Adaptive Speciation

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Speciation Modes: Pattern and Process

- **Pattern-based classification**

  Allopatric speciation

  Parapatric speciation

  Sympatric speciation

- **Process-based classifications**

  Competitive speciation

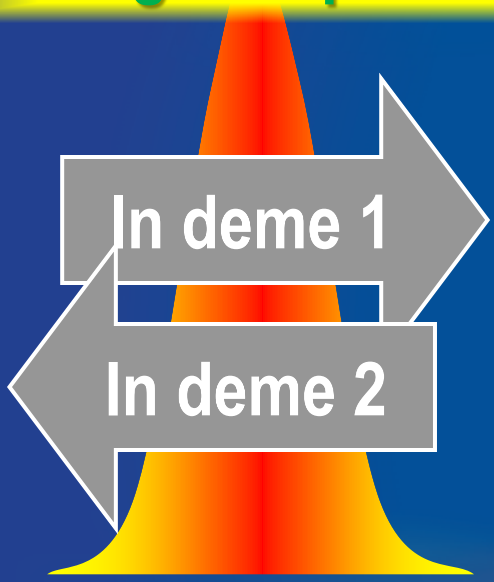
  Ecological speciation

  Adaptive speciation

Evolution of Reproductive Isolation

- Divergent selection

Ecological speciation



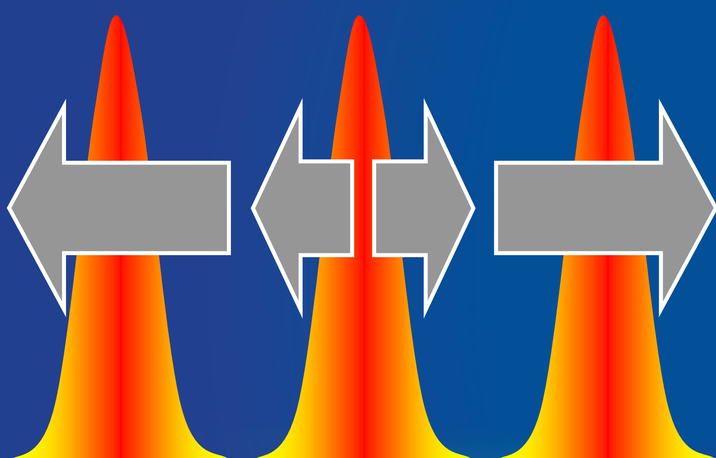
Reproductive isolation
may occur along the way

- Disruptive selection

Reproductive isolation
may be selected for directly

Long-lived Evolutionary Trapping

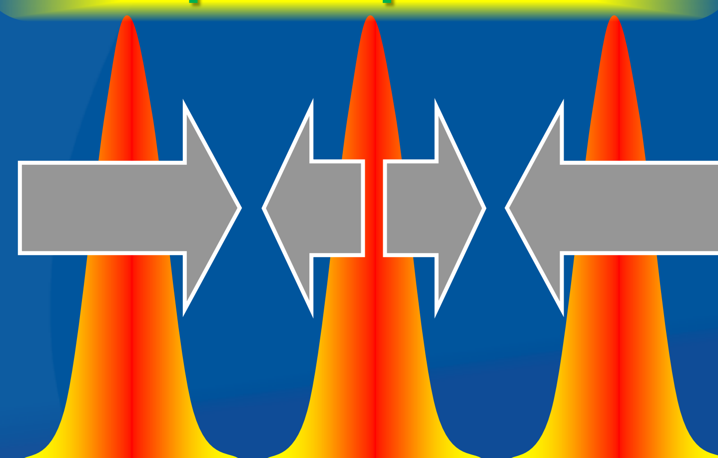
- Frequency-independent disruptive selection



Disruptiveness is unstable and thus short-lived

- Frequency-dependent disruptive selection

Adaptive speciation



Disruptiveness is stabilized and may thus be long-lived

Competitive speciation

is the expansion of a species from a single ecological opportunity to an unexploited ecological opportunity, followed by that species' sympatric breakup into two daughters, one using the original opportunity, the other the newly exploited one

Rosenzweig (1978)

Ecological speciation

happens through the evolution of reproductive isolation between populations as a result of ecologically-based divergent natural selection

Schluter (2000)

Adaptive speciation
occurs when a population escapes through speciation from remaining trapped at a fitness minimum

Dieckmann et al. (2004)

Adaptive speciation

is an adaptive response to disruptive selection caused by negatively frequency-dependent biological interactions

Dieckmann et al. (2004)

Ecological Drivers of Speciation

Competitive speciation

Divergent selection

Frequency-dependent disruptive selection

Existing niches

Emerging niches

Ecological speciation

Adaptive speciation

This talk

Overview

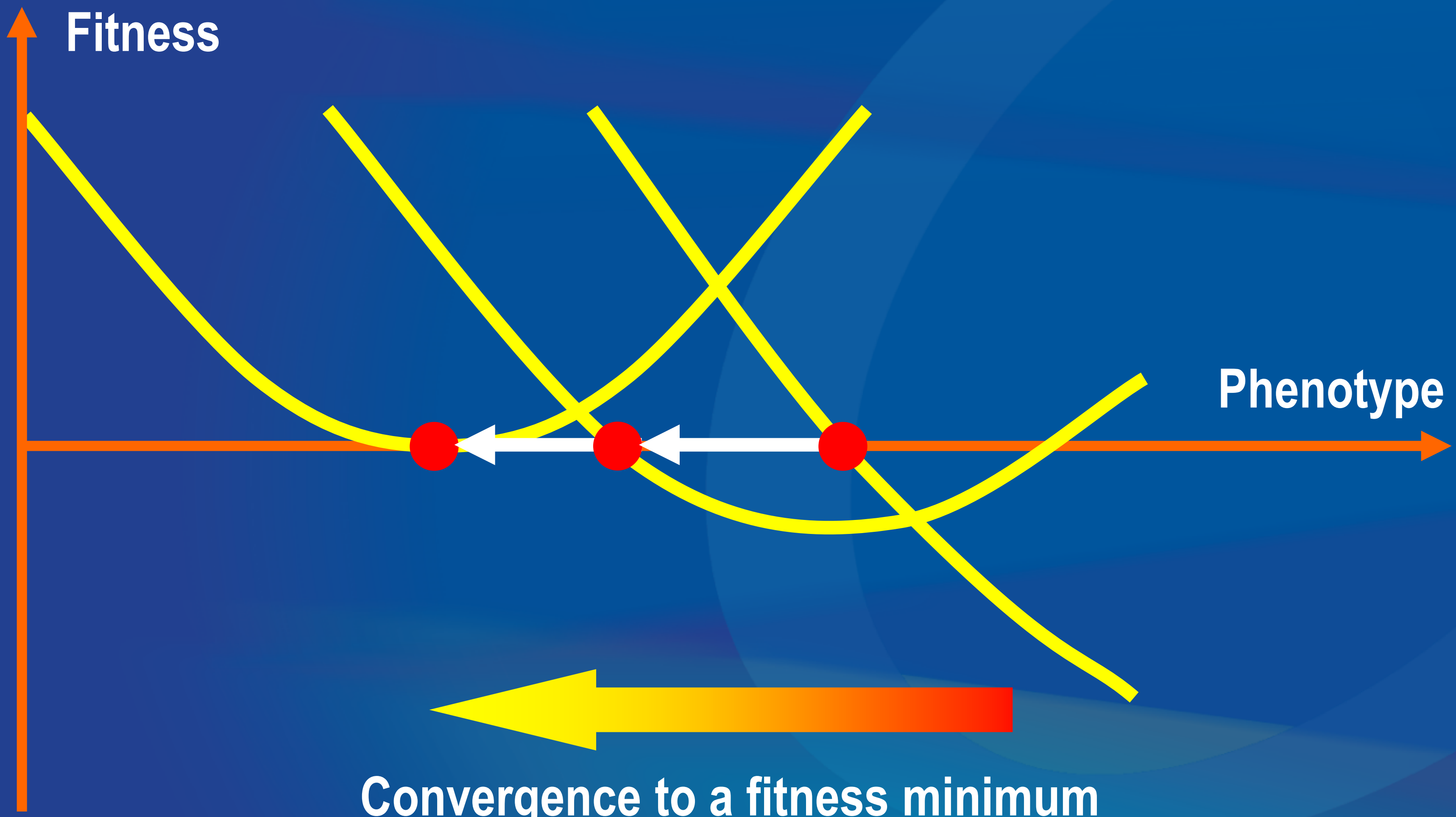
1. Adaptive Speciation
2. Robustness and Extensions
3. Extended Classification
4. Calibrated Speciation Models

1

Adaptive Speciation

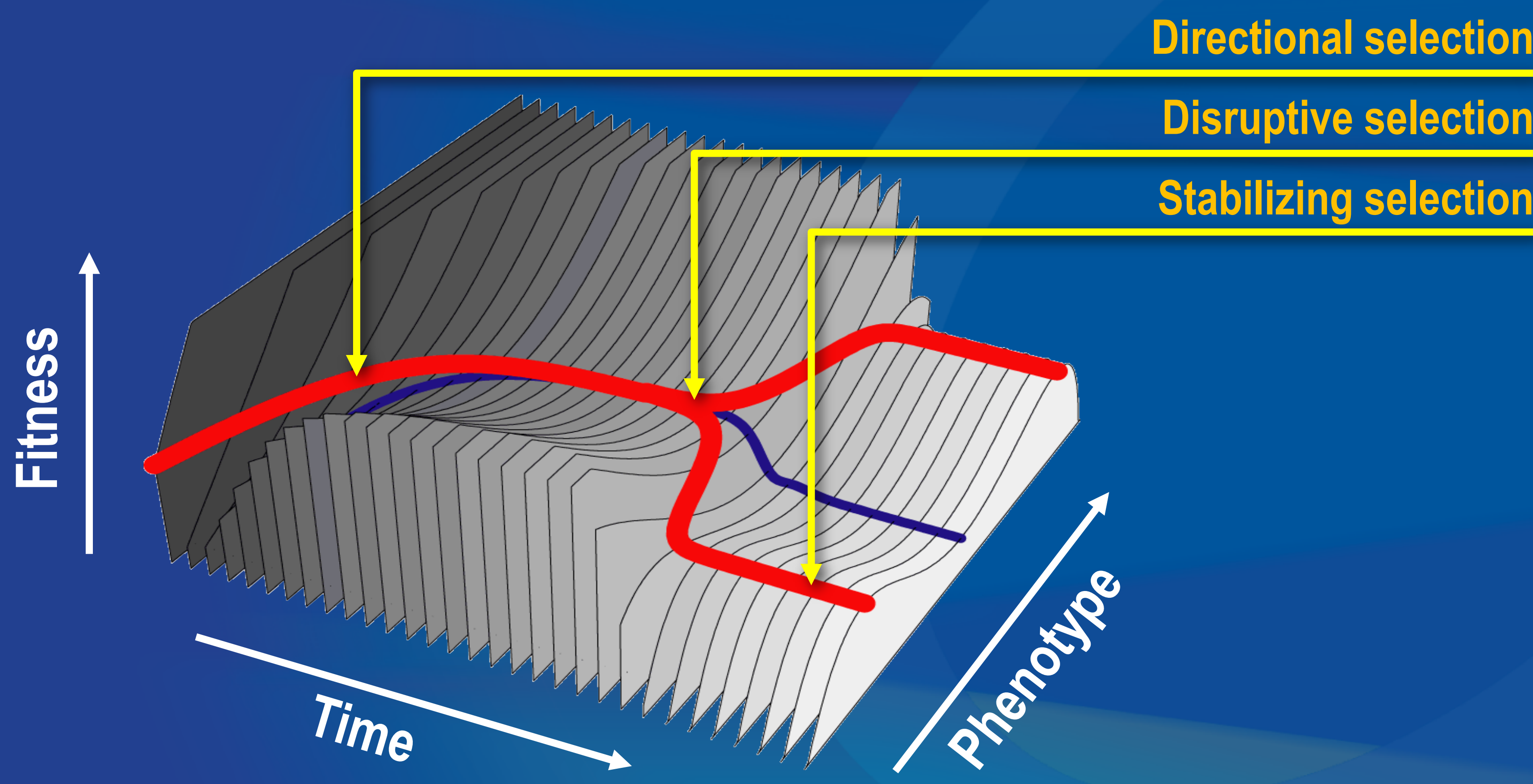
Reminder: Evolutionary Branching

Metz et al. (1992)



Reminder: Evolutionary Branching

Dieckmann et al. (2004)



Sexual Adaptive Speciation

Dieckmann & Doebeli (1999)

- With random mating and additive multi-locus genetics, sexual populations cannot easily become bimodal
- For sexual populations to become bimodal, ecological divergence and reproductive isolation need to evolve together
- Thus we allow evolution of the mating mode:

+1 Strongly assortative mating

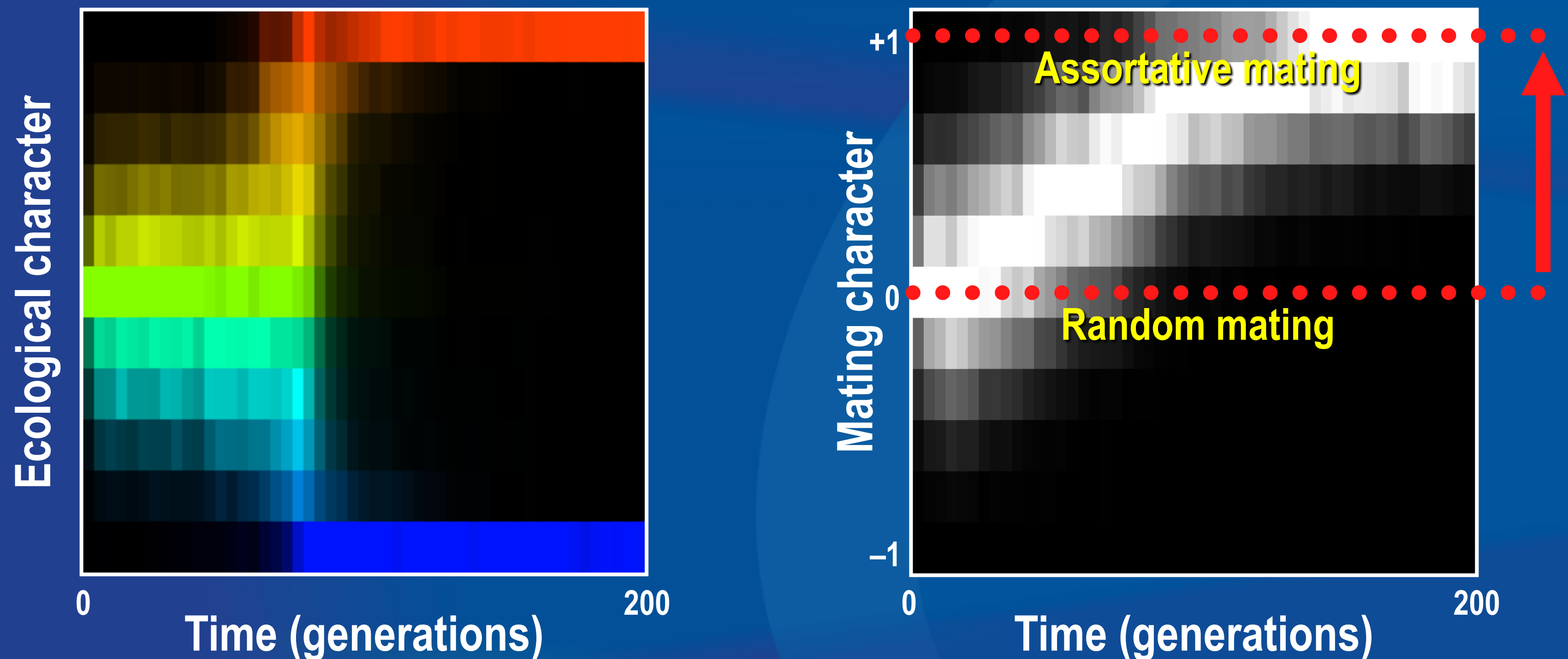
0 Random mating

–1 Strongly disassortative mating

Continuous adaptation

Sexual Adaptive Speciation

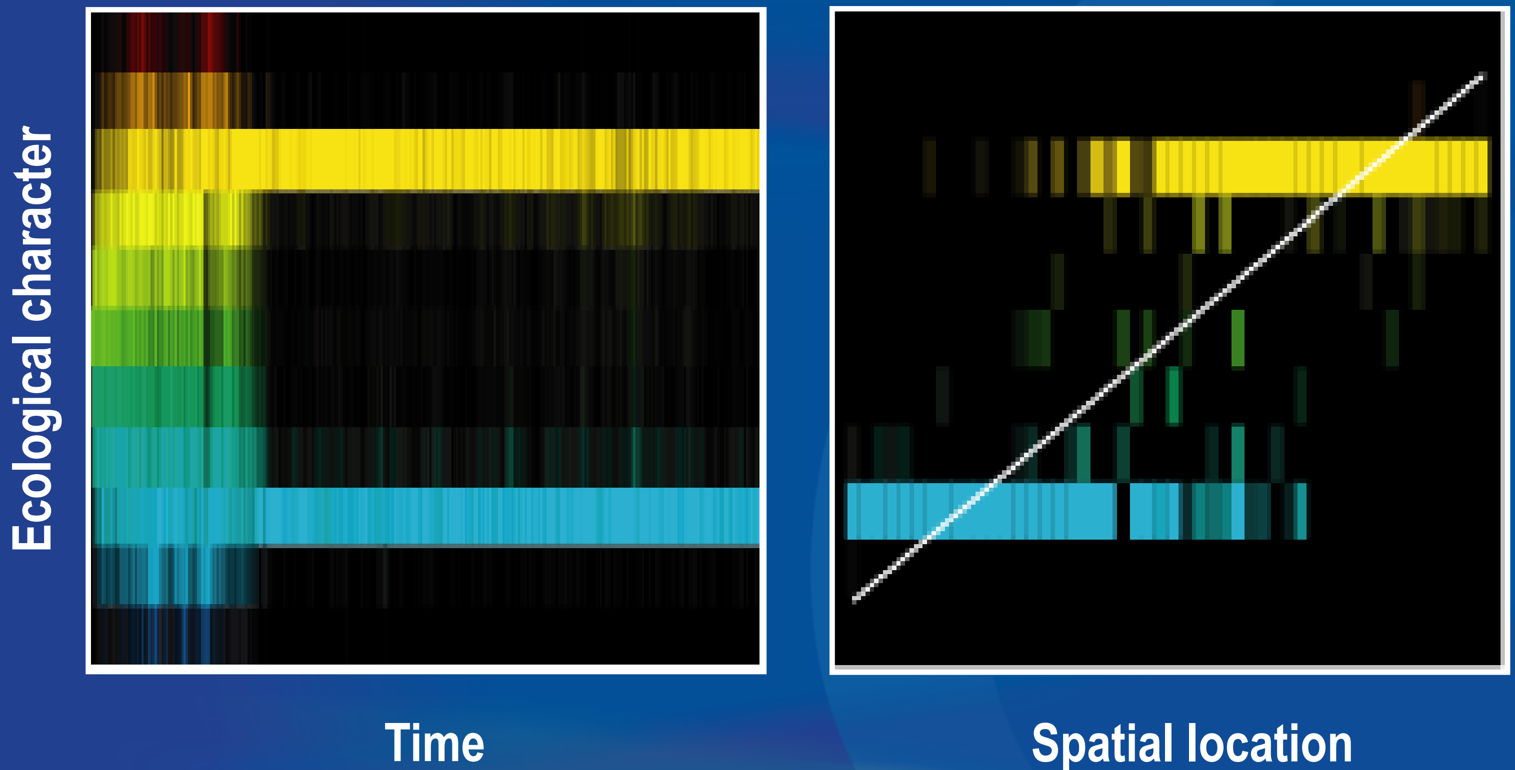
Dieckmann & Doebeli (1999)



Frequency-dependent disruptive selection favors assortative mating, which reduces the chance of offspring phenotypes to end up at the fitness minimum

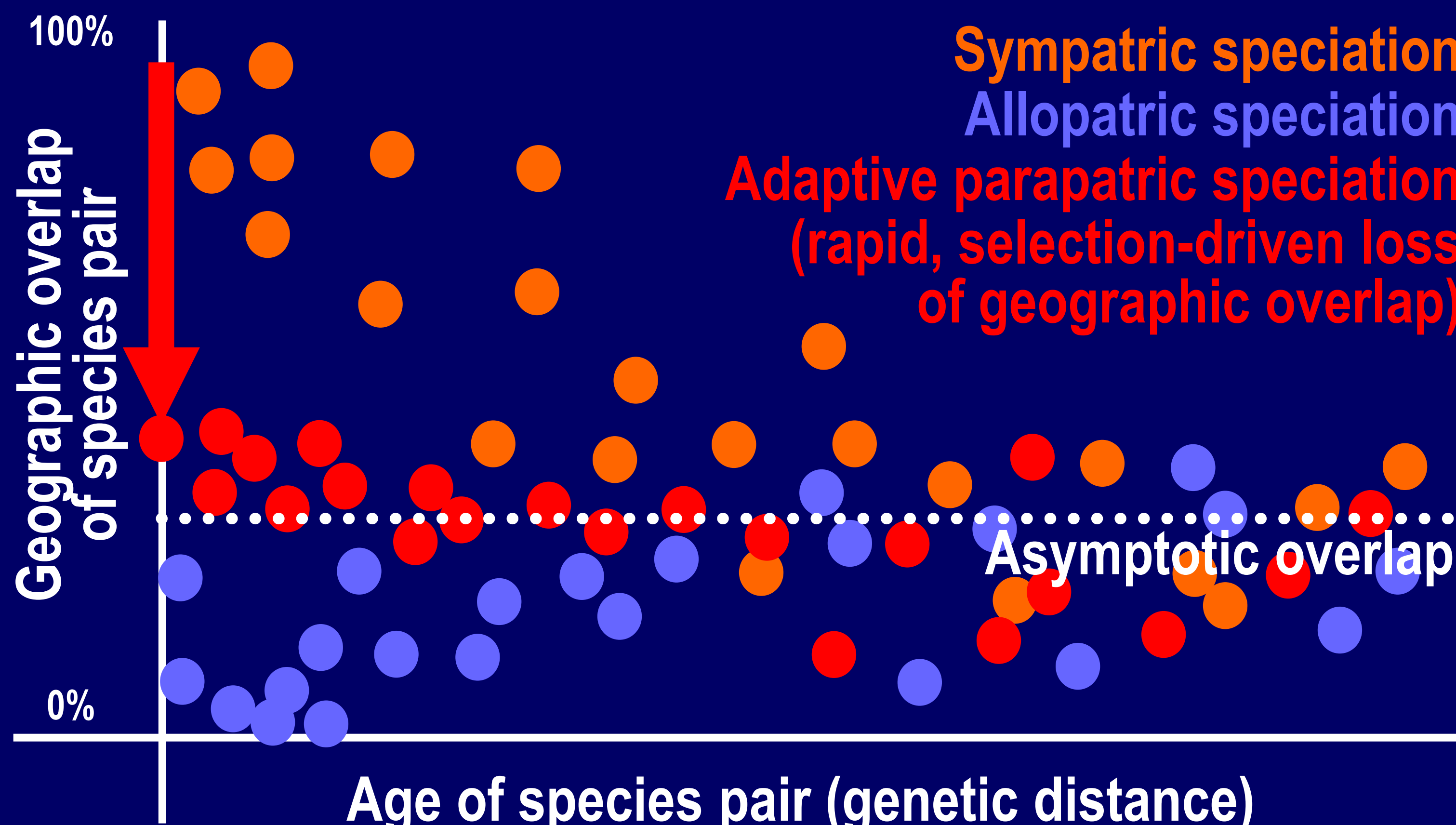
Spatial Adaptive Speciation

Doebeli & Dieckmann (2003)



Here spatial segregation is the **consequence**, rather than the **cause**, of speciation. This fundamentally changes how biogeographic patterns can be interpreted.

Expected Biogeographic Signatures



See also Barraclough & Vogler (2000)

2

Robustness and Extensions

Types of Competition 1/2

Adaptive speciation is promoted by

- **Indirect competition**

  All fundamental types of ecological interaction – competition, exploitation, and mutualism – can result in adaptive speciation, in the latter two cases through resource competition and apparent competition (Doebeli & Dieckmann 2000)

- **Platykurtic competition**

  Adaptive speciation is facilitated by competition kernels that are not positive definite, which in turn is more likely for box-like or platykurtic competition kernels (Pigolotti et al. 2007)

Types of Competition 2/2

Adaptive speciation is promoted by

- **Self-organized platykurtosis**

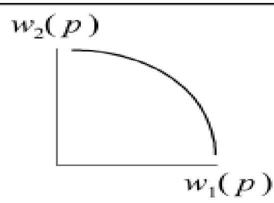
  Under the impact of residual disruptive selection, intraspecific phenotypic variation becomes platykurtic, with implications that are mathematically very similar to those of platykurtic competition kernels (Sasaki & Dieckmann 2011)

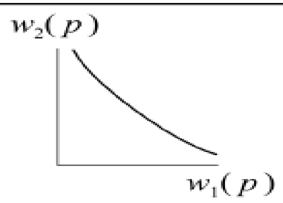
- **Wasteful consumption**

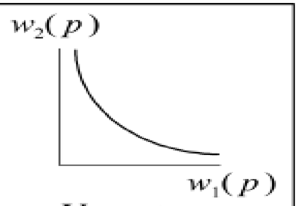
  Not all resources sequestered by a consumer contribute to its growth, increasing the expected prevalence of non-positive-definite competition kernels (Leimar et al. 2013)

Local Adaptation & Habitat Choice

Ravigné et al. (2009)

<table>
<tr><td colspan="2">Local-adaptation trade-offs</td><td>

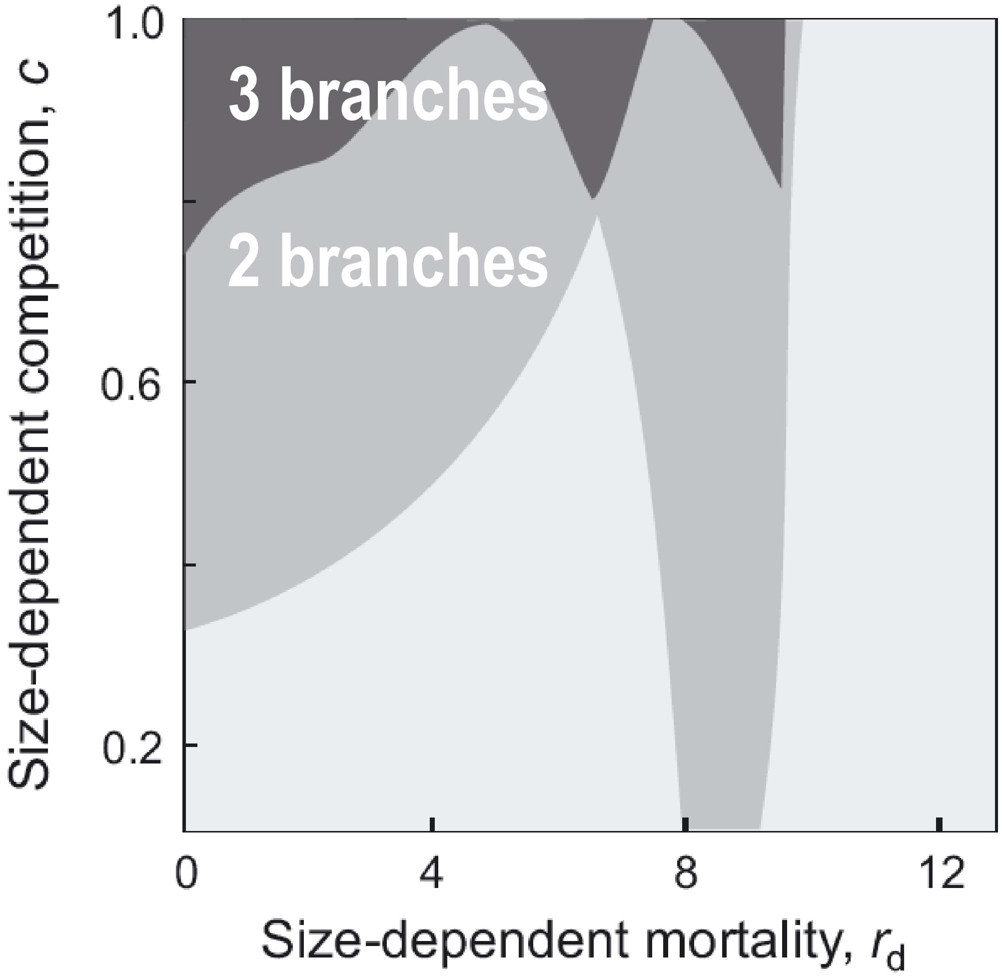
Weak trade-offs</td><td>

Moderately strong trade-offs</td><td>

Very strong trade-offs</td></tr>
<tr><td colspan="5">A Evolution of local adaptation under fixed and unconditional habitat choice</td></tr>
<tr><td colspan="2">Constant habitat outputs (Model 1)</td><td rowspan="2">Intermediate local adaptation
1 intermediate phenotype</td><td>Possible branching
2 specialists</td><td></td></tr>
<tr><td colspan="2">Variable habitat outputs (Models 2 and 3)</td><td colspan="2">Bistability
1 specialist</td></tr>
<tr><td colspan="5">B Evolution of habitat choice under fixed and monomorphic local adaptation</td></tr>
<tr><td colspan="2">Local regulation (Models 1 and 3)</td><td colspan="3">Intermediate habitat choice
Ideal free distribution</td></tr>
<tr><td colspan="2">Global regulation (Model 2)</td><td colspan="3">Maximal habitat choice
One habitat remains empty</td></tr>
<tr><td colspan="5">C Joint evolution of local adaptation and habitat choice</td></tr>
<tr><td>Constant habitat outputs (Model 1)</td><td rowspan="2">Local regulation (Models 1 and 3)</td><td colspan="2">Branching
2 specialists</td><td></td></tr>
<tr><td rowspan="2">Variable habitat outputs (Models 2 and 3)</td><td></td><td colspan="2">Bistability
1 specialist in ideal free distribution</td></tr>
<tr><td>Global regulation (Model 2)</td><td colspan="3">Bistability
1 specialist leaving the other habitat empty</td></tr>
</table>

Size Refuges

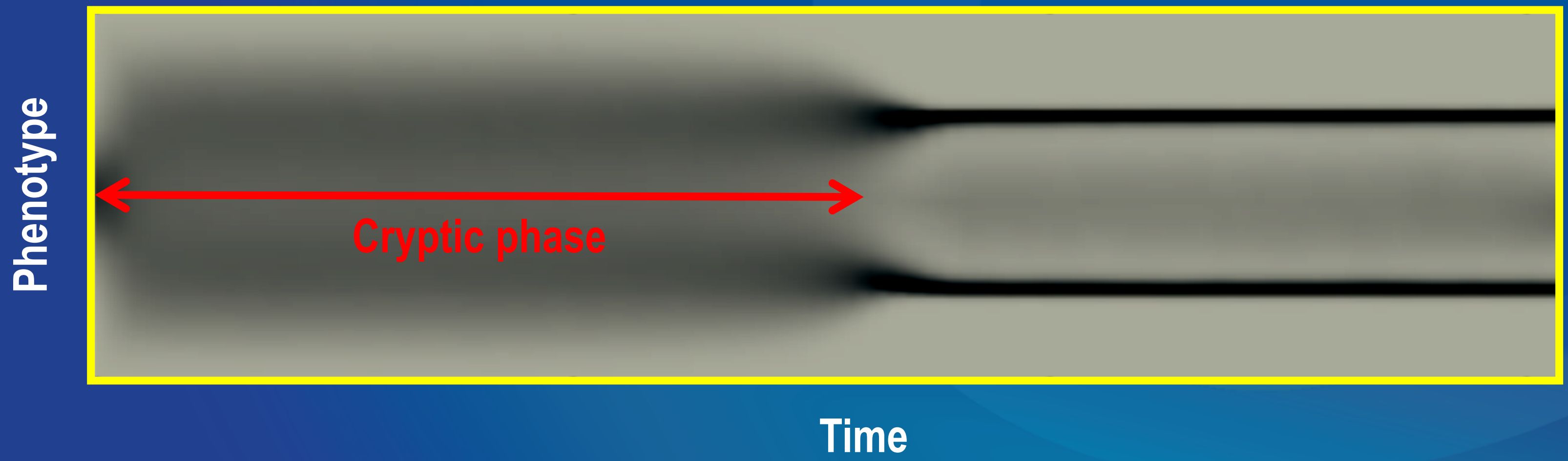
Taborsky et al. (2012)



Genetic Erosion

Meszéna & Dieckmann (unpublished)

When resource utilization can closely match resource availability, adaptive speciation may involve a cryptic phase of genetic erosion, during which within-phenotype genetic variation is gradually grinded away by phenotypically local stabilizing selection owing to natural selection and sexual selection:



Spatiotemporal Modes

Rettelbach et al. (2013)

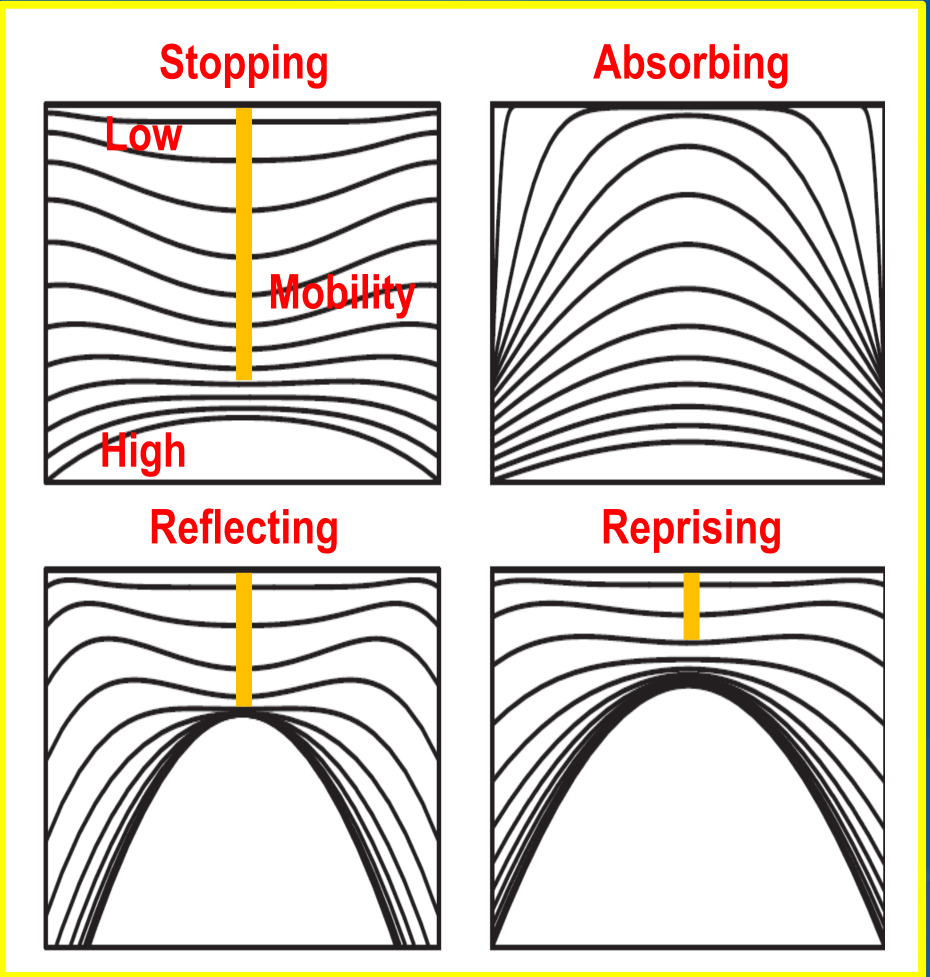
Adaptive speciation may occur through three qualitatively distinct spatiotemporal modes:

- **Migration-independent competitive mode:** occurs within demes due to intra-deme competition
- **Migration-driven ecological mode:** occurs between demes due to selection against mating with maladapted immigrants (reinforcement w/o allopatry)
- **Migration-induced competitive mode:** begins between demes due to selection against mating with maladapted immigrants, and is completed within demes due to intra-deme competition

Habitat Boundaries

Mazzucco et al. (unpublished)

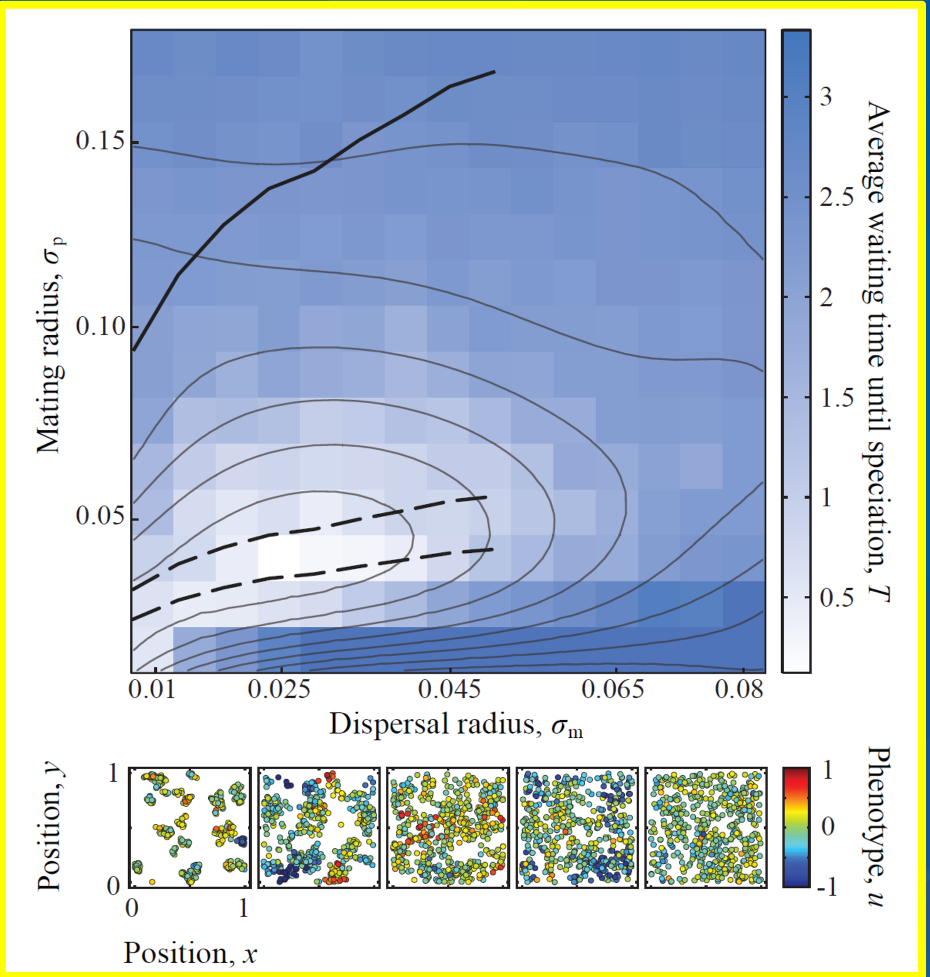
All populations experience spatial boundaries of their habitats. In conjunction with spatial environmental gradients, such boundaries exert selection pressures. At low mobilities, these tend to be disruptive (except for absorbing boundaries), promoting adaptive speciation.



Spatial Self-Structuring in Sexual Populations

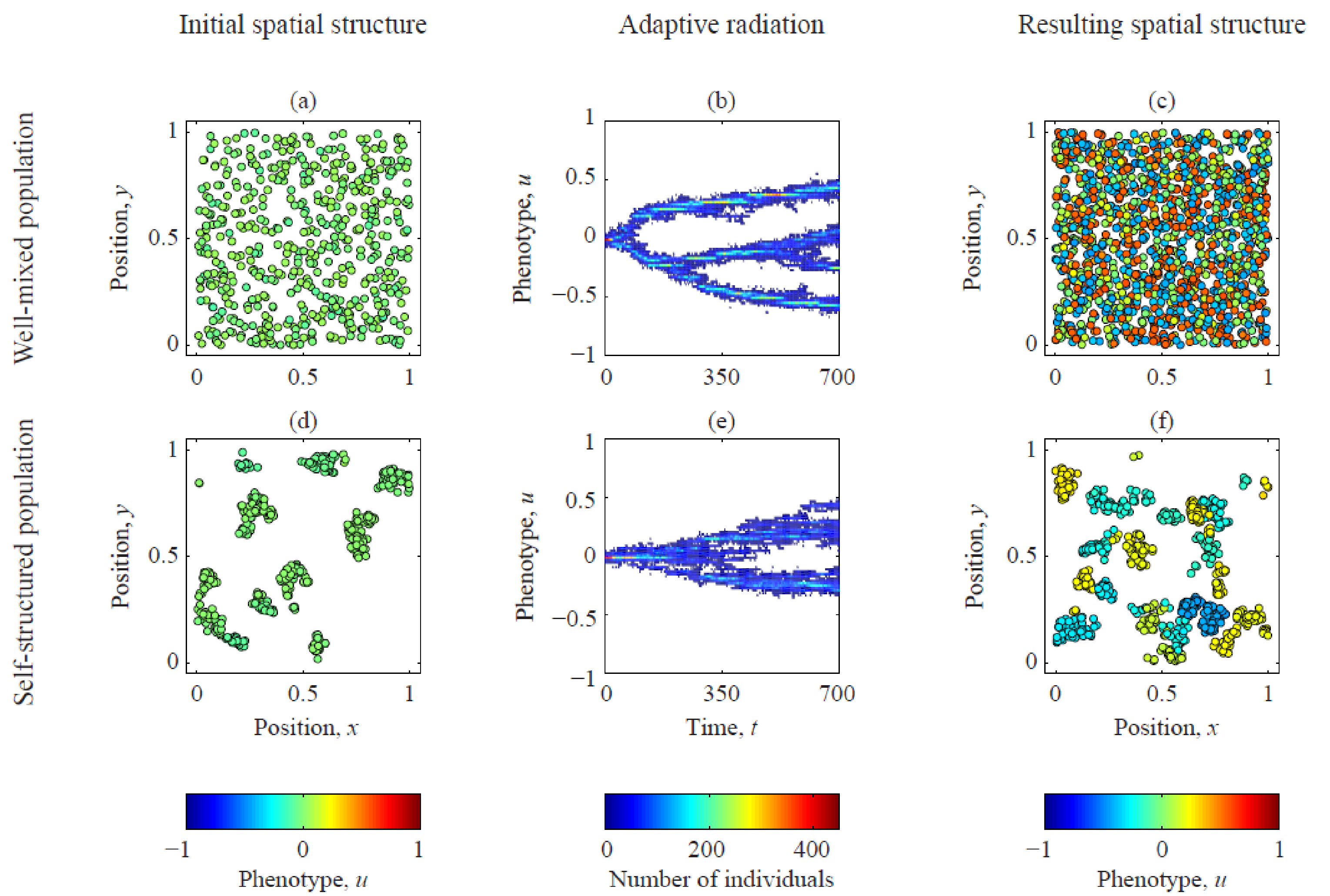
Fazalova & Dieckmann (2012)

Spatial adaptive speciation is accelerated in sexual populations by the spatial scale of mating matching that of dispersal.



Spatial Self-Structuring in Asexual Populations

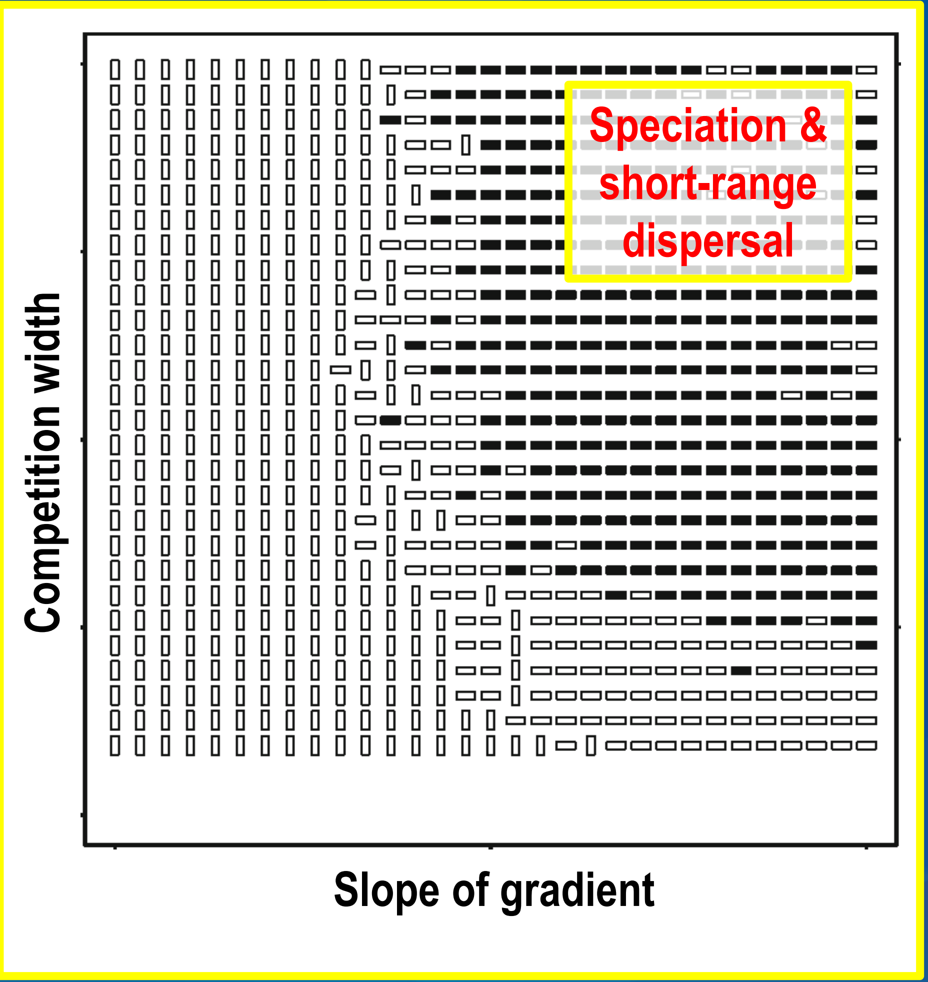
Fazalova & Dieckmann (unpublished)



Evolution of Unconditional Dispersal

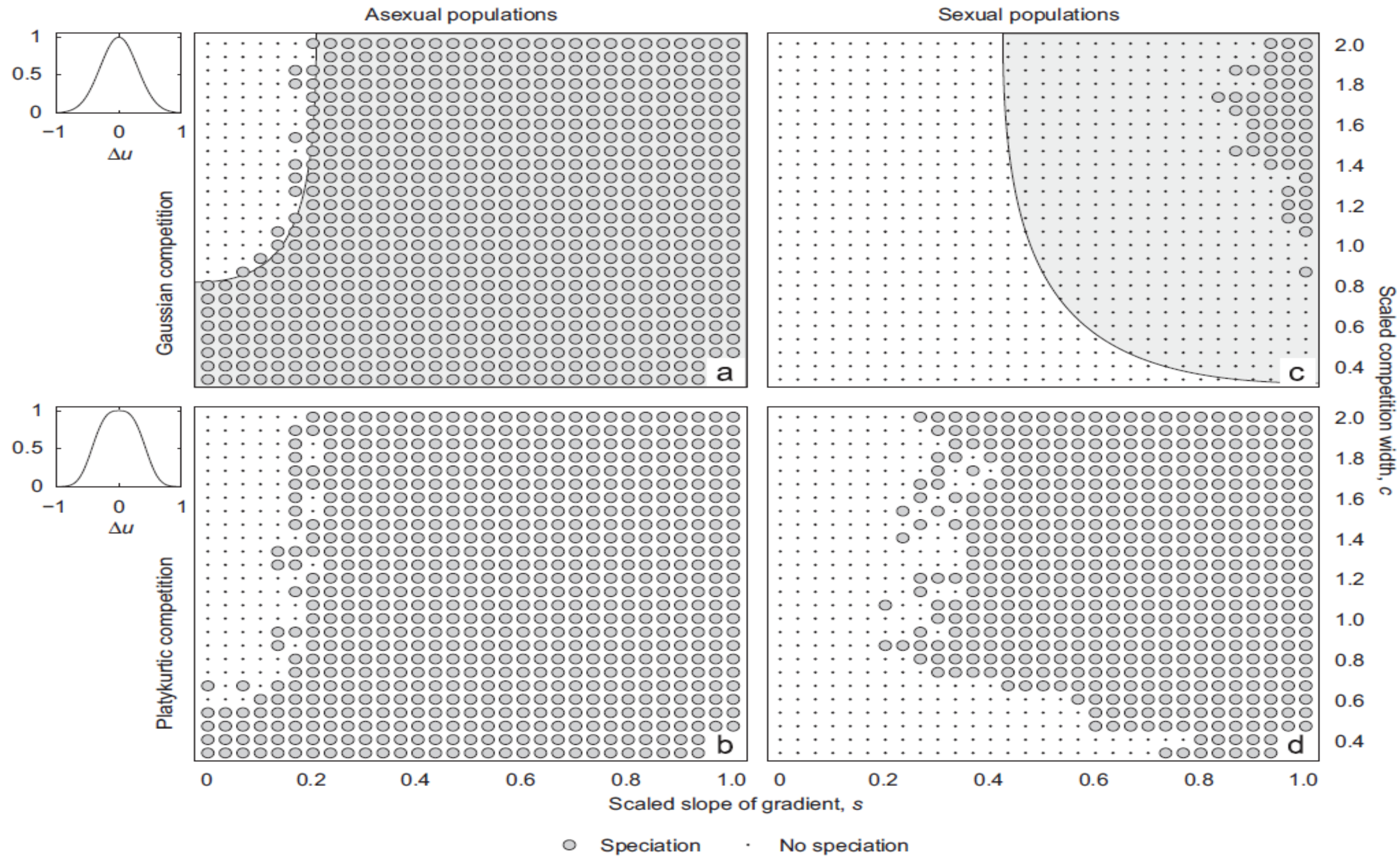
Heinz et al. (2009)

Along environmental gradients, adaptive speciation may be enabled by dispersal evolution – even in the absence of any direct assortative mating.

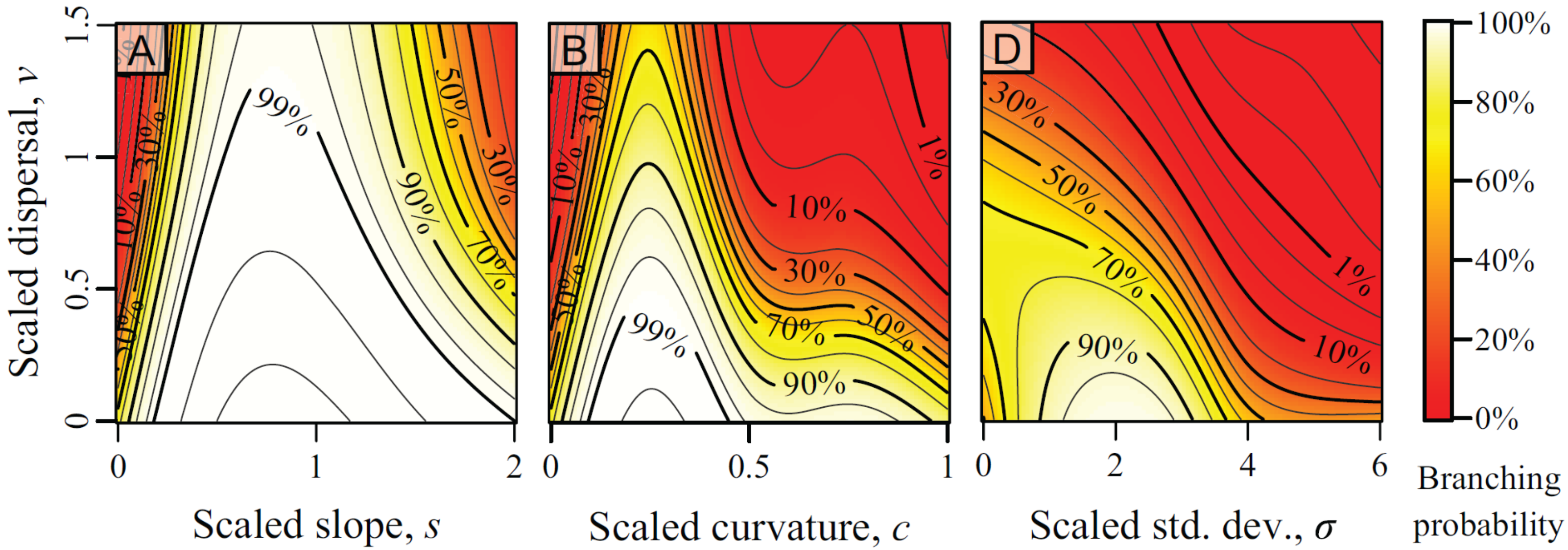


Evolution of Conditional Dispersal

Payne et al. (2011)



Heterogeneous Landscapes Haller et al. (2013)



The probability of evolutionary branching is maximal at intermediate levels of spatial heterogeneity, in terms of slope, curvature, and patchiness.

Neutral Coexistence through Costly Sexual Selection

M'Gonigle et al. (2012)

LETTER

nature

doi:10.1038/nature10971

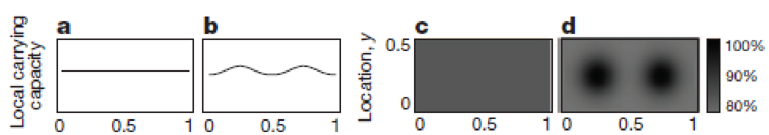
Sexual selection enables long-term coexistence despite ecological equivalence

Leithen K. M'Gonigle[1]†, Rupert Mazzucco[2], Sarah P. Otto[1] & Ulf Dieckmann[2]

Empirical data indicate that sexual preferences are critical for maintaining species boundaries[1–4], yet theoretical work has suggested that, on their own, they can have only a minimal role in maintaining biodiversity[5–9]. This is because long-term coexistence within overlapping ranges is thought to be unlikely in the absence of ecological differentiation[9]. Here we challenge this widely held view by generalizing a standard model of sexual selection to include two ubiquitous features of populations with sexual selection: spatial variation in local carrying capacity, and mate-search costs in females. We show that, when these two features are combined, sexual preferences can single-handedly maintain coexistence, even when spatial variation in local carrying capacity is so slight that it might go unnoticed empirically. This theoretical study demonstrates that sexual selection alone can promote the long-term coexistence of ecologically equivalent species with overlapping ranges, and it thus provides a novel explanation for the maintenance of species diversity.

associated with sexual selection, a recent review concluded that sexually divergent, but ecologically equivalent, species cannot coexist for significant lengths of time[9].

Here we report model results that suggest the contrary and demonstrate that sexual selection can promote long-term coexistence, even without any ecological differentiation. Building on a standard model of sexual selection[14], we develop an individual-based model to examine the long-term fate of species differing only in their secondary sexual characters in an ecologically neutral context with finite population sizes (details are given in Supplementary Information). Except where noted, we assume a simple genetic structure with two unlinked haploid

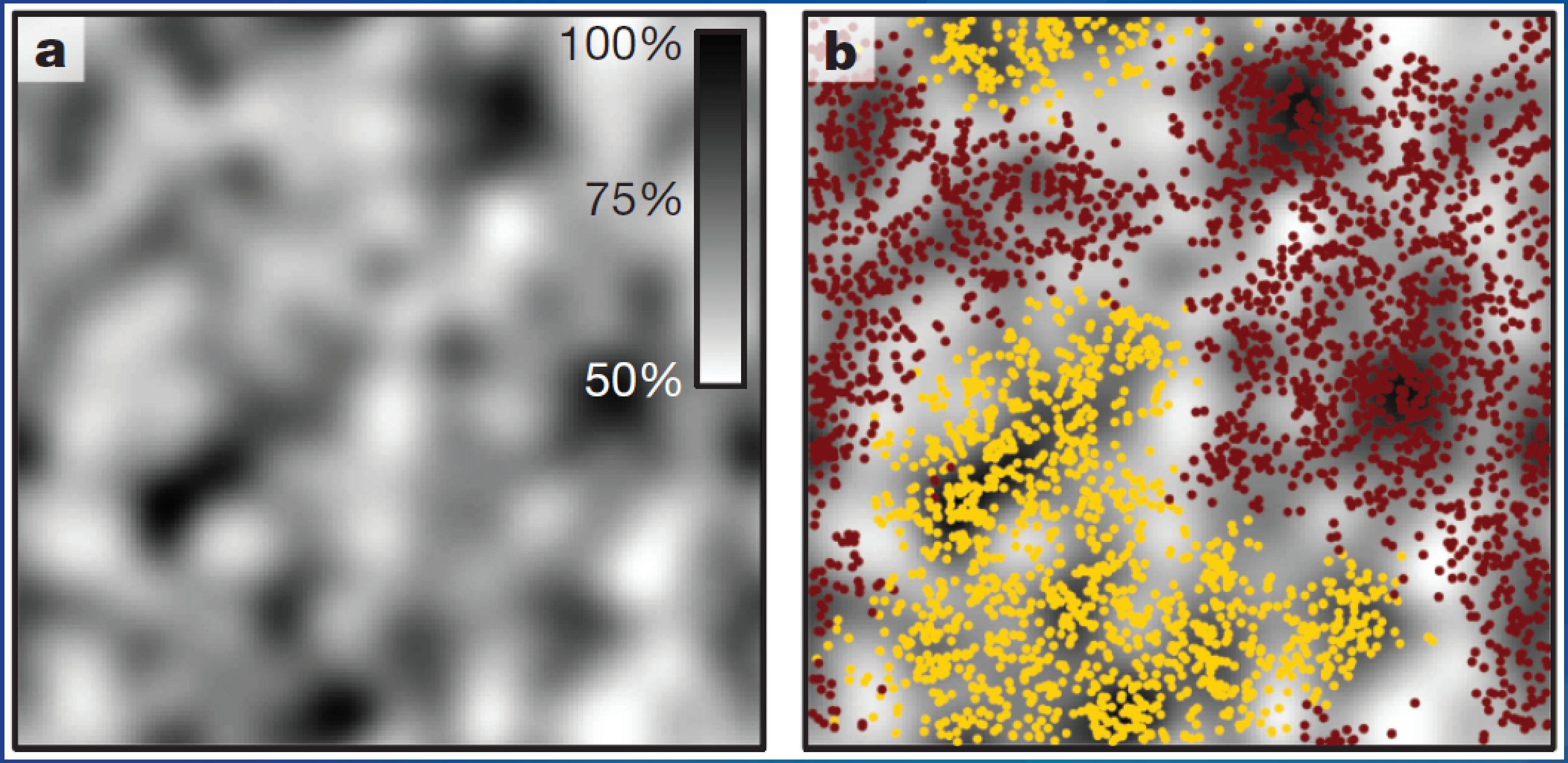


Neutral Coexistence through Costly Sexual Selection

M'Gonigle et al. (2012)

Slight spatial heterogeneity in local carrying capacity

Long-term coexistence despite full ecological equivalence



3

Extended Classification

IIASA

Three Key Characteristics

- **Ecological differentiation**

  Provides the only speciation criterion for asexuals

- **Spatial differentiation**

  Can either drive or be driven by speciation process

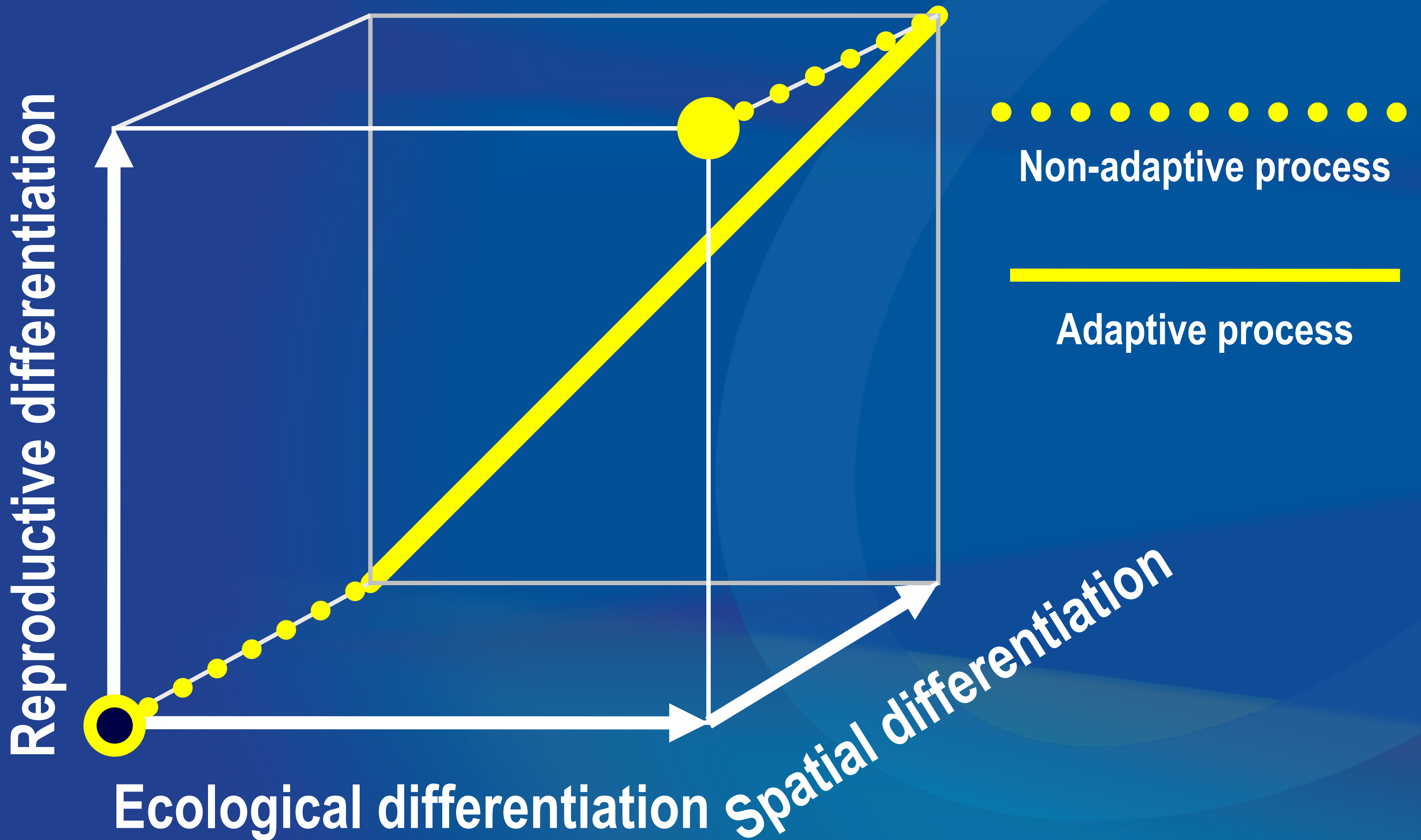
- **Reproductive differentiation**

  Needs to evolve for speciation in sexuals

- These characteristics can arise simultaneously or sequentially, and occur gradually or in externally determined phases

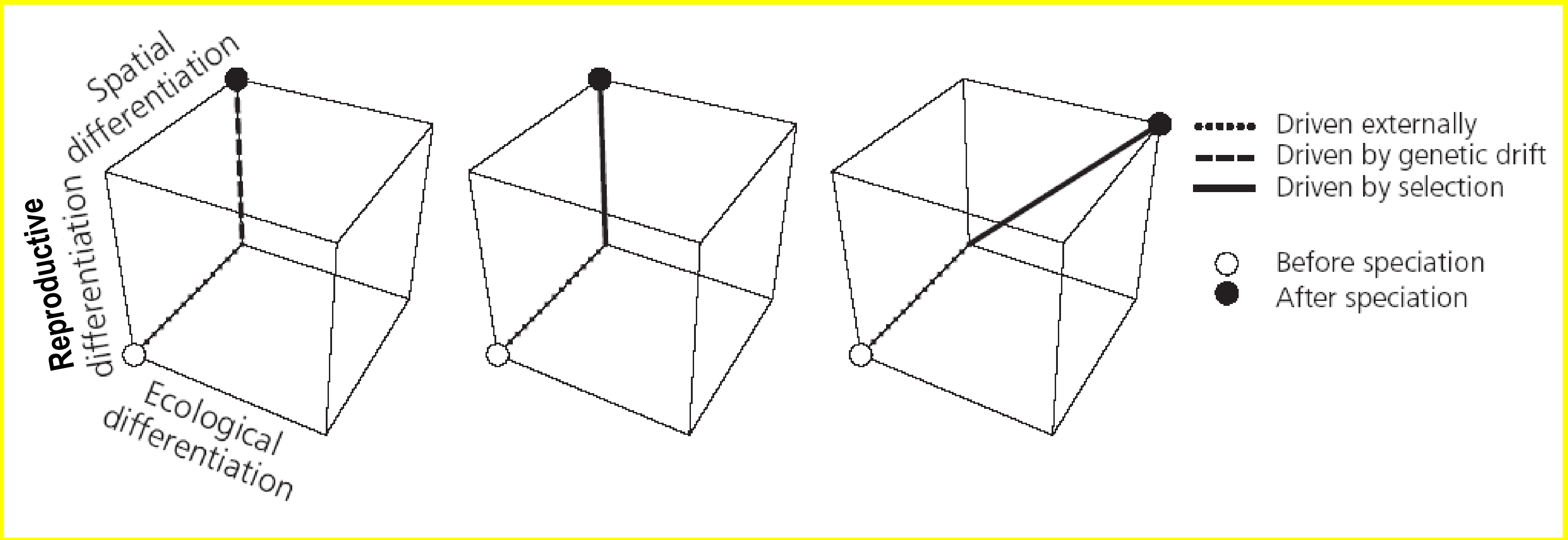
Speciation Cubes

Dieckmann et al. (2004)



Allopatric Speciation

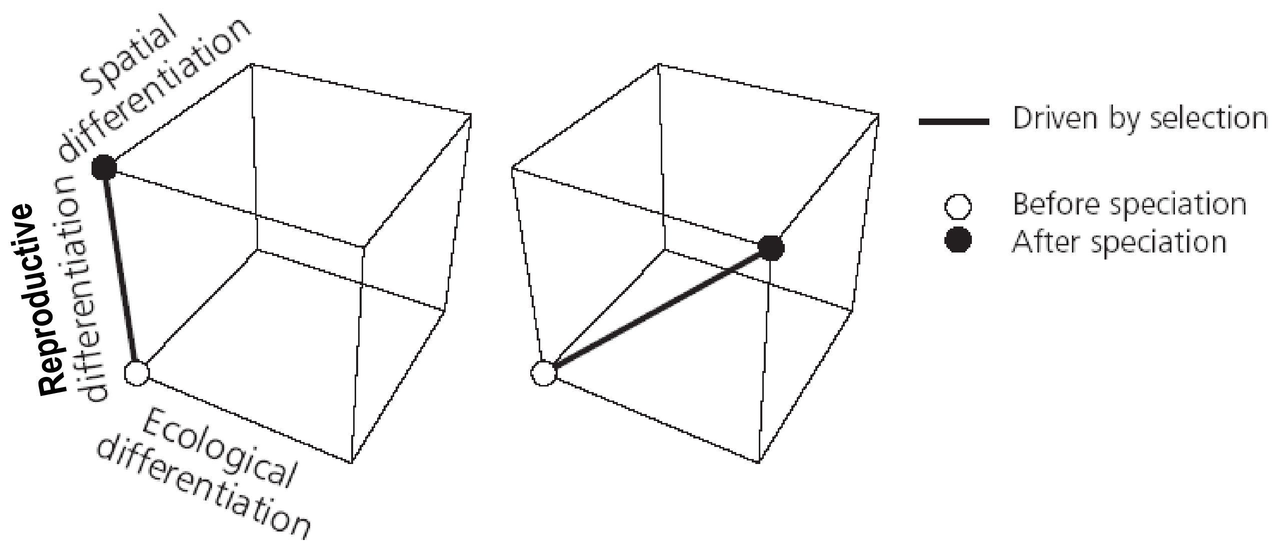
Dieckmann et al. (2004)



External causes first result in geographic isolation between two incipient species, and thus introduce a high degree of spatial differentiation. After that, either genetic drift (left) or sexual selection (middle) can increase reproductive differentiation. Alternatively, local adaptation with pleiotropic effects on mating (right) can increase ecological and reproductive differentiation concomitantly.

Sympatric Speciation

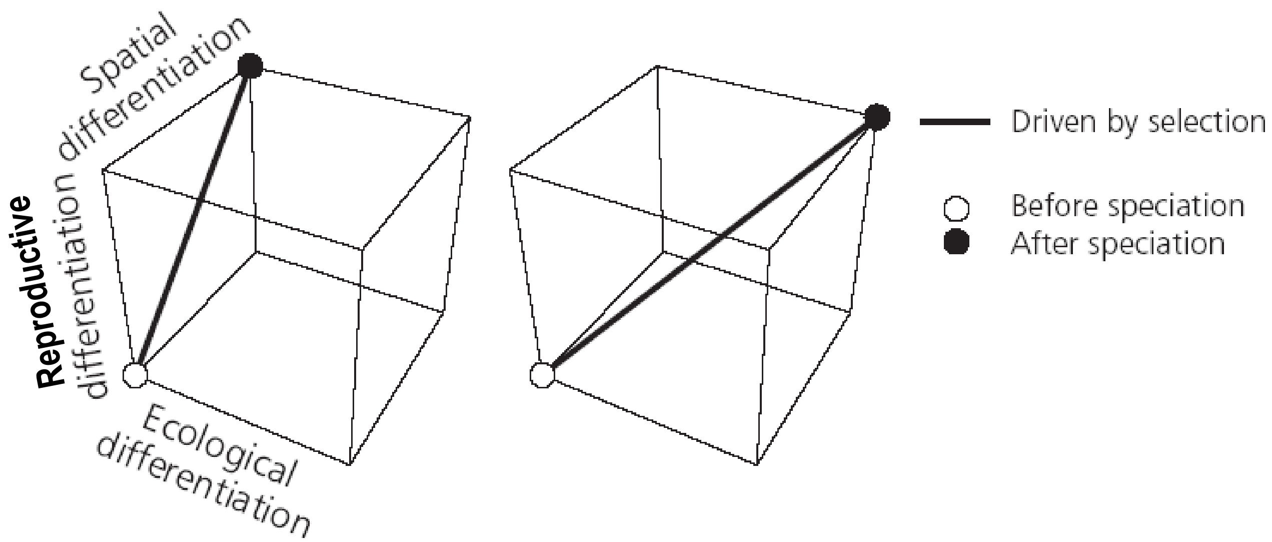
Dieckmann et al. (2004)



Either evolution driven by sexual selection induces reproductive isolation in the absence of concomitant ecological differentiation (left; unstable), or such ecological differentiation is accompanied by the evolution of assortative mating (right).

Parapatric Speciation

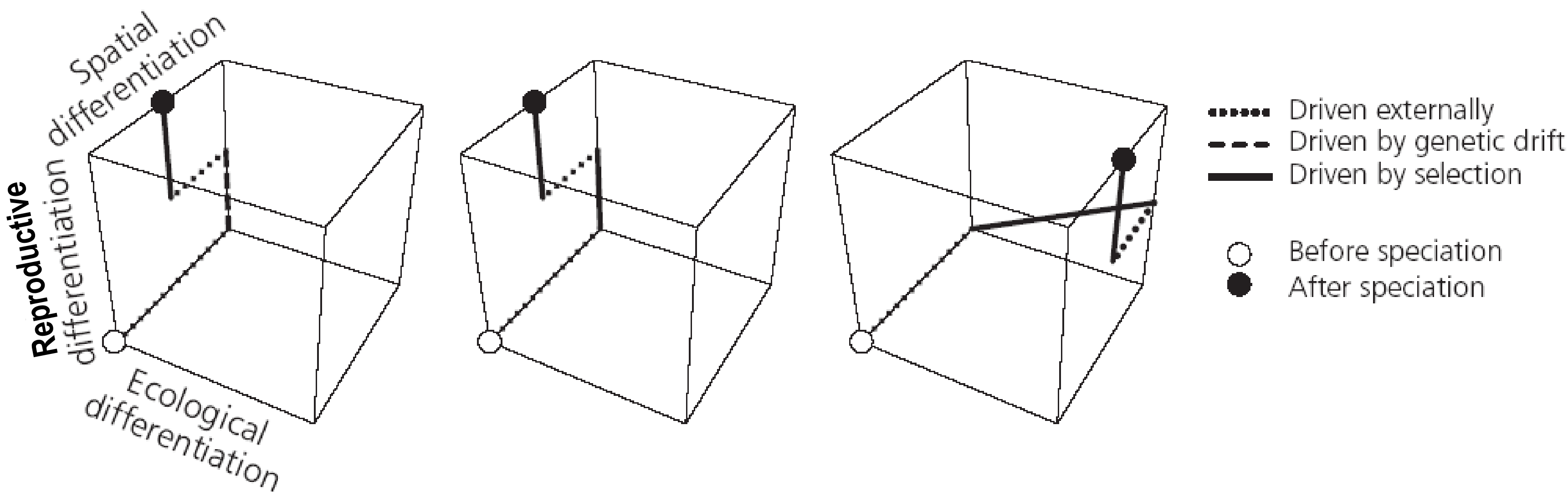
Dieckmann et al. (2004)



Either evolution driven by sexual selection induces reproductive isolation and spatial differentiation by giving rise to mating domains (left), or ecological differentiation is accompanied by the evolution of assortative mating and the emergence of spatial differentiation (right). The latter can occur at least in two guises: first in the course of host-race formation, and second through local adaptation and speciation along environmental gradients.

Two-Phase Speciation Processes

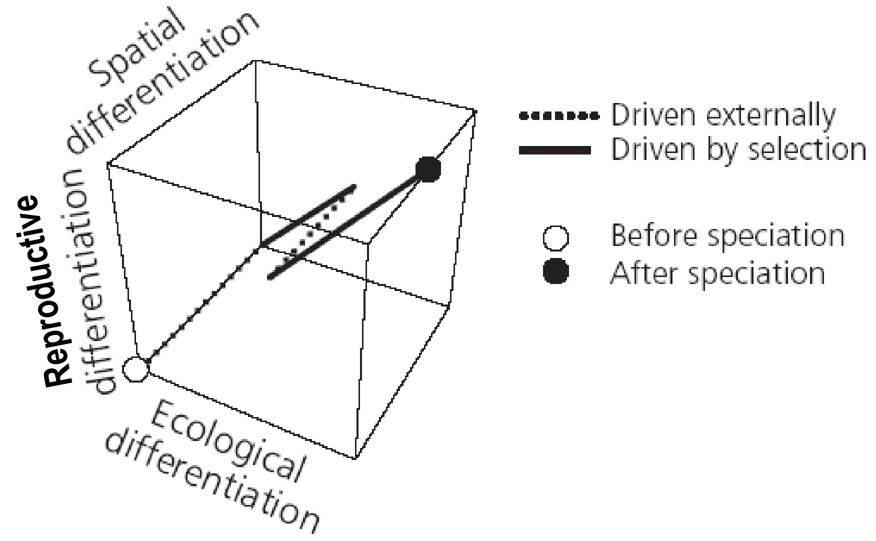
Dieckmann et al. (2004)



In the wake of geographic isolation, the incipient species develop partial reproductive isolation, through genetic drift (left), through sexual selection or conflict (middle), or through local ecological adaptation (right). This first phase is followed by the establishment of secondary contact and subsequent reinforcement.

Double Invasion Scenario

Dieckmann et al. (2004)



In the wake of geographic isolation, a first phase of evolution results in partial ecological differentiation and reproductive differentiation. In a second phase, contact between the incipient species is re-established, and further ecological and reproductive differentiation ensues; the second phase may also involve a further increase in spatial differentiation.

4

Calibrated Speciation Models

First Example

http://www.finerareprints.com/print_detail.html?stock_no=20386

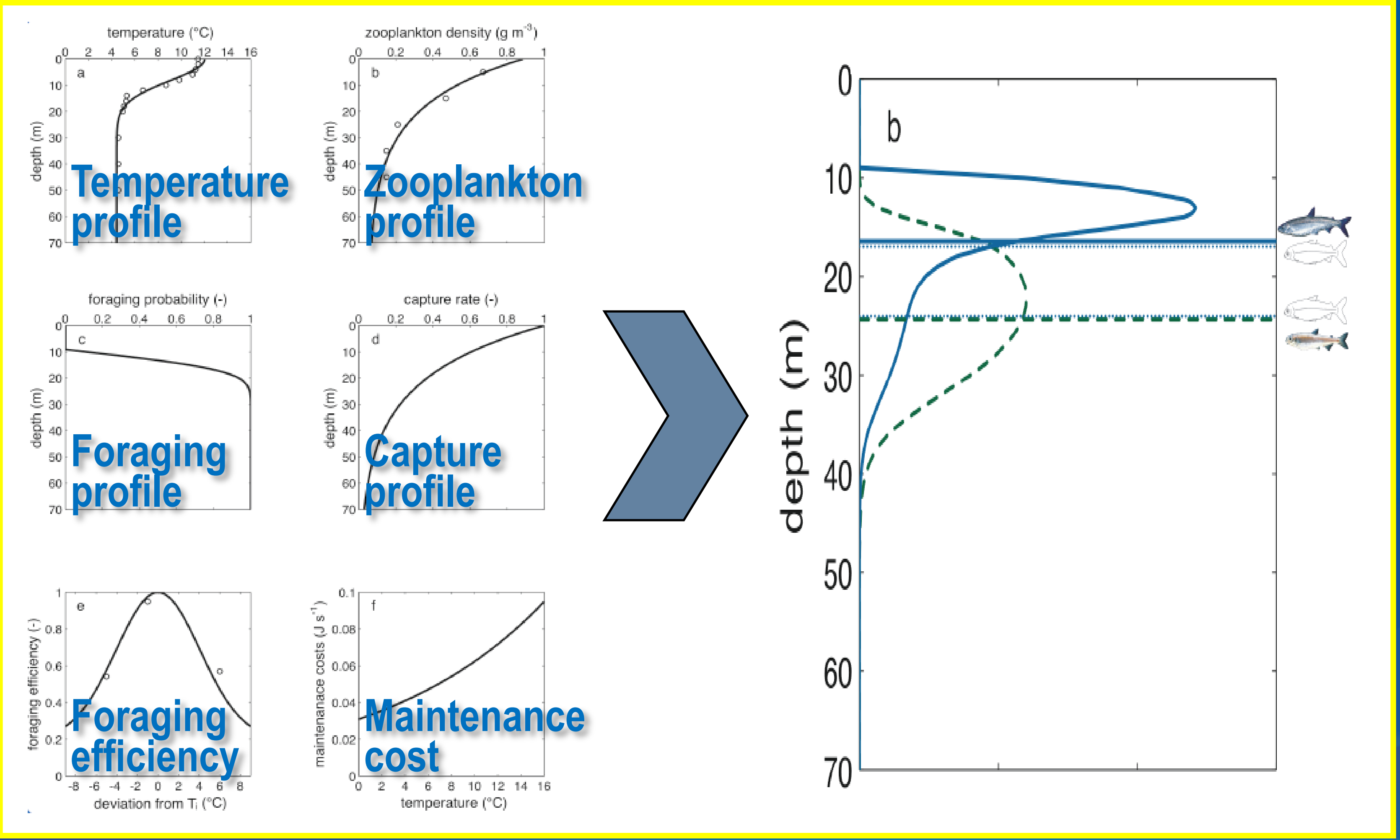
Lake Stechlin, Berlin, Germany

Vendace

Fontane cisco

Eco-Evolutionary Model of Fish Community

Ohlberger et al. (2013)

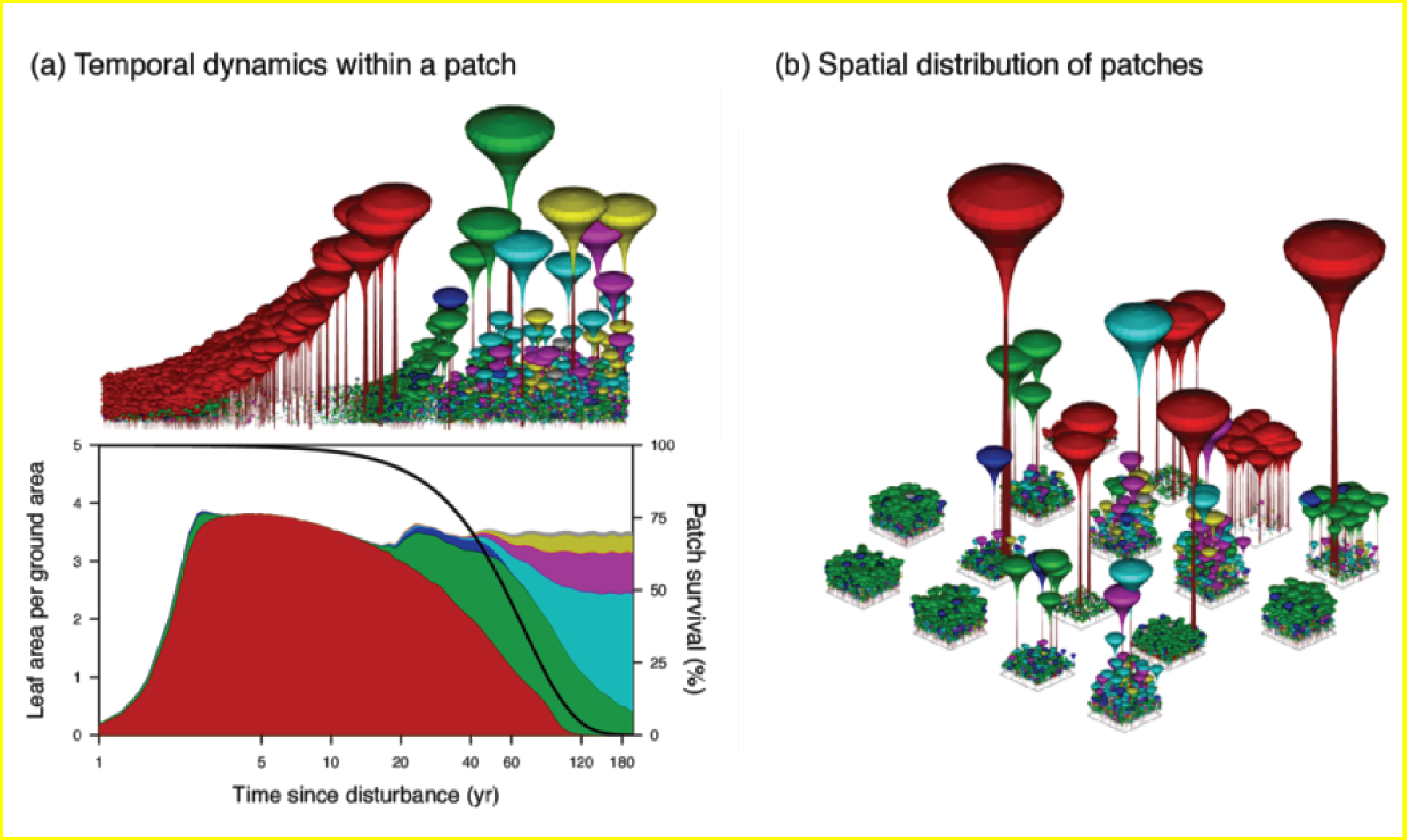


Second Example

http://fullmoon8.files.wordpress.com/2013/03/tree-scene-in-hawaii-jpeg.jpg

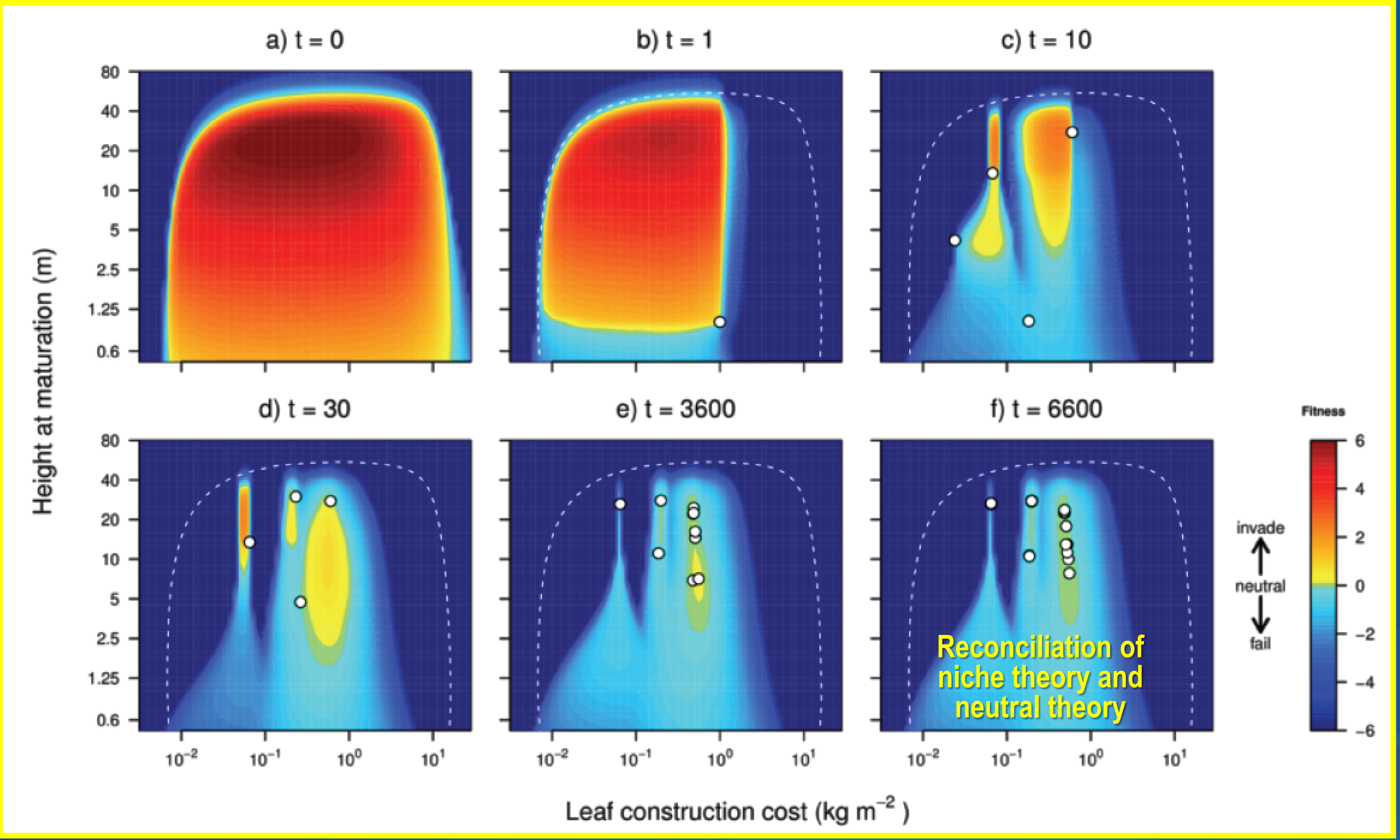
Eco-Evolutionary Model of Tree Community

Falster et al. (2016)

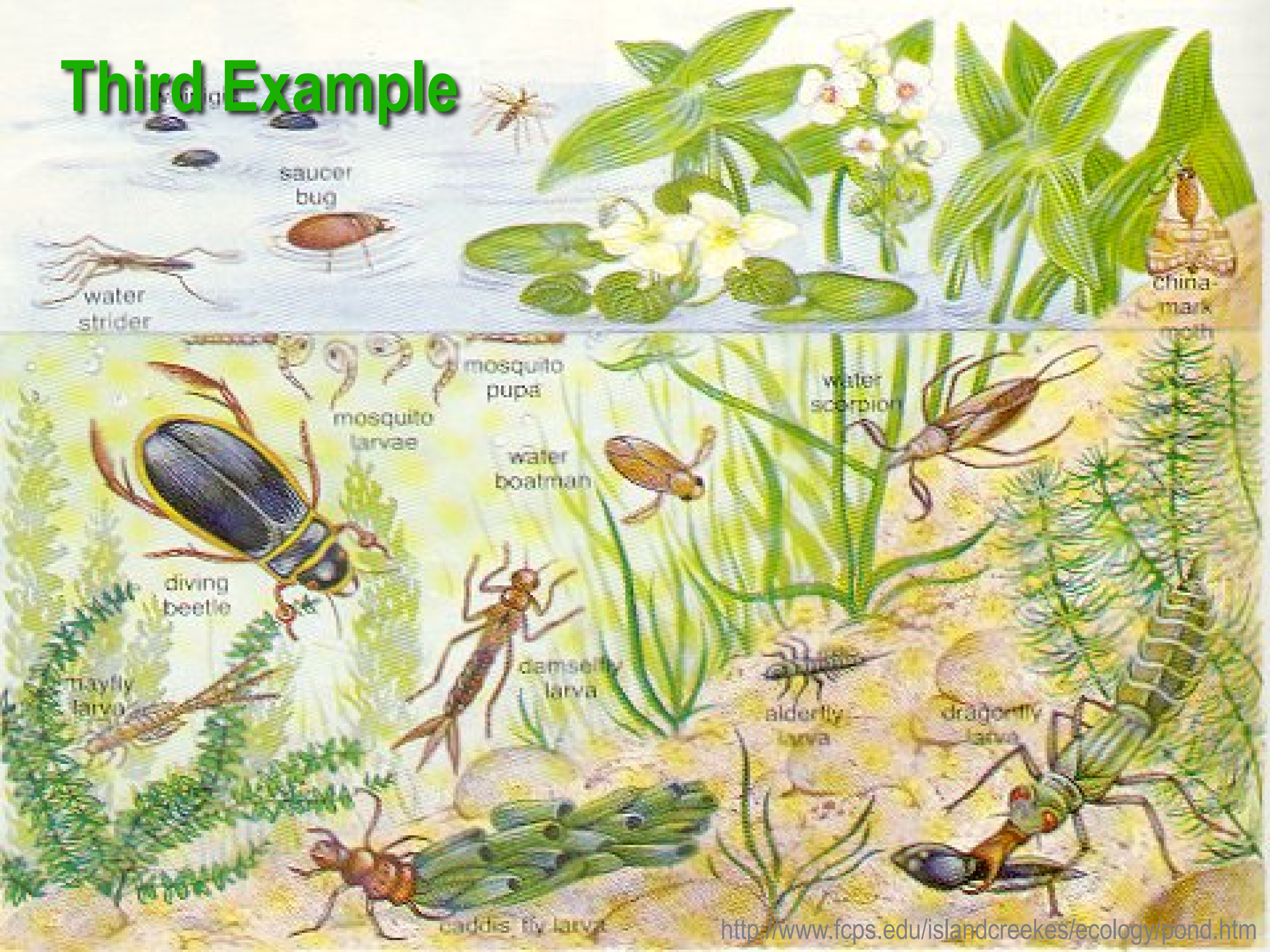


Eco-Evolutionary Model of Tree Community

Falster et al. (2016)



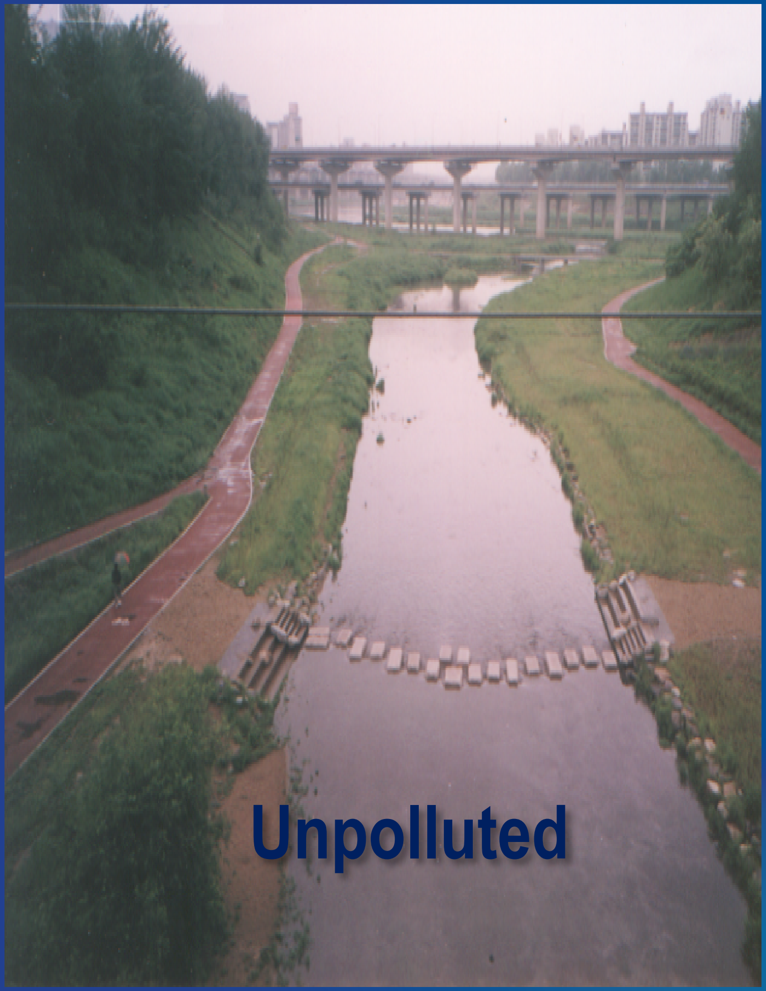
Third Example



http://www.fcps.edu/islandcreekes/ecology/pond.htm

Eco-Evolutionary Model of Insect Communities

Van Nguyen et al. (unpublished)



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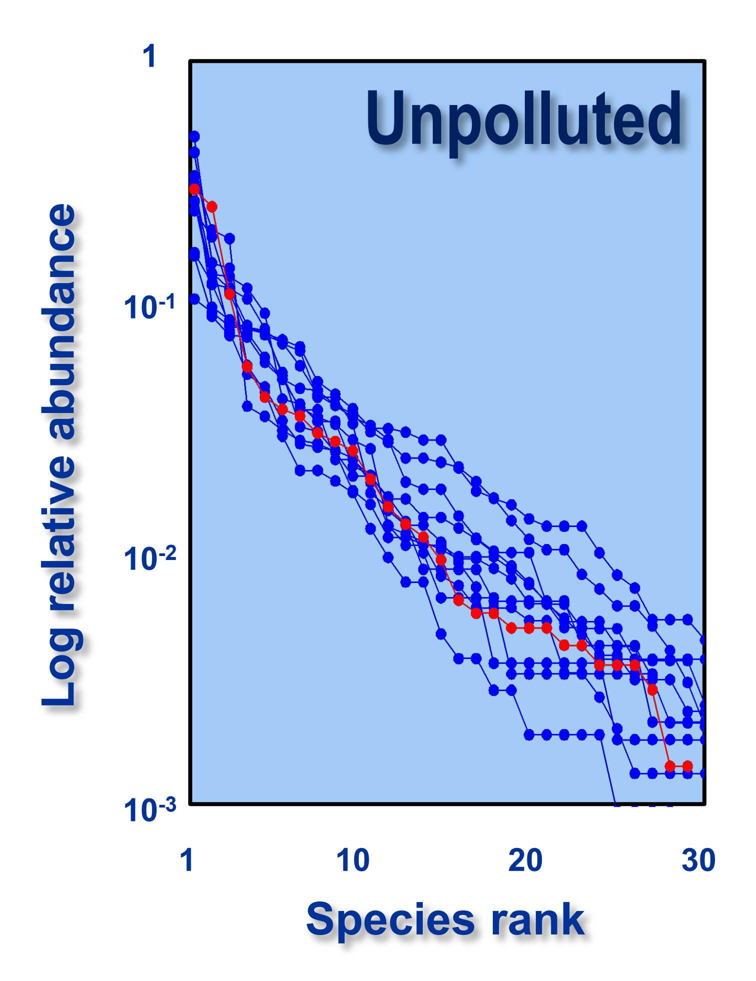

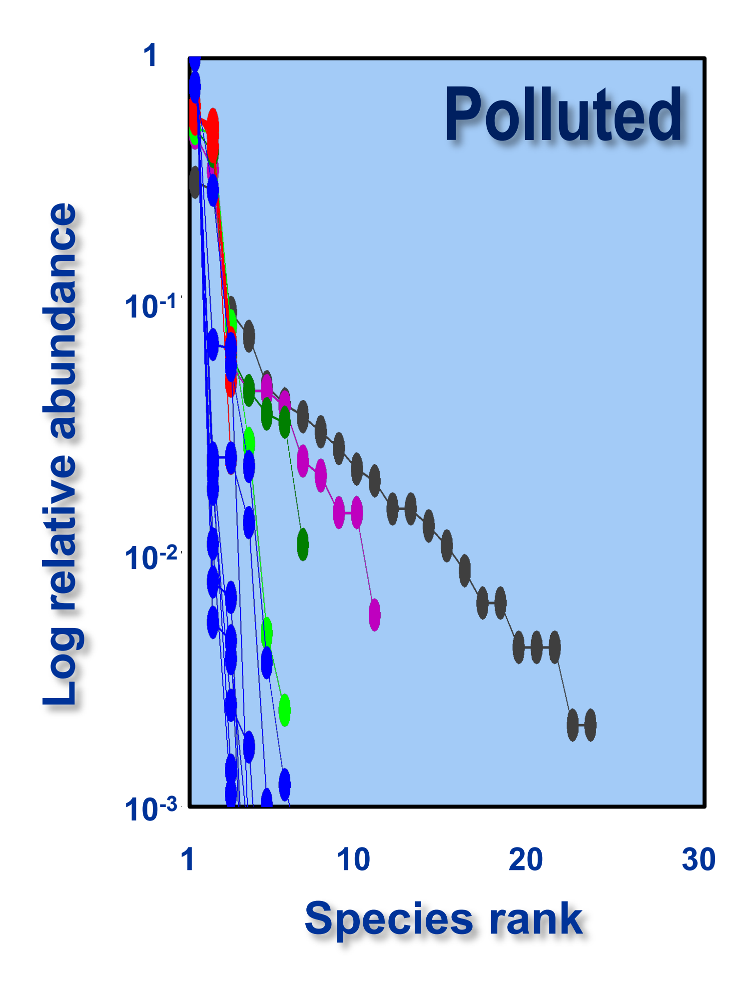

Adaptive Speciation: Summary

- Allows populations to escape fitness minima
- Occurs in asexual, sexual, and spatial populations
- Arises through all types of ecological interactions
- Promoted by platykurtic competition
- Can cause taxon cycles and recurrent radiations
- Promoted by habitat choice
- Promoted by body-size refuges
- May be preceded by a cryptic phase of genetic erosion
- Unfolds through three fundamental spatiotemporal modes
- Robust to habitat boundaries

Adaptive Speciation: Summary

- Promoted by spatial self-structuring in sexual populations, and accelerated by similar scales for dispersal and mating
- Hindered by spatial self-structuring in asexual populations
- Facilitated by the evolution of unconditional dispersal, but hindered by the evolution of conditional dispersal
- Promoted by intermediate levels of spatial heterogeneity
- Contributing processes and their sequences can be summarized in speciation cubes
- Can be studied in calibrated eco-evolutionary models