

## What is "Genetic Draft"?

It's not a fundamental "force" like mutation, selection, and drift.

It's an *effect* of mutation at a selected locus, that reduces variation at nearby (linked) loci, thereby reducing the apparent  $N$ .

Why should we care?

Neutral theory predicts that at *mutation-drift equilibrium*, DNA polymorphism should be proportional to  $N$ :

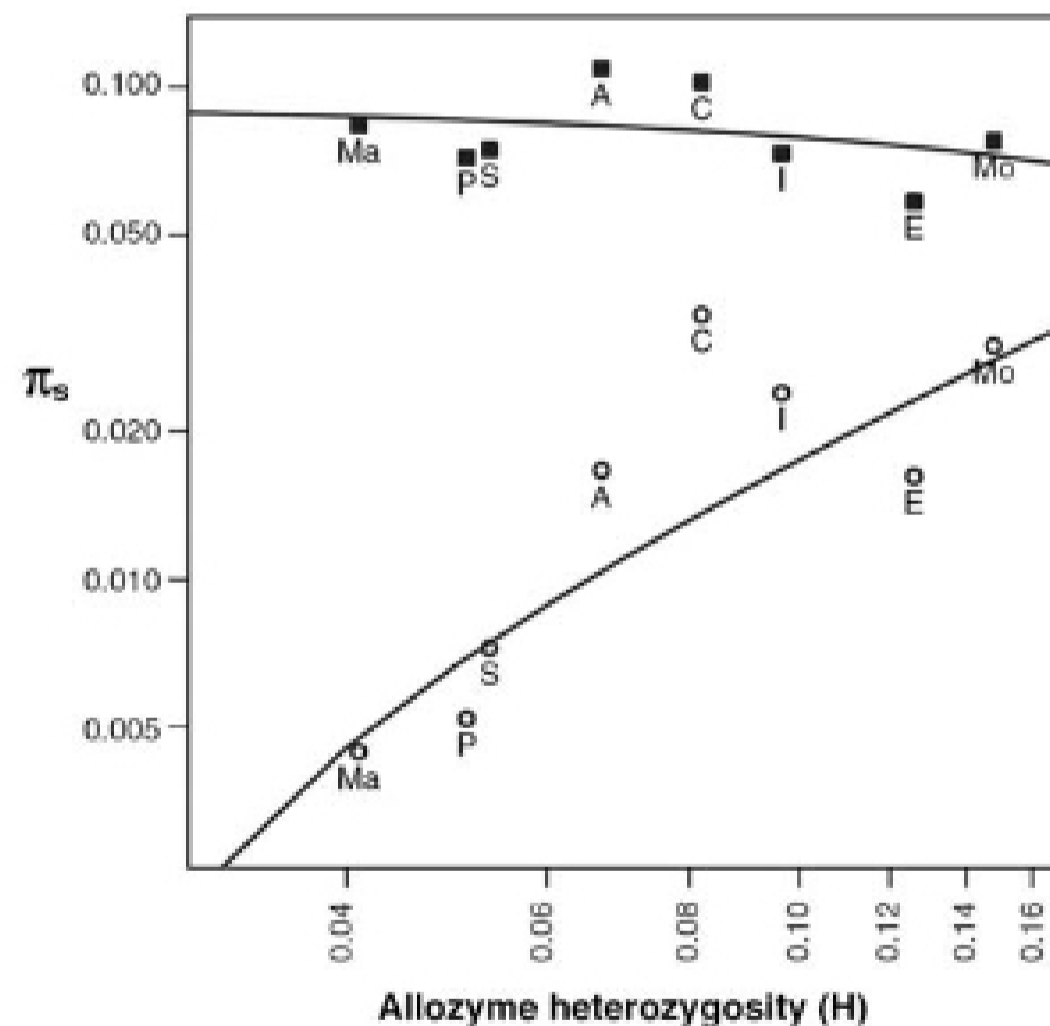
$$\pi \approx 2G\mu \quad (= 4N\mu \text{ for a diploid locus})$$

But it's *not!*

(Not even approximately, especially for mitochondria.)

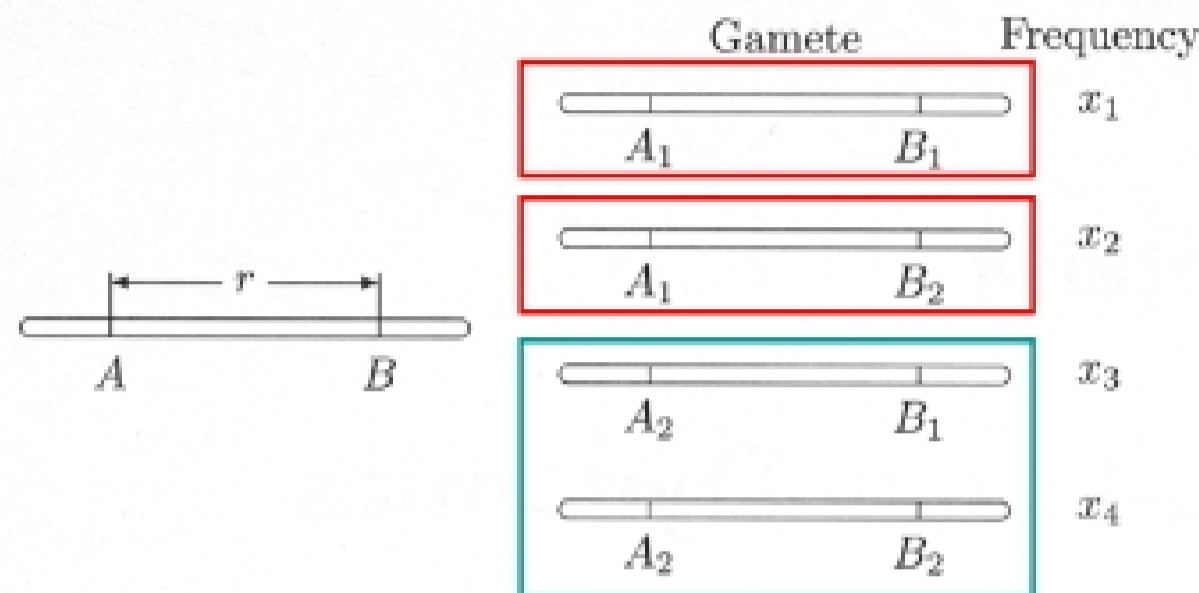
Anthro/Biol 5221, 7 November 2008

**Fig. 1.** Average allozymic, nuclear DNA, and mtDNA diversity in eight animal taxa. *x* axis: allozyme average heterozygosity. *y* axis: circles, nuclear DNA average synonymous diversity (kendall test:  $\tau = 0.87$ ,  $P < 0.05$ ); squares, mtDNA average synonymous diversity (kendall test:  $\tau = -0.14$ , not significant). Ma: Mammalia (allozymes: 184 species; nuclear: 30 species; mtDNA: 350 species); S: Sauropsida (reptiles and birds: 116, 20, 378); A: Amphibia (61, 4, 96); P: Pisces (bony fish and cartilaginous fish: 183, 22, 270); I: Insecta (156, 73, 511); C: Crustacea (122, 2, 78); E: Echinodermata (sea stars and urchins: 15, 14, 47); and Mo: Mollusca (46, 9, 125). The nuclear averages of the little-represented Amphibia (four species) and Crustacea (two species) are shown but were not used for the statistical test.



Eric Bazin, Sylvain Glémin, Nicolas Galtier (2006) *Science* 312, 570-572.

**The draft model: Locus "A" is selected, locus "B" is neutral**



**Figure 4.1:** The chromosome on the left shows the position of the  $A$  and  $B$  loci. The right side illustrates the four possible gametes with their frequencies.

Step 0: The population is fixed for  $A_2$ , polymorphic for  $B_1$  and  $B_2$ .

Frequency of  $B_1 = p_B$ , frequency of  $B_2 = q_B = (1 - p_B)$ .

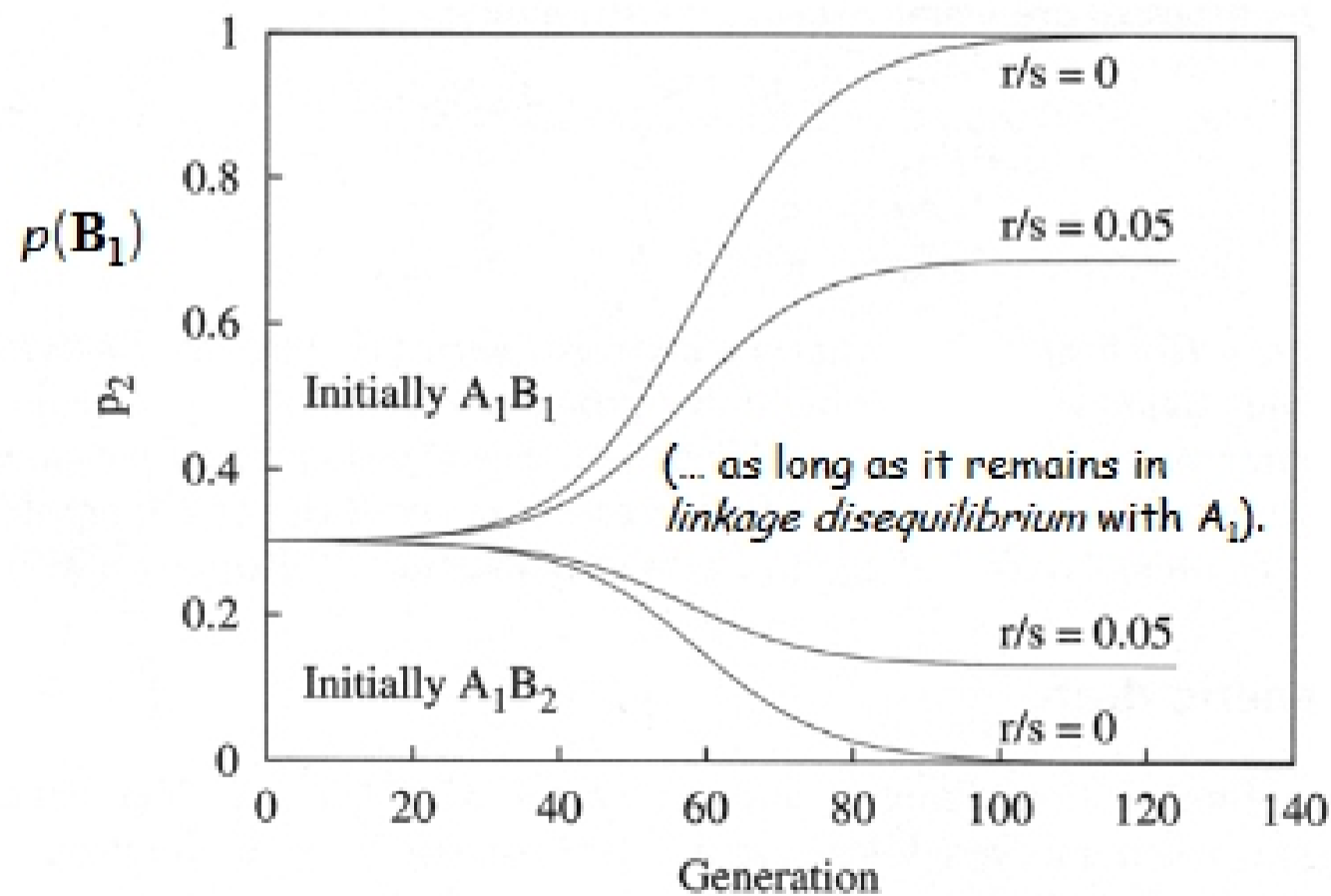
Step 1: A mutation to the selectively favored allele  $A_1$  occurs.

But on which genetic background?

$B_1$ ?

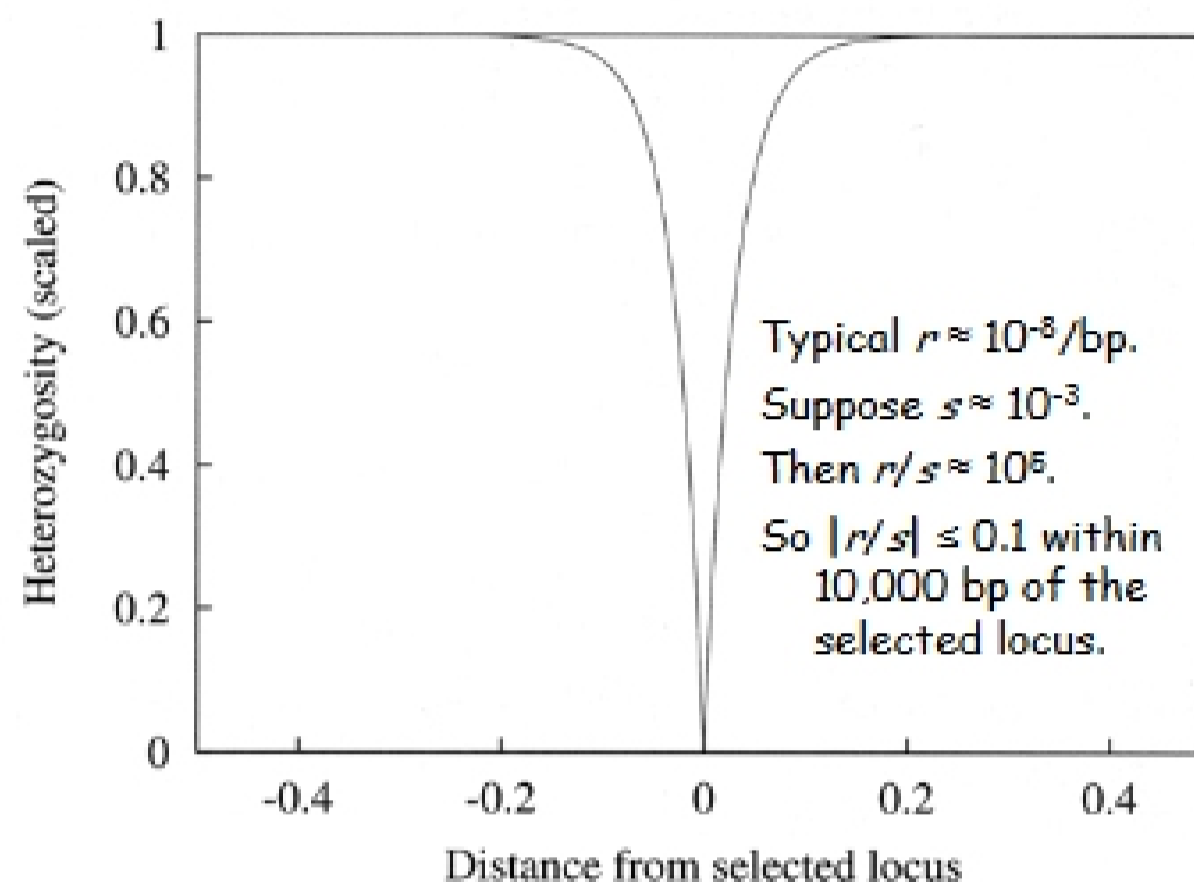
$B_2$ ?

**Step 2: The lucky B-allele "hitches a ride" with  $A_1$  ...**



**Figure 4.5:** The frequency of the  $B_2$  allele under different hitchhiking scenarios. For the upper two curves, the  $A_1$  allele is initially linked to the  $B_1$  allele; in the bottom two, it is linked to the  $B_2$  allele.  $s = 0.2$  for all trajectories.

An important consequence:  
hitchhiking "sweeps away" variation near the selected locus



**Figure 4.4:** The ratio of the final to initial heterozygosity at a neutral locus as a function of the distance from the selected locus as measured by  $r/s$ . Negative values of  $r/s$  are left of the selected locus, positive values are to the right.

4.3 The following program, written in Python, will print out the ratio of the final to starting heterozygosities at the  $B$  locus.

```

s, r, N = 0.1, 0.001, 5000
eps = 1.0 / ( 2 * N)
x1, x2 = eps, 0.0
x3, x4 = 0.5 - x1, 0.5
while x1 + x2 < 1.0 - eps:
    p1 = x1 + x2
    q1 = 1.0 - p1
    wBar1 = 1.0 - q1 * s / 2.0
    wBar3 = 1.0 - p1 * s / 2.0 - q1 * s
    wBar = 1.0 - q1 * s
    rWD = r * (1 - s / 2.0) * (x1 * x4 - x2 * x3)
    x1 = (x1 * wBar1 - rWD) / wBar
    x2 = (x2 * wBar1 + rWD) / wBar
    x3 = (x3 * wBar3 + rWD) / wBar
    x4 = (x4 * wBar3 - rWD) / wBar
p2 = x1 + x3
q2 = 1.0 - p2
print 2.0 * p2 * q2 / 0.5

```

Gamete	Frequency				
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$A_1$	$B_1$				
<table border="0" style="margin-left: auto; margin-right: auto;"> <tr> <td style="border-top: 1px solid black; width: 100px;"></td> <td style="border-top: 1px solid black; width: 100px;"></td> </tr> <tr> <td style="text-align: center;"><math>A_1</math></td> <td style="text-align: center;"><math>B_2</math></td> </tr> </table>			$A_1$	$B_2$	$x_2$
$A_1$	$B_2$				
<table border="0" style="margin-left: auto; margin-right: auto;"> <tr> <td style="border-top: 1px solid black; width: 100px;"></td> <td style="border-top: 1px solid black; width: 100px;"></td> </tr> <tr> <td style="text-align: center;"><math>A_2</math></td> <td style="text-align: center;"><math>B_1</math></td> </tr> </table>			$A_2$	$B_1$	$x_3$
$A_2$	$B_1$				
<table border="0" style="margin-left: auto; margin-right: auto;"> <tr> <td style="border-top: 1px solid black; width: 100px;"></td> <td style="border-top: 1px solid black; width: 100px;"></td> </tr> <tr> <td style="text-align: center;"><math>A_2</math></td> <td style="text-align: center;"><math>B_2</math></td> </tr> </table>			$A_2$	$B_2$	$x_4$
$A_2$	$B_2$				