

Is Adaptive Dynamics (non)invadable?



a contribution for further discussion
(feel free to interrupt!)

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1. Setting the Stage

Models are (families of) mathematical structures
together with an interpretation rule.

Theories are either
rules for constructing models (in the sciences), or
frameworks dealing with many different models of similar type
in one go (in mathematics).

Adaptive Dynamics belongs to the latter class.

The reason to go axiomatic is to delineate classes of problems
that keep recurring.

The interpretation rules for AD models are in terms of underlying
community models.

The interpretation rules for community models can be decomposed
in a step to some underlying individual-based stochastic model,
and from there to reality.

These considerations serve as guidelines for a proper choice of
definitions and axioms.

The modern synthesis has only shown
that
micro-evolutionary mechanisms
and
macro-evolutionary patterns
are compatible.

It did not add flesh and blood to the
connection.

Adaptive Dynamics aims at making
the transition to macro-evolution,
but concentrates on
only one component of
the evolutionary mechanism:
the filtering of novel mutations
by the ecology

Credo:

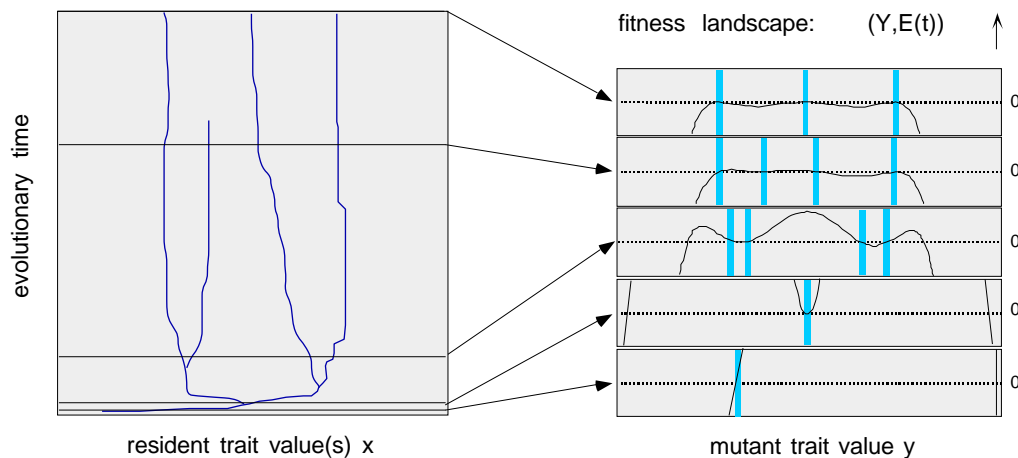
- The fitness of a given type
in a given stationary environment
can be defined as
the (asymptotic, average) exponential growth rate
of a (hypothetical) clone of individuals
of that type in that environment.
- For mutants the environment is set by the
population dynamics of the resident types.

<p>Note that as fitness is measured here on a logarithmic scale, zero is neutral.</p>
--

corollaries:

- Fitnesses are not given quantities, but depend
(1) the traits of the individuals,
(2) the environment in which they live.
- The ecological feedback loop sets the fitnesses
of all resident types equal to zero.
- Evolutionary progress is largely determined
by the signs and sizes of the fitnesses
of potential mutants.

Evolution proceeds through uphill movements in a fitness landscape that keeps changing so as to keep the fitness of the resident types at exactly zero.



2. The Population Dynamical Basis

Levels of Abstraction

illustrated by the spaces that play a role in adaptive dynamics theory:

1. the physical space in which the organisms live

2. the **state space** of their i(ndividual)-dynamics

3. the **state space** of their p(opulation)-dynamics

4. the abstract space of influences which they undergo, (the fluctuations in light, temperature food, enemies, conspecifics): their '**environment**'

5. the '**trait space**' in which their evolution takes place (= parameter space of their i- and therefore of their p-dynamics): the '**state space**' of their **adaptive dynamics**

6. the parameter spaces of simple families of adaptive dynamics

Credo:

- The fitness of a given type in a given stationary environment can be defined as the (asymptotic, average) exponential growth rate of a (hypothetical) clone of individuals of that type in that environment. (E, Y)
- For mutants the environment is set by the population dynamics of the resident types. $E_{\text{attr}}(X)$

Note that as fitness is measured here on a logarithmic scale, zero is neutral.

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$$s_X(Y) := (E_{\text{attr}}(X), Y)$$

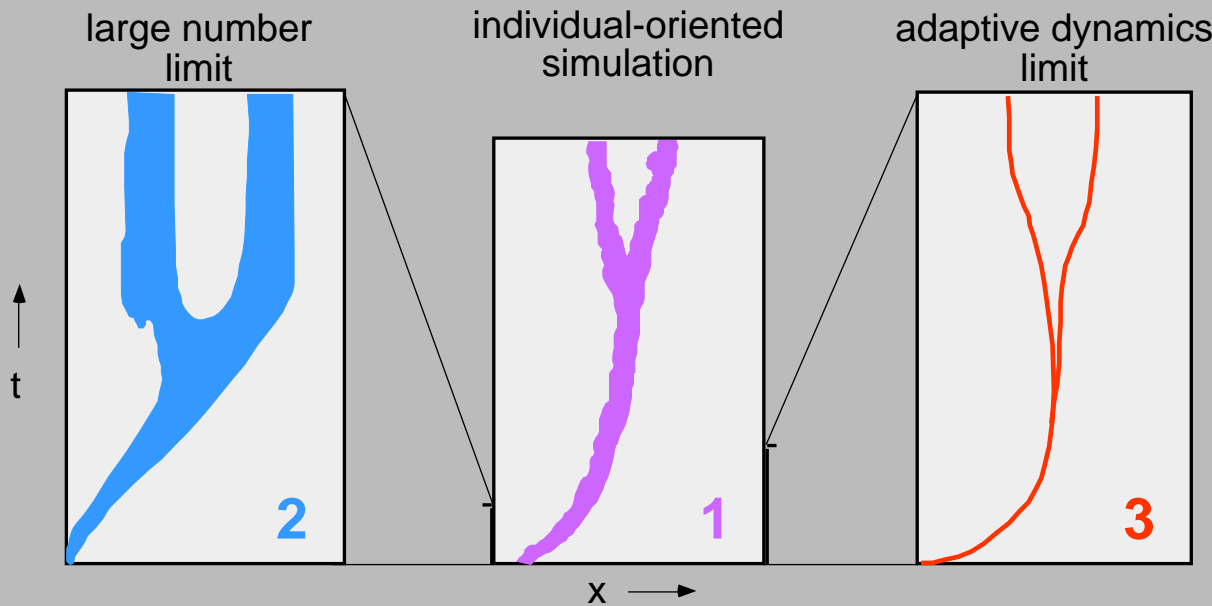
Simplifying assumptions

1. mutation limited evolution ^{1,2)}
2. good local mixing ²⁾
3. clonal reproduction ²⁾
4. largish system sizes,
5. "good" c-attractors
6. interior c-attractors unique ³⁾
7. smoothness of $s_X(Y)$ ³⁾
8. small mutational steps ³⁾

-
- 1) i.e. separated population dynamical and mutational time scales
 - 2) can often be relaxed !
 - 3) only made on some occasions

(often = often.....sometimes ?
some = some.....most ?)

On the individual-based justification of Adaptive Dynamics



1 Individual-oriented model ("the ecological basis"):

$X_i \rightarrow X_i + Y, Y = X_i$ at rate $1 -$
 $X_i \rightarrow X_i + Y, Y \in (y, y+dy)$ at rate $p(y-X)dy$
 $X_i \rightarrow X_j, j \neq i$ at rate $\frac{a(X_j, X_i)}{k(X_i)}$

2 "classical" deterministic limit: $\frac{1}{\Omega} \int_A n(x) dx = \frac{\#[\text{individuals in } A]}{A}$, and let $\Omega \rightarrow \infty$.

$$\frac{\partial n(x,t)}{\partial t} = \left(1 - \varepsilon - \frac{\int_{-1}^1 a(x,y)n(y,t)dy}{k(x)} \right) n(x,t) + \varepsilon \int_{-1}^1 p(x-y)n(y,t)dy$$

3 adaptive dynamics: let $\Omega \rightarrow \infty, \Omega\varepsilon \rightarrow 0$, and rescale time to on average one mutated birth per time unit

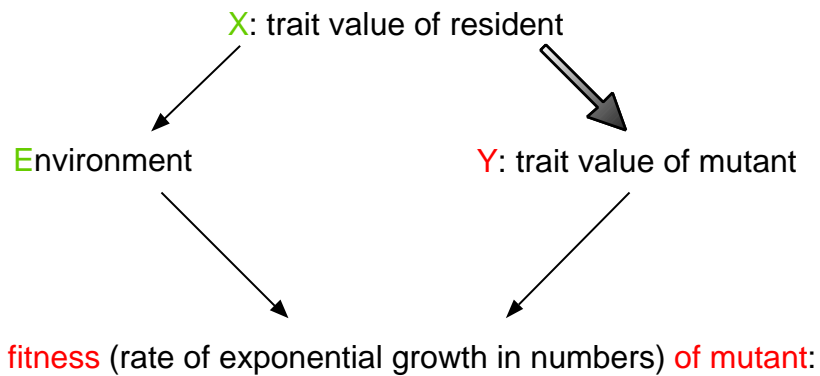
$X \rightarrow Y, Y \in (y, y+dy)$ at rate $\bar{n}(X) p(y-X)dy Q_x(y) [1 - H(s_y(x))]$
 $X \rightarrow (X, Y), Y \in (y, y+dy)$ at rate $\bar{n}(X) p(y-X)dy Q_x(y) H(s_y(x))$

3a canonical equation: subsequently let $\text{Var}_p \rightarrow 0$, and rescale time to keep the directional movement in view

$$\frac{dX}{dt} = \frac{1}{2} \bar{n}(X) \mathbf{C} \left(\frac{s_x(Y)}{Y} \Big|_{Y=X} \right)^T \quad \text{with} \quad = 2 T_f / (T_s^2)$$

3. Directional Adaptive Dynamics

Adaptive Dynamics: I the monomorphic case



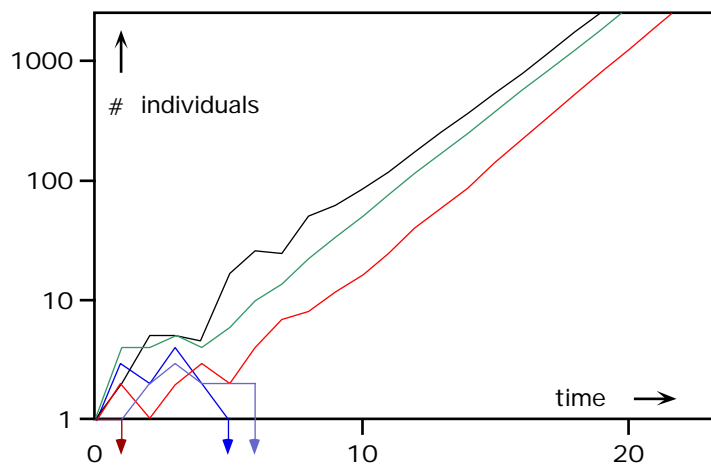
$$s_X(Y) := (E_{\text{attr}(X), Y})$$

- * Y has a positive probability to invade into an X community if and only if $s_X(Y) > 0$.

And after that:

- * X can be ousted by Y only if $s_Y(X) < 0$.

Starting from a single individual:

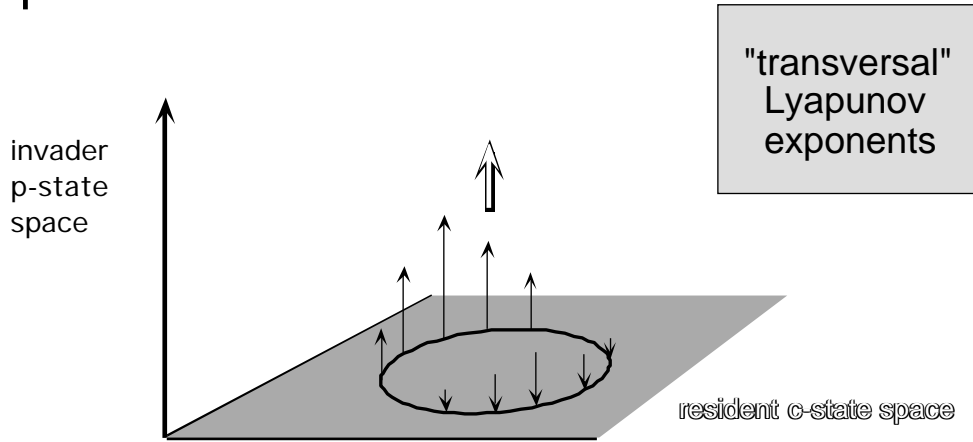


In an ergodic environment:

a population starting from a single individual either goes extinct, with probability $1-Q$, or "grows exponentially" at a relative rate (E) .

back to the deterministic theory

Interpretation:



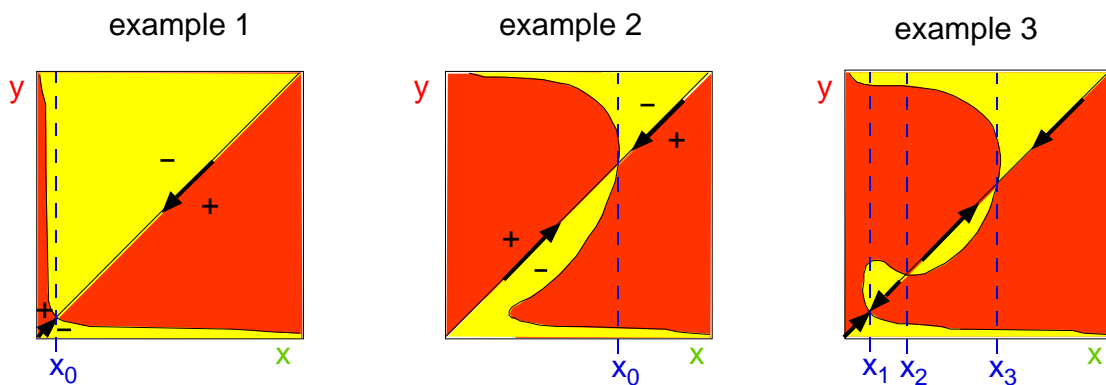
In the community model we linearise around an attractor in the $N_{mut} = 0$ boundary:

$$\begin{bmatrix} N_{mut}(t+1) \\ N_{res}(t+1) - \hat{N}_{res}(t+1) \end{bmatrix} = \begin{bmatrix} A_{mut}(E_{res}(t)) & 0 \\ \text{something} & \text{something} \end{bmatrix} \begin{bmatrix} N_{mut}(t) \\ N_{res}(t) - \hat{N}_{res}(t) \end{bmatrix}$$

tells local behaviour of mutant trajectories

tells local behaviour of trajectories in pure resident community

graphical representation for 1-dimensional trait spaces: Pairwise Invasibility Plots



- $s_x(y) > 0$: y -mutant can invade in x -population
- $s_x(y) < 0$: y -mutant disappears from x -population

$$s_x(X) = 0$$

for univariate (one-dimensional) traits the direction of evolution

Substitution resident by mutant I:

If $s_X(Y) > 0$ and $s_Y(X) < 0$,

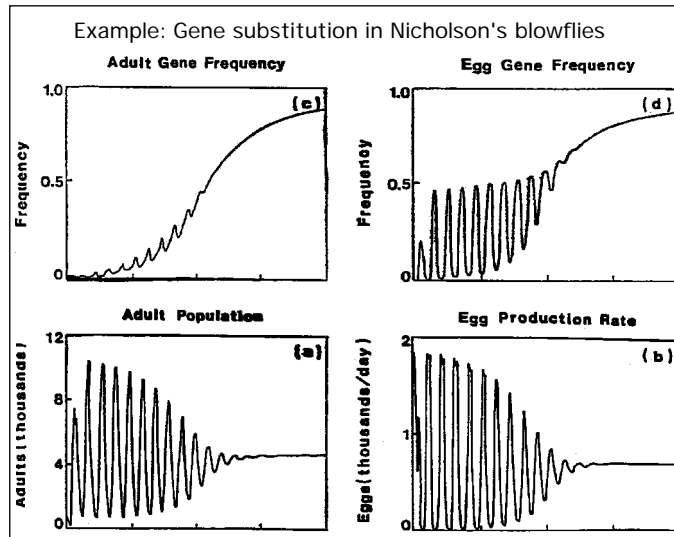
and nothing untowards happens in the interior of the c-state space,

the duration of a substitution

is essentially determined by

the initial and final exponential phases

and therefore by $s_X(Y)$ and $s_Y(X)$.



Substitution resident by mutant II:

Let X not be a c-dynamical bifurcation point, nor close to an evolutionarily singular point.

Moreover let $\epsilon = |Y-X|$ be sufficiently small.

- * Invasion of a "good" c-attractor of X leads to a substitution such that this c-attractor is "inherited" by Y , and

$$s_Y(X) = -s_X(Y) \quad \text{up to } O(\epsilon^2).$$

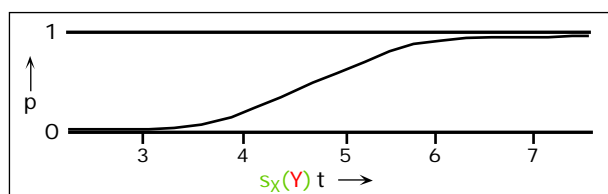
- * When an equilibrium point or a limit cycle is invaded, the relative frequency p of Y satisfies

$$\frac{dp}{dt} = s_X(Y) p(1-p) \quad \text{up to } O(\epsilon^2),$$

(the classical equation for gene frequency change)

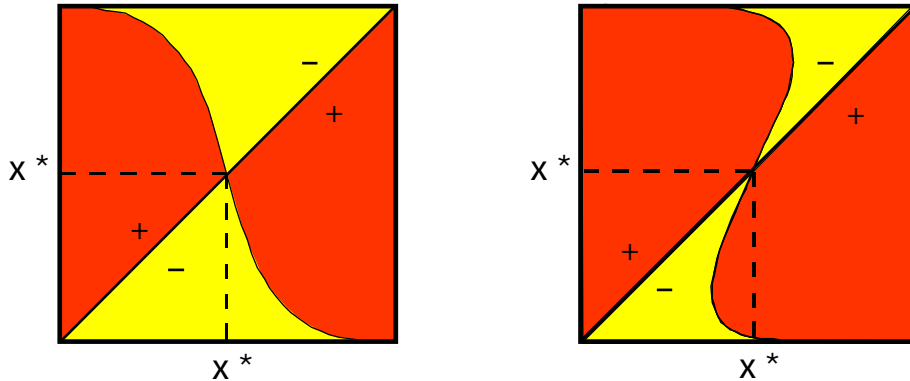
[note that $s_X(Y) = O(\epsilon)$],

while the convergence of the dynamics of the total population densities occurs $O(1)$.



x^* is a **singular point** iff

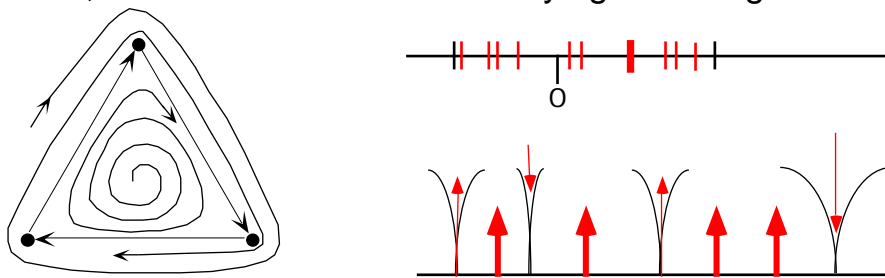
$$\left. \frac{ds_x(y)}{dy} \right|_{y=x=x^*} = 0 \quad (x^* \text{ is an extremum in the } y\text{-direction})$$



Problems with E determined by an attractor:

For bounded deterministic c-dynamics perturbed by the smallest possible amount of noise convergence to (so-called ep-chain) attractors is guaranteed.

However, these attractors do not always give an ergodic E .

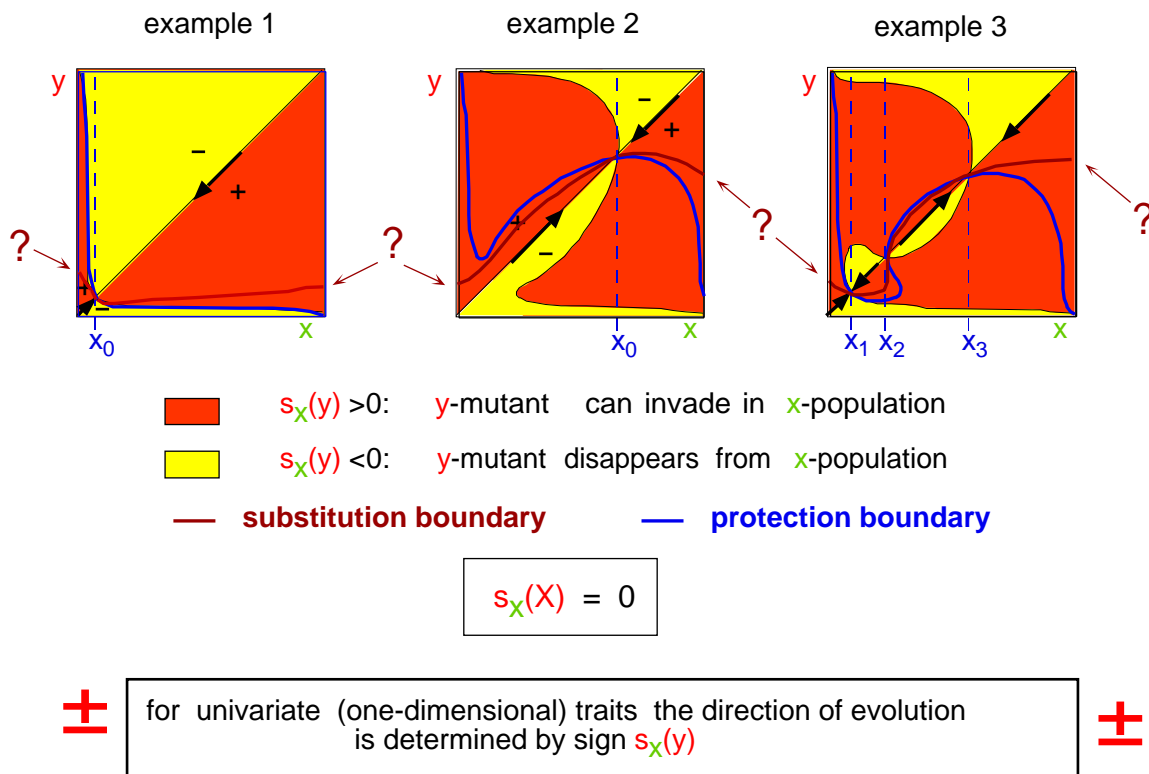


What is needed is a dense orbit.

Moreover, in chaotic attractors there are other, periodic, orbits, along which one gets different E 's and therefore different λ 's: (transversal) Lyapunov spectrum.

The E associated with the dense orbit is called **natural**.

This is the only E that persists with (a little) noise.



4. Beyond the directional mode: Stepping to Dimorphism

Dimorphisms I:

Let X not be a c-dynamical bifurcation point.

Moreover let $\epsilon = |Y-X|$ be sufficiently small,

and let $s_x(Y) > 0$ and $s_y(X) > 0$

(X is close to an evolutionarily singular point)

and let the monomorphic c-attractors of X and Y be "good"

Then an invasion of X by Y leads to a

"genetically protected" dimorphism

Dimorphisms II:

In general, $s_X(Y) > 0$ and $s_Y(X) > 0$ does not guarantee that invasion of X by Y leads to coexistence.

Example:

Consider the following recurrences for two mutualistic populations *

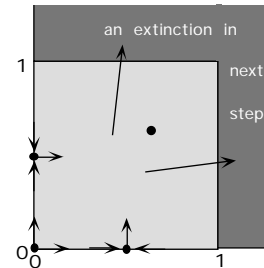
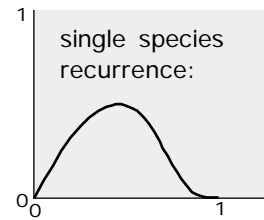
$$n' = R_0^{2+km+(n-1)^{-1}} n \quad \text{for } 0 < n < 1$$

$$= 0 \quad \text{for } n = 1$$

$$m' = R_0^{2+kn+(m-1)^{-1}} m \quad \text{for } 0 < m < 1$$

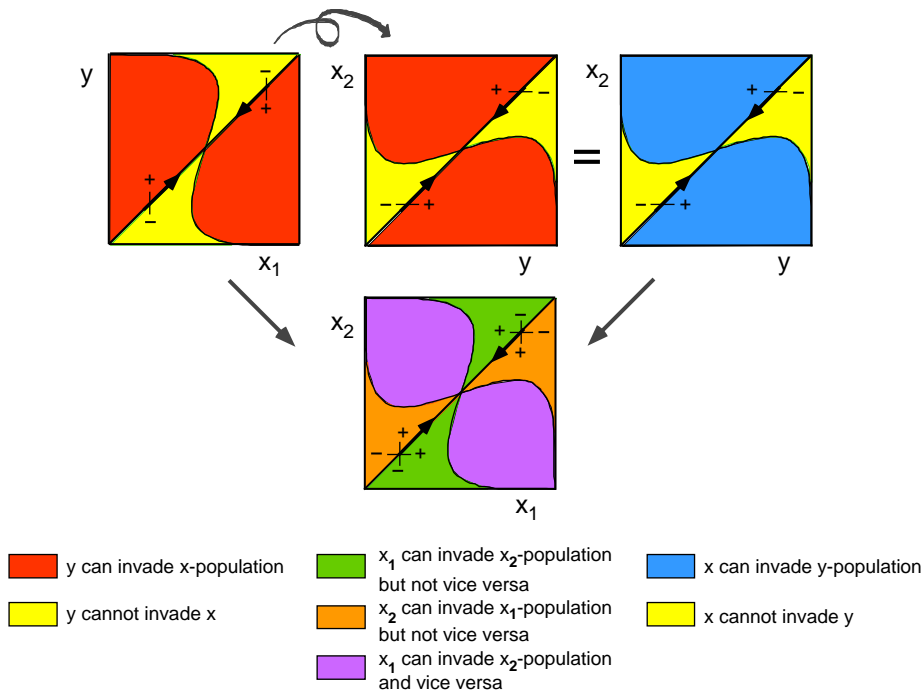
$$= 0 \quad \text{for } m = 1$$

* These equations may look pretty artificial, but they have all the mathematical properties required of a good population model



**when internal c-attractors are always unique
(slightly weaker: when dimorphisms are always protected):**

Mutual invasability: also consider "role reversal" of x and y



the purple set supports dimorphisms

Adaptive Dynamics, II polymorphisms:

In (spatially and/or physiologically structured) **locally largish** populations characterized by trait values (strategies) Y, X, X_1, \dots, X_n :

(E, Y) : asymptotic average rate of relative increase
(fitness) (dominant Lyapunov exponent) of Y population
 in a given ergodic environment E

$E_{\text{attr}}(C)$: the environment "created" by a strategy
 coalition $C = (X_1, \dots, X_n)$

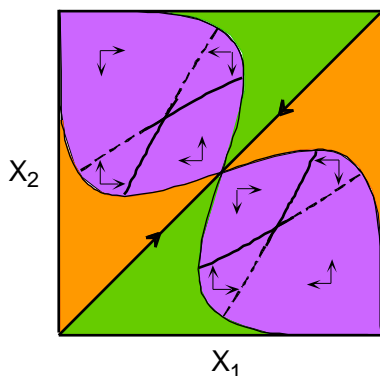
Implicit presupposition: An X_1, \dots, X_n (plus...) community has a **unique global attractor** (stationary probability measure on E) with all n strategies present [or else consider local theory only]

$$s_C(Y) := (E_{\text{attr}}(C), Y)$$

Invasion in a dimorphic population:

two residents: x_1, x_2 ; one mutant: y

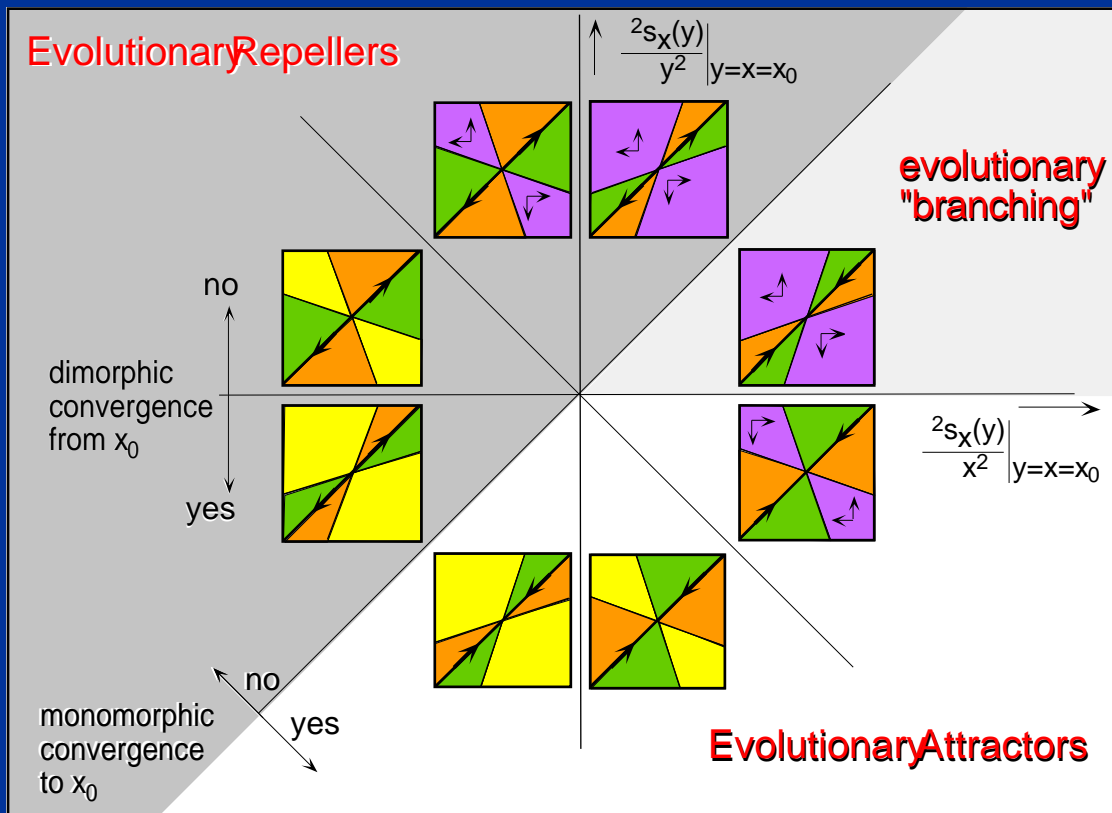
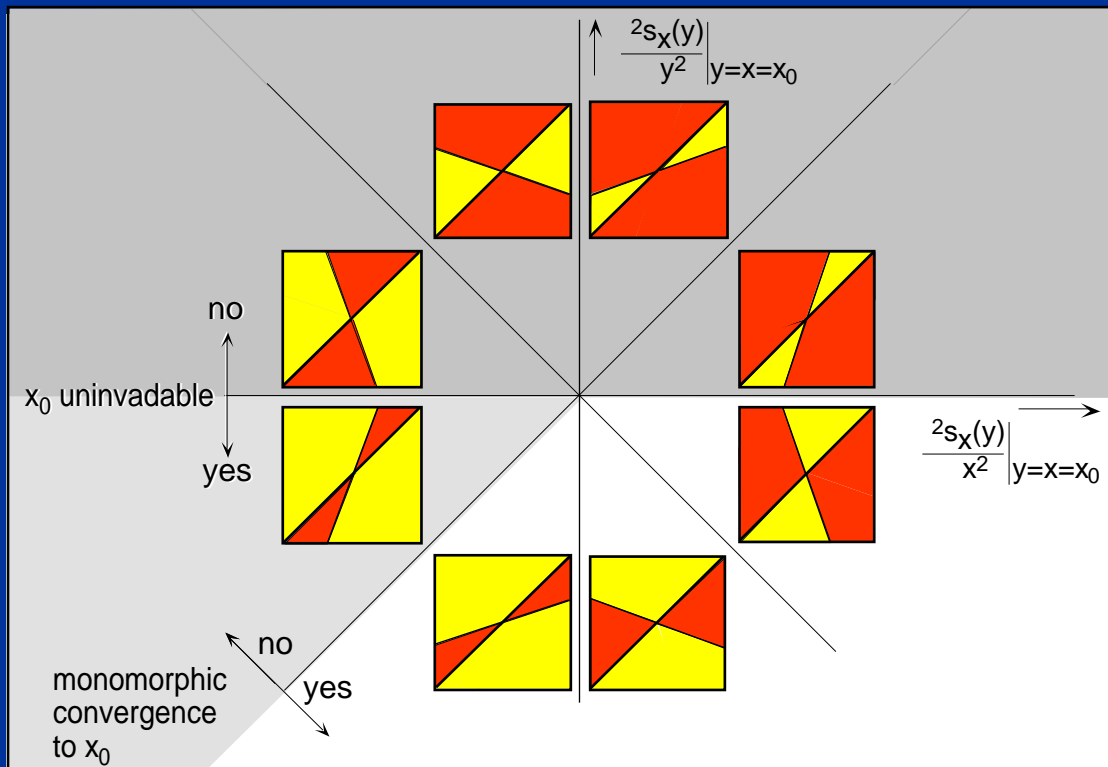
$$\text{fitness of mutant} = s_{x_1, x_2}(y)$$



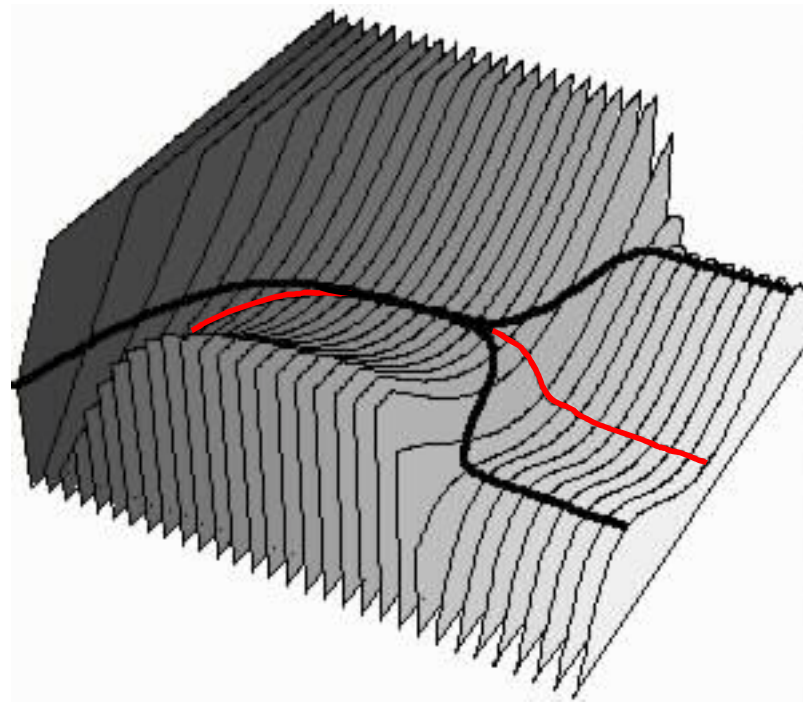
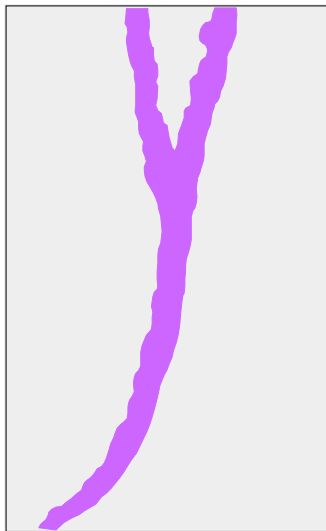
\rightarrow or \leftarrow :
 succesful mutation of x_1

\downarrow or \uparrow :
 succesful mutation of x_2

classifying the evolutionarily singular points

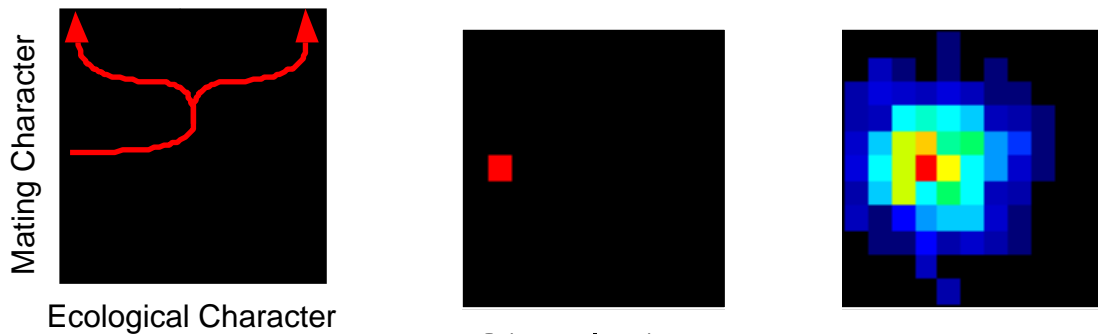


- One of the main results from AD is the discovery of a near ubiquitous potential mechanism for adaptive speciation.

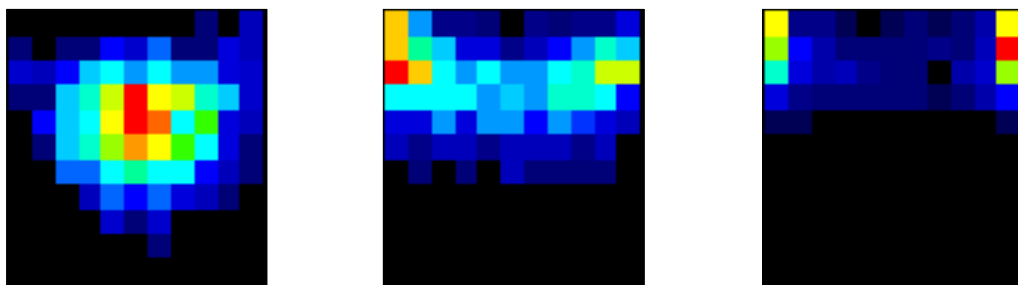


adding Mendelian genetics:

Summary



Simulation



1. Dieckmann & Doebeli considered a few ways of achieving assortative mating.
What about other ways?
In particular, which ones are easiest to realise?
(Spatial structure can help!)
2. There are more ways of achieving a split in the types around than thwarting the Mendelian mixer, like using a developmental switch to produce different types, and letting the types so produced evolve by means of modifier genes.
Possible switches:
 - (a) a single locus with a dominant-recessive allele pair,
 - (b) sex (a special case of 1; disadvantage: there are other selective pressures to let the types occur in special ratios).
 - (c) some incidental environmental cue.

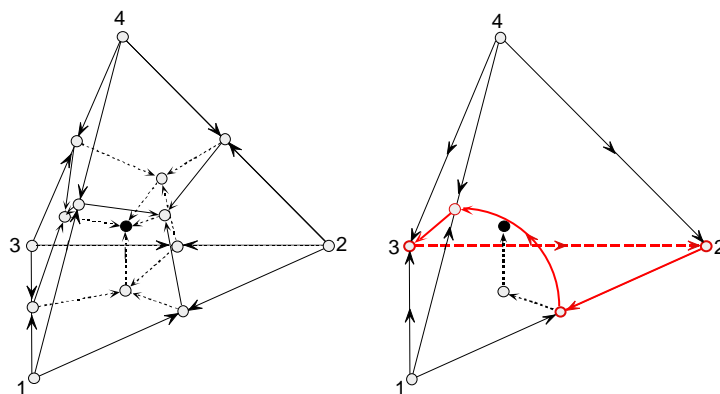
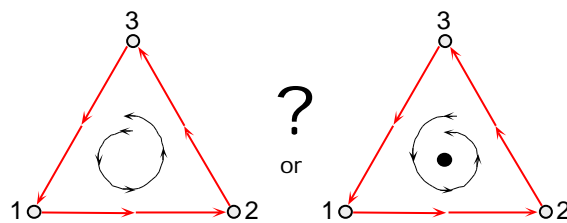
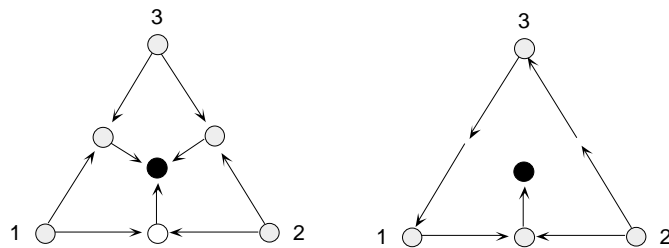
4. Polymorphisms / More than Two Species

More Species Coevolution:

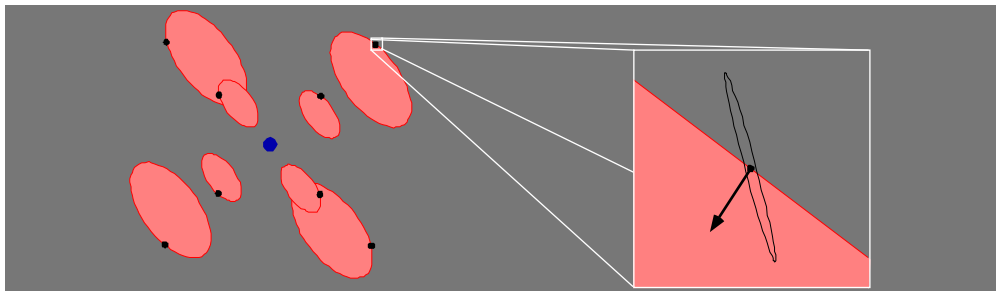
What are the regularities?

(cf. talk by Vincent Jansen)

We need to put in more ecological constraints,
or else



5. And beyond: Higher Dimensional Traits, Bifurcations



To first order of approximation for small mutational steps:

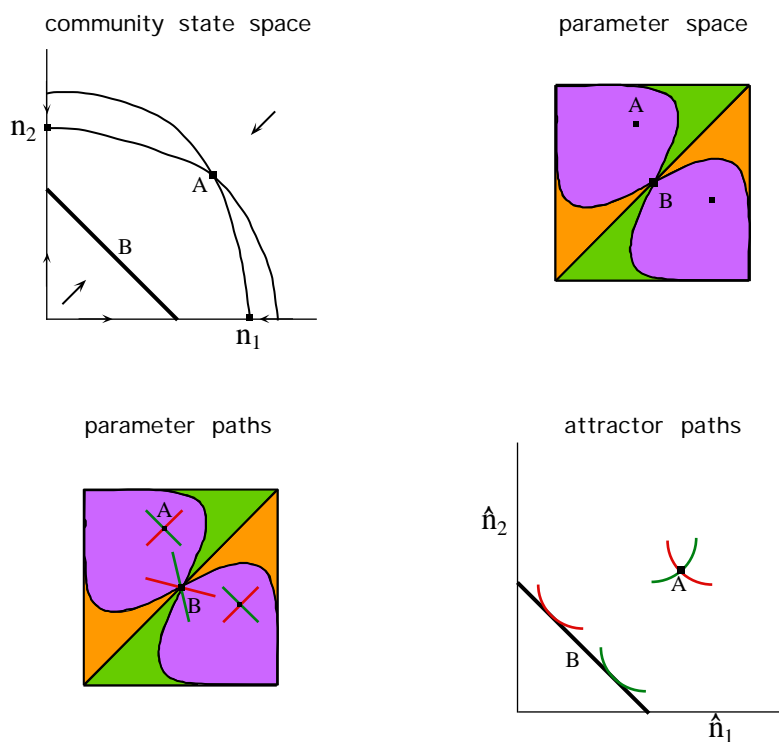
$$\frac{dX}{dt} = \frac{1}{2} \bar{N}(X) \mathbf{C} \left(\frac{s_x(Y)}{Y} \Big|_{Y=X} \right)^T$$

where $\frac{1}{2}$ is the probability of a mutation per birth event,
 \mathbf{C} is the mutational covariance matrix,
and $\left(\frac{s_x(Y)}{Y} \Big|_{Y=X} \right)^T$ depends i.a. on the reproductive variability.

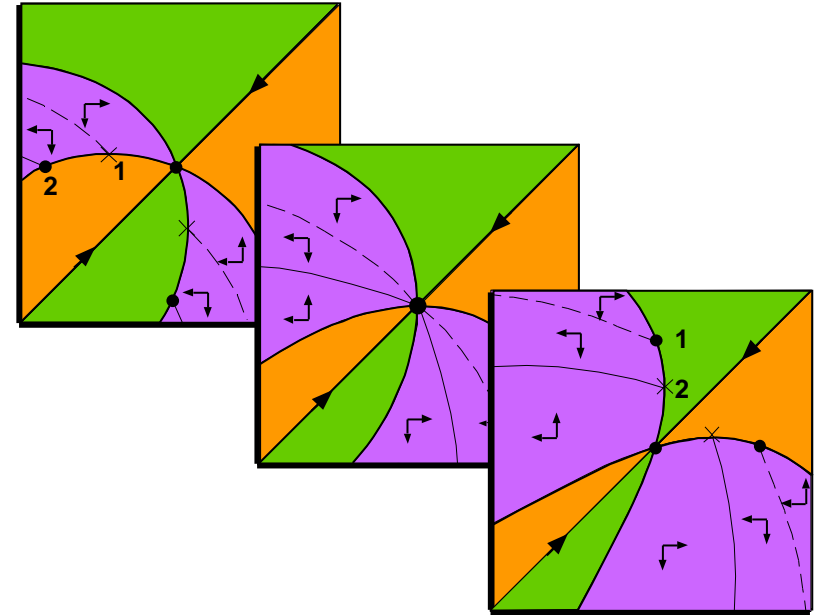
[When everybody is born equal & the community attractor is just a point:
 $\frac{1}{2} = 2 T_f / (T_s^2)$
 T_f = average age of giving birth, T_s = average lifetime (of resident)
 $2 = \text{Var}[\text{lifetime offspring number}]$.]

message: the canonical equation is now our main tool

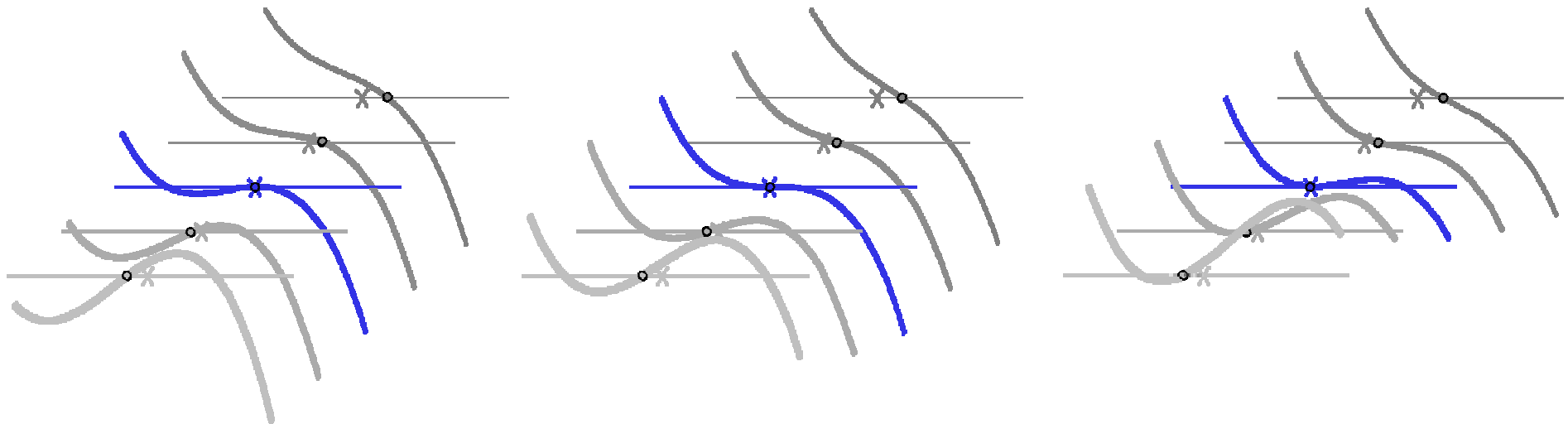
**in higher dimensional trait spaces
at higher degrees of polymorfism $s_x(Y)$ is no longer differentiable
near the lower dimensional singular points:**



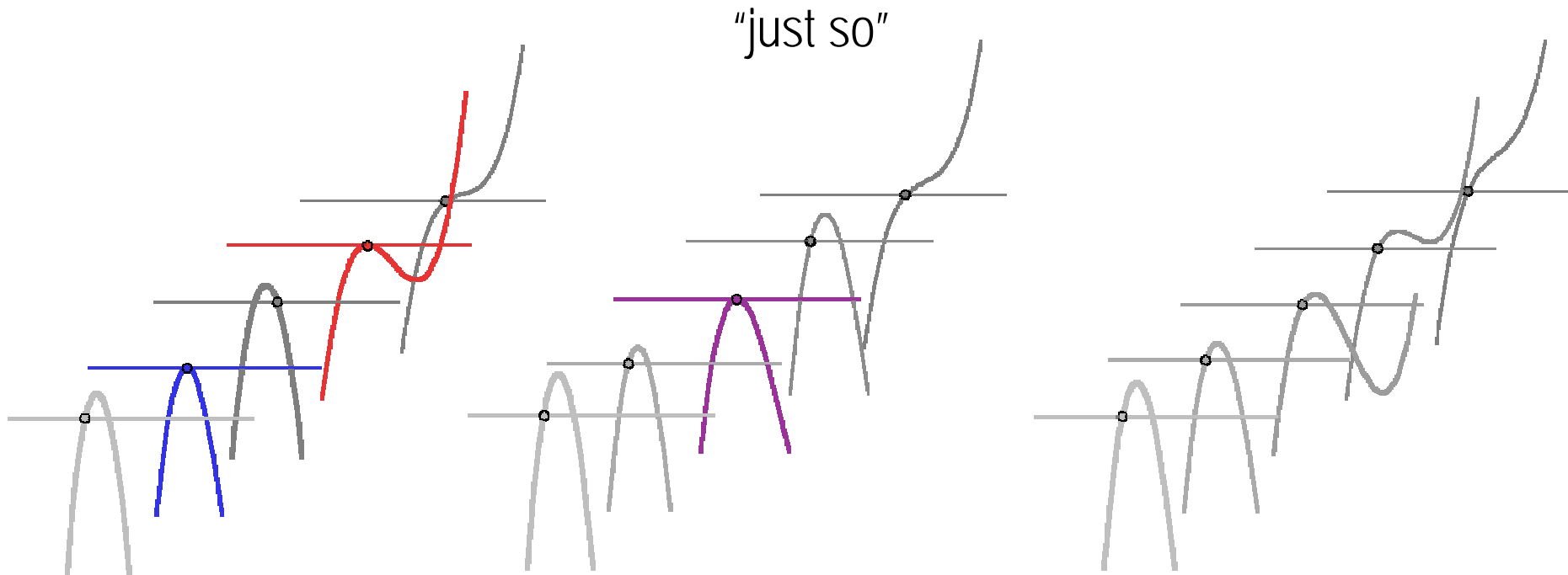
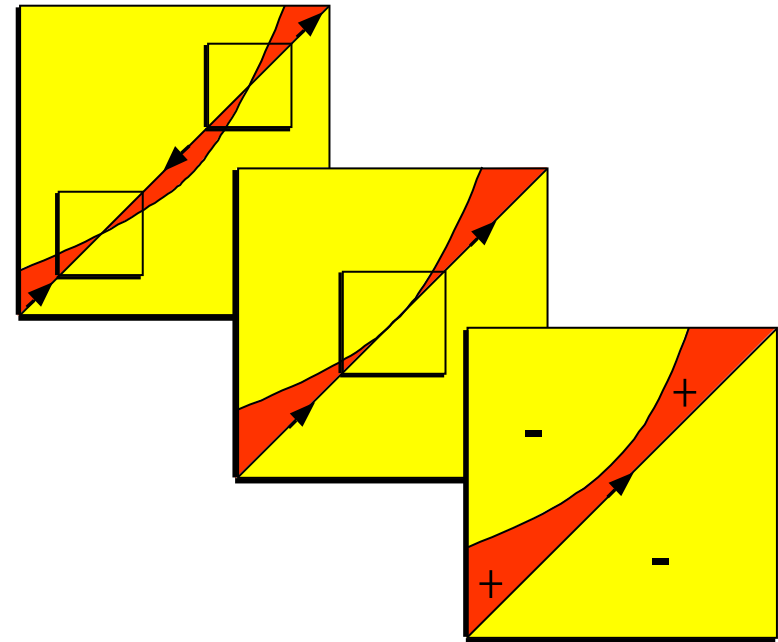
- In the fossil record we probably see mainly the slow tracking of adaptive equilibria, punctuated by phases of fast evolution when the equilibrium structure bifurcates.



starting with speciation

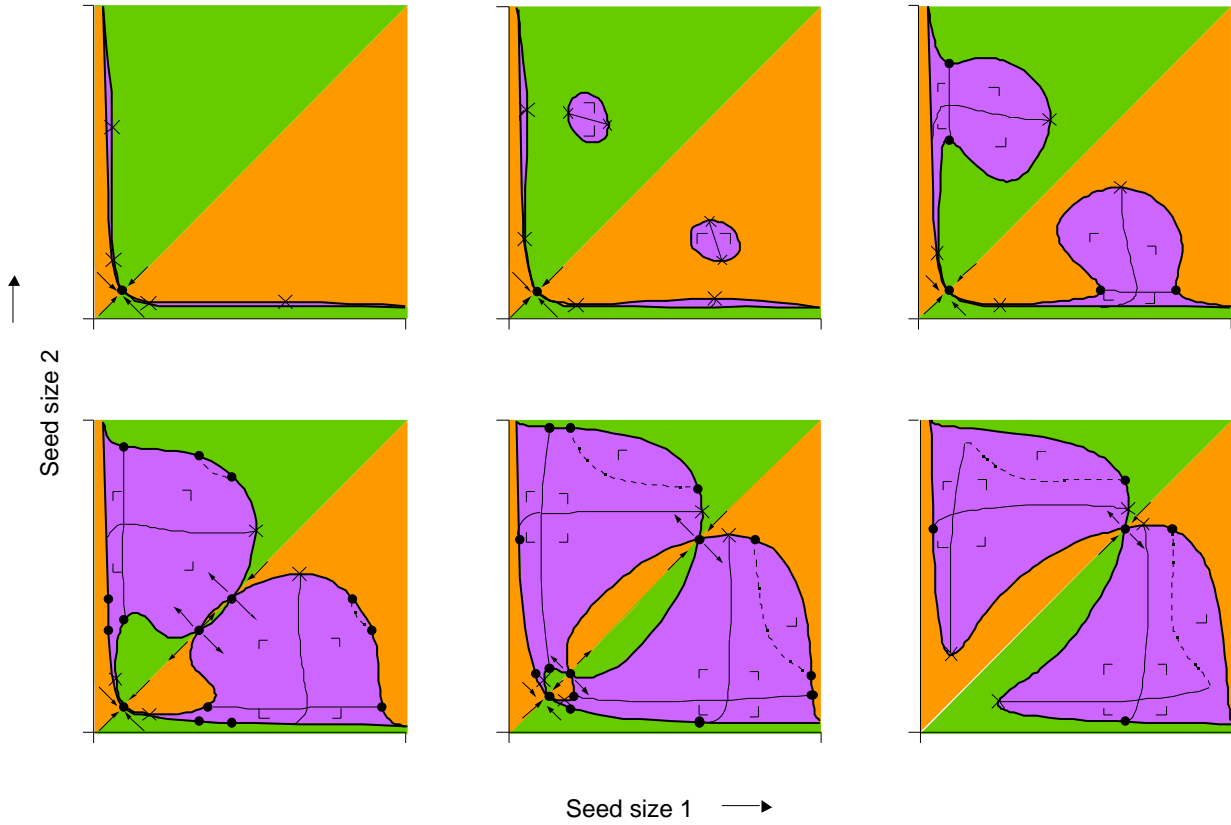


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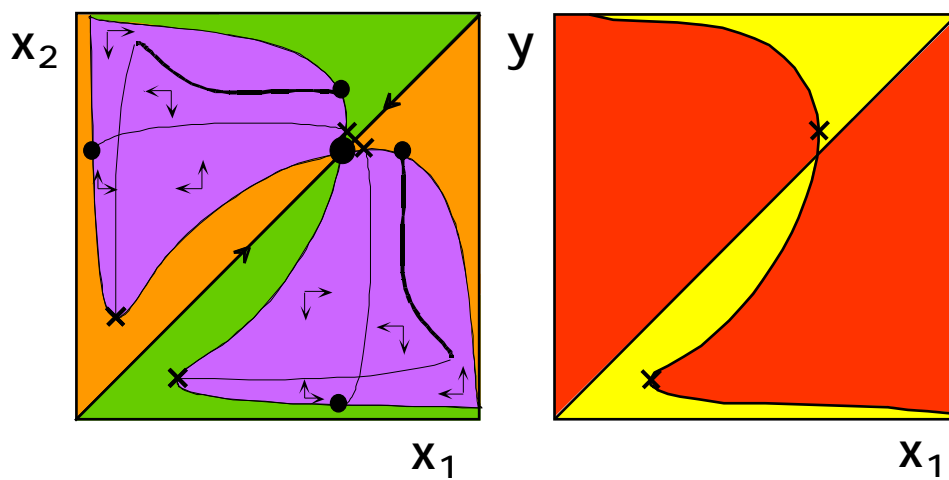


more bifurcations

From a model for the evolution of seed sizes



Global constraints on the isoclines:



6. Future

Open problems in AD:

Internal:

- * hard proofs
- * range of applicability of local results
- * fully classifying local behaviour for higher dimensional trait spaces
- * developing a full-fledged bifurcation theory (including good computational tools)
- * classifying generic properties

Population dynamical justification:

- * hard proofs of stochastic limit theorems
- * elucidating generic behaviour of community models on those points relevant for AD

Genetic considerations:

- * what survives under Mendelian inheritance?
- * when do the assumed smoothness properties (i.a. similarity of mutational and ecological metrics), apply, and how to proceed if they don't?

Applications:

- * analysing specific eco-evolutionary models
- * predicting generic macro-evolutionary patterns
- * improving the connection with real biology and the argumentation style of "real" biologists

7. Afterthoughts 1: Why small mutational steps?

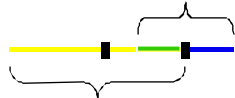
- **Internal selection processes**
Officially: selection processes occurring so early in life that they are largely independent of the ecological feedback loop.
In our case: such that their effect on the fitness landscape is always the same.
- Both functional morphologists and developmental biologists talk in terms of mechanisms that keep working properly through a sequence of small transformational steps.
- Only properly functioning organisms have fitnesses in a relevant range, malfunctioning ones have fitnesses near $-\infty$.
- This leads to a picture of narrow, slightly sloping, ridges, surrounded by a fitness abyss
- The trait spaces considered by morphologists and evo-devo-researchers are, at least in principle, very high dimensional.

NB For an n -dimensional trait space the top of a fitness ridge can easily have a dimension $k > 1$ while away from the ridge fitness decreases in an $(n-k)$ -dimensional set of directions

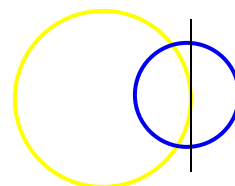
- The slope of the ridges is the domain of ecology, their location is largely ecology independent.

The ratio of the size of the intersection of two spheres with constant radii and the distance of their centers equal to the largest radius, to the size of the smallest sphere rapidly decreases when the number of dimensions increases.

1 dimensional spheres:



2 dimensional spheres:



To offset this effect one has to let the size of the smaller sphere go to zero.

2 Afterthoughts 2: Beyond Adaptive Dynamics

about trait spaces:

So far the implicit assumption was that the trait space has an 'ordinary', i.e., manifoldlike, geometry.

This need not be the case, as the geometry should reflect everything that can be generated by the developmental system.

some further long-term considerations

evolution tinkers (Jacob):

- The properties realised during evolution can often be realised by very different mechanisms.
- The first mechanism that does a sufficient job inherits the earth. →
Considering which mechanisms should be easiest to realise has considerable predictive power.
- Evolution does not necessarily solve a problem in the best possible manner.
- Evolution optimises only under very special circumstances, and only very locally.
- In the longer term different mechanisms for solving a problem lead to different mutational covariances and hence to different evolutionary routes.

The real evolutionary state space is not phenotype space but **genotype space**.

The mutational covariances reflect the geometry of genotype space (mutational distances) as well as the genotype to phenotype map.

This reflection is only adequate locally in genotype space, and therefore locally in evolutionary time.

Presently
the detailed nitty-gritty at the molecular level does not help yet in developing a predictive framework for dealing with large-scale evolution.

**The reason is
the evolved complexity of the developmental processes
and the resulting
convolutedness of the genotype to phenotype
map.**

There is a need for intermediate abstractions.

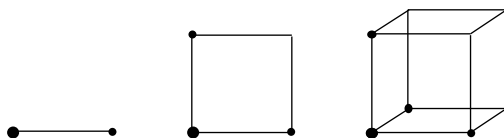
some arguments:

- There is a discrepancy between the good job done by random models at the level of molecular evolution versus the domination of adaptive processes perceived by ecologists, functional morphologists, and the like.
- This discrepancy nicely fits with the assumption of a great convolutedness of the genotype to genotype map.
- The exceptions to the random model also fit in nicely:
 - Different pieces of the genome evolve at different speeds, which tie in with the function a few translation steps away, but not further.
 - The variance in the number of substitutions is much too high. This presumably reflects repeated selective sweeps.

on adaptive walks in genotype space:

The very high dimension of genotype space

1. makes that every point has very many neighbours



2. makes that by far the most points in any set lie close to the boundary



Addendum: Topics in Adaptive Dynamics s.l. that presently have my interest

1. Development of the mathematical framework: Finding canonical forms of the invasion fitness function for higher degrees of polymorphism locally near evolutionarily singular points for higher dimensional trait spaces. Result: Up to quadratic terms the algebraic form derived on the basis of Lotka-Volterra population models is universal, or, equivalently, the monomorphic invasion fitness locally fully determines the polymorphic invasion fitnesses in a manner that does not depend on the underlying ecological model.
2. Ecological justification: Heuristically justifying the AD framework for physiologically structured (PS) population models, and more in particular the derivation of procedures for calculating the various quantities like invasion fitnesses and coefficients of the canonical equation for such models. Results: (a) For PS population models the canonical equation looks exactly the same as for simple ODE population models but for an additional multiplicative factor that relates to details of the resident life history, like the variance of the lifetime offspring production. (b) The result mentioned under 1 applies in full generality for PS population models.
3. Relationship with the Mendelian world (a): Exploring the consequences of male and female life history differences for measures of invasion fitness for polymorphic Mendelian PS populations. I do have interesting closed expressions for single locus genetics but I still have to explore their multi-locus extension, and to see what their consequences are for e.g. life-history evolution and the like.
4. Relationship with the Mendelian world (b): Exploring the influence of the genetic architecture on the choice made by Mendelian populations for the solution of ecologically posed branching problems as defined by AD theory, where the solution may be e.g. speciation, sexual role differences, random assignment of different types based on external cues, or the gradual evolutions of single locus dimorphisms with large phenotypic effect.