Environmental oscillations favor the evolution of adaptive transgenerational plasticity

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Abstract

Effects of parental environment on offspring traits have been well known for decades. Interest in this transgenerational form of phenotypic plasticity has recently surged due to advances in our understanding of its mechanistic basis. Theoretical research has simultaneously advanced by predicting the environmental conditions that should favor the adaptive evolution of transgenerational plasticity. Yet whether such conditions actually exist in nature remains largely unexplored. Here, using long-term climate data, we modeled optimal levels of transgenerational plasticity for an organism with a one-year life cycle at a spatial resolution of 4km$^2$ across the continental US. Both annual temperature and precipitation levels were often autocorrelated, but the strength and direction of these autocorrelations varied considerably across the continental US and even among nearby sites. When present, such environmental autocorrelations render offspring environments statistically predictable based on the parental environment, a key condition for the adaptive evolution of transgenerational plasticity. Our optimality models confirmed this prediction: high levels of transgenerational plasticity were favored at sites with strong environmental autocorrelations, and little-to-no transgenerational plasticity was favored at sites with weak or non-existent autocorrelations. These results suggest that transgenerational plasticity is highly variable in nature, depending on site-specific patterns of environmental variation.

Author Summary

Parental environments can alter progeny development, a phenomenon that has received renewed focus as interest in epigenetic inheritance has surged. Mathematical models indicate that these effects can evolve to adaptively match progeny phenotypes and environments when conditions change predictably, but few studies have explored whether such conditions actually exist in nature. This study reveals that patterns of precipitation and temperature variation in many regions of the US should favor the adaptive evolution of parental effects, but the optimal extent of these effects varies widely. Patterns of environmental fluctuations are heterogeneous across the landscape such that not only will there be variation in optimal phenotypes across space, but that there will also be variation for the optimal system of inheritance.
The capacity for life to evolve adaptively results in part from patterns in environmental variation. Selection can produce adaptation only if the selective environment is reliably encountered over generations, or in other words, if selective environments are statistically predictable. Early models of evolution envisioned fitness landscapes that were static, such that populations adapt over the course of generations to one or another environment (1). While this form of adaptation optimizes phenotypes for homogenous environments, the more realistic scenario of environmental heterogeneity in both space and time limits the adaptive value of such constitutive genetic expression. Rather, in variable environments, the capacity to modify phenotypes in response to predictive environmental cues allows organisms to adaptively match their traits to the specific patch of habitat in which they find themselves.

This key mode of adaptation to environmental heterogeneity is termed adaptive phenotypic plasticity, a strategy in which individual organisms make functionally appropriate changes to their physiology, development, or behavior in response to specific environmental cues (2,3). Over the last three decades, it has become clear that transgenerational plasticity is also remarkably common (reviewed by (4-9), yet highly variable (10-12) and nearly absent in some cases (13). This form of plasticity (also known as parental effects) occurs when environments experienced by parents influence the traits of their offspring, without changing the DNA sequence. Such inherited environmental effects can be transmitted from parent to offspring (and to additional generations in some cases) by diverse mechanisms, including heritable epigenetic modifications (i.e., DNA methylation marks, histone modifications, and small RNAs) and the allocation of nutritive resources, hormones, mRNAs, and regulatory proteins to seeds or eggs (note that these mechanisms are not mutually exclusive; (14,15). Additionally, rather than parental and current environment acting in an additive and independent fashion, some transgenerational effects only present themselves when offspring are exposed to particular environments, such as the same stress (e.g., priming, 8), and more generally parental x current environment interaction effects appear prevalent (10,11, 16, 17). Thus in addition to genetic inheritance, organisms have at their disposal relevant information from the environments they have experienced and the environments experienced by previous generations (18). Theoretically, these streams of information can be integrated in order to fine-tune the expression of a given trait for the selective environment that is most likely to be encountered. Whether organisms have in fact evolved to express adaptive transgenerational plasticity, and under what situations adaptive transgenerational plasticity is expected to evolve, has been the subject of intense research in recent years.
One of the major findings of these studies has been that natural selection should favor specific forms of within- and transgenerational plasticity depending on the precise patterns of environmental variation experienced by a population over time (19,20). For instance, within-generation adaptive plasticity is expected to evolve when individuals encounter variable conditions during their lives by either moving to different environments in a heterogeneous landscape, or by conditions changing temporally and with some degree of predictability within an individual’s lifetime. Furthermore, there must be little to no cost of responding to environmental cues and maintaining the molecular machinery to do so, and there must be genetic variation for individual phenotypic responses to the immediate environment (see e.g., 21,22; reviewed by 23,24).

These same factors – predictable environmental variation and genotype-by-environment interaction – also influence the evolution of transgenerational plasticity (18,25-30). First, environments must vary across generations, either due to temporal change in environmental states at the same site, or by offspring dispersal across spatially heterogeneous environments. Second, the environments experienced by parents must predict the selective environments that offspring experience. This scenario occurs when parental and offspring environments are correlated. Such intergenerational environmental correlations occur when the same environmental variable correlates with itself across years, as is the case for temperature when hot years are followed by hot years (i.e., a positive autocorrelation in temperature), or when several environmental factors change simultaneously to indicate the changing of seasons (31). Third, there must be genetic variation for transgenerational plasticity, that is to say, genotype-by-parental environment variation. This form of genetic variation appears to be common (10, 32-35).

From a more practical perspective, the ability of natural and agricultural populations to transmit environmental information transgenerationally will determine their ability to persist in the face of a rapidly fluctuating and changing environments, and thus profoundly influence the health and productivity of our planet as climate change proceeds. Thus, understanding how patterns of variation and predictability favor or hinder different forms of phenotypic expression represents an unexplored and potentially key factor in determining the populations that are most at risk under future climate change scenarios. While anthropogenic climate change differs greatly from natural climatic oscillations, both elevate the value of information from the prior generation relative to the long-term average conditions at a site, and thus transgenerational plasticity that has evolved in response to environmental oscillations may provide fitness benefits under climate change. On the other hand, climate change is expected to increase environmental variation, including more extreme
weather events, potentially decreasing the relative fitness of organisms that may have evolved
transgenerational plasticity to cope with previously reliable environmental patterns.

Empirical investigations in diverse plant and animal systems have confirmed that
transgenerational environmental effects can be adaptive when parent and progeny environments
match (i.e., under positive intergenerational environmental autocorrelations; see e.g., 36-46; reviewed
by 6,7,14). For instance, when *Mimulus guttatus* plants experience herbivory, their offspring increase
production of defensive leaf trichomes (11,47,48). Similarly, when the aquatic crustacean *Daphnia
cuculatta* is exposed to predator cues, it produces offspring with a defensive ‘helmet’ that protects
against predation by midge larvae and cladocerans (36).

Despite this surge of interest, to date no study has examined long-term environmental data
for the presence of inter-generational environmental correlations that are expected to favor the
adaptive evolution of transgenerational plasticity. Although we tend to think about how the average
environmental conditions differ across a landscape, there is no reason to expect that the scale and
predictability of environmental variation is any less complex or ubiquitous across a landscape. Here
we identify spatial variation in the temporal predictability of environmental variation, and leverage this
variation to compare the adaptive value of within-generation plasticity, transgenerational plasticity,
and multigenerational epigenetic inheritance across different local regimes of climate variability. We
utilize 120 years of fine-scale (4km²) climate data spanning the coterminous U.S. to test for auto- and
cross-correlations in temperature and precipitation levels across years. We found many significant
correlations that vary widely in both magnitude and direction across the US. We then construct
separate models for temperature and precipitation to determine the degree of transgenerational
plasticity that would maximize fitness in each of these sites across the U.S. with respect to the
observed environmental measurements. Additionally, we constructed each model using raw
environmental data and the residuals after factoring out the effects of directional climate change. By
considering both raw data values and residuals in tandem, we are able to parse out the role of
transgenerational effects and within generation plasticity in periodically oscillating environments
(residual model), as well as those with periodic oscillations in addition to a linear change in mean
temperature (raw data model). In all other ways, the two variants of this model are identical.
Differences in the results of raw vs. residual models highlight how climate change alters the benefits
associated with transgenerational plasticity. These models were constructed with summer annual
plants in mind, but are generalizable to other organisms with generation times of one year.
In our precipitation model, we examine transgenerational effects that persist for up to three generations (Figure 1a), as multiple experimental studies have found that environmentally induced epigenetic and phenotypic effects can persist for at least this long (e.g., 49,50), and in some cases for far longer (51,52). In our temperature model (Figure 1b), we also determine the degree of within-generation plasticity that would maximize fitness, in response to both early and late-season temperatures. In both of these models we calculate the fitness of genotypes as a product of the difference between the individual’s phenotype value and the environmental optimum for that year. With different genotypes producing their phenotypes based on different weightings of within-generation plasticity, transgenerational plasticity, multi-generation epigenetic inheritance, and genetic inheritance, we find that across the US there is extraordinary variation in the optimal ratio of how these various classes of information should inform an individual’s phenotype. These findings imply that just as landscape level variation in mean historical conditions selects for locally adapted populations, landscape level variation in the predictability of environmental variation may select for locally adapted patterns of plasticity within and across generations.

**Methods**

*Descriptive statistics*

Mean monthly temperature and precipitation at a 4km resolution from 1895-2014 (LT81m) were downloaded from the PRISM climate group web server (53). In short, PRISM uses climate normal from between 1981-2010 as a predictor grid, and then utilizes station networks with at least 20 years of data to model monthly temperature and precipitation across the US. The emphasis on this dataset is long-term consistency making it ideal for our purposes. Individual yearly values were concatenated using the QGIS merge raster function (54), and exported in the .RData format for downstream analysis. For precipitation data, October was chosen to represent the start of the “hydrologic” year in order to more accurately capture water availability patterns during the growing season. For temperature data, mean daily maximum temperature was calculated for March-May as a measure of early growing season temperature for a given year, and July-September mean daily maximum temperature for late growing season temperature. Custom R scripts were used to calculate descriptive statistics for precipitation and temperature separately. Autocorrelations were calculated at lags between 1 and 12 years (i.e., environmental correlations were calculated between year X and year X+1, year X and year X+2…year X and year X+12).
Mathematical models were constructed in R for both precipitation and temperature patterns to compare how individuals that utilize within-generation plasticity, transgenerational plasticity, and genetic inheritance to varying degrees differ in their capacity to match their phenotype with the environmentally optimal phenotype for a given year. In these models, there are hundreds (precipitation models) or thousands (temperature models) of competing genotypes, each representing unique points of parameter space for alleles that modify the extent to which environment affects phenotype. Trait value is a measure of the expected environment (temperature or precipitation), and is determined by a combination of the mean environment at a given site over all years, and terms that modify this value based on recent environmental information. Each genotype is in essence a climatologist, that utilizes genetic information (based on mean precipitation over the 120 years at a site), transgenerational plasticity, or within generation plasticity (only in temperature model) to come up with an expected environment that it will face. This expected environmental value is equivalent to a phenotype, and the closer this phenotype is to the actual environment experienced, the higher the fitness that genotype will have for a given generation.

While this framework is identical for precipitation and temperature modeling, inherent differences in precipitation and temperature variables lead to us considering a different set of parameters for each variable, allowing us to ask related but unique questions regarding transgenerational inheritance. Precipitation can accumulate as snowpack, bodies of water, or soil moisture, such that the cumulative precipitation over the course of the water year will determine to a large extent the amount of water available to a plant. On the other hand, the effects of temperature are much more immediate and transient, such that a particularly cold spring will not “keep the plant cool” over the summer, in the way that a particularly wet spring could provide moisture during a summer of drought. For this reason, we decided to extend our temperature models to compare patterns across different segments of the growing season, and different forms of plasticity both within and between a single generation. For precipitation we only considered annual hydrologic year precipitation without breaking it down by seasons, but did consider the possibility of multi-generation persistence of transgenerational plasticity.

For a given genotype, the absolute distance between the expected and actual environment at a given time imposes a linear cost on fitness. If the expected and actual environment in a given generation are identical, that genotype’s fitness will equal 1, and as the difference increases, fitness will drop down to a minimum value of 0.2. This minimum value was put in place to prevent a single
year with extremely low fitness from dominating final genotype frequencies, but was only used in
under 0.01% of fitness measurements. After every generation, there is a round of competition,
where the frequency of a given genotype will change based on the relative fitness of that genotype
compared to the mean phenotype for that year. This scenario is equivalent to an infinite population
size evolutionary model in which the relative frequency of genotypes changes due to selection and
reproduction once per year.

For each locale, mean annual precipitation (or temperature) across the 120 years ($\bar{P}$) is
calculated, and this statistic is used as the baseline phenotype of all genotypes in the raw data variant
of the model. Additionally, a linear regression of precipitation on year was fit for each site over the
120 years considered, and residuals were calculated for every year. In the residual variant of this
formula, the expected values are 0, and residuals are used as the precipitation values for each year.

Precipitation model

For a given generation $T$ the expected precipitation (phenotype) is defined as $\bar{P}_T$, while the
actual precipitation is $P_T$. The two parameters considered in this model are $m$ (maternal or parental
effect) and $g$ (multigenerational persistence). The $m$ value in this model alters the expected
precipitation (phenotype) for a given year ($\bar{P}_T$) based on how deviant the precipitation was during a
preceding year or years ($P_{T-k} - \bar{P}$). In other words, $m$ adjusts offspring phenotype based on how
different parental environment was from long term average environment. When there are
interannual autocorrelations, values of $m$ that match the degree of interannual autocorrelation will
be adaptive.

$$\bar{P}_T = \bar{P} + \frac{m(P_{T-1} - \bar{P}) + mg(P_{T-2} - \bar{P}) + mg^2(P_{T-3} - \bar{P})}{1 + g + g^2}$$

When $m = 0$ the expected precipitation will always be equivalent to the mean precipitation
at a site, when $m = 1$ and $g = 0$, the expected precipitation will always equal the precipitation
experienced the prior year. In the simplest case when $g = 0$ only the prior year’s information alters
the expected precipitation. The $g$ value in this model weighs how much the precipitation
experienced two and three generations back should change expected precipitation values relative to
the prior year’s precipitation. At a value of $g = 1$ the previous three years will all contribute equally
to the expected precipitation. As $g$ decreases, the relative information from two generations back decreases linearly, and the relative information contribution from three generations back decreases quadratically. At $g = 0.5$, the grandparental precipitation will contribute half as much information as the parental generation, and the great-grandparental generation will contribute one quarter the information of the parental generation. In other words, the $g$ parameter represents how much the transgenerational information diminishes each year after the first. The cumulative effect of the previous generations environment is scaled by a factor of $(1 + g + g^2)$ in order to standardize the total contribution of transgenerational effects for a given value of $m$ independent of $g$. That is to say, $m$ affects the total amount of transgenerational information transmitted between generations, and $g$ affects the distribution of the information disseminated from each of the prior three years.

A test of a random subset of 2000 sites led us to restrict the values of $m$ we investigated to between -0.6 and 0.9 at increments of 0.1 (from a possible range of -1 to 1). Values less than -0.6 and greater than 0.9 were not optimal in any of the 2000 sites and were therefore excluded for computational reasons. The full range of $g$ values (i.e., 0 to 1) was retained. We considered genotypes for every possible combination of $m$ and $g$ values selected at intervals of 0.1 (for a total of $16 \times 11 = 176$ genotypes). For each genotype we calculated expected phenotype for every year between 1897-2015. Next, for each genotype and each year, we calculated the difference between the expected phenotype and the actual phenotype for that year.

$$w_{MT} = 1 - \frac{|\bar{p}_T - p_T|}{\bar{p}}$$

Geometric mean fitness over the 118 years was calculated for each of the 176 genotypes. The values of $m$ and $g$ for which fitness was maximized was recorded for each of the 481,631 sites and plotted in qGIS. This approach identifies the most fit genotype at a given site over the generations, or more explicitly, the genotype that would be at the highest frequency in the year 2015.

In order to compare evolutionary dynamics in more detail, we constructed fitness landscapes and compared the relative frequency of competing genotypes over time for twelve sites representing a wide range of geographic and parameter space [may need to say more about the parameter space here]. For these sites, the mean fitness across the 176 genotypes was calculated for the first year (1897). The fitness of each genotype in that year was then divided by the mean fitness.
to produce the relative fitness of each genotype. This relative fitness was then used as the relative frequency of each genotype for the following year. For each year following the first, the absolute fitness of each genotype was divided by a weighted mean of the fitness of all individuals for that year:

\[ w_X^{rel} = \frac{w_X^{abs}}{\sum_{i=1}^{154} w_i^{abs} \cdot \text{Freq}(i)} \]

This relative fitness was then used as the relative frequency of each genotype for the following year. For each year following the first, the absolute fitness of each genotype was divided by a weighted mean of the fitness of all individuals for that year. This value was then multiplied by the frequency of that genotype in that generation to get the following generation’s frequency. The final generation frequency was used for the construction of fitness surface heatmaps.

**Temperature model**

The general framework of the temperature model is similar, but rather than allowing for the persistence of transgenerational effects across multiple years, it considers early and late season transgenerational effects, as well as within-generation plasticity. We ran the same model on raw data and residuals, calculated as in the precipitation model. Annual plants were used as the motivation for this model, with a growing season from March-September. The growing season was broken down into three parts: early growing season (March, April, May), transitional growing season (June), and late growing season (July, August, September). Within this model there are two bouts of selection, one after the early growing season, and one after the late season. While early season phenotype can only be modified by the previous year’s temperature (because organisms are newly born in the spring in this scenario, and therefore cannot respond themselves to temperatures), late growing season phenotype can be modified by the previous year’s temperature, and/or the temperature earlier in the growing season. Additionally, this model allows for both early and late season phenotype to be modified by both the previous season’s early and late temperatures independently. In other words, early season phenotype can be modified by the previous year’s early season temperature, or the previous year’s late season temperature; late season phenotype can be modified by these same two factors as well as the current year’s early season temperature (i.e., by within-generation plasticity).

Thus, this model includes five plasticity parameters, reflecting the effect of 1) the previous generation’s early season temperature on current early season phenotype \((m_{EE})\), 2) the previous generation’s late season temperature on current early season phenotype \((m_{LE})\), 3) the previous generation’s early season temperature on the current late season phenotype \((m_{EL})\), 4) the previous generation’s late season temperature on current late season phenotype \((m_{LL})\), and 5) the current early season temperature on the current late season phenotype \((b)\). Note that the mean and variance
of temperature data are not correlated, unlike precipitation data. For this reason, fitness is scaled by a constant 20 rather than the mean temperature of a given site. Results were exceedingly similar when fitness was scaled by constants of 10 and 100; 20 was chosen as it is closer to the mean annual temperature across the US.

\[
p_{TE}^* = \bar{P}_E + m_{EE}(P_{ET-1} - \bar{P}_E) + m_{LE}(P_{LT-1} - \bar{P}_L)
\]

\[
w_E = 1 - \frac{|p_{TE}^* - \bar{P}_E|}{20}
\]

\[
p_{TL}^* = \bar{P}_L + m_{EL}(P_{ET-1} - \bar{P}_E) + m_{LL}(P_{LT-1} - \bar{P}_L) + b(P_{ET} - \bar{P}_E)
\]

\[
w_L = 1 - \frac{|p_{TL}^* - \bar{P}_L|}{20}
\]

\[
w_F = w_E \ast w_L
\]

The geometric mean of genotype fitness was taken over the 119 years for each of the genotypes. For each of the five plasticity (transgenerational and within generational) terms in this model we considered possible values of -0.2 (negative plasticity), 0 (no plasticity), 0.1 (minor plasticity), 0.3 (moderate plasticity), and 0.5 (major plasticity). While this resolution is somewhat coarse, focusing on this subset of values allowed us to consider this model for the full factorial combination of parameter space. In total, fitness was calculated for 3125 genotypes, across each of 119 years, at all 481631 locations, for a total of 179 billion measures of fitness. The values of plasticity at which fitness was maximized were recorded from each grid point across the US. Finally, for the same 12 focal sites used in the precipitation model, we calculated the changes in genotype frequency across 119 years using the same methodology as above. All code for these simulations, and other modeling results are available at (github.com/XXXX).

Results

Both mean annual precipitation and growing season temperatures vary immensely across the US (Figure 2 and S1). Mean annual temperature and precipitation are both primary forces driving local adaptation to the diversity of climate regimes across the US, but for the evolution of locally adaptive phenotypic plasticity, it is the patterns of variation that are more relevant. The standard deviation of a site’s annual precipitation or growing season temperatures over the past 120 years also varied dramatically (Table 1 and S1), with precipitation inter-annual standard deviation (IASD)
varying from 40mm to 800m, spring temperature IASD from 0.77C to 1.95C, and summer temperature IASD from 0.35C to 1.32C (Figure 2 and S1 and Table S1). The southwest US generally had the highest precipitation IASD relative to its mean precipitation, with IASD being nearly equal to the mean precipitation in some regions (Figure 2). Interestingly, spring temperature IASD was significantly higher than summer temperature IASD across the US. This pattern was largely driven by extremely high spring temperature IASD over the north central US (Figure 2), and consistently low summer temperature IASDs across much of the coastal US.

Directional climate change over the past 120 years was prevalent and variable across the US (Figure 2). Mean annual precipitation has declined over much of the Sierra Nevada mountain range, southern California, and other scattered regions over the last 120 years, while precipitation levels have increased in the Midwestern and much of the northeastern US. Both spring and summer temperatures have gotten substantially higher with the exception of the southeast, where spring temperatures have decreased and summer temperatures have changed little (Figure 2). This phenomenon has been noted numerous times (55,56) and seems to be largely due to a switch from cropland to natural forest ecosystems across the southeastern US during the past 120 years that has led to greater transpiration cooling.

Although a variable environment is necessary for the evolution of adaptive phenotypic plasticity, it is the patterns of this variation that influence which forms of plasticity will be favored. Patterns of climatic oscillation varied substantially across the US over the last 120 years, suggesting the potential for climatically driven variation in locally adaptive plasticity (Figure 2 and S1, Table 1 and S1). We examined these patterns by calculating autocorrelations in annual temperature and precipitation between successive years. The climate (temperature or precipitation) of a given year and that of the prior year(s) were often significantly correlated across the US. However, the magnitude and direction of correlations varied depending on the region and climatic parameter.

Averaged across all sites, the precipitation autocorrelation (AC) at lag-1 (i.e., the correlation between the precipitation during one year and the next) was slightly positive (mean=0.04, Table 1, Figure S1), and was reduced by half after taking linear changes in precipitation into account (mean=0.02, Table 1, Figure S1). Spatially, we found that the southeastern gulf coast was the largest region with negative lag-1 ACF (dry years tend to be followed by wet years), while the northeastern US was the largest region of substantially positive lag-1 ACF (Figure 2). Somewhat surprisingly, there was higher mean and standard deviation for lag-2 partial ACF than lag-1 ACF (Figure S1). There were many more sites with significantly positive (62,693: lag-2 PACF > 0.2, vs. 21,671: lag-1
ACF >0.2) and significantly negative (5,088 lag-2 PACF < -0.2 vs. 441 lag-1 ACF < -0.2) lag-2 partial autocorrelation (PAC) than lag-1 ACF. These correlations suggest that climatic oscillations impacting annual precipitation tend to operate over more than two years in these regions, and that on a year to year basis, variation is more stochastic (leading to lower absolute lag-1 ACF). The northeastern and northwestern US show substantially positive precipitation lag-2 PACF; in these regions, multi-year climatic oscillations may dictate over 20% of the variation in inter-annual precipitation variation (Figure 2). By contrast, across the southeastern US, negative lag-1 ACF and lag-2 PACF suggest a negative feedback dynamic in which multiple dry years tend to be followed by a wet year, and vice versa (Figure 2).

Patterns of temperature autocorrelations extended over larger regions, and were often substantially more extreme, compared to the more complex patterns observed for precipitation autocorrelations (Figure 2). Lag-1 ACF for spring and summer temperatures varied a great deal, with patterns of summer temperature autocorrelation substantially more positive than those of spring (summer ACF-1 mean: 0.24, spring mean: -0.01, Figure S1). In both cases, however, the western US tended to have more positive autocorrelations than the rest of the country (with the exception of southern Florida; Figure 2).

Spring and summer temperatures displayed significant autocorrelations at lags 2 and 3. The mean lag-2 PACF for spring temperature was negative (mean: -0.04, Figure 3) and more variable than lag-1 ACF (sd=0.1 vs. 0.08), with much of the north-central US displaying lag-2 PACF of less than -0.2 (Figure 2). The mean lag-2 ACF for summer temperatures was positive (mean: 0.09), but substantially lower than the mean lag-1 ACF (mean: 0.24). At a lag of 3, both spring-temperature ACF (mean: 0.05) and summer-temperature ACF (mean: 0.11) were positive (Figure 3), suggesting that long-term climatic trends play a role in temperature variation during the past 120 years.

Modeling Results

Optimal levels of transgenerational plasticity: precipitation

As expected, the vast variability of climatic autocorrelations lead to a great deal of variation in the optimal levels of plasticity in the precipitation evolutionary model (Figure 3, Table S1). In the raw variant of the model, optimal parental effect values were positive in 314,118 cases (65%), zero in 32,352 (7%), and negative in 135,161 (28%), compared to 55%, 7%, and 38% respectively in the residual variant. The most common “parental effect” value ($m$) in the precipitation model was 0.1 (22.5% and 21.8% of sites in the raw and residual models, respectively, Figure 3a). This level of
parental effect indicates that 90% of phenotypic variance is dictated by the long-term average (genetic effects), and 10% by the difference between the parental environment and the long-term average environment. The second most common optimal value of $m$ was 0.2 (19.15% in the raw model, 18.6% in residual model), followed by -0.1 (14.3% in the raw model, 17.2% in the residual, Figure 3a). A value of -0.1 means that 10% of phenotypic variation stems from transgenerational plasticity and 90% from genetic variation, but that the precipitation experienced by parents will influence the progeny in the opposite direction. For example, if the mean annual precipitation at a site is 1000mm (dictating the genetic value), and the previous year’s precipitation was 1100mm, then the phenotype of the current generation would be 1010mm ($1000 \times 0.9 + (1,100-1000) \times 0.1)$ in the case of an allele value of 0.1, and 990mm in the case of an $m$ value of -0.1 (assuming there are no multigenerational environmental effects). Optimal values of $m$ ranged from -0.6 to 0.9, and were approximately normally distributed, except a dearth of sites for which the optimal allele value was 0 due to the lack of multigenerational environmental effects in this situation.

The multigenerational persistence ($g$) of transgenerational effects was also found to vary greatly across the US with the two most common values being 1 (40.7% raw, 39.5% residual) and 0 (18.6% raw, 16.8% residual) (Figure 3b). Here, a value of 1 indicates that the precipitation one, two, and three years prior all contribute equally to the expected precipitation at a given site. A $g$ value of 0 indicates that only the previous year’s precipitation is predictive of the current precipitation level. The remaining 40.7% of sites (in the raw variant) have intermediate optimal values of $g$, suggesting that in these locations the precipitation of each of the past three years is informative, but information from the immediately preceding year is of the highest value. Of the nine values considered between 0 and 1, all were represented by between 3.1% and 5.7% of sites, with a value of 0.8 being the most frequent strategy, and 0.1 being the least frequent (Figure 4). Interestingly, full multigenerational persistence ($g =1$) was more frequently optimal at sites with negative transgenerational effect values compared to those with positive values (44.9% vs. 38.9%, respectively), where intermediate multigenerational persistence was more common (Figure S2). Additionally, we found that the adaptive value of multigenerational persistence increases as the strength of the transgenerational effect increases, such that little-to-no multigenerational persistence is optimal when the transgenerational effect is close to zero, and strong multigenerational effects are optimal when the transgenerational effect is extreme (Figure S2).
Spatial variation for optimal precipitation plasticity values largely paralleled the spatial distribution of inter-annual precipitation autocorrelation patterns (compare Figure 2a to Figure 4a). At the broadest level, the northern latitudes show the highest optimal transgenerational precipitation plasticity values (Figure 4a), but not necessarily multi-generation persistence of transgenerational effects (Figure 4b). Optimal transgenerational plasticity values were 0.057 lower in the residual variant of the precipitation model compared to the raw data variant, with the vast majority of sites having equal values (56%), decreasing by 0.1 (24%), decreasing by 0.2 (8.5%), or increasing by 0.1 (4.3%). The northeast US and the Yellowstone National Park region, where precipitation increased most (Figure 2), also saw the greatest proportion of their optimal transgenerational plasticity values diminished after factoring out linear climate change (Figure 4c).

Optimal levels of transgenerational plasticity: Temperature

Purely positive transgenerational effects ($m_{EE} \geq 0, m_{EL} \geq 0, m_{LL} \geq 0, m_{LE} \geq 0$) of temperature were optimal in 70.2% of sites (338,327 out of 481,631) in the raw version of the model and 55.7% of sites (268,307) in the residual variant. Conversely, only 1.4% of sites (7,018) in the raw model and 3.1% (14,777) in the residual version included only negative transgenerational plasticity values. Only 0.4% (raw model) or 0.9% (residual model) of sites totally lacked transgenerational plasticity (either positive or negative) as part of the optimal strategy. The optimal strategies in the remaining sites (28% raw model, 40% residual model) comprised a mixture of positive and negative transgenerational plasticity values. Positive within-generation plasticity was favored in 79.7% of sites (383,667), compared to only 0.03% of sites (157) in which negative within-generation plasticity ($w$) was favored, and 20.3% of sites (97,807) in which no within-generation plasticity was favored (Figure 3g). Optimal levels of within-generation plasticity were generally positive and relatively weak across the US; e.g., 72% (346,603/481,631) of sites had an optimal $w$ value of 0.1 (Table S1).

The most common optimal form of transgenerational plasticity to temperature in both the raw and residual models was the effect of late growing season temperature on the next generation’s late growing season phenotype ($m_{LL}$, Figure 3f, Table 2a). Effects of late season temperature on the next generation’s early season phenotype ($m_{LE}$) were the most variable, with a substantial number of sites having negative transgenerational plasticity values (63,881 raw, 100,267 residual) and many others having moderate (98,524 raw, 66,625 residual) and major (26,967 raw, 10,080 residual) positive transgenerational plasticity values (Figure 3e). Effects of early growing season temperature
on the next generation’s early season phenotype ($m_{EE}$) were slightly more likely to be positive in the raw version of the model (98,089 vs. 89,547), and more likely to be negative in the residual variant (68,441 vs. 132,352). In both cases however, no $m_{EE}$ plasticity was the most common optimal strategy. Finally, the effect of early season temperature on the next generation’s late season phenotype ($m_{EL}$) was most often minor (0.1) in both raw (251,691) and residual (229,301) variants. When considering the combined plasticity value profile of a site, we find the most common combination of plasticity values is, EE: none (0), EL: minor (0.1), LE: minor (0.1), LL: moderate (0.3), WP: minor (0.1) (Table 2b). Summing the four transgenerational plasticity alleles together we find the southwest US has the highest optimal values of transgenerational plasticity, while the Great Lakes region has the lowest optimal values (Figure 4d). Texas and Florida tend to have the greatest variability for transgenerational plasticity values, with many areas within these regions having both positive and negative transgenerational values leading to intermediate total transgenerational plasticity (Figures 4e and 4h). Optimal total transgenerational plasticity values were on average 0.146 (+/− 0.21) higher in the raw relative to the residual models (although the most common change was 0). In the southwestern US, where temperature increased the most over the past 120 years (Figure 2), the difference between the raw and residual model was the greatest (Figure 4g).

Variation in different classes of temperature autocorrelations between seasons explains a large portion of the variation in the optimal transgenerational response to temperature at a given site. For example, the autocorrelation between early season growing temperature and the next year’s late season growing temperature is the factor that explains the largest amount of variation in optimal levels of $m_{EL}$ (Table 3). We assessed potential tradeoffs between different forms of transgenerational plasticity to temperature by first calculating the residuals of a particular plasticity term after accounting for the effects of environmental autocorrelations, then testing the effect of the other four plasticity terms on these residuals. There was a highly significant negative association between $m_{LE}$ and $m_{EE}$ plasticity, and between $m_{LL}$ and $m_{EL}$ plasticity (Figure S3a). As higher levels of late-late transgenerational plasticity were favored, the optimal levels of EL plasticity also decreased across all environmental autocorrelation values. These associations suggest that, for a given life history stage in this model, there are tradeoffs between using transgenerational information from the previous generation’s early vs. late season temperature (Table S2). For example, there are many sites where no plasticity, $m_{EE}$ plasticity, and $m_{LE}$ plasticity all have higher fitness than individuals exhibiting both $m_{EE}$ and $m_{LE}$ plasticity (Figure S3b).
Fitness Landscapes

In the previous analyses we used restricted parameter space to identify optimal site-specific combinations of plasticity values across the entire contiguous U.S., but further insight can be gained by comparing fitness landscapes across the full parameter space at individual sites. In the precipitation model we found that, among sites where fitness optima are located near zero transgenerational effects, a vertical fitness ridge formed that was centered near parental effect values of zero. This result is due to transgenerational persistence levels (y-axis) having a minimal impact on phenotype when parental effects are marginal. As absolute optimal parental effect values increased, however, the fitness landscape shifted from a ridge to a peak, with certain values of transgenerational persistence imparting extreme fitness advantages over others (Figure 5). Site B (North Central Minnesota) exemplifies a unique and unexpected outcome of this model: under certain conditions, there can be multiple local fitness maxima with divergent levels of transgenerational plasticity (Figure 5). Two fitness maxima exist at this site, one in which the optimal strategy comprises slightly negative parental effect values with no multigenerational persistence, and a second in which the optimal strategy comprises slightly to moderately positive parental effect values with high levels of multigenerational persistence. This situation occurs when two conditions hold: the lag-1 autocorrelation is in a different direction than the average of the lag-2 and lag-3 autocorrelations, and the absolute value of the lag-1 autocorrelation is less than the average of the lag-2 and lag-3 autocorrelations. In these cases, plasticity in the opposite direction of the previous generation, or in the same direction as the average environment of the past three generations, would be adaptive. This scenario occurs in approximately 90k out of the 480k sites, but only in 30k sites are lag-2 and lag-3 average values greater than 0.1 and therefore likely to show up as bimodal peaks in our model. Fitness landscapes provide a snapshot of the final frequency at the end of the 120 years of the modeling run, which is the product of differences in fitness within each generation and subsequent changes in frequency (Figure 6). Over the course of the 120 year simulation, the frequency of plasticity genotypes fluctuated somewhat dramatically, suggesting that the interactions between climatic oscillations and other effects might have favored positive plasticity values over some decades, and negative in the next (Figure 6).

Fitness landscapes for the temperature model are substantially more complex due to the larger number of terms, but do suggest that patterns of environmental variation can favor tradeoffs between multiple forms of plasticity. As the effect of parental early season temperature on offspring
late season phenotypes ($m_{EL}$) increased, optimal $m_{LL}$ values decreased (Figure S4) and vice versa. The same is true for $m_{EE}$ and $m_{LE}$. At a given stage in the offspring’s life cycle there is only so much information value that can be gleaned from the environments of previous generations; this total value ($m_{EL} + m_{LL}$) is one factor that varies across the US in this model. The optimal balance between the two forms of transgenerational plasticity that affect a given life history stage ($m_{EL}: m_{LL}$) is the other parameter that varies, and this balance is what controls the degree to which the early vs. late season parental conditions will modify offspring development at a given stage.

Discussion

Although transgenerational environmental effects on phenotypic expression have been recognized for decades (57,58), interest in these effects has surged recently due to increased appreciation for the potential role of transgenerational plasticity in adaptation (59). Despite this renewed interest, a critical question has remained unanswered: do natural patterns of environmental variation favor the adaptive evolution of transgenerational plasticity? Our analysis of 120 years of climatic data from the continental U.S. revealed that such patterns are indeed widespread. Specifically, we analyzed how inter-annual variation in precipitation and temperature impacts the optimal mode of adaptation for clonally reproducing organisms with a life cycle meant to mimic that of an annual plant. When there are correlations between the parental and offspring environments, neither traditional genetic selection nor within-generation plasticity take full advantage of the available information inherent in the environment. Instead, under such correlations selection should favor the genetic evolution of mechanisms that transmit plastic responses from one generation to the next. Absent such correlations, the information provided by the parental environment may not be relevant to offspring, and indeed may prove to be maladaptive (reviewed by 60).

Our modeling results revealed that the vast majority of sites in the contiguous US experienced autocorrelations in precipitation and temperature that should favor the evolution of adaptive transgenerational plasticity. As predicted by other models, the predictability of an environmental variable based on its autocorrelation or its association with other environmental variables is a major factor driving the optimal level of plasticity (e.g., 12,18,21,61). Furthermore, we find that the strength and direction of autocorrelations in precipitation and temperature varied substantially across the U.S., and consequently, the optimal levels of plasticity were also highly variable. Although both precipitation and temperature interact to shape the moisture availability and rates of transpiration for a plant, here we consider these terms separately. Future studies considering
temperature and precipitation in tandem should shed new light into the transmission of more complex environmental information.

Precipitation

The availability of water is one of the environmental factors that most directly impacts terrestrial plant life. Local adaptation to variable water regimes has been a major focus of plant evolutionary ecology for many years. This research shows that plants have evolved a wide range of physiological, phenological, and morphological adaptations to handle site-specific patterns of water availability (62). These adaptive phenotypes may be expressed constitutively or may be induced by an environmental cue that predicts a change in water availability later in the life of the organism. Increasingly, experimental studies show that the parental soil moisture regime can also adaptively influence the development of progeny (e.g., 35, 63), providing a third route by which plants can fine-tune their phenotypes of their offspring to local soil-moisture levels. For instance, in Massachusetts genotypes of the annual plant Polygonum persicaria, offspring of drought-stressed parents make more extensive root systems and deploy them faster in response to drought as compared to offspring of well-watered parents. This drought-induced change in growth and development can be inherited for at least two generations, resulting in increased survival of grandoffspring under severe drought stress (16, 38). Furthermore, these epigenetic effects of drought are genetically variable in P. persicaria: some genotypes strongly increase root length and biomass in response to parental drought, while other genotypes do so only moderately or not at all (10).

Our analysis revealed substantial and spatially variable interannual autocorrelations in precipitation, indicating that precipitation levels in one year are often predictive of precipitation levels up to three years later. For example, across the coterminous U.S., lag-1 interannual precipitation autocorrelations varied from moderately negative (-0.27) to strongly positive (0.69), including some values near zero. In turn, the optimal direction and strength of transgenerational effects of precipitation also varied. Positive parental effects, wherein individuals are developmentally predisposed to perform better in environments that match their parents’ environment, were optimal across more than twice as many regions (65% of sites) as negative transgenerational effects (28% of sites), wherein individuals perform better in a different environment compared to that of their parents. Relatively strong parental effect values of 0.3 or higher were optimal in nearly 30% of sites, but the most common transgenerational effect values were lower.
Intriguingly, multigenerational persistence values of 0 (18.7% of sites) and 1 (40.7% of sites) were the most common, representing strategies in which transgenerational effects lasted only a single generation or persisted fully through to the third generation, respectively. The remaining persistence values were somewhat evenly distributed between 0 and 1 and represent strategies in which environmental information gets passed through three generations, but the environment of more recent years is weighted more heavily. By contrast, complete absence of parental effects was favored in only 7% of sites.

The optimal level of transgenerational effects varied on multiple scales. On the largest scale, we found that the western and northern US experience conditions that select for the highest levels of transgenerational plasticity (Figure 4a). There was a striking contrast between the northeast, where positive transgenerational plasticity was generally optimal, and the southeast, where negative transgenerational plasticity predominated. These large-scale differences in plasticity levels stemmed from substantial differences in precipitation autocorrelations between these regions. There was also considerable variation in optimal levels of transgenerational plasticity on much finer scales. In some cases, optimal levels of transgenerational plasticity were highly divergent between adjacent sites (e.g., in central Texas and Minnesota). Furthermore, some sites had bimodal fitness landscapes, in which genotypes that express either positive or negative transgenerational effects were favored over genotypes that do not express plasticity (Figure 5b). For example, after a wetter-than-average year but two drier than average years prior to that, a genotype that prepares its offspring for another wetter-than-average year (i.e., a positive transgenerational effect), or one that prepares its offspring for a drier-than-average year (i.e., a negative transgenerational effect), will have higher fitness than a genotype that does not express transgenerational plasticity. To our knowledge, this represents the first demonstration that patterns of environmental variation can favor both positive and negative transgenerational effects in the same site. Our modeling results suggest that genetic variation for transgenerational precipitation effects may stem in part from fine-scale spatial variation in precipitation autocorrelations. We predict that such variation in precipitation autocorrelations translates into variable selection for transgenerationally plastic responses to precipitation, resulting in the maintenance of genetic variation for transgenerational plasticity within species.

**Temperature**

Temperature is vitally important to plant function and fitness, as it impacts the rate of physiological reactions, cues developmental transitions, and in extremes can cause stress and
mortality. Plants adapt to variable temperature regimes in a host of ways, including the production of heat shock proteins and cold-response factors, and the development of morphologies that mitigate the experience of temperature extremes. Experimental studies have identified adaptive plastic responses to temperature changes in plants, both within and across generations. For example, ambient temperature in Arabidopsis has been shown to influence the expression and splicing of hundreds of genes, leading to changes in underlying histone methylation (64), and significantly shifts flowering time (31) and many other phenotypes (65) in genotype-specific ways. Additionally, recent work has demonstrated the lasting impact of temperature regime on Arabidopsis thaliana plants for generations to come (12,49,66,67). In order for these responses to adaptively match phenotypes with natural environments, there must be substantial correlations in temperature within and between growing seasons.

We found significant autocorrelations in temperature, both within and between years. Within a single growing season, temperatures early and late in the growing season tended to be positively correlated across the U.S. Furthermore, we found that the temperatures of the late growing season months (July, August, September) were generally strongly autocorrelated between successive years. Interannual correlations between the temperatures of the early growing season months (February, March, April) were often much lower. Surprisingly, early growing season temperatures were generally more predictive of the following late seasons temperature than they were of the following early seasons temperature. These results suggest that early spring temperatures may be a harbinger of temperatures to come later in the same growing season and the latter half of the following growing season but provide little information regarding the following year’s early season temperature.

In our framework, temperature plays two roles related to fitness at both the early and late growing season time points. First, temperature acts as a selective agent, by which fitness is reduced according to the deviation between the actual temperature and a genotype’s phenotypic temperature optimum. Second, temperature is a source of information that a plant can use to alter its phenotype later in the growing season, and to alter the phenotype of its offspring in the following year. As a result, five classes of plasticity are available to plants in this model in order to best prepare themselves and their progeny for the most likely temperature conditions in the future. These plasticity classes include within-generation plasticity and four classes of transgenerational plasticity representing all permutations of early and late season temperature effects across the parent and offspring generations.
As expected, we find that, at a given site, the strength of the correlation between the average temperature during the season in which information is gathered and the average temperature during the season when selection occurs is highly predictive of both the type and degree of plasticity that will be favored. For example, warmer than average springs were very often followed by hotter than average summers, and this information yielded benefits via within-generation responses to temperature in many sites. The optimal strategy in more than 99% of sites across the U.S. contained some form of transgenerational plasticity, suggesting that environmental oscillations generally provide valuable information that allows transgenerational plasticity to improve the match between phenotypes and temperature regimes.

The most common form of transgenerational plasticity observed in this model entailed effects of late-growing season temperature on the following generation’s phenotype late in the growing season, which matches our expectations based on the patterns of temperature autocorrelation. Interestingly, patterns of environmental oscillations lead to favorable strategies in which the current late-season phenotype was more strongly impacted by the previous late-season temperature than it was by the current generation early season temperature. Indeed, this pattern was found in over half of the regions considered (270k/480k). Although intuition suggests that more recent information is of higher value, this result suggests that parental environments can be more predictive of offspring selective environments than environmental cues early in the offspring generation. This result stems from the cyclic nature of seasonal environments (68). For instance, cool temperatures in spring do not generally foreshadow similarly cool temperatures in late summer, but warm summer temperatures in the previous generation do correlate with warm temperatures in the following summer. Since autocorrelations between consecutive early growing seasons were generally low, it is not surprising that effects of early growing season temperatures on phenotypes in the following early growing season was the least common form of plasticity and was in the negative direction more often than the positive. Other forms of transgenerational plasticity were present at intermediate levels and varied greatly across the US.

Although we identified general patterns in temperature autocorrelations, a key finding was that these autocorrelations varied considerably across the U.S., leading to vastly different optimal levels of within- and transgenerational plasticity among sites. The west coast of the US and southern Florida experienced the highest optimal transgenerational plasticity values. Because these regions are due east of large bodies of water, their climates are heavily influenced by maritime airflow including the prevailing westerlies, loop current, and Coriolis affect (69). As water has a substantially higher
heat capacity than either rock or soil, the location of these land masses downstream of maritime air
may predispose them to temperature autocorrelations between years. Additionally, we found highly
variable correlations between late growing season temperature and the following generation’s early
growing season temperature. This result is intriguing because the temperature experienced during
seed maturation interacts with the post-dispersal temperature to strongly influence the dormancy
and germination behavior of seeds, with cascading effects throughout the life cycles of annual plants
(31,70). Consequently, site-specific correlations between maternal late-season temperature and the
early-season temperature in the next generation may select for divergent, site-specific effects of
maternal temperature on germination for species that set seed in late summer. Intriguingly, parental
effects of temperature on germination and flowering time are highly genetically variable in

*Arabidopsis thaliana* (12,70,71). In *Plantago lanceolata*, such genotype-by-maternal temperature effects
persist throughout the offspring life cycle to generate variation in offspring reproduction in the field
(72). Our results suggest that such genetic variation for maternal effects may derive in part from
variable selection imposed by differences among sites in intergenerational temperature correlations
(see also 12).

**Common Themes and Future Directions**

Although our precipitation and temperature models yielded distinct insights into the
dynamics of each of these factors, common themes emerged in both sets of analyses. For example,
we found higher levels of inter-annual autocorrelation, and therefore more prominent
transgenerational effects, at northern latitudes and along coastal regions within both models. Studies
that compare patterns of transgenerational plasticity across such large geographic regions will be
necessary to determine whether underlying differences in environmental patterns do in fact drive
differences in transgenerational plasticity. Another common finding of both the raw temperature
and precipitation models is that transgenerational effects are expected to provide greater benefits in
changing climates relative to purely oscillating climates, in which linear climate change has been
removed (i.e., the residual models). We also found that populations in regions undergoing the most
severe climate change are expected to benefit most by increasing transgenerational plasticity.

These results suggest that transgenerational effects may have an important role in adaptation
to human-induced climate change, and that rapid climate change should select for more
transgenerationally plastic individuals. However, there is an important caveat. In our models we
assume that genotypes are uniform in their mean phenotype, and do not allow for mutations that
could lead to genetic adaptation to changing conditions. The potential for transgenerational plasticity to either promote or hinder genetic adaptation has been explored (73), but our models do not address this issue. Instead, we set the baseline phenotype of an organism as the optimal phenotype for the average conditions over the 120 years for which we have data, and then compared the fitness of genotypes that vary in their expression of plasticity. In the absence of genetic evolution, it follows that if there is a linear trend towards hotter or drier years in addition to climatic oscillations (as in the raw model variants), then there is more transgenerational information relative to a situation in which only climatic oscillations are occurring (residual model variants). Theory indicates that these dynamics become much more complex when local genetic adaptation to changing conditions is allowed to occur along with transgenerational plasticity (12). For instance, in some scenarios transgenerational effects can increase fitness in the short term, while reducing it in the long term (74). In future studies, it will be critical to investigate the influence of standing genetic variation for transgenerational plasticity on evolutionary trajectories, and to examine the availability of novel mutations that alter the dynamics of transgenerational effects. Answering both of these questions in the same system will be necessary to determine the likelihood that selection on transgenerational plasticity is a viable route to adaptation in the face of changing conditions.

Temperature and precipitation autocorrelations and optimal plasticity values likely stem in part from the same broad-scale climatic oscillations, such as the El Niño Southern Oscillation (75), the Quasi-biennial oscillation (76), and the Pacific Decadal Oscillation (77,78). Aside from these climatic oscillations, autocorrelations will arise due simply to “red” or “pink” noise in which rare, large events and common, small events have equal power in explaining variation (79). It has been demonstrated that even without clear underlying phenomena explaining variation, pink-noise is often the model that best explains patterns of ecological and abiotic time-series variation (80). These oscillations and general patterns of red noise will interact with each other to varying degrees across different regions of the US, leading to variable levels of autocorrelation at all lags for both precipitation and temperature.

Furthermore, because temperature and precipitation interact to alter moisture availability, it is likely that organisms do not process temperature and precipitation information independently, but rather use them in tandem along with other sources of information to fine tune phenotypes for the most likely future environment. For instance, temperature influences water availability by influencing rates of evaporation and transpiration. Interactions between temperature and water availability also shape the collection of herbivores, pathogens, and competitors present in a given locality.
Understanding how these environmental factors jointly influence the expression of transgenerational plasticity is an important goal for future research. Another critical goal of future research is to better understand how within- and transgenerational plasticity interact to influence phenotypic expression. A key element of this research direction is to study environmental (auto)correlations at fine scales in the context of dispersal distances. It is possible that transgenerational plasticity may be a more common mode of adaptation for organisms with short dispersal distances, in which parents and offspring are more likely to grow and develop in similar microsites. Finally, differences in life history strategies and generation times will alter the time-scales and types of environmental autocorrelations relevant to transgenerational plasticity. Future studies drawing inspiration from other species will provide insight into how these variables might impact the evolution of transgenerational effects.

Conclusion

In summary, we demonstrate that patterns of climatic variation in nature may favor the adaptive evolution of transgenerational plasticity in organisms with approximately annual generation times, such as annual plants. Our models indicate that differing patterns of climatic oscillations across the US lead to strikingly different optimal patterns of within- and transgenerational plasticity. Thus, for a given species, one may expect that environmental variation across its range not only selects for different locally adapted mean trait values, but also different classes and magnitudes of plasticity. Perhaps the most meaningful result of this study is that the climatic patterns across relatively small geographic regions vary so dramatically that the optimal value of transgenerational plasticity ranges from extremely high to non-existent. It should therefore be expected that although many species, environmental variables, or phenotypes of interest may show no evidence of transgenerational plasticity, such results may be due to their specific situation rather than a fundamental biological limitation. This applies equally strongly to the other side of the coin: because a single population or species expresses strong transgenerational plasticity does not mean that this process is a key driver of evolutionary processes. Rather, variation in transgenerational plasticity should be expected, just as genetic variation is ubiquitous in natural populations. Transgenerational plasticity is best considered in the specific ecological and evolutionary context of the study organism, and broad generalizations about the role of these effects in evolution should be avoided until considerably more field data are in hand. The results described here provide a source of testable predictions for geographical variation in this mode of adaptation.
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Table 1: Summary statistics of climatic patterns relevant to the evolution of within and transgenerational plasticity. Mean (s.d.).

|                  | Mean   | IASD   | RACF-1  | ACF-1  | ACF-2   | ACF-3   |
|------------------|--------|--------|---------|--------|---------|---------|
| Precipitation    | 763 (443) | 145 (76) | 0.02 (0.08) | 0.04 (0.09) | 0.05 (0.13) | 0.01 (0.09) |
| Spring Temp      | 10.4 (5.5) | 1.2 (0.2) | -0.04 (0.07) | -0.01 (0.08) | -0.04 (0.1) | 0.05 (0.09) |
| Summer Temp      | 21.2 (4.2) | 0.9 (0.2) | 0.17 (0.1) | 0.24 (0.12) | 0.09 (0.1) | 0.11 (0.09) |
Table 2: Most common, second most common, and mean optimal plasticity values across all sites in the US.

| Climate Term | Raw | Residual |
|--------------|-----|----------|
|              | #1 / #2 | Mean (s.d.) | #1 / #2 | Mean (s.d.) |
| Precipitation | M  | 0.1/0.2 | 0.094 (0.22) | 0.1/0.2 | 0.036 (0.21) |
|              | G   | 1/0     | 0.63 (0.40) | 1/0     | 0.64 (0.40) |
| Temperature  | $m_{EE}$ | 0 / 0.1 | -0.016 (0.098) | 0 / -0.2 | -0.04 (0.11) |
|              | $m_{EL}$ | 0.1 / 0 | 0.057 (0.073) | 0.1 / 0 | 0.045 (0.073) |
|              | $m_{LE}$ | 0.1 / 0 | 0.096 (0.178) | 0 / 0.1 | 0.042 (0.17) |
|              | $m_{LL}$ | 0.3 / 0.1 | 0.204 (0.133) | 0.1 / 0.3 | 0.148 (0.117) |
|              | $w$    | 0.1 / 0 | 0.095 (0.072) | 0.1 / 0 | 0.092 (0.072) |
Table 3: Correlations between the temperature correlation between seasons and the optimal transgenerational plasticity values.

|        | $m_{EE}$   | $m_{EL}$   | $m_{LE}$   | $m_{LL}$   |
|--------|------------|------------|------------|------------|
| EE ACF | 0.757139   | -0.131583  | -0.049501  | -0.156768  |
| EL ACF | -0.036229  | 0.5968488  | -0.069245  | -0.153818  |
| LE ACF | 0.1256068  | -0.036048  | 1.3390581  | -0.067451  |
| LL ACF | 0.0135772  | -0.017808  | -0.120773  | 0.9757164  |
| Within ACF | -0.067861 | -0.160476  | 0.0595802  | 0.0701295  |
Figure 1: Schematic depicting the ecological motivations (summer annual plants) and theoretical underpinnings for the evolutionary modeling of plasticity traits (A and C), and the types of environmental fluctuations that may influence their evolution. (A) Temperature plasticity model. In the abbreviations, E denotes the Early growing season (spring) and L denotes the late growing season (summer). The first letter represents the relevant season during the parental generation and the second letter represents the relevant season in the offspring generation (e.g., EL denotes effects of parental early growing season temperature on offspring phenotypes late in the growing season). Within generation developmental changes in response to early season environment (W) are also considered in this model. Additionally, the longer term average environmental conditions at a specific area determine the genetic baseline phenotype of an individual (G). (B) On the left we see an example of an environment with high within season autocorrelations for temperature (hot springs tend to be followed by hot summers), but low inter-annual autocorrelations (a hot year does not tend to be followed by another hot year) that selects for within generation plasticity but not transgenerational plasticity. On the right, a situation where spring and summer temperatures are not correlated with each other, but we do find that environmental oscillations lead to a string of warmer than average springs and cooler than average summers, in this situation transgenerational plasticity (EE and LL) but not within generation plasticity is expected to be optimal. (C) Precipitation plasticity model. The amount of precipitation experienced by an individual can lead to transgenerational effects in the next generation (T), as well as persist for two (TG) or three (TGG) generations. (D) On the left, relatively gradual decadal oscillations give value to transgenerational effects that persist for multiple seasons (T, TG, and TGG). On the right shorter period climatic oscillations may favor parental effects (T), but not multi-generation effects (TG or TGG).

Figure 2: Maps depicting natural climatic variation across the conterminous US.
Figure 3: Distributions of optimal plasticity (A and B) and temperature (C-G) values across all 4km x 4km sites in the US. Histograms of optimal (A) precipitation transgenerational plasticity value \(T\), (B) precipitation multi-generation persistence \(G\), (C) temperature spring (early season) -> spring (early season) transgenerational plasticity \(m_{EE}\), (D) temperature spring (early season) -> summer (late season) transgenerational plasticity \(m_{EL}\), (E) temperature summer (late season) -> spring (early season) transgenerational plasticity \(m_{LE}\), (F) temperature summer (late season) -> summer (late season) transgenerational plasticity \(m_{LL}\), and within generation temperature plasticity \(W\).

Figure 4: Maps coded to show patterns of variability for optimal precipitation (A-C) and temperature (D-H) plasticity values across the US. (A) Optimal transgenerational plasticity values for the one-generation transmission of precipitation level information. (B) Optimal grandparental transgenerational plasticity values coded blue (green) or red (orange) based on the direction of effect (positive or negative). White regions have an optimal multi-generation persistence \(G\) of 0, while red and blue both have optimal multigeneration persistence of 1, intermediate values \(0>G>1\) in orange and green. (C) The difference between optimal transgenerational plasticity values in the raw vs. residual variant of the mode. Higher values suggest that the primary value associated with transgenerational plasticity over the past 120 years has been associated with allowing individuals to keep up with linearly changing precipitation patterns. (D) Optimal total levels of transgenerational temperature plasticity \((M_{EE} + M_{EL} + M_{LE} + M_{LL})/2\). (E) Optimal transgenerational plasticity of most extreme positive transgenerational plasticity allele. (F) Optimal transgenerational plasticity of lowest transgenerational plasticity allele. Regions in orange have at least one form of transgenerational plasticity for which negative transgenerational effects increase fitness. (G) The difference between optimal transgenerational plasticity values in the raw vs. residual variant of the
mode. Higher values suggest that the primary value associated with transgenerational plasticity over the past 120 years has been associated with allowing individuals to keep up with increasing temperature. (H) Optimal within generation plasticity (W) values.

Figure 5: Fitness landscapes of transgenerational precipitation alleles for twelve sites across the US. Sites with low optimal parental effects (D and I) have only very subtle fitness differences associated with changes in the multigeneration persistence (Y-axis) due to the minor role in any form of transgenerational effect on fitness in these cases. More defined fitness peaks tend to occur in areas where more substantial transgenerational effects are optimal (E, G, J, K, L). In some rare cases, bimodal fitness landscapes arise (B) where lines with either positive (with high persistence) or negative (with low persistence) transgenerational persistence have higher fitness than lines with no transgenerational inheritance.

Figure 6: Changes in the frequency of ten clonal types in a 120 year simulated competition experiment for four different sites across the US. The top three final frequency clones are denoted with stars.

Figure S1: Distribution of climatic summary statistics across the 481k 4x4km grids in the US. Dotted lines at 0 for autocorrelation histograms.

Figure S2: Mosaic plot showing the frequency of specific combinations of optimal transgenerational effects and multi-generational persistence values. More subtle transgenerational effects more frequently only have a single generation of persistence (G=0), while more extreme transgenerational effects tend to coincide with full transgenerational persistence (G=1) where each of the prior three
years contribute equally. Additionally, positive transgenerational effects were more likely to have intermediate levels of persistence than negative transgenerational effects.

Figure S3: Multi-panel fitness landscape comparing the relative fitness of clonal types with different levels of the four transgenerational temperature plasticity terms.
Figure 1

Temperature

Generation 0

Spring Summer Spring Summer

Generation 0 Generation 1

EE EL LE LL

Temperature Deviance

High: W Low: EE, EL, LE, LL

Annual Precip

High: T, G Low:

High: T Low: G

Seasonal Temperature Deviance

High: EE, LL Low: W, EL, LE

Precipitation

High: T, G Low:

High: T Low: G

Annual Precip

High: W Low: EE, EL, LE, LL

High: EE, LL Low: W, EL, LE

Generations 0 1 2 3 4

Generation Generation

1 2 3 4
Figure 2

Annual Precipitation

Mean Daily Maximum Temperature

Spring (March-May)

Summer (July-September)

Mean

Inter-Annual Variability

120 Year Change

Inter Annual ACF Lag-1

Inter Annual ACF Lag-2

Wet Cold

Hot Dry

Consistent Variable

Hotter Drier

Cooler Wetter

Negative Positive

Negative Positive
Figure 3

Precipitation Plasticity Model

Temperature Plasticity Model
Figure 6

Relative Abundance

Parental Effect
-0.2
0
0.2
0.4

Transgenerational Persistance
0
0.5
1

Final Abundance
First
Second
Third
Figure S3

A

**Optimal late-late transgenerational plasticity**

 Frequency of early-late transgenerational plasticity

| Frequency of early-late transgenerational plasticity | 0.1 | 0.2 | 0.3 | 0.4 |
|------------------------------------------------------|-----|-----|-----|-----|
| 0.0                                                  | -   | -   | -   | -   |
| 0.1                                                  | -   | -   | -   | -   |
| 0.2                                                  | -   | -   | -   | -   |
| 0.3                                                  | -   | -   | -   | -   |
| 0.4                                                  | -   | -   | -   | -   |
| 0.5                                                  | -   | -   | -   | -   |
| 0.6                                                  | -   | -   | -   | -   |
| 0.7                                                  | -   | -   | -   | -   |
| 0.8                                                  | -   | -   | -   | -   |
| 0.9                                                  | -   | -   | -   | -   |
| 1.0                                                  | -   | -   | -   | -   |

B

**Optimal early-late transgenerational plasticity**

- **Moderate (0.3)**
- **Minor (0.1)**
- **Zero (0)**
- **Negative (-0.2)**

**Fitness**

| Fitness | None | Both | Early | Late |
|---------|------|------|-------|------|
| 0.888   | -    | -    | -     | -    |
| 0.89    | -    | -    | -     | -    |
| 0.891   | -    | -    | -     | -    |
| 0.892   | -    | -    | -     | -    |
| 0.893   | -    | -    | -     | -    |
| 0.894   | -    | -    | -     | -    |
| 0.895   | -    | -    | -     | -    |
| 0.896   | -    | -    | -     | -    |
| 0.897   | -    | -    | -     | -    |
| 0.898   | -    | -    | -     | -    |
| 0.899   | -    | -    | -     | -    |

**Summer inter-annual temperature autocorrelation**

- **None**
- **Both**
- **Early**
- **Late**
