PREDICTION, OPTIMIZATION, CHAOS: THE ROLE OF FITNESS

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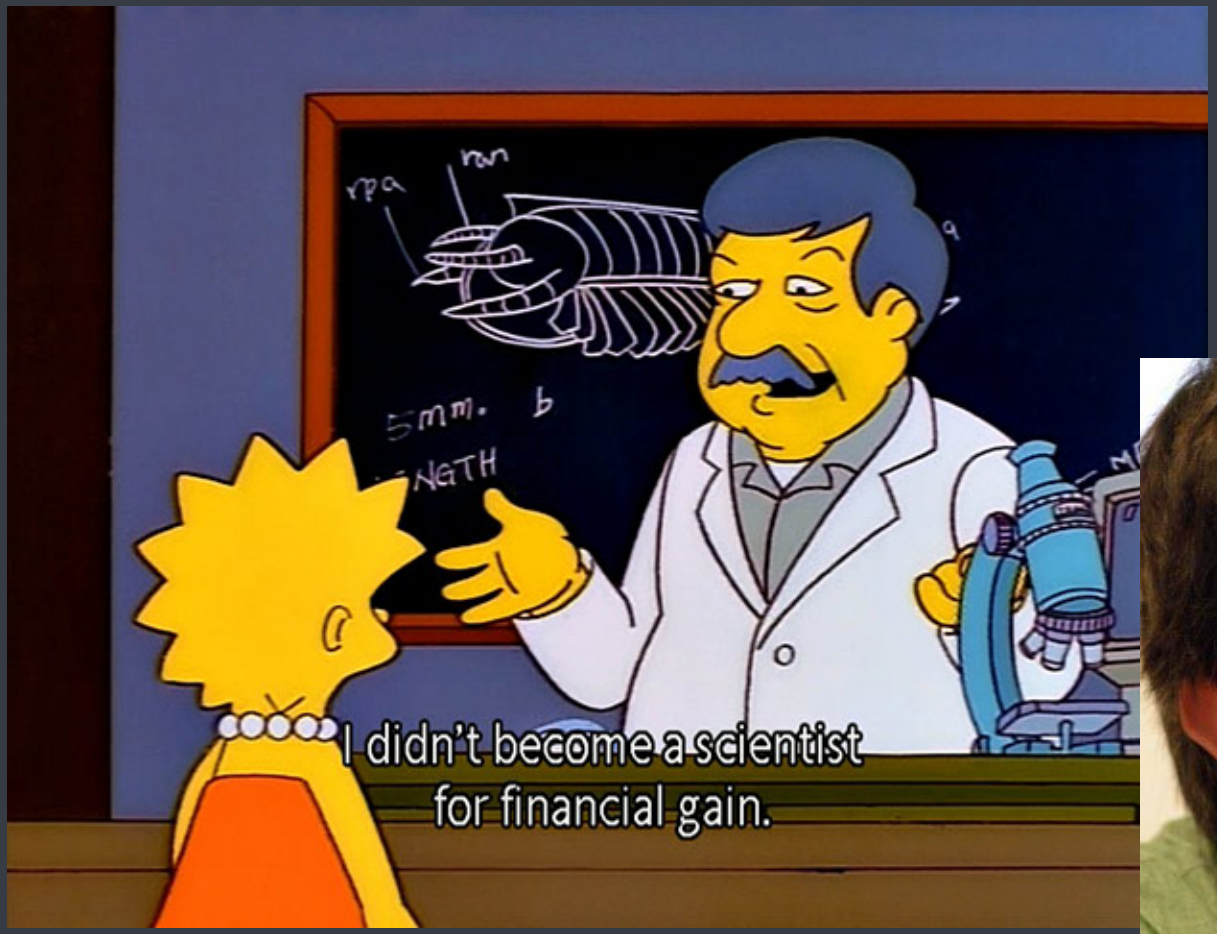
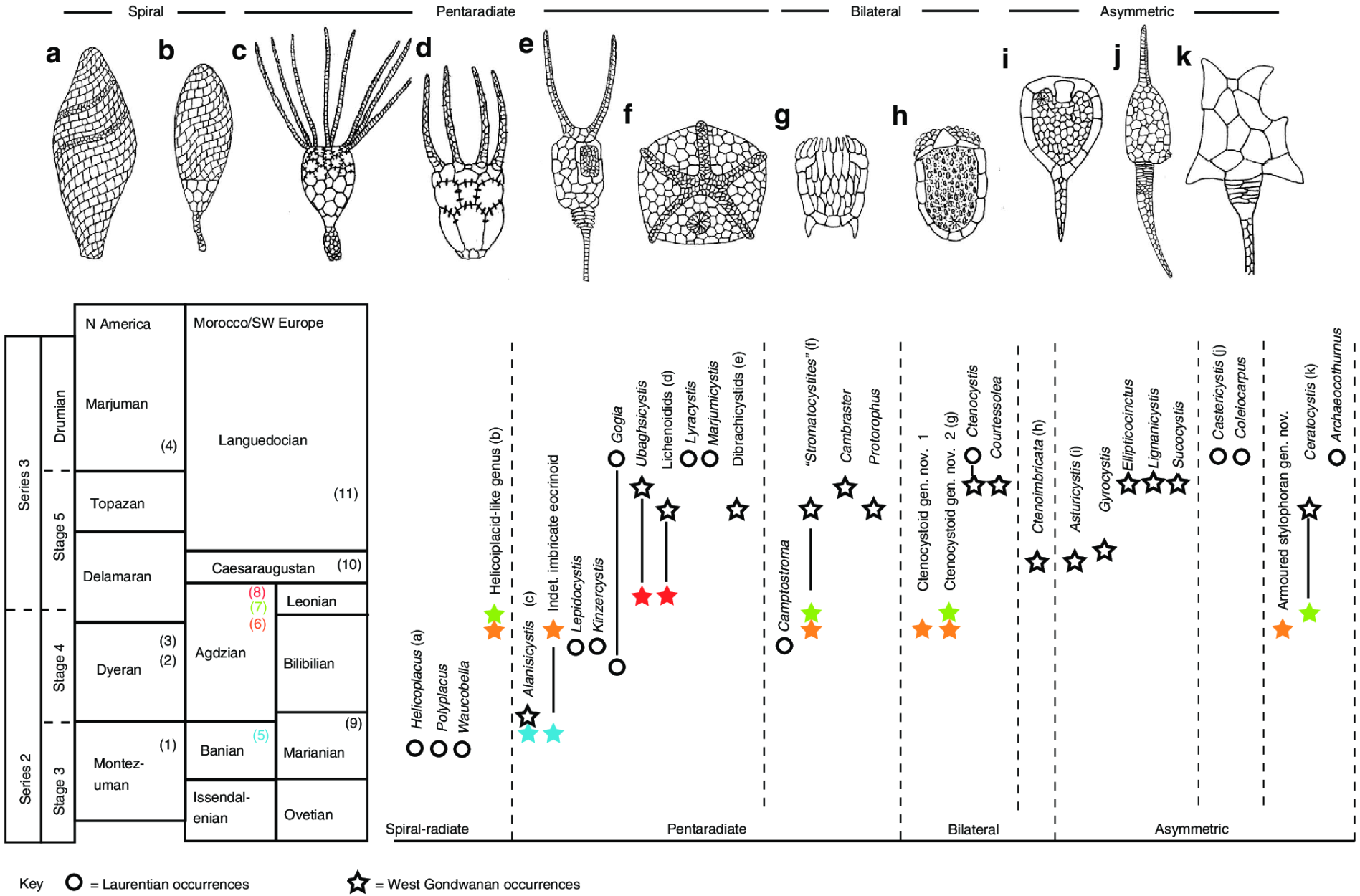

5mm. b
I didn't become a scientist
for financial gain.



Smith et. al., 10.1038/ncomms2391

A FOUNDATIONAL PERSPECTIVE?

Brit. J. Phil. Sci. **64** (2013), 851–881

A New Foundation for the Propensity Interpretation of Fitness

Charles H. Pence and Grant Ramsey

ABSTRACT

The propensity interpretation of fitness (PIF) is commonly taken to be subject to a set of simple counterexamples. We argue that three of the most important of these are not counterexamples to the PIF itself, but only to the traditional mathematical model of this propensity: fitness as expected number of offspring. They fail to demonstrate that a new mathematical model of the PIF could not succeed where this older model fails. We then propose a new formalization of the PIF that avoids these (and other) counterexamples. By producing a counterexample-free model of the PIF, we call into question one of the primary motivations for adopting the statisticalist interpretation of fitness. In addition, this new model has the benefit of

$$F = \exp\left(\lim_{t\to\infty} \frac{1}{t} \int_{\omega\in\Omega} \Pr(\omega) \cdot \ln(\phi(\omega, t))\, d\omega\right)$$

DEMOGRAPHIC WEAK ERGODICITY

Fine details of the initial state of the individual organism at issue must disappear in the limit of large times (Tuljapurkar and Orzack, 1980)

or

Two organisms experiencing the same selective history must have a constant ratio of fitness values for large times (Seneta, 1981)

CHAOTIC DYNAMICS

doi:10.1111/evo.12354

CHAOS AND UNPREDICTABILITY IN EVOLUTION

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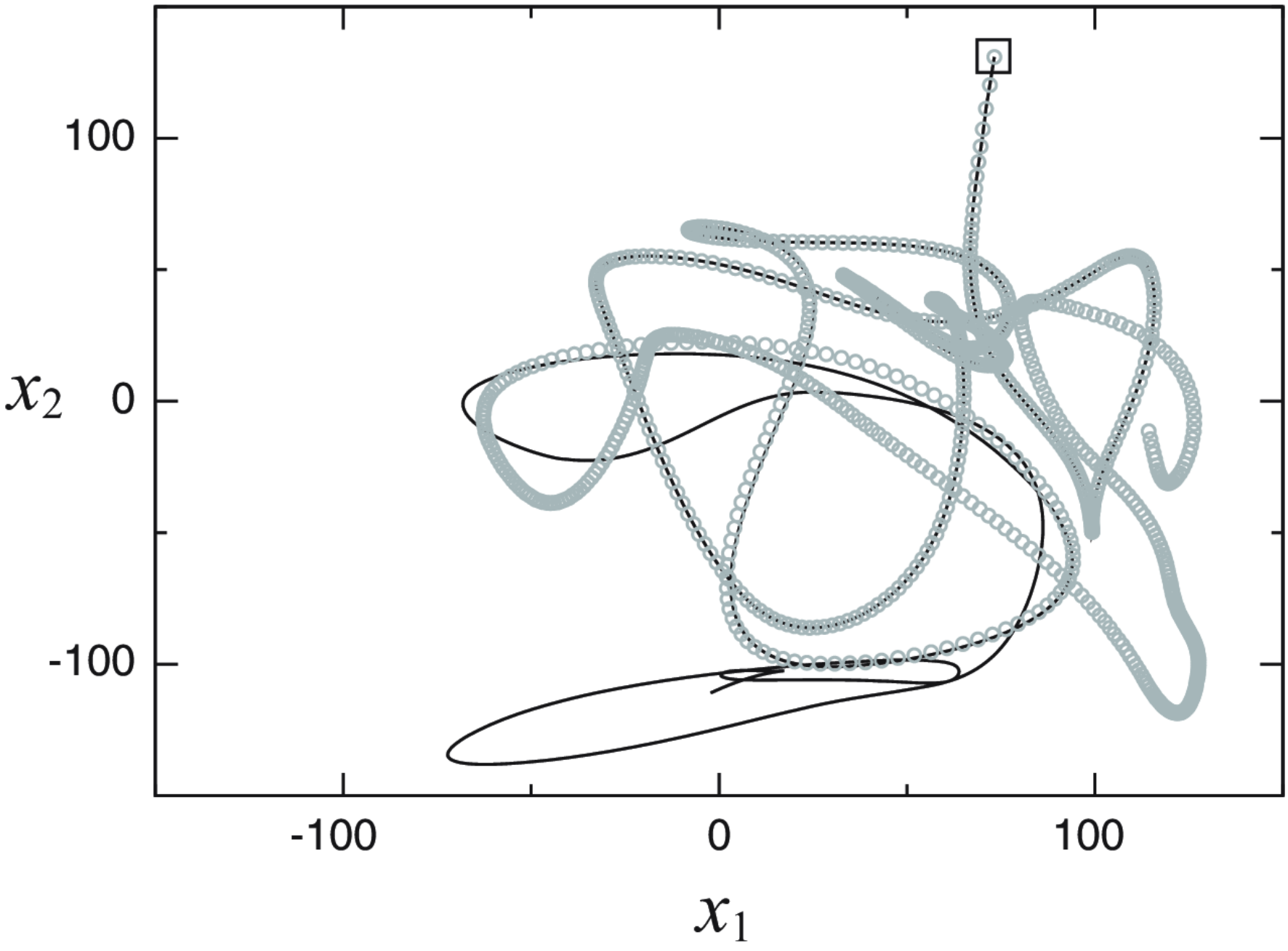
The possibility of complicated dynamic behavior driven by nonlinear feedbacks in dynamical systems has revolutionized science in the latter part of the last century. Yet despite examples of complicated frequency dynamics, the possibility of long-term evolutionary chaos is rarely considered. The concept of "survival of the fittest" is central to much evolutionary thinking and embodies a perspective of evolution as a directional optimization process exhibiting simple, predictable dynamics. This perspective is adequate for simple scenarios, when frequency-independent selection acts on scalar phenotypes. However, in most organisms many phenotypic properties combine in complicated ways to determine ecological interactions, and hence frequency-dependent selection. Therefore, it is natural to consider models for evolutionary dynamics generated by frequency-dependent selection acting simultaneously on many different phenotypes. Here we show that complicated, chaotic dynamics of long-term evolutionary trajectories in phenotype space is very common in a large class of such models when the dimension of phenotype space is large, and when there are selective interactions between the phenotypic components. Our results suggest that the perspective of evolution as a process with simple, predictable dynamics covers only a small fragment of long-term evolution.



Doebeli and Ispolatov, fig. 5

[T]he current phenotypic state of a population can never be understood as the result of an equilibrium or optimisation process, even though the process determining the phenotypic state is entirely adaptive and deterministic. (D&I, 1368–9)

Dynamics and evolution: evolutionarily stable attractors, invasion exponents and phenotype dynamics

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CONT

1.
2.

Selection pressures on vital rates in density-dependent populations

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3.
4.

SUMMARY

5.

For density-independent populations, the sensitivity of population growth rate to changes in individual vital rates indicates the strength of selection on different parts of the life history. Here I show how this approach may be extended to any density-dependent and/or stochastic population model, including those that show cyclic, quasi-periodic and chaotic dynamics. One calculates the influence of individual vital rates on the outcome of competition between two almost identical life histories. The outcome of this competition is determined by the invasion exponent ϑ introduced by Rand. This is the Lyapunov exponent of the linearized system describing the invasion of a population with one life history by a variant type with another. Demographic sensitivities are given by the partial derivatives of ϑ with respect to the individual vital rates of the invading type. The density-independent analysis is a special case of this

6.

A CHEAP HACK?

APPARENT CONTRADICTION:

The P&R model is definable over the long term

The D&I results indicate ubiquitous long-term chaos

Fitness and prediction of future evolutionary outcomes?

Fitness as the quantity that evolution optimizes in the long run?

PREDICTION

WHAT IS FITNESS FOR?

predictive *vs.* causal

- individual fitness: $N = 1$
- trait fitness, traits relativized to include genotype and environment for pleiotropic/GxE effects: $N = 1$
- trait fitness, in natural populations: N small, likely unrepresentative
- type fitness, in natural populations: N medium-sized, still likely unrepresentative
- type fitness, experimental evolution: large N

FITNESS:

Not very predictive.

OPTIMIZATION

Fitness isn't what evolution is optimizing.

generation 1	100% heterozygote (Aa)
generation 2	50% Aa, 25% AA, 25% aa

[T]he current phenotypic state of a population can never be understood as the result of an equilibrium or optimisation process, even though the process determining the phenotypic state is entirely adaptive and deterministic. (D&I, 1368–9)

- adaptation as equilibrium or optimal fitness distribution (e.g., Hartl and Taubes, 1998)
- adaptation as historical selection-for (e.g., Sober, 1984)
- adaptation as current contribution to fitness (e.g., Reeve and Sherman, 1993)

[The] general new implication of chaos for unpredictability is that for predicting any event at any level of precision $\epsilon > 0$, all sufficiently past events are approximately probabilistically irrelevant.

(Werndl, 2009, 215)

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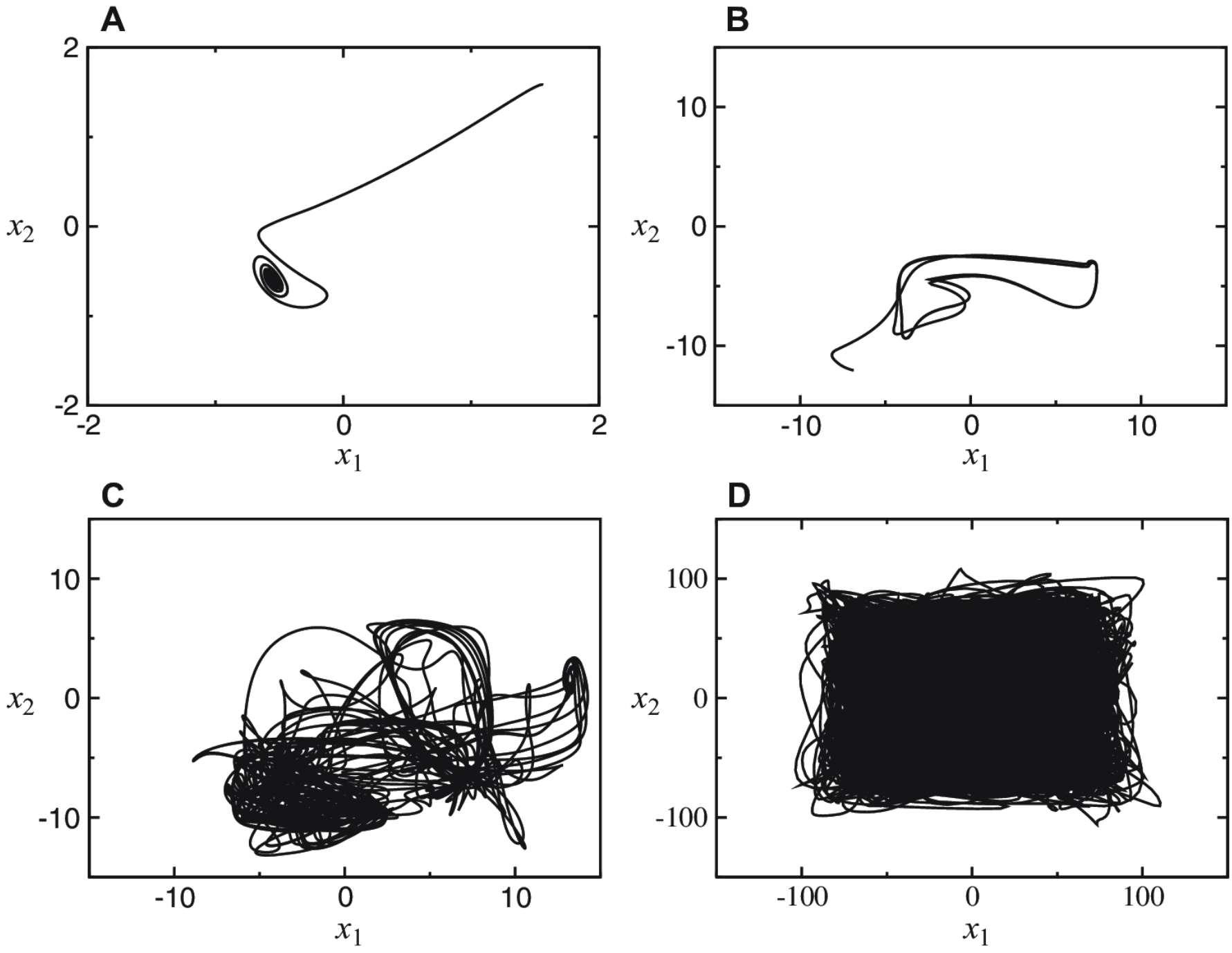

Doebeli and Ispolatov, fig. 1

TAKING STOCK

prediction: not that interesting – as fitness was never very predictive anyway

optimization: may make trouble for our concepts of adaptation

CONTINGENCY VS. CONVERGENCE

Fitness seems to be *screened off* from long-term evolutionary outcomes

A rift between the short-term, adaptive structure of evolution by natural selection and long-term evolutionary outcomes!

QUESTIONS?

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