Extended Heredity & the Extended Synthesis

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Queen's University

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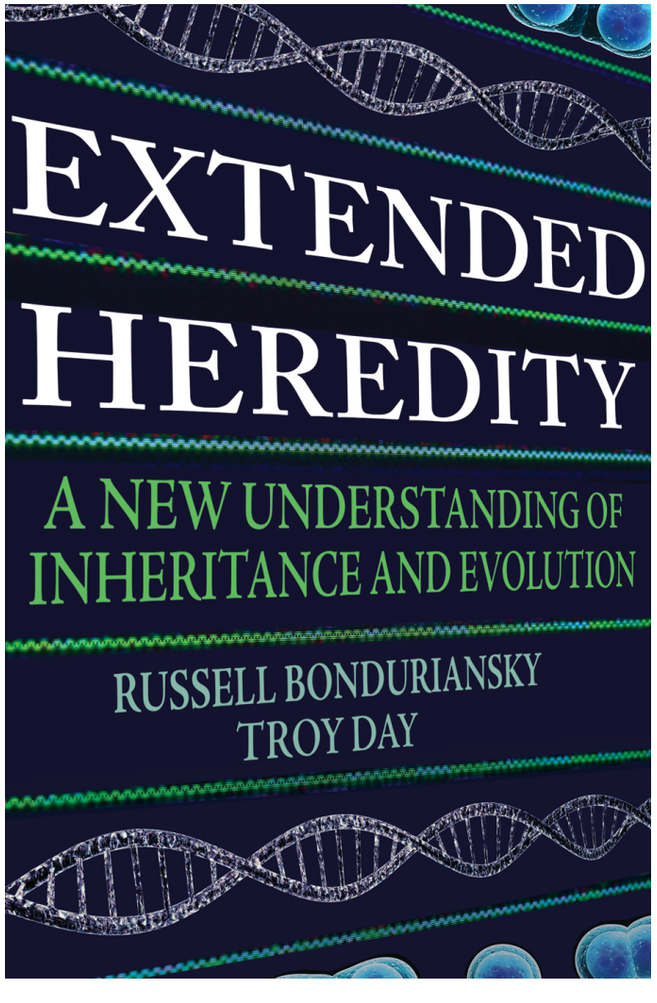


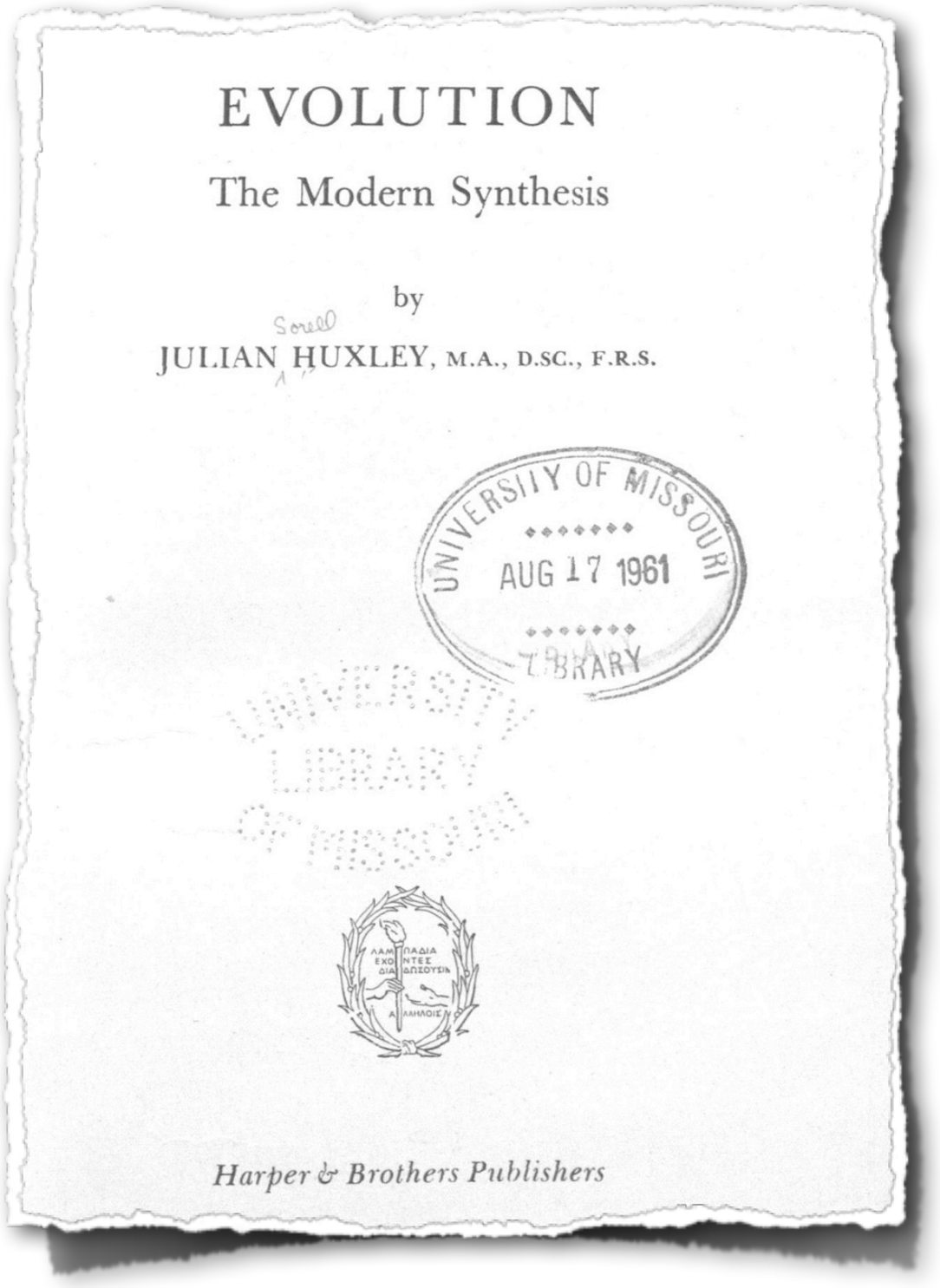
Outline

- The Modern Synthesis & Extended Heredity
- Extended Heredity & the Extended Synthesis: What is the Controversy?

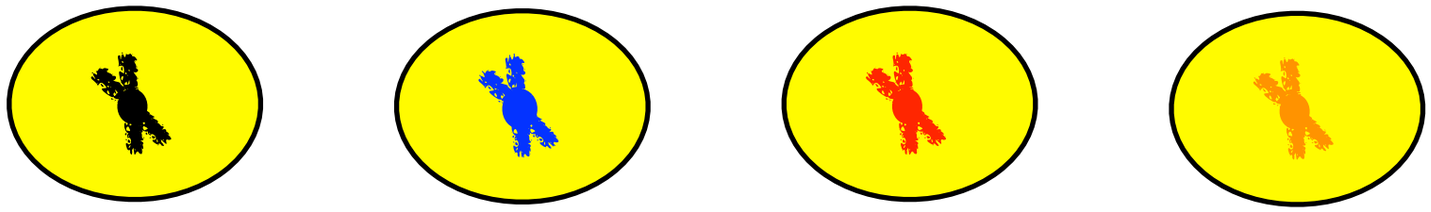
The Modern Synthesis

- Synthesis of ideas involving the nature of selection, inheritance, and species, that occurred during 1936-1947

- Reconciliation of Mendelian inheritance with evolution by natural selection



MS View of Evolution



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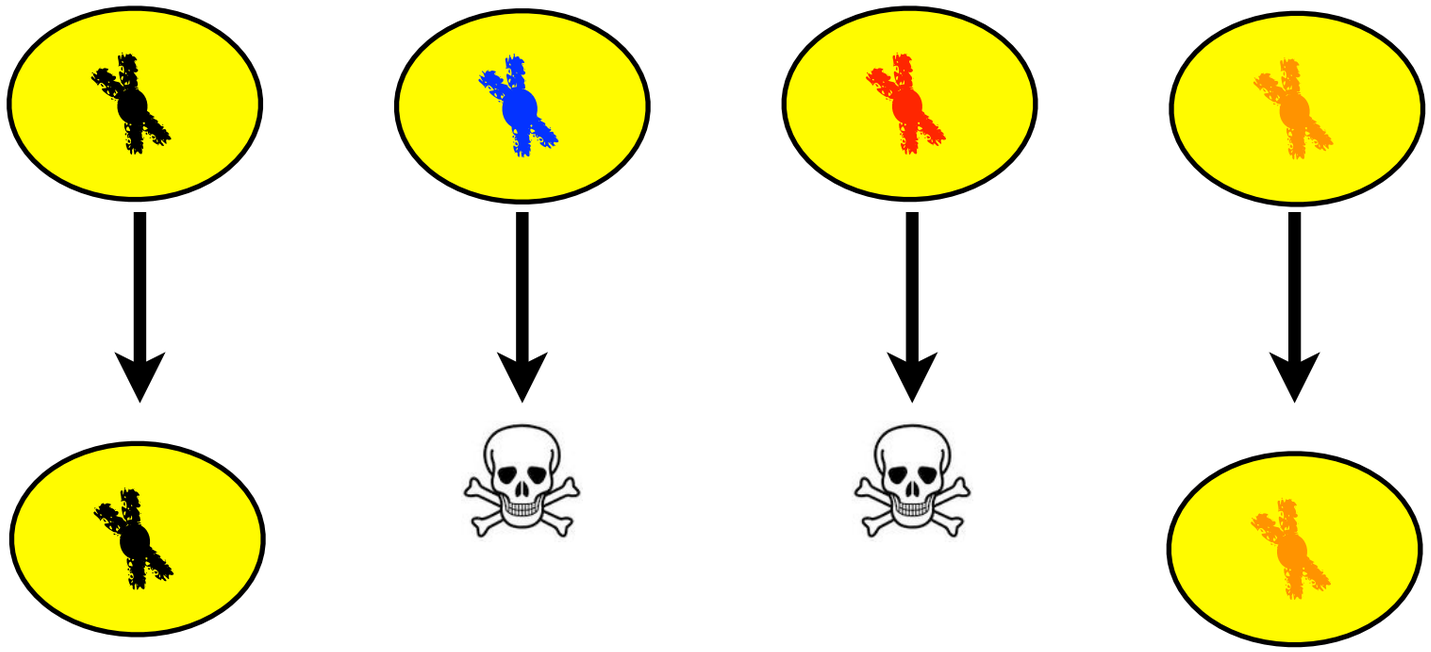
Natural Selection



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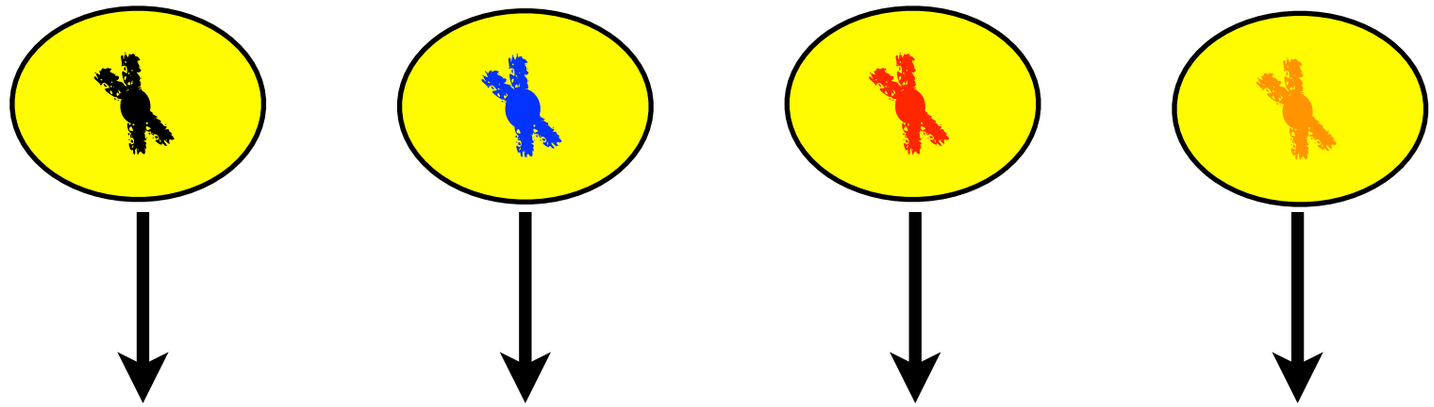
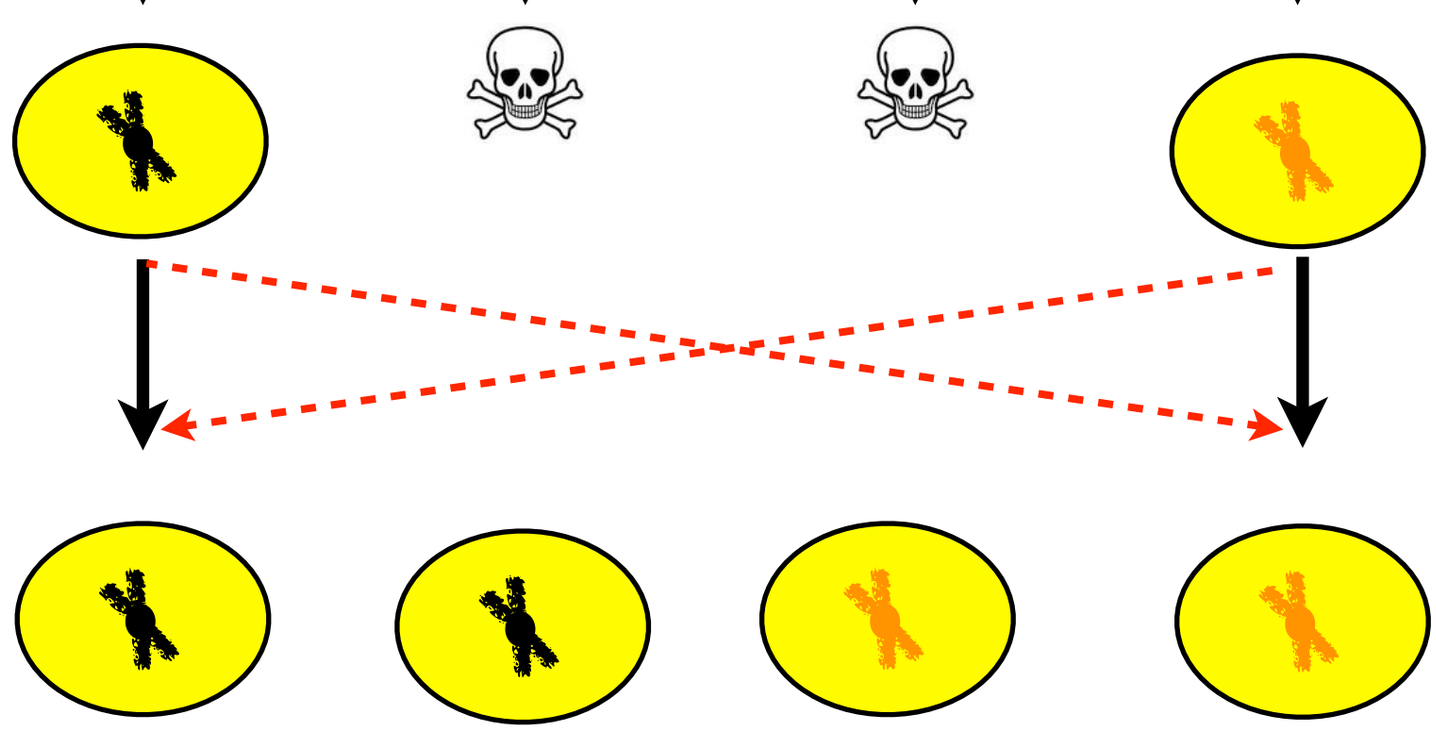
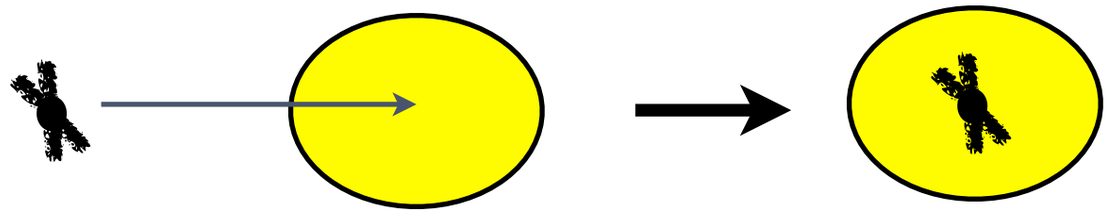


Mendelian Inheritance



The Logic of Inheritance



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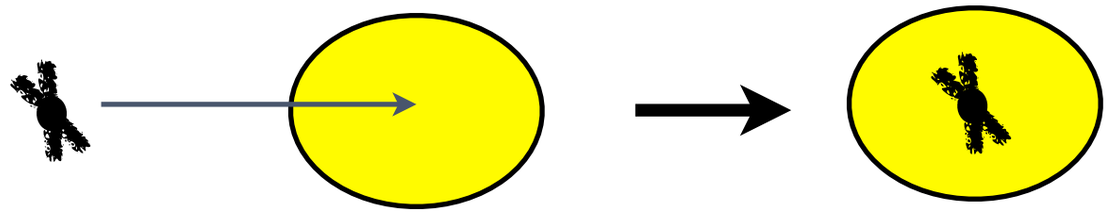
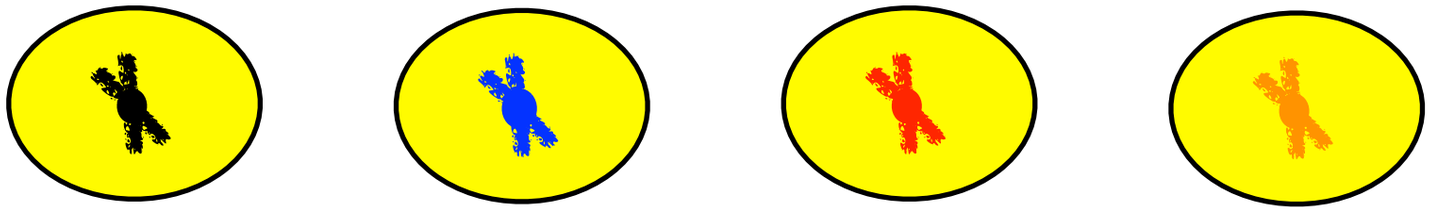


All living organisms inherit both genetic material and nongenetic “interpretative machinery”

A complete evolutionary synthesis should account for both

Does This Matter?

(1) Not if all individuals have the same nongenetic machinery



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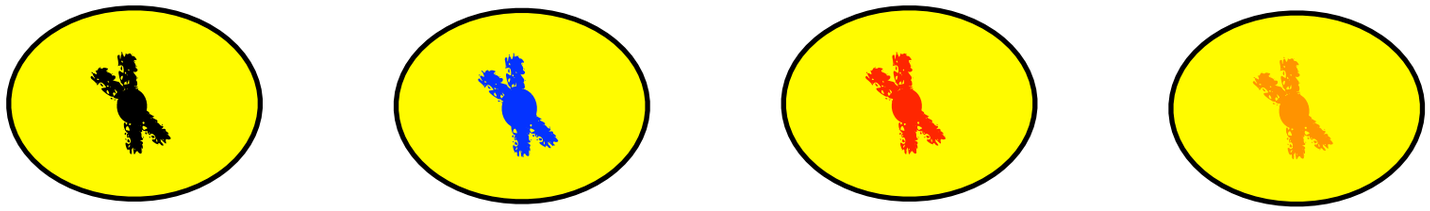

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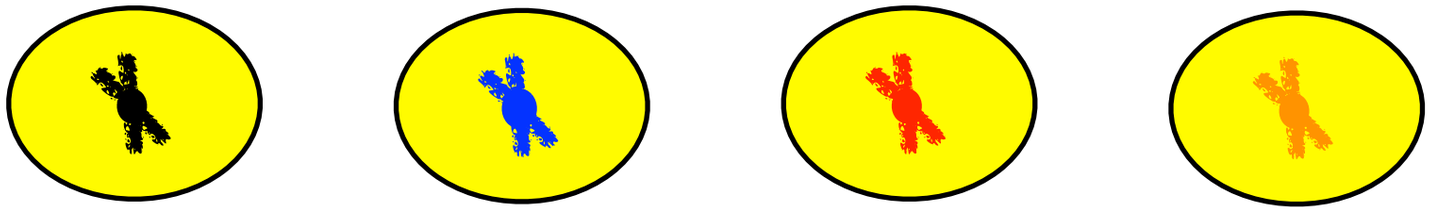

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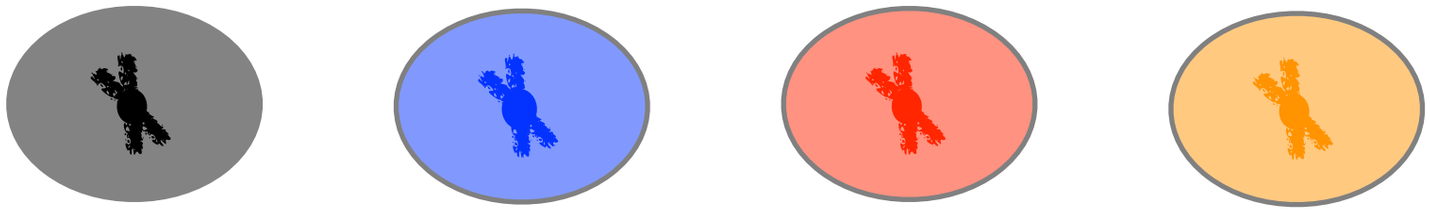

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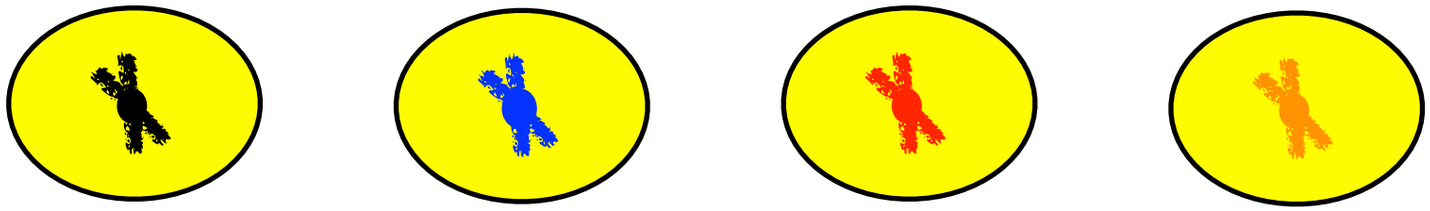

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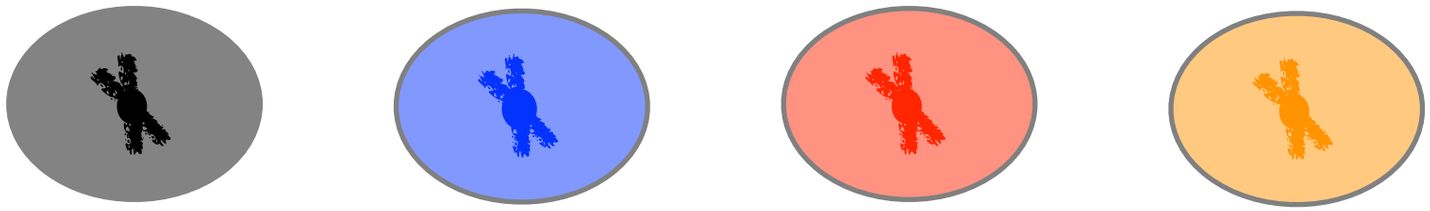
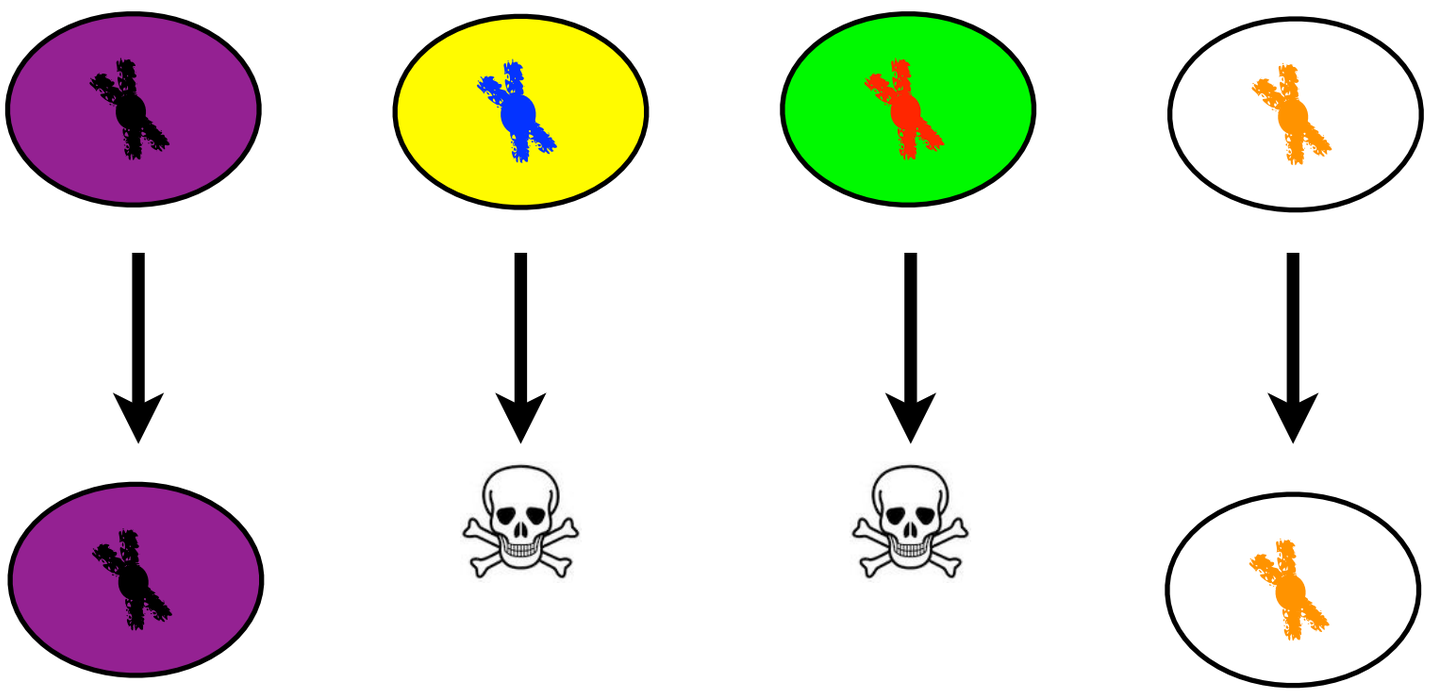


A Broader View



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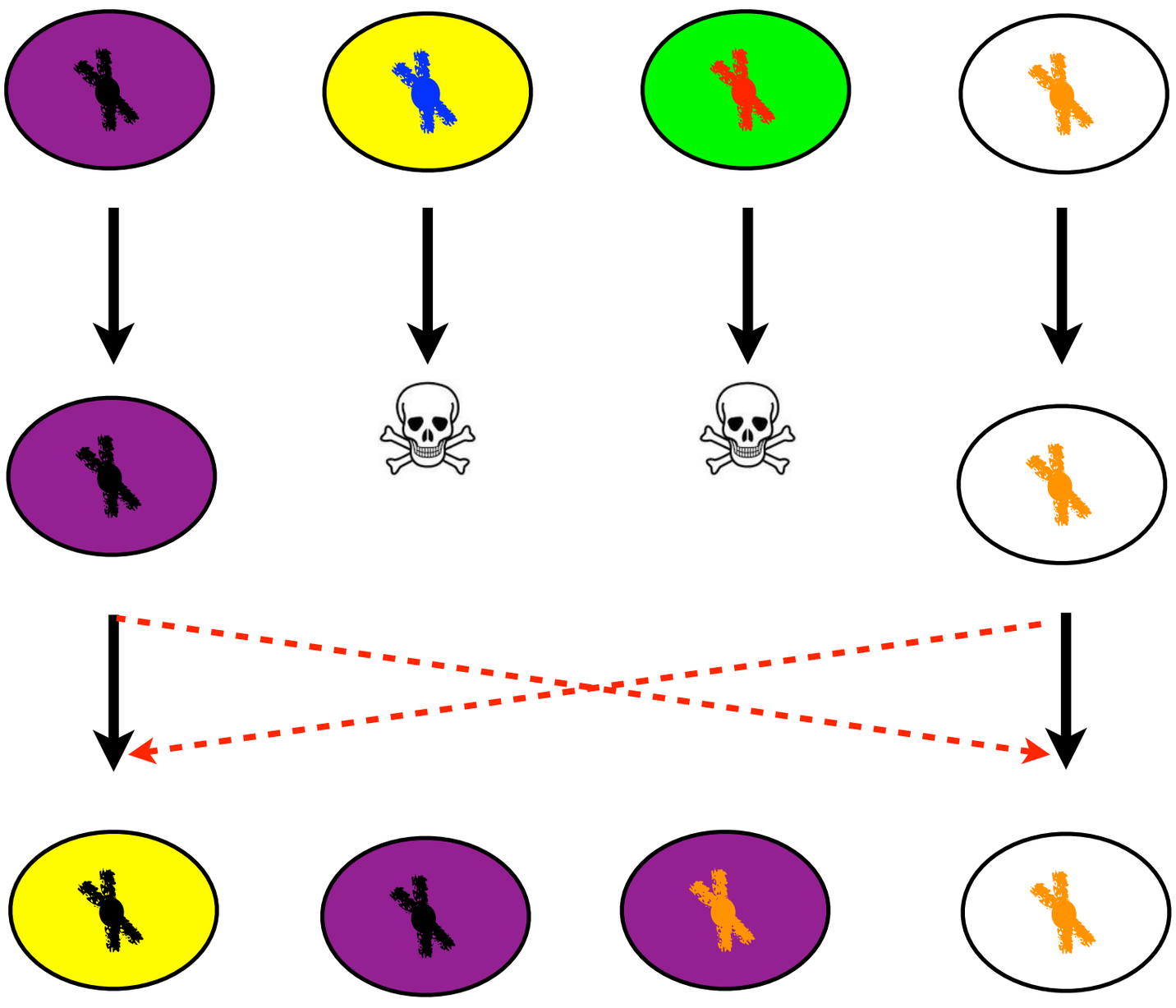


Examples of Nongenetic Inheritance

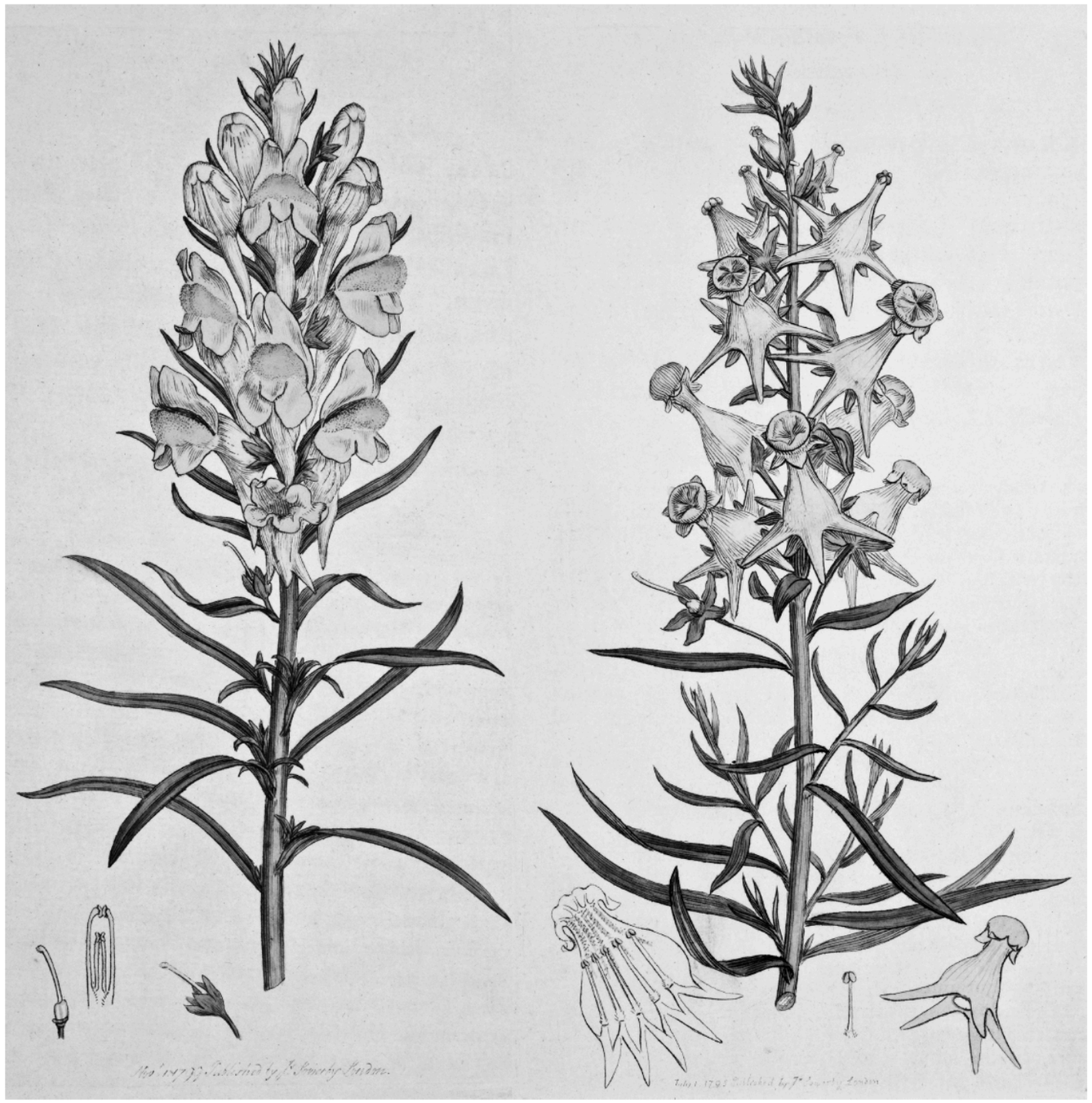


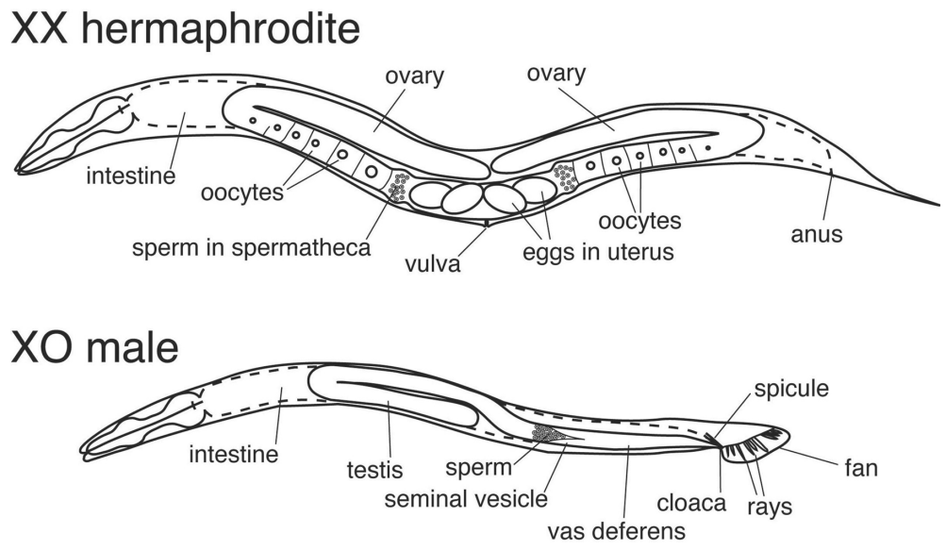
Figure 4.1. Toadflax (*Linaria vulgaris*) in its normal form (*left*) and "monstrous" peloric form (*right*). The peloric form turned out to be an epimutant rather than a genetic mutant. (Illustrations by James Sowerby, John Innes Historical Collections. Courtesy of the John Innes Foundation.)

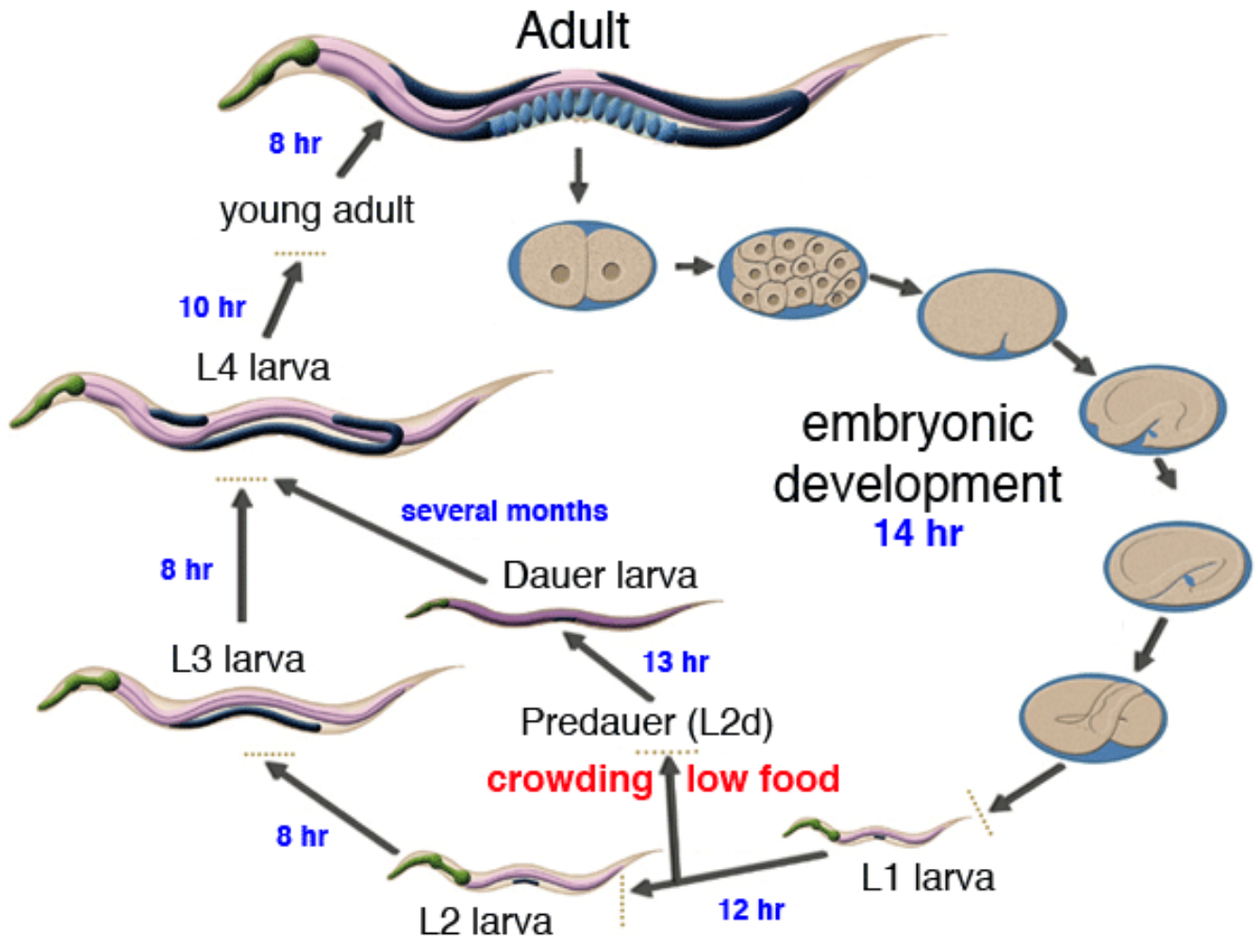
This is certainly no less remarkable than if a cow were to give birth to a calf with a wolf's head"
Linnaeus, 1744

Cubas et al. 1999. Nature 401:157-161

C. elegans

- *C. elegans* is a small (~1mm), transparent, free-living nematode worm
- Feeds on bacteria
- Hermaphrodites & Males





Examples of Nongenetic Inheritance

Allele wdr-5 “causes” increased lifespan

Greer et al. 2011. Nature 479:365-371

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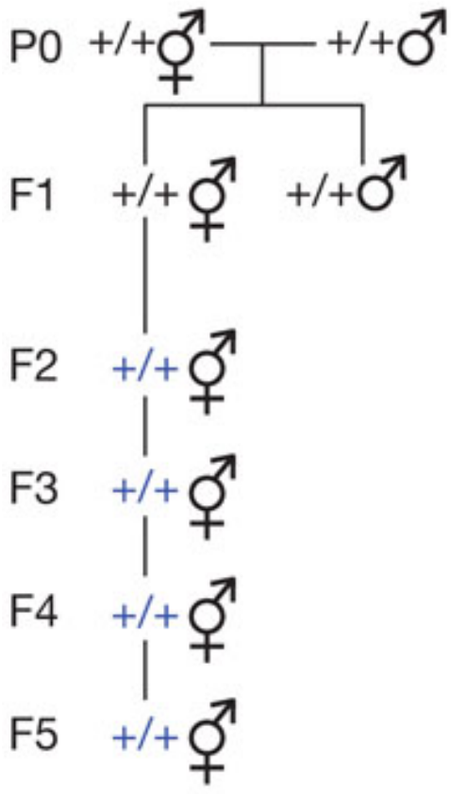

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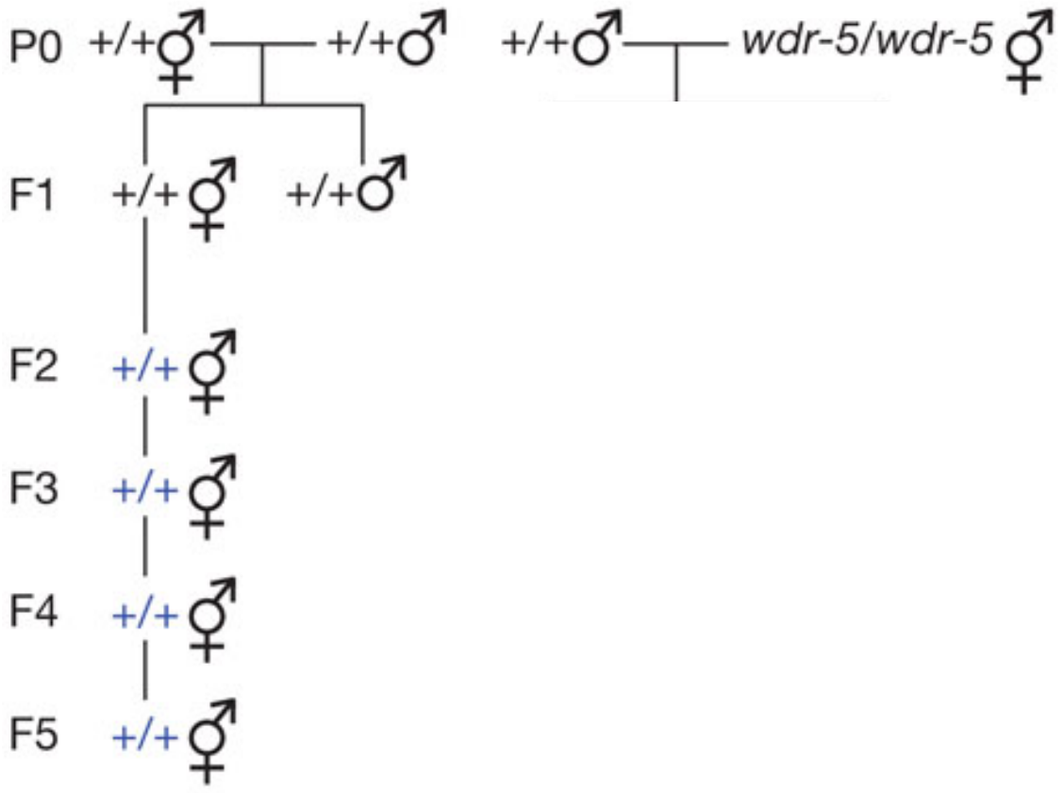

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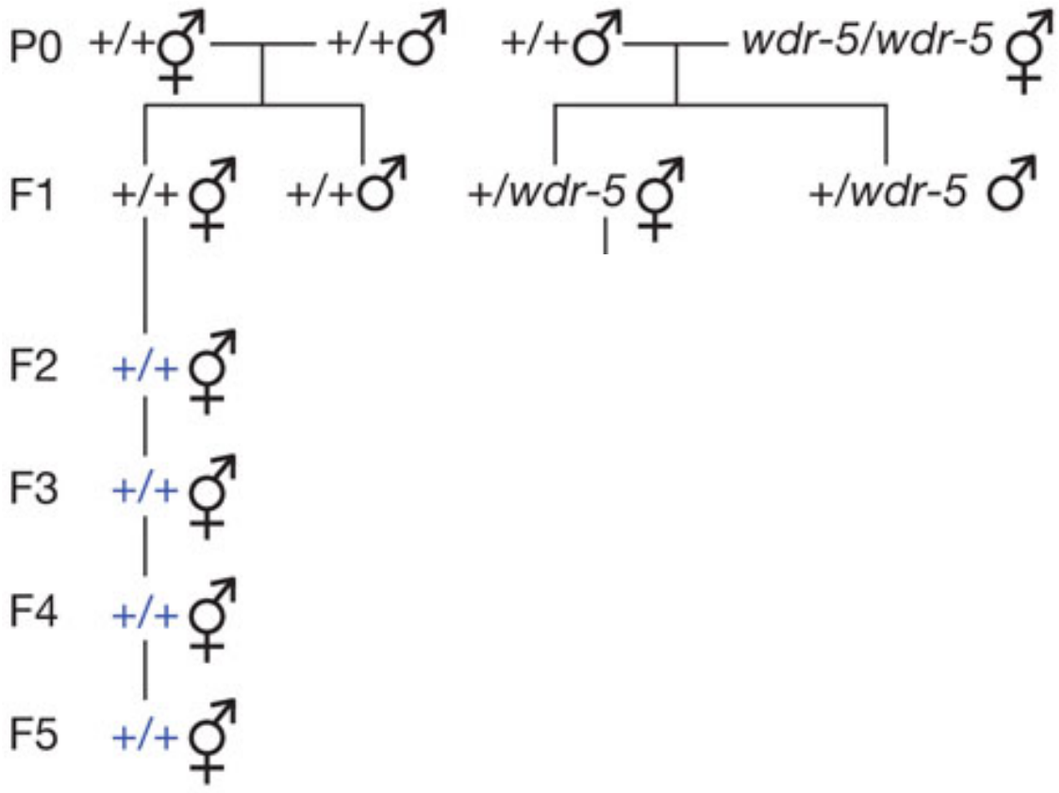

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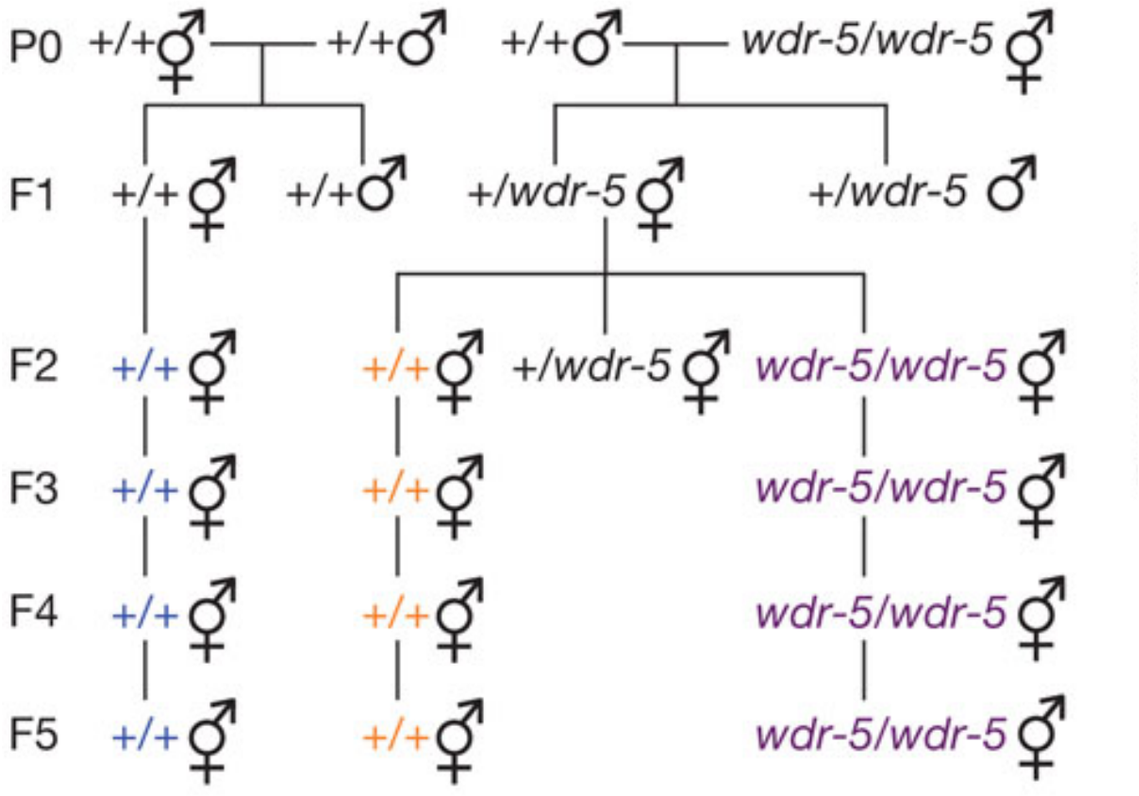

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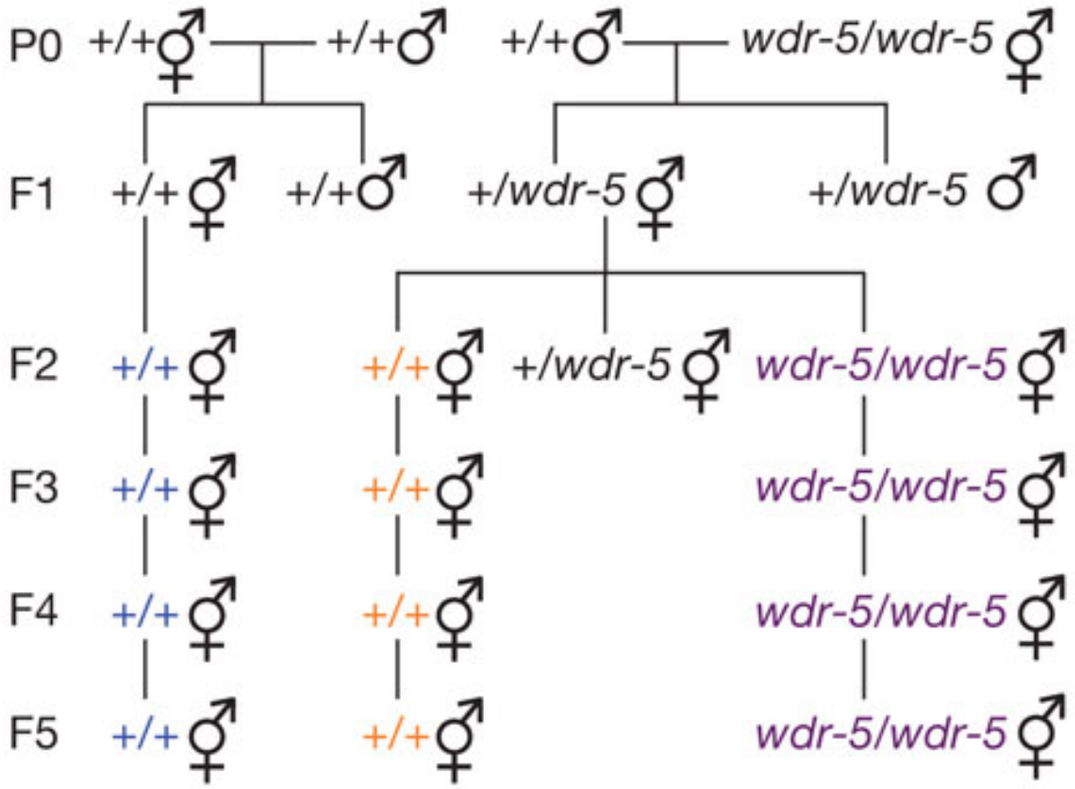
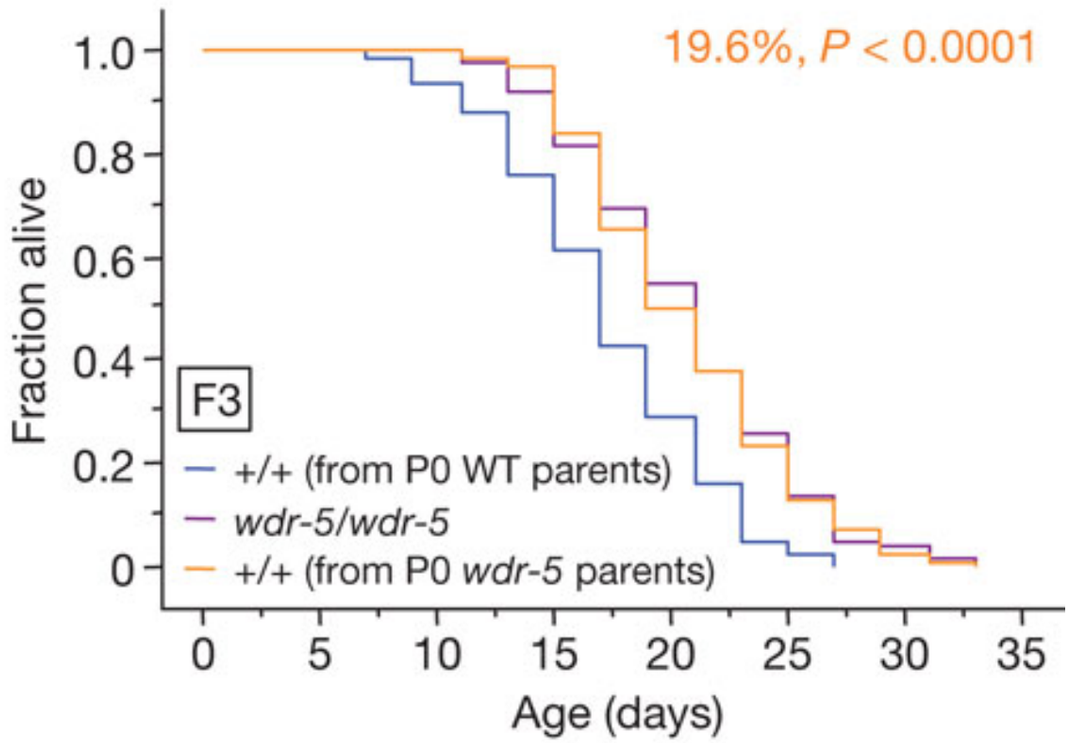


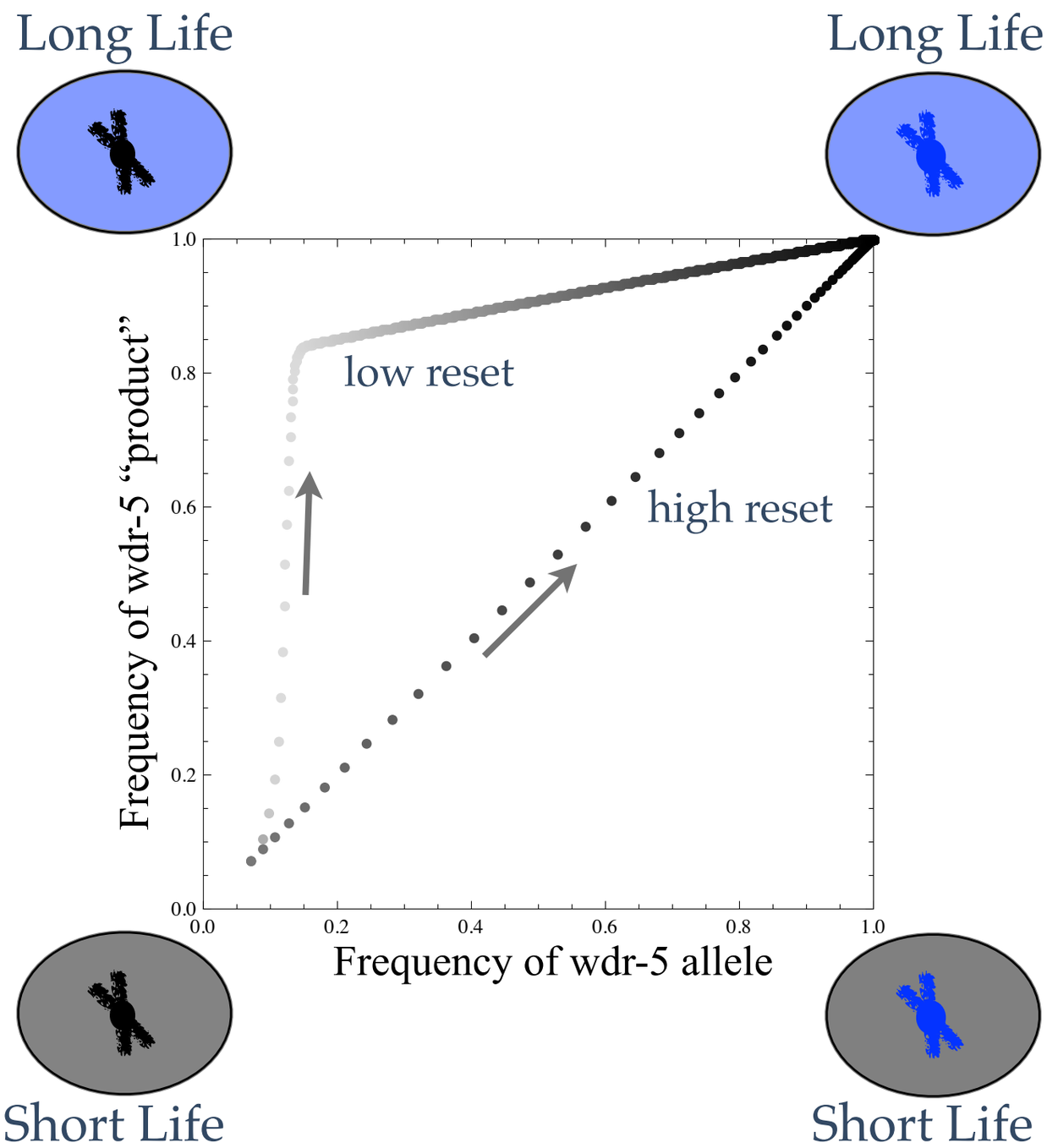


Genetically wild-type descendants from wdr-5 mutant parents nevertheless **have extended lifespan** for several generations.

Greer et al. 2011. Nature 479:365-371

Examples of Nongenetic Inheritance

Some product of allele wdr-5 actually causes increased lifespan

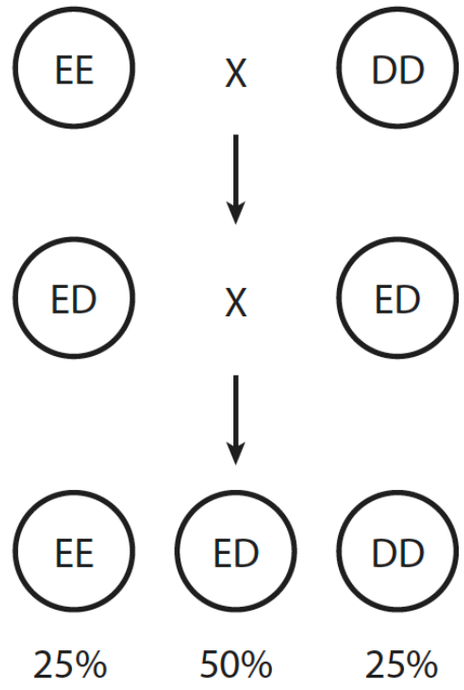


Day and Bonduriansky. 2011. Am Nat 178: E18-E36

Examples of Nongenetic Inheritance

Phytophthora sojae

Inheritance of Alleles



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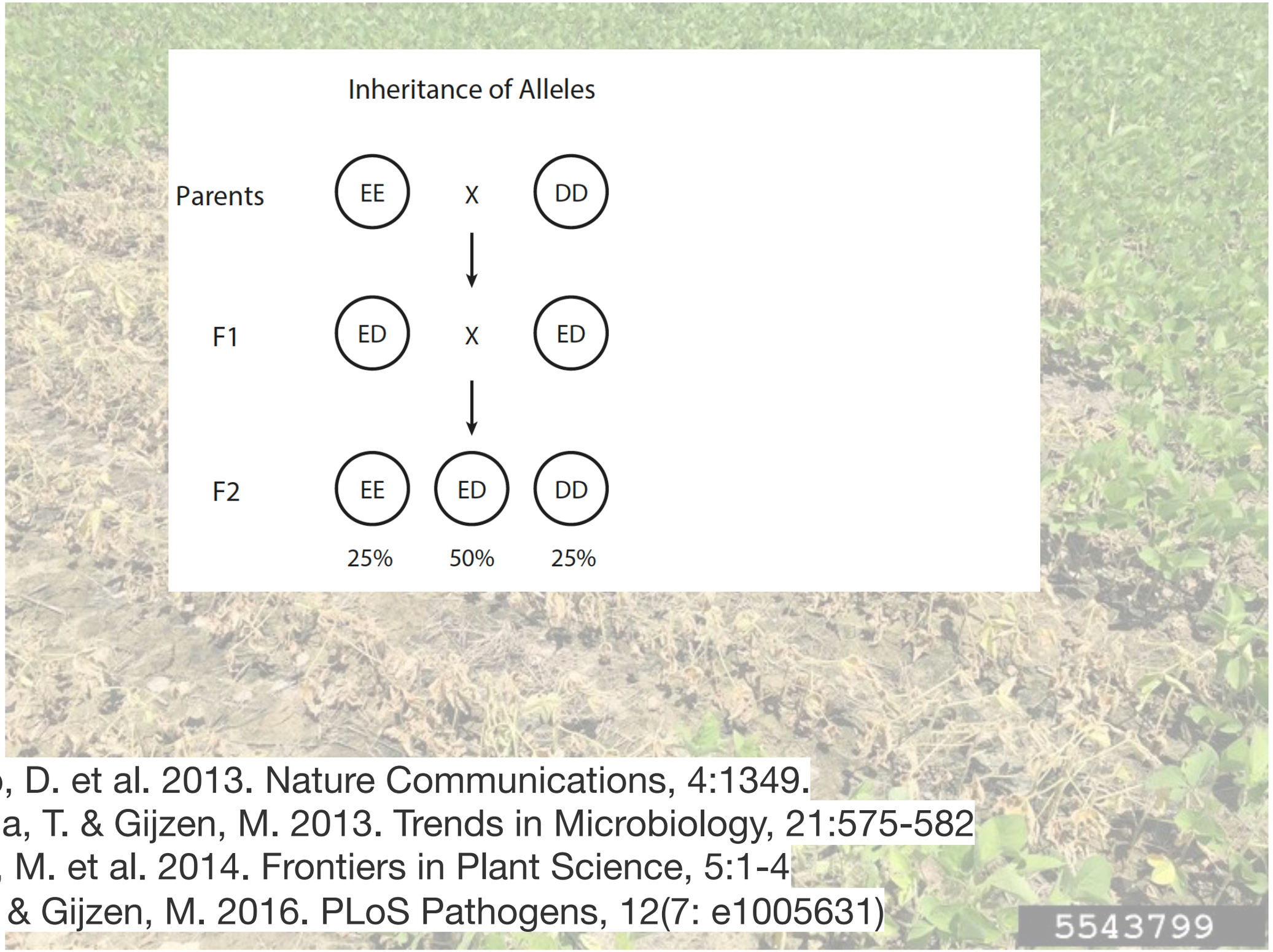

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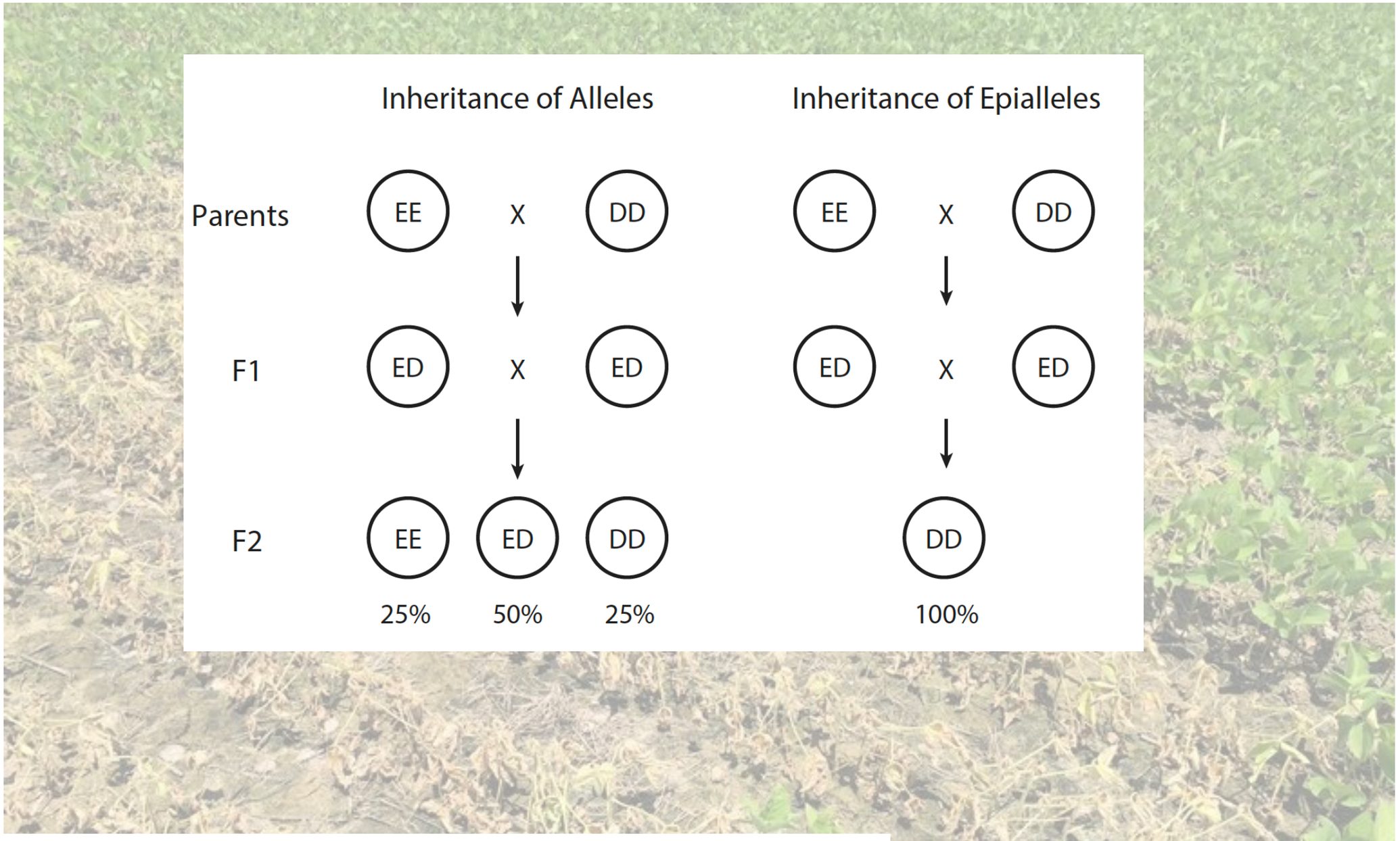

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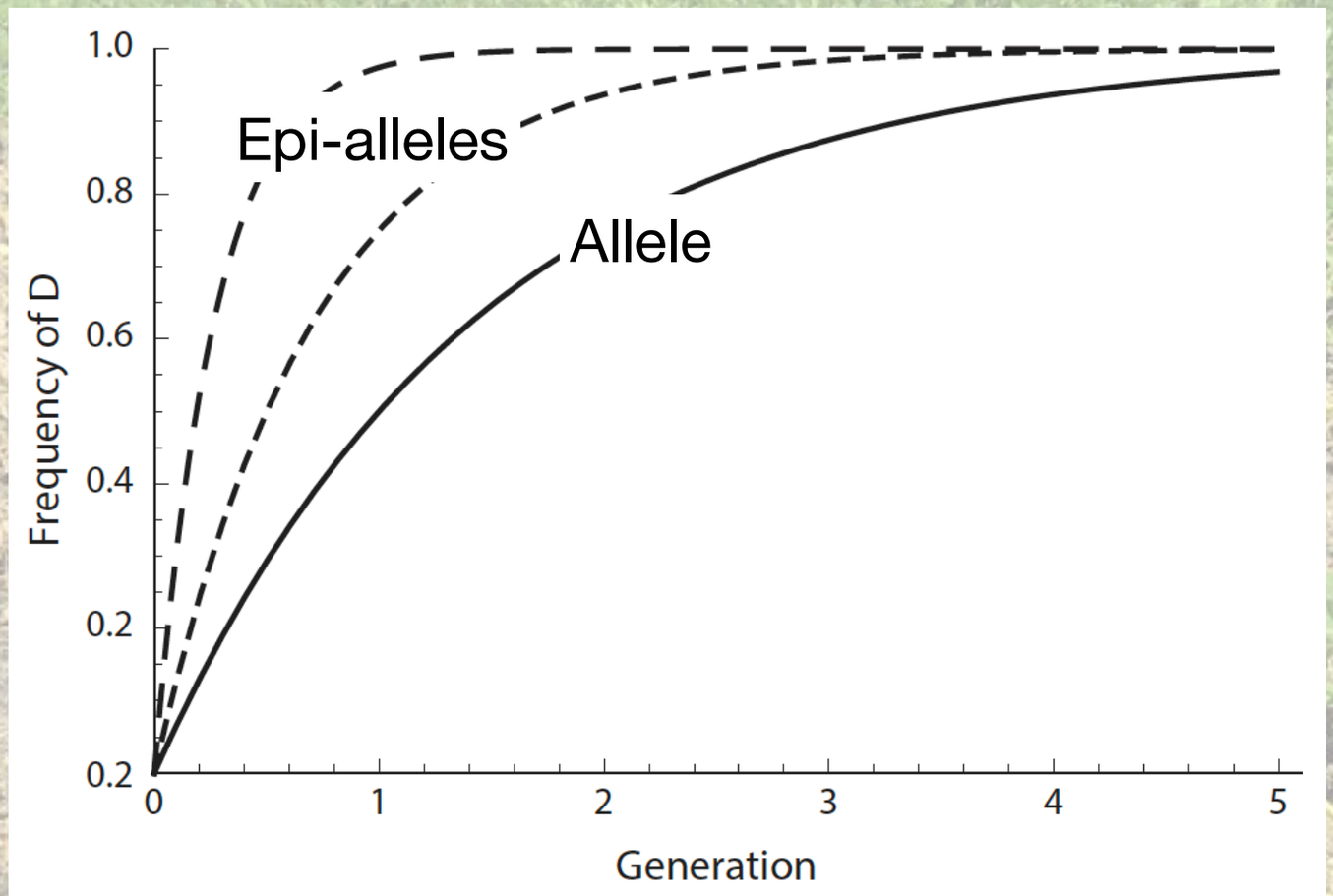

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Outline

- The Modern Synthesis & Extended Heredity
- Extended Heredity & the Extended Synthesis: What is the Controversy?

The Controversy

Extended Heredity

Except for cultural evolution in humans, we still don’t have good examples of adaptations that are underlain by NGI

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a. Trait must vary among individuals
b. Trait must be heritable
c. Trait must affect survival and/or reproductive success

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Extended Synthesis

Broader notions that somehow natural selection is not the sole source of adaptive evolution

The Controversy

- "…adaptation can arise through both natural selection and internal and external constructive processes."
- "the …(generation of adaptation) … does not rest on selection alone"
- "not enough [significance is afforded] to the developmental processes that create novel variants, contribute to heredity, *generate adaptive fit*,…"
- "Developmental processes play important evolutionary roles as causes of novel, potentially beneficial, phenotypic variants,…"

Laland et al. 2015. Proc B 282:21051019

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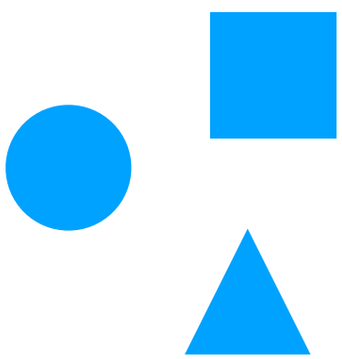
- "If … adaptive changes in phenotypes induced by external circumstances were often transmitted to the offspring, this would involve a major change in outlook."
- "…observations do not require directed mutations, and … a neo-Darwinian explanation is more likely…"
- "…allele frequency change caused by natural selection is the only credible process underlying the evolution of adaptive organismal traits."

Charlesworth et al. 2017. Proc B. 284:20162864

A Model of Evolution

Non-overlapping generations, no age-stage structure

Genetic or Nongenetic Types



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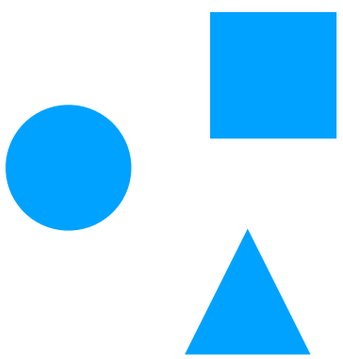

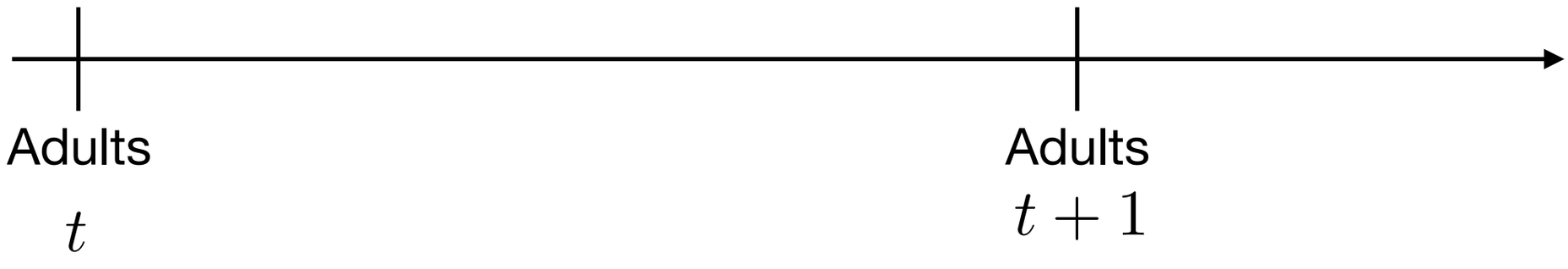

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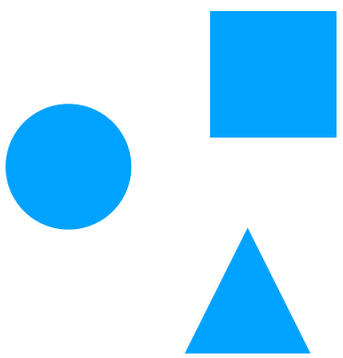

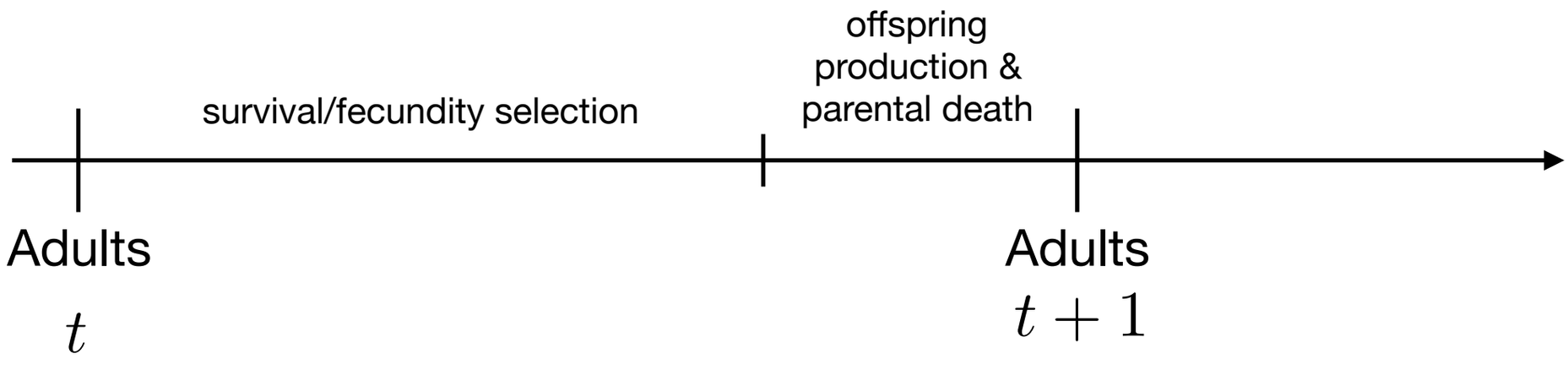

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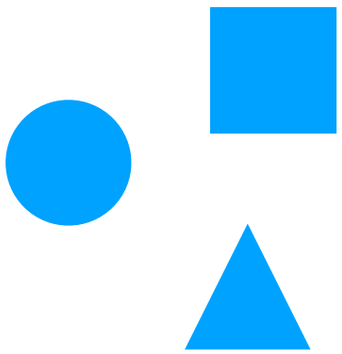

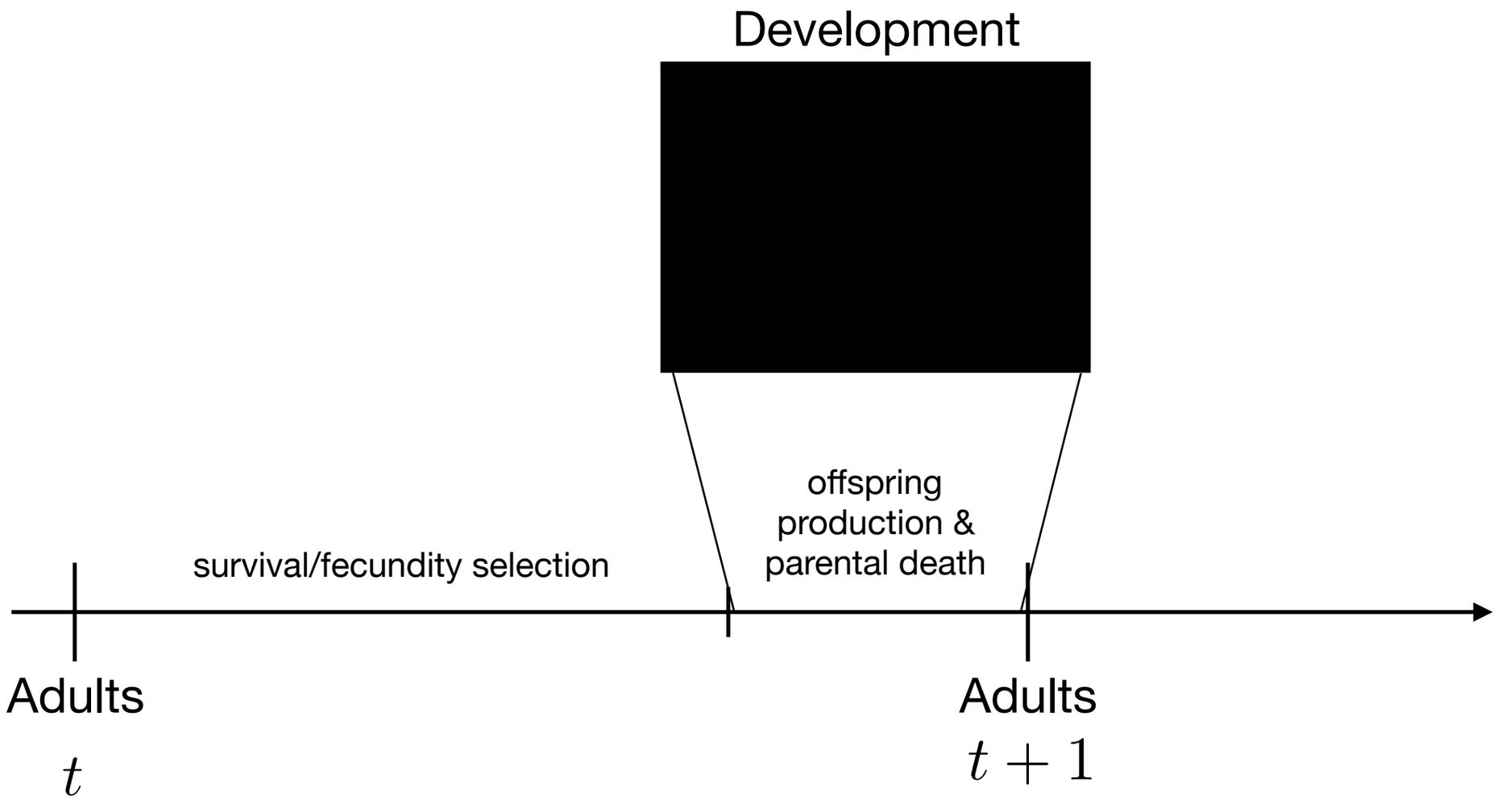

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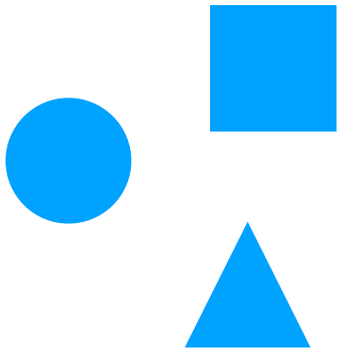

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x_i the value of some attribute *x* for individuals of type *i*

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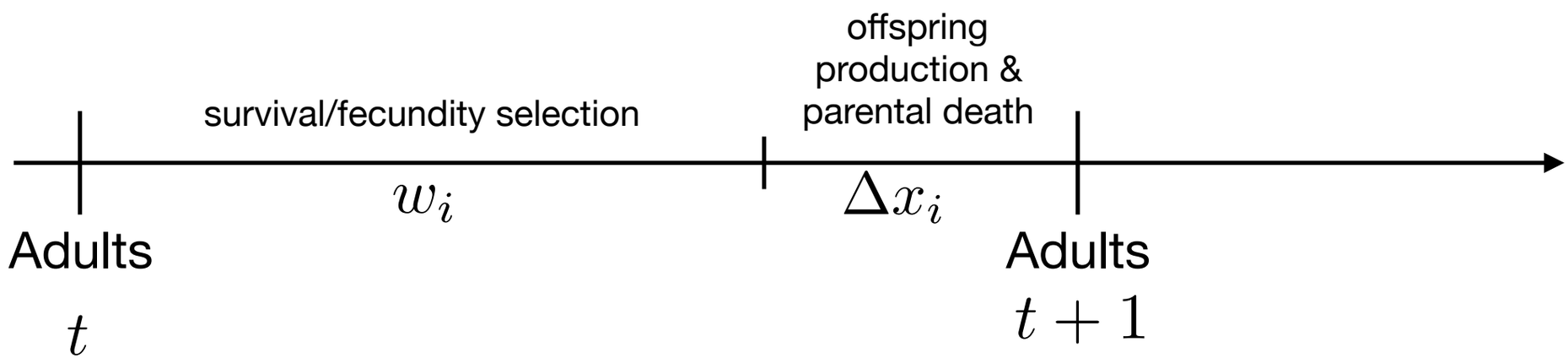

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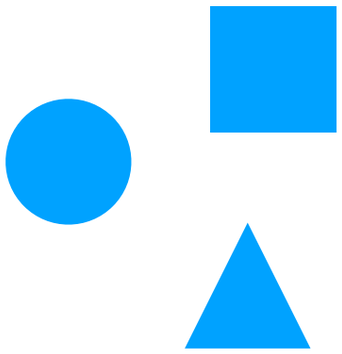

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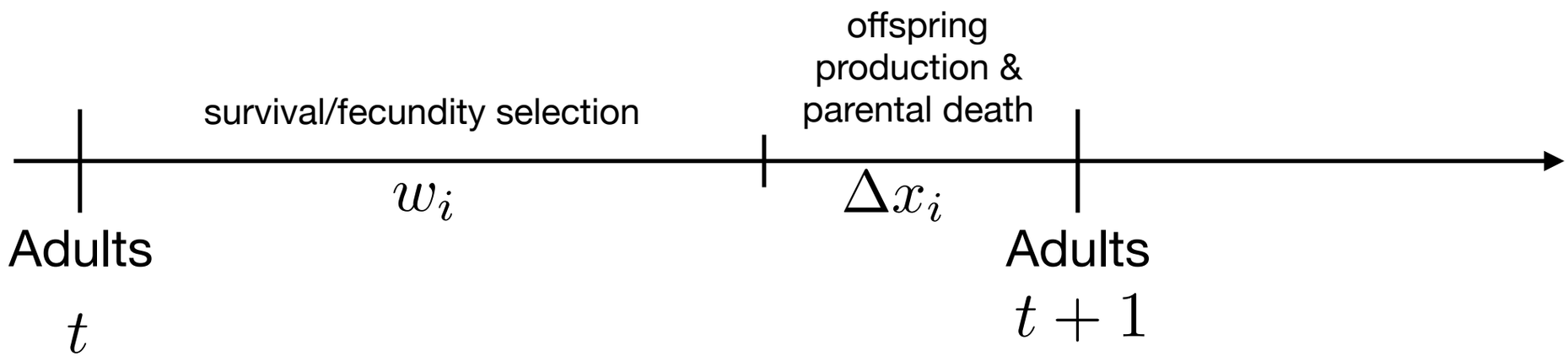

$$\bar{x}(t+1) = \sum \frac{n_i w_i}{\sum n_i w_i}(x_i + \Delta x_i)$$

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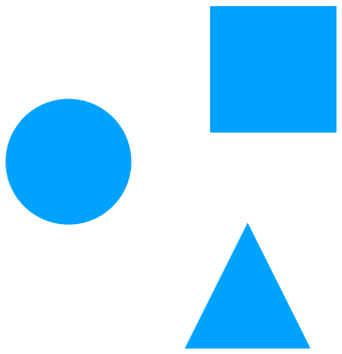

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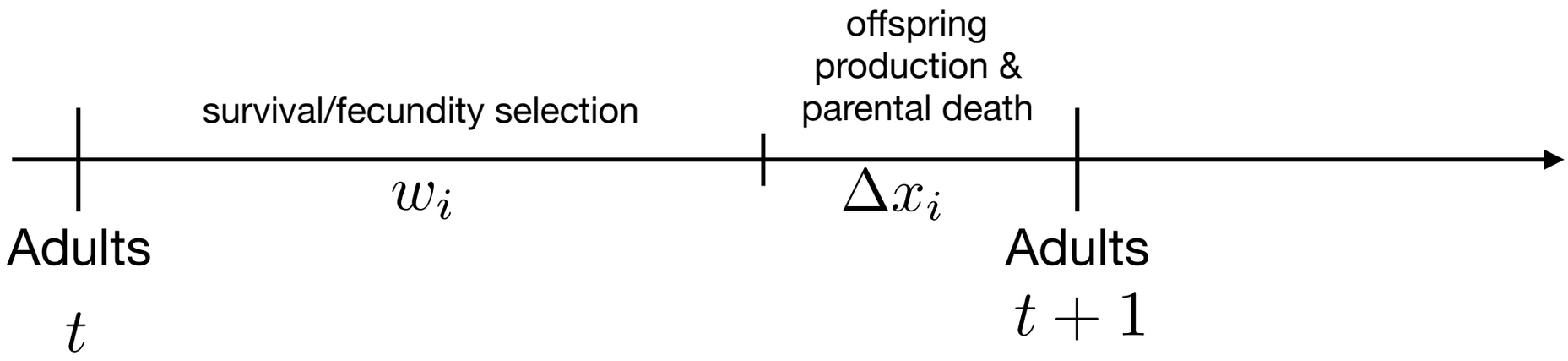

$$\bar{x}(t+1) - \bar{x}(t) = \frac{1}{\bar{w}}\mathrm{cov}[x, w] + \mathbb{E}[\Delta x]$$

Tracking Type Frequency

$x_i = \mathbb{I}_i$ indicator variable of type *i*

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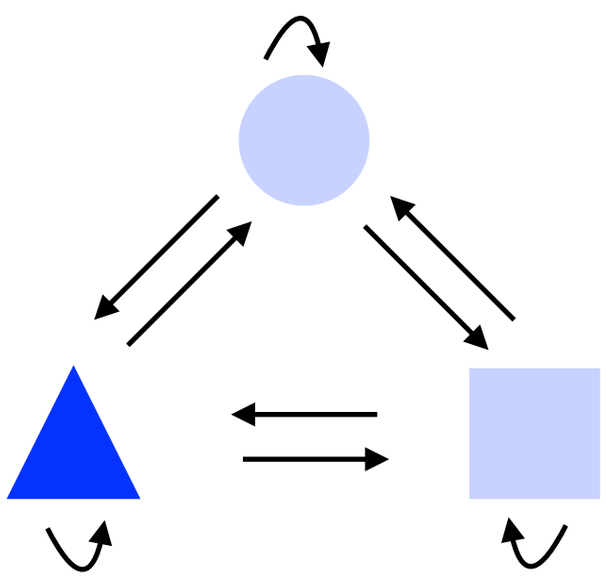
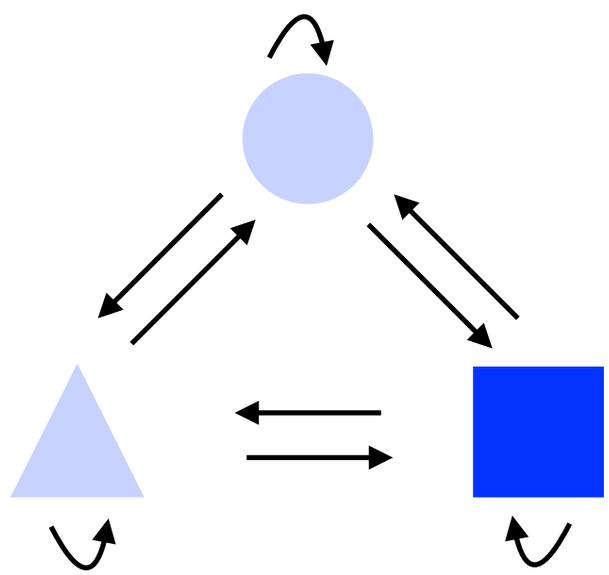
Environment 1



Darker =
Higher Fitness

Environment 2



Tracking Type Frequency

$x_i = \mathbb{I}_i$ indicator variable of type *i*

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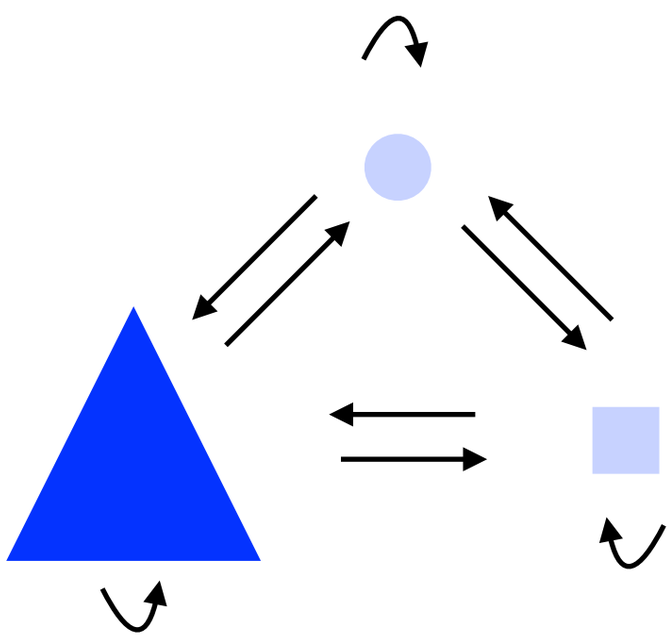

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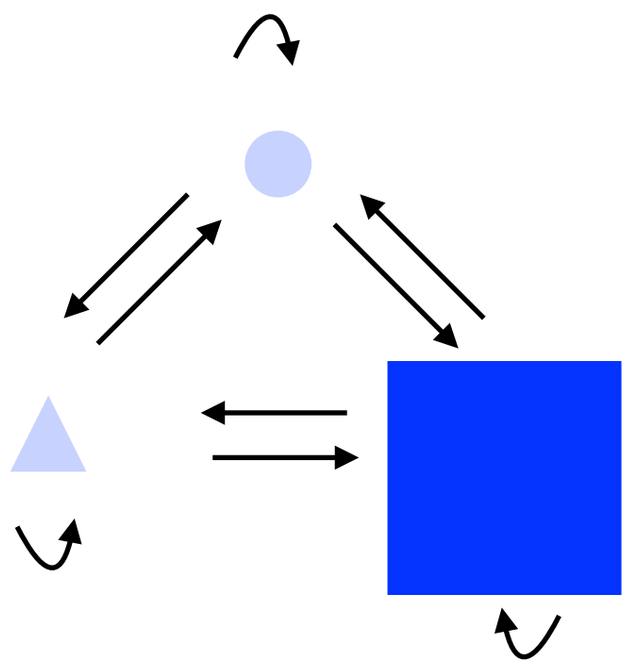

Drosophila Sex Comb Evolution

Ahuja & Singh. 2008. Genetics 179:503

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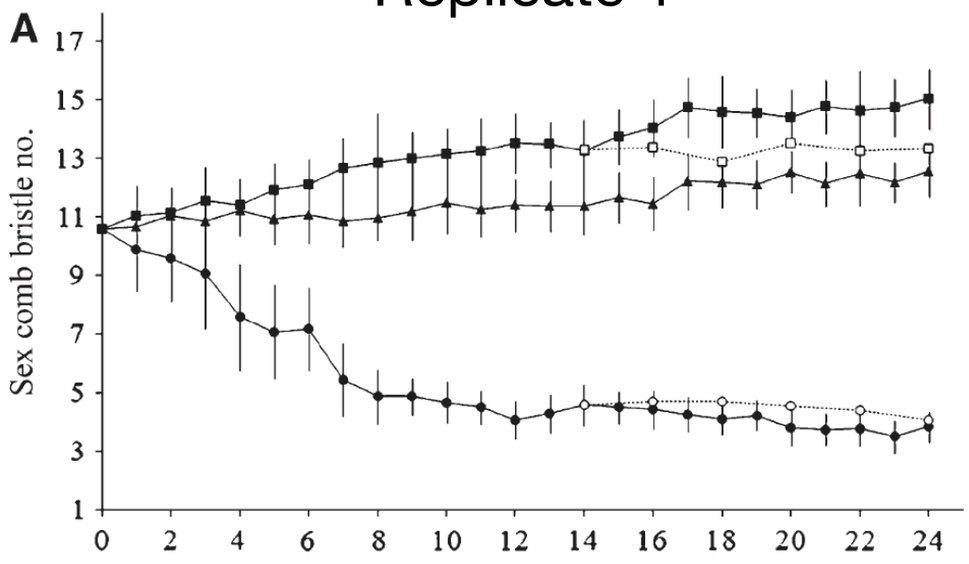

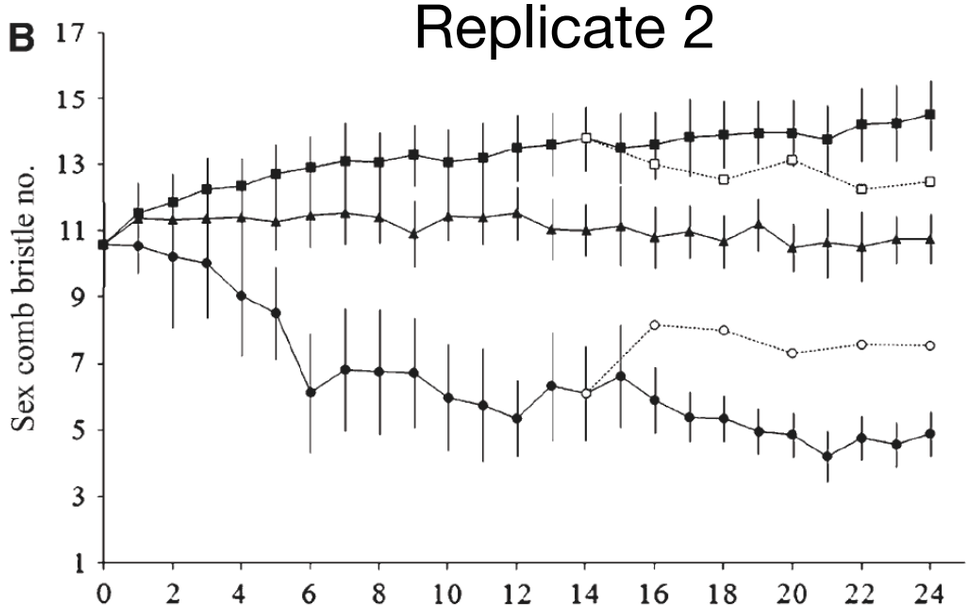

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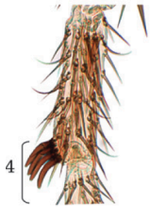

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Natural selection is not the sole determinant of phenotype

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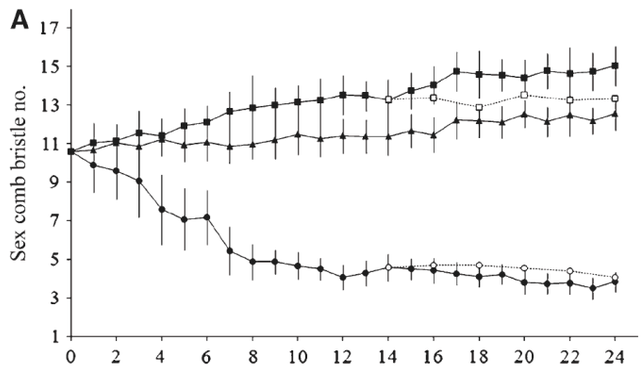

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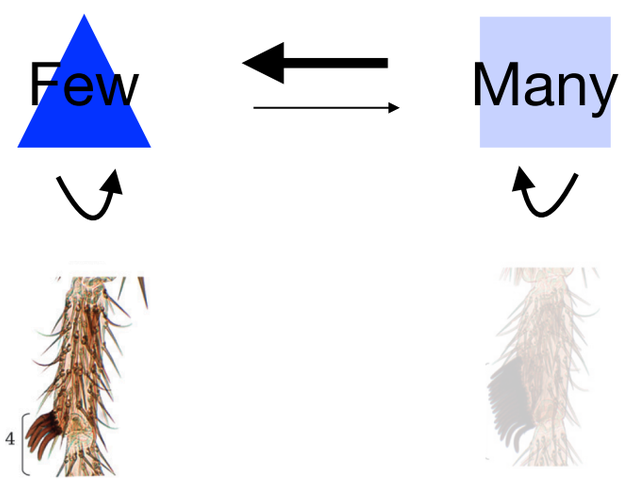

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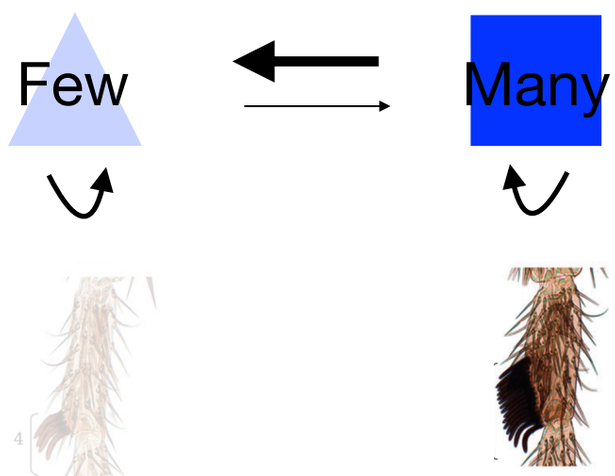

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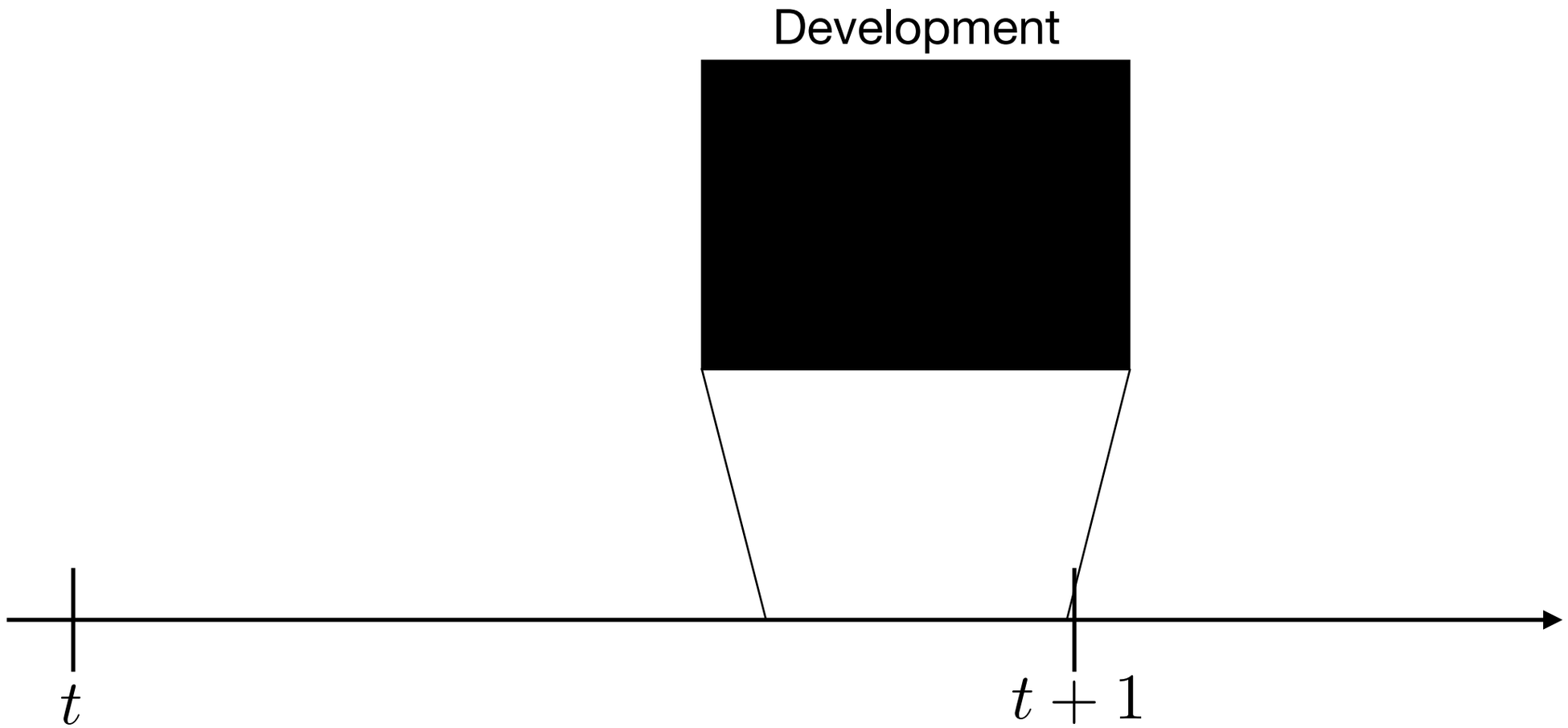

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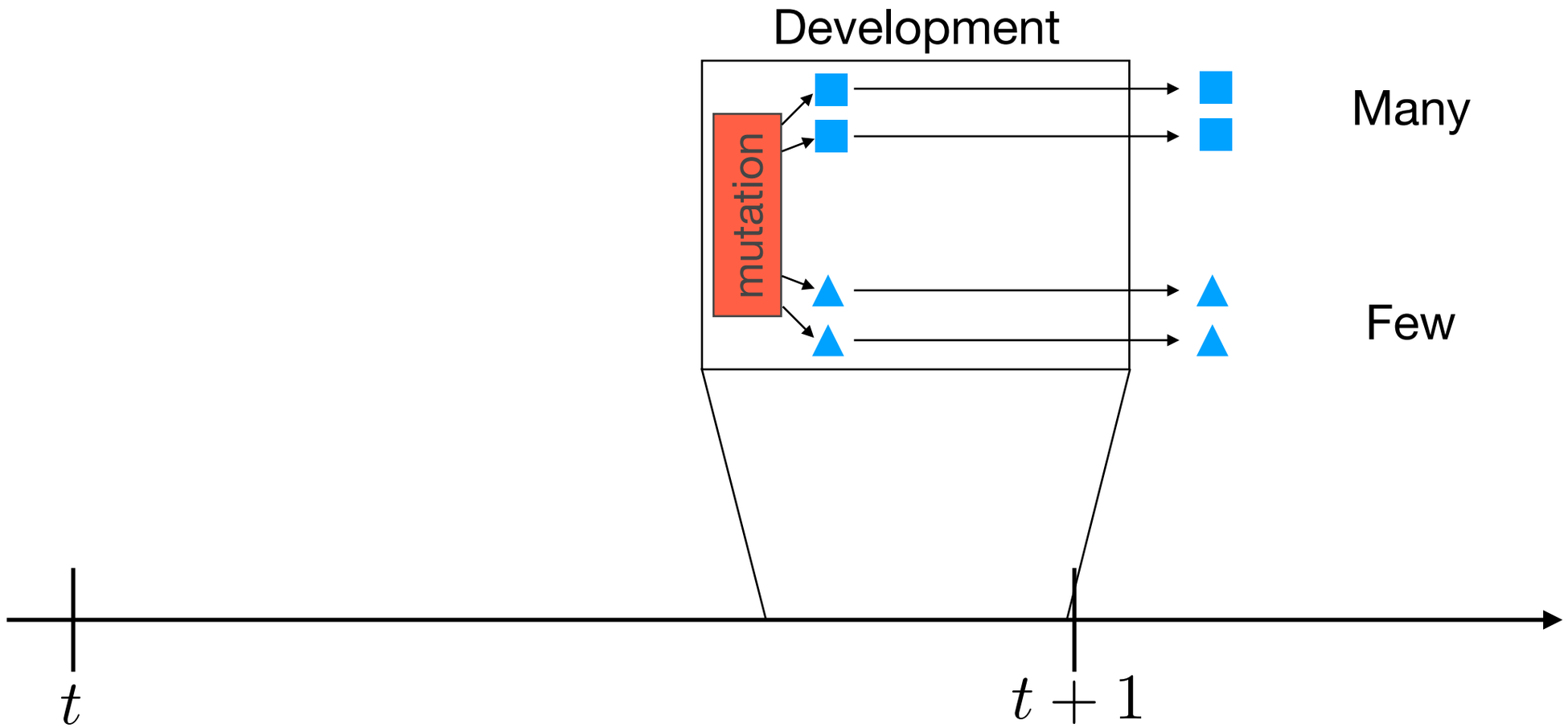

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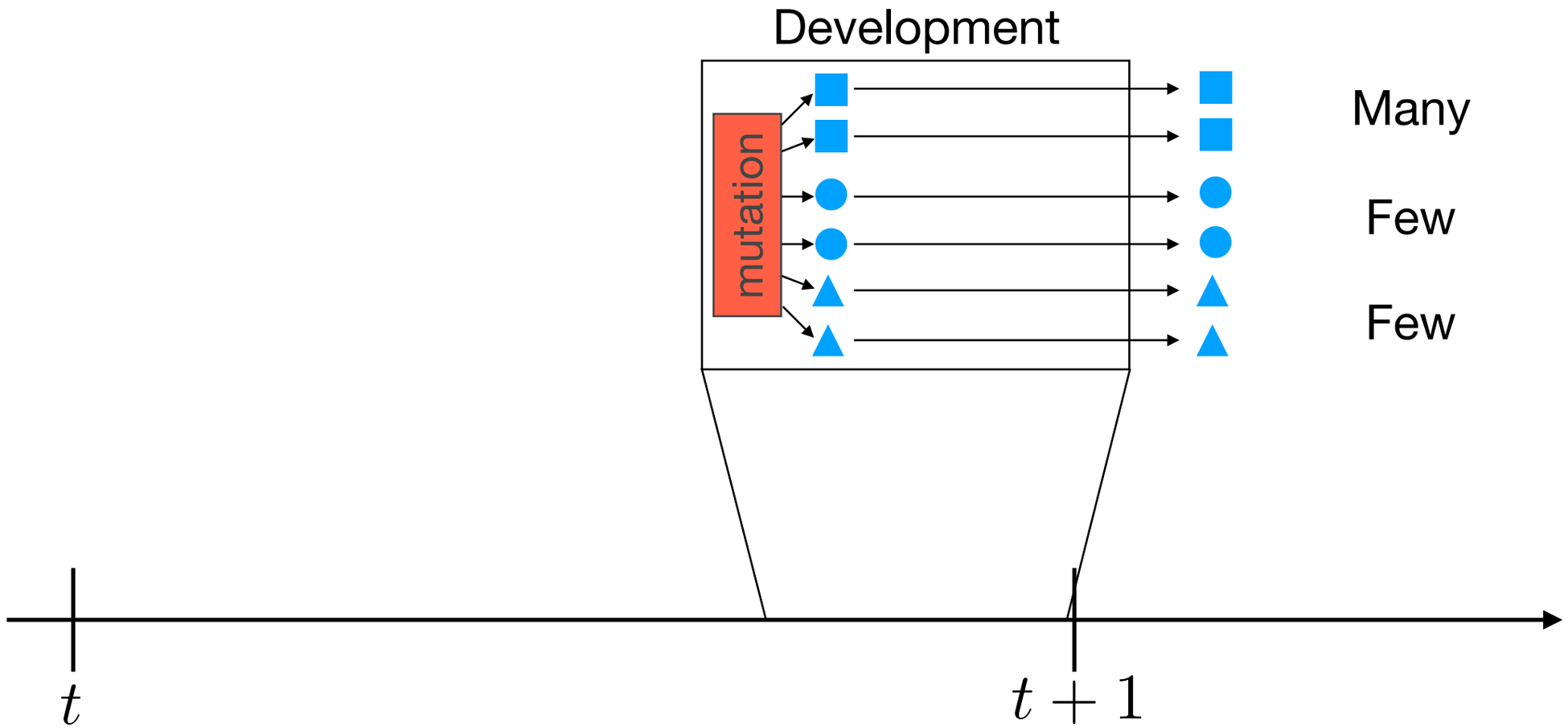

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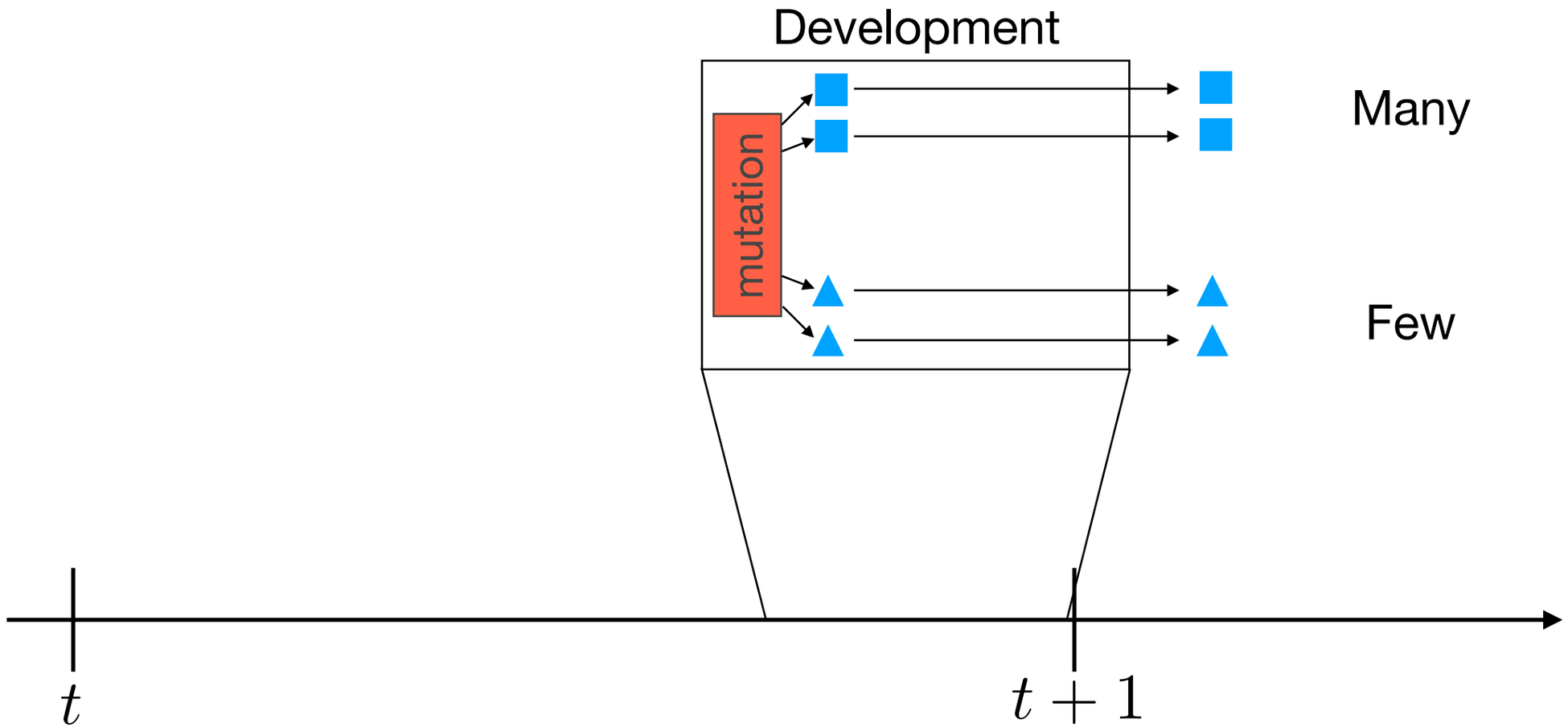

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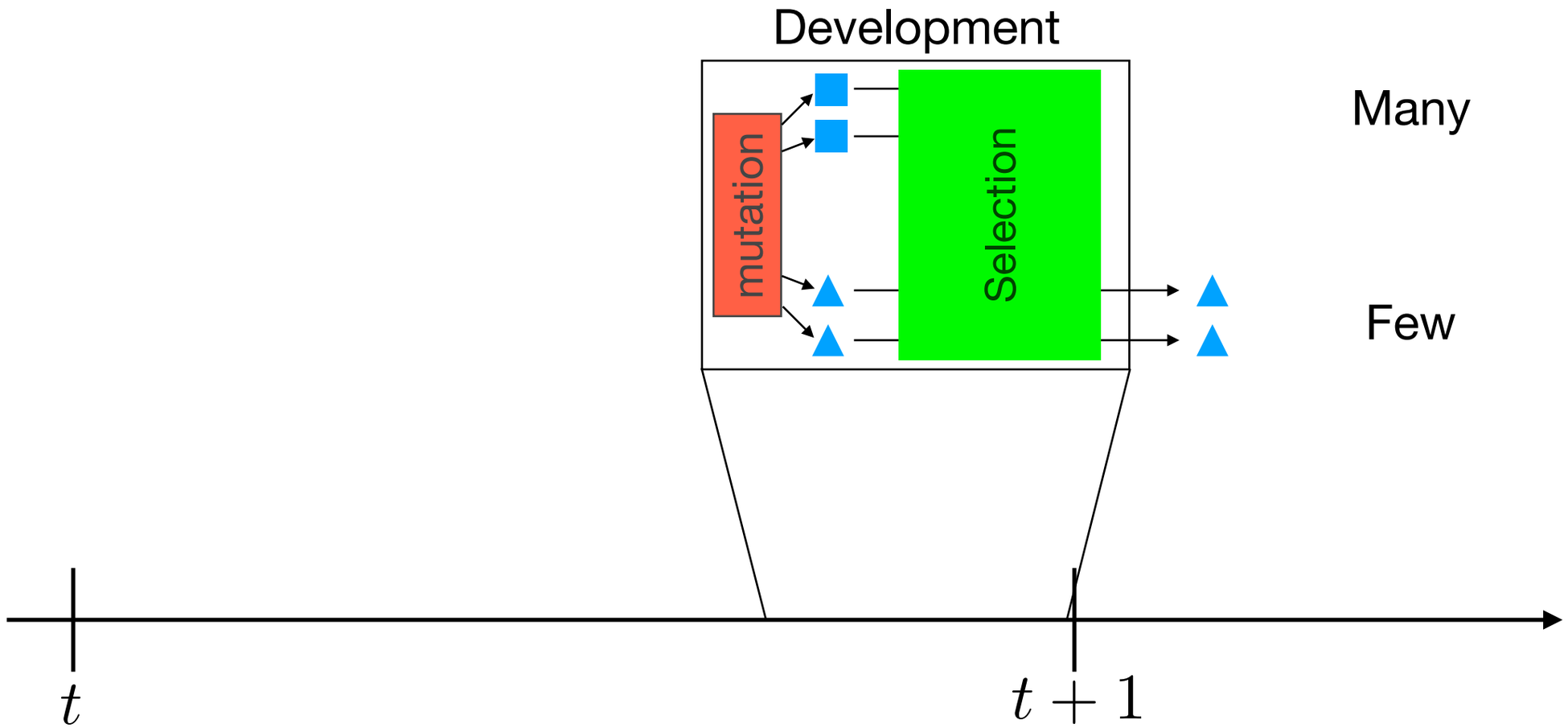

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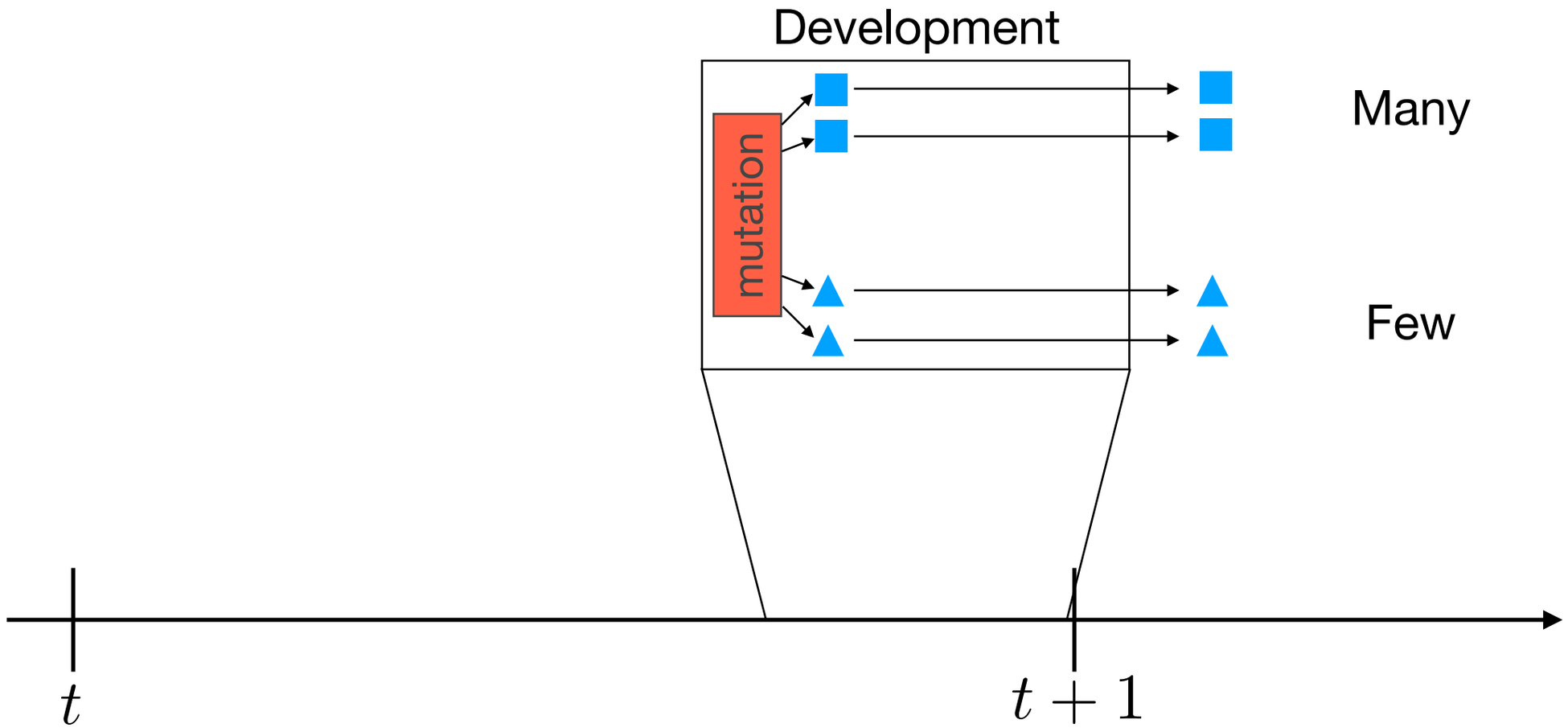

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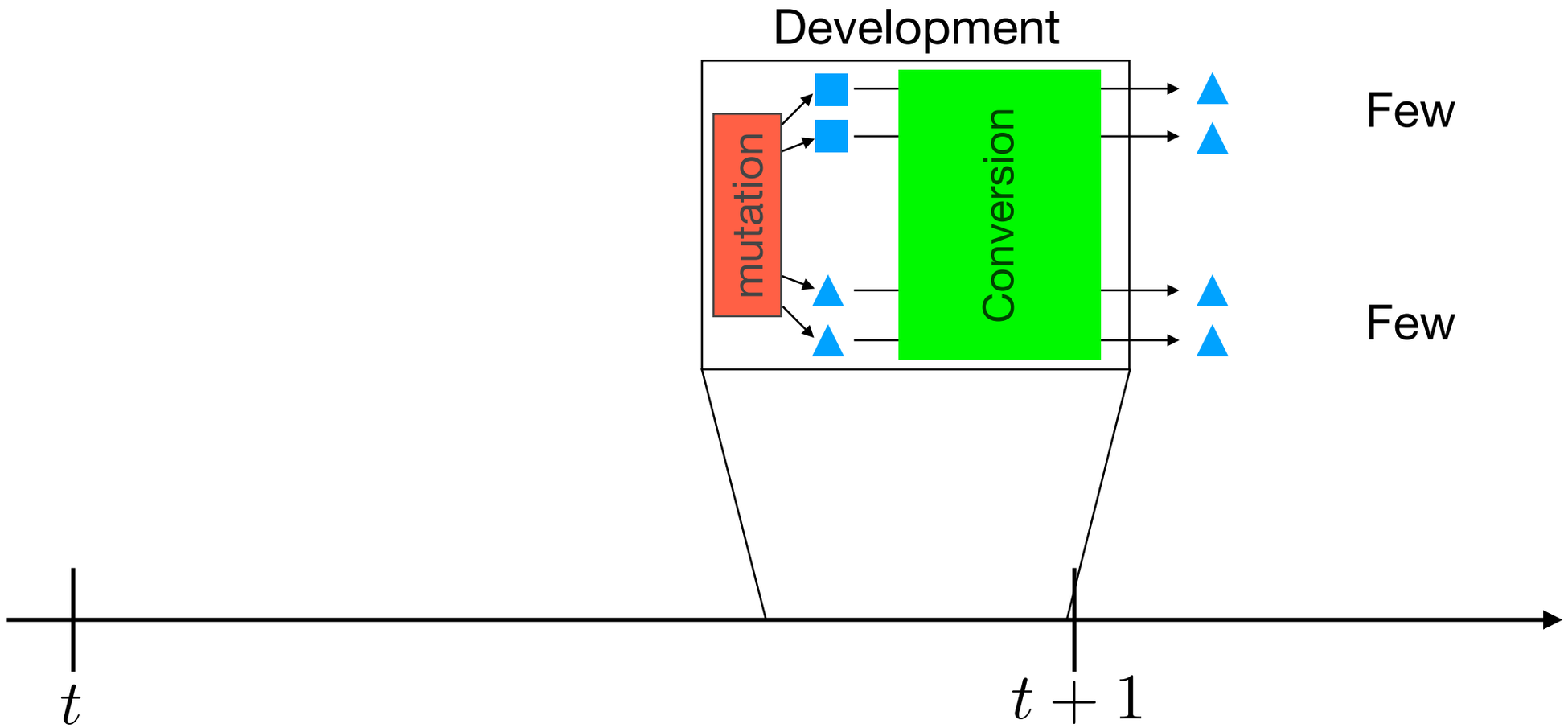

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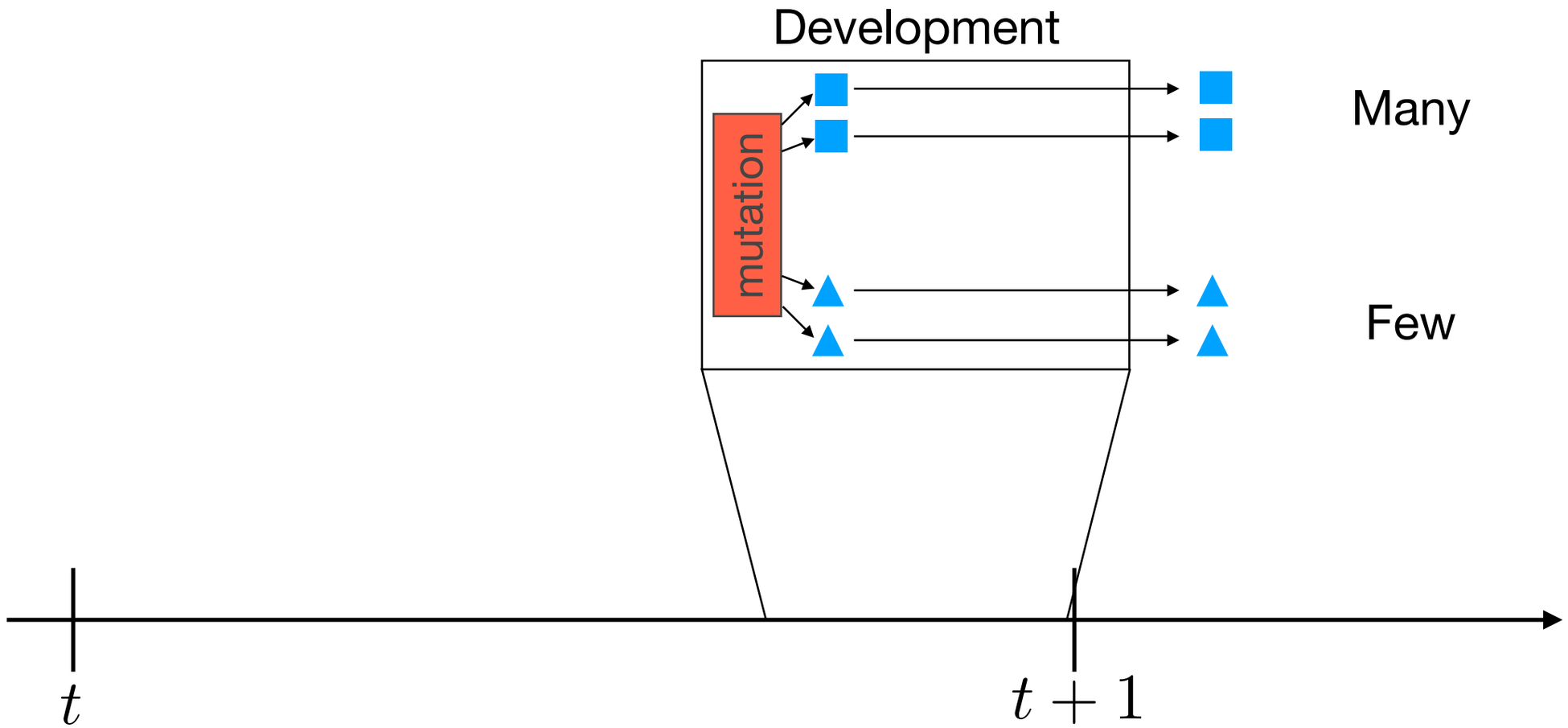

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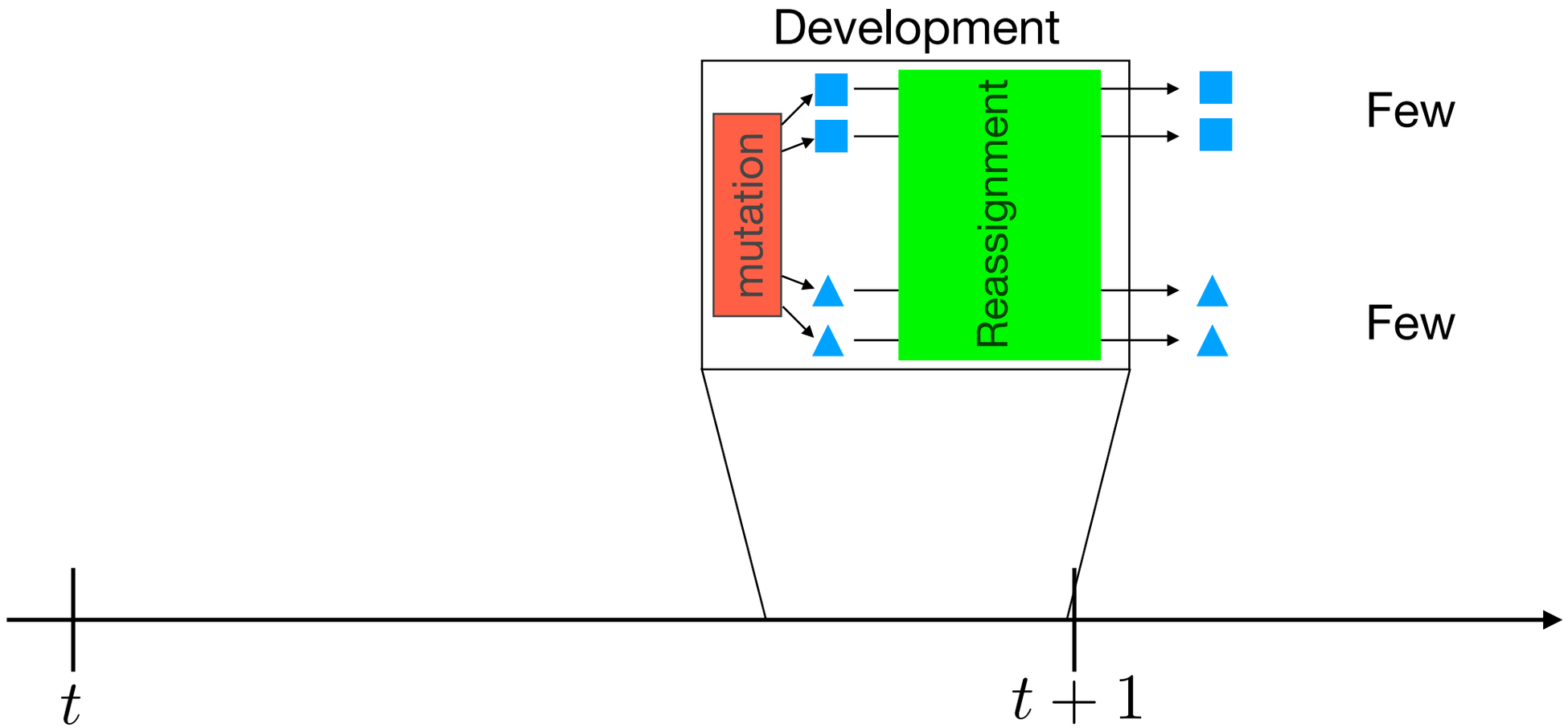

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Drosophila Sex Comb Evolution

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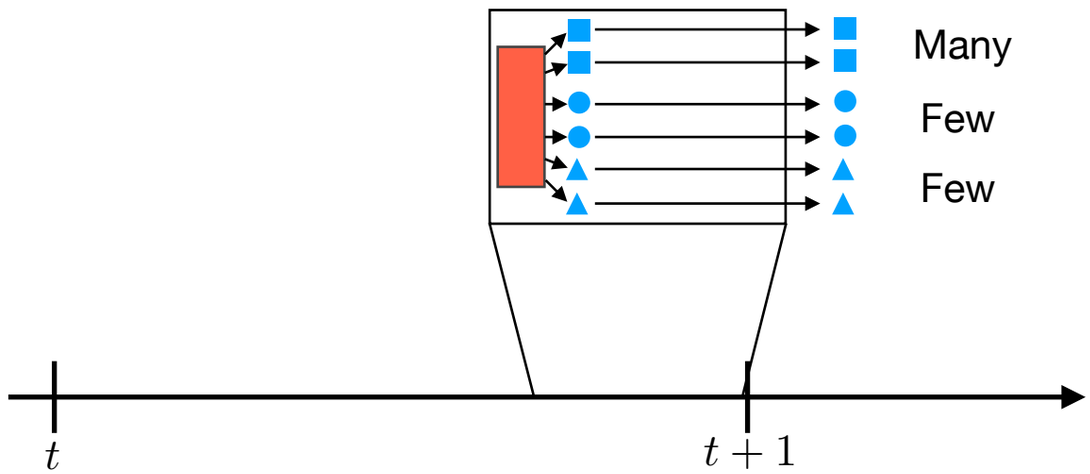

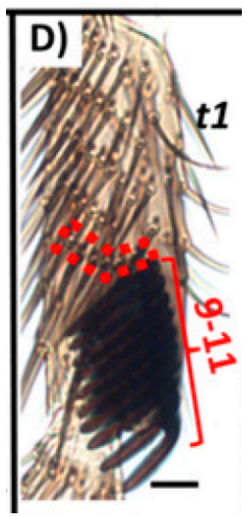

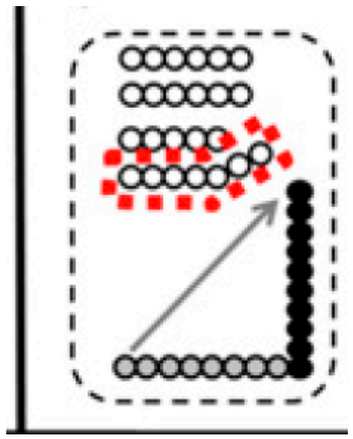

Malagon et al. 2014. PNAS 111:E4103

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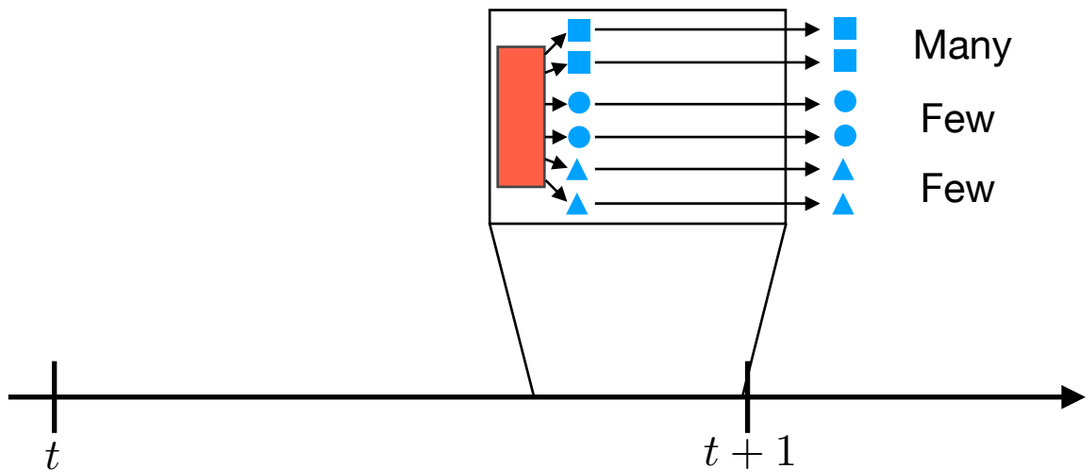

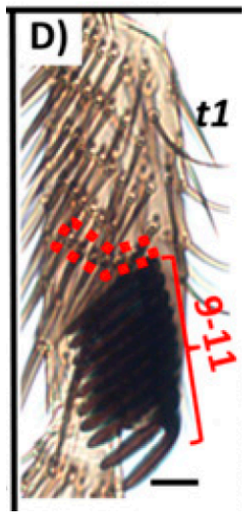

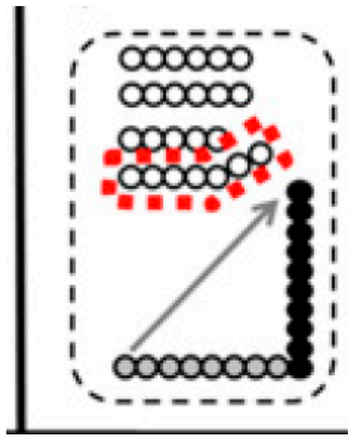

But this biased variation is not adaptive

Malagon et al. 2014. PNAS 111:E4103

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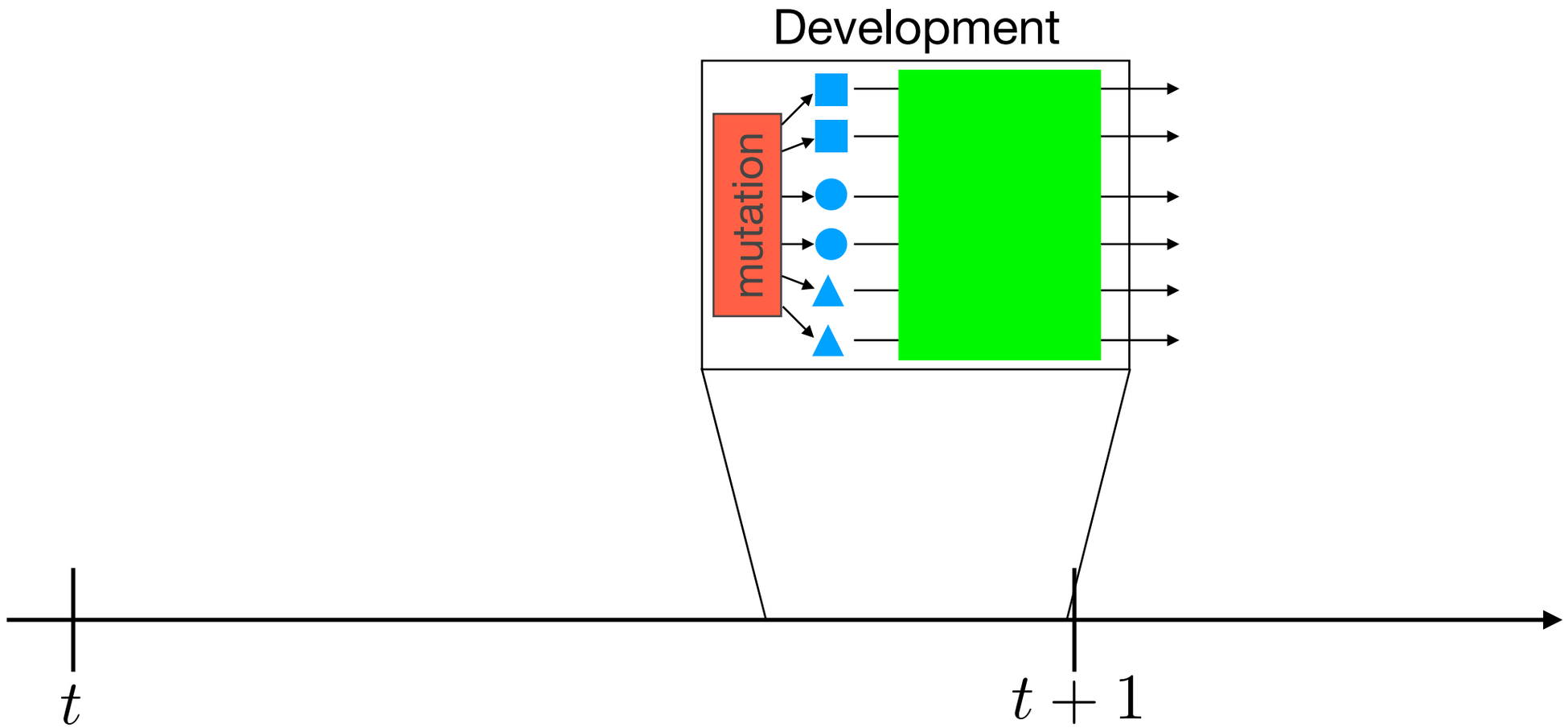
Why Would Bias be Adaptive in Novel Selective Environments?



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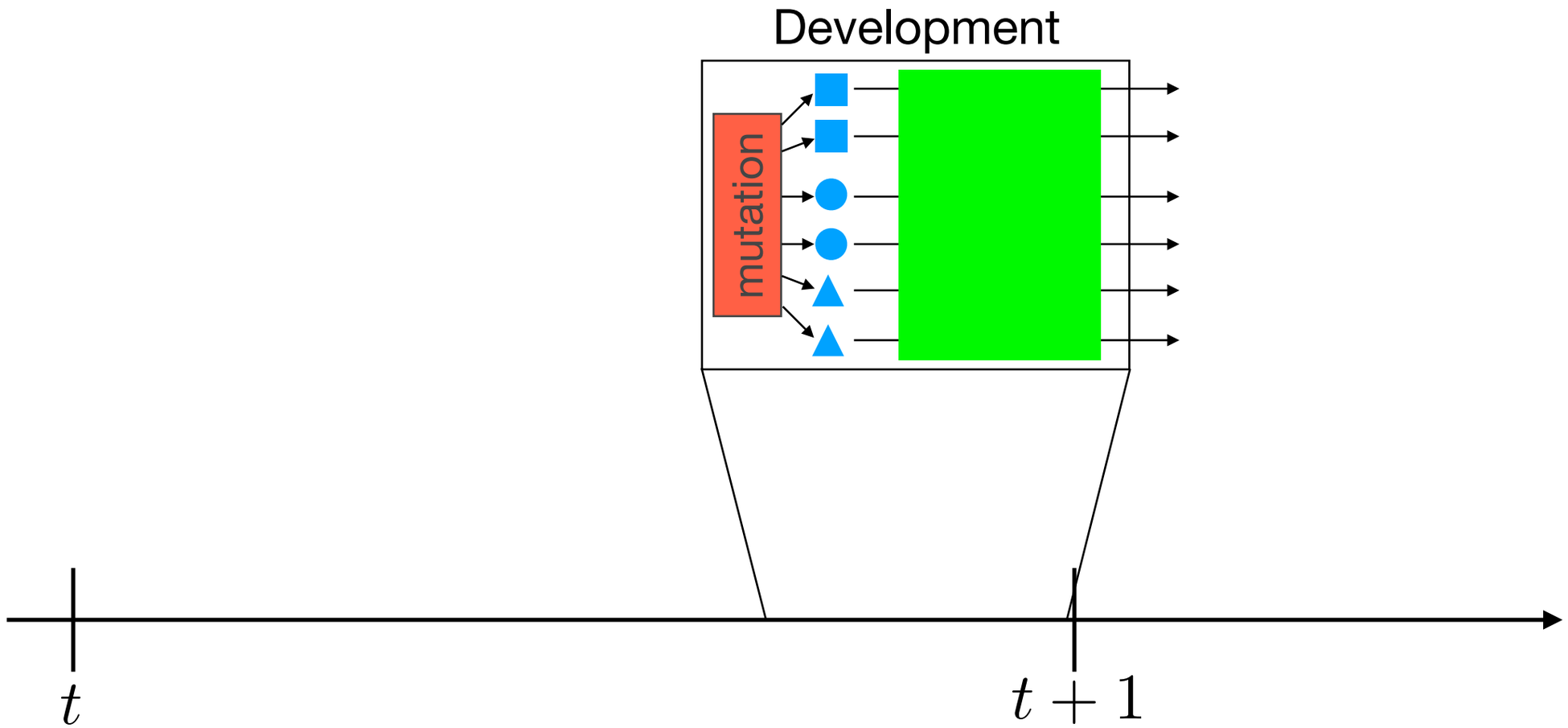

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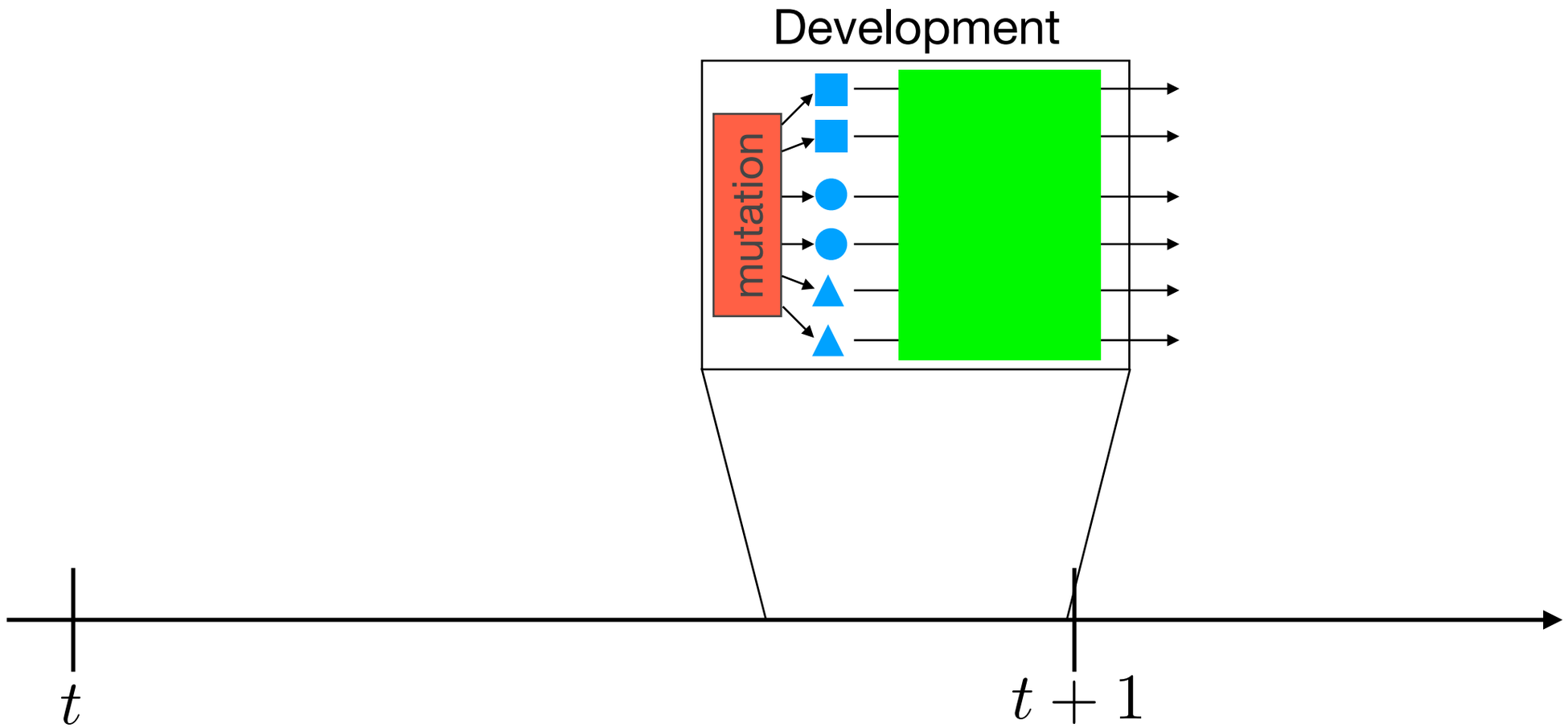

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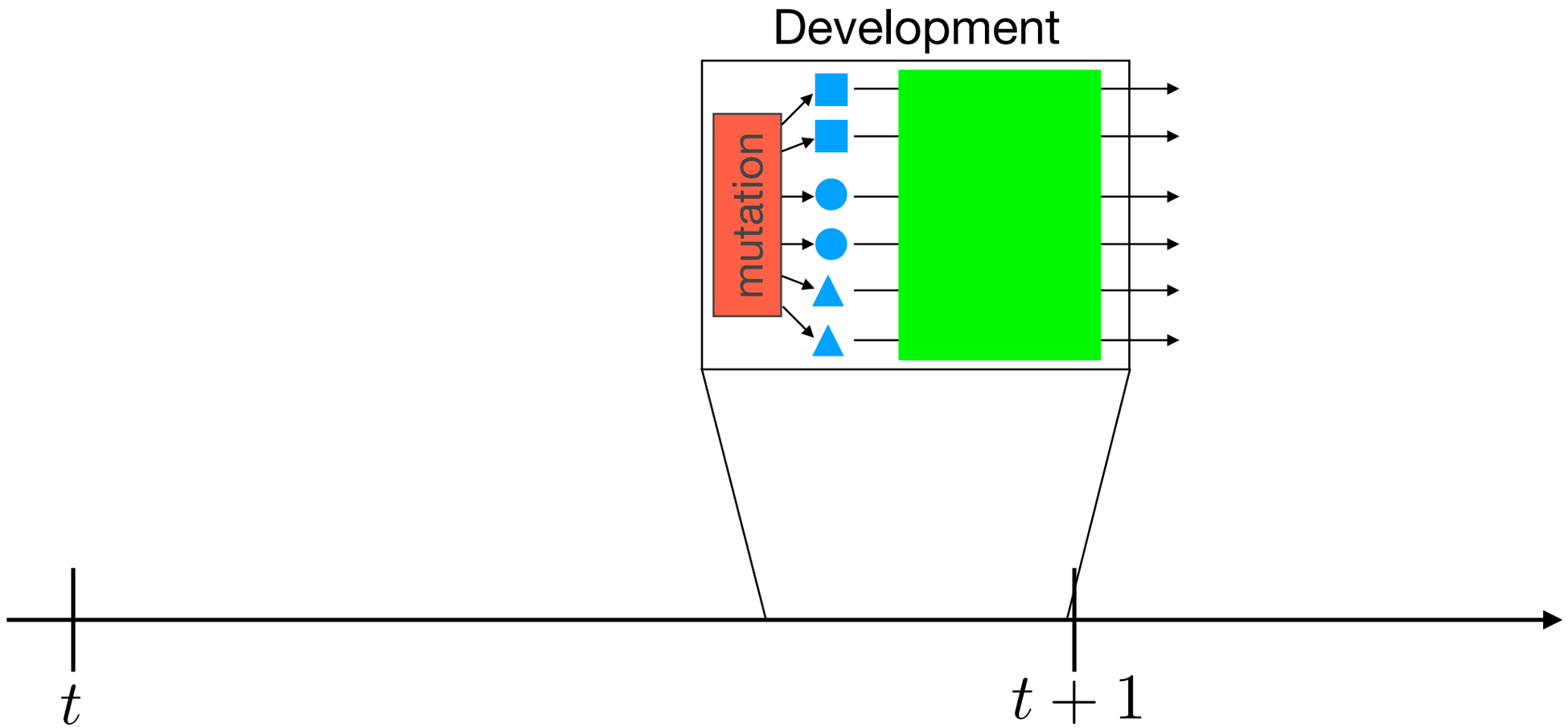

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Adaptive Variation Through Generalized Stress Response?

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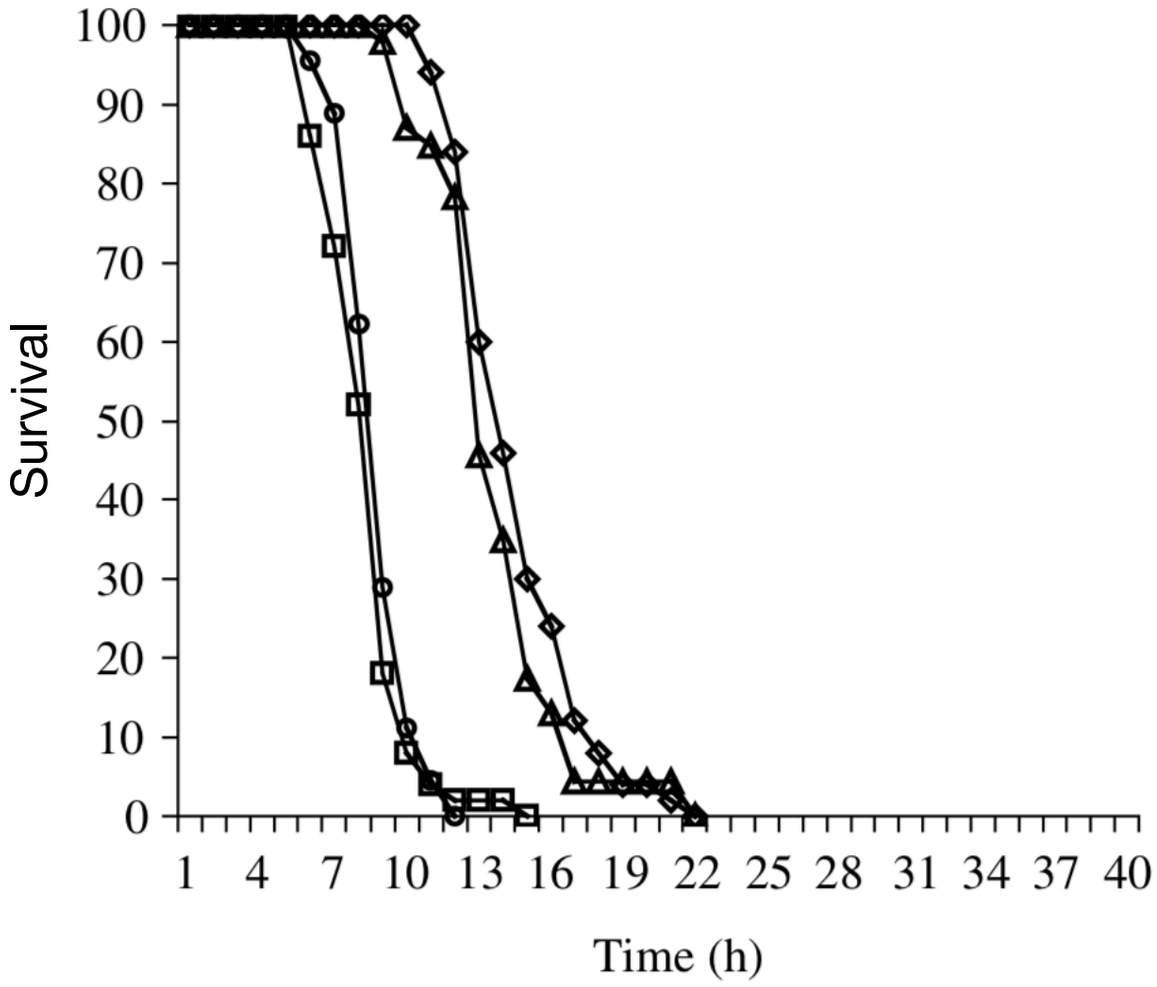
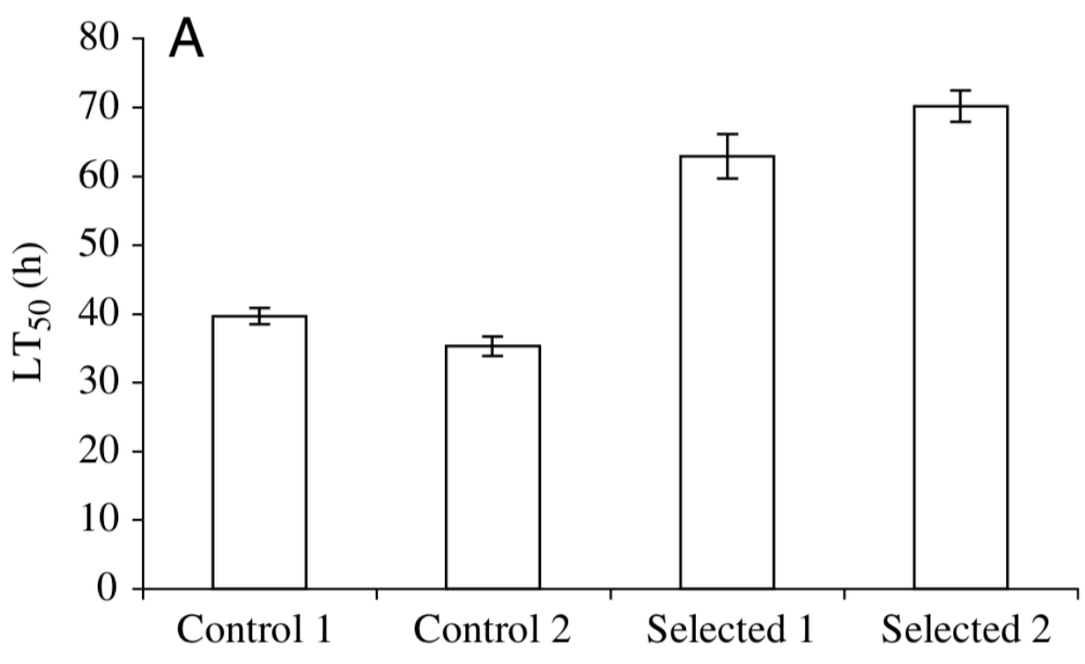


Select Drosophila for desiccation resistance

Telonis-Scott et al. 2006. J Experimental Biol 209:1837

Adaptive Variation Through Generalized Stress Response?

Starvation Stress



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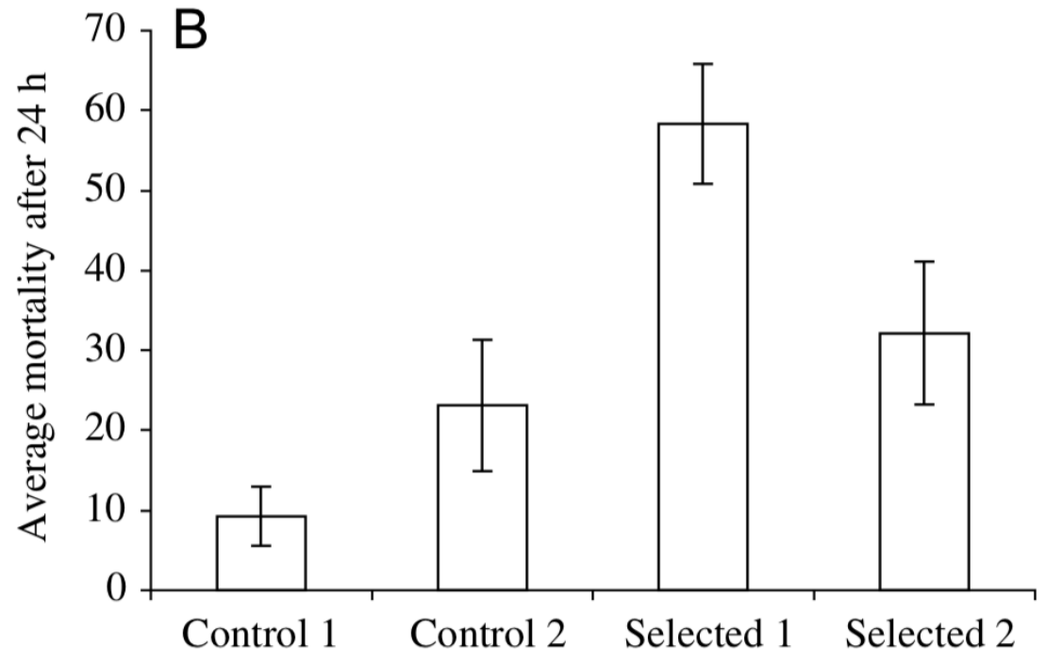

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Yellow Environment

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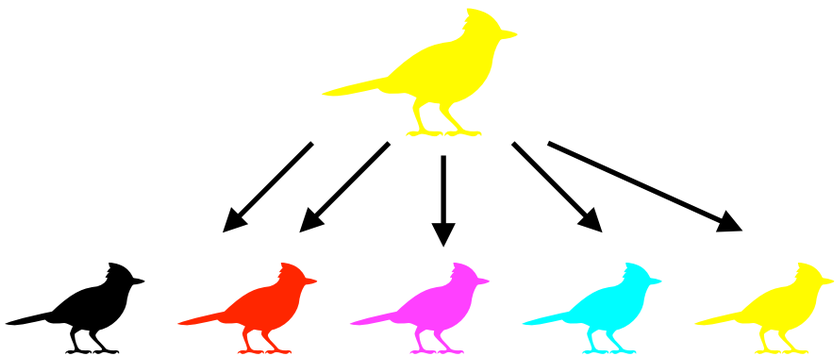

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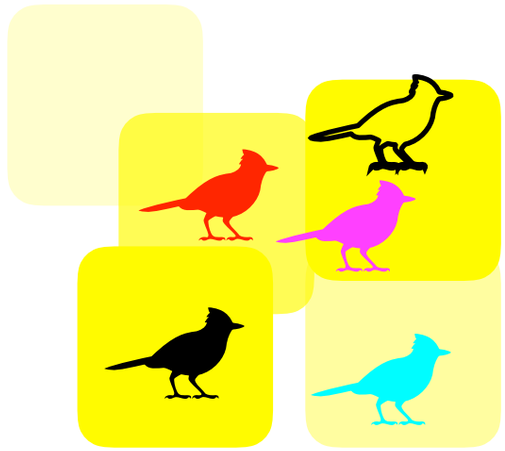

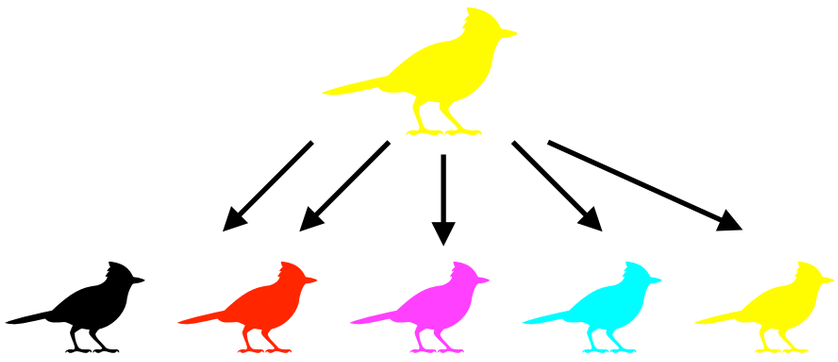

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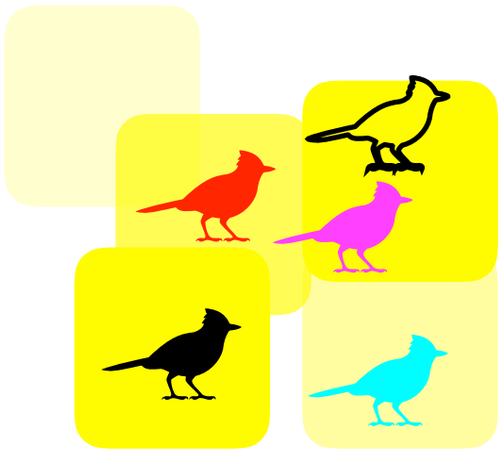

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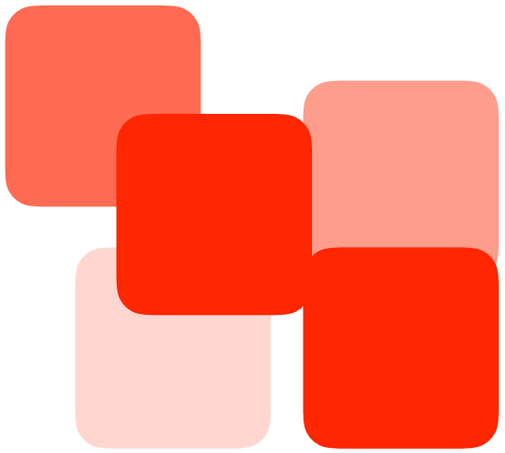

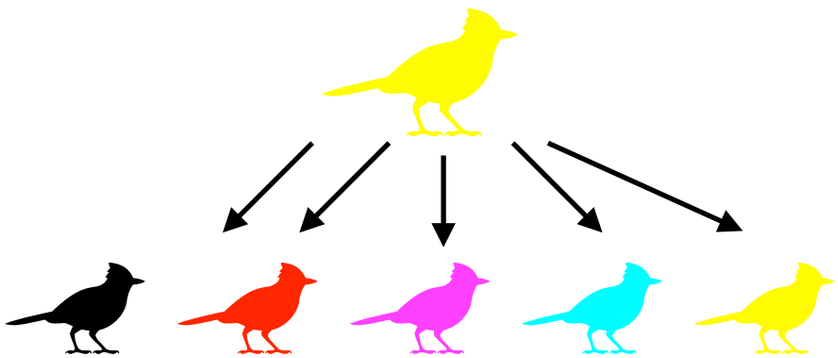

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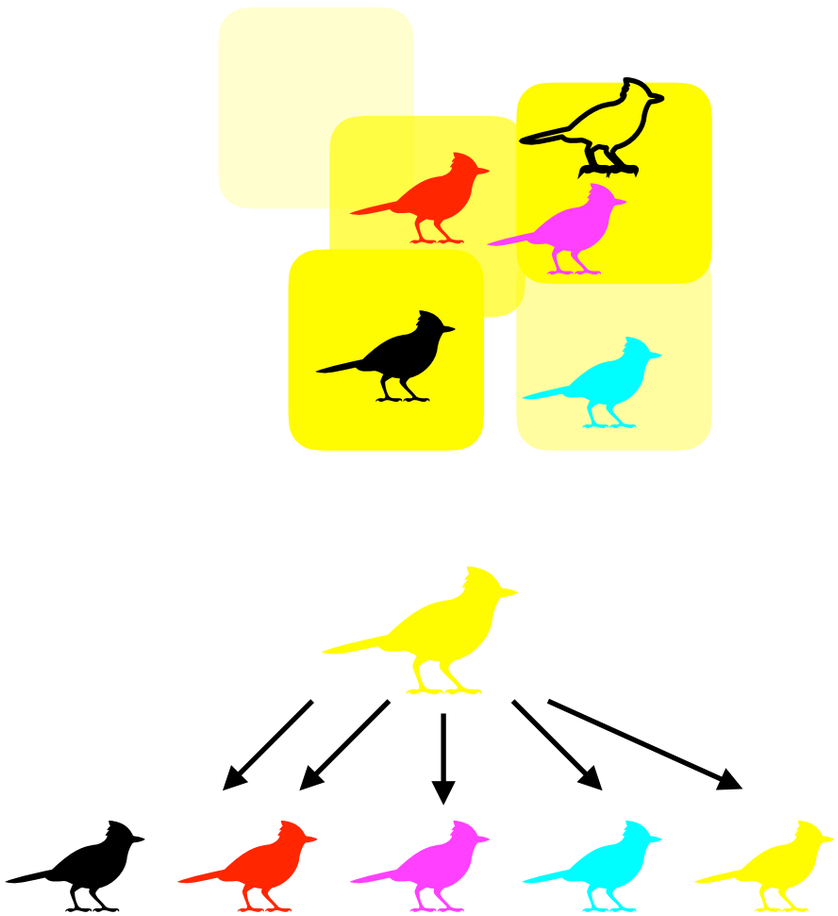

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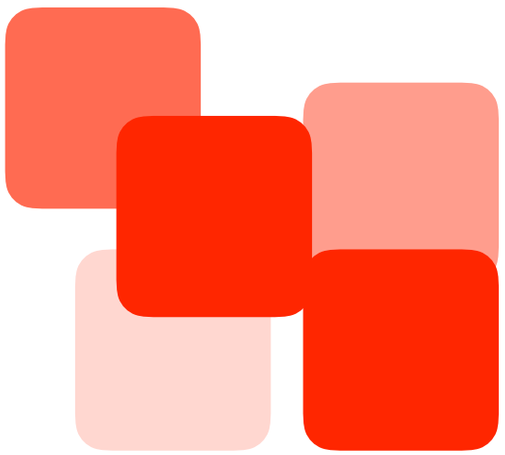

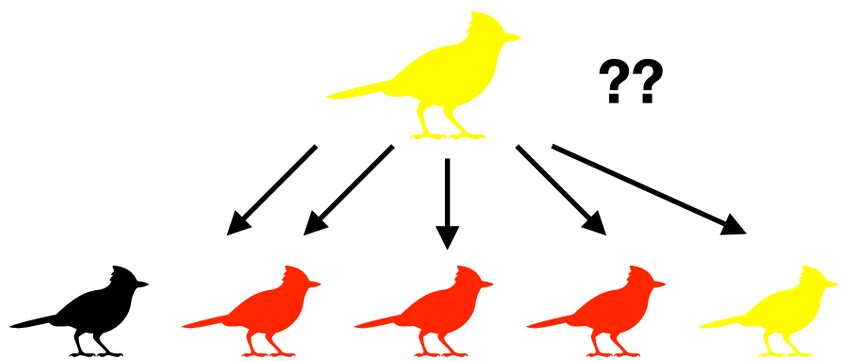

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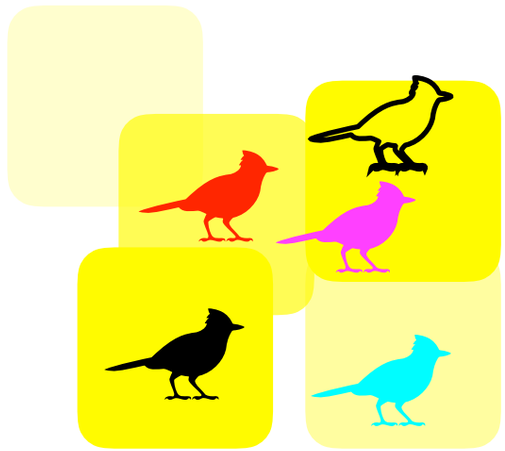

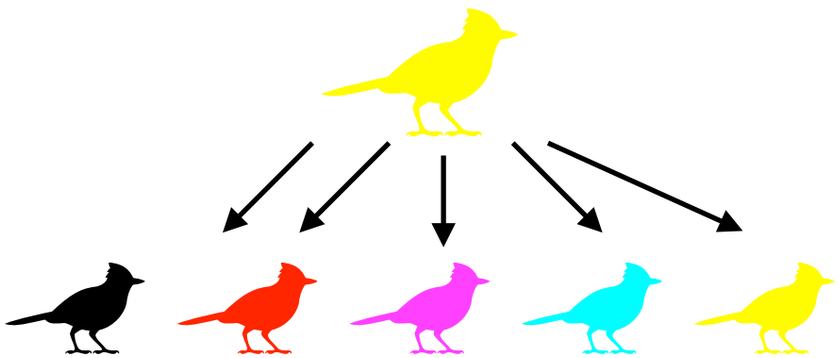

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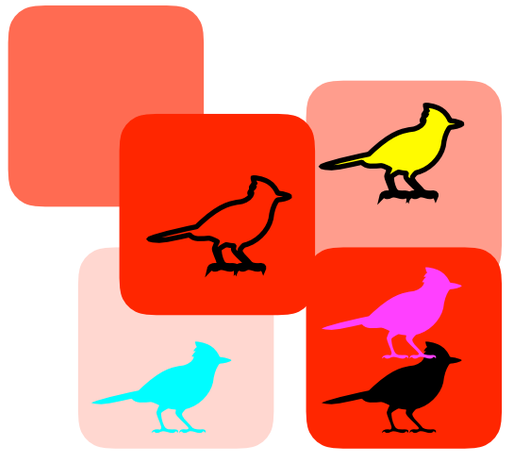

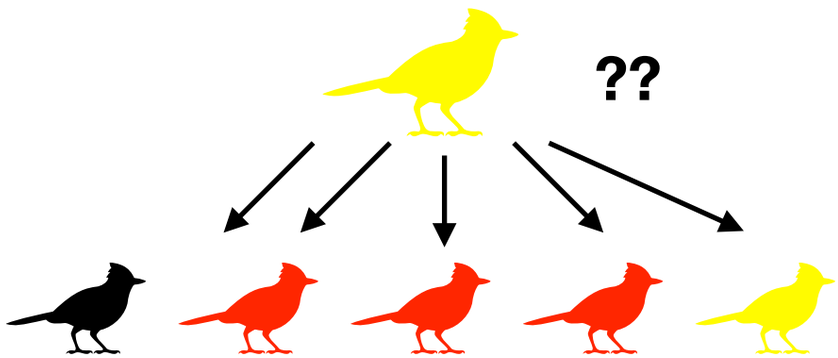

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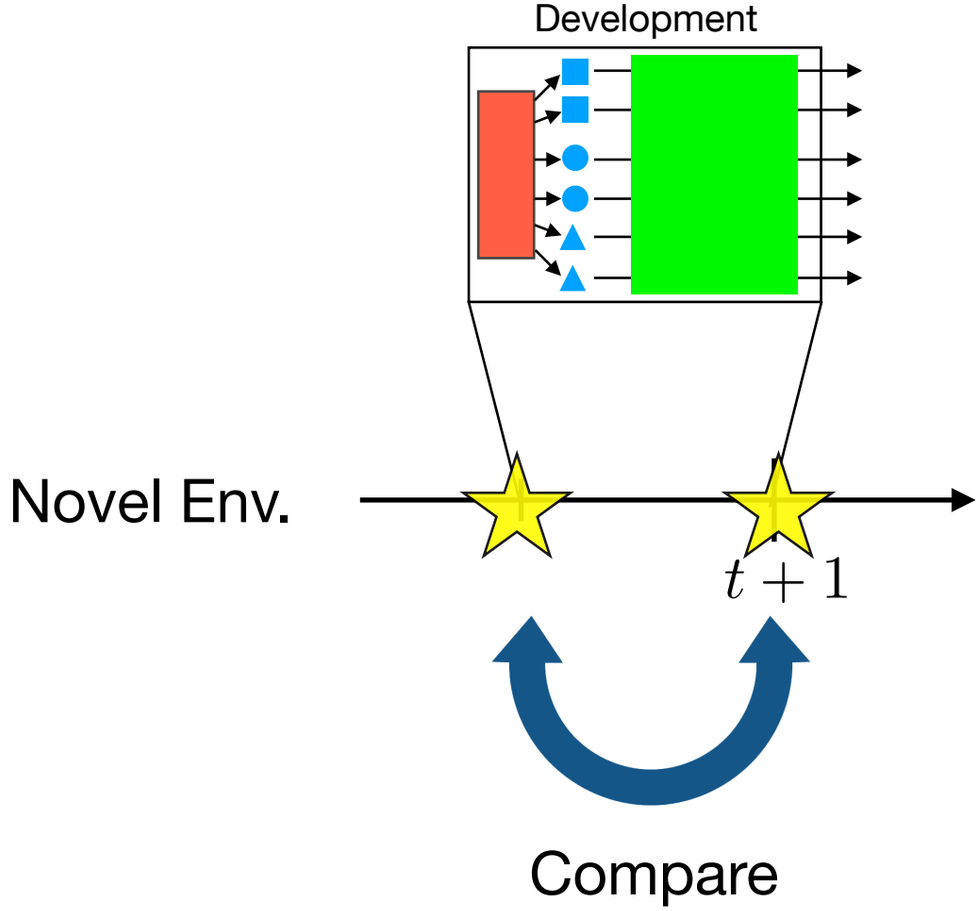

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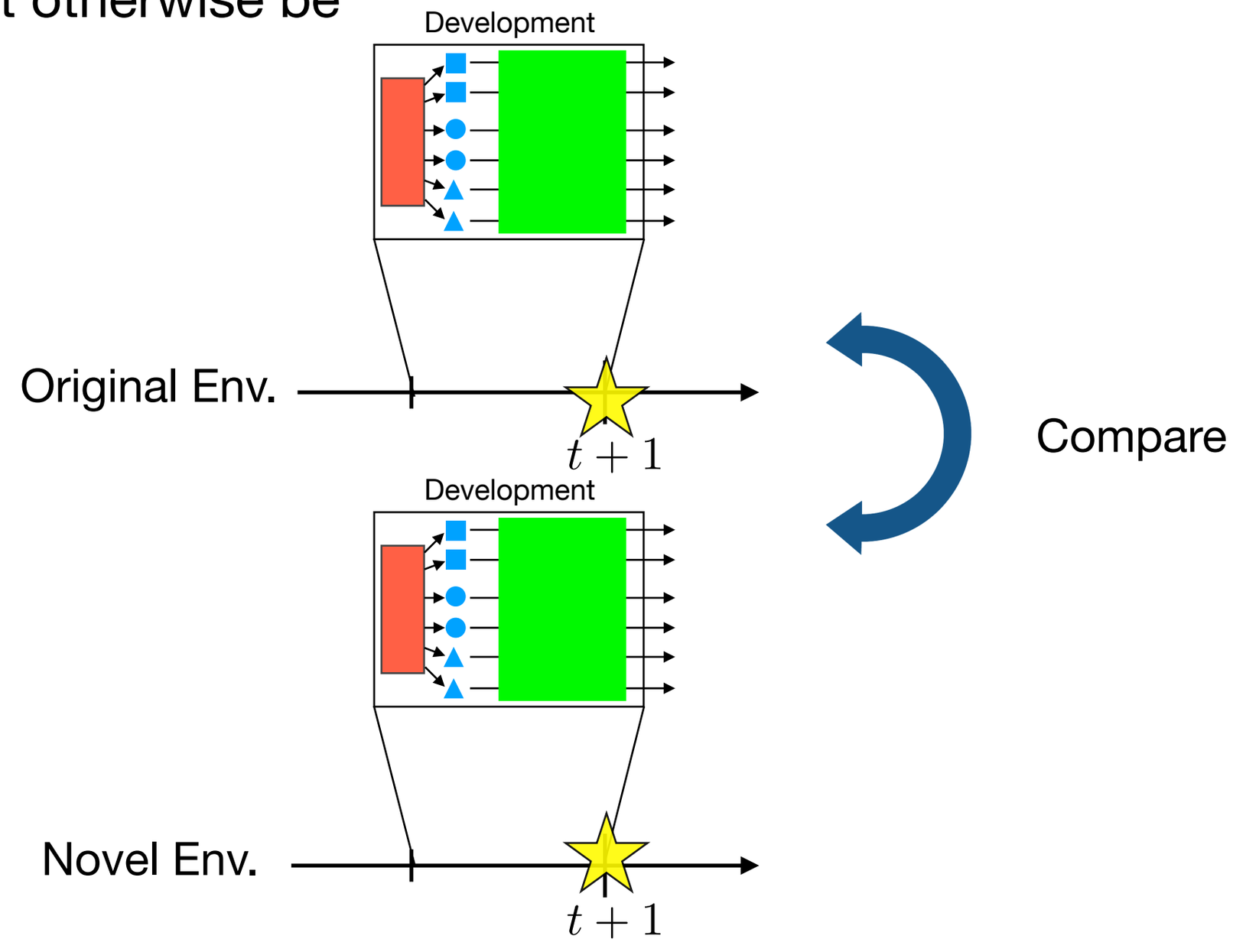

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<u>Thanks to</u>: Richard Watson, Kevin Laland, Tobias Uller

NSERC CRSNG

Queen's University