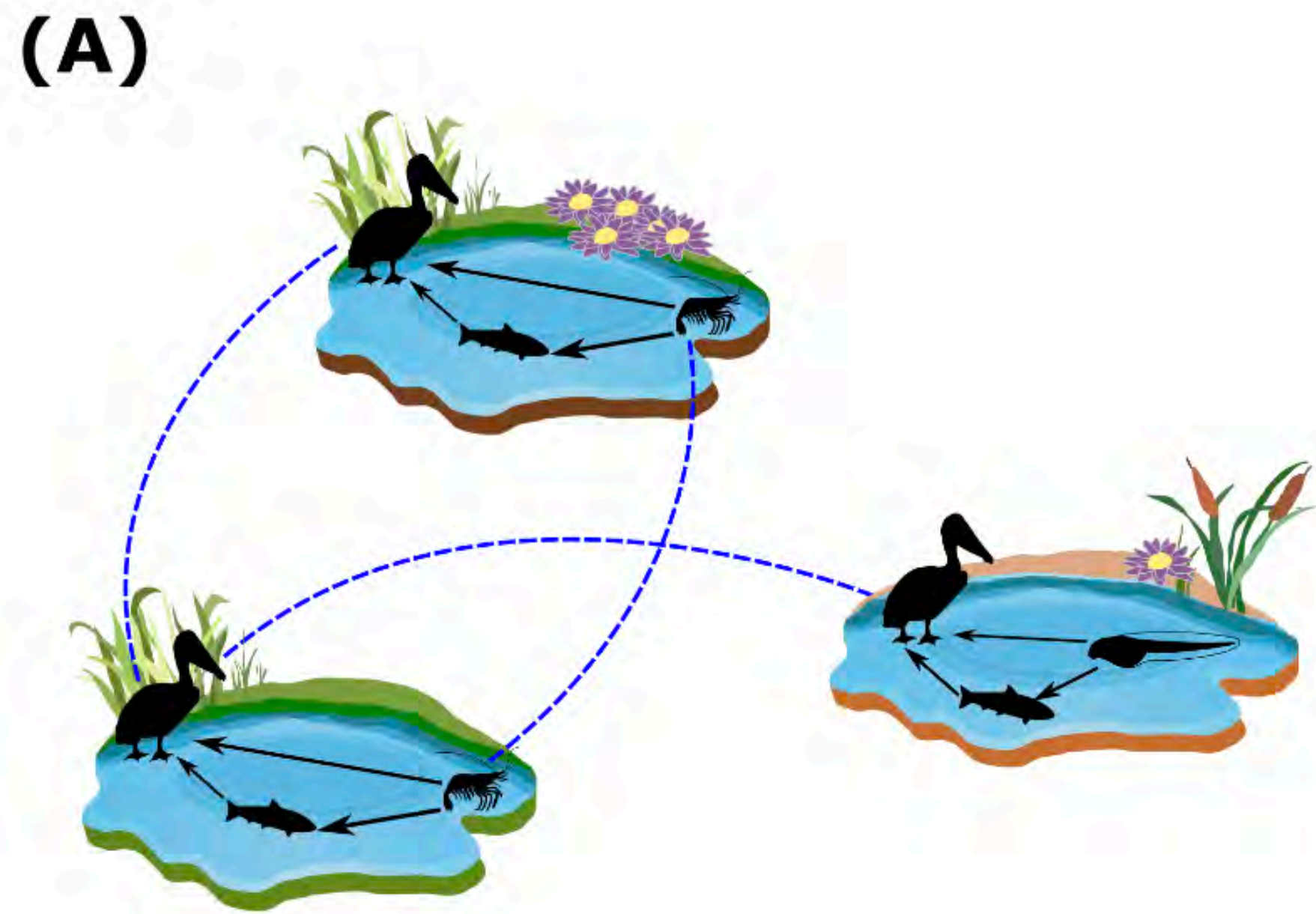
EMLN database



EMLN database



1. None.
2. Inferred.
3. Measured.

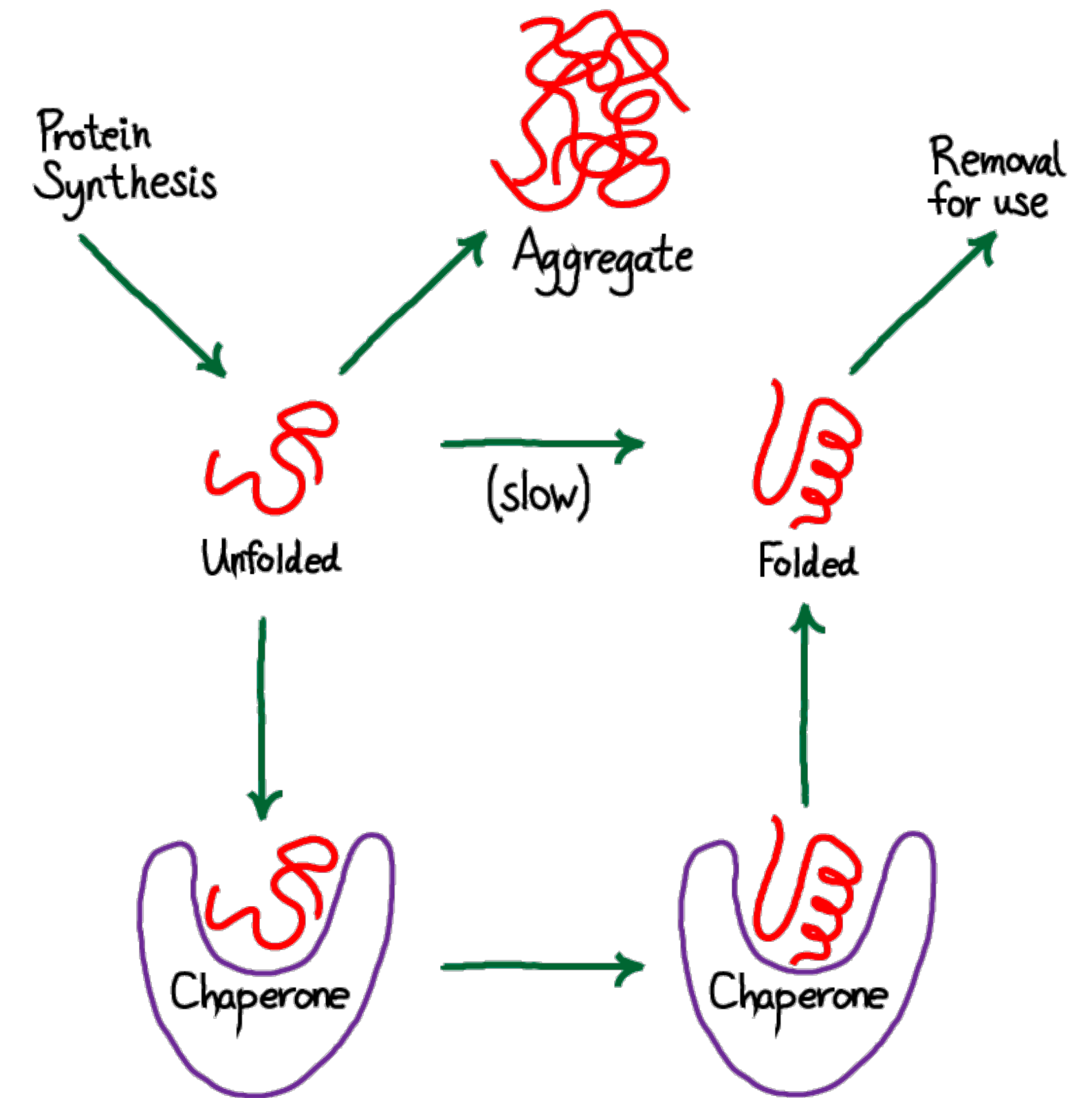


Constructing interlayer links

1. Are they needed?
2. What is the hypothesis encoded?
3. Intralayer vs interlayer number and weight distribution.
4. Algorithms and tools applied.

Protein interactions in changing cancer environments

- Proteins are folded by chaperones.
- Can we predict **chaperone-client interactions** across cancer environments?
- What are the network-wide consequences of targeting proteins?



Geut Galai



Prof. Barak Rotblat

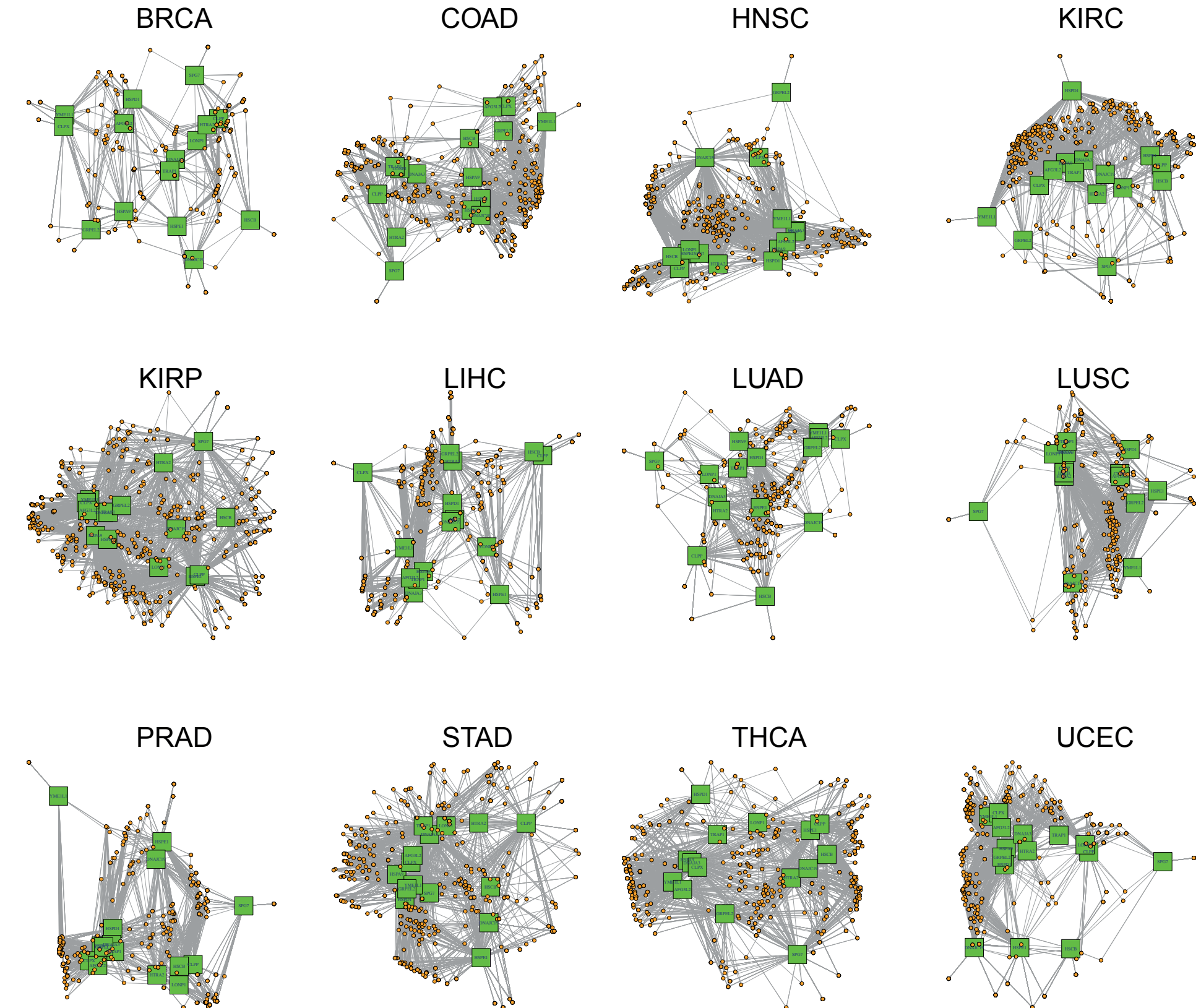


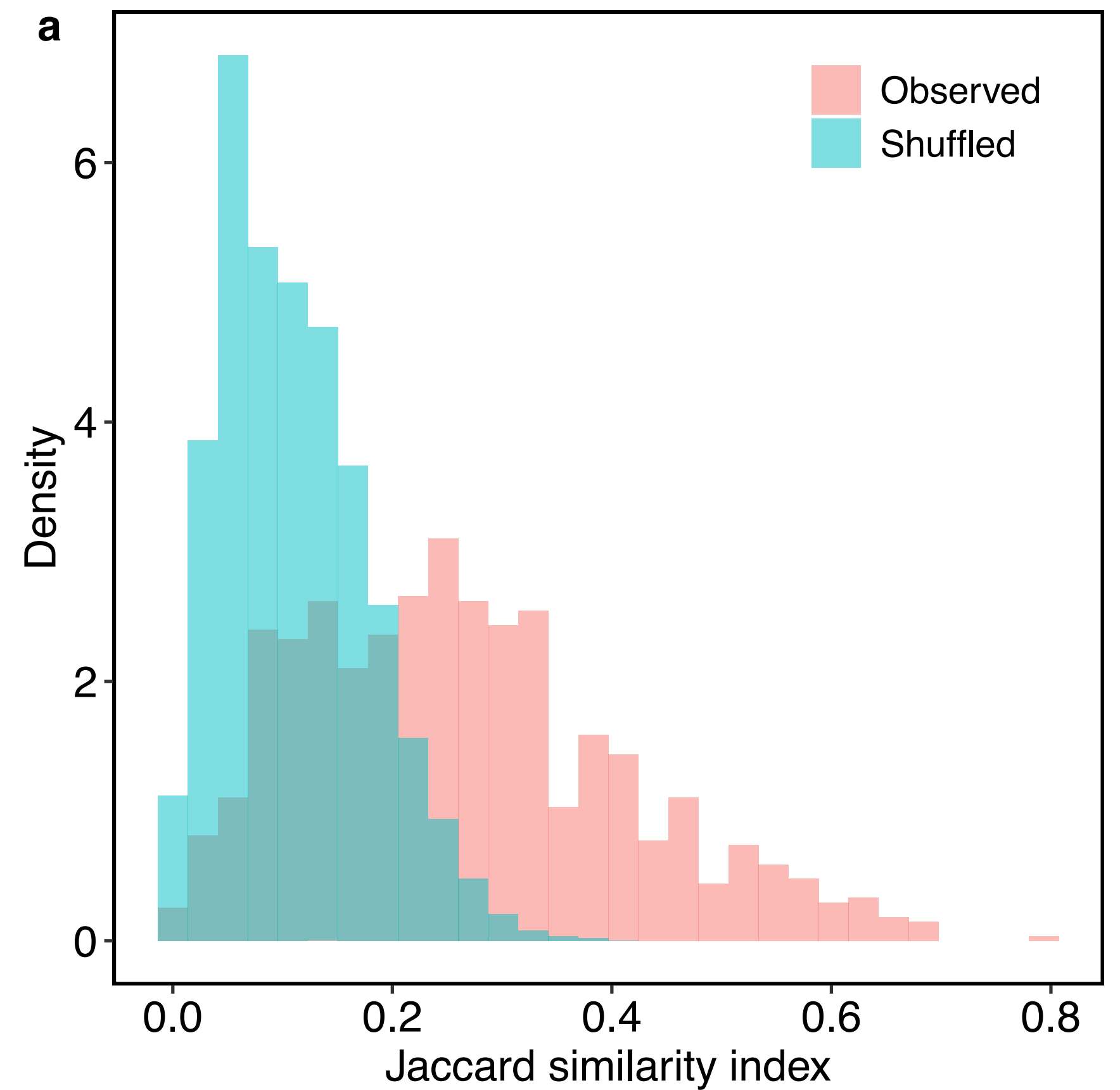
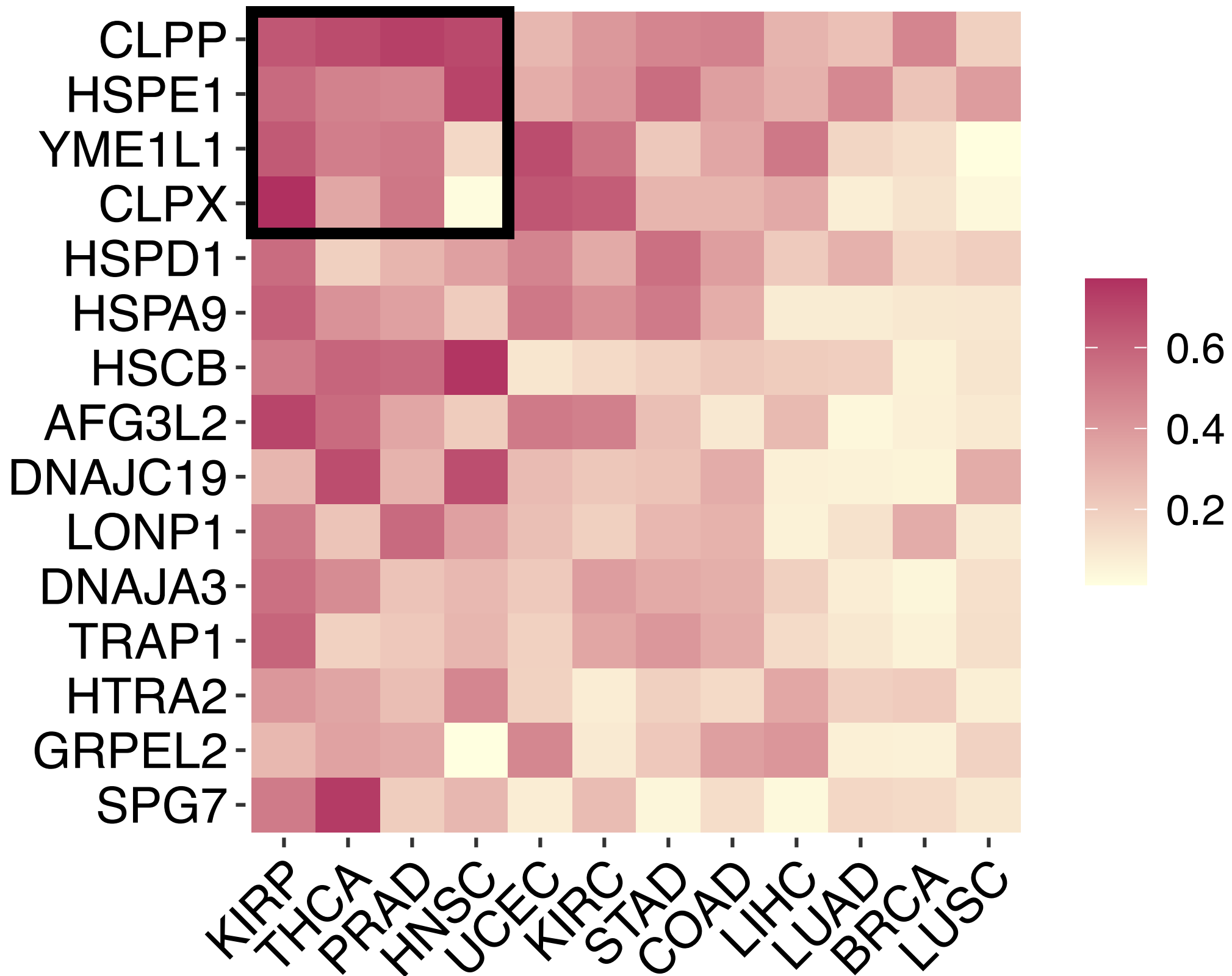
Xie He

Protein interactions in changing cancer environments

How do chaperone-client interactions vary across cancer environments?

What are the network-wide consequences of targeting proteins?



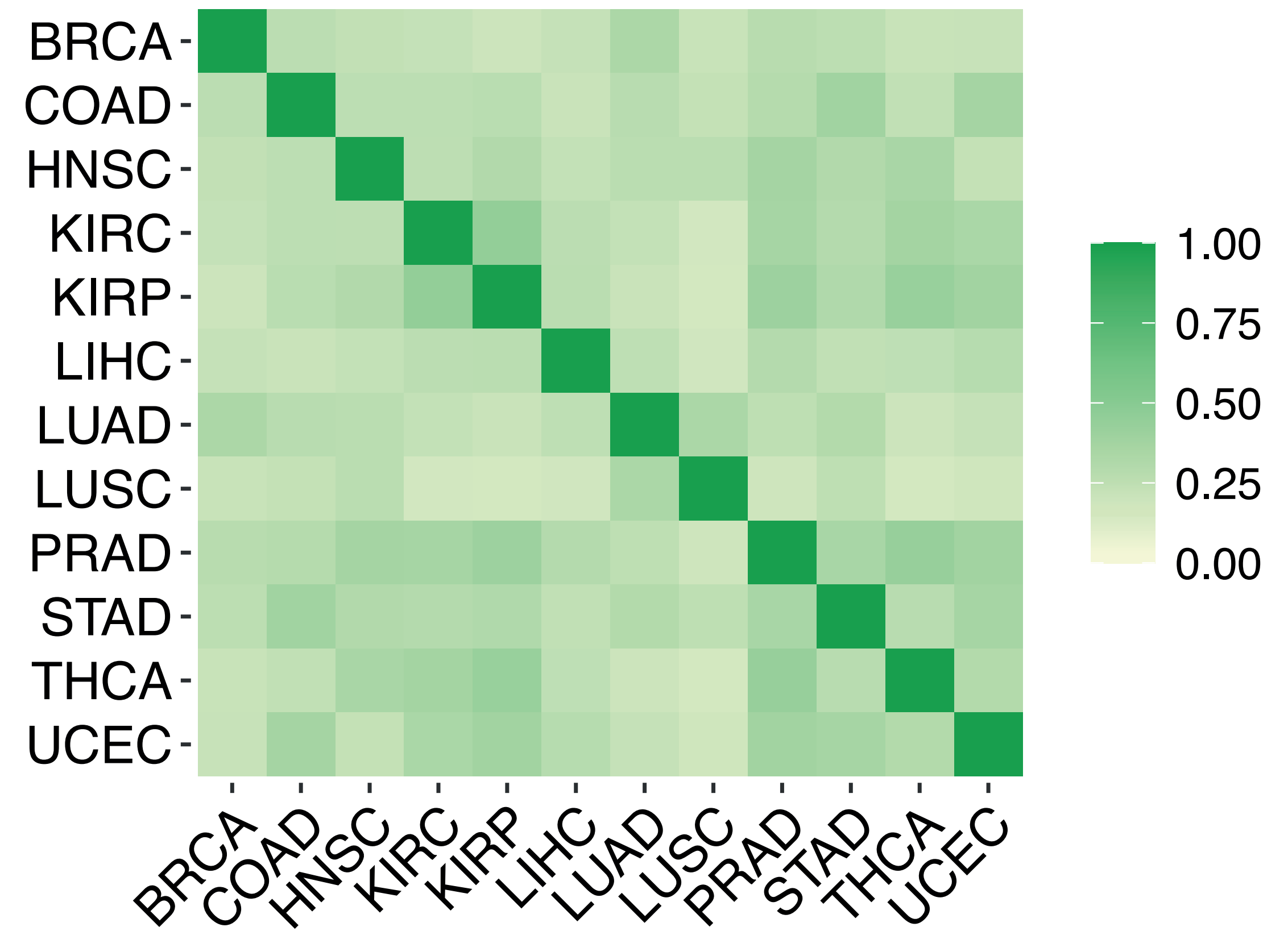
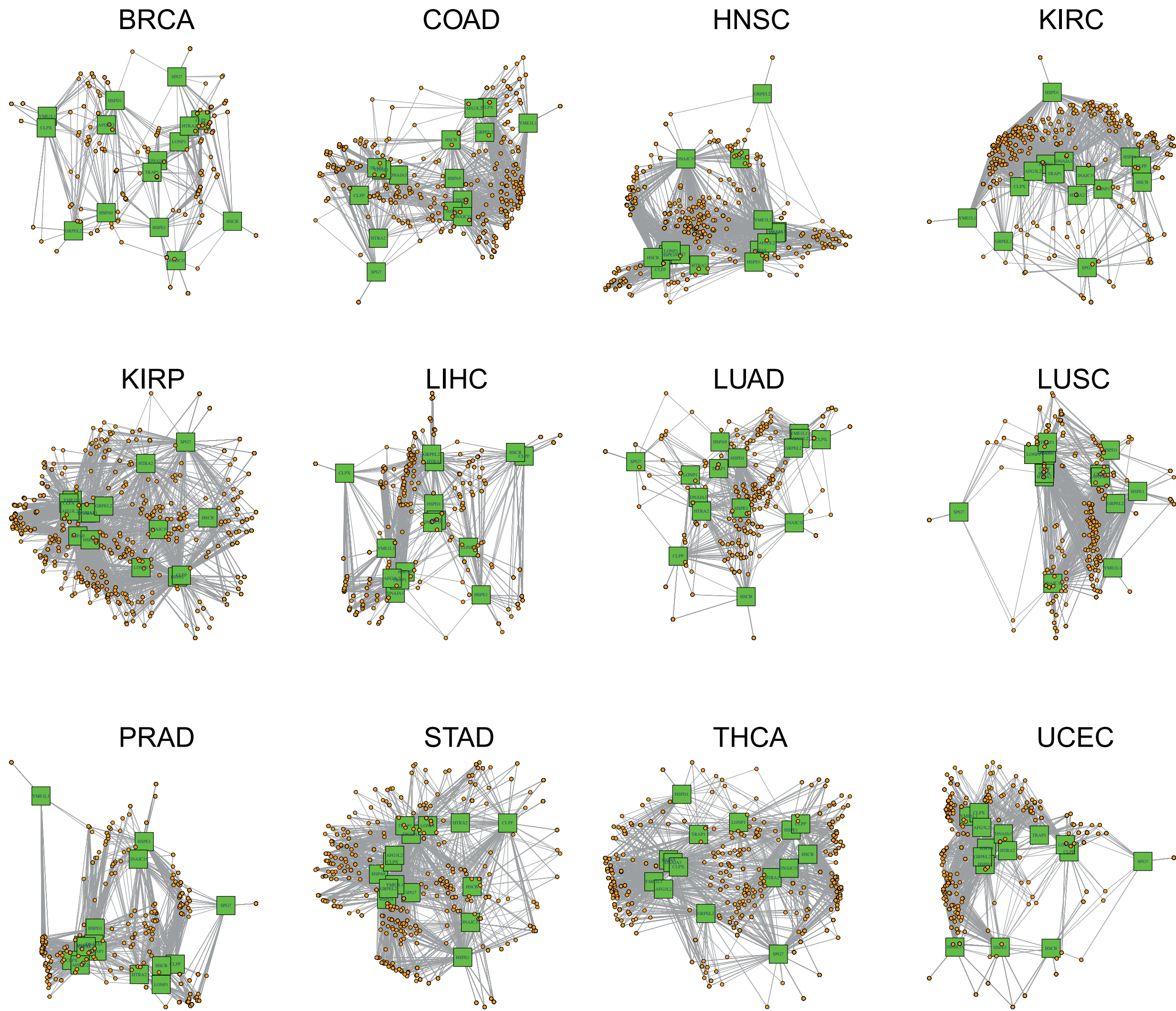


Non-random patterns in chaperone realized niche across cancer environments.

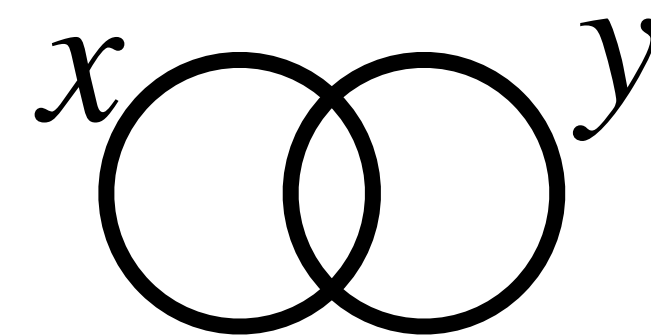
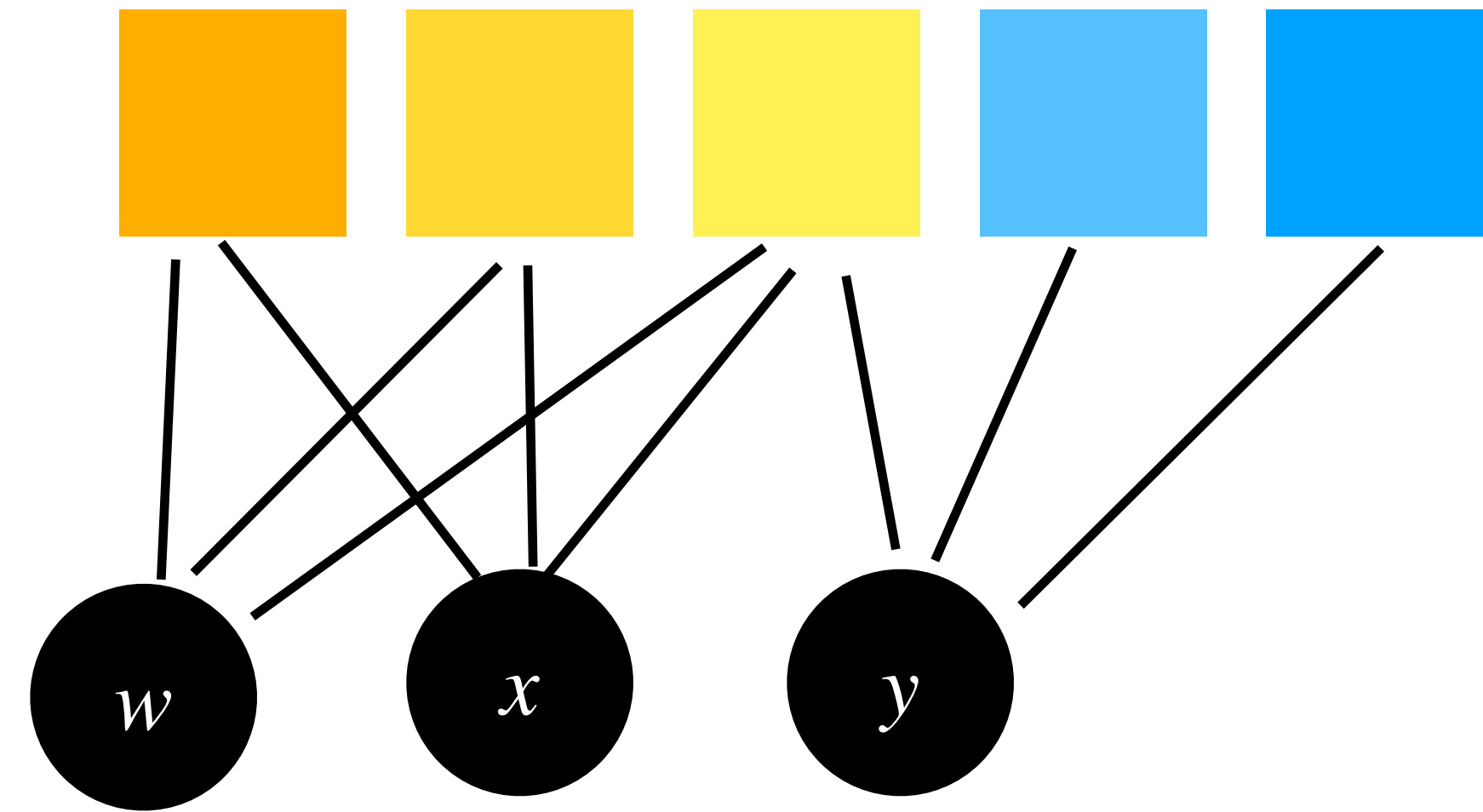
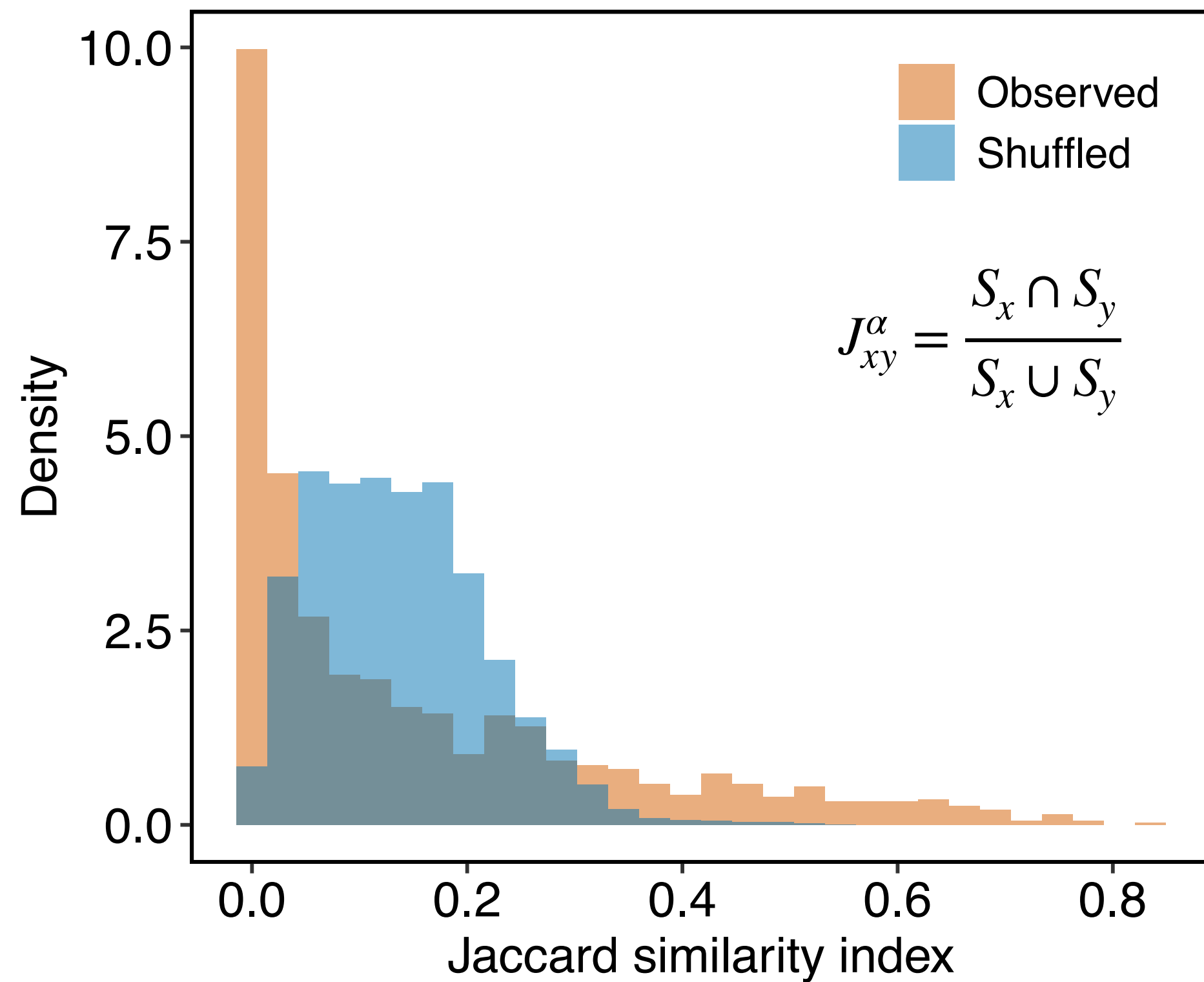
Chaperones share clients across cancers more than expected at random

$$R_c^\alpha = L_c^\alpha / P_c$$

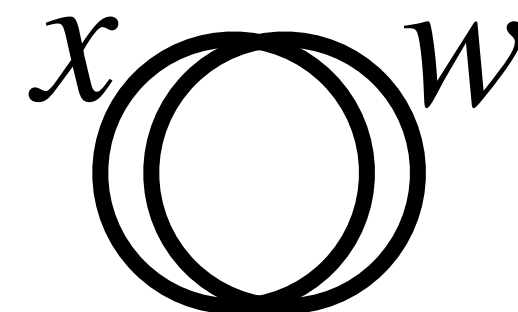
Low similarity in interactions across cancers



Chaperones have strong niche differentiation but some redundancy

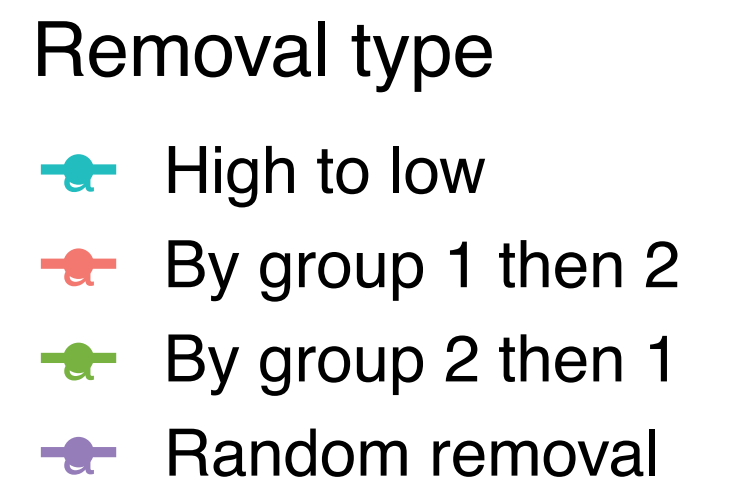
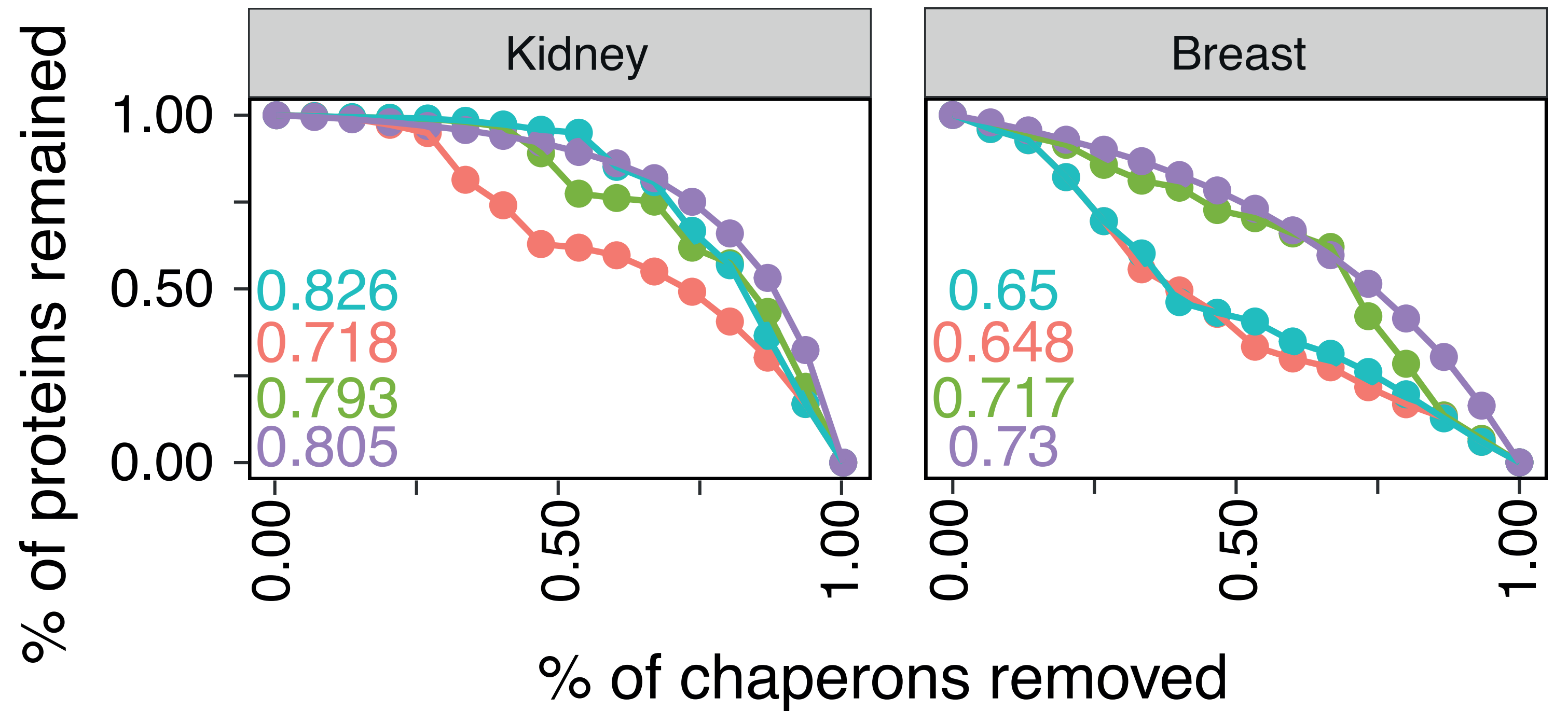
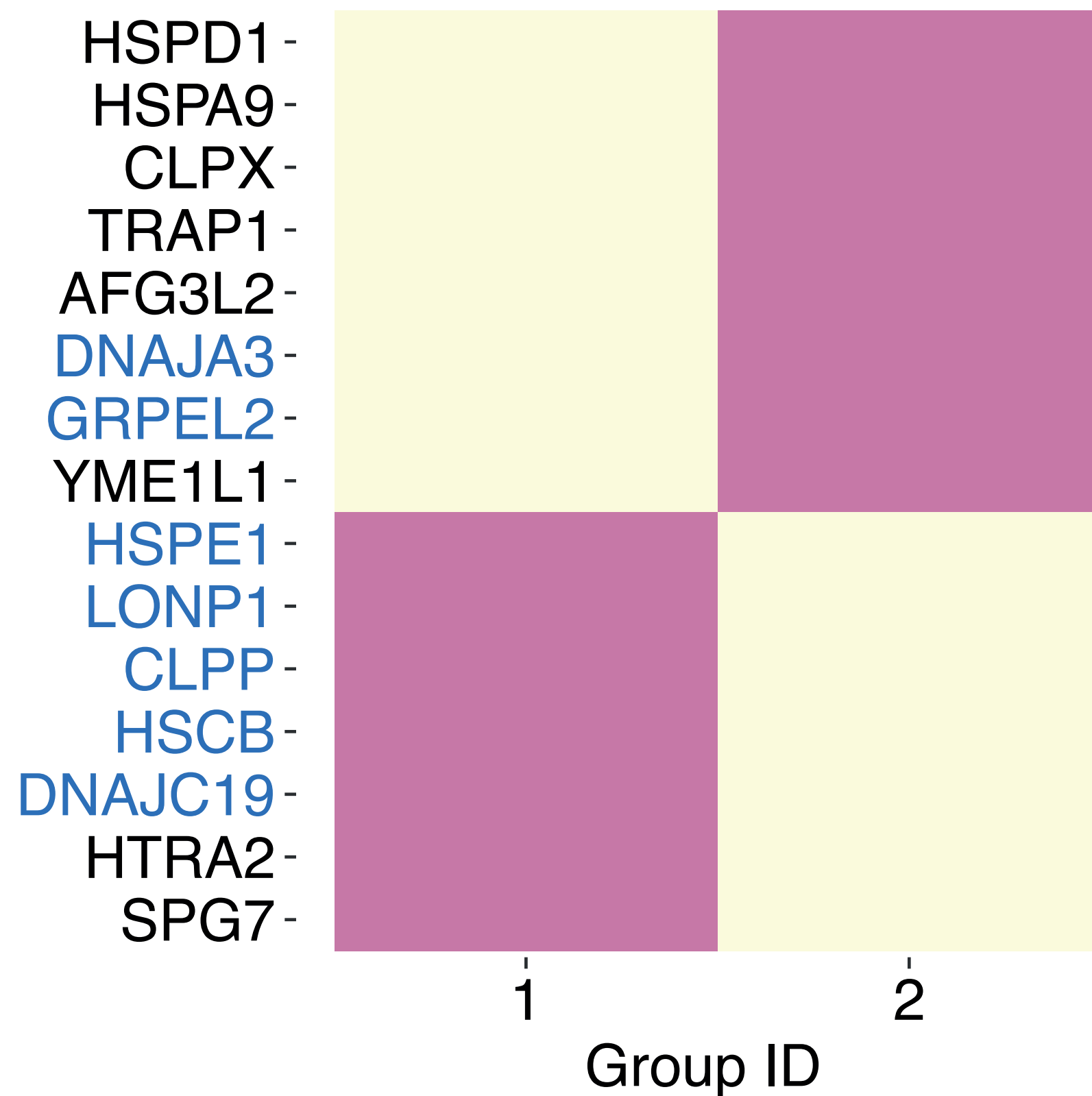


Niche separation

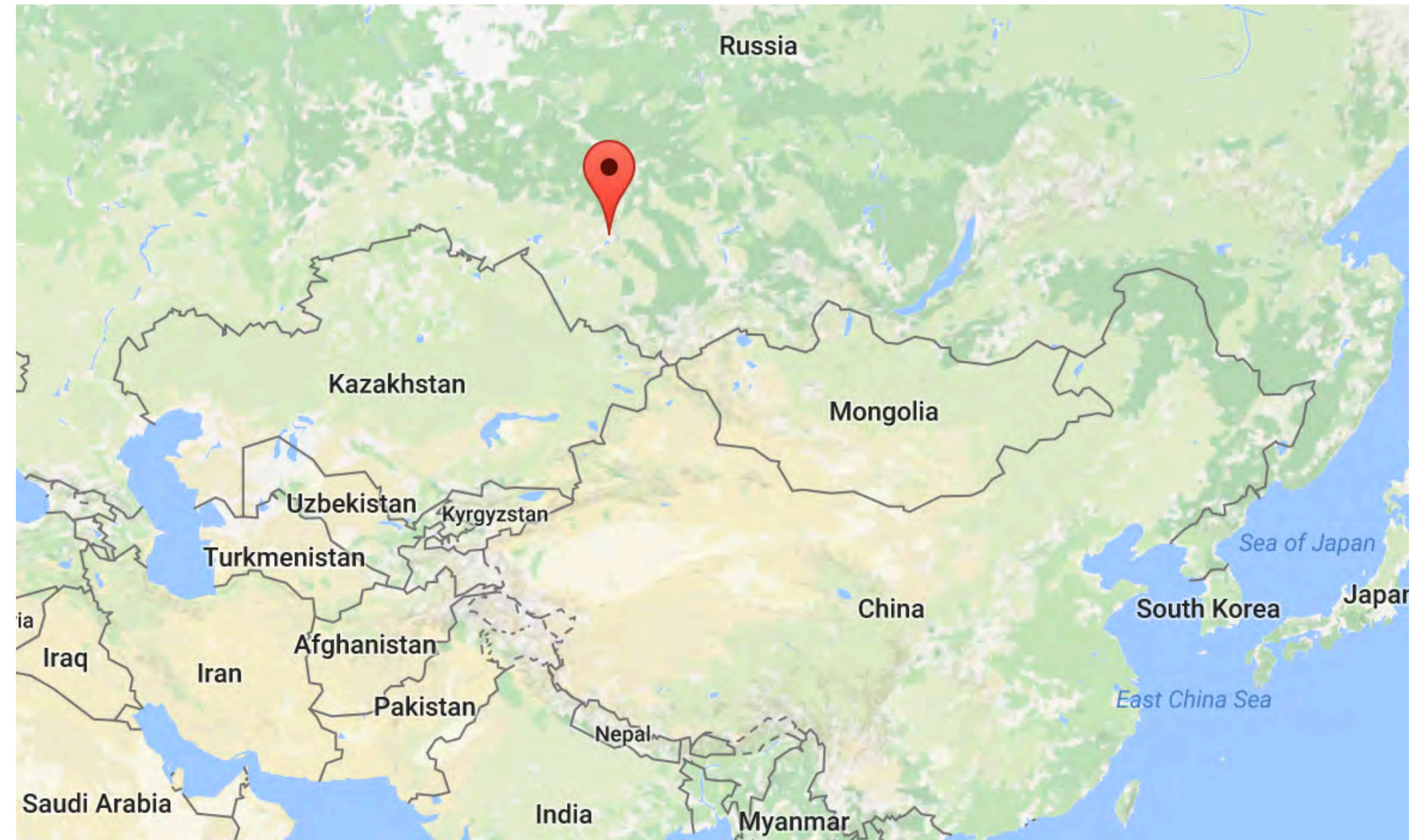


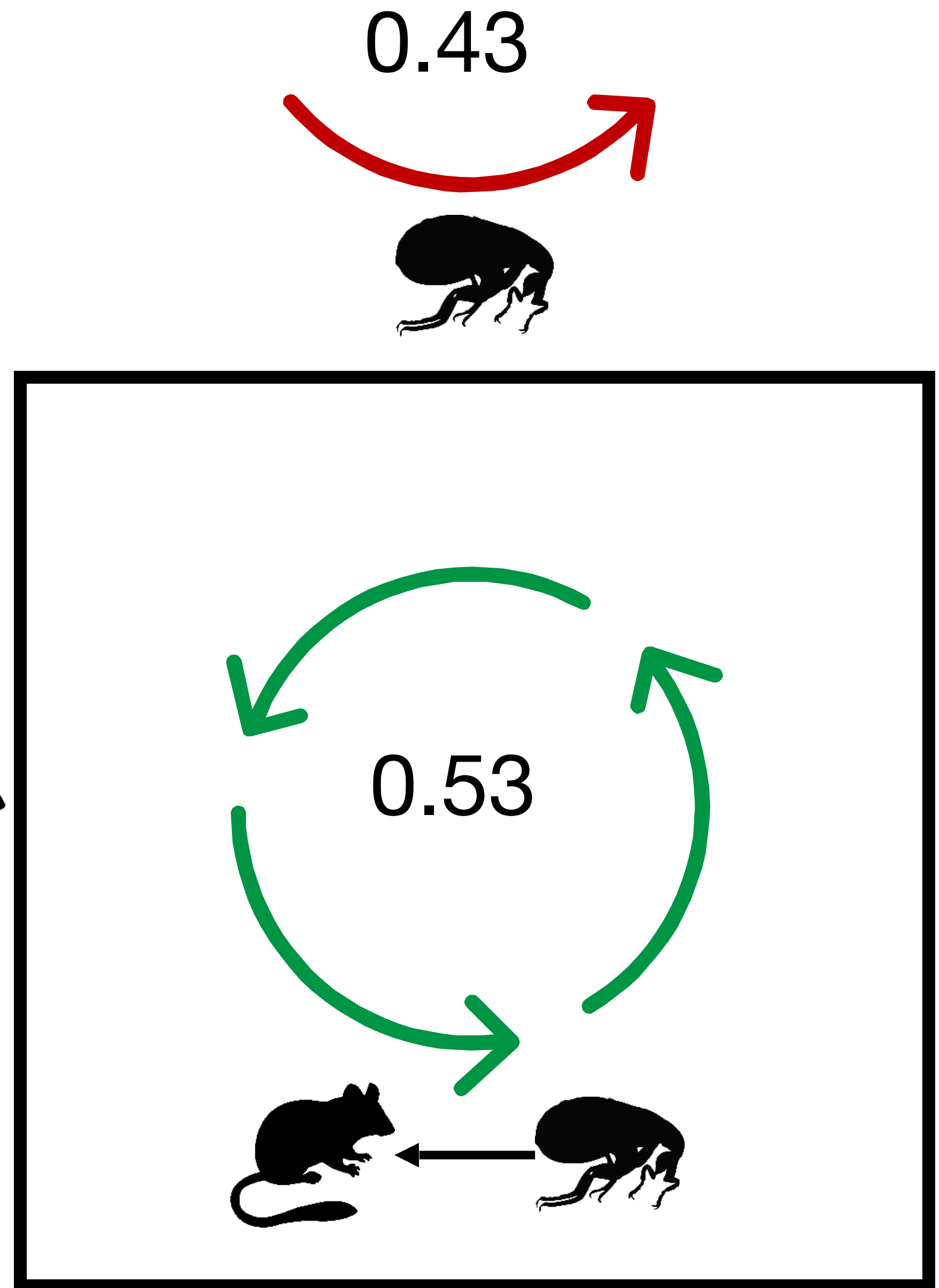
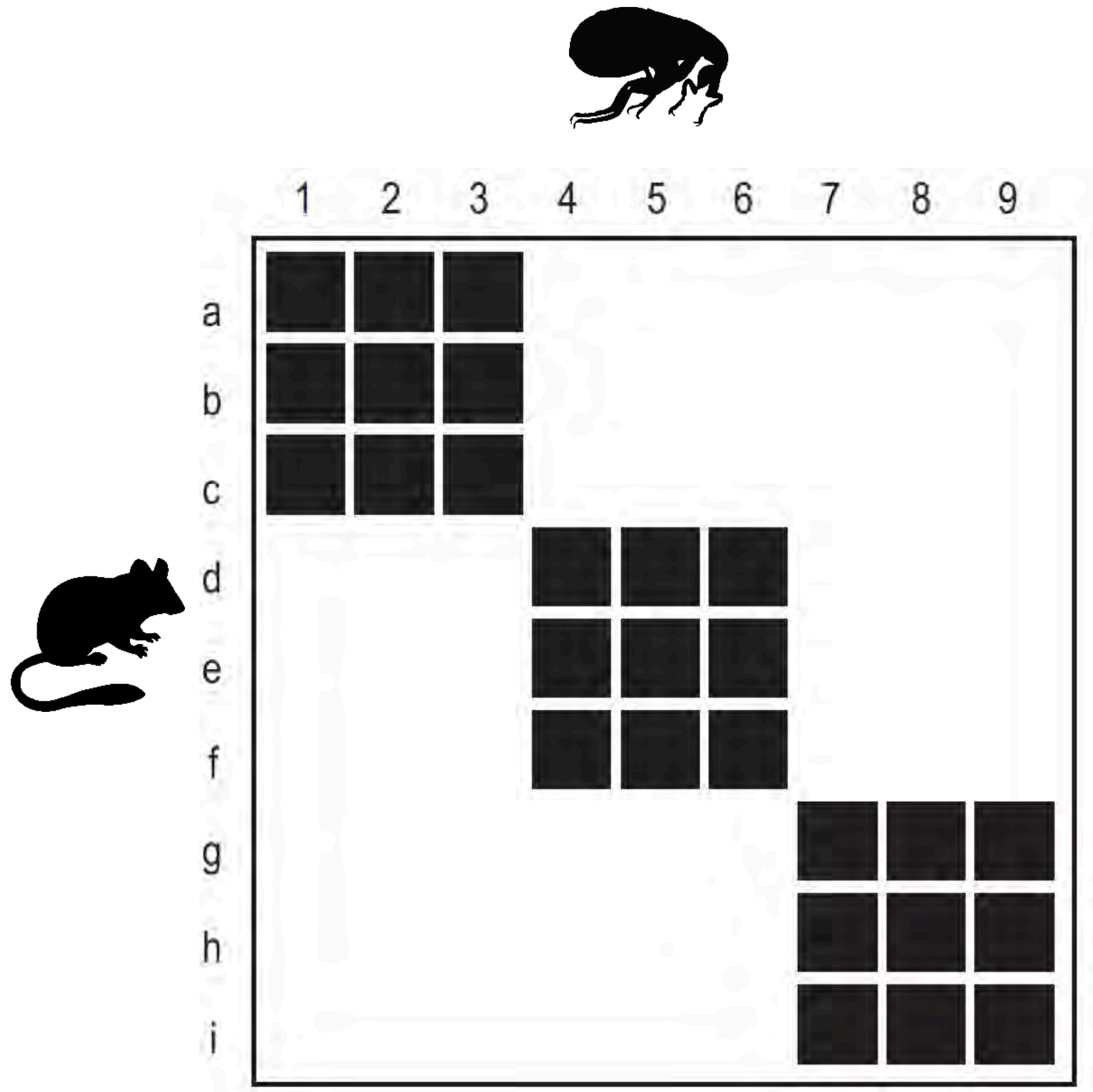
Redundancy

Chaperones are organized in two groups, affecting robustness

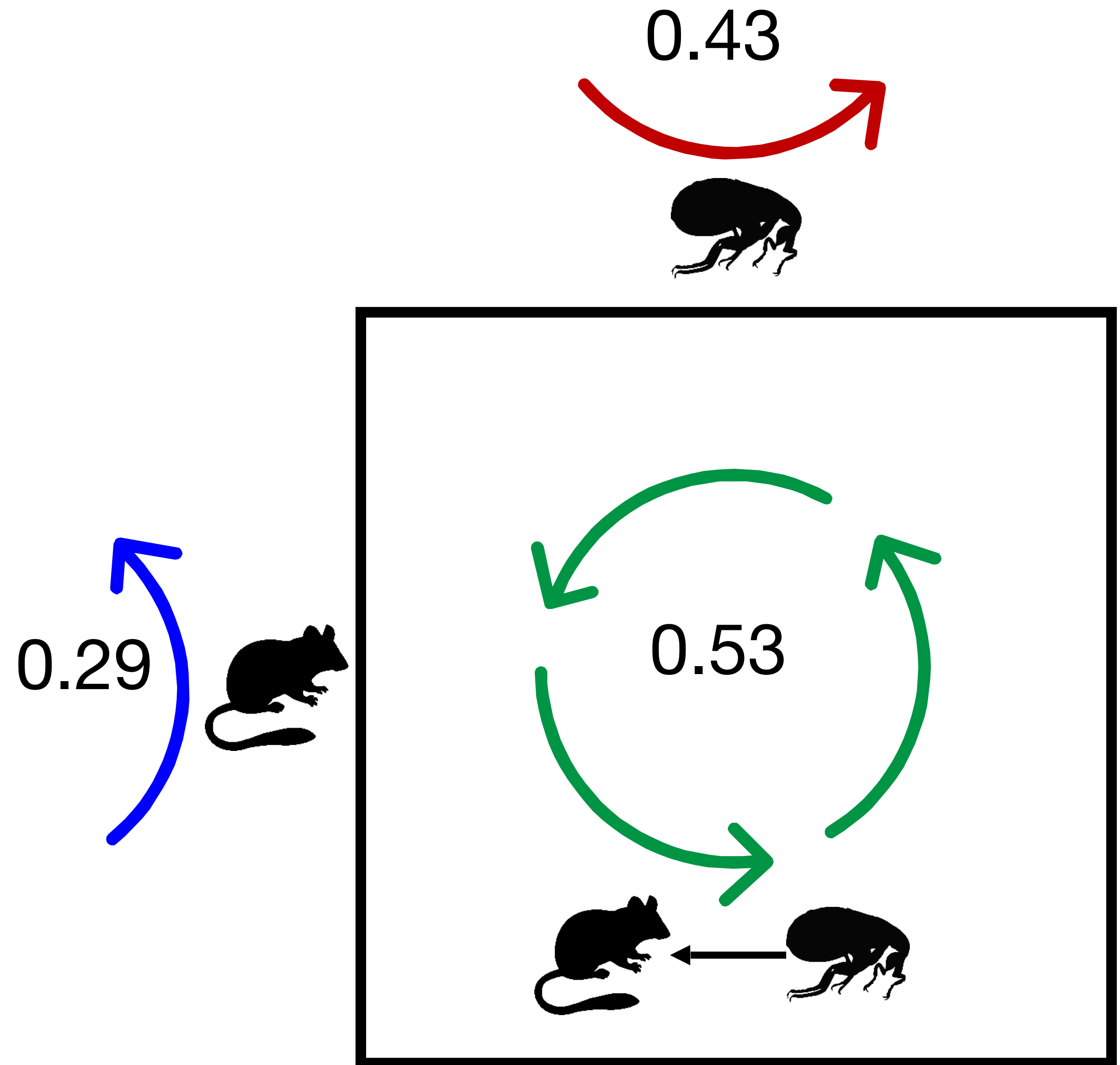


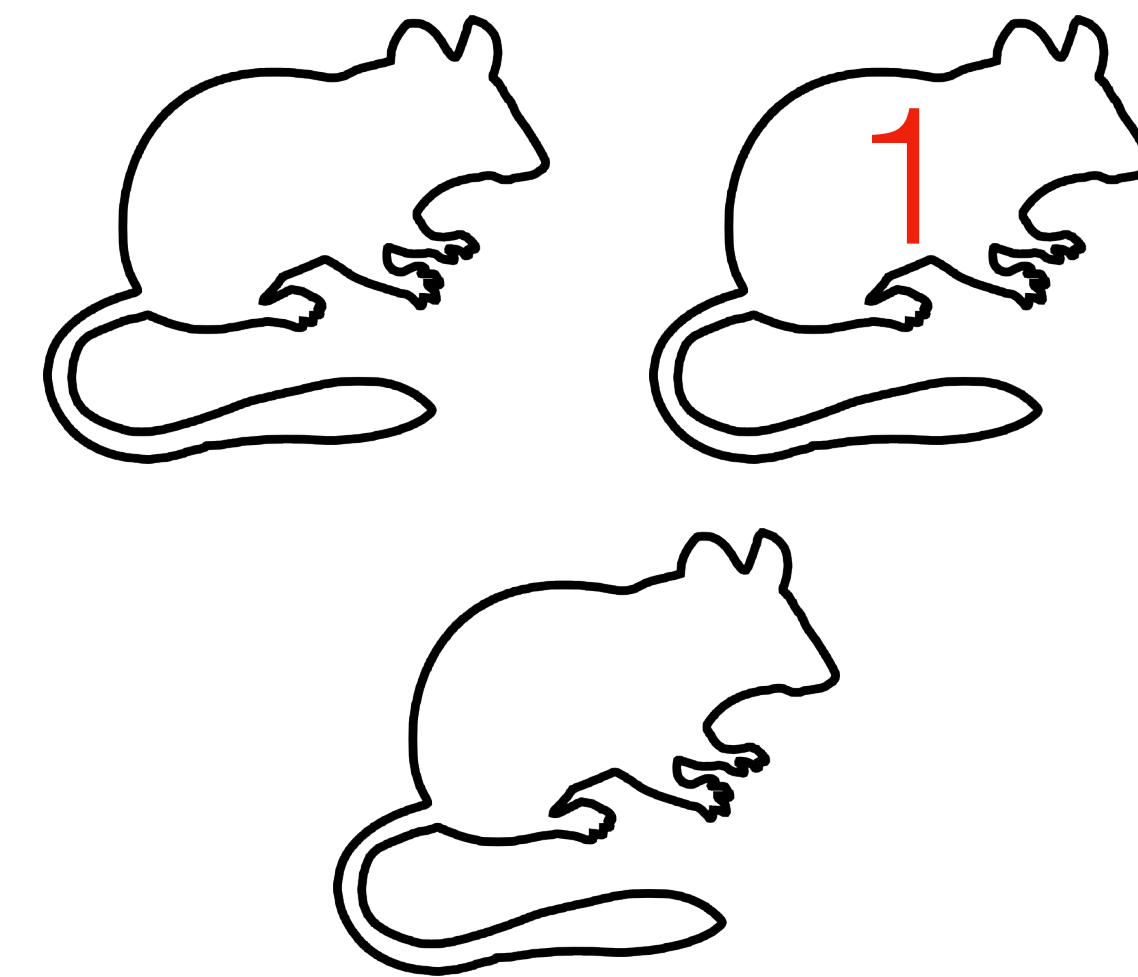
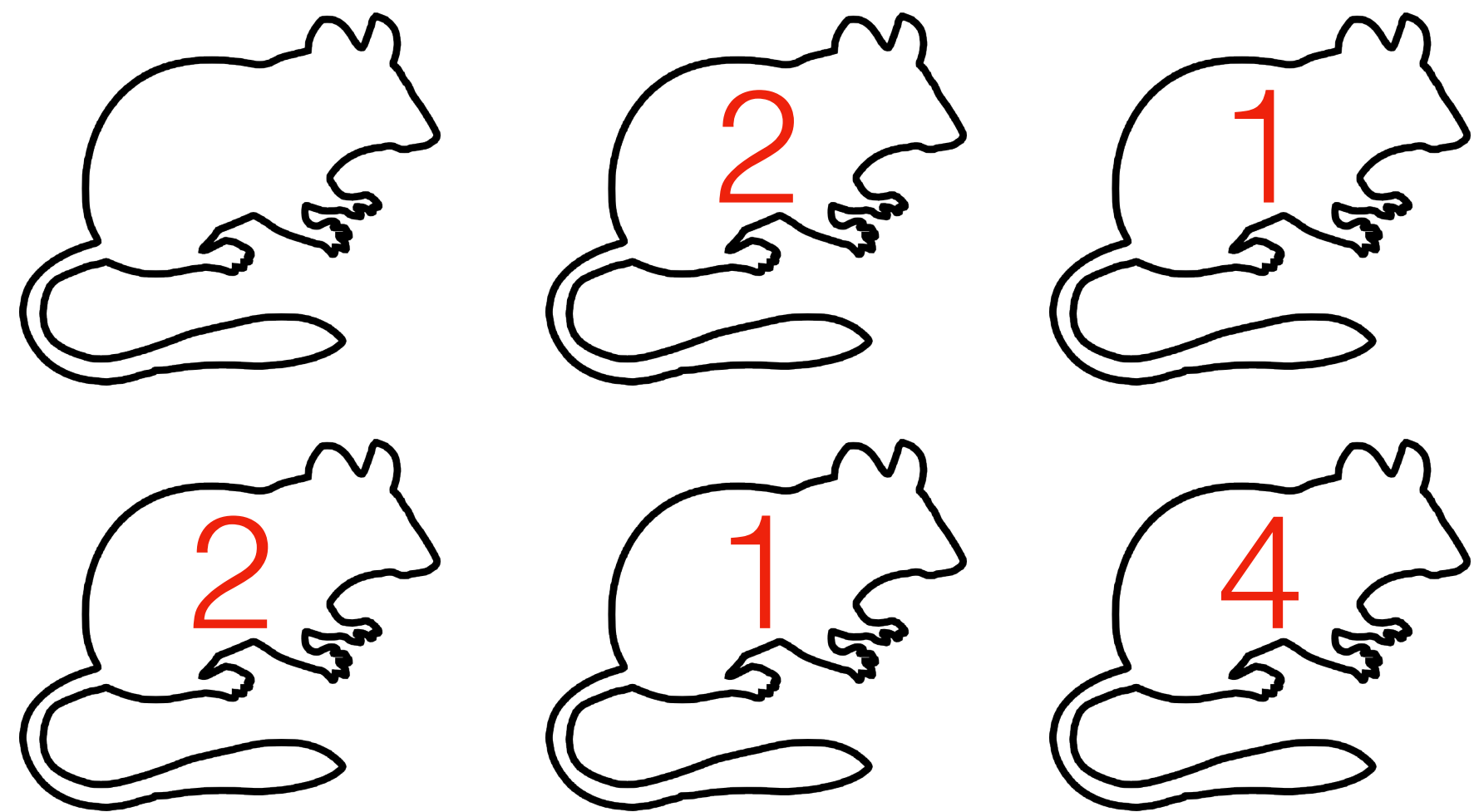
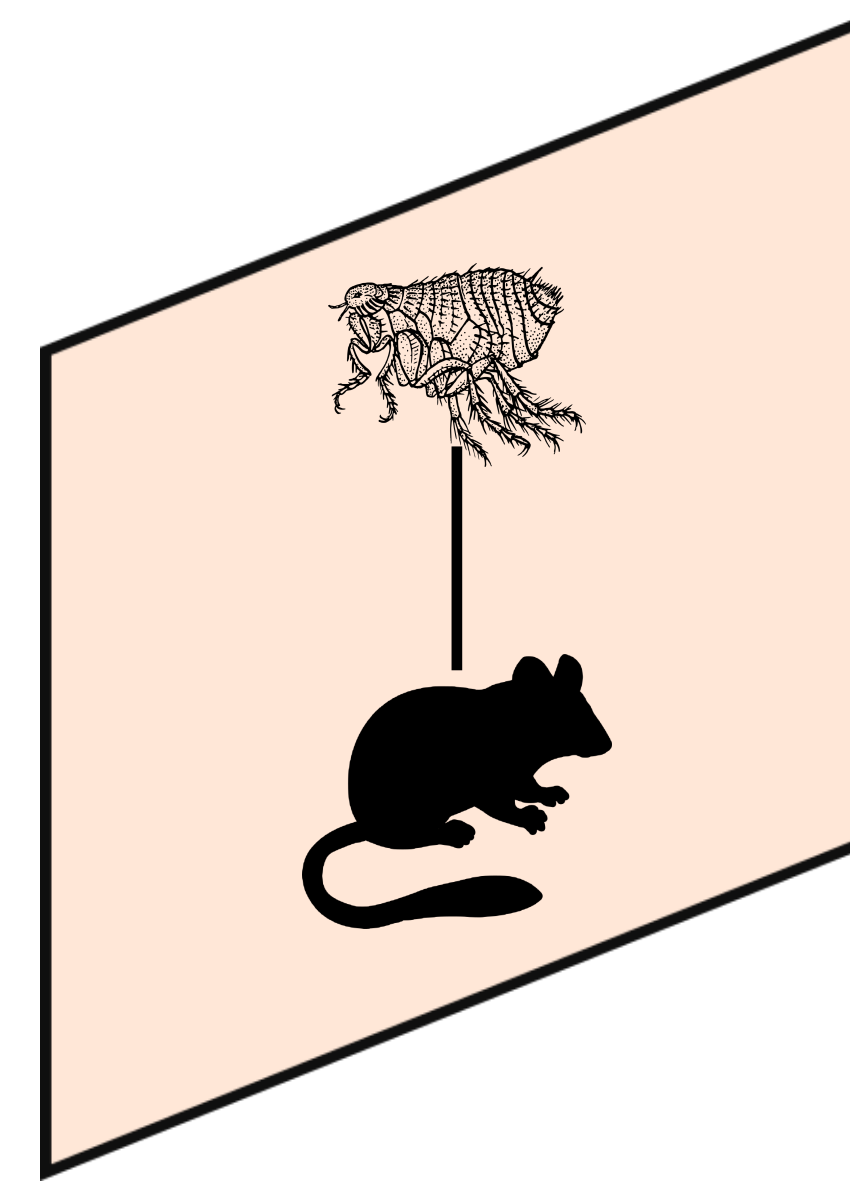
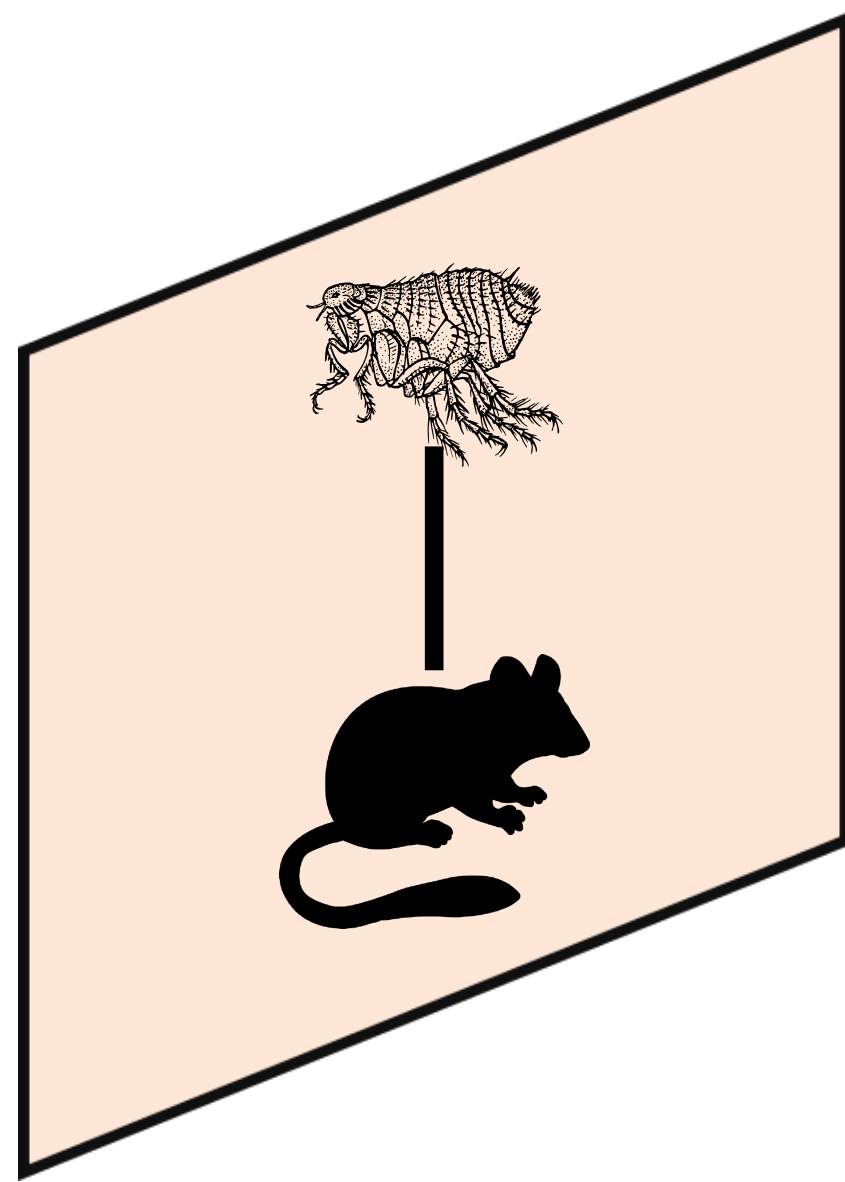
- 6 consecutive summers (1982-1987).
- 22 mammalian hosts.
- 56 ectoparasites (fleas and mites).





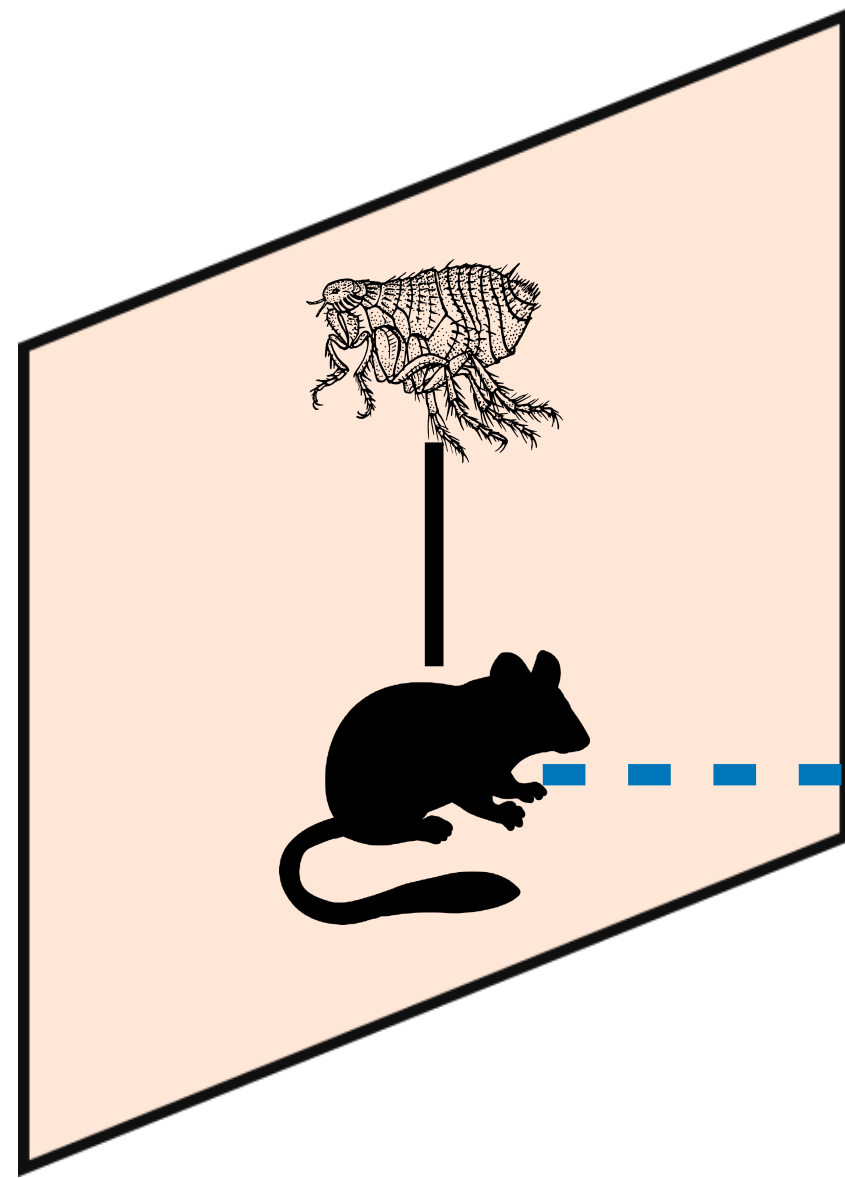
Does the structure of the
host-parasite community
evolve in time?



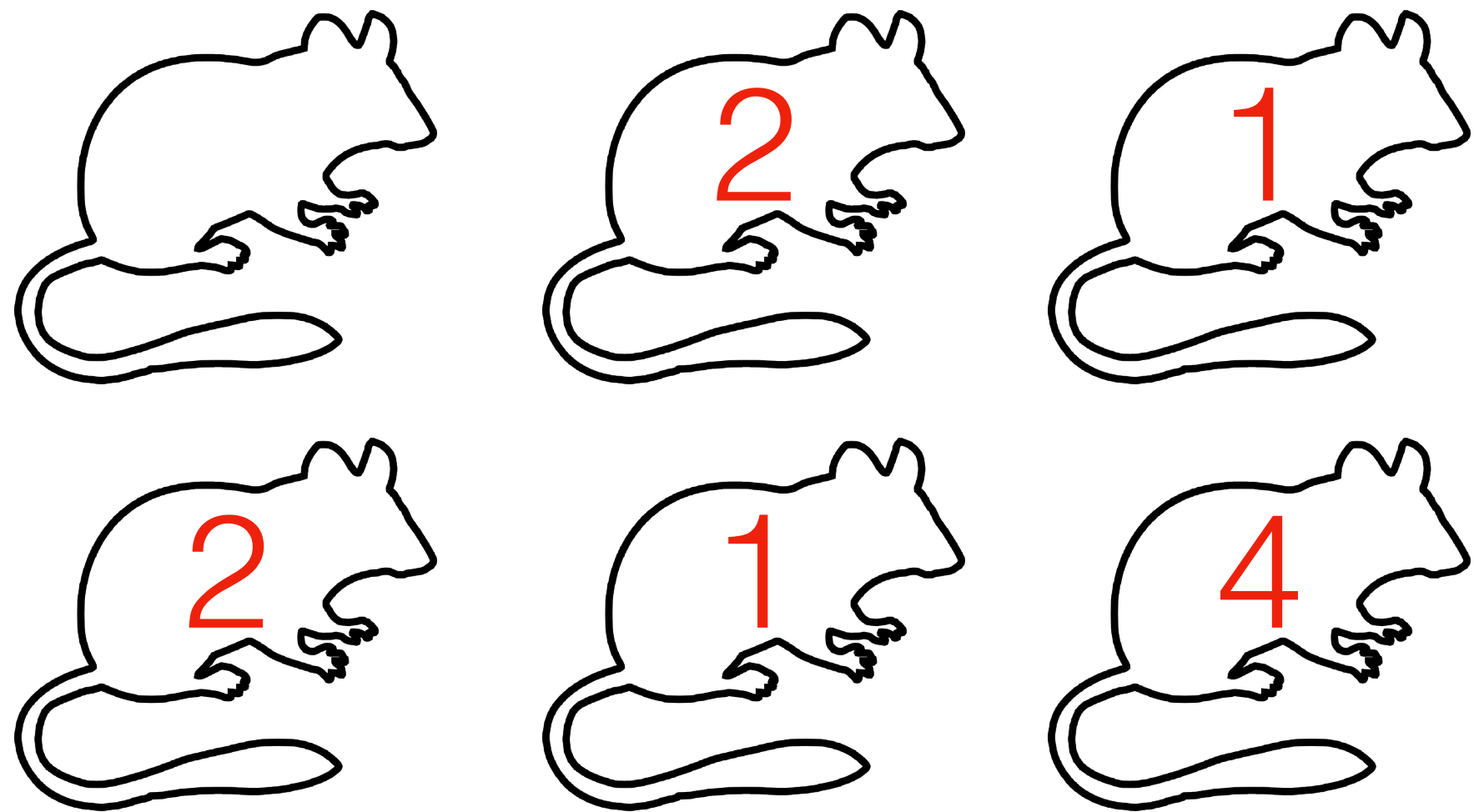
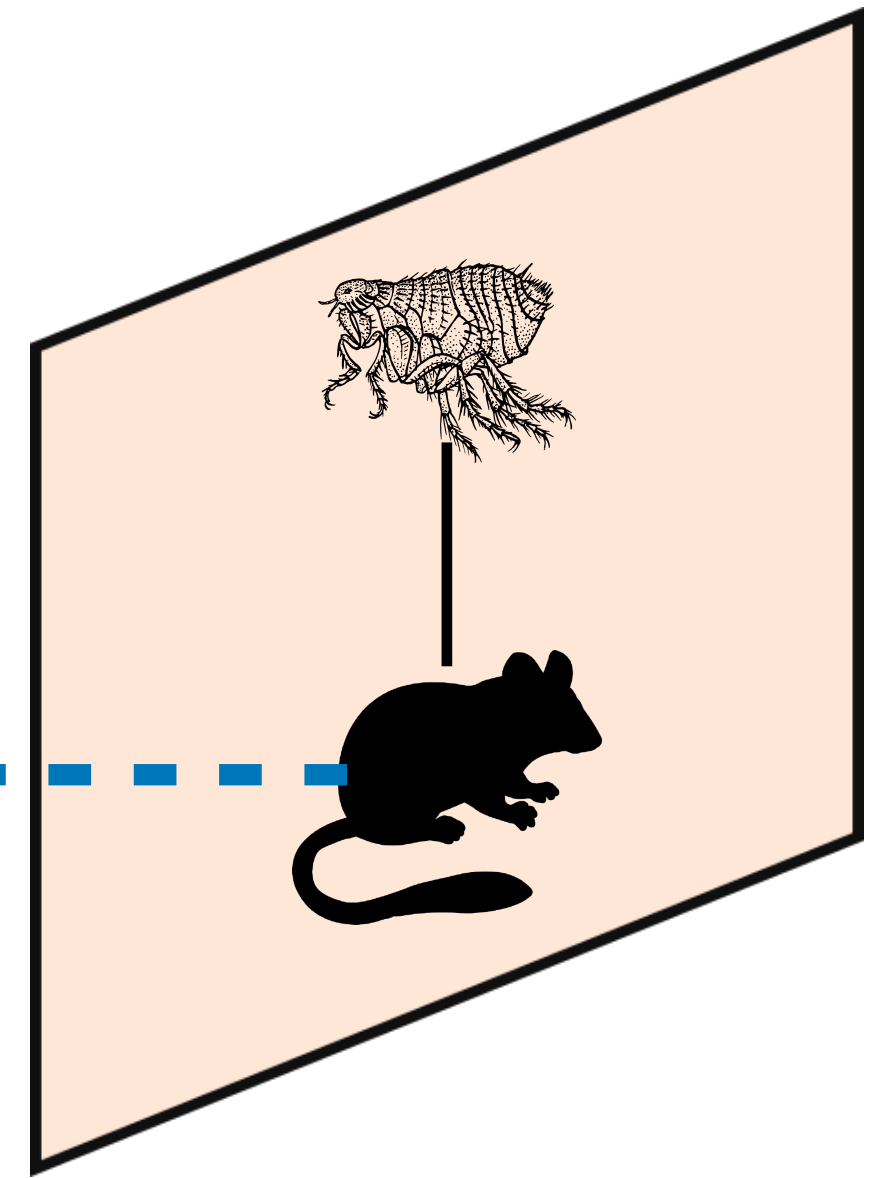


$$p_{ij}^t / a_i^t = 10/6$$

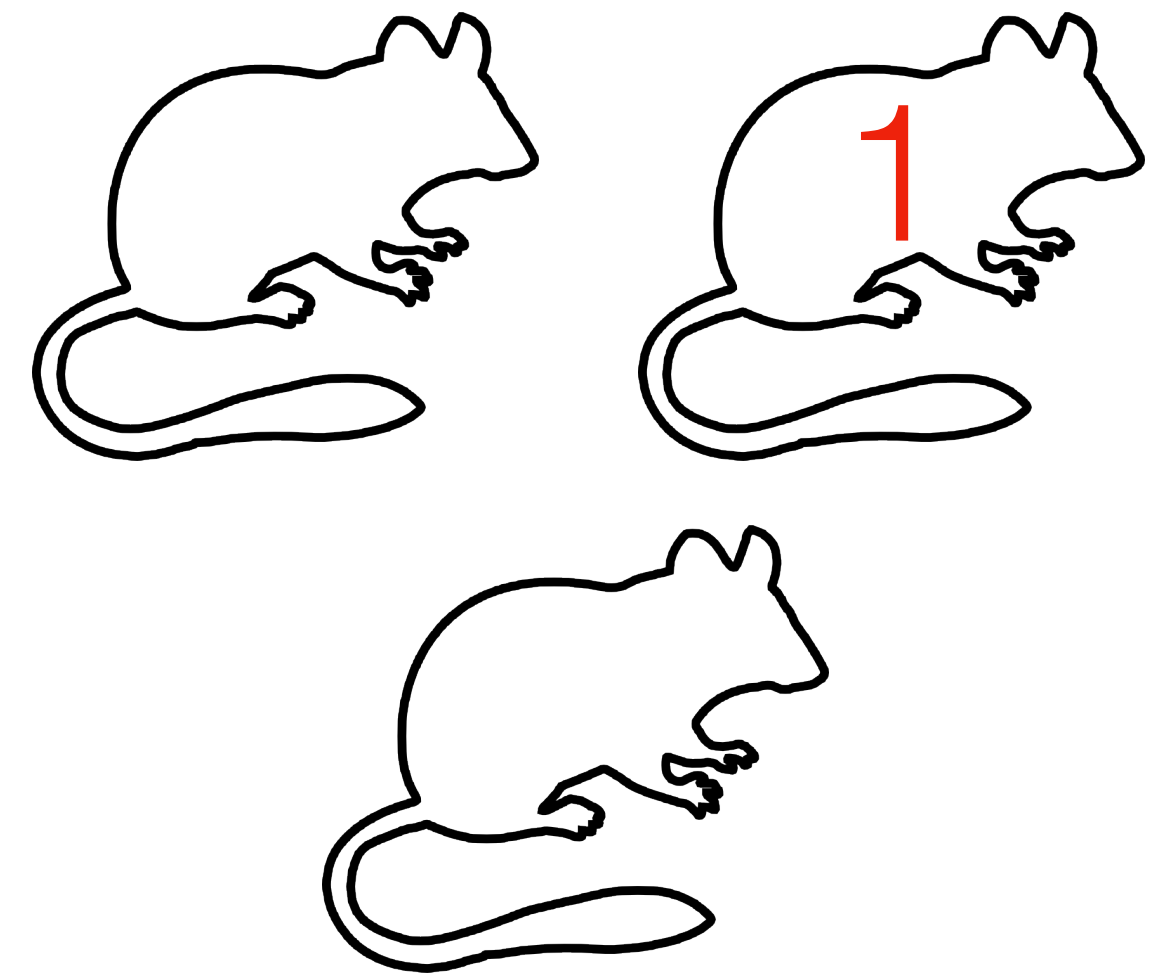
$$p_{ij}^{t+1} / a_i^{t+1} = 1/3$$



$$a_i^{t+1} / a_i^t = 3/6$$



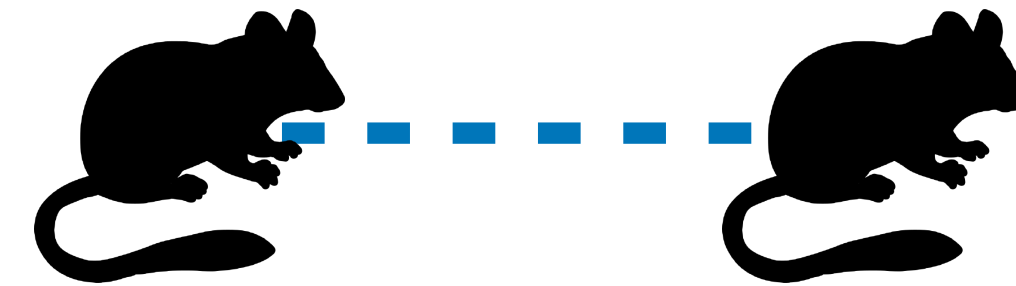
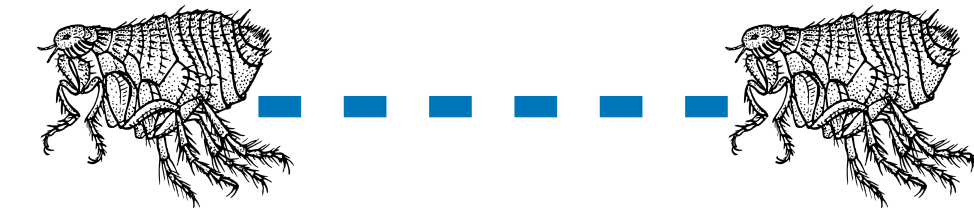
$$p_{ij}^t / a_i^t = 10/6$$



$$p_{ij}^{t+1} / a_i^{t+1} = 1/3$$

A future intra-layer interaction depends on past inter-layer interactions

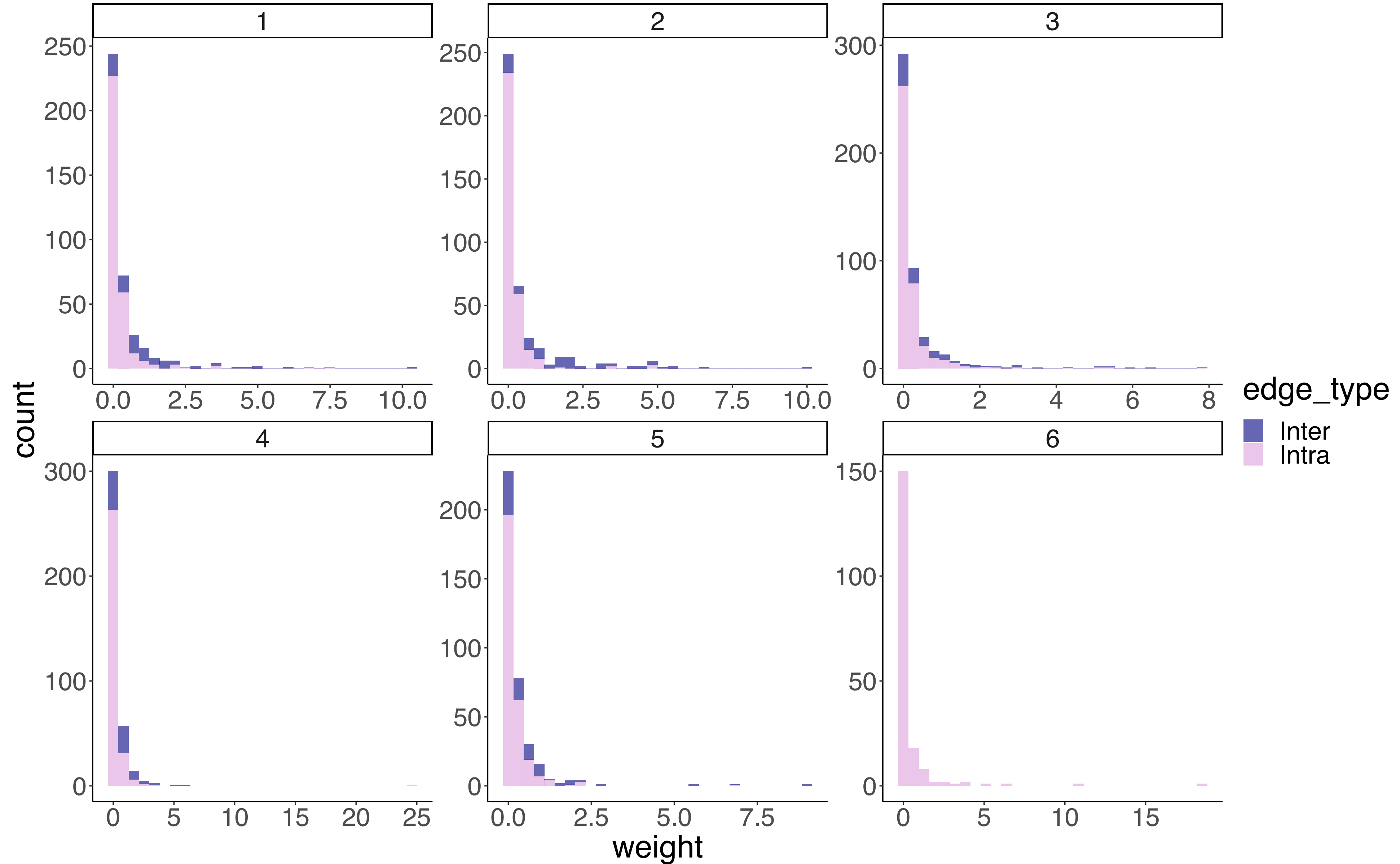
$$\left\{ \begin{array}{l} \boxed{n_i^{t \rightarrow t+1}} = \frac{p_i^{t+1}}{p_i^t} \Rightarrow p_i^{t+1} = p_i^t \cdot n_i^{t \rightarrow t+1} \\ \boxed{n_j^{t \rightarrow t+1}} = \frac{a_j^{t+1}}{a_j^t} \Rightarrow a_j^{t+1} = a_j^t \cdot n_j^{t \rightarrow t+1} \end{array} \right.$$

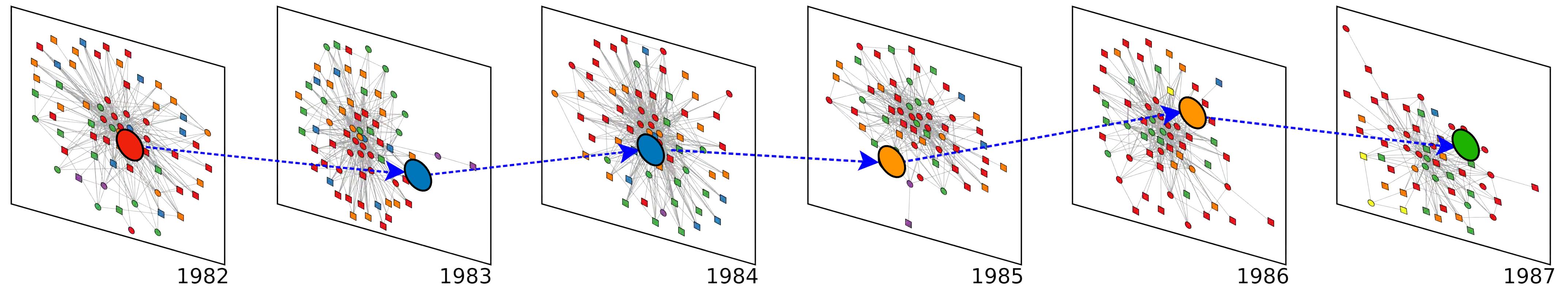


$$m_{ij}^{t+1} = \frac{p_i^{t+1}}{a_j^{t+1}} = \frac{p_i^t \cdot \boxed{n_i^{t \rightarrow t+1}}}{a_j^t \cdot \boxed{n_j^{t \rightarrow t+1}}}$$



Edge weight distribution





- ~6 modules with **non-random**, time-dependent structure.
- Species can change modules in time.



Non-flexible

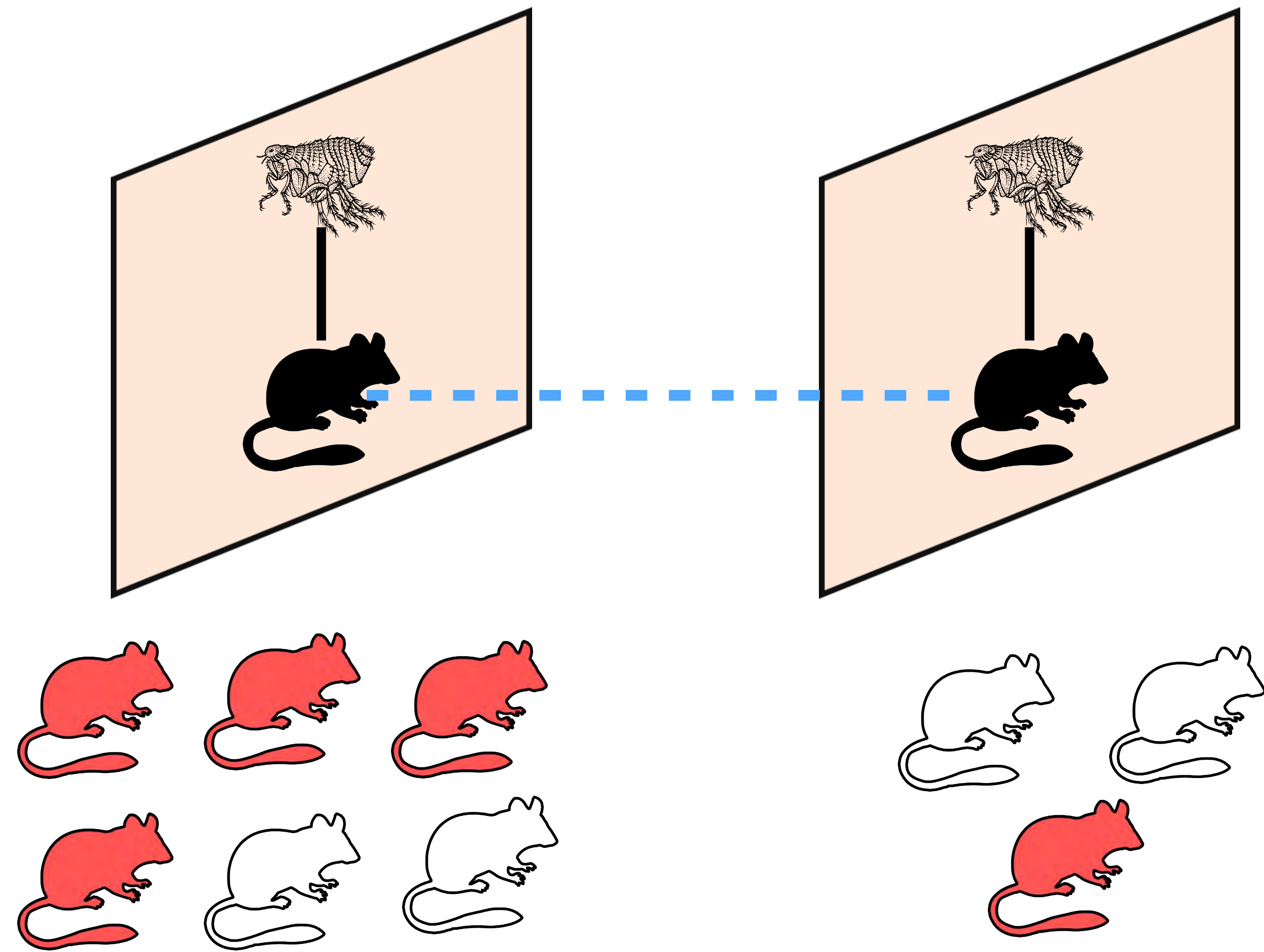
- Support consistent parasite assemblages.



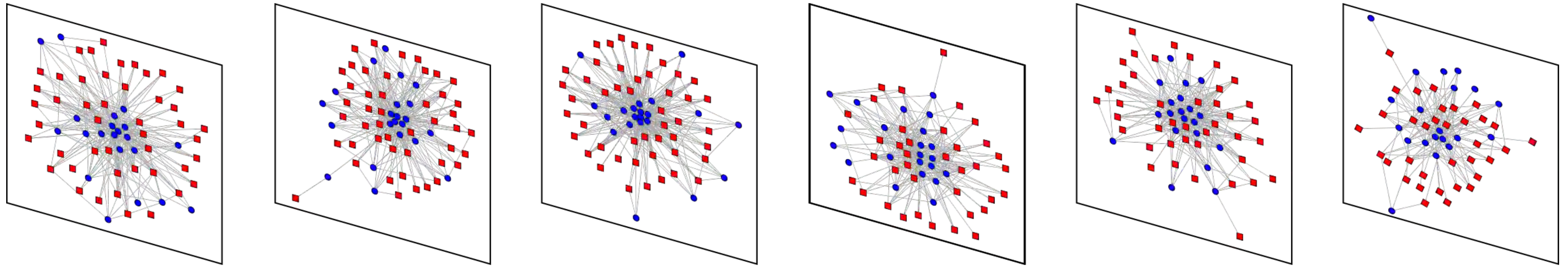
Flexible

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

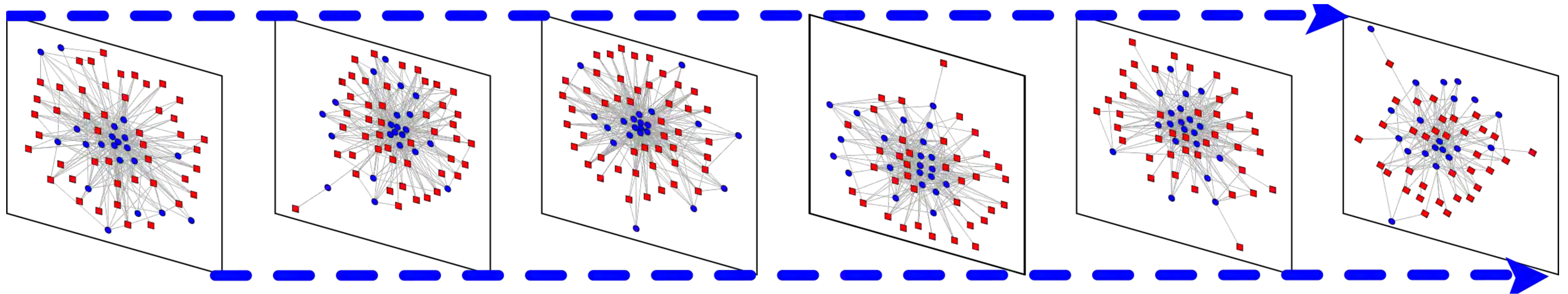
- Time-dependent distribution of parasites in hosts.
- The same species is functionally different at different times.



State nodes!



- No insights into the evolution of the modules.



- Infinity — Species do not change modules.

Interlayer edges measured in the field

$$w_{ij\alpha} = \frac{p_{ij}^{\alpha}}{b_j^{\alpha}}$$

number of bird individuals of j on which pollen grains of i was detected

Total number of bird individuals in α

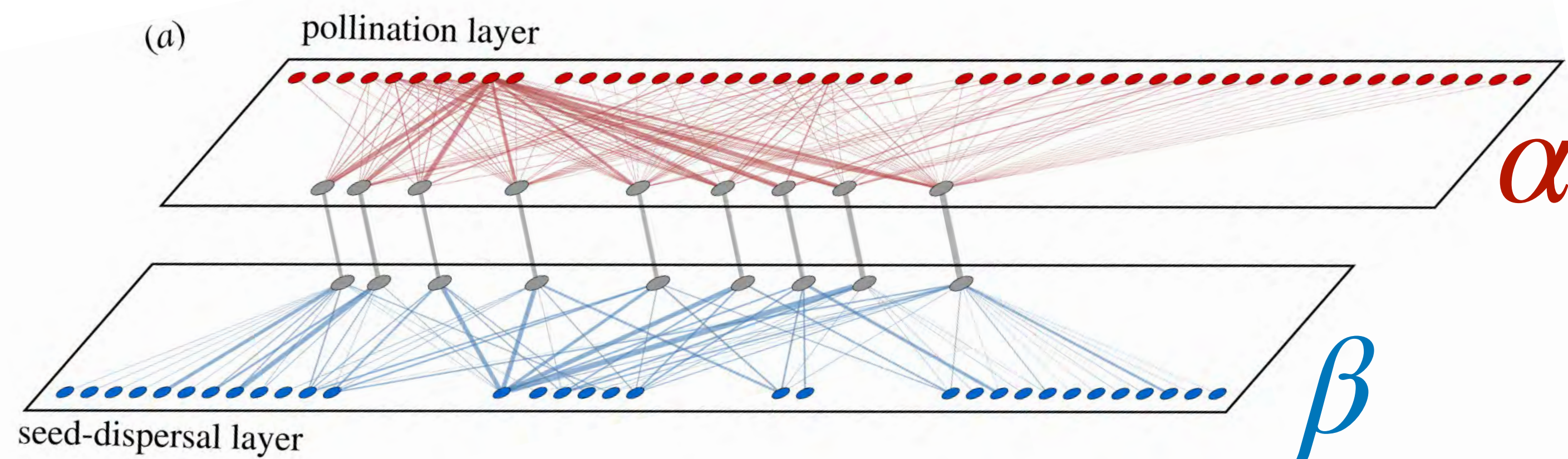
Intra (pollination)

$$w_{j\alpha\beta} = \frac{p_j^{\alpha\beta}}{b_j^{\alpha\beta}}$$

number of bird individuals of j on which pollen and seeds were detected

Total number of bird individuals of j

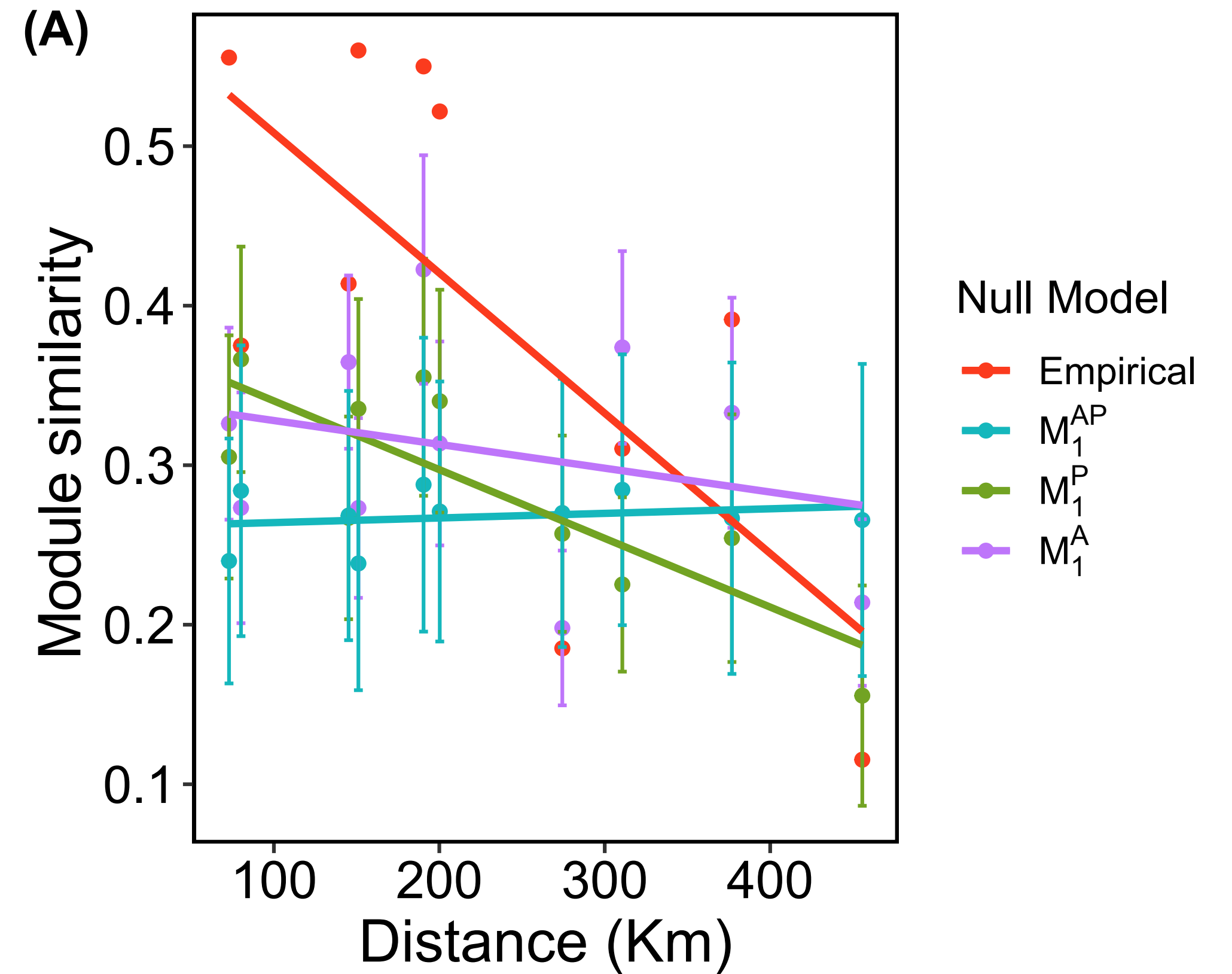
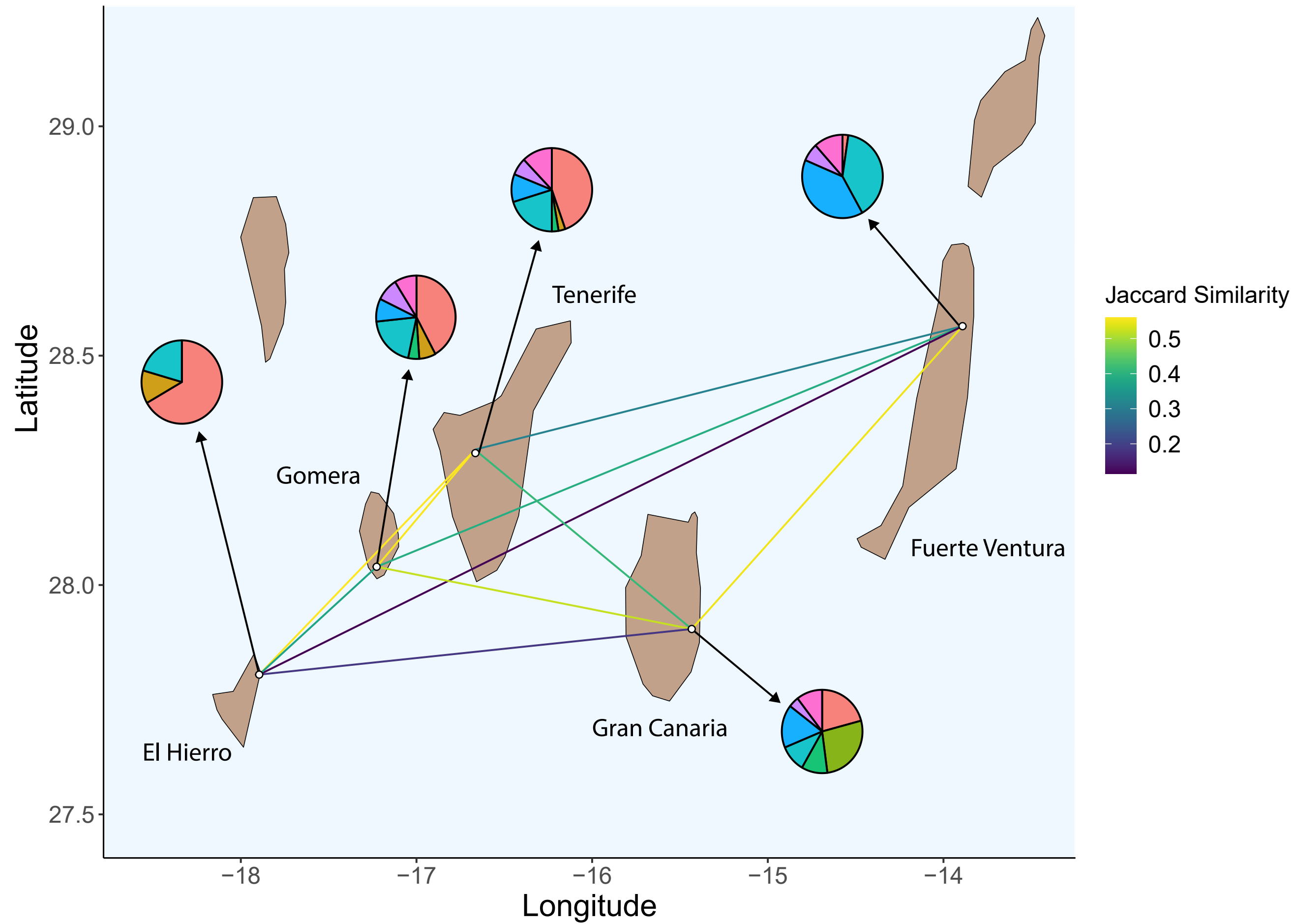
Interlayer (bounded [0,1])



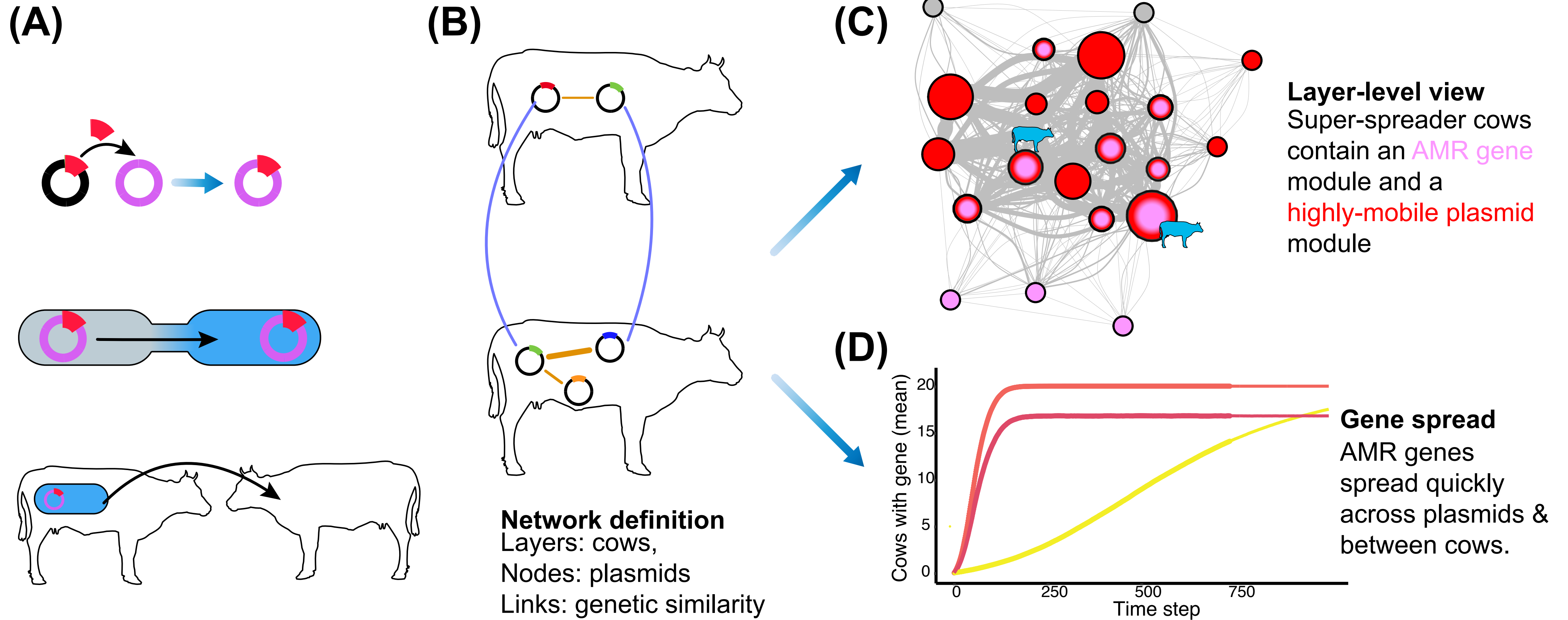
Example key questions

- How do multiple interaction types affect the stability of communities?
- Will a multilayer approach change understanding of ecological concepts (e.g., “key-stone species”)?
- How do processes that operate within and between layer interact to affect structure and dynamics?

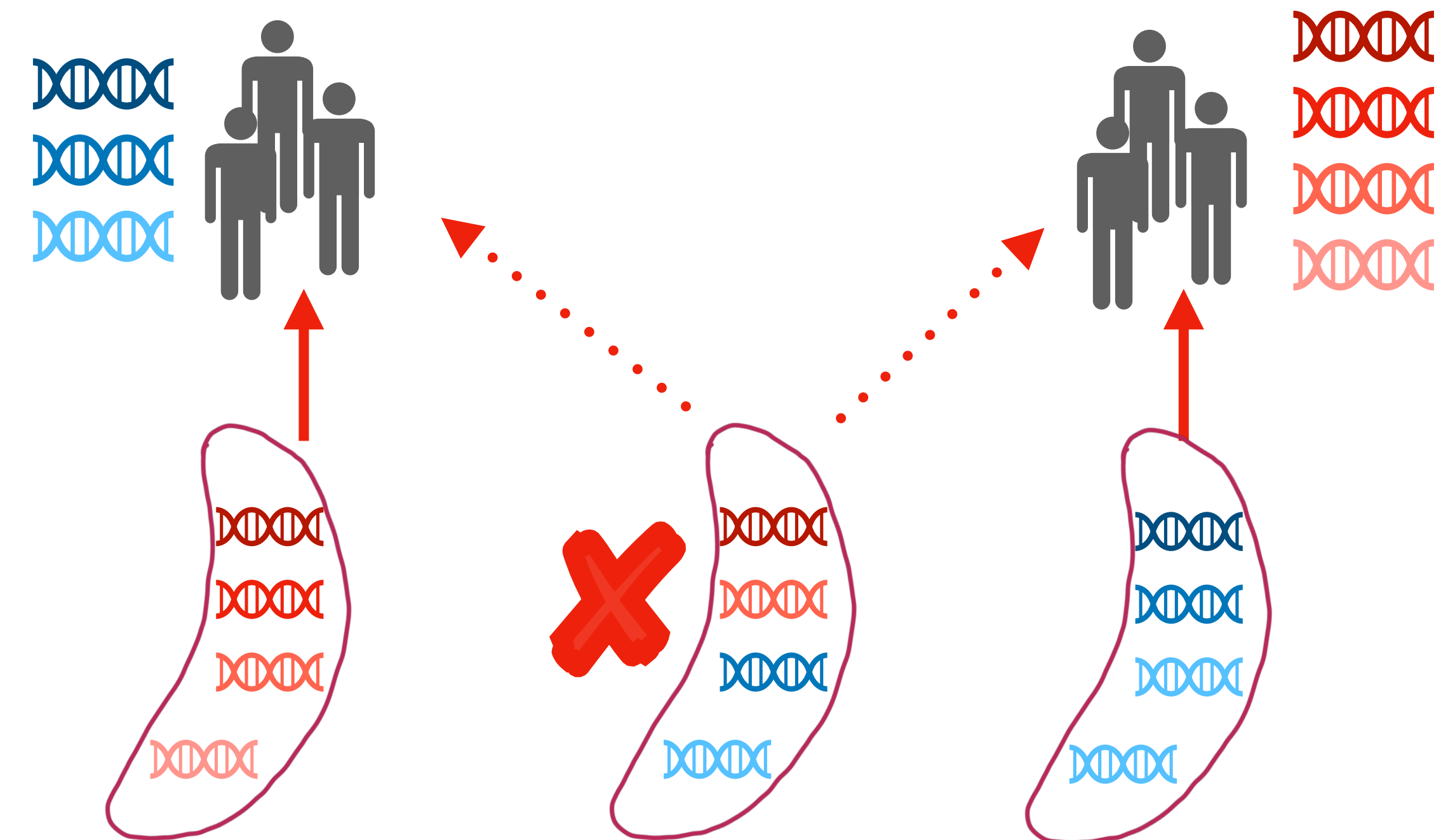
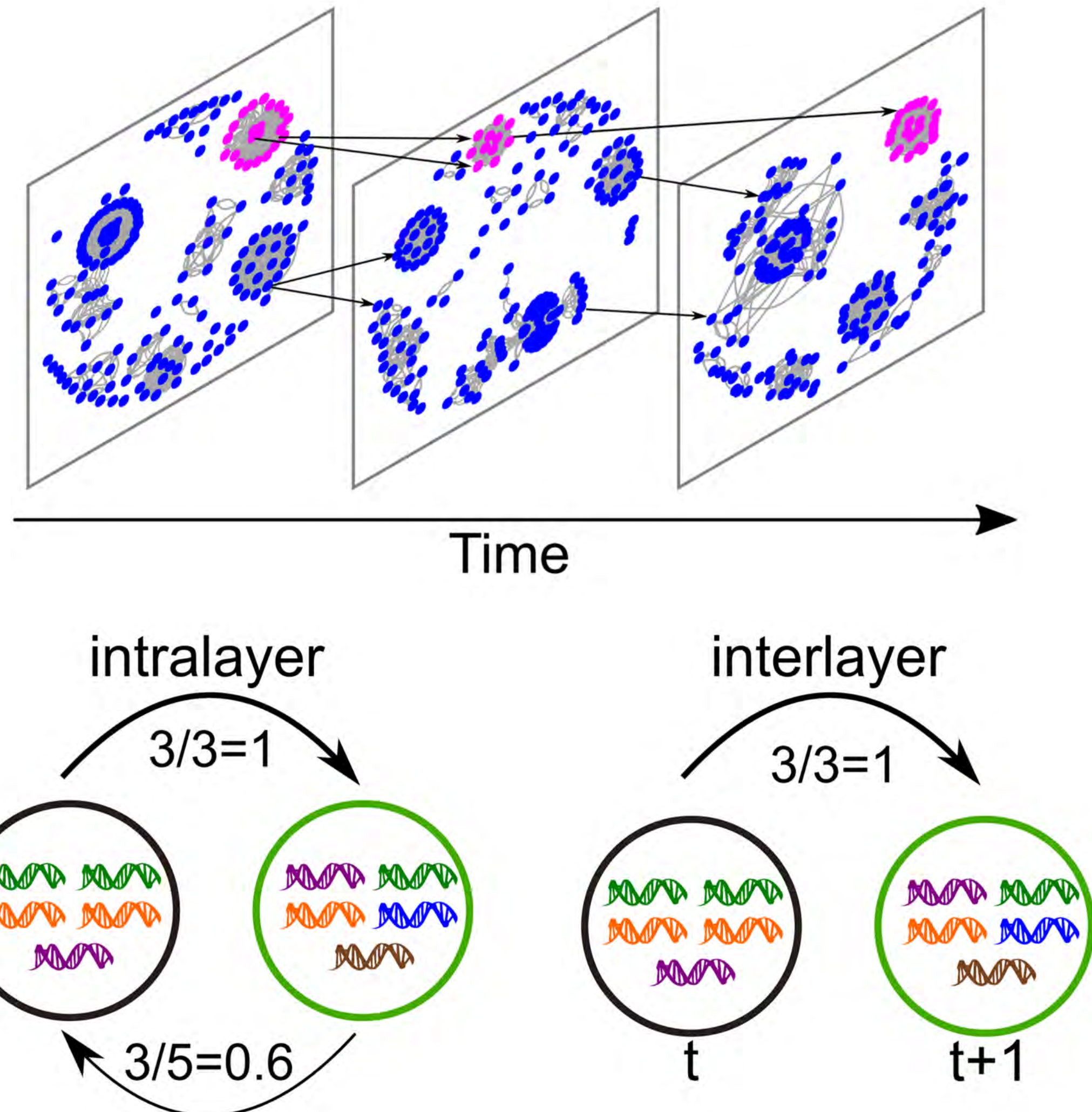
Spatial or meta-community dynamics



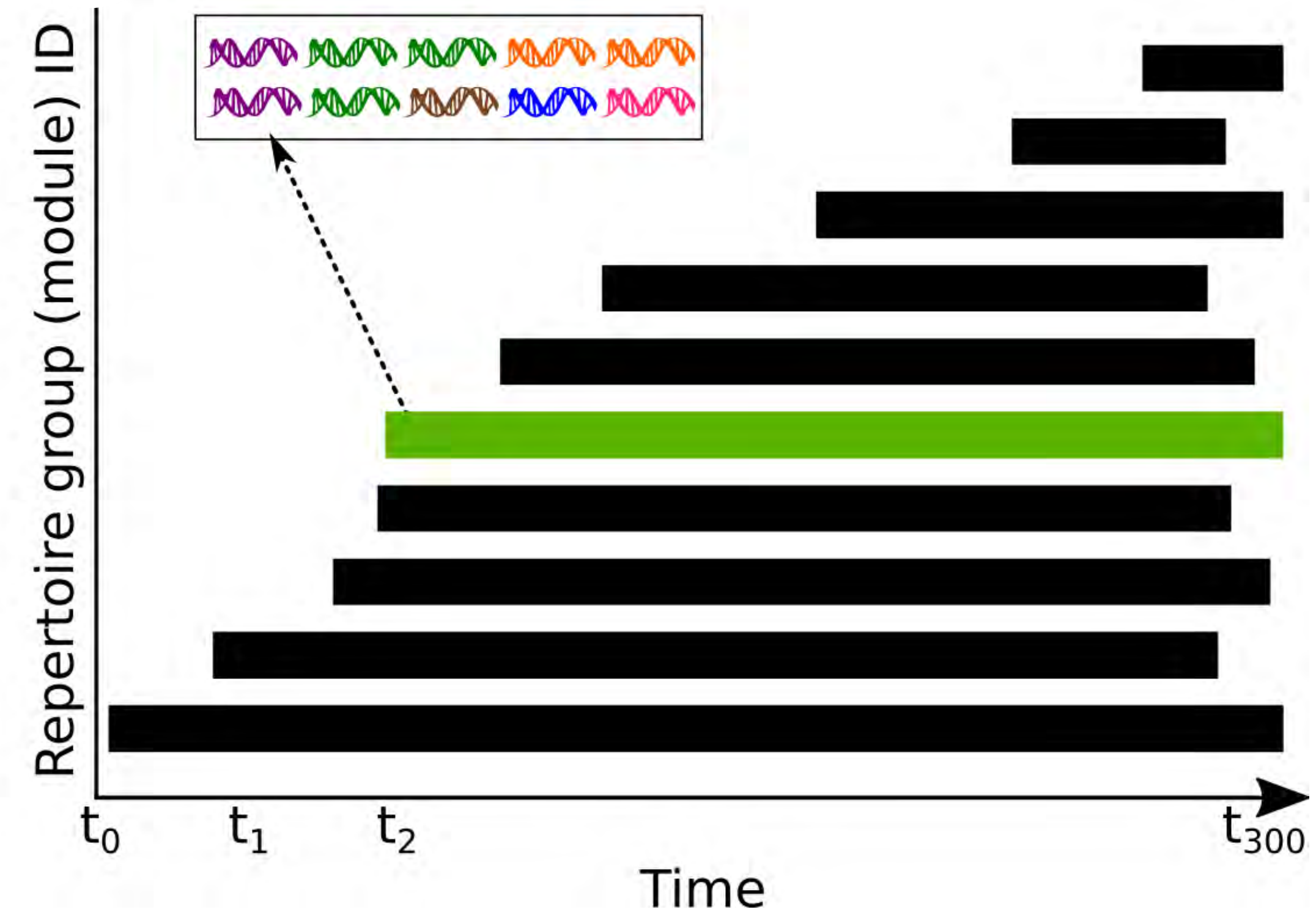
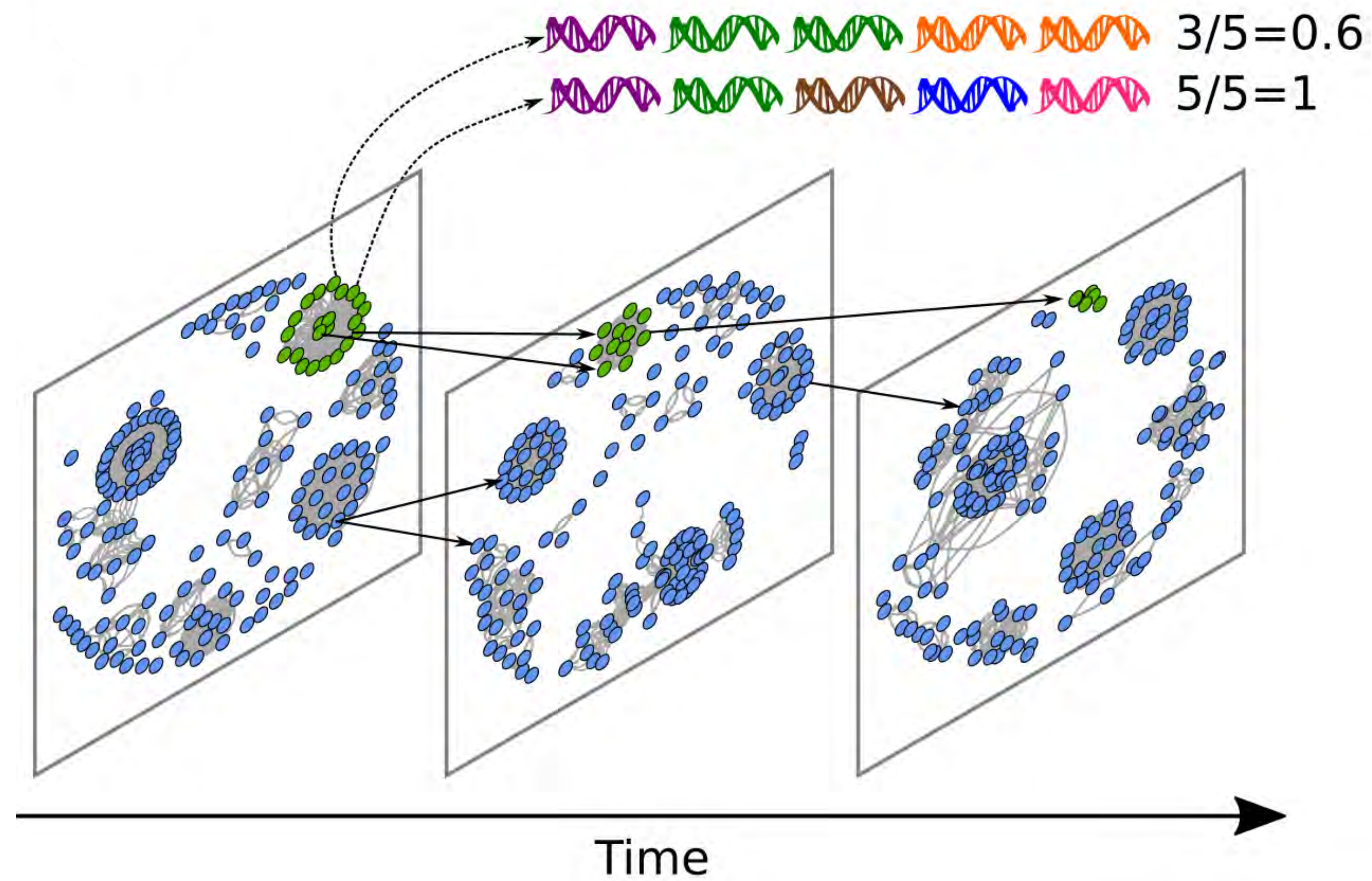
Meta-community structure



Temporal dynamics

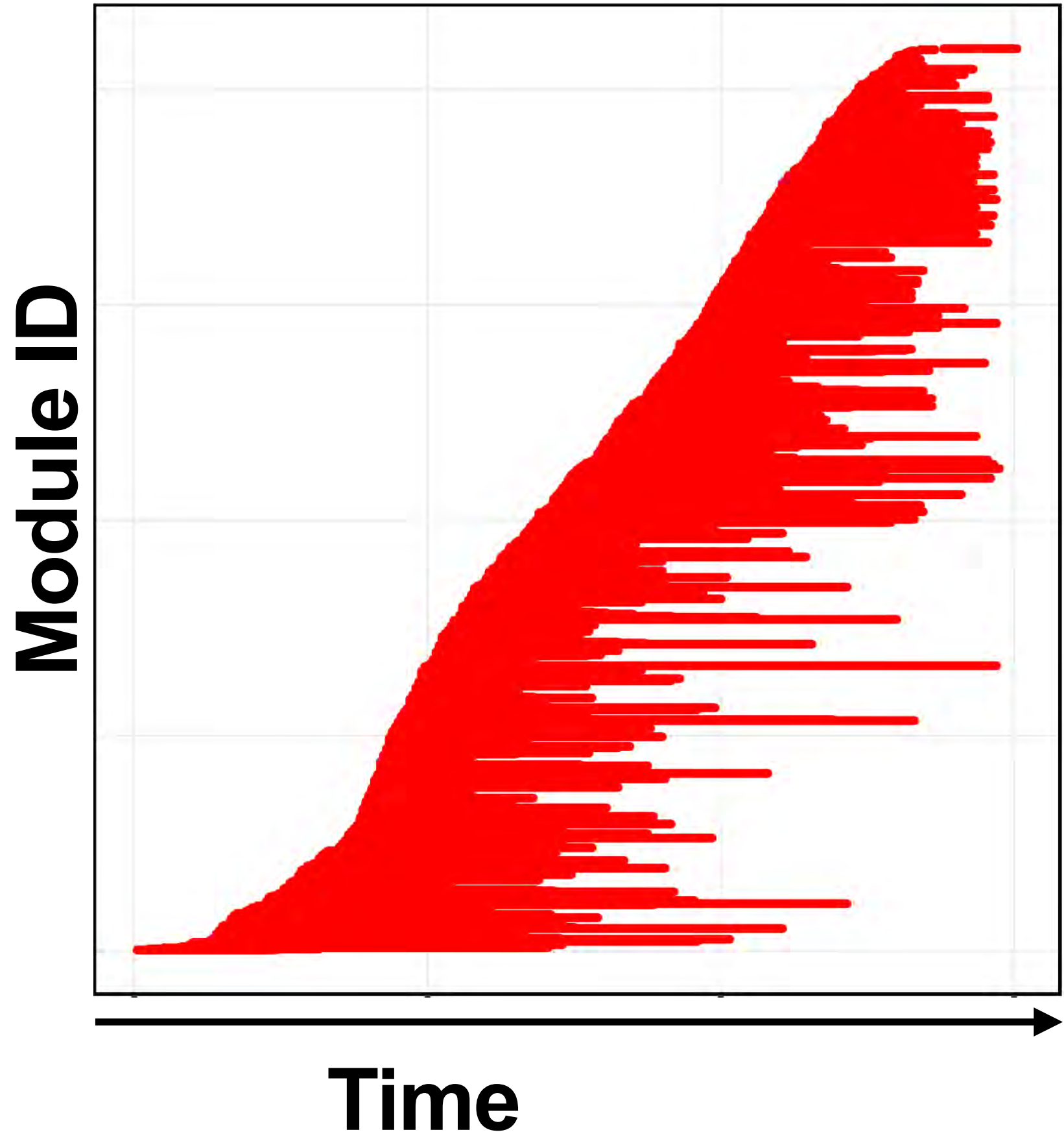


Revealing ecological niches using community detection

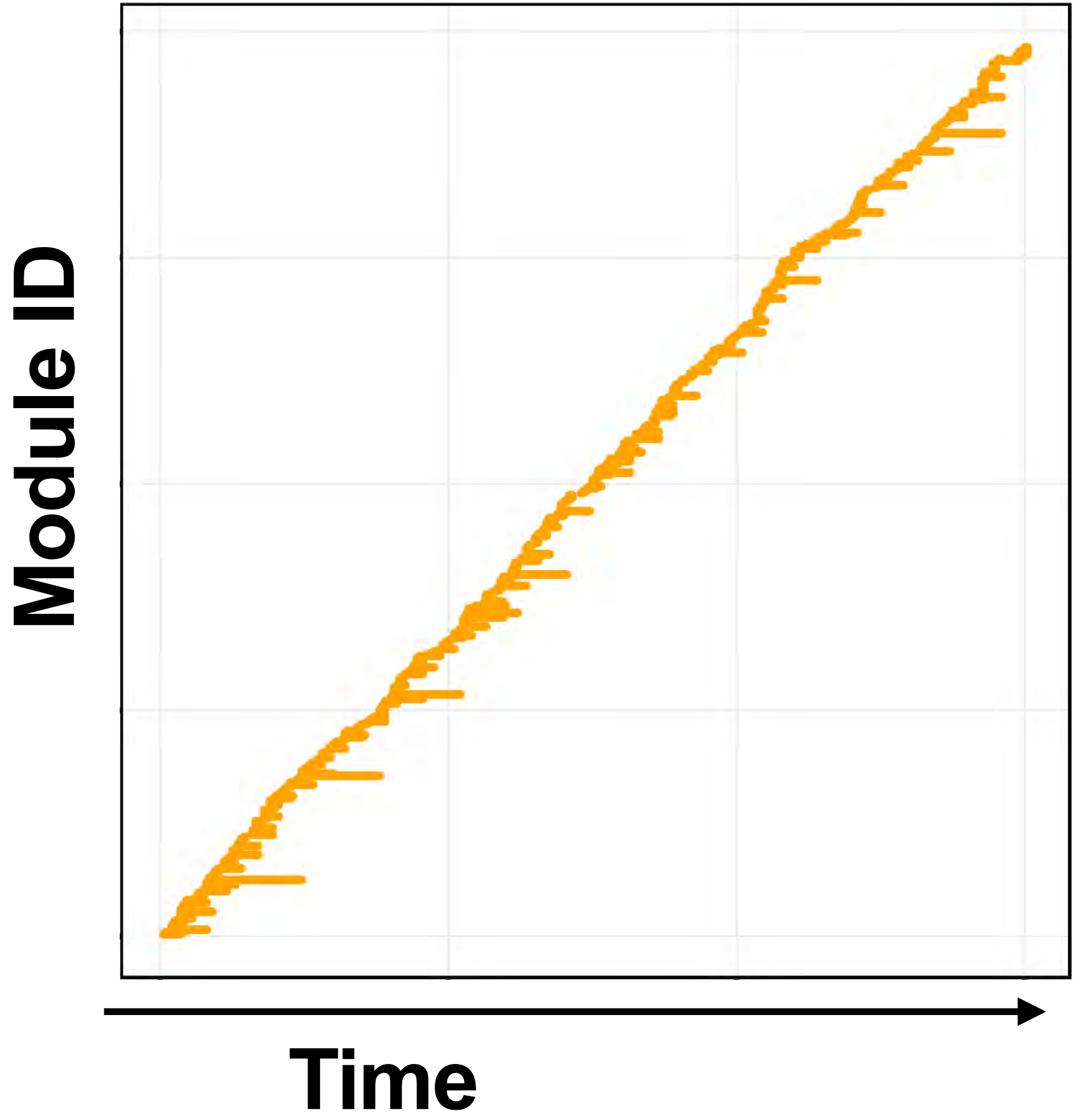


Human immunity determines structure

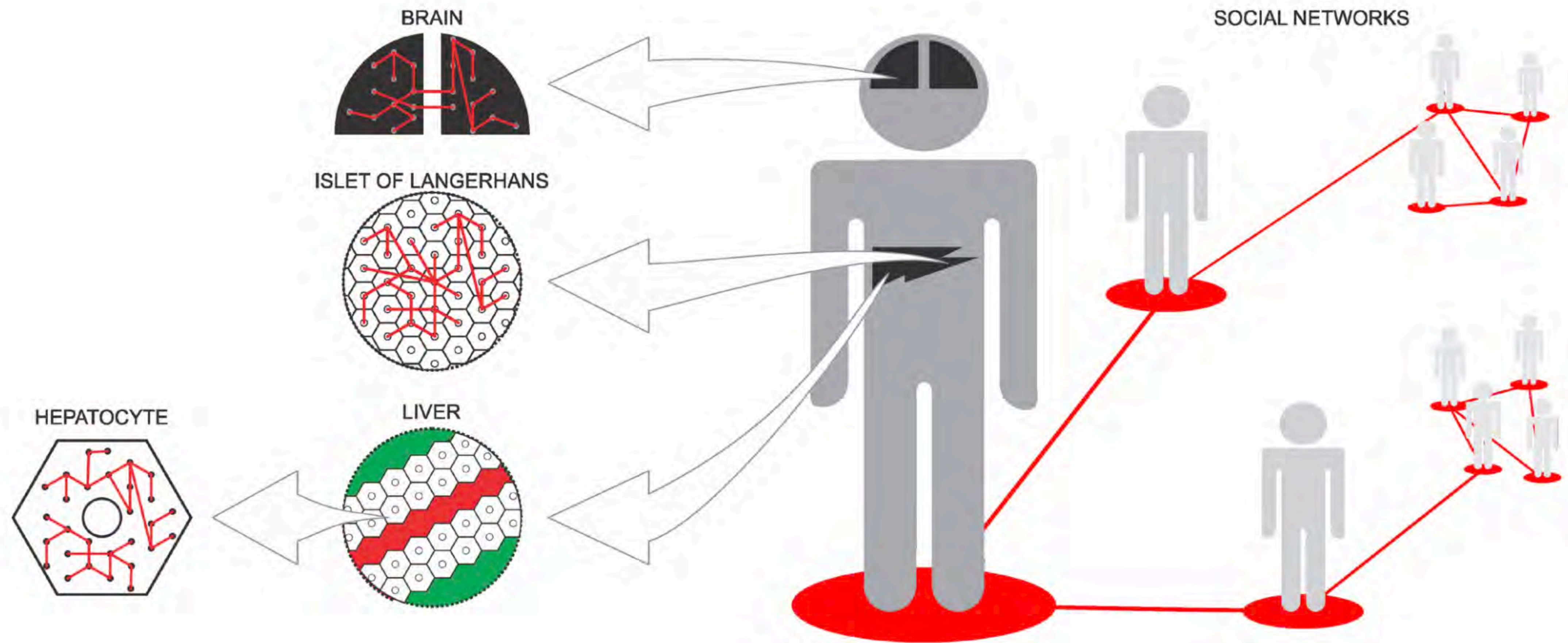
Human immunity



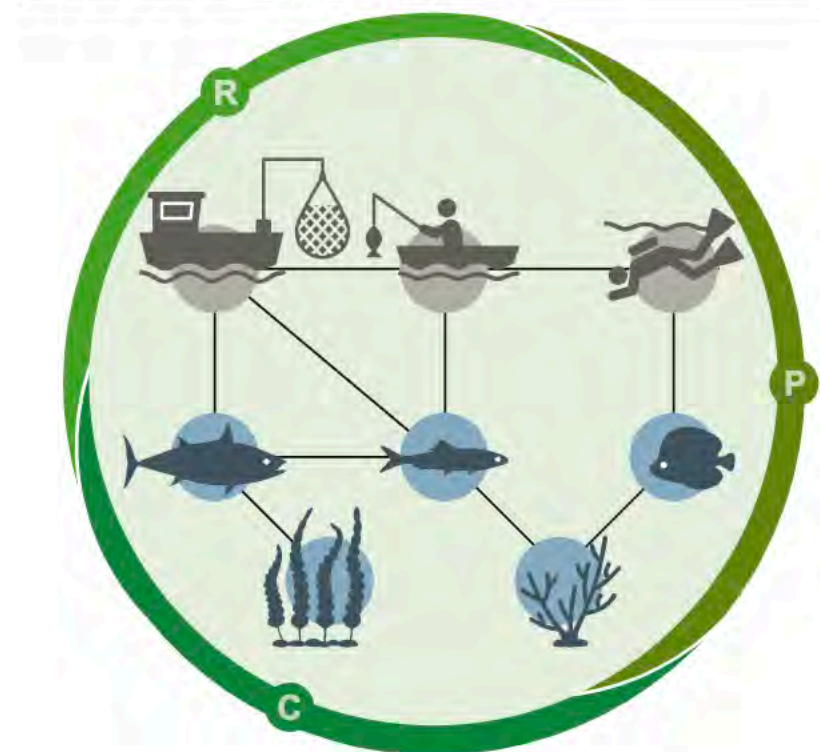
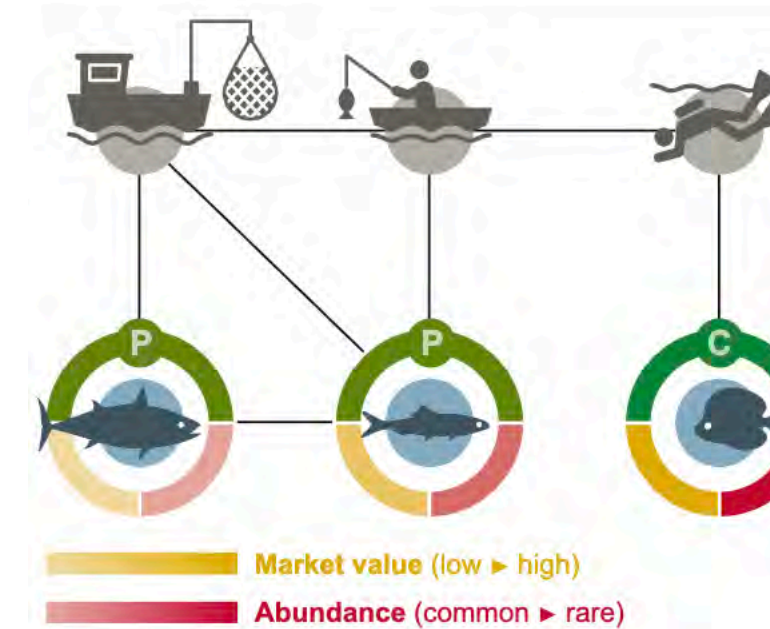
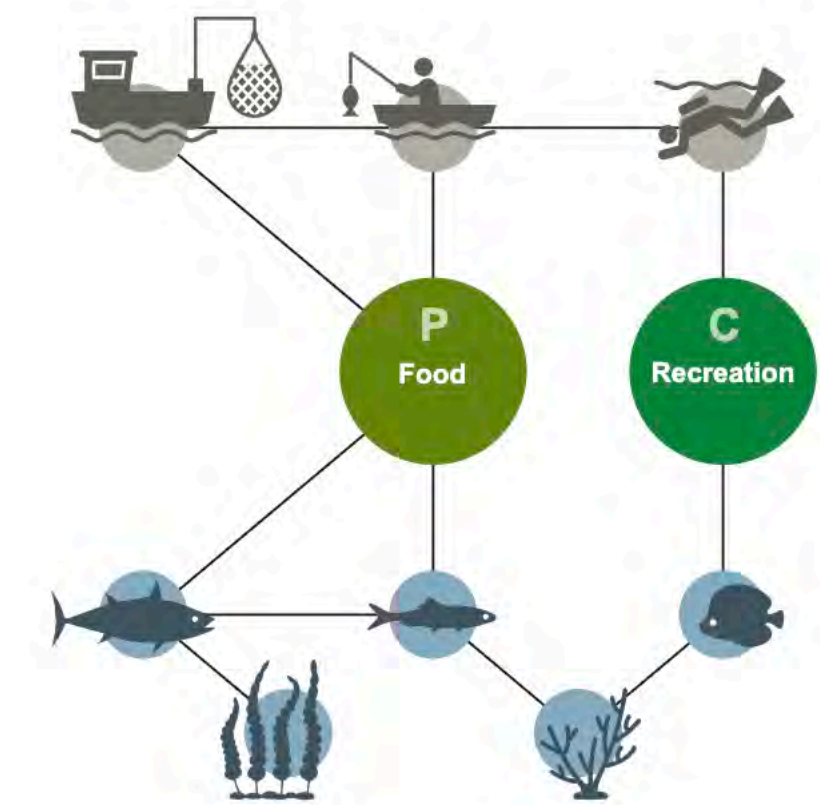
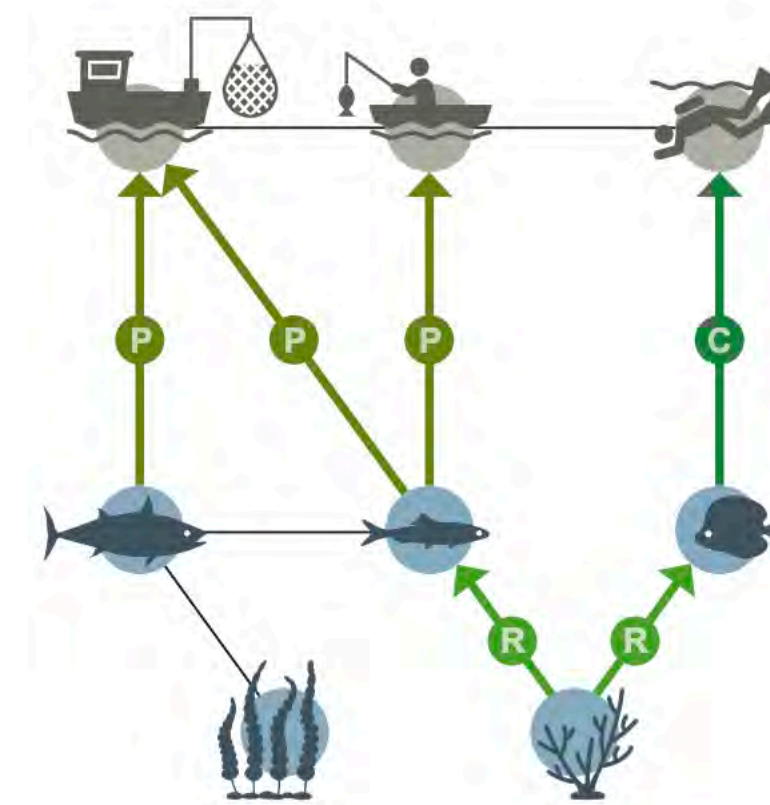
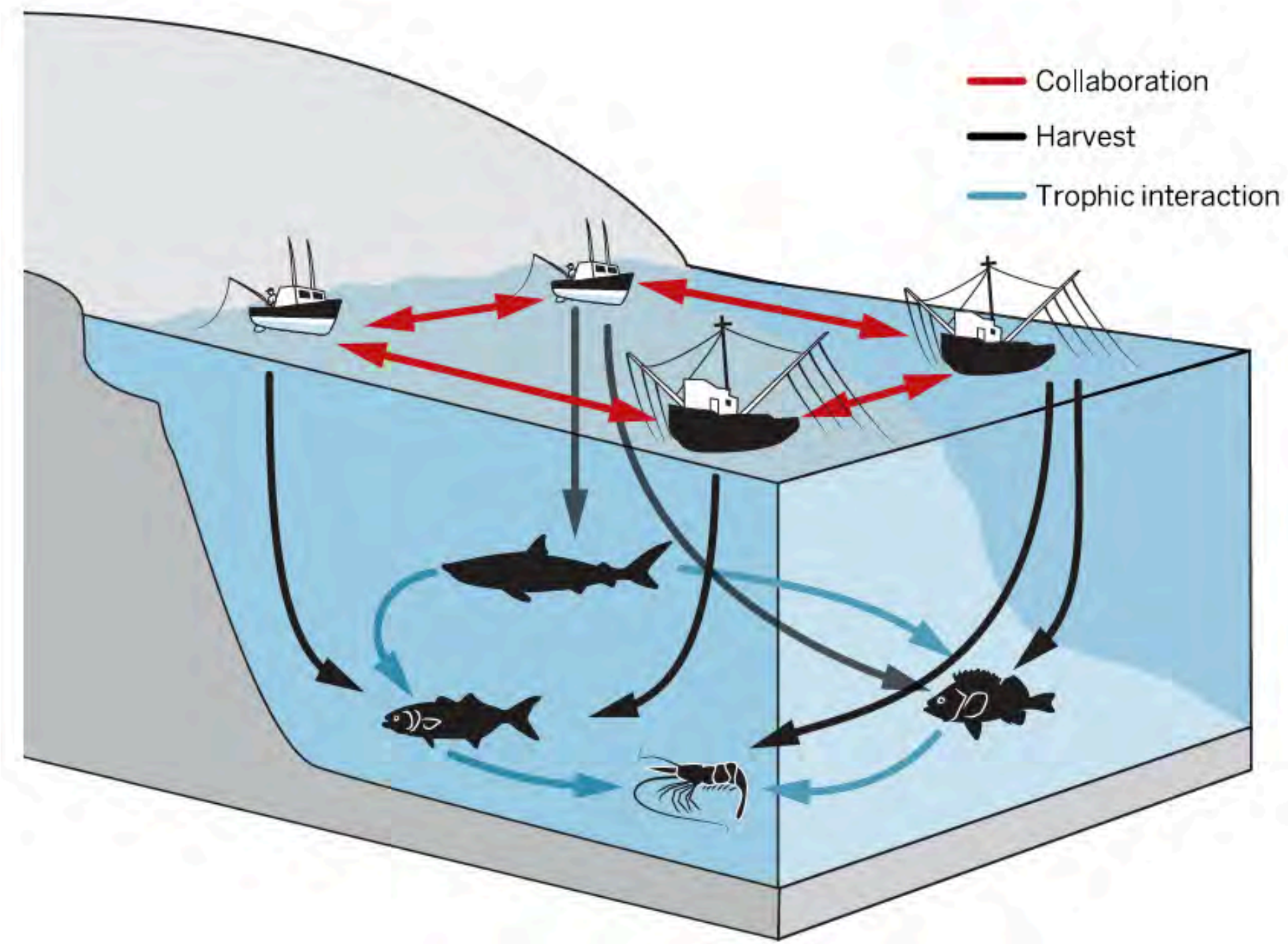
No human immunity



Interconnected scales



Social-ecological networks



Ecosystem services (ES)
R Regulating P Provisioning C Cultural

Social actors ● e.g. beneficiaries

Ecological actors ● e.g. species

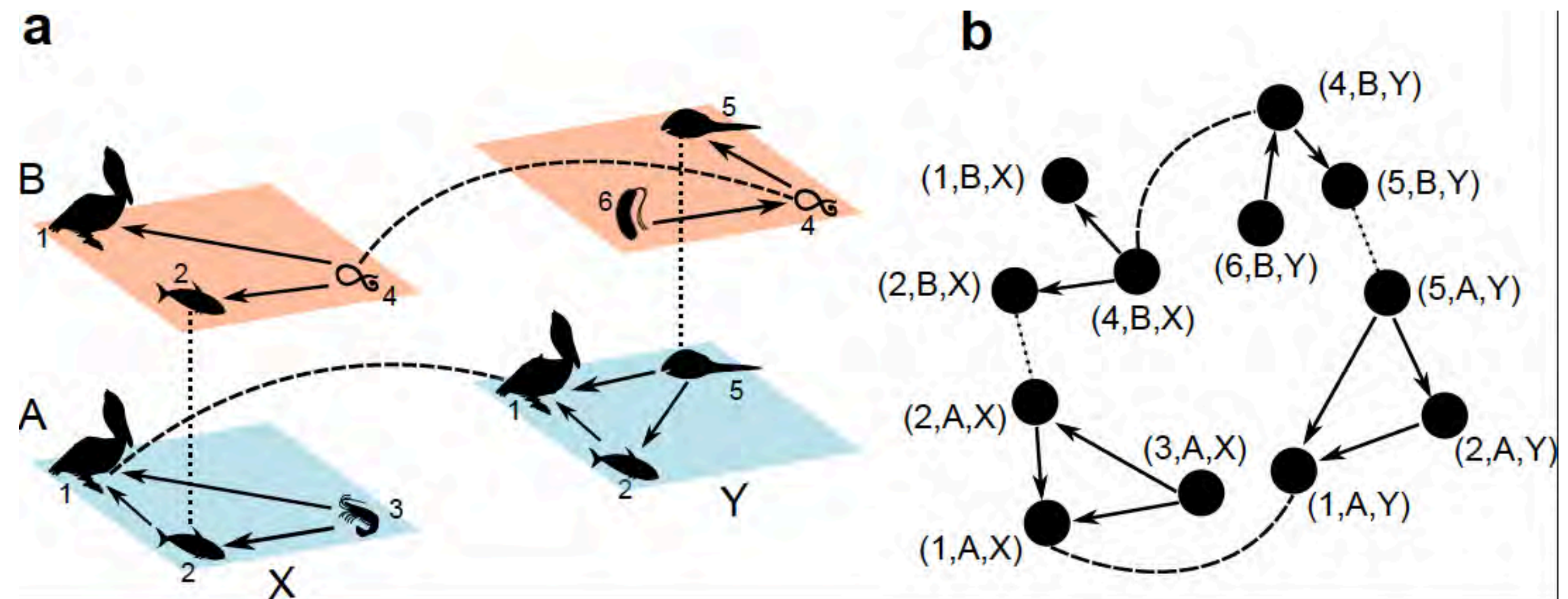
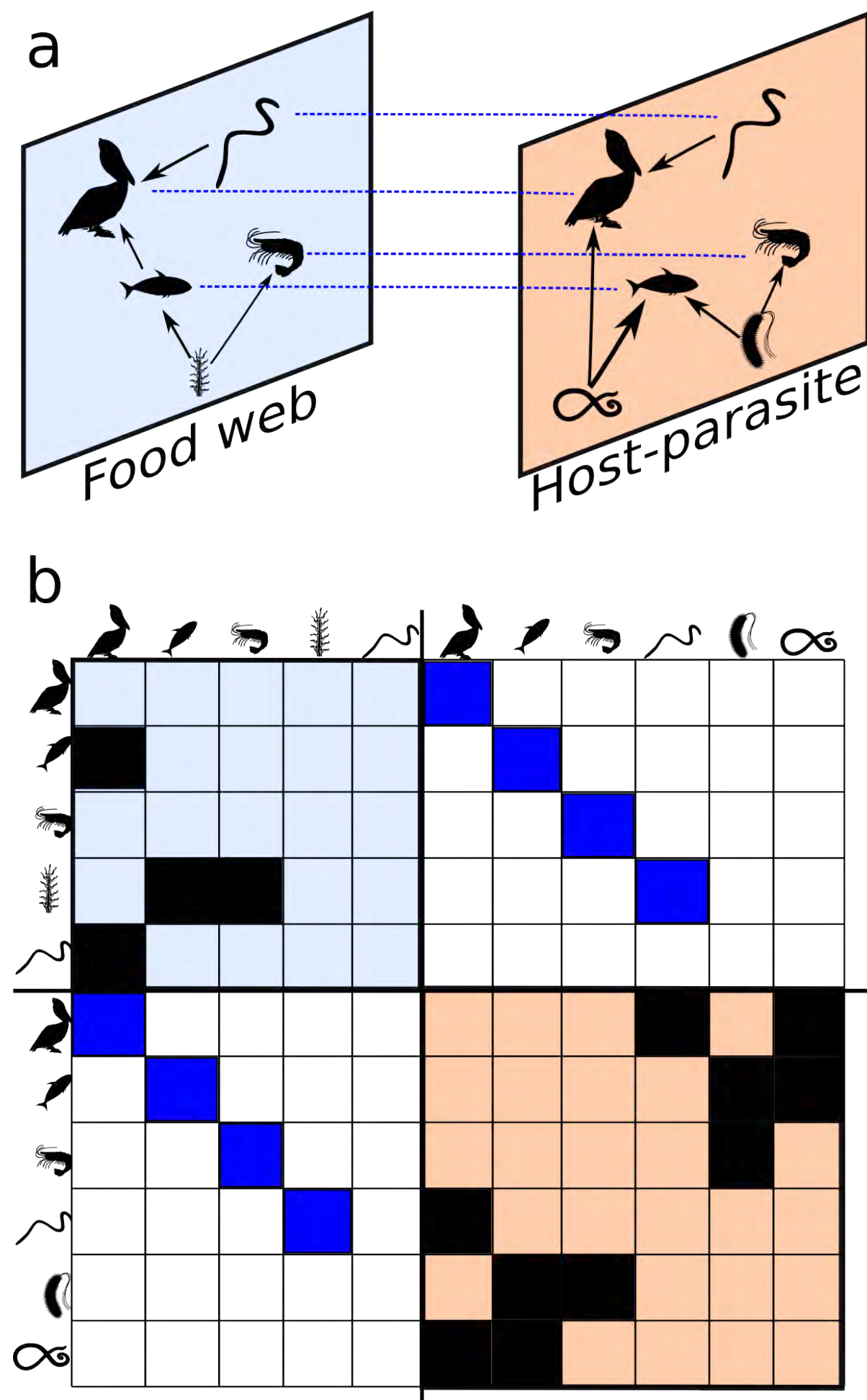
Interactions — ecological or social

Summary

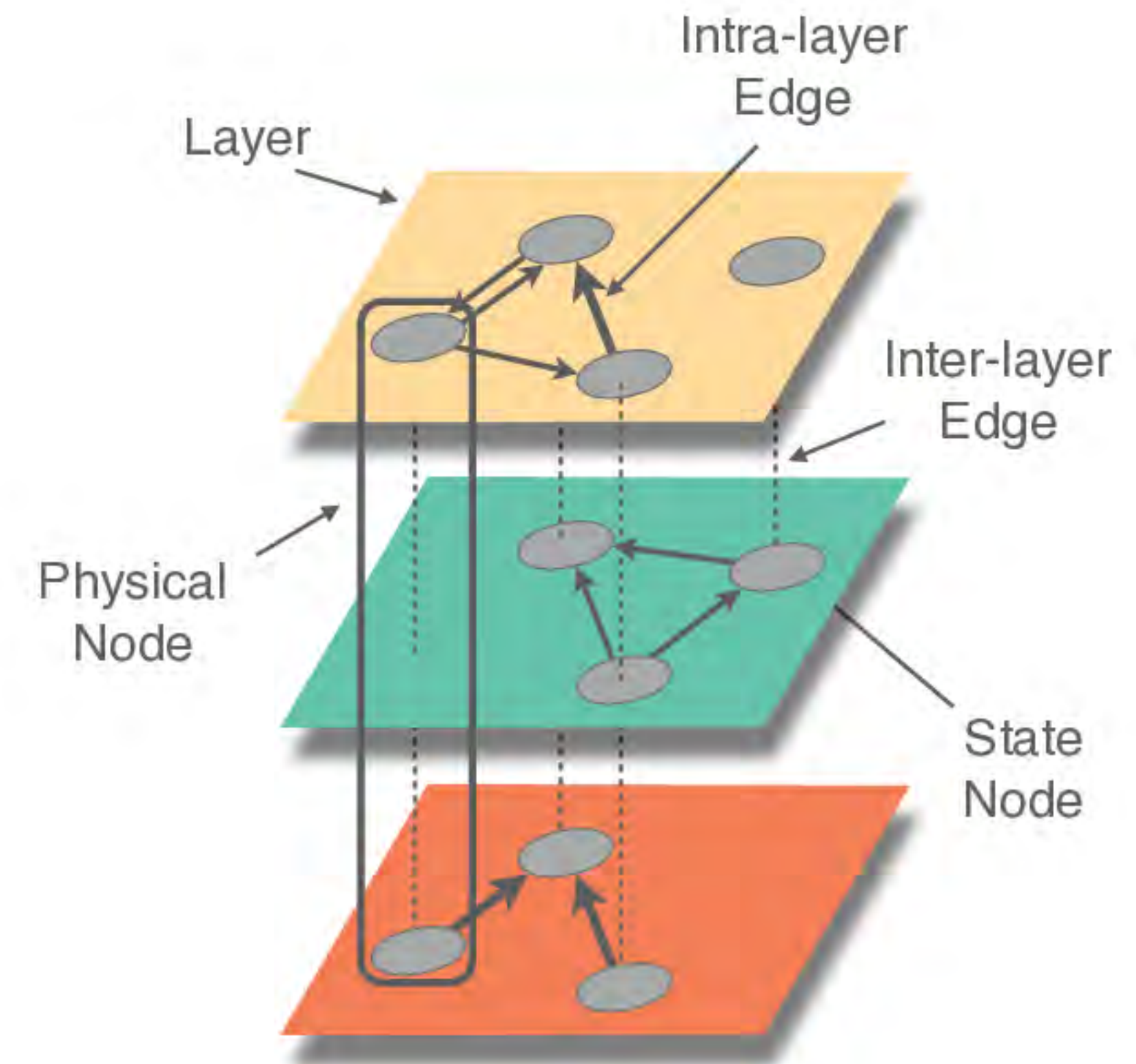
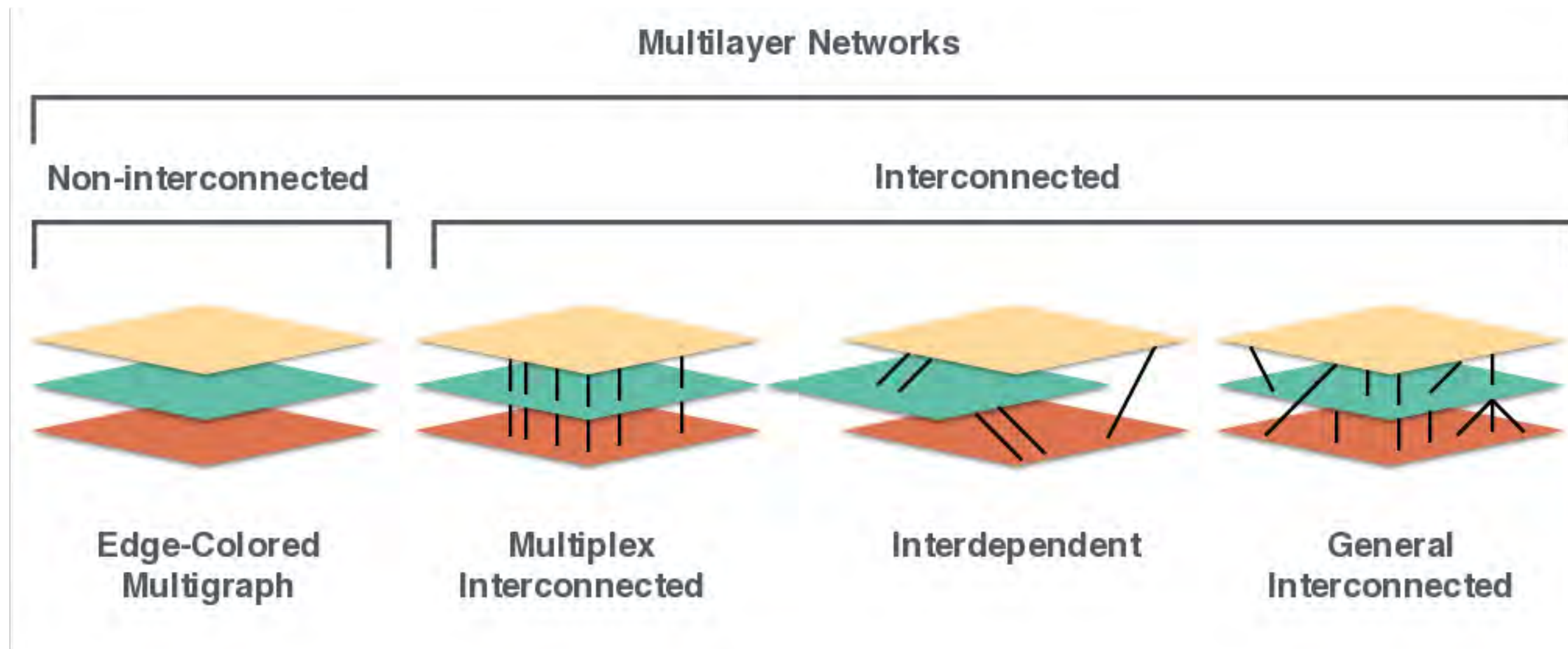
- Networks with multiple layers are not a new concept but multilayer networks is (relatively).
- Multiple types of interlayer edges.
- Interlayer edges (and state nodes) are key to encoding processes between layers.
- Many exciting questions!

Slides for exercise

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

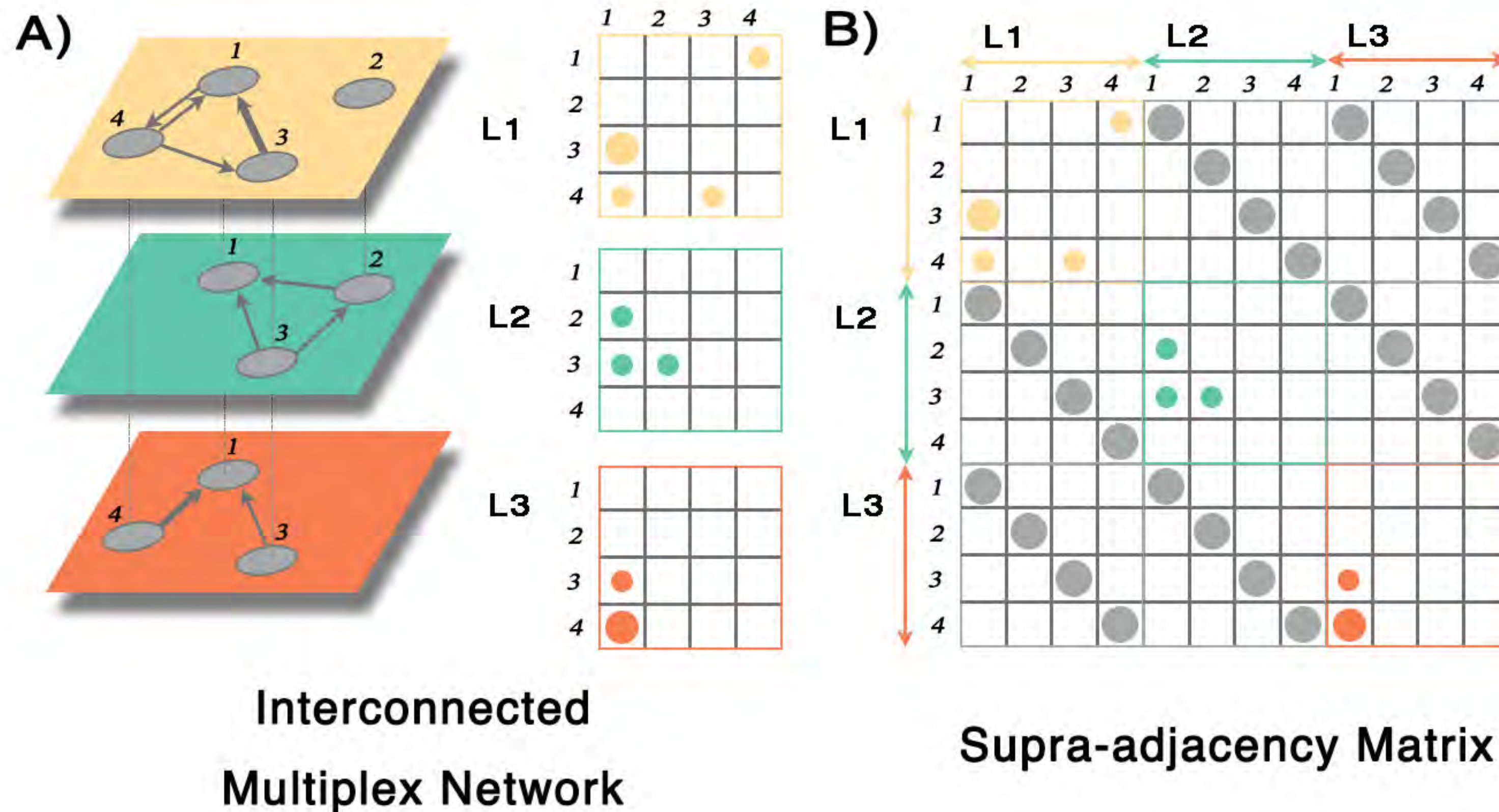


General definitions



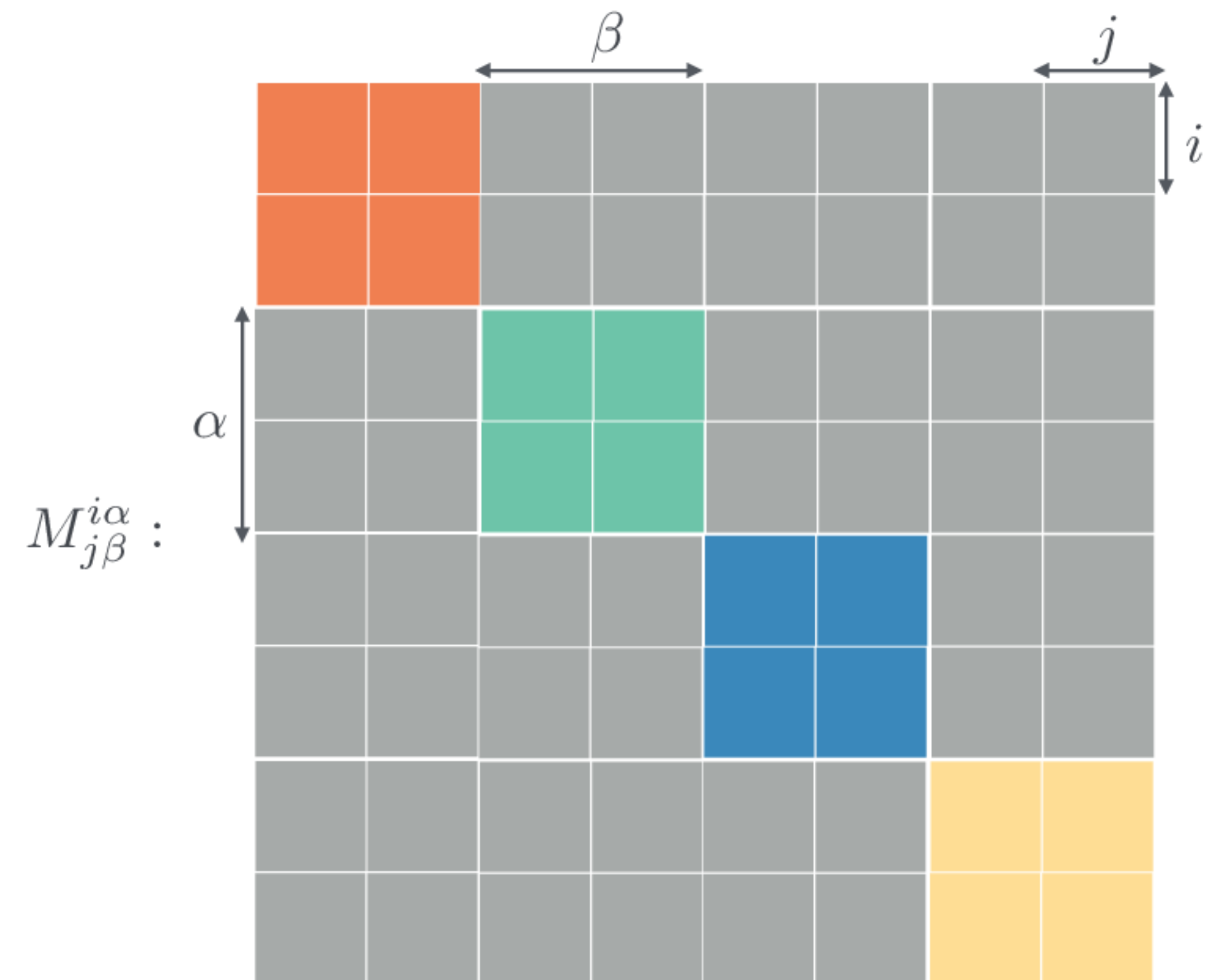
Matrix representation

Operatively, rank-4 tensors can be mapped into rank-2 supra-adjacency matrices to facilitate operations (with care)

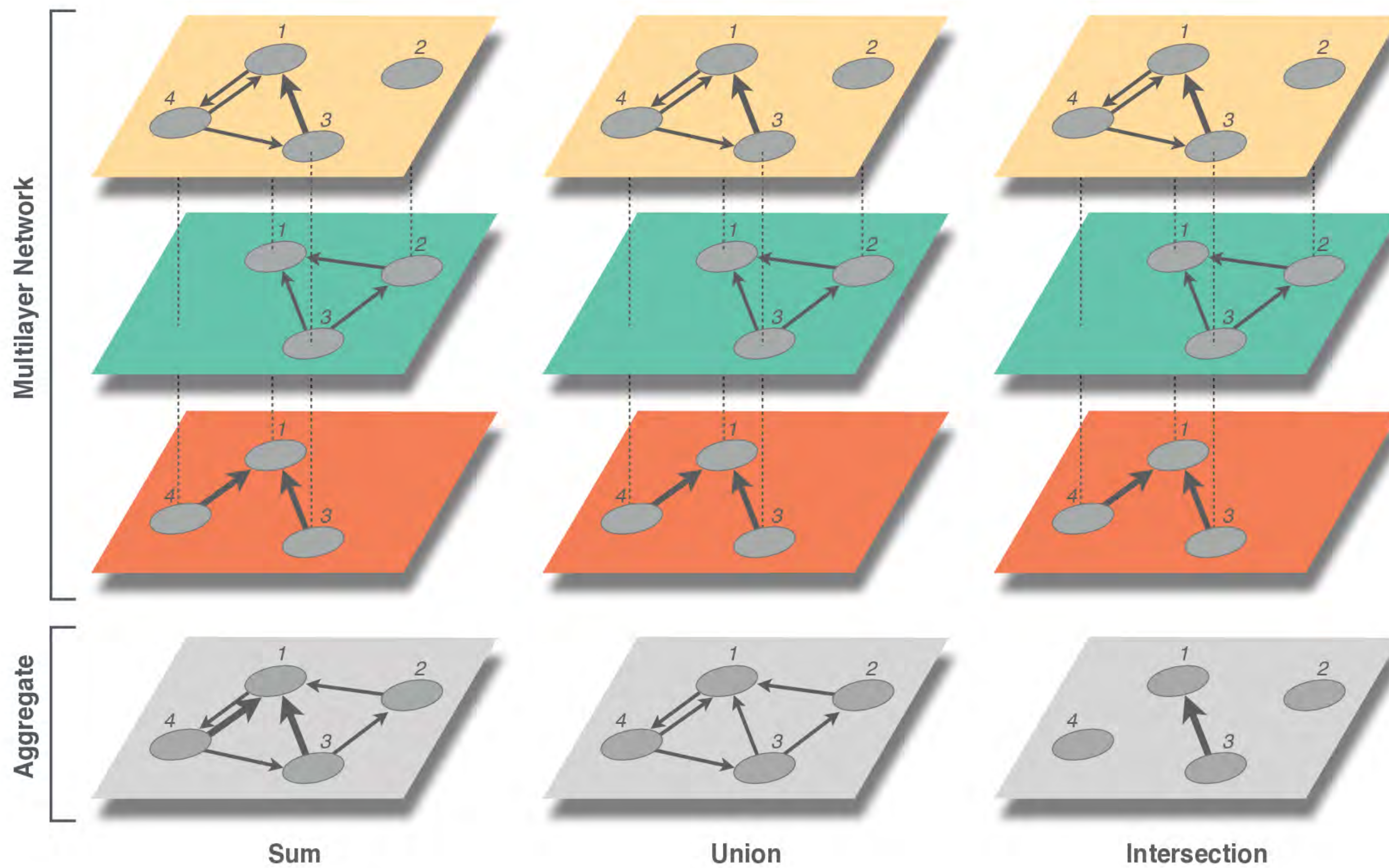


Tensor representation

A directed weighted connection between node i from layer α to node j in layer β



Aggregation

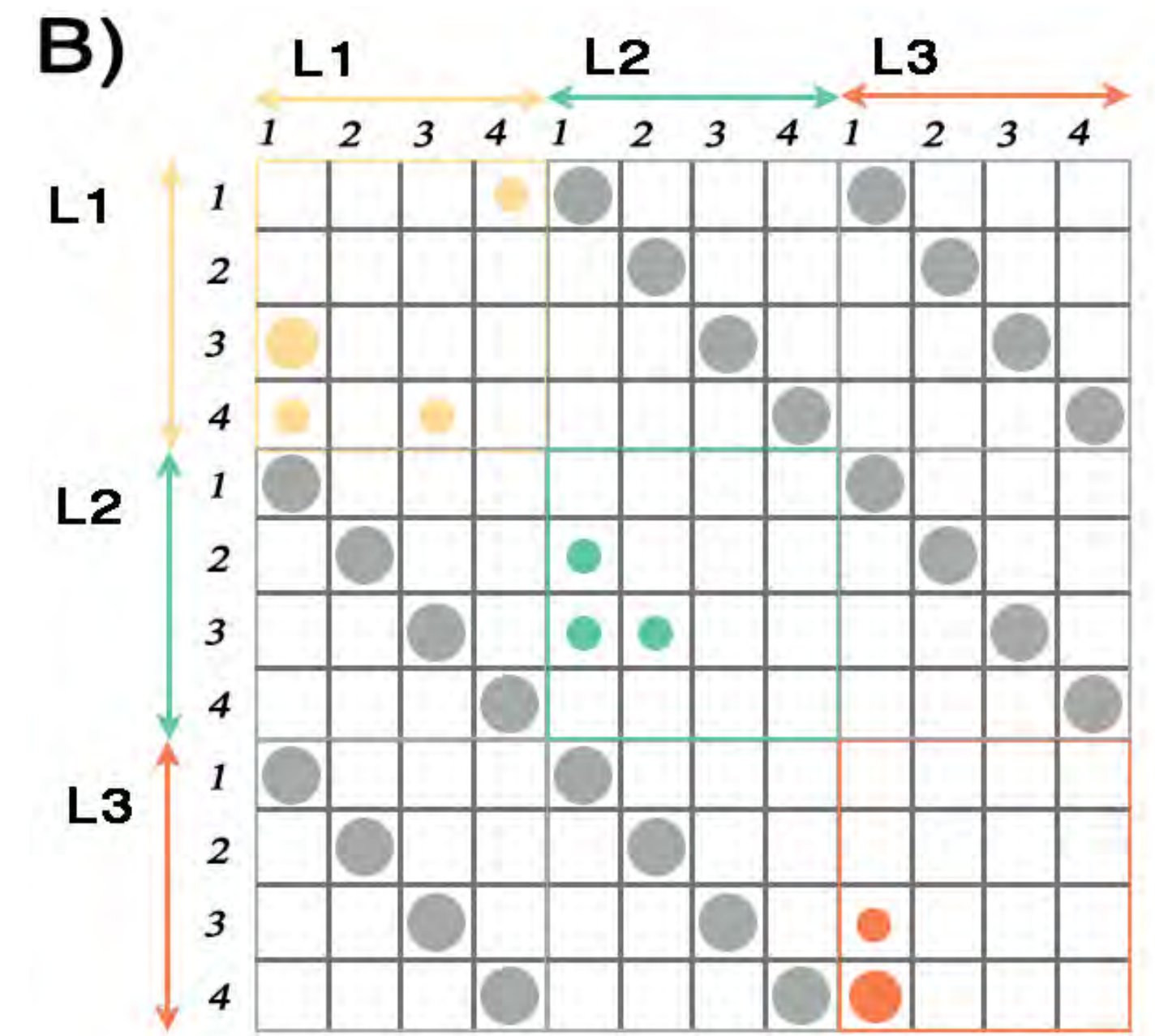


Centrality and versatility

Multi-degree of a node i is a vector (and you can do whatever you want with it...)

$$k_i = (k_i^{[1]}, \dots, k_i^{[M]})$$

EV versatility: “The versatility of each node is obtained by aggregating over layers the centrality of each node in each layer computed using the full multilayer structure.”



Centrality and versatility

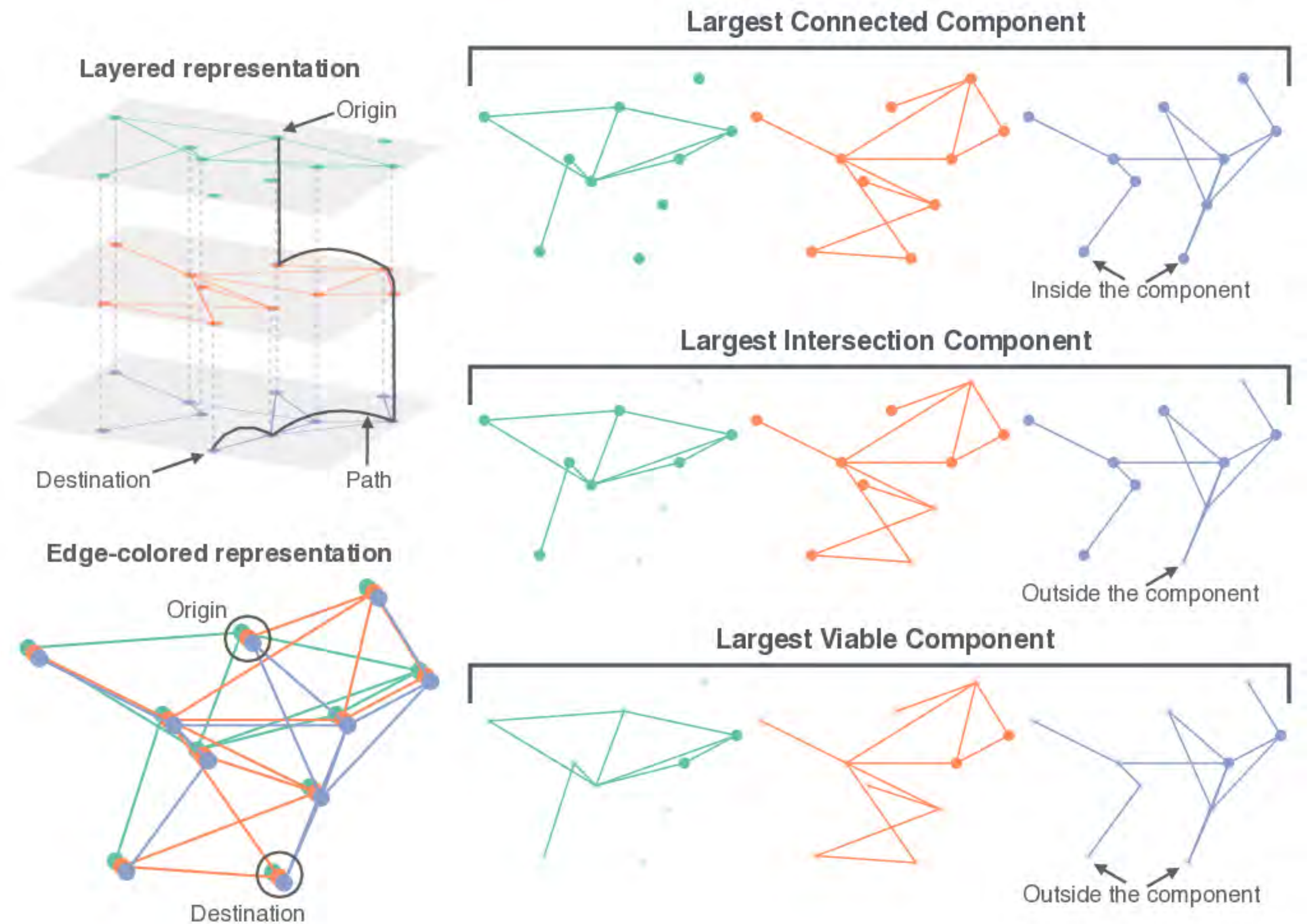
Betweenness versatility: can calculate on supra-adjacency matrix

$$l_{s\alpha \rightarrow t\beta}^* = \min(\mathcal{P}_{s\alpha \rightarrow t\beta})$$

$$l_{s \rightarrow t}^* = \min_{\alpha, \beta \in \{1, 2, \dots, L\}} (l_{s\alpha \rightarrow t\beta}^*)$$

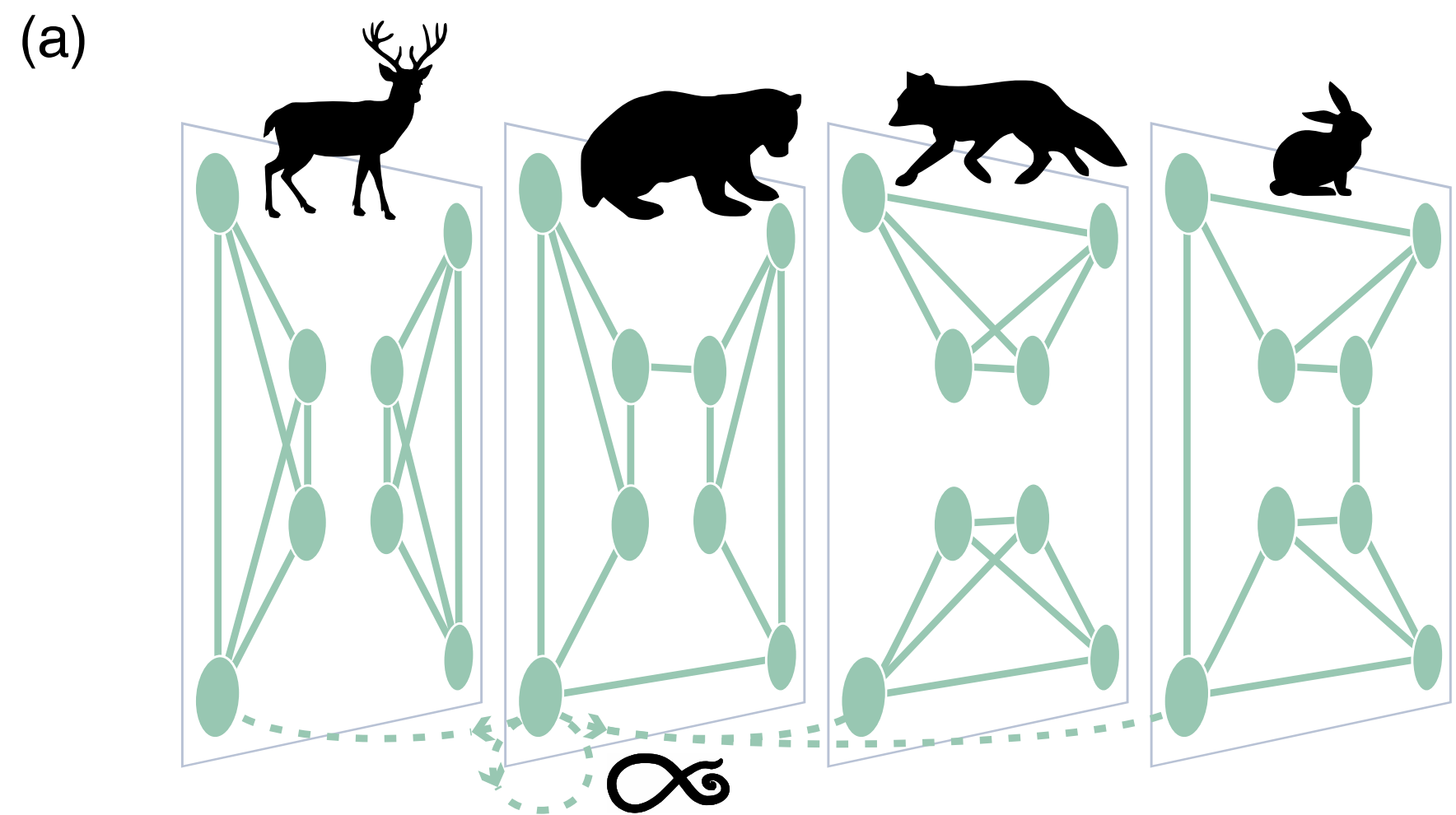
$$\sigma_{st}(j) = \|l_{s \rightarrow t}^*(j)\|$$

$$BC(j) = \sum_{s \neq j \neq t} \frac{\sigma_{st}(j)}{\sigma_{st}}$$

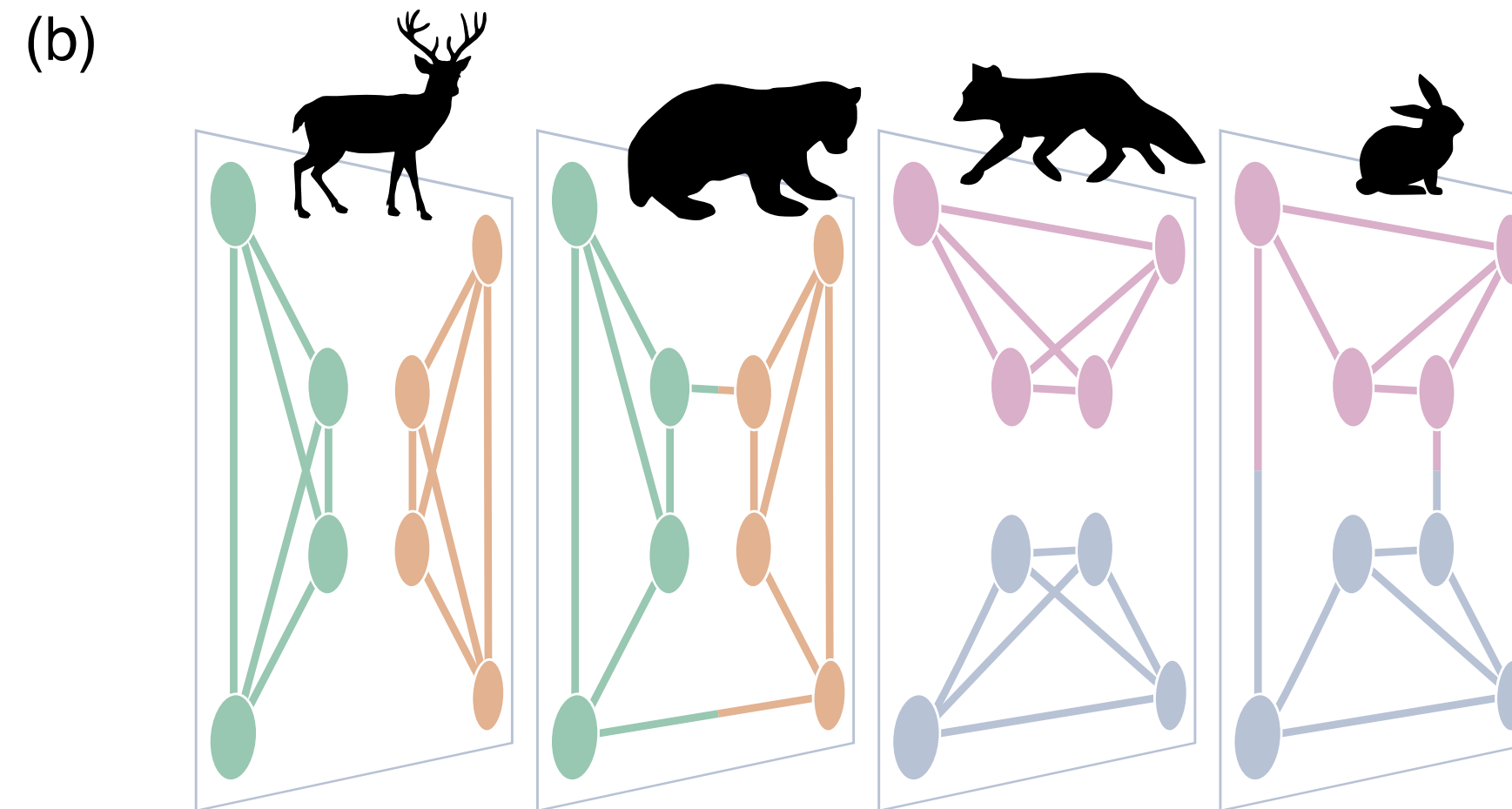


Infomap in multilayer networks

<https://www.mapequation.org/apps/multilayer-network/index.html>



$$L = H(12/96, 12/96, 12/96, 12/96, 12/96, 12/96, 12/96, 12/96) = 3 \text{ bits}$$



$$L = (8 + 48r)/96 H((2 + 12r)/96, (2 + 12r)/96, (2 + 12r)/96, (2 + 12r)/96) + (26 + 12r)/96 H(6/96, 6/96, 6/96, 6/96, (2 + 12r)/96) + (26 + 12r)/96 H(6/96, 6/96, 6/96, 6/96, (2 + 12r)/96) + (26 + 12r)/96 H(6/96, 6/96, 6/96, 6/96, (2 + 12r)/96) + (26 + 12r)/96 H(6/96, 6/96, 6/96, 6/96, (2 + 12r)/96) \approx 2.84 \text{ bits for } r = 0.1$$