Is there a more fundamental theorem of natural selection?

Joe Felsenstein

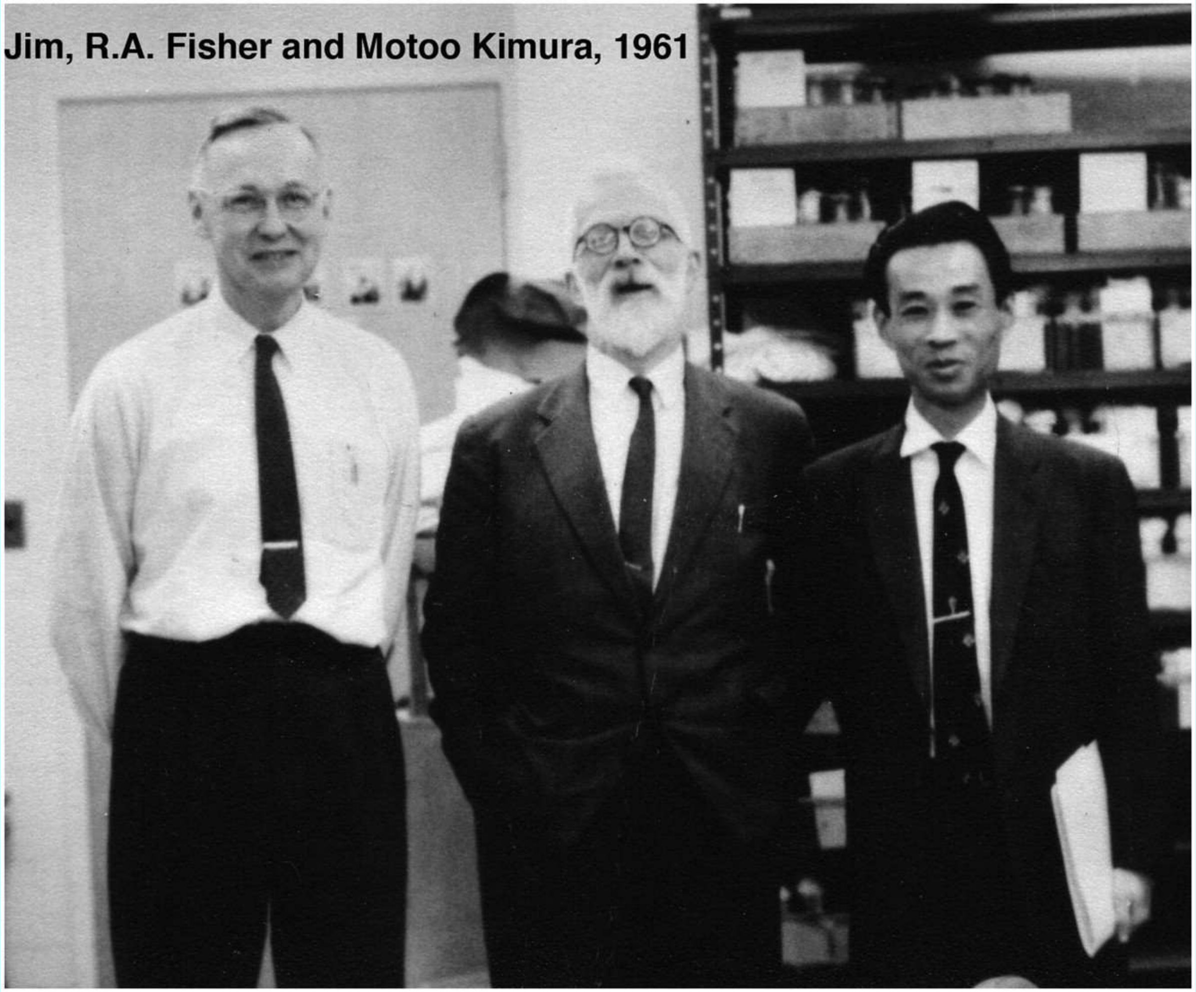
Fisher Memorial Lecture, 4 January 2018

Hello to ...

Walter Bodmer
(shown in 1973)

The PopGroup
at PGG #1, 50 years ago)

R.A. Fisher and (not-) me



The day I didn't stop by Jim Crow's lab ...

R.A. Fisher and his Fundamental Theorem

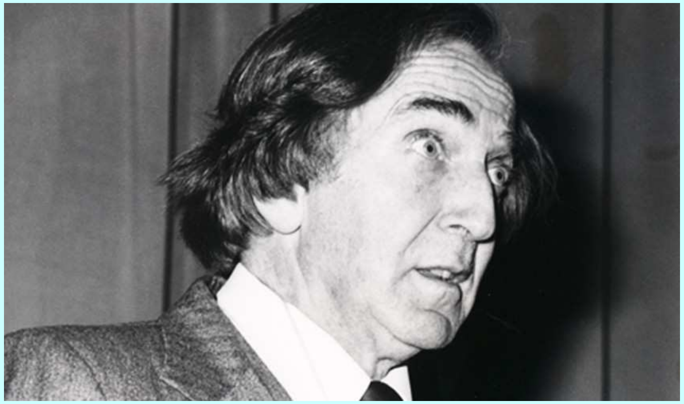
$$\frac{dM}{dt} + \frac{M}{C} = W - D$$

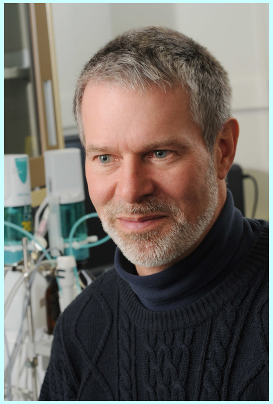
R. A. Fisher about 1928

The FTNS

Information measures relevant to adaptation

Specified information: (Defined by Leslie Orgel in 1973)





Leslie Orgel Jack Szostak Robert Hazen

1. Orgel: Life has information that makes it not only complex, but also specified.
2. Szostak (2003) and Hazen et al. (2007) have defined “functional information”, a better-defined version of specified information.
3. I also talked about “adaptive information” in similar terms in 1978.
4. The most relevant form of specification is fitness.

In effect, specified information is information that increases fitness.

Intelligent Design advocates have publicized it

William Dembski

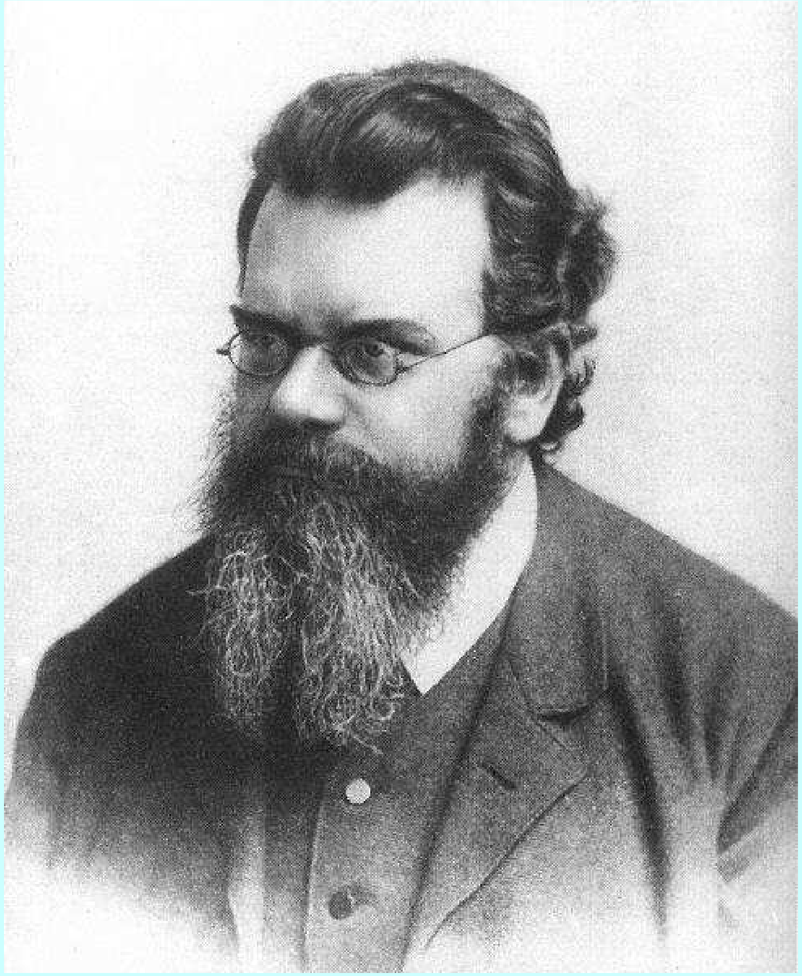
1. William Dembski: discussed it and argues (2002 ff.) that he has a Law of Conservation of Complex Specified Information that shows that natural selection and other natural evolutionary forces cannot put Complex Specified Information into the genome.

2. Dembski's LCCSI Theorem has fatal flaws involving violating its own assumptions and changing the specification in mid-stream.

3. This leaves it entirely possible that Complex Specified Information can be put into the genome by natural selection.

4. More recently (2006) Dembski has redefined CSI to be that information that cannot be put into the genome by ordinary evolutionary forces. It is therefore no longer of use in demonstrating that CSI cannot be put into the genome by natural selection. (It then can't, by definition, but that leaves open as to how you know that there is such information).

First to think about entropy and evolution



Ludwig Boltzmann (1844–1906)

Founder of statistical mechanics

Boltzmann on entropy, life, and and evolution

The general struggle for existence of animate beings is not a struggle for raw materials – these, for organisms, are air, water and soil, all abundantly available – nor for energy which exists in plenty in any body in the form of heat, but a struggle for [negative] entropy, which becomes available through the transition of energy from the hot sun to the cold earth.

Ludwig Boltzmann, 1875

If you ask me about my innermost conviction whether our century will be called the century of iron or the century of steam or electricity, I answer without hesitation: It will be called the century of the mechanical view of Nature, the century of Darwin.

Ludwig Boltzmann, 1886

Quoted and translated by Peter Schuster, 2007.

A Holy Grail of sorts

Many people have seen that there ought to be a quantitative theory of evolution that connects to thermodynamics.

Here I will try to make some simple models in which we can see what connection there is.

This is not a new quest.

A 37-year-old paper

Vol. 112, No. 983 The American Naturalist January–February 1978

MACROEVOLUTION IN A MODEL ECOSYSTEM*

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Suppose that we suddenly discovered that life existed somewhere else in the universe, but we knew nothing of its specific properties. There are two sources from which we might make inferences about them. One is the body of physical and chemical principles on which we could base consideration of the possible biochemistries of living systems. The other is the knowledge that they have evolved by natural selection and are maintained by the flow of energy through an ecosystem. From these sources alone we could hope to predict some of the properties of the evolving ecosystem. What would these predictions be? Were theoretical biology more mature, this question would have been addressed more extensively. Its interest transcends the narrow realm of exobiology. We ought to inquire which properties of our own biosphere are general to any

Its citations in Web of Science

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1. **The fitness value of information**
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   Check for Full Text | View Abstract
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   CURRENT ANTHROPOLOGY Volume: 21 Issue: 2 Pages: 274-275 Published: 1980
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4. **QUANTUM ADJUSTMENT, MACROEVOLUTION, AND THE SOCIAL FIELD - SOME COMMENTS ON EVOLUTION AND CULTURE**
   By: DIENER, P
   CURRENT ANTHROPOLOGY Volume: 21 Issue: 4 Pages: 423-443 Published: 1980
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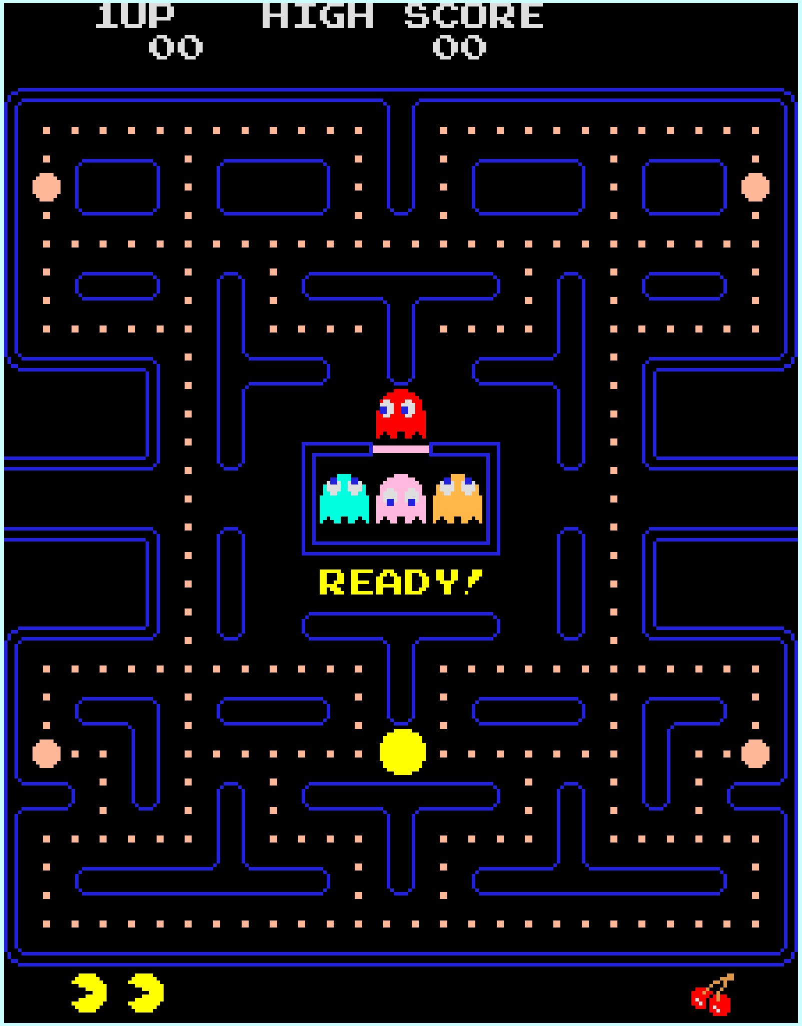
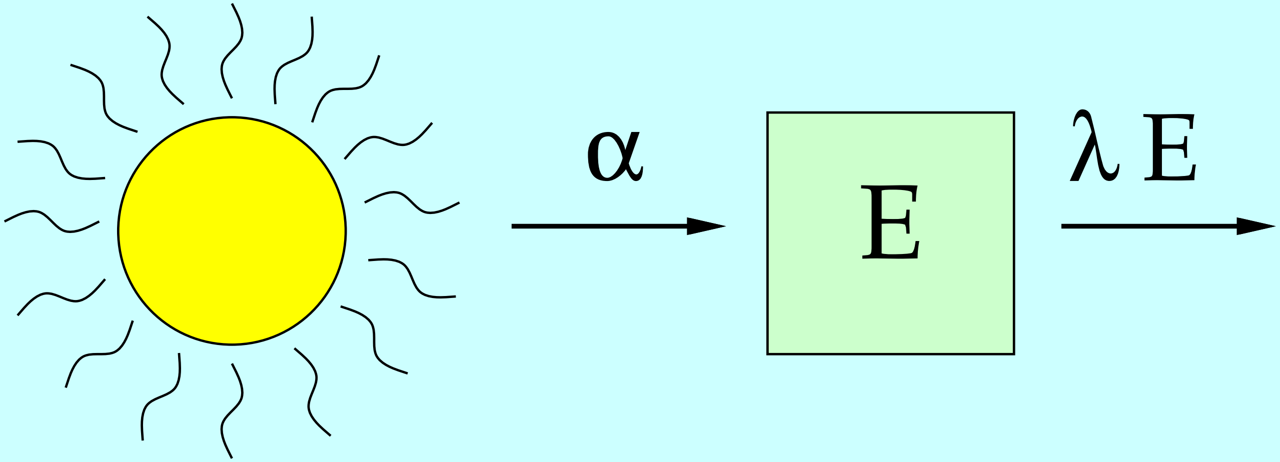
(A more recent, somewhat over-the-top, citation is by Matt Pennell and Mary O'Connor in 2017)

Sophisticated physics? Units of energy

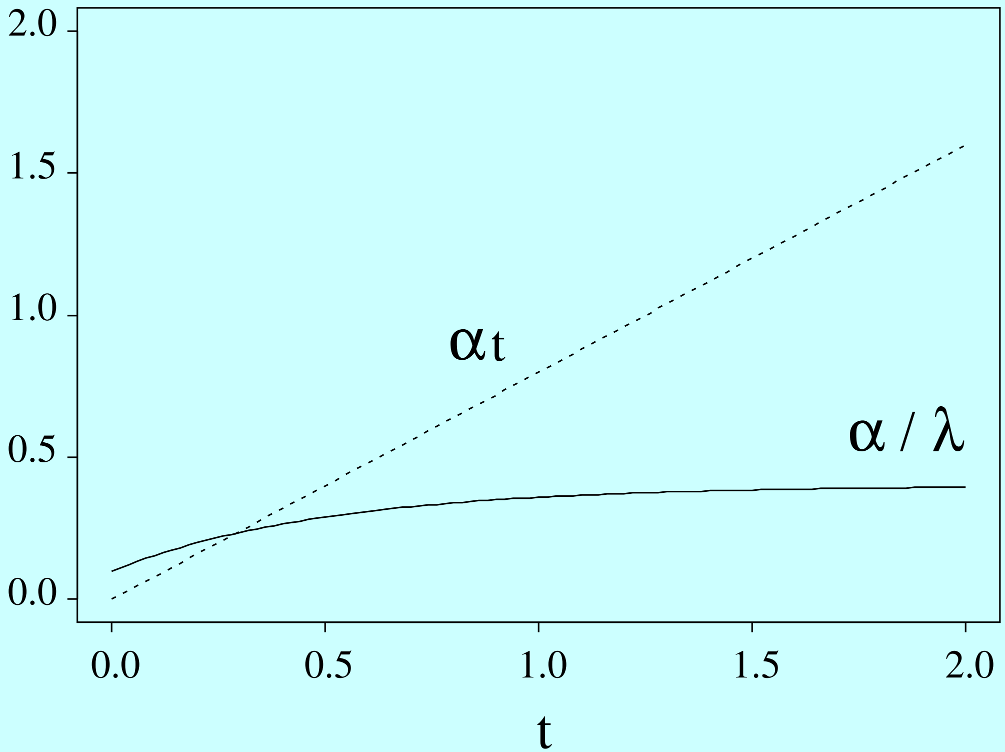


Pacman: the yellow dots are "energy dots"

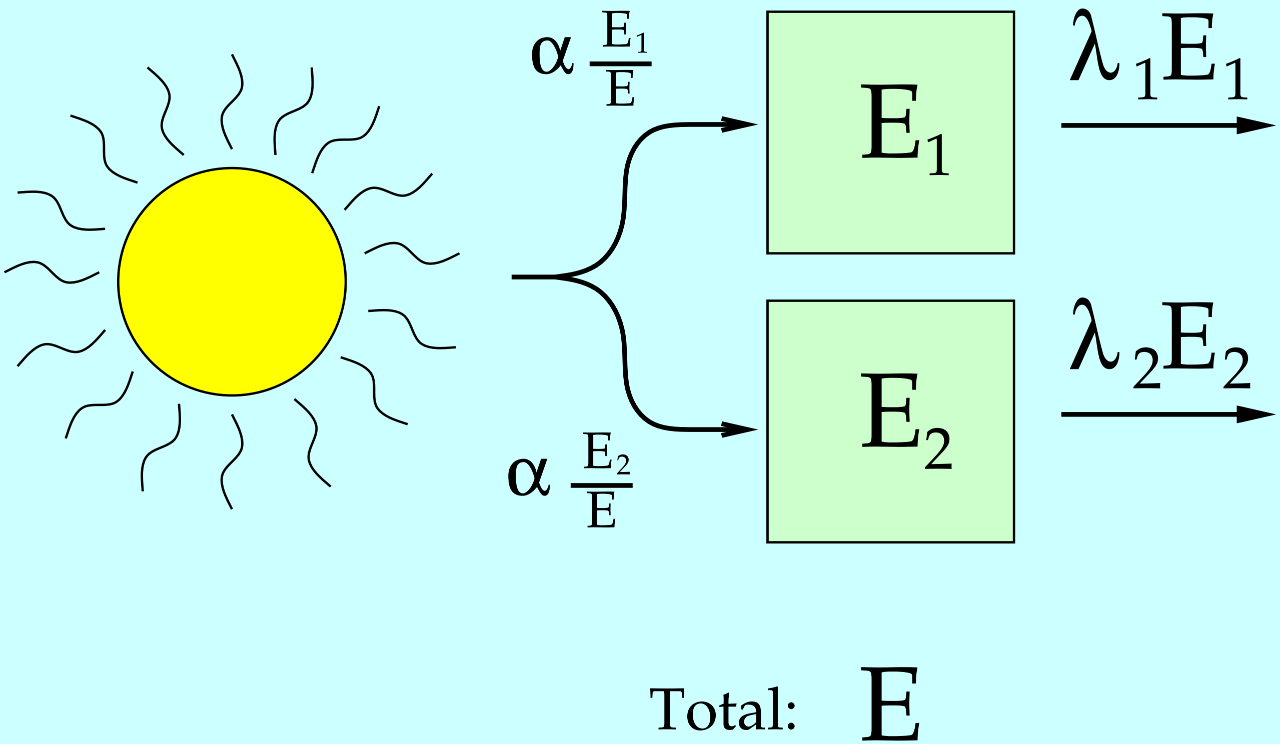
Organisms maintained by energy throughput



Change of energy content over time

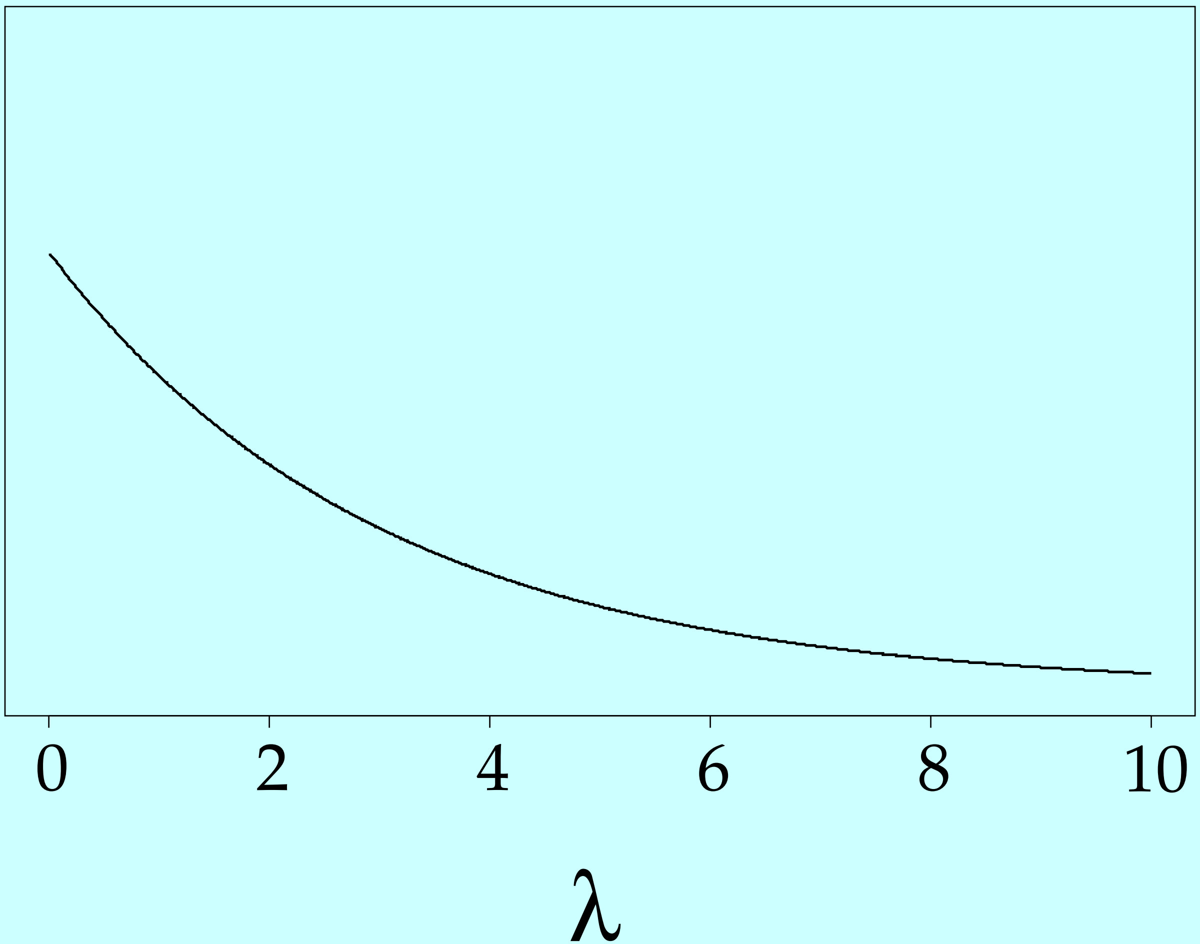


Competition based on different rates of loss



The inflow does not change the ratio of the two genotypes. The different rates of loss (λ_1 and λ_2) do. The one with the lower rate of loss takes over, with the usual kind of gene frequency change.

Assuming rates of loss are from this distribution ...



This is an Exponential distribution with expectation 3.

The result is continual improvement

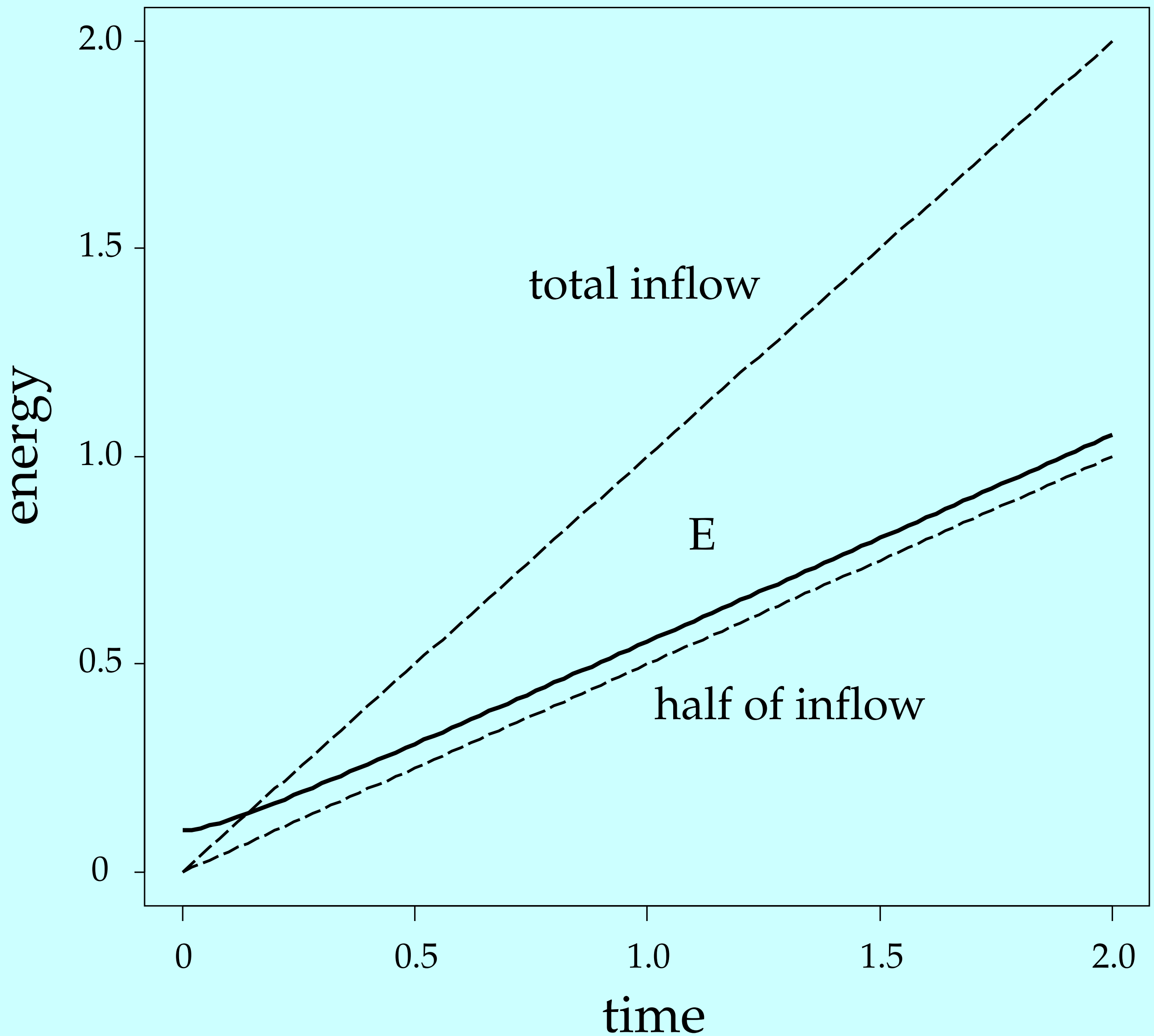
Key findings (after rather straightforward solution of a differential equation)

- The distribution remains an exponential distribution, with the expectation of λ decreasing toward zero.
- The formula for the mean λ is

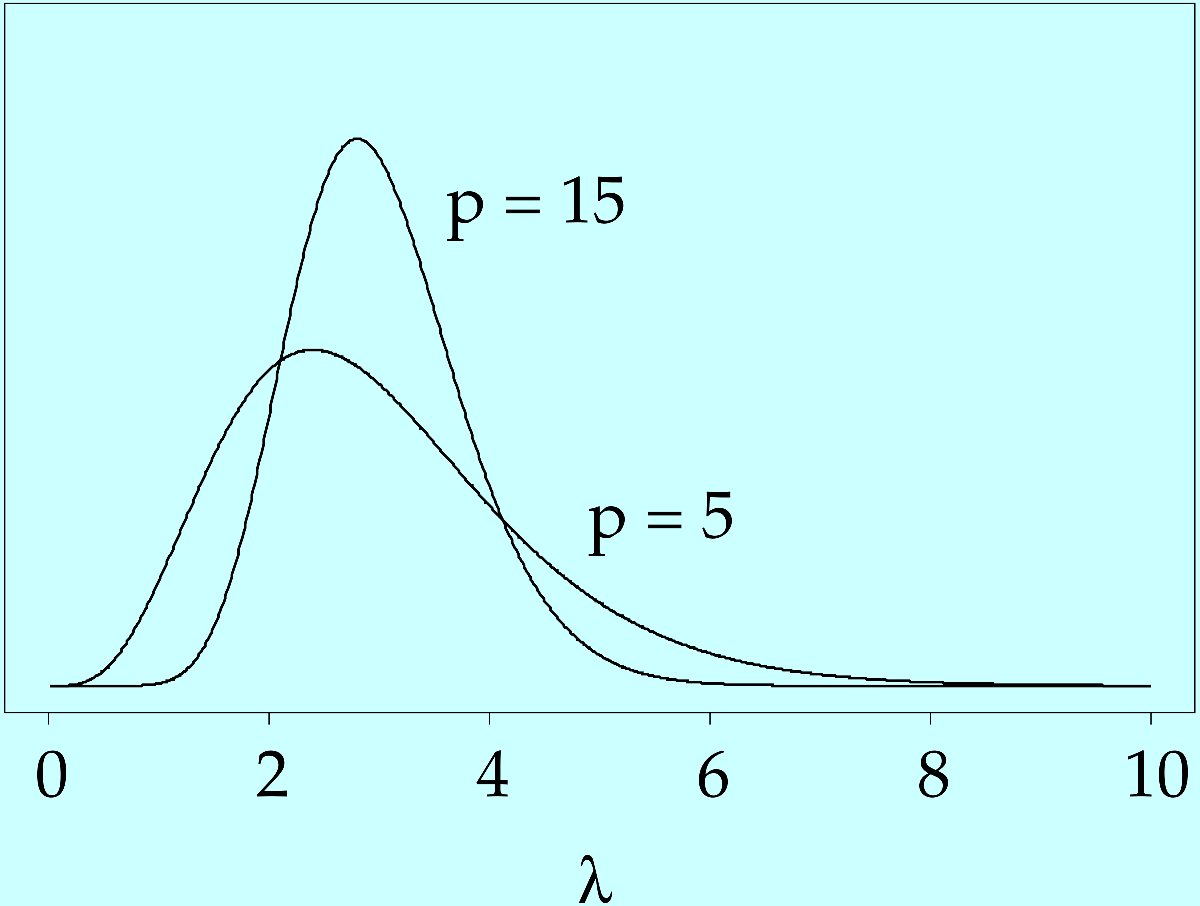
$$\bar{\lambda} = \frac{1}{\frac{1}{\bar{\lambda}_0} + t}$$

- ... and here's the surprise: the energy content E of the ecosystem increases linearly, and
- ... that means that the ecosystem contains within it at any time half of all the energy that ever flows into it!

Macroevolution from exponential rates of loss



Gamma distributions of rates of loss



Gamma distributions with different parameters but the same expected value (3). Note that the higher the value of p the rarer are the really efficient genotypes.

Macroevolution from a Gamma distribution of λ

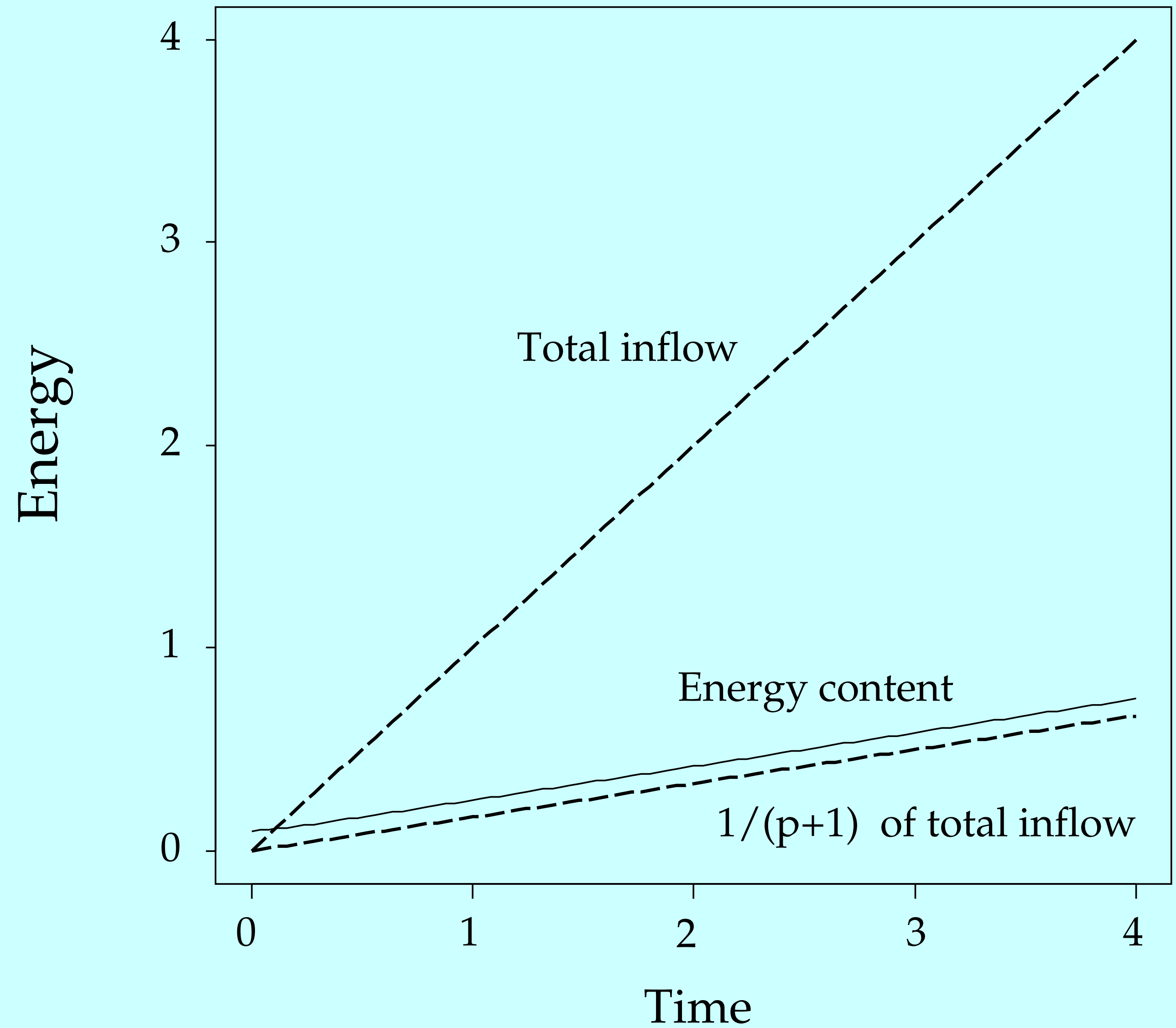
Similar results. We remain in a Gamma distribution, with the same value of p but decreasing mean rate of loss λ. Now

$$\bar{\lambda} = \frac{1}{\frac{1}{\bar{\lambda}_0} + \frac{t}{p}}$$

and again, we approach a linear increase of the energy content E, which implies that the ecosystem contains within it the constant fraction $\frac{1}{p+1}$ of all the energy that ever flows into it.

As a larger value of p means that good genotypes are rare, it is not surprising that it also means that the ecosystem retains a smaller fraction of all the energy that ever flows into it.

Macroevolution from Gamma rates of loss



Entropy

Considering three locations of energy in this model:

- The sun (s)
- The biosphere (b)
- Outer space (o)

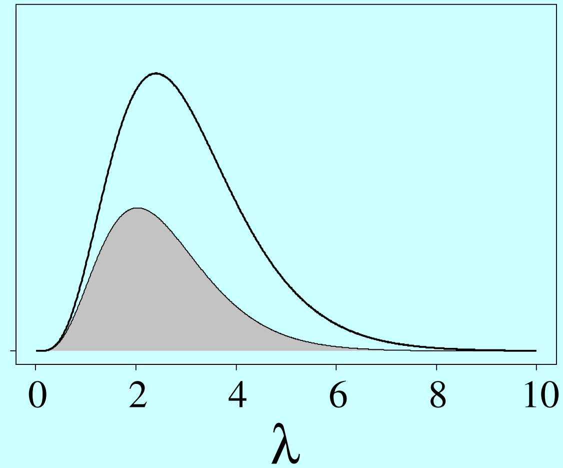
And the temperatures typical for each, T_s, T_b, and T_o, one can calculate the entropy at any time as

$$S = \frac{E_s}{T_s} + \frac{E_b}{T_b} + \frac{E_o}{T_o}$$

and record how much less the entropy increases when life is present.

That turns out to be $E_b(\frac{1}{T_o} - \frac{1}{T_b})$

Information?



- Is there a quantitative connection between increase of entropy and increase of biological information?
- If we get the Kullback-Leibler divergence between the initial and final distributions of λ, this ends up as $-\log(P) = \log(1 + \lambda_0 \mathtt{t}/\alpha)$
- This is in the long run proportional to $\log \mathtt{t}$.
- If we instead count a doubling of the population's total energy content as a doubling of its information content, then the proportionality will be with $\mathtt{t} \log \mathtt{t}$.

There's something that feels wrong about having information not be proportional to the increase of entropy.

Issues

- Is it reasonable to have energy inputs be proportional to current energy content?
- Is the family of Gamma distributions a reasonable one for initial distribution of rates of energy loss across genotypes?
- What about genetic drift?
- What about mutation?
- What about gene interactions?
- What about recombination?

The use of a model like this is to explore assumptions, and the relationships they imply. Not to give a quantitative account of the real world.

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