Simultaneous invasion by two species: consequences for their success and for the resident community

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CENTRE FOR ECOLOGICAL RESEARCH

INSTITUTE OF EVOLUTION

International Initiative for Theoretical Ecology
A think tank to promote our understanding of nature

Background and motivation

- regime shifts
- structure–function links

Á. Móréh et al.: **Overfishing and regime shifts in minimal food web models.**
Comm. Ecol., 10(2) 236-243 (2009)

- two-species disturbances
- additive/non-additive effects
- community response
- network position

Á. Móréh et al.: **Topology of additive pairwise effects in food webs.**
Ecol. Mod., 440:109414 (2021)

- Interactions among invaders matter
- How do invasive species interact when arriving together?
- Gaps in understanding multi-species invasions

Research background and modelling gap

- **Invasional meltdown** (Simberloff & Von Holle 1999)
- Strong empirical interest in multi-species invasions
  - field- and mesocosm experiments
  - meta-analyses
- Surprising lack of theoretical/mathematical models
- Theory focuses on **single-species invasions**
  - Traits predicting invasion success
  - Impacts on resident communities

D. Simberloff and B. Von Holle: **Positive Interactions of Nonindigenous Species: Invasional Meltdown?**
Biol. Inv, 1:21-32 (1999)

T. Romanuk et al.: **Predicting invasion success in complex ecological networks**
Phil. Trans. R. Soc. B, 364:1743-1754 (2009)

Multi-species invasion – metaanalyses

Jackson, M. C: **Interactions among multiple invasive animals**
Ecology, 96(8): 2035-2041 (2015)

- Global meta-analysis
- Mean effect is antagonistic or neutral
- No general support for invasional meltdown

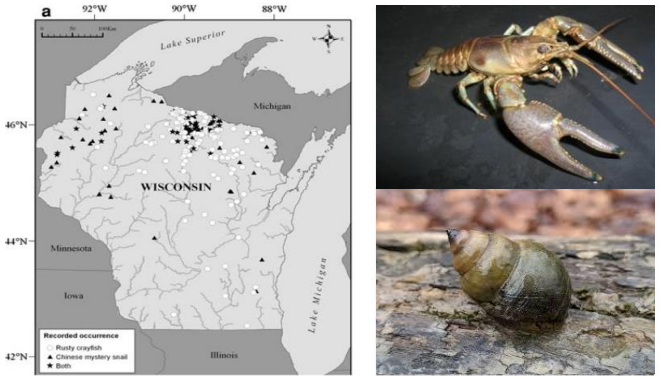
Cameron, E. K. et al.: **Global meta-analysis of the impacts of terrestrial invertebrate invaders on species, communities and ecosystems: Ecological impacts of terrestrial invertebrate invaders**
Global Ecology and Biogeography, 25(5): 596-606 (2016)

- 700 terrestrial invertebrate studies
- Strong negative impacts of invaders
- no stronger effects for multiple invaders

The outcomes are often additive or antagonistic, positive interactions among invaders are not universal.

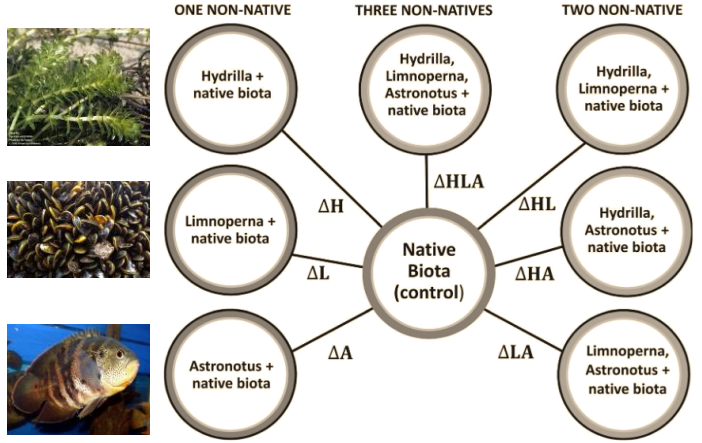
Multi-species invasion experiments

P. Johnson et al.: **Interactions among invaders: community and ecosystem effects of multiple invasive species in an experimental aquatic system.**
Oecologia, 159(1) 161-170 (2009)



- Both reduce native snails
- Combined impact > individual impacts
- Amplified effects without facilitation

R. R. Braga et al.: **Invasional meltdown: an experimental test and a framework to distinguish synergistic, additive, and antagonistic effects**
Hydrobiologia, 847(7): 1603-1618 (2020)



- Additive interactions, no meltdown

Modelling multi-species invasion

Rauschert, E. and Shea, K.: **Competition between similar invasive species: modeling invasional interference across a landscape**
Population Ecology, 59(1): 79-88 (2017)

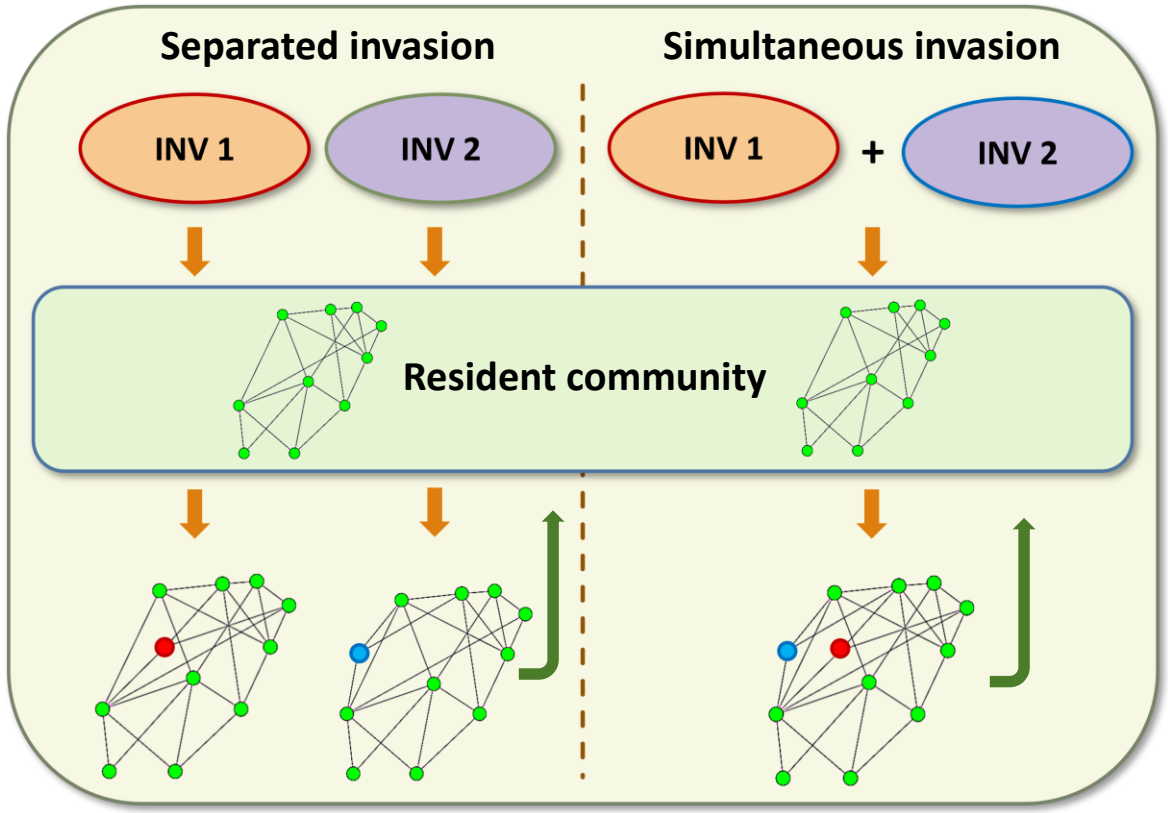
- Spatially explicit **competition model**
- Two thistle invaders (*Carduus* spp.)
- **Invasional interference:** negative interactions reduce spread
- Spatial segregation or coexistence depending on competition strength

Vagnon, Ch. et al.: **Inferring the trophic attributes and consequences of co-occurring lake invaders using an allometric niche model**
Biol. Inv., 24(6): 1661-1676 (2022)

- **Allometric niche model** (aNM)
- Mysid shrimp + catfish in Lake Bourget
- **Additive trophic impacts:** shared resources, food-web changes
- Predicts shifts in trophic roles and vulnerability of natives

Modelling connects different mechanisms and helps anticipate invasion outcomes.

Study design and main objectives



- **Two invasion scenarios:**
  - Single-species invasion
  - Joint invasion (both species together)
- **Network analysis** to determine:
  - Presence/absence of direct or indirect links between them
  - Invaders' positions in the food web
- **Comparison** of:
  - Invasion success under each scenario
  - Additive/non-additive effects on the resident community

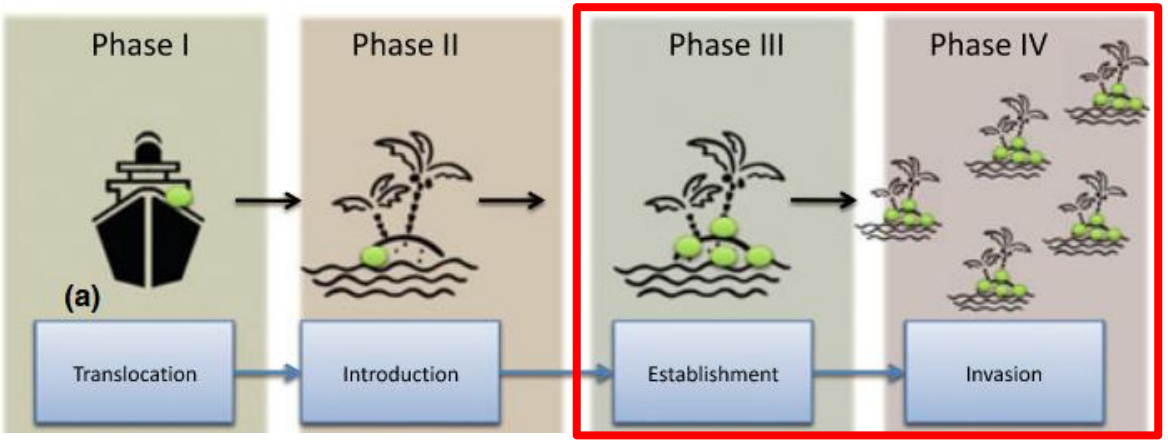
Q1: Does one invader affect the success of another?

Can a species remain successful/unsuccessful when invading together? Possible outcomes?

What do we consider "success"?

– General invasion steps: **translocation → introduction → establishment → spread**

– Success = completion of *establishment* and *spread*

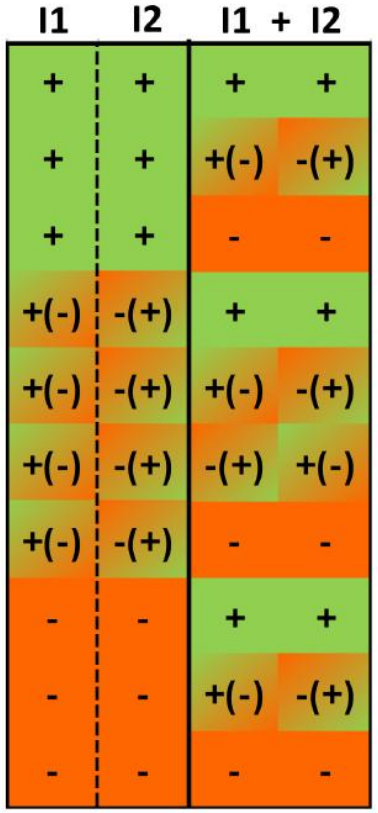


Hatcher et al., 2012

Operational definition in our simulations:

– Invader is successful if it persists at equilibrium with stable **positive biomass**

Q1: Does one invader affect the success of another?



I1	I2	I1 + I2	
+	+	+	+
+	+	+(-)	-(+)
+	+	-	-
+(-)	-(+)	+	+
+(-)	-(+)	+(-)	-(+)
+(-)	-(+)	-(+)	+(-)
+(-)	-(+)	-	-
-	-	+	+
-	-	+(-)	-(+)
-	-	-	-

- **Ten possible presence/absence outcomes** when treating the two invaders symmetrically (order irrelevant).
- **Outcome patterns:** from both invaders succeeding alone and together, through asymmetric or mutual exclusion, down to cases where neither species can establish.

Q1: Does one invader affect the success of another?

I1	I2	I1 + I2	
+	+	+	+
+	+	+(-)	-(+)
+	+	-	-
+(-)	-(+)	+	+
+(-)	-(+)	+(-)	-(+)
+(-)	-(+)	-(+)	+(-)
+(-)	-(+)	-	-
-	-	+	+
-	-	+(-)	-(+)
-	-	-	-

- We compare the equilibrium biomass of each invasive species when they are introduced separately vs. when they co-occur in the community.
- This allows us to assess whether the presence of a second invader increases or decreases an invader's biomass relative to its single-invader scenario.

Q2: Combined impact on the resident community

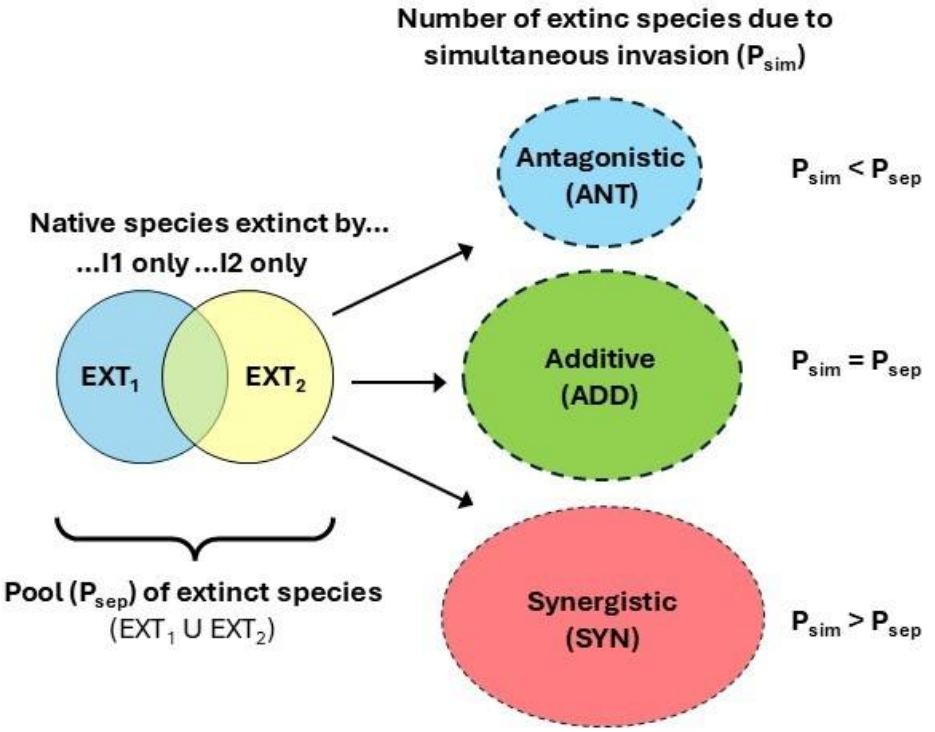
I1	I2	I1 + I2	
+	+	+	+
+	+	+(-)	-(+)
+	+	-	-
+(-)	-(+)	+	+
+(-)	-(+)	+(-)	-(+)
+(-)	-(+)	-(+)	+(-)
+(-)	-(+)	-	-
-	-	+	+
-	-	+(-)	-(+)
-	-	-	-

- **Additive effect:**
  - The joint impact equals the sum of their individual effects.
- **Antagonistic effect:**
  - The joint impact is **weaker** than expected from individual effects.
- **Synergistic effect:**
  - The joint impact is **stronger** than expected from individual effects.

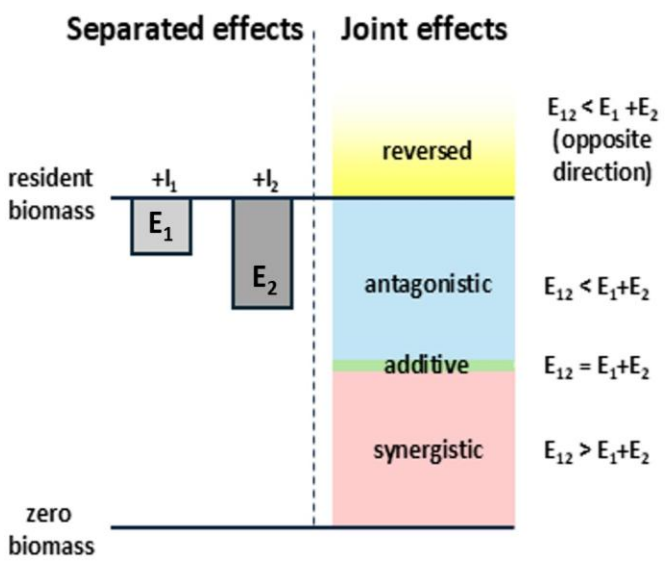
- **measurable, quantifiable properties to assess additivity**
- **simulated networks → two general, quantifiable metrics**

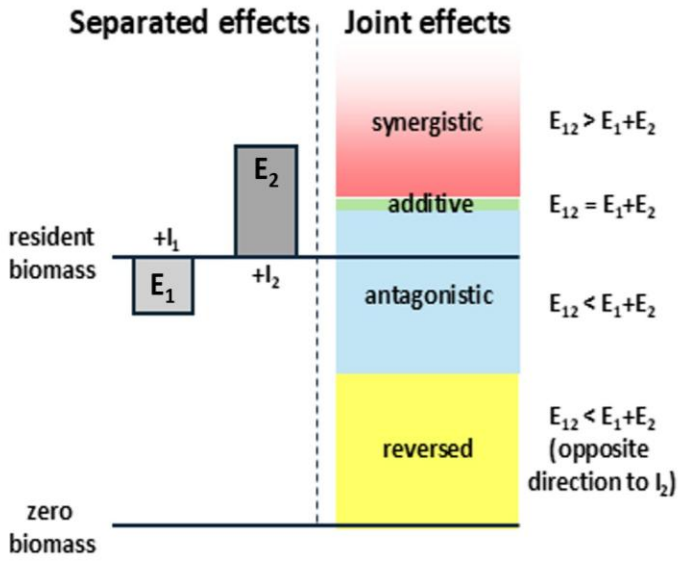
Q2: Combined impact on the resident community

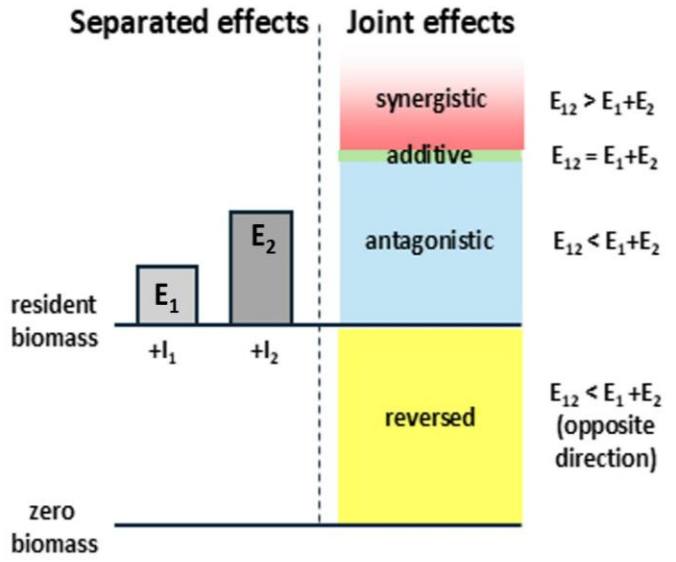
I1	I2	I1 + I2	
+	+	+	+
+	+	+(-)	-(+)
+	+	-	-
+(-)	-(+)	+	+
+(-)	-(+)	+(-)	-(+)
+(-)	-(+)	-(+)	+(-)
+(-)	-(+)	-	-
-	-	+	+
-	-	+(-)	-(+)
-	-	-	-



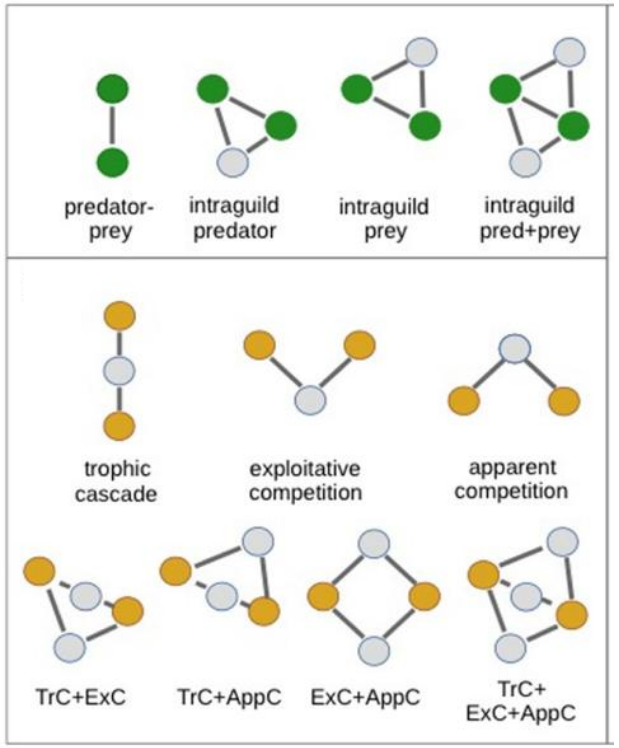
Q2: Combined impact on the resident community







Q3: Influencing factors

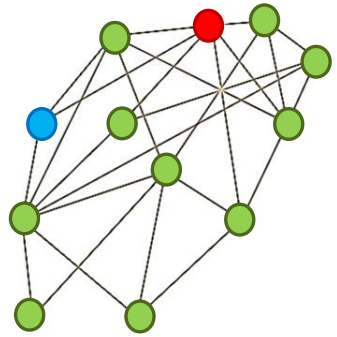


- **Direct (predator-prey) interaction:**
  - *PP*
  - Intraguild predator (*IGPred*)
  - Intraguild prey (*IGPrey*)
- **Indirect (no predator-prey) interaction (2 „steps”):**
  - Trophic cascade (*TrC*)
  - Exploitative competition (*ExC*)
  - Apparent competition (*AppC*)
- **Distant connection (>2 steps)**

Trophic level

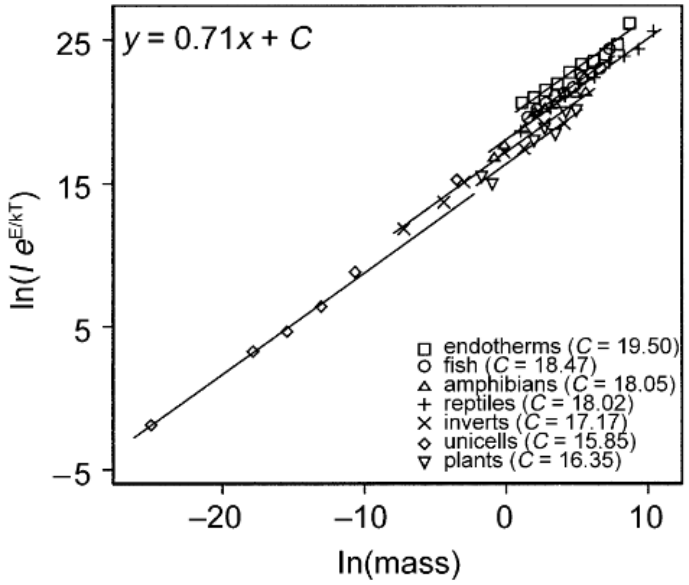
$$\overline{TL}_i = 1 + \frac{\sum_j TL_j}{n_j}$$

Top vs intermedier position



Simulation of dynamics – the *allometric bioenergetic model*

- **Body size determines metabolic demand:**
  - According to *Kleiber's law*, metabolic rate scales with approximately the ¾ power of body mass.
- **Body size shapes consumer-resource dynamics:**
  - It governs consumption rates and the strength/stability of trophic interactions.
- **Body size predicts trophic position:**
  - Larger species tend to be top predators, smaller species are typically prey.
- **Why this matters for our simulations:**
  - The framework uses these allometric principles to mechanistically link metabolism, feeding interactions, and food-web stability.



Yodzis and Innes, 1992, Am. Nat. 139(6), 1771-1789

Simulation of dynamics – the allometric bioenergetic model

$$\frac{dB_{i(basal)}}{dt} = r_i(M_i)B_iG_i - \sum_{c=cons} \frac{x_c(M_c)y_c}{e_{ci}} B_cF_{ci}$$

$$\frac{dB_{i(consumer)}}{dt} = \sum_{\rho=res} x_i(M_i)y_iB_iF_{i\rho} - \sum_{c=cons} \frac{x_c(M_c)y_c}{e_{ci}} B_cF_{ci} - x_i(M_i)B_i$$

Ecology Letters, (2006) **9**: 1228–1236 doi: 10.1111/j.1461-0248.2006.00978.x

LETTER

Allometric scaling enhances stability in complex food webs

Ulrich Brose,[1,2]* Richard J. Williams[2,3] and Neo D. Martinez[2]

Simulation of dynamics – the allometric bioenergetic model

$$\frac{dB_{i(basal)}}{dt} = r_i(M_i)B_iG_i - \sum_{c=cons} \frac{x_c(M_c)y_c}{e_{ci}} B_cF_{ci}$$

$$\frac{dB_{i(consumer)}}{dt} = \sum_{\rho=res} x_i(M_i)y_iB_iF_{i\rho} - \sum_{c=cons} \frac{x_c(M_c)y_c}{e_{ci}} B_cF_{ci} - x_i(M_i)B_i$$

$$G_i = \left(1 - \frac{B_i}{K_i}\right)$$

$$F_{ij} = \frac{B_j^h \omega_{ij}}{B_0^h + \sum_{k=res} \omega_{ik} B_k^h}$$

Reproduction:

$$R_P = a_r M_P^{-1/4}$$

Metabolism:

$$X_C = a_x M_C^{-1/4}$$

Max consumption:

$$Y_C = a_x M_C^{-1/4}$$

- *P*: producer (basal)
- *C*: consumer
- a_r, a_x, a_y: allometric constants

Brose et al., 2006, Ecol. Lett. 9, 1228-1236

Simulation of dynamics – the allometric bioenergetic model

$$\frac{dB_{i(basal)}}{dt} = r_i(M_i)B_iG_i - \sum_{c=cons} \frac{x_c(M_c)y_c}{e_{ci}} B_cF_{ci}$$

$$\frac{dB_{i(consumer)}}{dt} = \sum_{\rho=res} x_i(M_i)y_iB_iF_{i\rho} - \sum_{c=cons} \frac{x_c(M_c)y_c}{e_{ci}} B_cF_{ci} - x_i(M_i)B_i$$

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Reproduction:

$$R_P = a_r M_P^{-1/4}$$

Metabolism:

$$X_C = a_x M_C^{-1/4}$$

Max consumption:

$$Y_C = a_x M_C^{-1/4}$$

Mass-specific max growth rate

$$r_{basal} = 1$$

Mass-specific metabolic rate

$$x_i = \frac{X_C}{R_P} = \frac{a_x}{a_r}\left(\frac{M_C}{M_P}\right)^{-1/4}$$

max consumption rate

$$y_i = \frac{Y_C}{X_C} = \frac{a_y}{a_x}$$

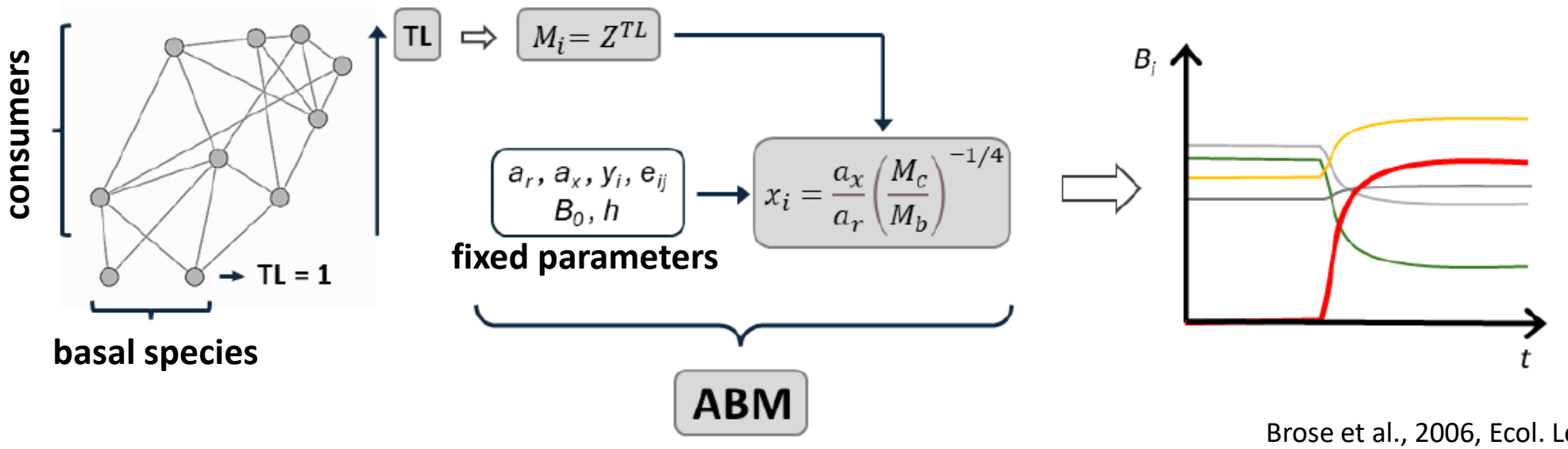
Brose et al., 2006, Ecol. Lett. 9, 1228-1236

Simulation of dynamics – the allometric bioenergetic model

$$\frac{dB_{i(basal)}}{dt} = r_i(M_i)B_iG_i - \sum_{c=cons} \frac{x_c(M_c)y_c}{e_{ci}} B_cF_{ci}$$

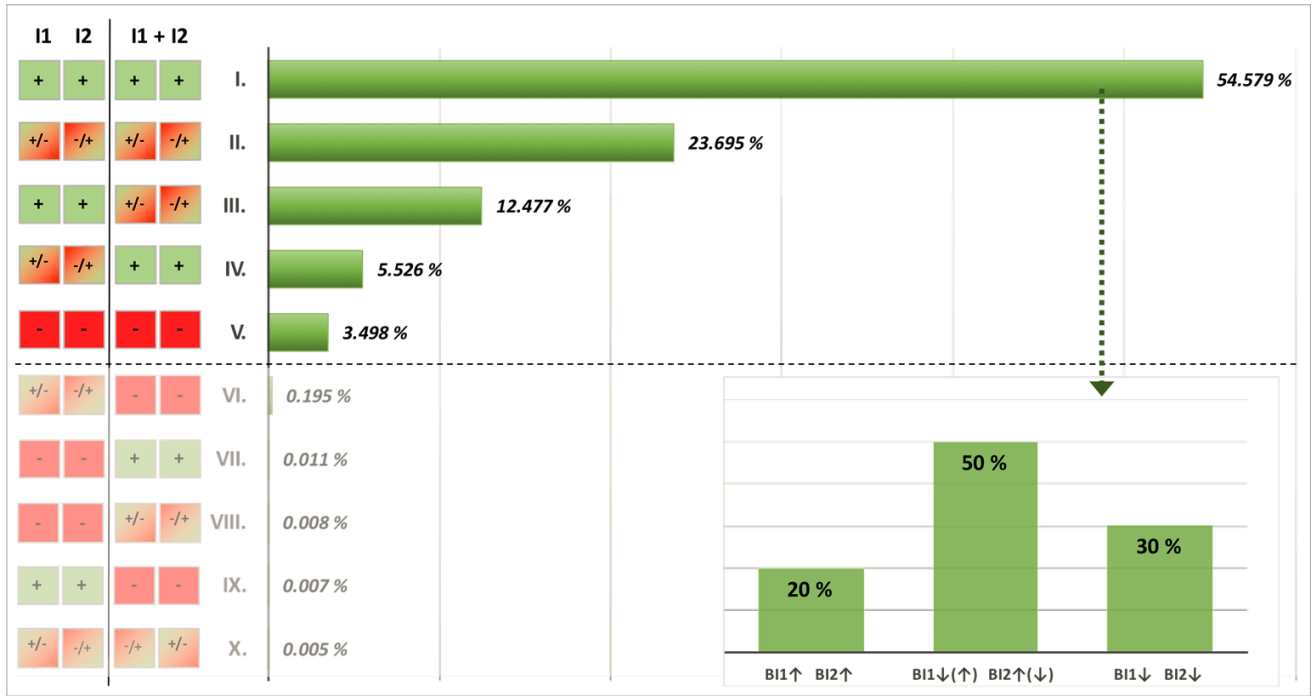
$$\frac{dB_{i(consumer)}}{dt} = \sum_{\rho=res} x_i(M_i)y_iB_iF_{i\rho} - \sum_{c=cons} \frac{x_c(M_c)y_c}{e_{ci}} B_cF_{ci} - x_i(M_i)B_i$$

Costant body-mass ratio (BMR): $Z = 10^2$



Brose et al., 2006, Ecol. Lett. 9, 1228-1236

Results


I1
I2
I1 + I2
I.
54.579 %
II.
23.695 %
III.
12.477 %
IV.
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V.
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VII.
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VIII.
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IX.
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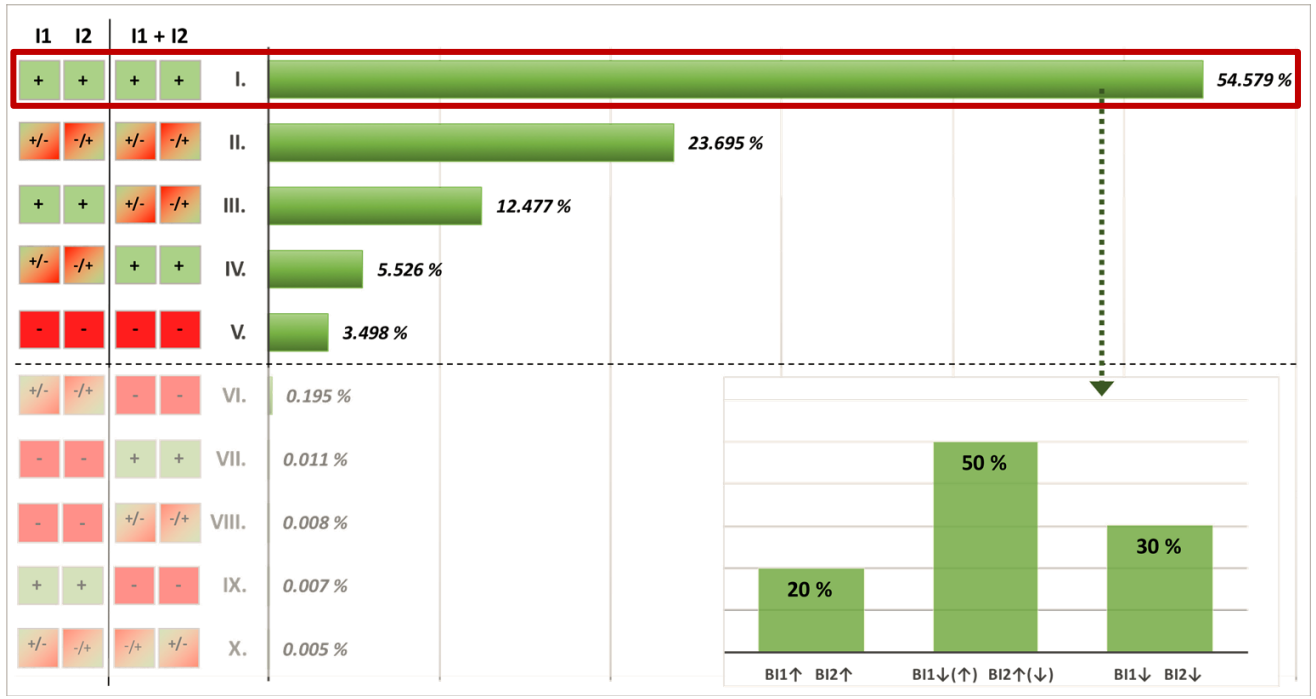
BI1↓(↑) BI2↑(↓)
BI1↓ BI2↓

Results


I1
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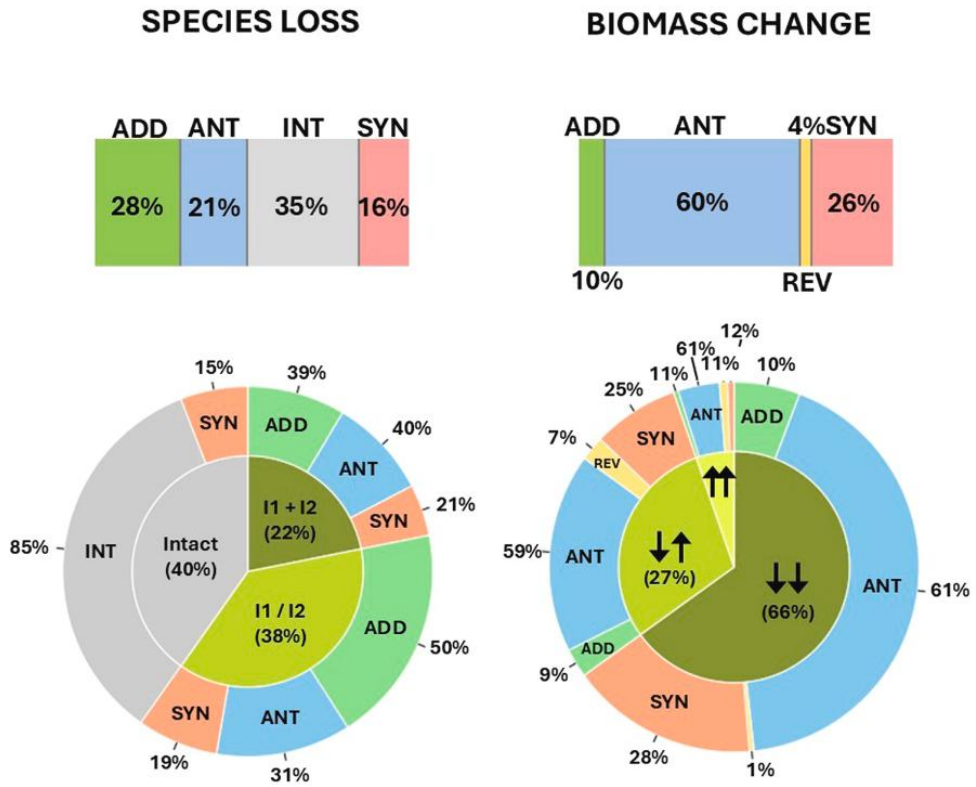
BI1↑ BI2↑
BI1↓(↑) BI2↑(↓)
BI1↓ BI2↓


SPECIES LOSS
ADD
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28%
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85%
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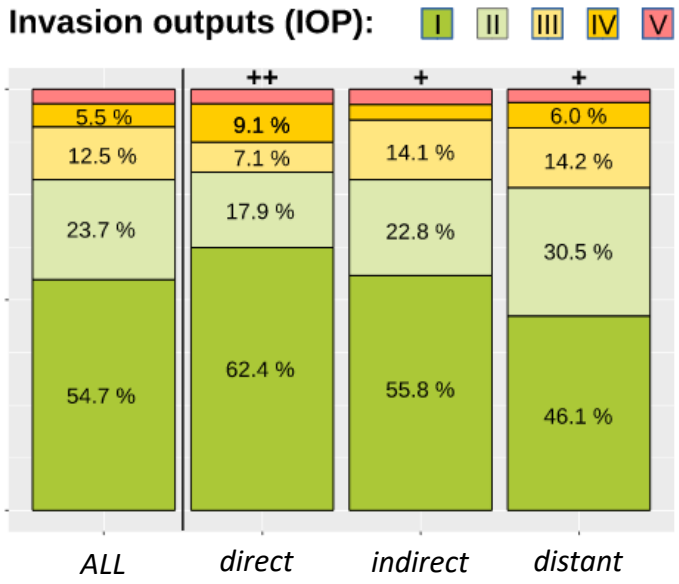
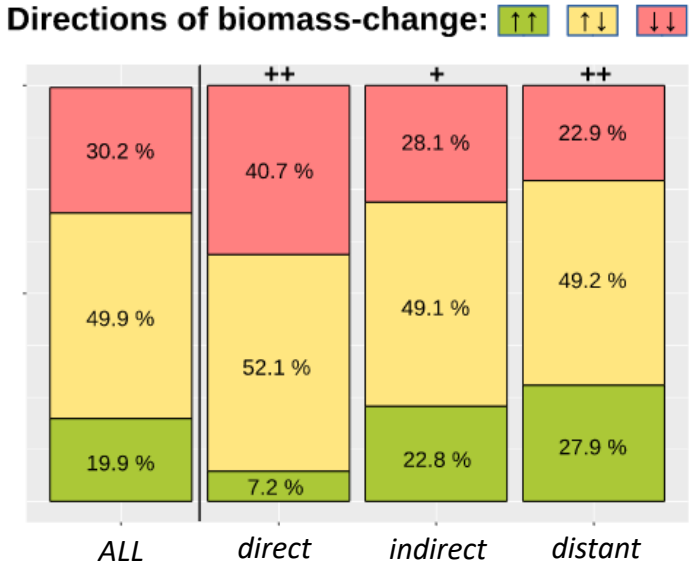
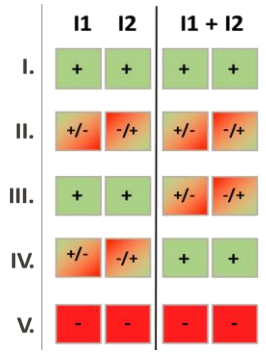




Results – effects of direct/indirect interactions

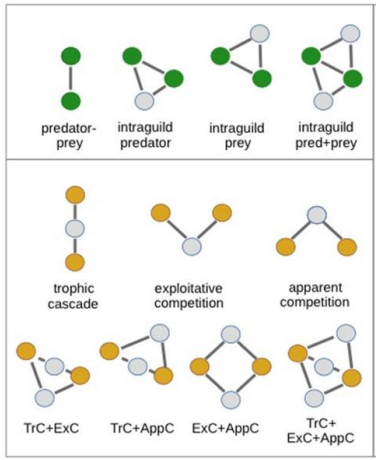
- **Effect sizes over p-values:** large sample → significance everywhere → effect sizes are more informative.
- **Interaction types shift outcome frequencies:** overall effects modest, but clear and consistent trends.
- **Direct trophic link** (one invader eats the other):
  - Higher probability that *both* invaders succeed (alone and together).
  - Higher probability that a normally failing invader persists when the other is present.
  - Decreasing biomass when invading together (cost of direct interaction).

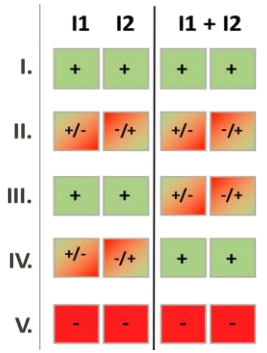


Results – effects of direct/indirect interactions

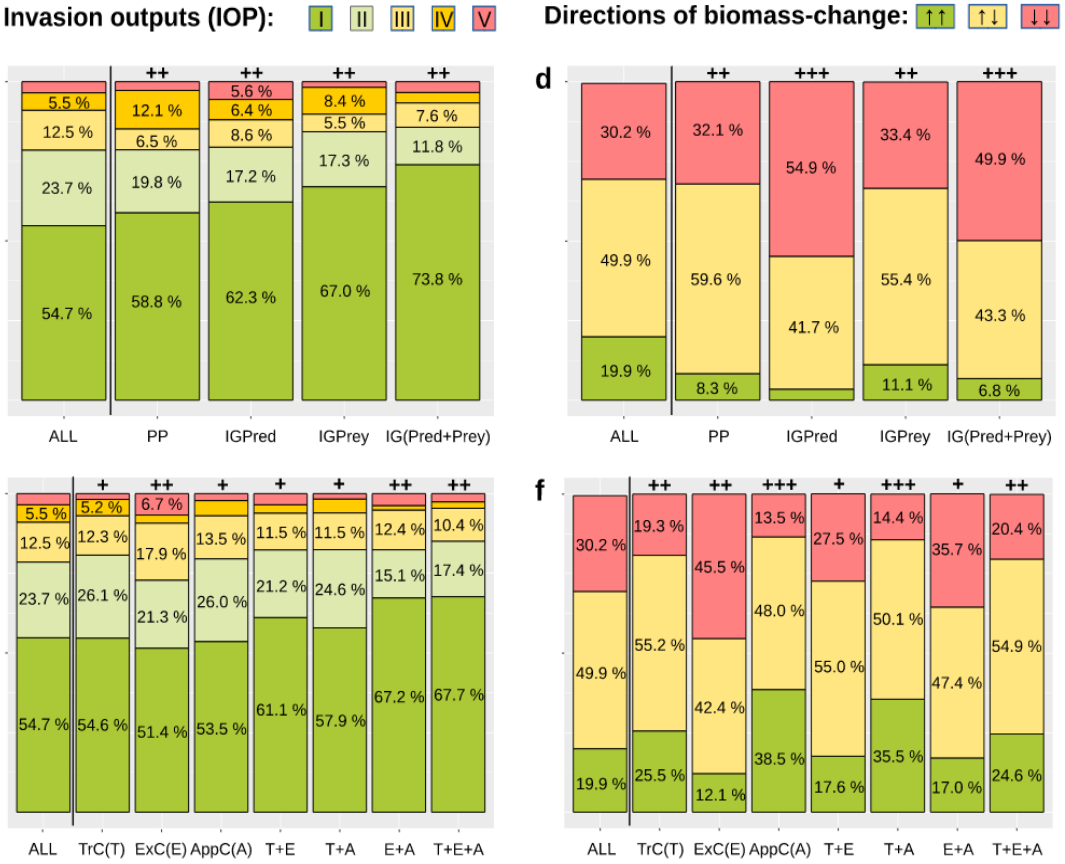
Direct interactions

- increasing joint success of both invaders (even stronger with shared prey/predator/both).
- **IGPred:**
  - ↑ probability that *both* individually unsuccessful invaders also fail together.
  - ↓ biomass for both invaders when co-occurring (negative effect not offset by shared prey).



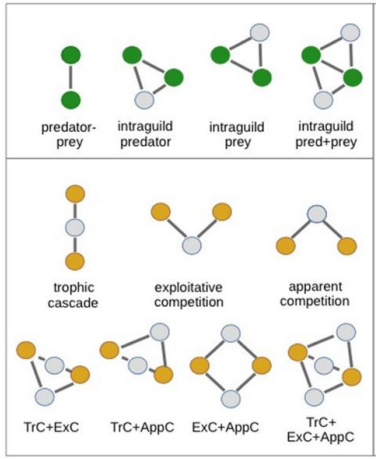


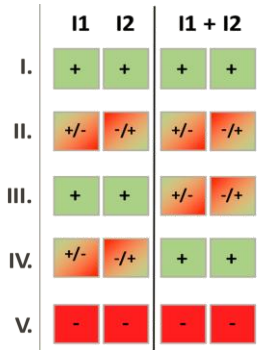
Results – effects of direct/indirect interactions

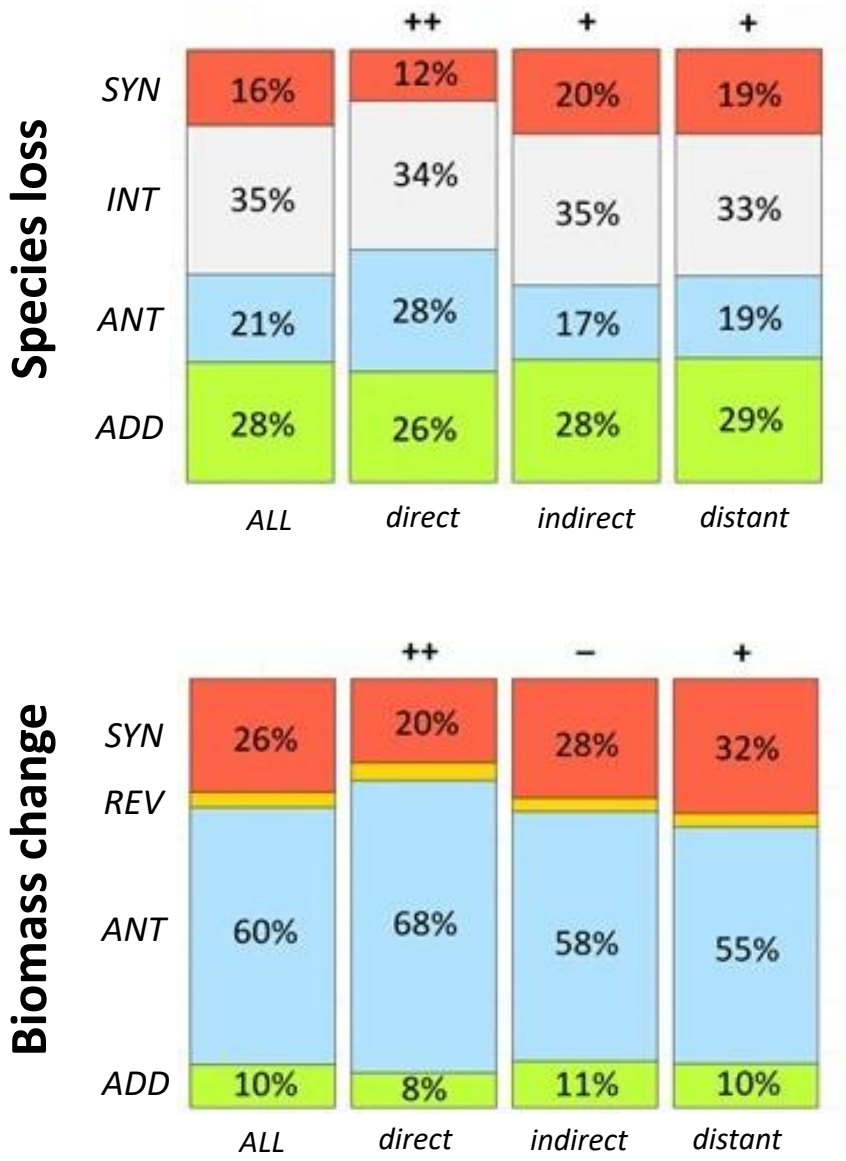


Indirect interactions

- **ExC**:
  - ↑ "both unsuccessful"
  - ↑ asymmetric exclusion among individually successful invaders
  - ↓ biomass for both
- **AppC**:
  - counteracts negative biomass effects
  - ↑ probability of biomass increase for both invaders





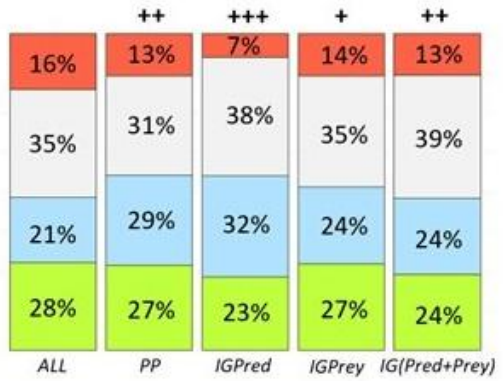


Results – effects of direct/indirect interactions

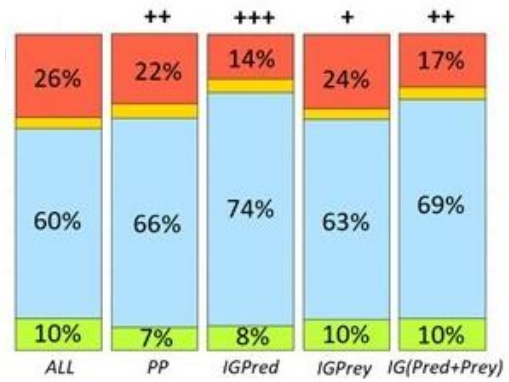
- **Overall impact is small:** interaction type explains little variation in diversity loss or net community biomass change.
- **Direct predator–prey link:**
  - ↑ likelihood of **antagonistic** combined effects;
  - ↓ probability of synergistic outcomes.
- **Greater trophic distance:**
  - ↑ likelihood of **synergistic**, mutually reinforcing effects on community biomass.

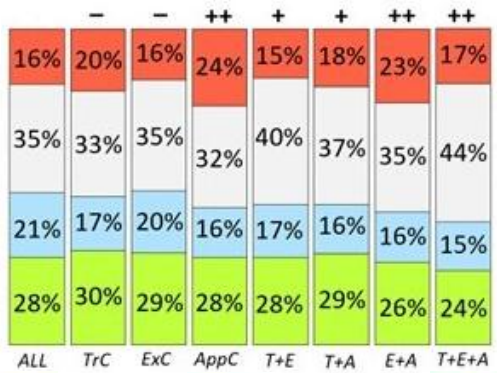
Results – effects of direct/indirect interactions

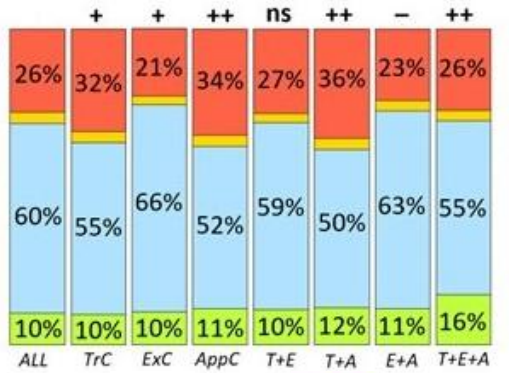
Species loss



Biomass change







additive antagonistic synergistic intact reversed

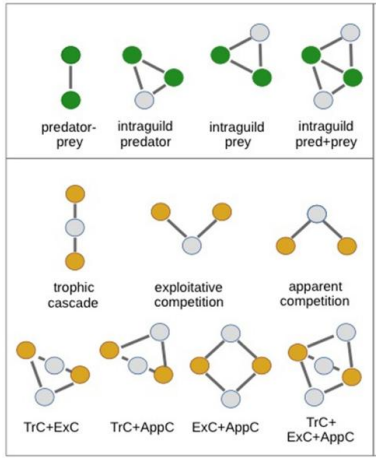
Predator–prey interactions

- **antagonistic effects** strengthened further when paired with **shared-prey competition (IGPred)**

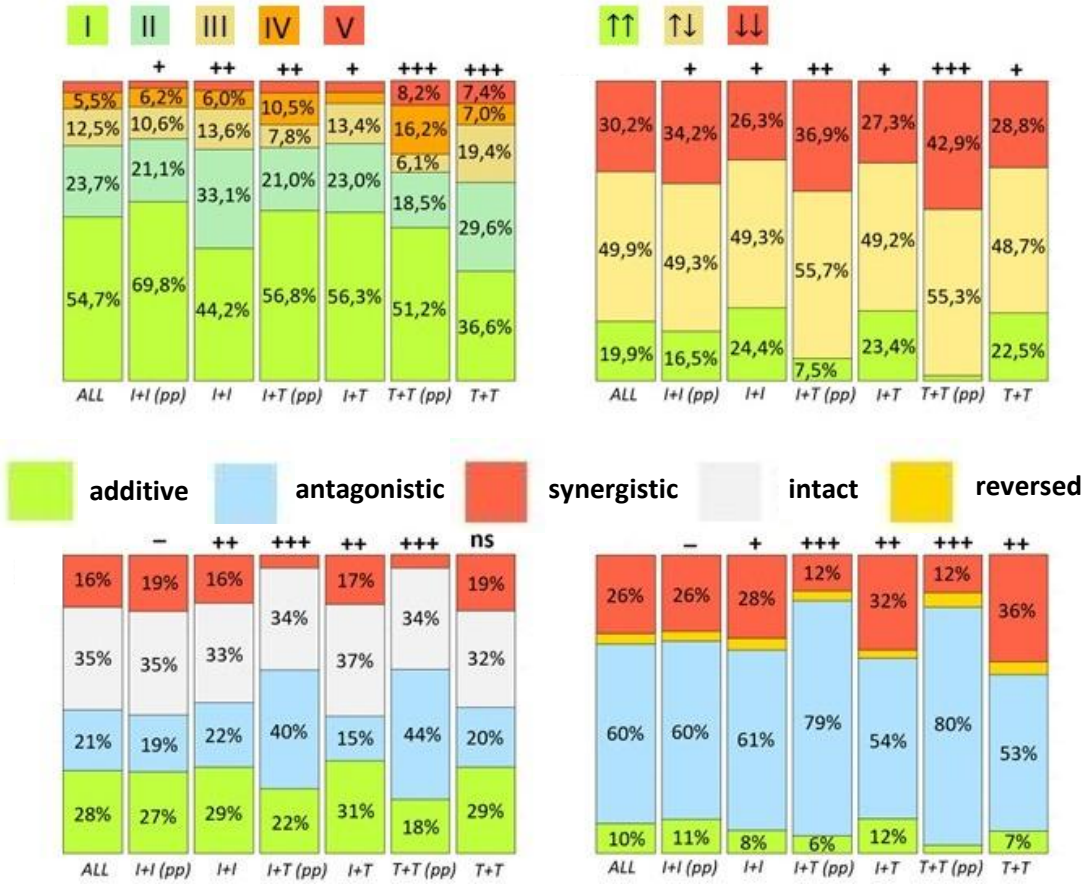
Indirect interactions:

- **Apparent competition** increases the likelihood of **synergistic** community effects
- **Trophic cascades** show a similar synergistic tendency (especially for biomass change)

Reversed case: very rare; not systematically affected by any interaction type.



Results – effects of top/intermedier position

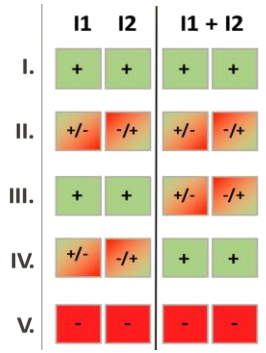


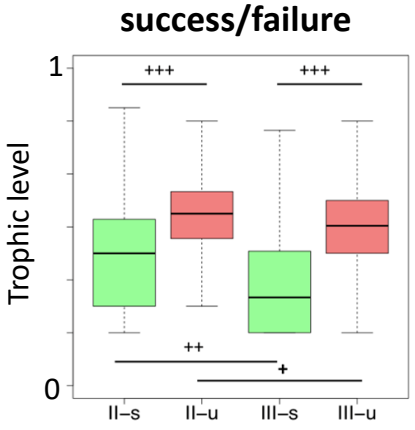
Invasion outcomes depend far more on the presence of a predator–prey link than on being top or intermediate consumers.

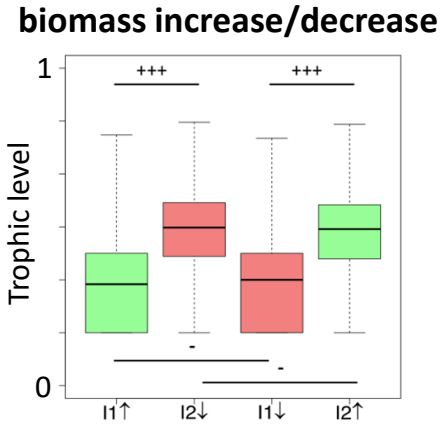
- PP relationship → higher chance that both invaders succeed
- Two top predators invading together → increasing chance that at least one fails.
- Biomass changes: predator–prey pairs typically reduce each other's biomass.

Combined community impact:

- Antagonistic effects more likely when a direct link exists, but only if one of them is a top predator.
- If both are intermediates, this difference largely disappears.

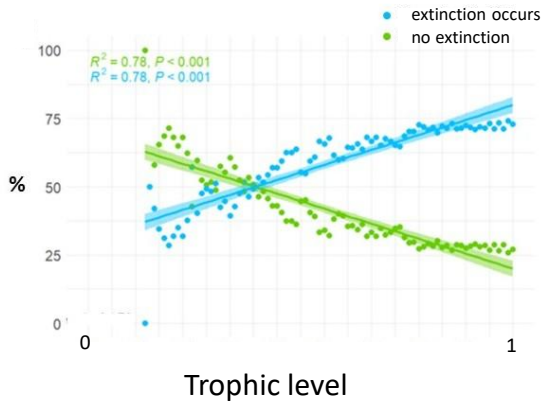


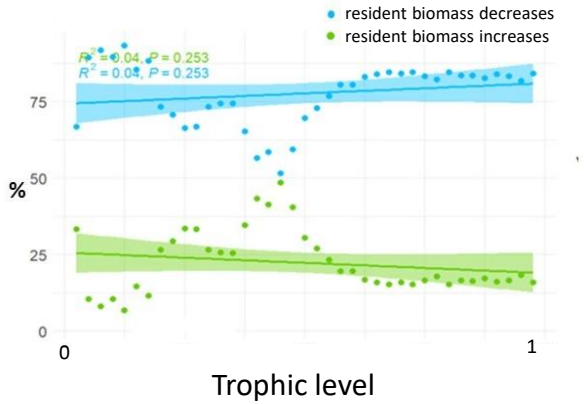




Results – effects of the trophic level

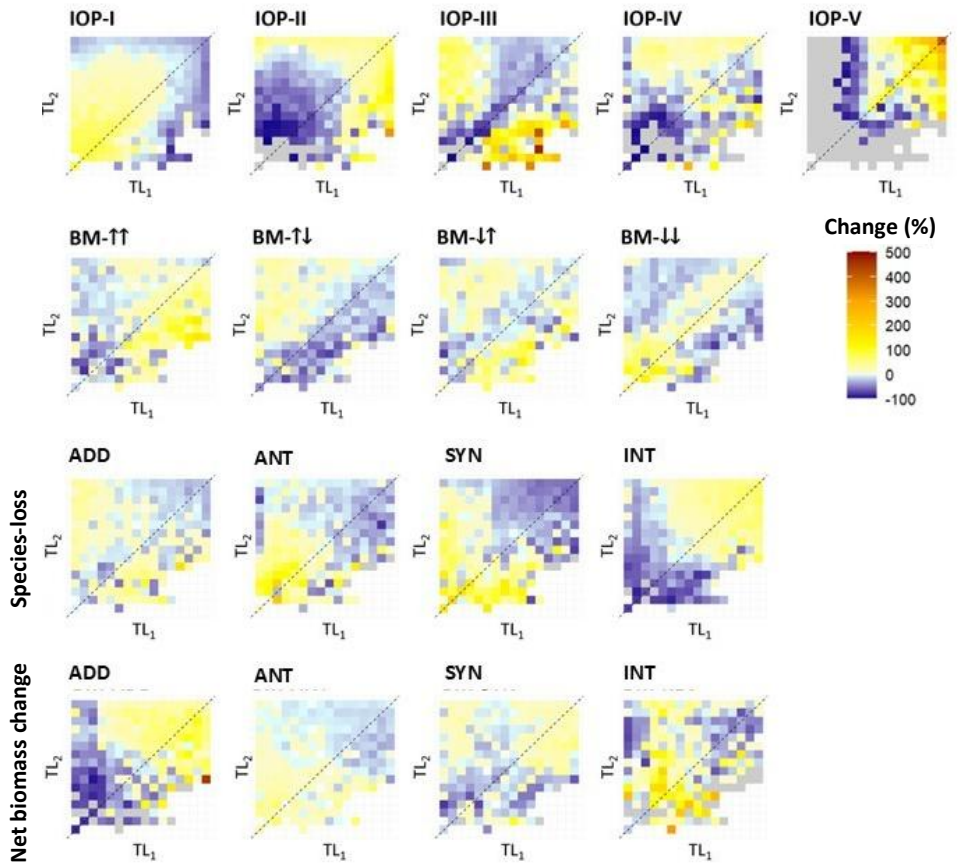
Invasion success declines with trophic level:
failed invaders typically enter at **higher trophic levels** than successful ones.





- **Community effects:**
  - Lower TL → higher chance that resident extinctions occur.
  - Net resident biomass usually decreases at low and high trophic levels,
    but may increase at intermediate trophic levels.

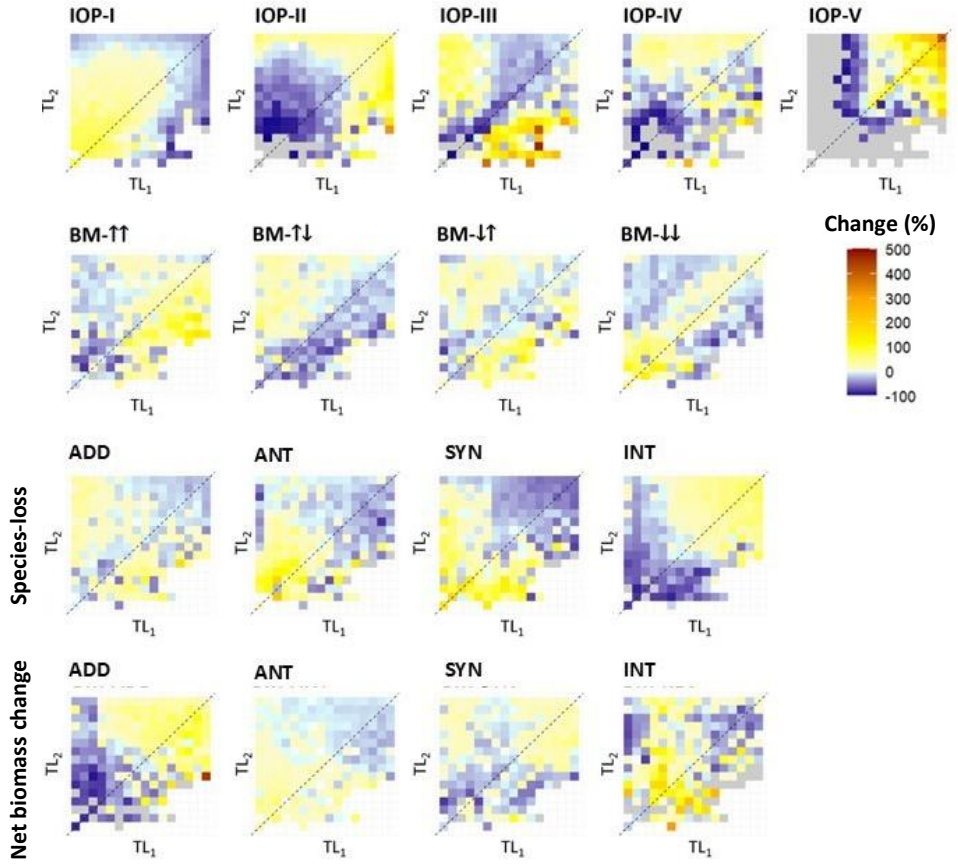
Results – effects of the trophic level



Invasion success and biomass patterns

- Lower trophic level → higher probability of successful establishment (alone or together).
- Increasing probability of unsuccessful invasion at high TL
- The TL-difference between invaders strongly shapes joint invasion outcomes.
- Biomass patterns are weaker: low-TL invaders tend to lose biomass, while high-TL invaders do so mainly when TLs are similar.

Results – effects of the trophic level



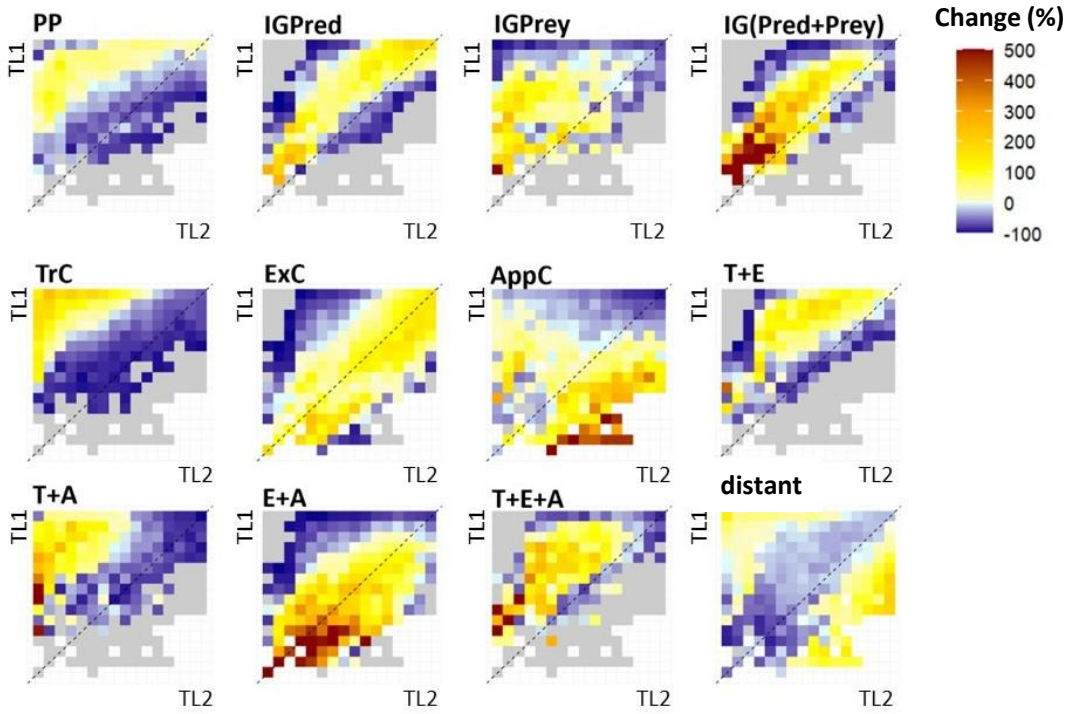
Species loss:

- Higher TL → resident food web is more likely to remain fully intact.
- Non-additive outcomes become more frequent at low trophic levels.
- Additive effects increase when the TL difference between invaders is large.

Resident biomass change:

- Higher-TL invaders more often produce additive effects, as the resident community is less affected.
- Synergistic effects also become more common at higher trophic levels.
- The rare reversed (antagonistic) effect appears mainly at intermediate trophic levels.

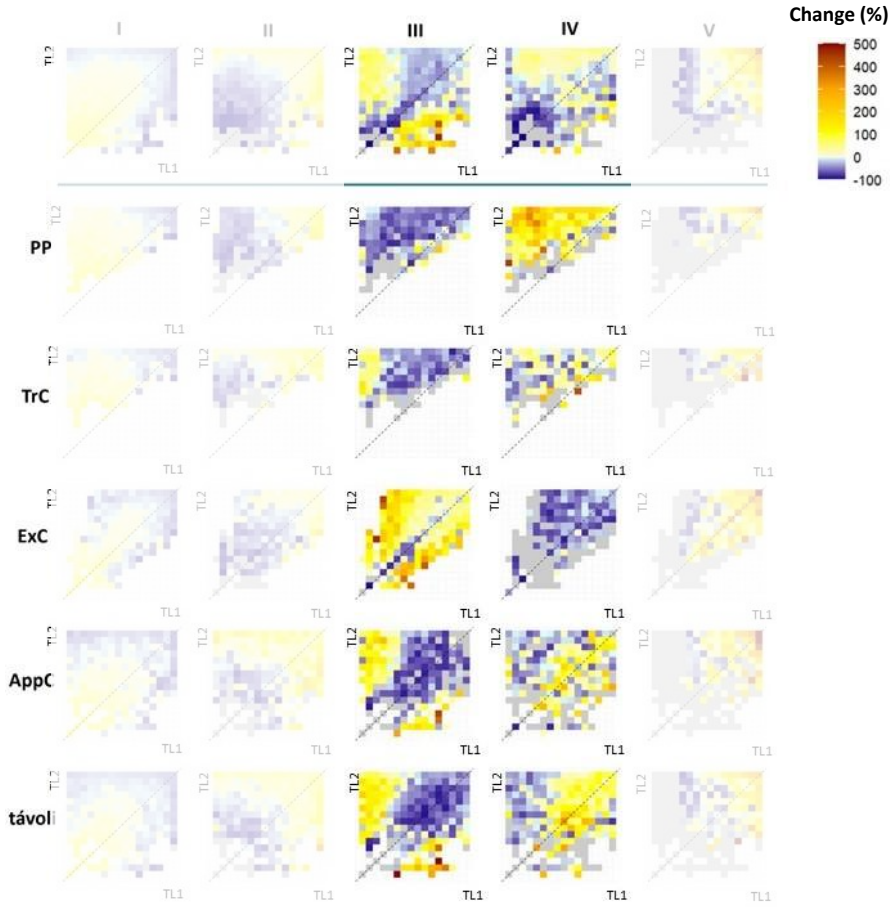
Trophic level AND connection-type



- Trophic level and interaction type are not independent.
- The trophic levels at which the two invaders enter largely determine which direct or indirect interactions can arise.
- Some interaction types become highly probable at certain TL combinations, while others are rare or impossible.

Invasion outcomes are best understood by considering trophic level *together with* the potential interaction types.

Trophic level AND connection-type



Two focal outcome:

- *IOP-III:* both succeed alone, one fails together
- *IOP-IV:* one fails alone but succeeds when co-invading

When considering **trophic level only**:

- both outcomes become more frequent when invaders enter at more different TLs

When including **interaction type**:

- **PP** strongly increases the chance that an otherwise unsuccessful invader persists together (IOP-IV)
- **ExC** increases the chance of IOP-III

Interaction type can be as important as, or more important than trophic level in determining these outcomes.

Summary

- **Most common outcome:** both invaders succeed (alone and together); the model produces a highly stable community with generally weak invader–invader effects.
- **Impact metric matters:** species richness often remains unchanged, while **biomass almost always shifts**.
- **Consistent with meta-analyses:** additive and antagonistic effects are the most frequent outcomes across empirical studies as well.
- **Low predictability:** multiple interacting factors limit predictive power, explaining why case studies often report contrasting patterns.

Á. Móréh et al.: **Effects of joint invasion: How co-invaders affect each other's success in model food webs?**
Ecol. Mod, 492:110735 (2024)

Á. Móréh and I. Scheuring: **Invaders' trophic position and their direct and indirect relationship influence on resident food webs**
Ecol. Mod, 508:111238 (2025)

Summary

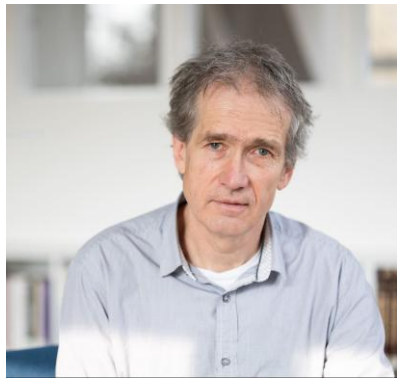
Strenghts and limitations of using ABM:

- highly stable food webs that make it suitable for comparative analyses
- allometric relationships reduce the number of free parameters (fixed allometric constants)
- best for aquatic (marine) food webs, where body size reliably predicts interactions.
- terrestrial ecosystems: body-size interaction relationship is much weaker
- omits important ecological factors, such as behavioural variation and seasonal dynamics

Other limitations:

- additional species traits and community-level properties can also play important roles
- communities may respond to invasions in multiple ways, focusing on a single trait is insufficient

The effects of multiple simultaneous invasions depend on *how invaders interact with each other **and** with the resident community*.



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Ferenc Jordán

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Thank you for your attention!