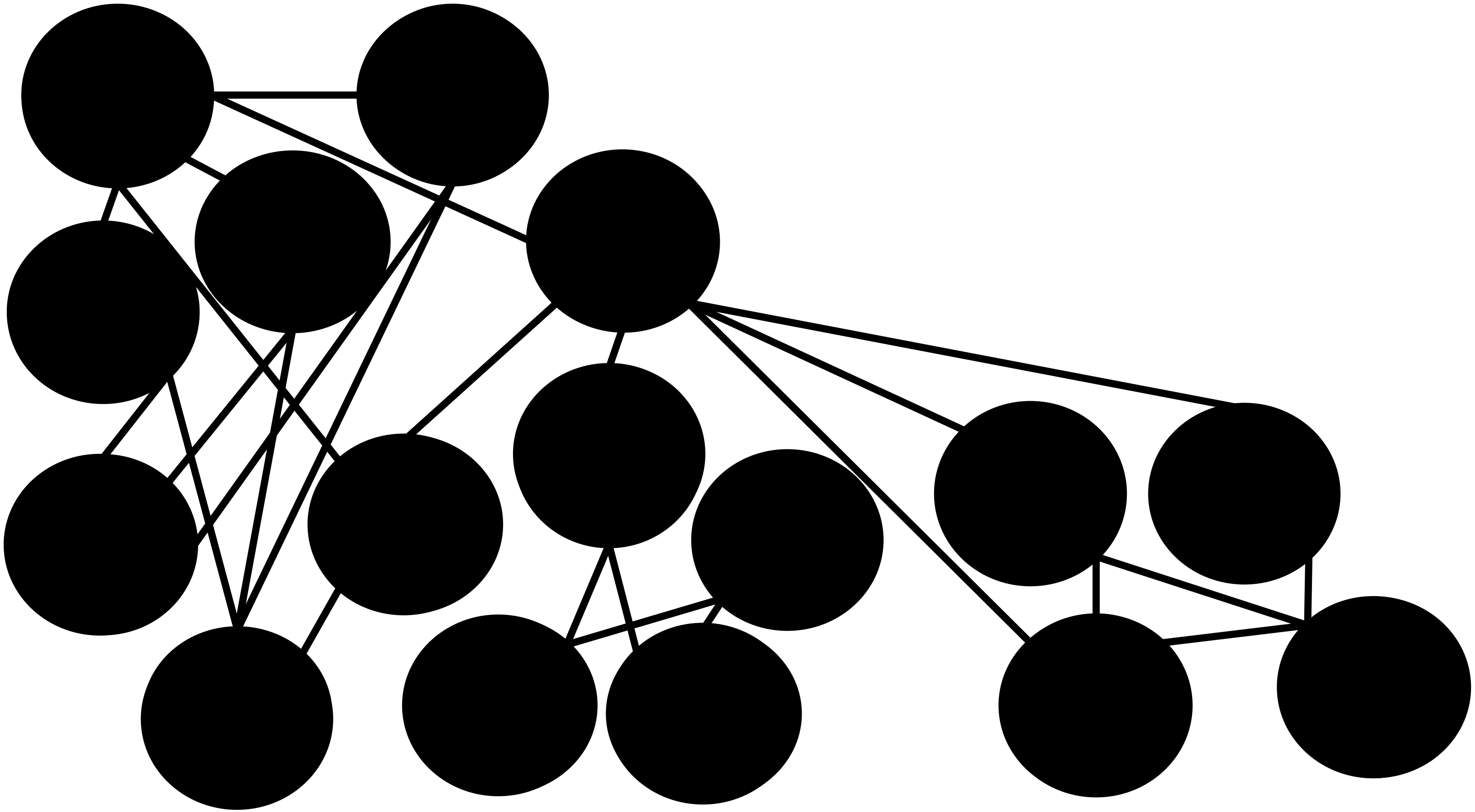
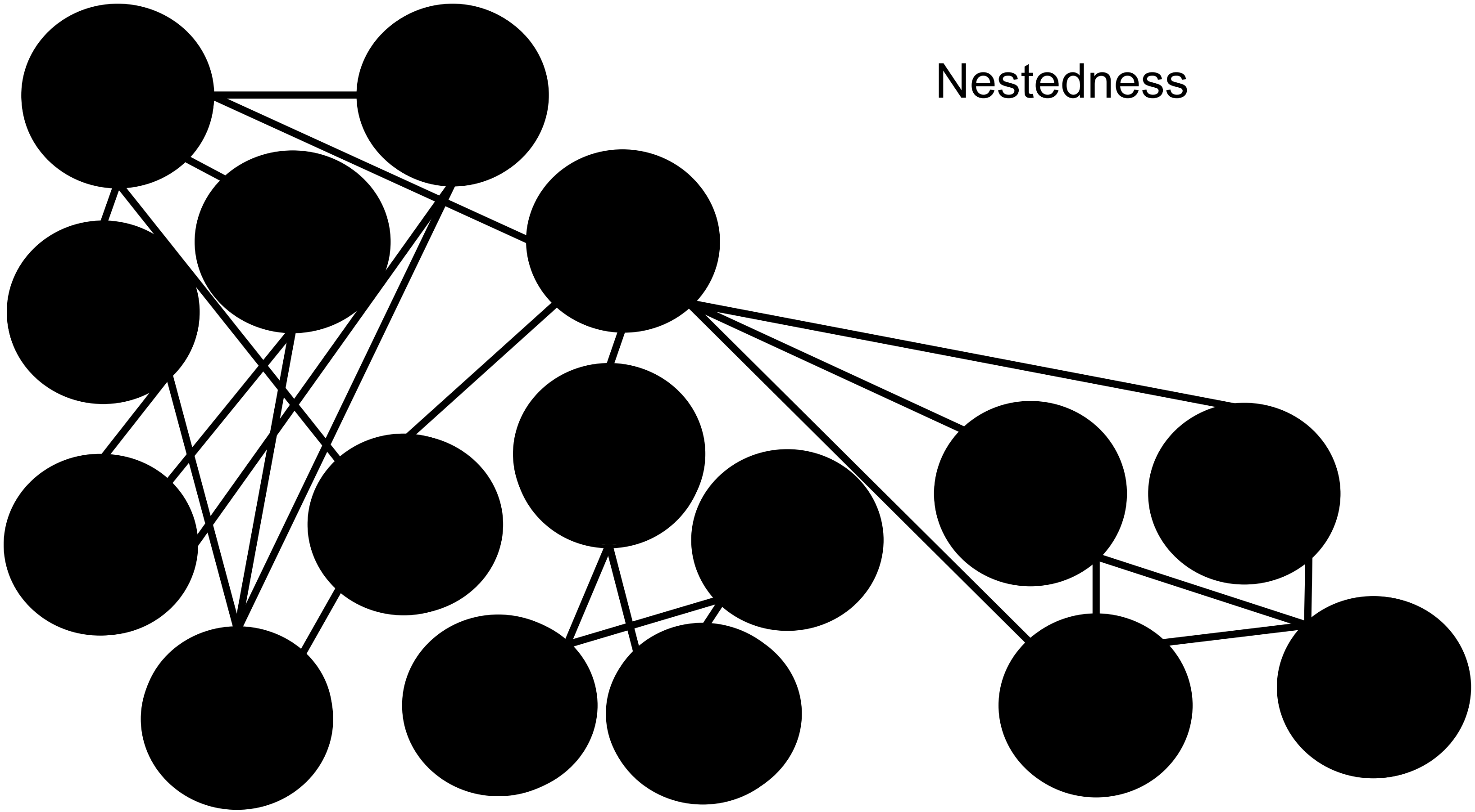
How are ecological networks made?


How are ecological networks made?
or, how does behavior shape network structure?

Networks are made of pairwise interactions

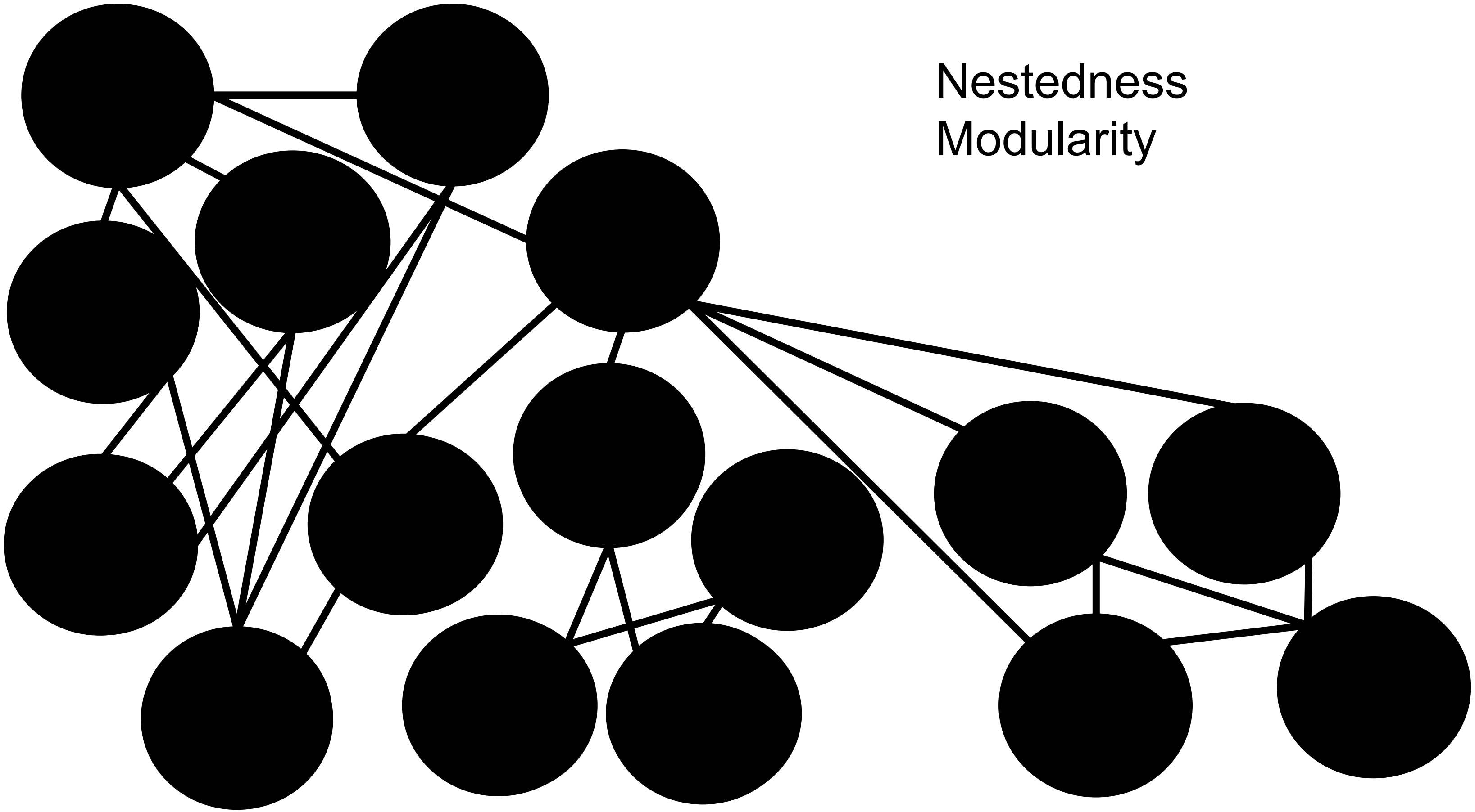


Networks are made of pairwise interactions



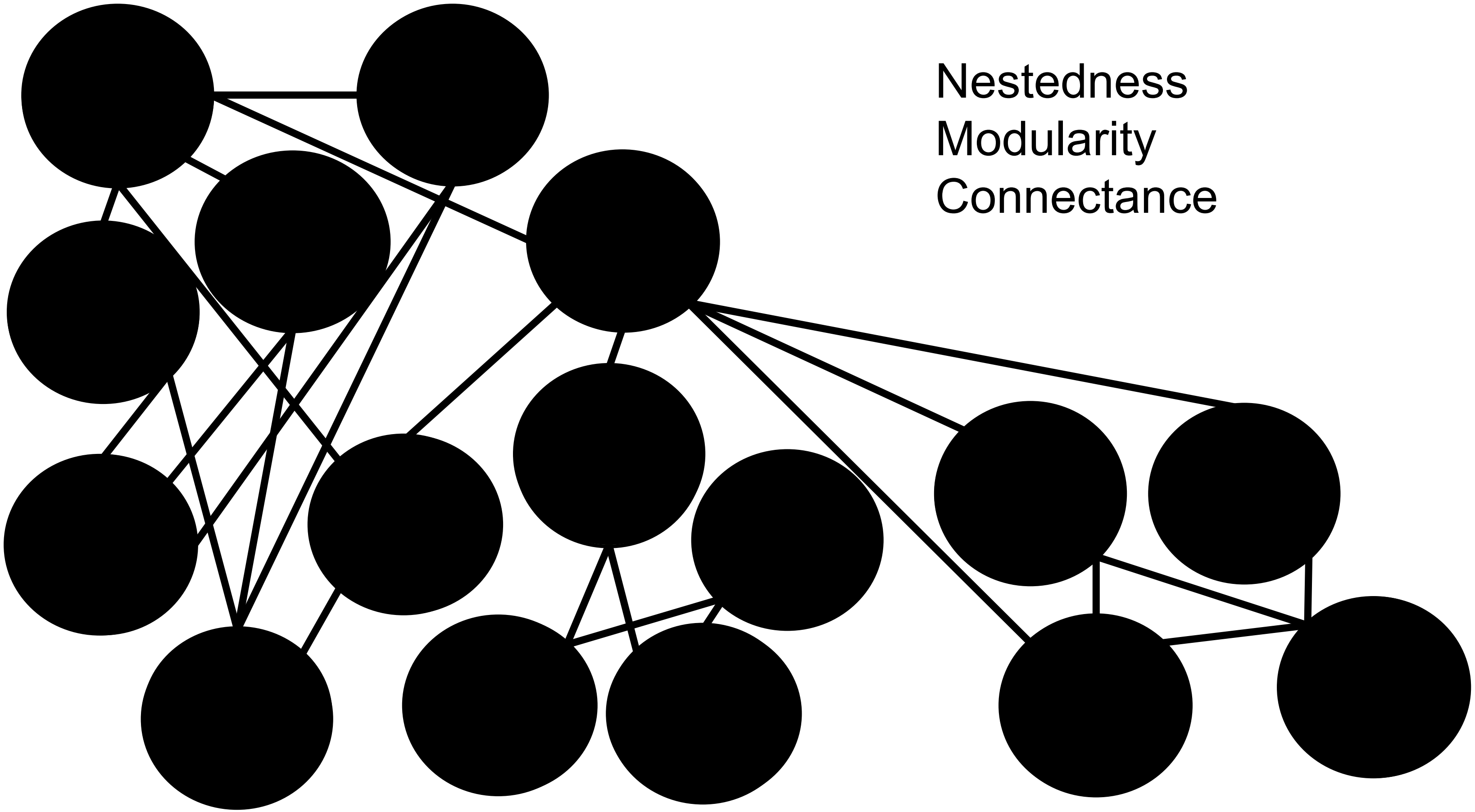
Nestedness

Networks are made of pairwise interactions



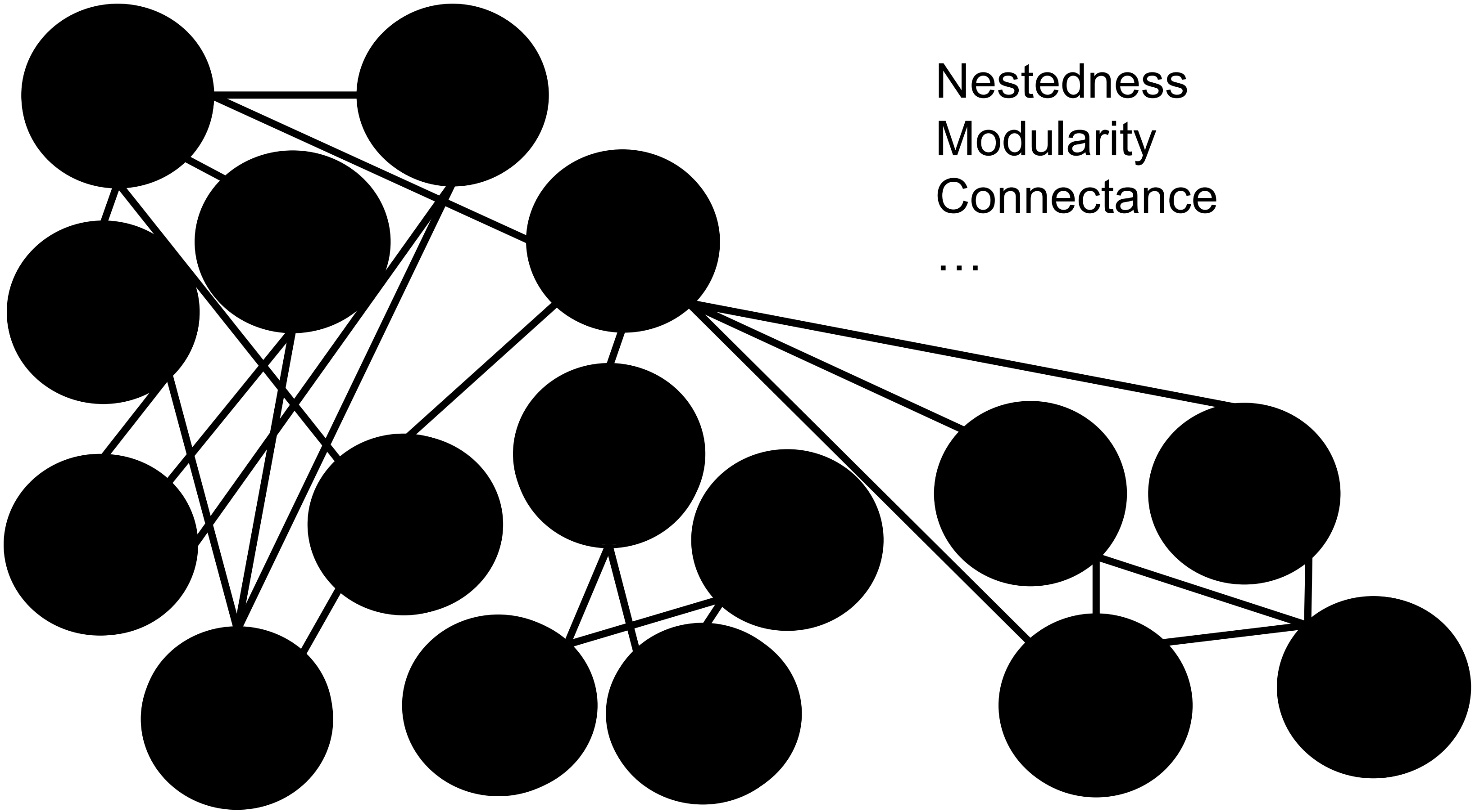
Nestedness
Modularity

Networks are made of pairwise interactions



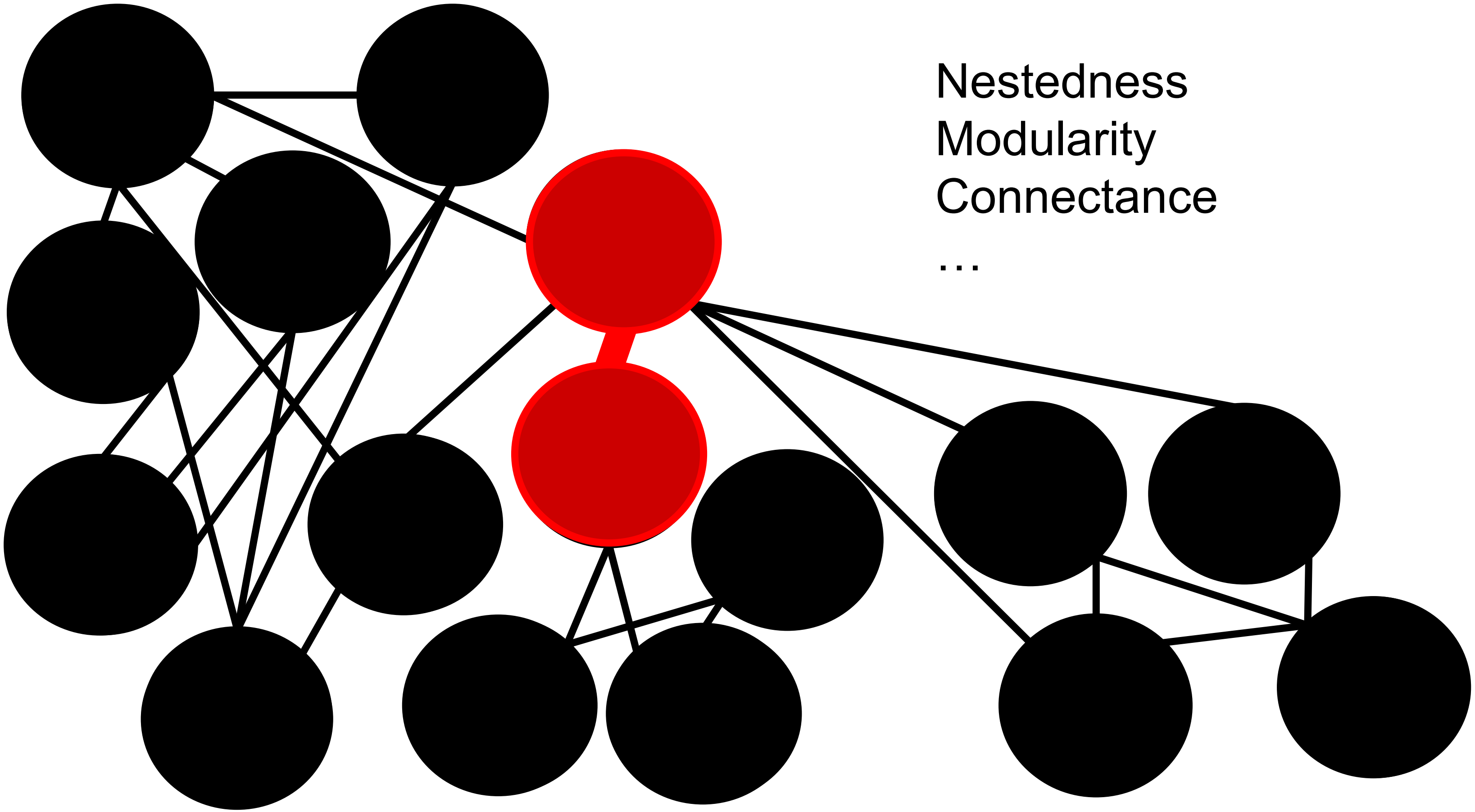
Nestedness
Modularity
Connectance

Networks are made of pairwise interactions



Nestedness
Modularity
Connectance
…

Networks are made of pairwise interactions



Nestedness
Modularity
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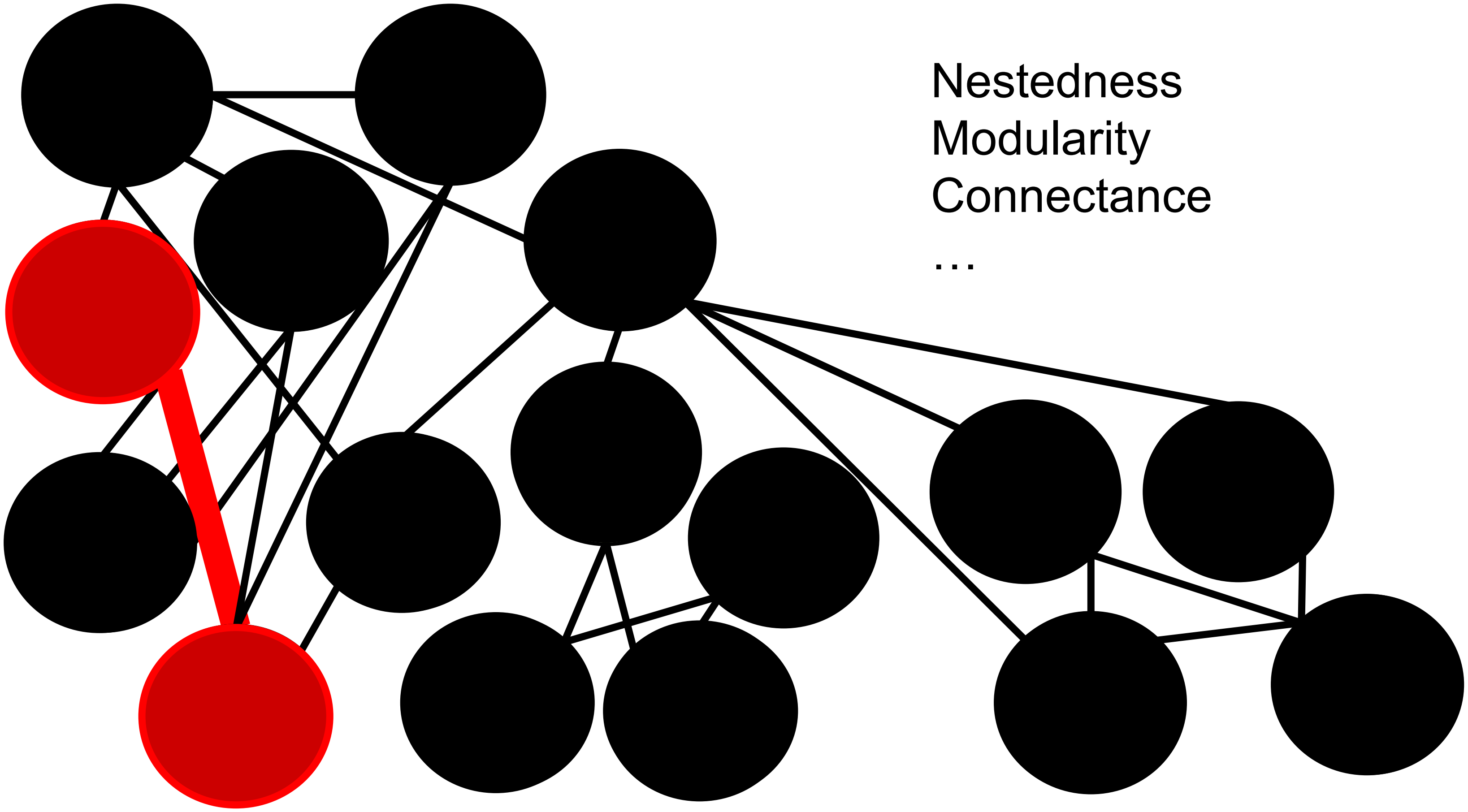
Networks are made of pairwise interactions



Nestedness
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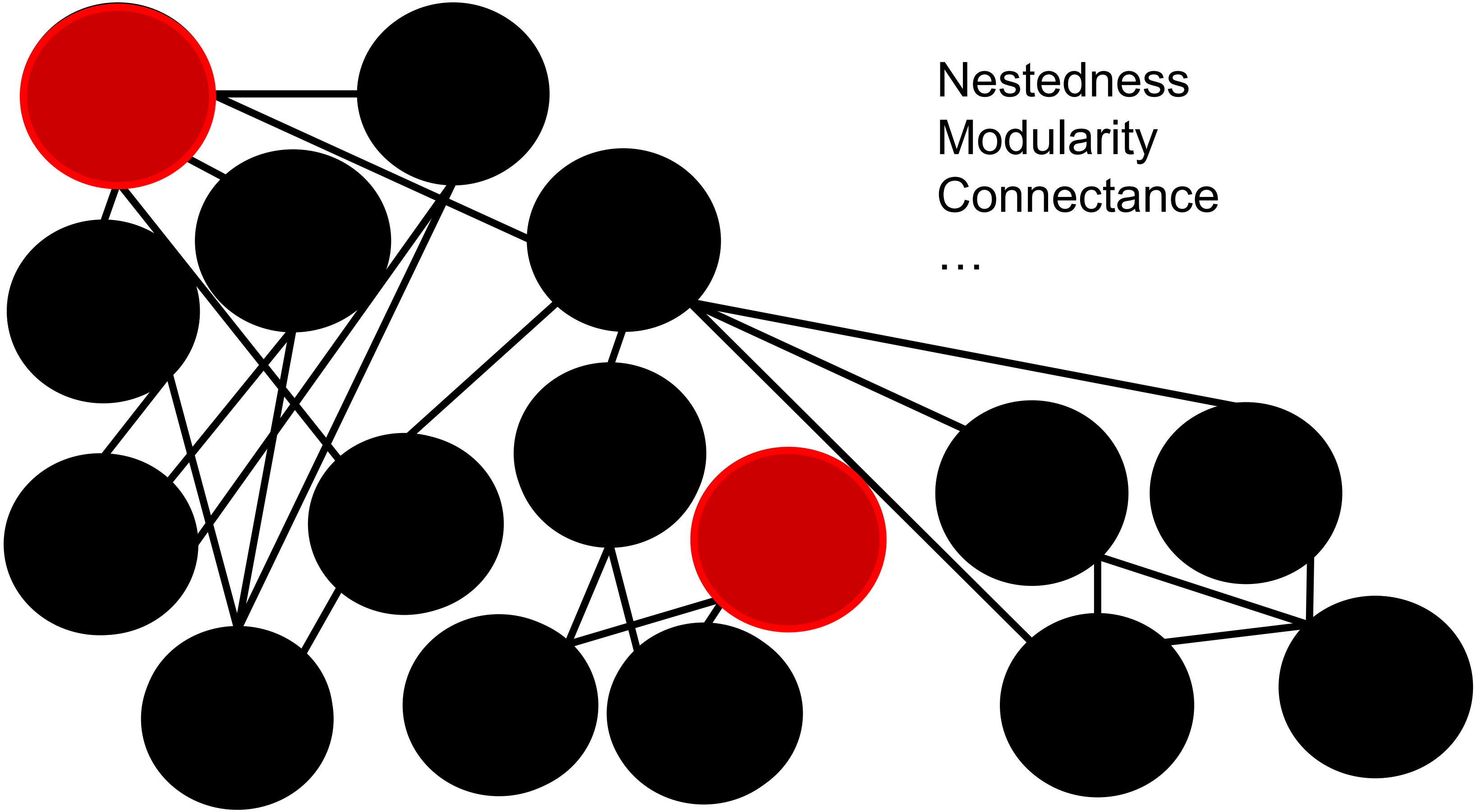

Nestedness
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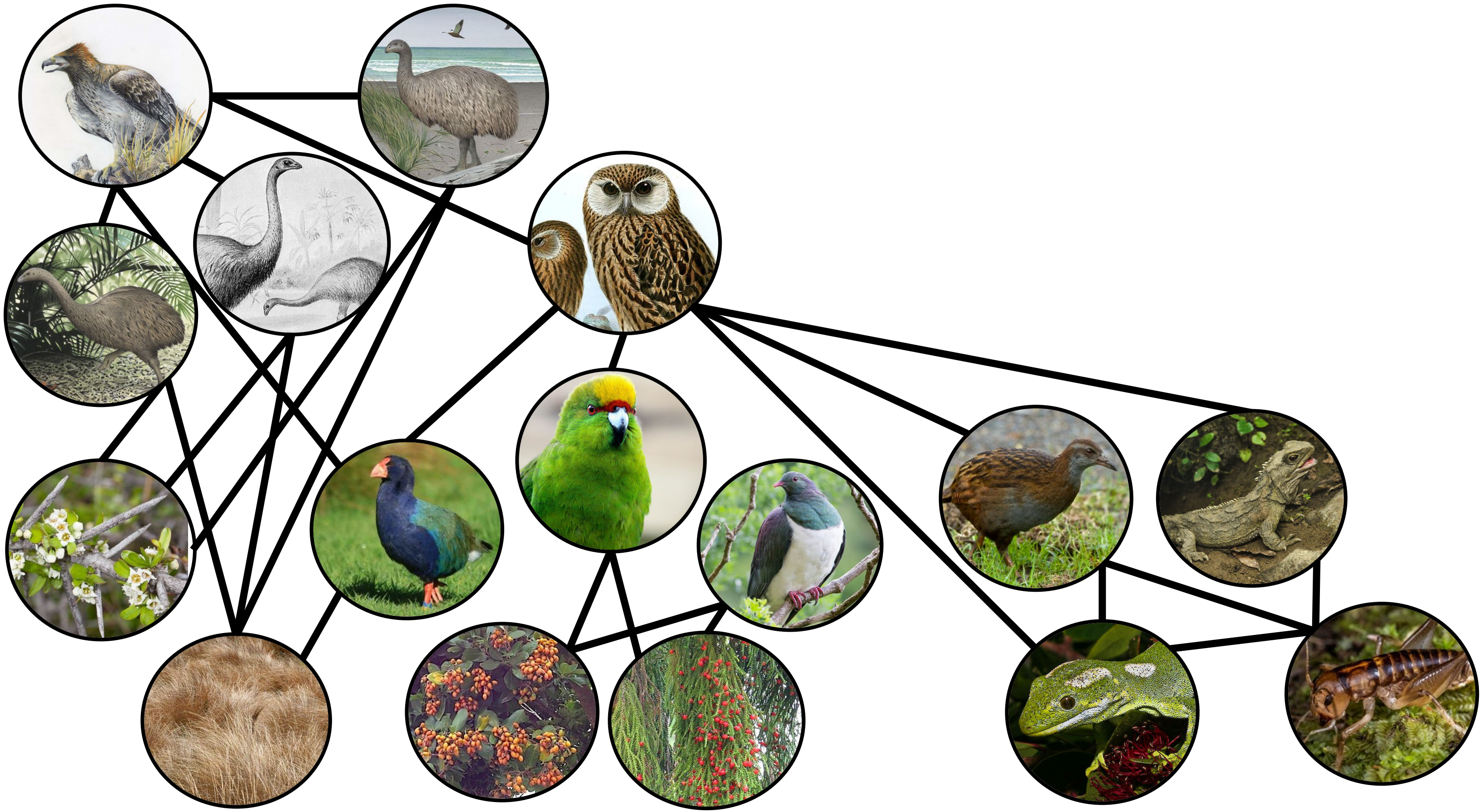
Networks are made of pairwise interactions



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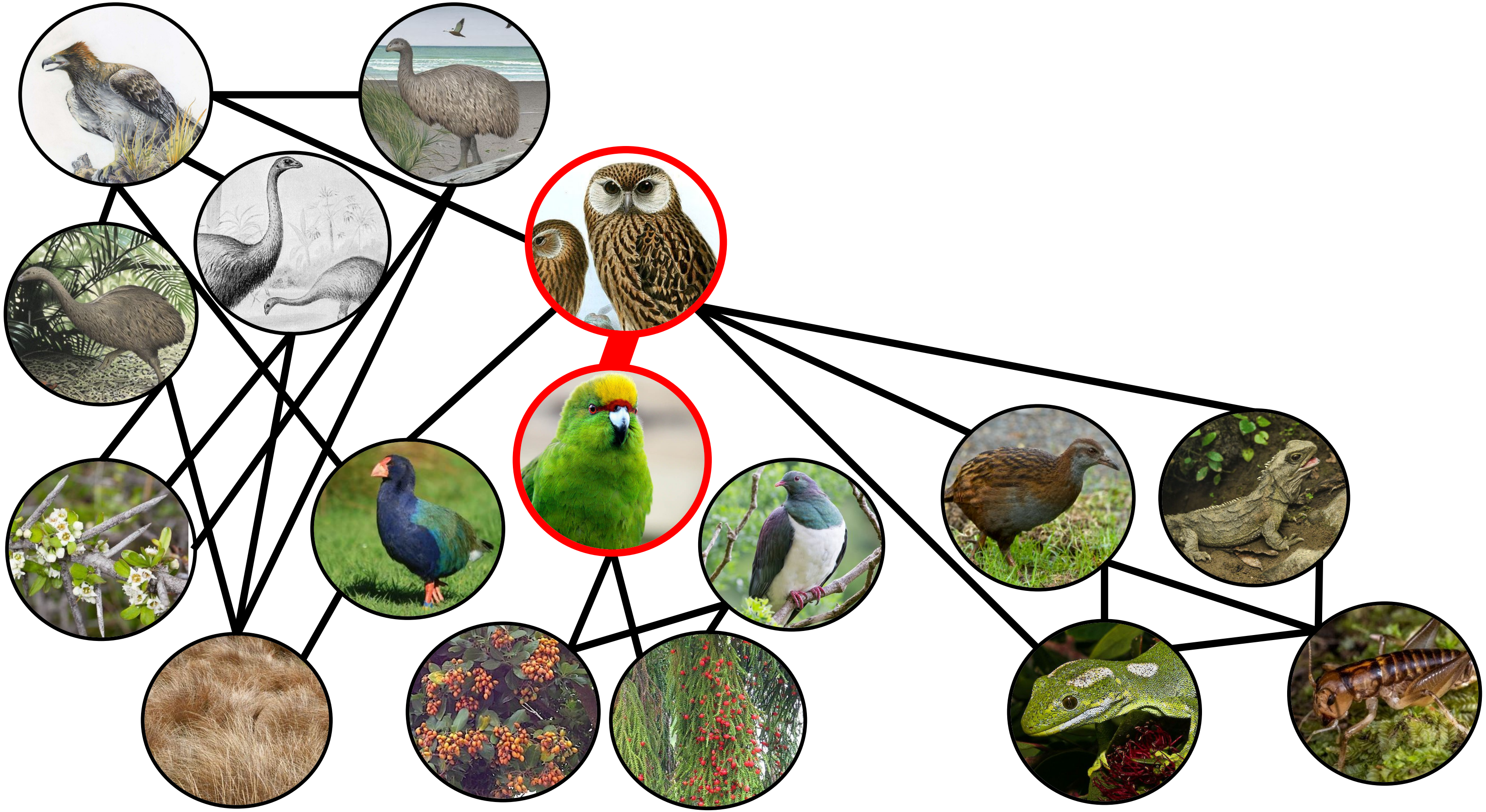

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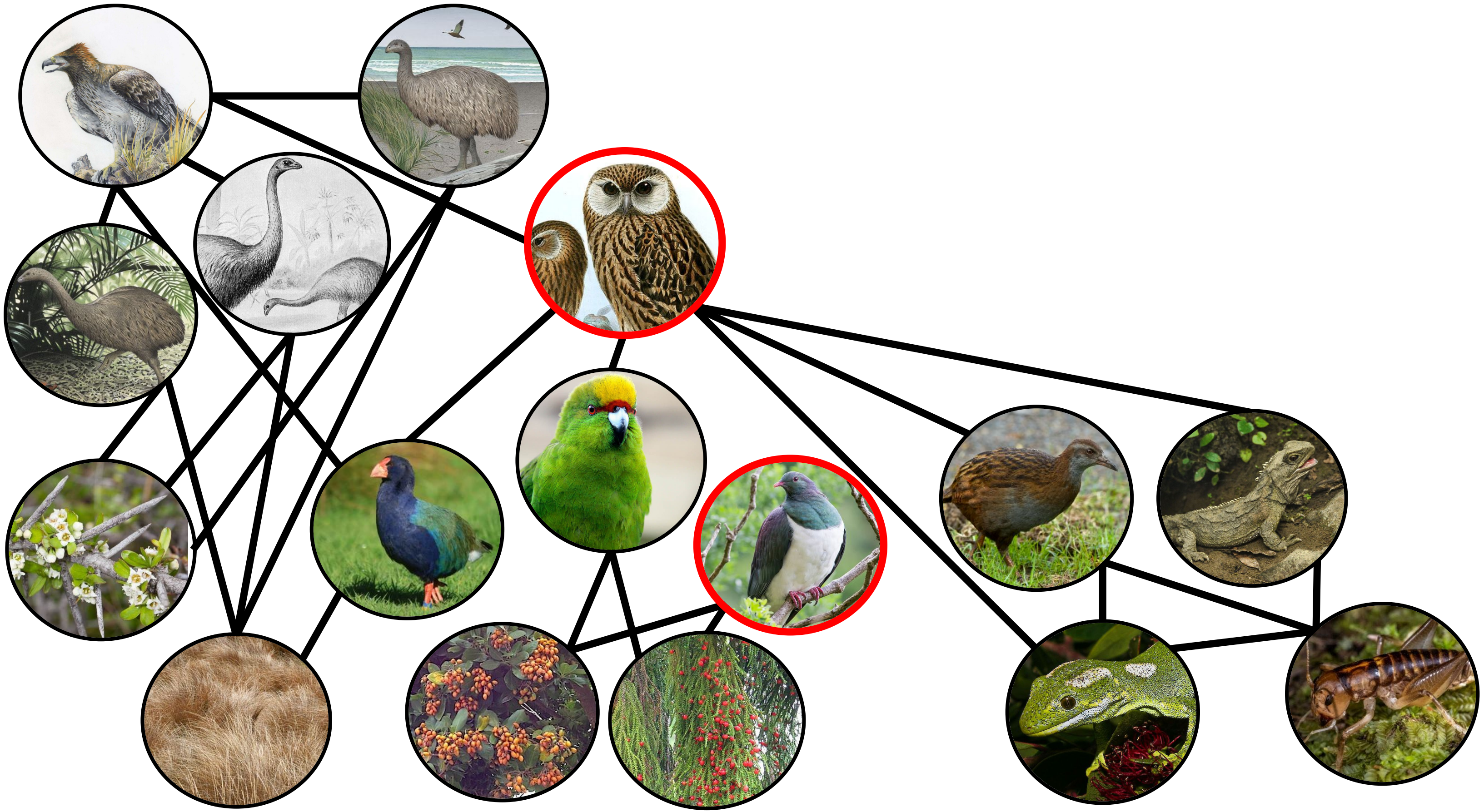

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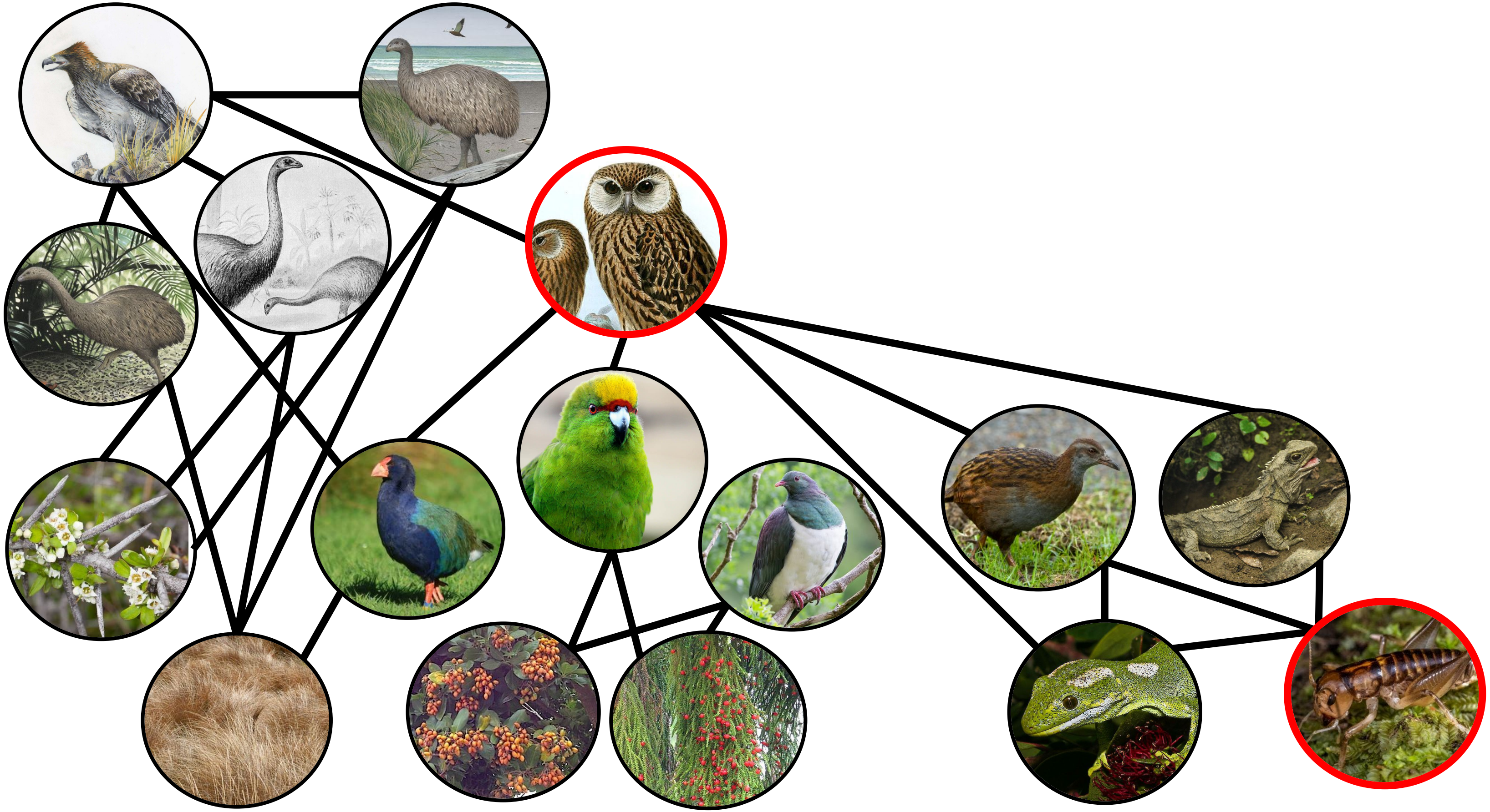


How do animals choose who to interact with?

How do animals choose who to interact with?

Answering this question:

- allows us to explain the interactions in empirical networks

- and make predictions about how networks should be structured in certain ecosystems and with certain species

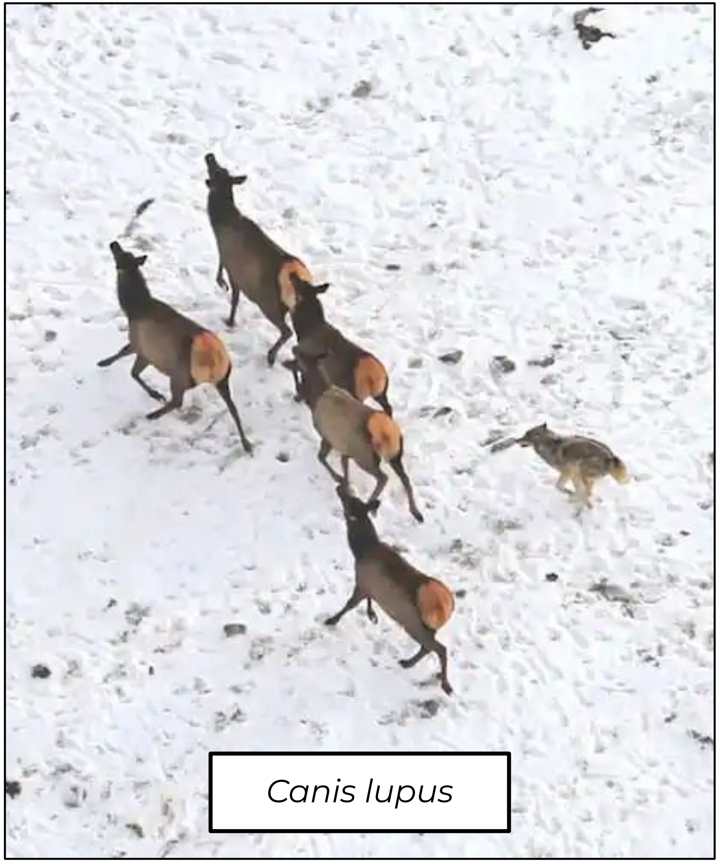
How do animals choose who to interact with?

Hippopotamus amphibius

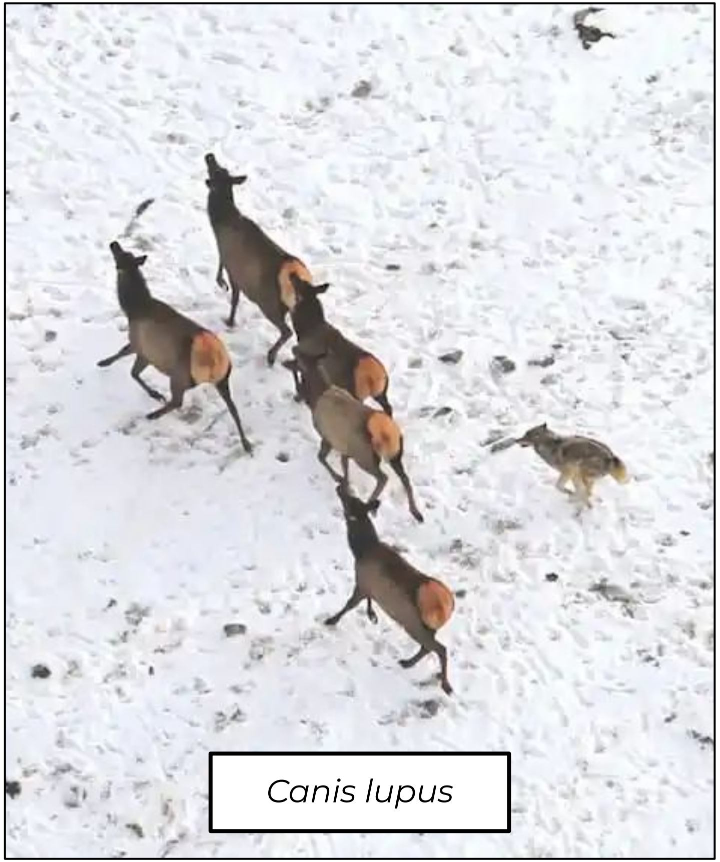
How do animals choose who to interact with?

Dudley et al. 2015 *Mammal Review*

How do animals choose who to interact with?



How do animals choose who to interact with?



Barton et al. 2018 *Ecology*

How do animals choose who to interact with?

Galeocerdo cuvier

How do animals choose who to interact with?

Drymon et al. 2019 *Ecology*

How do animals choose who to interact with?

How do animals choose who to interact with?

How do animals choose who to interact with?

Outline for today

Outline for today

How can behavior predict species interactions?
- (optimal) foraging theory
- functional responses

Outline for today

How can behavior predict species interactions?
- (optimal) foraging theory
- functional responses

How can ecological networks be predicted?
- body size and food-webs

Optimal foraging theory

What is it?

Optimal foraging theory

Optimal foraging theory

Vol. 100, No. 916 The American Naturalist November–December, 1966

THE ROLE OF TIME AND ENERGY IN FOOD PREFERENCE

J. MERRITT EMLEN*

Department of Zoology, University of Washington, Seattle

Vol. 100, No. 916 The American Naturalist November–December, 1966

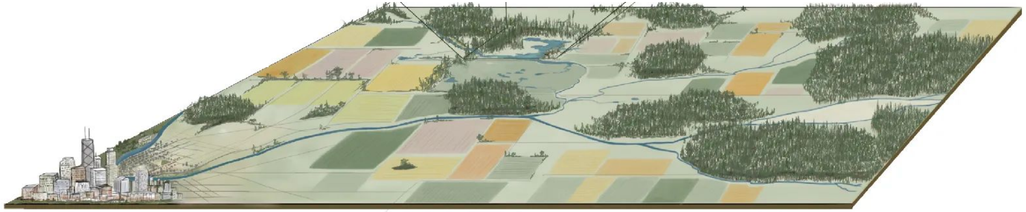
ON OPTIMAL USE OF A PATCHY ENVIRONMENT

ROBERT H. MACARTHUR AND ERIC R. PIANKA

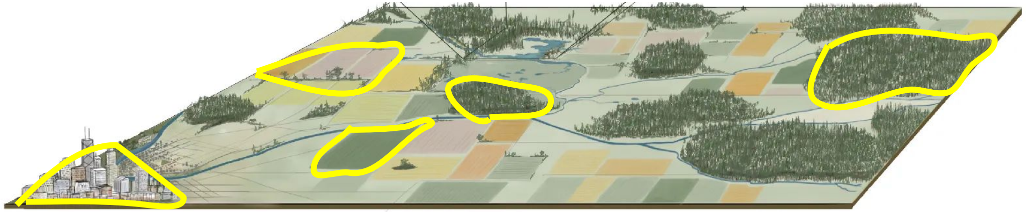
Department of Biology, Princeton University, Princeton, New Jersey

Optimal foraging theory

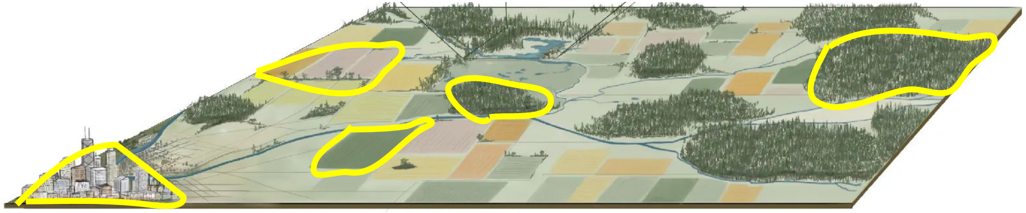
Optimal foraging theory



Optimal foraging theory



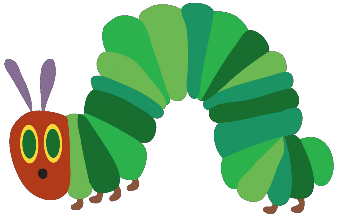
Optimal foraging theory



If habitat patches provide different amounts of food, **how many patches** should a predator use **to maximise** its **energy gain per time hunting**?

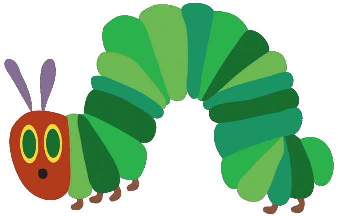
Optimal foraging theory



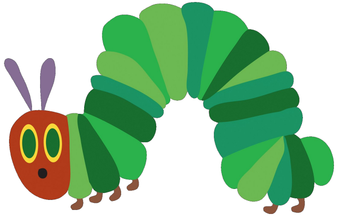



Optimal foraging theory

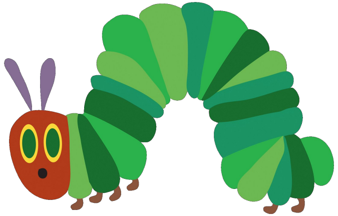
If prey species provide different amounts of calories, **how many species** should a predator eat **to maximise** its **energy gain per time hunting**?



Optimal foraging theory

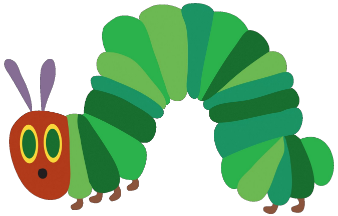


Optimal foraging theory



1. Encounter rate: how often can each prey species be found?

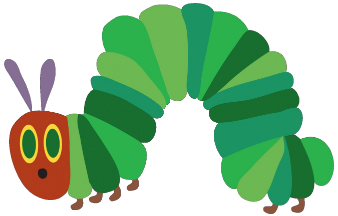
Optimal foraging theory



1. Encounter rate: how often can each prey species be found?

2. Net energy gain: how much energy does the predator get by capturing and eating each prey species?

Optimal foraging theory

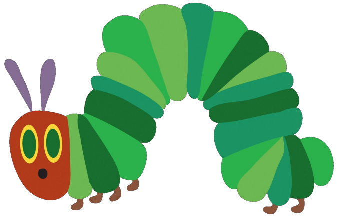


1. Encounter rate: how often can each prey species be found?

2. Net energy gain: how much energy does the predator get by capturing and eating each prey species?

3. Handling time: how long does it take for the predator to eat each prey species?

Optimal foraging theory



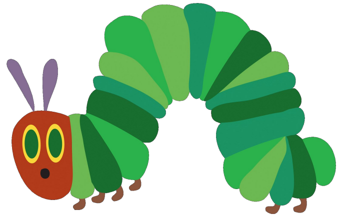
1. Encounter rate: how often can each prey species be found?

2. Net energy gain: how much energy does the predator get by capturing and eating each prey species?

3. Handling time: how long does it take for the predator to eat each prey species?

4. Attack rate: if the predator finds potential prey species, what is the chance it attacks them?

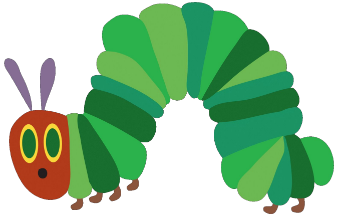
Optimal foraging theory



$$ET = \frac{\sum_{i-n} ER_i * NE_i * AR_i}{1 - \sum_{i-n} ER_i * HT_i * AR_i} - ES$$

Charnov 1973 *Uni. of Washington*; Schoener 1987 in *Foraging Behavior*

Optimal foraging theory



encounter rate

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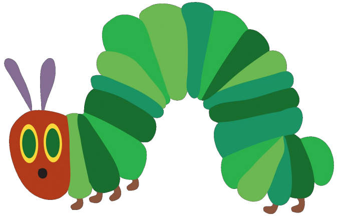

encounter rate

net energy gain

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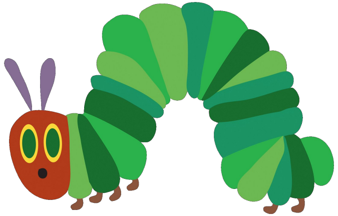

net energy gain

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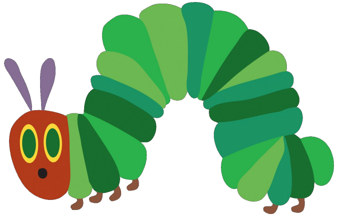
attack rate

Charnov 1973 *Uni. of Washington*; Schoener 1987 in *Foraging Behavior*

Optimal foraging theory



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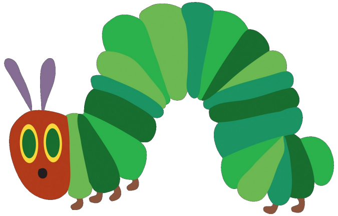
encounter rate

net energy gain

handling time

attack rate

Optimal foraging theory



$$ET = \frac{\sum_{i-n} ER_i * NE_i * AR_i}{1 - \sum_{i-n} ER_i * HT_i * AR_i} - ES$$

encounter rate

net energy gain

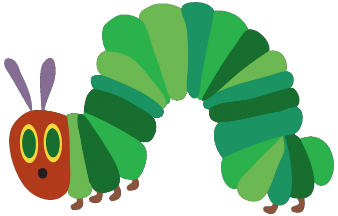
energy spent hunting

handling time

attack rate

Charnov 1973 *Uni. of Washington*; Schoener 1987 in *Foraging Behavior*

Optimal foraging theory



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encounter rate

net energy gain

energy spent hunting

total energy gain

handling time

attack rate

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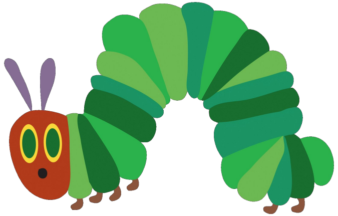
Optimal foraging theory



$$ET = \frac{\sum_{i-n} ER_i \cdot NE_i \cdot AR_i}{1 - \sum_{i-n} ER_i \cdot HT_i \cdot AR_i} - ES$$

encounter rate

net energy gain

energy spent hunting

handling time

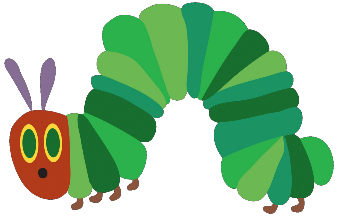
attack rate

total energy gain

the optimal diet is the set of prey that maximize total energy gain (per time spent foraging)

Charnov 1973 *Uni. of Washington*; Schoener 1987 in *Foraging Behavior*

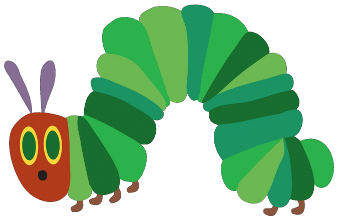
Optimal foraging theory



What are the features of an optimal diet?

MacArthur & Pianka 1966; Emlen 1966, *American Naturalist*

Optimal foraging theory

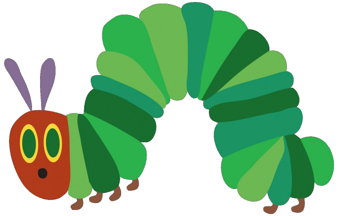


What are the features of an optimal diet?

An optimal diet becomes more specialized when:

MacArthur & Pianka 1966; Emlen 1966, *American Naturalist*

Optimal foraging theory



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An optimal diet becomes more specialized when:

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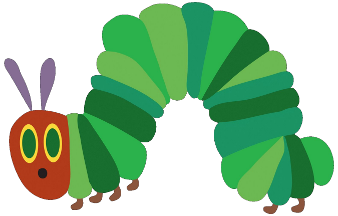
Optimal foraging theory



What are the features of an optimal diet?

An optimal diet becomes more specialized when:

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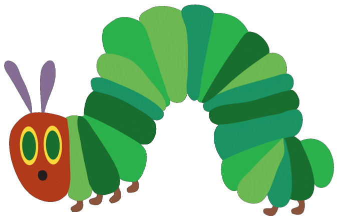
MacArthur & Pianka 1966; Emlen 1966, *American Naturalist*

Optimal foraging theory



What are the features of an optimal diet?

An optimal diet becomes more specialized when:

- food density increases

- the predator can move more easily

- prey "value" becomes more different

MacArthur & Pianka 1966; Emlen 1966, *American Naturalist*

Does it work?

Optimal foraging theory

Does it work?

Belovsky 1984 *American Naturalist*

Krebs et al. 1977 *Animal Behavior*

Werner & Hall 1974 *Ecology*

Does it work?

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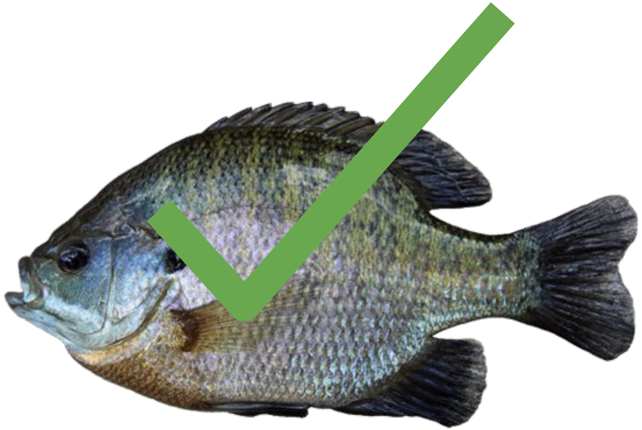

Werner & Hall 1974 *Ecology*

Optimal foraging theory

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Only considered broad groups of plants

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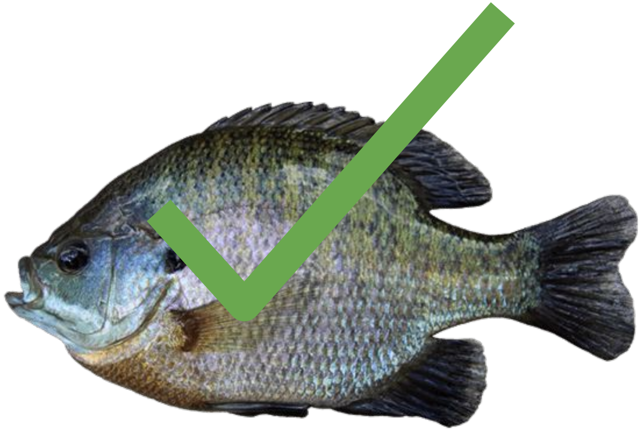

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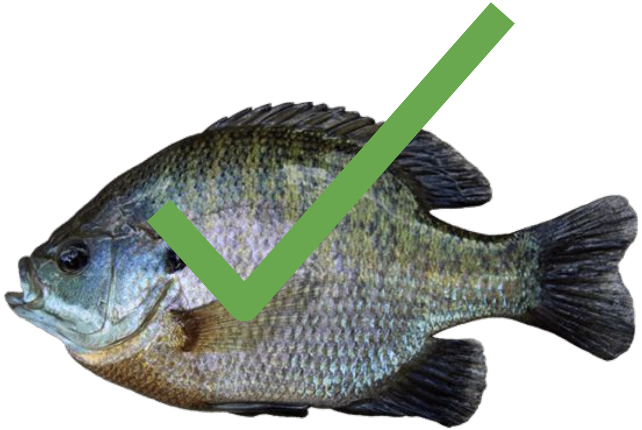
Tested between one good and one bad prey



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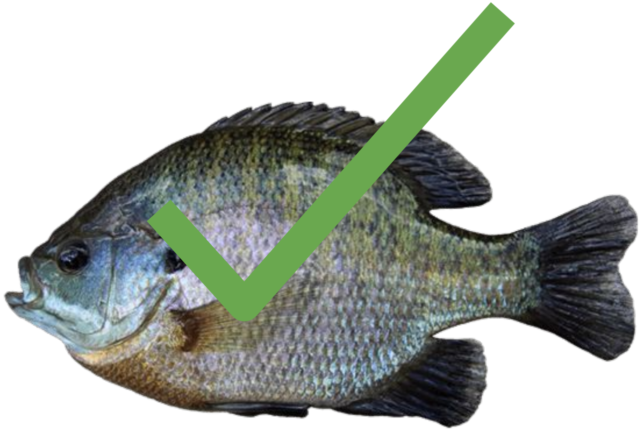


Werner & Hall 1974 *Ecology*

Used one prey at different growth stages

Elaborations

Elaborations

- changing the "currency": minimizing time, minimizing toxin ingestion, other nutrients, digestion

Optimal foraging theory

Elaborations

- changing the "currency": minimizing time, minimizing toxin ingestion, other nutrients, digestion

- allowing animals to "sample" their environment and learn

Elaborations

- changing the "currency": minimizing time, minimizing toxin ingestion, other nutrients, digestion

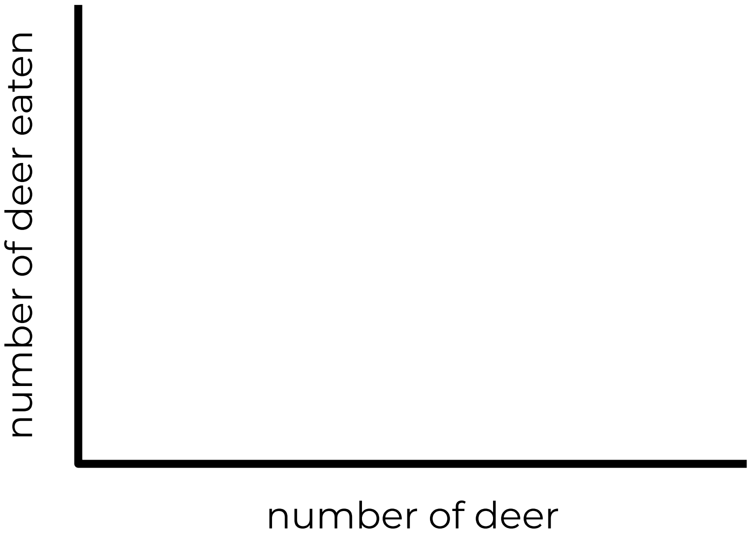
- allowing animals to "sample" their environment and learn

- accounting for the risk of being eaten

Functional responses

Not what to eat, but how much to eat.

If the number of deer increases, do wolves eat more of them?



Functional responses

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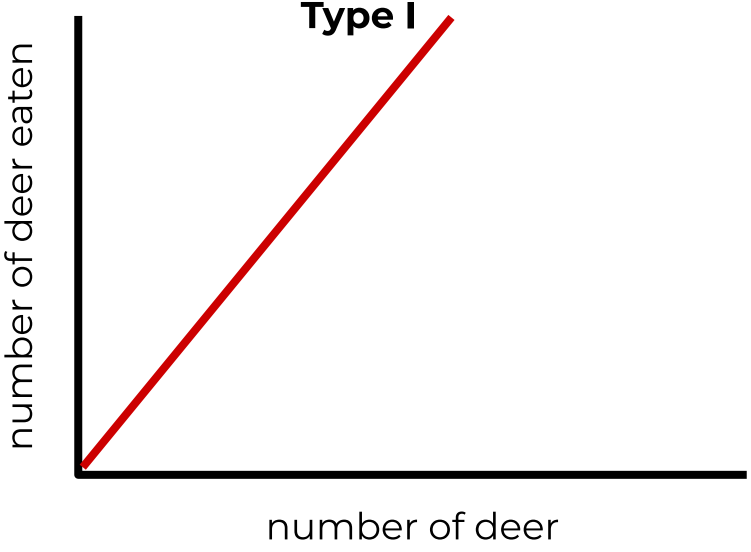

Holling 1959 *Canadian Entomologist*

Functional responses

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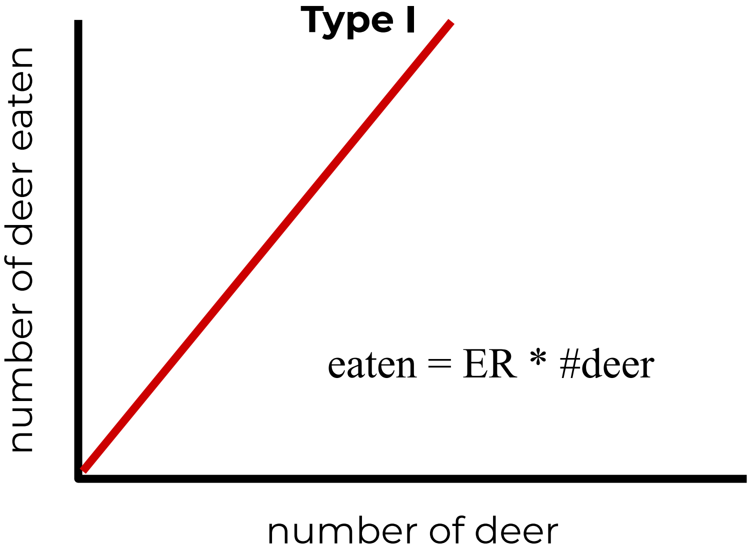

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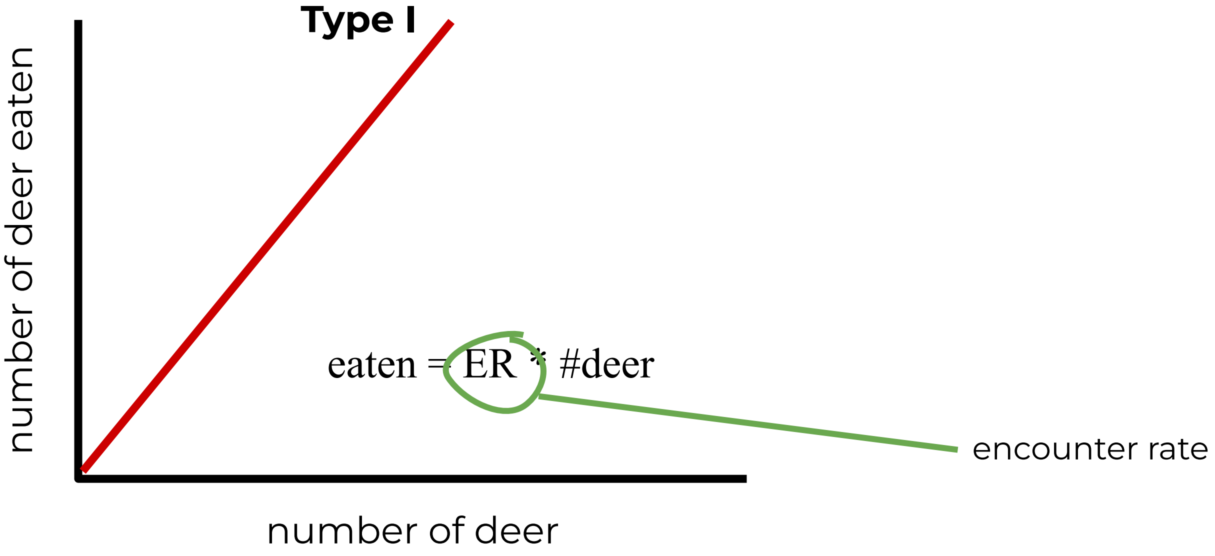

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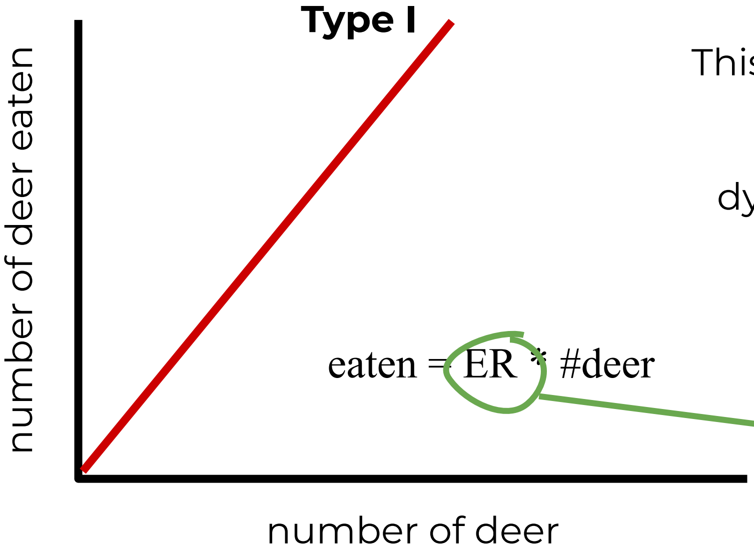
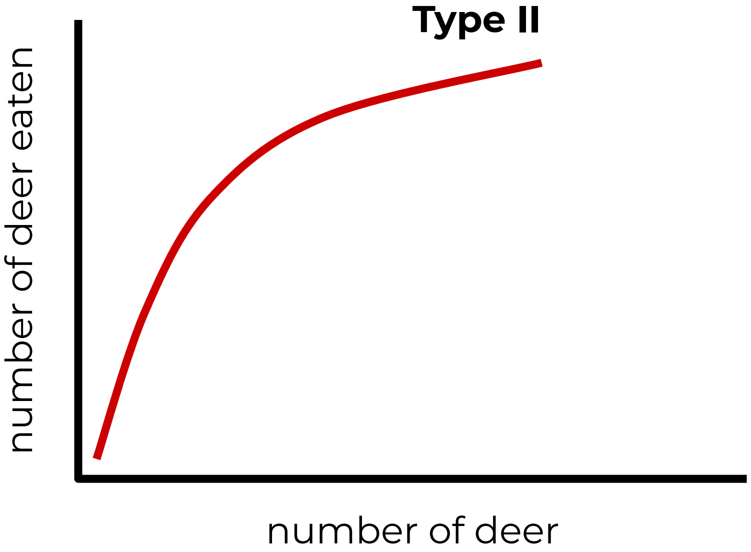


This is the assumed relationship in classical models of predator-prey population dynamics (e.g., Lotka-Volterra population models)

Holling 1959 *Canadian Entomologist*

Functional responses

If the number of deer increases, do wolves eat more of them?



Holling 1959 *Canadian Entomologist*

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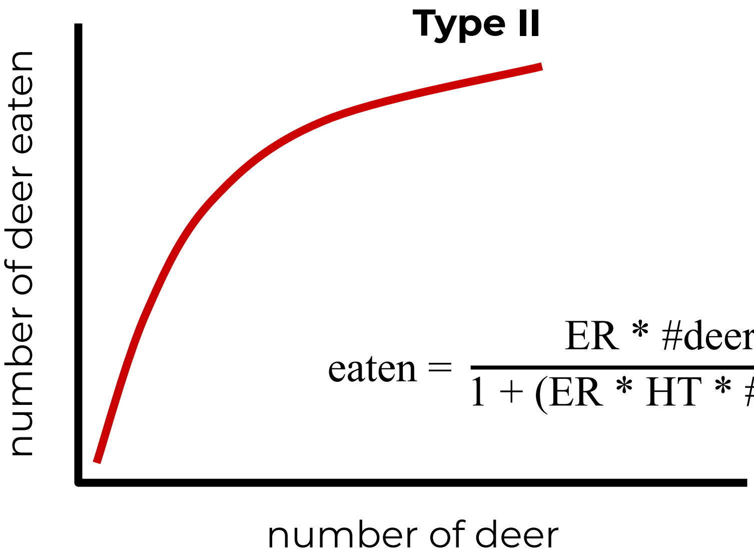
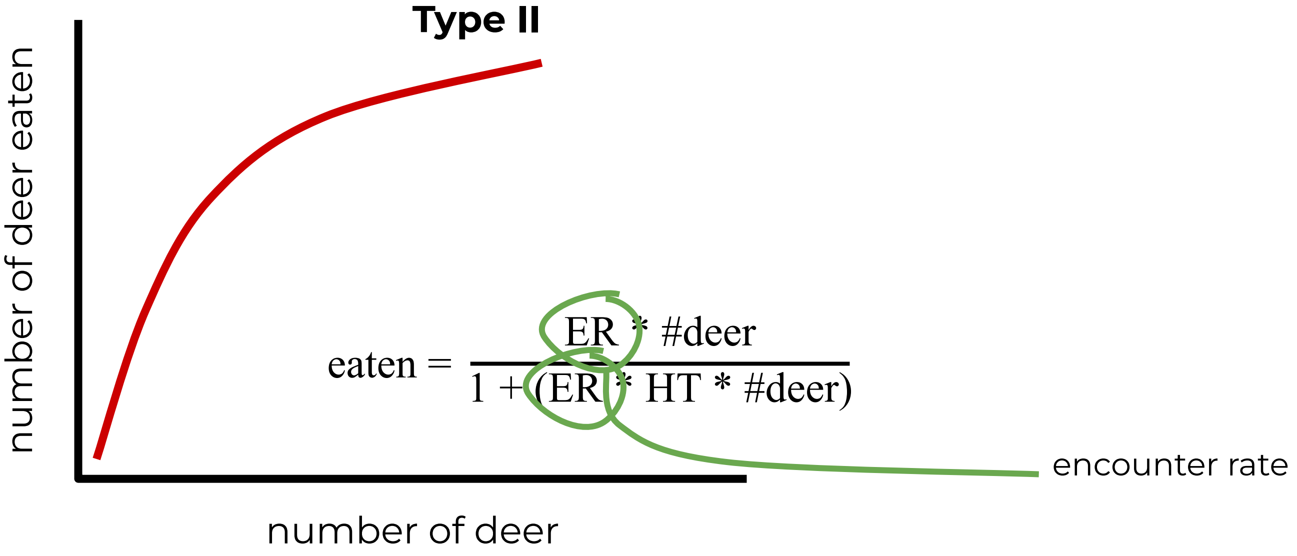


$$\text{eaten} = \frac{\text{ER} * \#\text{deer}}{1 + (\text{ER} * \text{HT} * \#\text{deer})}$$

Holling 1959 *Canadian Entomologist*

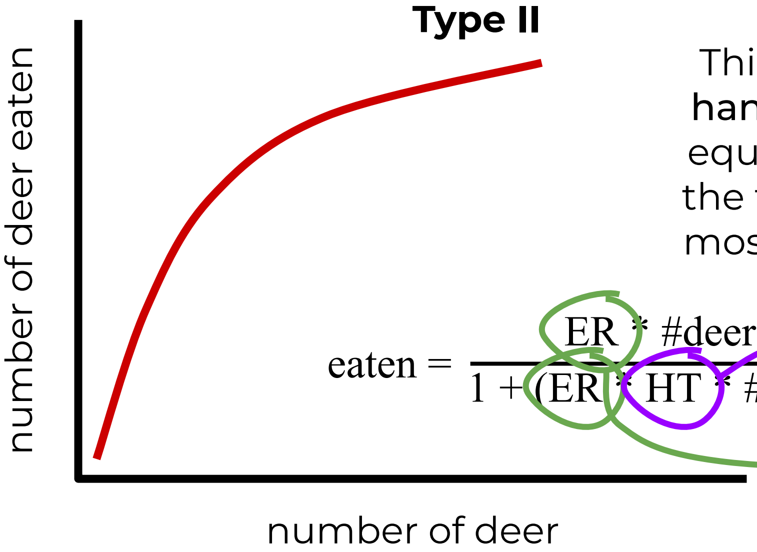
If the number of deer increases, do wolves eat more of them?



$$\text{eaten} = \frac{ER * \#deer}{1 + (ER * HT * \#deer)}$$

Holling 1959 *Canadian Entomologist*

If the number of deer increases, do wolves eat more of them?



This relationship is found when **handling time** is included in the equation. In most cases, it is also the functional form receiving the most support from the literature.

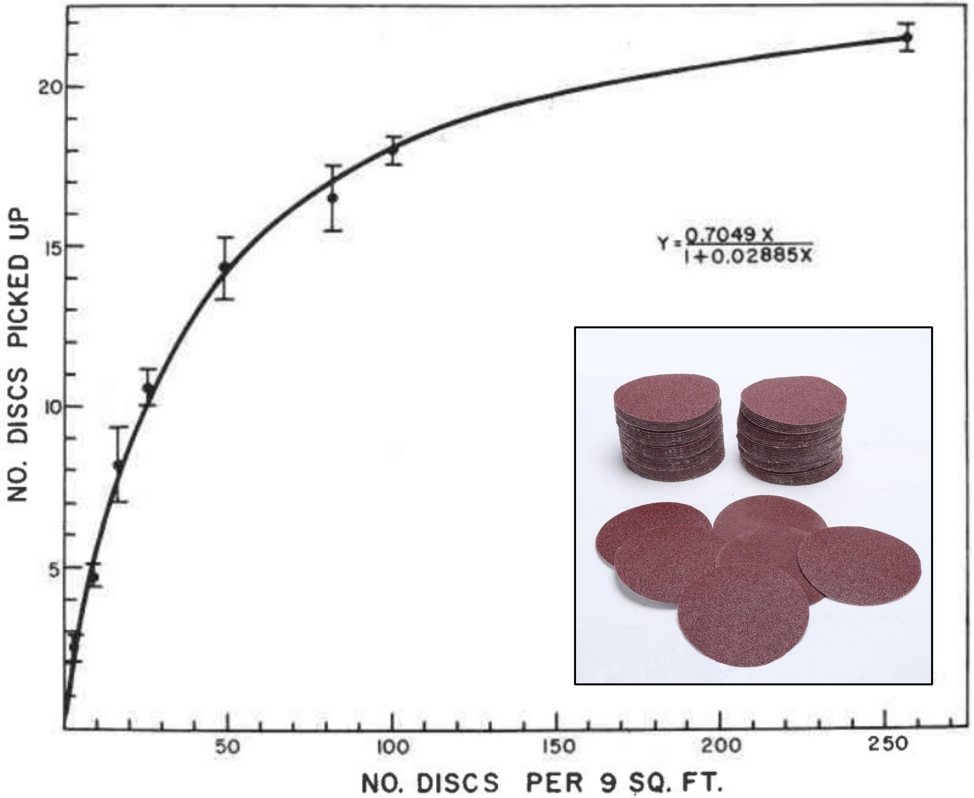
$$\text{eaten} = \frac{ER * \#deer}{1 + (ER * HT * \#deer)}$$

handling time

encounter rate

Holling 1959 *Canadian Entomologist*

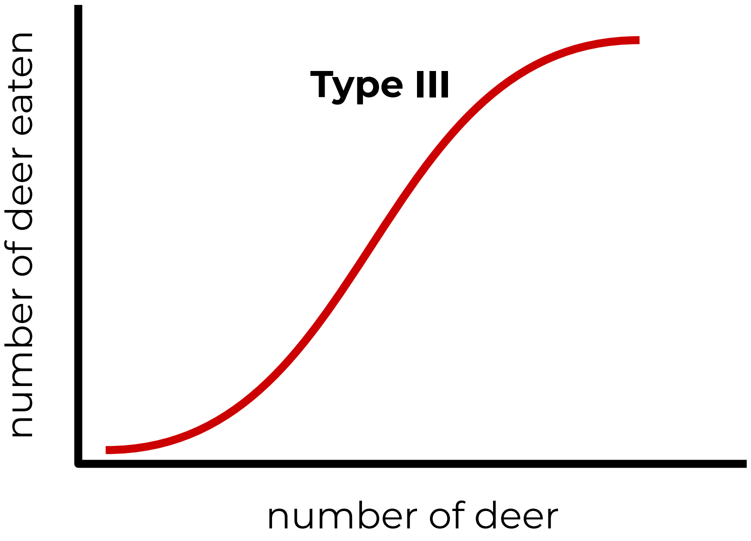
Functional responses



Holling 1959 *Canadian Entomologist*

Functional responses

If the number of deer increases, do wolves eat more of them?



Holling 1965 *Memoirs Ecol. Soc. Canada*; Real 1977 *American Naturalist*

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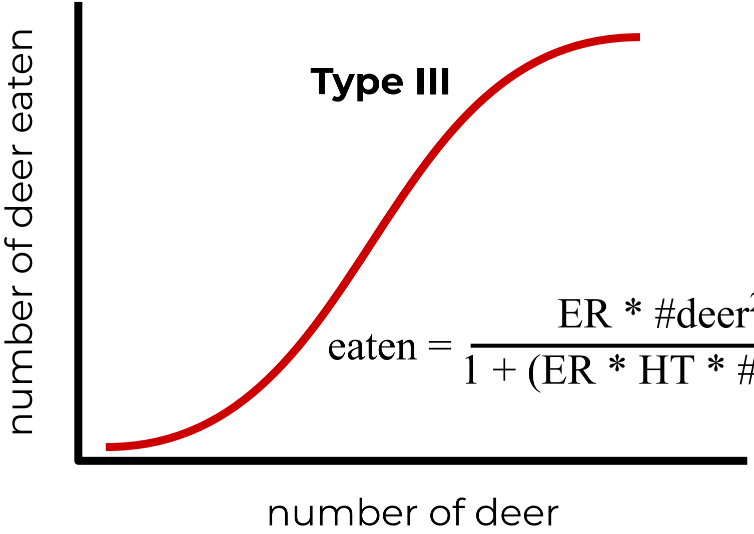

$$\text{eaten} = \frac{\text{ER} * \#\text{deer}^2}{1 + (\text{ER} * \text{HT} * \#\text{deer}^2)}$$

Holling 1965 *Memoirs Ecol. Soc. Canada*; Real 1977 *American Naturalist*

Functional responses

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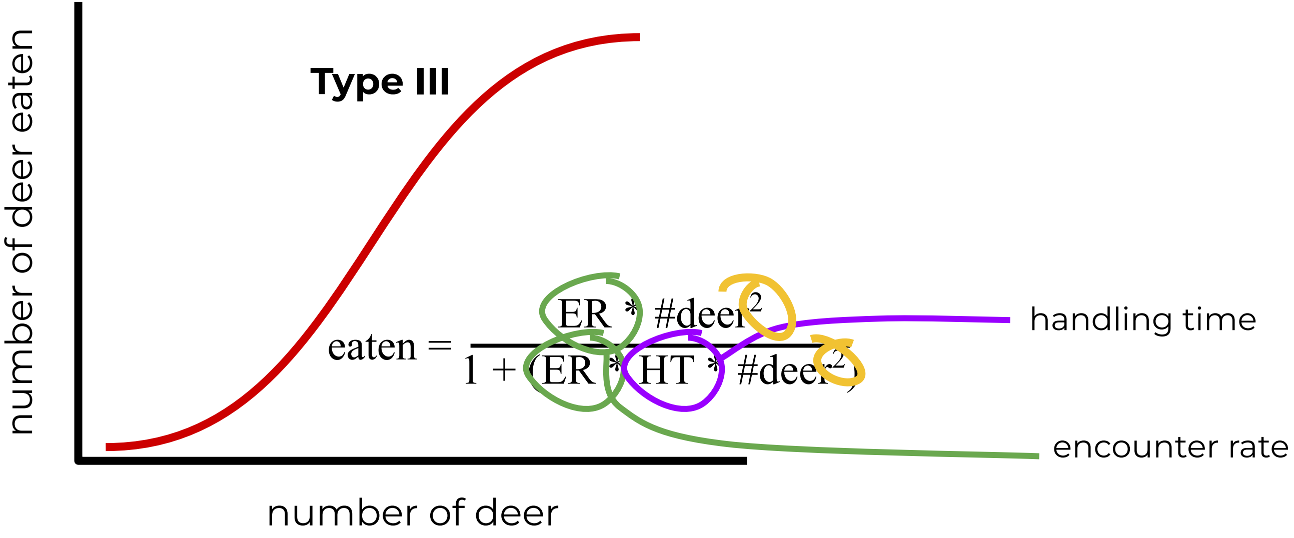

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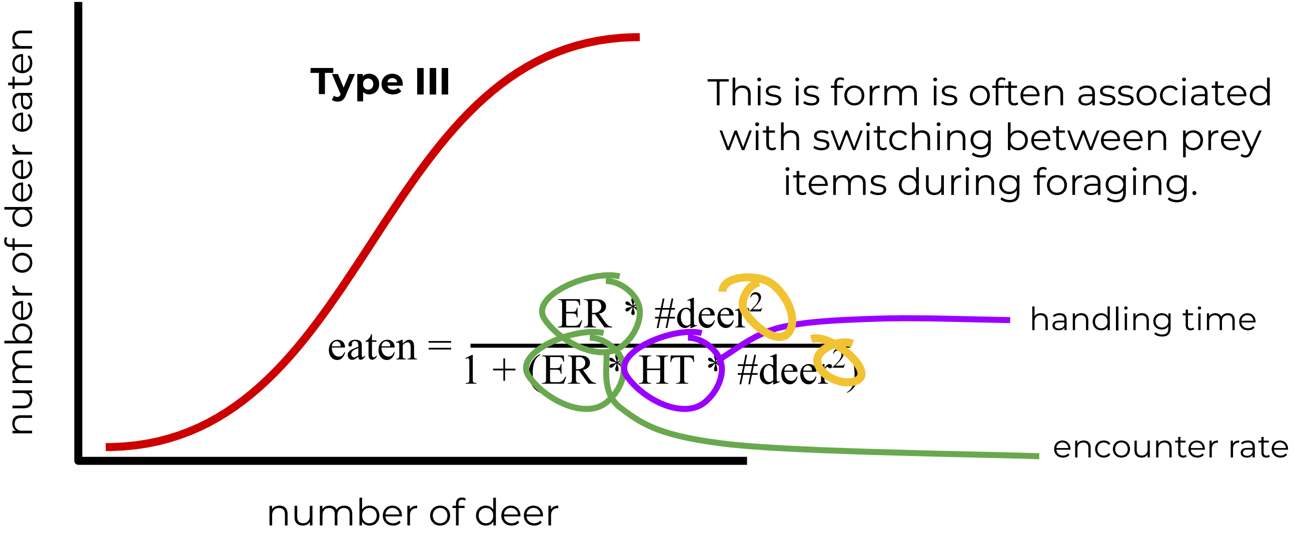

This is form is often associated with switching between prey items during foraging.

Holling 1965 *Memoirs Ecol. Soc. Canada*; Real 1977 *American Naturalist*

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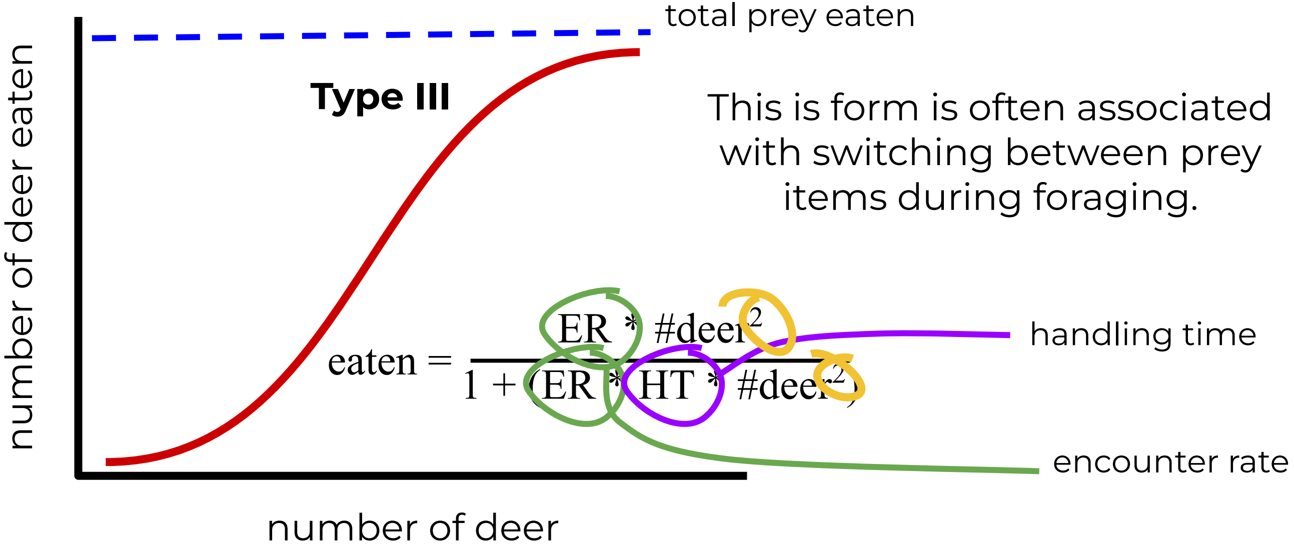

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In principle, these theories allow us to:

- explain why a predator eats certain prey

- explain interaction frequencies between predators and prey

So, how do we predict interactions?

Their narrow scope makes this difficult to actually do across entire networks

An alternative: predicting entire networks

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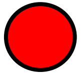
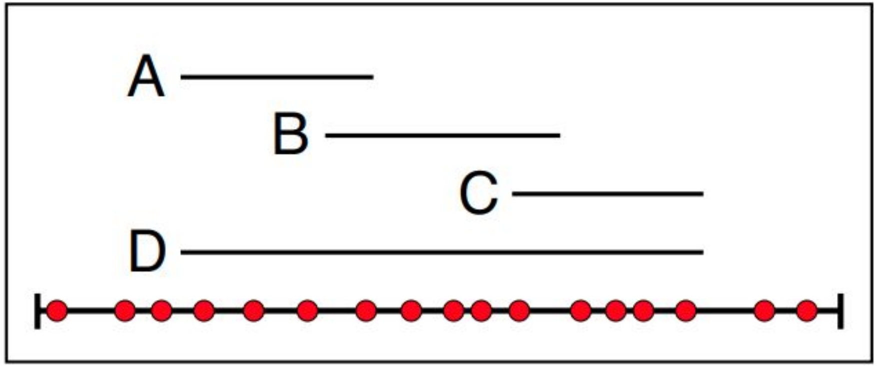
Do patterns within entire species assemblages reveal the rules of species' interactions?

An alternative: predicting entire networks

A-D = predators



= prey



all predators use one section of niche space

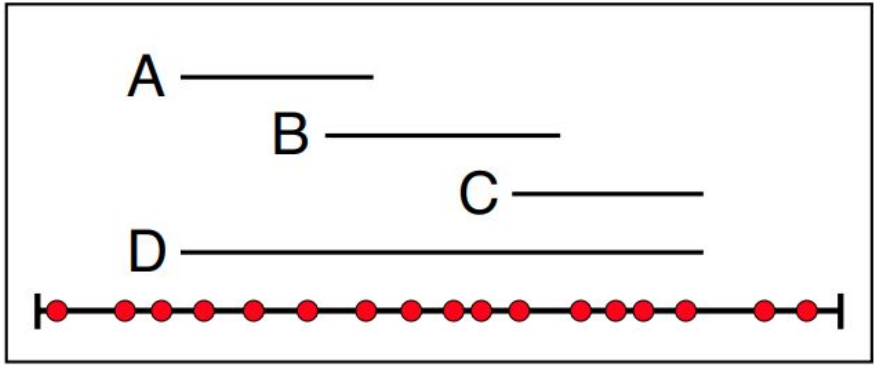
Cohen 1977 *PNAS*; Stouffer et al. 2006 *PNAS*

An alternative: predicting entire networks

food-web intervality

A-D = predators

= prey



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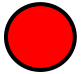
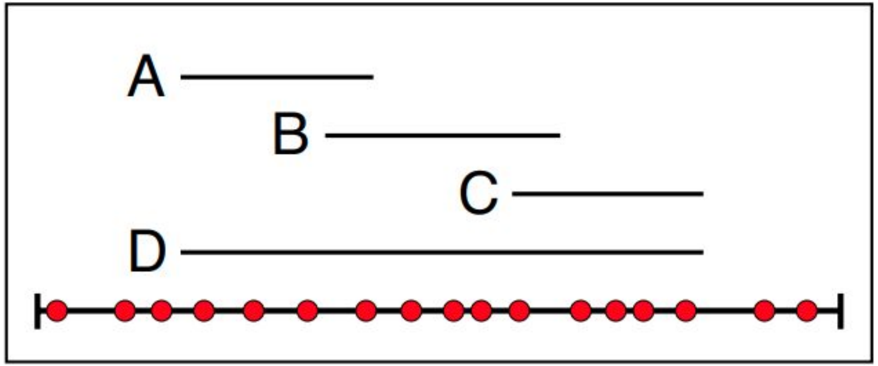
 = prey



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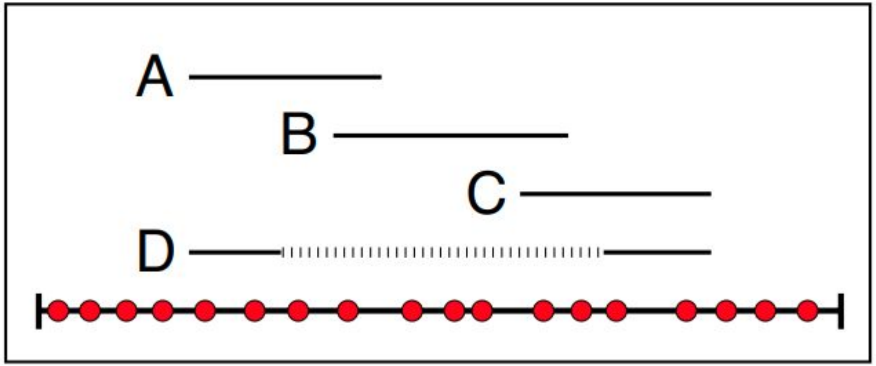
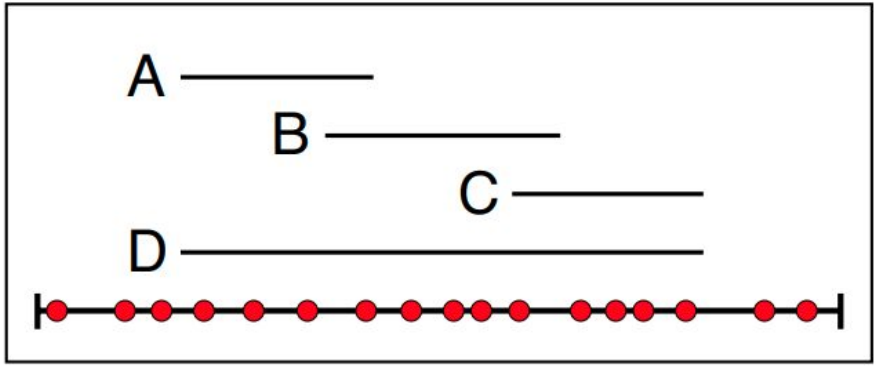


some predators (**D**) use multiple sections of niche space

Cohen 1977 *PNAS*; Stouffer et al. 2006 *PNAS*

An alternative: predicting entire networks

body mass explains diets and food-webs



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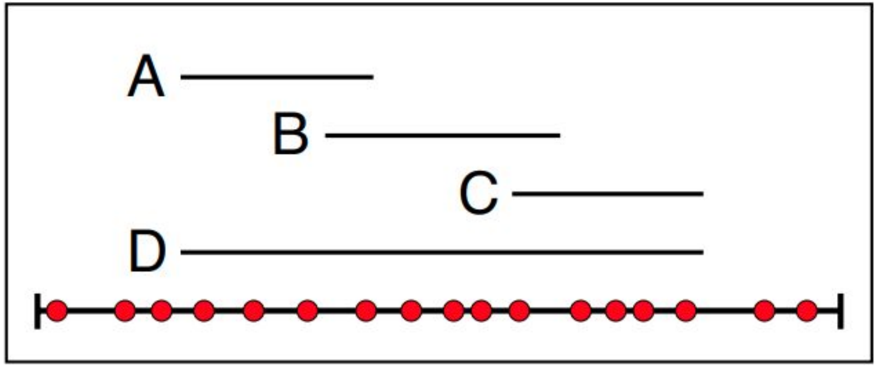

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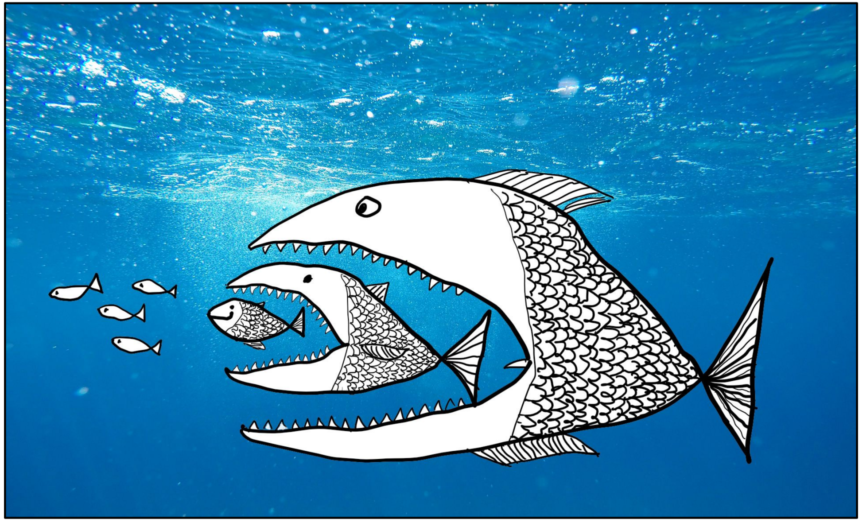

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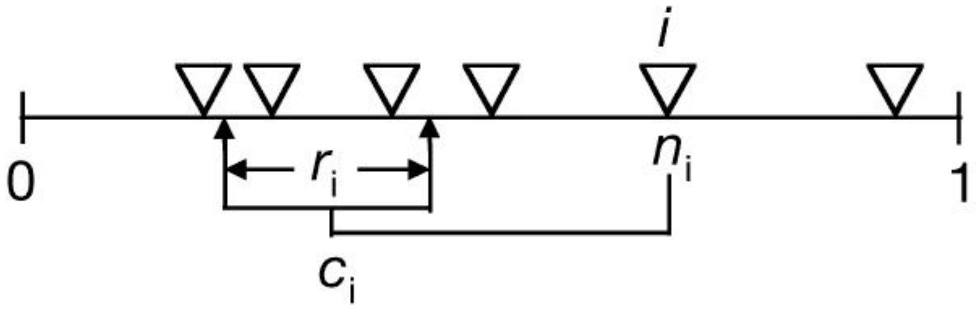

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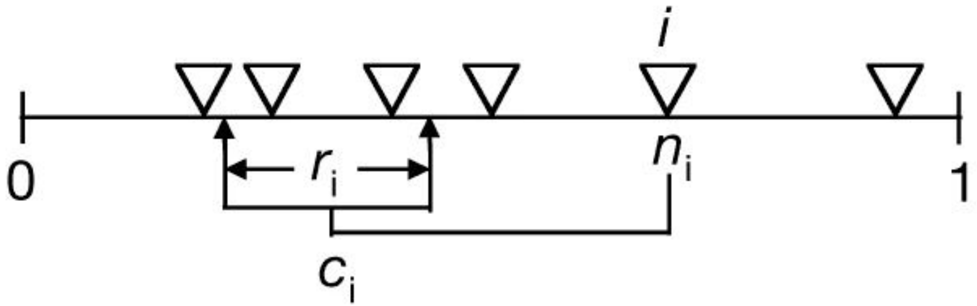

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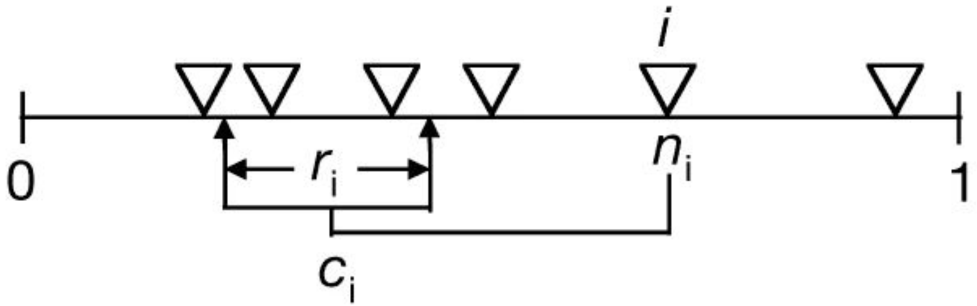
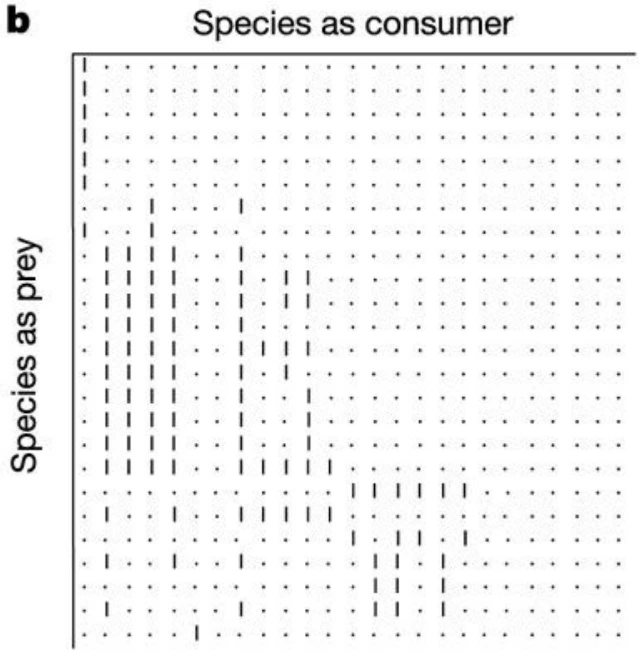


this model generates networks with similar structure to real networks
but how well does it predict specific interactions?

Williams & Martinez 2000 *Nature*; Stouffer et al. 2011 *Journal of Ani. Ecol.*

An alternative: predicting entire networks

real food-web



Cattin et al. 2004 *Nature*

An alternative: predicting entire networks

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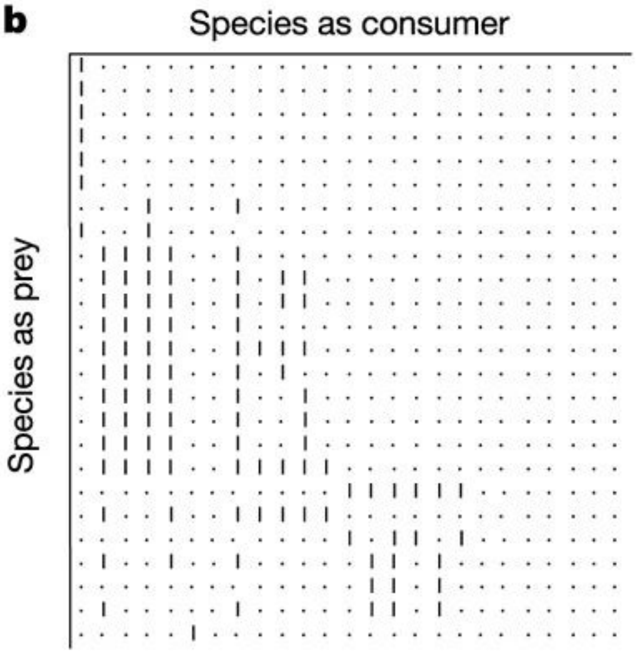
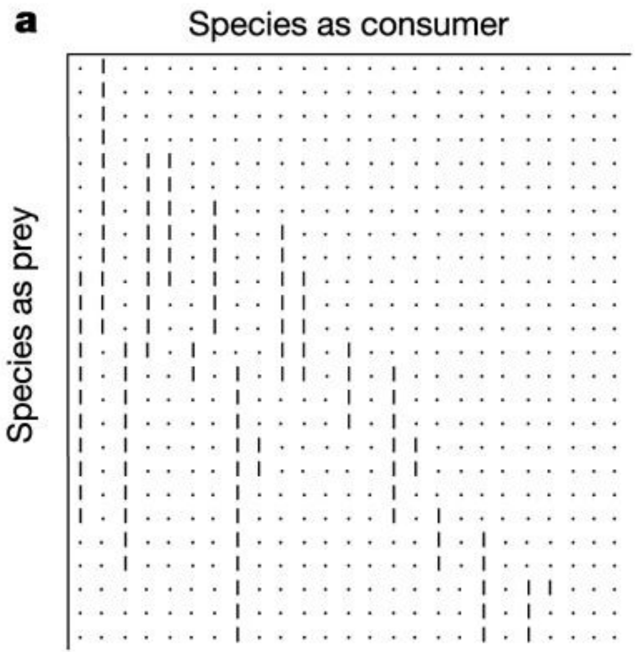


model-generated food-web



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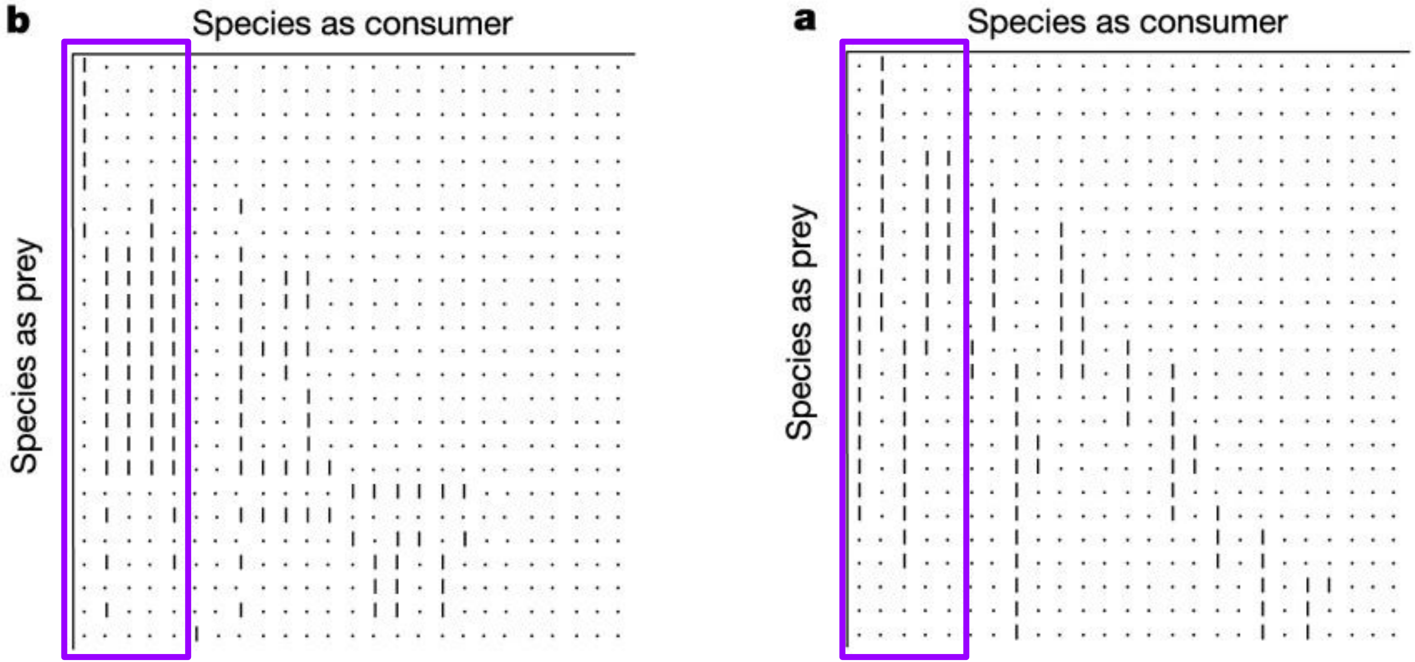

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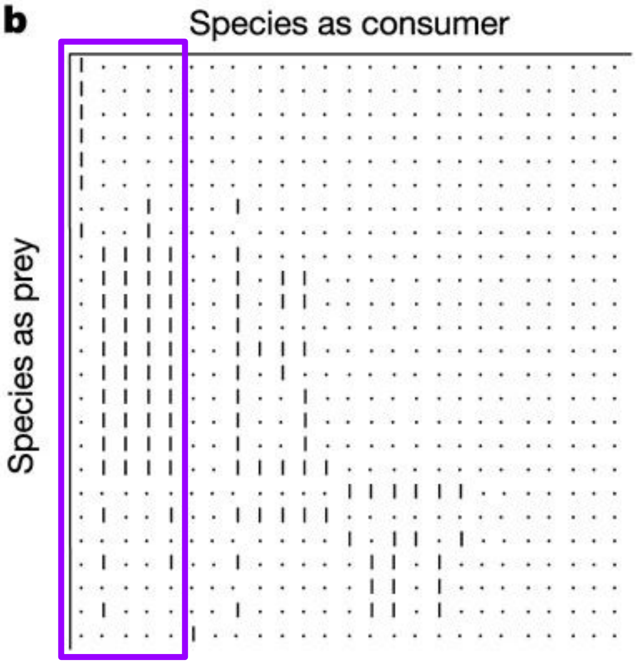

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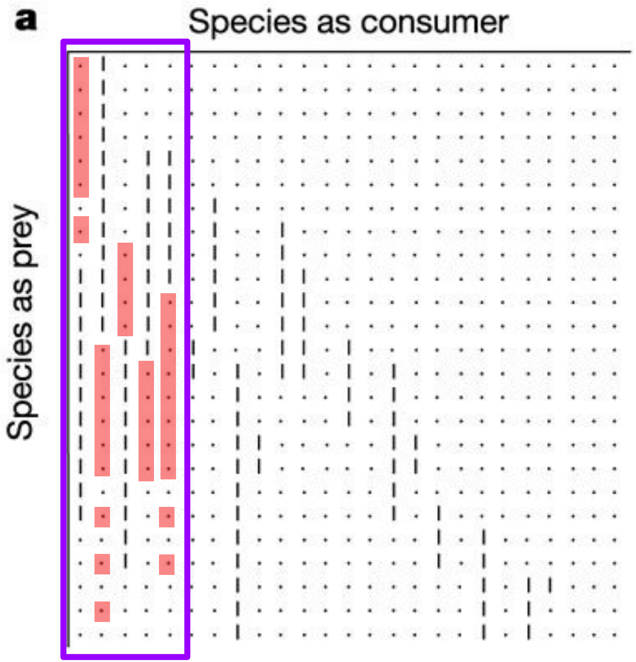

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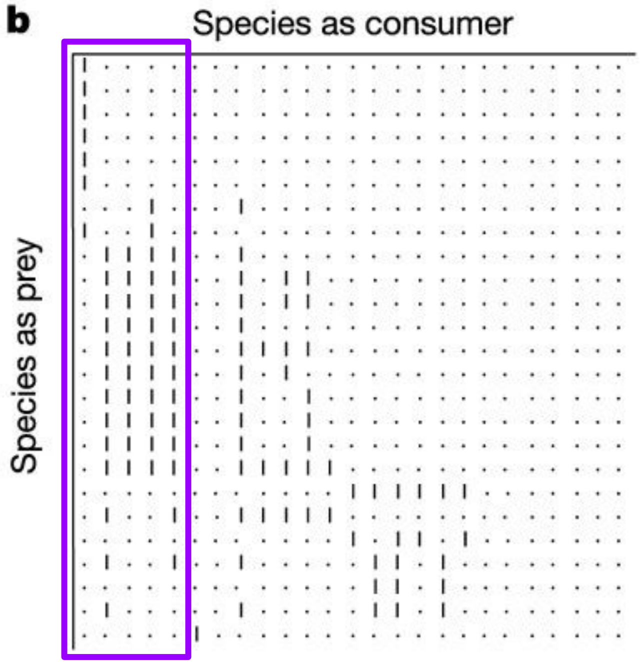

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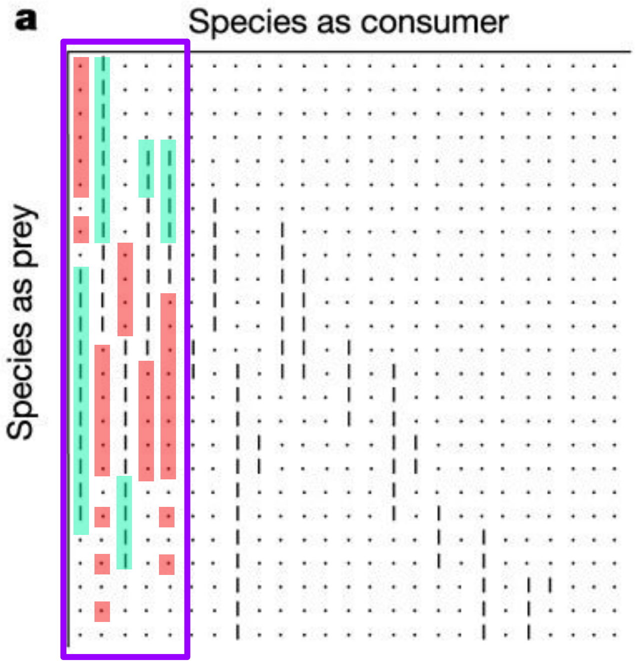

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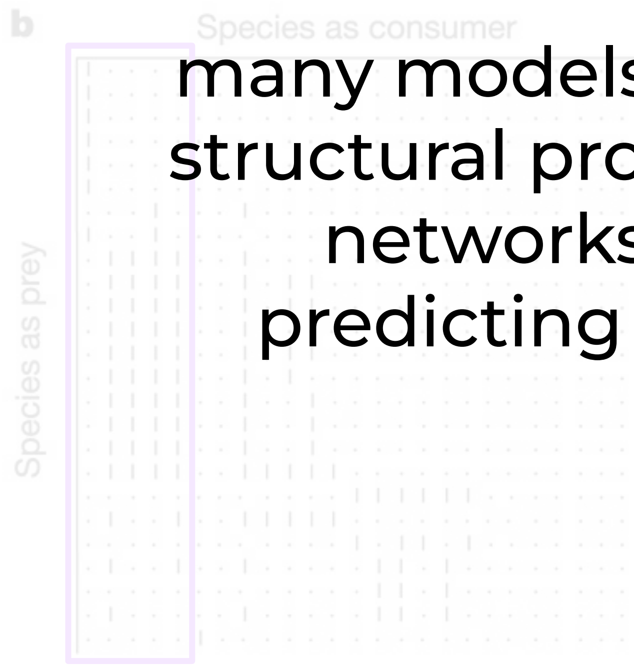

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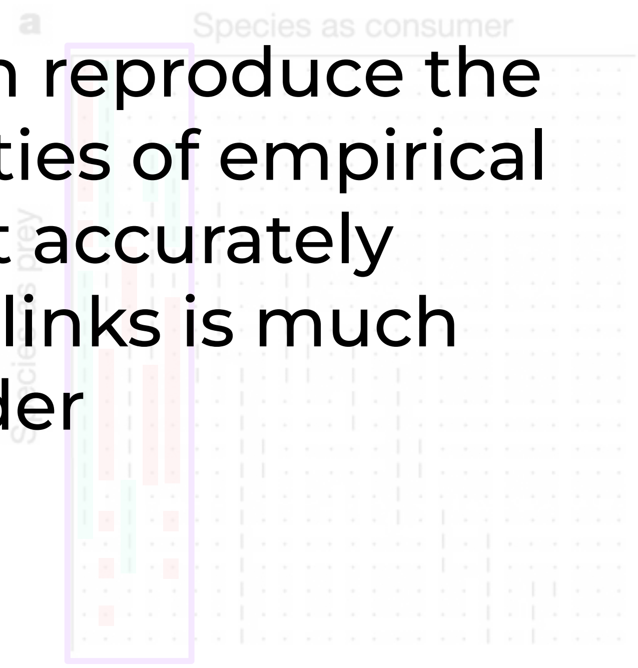


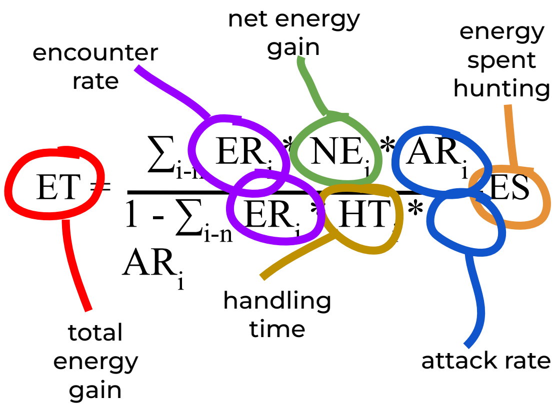
many models can reproduce the structural properties of empirical networks but accurately predicting the links is much harder

Combining behavior with networks

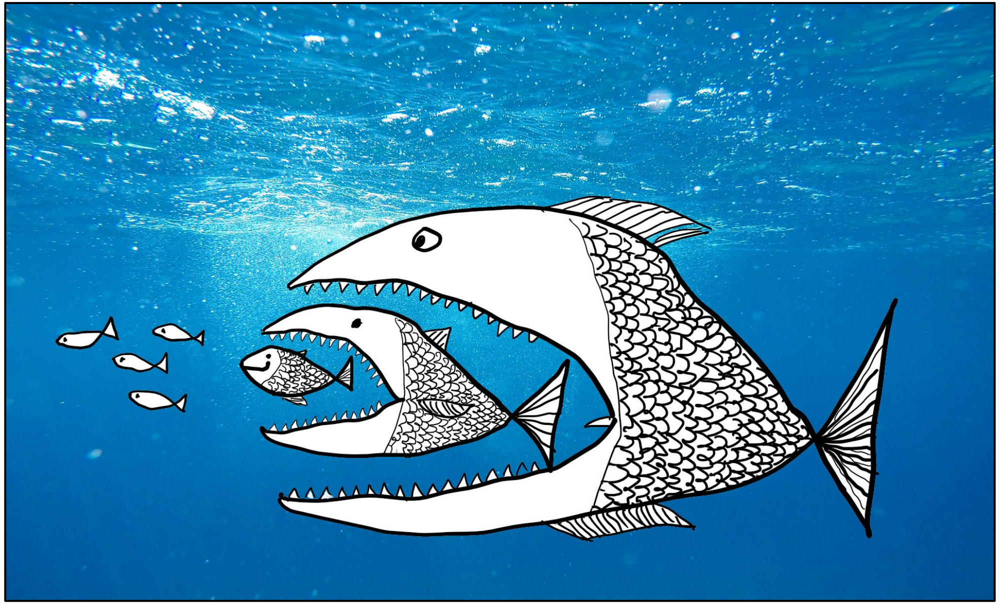
can optimal foraging theory be used to predict the interactions in a food-web?

Petchey et al. 2008 *PNAS*

problem: how do you estimate all the parameters for optimal foraging theory?



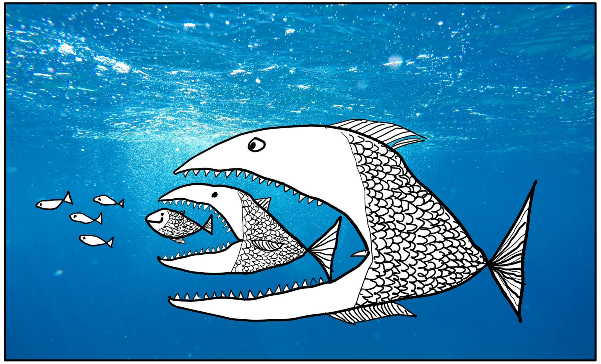
Combining behavior with networks



Petchey et al. 2008 *PNAS*

Combining behavior with networks

$$ET = \frac{\sum_{i-n} ER_i * NE_i * AR_i}{1 - \sum_{i-n} ER_i * HT_i * AR_i} ES$$



Petchey et al. 2008 *PNAS*

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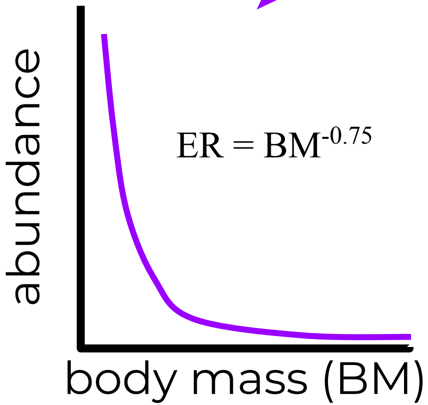

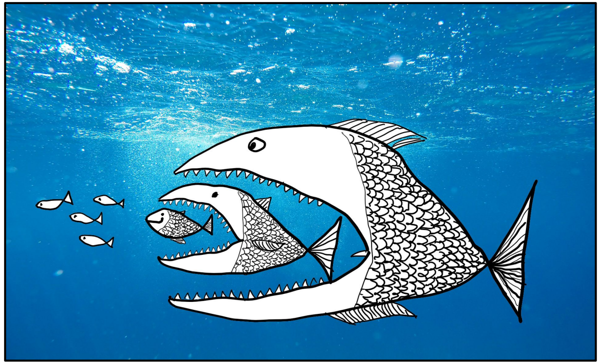

Petchey et al. 2008 *PNAS*

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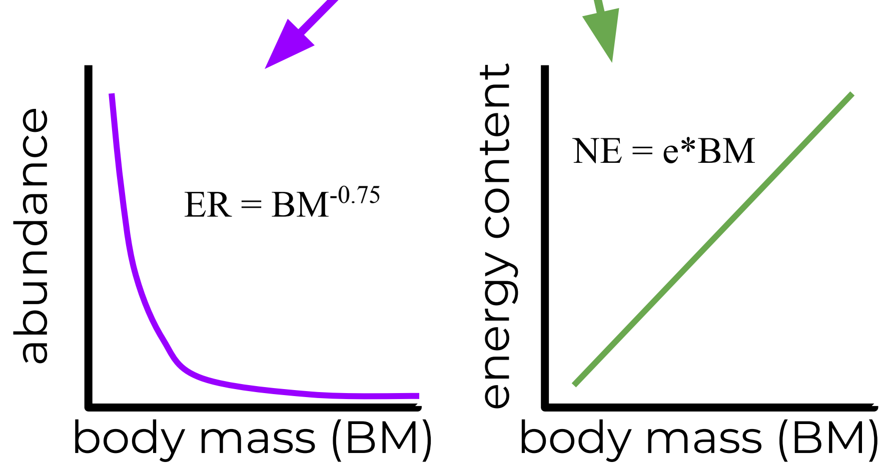

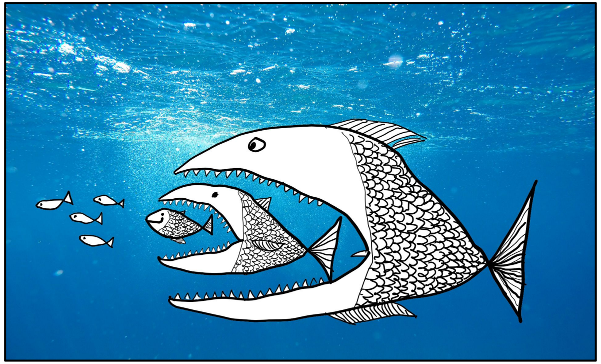

Petchey et al. 2008 *PNAS*

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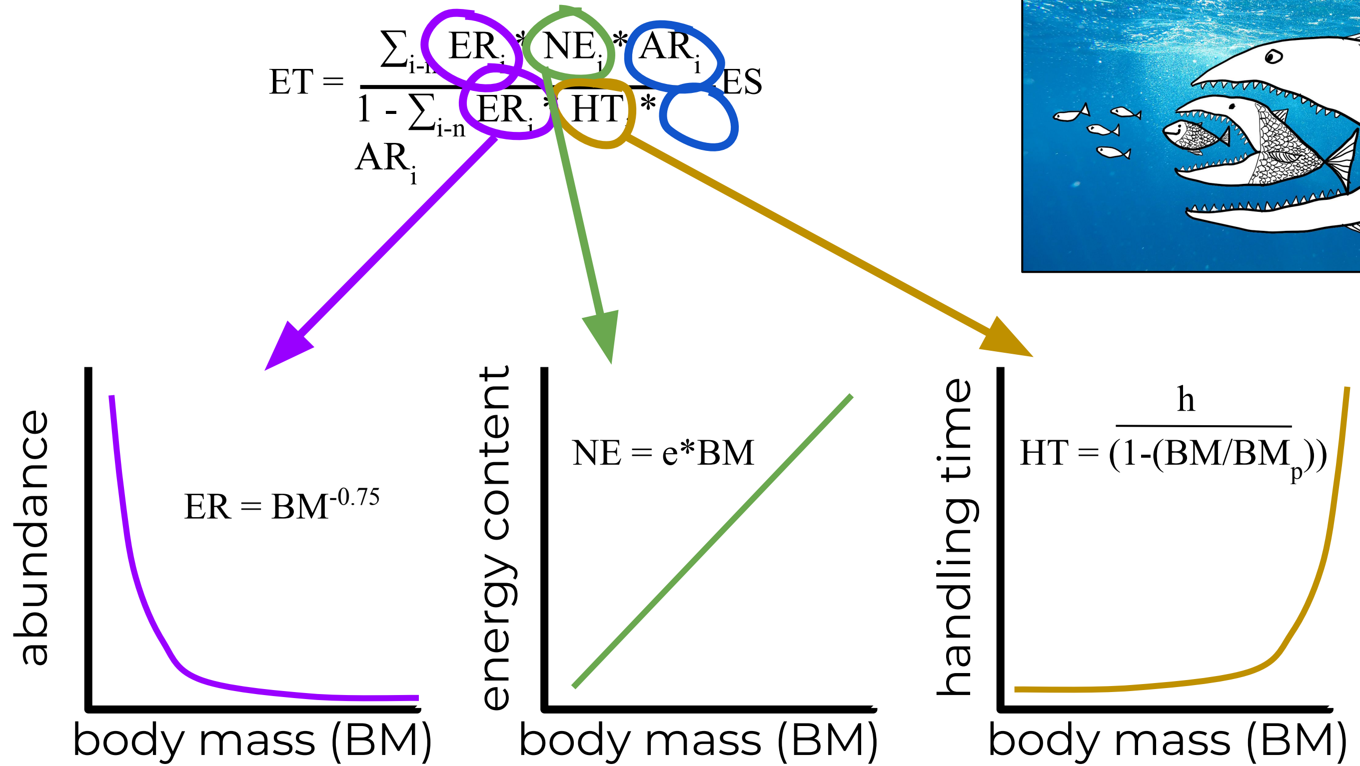

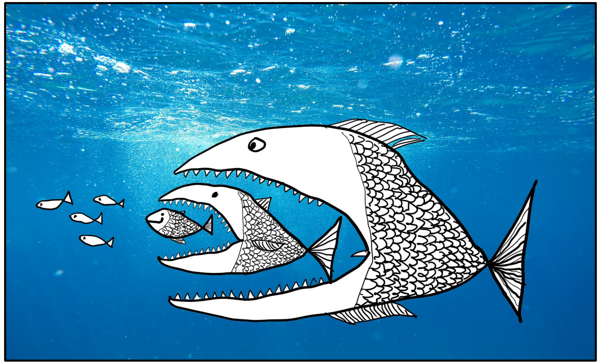

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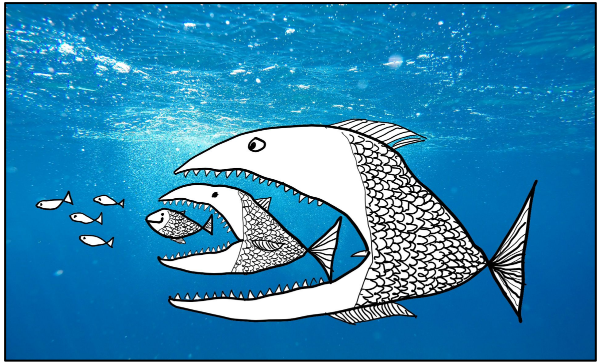

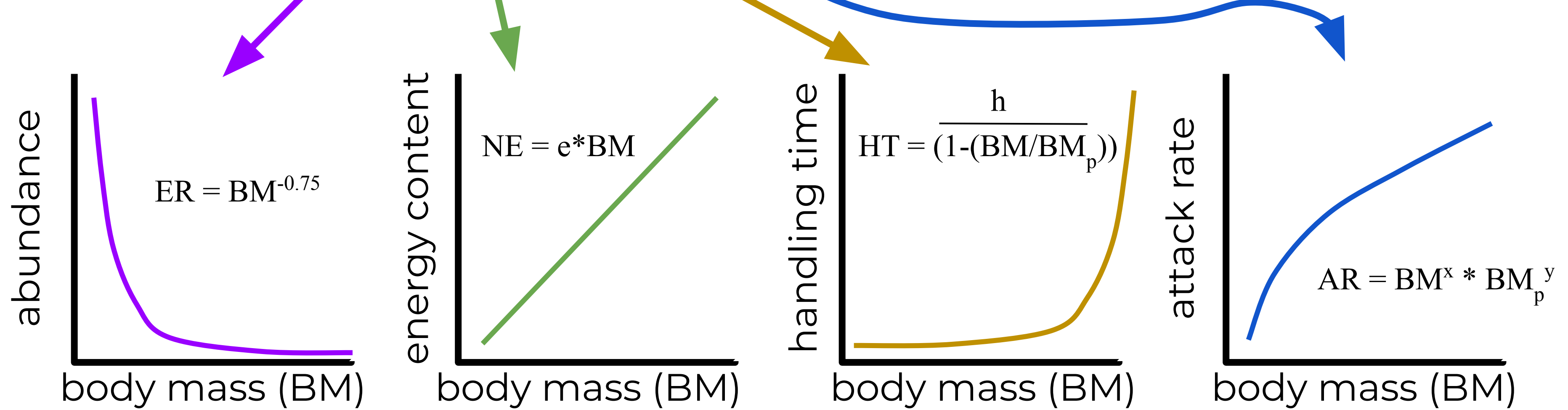

Petchey et al. 2008 *PNAS*

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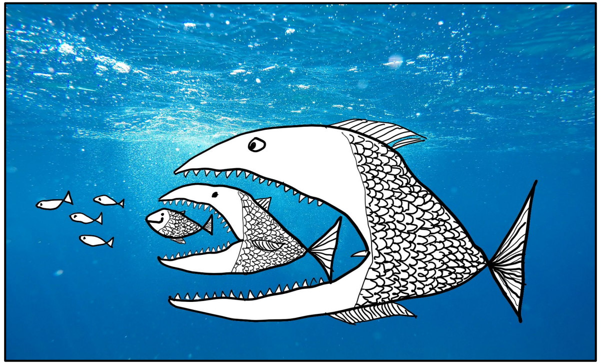

Petchey et al. 2008 *PNAS*

Combining behavior with networks

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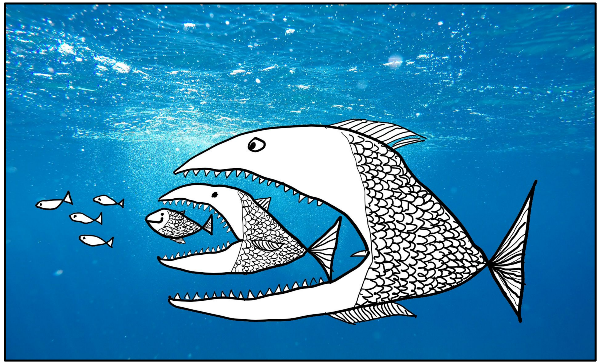

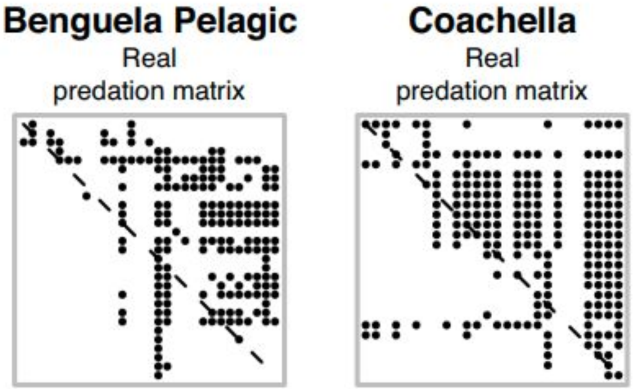

Petchey et al. 2008 *PNAS*

Combining behavior with networks

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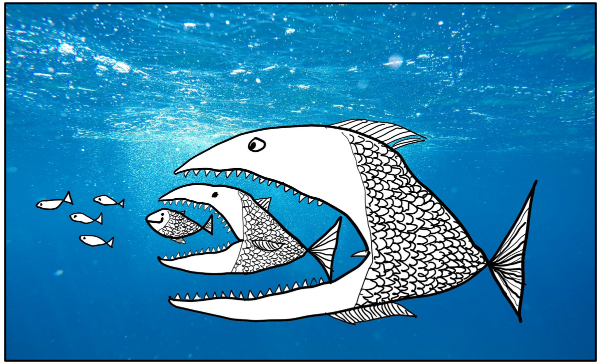
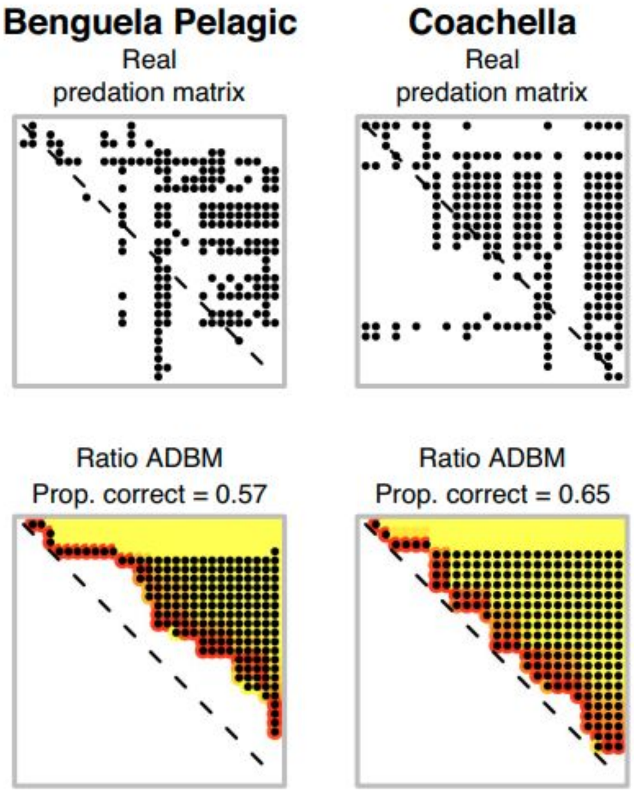
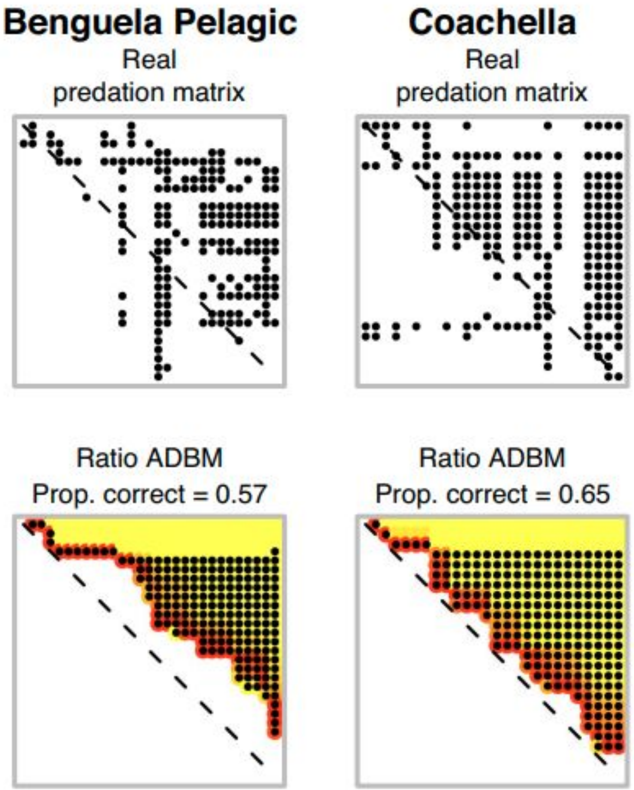




Petchey et al. 2008 *PNAS*

Combining behavior with networks

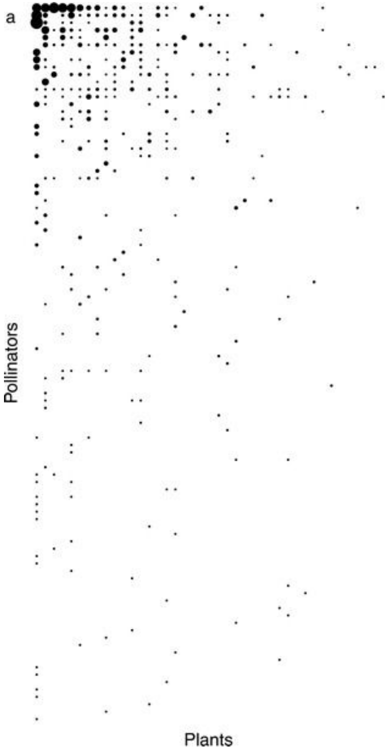
aren't there still a lot of errors?



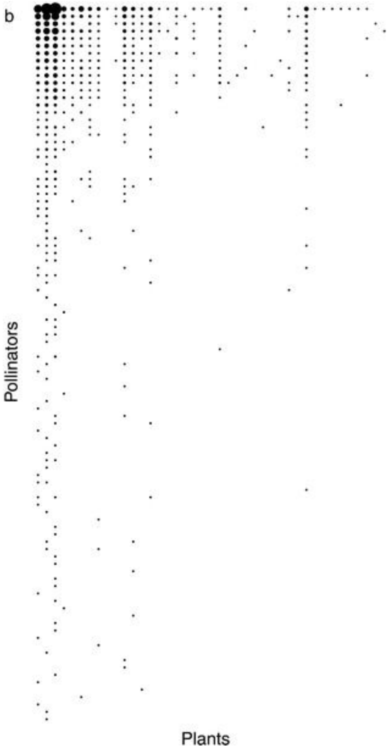
Petchey et al. 2008 *PNAS*

Combining behavior with networks

real network

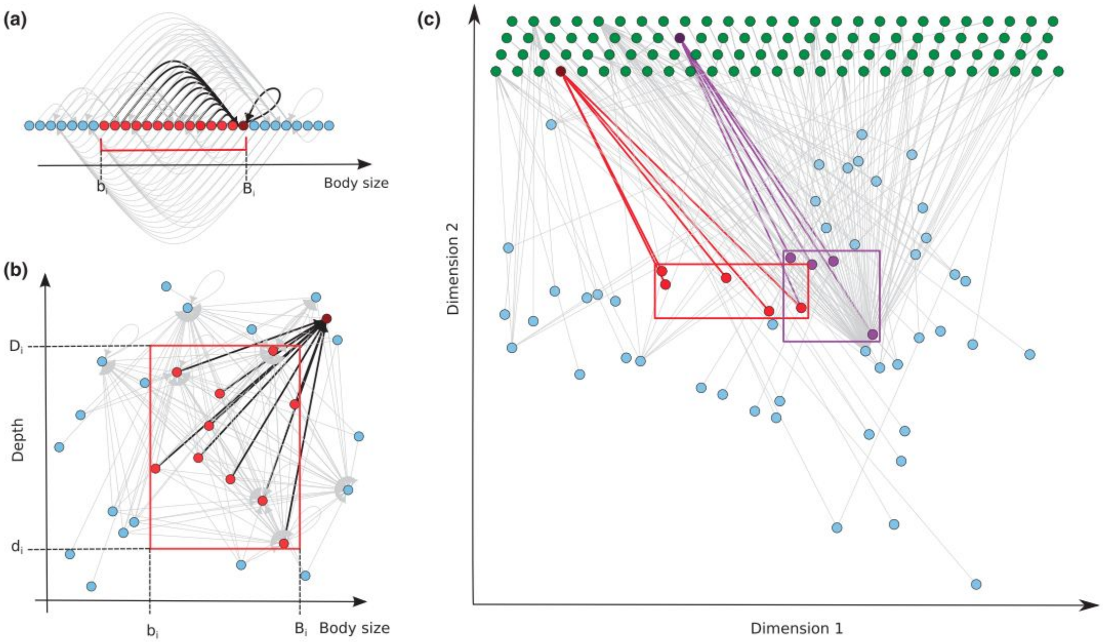


model-generated network



Vazquez et al. 2009 *Ecology*

Adding in more and more information



Eklof et al. 2013 *Ecology Letters*

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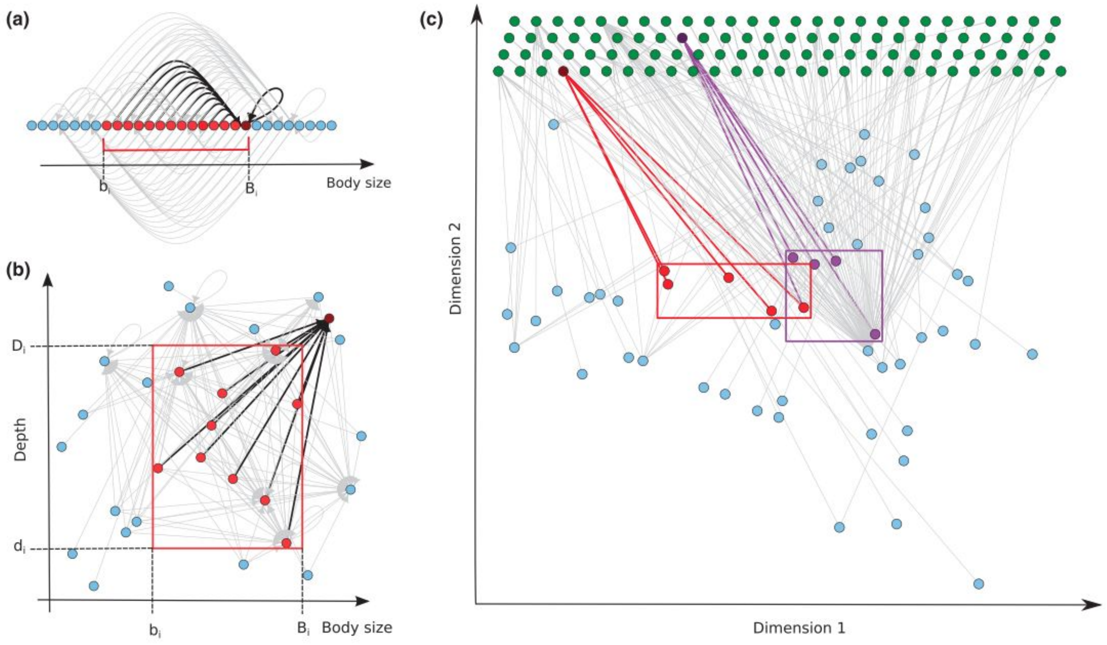

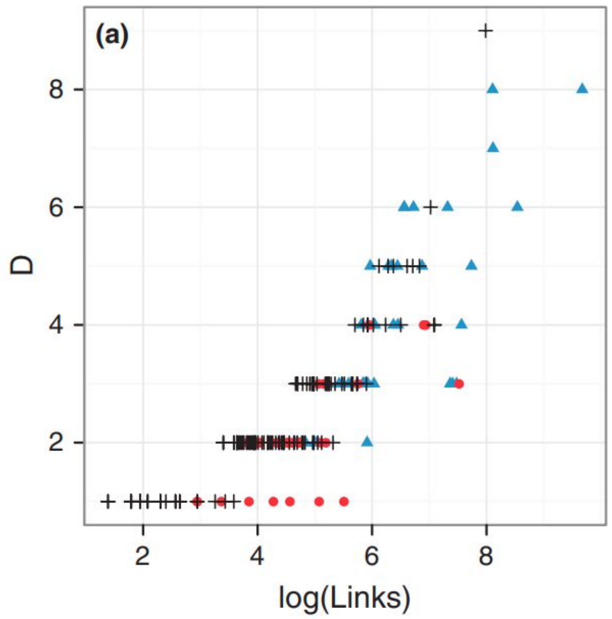

Eklof et al. 2013 *Ecology Letters*

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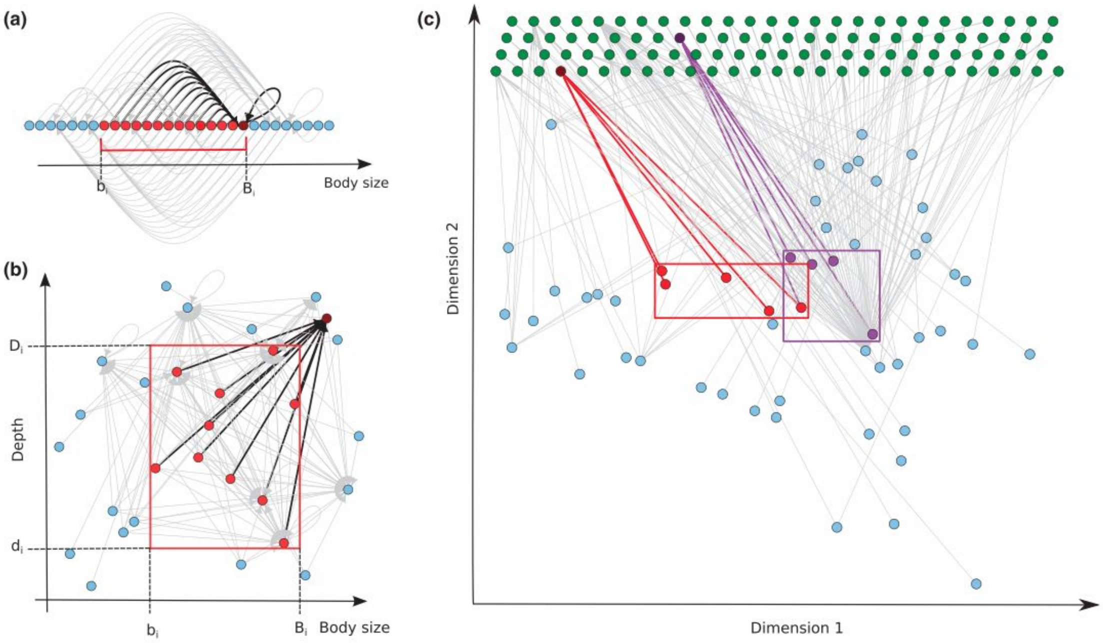

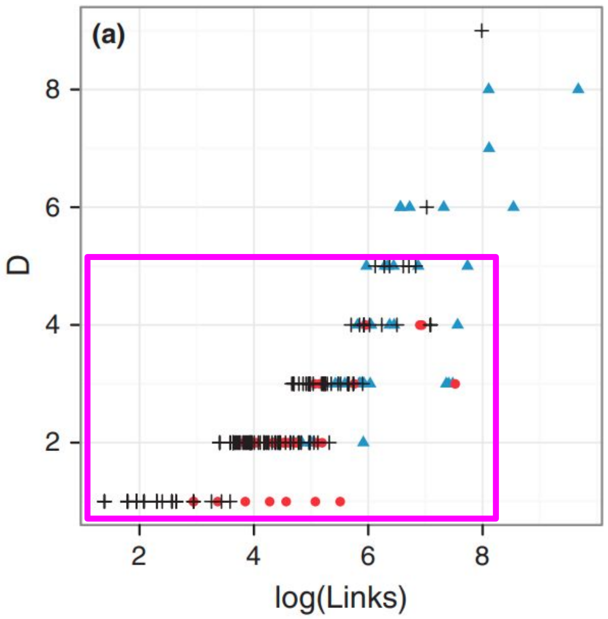

Eklof et al. 2013 *Ecology Letters*

What do we know?

Key takeaways

Optimal foraging theory describes what an animal should eat based on energy gain, handling time, encounter rates, and attack rates.

Functional responses show how consumption should change with prey abundance; they become more complex as more realism is added to them.

Both theories have a narrow focus. Few "currencies" are used in OFT; only one prey is considered in functional responses

Key takeaways

The narrow scope of these theories prompted ecologists to look for patterns in entire food-web and they noticed that body mass is a good predictor of food-web links

Relationships between body mass and biological traits are common and allow Optimal Foraging Theory to be incorporated with food-web analyses

Food-web models still struggle to predict interactions accurately. Current trends incorporate more data, but come with the trade-off of more complex theory

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