Mutualists, Parasites, and Microbes

Meandering Along the Entangled Bank

TransEvo Core Seminar, June 2024

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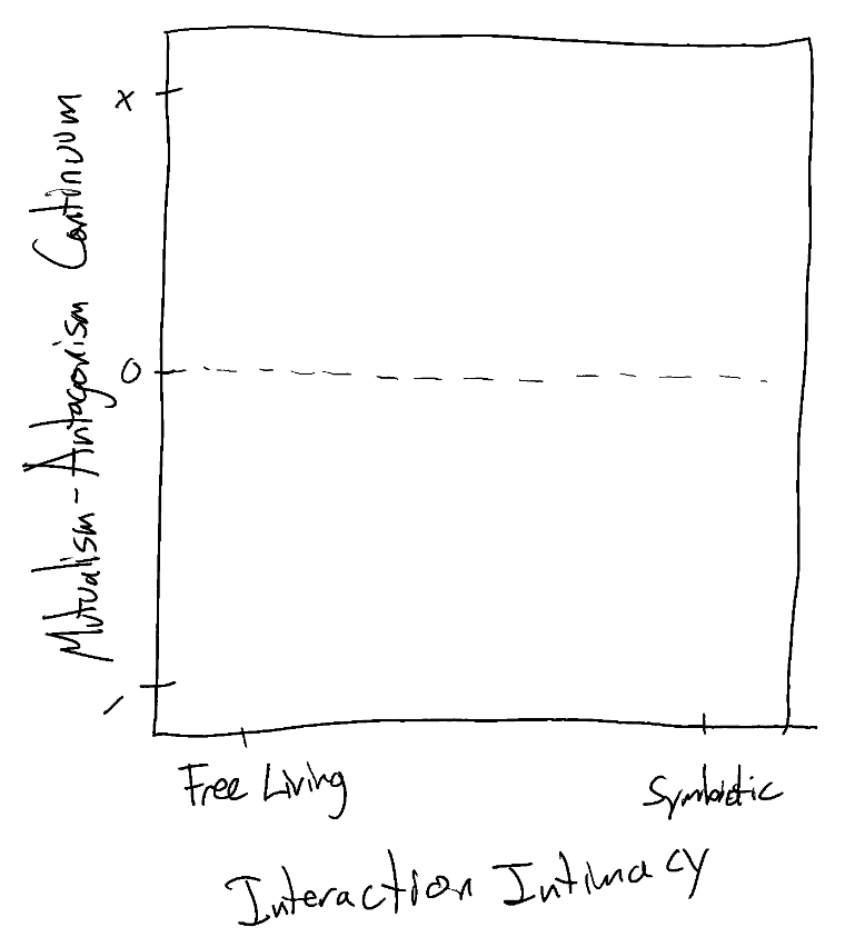
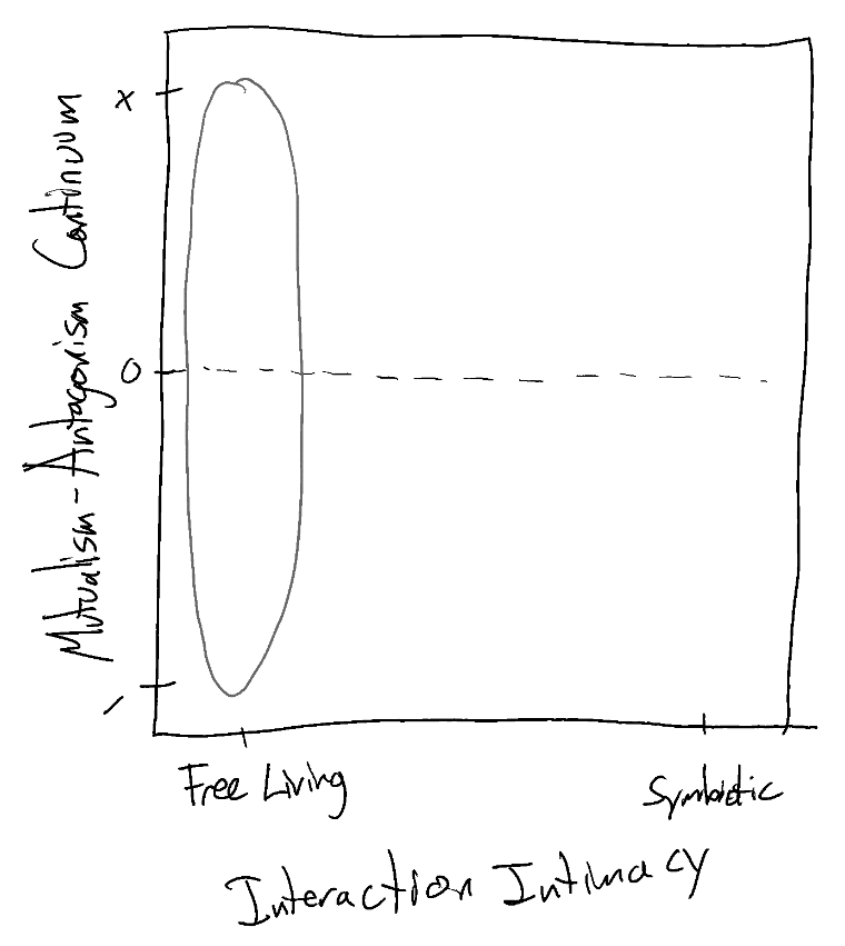
Entangled Bank

Unifying Theme



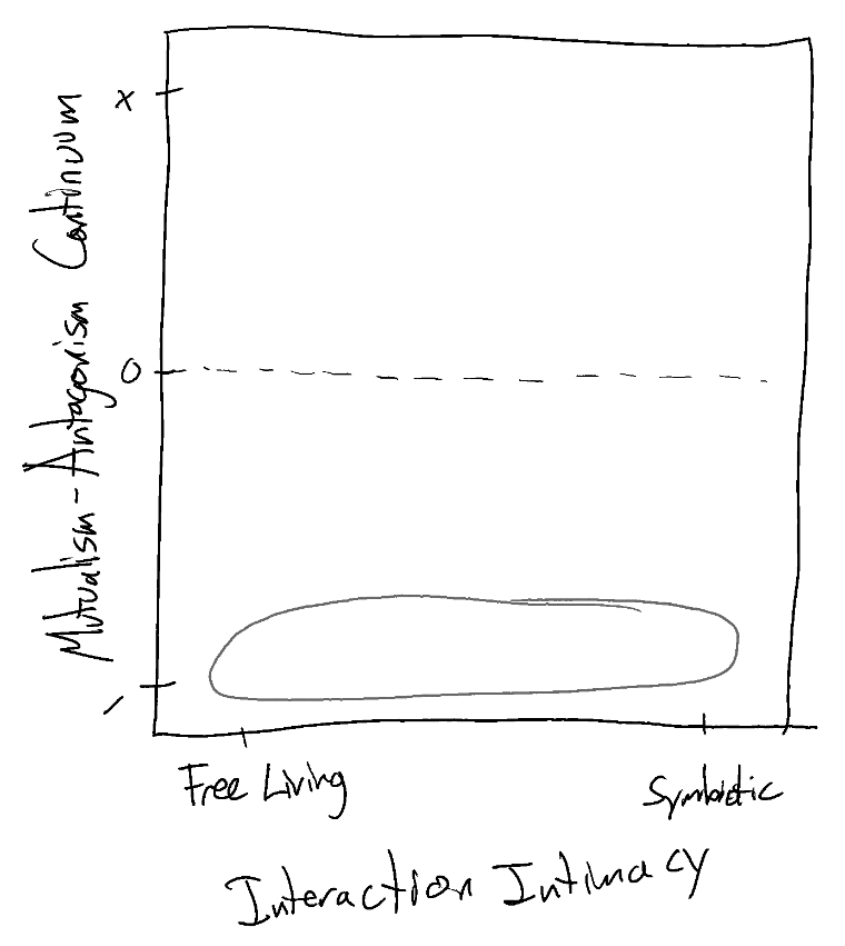
Mutualism-antagonism spectrum $\times$ degrees of interaction intimacy

Part One



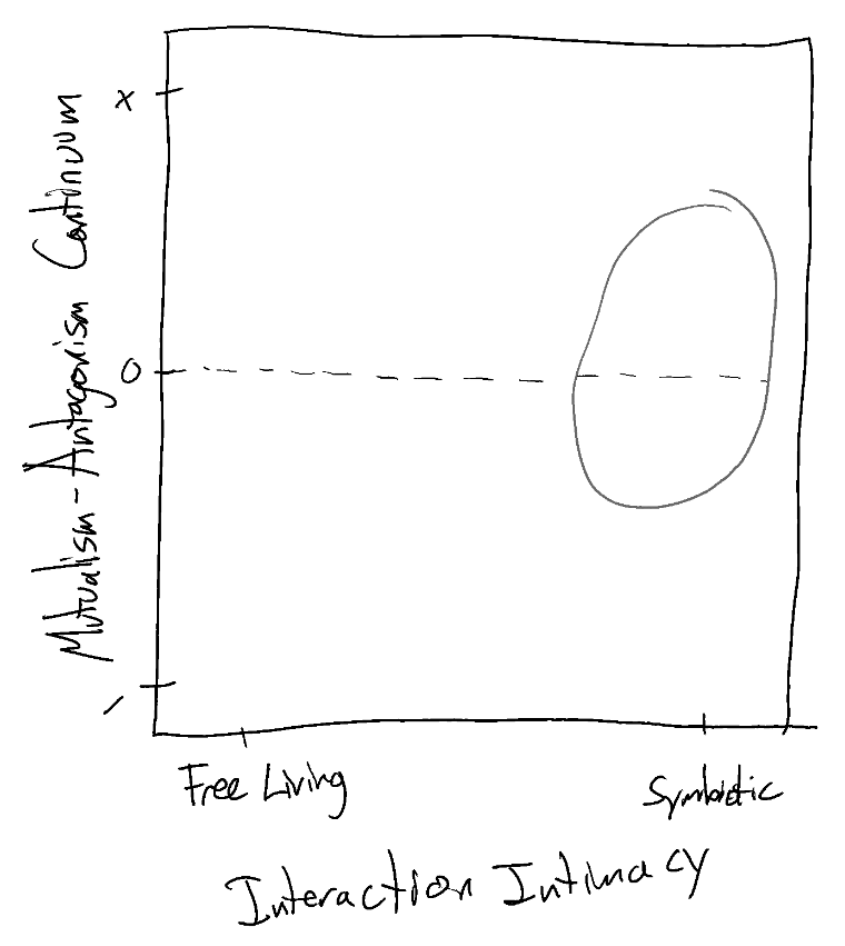
Coevolution along the mutualism-antagonism continuum

Part Two



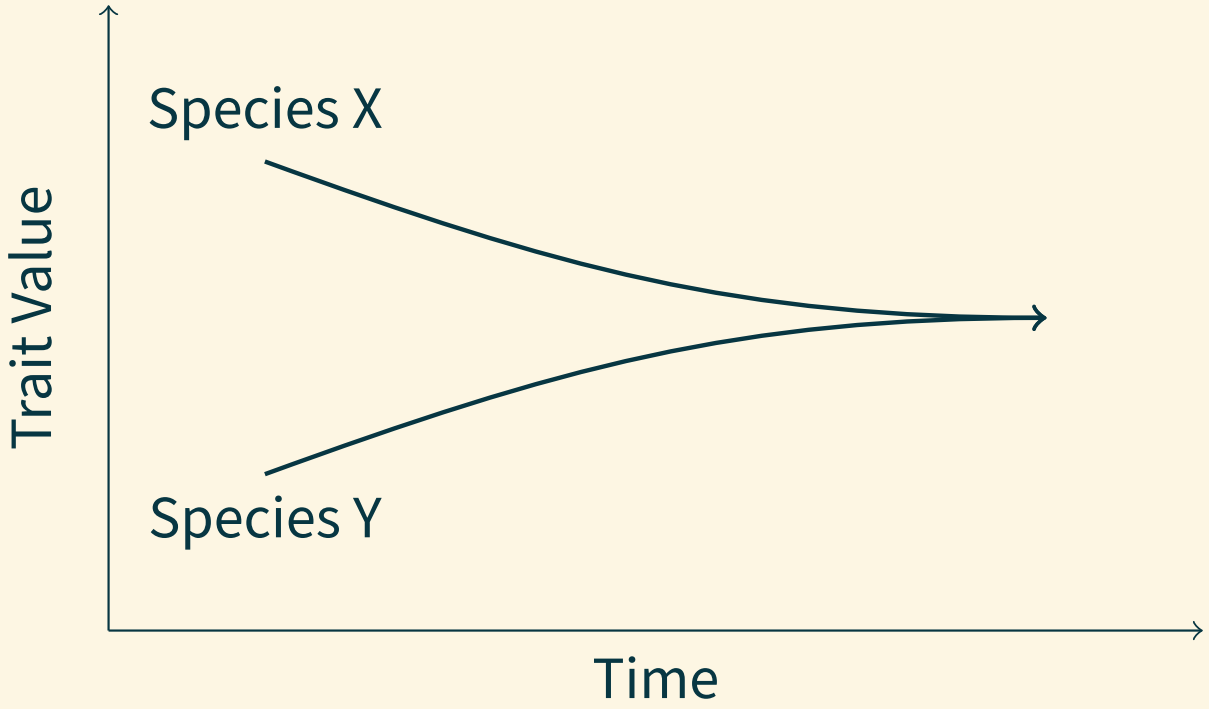
Host-parasite coevolution in continuous space

Part Three



Host-microbiome dynamics, and microbiome-mediated host evolution

Coevolving Mutualists



Mutualistic coevolution is often thought to cause convergence of traits

Trait-Matching Counterexamples

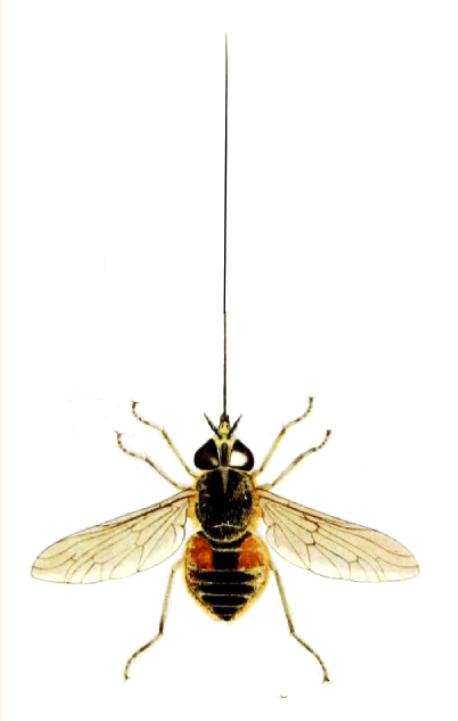
However, striking counterexamples exist in nature

Trait-Matching Counterexamples

Rediviva neliana visiting the oil-secreting flower of *Diascia capsularis*[1]

[1] Steiner & Whitehead (1990)

Trait-Matching Counterexamples



Philoliche longirostris (left) and *Roscoea purpurea* (right)[2]

[2] Paudel et al. (2015)

Trait-Matching Counterexamples

Moegistorhynchus longirostris visiting the flower of *Lapeirousia anceps*[3]

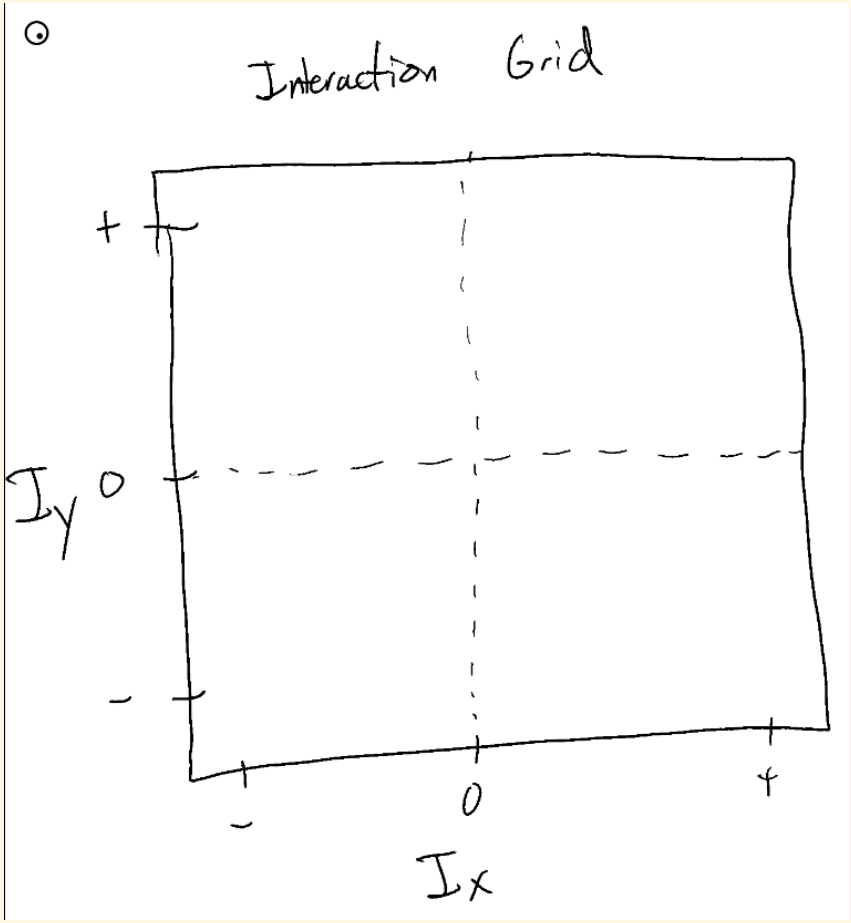
[3] Pauw et al. (2009)

Imbalance of Armaments

Moegistorhynchus longirostris visiting *Babiana thunbergii*[4]

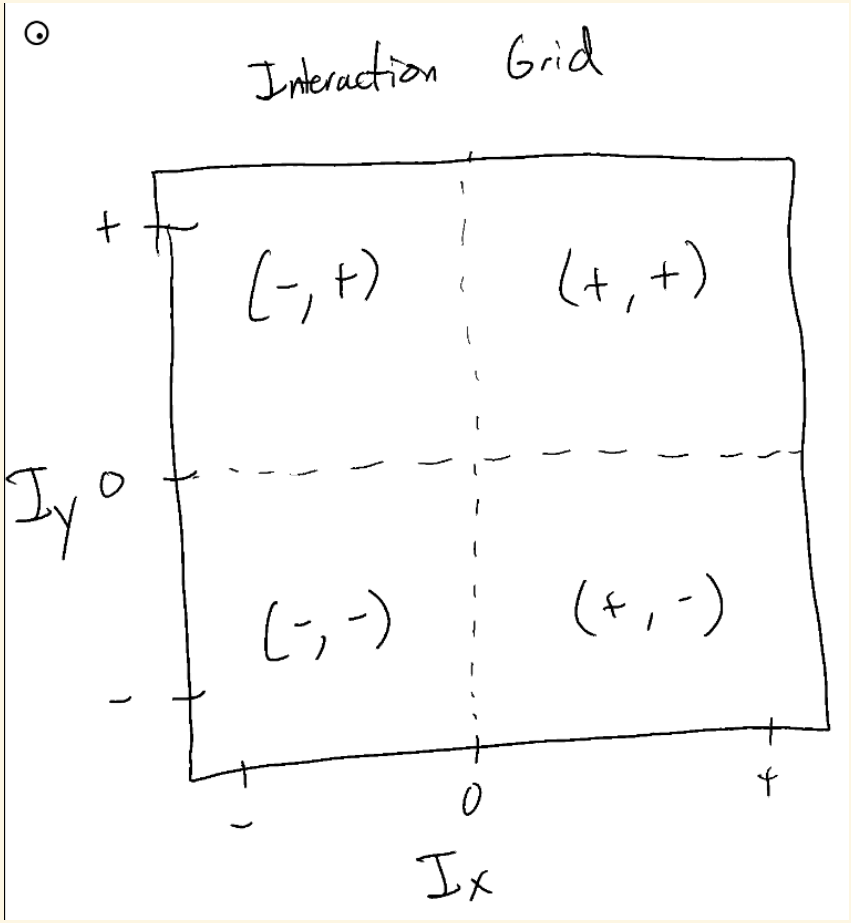
[4] Pauw et al. (2009)

Ecological Consequences of Coevolution



Grid of ecological interaction types

Ecological Consequences of Coevolution



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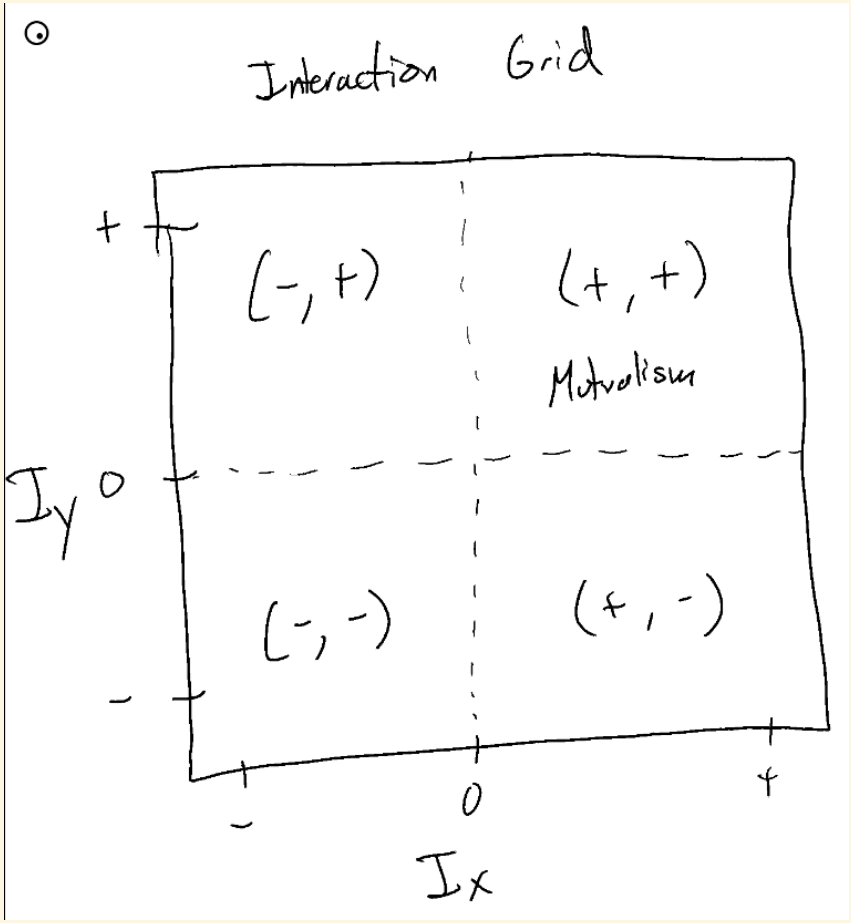

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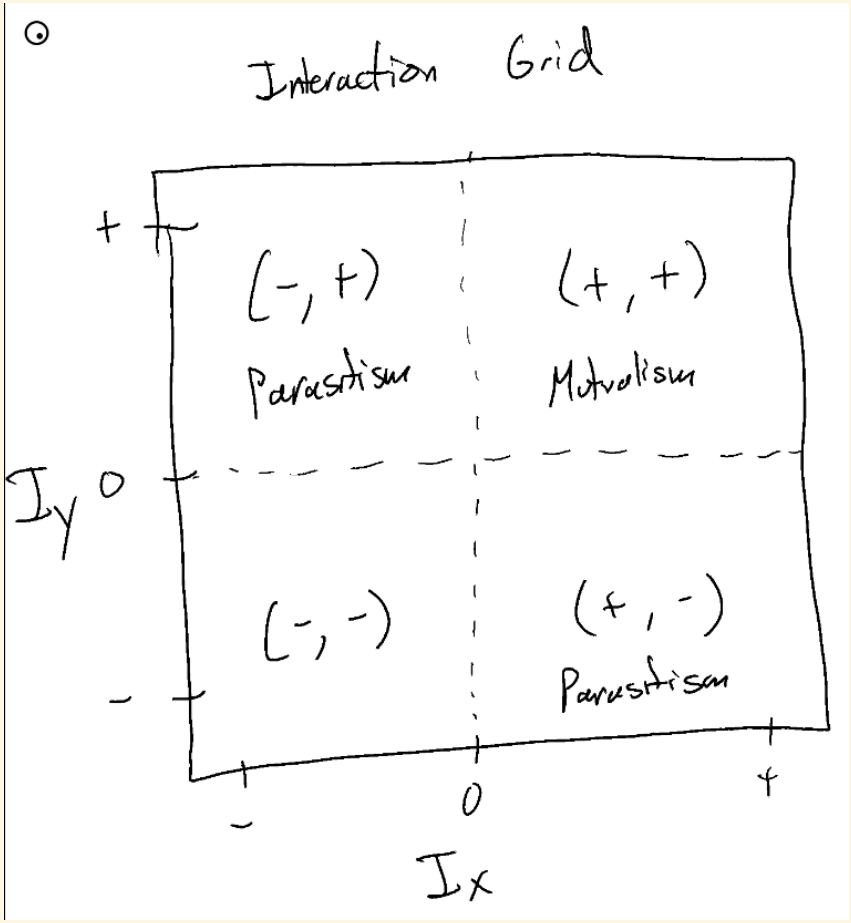
Ecological Consequences of Coevolution



Grid of ecological interaction types

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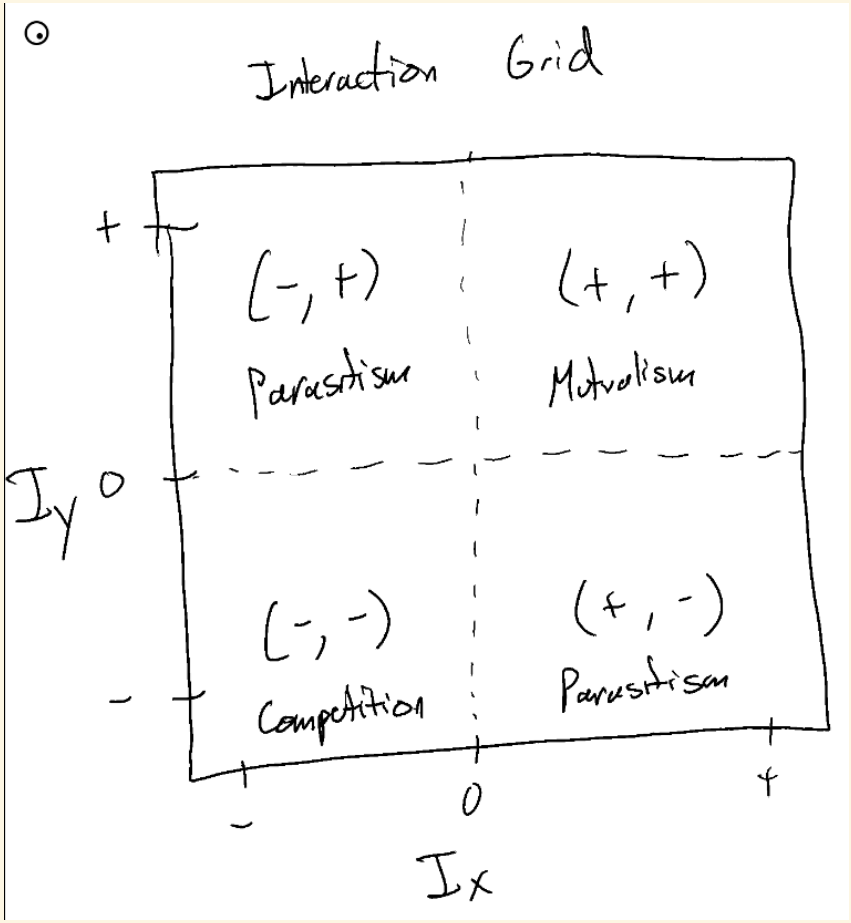
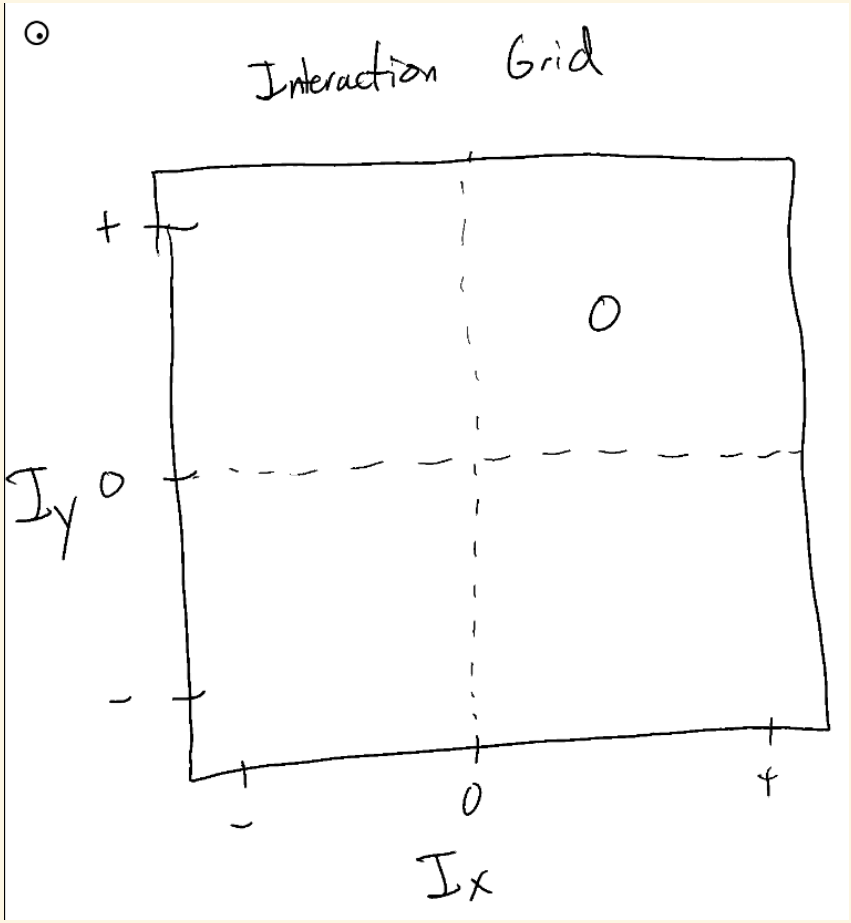


Grid of ecological interaction types

When does mutualism dissolve into parasitism?



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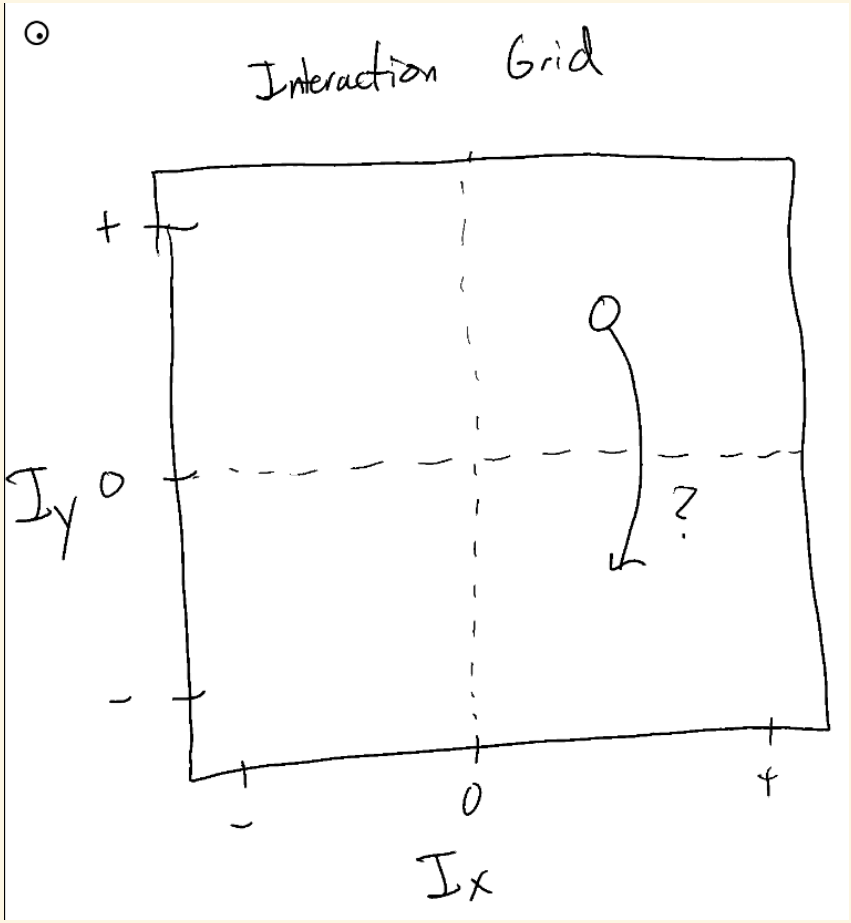
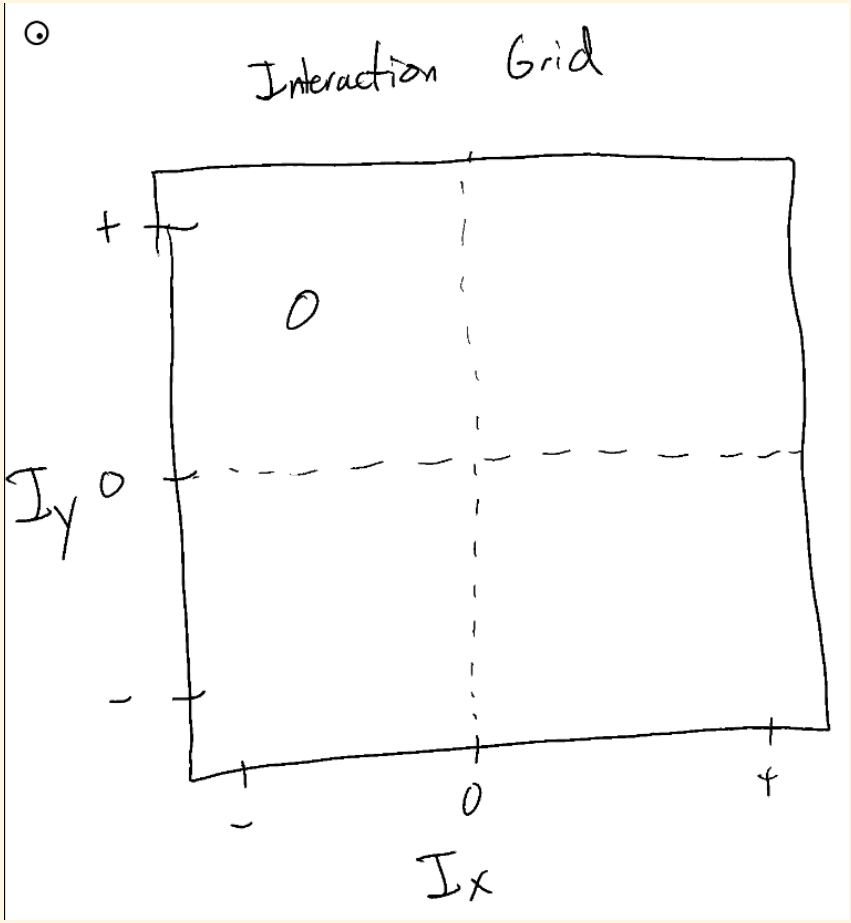


When is parasitism converted to mutualism?



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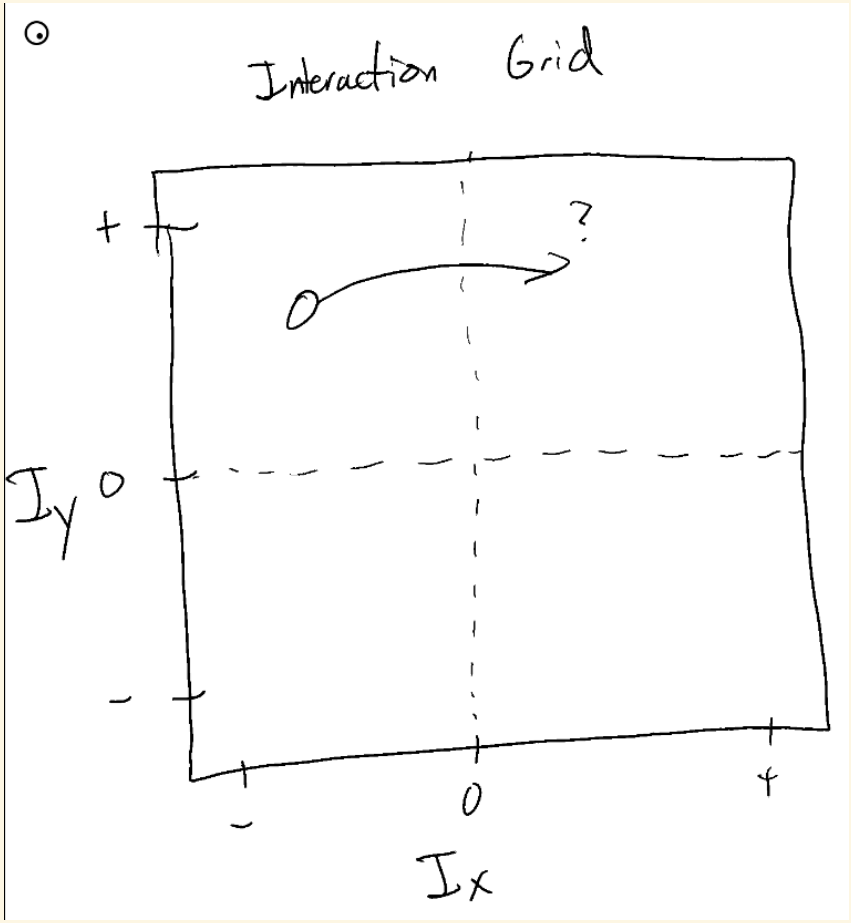

Exploitation of Mutualism

one way to interpret this pathway towards the dissolution of mutualism is through the framework of cheating

Cheating[5]

Definition

In an interspecific interaction, an individual is a **cheater** if

[5] Definition adapted from Jones et al. (2015)

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In an interspecific interaction, an individual is a **cheater** if

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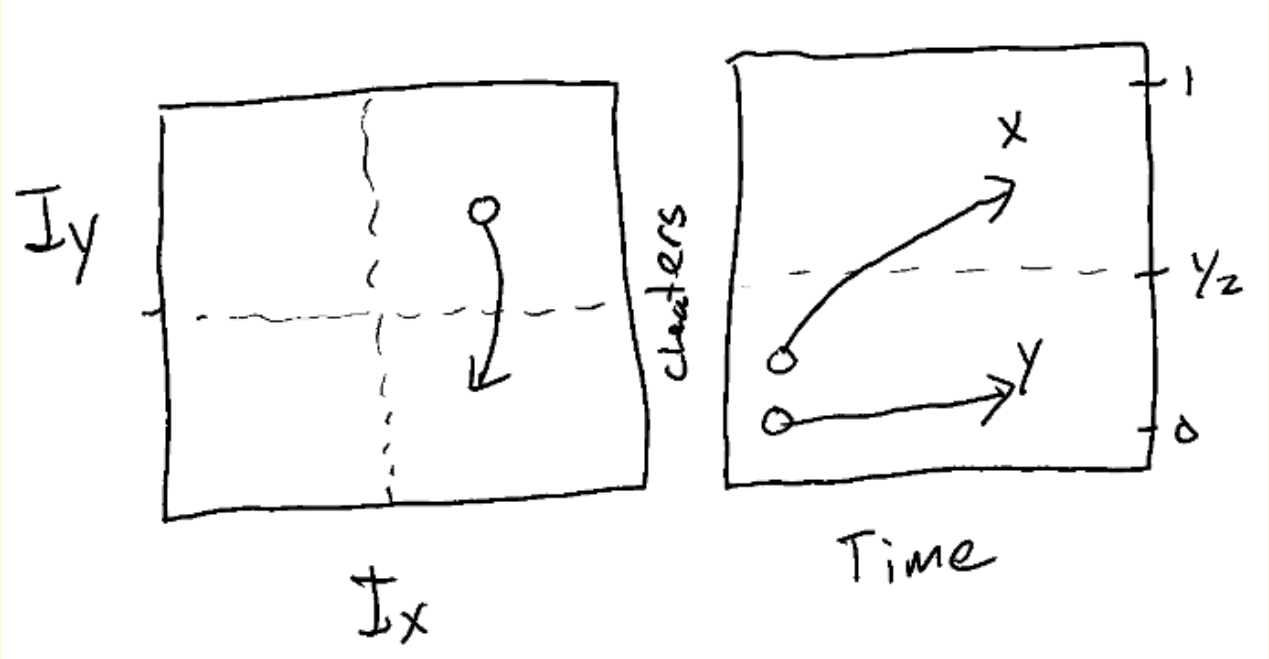
In an interspecific interaction, an individual is a **cheater** if

- it benefits from the interaction
- its partner incurs a cost from the interaction
- $\neq$ parasitism!
  - scale!

[5] Definition adapted from Jones et al. (2015)

Cheating and Mutualism Breakdown

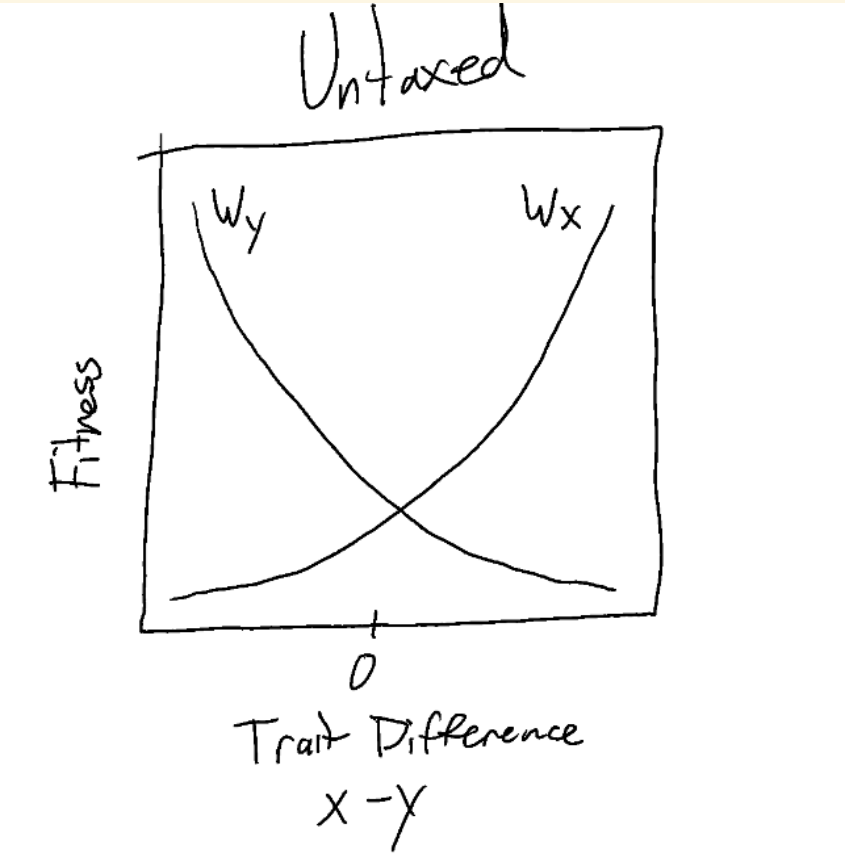


When does the mutualism breakdown = when is one species mostly cheaters?

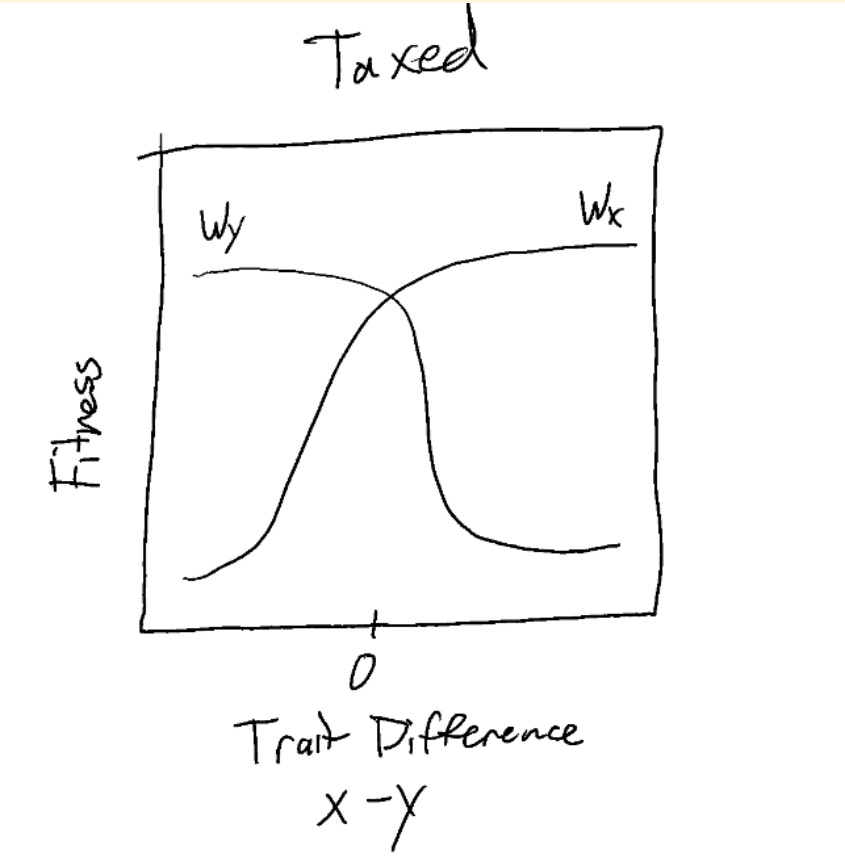
Approach

Consider two models of cheating: 1. untaxed cheating 2. taxed cheating

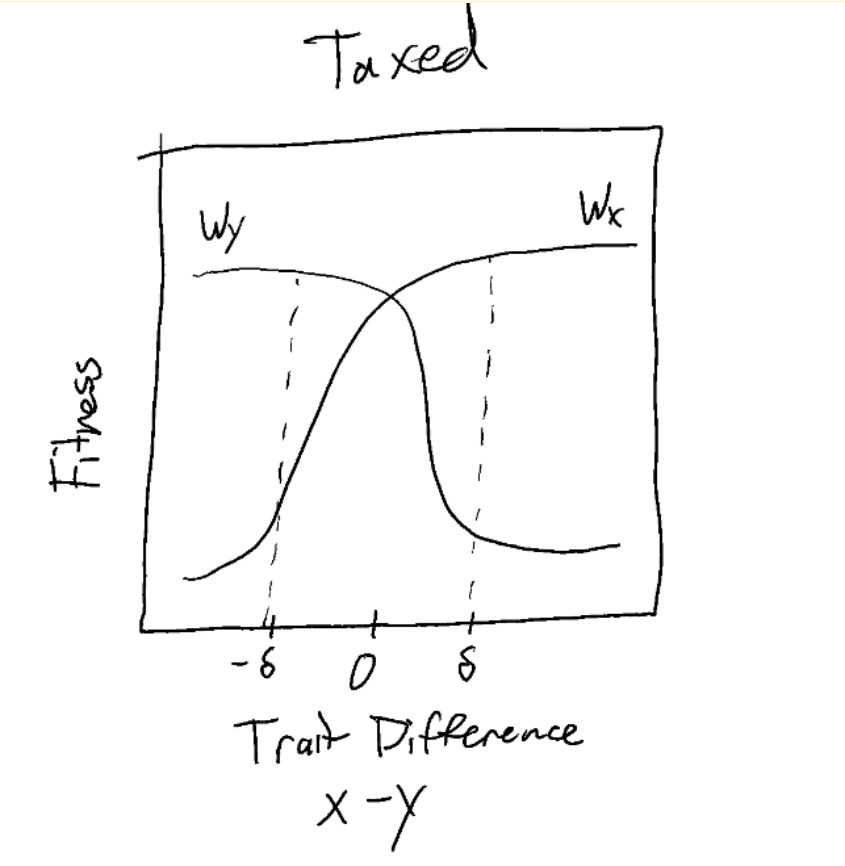
Untaxed Cheating



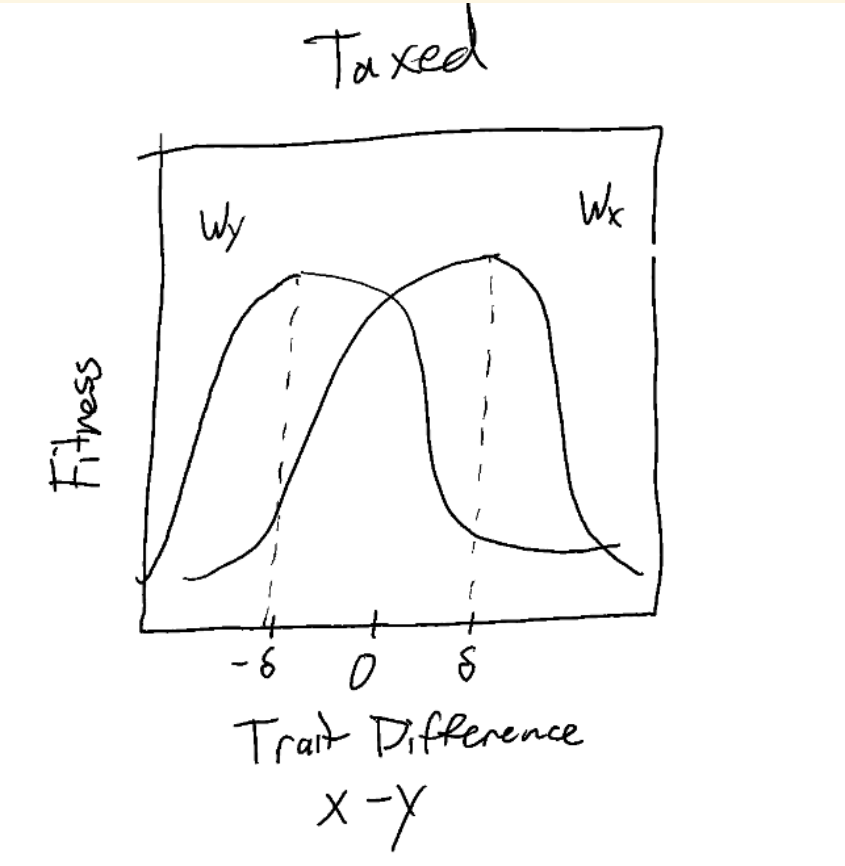
Taxed Cheating



Taxed Cheating



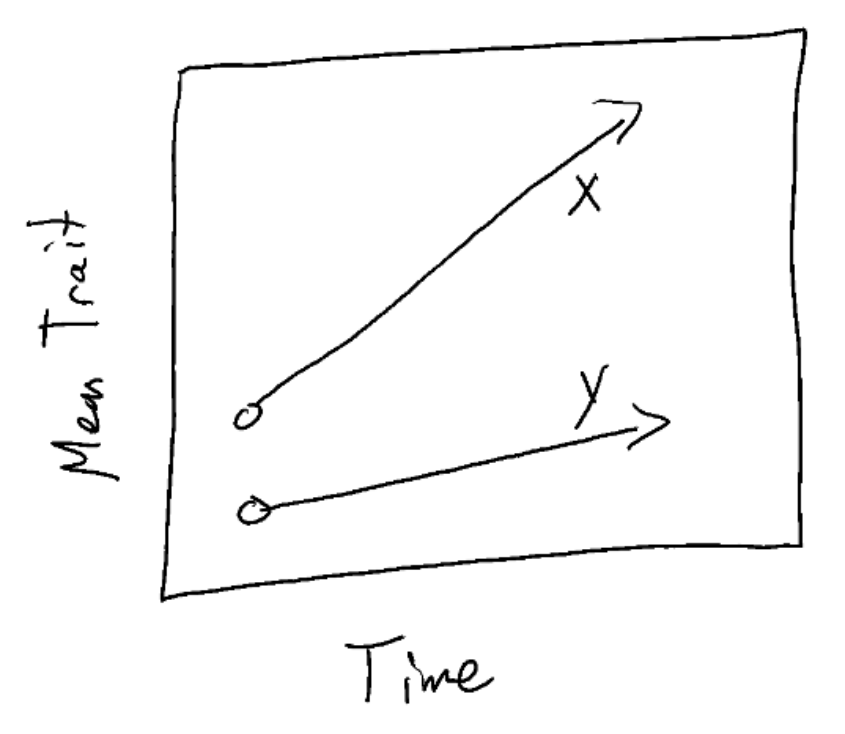
Taxed Cheating Approximation



Taxed Cheating in the Wild[6] - GIF

[6] Courtesy Stellenbosch University

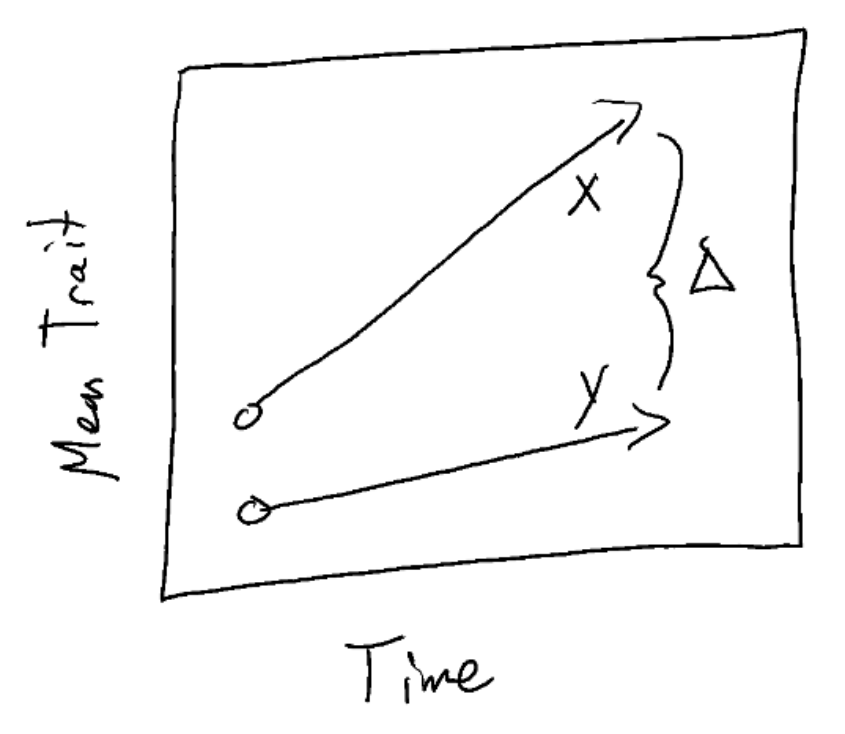
Coevolution under Untaxed Cheating



$$\dot{\bar{x}} = G_X B_X$$

$$\dot{\bar{y}} = G_Y B_Y$$

Coevolution under Untaxed Cheating



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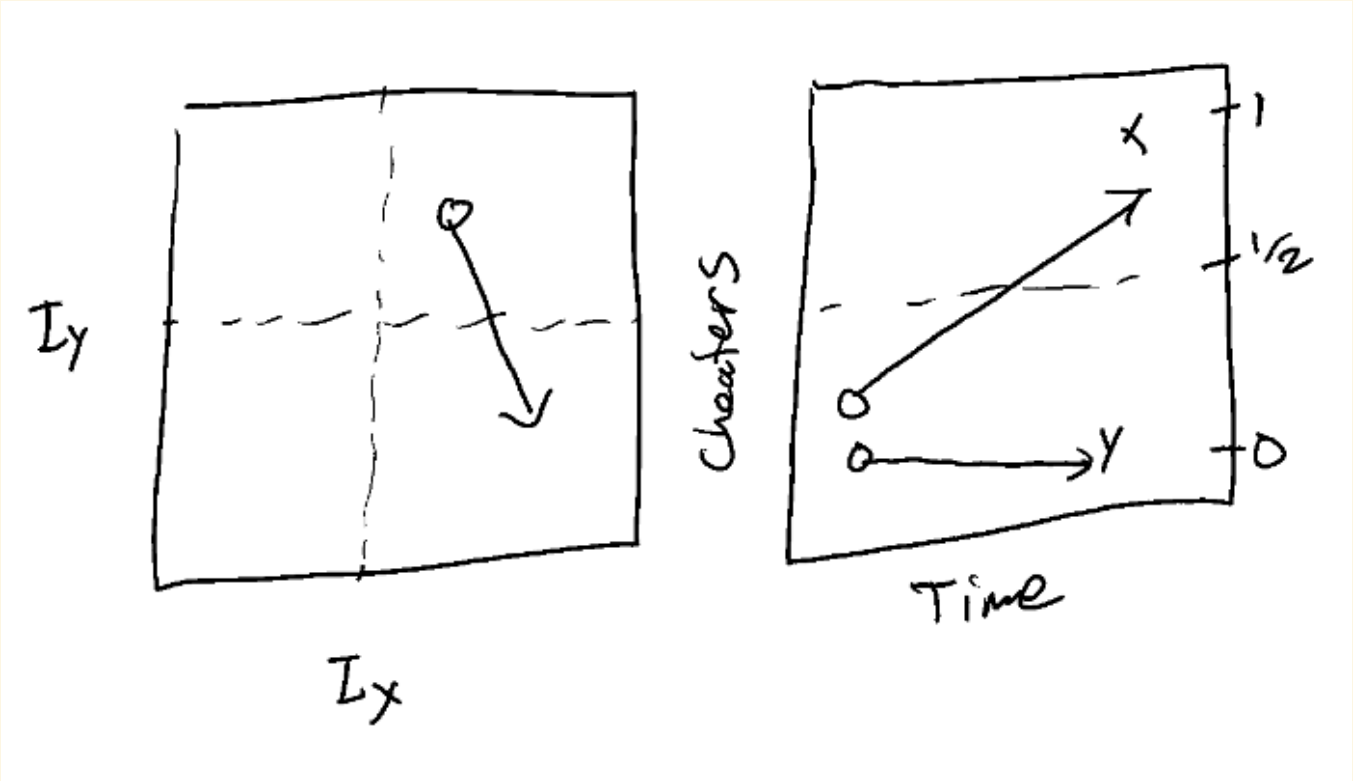
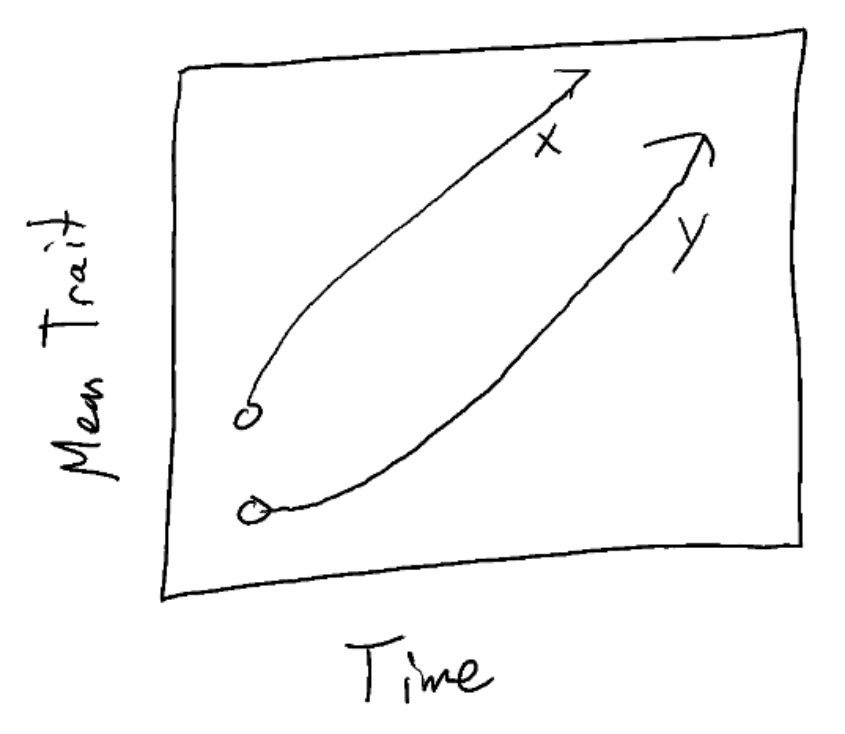
Untaxed Cheating Doomed to Parasitism



A mutualism dissolving into parasitism during an arms race

Coevolution under Taxed Cheating



$$\dot{\bar{x}} = G_X B_X (\bar{y} + \delta - \bar{x})$$

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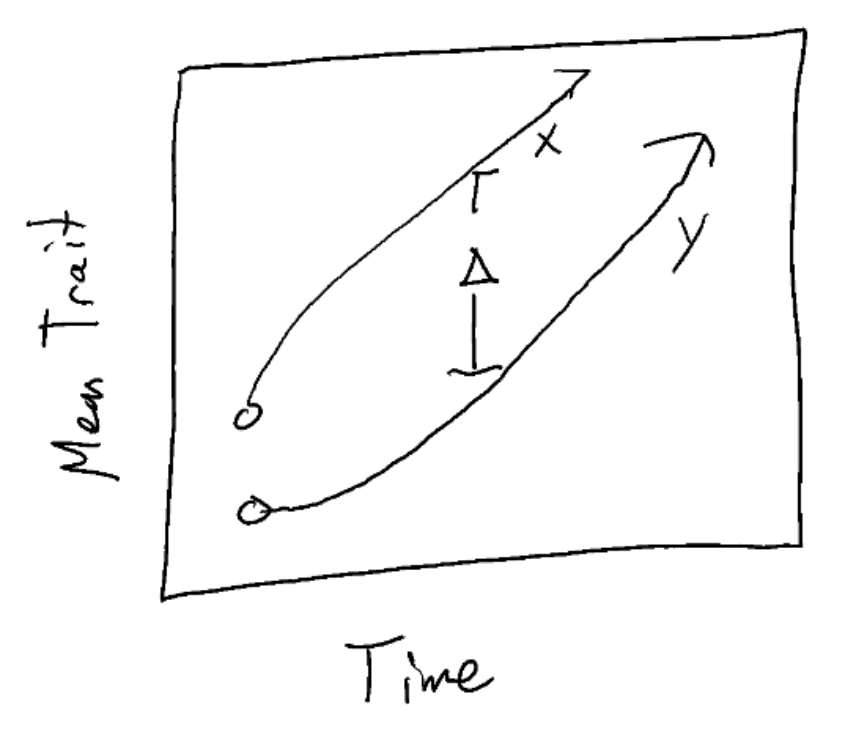

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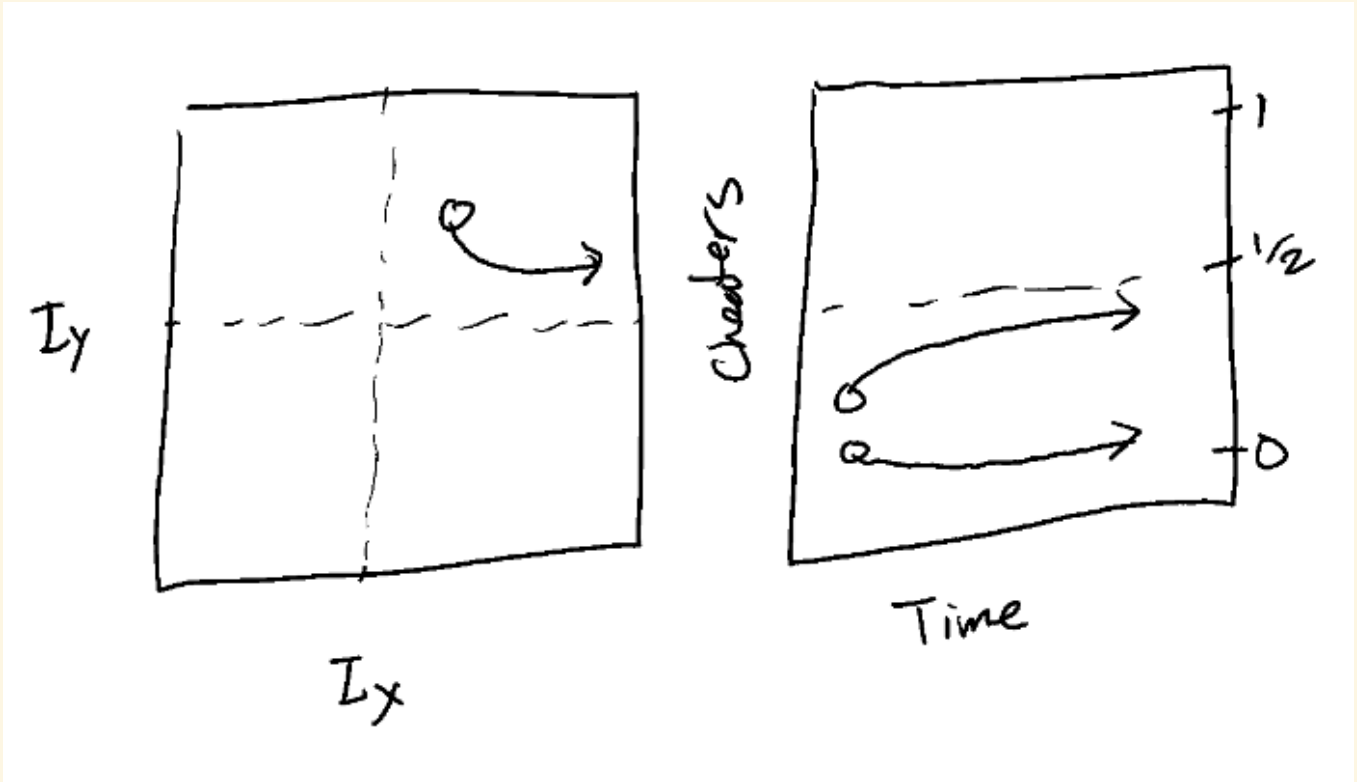
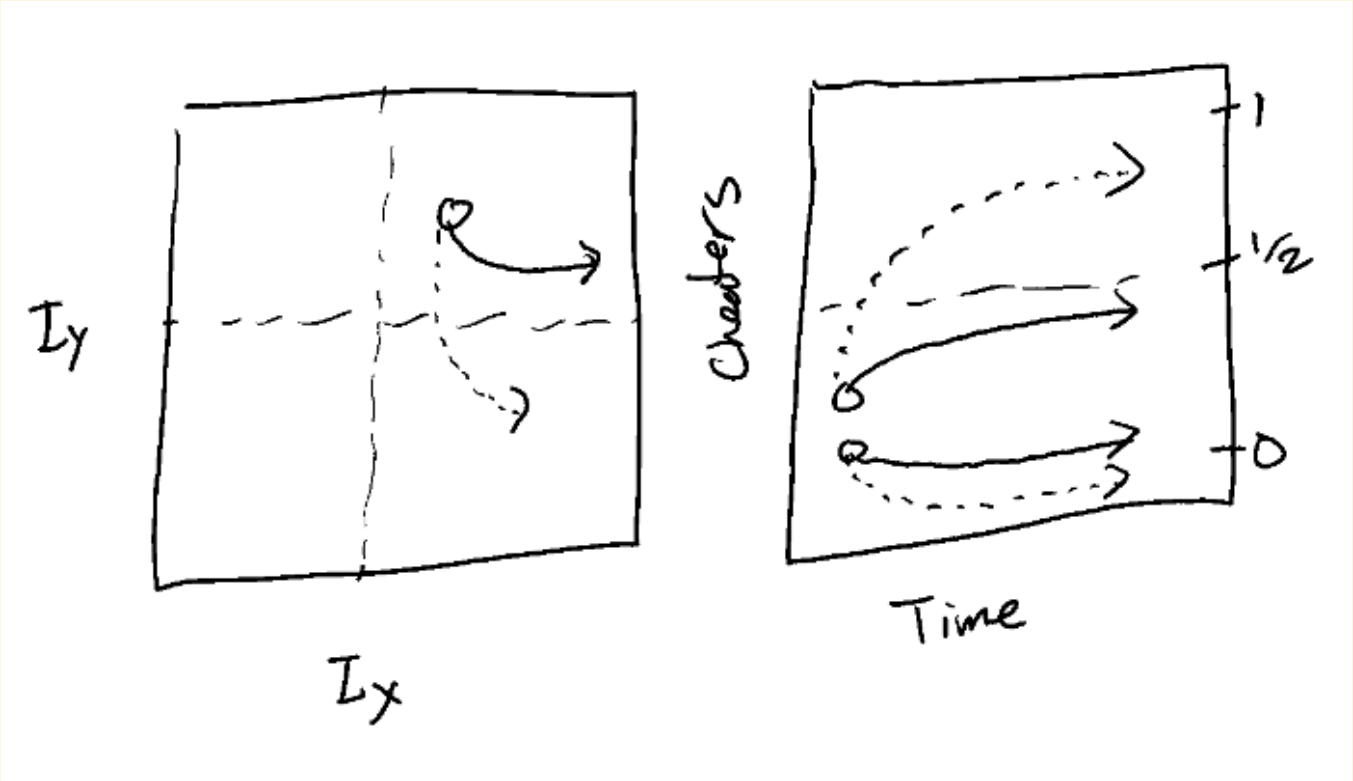
Taxed Cheating Prevents Parasitism



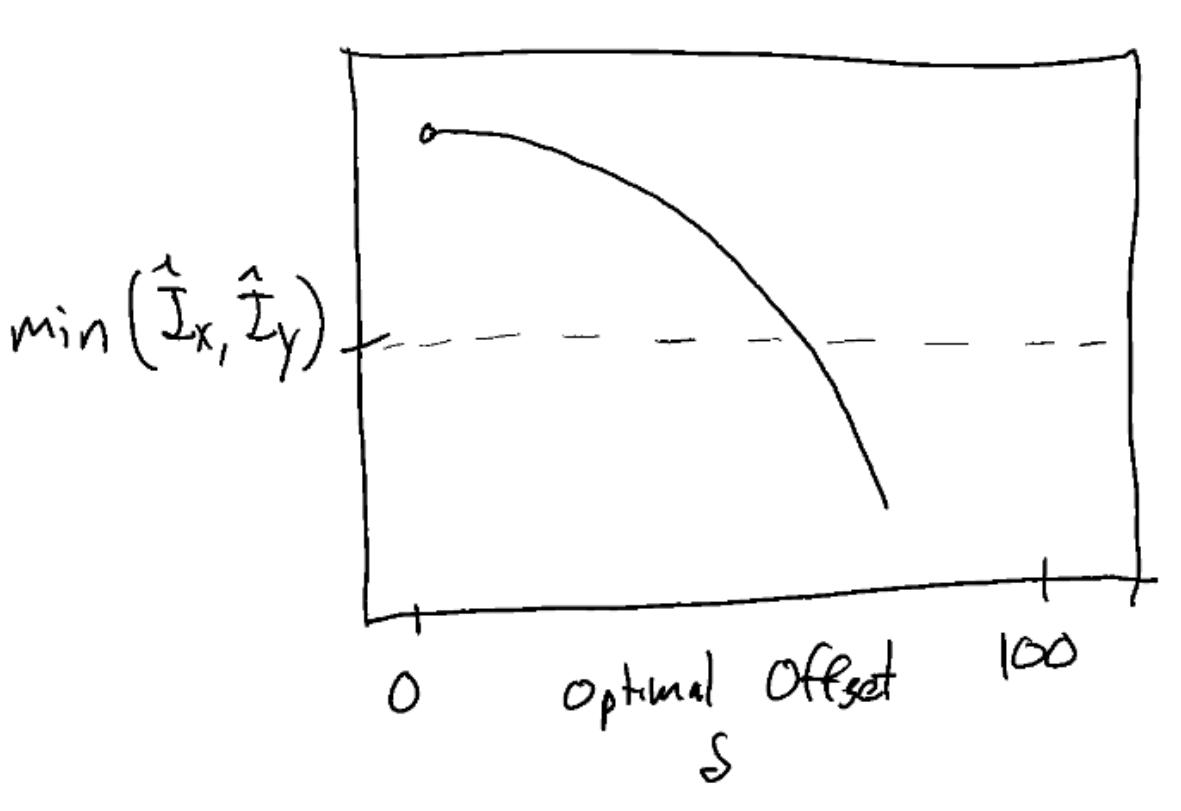
A mutualism avoiding parasitism during an arms race

Taxed Cheating Prevents Parasitism



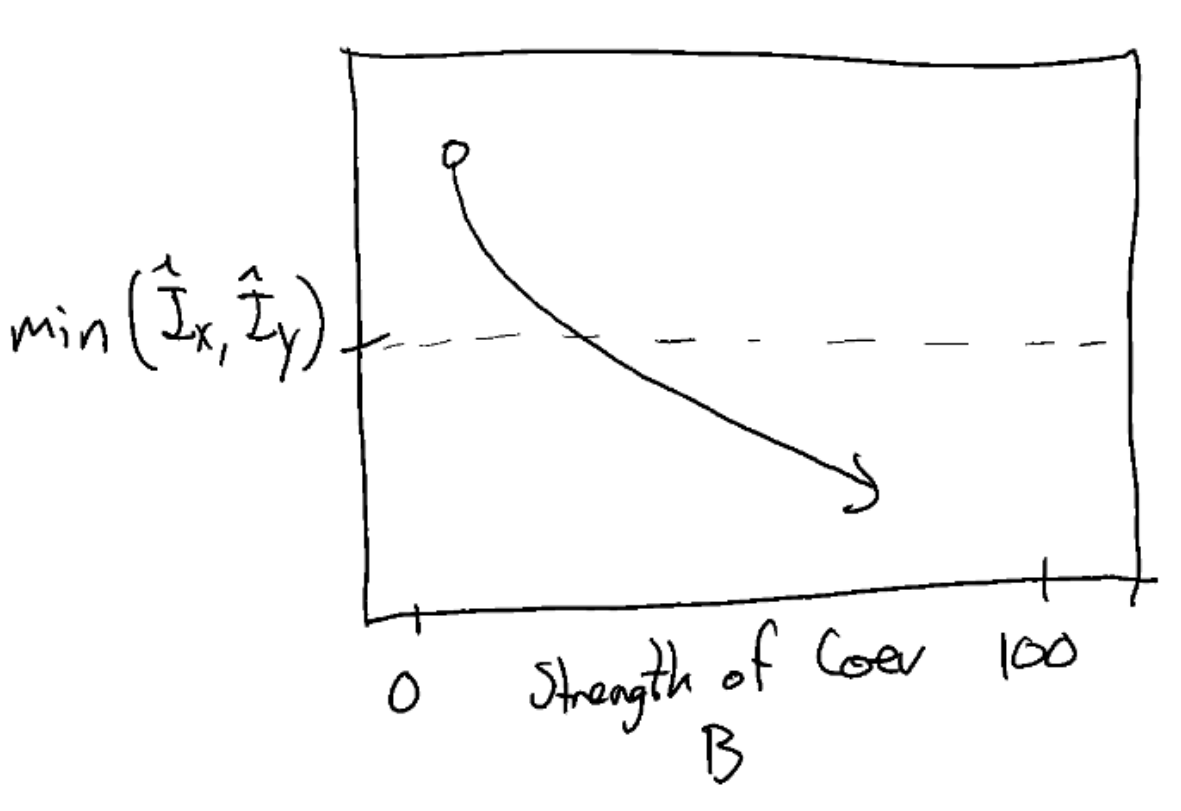
Variable outcomes are possible

Conditions for the Maintenance of Mutualism



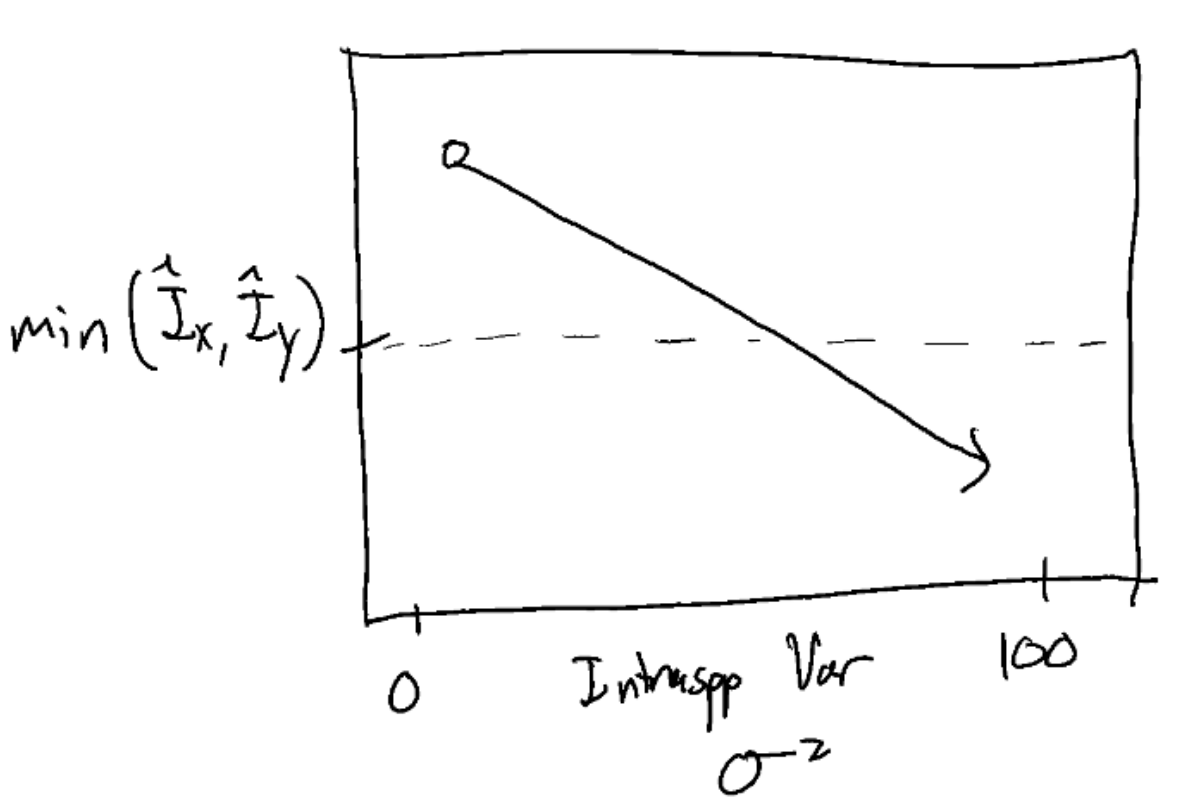
Equilibrium interaction effects as functions of optimal offset

Conditions for the Maintenance of Mutualism



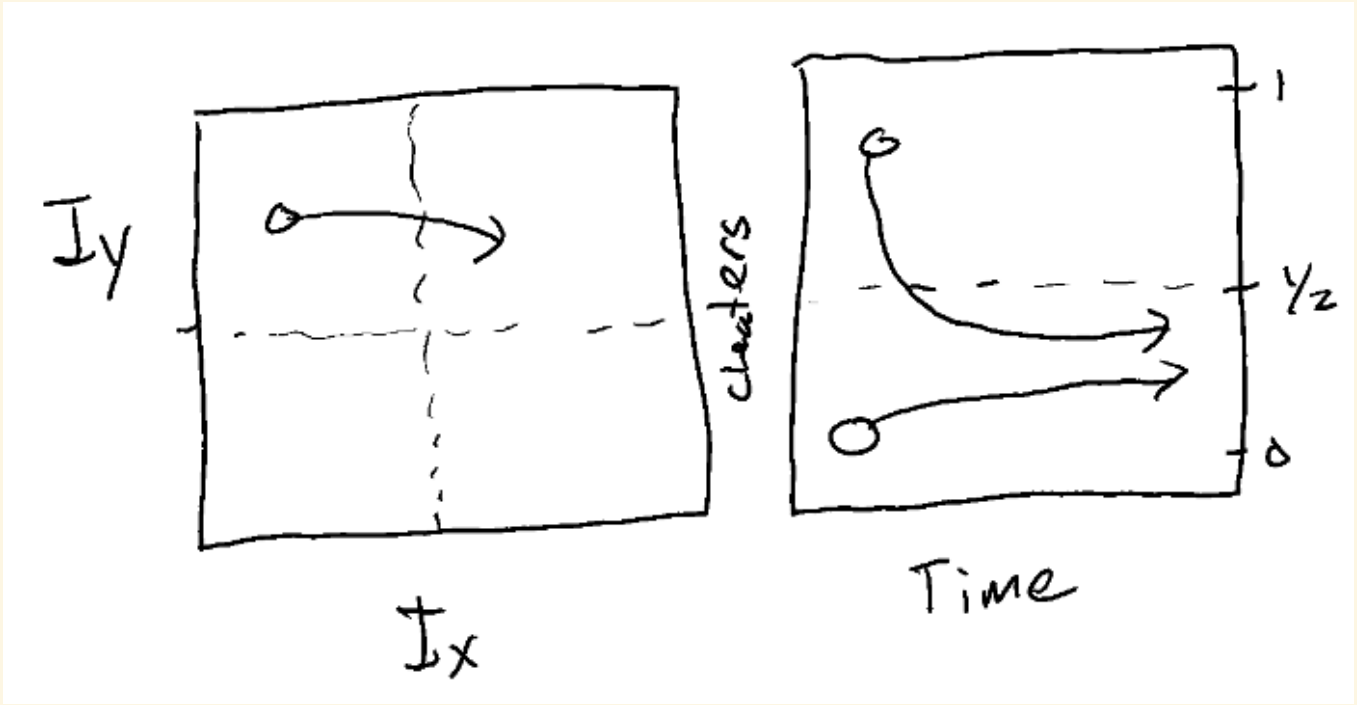
Equilibrium interaction effects as functions of biotic selection strength

Conditions for the Maintenance of Mutualism



Equilibrium interaction effects as functions of intraspecific variation

Taxed Cheating Converts Parasitism to Mutualism



M. longirostris Pollination Guild

Moegistorhynchus longirostris visiting *Babiana thunbergii*[7]

[7] Pauw et al. (2009)

Indirect Coevolutionary Effects?

Babiana thunbergii normally pollinated by malachite sunbirds[8]

[8] Pauw et al. (2009)

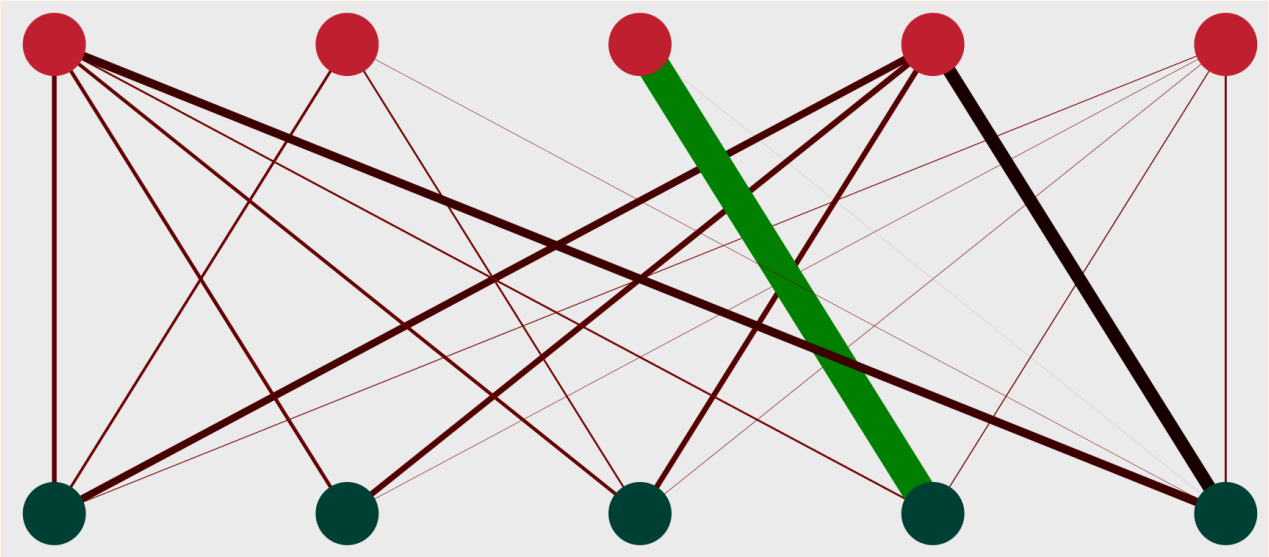
Implications for Mutualistic Networks

LETTER

doi:10.1038/nature24273

Indirect effects drive coevolution in mutualistic networks

Paulo R. Guimarães Jr[1], Mathias M. Pires[2], Pedro Jordano[3], Jordi Bascompte[4] & John N. Thompson[5]



Caveats

Ignores:

Caveats

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- Community context

Caveats

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- Feedback with abundance

Caveats

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- Spatial structure

Caveats

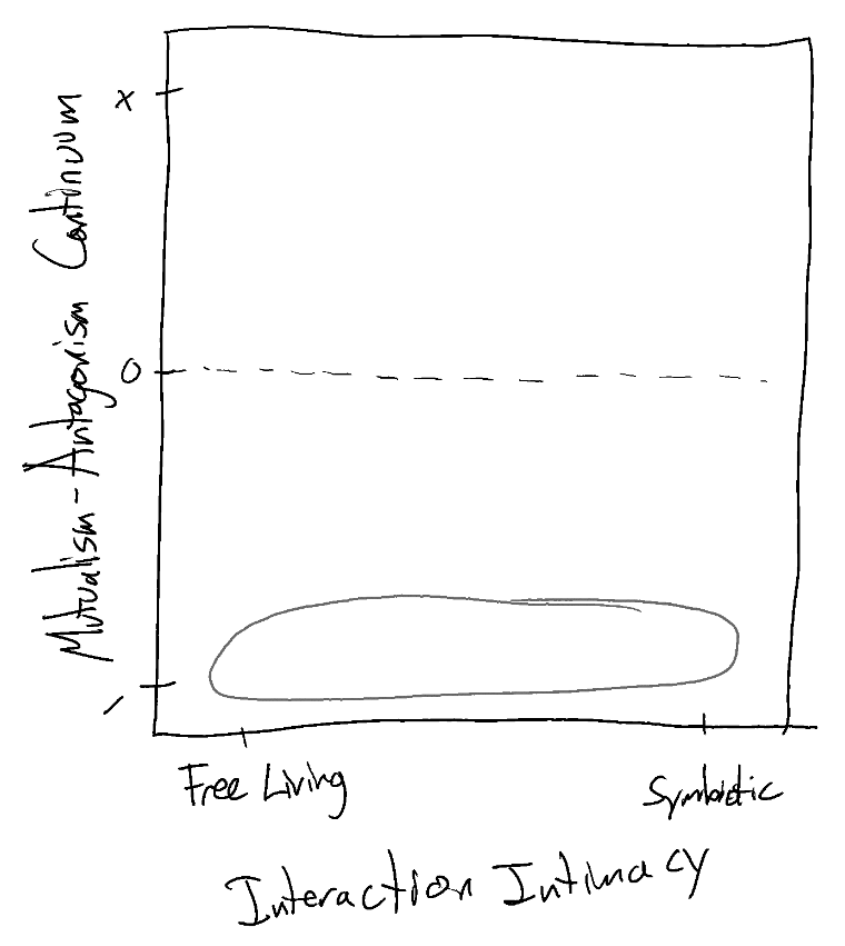
Ignores:

- Community context
- Feedback with abundance
- Spatial structure
  - Of particular interest today

The Geographic Mosaic of Coevolution

motivate study of local adaptation

Host-parasite coevolution in continuous space



Road-map

Spatial Host-Parasite Coevolution

[9] Best et al. (2010)
[10] Nuismer et al. (2003)
[11] Nuismer (2017)

Spatial Host-Parasite Coevolution

- Lowers pathogen transmissibility and virulence[9]

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Spatial Host-Parasite Coevolution

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Spatial Host-Parasite Coevolution

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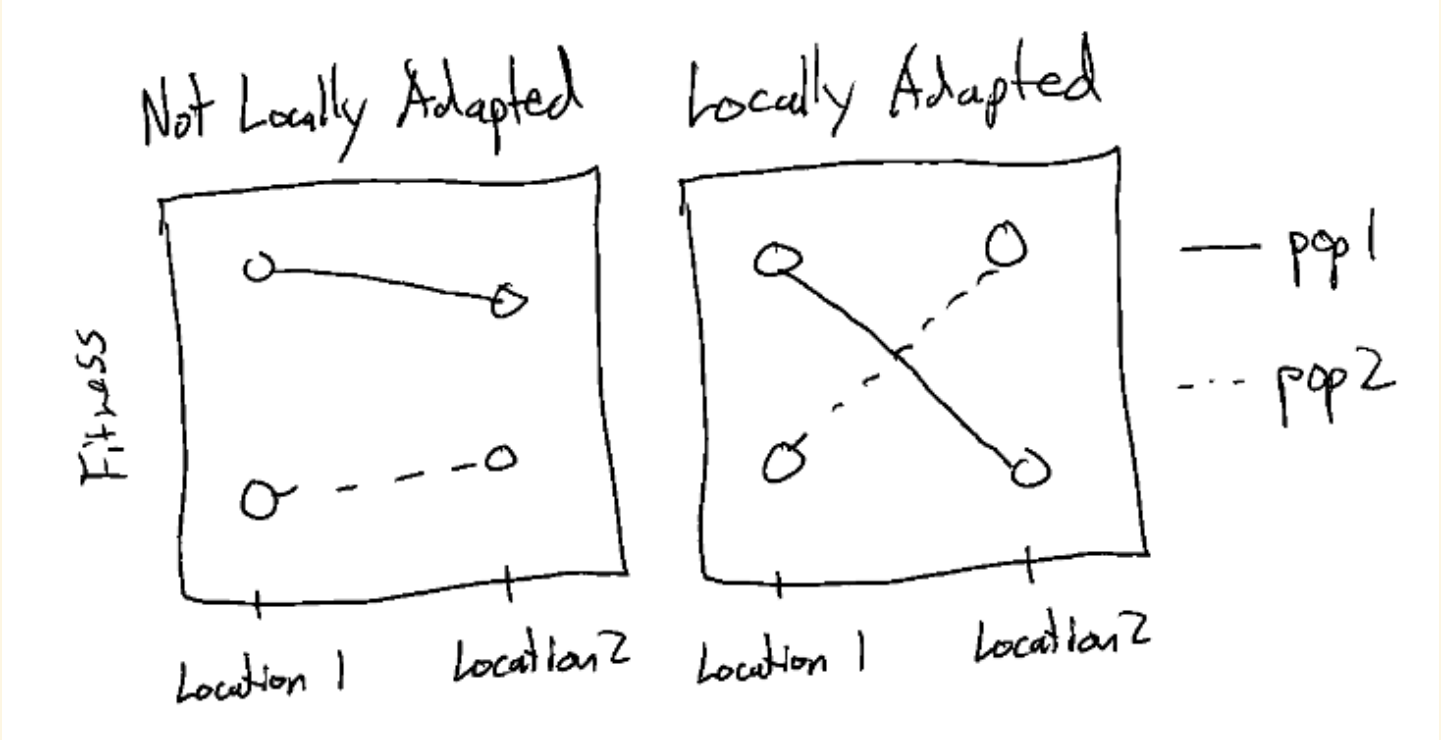
What is Local Adaptation?



Determinants of Host-Parasite Local Adaptation[12]

[12] Gandon & Nuismer (2009)

Determinants of Host-Parasite Local Adaptation[12]

- Relative selection strengths

[12] Gandon & Nuismer (2009)

Determinants of Host-Parasite Local Adaptation[12]

- Relative selection strengths
- Selection mosaics

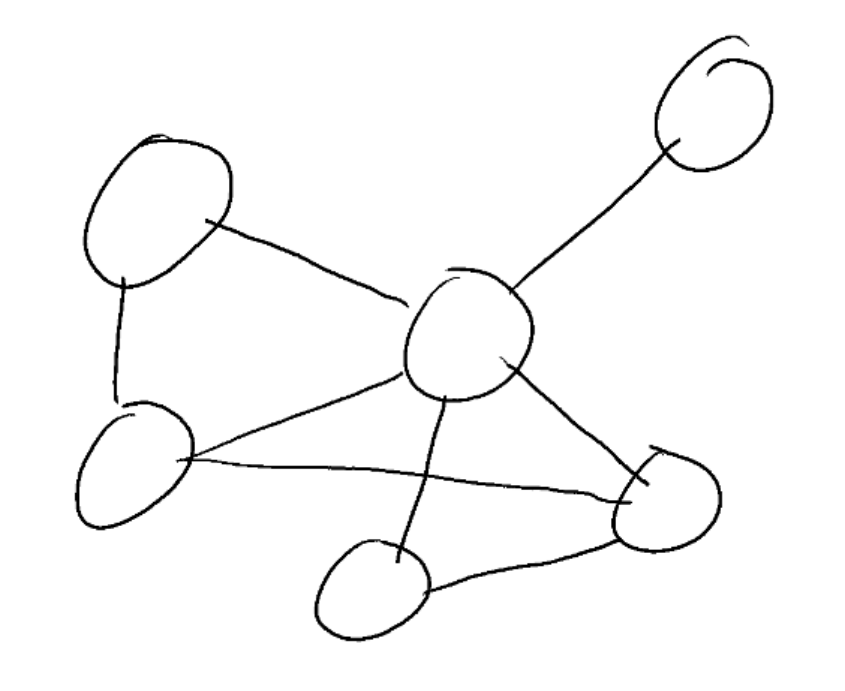
[12] Gandon & Nuismer (2009)

Determinants of Host-Parasite Local Adaptation[12]

- Relative selection strengths
- Selection mosaics
- Relative dispersal abilities

[12] Gandon & Nuismer (2009)

Host-Parasite Models Assume Discrete Space

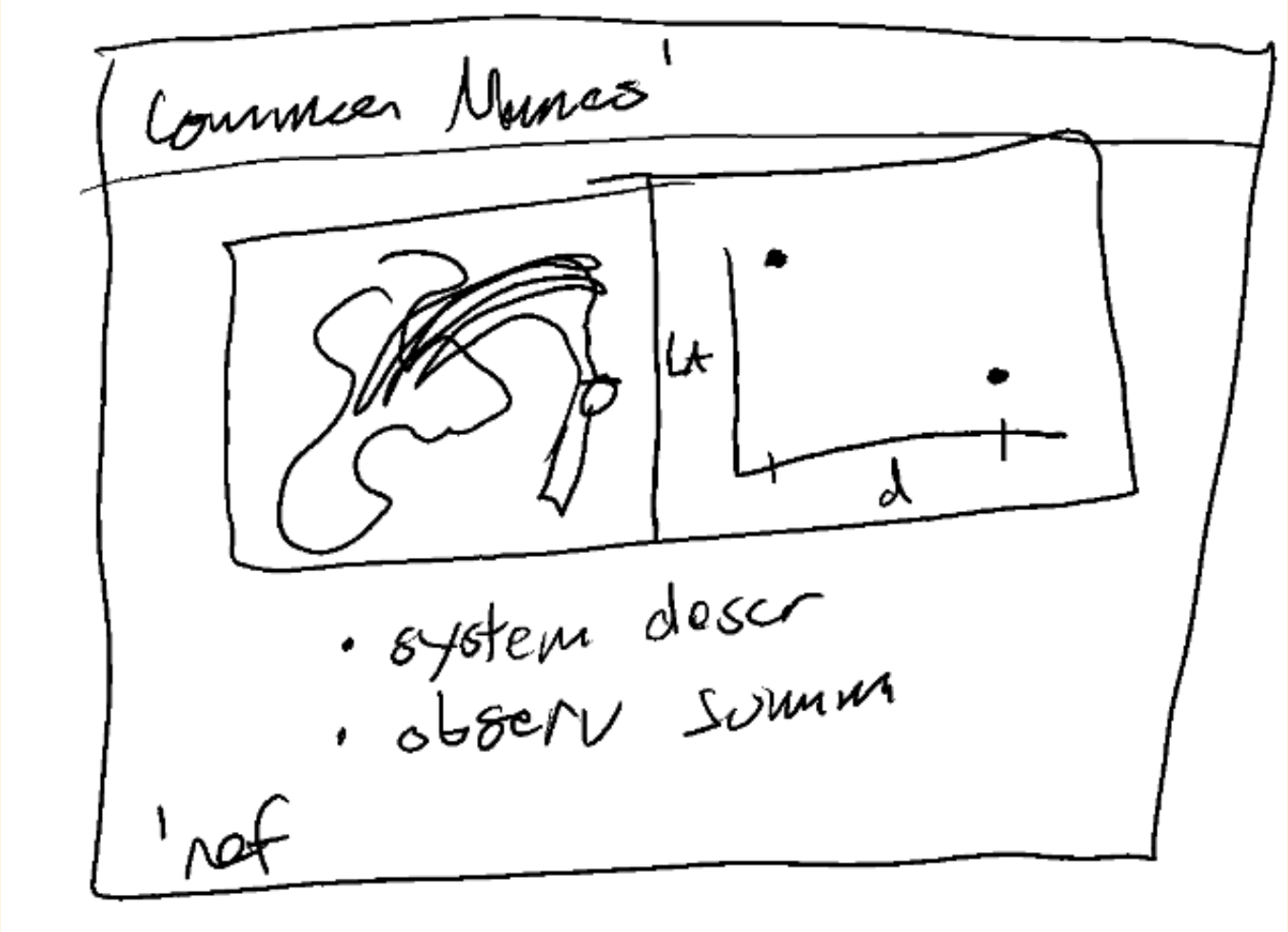


A metapopulation

Empirical Systems Exhibit Cross-Scale Variation

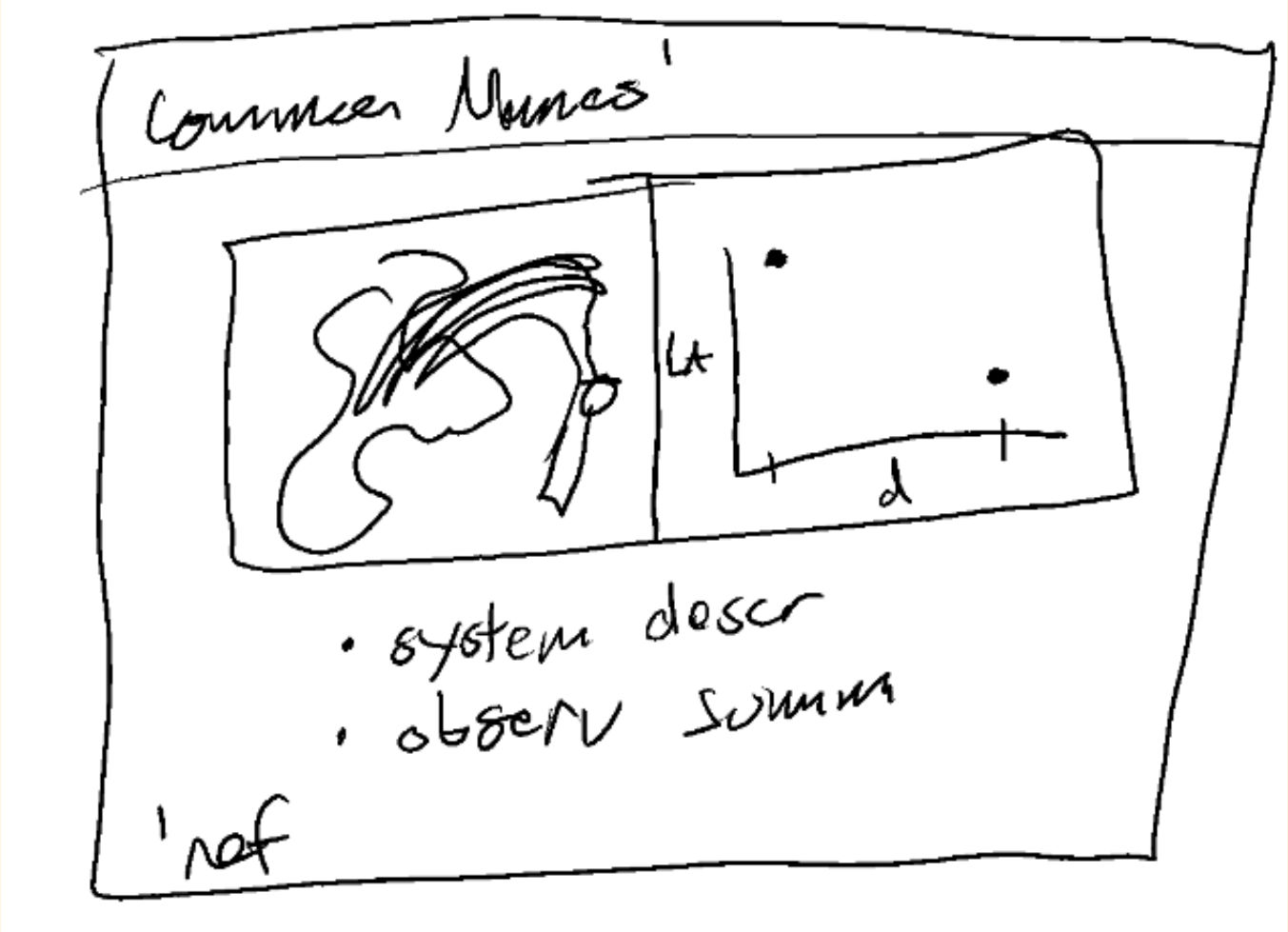
Local adapation can vary across distances measured

Rust Pathogen and Perennial Herb[13]



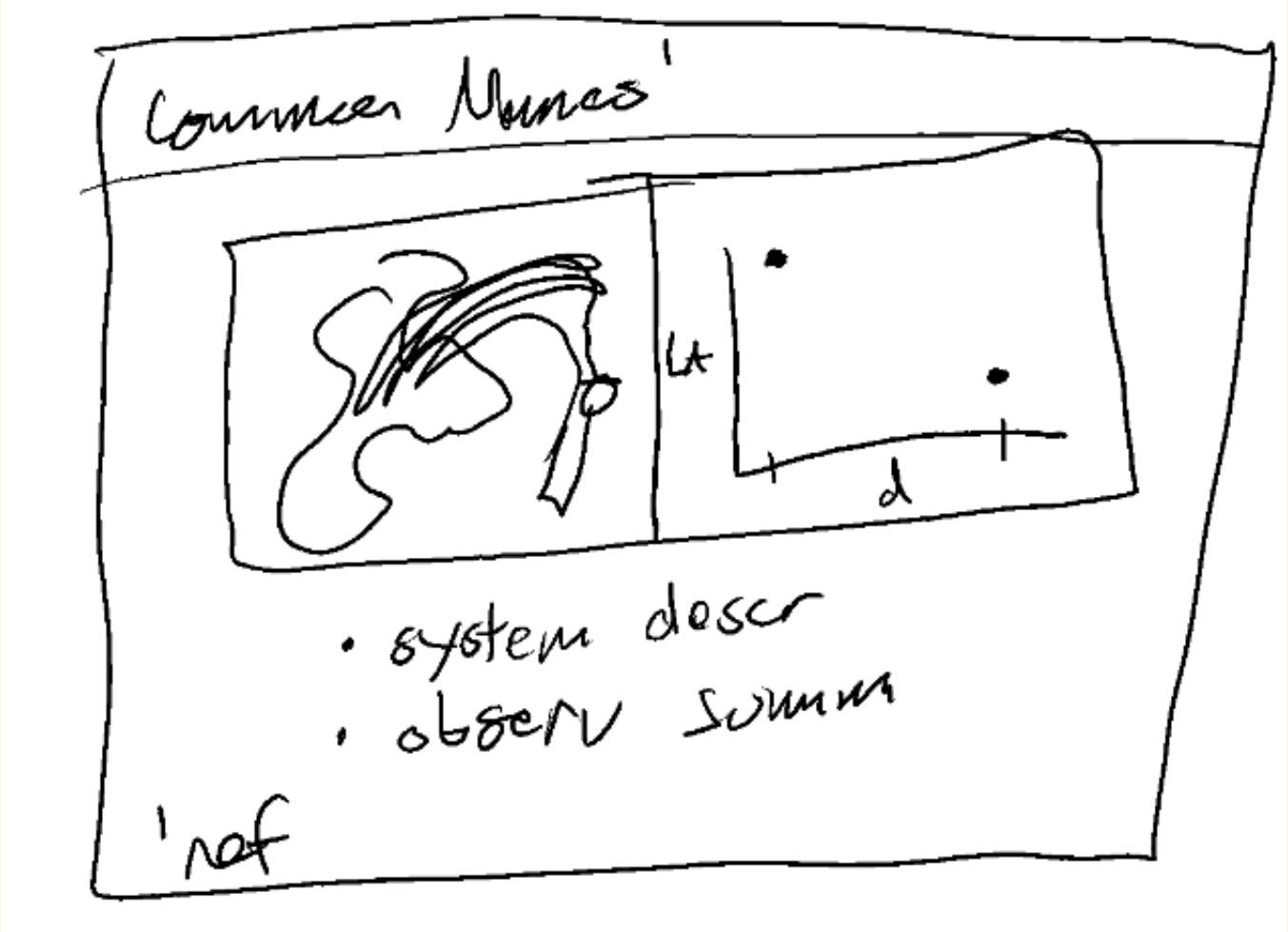
[13] Thrall et al. (2002)

Armored Scale Insect and Mulberry Trees[14]



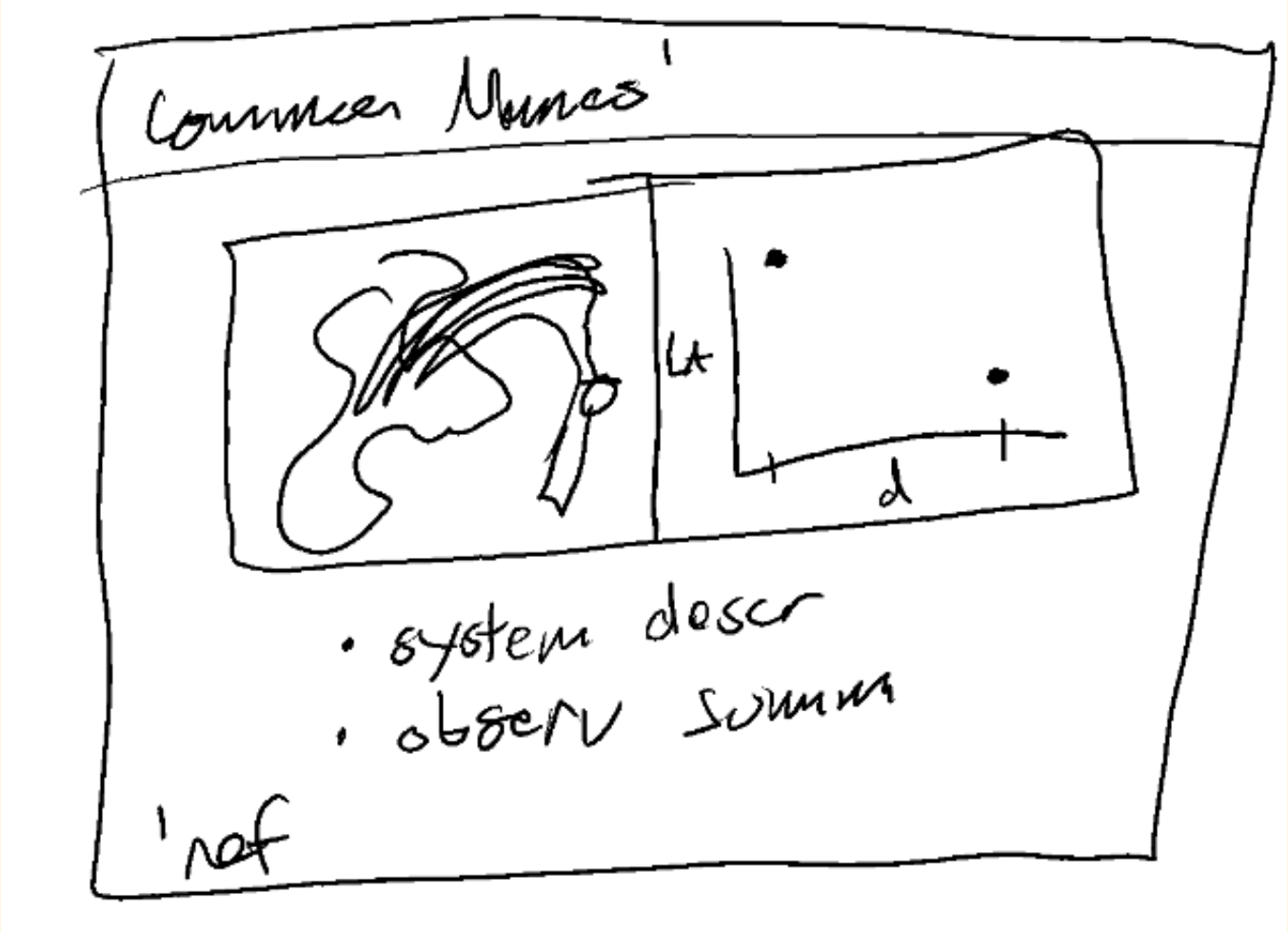
[14] Hanks & Denno (1994)

Hoverfly and Host Ant[15]



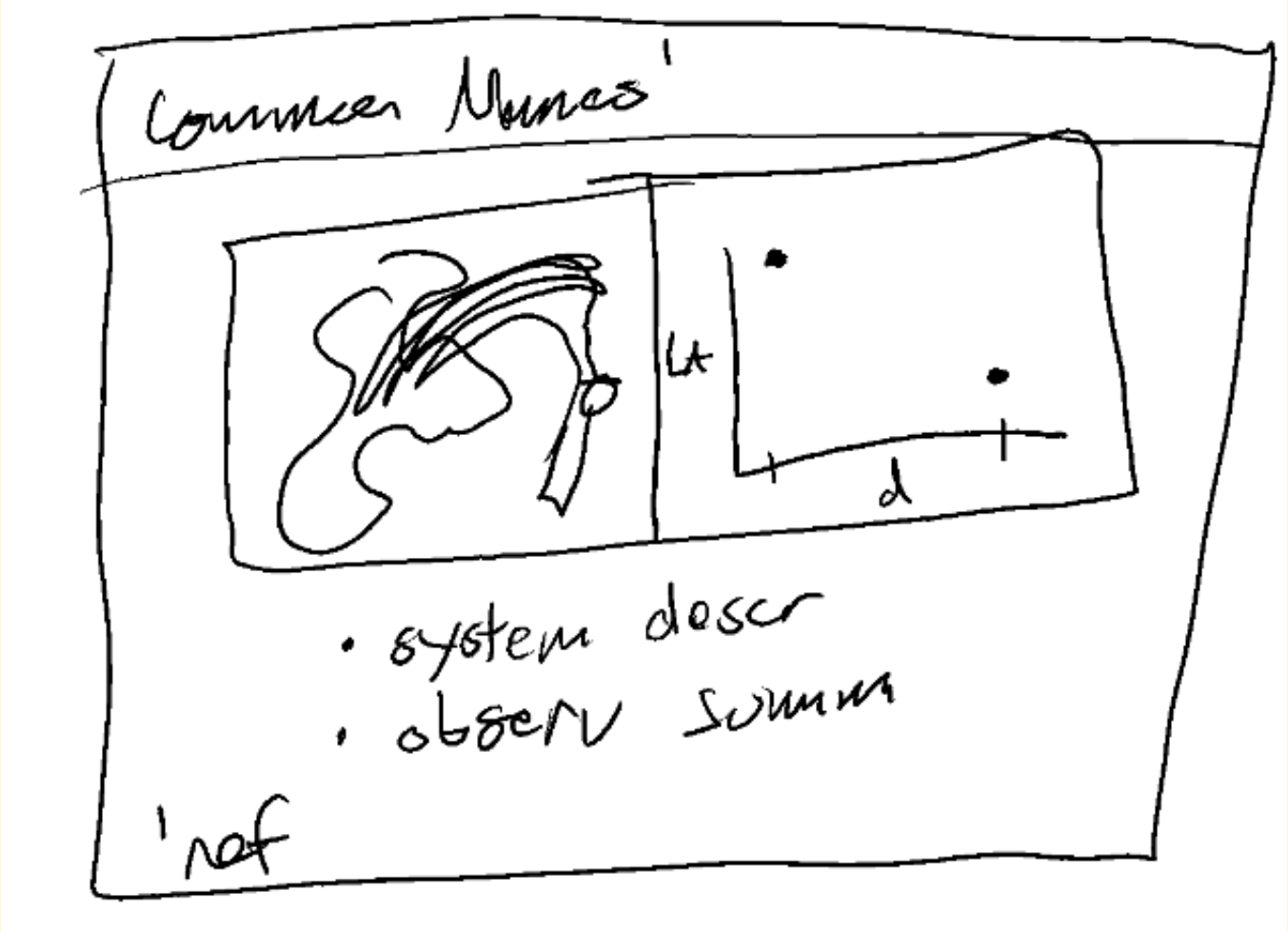
[15] Schonrogge et al (2006)

Anther-Smut Fungus and Host Plant[16]



[16] Kaltz et al (1999)

Powdery Mildew and Ribwort Plantain Host[17]



[17] Tack et al (2014)

Why do Host-Parasite Systems Exhibit Cross-Scale Variation?

insert figure of general pattern observed

Approach

A model of host-para coev in cont space an index of local adaptation that accounts for distance

The Model

The Model

- Dispersal

The Model

- Dispersal
- Abiotic Stabilizing Selection

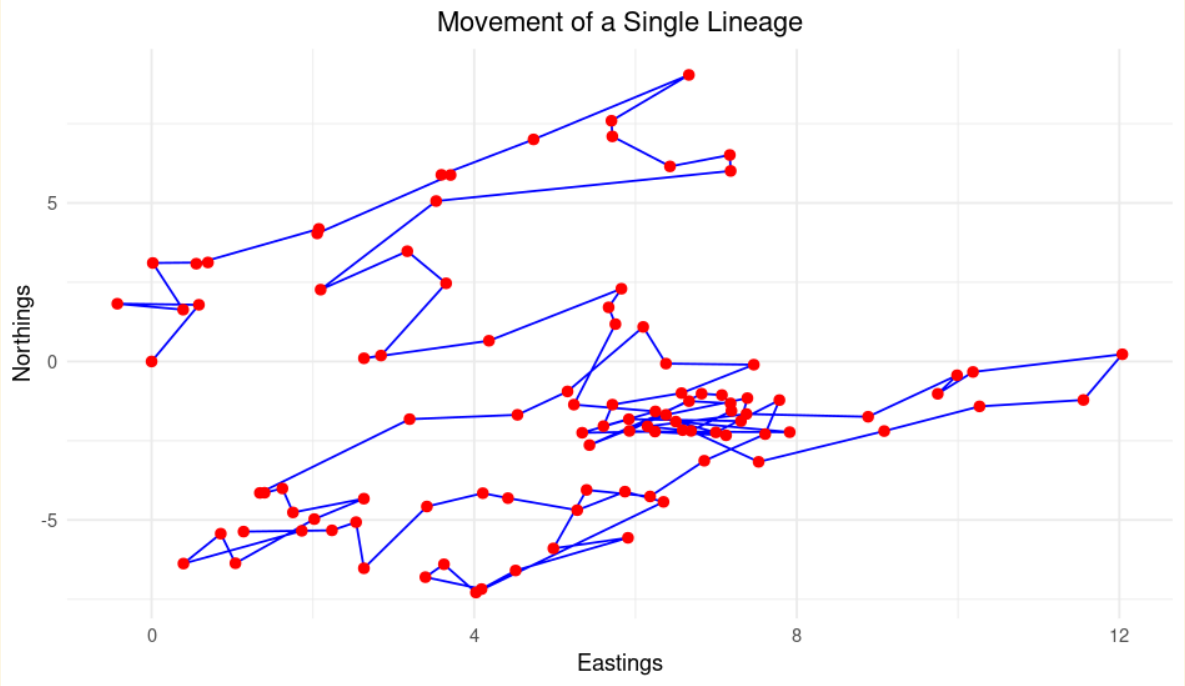
The Model

- Dispersal
- Abiotic Stabilizing Selection
- Interspecific Biotic Selection

The Model

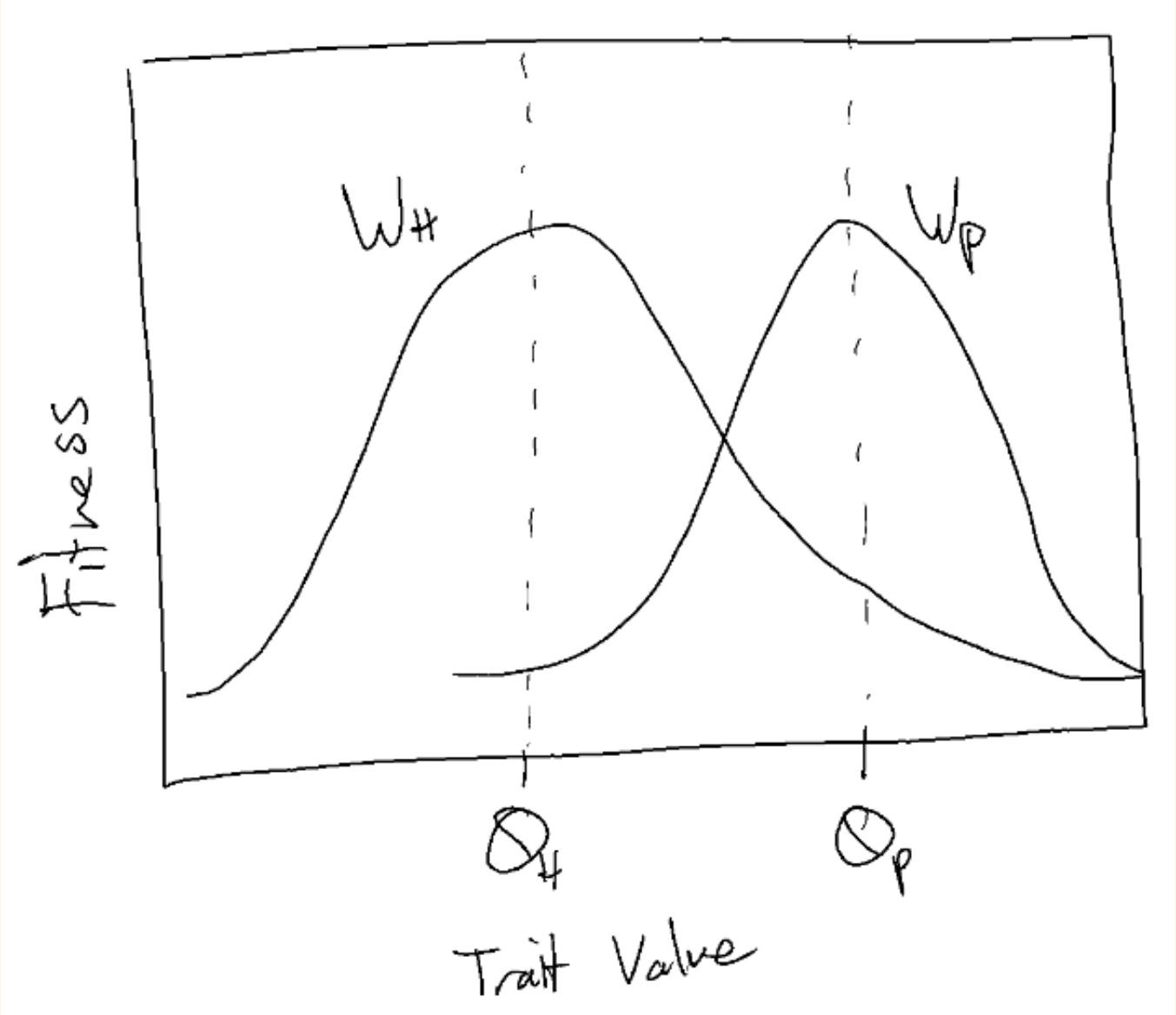
- Dispersal
- Abiotic Stabilizing Selection
- Interspecific Biotic Selection
- Random Genetic Drift

Dispersal



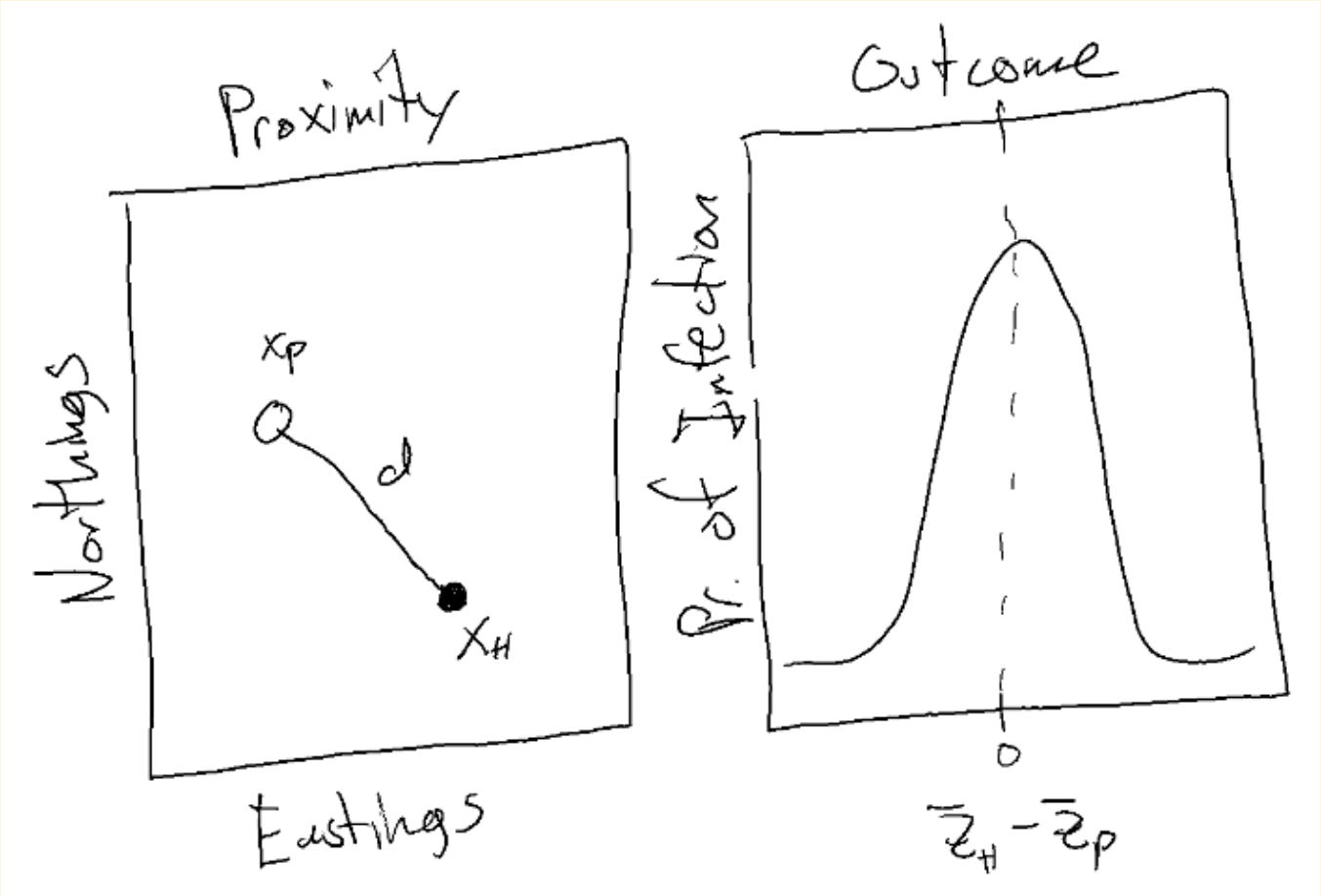
Movement of a single lineage

Abiotic Stabilizing Selection



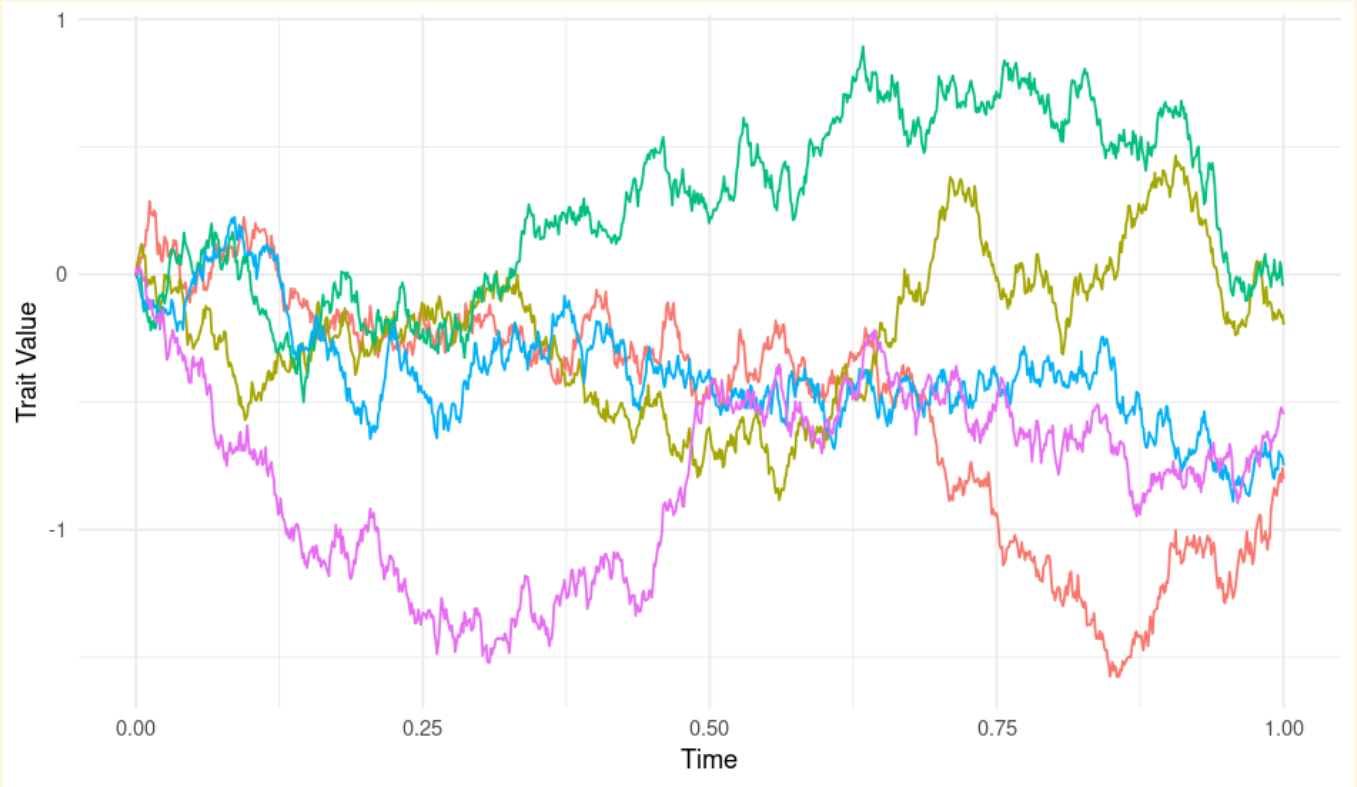
Included to guarantee model has equilbirium

Biotic Selection



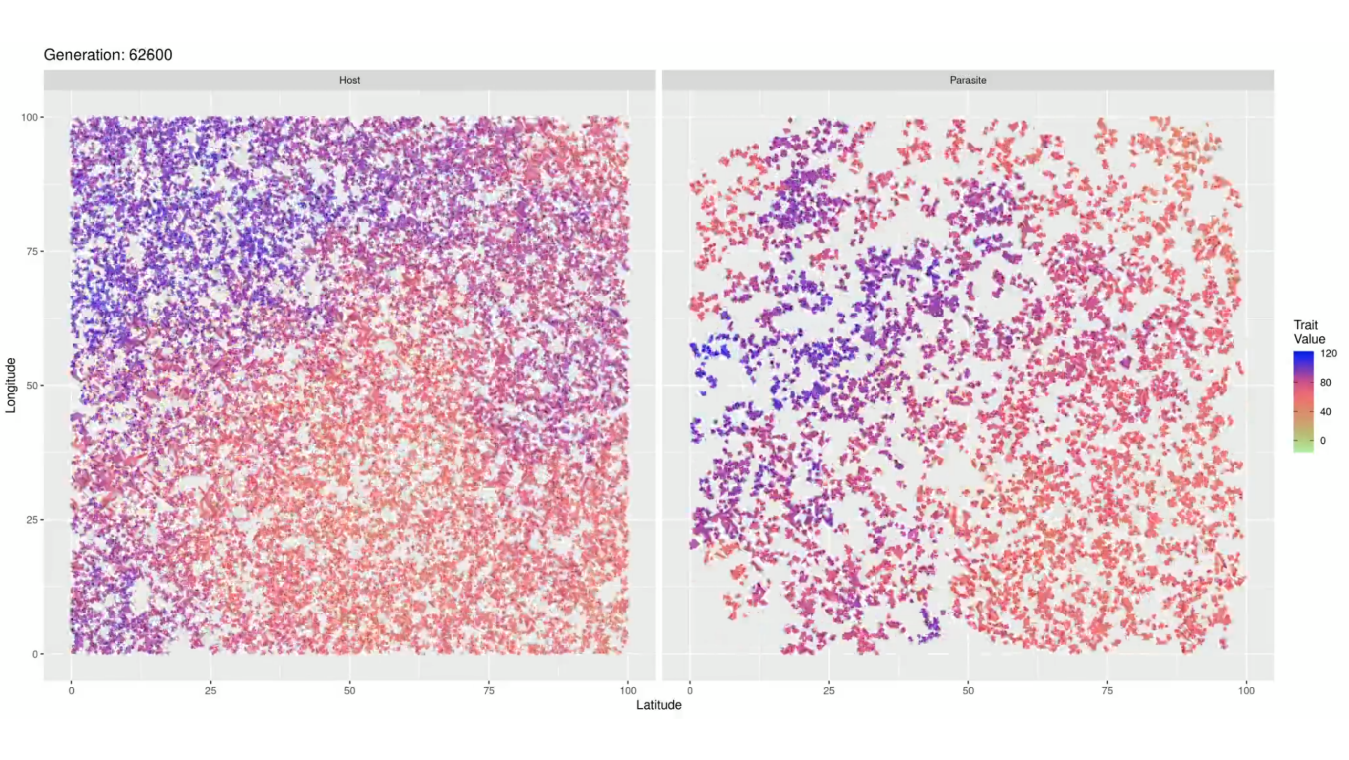
Encounters depend on proximity and infection probability depends on how well traits match

Random Genetic Drift



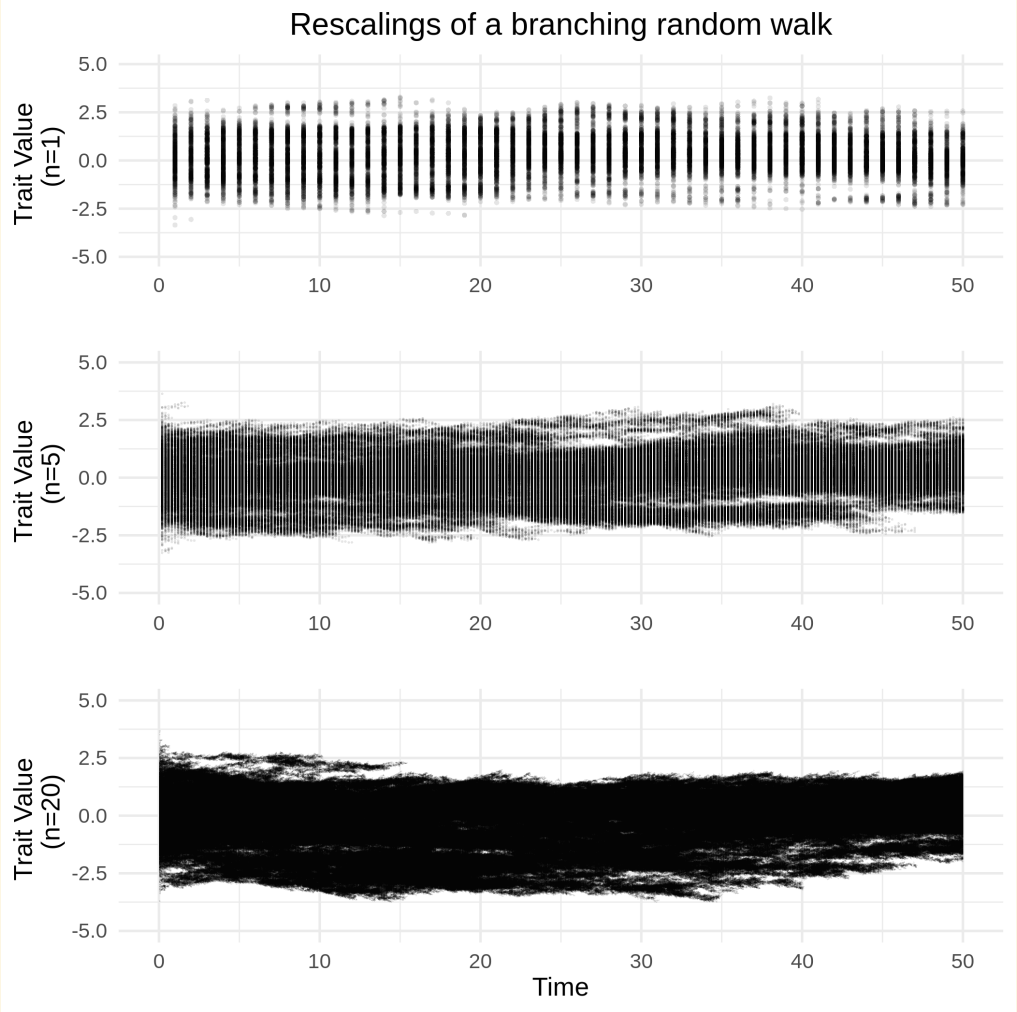
Evolution in Response to Random Genetic Drift

Individual-Based Model



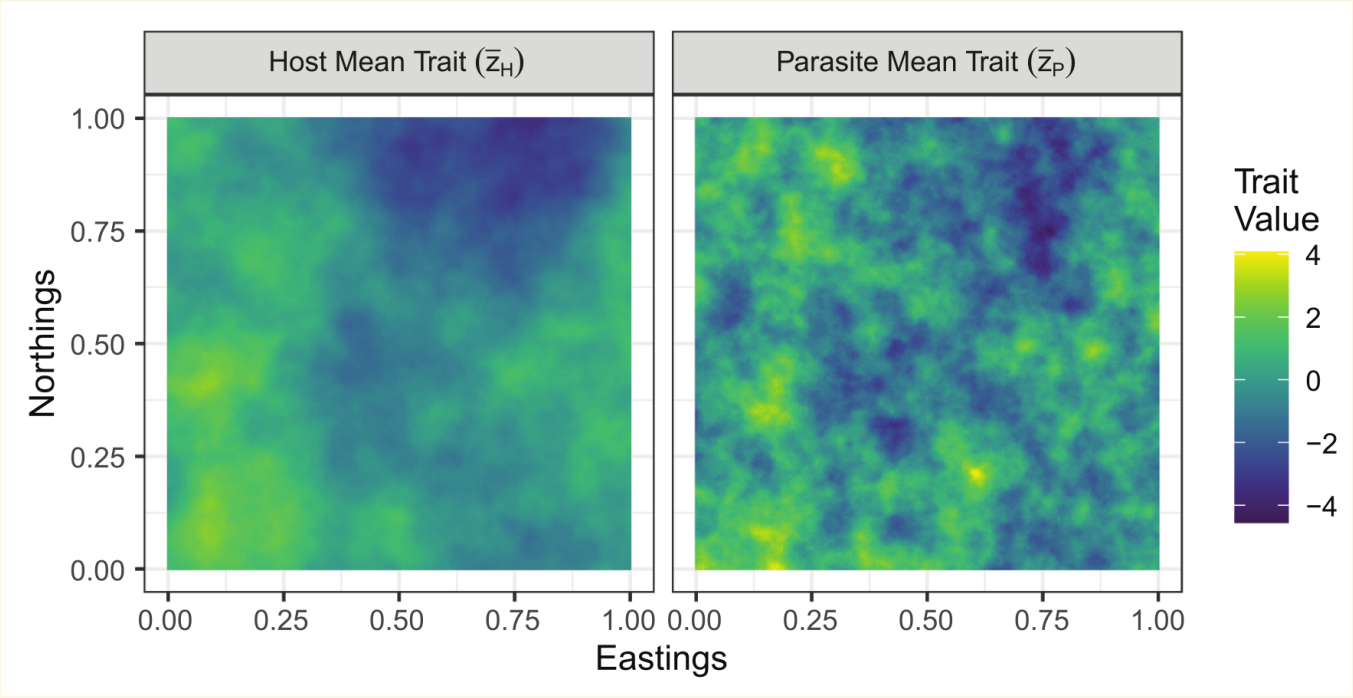
Animation

Diffusion Limit



Used to obtain population-level model from individual-based model

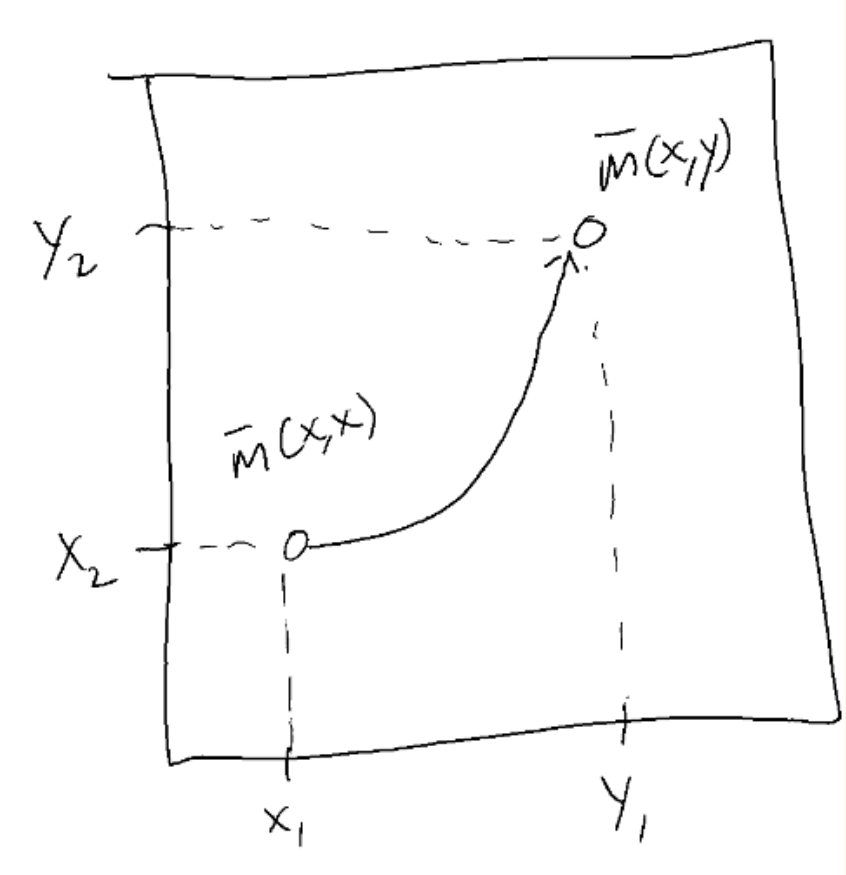
SPDE Model



$$\dot{\bar{z}}_H = -A_H\bar{z}_H - B_H(\bar{z}_P - \bar{z}_H) + \frac{\sigma_H^2}{2}\nabla^2\bar{z}_H + D_H\xi_H$$

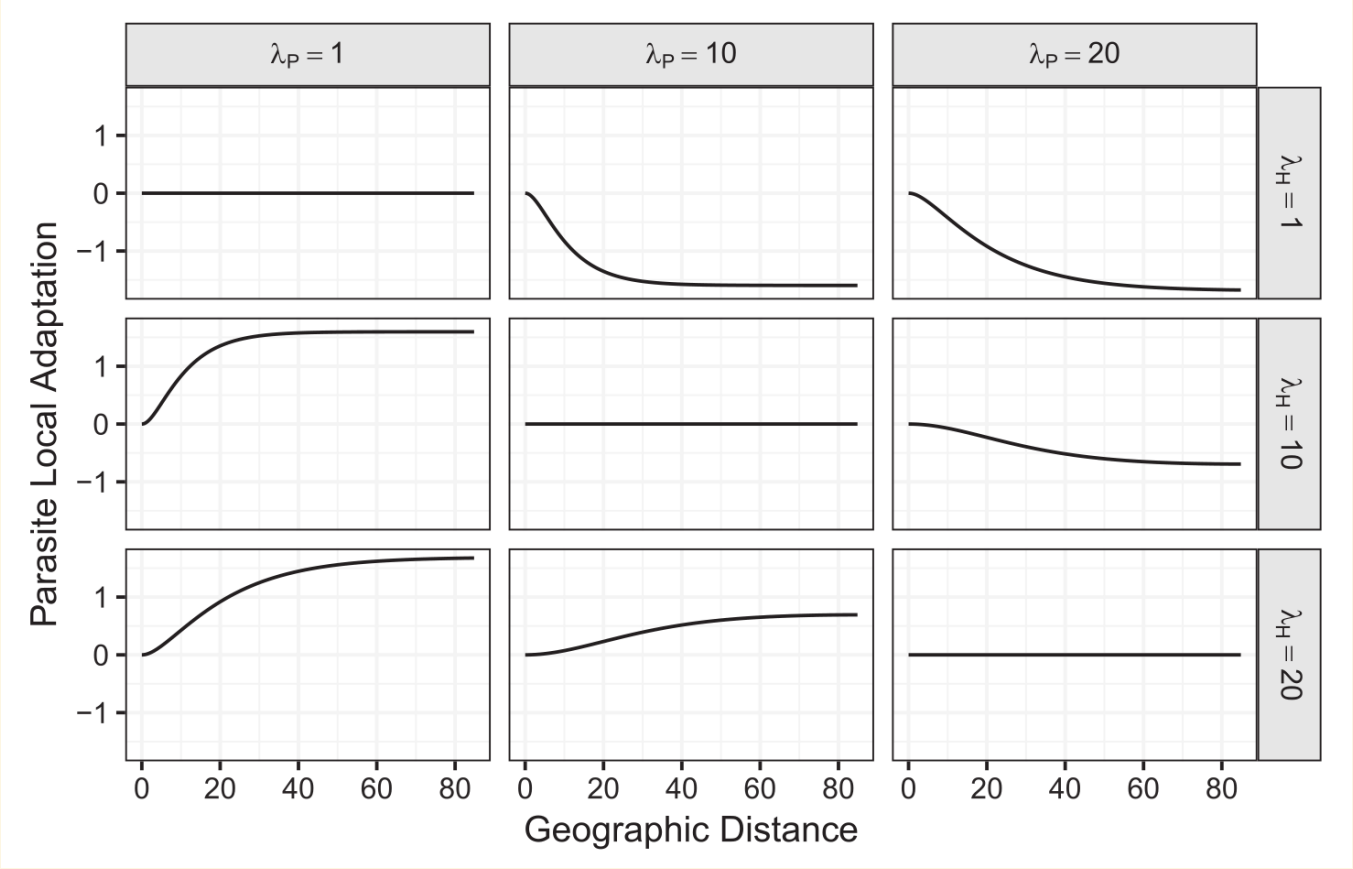
$$\dot{\bar{z}}_P = -A_P\bar{z}_P + B_P(\bar{z}_H - \bar{z}_P) + \frac{\sigma_P^2}{2}\nabla^2\bar{z}_P + D_P\xi_P$$

Local Adaptation in Continuous Space

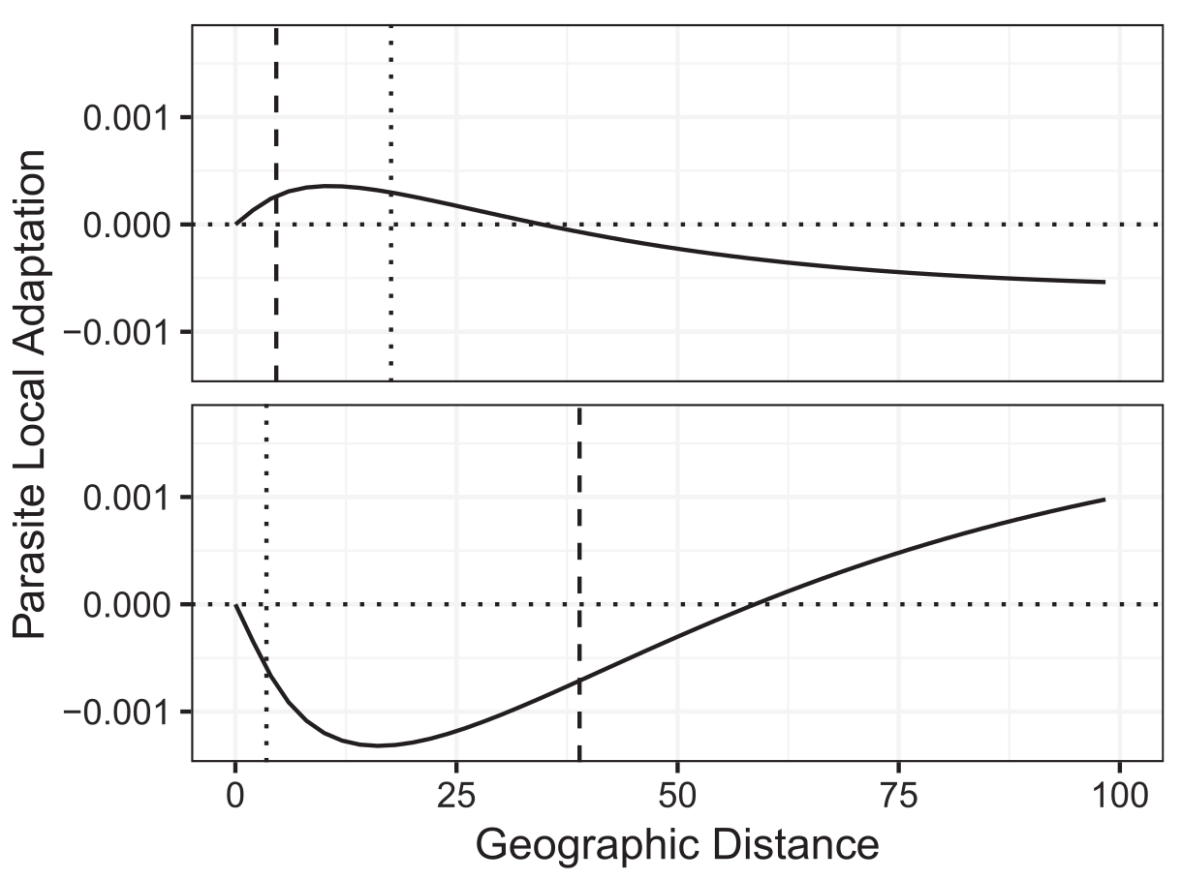


$$\mathcal{L}(\boldsymbol{x},\boldsymbol{y}) = \mathbb{E}[\bar{m}(\boldsymbol{x},\boldsymbol{x}) - \bar{m}(\boldsymbol{x},\boldsymbol{y})]$$

Parasite Local Adaptation

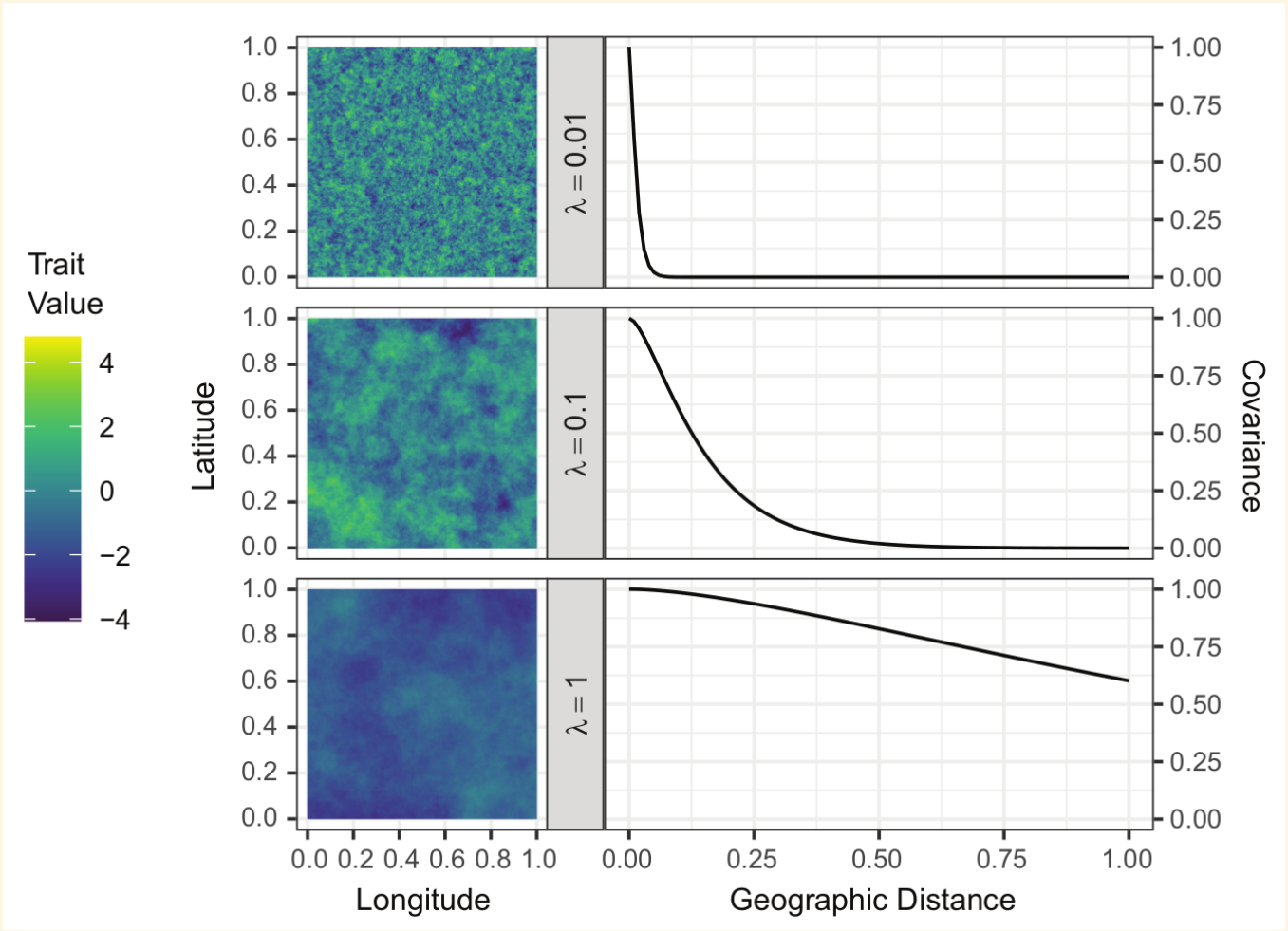


Which Species is Locally Adapted can Depend on Distance



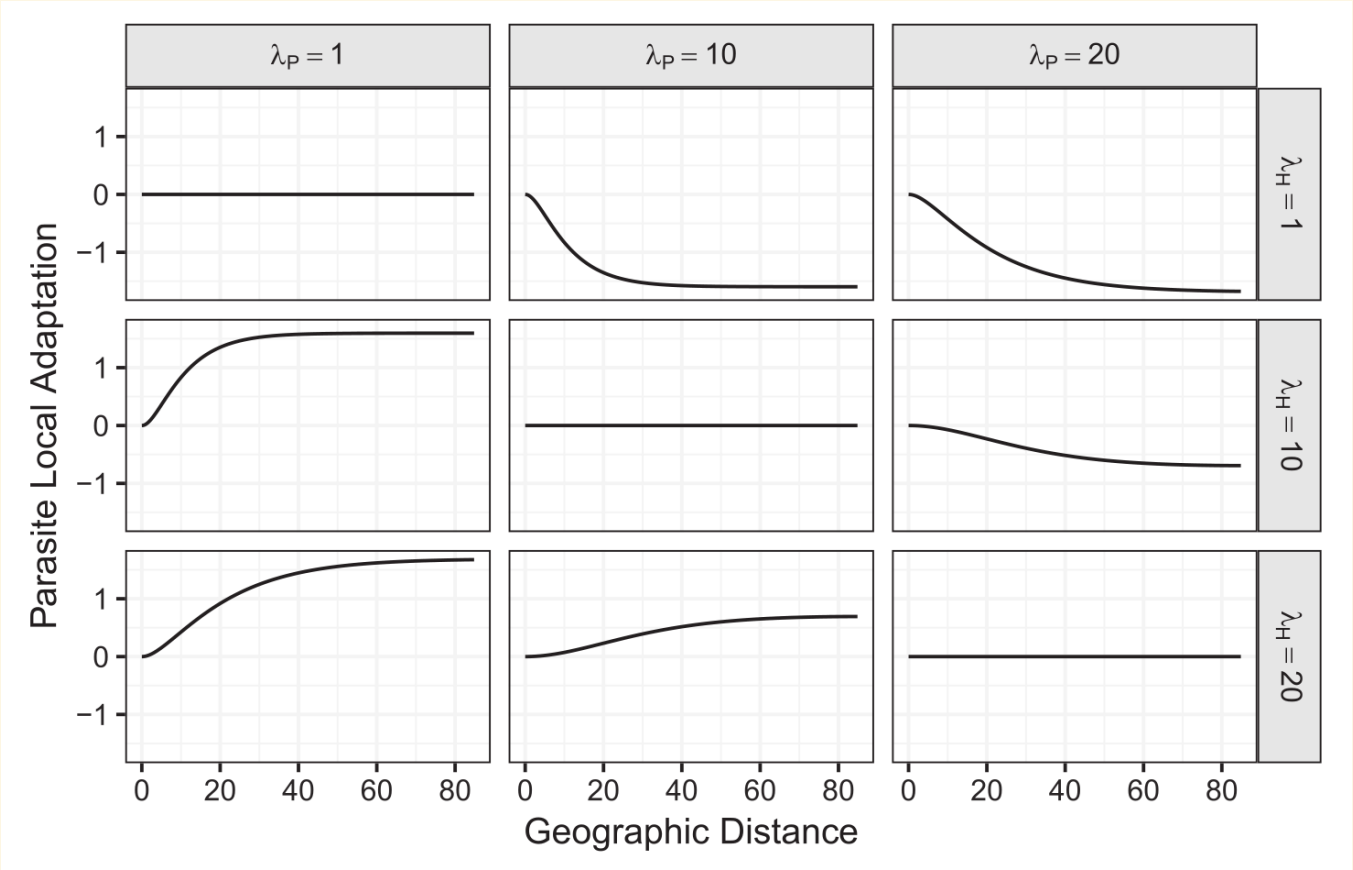
Results from asymmetry in selection strengths and rates of drift

Q: What Causes Cross-Scale Variation of Local Adaptation?



A: Spatial Autocorrelation

Consistent Measurements Require Sufficient Distances



Spatial autocorrelation dissappears with distance

Caveats

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- Spatiotemporal constancy of local abundances

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- Spatiotemporal constancy of local genetic variation

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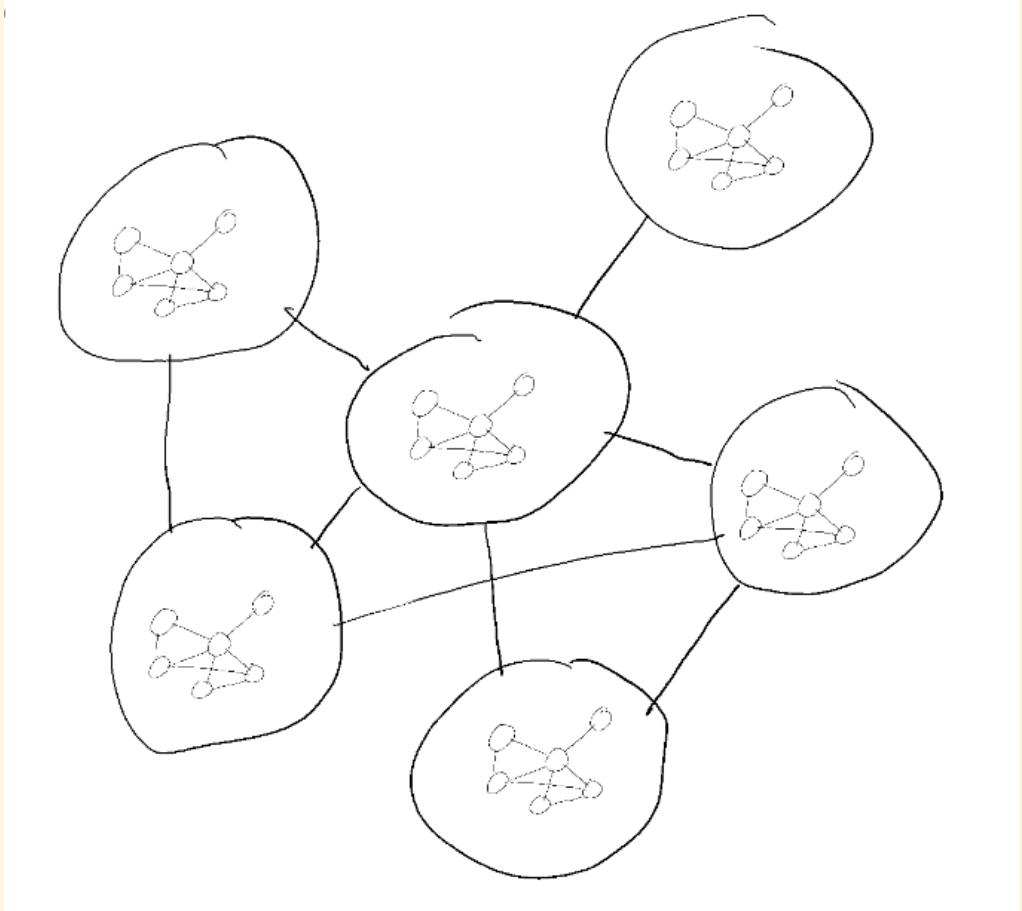
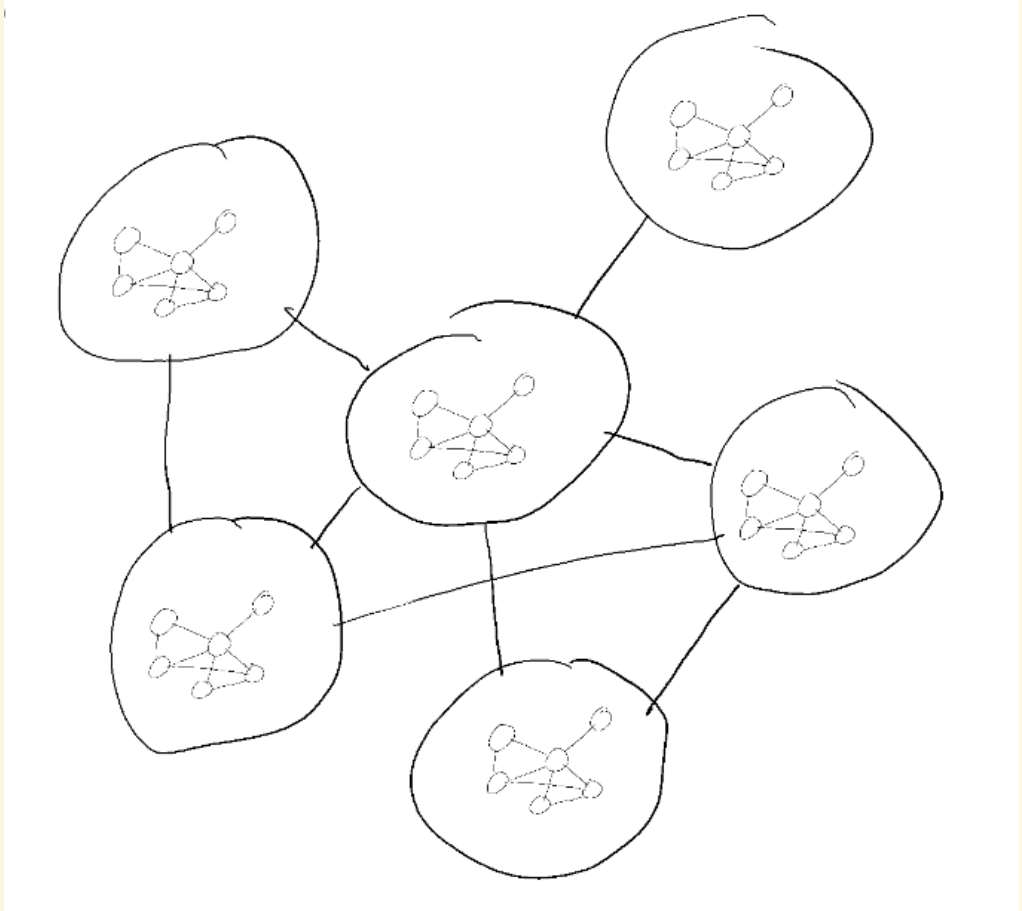
- Spatiotemporal constancy of local genetic variation
- Directionless Gaussian dispersal kernel

Future Direction: How General is This Result?



Future Direction: How General is This Result?



- Does the pattern emerge for other notions of spatial scale?

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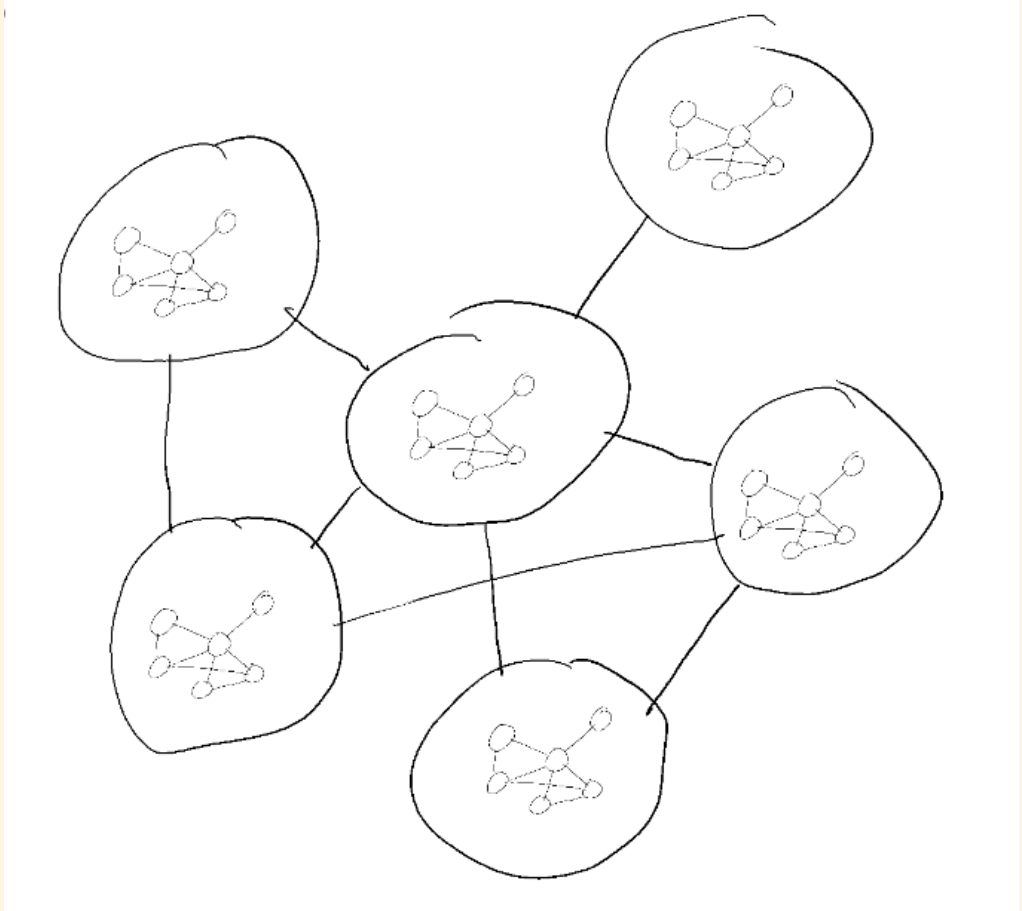
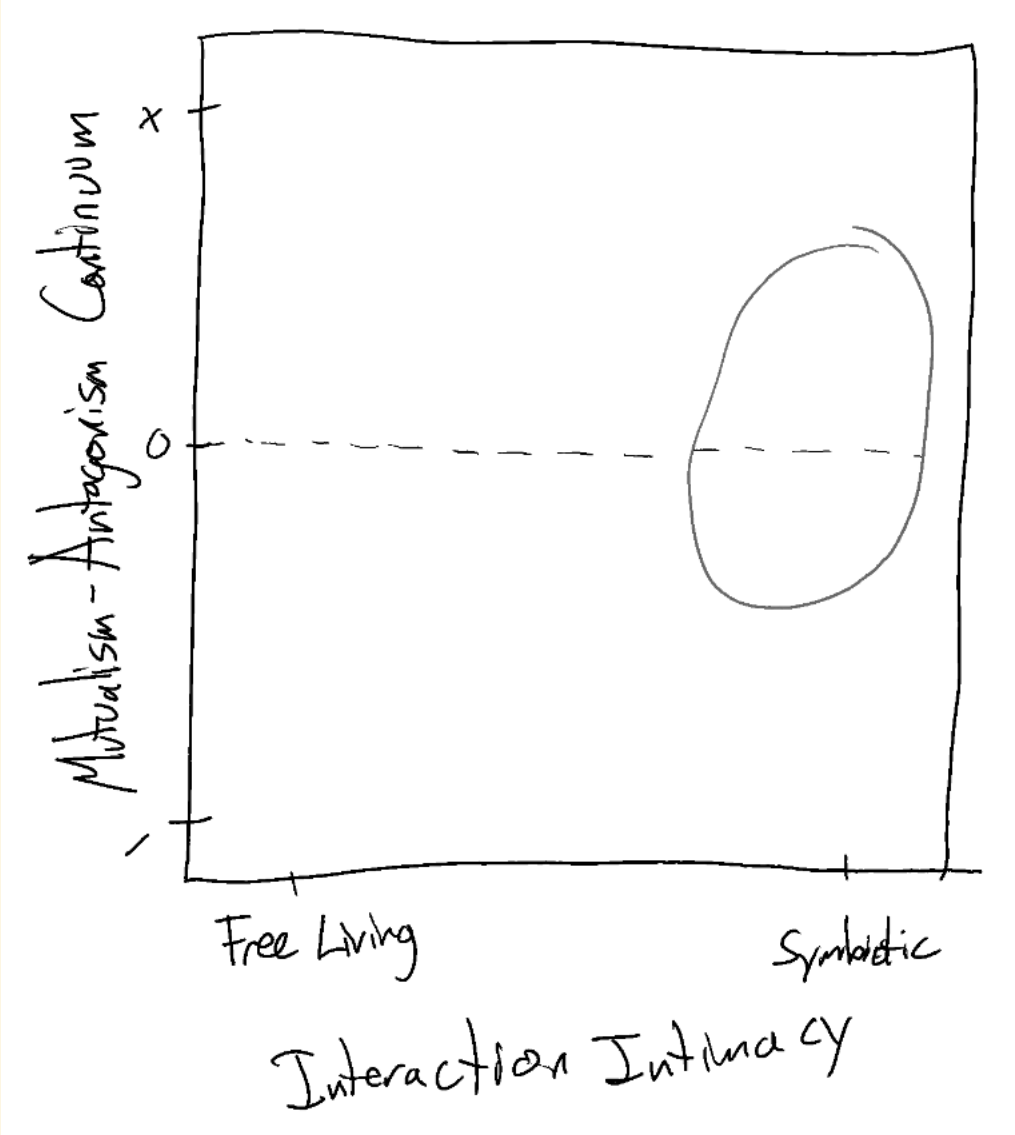


- Does the pattern emerge for other notions of spatial scale?
- If so, may be useful for spatial patterns of host-associated microbes

Host-Microbiome Dynamics



Roadmap

~~Two~~One Projects

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- Microbiome-mediated host trait evolution

~~Two~~One Projects

- Microbiome-mediated host trait evolution
  - with environmental transmission

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  - with environmental transmission
- ~~Microbe-host-gene interactions~~

~~Two~~One Projects

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  - with environmental transmission
- ~~Microbe-host-gene interactions~~
  - ~~with social transmission~~

What is a Microbiome Mediated Trait?

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- $P =$ host trait variance

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- $G =$ host genetic variance
- $M =$ *host microbiome variance*
- $P = G + M$
  - $M > 0$

Examples

Toxicity of rough-skin newt mediated by skin microbiome[18]

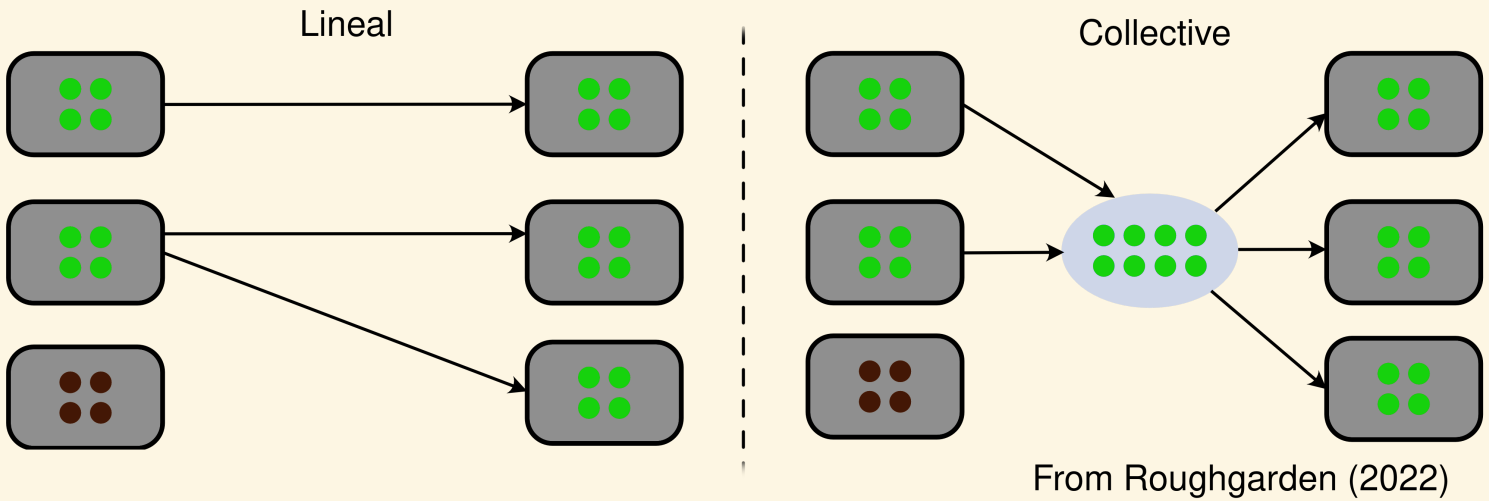
[18] ref

Examples

Cellulose digestion in cows mediated by gut microbiome[19]

[19] ref

Microbiomes Are Inherited



A comparison of lineal vs collective inheritance[20]

[20] Roughgarden (2022)

Q: How do Microbiome Mediated Host Traits Evolve?

?

Related Theoretical Frameworks

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- Niche Construction

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- Indirect Genetic Effects

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- Indirect Genetic Effects
- Maternal Characters
  - Each appear to apply to distinct aspects of microbiome mediated traits, but none provide a unified treatment
  - So new models are needed

The Model(s)

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- Analytical Model
  - additive genetic/microbial effects on host trait

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  - explicite microbiome community dynamics
  - finite host population size

Host Trait Architecture

$$z = g + m$$

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- $g =$ sum of additive effect across host loci

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- $z =$ host trait
- $g =$ sum of additive effect across host loci
- $m =$ sum of additive effect across microbial taxa

Host Life-Cycle

Microbiome Inheritance

Analytical Model

$$\Delta\bar{z} = G\beta + (\ell + \kappa)M\beta + (1 - \ell - \kappa)(\xi - \bar{m})$$

$$\Delta\xi = \kappa(M\beta + \bar{m} - \xi)/(1 - \ell)$$

Simulation Model

Comparison

Conclusion

Thanks!