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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.

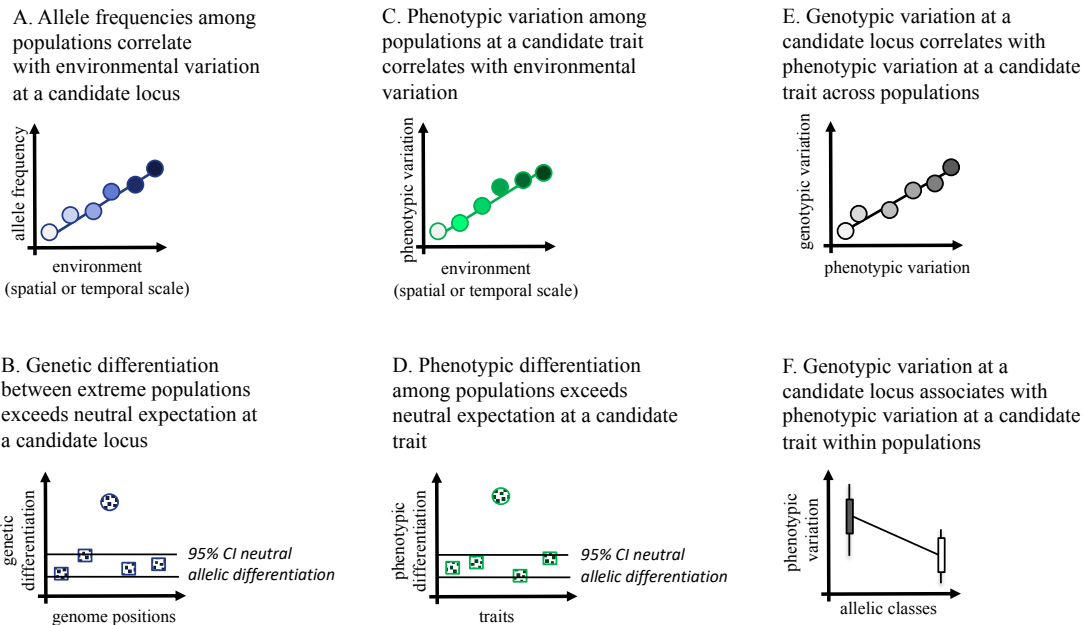
85 In this chapter, we focus on adaptation and phenotypic plasticity. We review methods used
86 to explore genetic adaptation and the factors constraining it. Next, we review empirical reports of
87 short- and long-term adaptation in maize and teosintes. Finally, we discuss the role genetic
88 convergence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

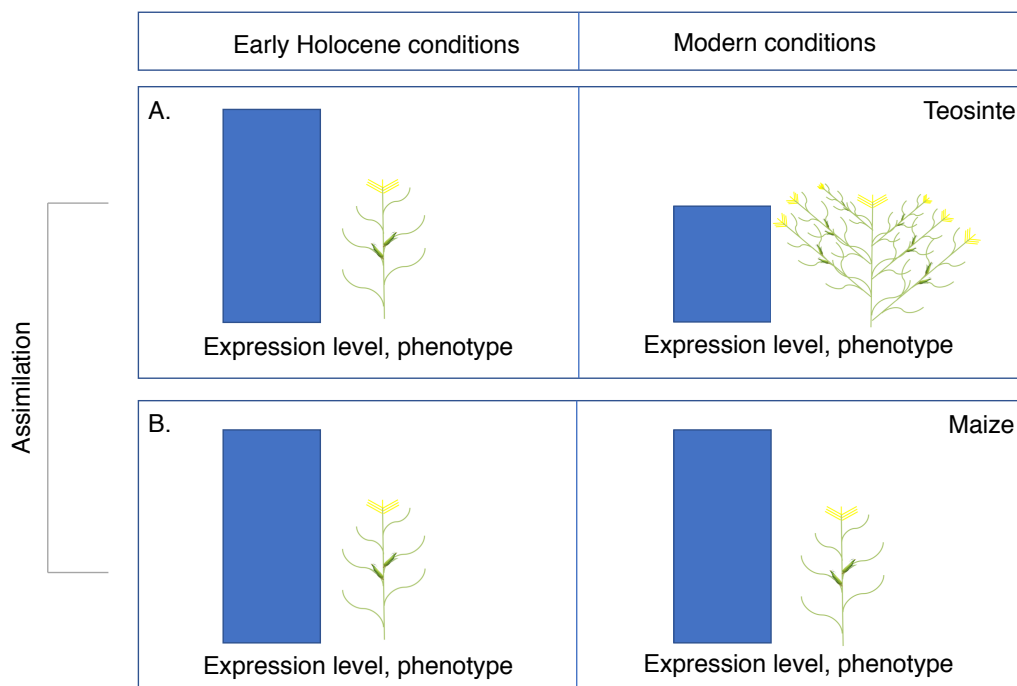
345 Plasticity has limits, however, and may entail a fitness cost. For instance, compared to
346 developmentally fixed phenotypes, plastic individuals in constant environments may display lower
347 fitness or produce a less adapted phenotype. Possible reasons include sensory mechanisms that
348 have 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).

420 [1]: Durand, E., M. I. Tenailon, C. Ridet, D. Coubriche, P. Jamin, S. Jouanne, A. Ressayre, A.
421 Charcosset, and C. Dillmann. 2010. "Standing Variation and New Mutations Both Contribute to a
422 Fast Response to Selection for Flowering Time in Maize Inbreds." *BMC Evolutionary Biology* 10:2.
423 <https://doi.org/10.1186/1471-2148-10-2>.

424 [2]: Durand, E., M. I. Tenailon, X. Raffoux, S. Thépot, M. Falque, P. Jamin, A. Bourgaïs, A. Ressayre,
425 and C. Dillmann. 2015. "Dearth of Polymorphism Associated with a Sustained Response to Selection
426 for Flowering Time in Maize." *BMC Evolutionary Biology* 15 (1):103.
427 <https://doi.org/10.1186/s12862-015-0382-5>.

428 [3]: Odhiambo, M. O., and W. A. Compton. 1987. "Twenty Cycles of Divergent Mass Selection for Seed
429 Size in Corn." *Crop Science* 27 (6). Crop Science Society of America:1113–16.

430 [4]: Moose, S. P., J. W. Dudley, and T. R. Rocheford. 2004. "Maize Selection Passes the Century Mark: A
431 Unique Resource for 21st Century Genomics." *Trends in Plant Science*.
432 <https://doi.org/10.1016/j.tplants.2004.05.005>.

433
434 [5]: Dudley, J. W., and R. J. Lambert. 2010. "100 Generations of Selection for Oil and Protein in Corn."
435 In *Plant Breeding Reviews*, 79–110. <https://doi.org/10.1002/9780470650240.ch5>.

436 [6]: Leon, N. De, and J. G. Coors. 2002. "Twenty-Four Cycles of Mass Selection for Prolificacy in the
437 Golden Glow Maize Population." *Crop Science* 42 (2):325–33.
438 <https://doi.org/10.2135/cropsci2002.3250>.

439 [7]: Maita, R., and J. G. Coors. 1996. "Twenty Cycles of Biparental Mass Selection for Prolificacy in the
440 Open-Pollinated Maize Population Golden Glow." *Crop Science* 36 (6). Crop Science Society of
441 America:1527–32.

442
443 [8]: Buckler, E. S., J. B. Holland, P. J. Bradbury, C. B. Acharya, P. J. Brown, C. Browne, E. Ersoz, et al.

- 444 2009. “The Genetic Architecture of Maize Flowering Time.” *Science* 325 (5941):714–18.
445 <https://doi.org/10.1126/science.1174276>.
446
- 447 [9]: Liu, J., J. Huang, H. Guo, L. Lan, H. Wang, Y. Xu, X. Yang, et al. 2017. “The Conserved and Unique
448 Genetic Architecture of Kernel Size and Weight in Maize and Rice.” *Plant Physiology* 175 (2). Am
449 Soc Plant Biol:774–85.
450
- 451 [10]: Lamkey, K. R. 1992. “Fifty Years of Recurrent Selection in the Iowa Stiff Stalk Synthetic Maize
452 Population.” *Maydica* 37 (1):19.
453
- 454 [11]: Hallauer, A. R., M. J. Carena, and J.B. M. Filho. 2010. “Quantitative Genetics in Maize Breeding.”
455 In *Handbook of Plant Breeding*, 1–680. <https://doi.org/10.1017/CBO9781107415324.004>.
- 456 [12]: Gerke, J. P., J. W. Edwards, K. E. Guill, J. Ross-Ibarra, and M. D. McMullen. 2015. “The Genomic
457 Impacts of Drift and Selection for Hybrid Performance in Maize.” *Genetics* 201 (3):1201–11.
458 <https://doi.org/10.1534/genetics.115.182410>.
- 459 [13]: Yang, J., S. Mezmouk, A. Baumgarten, E. S. Buckler, K. E. Guill, M. D. McMullen, R. H. Mumm,
460 and J. Ross-Ibarra. 2017. “Incomplete Dominance of Deleterious Alleles Contributes Substantially
461 to Trait Variation and Heterosis in Maize.” *PLoS Genetics* 13 (9).
462 <https://doi.org/10.1371/journal.pgen.1007019>.
463
- 464 [14]: Lopez-Reynoso, J. J. De. 1997. “Divergent Mass Selection for Ear Length in the Iowa Long Ear
465 Synthetic Maize Cultivar after Twenty-Seven Cycles of Selection.” Digital Repository@ Iowa State
466 University, <http://lib.dr.iastate.edu/>.
467
- 468 [15]: Ross, A. J., A. R. Hallauer, and M. Lee. 2006. “Genetic Analysis of Traits Correlated with Maize Ear
469 Length.” *Maydica* 51 (2):301–13.
470

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479 **REFERENCES**

- 480 1. Piperno DR, Flannery K V (2001) The earliest archaeological maize (*Zea mays* L.) from
481 highland Mexico: new accelerator mass spectrometry dates and their implications. *Proc*
482 *Natl Acad Sci U S A* 98:2101–2103 . doi: 10.1073/pnas.98.4.2101
- 483 2. Matsuoka Y, Vigouroux Y, Goodman MM, Sanchez G J, Buckler E, Doebley J (2002) A
484 single domestication for maize shown by multilocus microsatellite genotyping. *Proc Natl*
485 *Acad Sci U S A* 99:6080–6084 . doi: 10.1073/pnas.052125199
- 486 3. van Heerwaarden J, Doebley J, Briggs WH, Glaubitz JC, Goodman MM, de Jesus
487 Sanchez Gonzalez J, Ross-Ibarra J (2011) Genetic signals of origin, spread, and
488 introgression in a large sample of maize landraces. *Proc Natl Acad Sci* 108:1088–1092 .
489 doi: 10.1073/pnas.1013011108
- 490 4. Kwak M, Toro O, Debouck DG, Gepts P (2012) Multiple origins of the determinate growth
491 habit in domesticated common bean (*Phaseolus vulgaris*). *Ann Bot* 110:1573–1580 . doi:
492 10.1093/aob/mcs207
- 493 5. Poets AM, Fang Z, Clegg MT, Morrell PL (2015) Barley landraces are characterized by
494 geographically heterogeneous genomic origins. *Genome Biol* 16: . doi: 10.1186/s13059-
495 015-0712-3
- 496 6. Hufford MB, Xu X, van Heerwaarden J, Pyhäjärvi T, Chia J-M, Cartwright RA, Elshire RJ,
497 Glaubitz JC, Guill KE, Kaeppler SM, Lai J, Morrell PL, Shannon LM, Song C, Springer
498 NM, Swanson-Wagner RA, Tiffin P, Wang J, Zhang G, Doebley J, McMullen MD, Ware
499 D, Buckler ES, Yang S, Ross-Ibarra J (2012) Comparative population genomics of maize
500 domestication and improvement. *Nat Genet* 44:808–811 . doi: 10.1038/ng.2309
- 501 7. Hudson RR (2002) Generating samples under a Wright-Fisher neutral model of genetic
502 variation. *Bioinformatics* 18:337–338 . doi: 10.1093/bioinformatics/18.2.337
- 503 8. Eyre-Walker a, Gaut RL, Hilton H, Feldman DL, Gaut BS (1998) Investigation of the
504 bottleneck leading to the domestication of maize. *Proc Natl Acad Sci U S A* 95:4441–
505 4446 . doi: 10.1073/pnas.95.8.4441
- 506 9. Tenaillon MI, U'Ren J, Tenaillon O, Gaut BS (2004) Selection versus demography: A
507 multilocus investigation of the domestication process in maize. *Mol Biol Evol* 21:1214–
508 1225 . doi: 10.1093/molbev/msh102
- 509 10. Wright SI, Bi IV, Schroeder SG, Yamasaki M, Doebley JF, McMullen MD, Gaut BS (2005)
510 The effects of artificial selection on the maize genome. *Science* 308:1310–1314 . doi:
511 10.1126/science.1107891
- 512 11. Beissinger TM, Wang L, Crosby K, Durvasula A, Hufford MB, Ross-Ibarra J (2016)
513 Recent demography drives changes in linked selection across the maize genome. *Nat*
514 *Plants* 2:16084 . doi: 10.1038/nplants.2016.84
- 515 12. Doebley J, Stec A, Gustus C (1995) teosinte branched1 and the origin of maize: evidence
516 for epistasis and the evolution of dominance. *Genetics* 141:333–346
- 517 13. Cvijović I, Good BH, Desai MM (2018) The Effect of Strong Purifying Selection on
518 Genetic Diversity. *Genetics*. doi: 10.1534/genetics.118.301058
- 519 14. Vigouroux Y, Glaubitz JC, Matsuoka Y, Goodman MM, Sánchez G. J, Doebley J (2008)
520 Population structure and genetic diversity of New World maize races assessed by DNA
521 microsatellites. *Am J Bot* 95:1240–1253 . doi: 10.3732/ajb.0800097
- 522 15. Da Fonseca RR, Smith BD, Wales N, Cappellini E, Skoglund P, Fumagalli M, Samaniego

- 523 JA, Carøe C, Ávila-Arcos MC, Hufnagel DE, Korneliussen TS, Vieira FG, Jakobsson M,
524 Arriaza B, Willerslev E, Nielsen R, Hufford MB, Albrechtsen A, Ross-Ibarra J, Gilbert MTP
525 (2015) The origin and evolution of maize in the Southwestern United States. *Nat Plants* 1:
526 . doi: 10.1038/nplants.2014.3
- 527 16. Brandenburg JT, Mary-Huard T, Rigaille G, Hearne SJ, Corti H, Joets J, Vitte C,
528 Charcosset A, Nicolas SD, Tenaillon MI (2017) Independent introductions and admixtures
529 have contributed to adaptation of European maize and its American counterparts. *PLoS*
530 *Genet* 13: . doi: 10.1371/journal.pgen.1006666
- 531 17. Chuine I (2010) Why does phenology drives species distribution? *Philos Trans R Soc*
532 *London B* 365:3149–3160 . doi: doi: 10.1098/rstb.2010.0142
- 533 18. Swarts K, Gutaker RM, Benz B, Blake M, Bukowski R, Holland J, Kruse-Peeples M,
534 Lepak N, Prim L, Romay MC, Ross-Ibarra J, Sanchez-Gonzalez J de J, Schmidt C,
535 Schuenemann VJ, Krause J, Matson RG, Weigel D, Buckler ES, Burbano HA (2017)
536 Genomic estimation of complex traits reveals ancient maize adaptation to temperate
537 North America. *Science* (80-) 357:512–515 . doi: 10.1126/science.aam9425
- 538 19. Hufford MB, Bilinski P, Pyhäjärvi T, Ross-Ibarra J (2012) Teosinte as a model system for
539 population and ecological genomics. *Trends Genet.* 28:606–615
- 540 20. Pyhäjärvi T, Hufford MB, Mezouk S, Ross-Ibarra J (2013) Complex patterns of local
541 adaptation in teosinte. *Genome Biol Evol* 5:1594–1609 . doi: 10.1093/gbe/evt109
- 542 21. De Jesús Sánchez González J, Corral JAR, García GM, Ojeda GR, De La Cruz Larios L,
543 Holland JB, Medrano RM, Romero GEG (2018) Ecogeography of teosinte. *PLoS One.*
544 doi: 10.1371/journal.pone.0192676
- 545 22. Fukunaga K, Hill J, Vigouroux Y, Matsuoka Y, Sanchez J, Liu KJ, Buckler ES, Doebley J
546 (2005) Genetic diversity and population structure of teosinte. *Genetics* 169:2241–2254 .
547 doi: genetics.104.031393 [pii]r10.1534/genetics.104.031393
- 548 23. Ross-Ibarra J, Tenaillon M, Gaut BS (2009) Historical divergence and gene flow in the
549 genus *Zea*. *Genetics* 181:1399–1413 . doi: 10.1534/genetics.108.097238
- 550 24. Monleon VJ, Lintz HE (2015) Evidence of tree species' range shifts in a complex
551 landscape. *PLoS One* 10: . doi: 10.1371/journal.pone.0118069
- 552 25. Pauli H, Gottfried M, Dullinger S, Abdaladze O, Akhalkatsi M, Alonso JLB, Coldea G, Dick
553 J, Erschbamer B, Calzado RF, Ghosn D, Holten JI, Kanka R, Kazakis G, Kollar J,
554 Larsson P, Moiseev P, Moiseev D, Molau U, Mesa JM, Nagy L, Pelino G, Puscas M,
555 Rossi G, Stanisci A, Syverhuset AO, Theurillat J-P, Tomaselli M, Unterluggauer P, Villar
556 L, Vittoz P, Grabherr G (2012) Recent Plant Diversity Changes on Europe's Mountain
557 Summits. *Science* (80-) 336:353–355 . doi: 10.1126/science.1219033
- 558 26. Hufford MB, Martínez-Meyer E, Gaut BS, Eguiarte LE, Tenaillon MI (2012) Inferences
559 from the Historical Distribution of Wild and Domesticated Maize Provide Ecological and
560 Evolutionary Insight. *PLoS One* 7: . doi: 10.1371/journal.pone.0047659
- 561 27. Anderson JT, Geber MA (2010) Demographic source-sink dynamics restrict local
562 adaptation in Elliott's blueberry (*Vaccinium elliotii*). *Evolution* (N Y) 64:370–384 . doi:
563 10.1111/j.1558-5646.2009.00825.x
- 564 28. Fournier-Level A, Korte A, Cooper MD, Nordborg M, Schmitt J, Wilczek AM (2011) A map
565 of local adaptation in *Arabidopsis thaliana*. *Science* (80-) 334:86–89 . doi:
566 10.1126/science.1209271

- 567 29. Savolainen O, Lascoux M, Merilä J (2013) Ecological genomics of local adaptation. *Nat.*
568 *Rev. Genet.* 14:807–820
- 569 30. Endler JA (1986) Natural selection in the wild
- 570 31. Thompson J, Charpentier A, Bouguet G, Charmasson F, Roset S, Buatois B, Vernet P,
571 Gouyon P-H (2013) Evolution of a genetic polymorphism with climate change in a
572 Mediterranean landscape. *Proc Natl Acad Sci U S A* 110:2893–7 . doi:
573 10.1073/pnas.1215833110
- 574 32. Tiffin P, Ross-Ibarra J (2014) Advances and limits of using population genetics to
575 understand local adaptation. *Trends Ecol. Evol.* 29:673–680
- 576 33. Jaenicke-Despres V (2003) Early Allelic Selection in Maize as Revealed by Ancient DNA.
577 *Science* (80-) 302:1206–1208 . doi: 10.1126/science.1089056
- 578 34. Hermisson J, Pennings PS (2017) Soft sweeps and beyond: understanding the patterns
579 and probabilities of selection footprints under rapid adaptation. *Methods Ecol Evol* 8:700–
580 716 . doi: 10.1111/2041-210X.12808
- 581 35. Bell G, Collins S (2008) Adaptation, extinction and global change. *Evol Appl* 1:3–16 . doi:
582 10.1111/j.1752-4571.2007.00011.x
- 583 36. Burke MK, Dunham JP, Shahrestani P, Thornton KR, Rose MR, Long AD (2010)
584 Genome-wide analysis of a long-term evolution experiment with *Drosophila*. *Nature*
585 467:587–590 . doi: 10.1038/nature09352
- 586 37. Tenaillon O, Rodriguez-Verdugo A, Gaut RL, McDonald P, Bennett AF, Long AD, Gaut
587 BS (2012) The Molecular Diversity of Adaptive Convergence. *Science* (80-) 335:457–461
588 . doi: 10.1126/science.1212986
- 589 38. Burke MK, Liti G, Long AD (2014) Standing genetic variation drives repeatable
590 experimental evolution in outcrossing populations of *saccharomyces cerevisiae*. *Mol Biol*
591 *Evol* 31:3228–3239 . doi: 10.1093/molbev/msu256
- 592 39. Graves JL, Hertweck KL, Phillips MA, Han M V., Cabral LG, Barter TT, Greer LF, Burke
593 MK, Mueller LD, Rose MR, Singh N (2017) Genomics of parallel experimental evolution in
594 *drosophila*. *Mol Biol Evol* 34:831–842 . doi: 10.1093/molbev/msw282
- 595 40. Good BH, McDonald MJ, Barrick JE, Lenski RE, Desai MM (2017) The dynamics of
596 molecular evolution over 60,000 generations. *Nature* 551:45–50 . doi:
597 10.1038/nature24287
- 598 41. Schlötterer C, Kofler R, Versace E, Tobler R, Franssen SU (2014) Combining
599 experimental evolution with next-generation sequencing: a powerful tool to study
600 adaptation from standing genetic variation. *Heredity (Edinb)* 1–10 . doi:
601 10.1038/hdy.2014.86
- 602 42. Franssen SU, Kofler R, Schlötterer C (2017) Uncovering the genetic signature of
603 quantitative trait evolution with replicated time series data. *Heredity (Edinb)* 118:42–51 .
604 doi: 10.1038/hdy.2016.98
- 605 43. De Leon N, Coors JG (2002) Twenty-four cycles of mass selection for prolificacy in the
606 Golden Glow maize population. *Crop Sci* 42:325–333 . doi: 10.2135/cropsci2002.3250
- 607 44. Lopez-Reynoso JDJ, Hallauer AR (1998) Twenty-seven cycles of divergent mass
608 selection for ear length in maize. *Crop Sci* 38:1099–1107 . doi:
609 10.2135/cropsci1998.0011183X003800040035x
- 610 45. Lamkey KR (1992) Fifty years of recurrent selection in the Iowa Stiff Stalk Synthetic

- 611 maize population. *Maydica* 37:19
- 612 46. Moose SP, Dudley JW, Rocheford TR (2004) Maize selection passes the century mark: A
613 unique resource for 21st century genomics. *Trends Plant Sci.* 9:358–364
- 614 47. Dudley JW, Lambert RJ (2010) 100 Generations of Selection for Oil and Protein in Corn.
615 In: *Plant Breeding Reviews*. pp 79–110
- 616 48. Durand E, Tenailon MI, Raffoux X, Thépot S, Falque M, Jamin P, Bourgeois A, Ressayre
617 A, Dillmann C (2015) Dearth of polymorphism associated with a sustained response to
618 selection for flowering time in maize. *BMC Evol Biol* 15:103 . doi: 10.1186/s12862-015-
619 0382-5
- 620 49. Maita R, Coors JG (1996) Twenty cycles of biparental mass selection for prolificacy in the
621 open-pollinated maize population Golden Glow. *Crop Sci* 36:1527–1532
- 622 50. Odhiambo MO, Compton WA (1987) Twenty cycles of divergent mass selection for seed
623 size in corn. *Crop Sci* 27:1113–1116
- 624 51. Gerke JP, Edwards JW, Guill KE, Ross-Ibarra J, McMullen MD (2015) The genomic
625 impacts of drift and selection for hybrid performance in maize. *Genetics* 201:1201–1211 .
626 doi: 10.1534/genetics.115.182410
- 627 52. Durand E, Tenailon MI, Ridet C, Coubriche D, Jamin P, Jouanne S, Ressayre A,
628 Charcosset A, Dillmann C (2010) Standing variation and new mutations both contribute to
629 a fast response to selection for flowering time in maize inbreds. *BMC Evol Biol* 10:2 . doi:
630 10.1186/1471-2148-10-2
- 631 53. Messer PW, Petrov DA (2013) Population genomics of rapid adaptation by soft selective
632 sweeps. *Trends Ecol Evol* 28:659–669 . doi: 10.1016/j.tree.2013.08.003
- 633 54. Agrawal AF, Stinchcombe JR (2009) How much do genetic covariances alter the rate of
634 adaptation? *Proc R Soc B Biol Sci* 276:1183–1191 . doi: 10.1098/rspb.2008.1671
- 635 55. Lande R (1979) Quantitative Genetic Analysis of Multivariate Evolution, Applied to Brain:
636 Body Size Allometry. *Evolution (N Y)* 33:402 . doi: 10.2307/2407630
- 637 56. Le Thierry D'Ennequin M, Toupance B, Robert T, Godelle B, Gouyon PH (1999) Plant
638 domestication: A model for studying the selection of linkage. *J Evol Biol* 12:1138–1147 .
639 doi: 10.1046/j.1420-9101.1999.00115.x
- 640 57. Martínez-Ainsworth NE, Tenailon MI (2016) Superheroes and masterminds of plant
641 domestication. *C R Biol* 339:268–273 . doi: 10.1016/j.crv.2016.05.005
- 642 58. Lukens LN, Doebley J (1999) Epistatic and environmental interactions for quantitative
643 trait loci involved in maize evolution. *Genet Res* 74:291–302 . doi:
644 10.1017/S0016672399004073
- 645 59. Wallace JG, Larsson SJ, Buckler ES (2014) Entering the second century of maize
646 quantitative genetics. *Heredity (Edinb)*. 112:30–38
- 647 60. Beadle GW (1972) Mystery of Maize. *F Museum Nat Hist Bull*
- 648 61. Briggs WH, McMullen MD, Gaut BS, Doebley J (2007) Linkage mapping of domestication
649 loci in a large maize teosinte backcross resource. *Genetics* 177:1915–1928 . doi:
650 10.1534/genetics.107.076497
- 651 62. Stitzer MC, Ross-Ibarra J (2018) Maize domestication and gene interaction. *New Phytol.*
652 doi: 10.1111/nph.15350
- 653 63. Buckler ES, Holland JB, Bradbury PJ, Acharya CB, Brown PJ, Browne C, Ersoz E, Flint-
654 Garcia S, Garcia A, Glaubitz JC, Goodman MM, Harjes C, Guill K, Kroon DE, Larsson S,

- 655 Lepak NK, Li H, Mitchell SE, Pressoir G, Peiffer JA, Rosas MO, Rocheford TR, Romay
656 MC, Romero S, Salvo S, Villeda HS, Sofia da Silva H, Sun Q, Tian F, Upadaya N,
657 Ware D, Yates H, Yu J, Zhang Z, Kresovich S, McMullen MD (2009) The Genetic
658 Architecture of Maize Flowering Time. *Science* (80-) 325:714–718 . doi:
659 10.1126/science.1174276
- 660 64. Cook JP, McMullen MD, Holland JB, Tian F, Bradbury P, Ross-Ibarra J, Buckler ES, Flint-
661 Garcia SA (2012) Genetic Architecture of Maize Kernel Composition in the Nested
662 Association Mapping and Inbred Association Panels. *PLANT Physiol* 158:824–834 . doi:
663 10.1104/pp.111.185033
- 664 65. Romero Navarro JA, Willcox M, Burgueño J, Romay C, Swarts K, Trachsel S, Preciado
665 E, Terron A, Delgado HV, Vidal V, Ortega A, Banda AE, Montiel NOG, Ortiz-Monasterio I,
666 Vicente FS, Espinoza AG, Atlin G, Wenzl P, Hearne S, Buckler ES (2017) A study of
667 allelic diversity underlying flowering-time adaptation in maize landraces. *Nat Genet*
668 49:476–480 . doi: 10.1038/ng.3784
- 669 66. Tian F, Stevens NM, Buckler ES (2009) Tracking footprints of maize domestication and
670 evidence for a massive selective sweep on chromosome 10. *Proc Natl Acad Sci*
671 106:9979–9986 . doi: 10.1073/pnas.0901122106
- 672 67. Tenaillon MI, Sawkins MC, Long AD, Gaut RL, Doebley JF, Gaut BS (2001) Patterns of
673 DNA sequence polymorphism along chromosome 1 of maize (*Zea mays* ssp. *mays* L.).
674 *Proc Natl Acad Sci U S A* 98:9161–6 . doi: 10.1073/pnas.151244298
- 675 68. Buckler ES, Gaut BS, McMullen MD (2006) Molecular and functional diversity of maize.
676 *Curr. Opin. Plant Biol.* 9:172–176
- 677 69. Wang H, Nussbaum-Wagler T, Li B, Zhao Q, Vigouroux Y, Faller M, Bomblies K, Lukens
678 L, Doebley JF (2005) The origin of the naked grains of maize. *Nature* 436:714–719 . doi:
679 10.1038/nature03863
- 680 70. Zheng P, Allen WB, Roesler K, Williams ME, Zhang S, Li J, Glassman K, Ranch J, Nubel
681 D, Solawetz W, Bhatramakki D, Llaca V, Deschamps S, Zhong GY, Tarczynski MC,
682 Shen B (2008) A phenylalanine in DGAT is a key determinant of oil content and
683 composition in maize. *Nat Genet* 40:367–372 . doi: 10.1038/ng.85
- 684 71. Hancock AM, Brachi B, Faure N, Horton MW, Jarymowycz LB, Sperone FG, Toomajian
685 C, Roux F, Bergelson J (2011) Adaptation to Climate Across the *Arabidopsis thaliana*
686 Genome. *Science* (80-) 334:83–86 . doi: 10.1126/science.1209244
- 687 72. Chia JM, Song C, Bradbury PJ, Costich D, De Leon N, Doebley J, Elshire RJ, Gaut B,
688 Geller L, Glaubitz JC, Gore M, Guill KE, Holland J, Hufford MB, Lai J, Li M, Liu X, Lu Y,
689 McCombie R, Nelson R, Poland J, Prasanna BM, Pyhäjärvi T, Rong T, Sekhon RS, Sun
690 Q, Tenaillon MI, Tian F, Wang J, Xu X, Zhang Z, Kaeppler SM, Ross-Ibarra J, McMullen
691 MD, Buckler ES, Zhang G, Xu Y, Ware D (2012) Maize HapMap2 identifies extant
692 variation from a genome in flux. *Nat Genet* 44:803–807 . doi: 10.1038/ng.2313
- 693 73. Rodgers-Melnick E, Vera DL, Bass HW, Buckler ES (2016) Open chromatin reveals the
694 functional maize genome. *Proc Natl Acad Sci* 113:E3177–E3184 . doi:
695 10.1073/pnas.1525244113
- 696 74. Swanson-Wagner R, Briskine R, Schaefer R, Hufford MB, Ross-Ibarra J, Myers CL, Tiffin
697 P, Springer NM (2012) Reshaping of the maize transcriptome by domestication. *Proc Natl*
698 *Acad Sci U S A* 109:11878–11883 . doi: 10.1073/pnas.1201961109

- 699 75. Schnable PS, Ware D, Fulton RS, Stein JC, Wei F, Pasternak S, Liang C, Zhang J,
700 Fulton L, Graves TA, Minx P, Reily AD, Courtney L, Kruchowski SS, Tomlinson C, Strong
701 C, Delehaunty K, Fronick C, Courtney B, Rock SM, Belter E, Du F, Kim K, Abbott RM,
702 Cotton M, Levy A, Marchetto P, Ochoa K, Jackson SM, Gillam B, Chen W, Yan L,
703 Higginbotham J, Cardenas M, Waligorski J, Applebaum E, Phelps L, Falcone J, Kanchi K,
704 Thane T, Scimone A, Thane N, Henke J, Wang T, Ruppert J, Shah N, Rotter K, Hodges
705 J, Ingenthron E, Cordes M, Kohlberg S, Sgro J, Delgado B, Mead K, Chinwalla A,
706 Leonard S, Crouse K, Collura K, Kudrna D, Currie J, He R, Angelova A, Rajasekar S,
707 Mueller T, Lomeli R, Scara G, Ko A, Delaney K, Wissotski M, Lopez G, Campos D,
708 Braidotti M, Ashley E, Golser W, Kim H, Lee S, Lin J, Dujmic Z, Kim W, Talag J, Zuccolo
709 A, Fan C, Sebastian A, Kramer M, Spiegel L, Nascimento L, Zutavern T, Miller B,
710 Ambroise C, Muller S, Spooner W, Narechania A, Ren L, Wei S, Kumari S, Faga B, Levy
711 MJ, McMahan L, Van Buren P, Vaughn MW, Ying K, Yeh C-T, Emrich SJ, Jia Y,
712 Kalyanaraman A, Hsia A-P, Barbazuk WB, Baucom RS, Brutnell TP, Carpita NC,
713 Chaparro C, Chia J-M, Deragon J-M, Estill JC, Fu Y, Jeddelloh JA, Han Y, Lee H, Li P,
714 Lisch DR, Liu S, Liu Z, Nagel DH, McCann MC, SanMiguel P, Myers AM, Nettleton D,
715 Nguyen J, Penning BW, Ponnala L, Schneider KL, Schwartz DC, Sharma A, Soderlund
716 C, Springer NM, Sun Q, Wang H, Waterman M, Westerman R, Wolfgruber TK, Yang L,
717 Yu Y, Zhang L, Zhou S, Zhu Q, Bennetzen JL, Dawe RK, Jiang J, Jiang N, Presting GG,
718 Wessler SR, Aluru S, Martienssen RA, Clifton SW, McCombie WR, Wing RA, Wilson RK
719 (2009) The B73 Maize Genome: Complexity, Diversity, and Dynamics. *Science* (80-)
720 326:1112–1115 . doi: 10.1126/science.1178534
- 721 76. Tenaillon MI, Hollister JD, Gaut BS (2010) A triptych of the evolution of plant
722 transposable elements. *Trends Plant Sci.* 15:471–478
- 723 77. Muñoz-Diez C, Vitte C, Ross-Ibarra J, Gaut BS, Tenaillon MI (2012) Using nextgen
724 sequencing to investigate genome size variation and transposable element content. *Top.*
725 *Curr. Genet.* 24:41–58
- 726 78. Diez CM, Meca E, Tenaillon MI, Gaut BS (2014) Three Groups of Transposable Elements
727 with Contrasting Copy Number Dynamics and Host Responses in the Maize (*Zea mays*
728 *ssp. mays*) Genome. *PLoS Genet* 10: . doi: 10.1371/journal.pgen.1004298
- 729 79. Hollister JD, Gaut BS (2009) Epigenetic silencing of transposable elements: A trade-off
730 between reduced transposition and deleterious effects on neighboring gene expression.
731 *Genome Res* 19:1419–1428 . doi: 10.1101/gr.091678.109
- 732 80. Waters AJ, Makarevitch I, Noshay J, Burghardt LT, Hirsch CN, Hirsch CD, Springer NM
733 (2017) Natural variation for gene expression responses to abiotic stress in maize. *Plant J*
734 89:706–717 . doi: 10.1111/tpj.13414
- 735 81. Vitte C, Fustier MA, Alix K, Tenaillon MI (2014) The bright side of transposons in crop
736 evolution. *Briefings Funct Genomics Proteomics* 13:276–295 . doi: 10.1093/bfgp/elu002
- 737 82. Studer A, Zhao Q, Ross-Ibarra J, Doebley J (2011) Identification of a functional
738 transposon insertion in the maize domestication gene *tb1*. *Nat Genet* 43:1160–1163 . doi:
739 10.1038/ng.942
- 740 83. Springer NM, Ying K, Fu Y, Ji T, Yeh CT, Jia Y, Wu W, Richmond T, Kitzman J,
741 Rosenbaum H, Iniguez AL, Barbazuk WB, Jeddelloh JA, Nettleton D, Schnable PS (2009)
742 Maize inbreds exhibit high levels of copy number variation (CNV) and presence/absence

- 743 variation (PAV) in genome content. *PLoS Genet* 5: . doi: 10.1371/journal.pgen.1000734
- 744 84. Maron LG, Guimarães CT, Kirst M, Albert PS, Birchler JA, Bradbury PJ, Buckler ES,
745 Coluccio AE, Danilova T V, Kudrna D, Magalhaes J V, Piñeros MA, Schatz MC, Wing RA,
746 Kochian L V, Ronald Sederoff R (2013) Aluminum tolerance in maize is associated
747 with higher MATE1 gene copy number. *Proc Natl Acad Sci U S A* 110:5241–5246 . doi:
748 10.1073/pnas.1220766110
- 749 85. Baltazar BM, Sánchez-Gonzalez JDJ, De La Cruz-Larios L, Schoper JB (2005)
750 Pollination between maize and teosinte: An important determinant of gene flow in Mexico.
751 *Theor Appl Genet* 110:519–526 . doi: 10.1007/s00122-004-1859-6
- 752 86. Hufford MB, Lubinsky P, Pyhäjärvi T, Devengenzo MT, Ellstrand NC, Ross-Ibarra J
753 (2013) The Genomic Signature of Crop-Wild Introgression in Maize. *PLoS Genet* 9: . doi:
754 10.1371/journal.pgen.1003477
- 755 87. Lauter N, Gustus C, Westerbergh A, Doebley J (2004) The inheritance and evolution of
756 leaf pigmentation and pubescence in teosinte. *Genetics* 167:1949–1959 . doi:
757 10.1534/genetics.104.026997
- 758 88. Kawecki TJ, Ebert D (2004) Conceptual issues in local adaptation. *Ecol Lett* 7:1225–1241
759 . doi: 10.1111/j.1461-0248.2004.00684.x
- 760 89. Anderson JT, Lee CR, Rushworth CA, Colautti RI, Mitchell-Olds T (2013) Genetic trade-
761 offs and conditional neutrality contribute to local adaptation. In: *Molecular Ecology*. pp
762 699–708
- 763 90. Mercer K, Martínez-Vásquez Á, Perales HR (2008) Asymmetrical local adaptation of
764 maize landraces along an altitudinal gradient. *Evol Appl* 1:489–500 . doi: 10.1111/j.1752-
765 4571.2008.00038.x
- 766 91. Aguirre-Liguori JA, Tenaillon MI, Vázquez-Lobo A, Gaut BS, Jaramillo-Correa JP,
767 Montes-Hernandez S, Souza V, Eguiarte LE (2017) Connecting genomic patterns of local
768 adaptation and niche suitability in teosintes. *Mol Ecol* 26:4226–4240 . doi:
769 10.1111/mec.14203
- 770 92. Fustier MA, Brandenburg JT, Boitard S, Lapeyronnie J, Eguiarte LE, Vigouroux Y,
771 Manicacci D, Tenaillon MI (2017) Signatures of local adaptation in lowland and highland
772 teosintes from whole-genome sequencing of pooled samples. *Mol Ecol* 26:2738–2756 .
773 doi: 10.1111/mec.14082
- 774 93. Hung H-Y, Shannon LM, Tian F, Bradbury PJ, Chen C, Flint-Garcia SA, McMullen MD,
775 Ware D, Buckler ES, Doebley JF, Holland JB (2012) ZmCCT and the genetic basis of
776 day-length adaptation underlying the postdomestication spread of maize. *Proc Natl Acad*
777 *Sci* 109:E1913–E1921 . doi: 10.1073/pnas.1203189109
- 778 94. Yang Q, Li Z, Li W, Ku L, Wang C, Ye J, Li K, Yang N, Li Y, Zhong T, Li J, Chen Y, Yan J,
779 Yang X, Xu M (2013) CACTA-like transposable element in ZmCCT attenuated
780 photoperiod sensitivity and accelerated the postdomestication spread of maize. *Proc Natl*
781 *Acad Sci* 110:16969–16974 . doi: 10.1073/pnas.1310949110
- 782 95. Linhart YB, Grant MC (1996) EVOLUTIONARY SIGNIFICANCE OF LOCAL GENETIC
783 DIFFERENTIATION IN PLANTS. *Annu Rev Ecol Syst* 27:237–277 . doi:
784 10.1146/annurev.ecolsys.27.1.237
- 785 96. Valverde BE (2007) Status and Management of Grass-weed Herbicide Resistance in
786 Latin America. *Weed Technol* 21:310–323 . doi: 10.1614/WT-06-097.1

- 787 97. Moeller DA, Tiffin P (2008) Geographic variation in adaptation at the molecular level: A
788 case study of plant immunity genes. *Evolution* (N Y) 62:3069–3081 . doi: 10.1111/j.1558-
789 5646.2008.00511.x
- 790 98. Fang Z, Pyhäjärvi T, Weber AL, Dawe RK, Glaubitz JC, Sánchez González J de J, Ross-
791 Ibarra C, Doebley J, Morrell PL, Ross-Ibarra J (2012) Megabase-scale inversion
792 polymorphism in the wild ancestor of maize. *Genetics* 191:883–894 . doi:
793 10.1534/genetics.112.138578
- 794 99. Romero Navarro JA, Willcox M, Burgueño J, Romay C, Swarts K, Trachsel S, Preciado
795 E, Terron A, Delgado HV, Vidal V, Ortega A, Banda AE, Montiel NOG, Ortiz-Monasterio I,
796 Vicente FS, Espinoza AG, Atlin G, Wenzl P, Hearne S, Buckler ES (2017) A study of
797 allelic diversity underlying flowering-time adaptation in maize landraces. *Nat Genet.* doi:
798 10.1038/ng.3784
- 799 100. Schluter D (2009) Evidence for ecological speciation and its alternative. *Science* (80-).
800 323:737–741
- 801 101. Wood TE, Burke JM, Rieseberg LH (2005) Parallel genotypic adaptation: When evolution
802 repeats itself. In: *Genetica*. pp 157–170
- 803 102. Colosimo PF, Hosemann KE, Balabhadra S, Villarreal G, Dickson H, Grimwood J,
804 Schmutz J, Myers RM, Schluter D, Kingsley DM (2005) Widespread parallel evolution in
805 sticklebacks by repeated fixation of ectodysplasin alleles. *Science* (80-) 307:1928–1933 .
806 doi: 10.1126/science.1107239
- 807 103. Pearce RJ, Pota H, Evehe MSB, Bâ EH, Mombo-Ngoma G, Malisa AL, Ord R, Inojosa W,
808 Matondo A, Diallo DA, Mbacham W, Van Den Broek I V., Swarthout TD, Getachew A,
809 Dejene S, Grobusch MP, Njie F, Dunyo S, Kweku M, Owusu-Agyei S, Chandramohan D,
810 Bonnet M, Guthmann JP, Clarke S, Barnes KI, Streat E, Katokele ST, Uusiku P,
811 Agboghoroma CO, Elegba OY, Cissé B, A-Elbasit IE, Giha HA, Kachur SP, Lynch C,
812 Rwakimari JB, Chanda P, Hawela M, Sharp B, Naidoo I, Roper C (2009) Multiple origins
813 and regional dispersal of resistant dhps in African *Plasmodium falciparum* malaria. *PLoS*
814 *Med* 6: . doi: 10.1371/journal.pmed.1000055
- 815 104. Chan YF, Marks ME, Jones FC, Villarreal G, Shapiro MD, Brady SD, Southwick AM,
816 Absher DM, Grimwood J, Schmutz J, Myers RM, Petrov D, Jónsson B, Schluter D, Bell
817 MA, Kingsley DM (2010) Adaptive evolution of pelvic reduction in sticklebacks by
818 recurrent deletion of a pitxl enhancer. *Science* (80-) 327:302–305 . doi:
819 10.1126/science.1182213
- 820 105. Stern DL (2013) The genetic causes of convergent evolution. *Nat. Rev. Genet.* 14:751–
821 764
- 822 106. Roesti M, Gavrillets S, Hendry AP, Salzburger W, Berner D (2014) The genomic signature
823 of parallel adaptation from shared genetic variation. *Mol Ecol* 23:3944–3956 . doi:
824 10.1111/mec.12720
- 825 107. Riehle MM, Bennett AF, Long AD (2001) Genetic architecture of thermal adaptation in
826 *Escherichia coli*. *Proc Natl Acad Sci* 98:525–530 . doi: 10.1073/pnas.98.2.525
- 827 108. Gaut BS (2015) Evolution is an experiment: Assessing parallelism in crop domestication
828 and experimental evolution. *Mol Biol Evol* 32:1661–1671 . doi: 10.1093/molbev/msv105
- 829 109. Fuller DQ, Denham T, Arroyo-Kalin M, Lucas L, Stevens CJ, Qin L, Allaby RG,
830 Purugganan MD (2014) Convergent evolution and parallelism in plant domestication

- 831 revealed by an expanding archaeological record. *Proc Natl Acad Sci* 111:6147–6152 .
832 doi: 10.1073/pnas.1308937110
- 833 110. Lin Z, Li X, Shannon LM, Yeh CT, Wang ML, Bai G, Peng Z, Li J, Trick HN, Clemente TE,
834 Doebley J, Schnable PS, Tuinstra MR, Tesso TT, White F, Yu J (2012) Parallel
835 domestication of the *Shattering1* genes in cereals. *Nat Genet* 44:720–724 . doi:
836 10.1038/ng.2281
- 837 111. Takuno S, Ralph P, Swart K, Elshire RJ, Glaubitz JC, Buckler ES, Hufford MB, Ross-
838 Ibarra J (2015) Independent molecular basis of convergent highland adaptation in maize.
839 *Genetics* 200:1297–1312 . doi: 10.1534/genetics.115.178327
- 840 112. Lee KM, Coop G (2017) Distinguishing Among Modes of Convergent Adaptation Using
841 Population Genomic Data. *Genetics* genetics.300417.2017 . doi:
842 10.1534/genetics.117.300417
- 843 113. Gilbert SF, Epel D (2009) *Ecological developmental biology: integrating epigenetics,*
844 *medicine, and evolution.* Sinauer Assoc
- 845 114. Beldade P, Mateus ARA, Keller RA (2011) Evolution and molecular mechanisms of
846 adaptive developmental plasticity. *Mol Ecol* 20:1347–1363 . doi: 10.1111/j.1365-
847 294X.2011.05016.x
- 848 115. Wennersten L, Forsman A (2012) Population-level consequences of polymorphism,
849 plasticity and randomized phenotype switching: A review of predictions. *Biol. Rev.*
850 87:756–767
- 851 116. Des Marais DL, Hernandez KM, Juenger TE (2013) Genotype-by-environment interaction
852 and plasticity: exploring genomic responses of plants to the abiotic environment. *Annu*
853 *Rev Ecol Evol Syst* 44:5–29
- 854 117. DeWitt TJ, Sih A, Wilson DS (1998) Costs and limits of phenotypic plasticity. *Trends Ecol.*
855 *Evol.* 13:77–81
- 856 118. Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P,
857 Purugganan MD, Richards CL, Valladares F, van Kleunen M (2010) Plant phenotypic
858 plasticity in a changing climate. *Trends Plant Sci.* 15:684–692
- 859 119. Auld JR, Agrawal AA, Relyea RA (2010) Re-evaluating the costs and limits of adaptive
860 phenotypic plasticity. *Proc R Soc B Biol Sci* 277:503–511 . doi: 10.1098/rspb.2009.1355
- 861 120. Kuzawa CW, Bragg JM (2012) Plasticity in human life history strategy. *Curr Anthropol*
862 53:S369–S382
- 863 121. Diggle PK, Miller JS (2013) Developmental plasticity, genetic assimilation, and the
864 evolutionary diversification of sexual expression in *Solanum*. *Am J Bot* 100:1050–1060 .
865 doi: 10.3732/ajb.1200647
- 866 122. Standen EM, Du TY, Larsson HCE (2014) Developmental plasticity and the origin of
867 tetrapods. *Nature* 513:54–58 . doi: 10.1038/nature13708
- 868 123. Gage JL, Jarquin D, Romay C, Lorenz A, Buckler ES, Kaeppler S, Alkhalifah N, Bohn M,
869 Campbell DA, Edwards J, Ertl D, Flint-Garcia S, Gardiner J, Good B, Hirsch CN, Holland
870 J, Hooker DC, Knoll J, Kolkman J, Kruger G, Lauter N, Lawrence-Dill CJ, Lee E, Lynch J,
871 Murray SC, Nelson R, Petzoldt J, Rocheford T, Schnable J, Schnable PS, Scully B, Smith
872 M, Springer NM, Srinivasan S, Walton R, Weldekidan T, Wisser RJ, Xu W, Yu J, De Leon
873 N (2017) The effect of artificial selection on phenotypic plasticity in maize. *Nat Commun*
874 8: . doi: 10.1038/s41467-017-01450-2

- 875 124. Wallace JG, Bradbury PJ, Zhang N, Gibon Y, Stitt M, Buckler ES (2014) Association
876 Mapping across Numerous Traits Reveals Patterns of Functional Variation in Maize.
877 PLoS Genet 10: . doi: 10.1371/journal.pgen.1004845
- 878 125. Piperno DR, Holst I, Winter K, McMillan O (2015) Teosinte before domestication:
879 Experimental study of growth and phenotypic variability in late Pleistocene and early
880 Holocene environments. *Quat Int* 363:65–77
- 881 126. Lorant A, Pedersen S, Holst I, Hufford MB, Winter K, Piperno D, Ross-Ibarra J (2017)
882 The potential role of genetic assimilation during maize domestication. *PLoS One* 12: . doi:
883 10.1371/journal.pone.0184202
- 884 127. Lobell DB, Schlenker W, Costa-Roberts J (2011) Climate trends and global crop
885 production since 1980. *Science* 333:616–620 . doi: 10.1126/science.1204531
- 886 128. Ureta C, Martínez-Meyer E, Perales HR, Álvarez-Buylla ER (2012) Projecting the effects
887 of climate change on the distribution of maize races and their wild relatives in Mexico.
888 *Glob Chang Biol* 18:1073–1082 . doi: 10.1111/j.1365-2486.2011.02607.x
- 889 129. Crow JF, Kimura M, others (1970) An introduction to population genetics theory. *An*
890 *Introd to Popul Genet theory*
- 891 130. Liu J, Huang J, Guo H, Lan L, Wang H, Xu Y, Yang X, Li W, Tong H, Xiao Y, others
892 (2017) The conserved and unique genetic architecture of kernel size and weight in maize
893 and rice. *Plant Physiol* 175:774–785
- 894 131. Hallauer AR, Carena MJ, Filho JBM (2010) Quantitative genetics in Maize Breeding. In:
895 *Handbook of Plant Breeding*. pp 1–680
- 896 132. Yang J, Mezouk S, Baumgarten A, Buckler ES, Guill KE, McMullen MD, Mumm RH,
897 Ross-Ibarra J (2017) Incomplete dominance of deleterious alleles contributes
898 substantially to trait variation and heterosis in maize. *PLoS Genet* 13: . doi:
899 10.1371/journal.pgen.1007019
- 900 133. Lopez-Reynoso J de J (1997) Divergent mass selection for ear length in the Iowa Long
901 Ear Synthetic maize cultivar after twenty-seven cycles of selection
- 902 134. Ross AJ, Hallauer AR, Lee M (2006) Genetic analysis of traits correlated with maize ear
903 length. *Maydica* 51:301–313