



# Mutualists, Parasites, and Microbes

*Meandering Along the Entangled Bank*

*TransEvo Core Seminar, June 2024*

Bob Week

Postdoctoral Fellow, Bohannan Lab, University of Oregon

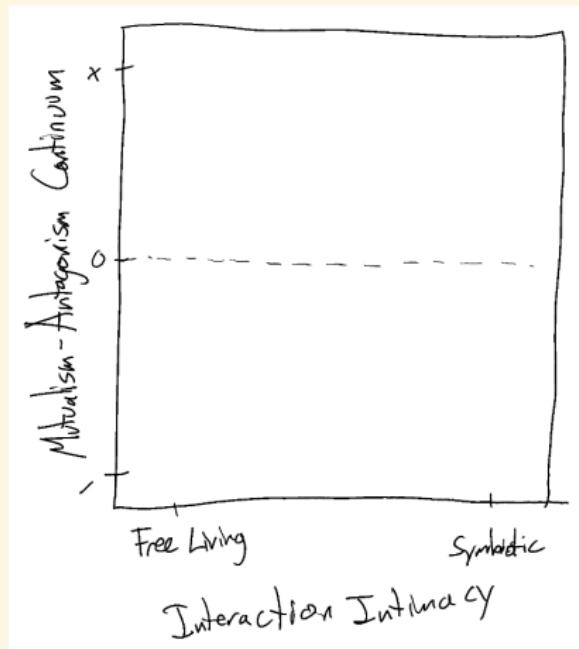
✉ bweek@uoregon.edu

🏡 bobweek.github.io

🐦 @\_bobweek\_

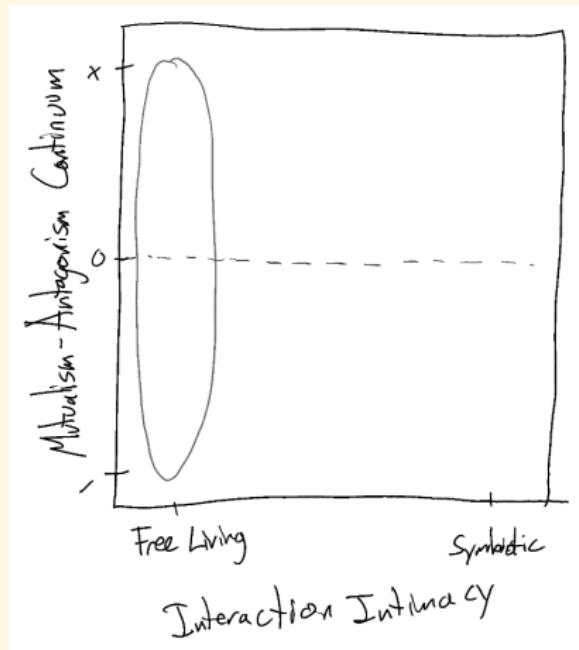
# Entangled Bank

# Unifying Theme



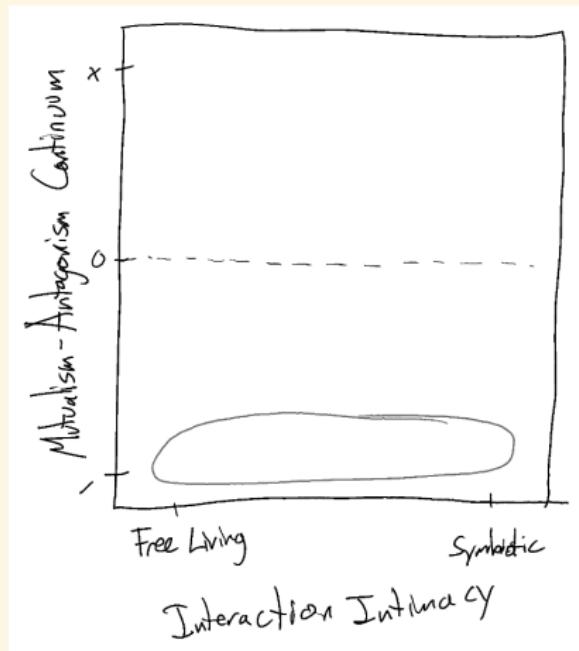
Mutualism-antagonism spectrum × degrees of interaction intimacy

# Part One



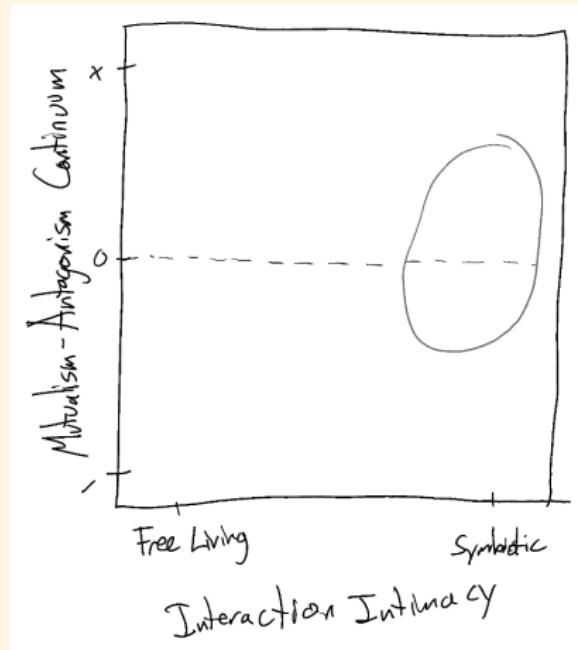
Coevolution along the mutualism-antagonism continuum

## Part Two



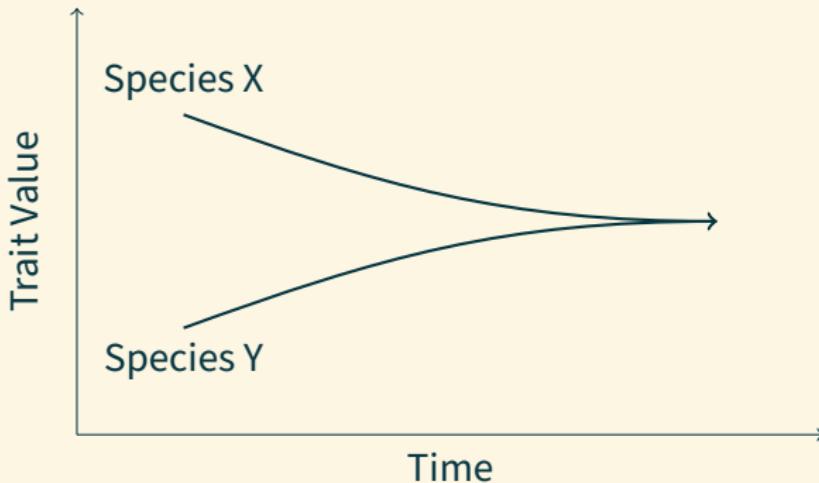
Host-parasite coevolution in continuous space

## 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

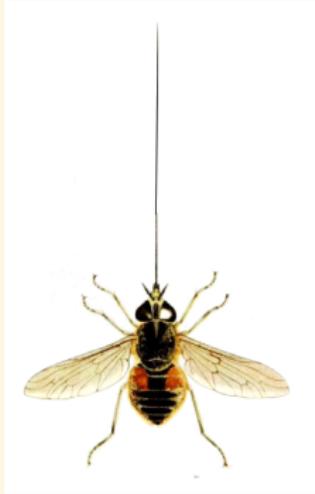


*Rediviva neliana* visiting the oil-secreting flower of *Diascia capsularis*<sup>1</sup>

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<sup>1</sup>Steiner & Whitehead (1990)

# Trait-Matching Counterexamples



*Philoliche longirostris* (left) and *Roscoea purpurea* (right)<sup>2</sup>

<sup>2</sup>Paudel et al. (2015)

# Trait-Matching Counterexamples



*Moegistorhynchus longirostris* visiting the flower of *Lapeirousia anceps*<sup>3</sup>

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<sup>3</sup>Pauw et al. (2009)

# Imbalance of Armaments

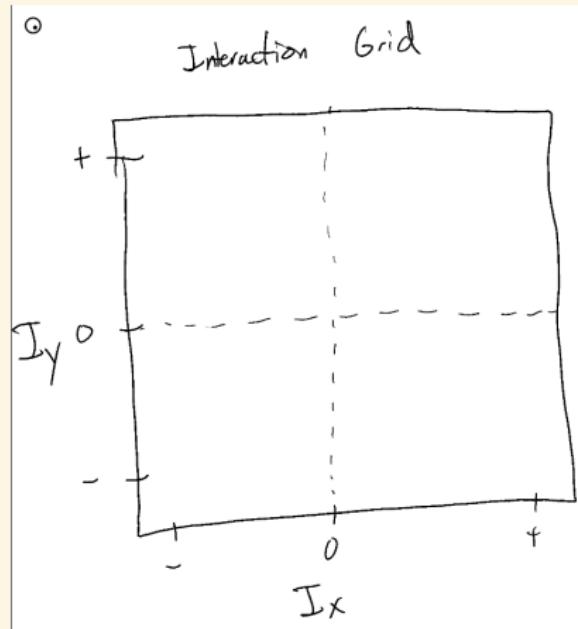


*Moegistorhynchus longirostris* visiting *Babiana thunbergii*<sup>4</sup>

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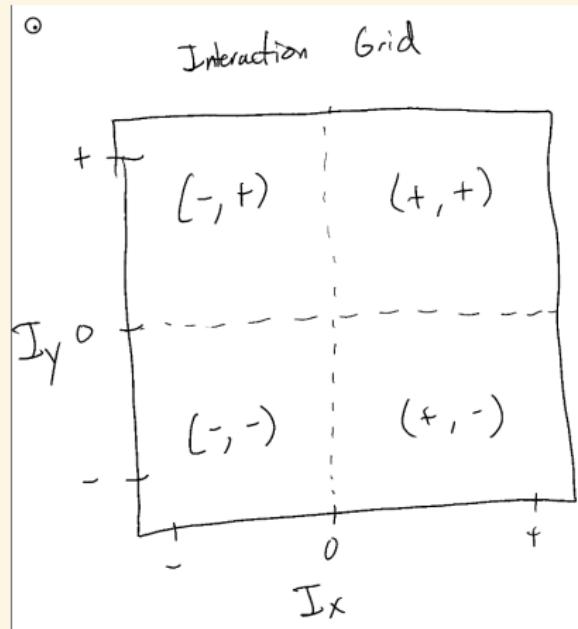
<sup>4</sup>Pauw et al. (2009)

# Ecological Consequences of Coevolution



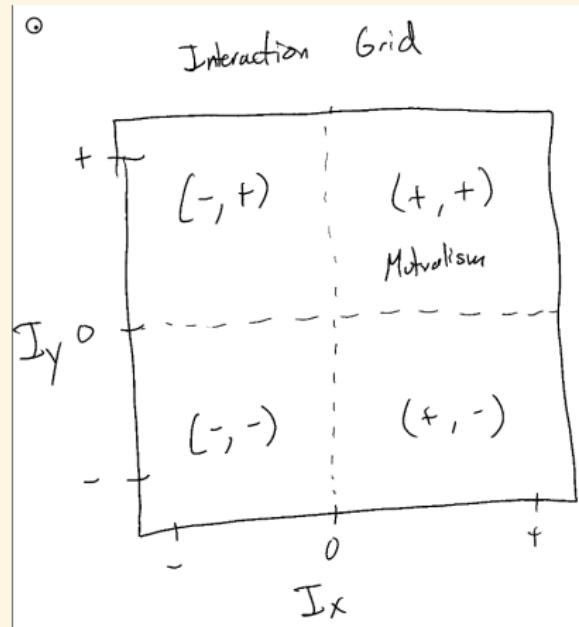
Grid of ecological interaction types

# Ecological Consequences of Coevolution



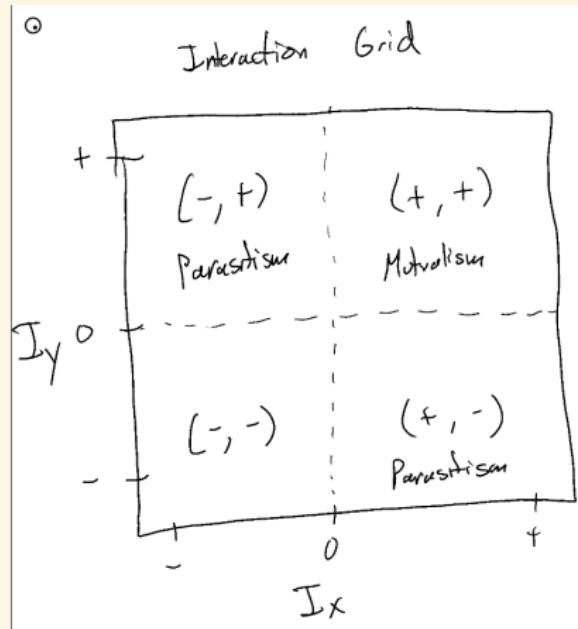
Grid of ecological interaction types

# Ecological Consequences of Coevolution



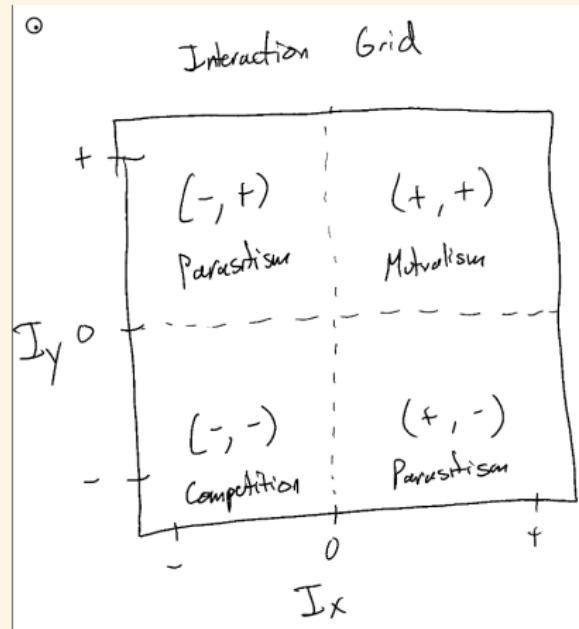
Grid of ecological interaction types

# Ecological Consequences of Coevolution



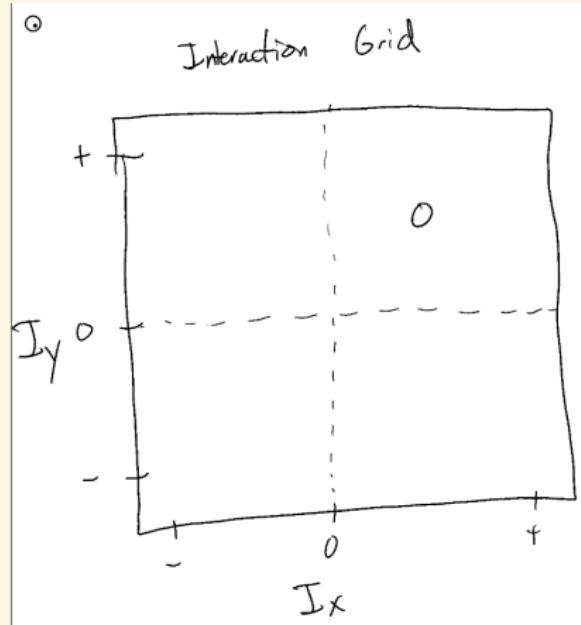
Grid of ecological interaction types

# Ecological Consequences of Coevolution

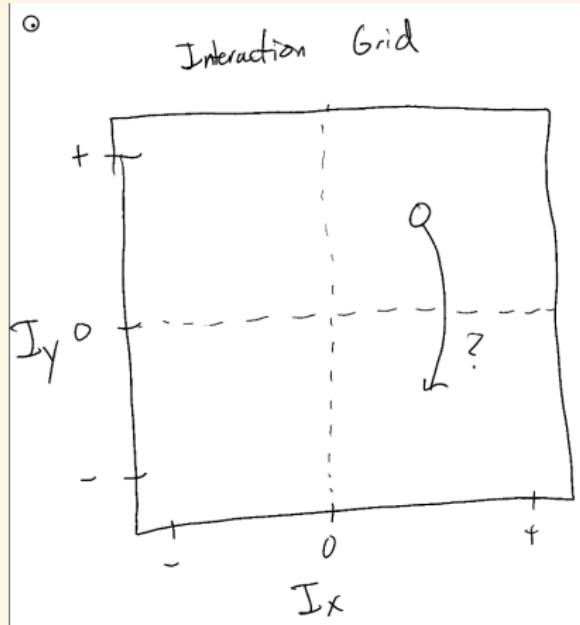


Grid of ecological interaction types

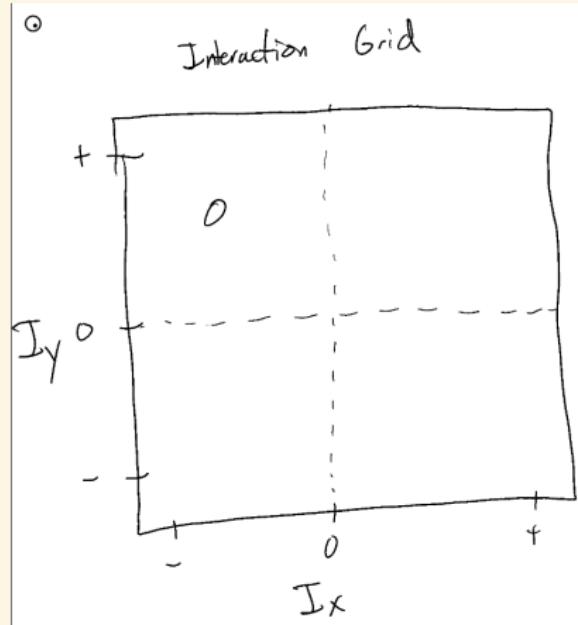
# When does mutualism dissolve into parasitism?



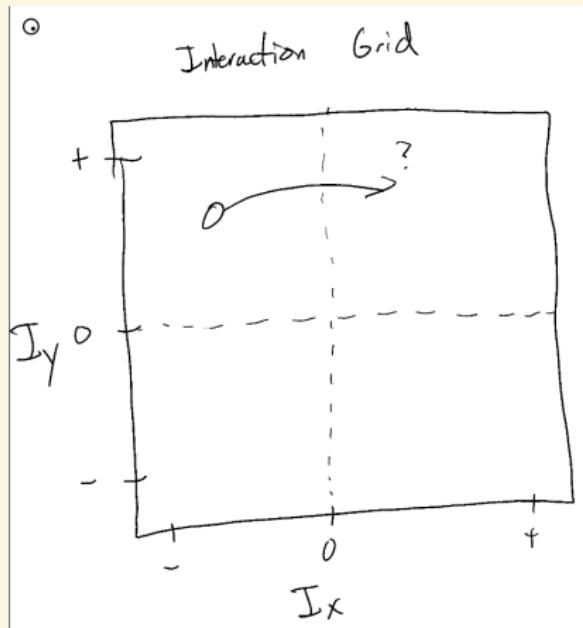
# When does mutualism dissolve into parasitism?



# When is parasitism converted to mutualism?



# When is parasitism converted to mutualism?



# Exploitation of Mutualism

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

# Cheating<sup>5</sup>

## ***Definition***

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

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<sup>5</sup>Definition adapted from Jones et al. (2015)

# Cheating<sup>5</sup>

## **Definition**

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## **Definition**

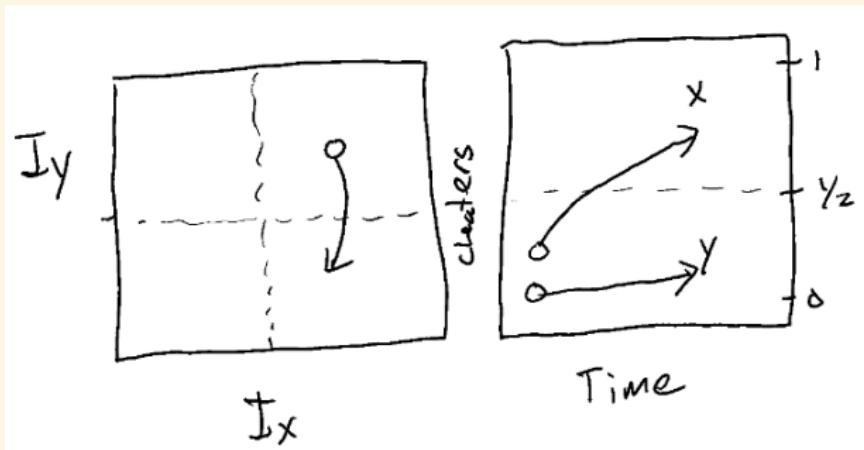
In an interspecific interaction, an individual is a **cheater** if

- it benefits from the interaction
- its partner incurs a cost from the interaction
- ≠ parasitism!
  - scale!

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<sup>5</sup>Definition adapted from Jones et al. (2015)

# Cheating and Mutualism Breakdown

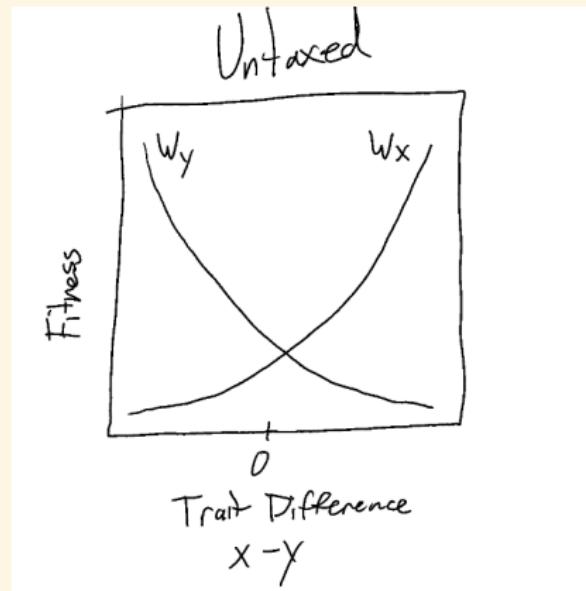


When does the mutualism breakdown = when is one species mostly cheaters?

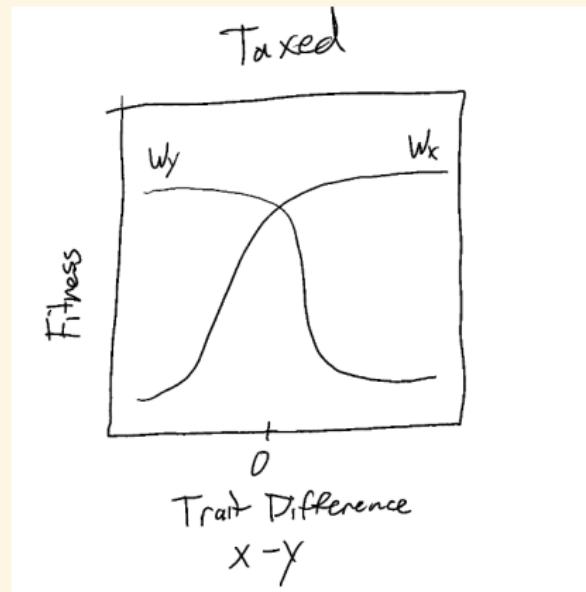
# Approach

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

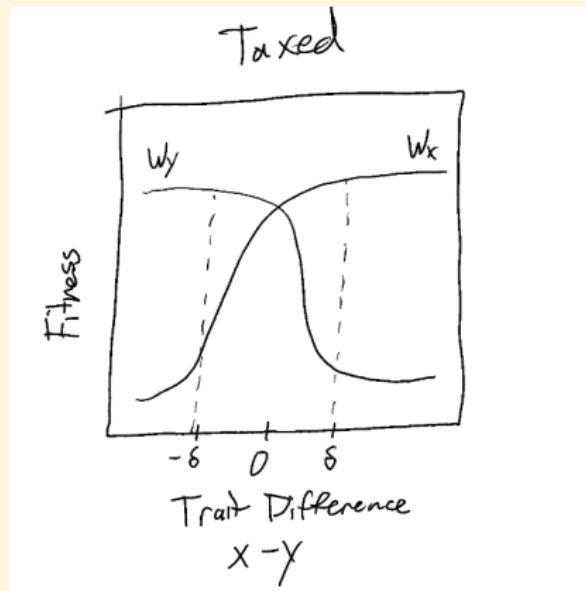
# Untaxed Cheating



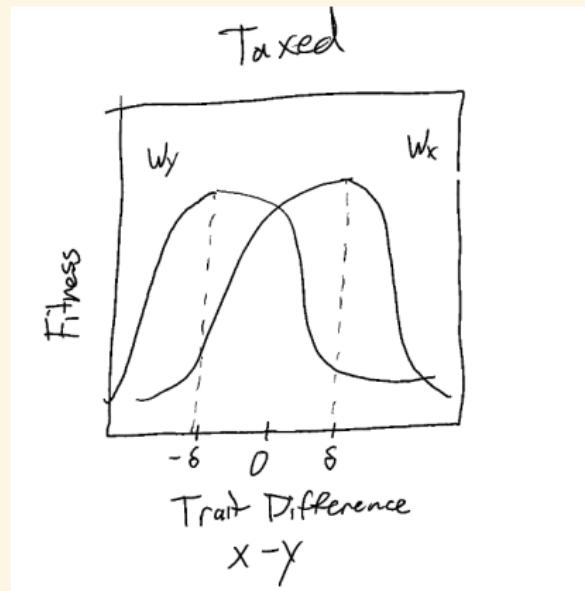
# Taxed Cheating



# Taxed Cheating



# Taxed Cheating Approximation

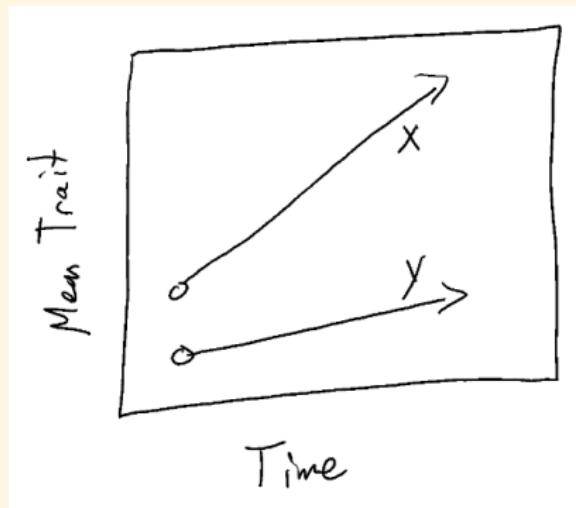


# Taxed Cheating in the Wild<sup>6</sup> - GIF ⚡



<sup>6</sup>Courtesy Stellenbosch University

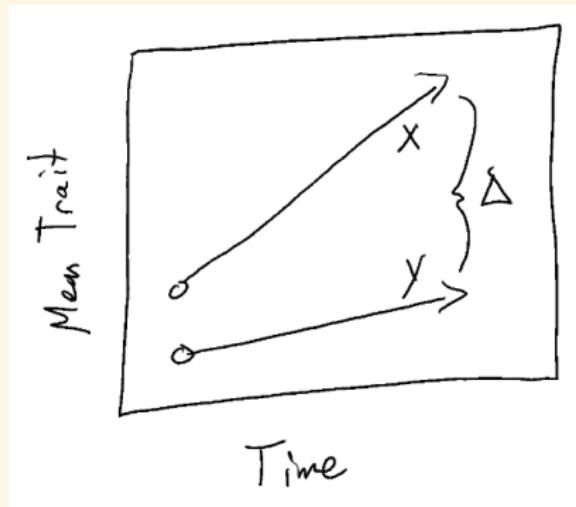
# Coevolution under Untaxed Cheating



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

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

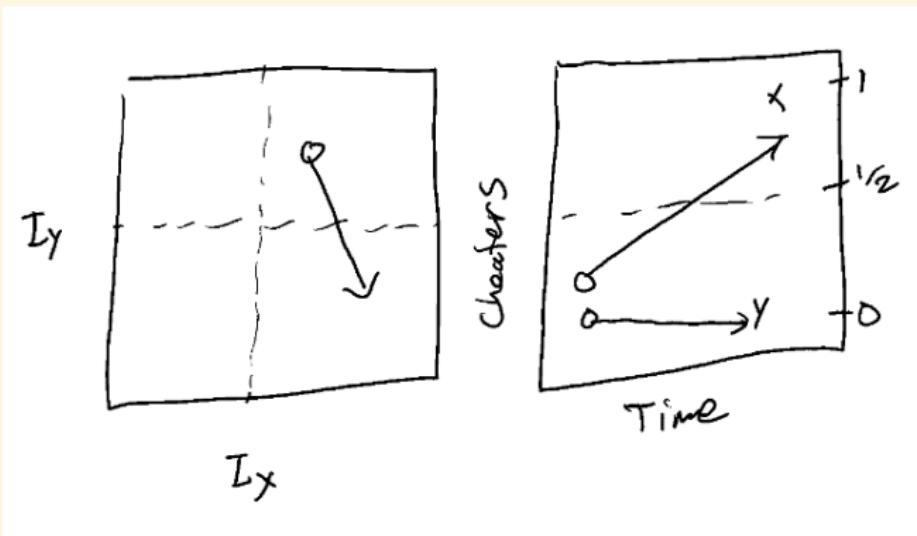
# Coevolution under Untaxed Cheating



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

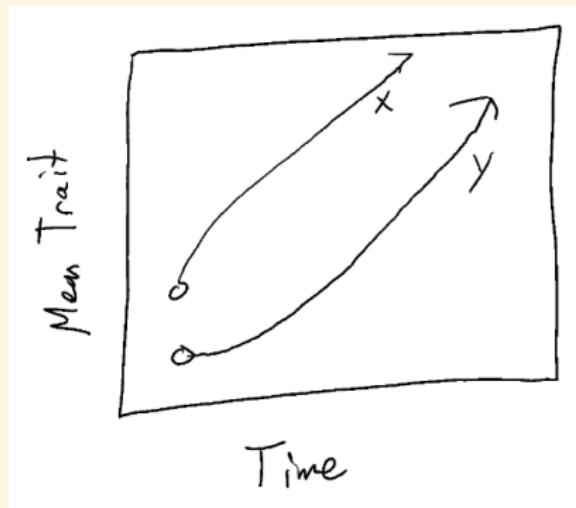
$$\dot{y} = G_Y B_Y$$

# Untaxed Cheating Doomed to Parasitism



A mutualism dissolving into parasitism during an arms race

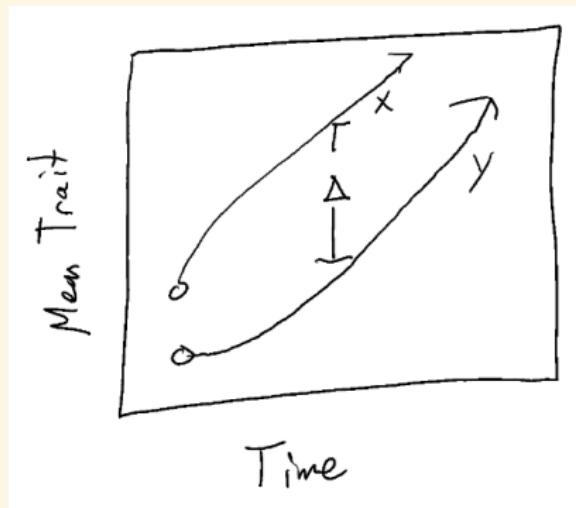
# Coevolution under Taxed Cheating



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

$$\dot{\bar{y}} = G_Y B_Y (\bar{x} + \delta - \bar{y})$$

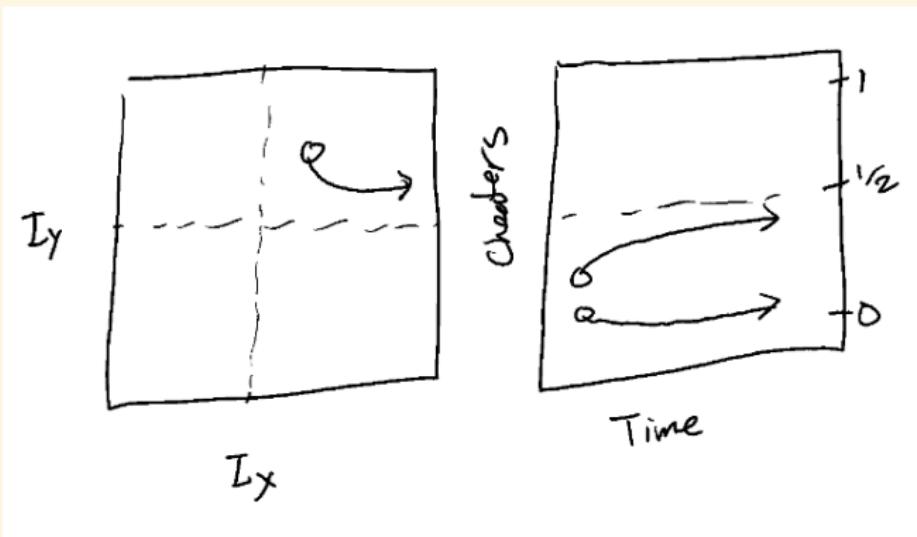
# Coevolution under Taxed Cheating



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

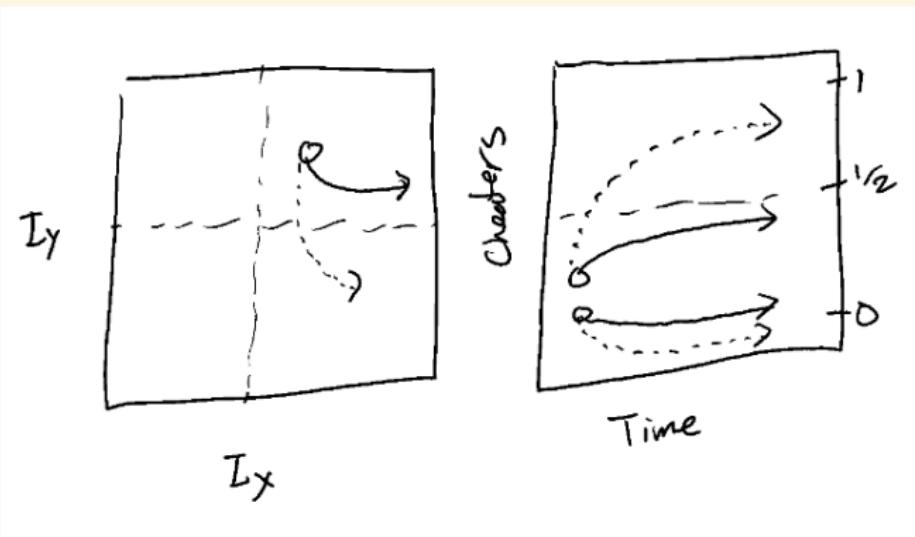
$$\dot{\bar{y}} = G_Y B_Y (\bar{x} + \delta - \bar{y})$$

# Taxed Cheating Prevents Parasitism



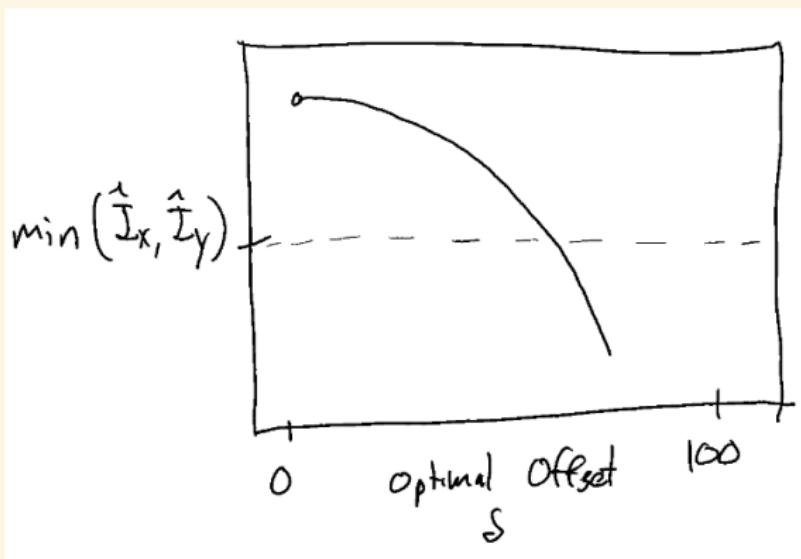
A mutualism avoiding parasitism during an arms race

# Taxed Cheating Prevents Parasitism



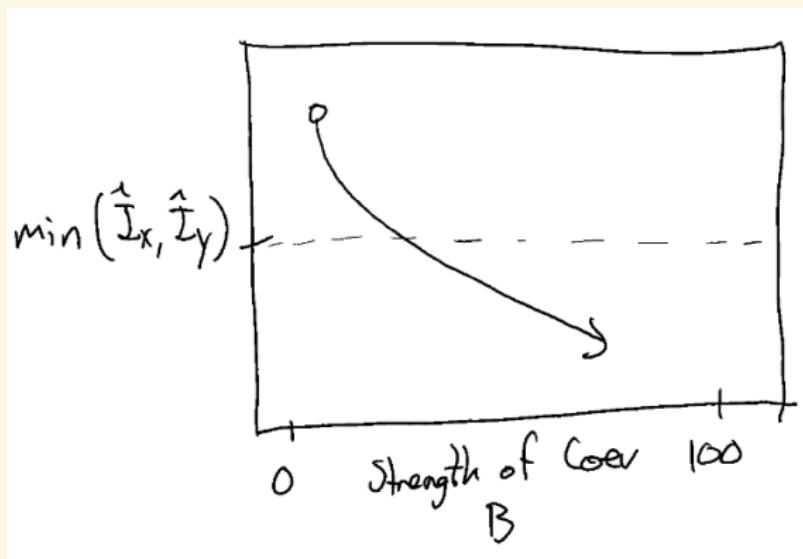
Variable outcomes are possible

# Conditions for the Maintenance of Mutualism



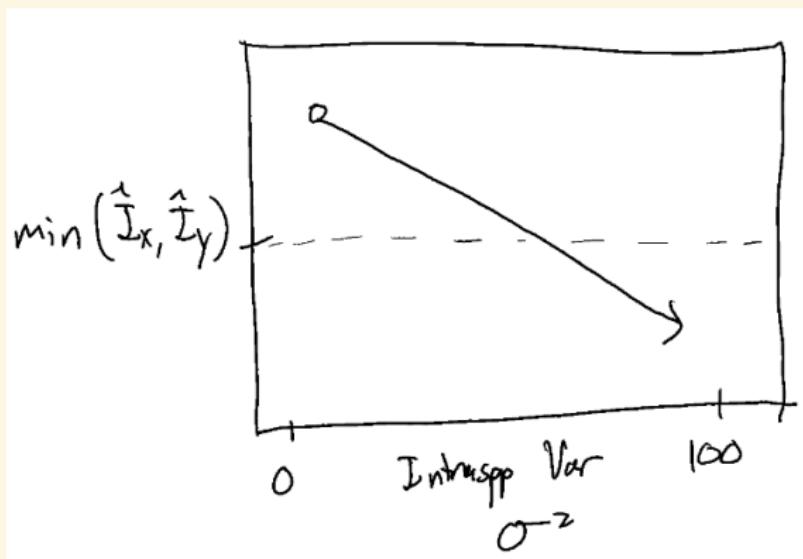
Equilibrium interaction effects as functions of optimal offset

# Conditions for the Maintenance of Mutualism



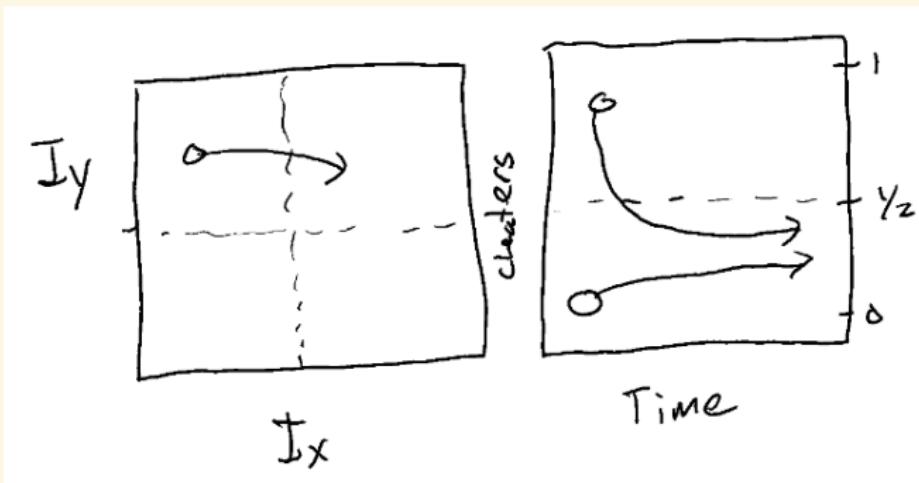
Equilibrium interaction effects as functions of biotic selection strength

# Conditions for the Maintenance of Mutualism



Equilibrium interaction effects as functions of intraspecific variation

# Taxed Cheating Converts Parasitism to Mutualism



## *M. longirostris* Pollination Guild

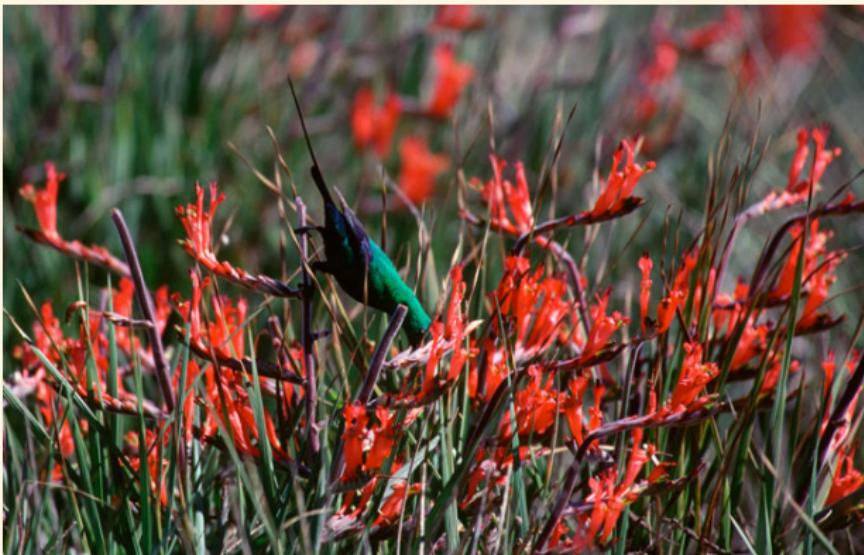


*Moegistorhynchus longirostris* visiting *Babiana thunbergii*<sup>7</sup>

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<sup>7</sup> Pauw et al. (2009)

# Indirect Coevolutionary Effects?



*Babiana thunbergii* normally pollinated by malachite sunbirds<sup>8</sup>

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<sup>8</sup>Pauw et al. (2009)

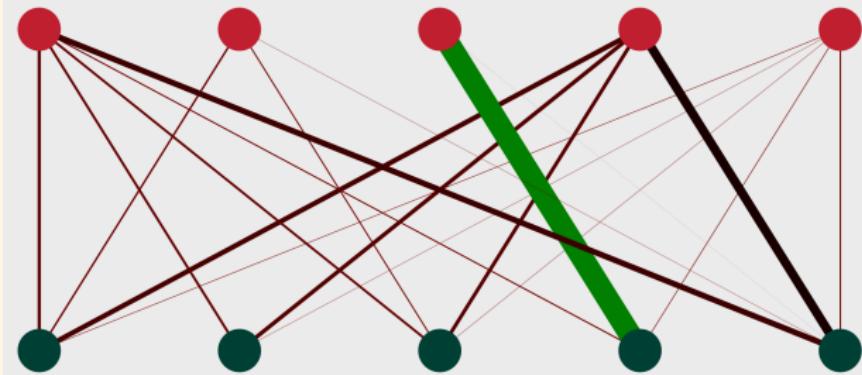
# Implications for Mutualistic Networks

LETTER

doi:10.1038/nature24273

## Indirect effects drive coevolution in mutualistic networks

Paulo R. Guimarães Jr<sup>1</sup>, Mathias M. Pires<sup>2</sup>, Pedro Jordano<sup>3</sup>, Jordi Bascompte<sup>4</sup> & John N. Thompson<sup>5</sup>



# Caveats

Ignores:

# Caveats

Ignores:

- Community context

# Caveats

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- Community context
- Feedback with abundance

# Caveats

Ignores:

- Community context
- Feedback with abundance
- Spatial structure

# Caveats

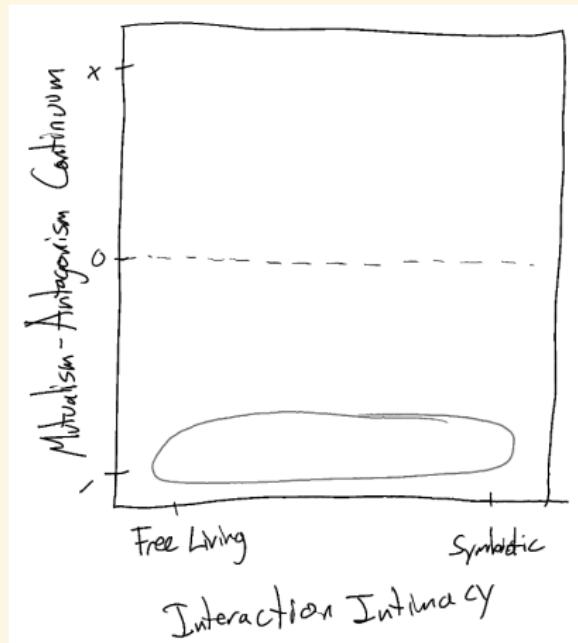
Ignores:

- 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

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<sup>9</sup> Best et al. (2010)

<sup>10</sup> Nuismer et al. (2003)

<sup>11</sup> Nuismer (2017)

# Spatial Host-Parasite Coevolution

- Lowers pathogen transmissibility and virulence<sup>9</sup>

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# Spatial Host-Parasite Coevolution

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# Spatial Host-Parasite Coevolution

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# Spatial Host-Parasite Coevolution

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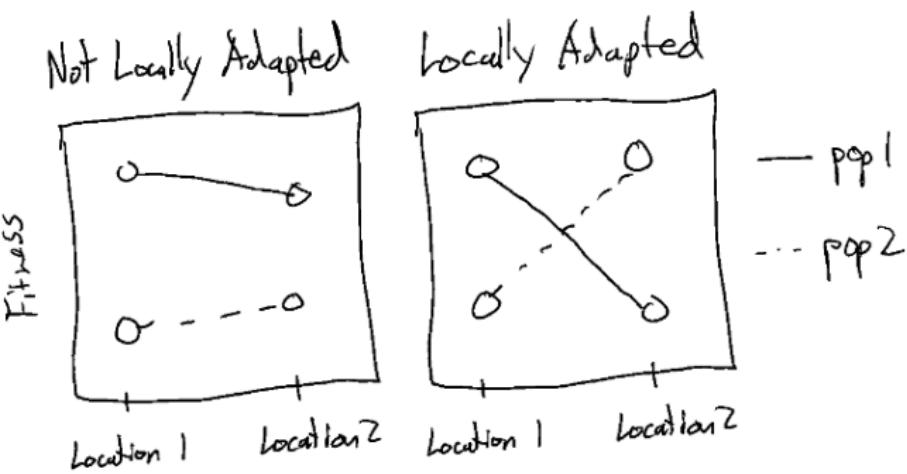
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<sup>9</sup> Best et al. (2010)

<sup>10</sup> Nuismer et al. (2003)

<sup>11</sup> Nuismer (2017)

# What is Local Adaptation?



# Determinants of Host-Parasite Local Adaptation<sup>12</sup>

<sup>12</sup>Gandon & Nuismer (2009) 

# Determinants of Host-Parasite Local Adaptation<sup>12</sup>

- Relative selection strengths

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# Determinants of Host-Parasite Local Adaptation<sup>12</sup>

- Relative selection strengths
- Selection mosaics

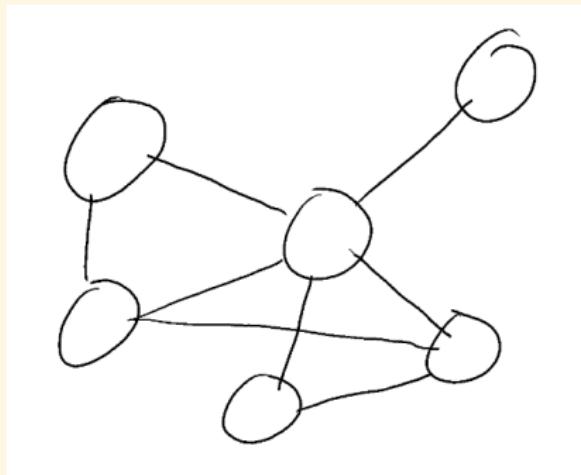
<sup>12</sup>Gandon & Nuismer (2009) 

# Determinants of Host-Parasite Local Adaptation<sup>12</sup>

- Relative selection strengths
- Selection mosaics
- Relative dispersal abilities

<sup>12</sup>Gandon & Nuismer (2009) 

# Host-Parasite Models Assume Discrete Space



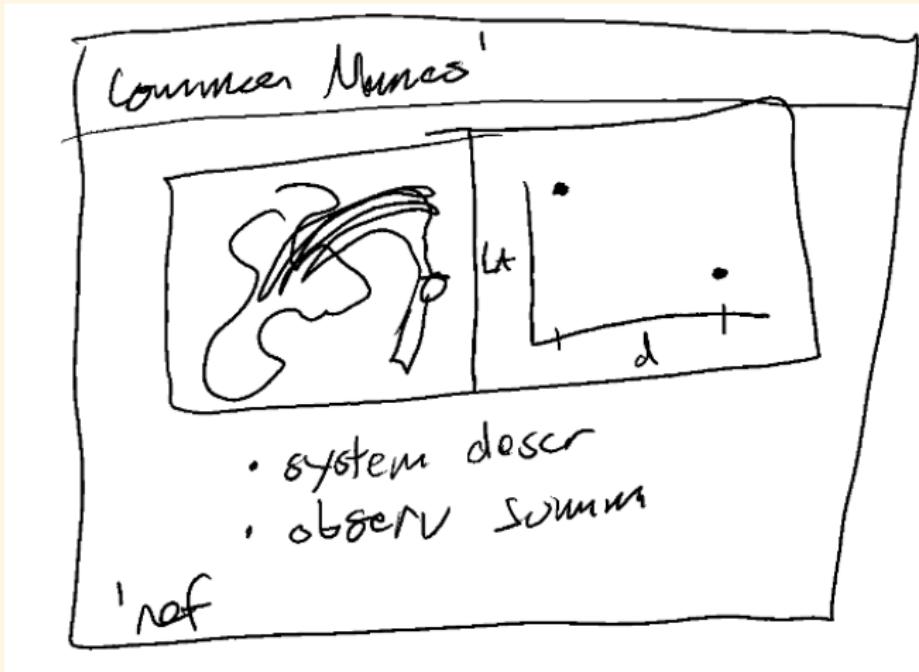
A metapopulation

# Empirical Systems Exhibit Cross-Scale Variation



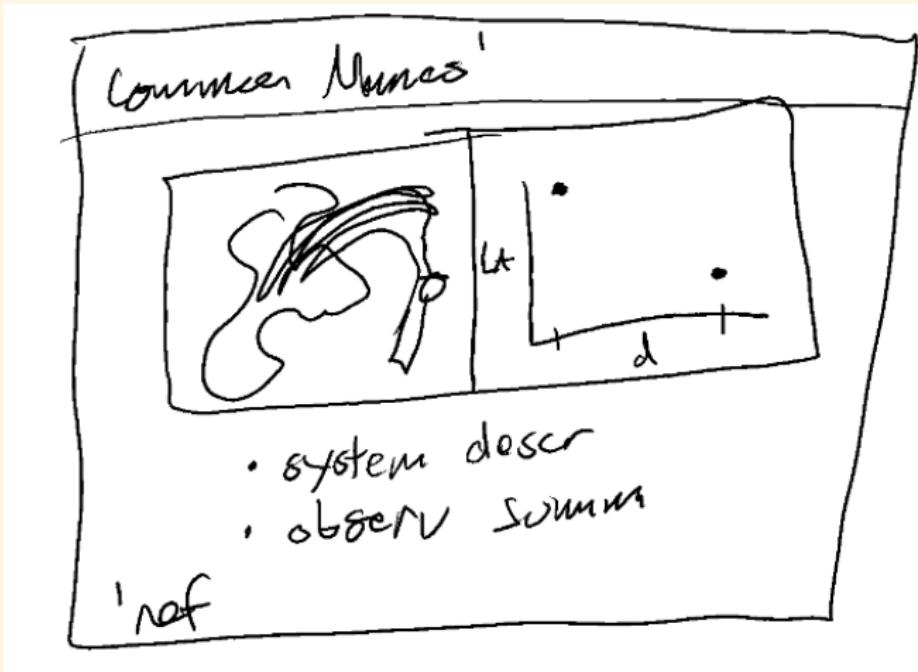
Local adaption can vary across distances measured

# Rust Pathogen and Perennial Herb<sup>13</sup>



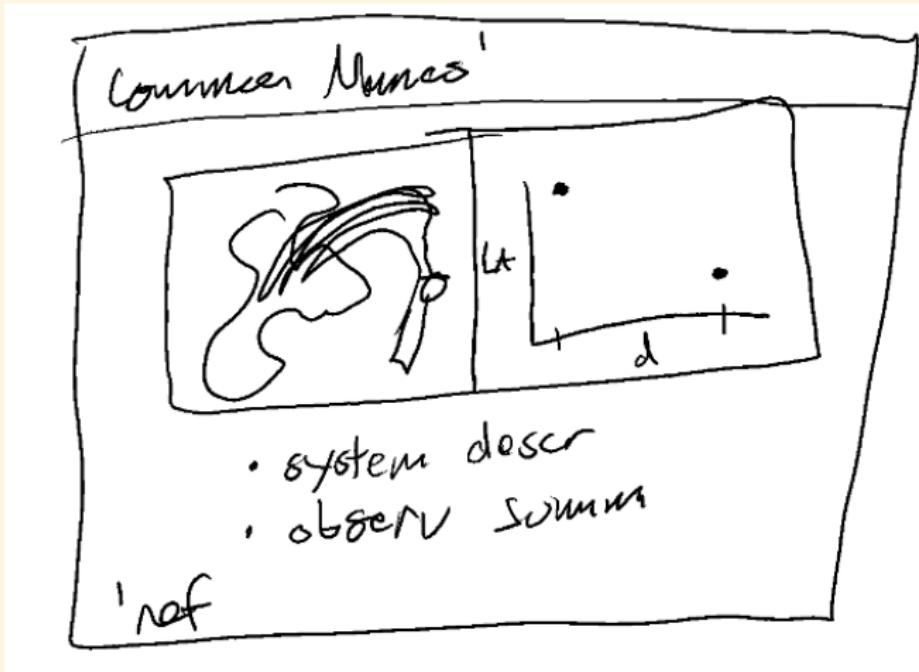
<sup>13</sup>Thrall et al. (2002)

# Armored Scale Insect and Mulberry Trees<sup>14</sup>



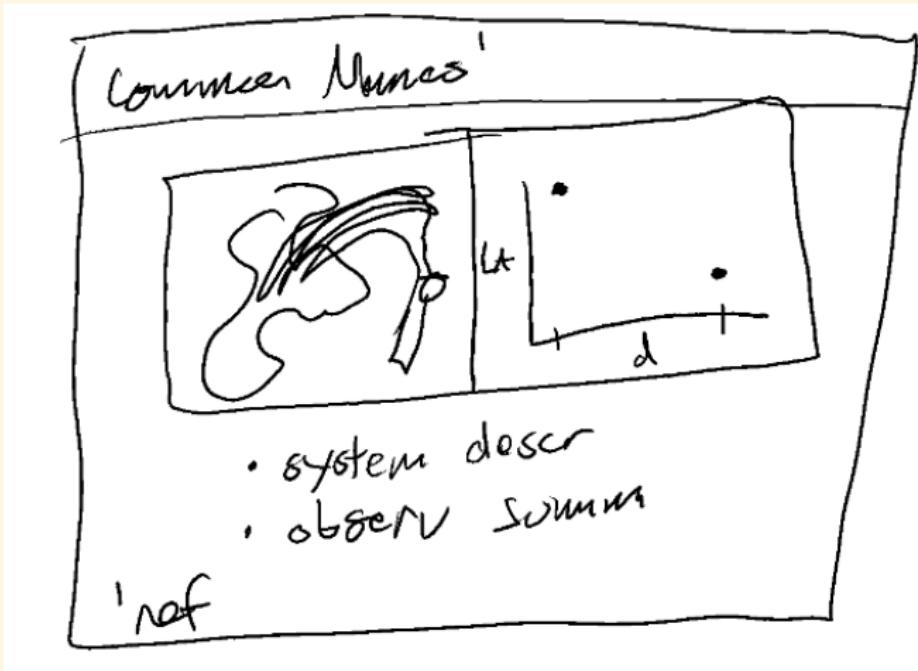
<sup>14</sup>Hanks & Denno (1994)

# Hoverfly and Host Ant<sup>15</sup>



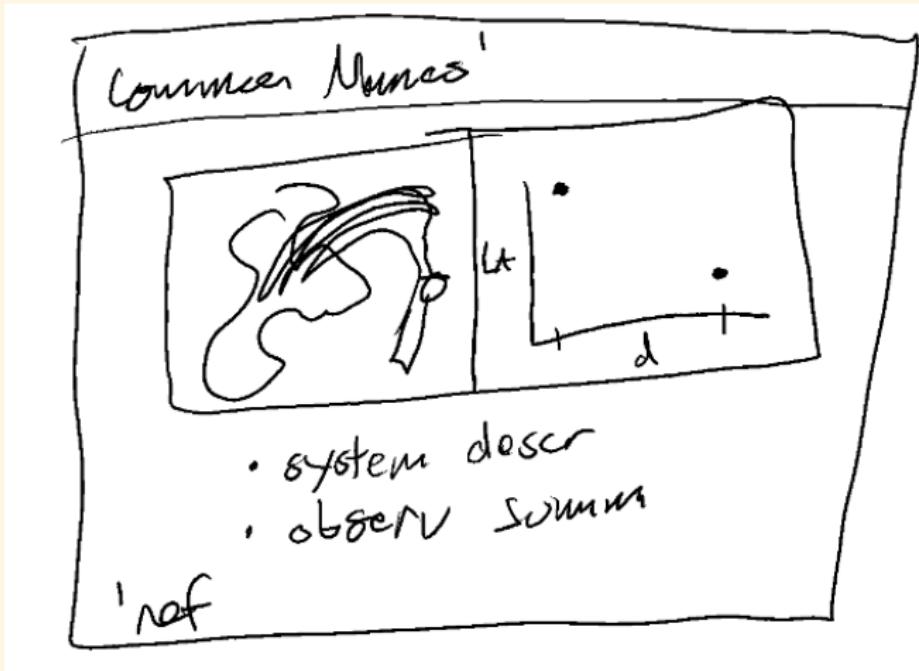
<sup>15</sup>Schonrogge et al (2006)

# Anther-Smut Fungus and Host Plant<sup>16</sup>



<sup>16</sup>Kaltz et al (1999)

# Powdery Mildew and Ribwort Plantain Host<sup>17</sup>



<sup>17</sup>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

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- Dispersal
- Abiotic Stabilizing Selection

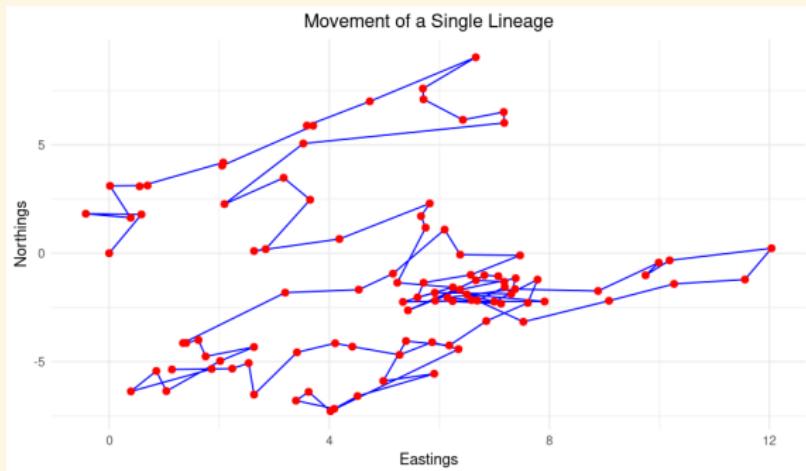
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- Dispersal
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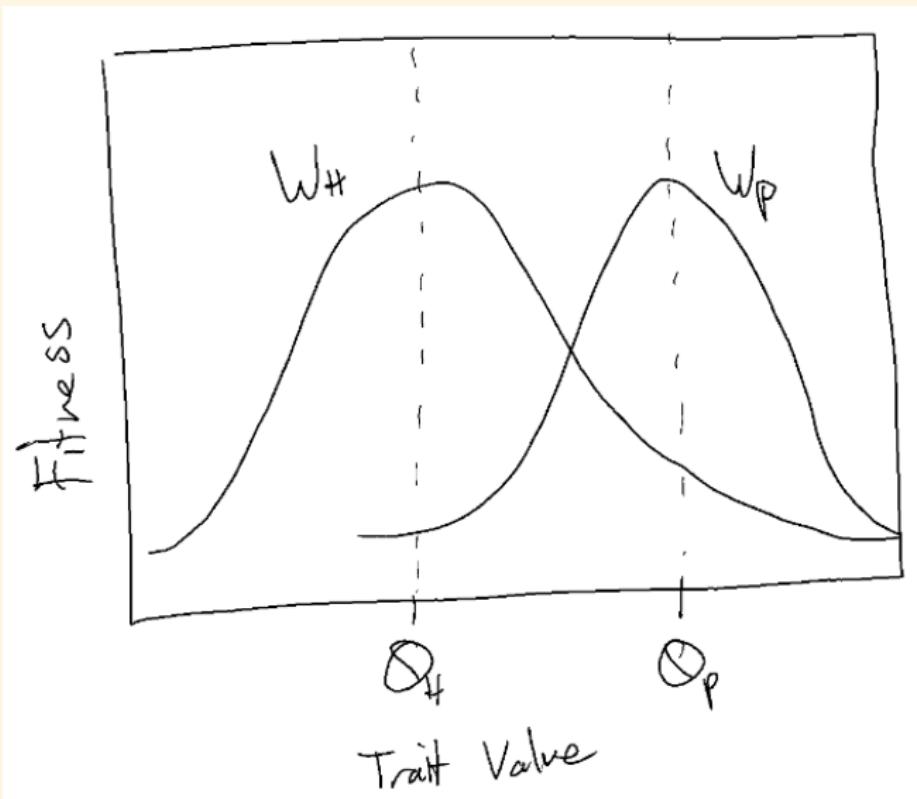
- Dispersal
- Abiotic Stabilizing Selection
- Interspecific Biotic Selection
- Random Genetic Drift

# Dispersal



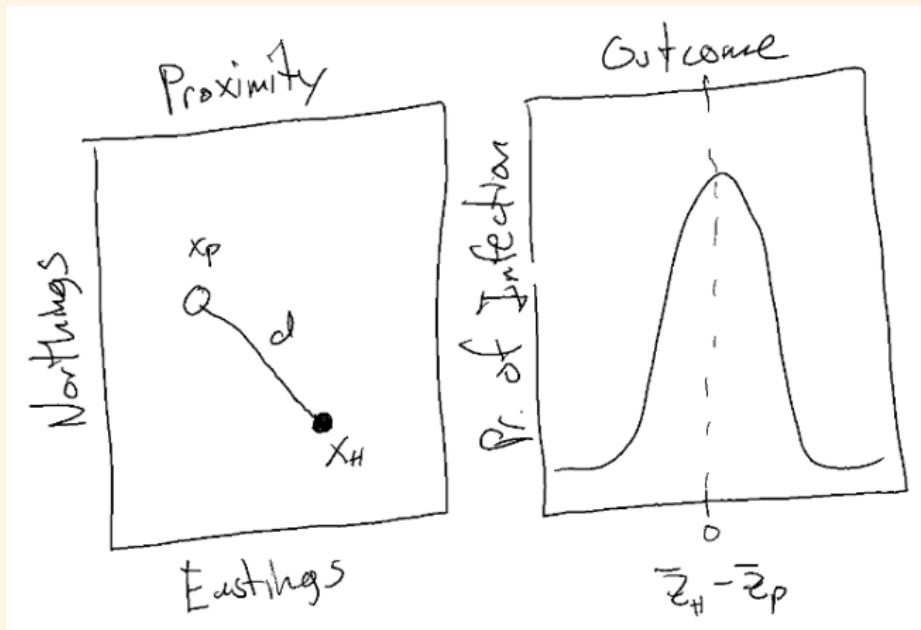
Movement of a single lineage

# Abiotic Stabilizing Selection



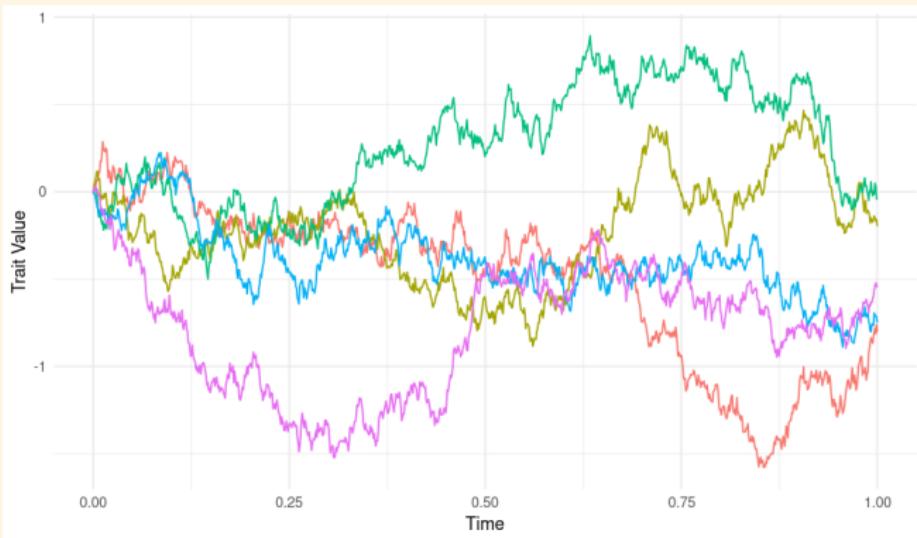
Included to guarantee model has equilibrium

# Biotic Selection



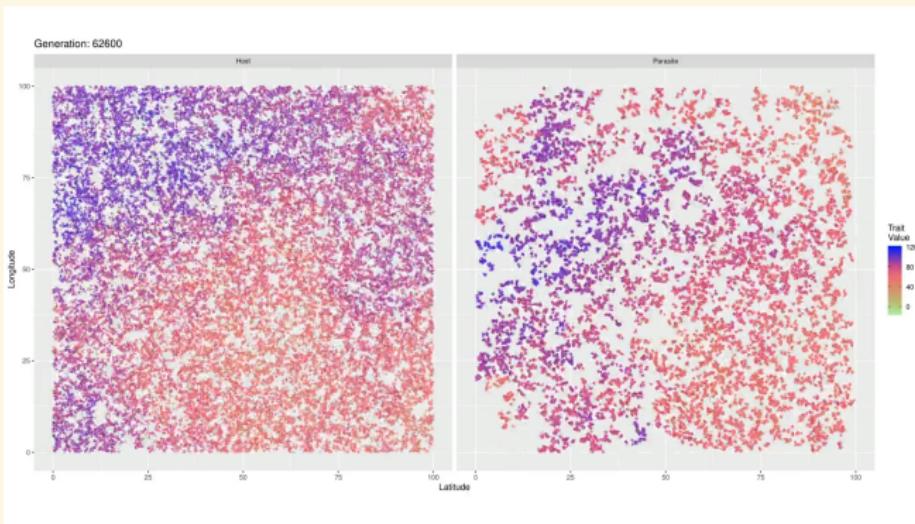
Encounters depend on proximity and infection probability depends on how well traits match

# Random Genetic Drift



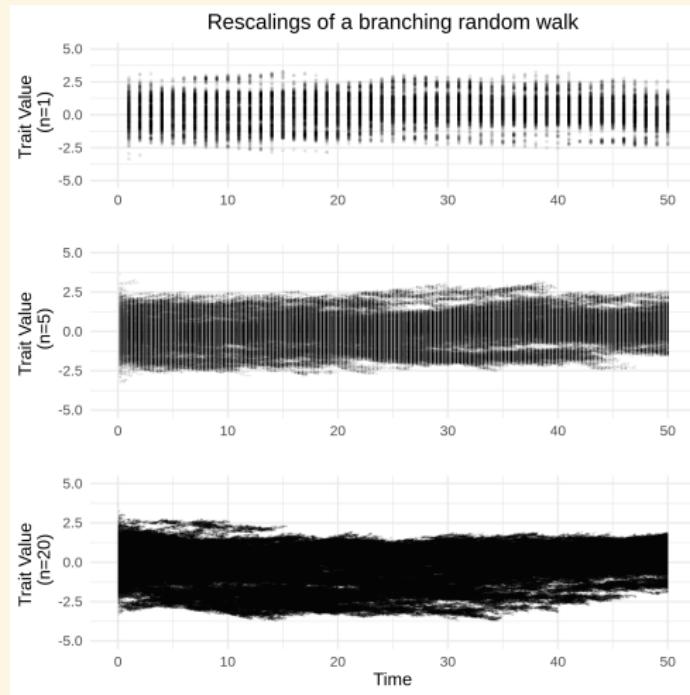
Evolution in Response to Random Genetic Drift

# Individual-Based Model



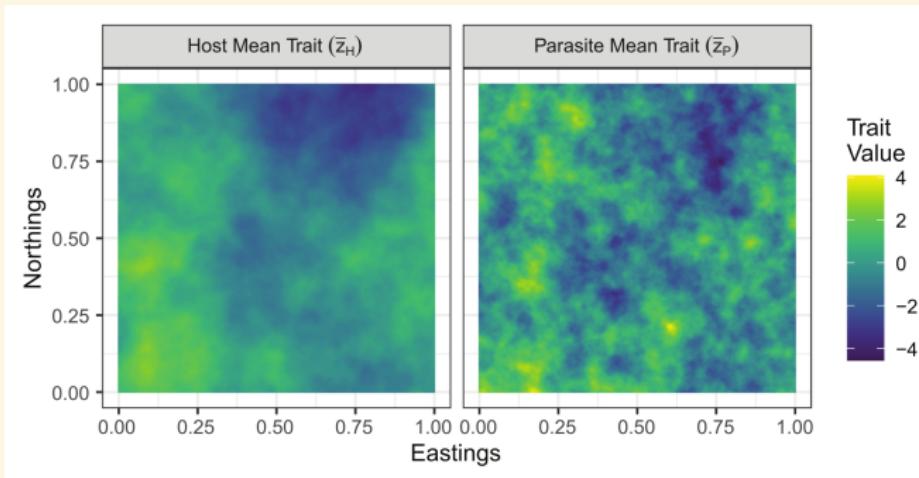
Animation

# Diffusion Limit



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

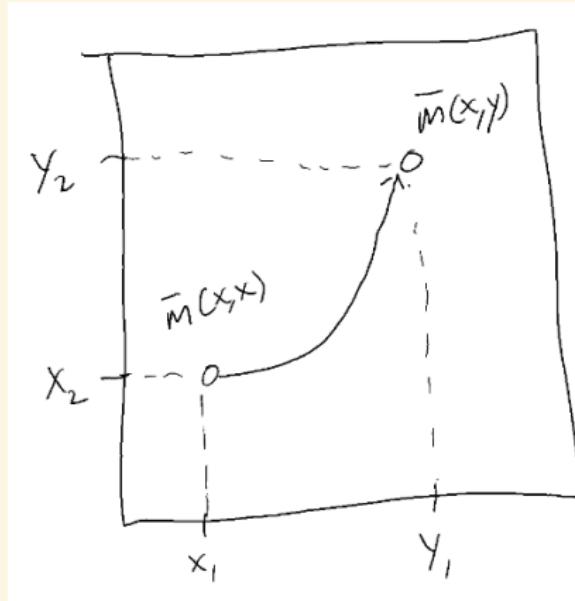
# SPDE Model



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

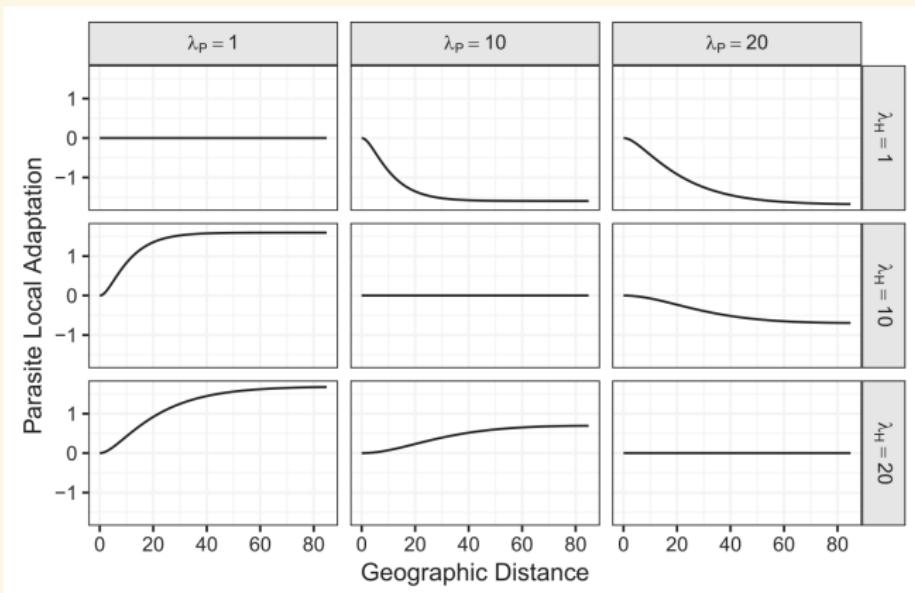
$$\dot{\bar{z}}_P = -A_P \bar{z}_P + B_P (\bar{z}_H - \bar{z}_P) + \frac{\sigma_P^2}{2} \nabla^2 \bar{z}_P + D_P \xi_P$$

# Local Adaptation in Continuous Space

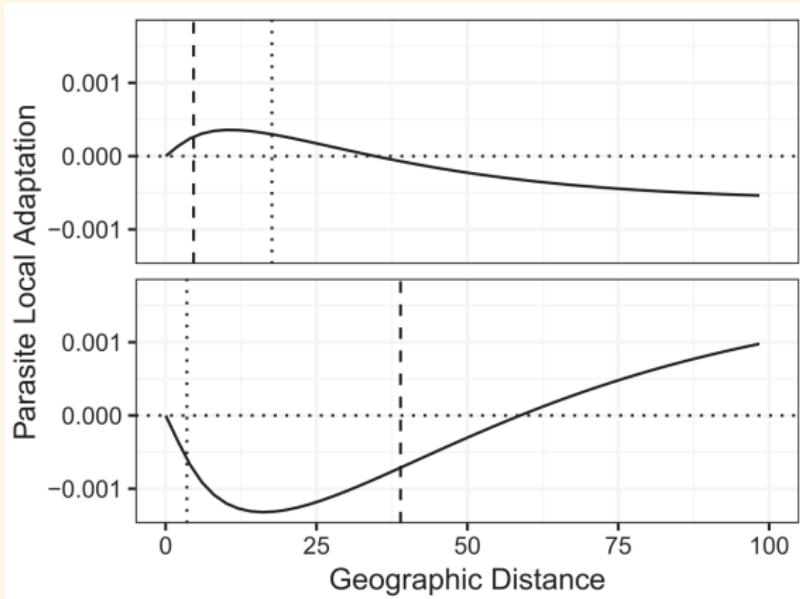


$$\mathcal{L}(\mathbf{x}, \mathbf{y}) = \mathbb{E}[\bar{m}(\mathbf{x}, \mathbf{x}) - \bar{m}(\mathbf{x}, \mathbf{y})]$$

# Parasite Local Adaptation

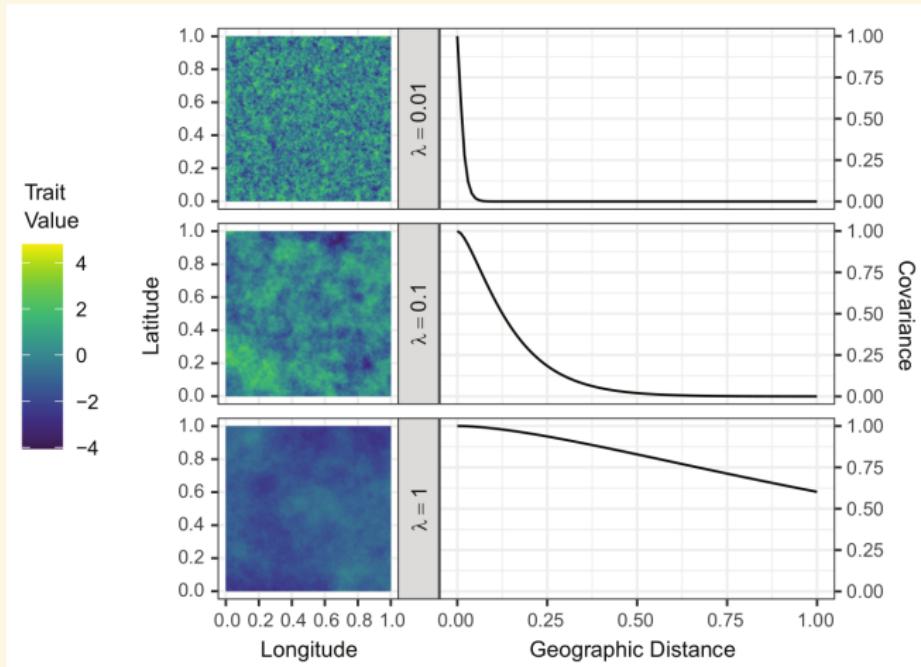


# Which Species is Locally Adapted can Depend on Distance



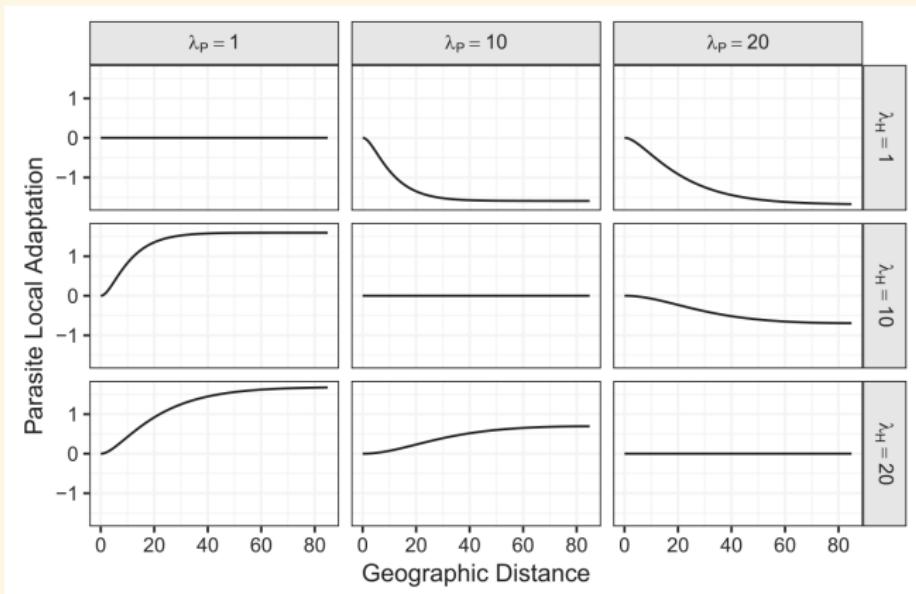
Results from asymmetry in selection strengths and rates of drift

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



A: Spatial Autocorrelation

# Consistent Measurements Require Sufficient Distances



Spatial autocorrelation disappears with distance

# Caveats

## Caveats

- Spatiotemporal constancy of local abundances

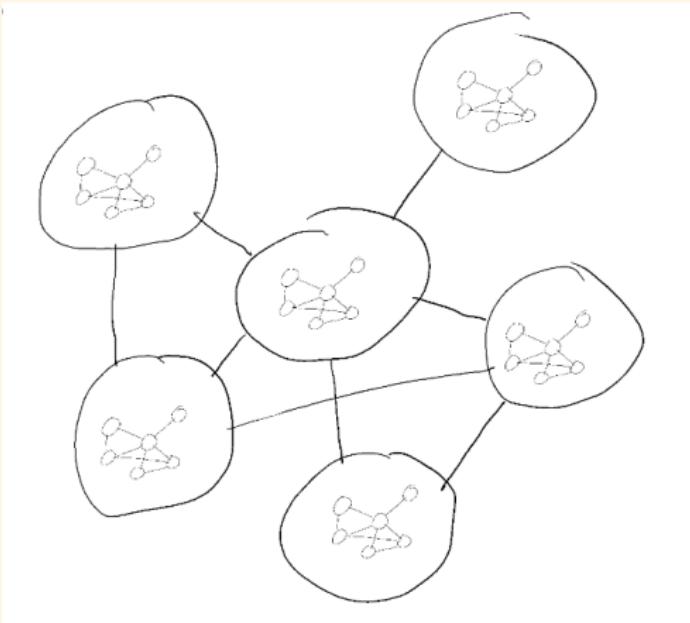
## Caveats

- Spatiotemporal constancy of local abundances
- Spatiotemporal constancy of local genetic variation

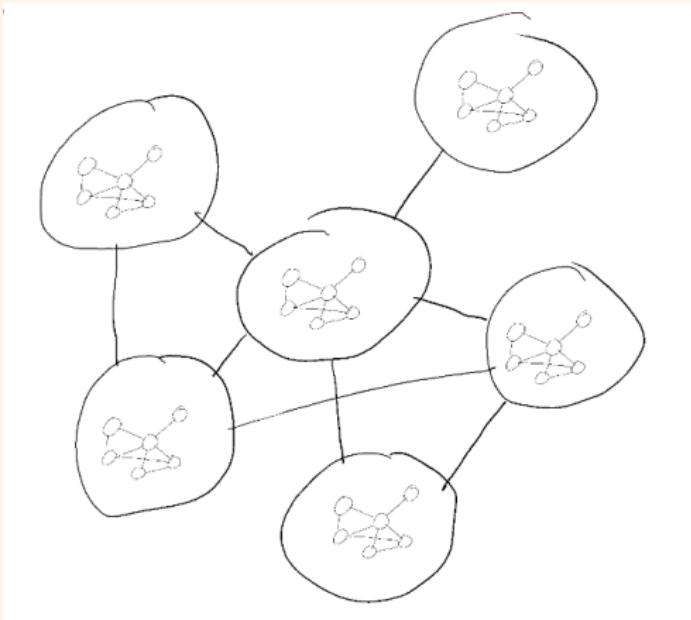
## Caveats

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

## Future Direction: How General is This Result?

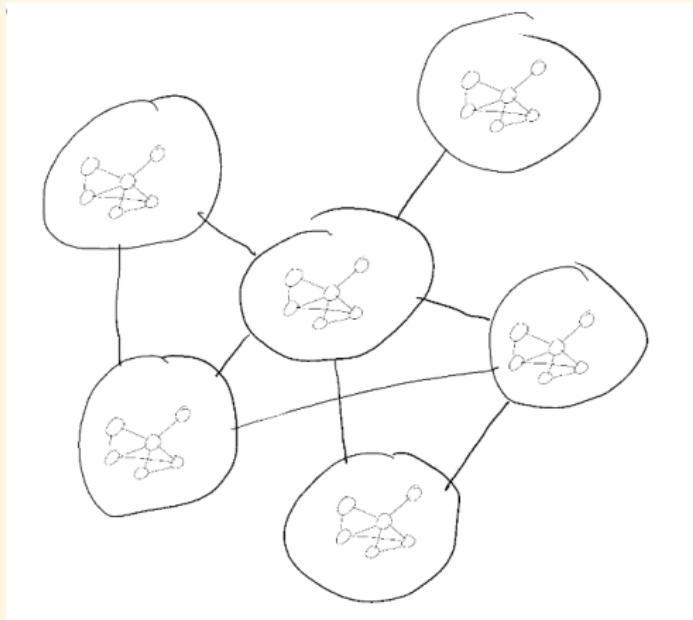


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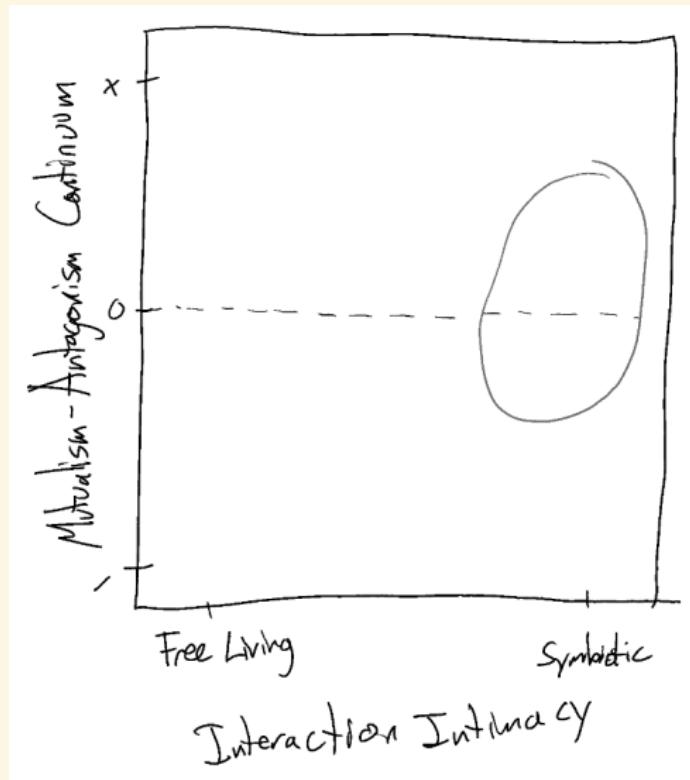
- Does the pattern emerge for other notions of spatial scale?

## Future Direction: How General is This Result?



- 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

# TwoOne Projects

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- Microbiome-mediated host trait evolution

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- Microbiome-mediated host trait evolution
  - with environmental transmission

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

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  - $M > 0$

## Examples



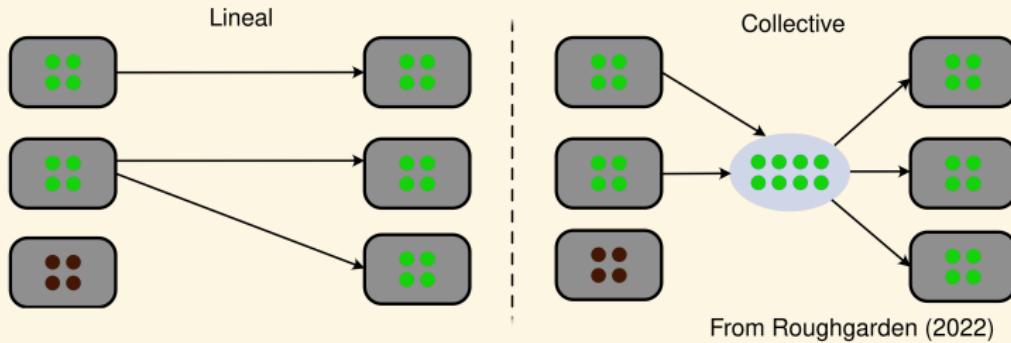
Toxicity of rough-skin newt mediated by skin microbiome<sup>18</sup>

# Examples



Cellulose digestion in cows mediated by gut microbiome<sup>19</sup>

# Microbiomes Are Inherited



A comparison of lineal vs collective inheritance<sup>20</sup>

<sup>20</sup>Roughgarden (2022)

# Q: How do Microbiome Mediated Host Traits Evolve?

?

## Related Theoretical Frameworks

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  - So new models are needed

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# Host Trait Architecture

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- $m$  = 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!