

Effect of Parasites on the Structure and Dynamics of Food Webs

Nicholas J. Kappler

April 8, 2018

Motivation

Structural Fingerprint of Parasites

Food Web Models

ATN Model

Motivation

Structural Fingerprint of Parasites

Goals

- ▶ Look for systematic difference between parasite and free liver communities

Goals

- ▶ Look for systematic difference between parasite and free liver communities
- ▶

6 Empirical Food Webs

- ▶ Intertidal ecosystems

6 Empirical Food Webs

- ▶ Intertidal ecosystems
- ▶ Notable for high resolution

6 Empirical Food Webs

- ▶ Intertidal ecosystems
- ▶ Notable for high resolution
 - ▶ Between 109 and 185 trophic species

6 Empirical Food Webs

- ▶ Intertidal ecosystems
- ▶ Notable for high resolution
 - ▶ Between 109 and 185 trophic species
 - ▶ Between 840 and 2841 feeding relationships

6 Empirical Food Webs

- ▶ Intertidal ecosystems
- ▶ Notable for high resolution
 - ▶ Between 109 and 185 trophic species
 - ▶ Between 840 and 2841 feeding relationships
 - ▶ 7-9% of possible links between species; “connectance”

6 Empirical Food Webs

- ▶ Intertidal ecosystems
- ▶ Notable for high resolution
 - ▶ Between 109 and 185 trophic species
 - ▶ Between 840 and 2841 feeding relationships
 - ▶ 7-9% of possible links between species; “connectance”
 - ▶ 17 to 68 parasite taxa, 14-46% of species in web.

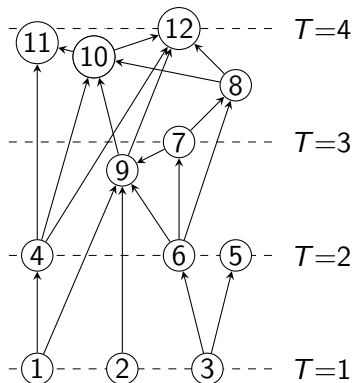
6 Empirical Food Webs

- ▶ Intertidal ecosystems
- ▶ Notable for high resolution
 - ▶ Between 109 and 185 trophic species
 - ▶ Between 840 and 2841 feeding relationships
 - ▶ 7-9% of possible links between species; “connectance”
 - ▶ 17 to 68 parasite taxa, 14-46% of species in web.
- ▶ Standardized data format

Properties Considered

Property	Name
g	Generality
v	Vulnerability
v_r	Mean. Vul. Resources
g_c	Mean. Gen. Consumers
T	Prey-Averaged
λ	Eigenvector based
C_B, C_{EB}	Betweenness
γ	Four types of directed clustering

Example Food Web

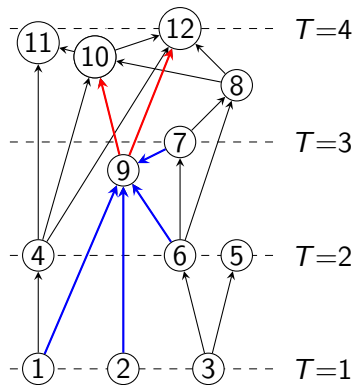


West Coastal Tundra, Barrow, Alaska Food Web

ID	Species Description
1	Monocots
2	Dicots
3	Detritus
4	Lemmings
5	Microorganisms
6	Saprovores
7	Carnivorous Arthropods
8	Shorebirds
9	Longspurs
10	Weasels
11	Owls
12	Jaegers

Source: Cohen, J. E. (compiler) 2010 Ecologists' Co-Operative Web Bank. Version 1.1. Machine-readable data base of food webs. New York: The Rockefeller University.

Example Food Web



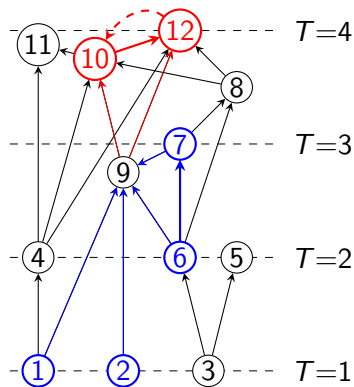
Longspurs:

$$v_9 = 2$$

$$g_9 = 2$$

$$T_9 = \frac{1 + 1 + 2 + 3}{4} + 1 = 2.75$$

Example Food Web



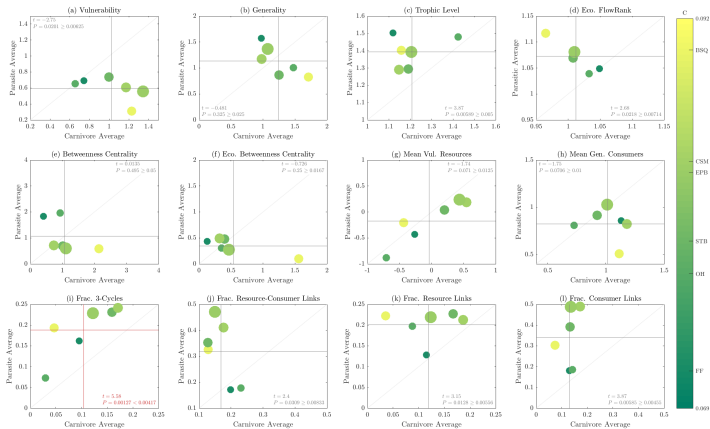
Longspurs:

$$\gamma_9^c = \frac{1}{2}$$

$$\gamma_9^r = \frac{1}{12}$$

$$\gamma_9^{rc} = \gamma^{cr} = 0$$

Observed Patterns



Patterns are there

- ▶ Network properties of individual nodes could differentiate parasite from free liver on about 85% of nodes

Patterns are there

- ▶ Network properties of individual nodes could differentiate parasite from free liver on about 85% of nodes
- ▶ Observed patterns were robust to decreases in trophic resolution

Add salt

- ▶ We are observing patterns in *data*

Add salt

- ▶ We are observing patterns in *data*
- ▶ Life stages were aggregated first

Add salt

- ▶ We are observing patterns in *data*
- ▶ Life stages were aggregated first
- ▶ Sampling Biases

Add salt

- ▶ We are observing patterns in *data*
- ▶ Life stages were aggregated first
- ▶ Sampling Biases
 - ▶ No parasites of plants

Add salt

- ▶ We are observing patterns in *data*
- ▶ Life stages were aggregated first
- ▶ Sampling Biases
 - ▶ No parasites of plants
 - ▶ No ectoparasites of birds, fish

Add salt

- ▶ We are observing patterns in *data*
- ▶ Life stages were aggregated first
- ▶ Sampling Biases
 - ▶ No parasites of plants
 - ▶ No ectoparasites of birds, fish
 - ▶ Poor resolution of microbes and viruses

Add salt

- ▶ We are observing patterns in *data*
- ▶ Life stages were aggregated first
- ▶ Sampling Biases
 - ▶ No parasites of plants
 - ▶ No ectoparasites of birds, fish
 - ▶ Poor resolution of microbes and viruses
 - ▶ Poor resolution of Fungi

Add salt

- ▶ We are observing patterns in *data*
- ▶ Life stages were aggregated first
- ▶ Sampling Biases
 - ▶ No parasites of plants
 - ▶ No ectoparasites of birds, fish
 - ▶ Poor resolution of microbes and viruses
 - ▶ Poor resolution of Fungi
 - ▶ Detritus as basal node

Food Web Models

Background

- ▶ Robert May (1972)

Background

- ▶ Robert May (1972)
- ▶ Cohen's Cascades (1990)

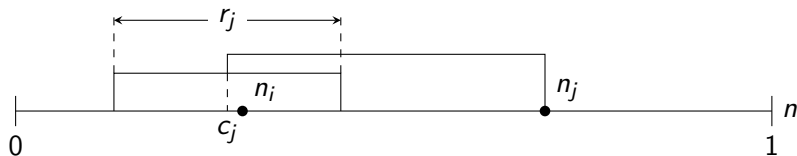
Background

- ▶ Robert May (1972)
- ▶ Cohen's Cascades (1990)
- ▶ Niche Model (2000)

Background

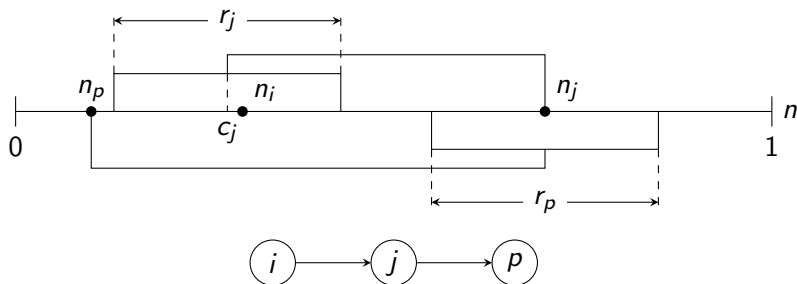
- ▶ Robert May (1972)
- ▶ Cohen's Cascades (1990)
- ▶ Niche Model (2000)
- ▶ Variants

The Niche and Inverse Niche Models



- ▶ $n_i \sim U(0, 1)$
- ▶ $y_i \sim \text{Beta}(1, \beta)$
- ▶ $r_i \sim n_i \cdot y_i$
- ▶ $c_i \sim U(\max(0, r_i/2), \min(1 - r_i/2, n_i))$

The Niche and Inverse Niche Models



- ▶ $n_p \sim U(0, 1)$
- ▶ $y_p \sim \text{Beta}(1, \beta_p)$
- ▶ $r_p \sim (1 - n_p) \cdot y_p$
- ▶ $c_p \sim U(\{n_j | j \in \text{free livers}, n_j > n_p\})$

Models Tested

- ▶ Niche model with randomly chosen parasites

Models Tested

- ▶ Niche model with randomly chosen parasites
- ▶ Inverse Niche Model, matching number of links within and between free liver and parasite communities

Models Tested

- ▶ Niche model with randomly chosen parasites
- ▶ Inverse Niche Model, matching number of links within and between free liver and parasite communities
 - ▶ e.g. free liver - parasite more common than parasite - parasite

How to Assess Fit

- ▶ Ensemble of food webs from each model

How to Assess Fit

- ▶ Ensemble of food webs from each model
- ▶ Calculate properties

How to Assess Fit

- ▶ Ensemble of food webs from each model
- ▶ Calculate properties
- ▶ Distribution of ensemble properties

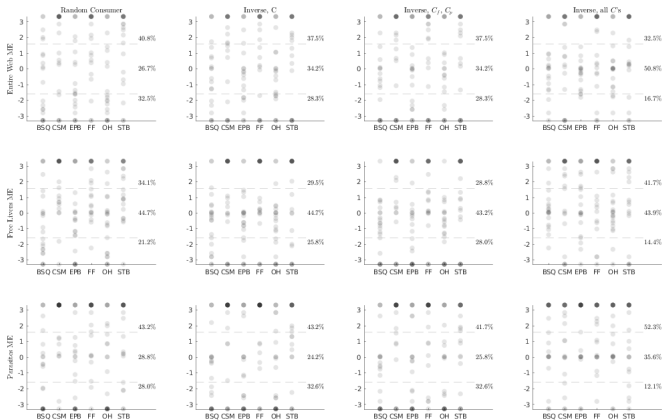
How to Assess Fit

- ▶ Ensemble of food webs from each model
- ▶ Calculate properties
- ▶ Distribution of ensemble properties
- ▶ How many of the empirical properties are reasonable viz. ensemble properties?

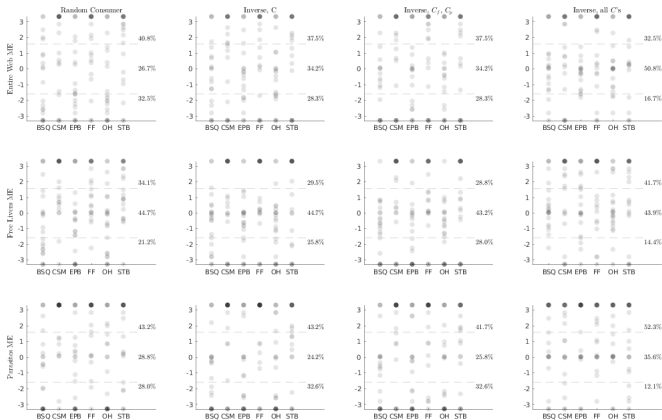
Laundry List of Properties

Property	Definition and Comments
Global and Comm. Props.	
Top,Int,Bas	The fraction of top, intermediate, and basal species in the web, respectively.
Herb,Carn	The fractions of herbivores and carnivores, respectively.
Omn	The fraction of species that consume both a basal and a non-basal species. The set {Top,Int,Bas,Herb,Carn,Omn} has only four degrees of freedom.
Cann	The fraction of cannibals in the food web.
ρ_{gV}	The correlation between generality and vulnerability.
σ_g	The standard deviation of generality.
σ_v	The standard deviation of vulnerability.
T	The mean prey-averaged trophic level.
FlowRankSD	The standard deviation of the FlowRank metric.
PATH	The average link distance of every species to every other.
Loop	The fraction of species involved in a loop.
EcoBtwn	The mean Ecological Betweenness over all species.
$\gamma^c, \gamma^r, \gamma^{rc}$, and γ^{cr} .	The clustering coefficients
MaxSim	The average of the maximum similarity of each species to all other species.
Community Properties	
\bar{v}, \bar{g}	Mean vulnerability and mean generality.
FlowRank	Based on eigenvalue of the augmented food web
C_{EB}	Ecological Betweenness
v_r and g_c	Mean vulnerability of resources and mean generality of consumers.

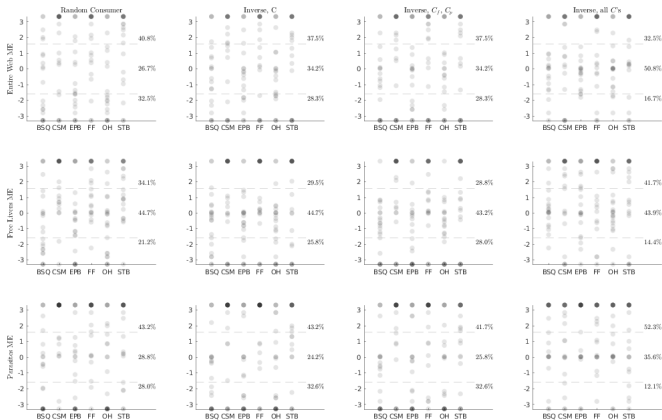
Entire Web Results



Free Liver Community Results



Parasite Community Results



Discussion

- ▶ Inverse niche model does better

Discussion

- ▶ Inverse niche model does better
- ▶ Matching subweb connectances is key

Discussion

- ▶ Inverse niche model does better
- ▶ Matching subweb connectances is key
- ▶ Scale dependence

Discussion

- ▶ Inverse niche model does better
- ▶ Matching subweb connectances is key
- ▶ Scale dependence
- ▶ Correlations in properties

ATN Model

Allometric Trophic Network Model

- ▶ All activity by a species is driven by metabolic rate

Allometric Trophic Network Model

- ▶ All activity by a species is driven by metabolic rate
- ▶ Metabolic rate scales allometrically

Allometric Trophic Network Model

- ▶ All activity by a species is driven by metabolic rate
- ▶ Metabolic rate scales allometrically
- ▶ $x_i = a_{x_i} M_i^{-0.25}$

Allometric Trophic Network Model

- ▶ All activity by a species is driven by metabolic rate
- ▶ Metabolic rate scales allometrically
- ▶ $x_i = a_{x_i} M_i^{-0.25}$
- ▶ Body size and body size ratios

Allometric Trophic Network Model

- ▶ All activity by a species is driven by metabolic rate
- ▶ Metabolic rate scales allometrically
- ▶ $x_i = a_{x_i} M_i^{-0.25}$
- ▶ Body size and body size ratios
- ▶ $M_i = Z^{T-1}$

Equations

$$\frac{dB_b}{dt} = r_b B_b \left(1 - \frac{\sum_{k \in \text{basal}} B_k}{K} \right) - \sum_k x_k B_k \frac{y_{bk} F_{bk}}{e_{bk}} \quad (1)$$

$$\frac{dB_c}{dt} = -x_c B_c + x_c B_c \sum_k y_{kc} F_{kc} - \sum_k x_k B_k \frac{y_{ck} F_{ck}}{e_{ck}} \quad (2)$$

Functional Response

“Attack rate on population of species i by a unit of species j ”

$$F_{ij} = \frac{\omega_{ij} B_i^{1+q}}{B_0^{1+q} + \sum_k \omega_{kj} B_k^{1+q}}$$

Consumer - Resource Body Size Ratio

- ▶ Want parasites Z_p times host and free livers Z_f times resource.

Consumer - Resource Body Size Ratio

- ▶ Want parasites Z_p times host and free livers Z_f times resource.
- ▶ Free liver i :

$$M_i = Z_f^{T_i-1}$$

Consumer - Resource Body Size Ratio

- ▶ Want parasites Z_p times host and free livers Z_f times resource.
- ▶ Free liver i :

$$M_i = Z_f^{T_i-1}$$

- ▶ p parasite: Maybe...?

$$M_i = Z_p^{T_i-1}$$

Consumer - Resource Body Size Ratio

- ▶ Want parasites Z_p times host and free livers Z_f times resource.
- ▶ Free liver i :

$$M_i = Z_f^{T_i-1}$$

- ▶ p parasite:

Wrong!

~~$$M_p = Z_p^{T_p-1}$$~~

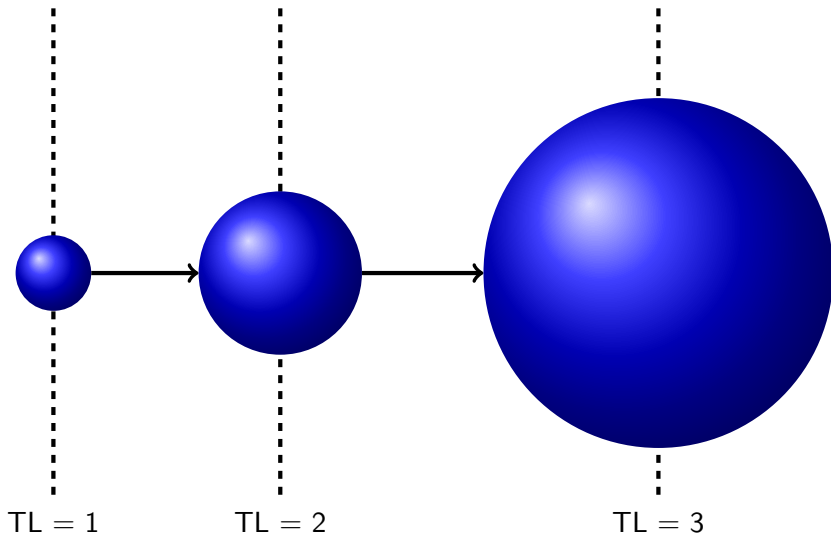
Body Size Hierarchy

$Z = 10$ (no parasites):

$M_f = 1$

$M_f = 10$

$M_f = 100$



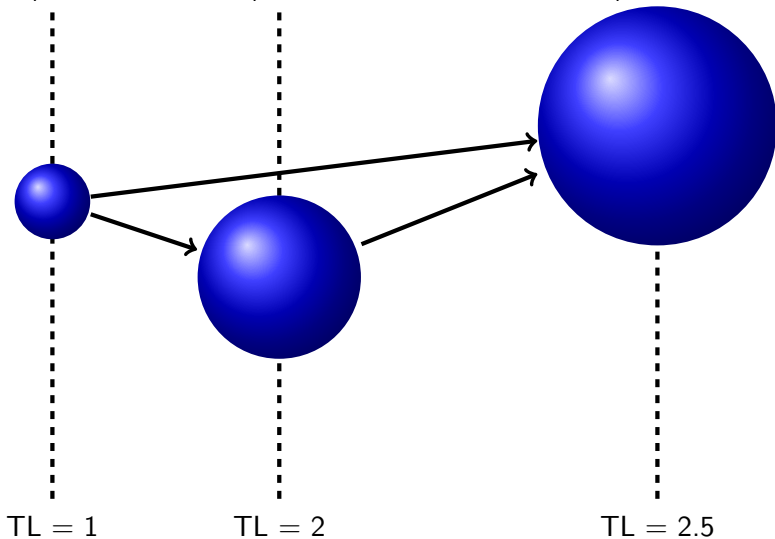
Body Size Hierarchy

$Z = 10$ (no parasites):

$M_f = 1$

$M_f = 10$

$M_f = 10^{1.5}$



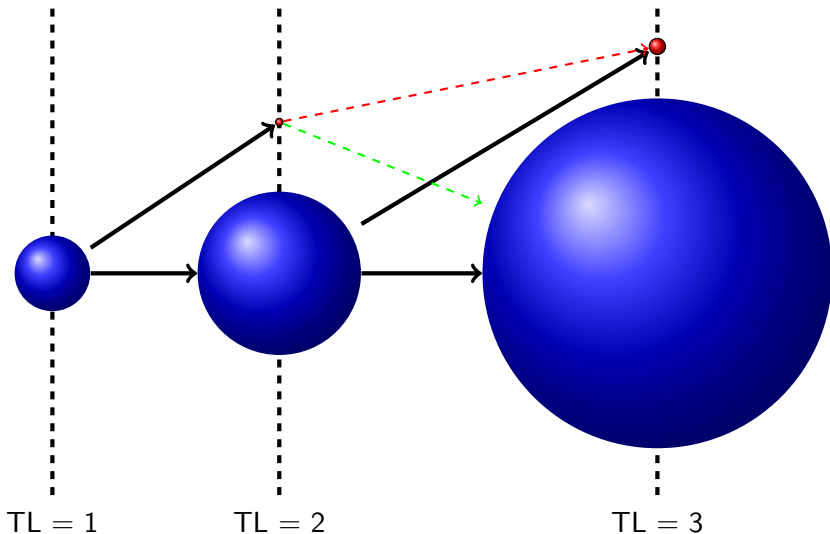
Body Size Hierarchy

$$Z_f = 10, Z_p = 10^{-3}$$

$$M_f = 1$$

$$M_f = 10, M_p = 10^{-3}$$

$$M_f = 100, M_p = 10^{-2}$$



Consumer - Resource Body Size Ratio

- ▶ If p and k : exponents of body size ratios of parasite-host and consumer-resource relationships,

Consumer - Resource Body Size Ratio

- ▶ If p and k : exponents of body size ratios of parasite-host and consumer-resource relationships,
- ▶ i free liver:

$$M_i = 10^{k(T_i-1)}$$

Consumer - Resource Body Size Ratio

- ▶ If p and k : exponents of body size ratios of parasite-host and consumer-resource relationships,

- ▶ i free liver:

$$M_i = 10^{k(T_i-1)}$$

- ▶ i parasite:

$$M_i = 10^{p+k(T_i-2)}$$

Modifications to ATN

- ▶ Concomittant predation

Modifications to ATN

- ▶ Concomittant predation
- ▶ Fraction of biomass outside host

Modifications to ATN

- ▶ Concomittant predation
- ▶ Fraction of biomass outside host
- ▶ Concomittant Diagram

Modifications to ATN

- ▶ Concomittant predation
- ▶ Fraction of biomass outside host
- ▶ Concomittant Diagram
- ▶ Cartoon of models

New Equations

$$\begin{aligned}\frac{dB_b}{dt} = & r_b B_b \left(1 - \frac{\sum_{k \in \text{basal}} B_k}{K} \right) - \sum_k \phi_k B_k x_k \frac{y_{bk} F_{bk}^{(\text{troph})}}{e_{bk}} \\ & - \sum_k (1 - \phi_k) B_k x_k \frac{y_{bk} F_{bk}^{(\text{para})}}{e_{bk}}\end{aligned}$$

$$\begin{aligned}\frac{dB_c}{dt} = & -x_c B_c + \phi_c x_c B_c \sum_k y_{kc} F_{kc}^{(\text{troph})} + (1 - \phi_c) x_c B_c \sum_k y_{kc} F_{kc}^{(\text{para})} \\ & - \sum_k \phi_k x_k B_k \frac{y_{ck} F_{ck}^{(\text{troph})}}{e_{ck}} - \sum_k (1 - \phi_k) x_k B_k \frac{y_{ck} F_{ck}^{(\text{para})}}{e_{ck}} - C_p\end{aligned}$$

New Functional Response

$$F_{ij}^{(troph)} = \frac{\omega_{ij}^{(troph)} (\phi_i B_i)^{1+h}}{B_0^{1+h} + \sum_k \omega_{kj}^{(troph)} (\phi_k B_k)^{1+h}}$$

$$F_{ij}^{(para)} = \frac{\omega_{ij}^{(para)} (\phi_i B_i)^{1+h}}{B_0^{1+h} + \sum_k \omega_{kj}^{(para)} (\phi_k B_k)^{1+h}}$$

Concomittant Losses



$$C_p = \sum_h a_{ph} L_h$$

Concomittant Losses



$$C_p = \sum_h a_{ph} L_h$$



$$a_{ph} = \frac{(1 - \phi_p) B_p}{B_h} \frac{y_{hp} F_{hp}^{(para)}}{\sum_k y_{kp} F_{kp}^{(para)}}$$

Concomittant Losses



$$C_p = \sum_h a_{ph} L_h$$



$$a_{ph} = \frac{(1 - \phi_p) B_p}{B_h} \frac{y_{hp} F_{hp}^{(para)}}{\sum_k y_{kp} F_{kp}^{(para)}}$$



$$L_h = \sum_k x_k B_k \frac{y_{kh} F_{kh}^{(troph)}}{e_{kh}}$$

Summary of Experiments

- ▶ $Z_f = 10,100$

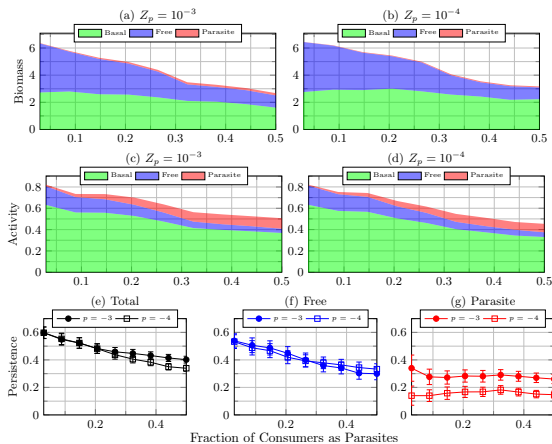
Summary of Experiments

- ▶ $Z_f = 10, 100$
- ▶ $Z_p = 10^{-3}, 10^{-4}$

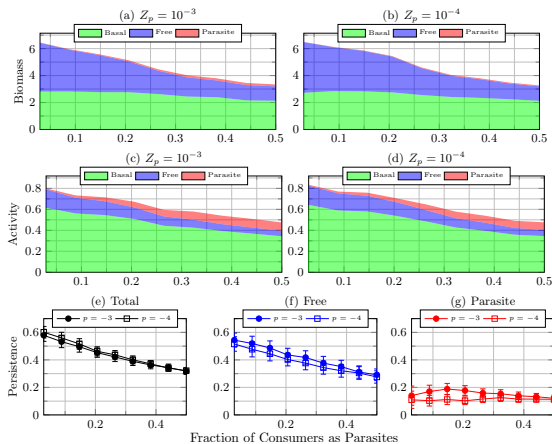
Summary of Experiments

- ▶ $Z_f = 10, 100$
- ▶ $Z_p = 10^{-3}, 10^{-4}$
- ▶ Different fractions of parasites

Results of Simulations: Null Model



Results of Simulations: Full Model



Final Thoughts

- ▶ Role of Parasites: Artifact or feature?

Final Thoughts

- ▶ Role of Parasites: Artifact or feature?
- ▶ Are the Food Web Models good enough?

Final Thoughts

- ▶ Role of Parasites: Artifact or feature?
- ▶ Are the Food Web Models good enough?
- ▶ Activity vs. Biomass