



The geometry of Meso-evolution

exploring the links
collecting mathematical
elements for a
postmodern synthesis
and
evo-devo



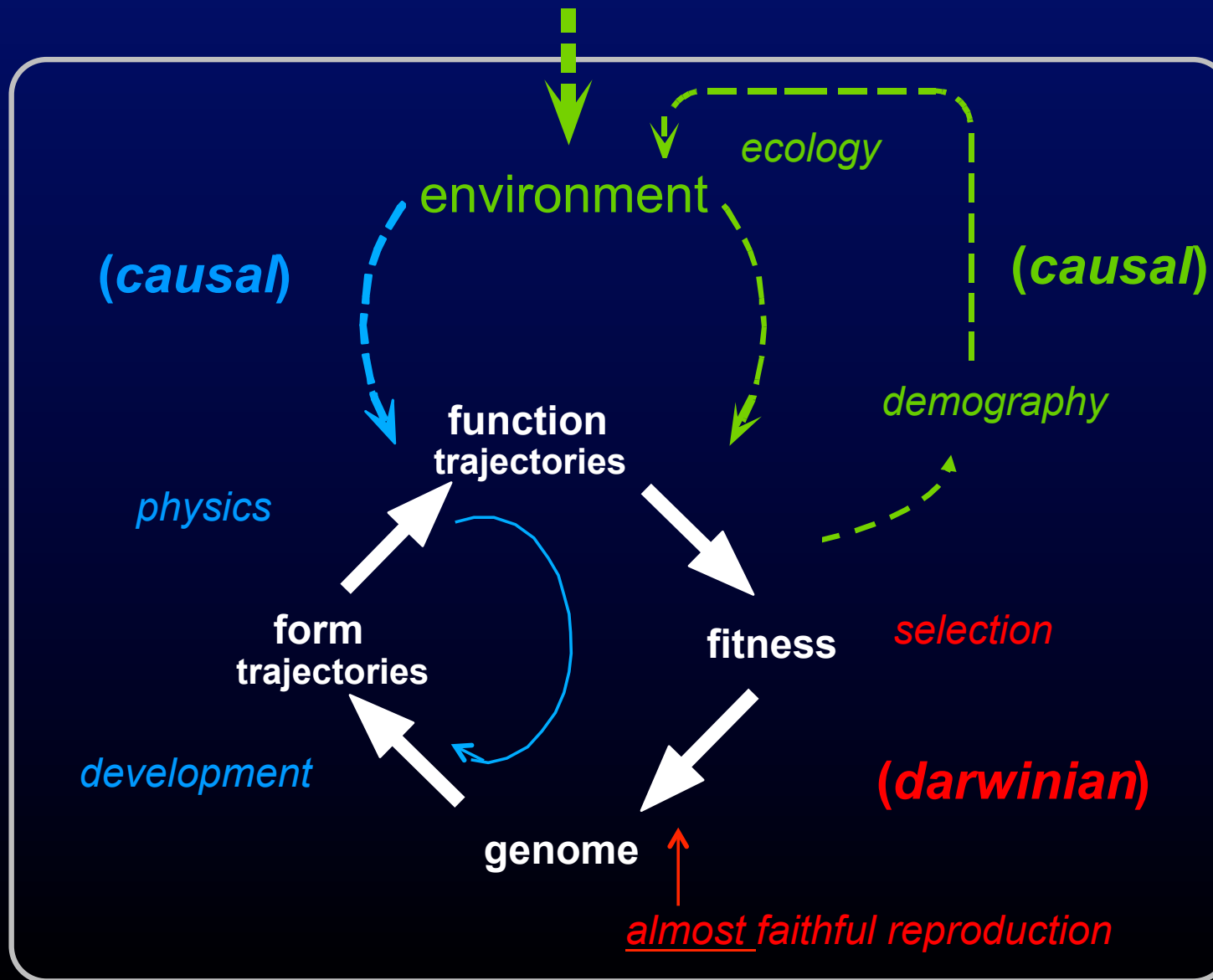
Hans Metz

EEP

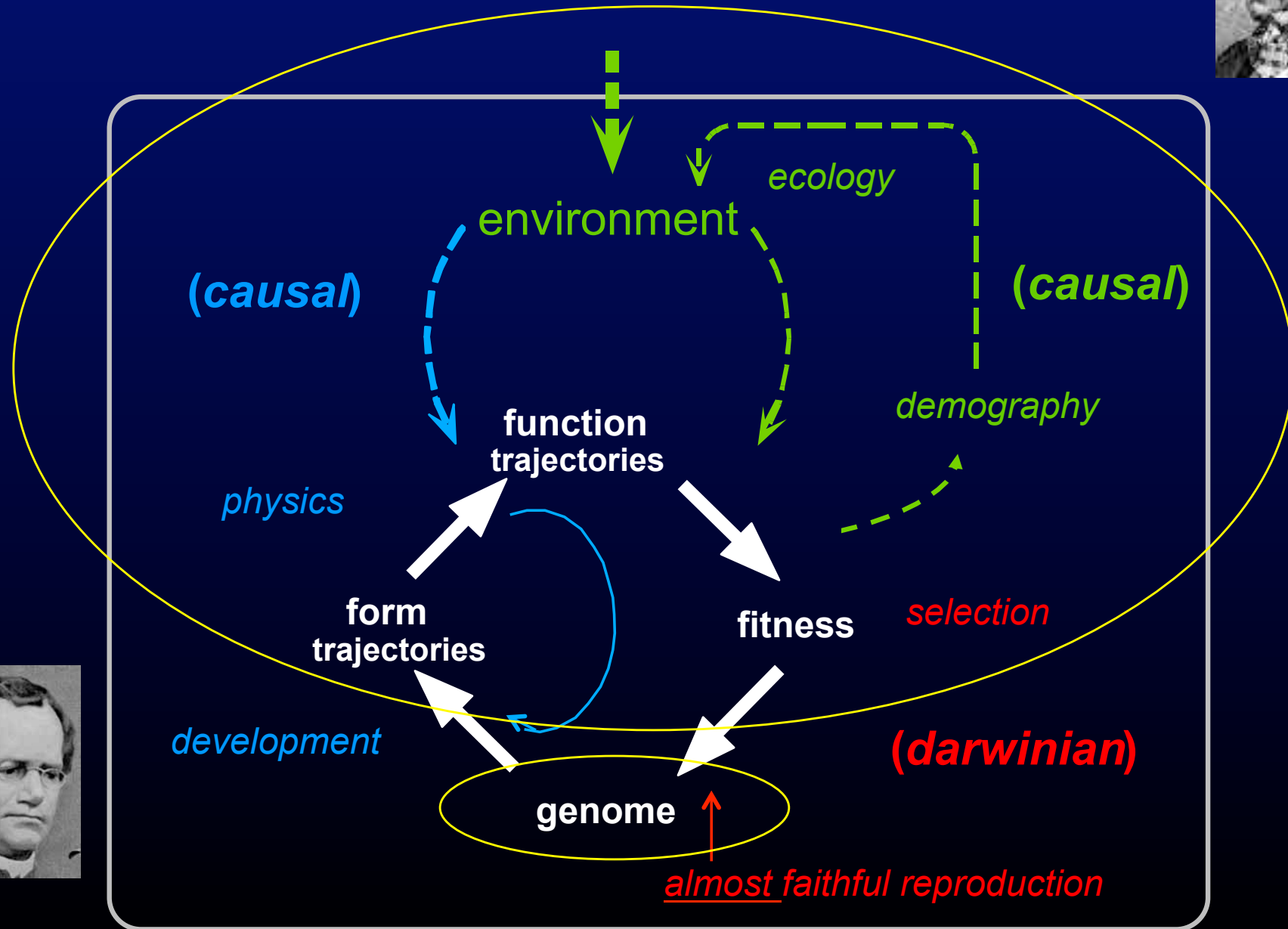
(formerly ADN)

IIASA

components of the evolutionary mechanism

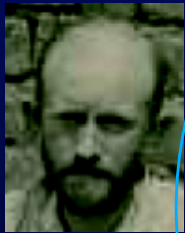


Darwin, Mendel

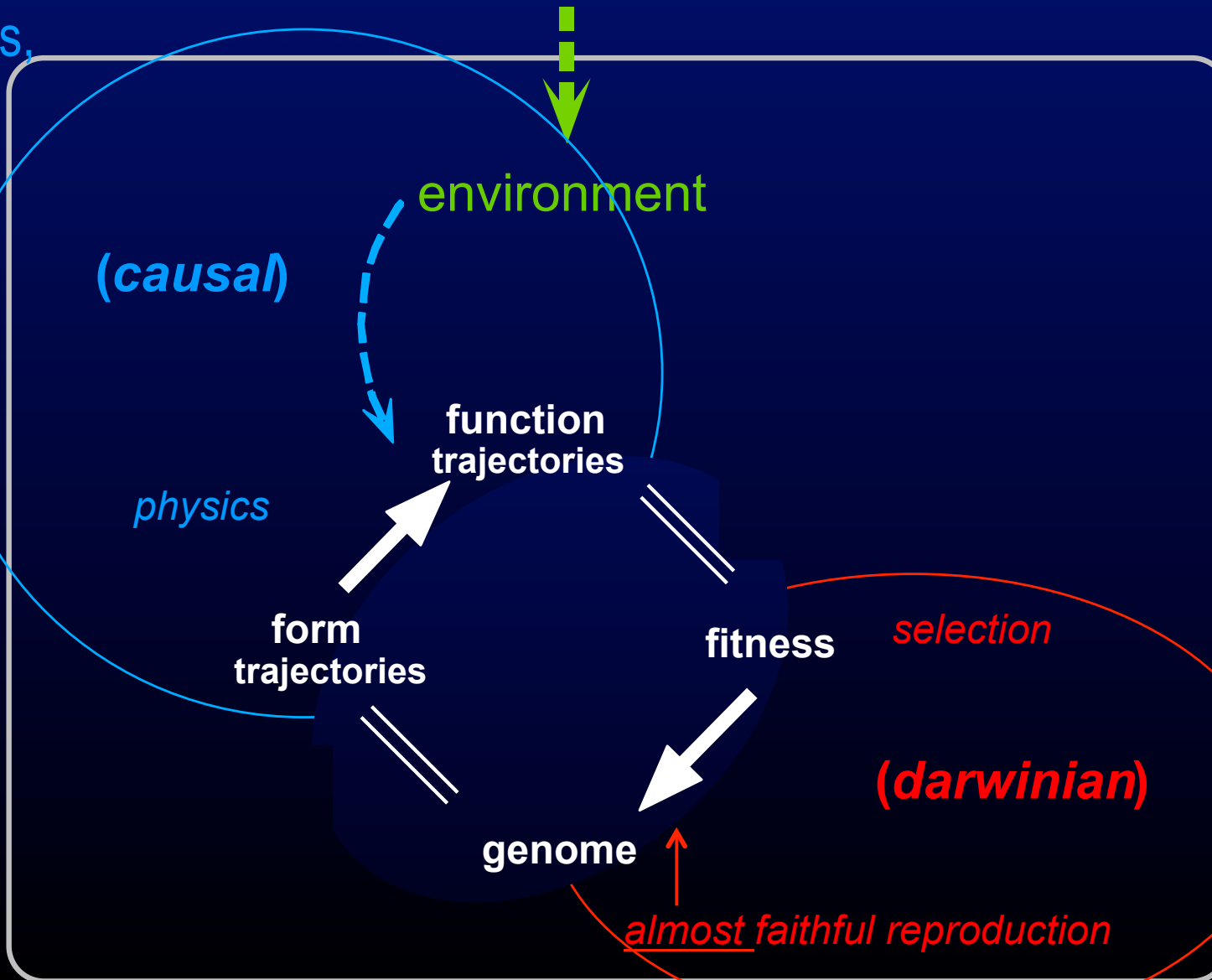
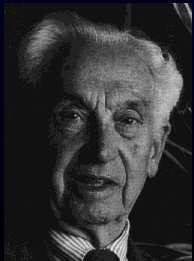


the Modern Synthesis: 1920 - 1950

paleontology,
systematics,
morphology



macro-
evolution

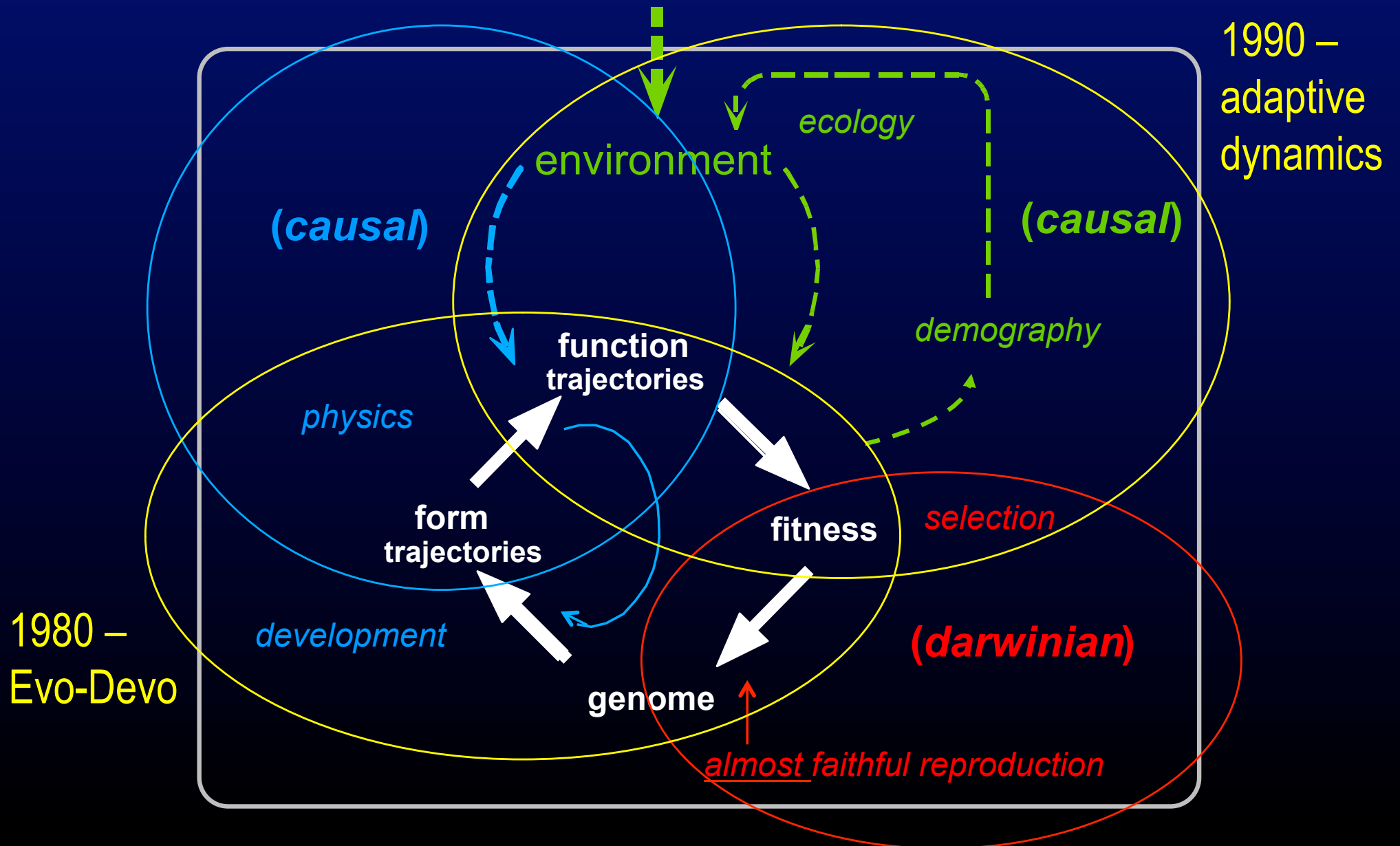


population
genetics



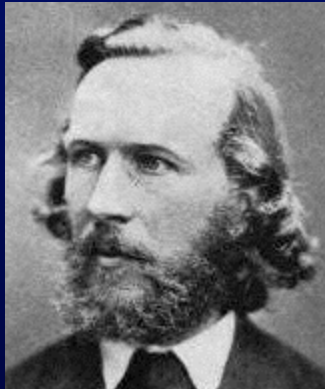
micro-
evolution

“postmodern” developments



various earlier roots

Evo-Devo:



Ernst H.P.A. Haeckel



Hans Spemann



Ivan I. Schmalhausen



Conrad H. Waddington

Adaptive Dynamics:



Russell Lande



W.D. (Bill) Hamilton



John Maynard Smith



Ilan Eshel

some contrasts

Evo-Devo

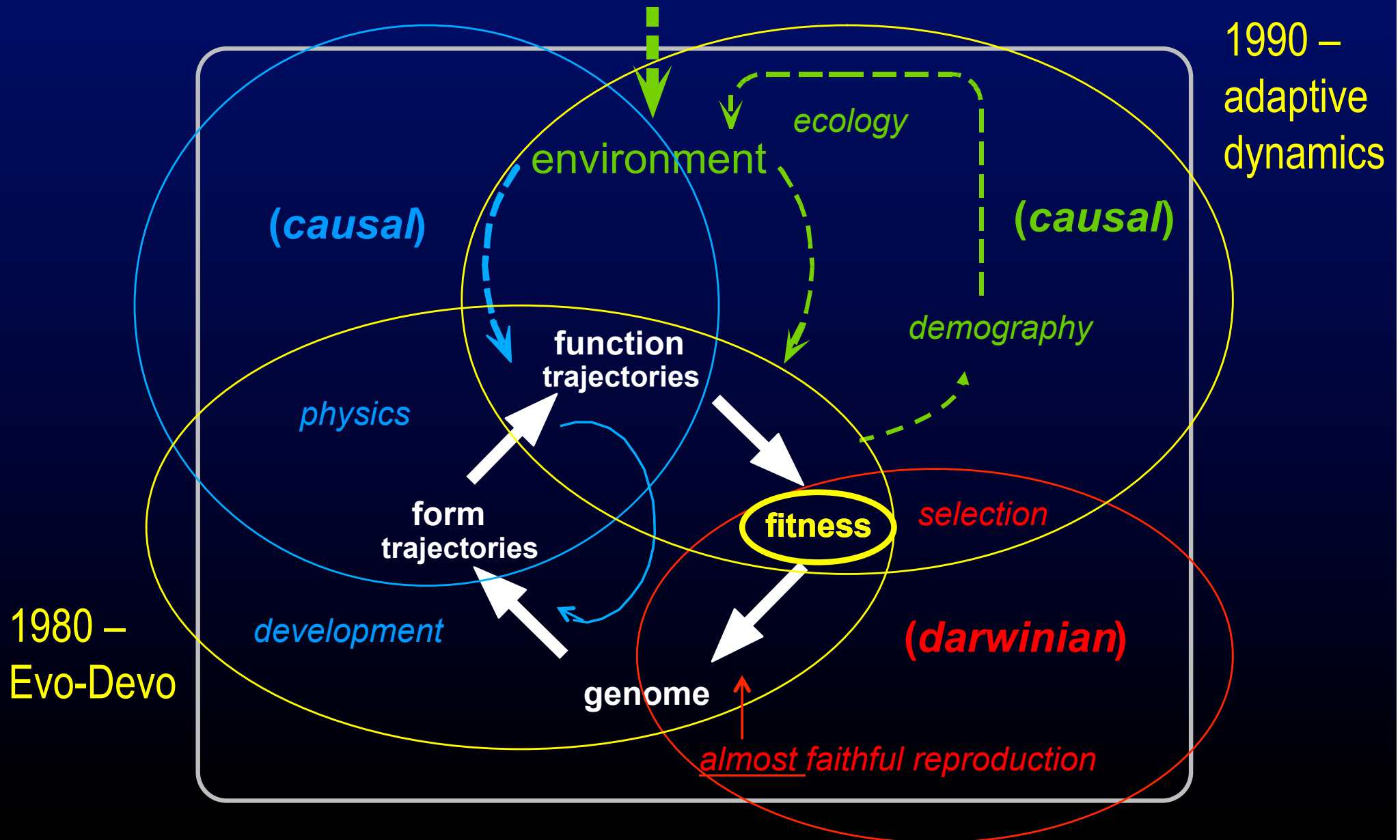
- focuses mainly on intra-individual processes
- macro-evolution
- the post-hoc explanation of realised patterns

Adaptive Dynamics

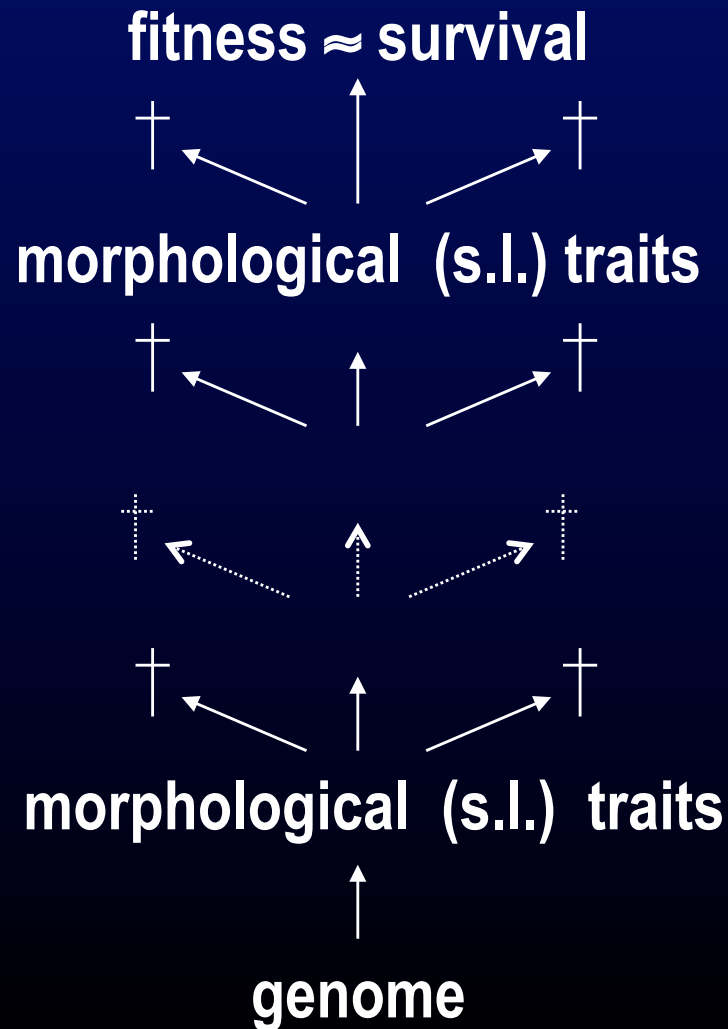
- focuses mainly on ecological processes
- meso-evolution
- prediction oriented theory

(AD was devised as a simple dynamic extension
of the evolutionary statics covered by ESS theory.)

the first connection



fitness: the intra-individual perspective



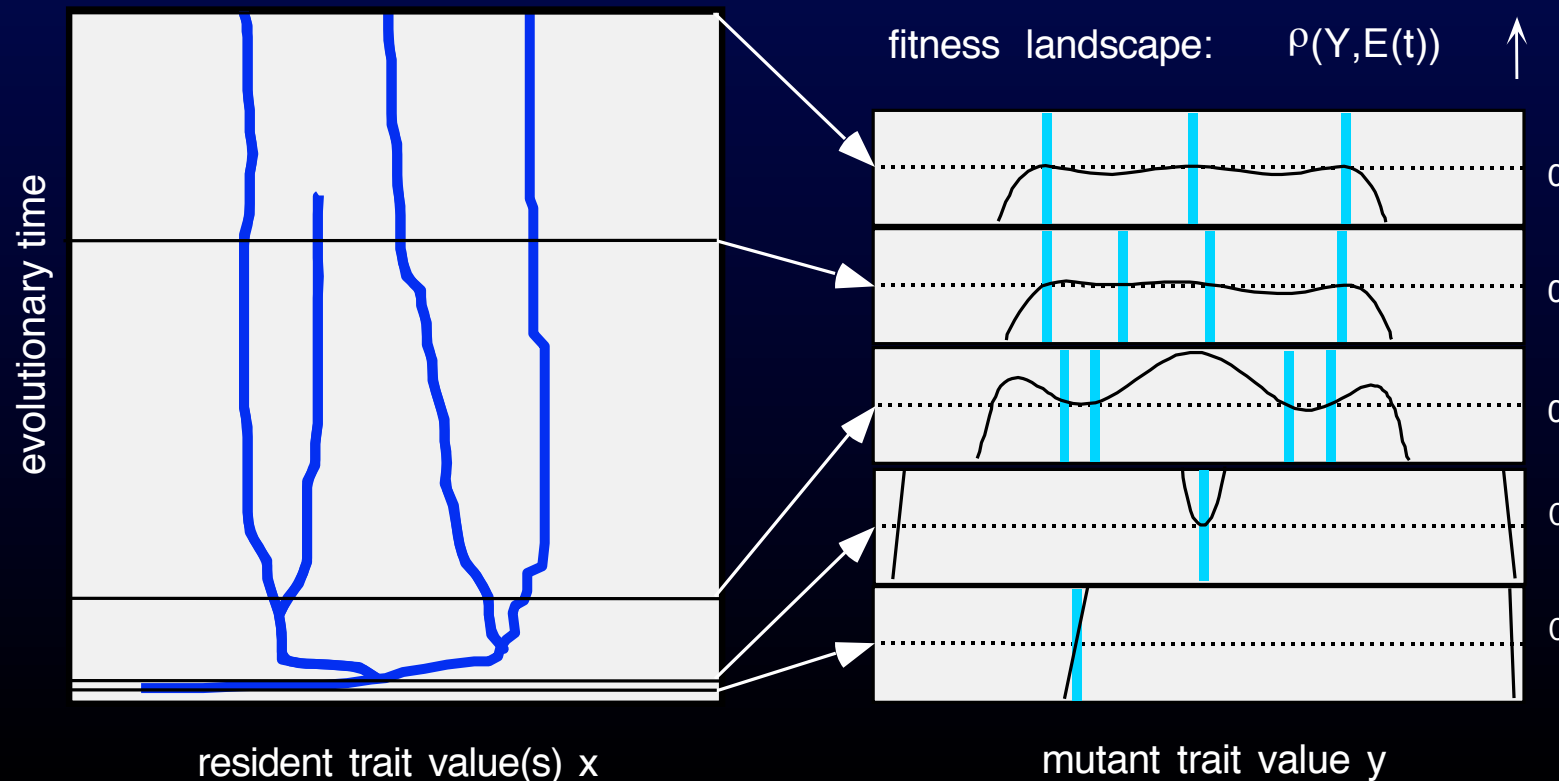
invasion fitness

- 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.

AD: fitness landscapes change with evolution

- 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.

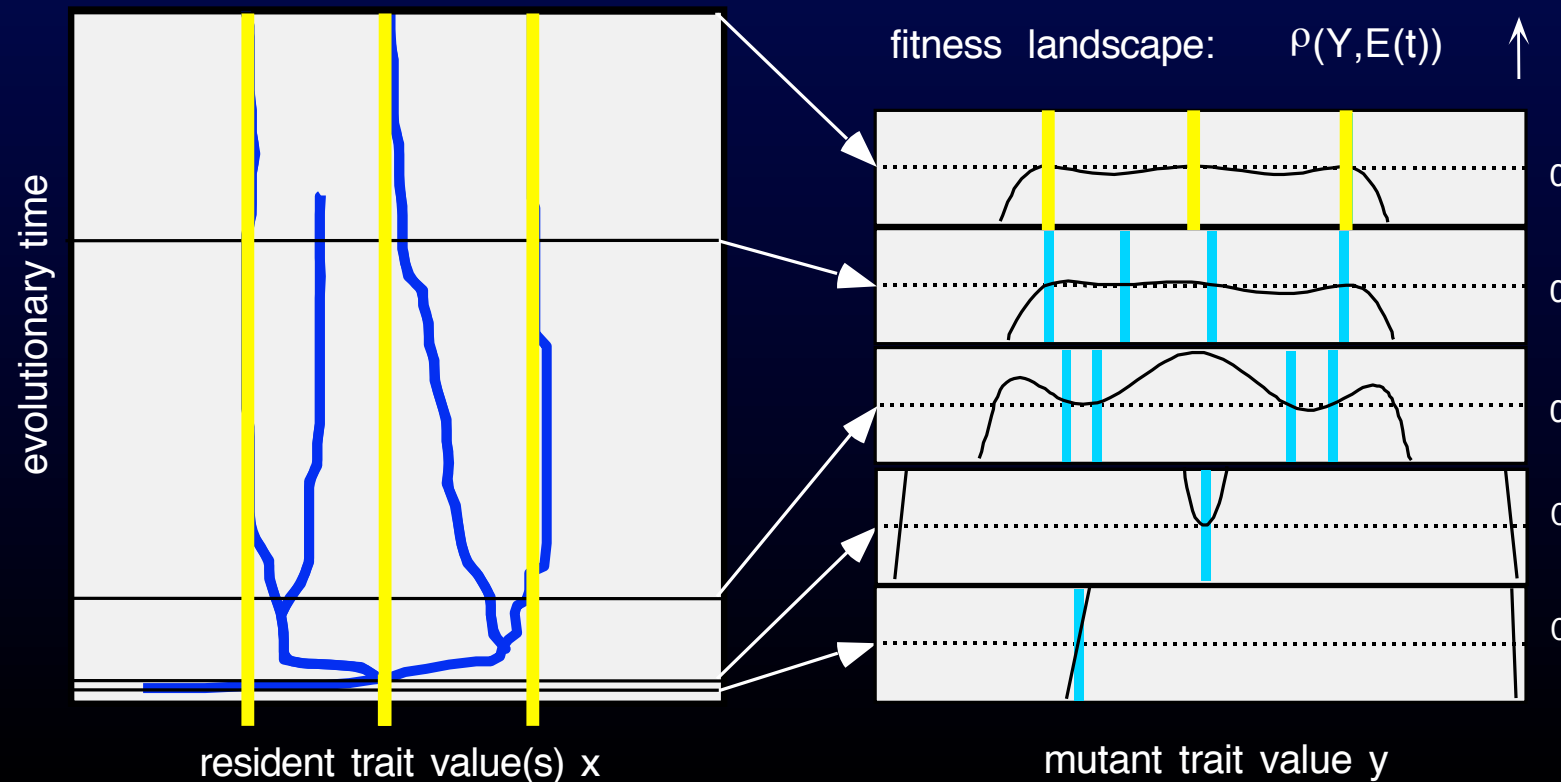


organisers of the landscape change



Evolutionarily Singular Strategies:

i.a. branching points and evolutionarily steady states



Evo-Devo: stresses fixed landscape features

■ internal selection

Origin of the name: selection occurring in the womb, and hence largely independent of the ecological feedback loop. **Generalisation:** any features of the fitness landscape that do not depend of the environmental condition (within the restrictions of a particular argument) are referred to as representing internal selection.

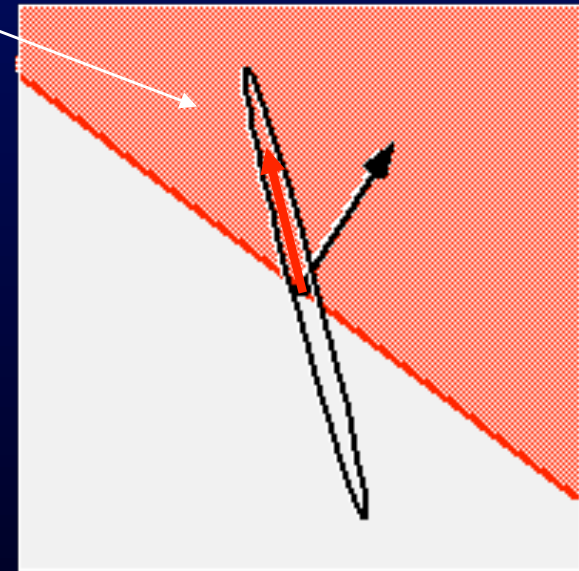
the second connection



“mutational covariances”

- In one dimensional trait spaces selection determines everything.

In higher dimensions
the distribution of mutational
effects also enters the equation.



⇒ For higher dimensional traits AD needs Evo-Devo !

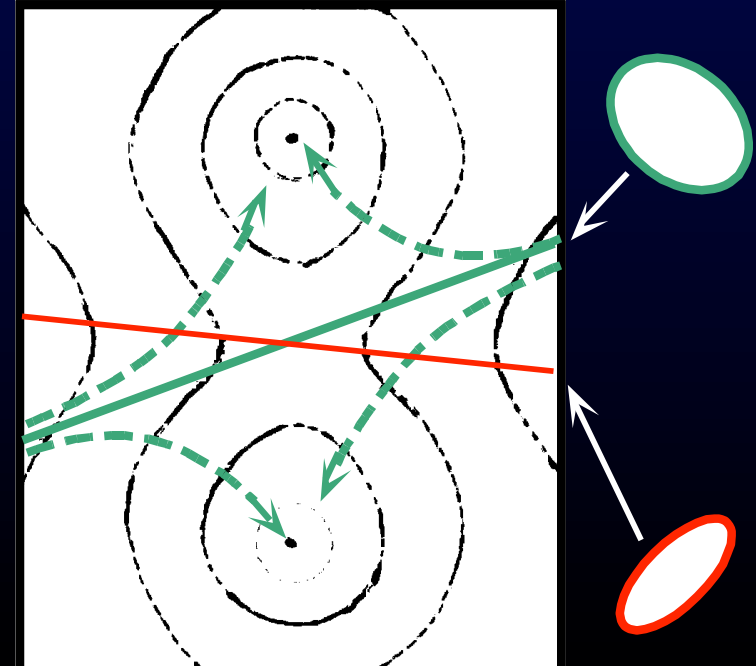
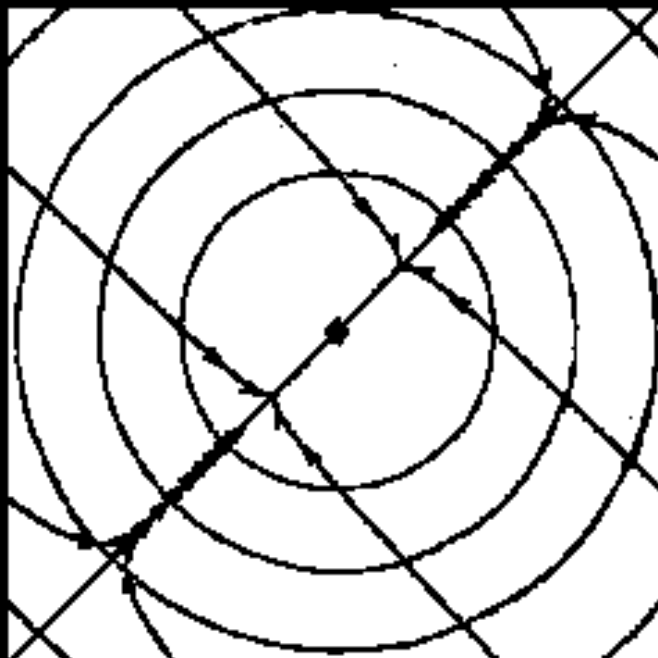
- The higher the dimension of the trait space, the larger the number of directions orthogonal to the selection gradient !

covariances can be very influential

Olof
Leimar



The mutational covariance matrix has an, often dominating, influence on the time scales of evolution, the basins of attraction of singular points, and even the attractiveness of singular points.



**So far we only considered
meso-evolutionary time scales.**

from meso- to macro-evolution



Evolution tinkers !

- 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.

from meso- to macro-evolution 2

- 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.

from meso- to macro-evolution 3

- So far the implicit assumption was that trait spaces have an 'ordinary' geometry.

- This need not be the case:

The geometry should reflect everything that can be generated by the developmental system.

- Yet, often simple Euclidian-like geometries seem to do a good job at least locally in trait space (and hence locally in time).

(The remainder of the talk is based on that presupposition.)

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

The cause probably has to be sought in the
tangledness of the genotype to phenotype map
(itself a result of
the evolved complexity of the developmental process)

some observational 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 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 way 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, in particular Arno Wouters, Fritson Galis, Günter Wagner and Sir Ronald Fisher.



essential theoretical ingredients

- **internal selection**

The focus will be on features of the fitness landscape that depend but little on the ecological feedback loop.

(Origin of the term: selection in the egg or womb, and hence little influenced by the world outside.)

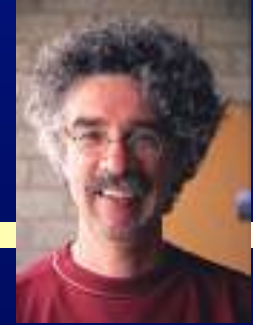
- **the ridgy nature of the fitness landscape**

(both over phenotype and over genotype space)

→ **“high fitness mazes”**

- **the high dimension of both these spaces**

functional biology & ridginess



- Functional biologist 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 zero
- 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.

evo-devo & rigidity: i.a. homology



- The long term conservation of developmental units can only be due to strong stabilising selection. (Think of homology, phylotypic stage.)
[Mutations causing large pattern changes generally have many side effects with dire consequences for fitness.]
- In general, ecological selection acts only on quantitative changes in the size or shape of homologous parts.
- ⇒ The picture emerging from evo-devo accords with that of the functional biologists.

effects of high dimensionality 1

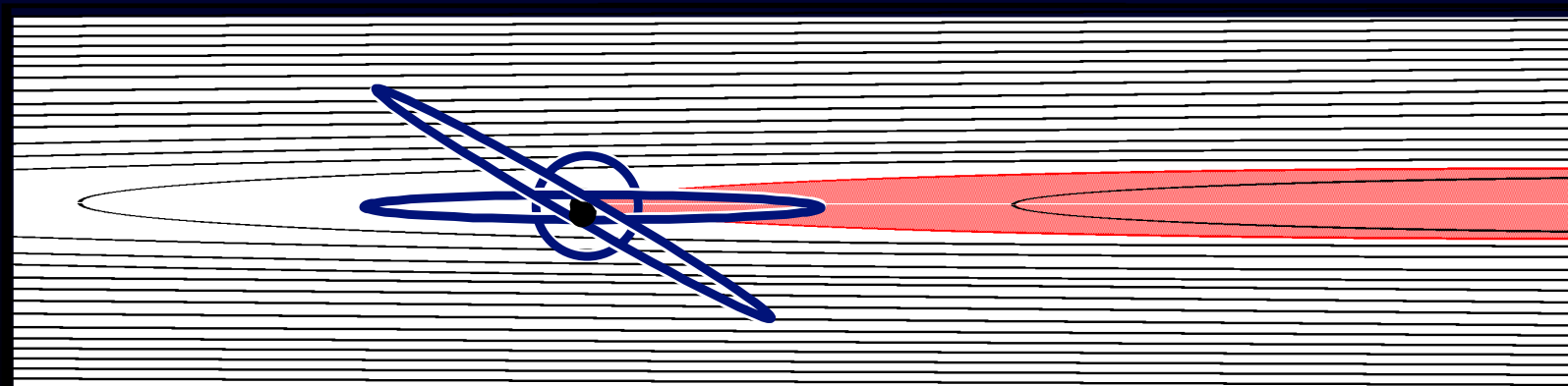
- The trait spaces considered by evo-devo researchers, morphologists, and the like have, in principle, very high dimension.

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.

ridgyness and development may conspire



- 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.



a mechanism leading to such a conspiracy

- 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

- Morphology evolved much faster in mammals than in insects, in particular indirectly developing ones.

lowest and highest estimated divergence times in Ma:

Dipteran families:

179

330

Drosophila

subgenera:

60

110

mammalian orders:

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.

rigidness cascades back through development

- The stabilising selection that underlies the long term conservation of developmental units should ultimately cause 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)

an Evo-Devo myth

However,

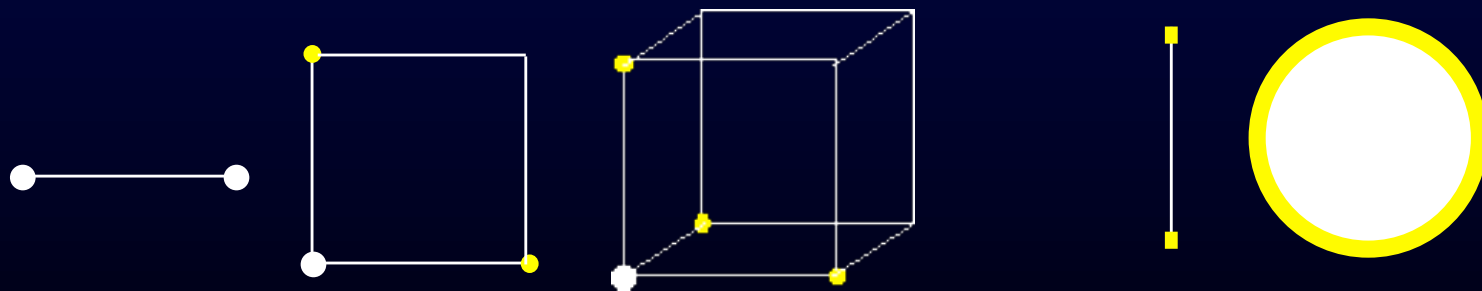
- Contrary to naive expectation, the robustness of parts of the developmental process cannot by itself conserve developmental units, or constrain their evolution.

⇒ Long term constraints have to come from selection !

- The reason lies in the high dimensionality of genotype space.

effects of high dimensionality 2

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



implications of
a high dimensional ridgyness
for the modeling of
meso-evolution

speciation as non-adaptive byproduct ?



- High dimensional ridgyness 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.

In random genotype to phenotype maps this phenomenon almost never occurs !

Another myth to be debunked ?

Or are evolved maps more conducive to speciation ?

effects of high dimensionality 3

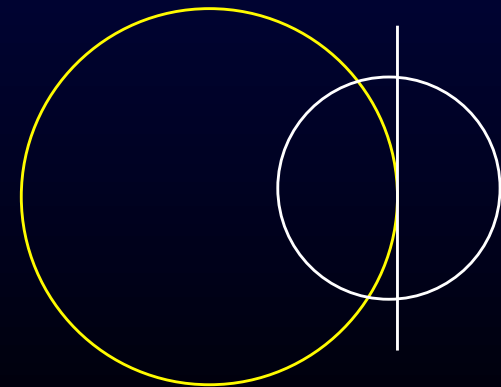


The ratio of the size of the intersection of two balls, with constant radii and the distance of their centers equal to the largest radius, to the size of the smallest ball rapidly decreases when the number of dimensions increases.

1 dimensional balls:



2 dimensional balls:



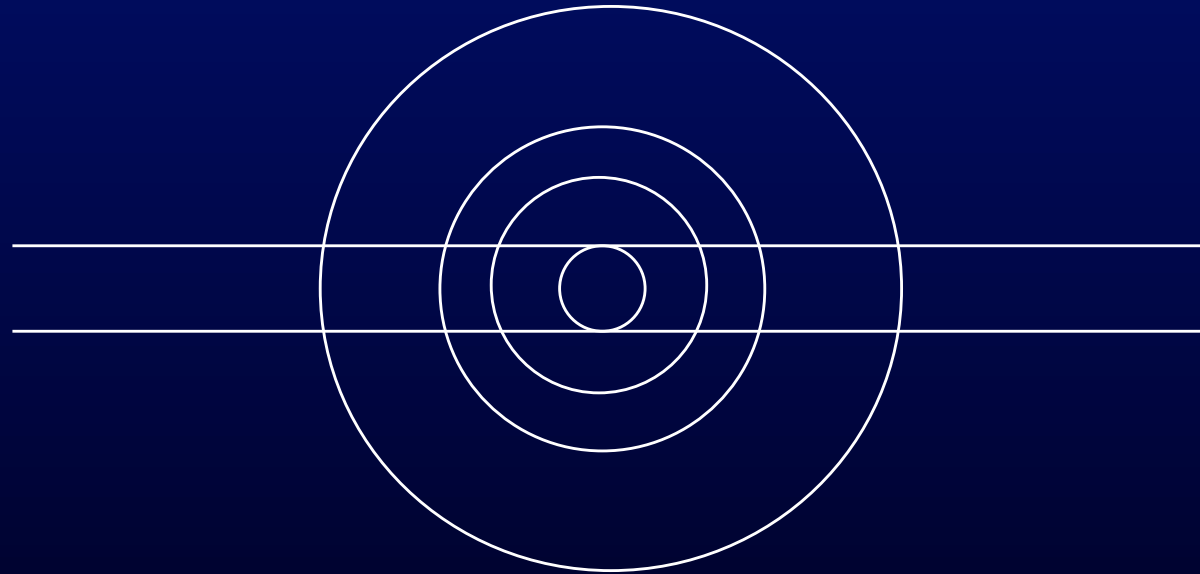
a justification of adaptive dynamics

- \Rightarrow Almost all mutational steps end up off-ridge, and are thus effectively aborted.



- The two main assumptions underlying the adaptive dynamics approach often will hold water:
 - (1) effective trait spaces are relatively low dimensional
 - (2) beneficial mutations are effectively rare

a justification of adaptive dynamics, cont'd



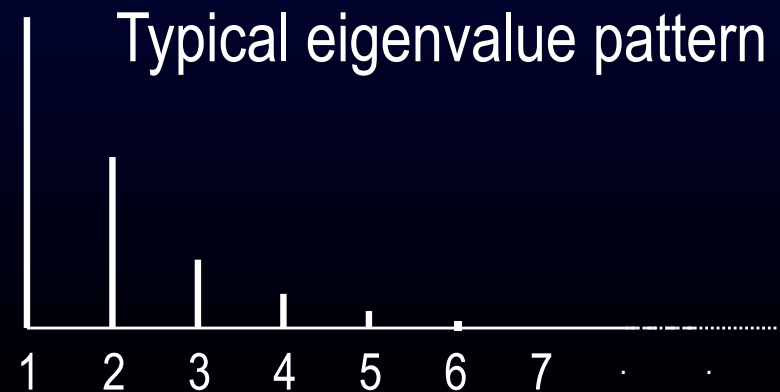
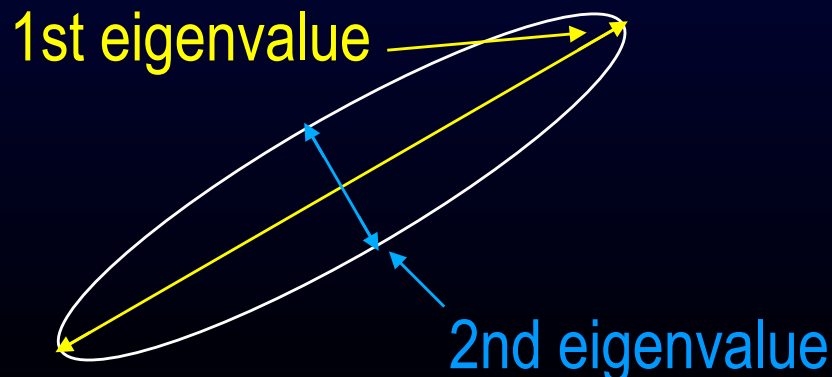
- The third main assumption of adaptive dynamics (3) effective mutational steps are relatively small also follows.

covariances make evolution even more gradual

Taking generally observed features of the developmental process into account strengthens the argument even further:

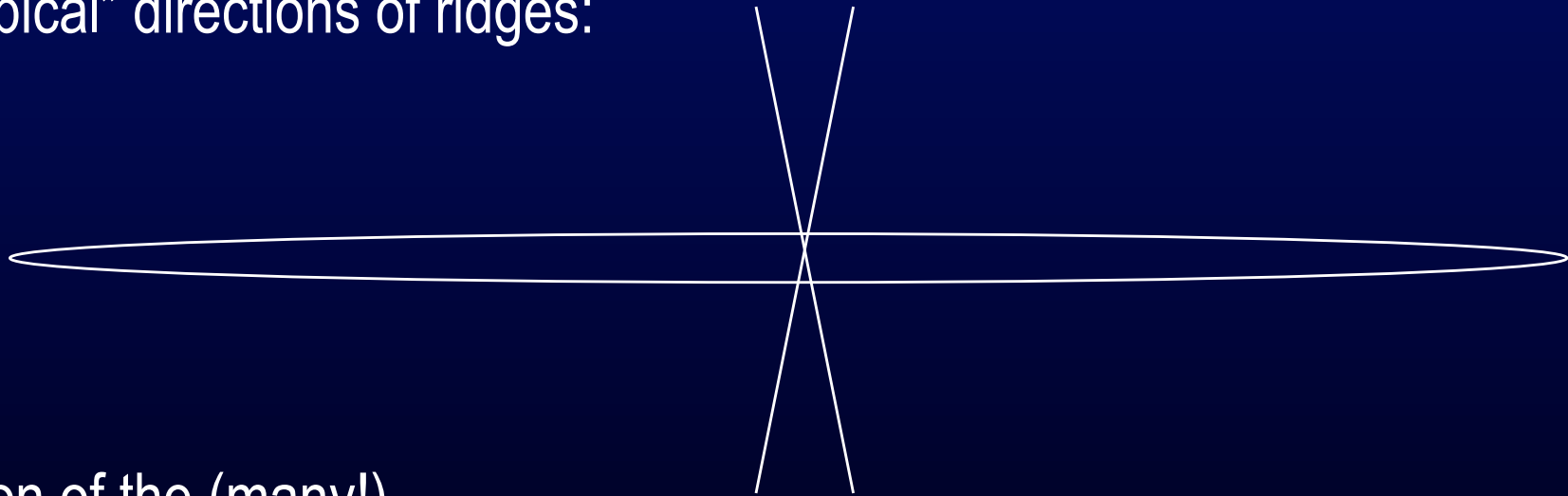
Almost no covariance structure is fully rotationally symmetric due to interdependencies between traits.

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



covariances make evolution even more gradual

“typical” directions of ridges:



direction of the (many!)
remaining eigenvectors



direction of the first
few eigenvectors



The End ?

2nd myth?: punctuated equilibria



Introduced by Eldredge & Gould, based on observations, and then ascribed by them to “morphological revolutions”

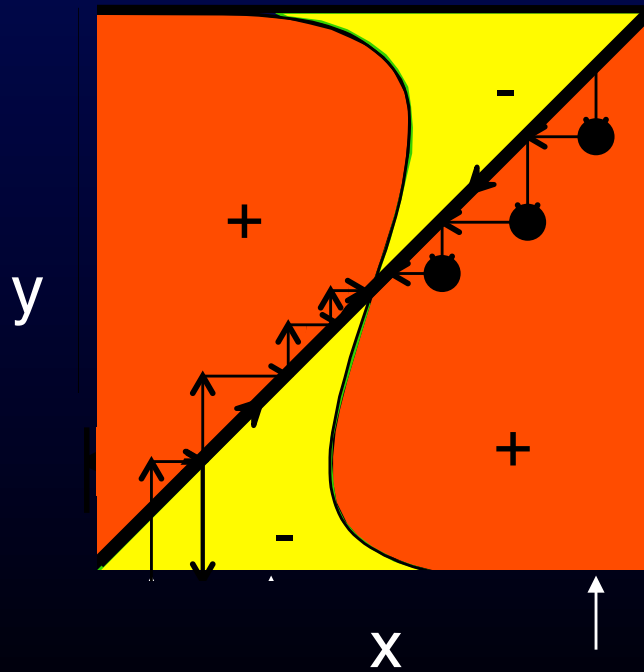
Objections and an alternative:

- The morphological scale involved is usually too small for developmental revolutions to be a plausible cause.
- Punctuated equilibria are common. There is little reason to expect that much scope for developmental revolutions.
- The time scale is at the upper end of the meso-evolutionary one, where adaptive dynamics predicts the common occurrence of ecologically driven punctuated equilibria.

short adaptive dynamics refresher

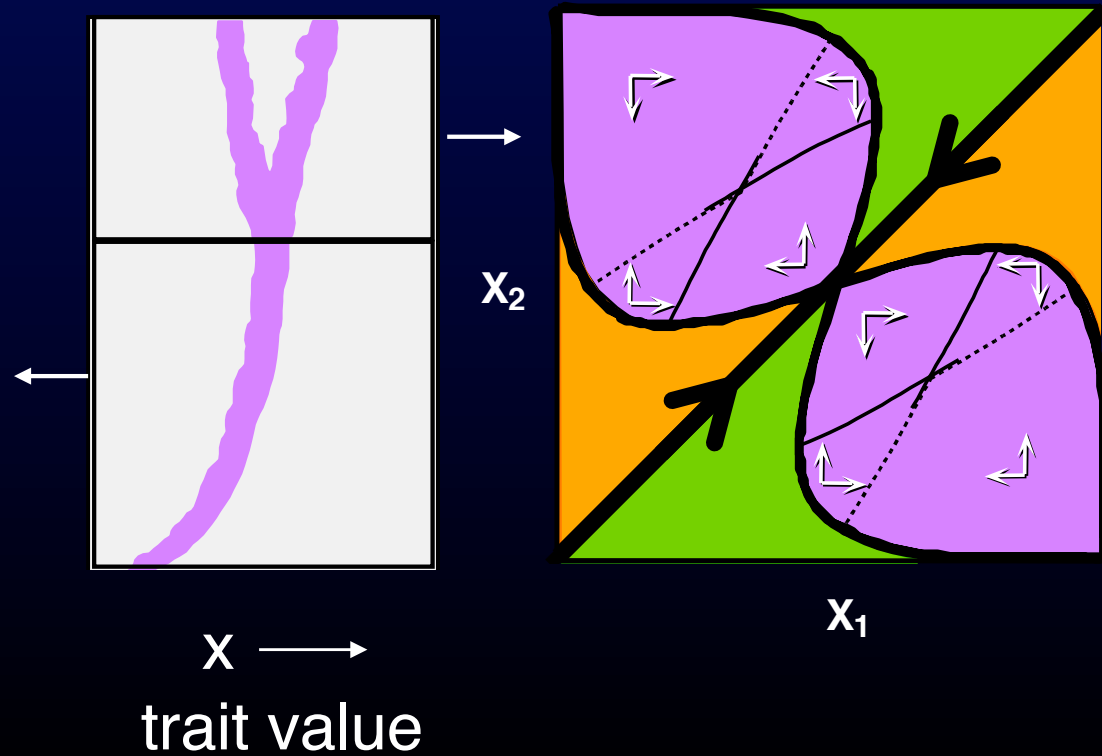
Pairwise Invasibility Plot

PIP



Trait Evolution Plot

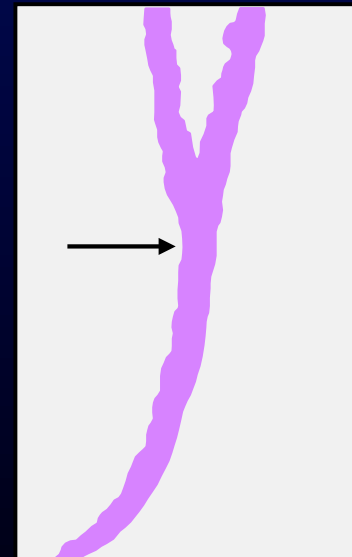
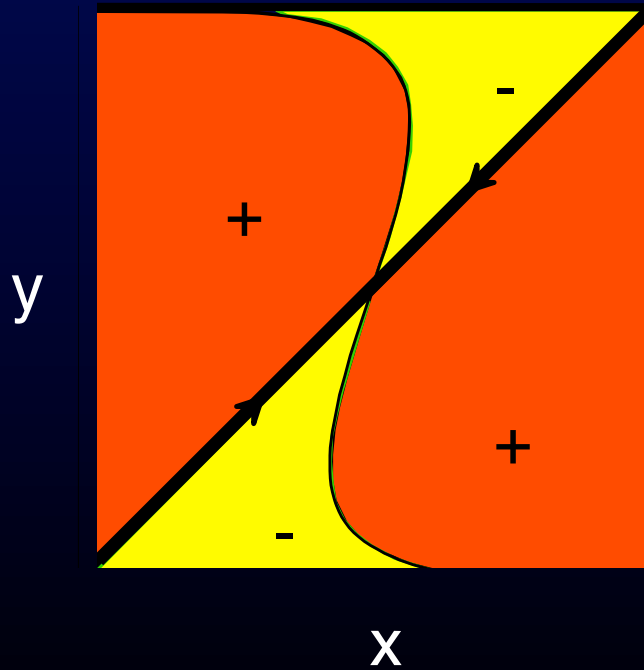
TEP



short adaptive dynamics refresher

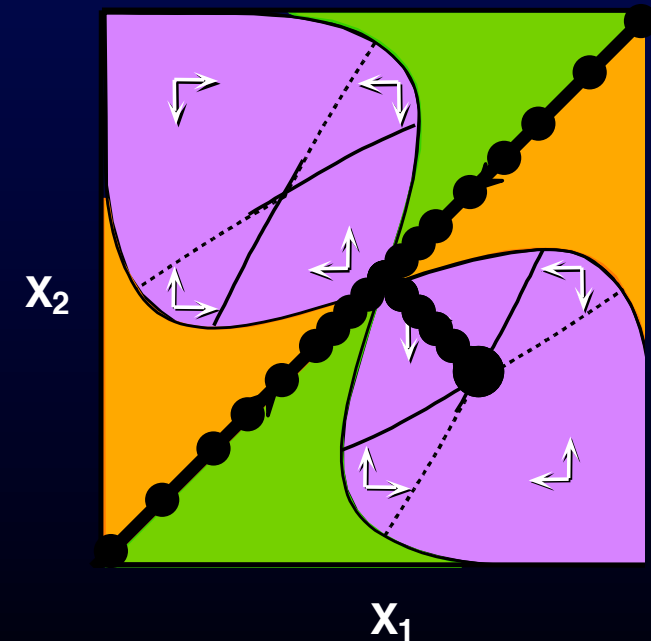
Pairwise Invasibility Plot

PIP



Trait Evolution Plot

TEP

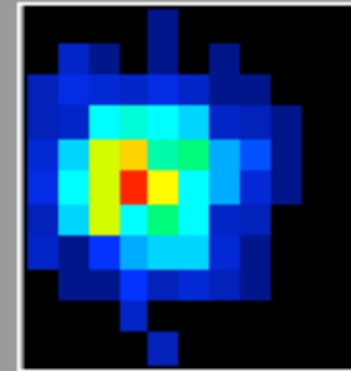
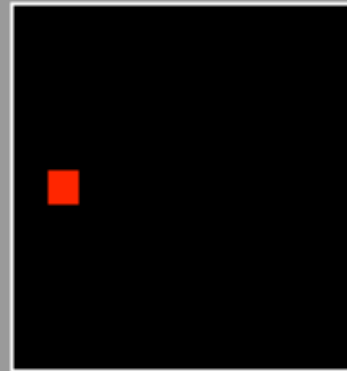
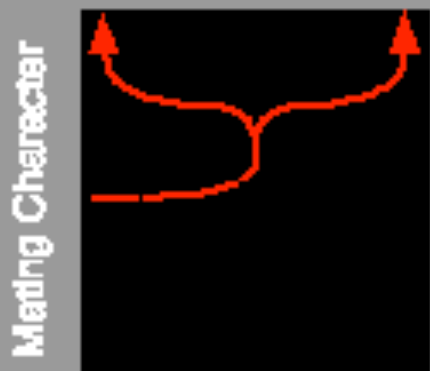


x →
trait value

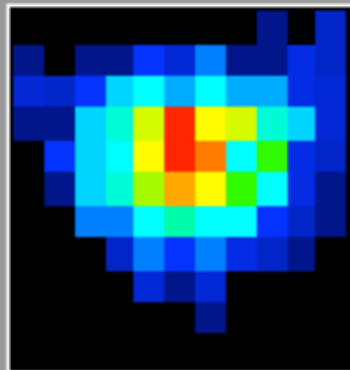
short adaptive dynamics refresher

branching in a Mendelian world

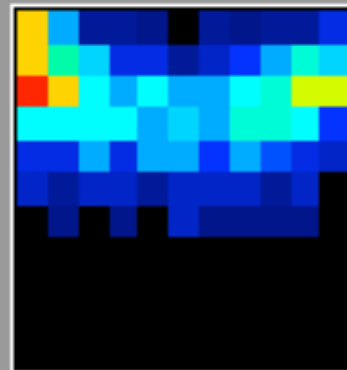
Summary



Ecological Character



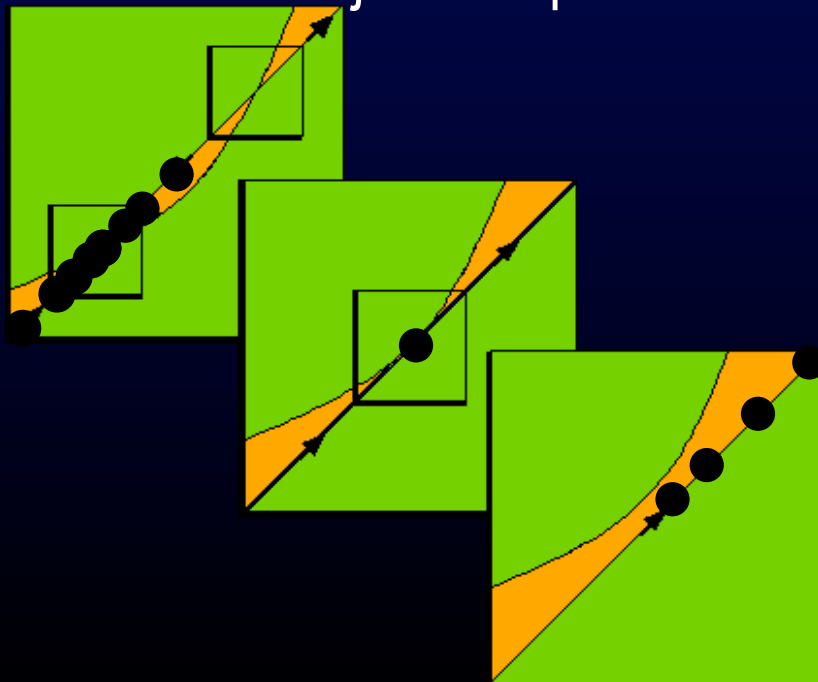
Simulation



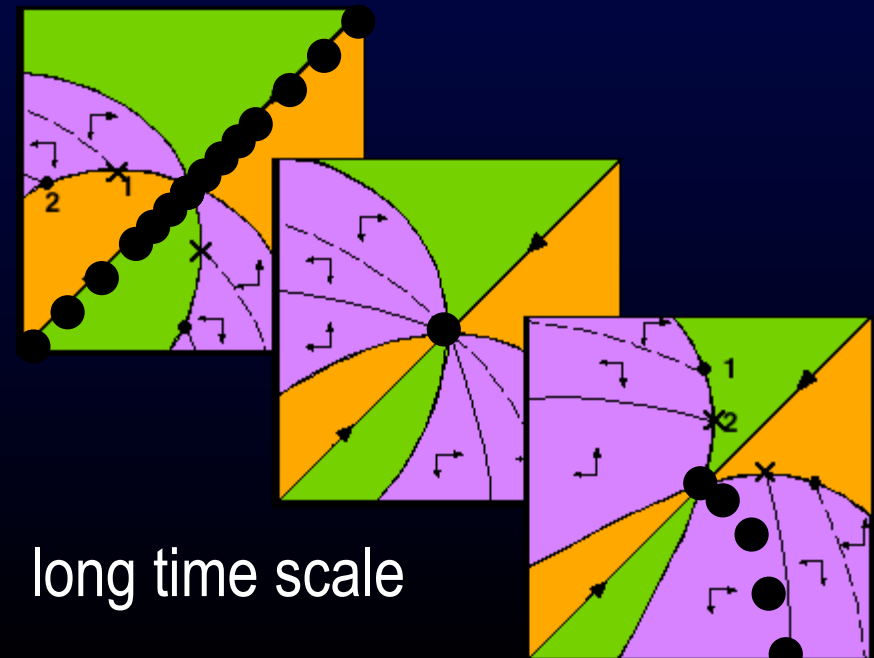
two types of punctuated equilibria

- 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.

“just so” punctuation



starting with speciation



long time scale



The End !





Attempts to contribute to a postmodern synthesis

explorations in the interface between
meso- and macro-evolution



Hans Metz

EEP

(formerly ADN)

IIASA

the seventies

