Genomic architecture controls multivariate adaptation to climate change

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As climate change advances, environmental gradients may decouple, generating novel multivariate environments that stress wild populations. A commonly invoked mechanism of evolutionary rescue is adaptive gene flow tracking climate shifts, but gene flow from populations inhabiting similar conditions on one environmental axis could cause maladaptive introgression when populations are adapted to different environmental variables that do not shift together. Genomic architecture can play an important role in determining the effectiveness and relative magnitudes of adaptive gene flow and *in situ* adaptation. This may have direct consequences for how species respond to climate change but is often overlooked. Here, we simulated microevolutionary responses to environmental change under scenarios defined by variation in the polygenicity, linkage, and genetic redundancy of two independent traits, one of which is adapted to a gradient that shifts under climate change. We used these simulations to examine how genomic architecture influences evolutionary outcomes under climate change. We found that climate-tracking (up-gradient) gene flow, though present in all scenarios, was strongly constrained under scenarios of lower linkage and higher polygenicity and redundancy, suggesting *in situ* adaptation as the predominant mechanism of evolutionary rescue under these conditions. We also found that high polygenicity caused increased maladaptation and demographic decline, a concerning result given that many climate-adapted traits may be polygenic. Finally, in scenarios with high redundancy we observed increased adaptive capacity. This finding adds to the growing recognition of the importance of redundancy in mediating *in situ* adaptive capacity and suggests opportunities for better understanding the climatic vulnerability of real populations.

adaptation | climate change | | landscape genomics | spatial simulation | gene flow | genomic architecture | genetic redundancy

Climate change is one of the foremost threats to biodiversity in the Anthropocene. The ability of species to persist within their current ranges will likely depend largely upon their abilities to locally adapt to new climate conditions — a concept frequently referred to as 'adaptive capacity' or 'evolutionary potential' (1–5). Because beneficial *de novo* mutations take a long time to arise, this adaptation will likely be facilitated by the reconfiguration of existing adaptive genetic diversity (6). A common conceptual model underlying this scenario is that of adaptive gene flow tracking a shifting climatic gradient (7, 8), which would bring beneficial genes into recipient populations from 'climate-suitable' populations whose current climates approximate future local conditions (9). This model of adaptive gene flow has both theoretical (10–12) and empirical (13, 14) support but meets resistance under conditions in which gene flow can be maladaptive (11, 15–19). In these circumstances, shifting allelic covariance — the *in situ* recombination of standing genetic variation into new, adaptive genotypes — could be a more efficient mechanism underlying local adaptation to environmental change.

In recent decades, research bridging the fields of molecular population genetics and quantitative genetics (20–23) has revealed that the genomic architecture of a trait is a core determinant of whether and how that trait becomes locally adapted (24). Among the key aspects of genomic architecture that influence adaptation (21, 24–26) are the number of loci underlying a trait (henceforth, 'polygenicity'), the rate of recombination between these loci (i.e., linkage), and the number of distinct genotypes that yield identical phenotypes (henceforth, 'genotypic redundancy'). Previous research suggests that ecologically-important traits can vary from having few loci of large effect (27, 28) to many loci of small effect (20, 29–32) and shows that variation in polygenicity can determine the rate and nature of local adaptation (33). Linkage controls the likelihood that adaptive alleles cluster together, essentially forming alleles of larger effect size that are stronger targets of selection and more resistant to swamping gene flow (25), thereby facilitating local adaptation (12). Genotypic redundancy — a form of genetic redundancy that is defined as when more than one genotype can produce the same phenotype (34) — can facilitate local adaptation by allowing the existence of a stable phenotypic cline governed by concerted shifts in underlying allele frequencies (33, 35, 36). We refer to this phenomenon as 'transient genomic architecture.'

The influence of genomic architecture on the nature and outcomes of local adaptation to changing environmental gradients has been studied to a limited extent, with nearly exclusive focus on univariate models of the selective environment (but see (37)). These models have limitations for studying adaptation to climate change because, in nature, species can be adapted to multiple, independent environmental gradients (38) that can shift differentially, and thus decouple, as climate change advances (39, 40), leading to the emergence of novel multivariate landscapes (41–43). Thus, it is important to investigate how the genomic architectures of multiple traits can combine to drive multivariate adaptation under climate change. Gene flow from 'climate-suitable' portions of a species' range is often assumed to be beneficial for adaptation to climate change. This may be accurate from the perspective of a single trait adapted to a shifting climatic gradient, but it may be an invalid assumption if the gene flow also carries linked variation for a trait adapted to a second environmental variable from

component	level	parameter value
genotypic redundancy	low:	`redund` = 1
	high:	`redund` = 2
polygenicity	low:	`n_loci` = 4 × `redund`
	mod:	`n_loci` = 20 × `redund`
	high:	`n_loci` = 100 × `redund`
linkage	low:	`recomb` = 0.5
	mod:	`recomb` = 0.05
	high:	`recomb` = 0.005

Table 1. Parameter values used for each of the three focal components of genomic architecture. The full factorial combinations of these parameter values constitute the set of 18 simulation scenarios for which we present results.

which the shifting gradient has decoupled. Under this scenario, gene flow may introduce alleles for the second trait that are disadvantageous and that could counteract any fitness advantage gained through the first trait. Thus, the genomic architectures of both traits may determine evolutionary outcomes by controlling the relative likelihoods of adaptation by gene flow and of *in situ* adaptation by shifting allelic covariance (10, 37).

Spatially-explicit simulation is one of our strongest tools for improving our understanding of the complex dynamics of gene flow and adaptation under climate change (44). In this study, we use individual-based, spatially-explicit simulations, constructed in `Geonomics` (45), to test how genomic architecture influences multivariate adaptation to climate change. We simulate the adaptation of a single population continuously distributed on a two-dimensional landscape composed of two environmental variables, each structured as a gradient that runs parallel to the x-axis (Fig. 1) and that exerts selection on a separate trait. In our main models, we then simulate climate change on that landscape by holding one gradient constant while gradually shifting the other gradient along the x-axis, such that the decoupling environment pushes local fitness peaks toward novel regions of two-dimensional trait space (Fig. 1). We run 100 pairs of climate change simulations and null (stable-climate) simulations for each of eighteen scenarios resulting from the full factorial crossing of three key components of genomic architecture: genotypic redundancy, polygenicity, and linkage (Table 1).

We analyze variation in the resulting spatiotemporal patterns of gene flow, population size and density, and phenotypic distributions — all of which are emergent properties of our simulation parameterizations (Code Sample S1) — to test a series of hypotheses about the influence of genomic architecture on multivariate adaptation under climate change. First, we hypothesize that up-gradient gene flow will be higher under climate change than under a stable climate across all scenarios but that gene flow contributes least to climate change adaptation when linkage is low and polygenicity is high. This is because we expect gene flow to always have at least some adaptive value, but we also expect low-linkage, high-polygenicity architectures (i.e., 'dispersed' architectures (24)) to exhibit quick *in situ* adaptation via shifting allelic covariance among many small-effect alleles, facilitating phenotypic shifts in the absence of up-gradient gene flow. Second, we hypothesize that stronger linkage and higher polygenicity will reduce a

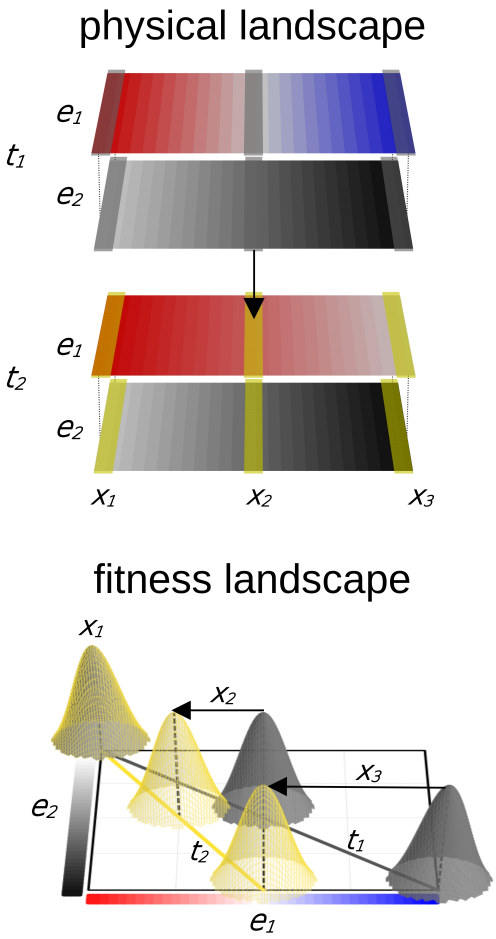


Fig. 1. Conceptual model of adaptation to climate change. The top panel depicts the two-layered physical landscape used in our simulations, showing the shifting environmental gradient (e_1) in a blue-red color ramp and the stable gradient (e_2) in a white-black color ramp. The landscape is shown both before climate change (t_1) and after (t_2). The bottom panel depicts a fitness landscape for two traits adapted to the shifting (e_1) and stable gradients (e_2). Three example positions on the physical landscape (x_1, x_2, x_3) are shown as boxes delinated y-axis cross-sections, both before climate change (gray) and after (yellow), and their corresponding fitness peaks are shown as color-matched kernels on the fitness landscape. The gray and yellow lines on the fitness landscape indicate the fitness optima defined by the environments that exist before (t_1) and after climate change (t_2). Shifts in local fitness peaks are shown as labeled arrows (x_2, x_3); the environment at the far left of the physical landscape does not change, so x_1's fitness peaks are overlapping and have no shift.

population's adaptive capacity under climate change, manifesting as greater reductions in population size and mean fitness and more persistent maladaptation, because both conditions impose longer expected wait times for the emergence of recombinant haplotypes that push phenotypes further from their pre-change fitness peaks. Finally, we hypothesize that higher genotypic redundancy will facilitate adaptation to shifting gradients, much as it does on stable gradients (33, 35, 36), resulting in smaller reductions in population size and mean fitness.

Methods

Simulations. We performed simulations using `Geonomics` (45), a Python (46) package for forward-time, agent-based, continuous-space landscape genomic simulations. All of our simulated scenarios feature a species with two traits, each of which experiences selection on the basis of a different environmental variable. Both environmental variables are modeled as linear gradients running along the x-axis (Fig. 1) that initially span environmental values from 1 to 0, left to right across the landscape. The genome is modeled as an array of length L, which in our 2-trait simulations equals 2 times the number of genes per trait. Instead of randomly assigning loci to either of the two traits, we alternated locus trait assignment along the genome to avoid creating islands of within-trait linkage that would vary across iterations and introduce noise in our results. The fitness of individuals is a function of the difference between their local environmental values and their phenotypes, which are determined by the additive effects of multiple loci (i.e., without pleiotropy or epistasis), a reasonable approximation of many traits in real populations (32). Individuals have continuous spatial coordinates, and their local environmental values are found in the landscape cells within which their coordinates fall. Each time step has a movement phase during which each individual moves along a vector composed of a randomly drawn direction (from a uniform circular distribution) and a randomly drawn distance (from a Wald(0.25, 0.5) distribution, such that most movements are less than one landscape cell in length).

Simulations start with a neutral burn-in period that does not include differential fitness. The burn-in is concluded when statistical tests of temporal and spatial population stability are passed, at which point individuals are randomly assigned genomes based on 0.5|0.5 allele frequencies at all loci. Simulations then run for 2,500 time steps with differential fitness, generating a pattern of local adaptation to the initial environment. After that, one environmental layer undergoes a change event in which the gradient's values shift over a period of 250 time steps, resulting in a final gradient that spans values from 1 to 0.5, left to right. This creates a scenario in which the two environmental variables become decoupled, leading to the emergence of novel environments (i.e. sites occupying new values in two-dimensional environmental space), effectively modeling a common phenomenon under climate change (41–43). This generates spatially heterogeneous rates of climate change, ranging from no change at the leftmost edge to 0.002 units per timestep at the rightmost edge. We chose this scenario because one with spatially homogeneous rates of change would generate an artefact of range expansion whose genomic signal could not reliably be disentangled from that of climate change adaptation. Hence, the approach we chose here allows us to isolate the evolutionary dynamics resulting from the components of genomic architecture that define our scenarios and hypotheses. The pre-climate change population sizes in our simulations varied around 5,800-6,100 individuals, which yields mean times to fixation of approximately 16,000-17,000 time steps (18, 45), roughly an order of magnitude larger than the total simulation length. Thus, the effects of drift during these simulations should be low given the relatively large population sizes.

We used a custom Python script to set values for the parameters of interest in our simulations: the number of loci underlying each trait (parameter `n_loci`), the recombination rate between neighboring loci (parameter `recomb`), and the level of genotypic redundancy (parameter `redund`). The values we assigned to these parameters are provided in Table 1, and a visual depiction of the difference between low- and high-redundancy scenarios for all phenotypes is provided in Fig. S1. We ran the simulations on the savio3 partition of UC Berkeley's Savio computing cluster (each node has 96 GB RAM and 32, 2.1-GHz Skylake processors). For each scenario, we ran a total of 100 iterations, featuring a 250 time-step climate change period with natural selection (henceforth, the 'main' scenarios), and 100 iterations of a paired null scenario without natural selection (henceforth, the 'null' scenarios). We set all other `Geonomics` parameters to their default values. Some values of interest that might be explicit parameter settings in other simulation programs are instead emergent properties in `Geonomics`; for example, the population size values we report emerge from the interaction of several explicit parameters, including the raster of local carrying capacities, the population intrinsic growth rate, the number of offspring per reproduction event, and the death rates resulting from the parameters controlling density-dependent mortality and natural selection. The complete set of `Geonomics` parameters and the values we assigned to them across all models are provided in Code Sample S1. The parameters we set correspond best to a scenario of a moderately mobile species with occasional longer-distance dispersal, overlapping generations, and repeat reproduction of small numbers of offspring.

Using a combination of internal `Geonomics` functions and custom Python code, we designed a set of data outputs from each model run to visualize results and test hypotheses. We saved tables of the locations and phenotypes for all individuals at the beginning and end of the climate change period. We also saved time series of population size, mean fitness, and the mean phenotype of the trait adapted to the shifting gradient. We gathered this data at every time step for the 250 time steps immediately before the onset of climate change, 250 time steps during the climate change period, and 250 time steps after climate change completed (hereafter, the 'post-change period').

We also saved data on the vector directions of gene flow occurring during climate change by keeping data for two randomly chosen loci underlying the trait adapted to the shifting environmental gradient (with positive effect) for all of the individuals remaining in the final time step. Capturing loci expected to facilitate adaptation to increasing environmental values allowed us to track up-gradient gene flow, and it provided equal sample sizes across scenarios for downstream analysis (which was constrained to the number of positive-effect loci in the low-polygenicity, low-redundancy scenarios). We collected

these data using an internal function that extracts data from the spatial pedigrees stored in the simulation's `tskit` (47) data structures. We also calculated a single summary metric of 'up-gradient gene flow' for each iteration:

$$GF_{up} = \frac{\sum_{i}^{n} \cos\theta}{n}, \ \cos\theta \geq 0,$$

where θ is the angle of gene flow, expressed counterclockwise from the right. The $\cos\theta \geq 0$ condition allowed us to track only rightward (up-gradient) gene flow and to omit leftward (down-gradient) gene flow which would be maladaptive for the positive-effect loci we tracked and, thus, low irrespective of scenario.

Analysis. We analyzed the results of our simulations using custom scripts written in Python (46) and R (48). To test our first hypothesis — that up-gradient gene flow should be greater under climate change scenarios — we first produced a visualization of the directional distributions of gene flow under all 18 scenarios, comparing between main and null simulations (Fig. 2) based on the random sample of the gene flow that occurred during the climate change period that we captured from our simulations. We then fitted a mixture of 4 von Mises distributions to that data using the R package `movMF` (49), yielding 12 parameter estimates defining each simulation's fitted mixture distribution. For each of the 18 scenarios, we then plotted the probability density function described by the means of all vectors of fitted parameters. We did this separately for null scenarios and for main scenarios then overlaid the results for the main scenarios (in red) on top of the null results (in blue; Fig. 2), providing a visualization of the directionality of gene flow within each climate change scenario compared to its null expectation.

We also ran a simple linear regression of the main vs. null difference in up-gradient gene flow density as a function of polygenicity, linkage, and redundancy. We coded the genomic architecture components as integer variables representing the levels of the parameter values used in the simulations (redundancy: low = 1, high = 2; polygenicity: low = 0, moderate = 1, high = 2; linkage: low = 0, moderate = 1, high = 2). We used the regression results to test both predictions for our first hypothesis: (1) that the main main - null difference in up-gradient gene flow should have 95% confidence intervals > 0 under all scenarios (calculated using the `stats` package's `predict.lm` function with the argument `interval='confidence'`), indicating significant up-gradient gene flow under climate change; and (2) that the coefficients for the linkage (β_l) and polygenicity (β_p) terms of the model should be significantly positive and negative, respectively, indicating that higher levels of gene flow are associated with stronger linkage and lower polygenicity.

To visually assess our second and third hypotheses, we created a series of plots comparing climate change-driven demographic shifts and maladaptation across all 18 scenarios and between our null and main models. First, we plotted the null and main time series of two demographic metrics, mean fitness and population size, for each of our 18 scenarios, combining the results for all 100 iterations under each scenario. For each time series we calculated the mean and 5th and 95th percentiles at each time step (Figs. 3 and S2). We also summarized all scenarios in a pair of box plots (Fig. S2).

To better understand changes in population size and distribution, we also mapped before and after comparisons of population densities for all 18 main scenarios (Fig. S3). Each population density map was calculated as the mean population density at each cell on the landscape, averaged across all 100 iterations.

Finally, to visualize maladaptation, we plotted each scenario's mean phenotypic distributions before and after climate change as scatter plots of the density of individuals occurring across two-dimensional trait space. We plotted lines and wedges depicting the average maladaptation observed across each scenario's 100 iterations (Fig. 4). We refer to the wedge as 'persistent maladaptation,' and we calculated it as the difference between: a) the area within two-dimensional trait space that the population's phenotypic distribution would have needed to shift through during the climate change event to remain optimally fit to its environment, and b) the observed area of phenotypic shift within a scenario's 100 simulations. We qualify this metric as 'persistent' to emphasize that it does not reflect transient maladaptation that arises but then resides during the period of climate change but rather reflects only maladaptation that remained at the end of the climate change period. To measure this area, we first determined the triangular area between the expected central tendency lines of the optimal two-dimensional phenotypic distributions before and after the climate change event. Then, for each model run, we used ordinary least squares (OLS) to fit a central tendency line to the 100-iteration ensemble phenotypic distribution observed at the end of the climate change event (fixing the y-intercept at the (1,1) point in phenotypic space, which represents the unchanging phenotypic optimum at the leftmost extent of the landscape). The area of the wedge between the expected and observed post-change central tendency lines provides our measure of a scenario's persistent maladaptation. We plotted before and after scatter plots of the ensemble datasets of individuals' two-dimensional phenotypes (binned to a grid of regular points for interpretability). We also produced these plots (Fig. S4) using data from our null simulations to demonstrate that all differences in maladaptation observed between scenarios were attributable to climate change.

To statistically evaluate our results, we ran simple linear regressions for each of our three response variables measuring population-level changes during the climate change event — change in mean fitness, change in population size, and persistent maladaptation — with polygenicity, linkage, redundancy, and nullness serving as explanatory variables. We modeled nullness as a binary categorical variable (null = 0, main = 1) and again modeled the genomic architecture components as integer variables, as described above. We used these regressions to test our second (polygenicity and linkage) and third (redundancy) hypotheses. Specifically, our second hypothesis predicts that the coefficients of the linkage and polygenicity terms are significantly non-zero and negative (for changes in fitness-change and population size) and positive (for the maladaptation model), while our third hypothesis predicts significantly non-zero redundancy coefficients with the opposite signs.

Results

Gene flow. Under our simulations, climate change led to a nearly universal increase in up-gradient gene flow compared to null simulations with no change to either environmental variable. For all 18 of our simulated scenarios (Fig. 2), the simula-

tions with climate change exhibited greater up-gradient gene flow than the null scenarios, and linear regressions modeling the effects of linkage, redundancy, and polygenicity on up-gradient gene flow found that the fitted 95% confidence intervals for up-gradient gene flow were > 0 for all but one scenario (the moderate-polygenicity, low-linkage, high-redundancy scenario; Table S1). However, the magnitude of this increase in gene flow was minimal under some scenarios. We found that the difference in up-gradient gene flow between climate change and null simulations was positively correlated with linkage ($\beta_l = 0.0129 \pm 0.0006, P < 1 \times 10^{-15}$) and inversely correlated with polygenicity ($\beta_p = -0.0142 \pm 0.0006, P < 1 \times 10^{-15}$), corroborating our first hypothesis. Correspondingly, and in line with expectations, down-gradient gene flow was universally suppressed under climate change (Fig. 2). Of the three components of genomic architecture that we tested, polygenicity had the most striking effect on the extent to which up-gradient gene flow contributed to adaptation; moderate and high polygenicity scenarios generally had much lower up-gradient gene flow than did low-polygenicity scenarios, with low-redundancy, independent-linkage scenarios being the main exception (Fig. 2). Moderate-polygenicity scenarios actually showed the lowest overall increase in up-gradient gene flow, though differences between moderate- and high-redundancy scenarios were minor.

Linkage and polygenicity. As expected, our null simulations showed essentially no changes in mean fitness (Fig. 2) or population size (Fig. S2), aside from small modeling artefacts present in both the null and climate-change scenarios, and the phenotypic distributions for the populations in these simulations were stable through time (Fig. S4). The results of our climate change simulations exhibited decreases in population size and mean fitness that are the expected results of increasing maladaptation (10). They also revealed environment-tracking phenotypic shifts (Fig. 4) in line with expectations (Fig. 1), though these shifts lagged behind environmental change to some extent, producing suboptimal mean fitness at the end of the climate change period. Across scenarios, the demographic responses to climate change, in terms of population size and fitness, increased with increasing linkage (change in fitness: $\beta_l = -0.0018 \pm 0.0001, P < 1 \times 10^{-15}$; change in population size: $\beta_l = -33.330 \pm 1.287, P < 1 \times 10^{-15}$). We also found greater maladaptation, defined as the area in two-dimensional trait space separating the central line of a population's post-change phenotypic distribution from the central line of the distribution that would optimally track the changing environment (Figs. 4 and S4), associated with increasing linkage (maladaptation: $\beta_l = 0.0038 \pm 0.0004, P < 1 \times 10^{-15}$).

The magnitude of demographic responses also showed a signal of overall increase with increasing polygenicity (change in fitness: $\beta_p = -0.0022 \pm 0.0001, P < 1 \times 10^{-15}$; change in population size: $\beta_p = -15.070 \pm 1.287, P < 1 \times 10^{-15}$; maladaptation: $\beta_p = 0.0097 \pm 0.0004, P < 1 \times 10^{-15}$), although the trend was non-monotonic and complex. Responses were smallest at moderate polygenicity, more pronounced at low polygenicity, and highest at high polygenicity and low redundancy (Figs. 3 and S2). In fact, under high polygenicity and low redundancy, populations declined so strongly that adaptive capacity was effectively outstripped, and the declines persisted throughout the climate change period, with little indication of evolutionary rescue (i.e., stabilization and re-

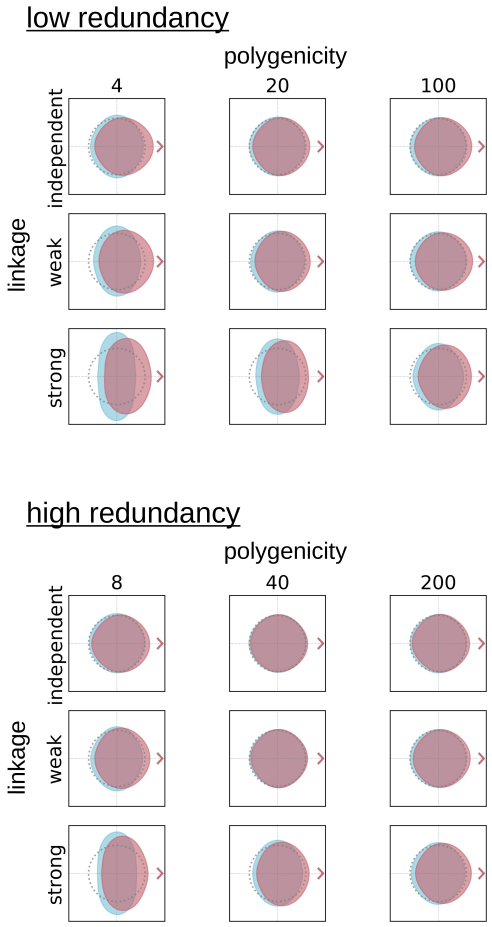


Fig. 2. Distributions of gene flow directions during the climate change period of our climate change simulations (red) compared to null simulations (blue) for our 18 scenarios. The shifting environmental gradient moves to the right (in the direction of the arrow) in our simulations, so rightward gene flow represents up-gradient gene flow, and upward and downward (i.e., 'on contour') gene flow is perpendicular to the environmental gradients. Down-gradient gene flow is expected to be maladaptive under all scenarios, explaining why it is universally suppressed relative to the null results (as evidenced by the blue distributional 'margins' extending to the left of the red distributions in all scenarios). There is a general trend toward increasing on-contour gene flow and decreasing up-gradient gene flow with decreasing linkage and increasing polygenicity.

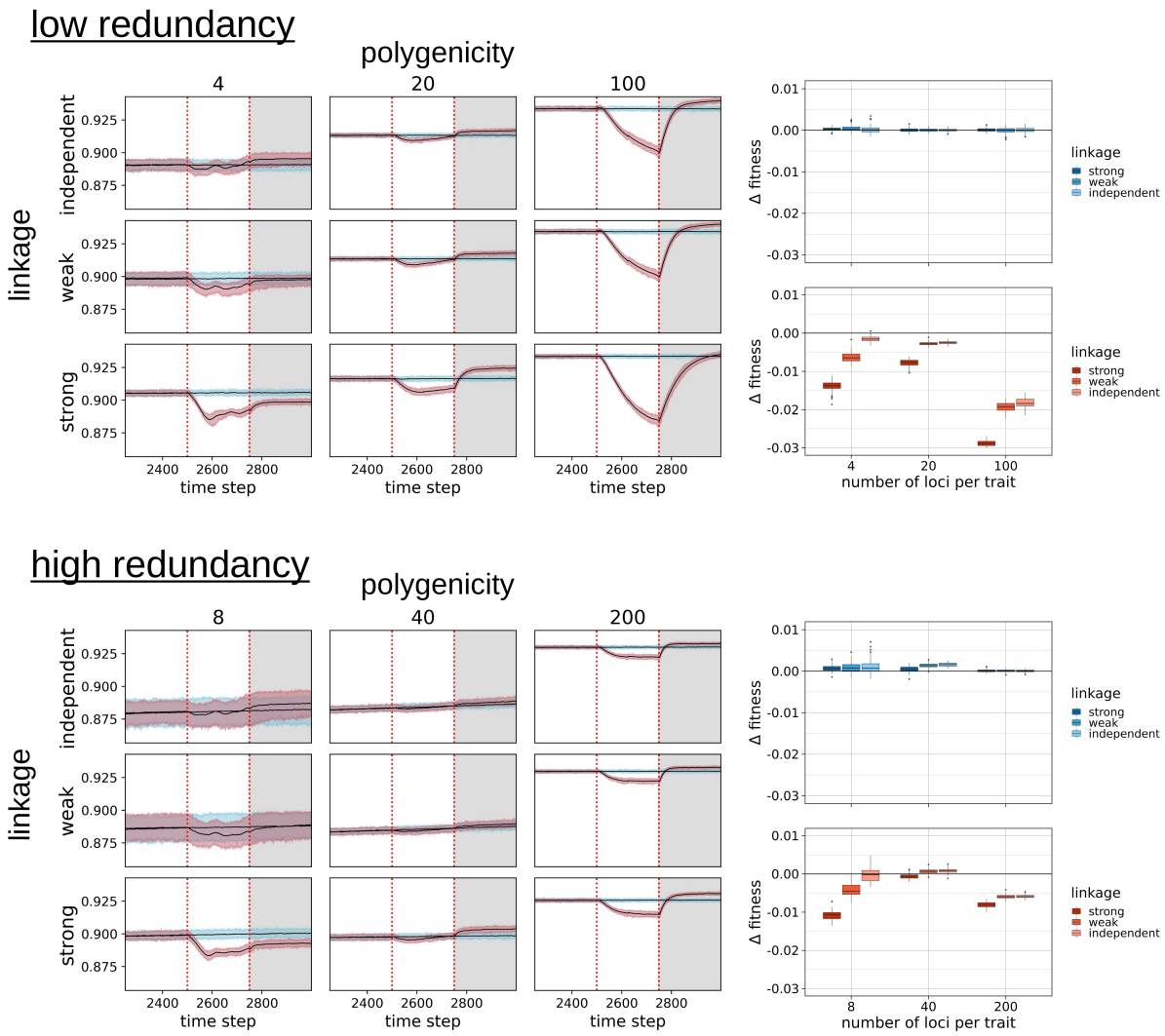


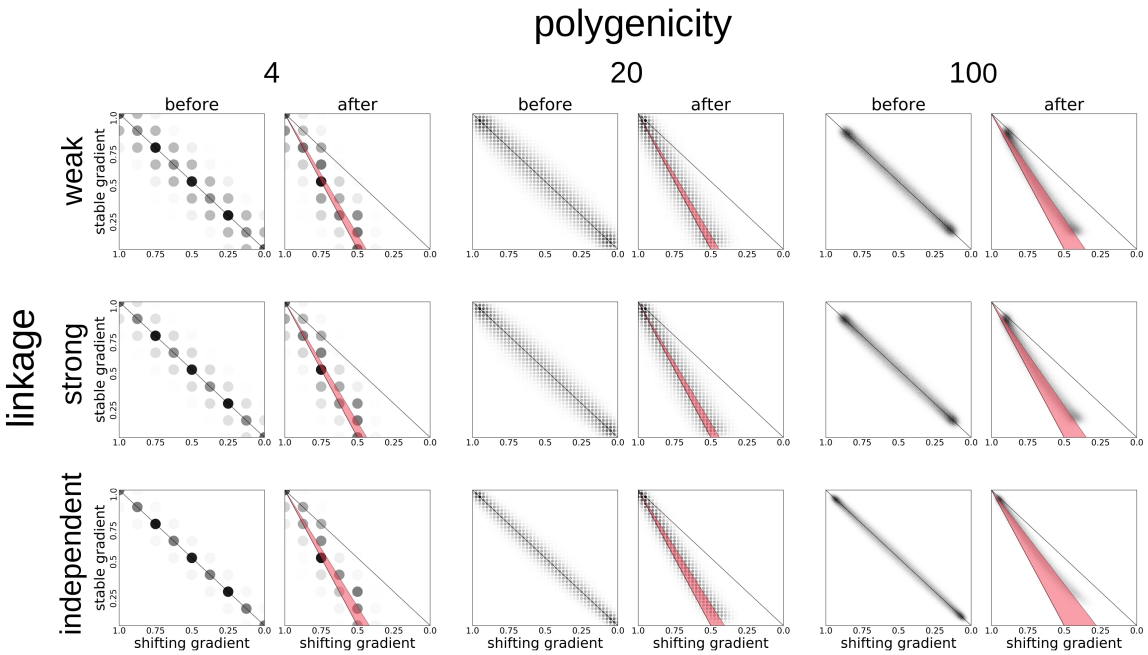
Fig. 3. Left: Mean fitness for all scenarios during the 250 time steps before, during, and after the climate change period (separated by red, dashed lines). Black lines represent the mean values, and the shaded red and blue areas represent variability envelopes (5th percentile to 95th percentile) for all replicates for climate change and null simulations, respectively. Right: Boxplots of changes in mean fitness during the climate change period for all scenarios. Null scenarios are plotted on the top in blue, and main scenarios are plotted on the bottom, in red. Within each plot, the scenarios are organized by polygenicity (number of loci per trait) on the x-axis and shaded by the strength of linkage.

bound) occurring until the post-change period (Figs. 3 and S2). The collapse of adaptive capacity in these scenarios is also visible in the large areas of phenotypic-shift shortfall in Fig. 4. The low-redundancy, high-polygenicity, strong-linkage scenario had such low adaptive capacity that mean fitness declined by 5.2% on average (from 0.934 to 0.885), mean population size declined by 17.1% on average (from 6326 to 5246 individuals), and the simulated population ceased to occupy the rightmost, fastest-changing portion of the landscape (Fig. 4).

Genotypic redundancy. Our high-redundancy scenarios showed consistently smaller demographic responses to climate change, less-prominent up-gradient gene flow, and higher adaptive capacity, than their low-redundancy counterparts (change in fitness: $\beta_r = 0.0040 \pm 0.0002, P < 1 \times 10^{-15}$; change in population size: $\beta_r = 39.060 \pm 2.101, P < 1 \times 10^{-15}$; maladaptation: $\beta_r = -0.0098 \pm 0.0006, P < 1 \times 10^{-15}$), consistent with our hypothesis that genotypic redundancy can facilitate adaptation to shifting environmental gradients (Figs. 2 and S2). This effect was most pronounced in the high-polygenicity scenarios, which exhibited much milder demographic decline under high redundancy compared to low redundancy, despite still showing no evidence of demographic rebound until after climate change (Fig. 3). Indeed, increased redundancy put the demographic declines under these scenarios on par with those of the low polygenicity scenarios (Figs. 3 and S2).

Discussion

Current theoretical understanding of evolutionary responses to climate change largely derives from a simplified mechanistic model in which adaptation is universally facilitated by up-gradient gene flow. This model also serves as the inspiration for some climate-smart approaches to biodiversity management (e.g., assisted gene flow; (10)). However, adopting this model as the basis for theoretical and mechanistic research risks overlooking the influence of genomic architecture on multivariate adaptation to environmental change. Starting from a



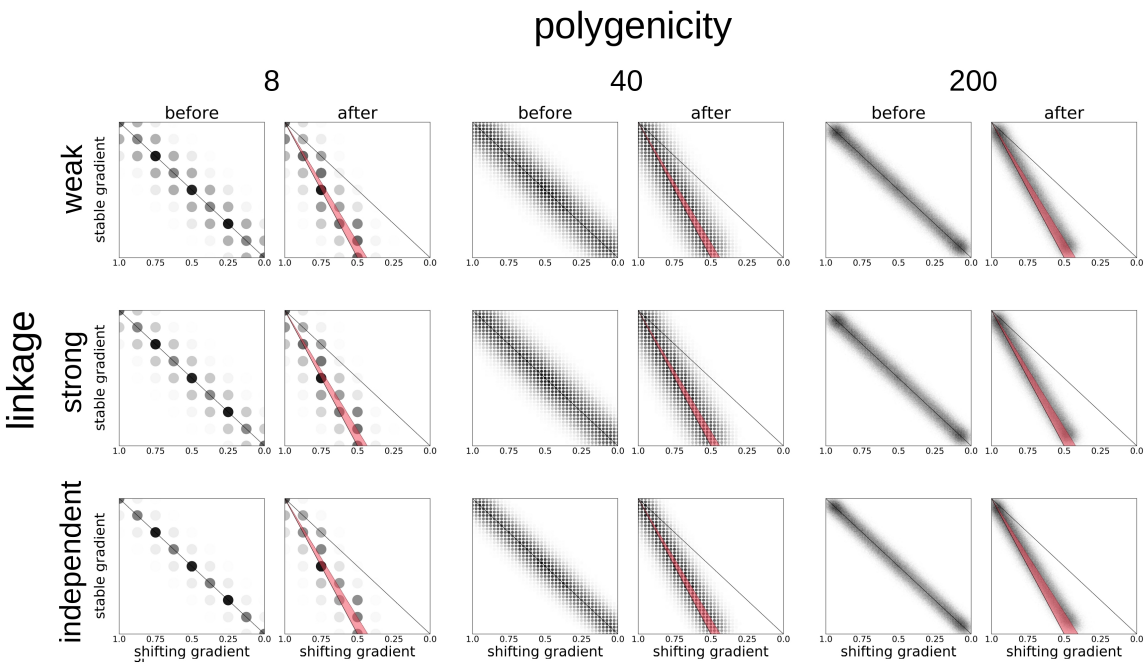


Fig. 4. Scatterplots of the observed versus expected phenotypic shift during the climate change period for all 18 of our simulated scenarios. For each scenario, the left ('before') scatterplot shows the distribution of phenotypes before climate change begins, and the right ('after') scatterplot shows how the distribution has shifted by the end of the climate change period. The trait adapted to the shifting environmental gradient is distributed along the x-axis, with the trait adapted to the stable gradient on the y-axis. Each plot is an ensemble of the results for all 100 replicates of each scenario. The size and opacity of each point represents the number of individuals exhibiting that two-dimensional phenotype. The gridded arrangement of the points in each scatterplot is a function of the number of loci per trait, which determines the set of possible phenotypes. Solid black lines delineate the shifts in the phenotypic distributions' central tendencies that are expected to take place during the climate change period, dotted black lines depict the observed distributions' central tendencies, and red wedges depict the differences between the expected and observed distributions ('phenotypic shortfall').

more realistic, multi-trait framework, our simulations demonstrate that up-gradient gene flow does indeed occur under climate change but that its contributions to local adaptation and persistence may be constrained by polygenicity, genotypic redundancy and, to a lesser extent, linkage. Given the range of plausible genomic architectures we simulate (6, 20, 29–32), these results raise the compelling possibility that up-gradient gene flow, while unlikely to be entirely maladaptive, could play a limited role in climate change adaptation in many systems. This may be especially true in systems where climate-adapted traits have more dispersed architectures — for example, architectures composed of many genes of small effect (24). This poses an important question for subsequent research: how often are the genomic architectures underlying climate-adapted traits dispersed versus concentrated?

We also show that the genomic architecture of climate-adapted traits can influence the nature and size of demographic responses to climate change. Our results suggest that strong linkage between non-neutral loci, especially under high polygenicity, can increase maladaptation and demographic decline during climate change. In the most extreme case, evolutionary rescue was absent; high polygenicity and low redundancy combined to drive dramatic and persistent demographic declines and even caused local extinction when linkage was strong. This was unexpected in light of previous work reporting that dispersed architectures produce stable, resilient phenotypic clines despite transient genotypic composition (24, 33) and, thus, that species with such architectures could exhibit rapid local adaptation (50). We did, nonetheless, expect evolutionary responses to climate change to be slower in these scenarios, because natural selection is less effective on smaller-effect alleles, gene flow may have more of a swamping effect for these alleles, and high linkage leads to longer expected wait times for the generation of novel, adaptive recombinant genotypes. We did not, however, expect adaptive capacity to be completely outstripped. Yet, it appears that the rate of environmental change simply exceeded the pace of adaptation. This is evidenced by the quick demographic rebound that occurred in the 'post-change' periods (Fig. 3). This rebound was likely driven by the same evolutionary dynamics that occur during evolutionary rescue, but in these extreme scenarios it only emerged once environmental change had ceased.

Remarkably, we also observed higher maladaptation and larger demographic declines in our low-polygenicity scenarios with fewer, larger-effect alleles. Demographic decline was least pronounced in our moderate-polygenicity models. This contrasts with previous work finding that adaptation to a gradient is more effective under either concentrated or dispersed genomic architectures (25). This disagreement may be attributable to the difference in timeframes between adaptation to a univariate environmental gradient and adaptation to a decoupled, multivariate gradient. Adaptation to a single, static gradient can proceed gradually, which may favor large-effect alleles or allele-clusters over longer time scales, once they have arisen by mutation, recombination, gene flow, or a combination thereof (24, 33). Longer term, gradual change scenarios may also favor dispersed architectures in temporally fluctuating environments (24, 25, 51, 52). However, the sudden onset of persistent environmental change in a population that is already locally adapted triggers a 'race against time,' and genomic architectures with optimal adaptive capacity may be the 'middle ground' architectures that comprise freely recombining loci with small enough effect sizes to avoid large declines in fitness from migration load but with large enough effect sizes to allow for effective natural selection and to avoid the long wait times necessary for recombination to cluster many adaptive loci into larger-effect haplotypes. This presents the surprising possibility that an 'evolutionary trade-off' may exist, such that mid-effect-size alleles may confer maximal adaptive capacity to environmental change.

The fact that high genotypic redundancy reduces demographic decline, across all scenarios, contributes to the growing recognition of the importance of redundancy as a driver of evolutionary outcomes for polygenic traits (24, 34). This also presents a possible mechanism to be explored in real-world populations living at colder range edges. Much like the local populations in the rightmost region of our low-redundancy scenarios, these local populations could already be at the edge of the phenotypic space defined by their standing genetic variation. In this case, segregating redundancy (34) and, thus, adaptive capacity would be low, so vulnerability to local extinction would be substantial. However, species whose cold range edges are predominantly determined by geographic barriers or biotic interactions rather than climate limits (53) could feature local populations more similar to our high-redundancy scenarios; segregating redundancy would be higher, so selection would be balancing rather than directional, and adaptive capacity would be substantial. Hence, *in situ* adaptation would be a substantial contributor to adaptive capacity in these scenarios — an implication supported by the fact that we observed reduced up-gradient gene flow across all high-redundancy scenarios.

Our findings also contribute new insight to the theoretical understanding of local adaptation with recombination. Recombination is generally regarded as disadvantageous in situations of clinal adaptation with gene flow, because it disrupts the association between adaptive loci underlying a single trait (12). Unstable environments experiencing stochastic temporal fluctuations are considered a major exception (12), but our results suggest that this may also extend to environments undergoing monotonic change such as that caused by climate change. In fact, recombination may be advantageous under these conditions, particularly when species have distinct traits simultaneously adapted to decoupled environmental gradients. This advantage likely arises because recombination allows for more effective *in situ* adaptation by shifting allelic covariance, despite still disrupting the associations between loci that would otherwise allow for the development of larger-effect gene clusters. This suggests that *in situ* shifts in allelic covariance provide an alternative to adaptive gene flow as a mechanism for evolutionary rescue, especially in multi-trait systems where gene flow can be adaptive for shifting climatic gradients but maladaptive with respect to other, decoupled gradients.

A major challenge in simulation-based research is the complexity of the high-dimensional parameter space that could be explored. Useful and informative studies can be constructed by focusing on a small set of key parameters while holding others at reasonable values, as we have done here. This nonetheless leaves unexplored a number of secondary parameters that can have non-negligible influence over the complex ecological phenomena of interest. In the case of evolutionary responses to climate change this provides various areas for future research.

These include population size, a major determinant of the relative strengths of drift and natural selection (54) and of the wait time to emergence of recombinant haplotypes (55); movement behavior, a key factor influencing migration-selection dynamics (17, 18, 21); allelic effect size distributions (56), which are omitted here in favor of a single, fixed effect size; and the spatiotemporal structure of the environment, including gradient geometries, slopes, orientations, and rates of change (57). Additionally, important and conservation-relevant insight could emerge from the integration of other dimensions of climate change ecology, including range shifts (58), plasticity (1), and range-wide variation in population densities (10). Finally, more complex evolutionary scenarios could also be explored, including pleiotropy and epistasis (59), hybridization (60), life history variation, and even multiple traits that differ in the complexity of their genomic architectures — a realistic scenario that could exhibit different evolutionary outcomes than the ones we describe here.

Conclusions

Adaptive gene flow and *in situ* adaptation are two of the main processes by which species may persist under climate change. Evaluating the conditions under which they are likely to contribute to species persistence is essential for better understanding microevolutionary responses to climate change and for informing management efforts. Our simulations show that genomic architecture can play an important, but largely overlooked, role in driving evolutionary outcomes. This includes determining the relative effectiveness of these two processes, the magnitude and persistence of maladaptation, and the likelihood of concomitant demographic decline or evolutionary rescue. These findings highlight the importance of considering multivariate environmental gradients for climate change research, and suggest that the genomic architecture underlying traits adapted to those gradients has direct consequences for how species respond to environmental change.

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