PhD Thesis Defense

Role of natural enemy complementarity and antagonism on herbivore dynamics and biocontrol

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Lise ROY, Université Paul Valéry Montpellier



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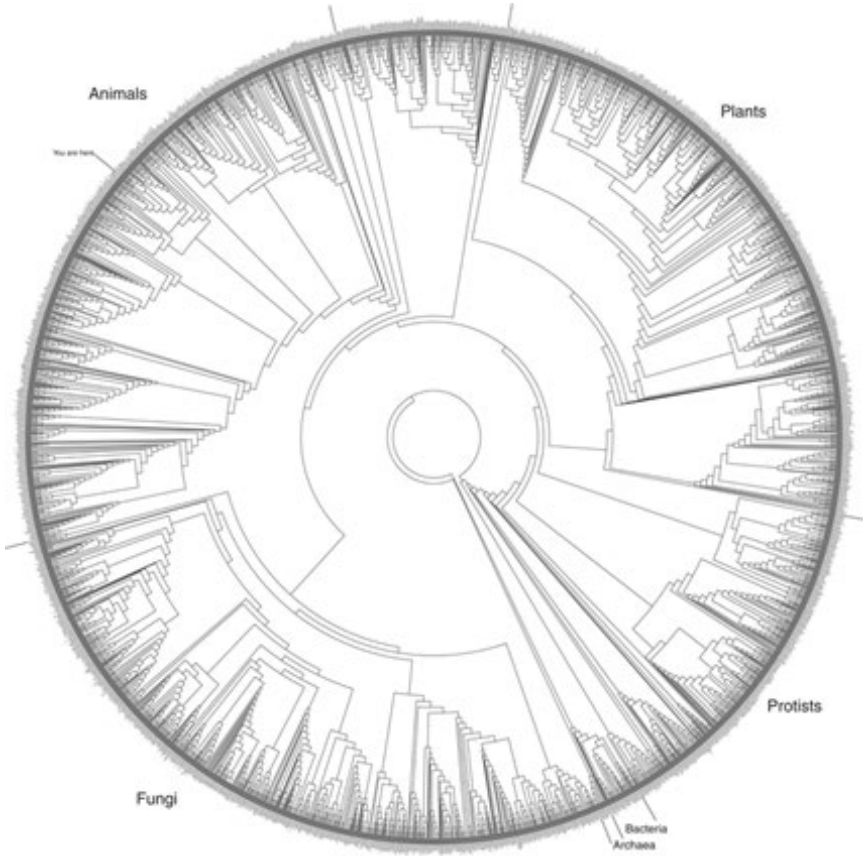
Biodiversity

Up to 30 million species are estimated



Erwin (2002), University Of Chicago Press.

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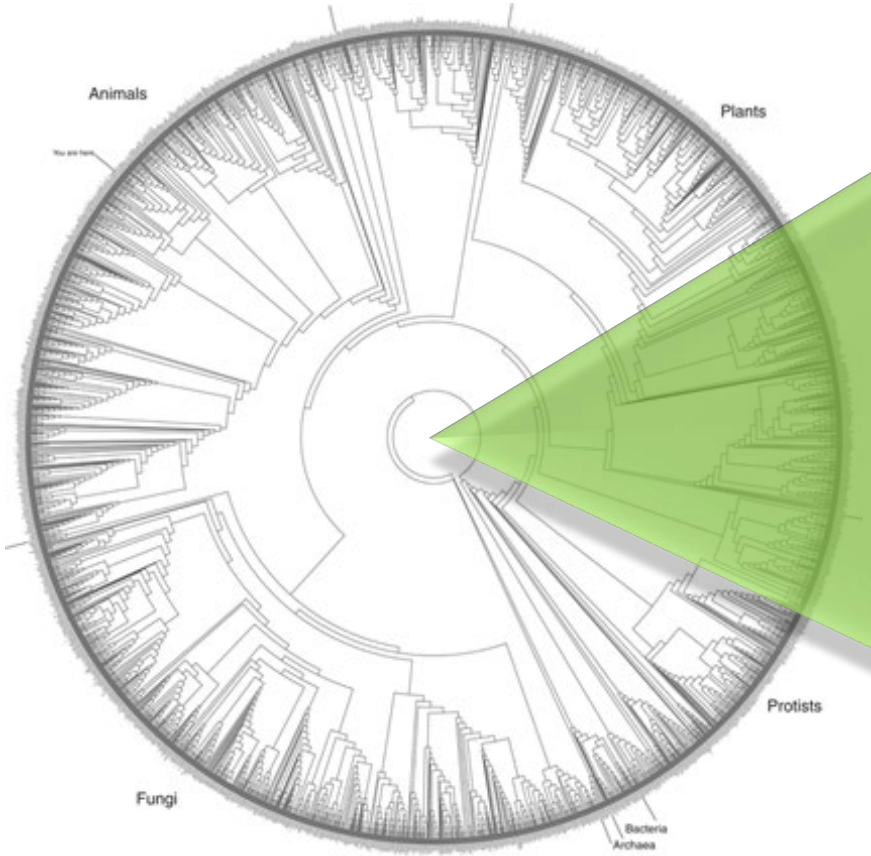


Ecosystem process and services

Water purification

Primary productivity

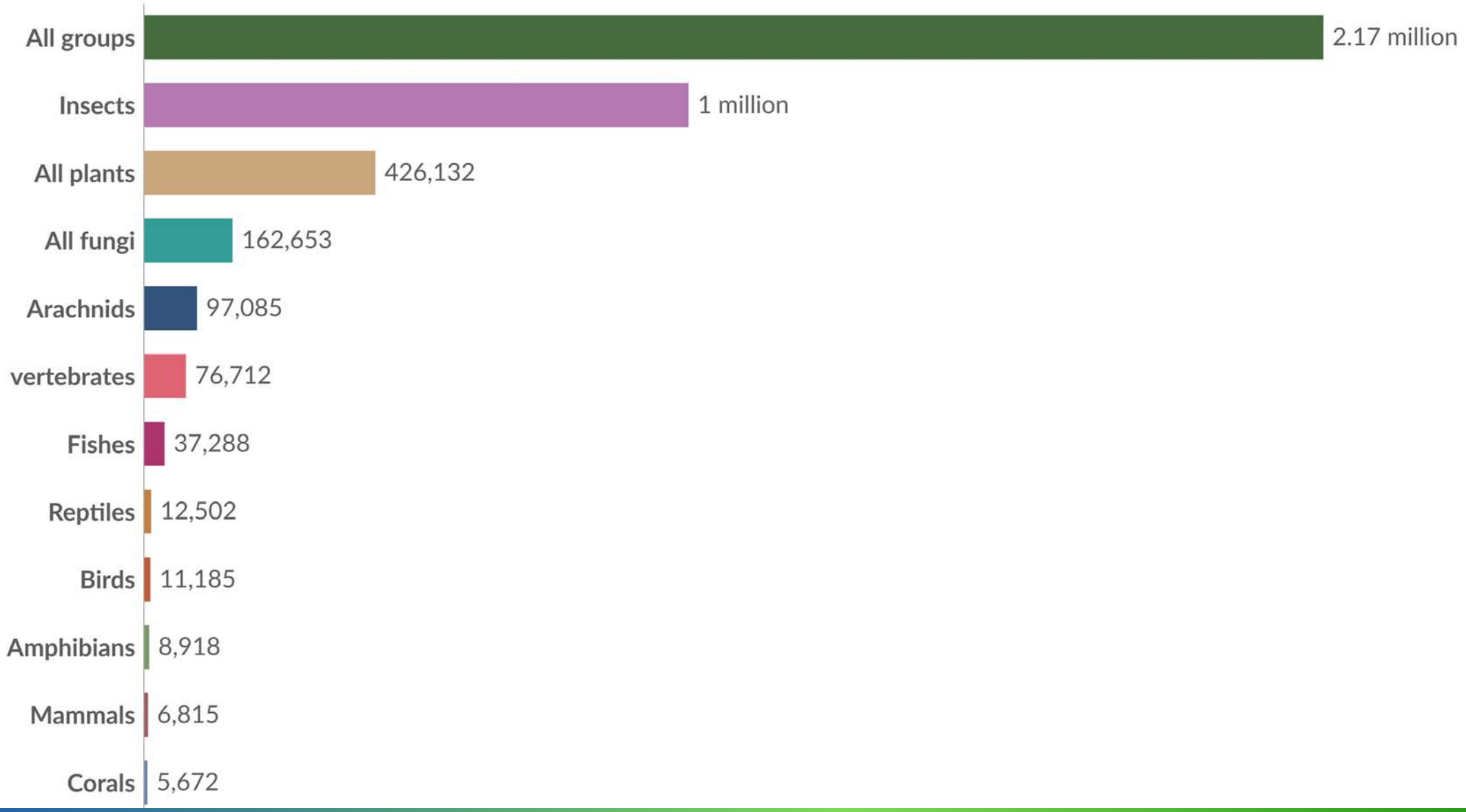
Nutrient cycling

Pollination

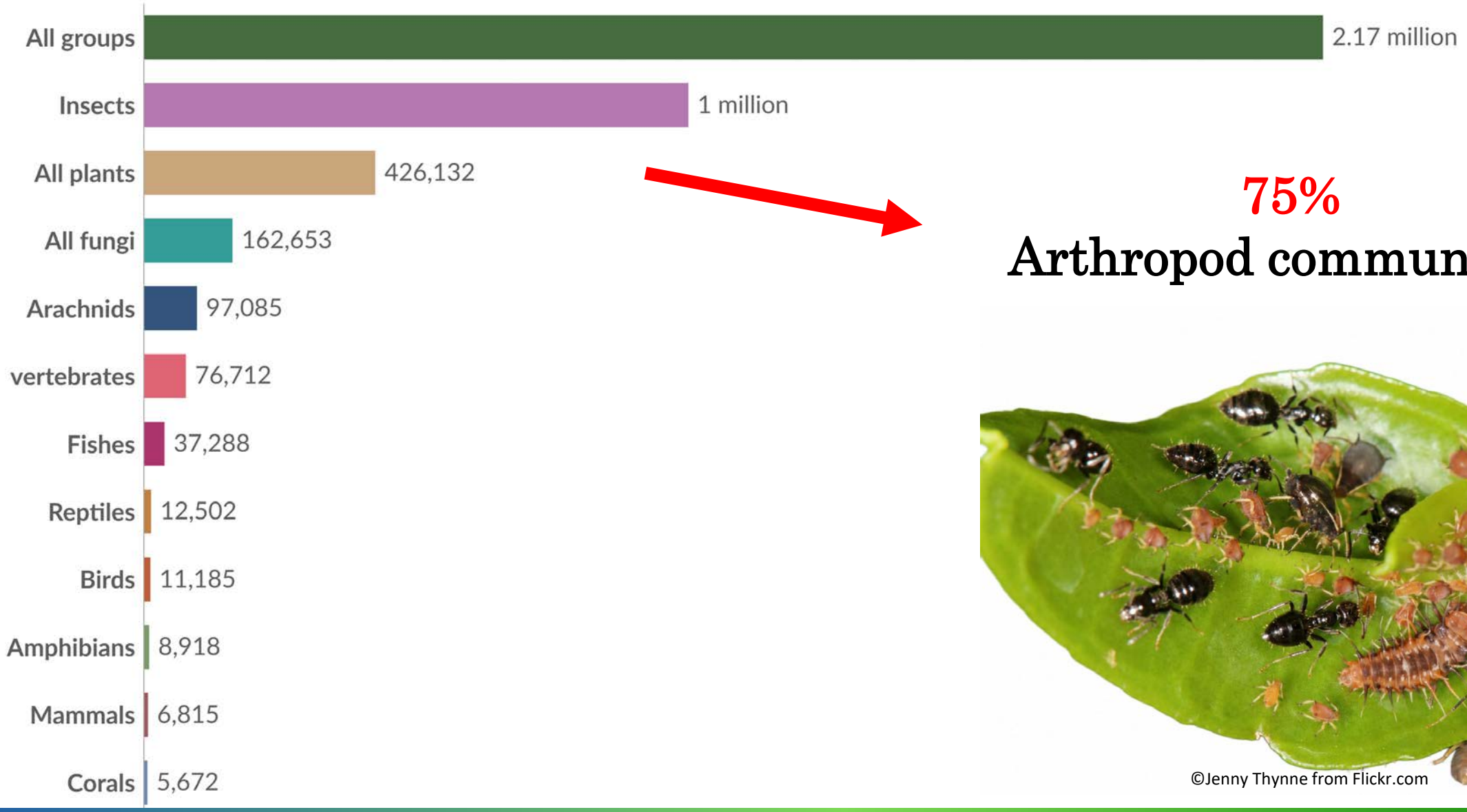
Herbivore Regulation

Cardinale et al. (2006), Nature.

Described species



Described species



75%

Arthropod communities

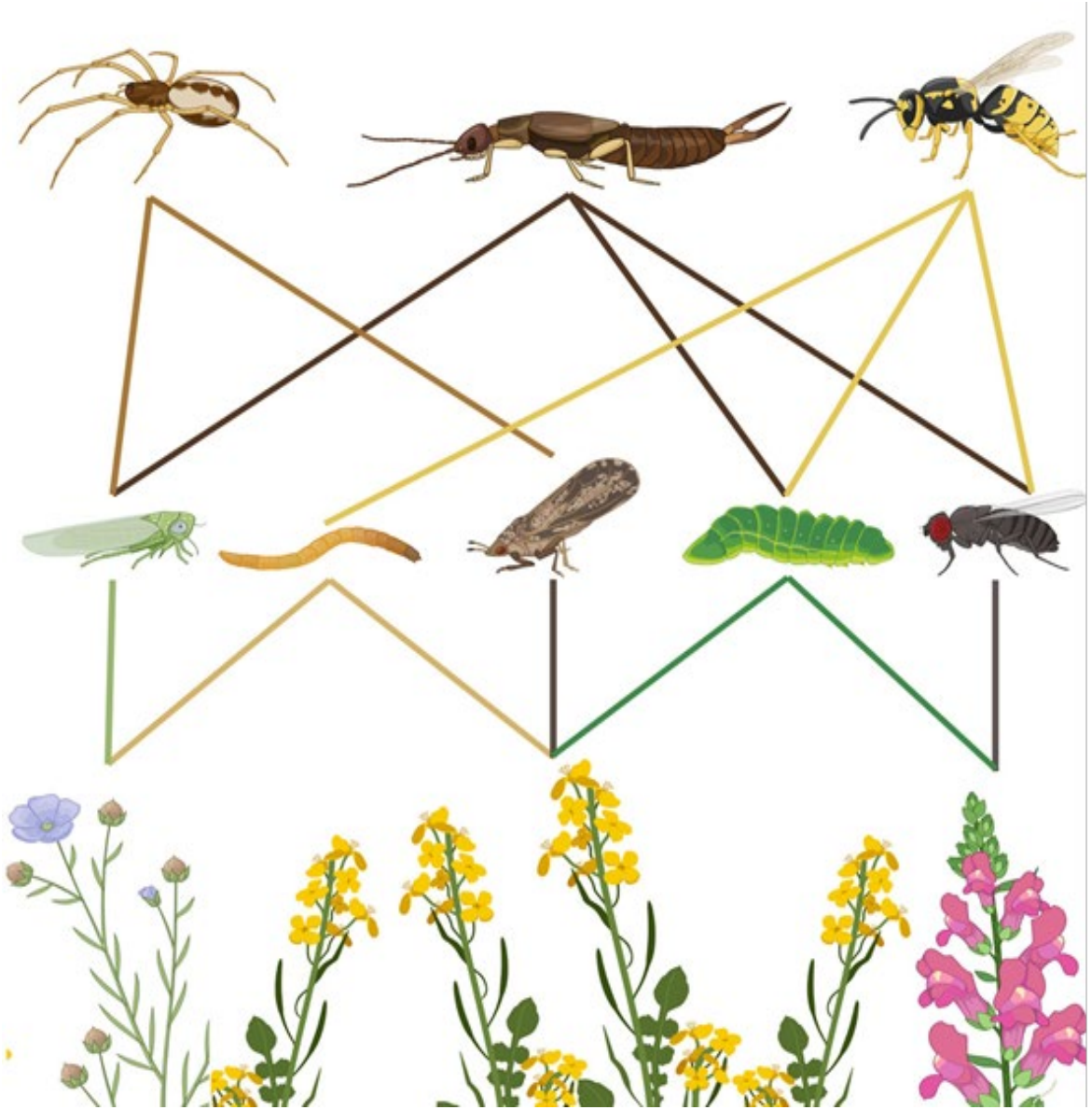
©Jenny Thynne from Flickr.com

Biodiversity (2025), OurWorldinData.org.

Terrestrial arthropod communities

Communities are composed of different trophic levels (predators-herbivores-plants)

Natural enemy diversity affects herbivores



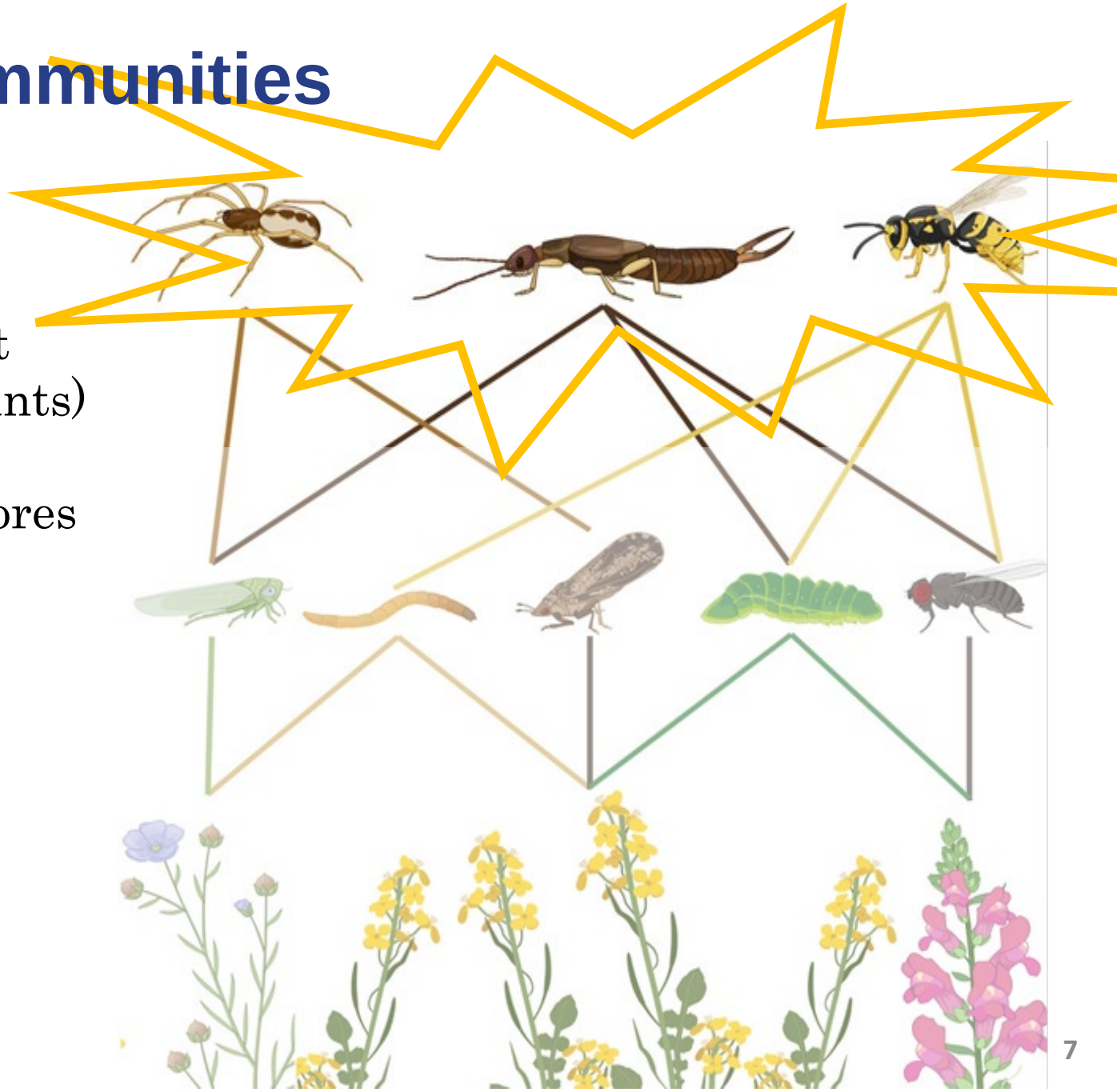
Morin (2011), Community ecology.

Terrestrial arthropod communities

Communities are composed of different trophic levels (predators-herbivores-plants)

Natural enemy diversity affects herbivores

Predator interactions determine biodiversity and biocontrol



Morin (2011), Community ecology.

Predator-predator interactions

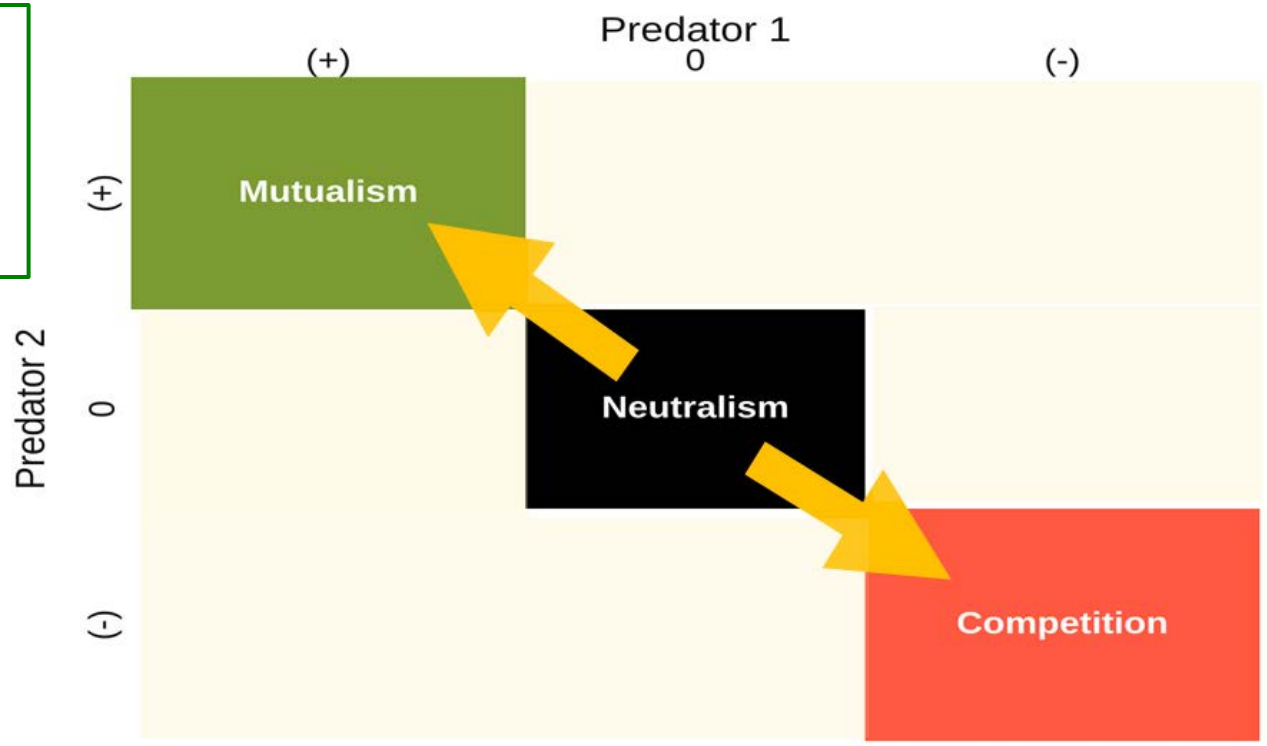
Predators can have **positive**, neutral or **negative** effect on diversity and biocontrol!

Pringle (2016), PLOS Biology.

Predator-predator interactions

Predators can have **positive**, neutral or **negative** effect on diversity and biocontrol!

Two predators
Improve
biocontrol



Disrupt biocontrol
Is better one predator?

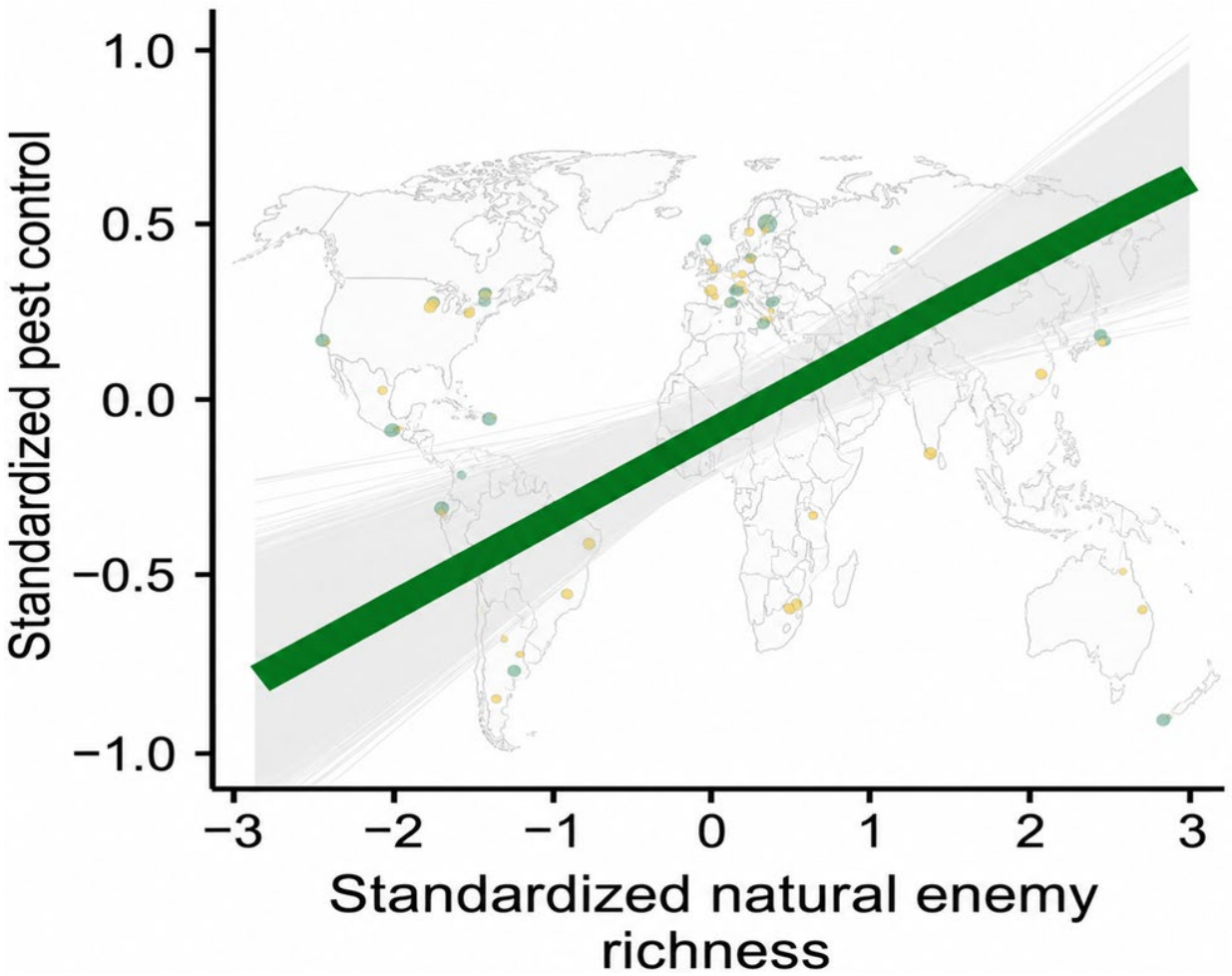
Pringle (2016), PLOS Biology.

The biodiversity-biocontrol relationship

Positive pattern

Driven by multiple mechanisms

1) Functional complementarity
2) Fitness differences
3) Intraguild predation



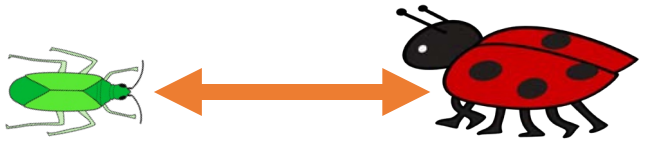
Dainese et al. (2019), Science Advances.

1) Functional complementarity

Natural enemies differ in prey use, microhabitats, feeding strategies, or activity periods. Together, these differences **enhance prey suppression**.

Measured by

1) Functional trait differences:
-Morphological, behavioural, and physical



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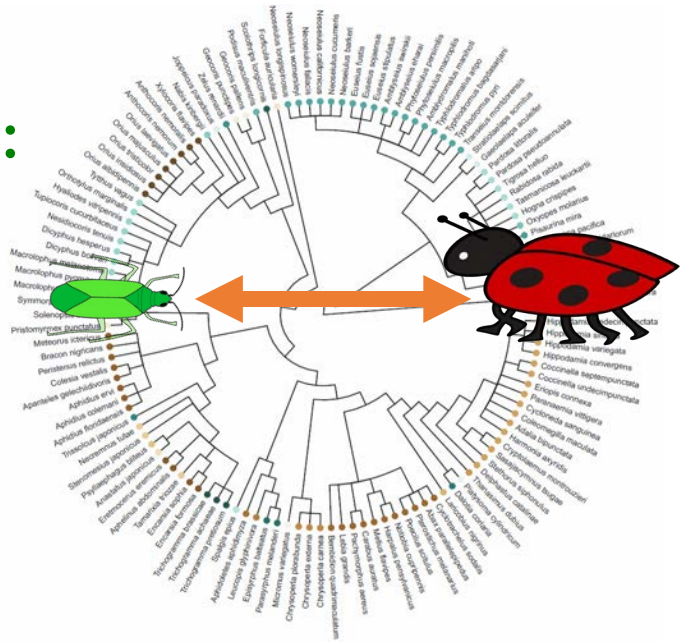
2) Phylogenetic distance
-Evolutionary history and trait differentiation



Snyder (2019), Biological Control.

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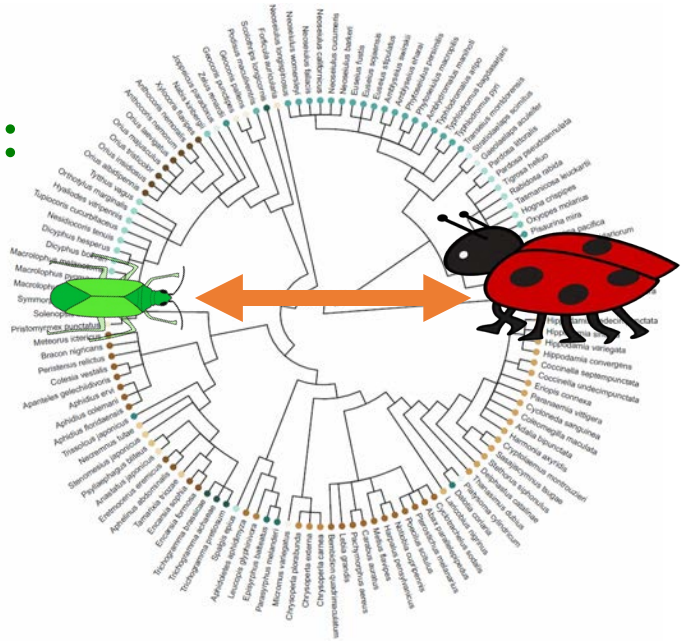


High functional differences

→ More complementarity

→ Coexistence

→ Better biocontrol

Snyder (2019), Biological Control.

2) Fitness differences

Competitive differences among predators in their **ability to prey** and maintain population growth.

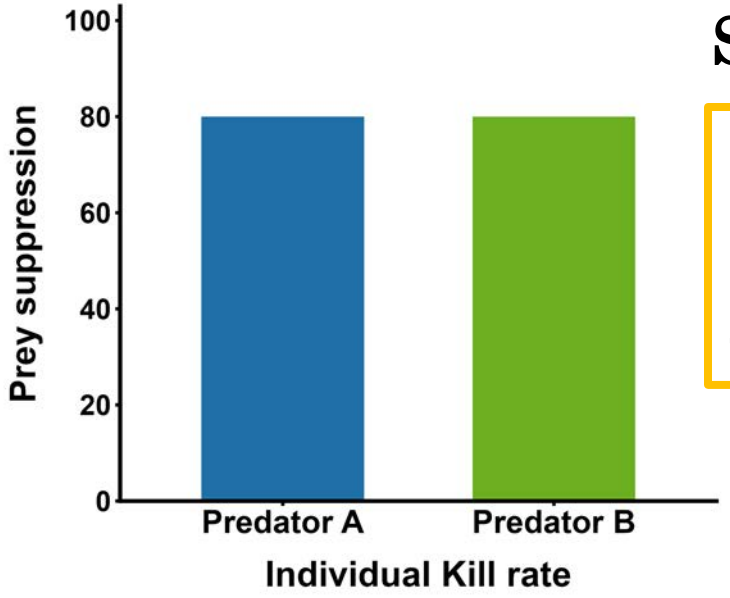
Measured by Kill rates

2) Fitness differences

Competitive differences among predators in their **ability to prey** and maintain population growth.

Measured by Kill rates

→ Similar kill rates



Similar Fitness

-No dominance

-Complementarity

-Better Biocontrol

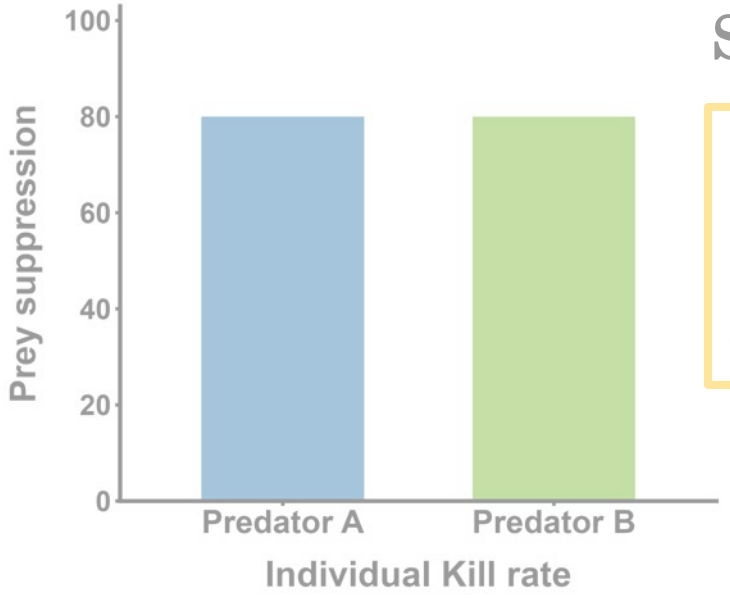
Chesson (2000), Annu. Rev. Ecol. Syst.

2) Fitness differences

Competitive differences among predators in their **ability to prey** and maintain population growth.

Measured by Kill rates

Similar kill rates



Similar Fitness

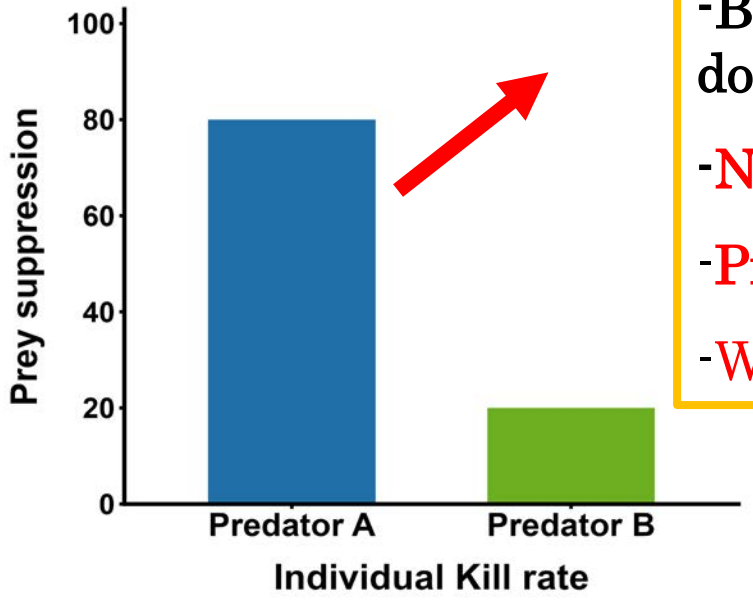
-No dominance

-Complementarity

-Better Biocontrol

Large kill rate differences

Fitness differences



-Best predator dominates

-No coexistence

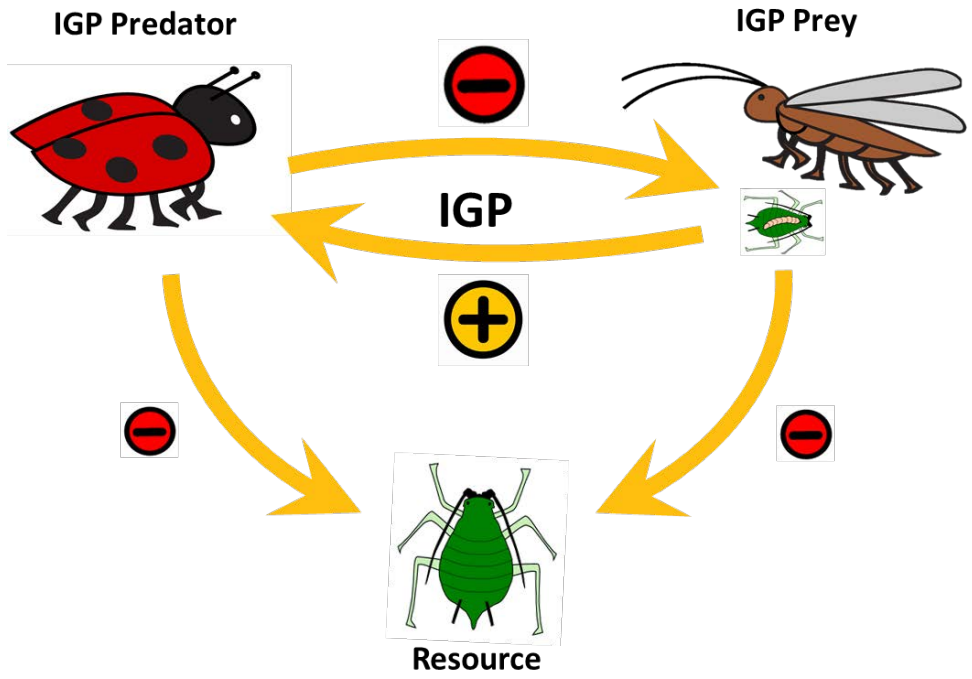
-Promote IGP

-Worse Biocontrol

Chesson (2000), Annu. Rev. Ecol. Syst.

3) Intraguild predation types

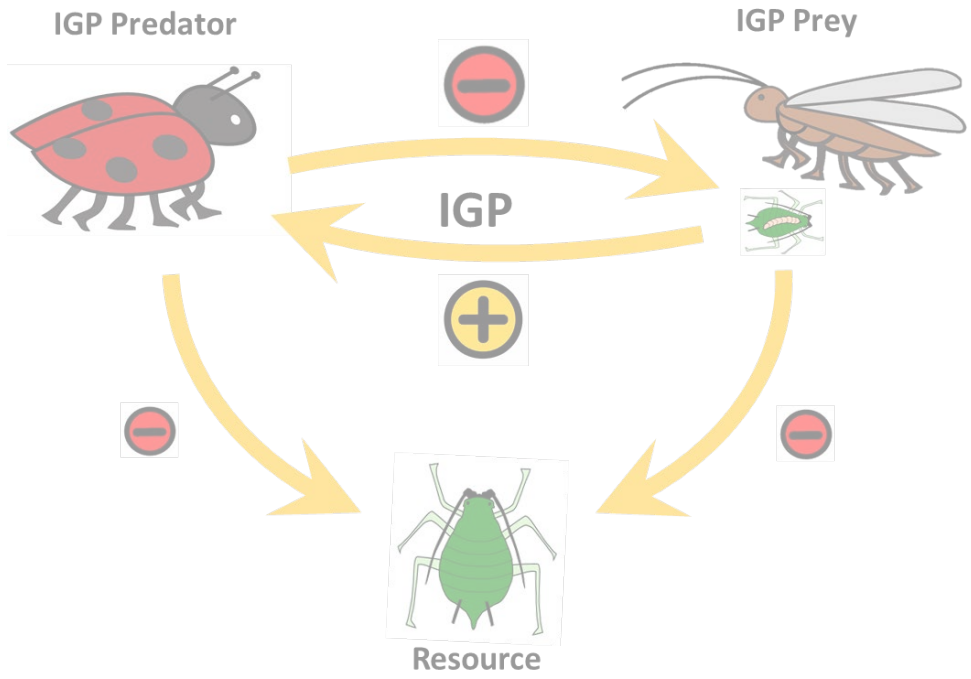
Asymmetrical IGP



Unbalanced competition

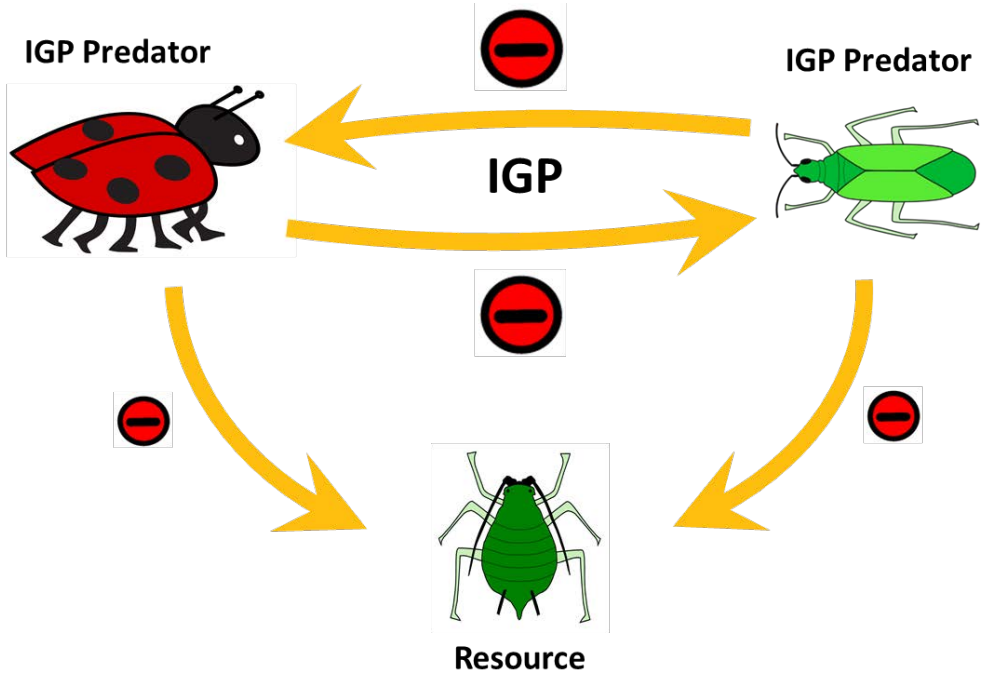
3) Intraguild predation types

Asymmetrical IGP



Unbalanced competition

Symmetrical IGP



Similar competition

Polis et al. (1989), Annu. Rev. Ecol. Syst.

Different studies address these mechanisms separately

Mechanism	Framework
1) Functional complementarity	Biodiversity-**Biocontrol** relationship
2) Fitness differences	Modern **coexistence** theory
3) Intraguild predation	Classic **IGP** theory

Letourneau et al. (2009), Chesson (2000), Polis et al. (1989).

Different studies address these mechanisms separately

Mechanism	Framework	
1) Functional complementarity	Biodiversity-**Biocontrol** relationship	High complementarity **-Better Biocontrol**
2) Fitness differences	Modern **coexistence** theory	
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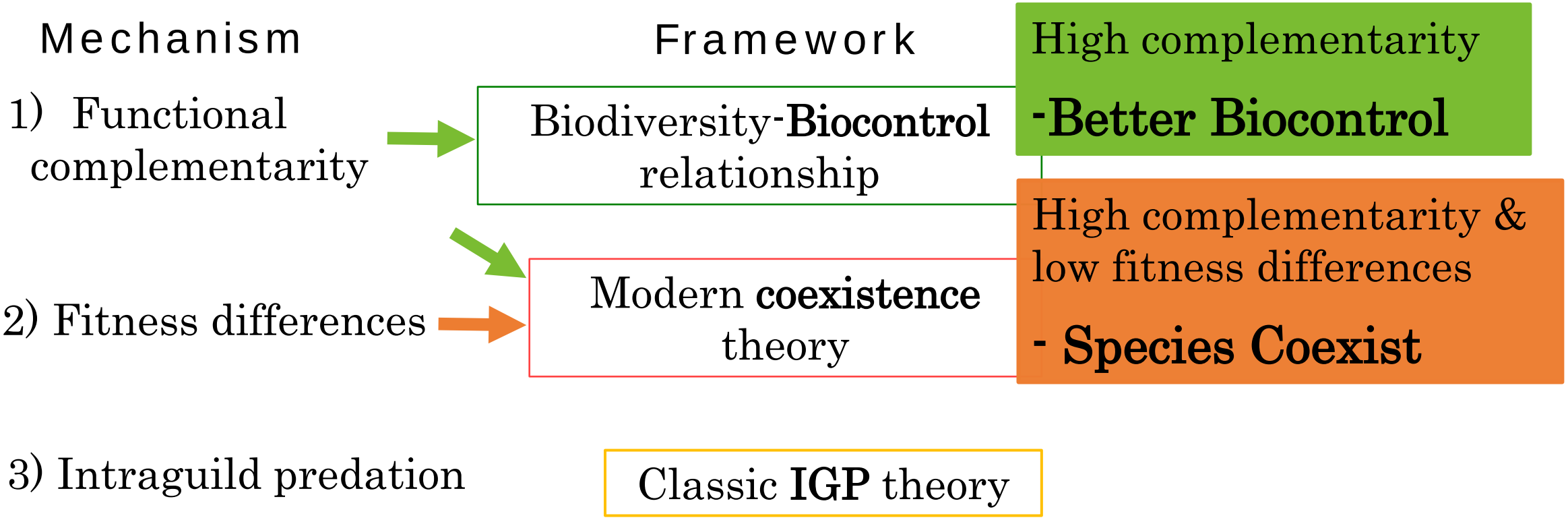

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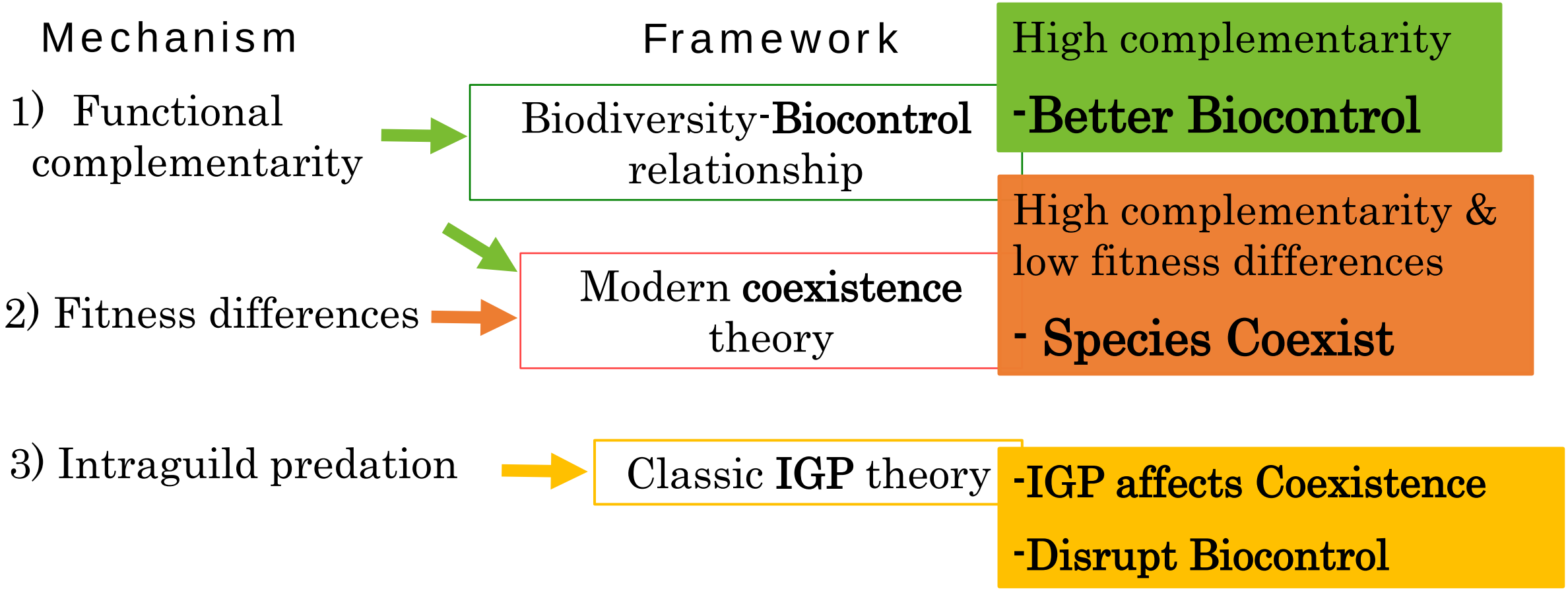


Letourneau et al. (2009), Chesson (2000), Polis et al. (1989).

Knowledge gap

No framework combines these 3 main mechanisms to explain coexistence and biocontrol!!!

1) Functional complementarity 

2) Fitness differences 

3) Intraguild predation 

Research question



How do predators coexist and promote better biocontrol?

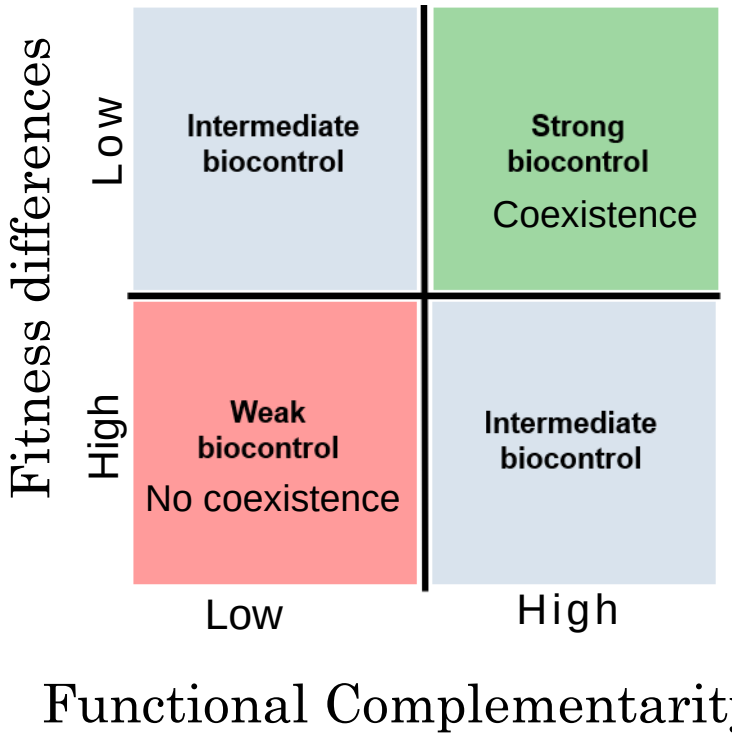
Main objective

"Identify how **functional complementarity**, **fitness differences**, and **intraguild predation** shape predator coexistence and biocontrol in **combinations of two predators (cocktails)**."



Coexistence
&
Better biocontrol

Hypotheses



H1

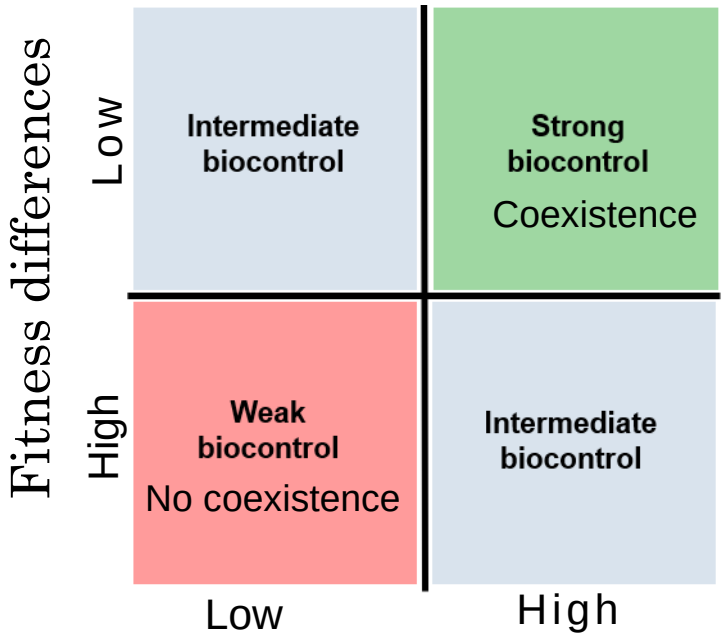
High complementarity &
Low fitness differences

→ **Coexistence**

→ **Better biocontrol**

Letourneau et al. (2009), Chesson (2000), Polis et al. (1989).

Hypotheses



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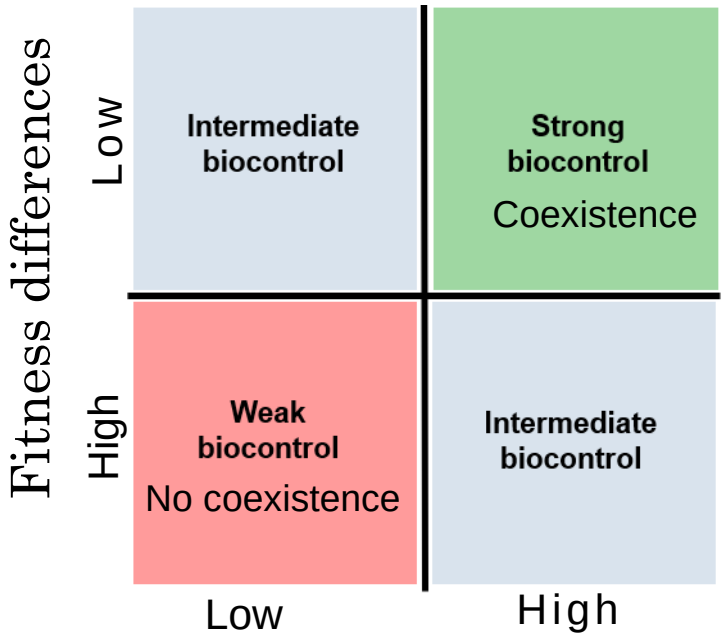

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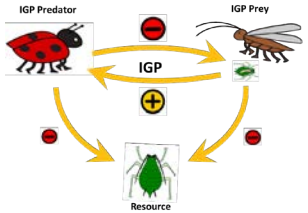
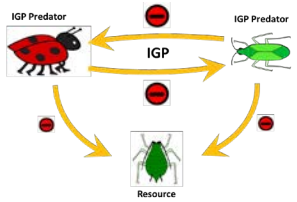


H2 Asymmetrical IGP

IGP prey is the best predator or **can reduce fitness differences**



H3 Symmetrical IGP

High complementarity & Low fitness differences (**kill rates or growth**)

Letourneau et al. (2009), Chesson (2000), Polis et al. (1989).

1. IGP interaction effects

- Experimental

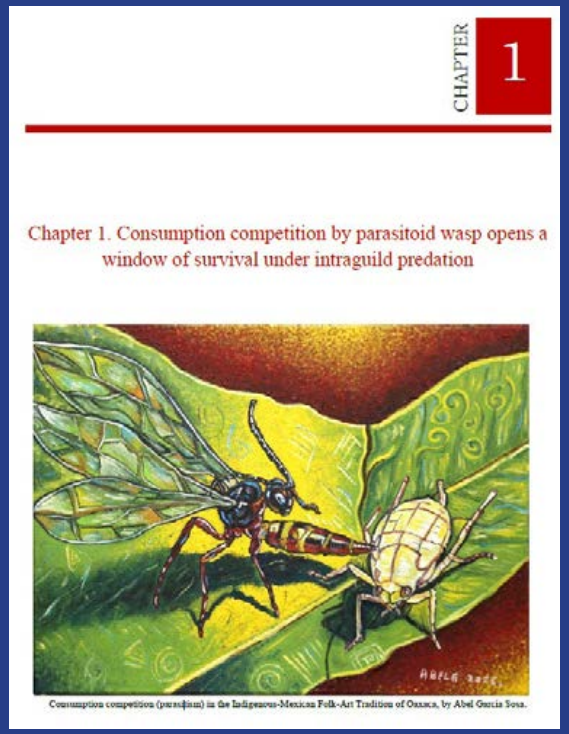
2. A meta-analysis

- Literature

3. Predator combinations

- Experimental

1. IGP interaction effects


CHAPTER 1

Chapter 1. Consumption competition by parasitoid wasp opens a window of survival under intraguild predation

Consumption competition (parasitism) in the Indigenous-Mexican Folk-Art Tradition of Oaxaca, by Abel García Sosa.

- Experimental

Predator-parasitoid

Coexistence mechanism

Biocontrol effect

2. A meta-analysis

3. Predator combinations

1. IGP interaction effects



- Experimental

Predator-parasitoid

Coexistence mechanism

Biocontrol effect

2. A meta-analysis



- Literature

Biocontrol patterns

Complementarity

Predation efficacy

IGP

3. Predator combinations

1. IGP interaction effects



- Experimental

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Complementarity

Predation efficacy

IGP

3. Predator combinations



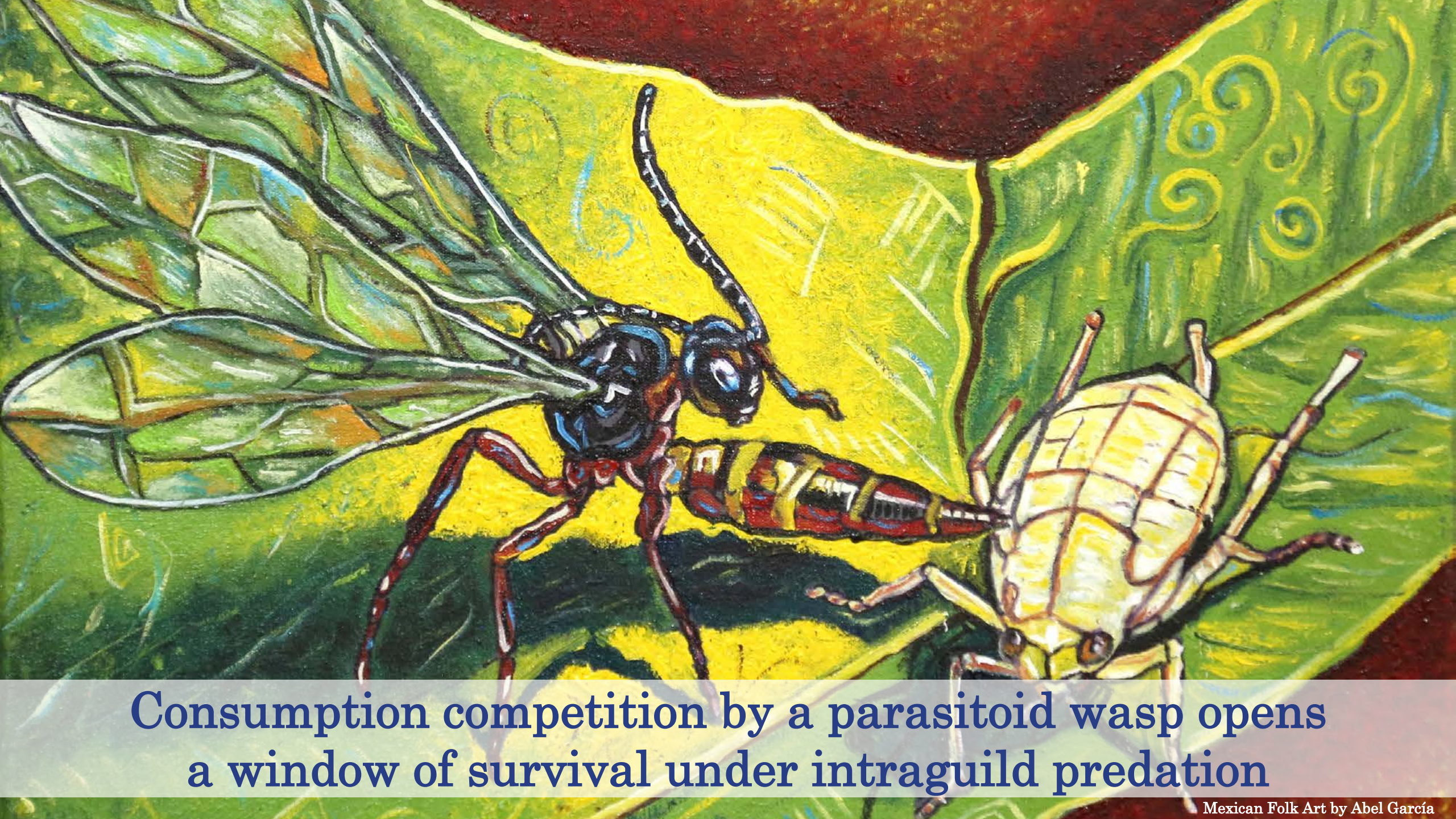
- Experimental

Complementarity

Fitness differences

IGP

Coexistence & biocontrol



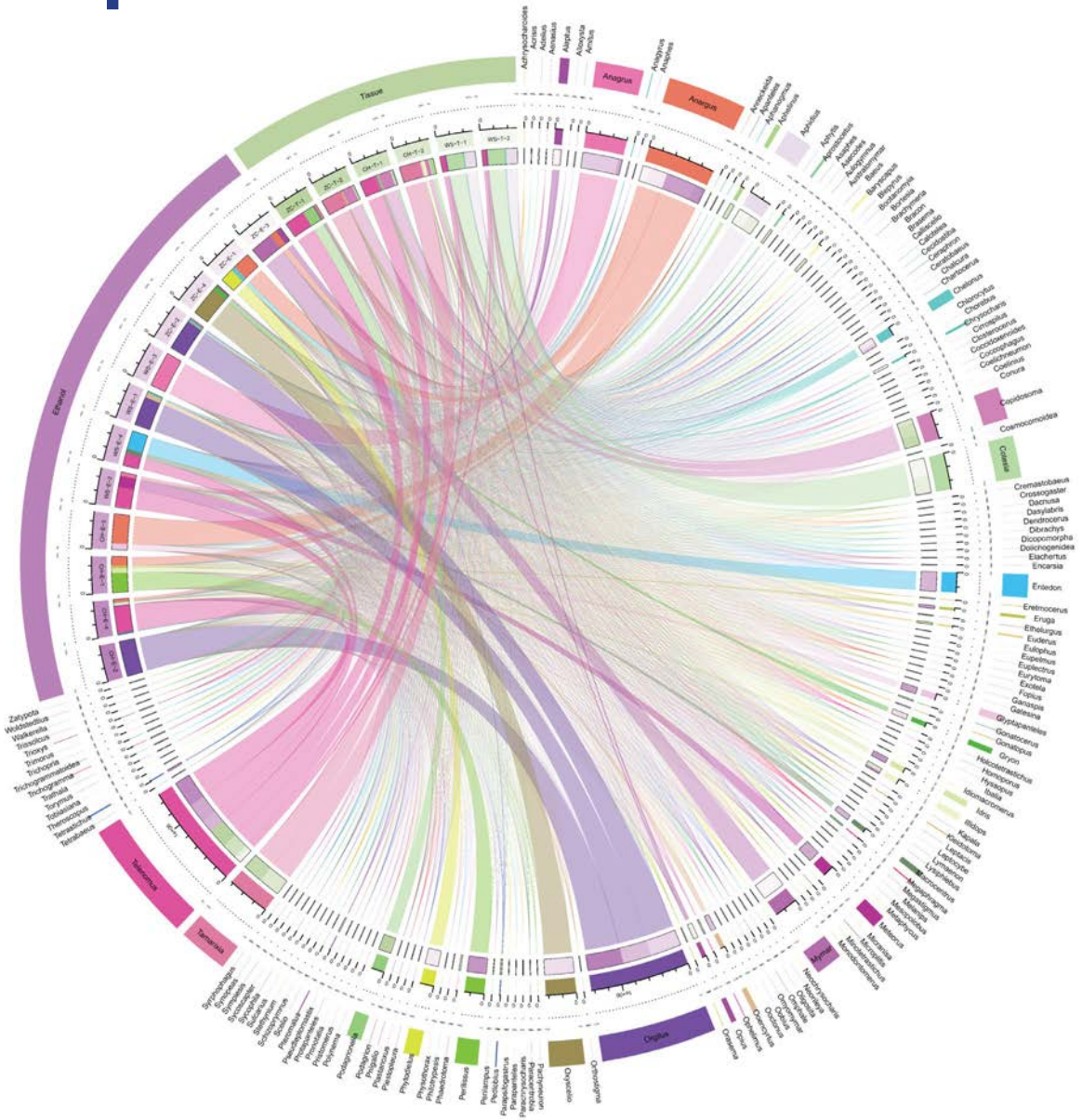
Consumption competition by a parasitoid wasp opens a window of survival under intraguild predation

Mexican Folk Art by Abel García

Parasitoids are a diverse group in nature

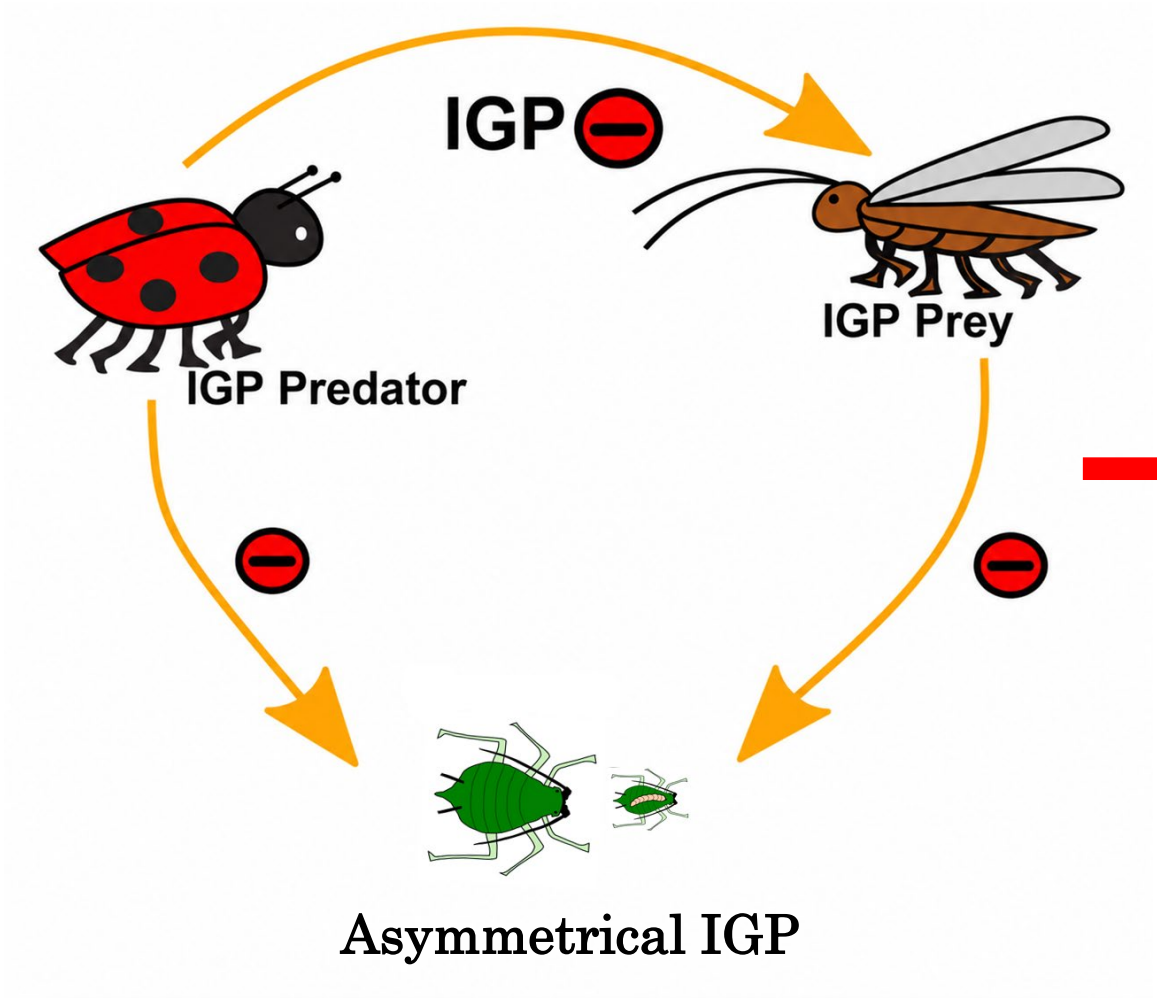
10% to 20% of all described insect species on Earth

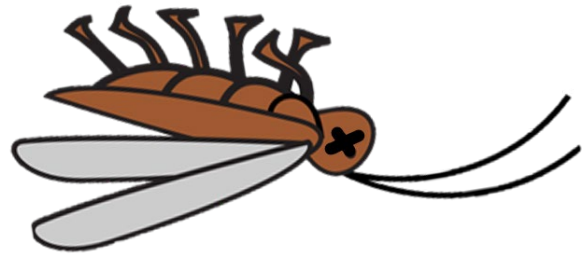
Important in pest control



Wang et al. (2024), Insects

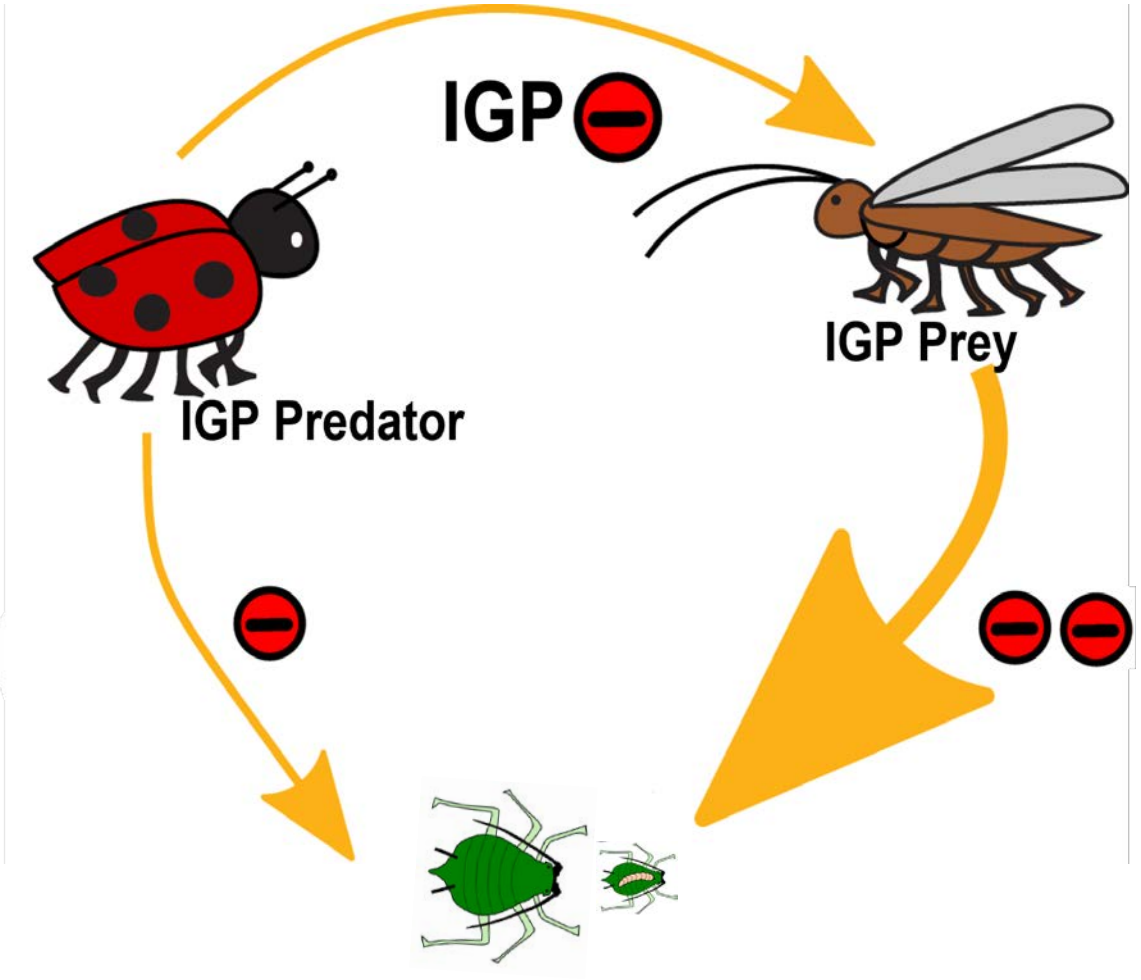
Parasitoid-predator system





Exclusion

How do parasitoids coexist?



Asymmetrical IGP

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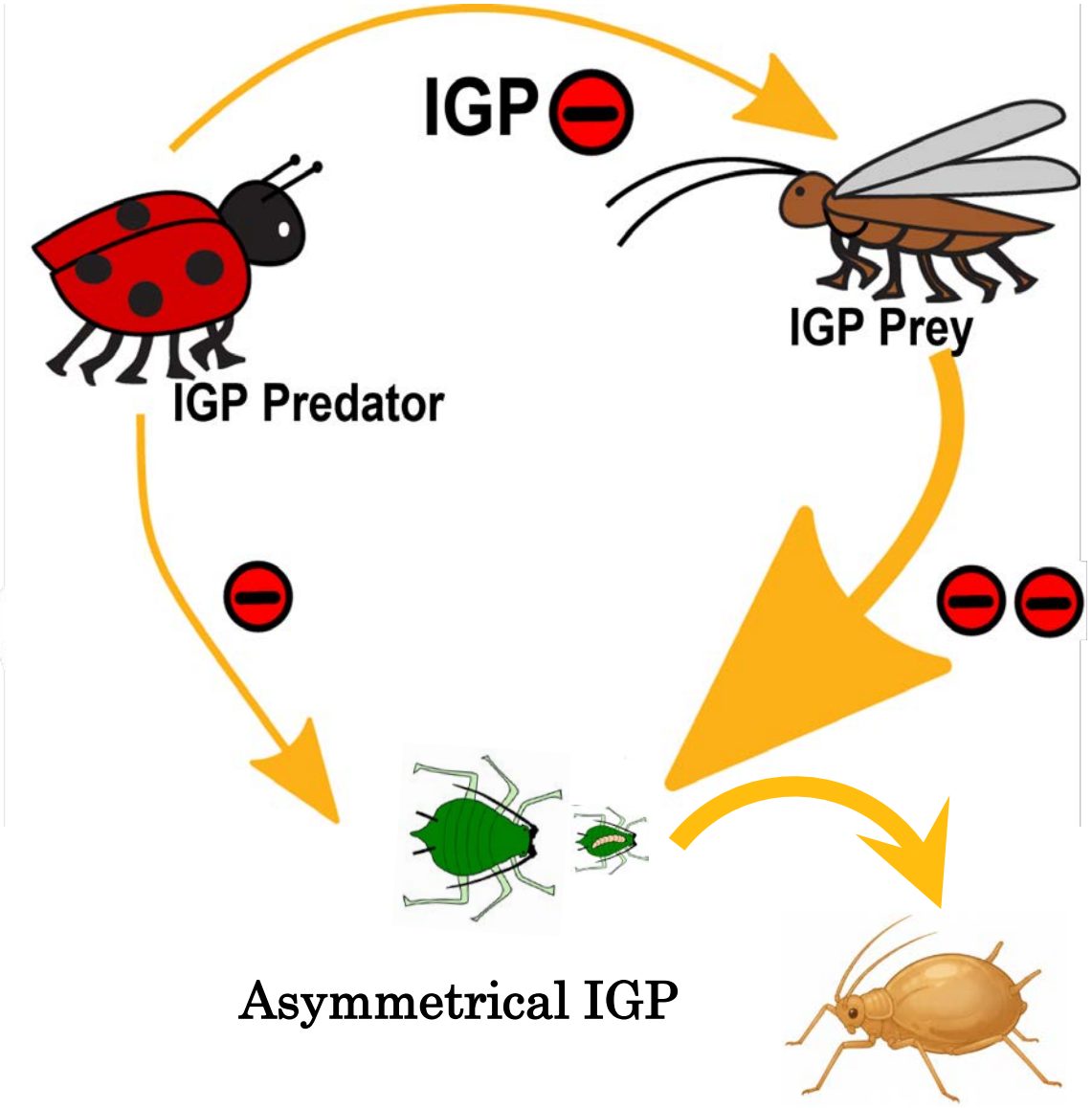


H2
Asymmetrical IGP

IGP prey is the best predator or can reduce fitness differences

a) Reduce prey availability (Consumption competition)

b) Predators avoid parasitised prey (low nutrient quality)

Chesson (2000), Polis et al. (1989).

Parasitoid-predator communities

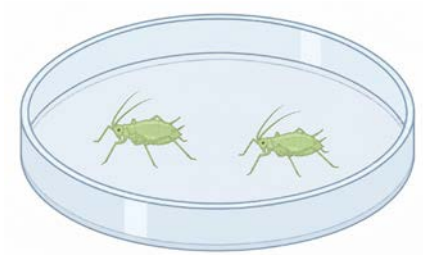
Community dynamics

-Better competitor



Predation rates

-Predator effectiveness



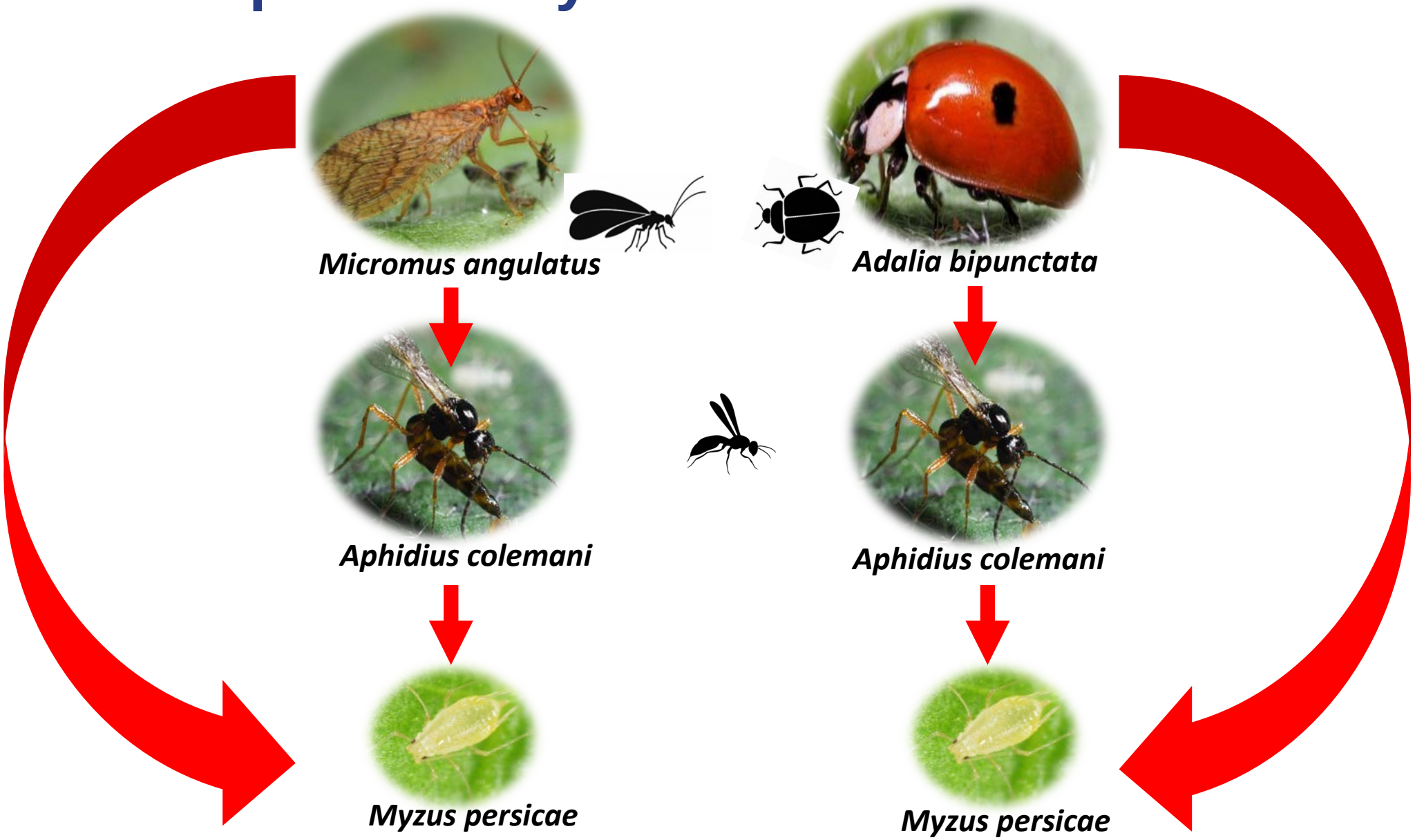
Choice test

-Predator selectiveness



Designs generated by BioRender.com

Parasitoid-predator system



Community dynamics

Experimental set-up

5 treatments each with 8 replicates:

1. *A. colemani*
2. *A. bipunctata*
3. *M. angulatus*
4. *A. colemani* + *A. bipunctata*
5. *A. colemani* + *M. angulatus*



n = 10 (5♀+5♂)



n = 300



n = 5♀





n = 5♀



40 cages







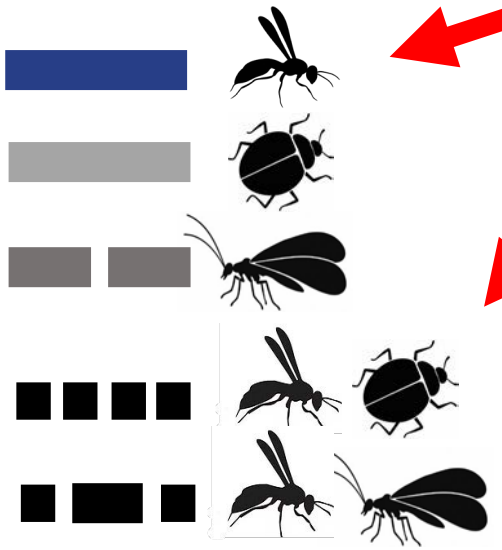
ENEMY COCKTAIL

Designing natural enemy cocktails for a better biocontrol

BRITISH ECOLOGICAL SOCIETY Journal of Animal Ecology

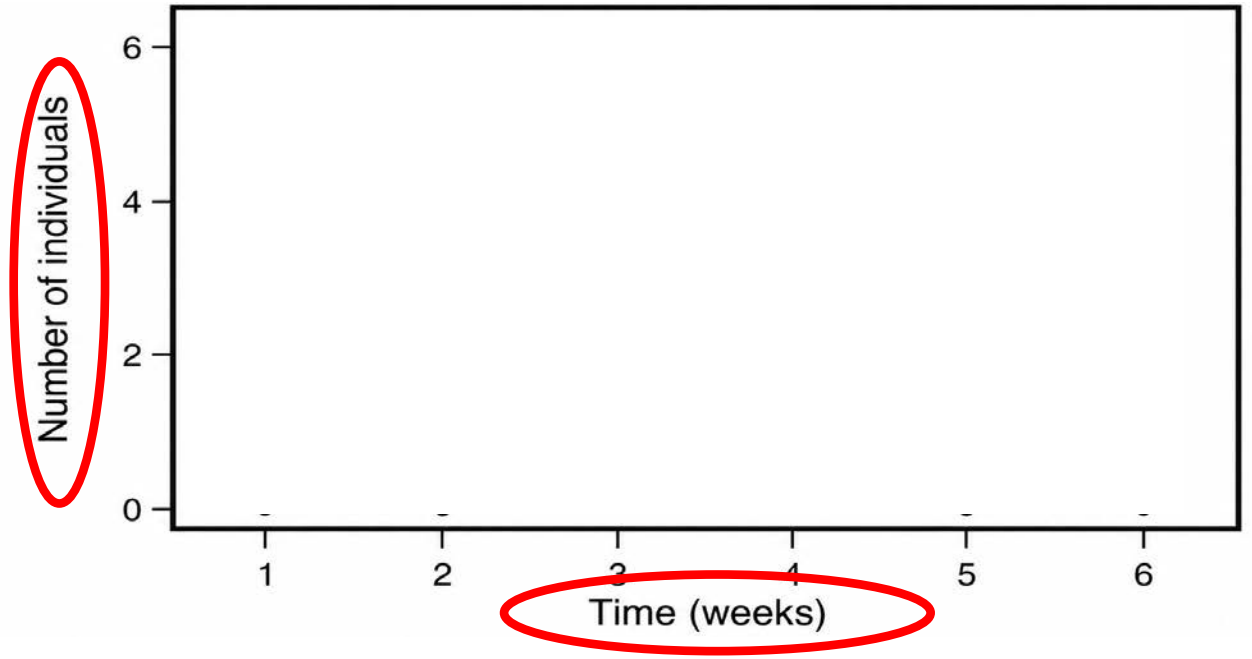
Results

1) Treatments



Parasitoid effects

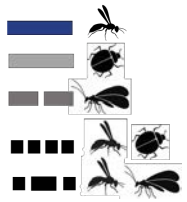
2) Dynamics

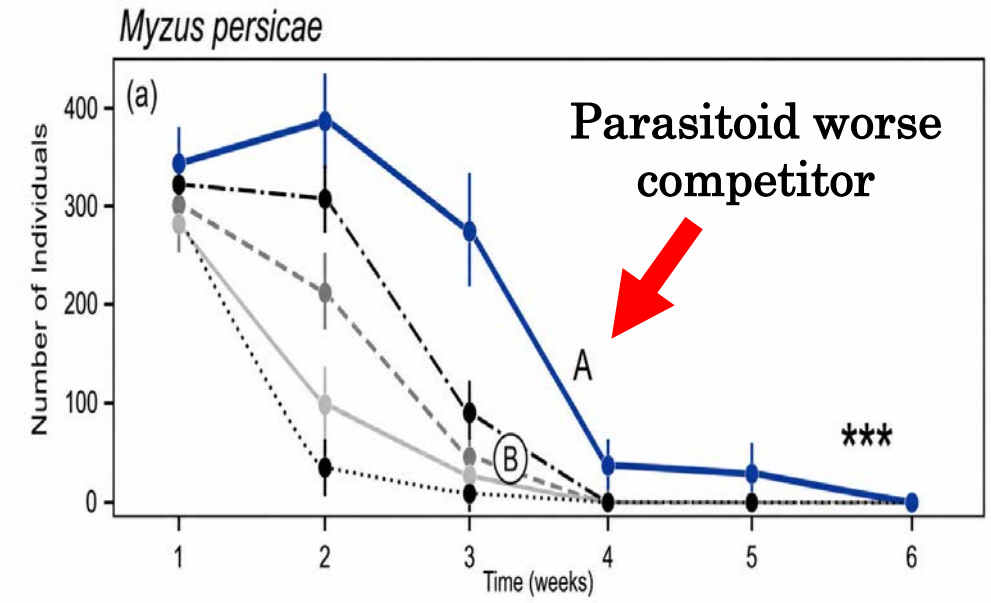


Community dynamics

BRITISH ECOLOGICAL SOCIETY Journal of Animal Ecology

Treatments





Community dynamics

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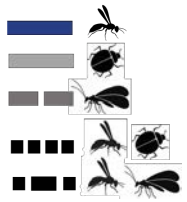
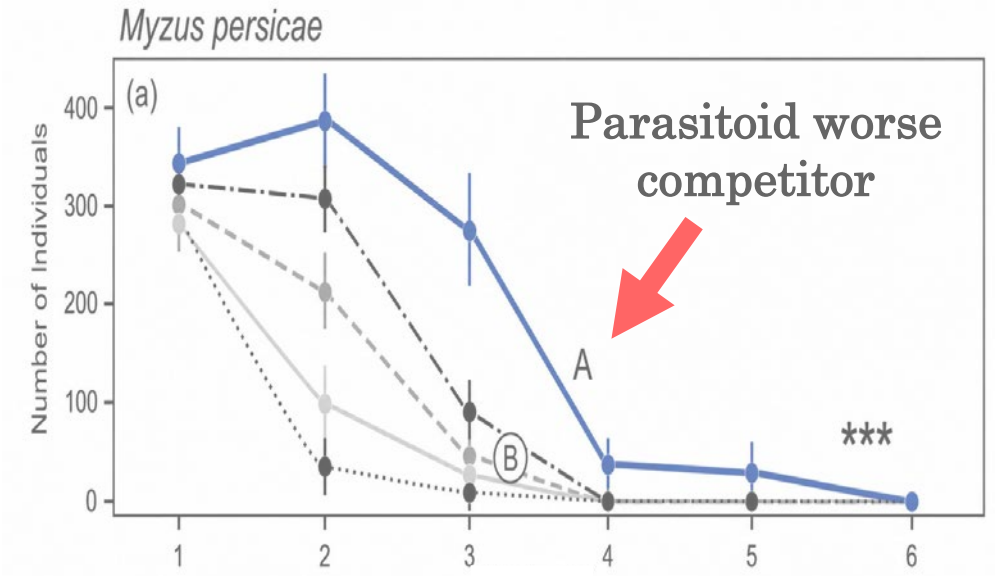
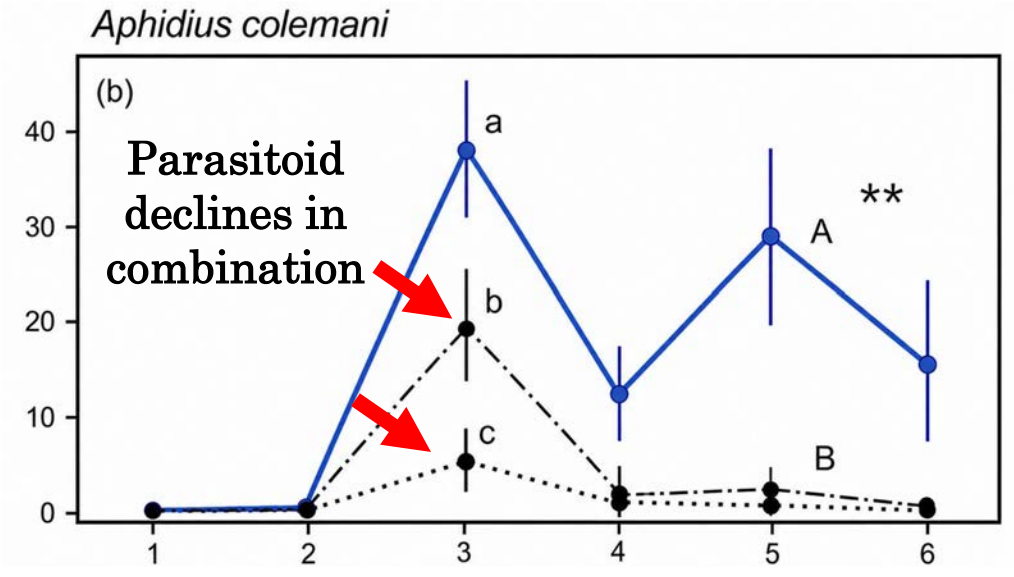
Treatments







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Community dynamics

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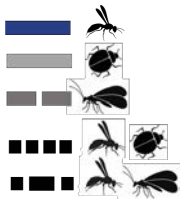
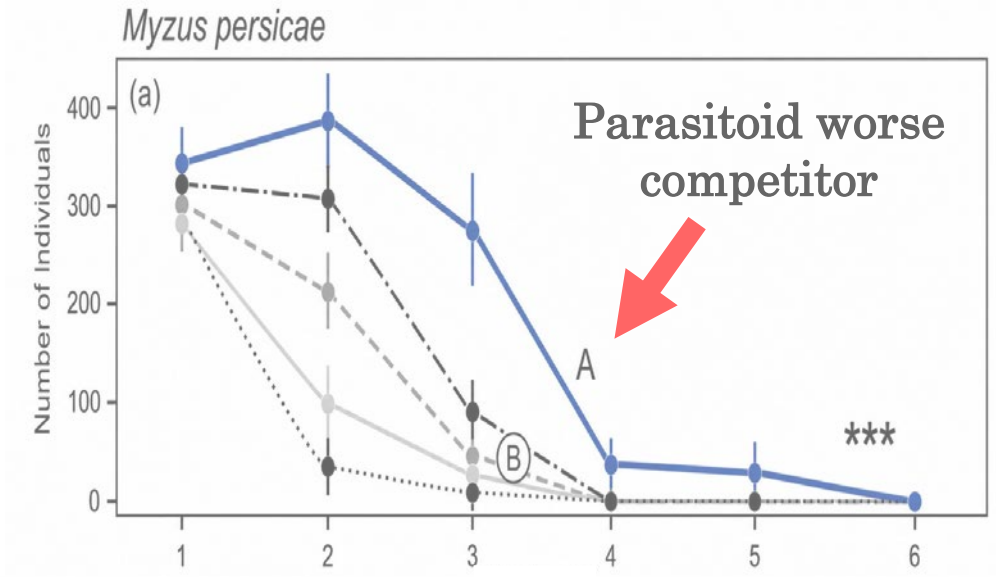
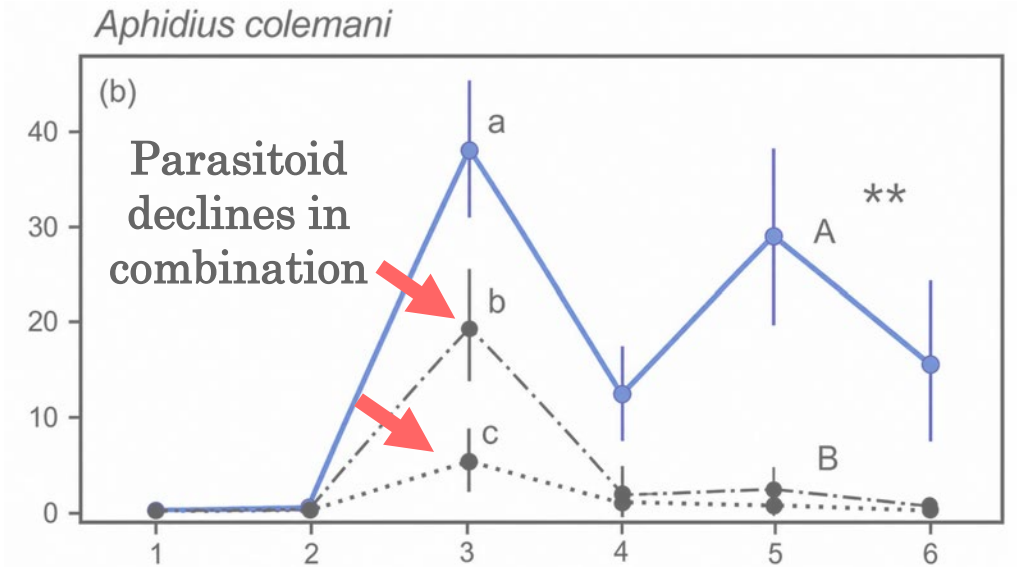
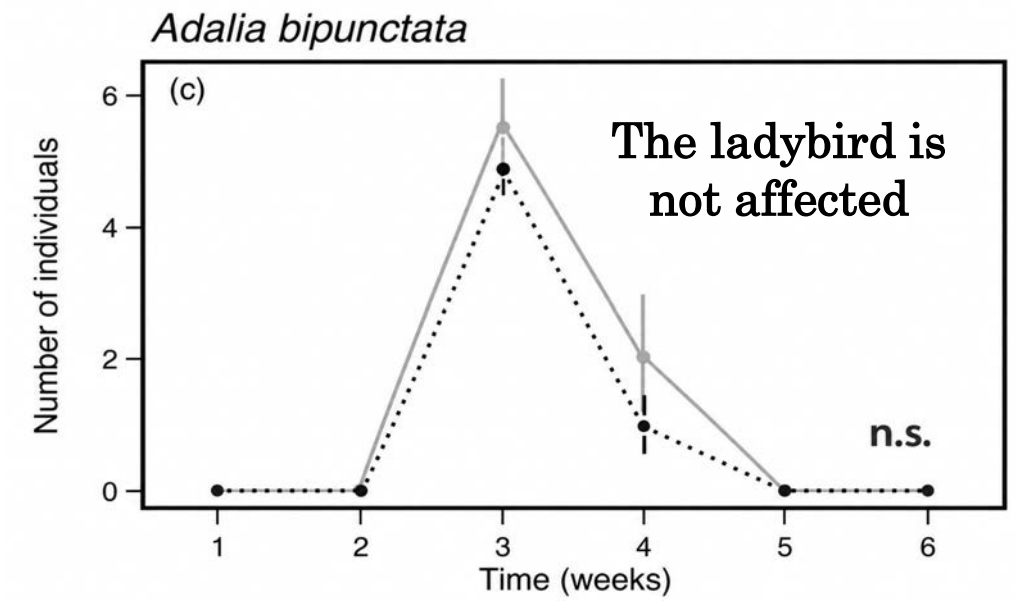




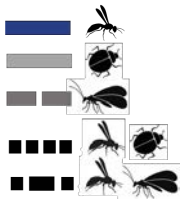


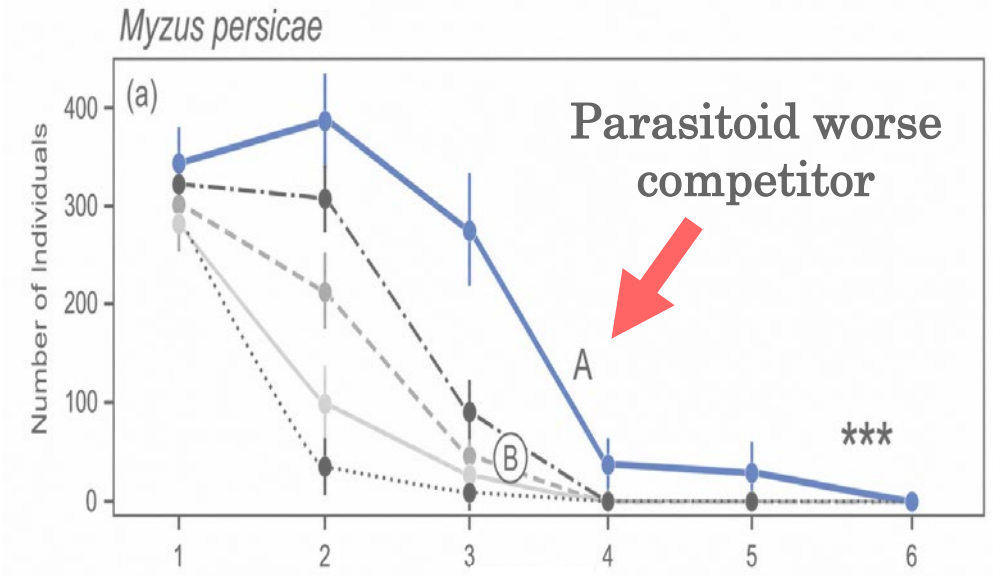


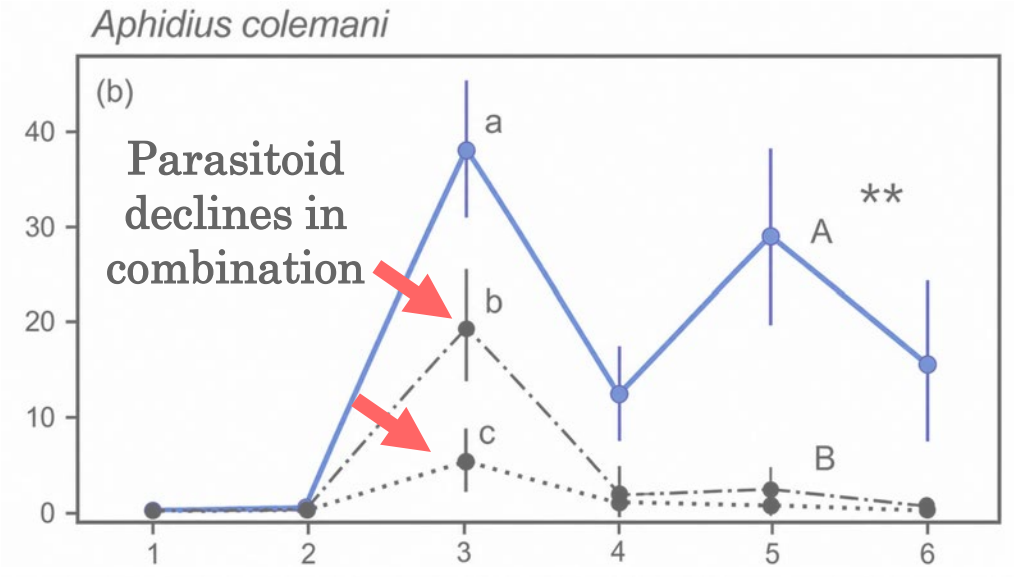
BRITISH ECOLOGICAL SOCIETY Journal of Animal Ecology

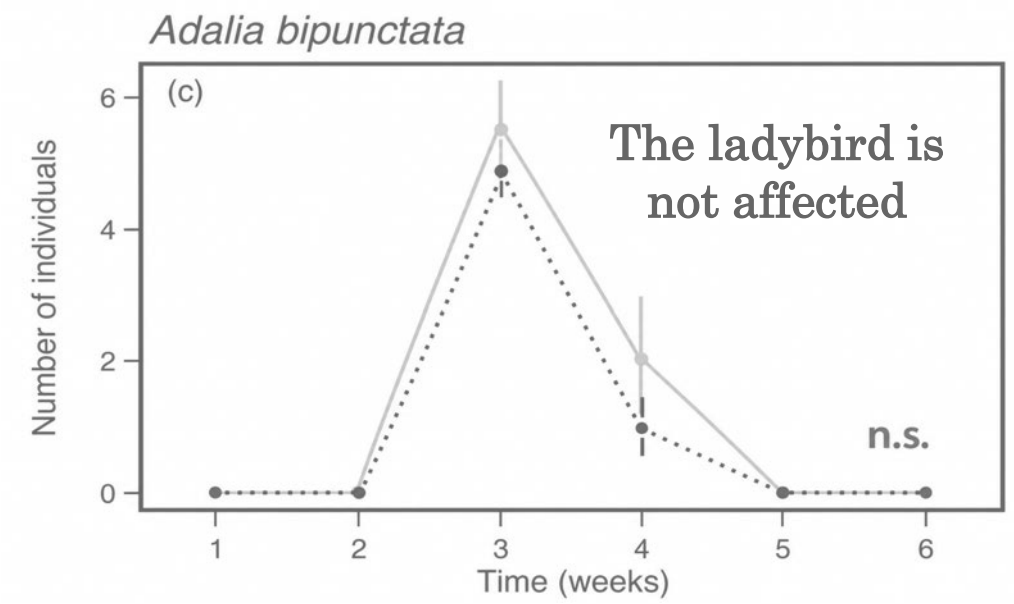
Community dynamics

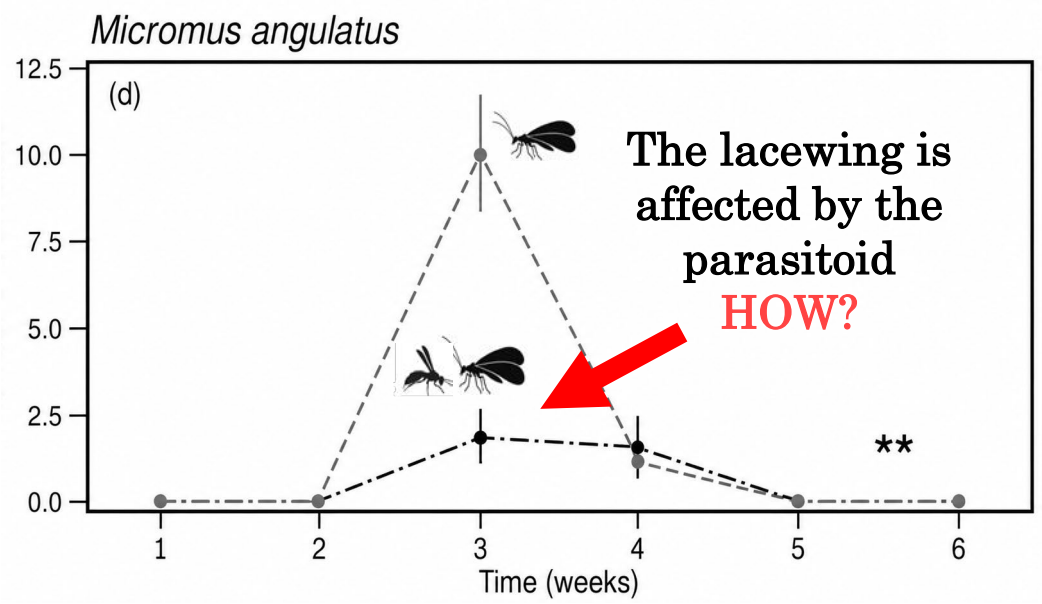
Treatments











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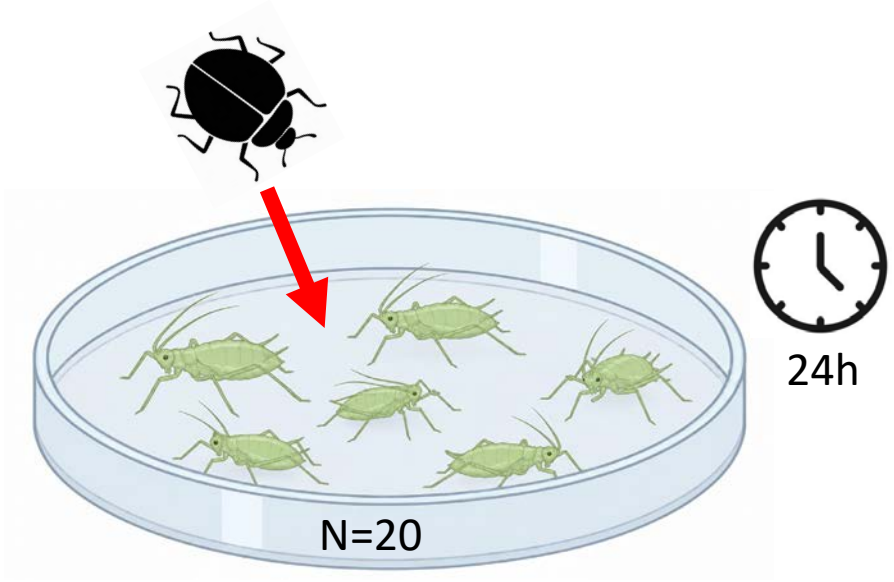
Predation rate (non-parasitised aphids)



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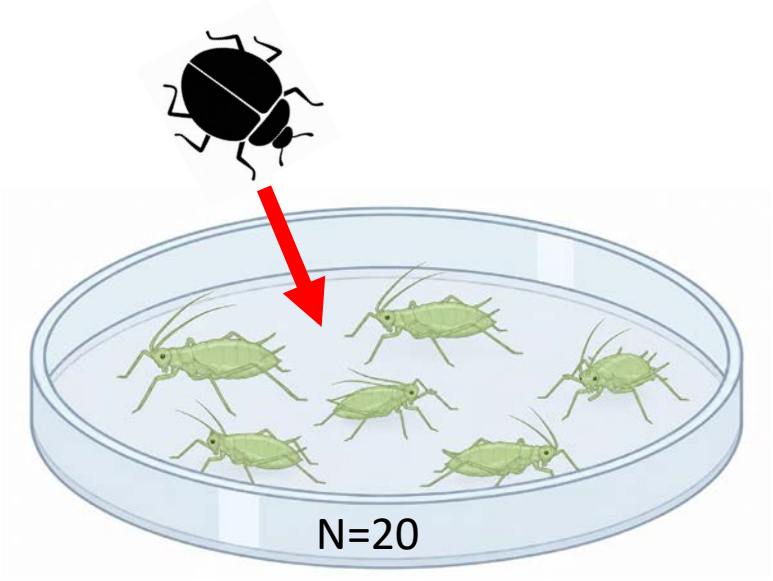
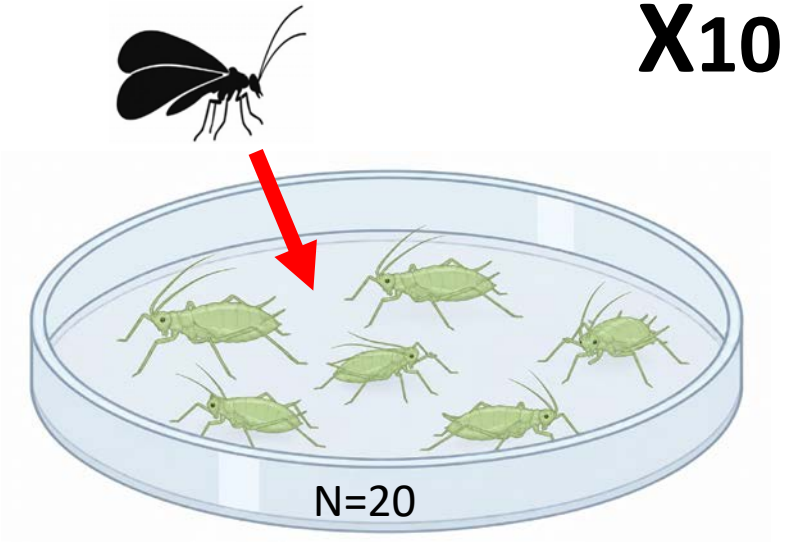
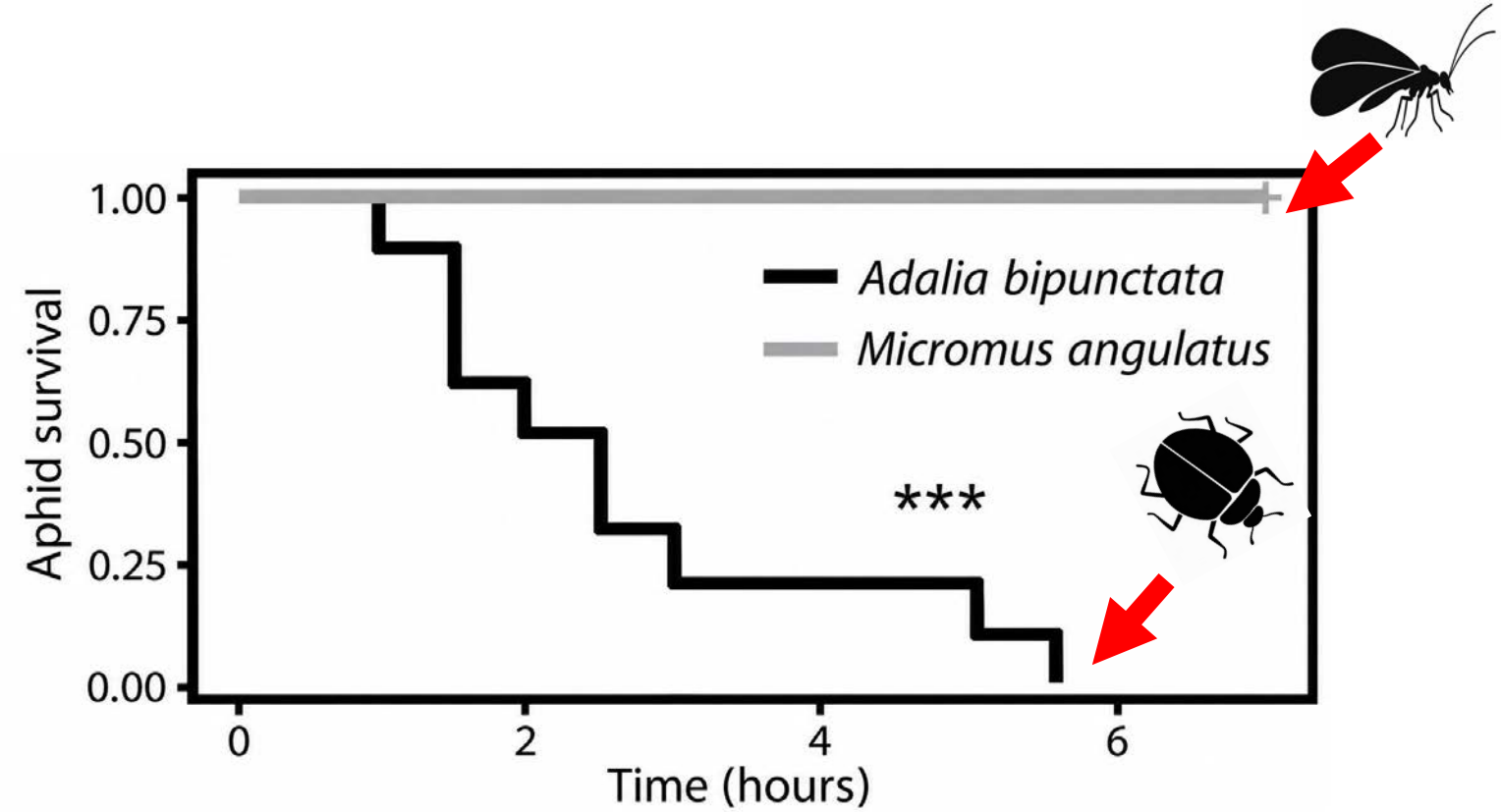
Predation rate (non-parasitised aphids)



X10





-Slower feeding by *M. angulatus*

-Parasitoids may compete by **consumption competition,** reducing aphid availability

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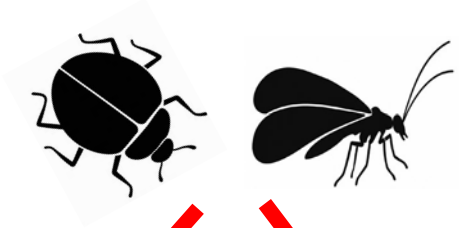
Choice test



Control
no predators

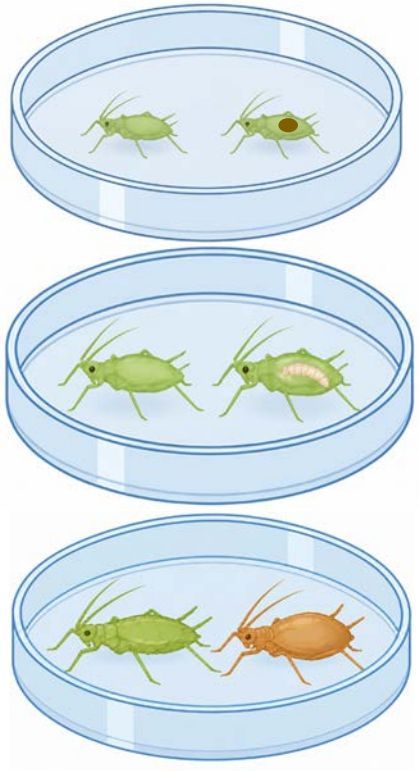
non-parasitised AND Parasitised

Aphid age

2days

6days

9days

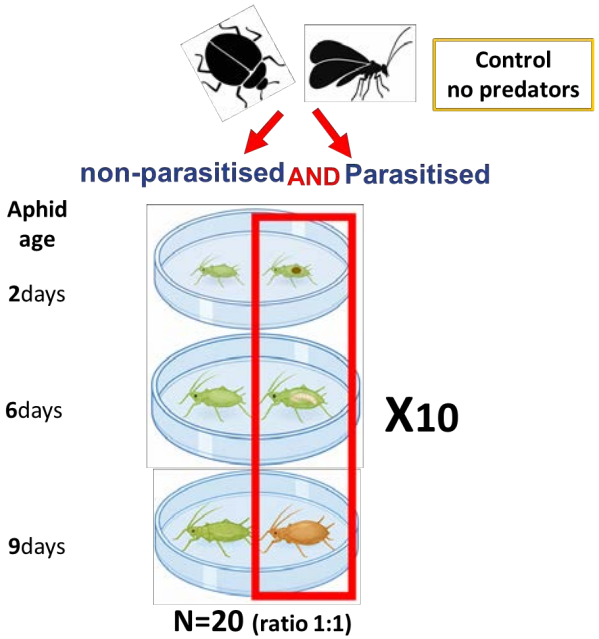


X10

N=20 (ratio 1:1)

Designs generated by BioRender.com

Choice test



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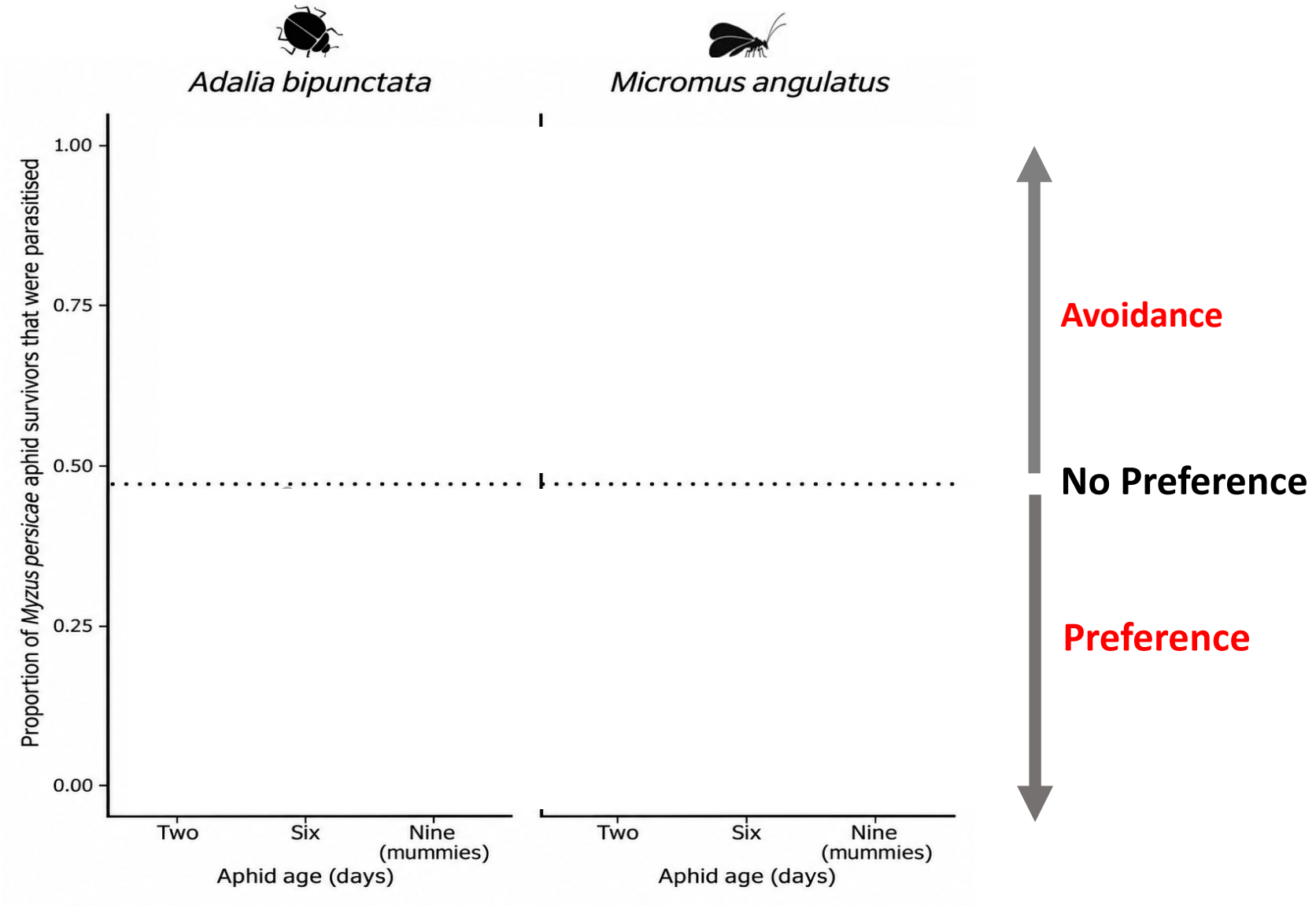
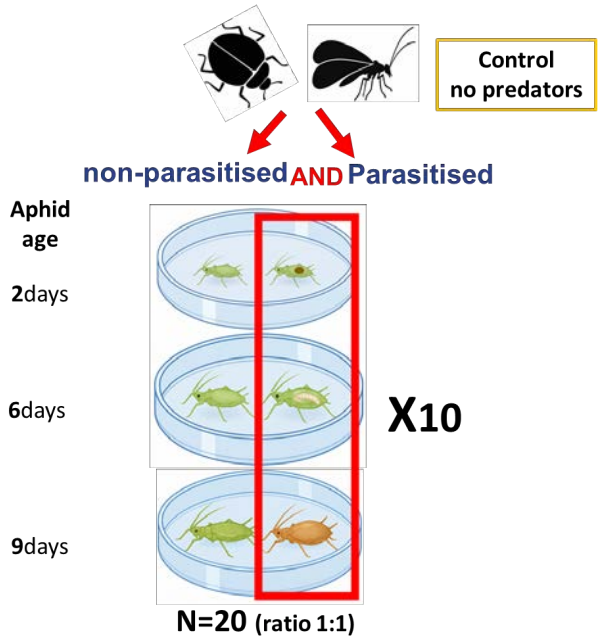
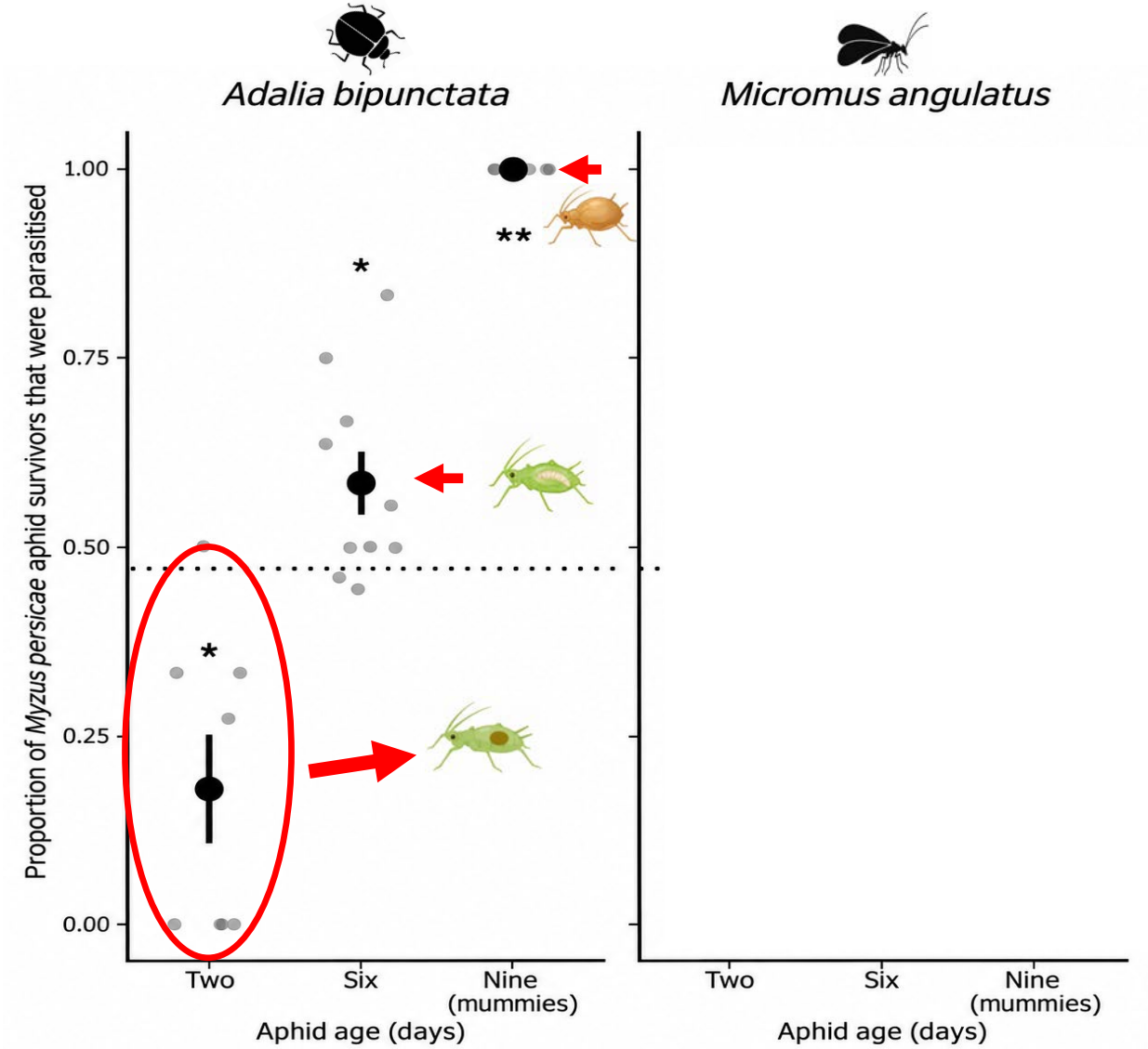


Choice test

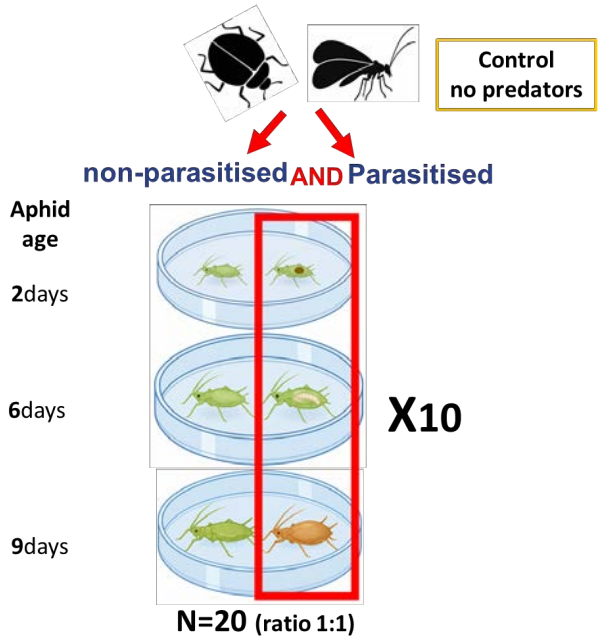


BRITISH ECOLOGICAL SOCIETY Journal of Animal Ecology

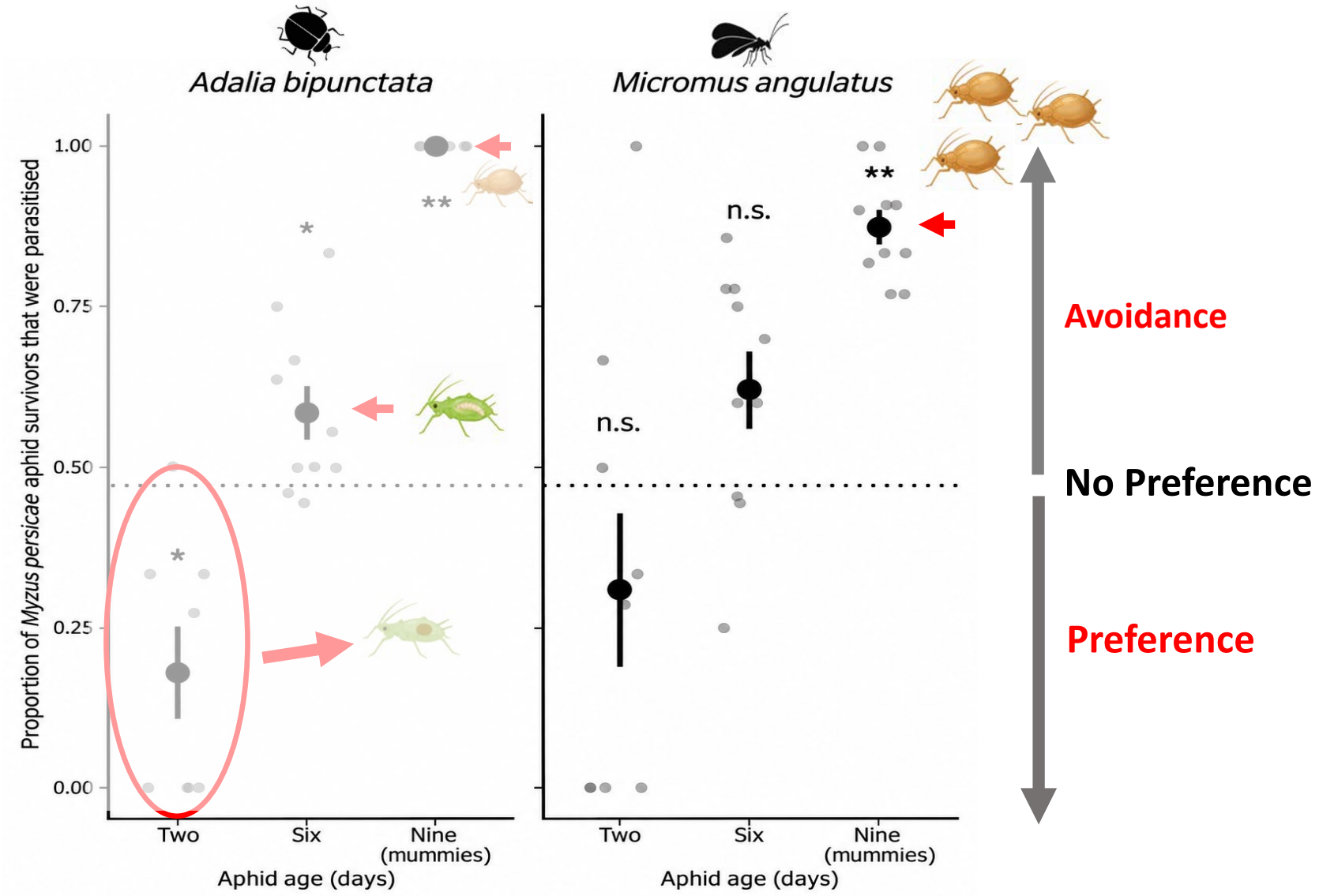


-The ladybird outcompetes parasitoids in the early stage to avoiding consumption competition!!

Choice test

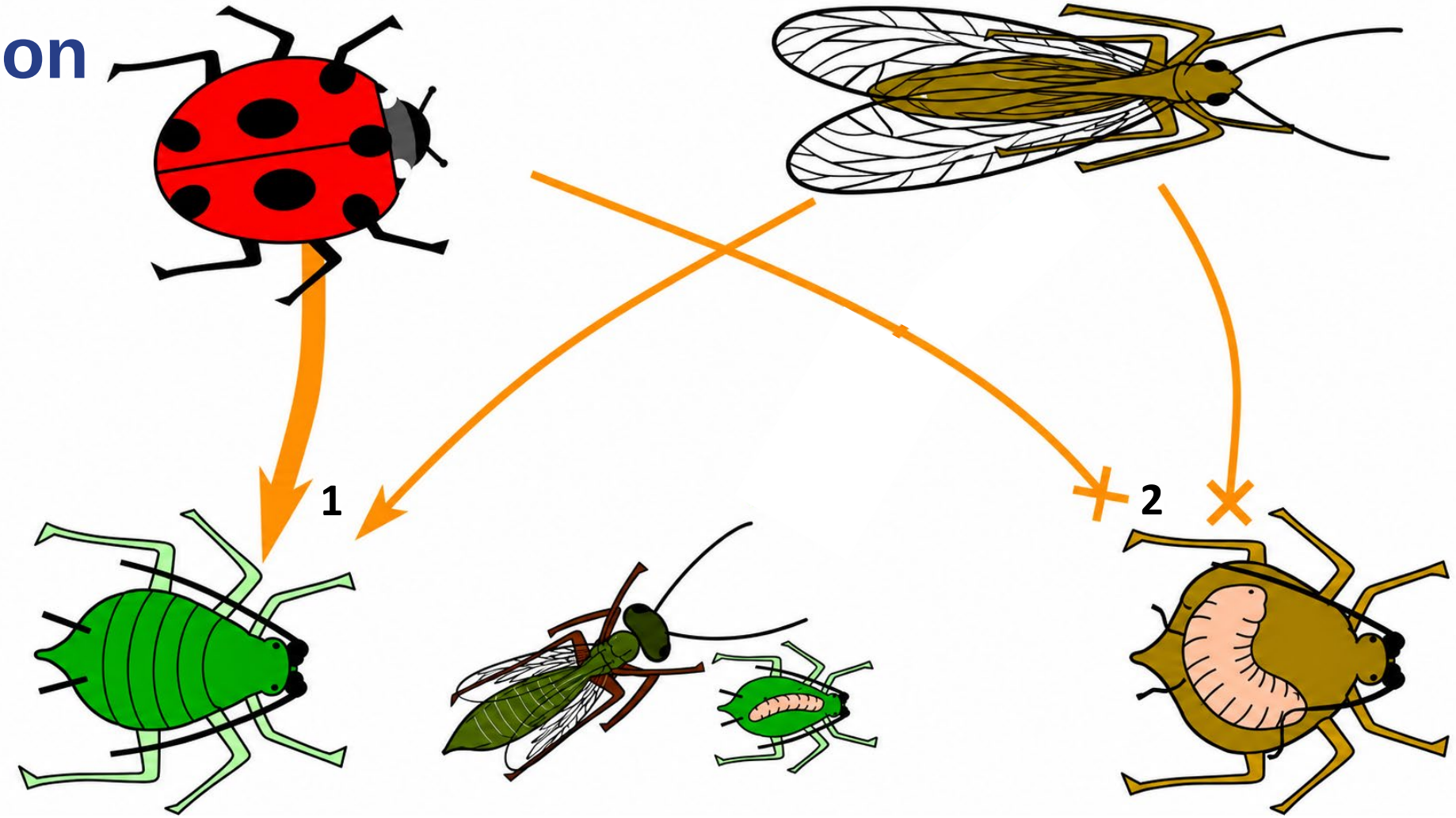


BRITISH ECOLOGICAL SOCIETY Journal of Animal Ecology



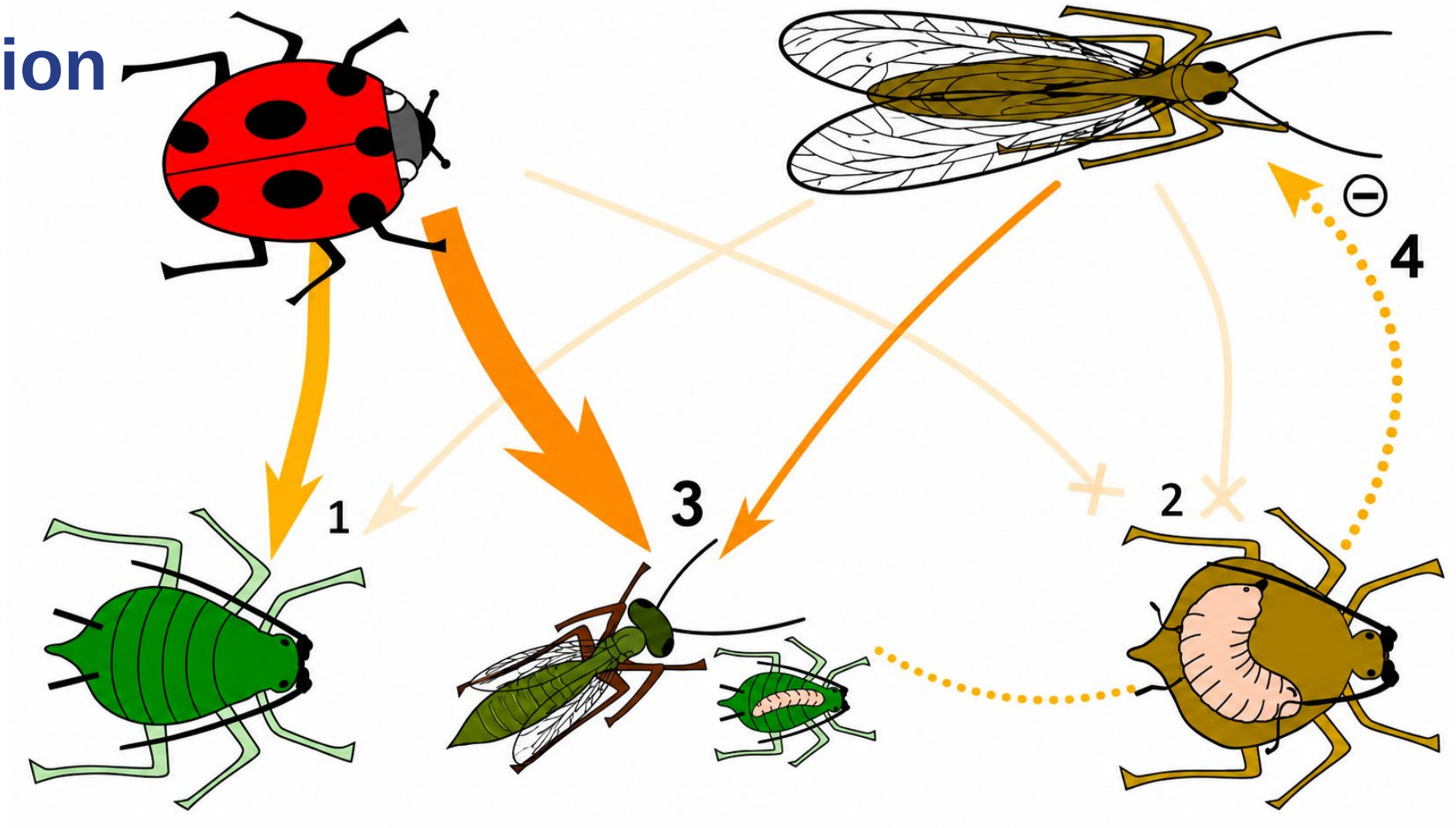
-The lacewing cannot stop consumption competition!

Conclusion



1. Lacewings feed slowly, which may favour consumption competition by parasitoids to coexist
2. When parasitoids reach the mummy stage, they are protected

Conclusion



1. Lacewings feed slowly, which may favour consumption competition by parasitoids to coexist
2. When parasitoids reach the mummy stage, they are protected
3. **Ladybirds reduce competition by consuming aphids containing early-stage parasitoids**
4. **Lacewings pay a fitness cost and parasitoids may coexist through consumption competition**

Martínez-Martínez et al. (2026), Journal of Animal Ecology.

1. IGP interaction effects



- Experimental

Predator-parasitoid

Coexistence mechanism

Biocontrol effect

2. A meta-analysis



- Literature

Biocontrol patterns

Complementarity

Predation efficacy

IGP

3. Predator combinations



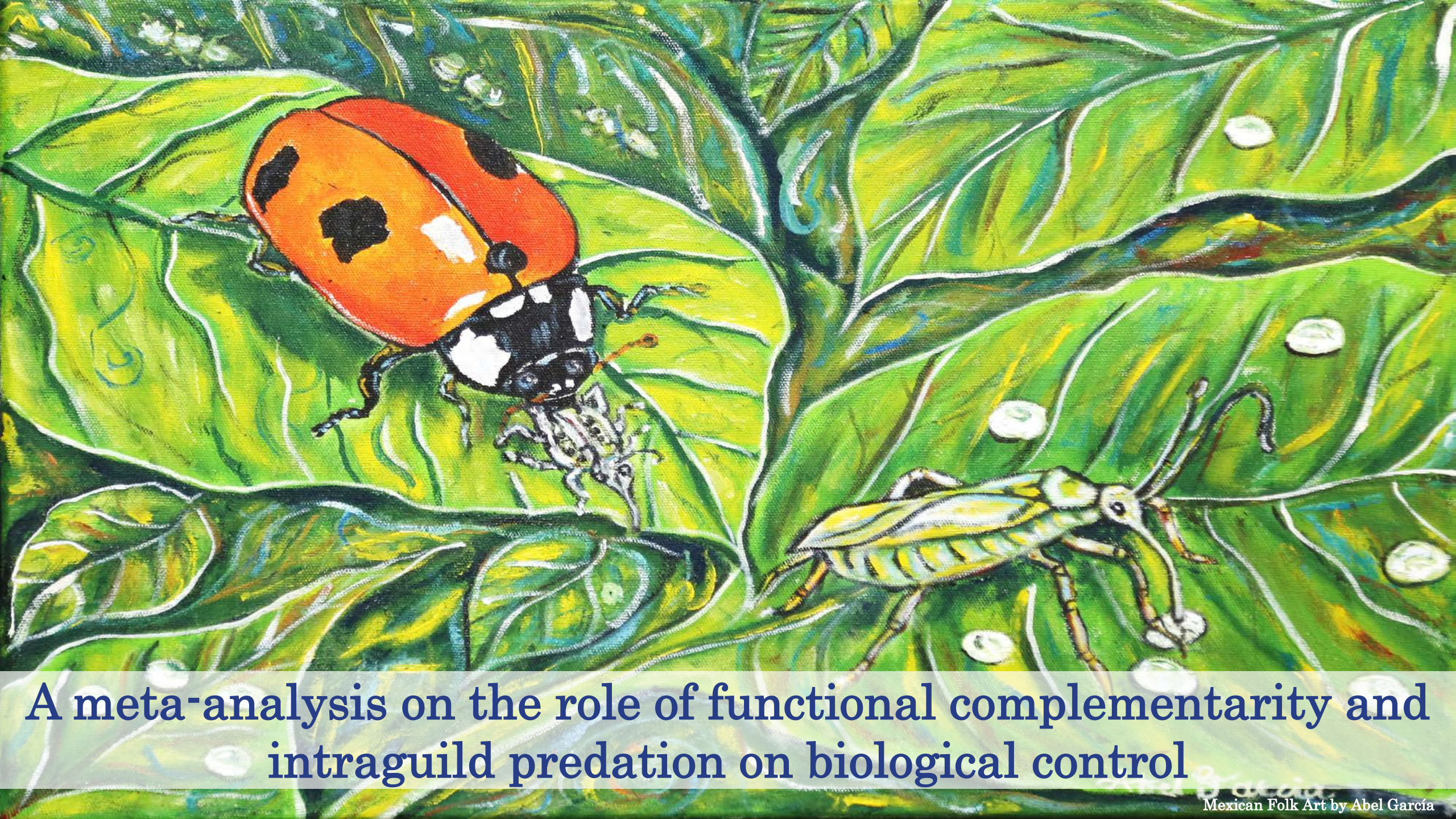
- Experimental

Patterns evaluation

Complementarity

Fitness differences

Coexistence & biocontrol



A meta-analysis on the role of functional complementarity and intraguild predation on biological control

Mexican Folk Art by Abel García

Earlier meta-analysis on predator diversity

A method that combines results from multiple studies with a similar research question

Predators complementarity

Cardinale et al. (2006)
High predator diversity
enhances prey suppression



Intraguild Predation

Vance-Chalcraft (2007)
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Herbivore biocontrol

Letourneau et al., 2009

Griffin et al., 2013

Taxonomy as descriptor

Antagonistic effects

Katano et al., 2015

Greenop et al., 2018

Phylogenetic approach and **functional traits**

Environmental conditions

Boldorini et al., 2024

Why a new meta-analysis?

New data that allows an integrative analysis and testing of **novel hypotheses to identify when combining natural enemies improves biocontrol**

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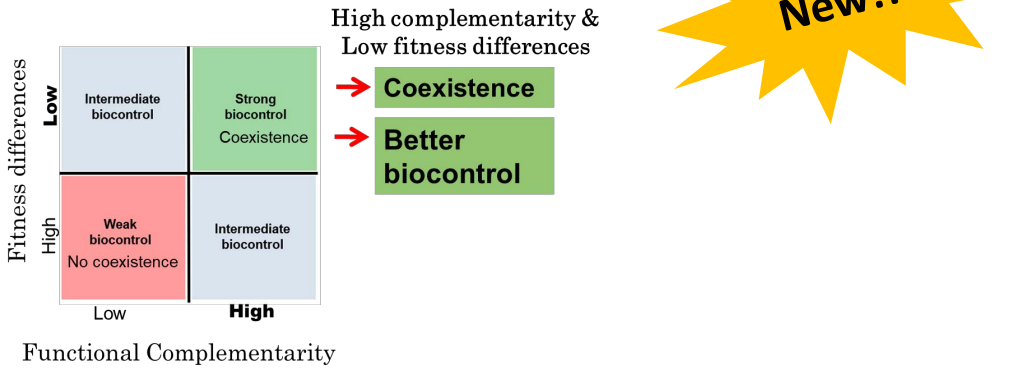
New data that allows an integrative analysis and testing of **novel hypotheses to identify when combining natural enemies improves biocontrol**

1. Biocontrol: When are two predators better than one?

H1

- Larger **functional** differences
- Larger **Phylogenetic** distances
- Similar **killing rates**



New!!

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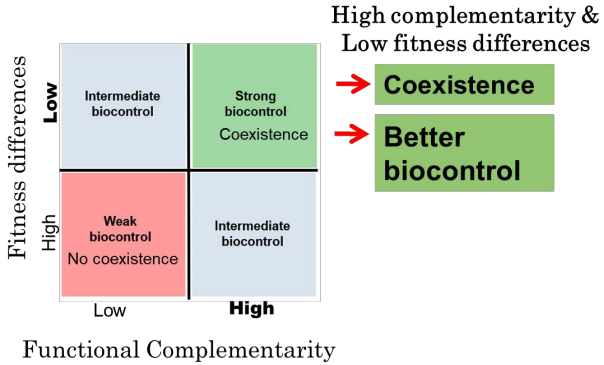


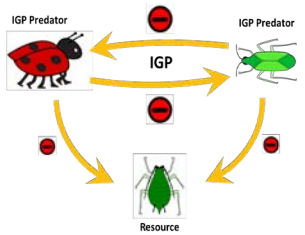
New!!

2. Do predator-predator interactions determine biocontrol?

H3

-Symmetrical IGP → Equilibrate competition

-Mutualism



New!!

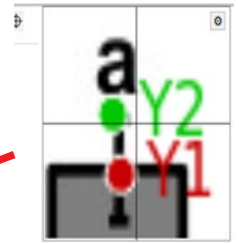
High complementarity & Low fitness differences
Coexistence
Better biocontrol

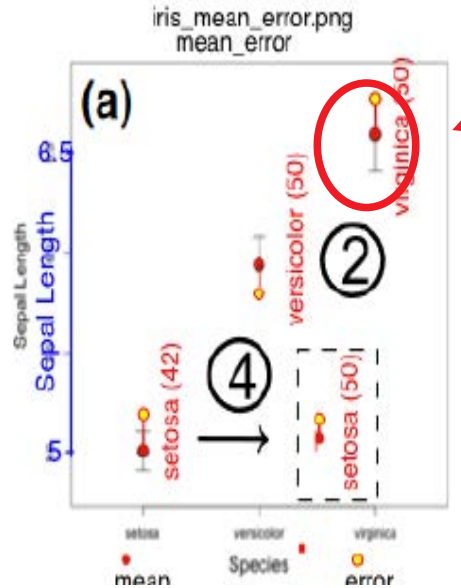
Meta-analysis main steps

1. **Literature search**
2. **Selection criteria (mean, SE and n)**
3. Screening articles
4. **Data extraction from text and figures**
5. Coding book
6. Data analysis
7. Communication









New Meta-analysis of two-predator cocktails

~2,000 studies screened → **159 studies selected**

Effect of cocktail measure

→ **470 Effect sizes: Cocktail vs best predator alone**

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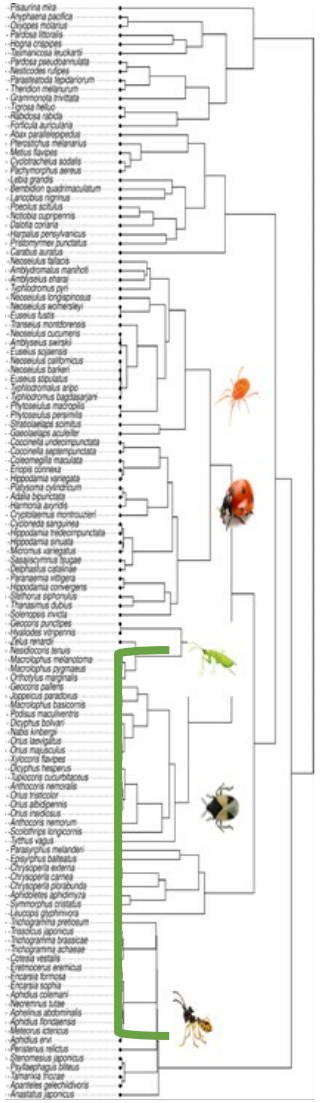
-**Functional complementarity** based on 10 traits
→ Gower's index



Greenop et al. (2018), Ecology.

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-**Functional complementarity** based on 10 traits
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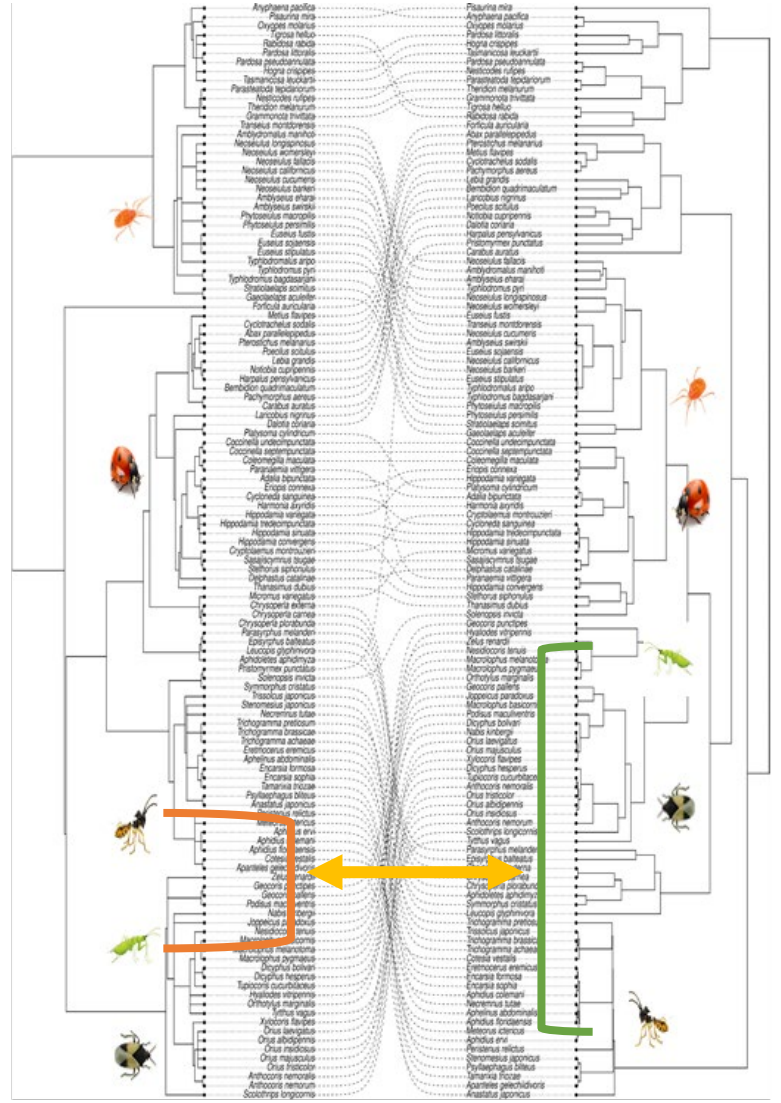
-**Phylogenetic distances**
→ Distance tree (OTL data)

-**Kill-rate:** differences in prey suppression when pred. alone

- **Environmental conditions**

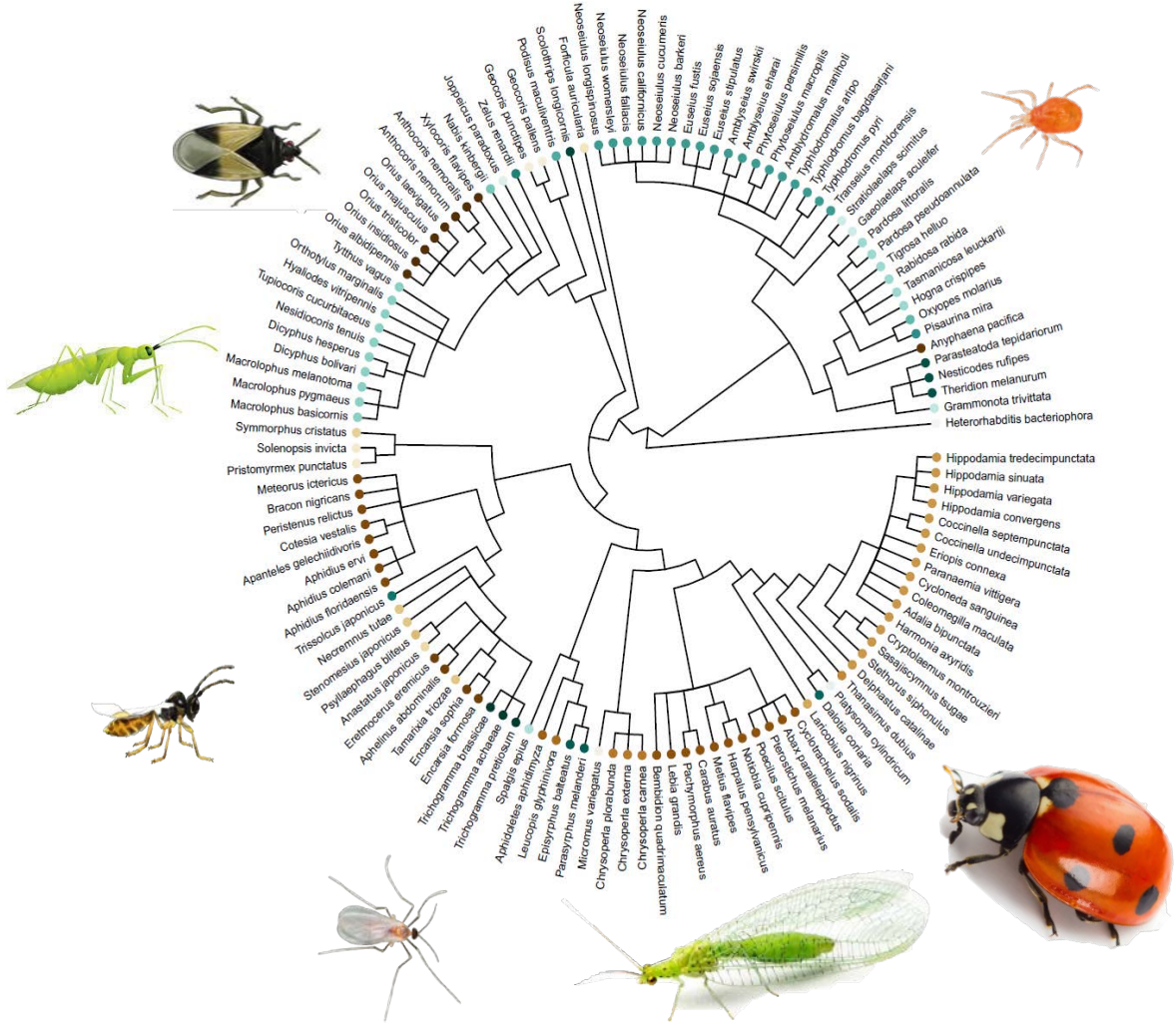


Greenop et al. (2018), Ecology.

1. Biocontrol: When are two predators better than one?

- Effect of **environmental conditions**
- Effect of **kill rate differences**
- Combined effects: **functional, phylogenetic and kill rate differences**

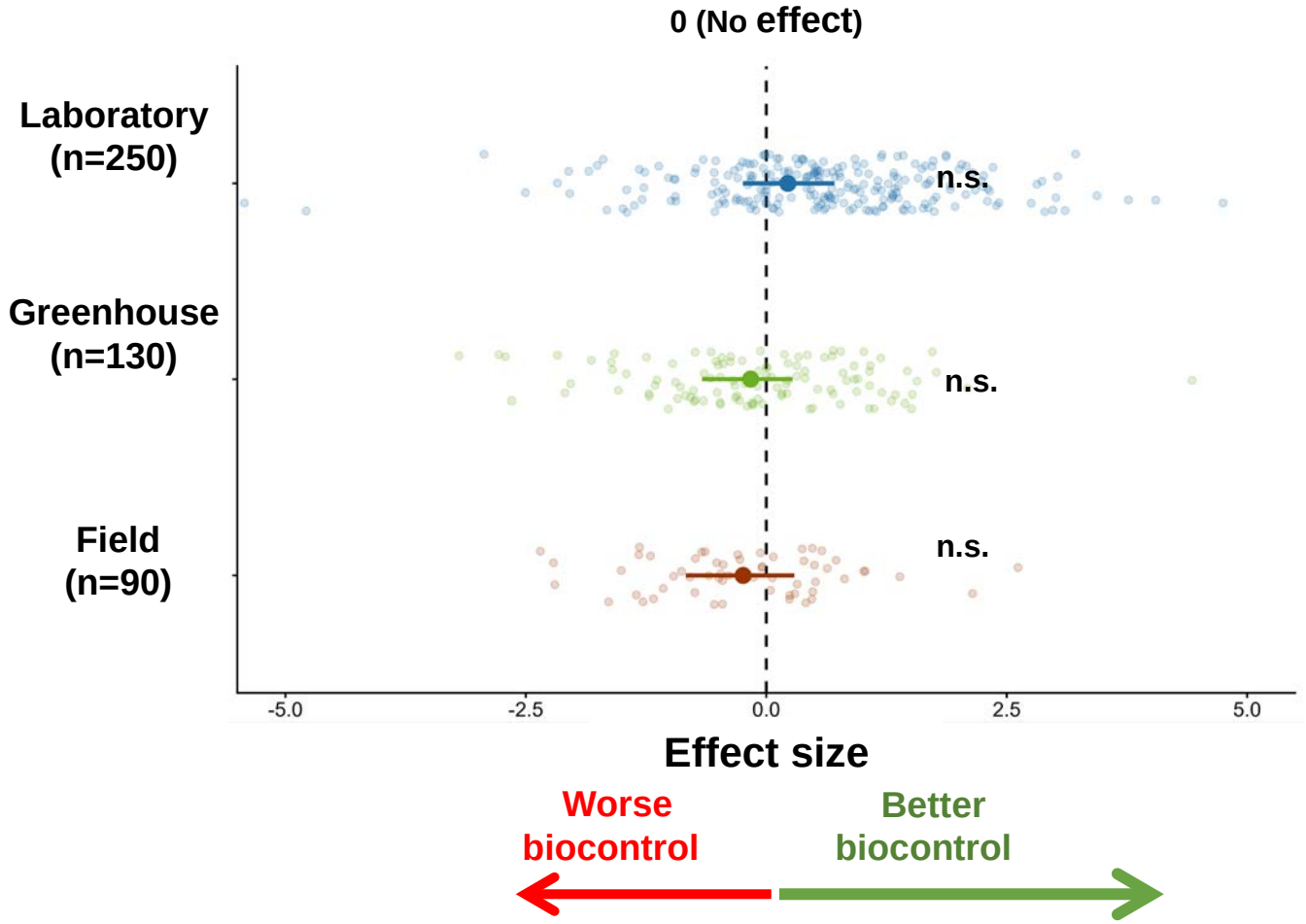
- **Phylogenetic Bayesian analysis** with the R package **MCMCglmm**



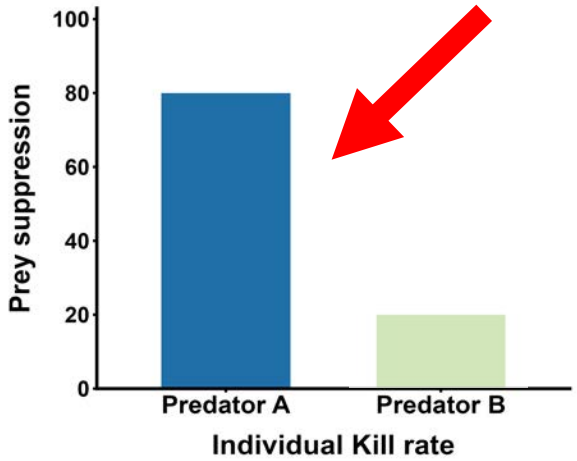
Jarrod (2010), Journal of Statistical Software.

Biocontrol: are two predators better than one?

Environmental condition: Cocktail vs Best predator (470 comparisons)



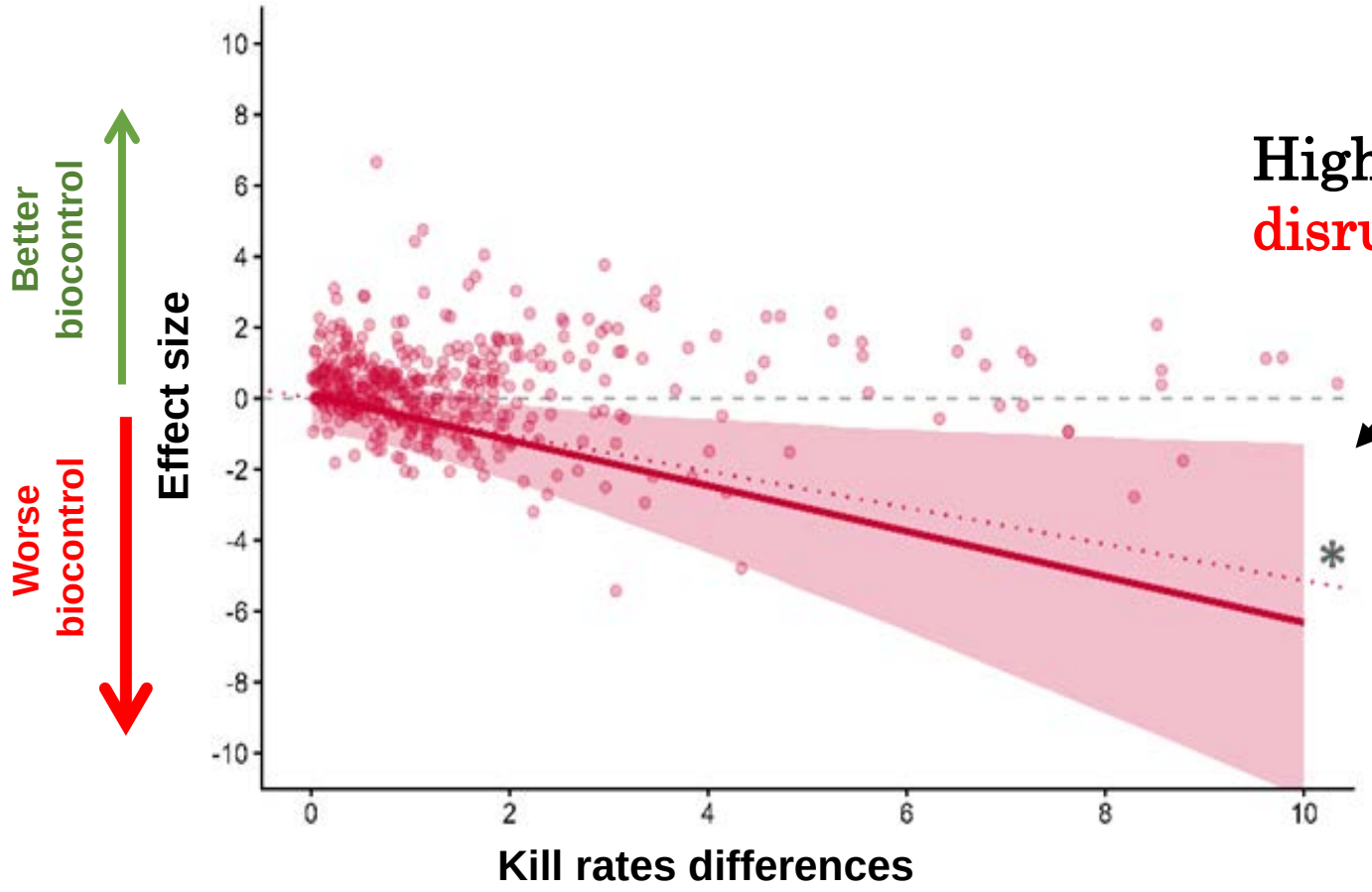
Cocktails vs **Best predators**



Cocktails perform similarly to the best predator

Biocontrol: are two predators better than one?

kill rates differences effects



High kill rate differences disrupt biocontrol

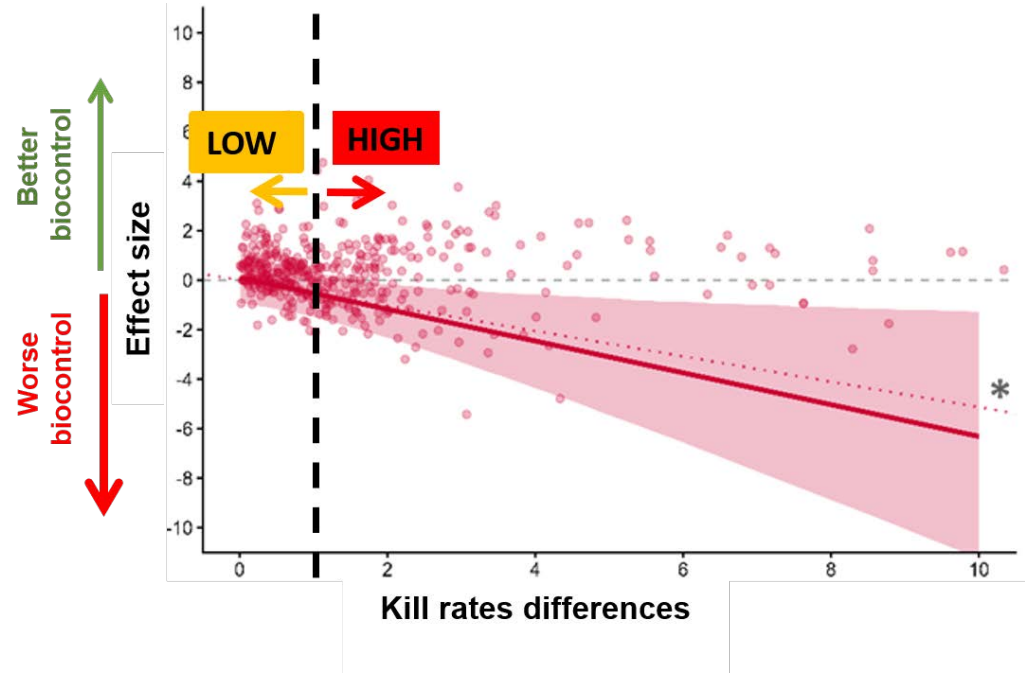
Mechanism
Competitive dominance= weak control

Biocontrol: are two predators better than one?

Model: 3-way interaction

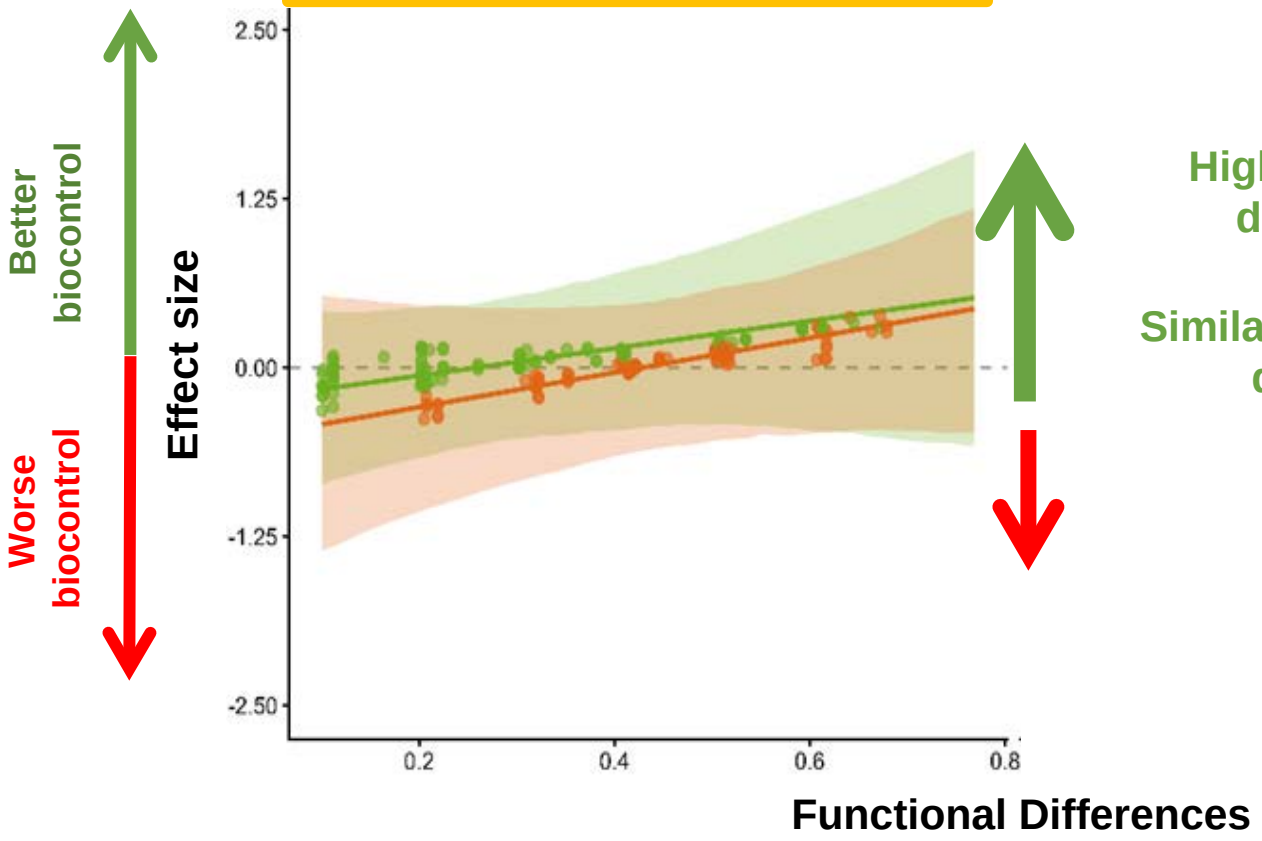
Biocontrol ~ FD*PD*Kill rates differences

Fitness differences



Joint effects of functional, phylogenetic, and kill-rate differences

LOW KILL RATES DIFFERENCES

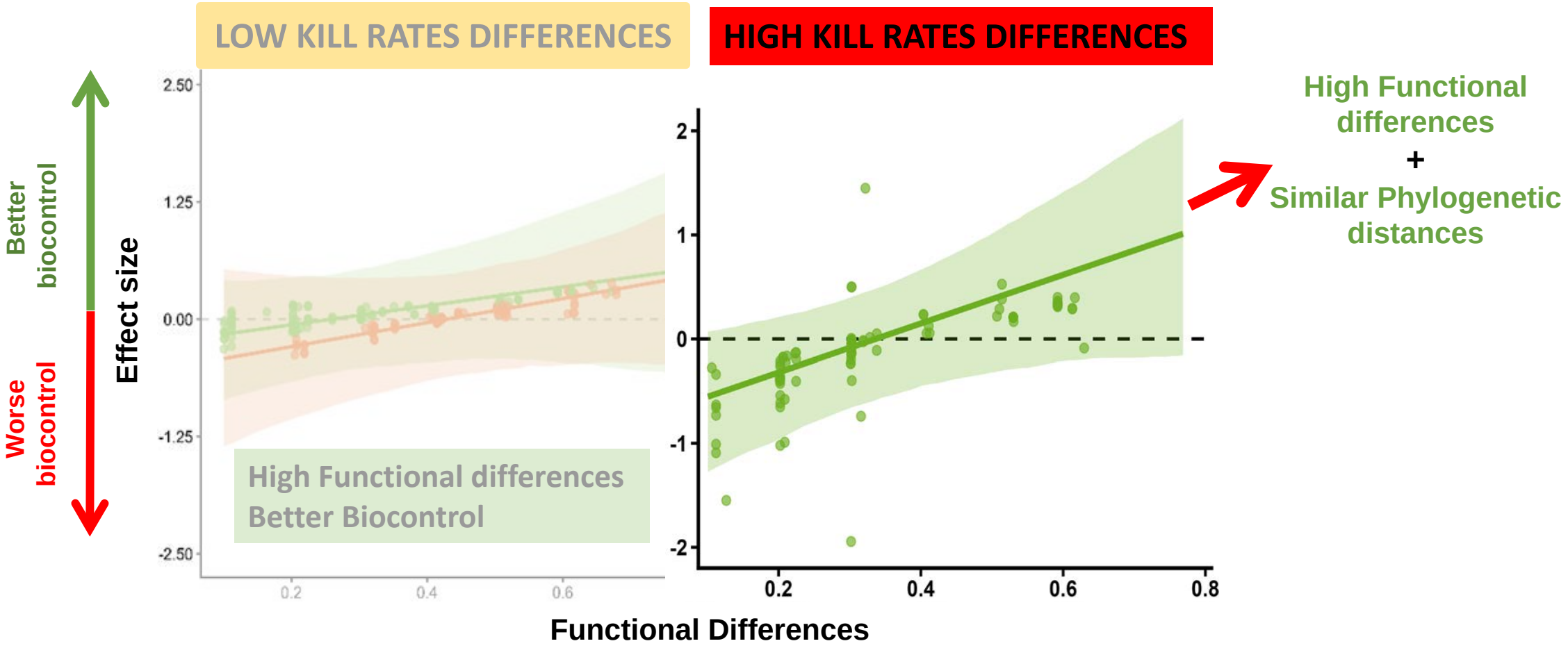


High Functional differences
+
Similar Phylogenetic distances

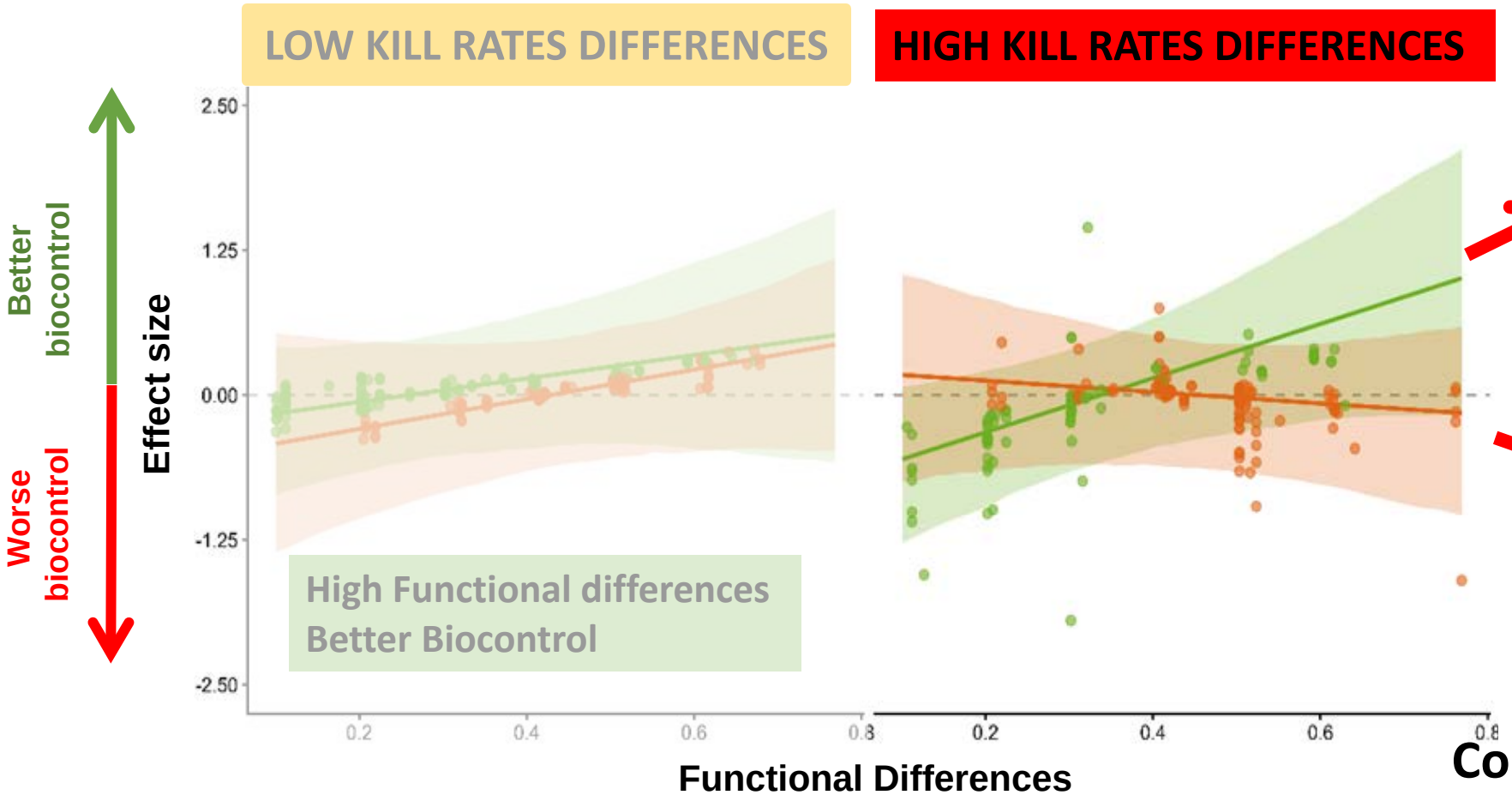
High Functional differences
+
High Phylogenetic distances

High Functional differences
Better Biocontrol

Joint effects of functional, phylogenetic, and kill-rate differences



Joint effects of functional, phylogenetic, and kill-rate differences



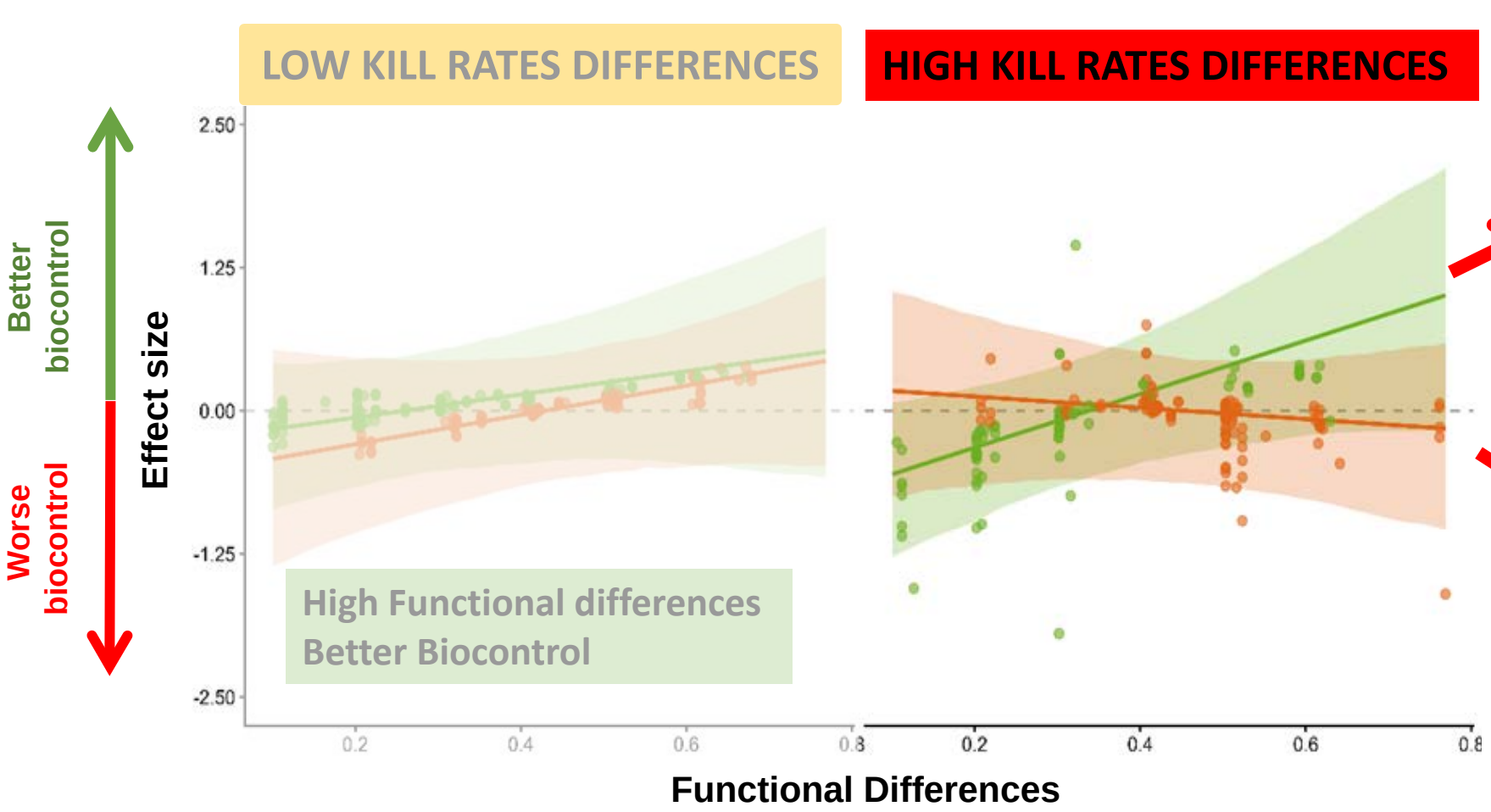
High Functional differences
+
Similar Phylogenetic distances

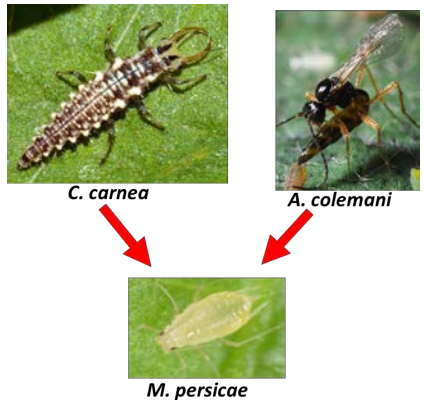
High Functional differences
+
High Phylogenetic distances

Contrary to our hypothesis!!

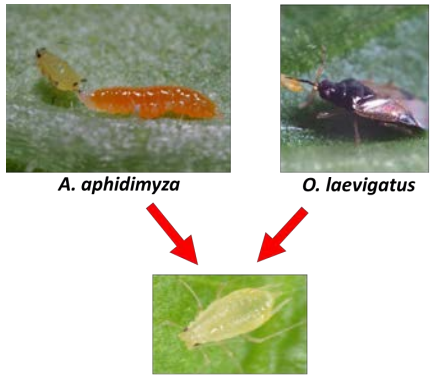
New open question?

Joint effects of functional, phylogenetic, and kill-rate differences





Better two predators!!



Better one predator!!



Predator-predator interaction effects

2. Do predator-predator interactions determine biocontrol?

Predator-predator interactions: 116 interactions

Effect of predator interaction on Biocontrol



Pringle (2016), PLOS Biology.

2. Do predator-predator interactions determine biocontrol?

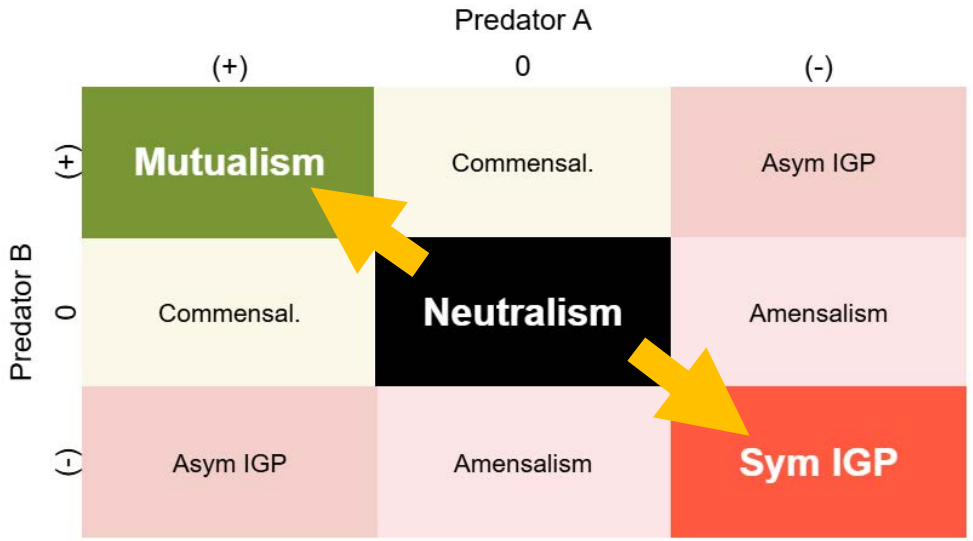
Predator-predator interactions: 116 interactions



Effect of predator interaction on Biocontrol

-Classified based on pairwise reciprocal effects on abundance **(6 types)**

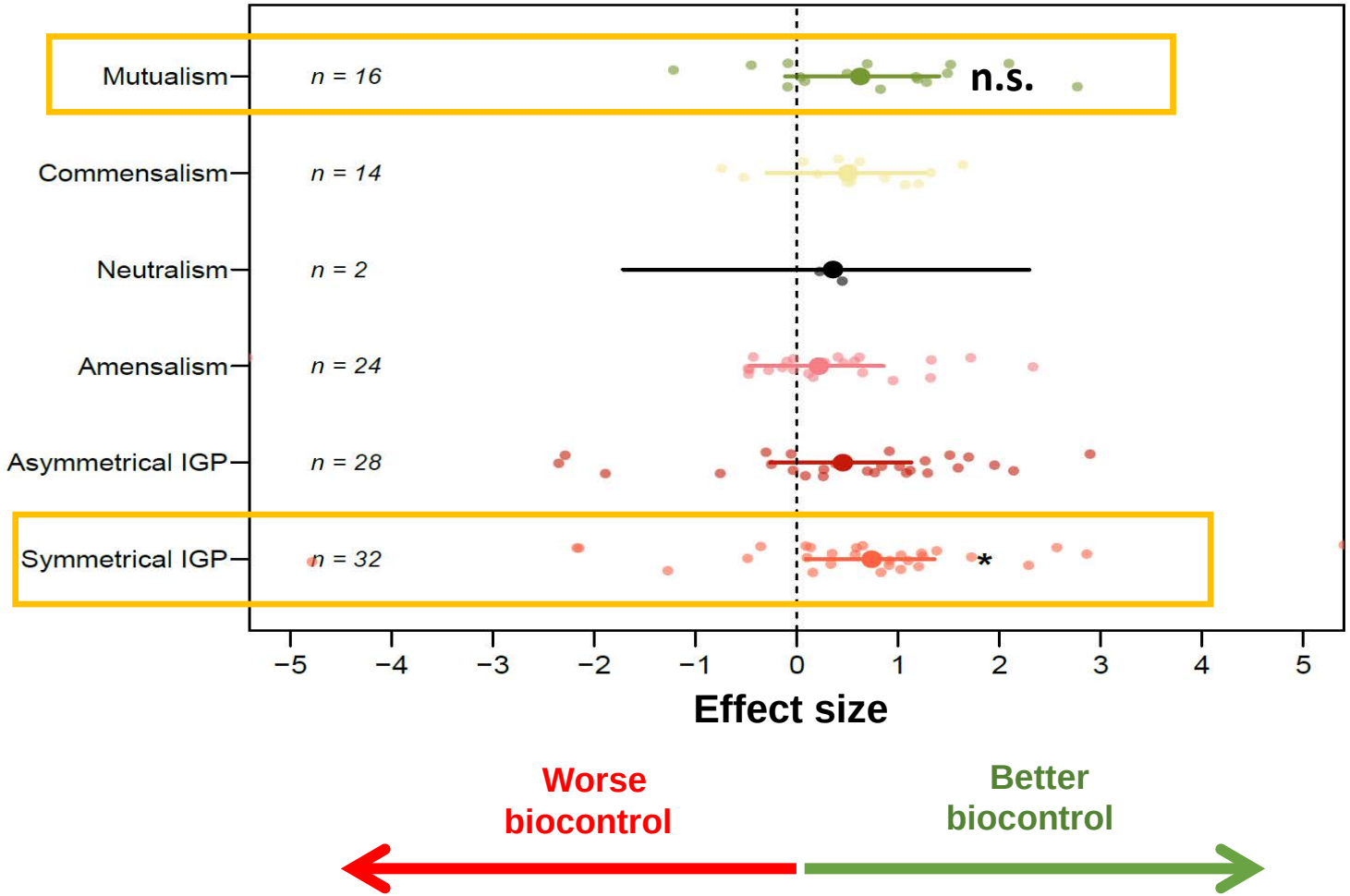
Density of predators
-A alone or in cocktail
-B alone or in cocktail



Pringle (2016), PLOS Biology.

Do predator-predator interactions determine biocontrol?

Interaction types effects on biocontrol



Symmetrical IGP
Reciprocal predation may reduce the likelihood of **dominance**

-Lack of data may drive the pattern

Conclusion

To make good cocktails for biocontrol!!



Biocontrol:

-Kill rate differences → **Weak cocktails biocontrol**

New!!

-Functional differences →
-Better biocontrol at **low kill rate differences**
-At high kill rates, only when predators are phylogenetically similar

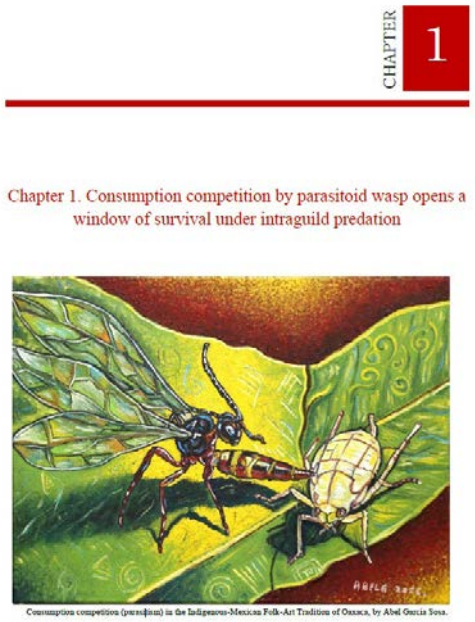
Predator-predator interactions:

-Symmetrical IGP → **No dominance by one predator**

New!!

→ **Support better biocontrol**

1. IGP interaction effects



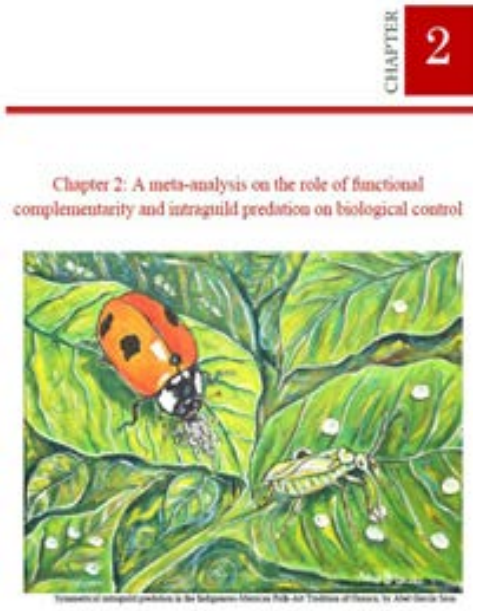
- Experimental

Predator-parasitoid

Coexistence mechanism

Biocontrol effect

2. A meta-analysis



- Literature

Biocontrol patterns

Complementarity

Predation efficacy

IGP

3. Predator combinations



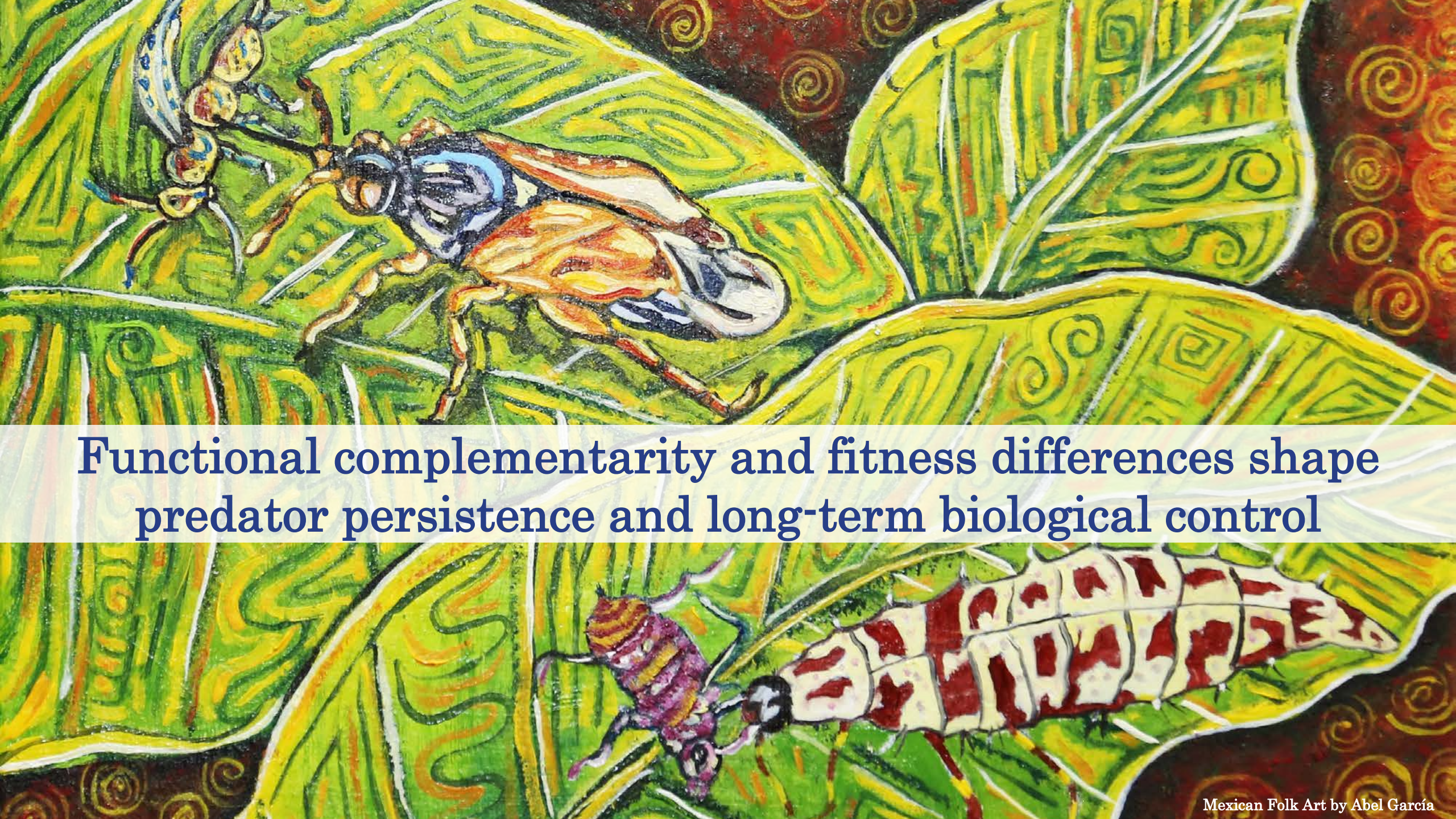
- Experimental

Patterns evaluation

Complementarity

Fitness differences

Coexistence & biocontrol



Functional complementarity and fitness differences shape predator persistence and long-term biological control

Mexican Folk Art by Abel García

How do predators coexist and promote better biocontrol?

Meta-analysis founds

Functional differences → **Promotes predators complementarity**

Fitness differences (kill rates) → **Can reduce predator combination efficacy**

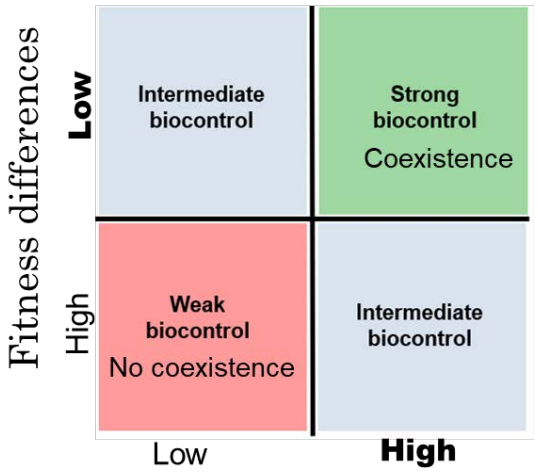
Predator-predator interactions → **Symmetrical IGP may equilibrate competition**

↓

Long-term community dynamics

How do predators coexist and promote better biocontrol?

H1



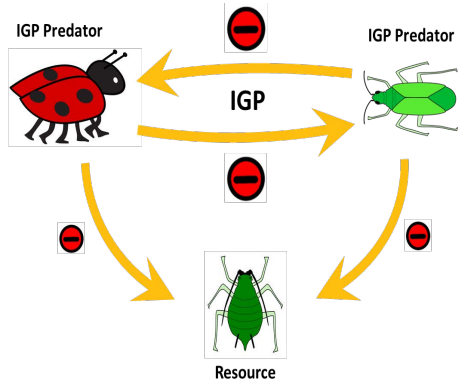
High complementarity &
Low fitness differences

→ **Coexistence**

→ **Better biocontrol**

H3

Symmetrical intraguild predation



High complementarity &
Low fitness differences

→ **Coexistence**

→ **Better biocontrol**

Long-term community dynamics

- Six predator pair combinations
- Varied functional complementarity
- Different fitness (growth)
- Two types of IGP



Designs generated by BioRender.com

Natural enemy selection for *M. persicae* control

A. colemani



A. matricariae



M. angulatus



C. carnea



M. pygmaeus



O. laevigatus



A. aphidimyza





C. annuum



M. persicae

Images from Biobest group.com

Complementarity estimation

Functional traits

Species	Microhabitat	Dispersal ability	Feeding guild	Specialisation level	Feeding mode	Guild type	Adult longevity (days)	Development time (days)	Body length (mm)	Fecundity
A. colemani	foliage	high	parasitoid	family	parasitoid	parasitoid	5.9	9.8	1.6	300
A. matricariae	foliage	high	parasitoid	family	parasitoid	parasitoid	7.3	11.6	1.8	116
A. aphidimyza	foliage	low	predator	family	chewing	gallmidge	5.7	13	2.5	94
C. carnea	foliage	med	predator	class	chewing	lacewing	43	21.36	7.1	583
M. pygmaeus	foliage	high	predator	phylum	sucking	bug	45	16.7	3.3	175
M. angulatus	foliage	med	predator	phylum	chewing	lacewing	34.9	16.3	8	223
O. laevigatus	foliage	high	predator	class	sucking	bug	28	17	3	202

Functional complementarity

Gower distances matrix

A. colemani	*A. matricariae*	*A. aphidimyza*	*C. carnea*	*M. angulatus*	*M. pygmaeus*	*O. laevigatus*
A. colemani	**0.0599**	**0.4844**	**0.8382**	**0.7458**	**0.6113**	**0.5604**
	A. matricariae	**0.4316**	**0.8536**	**0.7296**	**0.5755**	**0.5357**
		A. aphidimyza	**0.6391**	**0.5152**	**0.5611**	**0.5212**
			C. carnea	**0.2521**	**0.5882**	**0.5179**
				M. angulatus	**0.4124**	**0.5060**
					M. pygmaeus	**0.1561**
						O. laevigatus

Closer to 0 → More similar
Closer to 1 → More different

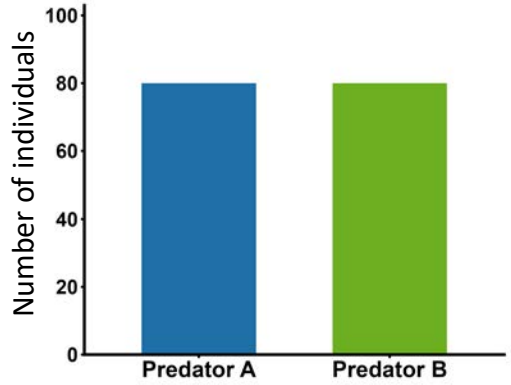
Fitness differences between predators estimation

Population growth rate $\boxed{\Delta r_{ij} = |r_i - r_j|}$

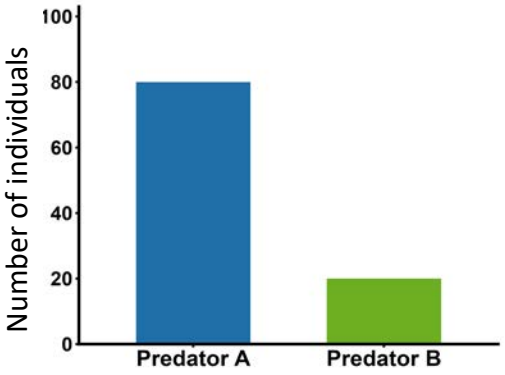
Closer to **0** → **Similar growth rates**

Larger than**1** → **More different growth rates**

Similar fitness



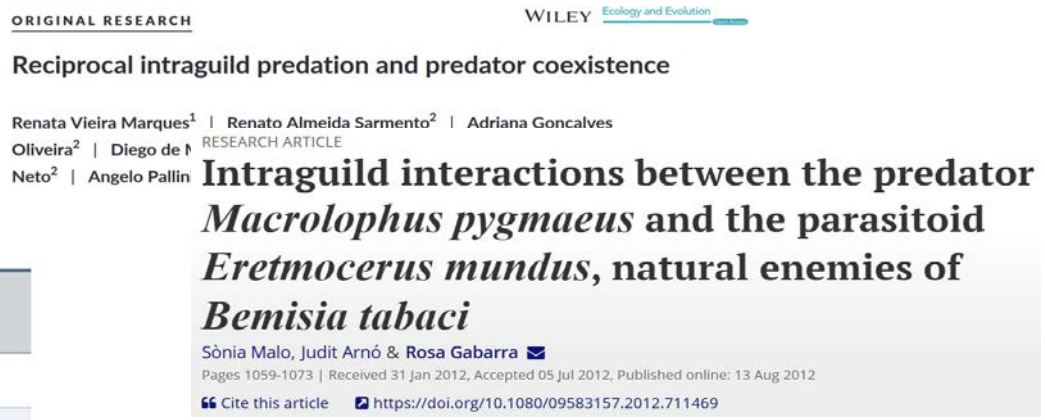
Fitness differences



Intraguild predation classification

Based on the literature

Species	IGP predator
A. colemani	yes
A. matricariae	no
A. aphidimyza	no
C. carnea	yes
M. pygmaeus	yes
M. angulatus	yes
O. laevigatus	yes



ORIGINAL RESEARCH

WILEY Ecology and Evolution

Reciprocal intraguild predation and predator coexistence

Renata Vieira Marques[1] | Renato Almeida Sarmento[2] | Adriana Goncalves Oliveira[2] | Diego de M Neto[2] | Angelo Pallin

RESEARCH ARTICLE

Intraguild interactions between the predator *Macrolophus pygmaeus* and the parasitoid *Eretmocerus mundus*, natural enemies of *Bemisia tabaci*

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Pages 1059-1073 | Received 31 Jan 2012, Accepted 05 Jul 2012, Published online: 13 Aug 2012

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Expected interaction

Asymmetrical IGP



Symmetrical IGP

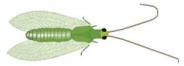
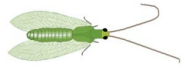


Predator combinations

Asymmetrical IGP

1. *A. colemani* + *A. matricariae*  vs
2. *A. colemani* + *O. laevigatus*  vs 
3. *M. pygmaeus* + *A. aphidimyza*  vs 

Symmetrical IGP

4. *C. carnea* + *M. angulatus*  vs 
5. *C. carnea* + *M. pygmaeus*  vs 
6. *M. angulatus* + *O. laevigatus*  vs 

Predator combinations

Asymmetrical IGP

1. *A. colemani* + *A. matricariae*  vs
2. *A. colemani* + *O. laevigatus*  vs
3. *M. pygmaeus* + *A. aphidimyza*  vs

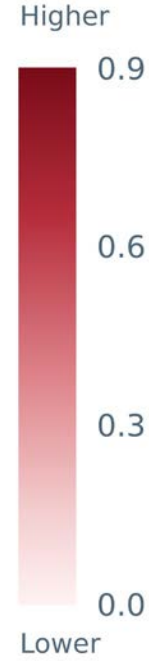
Symmetrical IGP

4. *C. carnea* + *M. angulatus* 
5. *C. carnea* + *M. pygmaeus* 
6. *M. angulatus* + *O. laevigatus* 

Functional complementarity



Fitness differences

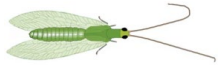


GlmmTMB → **Biocontrol**

Survival model → **Coexistence**

Long-term community dynamics

Experimental set-up

1. *A. colemani*  **n = 10** (5♀+5♂)
2. *A. matricariae* 
3. *M. angulatus* 
4. *C. carnea*  **n = 5♀**
5. *M. pygmaeus* 
6. *O. laevigatus* 
7. *A. aphidimyza*  **n = 10** pupae



n = 600



n = 60 cages









ENEMY COCKTAIL
Designing natural enemy cocktails for a better biocontrol

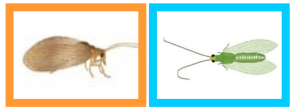
Results

Treatments

1 

2 

3 

4 

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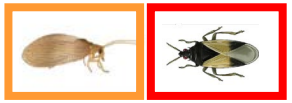
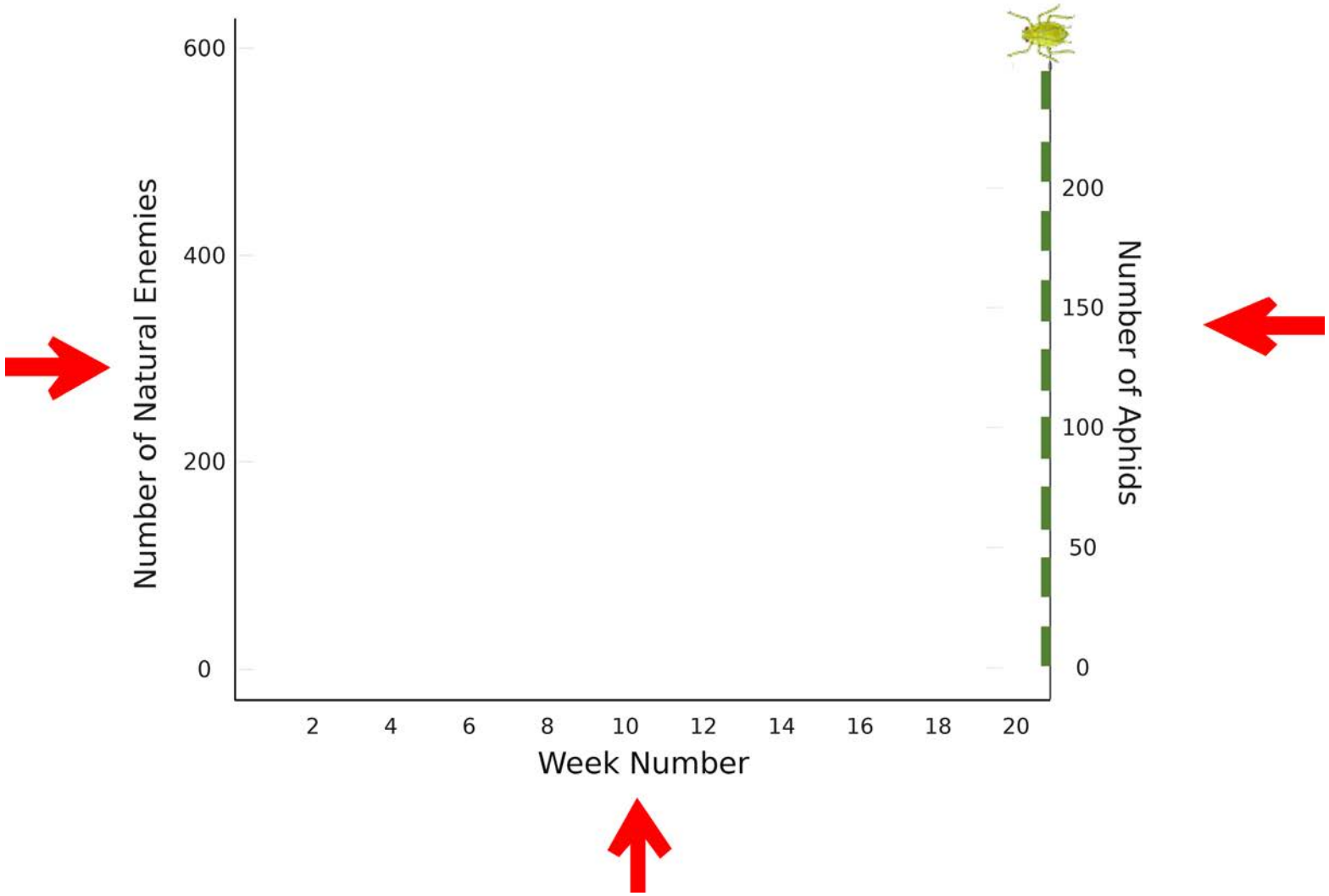
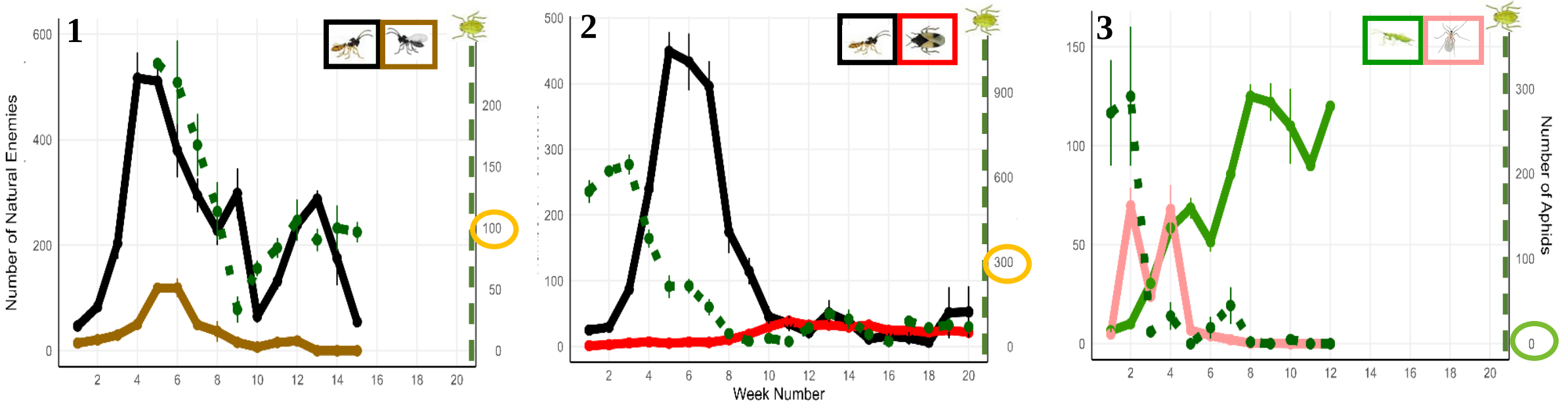
6 

Dynamics



Long-term community dynamics

Asymmetrical IGP



→ **No coexistence**

→ **Weak biocontrol**

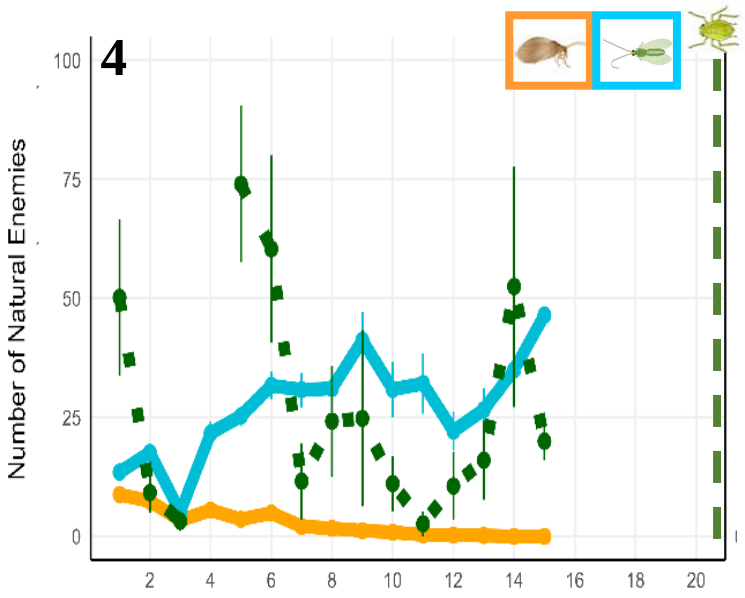
→ **No coexistence**

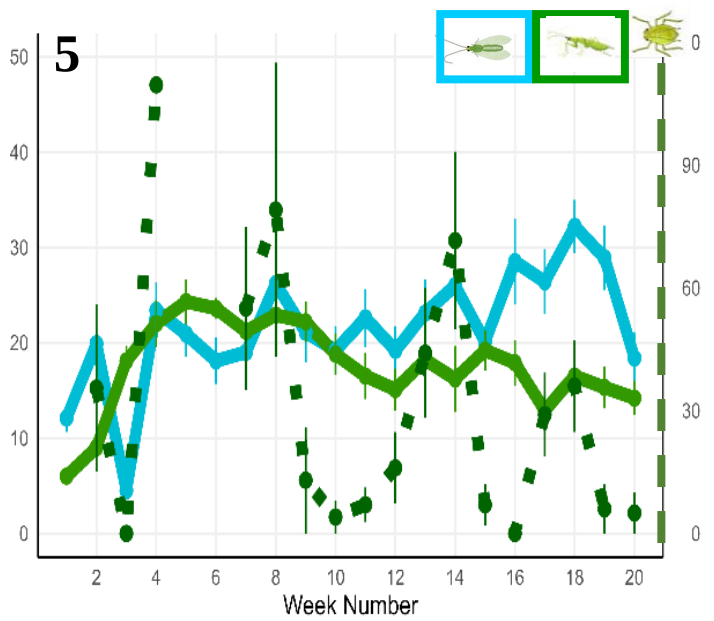
→ **Good biocontrol**

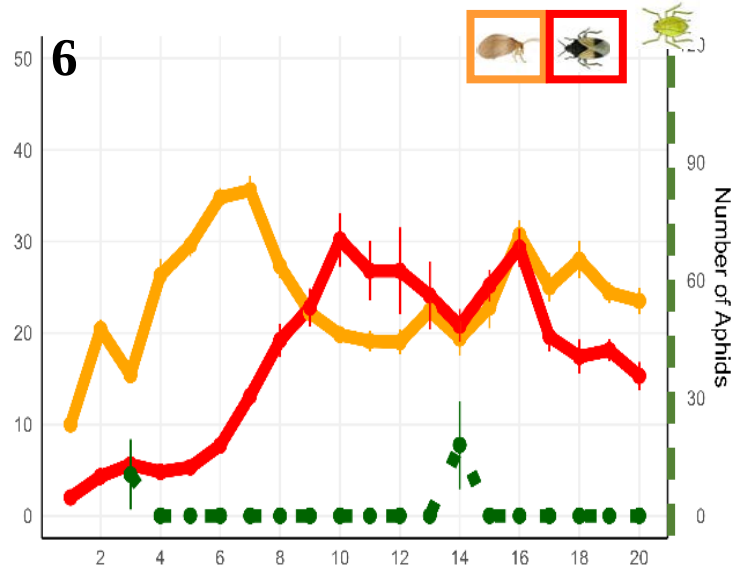
One predator better?

Long-term community dynamics

Symmetrical IGP







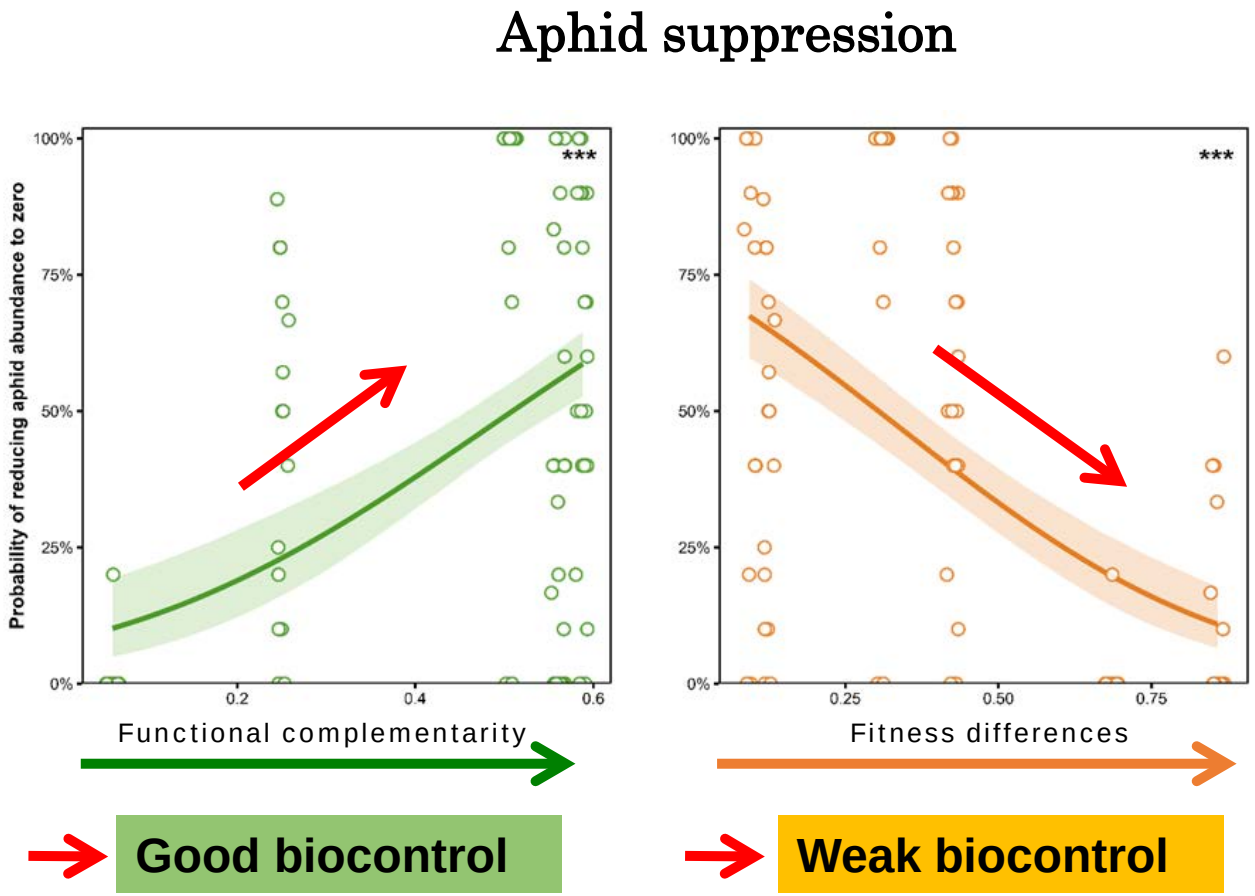
→ No coexistence

→ Good biocontrol

→ Coexistence

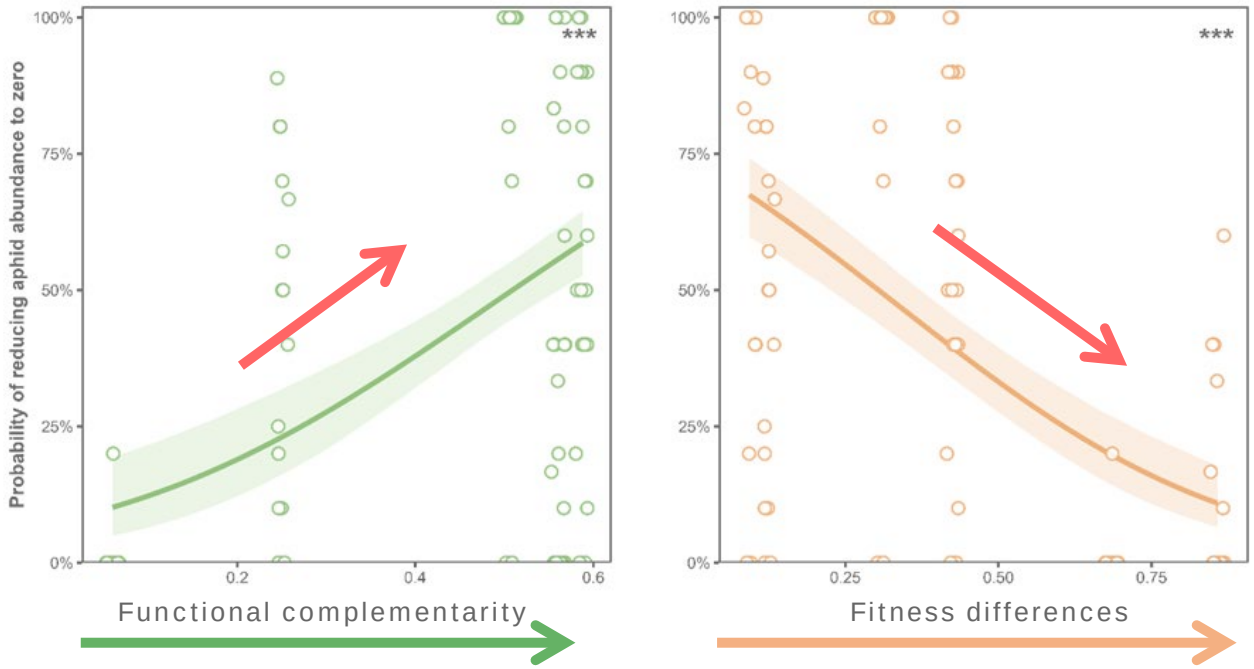
→ Good biocontrol

Functional complementarity and fitness differences effects



Functional complementarity and fitness differences effects

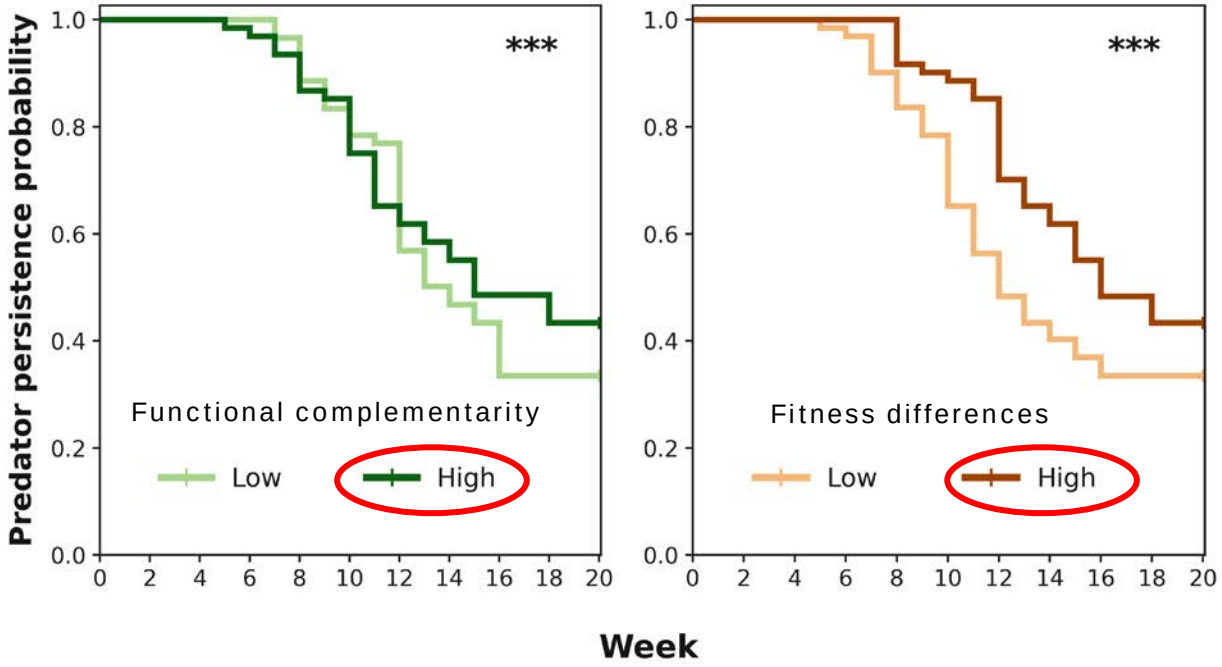
Aphid suppression



→ Good biocontrol

→ Weak biocontrol

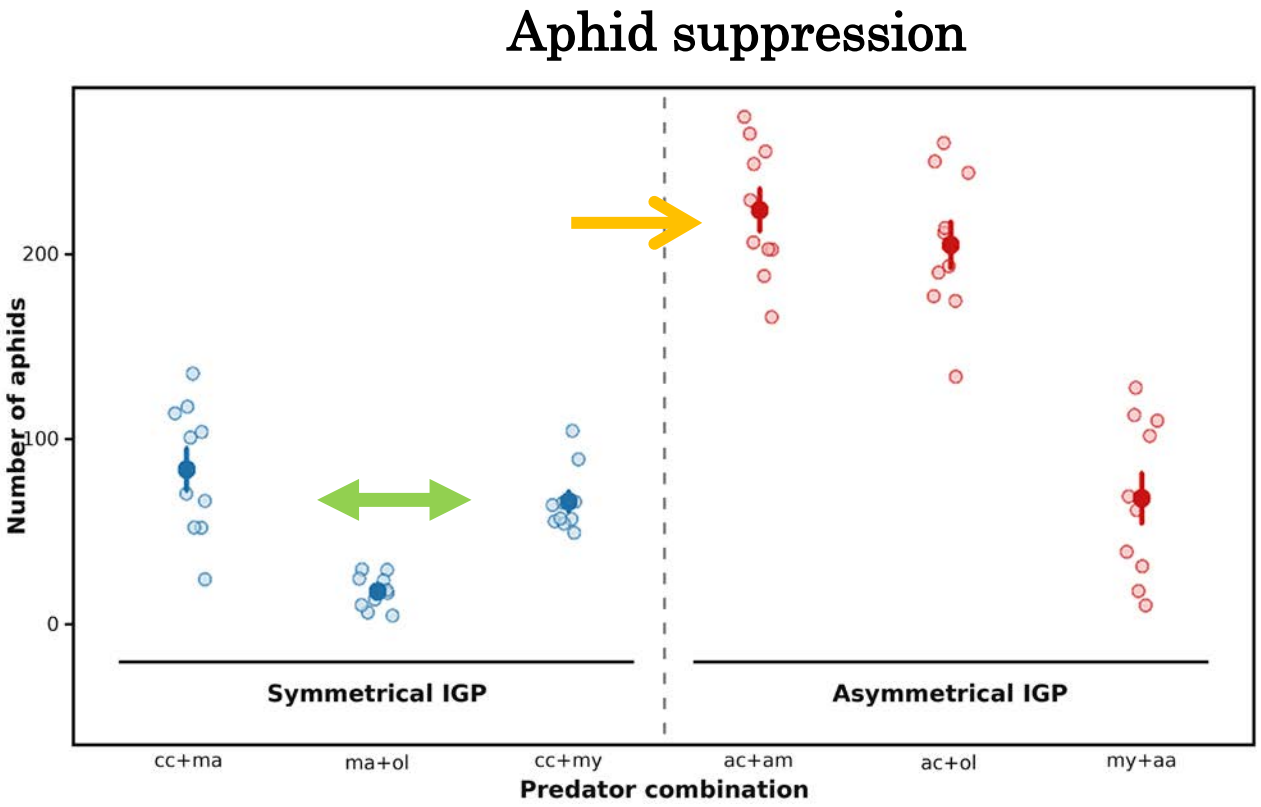
Predators coexistence



→ Coexistence

Functional complementarity large enough to offset high fitness differences!!

Intraguild predation effects

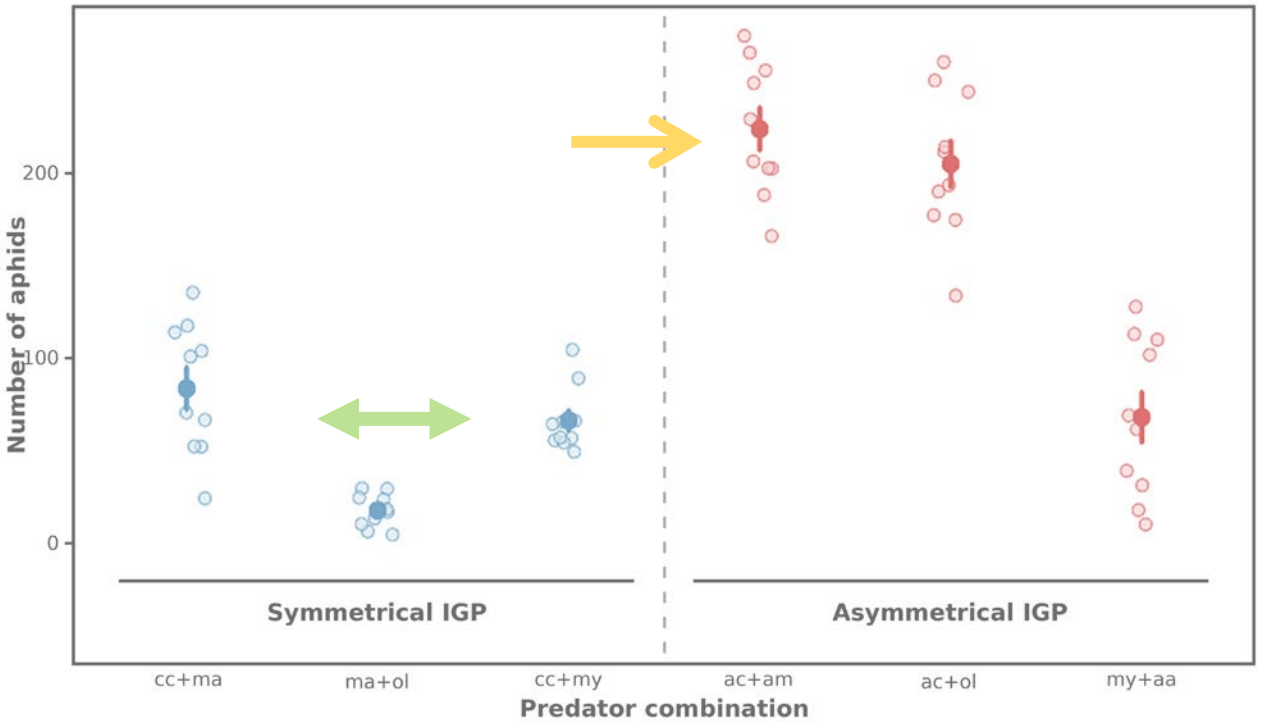


→ **Good biocontrol**

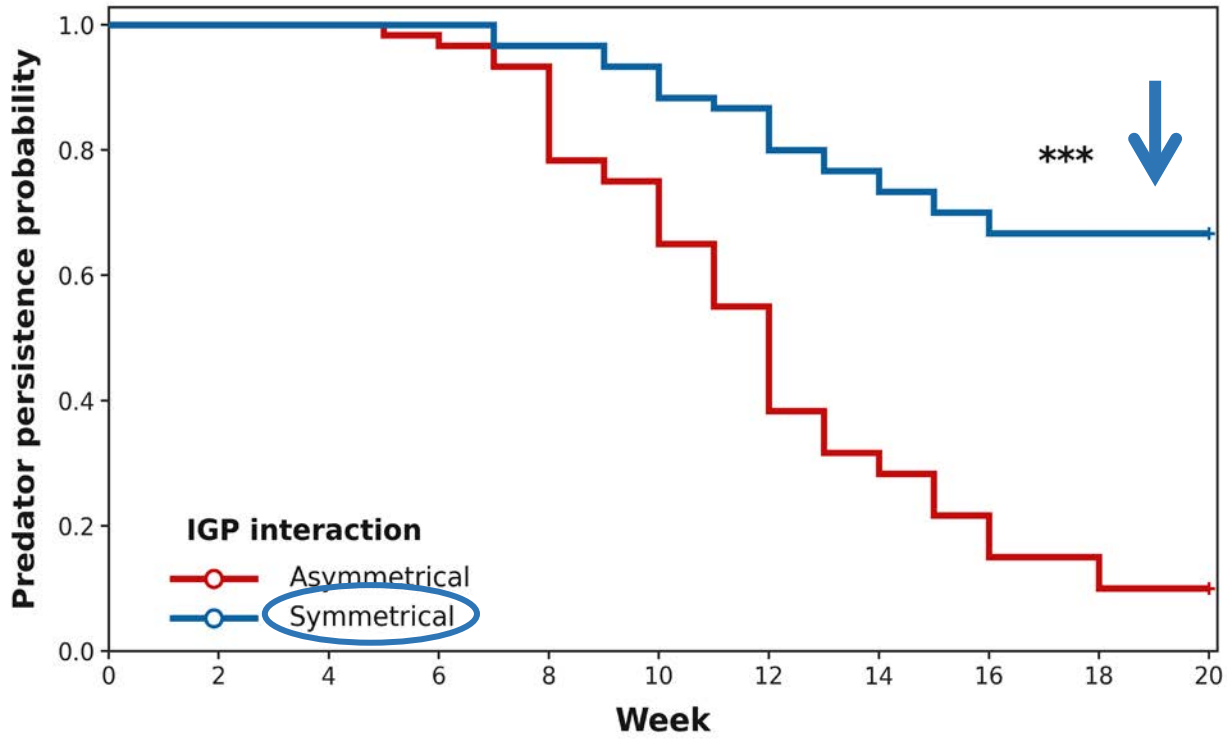
→ **Weak biocontrol**

Intraguild predation effects

Aphid suppression



Predators coexistence

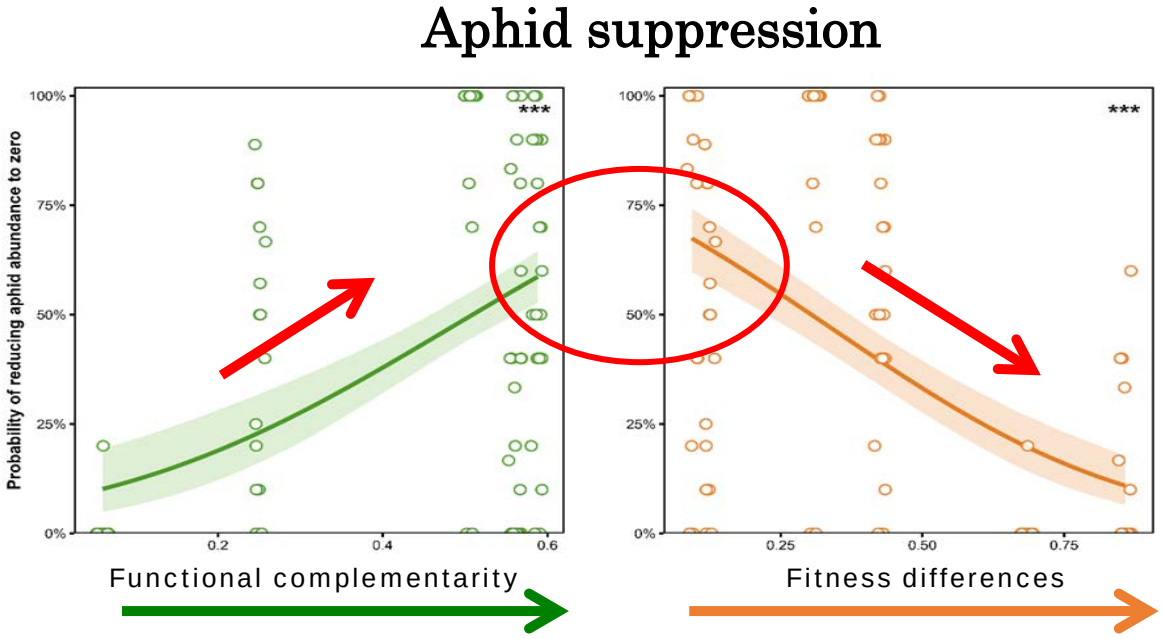


→ Good biocontrol

→ Weak biocontrol

Predators under symmetrical IGP coexist longer!!

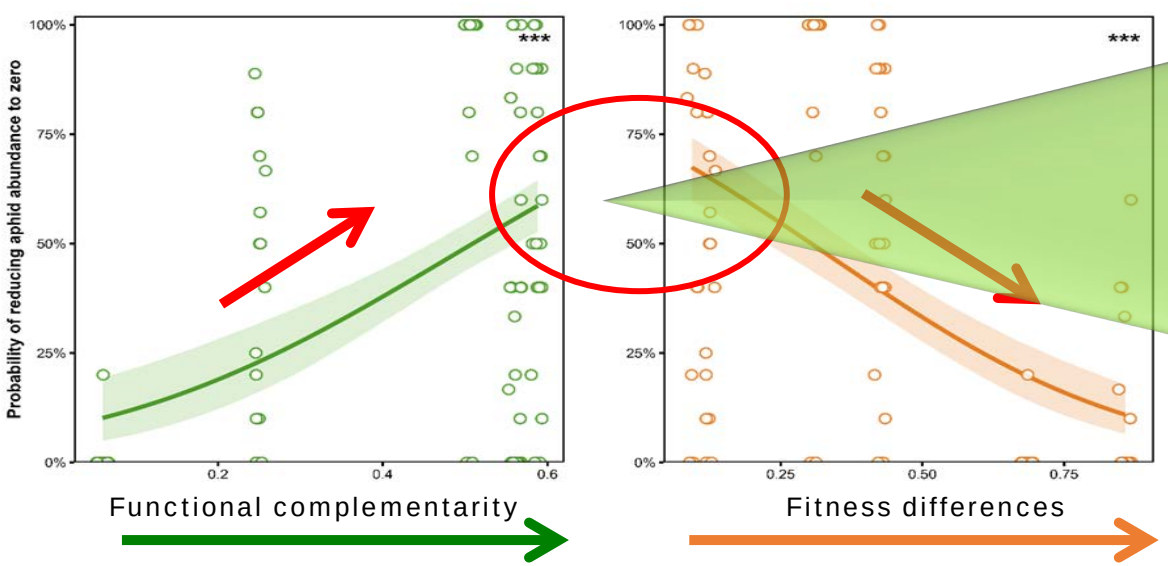
Conclusion

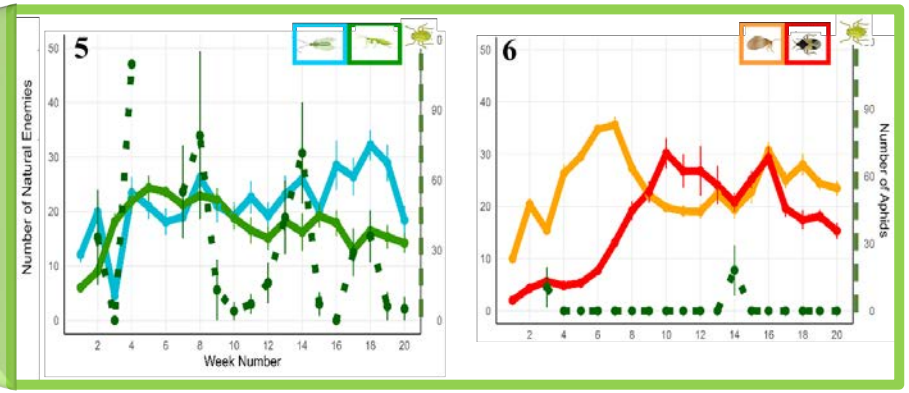


High functional complementarity and **low fitness differences** improve aphid suppression

Conclusion

Aphid suppression



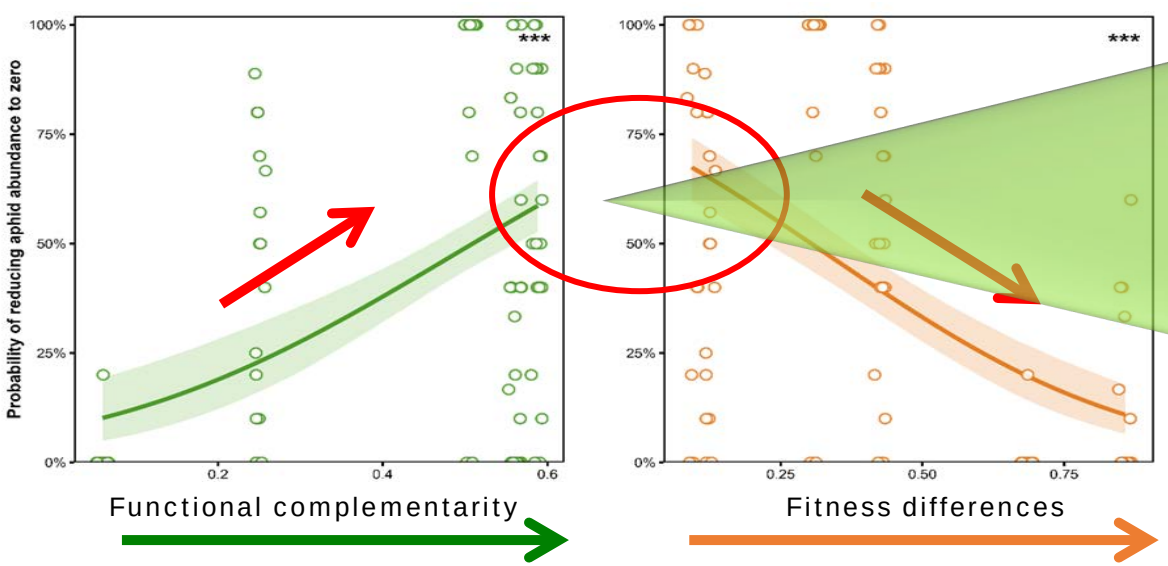


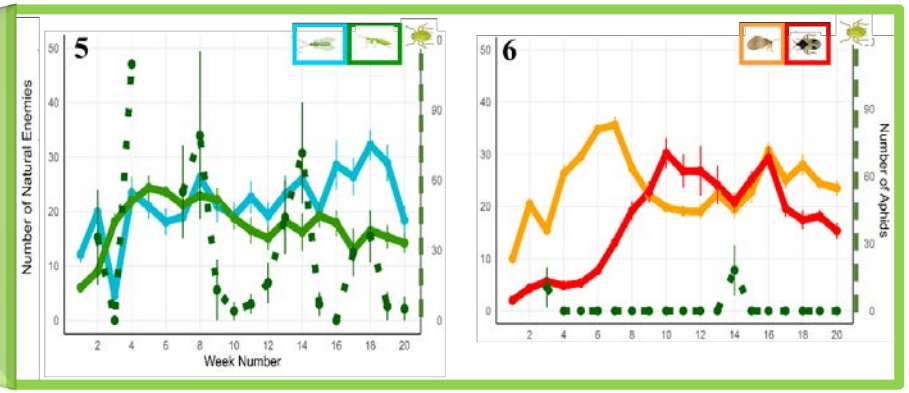
Two predator combinations coexist under symmetrical IGP

High functional complementarity and **low fitness differences** improve aphid suppression

Conclusion

Aphid suppression





Two predator combinations coexist under symmetrical IGP

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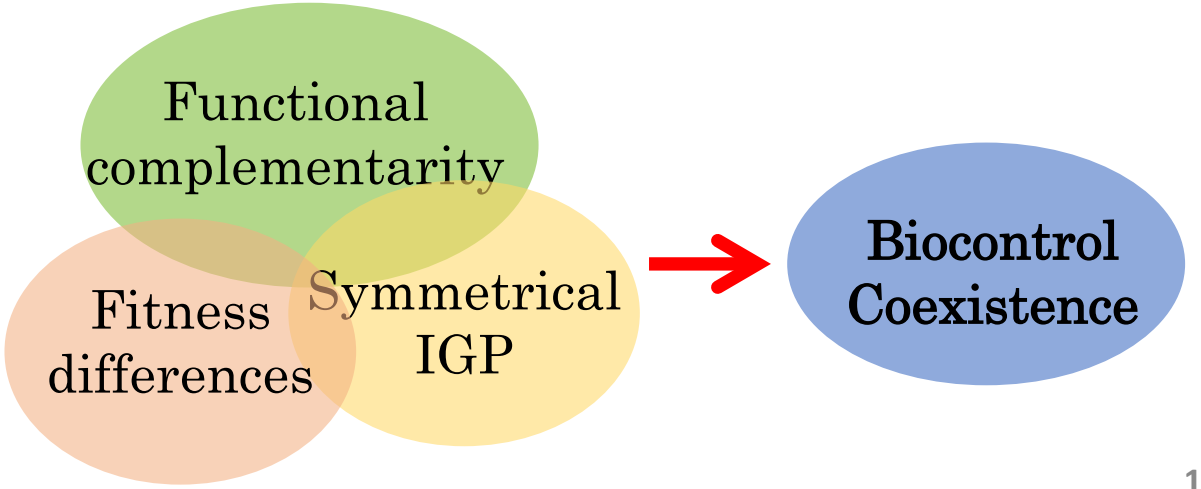
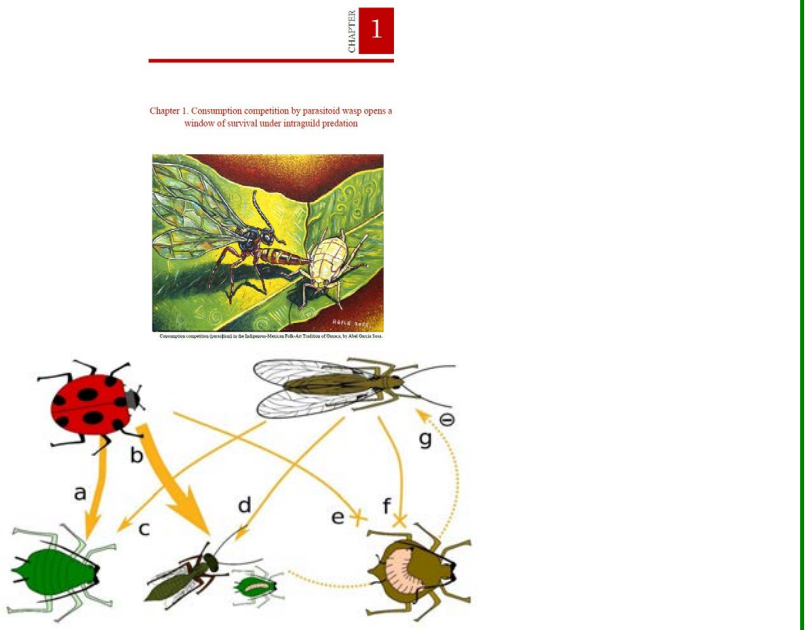


General discussion

General discussion

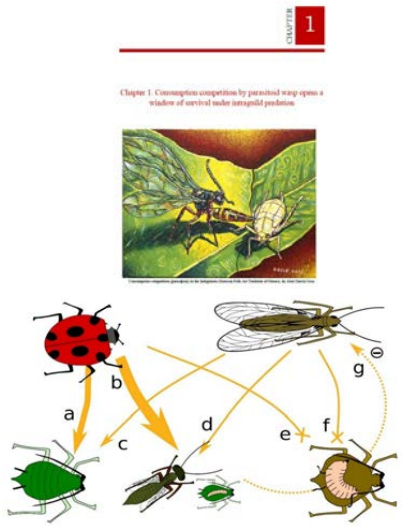


IG prey may persist through **consumption competition**

Preference reduces **fitness cost**

Slow feeding favors mummification

General discussion



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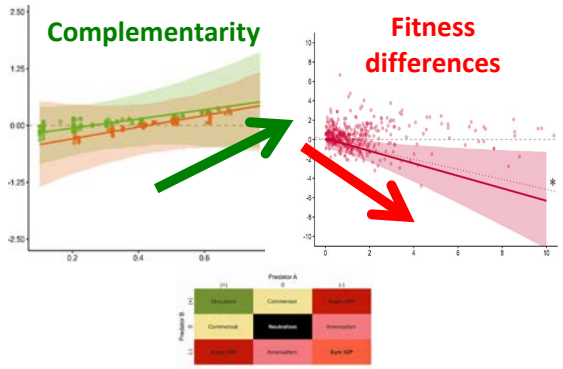
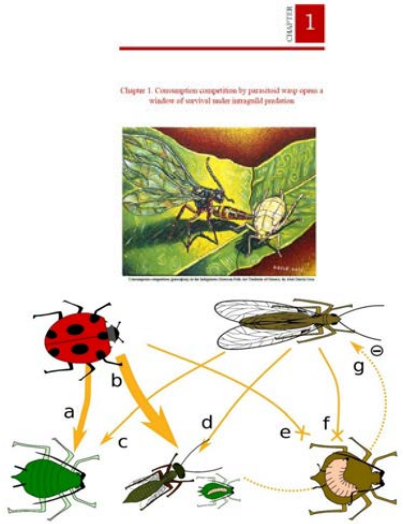


Complementarity favors biocontrol

Fitness asymmetry reduces benefits

Predator interactions alter the outcomes

General discussion



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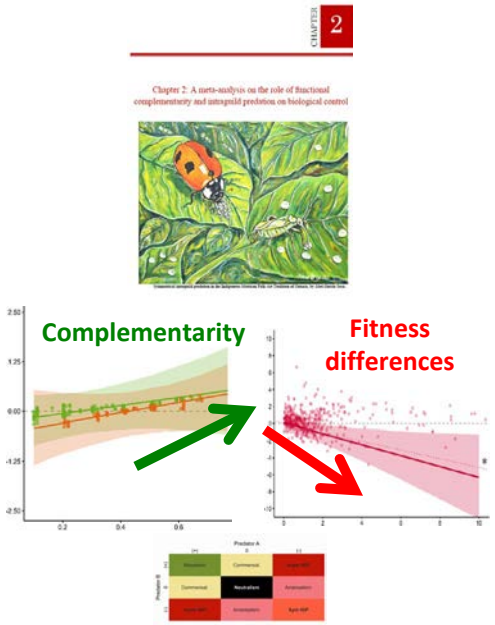

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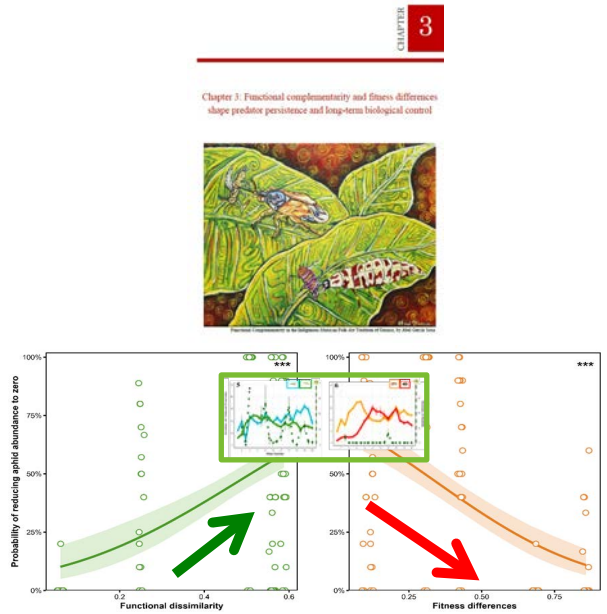
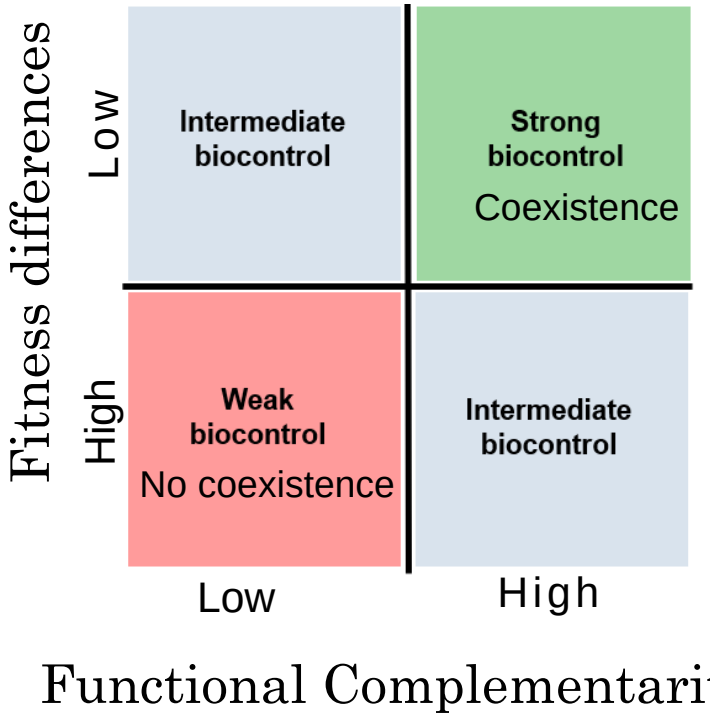


Predators that are functionally different with similar fitness can coexist under symmetrical IGP and provide strong biocontrol services!!!

General discussion



H1

High complementarity
&
Low fitness differences

+

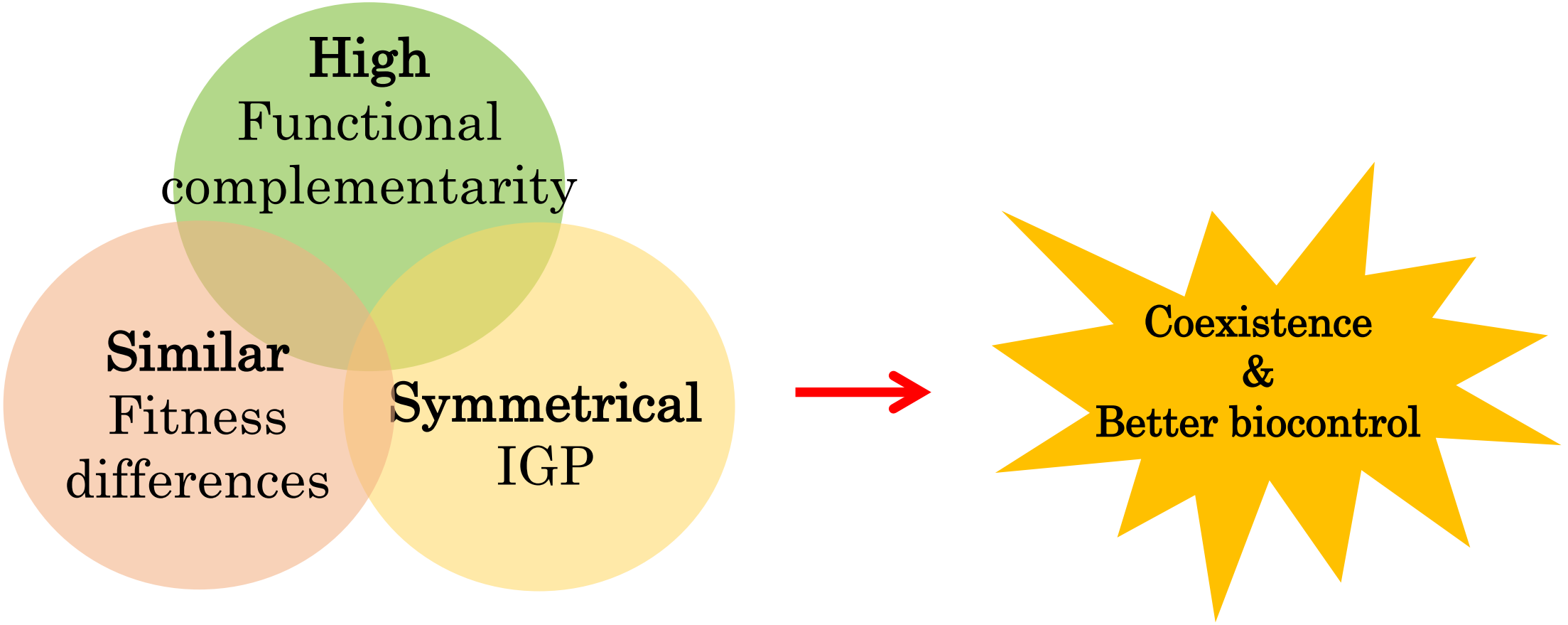
Intraguild predation

1/2 **H2** **Asymmetrical IGP**
Can reduce fitness differences to coexist
but neutral biocontrol effect

✓ **H3** **Symmetrical IGP**
High complementarity & Low fitness differences (**kill rates** or **growth**)

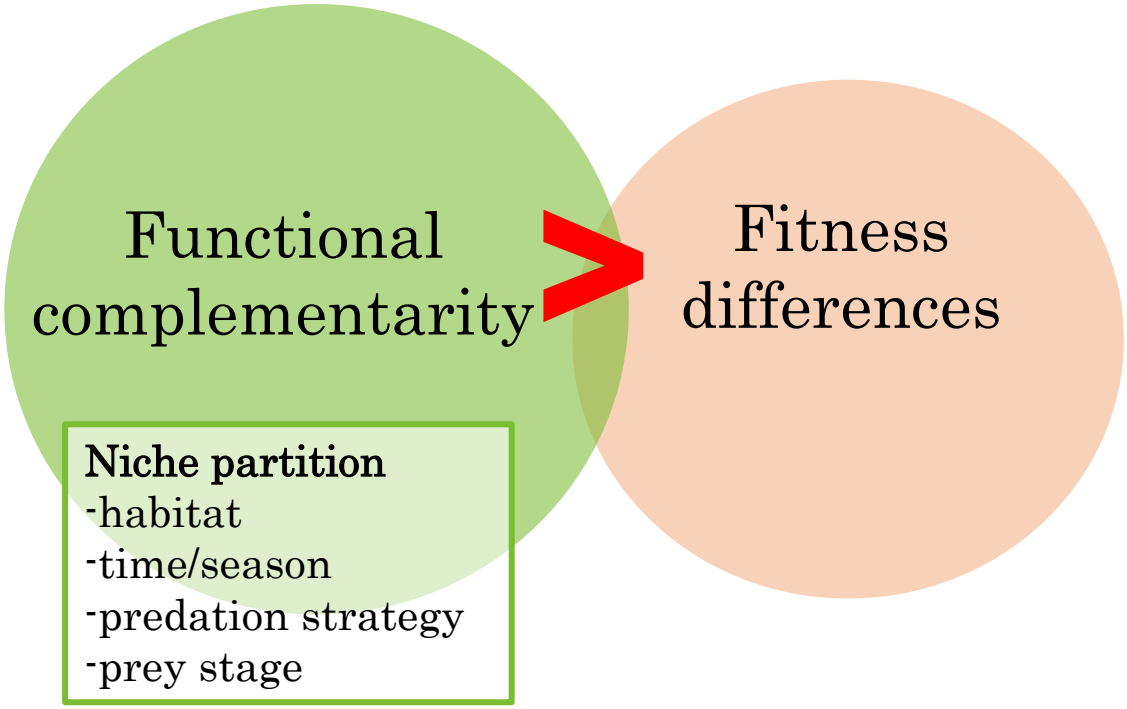
General discussion

A simple formula?



General discussion

Not quite, it's complex!



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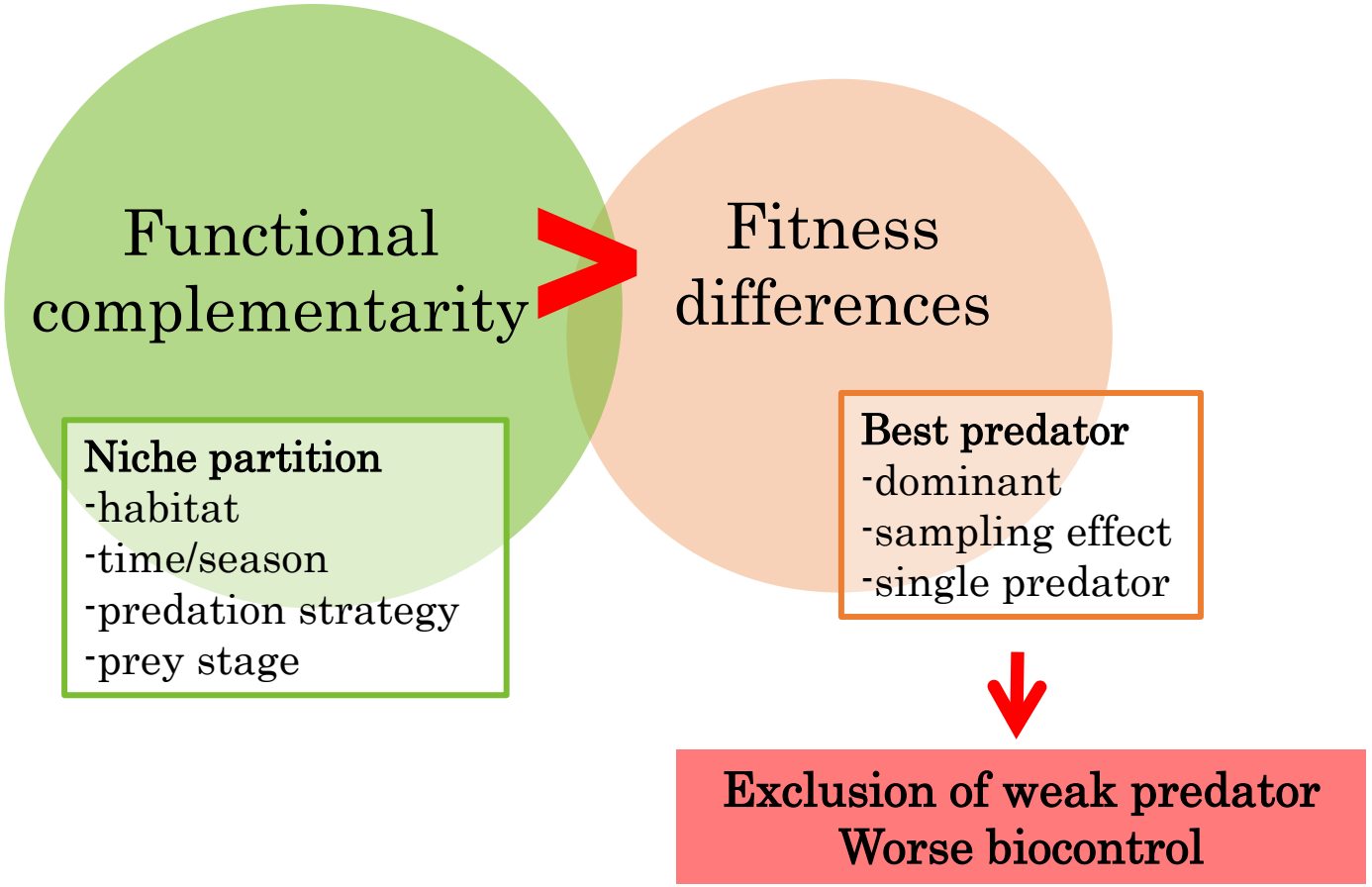

General discussion

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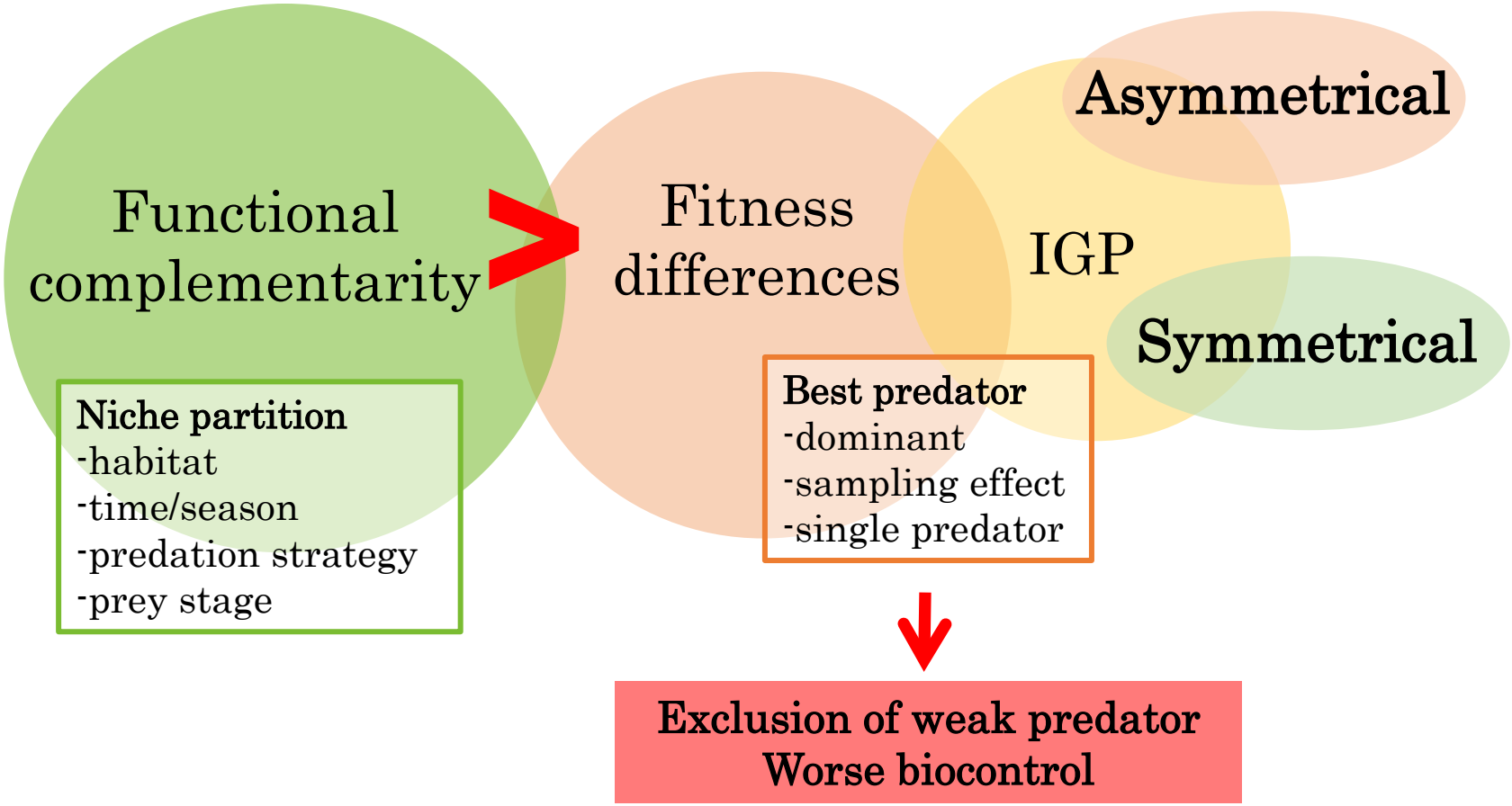

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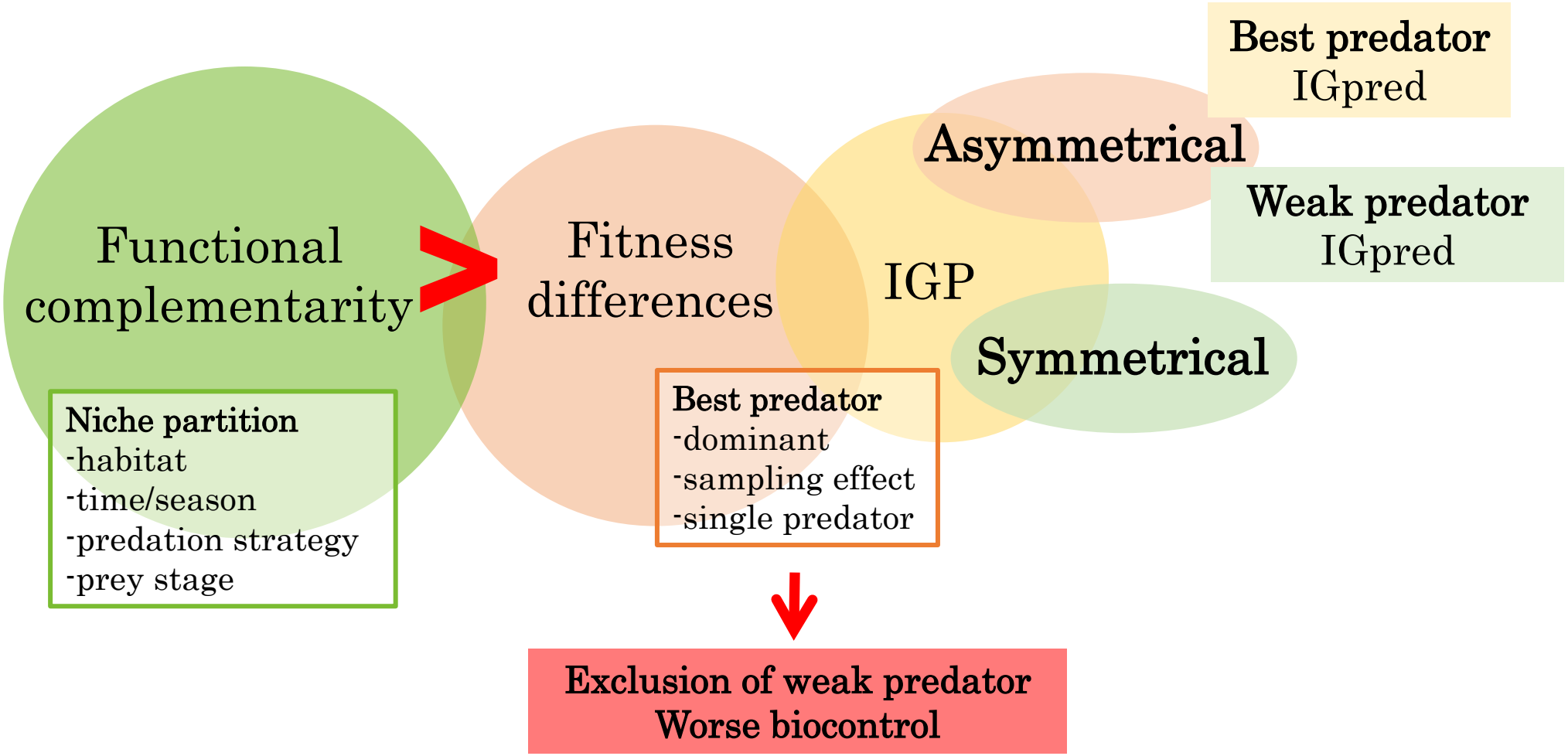
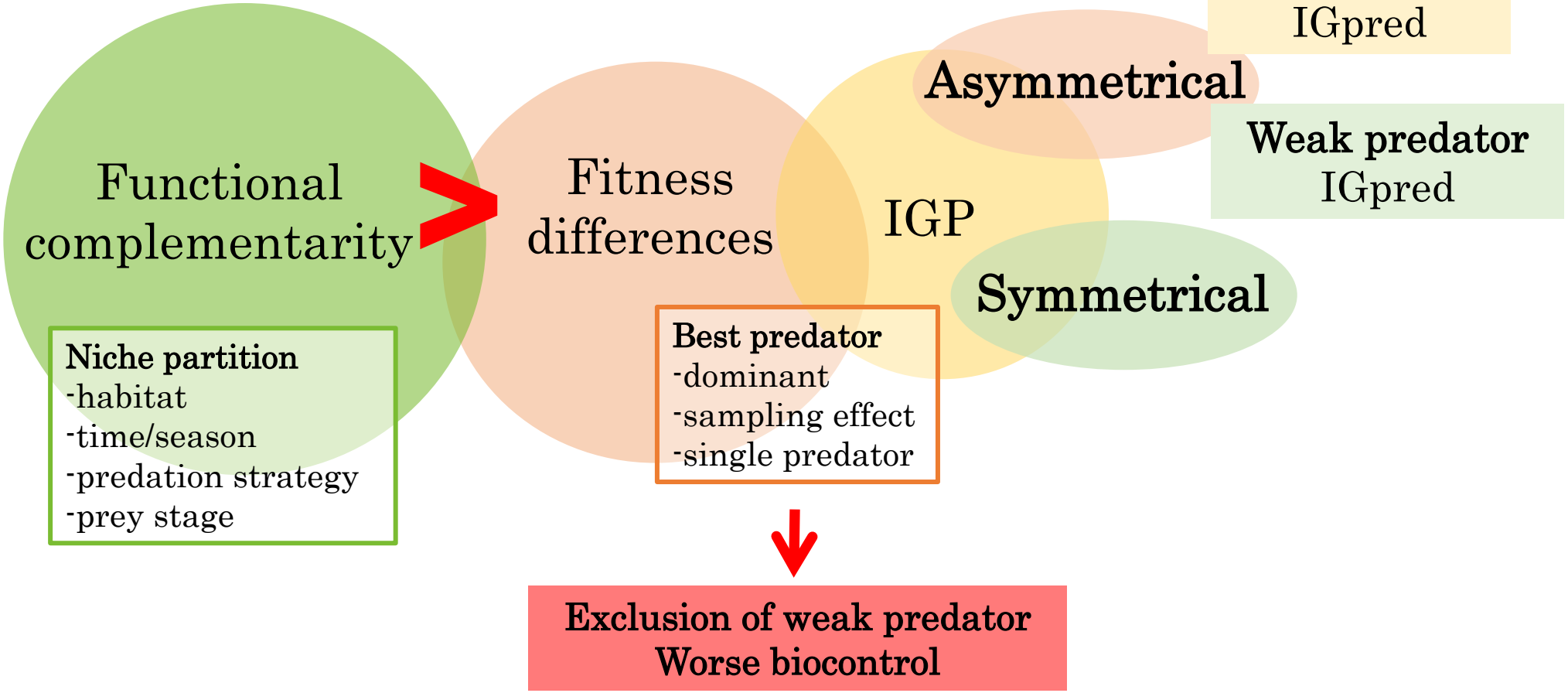


General discussion

Not quite, it's complex!



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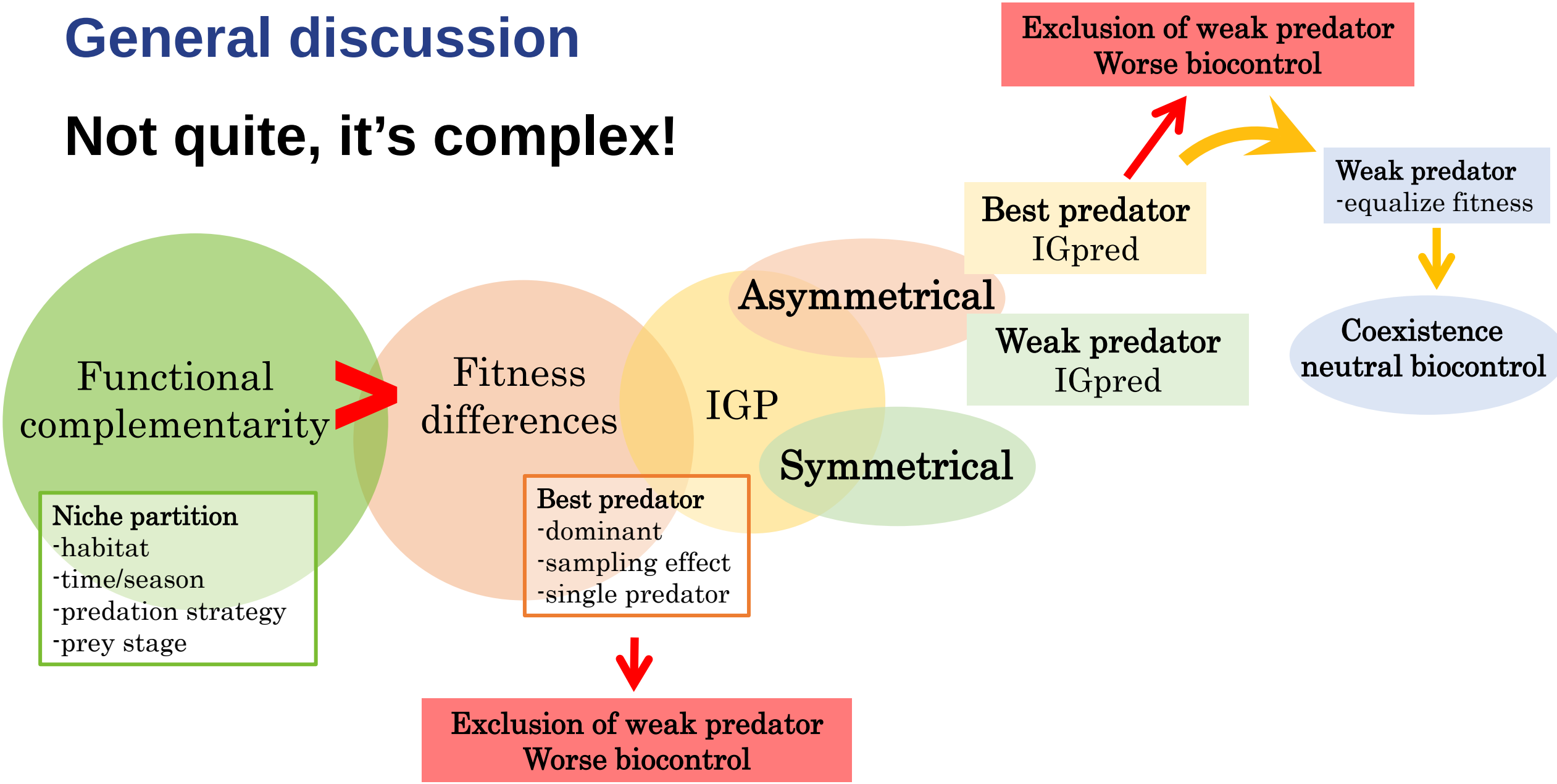

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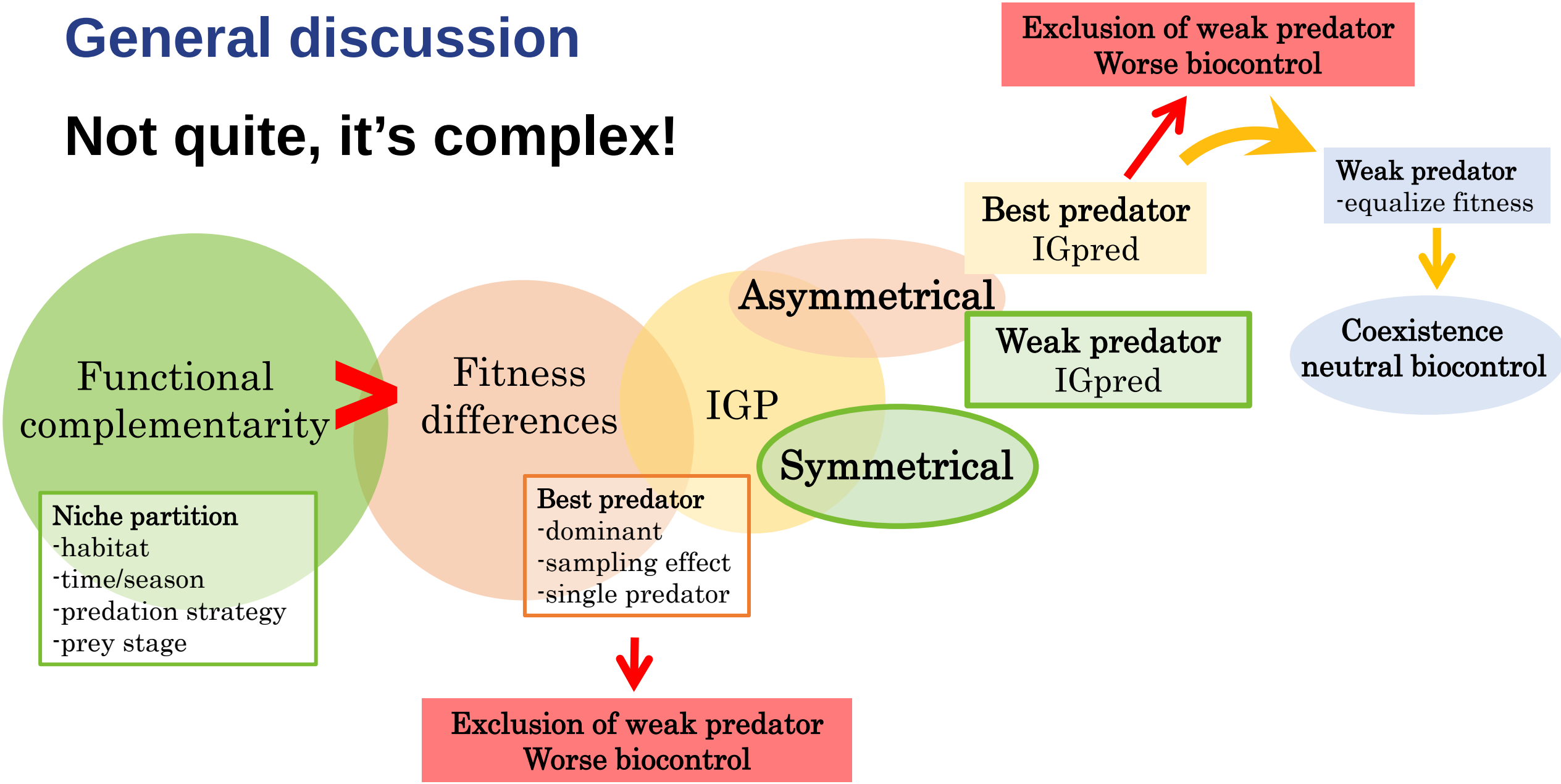

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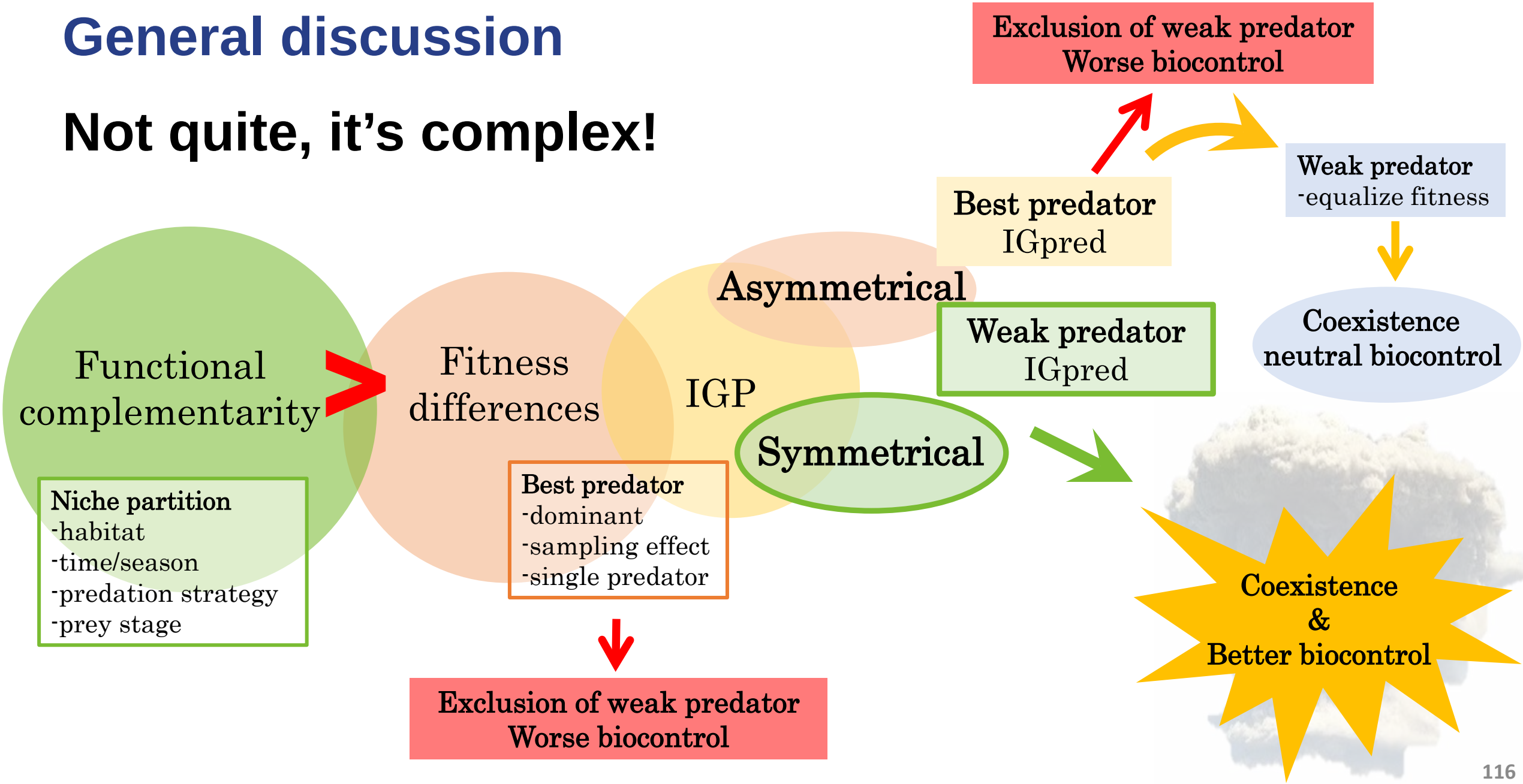

How to select your favorite cocktail?

1. **Similar fitness**: High functional and phylogenetic differences can enhance prey suppression

2. **Large fitness differences**: Functional complementarity may help, but a single predator can be preferable

3. **Symmetrical IGP**: Can support better biocontrol by cocktails

4. **Asymmetrical IGP**: Competitive advantages can promote IG prey persistence and sustain biocontrol



ENEMY COCKTAIL
Designing natural enemy cocktails for a better biocontrol

"The best predator cocktail depends on the balance between complementarity, fitness, and intraguild predation among predators"



©Nitohap from Flickr.com

Limits and perspectives

System limitation

- Cage experimental conditions may intensify competition and IGP
- Functional traits and fitness indices are proxies measures
- Study evaluations with one prey

Perspectives

- ✓ Validate mechanisms in a multi-prey system
- ✓ Evaluate multi-predators and multi-prey in greenhouses
- ✓ Explore **predator-microbial interactions**

Applied Biocontrol

Four predator combinations that lead to greater aphid suppression

Long-term strategy

1) ma+ol 

2) cc+my 

Strong biocontrol & coexistence

Short-term strategy

3) my+aa 

4) cc+ma 

Strong biocontrol

Enemycocktail

anr agence nationale de la recherche

isem Institut des Sciences de l'Evolution-Montpellier

University of Exeter

biobest SUSTAINABLE CROP MANAGEMENT



Project contribution

"Global development of biocontrol to promote the transition into more agroecological farming systems"

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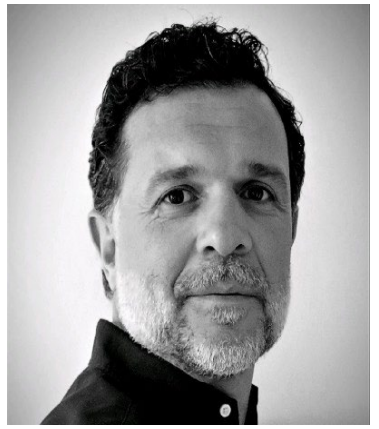

Apostolos Pekas

UNIVERSITAT POLITÈCNICA DE VALÈNCIA

Merci CBGP!

































Merci les amis!

Thanks to my family





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What is next??



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-Full travel grant for an oral presentation

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Thank you for your attention!!



Thank you for your attention!!