Innovation vs. improvement in eco-evolutionary dynamics

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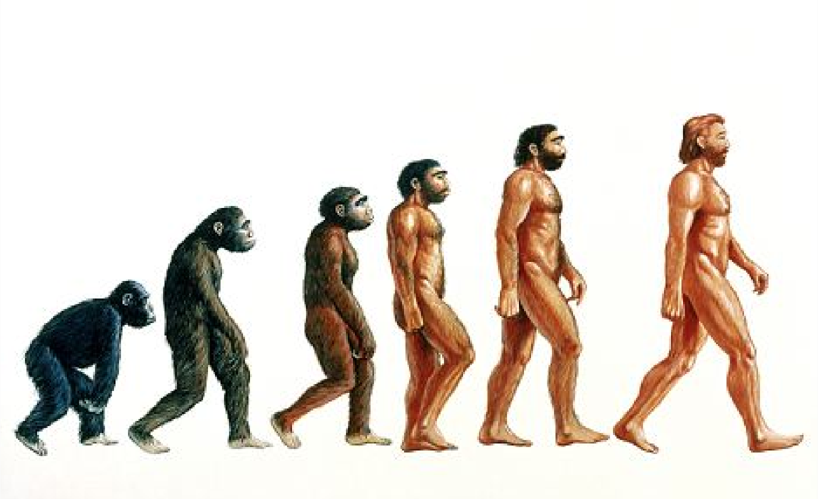
Evolution as improvement

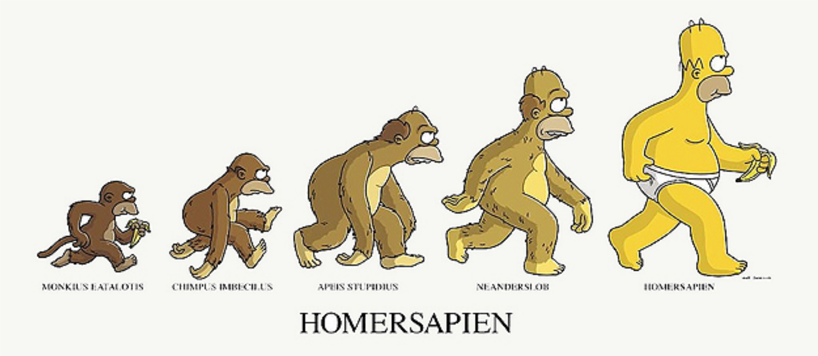
- In the classical evolution scenarios, natural selection acts towards the optimization of the species fitness
- This is often represented as a tendency of a life form to develop towards “more and more perfect forms”

Images of evolution



Daily Mail

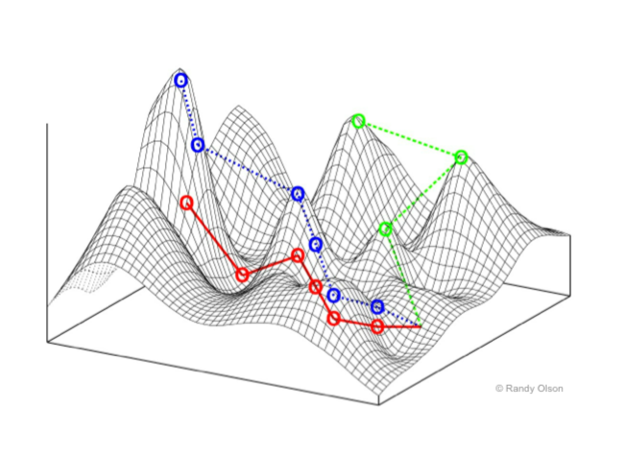
Images of evolution



BITREBELS

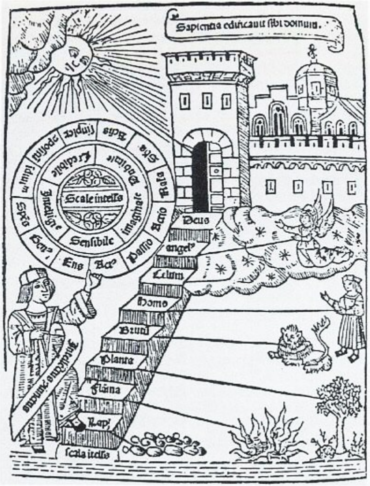
Fitness landscapes

This is often represented by describing life forms as climbing uphill in a *fitness landscape* (Wright, Kauffman, Gavrilets)



Scala Naturæ

This is not so different from the medieval concept of *Scala Naturæ*

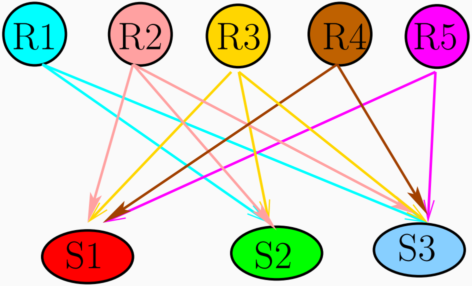


Evolution and ecology

So, why doesn't evolution stop?

- The "fitness landscape" is a seascape: it changes with time
- Most of its changes are due to the evolution of other, coexisting, life forms
- We need to understand the coevolution of a large number of coexisting life forms
- Novel aspects emerge when the number of coexisting life forms is large
- In this context, evolution is dominated by innovation ("creation" of new niches) rather than improvement (higher efficiency or lower cost)

MacArthur's model of Resource Competition



N resources

S species

MacArthur and Levins, 1967

MacArthur's model of Resource Competition

Resource flux: R_i, $i = 1, \ldots, N$
Population dynamics: $\mathrm{d}n_\mu/\mathrm{d}t = b_\mu n_\mu \, \Delta_\mu(\boldsymbol{h})$, $\boldsymbol{h} = (h_i)$
Resource surplus: $\Delta_\mu(\boldsymbol{h}) = \sum_i \sigma_{\mu i} h_i - \chi_\mu$, $\mu = 1, \ldots, S$
Metabolic Strategies: $\boldsymbol{\sigma}_\mu = (\sigma_{\mu 1}, \ldots, \sigma_{\mu N})$
Total demand: $T_i(\boldsymbol{n}) = \sum_\mu \sigma_{\mu i} n_\mu$
Resource availability: $h_i = R_i/T_i = H_i(T_i)$

Feedback loop:

- Growth of exploiting population leads to decrease in availability
- Decrease in availability leads to decrease in population growth

Lyapounov function (MacArthur, 1969):

$$F(\boldsymbol{n}) = \sum_i R_i \log T_i(\boldsymbol{n}) - \sum_\mu n_\mu \chi_\mu$$

$$\frac{\mathrm{d}F}{\mathrm{d}t} = \sum_\mu b_\mu n_\mu \Delta_\mu^2 \geq 0$$

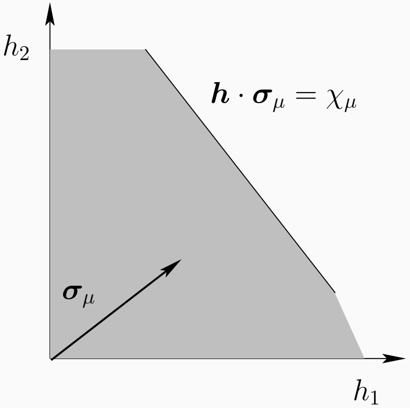
Global optimization of F for a given set of strategies and cost

MacArthur's model of Resource Competition

Steady state:

- If $n_\mu > 0$, $\Delta_\mu = 0$, i.e., $\boldsymbol{h} \cdot \boldsymbol{\sigma}_\mu = \chi_\mu$
- If $n_\mu = 0$, $\boldsymbol{h} \cdot \boldsymbol{\sigma}_\mu < \chi_\mu$ ("forbidden region")

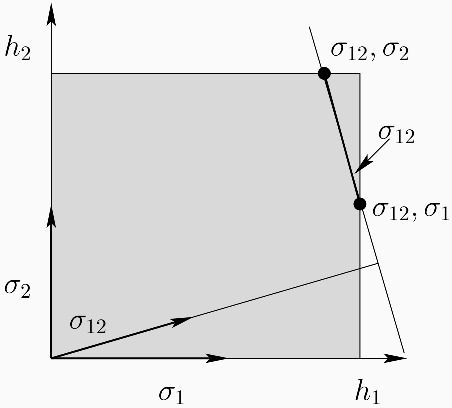
Geometric interpretation (Tilman, 1982):



Steady state:

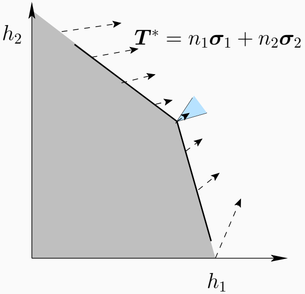
- σ_1, σ_2 are "specialists" with cost χ_0
- σ_{12} is a "generalist" with cost $\chi_{12} < \chi_0$

The steady state contains σ_{12} and possibly one of σ_1 or σ_2:



Locating the steady state

- At the steady state $\boldsymbol{h}^*$, $\boldsymbol{n}^*$, the *vector of total demand* $\boldsymbol{T}(\boldsymbol{n}^*)$ must point *strictly outward* from the unsustainable (gray) region, since $T^* = \sum_\mu n_\mu \boldsymbol{\sigma}_\mu$
- Define a vector field $\boldsymbol{T}_0(\boldsymbol{h})$ such that $T_{0i}(\boldsymbol{h}) = R_i/h_i$, then $\boldsymbol{T}_0(\boldsymbol{h^*}) = \boldsymbol{T}^*$
- Thus follow the vector field $\boldsymbol{T_0}$ along the boundary of the unsustainable region, till locating where it points strictly outwards



MacArthur's model in large dimensionality

What happens when $N \gg 1$?

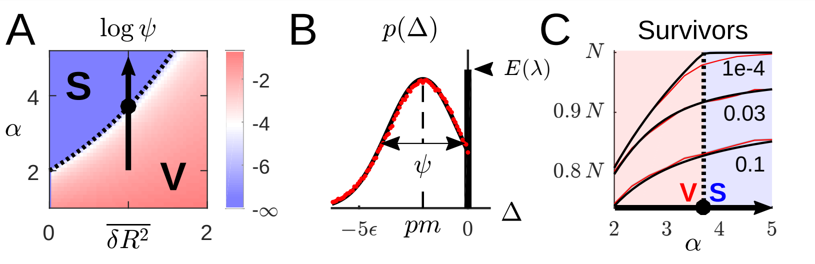
- M. Tikhonov (2015) introduced MacArthur's model with quenched disorder to the statphys community
- Several researchers analyzed the model in large dimensions by statphys methods (replica, cavity method): Tikhonov himself, and Advani, Bunin, Mehta, Monasson, …
- Tikhonov and Monasson find a phase transition in large ecosystems:

  V phase: "vulnerable": The number of surviving species is much smaller than N, the system is vulnerable to a change of external conditions

  S phase: "stable": There are exactly N species which can adapt to change in external conditions without going extinct
- More recently, they analyzed the evolutionary implications of the model

The transition

- $\sigma_{\mu i} = 1$ with probability p (else 0), $\chi_\mu = \sum_i \sigma_{\mu i} + \epsilon x_\mu$
- Control parameters: N, $\alpha = S/N$, p, ϵ, $\overline{\delta R^2}$
- Order parameters: $m = \overline{h}$, $\psi = \overline{(h_i - \overline{h})^2}$

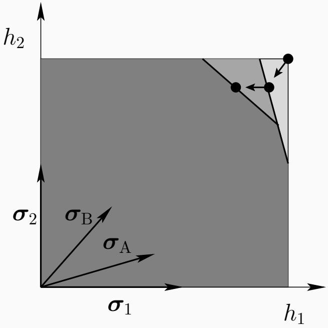


Tikhonov and Monasson, 2016

Evolution of communities

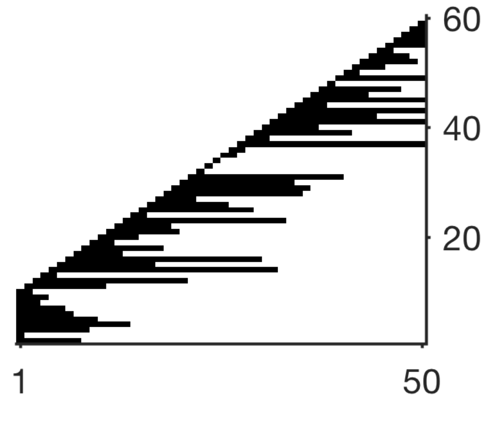
- # of possible species: $2^N \gg N$
- Keep introducing new species ($\alpha = S(t)/N$ measures time)
- Let the system reach steady state each time
- Allow “extinct” species to resurrect

Is “resurrection” moot?



Cost optimization?

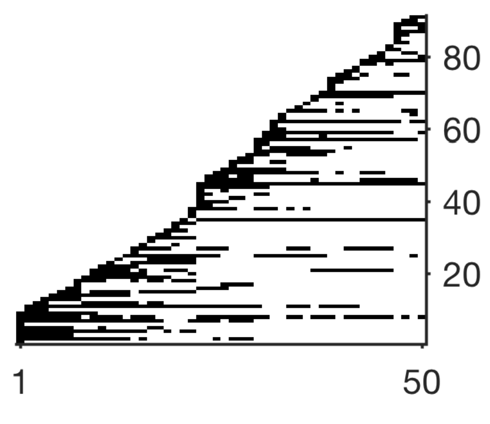
The “best species” model:



Tikhonov and Monasson, 2017

Cost optimization?

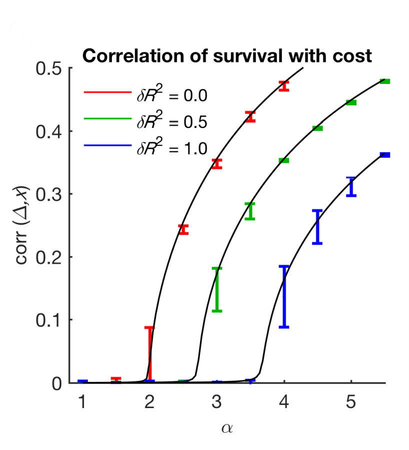
The actual simulation ($N = 15$, $\overline{\delta R^2} = 1.5$):



Tikhonov and Monasson, 2017

Is cost relevant?

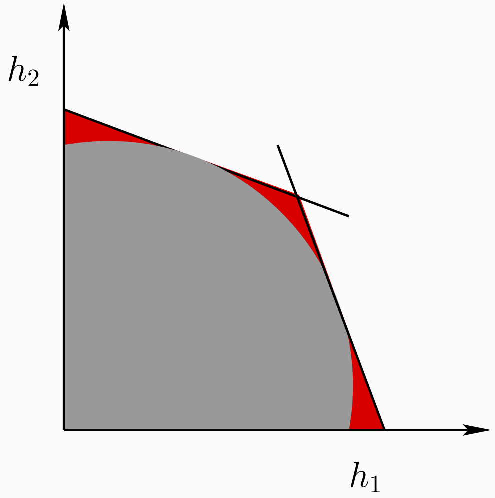
For $\alpha = S/N < \alpha_C$, the correlation between x_μ (cost) and Δ_μ (viability) vanishes:



Tikhonov and Monasson, 2017

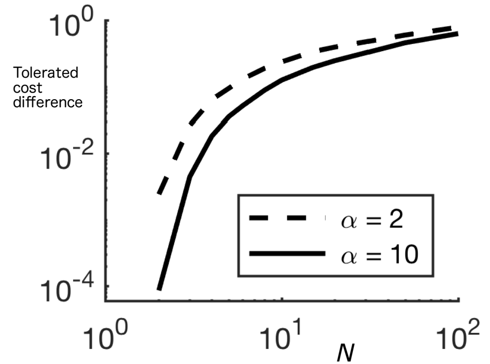
Is cost relevant?

Tolerated cost in the presence of random strategies of cost 1:



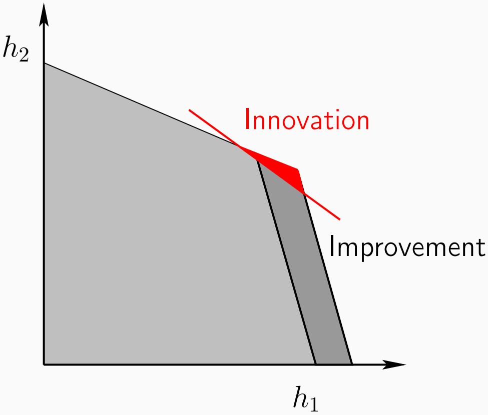
Tikhonov and Monasson, 2017

Tolerated cost difference for large N



Tikhonov and Monasson, 2017

Invasion strategies at large N



Tikhonov and Monasson, 2017

Summary

- Complex ecosystems may work in a “shielded” regime, which is not vulnerable to fluctuations in the outside environment
- This obtains by the introduction of species which operate a workable compromise in resource consumption, while cost is of lesser importance
- In large dimensionality, the room for innovation is exponentially larger than that of improvement (innovation as “environmental engineering”)
- Is a “one-dimensional” fitness concept a good cue in this situation?

Caveats:

- The model is very simple (no RSP)
- As soon as “producers” appear, there’s no Lyapounov function
- Good starting point (cf. Hopfield’s model)?

Thank you!

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