(Some explorations of the) evolution of functional responses

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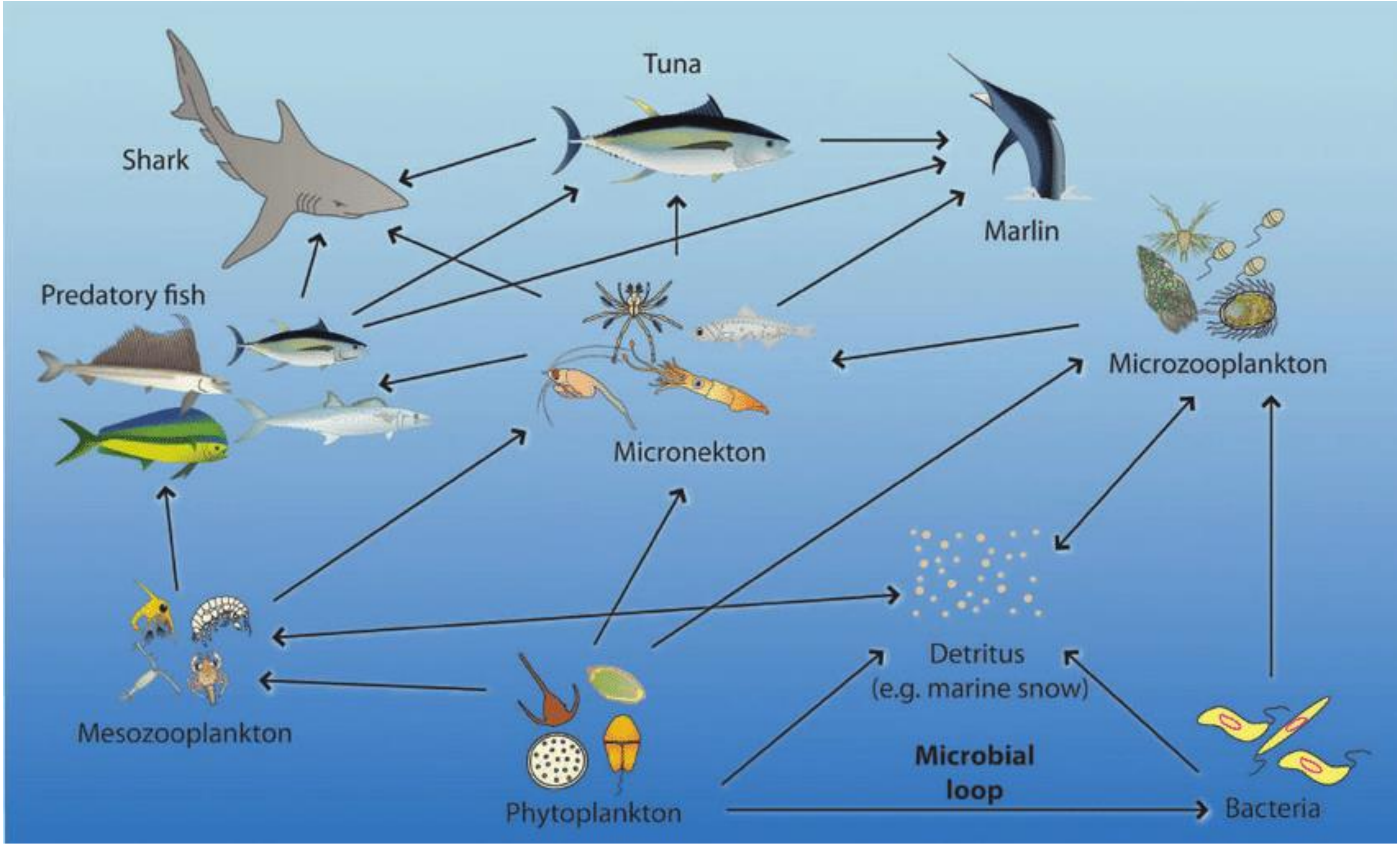
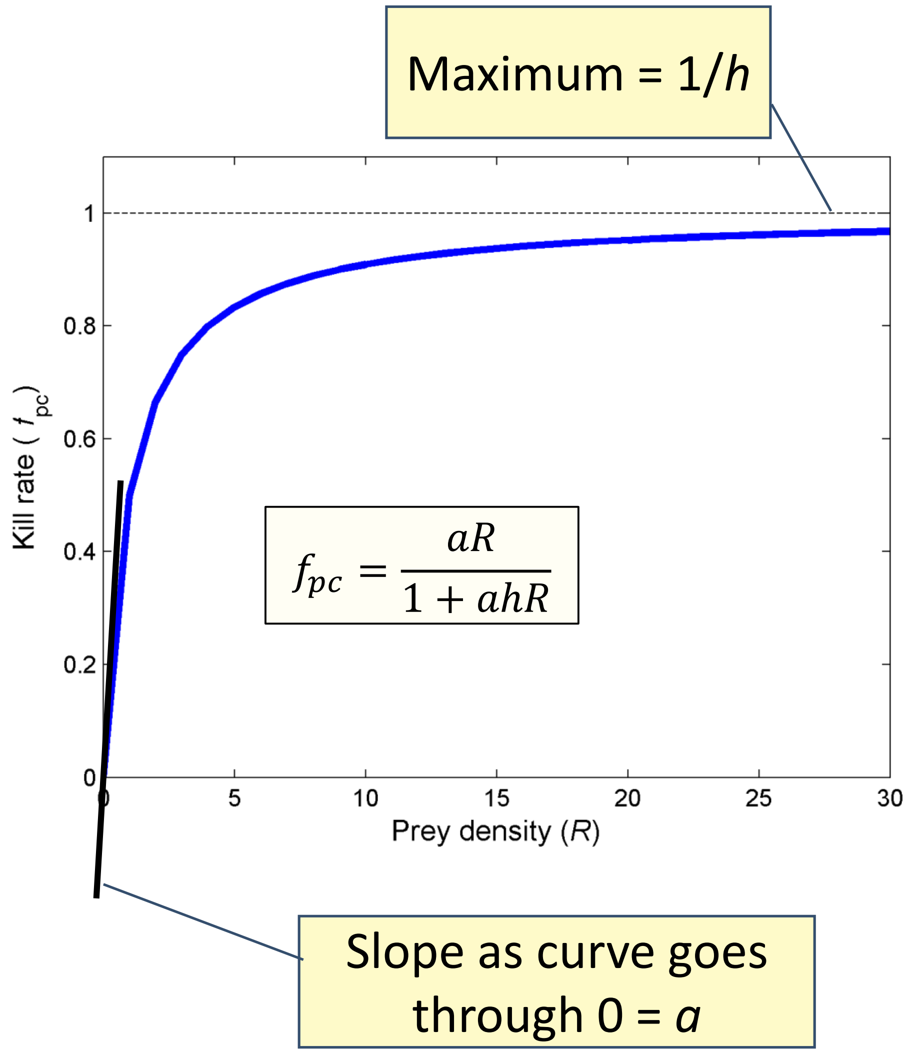
Food webs linked by consumption

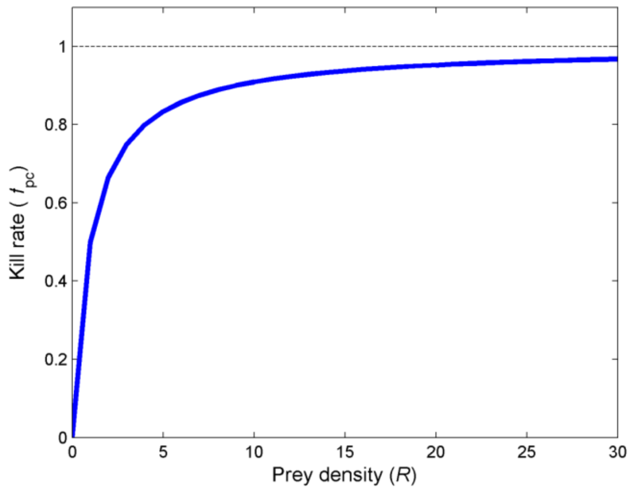


Allain et al 2015

Functional response



Why ‘space clearance rate’?



Units are rise/run:

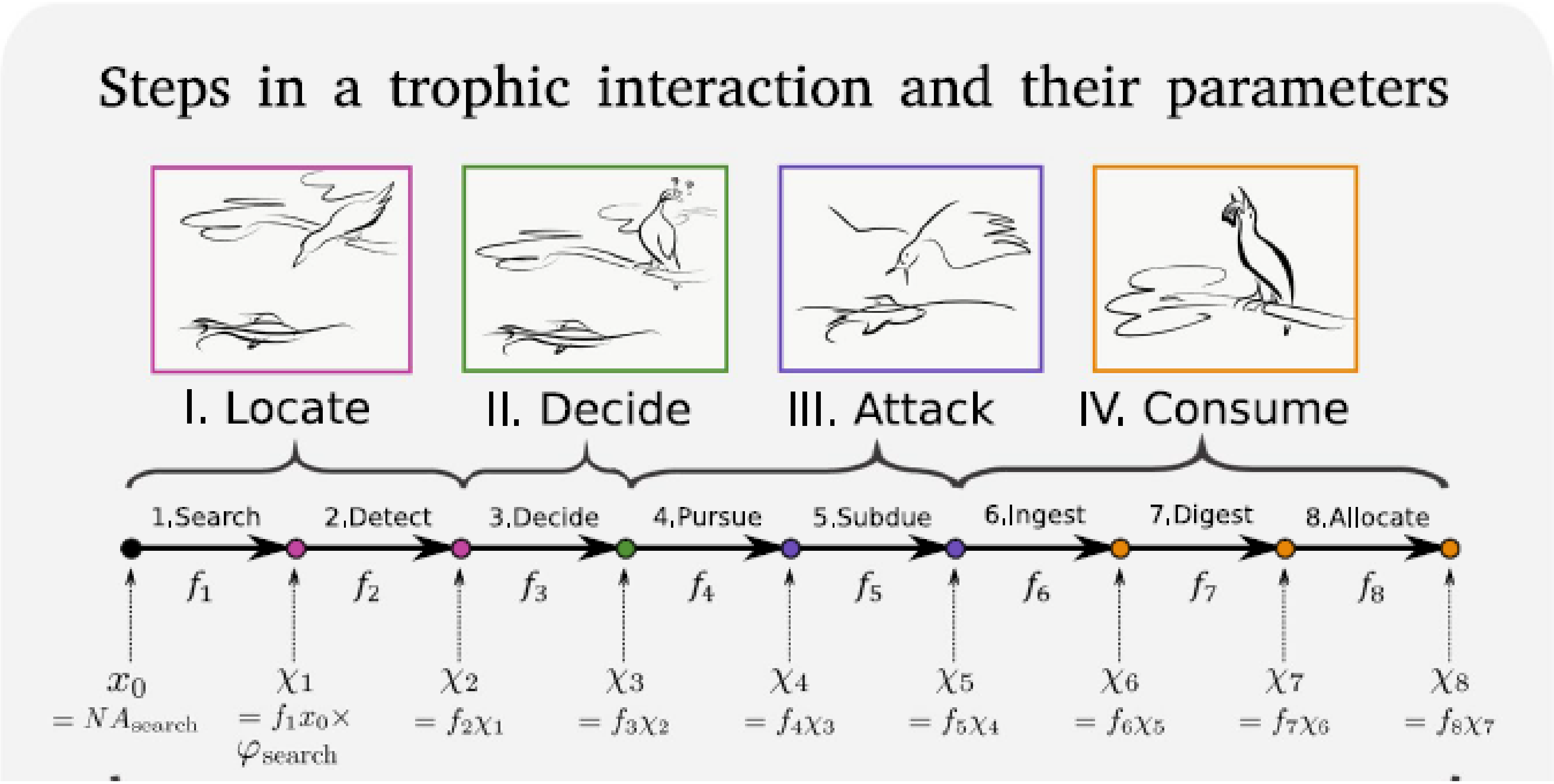
$$\frac{\left[\frac{prey}{pred \cdot time}\right]}{\left[\frac{prey}{space}\right]} = \left[\frac{space}{pred \cdot time}\right]$$

Why ‘space clearance rate’?

Names for ‘a’ in the literature:

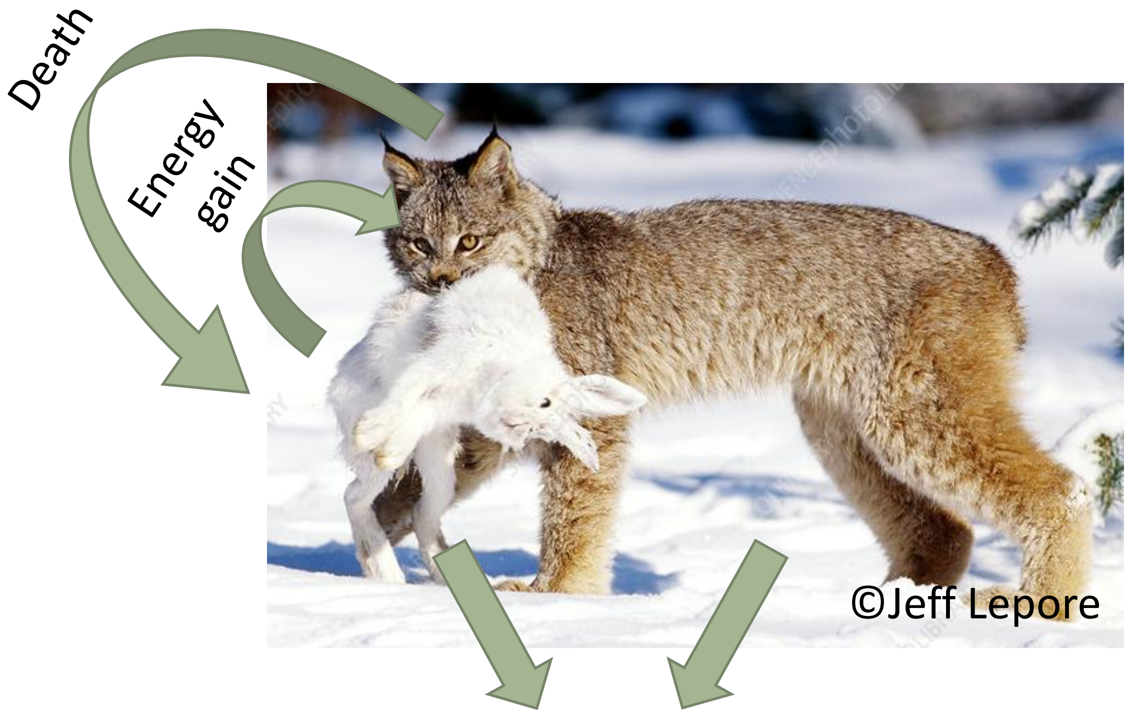
attack efficiency
attack rate
successful attack rate
attack constant
rate of successful search
capture rate
area of capture
maximum clearance rate
maximum per capita interaction strength
instantaneous rate of discovery
rate of potential detection
instantaneous search rate

Functional response parameters



Wootton et al 2021 FUN ECOL

Parameters emerge from interaction

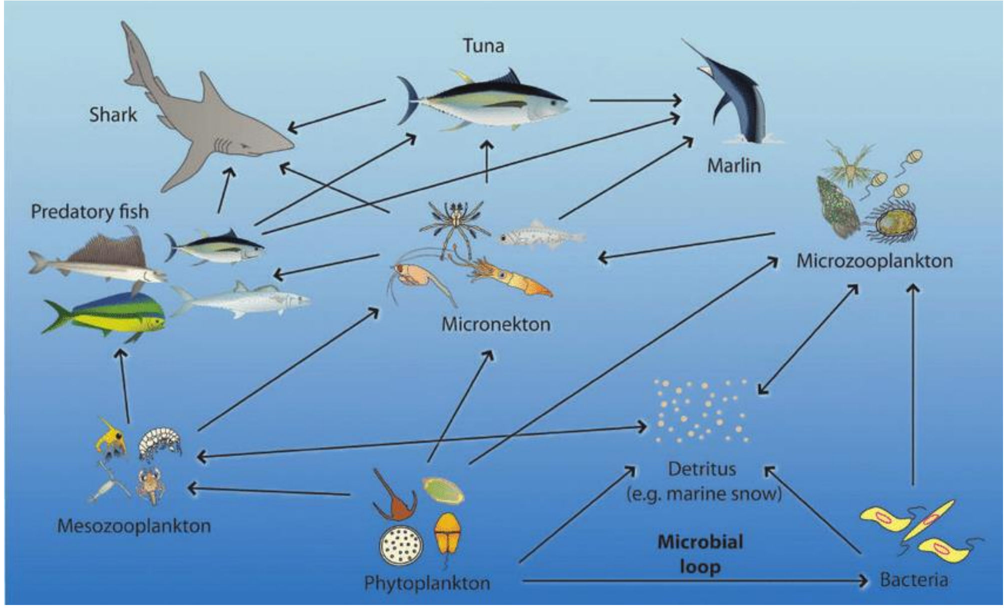


Encounters
Detections
Attacks
Success
Escape
Time costs

(a, h, … w, q)

Simple expectation

- ‘Better’ predators should be selected for
  - (higher ‘a’ and lower ‘h’)
- ‘Better’ prey should be selected for
  - (lower ‘a’ and higher ‘h’)



Two parts

1) How does increasing the number of prey types per se alter the evolution of ‘a’?
2) Co-evolution
    1) Does co-evolution alter selection on ‘a’?
    2) Does co-evolution of ‘a’ follow an arms-race, tug-of-war, or other paradigm?

Part 1. How does increasing the number of prey types alter the evolution of ‘a’?

DeLong and Coblentz 2022 Oikos

Fitness gradients

One prey species

$$\frac{dC}{dt} = e_1 \frac{a_1 R_1 C}{1 + a_1 h_1 R_1} - dC$$

$$\frac{\partial \frac{1}{C}\frac{dC}{dt}}{\partial a_1} = \frac{e_1 R_1}{(1 + a_1 h_1 R_1)^2}$$

Two prey species

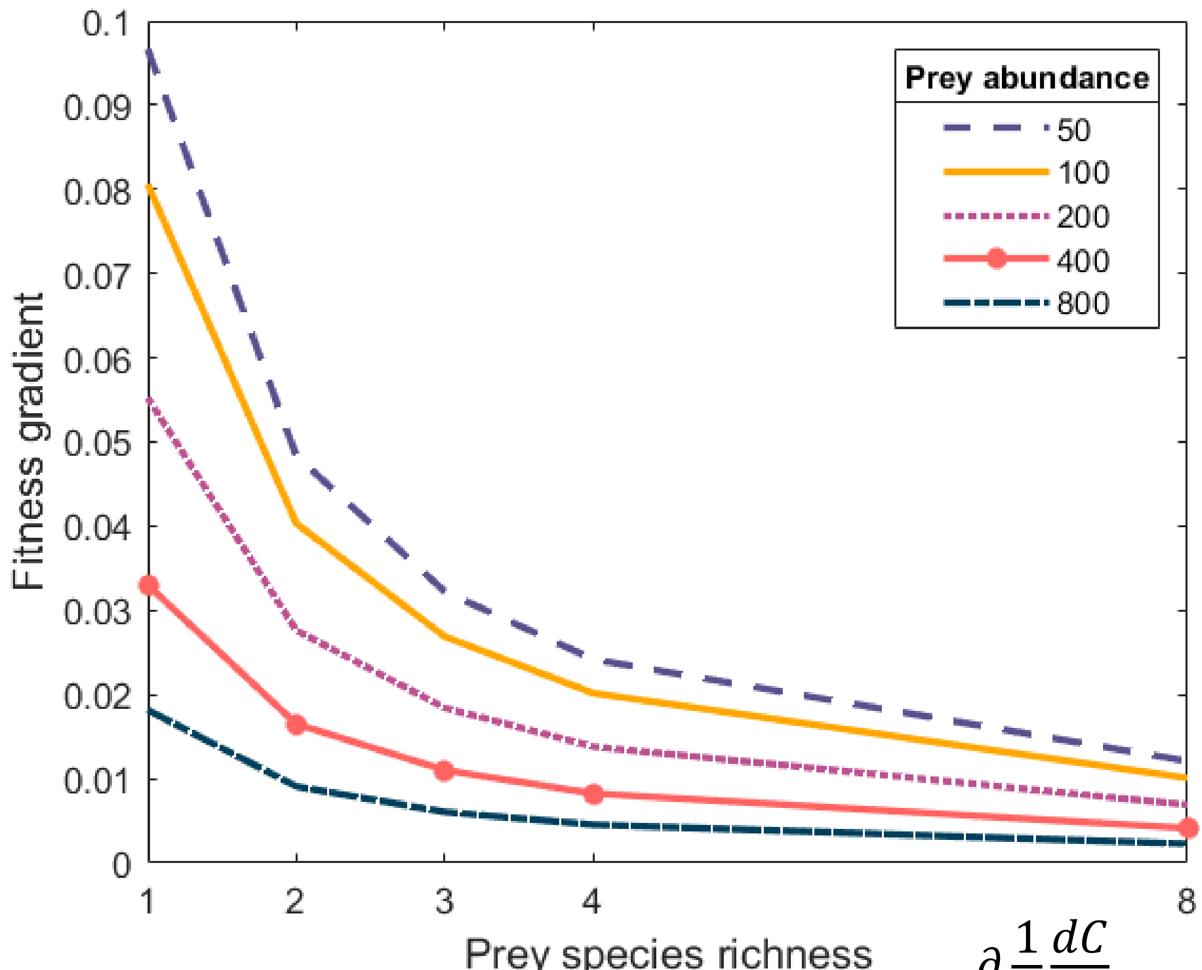
$$\frac{dC}{dt} = eC \frac{a_1 R_1 + a_2 R_2}{1 + a_1 R_1 h_1 + a_2 R_2 h_2} - dC$$

$$\frac{\partial \frac{1}{C}\frac{dC}{dt}}{\partial a_1} = \frac{eR_1(a_2 R_2 (h_2 - h_1) + 1)}{(1 + a_1 R_1 h_1 + a_2 R_2 h_2)^2}$$

Additional prey types can make denominator larger

DeLong and Coblentz 2022 Oikos

More prey -> shallower gradients



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$$\frac{\partial \frac{1}{C}\frac{dC}{dt}}{\partial a_1} = \frac{e_1 R_1}{(1 + a_1 h_1 R_1)^2}$$

Multi-species model

Multi-species functional response for *i* prey types

$$\frac{dC}{dt} = C\frac{\sum e_i a_i R_i}{1 + wC + \sum a_i R_i h_i} - dC$$

$$\frac{dR_i}{dt} = \left(b_{max,i} - \beta_i R_i - \sum \alpha_{ij} R_j\right) R_i - \left(d_{min,i} + \delta_i R_i + \sum \alpha_{ij} R_j\right) R_i - \frac{C a_i R_i}{1 + wC + \sum a_j h_j R_j}$$

Logistic with births and deaths separated out

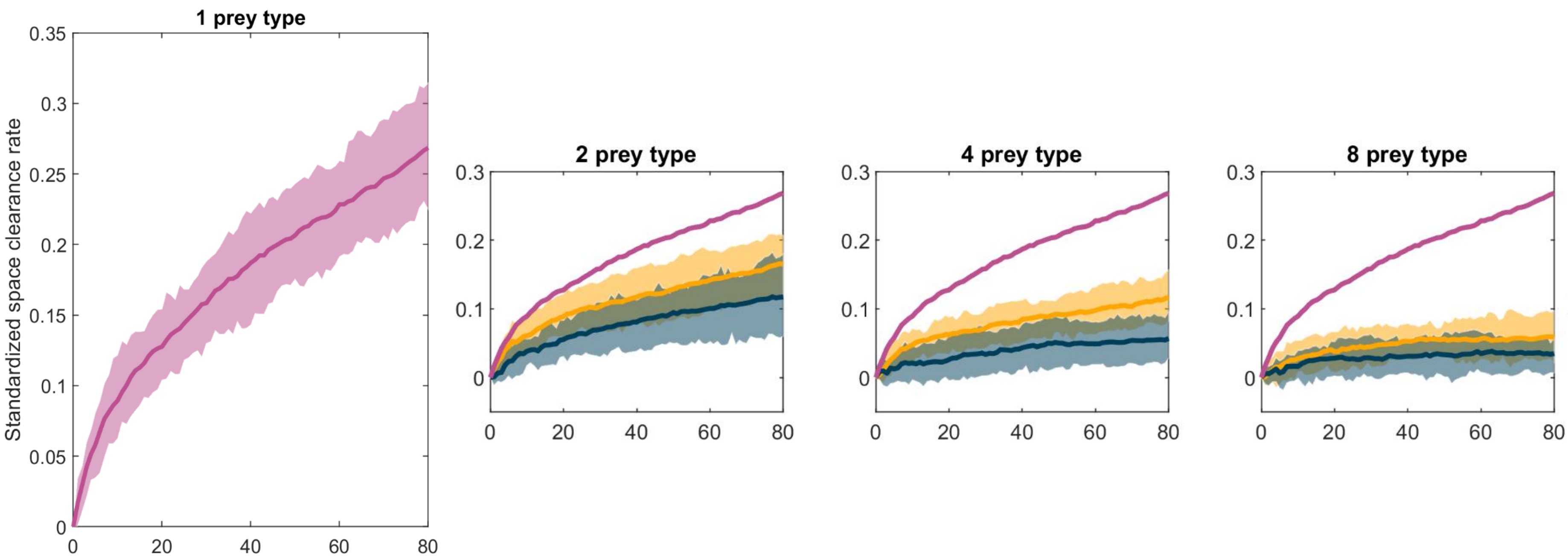
The *i* prey types can compete

DeLong and Coblentz 2022 Oikos

Gillespie Eco-evolutionary Model (GEM)

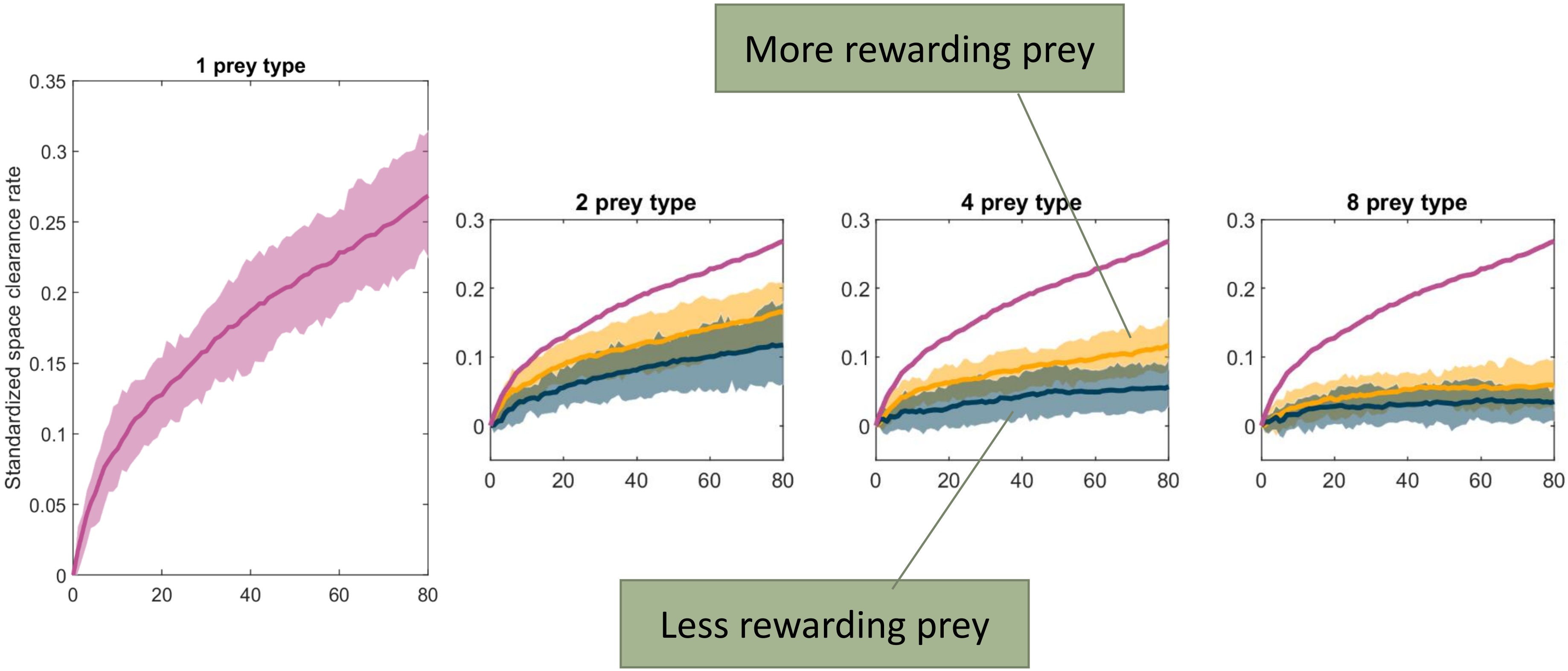
- Built on regular Gillespie approach to stochastic simulation of ODEs
- Use distribution of 'traits' instead of constants
- Sample those traits to run through the algorithm and advance time
- Traits that increase the likelihood of death get weeded out; traits that increase the likelihood of birth get bolstered
- GEMs are a computational analogue to natural selection

More prey lower increase in ‘a’



DeLong and Coblentz 2022 Oikos

Increase in ‘a’ higher for ‘better’ prey



DeLong and Coblentz 2022 Oikos

Part 2. Co-evolution of ‘a’.

Fitness gradients

$$\frac{dC}{dt} = e\frac{aRC}{1 + ahR} - dC$$

$$\boxed{\frac{\partial \frac{1}{C}\frac{dC}{dt}}{\partial a} = \frac{eR}{(1 + ahR)^2}}$$

DeLong and Coblentz *in prep*

Paradigms of co-evolution

- Arms race – toxins/resistance, acuity/camouflage
- Red Queen – ‘running to stand still’, with emphasis on persistence
- Tug-of-war – just pulling against each other
- Prey biased – shorter generation time of prey generally gives advantage over predators

DeLong and Coblentz *in prep*

When do these paradigms apply?

	Short	**Long**
Stable	*Prey biased*	*Tug-of-war*
Unstable	*Red Queen* *Arms race*	*Arms race*

DeLong and Coblentz *in prep*

MR model with ‘wasted time’

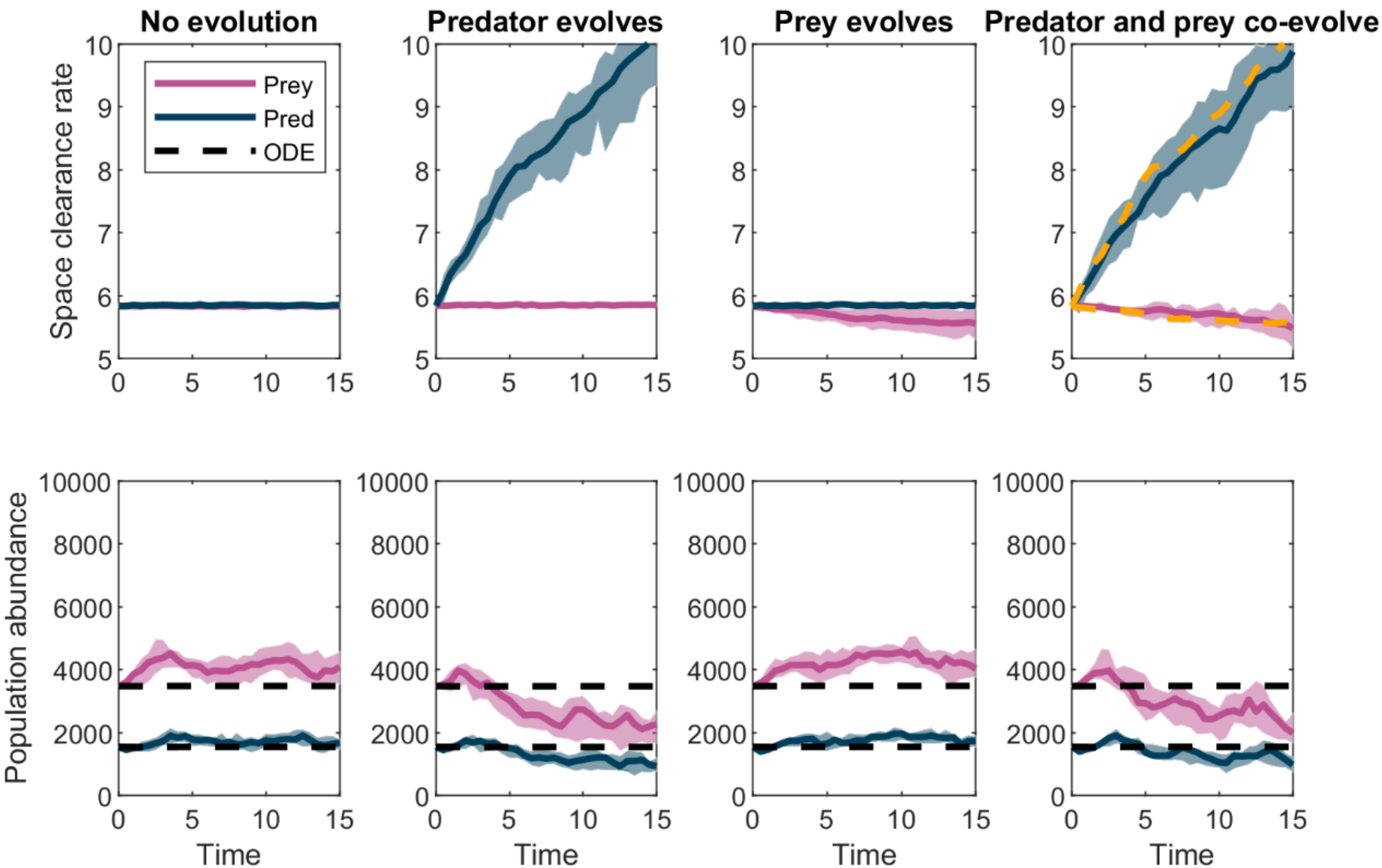
$$\frac{dC}{dt} = \frac{eaRC}{1 + w(C - 1) + ahR} - dC$$

$$\frac{dR}{dt} = (b_{max} - \beta R)R - (d_{min} + \delta R)R - \frac{CaR}{1 + w(C - 1) + ahR}$$

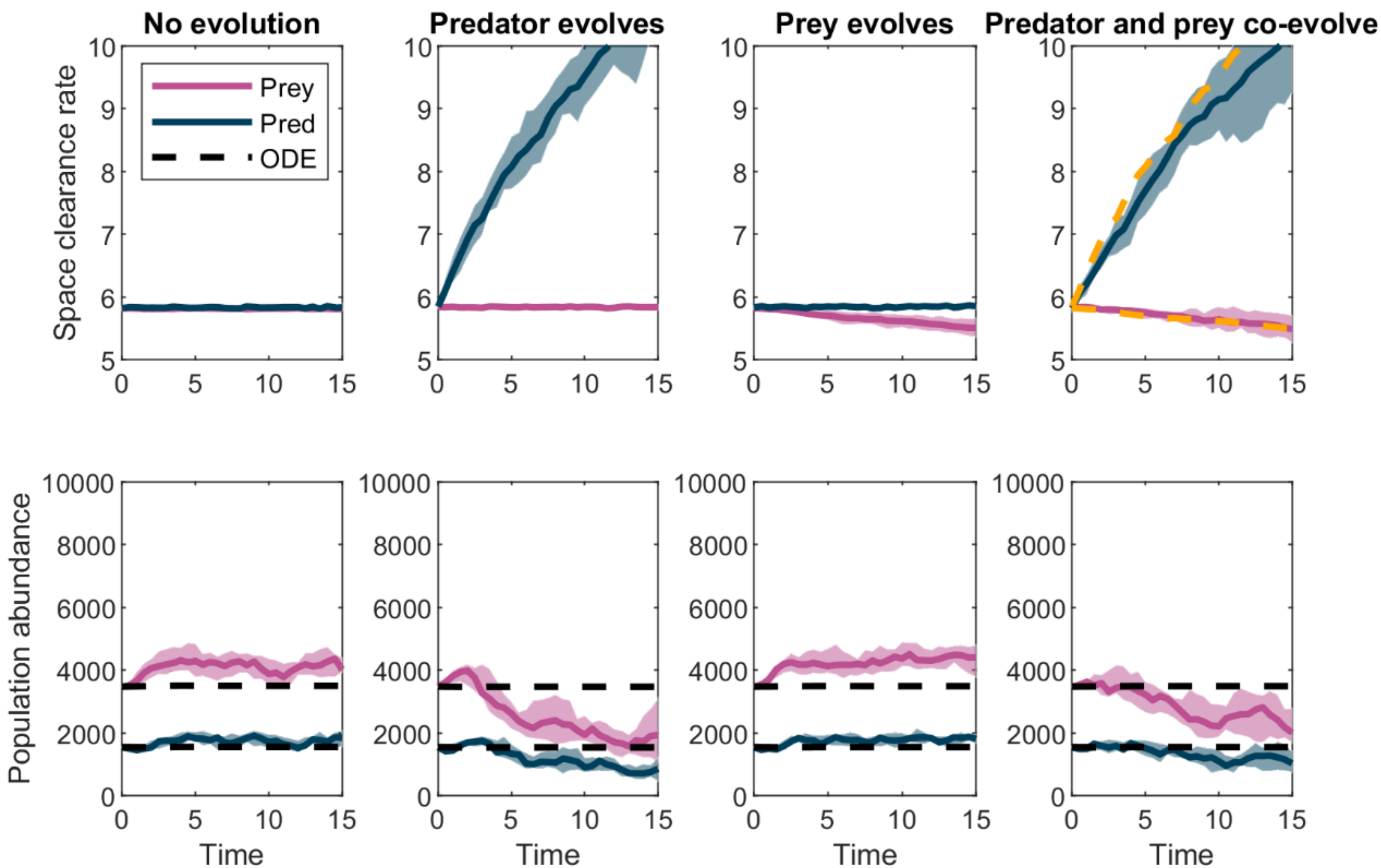
Logistic with births and deaths separated out – change magnitude of b and d to change generation time

Vary wasted time to vary stability

Short, stable

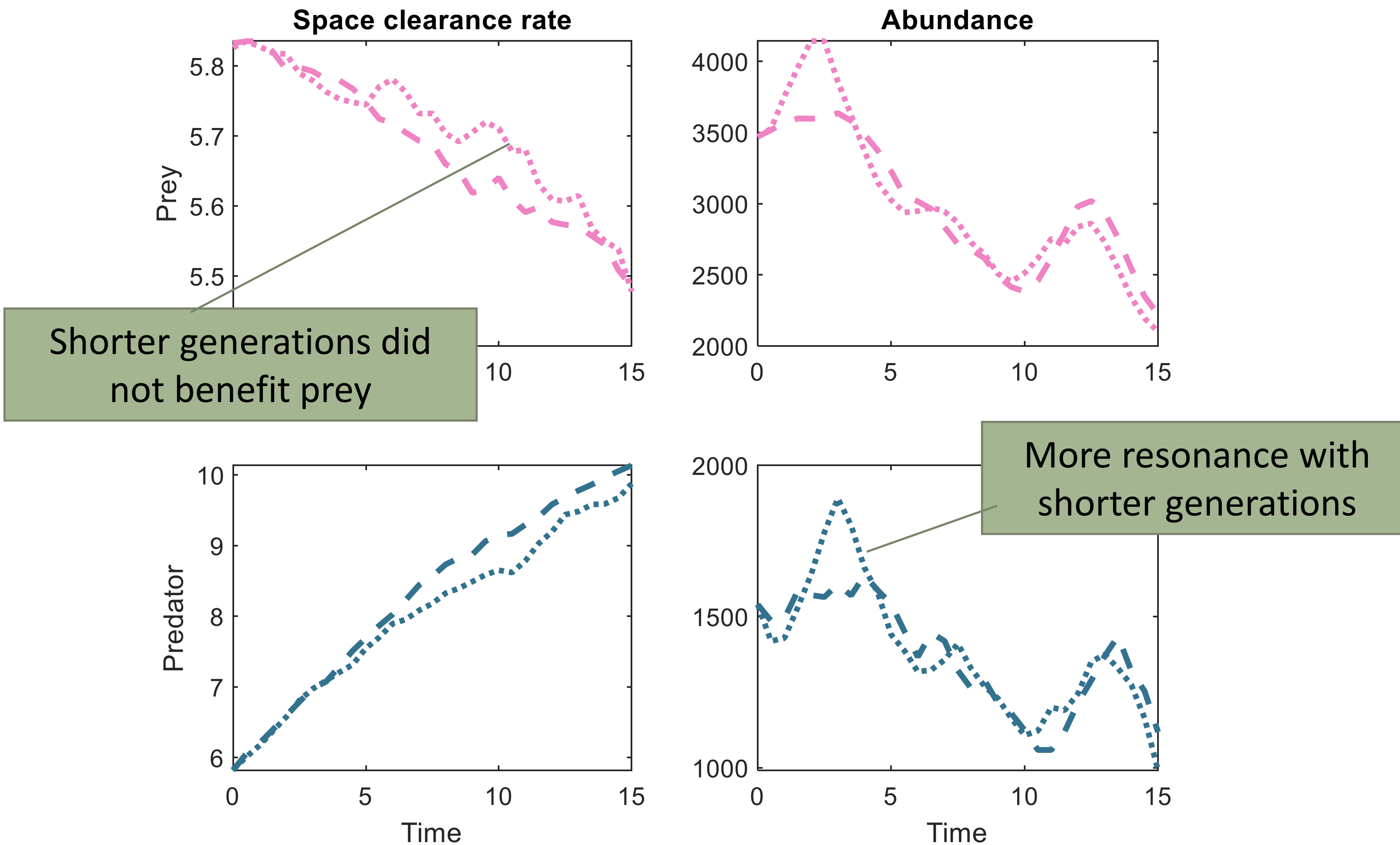


Long, stable

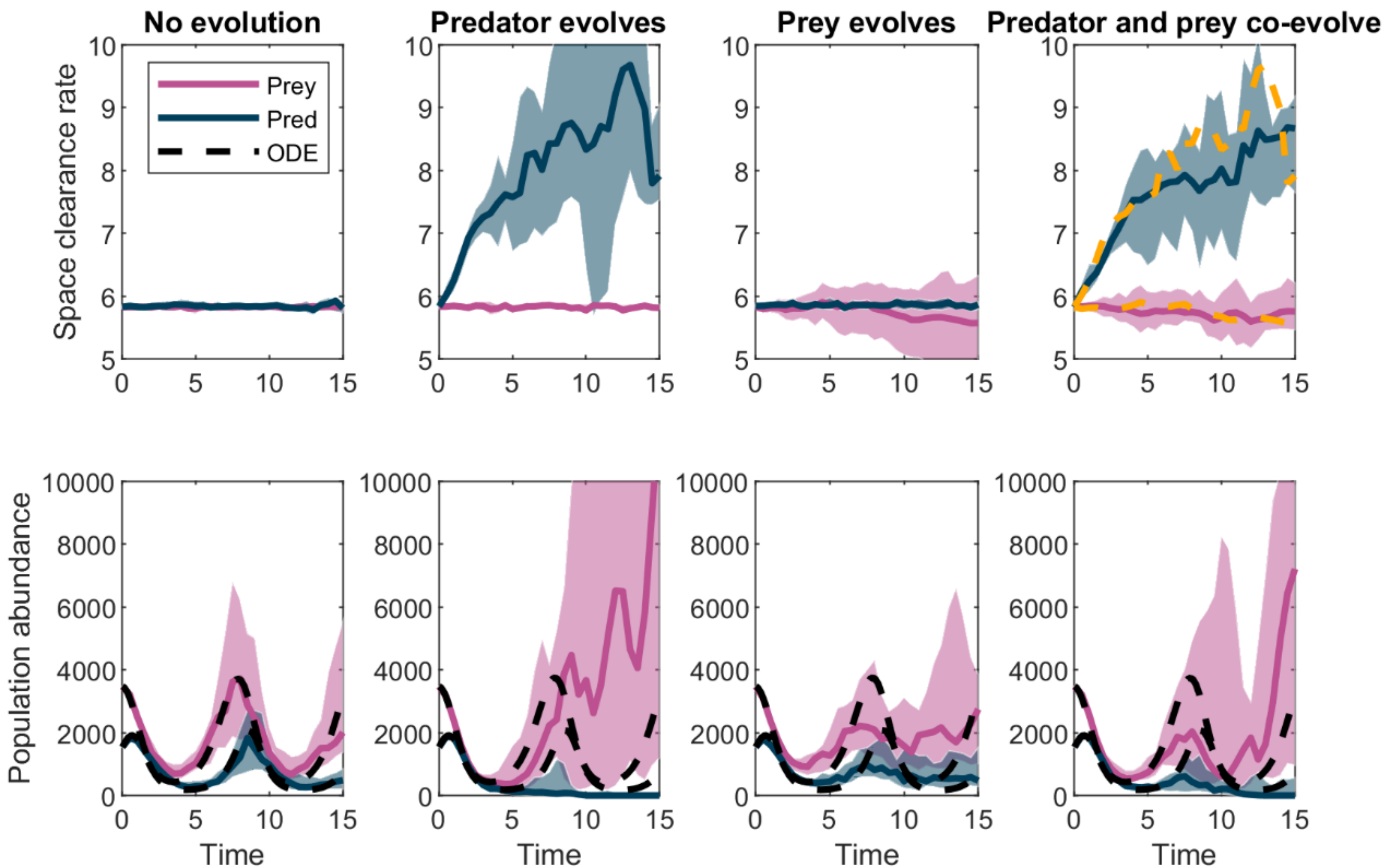


No evolution
Predator evolves
Prey evolves
Predator and prey co-evolve
Space clearance rate
Prey
Pred
ODE
10
9
8
7
6
5
0
5
10
15
Population abundance
10000
8000
6000
4000
2000
0
Time

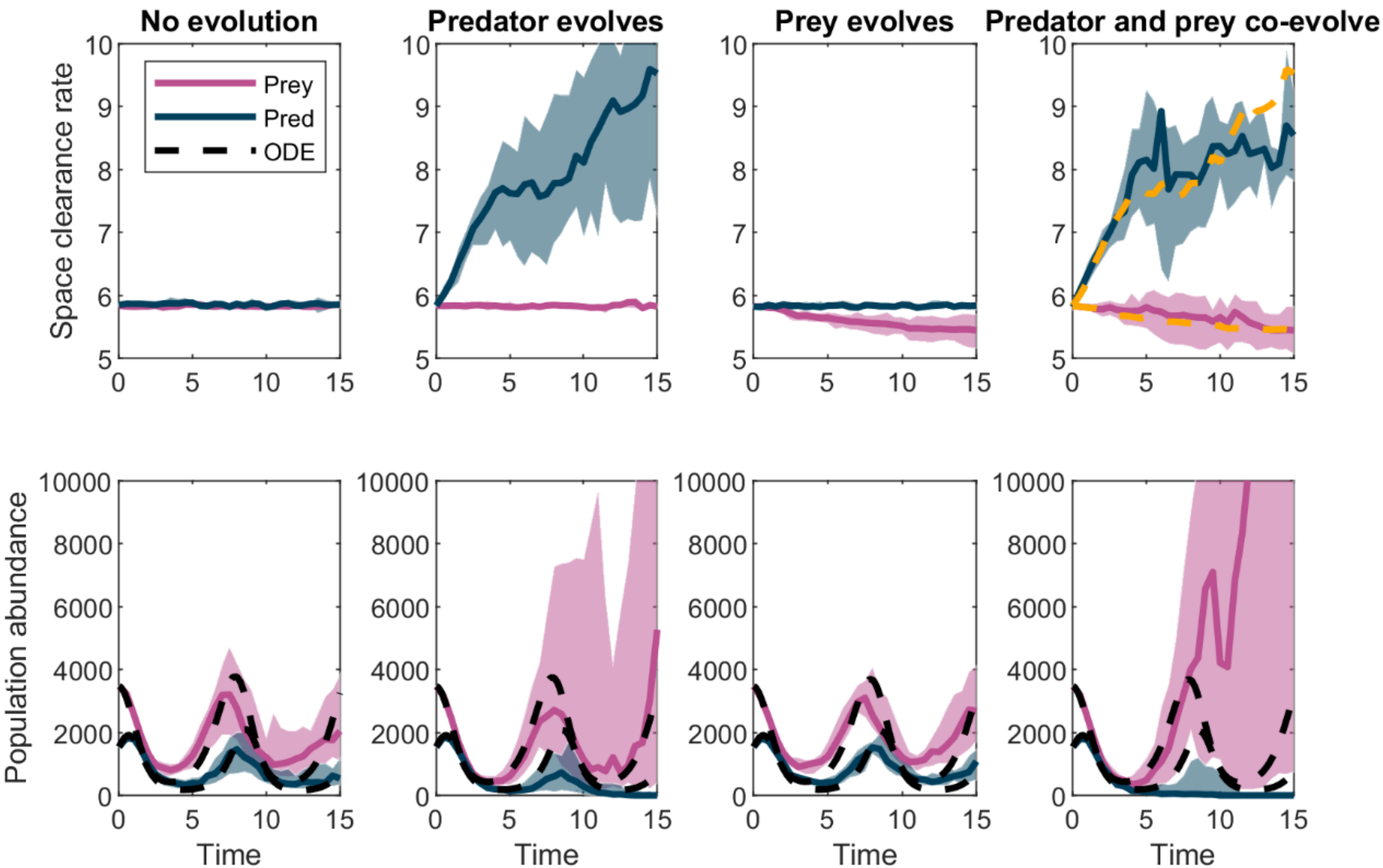
Short versus long



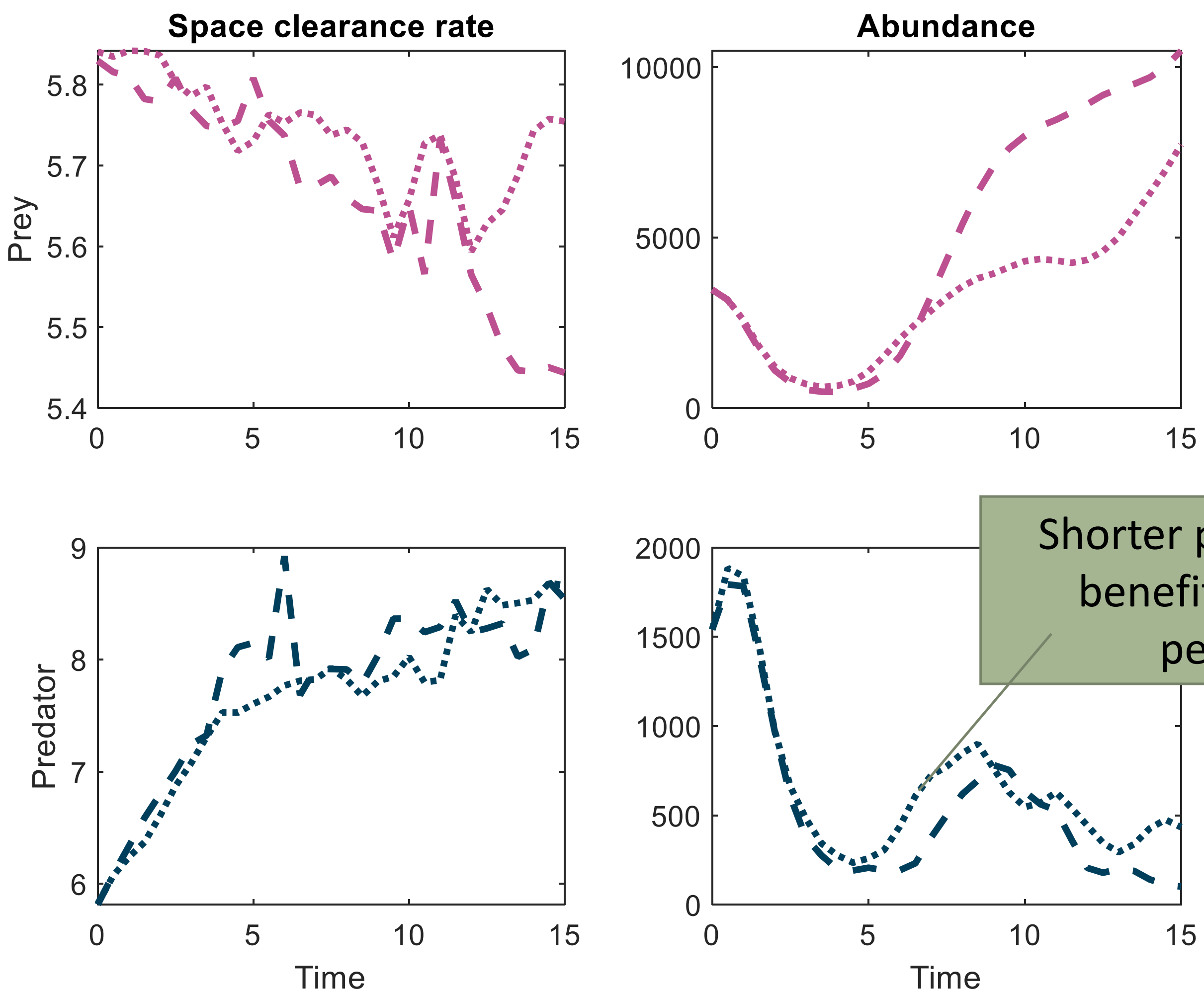
Short, unstable



Long, unstable



Together



Shorter prey generation benefitted predator persistence

Summary

- Functional responses
  - Process outcome
  - Parameters reflect underlying traits
  - Simple expectation of predator and prey getting better
- Part 1. Prey diversity
  - Increasing prey diversity reduces the value of increasing ‘a’, reducing evolution
  - ‘a’ increases more for more rewarding prey
  - Suggests many predators should retain broad diet with weak interactions
- Part 2. Co-evolution of ‘a’
  - Co-evolution not different than single-pop evolution
  - Mostly tug-of-war
  - Little evidence of Red Queen, Arms Race, or prey-favored outcomes

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