Genomics of long-and short-term adaptation in maize and teosinte
Anne Lorant, Jeff Ross-Ibarra, Maud Tenaillon

To cite this version:
Anne Lorant, Jeff Ross-Ibarra, Maud Tenaillon. Genomics of long-and short-term adaptation in maize and teosinte. 2019. hal-02345485

HAL Id: hal-02345485
https://hal.archives-ouvertes.fr/hal-02345485
Submitted on 4 Nov 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L’archive ouverte pluridisciplinaire HAL, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d’enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.
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

Anne Lorant1,4, Jeffrey Ross-Ibarra1,2,3, Maud Tenaillon4

1 Dept. of Plant Sciences, University of California, Davis, CA 95616, USA.
2 Center for Population Biology, University of California, Davis, CA 95616, USA.
3 Genome Center, University of California, Davis, CA 95616, USA.
4 Génétique Quantitative et Evolution – Le Moulon, Institut National de la Recherche agronomique, Université Paris-Sud, Centre National de la Recherche Scientifique, AgroParisTech, Université Paris-Saclay, Gif-sur-Yvette, 91190, France.

Corresponding Author:
Maud Tenaillon4
Le Moulon, Institut National de la Recherche agronomique, Université Paris-Saclay, Gif-sur-Yvette, 91190, France.
Email address: maud.tenaillon@inra.fr

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
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.

INTRODUCTION

A combination of archeobotanical records and genetic data has established that maize (Zea mays ssp. mays) was domesticated around 9,000 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 1990’s [7], researchers have repeatedly attempted to establish demographic scenarios of maize domestication. All concur with a simple bottleneck model, i.e. a reduction of effective population size ($N_e$), 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 $N_e$ 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 one hand, domestication has likely promoted strong positive selection at ~2% to 4% of loci [10] producing one of the most famous text-book 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 pre-existing 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 27m in altitude and 11kms northwards, towards 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.
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.
Figure 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 co-varies 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).

What constraints 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 [43]. 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 [44]. In the Iowa Stalk Synthetic (BSSS), the response was of 3.9% per cycle for higher grain yield [45]. 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 was observed [44]. The results were more equivocal for Burn’s White (BW), for which the response is much stronger and steadier towards 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 [48]. 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 [43, 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 [50]. In BSSS, in which the mutational target 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 [48, 52]. 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 [53]. Below 1, soft sweeps’ contribution diminishes with \( \theta \). In the experiments from Table 1, selection is strong but \( \theta << 1 \) 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 [54], several examples instead suggest that they may either constrain or facilitate adaptation as predicted by Lande [55]). For instance, in *Arabidopsis thaliana* a recent study indicates that polymorphisms with intermediate degrees of pleiotropy favored rapid adaptation to micro-habitats *in natura*. 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 co-adapted suites of alleles [56]. It turns out that rather than clustering, plant domestication genes identified so far are single locus which are mainly transcription factors (reviewed in [57]) 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 \( \sim 20\% \) of the inflorescence sex but the introgression of both alleles converts
90% of maize’s female flowers to male [58]. 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, 58]. Their association in maize has however facilitated the acquisition of the domesticated phenotype.

**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 towards optimal traits tailored to agriculture during a shorter time frame of ~9,000 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 [59]. This is supported by crosses between maize and teosinte that led to the discovery of six main QTLs responsible for major phenotypic differences between them, notably vegetative architecture and inflorescence sexuality [60, 61, reviewed in 62]. 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 to 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 [59, 63–65].

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 [66]. This diversity is even higher in intergenic regions [67, 68]. Some adaptive mutations are found in coding sequences. Examples include non-synonymous changes in the \( tga1 \) gene responsible for the “naked kernel” maize phenotype, and in the diacylglycerol acyltransferase (\( DGAT1\)-2) gene resulting in elevated kernel oil content in maize lines [69, 70]. But most observations support adaptation from regulatory non-coding sequences. Indeed, in comparison with *Arabidopsis*, where adaptive variants are enriched in coding sequences [71], in maize and teosinte these are predominantly found in non-coding region: estimates in *Zea*
show that non-coding variants may explain as much phenotypic variation as those in coding regions [72, 73]. 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 co-expression networks [74].

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 [75, 76]. Genome size varies considerably within Zea resulting in over 30% differences among maize lines or landraces [72, 77, 78]. Because of their deleterious effect, TEs are often negatively selected and silenced by DNA methylation [79]. 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 [80] or TE-mediated genomic rearrangements causing gene insertion, deletion or duplication (reviewed in [81]). A handful of examples of their beneficial impact has been reported in Zea. A classic example in maize is at the tb1 locus, where a transposon inserted in the cis-regulatory region, doubling expression [82]. 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 tb1 is the major contributor to this apical dominance [82]. Beyond TEs, Copy Number Variants (CNVs) are also common in the maize genome [83] and they contribute significantly to phenotypic variation [72, 84].

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 [85]. Highland maize shows up to 20% mexicana introgression, which has likely facilitated their adaptation to high elevations [3, 86]. 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 [86, 87], 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].
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 non-native genotypes [88]. Locally adapted alleles can be either neutral or deleterious in other environments. Two models depict those situations, namely conditional neutrality and antagonistic pleiotropy [89]. 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 [90], 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, 91, 92]. 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 [93, 94]. An example of adaptation driven by soil interactions is the tolerance of maize and teosinte 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 [84].

Numerous other biotic and abiotic factors are likely involved in adaptation in maize and teosinte, including predation, parasitism, moisture and herbicide [95, 96]. 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 [97].

Interestingly, four large inversion polymorphisms seem to play an important role in local adaptation. Among them, a 50Mb 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, 98]. 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, 99]. Local adaptation to different habitats or niches is a gradual process that can promote divergence and, in the long run, ecological speciation [100]. 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., [91] 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.

How convergent is adaptation?

Convergent adaptation is the result of independent events of similar phenotypic changes to adapt to analogous environmental constraints [101]. 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 [102–106]. The selected alleles can originate from independent mutation events in different lineages, from shared ancestral variation or by introgression [105].

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, 107]. 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 [108]. 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 [109]. 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 [110].

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. [92] 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 [111]. 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 [112], 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.

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 [113, 114]. 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 [115]. This process is particularly important for plants as they are fixed in a specific location and not sheltered from the environment [116].
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 [117–119].

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 [120–122]. 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 [118]. 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 [118].

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 [123]. 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 [123], an observation in agreement with previous findings indicating that most phenotypic variation in maize is due to gene regulation [124].

Recent work on maize and parviglumis growing under environmental conditions mimicking those encountered at the time of maize domestication (comparatively lower CO2
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 [125]. 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 (Figure 2; [126]). Such loss of phenotypic plasticity may limit the ability of maize to cope with environmental variability in the face of current climate changes.

**Figure 2:** Schematic representation of differences in plastic responses between maize and teosinte 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.

**CONCLUSIONS**

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 [127]. 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, 128]. 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 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 (BISLE) |
|----------------|-------------|--------------|----------------------|------------------|------------------|-----------------|-------------------------------|-------------------------------|
| 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                             |
| 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 | OP variety | OP variety |
| 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 [10] |
| 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 |
| N 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 i | 1 | 1 | 8 | 20 | 20 | 0.5 to 5 | 5 | 7.5 |
| Heritability j | 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 k | 2 haplotypes | 2 haplotypes | 100 founders | 24 ears (H) | 24 ears (H) | ~300 founders | 16 founders | 12 founders |
| Reproductive mode | Selling | Selling | Outcrossing | Outcrossing | Outcrossing | Outcrossing | Outcrossing | Outcrossing |
| Sampling l | 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 |

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.

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

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

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

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

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

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

g: For GG, 4250 individuals were evaluated from cycles 1 to 12, and 14250 in the following cycles.
Effective population size ($N_e$) estimates given from the variance of offspring number [129], range is given when $N_e$ was estimated at each generation.

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

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.

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

---

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

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

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

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

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

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

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

[8]: Buckler, E. S., J. B. Holland, P. J. Bradbury, C. B. Acharya, P. J. Brown, C. Browne, E. Ersoz, et al.
2009. “The Genetic Architecture of Maize Flowering Time.” *Science* 325 (5941):714–18. https://doi.org/10.1126/science.1174276.

[9]: Liu, J., J. Huang, H. Guo, L. Lan, H. Wang, Y. Xu, X. Yang, et al. 2017. “The Conserved and Unique Genetic Architecture of Kernel Size and Weight in Maize and Rice.” *Plant Physiology* 175 (2). Am Soc Plant Biol:774–85.

[10]: Lamkey, K. R. 1992. “Fifty Years of Recurrent Selection in the Iowa Stiff Stalk Synthetic Maize Population.” *Maydica* 37 (1):19.

[11]: Hallauer, A. R., M. J. Carena, and J.B. M. Filho. 2010. “Quantitative Genetics in Maize Breeding.” In *Handbook of Plant Breeding*, 1–680. https://doi.org/10.1017/CBO9781107415324.004.

[12]: Gerke, J. P., J. W. Edwards, K. E. Guill, J. Ross-Ibarra, and M. D. McMullen. 2015. “The Genomic Impacts of Drift and Selection for Hybrid Performance in Maize.” *Genetics* 201 (3):1201–11. https://doi.org/10.1534/genetics.115.182410.

[13]: Yang, J., S. Mezmouk, A. Baumgarten, E. S. Buckler, K. E. Guill, M. D. McMullen, R. H. Mumm, and J. Ross-Ibarra. 2017. “Incomplete Dominance of Deleterious Alleles Contributes Substantially to Trait Variation and Heterosis in Maize.” *PLoS Genetics* 13 (9). https://doi.org/10.1371/journal.pgen.1007019.

[14]: Lopez-Reynoso, J. J. De. 1997. “Divergent Mass Selection for Ear Length in the Iowa Long Ear Synthetic Maize Cultivar after Twenty-Seven Cycles of Selection.” Digital Repository@ Iowa State University, http://lib.dr.iastate.edu/.

[15]: Ross, A. J., A. R. Hallauer, and M. Lee. 2006. “Genetic Analysis of Traits Correlated with Maize Ear Length.” *Maydica* 51 (2):301–13.

**ACKNOWLEDGEMENTS**

Maud Tenaillon acknowledges the Kavli Institute for Theoretical Physics at UCSB, supported in part by the National Science Foundation under Grant No. NSF PHY-1125915. J.R.I. would like to acknowledge support from the USDA Hatch project (CA-D-PLS-2066-H). The authors wish to acknowledge funding support from the US National Science Foundation (IOS-0922703 and IOS-1238014) as well as Michelle Stitzer, Mirko Ledda and Domenica Manicacci for comments. Finally, the authors would like to acknowledge Yves Vigouroux for his helpful reviews.
REFERENCES

1. Piperno DR, Flannery K V (2001) The earliest archaeological maize (Zea mays L.) from highland Mexico: new accelerator mass spectrometry dates and their implications. Proc Natl Acad Sci U S A 98:2101–2103. doi: 10.1073/pnas.98.4.2101

2. Matsuoka Y, Vigouroux Y, Goodman MM, Sanchez G J, Buckler E, Doebley J (2002) A single domestication for maize shown by multilocus microsatellite genotyping. Proc Natl Acad Sci U S A 99:6080–6084. doi: 10.1073/pnas.052125199

3. van Heerwaarden J, Doebley J, Briggs WH, Glaubitz JC, Goodman MM, de Jesus Sanchez Gonzalez J, Ross-Ibarra J (2011) Genetic signals of origin, spread, and introgression in a large sample of maize landraces. Proc Natl Acad Sci 108:1088–1092. doi: 10.1073/pnas.1013011108

4. Kwak M, Toro O, Debouck DG, Gepts P (2012) Multiple origins of the determinate growth habit in domesticated common bean (Phaseolus vulgaris). Ann Bot 110:1573–1580. doi: 10.1093/aob/mcs207

5. Poets AM, Fang Z, Clegg MT, Morrell PL (2015) Barley landraces are characterized by geographically heterogeneous genomic origins. Genome Biol 16:. doi: 10.1186/s13059-015-0712-3

6. Hufford MB, Xu X, van Heerwaarden J, Pyhäjärvi T, Chia J-M, Cartwright RA, Elshire RJ, Glaubitz JC, Guilke KE, Kaepepler SM, Lai J, Morrell PL, Shannon LM, Song C, Springer NM, Swanson-Wagner RA, Tiffin P, Wang J, Zhang G, Doebley J, McMullen MD, Ware D, Buckler ES, Yang S, Ross-Ibarra J (2012) Comparative population genomics of maize domestication and improvement. Nat Genet 44:808–811. doi: 10.1038/ng.2309

7. Hudson RR (2002) Generating samples under a Wright-Fisher neutral model of genetic variation. Bioinformatics 18:337–338. doi: 10.1093/bioinformatics/18.2.337

8. Eyre-Walker a, Gaut RL, Hilton H, Feldman DL, Gaut BS (1998) Investigation of the bottleneck leading to the domestication of maize. Proc Natl Acad Sci U S A 95:4441–4446. doi: 10.1073/pnas.95.8.4441

9. Tenaillon MI, U'Ren J, Tenaillon O, Gaut BS (2004) Selection versus demography: A multilocus investigation of the domestication process in maize. Mol Biol Evol 21:1214–1225. doi: 10.1093/molbev/msh102

10. Wright SI, Bi IV, Schroeder SG, Yamasaki M, Doebley JF, McMullen MD, Gaut BS (2005) The effects of artificial selection on the maize genome. Science 308:1310–1314. doi: 10.1126/science.1107891

11. Beissinger TM, Wang L, Crosby K, Durvasula A, Hufford MB, Ross-Ibarra J (2016) Recent demography drives changes in linked selection across the maize genome. Nat Plants 2:16084. doi: 10.1038/nplants.2016.84

12. Doebley J, Stec A, Gustus C (1995) teosinte branched1 and the origin of maize: evidence for epistasis and the evolution of dominance. Genetics 141:333–346

13. Cvijović I, Good BH, Desai MM (2018) The Effect of Strong Purifying Selection on Genetic Diversity. Genetics. doi: 10.1534/genetics.118.301058

14. Vigouroux Y, Glaubitz JC, Matsuoka Y, Goodman MM, Sánchez G. J, Doebley J (2008) Population structure and genetic diversity of New World maize races assessed by DNA microsatellites. Am J Bot 95:1240–1253. doi: 10.3732/ajb.0800097

15. Da Fonseca RR, Smith BD, Wales N, Cappellini E, Skoglund P, Fumagalli M, Samaniego
JA, Carøe C, Ávila-Arcos MC, Hufnagel DE, Korneliussen TS, Vieira FG, Jakobsson M, Arriaza B, Willerslev E, Nielsen R, Hufford MB, Albrechtsen A, Ross-Ibarra J, Gilbert MTP (2015) The origin and evolution of maize in the Southwestern United States. Nat Plants 1: . doi: 10.1038/nplants.2014.3

16. Brandenburg JT, Mary-Huard T, Rigaill G, Hearne SJ, Corti H, Joets J, Vitte C, Charcosset A, Nicolas SD, Tenaillon MI (2017) Independent introductions and admixtures have contributed to adaptation of European maize and its American counterparts. PLoS Genet 13: . doi: 10.1371/journal.pgen.1006666

17. Chuine I (2010) Why does phenology drives species distribution? Philos Trans R Soc London B 365:3149–3160 . doi: doi:10.1098/rstb.2010.0142

18. Swarts K, Gutaker RM, Benz B, Blake M, Bukowski R, Holland J, Kruse-Peeples M, Lepak N, Prim L, Romay MC, Ross-Ibarra J, Sanchez-Gonzalez J de J, Schmidt C, Schuenemann VJ, Krause J, Matson RG, Weigel D, Buckler ES, Burbano HA (2017) Genomic estimation of complex traits reveals ancient maize adaptation to temperate North America. Science (80- ) 357:512–515 . doi: 10.1126/science.aam9425

19. Hufford MB, Bilinski P, Pyhäjärvi T, Ross-Ibarra J (2012) Teosinte as a model system for population and ecological genomics. Trends Genet. 28:606–615

20. Pyhäjärvi T, Hufford MB, Mezmouk S, Ross-Ibarra J (2013) Complex patterns of local adaptation in teosinte. Genome Biol Evol 5:1594–1609 . doi: 10.1093/gbe/evt109

21. De Jesús Sánchez González J, Corral JAR, García GM, Ojeda GR, De La Cruz Larios L, Holland JB, Medrano RM, Romero GEG (2018) Ecogeography of teosinte. PLoS One. doi: 10.1371/journal.pone.0192676

22. Fukunaga K, Hill J, Vigouroux Y, Matsuoka Y, Sanchez J, Liu KJ, Buckler ES, Doebley J (2005) Genetic diversity and population structure of teosinte. Genetics 169:2241–2254 . doi: genetics.104.031393 [pii]\r10.1534/genetics.104.031393

23. Ross-Ibarra J, Tenaillon M, Gaut BS (2009) Historical divergence and gene flow in the genus Zea. Genetics 181:1399–1413 . doi: 10.1534/genetics.108.097238

24. Monleon VJ, Lintz HE (2015) Evidence of tree species’ range shifts in a complex landscape. PLoS One 10: . doi: 10.1371/journal.pone.0118069

25. Pauli H, Gottfried M, Dullinger S, Abdaladze O, Akhalkatsi M, Alonso JLB, Coldea G, Dick J, Erschbamer B, Calzado RF, Ghosn D, Holten JI, Kanka R, Kazakis G, Kollár J, Larsson P, Moiseev P, Moiseev D, Molau U, Mesa JM, Nagy L, Pelino G, Puscas M, Rossi G, Stanisci A, Syverhuset AO, Theurillat J-P, Tomaselli M, Unterluggauer P, Villar L, Vittoz P, Grabherr G (2012) Recent Plant Diversity Changes on Europe’s Mountain Summits. Science (80- ) 336:353–355 . doi: 10.1126/science.1219033

26. Hufford MB, Martínez-Meyer E, Gaut BS, Eguiarte LE, Tenaillon MI (2012) Inferences from the Historical Distribution of Wild and Domesticated Maize Provide Ecological and Evolutionary Insight. PLoS One 7: . doi: 10.1371/journal.pone.0047659

27. Anderson JT, Geber MA (2010) Demographic source-sink dynamics restrict local adaptation in Elliott’s blueberry (Vaccinium elliottii). Evolution (N Y) 64:370–384 . doi: 10.1111/j.1558-5646.2009.00825.x

28. Fournier-Level A, Korte A, Cooper MD, Nordborg M, Schmitt J, Wilczek AM (2011) A map of local adaptation in Arabidopsis thaliana. Science (80- ) 334:86–89 . doi: 10.1126/science.1209271
29. Savolainen O, Lascoux M, Merilä J (2013) Ecological genomics of local adaptation. Nat. Rev. Genet. 14:807–820
30. Endler JA (1986) Natural selection in the wild
31. Thompson J, Charpentier A, Bouguet G, Charmasson F, Roset S, Buatois B, Vernet P, Gouyon P-H (2013) Evolution of a genetic polymorphism with climate change in a Mediterranean landscape. Proc Natl Acad Sci U S A 110:2893–7. doi: 10.1073/pnas.1215833110
32. Tiffin P, Ross-Ibarra J (2014) Advances and limits of using population genetics to understand local adaptation. Trends Ecol. Evol. 29:673–680
33. Jaenicke-Despres V (2003) Early Allelic Selection in Maize as Revealed by Ancient DNA. Science (80-) 302:1206–1208. doi: 10.1126/science.1089056
34. Hermisson J, Pennings PS (2017) Soft sweeps and beyond: understanding the patterns and probabilities of selection footprints under rapid adaptation. Methods Ecol Evol 8:700–716. doi: 10.1111/2041-210X.12808
35. Bell G, Collins S (2008) Adaptation, extinction and global change. Evol Appl 1:3–16. doi: 10.1111/j.1752-4571.2007.00011.x
36. Burke MK, Dunham JP, Shahrestani P, Thornton KR, Rose MR, Long AD (2010) Genome-wide analysis of a long-term evolution experiment with Drosophila. Nature 467:587–590. doi: 10.1038/nature09352
37. Tenaillon O, Rodriguez-Verdugo A, Gaut RL, McDonald P, Bennett AF, Long AD, Gaut BS (2012) The Molecular Diversity of Adaptive Convergence. Science (80-) 335:457–461. doi: 10.1126/science.1212986
38. Burke MK, Liti G, Long AD (2014) Standing genetic variation drives repeatable experimental evolution in outcrossing populations of saccharomyces cerevisiae. Mol Biol Evol 31:3228–3239. doi: 10.1093/molbev/msu256
39. Graves JL, Hertweck KL, Phillips MA, Han M V., Cabral LG, Barter TT, Greer LF, Burke MK, Mueller LD, Rose MR, Singh N (2017) Genomics of parallel experimental evolution in drosophila. Mol Biol Evol 34:831–842. doi: 10.1093/molbev/msw282
40. Good BH, McDonald MJ, Barrick JE, Lenski RE, Desai MM (2017) The dynamics of molecular evolution over 60,000 generations. Nature 551:45–50. doi: 10.1038/nature24287
41. Schlötterer C, Kofler R, Versace E, Tobler R, Franssen SU (2014) Combining experimental evolution with next-generation sequencing: a powerful tool to study adaptation from standing genetic variation. Heredity (Edinb) 1–10. doi: 10.1038/hdy.2014.86
42. Franssen SU, Kofler R, Schlötterer C (2017) Uncovering the genetic signature of quantitative trait evolution with replicated time series data. Heredity (Edinb) 118:42–51. doi: 10.1038/hdy.2016.98
43. De Leon N, Coors JG (2002) Twenty-four cycles of mass selection for prolificacy in the Golden Glow maize population. Crop Sci 42:325–333. doi: 10.2135/cropsci2002.3250
44. Lopez-Reynoso JDJ, Hallauer AR (1998) Twenty-seven cycles of divergent mass selection for ear length in maize. Crop Sci 38:1099–1107. doi: 10.2135/cropsci1998.0011183X003800040035x
45. Lamkey KR (1992) Fifty years of recurrent selection in the Iowa Stiff Stalk Synthetic
46. Moose SP, Dudley JW, Rocheford TR (2004) Maize selection passes the century mark: A unique resource for 21st century genomics. Trends Plant Sci. 9:358–364
47. Dudley JW, Lambert RJ (2010) 100 Generations of Selection for Oil and Protein in Corn. In: Plant Breeding Reviews. pp 79–110
48. Durand E, Tenaillon MI, Raffoux X, Thépot S, Falque M, Jamin P, Bourgain A, Ressaye A, Dillmann C (2015) Dearth of polymorphism associated with a sustained response to selection for flowering time in maize. BMC Evol Biol 15:103 . doi: 10.1186/s12862-015-0382-5
49. Maita R, Coors JG (1996) Twenty cycles of biparental mass selection for prolificacy in the open-pollinated maize population Golden Glow. Crop Sci 36:1527–1532
50. Odhiambo MO, Compton WA (1987) Twenty cycles of divergent mass selection for seed size in corn. Crop Sci 27:1113–1116
51. Gerke JP, Edwards JW, Guill KE, Ross-Ibarra J, McMullen MD (2015) The genomic impacts of drift and selection for hybrid performance in maize. Genetics 201:1201–1211 . doi: 10.1534/genetics.115.182410
52. Durand E, Tenaillon MI, Ridel C, Coubriche D, Jamin P, Jouanne S, Ressaye A, Charcosset A, Dillmann C (2010) Standing variation and new mutations both contribute to a fast response to selection for flowering time in maize inbreds. BMC Evol Biol 10:2 . doi: 10.1186/1471-2148-10-2
53. Messer PW, Petrov DA (2013) Population genomics of rapid adaptation by soft selective sweeps. Trends Ecol Evol 28:659–669 . doi: 10.1016/j.tree.2013.08.003
54. Agrawal AF, Stinchcombe JR (2009) How much do genetic covariances alter the rate of adaptation? Proc R Soc B Biol Sci 276:1183–1191 . doi: 10.1098/rspb.2008.1671
55. Lande R (1979) Quantitative Genetic Analysis of Multivariate Evolution, Applied to Brain: Body Size Allometry. Evolution (N Y) 33:402 . doi: 10.2307/2407630
56. Le Thierry D’Ennequin M, Toupance B, Robert T, Godelle B, Gouyon PH (1999) Plant domestication: A model for studying the selection of linkage. J Evol Biol 12:1138–1147 . doi: 10.1046/j.1420-9101.1999.00115.x
57. Martínez-Ainsworth NE, Tenaillon MI (2016) Superheroes and masterminds of plant domestication. C R Biol 339:268–273 . doi: 10.1016/j.crvi.2016.05.005
58. Lukens LN, Doebley J (1999) Epistatic and environmental interactions for quantitative trait loci involved in maize evolution. Genet Res 74:291–302 . doi: 10.1017/S0016672399004073
59. Wallace JG, Larsson SJ, Buckler ES (2014) Entering the second century of maize quantitative genetics. Heredity (Edinb). 112:30–38
60. Beadle GW (1972) Mystery of Maize. F Museum Nat Hist Bull
61. Briggs WH, McMullen MD, Gaut BS, Doebley J (2007) Linkage mapping of domestication loci in a large maize teosinte backcross resource. Genetics 177:1915–1928 . doi: 10.1534/genetics.107.076497
62. Stitzer MC, Ross-Ibarra J (2018) Maize domestication and gene interaction. New Phytol. doi: 10.1111/nph.15350
63. Buckler ES, Holland JB, Bradbury PJ, Acharya CB, Brown PJ, Browne C, Ersoz E, Flint-Garcia S, Garcia A, Glaubitsz JC, Goodman MM, Harjes C, Guill K, Kroon DE, Larsson S,
Lepak NK, Li H, Mitchell SE, Pressoir G, Peiffer JA, Rosas MO, Rocheford TR, Romay MC, Romero S, Salvo S, Villeda HS, Sofia da Silva H, Sun Q, Tian F, Upadayayula N, Ware D, Yates H, Yu J, Zhang Z, Kresovich S, McMullen MD (2009) The Genetic Architecture of Maize Flowering Time. Science (80-) 325:714–718. doi: 10.1126/science.1174276

Cook JP, McMullen MD, Holland JB, Tian F, Bradbury P, Ross-Ibarra J, Buckler ES, Flint-Garcia SA (2012) Genetic Architecture of Maize Kernel Composition in the Nested Association Mapping and Inbred Association Panels. PLANT Physiol 158:824–834. doi: 10.1104/pp.111.185033

Romero Navarro JA, Willcox M, Burgueño J, Romay C, Swarts K, Trachsel S, Preciado E, Terron A, Delgado HV, Vidal V, Ortega A, Banda AE, Montiel NOG, Ortiz-Monasterio I, Vicente FS, Espinoza AG, Atlin G, Wenzl P, Heame S, Buckler ES (2017) A study of allelic diversity underlying flowering-time adaptation in maize landraces. Nat Genet 49:476–480. doi: 10.1038/ng.3784

Tian F, Stevens NM, Buckler ES (2009) Tracking footprints of maize domestication and evidence for a massive selective sweep on chromosome 10. Proc Natl Acad Sci 106:9979–9986. doi: 10.1073/pnas.0901122106

Tenaillon MI, Sawkins MC, Long AD, Gaut RL, Doebley JF, Gaut BS (2001) Patterns of DNA sequence polymorphism along chromosome 1 of maize (Zea mays ssp. mays L.). Proc Natl Acad Sci U S A 98:9161–6. doi: 10.1073/pnas.151244298

Buckler ES, Gaut BS, McMullen MD (2006) Molecular and functional diversity of maize. Curr. Opin. Plant Biol. 9:172–176

Wang H, Nussbaum-Wagler T, Li B, Zhao Q, Vigouroux Y, Faller M, Bombilés K, Lukens L, Doebelley JF (2005) The origin of the naked grains of maize. Nature 436:714–719. doi: 10.1038/nature03863

Zheng P, Allen WB, Roesler K, Williams ME, Zhang S, Li J, Glassman K, Ranch J, Nubel D, Solawetz W, Bhattramakki D, Liaca V, Deschamps S, Zhong GY, Tarczynski MC, Shen B (2008) A phenylalanine in DGAT is a key determinant of oil content and composition in maize. Nat Genet 40:367–372. doi: 10.1038/ng.85

Hancock AM, Brachi B, Faure N, Horton MW, Jarymowycz LB, Sperone FG, Toomajian C, Roux F, Bergelson J (2011) Adaptation to Climate Across the Arabidopsis thaliana Genome. Science (80-) 334:83–86. doi: 10.1126/science.1209244

Chia JM, Song C, Bradbury PJ, Costich D, De Leon N, Doebley J, Elshire RJ, Gaut B, Geller L, Glaubitz JC, Gore M, Guil KE, Holland J, Hufford MB, Lai J, Li M, Liu X, Lu Y, McCombie R, Nelson R, Poland J, Prasanna BM, Pyhäjärvi T, Rong T, Sekhon RS, Sun Q, Tenaillon MI, Tian F, Wang J, Xu X, Zhang Z, Kaeppler SM, Ross-Ibarra J, McMullen MD, Buckler ES, Zhang G, Xu Y, Ware D (2012) Maize HapMap2 identifies extant variation from a genome in flux. Nat Genet 44:803–807. doi: 10.1038/ng.2313

Rodgers-Melnick E, Vera DL, Bass HW, Buckler ES (2016) Open chromatin reveals the functional maize genome. Proc Natl Acad Sci 113:E3177–E3184. doi: 10.1073/pnas.1525244113

Swanson-Wagner R, Briskine R, Schaefer R, Hufford MB, Ross-Ibarra J, Myers CL, Tiffin P, Springer NM (2012) Reshaping of the maize transcriptome by domestication. Proc Natl Acad Sci U S A 109:11878–11883. doi: 10.1073/pnas.1201961109
75. Schnable PS, Ware D, Fulton RS, Stein JC, Wei F, Pasternak S, Liang C, Zhang J, Fulton L, Graves TA, Minx P, Reily AD, Courtney L, Kruchowski SS, Tomlinson C, Strong C, Delehaunty K, Fronick C, Courtney B, Rock SM, Belter E, Du F, Kim K, Abbott RM, Cotton M, Levy A, Marchetto P, Ochoa K, Jackson SM, Gillam B, Chen W, Yan L, Higginbothom J, Cardenas M, Waligorski J, Applebaum E, Phelps L, Falcone J, Kanchi K, Waligorski J, Applebaum E, Phelps L, Falcone J, Kanchi K, Thane T, Scimone A, Thane N, Henke J, Wang T, Ruppert J, Shah N, Rotter K, Hodges J, Ingenthron E, Cordes M, Kohlberg S, Sgro J, Delgado B, Mead K, Chinwalla A, A, Fan C, Sebastian A, Kramer M, Spiegel L, Nascimento L, Zutavern T, Miller B, Ambroise C, Muller S, Spooner W, Narechania A, Ren L, Wei S, Kumari S, Faga B, Levy MJ, McMahan L, Van Buren P, Vaughn MW, Ying K, Yeh C-T, Emrich SJ, Jia Y, Kalyanaraman A, Hsia A-P, Barbazuk WB, Baucom RS, Brutnell TP, Carpita NC, Chaparro C, Chia J-M, Deragon J-M, Estill JC, Fu Y, Jeddeloh JA, Han Y, Lee H, Li P, Lisch DR, Liu S, Liu Z, Nagel DH, McCann MC, SanMiguel P, Myers AM, Nettleton D, Nguyen J, Penning BW, Ponnala L, Schneider KL, Schwartz DC, Sharma A, Soderlund C, Springer NM, Sun Q, Wang H, Waterman M, Westerman R, Wolfgruber TK, Yang L, Yu Y, Zhang L, Zhou S, Zhu Q, Bennetzen JL, Dawe RK, Jiang J, Jiang N, Presting GG, Wessler SR, Aluru S, Martinsson RA, Clifton SW, McCombie WR, Wing RA, Wilson RK (2009) The B73 Maize Genome: Complexity, Diversity, and Dynamics. Science (80-) 326:1112–1115. doi: 10.1126/science.1178534

76. Tenaillon MI, Hollister JD, Gaut BS (2010) A triptych of the evolution of plant transposable elements. Trends Plant Sci. 15:471–478

77. Munoz-Diez C, Vitte C, Ross-Ibarra J, Gaut BS, Tenaillon MI (2012) Using nextgen sequencing to investigate genome size variation and transposable element content. Top. Curr. Genet. 24:41–58

78. Diez CM, Meca E, Tenaillon MI, Gaut BS (2014) Three Groups of Transposable Elements with Contrasting Copy Number Dynamics and Host Responses in the Maize (Zea mays ssp. mays) Genome. PLoS Genet 10:. doi: 10.1371/journal.pgen.1004298

79. Hollister JD, Gaut BS (2009) Epigenetic silencing of transposable elements: A trade-off between reduced transposition and deleterious effects on neighboring gene expression. Genome Res 19:1419–1428. doi: 10.1101/gr.091678.109

80. Waters AJ, Makarevitch I, Noshay J, Burghardt LT, Hirsch CN, Hirsch CD, Springer NM (2017) Natural variation for gene expression responses to abiotic stress in maize. Plant J 89:706–717. doi: 10.1111/tpj.13414

81. Vitte C, Fustier MA, Alix K, Tenaillon MI (2014) The bright side of transposons in crop evolution. Briefings Funct Genomics Proteomics 13:276–295. doi: 10.1093/bfgp/elu002

82. Studer A, Zhao Q, Ross-Ibarra J, Doebley J (2011) Identification of a functional transposon insertion in the maize domestication gene tb1. Nat Genet 43:1160–1163. doi: 10.1038/ng.942

83. Springer NM, Ying K, Fu Y, Ji T, Yeh CT, Jia Y, Wu W, Richmond T, Kitzman J, Rosenbaum H, Iniguez AL, Barbazuk WB, Jeddeloh JA, Nettleton D, Schnable PS (2009) Maize inbreds exhibit high levels of copy number variation (CNV) and presence/absence...
variation (PAV) in genome content. PLoS Genet 5: . doi: 10.1371/journal.pgen.1000734

Maron LG, Guimaraes CT, Kirst M, Albert PS, Birchler JA, Bradbury PJ, Buckler ES, Coluccio AE, Danilova T V, Kudrna D, Magalhaes J V, Pineros MA, Schatz MC, Wing RA, Kochian L V, Ronald Sederoff (2013) Aluminum tolerance in maize is associated with higher MATE1 gene copy number. Proc Natl Acad Sci U S A 110:5241–5246 . doi: 10.1073/pnas.1220766110

Baltazar BM, Sánchez-Gonzalez JDJ, De La Cruz-Larios L, Schoper JB (2005) Pollination between maize and teosinte: An important determinant of gene flow in Mexico. Theor Appl Genet 110:519–526 . doi: 10.1007/s00122-004-1859-6

Hufford MB, Lubinsky P, Pyhäjärvi T, Devengenzo MT, Ellstrand NC, Ross-Ibarra J (2013) The Genomic Signature of Crop-Wild Introgression in Maize. PLoS Genet 9: . doi: 10.1371/journal.pgen.1003477

Lauter N, Gustus C, Westerbergh A, Doebley J (2004) The inheritance and evolution of leaf pigmentation and pubescence in teosinte. Genetics 167:1949–1959 . doi: 10.1534/genetics.104.026997

Kawecki TJ, Ebert D (2004) Conceptual issues in local adaptation. Ecol Lett 7:1225–1241 . doi: 10.1111/j.1461-0248.2004.00684.x

Anderson JT, Lee CR, Rushworth CA, Colautti RI, Mitchell-Olds T (2013) Genetic trade-offs and conditional neutrality contribute to local adaptation. In: Molecular Ecology. pp 699–708

Mercer K, Martínez-Vásquez Á, Perales HR (2008) Asymmetrical local adaptation of maize landraces along an altitudinal gradient. Evol Appl 1:489–500 . doi: 10.1111/j.1752-4571.2008.00038.x

Aguirre-Liguori JA, Tenaillon MI, Vázquez-Lobo A, Gaut BS, Jaramillo-Correa JP, Montes-Hernandez S, Souza V, Eguiarte LE (2017) Connecting genomic patterns of local adaptation and niche suitability in teosintes. Mol Ecol 26:4226–4240 . doi: 10.1111/mec.14203

Fustier MA, Brandenburg JT, Boitard S, Lapeyronnie J, Eguiarte LE, Vigouroux Y, Manicacci D, Tenaillon MI (2017) Signatures of local adaptation in lowland and highland teosintes from whole-genome sequencing of pooled samples. Mol Ecol 26:2738–2756 . doi: 10.1111/mec.14082

Hung H-Y, Shannon LM, Tian F, Bradbury PJ, Chen C, Flint-Garcia SA, McMullen MD, Ware D, Buckler ES, Doebly JF, Holland JB (2012) ZmCCT and the genetic basis of day-length adaptation underlying the postdomestication spread of maize. Proc Natl Acad Sci 109:E1913–E1921 . doi: 10.1073/pnas.1203189109

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, Yang X, Xu M (2013) CACTA-like transposable element in ZmCCT attenuated photoperiod sensitivity and accelerated the postdomestication spread of maize. Proc Natl Acad Sci 110:16969–16974 . doi: 10.1073/pnas.1310949110

Linhart YB, Grant MC (1996) EVOLUTIONARY SIGNIFICANCE OF LOCAL GENETIC DIFFERENTIATION IN PLANTS. Annu Rev Ecol Syst 27:237–277 . doi: 10.1146/annurev.ecolsys.27.1.237

Valverde BE (2007) Status and Management of Grass-weed Herbicide Resistance in Latin America. Weed Technol 21:310–323 . doi: 10.1614/WT-06-097.1
97. Moeller DA, Tiffin P (2008) Geographic variation in adaptation at the molecular level: A case study of plant immunity genes. Evolution (N Y) 62:3069–3081. doi: 10.1111/j.1558-5646.2008.00511.x

98. Fang Z, Pyhäjärvi T, Weber AL, Dawe RK, Glaubitz JC, Sánchez González J de J, Ross-Ibarra C, Doebley J, Morrell PL, Ross-Ibarra J (2012) Megabase-scale inversion polymorphism in the wild ancestor of maize. Genetics 191:883–894. doi: 10.1534/genetics.112.138578

99. Romero Navarro JA, Willcox M, Burgueño J, Romay C, Swarts K, Trachsel S, Preciado E, Terron A, Delgado HV, Vidal V, Ortega A, Banda AE, Montiel NOG, Ortiz-Monasterio I, Vicente FS, Espinoza AG, Atlin G, Wenzl P, Hearne S, Buckler ES (2017) A study of allelic diversity underlying flowering-time adaptation in maize landraces. Nat Genet. doi: 10.1038/ng.3784

100. Schluter D (2009) Evidence for ecological speciation and its alternative. Science (80-. ). 323:737–741

101. Wood TE, Burke JM, Rieseberg LH (2005) Parallel genotypic adaptation: When evolution repeats itself. In: Genetica. pp 157–170

102. Colosimo PF, Hosemann KE, Balabhadra S, Villarreal G, Dickson H, Grimwood J, Schmutz J, Myers RM, Schluter D, Kingsley DM (2005) Widespread parallel evolution in sticklebacks by repeated fixation of ectodysplasin alleles. Science (80-. ) 307:1928–1933. doi: 10.1126/science.1107239

103. Pearce RJ, Pota H, Evehe MSB, Bâ EH, Mombo-Ngoma G, Malisa AL, Ord R, Inojosa W, Matondo A, Diallo DA, Mbacham W, Van Den Broek I V., Swarthout TD, Getachew A, Dejene S, Grobusch MP, Njie F, Dunyo S, Kweku M, Owusu-Agyei S, Chandramohan D, Bonnet M, Guthmann JP, Clarke S, Barnes KL, Streat E, Katokele ST, Uusiku P, Agbogborhoocoma CO, Elegba OY, Cissé B, Al-Elbasit IE, Giha HA, Kachur SP, Lynch C, Rwakimari JB, Chanda P, Hawela M, Sharp B, Naidoo I, Roper C (2009) Multiple origins and regional dispersal of resistant dhps in African Plasmodium falciparum malaria. PLoS Med 6: . doi: 10.1371/journal.pmed.1000055

104. Chan YF, Marks ME, Jones FC, Villarreal G, Shapiro MD, Brady SD, Southwick AM, Absher DM, Grimwood J, Schmutz J, Myers RM, Petrov D, Jónsson B, Schluter D, Bell MA, Kingsley DM (2010) Adaptive evolution of pelvic reduction in sticklebacks by recurrent deletion of a pitx1 enhancer. Science (80-. ) 327:302–305. doi: 10.1126/science.1182213

105. Stern DL (2013) The genetic causes of convergent evolution. Nat. Rev. Genet. 14:751–764

106. Roesti M, Gavrillets S, Hendry AP, Salzburger W, Berner D (2014) The genomic signature of parallel adaptation from shared genetic variation. Mol Ecol 23:3944–3956. doi: 10.1111/mec.12720

107. Riehle MM, Bennett AF, Long AD (2001) Genetic architecture of thermal adaptation in Escherichia coli. Proc Natl Acad Sci 98:525–530. doi: 10.1073/pnas.98.2.525

108. Gaut BS (2015) Evolution is an experiment: Assessing parallelism in crop domestication and experimental evolution. Mol Biol Evol 32:1661–1671. doi: 10.1093/molbev/msv105

109. Fuller DQ, Denham T, Arroyo-Kalin M, Lucas L, Stevens CJ, Qin L, Allaby RG, Purugganan MD (2014) Convergent evolution and parallelism in plant domestication.
revealed by an expanding archaeological record. Proc Natl Acad Sci 111:6147–6152.
doi: 10.1073/pnas.1308937110

Lin Z, Li X, Shannon LM, Yeh CT, Wang ML, Bai G, Peng Z, Li J, Trick HN, Clemente TE,
Doebley J, Schnable PS, Tuinstra MR, Tesso TT, White F, Yu J (2012) Parallel
domestication of the Shattering1 genes in cereals. Nat Genet 44:720–724.
doi: 10.1038/ng.2281

Takuno S, Ralph P, Swart K, Elshire RJ, Glaubitz JC, Buckler ES, Hufford MB, Ross-
Ibarra J (2015) Independent molecular basis of convergent highland adaptation in maize.
Genetics 200:1297–1312. doi: 10.1534/genetics.115.178327

Lee KM, Coop G (2017) Distinguishing Among Modes of Convergent Adaptation Using
Population Genomic Data. Genetics genetics.300417.2017. doi:
10.1534/genetics.117.300417

Gilbert SF, Epel D (2009) Ecological developmental biology: integrating epigenetics,
medicine, and evolution. Sinauer Assoc

Beldade P, Mateus ARA, Keller RA (2011) Evolution and molecular mechanisms of
adaptive developmental plasticity. Mol Ecol 20:1347–1363. doi: 10.1111/j.1365-
294X.2011.05016.x

Wennersten L, Forsman A (2012) Population-level consequences of polymorphism,
plasticity and randomized phenotype switching: A review of predictions. Biol. Rev.
87:756–767

Des Marais DL, Hernandez KM, Juenger TE (2013) Genotype-by-environment interaction
and plasticity: exploring genomic responses of plants to the abiotic environment. Annu
Rev Ecol Evol Syst 44:5–29

DeWitt TJ, Sih A, Wilson DS (1998) Costs and limits of phenotypic plasticity. Trends Ecol.
Evol. 13:77–81

Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P,
Puttagunan MD, Richards CL, Valladares F, van Kleunen M (2010) Plant phenotypic
plasticity in a changing climate. Trends Plant Sci. 15:684–692

Auld JR, Agrawal AA, Relyea RA (2010) Re-evaluating the costs and limits of adaptive
phenotypic plasticity. Proc R Soc B Biol Sci 277:503–511. doi: 10.1098/rspb.2009.1355

Kuzawa CW, Bragg JM (2012) Plasticity in human life history strategy. Curr Anthropol
53:S369–S382

Diggle PK, Miller JS (2013) Developmental plasticity, genetic assimilation, and the
evolutionary diversification of sexual expression in Solanum. Am J Bot 100:1050–1060.
doi: 10.3732/ajb.1200647

Standen EM, Du TY, Larsson HCE (2014) Developmental plasticity and the origin of
tetrapods. Nature 513:54–58. doi: 10.1038/nature13708

Gage JL, Jarquin D, Romay C, Lorenz A, Buckler ES, Kaeplller S, Alkalifah N, Bohn M,
Campbell DA, Edwards J, Ertl D, Flint-Garcia S, Gardiner J, Good B, Hirsch CN, Holland
J, Hooker DC, Knoll J, Kolkman J, Kruger G, Lauter N, Lawrence-Dill CJ, Lee E, Lynch J,
Murray SC, Nelson R, Petzoldt J, Rocheford T, Schnable J, Schnable PS, Scully B, Smith
M, Springer NM, Srinivasan S, Walton R, Weldekind T, Wisser RJ, Xu W, Yu J, De Leon
N (2017) The effect of artificial selection on phenotypic plasticity in maize. Nat Commun
8: . doi: 10.1038/s41467-017-01450-2
124. Wallace JG, Bradbury PJ, Zhang N, Gibon Y, Stitt M, Buckler ES (2014) Association Mapping across Numerous Traits Reveals Patterns of Functional Variation in Maize. PLoS Genet 10: . doi: 10.1371/journal.pgen.1004845

125. Piperno DR, Holst I, Winter K, McMillan O (2015) Teosinte before domestication: Experimental study of growth and phenotypic variability in late Pleistocene and early Holocene environments. Quat Int 363:65–77

126. Lorant A, Pedersen S, Holst I, Hufford MB, Winter K, Piperno D, Ross-Ibarra J (2017) The potential role of genetic assimilation during maize domestication. PLoS One 12: . doi: 10.1371/journal.pone.0184202

127. Lobell DB, Schlenker W, Costa-Roberts J (2011) Climate trends and global crop production since 1980. Science 333:616–620 . doi: 10.1126/science.1204531

128. Ureta C, Martínez-Meyer E, Perales HR, Álvarez-Buylla ER (2012) Projecting the effects of climate change on the distribution of maize races and their wild relatives in Mexico. Glob Chang Biol 18:1073–1082 . doi: 10.1111/j.1365-2486.2011.02607.x

129. Crow JF, Kimura M, others (1970) An introduction to population genetics theory. An Introd to Popul Genet theory

130. Liu J, Huang J, Guo H, Lan L, Wang H, Xu Y, Yang X, Li W, Tong H, Xiao Y, others (2017) The conserved and unique genetic architecture of kernel size and weight in maize and rice. Plant Physiol 175:774–785

131. Hallauer AR, Carena MJ, Filho JBM (2010) Quantitative genetics in Maize Breeding. In: Handbook of Plant Breeding. pp 1–680

132. Yang J, Mezmouk S, Baumgarten A, Buckler ES, Guill KE, McMullen MD, Mumm RH, Ross-Ibarra J (2017) Incomplete dominance of deleterious alleles contributes substantially to trait variation and heterosis in maize. PLoS Genet 13: . doi: 10.1371/journal.pgen.1007019

133. Lopez-Reynoso J de J (1997) Divergent mass selection for ear length in the Iowa Long Ear Synthetic maize cultivar after twenty-seven cycles of selection

134. Ross AJ, Hallauer AR, Lee M (2006) Genetic analysis of traits correlated with maize ear length. Maydica 51:301–313