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Climate change shifts natural selection and the adaptive potential of the perennial forb *Boechera stricta* in the Rocky Mountains

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Heritable genetic variation is necessary for populations to evolve in response to anthropogenic climate change. However, antagonistic genetic correlations among traits may constrain the rate of adaptation, even if substantial genetic variation exists. We examine potential genetic responses to selection by comparing multivariate genetic variance–covariances of traits and fitness (multivariate Robertson–Price identities) across different environments in a reciprocal transplant experiment of the forb *Boechera stricta* in the Rocky Mountains. By transplanting populations into four common gardens arrayed along an elevational gradient, and exposing populations to control and snow removal treatments, we simulated future and current climates and snowmelt regimes. Genetic variation in flowering and germination phenology declined in plants moved downslope to warmer, drier sites, suggesting that these traits may have a limited ability to evolve under future climates. Simulated climate change via snow removal altered the strength of selection on flowering traits, but we found little evidence that genetic correlations among traits are likely to affect the rate of adaptation to climate change. Overall, our results suggest that climate change may alter the evolutionary potential of *B. stricta*, but reduced expression of genetic variation may be a larger impediment to adaptation than constraints imposed by antagonistic genetic correlations.

KEY WORDS: **Climate change, evolutionary potential, genetic correlations, genetic variation, Robertson–Price identity.**

To avoid local extinctions due to climate change projected for the next century and beyond (IPCC 2014), natural populations will need to respond to novel climates through a combination of migration to historically cooler environments, phenotypic plasticity, and adaptation to new environments (Aitken et al. 2008; Nicotra et al. 2010; Reed et al. 2011; Anderson et al. 2012b; Corlett and Westcott 2013). Assessing the adaptive potential of populations under climate change remains challenging (Shaw and Etterson 2012; Sheth et al. 2018; Torres-Martínez et al. 2019). Long-term studies of natural populations have sometimes suggested genetic adaptation to climate change (Bradshaw and Holzapfel 2008), but in general, evidence of evolution in response to ongoing climate change remains rare and is difficult to distinguish from ecological responses (Gienapp et al. 2008; Merilä 2012; but see Franks et al. 2007). Accurately predicting the potential for adaptation to contribute to population persistence in the future will first require establishing whether populations have sufficient genetic variation to adapt to ongoing environmental change.

Fisher's Fundamental Theorem of Natural Selection states that the evolutionary rate of change in fitness of a population is proportional to its additive genetic variance in fitness (Fisher 1930), and substantial genetic variation in fitness could suggest that populations may continue to adapt to contemporary conditions (Sheth et al. 2018). Genetic variation is ubiquitous in natural populations, even in traits under selection (Walsh and Blows 2009). However, environmental conditions affect the amount of genetic variation expressed (Hoffmann and Merilä 1999; Merilä 2012); therefore, the ability of populations to adapt

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to climate change will depend specifically on genetic variation under climate-change conditions, rather than in ambient environments. Theoretical arguments and data from empirical studies are both inconclusive as to whether genetic variation is generally more likely to increase, decrease, or remain the same in more stressful environments (Hoffmann and Merilä 1999). Experiments that transplant individuals along environmental gradients (Etterson and Shaw 2001; Shaw and Etterson 2012) or manipulate growing conditions (Torres-Martínez et al. 2019) can estimate genetic variation of populations under conditions that may resemble future climates.

In some cases, genetic variation substantially increases in novel conditions, which could help facilitate adaptive evolution. Cryptic genetic variation becomes apparent when a population is exposed to novel conditions (Gibson and Reed 2008) and can provide a source of standing genetic variation upon which selection can act (Paaby and Rockman 2014). Despite this potential, the actual prevalence of cryptic genetic variation and its importance in facilitating adaptation in natural populations is largely unknown (McGuigan and Sgrò 2009). Nonetheless, cryptic genetic variation can lead to rapid evolution (McGuigan et al. 2011), and may be particularly likely to emerge in conditions that were rare or absent from a lineage's evolutionary history (Ledón-Rettig et al. 2014).

Even if populations maintain substantial genetic variation in traits under selection in future climates, these traits may not evolve at the rate expected by the univariate breeder's equation (Morrissey et al. 2010). In particular, genetic correlations among traits can alter the rate of adaptation (Etterson and Shaw 2001; Hellmann and Pineda-Krch 2007; Agrawal and Stinchcombe 2009; Walsh and Blows 2009; Chevin 2013). Correlations antagonistic to the direction of selection could reduce the rate of evolution or potentially even reverse its direction compared with expectations when considering each trait in isolation (Walsh and Blows 2009). In contrast, correlations that align with the direction of selection may facilitate rapid adaptation (Agrawal and Stinchcombe 2009; Chevin 2013). Empirical studies have revealed many examples of both constraint and facilitation arising from genetic correlations in different systems (Agrawal and Stinchcombe 2009). Predictions about the rate and direction of adaptation in natural populations ought, therefore, to consider the multivariate nature of selection (Walsh and Blows 2009). Furthermore, because genetic correlations among traits depend upon environmental context (Sgrò and Hoffmann 2004; Teplitsky et al. 2011; Merilä 2012), studies that examine these correlations in environments representative of projected future climates are particularly needed.

Species inhabiting high-elevation ecosystems are susceptible to extensive habitat loss and reductions in range size due to anthropogenic climate change (Engler et al. 2011; Dullinger et al. 2012; Freeman et al. 2018), and may be forced to adapt, rather than migrate, as their habitats are lost. Here, we employ a reciprocal transplant experiment and climate manipulations to investigate the potential for adaptation as a response to climate change in *Boechera stricta* (A. Gray) A. Löve & D. Löve (Brassicaceae), a perennial plant native to the Rocky Mountains. In multiple common gardens arrayed across an elevational gradient, we exposed experimental transplants to contemporary conditions (control) and to snow removal, which simulates an advance in the timing of snowmelt and a reduction in the accumulation of snow, both of which are projected to continue to occur as climates change (Rangwala et al. 2012; IPCC 2014; Fyfe et al. 2017). This experiment quantifies fitness and functional traits in three situations relevant to climate change: accessions transplanted into warmer and drier lower elevation sites; local accessions exposed to simulated climate change (i.e., snow removal) in their home sites; and accessions transplanted into snow removal conditions in higher elevation sites, as these data reveal how upslope migrants respond to novel locales.

To assess the potential for adaptation, we quantified flowering phenology and size at flowering, specific leaf area (SLA), leaf water content, and foliar damage from insect herbivores. These heritable traits are subject to strong selection and exhibit genetically based clines across climatic gradients in *B. stricta* (Anderson et al. 2012a, 2015; Wadgymar et al. 2017). High-elevation populations have evolved to flower earlier and at a smaller size, and have greater SLA (often associated wtih thinner leaves), higher leaf water content, and increased susceptibility to insect herbivory in common gardens than low-elevation populations (Anderson and Gezon 2015; Wadgymar et al. 2017). These genetic clines reflect adaptation to the shorter growing seasons, lower drought stress and reduced herbivore pressure in high-elevation locations, and the longer growing season characterized by high drought stress and herbivory in low-elevation populations (Anderson and Gezon 2015; Wadgymar et al. 2017). Climate change likely imposes novel selection on these traits. For example, earlier timing of snowmelt could favor accelerated flowering (Anderson et al. 2012a; Wadgymar et al. 2018), increased drought stress (Rangwala et al. 2012; IPCC 2014; Fyfe et al. 2017) could favor drought tolerant traits (e.g., low SLA and low foliar water content) (Terashima et al. 2011; Maire et al. 2015), and increased herbivory (DeLucia et al. 2008; Liu et al. 2011; Robinson et al. 2012) could select for herbivore resistance.

Genetic trade-offs between these ecologically relevant traits could constrain an adaptive response to novel selection. Furthermore, climate change may alter the extent of genetic variation in these traits. Here, we test (1) whether simulated climate change reduces the expression of quantitative genetic variation in key traits and fitness, against the alternative hypothesis that cryptic genetic variation can emerge in novel environments. In addition, (2) we examine if climate change favors a greater rate of

evolution of these traits, against the alternative hypothesis that the increased abiotic stress associated with climate change could reduce the rate of trait evolution. Finally, we test (3) whether genetic trade-offs could constrain adaptive responses to novel climates, against the alternative hypothesis that genetic correlations could facilitate adaptation to environmental change.

Methods

STUDY SYSTEM

We evaluated our hypotheses in *B. stricta* (Brassicaceae), a short-lived perennial forb that shows clear patterns of local adaptation to elevation, latitude, and water availability (Lee and Mitchell-Olds 2013; Anderson et al. 2014; Anderson and Gezon 2015). The center of genetic diversity of *B. stricta* is in the Colorado Rocky Mountains (Kiefer et al. 2009), where genetic variation could potentially promote adaptation to changing environmental conditions. Along with 10–15% of plants (Goodwillie et al. 2005), *B. stricta* primarily self-pollinates (F_{IS}: 0.74–0.97) (Song et al. 2006). Selfers have lower adaptive potential than outcrossers, but a meta-analysis found no link between mating system and the extent of local adaptation (Hereford 2010).

In addition, *B. stricta* has gravity dispersed seeds; thus, this species may have limited migratory potential under anthropogenic climate change. Nevertheless, *B. stricta* rapidly recolonized high latitudes and elevations after the Pleistocene glacial retreat (Song et al. 2006; Kiefer et al. 2009; Rushworth et al. 2011), indicating that it responded to changing climates over relatively short geological timescales.

Boechera stricta flowers ~13 days earlier than in the mid-1970s; this shift likely resulted from both plasticity and adaptation in response to strong directional selection (Anderson et al. 2012a). The species expresses plasticity in flowering phenology in response to temperature, winter length, and the timing of snowmelt (Anderson et al. 2011, 2012a). These conditions will continue to change (IPCC 2014), which could alter phenology in *B. stricta* and other species that rely on multiple cues to elicit life-history transitions. In high-latitude and high-elevation systems, climate change has begun to shift some winter precipitation from snow to rain, which has reduced snowpack and snow water equivalent, accelerated the timing of snowmelt in the spring, and increased drought stress as rainfall is limited during the growing season before monsoonal rains occur in late July (Rangwala et al. 2012; IPCC 2014; Pepin et al. 2015; Fyfe et al. 2017). Additionally, early snowmelt exposes plants to frosts that they would not have experienced historically when they were insulated by snow (Inouye 2008). Near the Rocky Mountain Biological Lab (38.96°N, 106.99°W), snow removal in natural communities advanced the timing of snowmelt by 17.4 days and induced *B. stricta* to flower 7.0 days early (Anderson and Gezon 2015). Annual records from 1973 to 2012 predict a 5.5–10.3 day acceleration in flowering for a 17.4 days advance in snowmelt (Anderson et al. 2012a). Thus, climate manipulations in this system accurately reflect long-term phenological responses to climate change (Wadgymar et al. 2018).

EXPERIMENTAL DESIGN

To evaluate potential adaptive response to climate change, we conducted a reciprocal transplant experiment in five common gardens around the Rocky Mountain Biological Laboratory (elevations: 2553 m, 2710 m, 2890 m, 3133 m, 3340 m; Table S1). However, we were unable to obtain sufficient sample sizes for robust statistical inference in the lowest elevation garden due to mortality (0% germination of planted seeds, 64% mortality of planted rosettes prior to the first growing season, and >99% mortality by the end of the second field season). We excluded this garden from all analyses. In addition, we focus our analyses on genotypes planted locally or moved only one garden upslope or downslope relative to their origins, which corresponds to a ~200 m elevational difference; we excluded genotypes moved two or more gardens upslope or downslope, as migrations of ≥400 m elevational difference are unlikely to occur rapidly in this species.

In each garden, we established 16 experimental blocks and we exposed half of these blocks to contemporary snowmelt and half to early snow removal (Wadgymar et al. 2018). In March–May, when snowpack receded to 1 m in depth, we shoveled snow from removal blocks to a depth of 10 cm, to avoid damage to the vegetation (Wadgymar et al. 2018). Snow in these early removal blocks melted an average of 5.7–19.1 days earlier than the control blocks (Table S1). As snowmelt in this region is advancing by 7.4 days per decade (Harte et al. 2015), our protocol reflects climatic projections for the middle of the 21st century.

We transplanted both seeds and juvenile rosettes into our experiment. By including seeds, we evaluated the crucial seed-to-seedling transition, but seed germination rates in the field were <10%, seedlings typically do not reproduce until year 2–4, and leaves are too small for measurements of foliar morphology. Therefore, we also transplanted 3-month-old juvenile rosettes into the same treatments and gardens to generate data on survival and reproduction, flowering phenology, resistance to insect herbivory, and foliar morphology. Prior to the experiment, we collected seeds from natural populations outside of each garden, ensuring that we sampled naturally recruiting individuals at least 2 m apart from each other to reduce the risk of collecting seeds of close relatives. We propagated these seeds in a greenhouse for one generation to standardize maternal effects and produce full-sibling families for experimentation. In selfing plants, selection acts on total genetic variance, not just additive genetic variance (Roughgarden 1979); therefore, we used these full-sibling maternal families to evaluate broad-sense heritability and genetic variance–covariance matrices in this experiment.

In September and October of 2015, we reciprocally transplanted 9542 seeds (not including 2308 additional seeds transplanted into the excluded lowest elevation garden) from 124 accessions into the four gardens (N = 16–30 maternal families per source population). We planted one seed per family at a depth of ca. 2 mm into randomized cells of 13 cm × 13 cm plastic grids (experimental seed blocks), with each cell filled with 1 cm^3 of potting soil. We randomized the seed planting into each block and ensured that all maternal families from all source populations were represented in every block. Most seed families had two siblings planted into each block. We established 61 seed blocks total (15.25 per garden) across the four gardens evaluated in this study and we exposed 31 blocks to ambient conditions and 30 to early snow removal. We did not plant directly into native soil to avoid contamination from the soil seed bank. Natural seed dispersal typically occurs from July to September. At all sites, we planted after natural *B. stricta* had completed seed dispersal to reduce the risk of dispersal into the seed grids. We included empty cells (soil but no seed) in the seed grids to verify that germinating seedlings were experimental.

In addition, in October 2016, we transplanted 5483 juvenile rosettes (not including 1361 additional rosettes in the excluded 2553 m garden) from 123 accessions into the natural plant community in snow removal and control blocks in all gardens (N = 16–30 accessions per source population; Table S8). We randomized experimental individuals from each of the five source populations into each block within the four gardens considered here (N = 32 control blocks total, with eight per garden, and N = 35 snow removal blocks total with 8.75 per garden), such that each block contained at least one individual per maternal family per population.

TRAIT MEASUREMENTS AND DATASETS

We visited experimental grids and rosettes three to four times per week throughout each growing season to assess germination and survival of seeds, and survival, flowering, and reproduction of transplanted rosettes. We assessed leaf morphology and herbivore damage once per growing season for rosettes in 2017 and 2018. In total, we collected data on fitness plus three categories of phenotypic traits: seedling, leaf, and flowering traits. Complete details of trait measurement protocols are given in the Supporting Information Methods.

Seedling traits were measured on individuals planted as seeds, and included germination success and date of germination (expressed as the number of days after snowmelt, when each seed plot was completely snow-free) in the 2016 growing season, and survival to the end of the 2018 growing season. Germination success and survival are binary traits, and we modeled date of germination with a Gaussian distribution.

Leaf traits included SLA ($cm^2 \times g^{-1}$), leaf water content (proportion of the fresh mass composed of water), and leaf area removed by herbivores (proportion of total plant leaf area subject to herbivore damage). We natural log-transformed SLA, and modeled leaf water content and log-transformed SLA with Gaussian distributions, and leaf damage with a Poisson distribution. We multiplied leaf area removed by 10 to avoid loss of precision when rounding very small percentages to the nearest integer for the purpose of modeling a Poisson distribution.

Flowering traits included the date of first flowering (days after snowmelt), the duration of flowering (number of days), and the bolt height at initial flowering. We modeled flowering date and height with Gaussian distributions, and the duration of flowering with a Poisson distribution.

Our fitness data were highly zero-inflated, as >95% of individuals failed to set seed in either year. We used a hurdle model to split fitness into two components: whether the plant reproduced (i.e., reproductive success) and the number of seeds produced by reproductive plants only. To avoid attributing reproductive failure to mortality experienced during the previous year, we included only plants that were alive at the end of the prior year's growing season in our assessment of reproductive success: 2017 reproductive success included all rosettes planted in the fall of 2016, whereas 2018 reproductive success included only plants alive at the end of 2017. Due to the very low number of plants that reproduced overall, we were unable to make statistically meaningful inferences concerning seed number of reproductive plants (as described below). We therefore exclude this trait and present results only for our binary measure of fitness (i.e., reproductive success).

GENETIC VARIATION AND HERITABILITY

To evaluate the alternative hypotheses that novel environments could either depress quantitative genetic variation in traits subject to selection versus enable the expression of cryptic genetic variation, we estimated the total genetic variance (V_g) and broad-sense heritability (H^2) for all traits. We used generalized linear mixed models to estimate model parameters in the *R* package *MCMCglmm* version 2.26 (Hadfield 2010). These models employ a Bayesian framework using Markov chain Monte Carlo methods to aid in fitting non-Gaussian data, which is difficult to do using frequentist statistics (Hadfield 2010). For nonbinary traits, we calculated H^2 as V_g/V_p, where V_p is the total phenotypic variance, and $V_p = V_g + V_b + V_r$, where V_b is the variance due to block and V_r is the residual variance. For binary traits, H^2 is calculated in the same manner except that V_p includes an additional variance term of 1 to account for variance introduced by the probit link function (see Supporting Information Methods; de Villemereuil et al. 2013; Hadfield 2018), that is, $V_p = V_g + V_b + V_r + 1$.

We ran individual models for each trait for each year with data pooled across all gardens and including each of the six experimental environments consisting of the two snowpack treatments (control and snow removal) factorially crossed by the three directions that populations were moved relative to their elevation of origin (movement ~200 m upslope from the origin, planting at the local elevation of origin, and movement ~200 m downslope from the origin). Although we included all data for each trait and year in a single model, we obtained separate V_g and V_b estimates in each of the six experimental environments using *idh* covariance structure for random effects, and separate V_r estimates using *idh* residual covariance structure. Fixed effects in each model included initial size (rosette diameter at planting, centered at zero, and rescaled relative to the standard deviation), garden, and experimental environment. We included garden and experimental environment as fixed effects because our models included data from multiple gardens and experimental environments, and we anticipated that mean trait values could differ across these conditions. Random effects in each model included genetic effects of full-sib families (equivalent to total genetic variance, V_g) and block effects (V_b). We did not include garden or experimental environment as random effects because our models consider all gardens and experimental environments of interest, and because it is advisable to reduce the number of random effects in generalized linear-mixed models when possible (Sheth et al. 2018).

In addition to these main models pooled across all gardens, we also re-estimated V_g in models for each garden individually; these separate models still included each of the six movement by snow removal treatment combinations, except at the highest elevation garden where there were only four movement by treatment combination as we did not have any plants moved downslope. These models had reduced sample sizes and therefore reduced statistical power compared to the main models estimated across all gardens, but allowed us to examine whether unique patterns emerged in individual gardens and whether combining data from all gardens in the main models was justified. Fixed and random effects were the same as for the main models except that garden was not included as a fixed effect because only a single garden was represented in each model.

We ran models for 2×10^6 MCMC iterations, with the first 30% of iterations (6×10^5) discarded for burn-in and a total of 2000 iterations retained for estimating the mean and median values and 95% credible intervals of V_g and H^2. To assess the statistical significance of differences among V_g and H^2 estimates across each of the six experimental environments within each model, we sampled the differences between these parameter estimates for all pairwise environments at each of the 2,000 retained iterations and assessed whether 95% credible intervals on these pairwise differences overlapped with zero ($\alpha = 0.05$).

GENETIC VARIANCE–COVARIANCE MATRICES

To test the alternative hypotheses that genetic correlations could either constrain or facilitate adaptive response to novel environments, we estimated multivariate genetic variance–covariance matrices (Hadfield 2010) to calculate the multivariate Robertson–Price identity (Price 1970; Robertson 1966). According to the Robertson–Price identity, the genetic response to selection is the change in trait values ($\Delta\bar{z}$) after a single generation of selection, which can be estimated as the genetic covariance between relative fitness (w) and traits (z) in multivariate models: $\Delta\bar{z} = \sigma_g\,(w, z)$ (Etterson and Shaw 2001; Morrissey et al. 2010), where z is a vector of traits for each set of populations. The Robertson–Price identity is typically solved using relative fitness (Morrissey et al. 2010), but we used an absolute measure of fitness—reproductive success—in the estimation of multivariate genetic covariances of fitness and traits because it is not possible to relativize binary traits, and because using the second fitness component in our hurdle model (i.e., seed number of reproductive plants) would have resulted in dramatically reduced sample sizes due to excluding all data for nonreproductive plants. We also explored preliminary models using an alternative definition of fitness that would avoid these issues (i.e., relativized number of seeds produced with dead plants included as having produced zero seeds), but found that these models performed poorly and often did not produce reliable parameter estimates, likely due to the extremely large number of zeroes.

We estimated genetic (co)variance matrices (Robertson–Price identities) for each year. As flowering traits were available for only the small subset of plants that flowered, it was not possible to include flowering traits and leaf morphology in the same model without excluding large amounts of data for foliar traits. We therefore estimated two separate Robertson–Price identities for (1) all leaf traits only (i.e., leaf herbivory, SLA, and leaf water content), and (2) leaf herbivory and flowering traits (i.e., timing and duration of flowering, and height at flowering). These models allowed us to estimate the effects of genetic correlations among leaf traits and among flowering traits plus herbivore resistance, respectively.

For control and snow-removal treatments, we estimated both multivariate Robertson–Price identities that included fitness plus each complete set of traits, as well as separate univariate Robertson–Price identities for each trait that included only fitness plus one other trait at a time. By comparing the predicted response to selection from multivariate and univariate Robertson–Price identities, we assessed our hypothesis that genetic constraints on evolution could arise due to covariance among traits. If genetic trade-offs constrain adaptation, we expected our univariate Robertson–Price identities for a given trait to predict larger changes in trait values from one generation to the next. For example, if we found that univariate Robertson–Price identities

predicted a greater advancement in flowering time than multivariate models, we would conclude that trade-offs between traits restrict the rate of adaptation of flowering time. In contrast, if multivariate Robertson–Price identities predicted greater genetic responses to selection (e.g., in flowering time) than univariate models, we would conclude that genetic correlations could enhance the rate of trait evolution.

Finally, we also re-estimated multivariate genetic (co)variance matrices (Robertson–Price identities) in separate models for each garden and control or removal snowpack treatment individually, as well as separate models for each garden and each of the six experimental environments (i.e., snowpack treatments × direction of movement) individually, for traits and gardens where there were sufficient data for robust inference.

We modeled our data in the *R* package *MCMCglmm* version 2.26 (Hadfield 2010) for 2×10^6 MCMC iterations with a burn-in period of 6×10^5 iterations and 2000 iterations sampled for estimating model parameters. The fixed effects in our main models were the same as in models for estimating V_g and H^2 when we pooled data across gardens and experimental environment, but when we re-estimated Robertson–Price identities in separate models for each garden individually or each garden and experimental environment individually, we did not include garden or garden and experimental environment as fixed effects, respectively. We specified random effects (genetic effects and block effects) using *us* covariance structure in *MCMCglmm* (Hadfield 2010) (see Supporting Information Methods). To test whether covariance estimates significantly differed between snow-removal and control treatments and between model structures (i.e., univariate vs. multivariate), we calculated the difference between parameter estimates for the 2000 retained iterations of the separate MCMC chains for each pairwise model comparison and tested whether the 95% confidence interval on this difference overlapped with zero ($\alpha = 0.05$).

Results

DATA ASSEMBLY AND SAMPLE SIZES

Total sample sizes of traits ranged from 293 to 4919 (Tables S2 and S3), and were much smaller for flowering traits than for other traits or fitness, as only 11% and 5% of transplanted rosettes flowered in 2017 and 2018, respectively. In preliminary analyses of models to calculate V_g, we noted that 95% credible intervals rapidly became very large when the sample sizes were less than ~40 observations, suggesting that the data were inadequate for meaningful inference in these instances. We therefore only present results for models in which the sample sizes for each experimental environment were greater than 40 (Table S2). As expected, mean values of fitness and traits varied by source location, garden elevation, and snowpack treatment (Figs. S4–S6). In general, fitness (i.e., reproductive success) was highest in mid- to high-elevation sites (Figs. S5G and S6G).

GENETIC VARIANCE AND HERITABILITY

For traits related to flowering and germination phenology, we observed nonzero estimates of genetic variance (V_g) and broad-sense heritability (H^2), and statistically significant differences in these estimates among the six experimental environments, but we were less likely to observe significant patterns in other traits (Figs. 1–4, Figs. S1–S4). For date of germination, V_g was highest for plants moved upslope in the snow removal treatment (Fig. 1B). Additionally, for leaf water content in 2017, V_g of local plants in the control treatment significantly differed from zero and was significantly higher than V_g of plants moved upslope in the snow-removal treatment (Fig. 2C). For both the date and duration of flowering, V_g tended to be higher in local plants and plants moved upslope than in plants moved downslope, and in control rather than snow-removal treatments, and several of these differences were statistically significant (Fig. 3).

Although it is not possible to obtain V_g estimates exactly equivalent to zero, when the posterior distribution of V_g is pushed against zero and the lower end of the 95% credible interval is extremely small, we do not consider these estimates to differ statistically from zero. Using this definition, V_g did not significantly differ from zero and did not vary among environments in either year for height at flowering, reproductive success, germination success, germinant survival, or other leaf traits. Similarly, H^2 estimates for fitness and leaf traits were low (mean: 0.062; range: 0.011–0.165), even when they significantly differed from zero (Figs. S2 and S4). In contrast, H^2 estimates for flowering traits (Fig. S3) and date of germination (Fig. S1B) were generally moderate to high (mean: 0.297; range: 0.004–0.809).

Few novel patterns emerged when estimating genetic variance separately by garden rather than pooled across gardens (Figs. S5–S7), suggesting that pooling across gardens in our main analyses was justified (see Supporting Information Results for details).

GENETIC VARIANCE–COVARIANCE MATRICES

Genetic covariances between fitness (i.e., reproductive success) and leaf traits did not statistically differ from zero for any trait in either year for either control or snow-removal treatments (Fig. 5). These results might suggest that leaf traits had little effect on fitness; however, we caution against this interpretation because even though covariance estimates were not statistically significant, mean estimates were often consistently positive or negative across all models for specific traits. For example, the mean estimate of the covariance between fitness and leaf area removed by herbivores was always negative in 2017 and often only marginally nonsignificant (Fig. 5A). In addition, the mean estimate of the

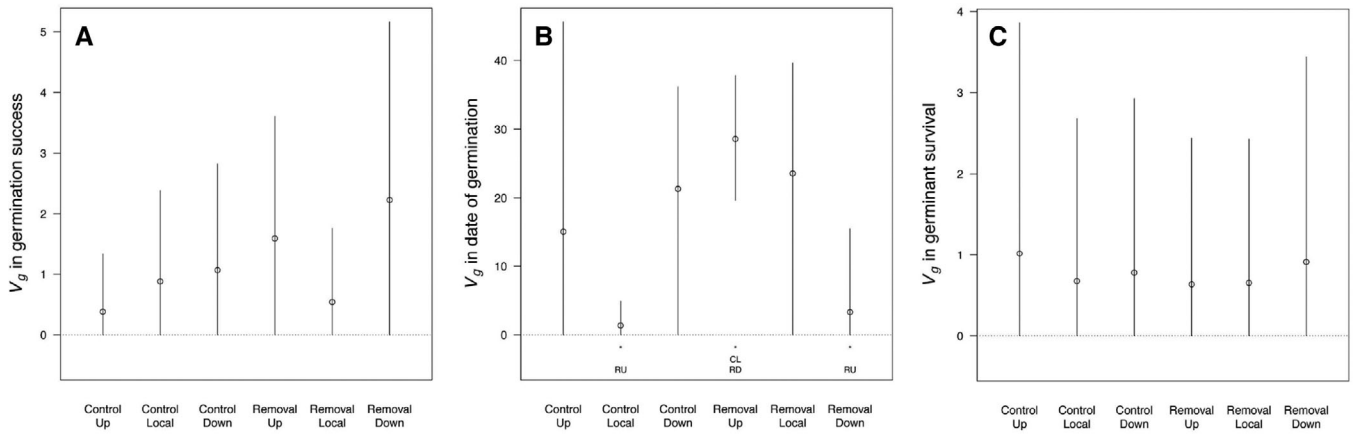


Figure 1. **Genetic variation (V_g) in seedling traits across each of the six experimental environments. An asterisk at the bottom of a panel indicates that V_g significantly differed ($P < 0.05$) from the estimate for at least one other environment, with the specific environment(s) abbreviated in small text (C, control; R, snow removal; U, movement upslope relative to the elevation of origin; L, local planting; D, movement downslope). Circle: mean estimate; solid lines: 95% credible interval.**

covariance between fitness and leaf water content was also consistently negative in 2017 (Fig. 5C).

In contrast, for flowering traits we often observed covariance estimates that significantly differed from zero (Fig. 6): the covariance between fitness and date of flowering was significantly negative in snow-removal treatments in both years (Fig. 6A,B); the covariance between fitness and duration of flowering was positive and marginally nonsignificant in both snowpack treatments in 2017, but not in 2018 (Fig. 6C,D); and the covariance between fitness and height at flowering was positive and either statistically significant or marginally nonsignificant in both snowpack treatments in both years (Fig. 6E,F). In addition, we observed two cases where covariance estimates significantly differed between snowpack treatments, indicating a significant effect of simulated climate change on the predicted response to selection: the covariance between fitness and date of flowering was significantly more negative in the snow-removal treatment (for the univariate model only) than in the control treatment in 2018 (Fig. 6B), and the covariance between fitness and duration of flowering was significantly more positive in the control treatment than in the snow-removal treatment (for the univariate model only) in 2017 (Fig. 6C).

To test our hypotheses that genetic correlations among traits may constrain or facilitate adaptation, we compared predicted responses to selection from the multivariate and univariate Robertson–Price identities. We observed no cases where covariance estimates significantly differed between the multivariate and univariate models. However, we note that the covariance between fitness and date of flowering was substantially more negative in the univariate model than in the multivariate model, for all treatments and years except for the control treatment in 2018 (Fig. 6A,B), although these patterns were not statistically significant.

In several cases, genetic covariances among traits were statistically significant (Table S7). Genetic covariances sometimes aligned with the direction of selection in both traits (e.g., negative genetic covariance between date of flowering and height at flowering in the 2017 control and 2018 snow removal treatments; and negative genetic covariance between date of flowering and duration of flowering in the 2017 control treatment, Table S7b), and sometimes involved traits not strongly correlated with fitness (e.g., a positive genetic covariance between leaf area removed by herbivores and SLA in the 2017 control and 2018 snow removal treatments, Table S7a). We did not observe any statistically significant examples of genetic correlations antagonistic to the direction of selection.

We found no statistically significant changes in genetic covariance estimates between fitness and traits when estimated separately by garden rather than pooled across gardens (Figs. S8 and S9), and 95% credible intervals were very large when covariances were estimated for each of the six experimental environments rather than pooled by control and snow-removal treatments (Fig. S10). These results suggest that pooling across gardens and by snowpack treatments in our main analyses was justified (see Supporting Information Results for details).

Discussion

Climate change is likely to alter patterns of selection and the process of adaptive evolution in natural populations (Etterson 2004; Hoffmann and Sgrò 2011; Franks et al. 2014, 2016). Our results revealed substantial genetic variation in flowering and germination phenology in *B. stricta*, and evidence suggesting these traits will be under selection in both current and future climates. However, the amount of genetic variation expressed in these traits and

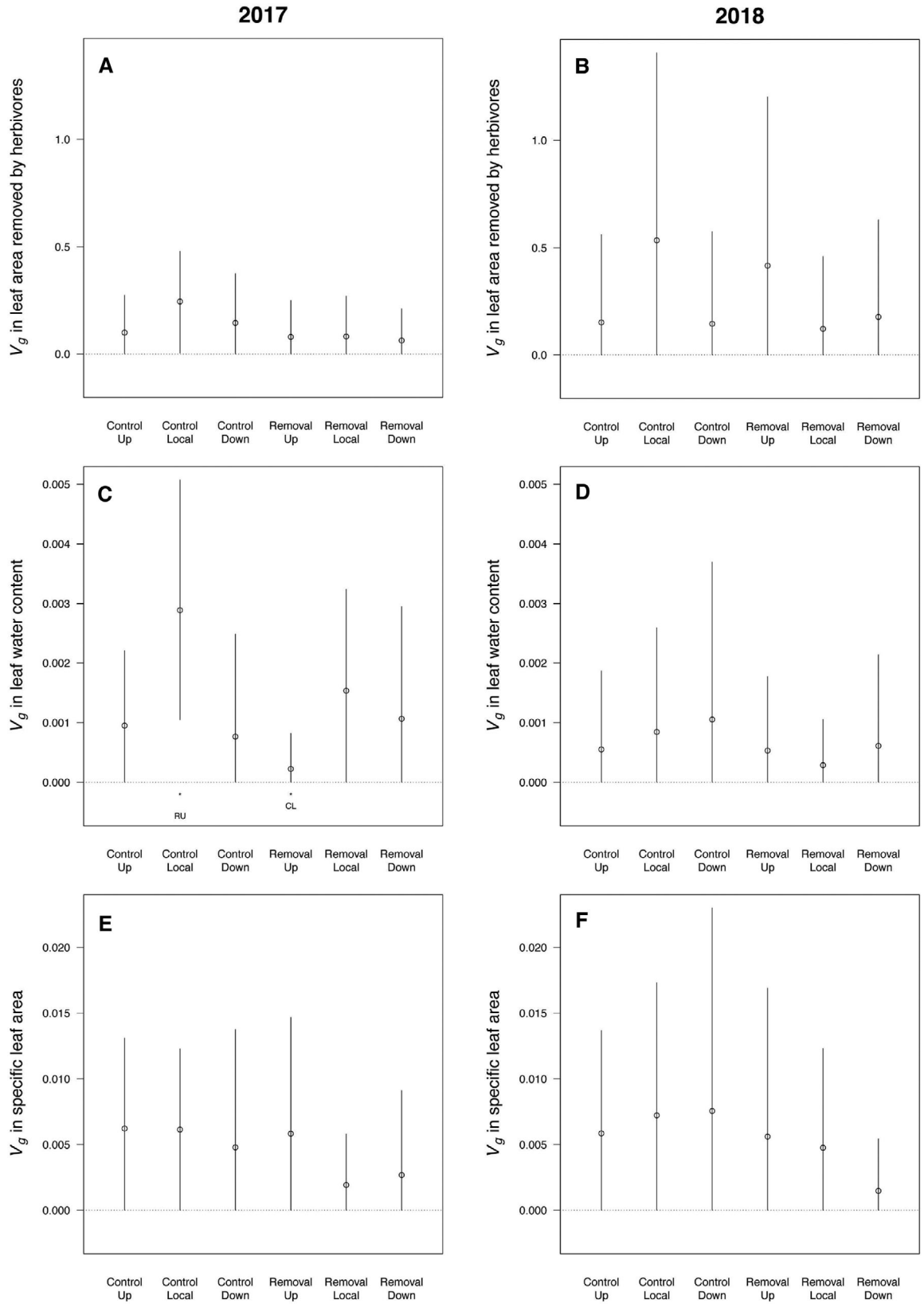


Figure 2. Genetic variation (V_g) in leaf traits across each of the six experimental environments, in 2017 (A, C, and E) and 2018 (B, D, and F). An asterisk at the bottom of a panel indicates that V_g significantly differed ($P < 0.05$) from the estimate for at least one other environment, with the specific environment(s) abbreviated in small text (C, control; R, snow removal; U, movement upslope relative to the elevation of origin; L, local planting; D, movement downslope). Circle: mean estimate; solid lines: 95% credible interval.

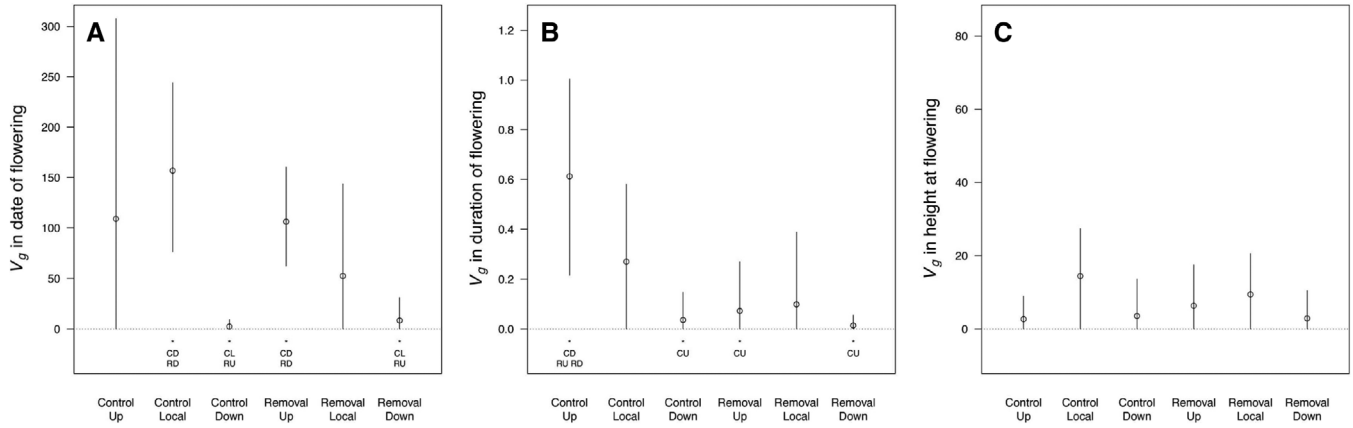


Figure 3. Genetic variation (V_g) in flowering traits across each of the six experimental environments in 2017. An asterisk at the bottom of a panel indicates that V_g significantly differed ($P < 0.05$) from the estimate for at least one other environment, with the specific environment(s) abbreviated in small text (C, control; R, snow removal; U, movement upslope relative to the elevation of origin; L, local planting; D, movement downslope). Circle: mean estimate; solid lines: 95% credible interval.

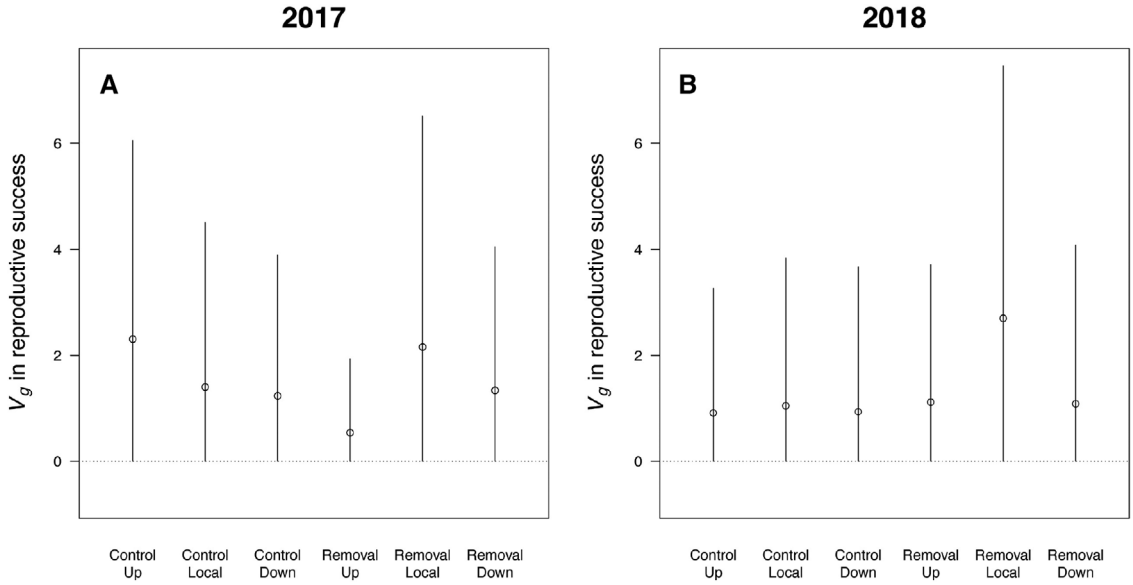


Figure 4. Genetic variation (V_g) in fitness (i.e., binary reproductive success) across each of the six experimental environments in 2017 (A) and 2018 (B). V_g did not significantly differ among environments for any trait. Circle: mean estimate; solid lines: 95% credible interval.

their relationship with fitness depended on the environmental context. In particular, populations moved downslope to warmer, drier climates often showed reduced expression of genetic variation, which may limit their potential to adapt to changing climates. In addition, simulated climate change via snowpack removal could increase the predicted rate of adaptation in timing of flowering, but reduce the predicted rate of adaptation in duration of flowering. In contrast, we found no evidence that genetic correlations among traits might constrain or facilitate the rate of genetic adaptation to climate change for any trait we studied.

Overall, our results suggest that climate change will alter selection pressures on *B. stricta* populations, but reduction of genetic variation may be a more important constraint on adaptation than genetic correlations among traits. However, we caution against broad generalizations, as patterns were often specific to particular traits and environments, and we did not find substantial genetic variation or statistically significant covariances with fitness in other traits we examined, including most leaf morphology traits, herbivore resistance, germination success, and germinant survival. One additional caveat of the study was that we could not analyze seed production among plants that reproduced because small sample sizes precluded models from converging; thus, our models of the genetic response to selection we focused on a crucial binary component of fitness (the probability of reproduction). Despite these caveats, our findings for flowering and germination phenology in particular suggest that climate change may

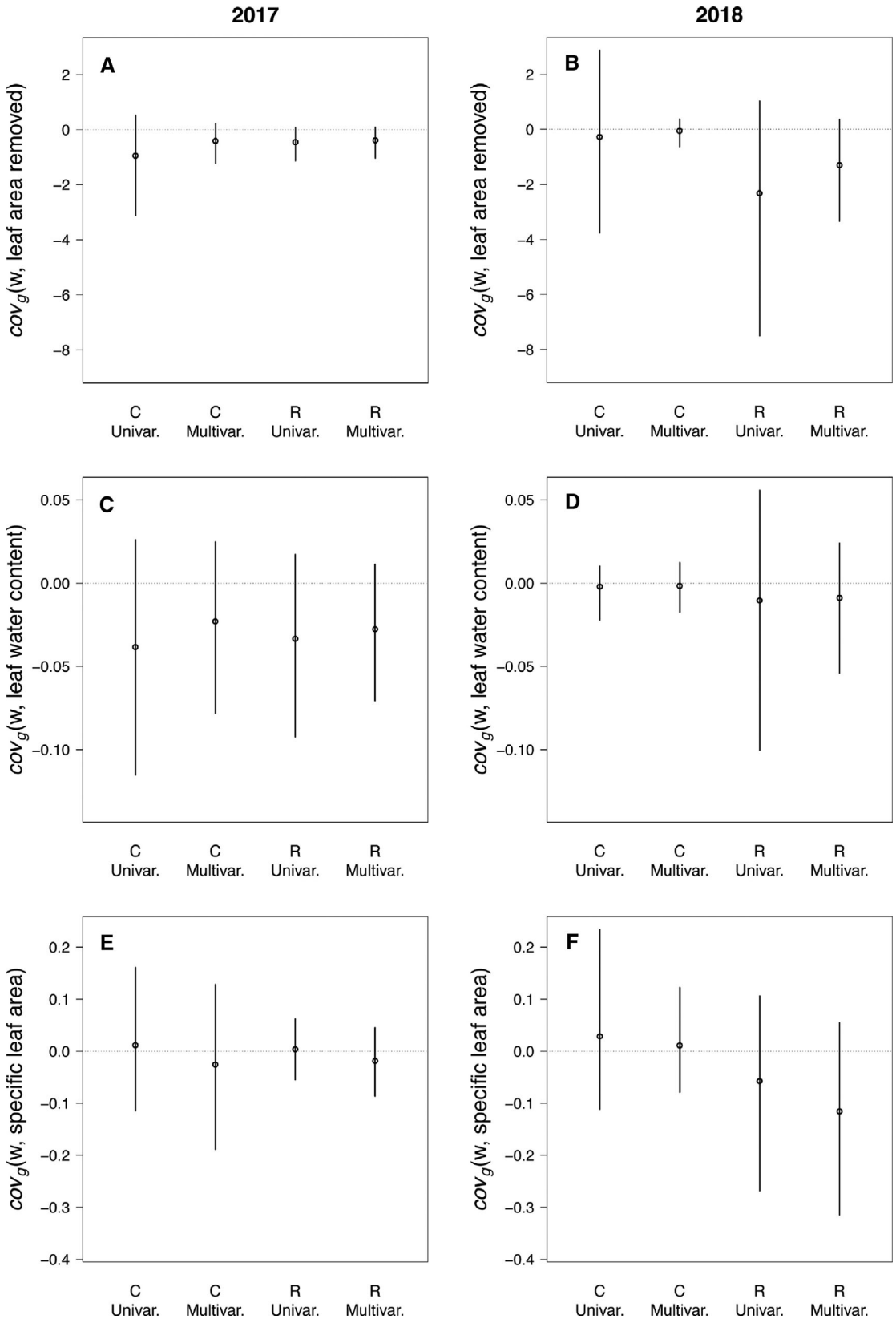


Figure 5. Genetic covariance estimates of fitness (w) versus leaf traits showing the predicted response to selection, from separate models for control (C) and snow-removal (R) treatments, and for both univariate and multivariate Robertson–Price identities, in 2017 (A, C, and E) and 2018 (B, D, and F). Covariance estimates did not significantly differ among models for any trait. Circle: mean estimate; solid lines: 95% credible interval.

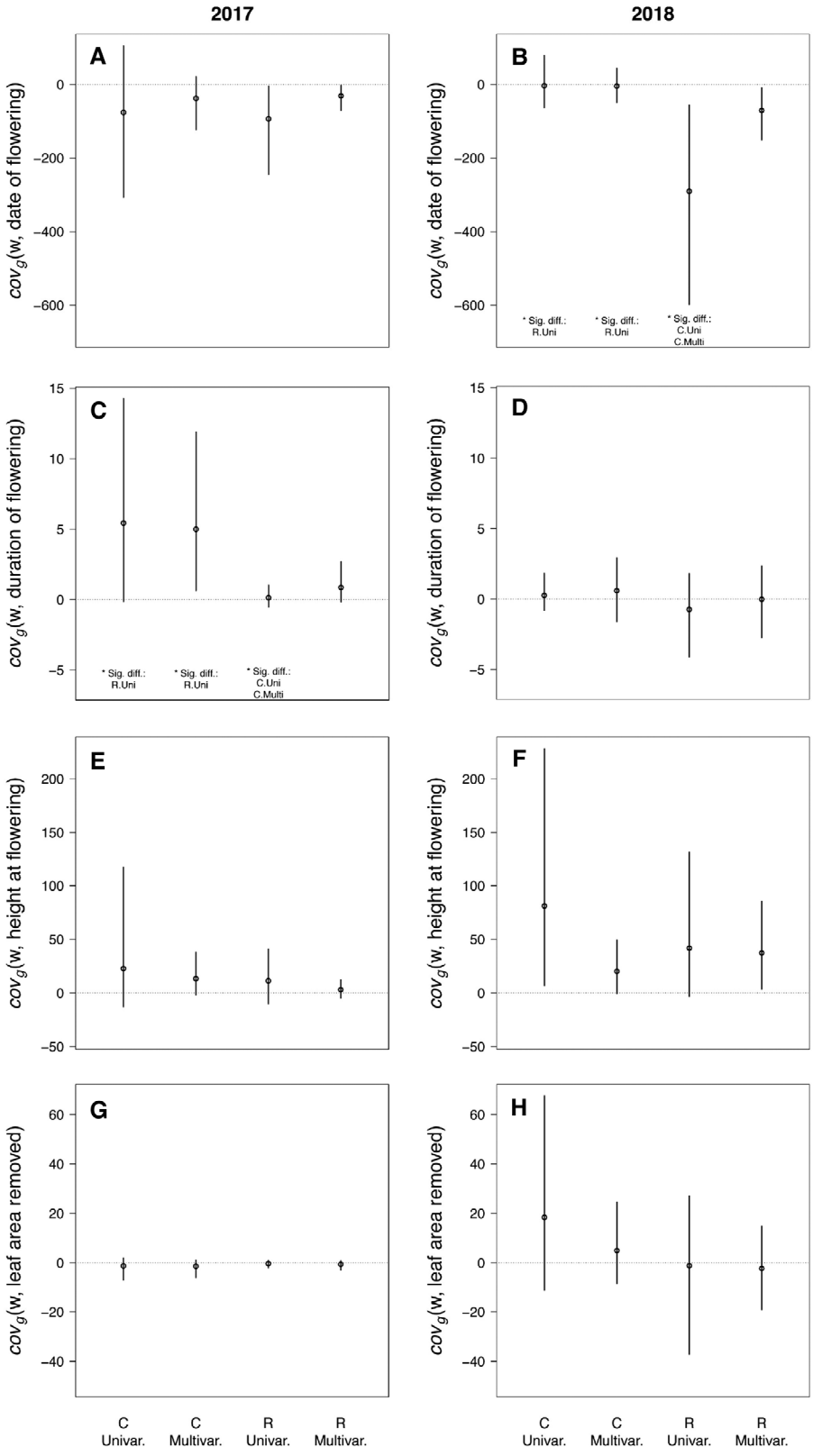


Figure 6. Genetic covariance estimates of fitness (w) versus leaf herbivory and flowering traits showing the predicted response to selection, from separate models for control (C) and snow-removal (R) treatments, and for both univariate and multivariate Robertson–Price identities, in 2017 (A, C, E, and F), and 2018 (B, D, F, and G). An asterisk at the bottom of a panel indicates that the covariance estimate significantly differed ($P < 0.05$) from the estimate for at least one other model, with the specific model(s) given in small text. Circle: mean estimate; solid lines: 95% credible interval.

substantially alter selection pressures and the potential for adaptation in *B. stricta* populations in these key traits.

EXPRESSION OF GENETIC VARIATION IN NOVEL ENVIRONMENTS

Our results partially support our hypothesis that simulated climate change may reduce the expression of quantitative genetic variation and do not support the alternative hypothesis that novel environments could facilitate the emergence of cryptic genetic variation. The amount of genetic variation expressed in flowering and germination phenology frequently changed when populations were exposed to novel environments (Figs. 1 and 3), but patterns depended on the environment and the specific trait. Genetic variation was always equal or greater in plants moved upslope relative to those planted at local elevations (Figs. 1–4), indicating that exposure to a novel locale does not in and of itself cause a decline in expression of genetic variation. Species inhabiting montane ecosystems may be expected to migrate upslope to track warming climates (Freeman et al. 2018), and our results suggest that upslope migrants will either retain or experience an increased expression of genetic variation on which selection can act.

In contrast, genetic variation in flowering and germination phenology often decreased in populations moved downslope relative to those moved upslope or planted at local elevations (Figs. 1B and 3a,b). Because the warmer, drier environments of downslope elevations may serve as a proxy for future climates (Rangwala et al. 2012; Fyfe et al. 2017), these results suggest that *B. stricta* populations that do not migrate upslope, but rather persist in situ as climates change, may experience reduced expression of genetic variation and a reduced ability to adapt. This conclusion contrasts with previous findings in other plant systems: Etterson and Shaw (2001) found that populations of *Chamaecrista fasciculata* moved latitudinally to warmer, drier environments retained substantial genetic variation in traits under selection, and Torres-Martínez et al. (2019) found that adaptive potential of *Lasthenia fremontii* is greater in drought than in wet or normal conditions. In general, determining whether genetic variation will increase, decrease, or remain the same under stressful conditions remains challenging, as theoretical arguments can be made for any one of these outcomes (Hoffmann and Merilä 1999), suggesting that responses to climate change may be difficult to predict and determined by case-specific factors.

Lack of genetic variation in fitness components such as germination success, germinant survival, and reproductive success (Figs. 1 and 4), as well as leaf traits in most environments (Fig. 2), suggests that there is little capacity for adaptation in these traits. Theory predicts that strong selection should purge genetic variation in fitness components (Mousseau and Roff 1987). Indeed, snow removal likely imposes strong selection and populations transplanted into foreign gardens either up- or downslope could also be subject to novel selection, which could deplete genetic variation in fitness components. In addition, ongoing climate change even under control conditions could exert novel selective patterns on local populations, thereby restricting the genetic variation expressed by these populations in our experiment. Despite this expectation, several empirical studies have documented genetic variation in fitness (Merilä and Sheldon 1999). For example, Sheth et al. (2018) found substantial genetic variation in fitness in a *C. fasciculata* population planted both at a novel site and at a site where it naturally occurs. However, only a handful of studies have explicitly examined the relationship between genetic variation in a trait and the strength of its association with fitness in the wild (Teplitsky et al. 2009), and further research will be needed to evaluate the capacity for evolution of fitness components in wild populations.

CLIMATE CHANGE ALTERS SELECTION PATTERNS

Depending on the specific trait and year, our results supported both of our competing hypotheses that simulated climate change could cause either an increase or a decrease in the predicted genetic response to selection. In other cases, we observed no significant effect of simulated climate change on the strength of selection. Significantly nonzero genetic covariances between flowering phenology traits and fitness (Fig. 6) suggest that flowering phenology will be under selection in both current and future climates. However, patterns often differed between years and snowpack treatments (Fig. 6), indicating that the strength of selection on these traits depends on environmental context. In particular, the significantly more negative covariance between date of flowering and fitness in snow-removal treatments relative to control treatments in 2018 (Fig. 6B) suggests that an advance in the timing of snowmelt could induce stronger selection on earlier flowering than under ambient snowmelt regimes; this effect may be particularly pronounced in dry years such as 2018, as the pattern was not observed in the relatively benign year 2017. During the winter of 2017–2018, the region experienced a severe winter drought, with total snowfall (490 cm) equaling only 46% of the average recorded at the Rocky Mountain Biological Lab since 1974 (1064.6 cm) (Wadgymar et al. 2018; Barr 2019). Similarly, the significantly more positive covariance between duration of flowering and fitness in the control treatment relative to the snow-removal treatment in 2017 (Fig. 6C) suggests that an advance in the timing of snowmelt could reduce selection for longer flowering plants; the strength of selection on duration of flowering may also be reduced in drier years such as 2018 (Fig. 6D). Finally, covariance between height at flowering and fitness was significantly positive and of much greater magnitude in 2018 relative to 2017, suggesting that selection for taller height at flowering may also increase in drier years.

In sum, these patterns highlight the influence of environment on patterns of natural selection and suggest that climate change will alter selection pressures in *B. stricta.* Both an advance in the timing of snowmelt and climatic drying may impose novel selection, although the strength of selection may either increase or decrease with climate change depending on the particular trait. Differences in precipitation regimes strongly influence variation in selection patterns at a global scale, suggesting that shifts in precipitation will alter natural selection as climates change (Siepielski et al. 2017). Furthermore, phenological traits are predicted to experience altered selection regimes under future climates due to selection for synchrony between phenology and changing environmental conditions (Gienapp et al. 2014).

In contrast, the absence of statistically significant covariances between leaf traits and fitness may indicate that the observed variation in these traits had little impact on fitness. However, shifts in selection on both reproductive phenology and leaf morphology have been observed in populations of *C. fasiculata* moved latitudinally to warmer, drier sites that may mimic future climates (Etterson 2004), suggesting that climate change also has the capacity to alter selection on plant morphology. Alternatively, the covariances close to zero we observed in *B. stricta* may suggest that leaf traits are under stabilizing selection, rather than directional selection. Visual inspection of data suggested that SLA might be under stabilizing selection, as most plants that reproduced had intermediate values of SLA (data not shown). However, this pattern was not observed for leaf area removed by herbivores nor for leaf water content, suggesting that these traits may have indeed been unrelated to fitness in our datasets or that effects were not pronounced enough to achieve statistical significance given our sample sizes.

LACK OF ANTAGONISTIC GENETIC CORRELATIONS

Although we did observe several statistically significant genetic correlations (Table S7), we found no evidence that these correlations are likely to either constrain or facilitate evolution. In particular, we observed a complete lack of significant differences when comparing covariance estimates from the multivariate Robertson–Price identities that included fitness plus multiple traits to covariance estimates from the univariate models that included only fitness plus a single trait at a time (Figs. 5 and -6). These results contrast with previous findings evaluating the effect of genetic correlations on the rate of adaptation in contexts relevant to climate change; for example, antagonistic genetic correlations are expected to slow the rate of adaptation in both *C. fasiculata* (Etterson and Shaw 2001) and barn swallows (Teplitsky et al. 2011). However, we note that genetic correlations among traits from plant and animal studies conducted in field, lab, and greenhouse settings more generally have been found to have a range of effects on the rate of evolution, include strong constraint, strong facilitation, or no effect at all (Agrawal and Stinchcombe 2009).

The positive genetic covariances between herbivore damage and SLA were expected (Wilson et al. 1999), as alleles that cause plants to have thinner leaves may also make them more palatable to herbivores through their effect on leaf thickness. Significantly negative genetic covariances between date of flowering and height at flowering (Table S7b) were unexpected, as we would have predicted a positive relationship between these traits (Troth et al. 2018). Physiological limitations on growth rate could mean that plants that flower rapidly would be smaller than those that are slower to flower. These limitations might create a positive phenotypic correlation between date of flowering and height at flowering but would not necessarily indicate an underlying genetic correlation. However, there is evidence that specific alleles control a large size-slow flowering versus small size-rapid flowering trade-off in *Mimulus guttatus* (Troth et al. 2018), indicating that these correlations may indeed have a genetic basis in some species. In contrast, our results revealed that rapid flowering was genetically correlated with larger size at flowering (Table S7b); the observed underlying genetic covariation therefore does not correspond to the expected phenotypic correlation. This pattern could arise if other genetic trade-offs operate in *B. stricta* populations; for example, alleles promoting rapid initial growth and flowering could make individuals less stress tolerant than alleles promoting slow growth, small stature, late reproduction, and high stress tolerance. Alternatively, even if life-history trade-offs involving stress tolerance are not involved, a genetic correlation could arise because of the reduction in water resources across the growing season from snowmelt in May–June until monsoon rains occur in mid-July. Alleles that promote early flowering may allow individuals to capitalize on high soil moisture from snowmelt early in the growing season, whereas alleles that delay flowering may also reduce height at flowering because late-flowering individuals may not have sufficient water resources to attain the stature that early-flowering individuals do. Given the trait data we had available, we were unable to fully address these hypotheses.

Although we do not find evidence of an effect of genetic correlations on the rate of adaptation, we have considered only a subset of traits that could potentially affect fitness, and it is possible that correlations between the traits we included and other unmeasured traits could alter the rate of adaptation. Correlations among traits depend on environmental conditions (Sgrò and Hoffmann 2004; Merilä 2012), and our experiments have not exhaustively examined the effects of all aspects of climate change *B. stricta* populations are likely to encounter. Genetic correlations among traits may continue to shift as climate change progresses, and it is possible that constraint or facilitation due to these correlations could arise at some point under future conditions.

CONCLUSIONS AND FUTURE DIRECTIONS

Responses to anthropogenic climate change are likely to be complex and may include a mixture of migration, adaptation, and ecological responses (Aitken et al. 2008; Anderson et al. 2012b). Our findings suggest that adaptation itself may be nuanced and interact with other responses. For example, *B. stricta* populations that migrate upslope to novel environments in response to climate change may retain genetic variation upon which selection can act in key phenological traits, whereas expression of genetic variation may decline in populations that fail to migrate and are exposed to warmer, drier climates. A simulated advance in the timing of snowmelt, which is projected to occur as climates change (Rangwala et al. 2012; IPCC 2014; Fyfe et al. 2017), also altered the strength of selection pressures on these traits. Finally, despite statistically significant genetic correlations among certain traits, these correlations were not sufficient to either facilitate or constrain the predicted response to selection. Our experimental approach represents one aspect of an integrated toolbox for assessing potential responses to climate change, and highlights the complex, trait- and context-specific dynamics that may be revealed by experiments that directly assess evolutionary potential in field settings. Approaches such as these, in combination with studies assessing migratory, plastic, and ecological responses, will continue to be needed to attain a holistic and detailed understanding of how natural populations may respond to changing climates.

AUTHOR CONTRIBUTIONS

JTA conceived the study, designed the experiment, and conducted fieldwork, JBB performed statistical analyses, and JBB and JTA wrote the manuscript.

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DATA ARCHIVING

The doi for our data is 10.5061/dryad.0p67v8g.

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Supporting Information

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

Table S1. Ordinal day of year of snowmelt in control and snow-removal treatments (mean $\pm$ SD) in the springs of all growing seasons of this experiment.
Table S2. Sample sizes of traits in models for estimating genetic variation (V_g) and heritability (H^2), split by each of the six experimental environments for which separate estimates were obtained.
Table S3. Sample sizes of traits in models for estimating genetic (co)variance matrices (Robertson–Price identities).
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