Environmental oscillations favor the evolution of adaptive transgenerational plasticity

Keywords: Transgenerational plasticity, epigenetics, local adaptation

Classification

Major: Biological Sciences

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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.

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 (Fisher 1930). 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 (Ghalambor et al. 2007; Nicotra et al. 2010). Over the last three decades, it has become clear that *transgenerational plasticity* is also remarkably common (reviewed by (Mousseau and Fox 1998; Uller 2008; Bonduriansky and Day 2009; Holeski et al. 2012; Conrath et al. 2015; Sultan 2015), yet highly variable (Herman and Sultan 2016; Colicchio 2017; Groot et al. 2017) and nearly absent in some cases (Ganguly et al. 2017). 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 (these mechanisms are not mutually exclusive; (Herman and Sultan 2011; Jablonka 2013). 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, Conrath et al. 2015), and more generally parental *x* current environment interaction effects appear prevalent (Herman and Sultan 2016; Colicchio 2017; Sultan et al. 2009; Galloway et al. 2009). 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 (English et al. 2015).

97 One of the major findings of these studies has been that natural selection should favor
98 specific forms of within- and transgenerational plasticity depending on the precise patterns of
99 environmental variation experienced by a population (Shea et al. 2011; Sultan and Spencer 2002).
100 For instance, within-generation adaptive plasticity is expected to evolve when individuals encounter
101 variable conditions during their lives, there is little to no cost of responding to environmental cues,
102 and there is genetic variation for individual phenotypic responses to the environment (Tufto 2015;
103 reviewed by Scheiner 1993; Schlichting and Pigliucci 1998). These same factors also influence the
104 evolution of transgenerational plasticity (Lachmann and Jablonka 1996; Räsänen and Kruuk 2007;
105 Kuijper et al. 2014; Prizak et al. 2014; Leimar and McNamara 2015). First, environments must vary
106 across generations, either due to temporal change in environmental states at the same site, or by
107 offspring dispersal across spatially heterogeneous environments. Second, the environments
108 experienced by parents must predict the selective environments that offspring experience. This
109 scenario occurs when parental and offspring environments are correlated. Third, there must be
110 genetic variation for transgenerational plasticity, that is to say, genotype-by-parental environment
111 variation. This form of genetic variation appears to be common (Herman and Sultan 2016, Schmitt
112 et al. 1992; Sultan 1996; Stjernman and Little 2011; Alsdurf et al. 2013).
113 From a more practical perspective, the ability of natural and agricultural populations to
114 transmit environmental information transgenerationally will determine their ability to persist in the
115 face of a rapidly fluctuating and changing environments, and thus profoundly influence the health
116 and productivity of our planet as climate change proceeds. While anthropogenic climate change
117 differs greatly from natural climatic oscillations, both elevate the value of information from the prior
118 generation relative to the long-term average conditions at a site, and thus transgenerational plasticity
119 that has evolved in response to environmental oscillations may provide fitness benefits under
120 climate change. On the other hand, climate change is expected to increase environmental variation,
121 including more extreme weather events, potentially decreasing the relative fitness of organisms that
122 may have evolved transgenerational plasticity to cope with previously reliable patterns.
123 Empirical investigations in diverse plant and animal systems have confirmed that
124 transgenerational environmental effects can be adaptive when parent and progeny environments
125 match (i.e., under positive intergenerational environmental autocorrelations; see e.g., Bilichak et al.
126 2012; Herman et al. 2012; Rasmann et al. 2012; Slaughter et al. 2012; Verhoeven and van Gurp 2012;
127 Dantzer et al. 2013; Lopez Sanchez et al. 2016; Walsh et al. 2016; Wibowo et al. 2016). For instance,
128 when *Mimulus guttatus* plants experience herbivory, their offspring increase production of defensive

129 leaf trichomes (Holeski 2007; Colicchio et al. 2015; Colicchio 2017). Similarly, when the aquatic
130 crustacean *Daphnia cuculatta* is exposed to predator cues, it produces offspring with a defensive
131 'helmet' that protects against predation by midge larvae and cladocerans (Agrawal et al. 1999).
132 Despite this surge of interest, to date no study has examined long-term environmental data
133 for the presence of inter-generational environmental correlations that are expected to favor the
134 adaptive evolution of transgenerational plasticity. Although we tend to think about how the average
135 environmental conditions differ across a landscape, there is no reason to expect that the scale and
136 predictability of environmental variation is any less complex or ubiquitous across a landscape. Here
137 we identify *spatial variation* in the *temporal predictability* of environmental variation, and leverage this
138 variation to compare the adaptive value of within-generation plasticity, transgenerational plasticity,
139 and multigenerational epigenetic inheritance across different local regimes of climate variability. We
140 utilize 120 years of fine-scale (4km^2) climate data spanning the coterminous U.S. to test for auto- and
141 cross-correlations in temperature and precipitation levels across years, and find many significant
142 correlations that vary widely in both magnitude and direction across the US. We then construct
143 separate models for temperature and precipitation to determine the degree of transgenerational
144 plasticity that would maximize fitness in each of these sites across the U.S. with respect to the
145 observed environmental measurements. Additionally, by running each model using raw
146 environmental data and the residuals after factoring out the effects of directional climate change we
147 were able to inspect how climate change alters the benefits associated with transgenerational
148 plasticity. These models were constructed with summer annual plants in mind, but are generalizable
149 to other organisms with generation times of one year.
150 In our precipitation model, we examine transgenerational effects that persist for up to three
151 generations (Figure 1a), as multiple experimental studies have found that environmentally induced
152 epigenetic and phenotypic effects can persist for at least this long (e.g., Whittle et al. 2009;
153 Akkerman et al. 2016), and in some cases for far longer (Vastenhouw et al. 20026; Rechavi et al.
154 2011). In our temperature model (Figure 1b), we also determine the degree of within-generation
155 plasticity that would maximize fitness, in response to both early and late-season temperatures. With
156 different genotypes producing their phenotypes based on different weightings of within generation
157 plasticity, transgenerational plasticity, multi-generation epigenetic inheritance, and genetic
158 inheritance, we find that across the US there is extraordinary variation in the optimal ratio of how
159 these various classes of information should inform an individual's phenotype. These findings imply
160 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 (Quantum GIS geographic information system 2012), 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

193 over the 120 years at a site), transgenerational plasticity, or within generation plasticity (only in
194 temperature model) to come up with an expected environment that it will face. This expected
195 environmental value is equivalent to a phenotype, and the closer this phenotype is to the actual
196 environment experienced, the higher the fitness that genotype will have for a given generation.
197 While this framework is identical for precipitation and temperature modeling, inherent
198 differences in precipitation and temperature variables lead to us considering a different set of
199 parameters for each variable, allowing us to ask related but unique questions regarding
200 transgenerational inheritance. Precipitation can accumulate as snowpack, bodies of water, or soil
201 moisture, such that the cumulative precipitation over the course of the water year will determine to a
202 large extent the amount of water available to a plant. On the other hand, the effects of temperature
203 are much more immediate and transient, such that a particularly cold spring will not "keep the plant
204 cool" over the summer, in the way that a particularly wet spring could provide moisture during a
205 summer of drought. For this reason, we decided to extend our temperature models to compare
206 patterns across different segments of the growing season, and different forms of plasticity both
207 within and between a single generation. For precipitation we only considered annual hydrologic year
208 precipitation without breaking it down by seasons, but did consider the possibility of multi-
209 generation persistence of transgenerational plasticity.
210 For a given genotype, the absolute distance between the expected and actual environment at
211 a given time imposes a linear cost on fitness. If the expected and actual environment in a given
212 generation are identical, that genotype's fitness will equal 1, and as the difference increases, fitness
213 will drop down to a minimum value of 0.2. This minimum value was put in place to prevent a single
214 year with extremely low fitness from dominating final genotype frequencies, but was only used in
215 under 0.01% of fitness measurements. After every generation, there is a round of competition,
216 where the frequency of a given genotype will change based on the relative fitness of that genotype
217 compared to the mean phenotype for that year. This scenario is equivalent to an infinite population
218 size evolutionary model in which the relative frequency of genotypes changes due to selection and
219 reproduction once per year.
220 For each locale, mean annual precipitation (or temperature) across the 120 years $(\bar{P})$ is
221 calculated, and this statistic is used as the baseline phenotype of all genotypes in the raw data variant
222 of the model. Additionally, a linear regression of precipitation on year was fit for each site over the
223 120 years considered, and residuals were calculated for every year. In the residual variant of this
224 formula, the expected values are 0, and residuals are used as the precipitation values for each year. A

225 description of the models developed can be found in Appendix 1, and code can be found at
226 github.com/XXXX.
227
228 **Results**
229 Both mean annual precipitation and growing season temperatures vary immensely across the
230 US (Figure 2 and S1), but for the evolution of locally adaptive phenotypic plasticity, it is the patterns
231 of variation that are more relevant. The standard deviation of a site's annual precipitation and
232 growing season temperatures over the past 120 years also varied dramatically (Table 1 and S1), with
233 precipitation inter-annual standard deviation (IASD) varying from 40mm to 800m, spring
234 temperature IASD from 0.77C to 1.95C, and summer temperature IASD from 0.35C to 1.32C
235 (Figure 2 and S1 and Table S1). The southwest US generally had the highest precipitation IASD
236 relative to its mean precipitation, with IASD being nearly equal to the mean precipitation in some
237 regions (Figure 2). Interestingly, spring temperature IASD was significantly higher than summer
238 temperature IASD across the US. This pattern was largely driven by extremely high spring
239 temperature IASD over the north central US (Figure 2), and consistently low summer temperature
240 IASDs across much of the coastal US.
241 Directional climate change over the past 120 years was prevalent and variable across the US
242 (Figure 2). Mean annual precipitation has declined over much of the Sierra Nevada mountain range,
243 southern California, and other scattered regions over the last 120 years, while precipitation levels
244 have increased in the Midwestern and much of the northeastern US. Both spring and summer
245 temperatures have gotten substantially higher with the exception of the southeast, where spring
246 temperatures have decreased and summer temperatures have changed little (Figure 2). This
247 phenomenon has been noted numerous times (Knappenberger et al. 2001; Ellenburg et al. 2016) and
248 seems to be largely due to a switch from cropland to natural forest ecosystems across the
249 southeastern US during the past 120 years that has led to greater transpiration cooling. \
250 Although a variable environment is necessary for the evolution of adaptive phenotypic
251 plasticity, it is the patterns of this variation that influence which forms of plasticity will be favored.
252 We examined these patterns by calculating autocorrelations in annual temperature and precipitation
253 levels between successive years, and found that their magnitude and directions were highly variable
254 across the US (Figure 2 and S1, Table 1 and S1).
255 Averaged across all sites, the precipitation autocorrelation (AC) at lag-1 (i.e., the correlation
256 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 were many more sites with moderately positive (62,693: lag-2 PACF > 0.2, vs. 21,671: lag-1 ACF >0.2) and negative (5,088 lag-2 PACF <-0.2 vs. 441 lag-1 ACF <-0.2) lag-2 partial autocorrelation (PAC) than lag-1 ACF. This 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 inter-annual precipitation variation (Figure 2).

Patterns of temperature autocorrelations extended over larger regions, and were often more extreme than the 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). 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 dramatic variability of precipitation autocorrelations across the US leads to a great deal of variation in the optimal levels of plasticity in our evolutionary models (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, see Appendix 1) 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. 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, Appendix 1) 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 on average 0.057 lower in the residual variant of the model compared to the raw 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, Appendix 1) 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; 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 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

351 of early season temperature on the next generation's late season phenotype (m_{EL}) was most often
352 minor (0.1) in both raw (251,691) and residual (229,301) variants. When considering the combined
353 plasticity value profile of a site, we find the most common combination of plasticity values is, EE:
354 none (0), EL: minor (0.1), LE: minor (0.1), LL: moderate (0.3), WP: minor (0.1) (Table 2b).
355 Summing the four transgenerational plasticity alleles together we find the southwest US has the
356 highest optimal values of transgenerational plasticity, while the Great Lakes region has the lowest
357 optimal values (Figure 4d). Texas and Florida tend to have the greatest variability for
358 transgenerational plasticity values, with many areas within these regions having both positive and
359 negative transgenerational values leading to intermediate total transgenerational plasticity (Figures 4e
360 and 4h). Optimal total transgenerational plasticity values were on average 0.146 (+/- 0.21) higher in
361 the raw relative to the residual models (although the most common change was 0). In the
362 southwestern US, where temperature increased the most over the past 120 years (Figure 2), the
363 difference between the raw and residual model was the greatest (Figure 4g).
364 Variation in different classes of temperature autocorrelations between seasons explains a
365 large portion of the variation in the optimal transgenerational response to temperature at a given
366 site. For example, the autocorrelation between early season growing temperature and the next year's
367 late season growing temperature is the factor that explains the largest amount of variation in optimal
368 levels of m_{EL} (Table 3). We assessed potential tradeoffs between different forms of
369 transgenerational plasticity to temperature by first calculating the residuals of a particular plasticity
370 term after accounting for the effects of environmental autocorrelations, then testing the effect of the
371 other four plasticity terms on these residuals. There was a highly significant negative association
372 between m_{LE} and m_{EE} plasticity, and between m_{LL} and m_{EL} plasticity (Figure S3a). As higher levels
373 of late-late transgenerational plasticity were favored, the optimal levels of EL plasticity also
374 decreased across all environmental autocorrelation values. These associations suggest that, for a
375 given life history stage in this model, there are tradeoffs between using transgenerational information
376 from the previous generation's early vs. late season temperature (Table S2). For example, there are
377 many sites where no plasticity, m_{EE} plasticity, and m_{LE} plasticity all have higher fitness than
378 individuals exhibiting both m_{EE} and m_{LE} plasticity (Figure S3b).
379
380 *Fitness Landscapes*
381 In the previous analyses we used restricted parameter space to identify optimal site-specific
382 combinations of plasticity values across the entire contiguous U.S., but further insight can be gained

383 by comparing fitness landscapes across the full parameter space at individual sites. In the
384 precipitation model we found that, among sites where fitness optima are located near zero
385 transgenerational effects, a vertical fitness ridge formed that was centered near parental effect values
386 of zero. This result is due to transgenerational persistence levels (y-axis) having a minimal impact on
387 phenotype when parental effects are marginal. As absolute optimal parental effect values increased,
388 however, the fitness landscape shifted from a ridge to a peak, with certain values of
389 transgenerational persistence imparting extreme fitness advantages over others (Figure 5). Site B
390 (North Central Minnesota) exemplifies a unique and unexpected outcome of this model: under
391 certain conditions, there can be multiple local fitness maxima with divergent levels of
392 transgenerational plasticity (Figure 5). Two fitness maxima exist at this site, one in which the optimal
393 strategy comprises slightly negative parental effect values with no multigenerational persistence, and
394 a second in which the optimal strategy comprises slightly to moderately positive parental effect
395 values with high levels of multigenerational persistence. This situation occurs when two conditions
396 hold: the lag-1 autocorrelation is in a different direction than the average of the lag-2 and lag-3
397 autocorrelations, and the absolute value of the lag-1 autocorrelation is less than the average of the
398 lag-2 and lag-3 autocorrelations. In these cases, plasticity in the opposite direction of the previous
399 generation, or in the same direction as the average environment of the past three generations, would
400 be adaptive. This scenario occurs in approximately 90k out of the 480k sites, but only in 30k sites are
401 lag-2 and lag-3 average values greater than 0.1 and therefore likely to show up as bimodal peaks in
402 our model. Over the course of the 120 year simulation, the frequency of plasticity genotypes
403 fluctuated somewhat dramatically, suggesting that the interactions between climatic oscillations and
404 other effects might have favored positive plasticity values over some decades, and negative in the
405 next (Figure S4)
406
407 **Discussion**
408 Although transgenerational environmental effects on phenotypic expression have been
409 recognized for decades (Falconer 1981; Roach and Wulff 1987), interest in these effects has surged
410 recently due to increased appreciation for the potential role of transgenerational plasticity in
411 adaptation (Donelson et al. 2018). Despite this renewed interest, a critical question has remained
412 unanswered: do natural patterns of environmental variation favor the adaptive evolution of
413 transgenerational plasticity? Our analysis of 120 years of climatic data from the continental U.S.
414 revealed that such patterns are indeed widespread. Specifically, we analyzed how inter-annual

415 variation in precipitation and temperature impacts the optimal mode of adaptation for clonally
416 reproducing organisms with a life cycle meant to mimic that of an annual plant. When there are
417 correlations between the parental and offspring environments, neither traditional genetic selection
418 nor within-generation plasticity take full advantage of the available information inherent in the
419 environment. Instead, under such correlations selection should favor the genetic evolution of
420 mechanisms that transmit plastic responses from one generation to the next. Absent such
421 correlations, the information provided by the parental environment may not be relevant to
422 offspring, and indeed may prove to be maladaptive (reviewed by Herman et al. 2014).
423 Our modeling results revealed that the vast majority of sites in the contiguous US
424 experienced autocorrelations in precipitation and temperature that should favor the evolution of
425 adaptive transgenerational plasticity. As predicted by other models, the predictability of an
426 environmental variable based on its autocorrelation or its association with other environmental
427 variables is a major factor driving the optimal level of plasticity (e.g., Groot et al. 2017; English et al.
428 2015; Sultan and Spencer 2002; Scheiner 2016). Furthermore, we find that the strength and direction
429 of autocorrelations in precipitation and temperature varied substantially across the U.S., and
430 consequently, the optimal levels of plasticity were also highly variable. Although both precipitation
431 and temperature interact to shape the moisture availability and rates of transpiration for a plant, here
432 we consider these terms separately. Future studies considering temperature and precipitation in
433 tandem should shed new light into the transmission of more complex environmental information.
434
435 *Precipitation*
436 Local adaptation to variable water regimes has been a major focus of plant evolutionary
437 ecology for many years. This research shows that plants have evolved a wide range of physiological,
438 phenological, and morphological adaptations to handle site-specific patterns of water availability
439 (Kooyers 2015). These adaptive phenotypes may be expressed constitutively or may be induced by
440 an environmental cue that predicts a change in water availability later in the life of the organism.
441 Increasingly, experimental studies show that the parental soil moisture regime can also adaptively
442 influence the development of progeny (e.g., Alsdurf et al. 2013; Alsdurf et al. 2015), providing a
443 third route by which plants can fine tune the phenotypes of their offspring to local soil-moisture
444 levels. For instance, in Massachusetts genotypes of the annual plant *Polygonum persicaria*, offspring of
445 drought-stressed parents make more extensive root systems and deploy them faster in response to
446 drought as compared to offspring of well-watered parents. This drought-induced change in growth

447 and development can be inherited for at least two generations, resulting in increased survival of
448 grandoffspring under severe drought stress (Sultan et al 2009; Herman et al. 2012). Furthermore,
449 these epigenetic effects of drought are genetically variable in *P. persicaria*: some genotypes strongly
450 increase root length and biomass in response to parental drought, while other genotypes do so only
451 moderately or not at all (Herman and Sultan 2011).

452 Our analysis revealed substantial and spatially variable interannual autocorrelations in
453 precipitation, indicating that precipitation levels in one year are often predictive of precipitation
454 levels up to three years later. For example, across the coterminous U.S., lag-1 interannual
455 precipitation autocorrelations varied from moderately negative (-0.27) to strongly positive (0.69),
456 including some values near zero. In turn, the optimal direction and strength of transgenerational
457 effects of precipitation also varied. Positive parental effects, wherein individuals are developmentally
458 predisposed to perform better in environments that match their parents' environment, were optimal
459 across more than twice as many regions (65% of sites) as negative transgenerational effects (28% of
460 sites), wherein individuals perform better in a different environment than their parents. Relatively
461 strong parental effect values of 0.3 or higher were optimal in nearly 30% of sites. By contrast,
462 complete absence of parental effects was favored in only 7% of sites.

463 Multigenerational persistence values of 0 (18.7% of sites) and 1 (40.7% of sites) were most
464 common, representing strategies in which transgenerational effects lasted only a single generation or
465 persisted fully to the third generation, respectively. The remaining persistence values were somewhat
466 evenly distributed between 0 and 1 and represent strategies in which environmental information gets
467 passed through three generations, but the environment of more recent years is weighted more
468 heavily.

469 The optimal level of transgenerational effects varied on multiple scales. On the largest scale,
470 we found that the western and northern US experience conditions that select for the highest levels
471 of transgenerational plasticity (Figure 4a). There was a striking contrast between the northeast,
472 where positive transgenerational plasticity was generally optimal, and the southeast, where negative
473 transgenerational plasticity predominated. These large-scale differences in plasticity levels stemmed
474 from substantial differences in precipitation autocorrelations between these regions. There was also
475 considerable variation in optimal levels of transgenerational plasticity on much finer scales. In some
476 cases, optimal levels of transgenerational plasticity were highly divergent between adjacent sites (e.g.,
477 in central Texas and Minnesota). Furthermore, some sites had bimodal fitness landscapes, in which
478 genotypes that express either positive or negative transgenerational effects were favored over

479 genotypes that do not express plasticity (Figure 5b). For example, after a wetter-than-average year
480 but two drier than average years prior to that, a genotype that prepares its offspring for another
481 wetter-than-average year (i.e., a positive transgenerational effect), or one that prepares its offspring
482 for a drier-than-average year (i.e., a negative transgenerational effect), will have higher fitness than a
483 genotype that does not express transgenerational plasticity. To our knowledge, this represents the
484 first demonstration that patterns of environmental variation can favor both positive and negative
485 transgenerational effects in the same site.
486
487 *Temperature*
488 Temperature is vitally important to plant function and fitness, as it impacts the rate of
489 physiological reactions, cues developmental transitions, and in extremes can cause stress and
490 mortality. Plants adapt to variable temperature regimes in a host of ways, including the production
491 of heat shock proteins and cold-response factors, and the development of morphologies that
492 mitigate the experience of temperature extremes. Experimental studies have identified adaptive
493 plastic responses to temperature changes in plants, both within and across generations. For example,
494 ambient temperature in Arabidopsis has been shown to influence the expression and splicing of
495 hundreds of genes, leading to changes in underlying histone methylation (Pajoro et al. 2017), and
496 significantly shifts flowering time (Donohue 2009) and many other phenotypes (Adams et al. 2016)
497 in genotype-specific ways. Additionally, recent work has demonstrated the lasting impact of
498 temperature regime on *Arabidopsis thaliana* plants for generations to come (Whittle et al. 2009; Suter
499 and Widmer 2013a; Suter and Widmer 2013b; Groot et al. 2017). In order for these responses to
500 adaptively match phenotypes with natural environments, there must be substantial correlations in
501 temperature within and between growing seasons.
502 We found significant autocorrelations in temperature, both within and between years. Within
503 a single growing season, temperatures early and late in the growing season tended to be positively
504 correlated across the U.S. Furthermore, we found that the temperatures of the late growing season
505 months (July, August, September) were generally strongly autocorrelated between successive years.
506 Interannual correlations between the temperatures of the early growing season months (February,
507 March, April) were often much lower. Surprisingly, early growing season temperatures were
508 generally more predictive of the following late seasons temperature than they were of the following
509 early seasons temperature.

In our framework, temperature both 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, and second as a source of information, that a plant can use to alter its phenotype later in the growing season or its offspring's phenotype in the following year. 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 provide valuable information that allows transgenerational plasticity to improve the match between phenotypes and temperature regimes.

The most common form of transgenerational plasticity in this model was late-growing season temperature impacting 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 (Auge et al. 2017). 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 across the US.

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 (Lorentz 1966). 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

542 between late growing season temperature and the following generation's early growing season
543 temperature. This result is intriguing because the temperature experienced during seed maturation
544 interacts with the post-dispersal temperature to strongly influence the dormancy and germination
545 behavior of seeds, with cascading effects throughout the life cycles of annual plants (Donohue 2009;
546 Burghardt et al. 2016). Consequently, site-specific correlations between maternal late-season
547 temperature and the early-season temperature in the next generation may select for divergent, site-
548 specific effects of maternal temperature on germination. Intriguingly, parental effects of temperature
549 on germination and flowering time are highly genetically variable in *Arabidopsis thaliana* (Burghardt et
550 al. 2016; Kerdaffrec and Nordburg 2017; Groot et al. 2017). In *Plantago lanceolata*, such genotype-by-
551 maternal temperature effects persist throughout the offspring life cycle to generate variation in
552 offspring reproduction in the field (Lacey and Herr 200). Our results suggest that such genetic
553 variation for maternal effects may derive in part from variable selection imposed by differences
554 among sites in intergenerational temperature correlations (see also Groot et al. 2017).
555
556 **Common Themes and Future Directions**
557 Although our precipitation and temperature models yielded distinct insights into the
558 dynamics of each of these factors, common themes emerged in both sets of analyses. For example,
559 we found higher levels of inter-annual autocorrelation, and therefore more prominent
560 transgenerational effects, at northern latitudes and along coastal regions within both models. Studies
561 that compare patterns of transgenerational plasticity across such large geographic regions will be
562 necessary to determine whether underlying differences in environmental patterns do in fact drive
563 differences in transgenerational plasticity. Another common finding of both the temperature and
564 precipitation models is that transgenerational effects are expected to provide greater benefits in
565 changing climates relative to purely oscillating climates, in which linear climate change has been
566 removed (i.e., the residual models). These results suggest that transgenerational effects may have an
567 important role in adaptation to human-induced climate change, and that rapid climate change should
568 select for more transgenerationally plastic individuals. However, there is an important caveat. In our
569 models we assume that genotypes are uniform in their mean phenotype, and do not allow for
570 mutations that could lead to genetic adaptation to changing conditions. The potential for
571 transgenerational plasticity to either promote or hinder genetic adaptation has been explored (Day
572 and Bonduriansky 2011), but our models do not address this issue. In the absence of genetic
573 evolution, it follows that if there is a linear trend towards hotter or drier years in addition to climatic

574 oscillations (as in the raw model variants), then there is more transgenerational information relative
575 to a situation in which only climatic oscillations are occurring (residual model variants). Theory
576 indicates that these dynamics become much more complex when local genetic adaptation to
577 changing conditions is allowed to occur along with plastic responses (Groot et al. 2017). For
578 instance, in some scenarios transgenerational effects can increase fitness in the short term, while
579 reducing it in the long term (Hoyle and Ezard 2012). In future studies, it will be critical to investigate
580 the influence of standing genetic variation for transgenerational plasticity on evolutionary
581 trajectories, and to examine the availability of novel mutations that alter the dynamics of
582 transgenerational effects.

583 Temperature and precipitation autocorrelations likely stem in part from the same broad-scale
584 climatic oscillations, such as the El Niño Southern Oscillation (Yang et al. 2018), the Quasi-biennial
585 oscillation (Baldwin et al. 2001), and the Pacific Decadal Oscillation (Mantua and Hare 2002;
586 Newman et al. 2016). Aside from these climatic oscillations, autocorrelations will arise due simply to
587 "red" or "pink" noise in which rare, large events and common, small events have equal power in
588 explaining variation (Szendro et al. 2001). It has been demonstrated that even without clear
589 underlying phenomena explaining variation, pink-noise is often the model that best explains patterns
590 of ecological and abiotic time-series variation (Halley 1996). These oscillations and general patterns
591 of red noise will interact with each other to varying degrees across different regions of the US,
592 leading to variable levels of autocorrelation at all lags for both precipitation and temperature.

593 Furthermore, because temperature and precipitation interact to alter moisture availability, it
594 is likely that organisms do not process temperature and precipitation information independently, but
595 rather use them in tandem along with other sources of information to fine tune phenotypes for the
596 most likely future environment. For instance, temperature influences water availability by influencing
597 rates of evaporation and transpiration. Interactions between temperature and water availability also
598 shape the collection of herbivores, pathogens, and competitors present in a given locality.
599 Understanding how these environmental factors jointly influence the expression of transgenerational
600 plasticity is an important goal for future research. A key element of this research direction is to study
601 environmental (auto)correlations at fine scales in the context of dispersal distances. It is possible that
602 transgenerational plasticity may be a more common mode of adaptation for organisms with short
603 dispersal distances, in which parents and offspring are more likely to grow and develop in similar
604 microsites. Finally, differences in life history strategies and generation times will alter the time-scales
605 and types of environmental autocorrelations relevant to transgenerational plasticity. Future studies

606 drawing inspiration from other species will provide insight into how these variables might impact
607 the evolution of transgenerational effects.
608
609 **Conclusion**
610 In summary, we demonstrate that patterns of climatic variation in nature may favor the
611 adaptive evolution of transgenerational plasticity in organisms with approximately annual generation
612 times, such as annual plants. Our models indicate that differing patterns of climatic oscillations
613 across the US lead to strikingly different optimal patterns of within- and transgenerational plasticity.
614 Thus, for a given species, one may expect that environmental variation across its range not only
615 selects for different locally adapted mean trait values, but also different classes and magnitudes of
616 plasticity. Perhaps the most meaningful result of this study is that the climatic patterns across
617 relatively small geographic regions vary so dramatically that the optimal value of transgenerational
618 plasticity ranges from extremely high to non-existent. It should therefore be expected that although
619 many species, environmental variables, or phenotypes of interest may show no evidence of
620 transgenerational plasticity, such results may be due to their specific situation rather than a
621 fundamental biological limitation. This applies equally strongly to the other side of the coin: because
622 a single population or species expresses strong transgenerational plasticity does not mean that this
623 process is a key driver of evolutionary processes. Rather, variation in transgenerational plasticity
624 should be expected, just as genetic variation is ubiquitous in natural populations. Transgenerational
625 plasticity is best considered in the specific ecological and evolutionary context of the study organism,
626 and broad generalizations about the role of these effects in evolution should be avoided until
627 considerably more field data are in hand. The results described here provide a source of testable
628 predictions for geographical variation in this mode of adaptation.
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634 **References**
635

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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

733 Figure 1: Schematic depicting the ecological motivations (summer annual plants) and theoretical
734 underpinnings for the evolutionary modeling of plasticity traits (A and C), and the types of
735 environmental fluctuations that may influence their evolution. (A) Temperature plasticity model. In
736 the abbreviations, **E** denotes the Early growing season (spring) and **L** denotes the late growing
737 season (summer). The first letter represents the relevant season during the parental generation and
738 the second letter represents the relevant season in the offspring generation (e.g., EL denotes effects
739 of parental early growing season temperature on offspring phenotypes late in the growing season).
740 Within generation developmental changes in response to early season environment (W) are also
741 considered in this model. Additionally, the longterm average environmental conditions at a specific
742 area determine the genetic baseline phenotype of an individual (G). (B) On the left we see an
743 example of an environment with high within season autocorrelations for temperature (hot springs
744 tend to be followed by hot summers), but low inter-annual autocorrelations (a hot year does not
745 tend to be followed by another hot year) that selects for within generation plasticity but not
746 transgenerational plasticity. On the right, a situation where spring and summer temperatures are not
747 correlated with each other, but we do find that environmental oscillations lead to a string of warmer
748 than average springs and cooler than average summers, in this situation transgenerational plasticity
749 (EE and LL) but not within generation plasticity is expected to be optimal. (C) Precipitation
750 plasticity model. The amount of precipitation experienced by an individual can lead to
751 transgenerational effects in the next generation (T), as well as persist for two (TG) or three (TGG)
752 generations. (D) On the left, relatively gradual decadal oscillations give value to transgenerational
753 effects that persist for multiple seasons (T, TG, and TGG). On the right shorter period climatic
754 oscillations may favor parental effects (T), but not multi-generation effects (TG or TGG).
755
756 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*)

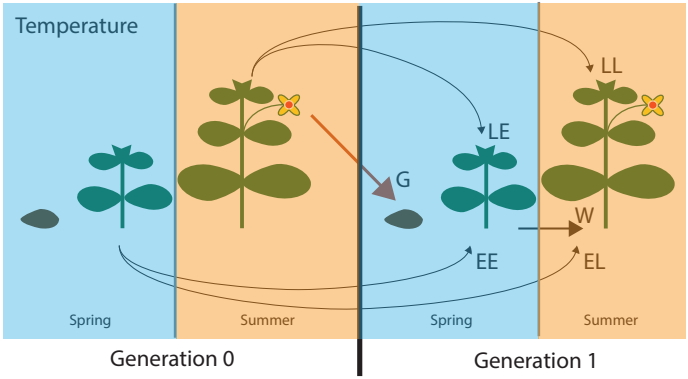
Figure 4: Maps coded to show patterns of variability for optimal precipitation (A-C) and temperature (D-H) plasticity values across the US. (A) Optimal transgenerational plasticity values for the one-generation transmission of precipitation level information. (B) Optimal grandparental transgenerational 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

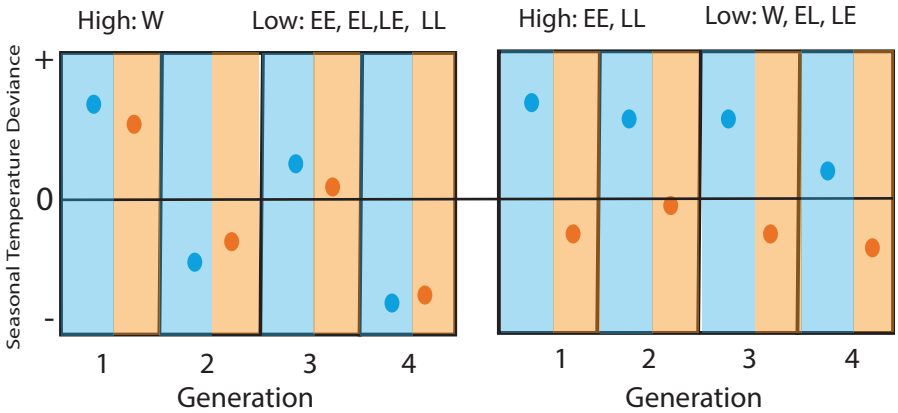
781 mode. Higher values suggest that the primary value associated with transgenerational plasticity over
782 the past 120 years has been associated with allowing individuals to keep up with increasing
783 temperature. (H) Optimal within generation plasticity (W) values.
784
785 Figure 5: Fitness landscapes of transgenerational precipitation alleles for twelve sites across the US.
786 Sites with low optimal parental effects (D and I) have only very subtle fitness differences associated
787 with chanes in the multigeneration persistence (Y-axis) due to the minor role in any form of
788 transgenerational effect on fitness in these cases. More defined fitness peaks tend to occur in areas
789 where more substantial transgenerational effects are optimal (E, G, J, K, L). In some rare cases,
790 bimodal fitness landscapes arise (B) where lines with either positive (with high persistence) or
791 negative (with low persistence) transgenerational persistence have higher fitness than lines with no
792 transgenerational inheritance.
793
794 Figure S1: Distribution of climatic summary statistics across the 481k 4x4km grids in the US.
795 Dotted lines at 0 for autocorrelation histograms.
796
797 Figure S2: Mosaic plot showing the frequency of specific combinations of optimal transgenerational
798 effects and multi-generational persistence values. More subtle transgenerational effects more
799 frequently only have a single generation of persistence (G=0), while more extreme transgenerational
800 effects tend to coincide with full transgenerational persistence (G=1) where each of the prior three
801 years contribute equally. Additionally, positive transgenerational effects were more likely to have
802 intermediate levels of persistence than negative transgenerational effects.
803
804

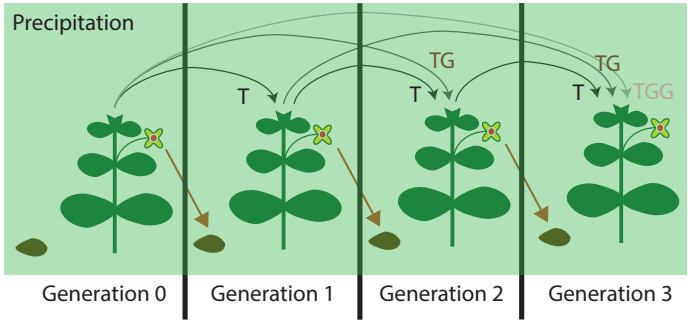
Figure S3: Figures demonstrating tradeoffs between classes of plasticity. (A) Tradeoffs between early-late (m12) and late-late (m22) transgenerational plasticity in relation to the autocorrelations in summer temperature. Generally, as inter-annual summer autocorrelations increase, so too does the frequency of minor and moderate early-late transgenerational plasticity. However, we also find that areas that favor higher levels of late-late transgenerational plasticity tend to favor lower levels of early-late plasticity compared to other sites with similar levels of temperature autocorrelation. (B) Within a single site there are many examples of localities where either early-late or late-late transgenerational plasticity lead to fitness increases relative to clones with no plasticity, but individuals expressing both forms of plasticity have the lowest fitness of all.

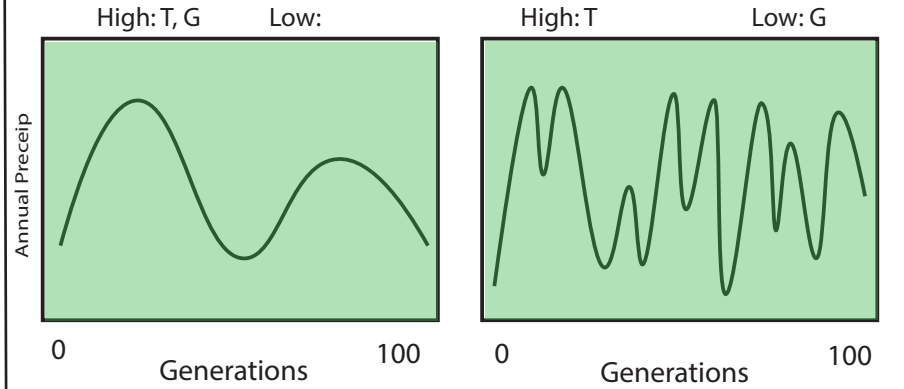
Figure S4: Changes in the frequency of ten clonal types in a 120 year simulated competition experiment for four different sites across the US. The top three final frequency clones are denoted with stars.

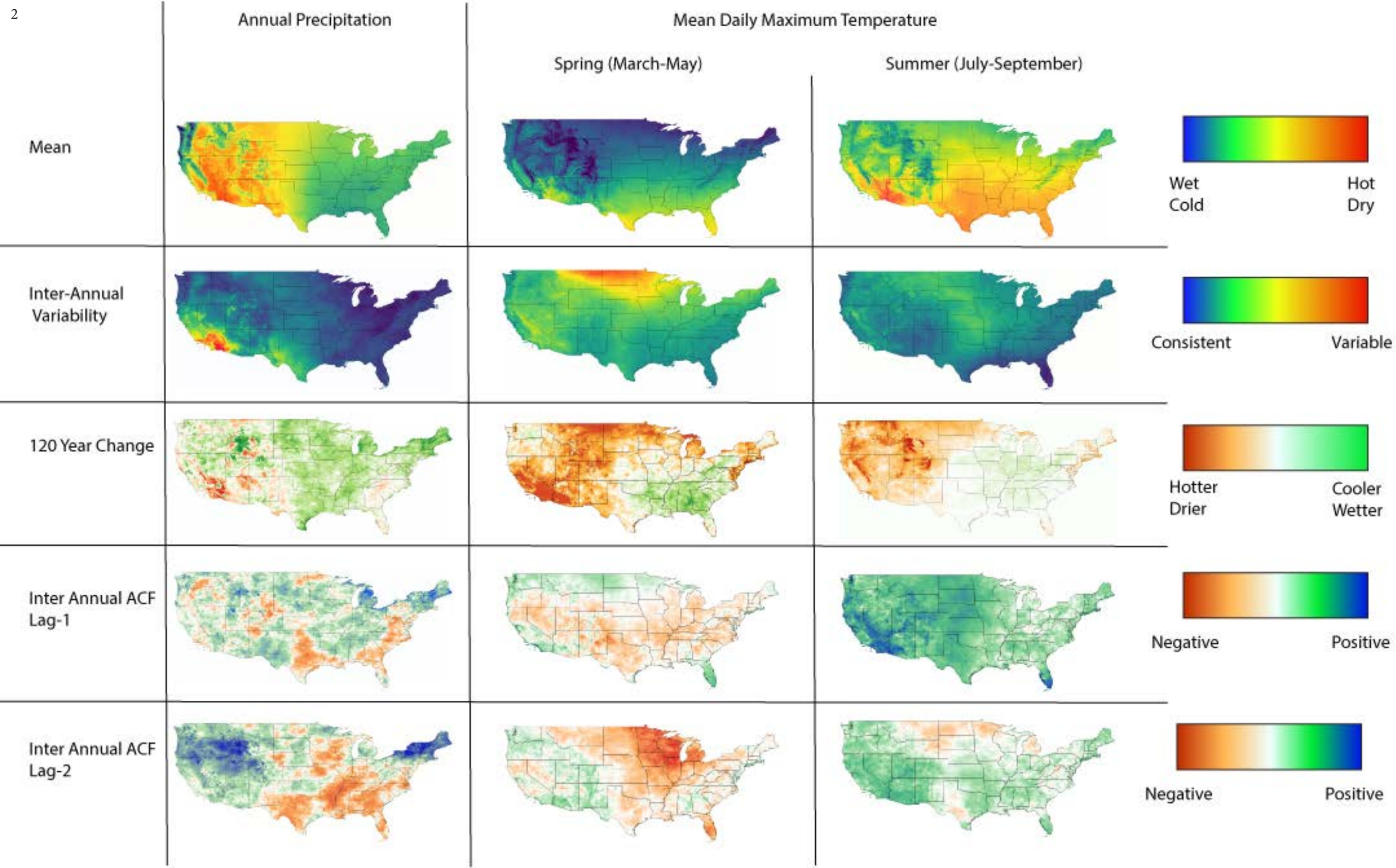
1

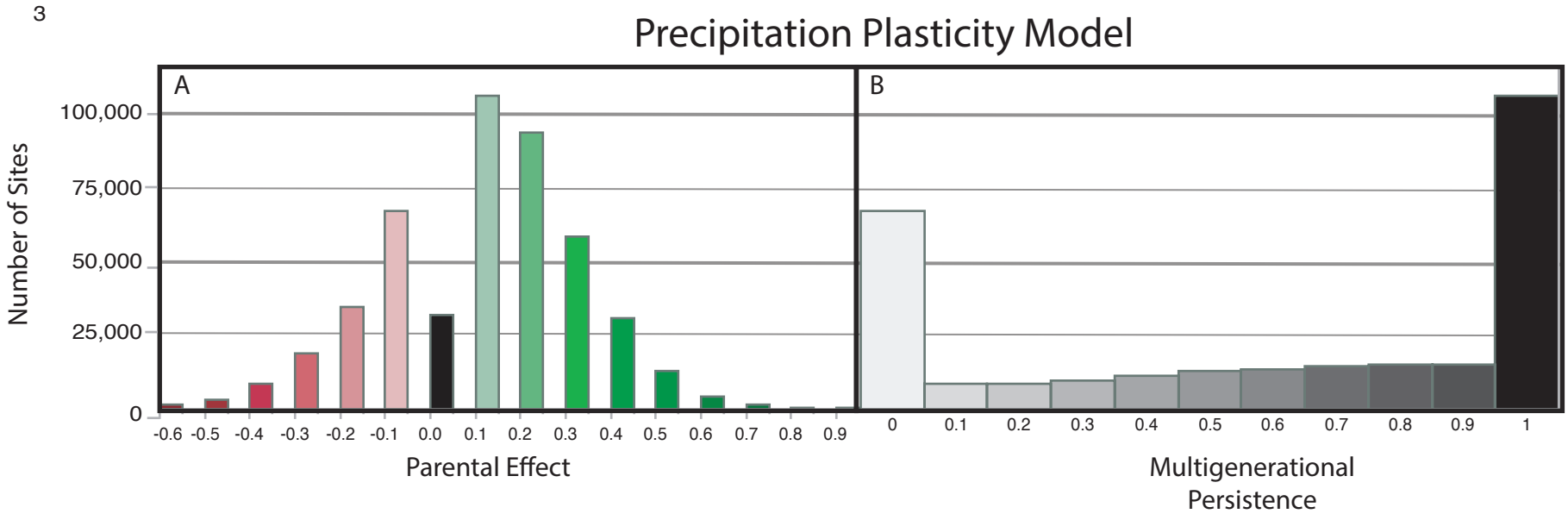

Temperature
LL
LE
G
W
EE
EL
Spring
Summer
Spring
Summer
Generation 0
Generation 1

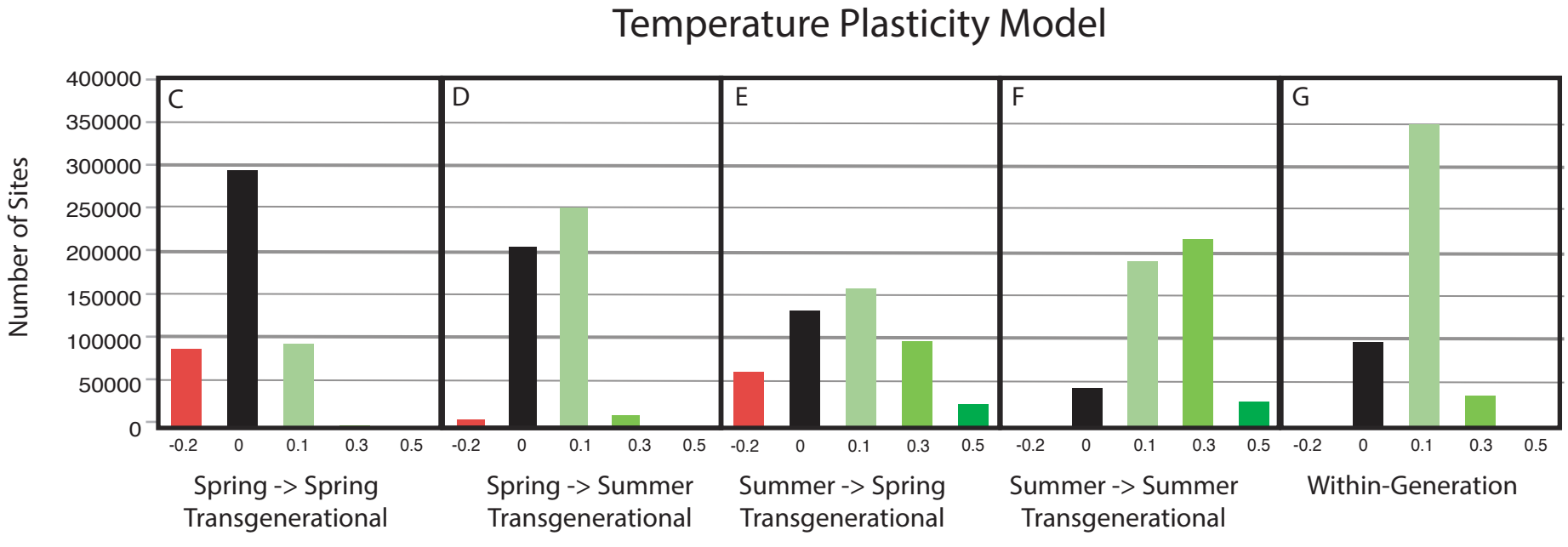

High: W
Low: EE, EL,LE, LL
High: EE, LL
Low: W, EL, LE
Seasonal Temperature Deviance
+
0
-
1
2
3
4
Generation
1
2
3
4
Generation

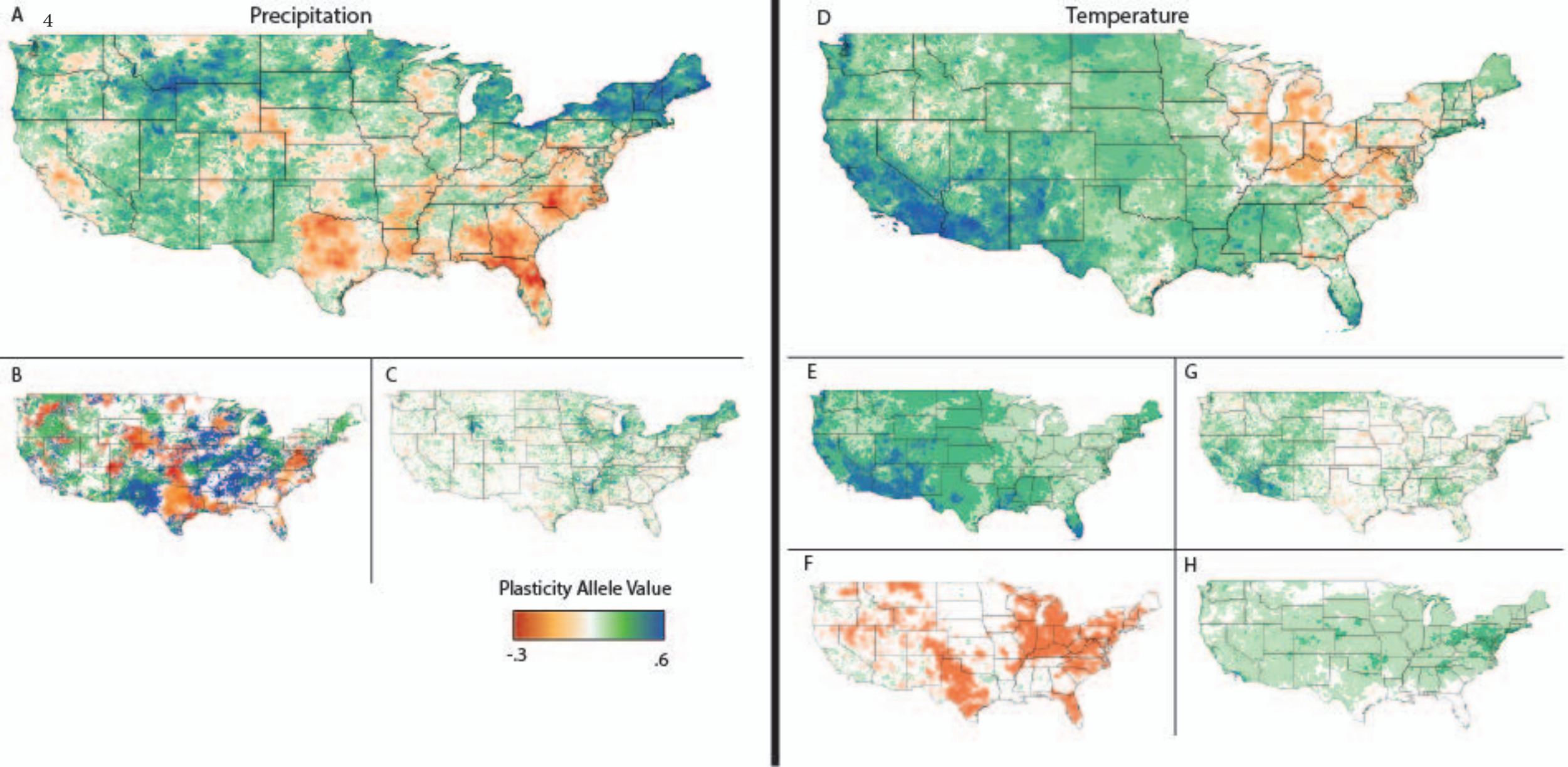

Precipitation
T
TG
T
TG
T
TGG
Generation 0
Generation 1
Generation 2
Generation 3

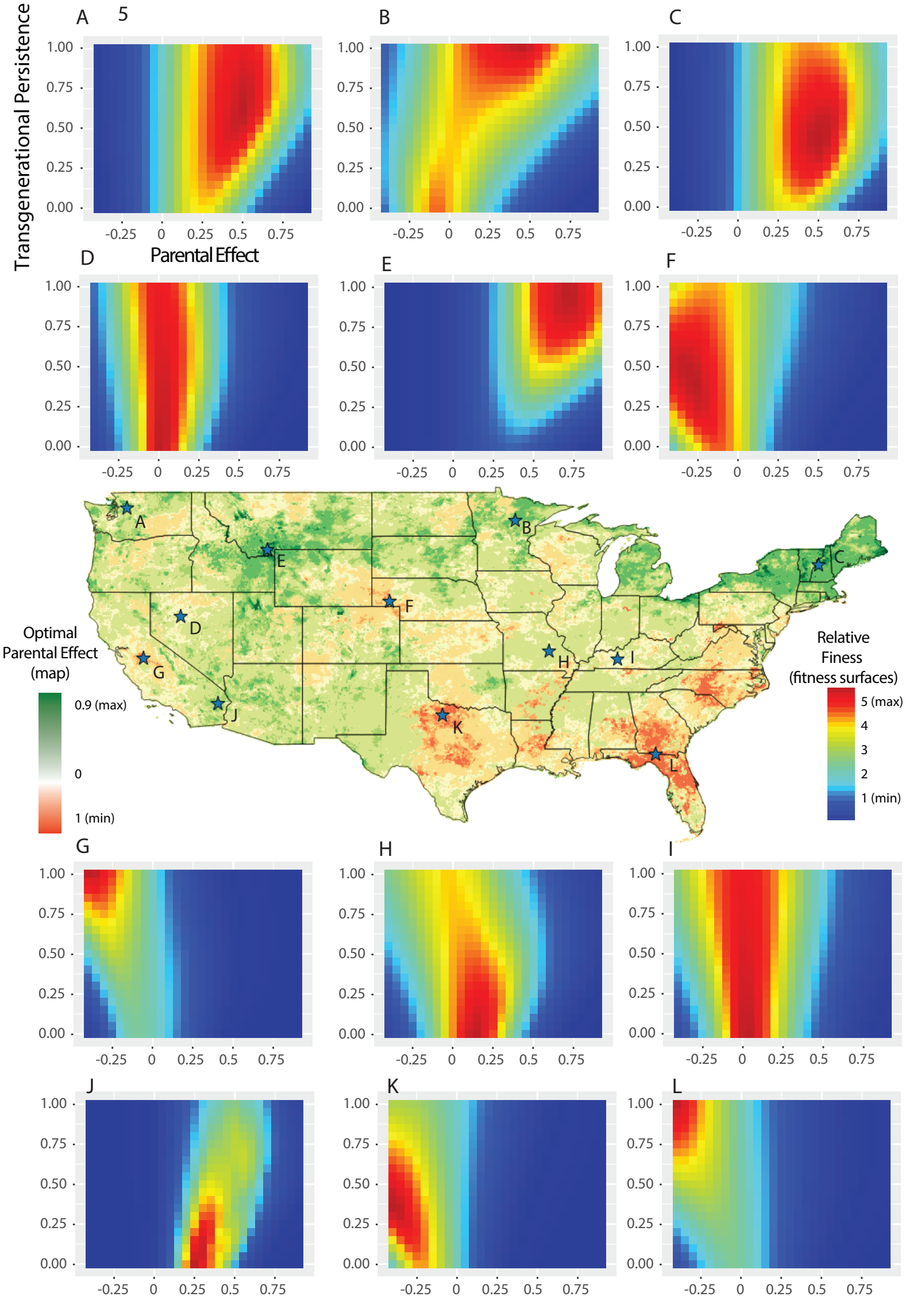

High: T, G
Low:
High: T
Low: G
Annual Preceip
0
100
Generations
0
100
Generations


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

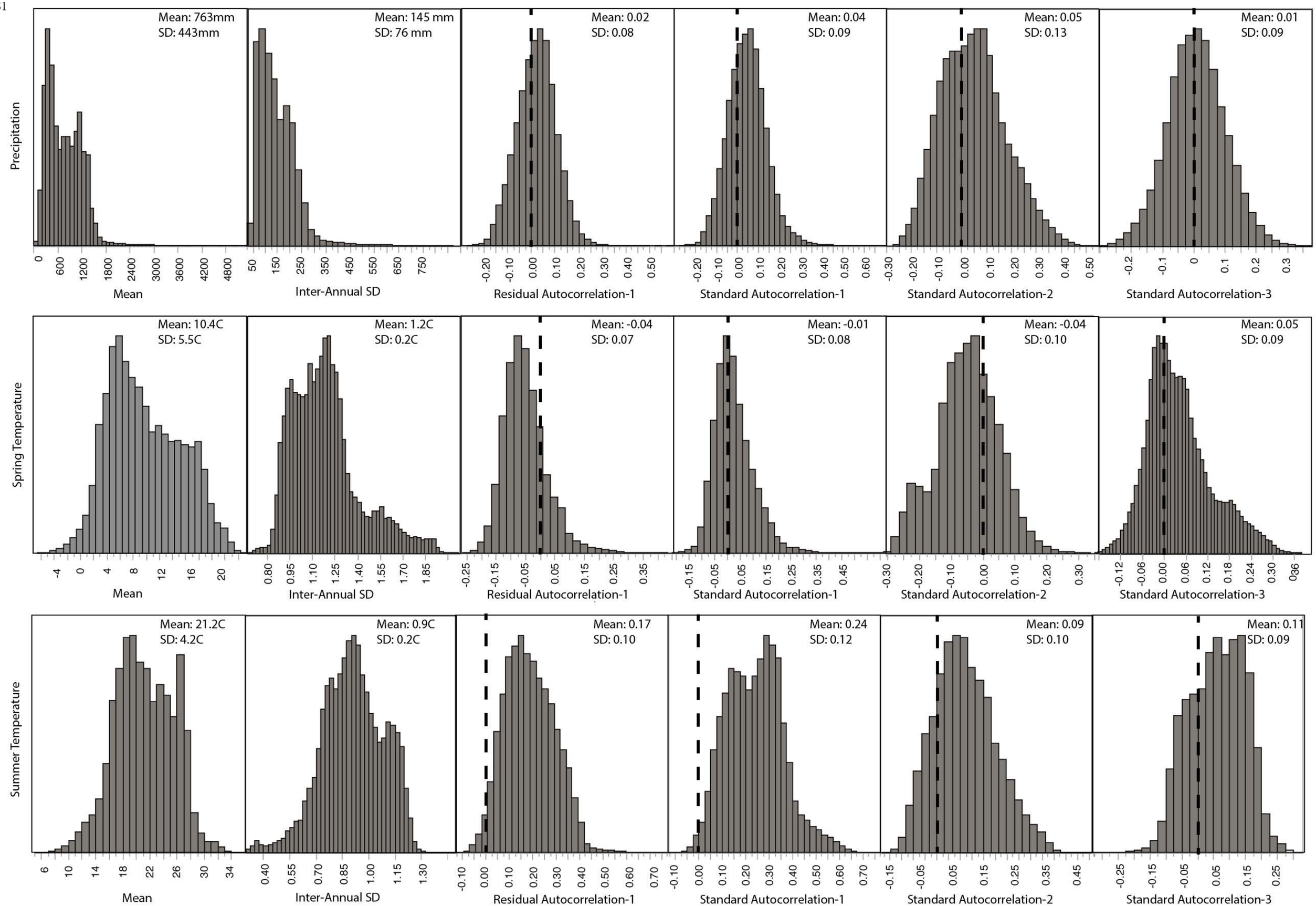

Precipitation Plasticity Model
A
B
Number of Sites
100,000
75,000
50,000
25,000
0
-0.6 -0.5 -0.4 -0.3 -0.2 -0.1 0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9
Parental Effect
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
Multigenerational Persistence


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

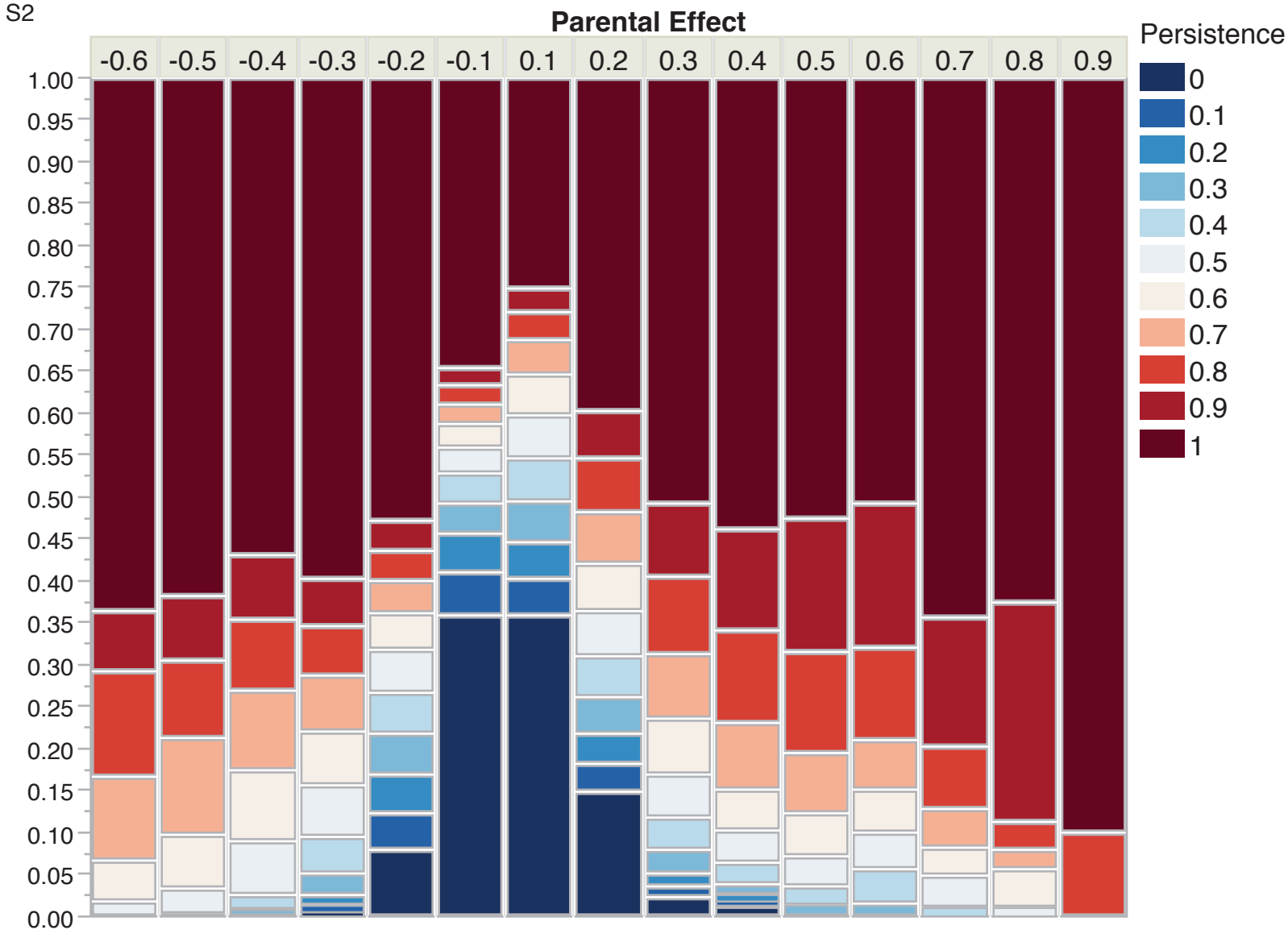

A
Precipitation
D
Temperature
B
C
E
G
F
H
Plasticity Allele Value
-.3
.6


A
5
B
C
D
E
F
G
H
I
J
K
L
Transgenerational Persistence
Parental Effect
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)

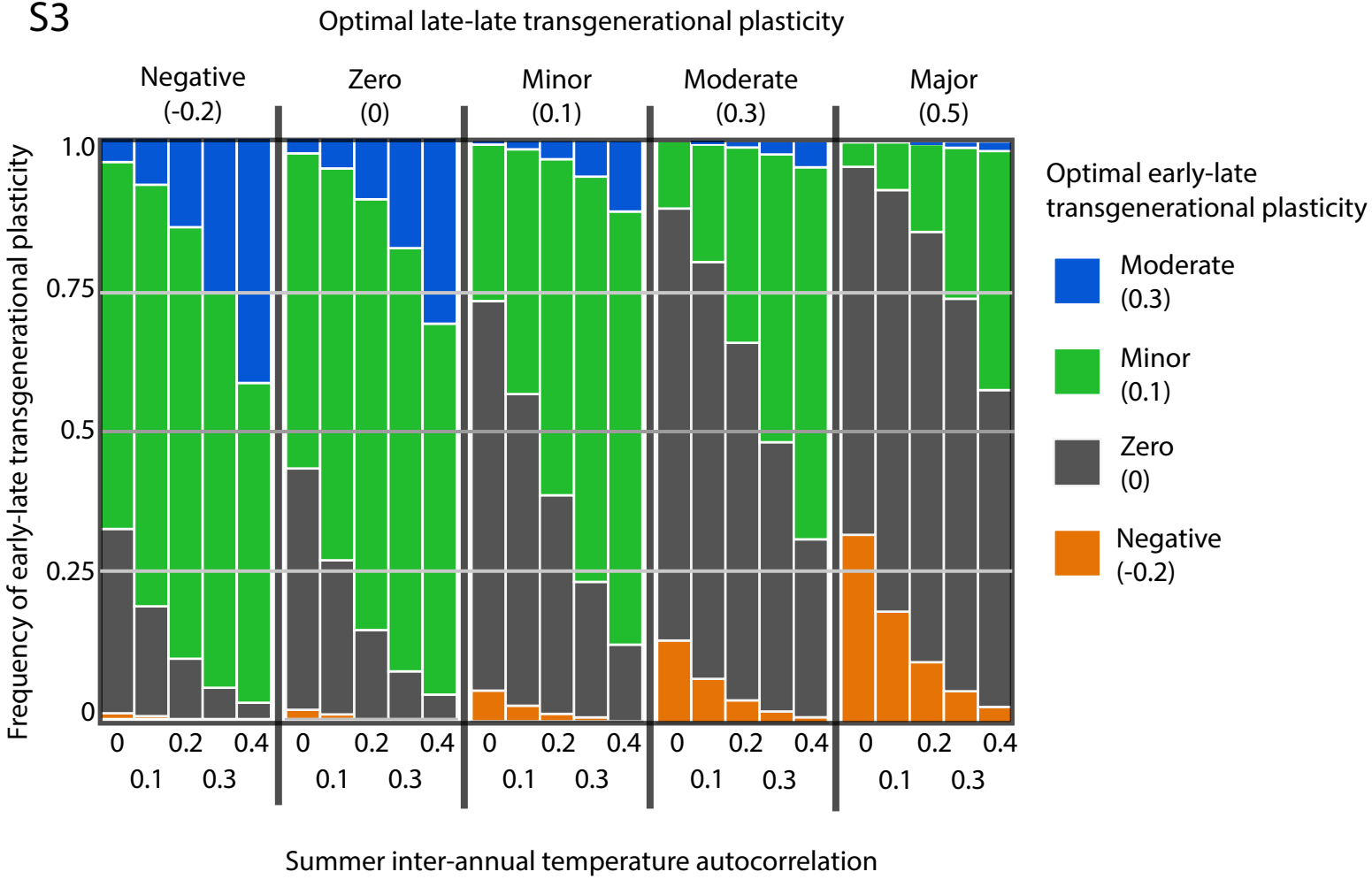
S1


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

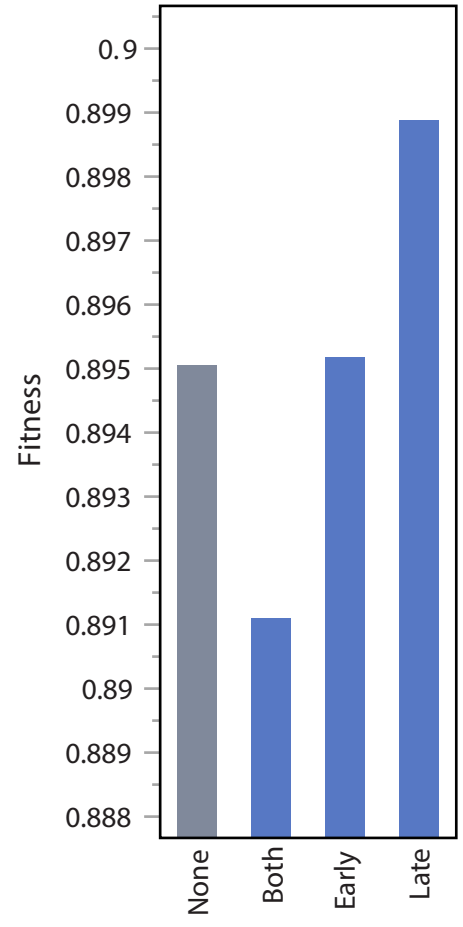
S2


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 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

S4

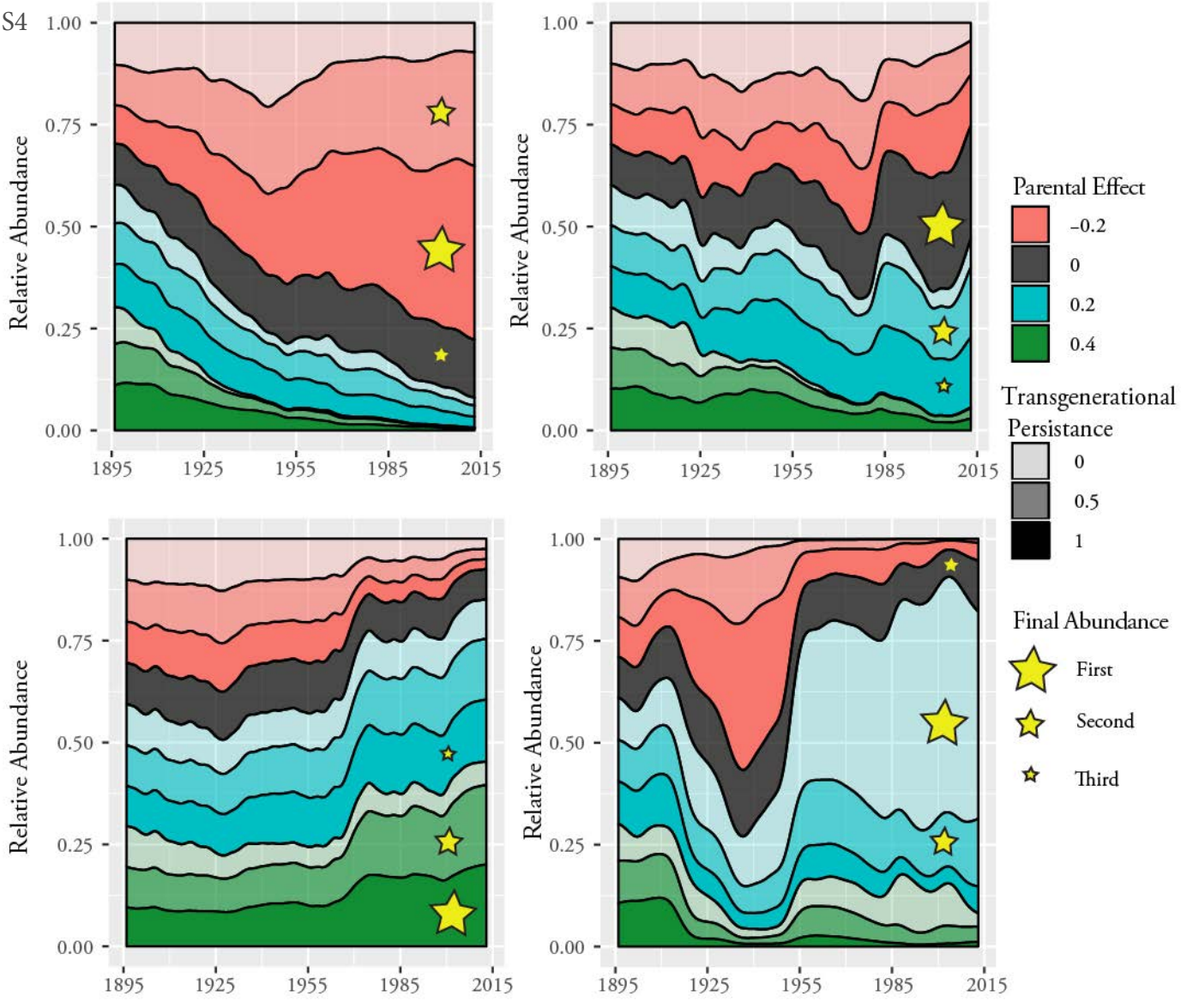

Relative Abundance
1.00
0.75
0.50
0.25
0.00
1895
1925
1955
1985
2015
Parental Effect
−0.2
0
0.2
0.4
Transgenerational Persistance
0
0.5
1
Final Abundance
First
Second
Third

Table S1

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Other (Video, Excel, large data files)

TableS1.xlsx

Table S2

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TableS2.xlsx