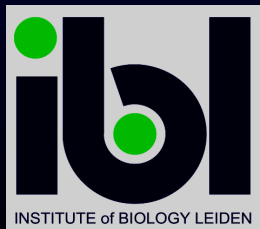


# Thoughts on the Geometry of Macro-Evolution

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steps towards  
a postmodern synthesis

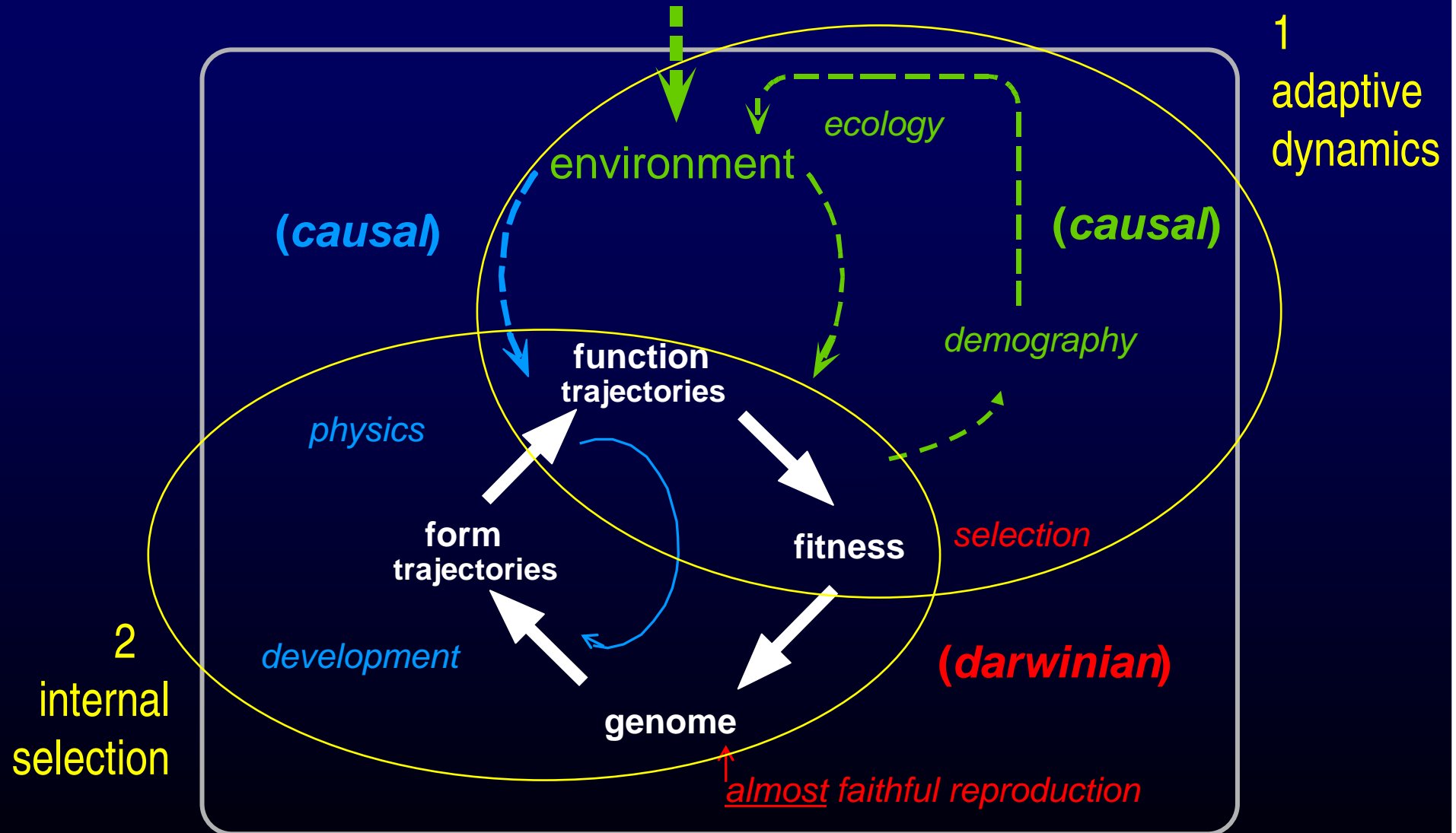


Hans Metz

ADN

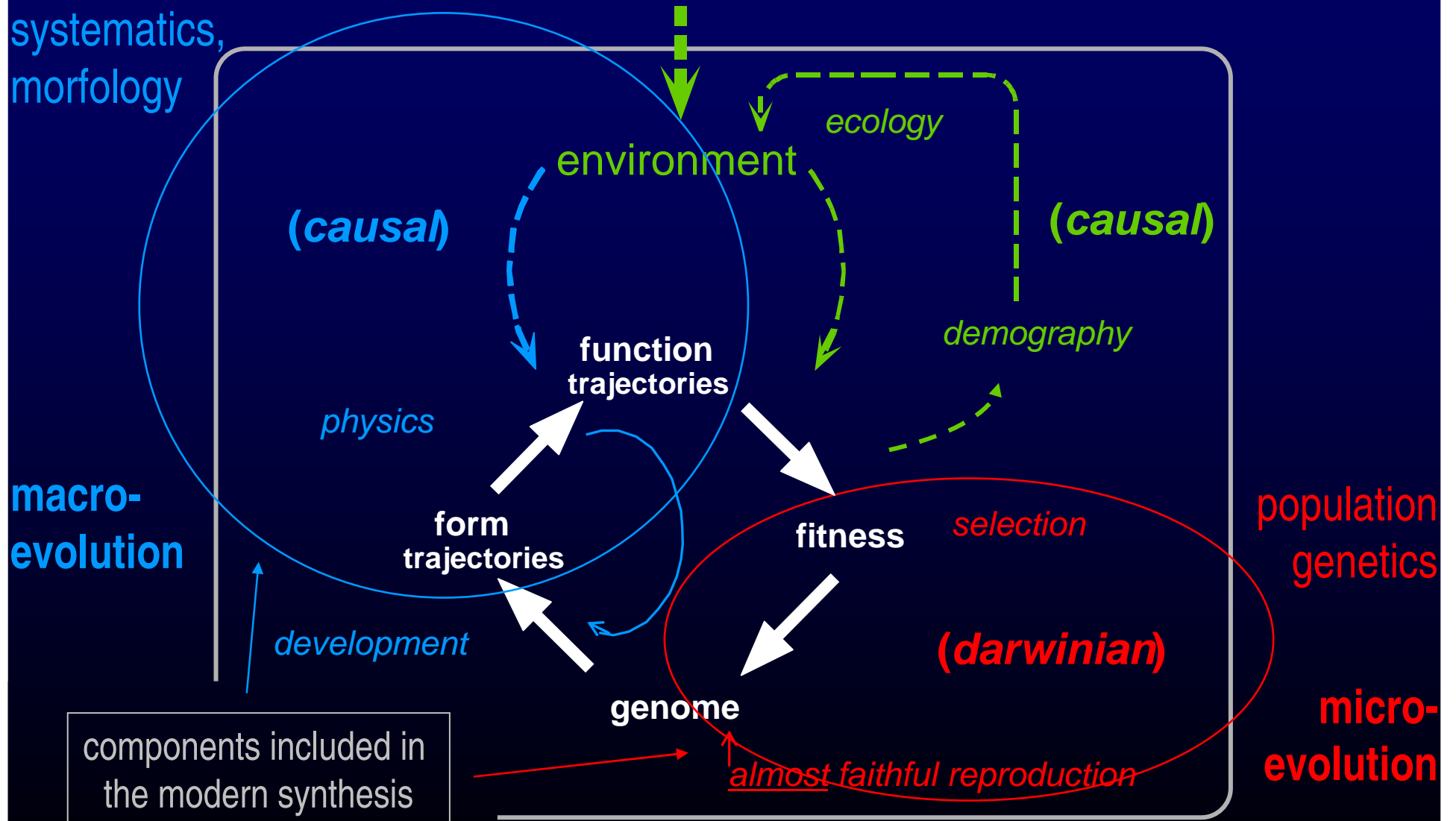
IIASA

# components of the evolutionary mechanism



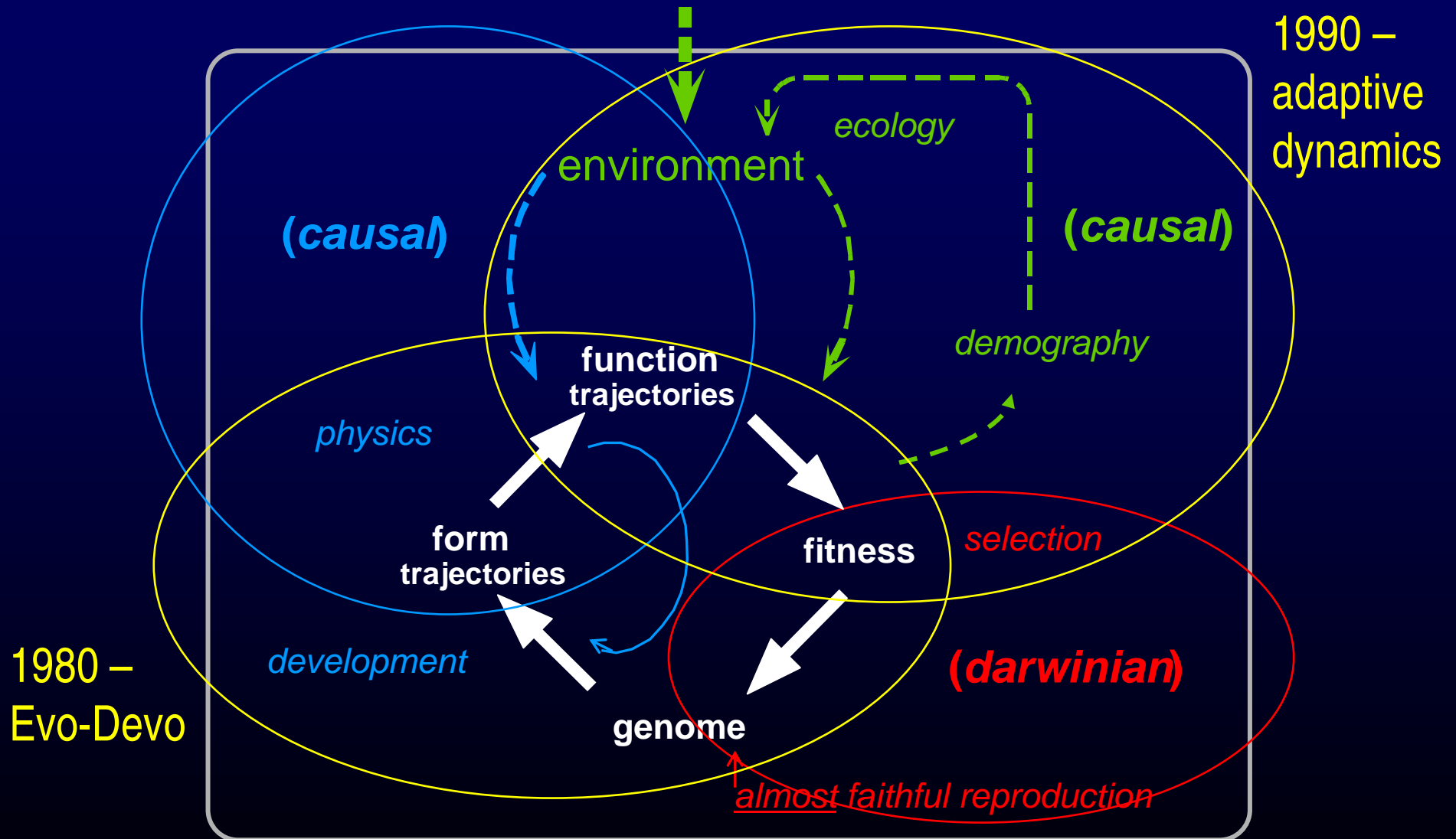
# the Modern Synthesis: 1920 - 1950

paleontology,  
systematics,  
morphology



The much revered  
**neo-Darwinian, or Modern, Synthesis**  
has shown little more than that  
**micro-evolutionary mechanisms**  
and  
**macro-evolutionary patterns**  
**are compatible.**

# more recent developments



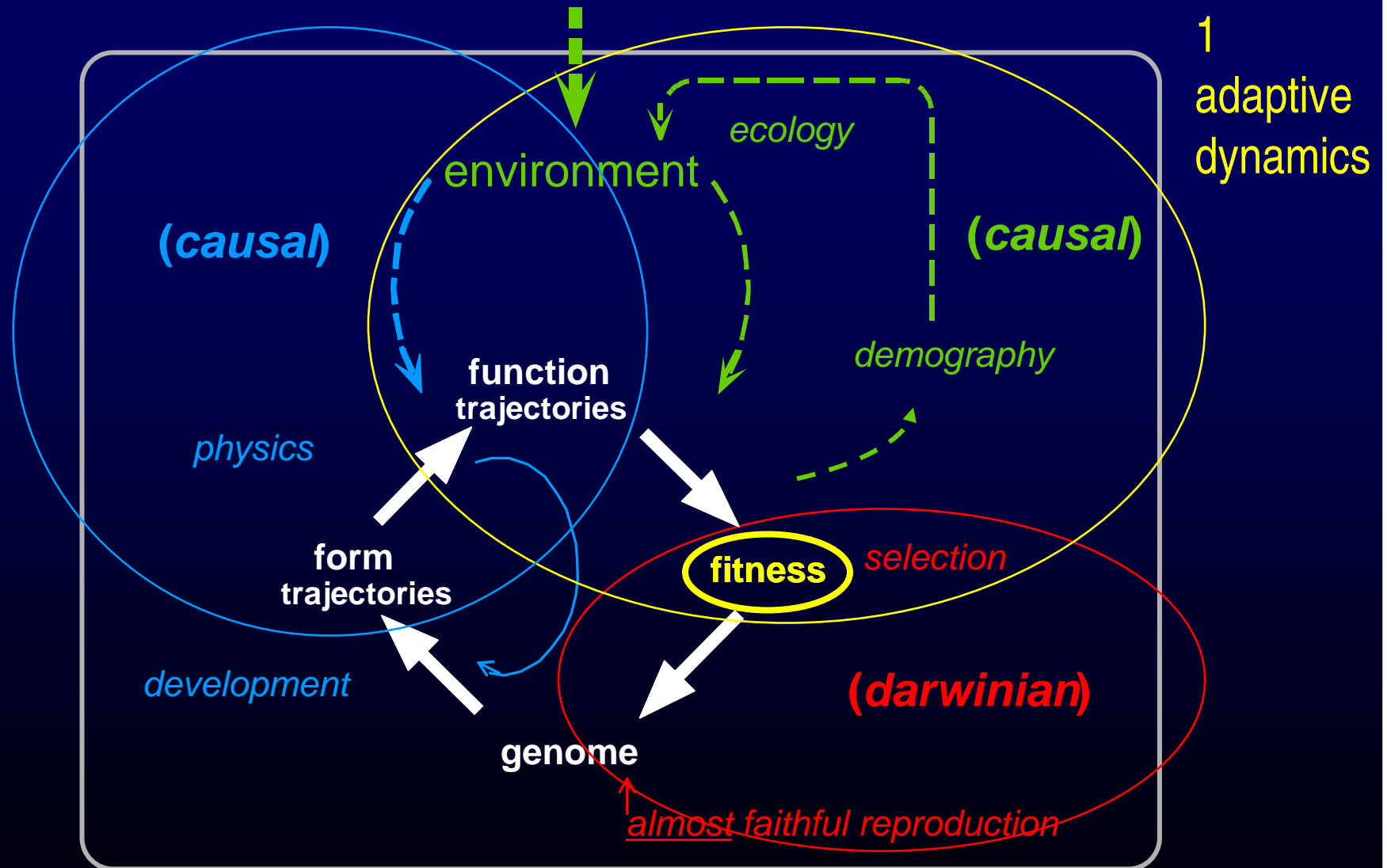
# **Adaptive Dynamics**

aims at making the transition from  
microevolution to macro-evolution,

but concentrates on  
only one component of  
the evolutionary mechanism:

**the filtering of novel mutations  
by the ecology.**

# the mathematical characteristics of the filter



# invasion fitness

~ dominant Lyapunov exponent  
(Furstenberg & Kesten, Oseledets)

⌘ 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.

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



# corollaries

---

⌘ Fitnesses are not given quantities, but depend on  
(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 determined by the (signs) (sizes) of the fitnesses of potential mutants.**

# some hidden mathematics 1

---

The different spaces that play a role in adaptive dynamics:

the physical space inhabited by the organisms

the state space of their i(ndividual)-dynamics

the state space of their p(opulation)-dynamics

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

**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**

the parameter spaces of families of adaptive dynamics

# some hidden mathematics 2

---

## The simplifying assumptions of adaptive dynamics

1. mutation limited evolution

2. clonal reproduction

3. good local mixing

4. largish system sizes

5. “good” c(ommunity)-attractors

6. interior c-attractors unique

essential

7. fitness smooth in traits

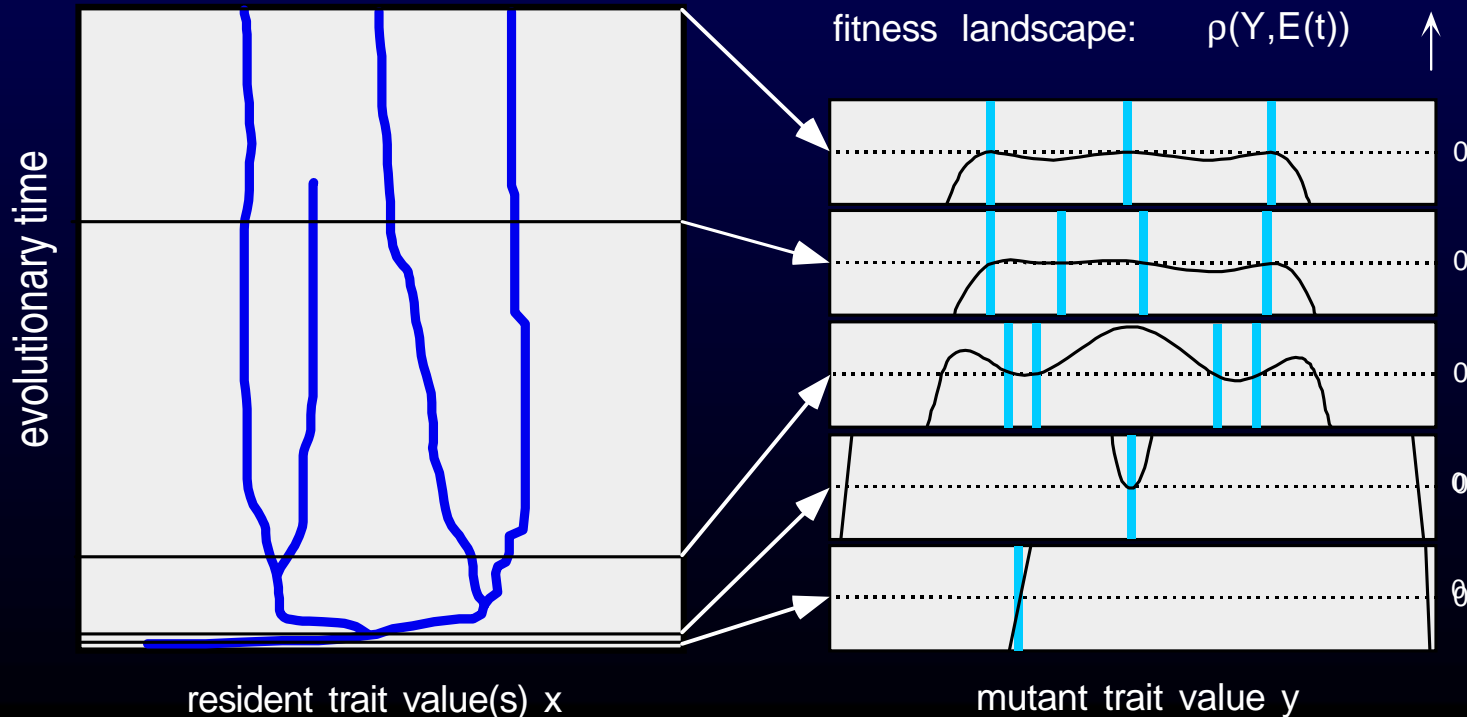
8. small mutational steps

---

i.e., separated population dynamical and mutational time scales:  
the population dynamics relaxes before the next mutant comes

# fitness landscapes

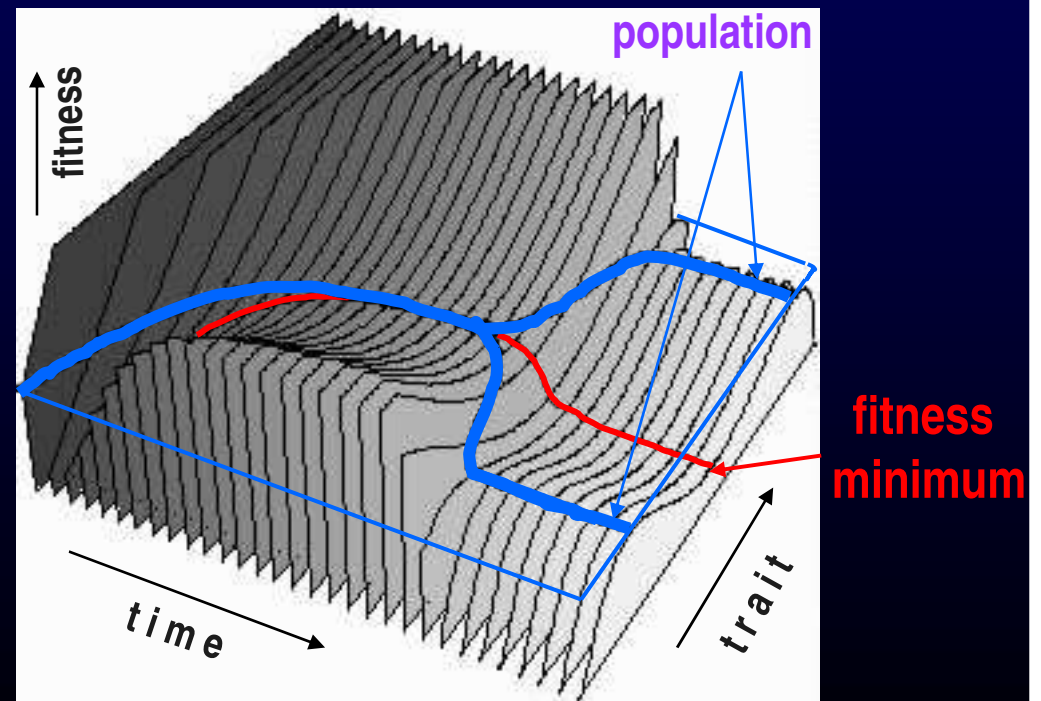
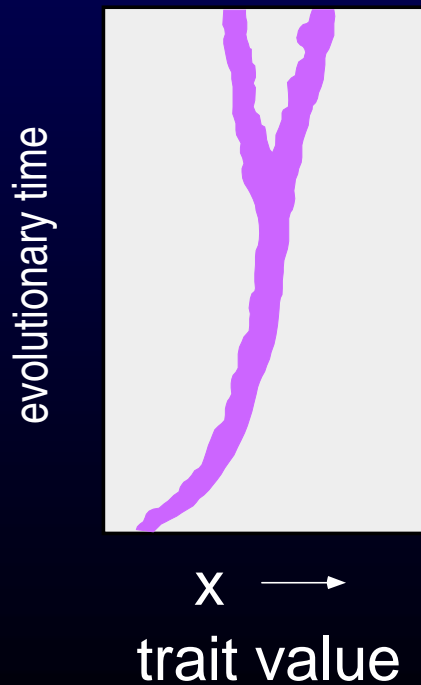
⌘ Evolution proceeds through uphill movements in a fitness landscape that keeps changing so as to keep the fitness of the resident types at exactly zero.



# speciation 1

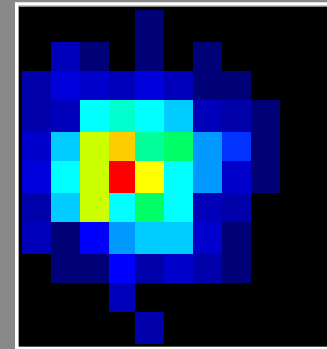
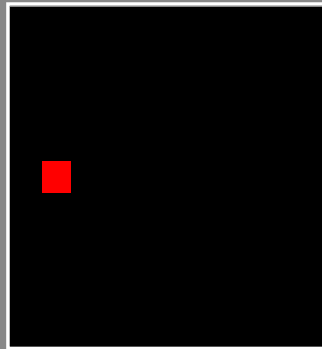
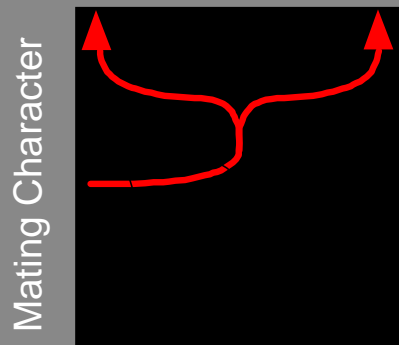
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⌘ One of the main results from AD is the discovery of a near ubiquitous potential mechanism for **adaptive speciation**.



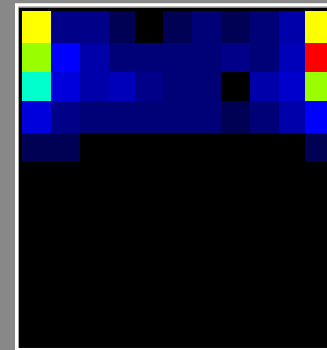
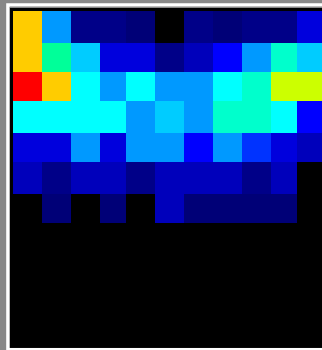
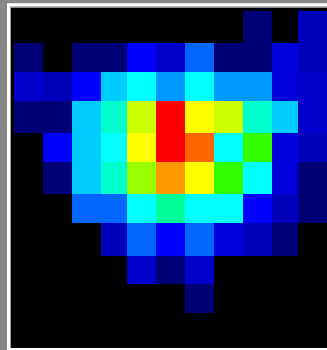
# beyond clonality: thwarting the Mendelian mixer

## Summary



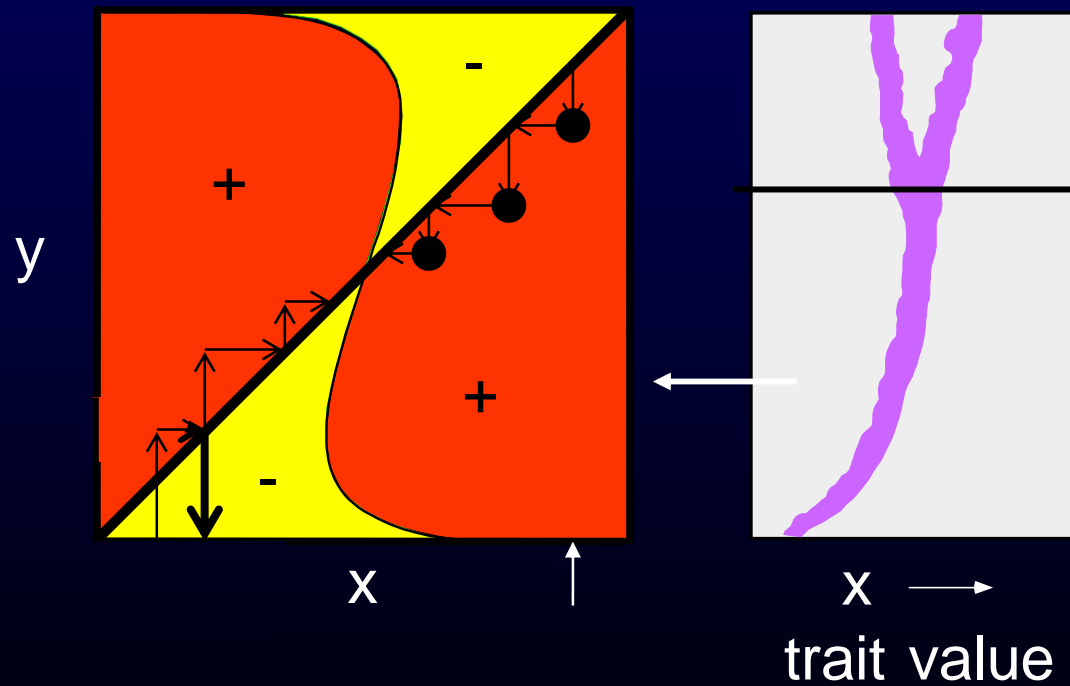
Ecological Character

## Simulation



# A bit more adaptive dynamics theory for later reference

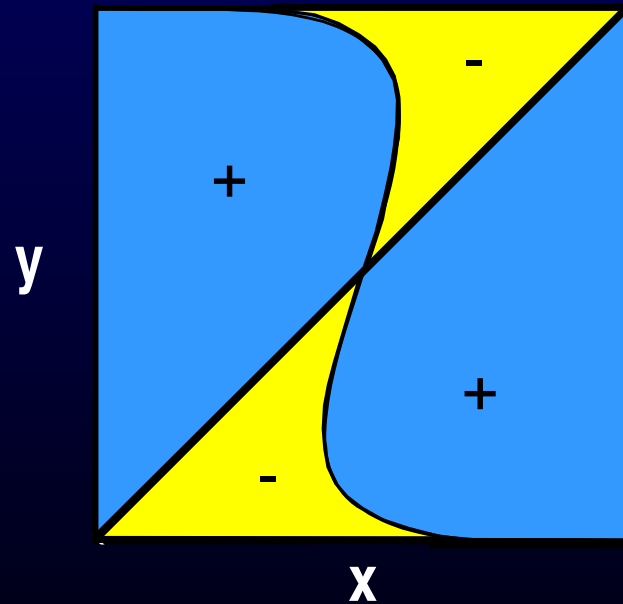
fitness contour plot  
x: resident  
y: potential mutant



# A bit more adaptive dynamics theory for later reference

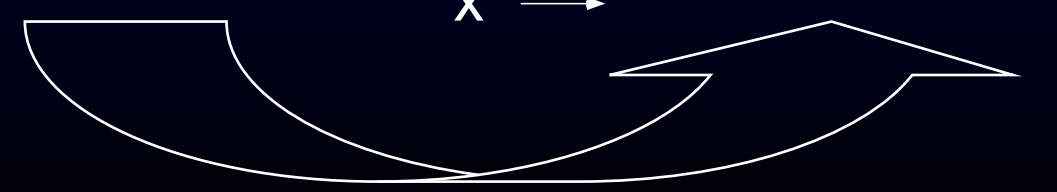
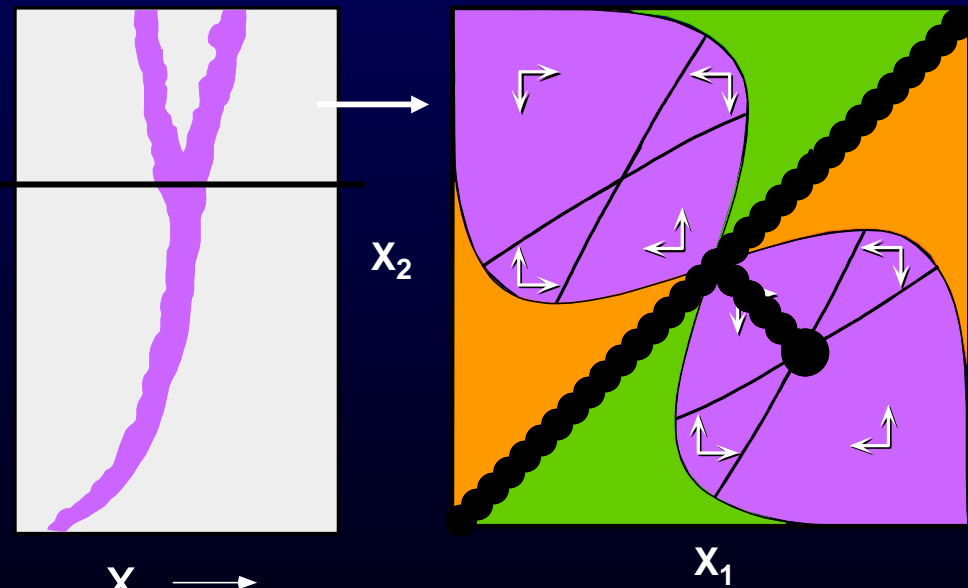
Pairwise Invasibility Plot

**PIP**



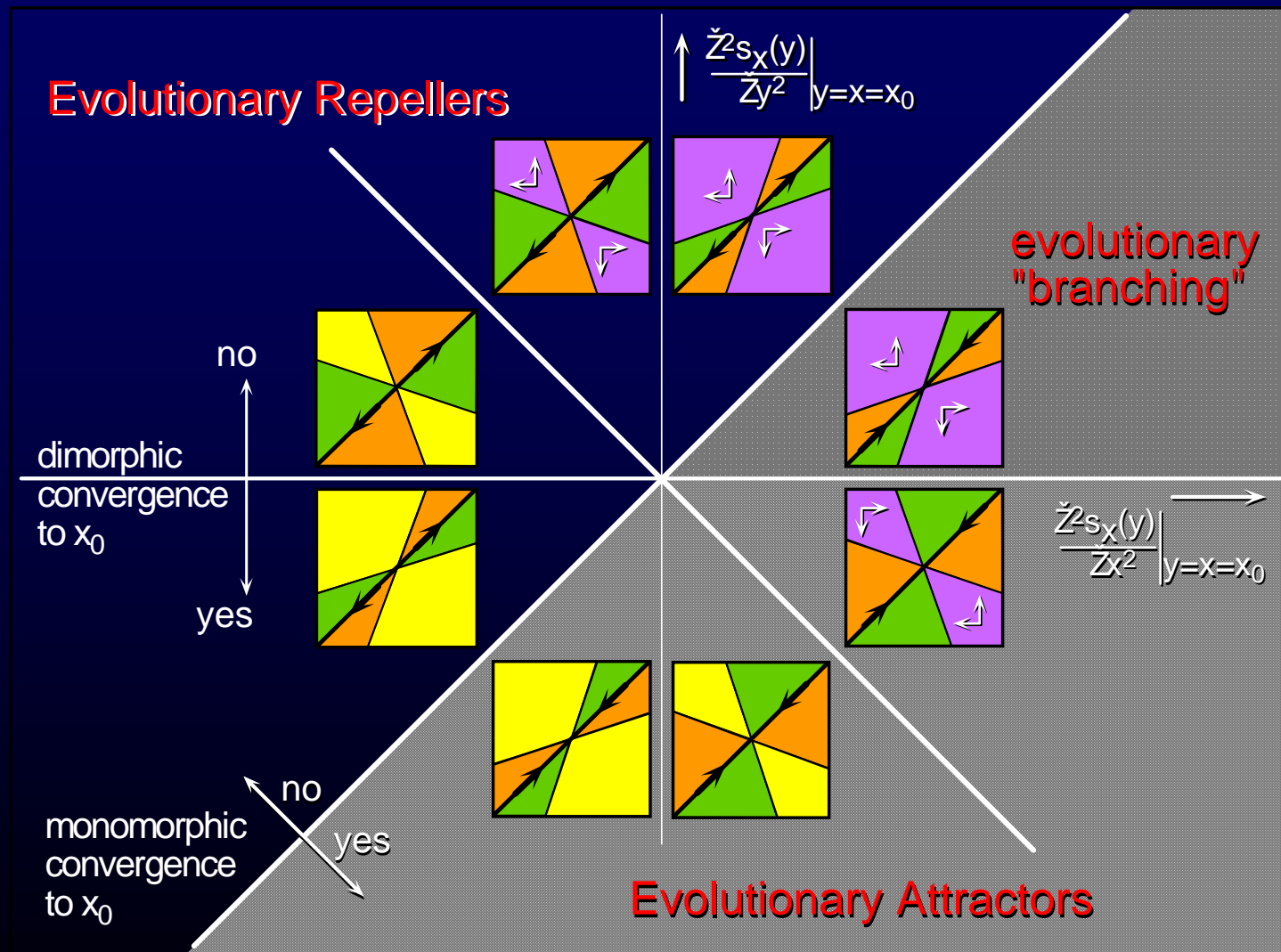
Trait Evolution Plot

**TEP**





# A bit more adaptive dynamics theory for later reference



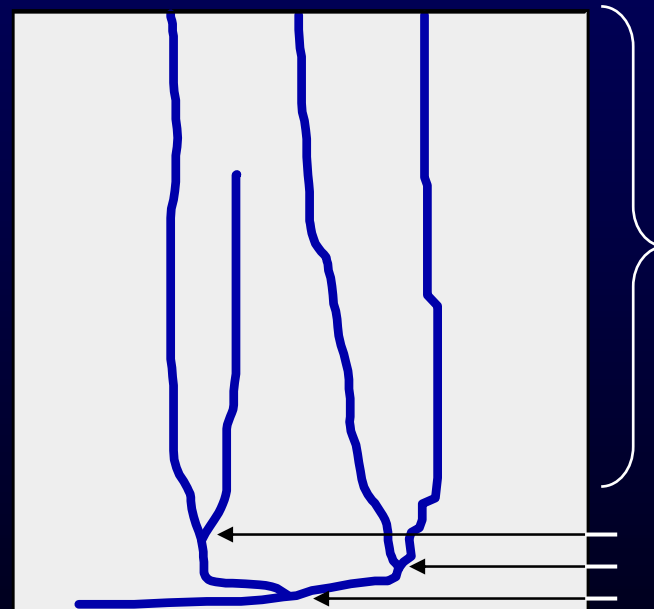
# some macro-evolutionary predictions 1

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⌘ After the colonisation of an empty habitat

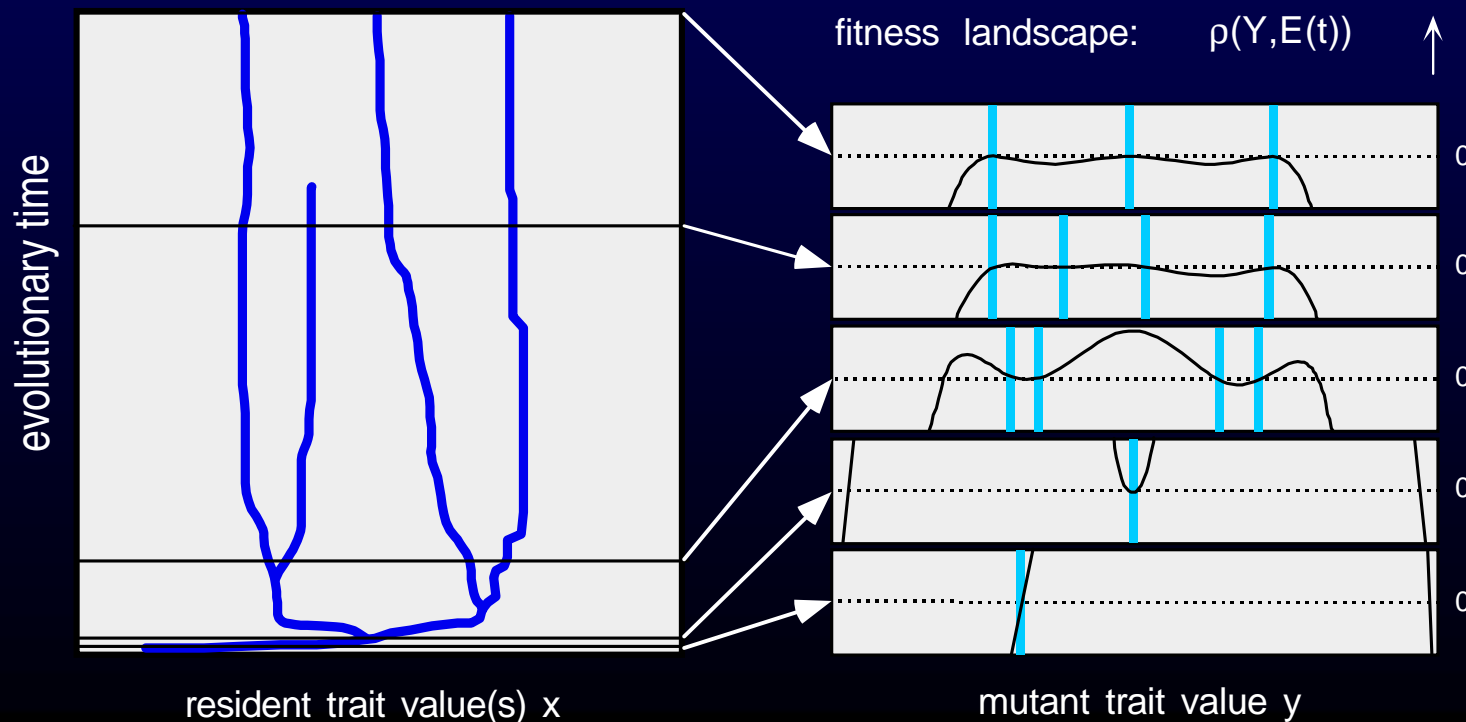
the speciation rate  
tends to be high,  
to decrease rapidly  
after the initial spurt.

(Conditional on the  
physical environment  
staying constant.)



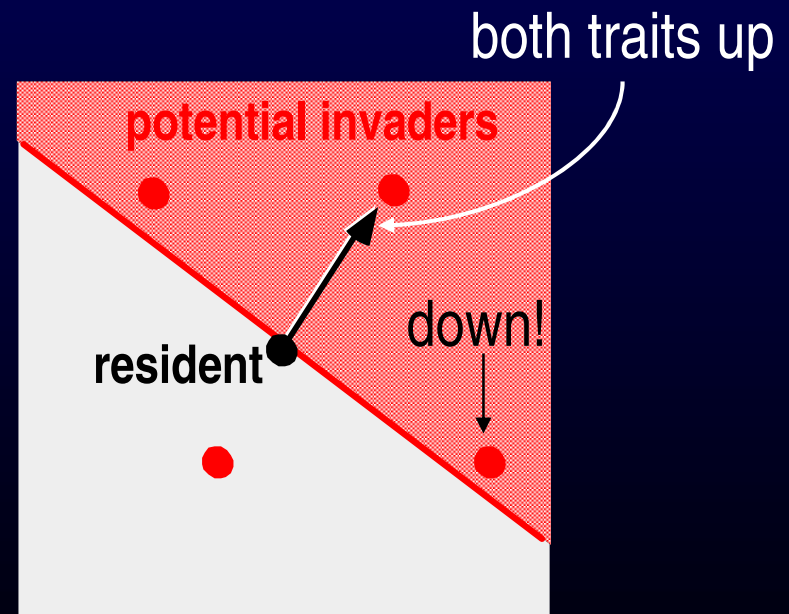
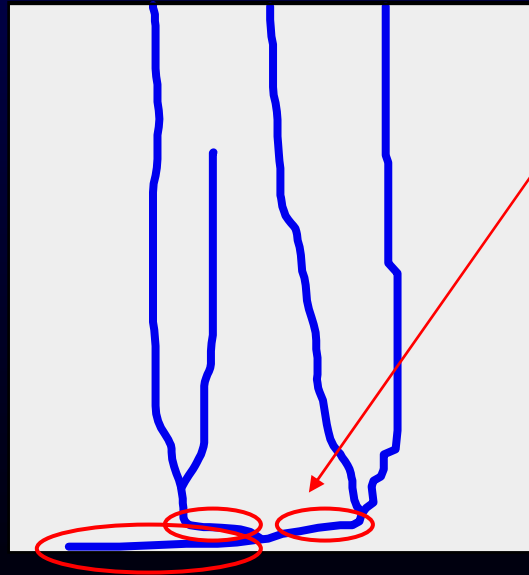
# rationale

The fitness landscape starts out as a single steep hill, but becomes overall flatter and more parceled up as it gets anchored at zero in more points.



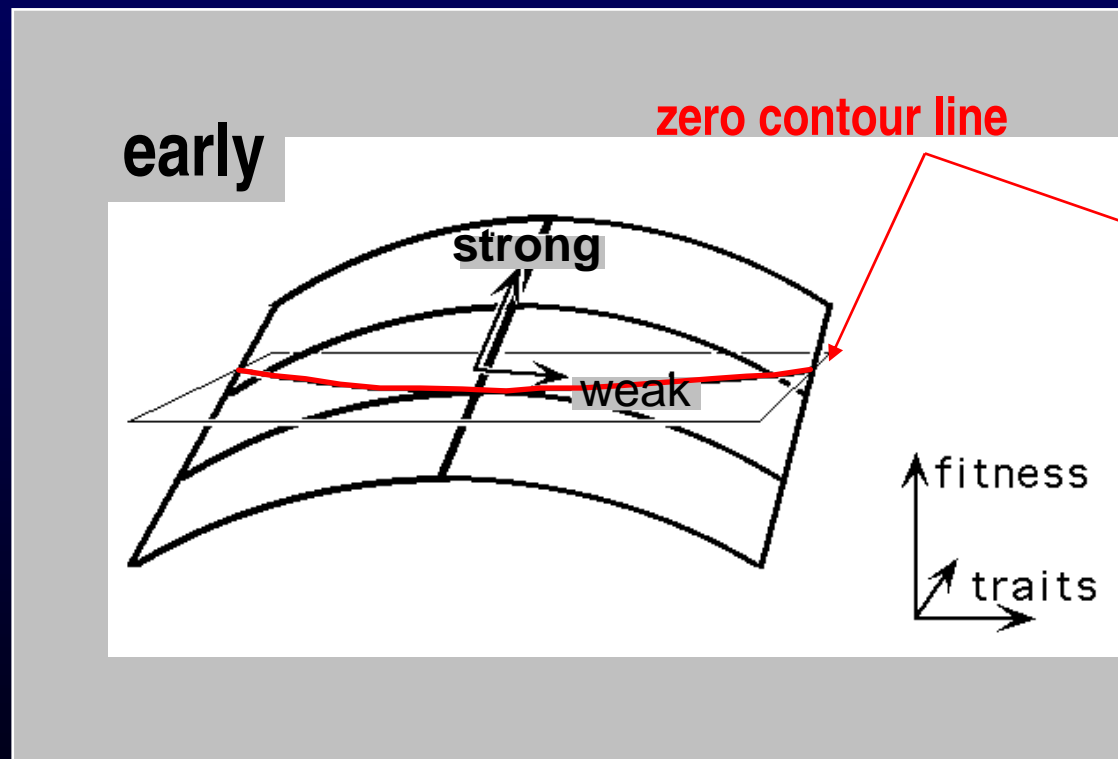
# some macro-evolutionary predictions 2

⌘ Initially, in the fast phases in between speciation events, a lot of random, non-adaptive, variation gets incorporated, but is weeded out in later stages of the process.



# rationale

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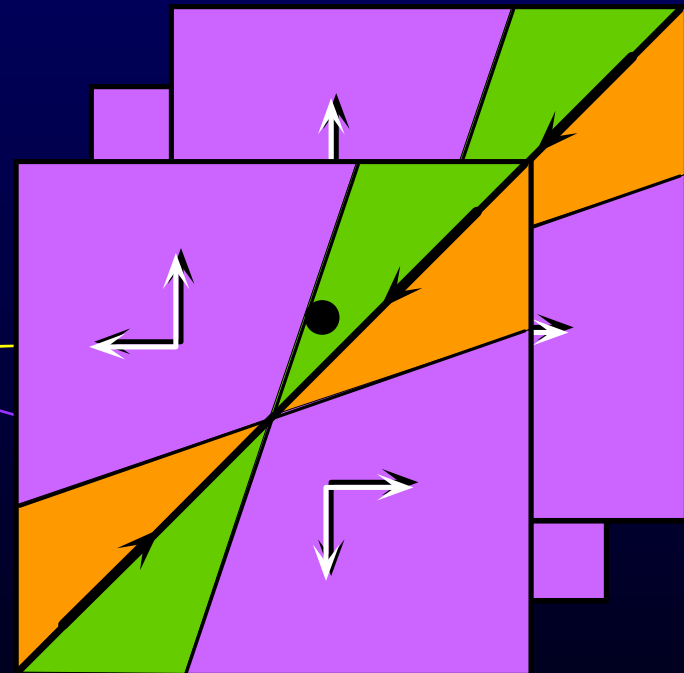
(second, instead of first order approximation)

# some macro-evolutionary predictions 3

---

⌘ Speciation should be rare in environments that fluctuate on a time scale between those of **directional evolution** and **speciation**.

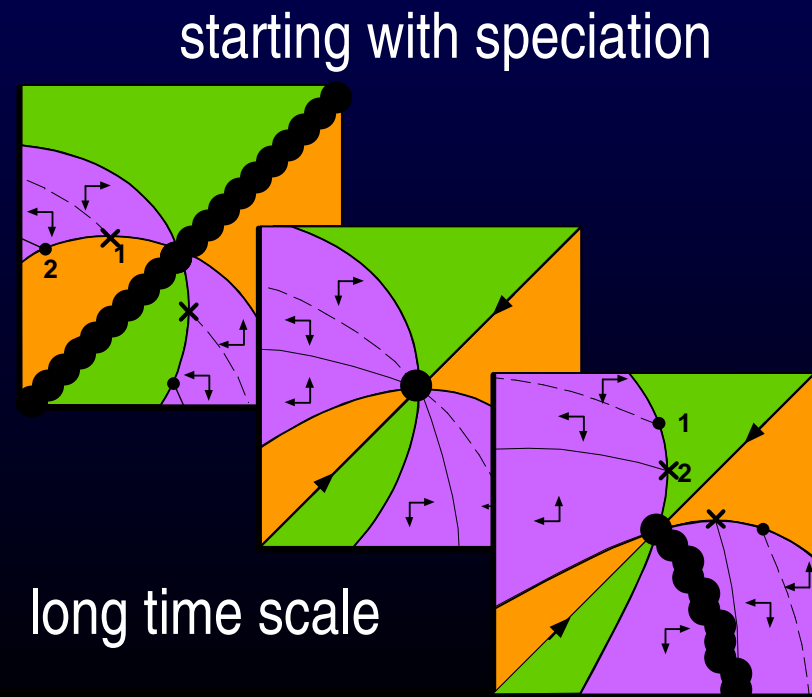
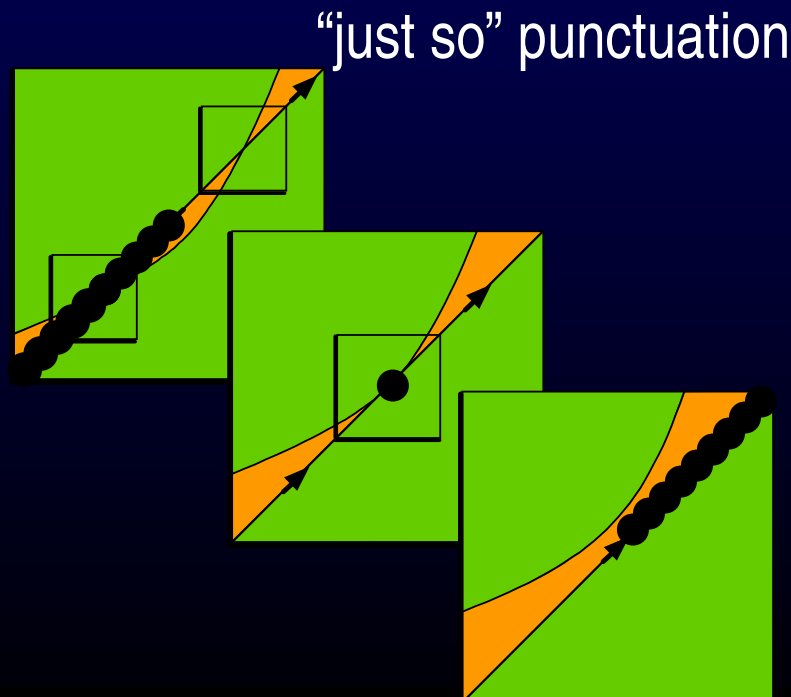
(Speciation is generally much slower than directional movement!)



# some macro-evolutionary predictions 4

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⌘ 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.

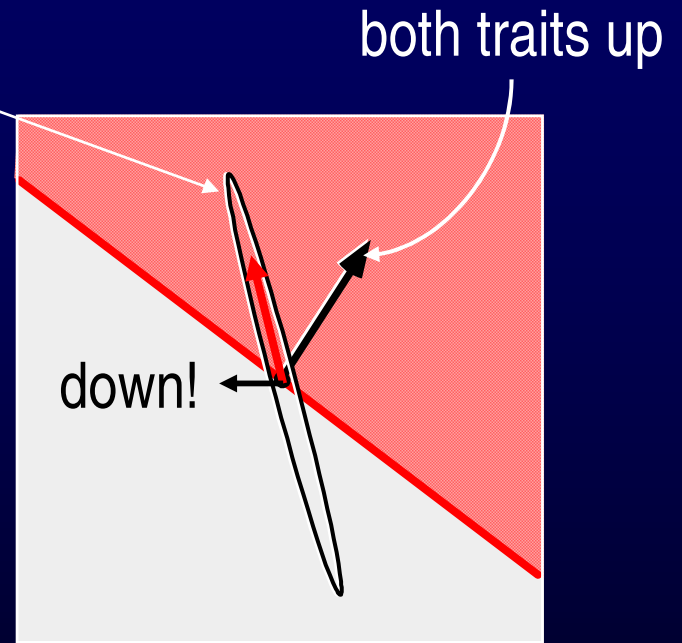


# against naive selectionism (style Richard Dawkins)

---

In one dimensional trait spaces selection dominates; this is no longer the case in higher dimensions.

mutational covariances



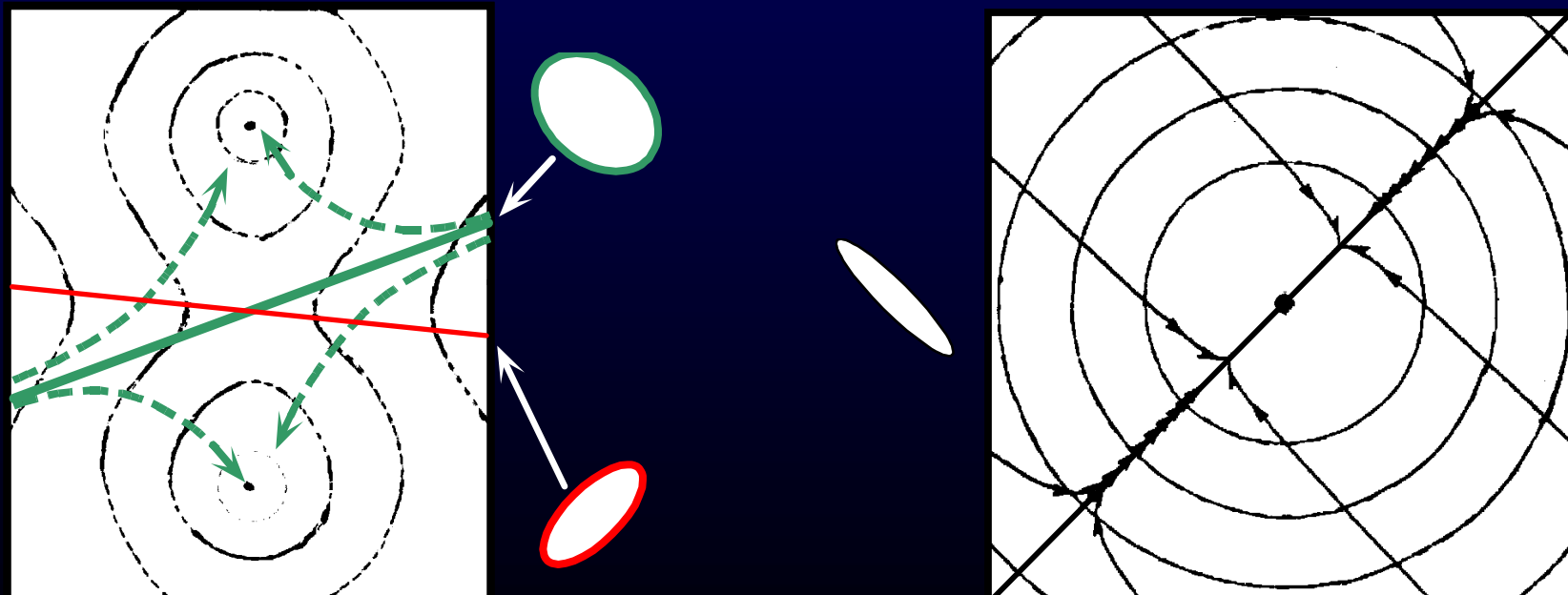
The higher the dimension of the trait space, the larger the number of directions orthogonal to the selection gradient!



# against naive selectionism, continued

---

The attractiveness of singular points and the shape of their basins, as well as the time scales of evolution, all depend on the covariance matrix.



# beyond Adaptive Dynamics

---

So far the implicit assumption was that the trait space has an 'ordinary' geometry.


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

**A conclusion will be  
that the picture sketched so far may well apply locally,  
but that additional geometrical mechanisms  
gain in importance on a more global scale.**

# 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.

# phenotype versus genotype

---

⌘ 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.

For larger time scale considerations we need  
different approaches,  
both  
to delineate the domain of applicability of the  
simpler framework,  
and  
to step beyond its confines.

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  
**tangledness of the genotype to phenotype map**  
(a result of  
the evolved complexity of the developmental process)

# some arguments

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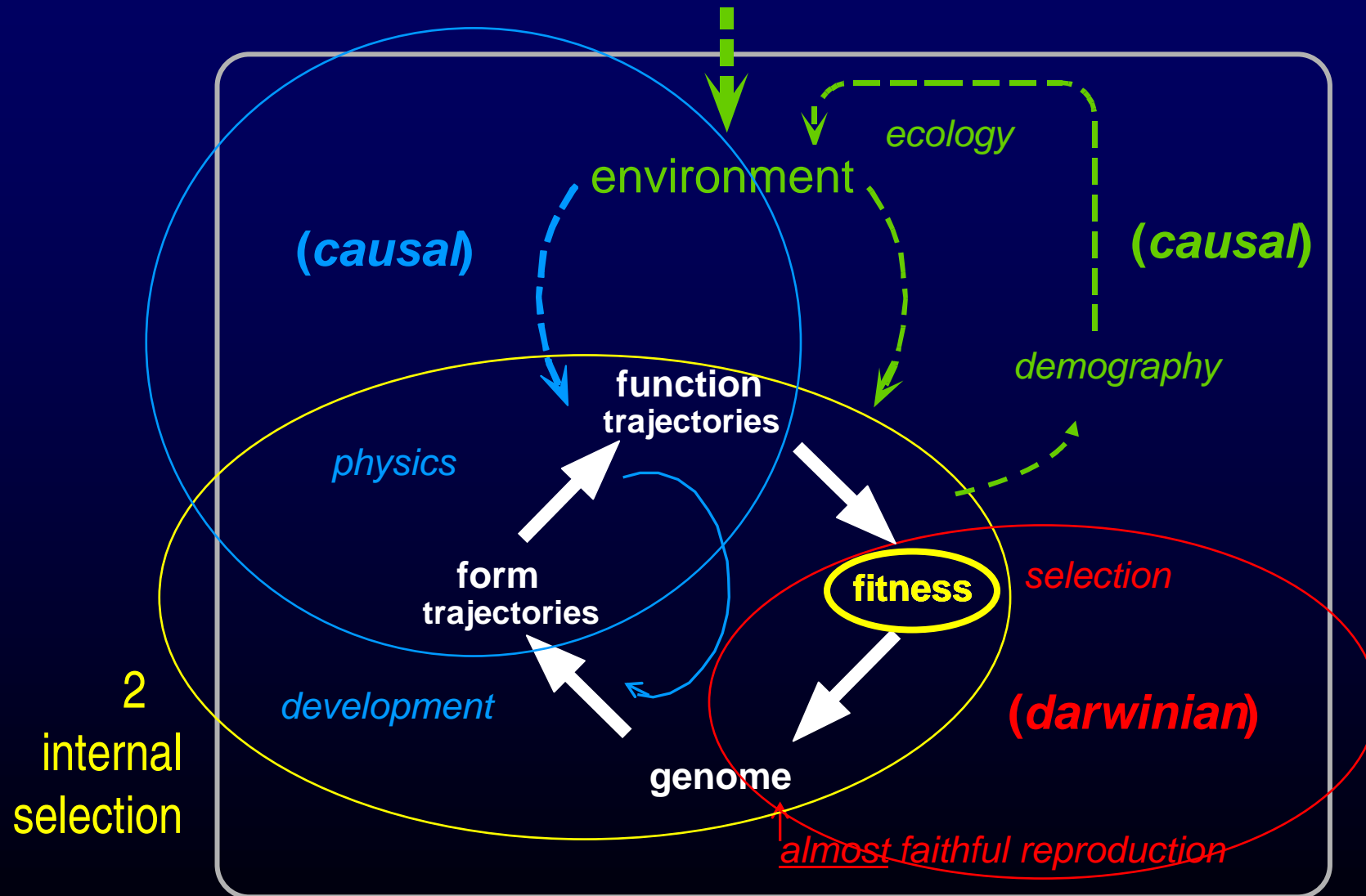
- ⌘ There is a discrepancy between the good job done by random models at the level of molecular evolution versus the domination of adaptive processes perceived by ecologists, functional morphologists, and the like.
- ⌘ This discrepancy nicely fits with the assumption of a great tangledness of the genotype 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 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.

**There is a need for intermediate abstractions.**

The ideas that follow are borrowed from a variety of people including Sir Ronald Fisher, Günther Wagner, Walter Fontana, Sergey Gavrilets, Arno Wouters, and Fritson Galis.



# constraints from development & morphology



# main topics of the 2nd part of the talk

---

## ⌘ internal selection

Origin: selection occurring so early in life that it is largely independent of the ecological feedback loop.

In our case: such that its effect on the fitness landscape is always the same.

## ⌘ the ridgy nature of the fitness landscape (both over phenotype and over genotype space)

→ “high fitness mazes”

## ⌘ the high dimension of both these spaces

# constructional morphology

---

- ⌘ Functional morphologists 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 slope of the ridges is the domain of ecology, their location is largely ecology independent.

# evolution of development research 1

---

⌘ The long term conservation of developmental units (homology, phylotypic stage) can only be due to strong stabilising selection.

[Mutations causing large pattern changes generally have many side effects with dire consequences for fitness.]

⌘ In general the fodder of selection are quantitative changes is the size or shape of homologous parts.

⌘  $\Rightarrow$  The picture emerging from evo-devo is roughly similar to that implicitly adhered to by morphologist.

# high dimensionality 1

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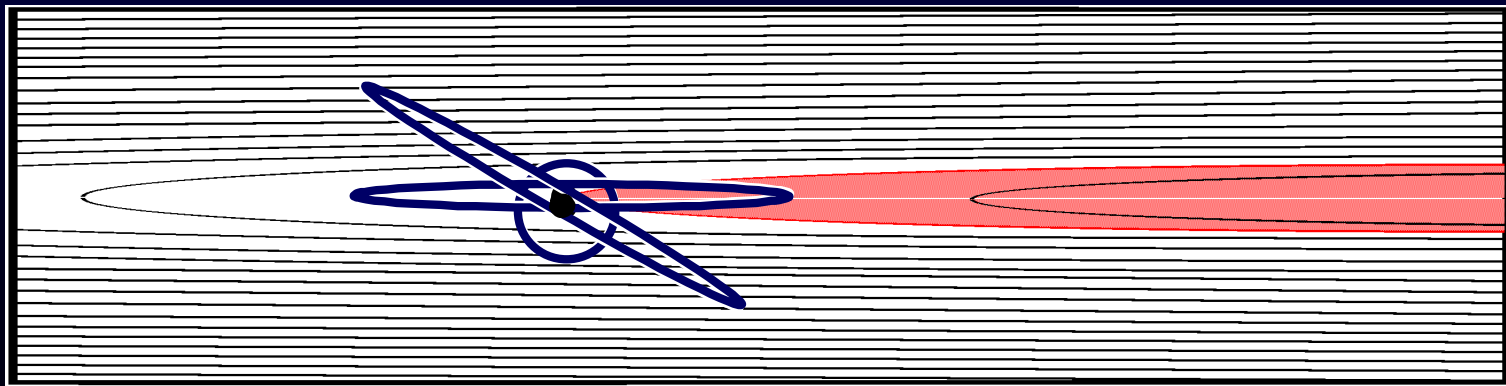
⌘ The trait spaces considered by morphologists, and evo-devo researchers have, in principle, very high dimension.

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.

# combining functional morphology & evo-devo

---

- ⌘ Developmental systems that produce relatively more mutational steps in the direction of the ridge will evolve much faster than systems that are not biased in such a manner.



# mechanism

---

⌘ Such a bias can occur when the development of an organ uses cues related to its later function.

## example:

⌘ In vertebrates, bones, muscles and nerve cells are modelled and/or grow in the embryo depending on their use.

# some data 1

---

⌘ Mammalian functional design evolved much faster than that of (indirectly developing) insects.

lowest and highest estimated divergence times in Ma:

Dipteran families:	179
330 Drosophila subgenera:	60
110 mammal orders:	38

70

This contrasts starkly with the fast speed of the evolution of e.g. resistance against agrochemicals in insects

relative to that in mammals

(due to their different population sizes and generation times)



## some data 2

---

⌘ In mammals teeth are exceptional, in that they develop ballistically, independent of their later function.

Teeth evolve so slowly that they are used to characterise the higher taxonomic levels, such as orders.

# speciation 2

---

⌘ High dimensional ridgyness also lies at the base of the usual ideas about **allopatric speciation**:

Separated populations independently wander around in the high fitness maze.

If confronted with each other, any mixed offspring ends up in the abyss.

# evolution of development research 2

---

- ⌘ The stabilising selection that underlies the long term conservation of developmental units necessarily leads to a great robustness of the developmental process.
- ⌘ This, and the tinkering nature of evolution, by itself will already cause a great tangledness of the genotype to phenotype map (but is by no means its only cause!).
- ⌘ In the language of fitness landscapes robustness translates into the existence of extensive near neutral sets in genotype space. ( → high fitness mazes)

# evolution of development research 2

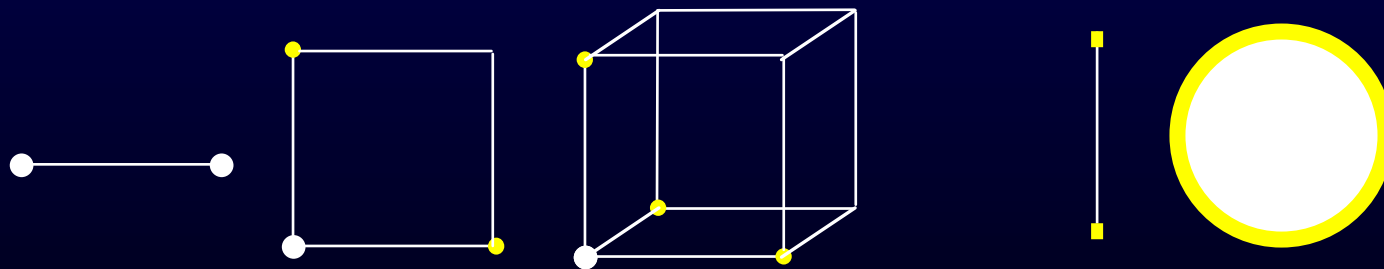
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- ⌘ Contrary to naive expectation, the robustness of parts of the developmental process cannot by itself conserve developmental units, or constrain their evolution.
- ⌘ The reason lies in the high dimensionality of genotype space.

# high dimensionality 2

---

In a very high dimensional space  
by far the most points in any set  
lie close to its boundary:



# further rationale 1

---

Most evolution probably amounts to a low pace tracking of environmental changes, interspersed with scarce punctuation events,

- ⌘ During the quasi-static periods the population state will “diffusionally ooze” within the neutral set, so that at a punctuation moment it is close to a lot of potential exits from the set.

## further rationale 2

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⌘ We are considering conservation over enormous time periods, in organisms potentially having enormous population sizes.

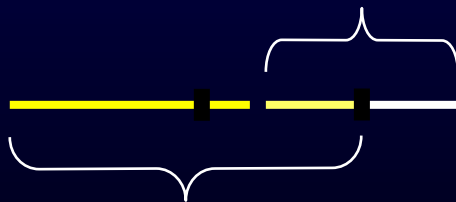


Neither the size nor the shape of the set of developmentally equivalent genotypes can keep the population from escaping from it, if this set is not surrounded by a fitness abyss (  $\Leftrightarrow$  very strong stabilizing selection).

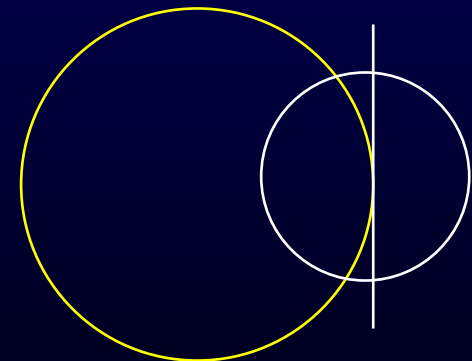
# high dimensionality 3

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

1 dimensional balls:



2 dimensional balls:



This effect disappears if we let the size of the smaller ball become smaller with increasing dimension.



# back to Adaptive Dynamics 1

---

⌘ ⇒ Almost all large mutational steps end up off-ridge, and are thus effectively aborted.



Two of the assumption often made in Adaptive Dynamics models, often will hold water:

- (1) relatively low dimensional trait space,
- (2) effectively rare mutational steps.

# back to Adaptive Dynamics 2

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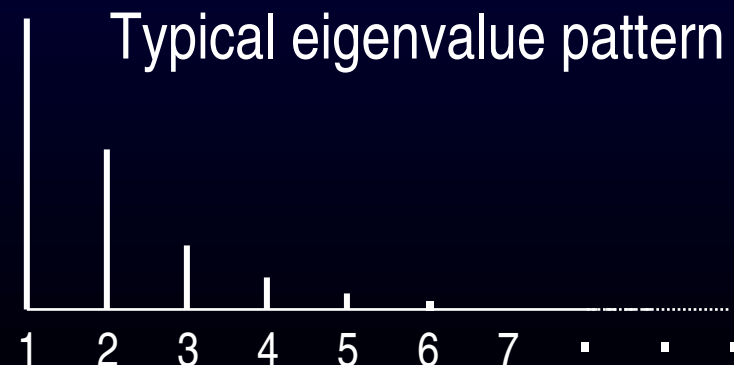
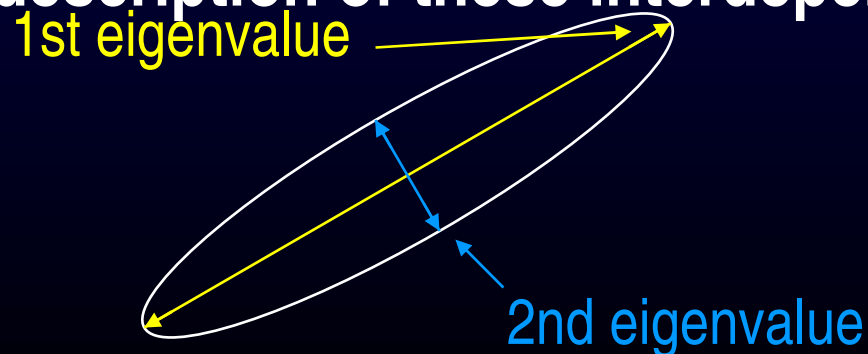
⌘ The third main assumption

(3) relatively small mutational steps

follows through a different argument:

Almost no covariance structure is fully rotationally symmetric due to interdependencies between traits.

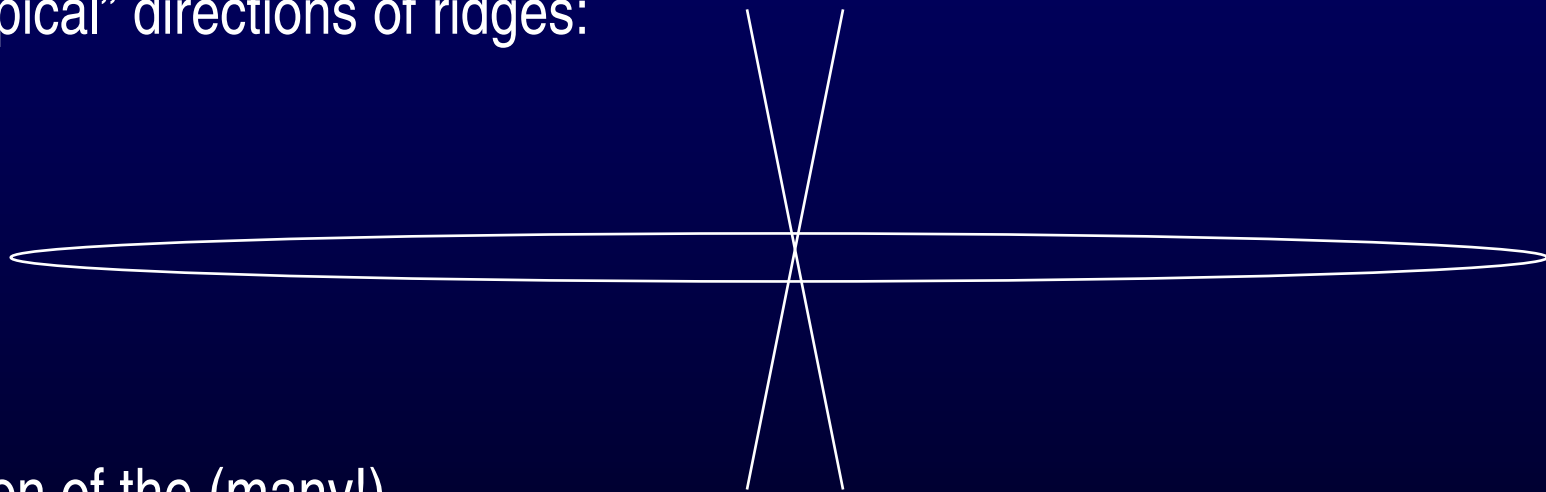
A principal component analysis can provide an organised description of these interdependencies:



# back to Adaptive Dynamics 2, continued

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“typical” directions of ridges:



direction of the (many!)  
remaining eigenvectors



direction of the first  
few eigenvectors

# Research issues

---

⌘ The consequences of high dimensionality combined with ridgyness are still far too little explored mathematically !

⌘ Some questions:

☒ How can we best characterise high fitness mazes?

☒ Are there options for a reduced characterisation of the genotype to phenotype map within a maze?

☒ How conducive to speciation are different combinations of genotype to phenotype maps and ecologies?

**The end**

