Crop Science

Local to continental-scale variation in fitness and heritability in common bean (Phaseolus vulgaris)

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Core Idea 1: Selection history impacts genetic variation, which enables adapting crops to new environment

Core Idea 2: We report spatiotemporal variation in dry bean yield, local adaptation and segregating genetics

Core Idea 3: Yields became more heritable in two of three dry bean races across North America over 35 years

Core Idea 4: Local adaptation (home field advantage) was worth up to 34 years of average breeding gains

Core Idea 5: Sites with high heritability and home field advantage are best for adapting to new environments

Local to continental-scale variation in fitness and heritability in common bean (*Phaseolus vulgaris*)

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CORE IDEAS

1. Selection history impacts genetic variation, which enables adapting crops to new environments and climates

2. We report spatiotemporal variation in dry bean yield, local adaptation and segregating genetics

3. Yields became more heritable in two of three dry bean races across North America over 35 years

4. Local adaptation (home field advantage) was worth up to 34 years of average breeding gains

5. Sites with high heritability and home field advantage are best for adapting to new environments

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ABSTRACT

Selection during plant domestication and improvement often decreases genetic variation, including variation that confers adaptation to local conditions. We report spatial and temporal variation in fitness (seed yield), local adaptation, and segregating genetic variation within three races of common bean (*Phaseolus vulgaris* L.) with differing domestication histories and genetic diversities. Three-hundred and twenty-seven common bean genotypes had seed yield measured at subsets of 70 sites across North America between 1981–2015, as part of the Cooperative Dry Bean Nursery (CDBN). We estimated local adaptation using the metric home field advantage (HFA) and segregating genetic variation using heritability. The Durango and Mesoamerican races (Middle American genepool) had higher-than-expected ($p = 0.002$) HFA, equal to up to 34 years of average yield gains. Surprisingly, Nueva Granada (Andean genepool) and Durango yields became more heritable across the study period ($p < 0.001$), while Mesoamerican heritability decreased ($p < 0.001$). Both metrics detected diversity loss corresponding to the timings of major historical gene introgressions. Local adaptation remains an agronomically important phenomenon within some common bean races. Common bean adaptation to new conditions will be most rapid at locations with large local adaptation benefits and high heritability.

Key Words: Cooperative Dry Bean Nursery (CDBN), domestication, home field advantage, local adaptation, *Phaseolus vulgaris* (common bean)

2

1. INTRODUCTION

48

49   Genetic variation in phenotypes is the basis for effective natural and artificial selection. Through

50   selection, crops become more productive and better adapted to new and changing environments.

51   However, the domestication of crops consistently corresponds with a loss of genetic variation in

52   "improved" or commercial genomes versus domesticated "landrace" or non-commercial genomes,

53   and in domesticated genomes versus the genomes of wild relatives (Miller and Gross 2011; Moyer et

54   al 2018). Domestication typically involves a genetic bottleneck followed by a long period of weak or

55   variable selection. During the process of crop improvement, intense selection over short time

56   frames is coupled with a reduction in effective population size and limited recombination, and often

57   followed by long-distance migration events and rapid population expansion. To date, losses of

58   genetic diversity between wild and improved populations range from 5 to 77% (Gray et al 2009, Lin

59   et al 2014), and the only reported case of a gain in genetic diversity is in the Andean domestication

60   event in common bean (*Phaseolus vulgaris* L.) (Schmutz et al 2014; Trucci et al, 2021).

61   Common bean is the most important food legume for direct human consumption. Common

62   bean is currently grown on over 35 million ha and in nearly every country that records agricultural

63   statistics (FAOSTAT 2015). This area encompasses across an enormous range of latitudes (from

64   52ºN-32ºS), altitudes (50-3000 m), growth temperatures (14-26 C), and average yearly precipitation

65   (400-1600 mm) and precipitation regimes (Singh 1989; FAOSTAT 2015). In contrast, the habitat

66   niche of wild common bean is narrow (Gepts 2009). The wild ancestors of common bean originated

67   in central America (Bitocchi et al 2012) and were dispersed to the Andes ~165,000 years ago with a

68   strong genetic bottleneck that lasted ~76,000 years (Schmutz et al 2014). From these two wild gene

69   pools, common bean was domesticated at least twice, once in Mesoamerica (the 'Middle American'

70   genepool) and once in the Andes (Gepts, et al. 1986; Schmutz, et al. 2014). The domestication

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71   bottleneck was stronger in the Middle American than in the Andean genepool, probably because

72   loss of diversity occurred in the Andes before domestication (Gepts et al., 1986; Bitocchi et al., 2012;

73   Bellucci et al., 2014; Schmutz et al., 2014). Common bean was widely cultivated in Mexico and

74   North America pre-European contact (Kaplan 1965), and New World settlers cultivated common

75   bean from landraces maintained by Native Americans, primarily from the Middle American

76   genepool, and later from European re-introductions, primarily from the Andean genepool

77   (Vandemark et al 2014). These complex histories led to differences in genetic diversity, yield

78   potential, and selection intensity among different races within these genepools. The first formal

79   North American improvement efforts were initiated in the late 1800s and early 1900s by the United

80   States state and federal governments (Vandemark et al 2014); since the 1950s, breeders have

81   assessed comparative performance in part via the Cooperative Dry Bean Nursery (CDBN), the

82   largest multi-environment trial of common bean in the United States and Canada (Myers 1988;

83   Singh 2000). CDBN cooperators develop germplasm in their home regions, and are most interested

84   in strong regional performance, typically releasing varieties with high seed yield that meet

85   commercial expectations for seed size, shape, and color. However, they also test promising material

86   for broad adaptation by measuring seed yield and other phenotypic traits across all participating

87   CDBN field locations. The impacts of selection at both regional and continental scales on the

88   genetic variation in common bean have not been measured; however, selection across

89   heterogeneous environments is theorized to have major effects on population fitness and the

90   suitability of different adaptive strategies (Levins, 1962; Botero et al 2015).

91   The CDBN dataset offers an exciting opportunity to examine the genetic component of fitness

92   in common bean in three races within two gene pools which differ in their genetic diversity, and to

93   determine the impact of this genetic variation on fitness and heritabilities at different spatial scales.

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94   CDBN entries are advanced breeding materials without 'locations of origin' in the sense of their wild

95   progenitors. However, progenitors of these entries were grown in North America in pre-Columbian

96   times, and these specific entries were developed for regional production by breeders at many

97   locations that took part in the CDBN trials; thus, local adaptation of CDBN entries to specific

98   North American regions may have arisen from long-term selection of improved material within

99   those regions. If present, local adaptation might be leveraged in breeding programs that have

100   focused on broad-scale adaptation to achieve fitness gains (Ewing et al., 2019). For individual-based

101   selection, breeding programs often measure the heritability of traits of interest, the proportion of

102   phenotypic variation that is genetically determined. High heritability is essential for efficient

103   selection, but environmental conditions also influence the heritability on which any response to

104   selection depends (Hoffman, Hercus 2000; Hoffman, Merila 1999). Heritability may also vary

105   temporally as the array of genotypes measured typically changes during the breeding process

106   (Feldman, Lewontin 1975). Understanding spatial and temporal patterns of seed yield heritability

107   and the interaction between heritability and the portion of seed yield variation attributable to local

108   adaptation could provide fundamental insights into the adaptation and domestication process of *P.*

109   *vulgaris* (Table 1; Papa & Gepts 2003; Papa et al., 2007; Eckert et al 2010; Kraft et al 2014; Rodriguez

110   et al 2015). These patterns and interactions may differ among races due to their unique

111   domestication histories and genetic variabilities, with implications for the potential of bean races to

112   continue to adapt to changing conditions.

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Table 1			
Implications of home field advantage and heritability for breeding and adaptation. Combining agroecological ecoregion information and heritability of specific traits may help improve selection efficiency while providing insights into processes driving past selection.			
		Heritability	
		Lower	**Higher**
Home Field Advantage	**Larger**	*Processes*: High environmental variation among locations, low genetic variation potentially enriched in locally important alleles. *Implications*: Inefficient selection on individuals for phenotypic improvement; testing at these sites may reveal conditionally beneficial alleles.	*Processes*: High environmental variation among locations, high genetic variation potentially enriched in locally important alleles. *Implications*: Efficient identification and selection of specialists that may contain large-effect candidate loci for introgression.
	Smaller	*Processes*: Low environmental variation among locations, low genetic variation potentially enriched in broadly important alleles. *Implications*: Inefficient selection on individual entries for phenotypic improvement, so family based methods are necessary.	*Processes*: Low environmental variation among locations, high genetic variation potentially enriched in broadly important alleles. *Implications*: Efficient selection on individual entries for phenotypic improvement.

114

115   We re-interpret the CDBN trials as a reciprocal transplant experiment to estimate local

116   adaptation and yield heritability among common bean races, experimental locations, and across

117   years. We first introduce a "home field advantage" (HFA) component for each CDBN entry into a

118   traditional partitioning of seed yield variation and explore patterns of HFA across three races within

119   the two genepools. Briefly, HFA is the fitness gain an entry realizes by growing in its home location,

120   which is empirically defined as the location of highest fitness relative to other entries (Ewing et al,

121   2019). We expected that HFA would explain a significant amount of yield variation within each bean

122   race. We then examined overall variation in yield heritability across years and locations in the CDBN

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123   and across races and genepools. We expected to observe substantial differences in heritability across

124   space due to environmental differences (Wilson et al 2006; Finlay and Wilkinson, 1963). We also

125   expected to observe decreases in heritability over time in the Middle American genepool as genetic

126   sources of yield variation were eliminated, and potential increases in heritability over time in the

127   Andean genepool, given its increase in genetic diversity from wild to domesticated gene pools.

128   Finally, through identifying sites with high HFA and yield heritability, we discuss potential strategies

129   for selection efforts to further incorporate local adaptation.

130   **2.   MATERIALS AND METHODS**

131   *2.1 Data Acquisition*

132   Common bean seed yield (hereafter: 'yield') data were retrieved from MacQueen et al. 2020;

133   briefly, yield data from digitized reports from 1981 to 2015 were obtained, which included data from

134   71 unique locations, and 327 entries (including released cultivars and unreleased advanced breeding

135   lines) with 11 common check entries (Figure 1). CDBN entries include released cultivars and

136   unreleased breeding lines at advanced breeding stages from at least 13 diverse North American

137   market classes of common bean. The majority of these entries are members of one of three of the

138   seven races of common bean; two of these races, Durango and Mesoamerican, arose from the

139   Middle American domestication event and are more genetically diverse than Nueva Granada, which

140   arose from the Andean domestication events (Mamidi, et al. 2011). 13,989 yield data points were
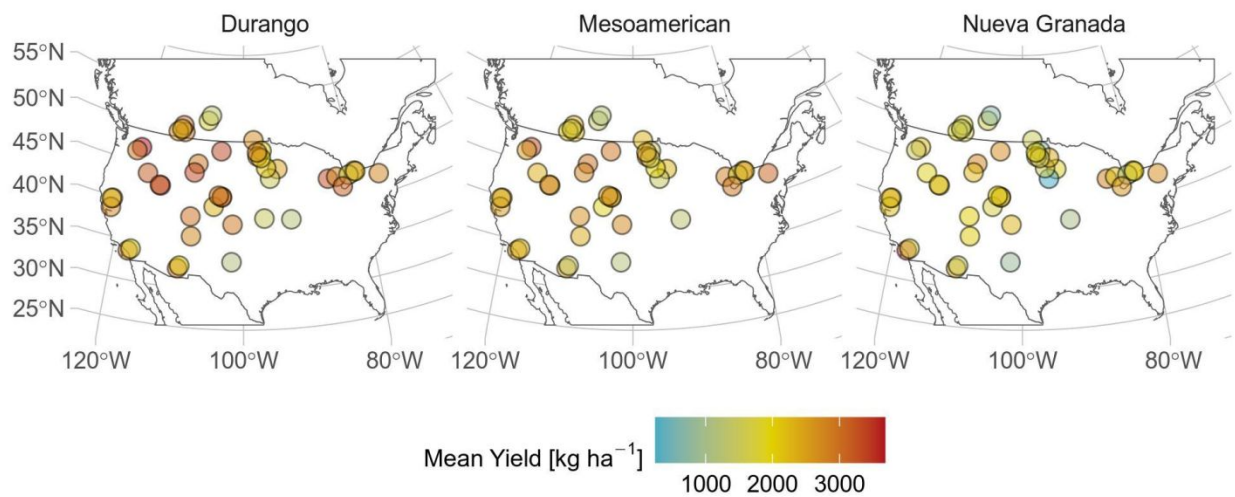
141   used in this analysis.

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142
143   **Figure 1:** Locations and mean yields at sites within the CDBN variety trials. The analysis was
144   restricted to continental North American sites used for at least three years.

145   The CDBN selection strategy for lines entered likely impacts partitioning of yield variance in

146   several ways. This strategy was developed to test dry bean material for broad adaptation across

147   CDBN locations. Within years, CDBN locations grew an identical complement of entries, with only

148   rare entries missing yield phenotypes at single locations. The entries shift gradually through the

149   years, with each entry typically present in the CDBN for three consecutive years. This shift is a

150   direct result of the improvement strategy employed by network cooperators over the trial years and

151   captures some of the regional breeding advances produced by additional non-CDBN field trials.

152   This strategy confounds partitioning of yield variation into genetic and environmental components

153   across years, but not across locations. Specifically, comparisons of heritability for different locations

154   within years are not confounded by the presence of different genotypes. Heritabilities from different

155   years within locations reflect both environmental differences across years and a change in the

156   complement of genotypes used to compute the heritability.

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157   *2.2 Yield and home field advantage expectations*

158   We first assessed overall fitness and fitness gains across the study period within three groups of

159   CDBN entries: entries from the Nueva Granada race from the Andean genepool, and entries from

160   two genetically distinct races within the Middle American genepool, the Durango and the

161   Mesoamerican race using linear modeling.

162   We then quantified HFA. Home field advantage is the fitness benefit an entry receives by

163   growing in its "home" location, after accounting for inherent site and genetic potential, and

164   therefore is an entry-specific outcome of genotype-by-environment interactions (Blanquart et al,

165   2013). We estimated HFA following a modified version of Ewing et al. (2019). Most importantly, we

166   included the additional step of accounting for entry genetic relationships to eliminate effects of

167   double counting similar CDBN entries.

168   To estimate HFA, we first filtered out sites with fewer than three years of data. Next, we

169   assigned each entry an empirical "home" site, the site where an entry performed best relative to

170   other varieties. We calculated relative yields within each site-year by centering (mean = 0) and scaling

171   (standard deviation = 1). Then, for each variety, we calculated the best linear unbiased predictor

172   (BLUP) of relative yield at each site by using site as a random intercept in *lme4* 1.1 (Bates et al, 2015).

173   The home site for each CDBN entry was the site with the largest BLUP.

174   With home site identified, we then tested whether it explained variation in CDBN yields using

175   model comparison, including in conjunction with genetic relatedness, by comparing formulations of

176   the ordinary least squares model:

177                                    $$y = \mathbf{X}\beta + \varepsilon$$

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178   Where y contains the n yields of each entry i at location j and year k, β contains coefficients of p

179   predictors in the n by p model matrix $\mathbf{X}$, and ε is the associated error term. In the base model, $\mathbf{X}$

180   included site, year, site-year, and entry identity. Model 2 added a predictor for HFA, a binary

181   indicator of whether a site was that variety's home. Model 3 added terms for genetic relatedness to

182   the base model. Genetic relatedness was determined using the *snp_autoSVD* function of the *bigsnpr* R

183   package (Prive et al 2017), using 1,221,540 SNPs genotyped previously using genotyping by

184   seqeuncing (MacQueen et al 2020); we used the first three principal components of the singular

185   value decompositions of linkage-adjusted SNP matrices (Figure S1). Model 4 added to the base

186   model both HFA and genetic relatedness terms, including an interaction. In models with an HFA

187   term, the coefficient β_{HFA} is the average home field advantage across entries.

188   We compared these models using Akaike's information criterion (AIC); Model 2 was always the

189   most parsimonious. We then calculated variance explained by each predictor in Model 2 using the

190   *Anova* function in *car* 3.0 (Fox and Weisberg, 2019). We then used 999 permutations to test the

191   significance of home field advantage (Ewing et al, 2019). After permuting yields within site-year, we

192   re-assigned home site and re-calculated home field advantage as described above. These permuted

193   HFAs were as expected based on variation in the dataset; we compared this with the observed HFA

194   using a two-tailed test.

195   To observe trends in HFA across the study period, we modified Model 1 to add a year by home

196   field interaction. The coefficients of these terms were the home field advantages within each year.

197   Likewise, we estimate home field advantage conferred by each site, by adding a site by home field

198   interaction to Model 1.

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199   *2.3 Spatial and temporal variation in heritability*

200   We calculated narrow sense heritability for yield per-site on an entry-mean basis, by combining

201   data from all breeding trials, then decomposing the variance components within each trial. Briefly,

202   we built linear models using the R package *lme4* version 1.1 to calculate heritability within each site-

203   year using the variance in components at each site with effects of entry, site, and year effects, as well

204   as entry-by-site and entry-by-year interactions. Heritability was calculated as

205     $$h^2 = V_{entries}(\frac{1}{rep * environment} * MS_{entries})^{-1}$$

206   Where $V_{entries}$ the variance among the entries, environment is the number of locations in the

207   study and $MS_{entries}$ is the squared value of expected yields for the entries (Bernardo, 2020, page 163).

208   To quantify the change in heritability over time, we used average heritability across a five-year sliding

209   window. For example, heritability for 1983 was the average heritability of 1981-1985. Finally, to

210   model the spatial variation of heritability across North America, we used ordinary kriging

211   implemented in *fields* version 11.6 (Furrer et al., 2009). For spatial variation, heritability was the

212   average heritability over the 35-year study period and across races.

213   *2.4 Relationship between home field advantage, heritability and kinship*

214   Finally, we identified locations suitable for breeding locally adapted crops. We defined such sites

215   as both having a higher-than-median heritability and conferring higher-than-median home field

216   advantages. We also quantified whether home site location had a genetic basis by correlating the

217   spatial distance among each variety's home site with the genetic distance among varieties. Home

218   distance was great circle distance using *sp* 1.3. Genetic distance was reconstructed from the first

219   three principal components of the linkage-corrected kinship matrices. We tested the correlation

220   using a Mantel test with 999 permutations in *vegan* 2.5 (Oksanen et al, 2019).

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221   *2.5 Statistical analysis*

222   All analyses were performed independently for each race. Unless otherwise noted: statistics were

223   performed in *R* 3.6.3 *base* and *stats* packages; plots were made with *ggplot2* 3.3.0 and annotated with

224   regression formulae using *ggpmisc* 0.3.3 (R Core Team, 2020; Wickham, 2016; Aphalo, 2019);

225   centering and scaling refer to a group mean of zero and standard deviation of one; errors are

226   standard.

227   **3. RESULTS**

228   *3.1 Home Field Advantage*

229   Each dry bean race studied had a different yield potential ($F_{2,13170}$ = 608; p < 0.001, Figure 2a;

230   Table S1): By 2015, Nueva Granada entries were expected to yield 2370 ± 40 kg ha^{-1}, Durango

231   entries, 3060 ± 30 kg ha^{-1}, and Mesoamerican entries, 2850 ± 40 kg ha^{-1}. In agreement with previous

232   studies (Vandemark et al 2014), yields of all races improved during the study period, albeit at

233   different rates ($F_{2,13170}$ = 4.00, p = 0.02). Nueva Granada yields grew by 16 ± 2 kg ha^{-1} yr^{-1} (p <

234   0.001), and Durango yields grew by 14 ± 1 kg ha^{-1} yr^{-1} (p < 0.001). Mesoamerican yields grew the

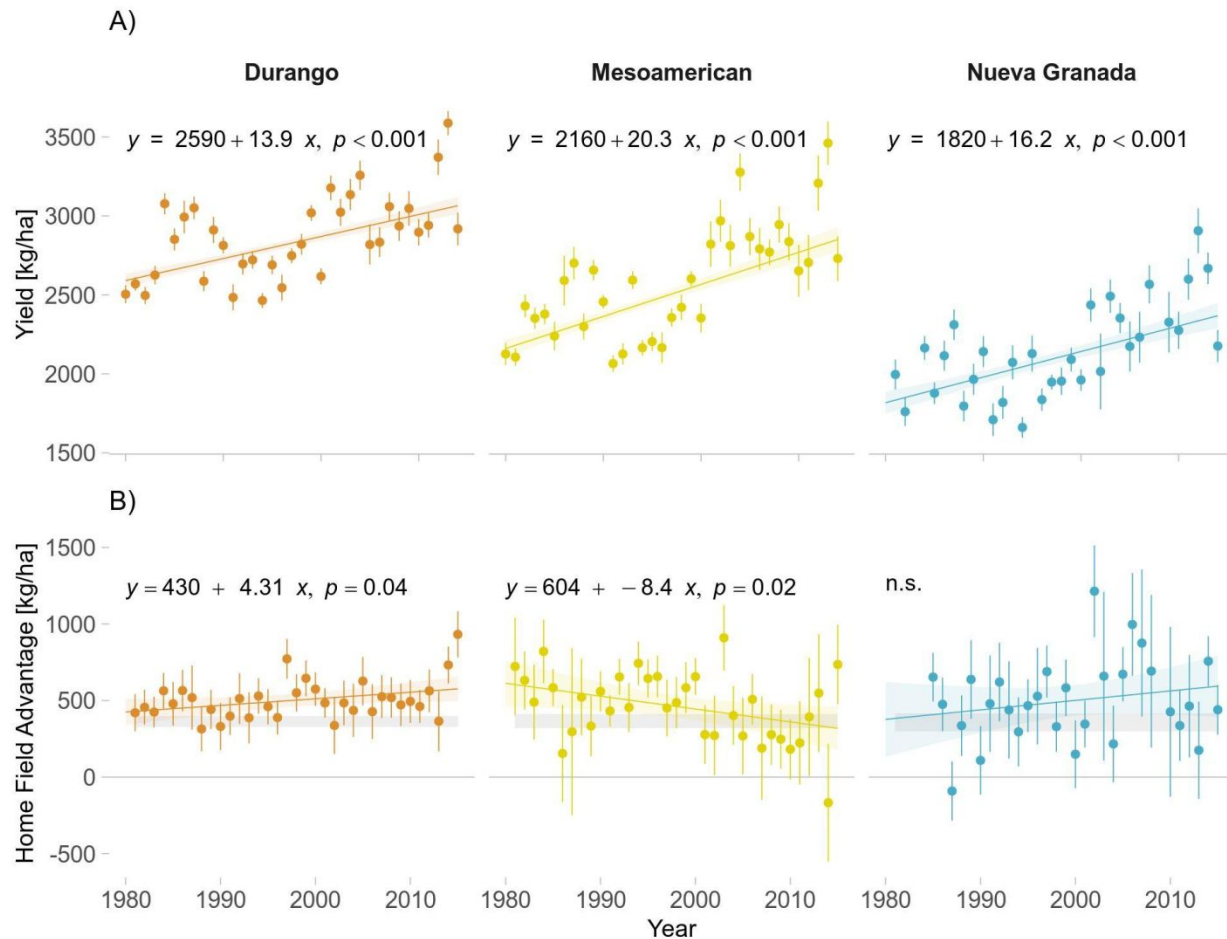235   fastest, by 20 ± 2 kg ha^{-1} yr^{-1} (p < 0.001).

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Figure 2: Trends in A) yield and B) home field advantage across the study period by race. In B), the gray bars indicate the 90% confidence interval of the expected home field advantage based on permutation within site-year. Error bars are standard errors. Shading around regression lines indicates 95% confidence intervals. n.s.: not significant at $p < 0.05$.

We partitioned yield variation into genetic and environmental components within the two genepools and three races (Table 2). Emphasizing the importance of local conditions, the largest source of variability in yield across all races was a location-by-year interaction (44.9-48.7%), followed by an effect of location alone (29-33.1%). In contrast, year-to-year variation and genotype variation were small (2.4-3% and 3.2-4.1%). To test for a contribution of local adaptation to these fitness gains, we also assessed the variation in yield explained by each CDBN entry's home field advantage (HFA). In Nueva Granada entries, HFA accounted for 1.1% of yield variation, and reduced unexplained yield variation by 6.4% (Table 2). In Durango entries, HFA accounted for 1.3% of yield

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249   variation and reduced residual variation by 8.3%. Similarly, HFA accounted for 1.3% of

250   Mesoamerican yield variation, and reduced residual variation by 7.7%. Including principal

251   components (PCs) as covariates for genetic relatedness did not reduce HFA; in fact, including

252   genetic relatedness as a predictor of yield reduced model parsimony (ΔAIC = 339 (Nueva Granada),

253   890 (Durango), and 608 (Mesoamerican); Table S2). These three PCs accounted for 39%, 44%, and

254   42% of genetic variance in the Nueva Granada, Durango, and Mesoamerican entries, respectively

255   (Figure S1).

Table 2
Partitioning of CDBN Yield Variances

	Race		
	Durango	**Mesoamerican**	**Nueva Granada**
Home Site	1.3%	1.3%	1.1%
Residuals	14.1%	15.8%	15.6%
Genotype	3.3%	4.1%	3.2%
Site	33.1%	30.9%	29.0%
Year	2.4%	3.0%	2.5%
Site-Year	45.7%	44.9%	48.7%
Residual Reduction[1]	8.3%	7.7%	6.3%

[1] Proportion of residual variance explained by home site

256

257   We next determined if race-average HFA were larger than expected and whether these average

258   HFA were agronomically significant. Nueva Granada entries had yield gains that were not

259   significantly different from the expectation of 357 kg ha^{-1} based on permutations of variation in

260   Nueva Granada yields (p = 0.21; Figure 2b). In Durango entries, HFA conferred an average yield

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261   gain of 472 kg ha^{-1}, 109 kg ha^{-1} larger than expected (90% confidence: 72-146 kg ha^{-1}; $p = 0.002$).

262   The Durango HFA was 15% of expected 2015 yields, equivalent to 34 years of yield gains for this

263   race. In Mesoamerican entries, HFA conferred a yield gain of 453 kg ha^{-1}, 89 kg ha^{-1} larger than

264   expected (90% confidence: 44 -134 kg ha^{-1}; $p = 0.002$). The average Mesoamerican HFA was 16% of

265   expected 2015 yields and equivalent to 22 years of yield gains for this race. Thus, some

266   environmental specialization had been preserved in modern North American varieties deriving from

267   the Mesoamerican race, but not the Nueva Granada race.

268   Though environmental specialization was present within two dry bean races, we found

269   inconsistent evidence that dry bean breeders tried to leverage HFA, in that there were inconsistent,

270   and only moderately significant changes in HFA among races and across time ($F_{2,94} = 4.82$; $p = 0.01$;

271   Table S3). HFA increased slightly across the study period in Durango entries, by 4.3 ± 2.0 kg ha^{-1} yr^{-1}

272   ^{1} ($p = 0.04$; Figure 2b). In Mesoamerican entries, however, HFA decreased by 8.4 ± 3.5 kg ha^{-1} yr^{-1} (p

273     $= 0.02$) and by the end of the study period, was no larger than expected based on permutation.

274   *3.2 Spatial and Temporal Decay in Heritability*

275   We next determined narrow-sense heritability in yield across 2170 location-year combinations in

276   the CDBN, without accounting for HFA. Yield heritabilities were highest in the northwestern

277   United States and southwestern Canada and decreased along a south-eastern gradient (Figure 3).

278   Heritabilities were stable over large geographic ranges (~1013 km), although year-to-year

279   fluctuations in the direction of the gradient in yield heritability were evident (Figure S2). More

280   commonly used trial locations did not have more consistent heritabilities: in fact, there was a

281   positive relationship between the number of trial years at a location and the standard deviation in

282   heritabilities (yield stability) across trial years ($p = 0.014$, Figure S3A). Location-specific heritability

283   was also unrelated to yield stability at the location ($p > 0.05$; Figure S3B). Heritability was higher in

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284   higher quality site-years ($p < 0.05$), with environmental quality measured as the average yield of

285   entries of a race in that site-year (Fig S3C; Finlay and Wilkinson, 1963). However, this trend was

286   confounded with values across time, which reflected the direct act of selection for improvement on

287   CDBN entries. Specifically, there were trends in yield heritability across years which varied by bean

288   race. As hypothesized, heritability decreased in Mesoamerican entries by 0.005 yr^{-1} ($p < 0.001$). In

289   contrast, Nueva Granada and Durango entries showed an increase in yield heritability over time,

290   with yield heritability increasing by 0.007 yr^{-1} and 0.004 yr^{-1}, respectively ($p < 0.001$). To test for a

291   genetic basis for environmental specialization, we determined whether more closely related CDBN

292   entries had spatially closer home sites. Entries in the Durango (Mantel's $r = 0.11$; $p = 0.001$) and

293   Mesoamerican (Mantel's $r = 0.068$; $p = 0.01$) races showed this relationship, while entries in the

294   Nueva Granada race did not ($p = 0.6$). Finally, we found no tradeoff between heritability and home

295   field advantage within races ($F_{2,97} = 1.27$; $p = 0.3$; Figure 4).
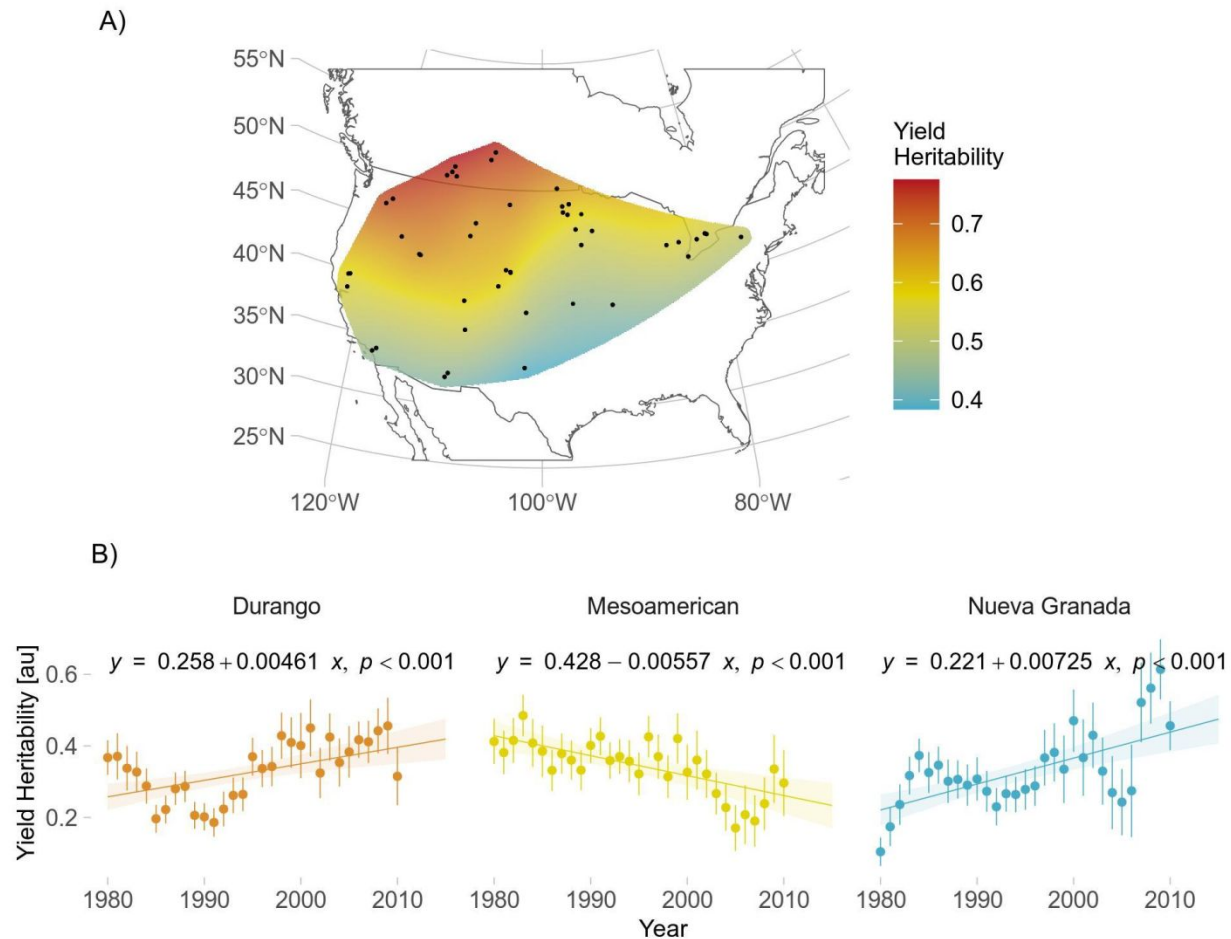
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A)

B)

296
297 **Figure 3:** A) Ordinary kriging of yield heritability based on the average heritability over 30-years of
298 trials at 70 field sites. B) Mean and standard deviation of site heritability for 70 field sites. Symbology
299 is as in Figure 2.

300

301 **4. DISCUSSION**

302 *4.1 Orthogonal Metrics to Interpret Past Selection and Guide Future Improvement*

303   Modern breeding techniques have achieved remarkable success in increasing the fitness and

304 phenotypic stability of cultivated plants through breeding programs that focus on broad adaptation

305 at large spatial scales. Efforts such as the CDBN have selected for both broad and regional

306 environmental adaptation; however, ecological theory suggests that across environments that vary

307 spatially or temporally, the most fit population will be a mix of narrowly adapted specialists (Levins,

17

308   1962). Ascertaining the presence and amount of environmental specialization remaining in broadly

309   adapted crop species may provide an opportunity to further improve crop fitness by leveraging local

310   adaptation. In other words, to continue improving common bean, we may need to select for locally

311   important alleles, (i.e., conditionally neutral alleles that affect performance in individual

312   environments without affecting performance in alternate environments). Yet unknown is whether

313   these locally adapted alleles or gene complexes are still segregating within advanced common bean

314   breeding material, or whether they have been removed as part of the genetic bottleneck during the

315   improvement of these races. Here, we measure HFA as a proxy for yield variation that may be

316   attributed to local adaptation. In Durango and Mesoamerican entries, local adaptation conferred

317   agronomically significant yield gains that were equivalent to decades worth of breeders' yield
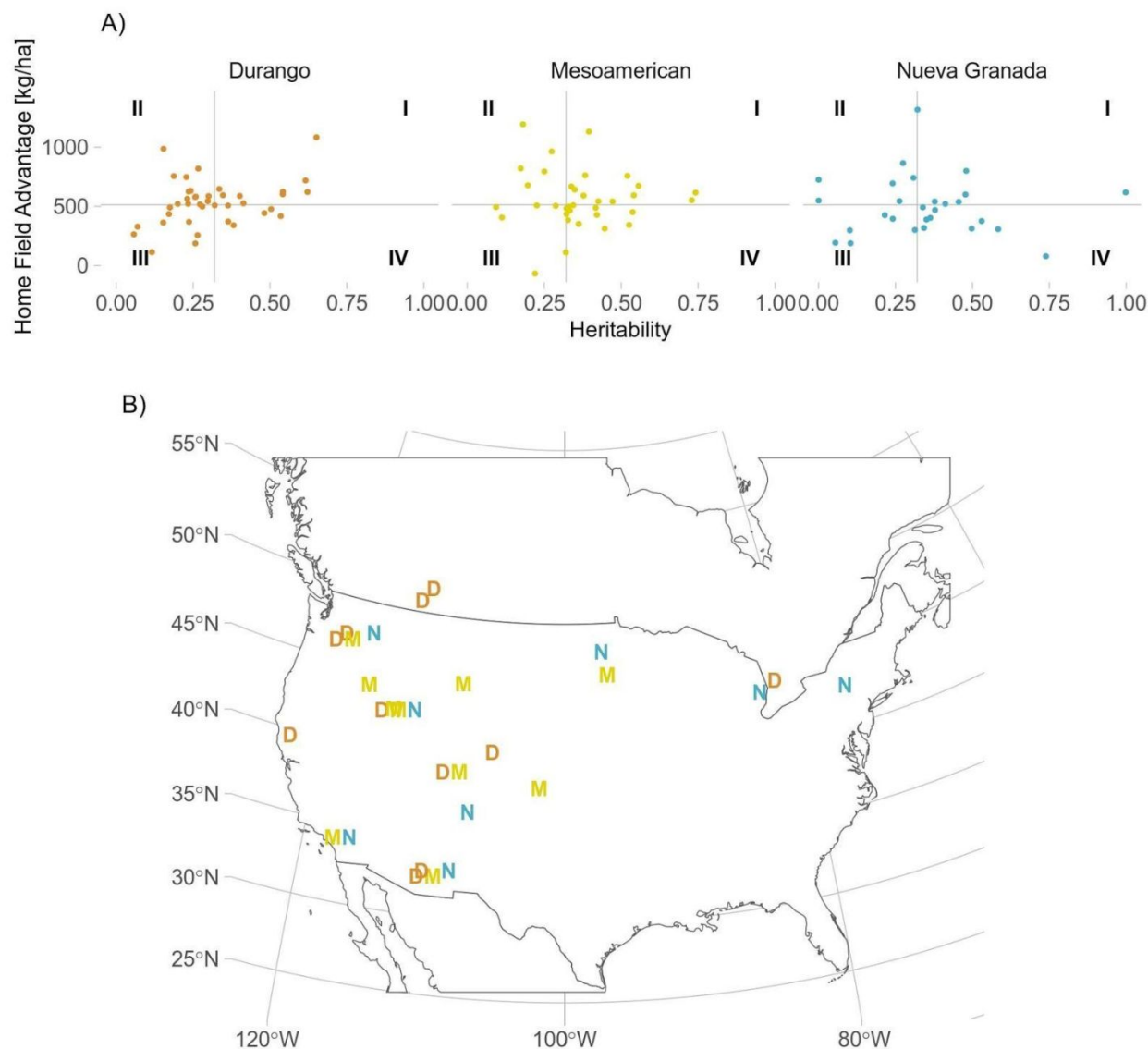
318   improvements.

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319
320 **Figure 4**: A) Relationship between yield heritability and home field advantage at each site, by race.
321 Lines indicate the median value for heritability and home field advantage across all sites. B) Top
322 locations (quadrant I) for selecting for home field advantage. D – Durango; M – Mesoamerican; N –
323 Nueva Granada races. Figure S3 identifies locations with CDBN abbreviations.

324   We correlate these HFAs with the amount of variance segregating for entry-mean heritability

325 (Figure 4). We envision that the interplay between HFA, an entry-specific quantity, and heritability, a

326 function of all genotypes grown at a location, could impact the kinds of selection practiced in the

327 future at specific locations of the CDBN (Table 1). When trait heritability is high and HFA are not

328 present for any CDBN entries (Table 1; Figure 4, quadrant IV), the current breeding approaches that

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329   select upon individual entries and families are appropriate. When trait heritability is high and HFA

330   are present for CDBN entries (Table 1; Figure 4, quadrant I), breeders have an additional

331   opportunity to screen and select for locally important alleles which may confer benefits at that

332   location without accruing trait costs at other locations. These alleles could be introgressed more

333   broadly into other material to improve performance in these environments. When trait heritability is

334   low and HFA is present for CDBN entries (Table 1; Figure 4, quadrant II), individual-based

335   selection is inefficient; however, entries at these locations could still be screened for locally

336   important alleles which may improve performance in these environments. When neither trait

337   heritability nor HFA are present (Table 1; Figure 4, quadrant III), neither traditional breeding

338   approaches nor screening for locally important alleles are likely to aid further common bean

339   improvement.

340   Given the different evolutionary histories of both genepools pre- and post-domestication, we

341   expected distinct responses to selection in the Andean and Middle American entries over the course

342   of the CDBN. The low-yielding, low genetic diversity Nueva Granada entries from the Andean

343   genepool experienced modest improvements in yield across the study period and showed little

344   evidence of local adaptation to specific regions within North America. Nonetheless, there was

345   strong evidence for increasing adaptation at a continental scale, in that yield heritability increased in

346   this race over the 35-year study period. These increases in yield heritability over time occurred

347   without an increase in HFA. We thus suggest that Andean CDBN entries still lack genetic variation

348   conferring adaptation to North American growing conditions. If this is true, then further

349   introgression from the Middle American genepool or from other species may offer opportunities for

350   continued yield improvement and local adaptation in this genepool. Alternatively, Andean entries

351   also require distinct management strategies and more inputs to maximize their yields; many CDBN

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352   locations may have managed for Middle American entries rather than Andean entries, which would

353   limit our ability to detect an HFA in Andean material.

354   The high-yielding, high genetic diversity Durango race also showed modest improvements in

355   yield across the study period, which coincided with a modest increase in local adaptation and

356   increases in adaptation at a continental scale over time. This increase in HFA and in yield heritability

357   suggests increasing adaptation to local and continental conditions in this race over the course of

358   improvement in the CDBN. We observe a drop in Durango yields and yield heritability from the

359   line-of-best-fit (Figure 2a, Figure 3b) beginning in the mid-1990s. This immediately follows the

360   introgression of rust resistance gene *Ur-3* into the Durango race from a Mesoamerican source, which

361   began in 1988 and was widely deployed in the mid-1990s (Hurtado-Gonzales et al 2017; MacQueen

362   et al 2020). We speculate that the broad introduction of rust resistance loci into the Durango race in

363   this time period resulted in a temporary (~6 year) reduction in segregating variation for yield within

364   this race.

365   Finally, the moderately yielding Mesoamerican race showed the largest improvements in yield

366   across the study period, at the expense of local adaptation and heritability of yield in more modern

367   entries. Both the decrease in heritability and HFA over time suggest a reduction in genetic diversity

368   in this race during the course of improvement. We observed a sustained drop in yields relative to the

369   line-of-best-fit (Figure 2a) in the Mesoamerican race in the 1990s. This observation was also made in

370   previous work which saw particularly low biomass and seed yields for Mesoamerican varieties

371   introduced in the 1990s that had upright determinate architecture (MacQueen et al 2020). After the

372   1990s, very few Mesoamerican CDBN entries have this architecture, as CDBN breeders had

373   adopted upright indeterminate architecture for newer CDBN entries in the Mesoamerican race

374   (Kelly 2001; Soltani et al 2016). This adoption highlights the complexity of defining fitness in

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375 agricultural systems: 'fitness' includes both overall seed yield, and numerous anthropocentric values

376 such as harvestability and commercial value that may override yield considerations. In the mid-

377 2000s, we also observed a sustained drop in yield heritability relative to the line-of-best-fit. Major

378 alleles for both lodging and plant height stopped segregating within the Mesoamerican race in this

379 time period; we speculate that loss of variation linked to these alleles could have caused this

380 temporary drop in heritability of yield. These major changes to entries in the Mesoamerican race

381 may also have caused the negative trend in HFA magnitude present in Mesoamerican entries, as

382 locally adaptive alleles may have been lost in genomic regions adjacent to architecture, height, and

383 lodging genes. In general, the introgression of major resistance or architecture alleles into

384 populations is equivalent to an artificially induced selective sweep. When this occurs, we expect to

385 see considerable linkage drag and the loss of locally adapted genetic variants. This signal was

386 observed in the CDBN, where following introgression, many years were required to regain local

387 adaptation (HFA) after using a common parent to introduce novel, important traits.

388 *4.2 HFA across species: comparing apples and oranges*

389 Previous work quantifying HFA in maize found that a large proportion of yield variation was

390 attributable to local adaptation (Ewing et al 2019) but was unable to determine if accounting for

391 genetic relatedness was an effective substitute for HFA. We found that HFA was robust to genetic

392 and familial relationships within CDBN material, supporting the utility of the HFA metric. We were

393 also able to compare HFA across these species. When compared to the annual breeding gains

394 observed in each trial, common bean HFA was four-fold larger than maize HFA. In absolute terms,

395 maize HFA was 1.0 Mg ha^{-1}year^{-1}, equivalent to 4.5 years of observed yield gains; in addition, the

396 HFA observed was smaller than expected (Ewing et al., 2019). In contrast, in this study, HFA was

397 450-470 kg ha^{-1} yr^{-1}, equivalent to 22 and 34 years of annual breeding gains for Mesoamerican and

398 Durango races, respectively; these HFA were larger than expected. There are several possible

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399 explanations for the difference in HFA between species. The current study encompasses yield trials

400 and improvement efforts over a much broader spatial scale and range of environments: thousands

401 of kilometers, versus a few hundred in Ewing et al (2019). Selection in common bean has occurred

402 in many regional breeding programs with disparate goals, which commonly develop specific sub-

403 races (market classes) (Vandermark et al, 2014); this may have enhanced regional adaptation in

404 common bean. Yet at the same time, several of these bean programs also employ shuttle breeding,

405 which commonly leads to the development of more broadly adapted germplasm (Ortiz et al, 2007).

406 The stable or decreasing HFA in Nueva Granada and Mesoamerican CDBN entries suggests that

407 the presence of regional adaptation is weakening, in line with CDBN goals. Irrespective of the

408 underlying cause of the size difference in HFA between dry bean and maize, in both species and

409 breeding systems (i.e. self-pollinated dicot, hybrid monocot), local adaptation is both valuable to

410 future breeding efforts and decreasing due to improvement efforts.

411 **5. CONCLUSION**

412   The interplay between local adaptation and total genetic variation may impact plant adaptation

413 to changing conditions. Local adaptation was worth decades of yield gains in genepools from both

414 domestication events over the 35 years of common bean improvement represented by the CDBN

415 but was decreasing or absent in two of three genepools. Surprisingly, we found that yield heritability

416 increased over time in races from both domestication events, indicating that genetic diversity in

417 races of both genepools may have increased, perhaps due to introgression from the other genepool

418 or from other species. The presence of yield variation attributable to local adaptation underscores

419 the possibility of selecting at particular CDBN locations for alleles that confer adaptation to those

420 environments. Resilient food systems of the future will take advantage of all potential avenues of

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421   improvement, including local adaptation, to sustainably produce food adapted to novel and changing

422   production environments.

6. ACKNOWLEDGEMENTS

7. DATA AVAILABILITY

428   Data and accompanying analyses are available at https://github.com/alice-MacQueen/cdbn-

429   home-away.

8. AUTHOR CONTRIBUTIONS

431   All authors contributed conceptualization and manuscript review. AHM, MK, and PME

432   designed and performed analyses, and wrote the manuscript with contributions from all authors.

433   PM, PEM, and JMO executed field trials. JWW and JMO compiled the phenotypic data from the

434   annual CDBN reports.

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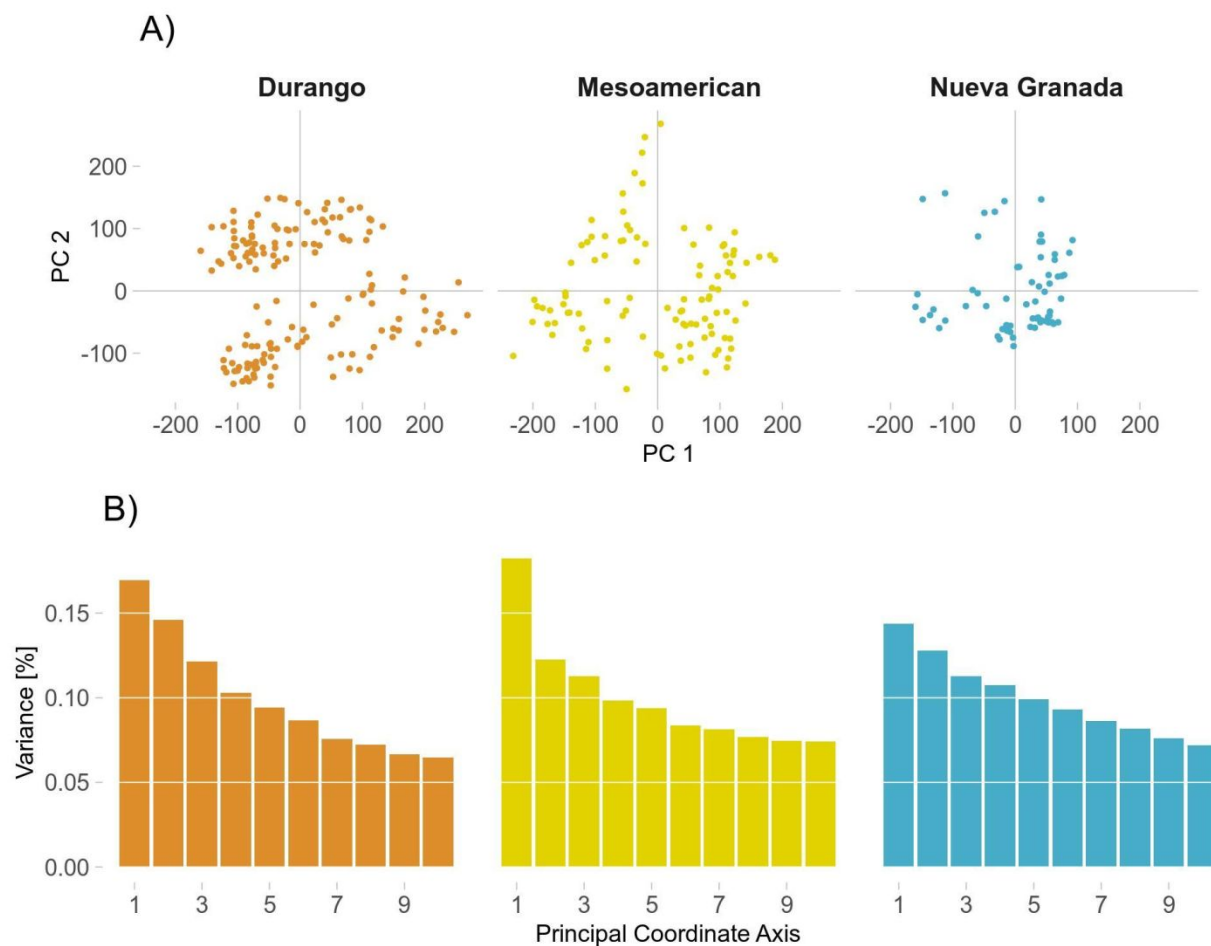
28

574 **10. SUPPLEMENT**

575
576 **Figure S1**: Summary of kinship among varieties within race. A) ordination of varieties along
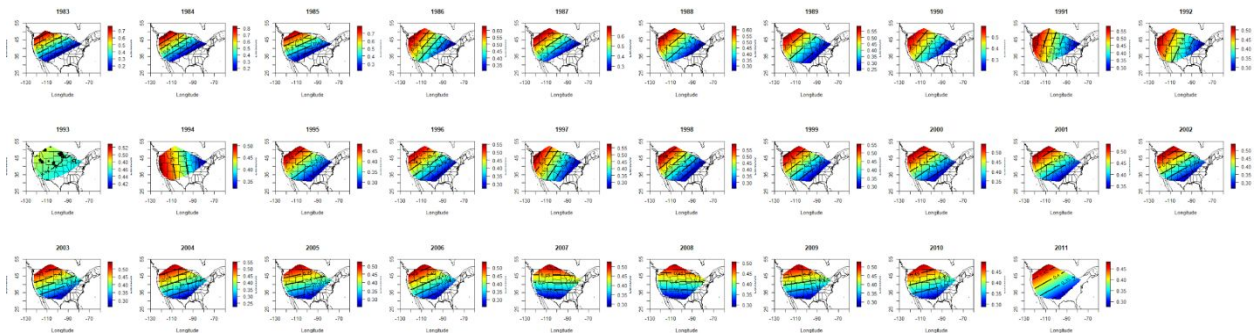577 principal component axes 1 and 2. B) Scree plot of variance explained by successive principal axes.

29

578
579   **Figure S2.** Ordinary kriging of yield heritability for each 5-year sliding window (1981-2013) centered
580   on the third year of the window.
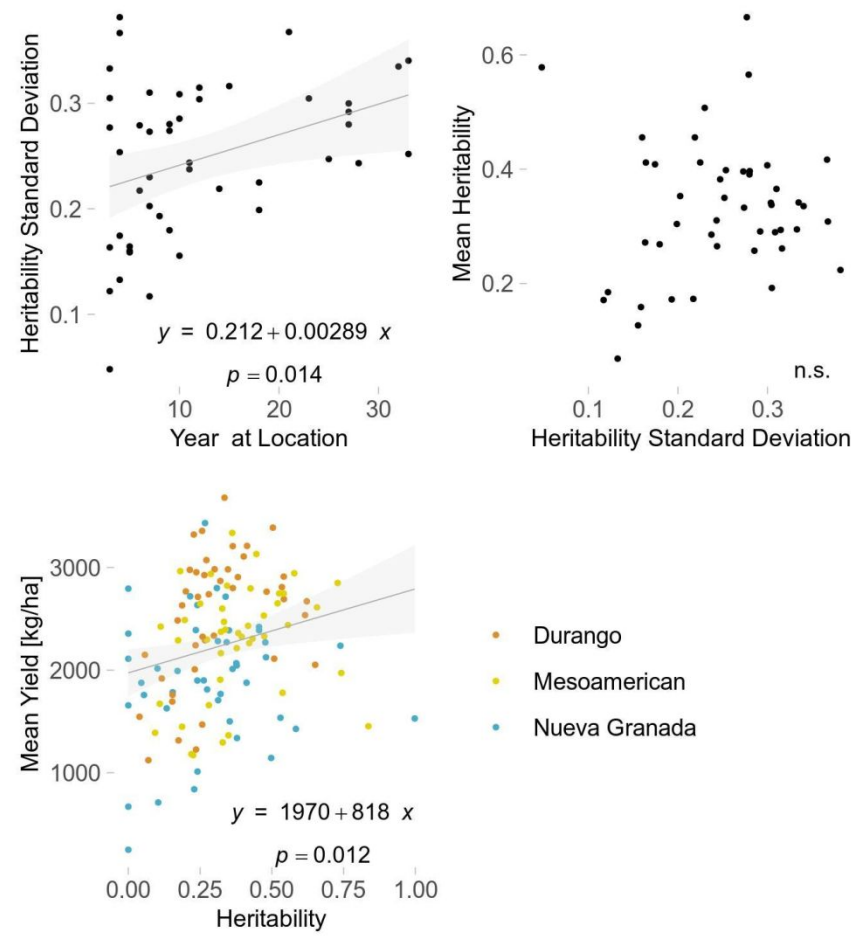
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583   **Figure S3**: a) relationship between standard deviation in heritability at each site, and the number of
584   trials at that site; b) relationship between mean and standard deviation in heritability at each site; c)
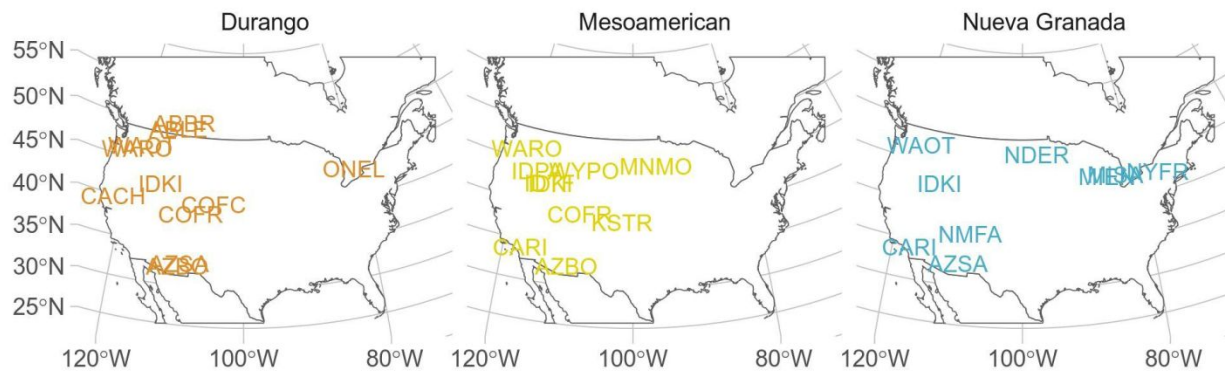585   relationship between mean yield and mean heritability at each site. n.s. – not significant at p < 0.10.

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Figure S4. High heritability and high HFA location combinations by bean race. Abbreviations
correspond to CDBN standard abbreviations.

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Table S1
ANOVA of Yield Across Time

	Sum Sq	Df	F value	Pr(>F)
Year	252,500,000	1	292.70	0.000
Race	1,050,000,000	2	608.26	0.000
Year*Race	6,895,000	2	4.00	0.018
Residuals	11,370,000,000	13174	-	-

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Table S2
AIC[1] of Competing Home Field Advantage Models

	Durango	Mesoamerican	Nueva Granada
With Home Field	6772	5095	3434
Base (Variety, Site, Year)	7323	5421	3599
With Home Field, Kinship	7662	5703	3773
With Kinship	8143	5997	3926

[1]Akaike Information Criterion

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Table S3
ANOVA of Home Field Advantage Across Time

	Sum Sq	Df	F value	Pr(>F)
Year	4.755	1	0.00	0.992
Race	36,290	2	0.43	0.654
Year * Race	410,000	2	4.82	0.010
Residuals	3,994,000	94	-	-

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