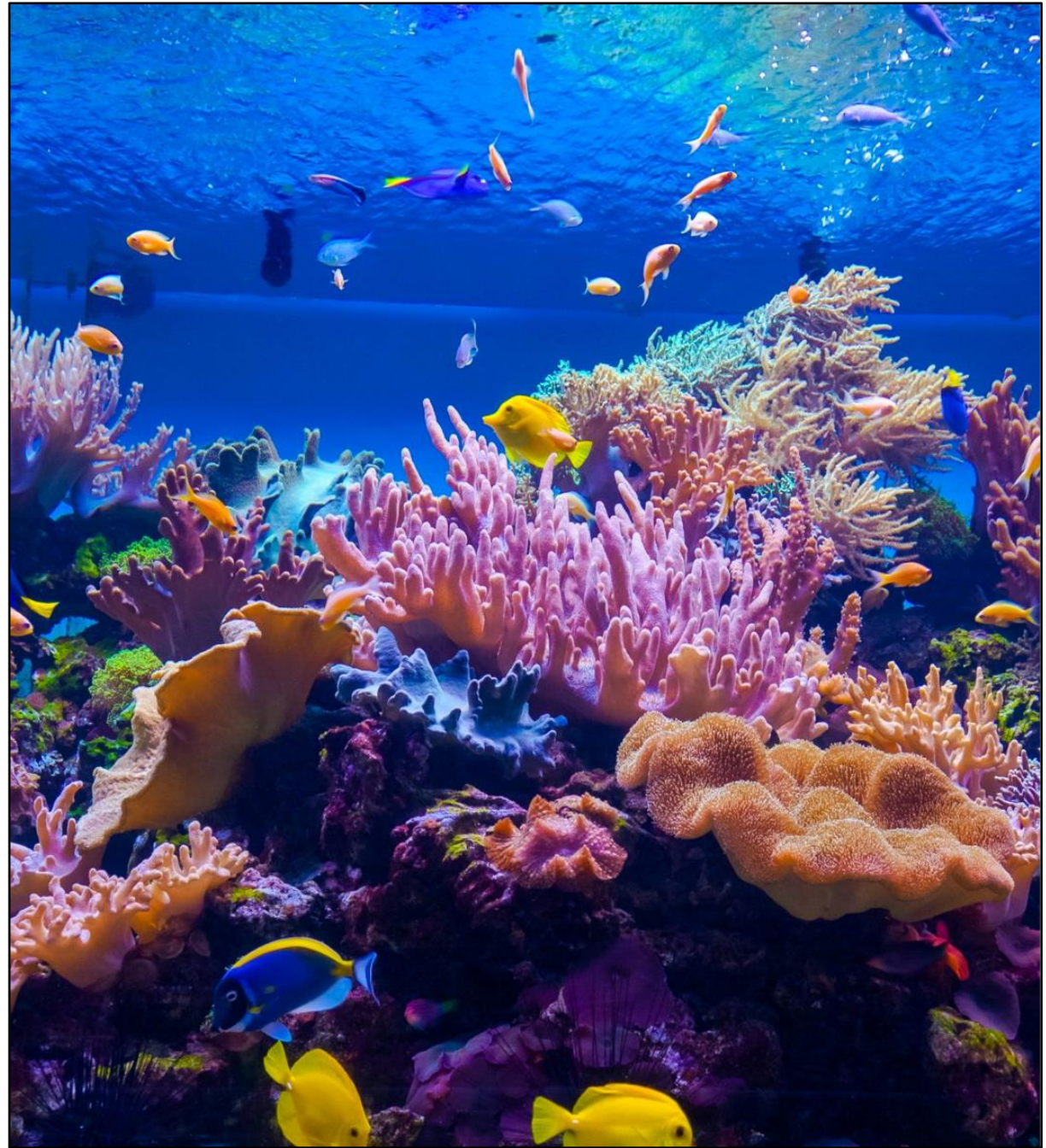
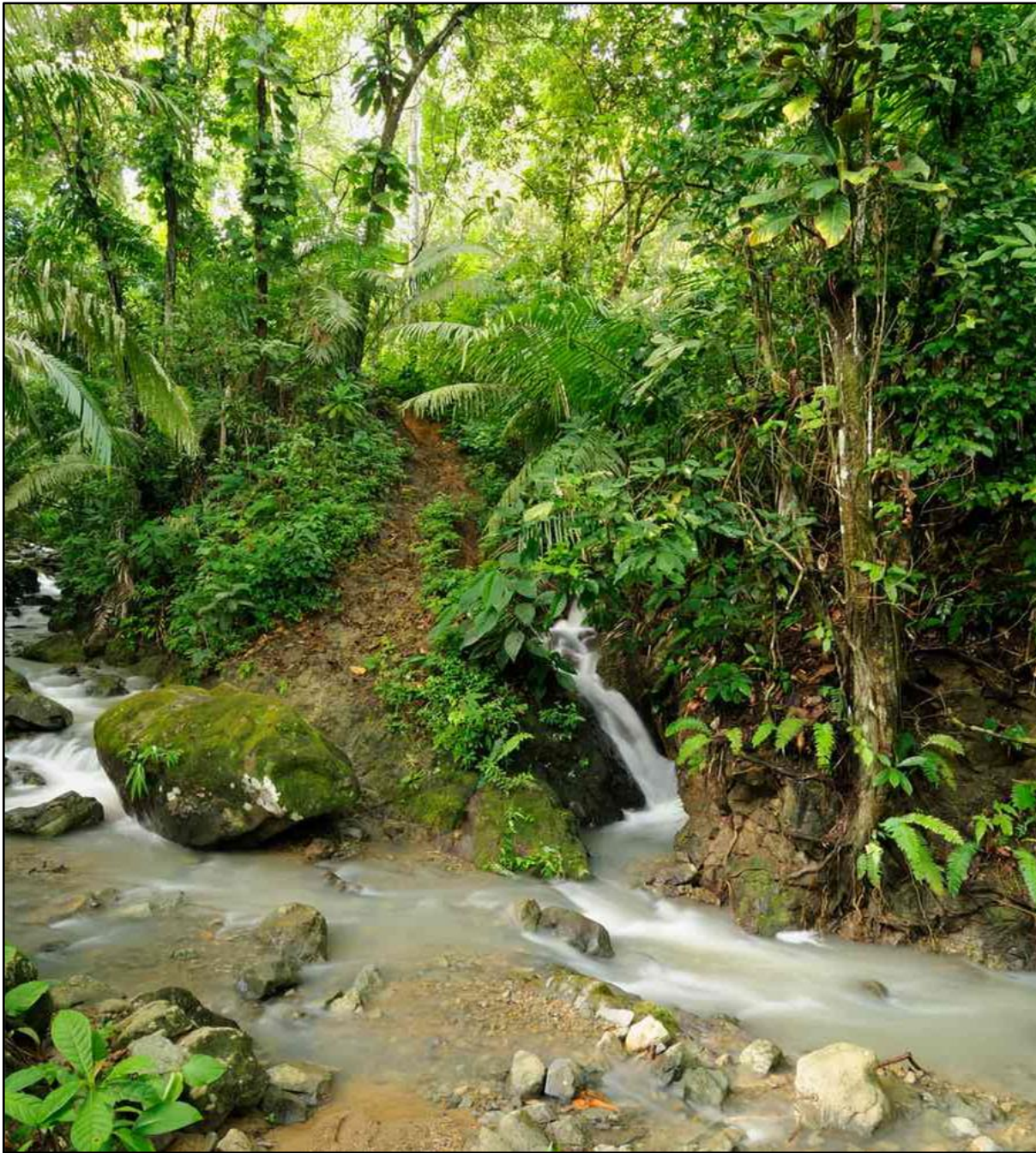


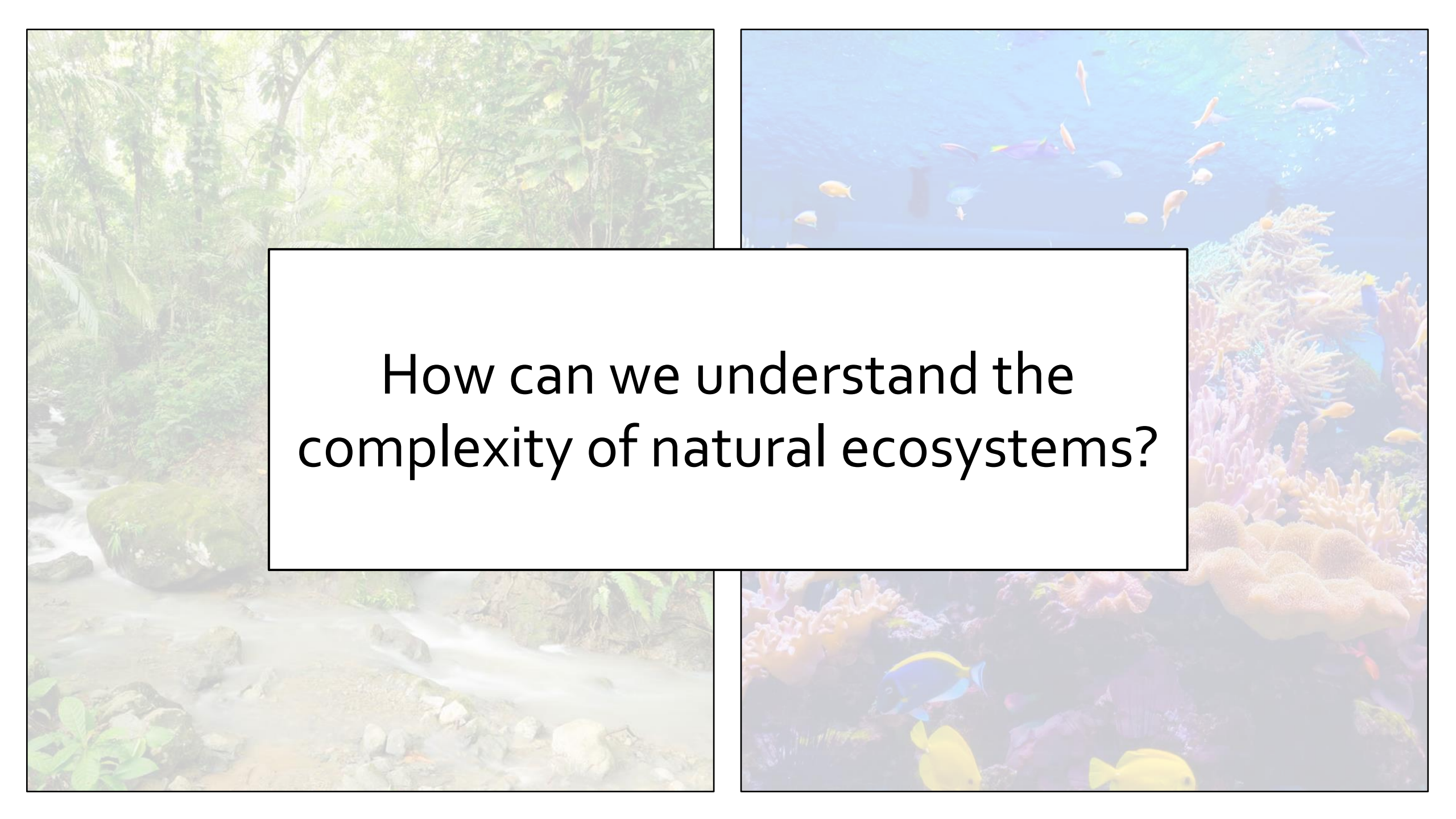


Topological patterns in ecological networks


BIO365 – Ecological Networks

Leandro G. Cosmo
leandro.giacobellicosmo@uzh.ch



The image is a collage of four nature scenes. The top-left panel shows a lush green forest with sunlight filtering through the trees. The top-right panel shows a vibrant coral reef with many colorful fish swimming in clear blue water. The bottom-left panel shows a small waterfall cascading over rocks in a forest. The bottom-right panel shows a close-up of a coral reef with several colorful fish, including a blue tang and a yellow tang. In the center of the collage is a white rectangular box with a black border containing the text.

How can we understand the complexity of natural ecosystems?




Quantifying interactions and understanding the role of species:

Direct interactions (degree)

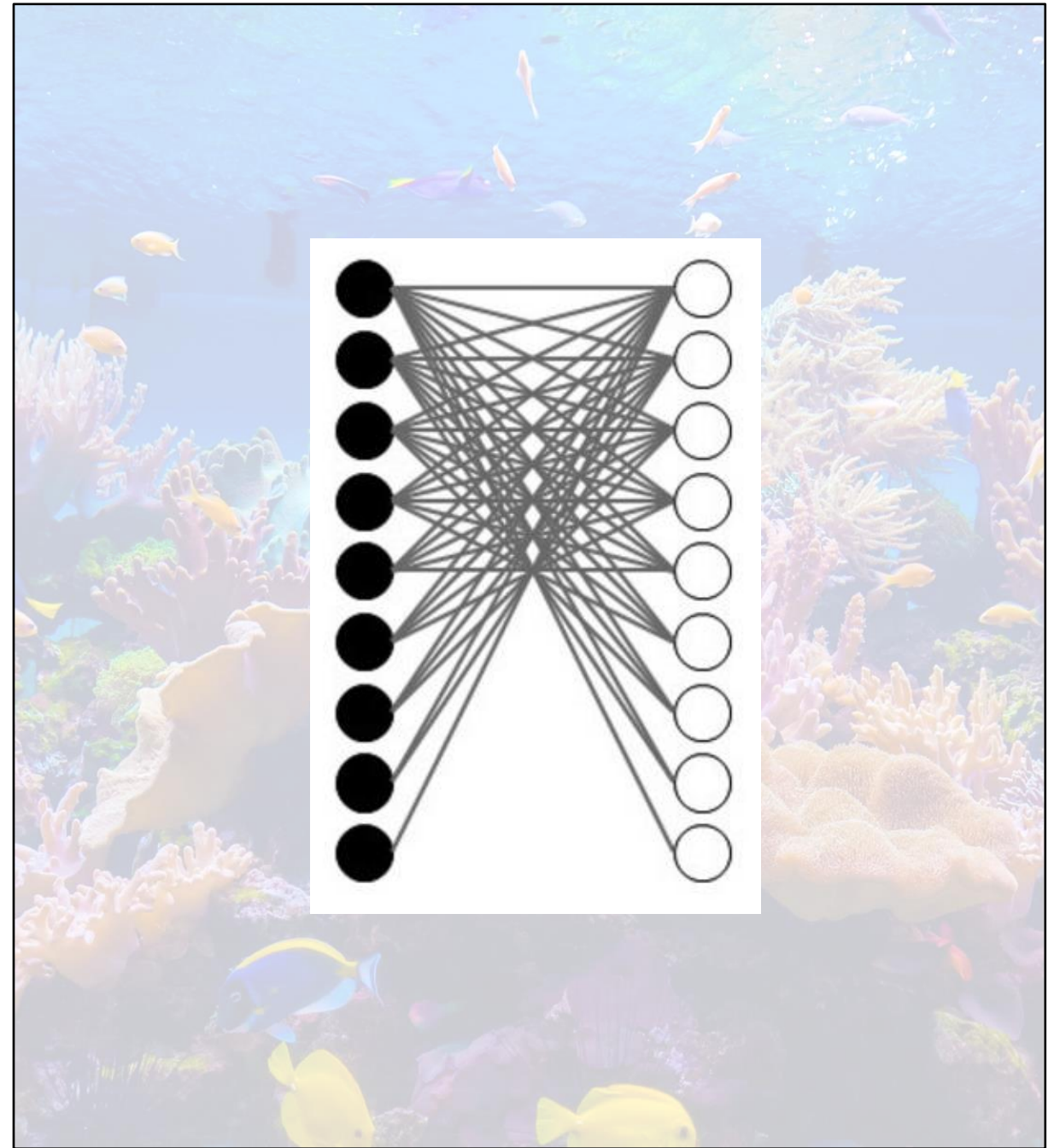
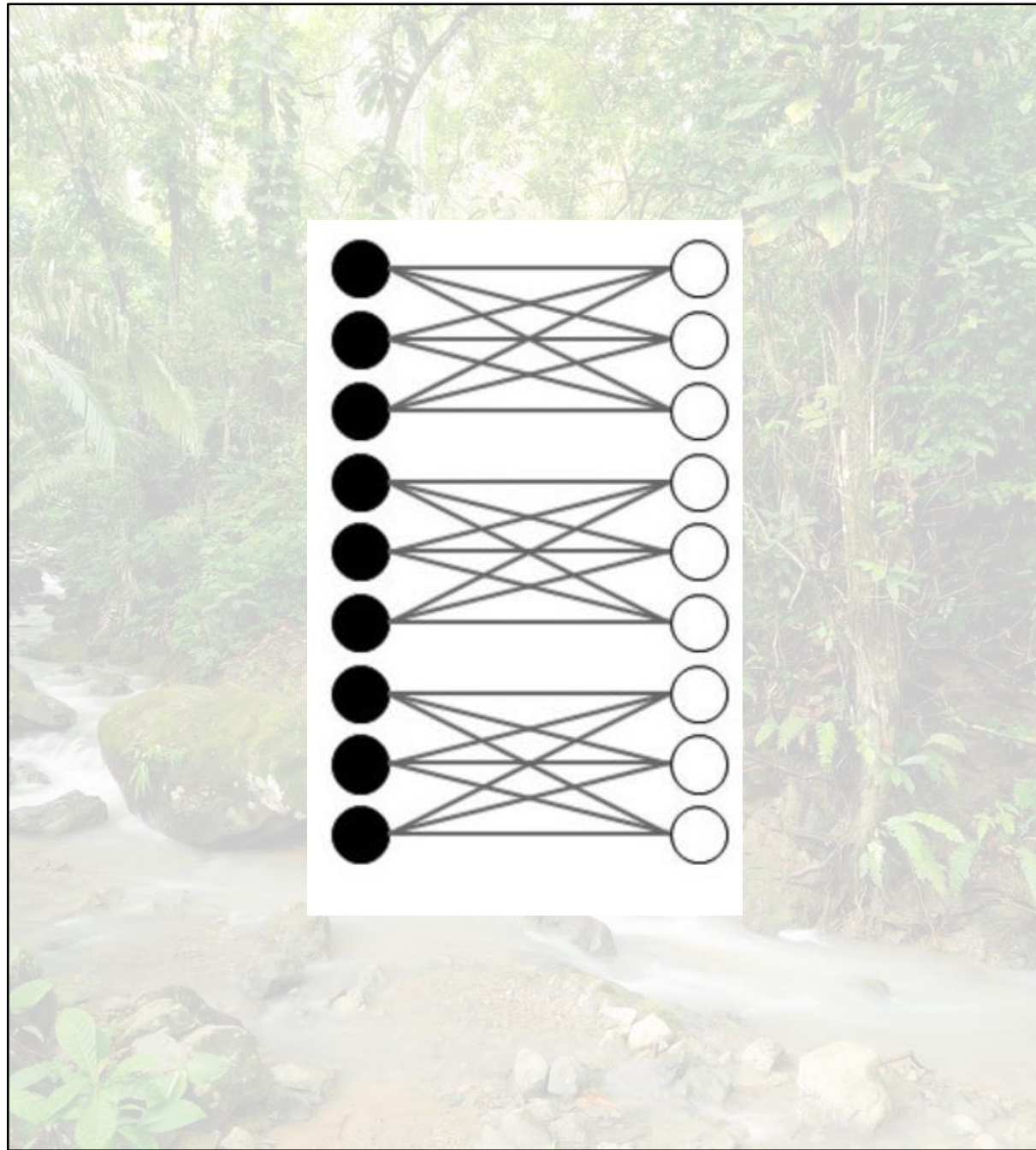
Indirect interactions through shortest pathways (closeness)

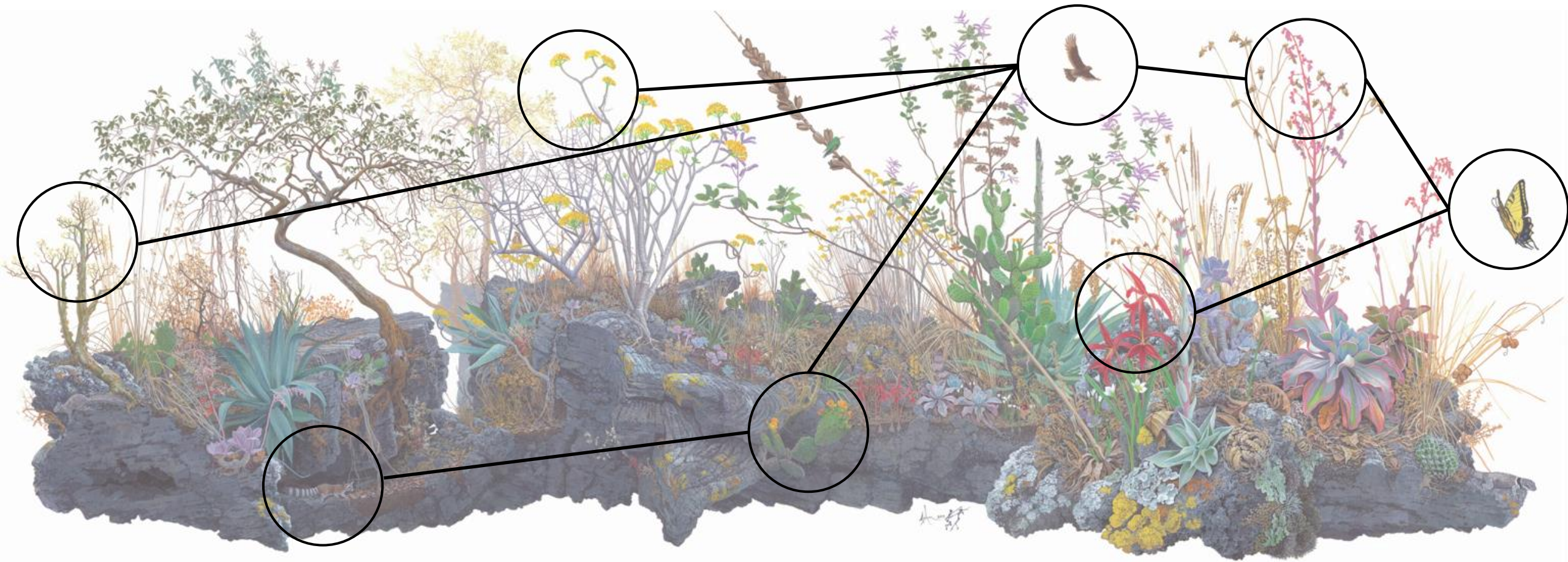
Indirect interactions through all possible pathways (Katz)

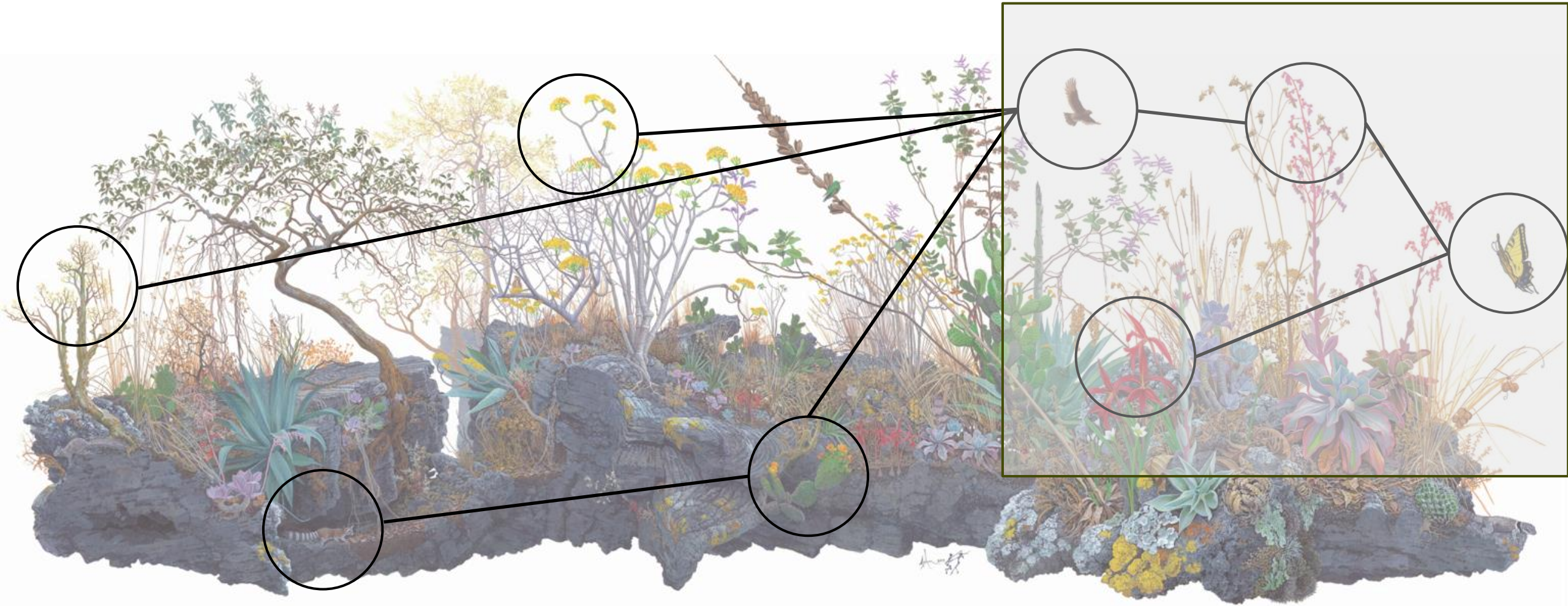


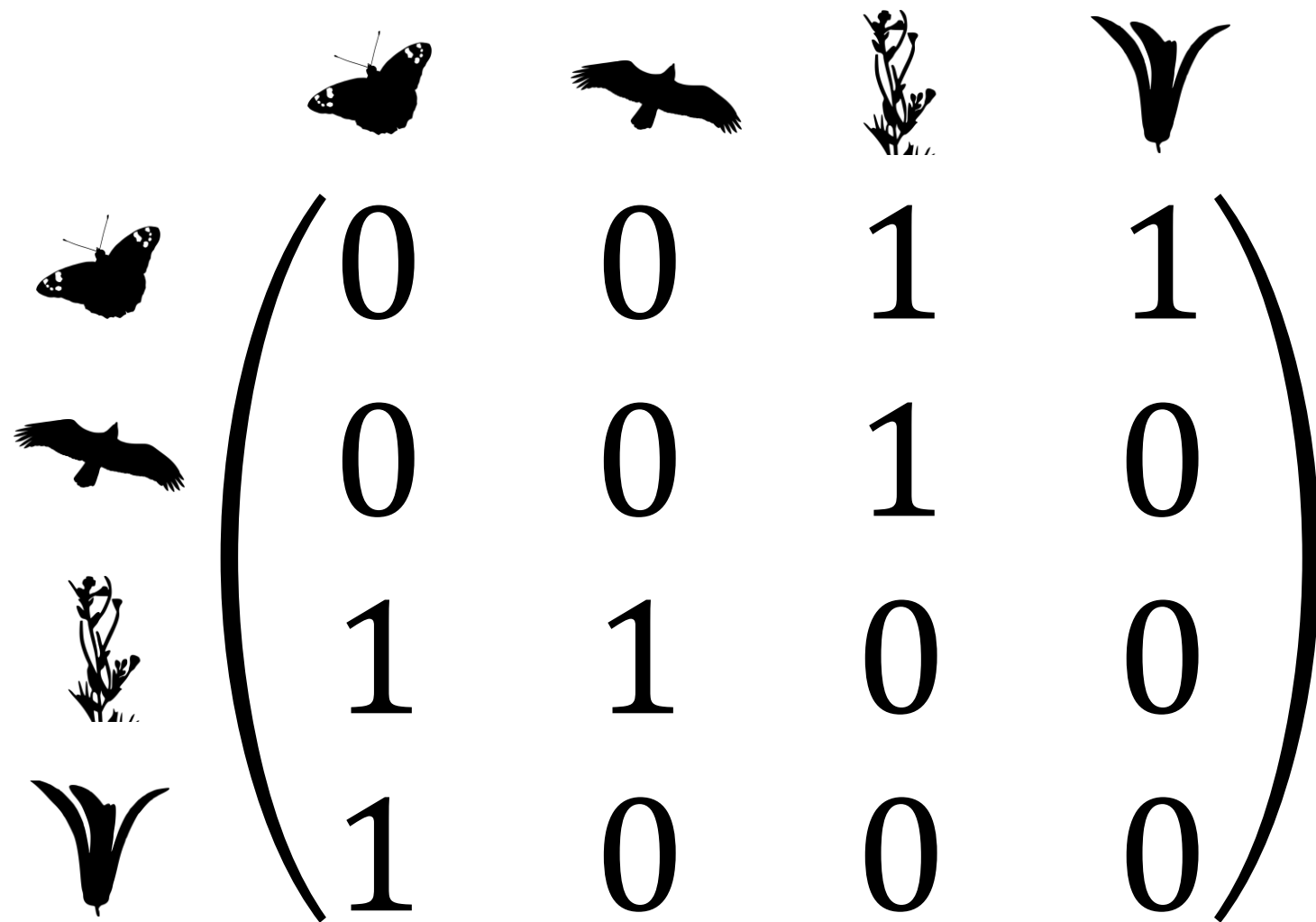
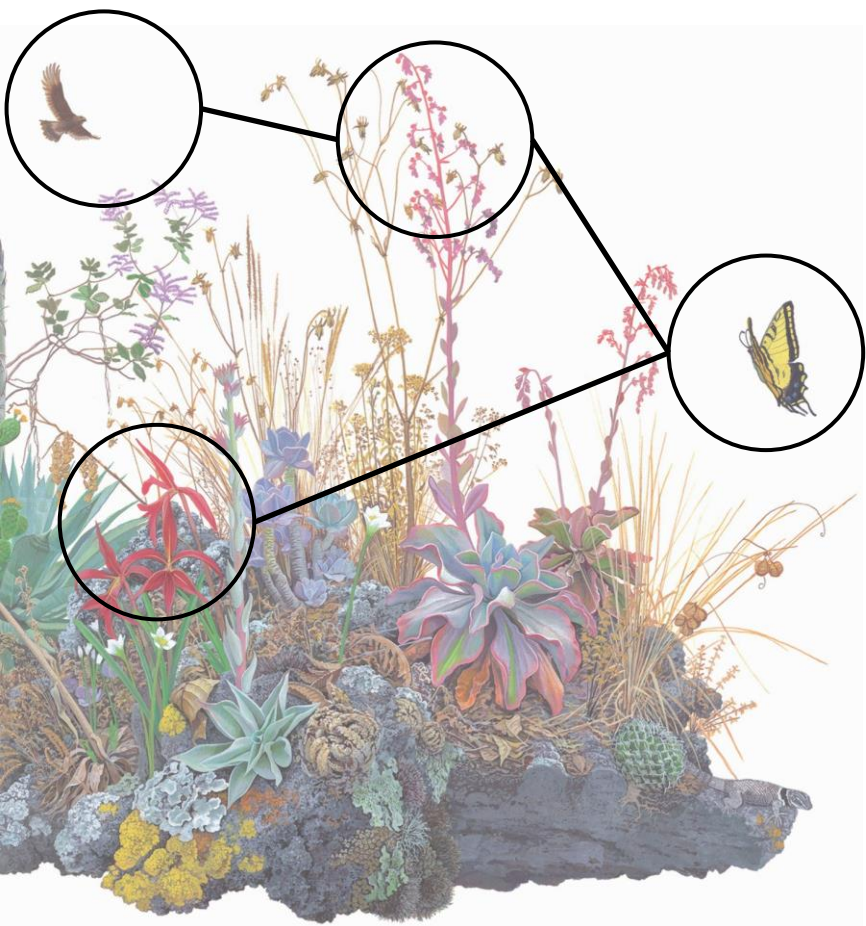


Are all networks the same?

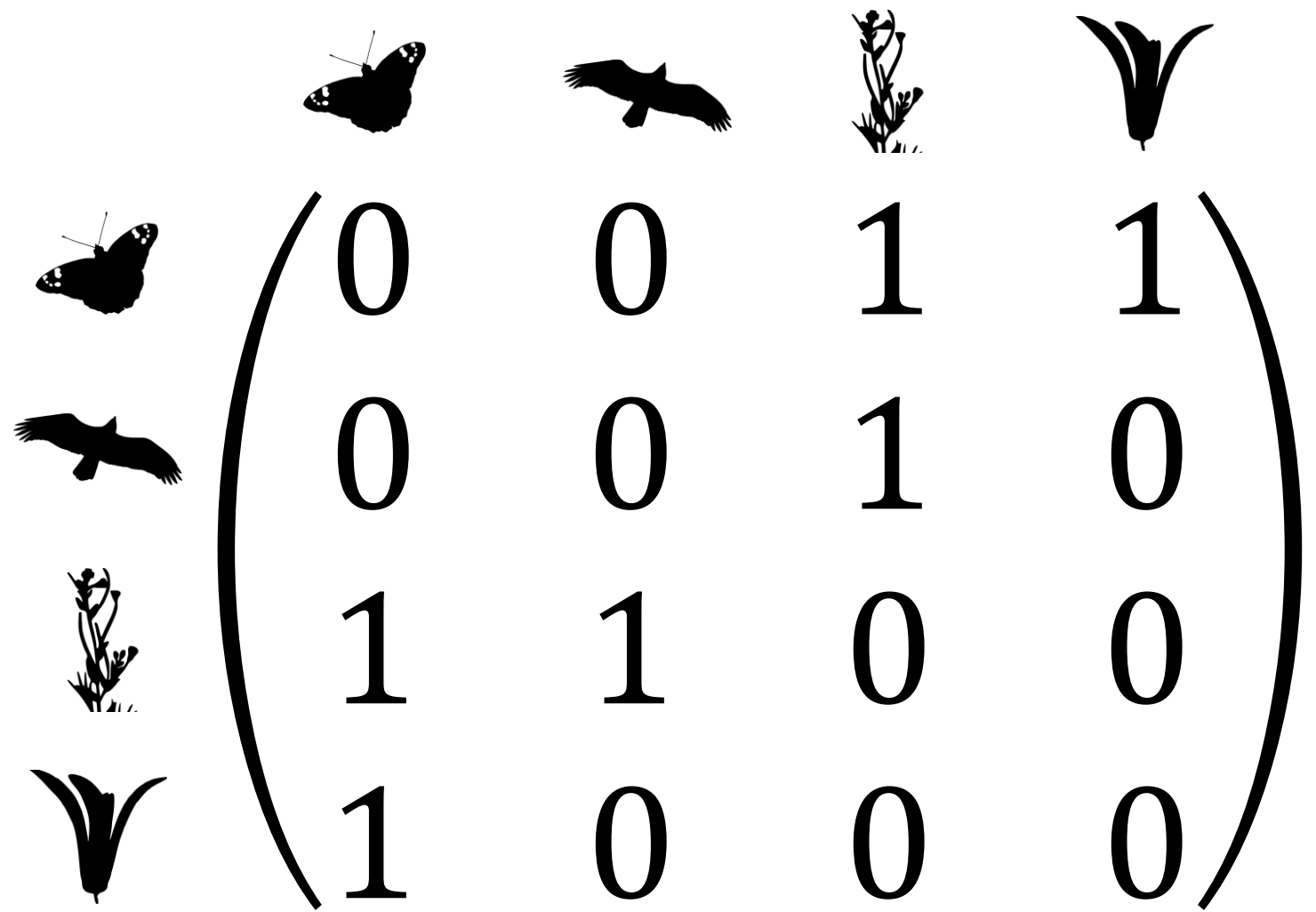
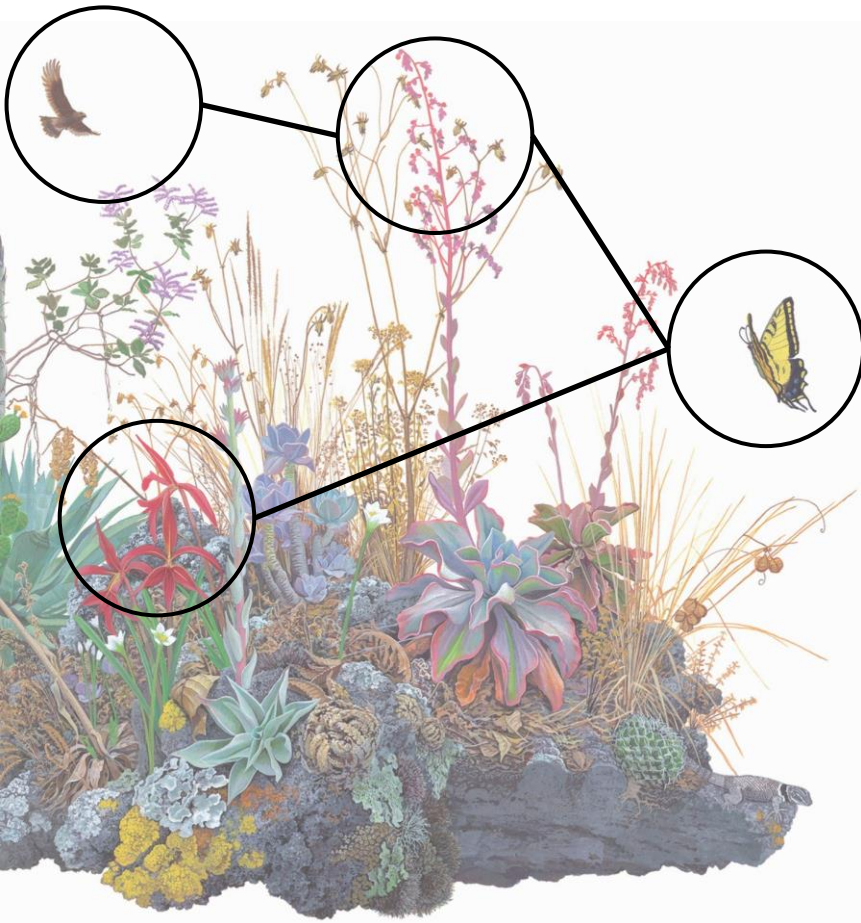




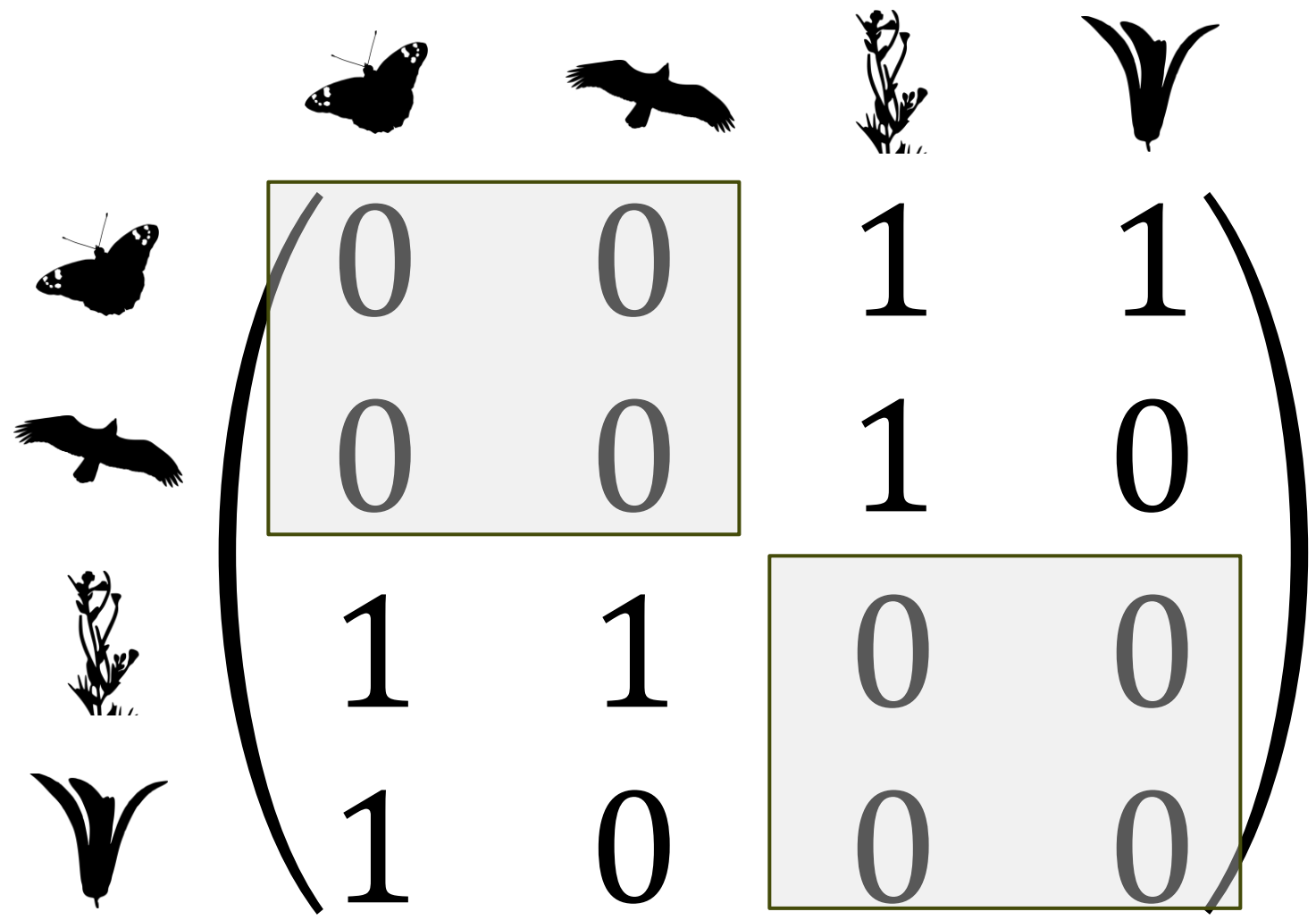
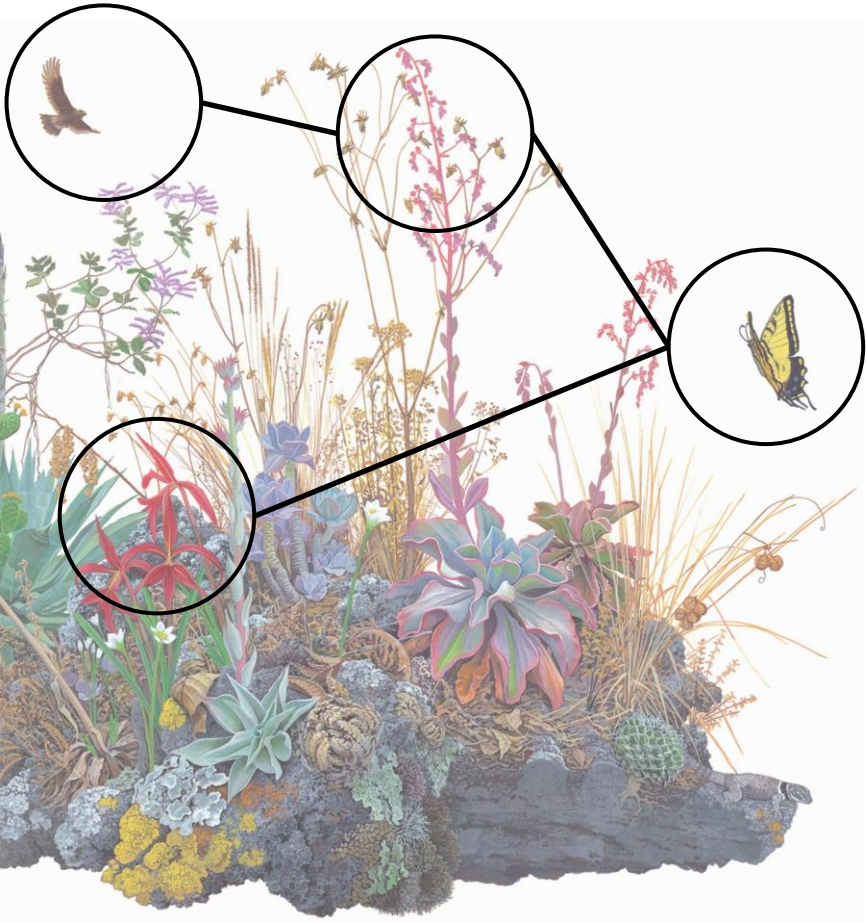




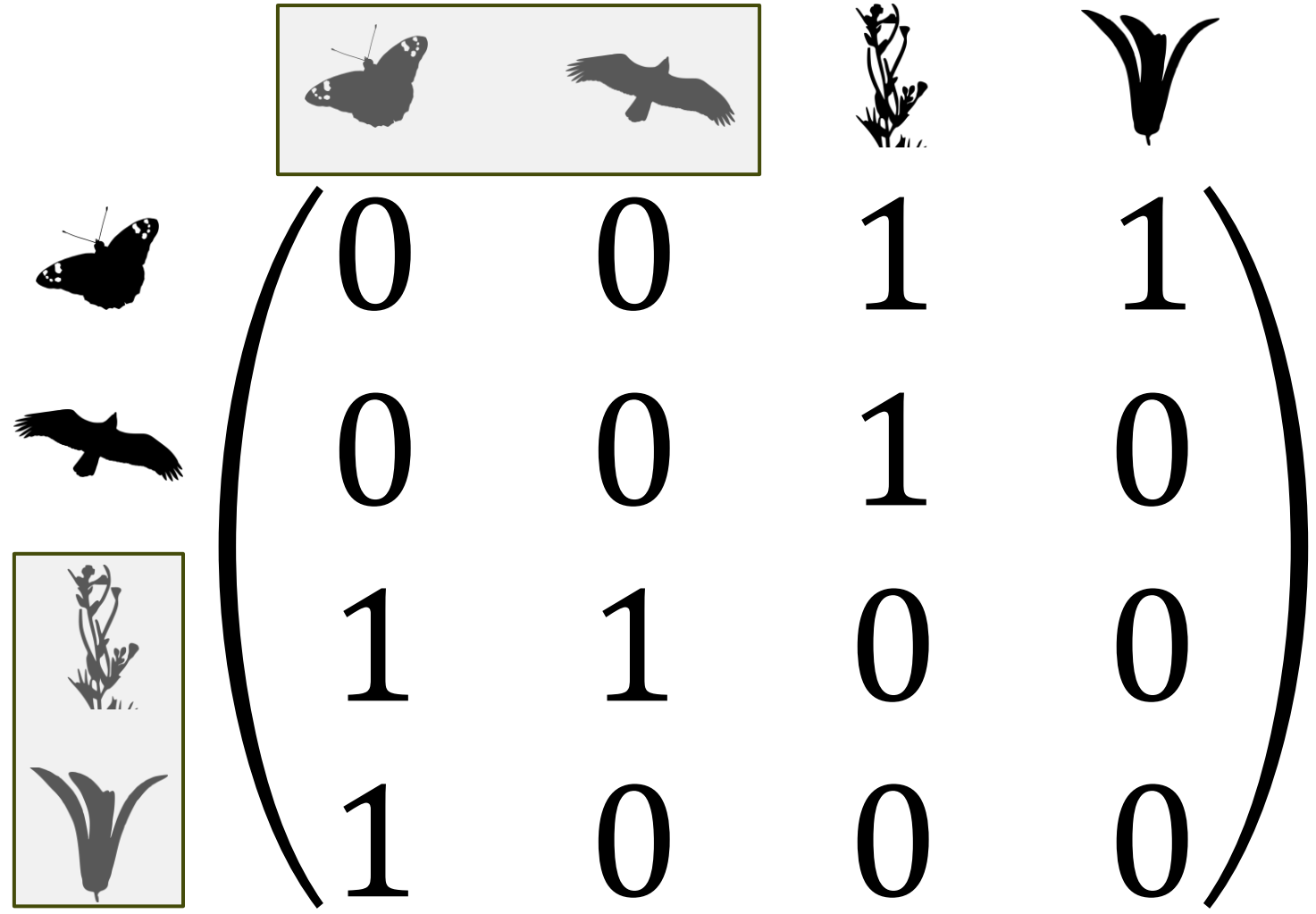
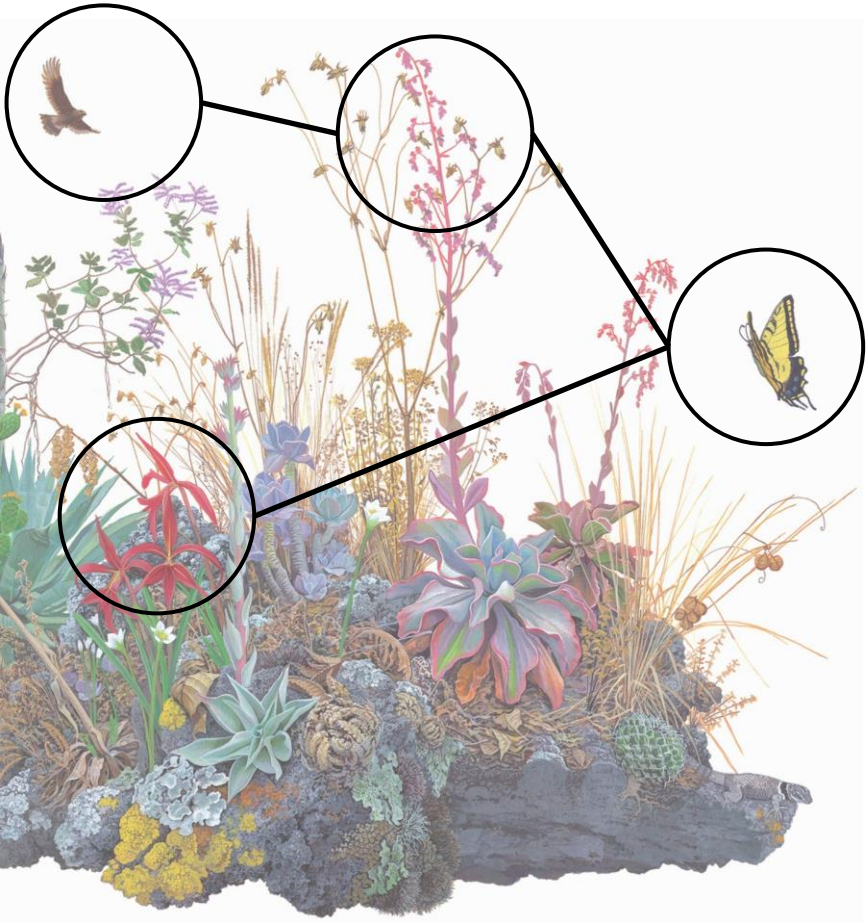
Networks can be represented as interaction matrices



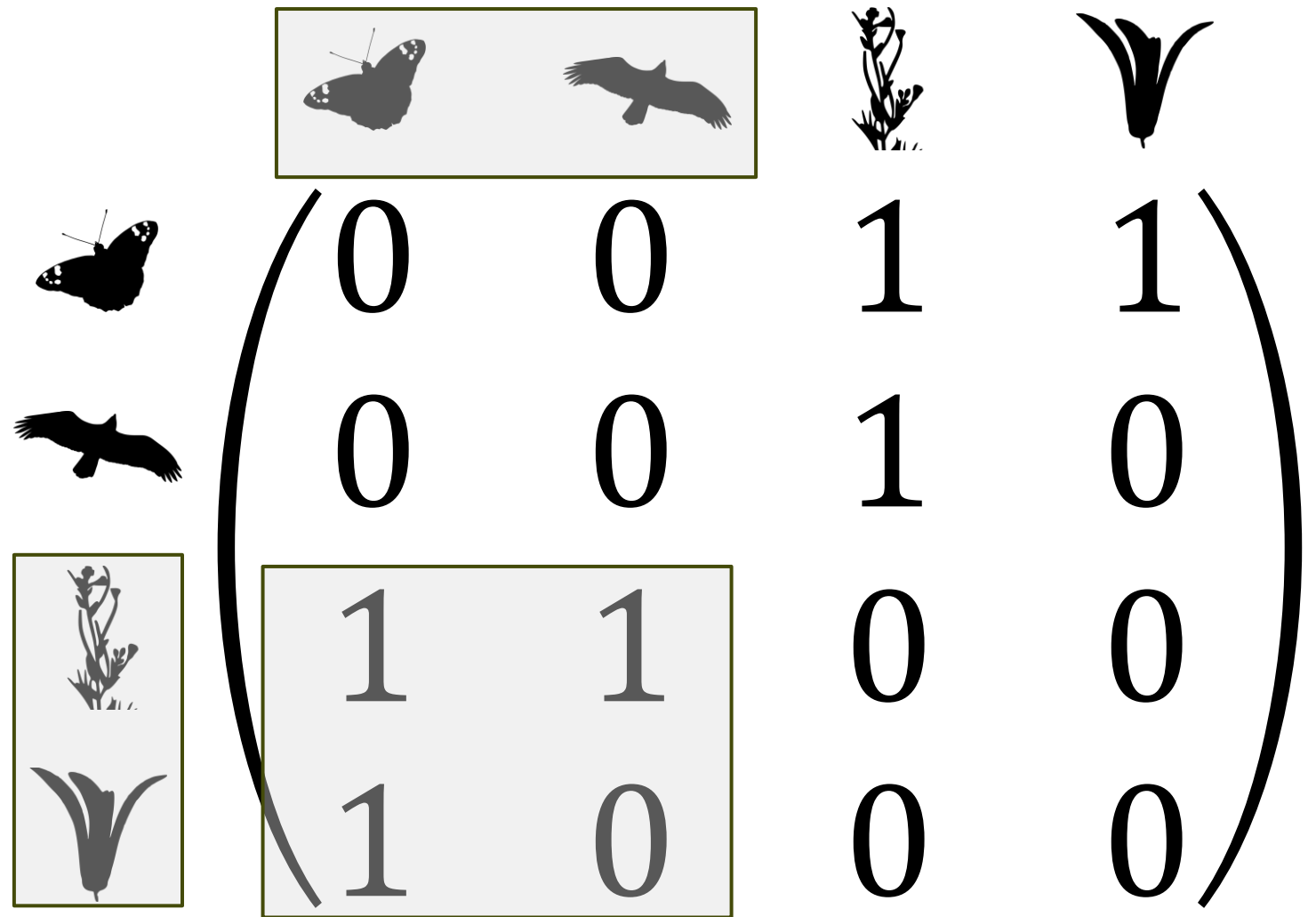
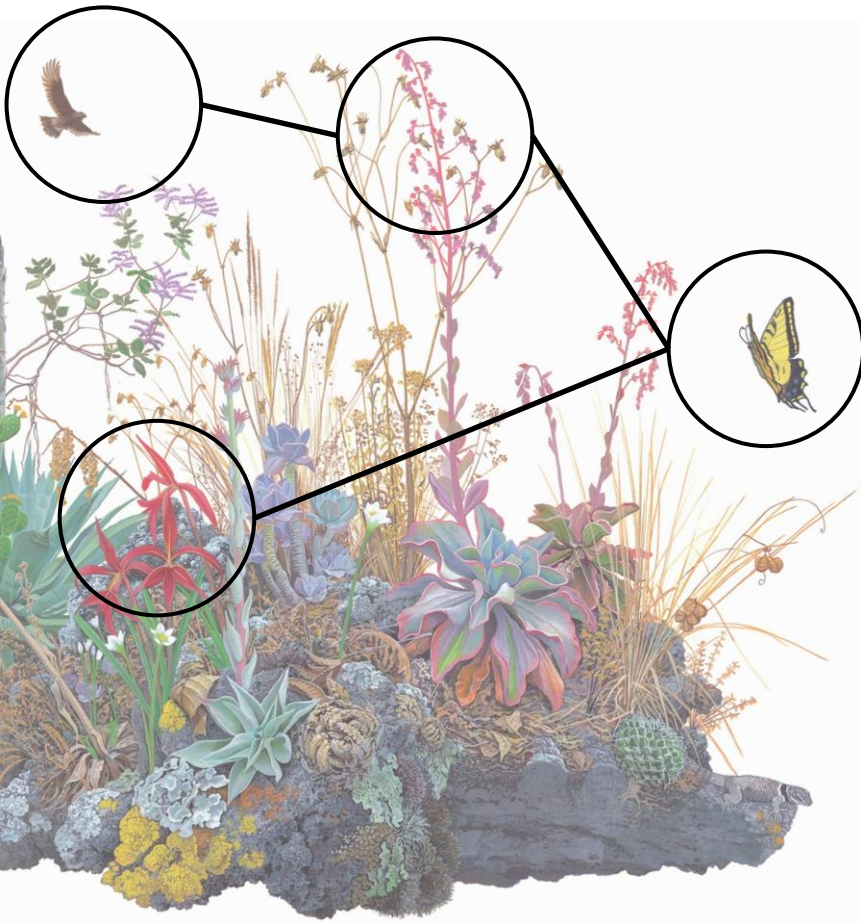
Adjacency matrix: all species in rows and columns



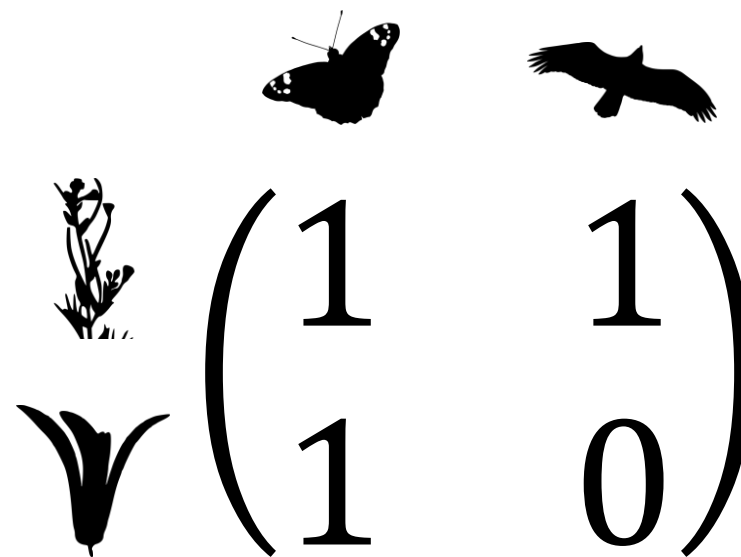
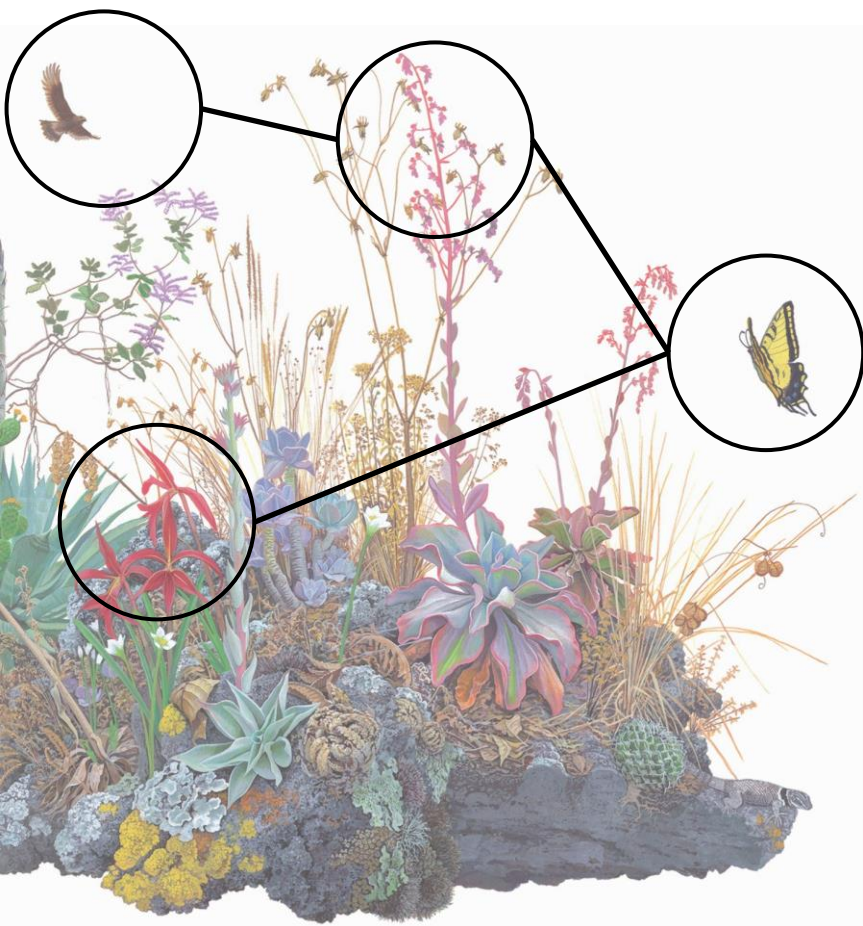
Adjacency matrix: all species in rows and columns



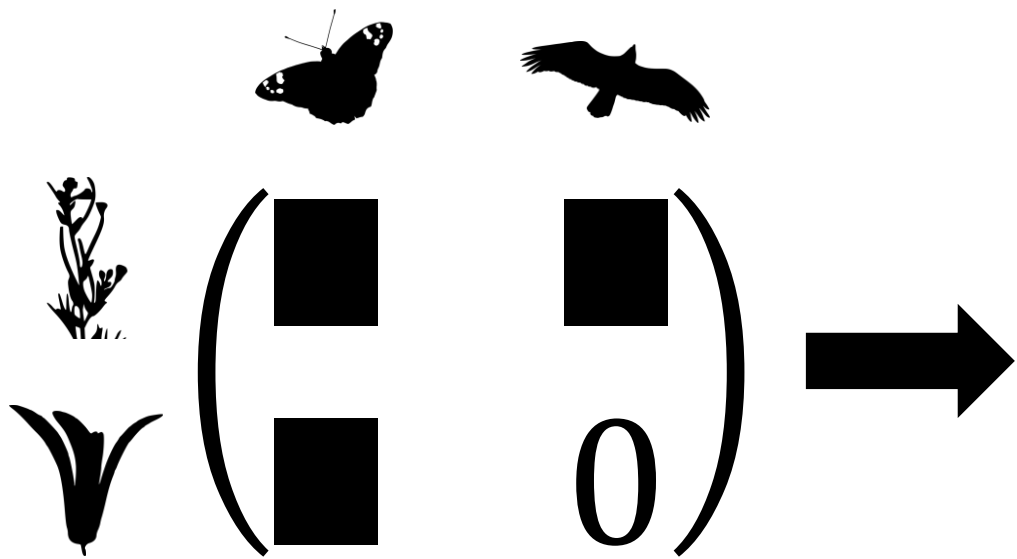
Incidence/Adjacency matrix: species from one set in rows and from another in columns



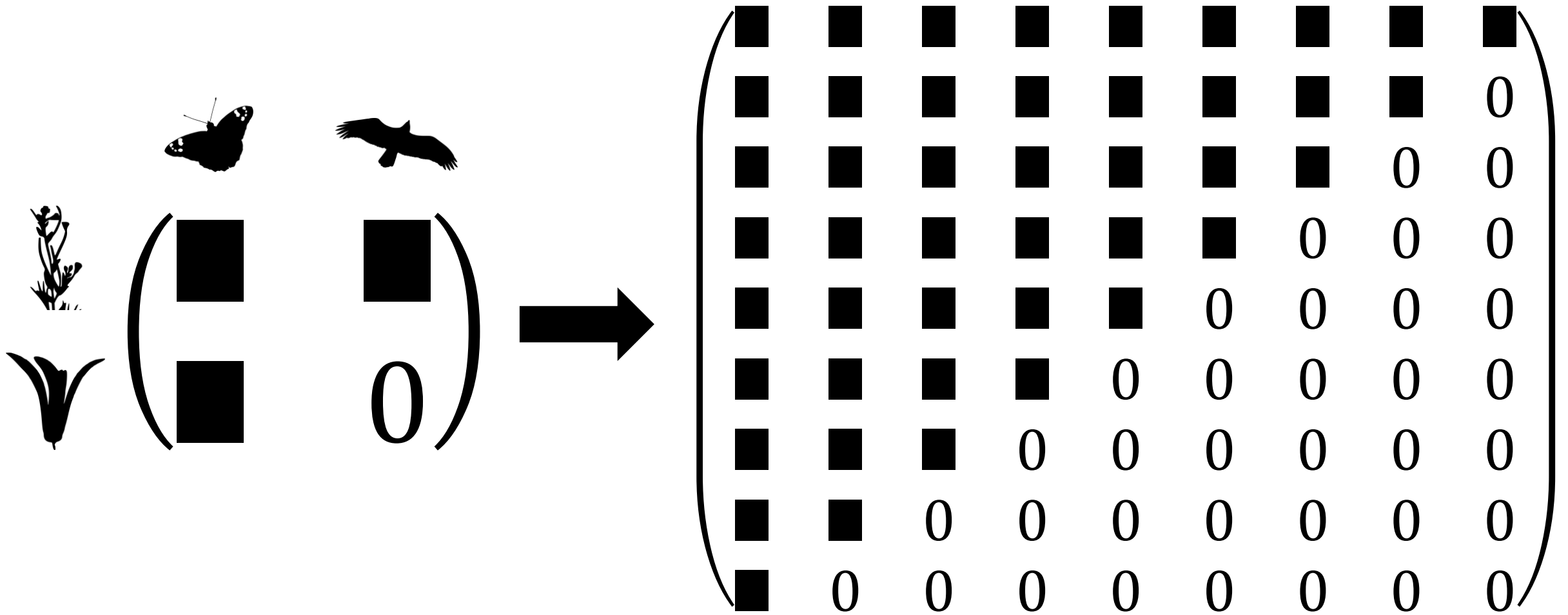
Incidence/Adjacency matrix: species from one set in rows and from another in columns



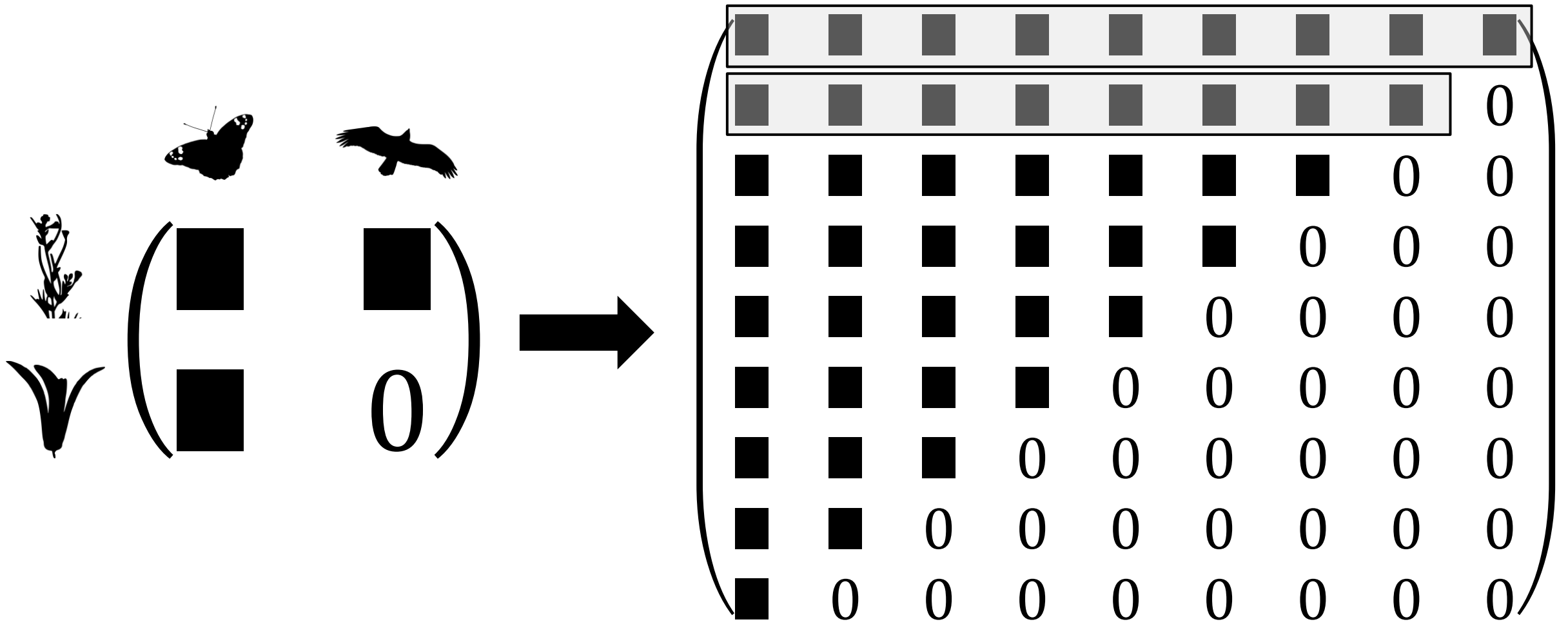
Incidence/Adjacency matrix: species from one set in rows and from another in columns



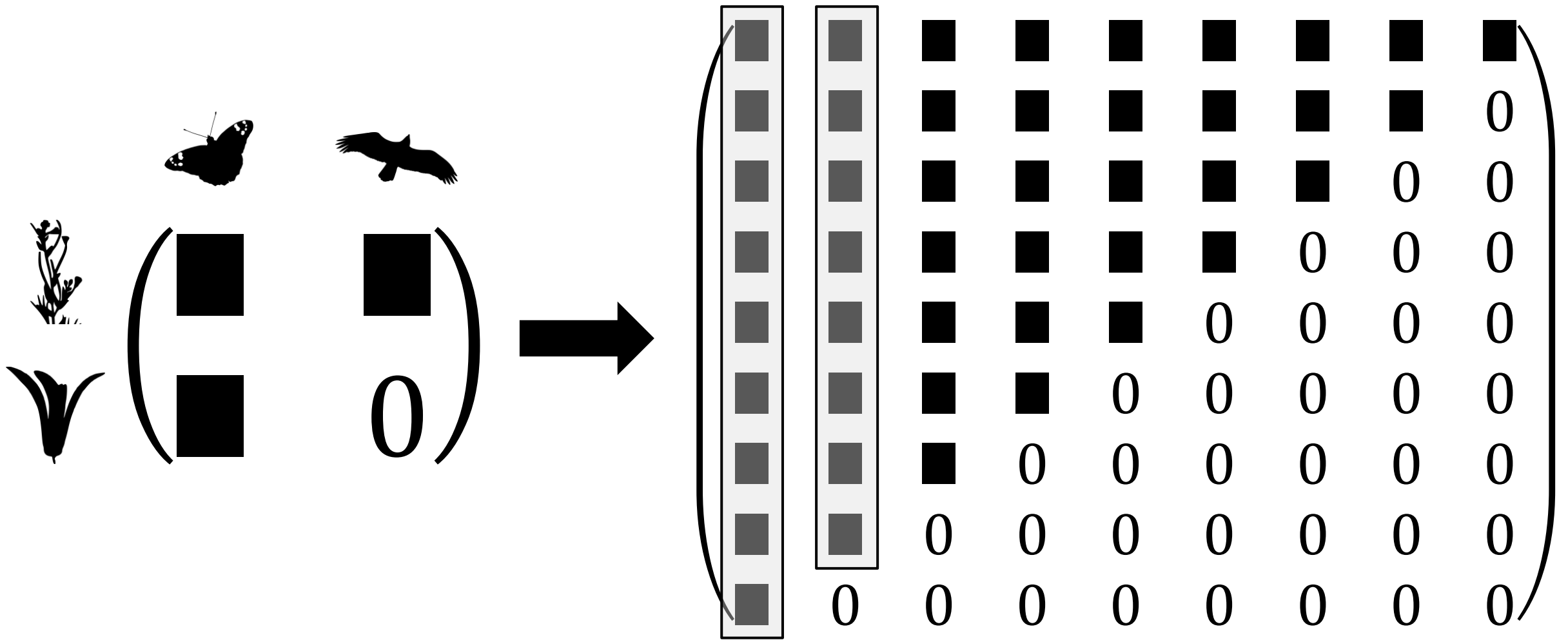
Scaling up to more plant and animal species: can we see any pattern in the incidence matrix?



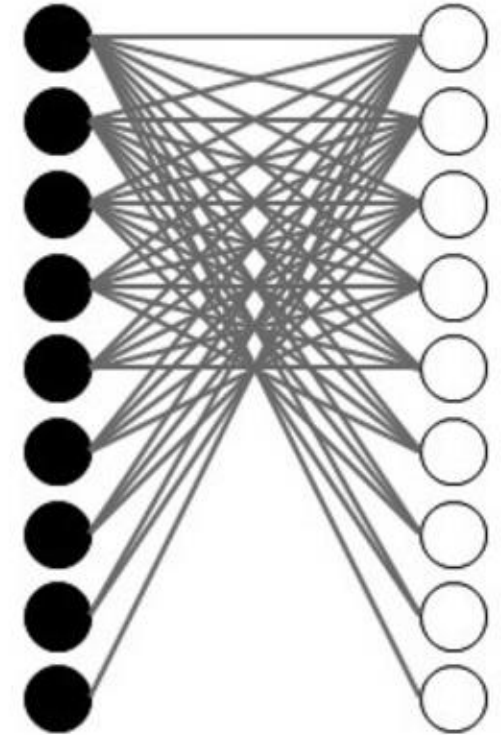
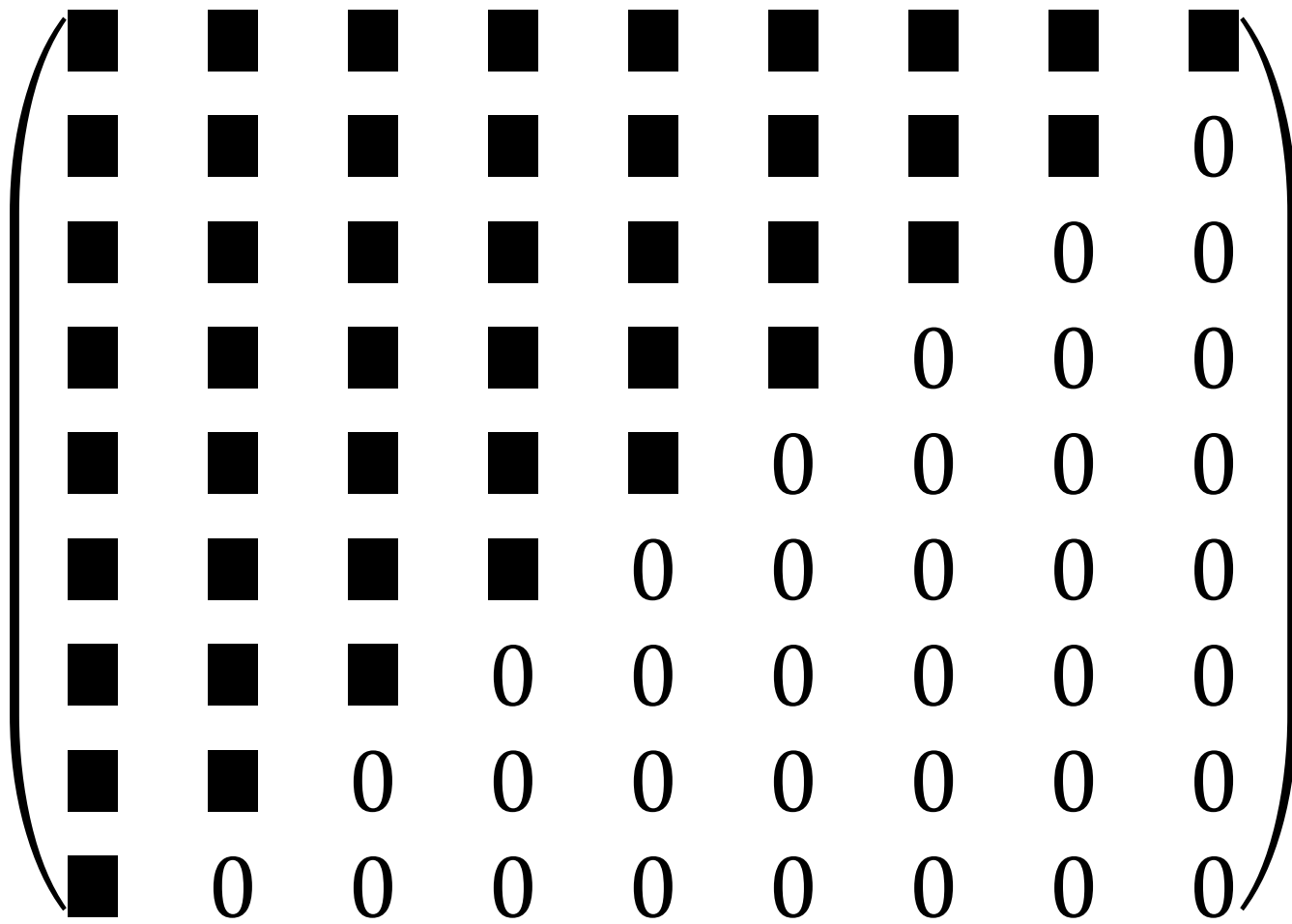
Scaling up to more plant and animal species: can we see any pattern in the incidence matrix?



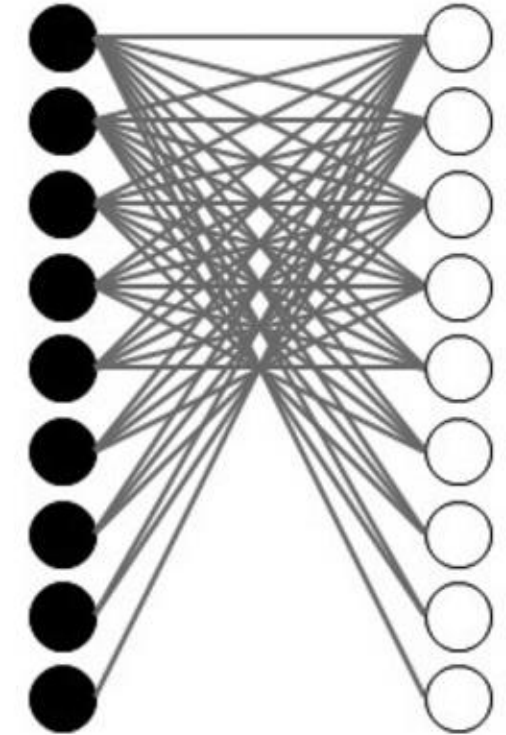
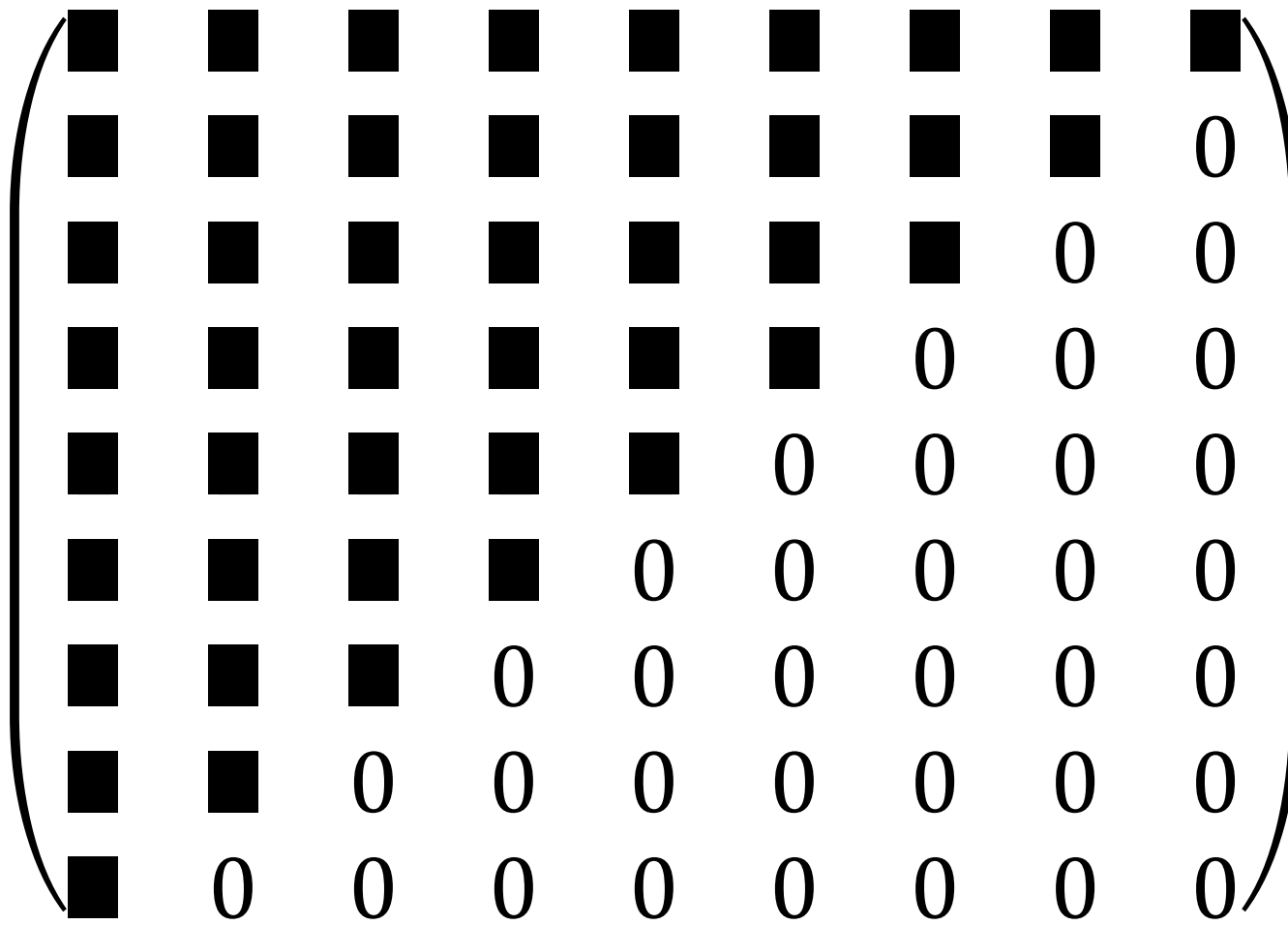
Interactions of plants with a lower degree are contained within the interactions of plants with a higher degree



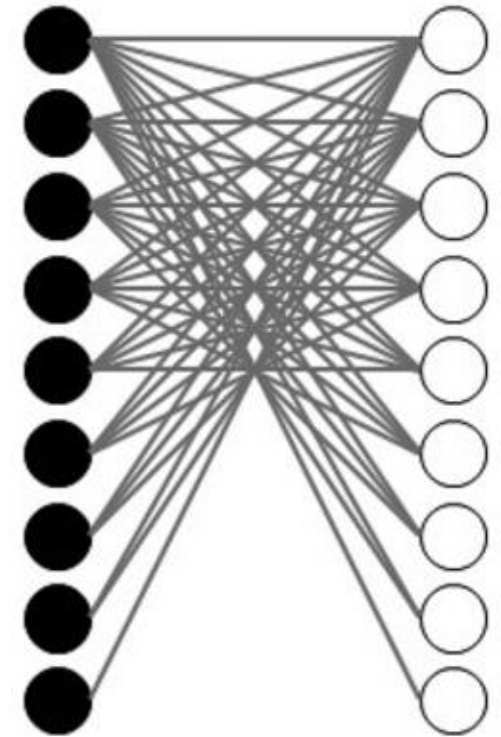
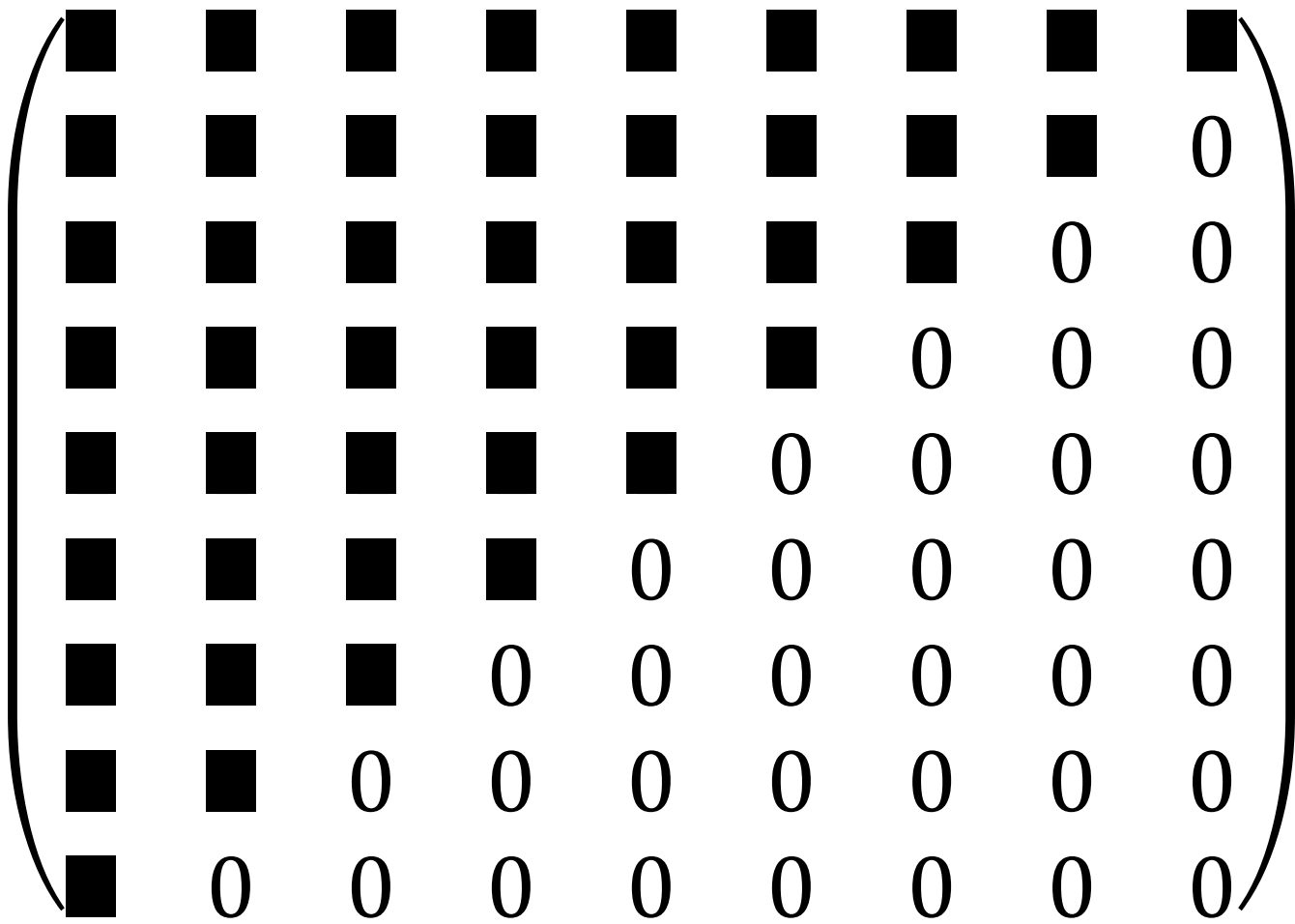
Interactions of animals with a lower degree are contained within the interactions of animals with a higher degree



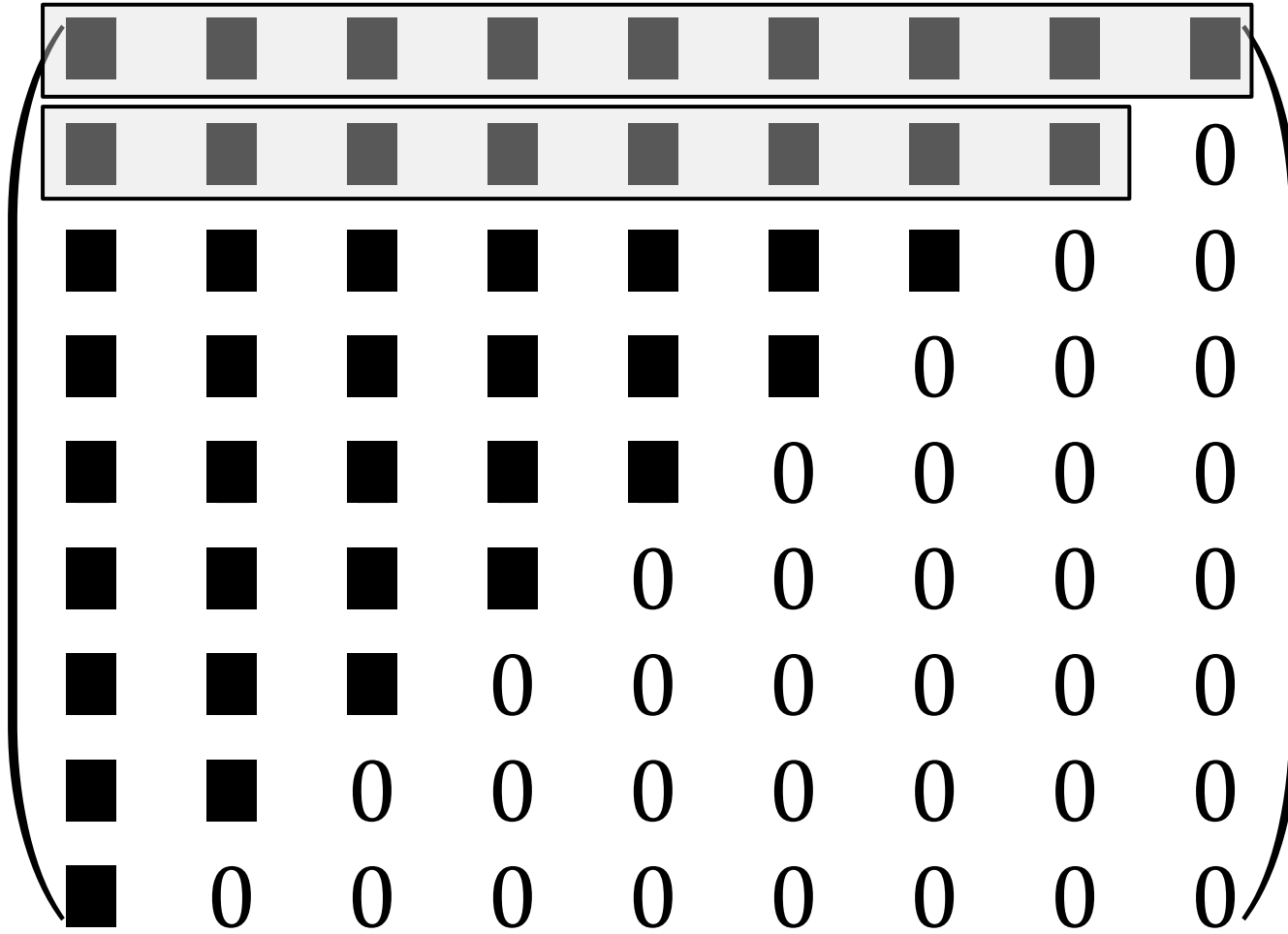
Can we see any pattern in the incidence matrix? Nestedness!



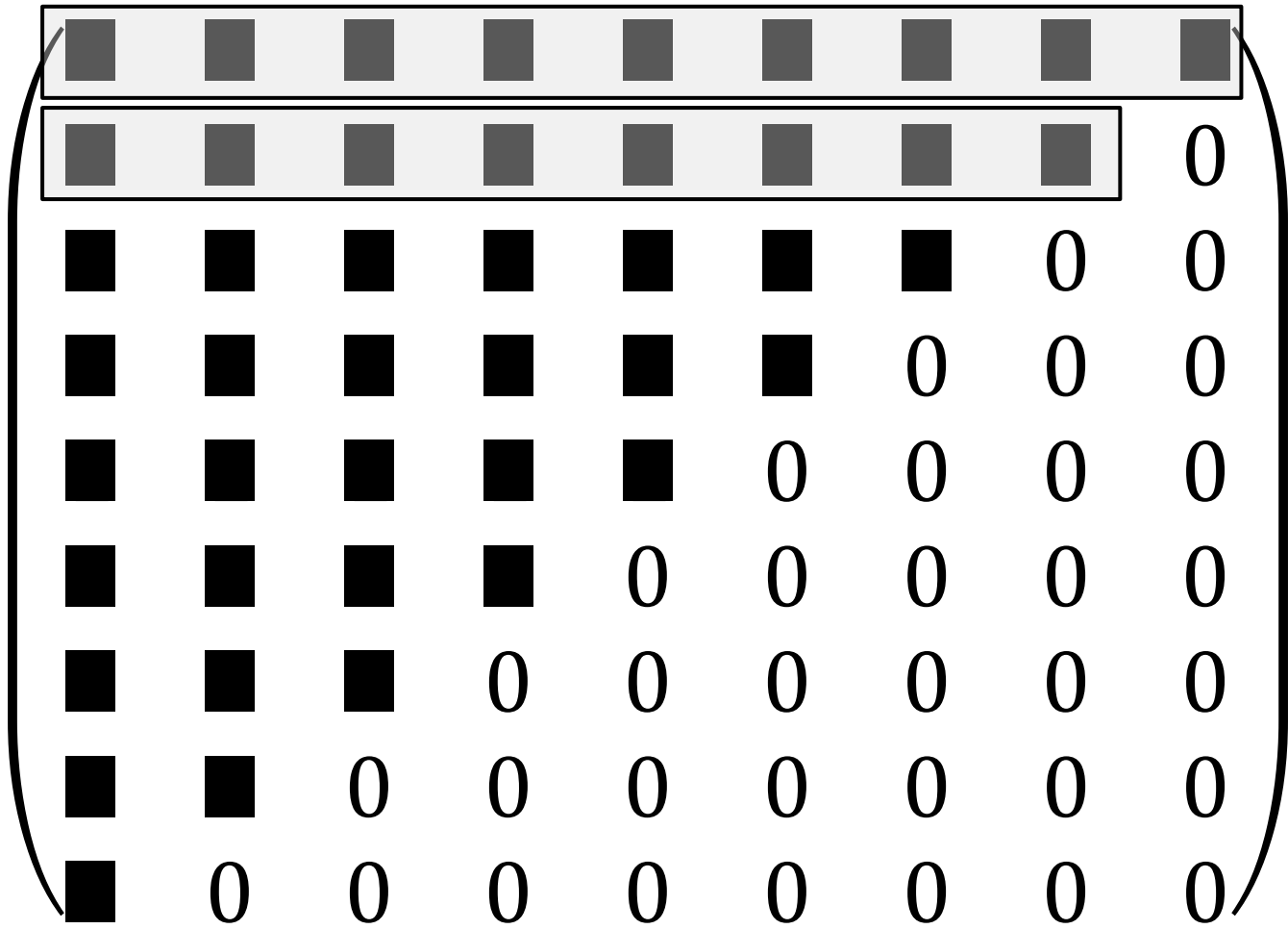
Nestedness: interactions of specialists are a subset of the interactions of generalists



How can we quantify this pattern?

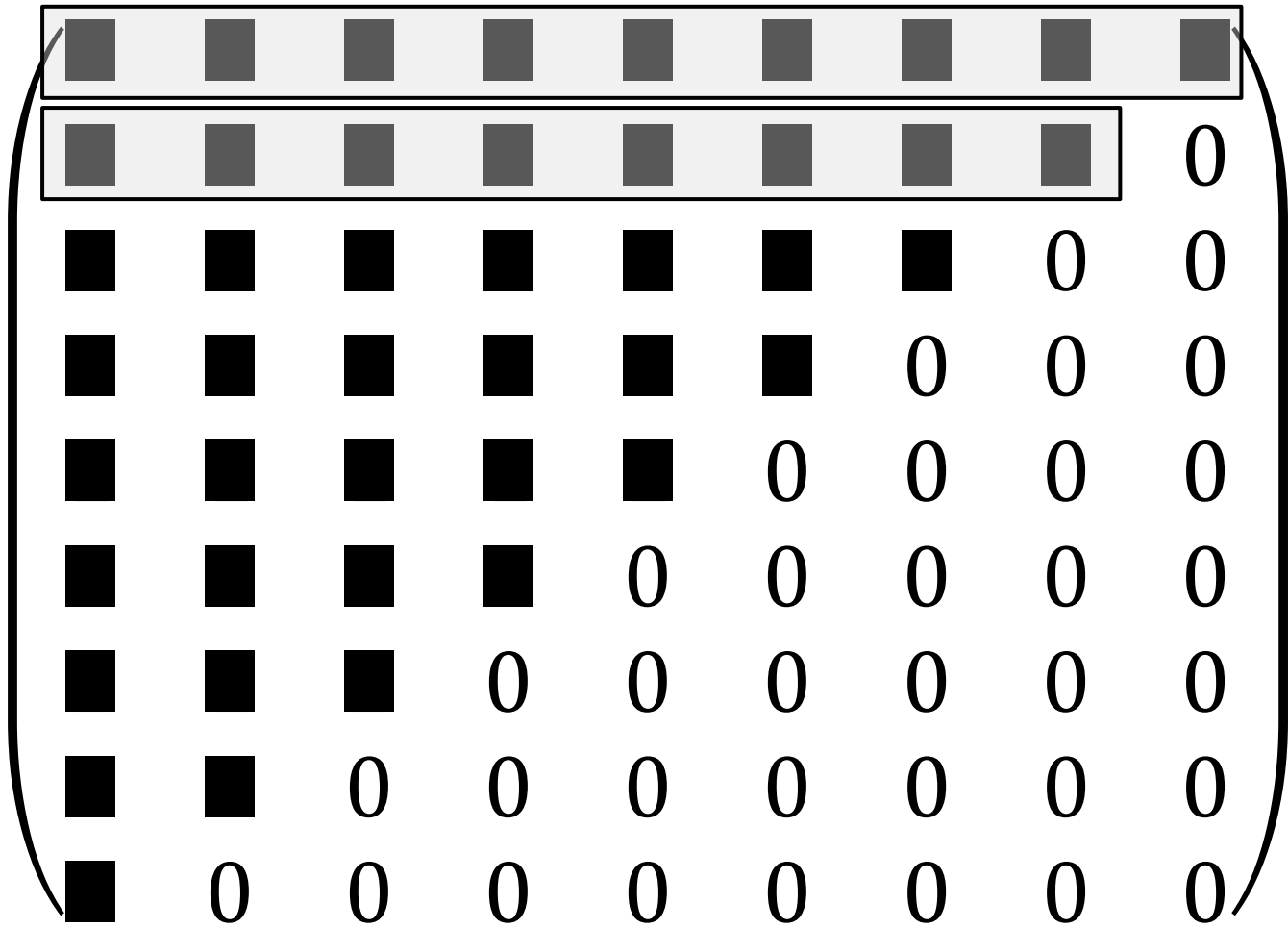


How can we quantify this pattern?
 Measuring overlap between pairs of plants (rows)



c_{ij} = Number of shared interactions between row i and j

How can we quantify this pattern?
 Measuring overlap between pairs of plants (rows)

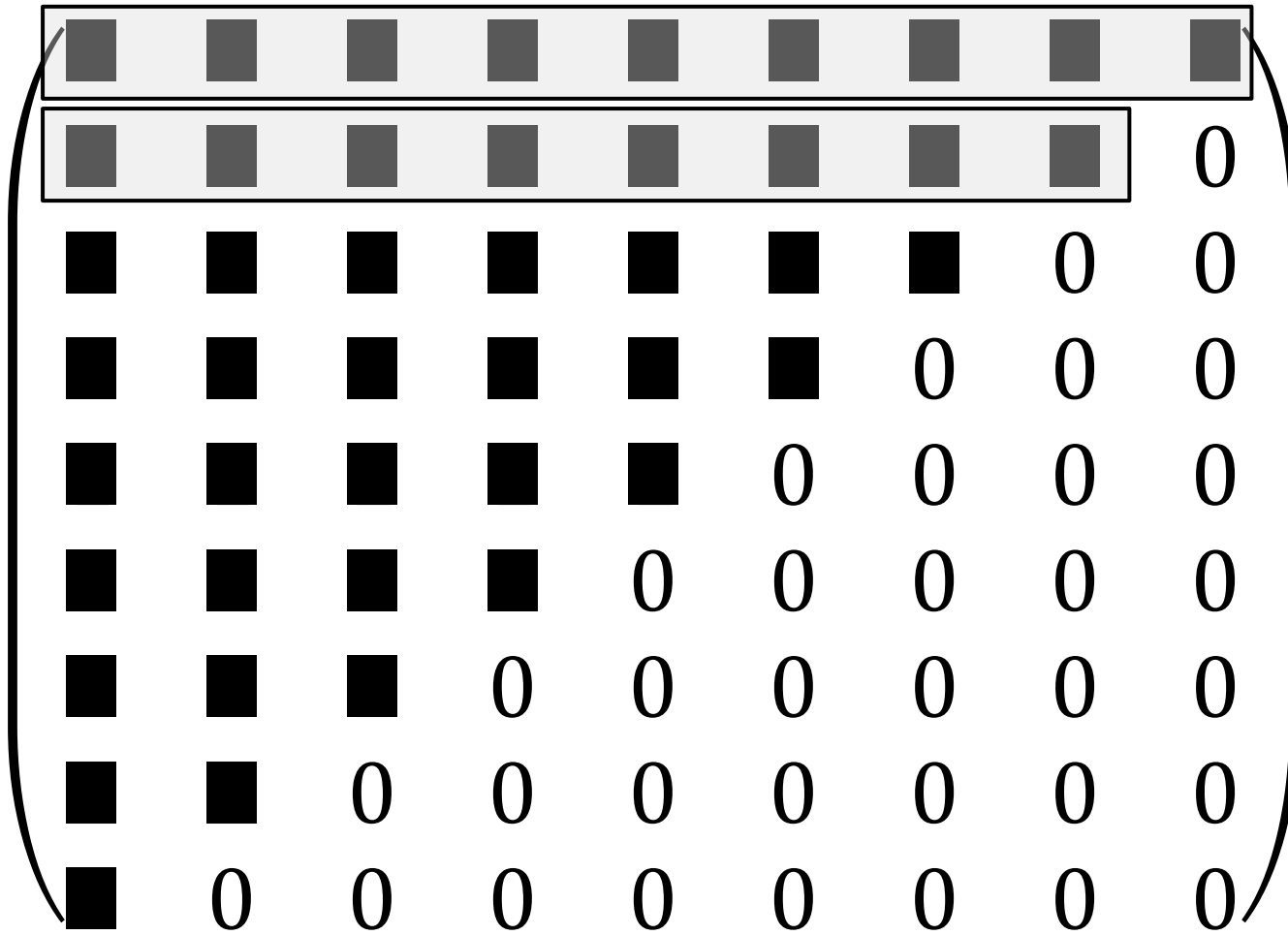


c_{ij} = Number of shared interactions between row i and j

k_i = Number of interactions in row i

k_j = Number of interactions in row j

How can we quantify this pattern?
 Measuring overlap between pairs of plants (rows)



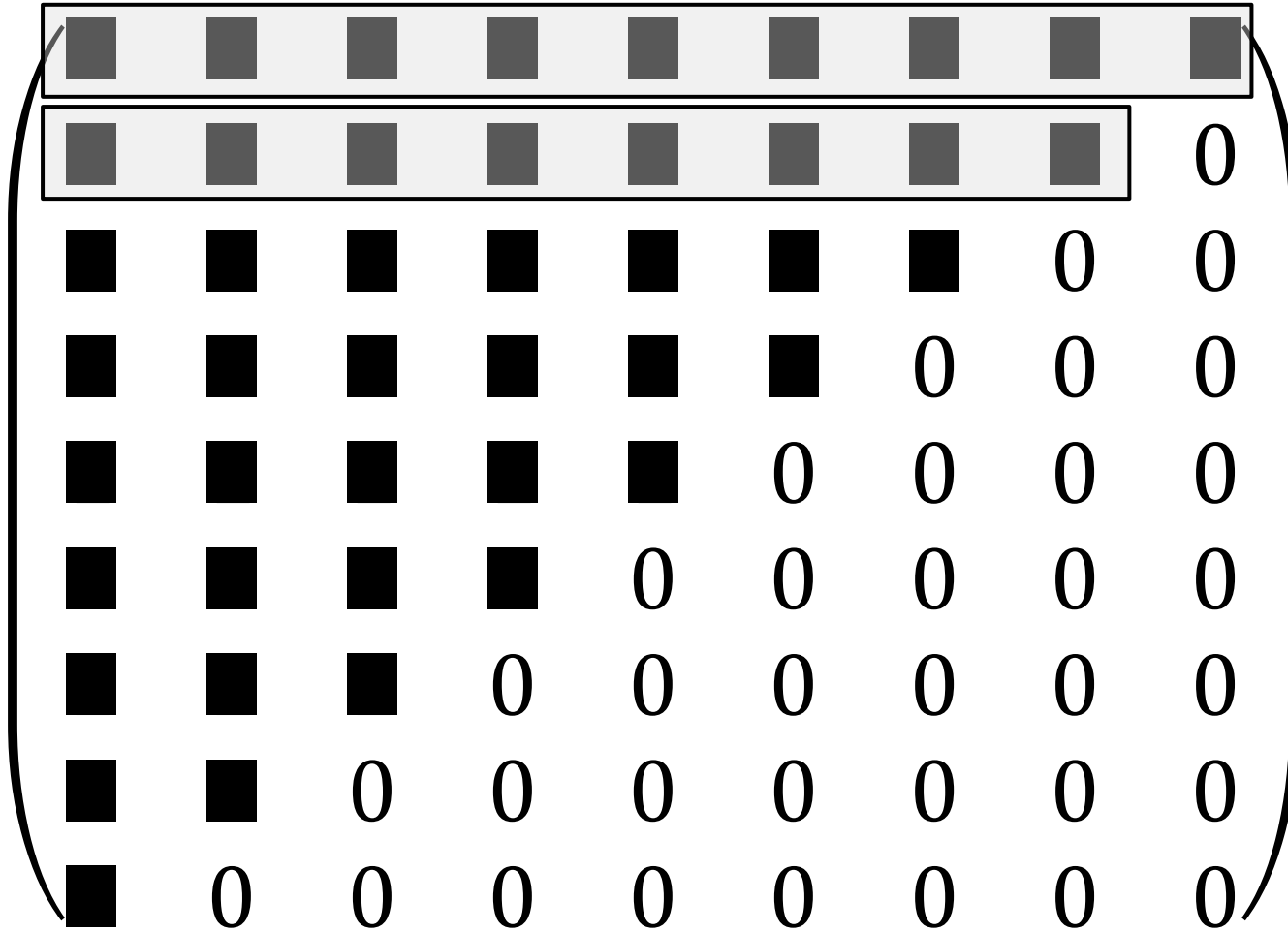
c_{ij} = Number of shared interactions between row i and j

k_i = Number of interactions in row i

k_j = Number of interactions in row j

$$o_{ij} = \frac{c_{ij}}{\min(k_i, k_j)}$$

How can we quantify this pattern?
 Measuring overlap between pairs of plants (rows)



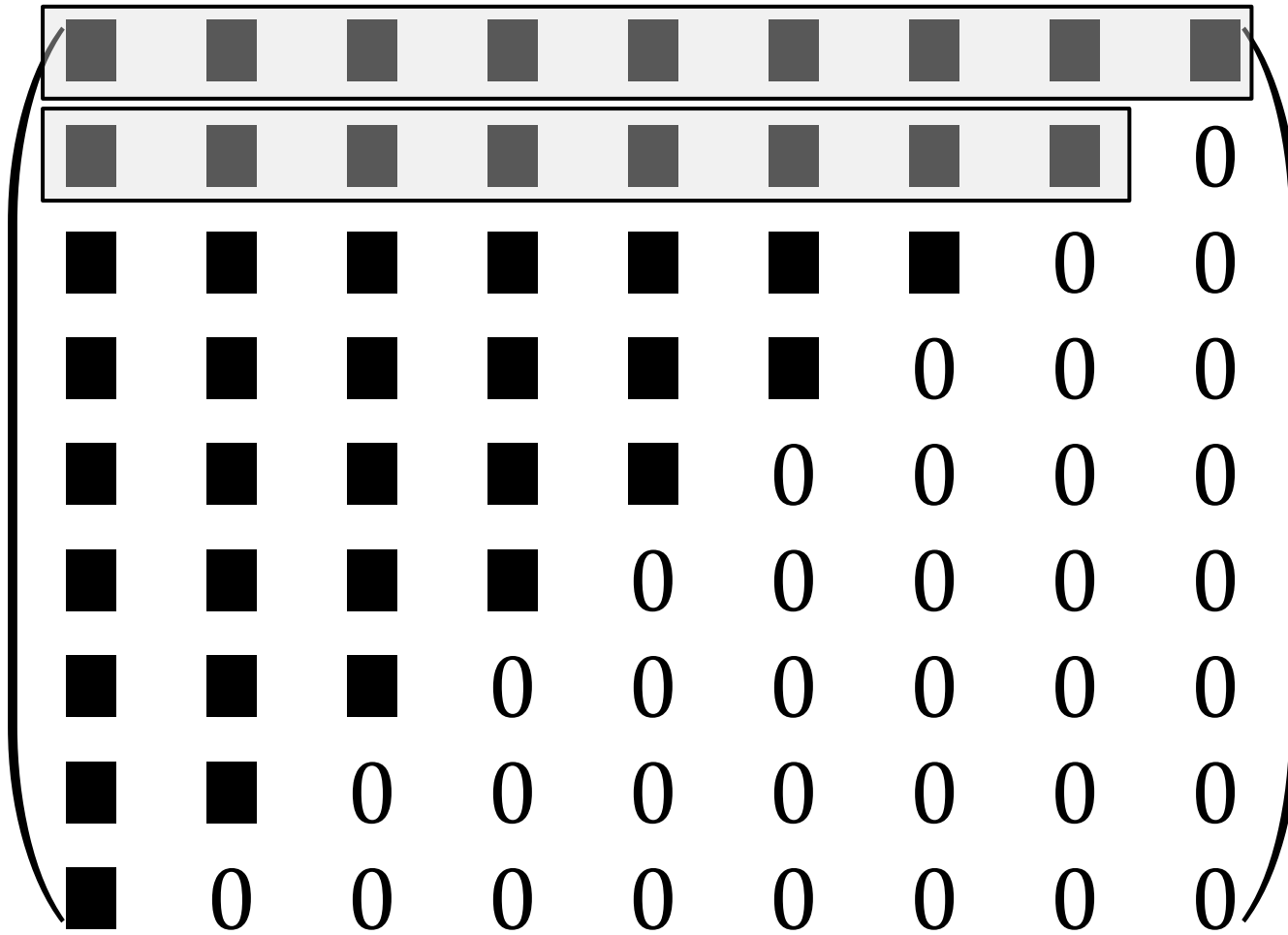
c_{ij} = Number of shared interactions between row i and j

k_i = Number of interactions in row i

k_j = Number of interactions in row j

$$o_{ij} = \frac{8}{8} = 1$$

How can we quantify this pattern?
 Measuring overlap between pairs of plants (rows)



c_{ij} = Number of shared interactions between row i and j

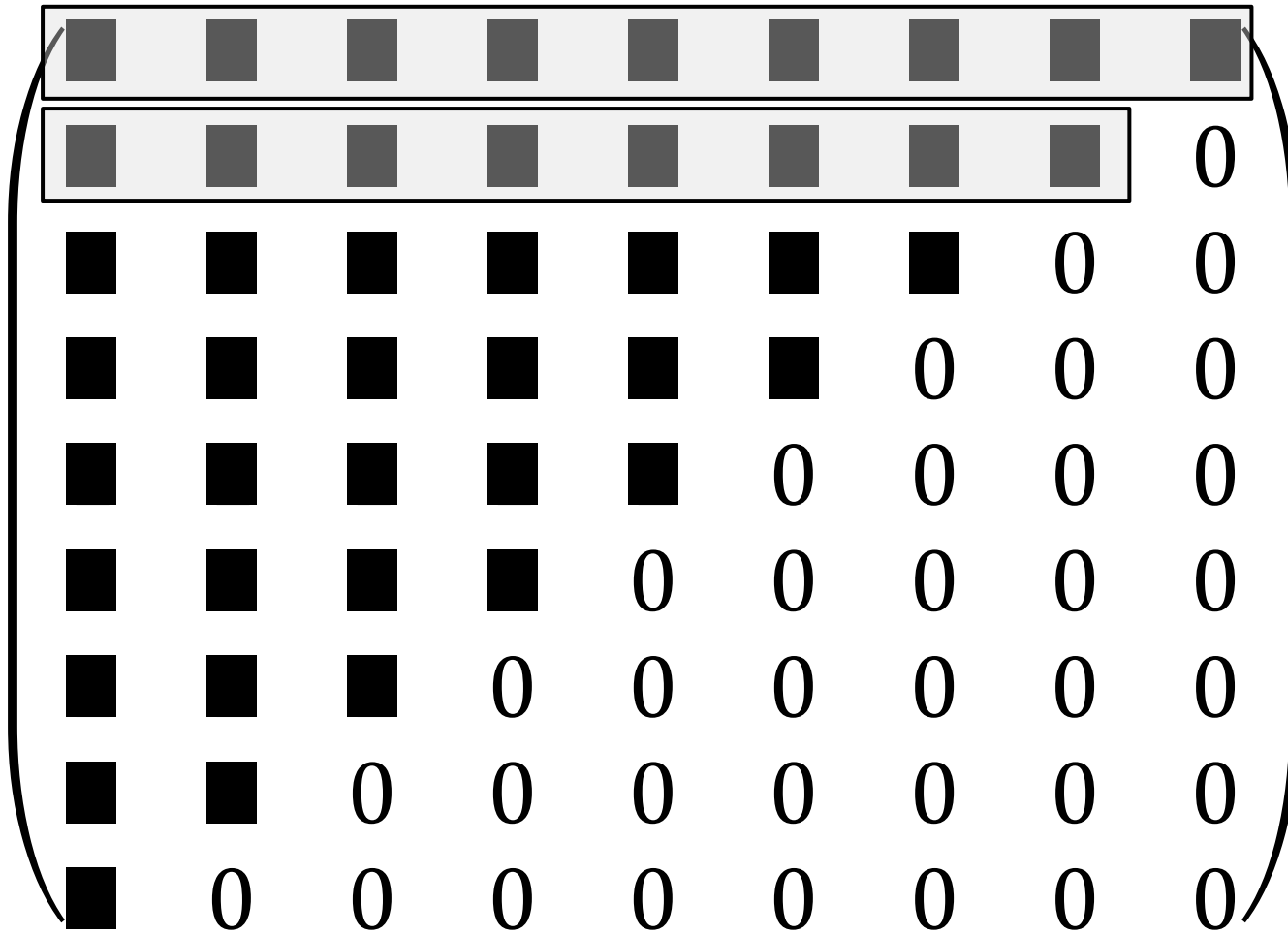
k_i = Number of interactions in row i

k_j = Number of interactions in row j

$$o_{ij} = \frac{c_{ij}}{\min(k_i, k_j)}$$

$$\sum_{i < j}^{NP} o_{ij}$$

How can we quantify this pattern?
 Measuring overlap between **all possible ij** pairs of rows



c_{ij} = Number of shared interactions between row i and j

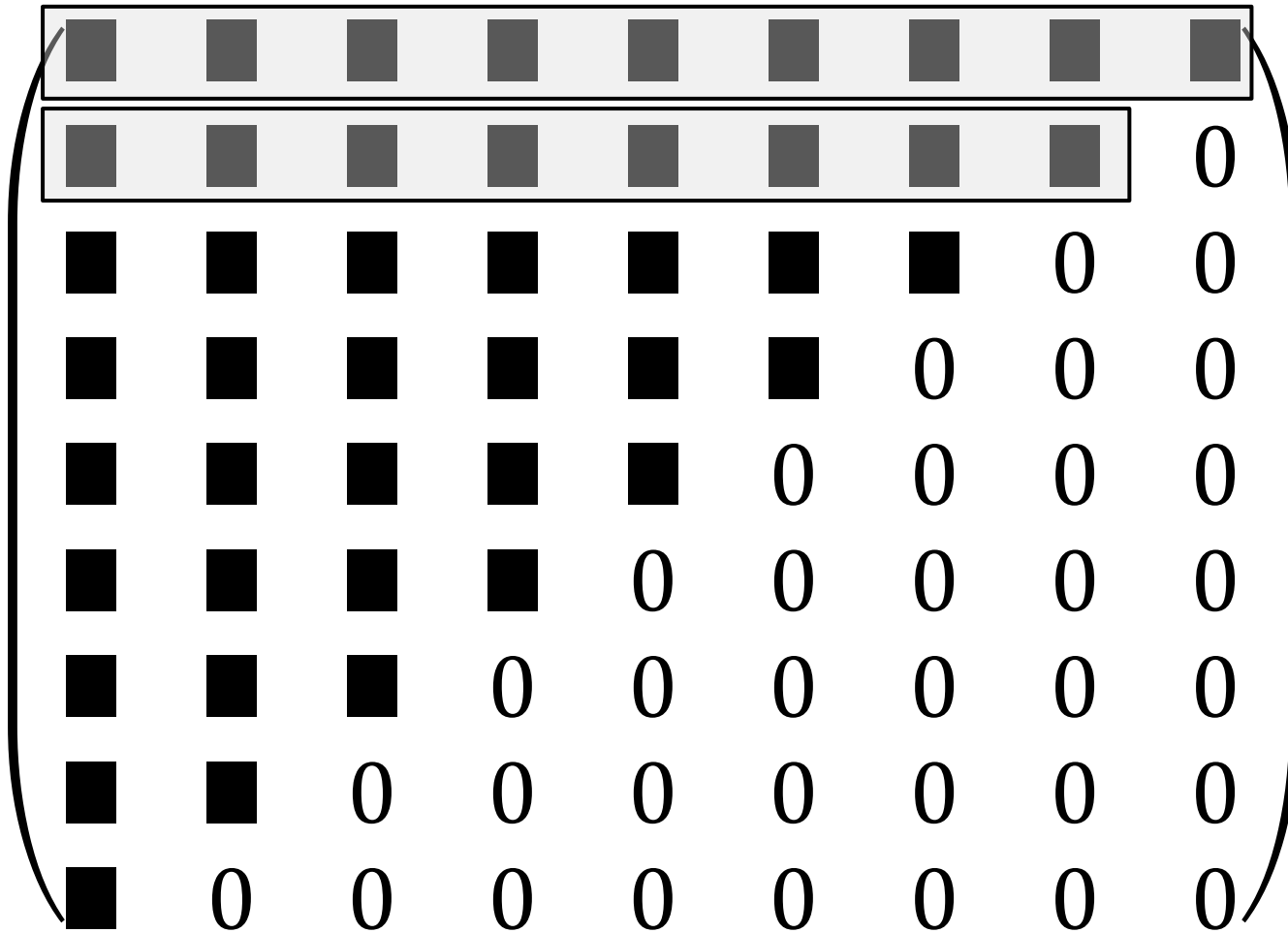
k_i = Number of interactions in row i

k_j = Number of interactions in row j

$$o_{ij} = \frac{c_{ij}}{\min(k_i, k_j)}$$

$$\frac{\sum_{i < j}^{NP} o_{ij}}{NP(NP - 1)/2}$$

Measuring overlap between **all possible** ij pairs of rows
 Divide by the number of possible pairs



c_{ij} = Number of shared interactions between row i and j

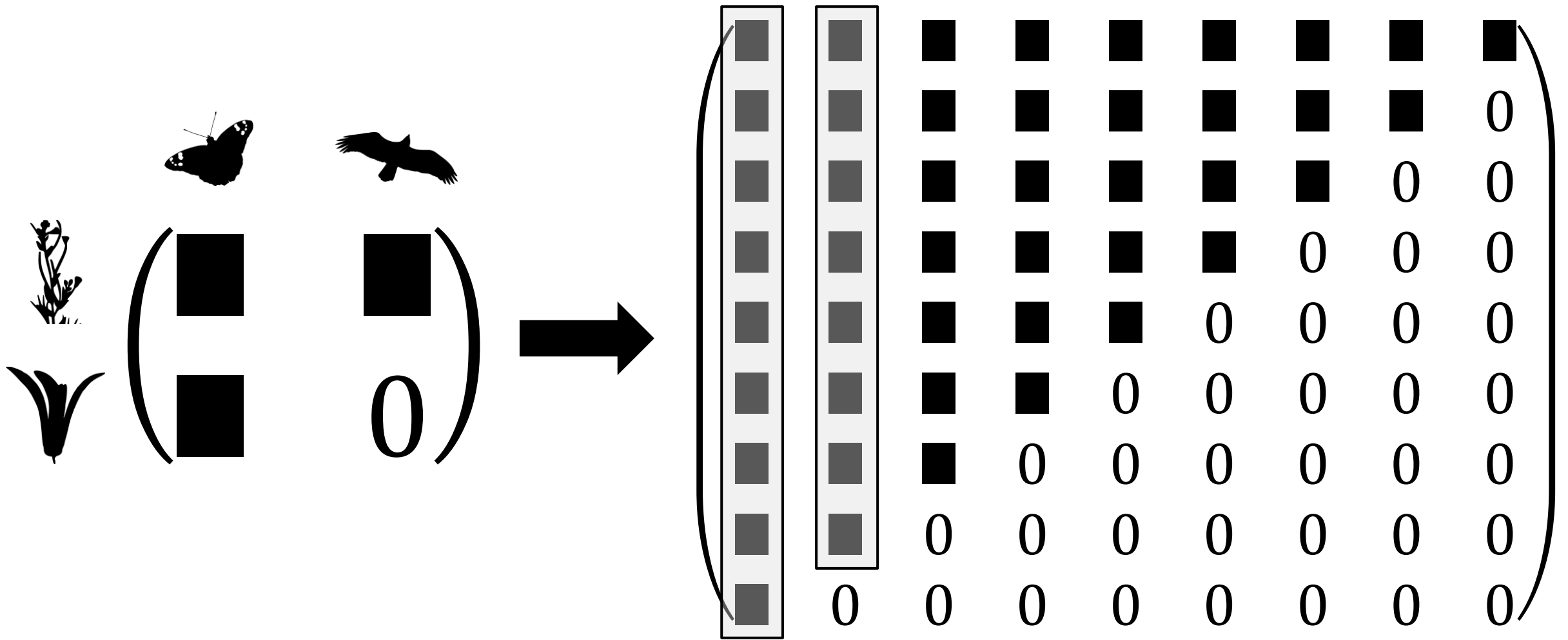
k_i = Number of interactions in row i

k_j = Number of interactions in row j

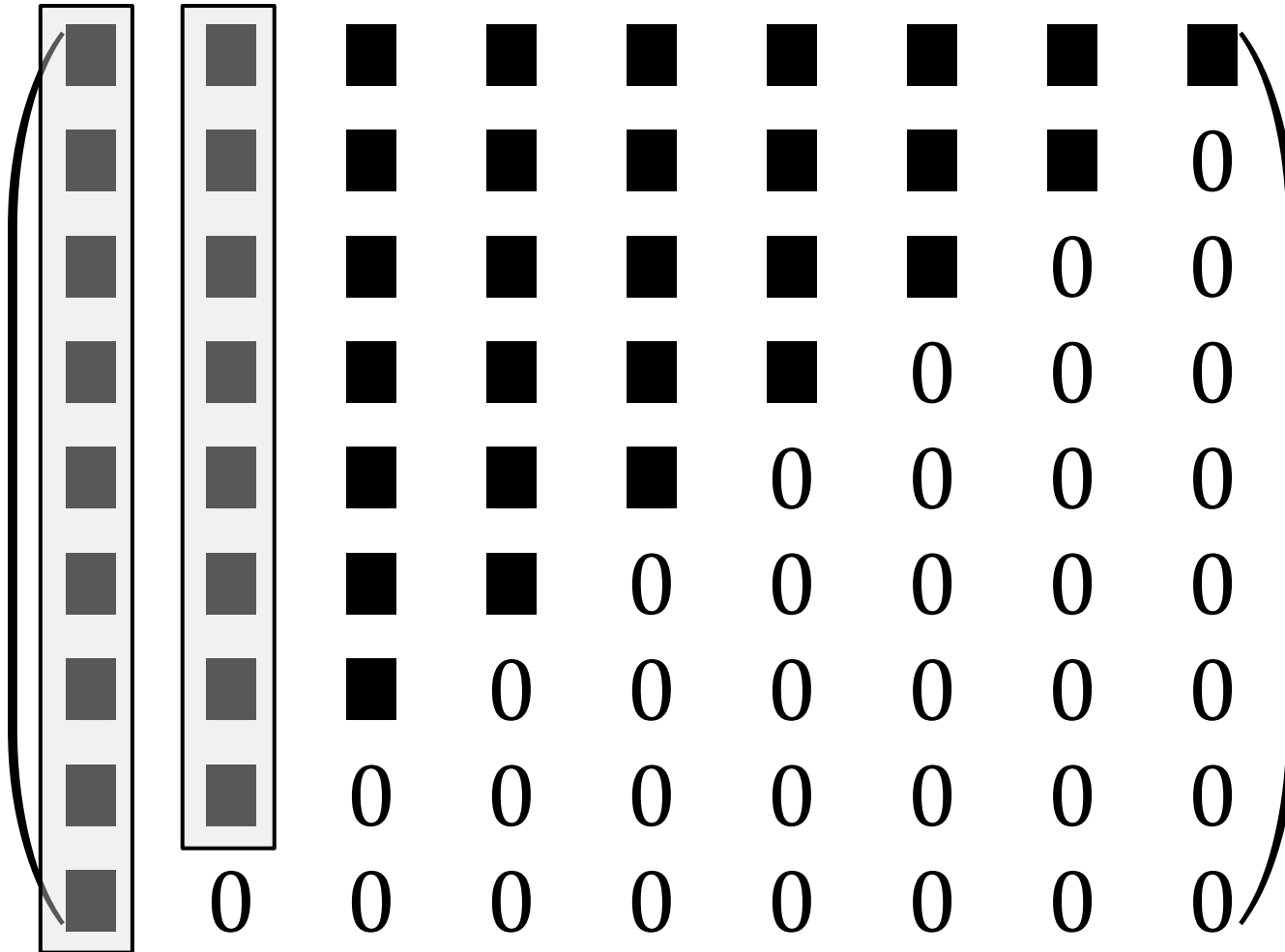
$$o_{ij} = \frac{c_{ij}}{\min(k_i, k_j)}$$

$$\frac{\sum_{i < j}^{NP} o_{ij}}{NP(NP - 1)/2}$$

Measuring overlap between **all possible** ij pairs of rows
 Divide by the number of possible pairs



Interactions of animals with a lower degree are contained within the interactions of animals with a higher degree



c_{ij} = Number of shared interactions between row i and j

k_i = Number of interactions in row i

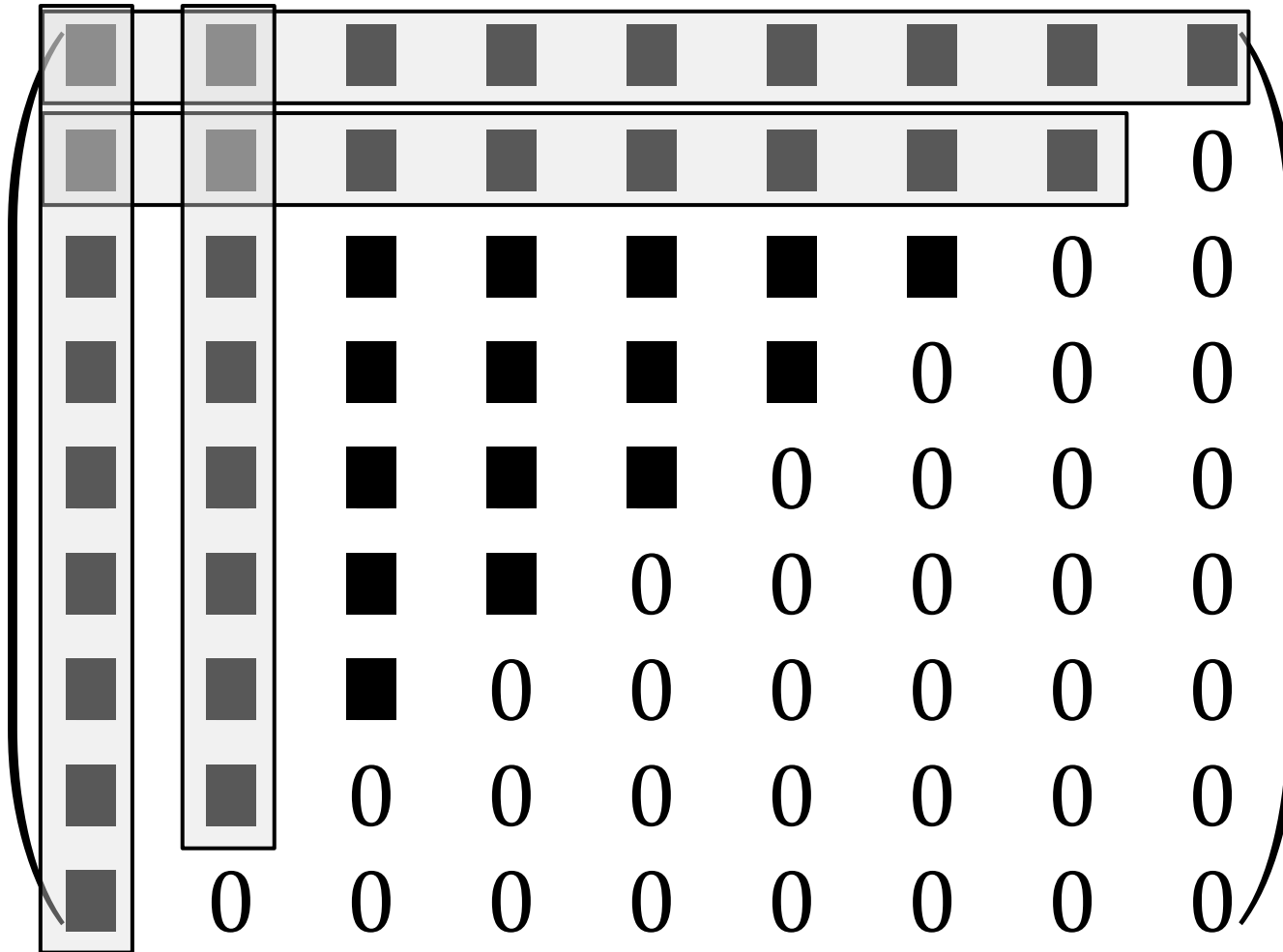
k_j = Number of interactions in row j

$$o_{ij} = \frac{c_{ij}}{\min(k_i, k_j)}$$

$$\frac{\sum_{i < j}^{NA} o_{ij}}{NA(NA - 1)/2}$$

Repeat for the columns:

Measuring overlap between **all possible ij** pairs of columns



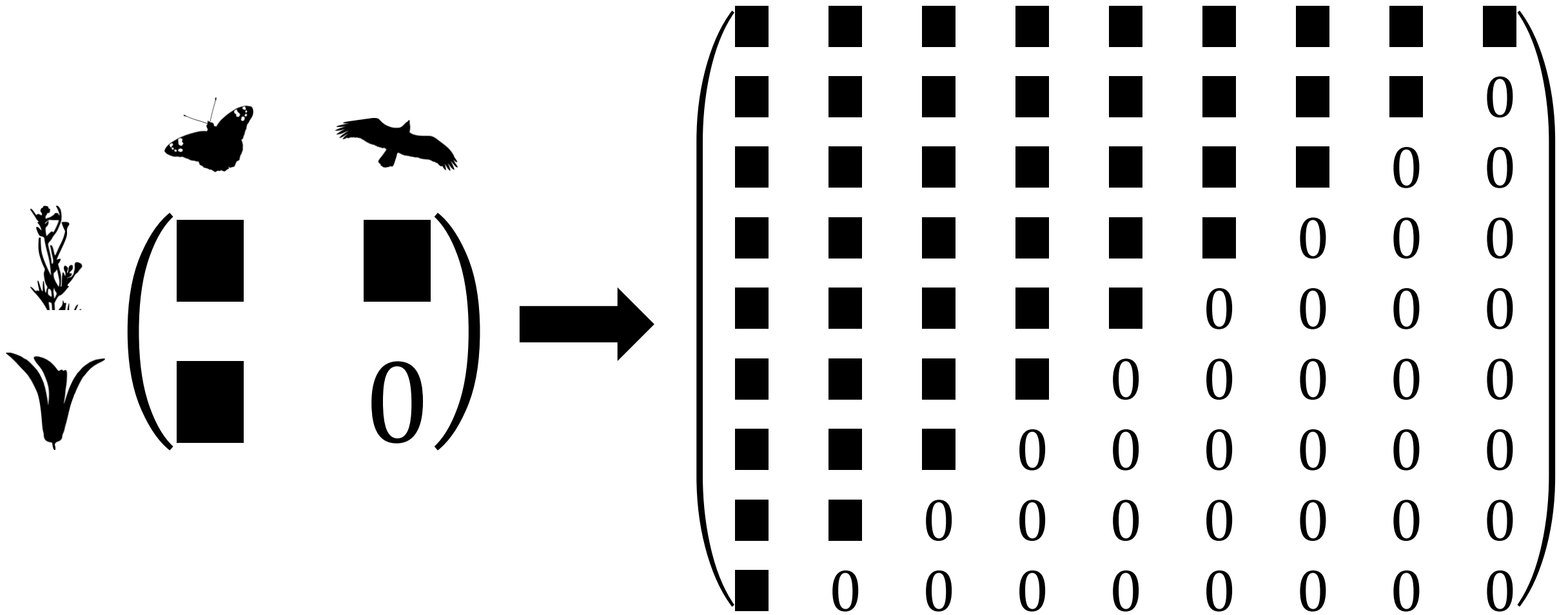
c_{ij} = Number of shared interactions between row i and j

k_i = Number of interactions in row i

k_j = Number of interactions in row j

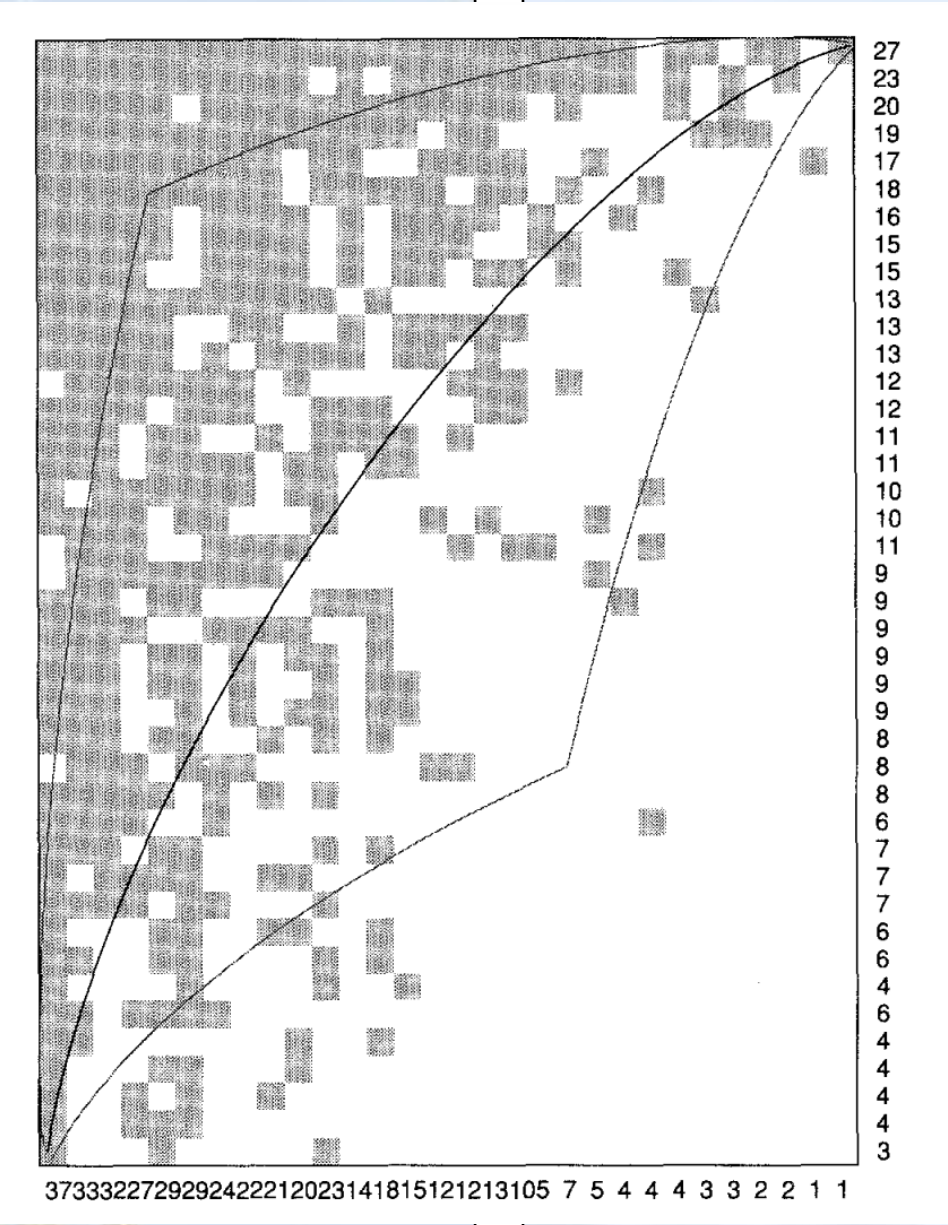
$$\eta = \frac{\sum_{i < j}^{NP} o_{ij} + \sum_{i < j}^{NA} o_{ij}}{\frac{NP(NP - 1)}{2} + \frac{NA(NA - 1)}{2}}$$

A general formula for quantifying nestedness:
 η varies between 0 and 1



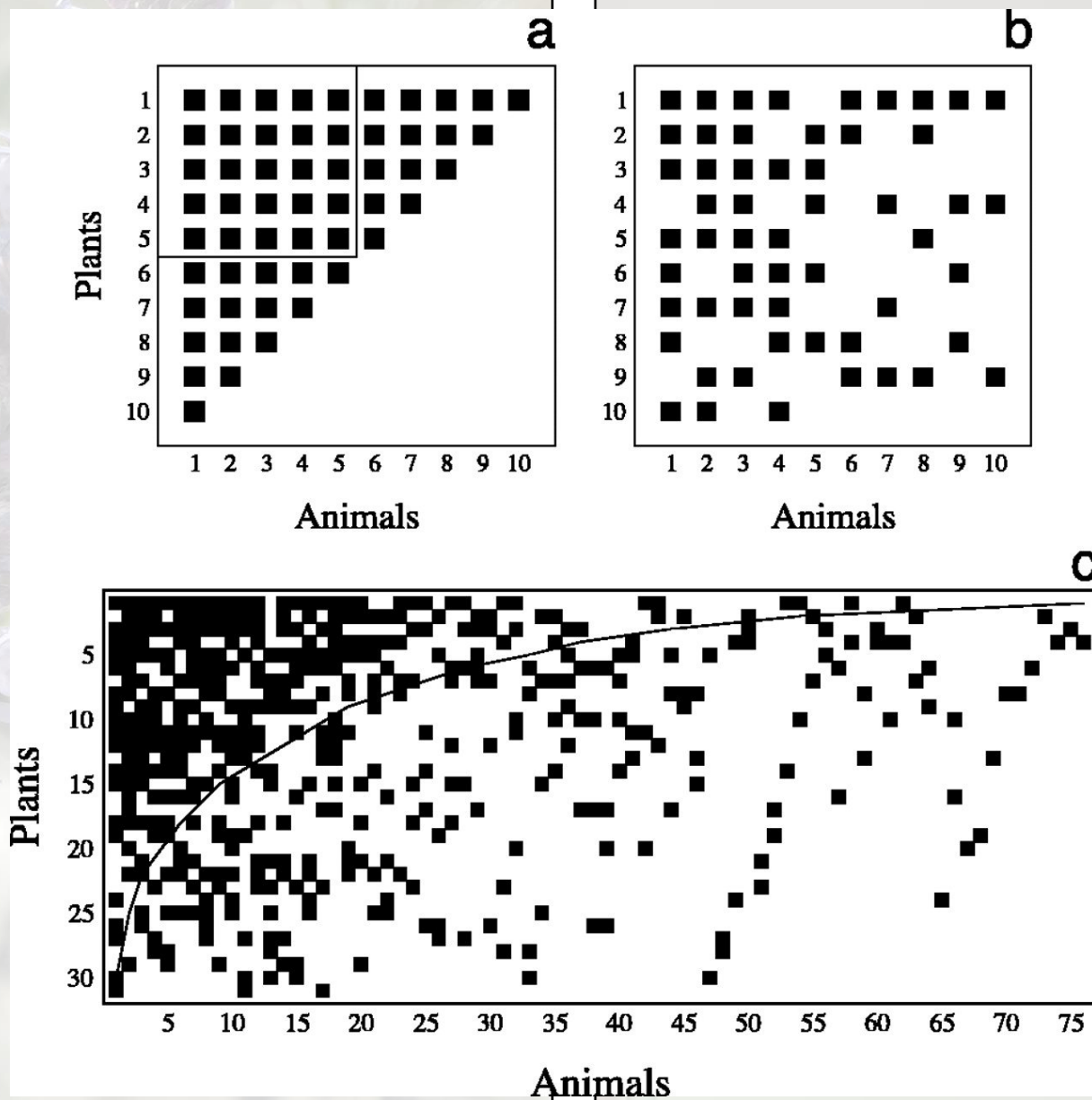
Now that we now how to quantify a nested pattern:
Where can we find it in nature?





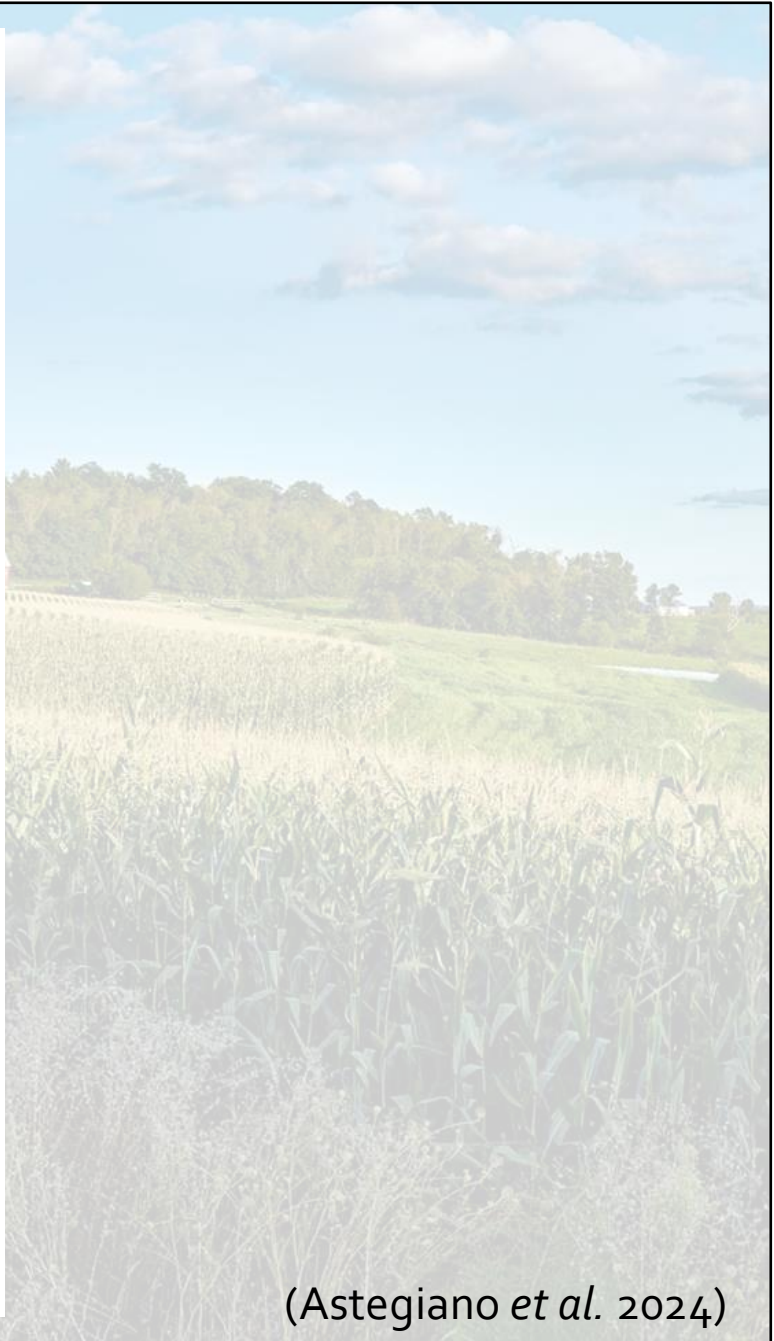
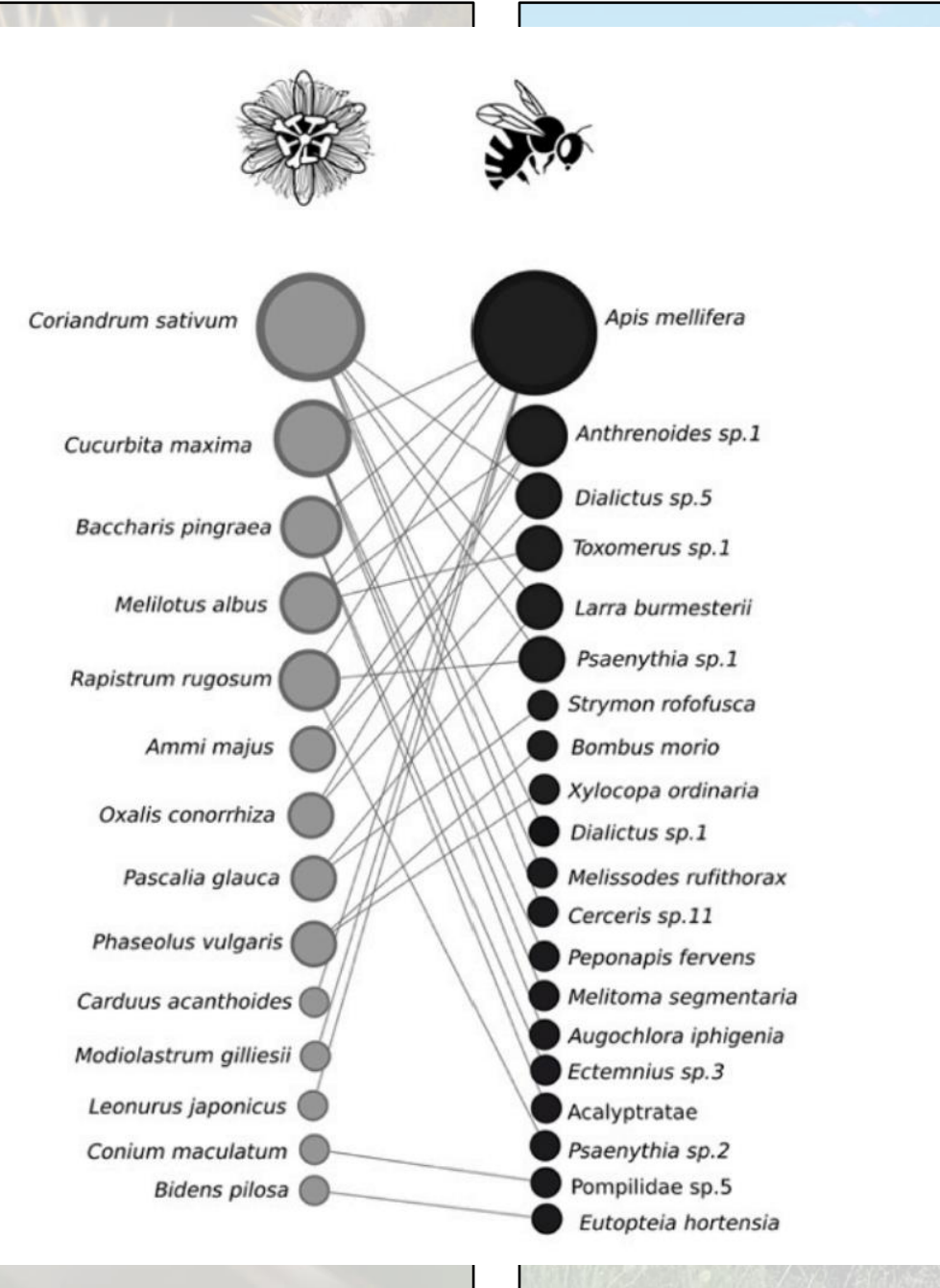
(Atmar & Patterson, 1993)





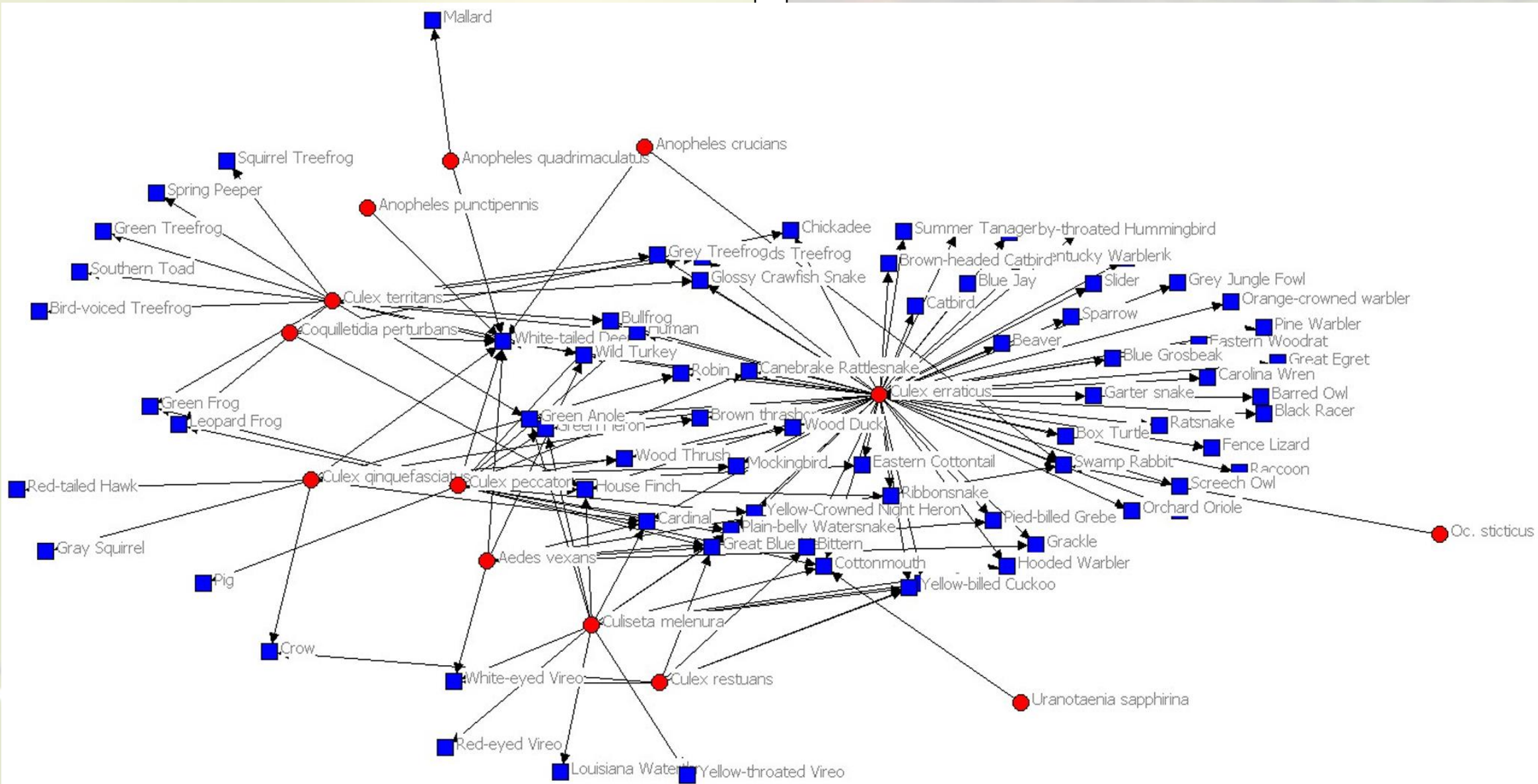
(Bascompte *et al.* 2003)



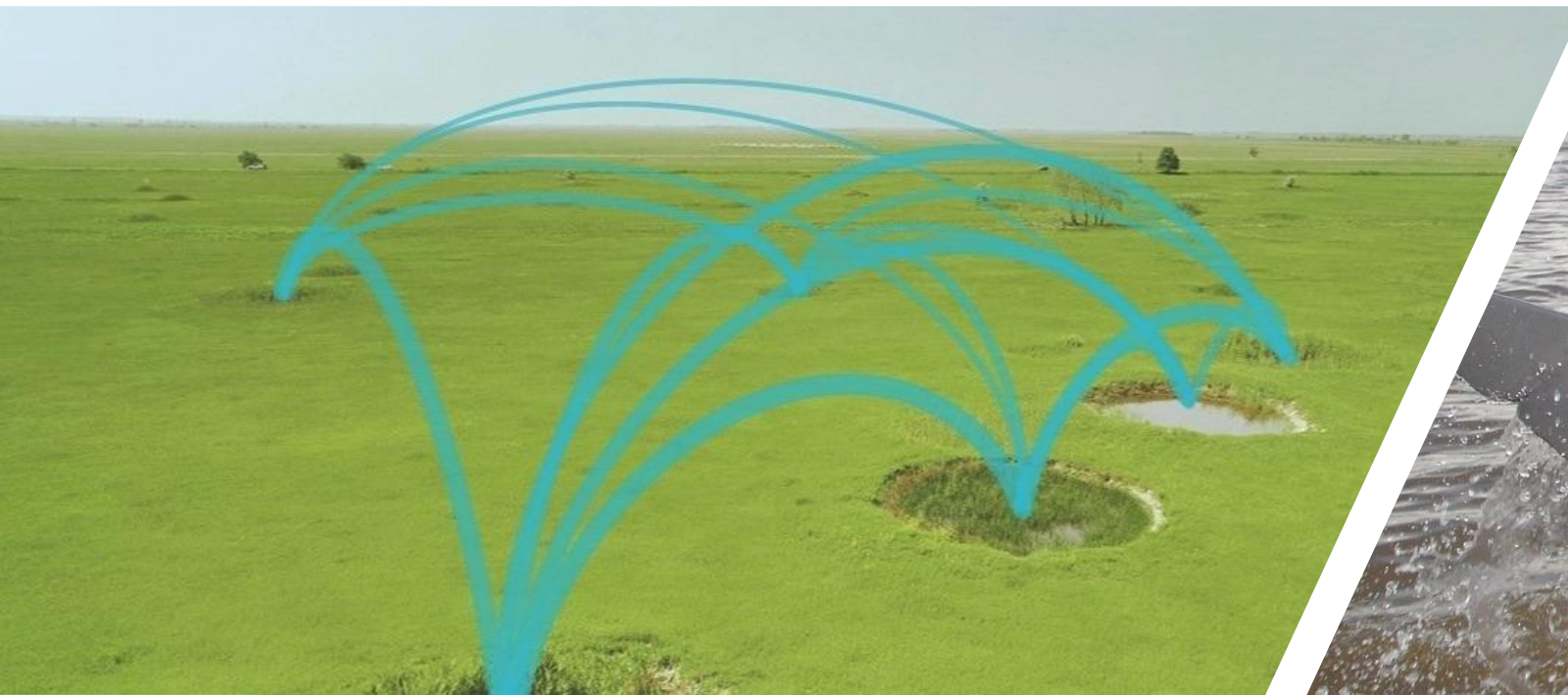
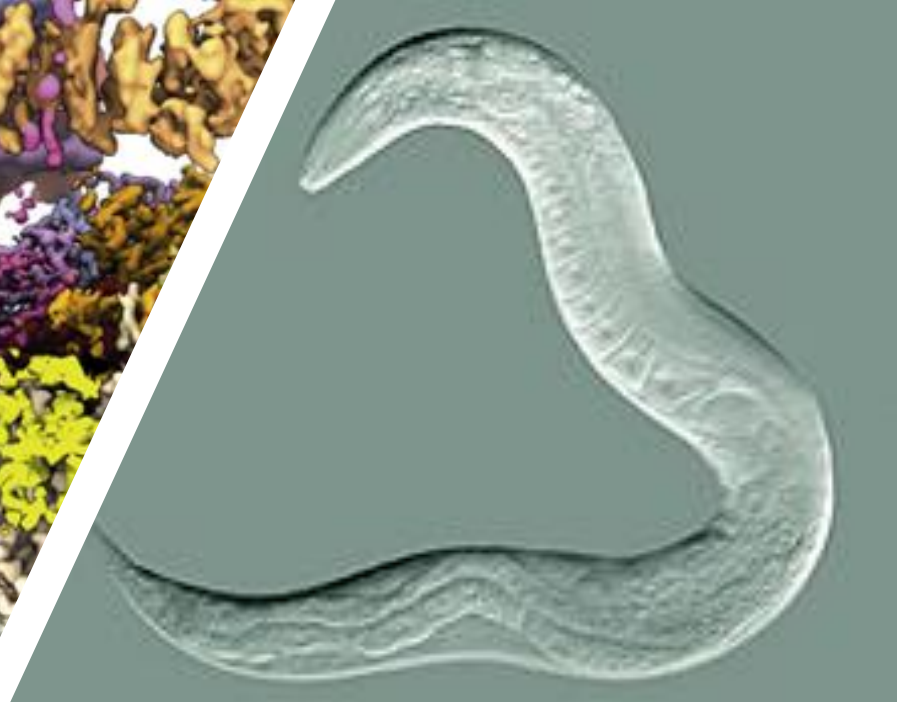


(Astegiano et al. 2024)



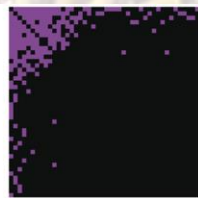
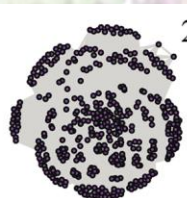
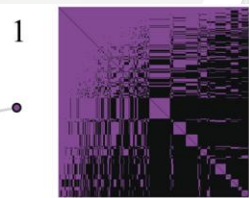
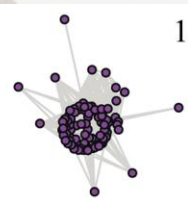
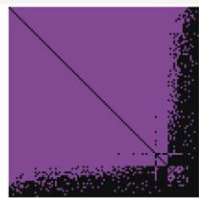


(Graham *et al.* 2009)

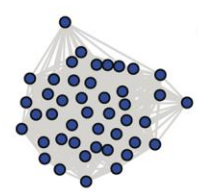
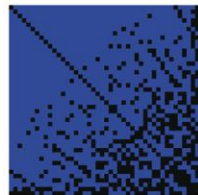
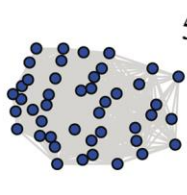
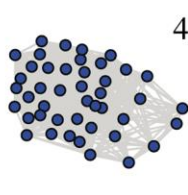




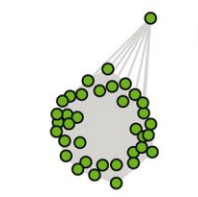
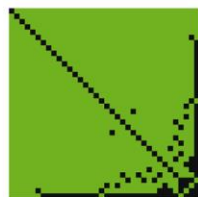
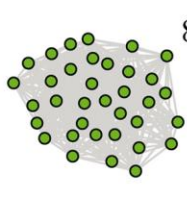
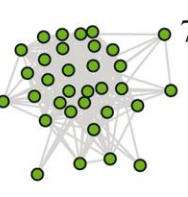
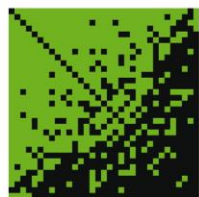
Molecular



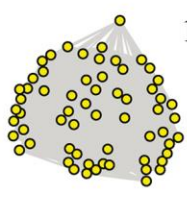
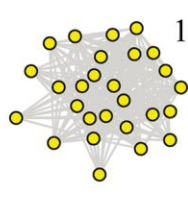
Individual



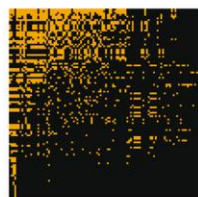
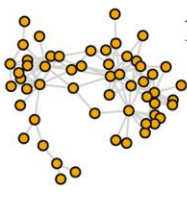
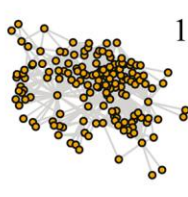
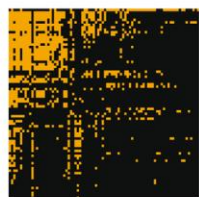
Population



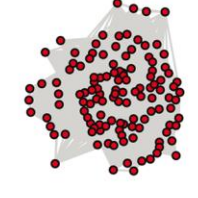
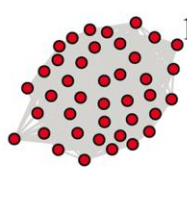
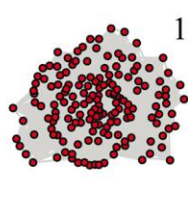
Metapopulation



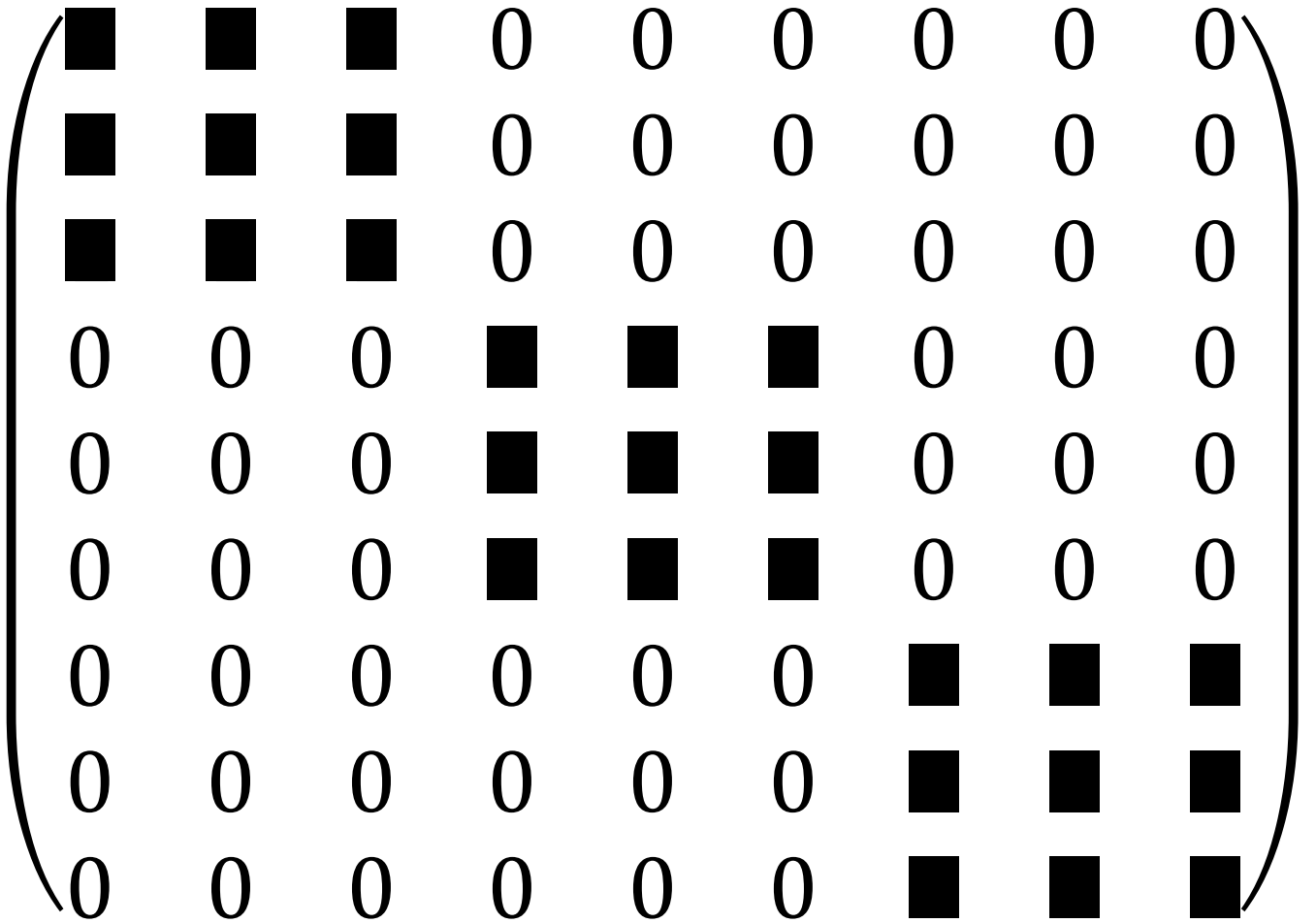
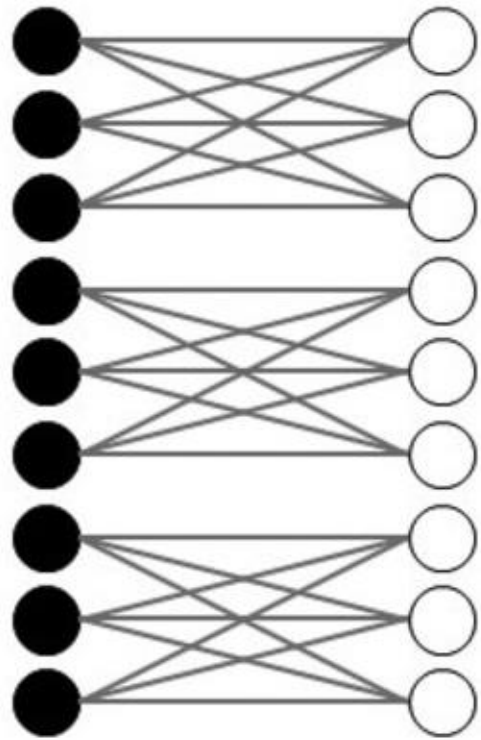
Community



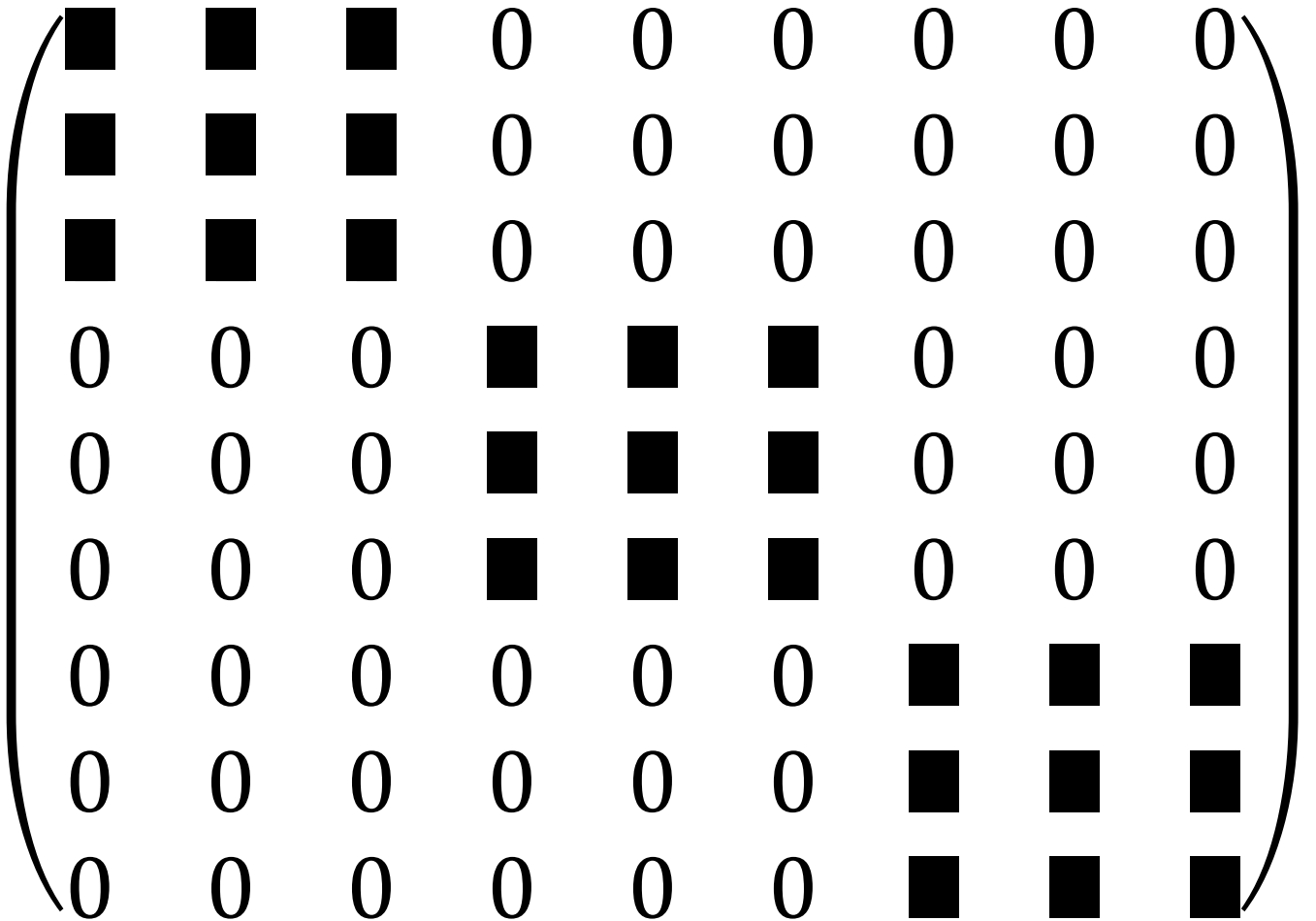
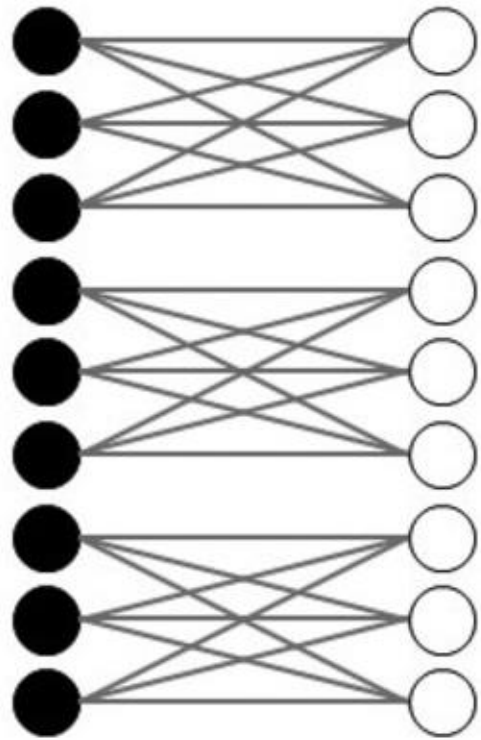
Metacommunity



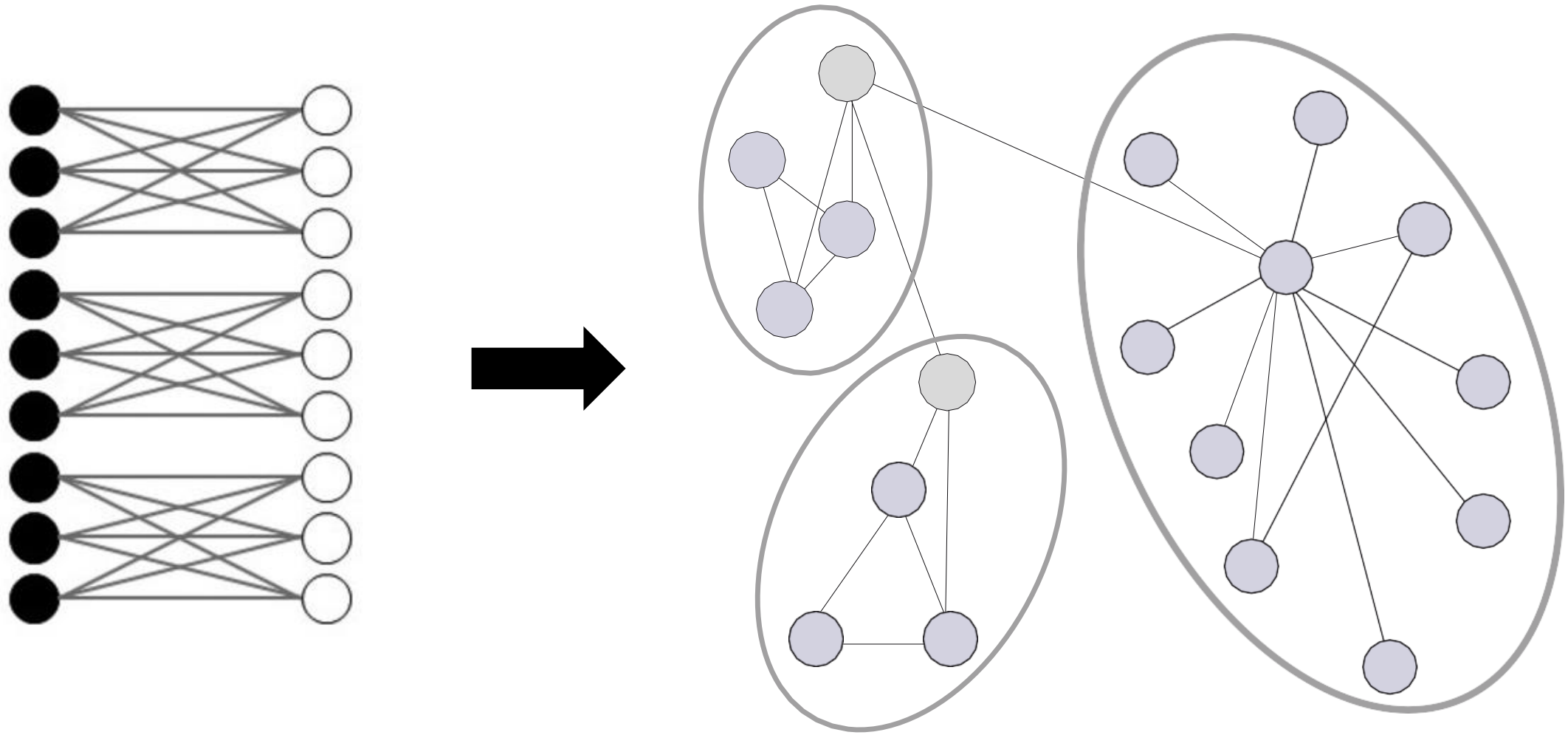
(Cantor *et al.* 2017)



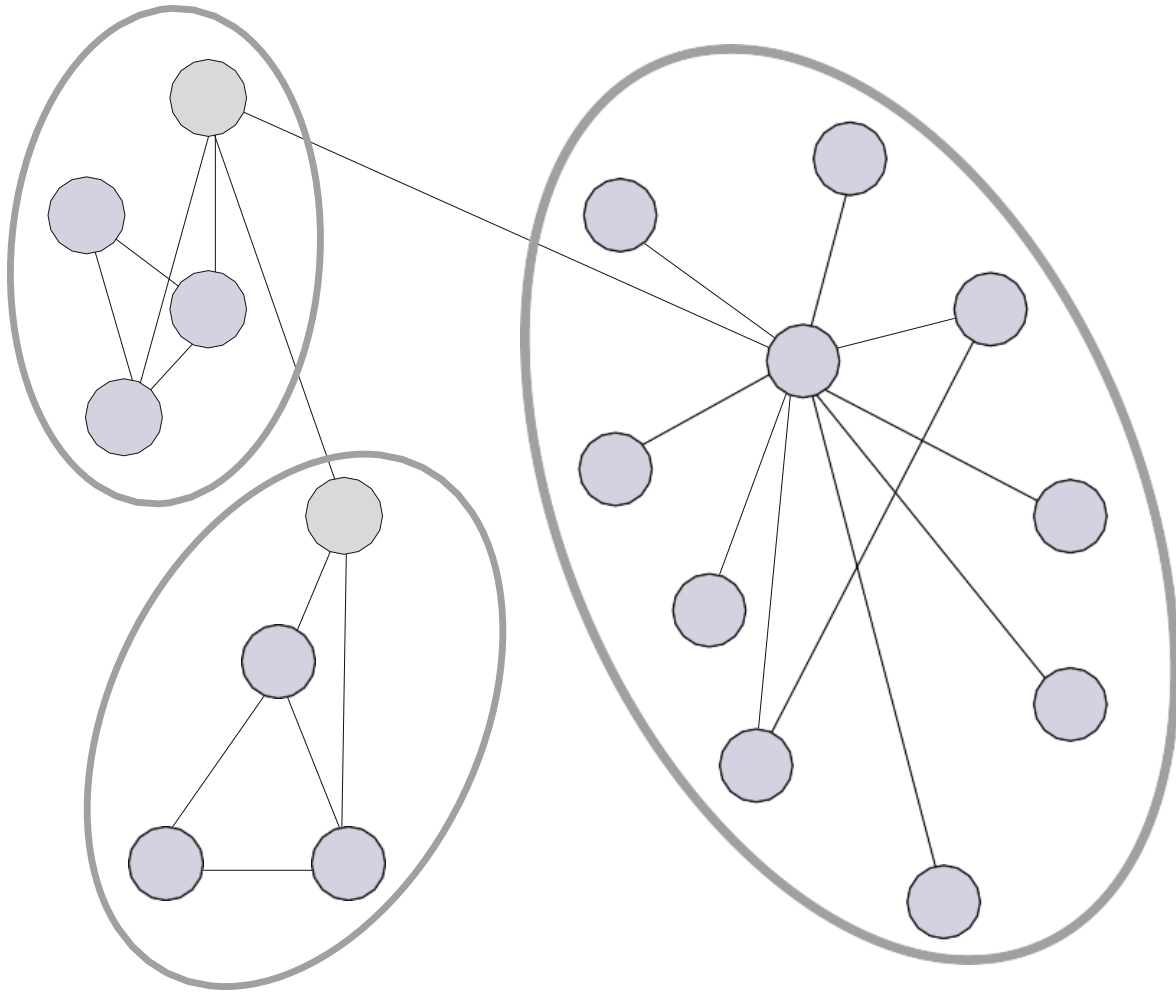
What about networks that look like this?
 Division into subgroups or "modules"



Division into subgroups or "modules"
 Extreme case: completely isolated subnetworks

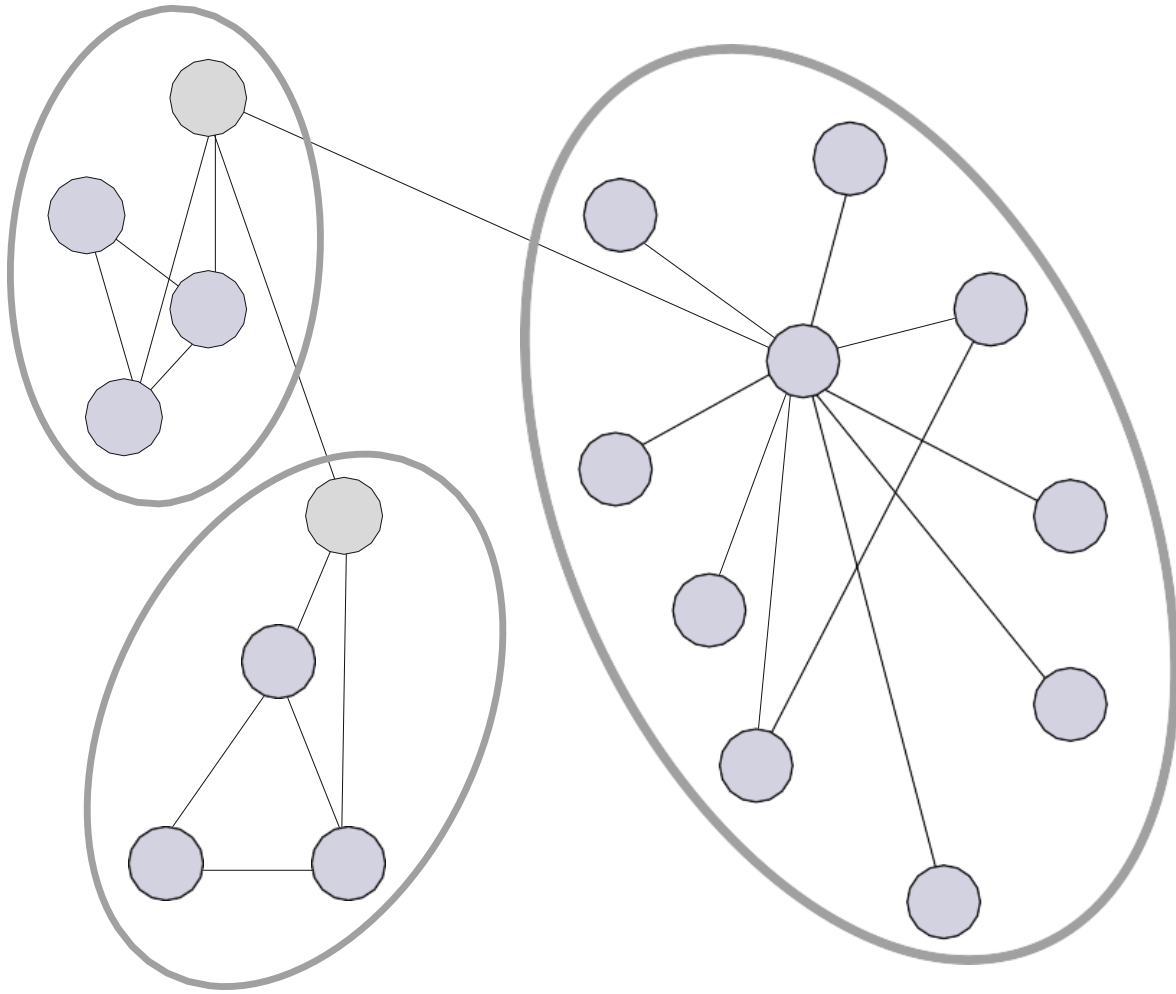


Modularity: species interact much more frequently within the same module than they do with species from other modules



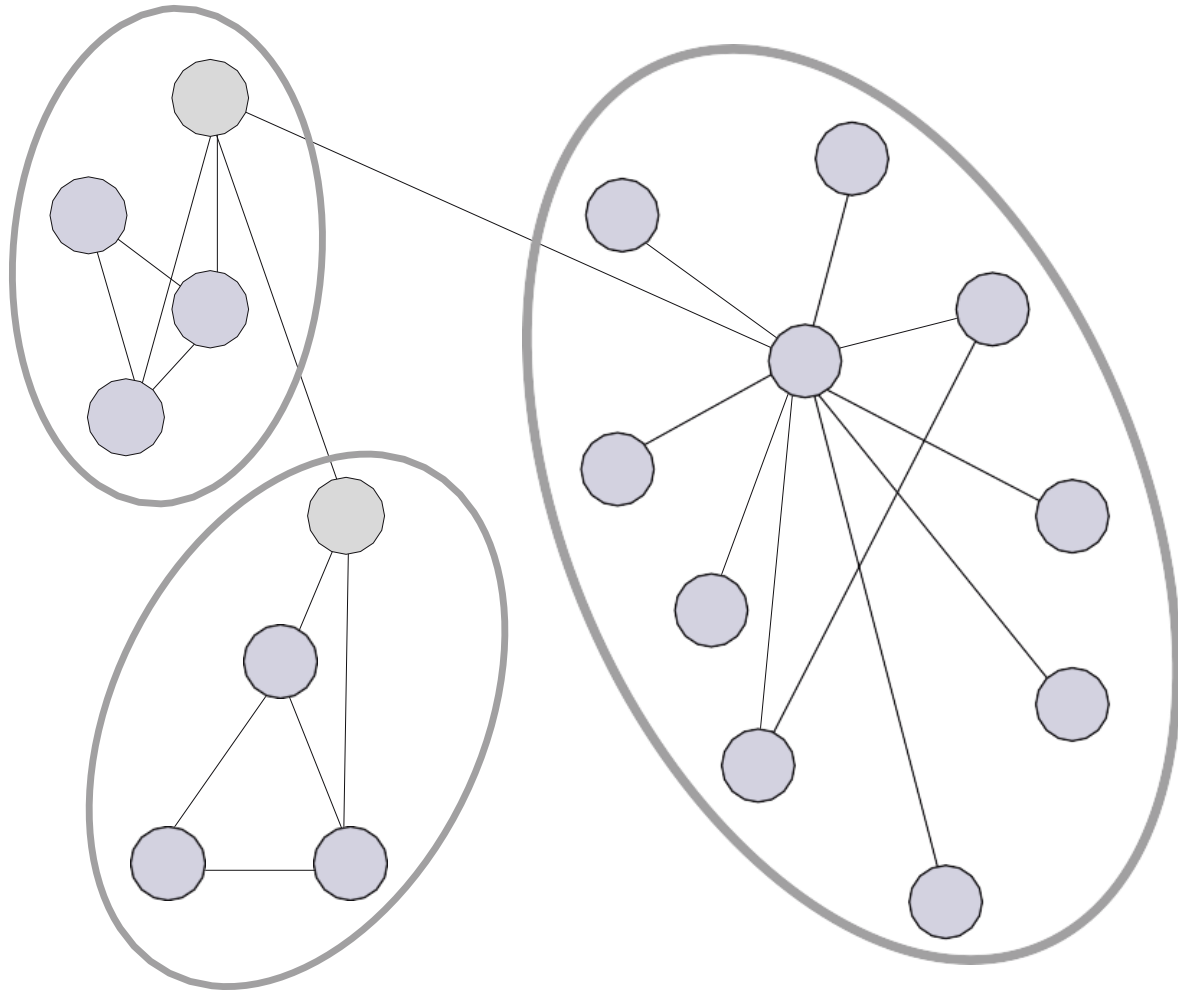
Fraction of
interactions within
modules vs among
modules

How can we measure modularity?



Fraction of
interactions within
modules vs among
modules

How to find the modules? What is the optimal way to divide
the network?



l_s = Number of interactions within module s

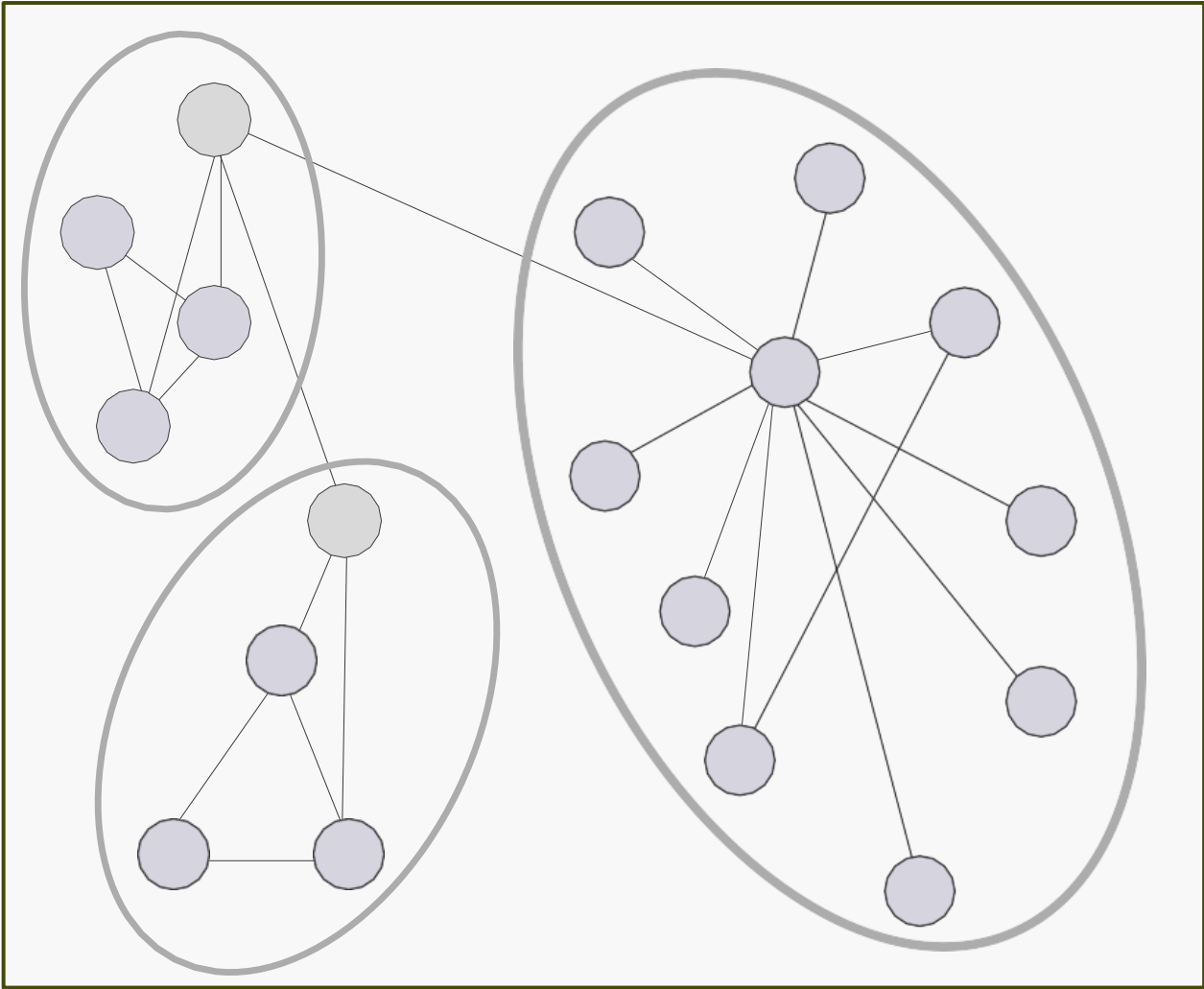
L = Number of interactions in the network

Maximize $\frac{l_s}{L}$

For all modules s

How to find the modules?

Dividing the network to maximize within modules interactions



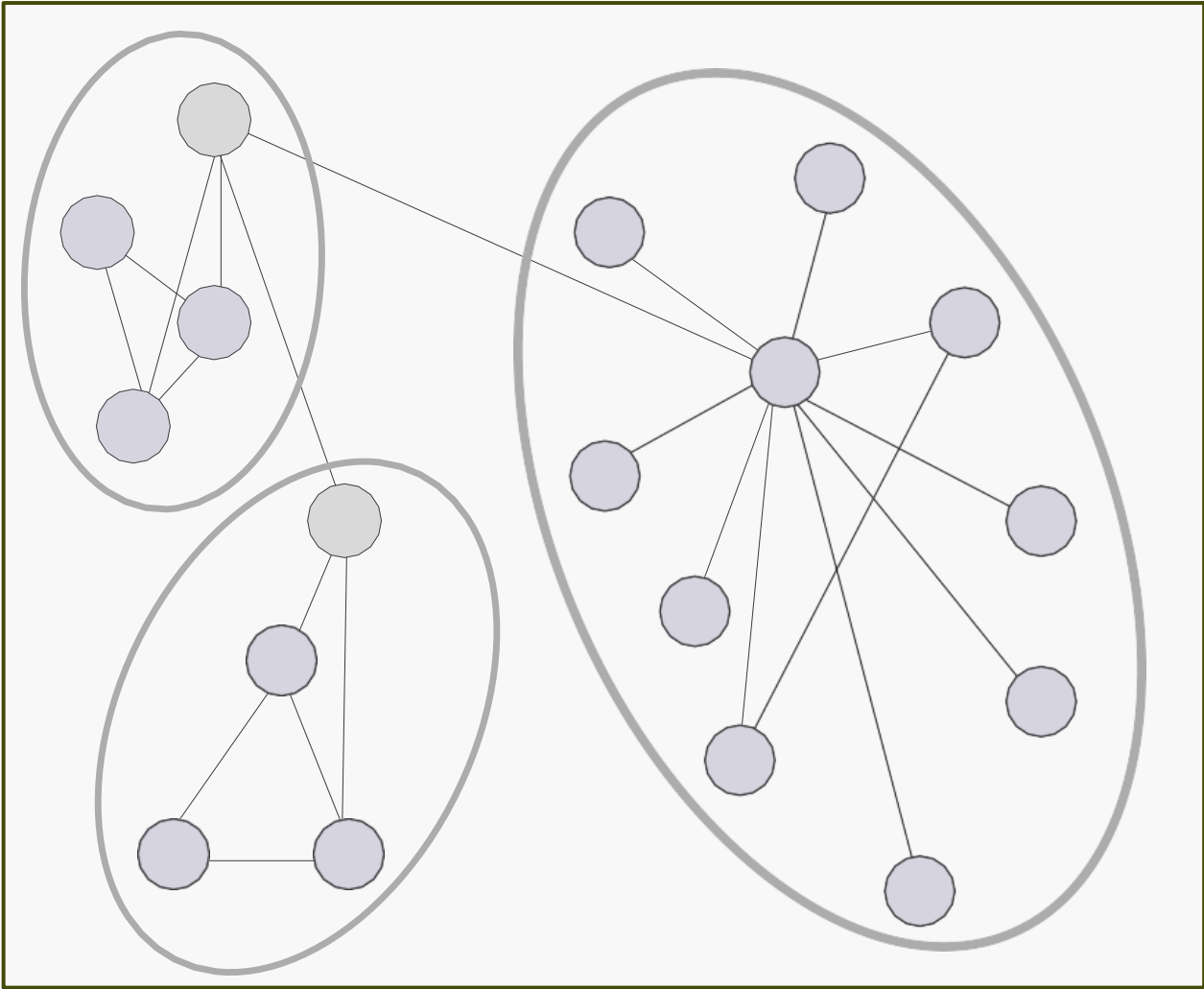
l_s = Number of interactions within module s

L = Number of interactions in the network



Maximize $\frac{l_s}{L}$
For all modules s

The problem: we may end up with trivial "optimal divisions"



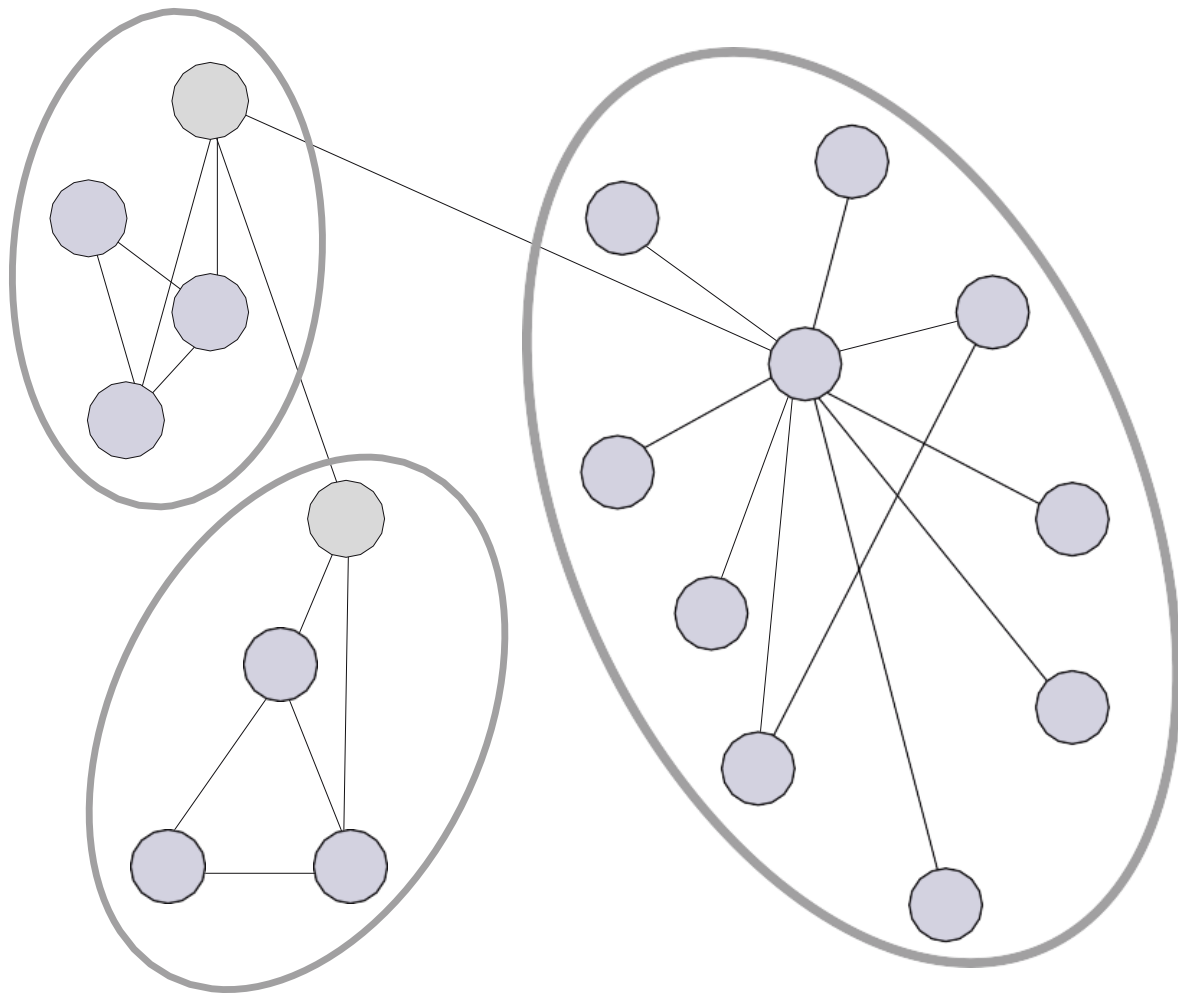
l_s = Number of interactions within module s

L = Number of interactions in the network



Maximize $\frac{l_s}{L}$
For all modules s

The solution: maximize within modules interactions relative to a randomized version of the same network



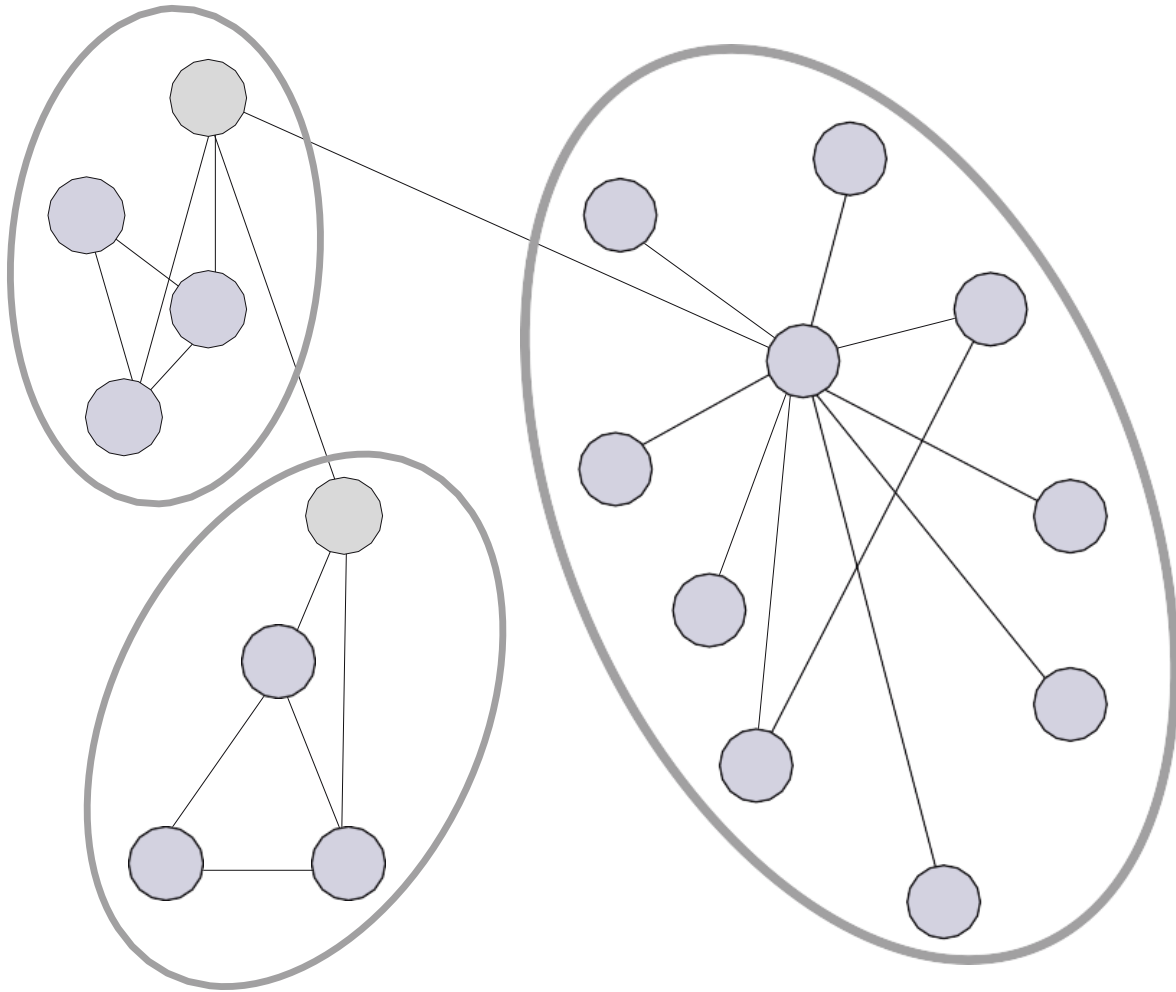
l_s = Number of interactions within module s

L = Number of interactions in the network



Maximize $\frac{l_s}{L}$
For all modules s

The solution: maximize within modules interactions relative to a randomized version of the same network



l_s = Number of interactions within module s

L = Number of interactions in the network



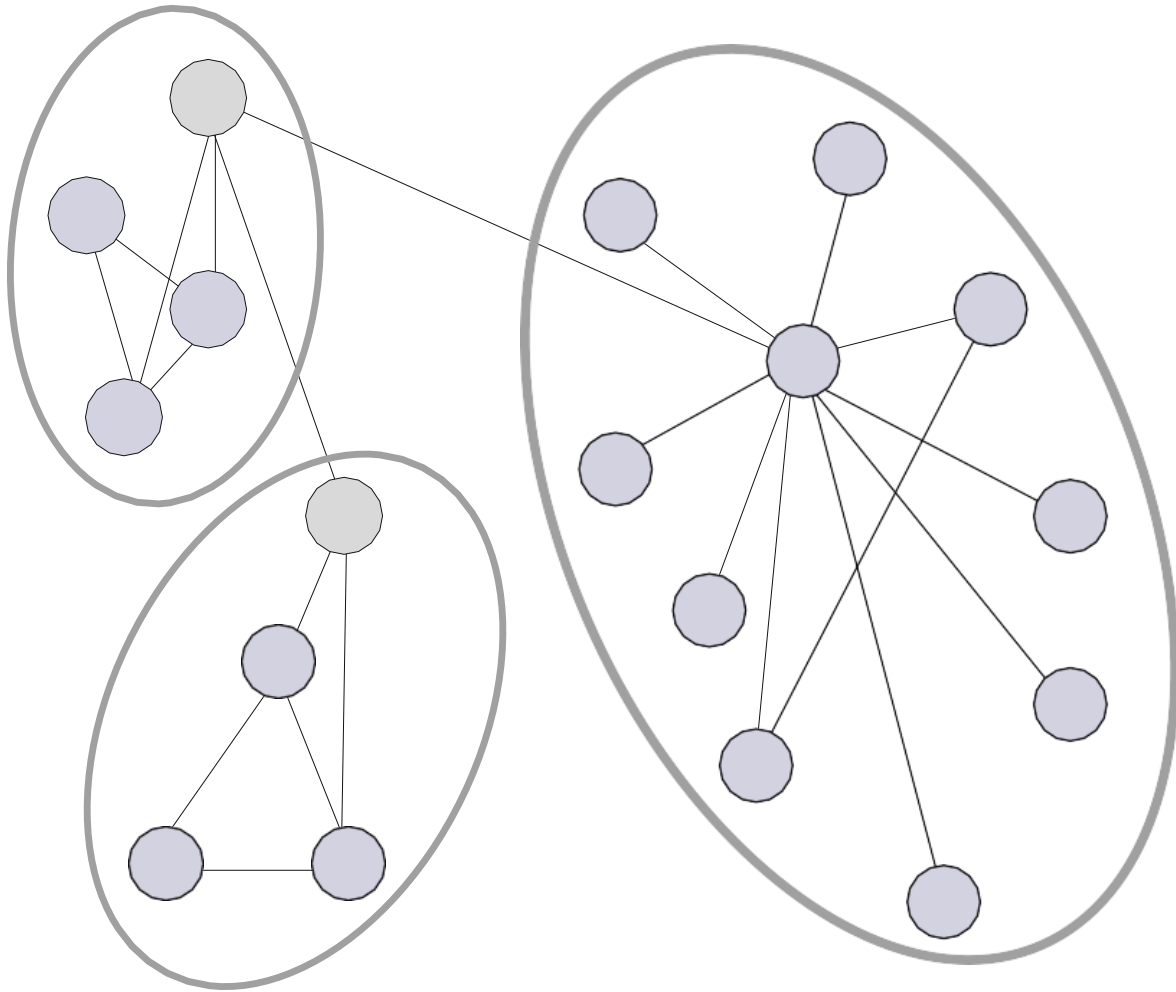
Maximize

$$\frac{l_s}{L} - \left(\frac{d_s}{L} \right)^2$$

For all modules s

d_s = Sum of the degrees of species in module s

The solution: maximize within modules interactions relative to a randomized version of the same network



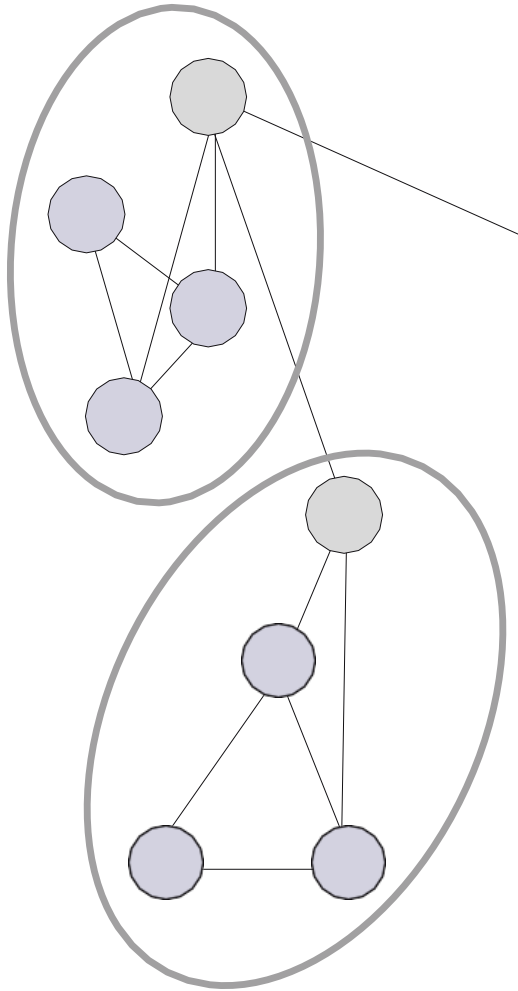
l_s = Number of interactions within module s

L = Number of interactions in the network

$$M = \sum_{s=1}^{N_m} \left[\frac{l_s}{L} - \left(\frac{d_s}{L} \right)^2 \right]$$

d_s = Sum of the degrees of species in module s

The solution: maximize within modules interactions relative to a randomized version of the same network



The term $\left(\frac{d_s}{L}\right)^2$ represents the expected fraction of interactions within modules for a network where interactions are randomly rewired

l_s = Number of interactions within module s

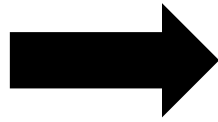
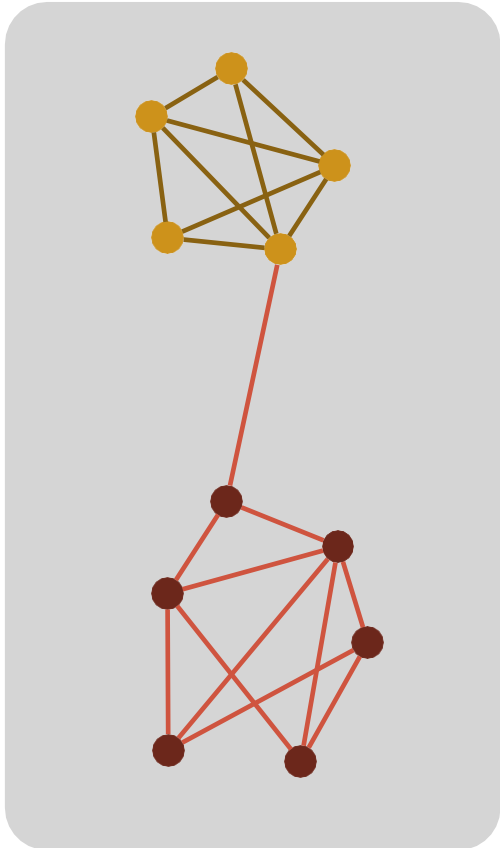
L = Number of interactions in the network



$$M = \sum_{s=1}^{N_m} \left[\frac{l_s}{L} - \left(\frac{d_s}{L} \right)^2 \right]$$

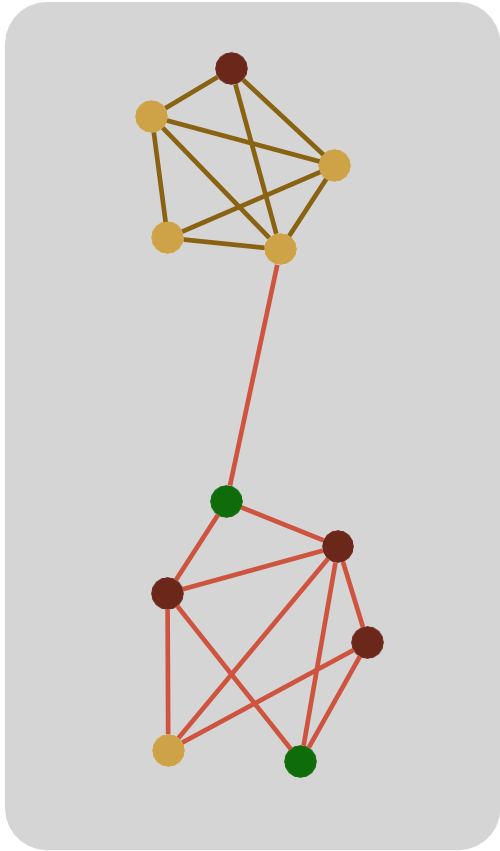
d_s = Sum of the degrees of species in module s

The term $\left(\frac{d_s}{L}\right)^2$ represents the expected fraction of interactions within module s for a network where interactions are randomly rewired



$$M = \sum_{s=1}^{N_m} \left[\frac{l_s}{L} - \left(\frac{d_s}{L} \right)^2 \right]$$

Measuring modularity: a practical example

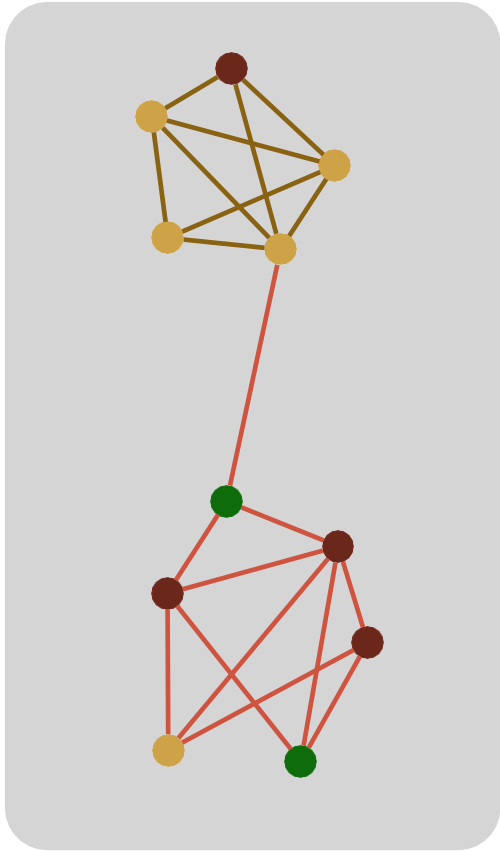


● $(2/20) - (15/40)^2$

● $(6/20) - (18/40)^2$

● $(0/20) - (6/40)^2$

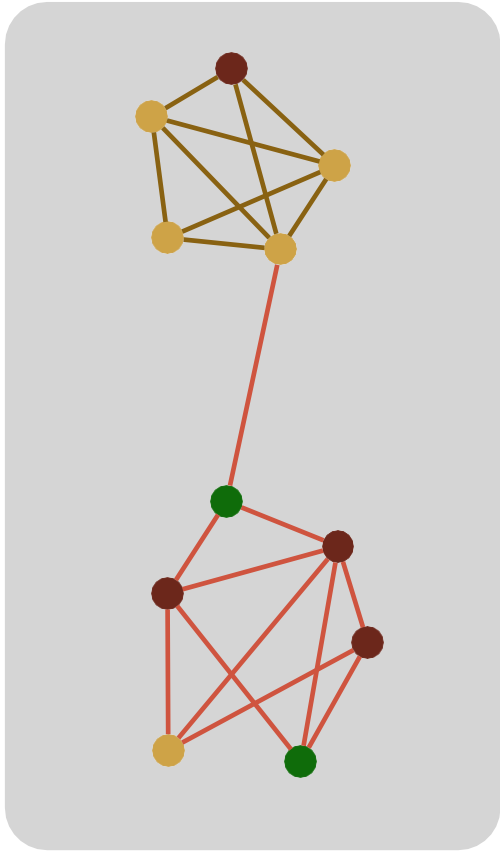
Measuring modularity: a practical example



- - 0.04
- 0.10
- - 0.02

$$M = \sum_{s=1}^{N_m} \left[\frac{l_s}{L} - \left(\frac{d_s}{L} \right)^2 \right]$$

Measuring modularity: a practical example



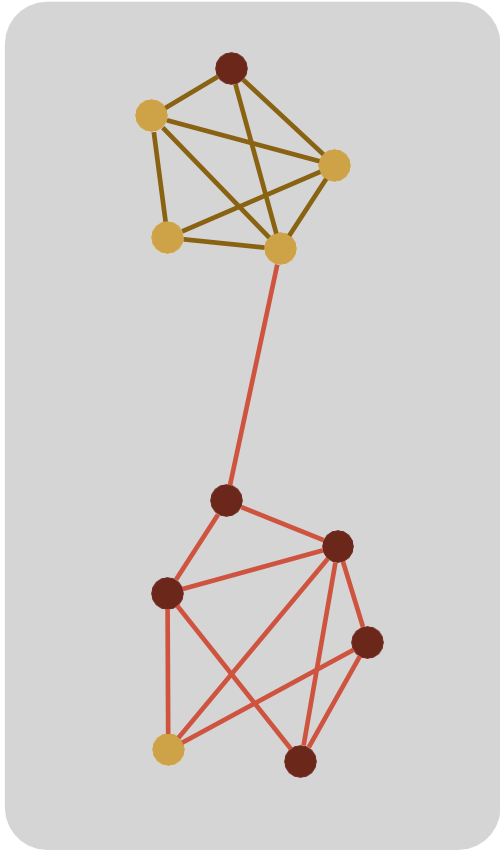
● - 0.04

● 0.10

● - 0.02

$$M = 0.04$$

Measuring modularity: a practical example

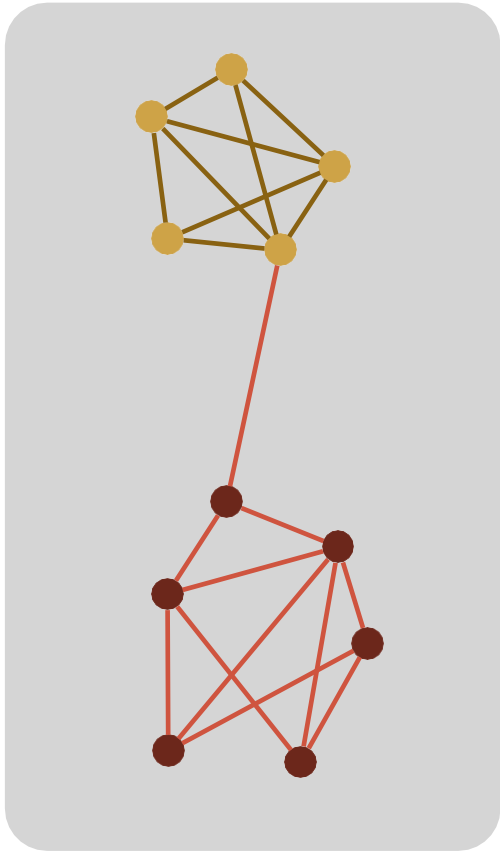


● 0.01

● 0.15

$$M = 0.16$$

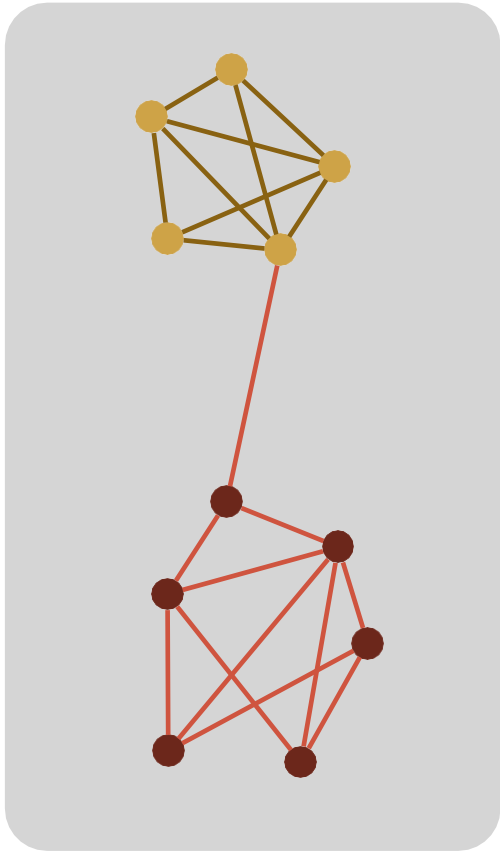
Measuring modularity: a practical example



- 0.22
- 0.25

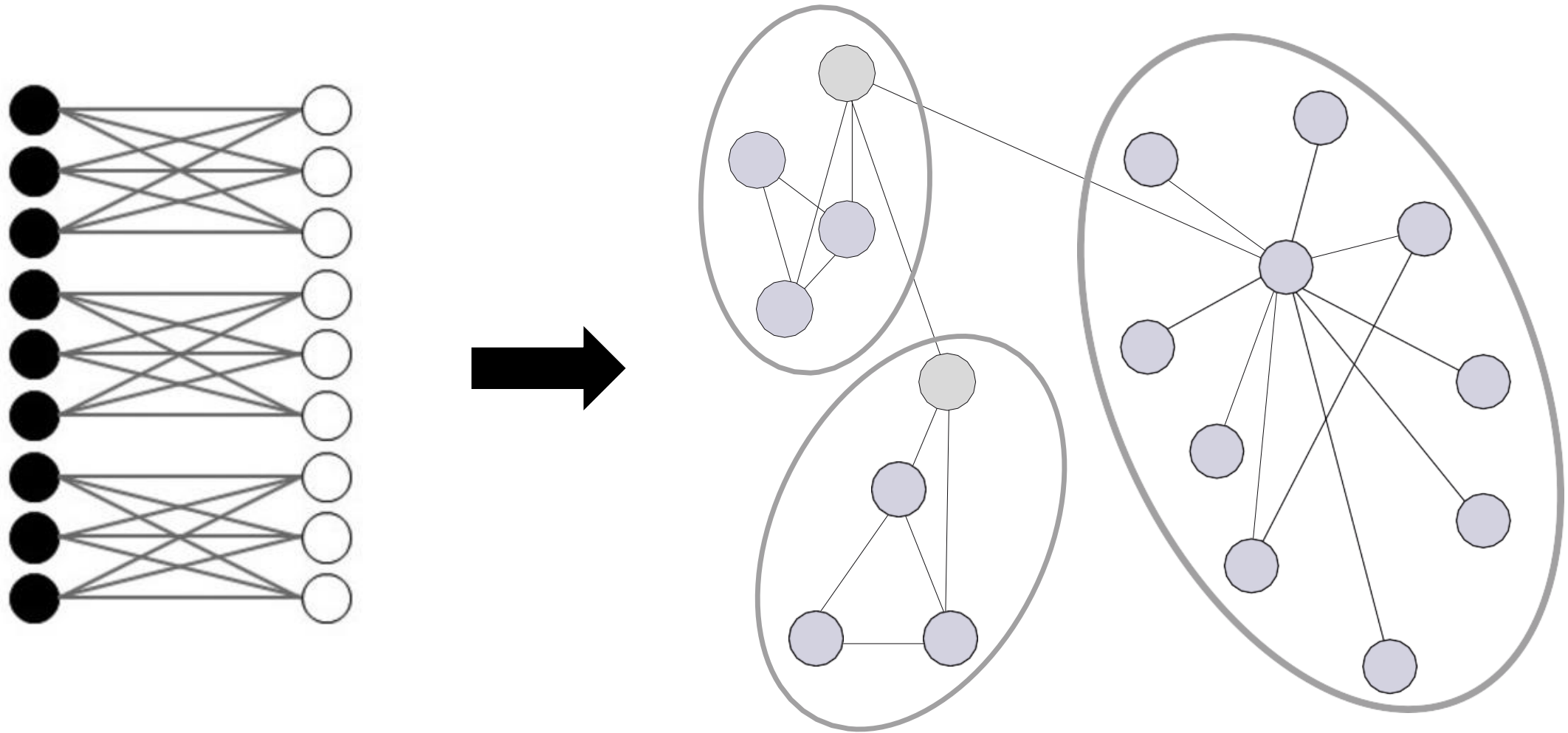
$$M = 0.47$$

Measuring modularity: a practical example



$$M = 0.47$$

Measuring modularity: optimization algorithms



Now that we now how to quantify a modular pattern:
Where can we find it in nature?

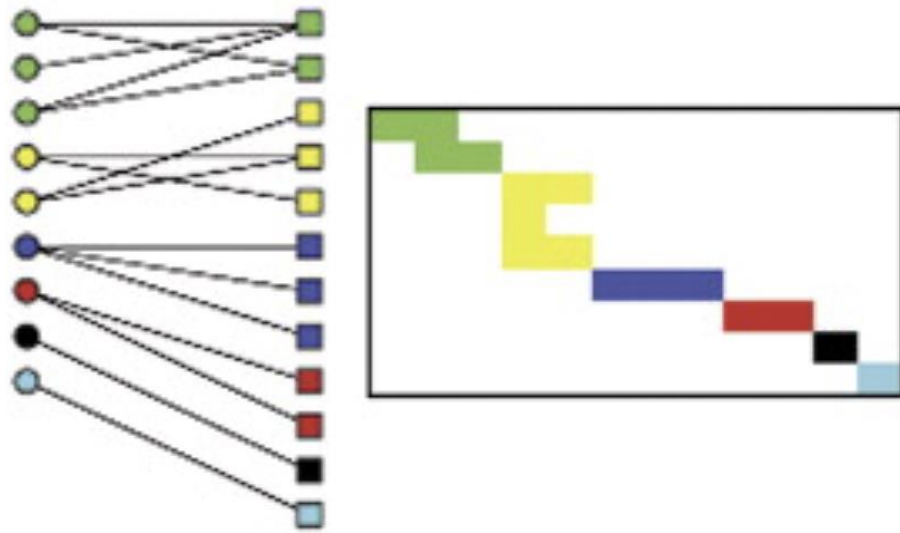




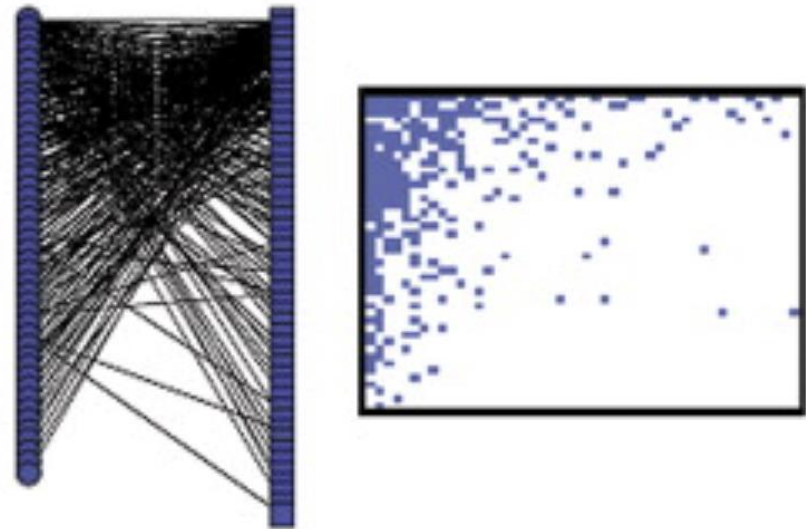
MYRMECOPHYTES & ANTS	<i>Cecropia purpuracens</i>	<i>Cecropia concolor</i>	<i>Cecropia distachya</i>	<i>Cecropia ficifolia</i>	<i>Pourouma heterophylla</i>	<i>Hirtella myrmecophila</i>	<i>Hirtella physophora</i>	<i>Duroia saccifera</i>	<i>Cordia nodosa</i>	<i>Cordia aff. nodosa</i>	<i>Tococa bullifera</i>	<i>Maieta guianensis</i>	<i>Maieta poeppigii</i>	<i>Tachigali polyphylla</i>	<i>Tachigali myrmecophila</i>	<i>Amatoua aff. guianensis</i>
<i>Camponotus balzanii</i>	11															
<i>Azteca alfari</i>	1															
<i>Azteca isthmica</i>	1	1	1	1												
<i>Azteca aff. isthmica</i>	1			2												
<i>Allomerus D</i>					23											
<i>Allomerus prancei</i>						5										
<i>Allomerus aff. octoarticulata</i>						3	70	27								
<i>Solenops A</i>						3	1									
<i>Allomerus auripunctata</i>								2		2						
<i>Crematogaster B</i>								1	1	1						
<i>Azteca HC</i>										3						
<i>Azteca G</i>										24	11	2				
<i>Crematogaster D</i>										3	2					
<i>Azteca CO</i>										1						
<i>Pheidole minutula</i>											1	93	28			
<i>Crematogaster A</i>						1					7	7	1			
<i>Azteca TO</i>											1					
<i>Crematogaster C</i>											3	3				
<i>Azteca schummani</i>														2	1	
<i>Pseudomyrmex nigrescens</i>														7	16	
<i>Pseudomyrmex concolor</i>														16	18	
<i>Azteca D</i>															1	
<i>Azteca polymorpha</i>															2	
<i>Crematogaster E</i>										1					1	
<i>Azteca Q</i>																3
Unoccupied plants	14	0	0	0	0	0	3	8	0	31	0	5	5	6	5	0



A

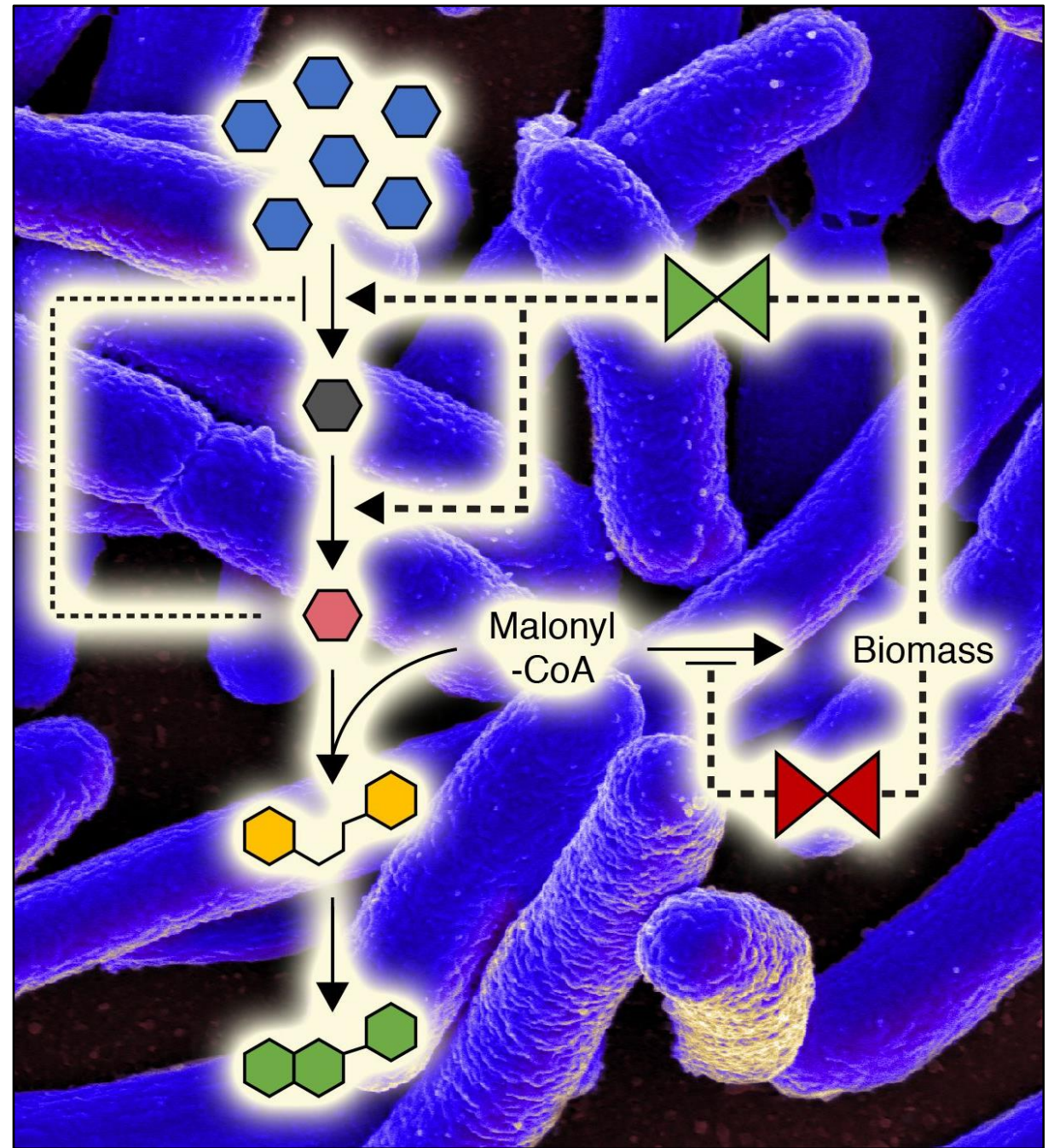
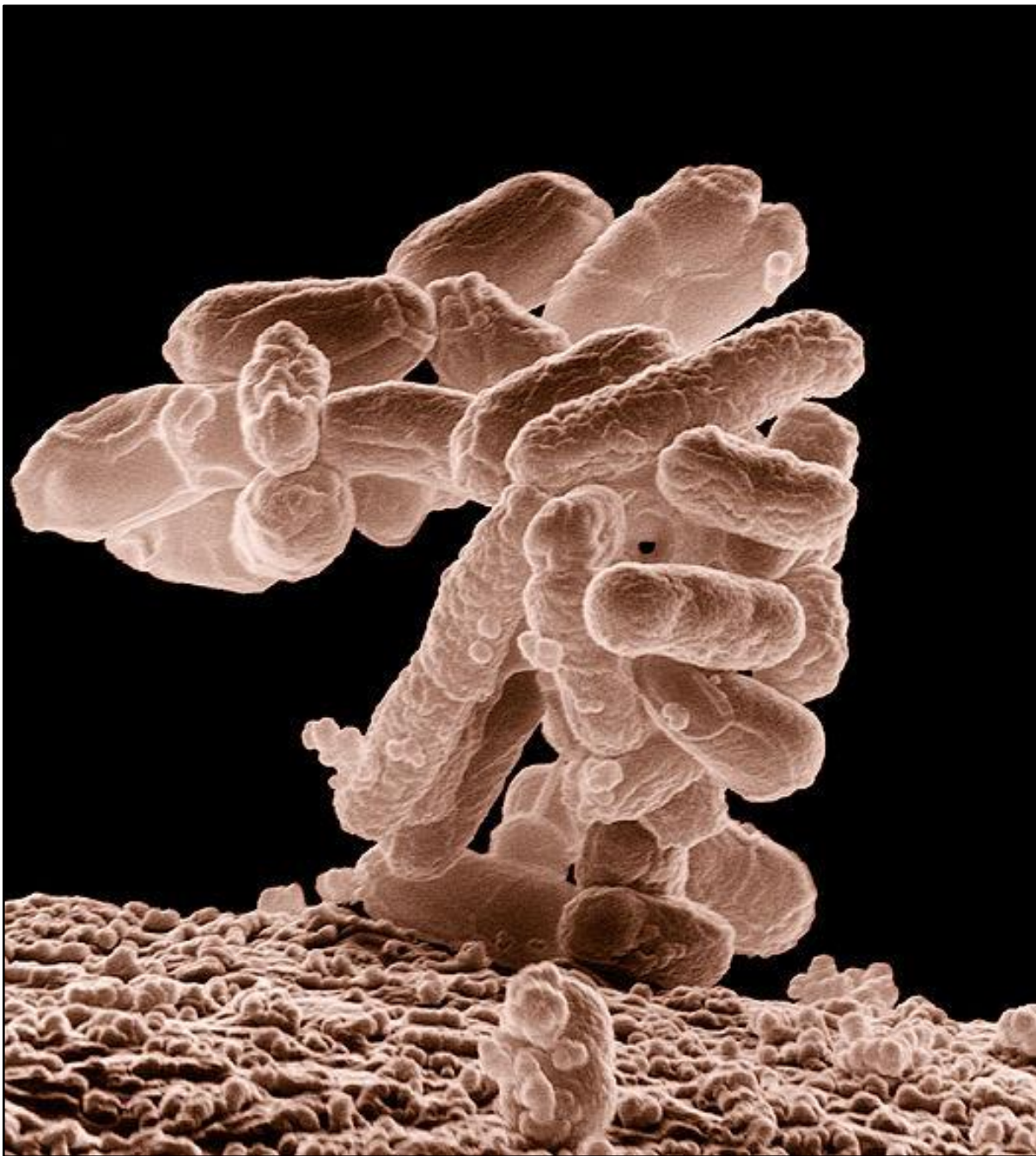


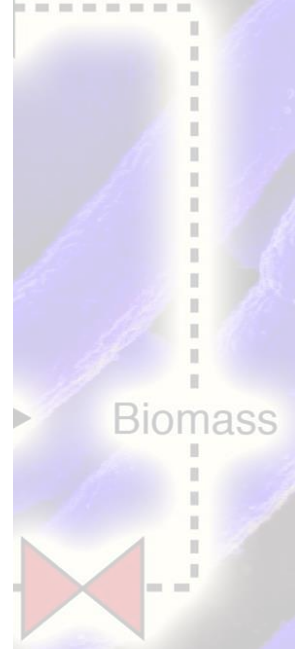
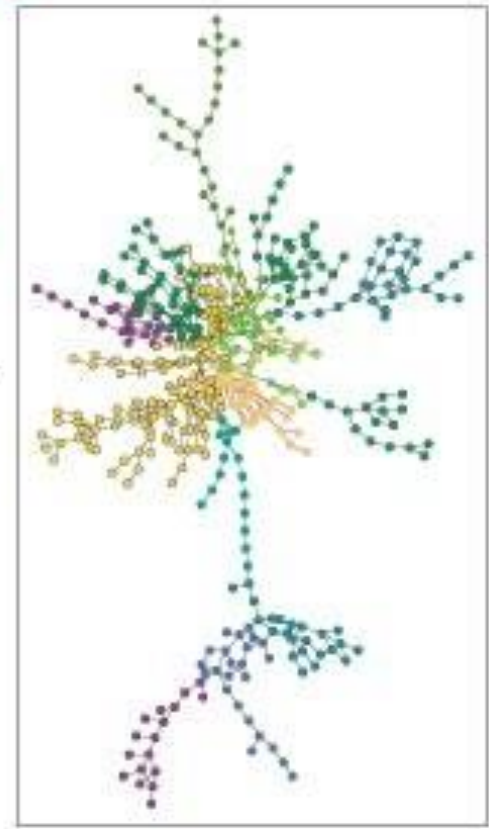
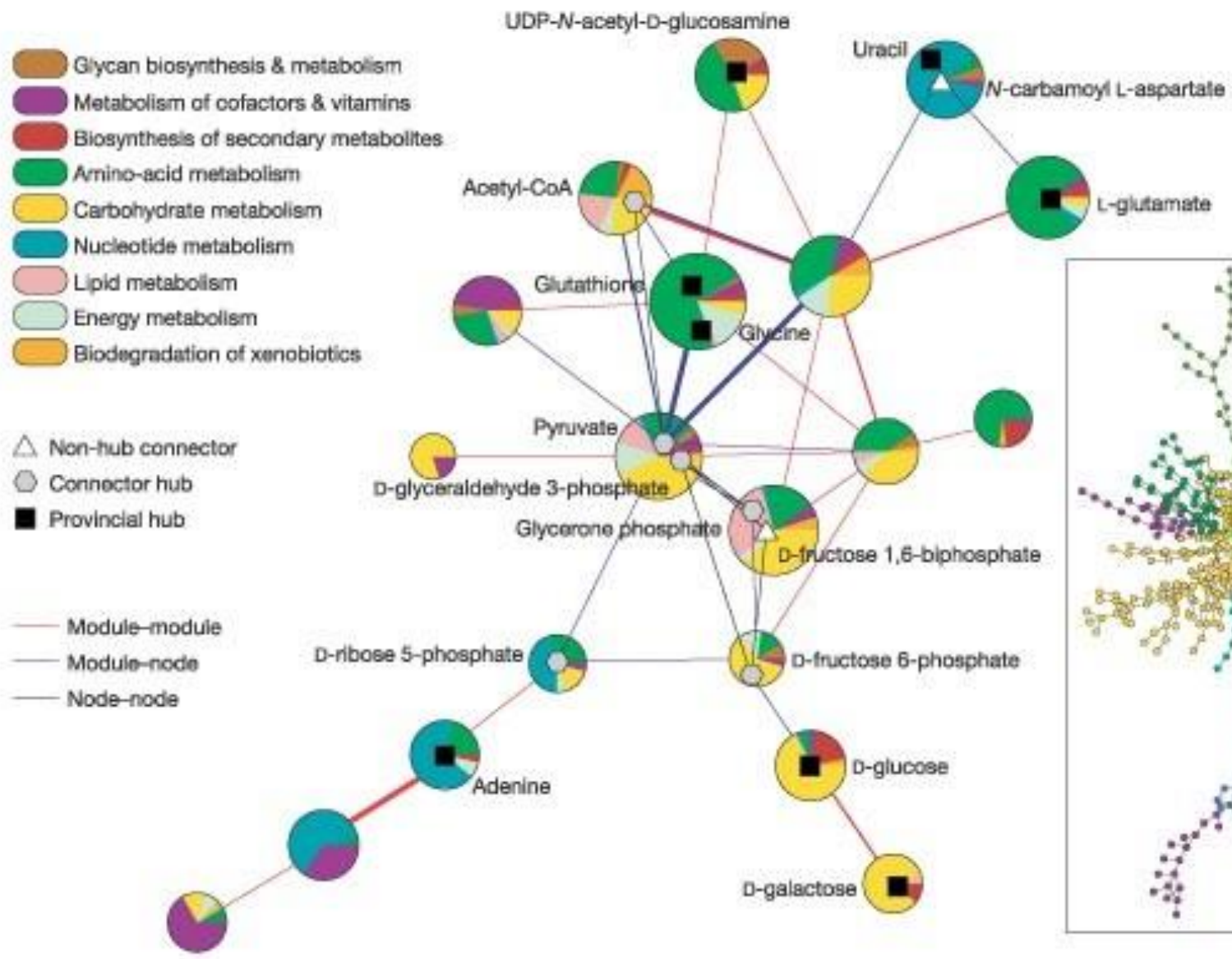
B





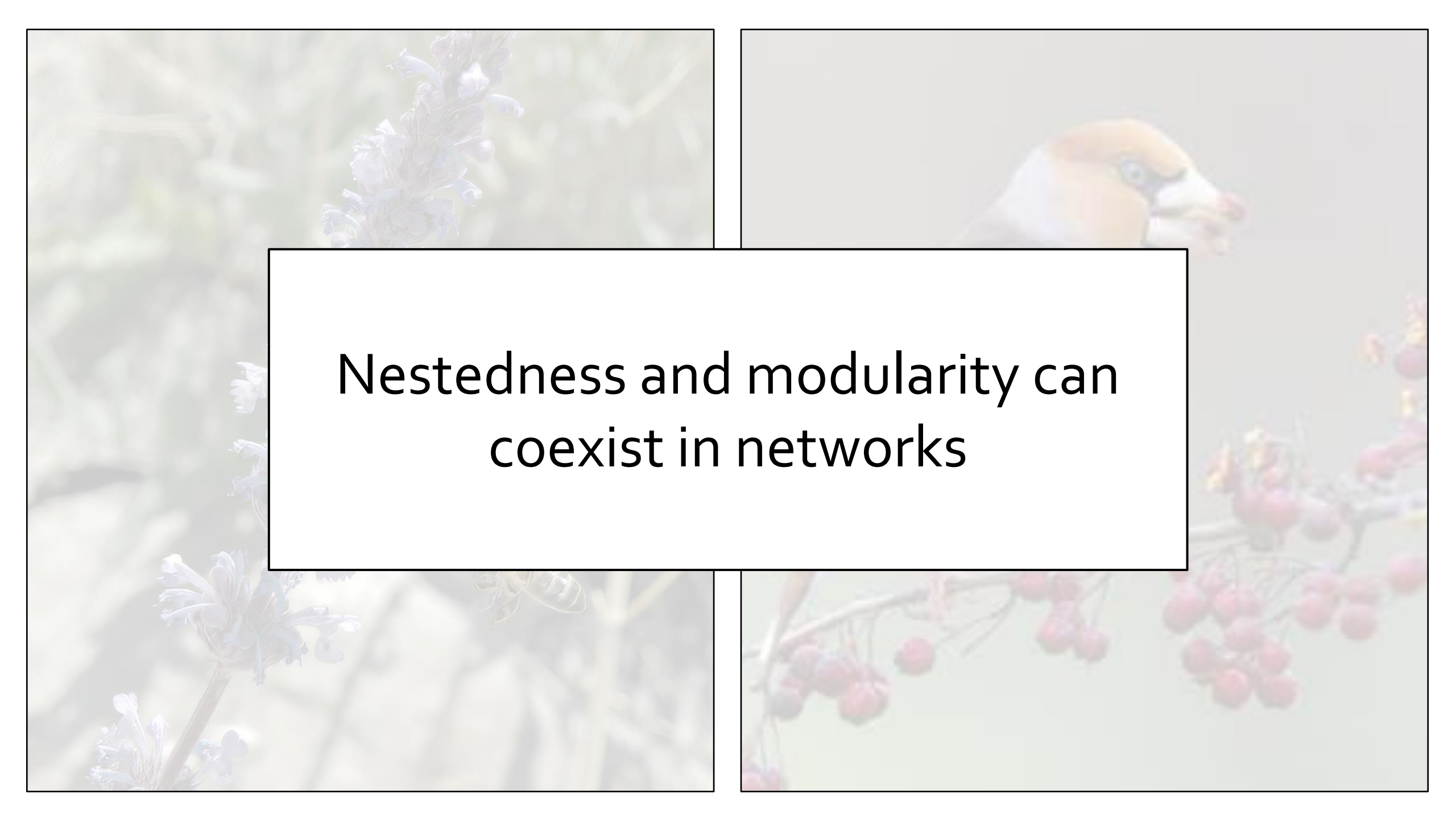
		1	2	3	4	5	6	Total																																	
		<i>Tomoplagia argentinensis</i>	<i>Tomoplagia pseudopenicillata</i>	<i>Tomoplagia fiebrigi</i>	<i>Tomoplagia reimoseri</i>	<i>Tomoplagia minuta</i>	<i>Tomoplagia grandis</i>	<i>Tomoplagia achromoptera</i>	<i>Tomoplagia brasiliensis</i>	<i>Dictyotrypa atacta</i>	<i>Tomoplagia cipoensis</i>	<i>Tomoplagia tripunctata</i>	<i>Tomoplagia incompleta</i>	<i>Xanthaciura biocellata</i>	<i>Dictyotrypa sp.1</i>	<i>Dictyotrypa sp.2</i>	<i>Tomoplagia sp.1</i>	<i>Tomoplagia dimorphica</i>	<i>Tomoplagia variabilis</i>	<i>Tetreaesta sp.1</i>	<i>Tomoplagia formosa</i>	<i>Tomoplagia punctata</i>	<i>Tetreaesta sp.2</i>	<i>Dictyotrypa sp.3</i>	<i>Tomoplagia bicolor</i>	<i>Tetreaesta sp.3</i>	<i>Trupanea sp.1</i>	<i>Acrotaeniini n.gen.1 sp.1</i>	<i>Tomoplagia interrupta</i>	<i>Tomoplagia acetii</i>	<i>Xanthaciura chrysuru</i>	<i>Tomoplagia voluta</i>	<i>Acrotaeniini n.gen.2 sp.1</i>	<i>Tomoplagia rupestris</i>	<i>Tomoplagia sp.2</i>	<i>Tetreaesta sp.4</i>	Total				
1	V	<i>Cyrtocymura scorpioides</i>	X	X																																				2	
	V	<i>Vernonanthura aff. lucida</i>		X	X																																			2	
	V	<i>Vernonanthura aff. laxa</i>			X																																			1	
	V	<i>Vernonanthura glanduloso-dentata</i>			X																																			1	
	V	<i>Vernonanthura membranacea</i>			X																																			1	
2	V	<i>Vernonanthura mucronulata</i>			X																																			1	
	V	<i>Vernonanthura phosphorica</i>			X																																			1	
	V	<i>Vernonanthura subverticillata</i>			X	X																																		2	
	V	<i>Vernonanthura westiniana</i>			X	X																																		1	
	V	<i>Vernonanthura mariana</i>			X	X																																		3	
	V	<i>Lessingianthus buddleifolius</i>				X																																		2	
	L	<i>Proteopsis sp.01</i>				X	X																																	2	
3	V	<i>Lessingianthus coriaceus</i>				X	X	X					X																												4
	V	<i>Lessingianthus roseus</i>				X	X	X					X																												4
	V	<i>Lessingianthus linearis</i>						X	X																																1
	V	<i>Lessingianthus vepretorum</i>					X	X	X			X	X	X																											6
	V	<i>Lessingianthus rosmarinifolius</i>					X																																		1
	V	<i>Lessingianthus linearifolius</i>					X	X																																	2
	V	<i>Lessingianthus carduoides</i>					X	X																																	2
	V	<i>Lessingianthus brevipetiolatus</i>					X	X																																	2
	V	<i>Lessingianthus pumillus</i>						X																																	1
	V	<i>Lessingianthus glabratus</i>						X																																	1
	V	<i>Lessingianthus simplex</i>						X																																	1
	V	<i>Lessingianthus aff. simplex</i>						X																																	1
	L	<i>Eremanthus sp.03</i>						X																																1	
	H	<i>Chresta sp.01</i>						X																																1	
	V	<i>Lessingianthus tomentellus</i>					X																																		2
	H	<i>Chresta sphaerocephala</i>						X																																	4
	V	<i>Lessingianthus sp.01</i>																																							1
	L	<i>Eremanthus erythropappus</i>																																							1
	V	<i>Lessingianthus psilophyllus</i>						X	X	X																															4
4	V	<i>Lessingianthus warmingianus</i>						X	X	X																															3
	V	<i>Lepidaploa spixiana</i>						X	X	X																															3
	V	<i>Echinocoryne schwenkiaefolia</i>						X	X	X																															3
	V	<i>Lessingianthus rubricaulis</i>						X																																	2
	V	<i>Lepidaploa lilacina</i>						X																																	2
	V	<i>Lepidaploa aff. rufogrisea</i>						X																																	2
	V	<i>Lessingianthus virgulatus</i>							X																																2
	V	<i>Echinocoryne holosericea</i>								X																															2
	V	<i>Stilpnopappus bicolor</i>														X																								1	
	V	<i>Lessingianthus hoveaeifolius</i>						X	X										X	X																				4	
	V	<i>Lepidaploa rufogrisea</i>						X											X																					3	
	V	<i>Chrysolaena herbacea</i>						X																																	3
	C	<i>Centratherum punctatum</i>																																						2	
	V	<i>Vernonanthura ferruginea</i>																																						1	
	V	<i>Lepidaploa sp.01</i>																																						1	
	V	<i>Lepidaploa salzmannii</i>																																						1	
	V	<i>Lepidaploa aurea</i>																																						1	



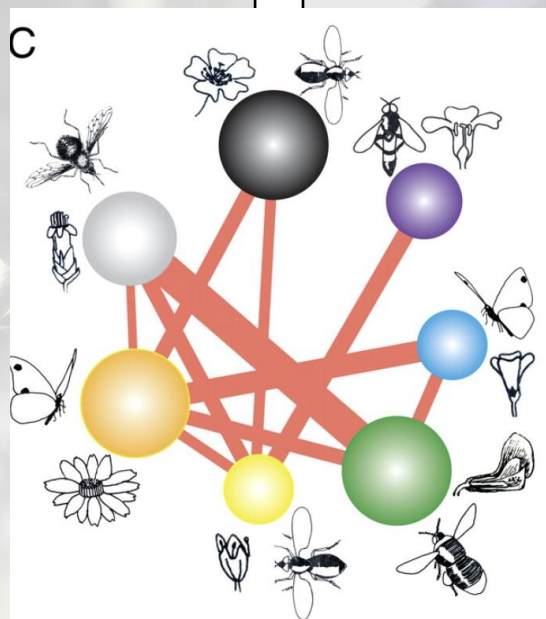
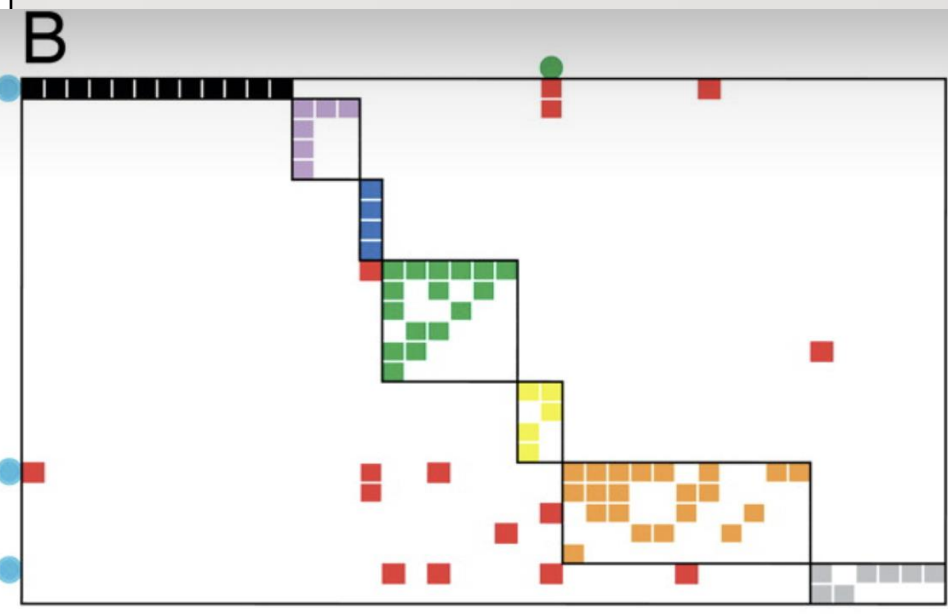


(Guimerà & Amaral 2005)

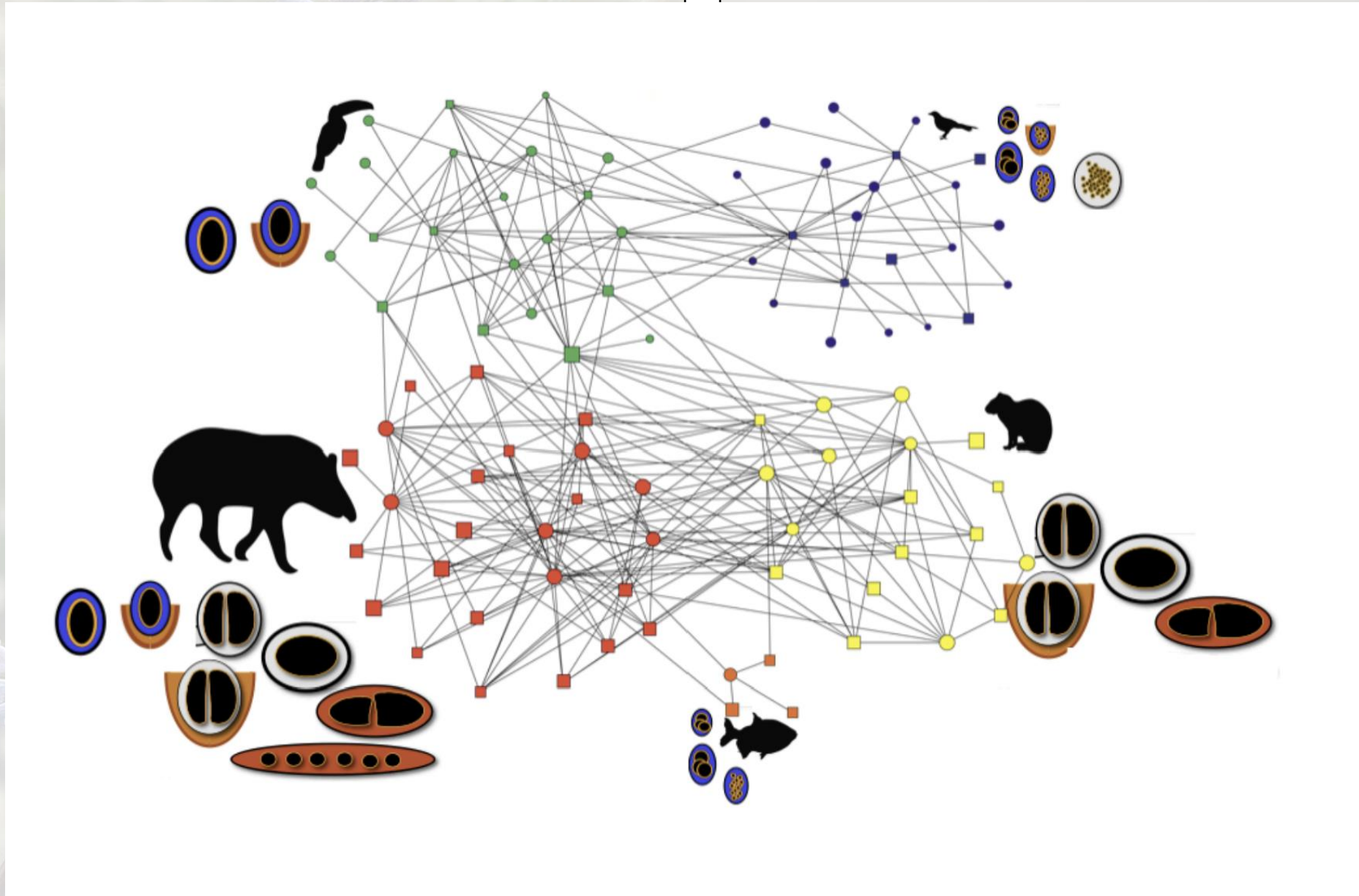


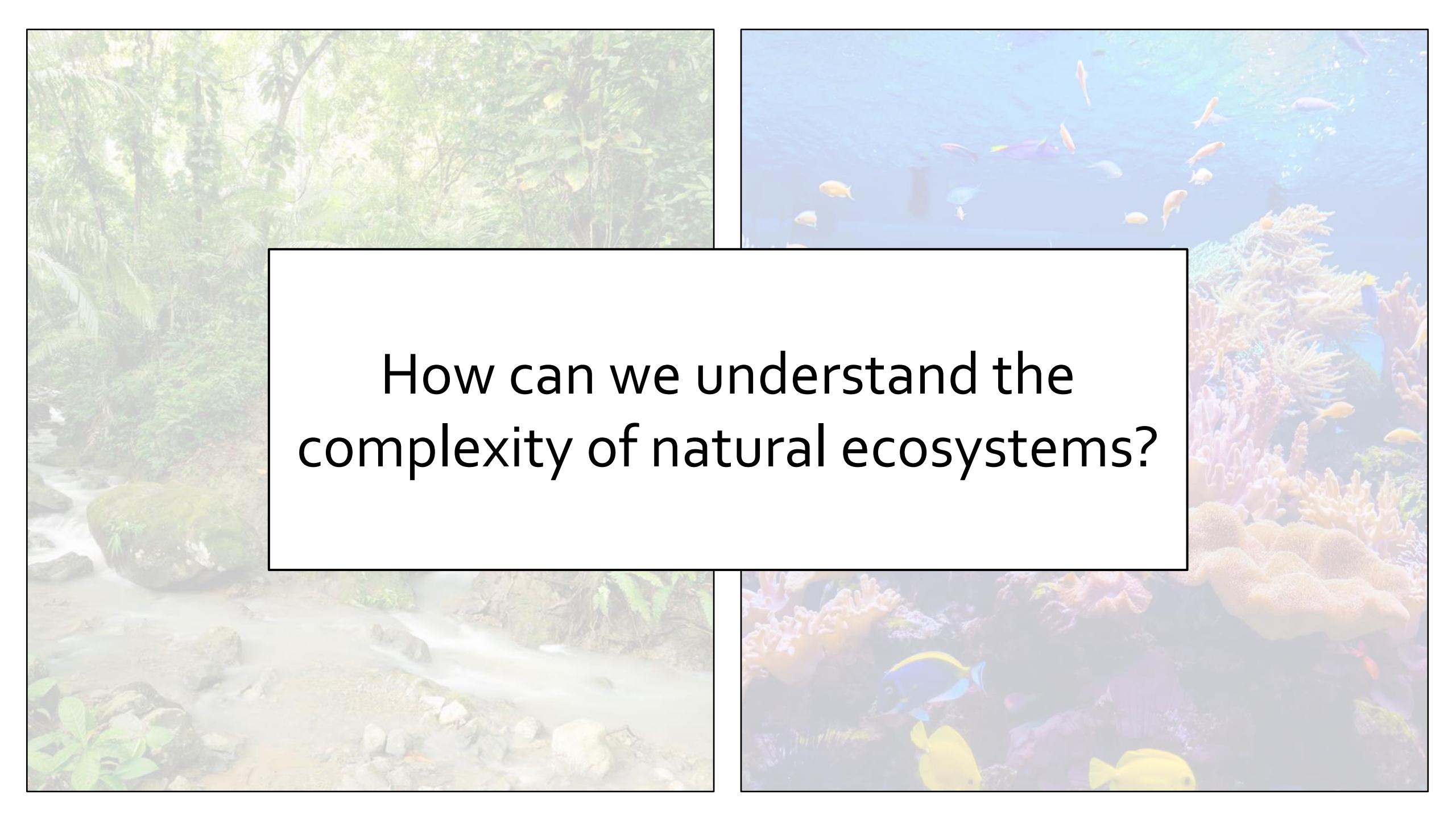


Nestedness and modularity can
coexist in networks



(Olesen et al. 2007)

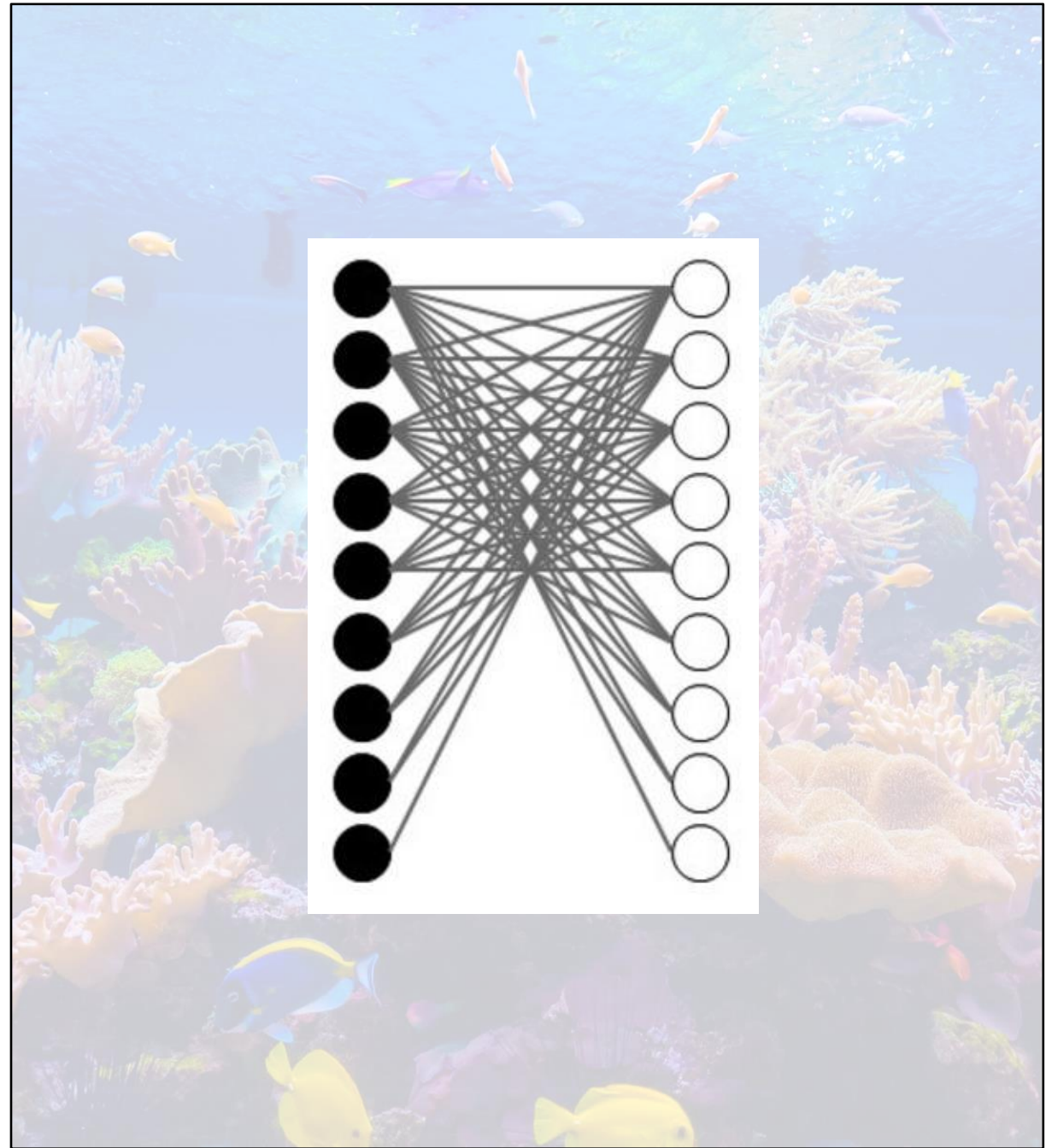
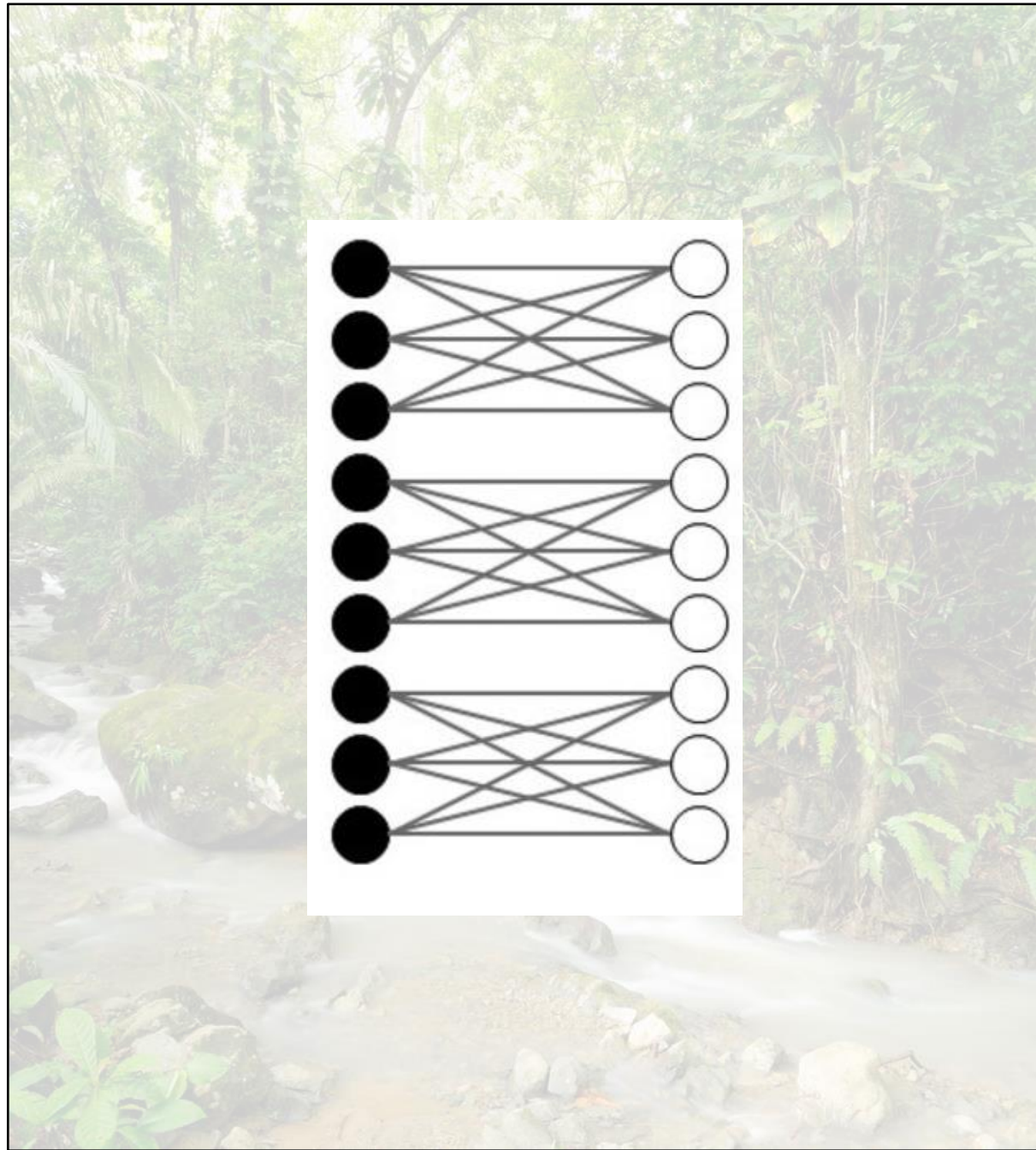


The image is a collage of four nature scenes. The top-left scene shows a lush green forest with a stream flowing over rocks. The top-right scene is an underwater view of a coral reef with many colorful fish. The bottom-left scene shows a stream flowing over rocks in a forest. The bottom-right scene is another underwater view of a coral reef with colorful fish. In the center, there is a white rectangular box with a black border containing the text "How can we understand the complexity of natural ecosystems?".

How can we understand the complexity of natural ecosystems?



Are all networks the same?






Quantifying topological patterns:



Nestedness:

Low interaction intimacy,
hierarchical organization of
interactions

Modularity

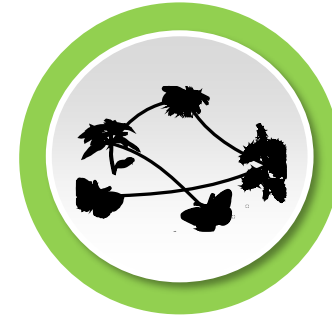
High interaction intimacy, tightly
connected, functional groups/units





How can understand the mechanisms underlying nestedness and modularity in networks?

What are the consequences of these patterns for the ecology and evolution of species?



Topological patterns in ecological networks

BIO365 – Ecological Networks

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