A Retrospective Analysis of Selection in the University of Nebraska – Lincoln Replicated Recurrent Selection (UNL-RRS) Program

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Introduction

- Hybrid maize breeding has been highly successful in terms of genetic gain for yield and creation of a well-defined heterotic pattern to maximize heterosis

- Selection for hybrid performance holds potential to increase population stratification, especially at loci exhibiting overdominance or pseudo-overdominance

- Previously it has not been possible to separate the effects of genetic drift from selection on population stratification
  - The UNL-RRS program offers a unique opportunity to study the effects of inter-population and intra-population selection on population stratification

- Findings could illuminate the population genetics of heterotic pattern formation and ultimately point toward genomic regions specifically influenced by inter-population selection

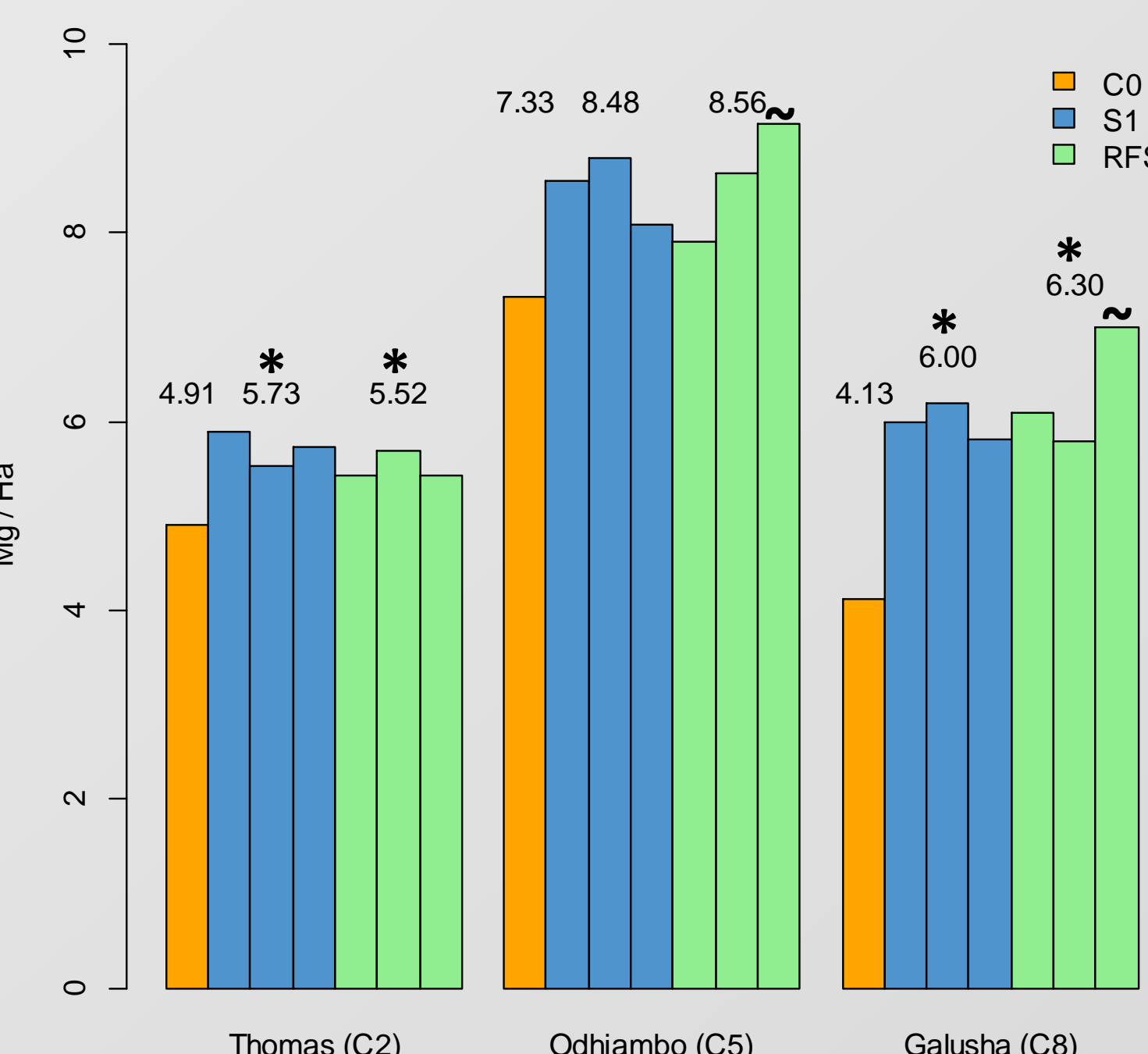- Figure 1 summarizes genetic gain made in the UNL-RRS program

Figure 1. Direct response of the population cross for index in the UNL-RRS program. Numbers above bars indicate the mean of cycle zero, S1 selection, or RFS selection.

Asterisks indicate if selection method was significantly different from cycle zero.

Tilda indicates if a replicate pair among breeding method was significantly different
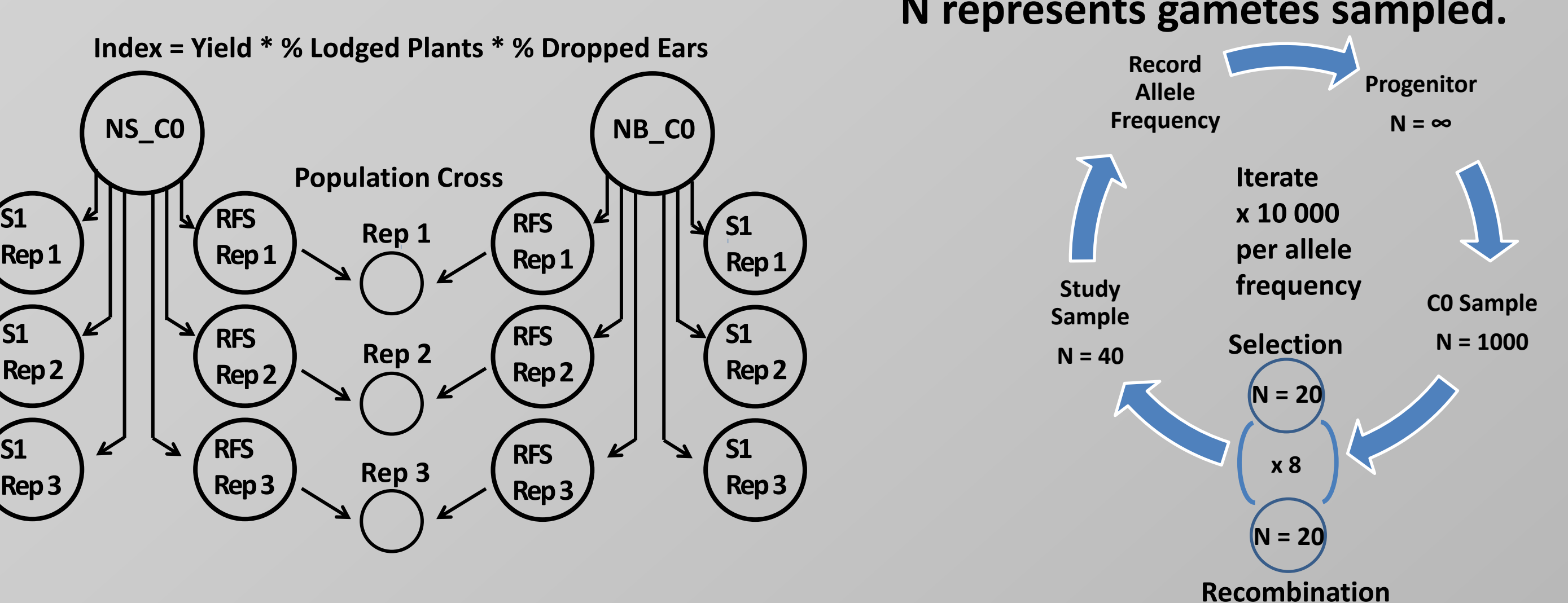
Objectives

1. Dissect changes in genetic diversity and population stratification due to intra-population improvement and inter-population recurrent selection

2. Identify genomic regions influenced by selection across multiple replicate populations

Materials and Methods

- Figure 2 illustrates the UNL-RRS system and populations
  - Nebraska B Synthetic (NB) and Nebraska Stiff Stalk Synthetic (NSS) cycle zero populations
  - 12 replicate populations from cycle 8

- Twenty individuals from each of two base populations and 12 cycle 8 populations were genotyped with Pioneer Hi-Bred public 768 Illumina GoldenGate Assay
  - MAF > 0.1 resulted in 524 SNPs for analysis

- Observed heterozygosity: $H_O = \left(\frac{1}{m}\right)\sum_{i=j}^{m} H_l$ where $\widehat{H_l} = \sum_{i=1}^{n}\frac{n_{lij}}{n}$, l is the number of loci, n is number of individuals, n_{lij} is observed heterozygote count for the lth locus for alleles i and j

- Expected heterozygosity: $\bar{D} = \sum_{l=1}^{m}\frac{D_l}{m}$ where $D_l = \frac{2n(1-\sum x_i^2)}{2n-1}$, n is number of individuals, m is number of loci, and x is frequency of the ith allele

- Effective population size: $\widehat{N_e} = \frac{1}{2*\left(1-\sqrt[t]{P}\right)}$ where t is time, and P is the panmictic index

- Modified Roger's Distance: $MRD = \frac{1}{\sqrt{2m}}\sqrt{\sum_{l=1}^{m}\sum_{j=1}^{n_j}\left(p_{ij}-q_{ij}\right)^2}$

- Figure 3 describes the workflow for the simulation developed for objective 2

Figure 2. UNL-RRS population structure.

Figure 3. Drift simulation diagram. N represents gametes sampled.
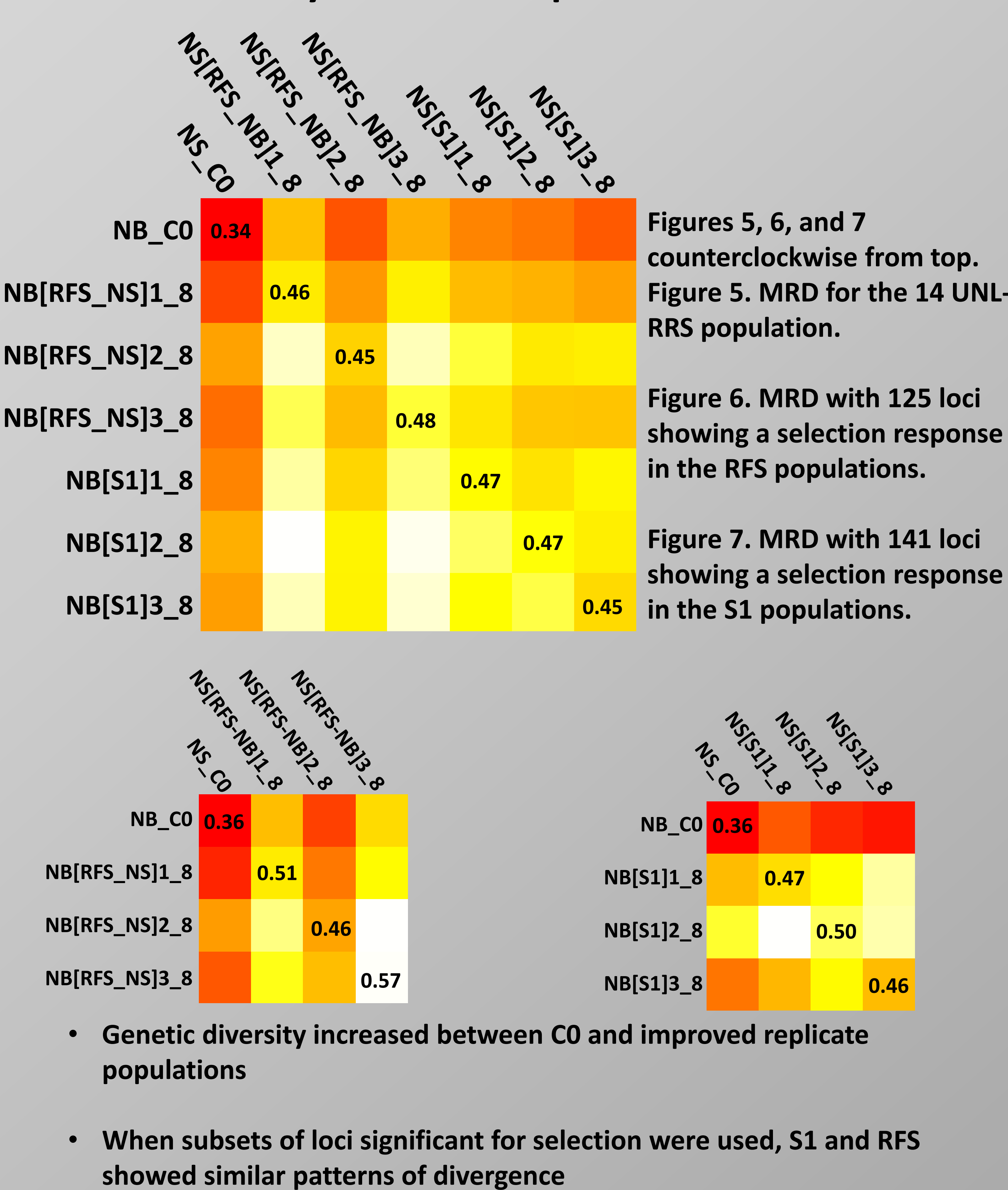

Genetic Diversity Within Populations

Table 1. Observed heterozygosity, expected heterozygosity, number of polymorphic markers (PM), and effective population size.

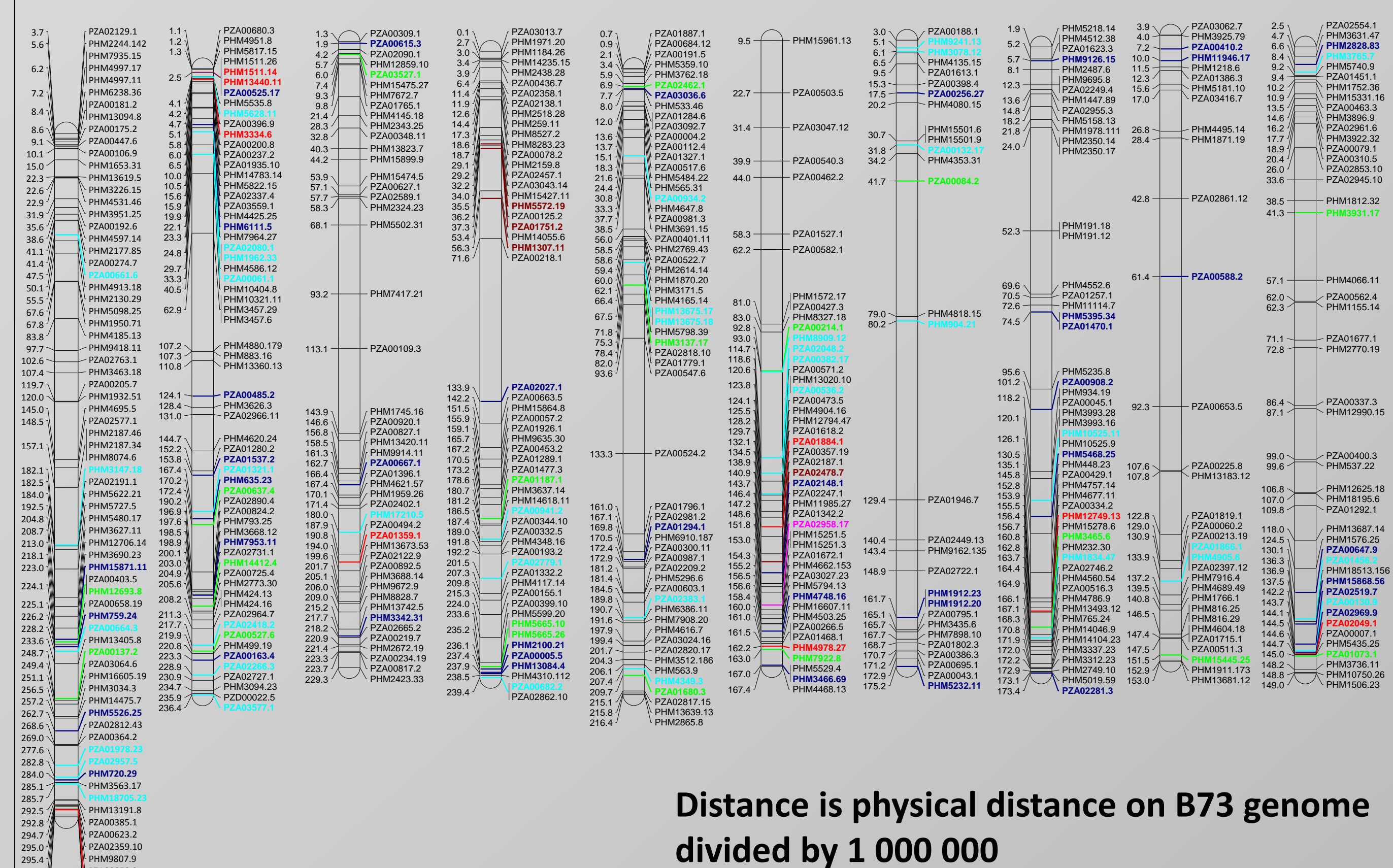| Population	H_O	D	PM	N_e
NB_C0	0.247	0.253	401	--
NB[RFS_NS]1_8	0.179	0.205	280	13
NB[RFS_NS]2_8	0.152	0.159	246	8
NB[RFS_NS]3_8	0.173	0.182	284	11
NB[S1]1_8	0.175	0.176	267	12
NB[S1]2_8	0.137	0.146	242	7
NB[S1]3_8	0.138	0.142	230	7
NS_C0	0.281	0.284	449	--
NS[RFS_NB]1_8	0.192	0.197	293	11
NS[RFS_NB]2_8	0.201	0.208	319	12
NS[RFS_NB]3_8	0.192	0.188	278	11
NS[S1]1_8	0.204	0.202	303	13
NS[S1]2_8	0.177	0.201	279	9
NS[S1]3_8	0.181	0.190	299	9

- After eight cycles of S1 and RFS selection, genetic diversity decreased within populations

- Replicate populations diverged to varying degrees within a breeding method

- Observed and expected heterozygosities agree well suggesting that inbreeding at cycle 8 is consistent with expectations under Hardy-Weinberg equilibrium and the effective population size

Genetic Diversity Between Populations

Figures 5, 6, and 7 counterclockwise from top.
Figure 5. MRD for the 14 UNL-RRS population.

Figure 6. MRD with 125 loci showing a selection response in the RFS populations.

Figure 7. MRD with 141 loci showing a selection response in the S1 populations.
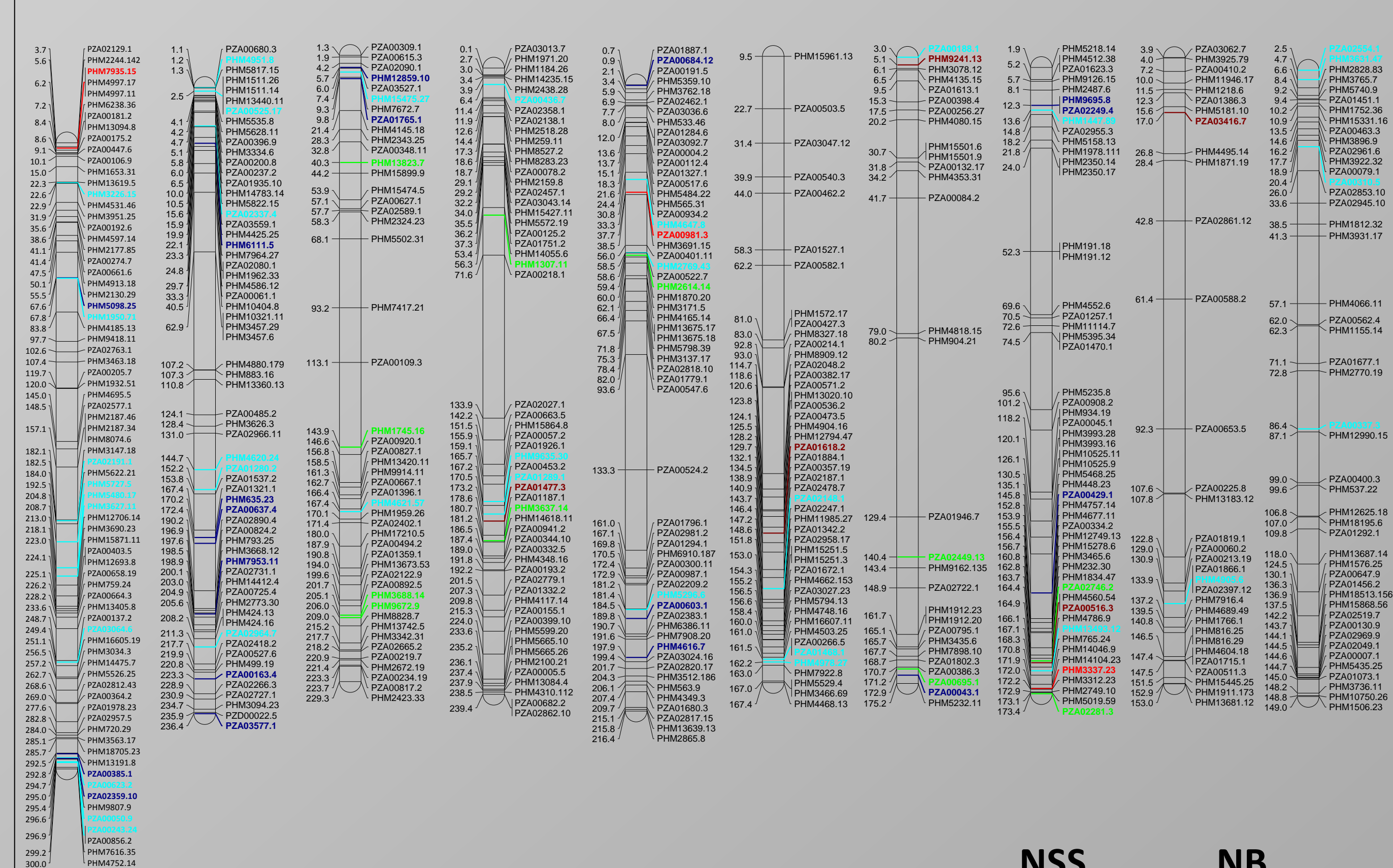

- Genetic diversity increased between C0 and improved replicate populations

- When subsets of loci significant for selection were used, S1 and RFS showed similar patterns of divergence
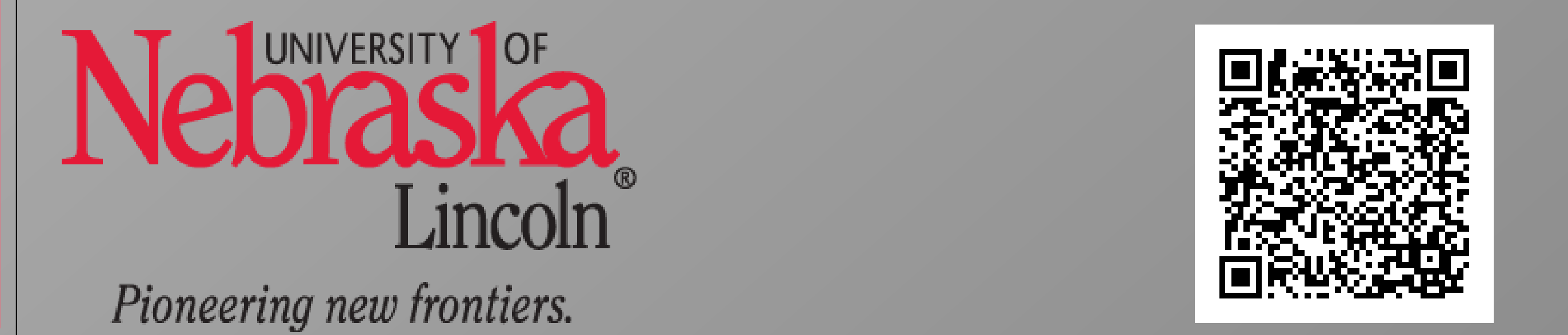
1. Inter-population selection did not stratify populations to a greater degree than intra-population improvement, suggesting genetic drift is the dominant force in shaping genetic variation in the UNL-RRS program.

2. Specific genomic regions, particularly in the telomeric regions, contain loci significant across replicates. Further study will reveal if these regions are important for increasing heterosis for yield in maize.

NSS Selection Candidates

Distance is physical distance on B73 genome divided by 1 000 000

NBS Selection Candidates

		NSS	NB
Blue	Significant in individual RFS replicates	41	18
Teal	Significant in individual S1 replicates	38	35
Green	Significant in one S1 and one RFS replicate	19	11
Red	Significant in any two RFS replicates	9	3
Dark Red	Significant in any two S1 replicates	4	5
Pink	Significant across three S1 replicates	1	0

- S1 and RFS selection both exhibited genome-wide selection signatures

- Locus PZA02958.17 was significant across all three S1 populations
  - Position relative to B73 physical map
    - Chr. = 6
    - Phys. Pos. = 151822737

- Loci significant in more than one replicate (red and dark red) tended to be located in the telomere regions in both populations

- Evidence for selection pressure on common loci across replicate populations was not found. Possible reasons include
  - Genotype by environment interaction
  - Founder effect
  - Epistasis

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