



## Genomics of Long- and Short-Term Adaptation in Maize and Teosintes

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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 basis 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.

**Key words** Maize, Teosinte, Adaptation, Plasticity, Convergence

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## 1 Introduction

A combination of archeobotanical records and genetic data has established that maize (*Zea mays* ssp. *mays*) was domesticated around 9000 years ago in the Balsas river valley of Mexico from the wild teosinte *Zea mays* ssp. *parviglumis* [1–3]. Unlike complex domestication scenarios involving multiple domestication events in the common bean (*Phaseolus vulgaris* L.) and the lima bean (*Phaseolus lunatus* L.) [4] or multiple progenitors from different regions in barley (*Hordeum vulgare*; [5], maize stands a relatively simple scenario involving only a single domestication event resulting in a moderate decrease of genetic diversity of roughly 20% [6].

With the rise of coalescent simulation tools since the late 1990s [7], researchers have repeatedly attempted to establish demographic scenarios of maize domestication. All concur with a simple bottleneck model, that is, a reduction of effective population size

( $N_c$ ), with <10% of the teosinte population contributing to the maize gene pool [8–11]. A recent investigation indicates that this bottleneck was followed by a major expansion resulting in an  $N_c$  for modern maize much larger than that of teosinte [11]. However, the complexity of the forces acting to shape diversity at a genome-wide scale makes it difficult to disentangle them. On the one hand, domestication has likely promoted strong positive selection at ~2% to 4% of loci [10] producing one of the most famous textbook example of selective sweeps at *tb1*, a gene responsible for the reduced branching phenotype in maize [12]. On the other hand, purifying selection has also reduced neutral genetic diversity [11]. Such selection may lead to an excess of rare variants, a footprint easily confounded with both positive selection and population expansion [13].

After its initial domestication, the geographic range of maize has rapidly exceeded that of its wild relatives, with documented routes of diffusion northward and southward out of Mexico [14, 15] and to the European continent [16]. Today the maize gene pool worldwide consists of locally adapted open-pollinated populations (landraces) as well as modern inbred lines, derived from landraces, that are used in hybrid production for modern breeding. Such spatial movement has exerted a diversity of selective pressures, triggering changes in the phenology of individuals that ultimately determines the completion of the annual cycle and individual fitness [17, 18].

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

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

Recent range shifts driven by global warming have been reported in tree species distributed in California, Oregon and Washington with an average shift compared to mature trees of about 27 m in altitude and 11kms northward, toward colder environments [24]. Likewise, rising temperatures have likely caused the

upslope migration reported for vascular plants species across European boreal-to-temperate mountains [25].

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

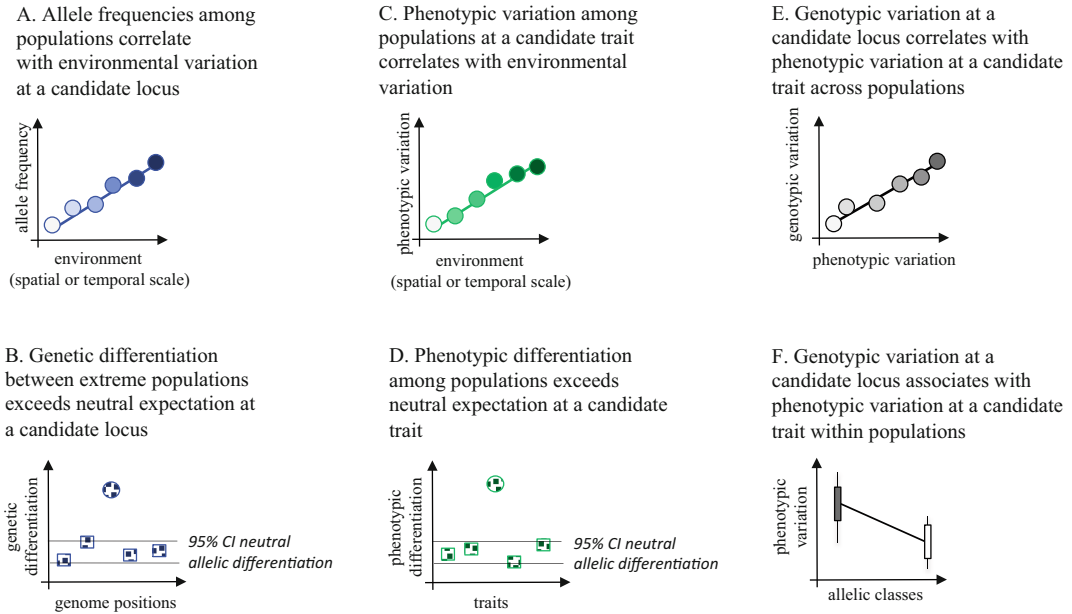
In this chapter, we focus on adaptation and phenotypic plasticity. We review methods used to explore genetic adaptation and the factors constraining it. Next, we review empirical reports of short- and long-term adaptation in maize and teosintes. Finally, we discuss the role genetic convergence and phenotypic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

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## 2 How to Explore Adaptation?

Genetic adaptation can be defined as the modulation of allele frequencies through natural and/or artificial selection. Natural selection is imposed by changes in environmental conditions, or artificial selection by humans. Identification of adaptive loci (Fig. 1a, b) and/or traits (Fig. 1c, d) uses spatial or temporal variation in conjunction with quantification of traits in native environments (Fig. 1f) or in common gardens (Fig. 1g) [27–30]. While the temporal approach includes retrospective studies that follow the phenotypic and genetic composition of populations through time (for instance [31] to infer past selective events, the spatial approach relies on samples of populations that are geographically separated [30, 32].

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



**Fig. 1** Experimental approaches to detect potentially adaptive polymorphisms and traits using population genetic (**a**, **b**) or phenotypic (**c**, **d**) data, or combining both (**e**, **f**). A candidate polymorphism whose allele frequency among populations varies with spatial or temporal variation can be detected using correlation-based methods (**a**) or genome-wide scans, where it displays an elevated differentiation of allele frequencies compared with neutral (squares) loci (**b**). A candidate trait that covaries with spatial or temporal variation among populations can be detected using correlation-based methods (**c**) or when phenotypic differentiation measured in common environment(s) exceeds genotypic differentiation at neutral (squares) loci (**d**). A link between candidate loci and traits can be established by correlating genotypic and phenotypic variation measures in common environment(s) across populations (**e**), and within populations (**f**)

### 3 What Constrains Adaptation?

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

Hard sweeps are characterized by local shifts in allele frequencies due to the hitchhiking of neutral sites around a selected *de novo* variant occurring on a specific haplotype. Such changes in allele frequencies can easily be detected by genome scans. In contrast, soft sweeps, which derive from multiple adaptive alleles sweeping in the population, are substantially harder to detect at a genome-wide scale.

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

One of the most puzzling observations across experiments is that the response to selection is generally steady over time. In the Golden Glow (GG) experiment, the response varies from 4.7% to 8.7% of the original phenotypic value per cycle of selection across 24 cycles [48]. In the Krug Yellow Dent (KYD), it was estimated at 1.6% and 2.5% per cycle respectively, for high and low seed size direction [59]. In the Iowa Stalk Synthetic (BSSS), the response was of 3.9% per cycle for higher grain yield [50]. In the Iowa Long Ear Synthetic (BSLE), an increase of 1.4% and a decrease of 1.9% per cycle for high and low ear length were observed [59]. The results were more equivocal for Burn's White (BW), for which the response is much stronger and steadier toward high (between 0.1% and 0.3%) than low values (between 0% and 0.32%) for both protein and oil content. This pattern of shift between a strong and steady response to a plateau-like response for the low trait values is explained by physiological limits. Hence after 65 generations a lower limit for protein content is reached where the percentage of oil in the grain (close to 0% in the late generations) is no longer detectable [46, 47]. A similar situation has been reported for some of the late flowering families of MBS847 and F252 that are not able to produce seeds in the local climate conditions where they are selected, while the early still display a significant response after 16 generations [43]. Overall, mutations do not appear limiting regardless of the design, whether it started from highly inbred material or a diverse set of intercrossed landraces (Table 1).

What differs from one experiment to another, however, is the genomic footprint of the response to selection. Such footprints have been investigated in all but the BW and BSLE design. In GG, in which the mutational target size—the number of sites affecting the trait—was restricted, the effective population size was the highest of all and the selection was intense. The signal is consistent with genome-wide soft sweeps [48, 49]. In KYD, characterized by a larger mutational target, stronger drift (smaller effective population size), but weaker selection, both hard and soft sweeps are observed [45]. In BSSS, in which the mutational target

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

DS experiments	F252 (F252)	MBS847 (MBS)	Krug Yellow Dent (KYD)	Burn's White (BW)	Burn's White (BW)	Golden Glow (GG)	lowa Stiff Stalk Synthetic (BSSS)	Iowa Long Ear Synthetic (BSLE)
References <sup>a</sup>	[43, 44]	[43, 44]	[45]	[46, 47]	[46, 47]	[48, 49]	[50-52]	[53]
Directions (High/low) <sup>b</sup>	H/L	H/L	H/L	H/L	H/L	H	H	H/L
Trait <sup>c</sup>	Flowering	Flowering	Seed size	Protein	Oil	Ears/plant	Grain yield	Ear length
Material type <sup>d</sup>	Inbred	Inbred	OP variety	OP variety	OP variety	OP variety	Synthetic population	Synthetic population
Mutational target <sup>e</sup>	>60 QTLs [54]	>60 QTLs [54]	>300 loci [55]	102-178 factors	14-69 factors	Limited [48]	Large [56]	25 QTLs [57]
Standing variation <sup>f</sup>	1.9%	0.19%	Pervasive	Pervasive	Pervasive	Pervasive	Pervasive	Pervasive
Census population size <sup>g</sup>	1000	1000	1200-1500	60-120	60-120	4250 (1-12) 14,250 (13-30)	>1240	4000
N <sub>e</sub> <sup>h</sup>	3.1-20.2	5.8-13.5	369	4-12	4-12	667	10-20	14
Selection coefficient (%)	1	1	8	20	20	0.5-5	5	7.5
Heritability <sup>i</sup>	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 <sup>l</sup>	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 <sup>k</sup>	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

<sup>a</sup>References from which values were taken for each DS experiment are indicated in superscript

<sup>b</sup>Direction of selection toward higher and/or lower values than the initial material

<sup>c</sup>Protein and Oil designate protein and oil content of the grain, Ears/plan relates to prolificacy

<sup>d</sup>Inbred: Inbred line; OP variety: Open Pollinated population

<sup>e</sup>Number of factors in BW was estimated from the trait value, predicted gain and additive genetic variance

<sup>f</sup>Standing variation was estimated from 50k SNP array for F252 and MBS

<sup>g</sup>For GG, 4250 individuals were evaluated from cycles 1–12, and 14,250 in the following cycles

<sup>h</sup>Effective population size ( $N_e$ ) estimates given from the variance of offspring number [58], range is given when  $N_e$  was estimated at each generation

<sup>i</sup>Broad-sense heritability estimated from genetic variation between progenies of the same family. Average values across generations is reported here

<sup>j</sup>Expressed either as number of haplotypes (a single founder = individual bears 2 haplotypes), number of founders, or number of ears (all individuals of a given ear share identical mother but different fathers). For GG, most selection cycles used 300 founders

<sup>k</sup>Seeds from all time points (All) are available, and were either collected separately on each selected individual (/ind) or in bulk (/bulk)

size is the largest, the effective population size small and the selection intense, the signal is consistent with hard sweeps [51]. The F252 and MBS populations display the most limited standing variation and at the same time the strongest drift and selection of all experiments; in these a rapid fixation of new mutations explains the response to selection [43, 44]. Effective population size primarily determines the likelihood of soft sweeps. Hence, when  $\theta$  (four times the product of effective population size and the beneficial mutation rate) is equal or above 1, and selection is strong enough, adaptation proceeds from multiple de novo mutations or standing variation [60]. Below 1, soft sweeps' contribution diminishes with  $\theta$ . In the experiments from Table 1, selection is strong but  $\theta \ll 1$  in all cases. Nevertheless, hard and soft sweeps were associated respectively with the lowest (F252 and MBS) and highest (GG) effective population size, consistent with  $N_e$  being a key player. Comparisons among experiments thus contribute to understanding the parameters of importance and their interactions that together shape the genomic patterns of the response to selection.

An additional layer of complexity that may substantially impact evolutionary trajectories is that of genetic correlations among traits. Such correlations may emerge from genes with pleiotropic effects, epistatic interactions among genes, and/or loci in tight linkage affecting various traits. While some studies have found that covariance between traits rarely affect adaptation [61], several examples instead suggest that they may either constrain or facilitate adaptation as predicted by Lande [62]. For instance, in *Arabidopsis thaliana* a recent study indicates that polymorphisms with intermediate degrees of pleiotropy favored rapid adaptation to microhabitats in natura [63]. In the case of domestication, tight linkage between genes conferring the so-called domestication syndrome has been invoked as a mechanism facilitating adaptation to the cultivated environment in allogamous species, preventing gene flow from wild relatives to break coadapted suites of alleles [64]. It turns out that rather than clustering, plant domestication genes identified so far are single locus which are mainly transcription factors (reviewed in [65]) most of which likely display strong epistatic interactions. *tb1* in maize, for instance, interacts with another locus on a different chromosome to alter the sex of maize inflorescences. The introgression of the *tb1* teosinte allele alone changes only ~20% of the inflorescence sex but the introgression of both alleles converts 90% of maize's female flowers to male [66]. The maize *tb1* allele segregates at low frequency in teosinte populations but is rarely found associated with the domesticated allele of chromosome 3, as both are likely to evolve under negative selection in teosinte [12, 66]. Their association in maize has however facilitated the acquisition of the domesticated phenotype.



## 4 Mechanisms of Genetic Adaptation in Maize and Teosintes

Populations of teosinte have long evolved under natural selection. In contrast, maize populations have been under artificial human selection that moved phenotypes toward optimal traits tailored to agriculture during a shorter time frame of ~9000 years [1, 2, 22]. These time scales have left distinct genetic signatures. In theory, traits fixed by domestication should involve genes with larger effect sizes, and standing variation should be a major contributor to domestication [67]. This is supported by crosses between maize and teosintes that led to the discovery of six main QTLs responsible for major phenotypic differences between them, notably vegetative architecture and inflorescence sexuality ([68, 69], reviewed in [70]). Among these QTLs, genes with major phenotypic effects have been discovered such as *tb1* and *tga1* (*teosinte glume architecture1*). In addition to these major genes, a collection of targets (2–4% of the genome according to [6, 10]) have likely contributed to the domesticated phenotype. In contrast, Genome Wide Association (GWA) studies on traits selected over much longer time scale such as drought tolerance or flowering time have highlighted only minor effect loci that rarely contribute to more than 5% of the phenotypic variation [54, 67, 71, 72].

In addition to the time frame over which adaptation occurs, another important factor for evolution is the nature of variation for selection to act on. Maize and teosintes are genetically very diverse, with as much nucleotide diversity in coding regions between two maize lines as there are between humans and chimpanzees [73]. This diversity is even higher in intergenic regions [74, 75]. Some adaptive mutations are found in coding sequences. Examples include nonsynonymous changes in the *tga1* gene responsible for the “naked kernel” maize phenotype, and in the *diacylglycerol acyltransferase* (*DGATI-2*) gene resulting in elevated kernel oil content in maize lines [76, 77]. But most observations support adaptation from regulatory noncoding sequences. Indeed, in comparison with *Arabidopsis*, where adaptive variants are enriched in coding sequences [78], in maize and teosintes these are predominantly found in noncoding region: estimates in *Zea* show that noncoding variants may explain as much phenotypic variation as those in coding regions [79, 80]. Selection on regulatory sequences drive important expression changes; hence, genes displaying footprints of selection in maize are usually more expressed than in teosintes [6], and are associated with modified coexpression networks [81].

Adaptive variation also results from structural variants. In contrast to the *Arabidopsis* or rice genomes where Transposable Elements (TEs) account for 20–40% of sequence, the maize genome is

composed of about 85% TEs [82, 83]. Genome size varies considerably within *Zea* resulting in over 30% differences among maize lines or landraces [79, 84, 85]. Because of their deleterious effect, TEs are often negatively selected and silenced by DNA methylation [86]. But some may also impact gene expression and function in a beneficial manner by various mechanisms such as gene inactivation or differential expression caused by insertion in regulatory regions [87] or TE-mediated genomic rearrangements causing gene insertion, deletion or duplication (reviewed in [88]). A handful of examples of their beneficial impact has been reported in *Zea*. A classic example in maize is at the *tbl* locus, where a transposon inserted in the cis-regulatory region, doubling expression [89]. Teosinte, like most grasses, produces numerous branches tipped by a male inflorescence. In contrast, maize has only one main stalk terminated by a single tassel with repressed development of lateral branches. The increased expression level of *tbl* is the major contributor to this apical dominance [89]. Beyond TEs, Copy Number Variants (CNVs) are also common in the maize genome [90] and they contribute significantly to phenotypic variation [79, 91].

Another important player in adaptation in *Zea* is gene flow. Indeed, teosinte populations are found in sympatry with maize and hybridization between them is common [92]. Highland maize shows up to 20% *mexicana* introgression, which has likely facilitated their adaptation to high elevations [3, 93]. An ancient DNA study revealed that ancestral highland maize already showed evidence of introgression from *mexicana* [15]. Introgressed regions found at high frequency in highland maize overlap with previously identified QTLs driving adaptive traits [93, 94], emphasizing the importance of introgression during post-domestication adaptation. Similarly, recent results suggest that admixture between distinct genetic groups has facilitated adaptation to mid-latitudes in North America and Europe [16].

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## 5 Local Adaptation in Maize and Teosintes

Strictly defined, a genotype can be considered locally adapted if it has a higher fitness at its native site than any other nonnative genotypes [95]. Locally adapted alleles can be either neutral or deleterious in other environments. Two models depict those situations, namely conditional neutrality and antagonistic pleiotropy [96]. Despite numerous studies, the genetic processes underlying local adaptation in natural populations are still poorly understood. This is mainly due to traits driving local adaptation being mostly quantitative [29]. This complex determinism may involve numerous, but not necessarily substantial, allele frequency changes.

Studies showed that highland maize landraces outperform lowland maize populations in their native environment but perform worse than any other population at lower elevation sites [97], suggesting strong adaptation for high altitude.

Natural selection acts on phenotypic traits, changing the frequency of underlying alleles and shifting population phenotypes toward local optima. Since these optima rely on local conditions, genes ecologically important usually differ between sub-populations in heterogeneous environments, resulting in divergence in allele frequencies over time. This characteristic has been utilized in genome scans to mine correlations between allele frequencies and environmental variables (Fig. 1a). Such studies have revealed that, in teosintes, these loci impact flowering time and adaptation to soil composition [20, 98, 99]. Flowering time was also a key component of maize's local adaptation to higher latitudes during post-domestication. Maize evolved a reduced sensitivity to photoperiod, in part due to a CACTA-like TE insertion in the promoter region of the *ZmCCT* gene that drives photoperiod response in early flowering maize [100, 101]. An example of adaptation driven by soil interactions is the tolerance of maize and teosintes to aluminum in highly acidic soils. In these lines, the adaptation is linked to tandem duplications of the *MATE1* gene involved in the extrusion of toxic compounds [91].

Numerous other biotic and abiotic factors are likely involved in adaptation in maize and teosintes, including predation, parasitism, moisture, and herbicide [102, 103]. For example, a study on *parviglumis* has shown that in response to herbivory, immunity genes involved in the inhibition of insects' digestive proteases experienced a recent selective sweep in a region of Mexico, probably reflecting local adaptation [104].

Interestingly, four large inversion polymorphisms seem to play an important role in local adaptation. Among them, a 50 Mb inversion on chromosome 1 is found at high frequency in *parviglumis* (20–90%), low frequency in *mexicana* (10%), and is absent in maize. This inversion is highly correlated with altitude and significantly associated with temperature and precipitation [20, 105]. Inversions on chromosomes 3, 4 and 9 also displayed environmental association in teosintes and maize landraces for the first two and in teosintes for the last one [20, 72]. Local adaptation to different habitats or niches is a gradual process that can promote divergence and, in the long run, ecological speciation [106]. Genotyping of a broad sample of 49 populations covering the entire geographic range of teosintes has recently provided some evidence of this. Aguirre-Liguori et al. [98] showed that both within *parviglumis* and *mexicana*, populations distributed at the edge of the ecological niche experience stronger local adaptation, suggesting that local adaptation may have contributed to divergence between these two subspecies.

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## 6 How Convergent Is Adaptation?

Convergent adaptation is the result of independent events of similar phenotypic changes to adapt to analogous environmental constraints [107]. In this review, we concentrated on genetic convergence in populations of the same, or closely related, species which are the result of convergent evolution at the molecular level. By molecular convergence, we include convergence at the same nucleotide positions, genes or orthologues. Several studies illustrate this, suggesting that genomes may respond in predictable ways to selection [108–112]. The selected alleles can originate from independent mutation events in different lineages, from shared ancestral variation or by introgression [111].

A classical way to study convergence is experimental evolution. During these experiments, replicates of the same genotype are grown for many generations in new environments. Such studies have often shown that convergent evolution is common [37, 113]. Domestication can be thought of as an example of long-term experimental evolution, and domesticates provide striking examples of phenotypic convergence, with common traits usually referred to as the domestication syndrome. These phenotypes include, but are not limited to, larger fruits or gains, less branching, loss of shattering, and loss of seed dormancy [114]. QTL mapping can be performed to identify the genes controlling these phenotypes in different species. As an example, seeds on wild grasses shed naturally at maturity. During domestication this trait was rapidly selected against since it causes inefficient harvesting [115]. QTL mapping of sorghum, rice and maize reveals that the *Shattering1* genes are involved in the loss of the dispersal mechanism and were under convergent evolution during their domestication [116].

But genetic convergence can also be observed over much shorter evolutionary time, at the intraspecific level across populations. Here genome scans for extreme differentiation in allele frequency between multiple pairs of diverged populations along gradients, for instance, are typically employed. This method has been used to test for convergent adaptation in highland maize landraces and teosintes. Fustier et al. [99] found several instances (24/40) of convergence involving the same haplotype in two gradients of adaptation to high altitude in teosintes. In maize, the Mesoamerican and South American populations independently adapted from distinct lowland populations to high elevation conditions [14]. These populations exhibit several similar phenotypic characteristics not observed in lowland populations such as changes in inflorescence morphology and stem coloration. A study found that highland adaptation is likely due to a combination of introgression events, selection on standing genetic variation and

independent de novo mutations [117]. These studies also showed that convergent evolution involving identical nucleotide changes is uncommon and most selected loci arise from standing genetic variation present in lowland populations. This is not surprising given the relative short time frame of highland adaptation in maize compared to teosinte subspecies.

Recently, a new method has been developed to infer modes of convergence [118], using covariance of allele frequencies in windows around a selected site to explicitly compare different models of origin for a selected variant. This novel method should give a better insight on the genetic mechanisms underlying convergence.

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## 7 What Is the Role of Phenotypic Plasticity?

Phenotypic plasticity is defined as the capacity of a genotype to produce a range of expressed phenotypes in distinct environments. This is achieved through differential developmental pathways in response to changing conditions [119, 120]. Plasticity can be an important process during adaptation. Indeed, populations with flexible phenotypes are predicted to better cope with environmental changes and to display a greater potential for expansion [121]. This process is particularly important for plants as they are fixed in a specific location and not sheltered from the environment [122].

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

Plasticity has limits, however, and may entail a fitness cost. For instance, compared to developmentally fixed phenotypes, plastic individuals in constant environments may display lower fitness or produce a less adapted phenotype. Possible reasons include sensory mechanisms that have a high energetic cost, the epistatic effects of regulatory genes involved in the plastic response, lag time between the perception and the phenotypic response and genetic correlations among traits [123–125].

Phenotypic plasticity is difficult to study as it arises from genetic and environmental interactions which are often hard to disentangle. After a number of generations of constant selection, for example, the fixation of genetic variation that constitutively expresses the trait can lead to a loss of plasticity via a process called genetic assimilation [126–128]. Hence an initially plastic phenotype may result in genetic adaptation after genetic assimilation. Some examples of plastic responses are well documented in plants, for example, the response to vernalization in *Arabidopsis* regulating flowering time in some ecotypes [122]. Another example is the change in

seed dormancy in response to the environment which prevents germination when conditions are unlikely to lead to the survival of the plant [124].

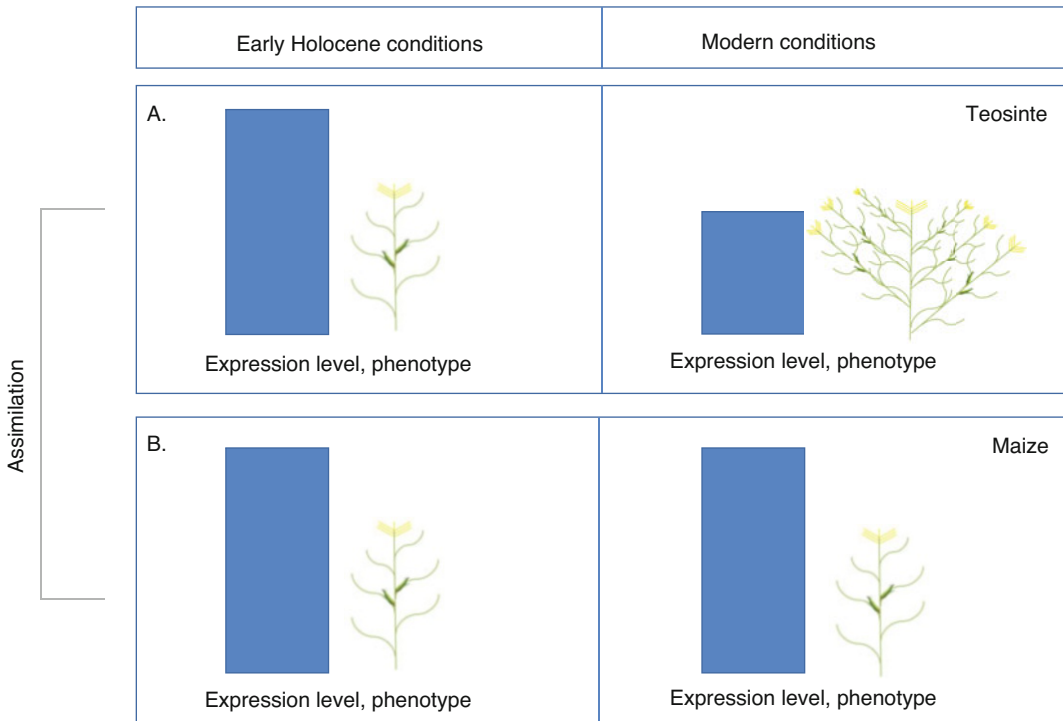
Taxa in *Zea* are good models to investigate plasticity as maize is grown worldwide and adapted to a diversity of environments. In addition, studies of teosintes allow comparison to ancestral levels of plasticity. A recent experiment evaluated plasticity in maize by studying Genotype by Environment interactions (GxE) for a number of phenotypes in 858 inbred lines across 21 locations across North America [129]. Results demonstrated that genes selected for high yield in temperate climates in North America correlated with low variance in GxE. This suggests a loss of plasticity accompanying selection for stable crop performance across environments, a major goal for breeders. In addition, GxE was mainly explained by regulatory regions [129], an observation in agreement with previous findings indicating that most phenotypic variation in maize is due to gene regulation [130].

Recent work on maize and *parviglumis* growing under environmental conditions mimicking those encountered at the time of maize domestication (comparatively lower CO<sub>2</sub> atmospheric concentration and lower temperatures) gives better insights into this phenomenon. The results showed that teosintes grown in these conditions exhibit contemporary maize-like phenotypes [131]. In contrast, modern maize has lost this plastic response. Over 2000 candidate loci associated with phenotypic changes showed altered expression in teosintes but not in maize, implying that they are no longer environmentally responsive (Fig. 2; [132]). Such loss of phenotypic plasticity may limit the ability of maize to cope with environmental variability in the face of current climate changes.

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## 8 Conclusion

Ongoing global warming has drastic effects on maize production, with an estimated impact of temperature and precipitation on yield of 3.8% worldwide between 1980 and 2008 [133]. Predicted changes that include further increases in temperatures and decline in rainfall, as well as shifts of pests and diseases, represent a huge challenge. There is thus a pressing need to better understand the dynamics and genomic basis of adaptation. Future climate projections predict that changes in temperature will impact the distribution and survival of both cultivated maize and its wild relatives [26, 134]. Most modeling studies, however, have focused on the climate tolerance of species, while the response to climate can depend on other factors such as plasticity and local adaptation. This suggests that the response should be studied at the level of individual populations to better understand the basis of adaptation.



**Fig. 2** Schematic representation of differences in plastic responses between maize and teosintes in Early-Holocene (EH) conditions. **(a)** *Parviglumis* plants exhibit maize-like phenotypes in the EH conditions (vegetative architecture, inflorescence sexuality and seed maturation). Phenotypes of *parviglumis* in modern conditions are typical of today's plants. These changes in phenotypes are associated with altered expression levels of over 2000 candidate loci in teosinte; here we represent the schematic expression of one gene between the two environments in teosinte. **(b)** In contrast, these same traits and underlying gene expression remain unchanged in maize between EH and modern conditions

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