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.

Introduction

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

129 weather events, potentially decreasing the relative fitness of organisms that may have evolved
130 transgenerational plasticity to cope with previously reliable environmental patterns.
131 Empirical investigations in diverse plant and animal systems have confirmed that
132 transgenerational environmental effects can be adaptive when parent and progeny environments
133 match (i.e., under positive intergenerational environmental autocorrelations; see e.g., 36-46; reviewed
134 by 6,7,14). For instance, when *Mimulus guttatus* plants experience herbivory, their offspring increase
135 production of defensive leaf trichomes (11,47,48). Similarly, when the aquatic crustacean *Daphnia*
136 *cuculatta* is exposed to predator cues, it produces offspring with a defensive 'helmet' that protects
137 against predation by midge larvae and cladocerans (36).
138 Despite this surge of interest, to date no study has examined long-term environmental data
139 for the presence of inter-generational environmental correlations that are expected to favor the
140 adaptive evolution of transgenerational plasticity. Although we tend to think about how the average
141 environmental conditions differ across a landscape, there is no reason to expect that the scale and
142 predictability of environmental variation is any less complex or ubiquitous across a landscape. Here
143 we identify *spatial variation* in the *temporal predictability* of environmental variation, and leverage this
144 variation to compare the adaptive value of within-generation plasticity, transgenerational plasticity,
145 and multigenerational epigenetic inheritance across different local regimes of climate variability. We
146 utilize 120 years of fine-scale (4km^2) climate data spanning the coterminous U.S. to test for auto- and
147 cross-correlations in temperature and precipitation levels across years. We found many significant
148 correlations that vary widely in both magnitude and direction across the US. We then construct
149 separate models for temperature and precipitation to determine the degree of transgenerational
150 plasticity that would maximize fitness in each of these sites across the U.S. with respect to the
151 observed environmental measurements. Additionally, we constructed each model using raw
152 environmental data and the residuals after factoring out the effects of directional climate change. By
153 considering both raw data values and residuals in tandem, we are able to parse out the role of
154 transgenerational effects and within generation plasticity in periodically oscillating environments
155 (residual model), as well as those with periodic oscillations in addition to a linear change in mean
156 temperature (raw data model). In all other ways, the two variants of this model are identical.
157 Differences in the results of raw vs. residual models highlight how climate change alters the benefits
158 associated with transgenerational plasticity. These models were constructed with summer annual
159 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).

General modeling framework

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

224 year with extremely low fitness from dominating final genotype frequencies, but was only used in
225 under 0.01% of fitness measurements. After every generation, there is a round of competition,
226 where the frequency of a given genotype will change based on the relative fitness of that genotype
227 compared to the mean phenotype for that year. This scenario is equivalent to an infinite population
228 size evolutionary model in which the relative frequency of genotypes changes due to selection and
229 reproduction once per year.

230 For each locale, mean annual precipitation (or temperature) across the 120 years $(\bar{P})$ is
231 calculated, and this statistic is used as the baseline phenotype of all genotypes in the raw data variant
232 of the model. Additionally, a linear regression of precipitation on year was fit for each site over the
233 120 years considered, and residuals were calculated for every year. In the residual variant of this
234 formula, the expected values are 0, and residuals are used as the precipitation values for each year.
235

236 *Precipitation model*

237 For a given generation *T* the expected precipitation (phenotype) is defined as $\dot{P}_T$, while the
238 actual precipitation is P_T. The two parameters considered in this model are m (maternal or parental
239 effect) and g (multigenerational persistence). The m value in this model alters the expected
240 precipitation (phenotype) for a given year ($\dot{P}_T$) based on how deviant the precipitation was during a
241 preceding year or years $(P_{T-X} - \bar{P})$. In other words, m adjusts offspring phenotype based on how
242 different parental environment was from long term average environment. When there are
243 interannual autocorrelations, values of m that match the degree of interannual autocorrelation will
244 be adaptive.
245

246 $$\dot{P}_T = \bar{P} + \frac{m(P_{T-1} - \bar{P}) + mg(P_{T-2} - \bar{P}) + mg^2(P_{T-3} - \bar{P})}{1 + g + g^2}$$

247

248 When $m = 0$ the expected precipitation will always be equivelant to the mean precipitation
249 at a site, when $m = 1$ and $g = 0$, the expected precipitation will always equal the precipitation
250 experienced the prior year. In the simplest case when $g = 0$ only the prior year's information alters
251 the expected precipitation. The g value in this model weighs how much the precipitation
252 experienced two and three generations back should change expected precipitation values relative to
253 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 effects 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 × 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.

$$w_{MT} = 1 - \frac{\left|\dot{P}_T - P_T\right|}{\bar{P}}$$

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

284 to produce the relative fitness of each genotype. This relative fitness was then used as the relative
285 frequency of each genotype for the following year. For each year following the first, the absolute
286 fitness of each genotype was divided by a weighted mean of the fitness of all individuals for that year
287 ($w_X^{Rel} = w_X^{Abs} / \sum_{i=1}^{154} w_i^{Abs} * Freq(i)$) to calculate the relative fitness of each genotype for each
288 generation. This value was then multiplied by the frequency of that genotype in that generation to
289 get the following generation's frequency. The final generation frequency was used for the
290 construction of fitness surface heatmaps.
291
292 *Temperature model*
293 The general framework of the temperature model is similar, but rather than allowing for the
294 persistence of transgenerational effects across multiple years, it considers early and late season
295 transgenerational effects, as well as within-generation plasticity. We ran the same model on raw data
296 and residuals, calculated as in the precipitation model. Annual plants were used as the motivation for
297 this model, with a growing season from March-September. The growing season was broken down
298 into three parts: early growing season (March, April, May), transitional growing season (June), and
299 late growing season (July, August, September). Within this model there are two bouts of selection,
300 one after the early growing season, and one after the late season. While early season phenotype can
301 only be modified by the previous year's temperature (because organisms are newly born in the spring
302 in this scenario, and therefore cannot respond themselves to temperatures), late growing season
303 phenotype can be modified by the previous year's temperature, and/or the temperature earlier in the
304 growing season. Additionally, this model allows for both early and late season phenotype to be
305 modified by both the previous season's early and late temperatures independently. In other words,
306 early season phenotype can be modified by the previous year's early season temperature, or the
307 previous year's late season temperature; late season phenotype can be modified by these same two
308 factors as well as the current year's early season temperature (i.e., by within-generation plasticity).
309 Thus, this model includes five plasticity parameters, reflecting the effect of 1) the previous
310 generation's early season temperature on current early season phenotype (m_{EE}), 2) the previous
311 generation's late season temperature on current early season phenotype (m_{LE}), 3) the previous
312 generation's early season temperature on the current late season phenotype(m_{EL}), 4) the previous
313 generation's late season temperature on current late season phenotype (m_{LL}), and 5) the current
314 early season temperature on the current late season phenotype (b). Note that the mean and variance

315 of temperature data are not correlated, unlike precipitation data. For this reason, fitness is scaled by
316 a constant 20 rather than the mean temperature of a given site. Results were exceedingly similar
317 when fitness was scaled by constants of 10 and 100; 20 was chosen as it is closer to the mean annual
318 temperature across the US.
319

320 $$\dot{P_{TE}} = \overline{P_E} + m_{EE}(P_{ET-1} - \overline{P_E}) + m_{LE}(P_{LT-1} - \overline{P_L})$$

321 $$w_E = 1 - \frac{|\dot{P_{TE}} - P_{TE}|}{20}$$

322 $$\dot{P_{TL}} = \overline{P_L} + m_{EL}(P_{ET-1} - \overline{P_E}) + m_{LL}(P_{LT-1} - \overline{P_L}) + b(P_{ET} - \overline{P_E})$$

323 $$w_L = 1 - \frac{|\dot{P_{TL}} - P_{TL}|}{20}$$

324 $$w_F = w_E * w_L$$

325

326 The geometric mean of genotype fitness was taken over the 119 years for each of the
327 genotypes. For each of the five plasticity (transgenerational and within generational) terms in this
328 model we considered possible values of -0.2 (negative plasticity), 0 (no plasticity), 0.1 (minor
329 plasticity), 0.3 (moderate plasticity), and 0.5 (major plasticity). While this resolution is somewhat
330 coarse, focusing on this subset of values allowed us to consider this model for the full factorial
331 combination of parameter space. In total, fitness was calculated for 3125 genotypes, across each of
332 119 years, at all 481631 locations, for a total of 179 billion measures of fitness. The values of
333 plasticity at which fitness was maximized were recorded from each grid point across the US. Finally,
334 for the same 12 focal sites used in the precipitation model, we calculated the changes in genotype
335 frequency across 119 years using the same methodology as above. All code for these simulations,
336 and other modeling results are available at (github.com/XXXX).
337

338 **Results**

339 Both mean annual precipitation and growing season temperatures vary immensely across the
340 US (Figure 2 and S1). Mean annual temperature and precipitation are both primary forces driving
341 local adaptation to the diversity of climate regimes across the US, but for the evolution of locally
342 adaptive phenotypic plasticity, it is the patterns of variation that are more relevant. The standard
343 deviation of a site's annual precipitation or growing season temperatures over the past 120 years also
344 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

409 parental effect indicates that 90% of phenotypic variance is dictated by the long-term average
410 (genetic effects), and 10% by the difference between the parental environment and the long-term
411 average environment. The second most common optimal value of m was 0.2 (19.15% in the raw
412 model, 18.6% in residual model), followed by -0.1 (14.3% in the raw model, 17.2% in the residual,
413 Figure 3a). A value of -0.1 means that 10% of phenotypic variation stems from transgenerational
414 plasticity and 90% from genetic variation, but that the precipitation experienced by parents will
415 influence the progeny in the opposite direction. For example, if the mean annual precipitation at a
416 site is 1000mm (dictating the genetic value), and the previous year's precipitation was 1100mm, then
417 the phenotype of the current generation would be 1010mm (1000*0.9 + (1,100-1000)*0.1) in the
418 case of an allele value of 0.1, and 990mm in the case of an m value of -0.1 (assuming there are no
419 multigenerational environmental effects). Optimal values of m ranged from -0.6 to 0.9, and were
420 approximately normally distributed, except a dearth of sites for which the optimal allele value was 0
421 due to the lack of multigenerational environmental effects in this situation.
422 The multigenerational persistence (g) of transgenerational effects was also found to vary
423 greatly across the US with the two most common values being 1 (40.7% raw, 39.5% residual) and 0
424 (18.6% raw, 16.8% residual) (Figure 3b). Here, a value of 1 indicates that the precipitation one, two,
425 and three years prior all contribute equally to the expected precipitation at a given site. A g value of
426 0 indicates that only the previous year's precipitation is predictive of the current precipitation level.
427 The remaining 40.7% of sites (in the raw variant) have intermediate optimal values of g, suggesting
428 that in these locations the precipitation of each of the past three years is informative, but
429 information from the immediately preceding year is of the highest value. Of the nine values
430 considered between 0 and 1, all were represented by between 3.1% and 5.7% of sites, with a value of
431 0.8 being the most frequent strategy, and 0.1 being the least frequent (Figure 4). Interestingly, full
432 multigenerational persistence (g =1) was more frequently optimal at sites with negative
433 transgenerational effect values compared to those with positive values (44.9% vs. 38.9%,
434 respectively), where intermediate multigenerational persistence was more common (Figure S2).
435 Additionally, we found that the adaptive value of multigenerational persistence increases as the
436 strength of the transgenerational effect increases, such that little-to-no multigenerational persistence
437 is optimal when the transgenerational effect is close to zero, and strong multigenerational effects are
438 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

470 on the next generation's early season phenotype (m_{EE}) were slightly more likely to be positive in the
471 raw version of the model (98,089 vs. 89,547), and more likely to be negative in the residual variant
472 (68,441 vs. 132,352). In both cases however, no m_{EE} plasticity was the most common optimal
473 strategy. Finally, the effect of early season temperature on the next generation's late season
474 phenotype (m_{EL}) was most often minor (0.1) in both raw (251,691) and residual (229,301) variants.
475 When considering the combined plasticity value profile of a site, we find the most common
476 combination of plasticity values is, EE: none (0), EL: minor (0.1), LE: minor (0.1), LL: moderate
477 (0.3), WP: minor (0.1) (Table 2b). Summing the four transgenerational plasticity alleles together we
478 find the southwest US has the highest optimal values of transgenerational plasticity, while the Great
479 Lakes region has the lowest optimal values (Figure 4d). Texas and Florida tend to have the greatest
480 variability for transgenerational plasticity values, with many areas within these regions having both
481 positive and negative transgenerational values leading to intermediate total transgenerational
482 plasticity (Figures 4e and 4h). Optimal total transgenerational plasticity values were on average 0.146
483 (+/- 0.21) higher in the raw relative to the residual models (although the most common change was
484 0). In the southwestern US, where temperature increased the most over the past 120 years (Figure
485 2), the difference between the raw and residual model was the greatest (Figure 4g).
486 Variation in different classes of temperature autocorrelations between seasons explains a
487 large portion of the variation in the optimal transgenerational response to temperature at a given
488 site. For example, the autocorrelation between early season growing temperature and the next year's
489 late season growing temperature is the factor that explains the largest amount of variation in optimal
490 levels of m_{EL} (Table 3). We assessed potential tradeoffs between different forms of
491 transgenerational plasticity to temperature by first calculating the residuals of a particular plasticity
492 term after accounting for the effects of environmental autocorrelations, then testing the effect of the
493 other four plasticity terms on these residuals. There was a highly significant negative association
494 between m_{LE} and m_{EE} plasticity, and between m_{LL} and m_{EL} plasticity (Figure S3a). As higher levels
495 of late-late transgenerational plasticity were favored, the optimal levels of EL plasticity also
496 decreased across all environmental autocorrelation values. These associations suggest that, for a
497 given life history stage in this model, there are tradeoffs between using transgenerational information
498 from the previous generation's early vs. late season temperature (Table S2). For example, there are
499 many sites where no plasticity, m_{EE} plasticity, and m_{LE} plasticity all have higher fitness than
500 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

533 late season phenotypes (m_{EL}) increased, optimal m_{LL} values decreased (Figure S4) and vice versa.
534 The same is true for m_{EE} and m_{LE}. At a given stage in the offspring's life cycle there is only so
535 much information value that can be gleaned from the environments of previous generations; this
536 total value (m_{EL} +m_{LL}) is one factor that varies across the US in this model. The optimal balance
537 between the two forms of transgenerational plasticity that affect a given life history stage (m_{EL} :
538 m_{LL}) is the other parameter that varies, and this balance is what controls the degree to which the
539 early vs. late season parental conditions will modify offspring development at a given stage.
540

541 **Discussion**

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

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

565 temperature and precipitation in tandem should shed new light into the transmission of more
566 complex environmental information.
567
568 *Precipitation*
569 The availability of water is one of the environmental factors that most directly impacts
570 terrestrial plant life. Local adaptation to variable water regimes has been a major focus of plant
571 evolutionary ecology for many years. This research shows that plants have evolved a wide range of
572 physiological, phenological, and morphological adaptations to handle site-specific patterns of water
573 availability (62). These adaptive phenotypes may be expressed constitutively or may be induced by
574 an environmental cue that predicts a change in water availability later in the life of the organism.
575 Increasingly, experimental studies show that the parental soil moisture regime can also adaptively
576 influence the development of progeny (e.g., 35, 63), providing a third route by which plants can fine
577 tune their phenotypes of their offspring to local soil-moisture levels. For instance, in Massachusetts
578 genotypes of the annual plant *Polygonum persicaria*, offspring of drought-stressed parents make more
579 extensive root systems and deploy them faster in response to drought as compared to offspring of
580 well-watered parents. This drought-induced change in growth and development can be inherited for
581 at least two generations, resulting in increased survival of grandoffspring under severe drought stress
582 (16, 38). Furthermore, these epigenetic effects of drought are genetically variable in *P. persicaria*:
583 some genotypes strongly increase root length and biomass in response to parental drought, while
584 other genotypes do so only moderately or not at all (10).
585 Our analysis revealed substantial and spatially variable interannual autocorrelations in
586 precipitation, indicating that precipitation levels in one year are often predictive of precipitation
587 levels up to three years later. For example, across the coterminous U.S., lag-1 interannual
588 precipitation autocorrelations varied from moderately negative (-0.27) to strongly positive (0.69),
589 including some values near zero. In turn, the optimal direction and strength of transgenerational
590 effects of precipitation also varied. Positive parental effects, wherein individuals are developmentally
591 predisposed to perform better in environments that match their parents' environment, were optimal
592 across more than twice as many regions (65% of sites) as negative transgenerational effects (28% of
593 sites), wherein individuals perform better in a different environment compared to that of their
594 parents. Relatively strong parental effect values of 0.3 or higher were optimal in nearly 30% of sites,
595 but the most common transgenerational effect values were lower.

596 Intriguingly, multigenerational persistence values of 0 (18.7% of sites) and 1 (40.7% of sites)
597 were the most common, representing strategies in which transgenerational effects lasted only a
598 single generation or persisted fully through to the third generation, respectively. The remaining
599 persistence values were somewhat evenly distributed between 0 and 1 and represent strategies in
600 which environmental information gets passed through three generations, but the environment of
601 more recent years is weighted more heavily. By contrast, complete absence of parental effects was
602 favored in only 7% of sites.
603 The optimal level of transgenerational effects varied on multiple scales. On the largest scale,
604 we found that the western and northern US experience conditions that select for the highest levels
605 of transgenerational plasticity (Figure 4a). There was a striking contrast between the northeast,
606 where positive transgenerational plasticity was generally optimal, and the southeast, where negative
607 transgenerational plasticity predominated. These large-scale differences in plasticity levels stemmed
608 from substantial differences in precipitation autocorrelations between these regions. There was also
609 considerable variation in optimal levels of transgenerational plasticity on much finer scales. In some
610 cases, optimal levels of transgenerational plasticity were highly divergent between adjacent sites (e.g.,
611 in central Texas and Minnesota). Furthermore, some sites had bimodal fitness landscapes, in which
612 genotypes that express either positive or negative transgenerational effects were favored over
613 genotypes that do not express plasticity (Figure 5b). For example, after a wetter-than-average year
614 but two drier than average years prior to that, a genotype that prepares its offspring for another
615 wetter-than-average year (i.e., a positive transgenerational effect), or one that prepares its offspring
616 for a drier-than-average year (i.e., a negative transgenerational effect), will have higher fitness than a
617 genotype that does not express transgenerational plasticity. To our knowledge, this represents the
618 first demonstration that patterns of environmental variation can favor both positive and negative
619 transgenerational effects in the same site. Our modeling results suggest that genetic variation for
620 transgenerational precipitation effects may stem in part from fine-scale spatial variation in
621 precipitation autocorrelations. We predict that such variation in precipitation autocorrelations
622 translates into variable selection for transgenerationally plastic responses to precipitation, resulting in
623 the maintenance of genetic variation for transgenerational plasticity within species.
624
625 *Temperature*
626 Temperature is vitally important to plant function and fitness, as it impacts the rate of
627 physiological reactions, cues developmental transitions, and in extremes can cause stress and

628 mortality. Plants adapt to variable temperature regimes in a host of ways, including the production
629 of heat shock proteins and cold-response factors, and the development of morphologies that
630 mitigate the experience of temperature extremes. Experimental studies have identified adaptive
631 plastic responses to temperature changes in plants, both within and across generations. For example,
632 ambient temperature in Arabidopsis has been shown to influence the expression and splicing of
633 hundreds of genes, leading to changes in underlying histone methylation (64), and significantly shifts
634 flowering time (31) and many other phenotypes (65) in genotype-specific ways. Additionally, recent
635 work has demonstrated the lasting impact of temperature regime on *Arabidopsis thaliana* plants for
636 generations to come (12,49,66,67). In order for these responses to adaptively match phenotypes
637 with natural environments, there must be substantial correlations in temperature within and between
638 growing seasons.

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

649 In our framework, temperature plays two roles related to fitness at both the early and late
650 growing season time points. First, temperature acts as a selective agent, by which fitness is reduced
651 according to the deviation between the actual temperature and a genotype's phenotypic temperature
652 optimum. Second, temperature is a source of information that a plant can use to alter its phenotype
653 later in the growing season, and to alter the phenotype of its offspring in the following year. As a
654 result, five classes of plasticity are available to plants in this model in order to best prepare
655 themselves and their progeny for the most likely temperature conditions in the future. These
656 plasticity classes include within-generation plasticity and four classes of transgenerational plasticity
657 representing all permutations of early and late season temperature effects across the parent and
658 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

691 heat capacity than either rock or soil, the location of these land masses downstream of maritime air
692 may predispose them to temperature autocorrelations between years. Additionally, we found highly
693 variable correlations between late growing season temperature and the following generation's early
694 growing season temperature. This result is intriguing because the temperature experienced during
695 seed maturation interacts with the post-dispersal temperature to strongly influence the dormancy
696 and germination behavior of seeds, with cascading effects throughout the life cycles of annual plants
697 (31,70). Consequently, site-specific correlations between maternal late-season temperature and the
698 early-season temperature in the next generation may select for divergent, site-specific effects of
699 maternal temperature on germination for species that set seed in late summer. Intriguingly, parental
700 effects of temperature on germination and flowering time are highly genetically variable in
701 *Arabidopsis thaliana* (12,70,71). In *Plantago lanceolata*, such genotype-by-maternal temperature effects
702 persist throughout the offspring life cycle to generate variation in offspring reproduction in the field
703 (72). Our results suggest that such genetic variation for maternal effects may derive in part from
704 variable selection imposed by differences among sites in intergenerational temperature correlations
705 (see also 12).
706
707 **Common Themes and Future Directions**
708 Although our precipitation and temperature models yielded distinct insights into the
709 dynamics of each of these factors, common themes emerged in both sets of analyses. For example,
710 we found higher levels of inter-annual autocorrelation, and therefore more prominent
711 transgenerational effects, at northern latitudes and along coastal regions within both models. Studies
712 that compare patterns of transgenerational plasticity across such large geographic regions will be
713 necessary to determine whether underlying differences in environmental patterns do in fact drive
714 differences in transgenerational plasticity. Another common finding of both the raw temperature
715 and precipitation models is that transgenerational effects are expected to provide greater benefits in
716 changing climates relative to purely oscillating climates, in which linear climate change has been
717 removed (i.e., the residual models). We also found that populations in regions undergoing the most
718 severe climate change are expected to benefit most by increasing transgenerational plasticity.
719 These results suggest that transgenerational effects may have an important role in adaptation
720 to human-induced climate change, and that rapid climate change should select for more
721 transgenerationally plastic individuals. However, there is an important caveat. In our models we
722 assume that genotypes are uniform in their mean phenotype, and do not allow for mutations that

723 could lead to genetic adaptation to changing conditions. The potential for transgenerational plasticity
724 to either promote or hinder genetic adaptation has been explored (73), but our models do not
725 address this issue. Instead, we set the baseline phenotype of an organism as the optimal phenotype
726 for the average conditions over the 120 years for which we have data, and then compared the fitness
727 of genotypes that vary in their expression of plasticity. In the absence of genetic evolution, it follows
728 that if there is a linear trend towards hotter or drier years in addition to climatic oscillations (as in the
729 raw model variants), then there is more transgenerational information relative to a situation in which
730 only climatic oscillations are occurring (residual model variants). Theory indicates that these
731 dynamics become much more complex when local genetic adaptation to changing conditions is
732 allowed to occur along with transgenerational plasticity (12). For instance, in some scenarios
733 transgenerational effects can increase fitness in the short term, while reducing it in the long term
734 (74). In future studies, it will be critical to investigate the influence of standing genetic variation for
735 transgenerational plasticity on evolutionary trajectories, and to examine the availability of novel
736 mutations that alter the dynamics of transgenerational effects. Answering both of these questions in
737 the same system will be necessary to determine the likelihood that selection on transgenerational
738 plasticity is a viable route to adaptation in the face of changing conditions.
739 Temperature and precipitation autocorrelations and optimal plasticity values likely stem in
740 part from the same broad-scale climatic oscillations, such as the El Niño Southern Oscillation (75),
741 the Quasi-biennial oscillation (76), and the Pacific Decadal Oscillation (77,78). Aside from these
742 climatic oscillations, autocorrelations will arise due simply to "red" or "pink" noise in which rare,
743 large events and common, small events have equal power in explaining variation (79). It has been
744 demonstrated that even without clear underlying phenomena explaining variation, pink-noise is
745 often the model that best explains patterns of ecological and abiotic time-series variation (80). These
746 oscillations and general patterns of red noise will interact with each other to varying degrees across
747 different regions of the US, leading to variable levels of autocorrelation at all lags for both
748 precipitation and temperature.
749 Furthermore, because temperature and precipitation interact to alter moisture availability, it
750 is likely that organisms do not process temperature and precipitation information independently, but
751 rather use them in tandem along with other sources of information to fine tune phenotypes for the
752 most likely future environment. For instance, temperature influences water availability by influencing
753 rates of evaporation and transpiration. Interactions between temperature and water availability also
754 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.

		Raw		Residual	
Climate Term		#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

1046 Figure 1: Schematic depicting the ecological motivations (summer annual plants) and theoretical
1047 underpinnings for the evolutionary modeling of plasticity traits (A and C), and the types of
1048 environmental fluctuations that may influence their evolution. (A) Temperature plasticity model. In
1049 the abbreviations, **E** denotes the Early growing season (spring) and **L** denotes the late growing
1050 season (summer). The first letter represents the relevant season during the parental generation and
1051 the second letter represents the relevant season in the offspring generation (e.g., EL denotes effects
1052 of parental early growing season temperature on offspring phenotypes late in the growing season).
1053 Within generation developmental changes in response to early season environment (W) are also
1054 considered in this model. Additionally, the longterm average environmental conditions at a specific
1055 area determine the genetic baseline phenotype of an individual (G). (B) On the left we see an
1056 example of an environment with high within season autocorrelations for temperature (hot springs
1057 tend to be followed by hot summers), but low inter-annual autocorrelations (a hot year does not
1058 tend to be followed by another hot year) that selects for within generation plasticity but not
1059 transgenerational plasticity. On the right, a situation where spring and summer temperatures are not
1060 correlated with each other, but we do find that environmental oscillations lead to a string of warmer
1061 than average springs and cooler than average summers, in this situation transgenerational plasticity
1062 (EE and LL) but not within generation plasticity is expected to be optimal. (C) Precipitation
1063 plasticity model. The amount of precipitation experienced by an individual can lead to
1064 transgenerational effects in the next generation (T), as well as persist for two (TG) or three (TGG)
1065 generations. (D) On the left, relatively gradual decadal oscillations give value to transgenerational
1066 effects that persist for multiple seasons (T, TG, and TGG). On the right shorter period climatic
1067 oscillations may favor parental effects (T), but not multi-generation effects (TG or TGG).
1068
1069 Figure 2: Maps depicting natural climatic variation across the conterminous US.

1070

1071 Figure 3: Distributions of optimal plasticity (A and B) and temperature (C-G) values across all 4km x
1072 4km sites in the US. Histograms of optimal (A) precipitation transgenerational plasticity value (*T*),
1073 (B) precipitation multi-generation persistence (*G*), (C) temperature spring (early season) -> spring
1074 (early season) transgenerational plasticity (m_{EE}) , (D) temperature spring (early season) -> summer
1075 (late season) transgenerational plasticity (m_{EL}), (E) temperature summer (late season) -> spring(early
1076 season) transgenerational plasticity (m_{LE}), (F) temperature summer (late season) -> summer (late
1077 season) transgenerational plasticity (m_{LL}), and within generation temperature plasticity (*W*)

1078

1079 Figure 4: Maps coded to show patterns of variability for optimal precipitation (A-C) and temperature
1080 (D-H) plasticity values across the US. (A) Optimal transgenerational plasticity values for the one-
1081 generation transmission of precipitation level information. (B) Optimal grandparental
1082 transgenerational plasticity values coded blue (green) or red (orange) based on the direction of effect
1083 (positive or negative). White regions have an optimal multi-generation persistence (G) of 0, while
1084 red and blue both have optimal multigeneration persistence of 1, intermediate values (0>G>1) in
1085 orange and green. (C) The difference between optimal transgenerational plasticity values in the raw
1086 vs. residual variant of the mode. Higher values suggest that the primary value associated with
1087 transgenerational plasticity over the past 120 years has been associated with allowing individuals to
1088 keep up with linearly changing precipitation patterns. (D) Optimal total levels of transgenerational
1089 temperature plasticity ((M_{EE} + M_{EL} + M_{LE} + M_{LL})/2). (E) Optimal transgenerational plasticity of
1090 most extreme positive transgenerational plasticity allele. (F) Optimal transgenerational plasticity of
1091 lowest transgenerational plasticity allele. Regions in orange have at least one form of
1092 transgenerational plasticity for which negative transgenerational effects increase fitness. (G) The
1093 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 chanes 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

1118 years contribute equally. Additionally, positive transgenerational effects were more likely to have

1119 intermediate levels of persistence than negative transgenerational effects.

1120

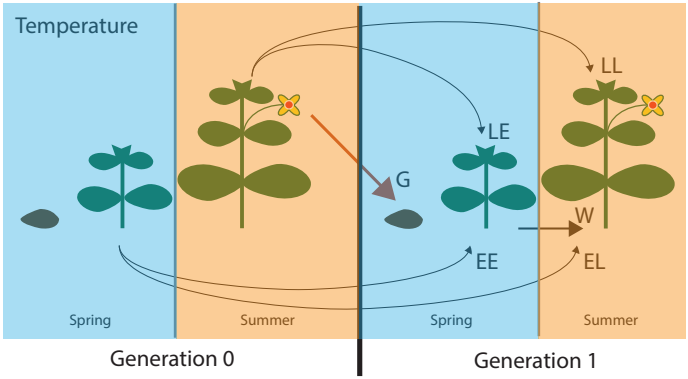
1121 Figure S3: Multi-panel fitness landscape comparing the relative fitness of clonal types with different

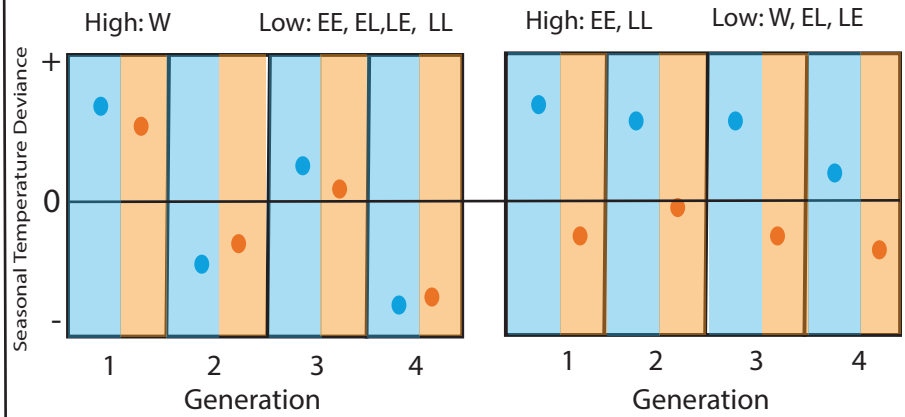
1122 levels of the four transgenerational temperature plasticity terms.

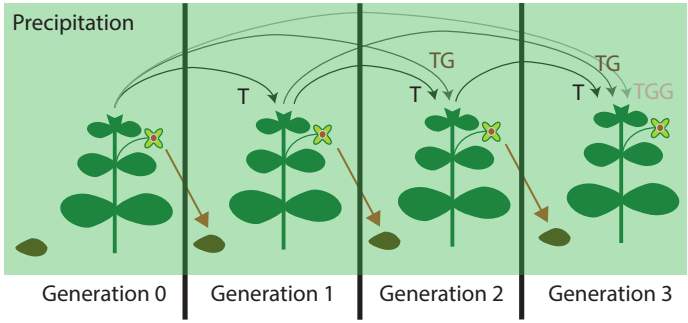
1123

1124

Figure 1


Temperature
LL
LE
G
W
EE
EL
Spring
Summer
Spring
Summer
Generation 0
Generation 1


High: W
Low: EE, EL,LE, LL
High: EE, LL
Low: W, EL, LE
Seasonal Temperature Deviance
+
0
-
1
2
3
4
Generation
1
2
3
4
Generation


Precipitation
T
TG
T
TG
T
TGG
Generation 0
Generation 1
Generation 2
Generation 3

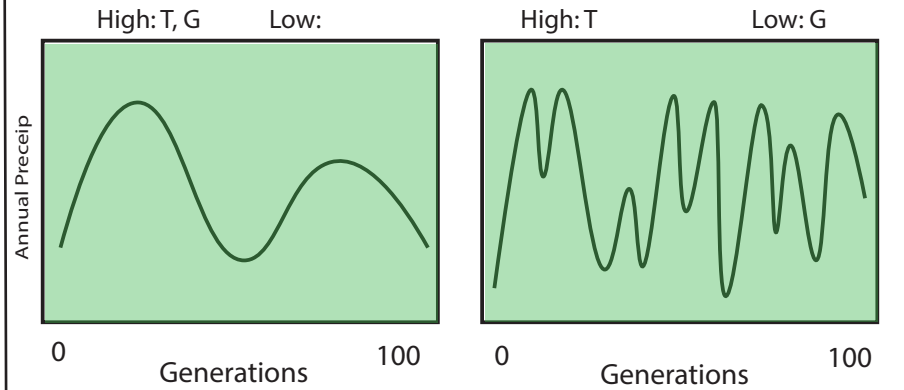

High: T, G
Low:
High: T
Low: G
Annual Preceip
0
Generations
100
0
Generations
100

Figure 2

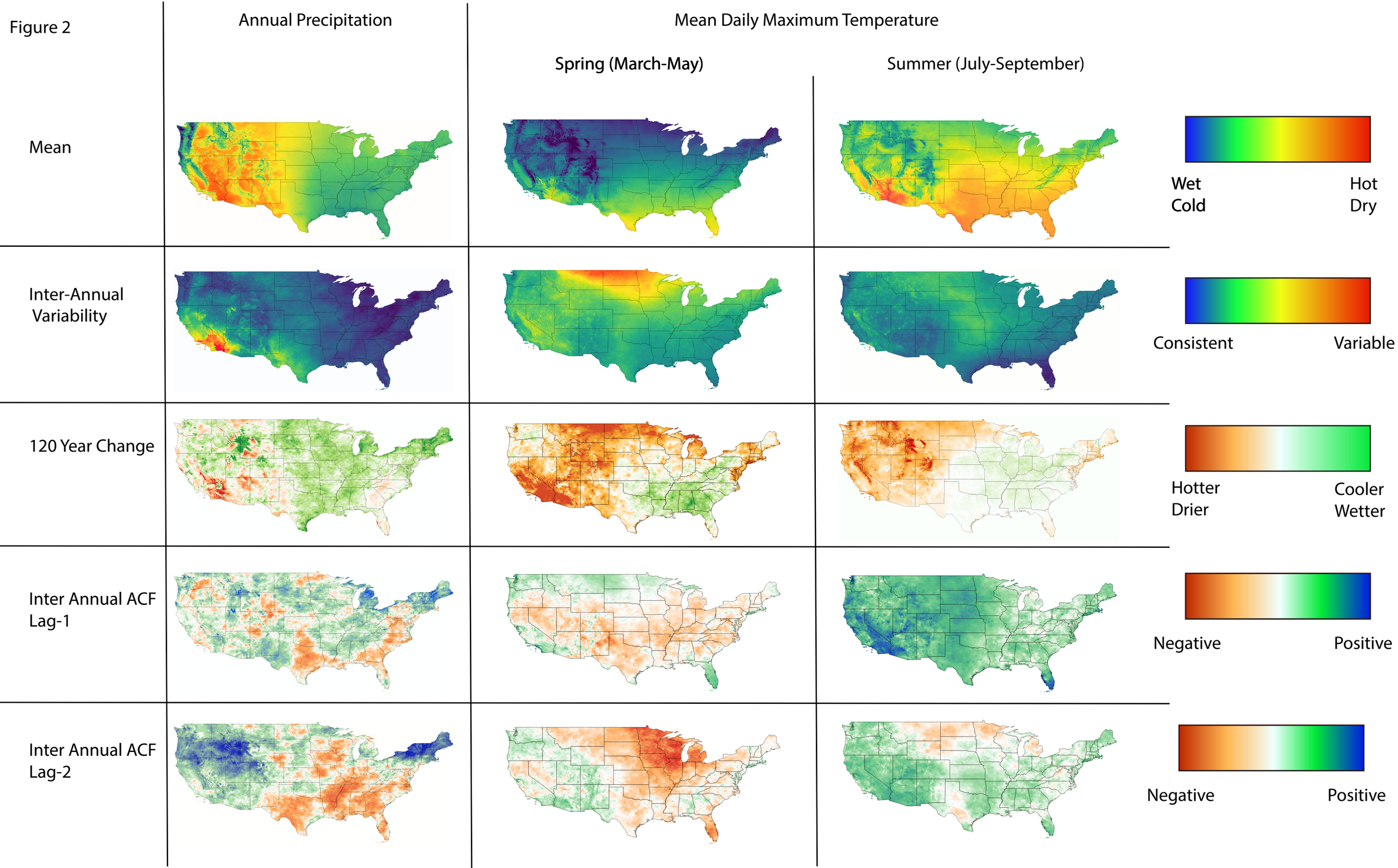
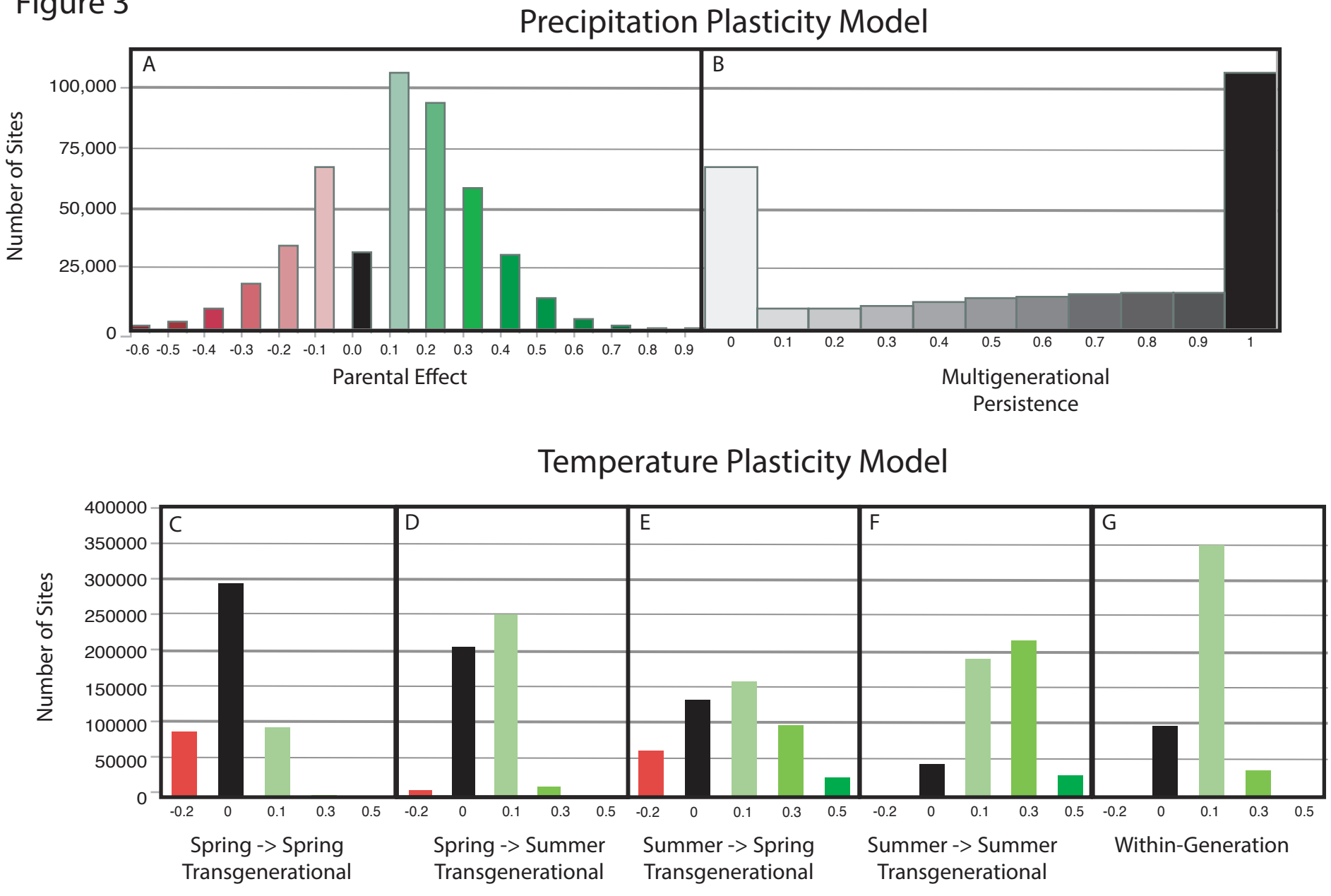
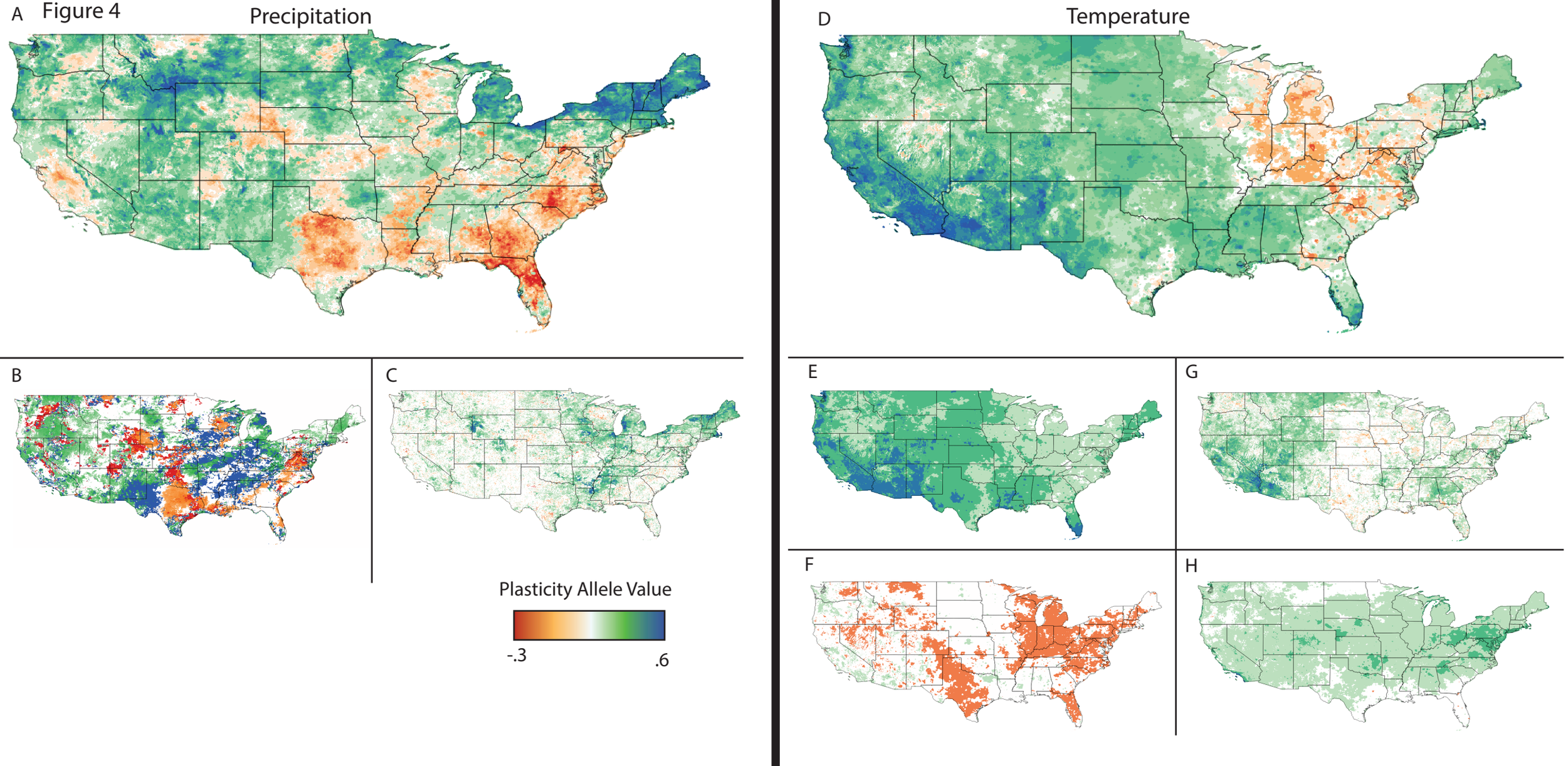

Annual Precipitation
Mean Daily Maximum Temperature
Spring (March-May)
Summer (July-September)
Mean
Wet
Cold
Hot
Dry
Inter-Annual Variability
Consistent
Variable
120 Year Change
Hotter
Drier
Cooler
Wetter
Inter Annual ACF Lag-1
Negative
Positive
Inter Annual ACF Lag-2
Negative
Positive

Figure 3


Precipitation Plasticity Model
A
B
Number of Sites
100,000
75,000
50,000
25,000
0
-0.6 -0.5 -0.4 -0.3 -0.2 -0.1 0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9
Parental Effect
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
Multigenerational Persistence
Temperature Plasticity Model
C
D
E
F
G
Number of Sites
400000
350000
300000
250000
200000
150000
100000
50000
0
-0.2 0 0.1 0.3 0.5
Spring -> Spring Transgenerational
Spring -> Summer Transgenerational
Summer -> Spring Transgenerational
Summer -> Summer Transgenerational
Within-Generation


A
Figure 4
Precipitation
D
Temperature
B
C
E
G
F
H
Plasticity Allele Value
-.3
.6

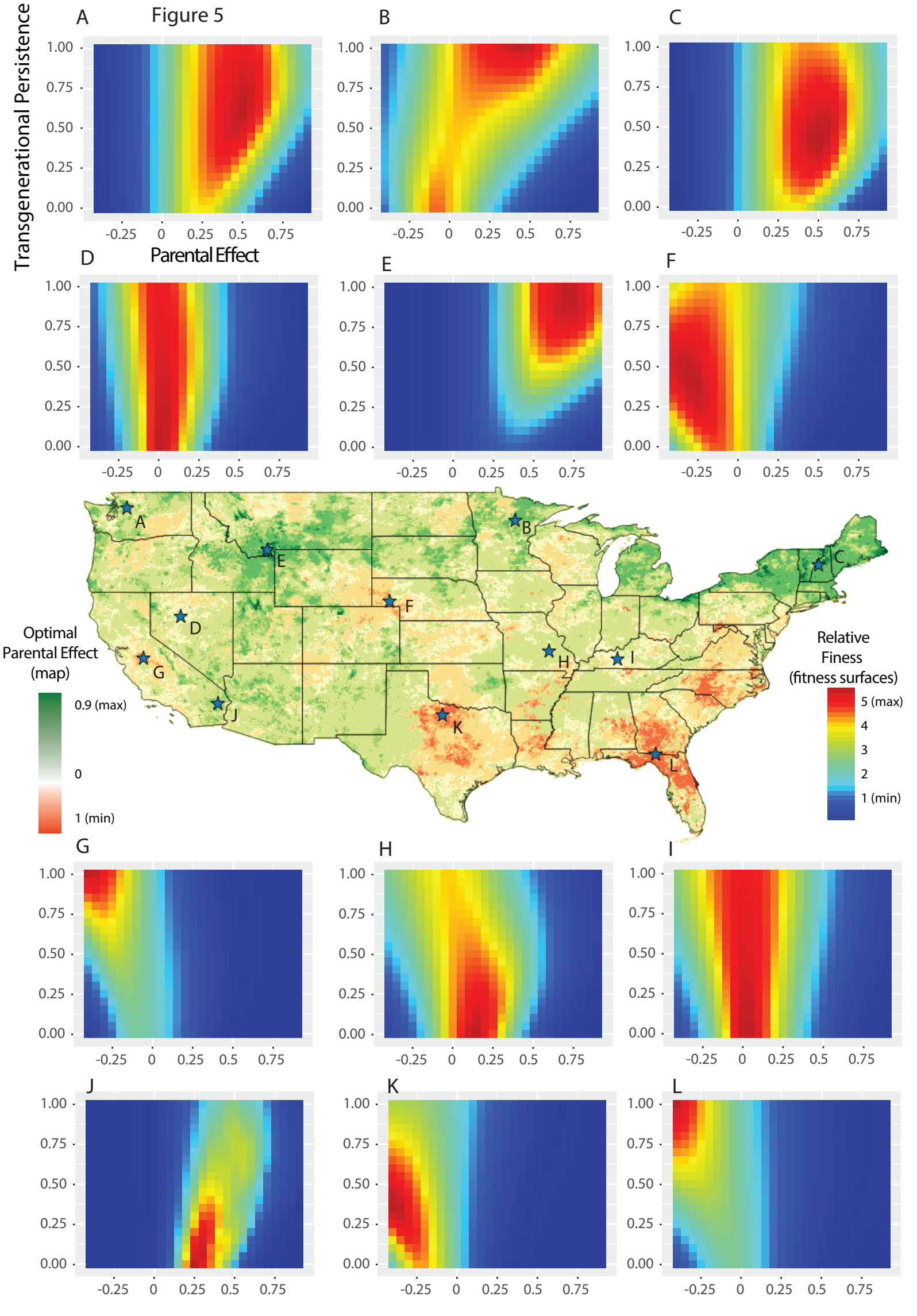


Figure 5
Transgenerational Persistence
Parental Effect
A
B
C
D
E
F
G
H
I
J
K
L
1.00
0.75
0.50
0.25
0.00
-0.25
0
0.25
0.5
0.75
Optimal Parental Effect (map)
0.9 (max)
0
1 (min)
Relative Finess (fitness surfaces)
5 (max)
4
3
2
1 (min)

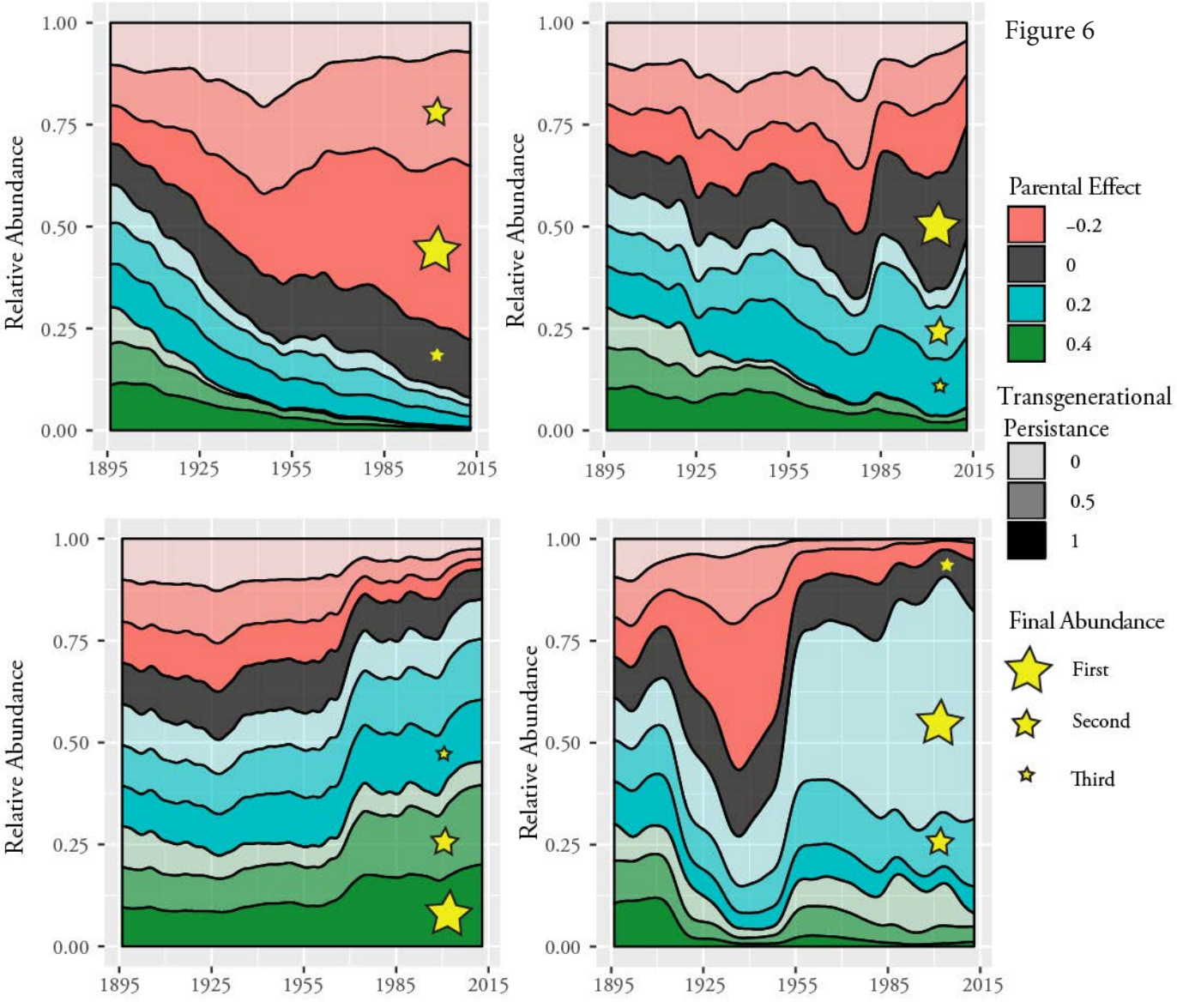


Figure 6
Relative Abundance
1.00
0.75
0.50
0.25
0.00
1895
1925
1955
1985
2015
Parental Effect
−0.2
0
0.2
0.4
Transgenerational Persistance
0
0.5
1
Final Abundance
First
Second
Third

Figure S1

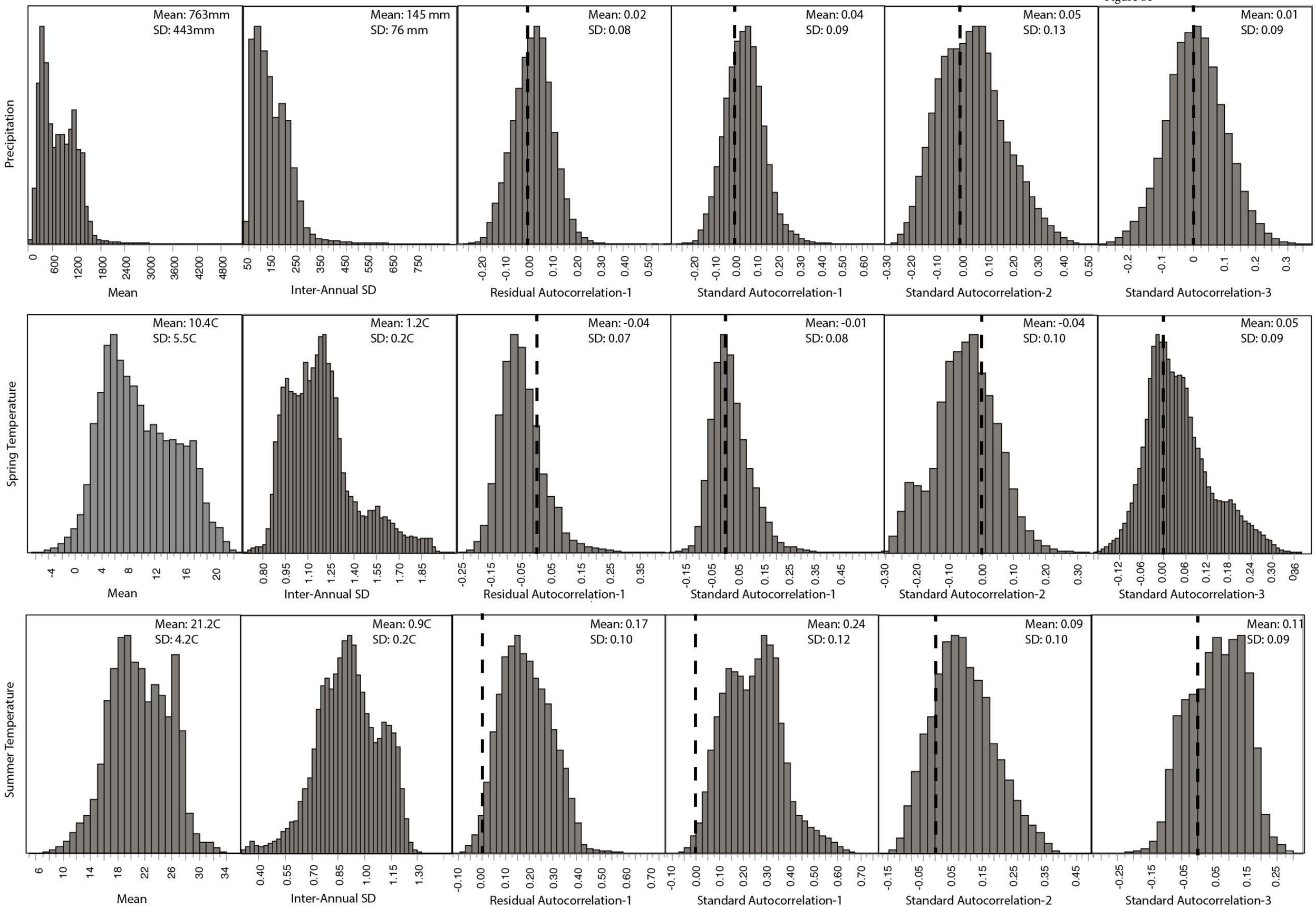
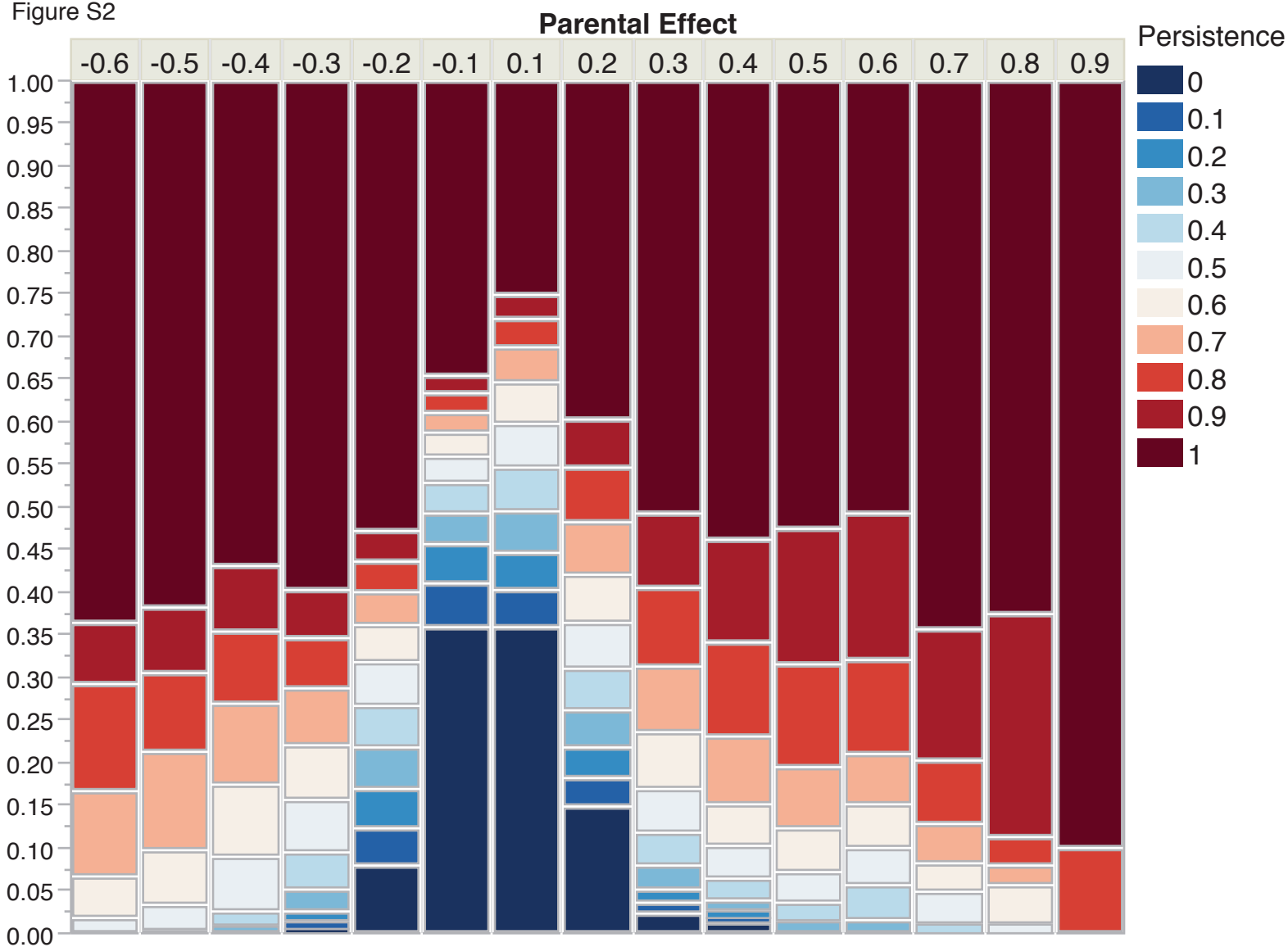
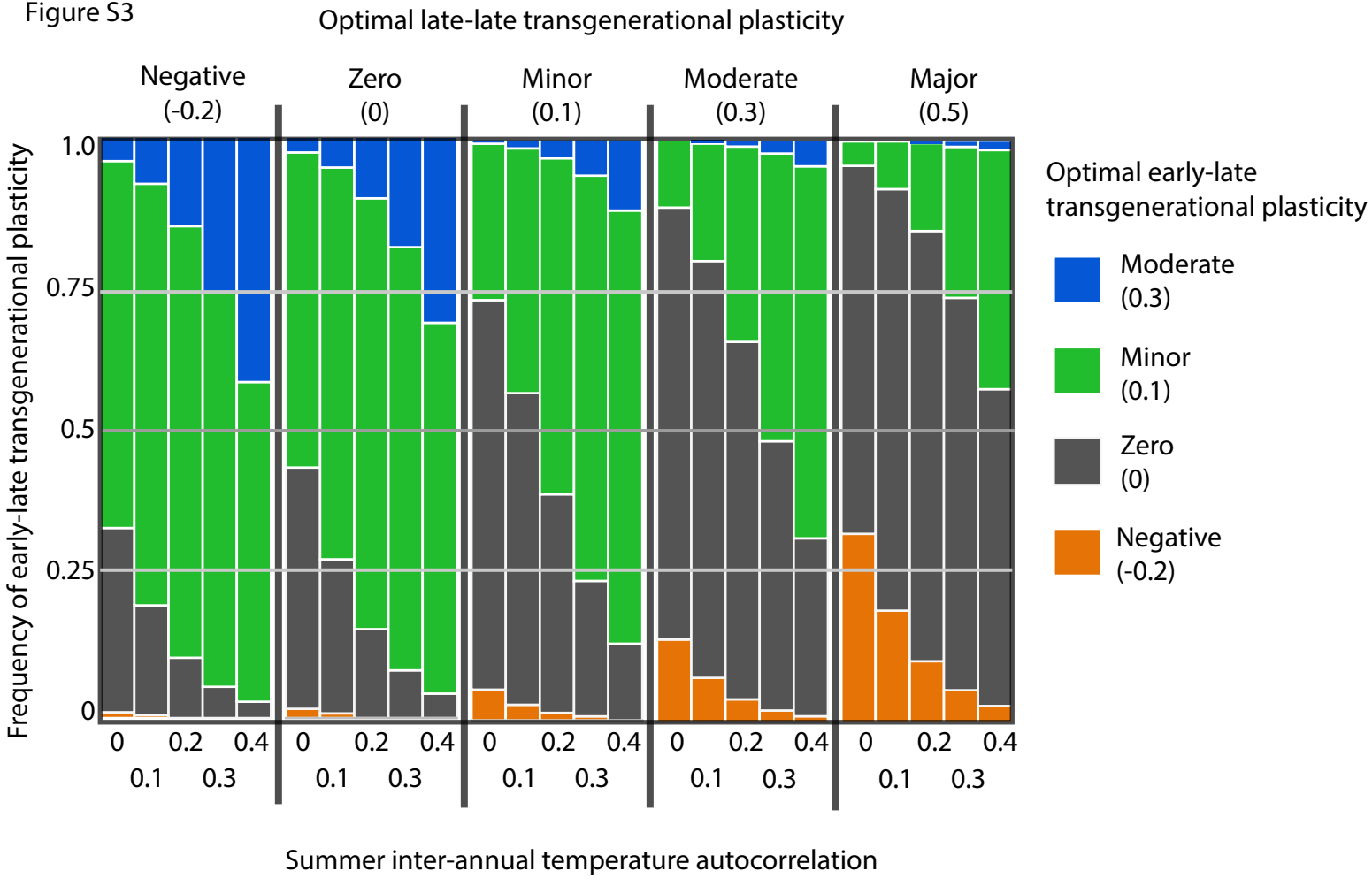

Precipitation
Mean: 763mm
SD: 443mm
Mean
Mean: 145 mm
SD: 76 mm
Inter-Annual SD
Mean: 0.02
SD: 0.08
Residual Autocorrelation-1
Mean: 0.04
SD: 0.09
Standard Autocorrelation-1
Mean: 0.05
SD: 0.13
Standard Autocorrelation-2
Mean: 0.01
SD: 0.09
Standard Autocorrelation-3
Spring Temperature
Mean: 10.4C
SD: 5.5C
Mean
Mean: 1.2C
SD: 0.2C
Inter-Annual SD
Mean: -0.04
SD: 0.07
Residual Autocorrelation-1
Mean: -0.01
SD: 0.08
Standard Autocorrelation-1
Mean: -0.04
SD: 0.10
Standard Autocorrelation-2
Mean: 0.05
SD: 0.09
Standard Autocorrelation-3
Summer Temperature
Mean: 21.2C
SD: 4.2C
Mean
Mean: 0.9C
SD: 0.2C
Inter-Annual SD
Mean: 0.17
SD: 0.10
Residual Autocorrelation-1
Mean: 0.24
SD: 0.12
Standard Autocorrelation-1
Mean: 0.09
SD: 0.10
Standard Autocorrelation-2
Mean: 0.11
SD: 0.09
Standard Autocorrelation-3

Figure S2


Parental Effect
-0.6
-0.5
-0.4
-0.3
-0.2
-0.1
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.60
0.55
0.50
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
Persistence
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1

A Figure S3


Optimal late-late transgenerational plasticity
Negative (-0.2)
Zero (0)
Minor (0.1)
Moderate (0.3)
Major (0.5)
Frequency of early-late transgenerational plasticity
1.0
0.75
0.5
0.25
0
0 0.2 0.4
0.1 0.3
Summer inter-annual temperature autocorrelation
Optimal early-late transgenerational plasticity
Moderate (0.3)
Minor (0.1)
Zero (0)
Negative (-0.2)

B

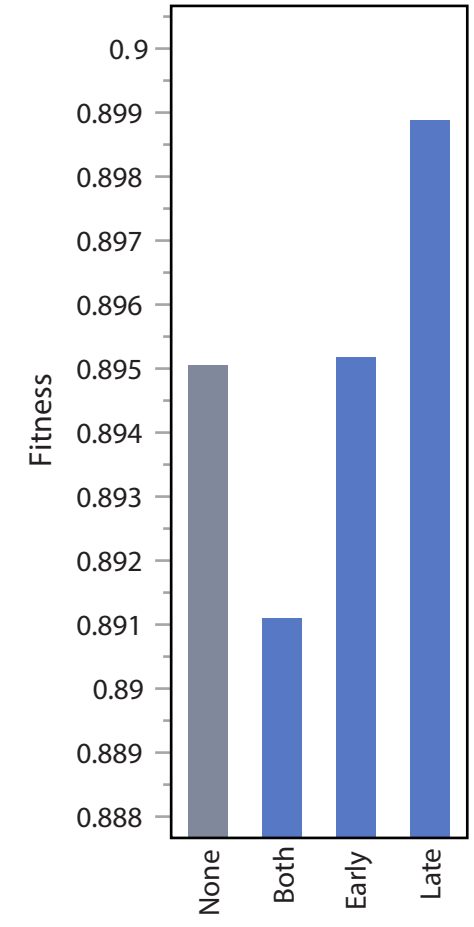
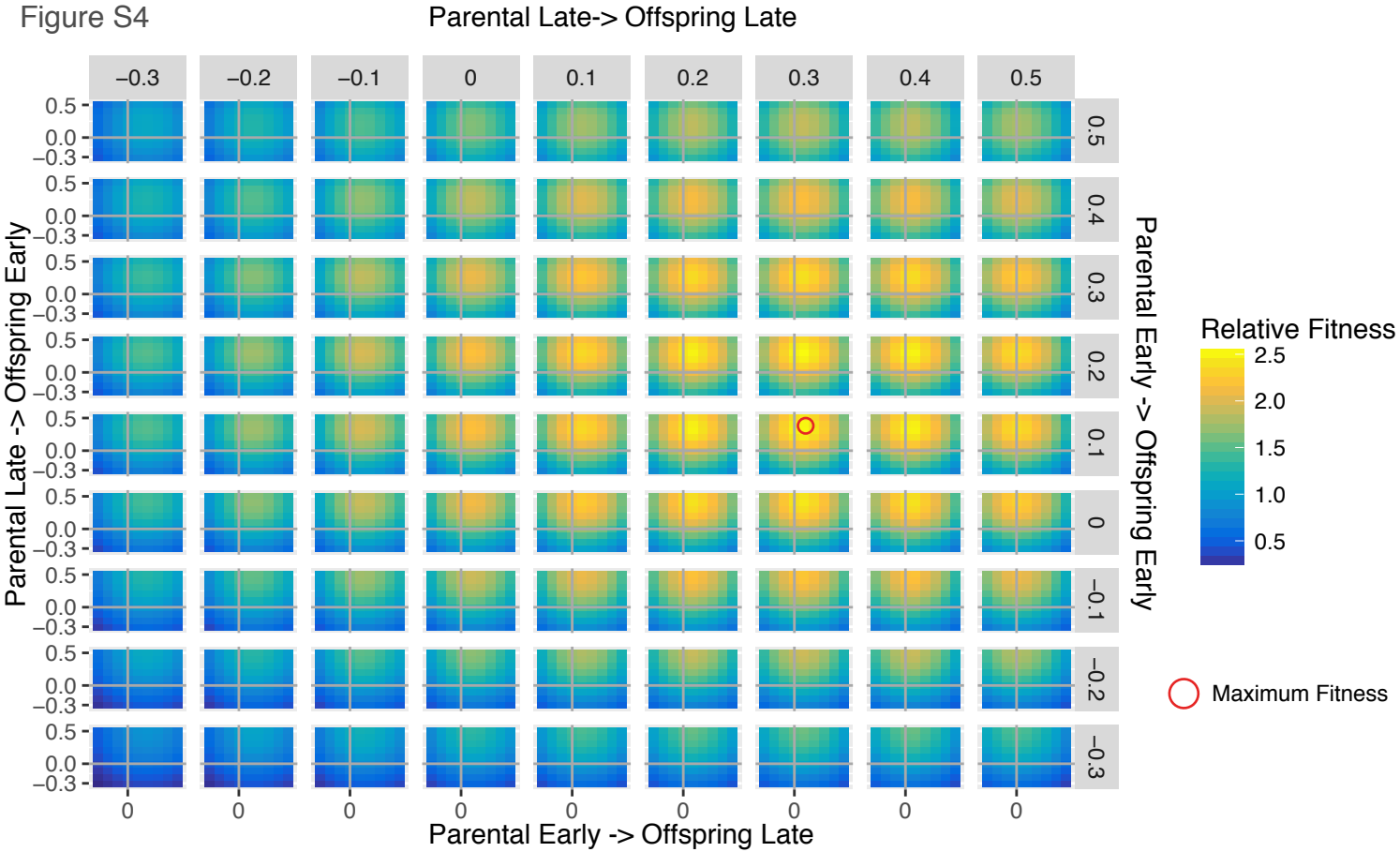

Fitness
0.9
0.899
0.898
0.897
0.896
0.895
0.894
0.893
0.892
0.891
0.89
0.889
0.888
None
Both
Early
Late

Figure S4


Parental Late-> Offspring Late
−0.3
−0.2
−0.1
0
0.1
0.2
0.3
0.4
0.5
Parental Early -> Offspring Early
Parental Late -> Offspring Early
Parental Early -> Offspring Late
Relative Fitness
2.5
2.0
1.5
1.0
0.5
Maximum Fitness