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Research

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Summary

- Crop genetic diversity for climate adaptations is globally partitioned. We performed experimental evolution in maize to understand the response to selection and how plant germplasm can be moved across geographical zones.
- Initialized with a common population of tropical origin, artificial selection on flowering time was performed for two generations at eight field sites spanning 25° latitude, a 2800 km transect. We then jointly tested all selection lineages across the original sites of selection, for the target trait and 23 other traits.
- Modeling intergenerational shifts in a physiological reaction norm revealed separate components for flowering-time plasticity. Generalized and local modes of selection altered the plasticity of each lineage, leading to a latitudinal pattern in the responses to selection that were strongly driven by photoperiod. This transformation led to widespread changes in developmental, architectural, and yield traits, expressed collectively in an environment-dependent manner. Furthermore, selection for flowering time alone alleviated a maladaptive syndrome and improved yields for tropical maize in the temperate zone.
- Our findings show how phenotypic selection can rapidly shift the flowering phenology and plasticity of maize. They also demonstrate that selecting crops to local conditions can accelerate adaptation to climate change.

Introduction

Evolutionary biologists have long recognized that individuals perform better in locations where their ancestral populations originated, a phenomenon referred to as local adaptation (Darwin, 1868; Kawecki & Ebert, 2004). Local adaptation is driven by selection over time and across geographical space, which leads to phenotypic and genotypic divergence between local, at least partially isolated, populations (Savolainen *et al.*, 2013). Phenotypic plasticity can also be locally adaptive and respond to selection on genetic variation in reaction norms, potentiating rapid adaptation to sudden environmental change (Lande, 2009). The interplay between selection and plasticity is particularly relevant to plants because they are sessile organisms that must cope with their environment. For crops, a deeper understanding of their adaptive mechanisms can offer insights for breeding in a fast-changing climate.

Phenological traits including the rates and timing of plant development are critical components of plant adaptation (Ducrocq *et al.*, 2008; Hancock *et al.*, 2011; Harrison *et al.*, 2014). Flowering time is essential for fitness in natural plant populations and for yield in cultivated varieties. Optimal timing of flowering in a given environment balances the production of vegetative photosynthesizing tissues against the time required to produce healthy seeds (Hall & Willis, 2006; Mercer & Perales, 2019). This enabled the global spread of maize from a relatively small geographical range in Southern Mexico to a vast range across the Americas before European contact (Weatherwax, 1954; Ross-Ibarra & Piperno, 2020), resulting in varieties adapted to an array of ecologies (Ruiz Corral *et al.*, 2008; Shiferaw *et al.*, 2011). Even within the territory of Mexico, historical varieties of maize show evidence of local adaptation to altitude (Mercer *et al.*, 2008). In association with differences in phenology, local varieties from one range in elevation outperform those from other elevations (Mercer & Perales, 2019). Thus,

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understanding the geographical scale and the degree to which local adaptation affects phenology is important for the exchange of germplasm and maximizing productivity.

Flowering time in maize is a complex trait, with a facultative physiological response to short-day : long-night photoperiods and other mechanisms of control conditioned by oligogenic and finite polygenic architectures, respectively (Buckler *et al.*, 2009; Hung *et al.*, 2012). Several key genes underlying phenotypic variation in flowering time have been identified, including *Vgt1* (Salvi *et al.*, 2007), *ZmCCT10* (Hung *et al.*, 2012; Yang *et al.*, 2013), *ZCN8* (Guo *et al.*, 2018), *ZmCCT9* (Huang *et al.*, 2017), MADS-box genes *ZMM4* and *ZmMADS69* (Liang *et al.*, 2019), *Dlf1* (Sun *et al.*, 2020), and *ZCN12* (Castelletti *et al.*, 2020). These genes show signatures of historical selection linked to the adaptation of maize across geographical zones. During recurrent selection on flowering time, selective sweeps for larger-effect variants at some of these genes occur in early generations, while many smaller-effect variants undergo transient frequency shifts that sustain the phenotypic response across additional generations (Wisser *et al.*, 2019).

In maize, genetic variation has fueled substantial gains in productivity over time (Hallauer & Carena, 2014). However, elite hybrids developed for production in temperate North America and Europe originate from a restricted breeding pool, tracing back to a few varieties preadapted to the temperate zone (Goodman, 2005; Mikel & Dudley, 2006), representing a small fraction of global maize diversity (Goodman, 1998). Tropical maize, in particular, contains greater genetic variation than temperate-adapted maize (Tenaillon *et al.*, 2001; Liu *et al.*, 2003), including unique alleles for disease resistance and yield potential (Holland *et al.*, 1996; Goodman, 2004; Frey *et al.*, 2011; Laude & Carena, 2015). However, tropical maize is poorly adapted to the temperate zone, where longer daylengths and lower average temperatures occur, both of which delay flowering time. Due to photoperiod sensitivity and lateness per se, tropical maize grown in temperate environments has a prolonged vegetative phase, leading to a maladaptive syndrome characterized by extremely late-flowering plants that are tall and susceptible to lodging, with greatly reduced grain yield (Stevenson & Goodman, 1972; Castillo-Gonzalez & Goodman, 1989; Holland & Goodman, 1995; Edmeades *et al.*, 2000; Teixeira *et al.*, 2015). Consequently, there has been a reluctance to work with tropical maize in temperate environments, as favorable genotypes and alleles are difficult to incorporate (Goodman, 2004).

For tropical germplasm to be a useful source of diversity in temperate breeding programs, selection for earliness is required to shift flowering time of late tropical populations toward the optimum for temperate environments. With an average phenotypic response of 1–2 d per cycle of selection, breeding within tropical populations that initially flower 20–40 d later than local varieties can take a decade to reach the optimal timing (Teixeira *et al.*, 2015). Understanding the influence of selection environments on response to selection could reveal ideal conditions for more rapid adaptation. However, the extent of variability in the effects of selection conducted in different locations is largely unknown. Furthermore, selection response depends not only on the environment in which selection is performed but also on the environment in which selection response is evaluated, as a function of trait heritability within each environment and genetic correlations between environments (Atlin & Frey, 1989, 1990; Simmonds, 1991; Falconer & Mackay, 1996). Specifically, response to selection practiced in environment X and evaluated in environment Y can be formulated as: $R_Y = ih_X h_Y r_{AXY} \sigma_{PY}$, where i is the selection intensity, h_X is the square root of trait heritability in selection environment X, h_Y is square root of trait heritability in evaluation environment Y, r_{AXY} is the genetic correlation between the environments, and σ_{PY} is the phenotypic standard deviation in the evaluation environment (Falconer & Mackay, 1996). Interactions between selection and evaluation environments can also arise due to genetic correlations between specific pairs of environments (r_{AXY}) that deviate from the pattern of average correlations involving those environments ($r_{AX.}$ and $r_{A.Y}$). Here, we sought to quantify the relative importance of selection and evaluation environments, test whether they interact in their effects on selection response, and identify environmental factors that influence the effectiveness of selection.

Across a spatiotemporal landscape, local and generalized modes of selection can drive adaptation, with the former contributing to responses in only parts of the landscape and the latter contributing to responses across the entire landscape. If local effects predominate over generalized selection responses, selection is expected be most effective when it occurs directly within those conditions. By contrast, within-environment heritabilities and between-environment genetic correlations for selected traits may be structured such that indirect gain from selection (where selection and evaluation locations differ) may be greater than direct selection response (where selection and evaluation locations are the same) in some cases (Atlin & Frey, 1990; Calhoun *et al.*, 1994). Combining selection studies, common garden evaluations, and reciprocal transplant experiments can help in understanding how selection in different environments leads to population divergence and adaptation and can disentangle local from generalized effects (Kawecki & Ebert, 2004).

Here, we used experimental evolution across a wide latitudinal range to address questions about the phenological adaptation of maize. Beginning with a common, multiparent intercross population from tropical lines, parallel selection was performed at eight field sites, traversing tropical climates in which the population was essentially preadapted to temperate climates in which it was poorly adapted. A standardized selection procedure was used at all sites for two generations, leading to the creation of site-specific selection lineages. Afterward, all selection lineages were evaluated together in a common garden at all of the original sites of selection, where developmental, architectural, and yield traits were recorded for multiple years (Fig. 1a). We dissected the observed variation in response to selection by differentiating local and broad mechanisms of adaptation, testing for environmental factors that affected selection progress, characterizing the interaction between trait plasticity and selection, and determining how target-trait selection affects numerous other traits. Our findings show how the rich diversity of tropical maize can be rapidly incorporated into the northern temperate zone. They

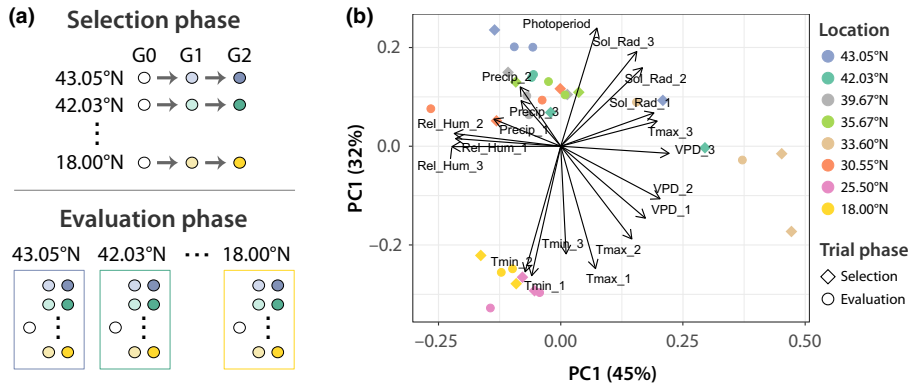

Fig. 1 Maize parallel selection experiment. (a) Schematic of study design. Initiated from a common base population (G0; white circles), directional selection was performed at eight field sites spanning a latitudinal range of 43.05°N to 18.00°N. Following the first generation of selection applied to G0, the second generation of selection used the locally selected G1 population, leading to the production of eight site-specific lineages comprising 16 separate populations (circles filled using a color scheme for separate lineages and their generations). During the evaluation phase, the populations were jointly evaluated in a two-year common garden experiment (including controls not depicted). (b) The experiment took place across 32 site-year environments, comprising 16 selection environments (diamonds) and 16 evaluation (circles) environments. The biplot shows the first two principal components based on envirotype data from each environment. Each of the site-year environments is color-coded as in (a) with the latitude coordinate for each location indicated. Diamond points indicate selection environments and circle points indicate evaluation environments.

also validate the importance of local selection for crop improvement and provide new insights for adapting crops to novel environments.

Materials and Methods

Study design

Selection and evaluation phases This study used parallel-selected populations of maize (*Zea mays* ssp. *mays* L.), created by first intermating seven tropical inbred lines to establish a common base population (G0) and subsequently selecting the population for early flowering time at eight field sites for two generations (Fig. 1a; Supporting Information Table S1). Details about population development and the experimental conditions used for parallel selection were described in a germplasm registration article (Weldekidan *et al.*, 2022); the populations are publicly available via the US National Germplasm System. Additional information about the parallel selection experiment and evaluation trials is described in Methods S1. Briefly, 2 yr of selection metadata and 2 yr of multitrait evaluation data were combined for this study. During the selection phase, at each field site, the 500 earliest individuals among 10 000 total individuals were selected and intermated using a standardized protocol (doi: 10.17504/protocols.io.bieakbae). The initial generation of selection used G0 as a common founder population for all sites, whereas the following generation of selection used the G1 generation created at each local site (> 10 000 seed for planting were made from a balanced bulk of 30 seeds from the 500 selected plants). During the evaluation phase, all selected populations were compared in a common trial, along with the common founder population and additional controls, at all of the original sites of selection and repeated for 2 yr (this was done during the same site-specific growing season when selection previously took place). Two types of controls were included: (1) a standard hybrid developed for the US temperate zone; and (2) four additional populations that were created from open-pollinated (randomly selected) plants from the first and second generation at each of two locations. The former control was used a reference for estimating certain environment parameters (see below). The latter controls were used to test for unintended selection. In each evaluation environment (i.e. 8 sites for 2 separate yr), a randomized complete block design was used with eight replications including four intrablock replicates of G0 comprising a total of 200 single-row plots (Methods S1).

Trait measurements In the 16 selection environments (combination of 2 yr at each of eight sites), the date of seedling emergence was recorded as a single day for the whole plot of 10 000 plants to which selection was applied. In the 16 evaluation environments, seedling emergence was recorded for each single-row plot. Following germination, eight individual plants from within each single-row plot were tracked and measured for as many as 25 traits (not all traits were measured in both years; Table S2). Therefore, trait measurements were recorded on 1600 individual plants at each of 16 evaluation environments, constituting a final dataset with *c.* 450 000 phenotypic data points.

Weather variables and summarization for separate periods of development Using the geographical coordinate of each field site, daily environmental variables from the 32 site-year environments were obtained using nasapower (Sparks, 2018). Environmental variables consisted of maximum temperature (T_{max}), minimum temperature (T_{min}), relative humidity (RH), solar radiation (SR), and precipitation (P). Precipitation consisted of just rainfall, even though most fields were irrigated. Additionally, vapor pressure deficit (VPD) was calculated using the R package PLANTECOPHYS (Duursma, 2015).

To control for the impact of temperature on flowering time variation within each environment, days from sowing to anthesis (male flowering) and to silking (female flowering) were converted into growing degree days (GDD), using the SM(B,30-) equation (Bonhomme *et al.*, 1994), with a base temperature of

10°C for planting to emergence and 8°C for emergence to flowering (Kiniry, 1991). The GDD data were used to define three phases of plant development in each selection and evaluation environment, including periods for emergence, tassel initiation, and flowering time (Methods S1). Weather data from within each site-year environment were then averaged across days per period. Also, for each environment, a point value for the photoperiod perceived by plants at tassel initiation (when maize becomes photoperiod sensitive; Kiniry *et al.*, 1983b) was included as a climate variable. Daylength was calculated according to the CMB model using civil twilight (Forsythe *et al.*, 1995).

Data analysis

Here, we briefly describe seven analysis models used for this study (Table 1). Detailed descriptions for Models 1–7 are presented in Methods S2. ASReml-R v.4.2 (Butler *et al.*, 2017) was used to fit all linear mixed models, using Wald tests to determine significant effects.

Common garden: estimating responses to selection and population-specific effects (Models 1 and 2) Two separate mixed linear models were developed for the common garden experiment. The experiment included all of the selection lineages comprising separate sets of populations but sharing the same G0 founder population (Fig. 1a; Methods S1).

Model 1 (Methods S2) was used to estimate linear responses to selection for each of the eight selection lineages with a common intercept of G0 in each evaluation site. The key variable estimates used for further analysis included regression coefficients for the response to selection, which were estimated among all selection lineages and evaluation sites, among selection lineages at each evaluation site, across evaluation sites for each selection lineage, and for all selection lineage by evaluation site combinations (interaction effects). The estimated responses to selection were then computed as linear combinations of the overall mean response to selection, the marginal responses for selection lineages and evaluation sites, and their specific interaction. This was used to quantify generalized and local responses to selection, to test for local adaptation, and to investigate indirect responses for nonselected traits (described below).

Model 2 (Methods S2) was used to obtain population-specific effects for G0, the 16 selected populations, and five separate controls (i.e. generation levels were treated as a categorical instead of a regressor variable). These estimates were used as input values to subsequent analyses aimed at characterizing flowering time plasticity and to dissect environment variable associations with phenotypic changes across selection and evaluation environments (described below).

Table 1 Summary of models used for analysis.

Model[1]	Model type	Purpose
1	Mixed linear model (regression model)	Estimate response to selection across generations per environment
2	Mixed linear model (means model)	Estimate population-specific means per environment
3	*t*-test (unequal variances)	Test for local adaptation
4	Piecewise regression (hinge model)	Estimate parameters for physiological reaction norm
5	Linear regression (forward selection)	Test for environmental variables associated with response to selection
6	Quadratic regression (forward selection)	Test environment variables associated with interactions between selection and evaluation environments
7	Pearson correlation	Test correlation between flowering time selection responses and nontarget trait responses

[1]See Supporting Information Methods S2 for detailed descriptions of the models.

Testing for local adaptation (Model 3) The null hypothesis of no local (site-specific) adaptation was tested by comparing the mean of selection interaction effects for populations evaluated at their original selection location to the mean of selection interaction effects evaluated at other locations (*Model 3*, Model 2; Fig. S1). For this, we isolated the site-specific interaction effects by removing the marginal effects of evaluation and selection environments from the linear combinations from the *Model 1* results. The leftover effects are interactions that are specific (above or below the mean values) to each combination of selection and evaluation environment. A *t*-test was used to compare the means of the diagonal elements (local effects) and off-diagonal elements. The interaction effects and testing approach are depicted in Fig. S1.

Modeling a physiological reaction norm for flowering time (Model 4) Population-specific estimates for the 16 evaluation environments (*Model 4*, Model 2) were used to model the relationship between GDD to flowering time and photoperiod. A piecewise linear regression model ('hinge model'; Fong *et al.*, 2017) was used to estimate three parameters for each population: the threshold photoperiod, the mean GDD to flowering below the threshold (intercept), and the regression coefficient for the change in GDD to flowering with increasing photoperiod above the threshold (slope). After comparing estimates and the raw data, it was determined that the threshold value was nearly identical for all populations, ranging only from 13.9 to 14.1 h with similar log-likelihoods. The latter value was more frequently estimated and was apparent from inspection of the data with estimated values of 13.9 h. Therefore, we fixed the threshold to 14.1 h and refit the model for each population, allowing for direct comparisons of slope estimates across populations. For each selection lineage, changes in the linear combination of the intercept and slope estimates were also compared with variation in the magnitudes of response to selection.

Dissecting environment variables associated with response to selection (Models 5 and 6) Using the population-specific means for each evaluation site, we computed the difference between sequential pairs of generations in the same selection lineage (G0 vs G1 and G1 vs G2). This quantifies the magnitude of phenotypic change for each step of selection, generating 256 estimates

corresponding to selection responses linked to the original 16 selection environments (e.g. G1 is selected from G0 grown in a given selection environment) and the 16 evaluation environments (Fig. 3). Here, we distinguish sites (fixed locations) from the separate year-environments at each site.

Combining the estimates of phenotypic change (dependent variable) and period-specific envirotype data (independent variables), a forward model selection procedure using Bayesian information criterion (Schwarz, 1978) was used to identify significant explanatory variables, considering main and interaction effects (*Model 5*, Methods S2; Fig. 3). Both GDD to flowering time and calendar days to flowering time were evaluated as dependent variables.

Separately, we tested whether phenotypic changes specific to each combination of selection and evaluation environment (interaction effects) were explained by the environmental or geographic similarity between those environments (*Model 6*, Methods S2; Fig. S2).

Testing the impact of flowering-time selection on nontarget traits (Model 7) In addition to flowering time, 23 traits that were not targeted for selection were also measured for this study (*Model 7*, Methods S2; Table S2). *Models 1* and *2* were fit to the data for each trait. For binary traits, we used a generalized mixed linear model with a logit link function (Butler *et al.*, 2017).

Only traits with significant population and evaluation-site effects (*Model 2*) which were also significant for at least one of the regression coefficients for selection responses (*Model 1*) were considered for further analyses. For each of these traits, the plastic response across latitude was inspected for G0 (*Model 2*) to establish whether it was associated with maladaptation (e.g. less favorable for yield). Finally, the indirect responses were estimated as above using the linear combination of regression coefficients. Pearson's correlations were used to measure the relationship between the indirect responses for each nontarget trait with the direct responses for flowering time.

Results

Selection response depends on both selection and evaluation locations

Selection for early flowering resulted in significant phenotypic responses in the expected direction for every selected lineage (Fig. 2; Table S3), but their progress varied substantially. For the eight selection lineages, ordered from northern to southern latitude, the per generation rate of progress for GDD to silking (female flowering) was: −50.5 ± 12.6 (43.05°N), −52.3 ± 12.6 (42.03°N), −45.9 ± 12.6 (39.67°N), −54.9 ± 12.6 (35.67°N), −35.0 ± 12.6 (33.60°N), −31.3 ± 8.2 (30.55°N), −26.9 ± 13.9 (25.50°N), and −11.7 ± 13.5 (18.00°N). Across the two generations of selection, this corresponds to total reductions in thermal time to flowering ranging from −23 to −110 GDD (*c.* 1–7 d). The main effect of selection lineages (averaged across evaluation sites) increased in association with latitude, but this relationship was not linear (Fig. 2). First, a large difference in the rate of change occurred between latitudes 33.60°N and

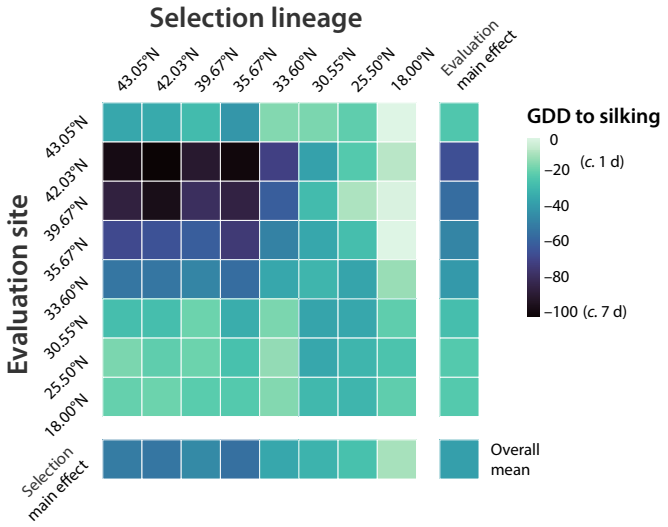

Fig. 2 Selection-by-evaluation matrix of phenotypic responses to selection for early flowering time. Estimated responses to selection are shown for each selection lineage (columns) at each evaluation site (rows), with corresponding latitudes indicated. Marginal means (main effects) for selection lineages, evaluation sites, and the overall mean are also shown. Each tile is colored according to the magnitude of response to selection for growing degree days (GDD) to silking (female flowering). Averaged across evaluation environments, 14 GDD corresponds to *c.* 1 calendar day.

35.67°N. Second, the higher rates of change plateaued in the four northernmost selection lineages, but selection at the mid-latitude location (35.67°N) resulted in the greatest overall selection response.

Response to selection also depended on the evaluation site. Selection responses averaged across all lineages were significant at each evaluation site, but the location impacted the strength of the response (Fig. 2; Table S3). The mean responses to selection for silking ranged from −23.0 to −65.9 GDD among the evaluation sites. Similar to the main effect of selection lineages, the observed response to selection also increased with the latitude for evaluation sites, except at the highest latitude (43.05°N). Although the selection lineage from this location ranked third among selection lineages, responses to selection at this location ranked sixth among evaluation sites. This location was substantially more effective at expressing heritable variation for flowering time that selection was able to act on than it was at discriminating differences in flowering time due to previous selections.

Interaction effects between selection lineages and evaluation sites measure deviations between the observed response in a specific combination of selection and evaluation locations and the response predicted by the average effects of those locations. The interaction effects were significant ($P < 0.001$; Table S3), modulating the selection response for silking by as much as −76 to +20 GDD per generation.

These results demonstrate that the response to selection for flowering time depends on both the site where selection is practiced and the site where selection lineages are compared. Furthermore, observed responses for specific combinations of selection lineages and evaluation sites are generally different from what would be predicted from their average effects.

Local adaptation is a significant component of the response to selection

Common garden data on the parallel-selected populations allowed us to test whether selection response was enhanced by site-specific adaptation. Such local adaptation is expected to result in greater selection responses when selection lineages are evaluated at the location where they were selected than at other locations. We measured this effect by comparing the average interaction effects for local responses (same sites for selection and evaluation) to those for nonlocal responses (different sites for selection and evaluation) (Fig. S1). We observed that local interaction effects resulted in an average increase in the response to selection (reduction in time to flowering) by −10 GDD (P = 0.007) and −13 GDD (P = 0.002) per generation for anthesis and silking, respectively. This represented *c.* 30% of the average gains from selection for both traits, a meaningful component of the overall mean progress. By contrast, the average interaction effects for responses to selection measured at different sites than where it was practiced were negligible (0.6 and 1.9 for GDD to anthesis and silking). Thus, for the phenological adaptation of maize to specific environments, local conditions accelerate the phenotypic change from selection.

Photoperiod strongly affects the strength of selection

A biplot of the first two principal components of the envirotype data showed similar contributions of the variables (vector lengths for the loadings) to the dispersion of environments where selection and evaluation were performed (Fig. 1b). The first two principal components explained a large proportion (77%) of the environmental variation. The 4-yr environments at a common field site clustered in the biplot for only some locations. For example, all environments at the two southernmost locations (25.50°N and 18.00°N) were strongly clustered, and they were also separated from environments for other locations. This clustering was driven primarily by their similar nighttime (minimum) temperatures and photoperiods. By contrast, many other environments did not cluster by location, reflecting how interannual weather variation at some field sites was as large as the climatic differences between them. Accordingly, the correlation structures of envirotype data were different between selection and evaluation environments (Figs S3, S4). Extreme examples occurred at 42.03°N (Iowa) and 43.05°N (Wisconsin), where differences in solar radiation, average daily (maximum) temperature, relative humidity, and to a lesser extent precipitation, resulted in a strong separation of the 2012 selection environments from other years, such that they grouped more closely with the environments at northern Texas (33.60°N), a uniquely dry climate compared with the other sites used in this study. As these were the only locations that did not use supplemental irrigation, this was likely due to the intense drought event which occurred across the Midwestern USA in 2012 (Mallya *et al.*, 2013).

Environments did not consistently group by geography, and some environment variables were partially correlated with others. Given that, we used variable selection in a mixed linear model to identify the most important environmental factors associated with the observed selection responses (Fig. 3). This analysis indicated that photoperiod alone had a consistently large impact on the responses to selection for early flowering time (Table S4). Longer photoperiods in both selection and evaluation environments were associated with larger responses to selection.

Only one additional variable was significantly associated with the responses to selection: precipitation in development period 1 in selection environments (Table S4). The sign of the regression coefficient indicated that less precipitation during this period was associated with greater selection responses. Given an average difference of < 0.5 mm for period 1 precipitation across the latitudinal range, it is unlikely that this was a causal factor.

The effect of photoperiod also interacted in a synergistic manner, whereby the response to selection was enhanced beyond the average effects of photoperiod when both selection and evaluation environments had longer daylenghts, giving rise to a geogrphical pattern of local adaptation. Local vs remote effects on selection response were quantified as interactions between pairs of selection and evaluation environments. We tested how these interaction effects associated with similarities of the environmental factors between pairs of selection and evaluation environments (Fig. S2d). Again, photoperiod showed a strong association: differences in photoperiod between selection and evaluation environments were quadratically related to interaction effects for both GDD to anthesis (r^2 = 0.22) and silking (r^2 = 0.20) (Table S5). This suggests that there was greater than expected response when the photoperiod of the selection environment was more similar to that of the evaluation environment; as the photoperiods differed more between selection and evaluation environments, the additional response to selection for flowering time decreased quadratically. This is concordant with the significant interaction between photoperiod in selection and evaluation environments on the response to selection detected in the previous analysis. We included linear and quadratic geographical distances between environment pairs as an additional measure of environmental distance in this analysis, but they were not significantly associated with the response interactions. Photoperiodic similarity between selection and evaluation environments, rather than simple geographical distance, had the largest impact on the structure of local responses in the parallel selection experiment.

Modeling a physiological reaction norm exposes distinct flowering time mechanisms for latitudinal adaptation

A simple physiological model was used to characterize components of flowering time plasticity for each population based on the relationship between GDD to flowering time and photoperiod across environments (Fig. 4a). For G0 and each selected population, a common threshold for photoperiod sensitivity was estimated as 14.1 ± 1.0 h for both anthesis and silking (Fig. 4a). This defines an inflection point between environments with shorter daylengths that do not cause a photoperiodic response

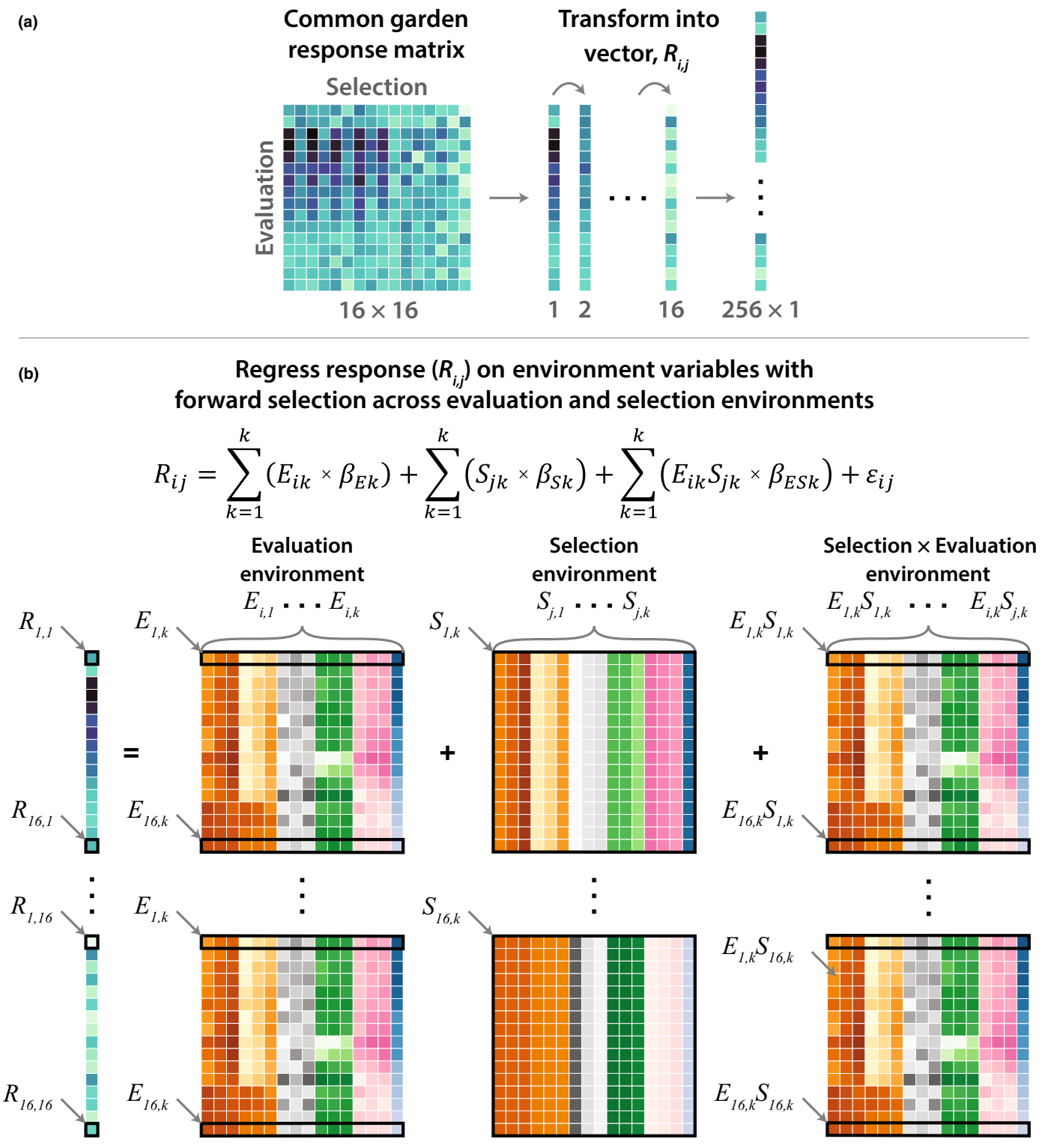

Fig. 3 Modeling framework for testing the influence of environment factors on responses to selection. (a) The common garden response matrix shows the magnitudes of phenotypic change (darker color corresponds to greater change) from selection between each pair of sequential generations (columns) in each evaluation environment (rows). As depicted, columns 1 to 16 of the matrix are stacked into a 256 × 1 vector. (b) The vector of phenotypic changes is then used as the dependent variable for the multiple linear regression model. Envirotype data from evaluation environments, selection environments, and their interaction were aggregated as corresponding regressor variables for each environmental factor in three development periods. Common color schemes depict the different environmental factors across the three periods of development (maximum temperature, minimum temperature, precipitation, humidity, and solar radiation) in addition to one column for photoperiod.

and environments with longer daylengths that stimulate photoperiod sensitivity. It separates all annual environments of the three southernmost sites (18.00°N–30.55°N) as non-inductive photoperiod environments from those of the five northernmost sites (33.60°N–43.05°N) as inductive photoperiod environments.

The intercept, estimated from observations in noninductive environments, corresponds to the basic vegetative phase (BVP) or minimal thermal time required for floral transition (Kiniry *et al.*, 1983a). Relative to the founding G0 population, the BVP was reduced overall by 2–7% among the selection lineages (Fig. 4b). For GDD to anthesis, lineages selected in noninductive environments showed slightly larger reductions in the BVP (changes in the BVP were more similar for silking; Table S6).

Slope estimates in inductive environments correspond to the degree of photoperiod sensitivity. For selection-lineages from noninductive photoperiod ennvironments, there were either moderate increases (10% and 16%) or a minor decrease (3%) to the founder population's degree of photoperiod sensitivity. However, all of the selection-lineages from inductive environments had consistently large reductions in photoperiod sensitivity, ranging from 40% to 53%. These results reveal how selection acted on separate modules of flowering time in an environment-specific manner. They also demonstrate largely independent physiological mechanisms for flowering time (i.e. the BVP is not tightly integrated with photoperiod sensitivity).

Experimental evolution with negligible unintended selection or drift

To test the possibility that natural selection, unintended artificial selection, or genetic drift caused phenotypic changes in the parallel selection experiment, we generated randomly mated control populations in two selection sites at latitudes 39.67°N (DE) and 25.50°N (FL). These were made from within the same populations that underwent selection, resulting in four independent control populations (G1-DE.C; G2-DE.C; G1-FL.C; G2-FL.C).

Averaged over evaluation environments, significant differences in flowering time were observed in the DE but not the FL control populations compared with the corresponding reference population, based on a least significant difference of 7.5 GDD for both anthesis and silking (14 GDD corresponds to *c.* 1 calendar day). The G1-DE.C control showed the largest phenotypic change, with a 14 and 16 GDD delay in the time to anthesis and silking, respectively. Among many other traits that were measured, there was only a significant increase in plant (4.7 cm) and ear height (6 cm) in this one control population, given least significant differences of 3.2 and 2.5 cm for the respective traits. The independent control from the second generation (G2-DE.C) also shifted to later flowering (9 GDD in anthesis and 11 GDD in silking) but had no significant differences in plant or ear height. These changes in flowering time were in the opposite direction of selection for earliness, indicating that responses in the parallel selection lineages resulted from direct selection, with the possibility of a small downward bias in the estimated changes from selection at some sites.

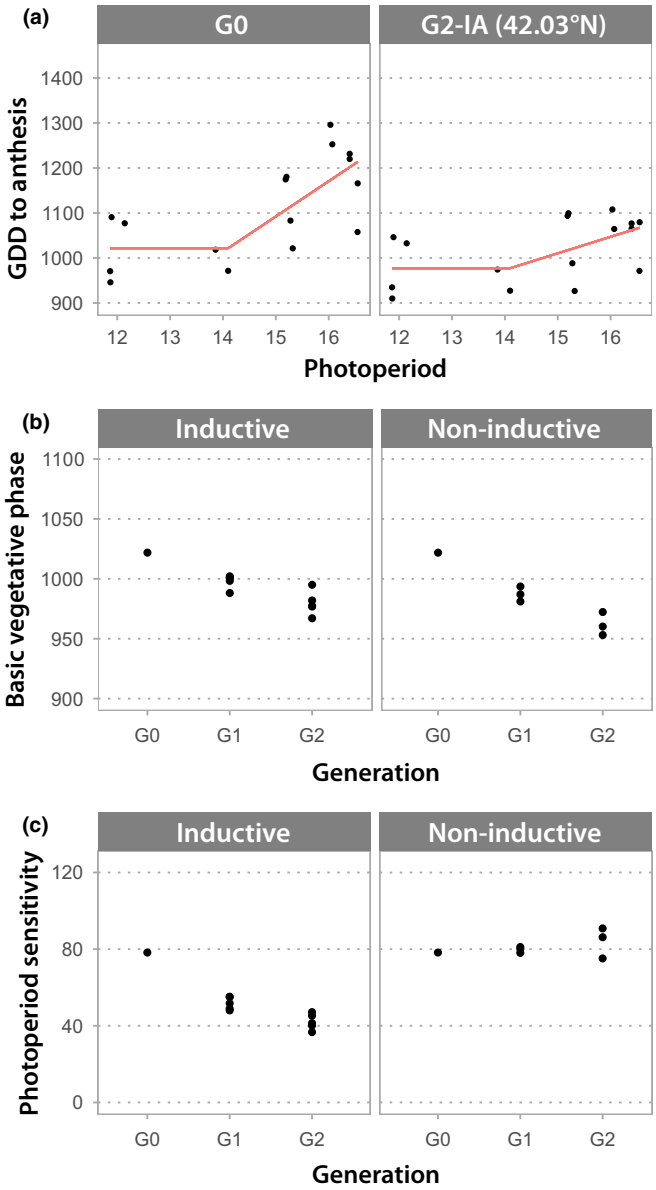

Fig. 4 Changes in ecophysiological components of flowering time from selection. (a) Piecewise linear regression functions estimated (red line) for the physiological reaction norm of flowering time are shown for G0 and G2-IA (second generation from lineage selected at 42.03°N). Points correspond to the growing degree days (*y*-axis) to anthesis (male flowering) for the given population (G0 or G2-IA) at photoperiods across the 16 evaluation environments. The intercept defines the basic vegetative phase, while the slope corresponds to the degree of photoperiod sensitivity. (b) Changes across generations in the basic vegetative phase (estimated intercept; *y*-axis) and (c) photoperiod sensitivity (estimated slope; *y*-axis) for populations selected in either inductive (33.60°N–43.05°N) or noninductive (18.00°N–30.55°N) photoperiod environments.

Selecting for flowering time ameliorates a maladaptive syndrome and increases yields for tropical maize in the temperate zone

During the evaluation phase, 23 additional traits were measured to test how selection on flowering time impacted maize development, architecture, and yield across latitude. Eighteen of these

traits varied significantly among evaluation sites, among populations, and for population-by-site interactions (Tables S6, S7).

The G0 population exhibited a maladaptive syndrome at higher latitudes. This phenomenon has been described previously (Stevenson & Goodman, 1972; Castillo-Gonzalez & Goodman, 1989; Holland & Goodman, 1995; Edmeades *et al.*, 2015; Teixeira *et al.*, 2015), but it has not been systematically characterized across the broad range of field sites and traits measured here. Along with delayed flowering time occurring at higher latitudes, G0 showed excessive vegetative growth (greater plant height, ear height, leaf length, and total number of leaves), more frequent aberrant ear morphology (greater probability of axillary ears, staminate ear tips, and exposed ear tips), and lower values of traits related to seed fertility (ear diameter, total kernel number, and kernel weight) (Figs S5–S7). Dry tassel weight also increased with latitude (Fig. S6), suggesting a shift of resources from female to male fertility at higher latitudes.

While none of these nontarget traits were selected in our experiment nor were they affected in unselected controls (see previous section), we nevertheless detected significant indirect responses to selection for most of them (Table S7). Combinations of selection and evaluation environments with stronger direct responses to selection for flowering time also had stronger indirect responses for other traits (Figs 5, S8–S10), which reduced the suite of phenotypic symptoms for maladaptation in G0. Specifically, stronger responses for flowering time were associated with stronger generational shifts toward shorter plant and ear heights, fewer and shorter leaves, smaller tassels, and a lower probability of forming axillary ears. Yields were also enhanced via both increases in seed number and total seed weight, from an underlying increase in yield potential measured as cob size (length and diameter) and number of cupules per ear, while individual seed weight remained the same (Figs 5, S8, S9). These results demonstrate that selection for earlier flowering time alone alleviates the tropical-to-temperate maladaptation syndrome in maize; this reshapes the form and function of tropical maize for better fitness in the temperate zone.

Discussion

We used experimental evolution in maize to demonstrate a novel design and modeling framework for studying environmental adaptation. Following a parallel selection regime, all selection lineages are evaluated jointly at the original locations of selection. This helps to unconfound the effects of selection and evaluation environments on the response to selection, while also allowing for characterization of environmental associations and the evolution of plasticity. With the urgent challenge of adapting crops to climate change, we investigated how artificial selection in a tropical maize population overcomes a phenology-associated maladaptive syndrome (Castillo-Gonzalez & Goodman, 1989; Tarter & Holland, 2006; Teixeira *et al.*, 2015) that hinders the injection of genetic diversity into the temperate zone (Goodman, 1999).

Using common garden data on the progression of directional selection in eight field sites, we distinguished broad and local modes of selection on flowering time adaptation. A generalized effect was observed across an extensive latitudinal range of the United States, from the northern state of Wisconsin at 43.05°N to the Caribbean Island of Puerto Rico at 18.00°N, indicating both significant trait heritabilities within, and positive genetic correlations among, the 32 site-year environments. Among these environments, temperature and photoperiod, which are key drivers of phenology, ranged from 22–33°C (mean of daily maximum temperatures), 10–26°C (mean of daily minimum temperatures) and 11.8–16.5 h (growth-stage specific photoperiod). This shows the wide spectrum of environmental conditions in which selection operates to shift flowering time. Responses to selection also showed substantial local effects, which depended on both the selection environment and the evaluation environment, as well as their interaction. This reflects variation in heritability within different environments, and in the pairwise genetic correlations among environments. These local responses were strongly influenced by photoperiod, revealing how rates of flowering time adaptation of tropical maize is determined by the photoperiodic similarity between environments in which a variety has been previously selected and where it is (or would be) grown. Still, *c.* 80% of the variation in local effects were not explained by other environmental factors or geographic proximity and remain unexplained. Contributing to this, environments did not always cluster by location based on meteorological data, reflecting interannual variation within sites, which could result in generation-by-environment selection effects that were not reproduced during the evaluation phase. This may explain genomic footprints of transient selection during directed evolution for flowering time adaptation described in another tropical-to-temperate selection study on maize (Wisser *et al.*, 2019). We also note that despite evidence for local adaptation, we also observed several cases of stronger indirect than direct response to selection for some sites. For example, five selection lineages from other sites had stronger responses than the locally selected lineage at 33.60°N Fig. 2). Similarly, the selection lineage from 35.67°N outperformed locally selected lineages at four of the eight sites. This result may reflect reduced heritability within a local environment where maladaptation overwhelms the expression of trait variation.

Ecophysiological and quantitative genetic concepts of flowering time adaptation provide complementary contexts for understanding generalized and local responses to selection. In plants, flowering time is regulated by separate genetic networks that converge in the control of vegetative-to-reproductive transition (Mouradov *et al.*, 2002; Dong *et al.*, 2012). The autonomous and photoperiod-dependent signaling pathways are major components of this system, which have been linked to the domestication and subsequent geographical spread of maize (Hung *et al.*, 2012; Minow *et al.*, 2018). Interpreting intergenerational shifts in the physiological reaction norm for flowering time among selection lineages (Fig. 4), we conclude that co-selection on the autonomous (corresponding to ubiquitous changes in the BVP among selection lineages) and photoperiod-dependent modules underlies broad and local modes of adaptation, respectively. The profile of adaptation at different geographical scales was affected by environment-specific changes in the combined

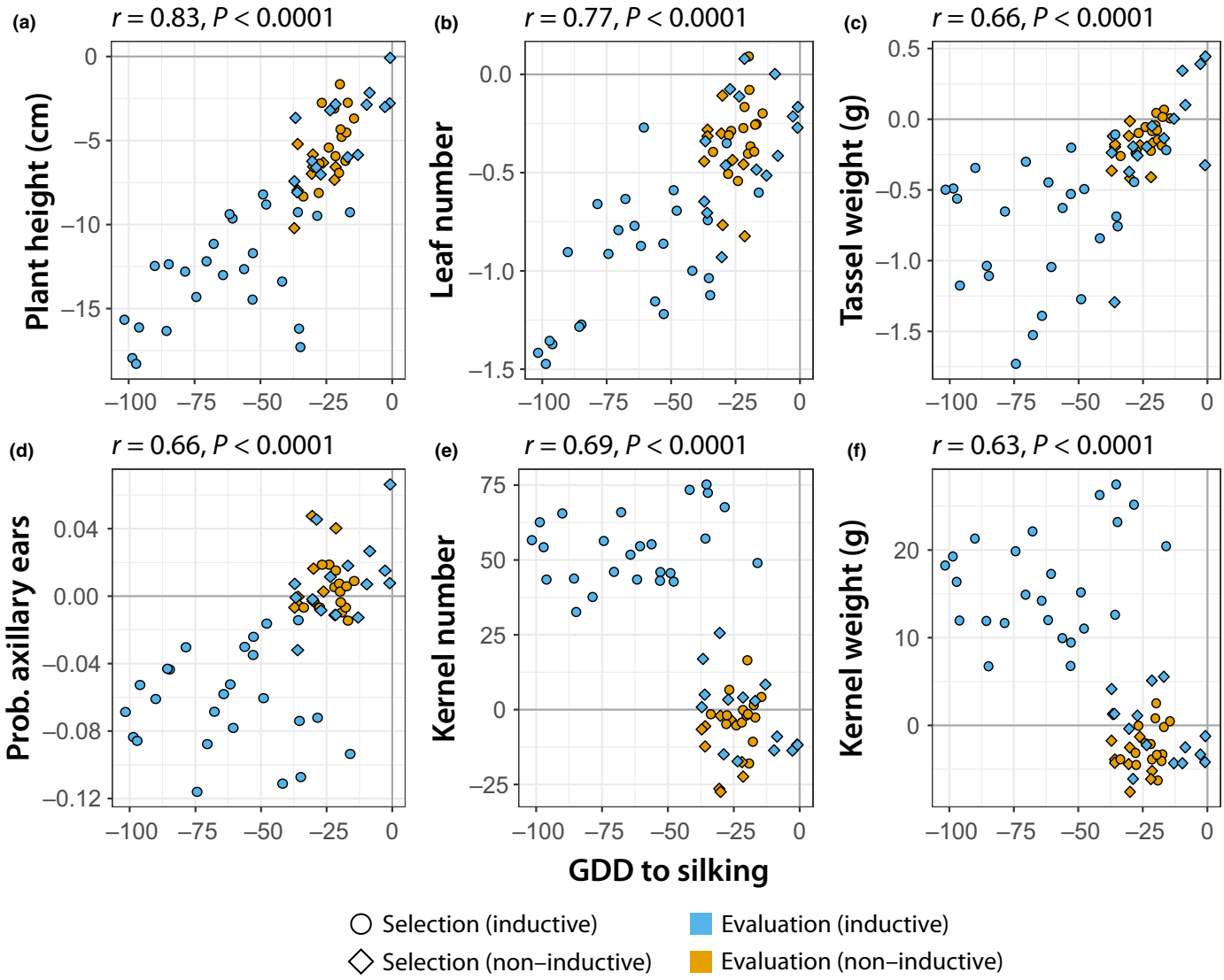

Fig. 5 Phenotypic responses for nonselected traits from direct selection on flowering time. (a–f) Estimated responses to selection for each nonselected trait (*y*-axis) regressed on the responses to selection for flowering time (*x*-axis). Points correspond to the 32 environment-specific estimates of response to selection. Point shapes and colors indicate whether selection or evaluation occurred in a photoperiod inductive (circle; 33.60°N–43.05°N) or photoperiod noninductive (diamond; 18.00°N–30.55°N) field site environment, respectively. GDD, growing degree days.

effects of selection on the BVP and photoperiod sensitivity, clarifying how locally selected populations differed in their behavior across evaluation environments.

The generalized and local effects observed for selection response can also be understood in light of quantitative genetics as functions of the heritability of flowering time in different environments and the genetic correlations of flowering time between selection and evaluation environments. Generally, the two components of flowering time are responsive to different climate variables: autonomous flowering is primarily affected by the impact of temperature on growth in all environments (Bonhomme *et al.*, 1994; Parent *et al.*, 2010), whereas photoperiod-dependent flowering is affected by the expression of genes that suppress reproductive transition (Yang *et al.*, 2013), but only in environments where photoperiod exceeds a sensitivity threshold (Bonhomme *et al.*, 1991). Locations where photoperiod sensitivity was triggered allowed for the phenotypic expression of photoperiod-sensitive genetic effects in addition to loci affecting autonomous flowering time regulation. The larger genetic variance exposed in these environments led to greater responses to selection, reducing both the BVP and photoperiod sensitivity (Fig. 4). In noninductive photoperiod locations, only genes impacting autonomous flowering would have been expressed. This reduced the genetic variance for flowering time, where only changes in the BVP could drive the response to selection. Similarity in photoperiod between environments was associated with positive interaction effects on selection response, likely due to increased genetic correlations across environments. Taken together, these results explain why photoperiod-inductive environments are better at expressing heritable variation, leading to interactions between trait plasticity and selection that accelerate the pace of adaptation.

Diversifying crops can help develop agricultural systems better able to cope with the cascade of effects from climate change

(Hufford *et al.*, 2019). Often, a key assumption for breeding within a crop is that we can capture climate adaptations from exotic varieties that have evolved locally for millennia, and then move these across ecological or geographical zones. Maladaptation of flowering phenology is the first roadblock to this approach, which maize breeders confront when trying to access the rich diversity of the tropical gene pool for the temperate zone (Castillo-Gonzalez & Goodman, 1989; Gouesnard *et al.*, 2002). Here, and previously (Teixeira *et al.*, 2015), we have found that tropical populations of maize can be shifted toward earlier flowering time through selection in novel environments, which occurs more rapidly when selection acts on segregating variation in photoperiod sensitivity.

The parallel selection experiment directly shows that maize undergoes a major pleiotropic transformation resulting from selection on flowering time alone: when the selection response for early flowering time was large, indirect responses were also stronger for shorter plant and ear heights, fewer total leaves, shorter leaves, and smaller tassels; an increase in the total number of seeds per ear, driving up total yield; and lower probabilities of developing unfavorable features such axillary ears, staminate tips, or exposed ears (Fig. 5). For lineages evaluated at their original site of selection, the magnitudes of indirect response were boosted for most nontarget traits including ear components that increased yield potential and realized yields (Figs 5, S8), while the mean indirect responses among selection lineages and across evaluation environments were negligible. This local effect was only significant in photoperiod inductive environments for the selection lineages with reductions in photoperiod sensitivity, where larger shifts in flowering time were observed. These findings are consistent with strong pleiotropic effects of flowering time genes (Auge *et al.*, 2019) but uniquely highlights pervasive environment-dependent pleiotropies, whereby selection on flowering time for a few generations overcomes a maladaptive syndrome for tropical maize in temperate environments. Together, this study validates the importance of understanding and using local adaptation for crop improvement.

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Competing interests

None declared.

Author contributions

Principal investigators JBH, NL, SF-G, NL, SCM, WX and RJW collaborated to design the study and RJW led the overall project. Each of these investigators conducted the selection and evaluation experiments at their home institution (exceptions: SF-G conducted the experiments in Puerto Rico, USA; RJW conducted the experiments in Delaware and Florida, USA). TW assisted the project team with the protocol development and multi-site fieldwork. NEC, JBH, JD and RJW analyzed the data. Specifically, NEC and JBH performed the mixed linear model analyses (*Models 1–3* and *Models 5–7*); JD and RJW performed the reaction norm analysis (*Model 4*). NEC, JBH and RJW wrote the manuscript.

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Data availability

The data that support the findings of this study are openly available in FigShare at doi: 10.6084/m9.figshare.21916140.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Test for local adaptation.

Fig. S2 Diagram of modeling approach used to test relationships between environmental similarities and responses to selection.

Fig. S3 Pairwise correlations between environment variables across selection environments during three periods of maize development.

Fig. S4 Pairwise correlations between environment variables across evaluation environments during three periods of maize development.

Fig. S5 TropicS-G0 means across years plotted against latitude of evaluation sites for traits measured in both 2014 and 2015.

Fig. S6 TropicS-G0 means across years plotted against latitude of evaluation sites for traits measured in only 2014.

Fig. S7 TropicS-G0 means across years plotted against latitude of evaluation sites for binary traits measured in only 2014.

Fig. S8 Indirect selection responses of traits measured in both years regressed on to GDD to silking direct selection responses (GDD_DTSsum).

Fig. S9 Indirect selection responses of traits measured only in 2014 regressed on to GDD to silking direct selection responses (GDD_DTSsum).

Fig. S10 Indirect selection responses of binary traits measured in 2014 regressed on GDD to silking direct selection responses (GDD_DTSsum).

Methods S1 Study design and data preparation.

Methods S2 Model specification and data analysis.

Table S1 Field sites and planting dates used for the maize parallel selection experiment.

Table S2 Data collected at evaluation sites.

Table S3 Wald tests for response to selection effects of flowering time.

Table S4 Environmental factors associated with response to selection for flowering time.

Table S5 Significant terms for the relationship between environment distances in photoperiods and phenotypic changes for flowering time.

Table S6 Wald tests for population mean effects of nontarget traits.

Table S7 Wald tests for response to selection effects of nontarget traits.

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