
Astrobio 2015 Santiago Chile

**CHAOS AND
UNPREDICTABILITY IN
BIOLOGICAL
EVOLUTION**

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How does a typical sequence of phenotypic changes, or evolutionary trajectory, look like?

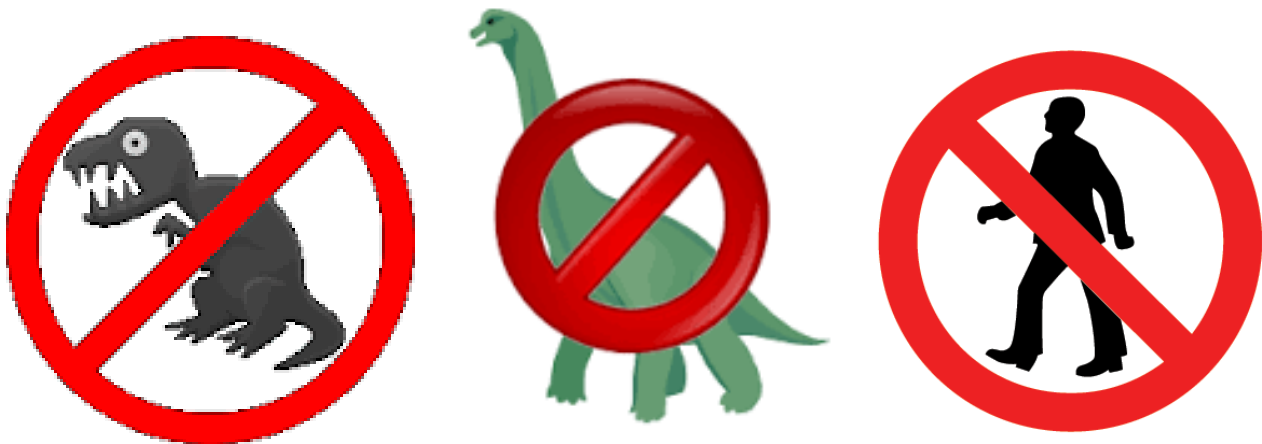
How micro-evolutionary processes generate macro-evolutionary patterns known from fossil record, such as “punctuated equilibria”?

Does species diversity saturate over evolutionary time in a given environment?

- Traditional paradigms of evolution: “survival of the fittest” , static fitness landscape, frequency dependence
- Ecological interactions as evolutionary feedbacks and drivers of complexity
- Logistic model
- Adaptive dynamics, trajectories in phenotype space
- Individual-based and PDE models
- Diversification
- Evolutionary speed and stability

Wind back the tape of life to the early days of the Burgess Shale; let it play again from an identical starting point, and the chance becomes vanishingly small that anything like human intelligence would grace the replay.

Stephen Jay Gould, 1989.



“SURVIVAL OF THE FITTEST”

“Traditional” concepts:

- evolution optimizes simple, scalar phenotypes such as body size, age and size at maturity, fecundity, stress tolerance, antibiotic resistance, etc.
- The “fittest” type wins, and hence evolution is often envisioned as a dynamical system that converges to an equilibrium in phenotype space, representing the optimally adapted type.
- Non-stationarity of evolution at large time scales is usually attributed to long-term changes in the external environment causing shifts in evolutionary optima.

Ecological interactions

Competition, symbiosis, predation, etc, lead to

Frequency-dependent selection,

in which the current phenotypic composition of a population determines whether a particular phenotype is advantageous or not.

Frequency-dependent selection

generates an

Evolutionary feedback loop,

because selection pressures, which cause evolutionary change, change themselves as a population's phenotype distribution evolves.

MULTIDIMENSIONAL PHENOTYPES

- Individual birth and death rates are determined by ecological interactions, which, in their turn, depend in a complex way on many phenotypic properties or **dimensions**.
- Phenotypic dimensions could be as diverse as the molecular efficiency of photosynthesis, ability to retain water, and the height of trees.
- Even for single species, it is natural to study evolutionary dynamics in high-dimensional phenotype spaces, where it is a fitness maximization process but in a dynamic landscape.

LOGISTIC MODEL

A simple evolutionary model for the simplest ecological interaction, competition for resources,

$$\frac{\partial N(x, t)}{\partial t} = rN(x, t) \left(1 - \frac{\int \alpha(x, y) N(y, t) dy}{K(x)} \right) + D\nabla^2 N(x, t).$$

$N(x, t)$ is the density of individuals of d -dimensional phenotype $x \in \mathbb{R}^d$ at time t , and $K(x)$ is the carrying capacity of a monomorphic population consisting entirely of x -individuals.

The competitive impact of individual with phenotype y on individual with phenotypes x is given by the competition kernel $\alpha(x, y)$, so that an x -individual experiences an effective density $\int \alpha(x, y) N(y, t) dy$.

Intuitive approximation: ADAPTIVE DYNAMICS

Consider a resident population that is monomorphic for trait x , which is at its ecological equilibrium $K(x)$. The invasion fitness $f(x, y)$ of a rare mutant y is its per capita growth rate in the resident population x ,

$$f(x, y) = 1 - \frac{\alpha(y, x)K(x)}{K(y)}.$$

The selection gradient $s(x) = (s_1(x), \dots, s_d(x))$ is derived from the invasion fitness as

$$s_i(x) = \left. \frac{\partial f(x, y)}{\partial y_i} \right|_{y=x} = - \left. \frac{\partial \alpha(y, x)}{\partial y_i} \right|_{y=x} + \frac{\partial K(x)}{\partial x_i} \frac{1}{K(x)}.$$

We assume that the complexity of the interactions between phenotypic components is contained in the competition kernel $\alpha(x, y)$.

For example, it has linear and quadratic terms,

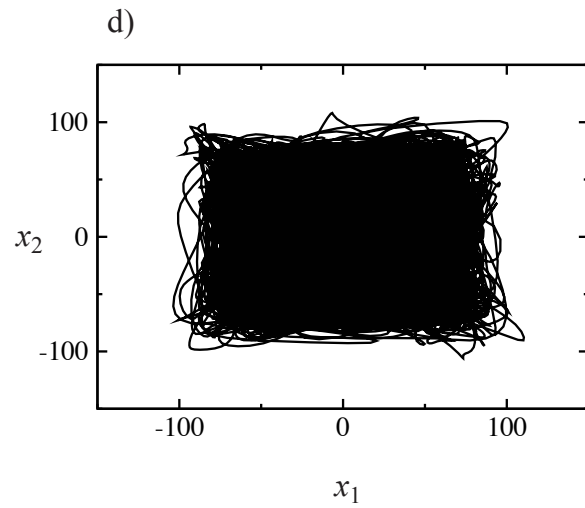
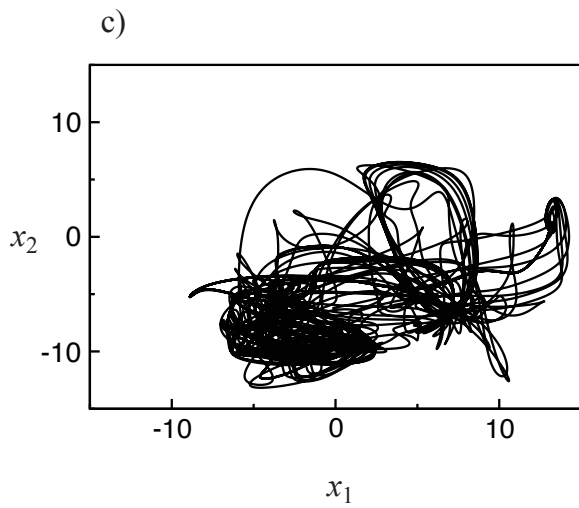
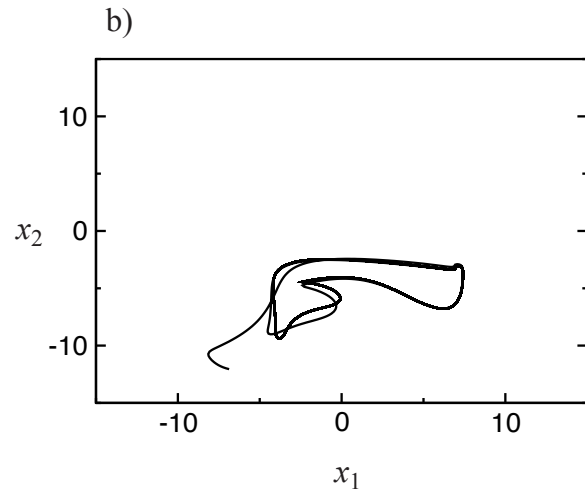
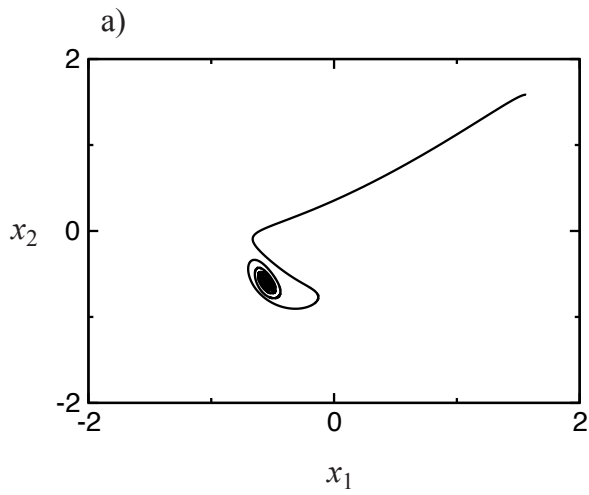
$$\left. \frac{\partial \alpha(y, x)}{\partial y_i} \right|_{y=x} = - \sum_{j=1}^d b_{ij} x_j - \sum_{j,k=1}^d a_{ijk} x_j x_k$$

For the carrying capacity, we assume a simple symmetric form: $K(x) = \exp(-\sum_i x_i^4/4)$

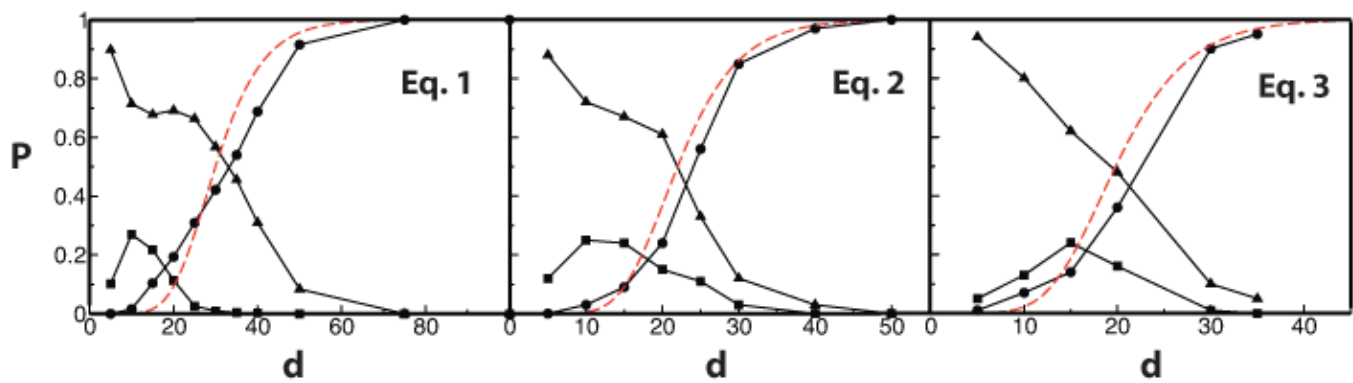
With these assumptions, the adaptive dynamics, describing the evolution of the multidimensional phenotype x , becomes

$$\frac{dx_i}{dt} = \sum_{j=1}^d b_{ij} x_j + \sum_{j,k=1}^d a_{ijk} x_j x_k - x_i^3, \quad i = 1, \dots, d.$$

CLASSES OF TRAJECTORIES



PROBABILITY OF CHAOS



UBIQUITY OF CHAOS

Trajectories of a generic non-linear confined system become mostly chaotic for sufficiently large d ($d \sim 10 - 100$)

I. Ispolatov, V. Madhok, S. Allende, and M. Doebeli, *Chaos in high-dimensional dissipative dynamical systems*, Sci. Rep. **5**, 12506, (2015), doi: 10.1038/srep12506.

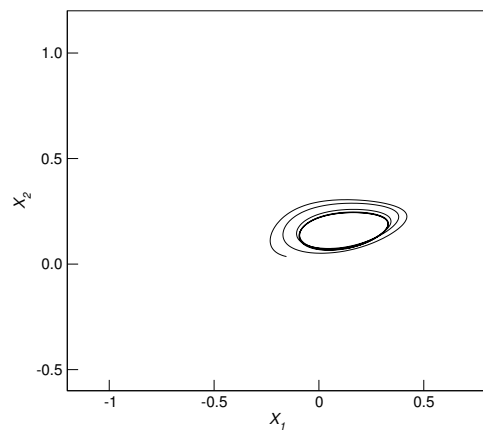
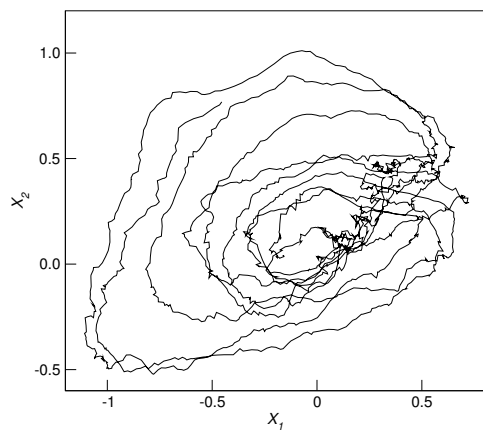
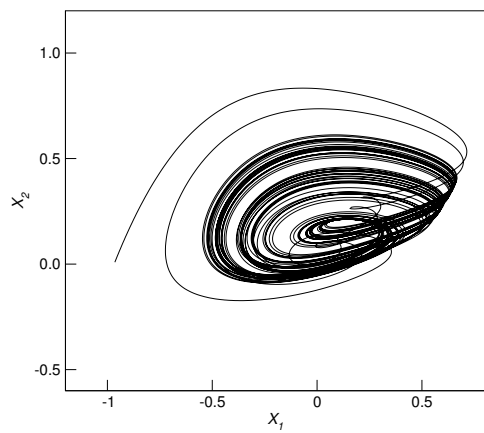
Hence, for complex multidimensional phenotypes, we expect even the simplest single-species evolutionary trajectories to be chaotic.

DIRECT SOLUTION OF LOGISTIC EQUATION

Reconstructing the competition kernel from the selection gradient

$$\alpha(\mathbf{y}, \mathbf{x}) = \exp \left[\sum_{i,j=1}^d b_{ij} x_j (x_i - y_i) + \sum_{i,j,k=1}^d a_{ijk} x_j x_k (x_i - y_i) \right],$$

yields a single-species (monomorphic) evolutionary dynamics similar to adaptive dynamics.



ADAPTIVE DIVERSIFICATION

Adding a Gaussian term to the competition kernel

$$\alpha(\mathbf{y}, \mathbf{x}) = \exp \left[\sum_{i,j=1}^d b_{ij}(x_i - y_i)x_j - \sum_{i=1}^d \frac{(x_i - y_i)^2}{2\sigma_i^2} \right],$$

does not change the single-species adaptive dynamics.

However, it leads to diversification, modeling
Sympatric speciation.

MULTICLUSTER ADAPTIVE DYNAMICS

The ecological dynamics of the m clusters are given by

$$\frac{dN_r(t)}{dt} = N_r(t) \left(\frac{1 - \sum_{s=1}^m \alpha(\mathbf{x}_r, \mathbf{x}_s) N_s(t)}{K(\mathbf{x}_r)} \right).$$

Selection gradient

$$s_{ri} = \sum_s N_s^* \left(-\frac{1}{K(\mathbf{x}_r)} \frac{\partial \alpha(\mathbf{x}_{r'}, \mathbf{x}_s)}{\partial x'_{ri}} \Big|_{\mathbf{x}'_r = \mathbf{x}_r} + \frac{\alpha(\mathbf{x}_r, \mathbf{x}_s)}{K^2(\mathbf{x}_r)} \frac{\partial K(\mathbf{x}_r)}{\partial x_{ri}} \right).$$

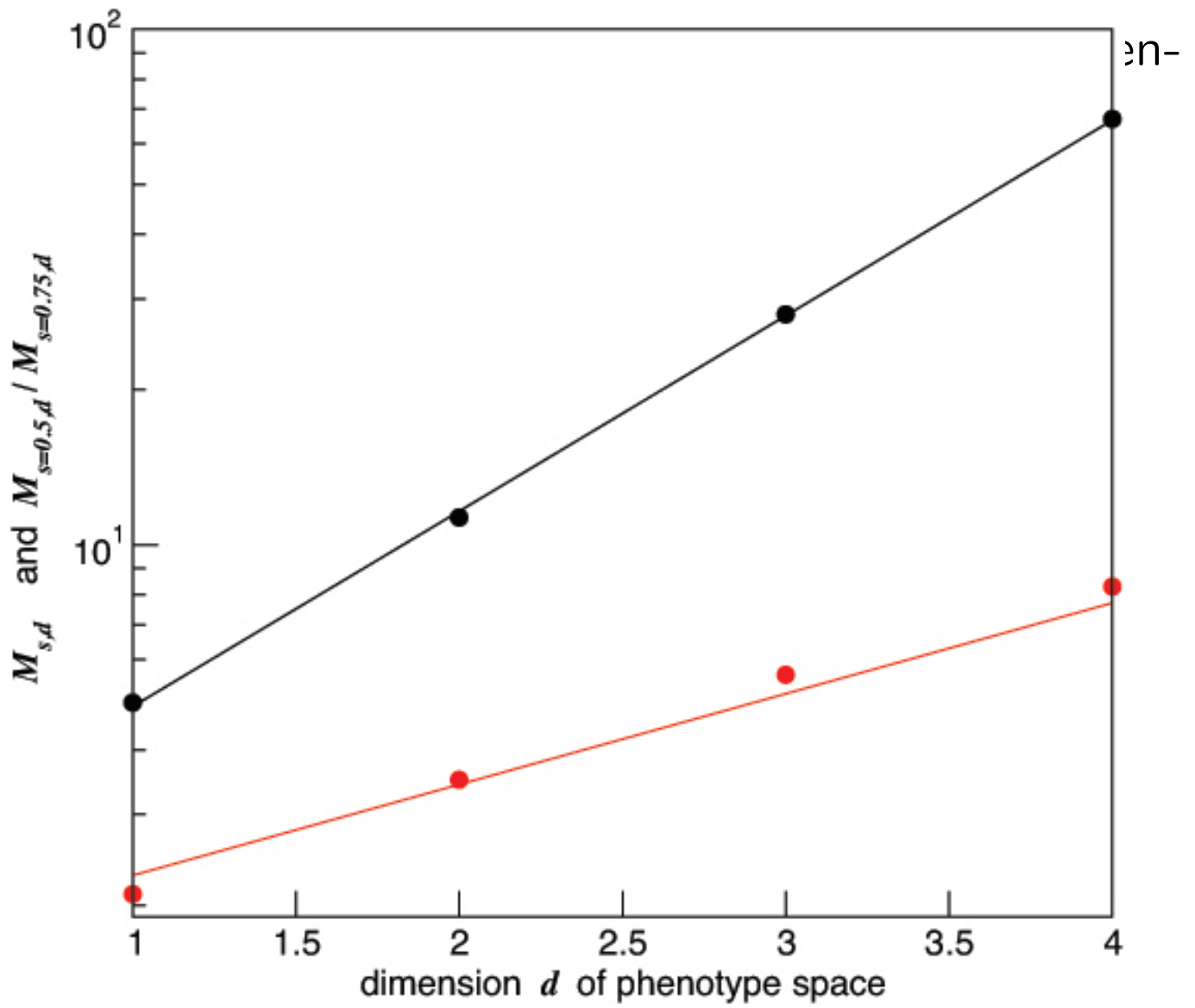
Equations of motion

$$\frac{dx_{ri}}{dt} = N_r^* s_{ri}, \quad i = 1, \dots, d, \quad r = 1, \dots, m.$$

SIMULATION PROCEDURE

1. A system is initiated with randomly generated coefficients for the competition kernel and initial clusters.
2. The ecological dynamics is integrated to get new populations N_r^* , $r = 1, \dots, m$, small-population clusters are eliminated.
3. The adaptive dynamics of the phenotypes of clusters is advanced.
4. Nearby clusters are merged.
5. If the current number of clusters is below the target one, a randomly chosen cluster is split into halves, which are slightly offset from each other.

EQUILIBRIUM DIVERSITY



MONITORING EVOLUTIONARY SPEED

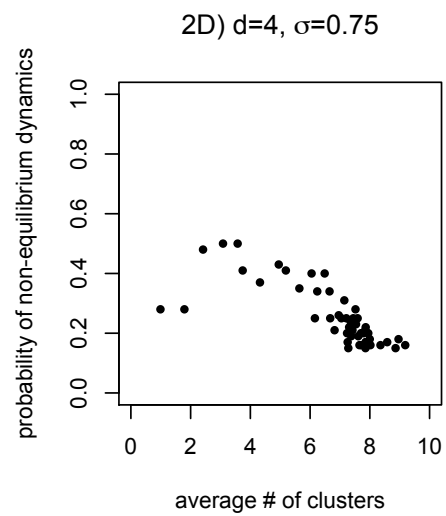
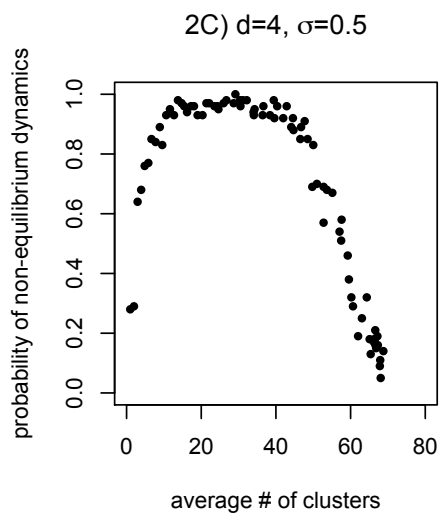
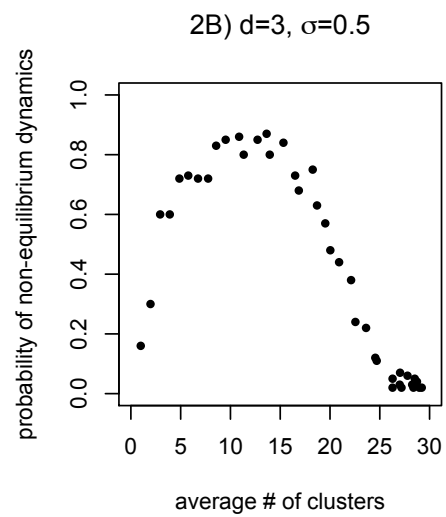
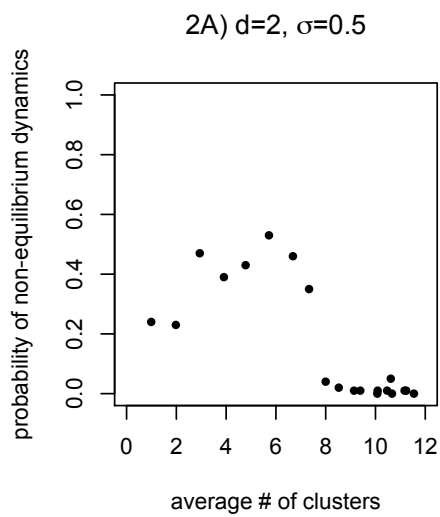
We defined average per capita evolutionary speed,

$$v = \sum_{r=1}^m \frac{N_r \sqrt{\sum_{i=1}^d (dx_{ri}/dt)^2}}{\sum_{r=1}^m N_r}.$$

and averaged it over several time units.

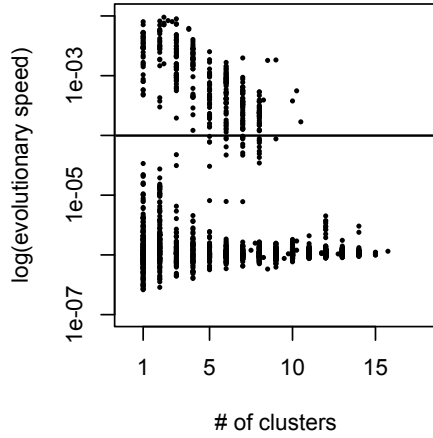
- Stationary $v < 10^{-5}$
- Non-stationary $v > 10^{-5}$

PROBABILITY OF NON-EQUILIBRIUM DYNAMICS VS. NUMBER OF CLUSTERS

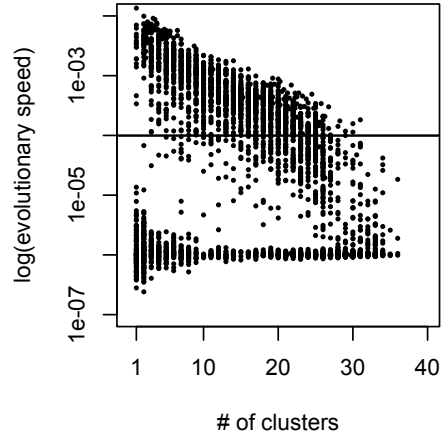


AVERAGE EVOLUTIONARY SPEED VS. NUMBER OF CLUSTERS

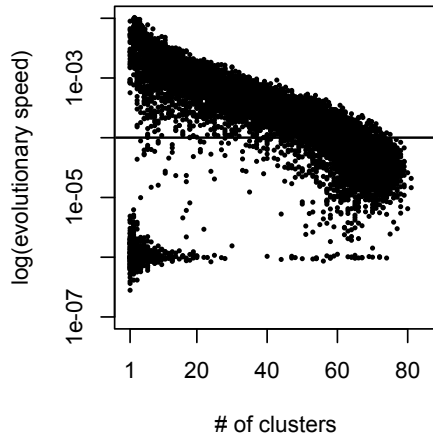
3A) $d=2, \sigma=0.5$



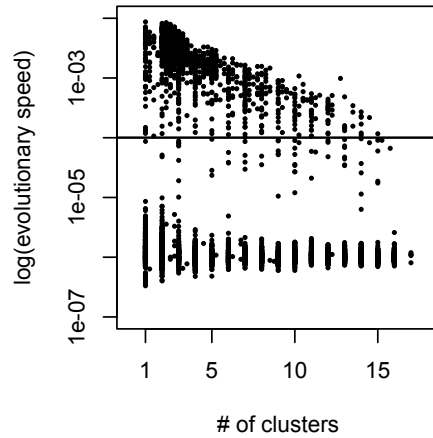
3B) $d=3, \sigma=0.5$



3C) $d=4, \sigma=0.5$

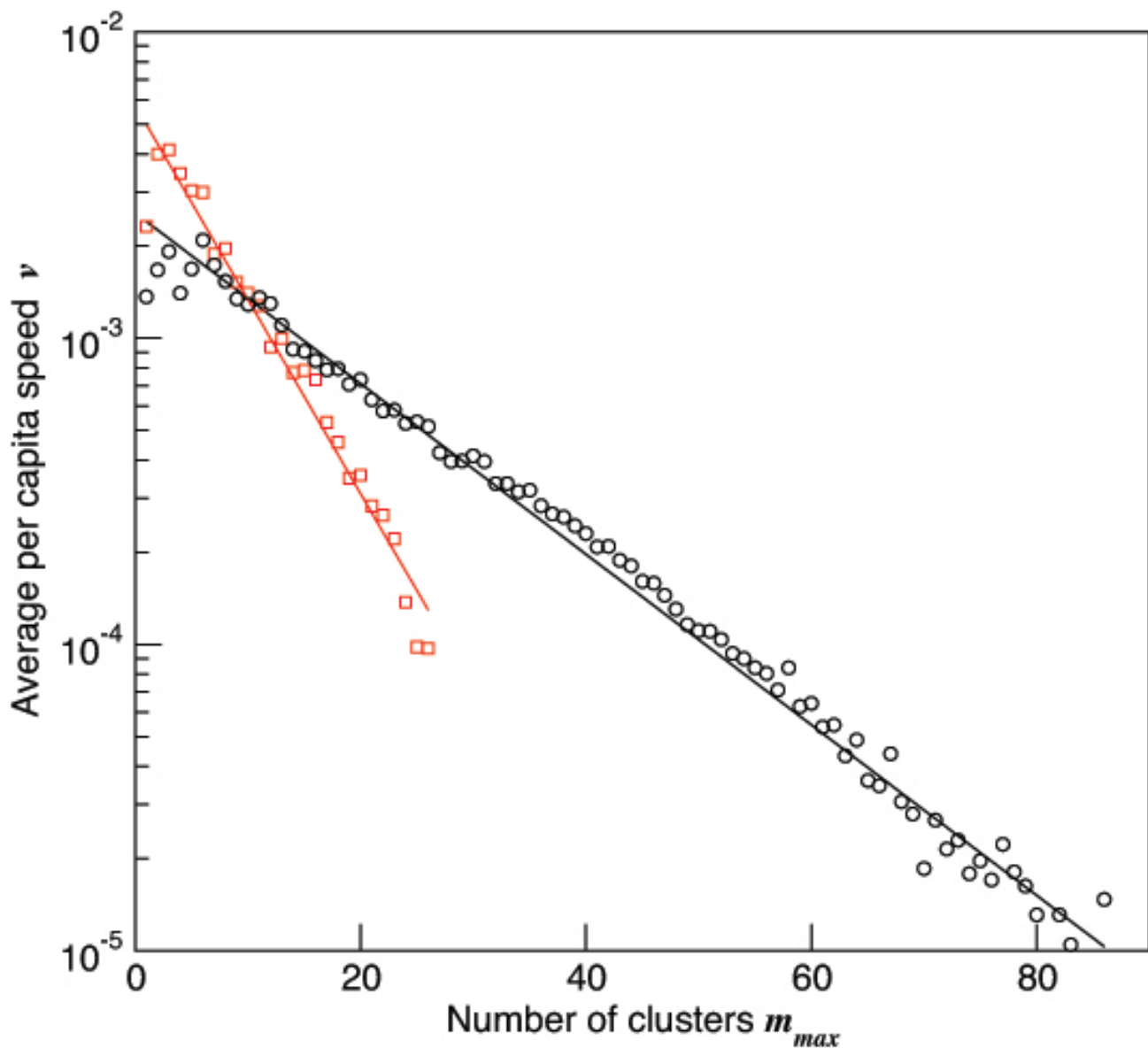


3D) $d=4, \sigma=0.75$



EVOLUTIONARY SPEED VS. NUMBER OF CLUSTERS FOR A SINGLE SYSTEM

For competition kernel width $\sigma = 0.5$ and dimensions $d = 3, 4$. Both systems exhibit non-stationary single-cluster dynamics.



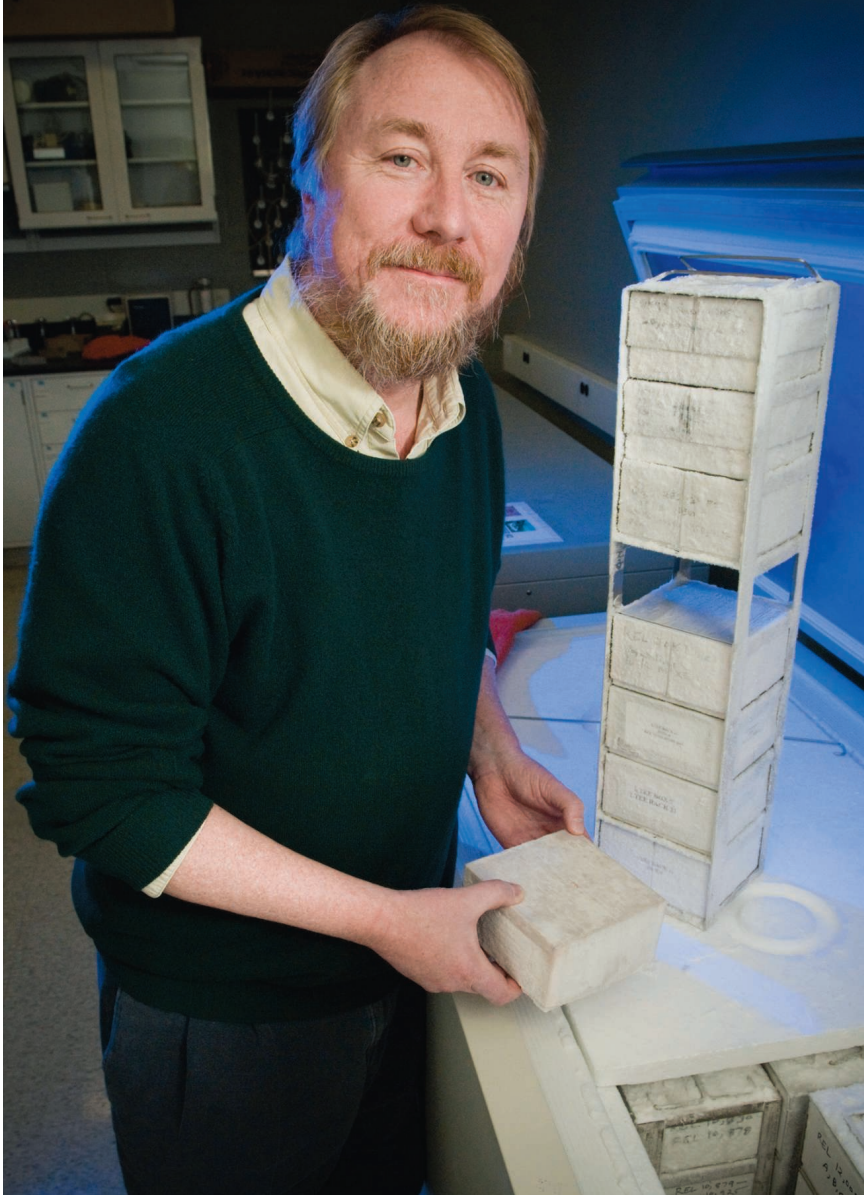
EXAMPLES FOR $\sigma = 0.5$ and $d = 3$

CONCLUSIONS

- Frequency-dependent ecological interactions can generate complicated evolutionary trajectories for multidimensional phenotypes that visit all feasible regions of phenotype space in the long run even if the external environment (given by system parameters) is constant.
- Deterministically-chaotic evolutionary trajectories are intrinsically unpredictable on top of the fundamental, quantum-mechanical stochasticity of mutations.
- Saturated diversity exponentially grows with the complexity (dimensionality) of phenotype
- Non-stationarity of evolution exhibits a hump-like dependence on diversity: it first increases, then drops.
- Punctuated equilibrium can be understood as cycles of mutations (gene duplications), opening up new dimensions, followed by repeated periods of slow-fast-slow diversification.

The Man Who Bottled Evolution

Richard Lenski's 25-year experiment in bacterial evolution shows no signs of running out of surprises about how mutation and selection shape living things



EAST LANSING, MICHIGAN—When most biologists want to understand how evolution unfolds, they look for clues in the fossil record or the natural world. Richard Lenski simply walks across his Michigan State University lab to his freezers. There, stored in 4000 vials, are bacteria dating back to 1988. That was the year Lenski started a simple but radical experiment. He put samples of *Escherichia coli* into a sugar solution, stoppered the flasks, and waited to see what would happen. It was a study with no defined endpoint, so risky that he didn't try very hard to get outside funding for it.

After 25 years and 58,000 bacterial generations, Lenski's bacteria are still growing, mutating, and evolving. They are proving as critical to understanding the workings of evolution as classic paleontology studies such as Stephen Jay Gould's research on the pace of change in mollusks. Lenski's humble *E. coli* have shown, among other things, how multiple small mutations can prepare the ground for a major change; how new species can arise and diverge; and that Gould was mistaken when he claimed that, given a second chance, evolution would likely take a completely different course. Most recently, the colonies have demonstrated that, contrary to what many biologists thought, evolution never comes to a stop, even in an unchanging environment. The work is "an absolutely magnificent achievement," says Douglas Futuyma, an evolutionary biologist at Stony Brook University in New York.

Other researchers have done experimental evolution, setting up populations of insects, yeast, and even fish in the lab and in controlled field conditions, and subjecting the organisms to a particular environmental stress for relatively short periods. But Lenski's long-term experiment "is just orders of magnitude beyond what anyone else has done," Futuyma says.

The project's quarter-century has witnessed the rise of bioinformatics and the birth of whole-genome sequencing, and Lenski has taken advantage of both technologies to glean new insights. Generations of students have tended and analyzed the microbes, and the project sparked a memorable conflict between Lenski and creationists. Fifteen years ago, he almost abandoned it for digital models of evolution, then reconsidered—and was vindicated when his bacteria took one of their most dramatic evolutionary leaps. As

Time traveler. To turn back evolution's clock, Richard Lenski dips into his freezer.

Downloaded from www.sciencemag.org on November 19, 2013

CREDIT: G. L. KOHUTH/MICHIGAN STATE UNIVERSITY (2009)

Lenski's LONG-TERM Evolution Experiment

Twelve batches of bacteria, replicating and evolving for 25 years, yield some pretty big numbers.

58,000* GENERATIONS
(*as of June 2013)

GENERATIONS
PER
DAY **6.6**



10¹⁴ ROUGH NUMBER OF
BACTERIAL CELLS

REPLICATE
POPULATIONS **12**

All started with identical *E. coli*,
but are now all different

The number of
FROZEN VIALS **>4000**

that hold ancestral and evolved bacteria

LIQUID MEDIA
>10,000
LITERS



FREEZERS
6

Lenski's experiment has
been running for more than

25
years

at an
ESTIMATED COST of

\$4 MILLION

Workforce involvement
equals about



75 PERSON
YEARS

30 PARTICIPATING
GRADUATE STUDENTS
AND POSTDOCS

OUTSIDE COLLABORATORS

40

>50 PUBLICATIONS

Michael Doebeli, Department of Mathematics and
Centre for Biodiversity, UBC, Canada

FONDECYT project #1151524.