

Four Perspectives on Transitions and Evolution

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Evolution workshop, Tsfat, Israel, 9/2019

Perspective 1. Evolution of resilience

Perspective 2. Demography and genomics of
Neolithic replacement: cultural hitchhiking

Perspective 3. Unpredictable cultural change

Perspective 4. Evolution of conformity: New complexities

Evolution of Resilience ...

“Evolution of resilience in protein interactomes across the tree of life”

Marinka Zitnik, Rok Susic, Marcus W. Feldman, and Jure Leskovec.

PNAS **116**(10): 4426–4423 (March 5, 2019)

TRANSFAC database

KEGG database

CORUM database

STRING database (EMBL)

IMEx consortium database

BIOGRID database

1,840 species, 8,762,166 protein-protein interactions.

Defined on 1,450,633 proteins.

1,539 bacteria, 111 archaea, 190 eukarya.

Each species s is represented by its protein-protein interaction network (PPI).

$$\text{Network } G^{(s)} = (V^{(s)}, E^{(s)})$$

$V^{(s)}$ nodes (protein-protein coding genes)

$E^{(s)}$ edges (protein-protein interactions)

Resilience

1. How fragmented the interactions become when a fraction f of the proteins are randomly removed. f is failure rate.
2. Calculate Shannon diversity on the resulting fragmented interactome G_f by taking the k isolated components in f . $\{C_1, C_2, \dots, C_k\}$ is an interactome of size N . Compute

$$H_{msh}(G_f) = -\frac{1}{\log N} \sum_{n=1}^k p_i \log p_i,$$

where $p_i = |C_i|/N$.

3. Resilience $(G) = 1 - \int_0^1 H_{msh}(G_f) df$.

Note: *H influenzae* fragments very quickly with f . Human interactome stays together for quite high f .

Results

1. *Evolutionary Distance*. Total branch length from root to leaf taxon in a tree of life.
Larger evolutionary distance \Rightarrow more resilience.
i.e., Connectivity (biological function) not much affected by small random failures.
2. Bacteria with more resilient interactomes have significantly more regulatory genes.
3. Bacteria living in the most complex habitats have highest resilience; e.g., aerobic bacteria. Host-associated bacteria have lowest resilience. Resilience strongly associated with oxygen dependence.
4. Resilient interactomes could harbor many neutral mutations.

Demography and genomics of Neolithic replacement: cultural hitchhiking

Cultural hitchhiking and competition between patrilineal kin groups explain the post-Neolithic Y-chromosome bottleneck

Tian Chen Zeng, Alan J. Aw, and Marcus W. Feldman

Nature Communications (2018) 9:2077

doi: [10.1038/s41467-018-04375-6](https://doi.org/10.1038/s41467-018-04375-6)

Part 1. The Data

Karmin et al.; Kivisild (2018) *Genome Research*
456 samples; 35,700 SNPs

Batini et al.; Jobling (2015) *Nature Communications*
334 meles; 3.7 Mb of MSY DNA

Poznik et al.; Bustamante (2016) *Nature Genetics*
1244 worldwide sequenced 4.3 ×.

Kivisild (2017) *Human Genetics*
(review and synthesis of all studies)

Part 2. Some models

THE BOTTLENECK

Karmin et al (2015)

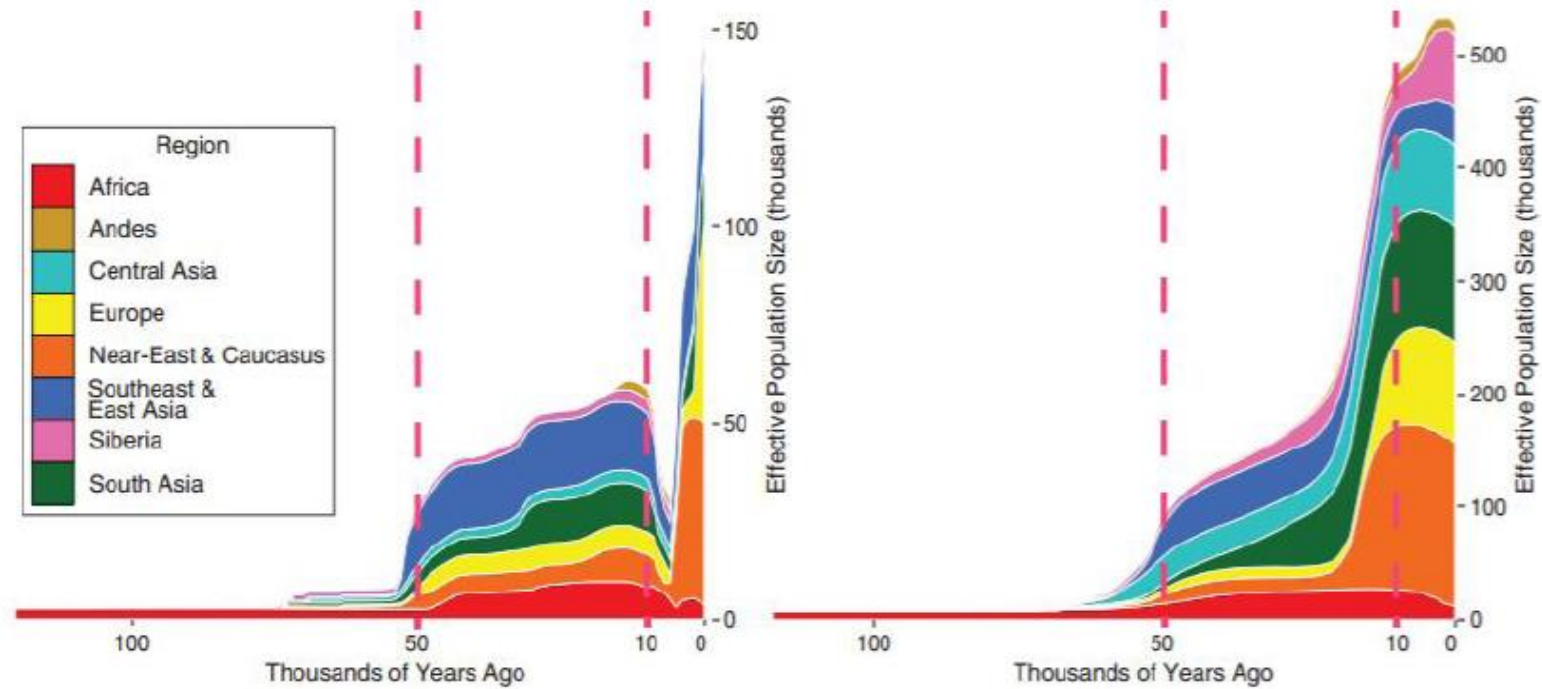


Figure 2. Cumulative Bayesian skyline plots of Y chromosome and mtDNA diversity by world regions. The red dashed lines highlight the horizons of 10 kya and 50 kya. Individual plots for each region are presented in Supplemental Figure S4A.

THE BOTTLENECK

Karmin et al (2015)

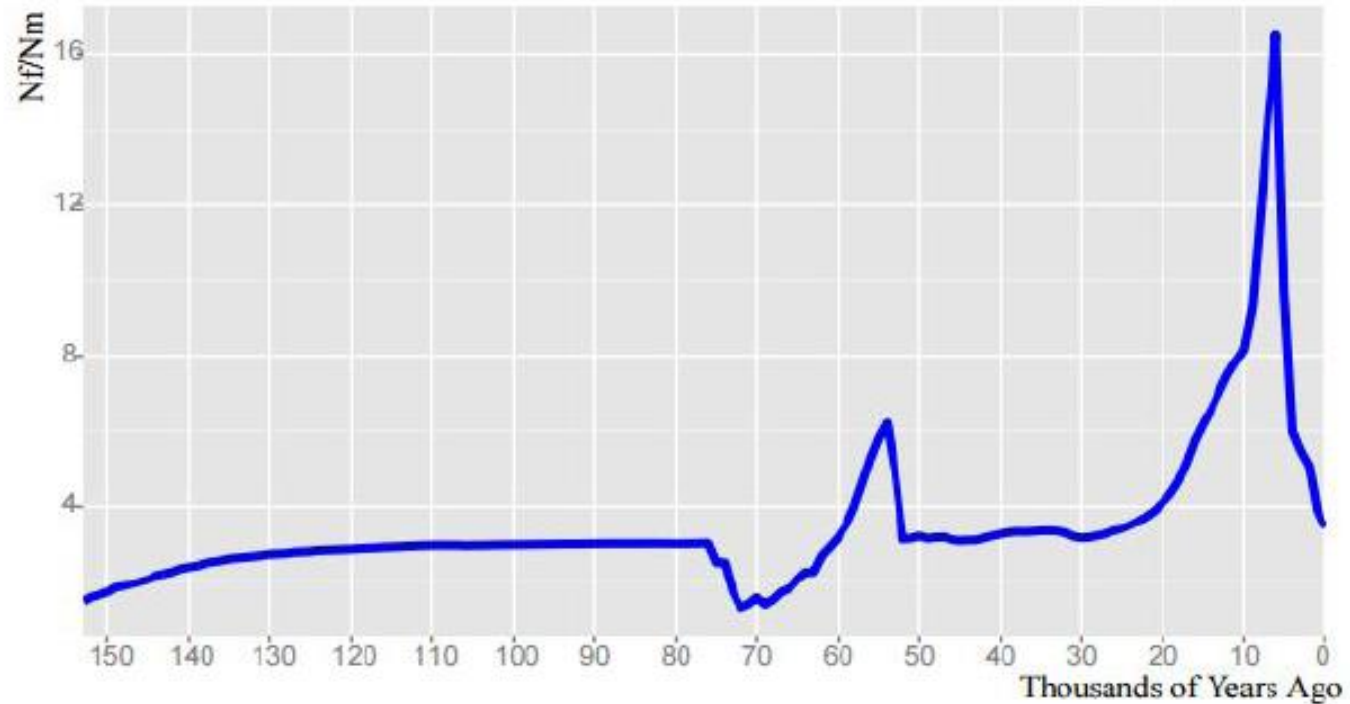


Figure S5 – The temporal dynamics of the **ratio of female (N_f) and male (N_m) effective population size in the last 140KY.** The ratios of the global accumulative N_e estimates of mtDNA (N_f) and Y chromosome (N_m), as presented in Figure 2, are plotted against the time (in thousands of years) back from the present (0). The BSPs estimates of N_e were obtained in BEAST using a piecewise-linear coalescence model.

OUR HYPOTHESIS

Intense intergroup
competition between
patrilineal descent
groups/'fraternal kin
groups'

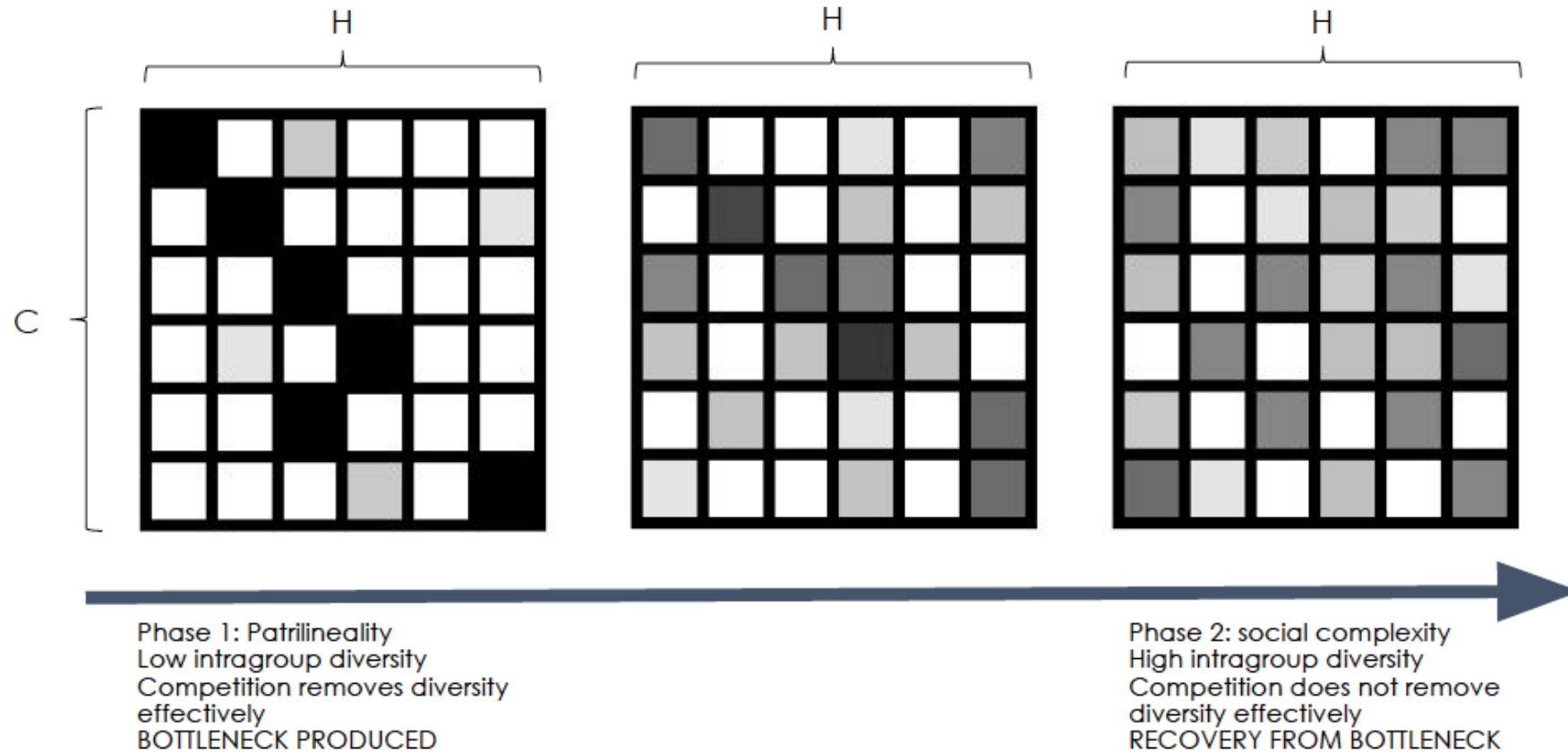
SUPPORTING EVIDENCE

Heyer et al 2006

Pastoral and farmer populations, who have coexisted in Central Asia since the fourth millennium B.C., present not only different lifestyles and means of subsistence but also various types of social organization. Pastoral populations are organized into so-called descent groups (tribes, clans, and lineages) and practice exogamous marriages (a man chooses a bride in a different lineage or clan). In Central Asia, these descent groups are patrilineal: the children are systematically affiliated with the descent groups of the father. By contrast, farmer populations are organized into families (extended or nuclear) and often establish endogamous marriages with cousins. This study aims at better understanding the impact of these differences in lifestyle and social organization on the shaping of genetic diversity. **We show that pastoral populations exhibit a substantial loss of Y-chromosome diversity in comparison to farmers but that no such a difference is observed at the mitochondrial-DNA level. Our analyses indicate that the dynamics of patrilineal descent groups, which implies different male and female sociodemographic histories, is responsible for these sexually asymmetric genetic patterns.** This molecular signature of the pastoral social organization disappears over a few centuries only after conversion to an agricultural way of life.

OUR HYPOTHESIS

Intense intergroup competition between patrilineal descent groups/'fraternal kin groups'



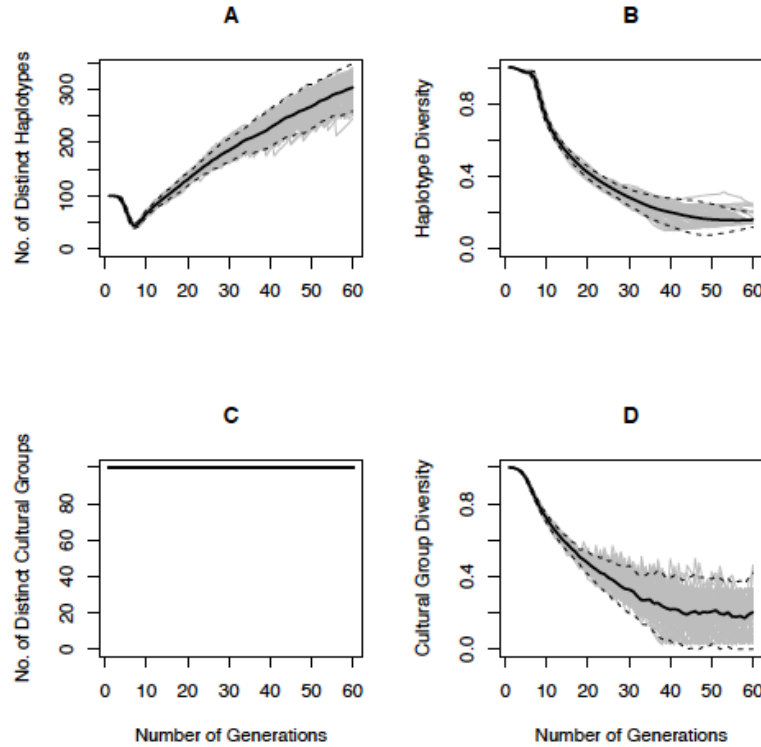
Computational Grid Model

1. Have large population (size = N^{total}) males partitioned into a grid of $|C|$ cultural groups and $|H|$ distinct haplogroups
2. Over T generations,
 - ☞ competition between cultural groups (probabilistic)
 - ☞ mutation of haplogroups (deterministic)
 - ☞ but N^{total} is kept fixed (deterministic)
3. During competition, individuals from each cultural group-haplogroup pair (c, h) (where $c \in C, h \in H$) are killed; number killed depends on cultural group c
 - ☞ Some cultural groups have greater survivability than others
 - ☞ Linear ordering of survivability
4. During mutation, within each c , a proportion of individuals from major haplogroup (i.e., $h = h(c)$ such that number of individuals in (c, h) is maximized) mutate into different haplogroups, but remain in same cultural group
5. To ensure N^{total} is fixed, grid sum is always scaled back
6. Other control mechanisms include
 - ☞ Preventing cultural group sizes from ballooning
 - ☞ Preventing extremely small cultural group sizes

Simulation Details

- ▶ Perform simulations across **18** distinct parameterizations
- ▶ Each simulation consists of 100 reps; $T = 60$ generations (≈ 1.5 millenia)
- ▶ Total population size $N^{\text{total}} \in \{10^4, 2 \times 10^4, 3 \times 10^4\}$
 - ☞ grid size is always $|C| = 100$, $|H| = 500$ (think of the labels for $C = \{1, 2, \dots, 100\}$ and the labels for $H = \{1, 2, \dots, 500\}$)
- ▶ Initial configuration is either **patrilineal** or **non-patrilineal**
 - ☞ patrilineal means for all $c \in C$, the number of individuals in $(c, c) = N^{\text{total}}/|C|$
 - ☞ non-patrilineal means for all $c \in C$ and for all $h \in C$, $(c, h) = N^{\text{total}}/|C|^2$
- ▶ The number of individuals killed in each cultural group at each generation follows a Poisson distribution
 - ☞ toggle between **15%, 25% and 50% proportion of individuals killed** in the beginning
- ▶ Mutation rate is a measure of how many new haplogroups can emerge after one generation
 - ☞ assume that in a population of 1000 individuals, their offspring can give rise to 2 new haplogroups in one generation

Simulation Results (Patrilineal)

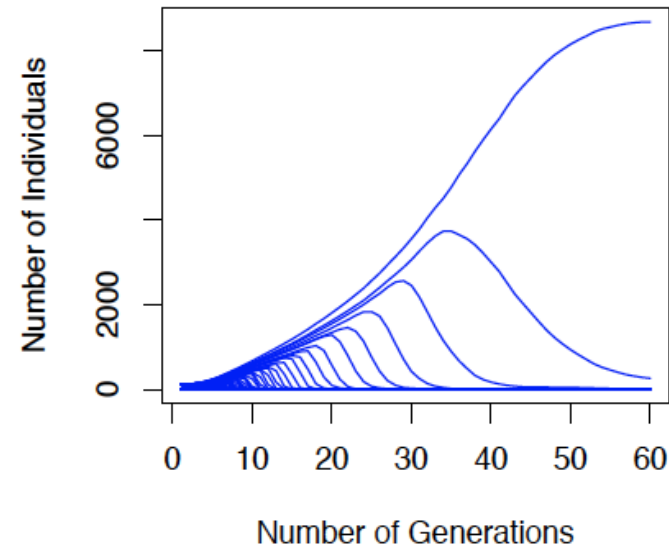


(A) Number of distinct haplotypes over time. (B) Haplotype diversity (normalized Shannon entropy) over time. (C) Number of distinct cultural groups over time. (D) Cultural group diversity over time. (\uparrow)

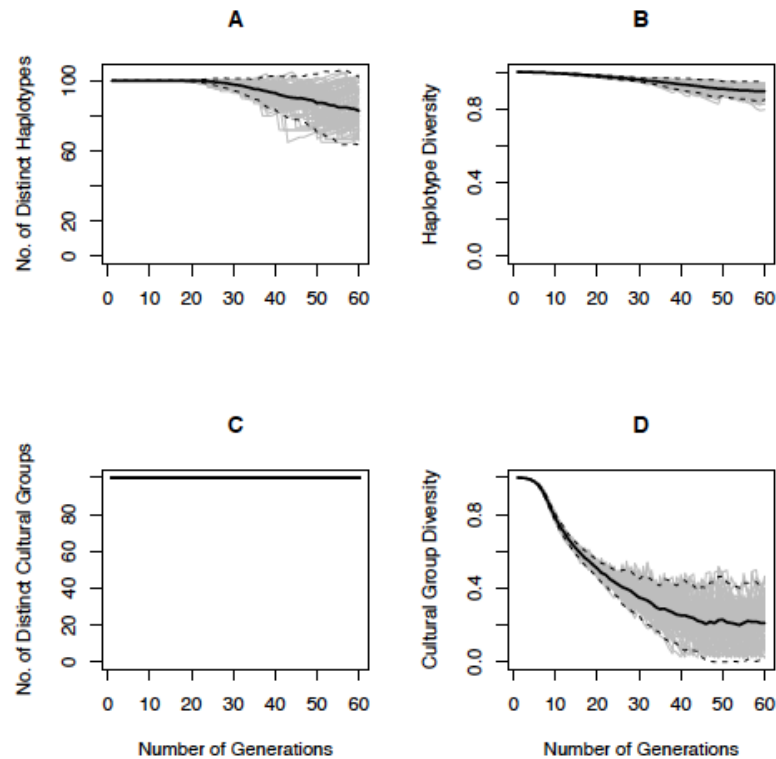
Parametrization

- ▶ $N^{\text{total}} = 10^4$
- ▶ 25% proportion of individuals killed in beginning

Numbers of individuals of each haplotype over time. (\downarrow)



Simulation Results (Non-patrilineal)

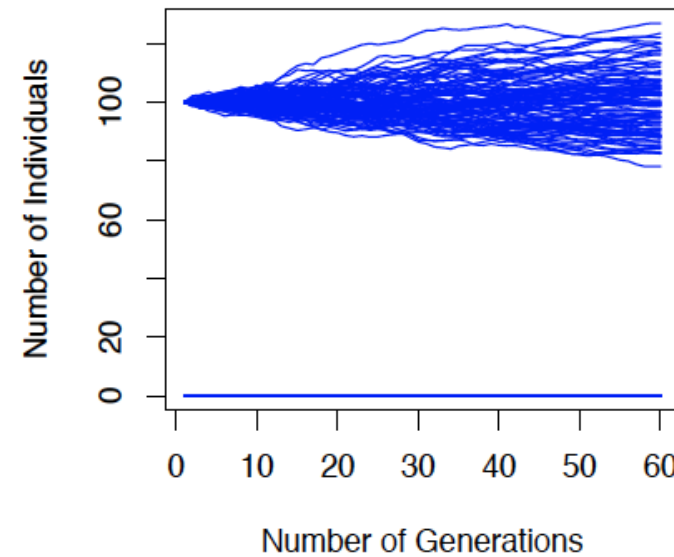


(A) Number of distinct haplotypes over time. **(B)** Haplotype diversity (normalized Shannon entropy) over time. **(C)** Number of distinct cultural groups over time. **(D)** Cultural group diversity over time. (↑)

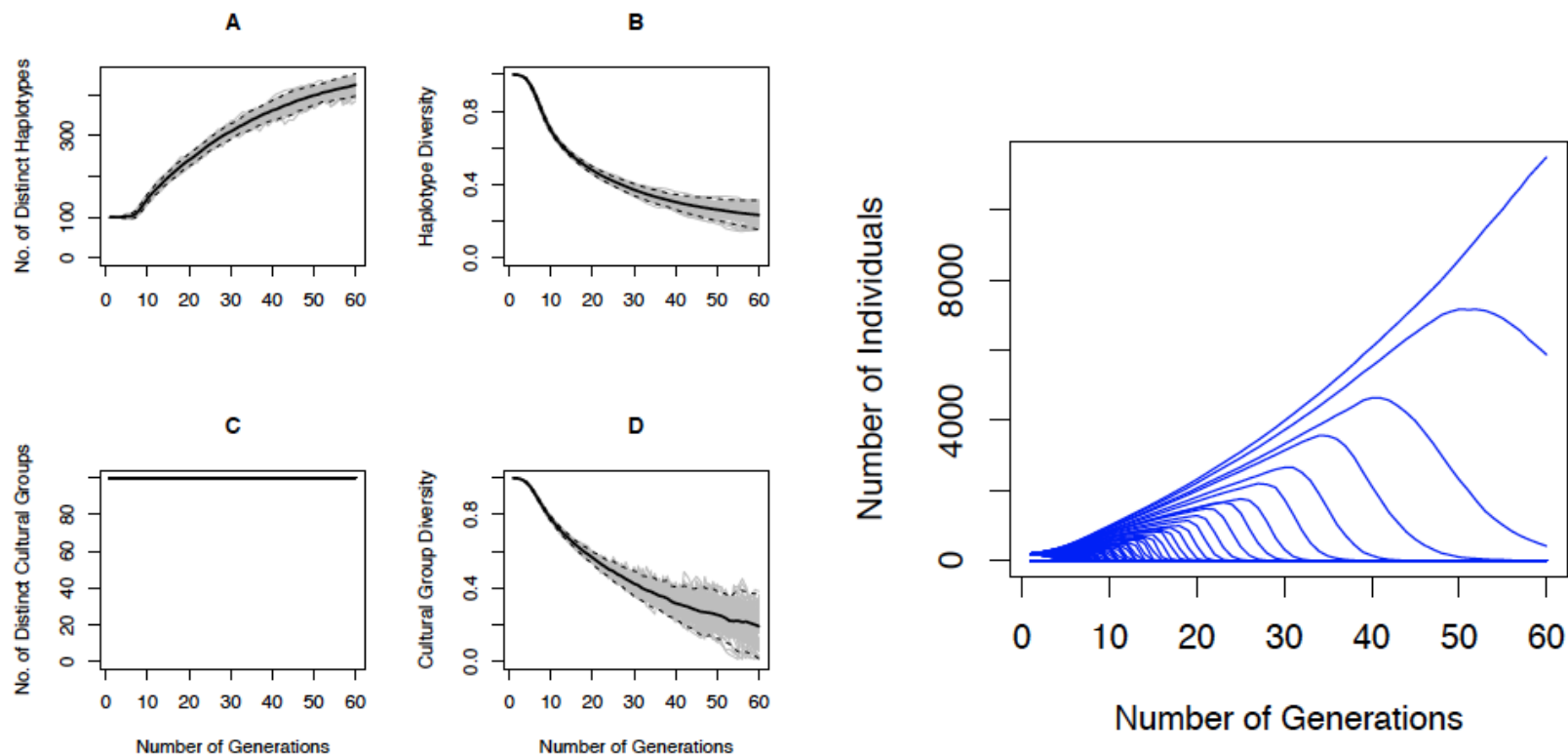
Parametrization

- ▶ $N^{\text{total}} = 10^4$
- ▶ 25% proportion of individuals killed in beginning

Numbers of individuals of each haplotype over time. (↓)

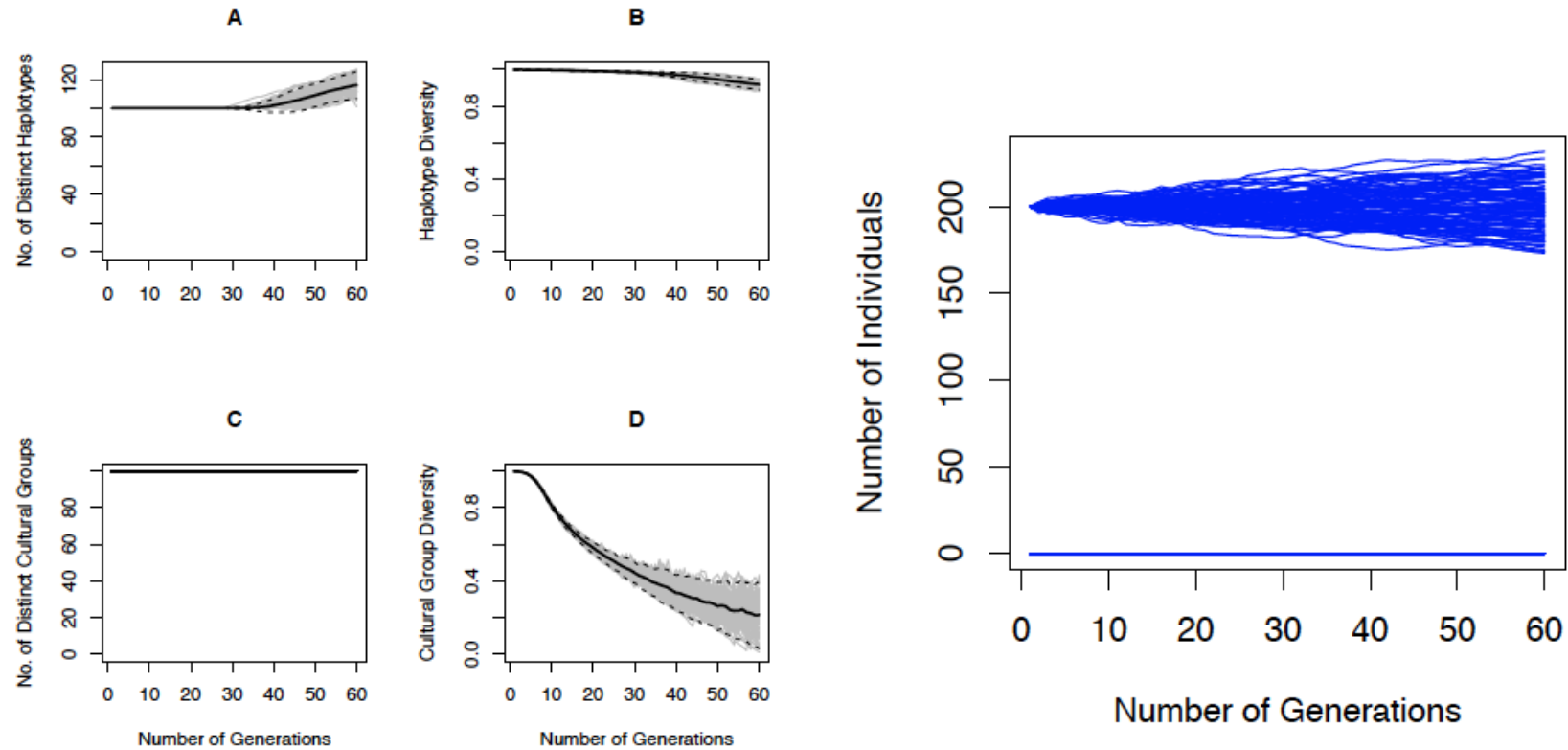


Increasing N^{total} (Patrilineal Case)



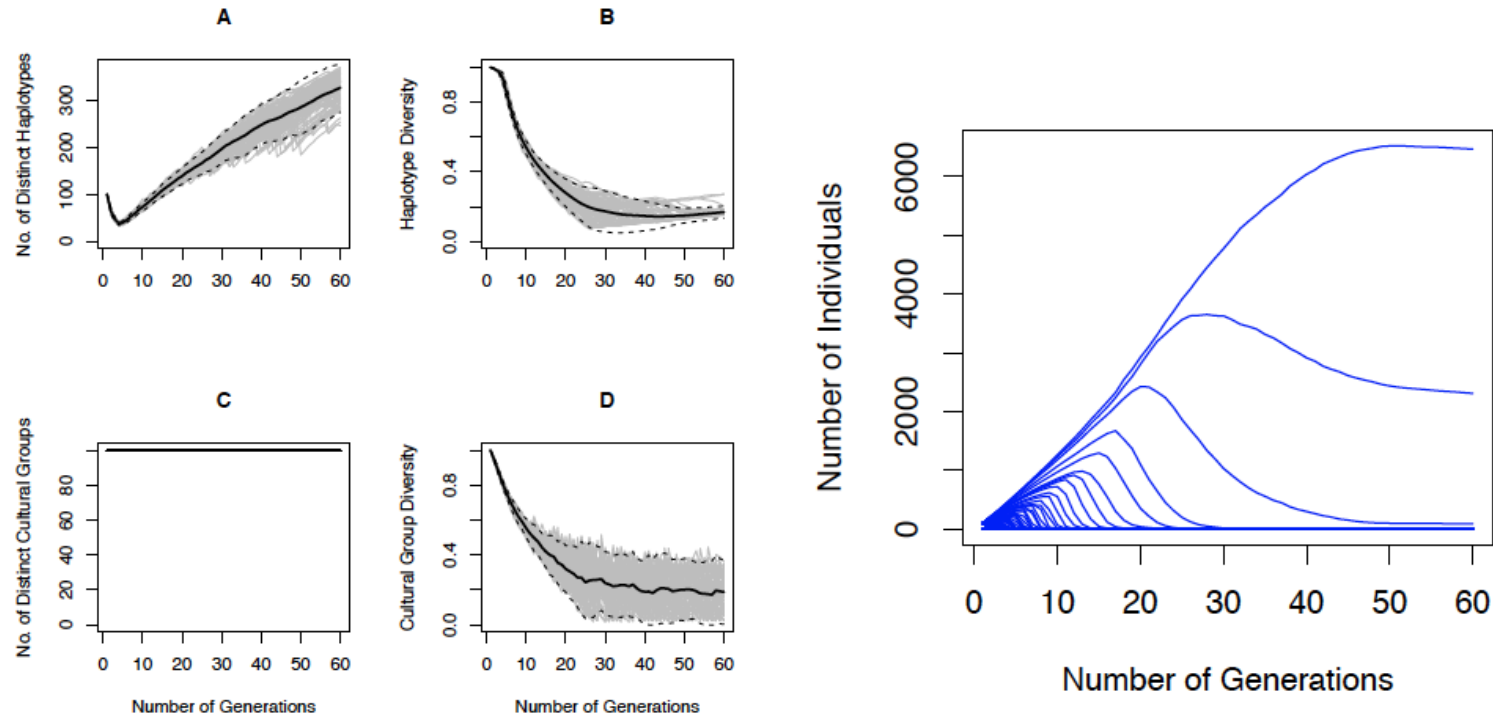
$$N^{\text{total}} = 2 \times 10^4, 25\% \text{ proportion of individuals killed}$$

Increase N^{total} (Non-patrilineal Case)



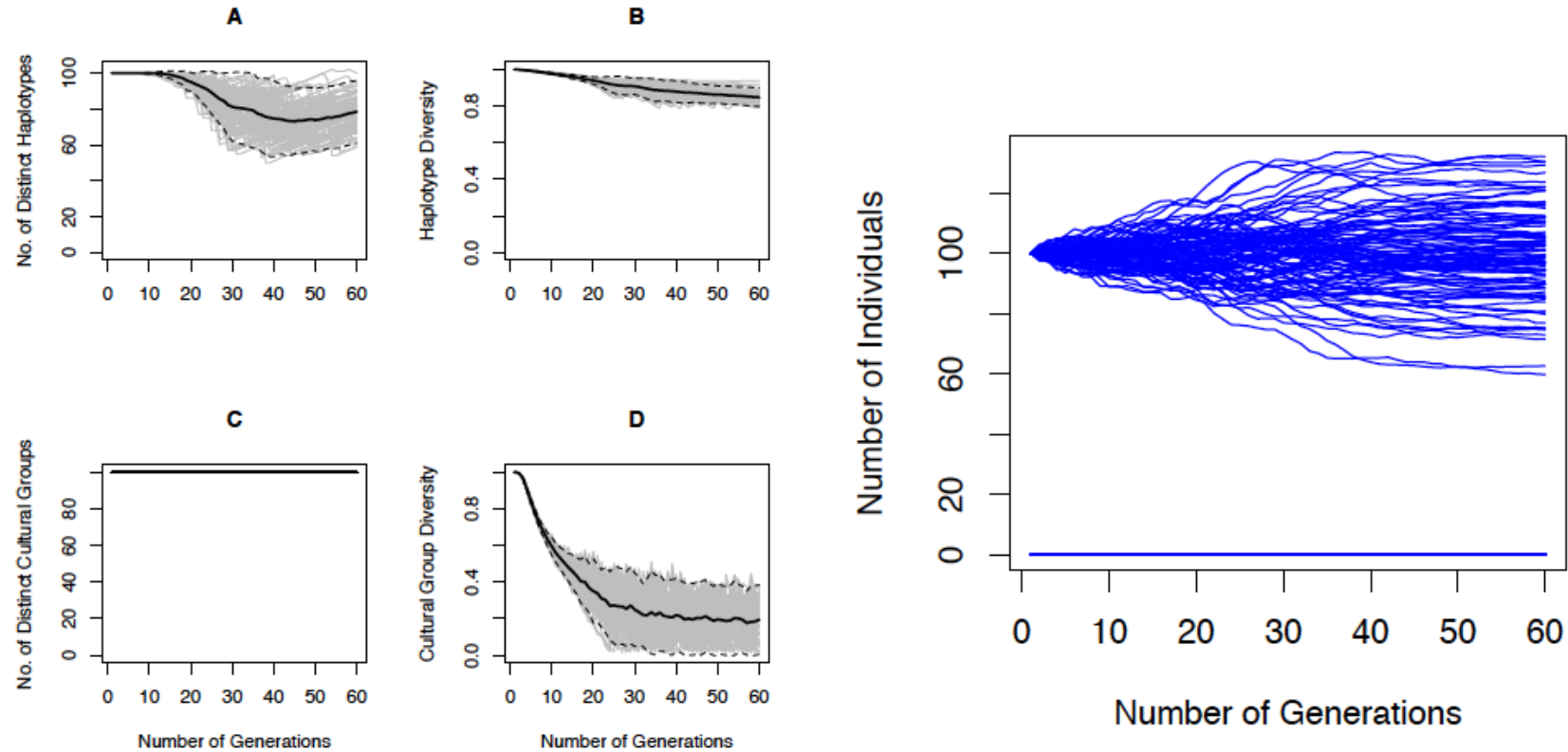
$N^{\text{total}} = 2 \times 10^4$, 25% proportion of individuals killed

Increasing Proportion of Individuals Killed (Patrilineal Case)



$$N^{\text{total}} = 10^4, 50\% \text{ proportion of individuals killed}$$

Increasing Proportion of Individuals Killed (Non-patrilineal Case)



$$N^{\text{total}} = 10^4, 50\% \text{ proportion of individuals killed}$$

Unpredictable cultural change

Cultural niche construction and cultural epistasis in Taiwan: 1895–1945

Brown, M. J., and M. W. Feldman. 2009. Sociocultural epistasis and cultural exaptation in footbinding, marriage form, and religious practices in early 20th century Taiwan. *Proc. Natl. Acad. Sci. USA*. **106**: 22139–22144.

PRE-COLONIAL ERA ETHNIC GROUPS

- Han (漢人, 華人)
 - Hoklo (福佬, 閩南)
 - Hakka (客家)
- Indigènes or Aborigines (原主民族)
 - mountain (高山族)
 - including Ami, Paiwan
 - plains (平埔族)
 - including Siraya

NOTE: Mainlanders arrived after 1945.



A Hakka couple



Empirical Problem

- Why did a change in footbinding lead to a change in religious & burial practices??



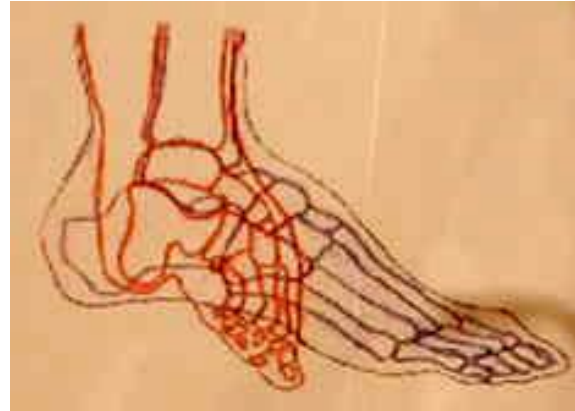
TYPES OF FOOTBINDING

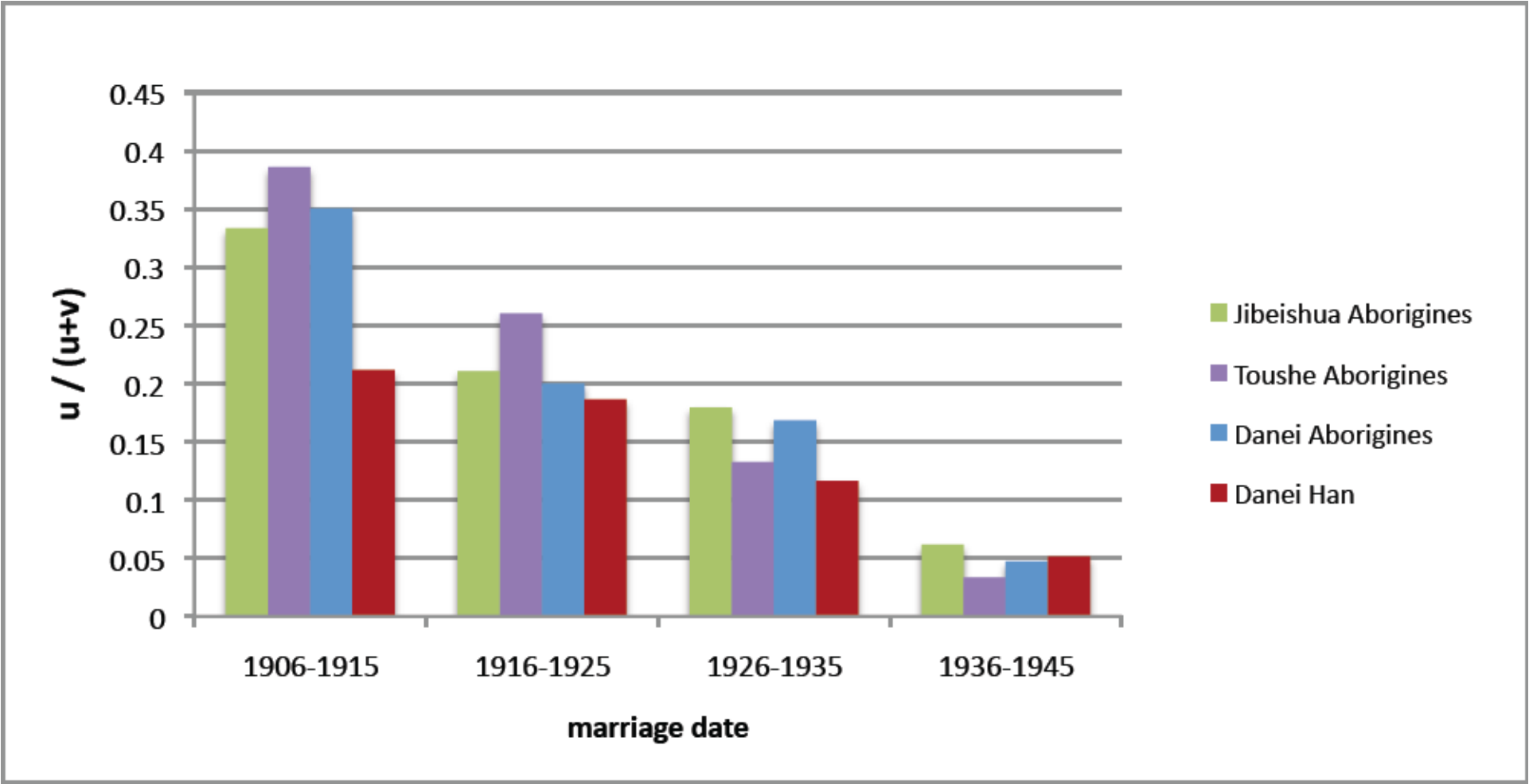
● “lotus” feet

- bind early (~ 6 years)
- extremely (3 inches)
- permanently (break arch)

● “cucumber” or “half sloping” feet

- bind late (~ 8-10 yrs)
- less radically
- not permanently





u is the number of first uxorilocal marriages among all the women from a particular village or township during a particular period of time.

v is the corresponding number of first virilocal marriages.

Religious Practices

- Spirit medium to Thai Tsoo / Ali Tsoo
 - men take over traditionally female role
 - last woman cannot find female replacement
- New worship practices
 - e.g., raised altar, use of incense, proliferation of vases, use of flag with Chinese writing



Evolution of Conformity: New complexities

Kaleda Denton, Uri Liberman, Yoav Ram, and
Marc Feldman

A social learner exhibits conformist bias when the probability that it will adopt the majority trait exceeds the frequency of that trait.

Some questions about conformity and its evolution

1. How to model conformity in terms of number of models, type of selection, population subdivision?
Special features of the dynamics.
2. How does the general pattern of social learning interact with conformist bias in cultural transmission?
3. Relationship of conformity to cooperation.
4. Evolution of conformity vs. anti-conformity.

A simple example of frequency-dependent cultural transmission

Cultural Variant of			Probability That Offspring Acquires Cultural Variant	
Model 1	Model 2	Model 3	<i>c</i>	<i>d</i>
<i>c</i>	<i>c</i>	<i>c</i>	1	0
<i>c</i>	<i>c</i>	<i>d</i>		
<i>c</i>	<i>d</i>	<i>c</i>	$2/3 + D/3$	$1/3 - D/3$
<i>d</i>	<i>c</i>	<i>c</i>		
<i>d</i>	<i>d</i>	<i>c</i>		
<i>d</i>	<i>c</i>	<i>d</i>	$1/3 - D/3$	$2/3 + D/3$
<i>c</i>	<i>d</i>	<i>d</i>		
<i>d</i>	<i>d</i>	<i>d</i>	0	1

$D > 0$ implies conformity.

With random mating the probability of forming a set of parents with i c individuals given that the frequency of c is p , $M(i|p)$, is

$$M(i|p) = \binom{3}{i} p^i (1-p)^{3-i}$$

The frequency of c after transmission, p' , is

$$p' = 1 \times M(3|p) + \left(\frac{2}{3} + \frac{D}{3}\right) M(2|p) + \left(\frac{1}{3} - \frac{D}{3}\right) M(1|p)$$

$$= p^3 + \left(\frac{2}{3} + \frac{D}{3}\right) [3p^2(1-p)] + \left(\frac{1}{3} - \frac{D}{3}\right) [3p(1-p)^2]$$

$$= p[p^2 + 2p(1-p) + (1-p)^2] + D[p^2(1-p) - p(1-p)^2]$$

$$= p + Dp(1-p)(2p-1)$$

Boyd and Richerson, 1985

Three models


$$p' = p + Dp(1 - p)(2p - 1)$$

***D* is the coefficient of conformity.**

Four models

$$p' = 1 \times M(4|p) + \left(\frac{3}{4} + \frac{D}{4}\right)M(3|p) + \frac{2}{4}M(2|p) + \left(\frac{1}{4} - \frac{D}{4}\right)M(1|p) + 0$$
$$= p + Dp(1-p)(2p-1) \quad \text{(Note: same as three models)}$$

Five models

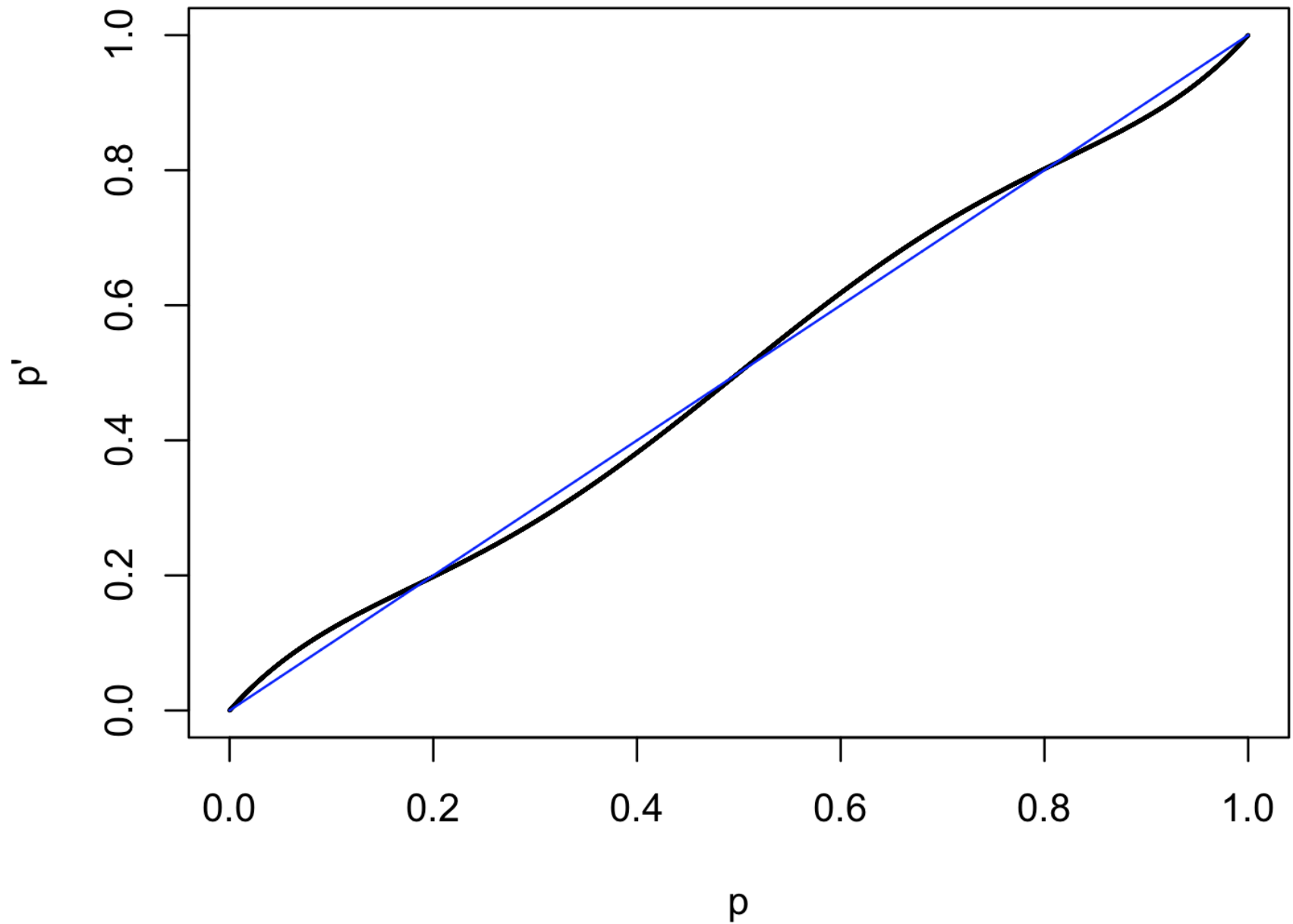
$$p' = 1 \times M(5|p) + \left(\frac{4}{5} + \frac{D(4)}{5}\right)M(4|p) + \left(\frac{3}{5} + \frac{D(3)}{5}\right)M(3|p) + \left(\frac{2}{5} - \frac{D(3)}{5}\right)M(2|p) + \left(\frac{1}{5} - \frac{D(4)}{5}\right)M(1|p) + 0$$
$$= p + p(1-p)(2p-1) [D(4)((p-1)p+1) + D(3)(-2p(p-1))]$$


(Note: two conformity parameters)

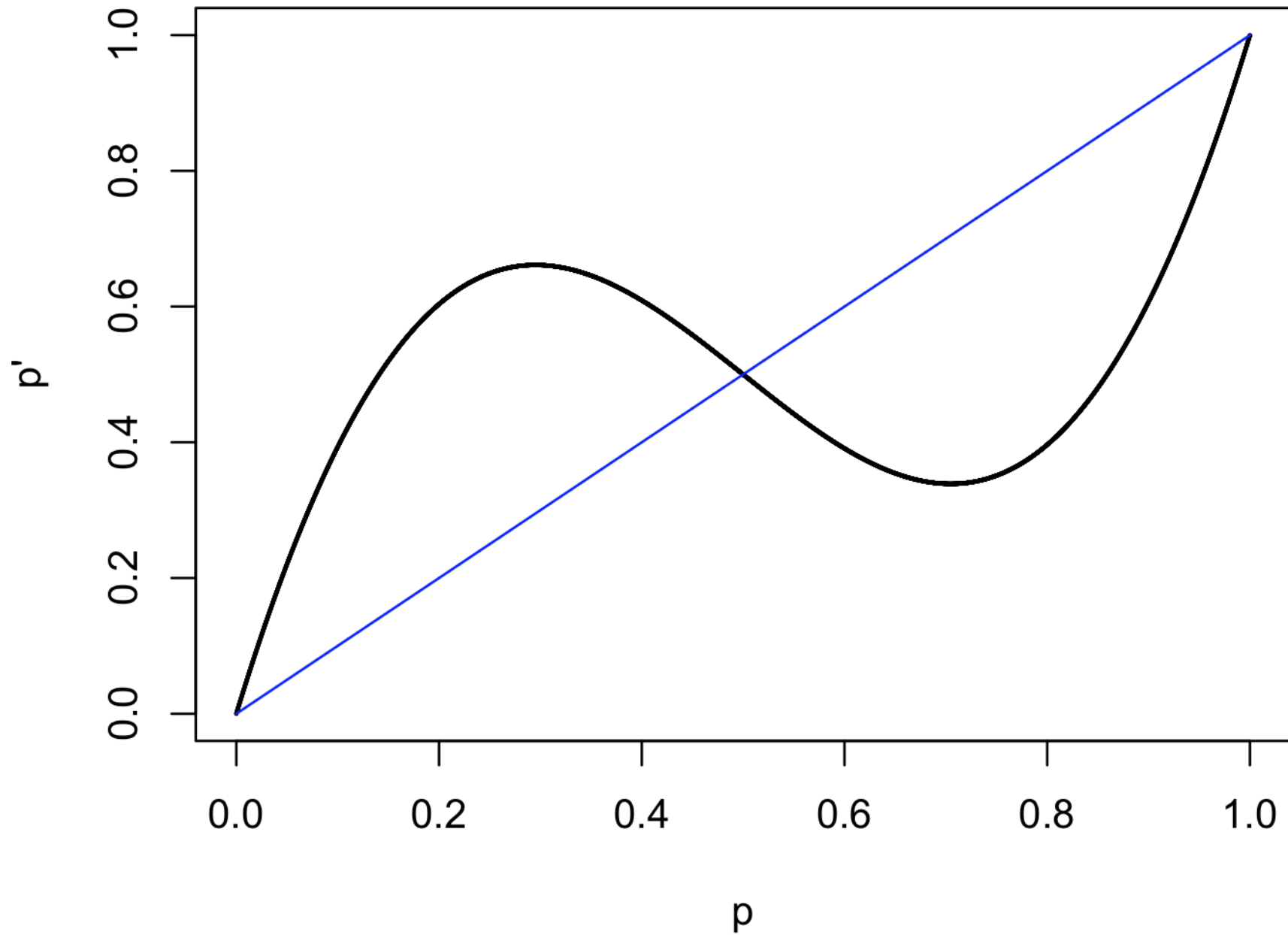
Constraints on conformity parameters

Number of models n	$D(n) = D(0) = 0; D(j) = -D(n - j)$
3	$1/3 \geq D \geq -2/3 \quad (D(2) = -D(1))$
4	$1/4 \geq D \geq -3/4 \quad (D(3) = -D(1))$
5	$1/5 \geq D(4) \geq -2/5; \quad 2 \geq D(3) \geq -3/5$
6	$1/6 \geq D(5) \geq -2/6; \quad 2 \geq D(4) \geq -4/6$
7	$1/7 \geq D(6) \geq -2/7; \quad 2 \geq D(5) \geq -5/7; \quad 3/7 \geq D(4) \geq -4/7$
etc.	

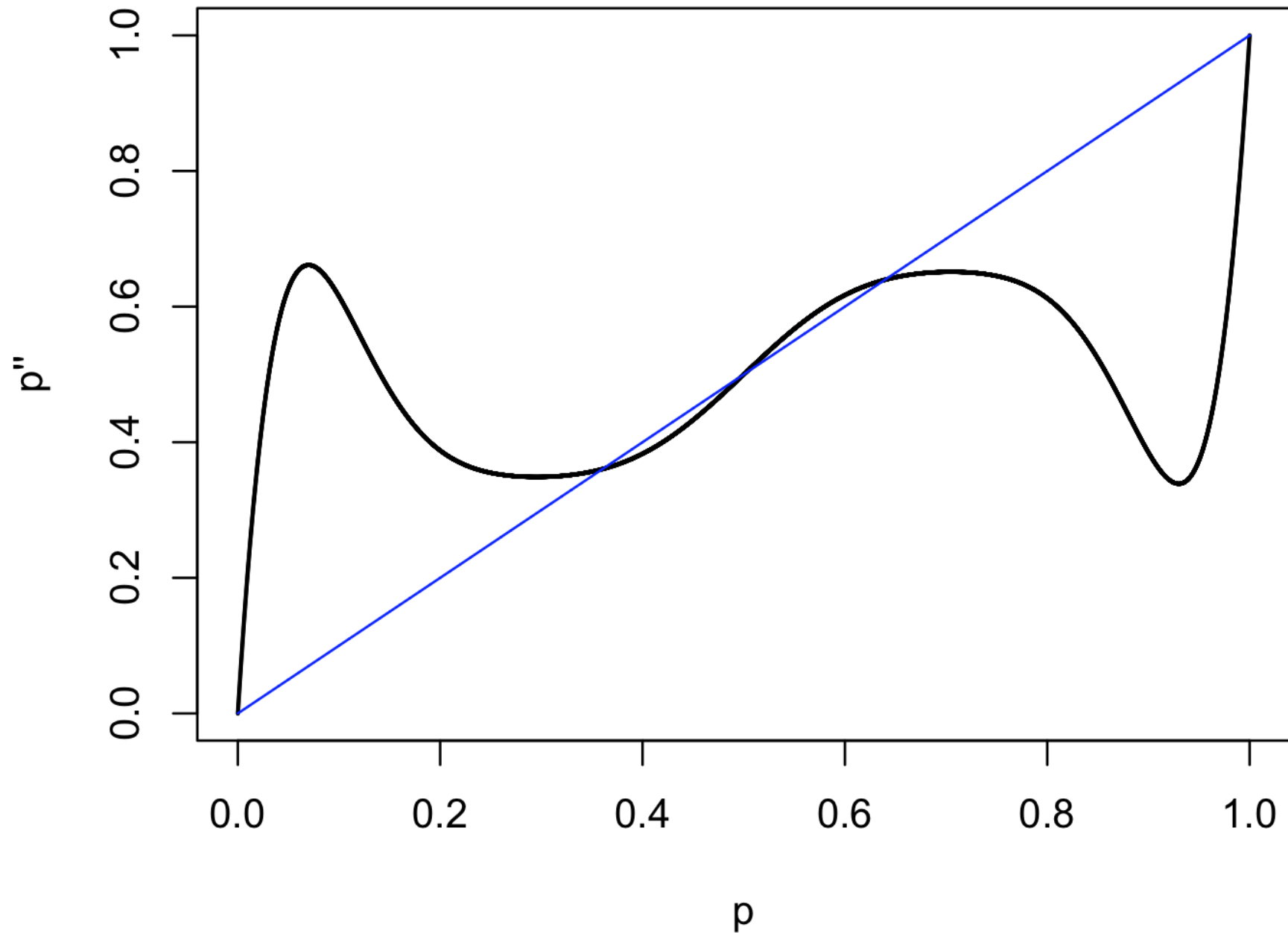
These constraints matter in understanding dynamics, and incorporating selection.



p' is plotted against p for the $n = 5$ model with $D(4) = -0.7$ and $D(3) = 1.9$.
The blue line is $p' = p$.



p' is plotted against p for the $n = 5$ model with $D(4) = -3.9$ and $D(3) = -2.9$. The blue line illustrates $p' = p$.



p'' is plotted against p for the $n = 5$ model with $D(4) = -3.9$ and $D(3) = -2.9$.
The blue line is $p'' = p$.

Results I

- i. If $D(1) = -D(n - 1) < 0$, then both $p^* = 0$ and $p^* = 1$ are locally stable (e.g., if $n = 5, D(4) > 0$).
- ii. If $-2^{n-1} < \sum_{j=k}^{n-1} D(j) \binom{n}{j} (2j - n) < 0$, then $p^* = 1/2$ is locally stable.

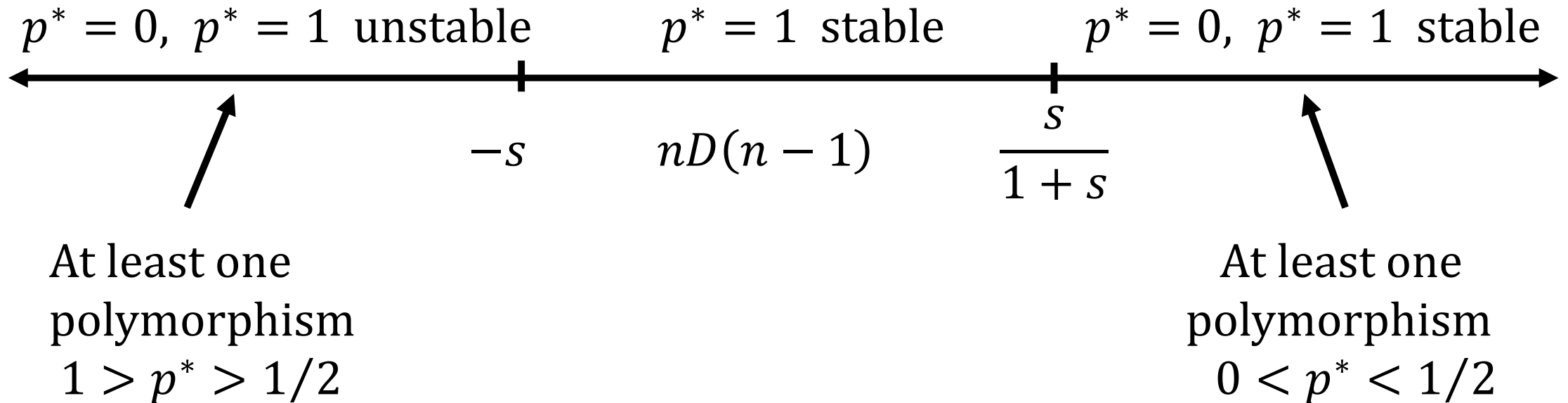
Note: constraints on $D(j)$: $-\frac{j}{n} < D(j) < 1 - \frac{j}{n}$.

Results II (*remarkable*)

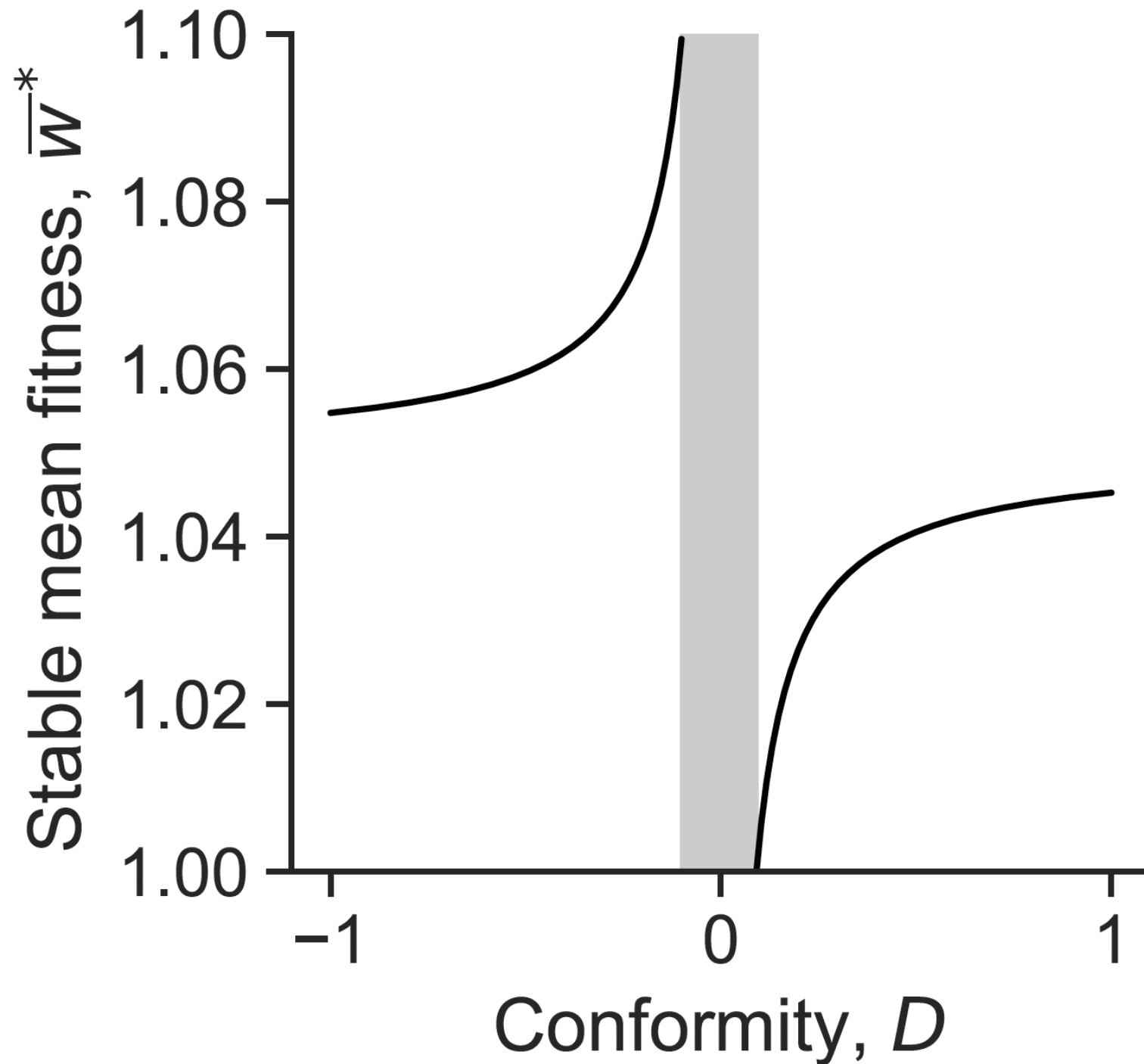
- iii. $p^* = 0$, $p^* = 1$, and $p^* = 1/2$ can all be locally unstable. No stable equilibria for $n \geq 5$.
- iv. With no stable equilibria, a two-cycle is possible.
- v. When the conformity parameters are of different signs, at least three polymorphic equilibria are possible for $n \geq 5$.

Selection: viability of $c:d$ is $1+s:1$. Then*

$$p' = \frac{(1+s)[p + F_n(p)]}{1 + s[p + F_n(p)]} \quad (1)$$



$$* F_n(p) = \sum_{j=1}^{n-1} D(j) \binom{n}{j} p^j (1-p)^{n-j}$$

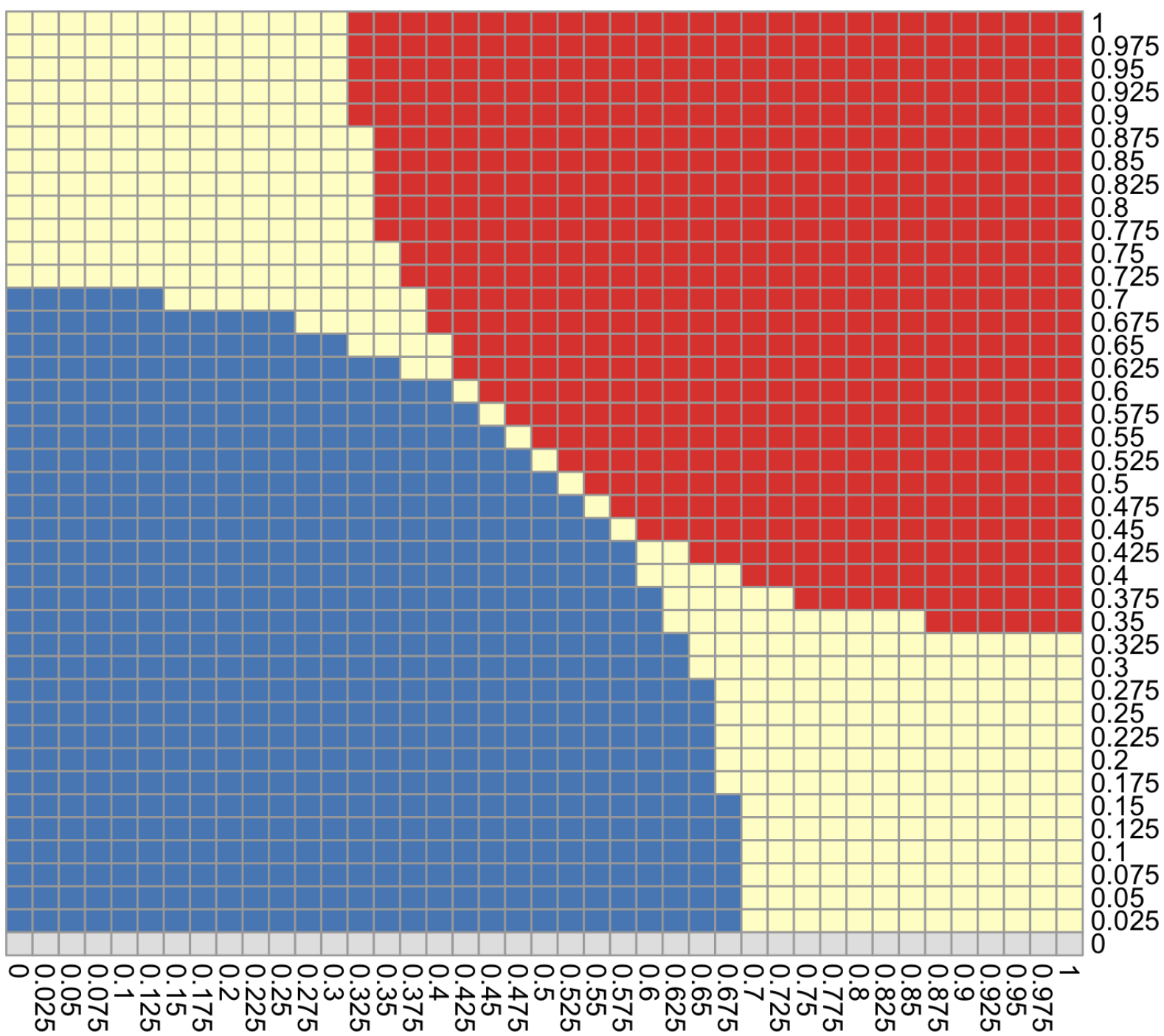


Mean fitness increases with frequency-dependent bias. The figure shows the population mean fitness \bar{w}^* (eq. 1 at the protected polymorphism x^* (the solution to eq. 1, if it exists) as a function of the frequency-dependent bias parameter D . In the shaded area $s < D < s/(1 + s)$ and x^* does not exist. Here, $s = 0.1$, $n = 3$.

Evolution of conformity. A modifier approach when fitness of $c:d$ is $1 + s:1$.

Suppose that allele M produces $D(1), D(2), \dots, D(n-1)$ and that these produce (x_1^*, x_2^*) for Mc, Md , which is stable with $x_1^* > 1/2$. Now introduce m , which produces $\tilde{D}(1), \tilde{D}(2), \dots, \tilde{D}(n-1)$. Then m invades under a rather complicated condition. But if $\tilde{D}(j) > D(j)$ for $k \leq j \leq n-1$, then m invades ($k = (n+1)/2, n$ odd; $k = n/2 + 1, n$ even).

Since the stable polymorphism must have $nD(n-1) < s$, modifier m succeeds if it reduces transmission bias against the disadvantaged type c .



Two populations with no selection and equal conformity coefficients, $D_1 = D_2 = 0.4$. Migration rate is $m = 0.05$. Starting from the two population frequencies in the red area, there is convergence to (1,1), from the blue area, to (0,0) and to the polymorphism (x^*, y^*) different from $(\frac{1}{2}, \frac{1}{2})$ from the yellow area.

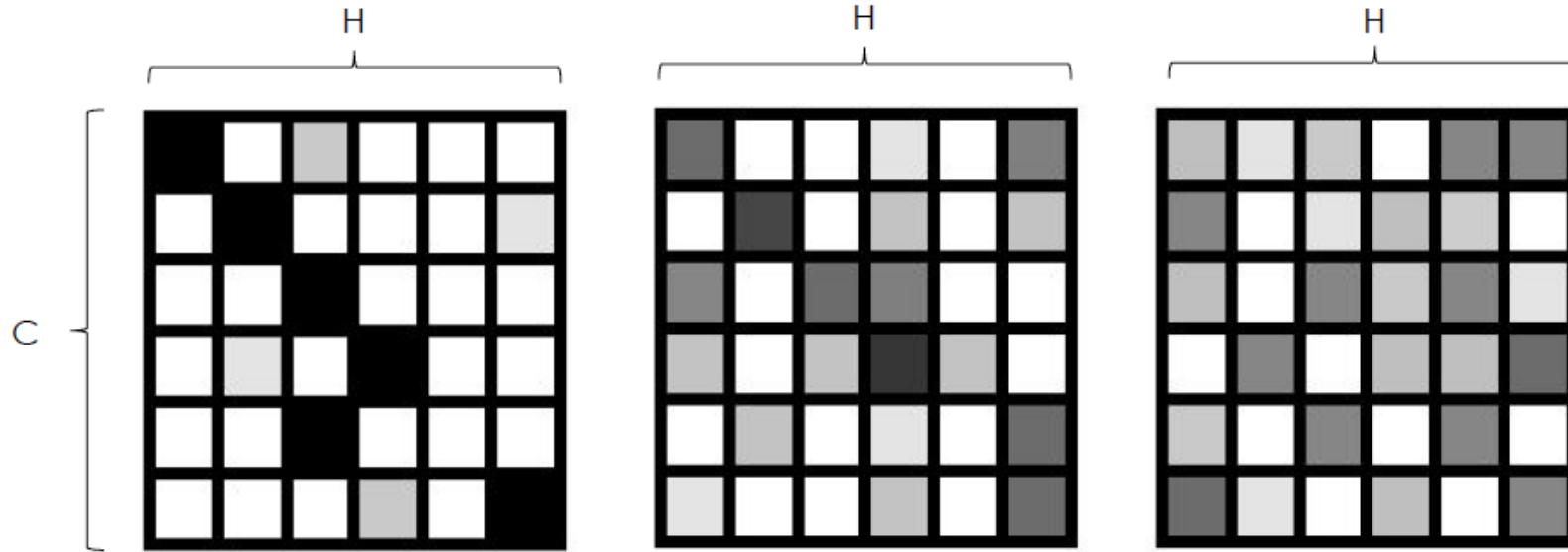
Review of: “Gods of the Upper Air” by Charles King

Written by Louis Menand, *New Yorker*, August 26, 2019

‘Other species are programmed to “know” how to cope with the world, but our biological endowment evolved to allow us to choose how to respond to our environment. We can’t rely on our instincts; we need an instruction manual. And culture is the manual.’

PATRILINEALITY VS NONPATRILINEALITY

Effects of competition on diversity in each scenario



In general

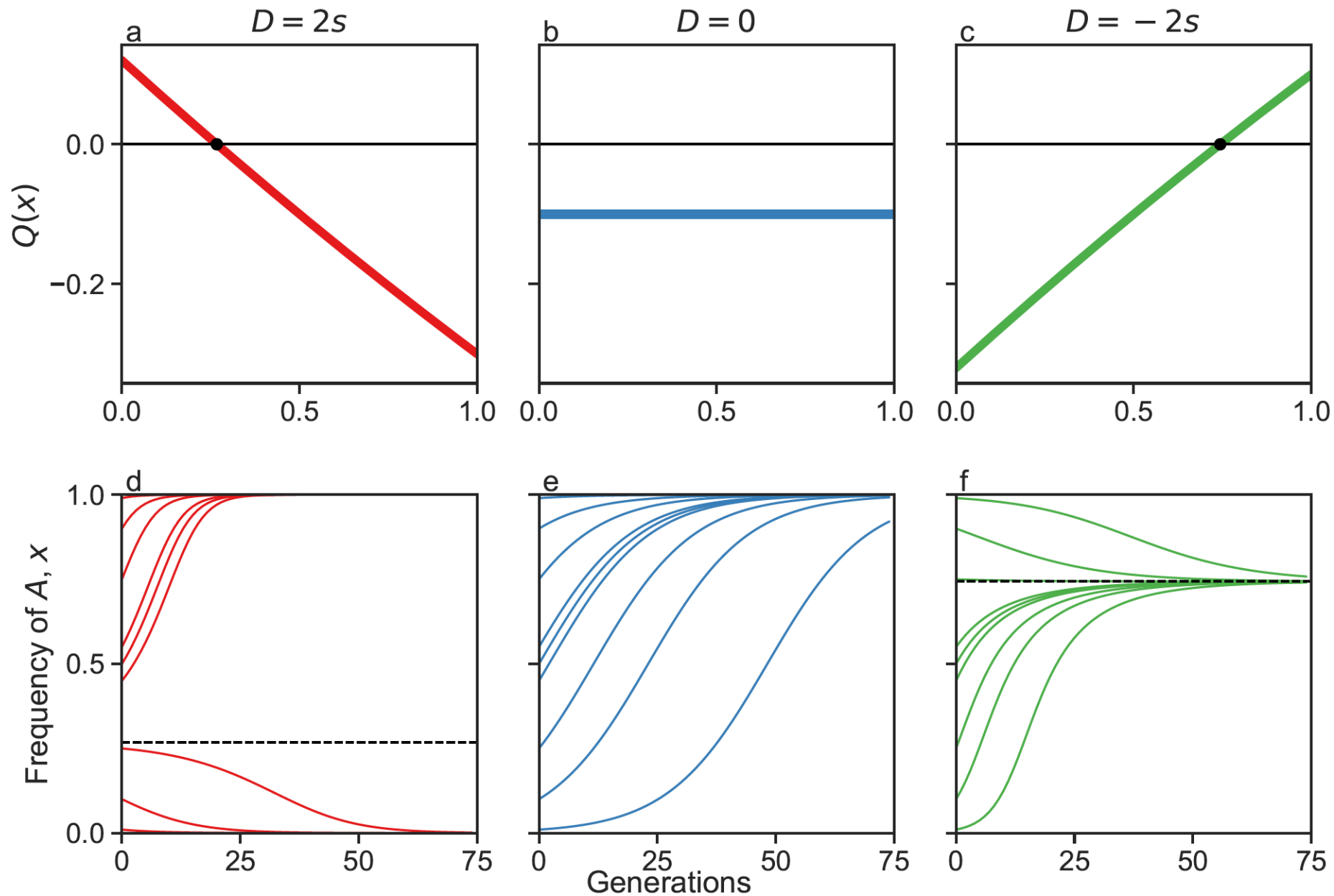
$$p' = p + \sum_{j=1}^{n-1} D(j) \binom{n}{j} p^j (1-p)^{n-j}$$

Note $D(n) = D(0) = 0$ and $D(j) = -D(n-j)$.

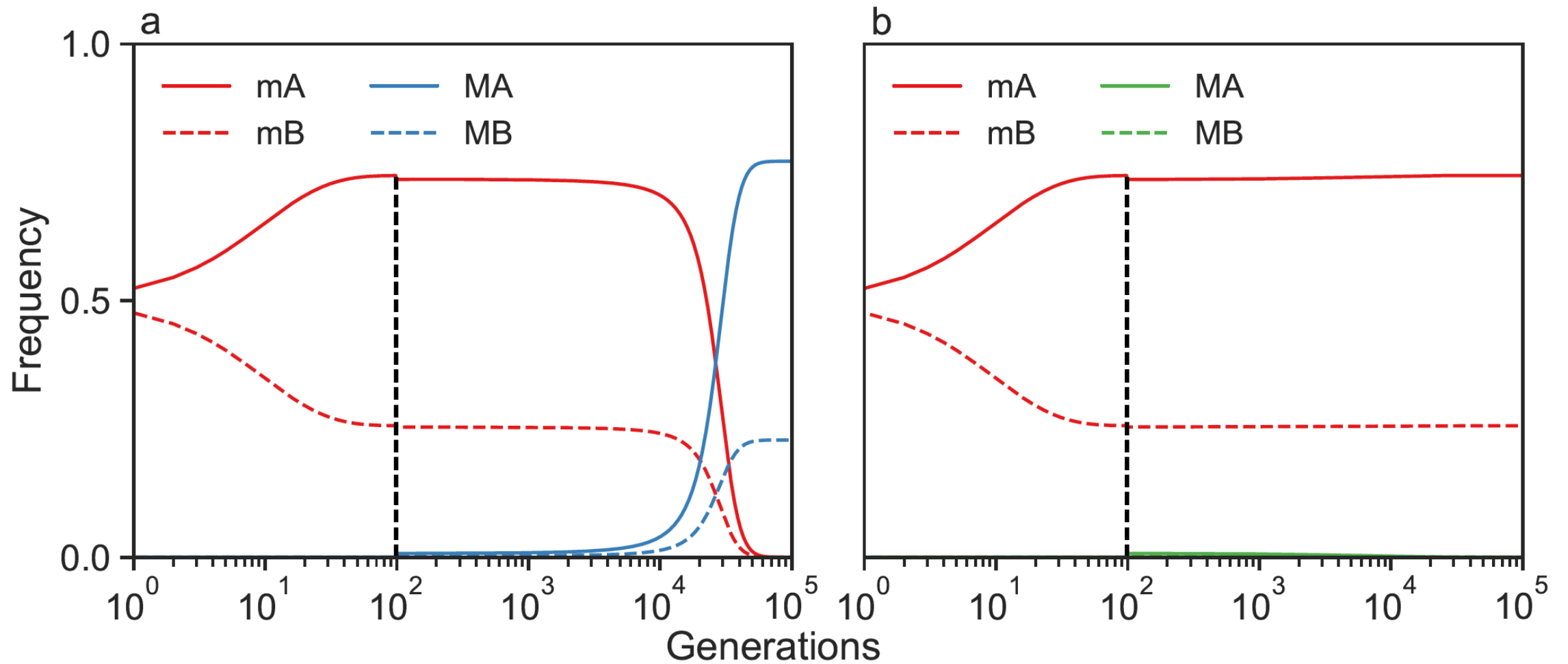
Can also write it as $p' = p + F_n(p) = p + (2p-1)G_n(p)$

$$p' = p + \sum_{j=k}^{n-1} D(j) \binom{n}{j} [p(1-p)]^{n-j} [p^{2j-n} - (1-p)^{2j-n}],$$

where $k = \frac{n}{2} + 1$ if n is even, $\frac{n+1}{2}$ if n is odd. Also, if $z = p(1-p)$, then $G(0) = 0$.



Frequency-dependent bias. The top row shows the shape of $Q(x)$ = in eq. ?? For three values of D , the frequency-dependent bias parameter (eq. ??): (a) conformity bias with $D = -2s$, which gives $x^* < \frac{1}{2}$, (b) unbiased transmission with $D = 0$, (c) non-conformity bias with $D = -2s$, which gives $x^* > \frac{1}{2}$. The circles mark the value of polymorphic equilibrium x^* (which solves $Q(x) = 0$), if it exists. Here phenotype A has a selective advantage of $s = 0.1$.



Reduction principle for negatively biased transmission. The frequencies of phenotypes A (solid lines) and B (dashed lines) over time during invasions by modifier allele M of a population of m alleles. The resident modifier allele m (red lines) produces bias parameter $D = -2s = -0.2$, while the invading modifier allele M (blue lines) produces $\tilde{D} = 0.9D > D$ in panel (a), and $\tilde{D} = 1.1D < D$ (green lines, barely seen) in panel (b). Modifier allele M that increases the bias parameter D to be less negative invades (panel (a)), while if it decreases D to make it more negative, it does not invade (panel (b)). Invasions start at generation 10 (shown by vertical dashed lines. Here, $w_A = 1 + s = 1.1$, $w_{B_2} = 1$, and the frequency of M is initially 0.01.

Culture

A pattern of (human) behavior and its products embodied in thought, speech, action, and artifacts, and dependent upon (humans') an organism's capacity for learning and transmitting knowledge to others, including succeeding generations.