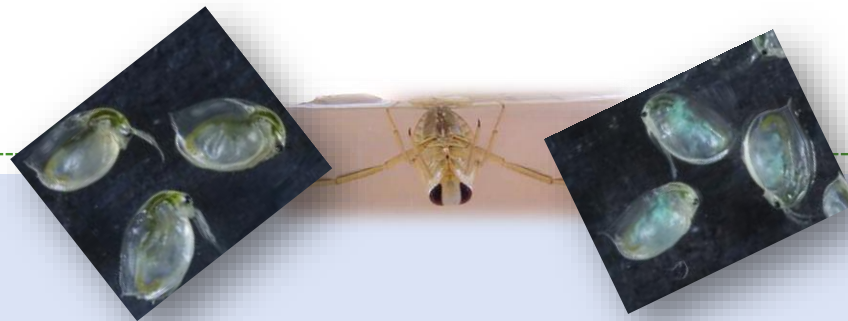


Prey infection alters predator diet



Loïc Prosnier, Florence Hulot, David Renault, Christophe Piscart,
Baptiste Biccocchi, Matthieu Lam, Vincent Médoc & Nicolas Loeuille

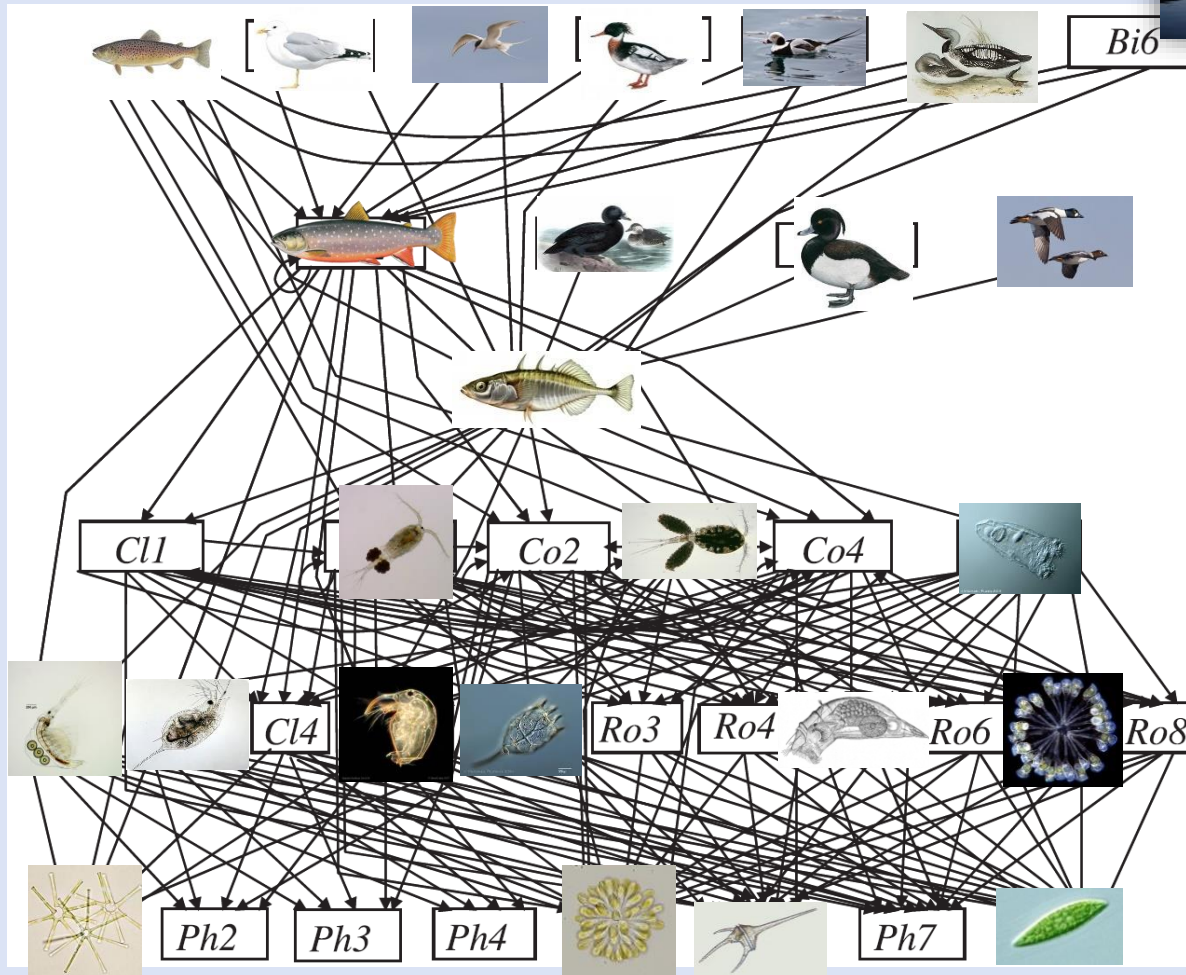
institute of Ecology and Environmental Sciences - Paris
Equipe de Neuro-Ethologie Sensorielle – Saint-Etienne
Ecologie Systematique Evolution – Orsay
Ecosystème, Biodiversité, Evolution - Rennes

Chaire MMB,
école de printemps d'Aussois
16 Juin 2021



From food webs without parasites ...

Pelagic food web of the subarctic lake Takvatn

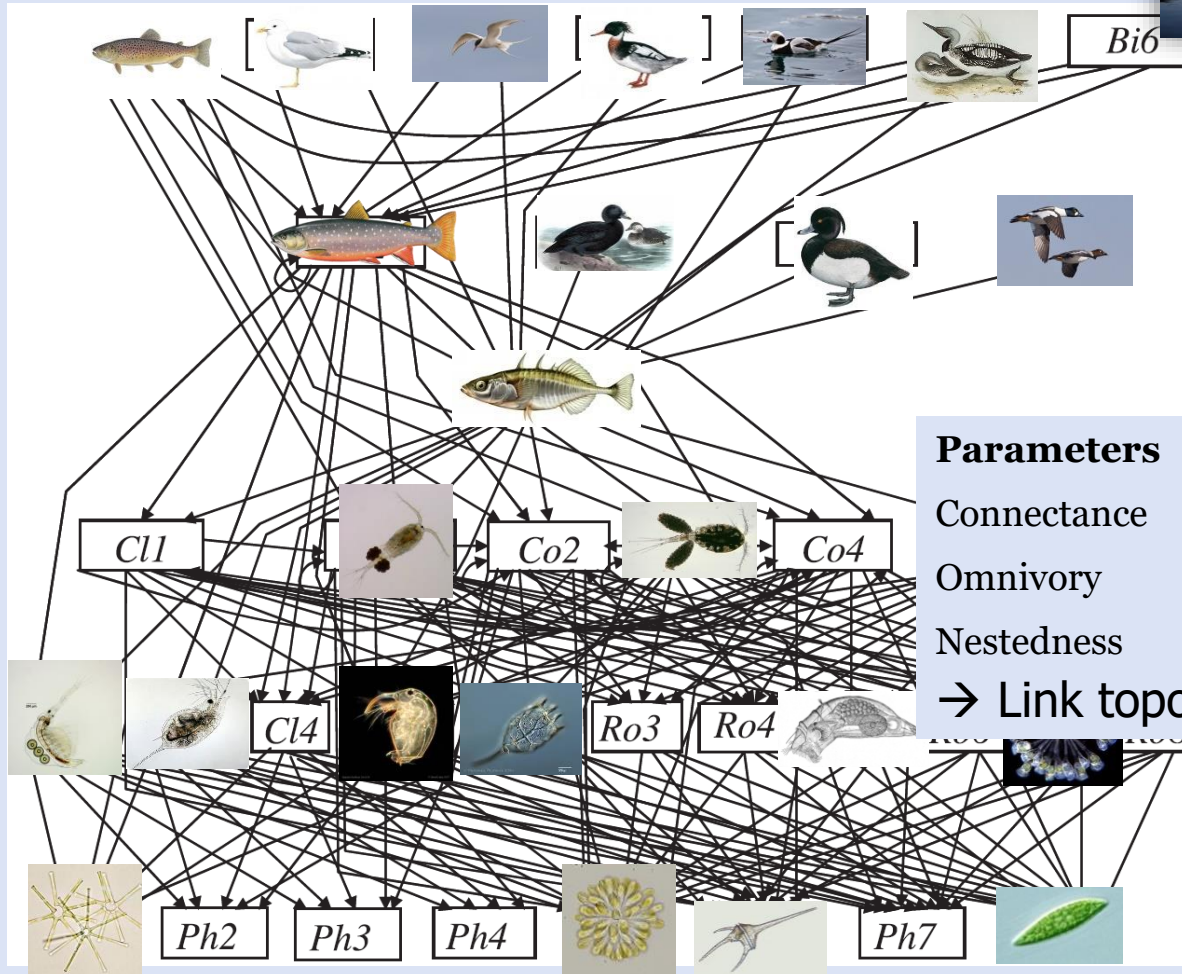


(Amundsen *et al.* 2009)

From food webs without parasites ...



Pelagic food web of the subarctic lake Takvatn



Parameters food web

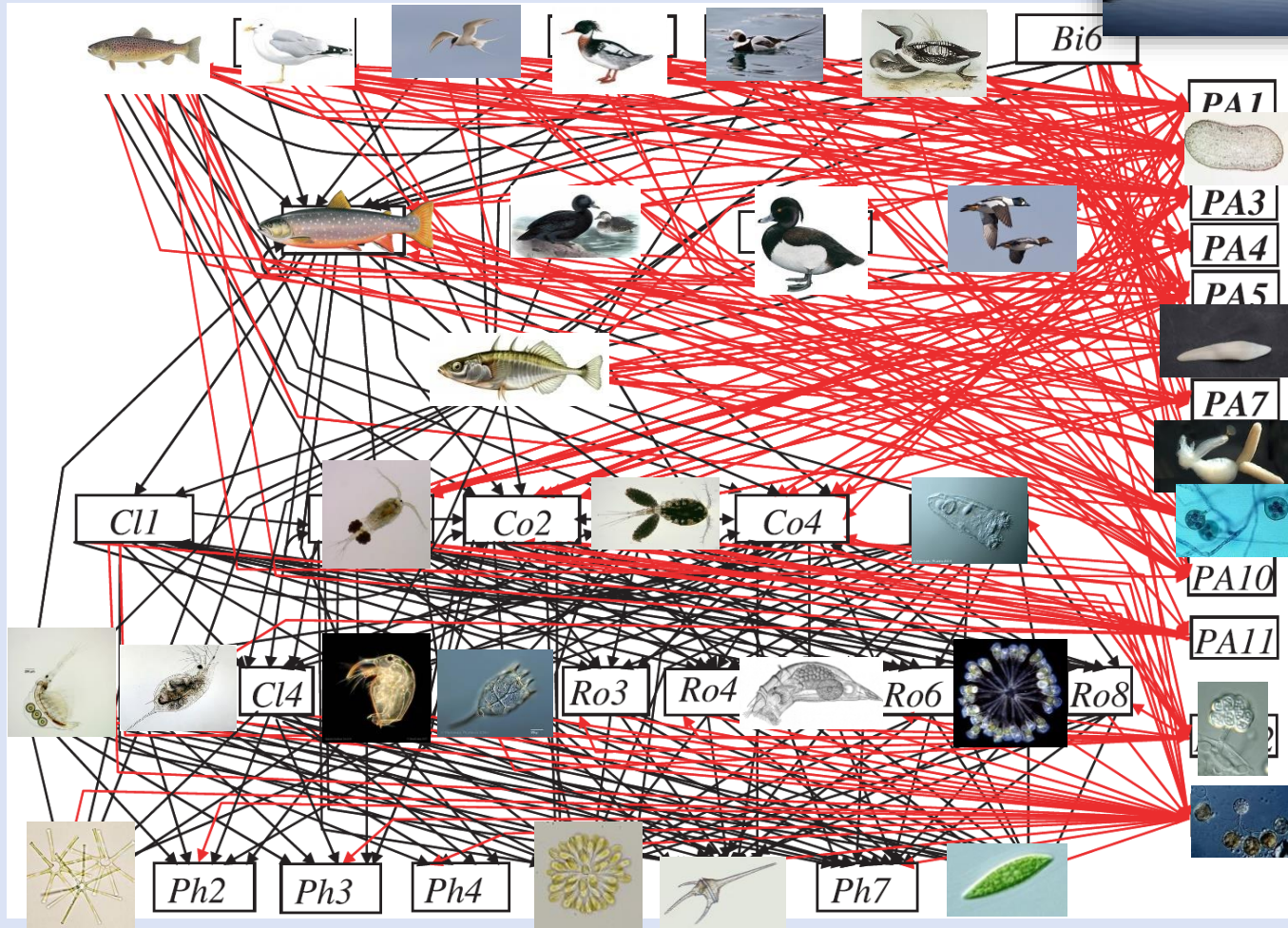
Connectance	0.145
Omnivory	1.86
Nestedness	0.10

→ Link topology to ecological property

(Amundsen *et al.* 2009)

... to food webs with parasites

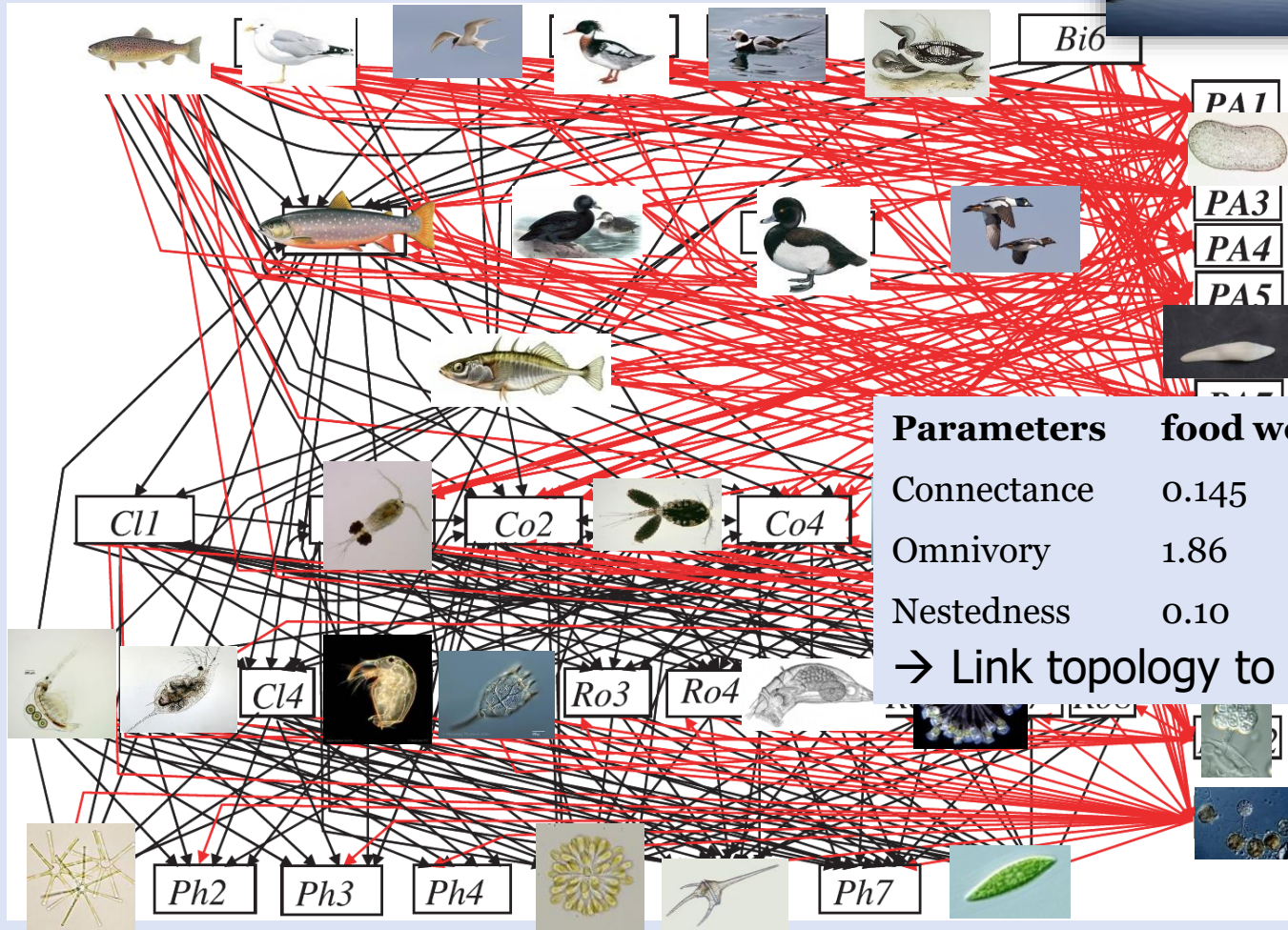
Pelagic food web of the subarctic lake Takvatn



(Amundsen *et al.* 2009)

... to food webs with parasites

Pelagic food web of the subarctic lake Takvatn



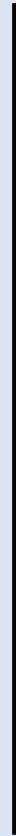
Parameters	food web	With parasites
Connectance	0.145	0.173
Omnivory	1.86	2.05
Nestedness	0.10	0.23

→ Link topology to ecological property?

(Amundsen *et al.* 2009)

Parasites

- Host alterations



Parasites

- Host alterations

Virulence effects

- ↗ mortality
- ↘ reproduction

(Schwartz & Cameron, 1993)

Trematodes



Daphnia obtusa

Parasites

- Host alterations

Virulence effects

- ↗ mortality
 - ↘ reproduction
- (Schwartz & Cameron, 1993)

Trematodes



Daphnia obtusa

Interaction effects

- Infected predator:
energy requirement

(Dick *et al.* 2010)

Acanthocephalan



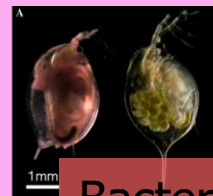
Gammarus pulex

- Infected prey:
vulnerability

(Médoc & Beisel, 2011)

(Goren & Ben Ami, 2017)

Acanthocephalan



Bacterial



Asellus aquaticus

Daphnia magna

Parasites

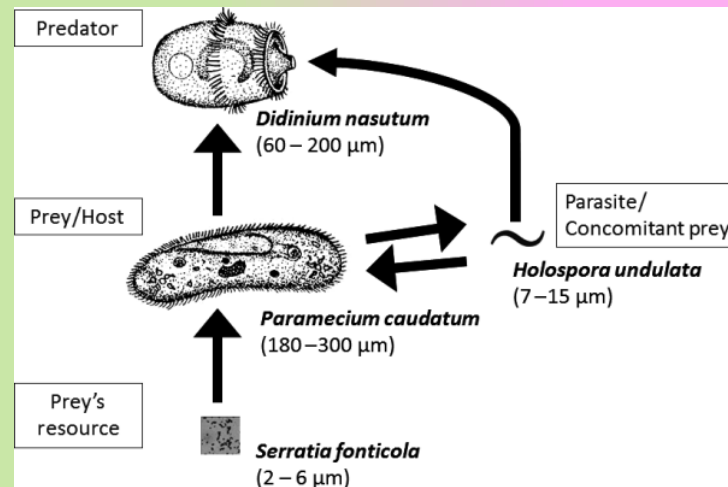
- Host alterations

Virulence effects

- ↗ mortality
 - ↘ reproduction
- (Schwartz & Cameron, 1993)

Interaction effects

- Energy requirement
- Vulnerability



(Banerji *et al.*, 2015)

Parasites

- Host alterations

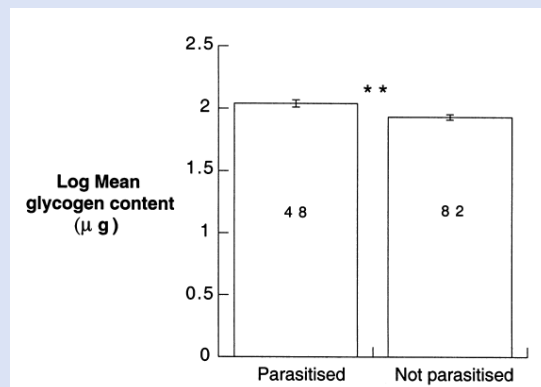
Virulence effects

- ↗ mortality
 - ↘ reproduction
- (Schwartz & Cameron, 1993)

Interaction effects

- Energy requirement
- Vulnerability

- Due to reallocation of host energetic resources



Gammarus pulex



(Plaistow *et al.*, 2001)

Predator diet

- Optimal foraging (Charnov, 1976)

An equation giving the rate of energy intake in a random encounter (non-patchy) situation may be derived as follows. Let E be the energy taken in during a feeding period of length T , which is made up of T_s (time searching) and T_h (time handling all prey items). A net rate of energy intake (En/T) is

$$\frac{En}{T} = \frac{E}{T_h + T_s}.$$

Predator diet

- Optimal foraging (Charnov, 1976)
 - Predators consume the most profitable prey

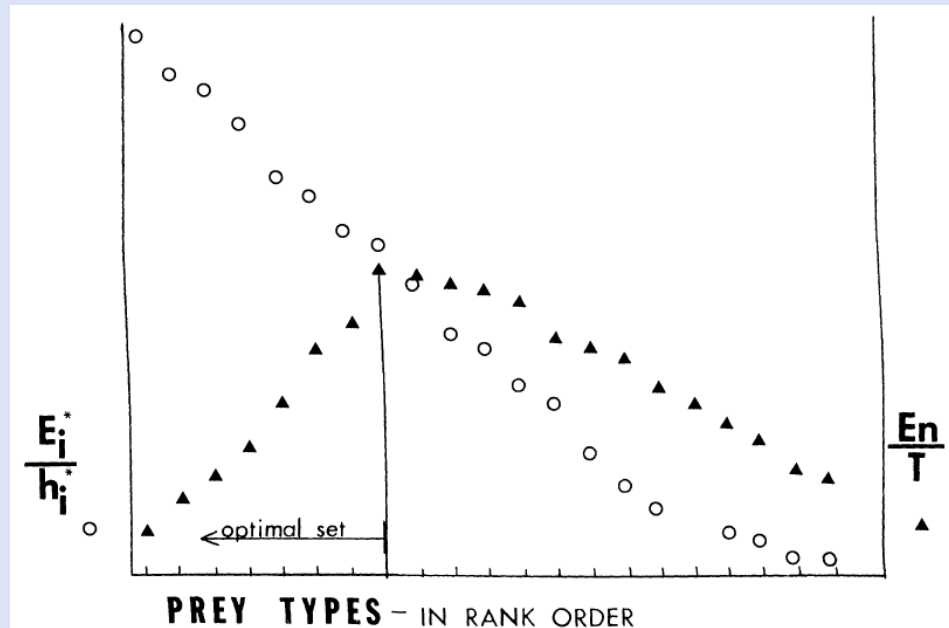


FIG. 1.—Choice of an optimal set of prey types. Prey types are first ranked by the E_i^*/h_i^* ratio, and then the cumulative En/T is calculated by adding prey types to En/T in rank order. En/T is maximized for a set of prey types of rank above the prey type (m) where En/T first becomes $> E_m^*/h_m^*$.

Predator diet

- Optimal foraging (Charnov, 1976)
 - Predators consume the most profitable prey

Prey energy content

Predator search time + Predator handling time

Predator diet

- Optimal foraging (Charnov, 1976)
→ Predators consume the most profitable prey

e.g. more glycogen but less lipid due to
infection (Plaistow *et al.*, 2001)

Prey energy content

Predator search time + Predator handling time

virulence and interaction effects

interaction effects

The prey infection: experiments

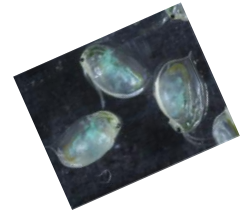
- Various measures on a parasite-host couple:
 - *Daphnia magna* and DIV-1 (White Fat Cell Disease)



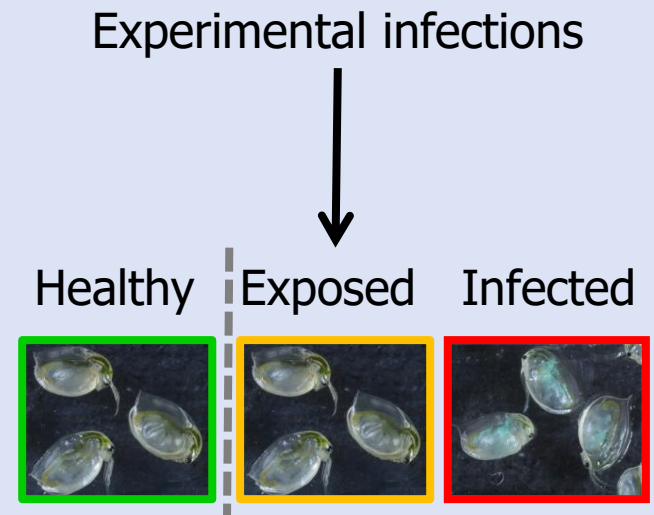
- Predator: *Notonecta sp.*

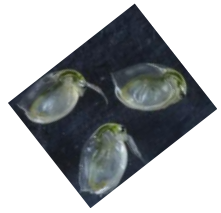


Assessment of virulence effects

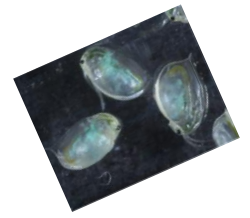


- Measures:
 - **Mortality**
 - **Fecundity**
 - **Fitness**

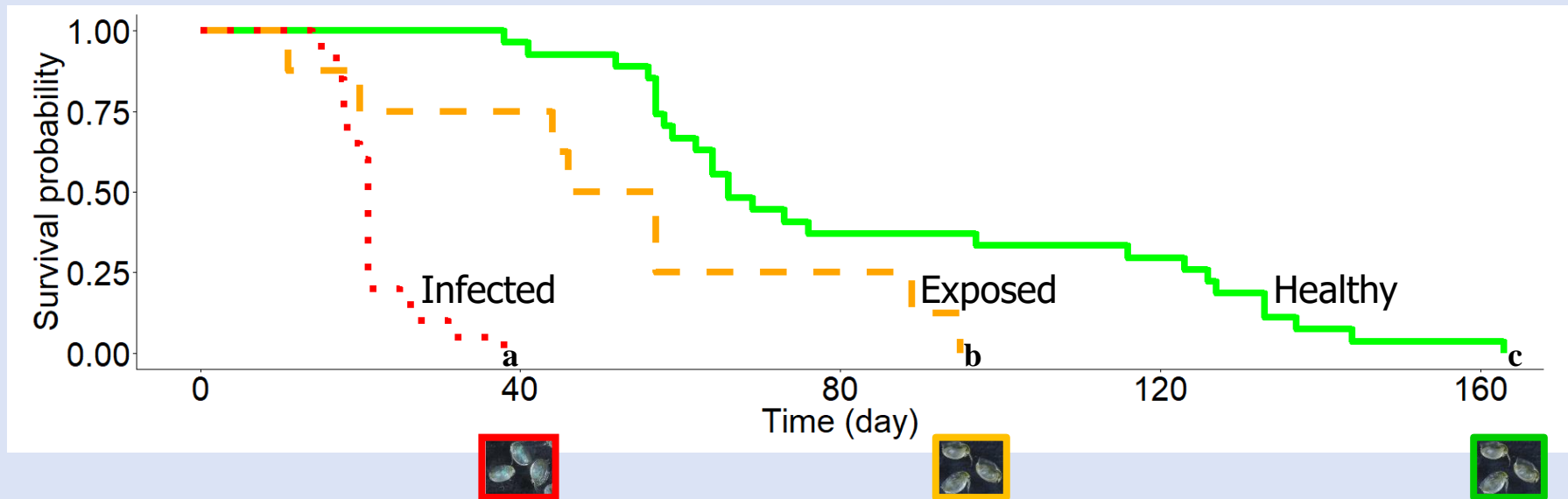




Virulence effects

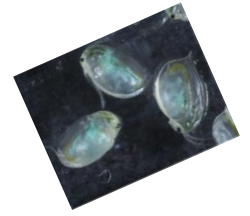


- Mortality
 - Increase of mortality





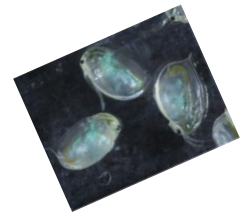
Virulence effects



- Mortality
 - Increase of mortality
 - No modification of juvenile mortality



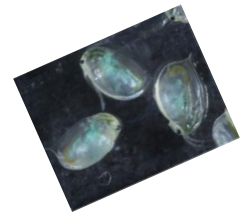
Virulence effects



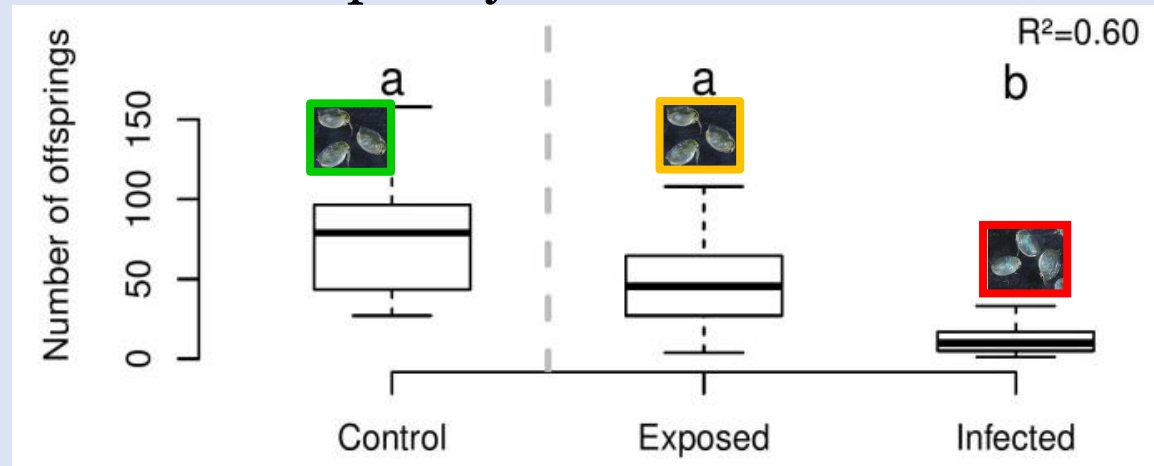
- Mortality
 - Increase of mortality
 - No modification of juvenile mortality
- Fecundity
 - Early first clutch of infected (age at maturity)
 - No modification of Clutches frequency and Mean clutches size



Virulence effects

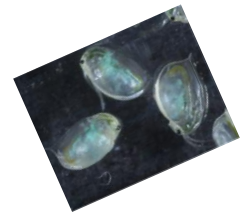


- Mortality
 - Increase of mortality
 - No modification of juvenile mortality
- Fecundity
 - Early first clutch of infected (age at maturity)
 - No modification of Clutches frequency and Mean clutches size
- Fitness
 - **Reduction of host fitness**





Assessment of visual alteration

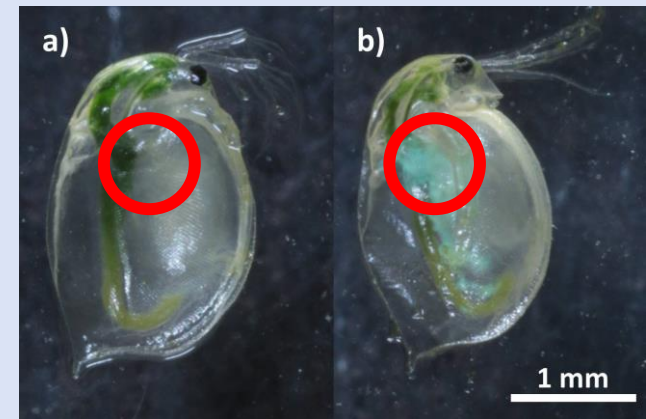


- Measures:

- Mortality
- Fecundity
- Fitness

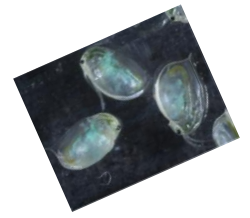
- **Reflectance**

→ In UV and Visible

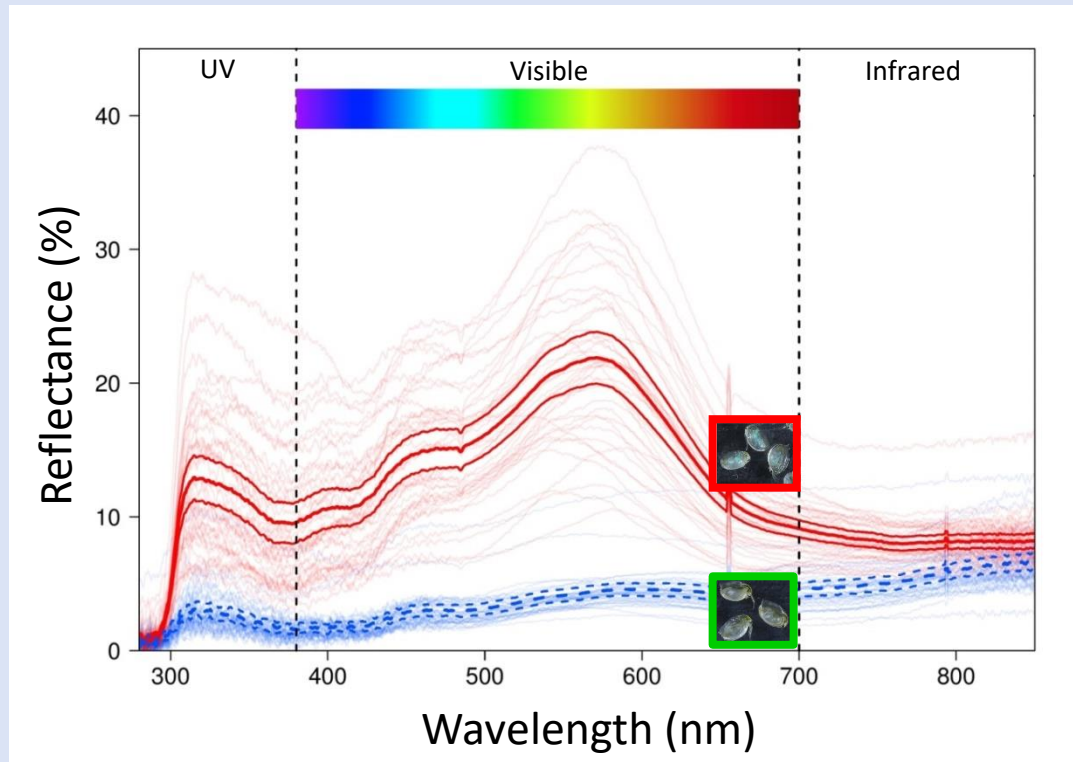


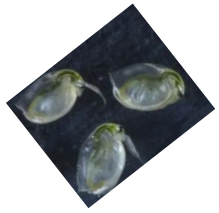


Interaction effects: reflectance

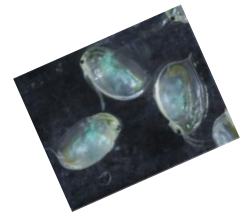


→ Higher reflectance of infected (UV and Visible)

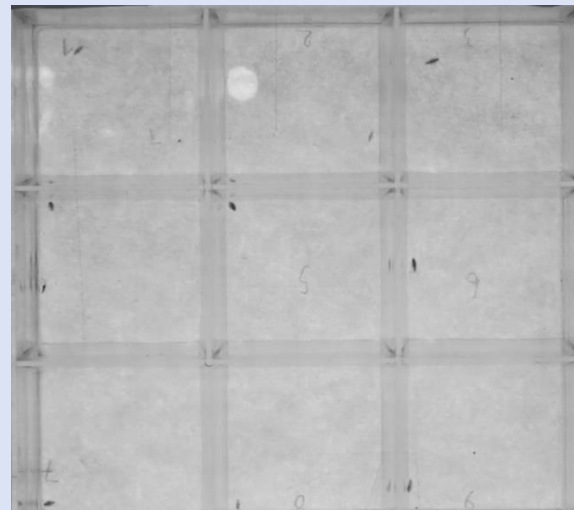




Assessment of visual alteration



- Measures:
 - Mortality
 - Fecundity
 - Fitness
 - Reflectance
 - **Behaviour**

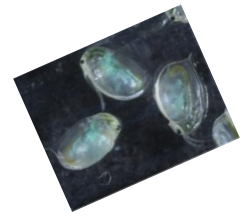


Day 14th

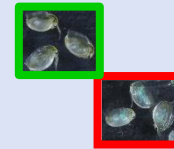
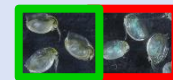
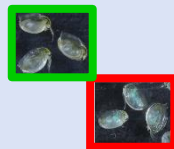
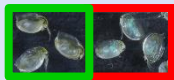
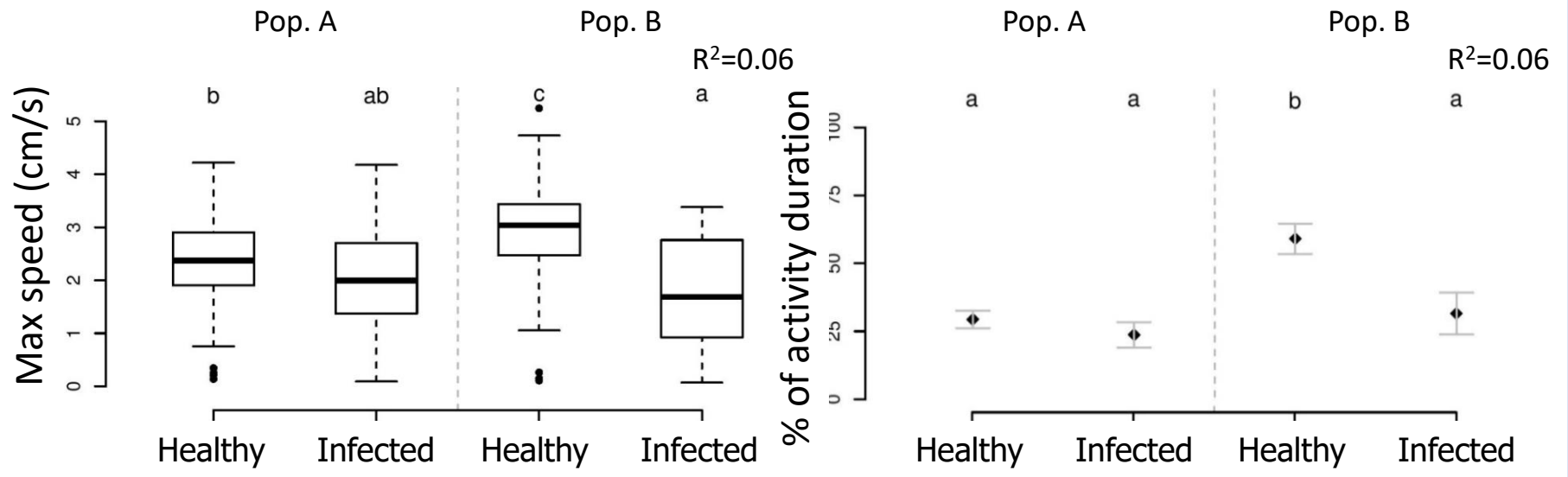


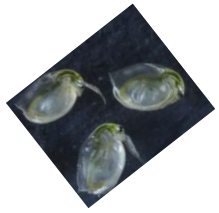


Interaction effects: behaviour

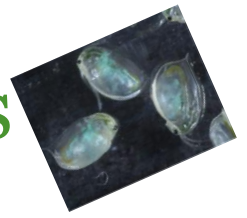


→ No effect or Lower activity of infected

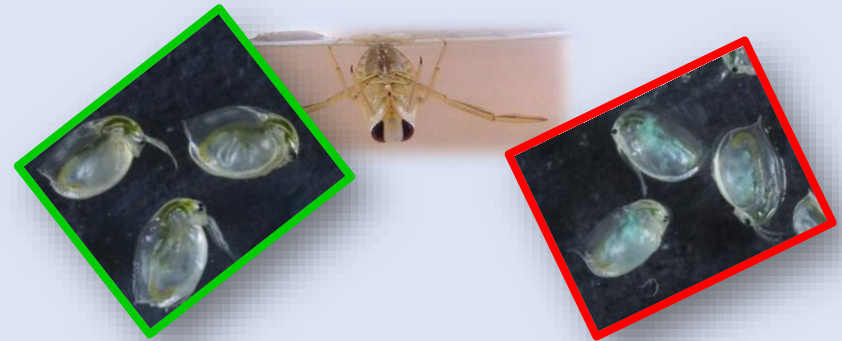




Assessment of interaction effects

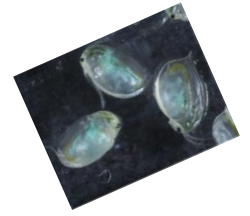


- Measures:
 - Mortality
 - Fecundity
 - Fitness
 - Reflectance
 - Behaviour
 - **Search time**
 - **Handling time**
 - **Predator preference**

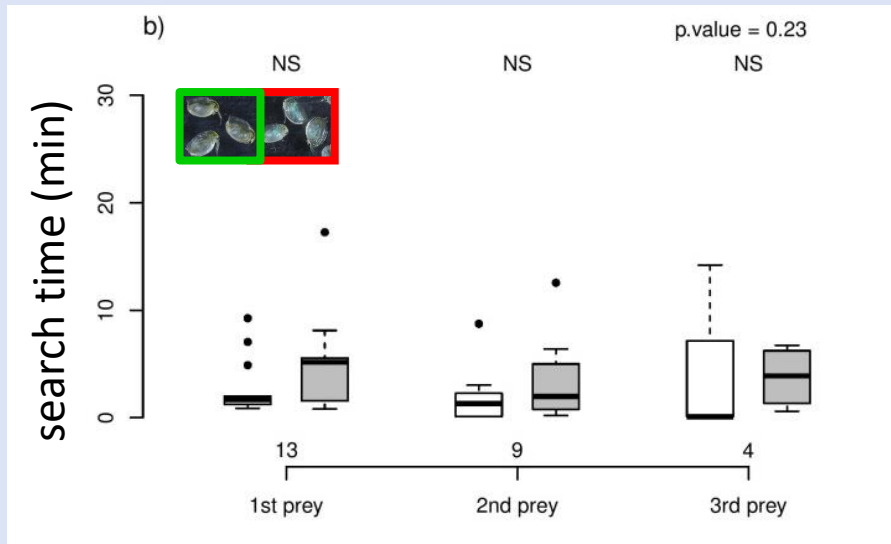


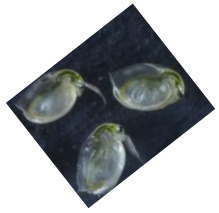


Interaction effects: search time

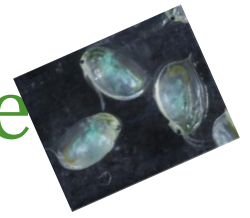


→ No modification of search time

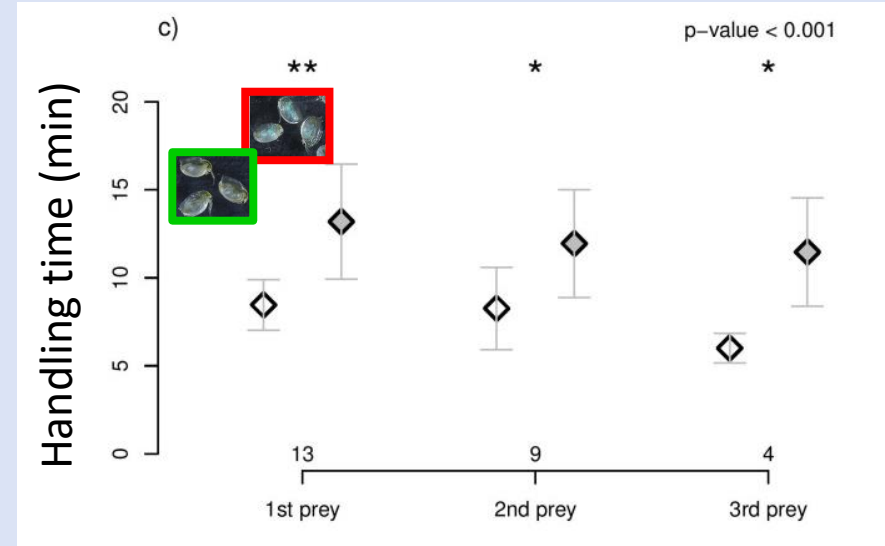
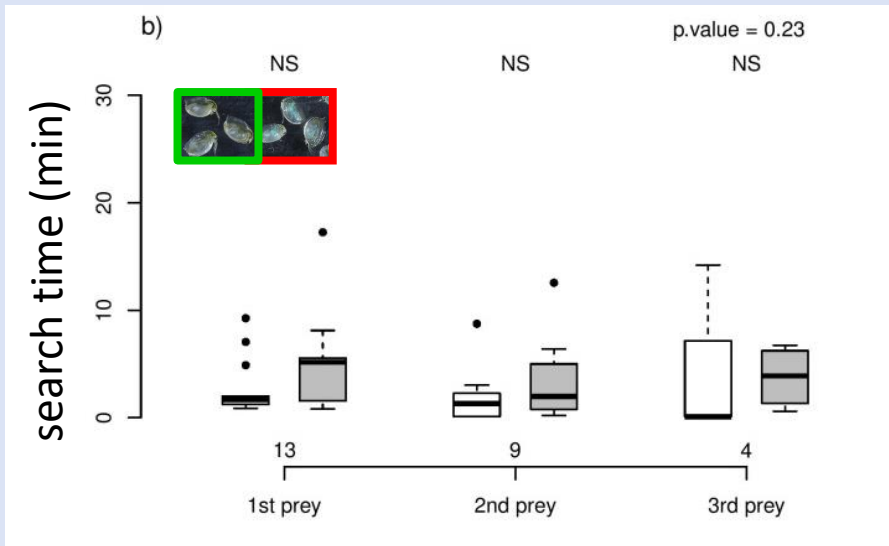




Interaction effects: handling time

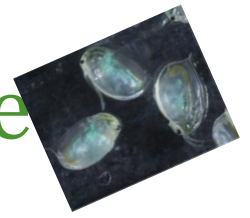


- No modification of search time
- Increased handling time



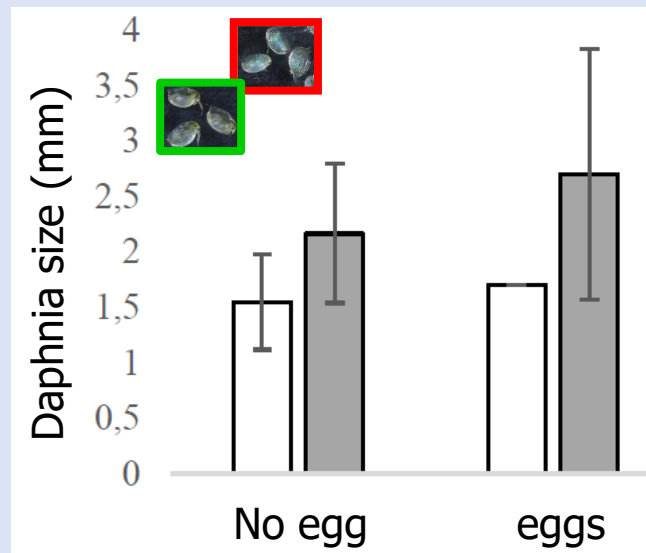


Interaction effects: handling time



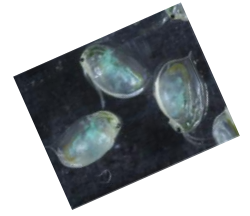
- Increased handling time
- Due to higher size?

Field observations:

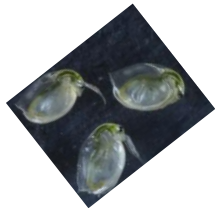




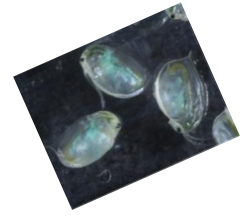
Assessment of profitability



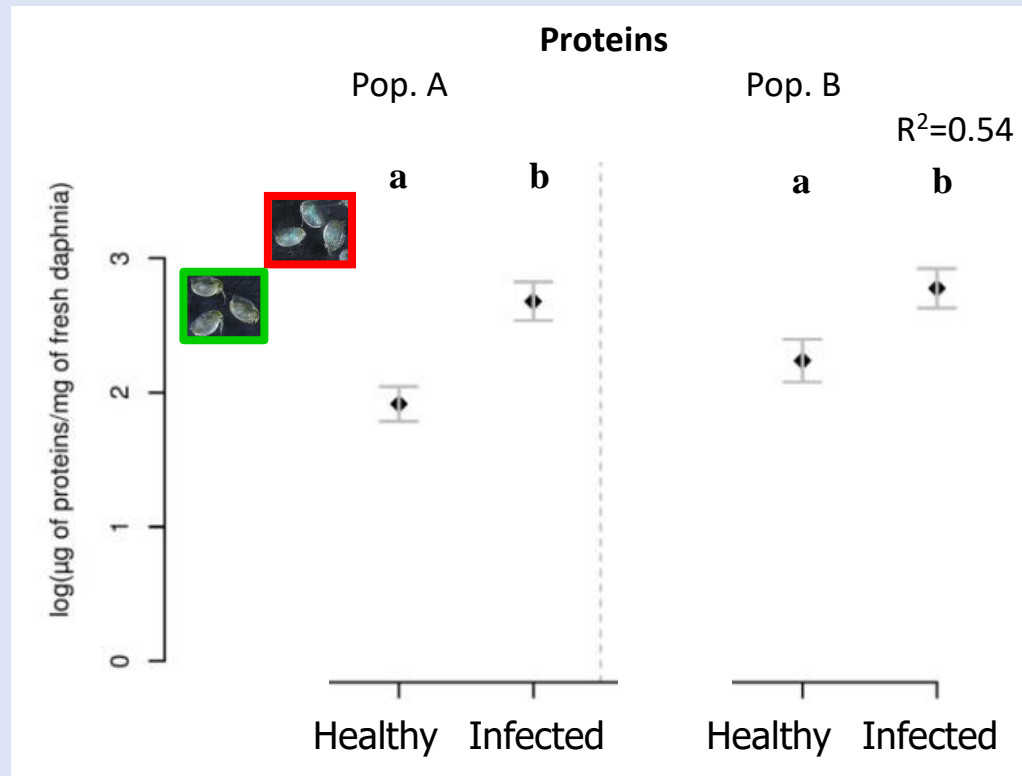
- Measures:
 - Mortality
 - Fecundity
 - Fitness
 - Reflectance
 - Behaviour
 - Search time
 - Handling time
 - Predator preference
 - **Energy content** → Proteins, Carbohydrates, Lipids

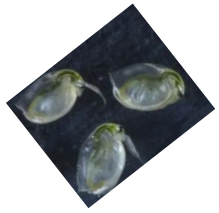


Host energy content

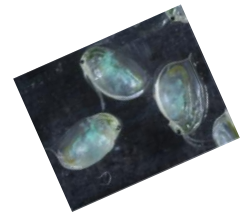


→ Higher protein contents



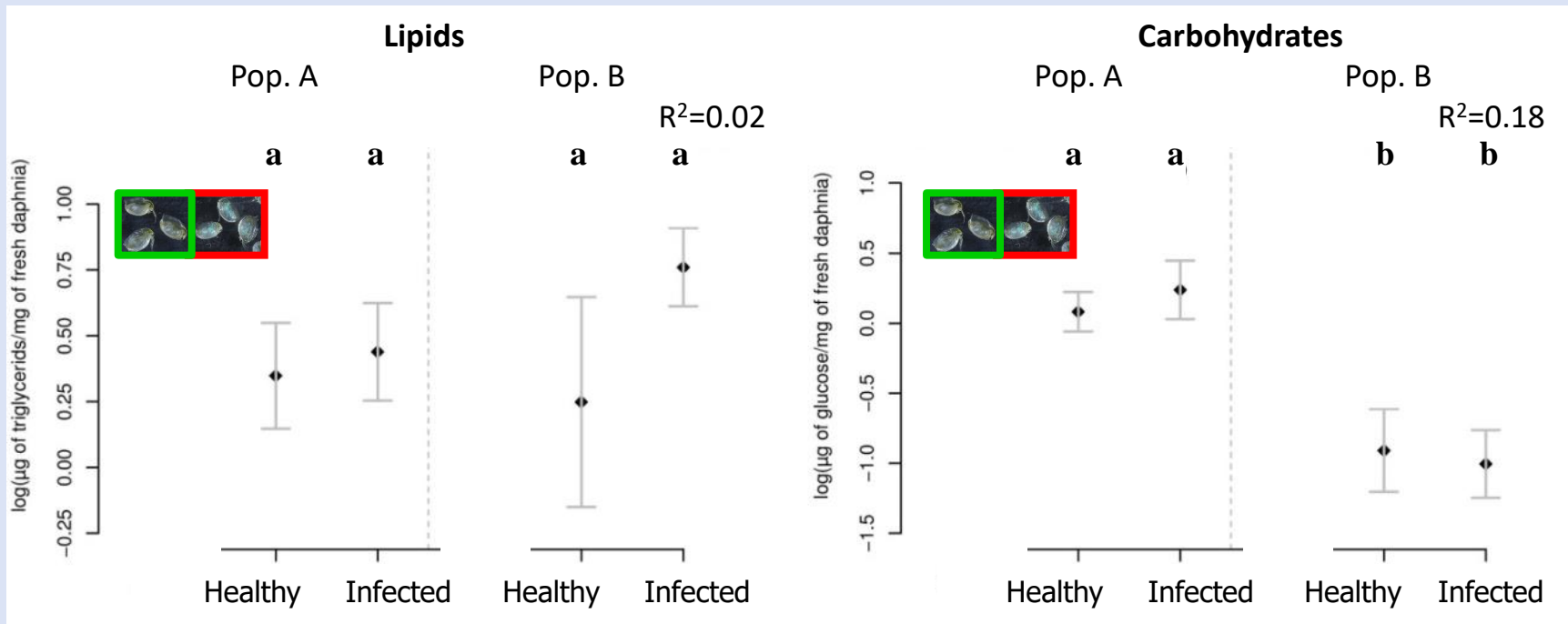


Host energy content



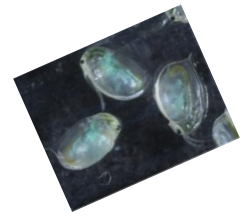
→ Higher protein contents

→ No modification of lipid and carbohydrate contents

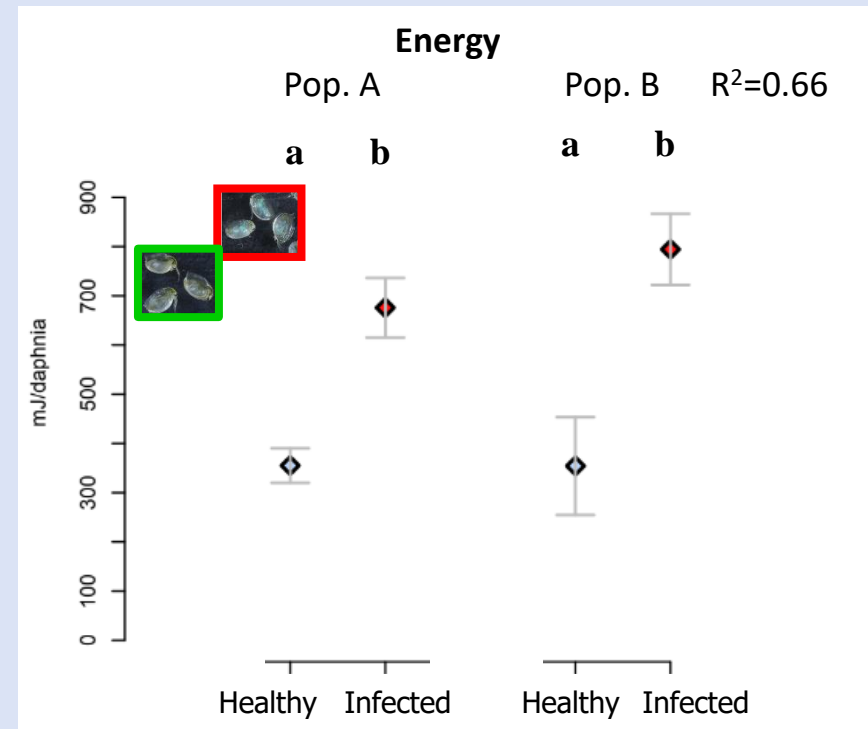




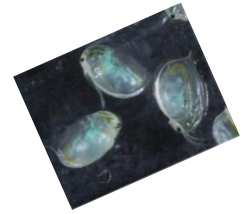
Host energy content



- Higher protein contents
- No modification of lipid and carbohydrate contents
- Higher energy content



Host profitability



- Higher handling time
- Higher energy content

→ Higher profitability



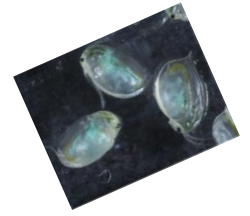
Healthy : 30 mJ/s



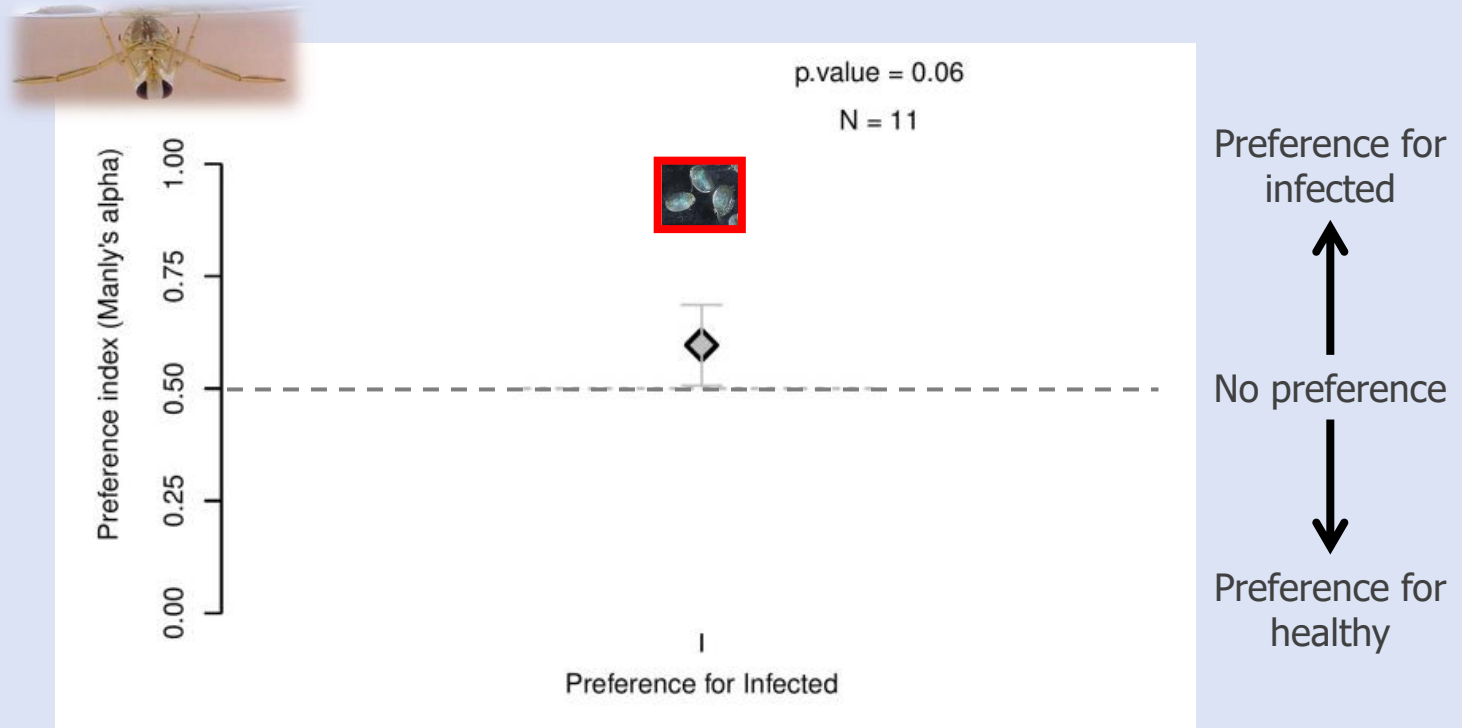
Infected : 37 mJ/s



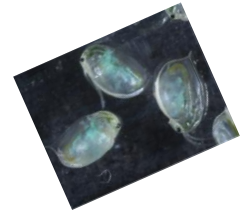
Interaction effects: Preference



→ Tendency for preference for infected

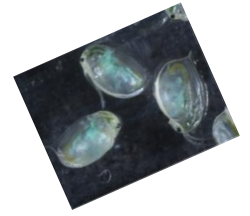


Conclusions



- Effects of DIV-1
 - Virulence effect > Interaction effect
 - Increase energy content
→ affect profitability

Host profitability



Proteins, Carbohydrates, Lipids
↙ (+)

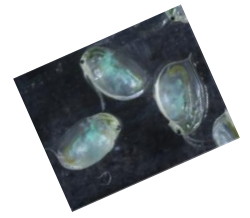
Prey energy content

Predator search time + Predator handling time

↗ (0)
interaction effects

↖ (+)
interaction effects

Host profitability



Proteins, Carbohydrates, Lipids
↙ (+)

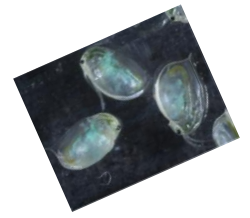
Prey energy content

Predator search time + Predator handling time

(+) ↗ (0)
virulence and interaction effects

(+) ↖
interaction effects

Host profitability



Proteins, Carbohydrates, Lipids
↙ (+)

Prey energy content

Predator search time + Predator handling time

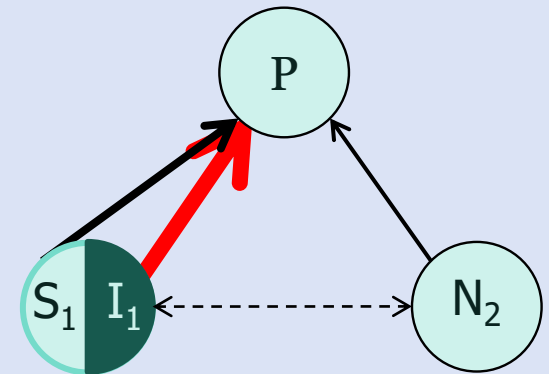
(+) virulence and (0) interaction effects

(+) interaction effects

Effects of DIV-1 on predator diet?

Infected prey: the structured model

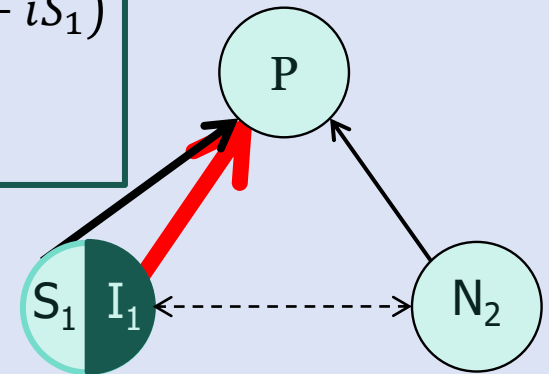
- Infected prey in Susceptible and Infected (SI)



Infected prey: the structured model

- Infected prey in Susceptible and Infected (SI)

$$\begin{cases} \frac{dS_1}{dt} = S_1(f_1 - m_1 - b_{11}N_1 - b_{12}N_2 - a_1P) + I_1((f_1 - n) - iS_1) \\ \frac{dI_1}{dt} = I_1(iS_1 - b_{11}N_1 - b_{12}N_2 - (a_1 + j)P - m_1) \\ \frac{dN_2}{dt} = N_2(r_2 - b_{21}N_1 - b_{22}N_2 - a_2P) \\ \frac{dP}{dt} = P(ea_1N_1 + ejI_1 + ea_2N_2 - m) \end{cases}$$



- Virulence, n (reduction of fecundity)
- Interaction, j (increase of vulnerability)

(Prosnier et al, 2018)

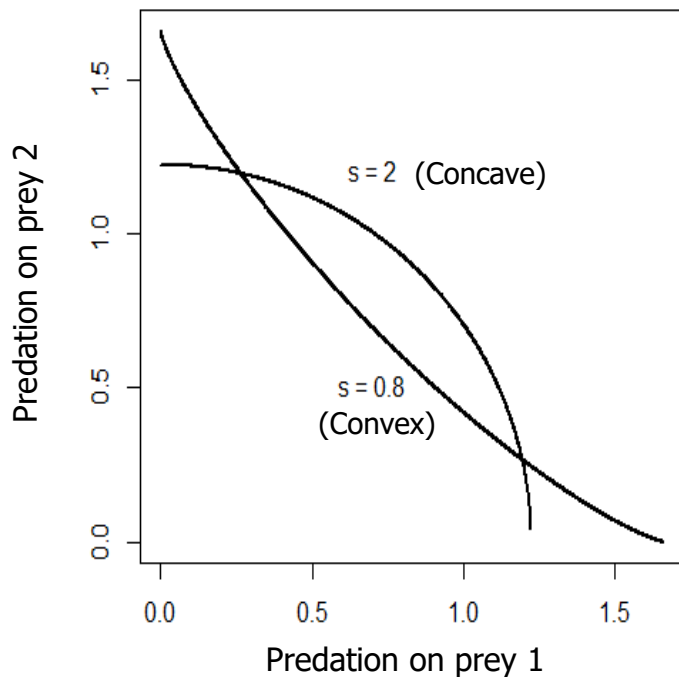
The Evolutionary model: adaptive foraging

- Adding a trade-off for predation (prey choice)

The Evolutionary model: adaptive foraging

- Adding a trade-off for predation (prey choice)

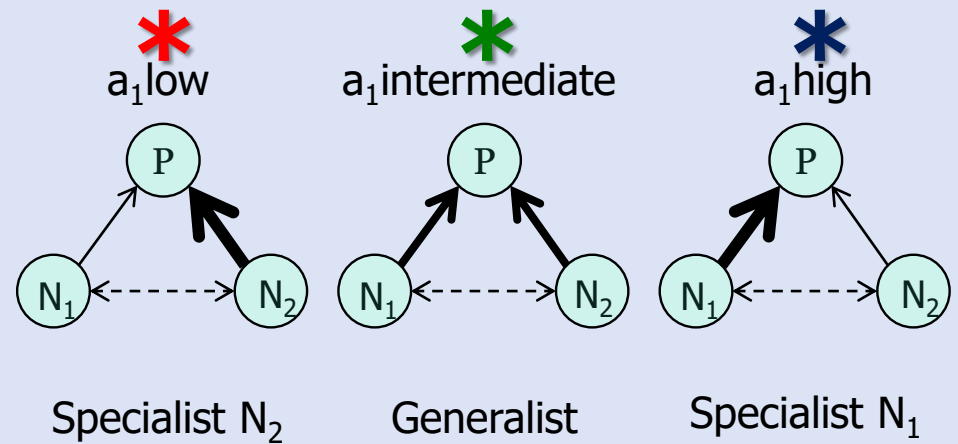
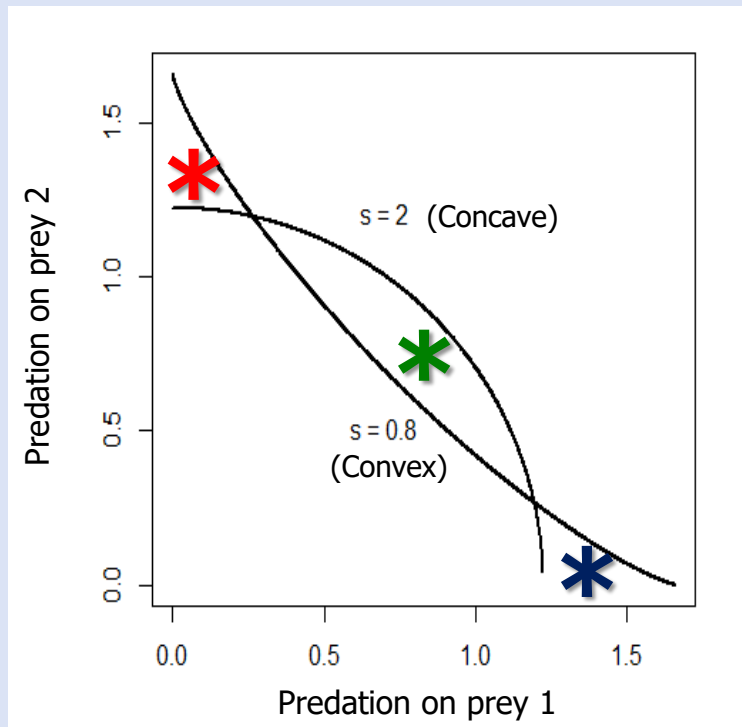
$$a_1^s + a_2^s = k_0$$



The Evolutionary model: adaptive foraging

- Adding a trade-off for predation (prey choice)

$$a_1^s + a_2^s = k_0$$



Adaptive dynamics

- Hypothesis:
 - clonal reproduction
 - Slow evolution compared to ecological dynamics
 - Rare mutations
 - Small mutation

(Dieckmann and Law, 1996)

Adaptive dynamics

- Canonical equation

Evolution of
attack rate on N_1

$$\frac{da_1}{dt} = \frac{1}{2} \mu \sigma^2 P^*(a_1) \underbrace{\left. \frac{\partial \omega(a_{1m}, a_1)}{\partial a_{1m}} \right|_{a_{1m} \rightarrow a_1}}_{\text{Selection gradient}}$$

Relative fitness
of mutants

Trade-off of
predation

$$a_1^s + a_2^s = k_0$$

- Singularities

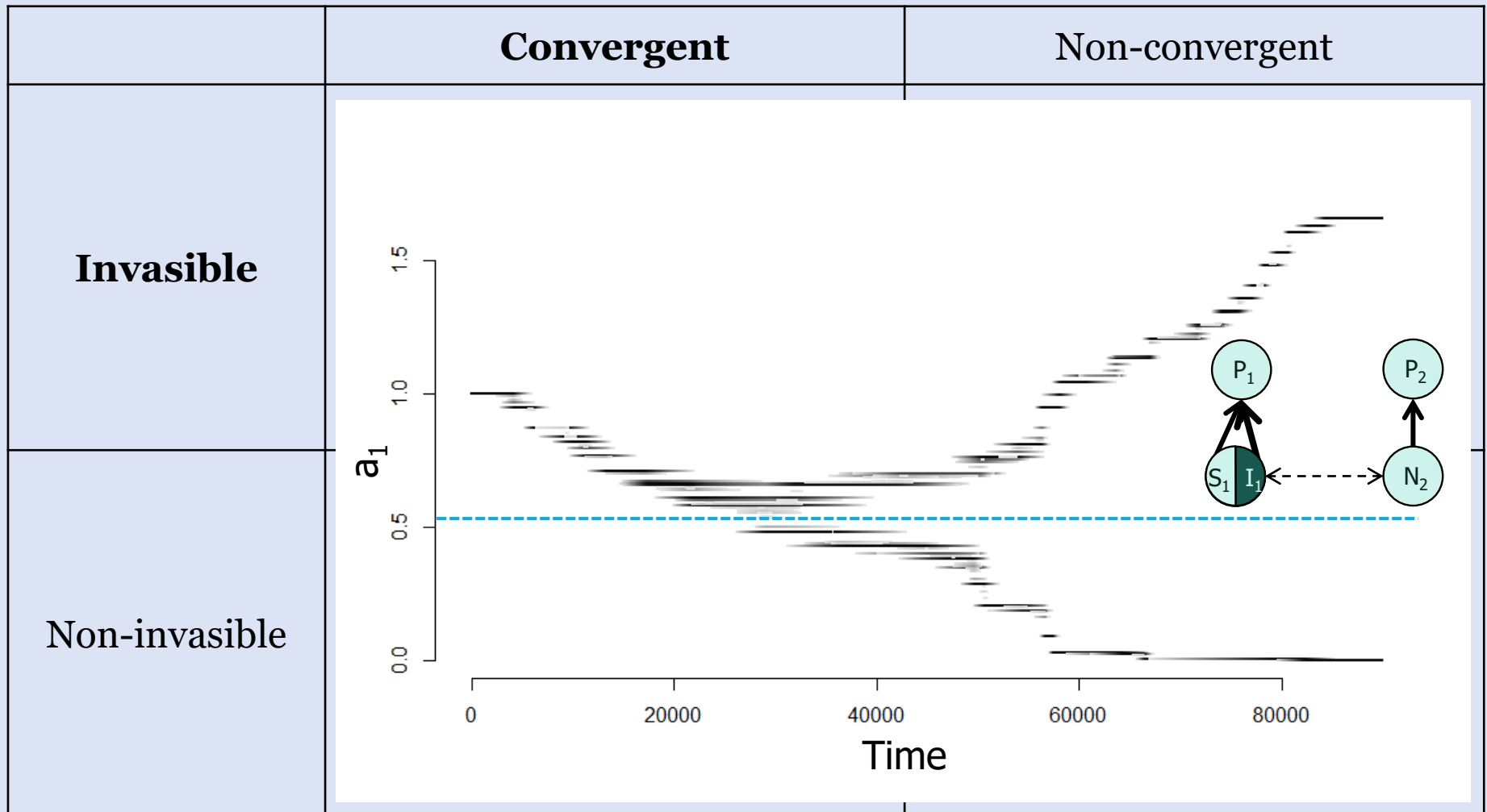
$$\left. \frac{\partial \omega(a_{1m}, a_1)}{\partial a_{1m}} \right|_{a_{1m} \rightarrow a_1 \rightarrow \bar{a}_1} = 0$$

(Dieckmann and Law, 1996)

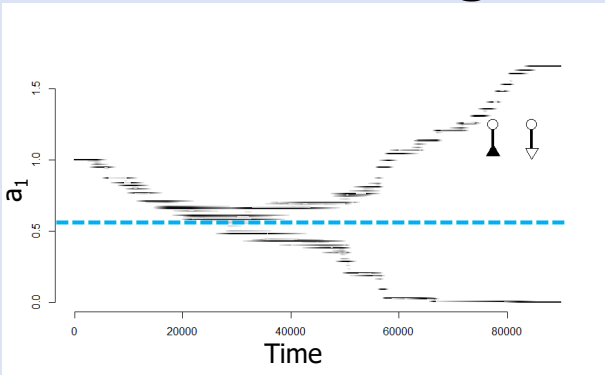
Singularities

	Convergent	Non-convergent
Invasible	EBP (Branching)	Repellor
Non-invasible	CSS (Continuously Stable)	<i>Not observed</i>

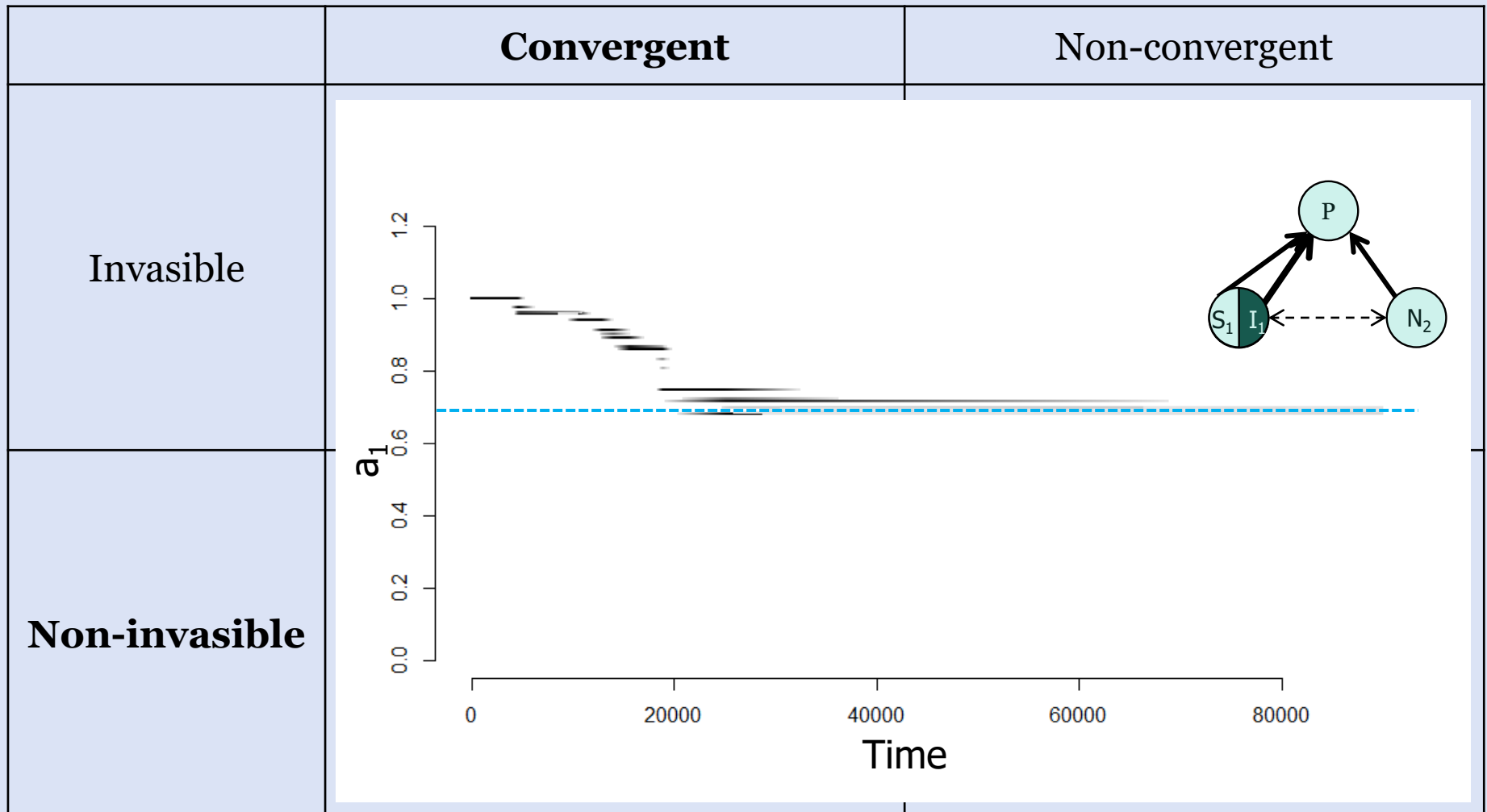
Singularities



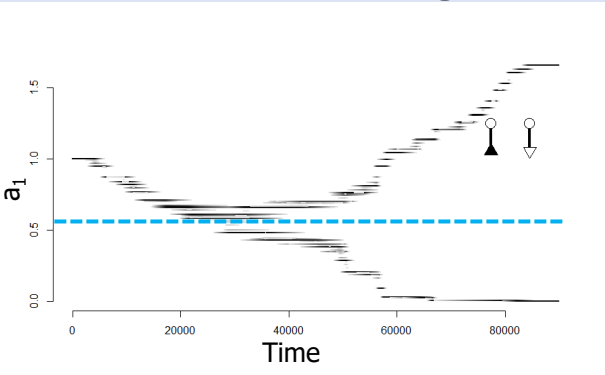
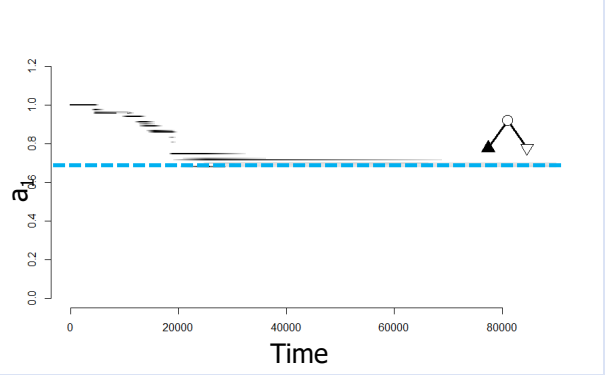
Singularities

	Convergent	Non-convergent
Invasible	EBP (Branching) 	Repellor
Non-invasible	CSS (Continuously Stable)	Not observed

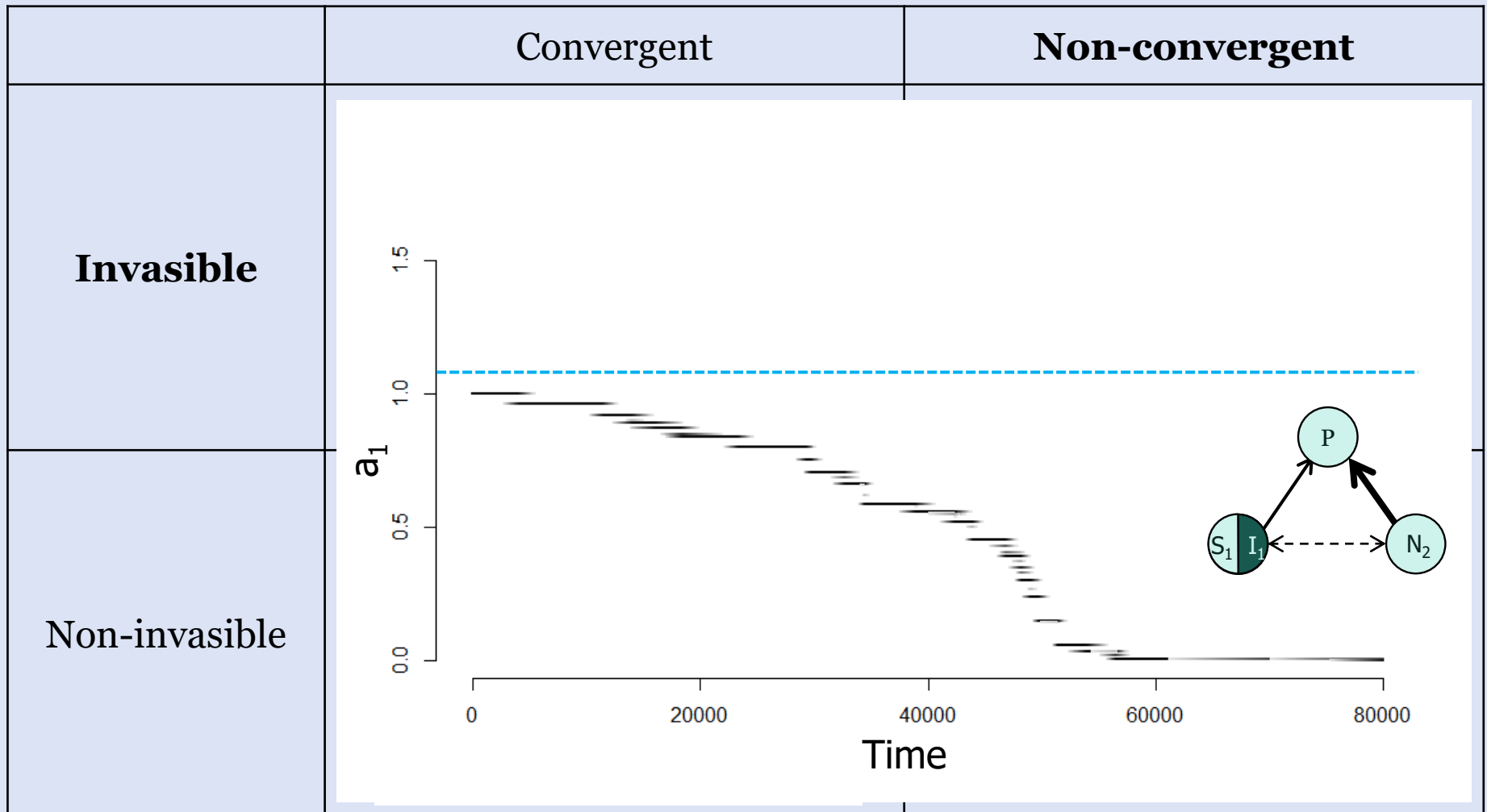
Singularities



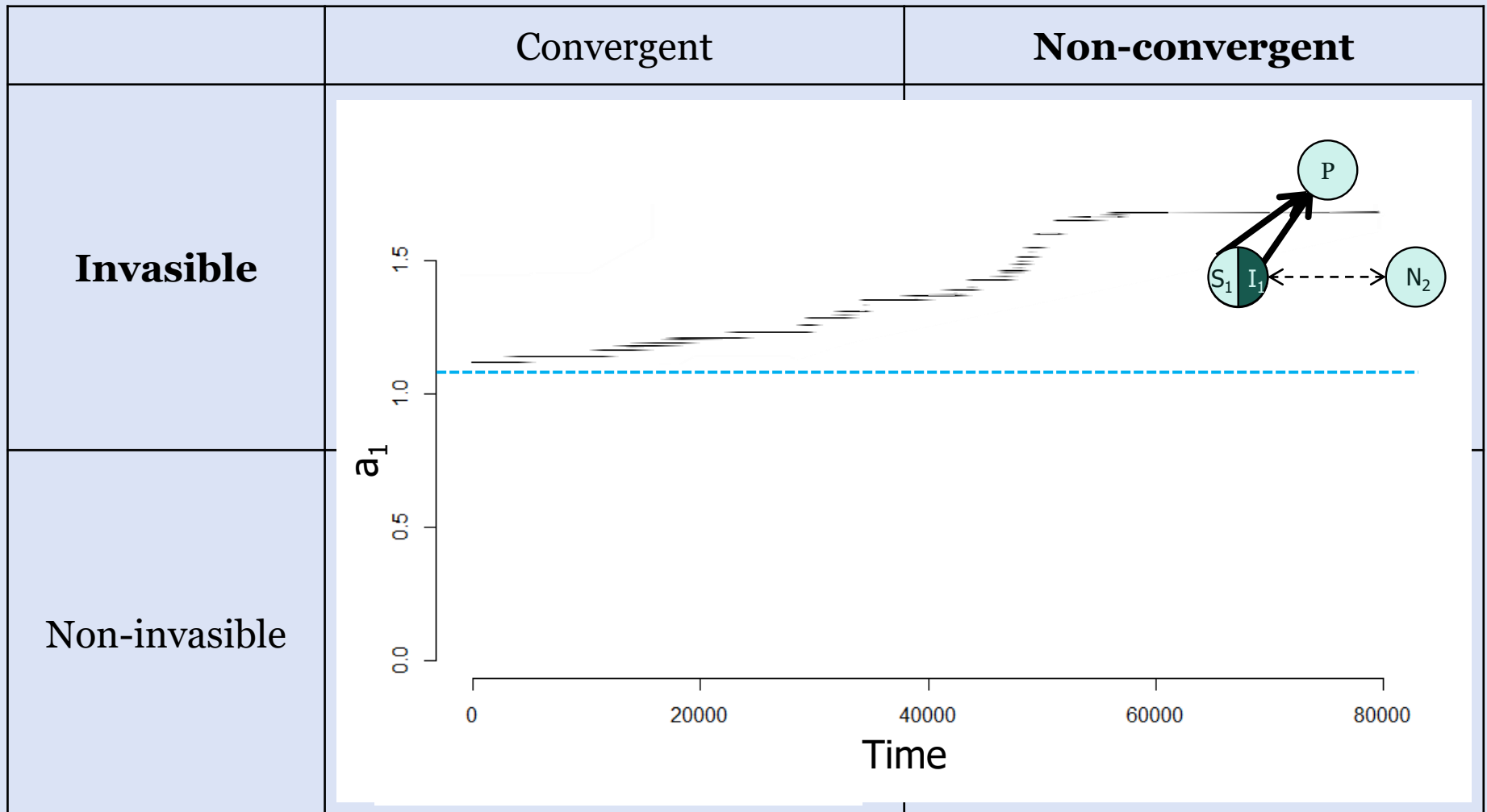
Singularities

	Convergent	Non-convergent
Invasible	EBP (Branching) 	Repellor
Non-invasible	CSS (Continuously Stable) 	Not observed

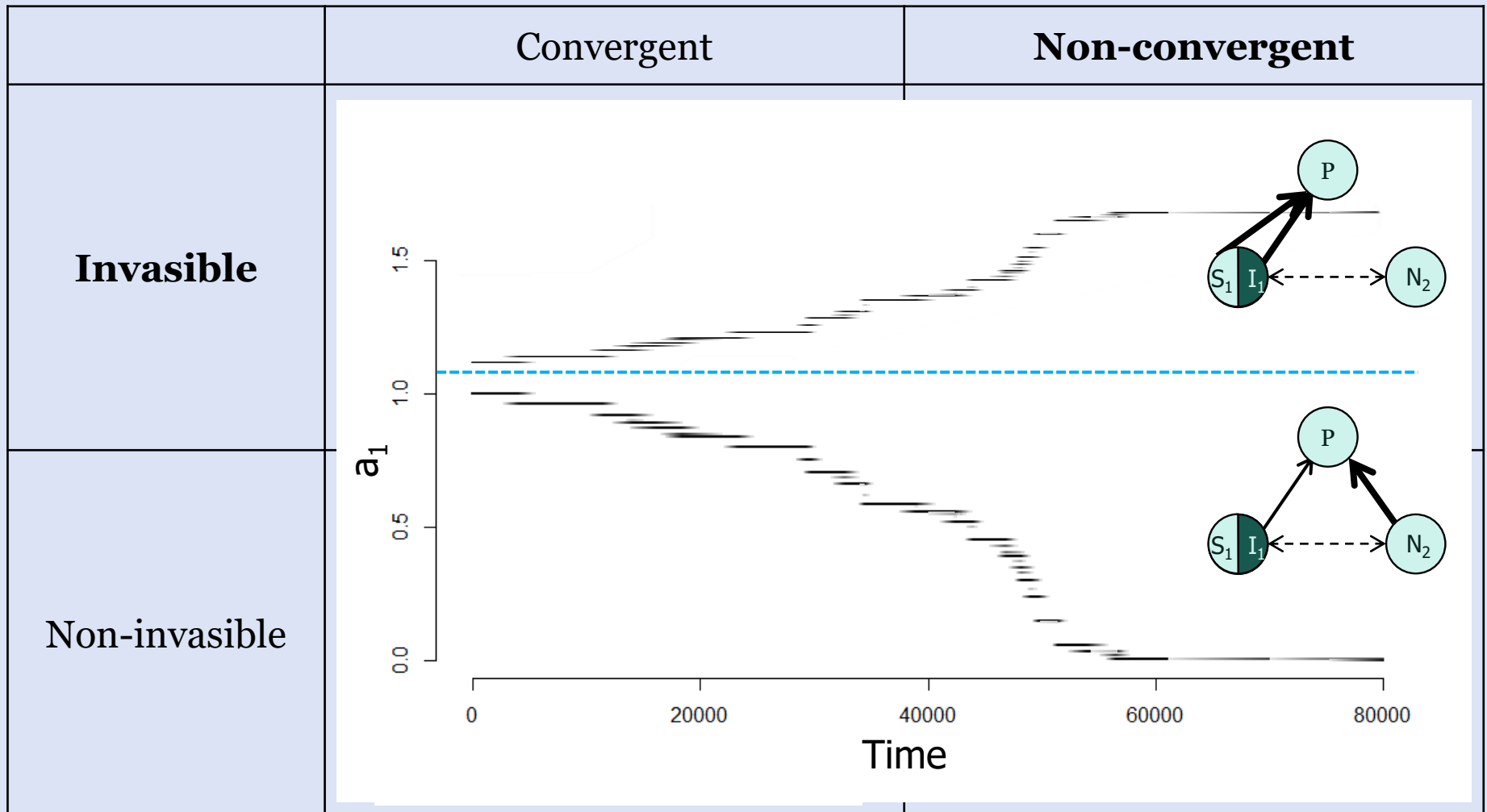
Singularities



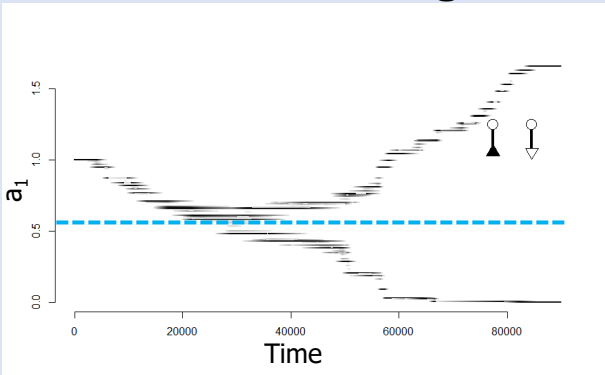
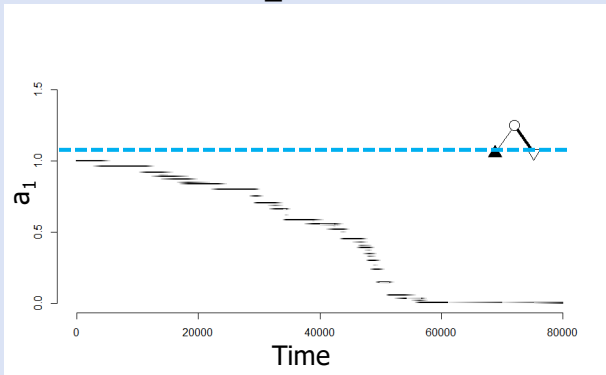
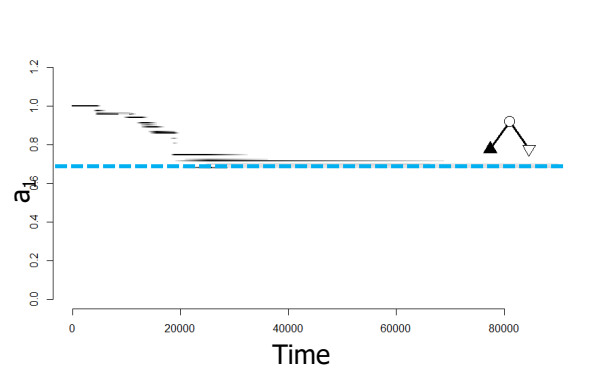
Singularities



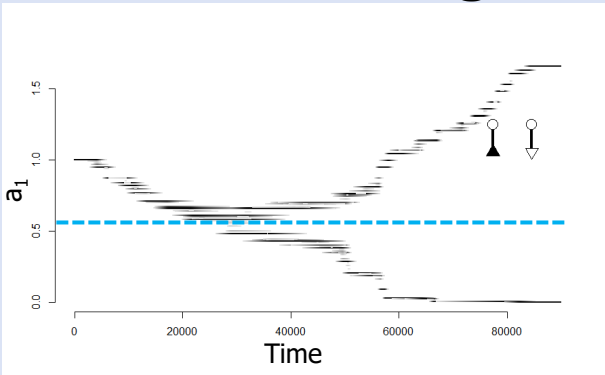
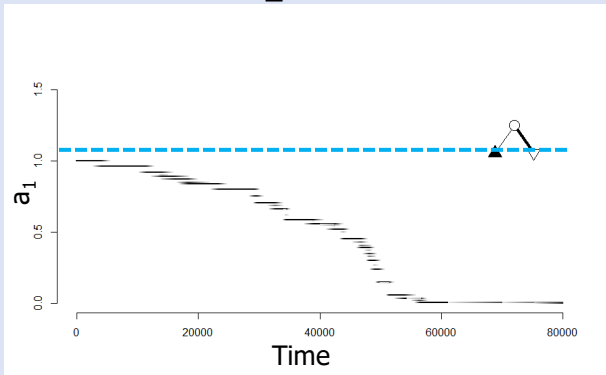
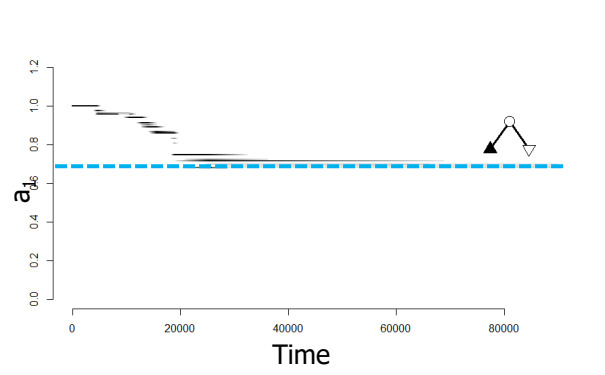
Singularities



Singularities

	Convergent	Non-convergent
Invisible	<p>EBP (Branching)</p> 	<p>Repellor</p> 
Non-invisible	<p>CSS (Continuously Stable)</p> 	<p>Not observed</p>

Singularities

	Convergent	Non-convergent
Invisible	<p>EBP (Branching)</p> 	<p>Repellor</p> 
Non-invisible	<p>CSS (Continuously Stable)</p> 	<p>Not observed</p>

Adaptive dynamics

- Singularities

$$\left. \frac{\partial \omega(a_{1m}, a_1)}{\partial a_{1m}} \right|_{a_{1m} \rightarrow a_1 \rightarrow \bar{a}_1} = 0$$

Trade-off of predation

$$a_1^s + a_2^s = k_0$$

- Non-invasible

$$c_{22} = \left. \frac{\partial^2 \omega}{\partial a_{1m}^2} \right|_{a_{1m} \rightarrow a_1 \rightarrow \bar{a}_1} < 0$$

$$-\bar{a}_1^{s-2} k_0 (k_0 - \bar{a}_1^s)^{\frac{1}{s}-2} N_2^*(s-1) < 0$$

$s > 1 \rightarrow$ Concave-trade-off

Adaptive dynamics

- Singularities

$$\left. \frac{\partial \omega(a_{1m}, a_1)}{\partial a_{1m}} \right|_{a_{1m} \rightarrow a_1 \rightarrow \bar{a}_1} = 0$$

Trade-off of predation

$$a_1^s + a_2^s = k_0$$

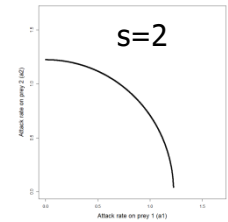
- Non-invasible

$$c_{22} = \left. \frac{\partial^2 \omega}{\partial a_{1m}^2} \right|_{a_{1m} \rightarrow a_1 \rightarrow \bar{a}_1} < 0$$

- Convergent

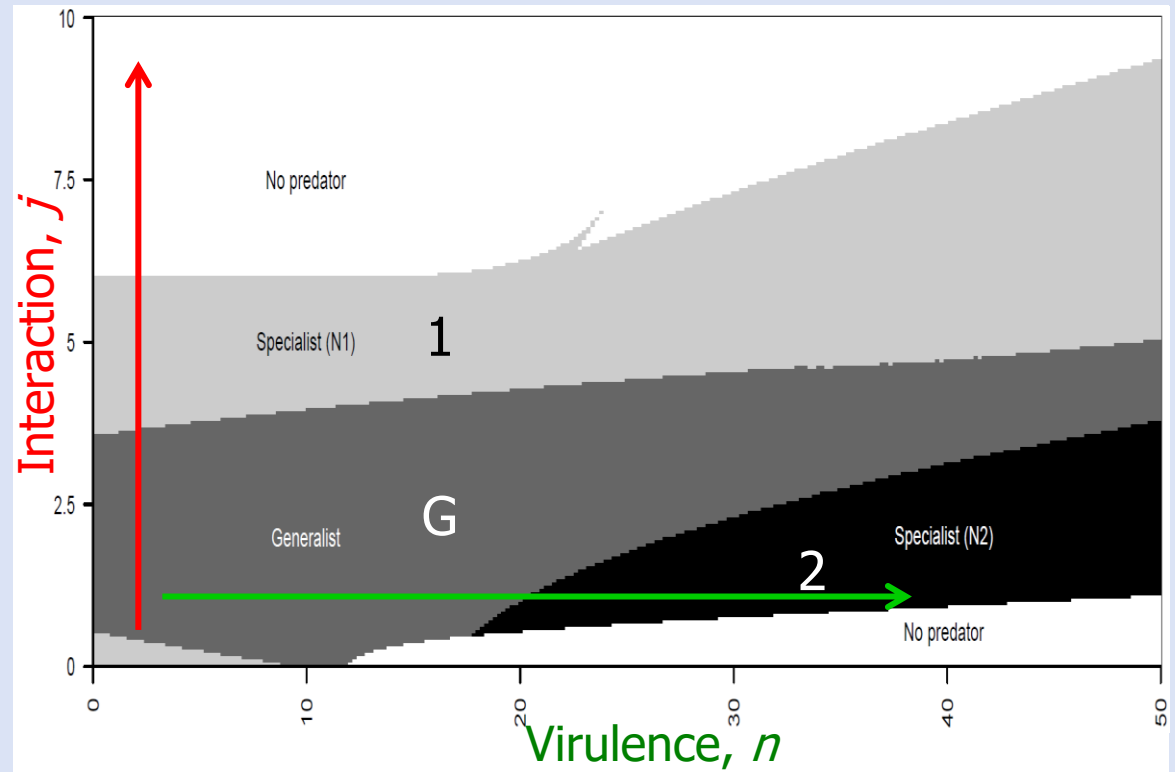
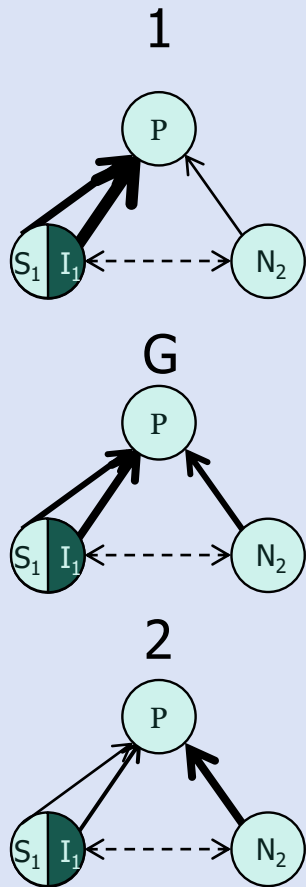
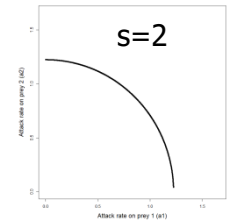
$$c_{12} + c_{22} < 0$$

Predator diet: concave trade-off

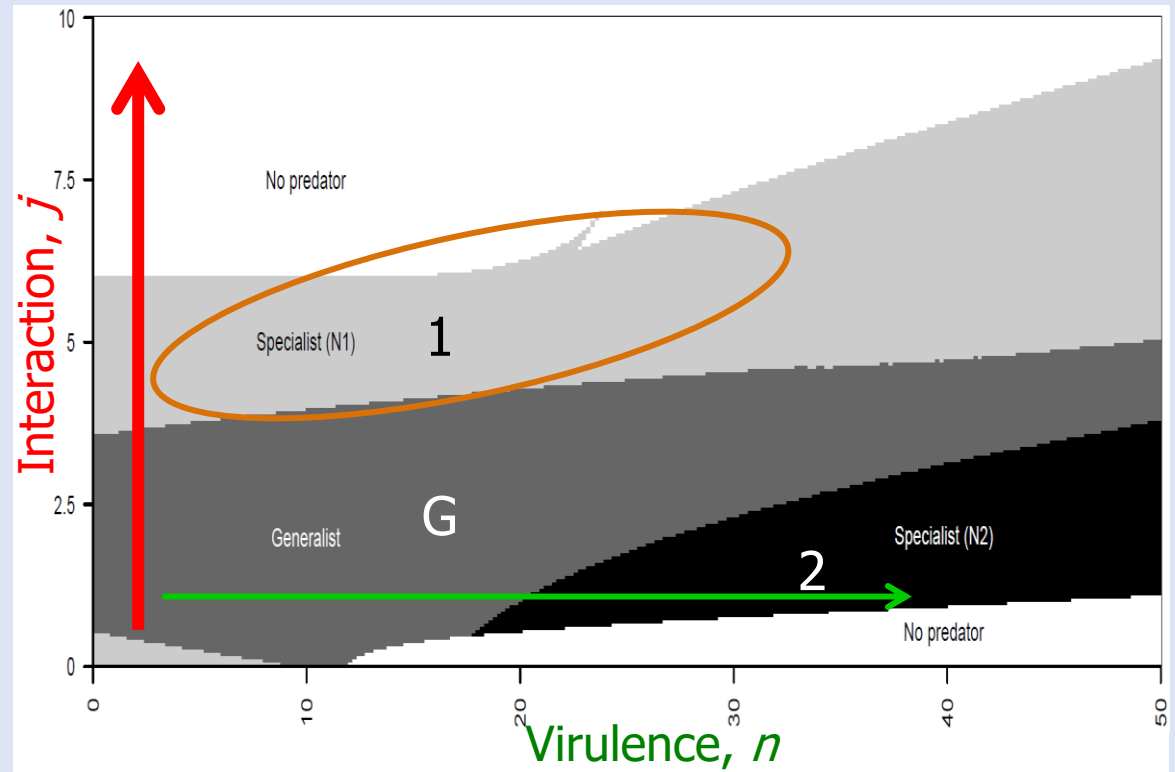
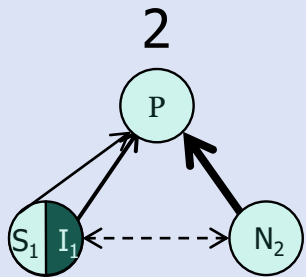
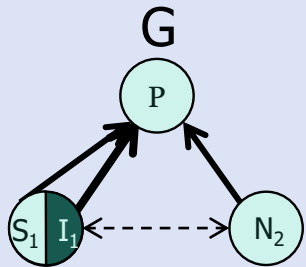
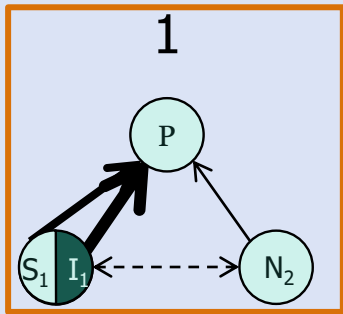
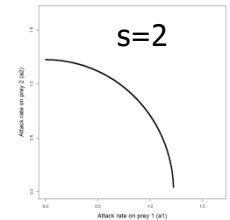


	Convergent	Non-convergent
Invisible	<p>EBP (Branching)</p>	<p>Repellor</p>
Non-invisible	<p>CSS (Continuously Stable)</p>	<p>Not observed</p>

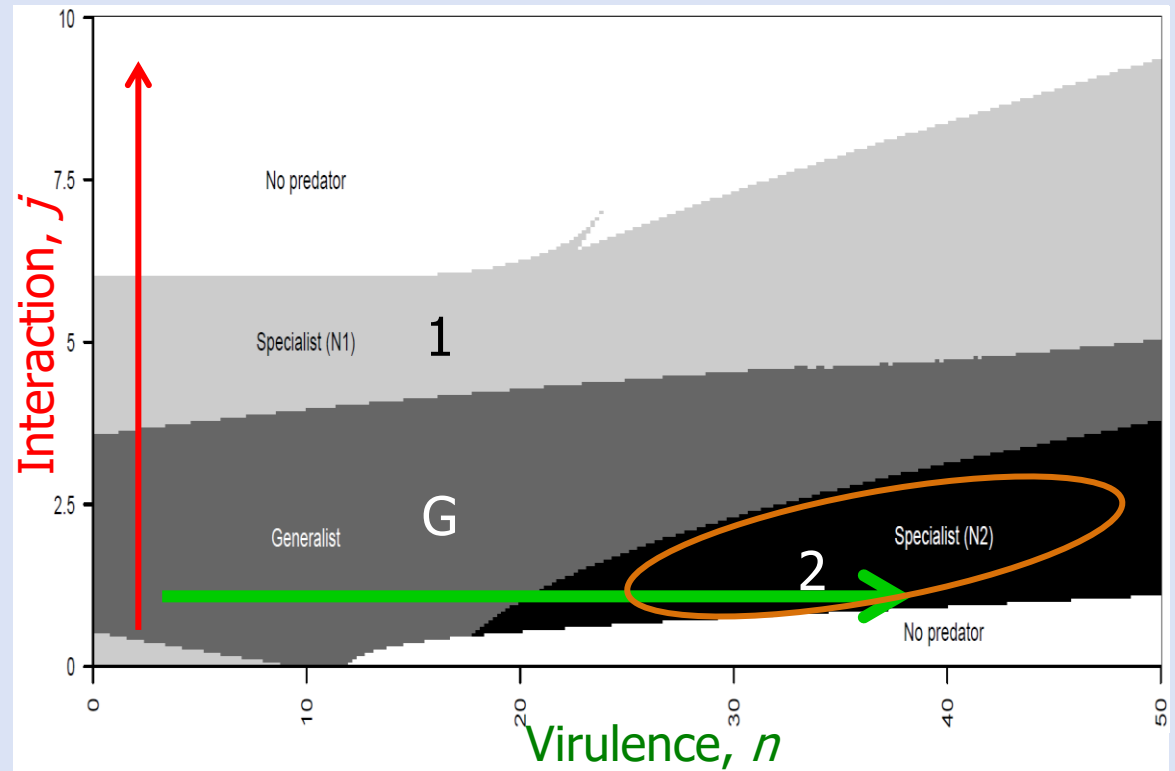
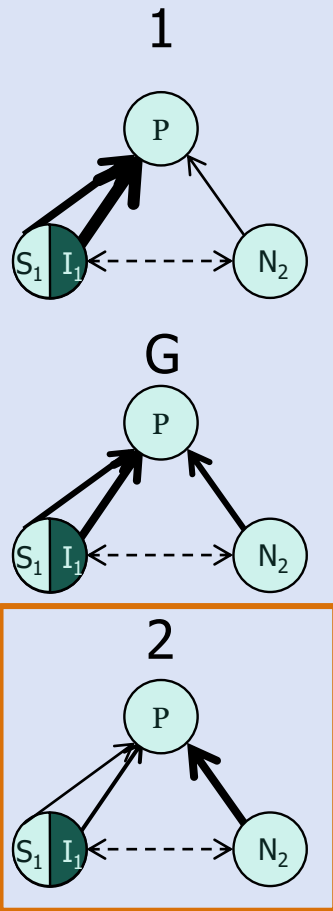
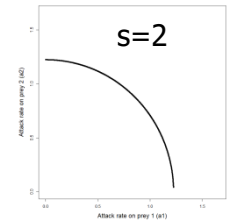
Predator diet: concave trade-off



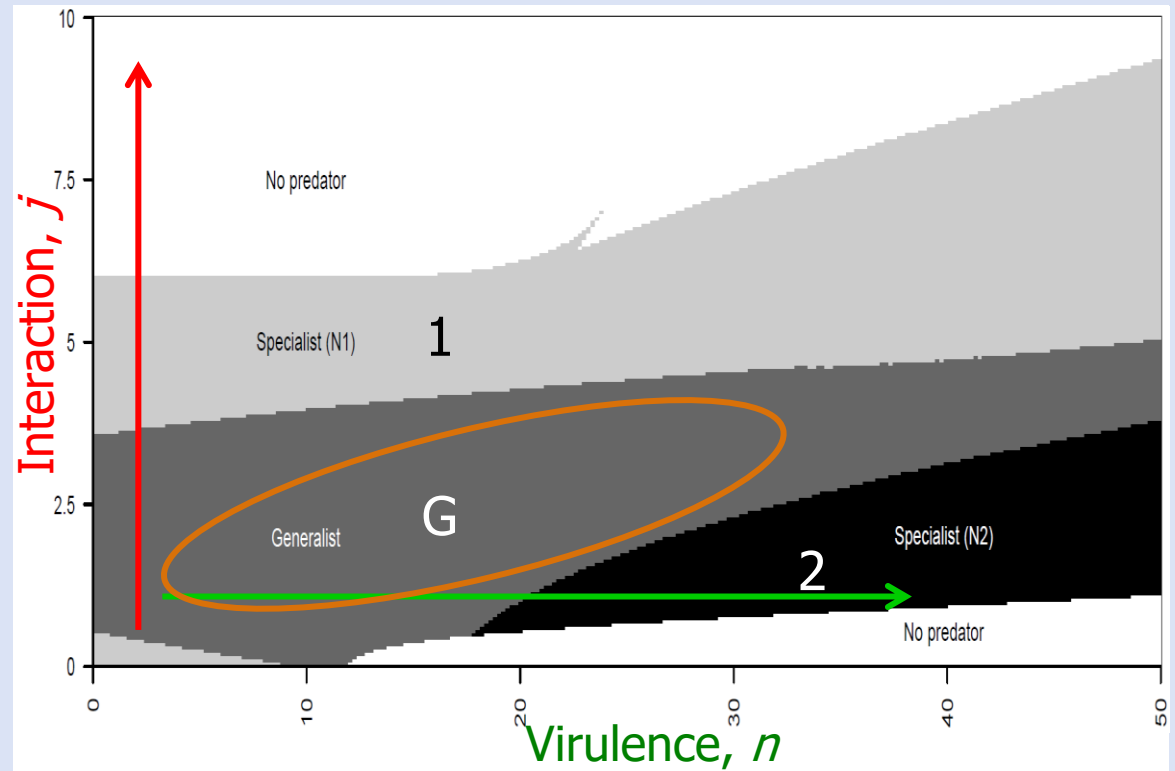
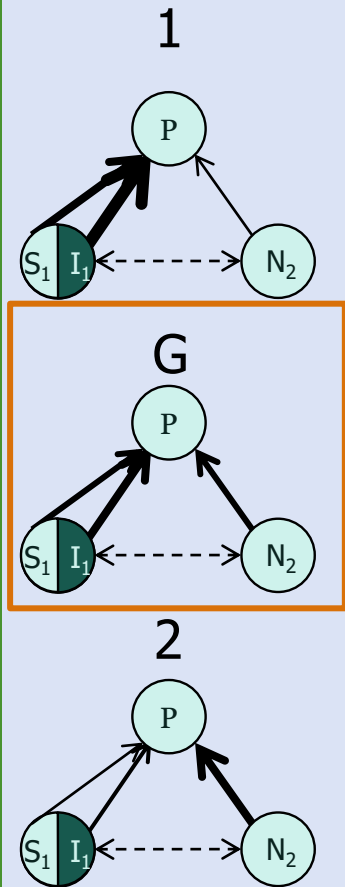
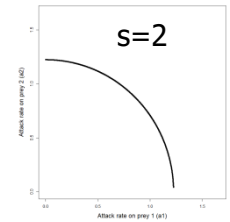
Predator diet: concave trade-off



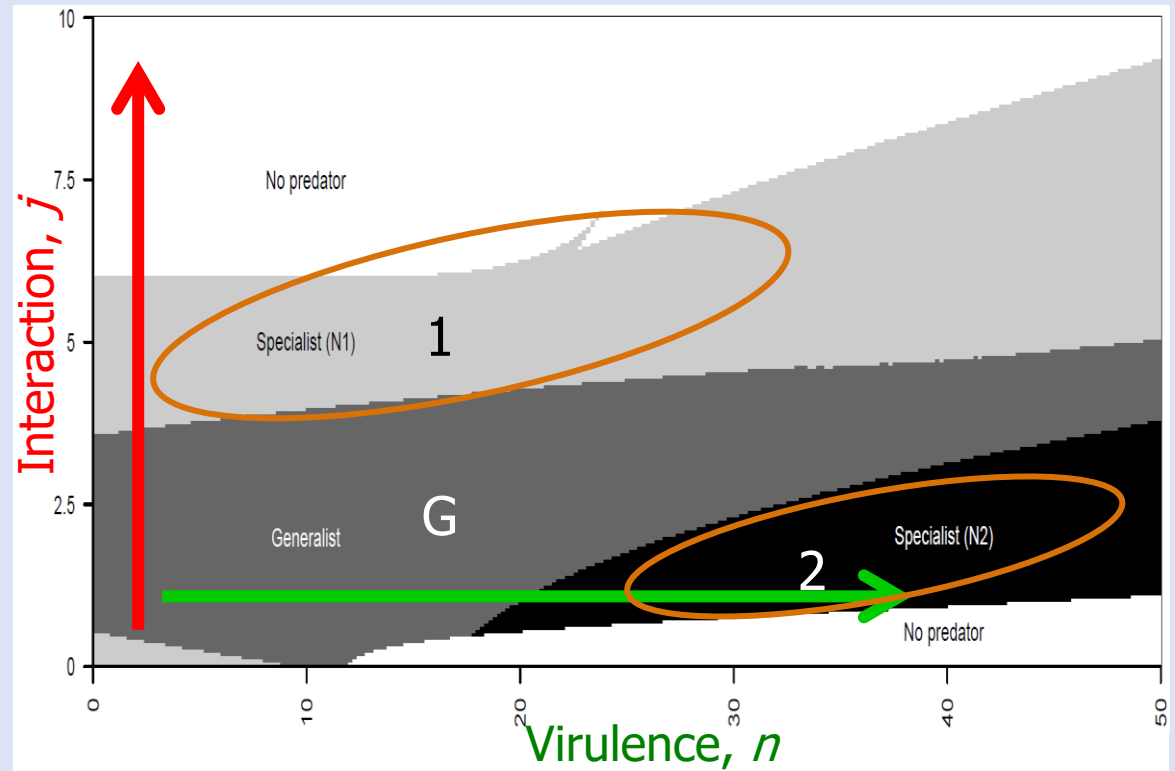
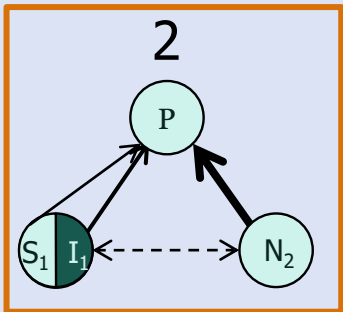
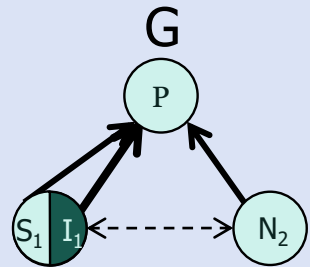
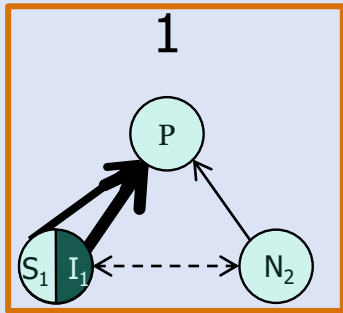
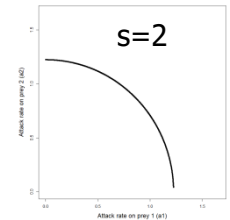
Predator diet: concave trade-off



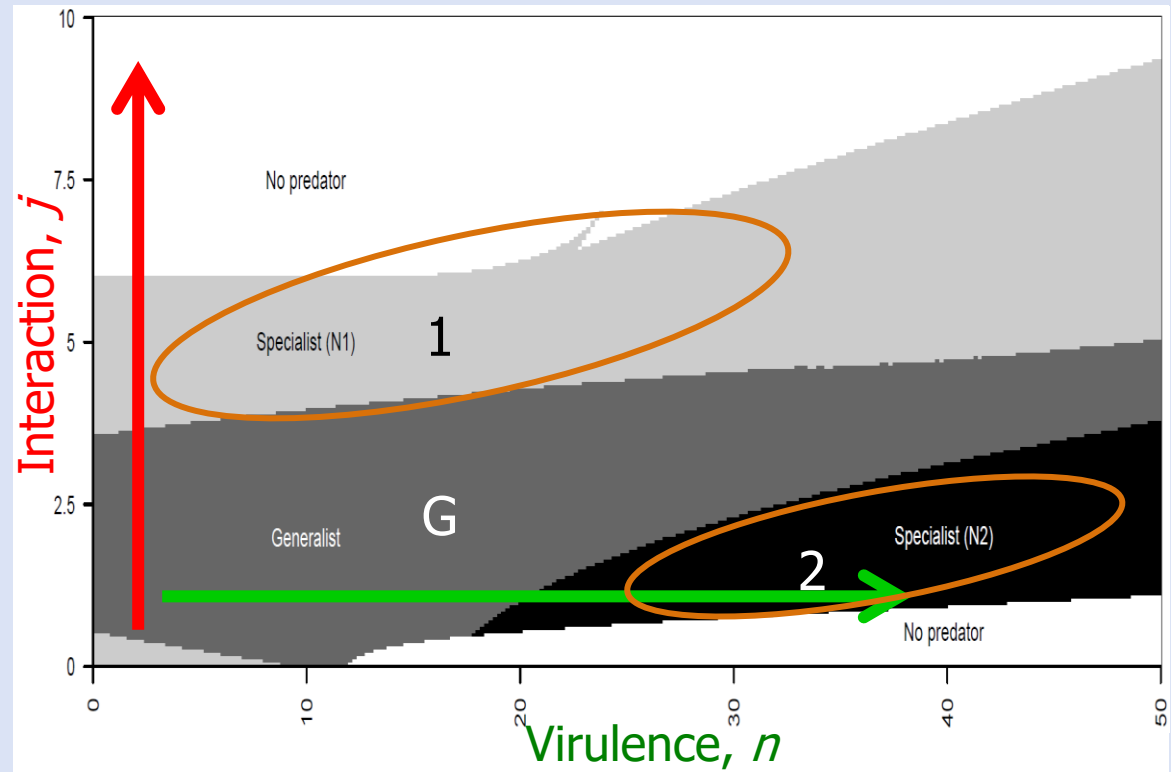
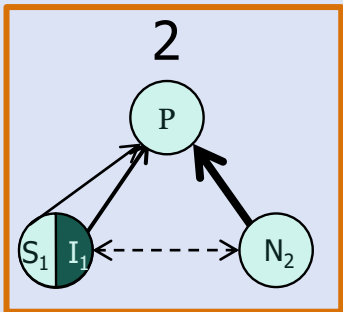
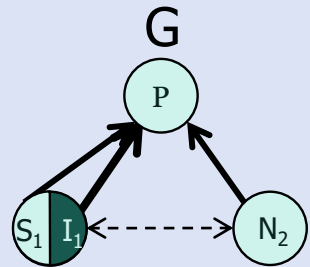
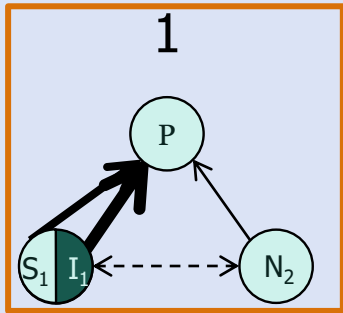
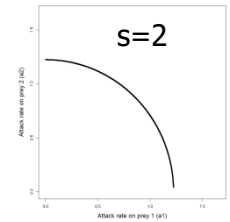
Predator diet: concave trade-off



Predator diet: concave trade-off

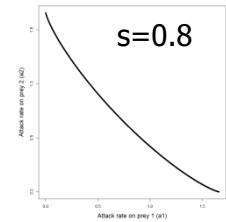


Predator diet: concave trade-off



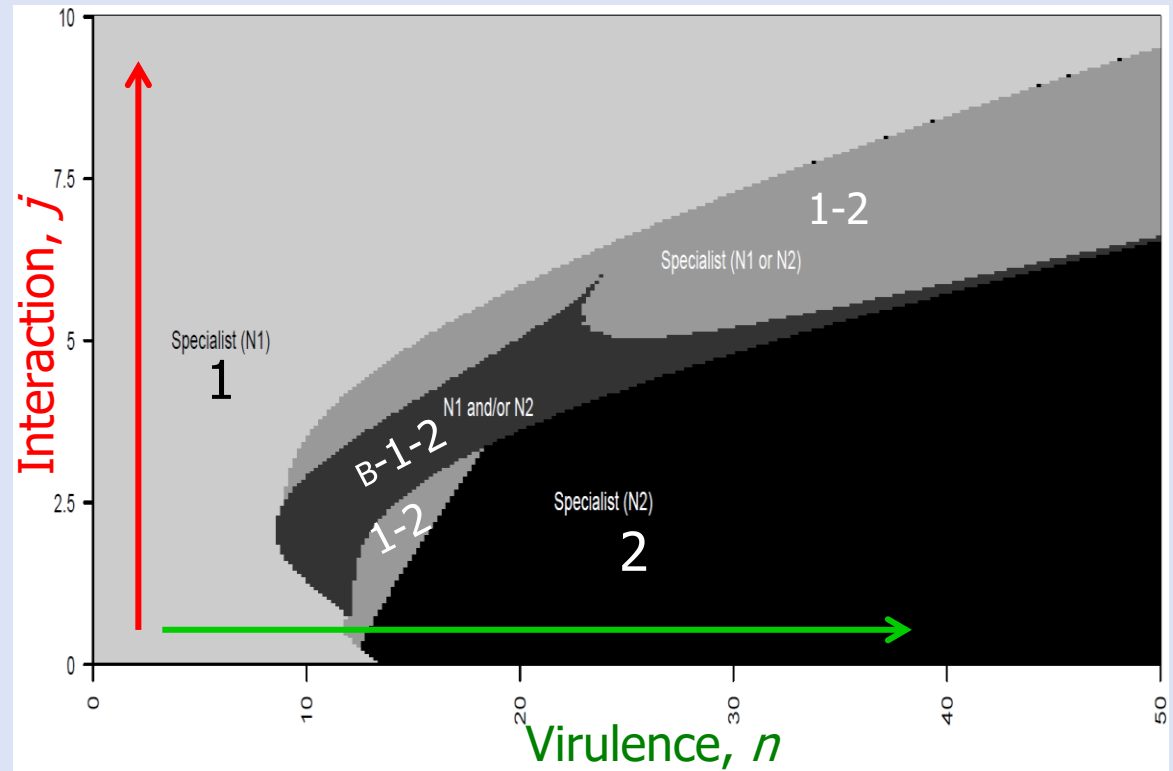
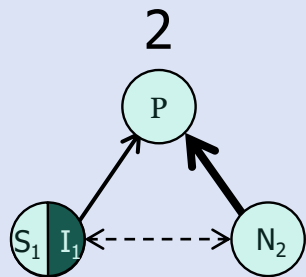
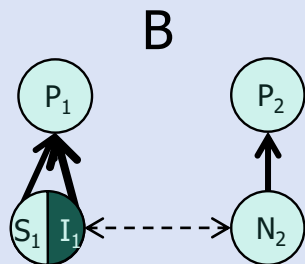
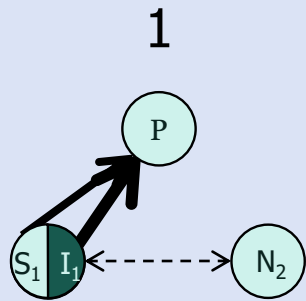
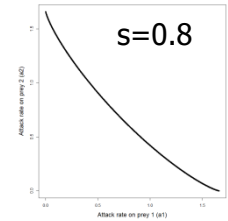
Virulence and interaction effects on profitability

Predator diet: convex trade-off

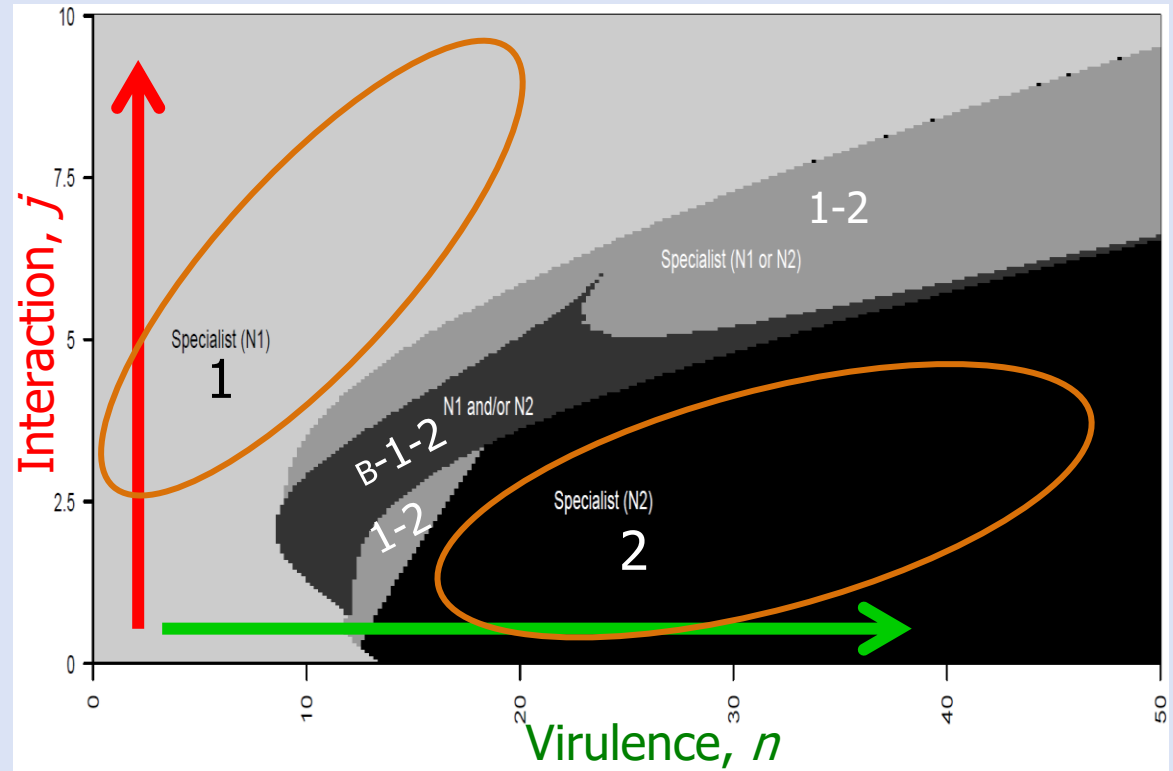
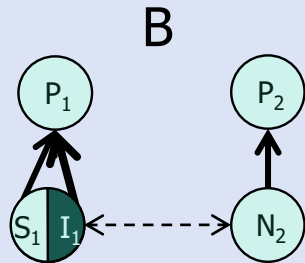
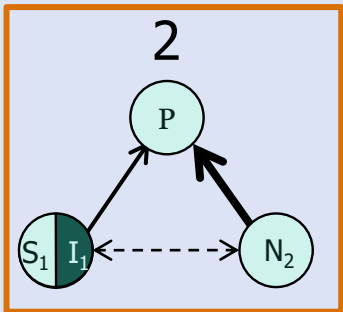
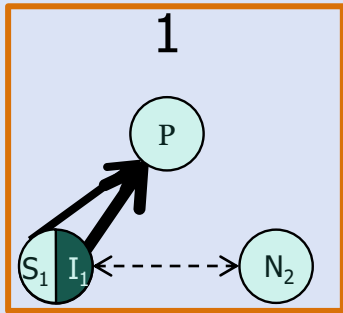
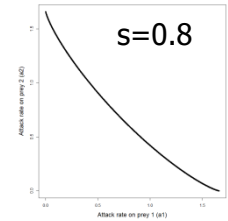


	Convergent	Non-convergent
Invisible	<p>EBP (Branching)</p>	<p>Repellor</p>
Non-invisible	<p>CSS (Continuously Stable)</p>	<p>Not observed</p>

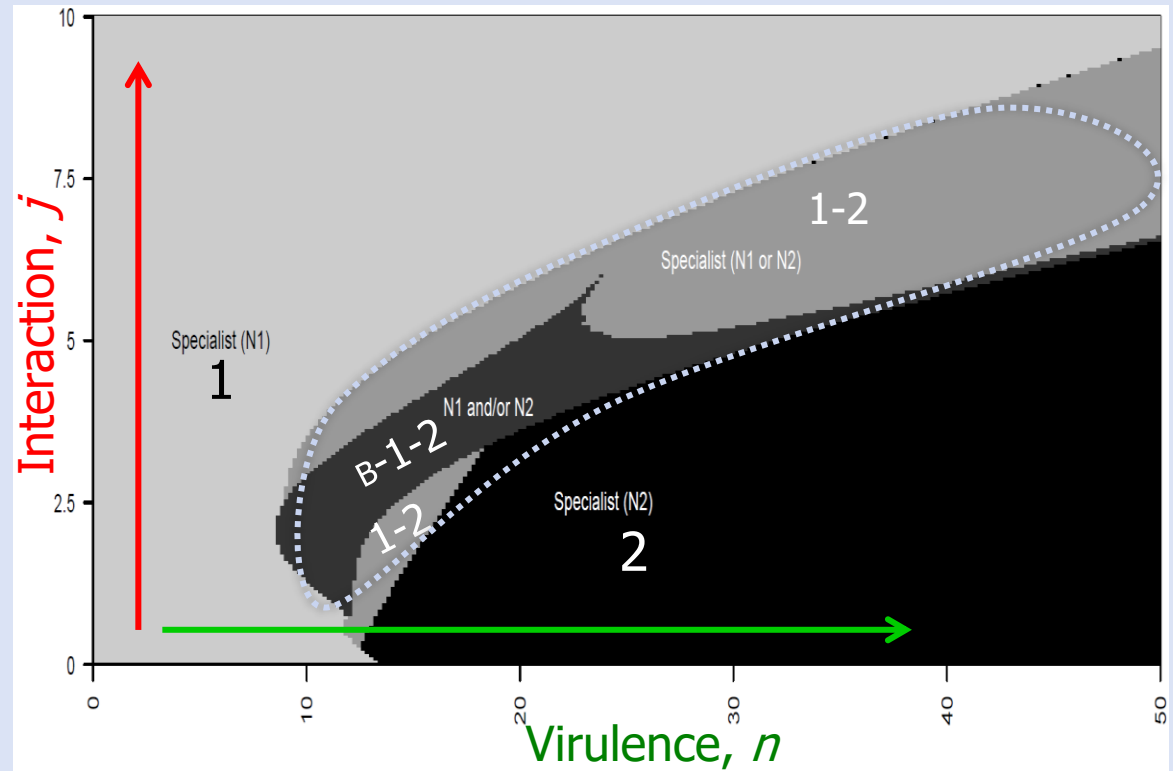
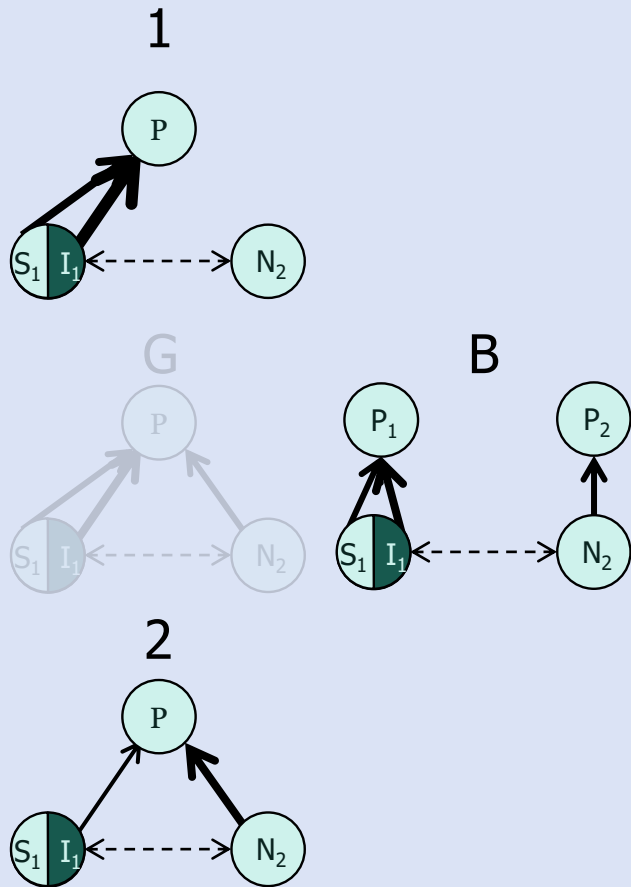
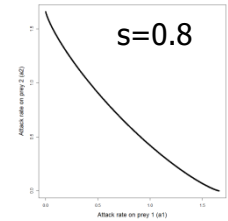
Predator diet: convex trade-off



Predator diet: convex trade-off

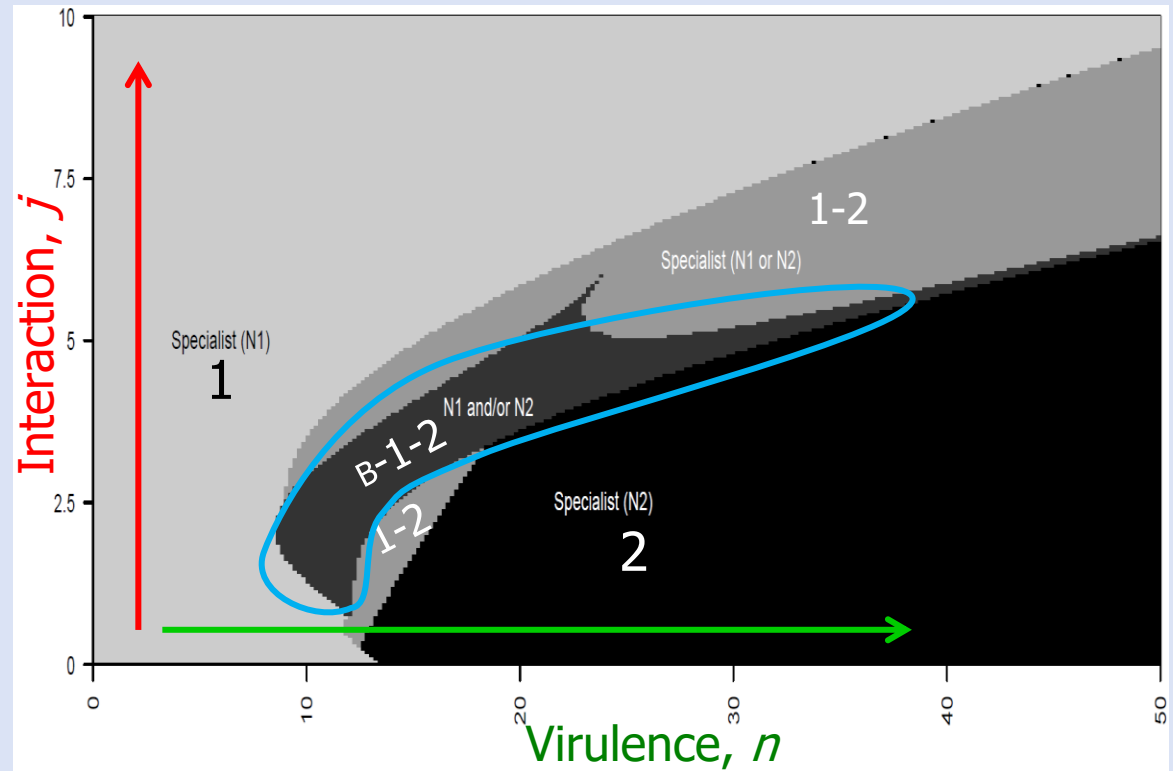
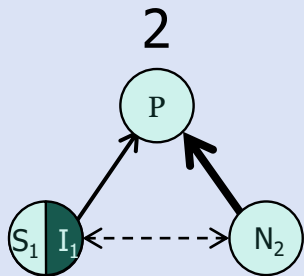
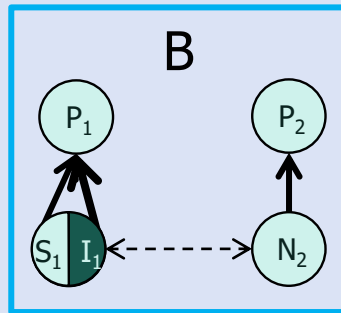
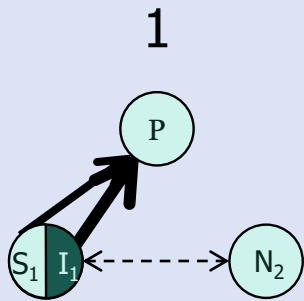
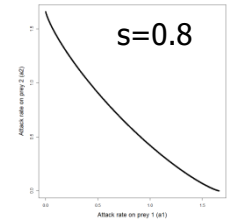


Predator diet: convex trade-off



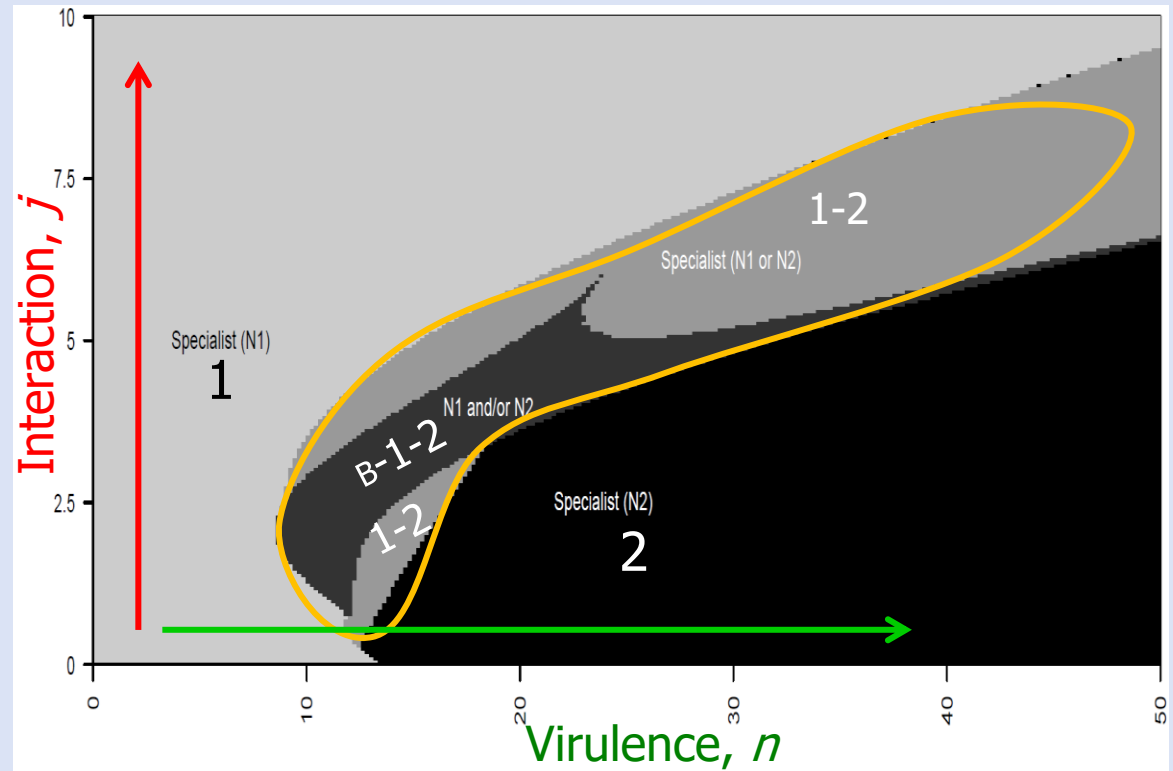
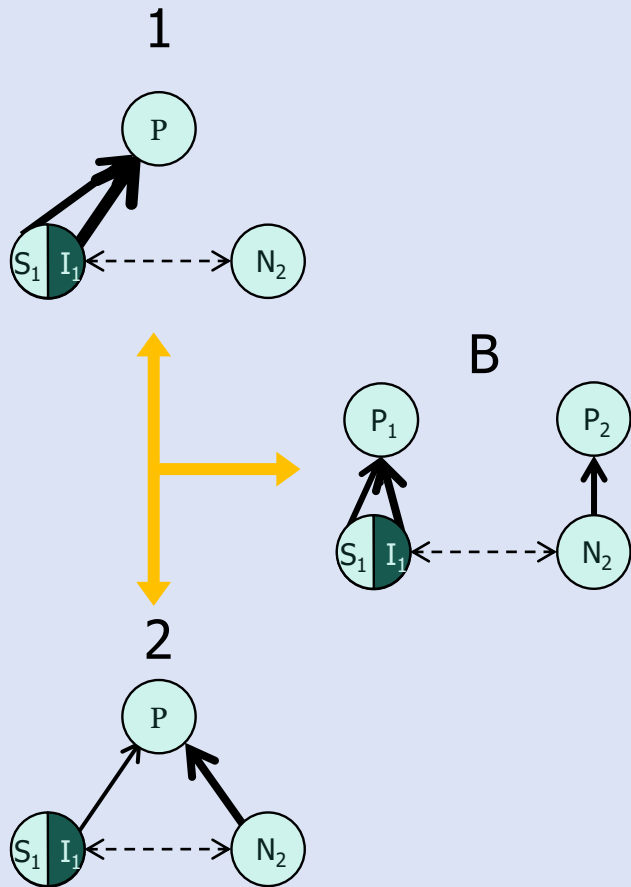
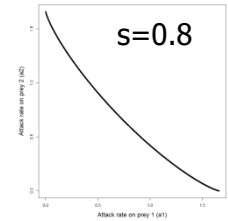
No generalist

Predator diet: convex trade-off



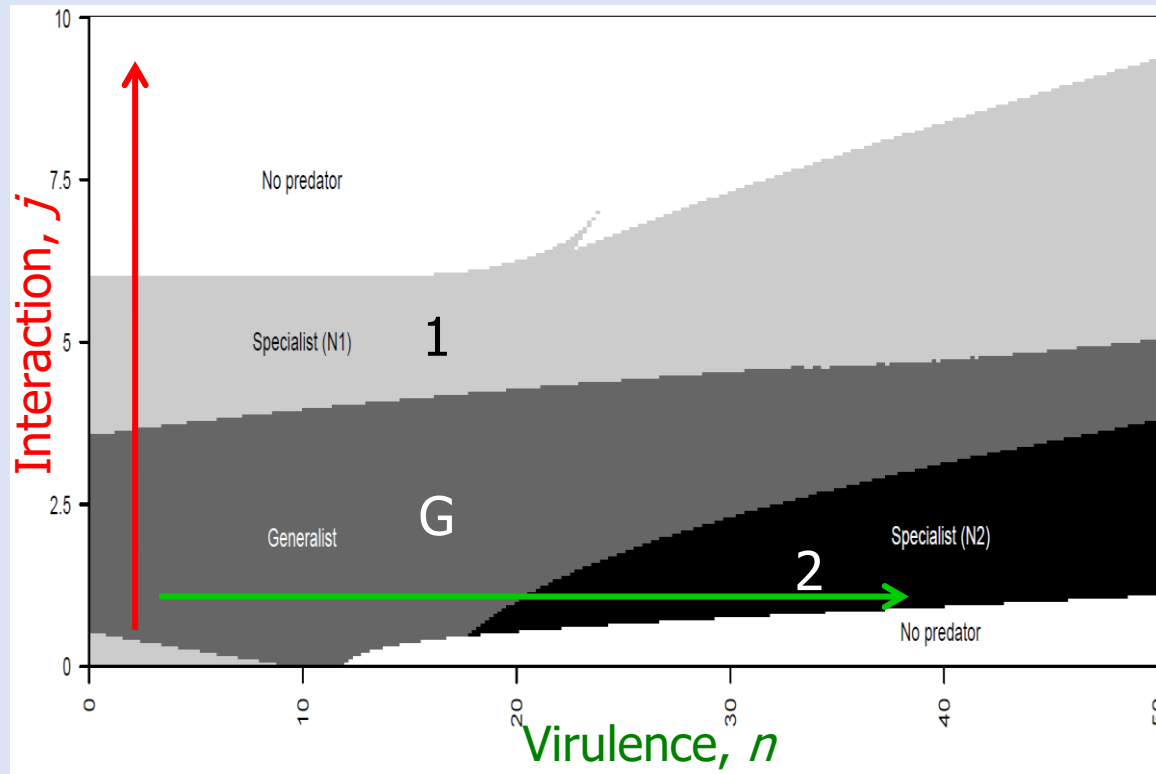
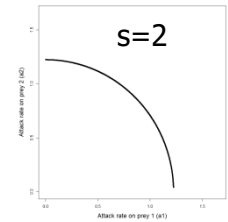
Diversification

Predator diet: convex trade-off

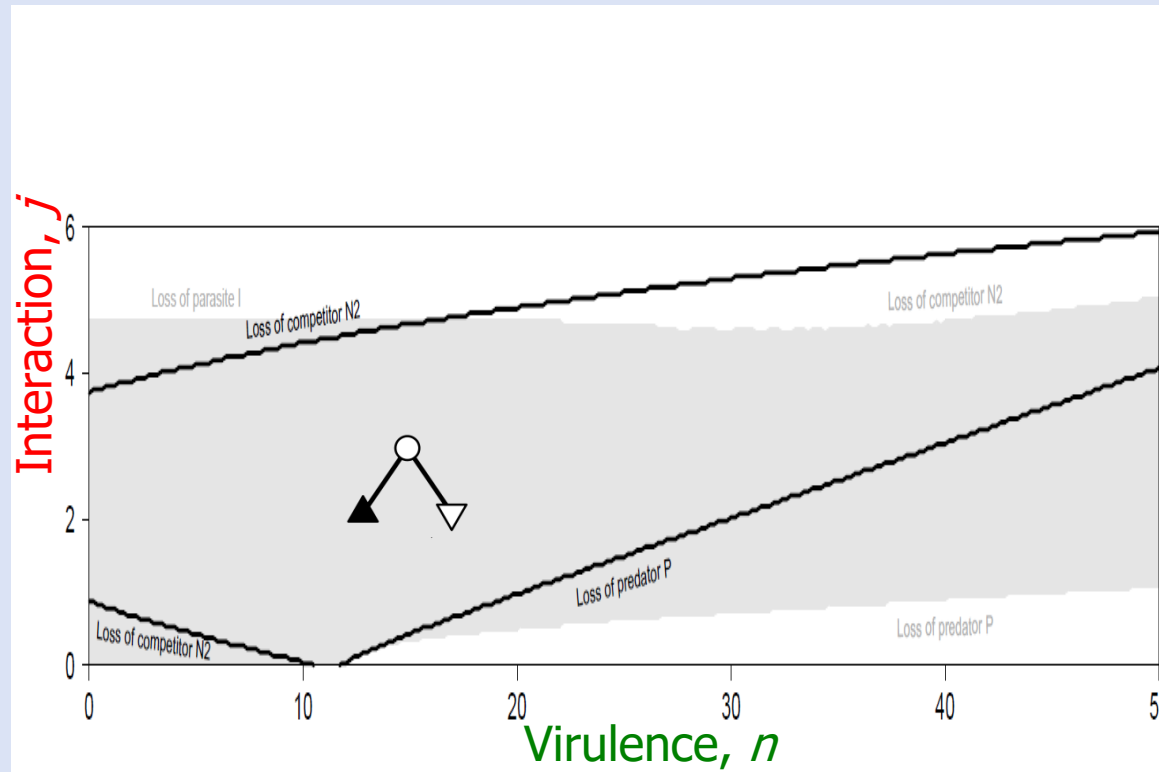
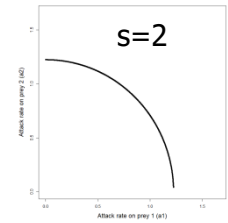


Evolutionary Multistability

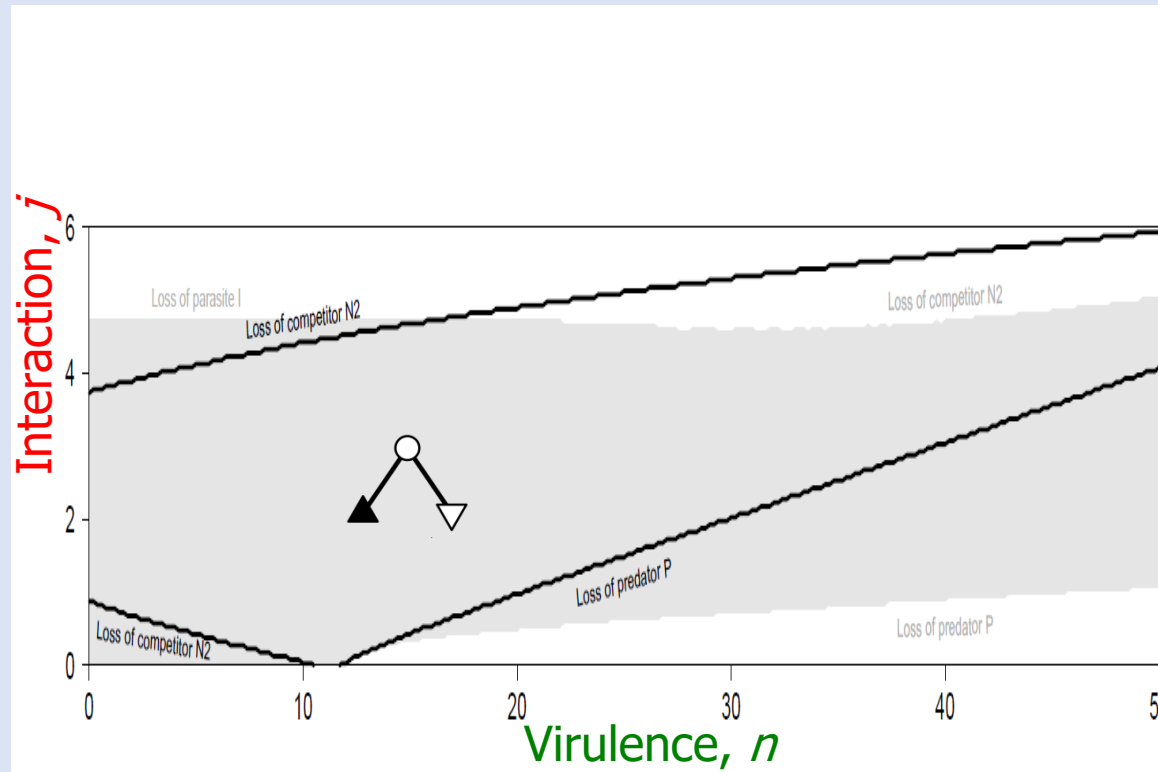
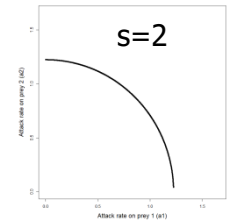
Coexistence: concave trade-off



Coexistence: concave trade-off



Coexistence: concave trade-off



Adaptive foraging increase coexistence

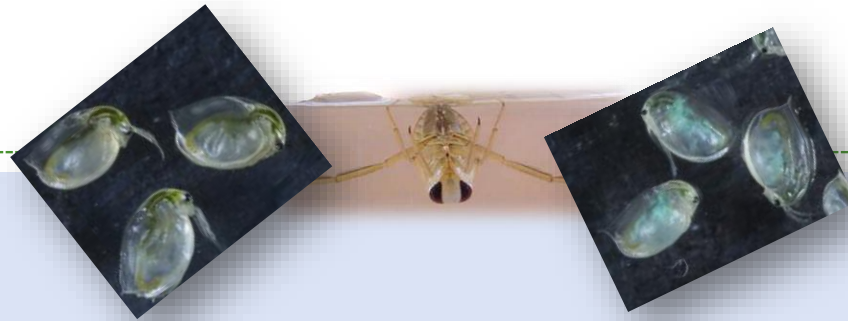
Conclusions

- Prey infection and adaptive foraging
 - Interaction effect: predation on host
 - Virulence effect: predation alternative prey
- Including evolution increases coexistence

Conclusions

- Prey infection and adaptive foraging
 - Interaction effect: predation on host
 - Virulence effect: predation alternative prey
 - Including evolution increases coexistence
- DIV-1 infection
 - Increase profitability but high virulence effect
 - Expected niche separation allowing coexistence

Prey infection alters predator diet



Thank you for your attention

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Baptiste Biccocchi, Matthieu Lam



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