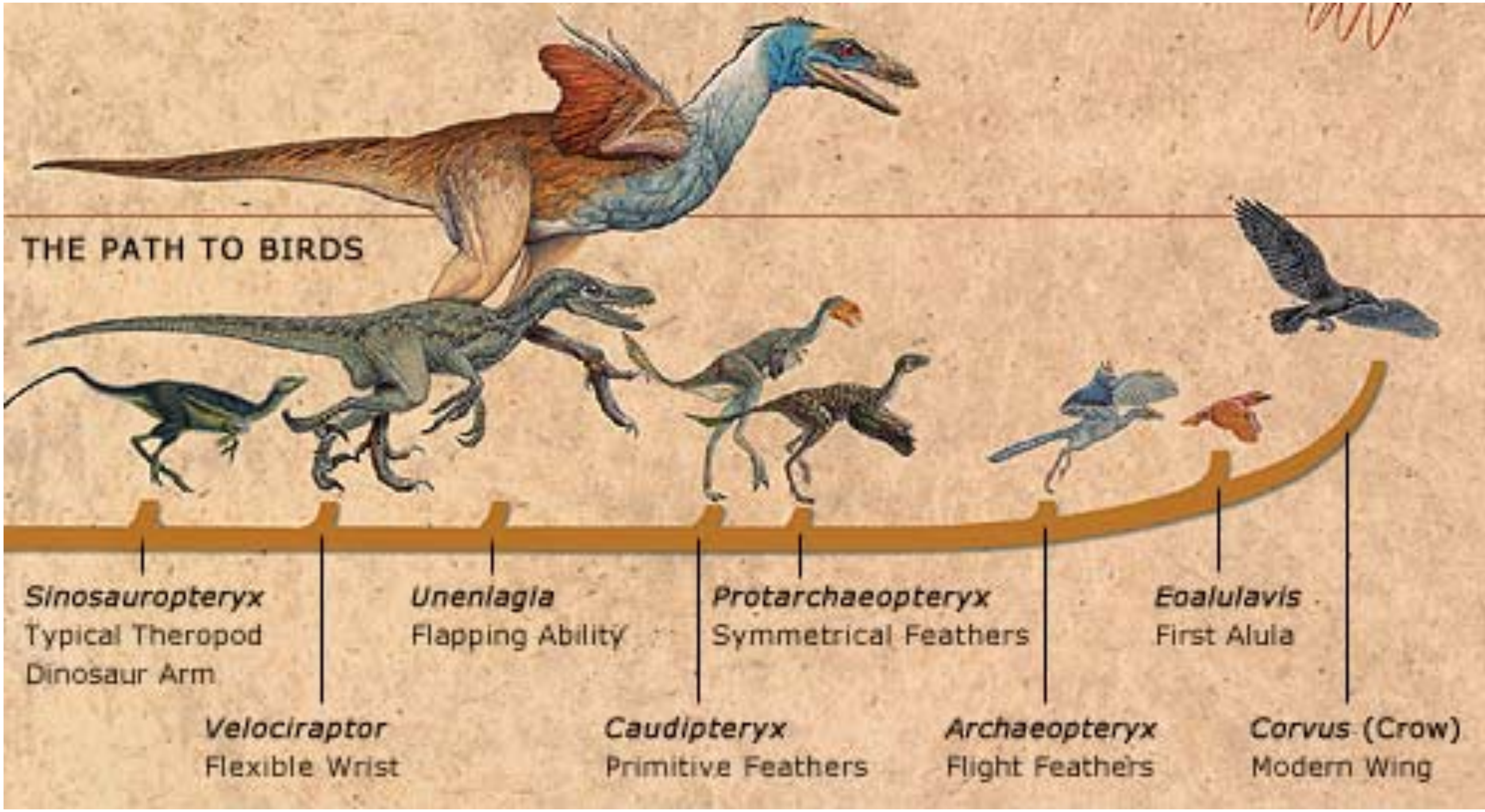
L'apparition et la perte subséquente de la diversité de ploïdie durant l'évolution expérimentale chez *Saccharomyces cerevisiae*

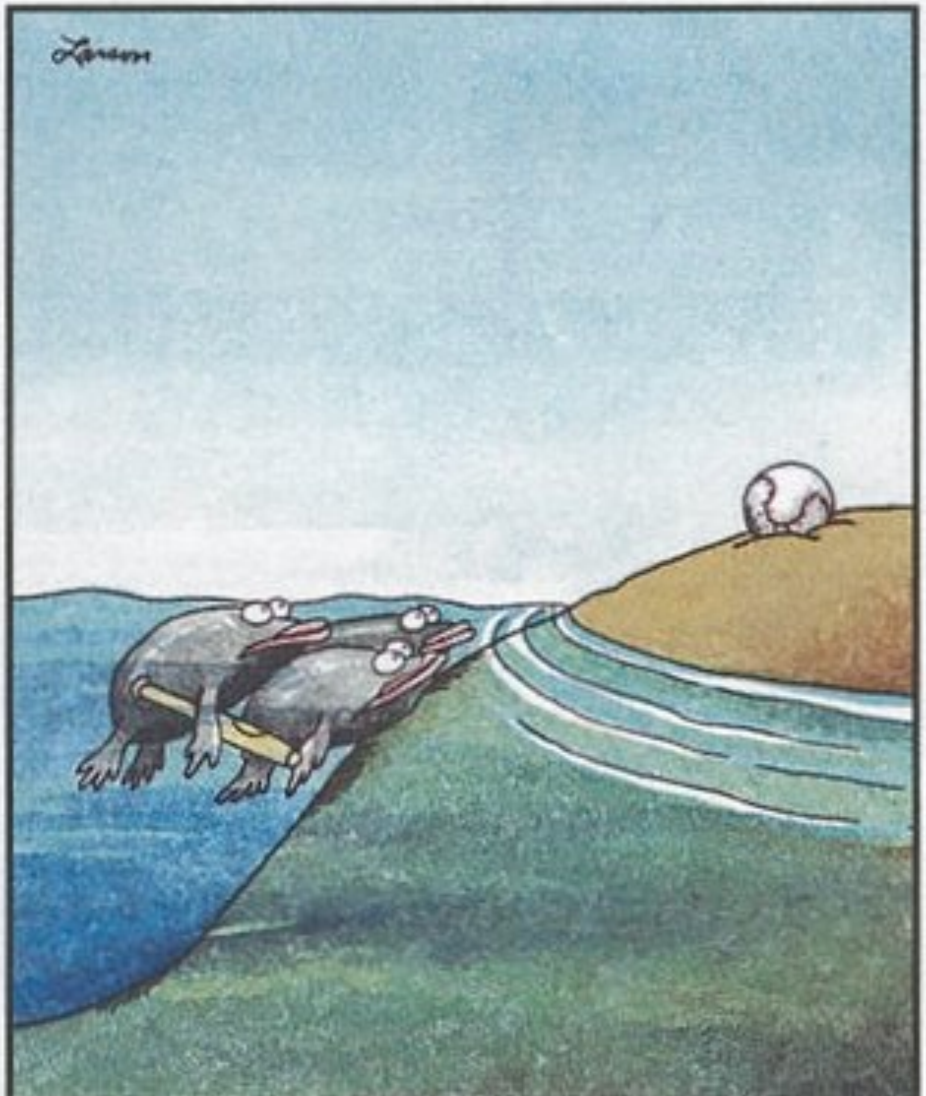
The appearance and subsequent loss of ploidy diversity in experimental evolution with *Saccharomyces cerevisiae*

Aleeza Gerstein
PhD Candidate, Otto Lab
SCEE/CSEE 2010

Transitions in form over evolutionary time

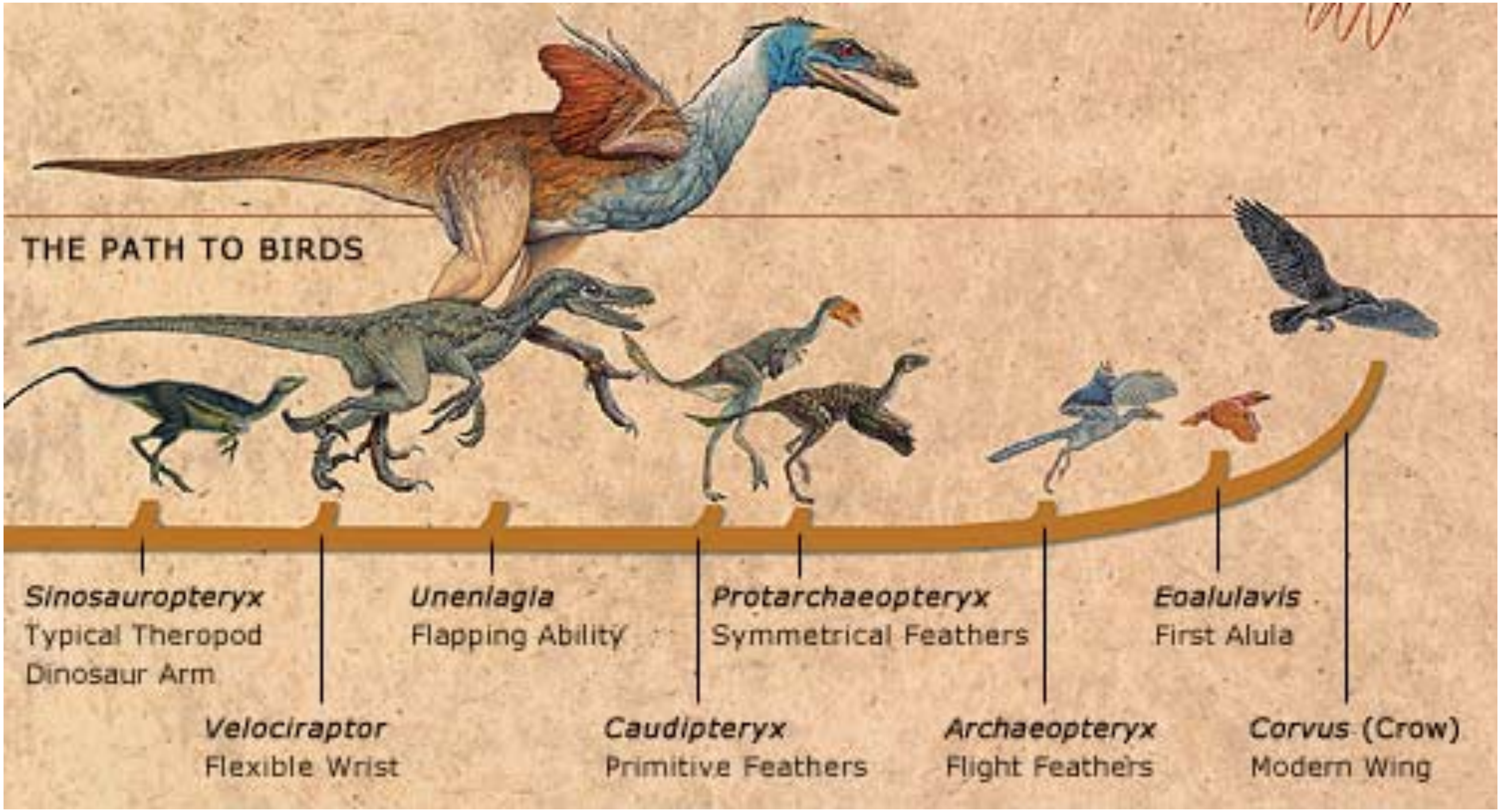


What are the selective forces?

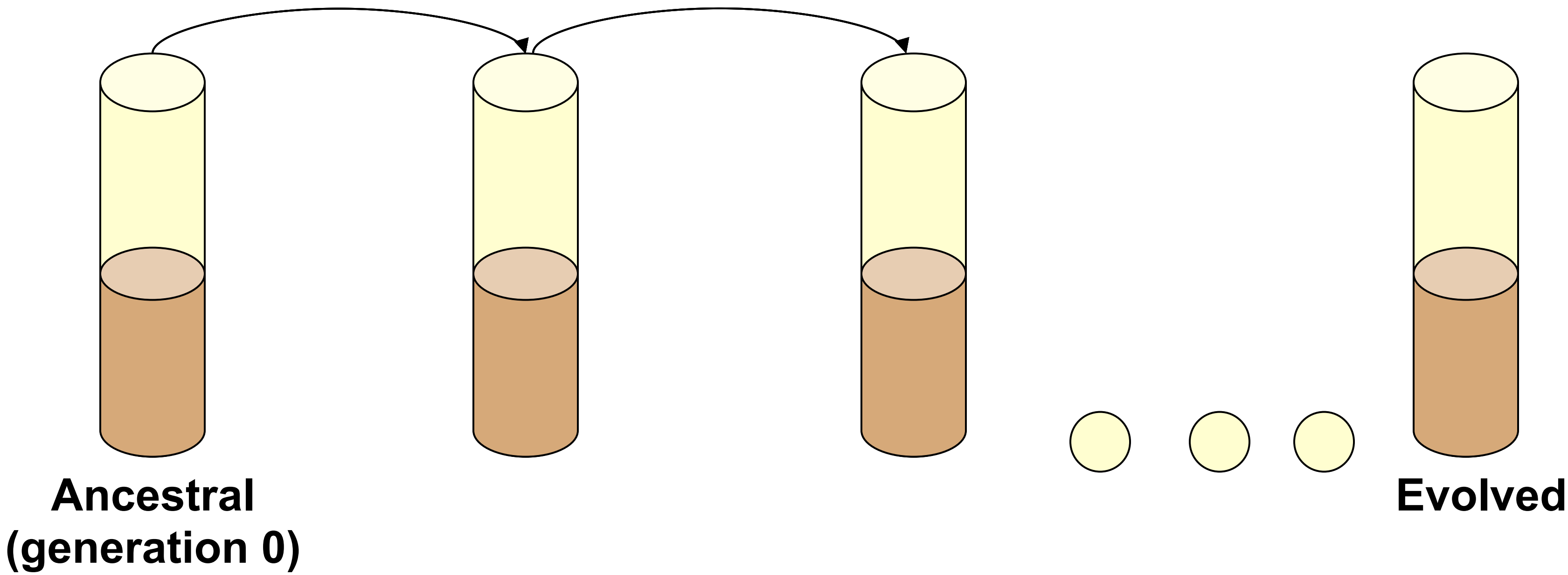


Great moments in evolution

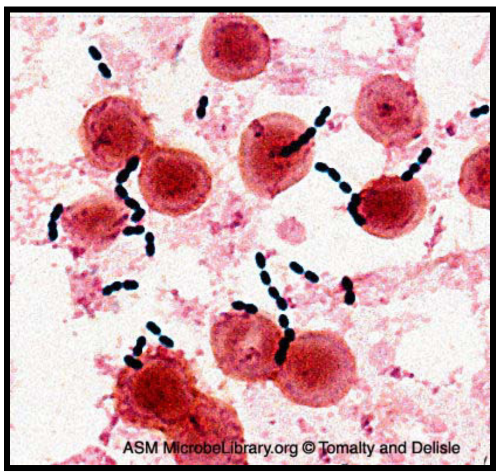
Hard to test hypotheses through the fossil record



We use batch culture evolution to track the fossil record



Ploidy varies between species

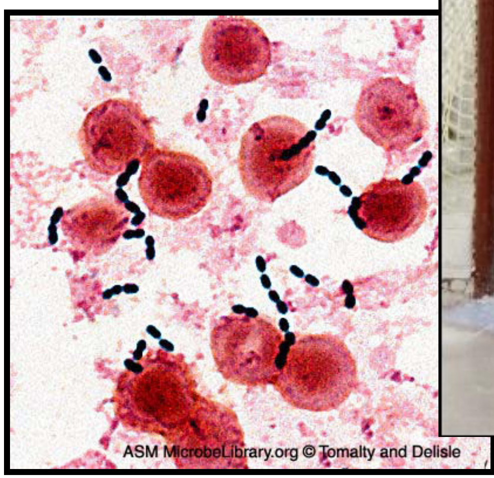


Haploid (N)

Diploid(s) (2N)

Polyploid (4N)

Ploidy varies between species

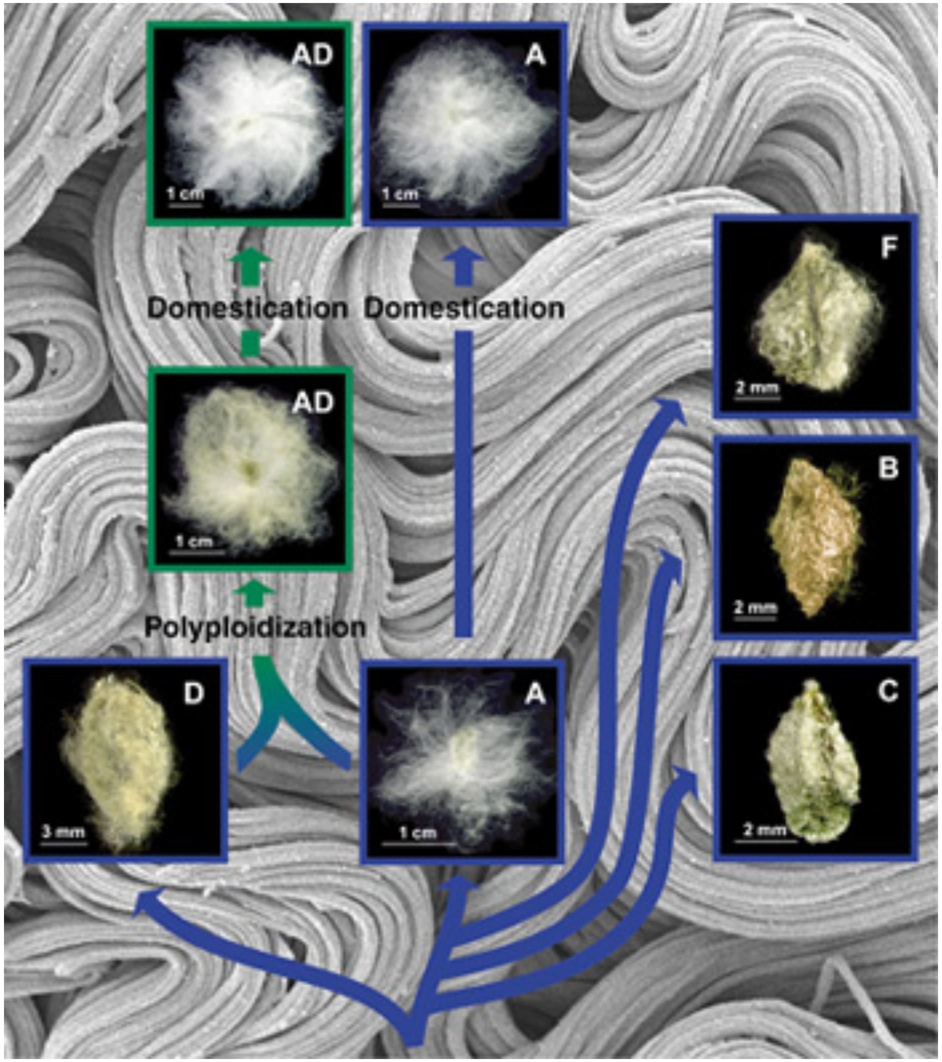


Haploid (N)

Diploid(s) (2N)

Polyploid (4N)

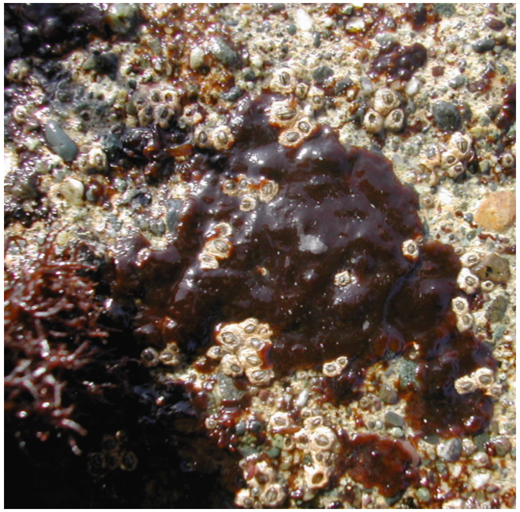
and across a phylogeny



Wendel lab

Ploidy can also vary within species

Haploid – Male honey bee



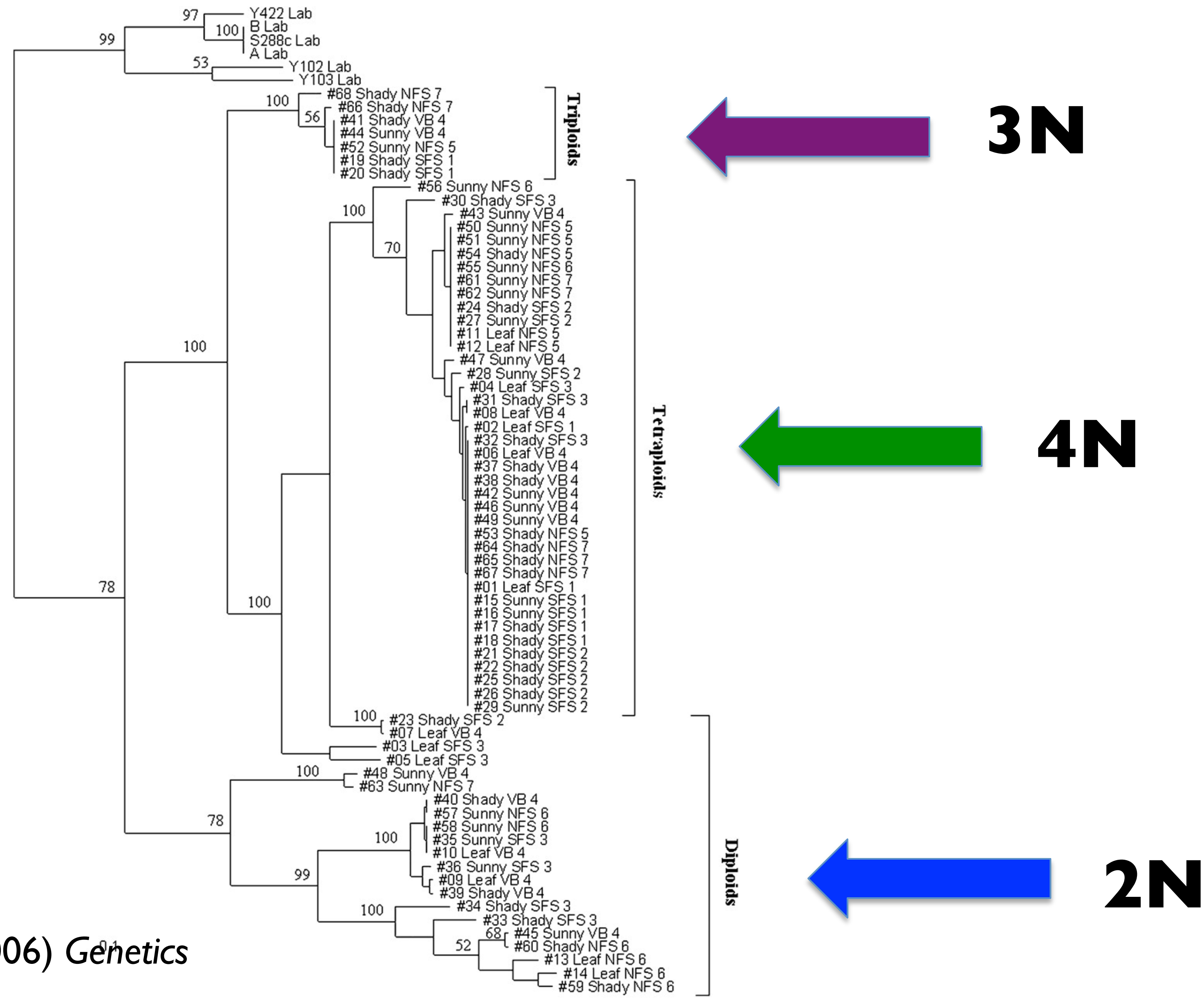
Haploid – *Mastocarpus papillatus* (gametophyte)

Haploid/Diploid – *Ulva lactuca*

Diploid– Female honey bee

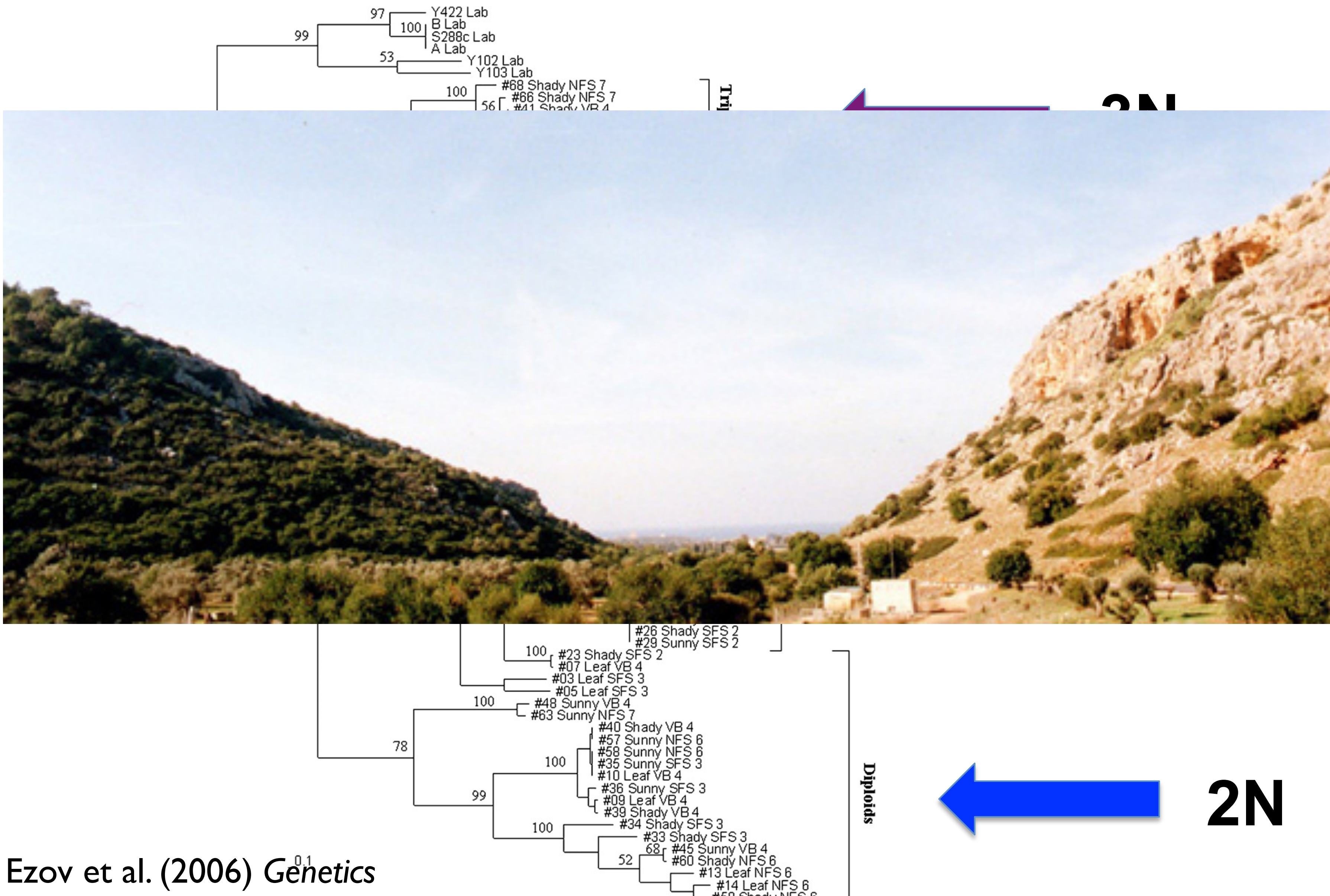
Diploid– *Mastocarpus papillatus* (sporophyte)

Yeast Ploidy



Ezov et al. (2006) *Genetics*

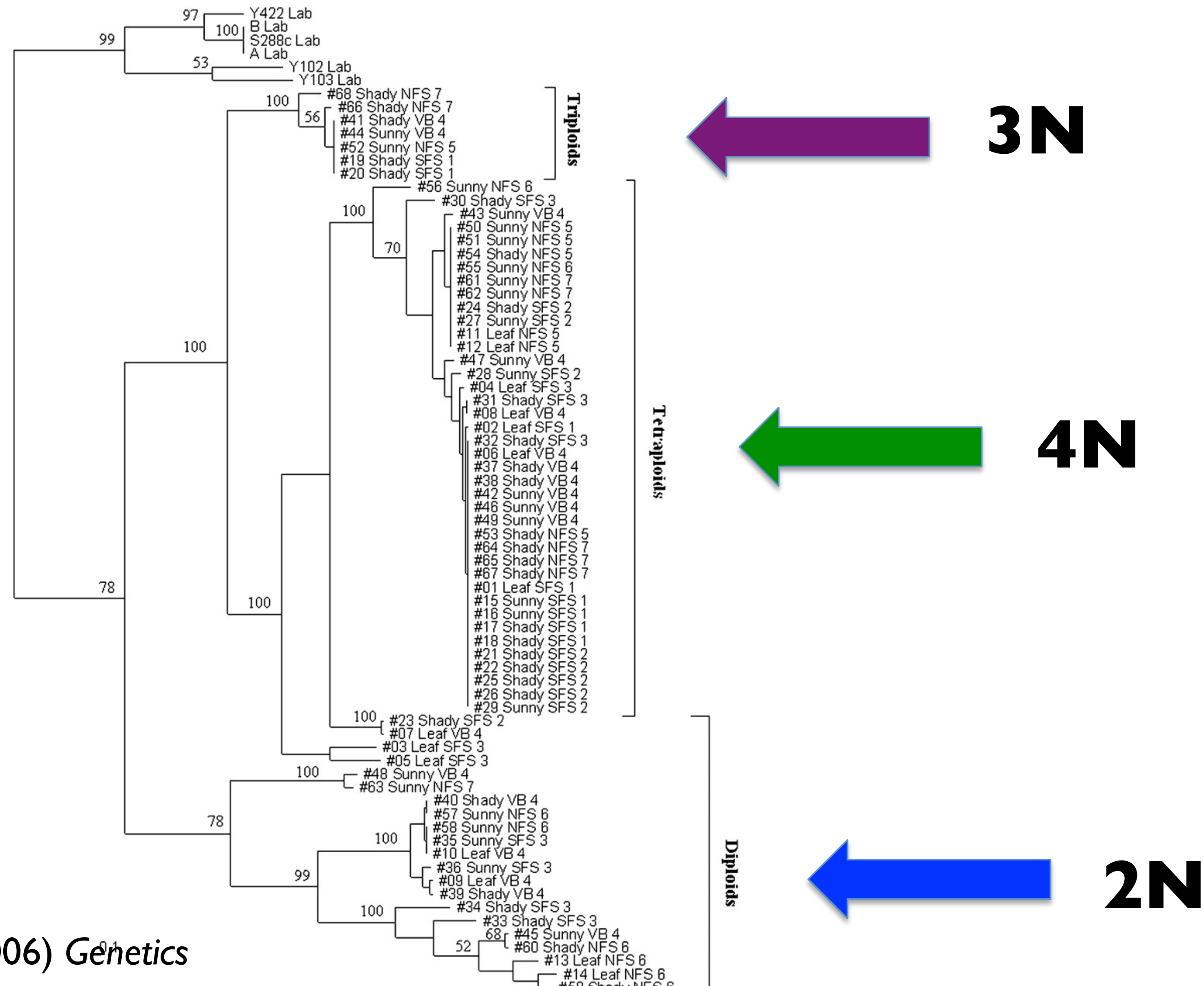
Yeast Ploidy in Nature!



2N

Ezov et al. (2006) *Genetics*

Yeast Ploidy

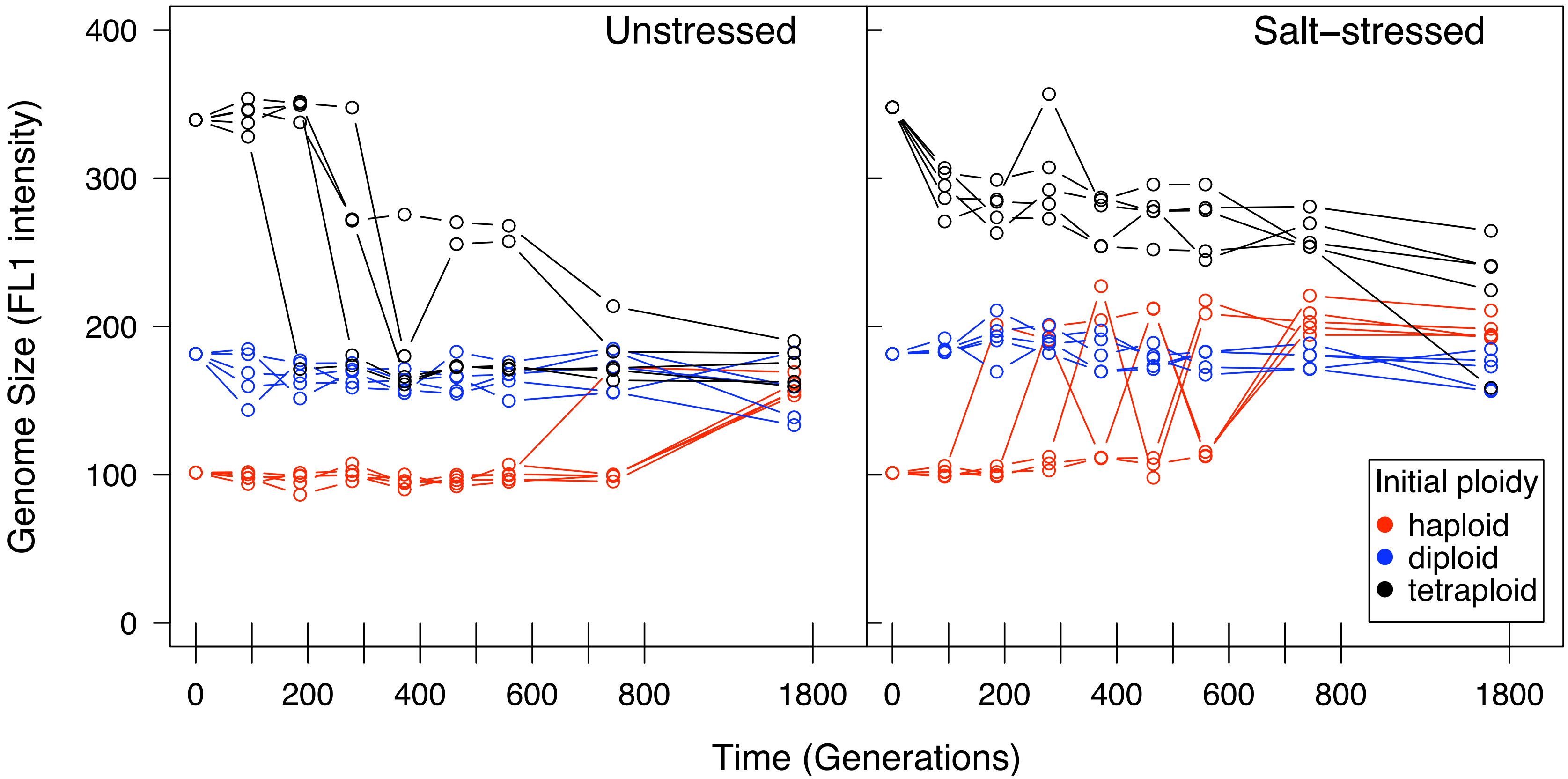


Ezov et al. (2006) *Genetics*

Ploidy can directly affect evolution

- Mutation rate
- Mutation effect size (*s* vs. *sh*)
- Rate of adaptation

Convergence toward diploidy in 1800 generations

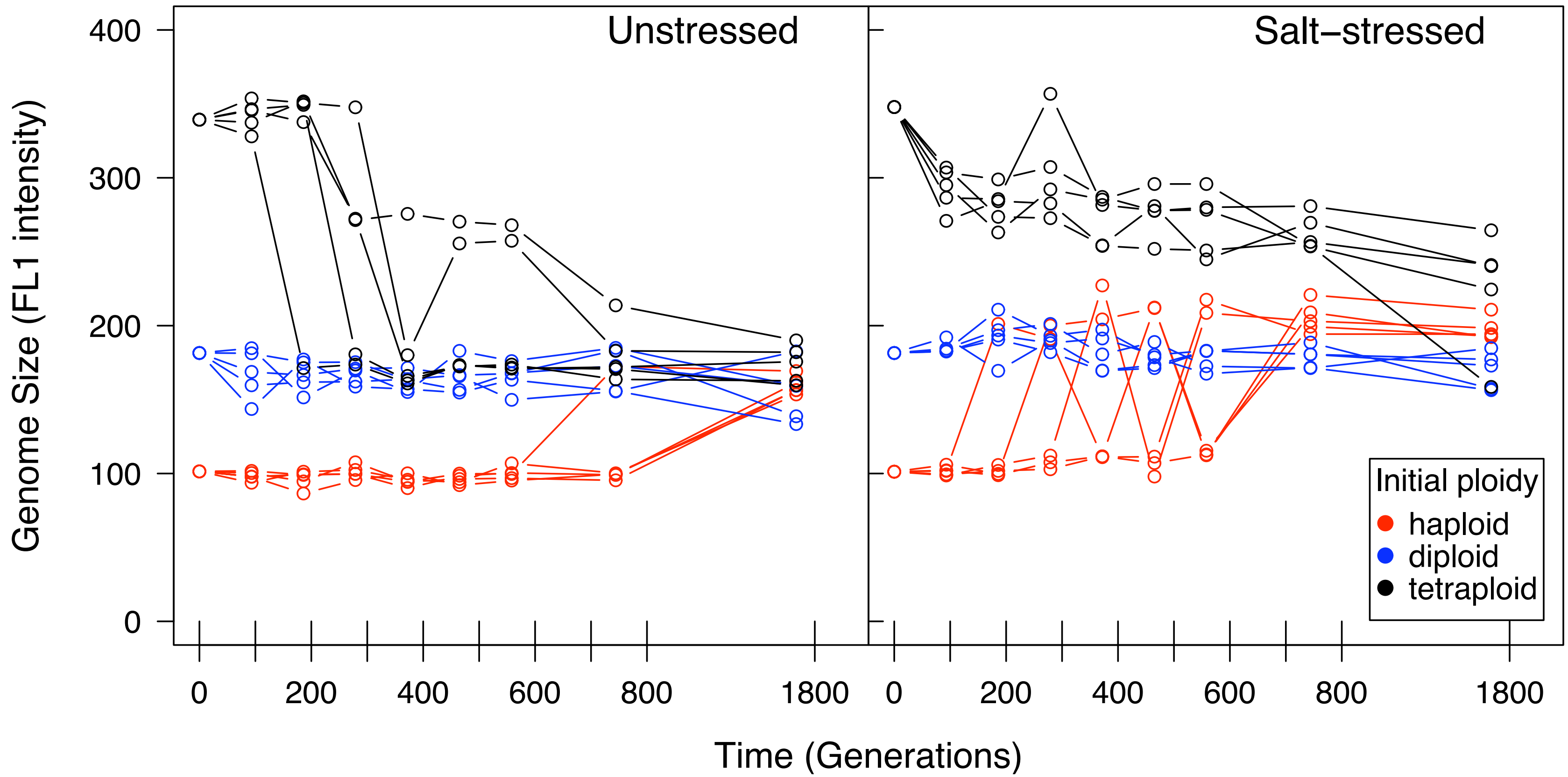


PLoS Genetics (2006)

Convergence toward diploidy in 1800 generations (not in nature)

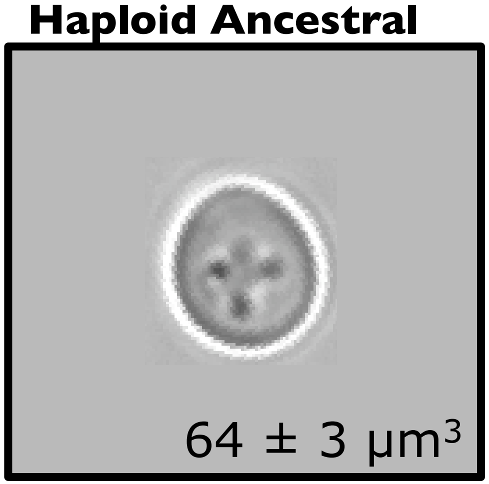
PLoS Genetics (2006)

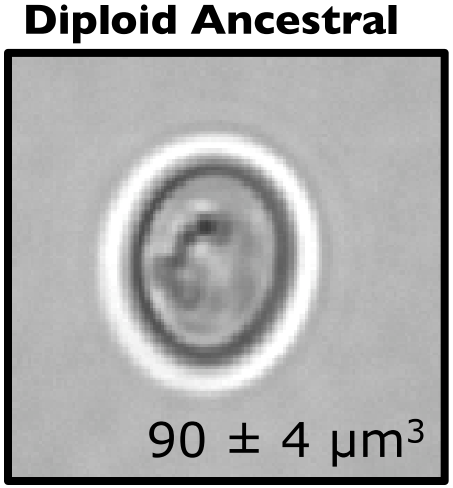
Convergence toward diploidy in 1800 generations



PLoS Genetics (2006)

What is different between haploid and diploid yeast?

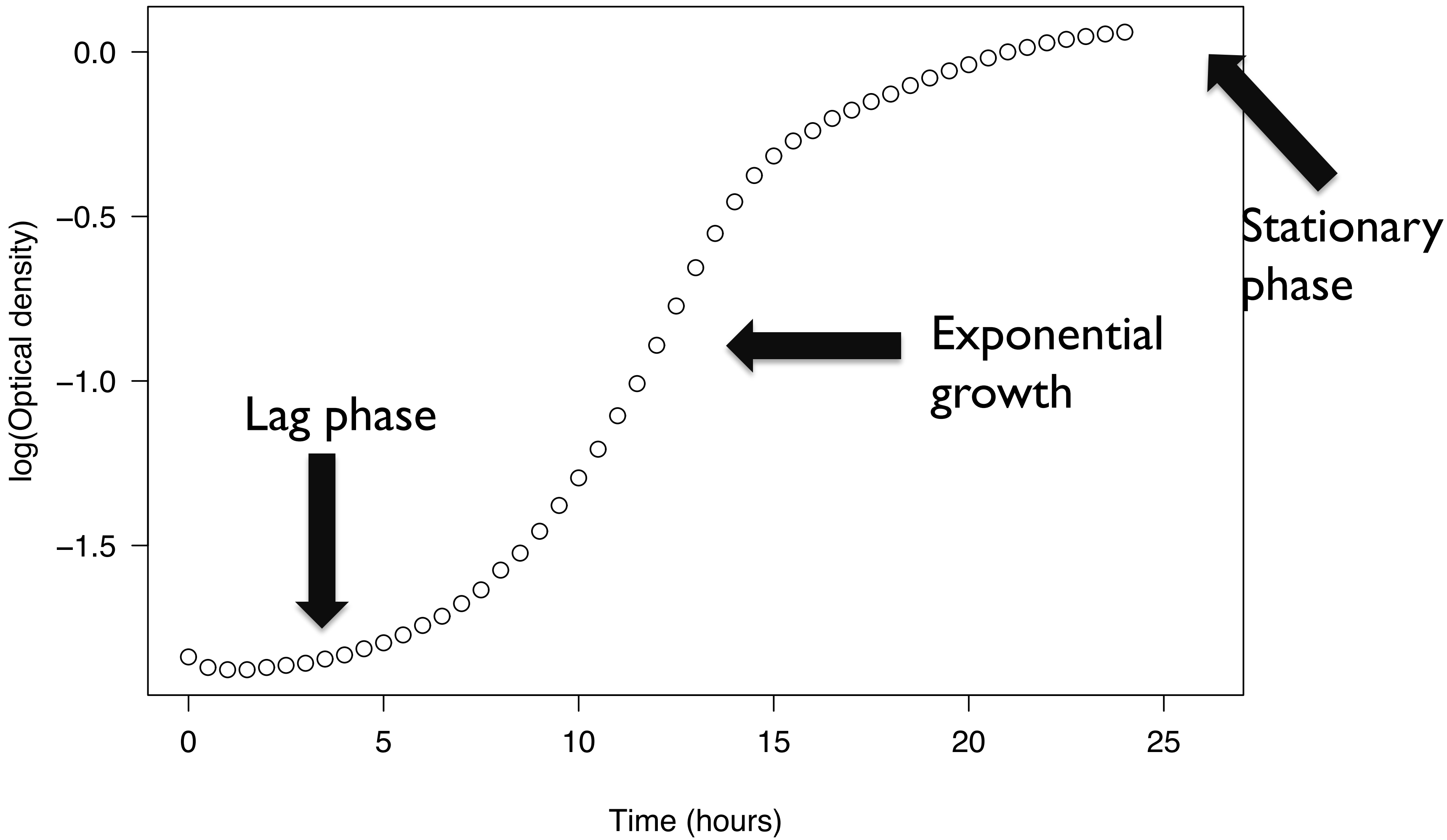




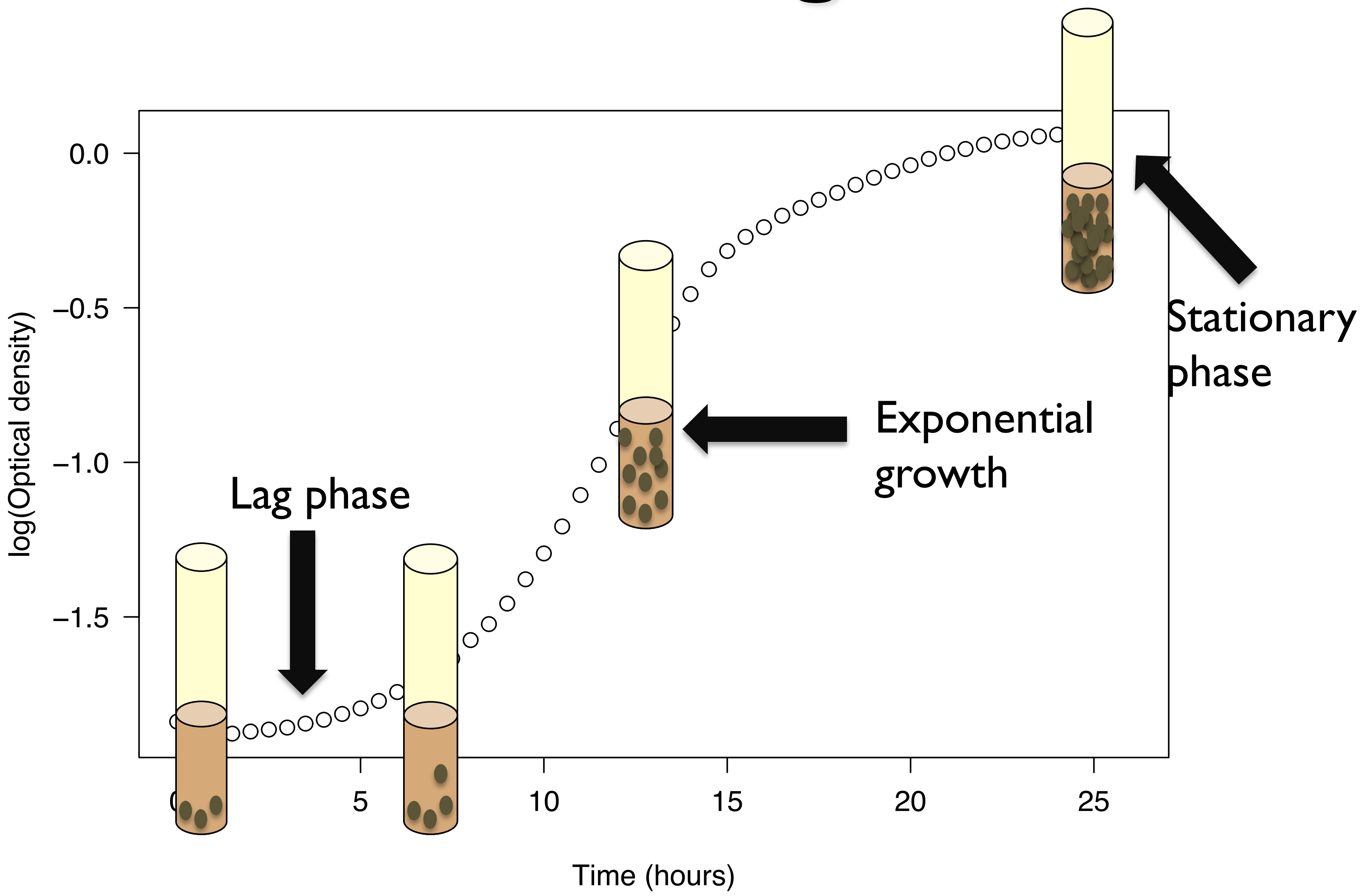
17 genes differ in expression *(Galitski, 1999)*

2.7% of the proteome changes more than 50% in abundance
(de Godoy, 2008)

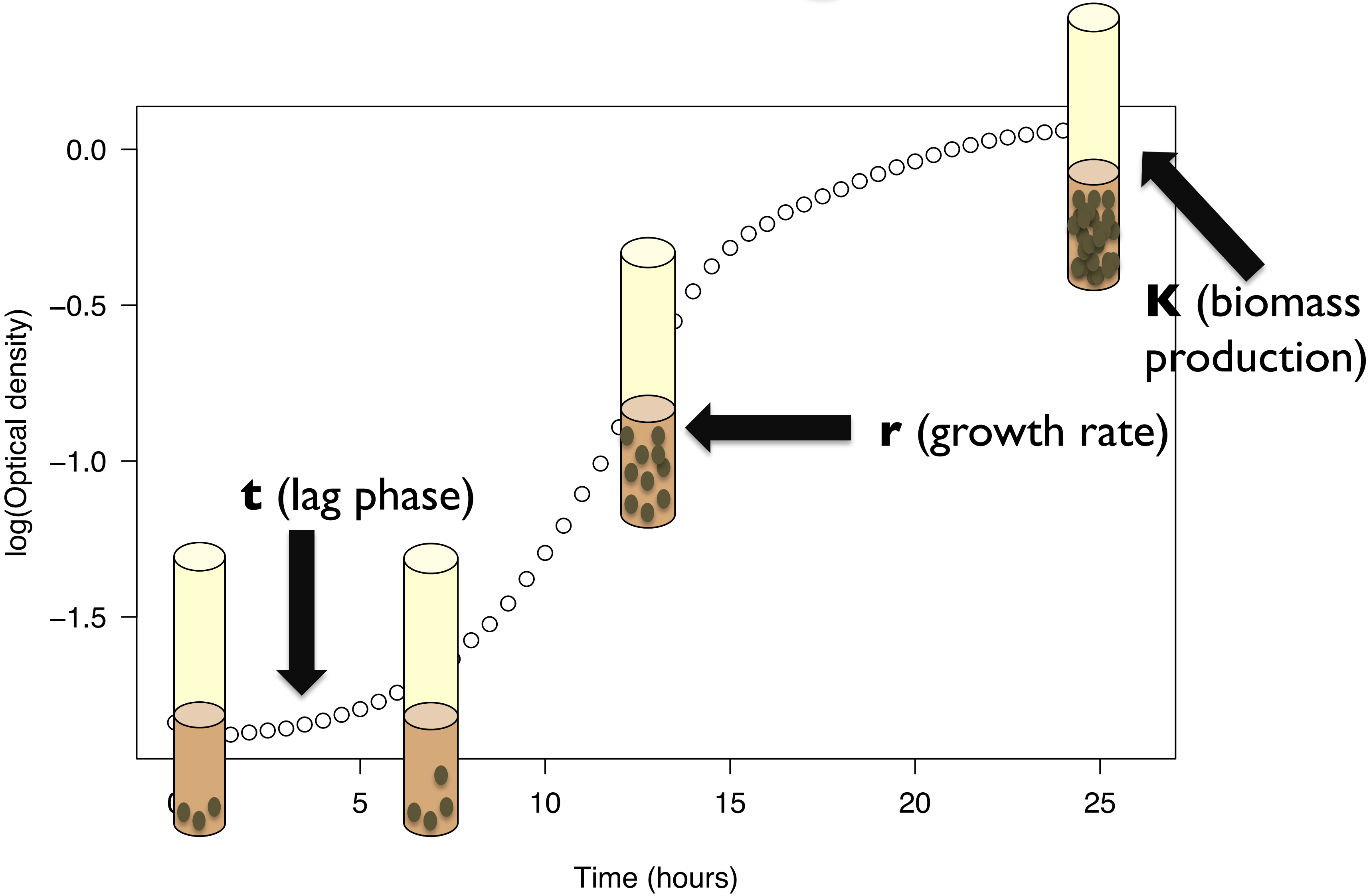
Batch culture growth



Batch culture growth



Batch culture growth

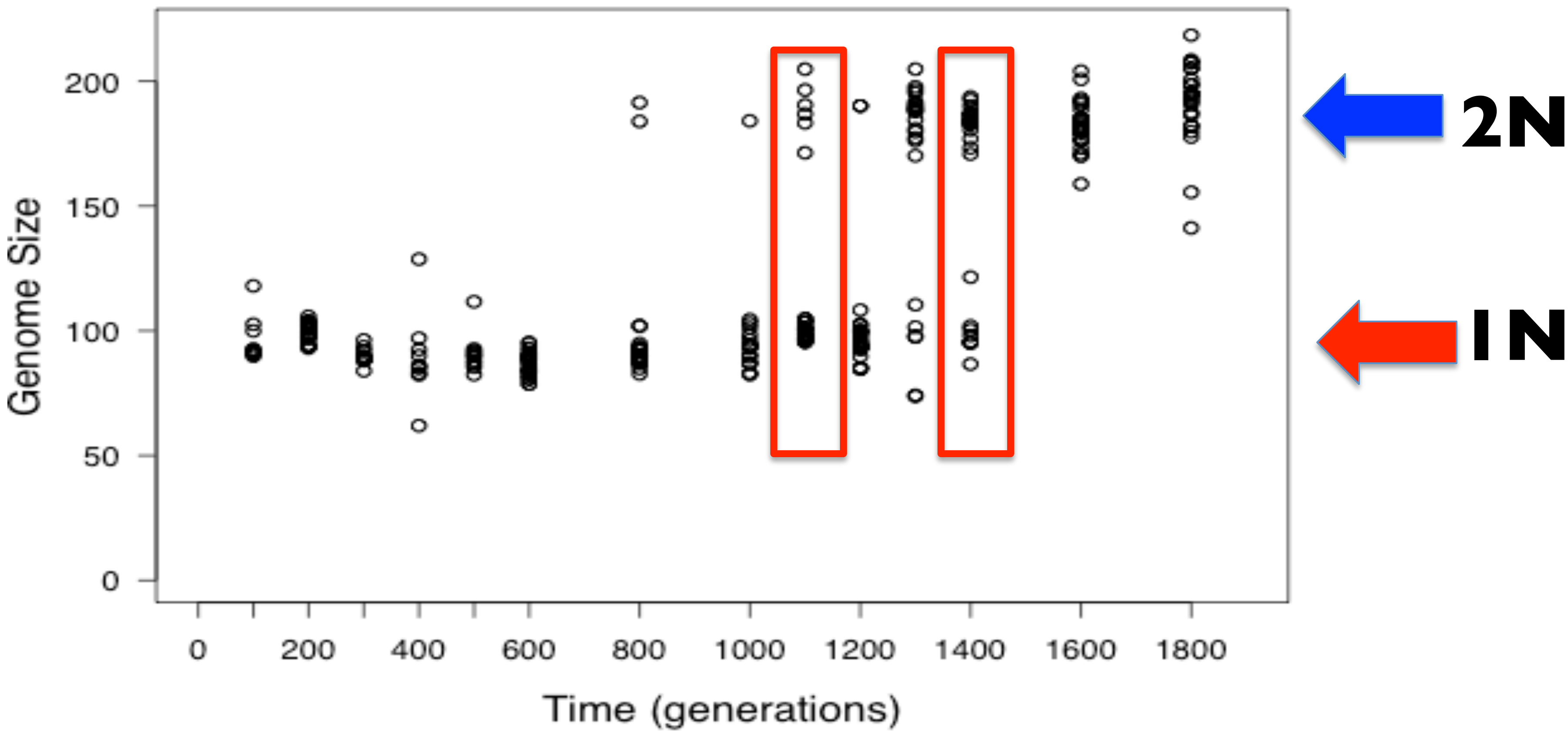


Qu'est-ce qui rend les diploïdes meilleurs?

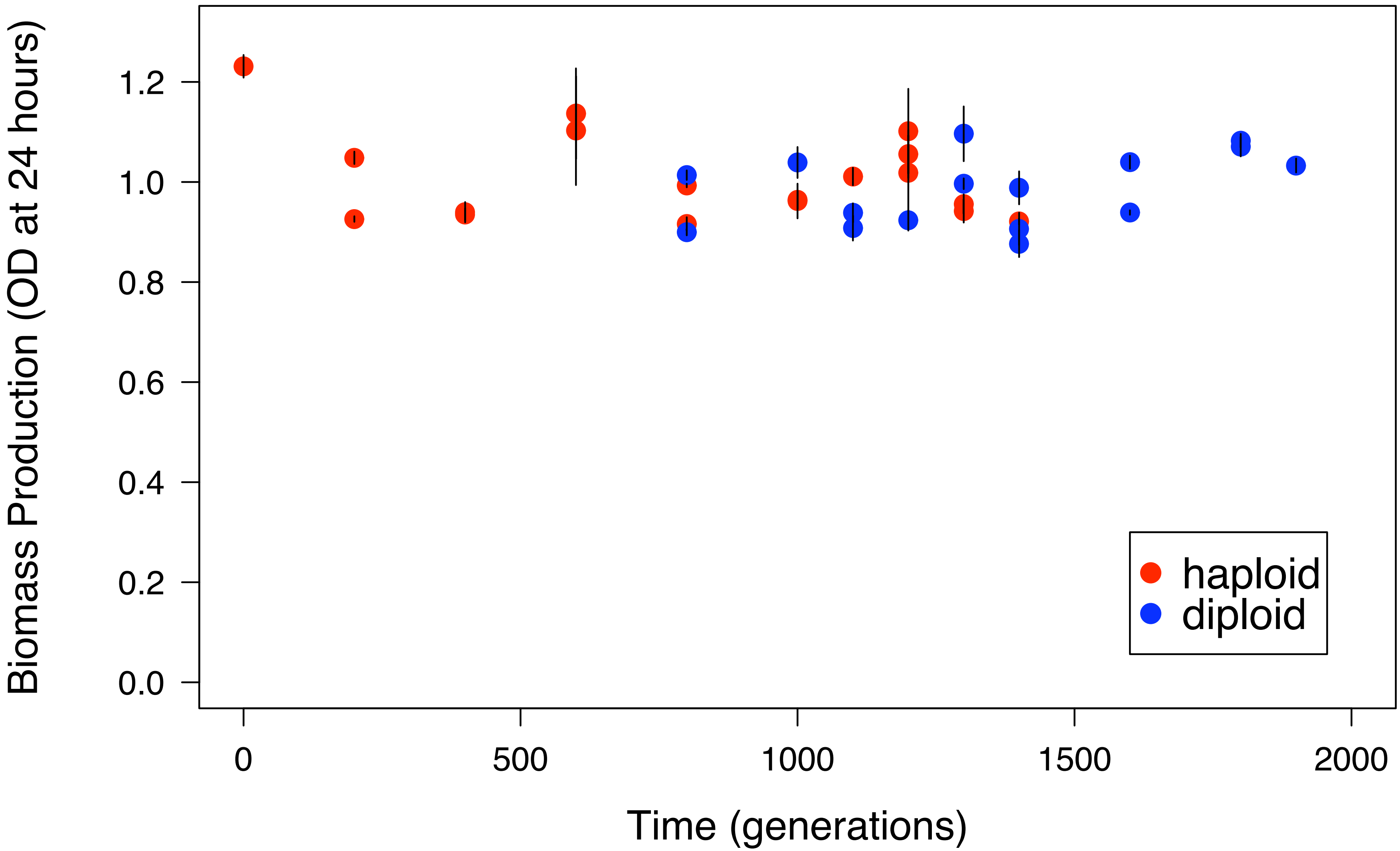
Hypothèse # 1 – Les diploïdes se multiplient mieux dans une culture discontinue (rendement de biomasse plus élevé, croissance exponentielle plus rapide, et/ou temps de latence plus courts).

Hypothesis # 1 – Diploids are better at growth during batch culture (higher biomass yield, faster exponential growth, and/or shorter lag phase).

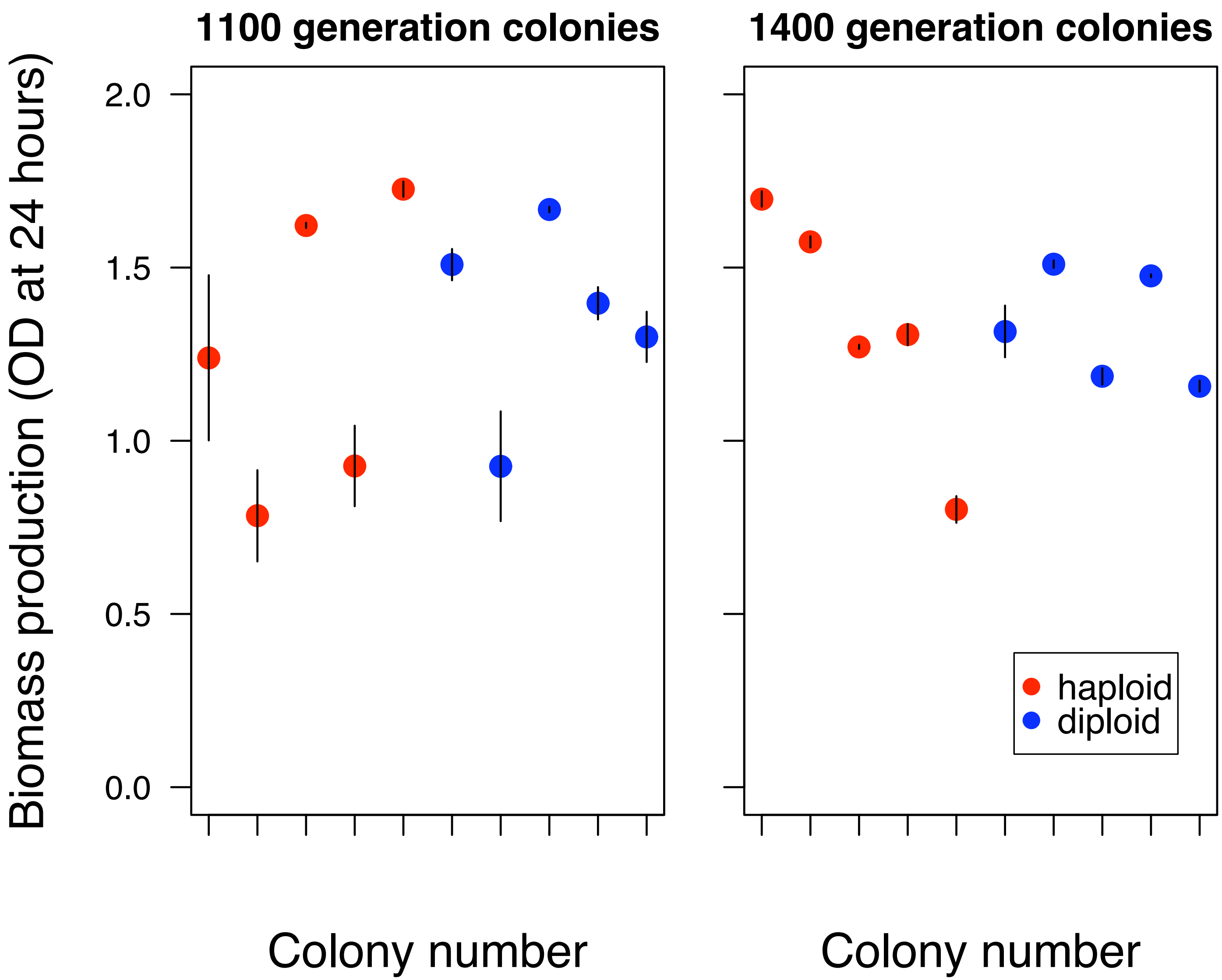
Directly compare haploids and diploids isolated throughout the fossil record



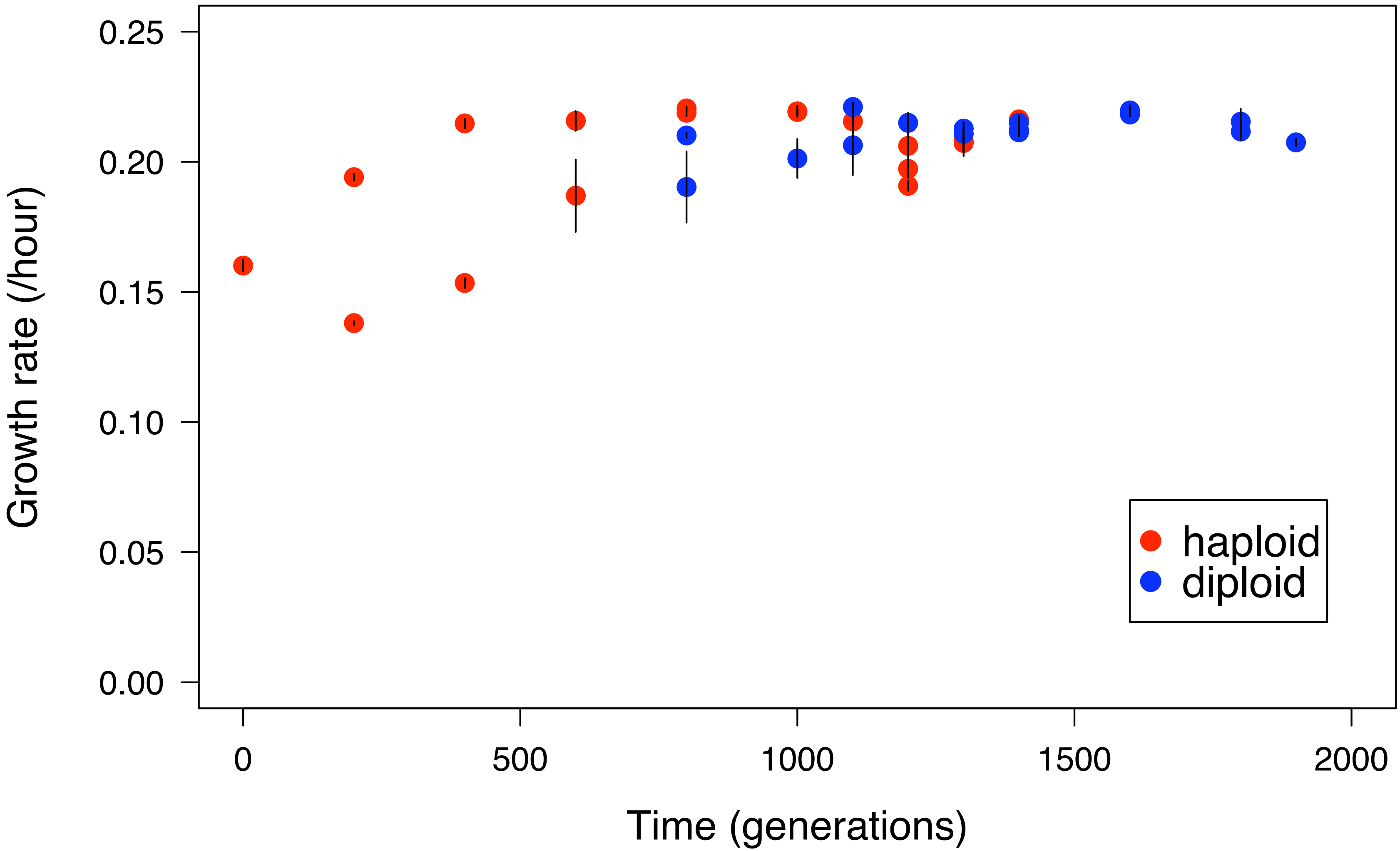
Biomass production through the fossil record



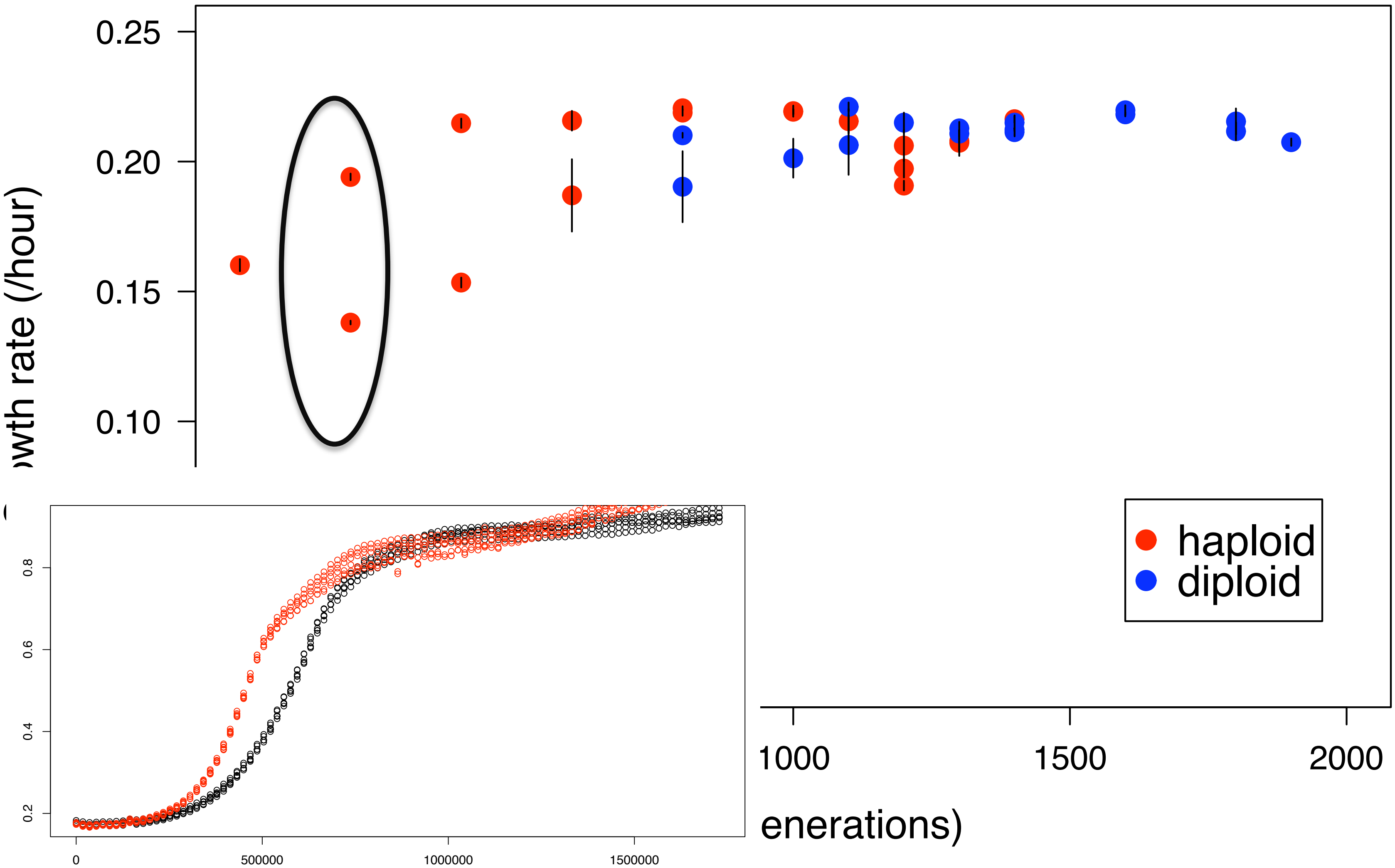
Variation in biomass production



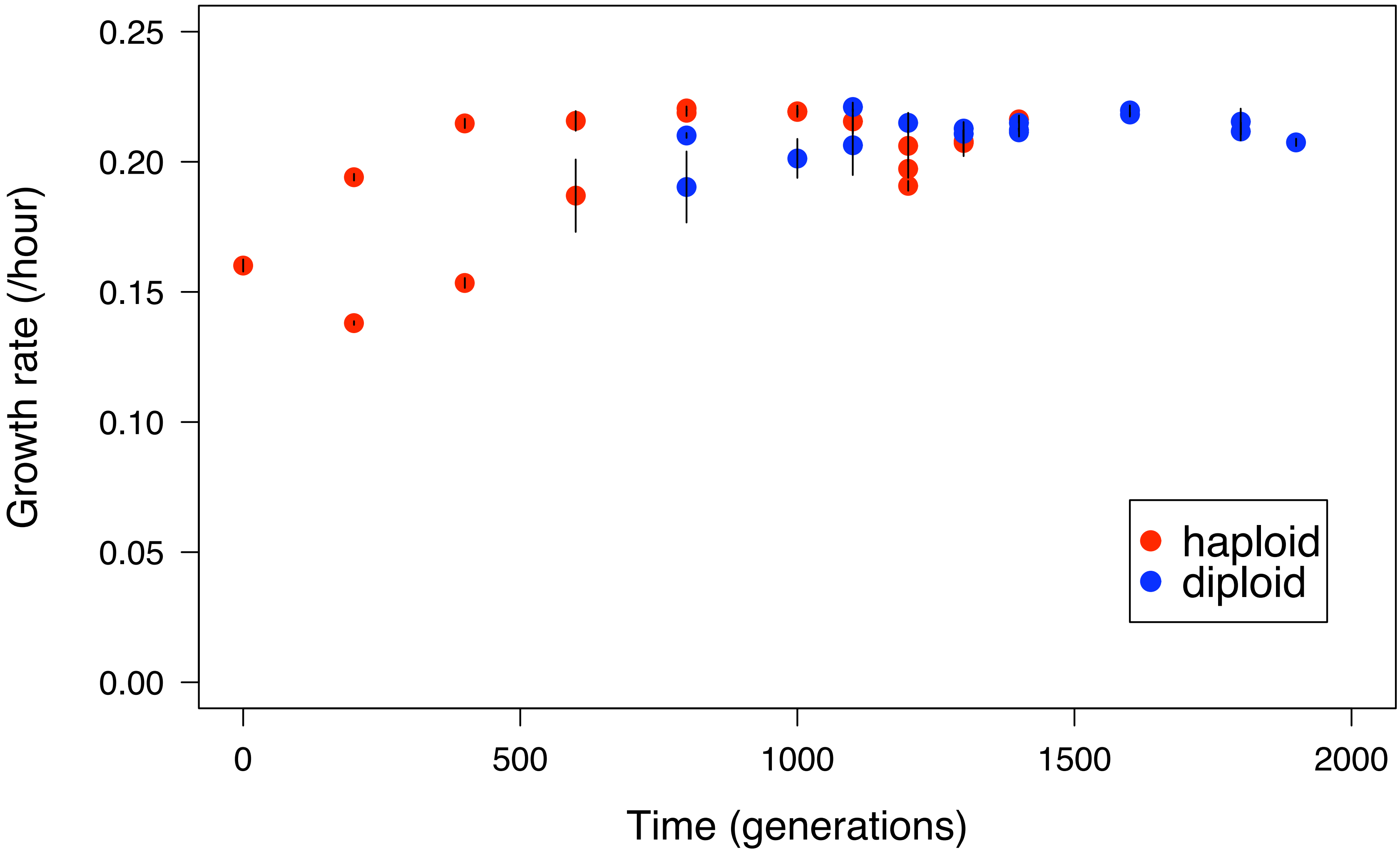
Growth rate through the fossil record



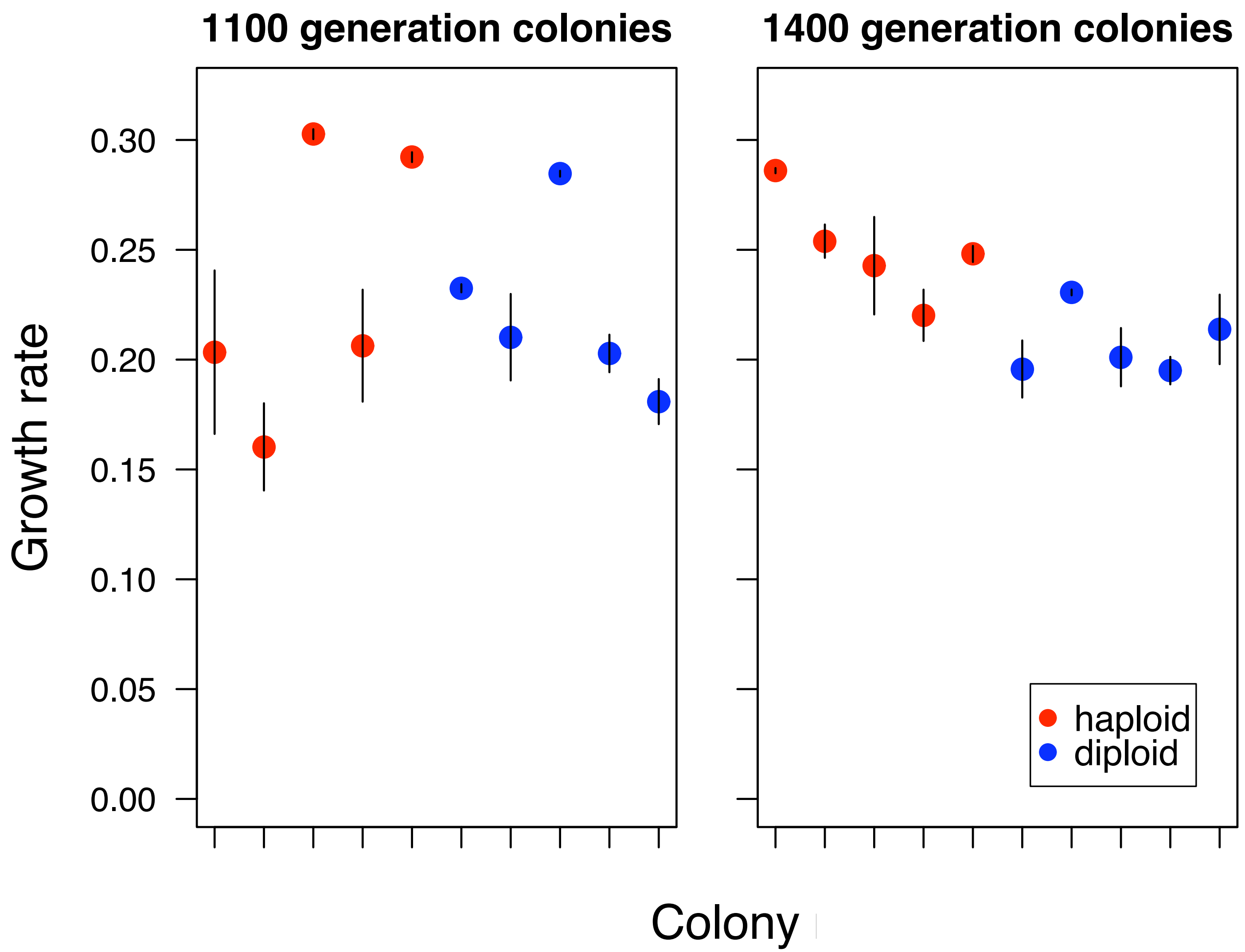
Growth rate through the fossil record



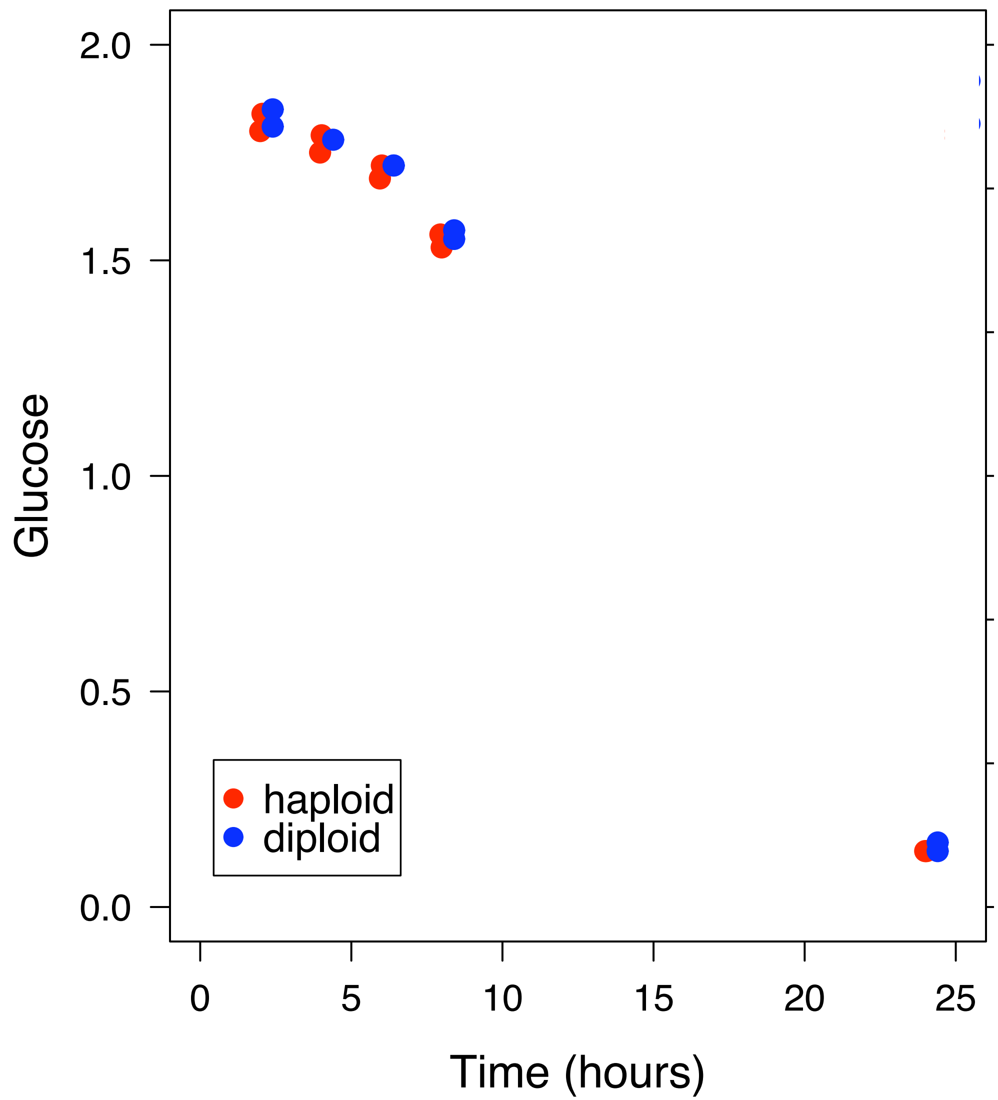
Growth rate through the fossil record



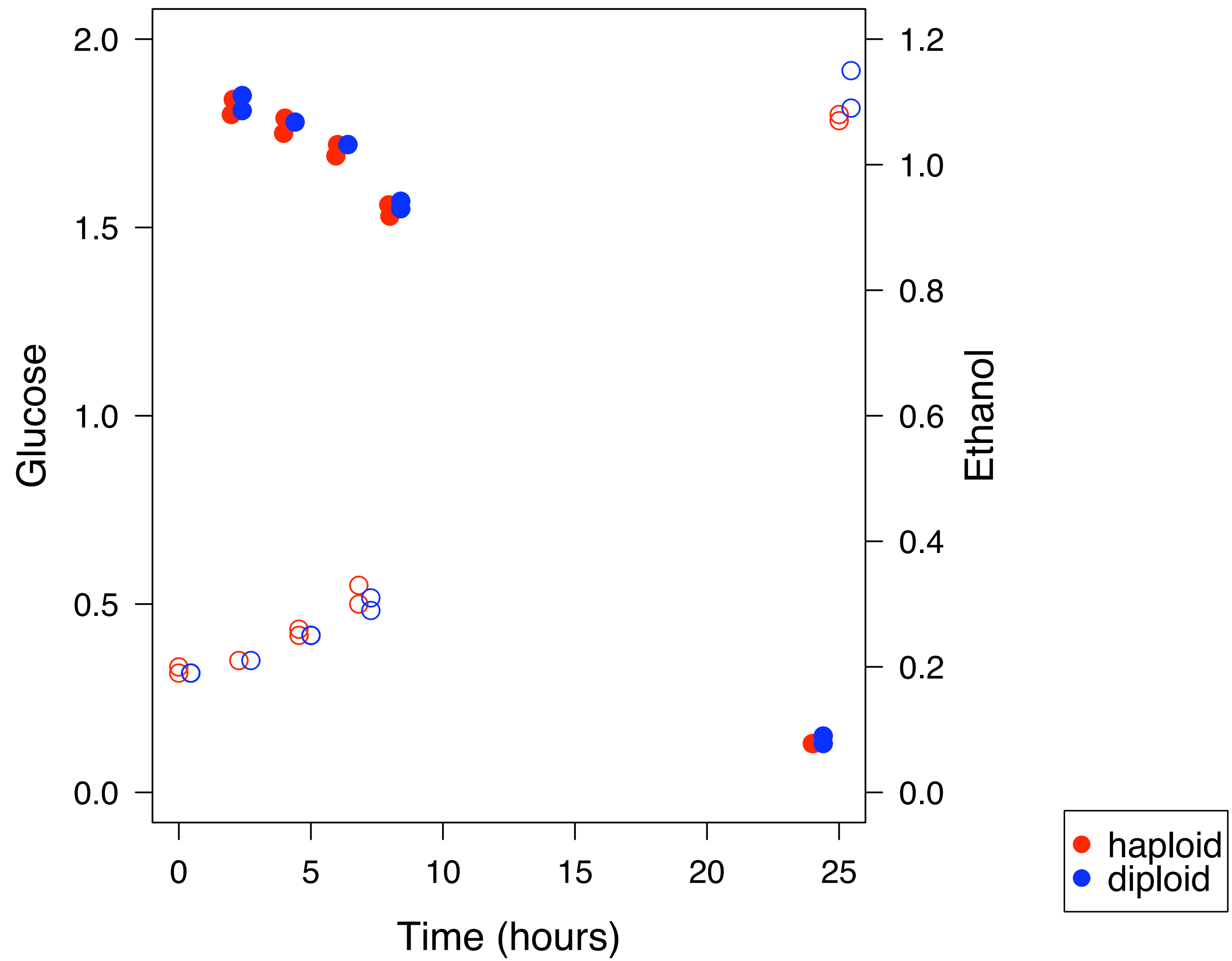
Variation in growth rate



Lag phase - glucose utilization



Lag phase - glucose utilization & ethanol production



Qu'est-ce qui rend les diploïdes meilleurs?

Conclusion # 1 – Les diploïdes ne produisent pas de biomasse plus élevée, ne montre pas de croissance exponentielle plus rapide, et n'ont pas de temps de latence plus courts.

Conclusion # 1– Diploids do not produce biomass more efficiently, grow faster, or have a shorter lag phase than haploids.

Qu'est-ce qui rend les diploïdes meilleurs?

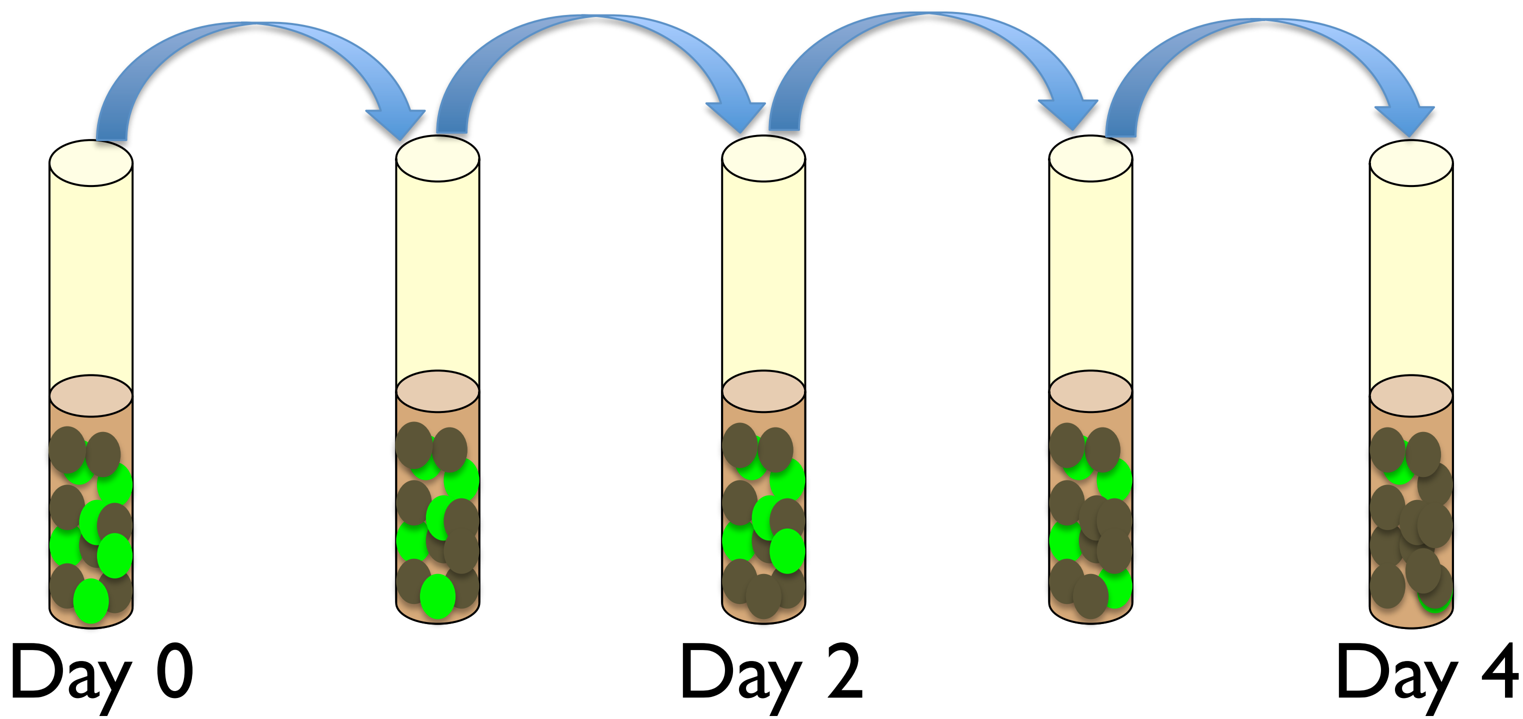
Conclusion # 1 – Les diploïdes ne produisent pas de biomasse plus élevée, ne montre pas de croissance exponentielle plus rapide, et n'ont pas de temps de latence plus courts.

Hypothèse # 2 – Les diploïdes sont plus compétitifs que les haploïdes.

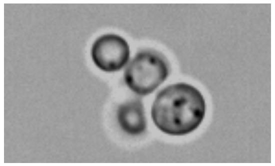
Conclusion # 1– Diploids do not produce biomass more efficiently, grow faster, or have a shorter lag phase than haploids.

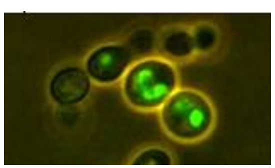
Hypothesis # 2 – Diploids are more competitively fit than haploids.

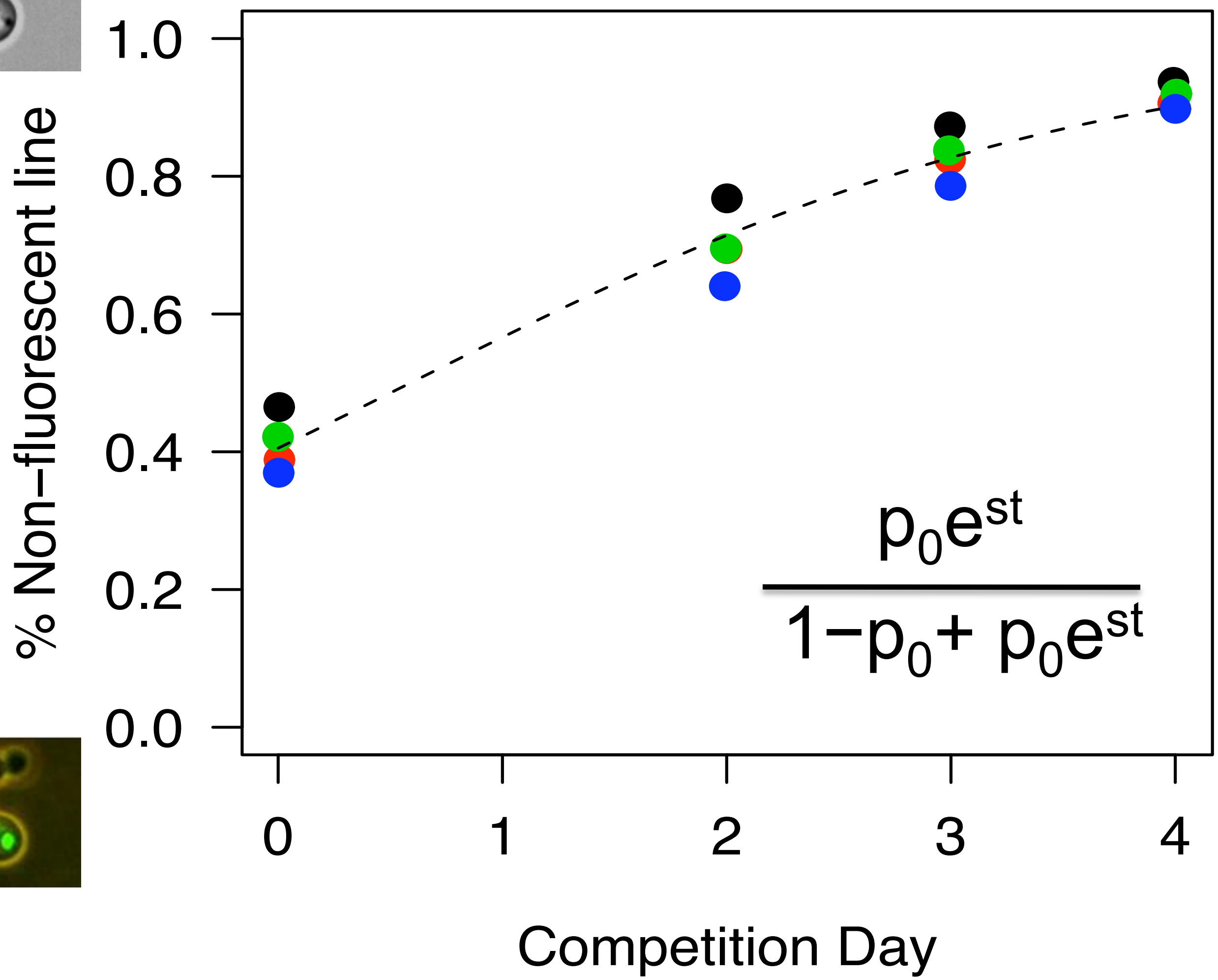
Competitive fitness



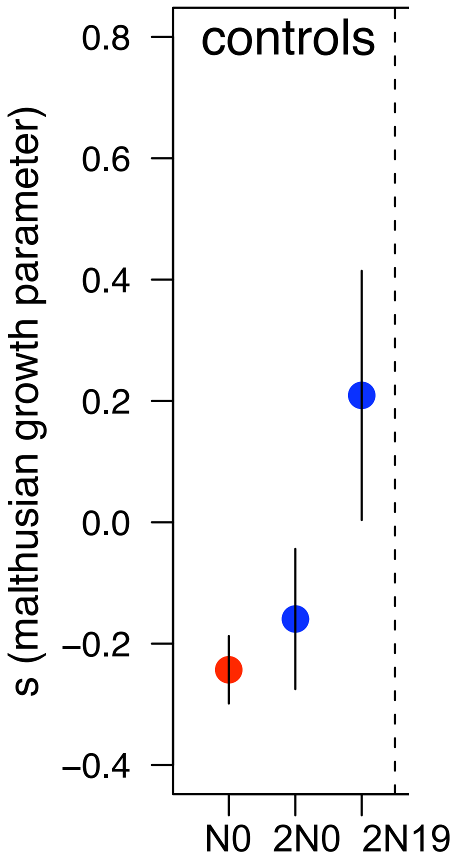
Competitive fitness (s)



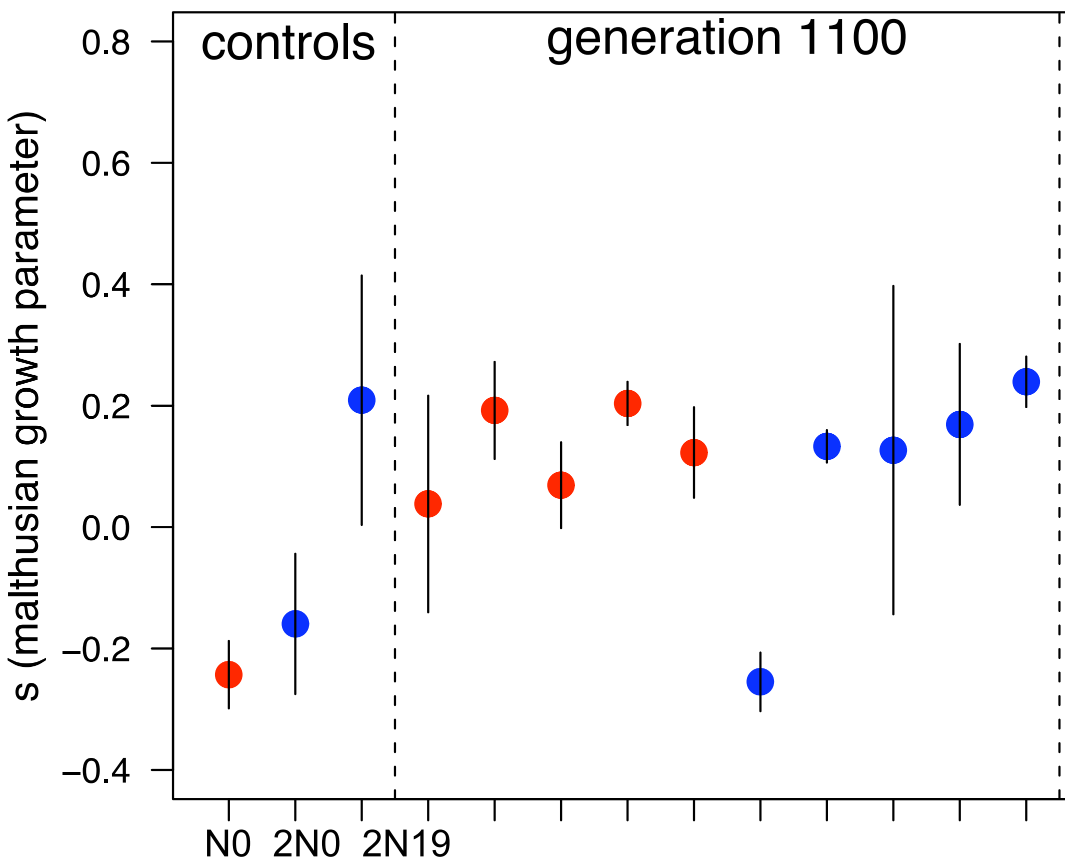




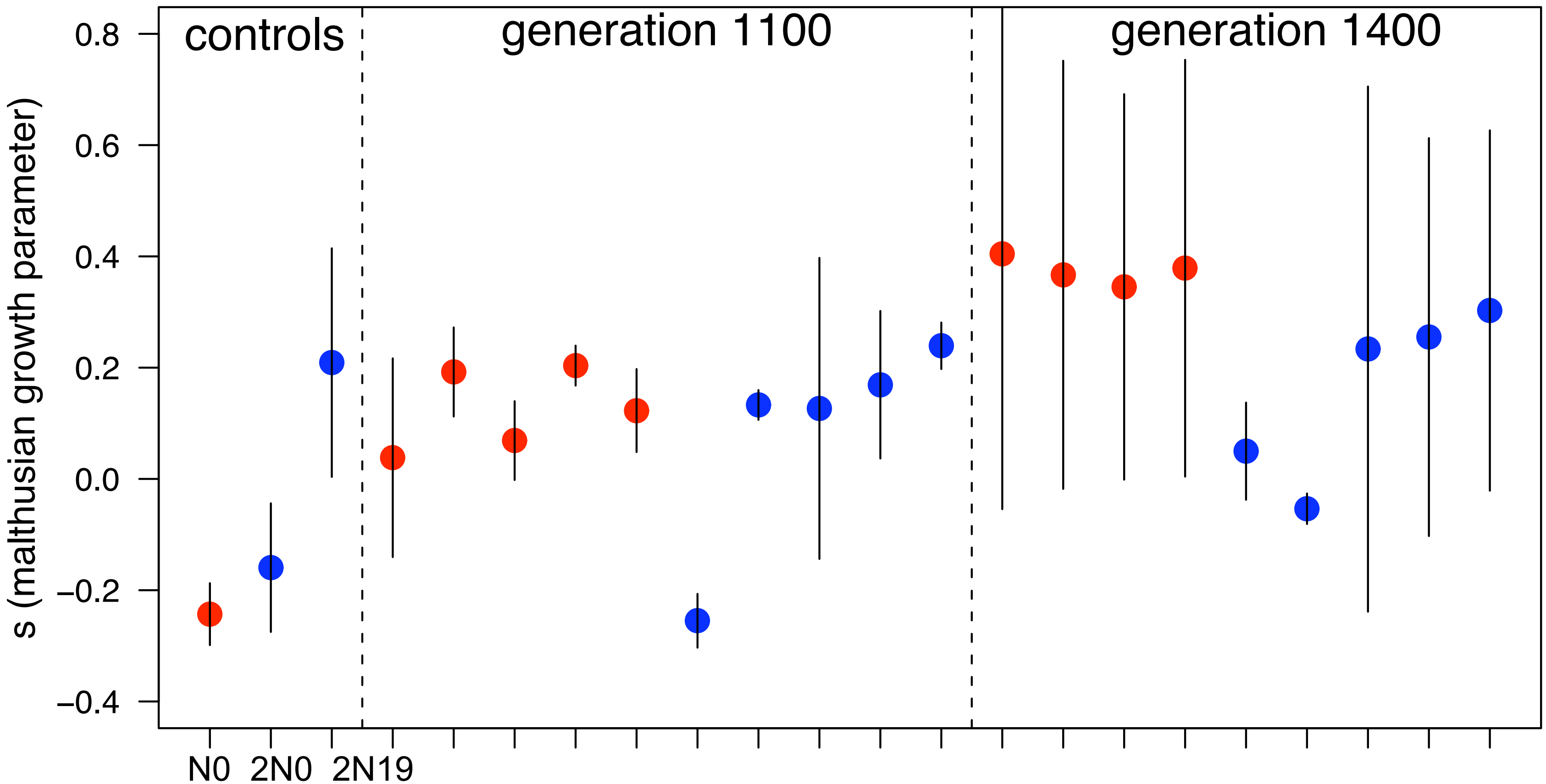
Competitive fitness (to a common competitor)



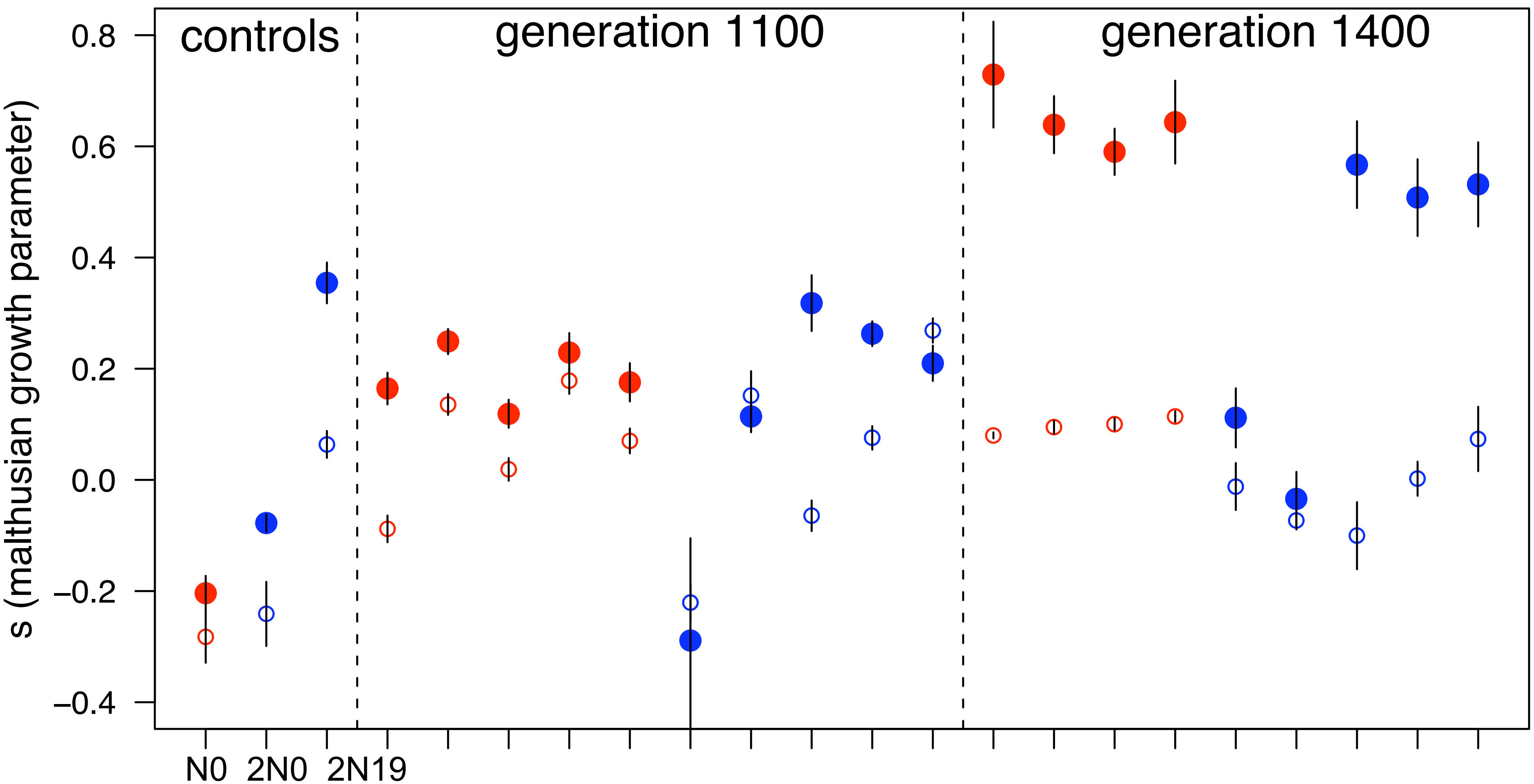
Competitive fitness (to a common competitor)



Competitive fitness (to a common competitor)



Competitive fitness (to a common competitor)



Qu'est-ce qui rend les diploïdes meilleurs?

Conclusion # 2 – Les diploïdes ne sont pas plus compétitifs que les haploïdes.

Conclusion # 2 – Diploids are not more competitively fit against a common competitor.

Qu’est-ce qui rend les diploïdes meilleurs?

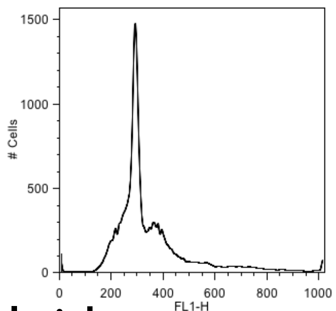
Conclusion # 2 – Les diploïdes ne sont pas plus compétitifs que les haploïdes.

Hypothèse # 3 – J’ai besoin d’une nouvelle hypothèse.

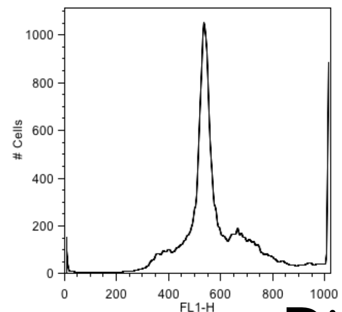
Conclusion # 2 – Diploids are not more competitively fit against a common competitor.

Hypothesis # 3 – I need a new hypothesis.

Directly compete haploids and diploids

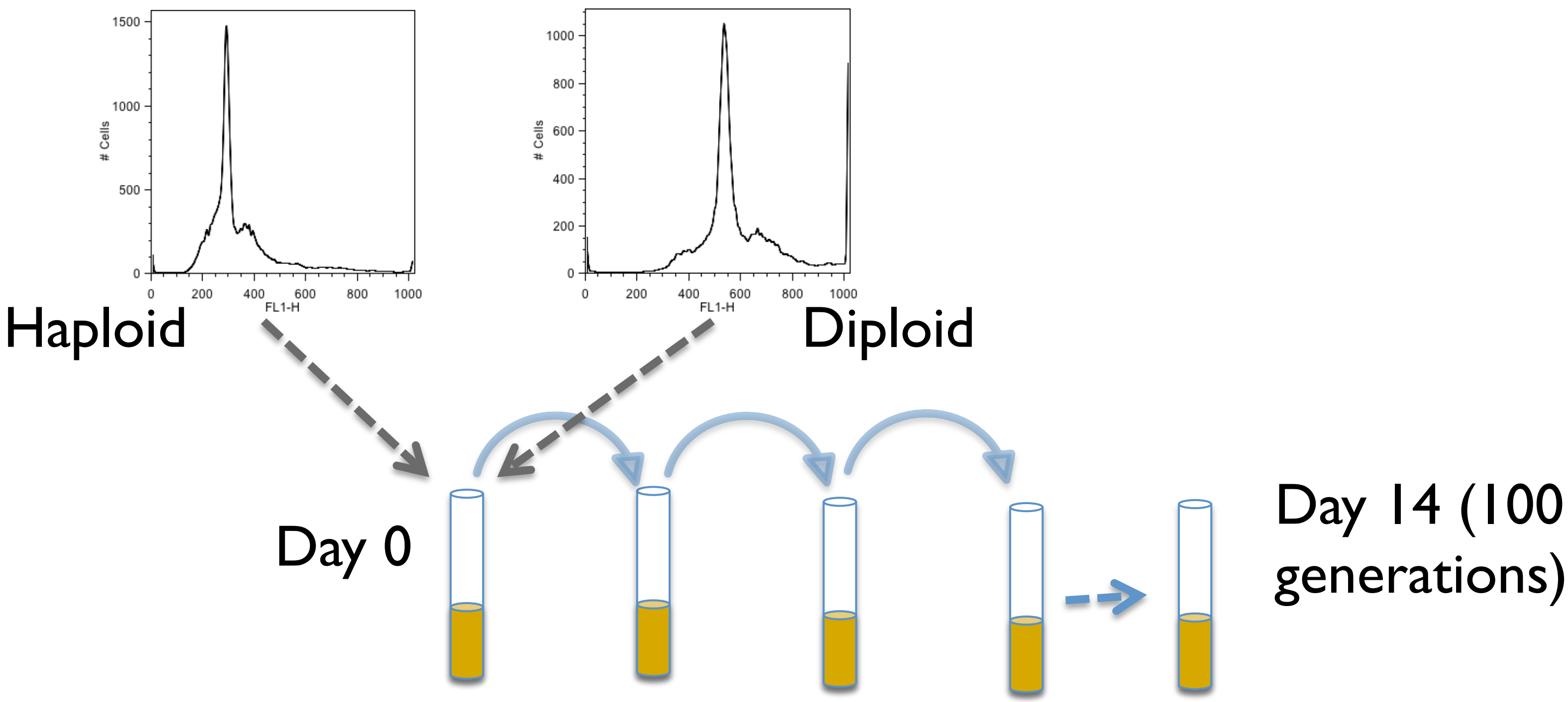


Haploid

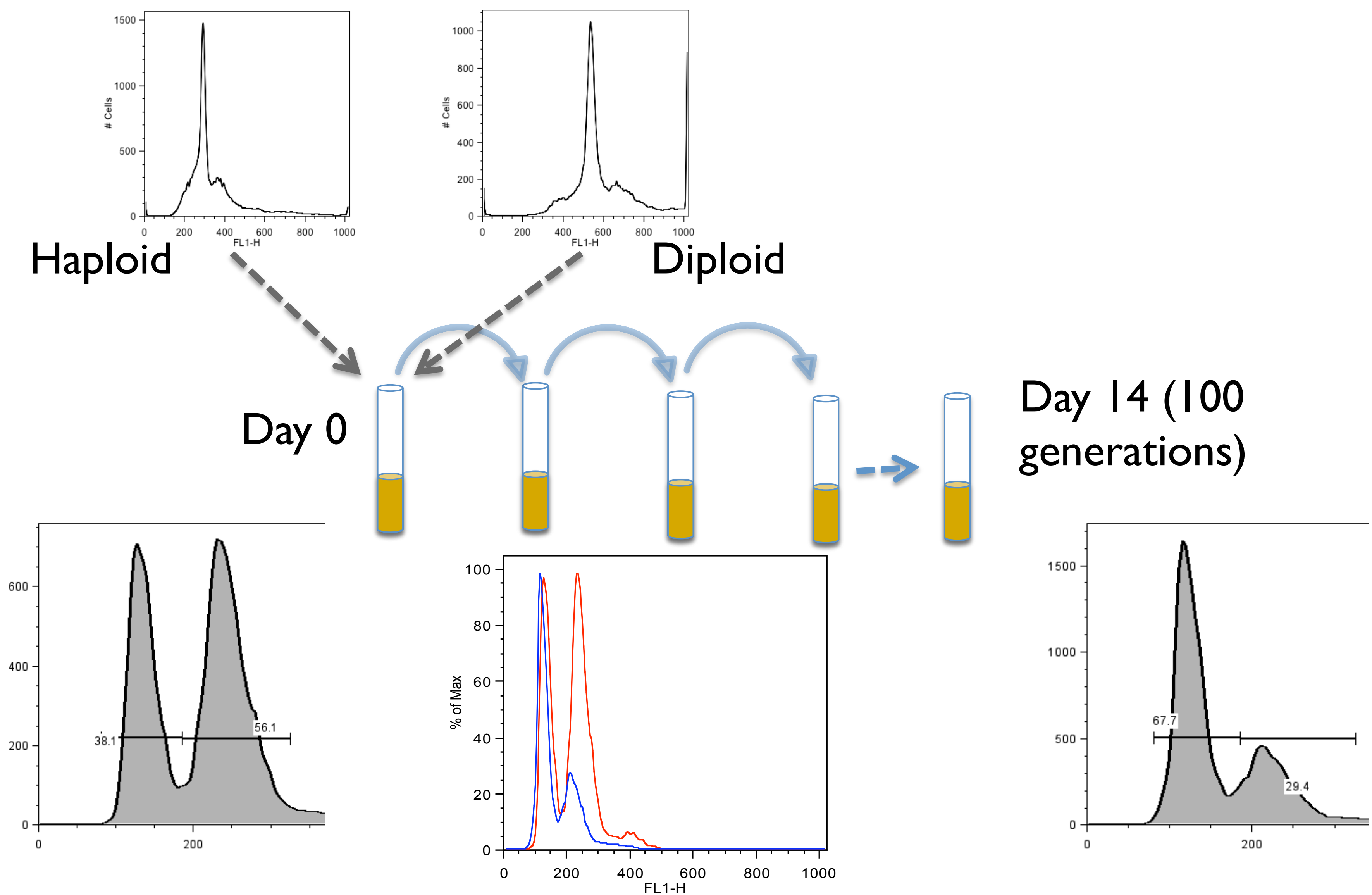


Diploid

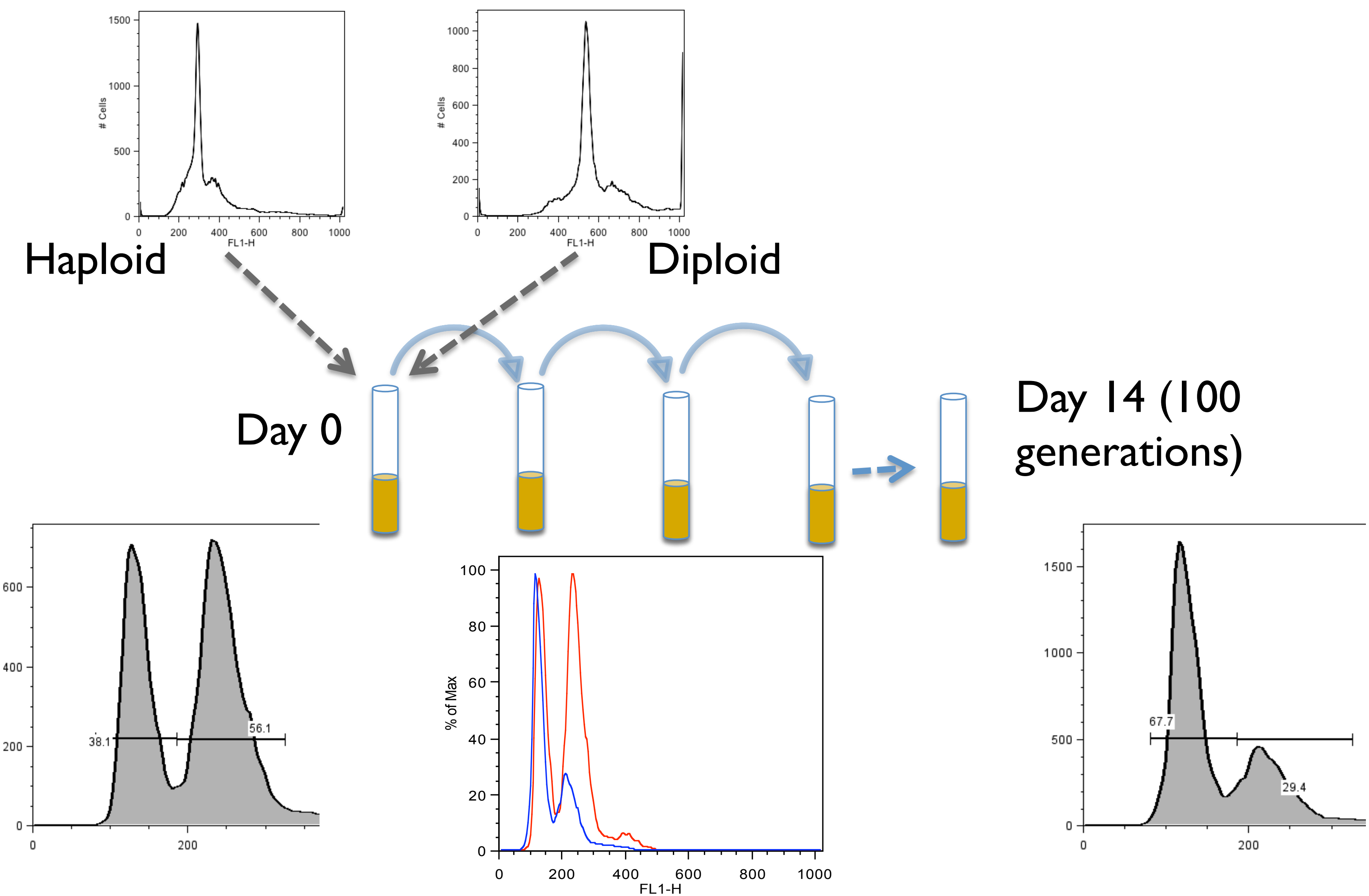
Directly compete haploids and diploids



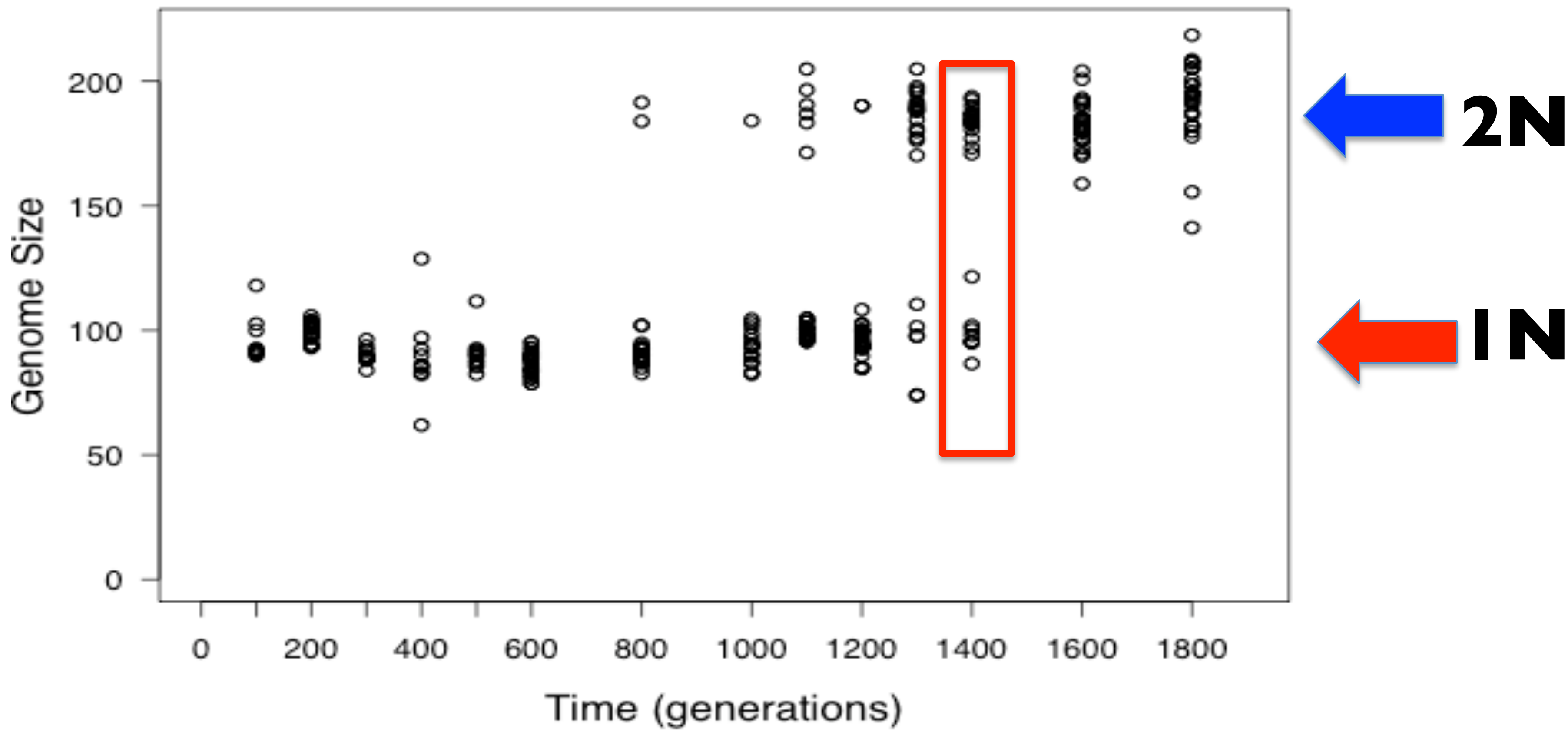
Directly compete haploids and diploids



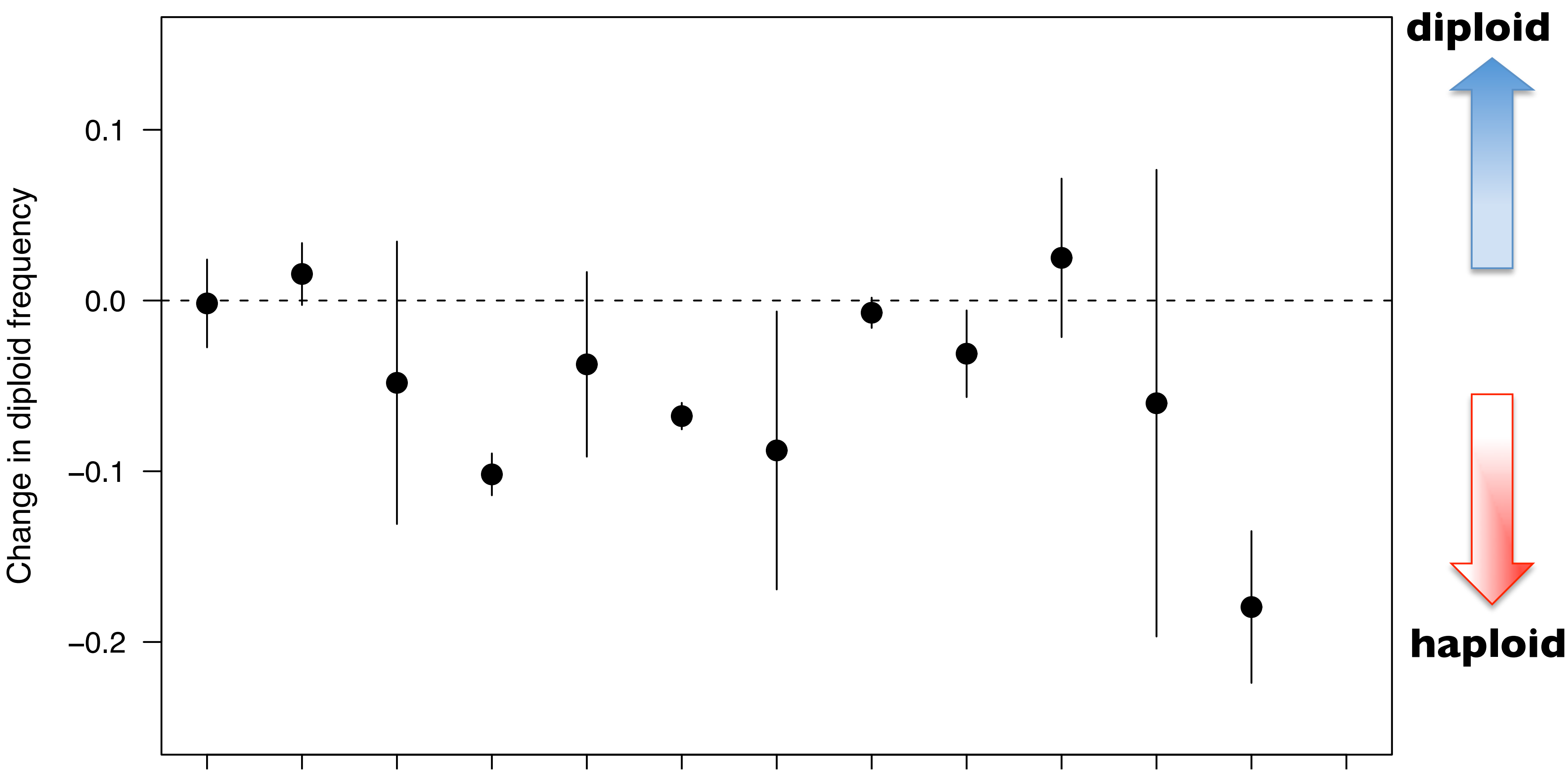
Directly compete haploids and diploids



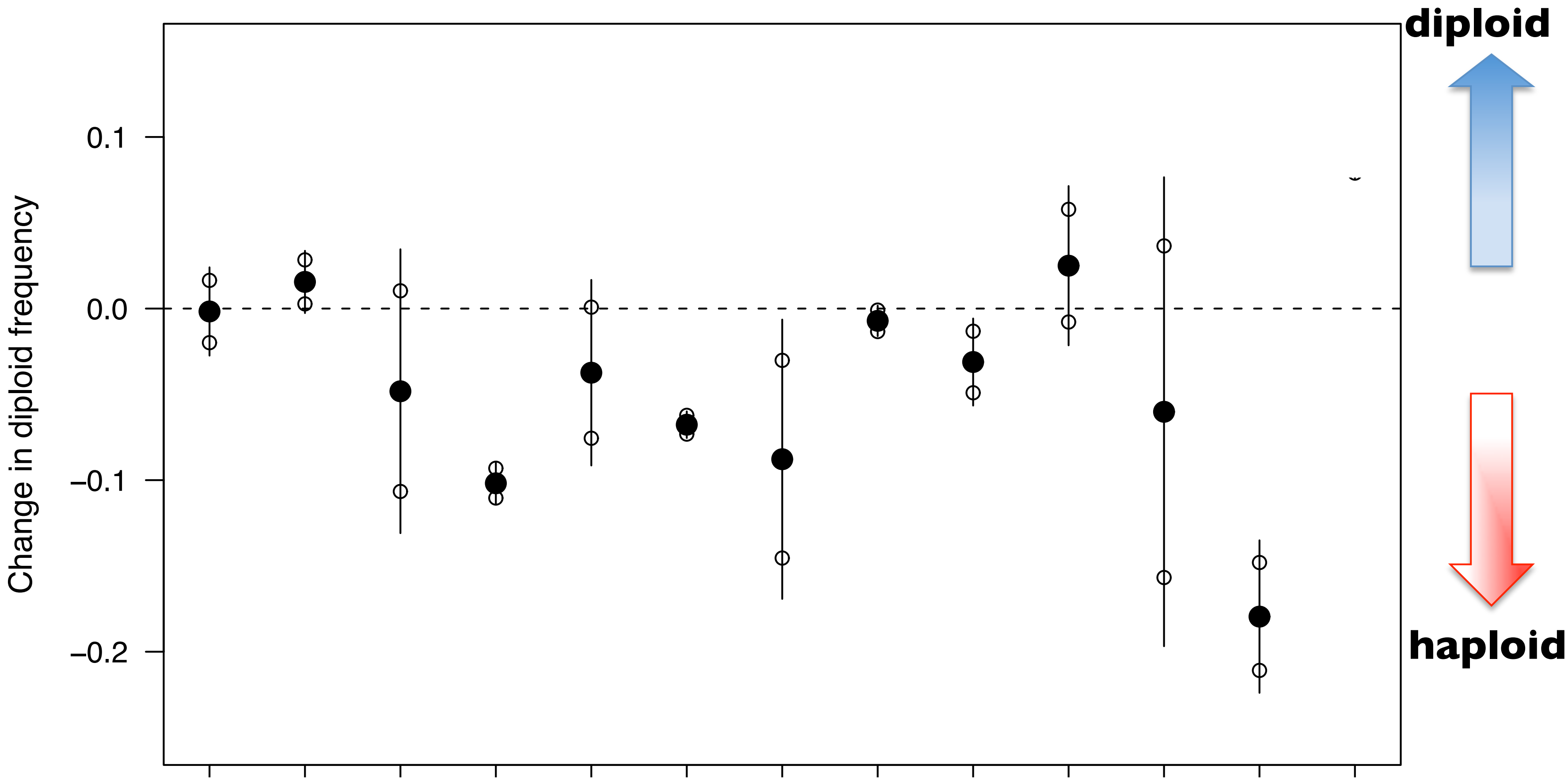
Directly compare (this time for sure!) haploids and diploids



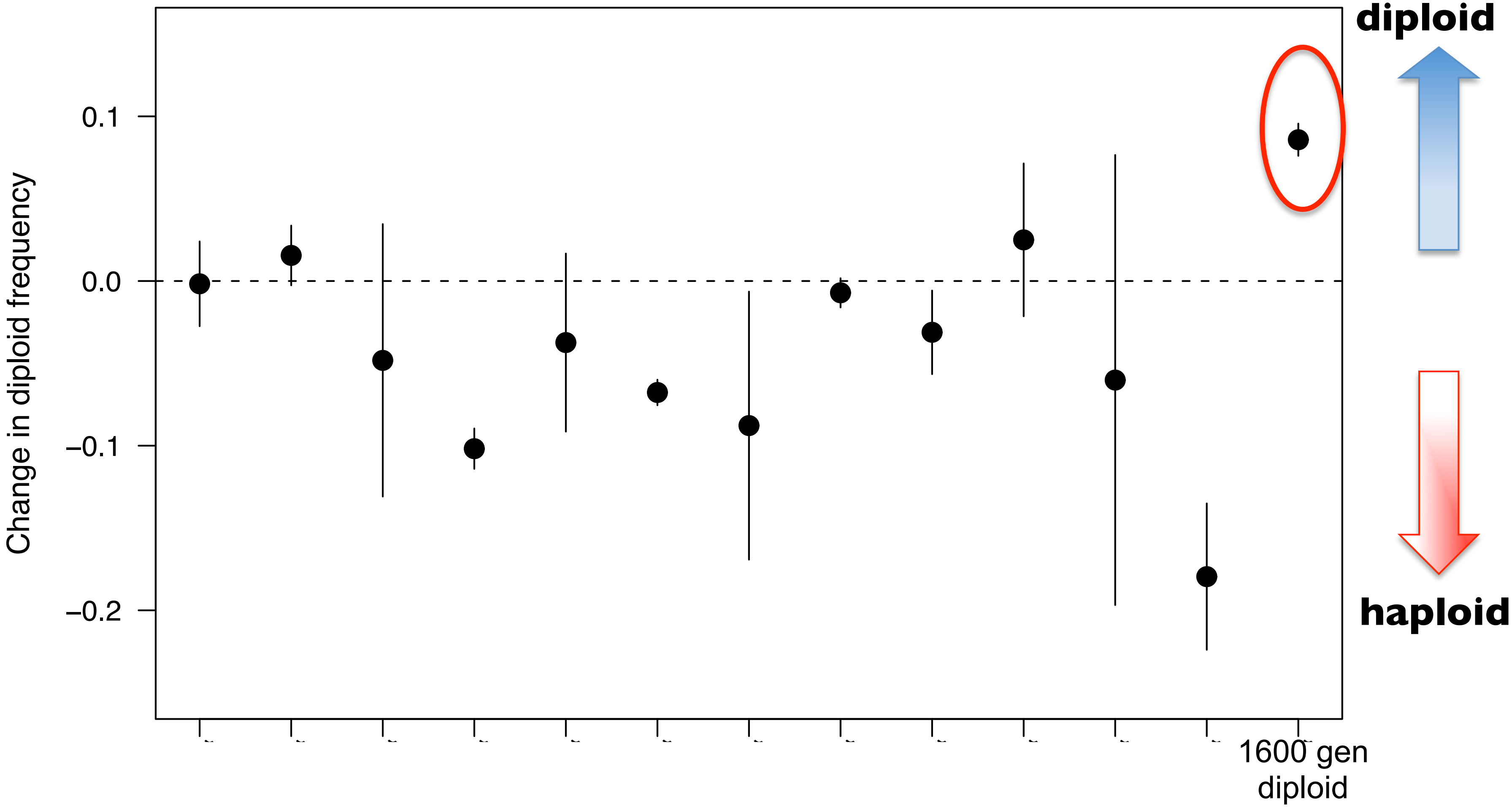
1400 generation diploid colonies against haploid population



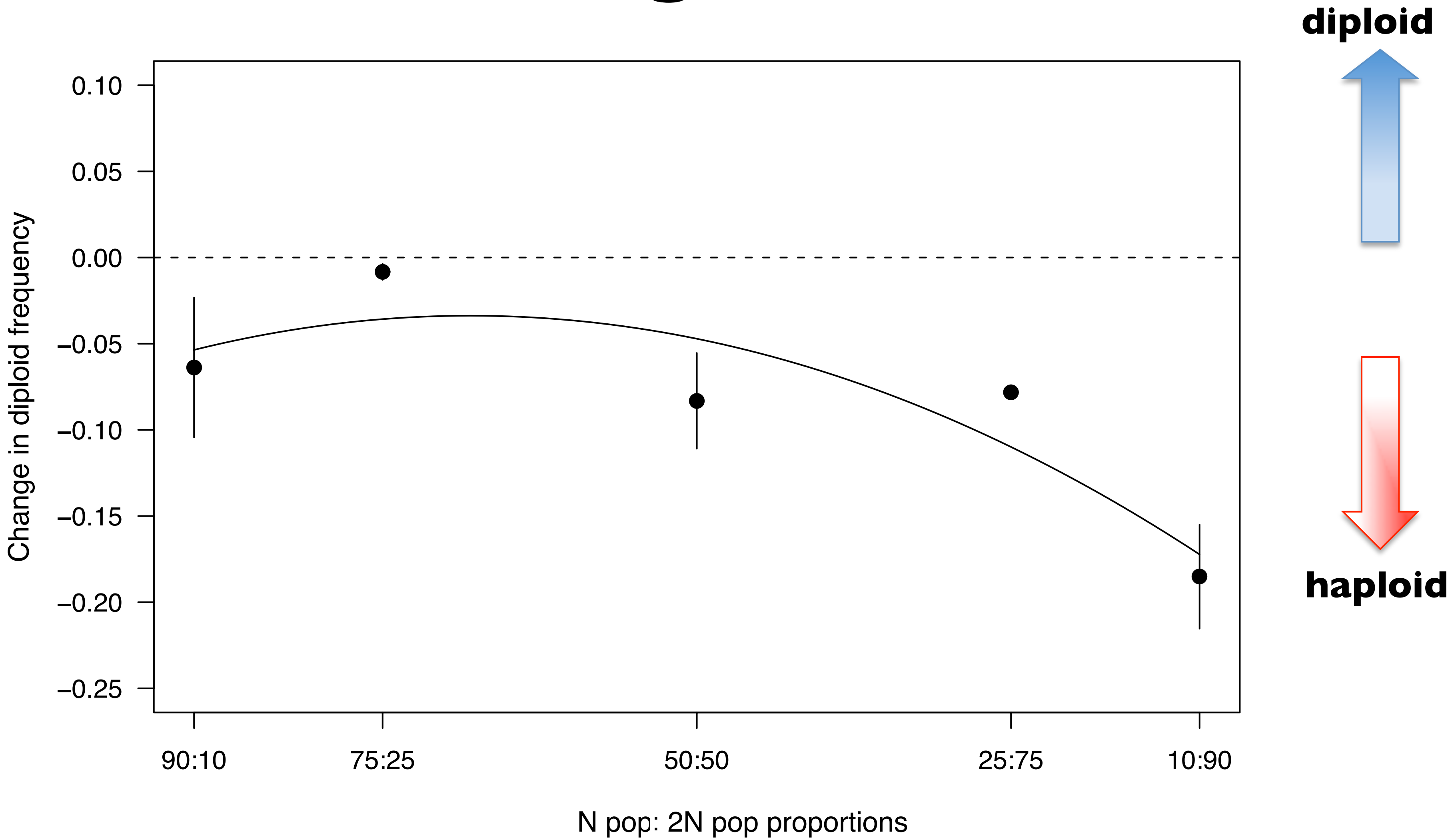
1400 generation diploid colonies against haploid population



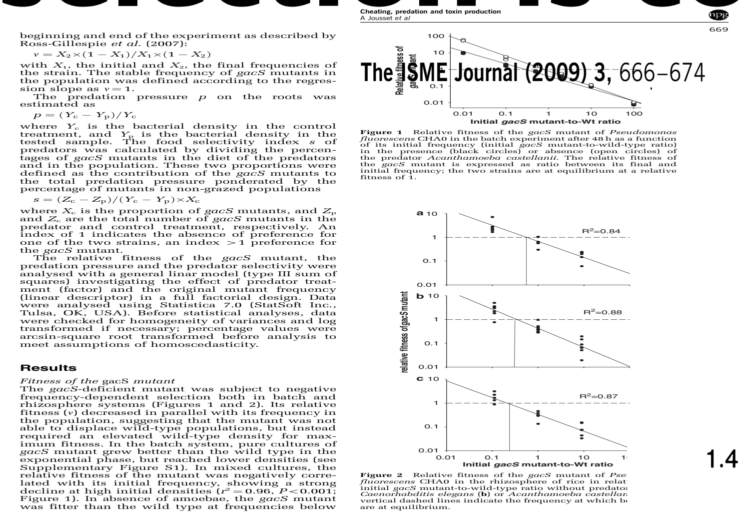
1400 generation diploid colonies against haploid population



N population vs. 2N population at 1400 generations



Negative frequency dependent selection is common



Cheating, predation and toxin production
A Jousset *et al*

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beginning and end of the experiment as described by Ross-Gillespie *et al.* (2007):

$v = X_2 \times (1 - X_1)/X_1 \times (1 - X_2)$

with X_1, the initial and X_2, the final frequencies of the strain. The stable frequency of *gacS* mutants in the population was defined according to the regression slope as $v = 1$.

The predation pressure p on the roots was estimated as

$p = (Y_c - Y_p)/Y_c$

where Y_c is the bacterial density in the control treatment, and Y_p is the bacterial density in the tested sample. The food selectivity index s of predators was calculated by dividing the percentages of *gacS* mutants in the diet of the predators and in the population. These two proportions were defined as the contribution of the *gacS* mutants to the total predation pressure ponderated by the percentage of mutants in non-grazed populations

$s = (Z_c - Z_p)/(Y_c - Y_p) \times X_c$

where X_c is the proportion of *gacS* mutants, and Z_p and Z_c are the total number of *gacS* mutants in the predator and control treatment, respectively. An index of 1 indicates the absence of preference for one of the two strains, an index >1 preference for the *gacS* mutant.

The relative fitness of the *gacS* mutant, the predation pressure and the predator selectivity were analysed with a general linar model (type III sum of squares) investigating the effect of predator treatment (factor) and the original mutant frequency (linear descriptor) in a full factorial design. Data were analysed using Statistica 7.0 (StatSoft Inc., Tulsa, OK, USA). Before statistical analyses, data were checked for homogeneity of variances and log transformed if necessary; percentage values were arcsin-square root transformed before analysis to meet assumptions of homoscedasticity.

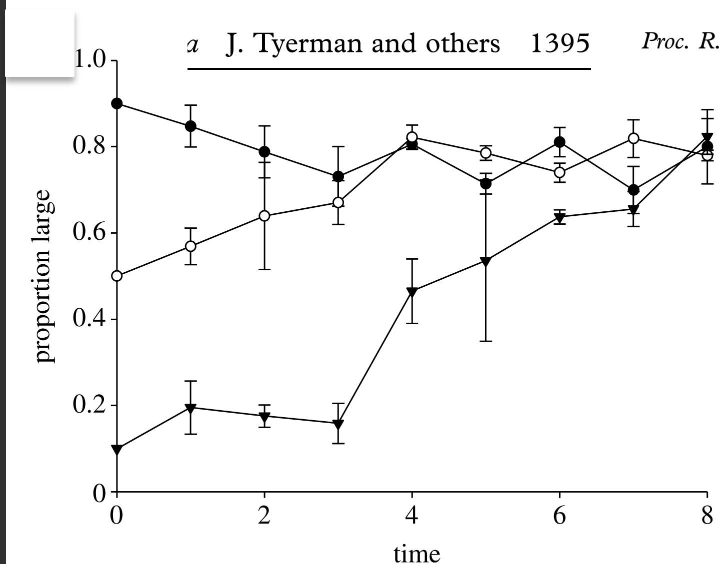
Results

Fitness of the gacS *mutant*
The *gacS*-deficient mutant was subject to negative frequency-dependent selection both in batch and rhizosphere systems (Figures 1 and 2). Its relative fitness (v) decreased in parallel with its frequency in the population, suggesting that the mutant was not able to displace wild-type populations, but instead required an elevated wild-type density for maximum fitness. In the batch system, pure cultures of *gacS* mutant grew better than the wild type in the exponential phase, but reached lower densities (see Supplementary Figure S1). In mixed cultures, the relative fitness of the mutant was negatively correlated with its initial frequency, showing a strong decline at high initial densities ($r^2 = 0.96$, $P < 0.001$; Figure 1). In absence of amoebae, the *gacS* mutant was fitter than the wild type at frequencies below

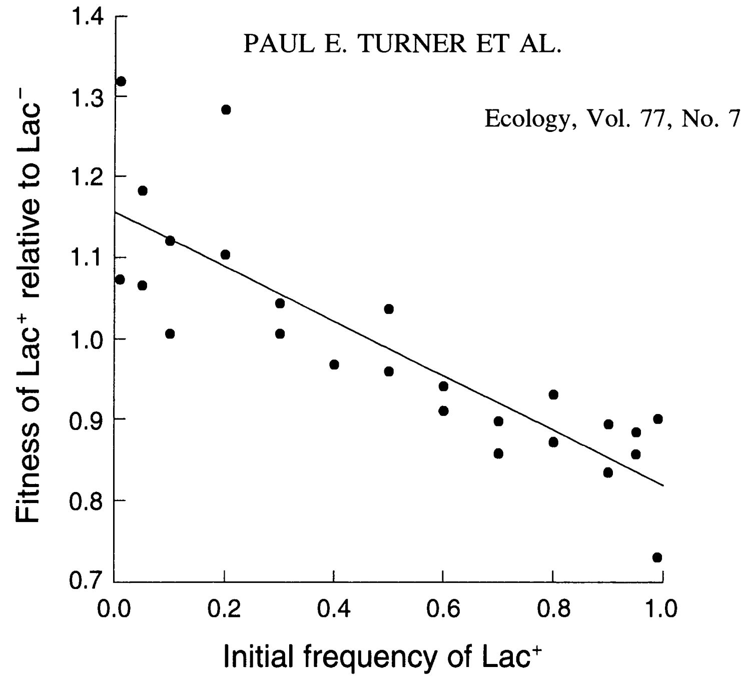
Figure 1 Relative fitness of the *gacS* mutant of *Pseudomonas fluorescens* CHA0 in the batch experiment after 48 h as a function of its initial frequency (initial *gacS* mutant-to-wild-type ratio) in the presence (black circles) or absence (open circles) of the predator *Acanthamoeba castellanii*. The relative fitness of the *gacS* mutant is expressed as ratio between its final and initial frequency; the two strains are at equilibrium at a relative fitness of 1.

Figure 2 Relative fitness of the *gacS* mutant of *Pse*
fluorescens CHA0 in the rhizosphere of rice in relat
initial *gacS* mutant-to-wild-type ratio without predato
Caenorhabditis elegans (**b**) or *Acanthamoeba castellan*
vertical dashed lines indicate the frequency at which b
are at equilibrium.

The ISME Journal (2009) 3, 666–674



Proc. R. Soc. B (2005)



Qu'est-ce qui rend les diploïdes meilleurs?

Conclusion # 3 – les diploïdes de génération 1400 ne remplace pas les haploïdes de génération 1400; mais les diploïdes de génération 1600 peuvent.

Conclusion # 4 – La sélection négative relative à la fréquence maintient les polymorphismes dans le système.

Conclusion # 3 –1400 generations diploids do not outcompete the 1400 generation haploid population; though generation 1600 diploids can.

Conclusion # 4 – Negative frequency dependent selection may act to maintain polymorphism in the system.

Ma perspective moléculaire sur la biodiversité

- Même dans les environnements simples, les polymorphismes peuvent être maintenus pour des centaines de générations
- La métaphore des paysages adaptatifs ne s'applique pas ici – ce n'est pas une mutation peu avantageuse essayant de grimper une colline

- Even in simple environments, polymorphism can be maintained for hundreds of generations
- Adaptive landscape metaphor doesn't work here – not a simple hill climbing low s mutation

Ma perspective moléculaire sur la biodiversité

- Il n’est pas trivial d’expliquer pourquoi la diversité se maintient ou est éventuellement perdue
- Les forces stochastiques & déterministiques sont probablement présentes pour maintenir et pour réduire la diversité ploïdique

- Not trivial to explain why diversity is either maintained, or eventually lost
- Stochastic & deterministic forces likely present to both maintain and remove diversity

Ploidy can directly affect evolution

- Mutation rate **?**
- Mutation effect size (*s* vs. *sh*) **?**
- Mutational neighbourhood **?**

The Next Generation

- Sequence!
- What mutations are fixed at 1600 generations?
- How many appear in only a diploid background?
- How rapidly did they sweep?

2011?

Acknowledgements

- Mike Anderson, Vivien Measday (Measday Lab, UBC) & John Koschwanez (Murray Lab, Harvard) for technical yeast assistance
- Excellent undergrads – Sherry Li, William Li, Dara Lo, Lisa Anderson, Emma Hodgson, Will Tang, Yukon Chen
- Otto Lab and Delta Tea
- Jean-Sébastien Moore pour la traduction

NSERC
CRSNG

Les Fiducies
Killam
Trusts

Restart evolution at 1400 generations