Ecology and the evolution of sex

1) What is sex

2) Sex in prokaryotes

3) Sex in eukaryotes

4) The cost of producing males

5) The macroevolutionary advantage of sex

6) The microevolutionary advantage of sex

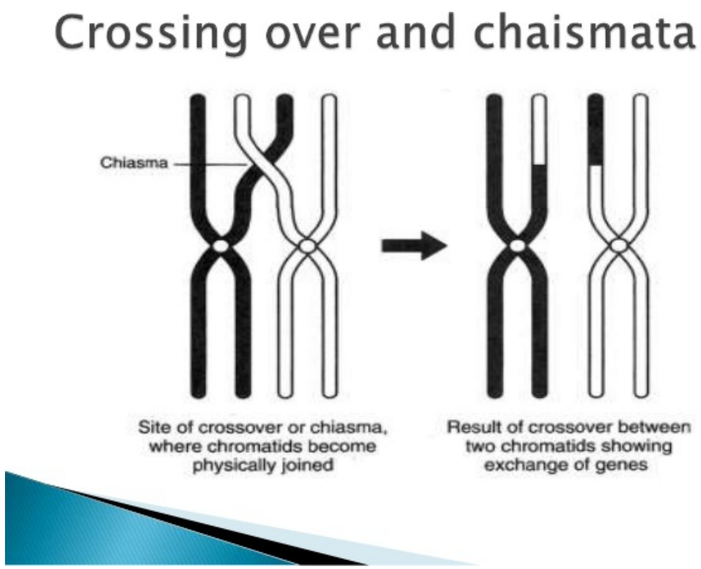
7) Mechanisms favoring the evolution of sex

8) Example exam questions

1) What is sex

The essence of sex is recombination: the process whereby genes from separate individuals (e.g., parents) are brought together in a single organism (e.g., offspring)

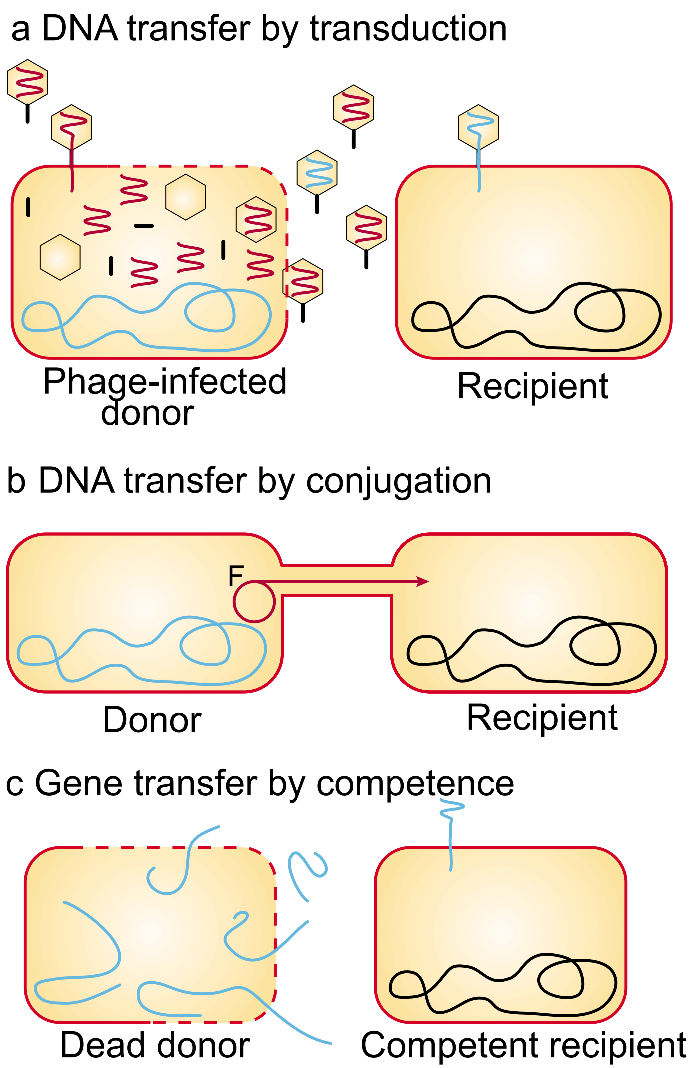
It results from both "crossing over" during meiosis, and from the free assortment of genes on different chromosomes.



https://www.slideshare.net/muhammadwaqasshahid35/crossing-over-37072685

2) Sex in prokaryotes

Involves transfer of DNA. Is not tied to reproduction



a | Transduction is the phage-mediated transfer of host genetic information. In a phage-infected bacterial cell, fragments of the host DNA are occasionally packaged into phage particles and can then be transferred to a recipient cell.

b | Conjugation is the transfer of DNA from a donor cell to a recipient that requires cell-to-cell contact. Genes on conjugative plasmids, such as the F plasmid, encode products that are necessary for this contact, and replication and transfer of the plasmid to the recipient. When, on rare occasions, the F plasmid becomes integrated into the host chromosome (Hfr), conjugation results in a partial transfer of the donor chromosome.

c | Cells that are competent can take up free DNA from their environment.

For all three methods of DNA transfer, the DNA will be expressed in the recipient cell if it is integrated into the recipient genome

Redfield (2002) Nature Reviews Genetics

3) Sex in eukaryotes

Tied to reproduction

Features:

I) Meiosis - the halving of chromosome number in the production of gametes. Followed by fertilization, the fusion of two gametes (male and female) to produce a zygote, the new individual.

ii) Degree of outcrossing - Fusion of gametes might be produced by the same individual (selfing), by relatives (inbreeding), or by unrelated individuals (outcrossing). This varies a great deal among species.

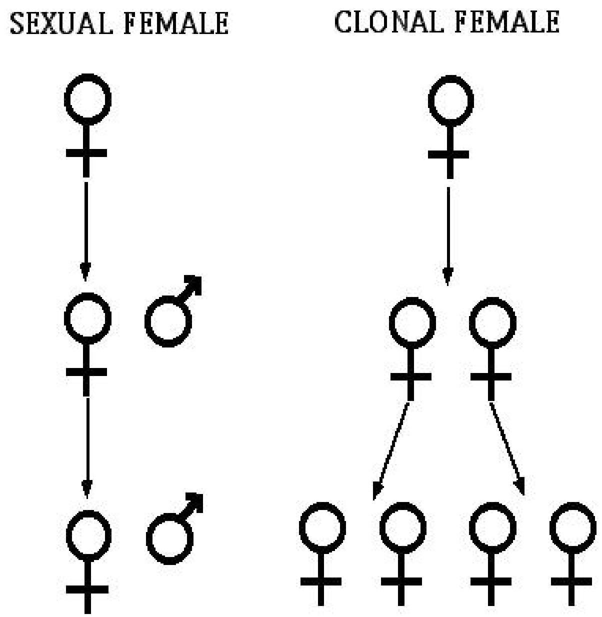
iii) Anisogamy - In most animals and plants a large morphological difference exists between gametes produced by males and females (small sperm vs large eggs). In many protozoa and green algae, gametes produced by the two sexes are the same size (isogamy).

iv) Origin vs maintenance: Sex originated a long time ago, and it is presently maintained. Are the processes the same?

4) The cost of producing males

Has been one of the most important issues in out understanding of the evolution of sexual reproduction.

With anisogamy, there is an immediate and approximate twofold disadvantage to sexual reproduction. Males contribute only DNA, so it seems a waste to produce them.



http://www.indiana.edu/~curtweb/Research/cost%20of%20males.html

4) The cost of producing males

Under this scenario, any advantage to sex must be large to overcome this 2-fold disadvantage.

There is no cost of producing males with isogamy.

Add to this the basic costs of sex: time and energy to mate (searching for mates; the cost of producing flowers; etc), the cost of sexual conflict (e.g., seminal fluid in *Drosophila*), the risk of acquiring sexually transmitted diseases...

Why did sex evolve, why is it maintained?

5) The macroevolutionary advantage of sex

Most asexual taxa are short-lived on a geological time scale. Most asexual species we find in nature are recently derived from sexual ancestors.

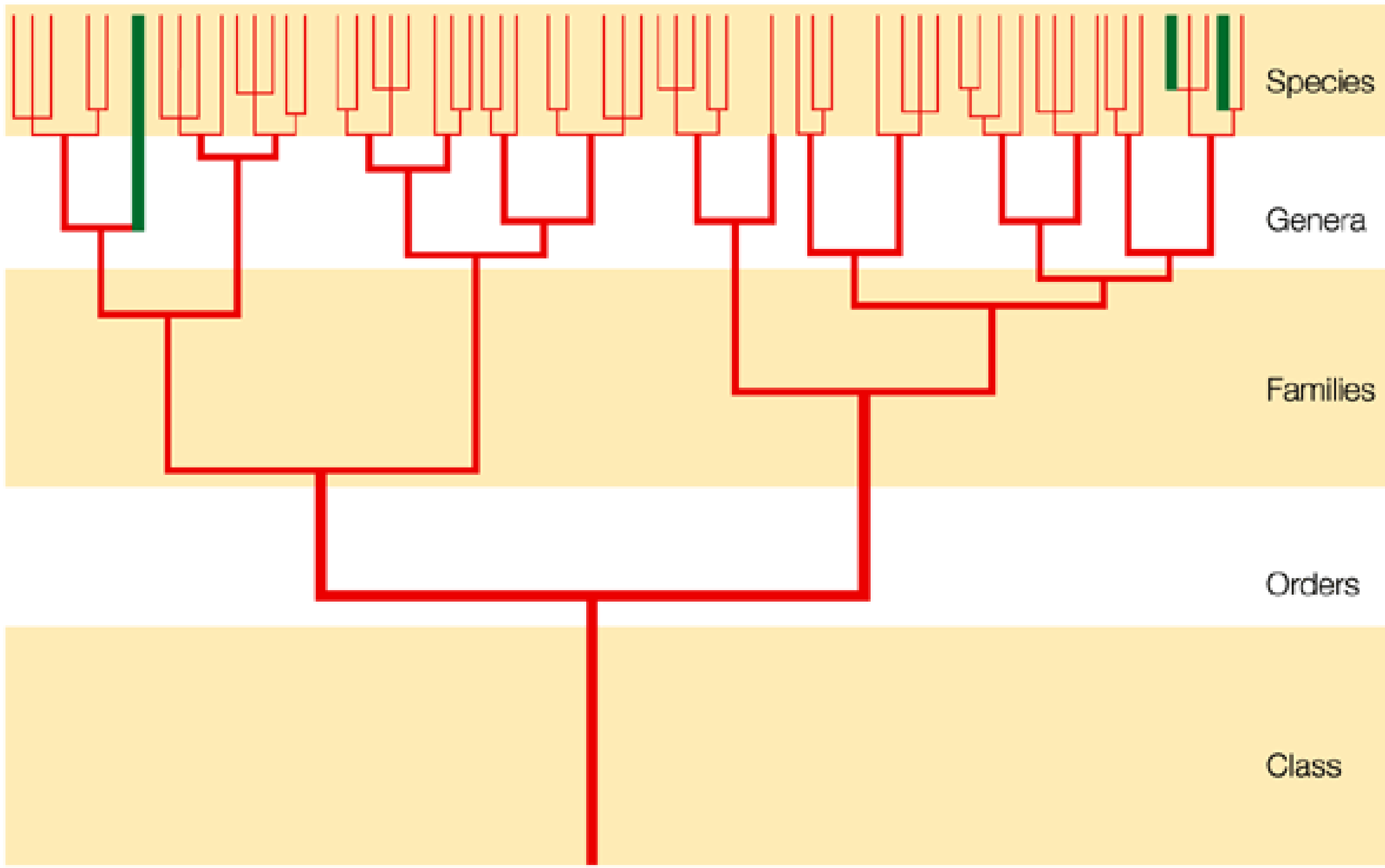
For example, dandelions: ~1000 asexual "species" of *Taraxacum* and ~50 sexual species. The asexual taxa are closely related to the sexual species and are relatively recently derived -- they still have petals and pollen.

With only one exception (the bdelloid rotifers), no major taxon (subfamily or higher) consists mainly of parthenogenetic forms. (Parthenogenesis: development of an embryo from an unfertilized egg.)

This pattern implies that asexual taxa go extinct at a higher rate than sexual species. This disadvantage over macroevolutionary times scales might contribute to the maintenance of sexual reproduction.

5) The macroevolutionary advantage of sex

Typical phylogenetic distribution of asexual species



A schematic of a typical animal phylogeny. Asexual species (green) are rare (<0.1% of all animal species) and their lineages are short lived on a geological timescale. With a single exception (the bdelloid rotifers, no genus of substantial size, or any higher taxonomic group, is composed entirely of asexual lineages

Rice (2002) Nature Reviews Genetics

5) The macroevolutionary advantage of sex

Bdelloid rotifers never have sex

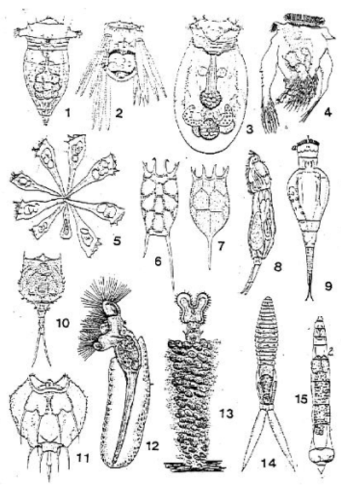
Science 19 May 2000:
Vol. 288 no. 5469 pp. 1211–1215

Evidence for the Evolution of Bdelloid Rotifers Without Sexual Reproduction or Genetic Exchange

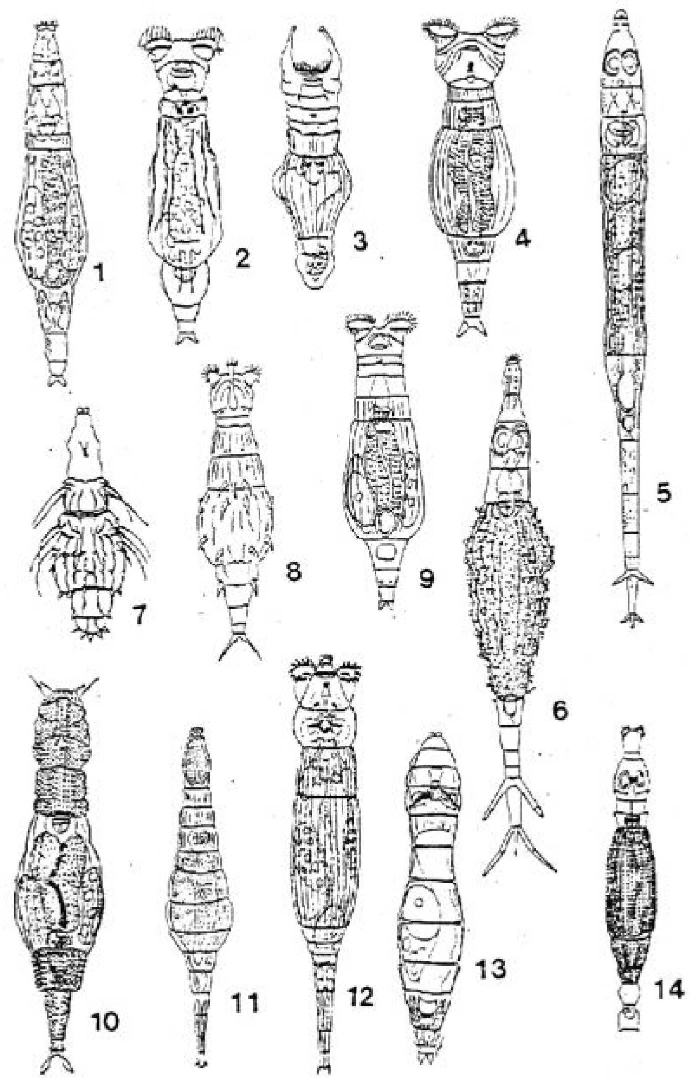
David B. Mark Welch, Matthew Meselson*

ABSTRACT

The Class Bdelloidea of the Phylum Rotifera is the largest metazoan taxon in which males, hermaphrodites, and meiosis are unknown. We conducted a molecular genetic test of this indication that bdelloid rotifers may have evolved without sexual reproduction or genetic exchange. The test is based on the expectation that after millions of years without these processes, genomes will no longer contain pairs of closely similar haplotypes and instead will contain highly divergent descendants of formerly allelic nucleotide sequences. We find that genomes of individual bdelloid rotifers, representing four different species, appear to lack pairs of closely similar sequences and contain representatives of two ancient lineages that began to diverge before the bdelloid radiation many millions of years ago when sexual reproduction and genetic exchange may have ceased.



monogonont



bdelloid

6) The microevolutionary advantage of sex

Short term advantage

Many species in nature reproduce both sexually and asexually, such as at different times of the year (called facultative or cyclical parthenogenesis). Examples include *Daphnia*, aphids, cynipid wasps, monogonont rotifers. Many plant species can produce offspring both sexually and asexually.

This implies that sexual reproduction must have an advantage in the shorter term.

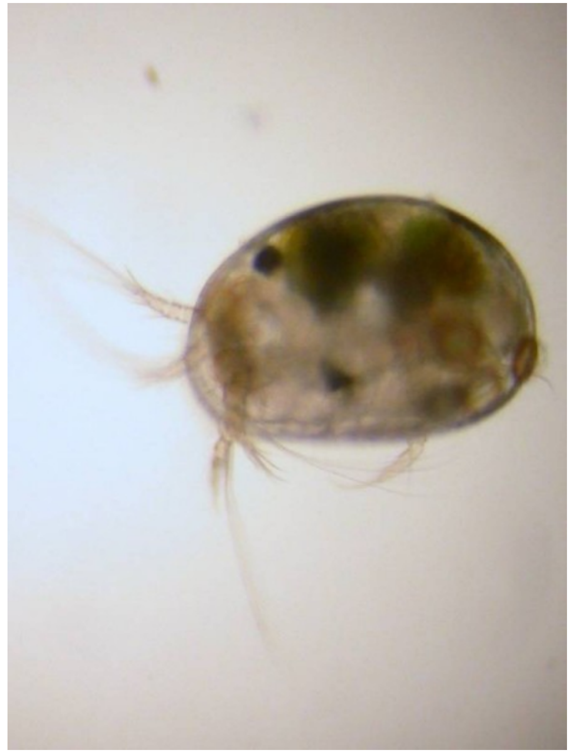
By Shipher Wu (photograph) and Gee-way Lin (aphid provision), National Taiwan University - PLoS Biology, February 2010 direct link to the image description, CC BY 2.5, https://commons.wikimedia.org/w/index.php?curid=9590073

6) The microevolutionary advantage of sex

Ecological distribution of sex

Table 3.11: Habitats of Free-living North American Freshwater Ostracods. Only genera with five or more species included. Figures in cells are the numbers of times that a particular habitat type is mentioned in Tressler's descriptions (Tressler, 1959). The classification of habitats attempts to express degree of permanence, as follows: (1) lakes and rivers; (2) ponds, streams, canals, small shallow lakes and littoral of lakes; (3) pools, rock pools, marshes and small shallow ponds; (4) ditches and temporary ponds, marshes and streams. Some habitat types (fish ponds, brackish water, springs and caves) do not fit readily into the classification and have been excluded: they comprise only seven per cent of the habitats named by Tressler.

Genus	Parthenogenetic spp. (%)	Habitat type			
		1	2	3	4
Cyclocypris	0	5	9	0	0
Cypria	11	4	5	2	0
Limnocythere	14	5	2	0	0
Cypricercus	27	1	7	8	0
Candona	34	8	22	12	13
Cyprinotus	42	6	10	6	6
Physocypria	50	4	4	3	0
Potamocypris	56	0	1	4	1
Cypretta	60	0	0	3	0
Cypridopsis	60	4	2	10	2
Chlamydotheca	84	0	3	3	1
Eucypris	100	0	2	1	5



http://dept.harpercollege.edu/biology/guide/gallery/small_crustaceans/original/seed_shrimp_eucypris_sp.jpg

Bell (1982) The masterpiece of nature

6) The microevolutionary advantage of sex

Environmental correlates of parthenogenesis usually show that it is typically least often found in "stable" environments and most often at high latitudes or disturbed habitats.

This suggests that variability in abiotic environments might not be a strong predictor of where sexual reproductive is most strongly favored. This observation has led to the suggestion that sexual reproduction is an adaptation to variability in the biotic environment.

by hecht801 https://www.flickr.com/photos/42867645@N03/4461572000

7) Mechanisms favoring the evolution of sex

The immediate consequence of sex and recombination is to make non-random associations between alleles in the genome more random.

If the association between alleles is already random (only possible in an infinite population), then sex accomplishes nothing and is not favored.

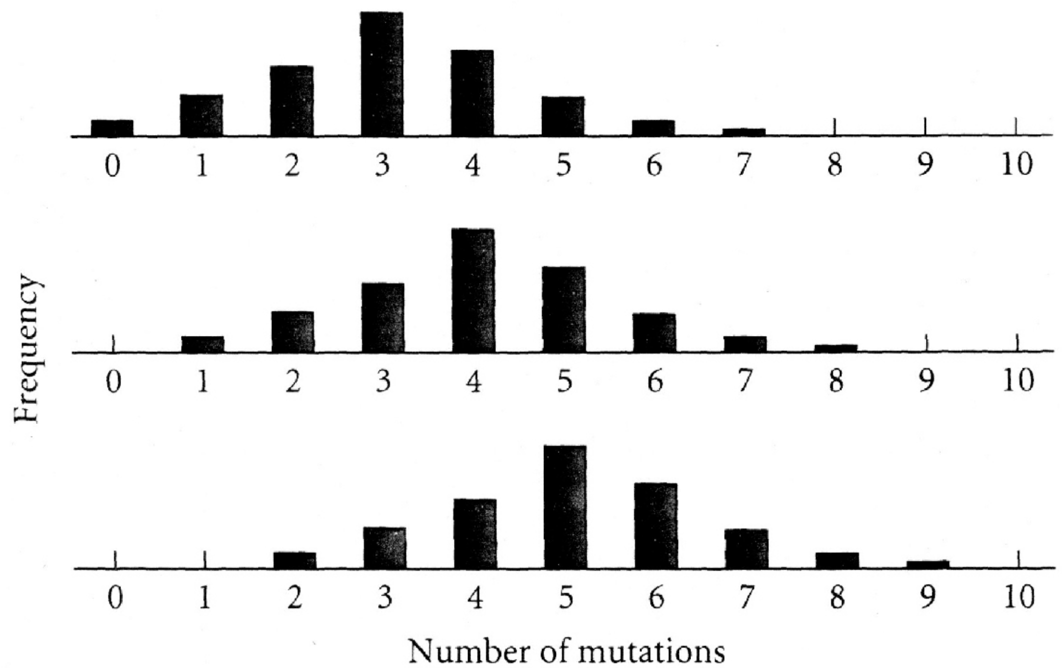
However, mutation, genetic drift and natural selection generate non-random associations between alleles.

If the breakdown of these associations is advantageous, then sex is favored.

7) Mechanisms favoring the evolution of sex

Muller's ratchet: an outcome of genetic drift in the absence of sex

FIGURE 21.6 Muller's ratchet. The frequency of individuals with different numbers of deleterious mutations (0–10) is shown for an asexual population at three successive times. The least loaded class (0 in top graph, 1 in middle graph) is lost over time, both by genetic drift and by its acquisition of new mutations. In a sexual population, class 0 can be reconstituted, since recombination between genomes in class 1 that bear different mutations can generate progeny with none. (After Maynard Smith 1988.)



The ratchet will be fastest when mutation rates are high, selection is weak, and population sizes are small: The advantage to sex is greatest under these circumstances.

7) Mechanisms favoring the evolution of sex

Sex allows faster fixation of advantageous mutations

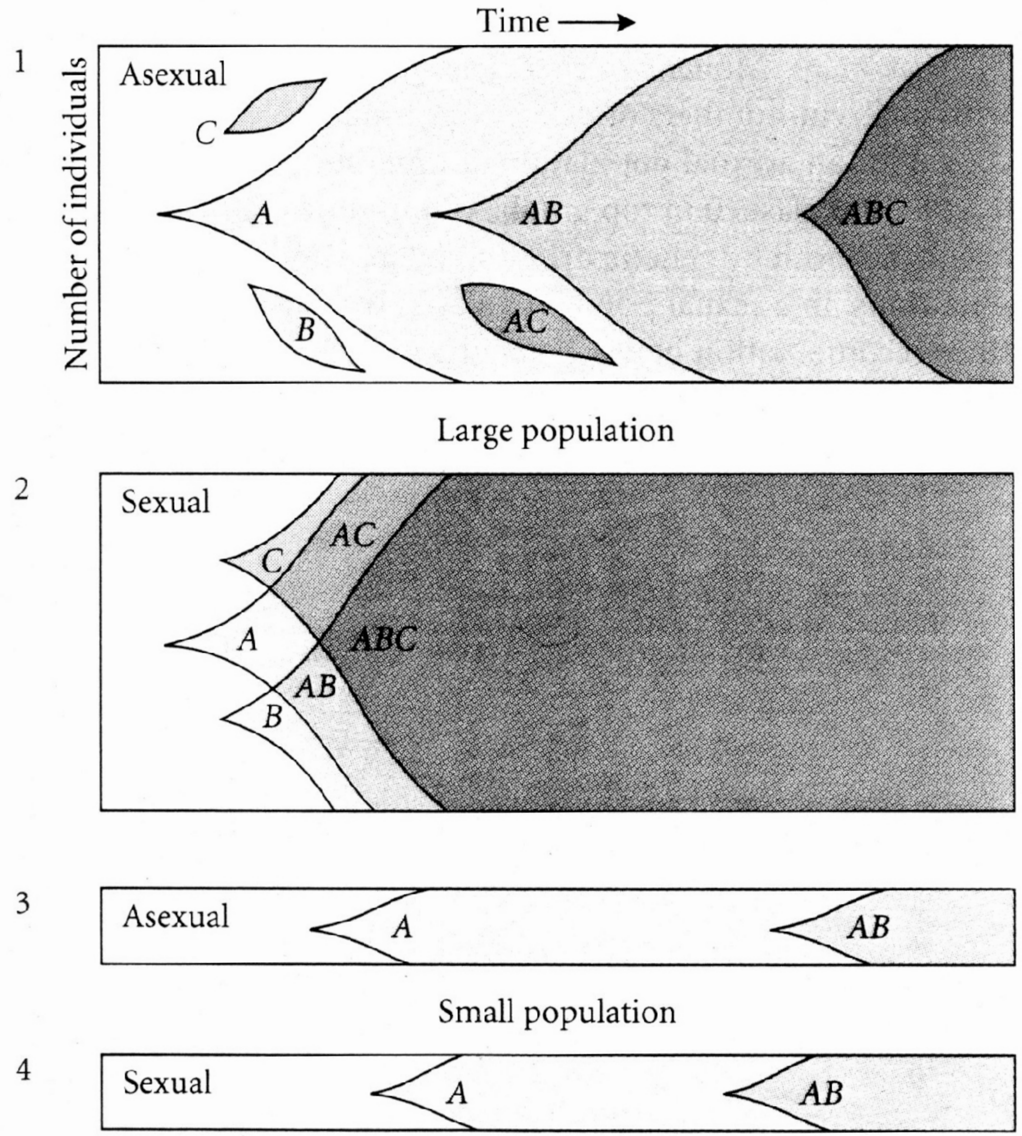
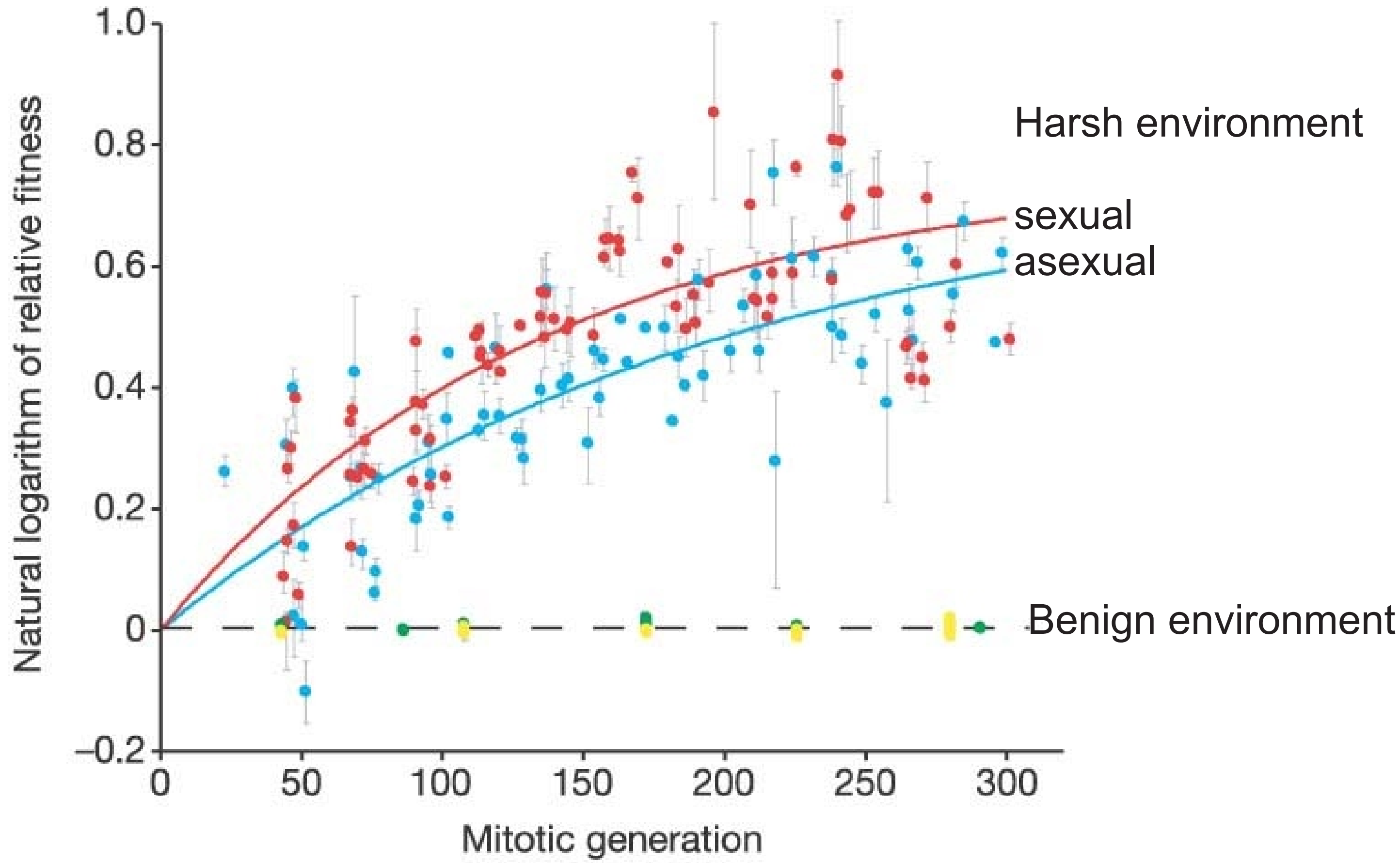


FIGURE 21.4 Effects of recombination on the rate of evolution. *A*, *B*, and *C* are new mutations that are advantageous in concert. In asexual populations (1 and 3), combination *AB* (or *ABC*) is not formed until a second mutation, such as *B*, occurs in a lineage that already bears the first mutation, *A*. In a large sexual population, independent mutations can be assembled more rapidly by recombination, so adaptation is more rapidly achieved. In small populations, however (panels 3 and 4), the interval between the occurrence of favorable mutations is so long that a sexual population does not adapt more rapidly than an asexual population. (After Crow and Kimura 1965.)

7) Mechanisms favoring the evolution of sex

Adaptation is faster in sexual than asexual populations

Goddard et al. measured the rate of adaptation of 8 sexual and 8 asexual yeast populations in chemostats when exposed to either a new benign environment in which growth was limited by glucose concentration (0.08%), or a harsher environment with the same glucose concentration but in which the temperature was raised from 30 to 37 8C, and where osmolarity was elevated from 0 to 0.2M NaCl.

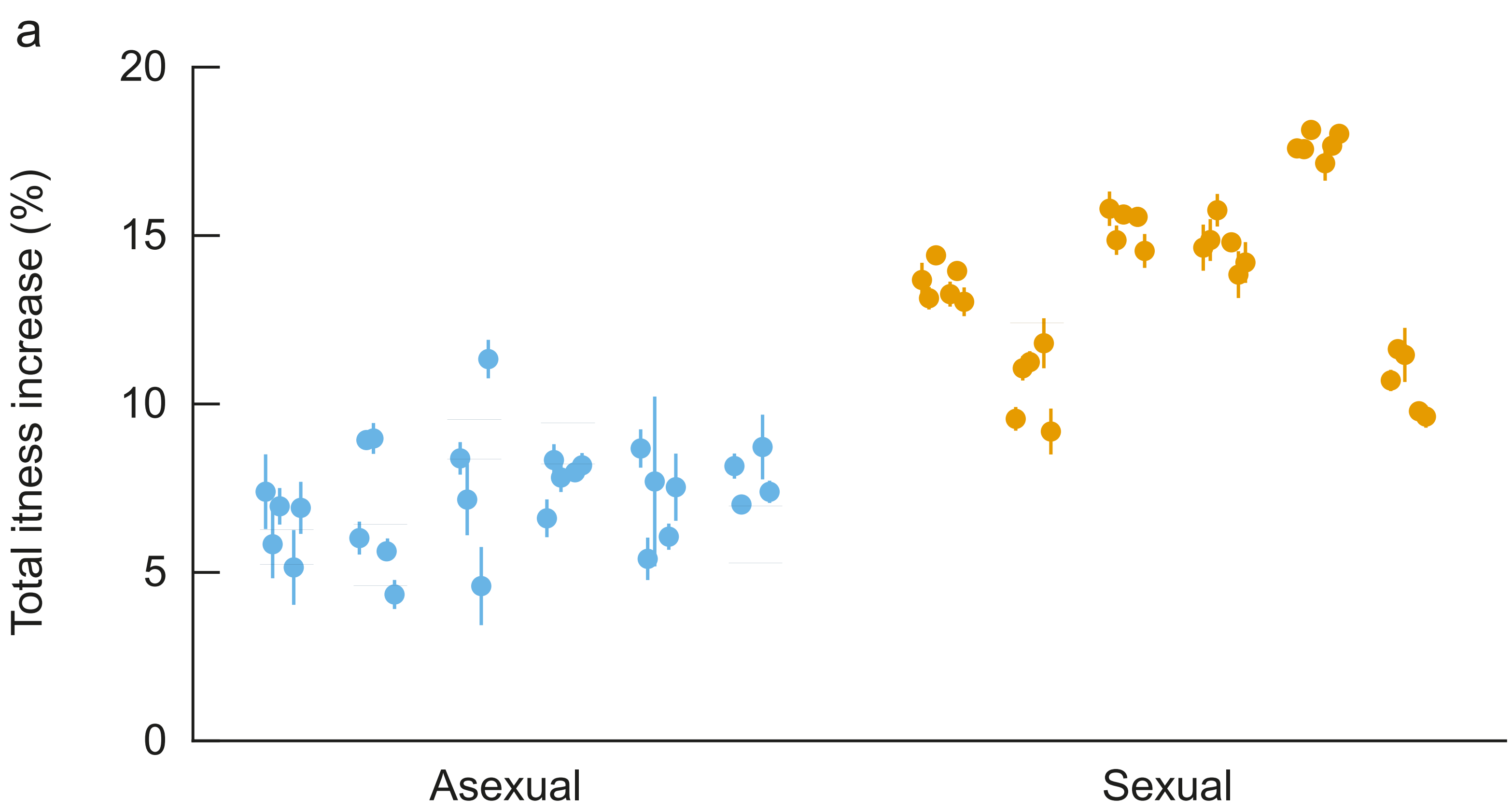


Goddard et al (2005) Nature

7) Mechanisms favoring the evolution of sex

Adaptation is faster in sexual than asexual populations

McDonald et al. (2016) propogated 6 replicate sexual populations of yeast and 12 asexual controls in 30 C in 96-well plates containing yeast extract peptone dextrose (a new environment?).



McDonald et al. (2016) Nature

7) Mechanisms favoring the evolution of sex

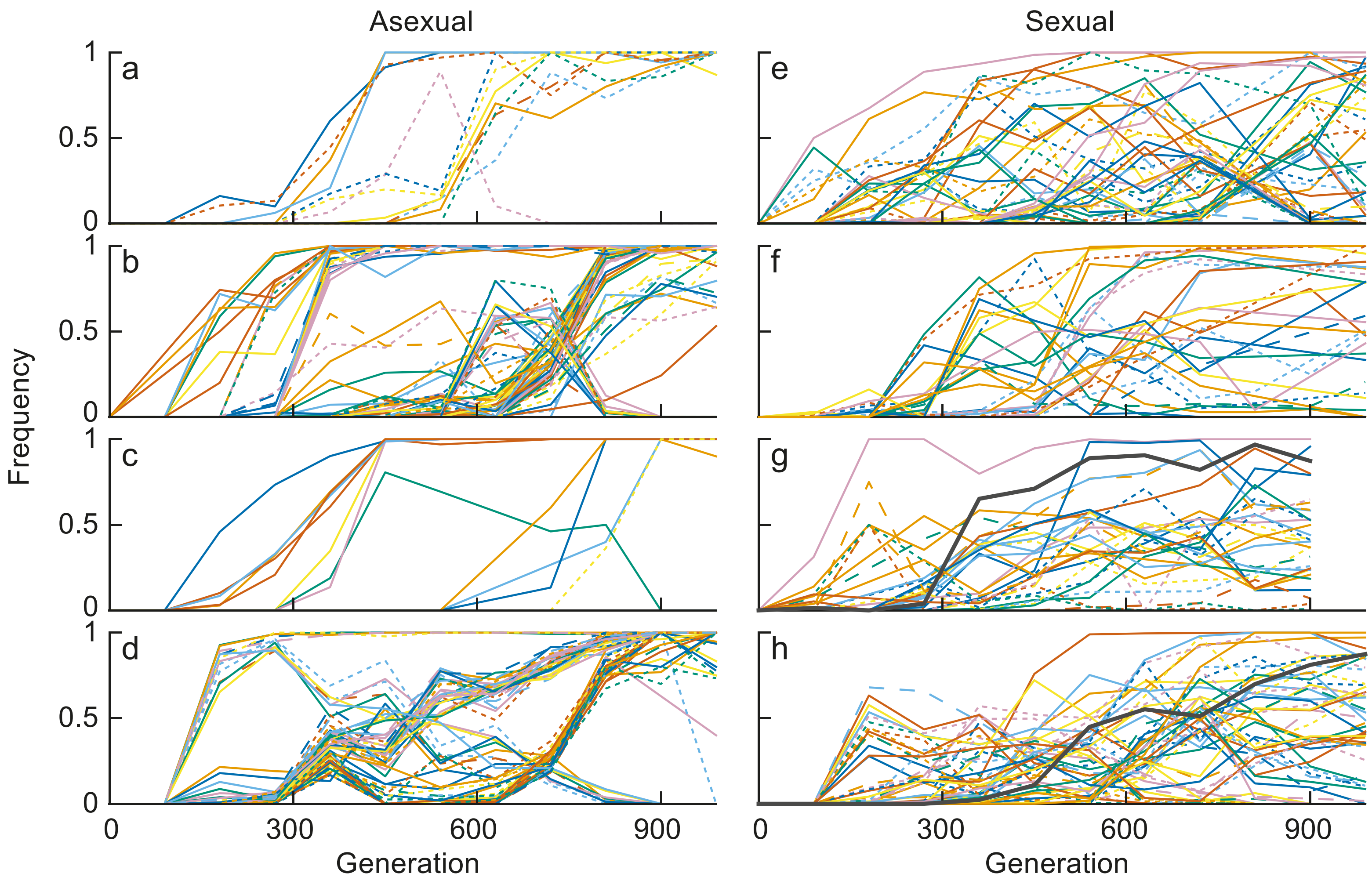
The frequencies of all identified de novo mutations through ~1,000 generations in four asexual populations and four sexual populations (sequenced every 90 generations).

Solid lines:
nonsynonymous mutations

Dashed lines:
synonymous mutations

Dotted lines:
intergenic

Black:
mutations in *Erg3* (known to be under balancing selection)



McDonald et al. (2016) Nature

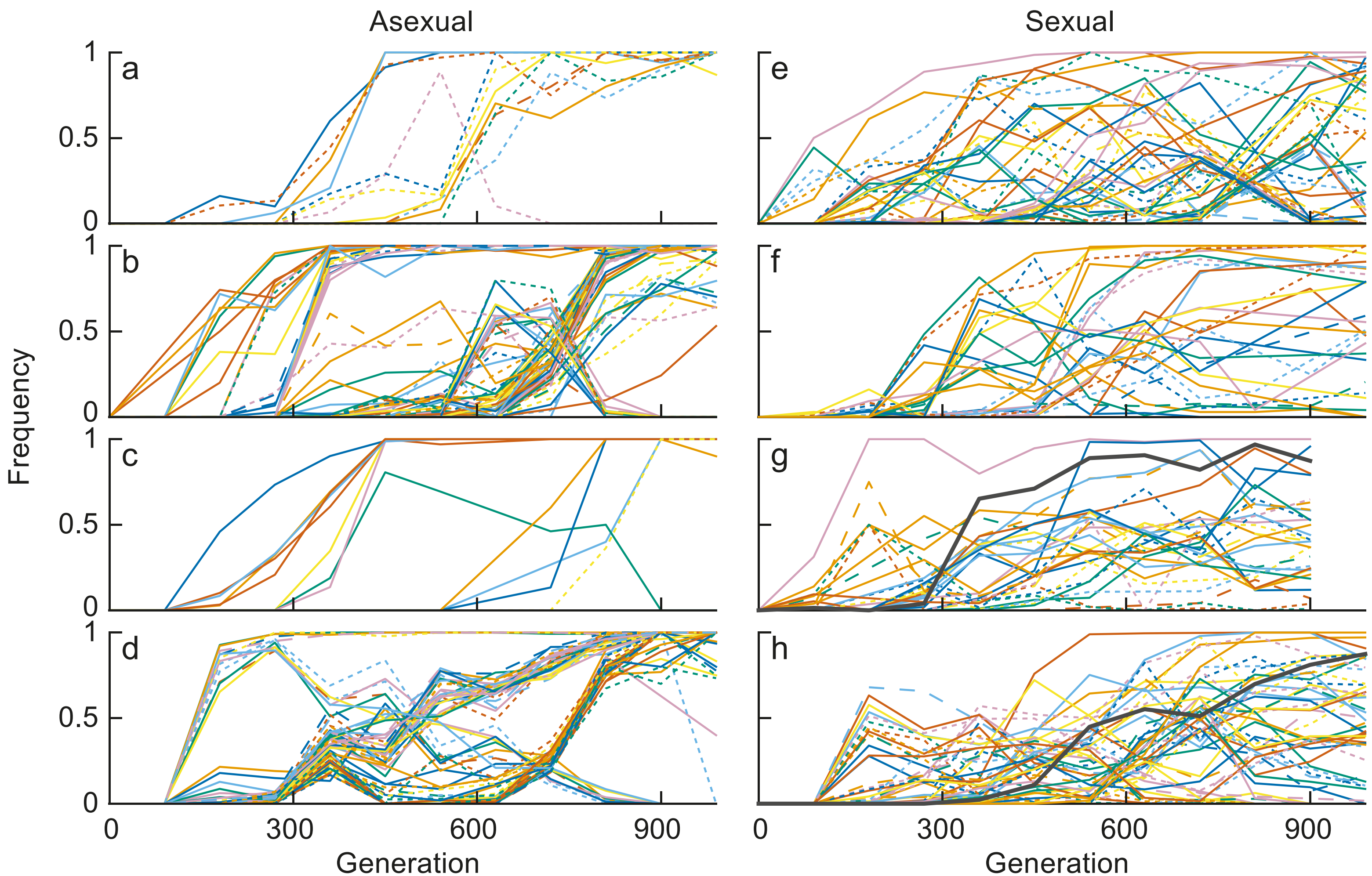
7) Mechanisms favoring the evolution of sex

The outcome of evolution is determined by competition between cohorts of mutations.
In sexual populations dynamics of each mutation is largely independent of others.

In the asexual populations, mutations rise to high frequency (fix) in cohorts.

All types of mutations fix in the asexual populations (synonymous, non-synonymous, and intergenic mutations).

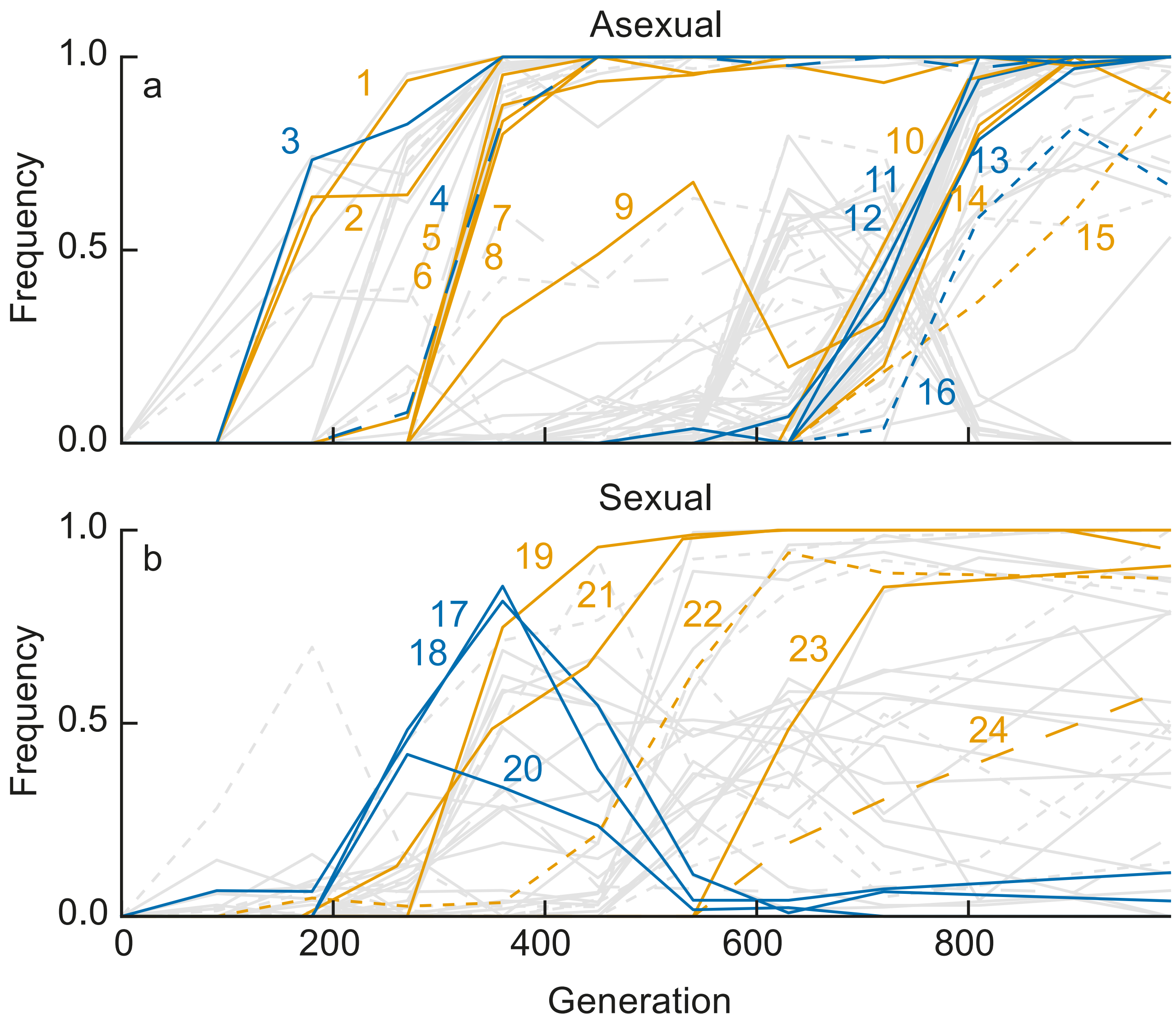
Fewer mutations fix in the sexual populations. They are mainly non-synonymous.



McDonald et al. (2016) Nature

7) Mechanisms favoring the evolution of sex

Trajectories of individual mutations in an asexual (a) and a sexual (b) line. Orange mutations are beneficial; blue are deleterious; grey are unmeasured or consistent with neutrality.



McDonald et al. (2016) Nature

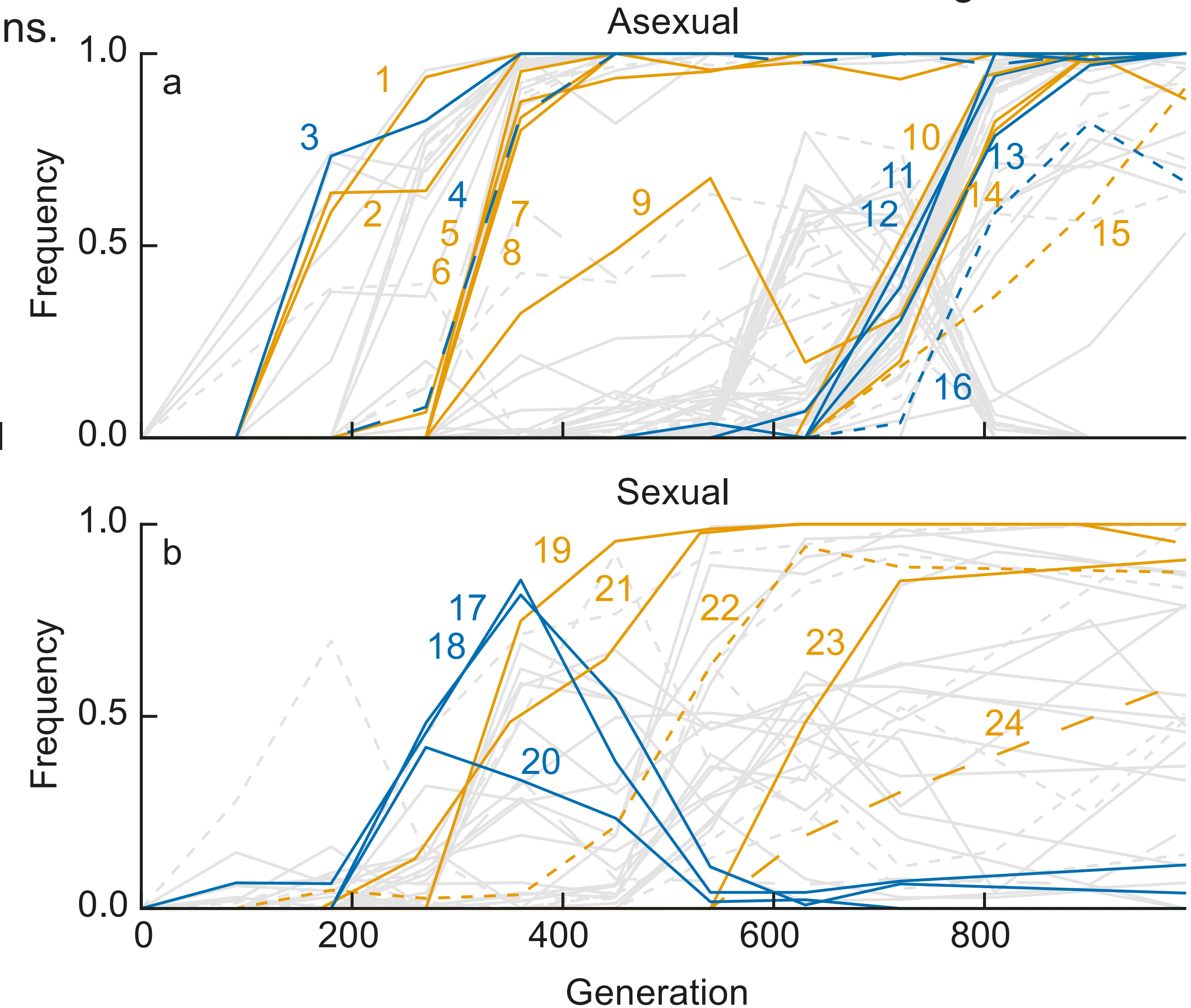
7) Mechanisms favoring the evolution of sex

Sex increases the rate of adaptation both by combining beneficial mutations into the same background and by separating deleterious mutations from advantageous backgrounds that would otherwise drive them to fixation. Sex makes natural selection more efficient at sorting both beneficial and deleterious mutations.

Cohorts of mutations that fix in asexual populations contain at least one beneficial mutation. But linked deleterious mutations also go to fixation.

In contrast, sex (recombination) decouples mutations from their initial background, and no deleterious mutations fixed in the sexual populations.

orange = beneficial;
blue = deleterious;
grey = unknown or neutral.



McDonald et al. (2016) Nature

8) Example exam questions

Explain the “cost of producing males” and why it is a problem for the evolution or maintenance of sexual reproduction.

What is Muller's ratchet, and how might it explain the evolution of sexual reproduction?

Why might sexual reproduction be advantageous during the process of adaptation to a new environment?

Comparative studies show that parthenogenesis (asexual reproduction) is most often found in organisms at high latitudes, high altitudes, and in disturbed habitats, than in related organisms at lower latitudes and altitudes, and more stable habitats. Suggest an evolutionary explanation for this pattern, and a means by which it might be tested.

In theory, what is the importance of anisogamy in the evolution of sex?

In lab experiments, asexual populations adapting to a new environment fix more deleterious mutations than do sexual populations. Explain why this occurs and what effect this has on the rate of increase in population mean fitness.