

Journées de Rochebrune – Janvier 2022

Evolution, Complexité et Flèche du Temps

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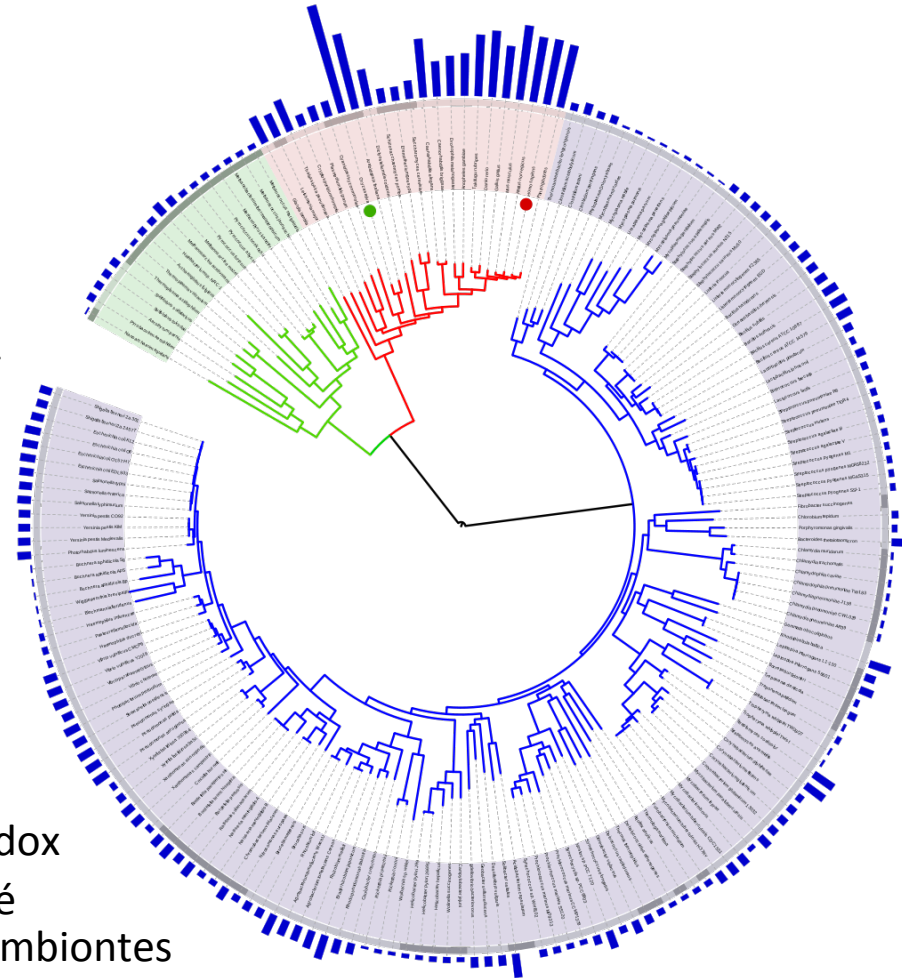
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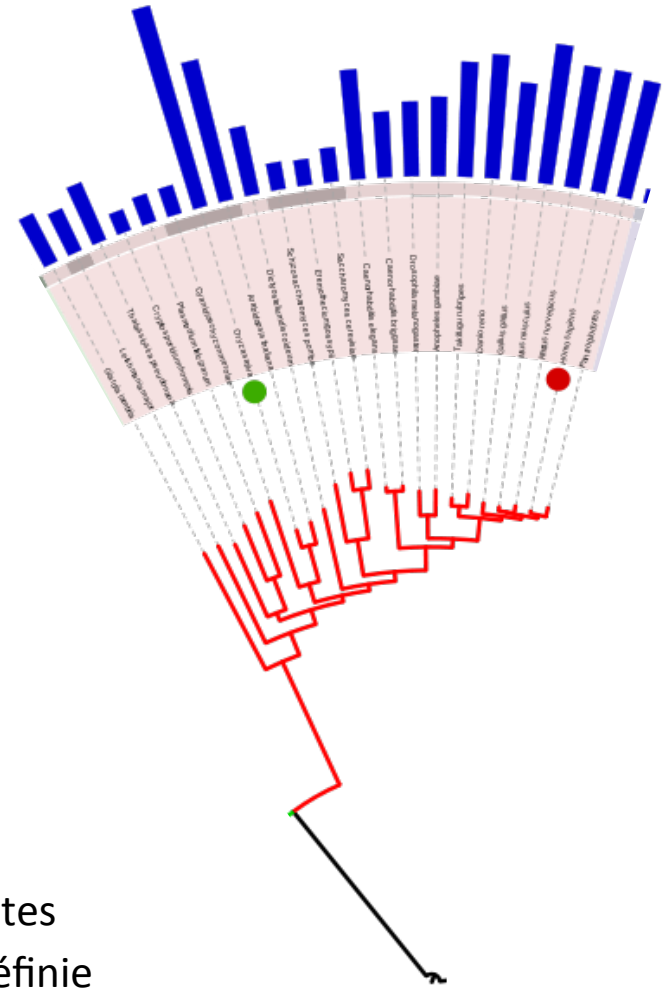
L'évolution est un processus inscrit dans le temps

- Observation naïve :
 - Les systèmes vivants se complexifient au cours de l'évolution
 - Il y aurait une « flèche de la complexité » au cours des temps évolutifs
 - Mais cette idée repose sur un anthropomorphisme
- Une analyse plus avancée de la complexité des systèmes biologiques offre une vision plus nuancée
 - La complexité n'est pas corrélée entre les « niveaux d'organisation » → C-value paradox
 - Plusieurs organismes ont vu leur complexité décroître au cours de l'évolution → endosymbiontes
 - Et en plus la complexité biologique est très mal définie
- Reste que la complexité s'est accrue, au moins dans certaines lignées ...



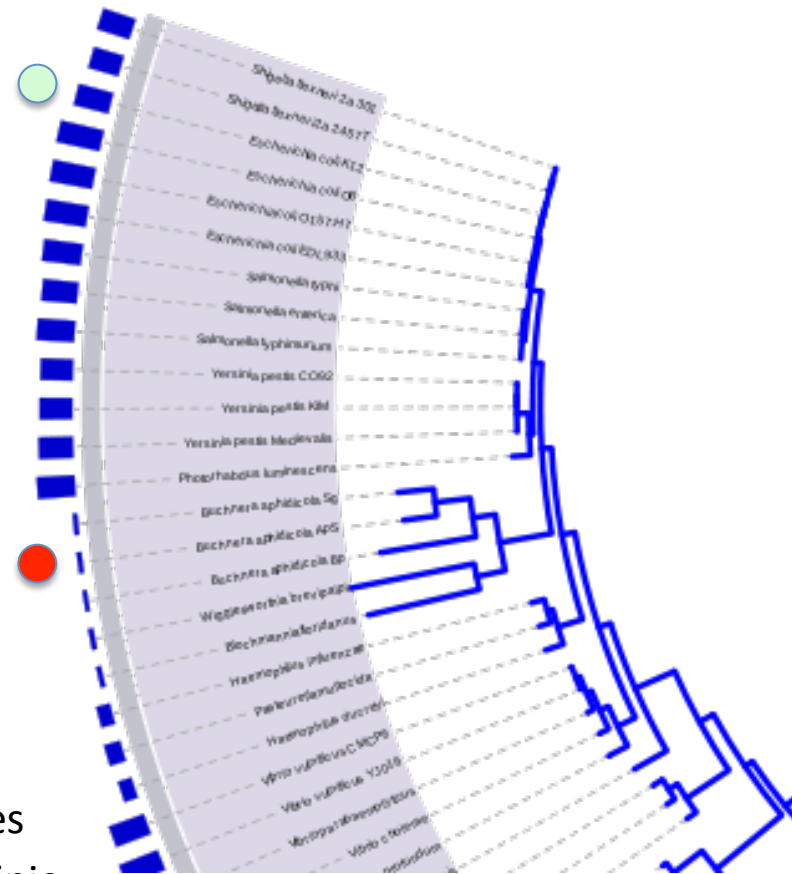
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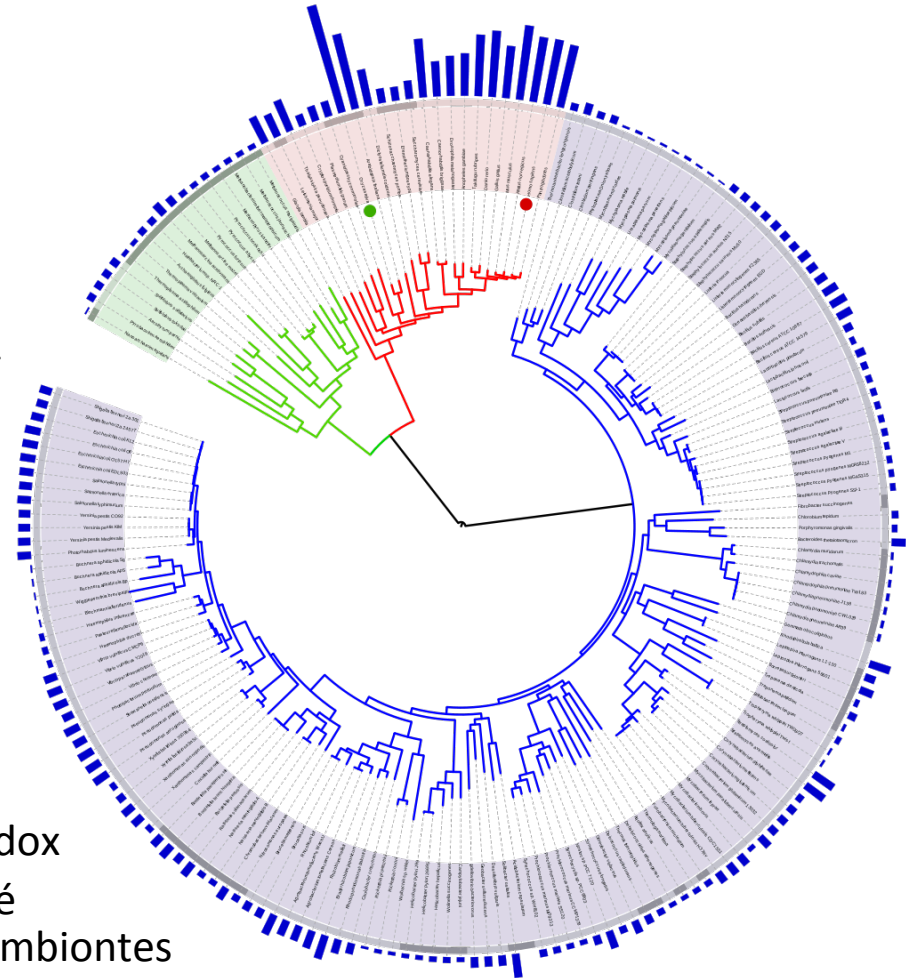
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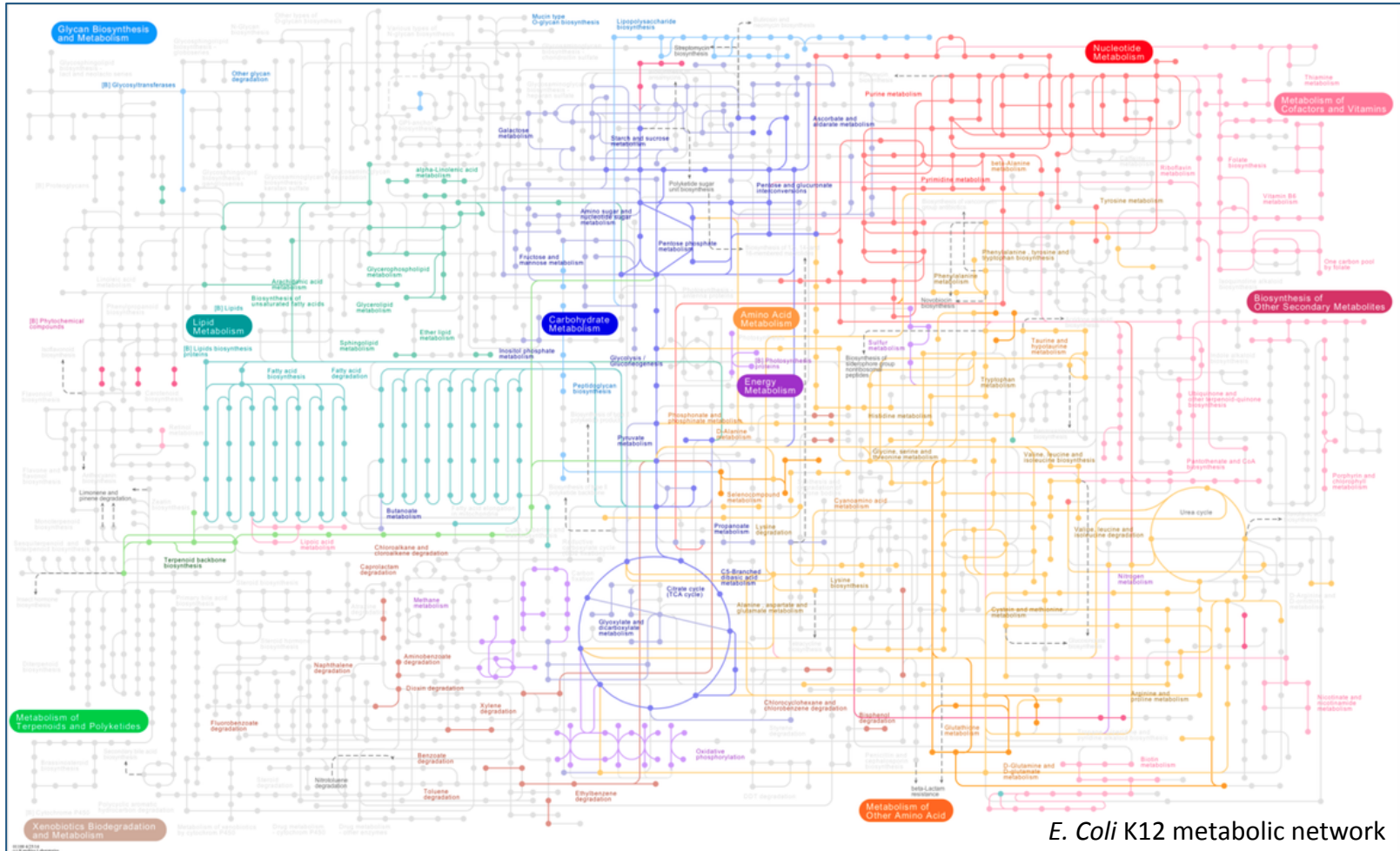


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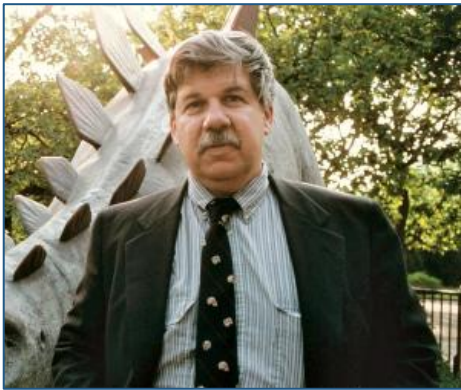
What is the evolutionary origin of biological complexity ?



→ Necessity or historical contingency (“Tinkering”) ?

Why are biological organisms so complex?

- Two families of evolutionary hypotheses
 - Neutral (simple consequence of random mutation accumulation)
 - Selective (complex organisms are better adapted)



Stephen Jay Gould:
"Drunkards walk model"

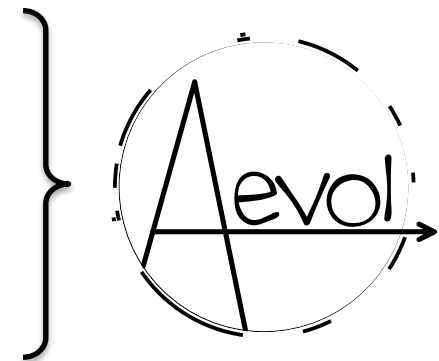


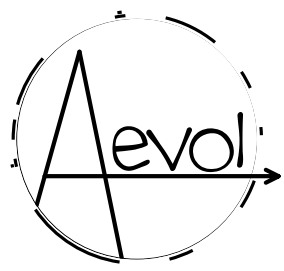
Richard Dawkins:
"Progressive increase in [...] complexity is to be expected only in taxa [that benefit from] complexity."

→ *How can we discriminate both explanations? Or propose others?*

A null (and impossible) experiment

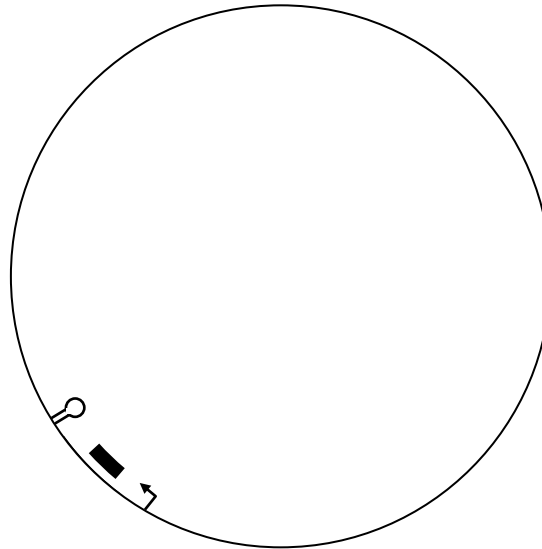
- Let populations evolve in situations where there is no selective pressure for complexity (i.e. evolution in a “simple” environment)
 - “Impossible experiment” (with real organisms)
- Let’s turn to artificial organisms → *in silico* experimental evolution (aka “digital genetics”)
 - Need for a platform in which complexity can evolve
 - Need for a platform that dissociates complexity at:
 1. Genomic level
 2. Functional level 1 (proteome)
 3. Functional level 2 (phenotype)
 4. Population/environment levels (fitness)





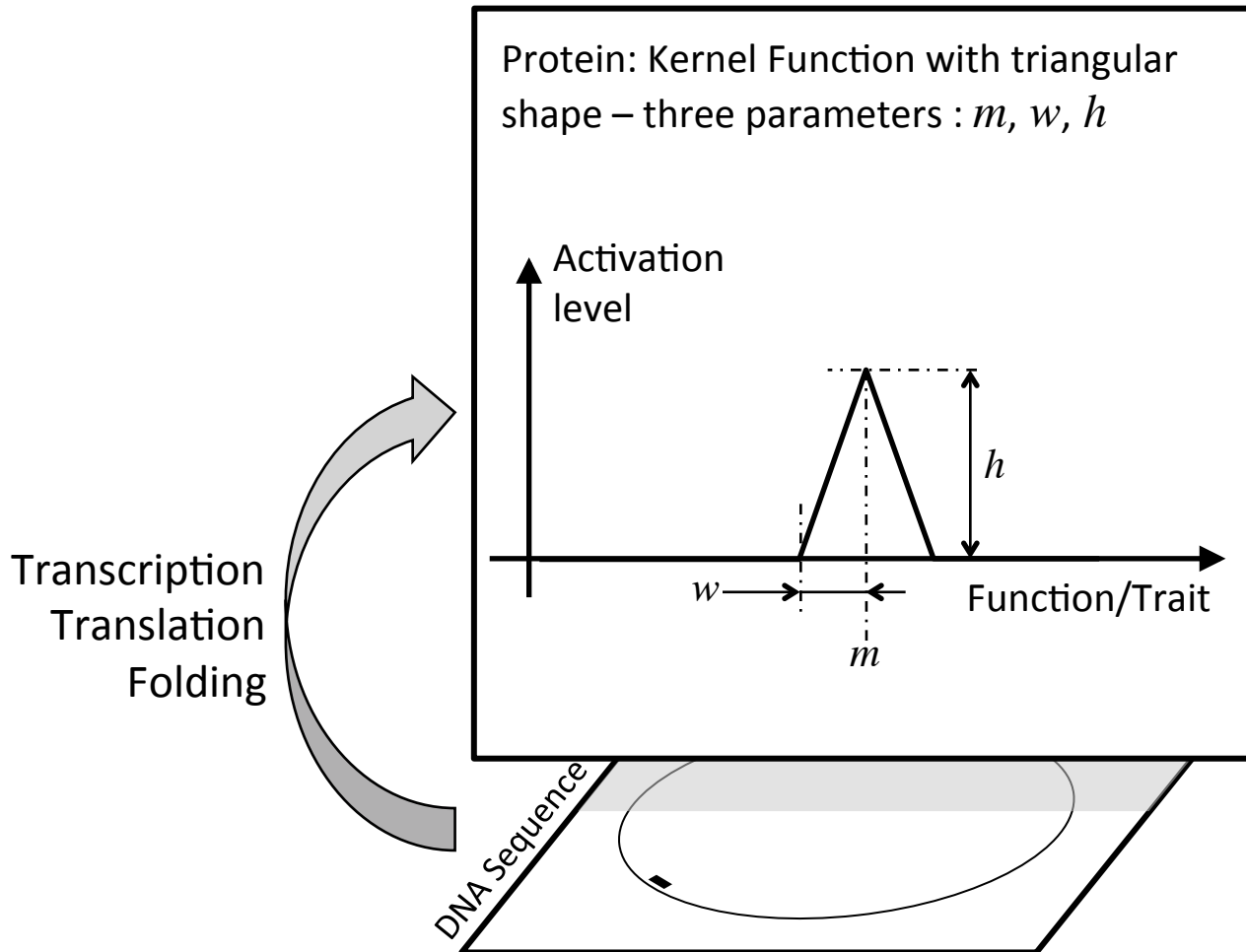
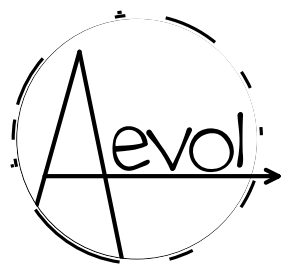
Aevol: an in silico experimental evolution platform with a realistic genome structure

Double-stranded circular binary sequence ;
Genes identified by signaling sequences

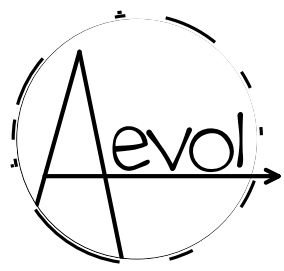


Genomic complexity: C_G

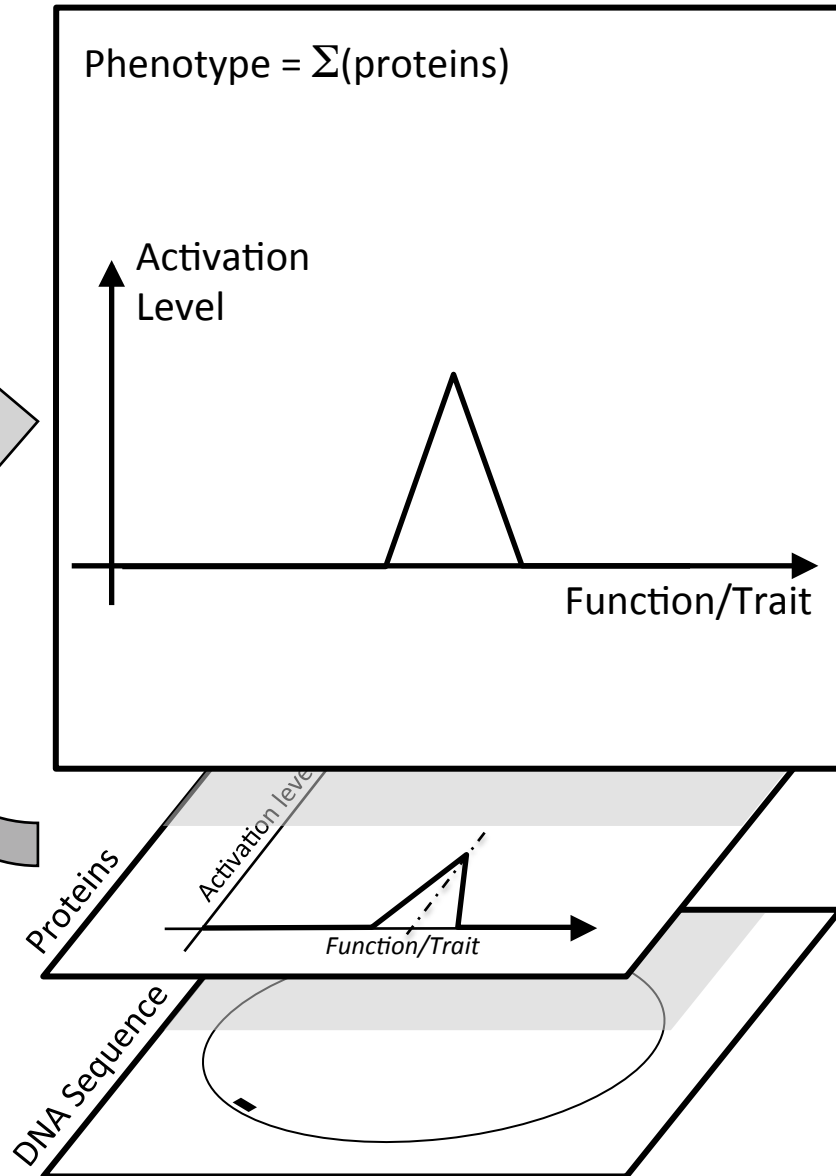
*Measured by the quantity of information stored in the genome (Adami, 2000).
The quantity of information is equal to the number of base-pairs which mutation would change the phenotype (aka “essential genome”)*



Functional complexity: C_P
Measured by the quantity of information stored in the proteome (Adami, 2000). The quantity of information is equal to the number of parameters needed to describe the proteome (i.e. number of different m , w , h values).



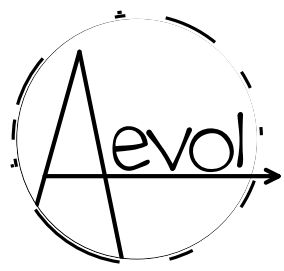
Linear
combination



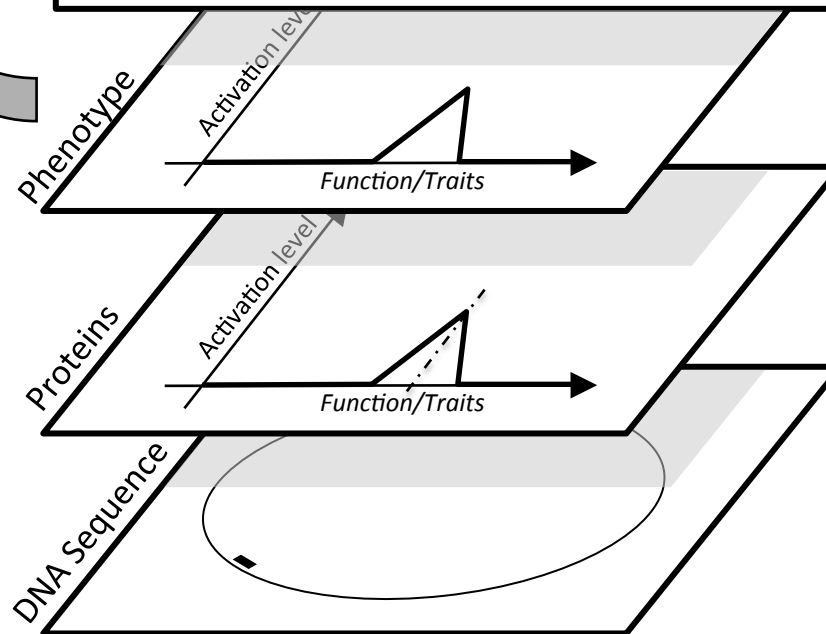
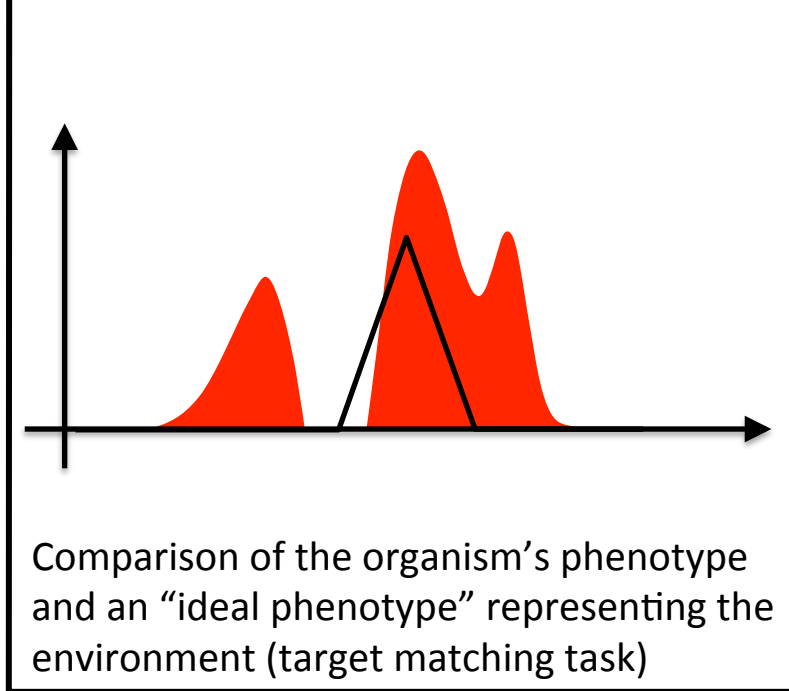
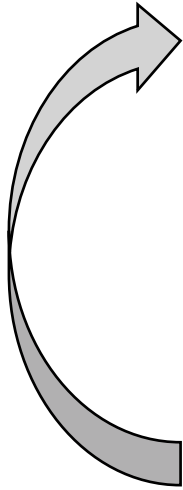
Simple (S) vs Complex (C) phenotypes

An organism/phenotype is considered “simple” if all its proteins contribute to a same function s (possibly with different activation levels).

An organism with only one gene is always simple but organisms with multiple genes can also be simple...

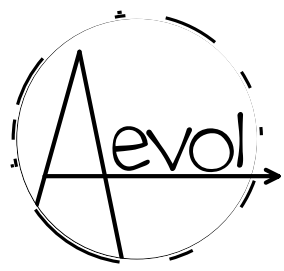


Fitness
computation

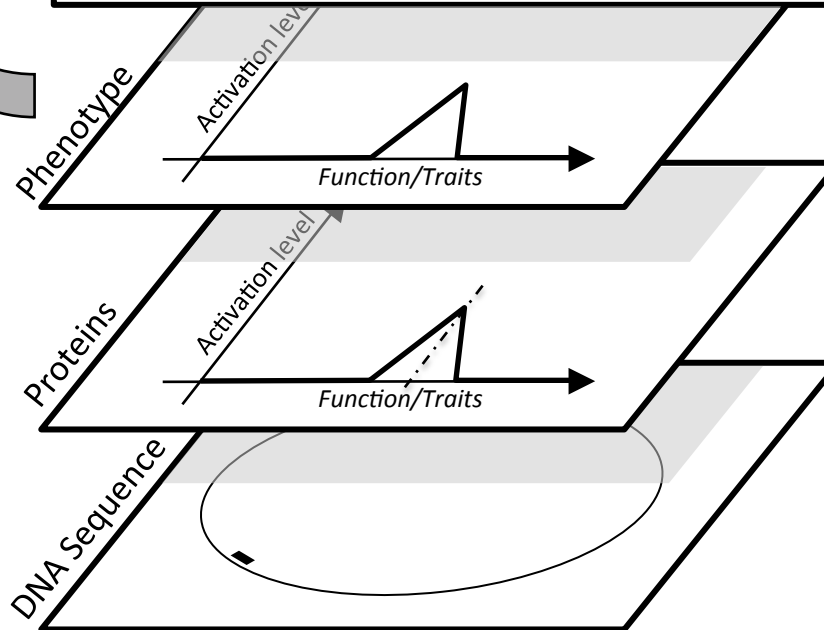
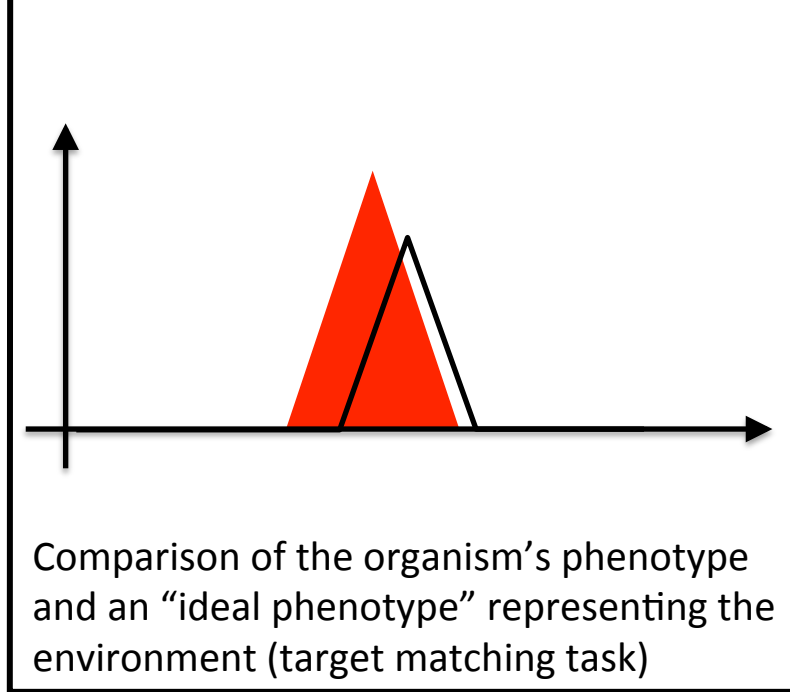
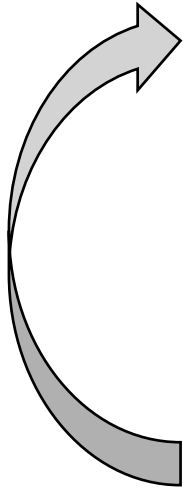


Simple vs Complex environments

*An environment is
considered to be simple if the
target function can be fitted
by a single gene/protein.
Classical aevol experiments
use a combination of
Gaussian functions to force
evolution of complexity*

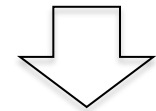


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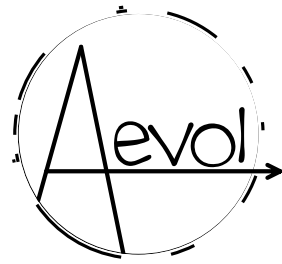
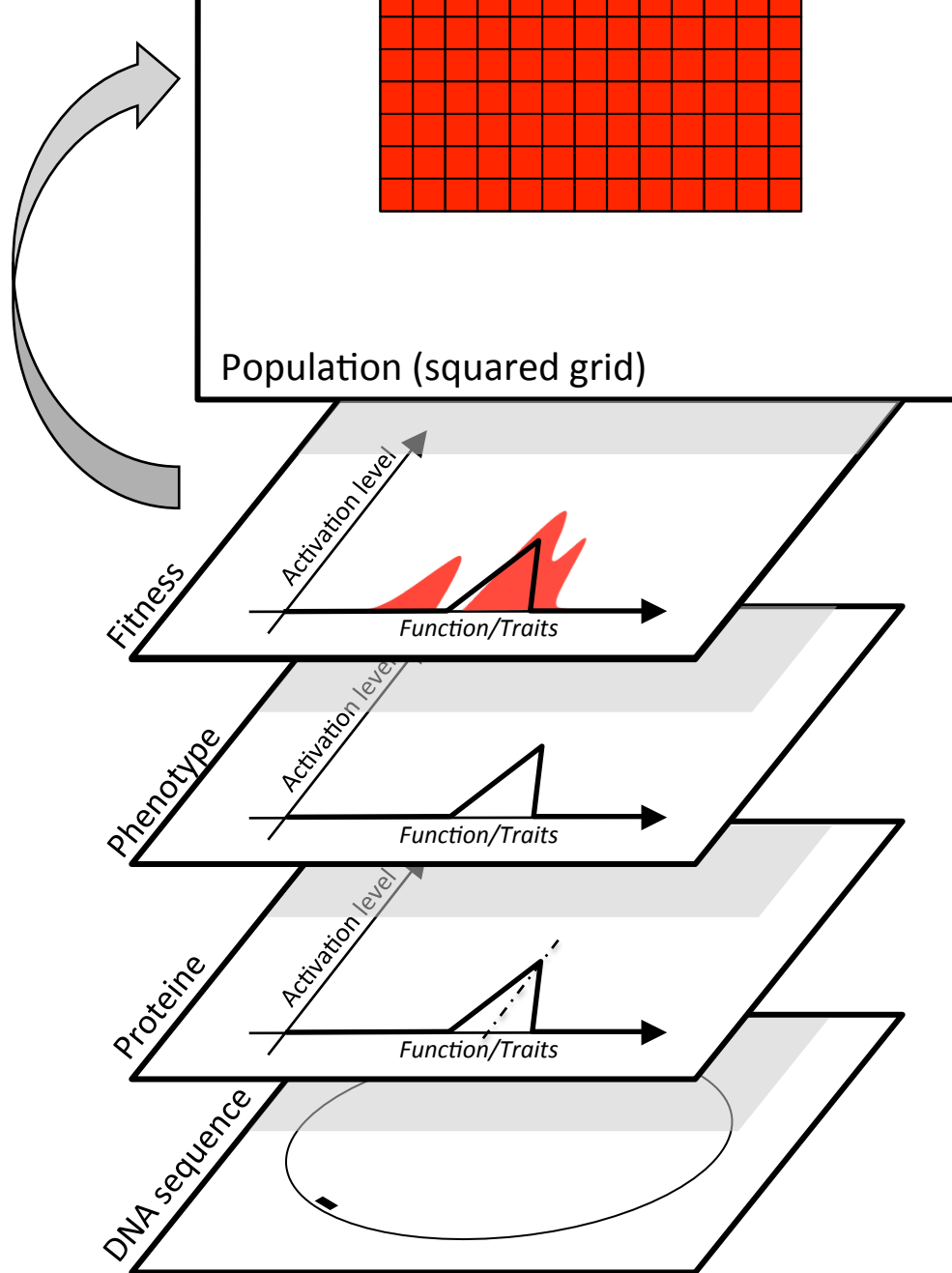
Simple vs Complex environments

An environment is considered to be simple if the target function can be fitted by a single gene/protein. Classical aevol experiments use a combination of Gaussian functions to force evolution of complexity



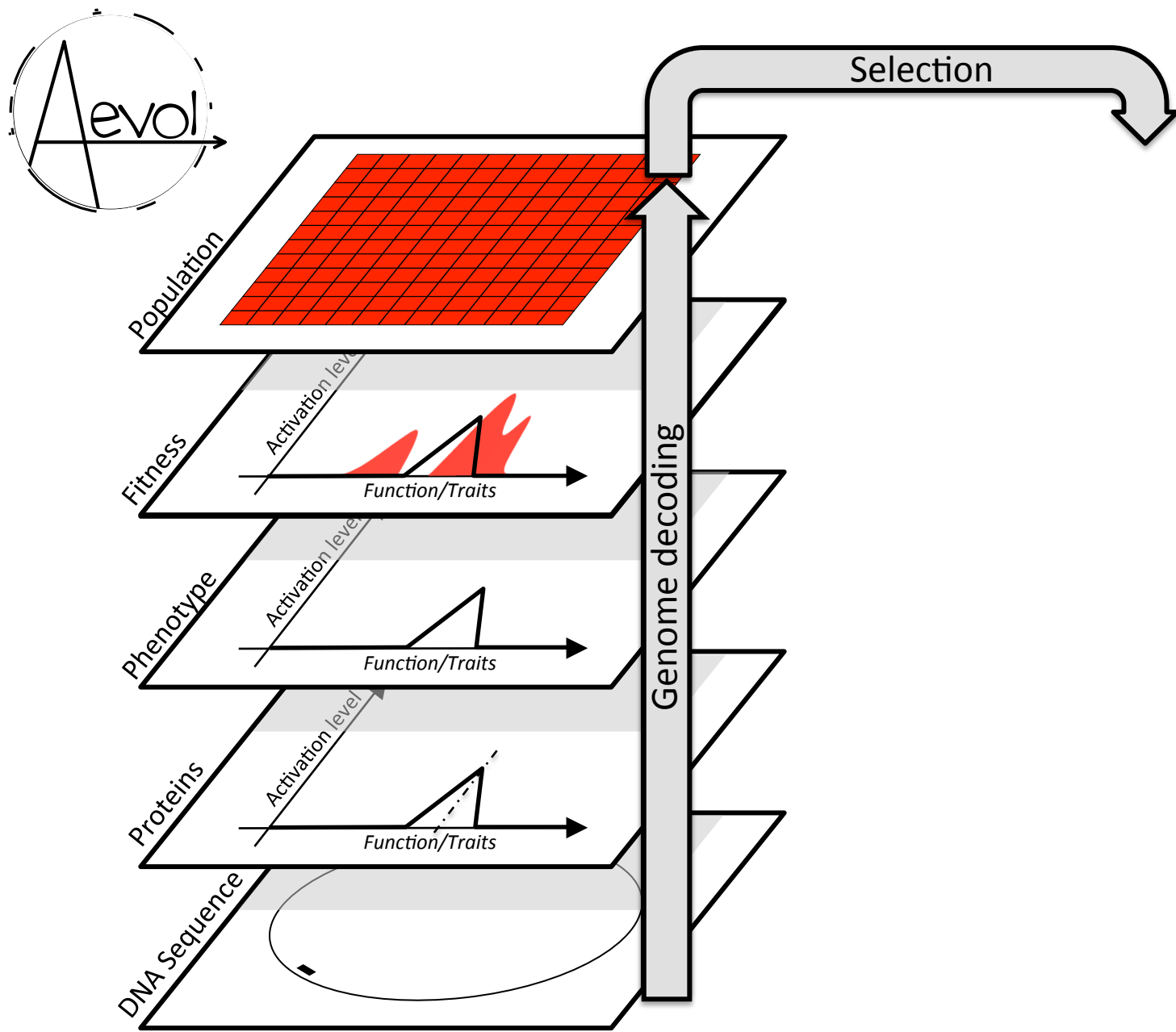
Here we will use a triangular target, ensuring that simple organisms can easily thrive and that complex organisms are not favored in this environment.

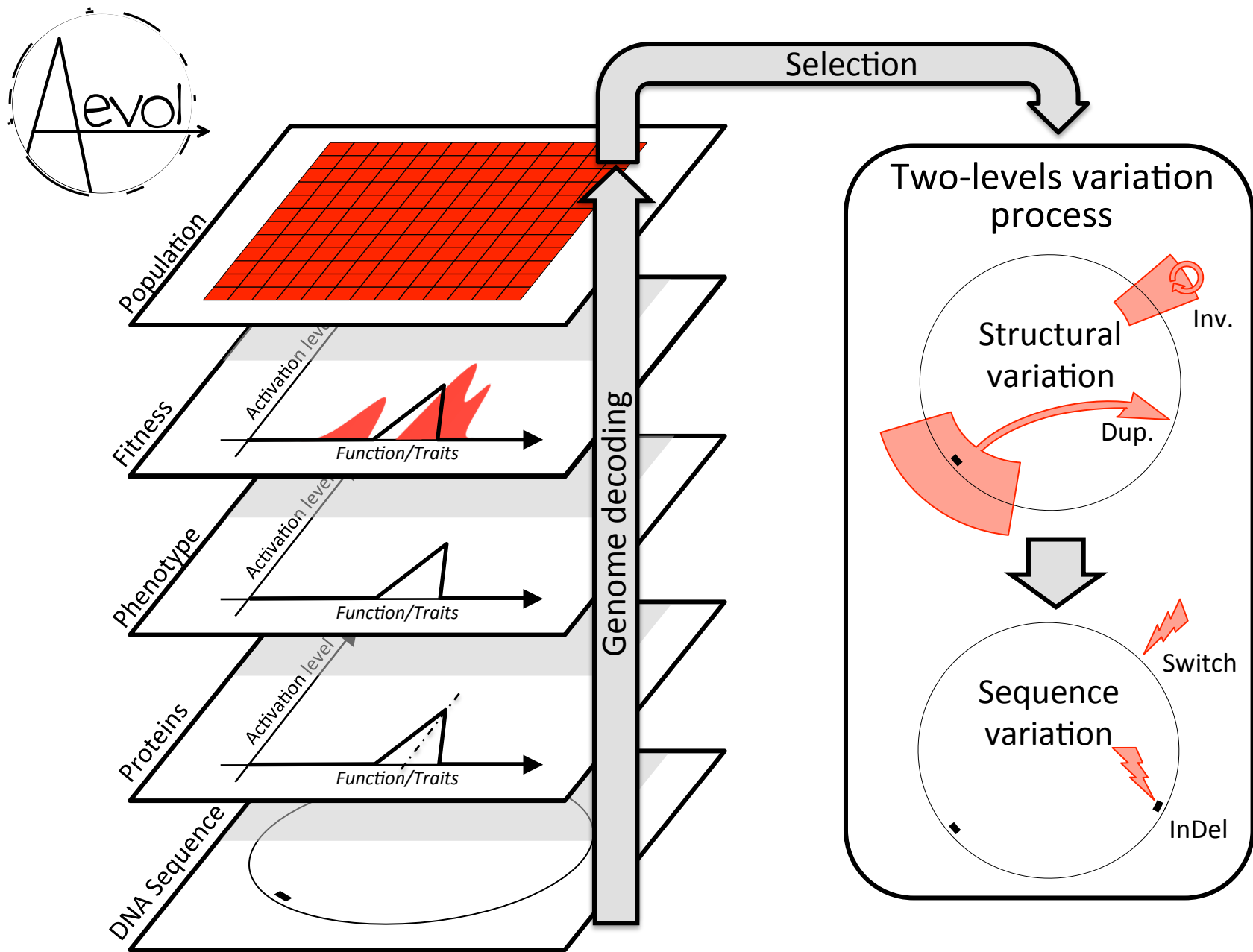
N individuals

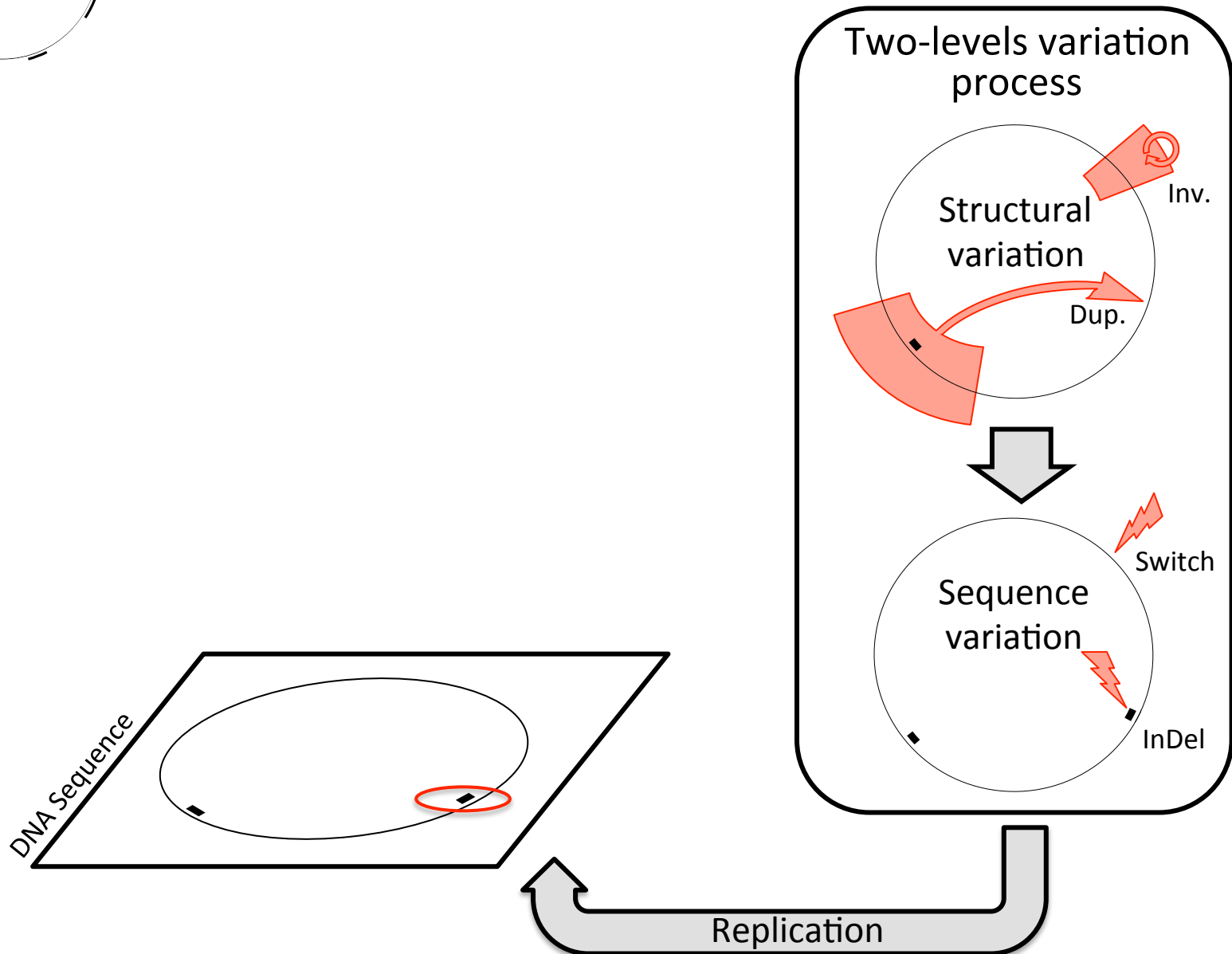
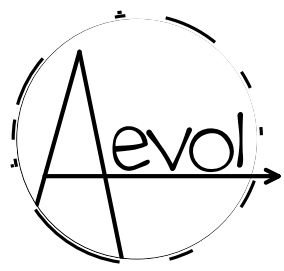


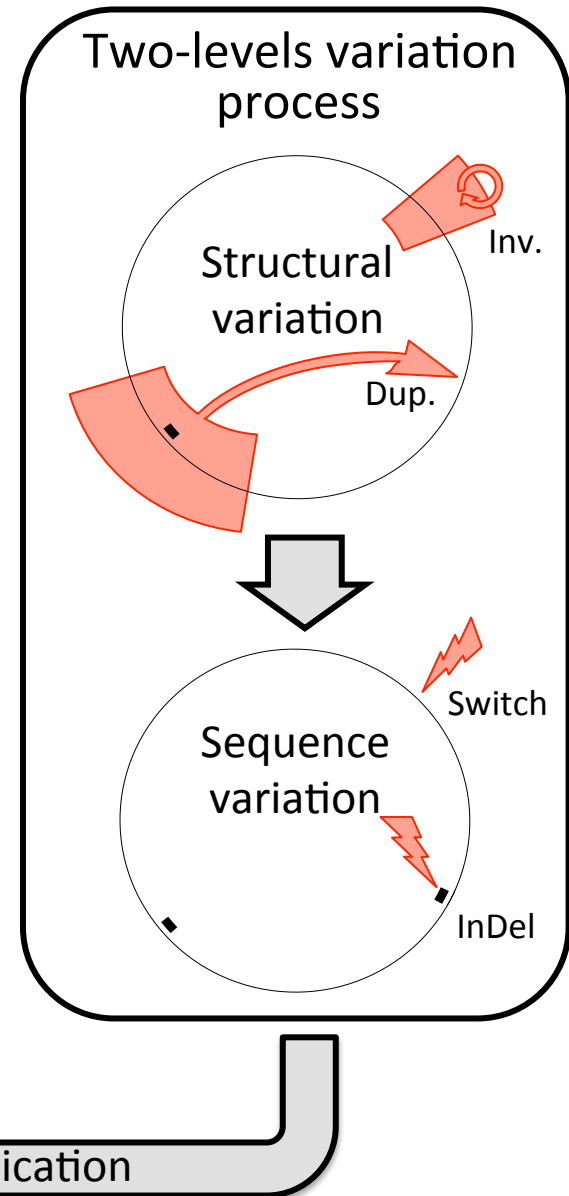
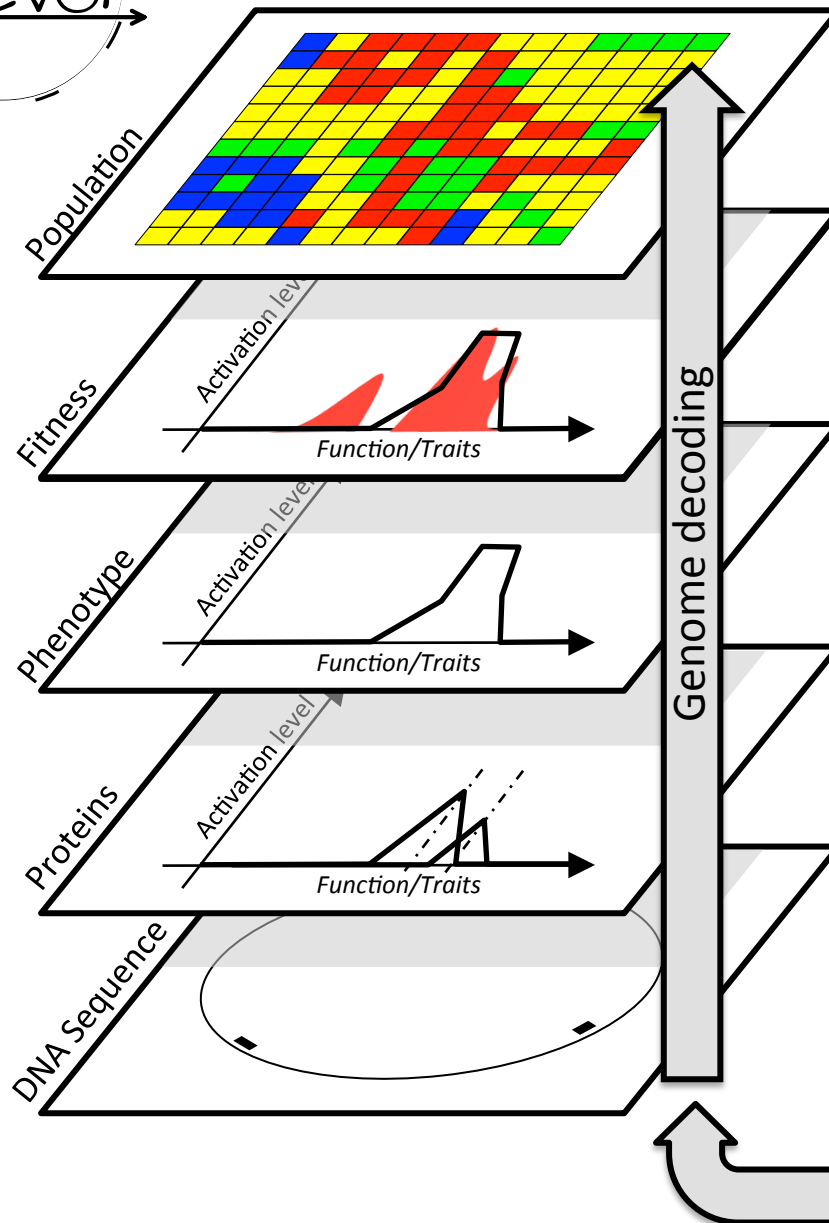
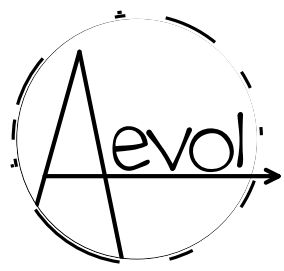
Population complexity

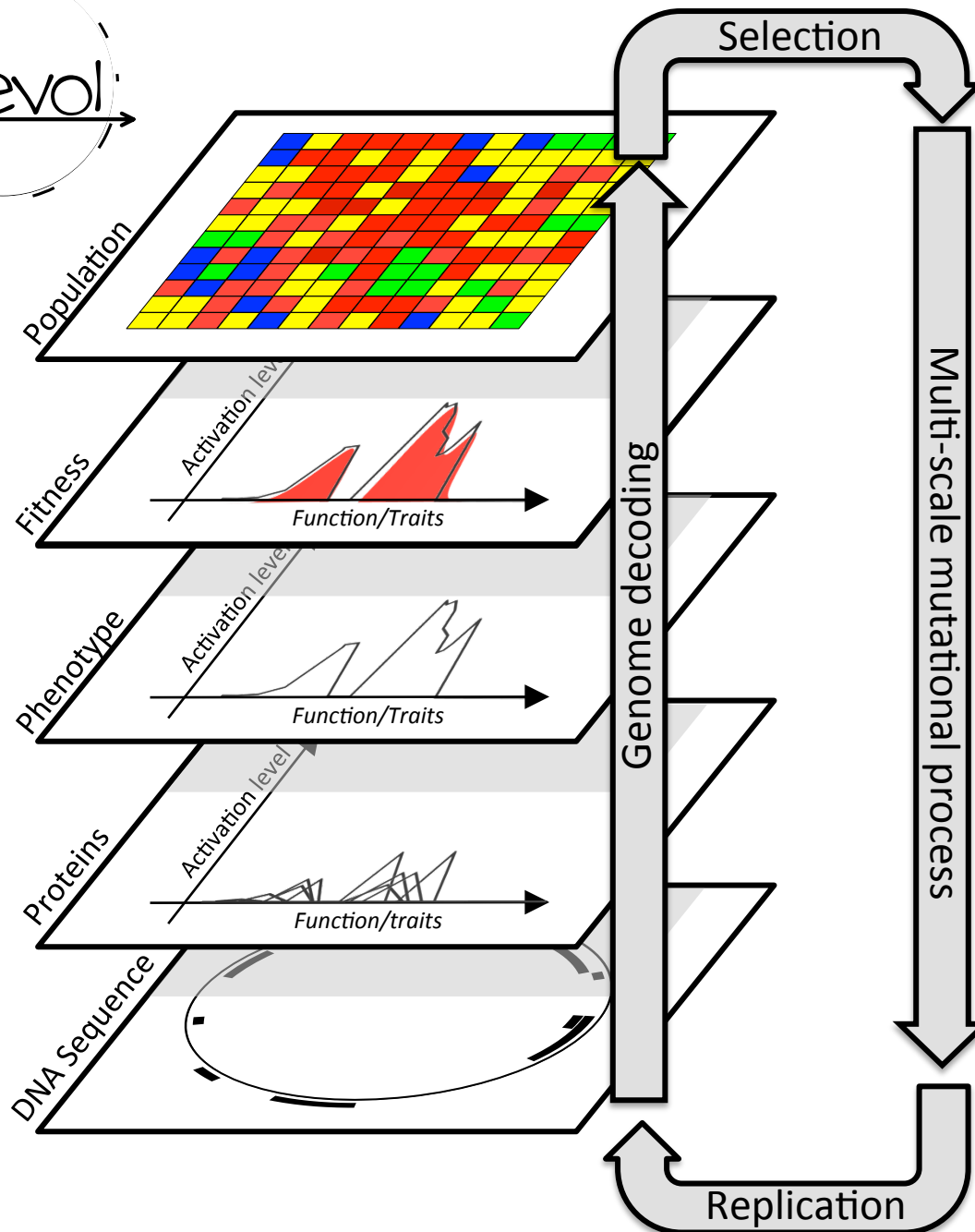
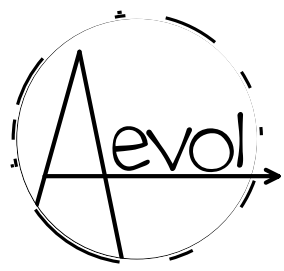
Population complexity can be estimated by the level of polymorphism in the population. This level is not taken into account in this study.





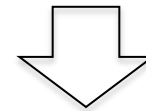






10 000 generations later...

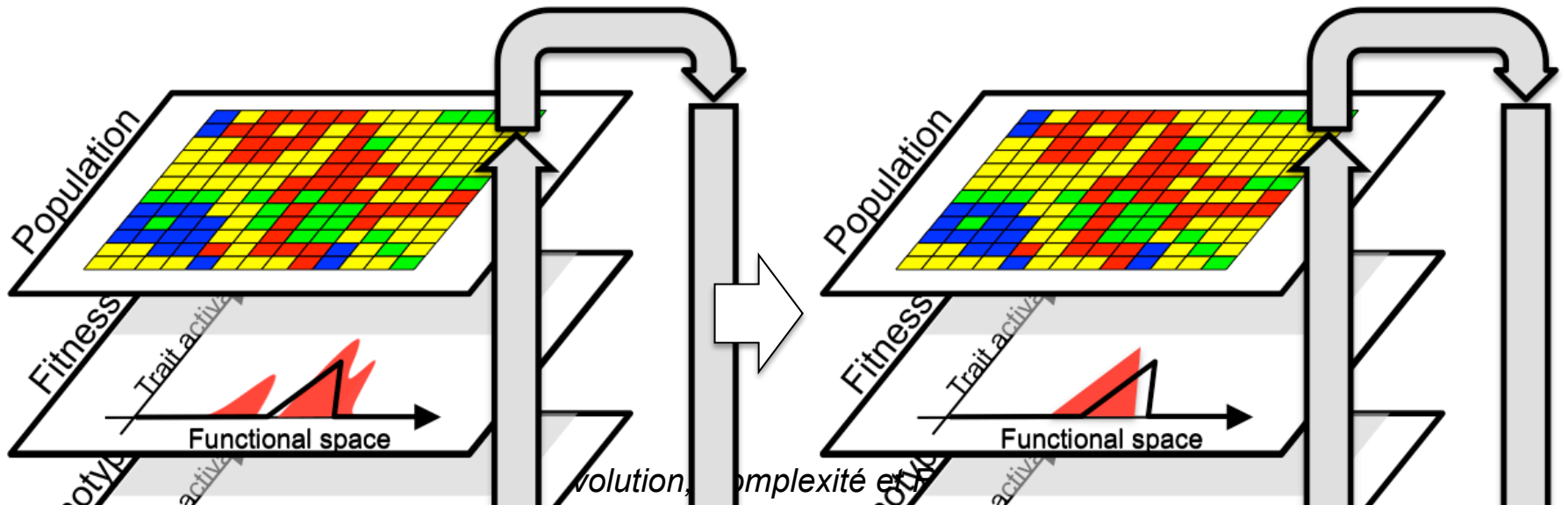
*Complexity increased at all levels (C_G , C_P , C).
But complexity is likely to be driven by target complexity...*



What will occur if we replicate this experiment in a simple environment (i.e. a triangular target function)?

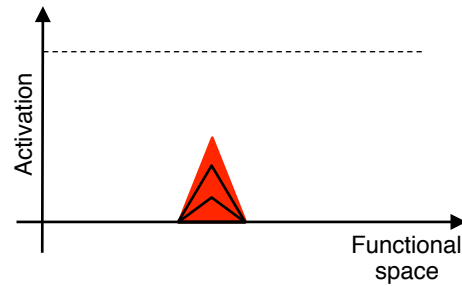
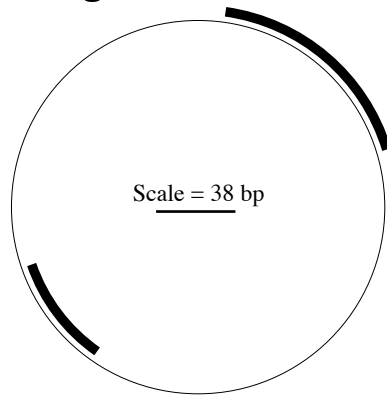
Experimental setup

- Modified Aevol: the phenotypic target is a “simple” function
 - i.e. a function that can be fitted by a single protein (a single triangle with $m = 0.5$, $w = 0.1$, $h = 0.5$).
 - Static environment, no niche construction, no arm race
 - Three different mutation rates (10^{-4} ; 10^{-5} ; 10^{-6} mut.bp $^{-1}$.gen $^{-1}$)
 - 100 repetitions per mutation rate, 250.000 generations
 - Monitoring of fitness, genetic complexity (C_G), functional complexity (C_P) and phenotypic complexity (S/C organisms)



Results (1/5): even in a simple environment, complex organisms evolve in 210/300 simulations

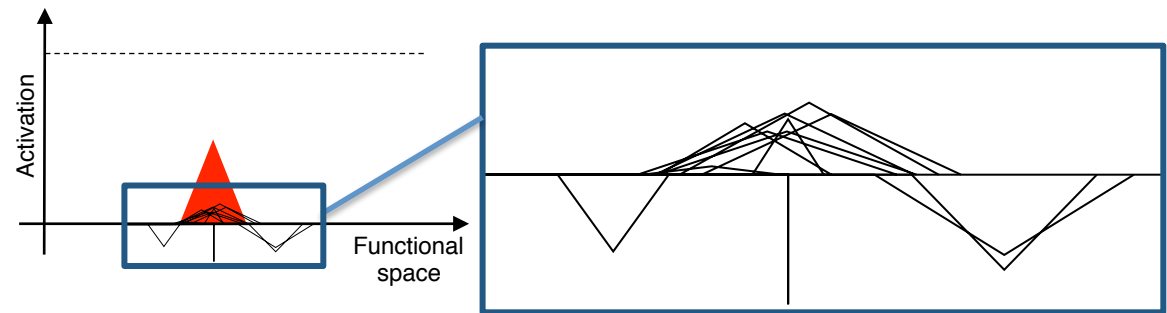
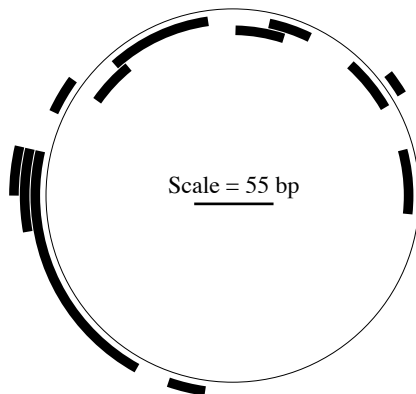
Simple organism



Mut. Rate	Nb S	Nb C
10^{-4}	39 ± 9.6	61 ± 9.6
10^{-5}	29 ± 8.8	71 ± 8.8
10^{-6}	22 ± 8.0	78 ± 8.0

All mutation rates in mutations.bp⁻¹.generation⁻¹

Complex organism



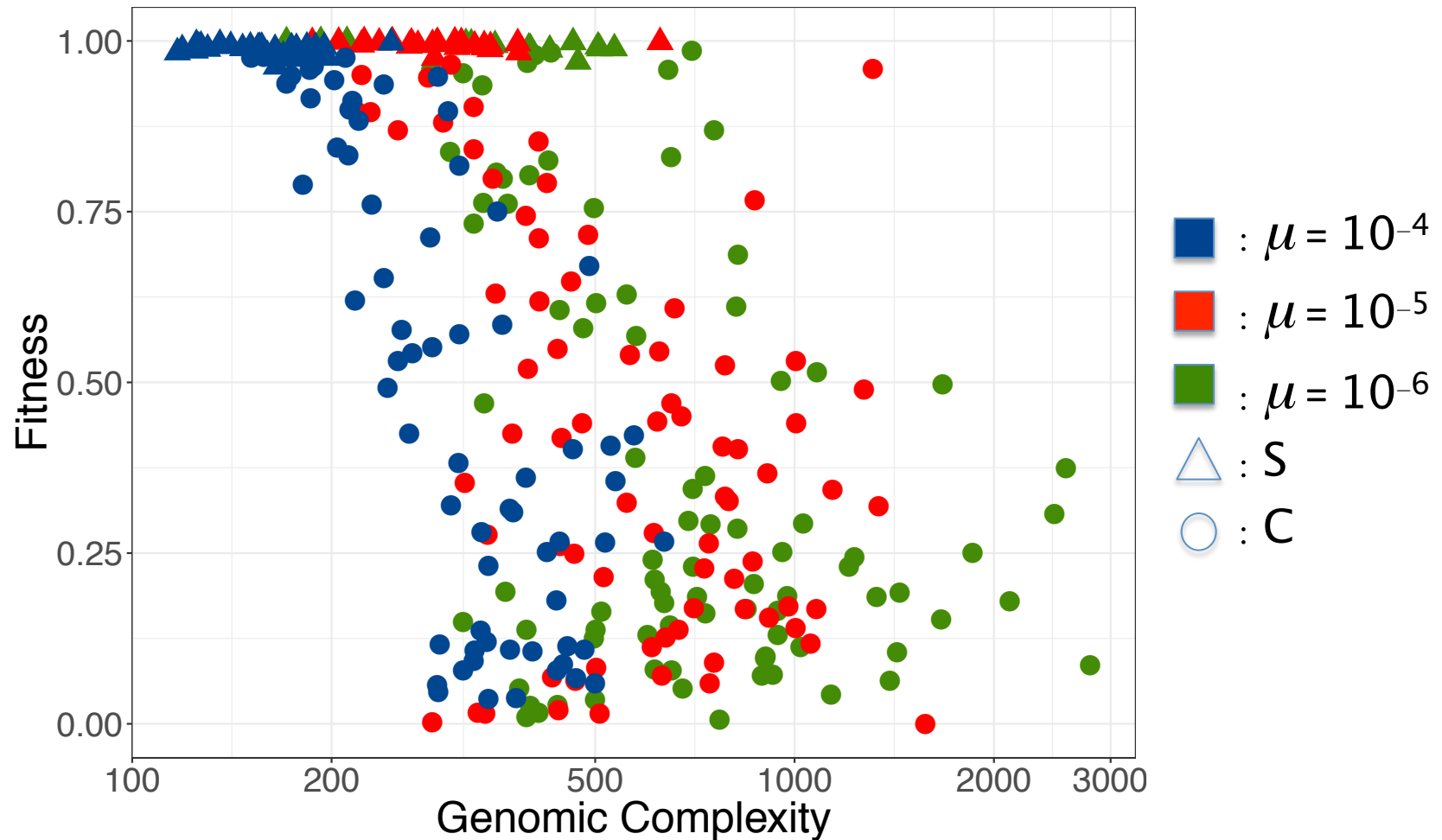
Why?

- Hypotheses from literature
 1. Selective hypotheses
 - a. Direct selection: complex are better
(Dawkins, 1997 ; Albantakis et al., 2014 ; Zaman et al., 2014 ; Maslov et al., 2009)
 - b. Indirect selection: complex evolve better due to selection for robustness or evolvability
(Simon, 1962 ; Lenski et al., 1999 ; Soyer & Bonhoffer, 2006)
 2. Neutral mechanism: accumulation of variation
(Gould, 1996 ; McShea & Brandon, 2010 ; Lukes et al., 2011)

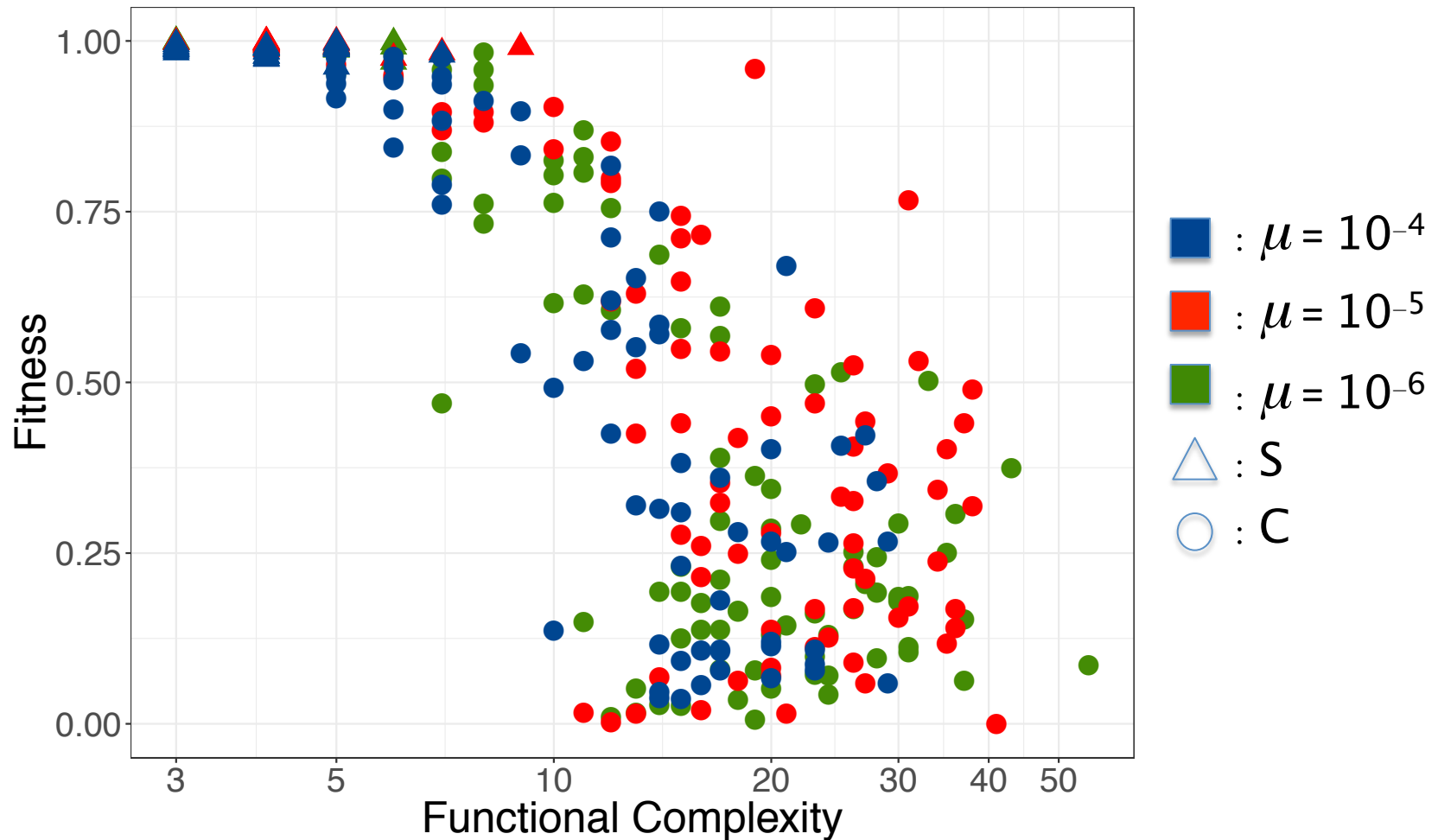
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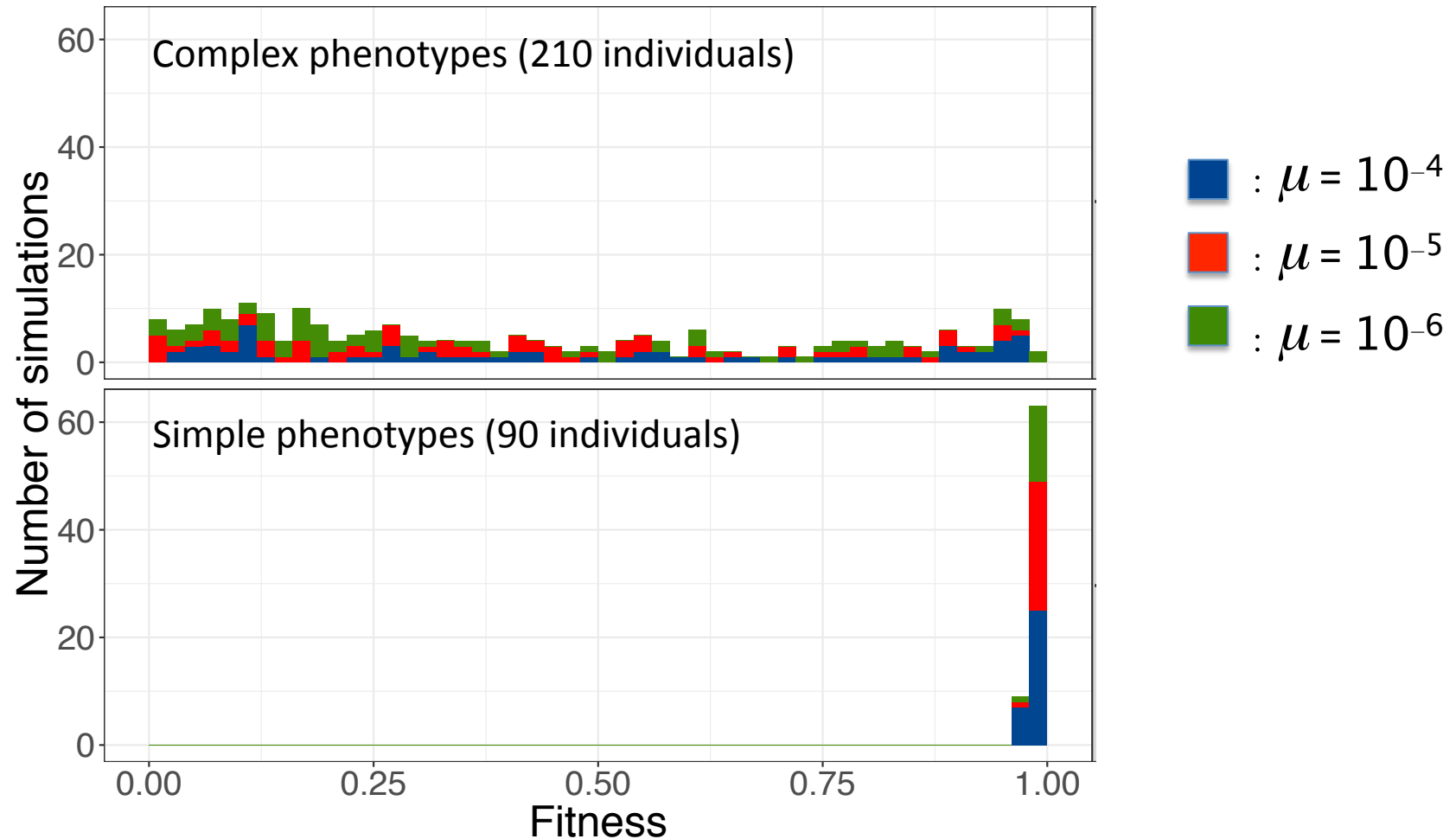
Results (2/5): simple organisms are better than complex ones whatever the complexity measure



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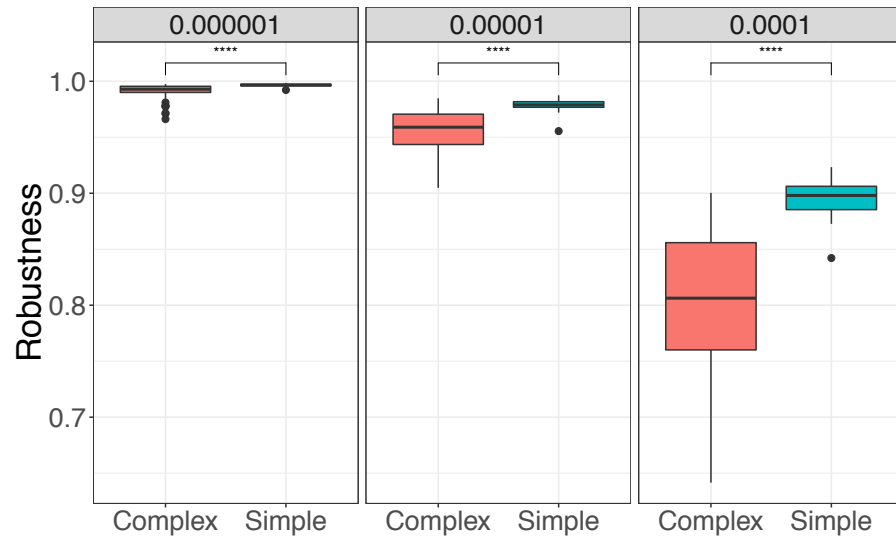
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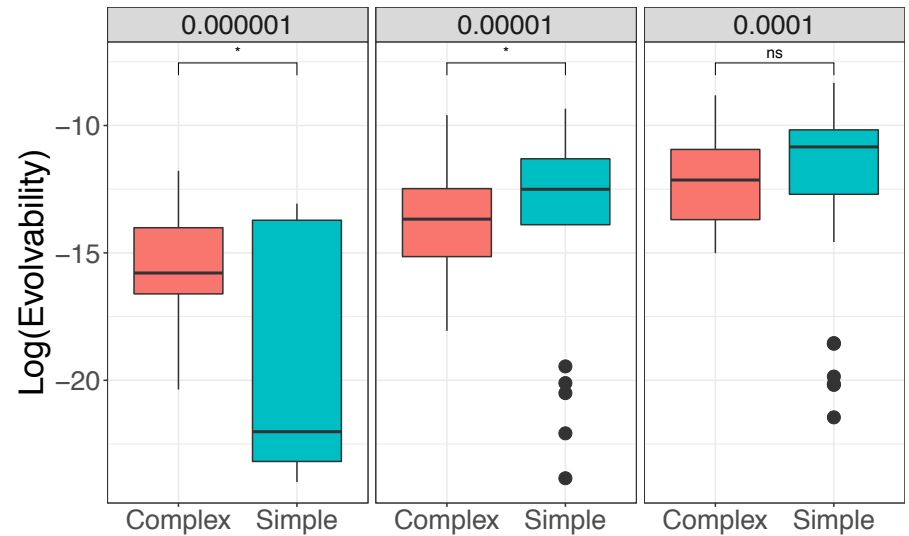
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Result (3/5): Being complex gives no robustness or evolvability advantage (on the opposite!)



Simple individuals (blue) are more robust than complex ones (red) whatever the mutation rate



Evolvability of simple (blue) and complex (red) individuals show no advantage of one class among the other

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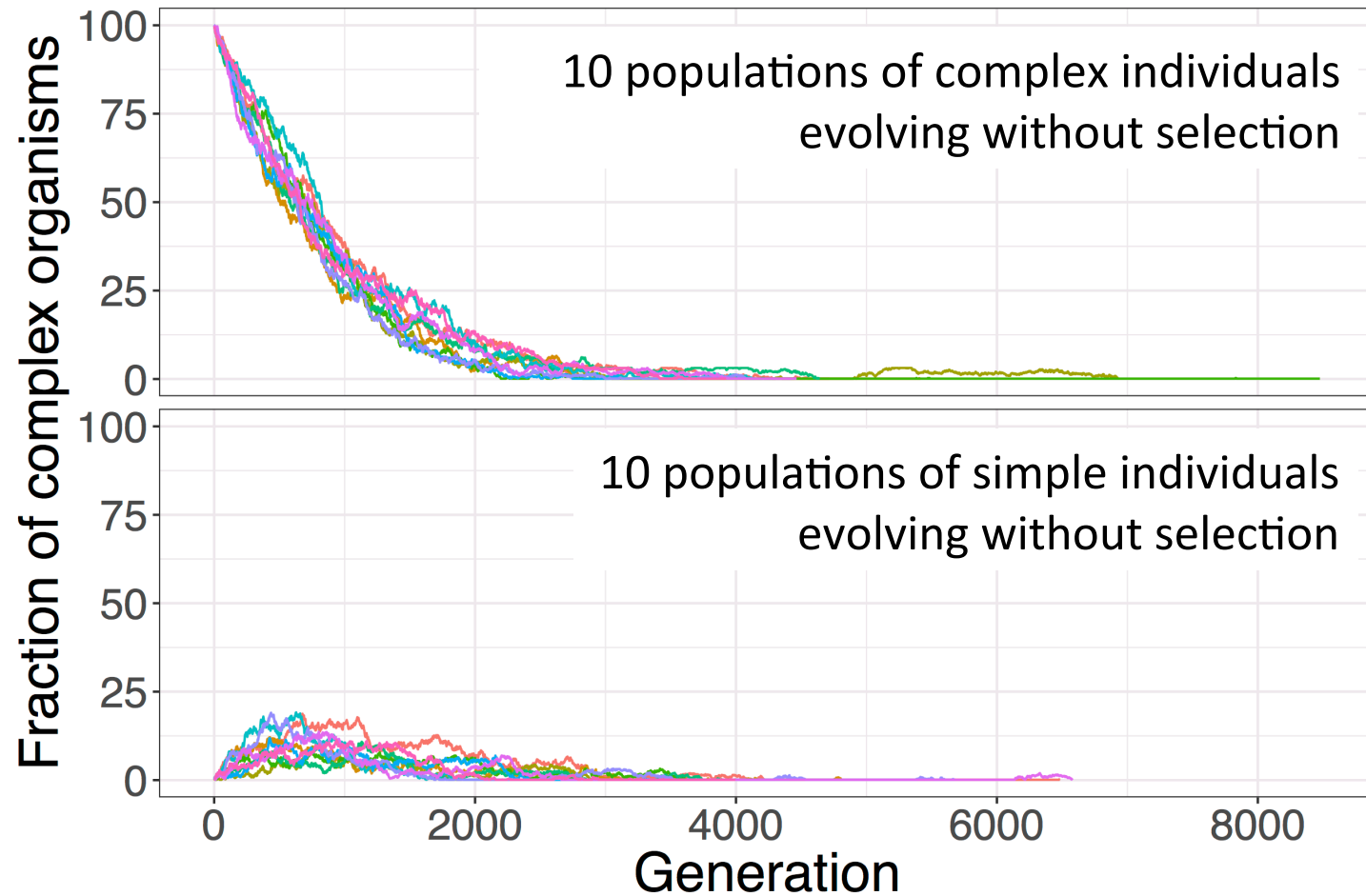
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2. **Neutral mechanism: accumulation of variation**

(Gould, 1996 ; McShea & Brandon, 2010 ; Lukes et al., 2011)

Results (4/5): Without selection functional complexity always vanishes on the long run (but a transient increase is observed in simple organisms)



So?

- Hypotheses from literature

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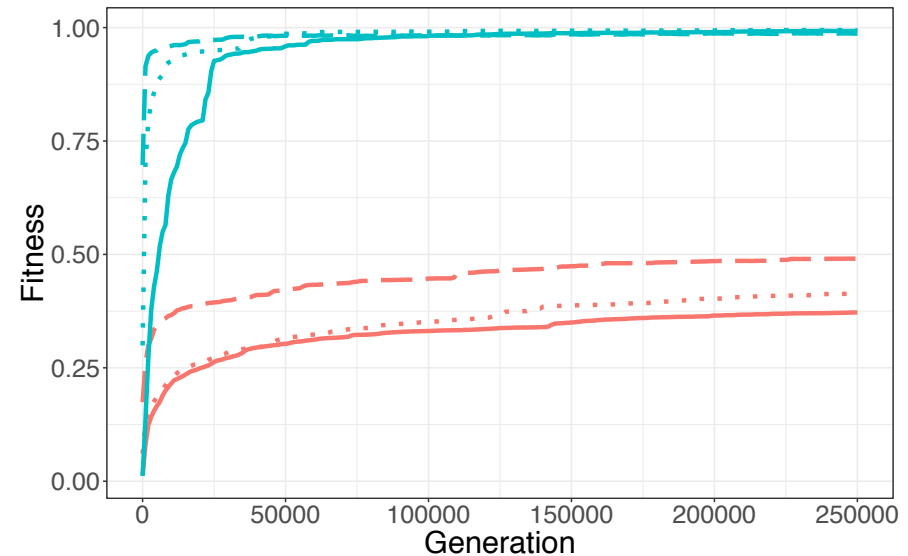
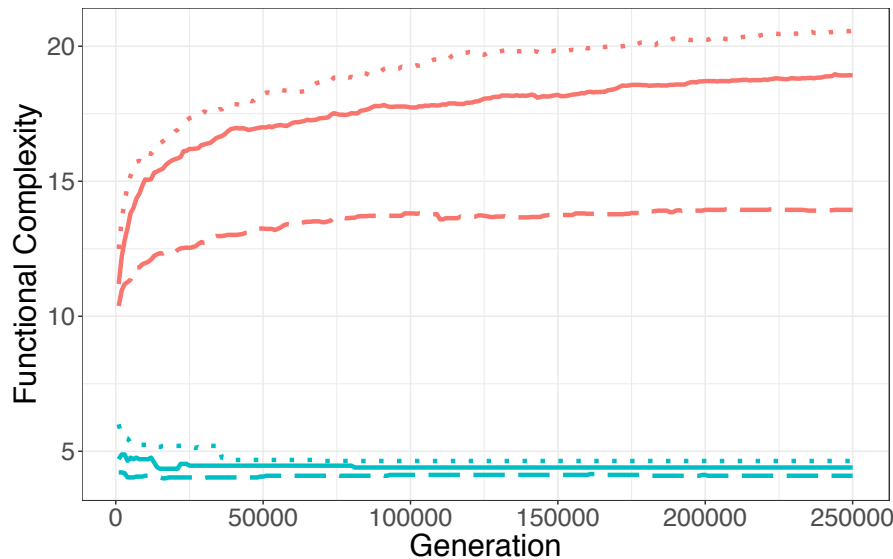
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→ Let's observe the long-term dynamics of simple and complex individuals

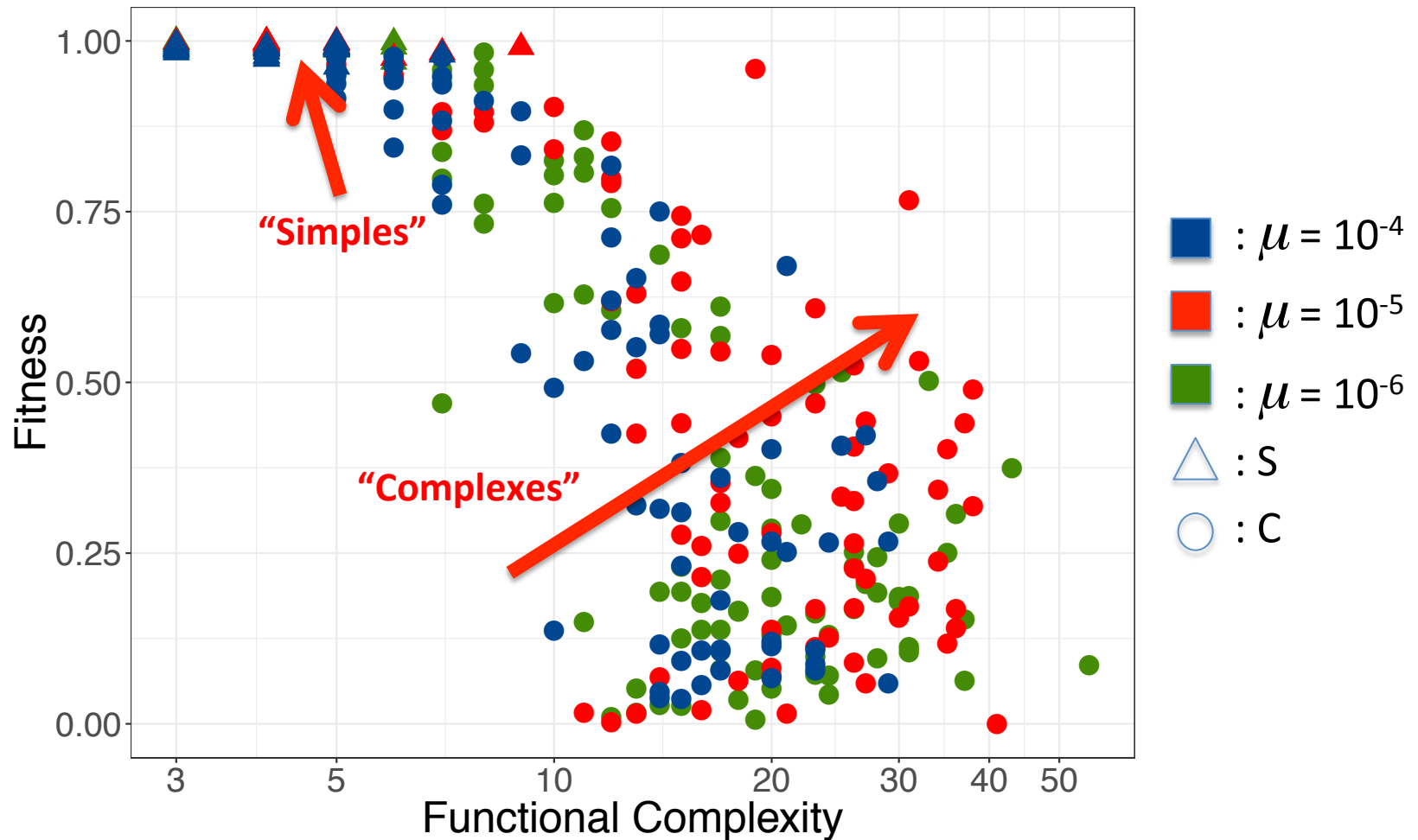
Results (5/5): For complex individuals, fitness and complexity increase simultaneously



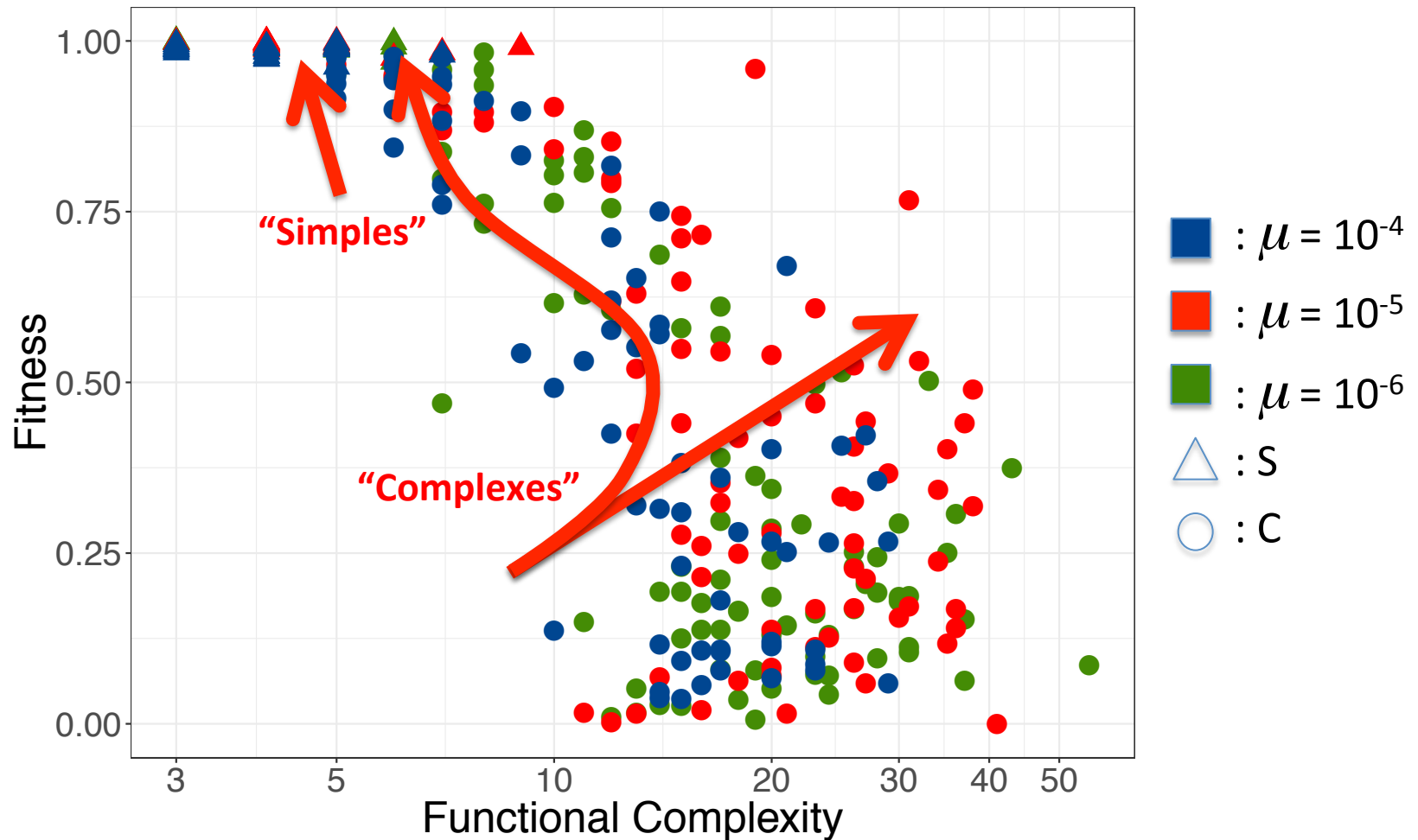
— : simples — : complexes - - : $\mu = 10^{-4}$ ··· : $\mu = 10^{-5}$ / : $\mu = 10^{-6}$

→ Even though the gain in fitness is much lower than what a dramatic complexity loss would yield, **complexity gain still yields a fitness gain**

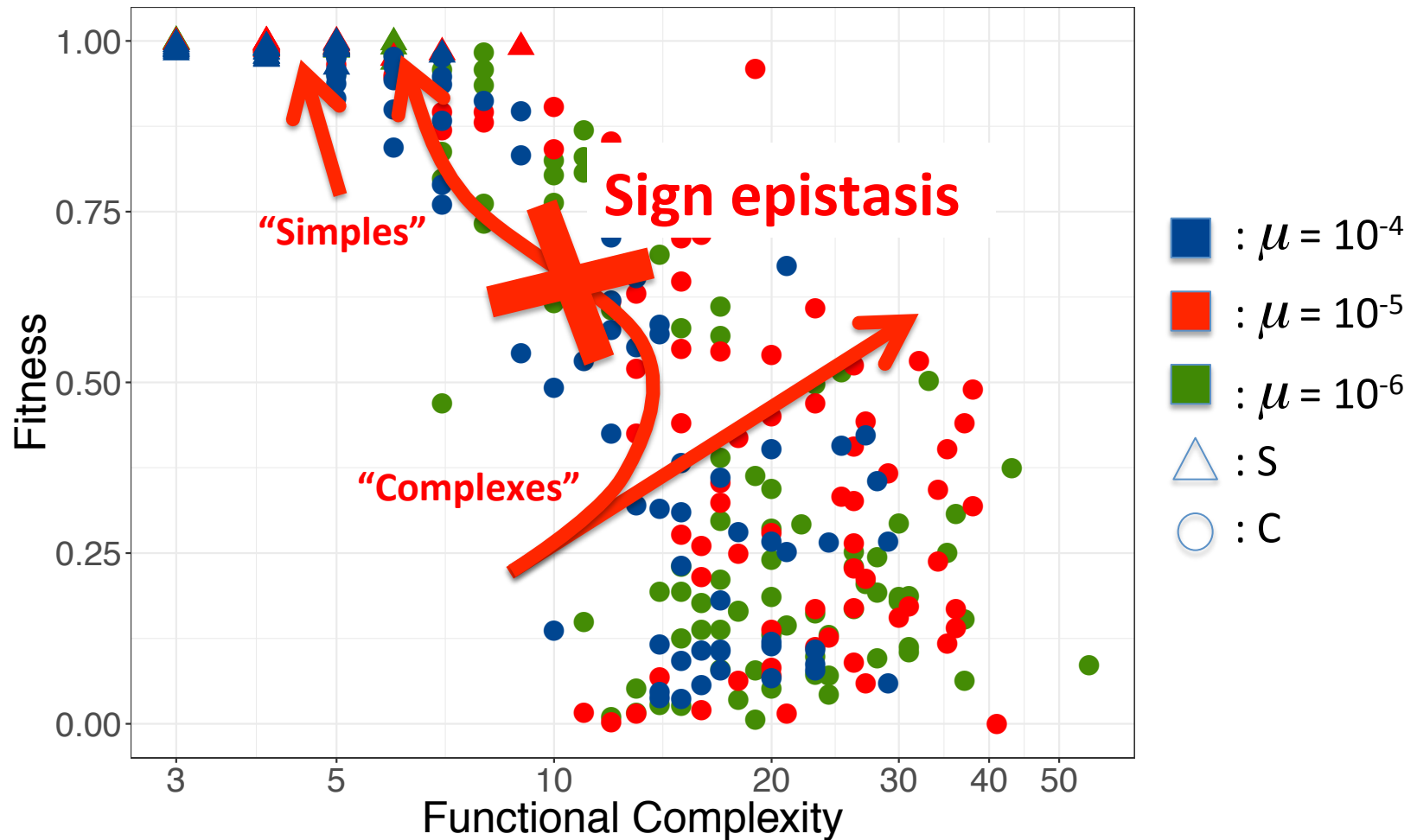
Conclusion: Simple and Complex organisms have opposing evolutionary dynamics



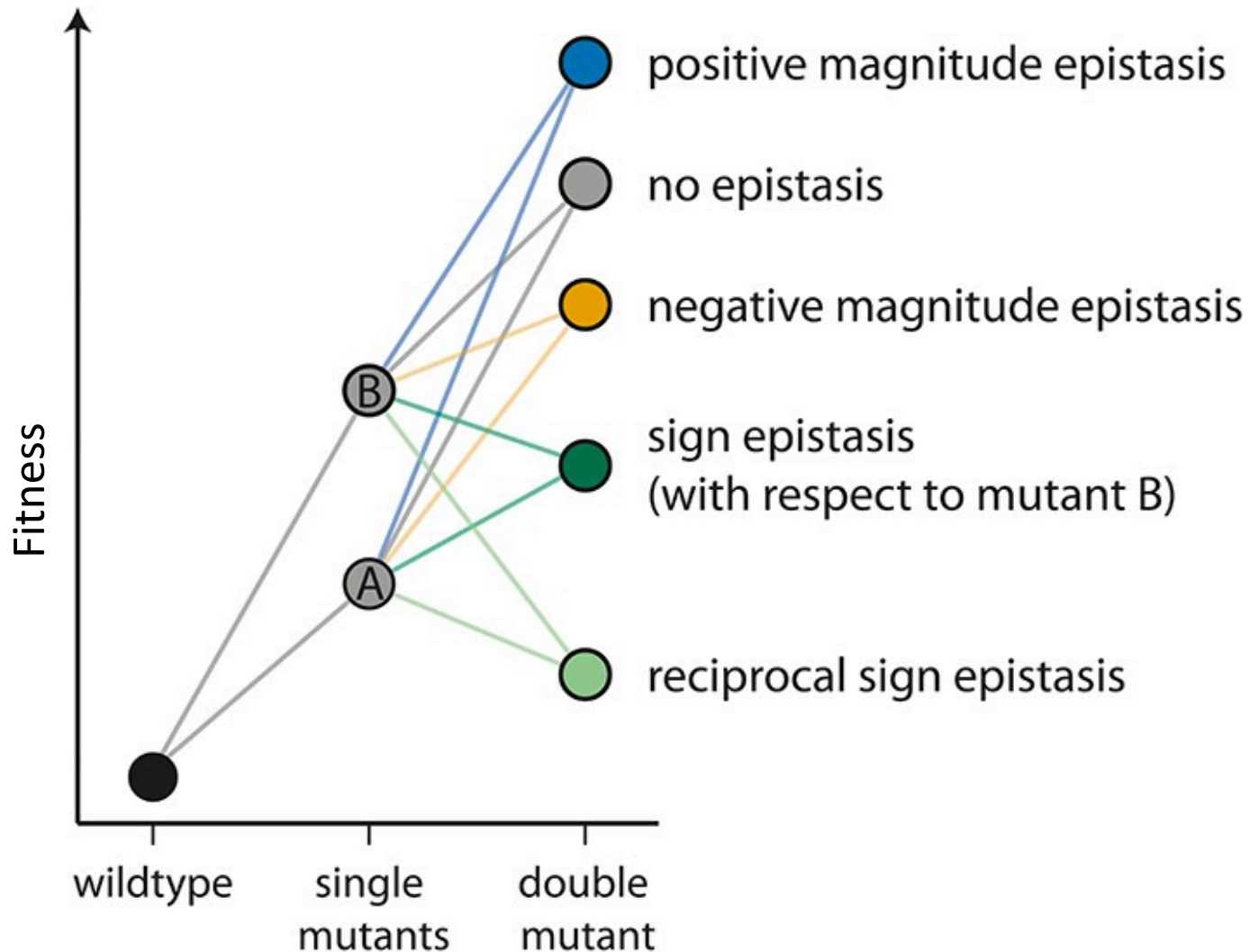
Why don't Complex individuals follow the same evolutionary dynamics as the Simple ones?



Sign epistasis is on the way: simplifying mutations have become unreachable



Digression: sign epistasis ?

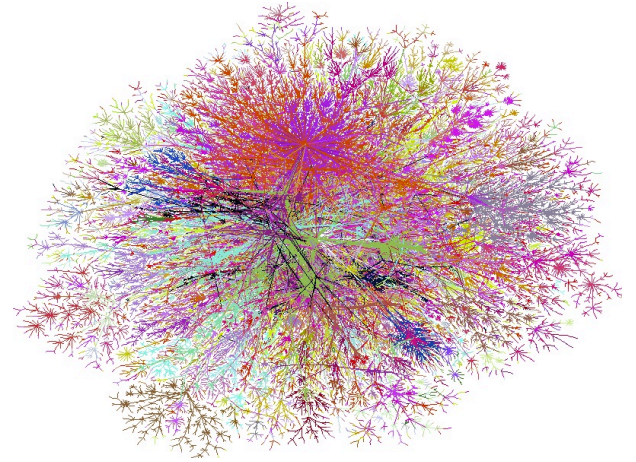
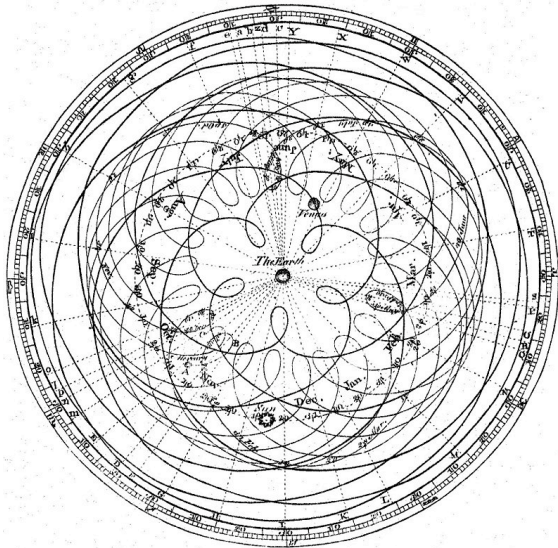


Discussion/Conclusion

- Although simple individuals are favored on all aspects (drift, selection, indirect selection), complexity accumulates along evolution
 - *Complexity in simple environments is comparable to complexity in complex environments!*
- We observed a “complexity ratchet”
 - *The complexity ratchet is stronger than selection*
 - *But the complexity ratchet is fueled by selection*
- The complexity ratchet is enforced by sign epistasis
 - *Mutations/genes/proteins that would be favorable in the a Simple context are highly deleterious in a Complex context*
- Sign epistasis is due to competition between different variation processes (structural variation vs. sequence variation)
 - *In the absence of structural variation all simulations lead to simple organisms*
- Can the ratchet be stopped or even inverted?
 - *Under strong increase of mutation rates, complexes switch back to simplicity (“simplification chock”)*

An open question...

- Complexification dynamics is observed in many other systems including social and socio-technical systems (economy, science, law, agencies...)
 - *Is there a complexity ratchet in social systems?*
 - *Structural variants ~ path dependence?*
 - *If yes, is there an equivalent to the simplification chock induced by increased mutation rate?*

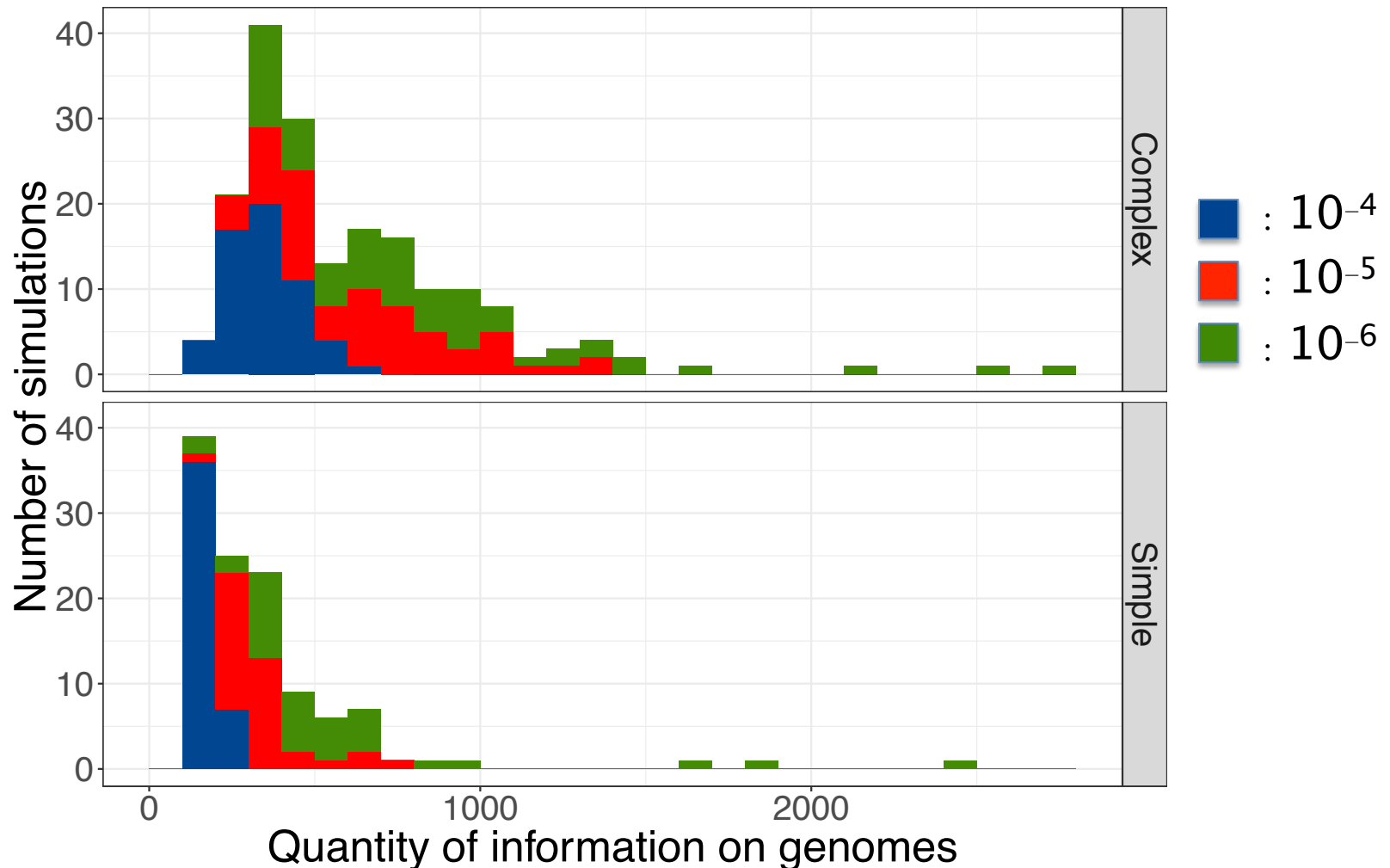


Inverting the complexity ratchet

- What could invert the complexity ratchet?
 - Mutation rates constrain the genome information content (Eigen and Schuster, 1977; Knibbe et al., 2007; Fischer et al., 2014)
 - What if the organisms undergo a strong *increase* in mutation rate?
- Fraction of C→S transitions under an elevated mutation rate

	$\mu = 10^{-4}$	$\mu = 10^{-5}$	$\mu = 10^{-6}$
$\mu_{new} = 10^{-3}$	$60 \pm 12\%$ (37/61)	$86 \pm 8\%$ (61/71)	$91 \pm 6\%$ (71/78)
$\mu_{new} = 10^{-4}$	/	$8 \pm 6\%$ (6/71)	$13 \pm 8\%$ (13/78)
$\mu_{new} = 10^{-5}$	/	/	$4 \pm 4\%$ (3/78)

Mutation rates bound the quantity of information stored on genomes (Knibbe et al., 2007)



Constraints on genomes are partly relaxed at the functional level

