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Genomics of long- and short- term adaptation in maize and teosinte

Maize is an excellent model for the study of plant adaptation. Indeed, post domestication maize quickly adapted to a host of new environments across the globe. And work over the last decade has begun to highlight the role of the wild relatives of maize – the teosintes *Zea mays* ssp. *parviglumis* and ssp. *mexicana* – as excellent models for dissecting long-term local adaptation. Although human-driven selection associated with maize domestication has been extensively studied, the genetic bases of natural variation is still poorly understood. Here we review studies on the genetic basis of adaptation and plasticity in maize and its wild relatives. We highlight a range of different processes that contribute to adaptation and discuss evidence from natural, cultivated, and experimental populations. From an applied perspective, understanding the genetic bases of adaptation and the contribution of plasticity will provide us with new tools to both better understand and mitigate the effect of climate changes on natural and cultivated populations.

GENOMICS OF LONG- AND SHORT- TERM ADAPTATION IN MAIZE AND TEOSINTE

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ABSTRACT

Maize is an excellent model for the study of plant adaptation. Indeed, post domestication maize quickly adapted to a host of new environments across the globe. And work over the last decade has begun to highlight the role of the wild relatives of maize – the teosintes *Zea mays* ssp. *parviglumis* and ssp. *mexicana* – as excellent models for dissecting long-term local adaptation.

Although human-driven selection associated with maize domestication has been extensively studied, the genetic bases of natural variation is still poorly understood. Here we review studies on the genetic basis of adaptation and plasticity in maize and its wild relatives. We highlight a range of different processes that contribute to adaptation and discuss evidence from

31 natural, cultivated, and experimental populations. From an applied perspective, understanding the
32 genetic bases of adaptation and the contribution of plasticity will provide us with new tools to both
33 better understand and mitigate the effect of climate changes on natural and cultivated populations.
34

35 INTRODUCTION

36 A combination of archeobotanical records and genetic data has established that maize (*Zea*
37 *mays* ssp. *mays*) was domesticated around 9 000 years ago in the Balsas river valley of Mexico
38 from the wild teosinte *Zea mays* ssp. *parviglumis* [1–3]. Unlike complex domestication scenarios
39 involving multiple domestication events in the common bean (*Phaseolus vulgaris* L.) and the lima
40 bean (*Phaseolus. lunatus* L.) [4] or multiple progenitors from different regions in barley (*Hordeum*
41 *vulgare*; [5], maize stands a relatively simple scenario involving only a single domestication event
42 resulting in a moderate decrease of genetic diversity of roughly 20% [6].

43 With the rise of coalescent simulation tools since the late 1990's [7], researchers have
44 repeatedly attempted to establish demographic scenarios of maize domestication. All concur with
45 a simple bottleneck model, i.e. a reduction of effective population size (N_e), with <10% of the
46 teosinte population contributing to the maize gene pool [8–11]. A recent investigation indicates
47 that this bottleneck was followed by a major expansion resulting in an N_e for modern maize much
48 larger than that of teosinte [11]. However, the complexity of the forces acting to shape diversity at
49 a genome-wide scale makes it difficult to disentangle them. On one hand, domestication has likely
50 promoted strong positive selection at ~2% to 4% of loci [10] producing one of the most famous
51 text-book example of selective sweeps at *tb1*, a gene responsible for the reduced branching
52 phenotype in maize [12]. On the other hand, purifying selection has also reduced neutral genetic
53 diversity [11]. Such selection may lead to an excess of rare variants, a footprint easily confounded
54 with both positive selection and population expansion [13].

55 After its initial domestication, the geographic range of maize has rapidly exceeded that of
56 its wild relatives, with documented routes of diffusion northward and southward out of Mexico
57 [14, 15] and to the European continent [16]. Today the maize gene pool worldwide consists of
58 locally adapted open-pollinated populations (landraces) as well as modern inbred lines, derived
59 from landraces, that are used in hybrid production for modern breeding. Such spatial movement

60 has exerted a diversity of selective pressures, triggering changes in the phenology of individuals
61 that ultimately determines the completion of the annual cycle and individual fitness [17, 18].

62 In the last decade, the annual teosintes *Zea mays* ssp. *parviglumis* and ssp. *mexicana* have
63 emerged as models for dissecting long-term adaptation to natural selection [19]. While their
64 distribution is rather limited geographically, teosintes span extremely various environmental
65 conditions in terms of temperatures, precipitations and elevations. Migration is also somewhat
66 limited by the complex landscape of Mexico [20, 21]. Moreover, both teosinte taxa display a high
67 level of nucleotide diversity [22] consistent with large estimates of effective population sizes from
68 120k to 160k [23]. Together, these conditions set the stage for extensive local adaptation.

69 Populations respond to environmental changes in three ways: (1) by shifting their range
70 via migration to environments whose conditions are similar to their original conditions; (2) by
71 genetic adaptation through the recruitment of pre-existing or new alleles that increase the fitness
72 of individuals carrying them; or (3) by phenotypic adjustments without genetic alterations, a
73 mechanism called phenotypic plasticity.

74 Recent range shifts driven by global warming have been reported in tree species distributed
75 in California, Oregon and Washington with an average shift compared to mature trees of about
76 27m in altitude and 11kms northwards, towards colder environments [24]. Likewise, rising
77 temperatures have likely caused the upslope migration reported for vascular plants species across
78 European boreal-to-temperate mountains [25].

79 Such measurement in natural populations of teosintes are currently unavailable making the
80 assessment of recent migration in response to climate change unknown. However, a niche
81 modeling study showed that the range of annual teosintes appears to be quite similar to what it was
82 at the time of domestication [26]. From the same study, relatively minor shifts of the niche have
83 occurred even over the dramatic changes of the last glacial maximum, suggesting that migration
84 over long ranges was not necessary.

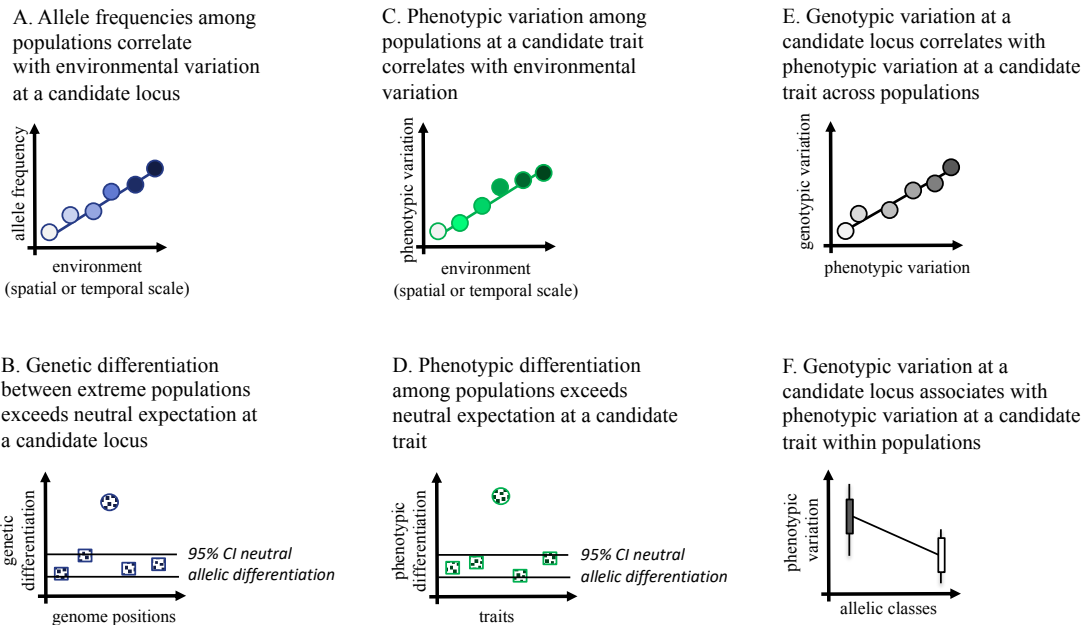
85 In this chapter, we focus on adaptation and phenotypic plasticity. We review methods used
86 to explore genetic adaptation and the factors constraining it. Next, we review empirical reports of
87 short- and long-term adaptation in maize and teosintes. Finally, we discuss the role genetic
88 convergence and phenotypic plasticity have played during adaptation.

89 **How to explore adaptation?**

90 Genetic adaptation can be defined as the modulation of allele frequencies through natural
91 and/or artificial selection. Natural selection is imposed by changes in environmental conditions, or
92 artificial selection by humans. Identification of adaptive loci (Fig. 1A-B) and/or traits (Fig. 1C-D)
93 uses spatial or temporal variation in conjunction with quantification of traits in native
94 environments (Fig. 1F) or in common gardens (Fig. 1G) [27–30]. While the temporal approach
95 includes retrospective studies that follow the phenotypic and genetic composition of populations
96 through time (for instance [31] to infer past selective events), the spatial approach relies on samples
97 of populations that are geographically separated [30, 32].

98 In *Zea*, experimental approaches have been coupled with genotyping of sampled/evolved
99 populations to identify the genomic bases of observed phenotypic changes. More often, however,
100 studies have focused only on species-wide population genomic analyses tracing patterns of
101 variation. These include searches for (1) spatial associations of allele frequencies with
102 environmental factors or phenotypes (Fig. 1A); (2); shifts in allele frequencies across genetic
103 groups (e.g. comparing wild and cultivated samples) using genome scans (Fig. 1B); and (3)
104 differential gene expressions related to population/subspecies differentiation. An increasingly
105 popular approach that was initiated in 2003 by Jaenicke-Despres [33] is the use of ancient DNA,
106 as maize cobs are often well preserved making them an attractive source for ancient DNA studies.
107 Such studies provide access to temporal samples to address past selective events that shaped
108 genomes.

109



110

111 **Figure 1: Experimental approaches to detect potentially adaptive polymorphisms and traits using**
 112 **population genetic (A-B) or phenotypic (C-D) data, or combining both (E-F).**

113 A candidate polymorphism whose allele frequency among populations varies with spatial or temporal
 114 variation can be detected using correlation-based methods (A) or genome-wide scans, where it displays an
 115 elevated differentiation of allele frequencies compared with neutral (squares) loci (B). A candidate trait that
 116 co-varies with spatial or temporal variation among populations can be detected using correlation-based
 117 methods (C) or when phenotypic differentiation measured in common environment(s) exceeds genotypic
 118 differentiation at neutral (squares) loci (D). A link between candidate loci and traits can be established by
 119 correlating genotypic and phenotypic variation measures in common environment(s) across populations
 120 (E), and within populations (F).

121

122 **What constraints adaptation?**

123 Genetic adaptation can proceed through a single beneficial mutation that occurs after the
 124 onset of selection pressure, in which case the classical genetic footprint of a “hard” selective sweep
 125 is observed. Alternatively, it can proceed through a single mutation segregating in the population
 126 before the onset of selection (standing genetic variation), or through recurrent beneficial mutations.
 127 In these latter cases, adaptation produces a “soft” sweep footprint [34].

128 Hard sweeps are characterized by local shifts in allele frequencies due to the hitchhiking
 129 of neutral sites around a selected *de novo* variant occurring on a specific haplotype. Such changes
 130 in allele frequencies can easily be detected by genome scans. In contrast, soft sweeps, which derive

131 from multiple adaptive alleles sweeping in the population, are substantially harder to detect at a
132 genome-wide scale.

133 The relative contribution of hard and soft sweeps has been a long-standing debate and
134 ultimately raises the important question of what limits adaptation. Experimental evolution in model
135 organisms with short generation time such as *Escherichia Coli*, yeast and *Drosophila*
136 *melanogaster* have provided insights into those questions [35–40]. What emerges from these
137 studies is that relevant parameters include the mutation rate, drift and selection [41, 42]. We
138 surveyed these parameters in eight divergent selection experiments undertaken in maize (Table 1)
139 and detail below our interpretations. By applying continuous directional selection on a given
140 quantitative trait, such experiments aim to quantify and understand the limits of selection.
141 However, it should be noted none of the cited work has included multiple replicates.

142 One of the most puzzling observations across experiments is that the response to selection
143 is generally steady over time. In the Golden Glow (GG) experiment, the response varies from 4.7%
144 to 8.7% of the original phenotypic value per cycle of selection across 24 cycles [43]. In the Krug
145 Yellow Dent (KYD), it was estimated at 1.6% and 2.5% per cycle respectively, for high and low
146 seed size direction [44]. In the Iowa Stalk Synthetic (BSSS), the response was of 3.9% per cycle
147 for higher grain yield [45]. In the Iowa Long Ear Synthetic (BSLE), an increase of 1.4% and a
148 decrease of 1.9% per cycle for high and low ear length was observed [44]. The results were more
149 equivocal for Burn's White (BW), for which the response is much stronger and steadier towards
150 high (between 0.1% and 0.3%) than low values (between 0% and 0.32%) for both protein and oil
151 content. This pattern of shift between a strong and steady response to a plateau-like response for
152 the low trait values is explained by physiological limits. Hence after 65 generations a lower limit
153 for protein content is reached where the percentage of oil in the grain (close to 0% in the late
154 generations) is no longer detectable [46, 47]. A similar situation has been reported for some of the
155 late flowering families of MBS847 and F252 that are not able to produce seeds in the local climate
156 conditions where they are selected, while the early still display a significant response after 16
157 generations [48]. Overall, mutations do not appear limiting regardless of the design, whether it
158 started from highly inbred material or a diverse set of intercrossed landraces (Table 1).

159 What differs from one experiment to another, however, is the genomic footprint of the
160 response to selection. Such footprints have been investigated in all but the BW and BSLE design.
161 In GG, in which the mutational target size – the number of sites affecting the trait – was restricted,

162 the effective population size was the highest of all and the selection was intense. The signal is
163 consistent with genome-wide soft sweeps [43, 49]. In KYD, characterized by a larger mutational
164 target, stronger drift (smaller effective population size), but weaker selection, both hard and soft
165 sweeps are observed [50]. In BSSS, in which the mutational target size is the largest, the effective
166 population size small and the selection intense, the signal is consistent with hard sweeps [51]. The
167 F252 and MBS populations display the most limited standing variation and at the same time the
168 strongest drift and selection of all experiments; in these a rapid fixation of new mutations explains
169 the response to selection [48, 52]. Effective population size primarily determines the likelihood of
170 soft sweeps. Hence, when θ (four times the product of effective population size and the beneficial
171 mutation rate) is equal or above 1, and selection is strong enough, adaptation proceeds from
172 multiple *de novo* mutations or standing variation [53]. Below 1, soft sweeps' contribution
173 diminishes with θ . In the experiments from Table 1, selection is strong but $\theta \ll 1$ in all cases.
174 Nevertheless, hard and soft sweeps were associated respectively with the lowest (F252 and MBS)
175 and highest (GG) effective population size, consistent with N_e being a key player. Comparisons
176 among experiments thus contribute to understanding the parameters of importance and their
177 interactions that together shape the genomic patterns of the response to selection.

178 An additional layer of complexity that may substantially impact evolutionary trajectories
179 is that of genetic correlations among traits. Such correlations may emerge from genes with
180 pleiotropic effects, epistatic interactions among genes, and/or loci in tight linkage affecting various
181 traits. While some studies have found that covariance between traits rarely affect adaptation [54],
182 several examples instead suggest that they may either constrain or facilitate adaptation as predicted
183 by Lande [55]). For instance, in *Arabidopsis thaliana* a recent study indicates that polymorphisms
184 with intermediate degrees of pleiotropy favored rapid adaptation to micro-habitats *in natura*. In
185 the case of domestication, tight linkage between genes conferring the so-called domestication
186 syndrome has been invoked as a mechanism facilitating adaptation to the cultivated environment
187 in allogamous species, preventing gene flow from wild relatives to break co-adapted suites of
188 alleles [56]. It turns out that rather than clustering, plant domestication genes identified so far are
189 single locus which are mainly transcription factors (reviewed in [57]) most of which likely display
190 strong epistatic interactions. *tb1* in maize, for instance, interacts with another locus on a different
191 chromosome to alter the sex of maize inflorescences. The introgression of the *tb1* teosinte allele
192 alone changes only ~20% of the inflorescence sex but the introgression of both alleles converts

193 90% of maize's female flowers to male [58]. The maize *tb1* allele segregates at low frequency in
194 teosinte populations but is rarely found associated with the domesticated allele of chromosome 3,
195 as both are likely to evolve under negative selection in teosinte [12, 58]. Their association in maize
196 has however facilitated the acquisition of the domesticated phenotype.

197

198 **Mechanisms of genetic adaptation in maize and teosintes**

199 Populations of teosinte have long evolved under natural selection. In contrast, maize
200 populations have been under artificial human selection that moved phenotypes towards optimal
201 traits tailored to agriculture during a shorter time frame of ~9,000 years [1, 2, 22]. These time
202 scales have left distinct genetic signatures. In theory, traits fixed by domestication should involve
203 genes with larger effect sizes, and standing variation should be a major contributor to
204 domestication [59]. This is supported by crosses between maize and teosinte that led to the
205 discovery of six main QTLs responsible for major phenotypic differences between them, notably
206 vegetative architecture and inflorescence sexuality [60, 61, reviewed in 62]. Among these QTLs,
207 genes with major phenotypic effects have been discovered such as *tb1* and *tga1* (*teosinte glume*
208 *architecture1*). In addition to these major genes, a collection of targets (2 to 4% of the genome
209 according to [6, 10]) have likely contributed to the domesticated phenotype. In contrast, Genome
210 Wide Association (GWA) studies on traits selected over much longer time scale such as drought
211 tolerance or flowering time have highlighted only minor effect loci that rarely contribute to more
212 than 5% of the phenotypic variation [59, 63–65].

213 In addition to the time frame over which adaptation occurs, another important factor for
214 evolution is the nature of variation for selection to act on. Maize and teosintes are genetically very
215 diverse, with as much nucleotide diversity in coding regions between two maize lines as there are
216 between humans and chimpanzees [66]. This diversity is even higher in intergenic regions [67,
217 68]. Some adaptive mutations are found in coding sequences. Examples include non-synonymous
218 changes in the *tga1* gene responsible for the “naked kernel” maize phenotype, and in the
219 *diacylglycerol acyltransferase* (*DGATI-2*) gene resulting in elevated kernel oil content in maize
220 lines [69, 70]. But most observations support adaptation from regulatory non-coding sequences.
221 Indeed, in comparison with *Arabidopsis*, where adaptive variants are enriched in coding sequences
222 [71], in maize and teosinte these are predominantly found in non-coding region: estimates in *Zea*

223 show that non-coding variants may explain as much phenotypic variation as those in coding
224 regions [72, 73]. Selection on regulatory sequences drive important expression changes; hence,
225 genes displaying footprints of selection in maize are usually more expressed than in teosintes [6],
226 and are associated with modified co-expression networks [74].

227 Adaptive variation also results from structural variants. In contrast to the *Arabidopsis* or
228 rice genomes where Transposable Elements (TEs) account for 20-40% of sequence, the maize
229 genome is composed of about 85% TEs [75, 76]. Genome size varies considerably within *Zea*
230 resulting in over 30% differences among maize lines or landraces [72, 77, 78]. Because of their
231 deleterious effect, TEs are often negatively selected and silenced by DNA methylation [79]. But
232 some may also impact gene expression and function in a beneficial manner by various mechanisms
233 such as gene inactivation or differential expression caused by insertion in regulatory regions [80]
234 or TE-mediated genomic rearrangements causing gene insertion, deletion or duplication (reviewed
235 in [81]). A handful of examples of their beneficial impact has been reported in *Zea*. A classic
236 example in maize is at the *tb1* locus, where a transposon inserted in the cis-regulatory region,
237 doubling expression [82]. Teosinte, like most grasses, produces numerous branches tipped by a
238 male inflorescence. In contrast, maize has only one main stalk terminated by a single tassel with
239 repressed development of lateral branches. The increased expression level of *tb1* is the major
240 contributor to this apical dominance [82]. Beyond TEs, Copy Number Variants (CNVs) are also
241 common in the maize genome [83] and they contribute significantly to phenotypic variation [72,
242 84].

243 Another important player in adaptation in *Zea* is gene flow. Indeed, teosinte populations
244 are found in sympatry with maize and hybridization between them is common [85]. Highland
245 maize shows up to 20% *mexicana* introgression, which has likely facilitated their adaptation to
246 high elevations [3, 86]. An ancient DNA study revealed that ancestral highland maize already
247 showed evidence of introgression from *mexicana* [15]. Introgressed regions found at high
248 frequency in highland maize overlap with previously identified QTLs driving adaptive traits [86,
249 87], emphasizing the importance of introgression during post-domestication adaptation. Similarly,
250 recent results suggest that admixture between distinct genetic groups has facilitated adaptation to
251 mid-latitudes in North America and Europe [16].

252 Local adaptation in maize and teosintes

253 Strictly defined, a genotype can be considered locally adapted if it has a higher fitness at
254 its native site than any other non-native genotypes [88]. Locally adapted alleles can be either
255 neutral or deleterious in other environments. Two models depict those situations, namely
256 conditional neutrality and antagonistic pleiotropy [89]. Despite numerous studies, the genetic
257 processes underlying local adaptation in natural populations are still poorly understood. This is
258 mainly due to traits driving local adaptation being mostly quantitative [29]. This complex
259 determinism may involve numerous, but not necessarily substantial, allele frequency changes.

260 Studies showed that highland maize landraces outperform lowland maize populations in
261 their native environment but perform worse than any other population at lower elevation sites [90],
262 suggesting strong adaptation for high altitude.

263 Natural selection acts on phenotypic traits, changing the frequency of underlying alleles
264 and shifting population phenotypes toward local optima. Since these optima rely on local
265 conditions, genes ecologically important usually differ between sub-populations in heterogeneous
266 environments, resulting in divergence in allele frequencies over time. This characteristic has been
267 utilized in genome scans to mine correlations between allele frequencies and environmental
268 variables (Fig. 1A). Such studies have revealed that, in teosintes, these loci impact flowering time
269 and adaptation to soil composition [20, 91, 92]. Flowering time was also a key component of
270 maize's local adaptation to higher latitudes during post-domestication. Maize evolved a reduced
271 sensitivity to photoperiod, in part due to a CACTA-like TE insertion in the promoter region of the
272 *ZmCCT* gene that drives photoperiod response in early flowering maize [93, 94]. An example of
273 adaptation driven by soil interactions is the tolerance of maize and teosinte to aluminum in highly
274 acidic soils. In these lines, the adaptation is linked to tandem duplications of the *MATE1* gene
275 involved in the extrusion of toxic compounds [84].

276 Numerous other biotic and abiotic factors are likely involved in adaptation in maize and
277 teosinte, including predation, parasitism, moisture and herbicide [95, 96]. For example, a study on
278 *parviglumis* has shown that in response to herbivory, immunity genes involved in the inhibition of
279 insects' digestive proteases experienced a recent selective sweep in a region of Mexico, probably
280 reflecting local adaptation [97].

281 Interestingly, four large inversion polymorphisms seem to play an important role in local
282 adaptation. Among them, a 50Mb inversion on chromosome 1 is found at high frequency in

283 *parviglumis* (20-90%), low frequency in *mexicana* (10%), and is absent in maize. This inversion
284 is highly correlated with altitude and significantly associated with temperature and precipitation
285 [20, 98]. Inversions on chromosomes 3, 4 and 9 also displayed environmental association in
286 teosintes and maize landraces for the first two and in teosintes for the last one [20, 99]. Local
287 adaptation to different habitats or niches is a gradual process that can promote divergence and, in
288 the long run, ecological speciation [100]. Genotyping of a broad sample of 49 populations covering
289 the entire geographic range of teosintes has recently provided some evidence of this. Aguirre-
290 Liguori et al, [91] showed that both within *parviglumis* and *mexicana*, populations distributed at
291 the edge of the ecological niche experience stronger local adaptation, suggesting that local
292 adaptation may have contributed to divergence between these two subspecies.

293 **How convergent is adaptation?**

294 Convergent adaptation is the result of independent events of similar phenotypic changes to
295 adapt to analogous environmental constraints [101]. In this review, we concentrated on genetic
296 convergence in populations of the same, or closely related, species which are the result of
297 convergent evolution at the molecular level. By molecular convergence, we include convergence
298 at the same nucleotide positions, genes or orthologues. Several studies illustrate this, suggesting
299 that genomes may respond in predictable ways to selection [102–106]. The selected alleles can
300 originate from independent mutation events in different lineages, from shared ancestral variation
301 or by introgression [105].

302 A classical way to study convergence is experimental evolution. During these experiments,
303 replicates of the same genotype are grown for many generations in new environments. Such studies
304 have often shown that convergent evolution is common [37, 107]. Domestication can be thought
305 of as an example of long-term experimental evolution, and domesticates provide striking examples
306 of phenotypic convergence, with common traits usually referred to as the domestication syndrome.
307 These phenotypes include, but are not limited to, larger fruits or gains, less branching, loss of
308 shattering, and loss of seed dormancy [108]. QTL mapping can be performed to identify the genes
309 controlling these phenotypes in different species. As an example, seeds on wild grasses shed
310 naturally at maturity. During domestication this trait was rapidly selected against since it causes
311 inefficient harvesting [109]. QTL mapping of sorghum, rice and maize reveals that the *Shattering1*

312 genes are involved in the loss of the dispersal mechanism and were under convergent evolution
313 during their domestication [110].

314 But genetic convergence can also be observed over much shorter evolutionary time, at the
315 intraspecific level across populations. Here genome scans for extreme differentiation in allele
316 frequency between multiple pairs of diverged populations along gradients, for instance, are
317 typically employed. This method has been used to test for convergent adaptation in highland maize
318 landraces and teosintes. Fustier *et al.*, [92] found several instances (24/40) of convergence
319 involving the same haplotype in two gradients of adaptation to high altitude in teosintes. In maize,
320 the Mesoamerican and South American populations independently adapted from distinct lowland
321 populations to high elevation conditions [14]. These populations exhibit several similar phenotypic
322 characteristics not observed in lowland populations such as changes in inflorescence morphology
323 and stem coloration. A study found that highland adaptation is likely due to a combination of
324 introgression events, selection on standing genetic variation and independent *de novo* mutations
325 [111]. These studies also showed that convergent evolution involving identical nucleotide changes
326 is uncommon and most selected loci arise from standing genetic variation present in lowland
327 populations. This is not surprising given the relative short time frame of highland adaptation in
328 maize compared to teosinte subspecies.

329 Recently, a new method has been developed to infer modes of convergence [112], using
330 covariance of allele frequencies in windows around a selected site to explicitly compare different
331 models of origin for a selected variant. This novel method should give a better insight on the
332 genetic mechanisms underlying convergence.

333 **What is the role of phenotypic plasticity?**

334 Phenotypic plasticity is defined as the capacity of a genotype to produce a range of
335 expressed phenotypes in distinct environments. This is achieved through differential
336 developmental pathways in response to changing conditions [113, 114]. Plasticity can be an
337 important process during adaptation. Indeed, populations with flexible phenotypes are predicted
338 to better cope with environmental changes and to display a greater potential for expansion [115].
339 This process is particularly important for plants as they are fixed in a specific location and not
340 sheltered from the environment [116].

341 When the environment changes, the phenotypic optimum of a population is likely altered
342 as well. As a result, individuals that show a plastic response in the direction of the new optimum
343 will have a fitness advantage. In contrast, individuals that exhibit no plasticity or that produce
344 phenotypes too far from the optimum will be selected against.

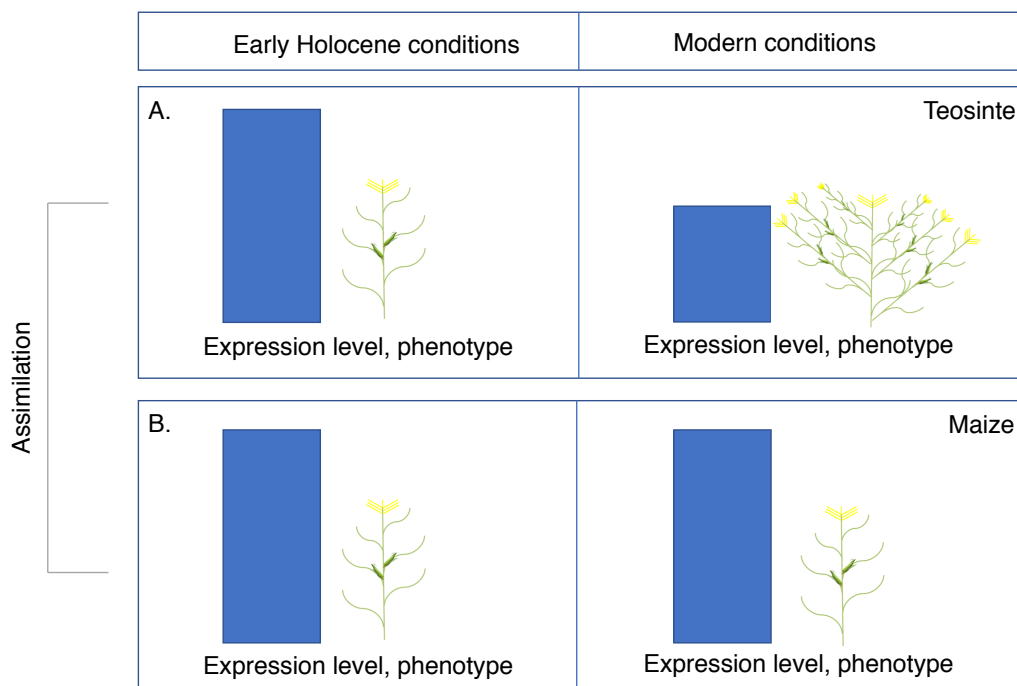
345 Plasticity has limits, however, and may entail a fitness cost. For instance, compared to
346 developmentally fixed phenotypes, plastic individuals in constant environments may display lower
347 fitness or produce a less adapted phenotype. Possible reasons include sensory mechanisms that
348 have a high energetic cost, the epistatic effects of regulatory genes involved in the plastic response,
349 lag time between the perception and the phenotypic response and genetic correlations among traits
350 [117–119].

351 Phenotypic plasticity is difficult to study as it arises from genetic and environmental
352 interactions which are often hard to disentangle. After a number of generations of constant
353 selection, for example, the fixation of genetic variation that constitutively expresses the trait can
354 lead to a loss of plasticity via a process called genetic assimilation [120–122]. Hence an initially
355 plastic phenotype may result in genetic adaptation after genetic assimilation. Some examples of
356 plastic responses are well documented in plants, for example, the response to vernalization in
357 *Arabidopsis* regulating flowering time in some ecotypes [118]. Another example is the change in
358 seed dormancy in response to the environment which prevents germination when conditions are
359 unlikely to lead to the survival of the plant [118].

360 Taxa in *Zea* are good models to investigate plasticity as maize is grown worldwide and
361 adapted to a diversity of environments. In addition, studies of teosintes allow comparison to
362 ancestral levels of plasticity. A recent experiment evaluated plasticity in maize by studying
363 Genotype by Environment interactions (GxE) for a number of phenotypes in 858 inbred lines
364 across 21 locations across North America [123]. Results demonstrated that genes selected for high
365 yield in temperate climates in North America correlated with low variance in GxE. This suggests
366 a loss of plasticity accompanying selection for stable crop performance across environments, a
367 major goal for breeders. In addition, GxE was mainly explained by regulatory regions [123], an
368 observation in agreement with previous findings indicating that most phenotypic variation in maize
369 is due to gene regulation [124].

370 Recent work on maize and *parviglumis* growing under environmental conditions
371 mimicking those encountered at the time of maize domestication (comparatively lower CO₂

372 atmospheric concentration and lower temperatures) gives better insights into this phenomenon.
 373 The results showed that teosintes grown in these conditions exhibit contemporary maize-like
 374 phenotypes [125]. In contrast, modern maize has lost this plastic response. Over 2000 candidate
 375 loci associated with phenotypic changes showed altered expression in teosintes but not in maize,
 376 implying that they are no longer environmentally responsive (Figure2; [126]). Such loss of
 377 phenotypic plasticity may limit the ability of maize to cope with environmental variability in the
 378 face of current climate changes.



379
 380 **Figure 2: Schematic representation of differences in plastic responses between maize and teosinte in**
 381 **Early-Holocene (EH) conditions.**

382 (A) *parviglumis* plants exhibit maize-like phenotypes in the EH conditions (vegetative architecture,
 383 inflorescence sexuality and seed maturation). Phenotypes of *parviglumis* in modern conditions are typical
 384 of today's plants. These changes in phenotypes are associated with altered expression levels of over 2000
 385 candidate loci in teosinte, here we represent the schematic expression of one gene between the two
 386 environments in teosinte. (B) In contrast, these same traits and underlying gene expression remain
 387 unchanged in maize between EH and modern conditions.

388

389 CONCLUSIONS

390 Ongoing global warming has drastic effects on maize production, with an estimated impact of
 391 temperature and precipitation on yield of 3.8% worldwide between 1980 and 2008 [127]. Predicted
 392 changes that include further increases in temperatures and decline in rainfall, as well as shifts of

393 pests and diseases, represent a huge challenge. There is thus a pressing need to better understand
 394 the dynamics and genomic basis of adaptation. Future climate projections predict that changes in
 395 temperature will impact the distribution and survival of both cultivated maize and its wild relatives
 396 [26, 128]. Most modeling studies, however, have focused on the climate tolerance of species, while
 397 the response to climate can depend on other factors such as plasticity and local adaptation. This
 398 suggests that the response should be studied at the level of individual populations to better
 399 understand the basis of adaption

DS experiments	F252 (F252)	MBS847 (MBS)	Krug Yellow Dent (KYD)	Burn's White (BW)	Burn's White (BW)	Golden Glow (GG)	Iowa Stiff Stalk Synthetic (BSSS)	Iowa Long Ear Synthetic (BSLE)
References ^a	[1,2]	[1,2]	[3]	[4,5]	[4,5]	[6,7]	[10,11,12]	[14]
Directions (High/Low) ^b	H/L	H/L	H/L	H/L	H/L	H	H	H/L
Trait ^c	Flowering	Flowering	Seed size	Protein	Oil	Ears/plant	Grain yield	Ear length
Material type ^d	Inbred	Inbred	OP variety	OP variety	OP variety	OP variety	Synthetic population	Synthetic population
Mutational target ^e	>60 QTLs ^[8]	>60 QTLs ^[8]	>300 loci ^[9]	102 to 178 factors	14 to 69 factors	limited ^[6]	large ^[13]	25 QTLs ^[15]
Standing variation ^f	1.9%	0.19%	pervasive	pervasive	pervasive	pervasive	pervasive	pervasive
Census population size ^g	1000	1000	1200 to 1500	60 to 120	60 to 120	4250 (1-12) 14250 (13-30)	>1240	4000
N _e ^h	3.1 to 20.2	5.8 to 13.5	369	4 to 12	4 to 12	667	10 to 20	14
Selection coefficient (%)	1	1	8	20	20	0.5 to 5	5	7.5
Heritability ⁱ	0.14/0.13	0.13/0.16	-	0.21/0.07	0.23/0.23	0.88	0.4	0.05
Number of founders ^j	2 haplotypes	2 haplotypes	100 founders	24 ears (H) 12 ears (L)	24 ears (H) 12 ears (L)	~300 founders	16 founders	12 founders
Reproductive mode	Selfing	Selfing	Outcrossing	Outcrossing	Outcrossing	Outcrossing	Outcrossing	Outcrossing
Sampling ^k	All/ind	All/ind	All/bulk	All/bulk	All/bulk	All/bulk	All/bulk	All/bulk
Number of generations	16	16	30	114	114	30	17	27

400

401 **Table 1. Description of eight long-term (>16 generations) Divergent Selection (DS) experiments in**
 402 **maize with groups of features primarily (but not exclusively) related to Mutations (3), Drift (1),**
 403 **Selection (2) and Power to detect selection targets (5) highlighted by groups.**

404 ^a: References from which values were taken for each DS experiment are indicated in superscript.

405 ^b: Direction of selection towards higher and/or lower values than the initial material.

406 ^c: Protein and Oil designate protein and oil content of the grain, Ears/plan relates to prolificacy.

407 ^d: Inbred: Inbred line; OP variety: Open Pollinated population.

408 ^e: Number of factors in BW was estimated from the trait value, predicted gain and additive genetic variance.

409 ^f: Standing variation was estimated from 50k SNP array for F252 and MBS.

410 ^g: For GG, 4250 individuals were evaluated from cycles 1 to 12, and 14250 in the following cycles.

411 ^h: Effective population size (N_e) estimates given from the variance of offspring number [129], range is given
412 when N_e was estimated at each generation

413 ⁱ: Broad-sense heritability estimated from genetic variation between progenies of the same family. Average
414 values across generations is reported here.

415 ^j: expressed either as number of haplotypes (a single founder=individual bears 2 haplotypes), number of
416 founders, or number of ears (all individuals of a given ear share identical mother but different fathers). For
417 GG, most selection cycles used 300 founders.

418 ^k: Seeds from all time points (All) are available, and were either collected separately on each selected
419 individual (/ind) or in bulk (/bulk).

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478

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