On the evolutionary transitions from free-living organisms to obligate symbioses

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The story of my academic life

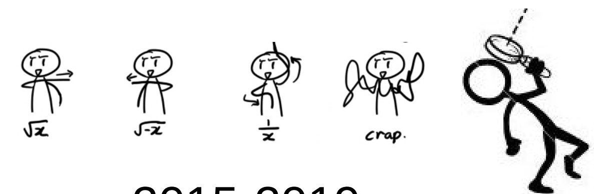
2007-2011

Bachelor in Biology
Hanoi College of Science
Vietnam National University

2011-2013

2013-2015

Erasmus Mundus
Master Programme in
Evolutionary Biology



2015-2019

Imalis International
PhD Programme

The diverse world of symbiosis

The diverse world of symbiosis

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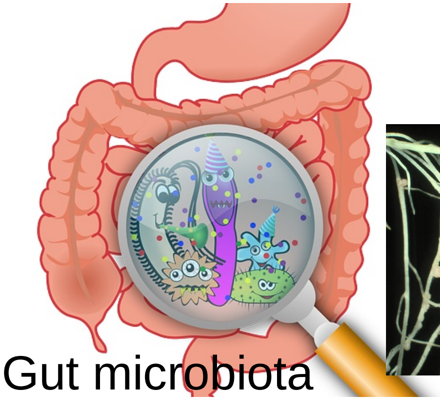
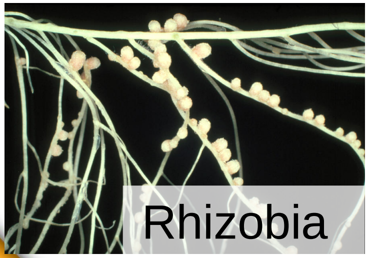
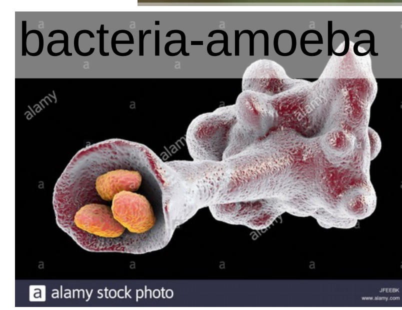


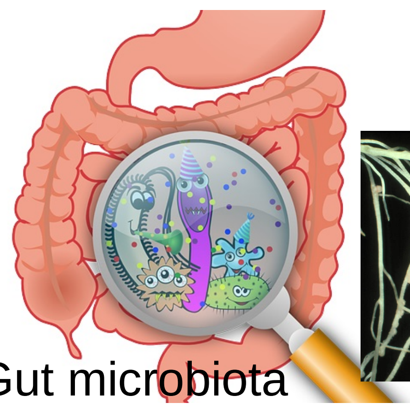


The diverse world of symbiosis


Lichen

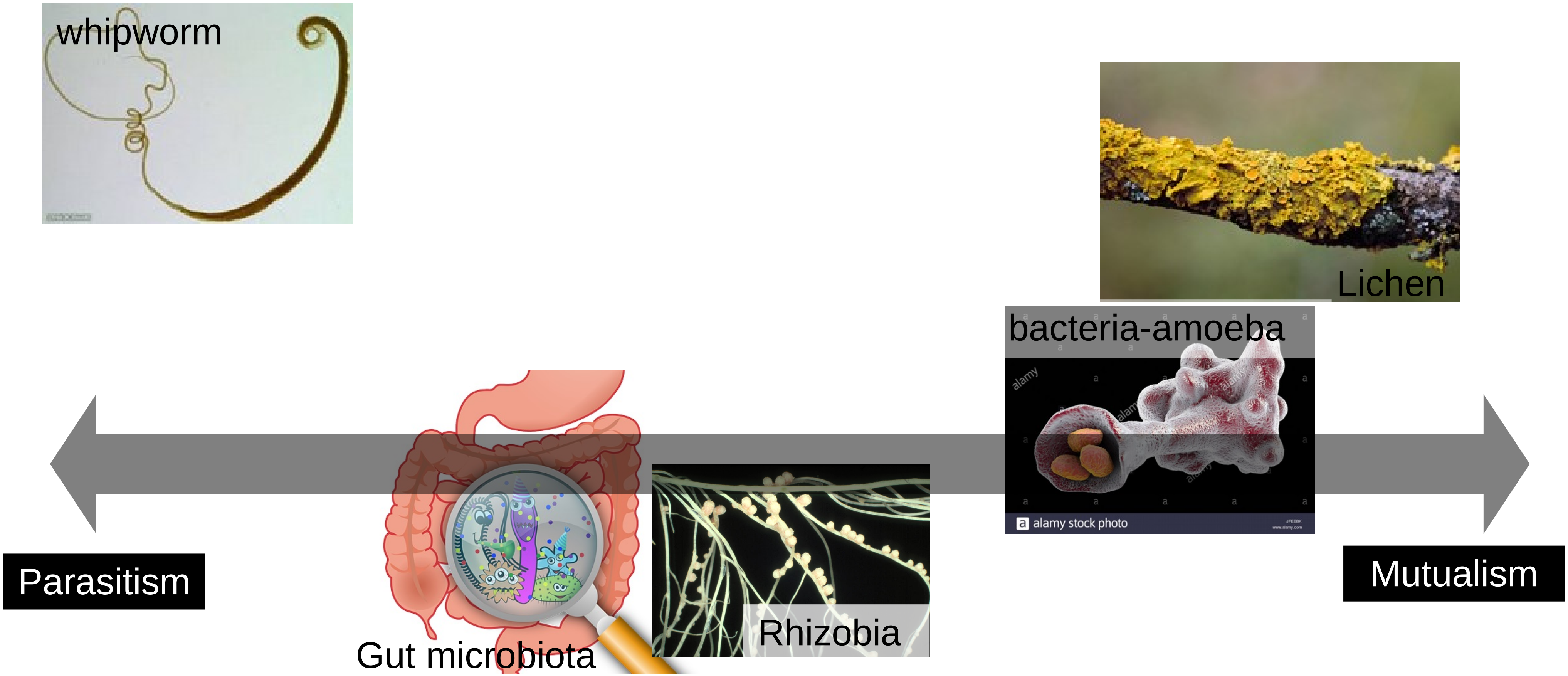


bacteria-amoeba

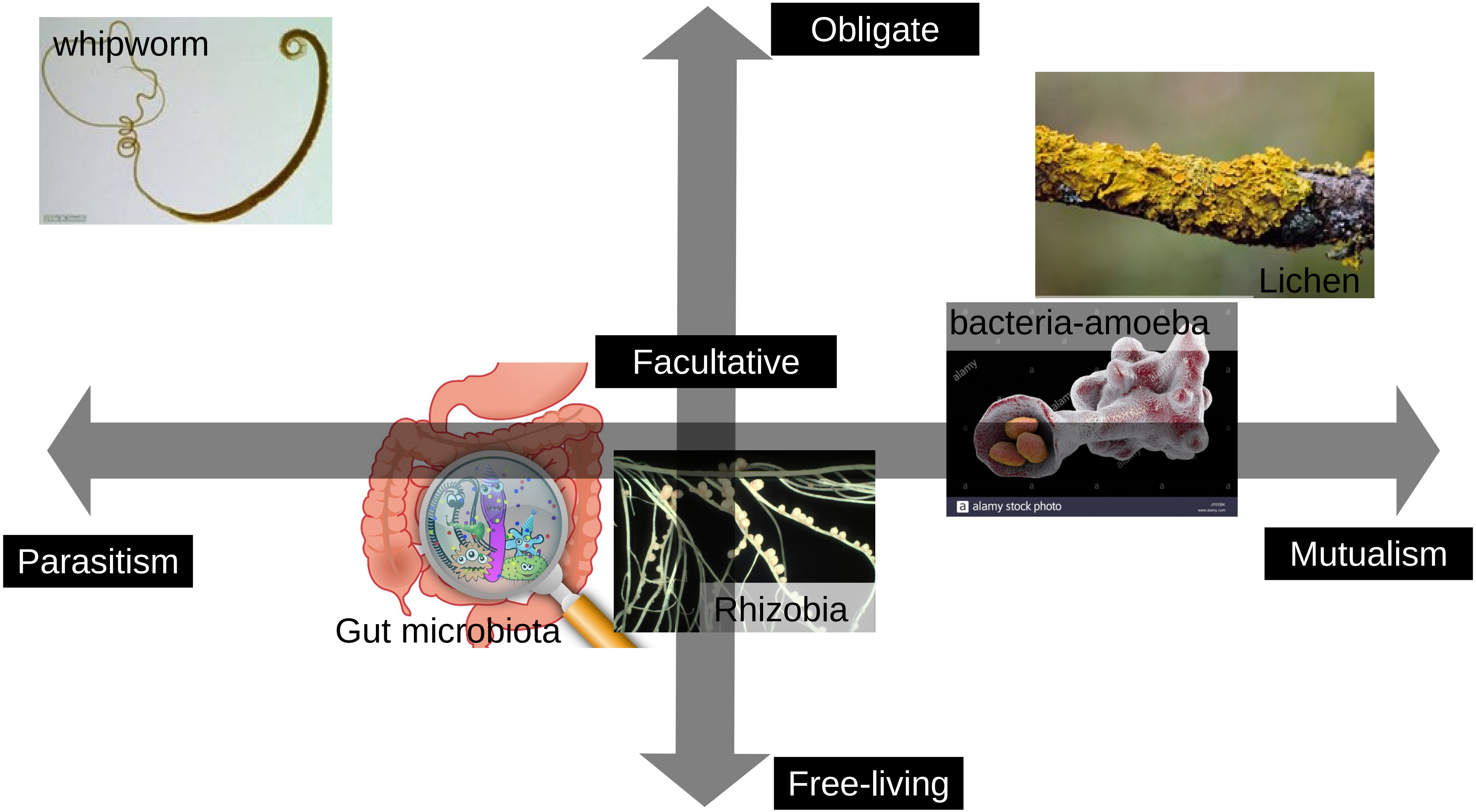

Gut microbiota


Rhizobia

The diverse world of symbiosis



The diverse world of symbiosis



Obligate symbiosis is an evolutionary riddle

- The dependency of on partner to the other is asymmetric
- There has to be a general rule for facultative-obligate transitions regardless of the ecological interactions

Obligate

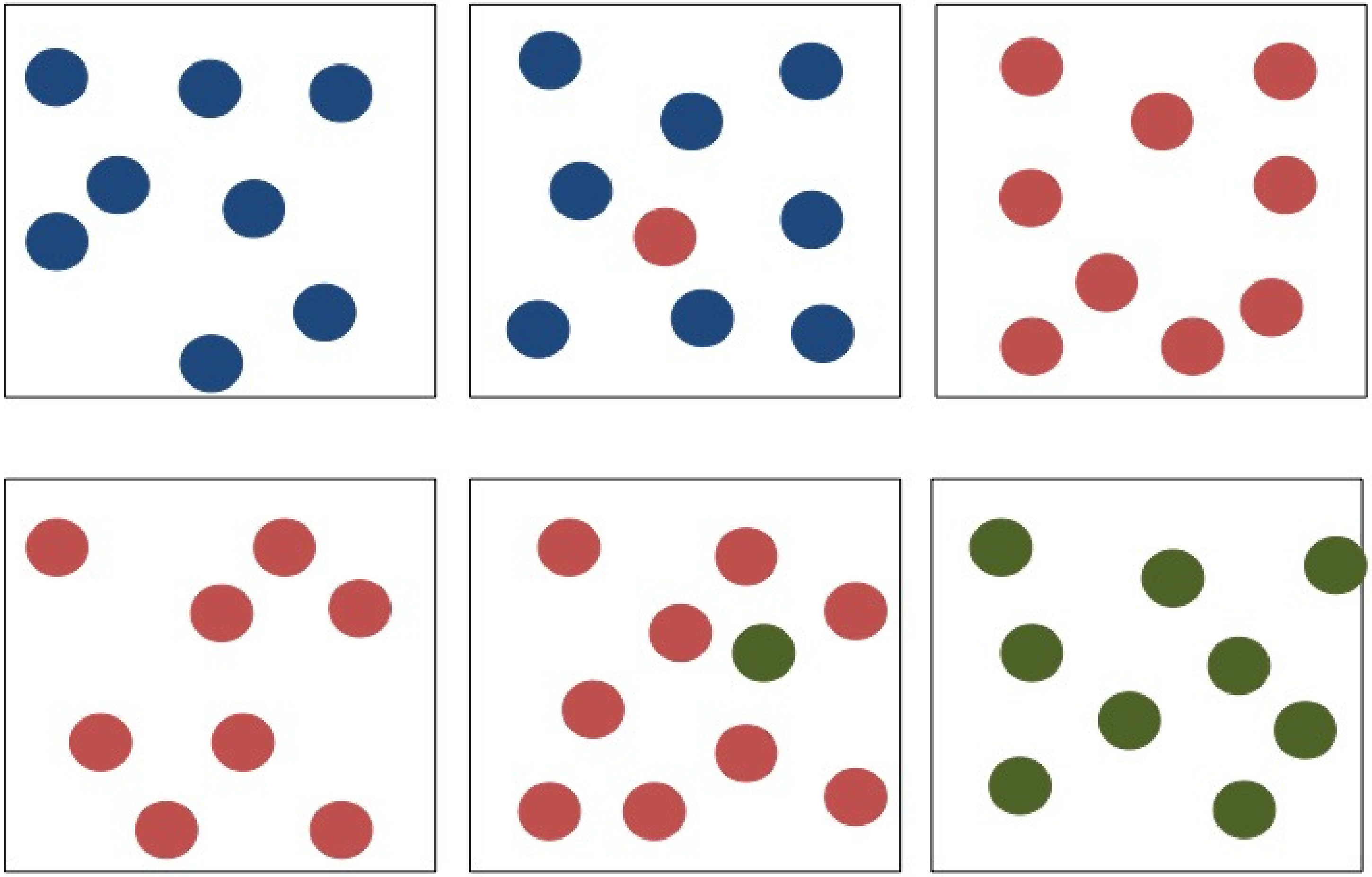
Individuals cannot survive and reproduce without the hosts

Facultative

Individuals can survive and reproduce without the hosts

Free-living

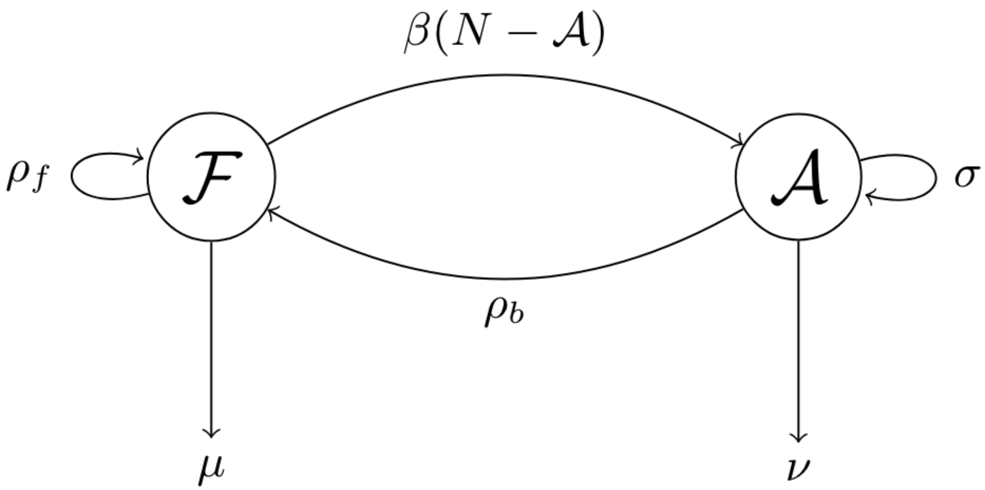
Adaptive dynamics approach



Evolutionary stable strategy: the strategy once adopted by a resident cannot be invaded by any mutant

Model with fixed host dynamics

Ecological dynamics

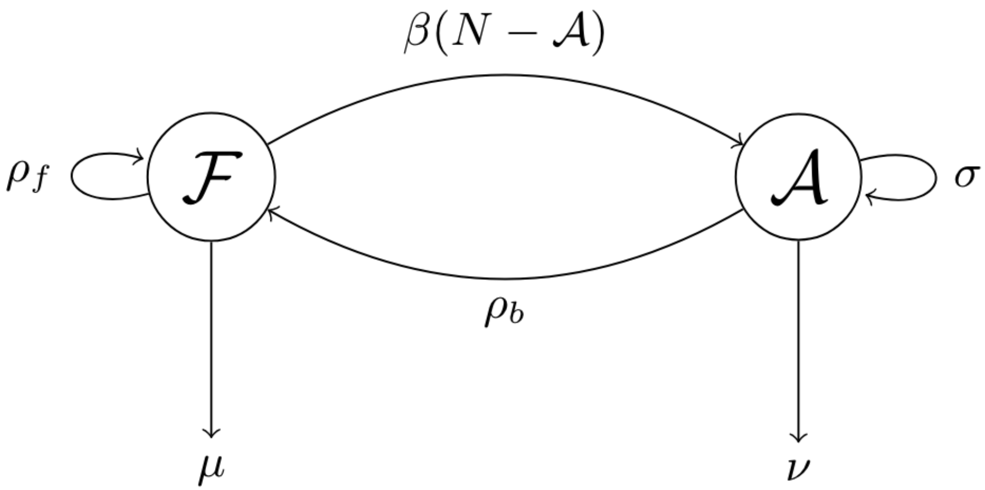


$$\frac{d\mathcal{F}}{dt} = \rho_f\mathcal{F} + \rho_b\mathcal{A} - \beta(N-\mathcal{A})\mathcal{F} - \mu(1+c\mathcal{F})\mathcal{F}$$

$$\frac{d\mathcal{A}}{dt} = \beta(N-\mathcal{A})\mathcal{F} + \sigma\mathcal{A} - \nu\mathcal{A}$$

Model with fixed host dynamics

Ecological dynamics



$$\frac{d\mathcal{F}}{dt} = \rho_f\mathcal{F} + \rho_b\mathcal{A} - \beta(N-\hat{\mathcal{A}})\mathcal{F} - \mu(1+c\mathcal{F})\mathcal{F}$$

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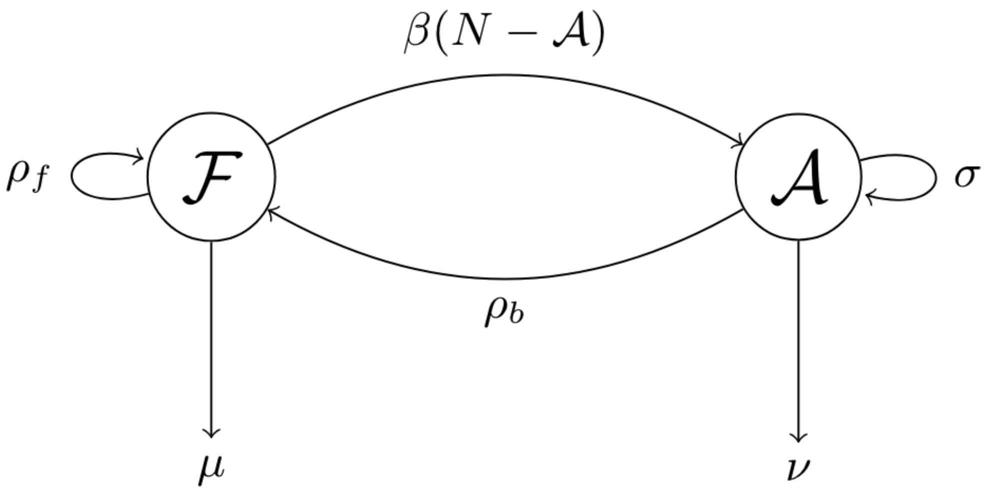
Reproduction ratio

$$R_0 = \frac{1}{\beta(N-\hat{\mathcal{A}}) + (1+c\hat{\mathcal{F}})\mu}\left(\rho_f + \beta\frac{\rho_b(N-\hat{\mathcal{A}})}{\nu-\sigma}\right)$$

Model with fixed host dynamics

Ecological dynamics



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Reproduction ratio

Bound component

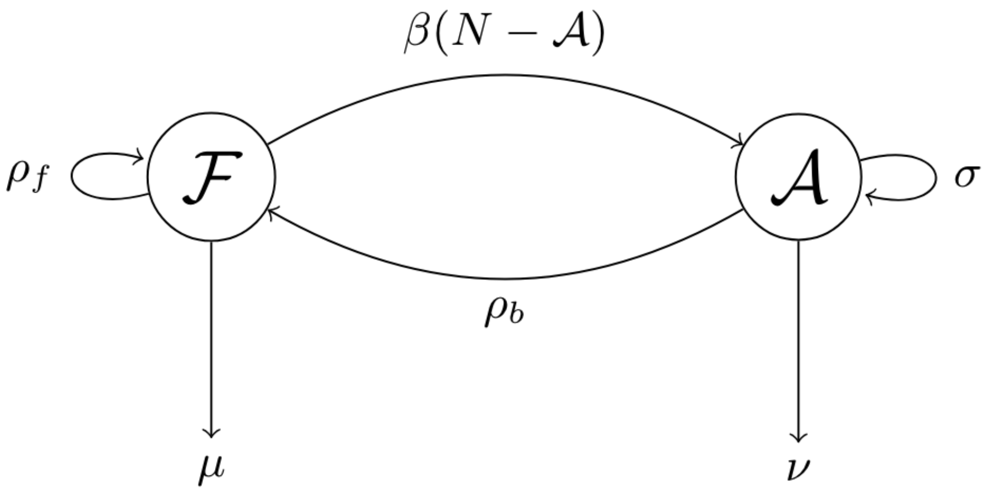
$$R_0 = \frac{1}{\beta(N-\hat{\mathcal{A}}) + (1+c\hat{\mathcal{F}})\mu}\left(\rho_f + \beta\frac{\rho_b(N-\hat{\mathcal{A}})}{\nu-\sigma}\right)$$

Duration in the free-living state

Free component

Model with fixed host dynamics

Ecological dynamics



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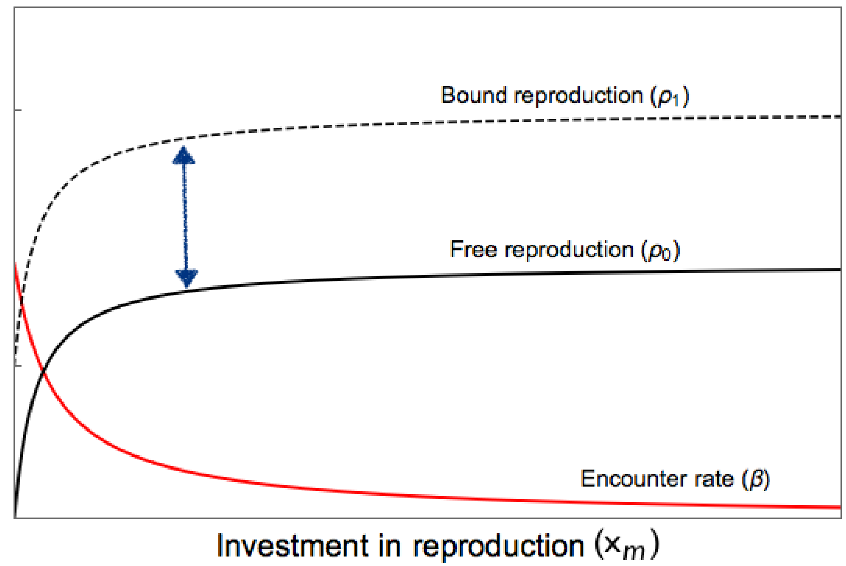
Duration in the free-living state

Free component

Trade-off



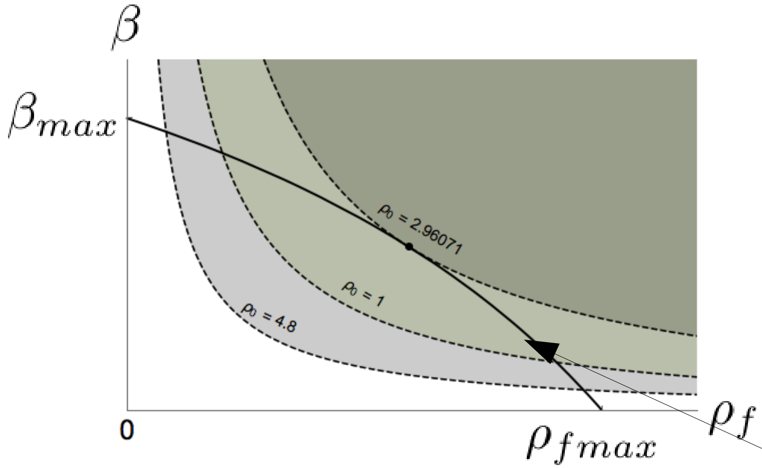
Underlying physiological trait

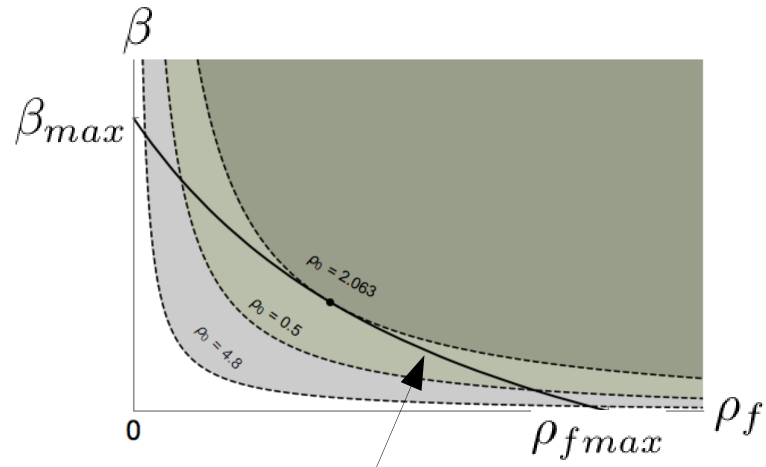
$$\rho_f(x) = \frac{\rho_{fmax}x}{\sigma x + 1}$$

$$\rho_b(x) = \rho_f(x) + b$$

$$\beta(x) = \frac{\beta_{max}}{\alpha x + 1}$$

Model with fixed host dynamics





$$\frac{d\mathcal{F}}{dt} = \rho_f \mathcal{F} + \rho_b \mathcal{A} - \beta(N - \hat{\mathcal{A}})\mathcal{F} - \mu(1 + c\mathcal{F})\mathcal{F}$$

$$\frac{d\mathcal{A}}{dt} = \beta(N - \hat{\mathcal{A}})\mathcal{F} + \sigma\mathcal{A} - \nu\mathcal{A}$$

Reproduction ratio

Bound component

$$R_0 = \frac{1}{\beta(N - \hat{\mathcal{A}}) + (1 + c\hat{\mathcal{F}})\mu}\left(\rho_f + \beta\frac{\rho_b(N - \hat{\mathcal{A}})}{\nu - \sigma}\right) > 1$$

Duration in the free-living state

Free component

Underlying physiological trait

$$\rho_f(x) = \frac{\rho_{fmax}\, x}{\sigma x + 1}$$

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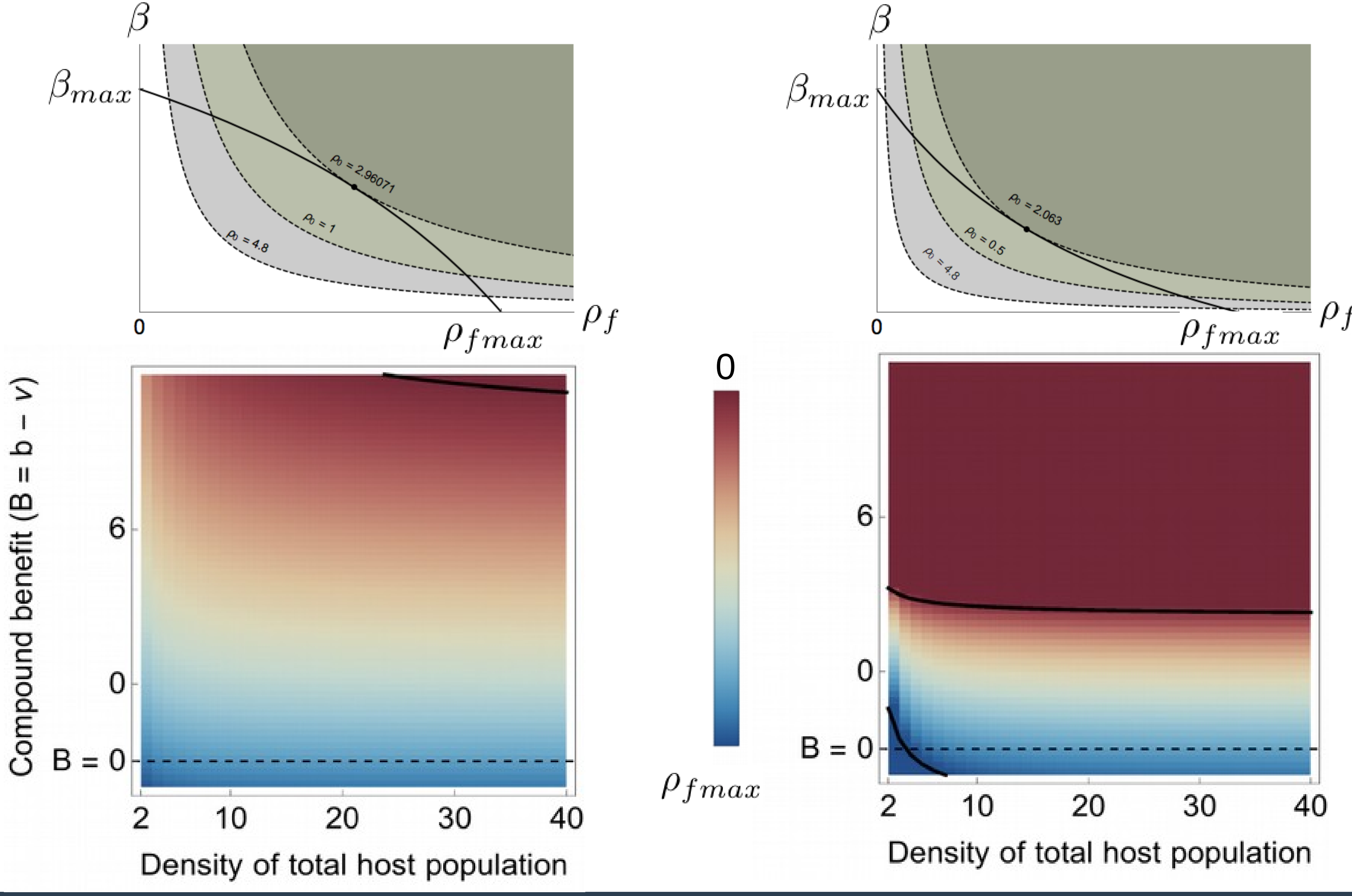
On the difficult transitions from free-living organisms to obligate symbiosis



Simplicity: the pros and cons

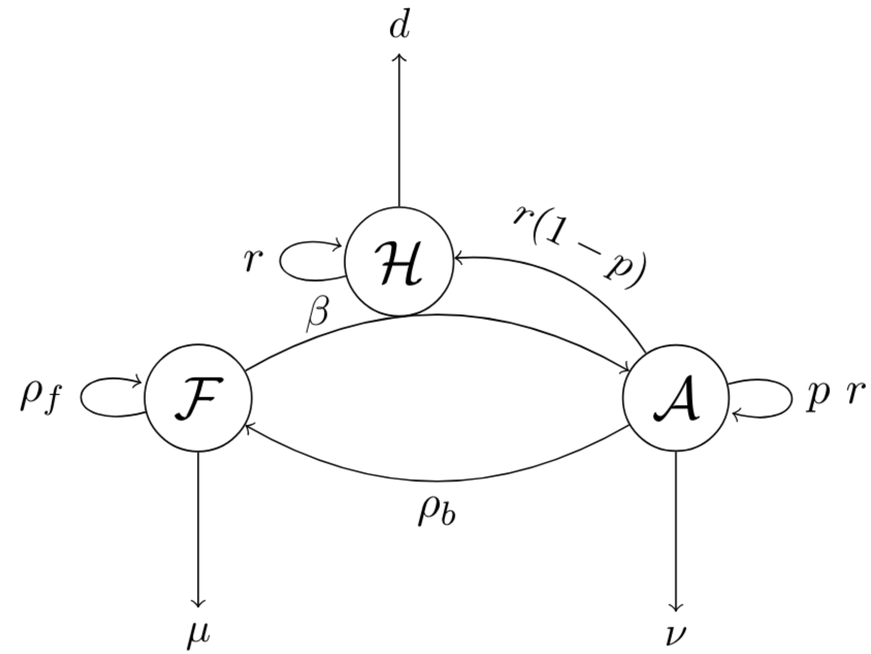
- **What I find exciting about this model:**
  - The effects of the trade-off and the ecological feedback are disentangled
  - Simple model but interesting and useful biological insights
- **Limitations:**
  - Host dynamics are not taken into account
  - Analysis using specific and simple trade-off
  - The evolution toward obligate symbiosis is not only about losing independent reproduction but also about gaining adaptation.

Building on the simple model

$$\frac{d\mathcal{F}}{dt} = \rho_f \frac{\kappa}{1+\phi\mathcal{F}}\mathcal{F} + \rho_b\mathcal{A} - \beta\mathcal{F}\mathcal{H} - \mu\mathcal{F}$$

$$\frac{d\mathcal{A}}{dt} = \beta\mathcal{F}\mathcal{H} - \nu(1+(\mathcal{A}+\mathcal{H})\gamma)\mathcal{A} + rpA$$

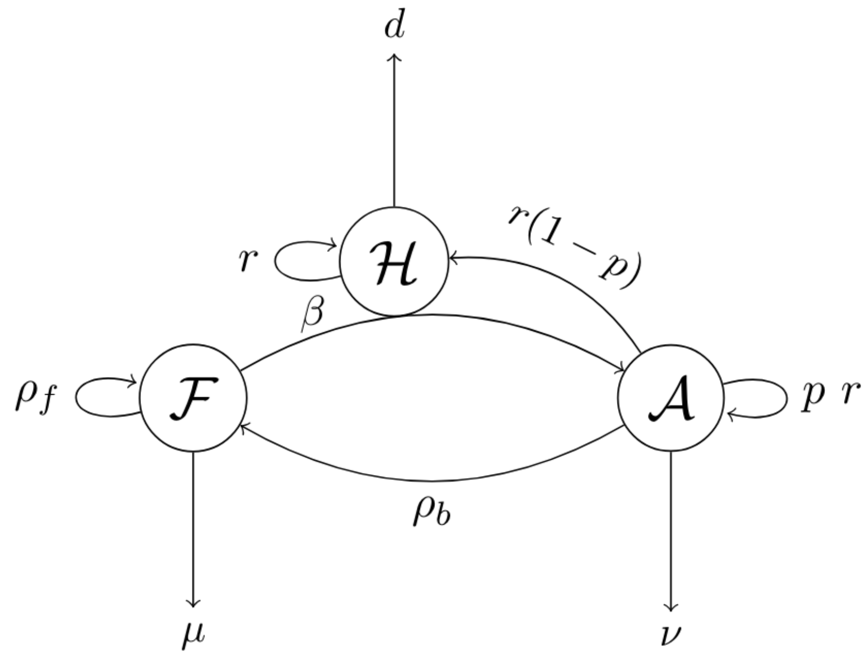
$$\frac{d\mathcal{H}}{dt} = r(1-p)\mathcal{A} + r\mathcal{H} - \beta\mathcal{F}\mathcal{H} - d(1+(\mathcal{H}+\mathcal{A})\zeta)\mathcal{H}$$



Building on the simple model

$$\frac{d\mathcal{F}}{dt} = \rho_f \frac{\kappa}{1+\phi\hat{\mathcal{F}}}\mathcal{F} + \rho_b\mathcal{A} - \beta\mathcal{F}\hat{\mathcal{H}} - \mu\mathcal{F}$$

$$\frac{d\mathcal{A}}{dt} = \beta\mathcal{F}\hat{\mathcal{H}} - \nu(1 + (\hat{\mathcal{A}} + \hat{\mathcal{H}})\gamma)\mathcal{A} + rpA$$



Neutral mutant has zero invasion fitness

$$\left(\frac{\kappa\rho_f}{(1+\phi\hat{\mathcal{F}})\mu} - 1\right)\left(\frac{rp}{(1+\gamma(\hat{\mathcal{A}}+\hat{\mathcal{H}}))\nu} - 1\right) = \left(\frac{rp}{(1+(\hat{\mathcal{A}}+\hat{\mathcal{H}})\gamma)\nu} + \frac{\rho_b}{(1+(\hat{\mathcal{A}}+\hat{\mathcal{H}})\gamma)\nu} - 1\right)\frac{\hat{\mathcal{H}}\beta}{\mu}$$

Building on the simple model

$$\frac{d\mathcal{F}}{dt} = \rho_f \frac{\kappa}{1+\phi\hat{\mathcal{F}}}\mathcal{F} + \rho_b\mathcal{A} - \beta\mathcal{F}\hat{\mathcal{H}} - \mu\mathcal{F}$$

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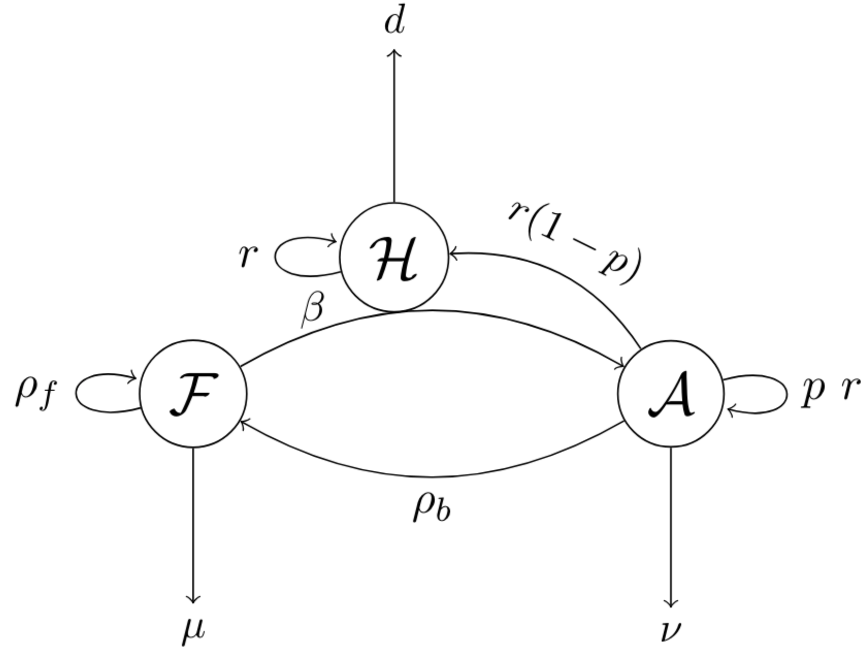


Neutral mutant has zero invasion fitness

$$(R_{ff}-1)(R_{aa}-1) = (R_{aa} + R_{af} - 1)\mathcal{T}$$

Reproduction ratio of free-living individual

Reproduction ratio of vertically transmitted individual

Reproduction ratio of horizontally transmitted individual

Effective number of host encounter

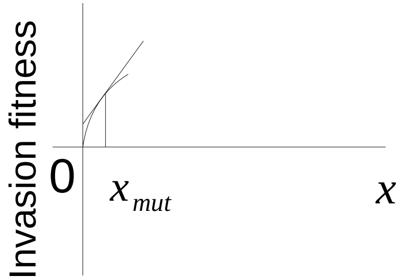
Insights from analysing invasion fitness

1. When can a mutant with small adaptation $x_{mut} \approx 0$ to the symbiotic lifestyle invade a resident population without any adaptation $x_{res} = 0$, hence $R_{ff}(x_{res}) = 0$?
2. If a singular strategy exists where adaptation to the symbiotic lifestyle is sufficient $R_{af}(x_{ss}) > 0$, is such a strategy at the minimum or maximum of the fitness landscape?
3. What are the effects of the ecological interactions on the evolution of the adaptation to the symbiotic lifestyle?

1. Evolution of small symbiotic adaptation

- **A mutant with small adaptation to the symbiotic lifestyle invades a resident population without any adaptation when the selection gradient is positive**

$$\frac{1}{R_{ff}-1}\frac{\partial R_{ff}}{\partial x_{mut}} - \left(\frac{1}{R_{af}+R_{aa}-1}\frac{\partial R_{af}}{\partial x_{mut}}\right)\Bigg|_{\substack{x_{res}=0\\ x_{mut}\approx 0}} > 0$$



Assumptions:

- $\frac{\partial R_{aa}}{\partial x_{mut}}=0;\ \frac{\partial T}{\partial x_{mut}}=0$

- Very small vertical transmission

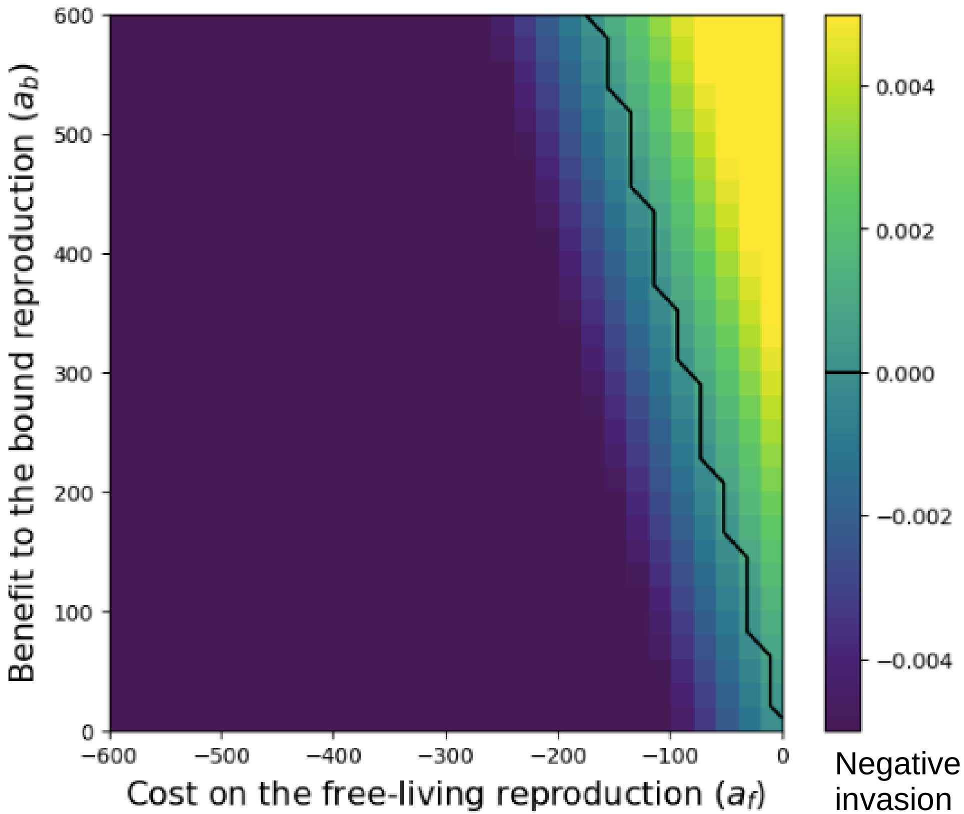
- **With local analysis around the resident value, any function can be linearised. What matters is the coefficients.**

Evolution of small symbiotic adaptation

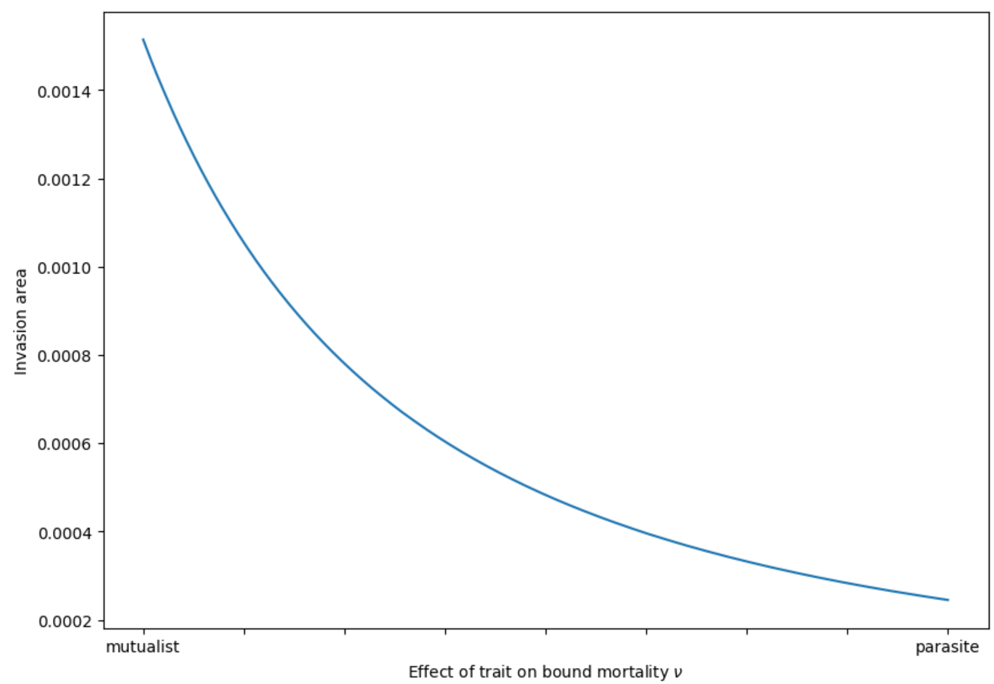
a_f Coefficient for R_{ff} linearised function < 0

a_b Coefficient for R_{af} linearised function > 0

Positive invasion fitness



Negative invasion fitness



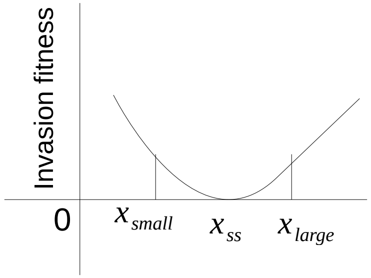
2. The singular strategy has to satisfy

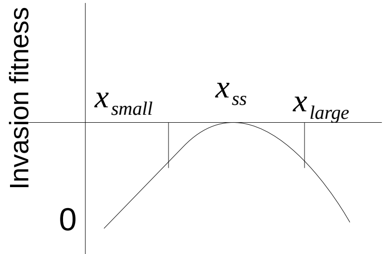
- **Selection gradient is zero**

$$\left(\frac{1}{R_{ff}-1}\frac{\partial R_{ff}}{\partial x_{mut}} = \frac{1}{R_{aa}+R_{af}-1}\frac{\partial R_{af}}{\partial x_{mut}}\right)\Big|_{x_{mut}=x_{res}=x_{ss}}$$

Assumptions:

- $\frac{\partial R_{aa}}{\partial x_{mut}}=0;\frac{\partial T}{\partial x_{mut}}=0$
- Very small vertical transmission





- **Condition for minimum and maximum**
  - ~~Second derivative of the fitness function~~ Selection gradients on neighbour mutants
  - Minimum singular strategy → polymorphism
  - Maximum singular strategy → monomorphism

2. The singular strategy has to satisfy

- **Selection gradient is zero**

$$\left(\frac{1}{R_{ff}-1}\frac{\partial R_{ff}}{\partial x_{mut}} = \frac{1}{R_{aa}+R_{af}-1}\frac{\partial R_{af}}{\partial x_{mut}}\right)\Big|_{x_{mut}=x_{res}=x_{ss}}$$

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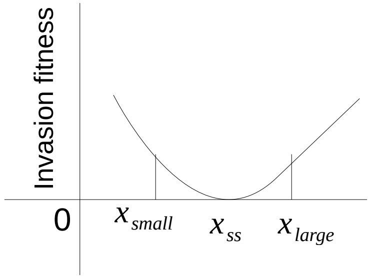

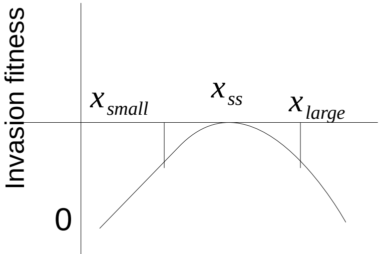

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$$\left(\frac{1}{R_{ff}-1} \boxed{\frac{\partial R_{ff}}{\partial x_{mut}}} = \frac{1}{R_{aa}+R_{af}-1} \boxed{\frac{\partial R_{af}}{\partial x_{mut}}} \right) \Big|_{x_{mut}=x_{res}=x_{ss}}$$

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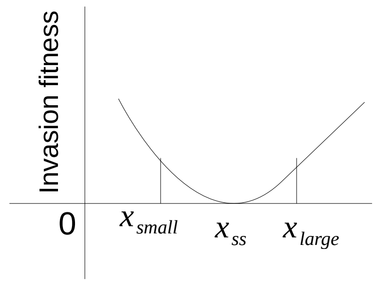

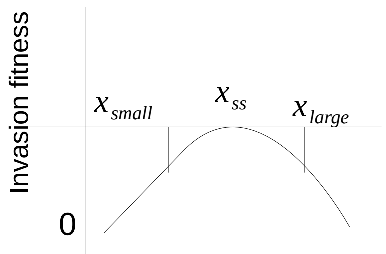

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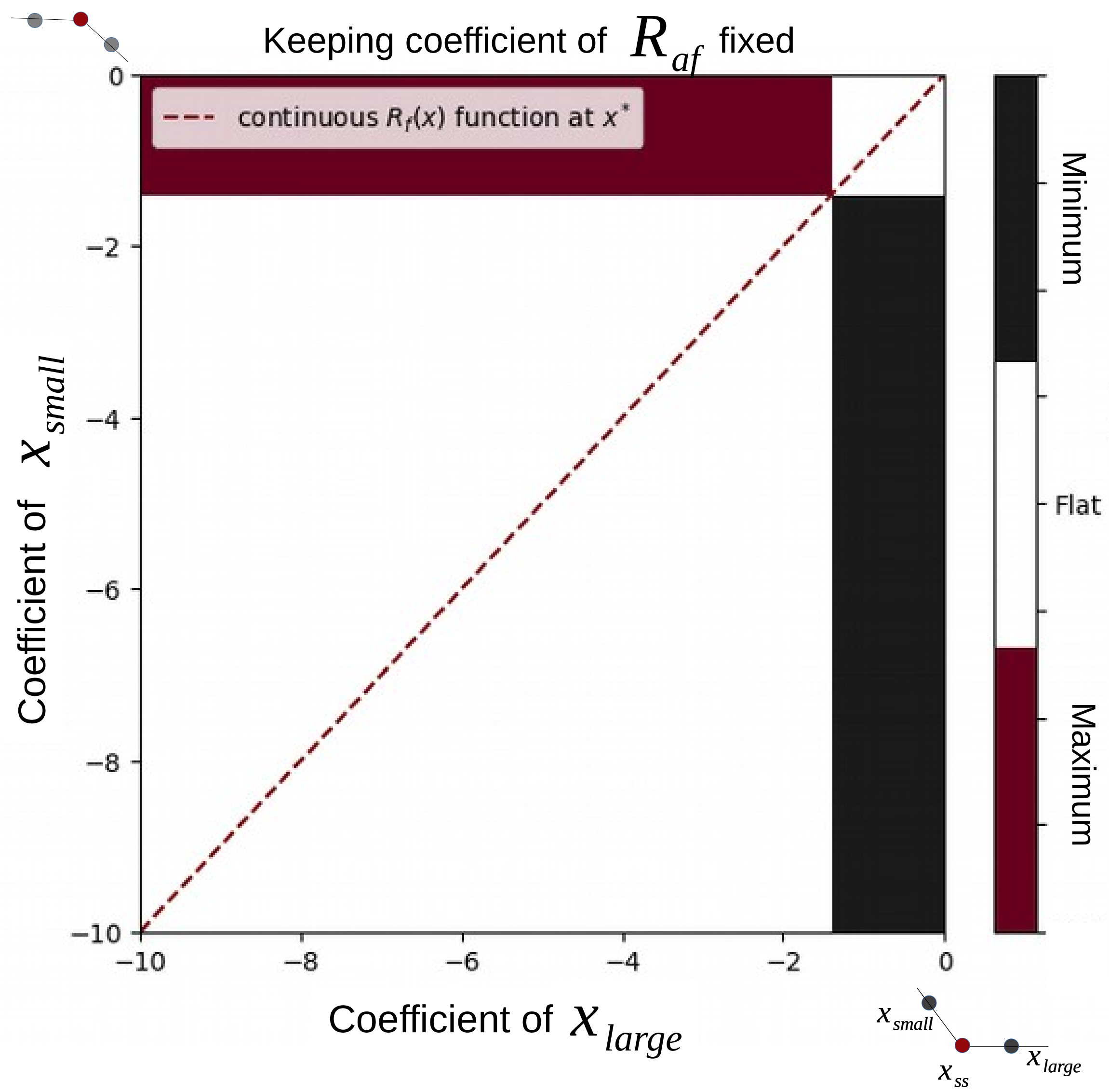

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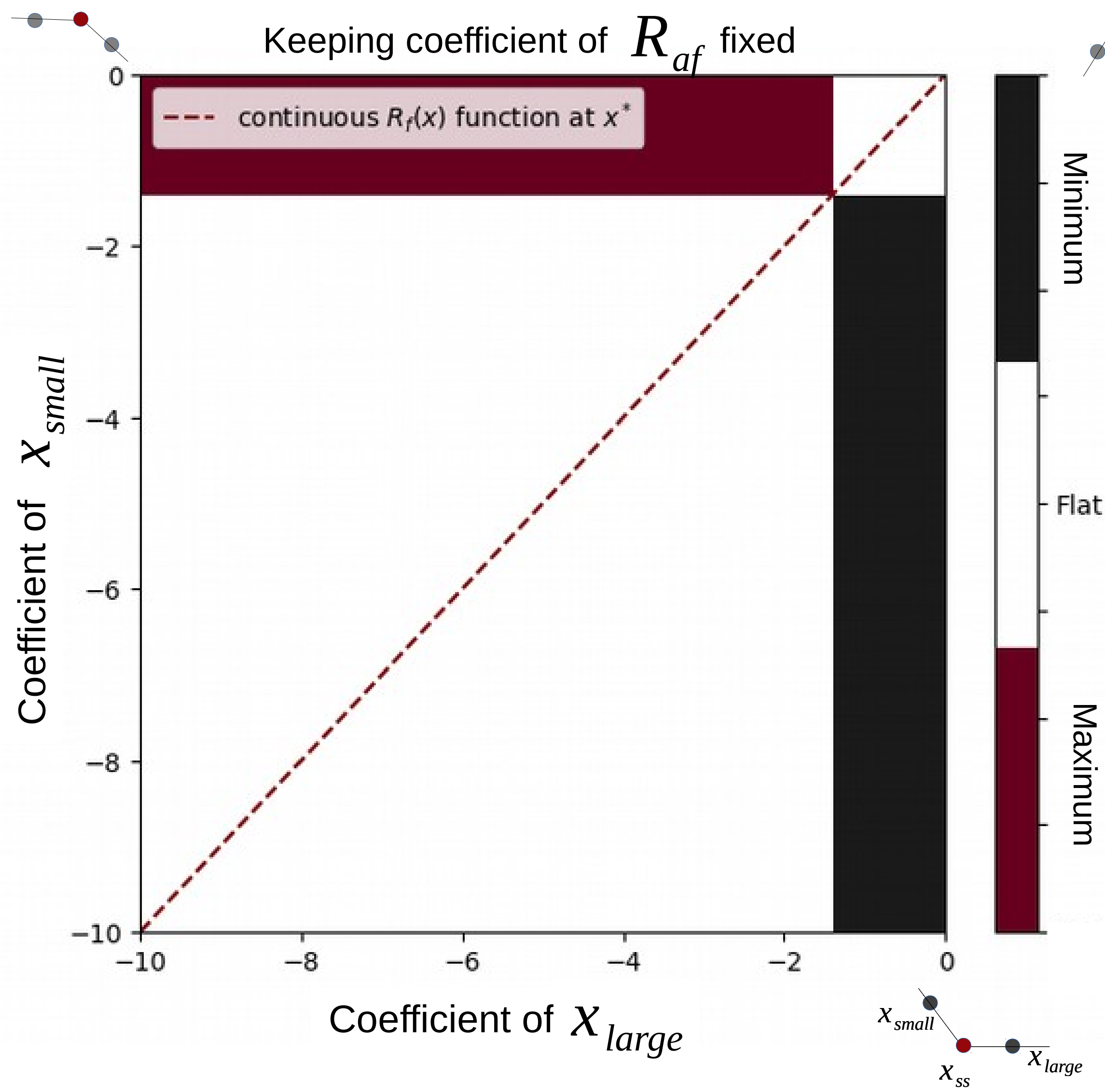
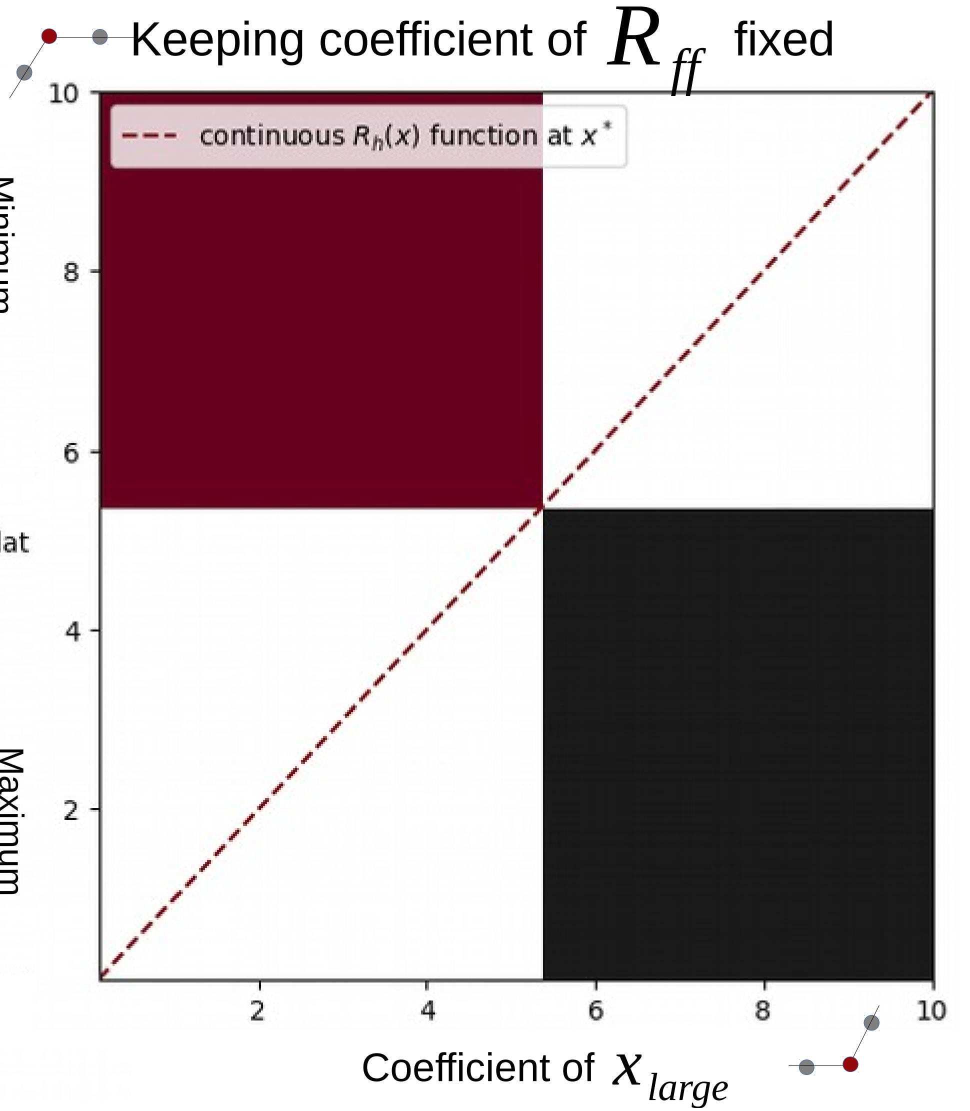
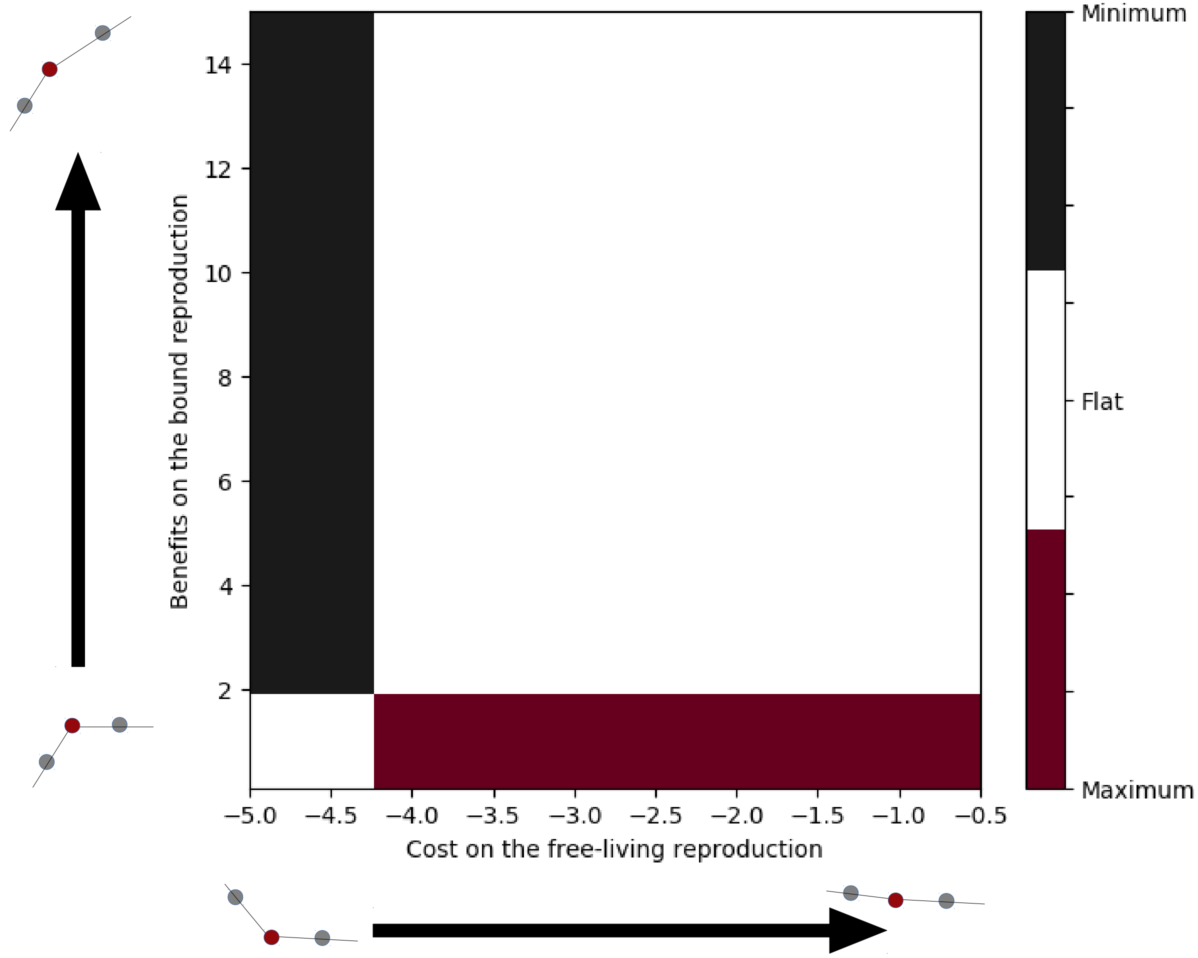




2. Condition for minimum and maximum

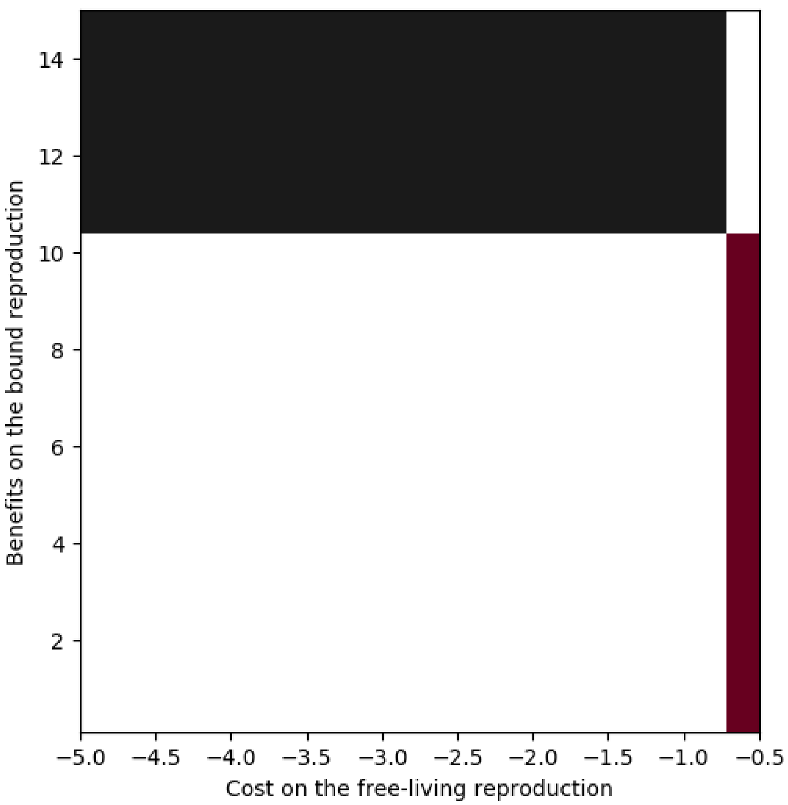
A saturated to continuously increasing benefit
A saturated to continuously decreasing benefit



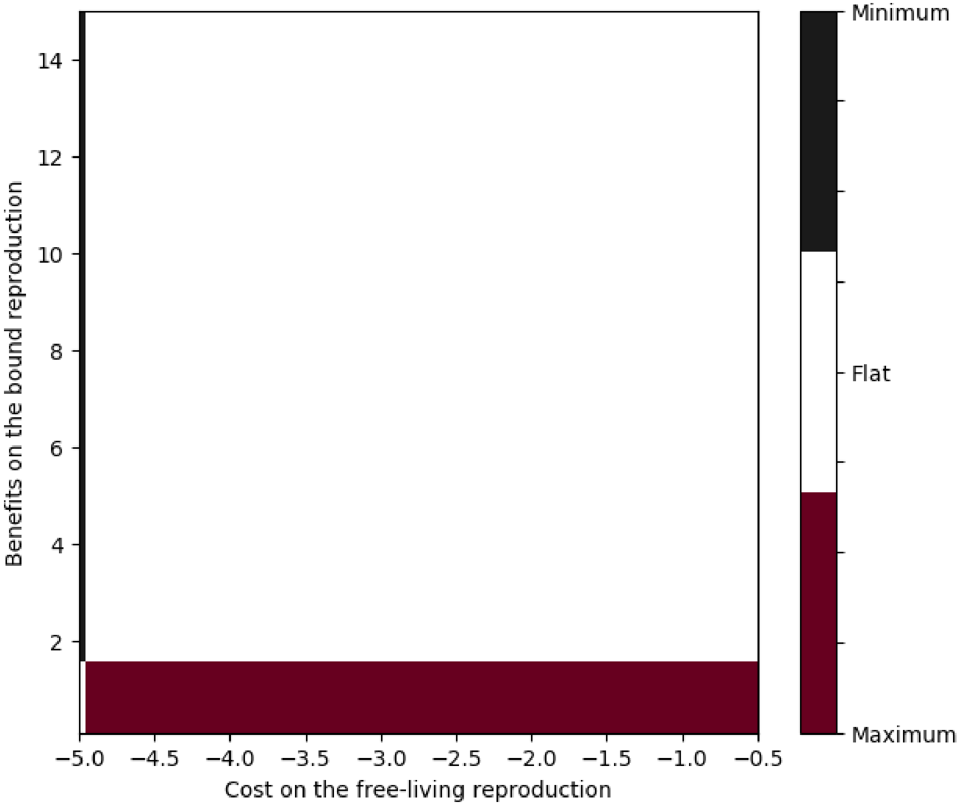
3. Effect of ecological interactions

A saturated to continuously increasing benefit
A saturated to continuously decreasing benefit

Parasitism



Mutualism



Exciting results

- Different production ratios for different reproduction strategies are disentangled
- Useful insights can be obtained from the analysis of invasion at the boundary and the local singular strategy
- Effect of the ecological interactions can be observed without specifying trade-off functions
- Understand the limit of analysis when specific trade-off is not stated

Thank you for your attention!