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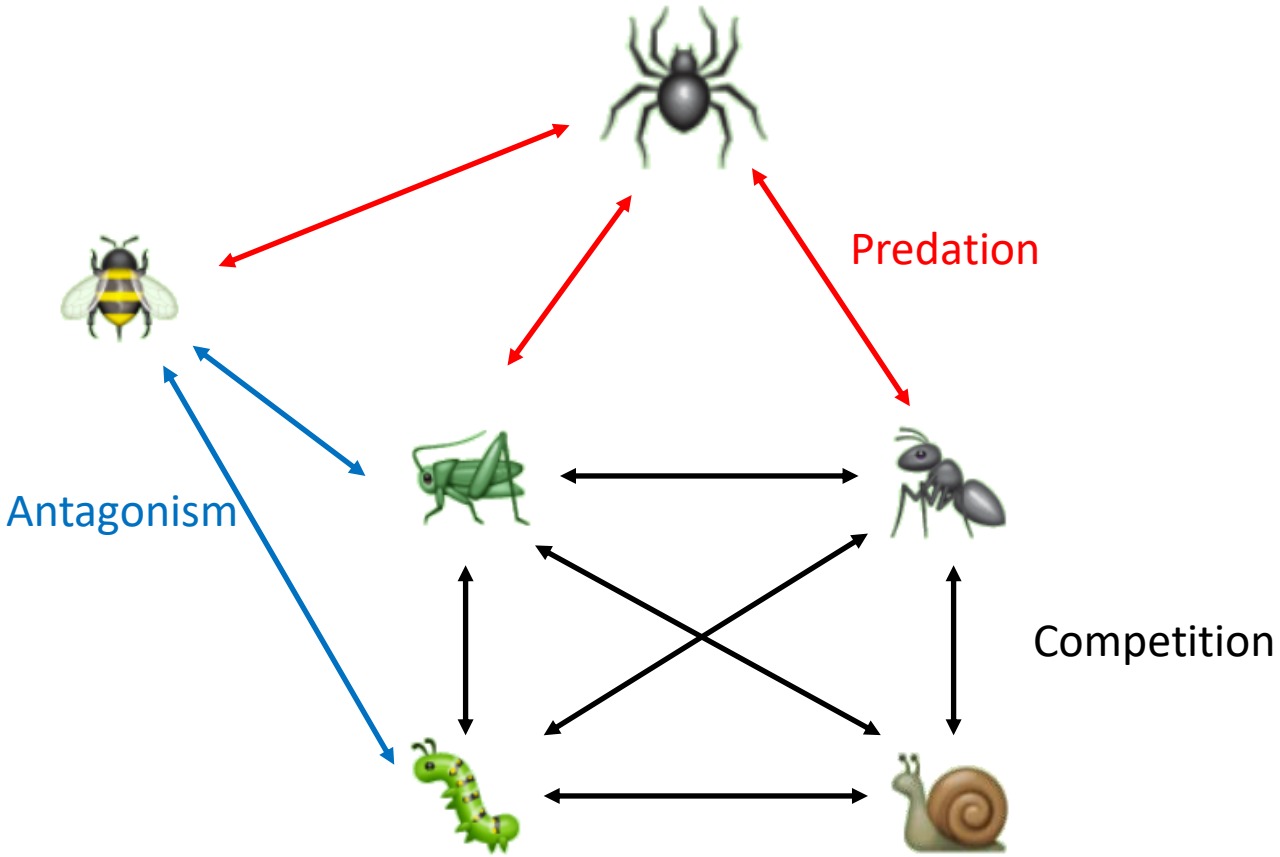
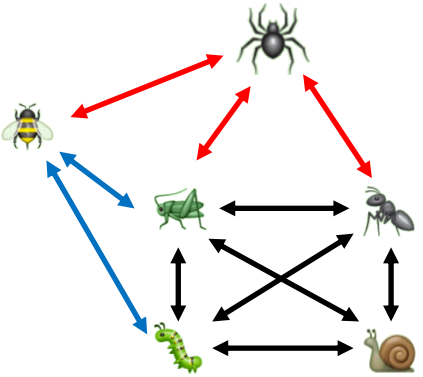
Modern Non-Coexistence theory

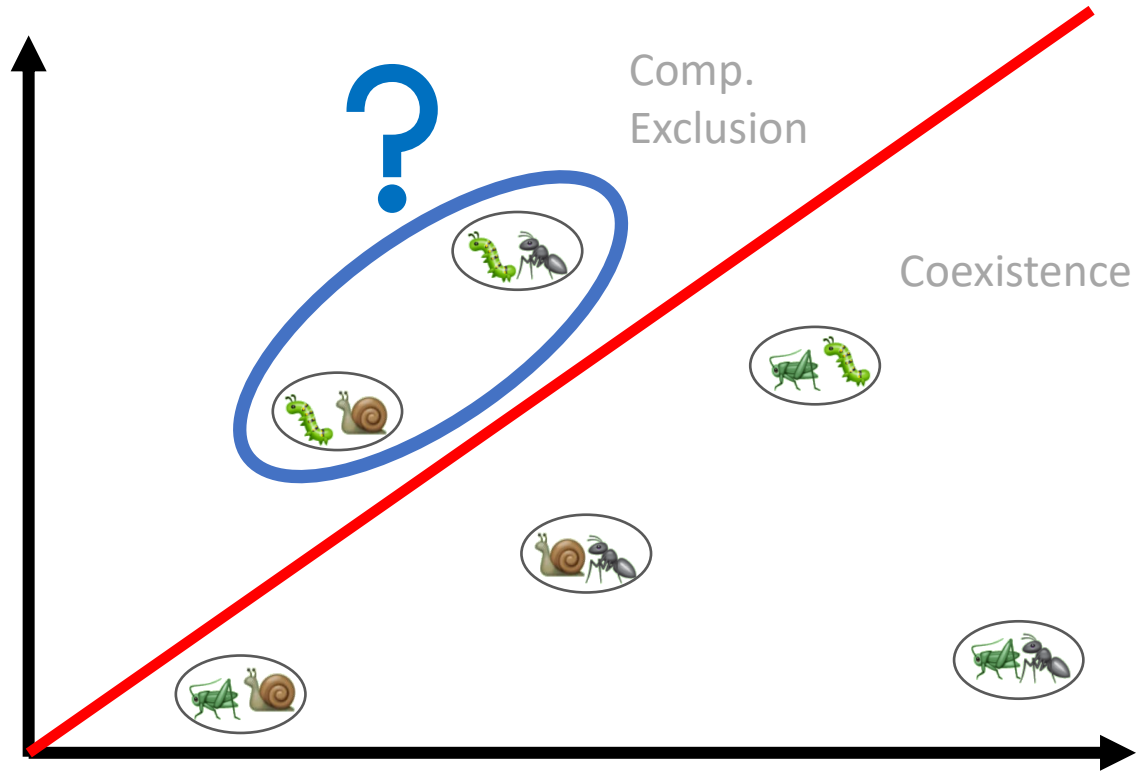
Jürg W. Spaak and Sebastian Schreiber

MCT attempts to explain observed biodiversity...



...but often focuses solely on pairwise interactions





Of 29 paper experimentally measuring niche and fitness differences we found

- 28 focus on pair-wise niche and fitness differences
  - Only 1 on multispecies niche and fitness differences
- 25 focus on primary producers (plants and phytoplankton)
- Only 4 focus on other organisms (yeasts 1, bacteria 3)

Buche et al. 2022, Journal of Ecology, data included up to Dec. 2020

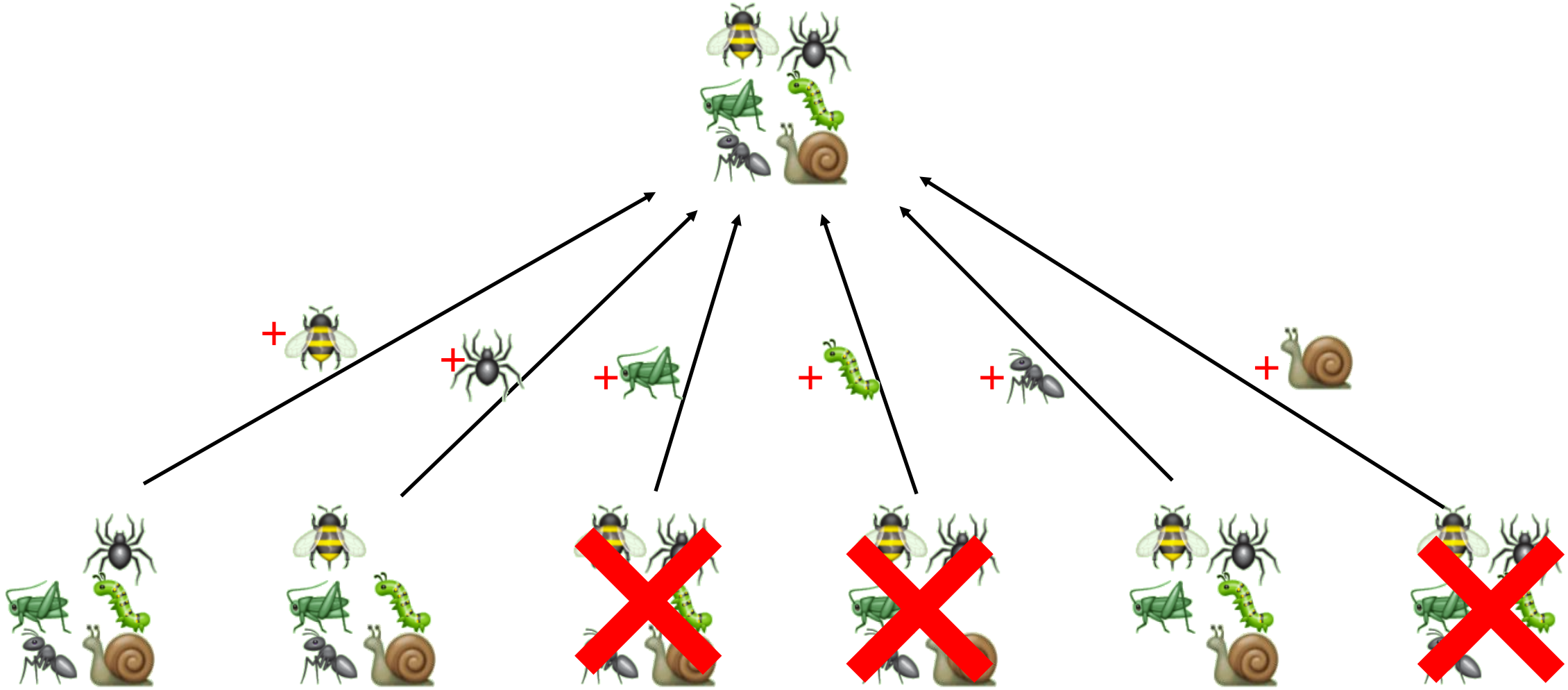
Historically, two issues hindered applications to species rich communities

- 1a Niche and fitness differences defined pair-wise
  - $\rho = \sqrt{\frac{a_{ij}a_{ji}}{a_{ii}a_{jj}}}, \frac{\kappa_i}{\kappa_j} = \frac{\mu_i}{\mu_j}\sqrt{\frac{a_{jj}a_{ji}}{a_{ii}a_{ij}}}$

  Solved (Spaak et al. 2021, Carroll et al. 2011)
- 1b Storage effect etc. Are pair-wise comparisons of resident

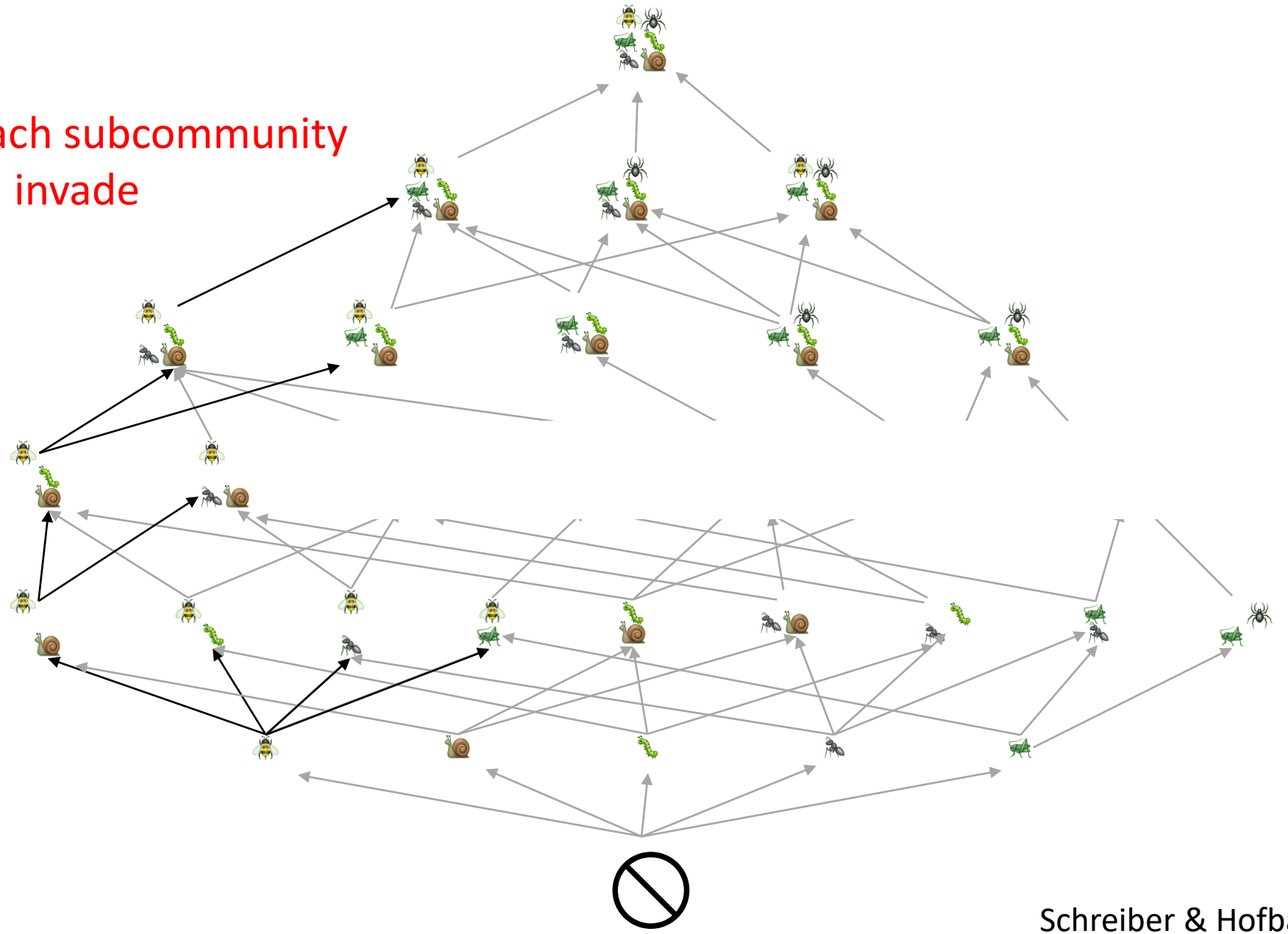
  Solved (Ellner et al. 2019)
- 2. Invasion growth rates...
  - Are sometimes undefined in species rich communities (Spaak et al. 2021)
  - Do not match with coexistence (Barabas et al. 2018)

Naïve invasion approach



Permanence theory

Species coexist, if for each subcommunity at least one species can invade



Schreiber & Hofbauer 2022

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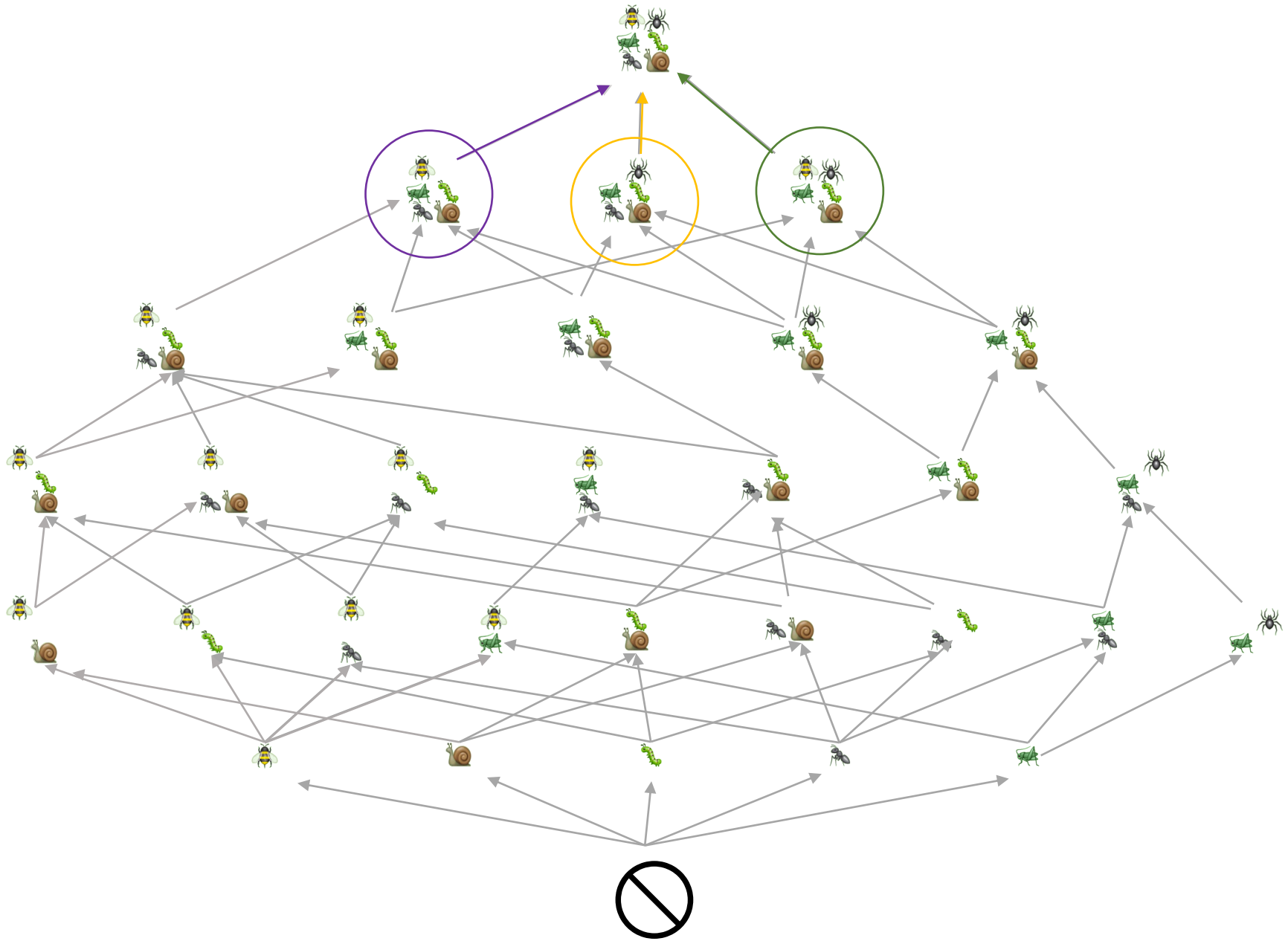
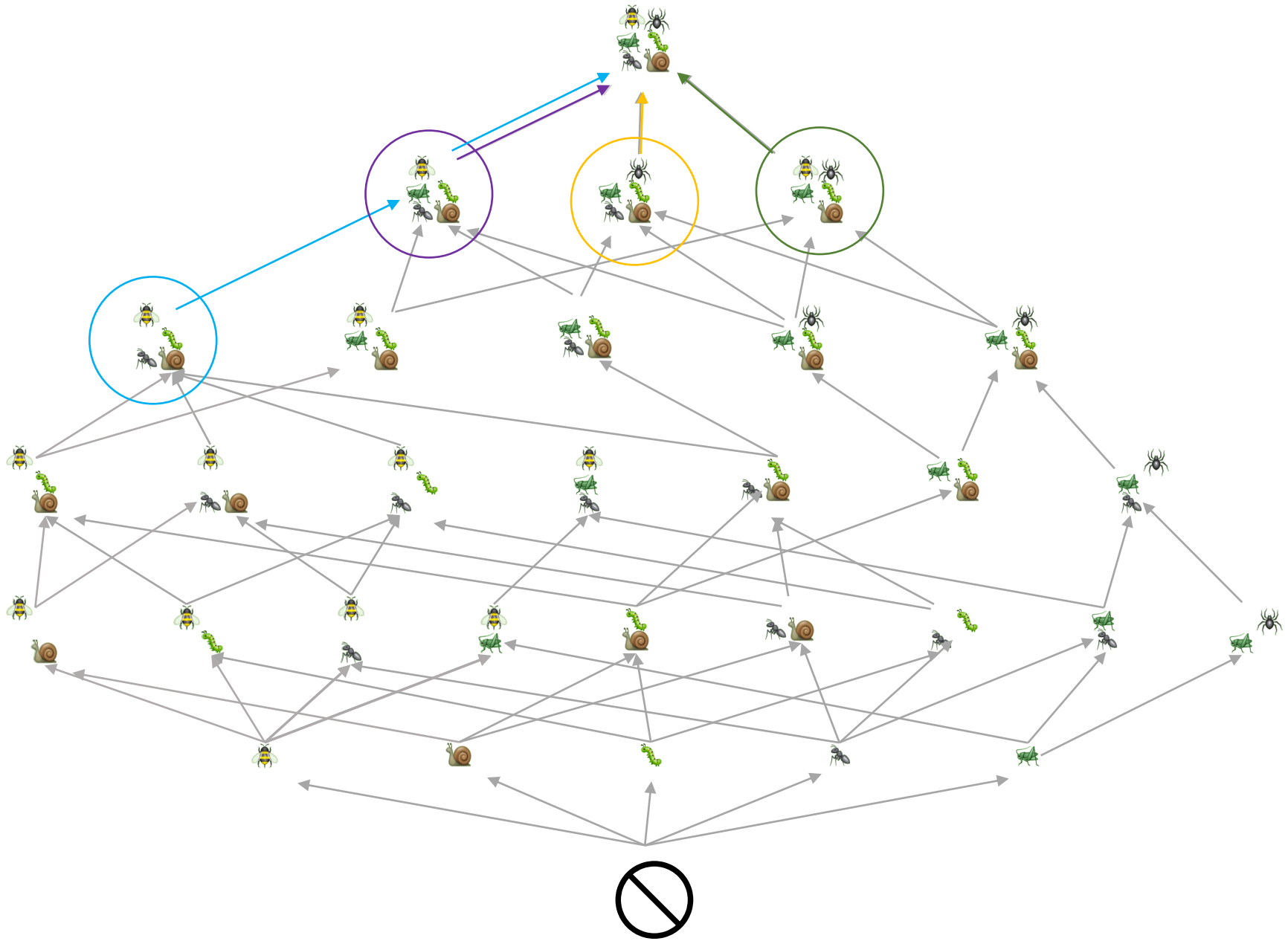
  Solved (Schreiber & Hofbauer 2022)

Which invasion growth rates are most important?

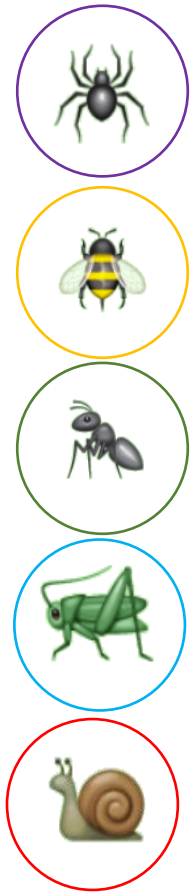
Permanence theory

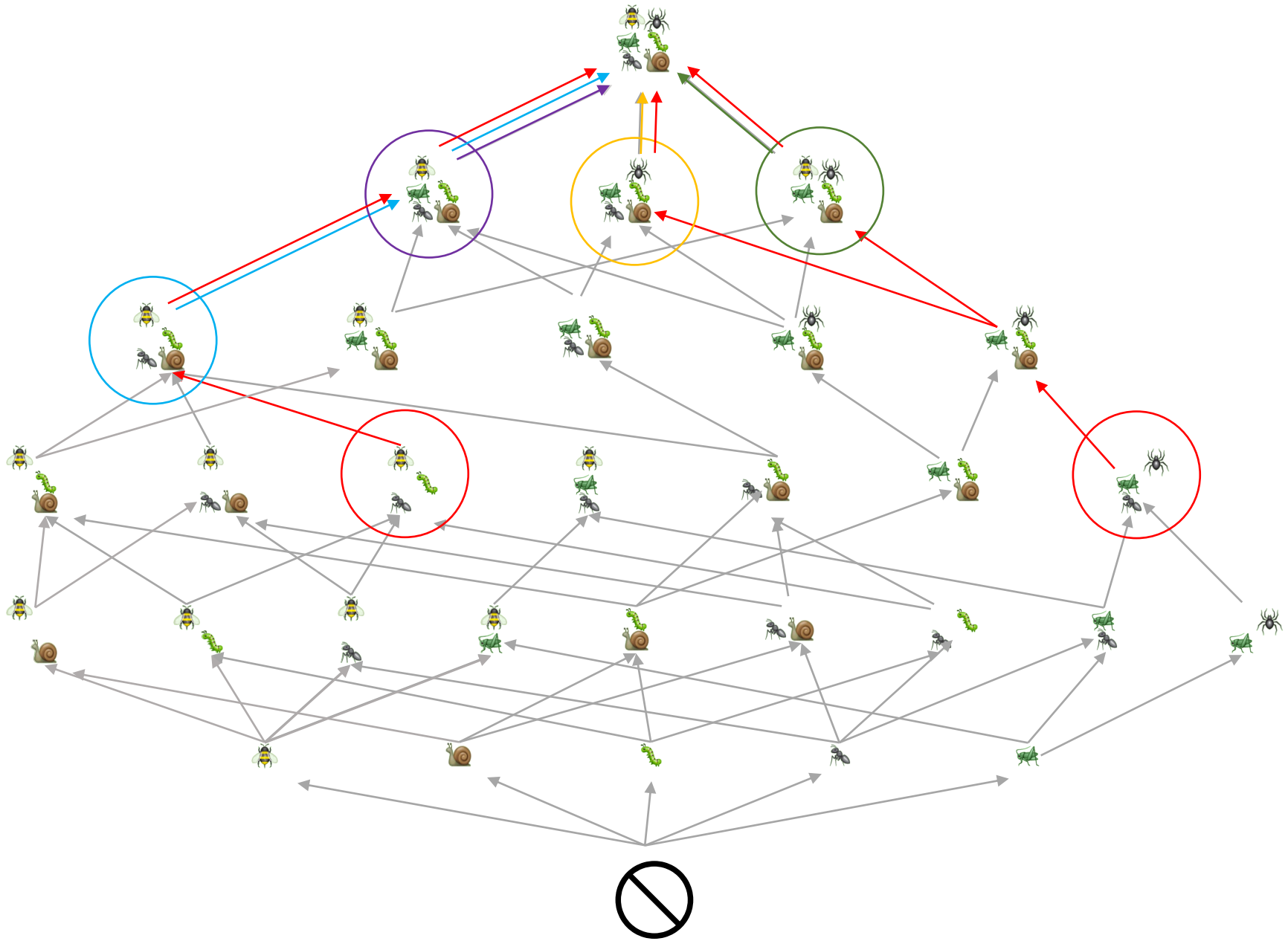


Permanence theory

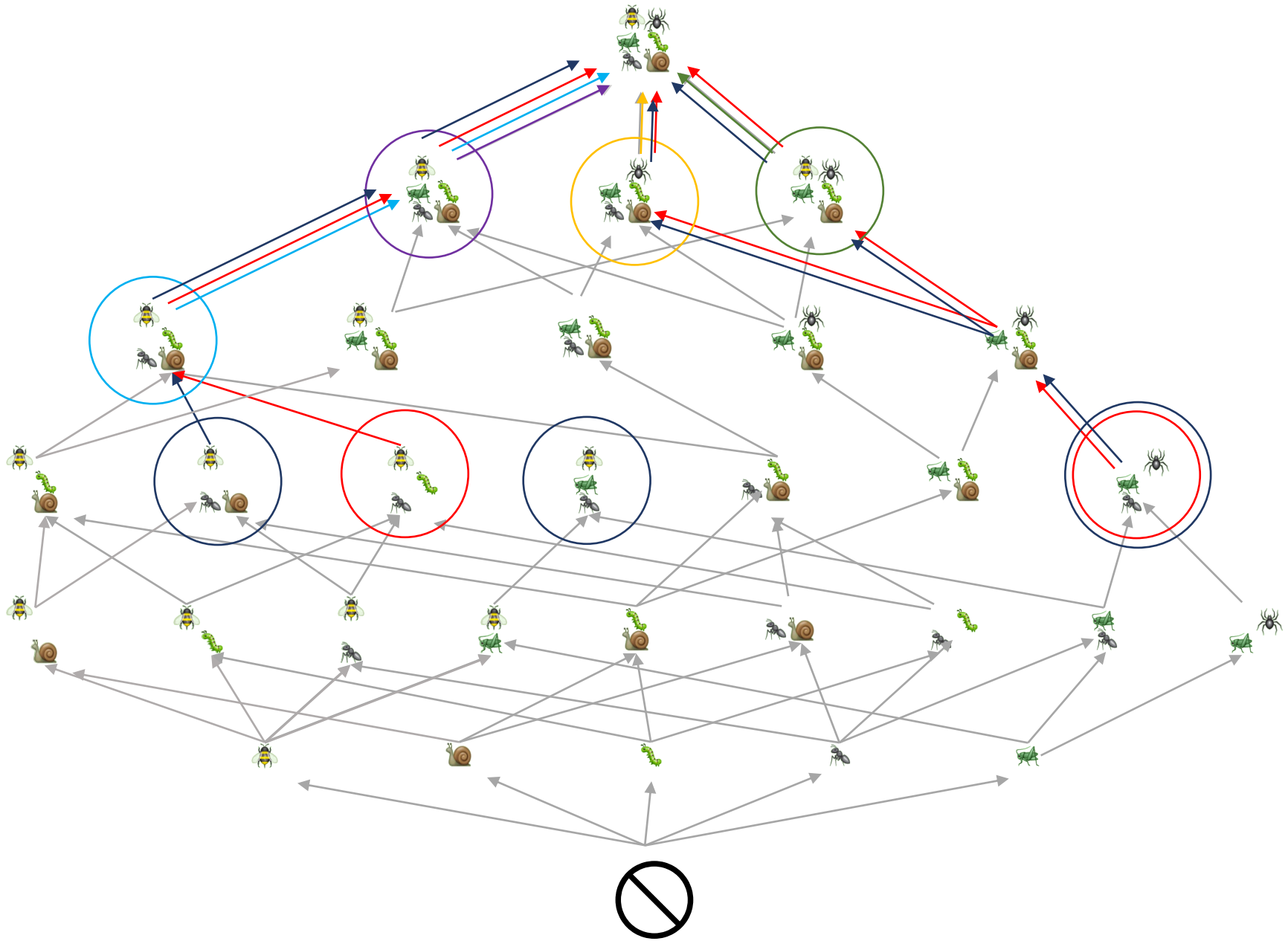


Permanence theory





Permanence theory



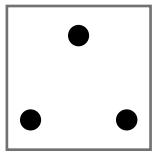
MCT should focus on
the last invasion step!

Naive
Invasion growth
Rate approach

	Sp1	Sp2	Sp3
	0	0	0.5
	0	0.5	0
	0.5	0	0

Apply modern
coexistence theory
metrics

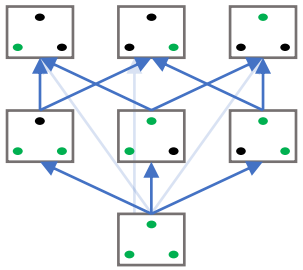
Community
of interest



Invasion
scheme

	Sp1	Sp2	Sp3
	1	1	1
	0	0.8	0.8
	0.8	0	0.8
	0.8	0.8	0
	0	0	0.5
	0	0.5	0
	0.5	0	0

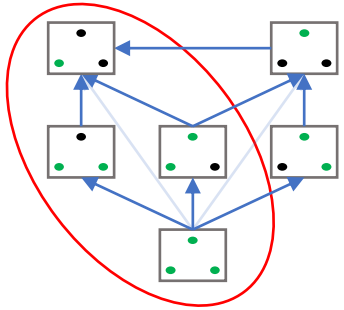
Invasion
graph



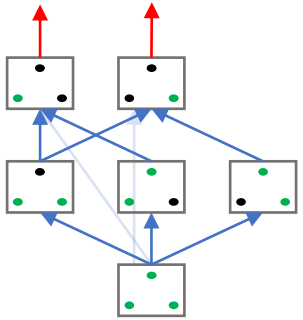
Cycles

Hofbauer
Criterion?

Select Maximal
Subcommunity



Select relevant
invasion growth rates

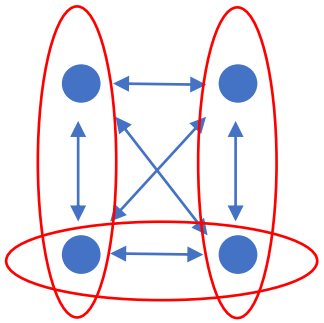


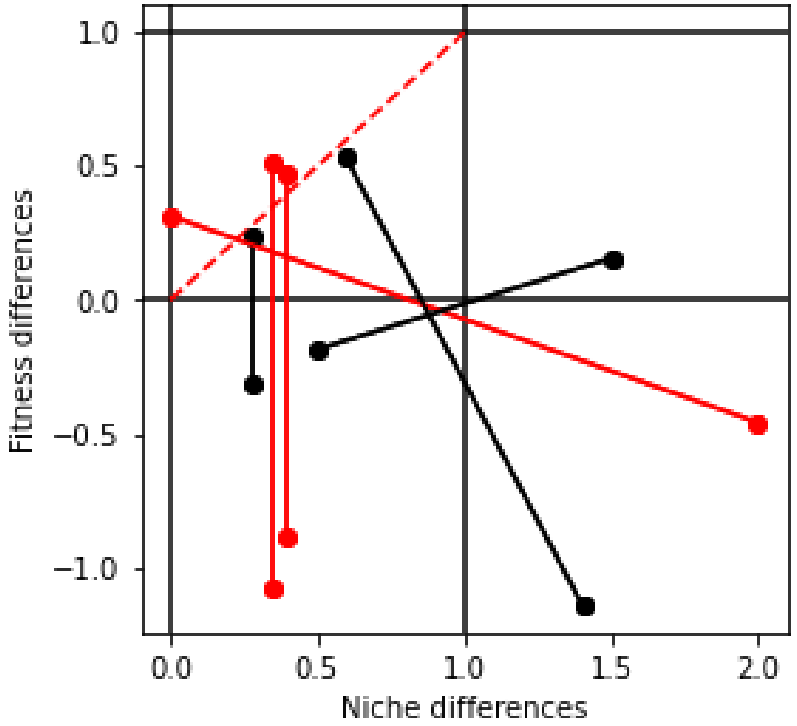
But then, what has changed???

- Nothing for two-species communities (which is good news)
- Nothing for multispecies communities where all invasion growth rates exist (which is good news)
- We can now apply MCT to more complicated communities, including trophic networks, obligatory mutualists and other
  - Two examples from Spaak et al 2021

We can analyse the entire community, instead of sub-communities

An empirical community with 4 species,
all interacting




1.0
0.5
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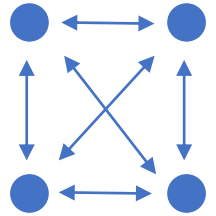
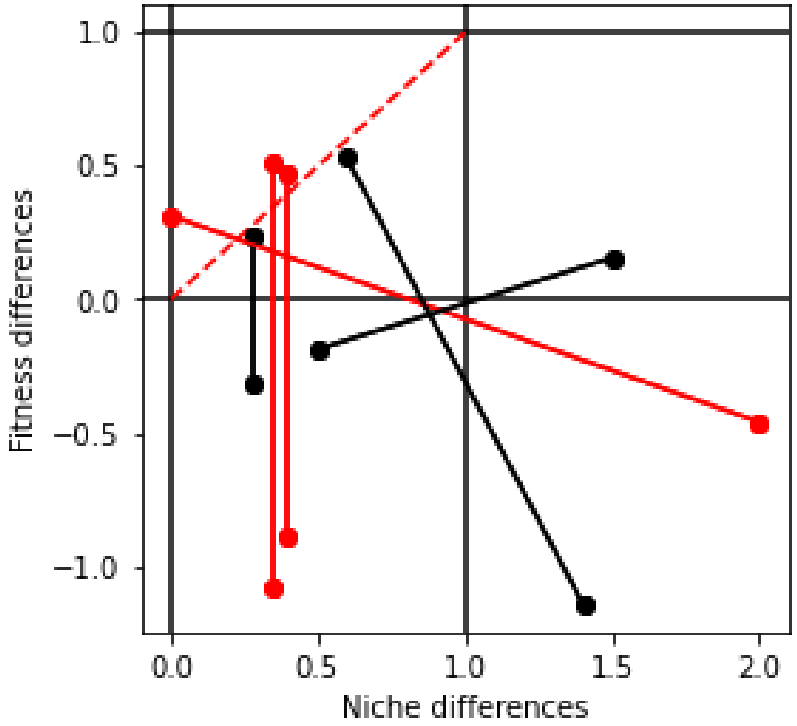
−0.5
−1.0
Fitness differences
0.0
0.5
1.0
1.5
2.0
Niche differences

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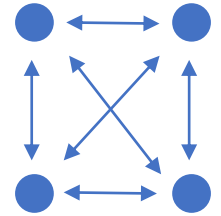
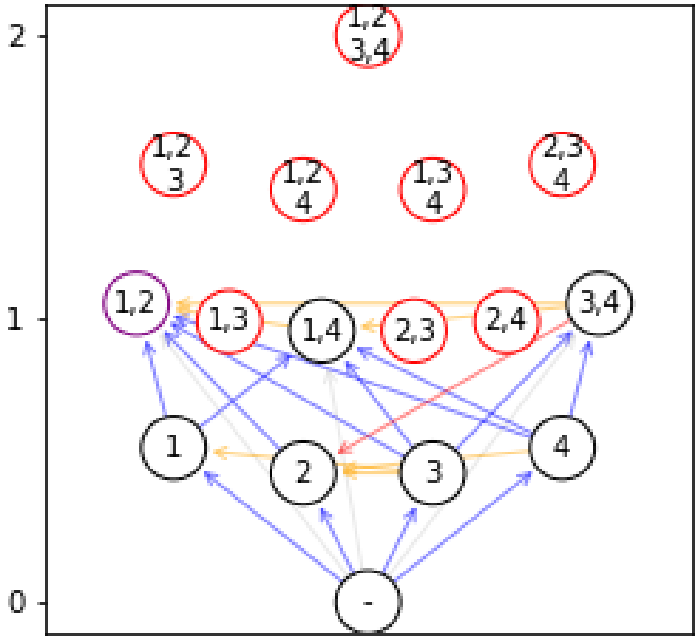
2.0
Niche differences

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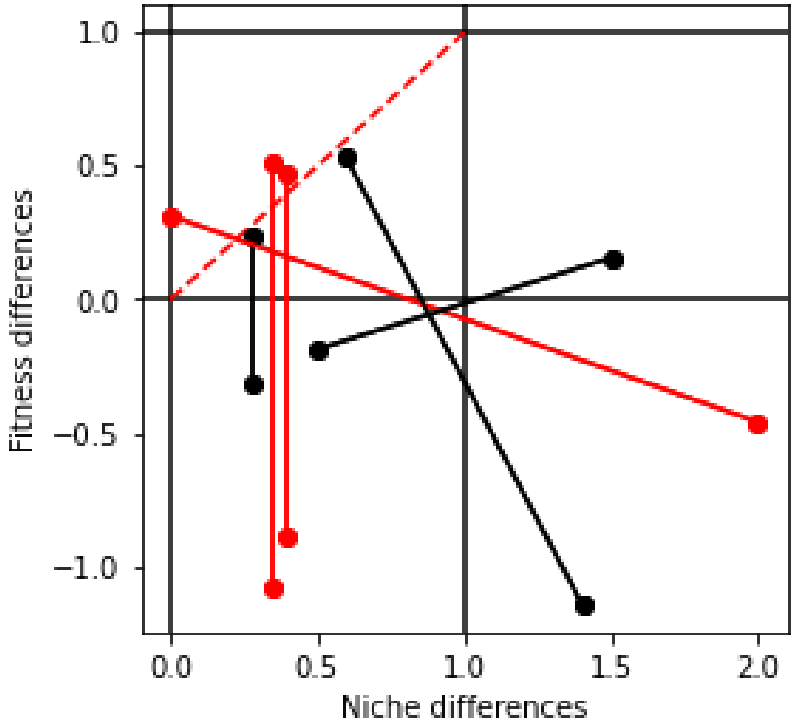
Fitness differences
Niche differences
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−0.5
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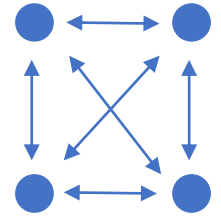

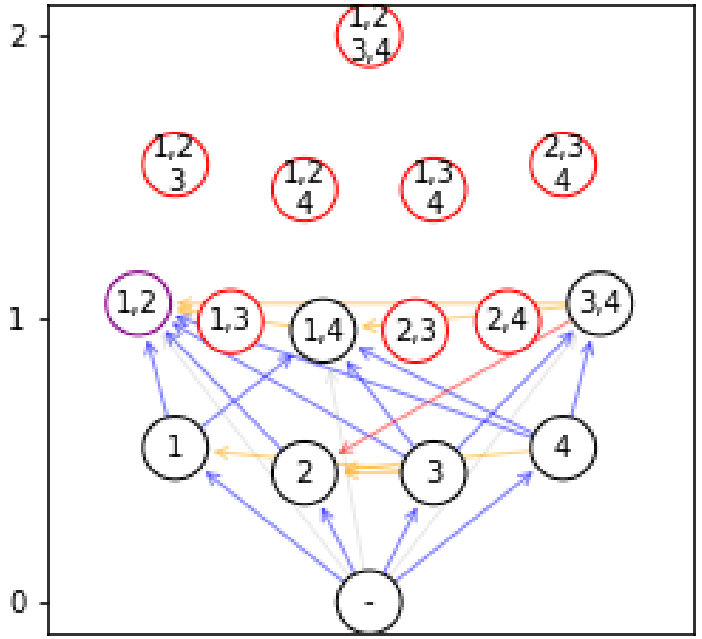
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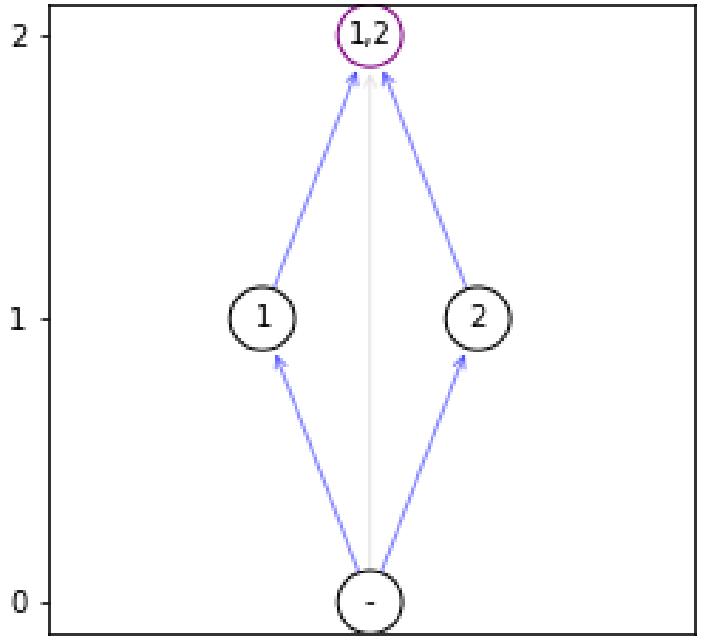
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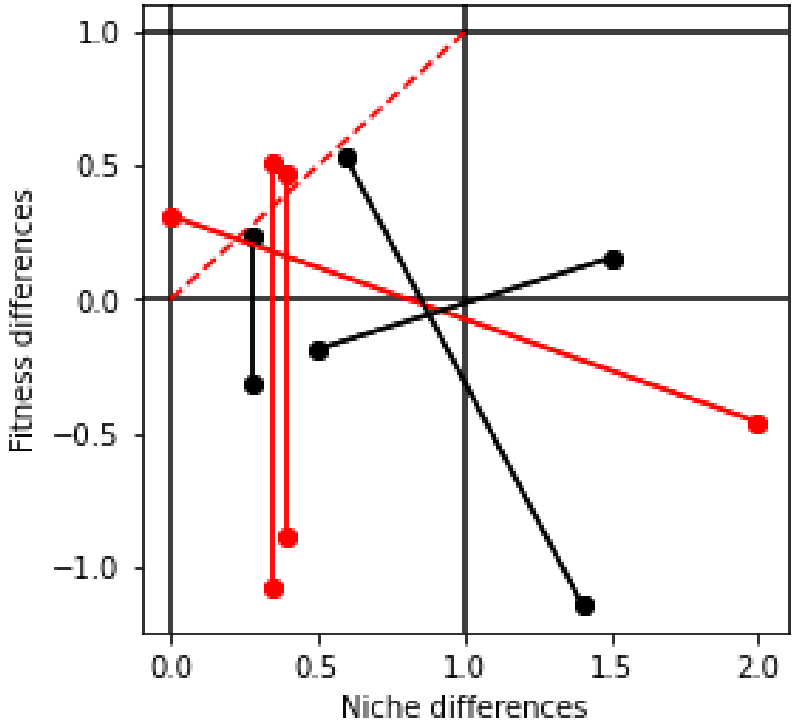
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Niche differences
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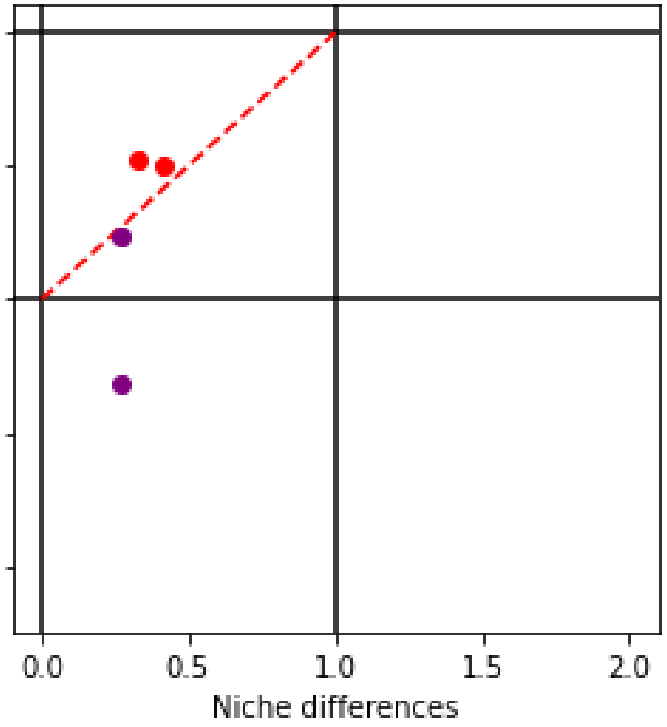
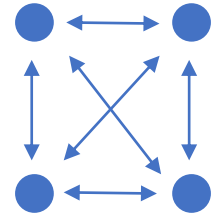
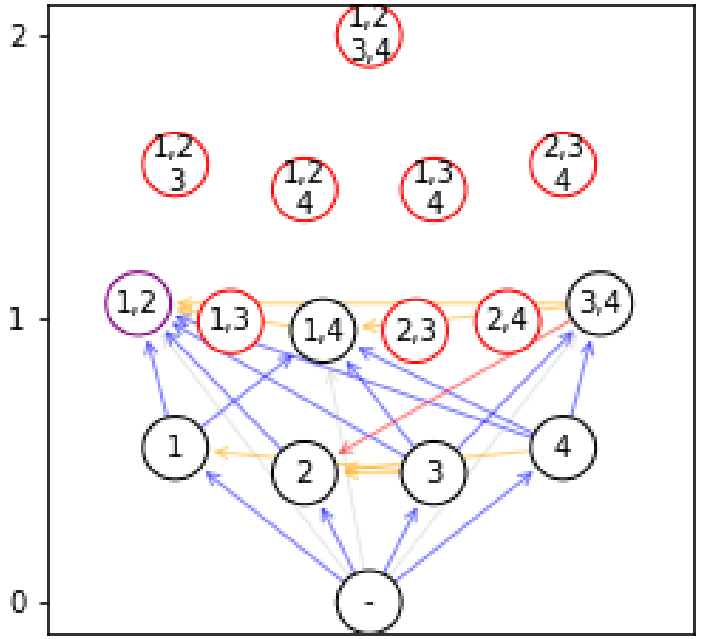
0.0
−0.5
−1.0
0.0
0.5
1.0
1.5
2.0


Niche differences
0.0
0.5
1.0
1.5
2.0

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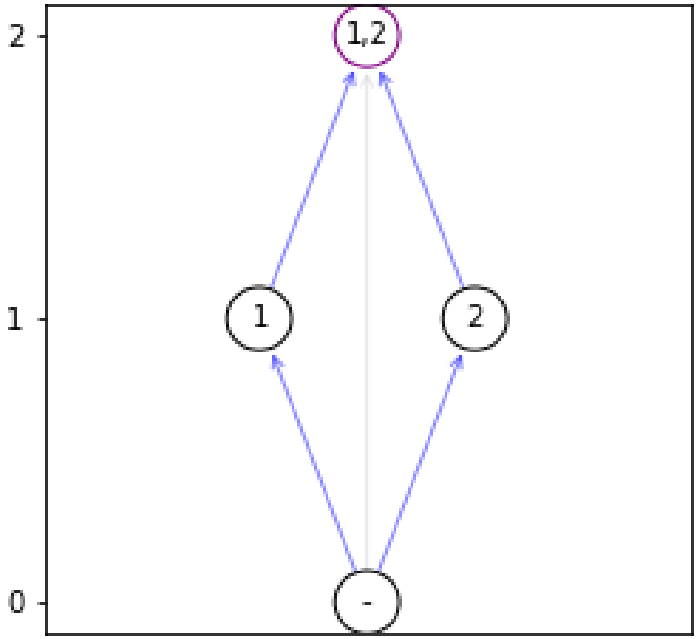
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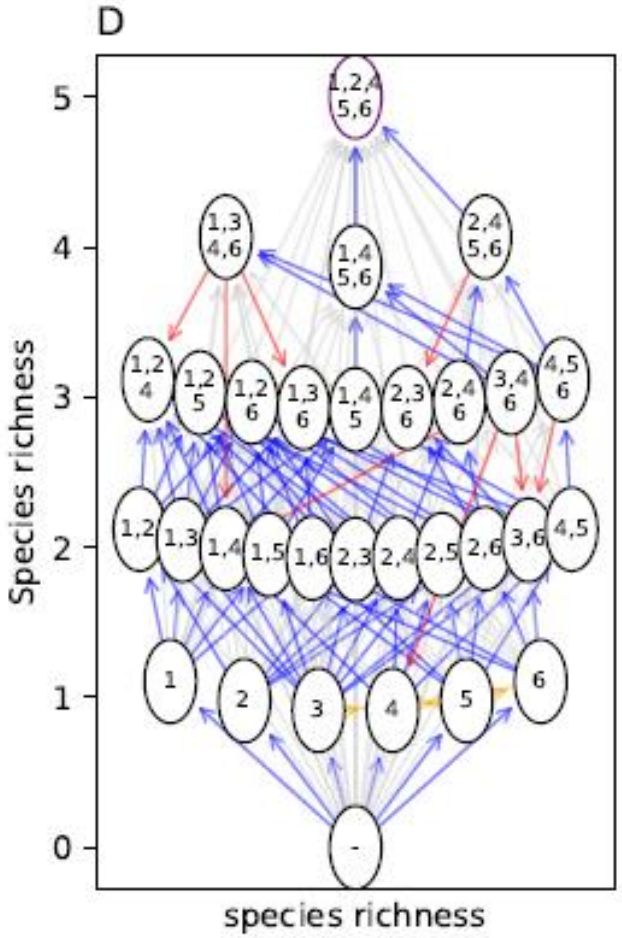
We can analyse new communities, previously outside the reach of MCT



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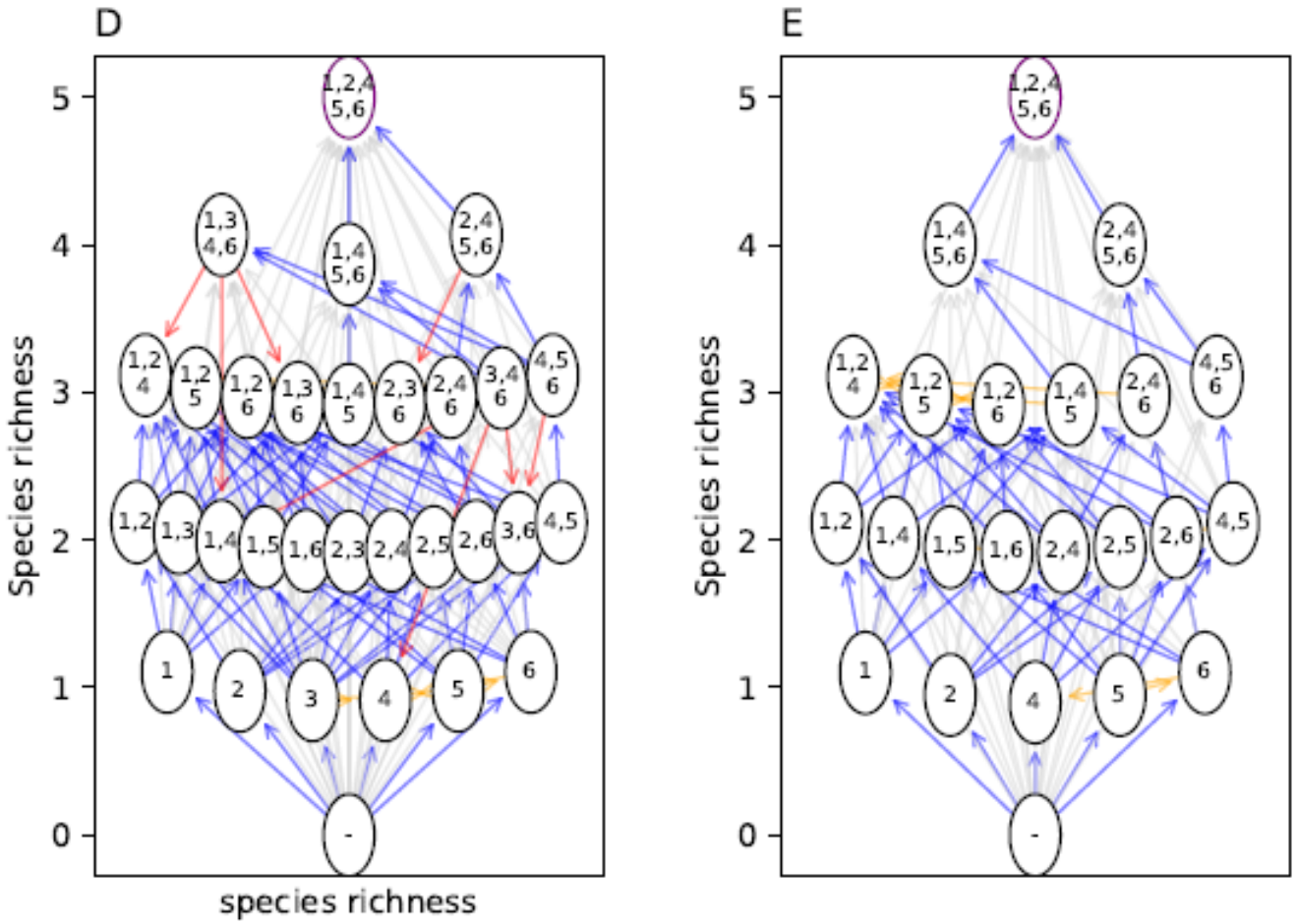

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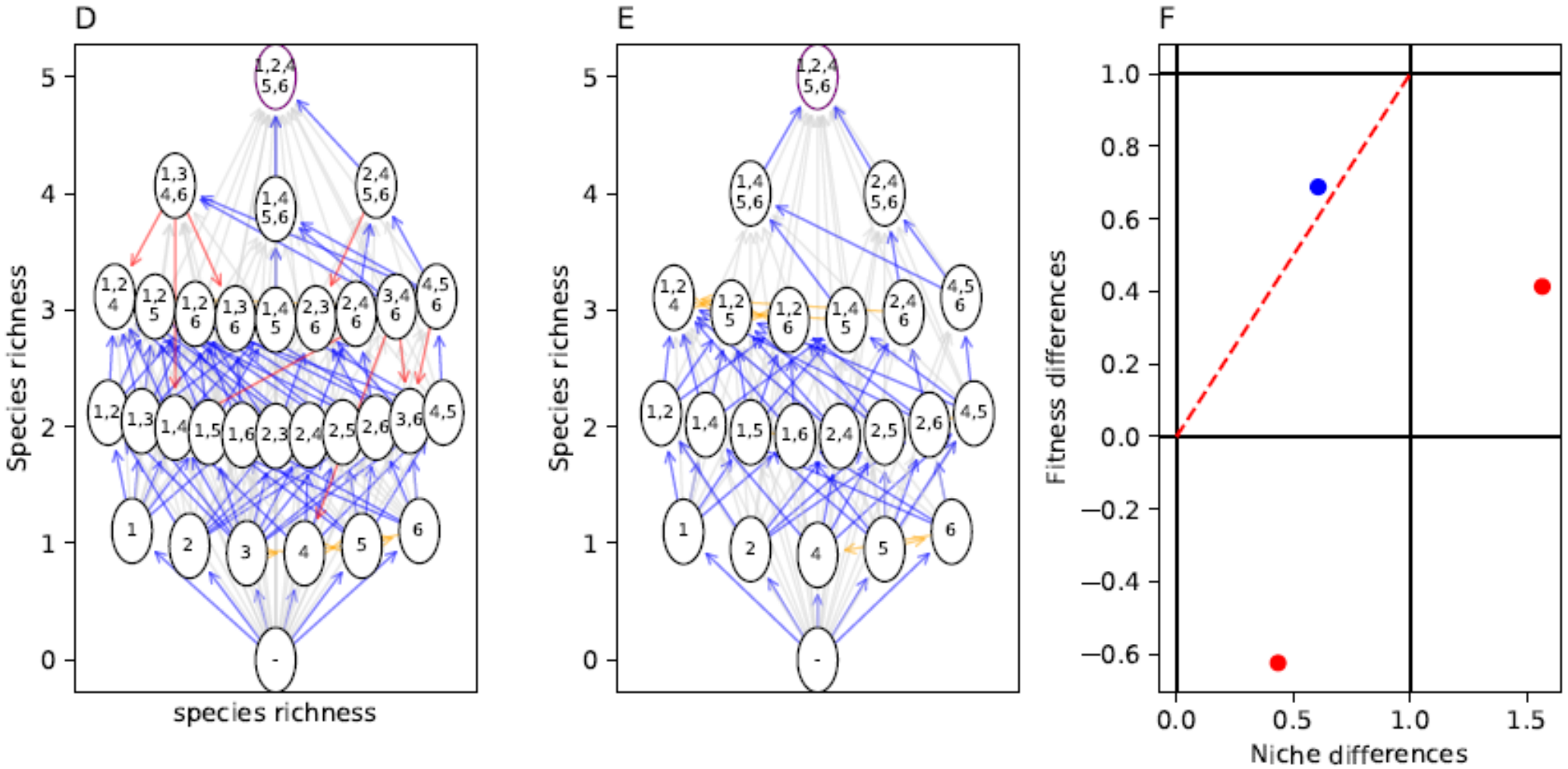
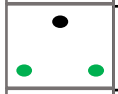
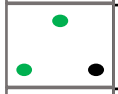
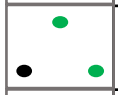
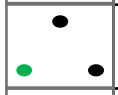
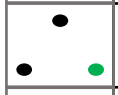


Formal definition of invasion scheme

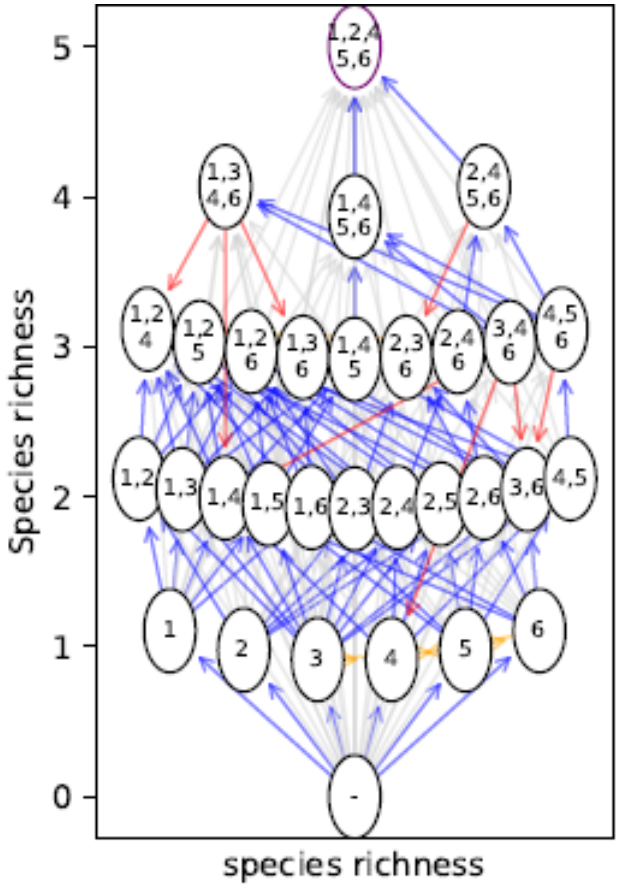
- Per-capita growth rates $\frac{1}{N_i}\frac{dN_i}{dt} = f_i(N, A)$
- Auxiliary variables $\frac{dA_j}{dt} = g_j(N, A)$
  - E.g. resources, predators, habitat suitability etc.
- Equilibrium (or stationary state) $\left(\hat{N}, \hat{A}\right)$ by a subcommunity S
- Define the invasion scheme $r_i(S) = f_i\left(\hat{N}, \hat{A}\right)$
  - By assumption, $r_i(S) = 0$ for $i \in S$
- If one subcommunity has two equilibria $\left(\hat{N}_1, \hat{A}_1\right)$ and $\left(\hat{N}_2, \hat{A}_2\right)$ then we require $sign\left(r_i\left(\hat{N}_1, \hat{A}_1\right)\right) = sign\left(r_i\left(\hat{N}_2, \hat{A}_2\right)\right)$

Invasion scheme

	Sp1	Sp2	Sp3
	1	1	1
	0	0.8	0.8
	0.8	0	0.8
	0.8	0.8	0
	0	0	0.5
	0	0.5	0
	0.5	0	0

Formal definition of invasion graph

- The vertex set V is the set of all subcommunities S for which there is (at least) one stationary state (not necessarily stable)
- Draw a directed edge from S to T if
  - For all species j in $T \backslash S$ $r_j(S) > 0$,
    i.e. all absent species can invade
  - For all species i in $S \backslash T$ $r_i(T) < 0$,
    i.e. lost species can‘t reinvade
- This allows for many edges to combine multiple invasions!



Formal definition of permanence

- First check, the invasion graph should be cycle free
  - If not cycle free the community assembly might get stuck in a cycle,
    - e.g. rock-paper-scissors
  - If there are cycles, try Hofbauer cirterion or Hofbauer criterion per cycle
- The community is permanent if for each subcommunity at least one species can invade
  - The graph is not necessary anymore to test permanence, it’s only to test for cycles

Conclusion

- Robust definition of coexistence (called permanence), invasion growth rates are saved

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- We change how we assess coexistence, not how we interpret coexistence (MCT stays the same)
- For communities where MCT could be applied nothing changes
- We provide automated code which does all the heavy lifting for you

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Thank you very much