Trade-Offs and Specialization: An Adaptive Dynamics Approach

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Introduction

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- Many empirical systems might best be approximated by this set up (e.g. Crossbills, Black-bellied Seedcrackers, Purple-throated Caribs, scale eating Cichlids).

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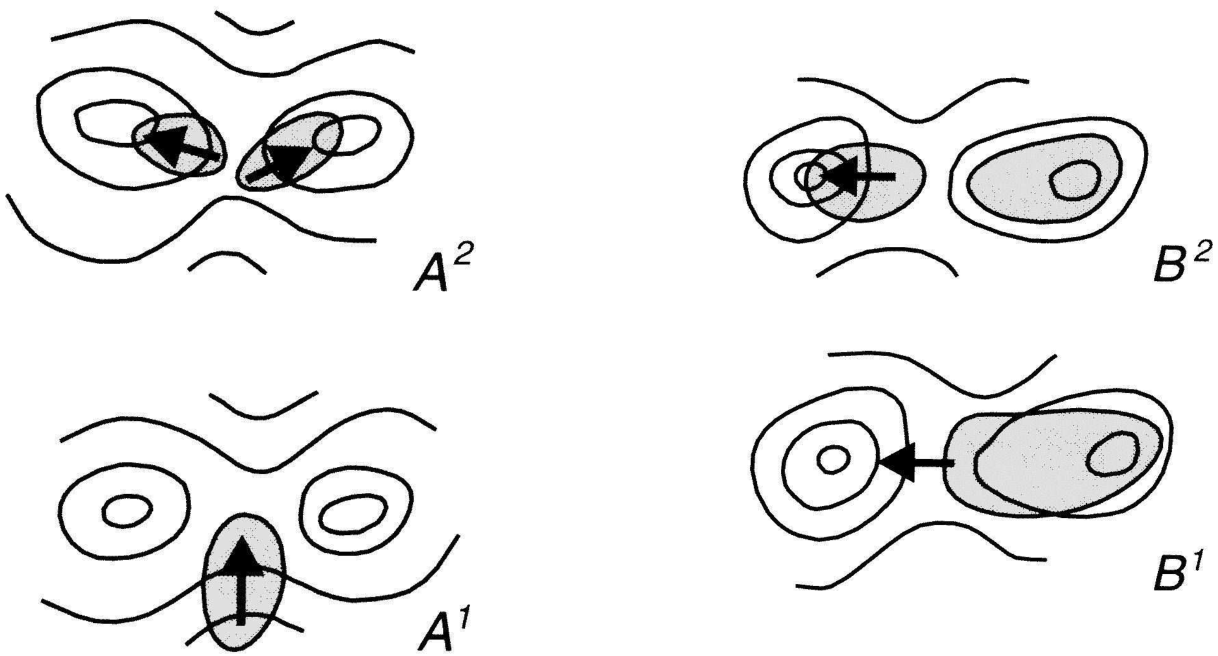
- Many empirical systems might best be approximated by this set up (e.g. Crossbills, Black-bellied Seedcrackers, Purple-throated Caribs, scale eating Cichlids).
- We re-analyze and extend a model of Wilson & Turelli (1986) using AD approximations.

Theory So Far

- Verbal model by Simpson (1953).

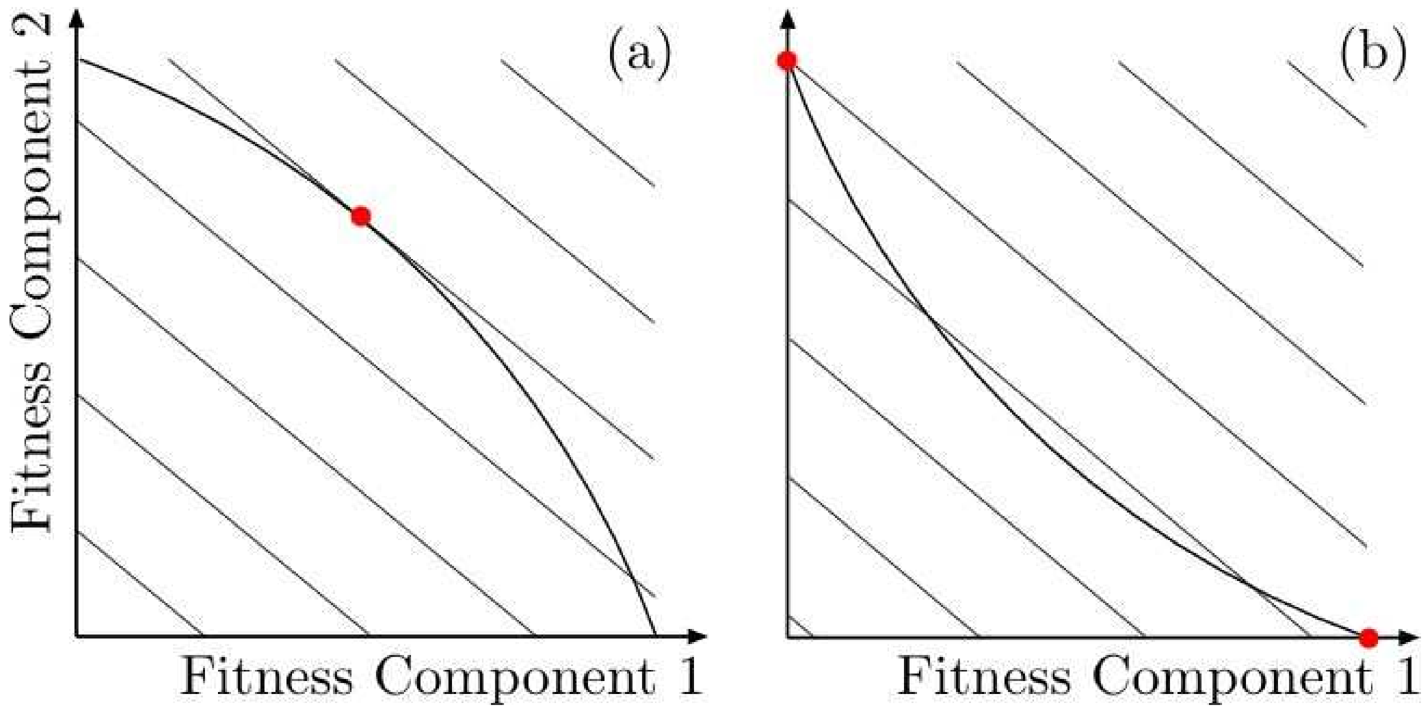


generalist colonizes two adaptive peaks

specialist colonizes ‘empty’ adaptive peak

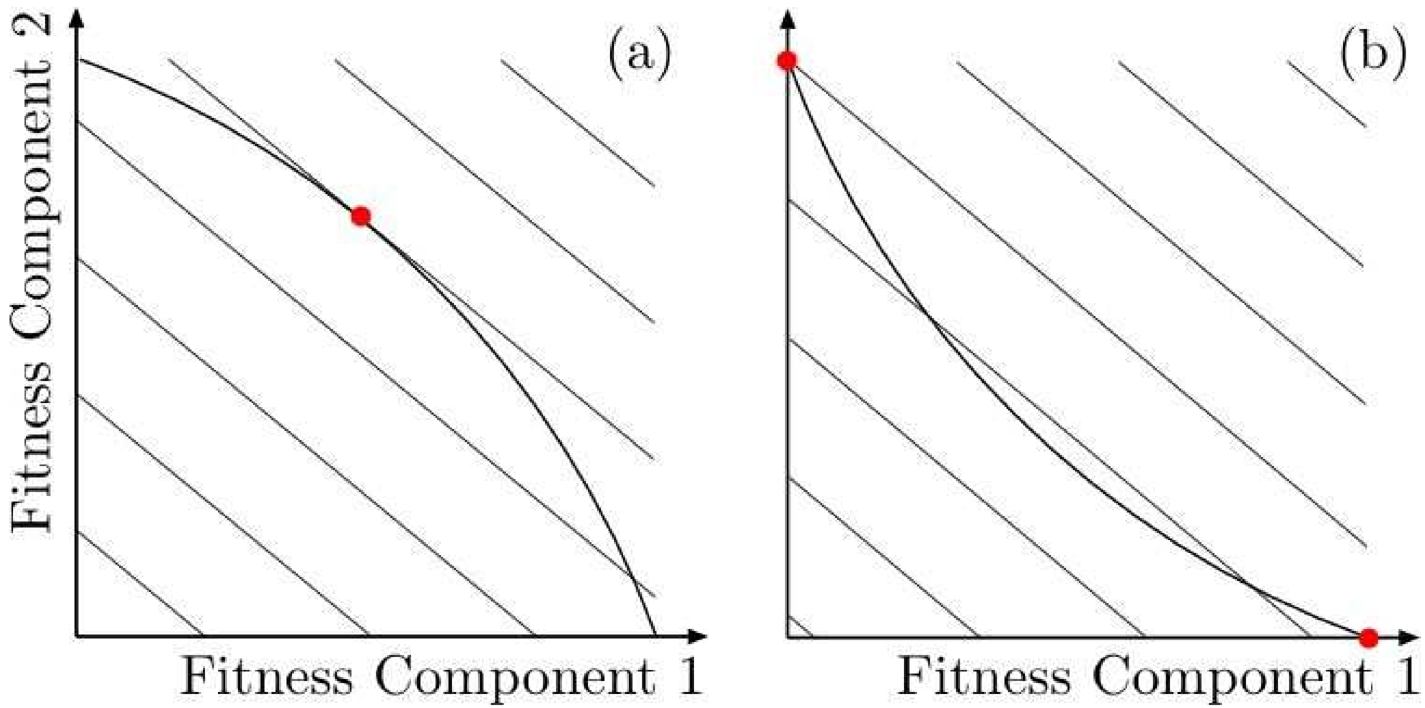
Levins 1962

- Spatially varying environment:
  Convex Phenotype Set $\Longrightarrow$ Generalist (a)
  Concave Phenotype Set $\Longrightarrow$ Specialist (b)



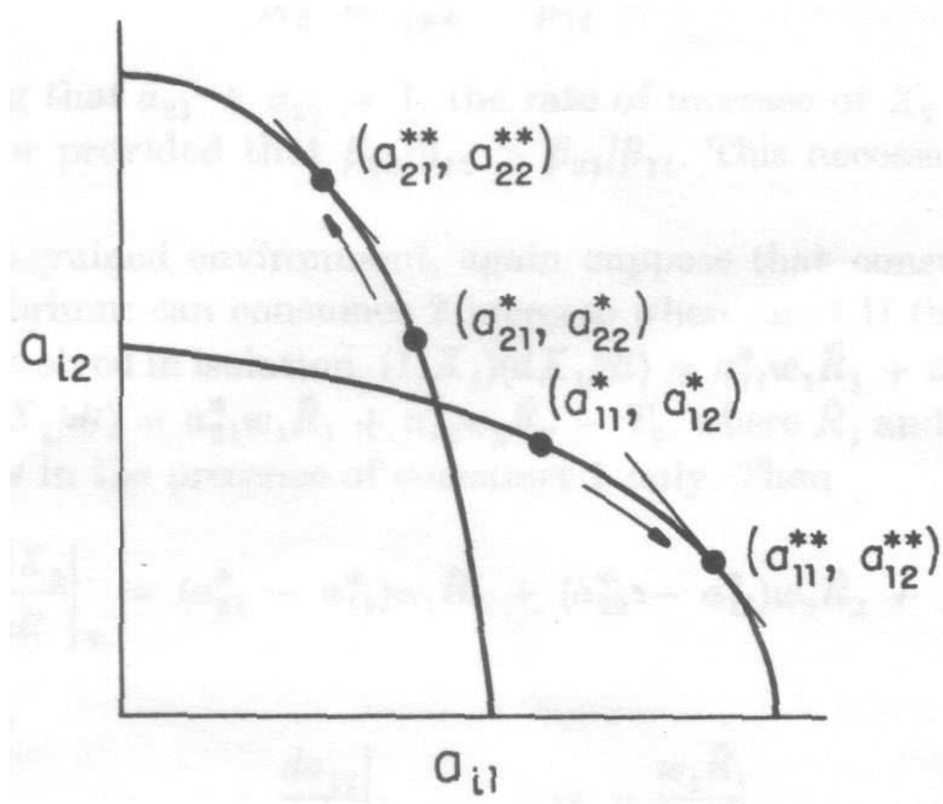
Levins 1962

- Spatially varying environment:
  Convex Phenotype Set $\Longrightarrow$ Generalist (a)
  Concave Phenotype Set $\Longrightarrow$ Specialist (b)
- However: Levins explicitly excluded density- and frequency dependence $\Longrightarrow$ No coexistence possible



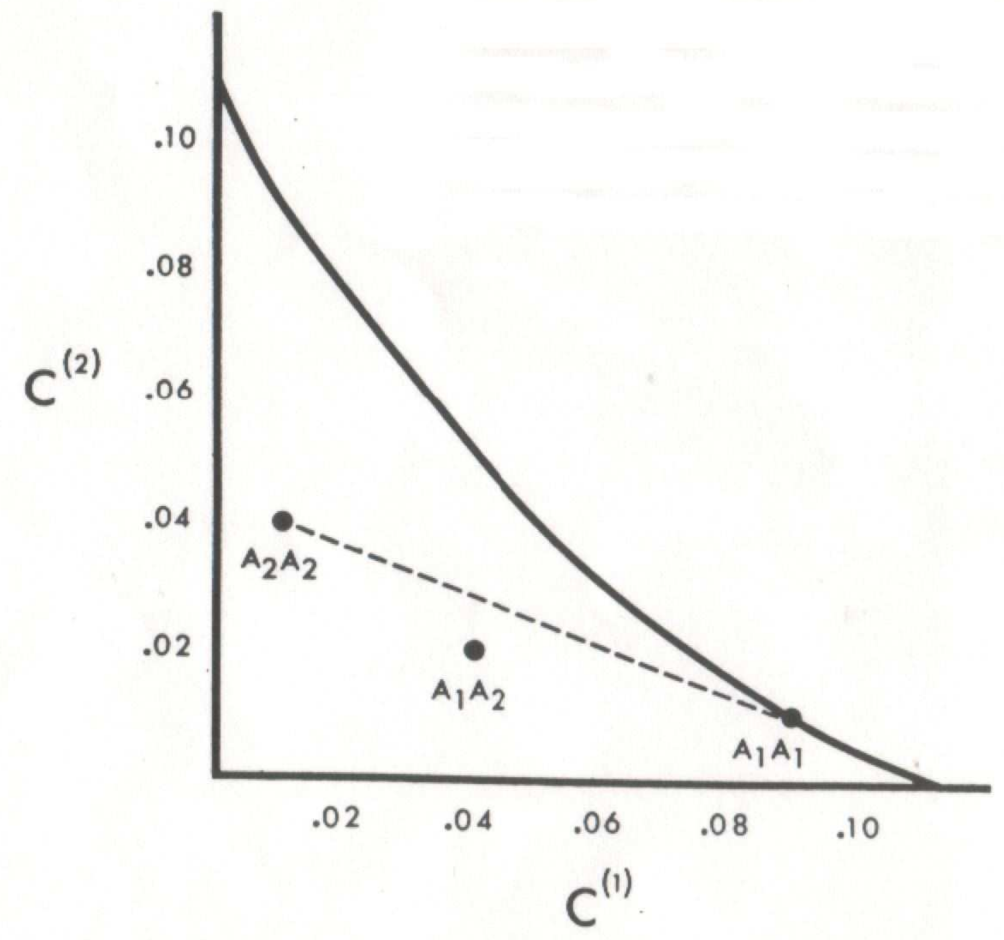
Lawlor & Maynard Smith 1976, Abrams 1986

- Derived fitness function from explicit resource consumption and renewal.
- Density- and frequency-dependent selection $\Longrightarrow$ coexistence.
- Character displacement of ESSs on two convex phenotype sets.



Wilson & Turelli 1986

- Two-alleles on one locus code for two consumption rates.
- Homozygote A_1A_1 well adapted to resource 1 but poor for resource 2.
- A_1A_2 and A_2A_2 slightly better for resource 2 but much worse for resource 1.
- Stable polymorphism with underdominance
  Deviations from population geneti cal equilibrium shift resource abun dances to favor rare allele.



Open Questions

- All approaches predict generalist for convex phenotype set.

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- Do polymorphisms arise if mutational steps are small?
- Do polymorphisms arise in all foraging traits?
- How does foraging behavior influence evolution?

The Foraging Process

$$\underbrace{\alpha \frac{eRpf}{1 + eRp(t_p + f t_m)}}_{\text{population growth rate}}$$

e	:	search efficiency
R	:	resource density
p	:	probability of attack
f	:	capture success
t_p	:	pursuit time
t_m	:	manipulation time
α	:	conversion factor of prey into offspring

The Foraging Process II

$$\underbrace{\frac{\alpha_1 e_1 R_1 p_1 f_1 + \alpha_2 e_2 R_2 p_2 f_2}{1 + e_1 R_1 p_1 (t_{p1} + f_1 t_{m1}) + e_2 R_2 p_2 (t_{p2} + f_2 t_{m2})}}_{\text{population growth rate on two resources}}$$

e	:	search efficiency
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The Foraging Process III

Without prey choice $(p_1 = 1 = p_2)$ and negligible pursuit time t_p, population growth rate simplifies to:

$$\underbrace{\frac{\alpha_1 e_1 R_1 + \alpha_2 e_2 R_2}{1 + e_1 R_1 t_{m1} + e_2 R_2 t_{m2}}}_{\text{population growth rate on two resources}} = t_s(\alpha_1 e_1 R_1 + \alpha_2 e_2 R_2)$$

- e : search efficiency
- R : resource density
- t_m : manipulation time
- α : conversion factor of prey into offspring
- t_s : search time

Resource Dynamics

- Resource abundance R_i derived from chemostat dynamics and in quasi steady state:

$$\hat{R}_i = \frac{b_i}{d_i + e_i p_i f_i t_s N}$$

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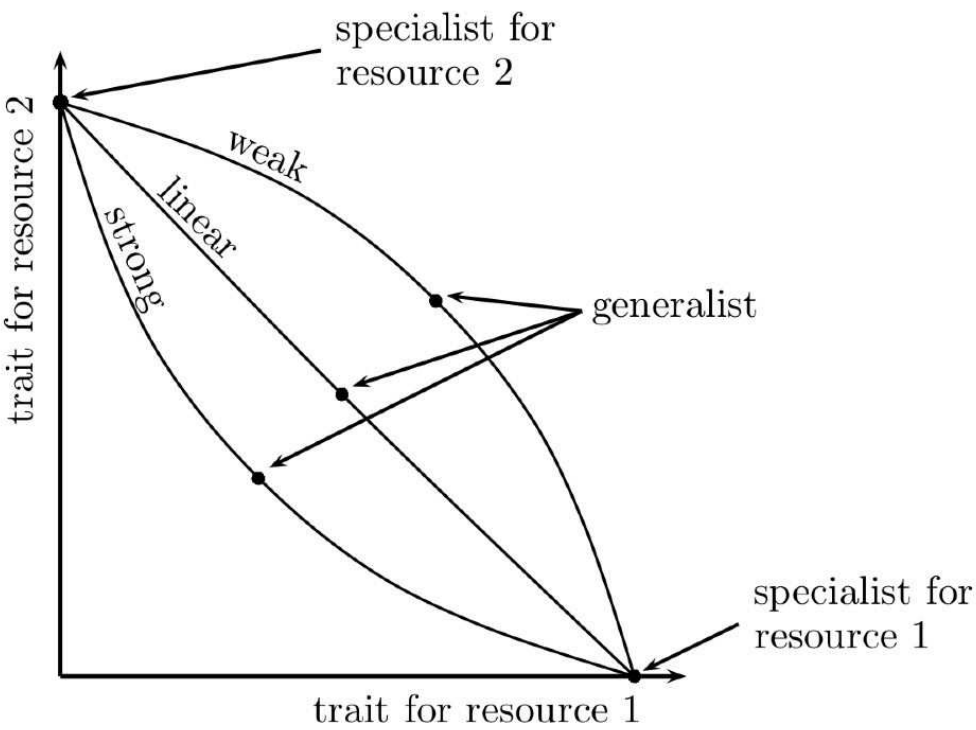
- Note:
  1) e_i, p_i and f_i influence resource abundance $\hat{R}_i$ explicit
  2) t_{pi}, t_{mi} and α_i influence $\hat{R}_i$ only implicit via consumer population size N and search time t_s and therefore both resources in the same way.

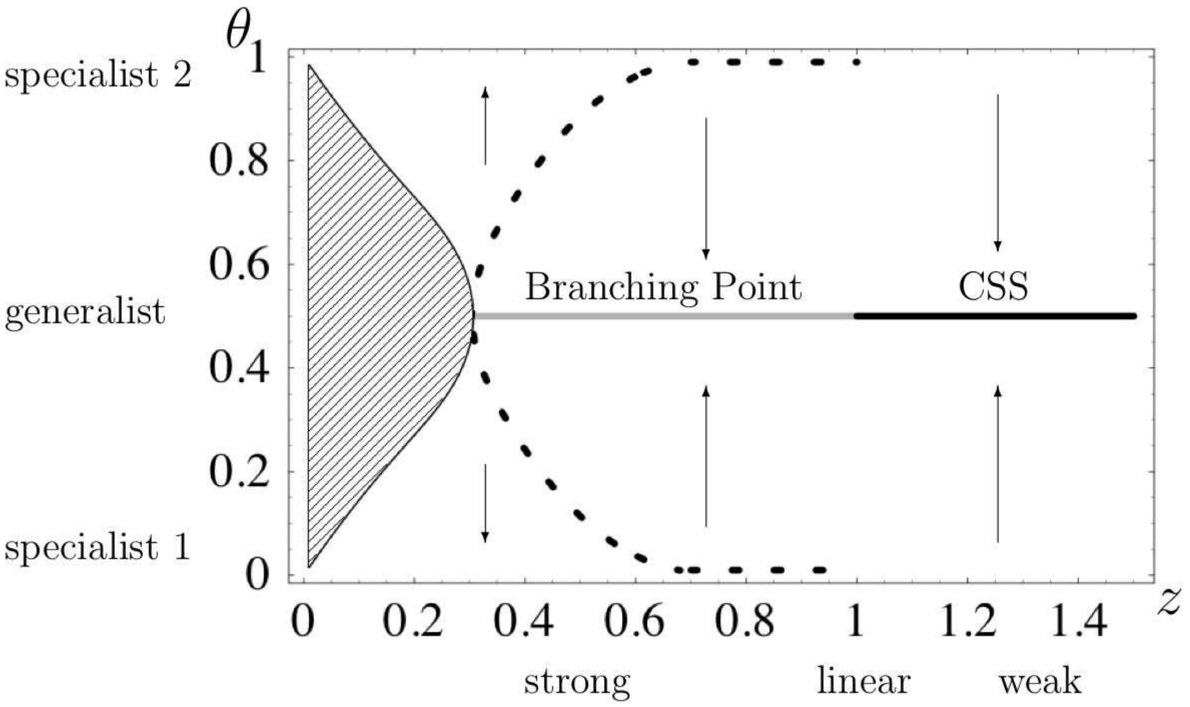
The Trade-Off

- Foraging success is determined by morphological and physiological traits.
- Predators face a trade-off
  $\Rightarrow$ they cannot be specialized on two prey-types.
- Evolution proceeds along the trade-off curve
  $\Rightarrow$ one-dimensional trait space, parameterized in $\theta \in [0,1]$
- We concentrate on trade-offs in:
  $\rightarrow$ in manipulation time t_m
  $\rightarrow$ in capture success f



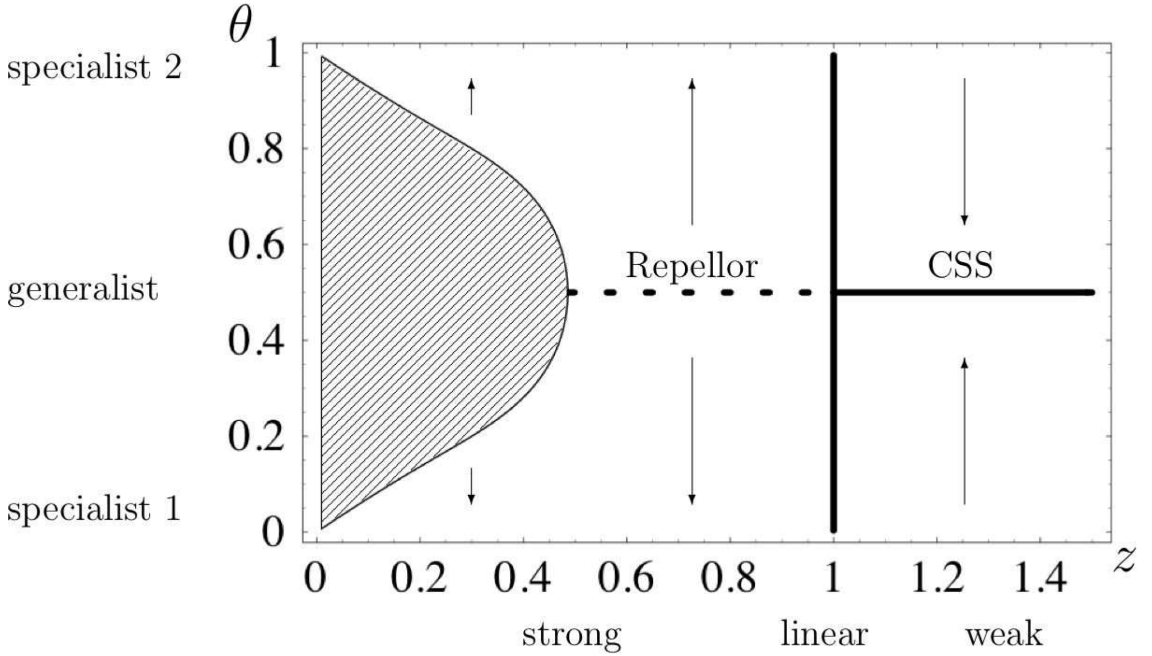
Trade-Off in Capture Success f

- Weak trade-off: generalist is CSS.
- Strong trade-off: monomorphic population evolves towards generalist. Selection turns disruptive $\Longrightarrow$ branching point.
- Very strong trade-off: only populations close to BP evolve towards it. Otherwise specialization. Coexistence with other specialist still possible.
- Same result for trade-off in search efficiency e.



Trade-Off in Manipulation Time t_m

- No frequency-dependence, no coexistence.
- Strong trade-off: both specialists are CSS. Realized CSS depends on initial conditions.
- Weak trade-off: generalist is CSS
- Same result for trade-off in pursuit time t_p and conversion efficiency α.



Results So Far and a Caveat

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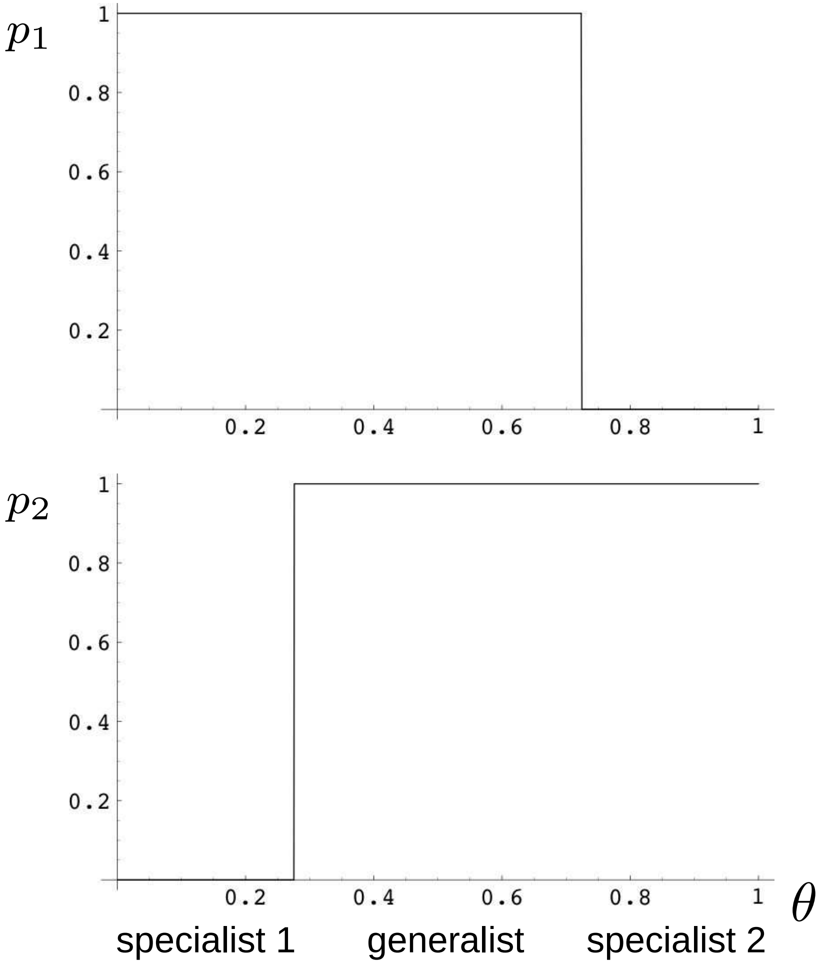
- Extension: including diet choice applying optimal foraging theory.

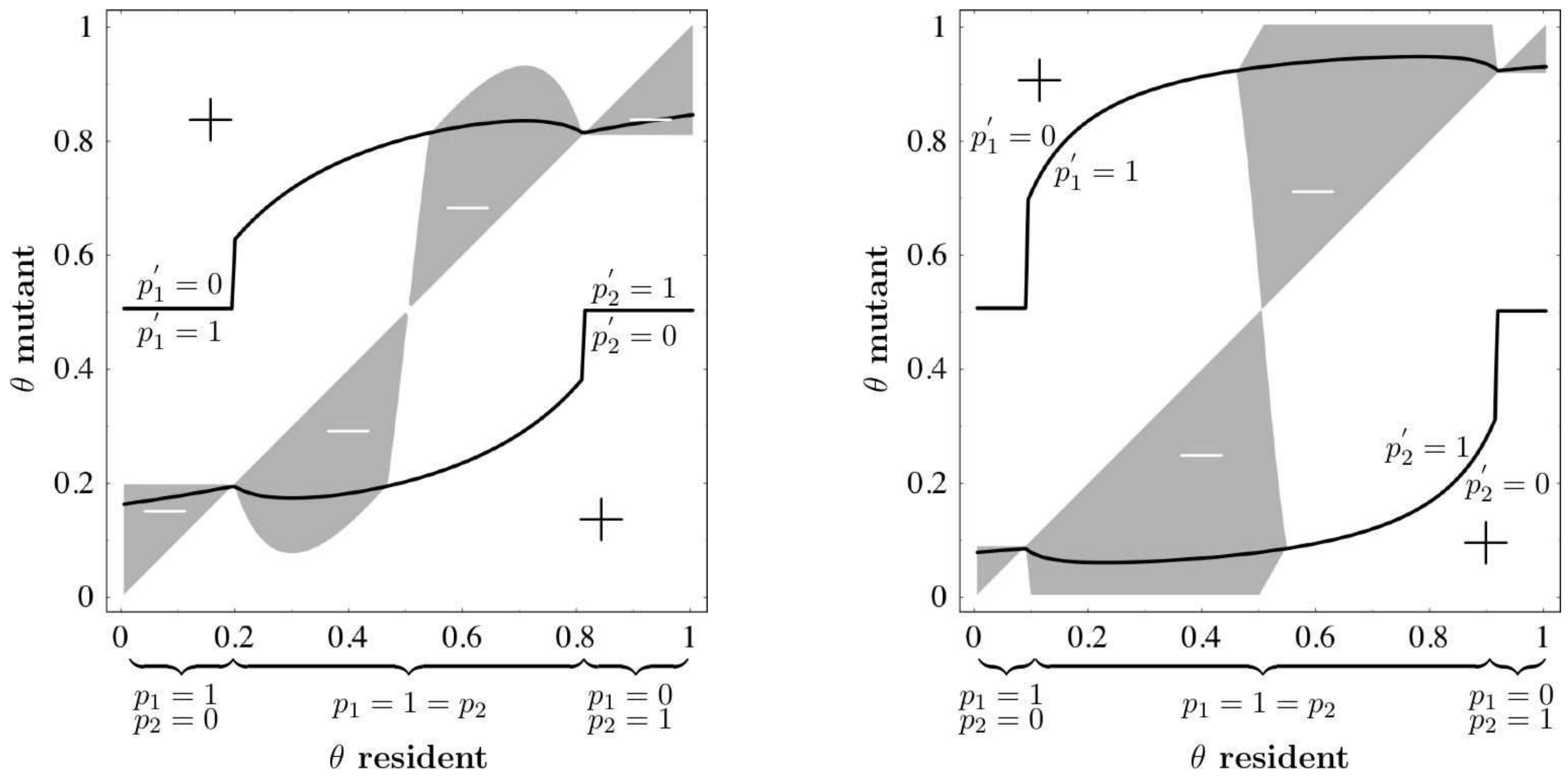
Optimal Diet Choice

- Prey profitability (fitness gain per investment of time) conditional on genetic trait.
- Zero-one rule:
  A prey type is either always or never taken.



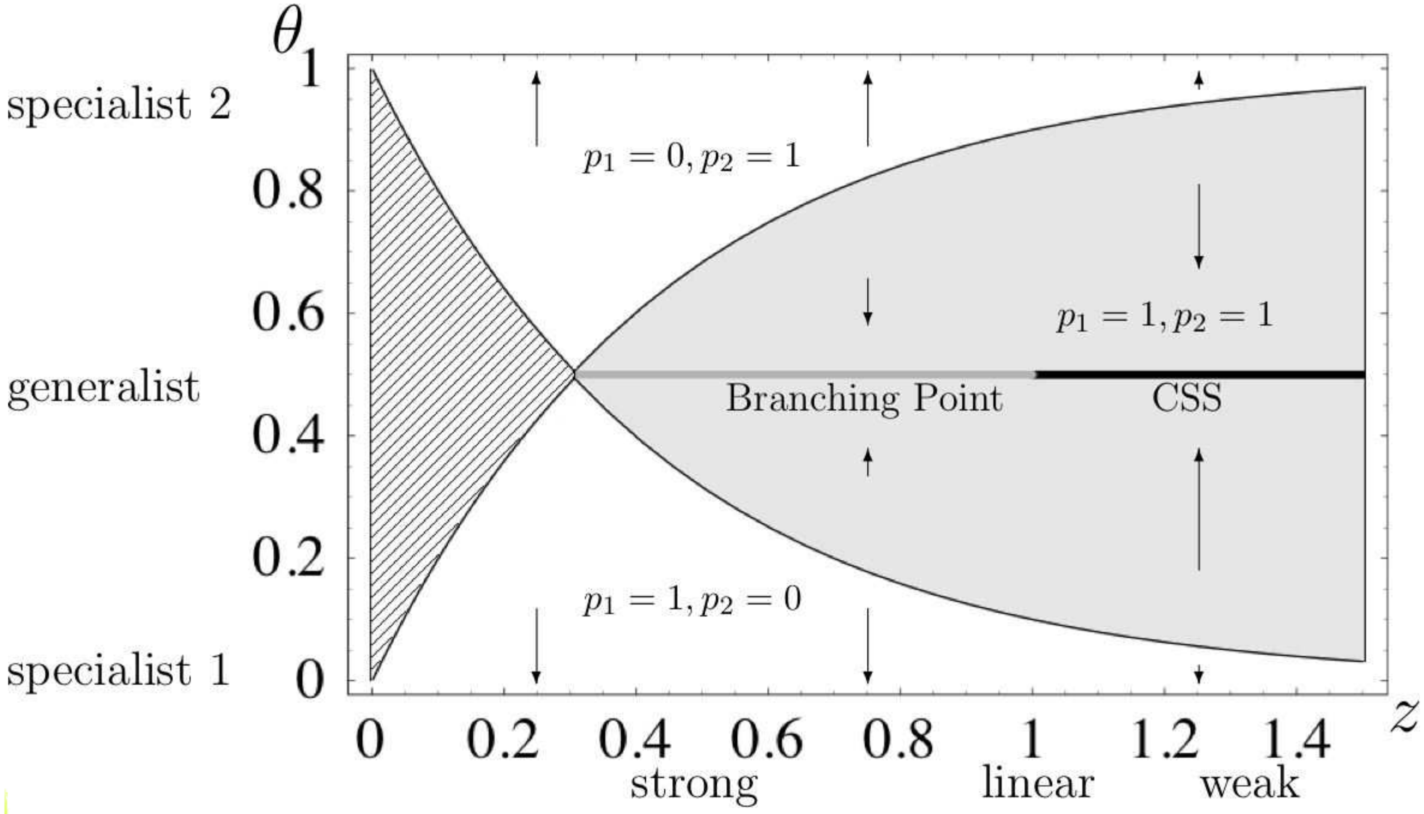
Extended PIPs: Capture Success

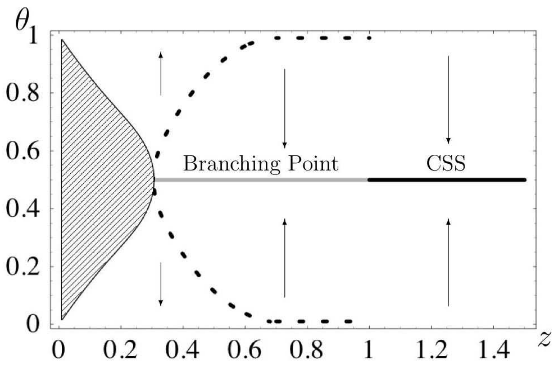
- Fitness function is non-differentiable where prey switch takes place.
- Mutant choice boundaries indicate prey switch of mutant.



Trade-Off in Capture Success II

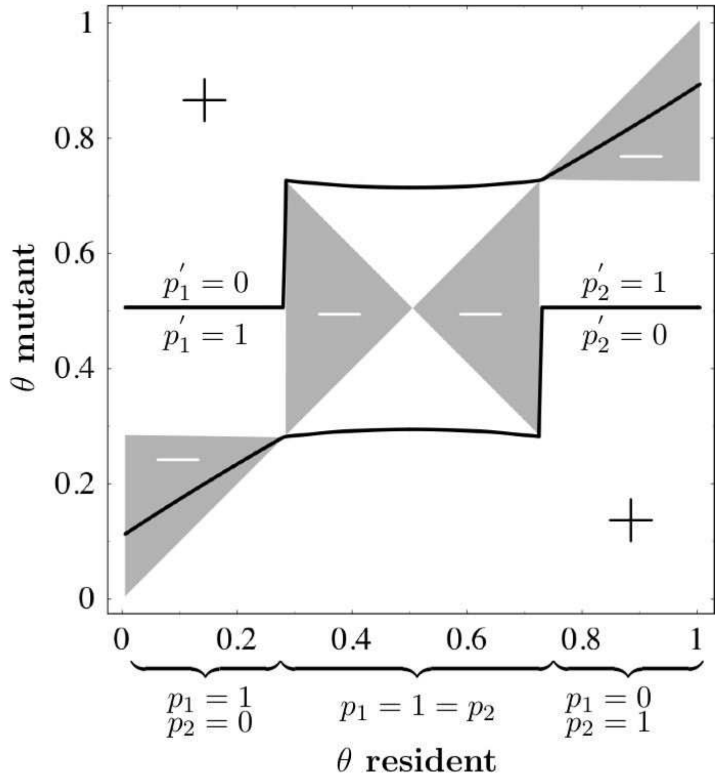
- If both resources are chosen $\Longrightarrow$ Equals scenario without diet choice
- If only one resource is chosen $\Longrightarrow$ Specialization

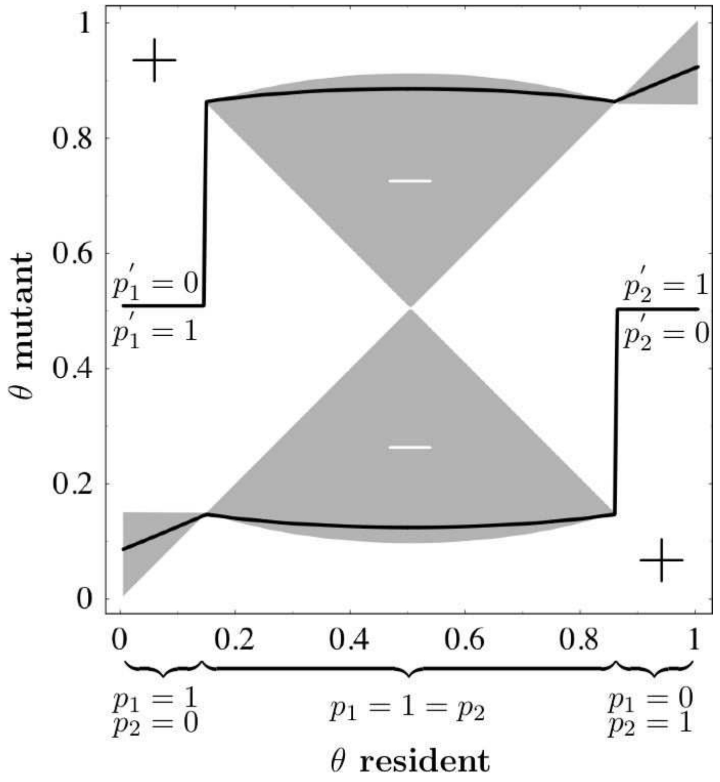




Extended PIPs: Manipulation Time

- Polymorphisms can emerge through small mutational steps at non-generic branching points.





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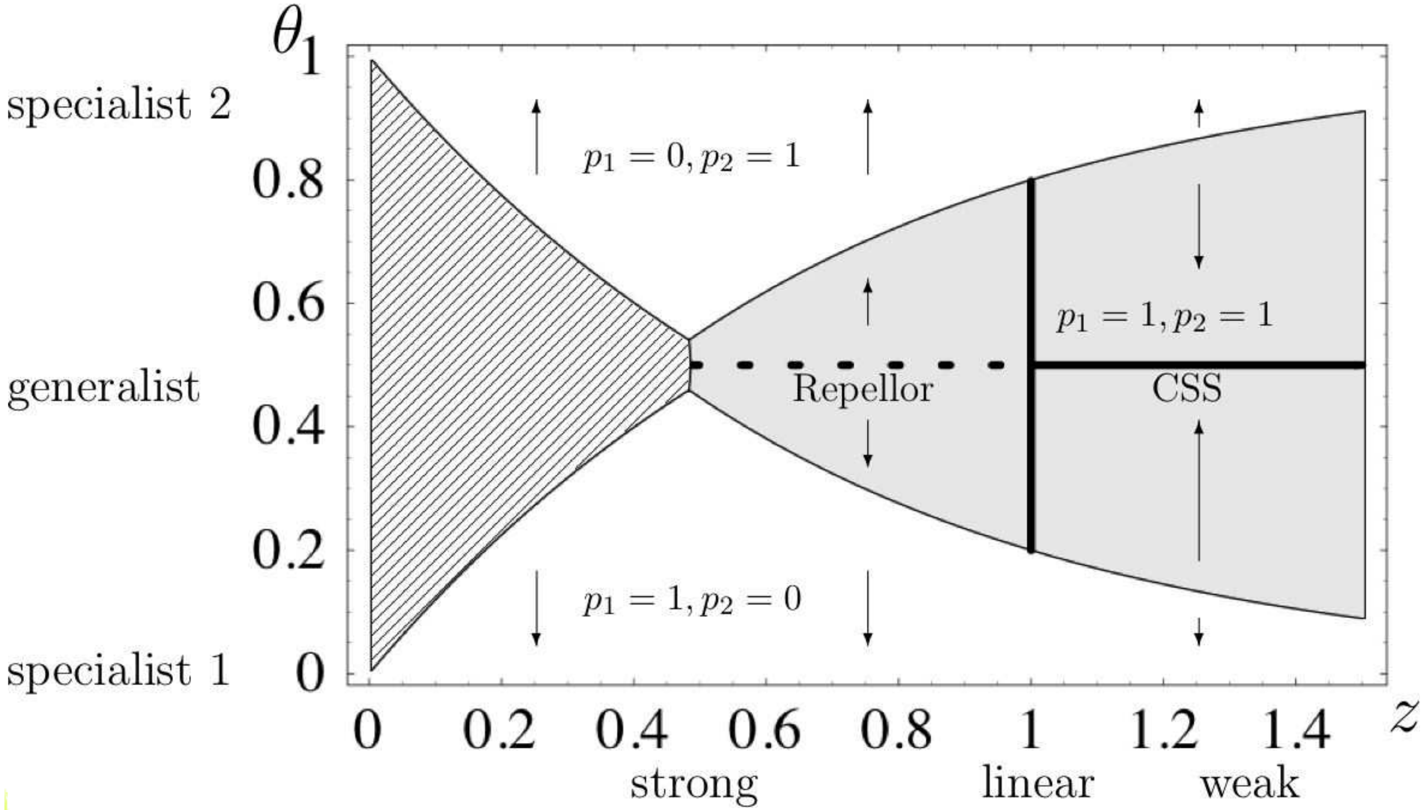
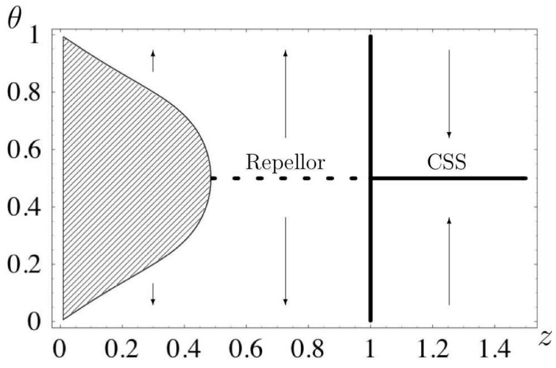
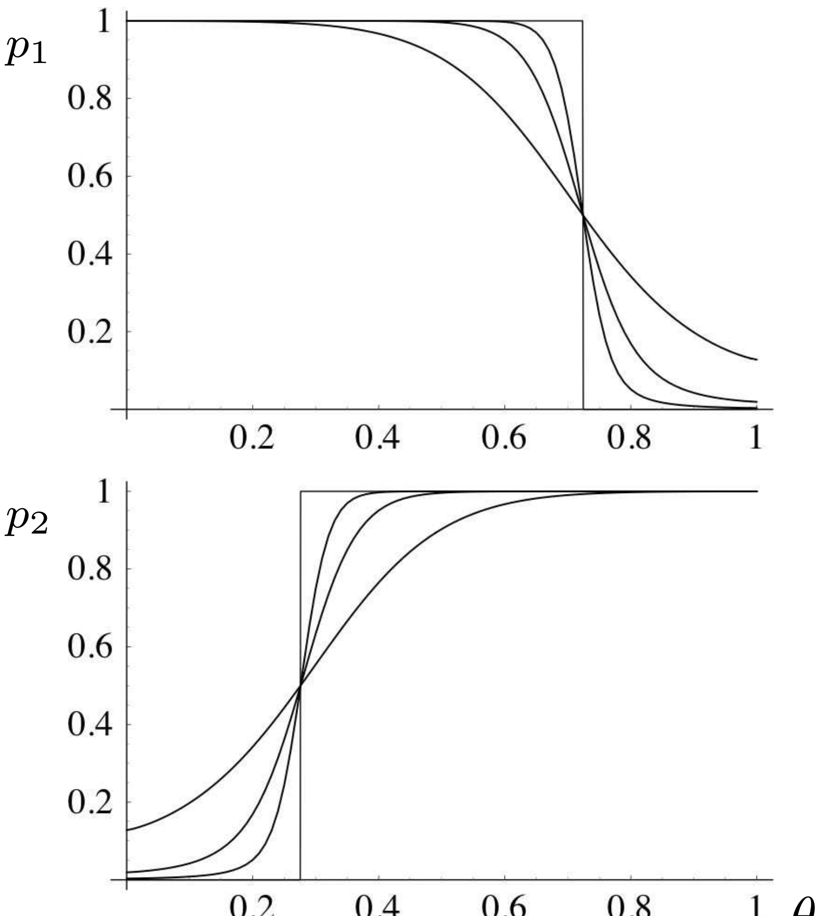
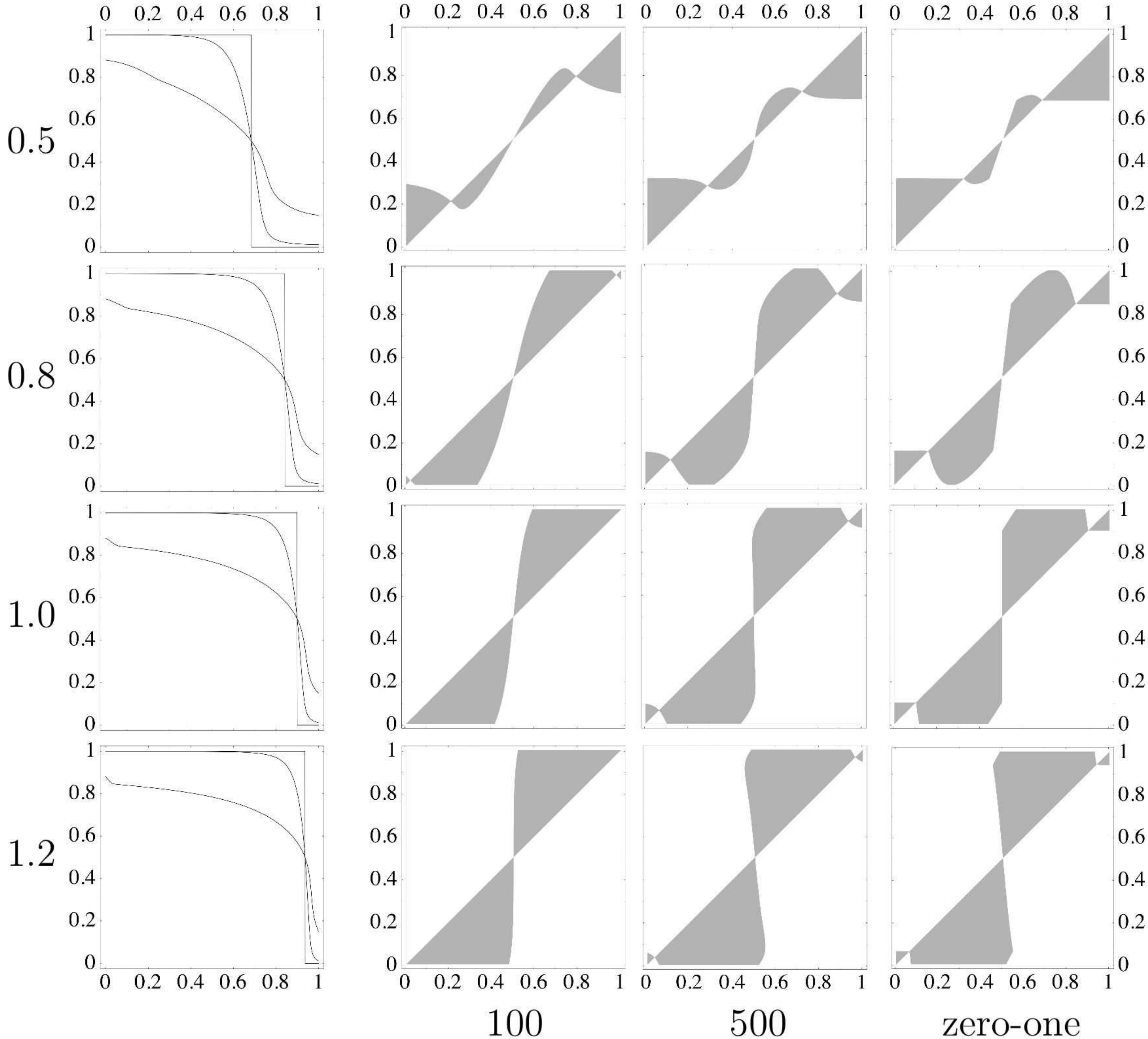




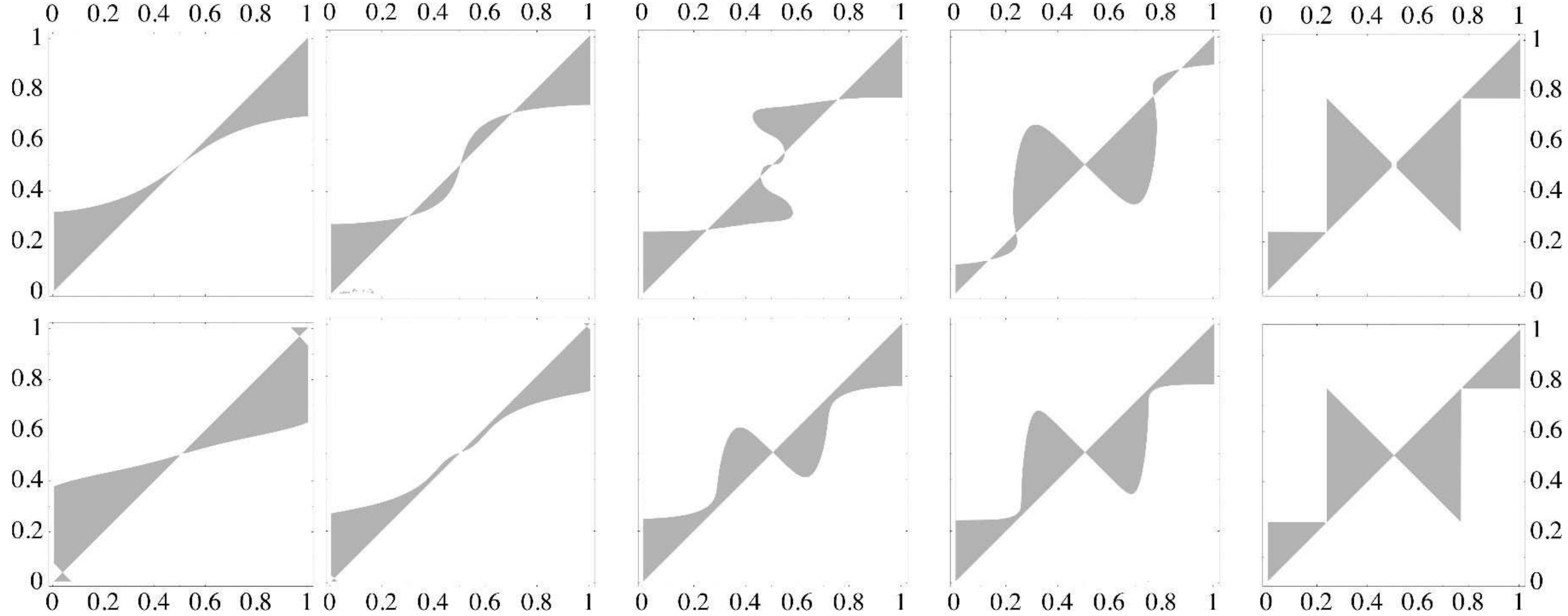
Foraging Inaccuracy

- In nature no zero-one rule.
- Foraging inaccuracy and incomplete information "smoothens" zero-one rule.
- Fitness function becomes differentiable.

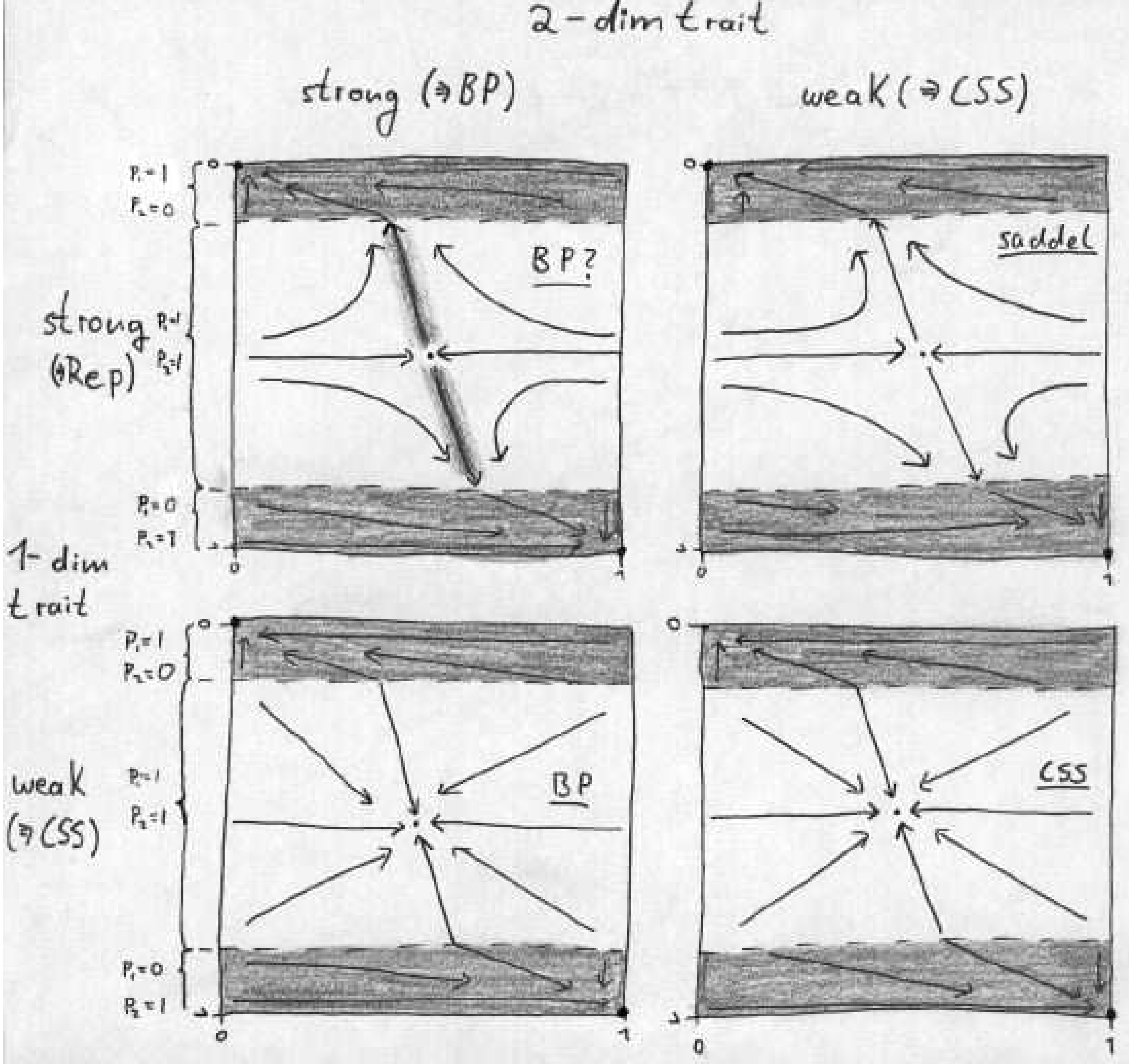



0.5
0.8
1.0
1.2
100
500
zero-one
0 0.2 0.4 0.6 0.8 1

Trade-Off in Manipulatio Time



$\Longrightarrow$ Increasing Accuracy


2-dim trait
strong (⇒BP)
weak (⇒CSS)
strong (⇒Rep)
weak (⇒CSS)
1-dim trait
BP?
saddel
BP
CSS
$P_1=1$
$P_2=0$
$P_1=0$
$P_2=1$

Take-Home Message

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- Prey choice facilitates coexistence and the evolution of polymorphisms.
- Which specific type of polymorphism evolves under disruptive selection depends on genetic architecture.
- In higher dimensions prey choice can prevent branching.