Founders predict trait evolution and population dynamics after evolutionary rescue

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Evolutionary rescue helps populations survive environmental change, but the phenotypic and demographic factors underlying rescue and its long-term effects remain unclear. We experimentally evolved 10 source populations of flour beetles from across India in a suboptimal corn resource for 70 generations (~5 years), collecting >10,000 population census points book-ended by measurements of fitness-related traits for 30 experimental lines. Despite clear ancestral differences, all lines showed highly parallel evolutionary rescue within ~20 generations. Long-term population size varied across source populations and was positively correlated with ancestral development rate, which increased convergently across populations and emerged as the single best predictor of population performance during and after evolutionary rescue. Notably, rescue dynamics were uncorrelated both with ancestral trait distributions and post-rescue adaptation. Our results justify the current focus on founders as key predictors of adaptation, but also highlight several disconnects between founder traits, rescue events, and long-term adaptation and trait evolution.

INTRODUCTION

Abrupt environmental changes (e.g., climate change or urbanization) can cause species abundance to decline rapidly, potentially causing extinction (Bell & Collins 2008; Lindsey et al. 2013) and reduction in local biodiversity (Bellard et al. 2012; Pereira et al. 2012). Evolutionary rescue — likely an important mechanism driving species persistence in such conditions (Azevedo et al. 2024; Bell & Collins 2008; Moritz & Agudo 2013) — refers to the demographic recovery of declining populations due to rapid adaptive evolution, with a hallmark U-shaped curve of population size over time (Bell 2017; Gomulkiewicz & Holt 1995; Orr & Unckless 2008, 2014). Although rescue has wide-ranging applications in conservation, pest control and medicine (Bell 2017), detecting and predicting evolutionary rescue outside the laboratory is fraught with logistical and technical challenges (Gomulkiewicz & Shaw 2013), leaving many questions unanswered and predictions untested.

Evolutionary rescue is aided by several genetic and demographic factors (Bay et al. 2017; Bell 2017; Carlson et al. 2014; Hufbauer et al. 2015; Martin et al. 2013; Szűcs et al. 2014; Vander Wal et al. 2013), such as founding population size (Bell & Gonzalez 2009, 2011; Oliveira & Campos 2024; Ramsayer et al. 2013; Willi & Hoffmann 2009), standing genetic variation (Agashe et al. 2011; Lachapelle & Bell 2012; Ramsayer et al. 2013; Stewart et al. 2017), and demographic history (Bouzat 2010; Draghi et al. 2024; Klerks et al. 2019; Olazcuaga et al. 2023). However, despite the large body of work on this topic, several important gaps remain in our empirical understanding of evolutionary rescue. For instance, founding genetic diversity facilitates rescue (Agashe et al. 2011; Lachapelle & Bell 2012; Ramsayer et al. 2013; Stewart et al. 2017) and it is likely that much of rapid adaptation is driven by such standing genetic variation (Barrett & Schluter 2008). However, this effect must be driven by genetic variation in specific phenotypic traits that aid survival and reproduction in the new environment (Orr 2005, 2009), and are directly visible to selection (Hendry 2017). In contrast, neutral genetic diversity is unlikely to have as large an impact on rapid adaptation

(Whitlock 2014), may not be directly linked with it (Chung et al. 2023; Holderegger et al. 2006), and does not always predict the adaptive potential of populations (Teixeira & Huber 2021; Yıldırım et al. 2018). Thus, the specific nature and type of founding genetic variation is likely more important than genetic diversity per se (Kasada et al. 2014). The challenges in mapping such functional genetic diversity for a given species can be partially circumvented by focusing on phenotypic diversity in specific fitness-related traits. But which traits matter, and at what stage of rescue?

Given the observed positive effect of initial genetic diversity, studies of evolutionary rescue typically focus on the genetic and phenotypic diversity of founders. Is this focus justified, beyond logistical ease? Founder phenotypic variation may be disconnected from rescue dynamics for several reasons, such as plastic responses to the new environment that affect population dynamics and evolution (also known as "plastic rescue") (Bonduriansky 2021; Brass et al. 2021; Chevin et al. 2013a; Fox et al. 2019; Ghalambor et al. 2007; Harmon & Pfennig 2021; Snell-Rood et al. 2018; Van Allen & Rudolf 2013), or carry-over effects (Beckerman et al. 2002; Plaistow & Benton 2009; Savković et al. 2016; Stuligross & Williams 2021). For instance, short-term *Tribolium castaneum* population dynamics depend on both the past resource in which colonizing individuals developed, and the newly colonized resource (Van Allen & Rudolf 2013). Founder diversity may also be an unreliable predictor of rescue if high mortality in the new environment changes trait distributions strongly (Ciotti & Planes 2019), which can determine subsequent responses to selection. Could such temporal changes in phenotypic trait values reduce the contribution of founder variation to evolutionary rescue? The answer determines whether the effect of founders on rescue dynamics is direct or indirect, and whether the focus on founding individuals as predictors of rescue is a good strategy.

Founder variation may also get disconnected from rescue dynamics during the process of adaptation. Different traits may contribute to population performance at different stages of adaptation, because the magnitude and nature of selection may change during the course of rescue, as populations traverse dynamic fitness landscapes. Selection may also simultaneously act on multiple phenotypic traits in the new environment, which may interact with each other (e.g., via genetic correlations) (Walsh & Blows 2009) in ways that differ from the ancestral environment. In light of these complexities, some founder trait distributions may change more slowly than others, with no single trait (or set of traits) consistently contributing to evolutionary rescue. Very few studies examine multi-trait responses to abrupt environmental change (Chown & Gaston 2016), though such data are critical to predict both the probability and outcome of rescue (O'Connor et al. 2020). Lastly, demographic and genetic stochasticity imposed by rapid initial population decline in the new environment (Carlson et al. 2014; Gomulkiewicz & Holt 1995) can alter trait distributions before and during rescue, breaking the expected correlation between founder trait variation and population performance. Thus, without empirical tests of the ancestral phenotypic drivers of evolutionary rescue — and more importantly, what factors may disconnect the two — it is difficult to predict evolutionary rescue for applications such as population restoration and combating the emergence of resistance to pesticides or antibiotics.

Finally, since most experimental studies of evolutionary rescue are concluded soon after rescue is successful, it also remains unclear whether initial trait variation and population dynamics during rescue have lasting effects on population performance. Does the length or magnitude of the initial population size bottleneck or the rate of subsequent recovery impact post-rescue dynamics? Do the same traits that facilitate rescue also enhance long-term population performance, or does this dependence change post-rescue? To address these gaps, we used laboratory experimental evolution in a harsh novel resource (corn flour), using ten wild-collected source populations of the red flour beetle *Tribolium castaneum* with high fitness in their ancestral wheat flour environment. We tested (a) whether source populations were phenotypically distinct and whether their performance during adaptation (population size and stability) was determined by source population identity, (b) if yes, which phenotypic traits aided population performance, (c) which traits were associated with specific demographic events during evolutionary rescue in corn and subsequent longer-term population dynamics, (d) whether trait distributions of the founders were correlated with those of their offspring (after entering the harsh new environment), (e) which of these distributions had a stronger impact on population performance, and finally, (f) whether these key traits had evolved during evolutionary rescue. Our results provide new insights about specific fitness components that may be important during and after evolutionary rescue in a novel environment and suggest that the focus on founding trait distributions is generally justified, with potential applications for predicting population survival in the wild (Gomulkiewicz & Shaw 2013).

METHODS

Collection and maintenance of source populations and selection lines

We used 10 wild-collected populations of *T. castaneum* from different locations in India (Figure 1; Figure S1) and established large laboratory stocks of these populations in plastic boxes (diameter 21 cm, height 8.5 cm) with holes in the lid for ventilation. To propagate stocks, we allowed ~2000 adults (1-2 weeks post-eclosion) to oviposit in ~750g whole wheat flour for 7 days, following a discrete generation cycle, after which we allowed offspring to develop for ~28 days. This regime ensured at least 2000 individuals every generation, facilitating maintenance of genetic diversity. Stocks were acclimatized to laboratory

conditions in dark Percival incubators at 32°C (±1°C) for 2-3 years (~20-30 generations) prior to initiating the selection lines. Note that populations are not numbered consecutively – they correspond with laboratory IDs.

To study evolutionary rescue, we used a highly suboptimal novel resource, corn flour. *T. castaneum* populations established in corn show low population growth rates (Szűcs et al. 2014), and are often driven to extinction (Agashe 2009). We established a total of 30 experimental lines in corn (10 source populations x 3 replicates each; Figure 1) founded with 100 pupae each from the respective source population stocks, which have a typical sex ratio of 1:1. We initiated lines in a staggered manner over 6 months, so that the three replicates of each source population were started on different days. We maintained all lines in 50 g (±0.5 g) corn flour in plastic boxes (6.7 cm diameter) with small holes in the lid for ventilation. We purchased flour from the same supplier throughout and documented any changes in the texture of the corn (Figure S2). To kill any prior pest infestations, new flour packets were sterilized by freezing at –80°C for 24 hours. We maintained the lines in incubators as above.

Every 28 days (± 1 day) — corresponding to the average development time from egg to pupae in corn (i.e., the approximate generation time) — we replenished the resource by transferring populations to fresh flour. At each transfer, we censused all life stages except eggs (i.e., we counted dead and alive larvae, pupae and adults), by sifting the contents of the box through meshes of different pore sizes (600-µm and 710-µm; Daigger), and discarding dead individuals. Eggs typically take ~48 hours to hatch, so all eggs laid 2-3 days prior to the census were discarded along with the used flour. We heat-sterilized all equipment for a minimum of 10 minutes at 65°C to prevent cross-contamination.

Assessing population performance

One line (replicate 2 of source population 2) went extinct within 5 generations and was excluded from all further analyses. We also excluded census data between generations 60-70 from subsequent analysis since we encountered many COVID19-related disruptions to the workflow during this time. We evaluated the overall population performance for each selection line from the census data for adults and larvae (the most abundant life-stages in the lines) by calculating the geometric and harmonic mean population size. Additionally, we estimated population stability by quantifying population size oscillations using the coefficient of variation (CV). We split the dynamics (and calculations) into bins of ten successive transfers (i.e., transfers 1–10, 11–20, till generation 60) and evaluated population performance (average size and CV) per bin to minimize autocorrelation effects. The harmonic and geometric means were strongly correlated for both adults and larvae (Pearson's correlation > 0.99, Figure S3), so we only report geometric means throughout. In addition, as a direct assay of adaptation we measured two important traits in each evolved line at generation 70, as described in the next section.

Measuring fitness-related phenotypic traits

We assayed the ten source populations for five fitness-related traits: adult longevity (lifespan after eclosion with access to food), adult starvation resistance (lifespan after eclosion without food), larval cannibalism (number of eggs cannibalized per larva per day), offspring development rate (proportion of eggs that developed to the pupal or adult stage in 4 weeks), and adult reproductive fitness (total viable offspring and viable adult offspring per female) (Figure 1; Figure S4; SI methods). To mimic founder trait distributions ('G1', hereafter 'founder phenotypes'), we allowed individuals from each of the 10 ancestral populations to develop in wheat, and then transferred them to corn to measure the phenotypes. We also used a proxy for the phenotypic distributions of the first generation of individuals that developed in corn ('G2', i.e., the offspring of the founders, hereafter 'offspring phenotypes'), by measuring all the above phenotypes for stock individuals whose parents developed in wheat but reproduced in corn, leading to the test individuals developing in corn too). Doing so allowed us to test the relative importance of the phenotypic distributions of the founders versus their offspring (with different development resources), giving us more insight into potential disconnects between ancestral variation and population dynamics. Finally, to test a hypothesis that arose during data analysis (discussed in Results), we re-measured two traits (development rate and reproductive fitness) after ~70 generations of evolution of each population (hereafter 'evolved phenotypes'). We did this by deriving smaller sub-lines from the evolving lines, which we then measured (SI methods).

Model fitting to adult population dynamics using piecewise linear models

To determine distinct stages of evolutionary rescue, we divided the population dynamic trajectories to reflect population recoveries, declines and bottlenecks. We first fit a piecewise model to the combined data from all populations. We only used data until 40 transfers (or generation cycles) for this analysis since the lines showed more divergent dynamics after this time. After trying several alternate models with different numbers of breakpoints, we chose the simplest model that captured the most variance in the data, settling on a model with 6 breakpoints that captured 51.8% of variance in the combined dataset. The breakpoint parameters from this 'global' model were then used to fit the same model to each individual line to prevent overfitting and to enable easy comparison. The global model captured fundamental population processes such as change in population size and bottlenecks. For the individual model fits, 6 models captured >90% variation; 17 captured 80-90% variation, and 5 captured 60-80% of the variation in the respective population dynamics. We excluded two lines from

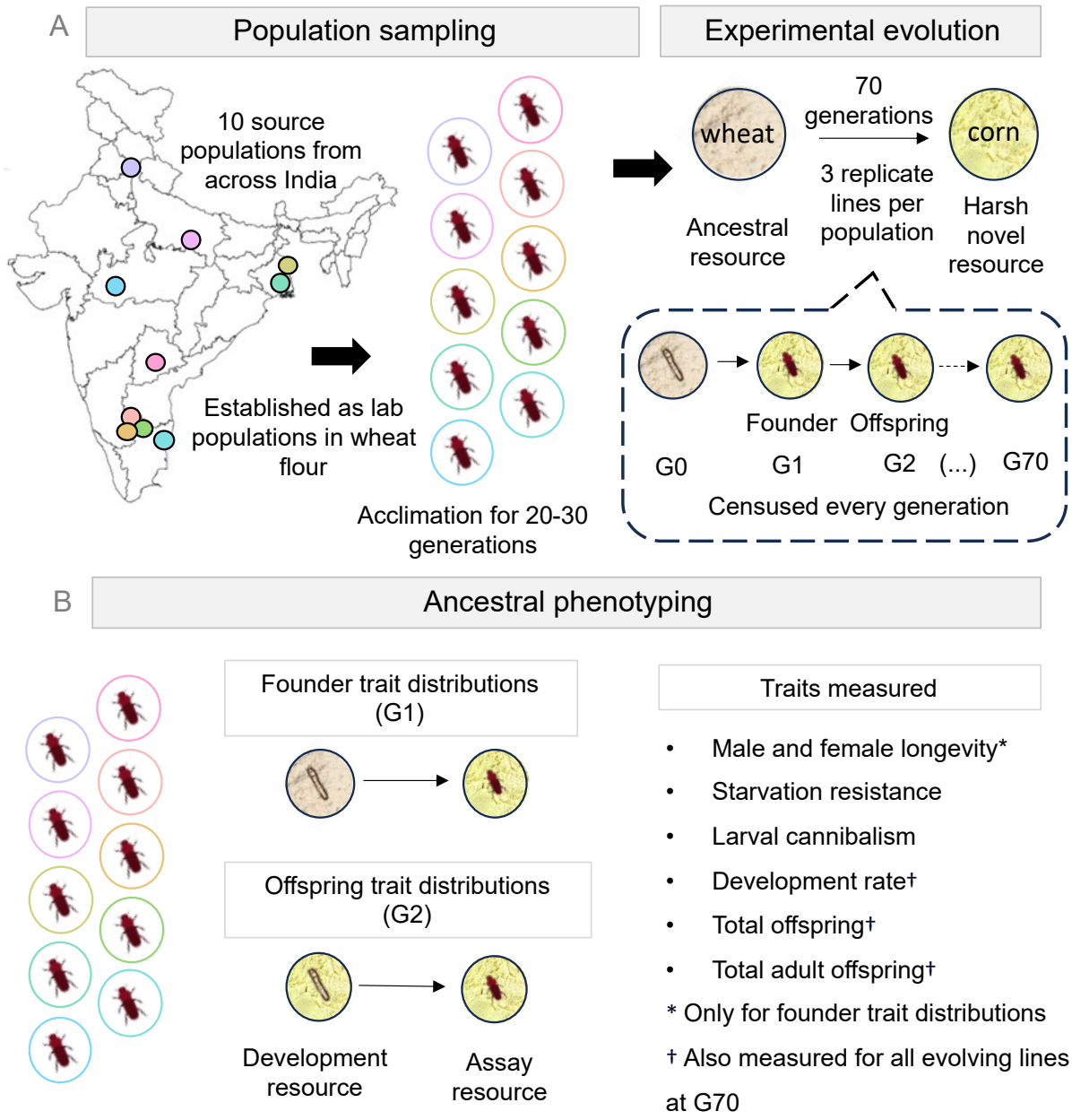

Figure 1. Schematic of the experimental design. **(A)** Population sampling, lab acclimation. Ten source populations were collected from across the Indian mainland (map: Survey of India), brought into the lab and acclimated to lab conditions in wheat flour (ancestral resource) for 20-30 generations. **(B)** Experimental evolution. We initiated selection lines in corn flour (a harsh novel environment), and transferred lines every 4 weeks (1 generation cycle) to fresh corn flour, for 70 generation cycles (280 weeks), with a complete census every generation cycle. **(C)** Ancestral phenotyping of the source populations. We measured seven fitness-related traits after rearing stock-derived individuals under two conditions – one mimicking the founders of the lines (G1), and the other mimicking their immediate offspring (G2). We also measured three of these traits indicated by our results (see 'Results') in all evolved lines at generation cycle 70.

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further analysis, one for which the model captured <60% of variation (population 7 replicate 3), and one that went extinct at transfer 5 (population 2 replicate 2). We extracted slopes and breakpoints to quantify the variation in dynamics for each individual line, then used these data for further analyses to test for correlations with ancestral traits and post-rescue performance.

Data analysis and visualization

All analyses and plots were generated in R version 3.4.4 in RStudio version 1.0.143 on a Windows 11 system. Figures were created in Microsoft Powerpoint, GIMP and Affinity Photo. Statistical tests are reported directly in the main text or Supplementary Information

legends for clarity. Packages used for analysis and visualisation were: ggplot2, gridExtra, paletteer, dplyr, tidyr, forcats, hrbrthemes, viridis, corrplot, RColorBrewer, survival, sjstats, segmented, broom, ggpubr, MASS, and vegan.

RESULTS

Source population identity influenced population performance during adaptation to corn

Across 60 transfers, all lines adapted to corn flour in a strikingly parallel manner, with dynamics during the first 20 transfers (~20 continuous generations) consistent with the classic U-shaped curve associated with evolutionary rescue (Figure 2A, 2B). We observed several signatures of adaptation – a gradual increase in both population size (Figure S5A-B, Table S1) and stability over time (Figure S5C-D, Table S2), with the average number of larvae staying consistent after ~40 transfers (Figure S5B), possibly indicating that the populations were close to the habitat carrying capacity soon after rescue. Despite the broad parallelism in the overall dynamics of both life stages across independently evolving lineages, average population size varied significantly across source population identity for much of the experiment for both life stages (Figure 2C; Figures S6-S8; Table S3). In contrast, population stability did not vary by founding population identity at any time (Figure 2D, Figure S8B, Table S4). Further, the relative performance of individual selection lines was weakly consistent during rescue (till transfer bin 2, or ~ generation 20, Table S5), then strengthened for the rest of the experiment, supporting the overall impact of source population identity on population performance.

Ancestral trait distributions varied across source populations and changed after a single generation of development in corn

We measured founder and offspring phenotypes in the ancestral stock populations (Figure 1C). Source populations were phenotypically distinct for all measured traits except longevity (ANOVA, phenotype ~ population x development resource; Table S6). Strikingly, all measured trait distributions also changed significantly after a single generation of development in corn, from founders to the first generation of offspring (Figure 3, Table S6). Development in corn (vs. wheat) decreased beetle lifespan by ~35 days (both sexes and all populations combined, GLM (days survived ~ development resource), $p<0.01$; full model in Table S6; population-specific analysis in Table S7; Kaplan-Meier survivorship curves in Figure S9). Surprisingly, offspring developed faster when the mother was also reared in the suboptimal corn rather than wheat (Figure 3C; Table S6, $p_{development\ resource} <0.001$). This parental effect persisted after controlling for offspring density in the assay plate (binomial GLM, proportion of pupated/ adults at week 4 ~ development resource x density, $p_{development\ resource} < 0.01$, other p values > 0.05), suggesting a direct parental contribution to offspring fitness in corn, e.g., due to parental body condition. Maternal development in corn (vs. wheat) also increased total offspring production in corn by ~1 offspring per female (all populations combined, GLM (development rate ~ development resource), $p<0.001$). Thus, within a single generation in corn, the number of adults available for reproduction at a given time should increase in all populations.

Notably, the relative fitness values of wheat-developed vs. corn-developed beetles from a given population were not correlated for any of the measured traits (Spearman correlation ranks in Table S8, Figure S10). Thus, ancestral fitness in wheat was a poor predictor of fitness in corn. Instead, we observed significant resource x source population interaction effects for all traits except larval cannibalism (Table S6). For instance, average lifespan under starvation generally decreased in individuals that developed in corn rather than wheat, but the magnitude of this effect varied across populations (Figure 3A; Table S6). The significant interactions may explain specific cases where populations with high initial fitness (i.e., as founders) did not turn out to be the best-performing populations later, due to a reduction in fitness of the first generation that developed in corn.

Overall, we observed pervasive effects of both development resource and source population identity on individual fitness for all measured fitness-related traits. The source population effect could potentially drive the distinct population size trajectories across time, via different rates of adaptation. For instance, development rate and total adult offspring are important traits that are directly relevant for population size, and are also strongly correlated with each other (Spearman's rho = 0.55, $p < 0.001$). These two traits varied the most across source populations (eta-squared of main effects for both traits = 0.14; Table S9). Additionally, development rate varied the most across development resource (eta-squared of main effect = 0.2; Table S9). Hence, we hypothesized that these traits may explain variation in population performance during the early stages of adaptation. Next, we tested whether specific founder or offspring phenotypic trait values were indeed correlated with population performance.

Population performance is most strongly associated with founder development rate

If specific traits drove differential population performance during and after rescue, we would see (a) significantly differentiated phenotypes across source populations (reported above), and (b) a correlation between performance and the mean and variance of phenotypic trait values for founders and their offspring (described in the previous section). In this manner, we identified which fitness component(s) may be responsible for the observed source population-specific differences in adaptation to corn (Figure 2C). An initial principal component analysis showed that the first two principal components accounted for only 53%

variance in the entire dataset (Figure S11), therefore we used original trait values for all correlations with performance and demography (Keller et al. 2023), using the false discovery rate (FDR) method (Benjamini & Hochberg 1995) to correct for multiple comparisons. After correcting for multiple comparisons, only three traits were strongly positively correlated with population size for several tens of generations during adaptation (Figure 4A-B) — development rate, reproductive fitness and female longevity. Aligning with our prediction in the previous section, the strongest and most consistent association was observed for the mean and variance of development rate of founding individuals (i.e., wheat-developed parents). These were positively correlated with average population size throughout the experiment (Figure 4C, Spearman's rho ranging from 0.41–0.67, all coloured squares have $p < 0.05$). Interestingly, the strength of both these correlations

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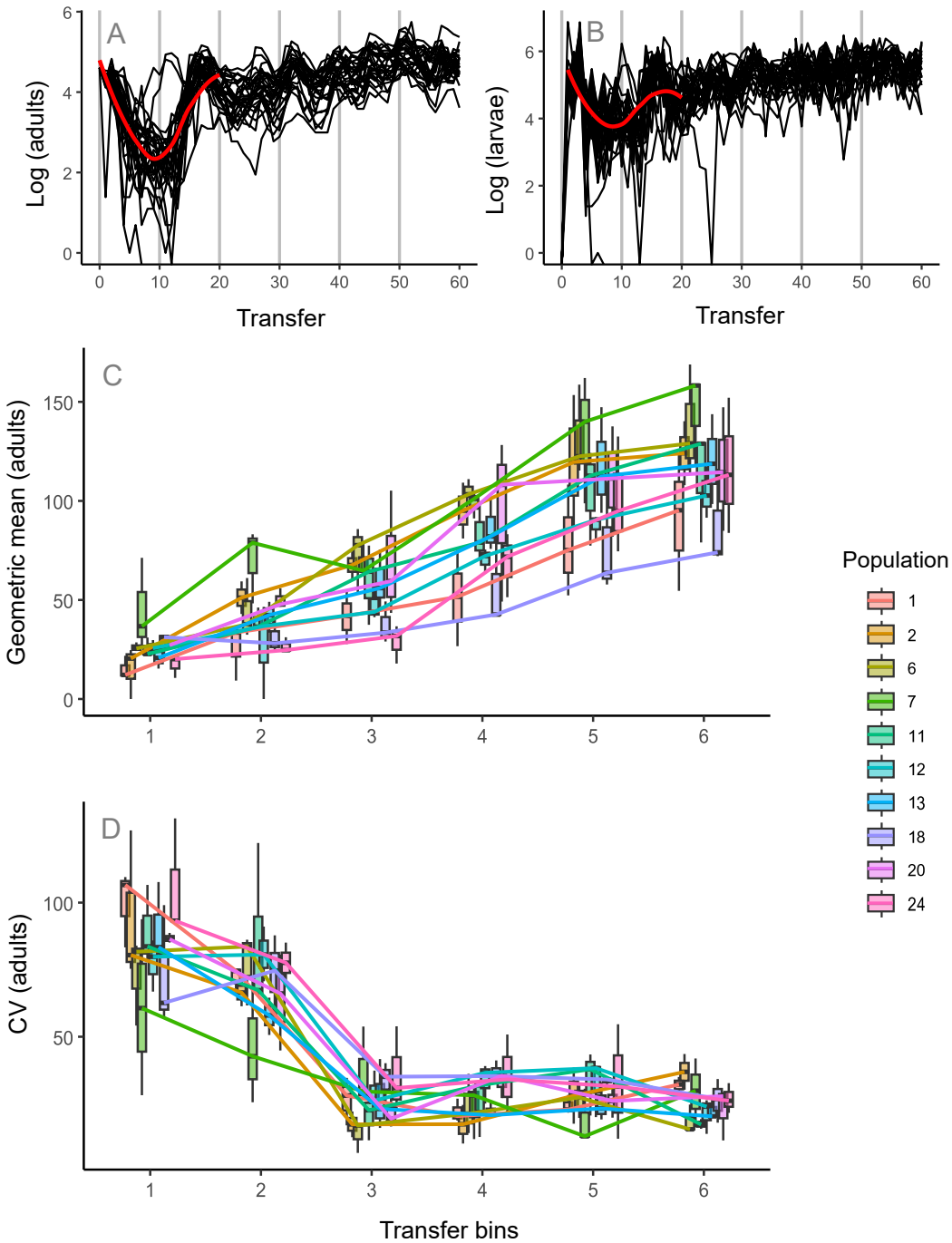

Figure 2. Overall demographic trends observed in corn-adapting lines. Time series of lines adapting to corn flour for **(A)** adults and **(B)** larvae, plotted on a natural log scale. The smoothed red curve (using loess) helps visualize the hallmark U-shaped curve of evolutionary rescue. Vertical grey lines represent transfer bins. **(C)** Average population size and **(D)** coefficient of variation (inverse of stability) across the adult time series, for triplicates of each source population (three data points per boxplot; source populations are indicated by different colours). See Tables S3-S4 for ANOVA statistics of population performance across founding populations, and Figure S8 for larval time series.

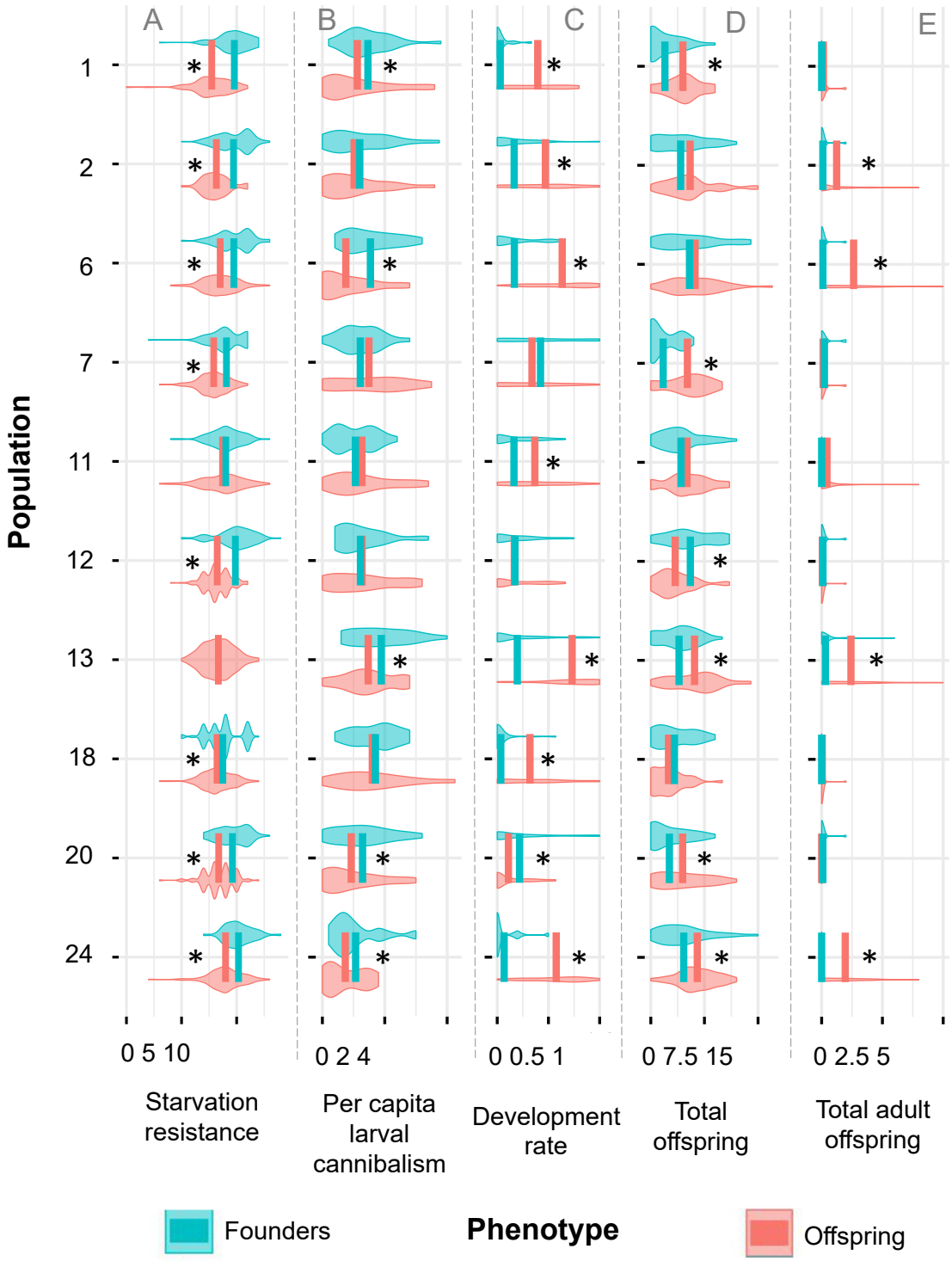

Figure 3. Change in ancestral phenotypic traits after developing in wheat vs corn, representing the phenotypic trait distributions of the founders vs their offspring respectively. Phenotypic trait distributions for each source population (y-axis) for different fitness-related traits (x-axis), with solid lines comparing distribution means for the same population across development resource. **(A)** Starvation resistance (n = 48 per population per resource); **(B)** larval cannibalism (n = 25 per population per resource) and (C–E) various measures of reproductive fitness per female (n = 25-40 females per population per resource) such as **(C)** offspring development rate **(D)** number of total offspring, and **(E)** number of adult offspring. Founder starvation resistance assays for population 13 in panel A were lost to an accident, so this comparison is not included in the statistics. One extreme data point each is not shown in panels D (Population 12, wheat, 42 total offspring) and E (Population 6, corn, 10 total adult offspring) for ease of visualization, but the data were included in the reported statistics. Asterisks represent statistically significant differences ($p<0.05$) for the following tests in the respective panels: (A, D, E) GLM with normally distributed errors and (B, C) GLM with binomially distributed errors. See Table S6 for summary statistics.

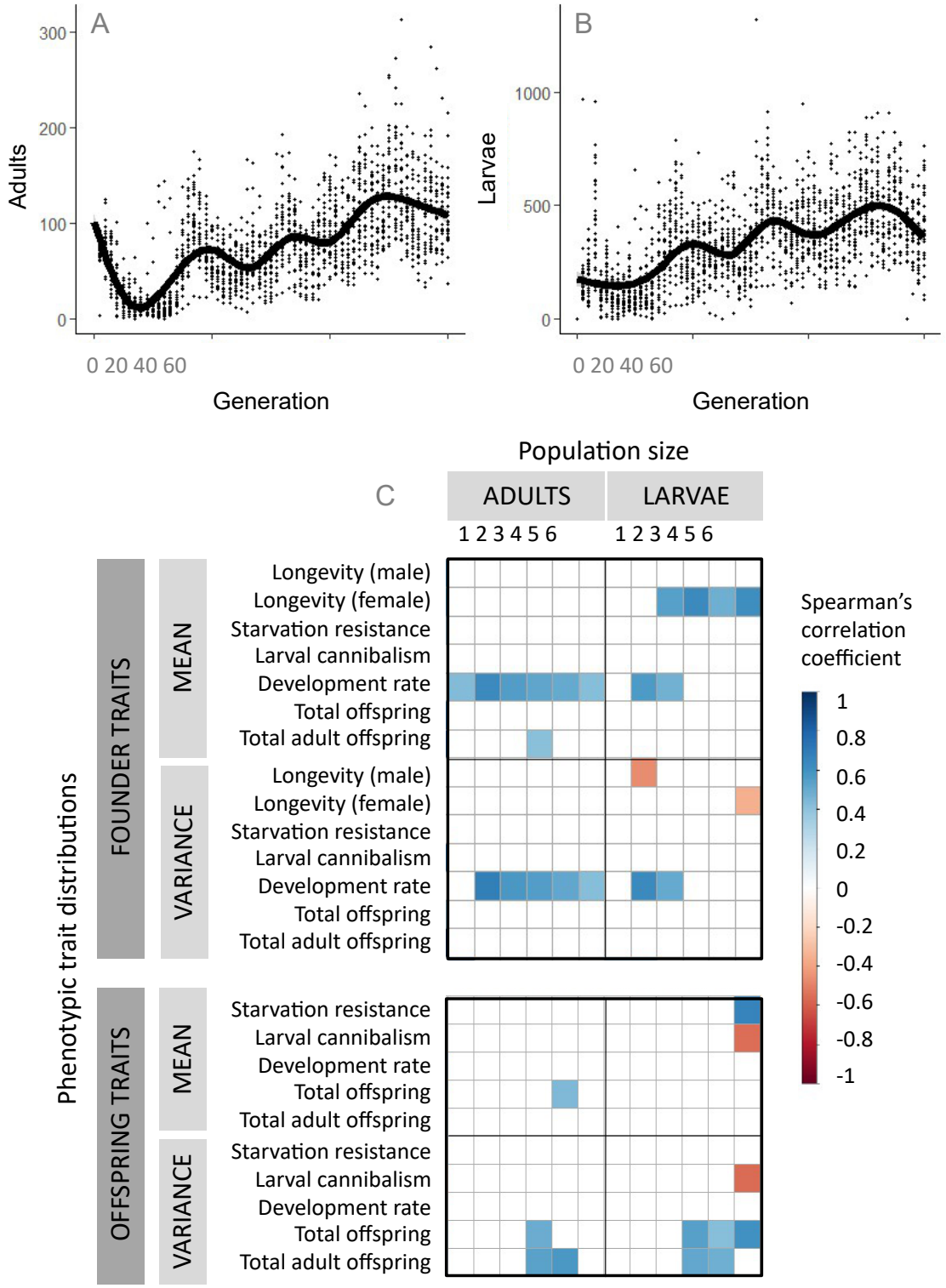

Figure 4. Ancestral phenotypic correlations for founder and offspring trait distributions (means and variances) with population size over time. Time series of **(A)** adults and **(B)** larvae combined across populations and replicates for visual reference. Black curves in both panels represent a smoothened fit of all data points at any time point. **(C)** Matrices showing significant correlations corrected for multiple comparisons (blue: positive, red: negative) between ancestral phenotypic traits and the geometric mean of the number of adults and larvae evolving in corn per 10-generation bin. Only statistically significant Spearman's rho correlation coefficients after correction for multiple comparisons are shown.

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decreased during evolution (reducing from 0.67 to 0.41 (mean), and 0.71 to 0.41 (variance) from transfer bin 2 to 6).

Variance in offspring reproductive fitness (i.e.,the second generation in the selection lines) was positively correlated with adult and larval population size only in the second half of our experiment (Figure 4C, after generation 30; Spearman's rho estimates ranging from 0.42–0.61).

Lastly, mean female longevity in corn (measured for founders, as above) was also positively correlated with the average number of larvae in the second half of our experiment (Figure 4C, after transfer 20; Spearman's rho values ranging from 0.4–0.64). Other significant but sporadic correlations between ancestral traits and population performance involved offspring phenotypic traits. For instance, the number of larvae in the last 10 generations was negatively correlated with the mean and variance of larval cannibalism for offspring (Figure 4C; Spearman's rho estimates of -0.55 and -0.56 respectively) and positively correlated with mean starvation resistance of offspring (Figure 4C, Spearman's rho, 0.66).

Thus, the mean population size of adults (as well as larvae) was overall most consistently and strongly correlated with offspring development time for the (wheat-reared) founders. In contrast, none of the ancestral traits were significantly and consistently correlated with population stability (Figure S12), except for development rate which was positively correlated with adult and larval population stability in transfer bin 2 (the bottleneck and rescue event) (Spearman's rho, -0.37 and -0.49 respectively).

Ancestral traits do not predict population dynamics during or after rescue, and rescue demography does not predict later population dynamics

In contrast to our results with the 10-transfer bins (Figure 4), we observed almost no correlations in our demographic analysis testing for associations between ancestral traits and specific features of population dynamics during and after rescue (Figure 5A-B; individual piecewise models shown in Figure S13). The only significant correlations after correcting for multiple comparisons involved founder traits that were distinct from those in the previous analysis, typically correlated with the start time of the third population recovery (Figure 5B, all coloured squares have $P < 0.05$). For instance, the third recovery started later in populations with higher mean total offspring of founders (Spearman's rho=0.31), higher mean starvation resistance of corn-developed offspring (Spearman's rho=0.41), and/or low variance in female longevity in corn (Spearman's rho=-0.534). The rates and timings of specific rescue demographic events also did not correlate with post-rescue demographic events (Figure S14).

Overall, these results suggest that while specific ancestral trait values had broad and consistent effects on population dynamics during corn adaptation, they had weak predictive power with respect to specific demographic changes during rescue. Further, specific demographic phases during the evolutionary rescue itself were poor predictors of long-term population performance.

Development rate and reproductive fitness increased after 70 generations

Our correlative analyses above indicated a major role for development rate in mediating adaptation to corn (Figure 4). To directly test this, we measured development rate in each evolved line. Since we also obtain data on total offspring and total adult offspring from the same assay (which are also correlated with average population size), we report them below as well. All three traits had increased significantly relative to both the founding individuals and their offspring (Figure 6A; Table S10). Beetles in the evolved lines were overall 11 times and 4 times more likely to have successfully pupated in 4 weeks relative to the (founding) wheat-developed ancestors and (offspring) corn-developed ancestral individuals (Table S11). Further, females from evolved lines produced ~4 more offspring (at all life stages) in corn relative to their wheat- and corn- developed ancestors, with a corresponding increase of ~2 adult offspring (Table S11). However, the evolved and ancestral development rates were not correlated (Spearman's rank correlation coefficient with founder and offspring development rate = 0.24 and 0.20; $p > 0.05$ for both). Further, linear discriminant analysis revealed clear separation between the phenotypic space occupied by founders, their offspring, and evolved populations based on the measured traits shown in Figure 6A (Figure 6B; PERMANOVA using Bray-Curtis distance, $F = 51.243$, $R2 = 0.69$, $p = 0.001$).

A linear discriminant analysis of only the evolved trait distributions (at generation 70) showed that the distributions were not clustered by ancestral source population (Figure 6C; PERMANOVA using Bray-Curtis distance, $F = 1.6123$, $R2 = 0.056$, $p = 0.192$). We also did not find any meaningful correlations between the demographic phases of rescue (see the previous section) and evolved trait values (Figure S14C), indicating that demographic events during evolutionary rescue do not shape later trait evolution.

DISCUSSION

We used comprehensive census data for 60 transfers (~60 generations) of experimental evolution in a harsh novel environment to determine the phenotypic contributors to evolutionary rescue, and to assess how founding trait variation was connected to rescue. Evolutionary rescue occurred within ~20 transfers, leading to large parallel increases in population size and stability. Development rate of founder offspring stood out as a strong and consistent driver of adaptation, with mean and variance in this trait being positively correlated with population performance (average population size). This trait also showed the highest initial variation between source populations compared to other fitness-related traits, potentially indicating past divergent selection. Development rate also increased dramatically within a single generation of exposure to corn (potentially reflecting both selective and plasticity effects), as well as over 70 generations of evolution. Interestingly, the impact of ancestral development rate was strongest during rescue and

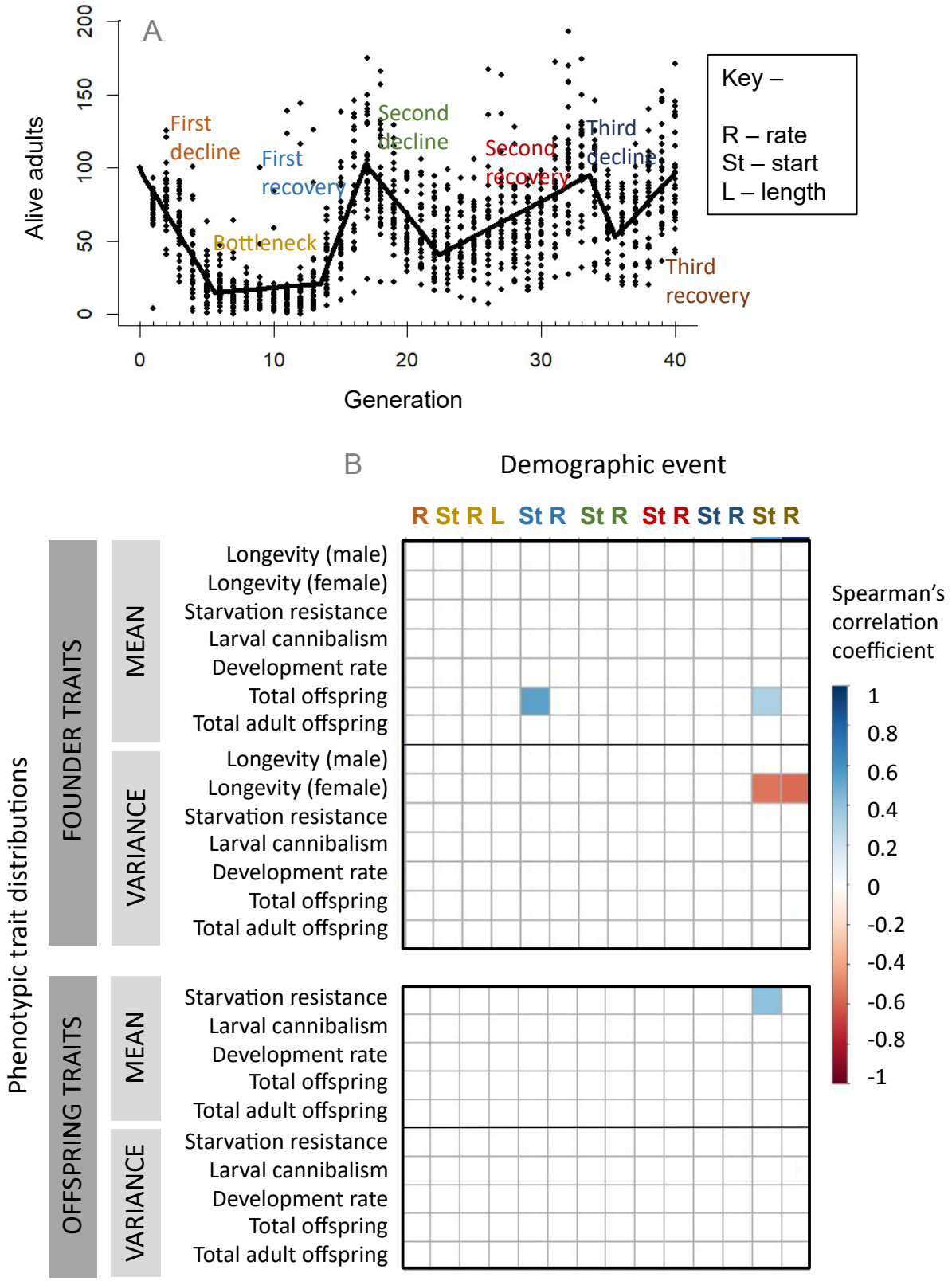

Figure 5. Ancestral phenotypic correlations for founder and offspring trait distributions (means and variances) with individual demographic parameters over time. **(A)** Time series of the adult population size, with the fitted global model combined across populations and replicates for visual reference, highlighting our identification of individual demographic events during and after the initial rescue. **(B)** Matrices showing significant correlations corrected for multiple comparisons (blue – positive, red - negative) between the individual demographic events with ancestral phenotypic traits. Only statistically significant Spearman's rho correlation coefficients after correction for multiple comparisons are shown. 'Rates' are extracted slopes from models fit individually to each line, 'starts' indicate the fitted breakpoint where one event ends and the other begins, and the bottleneck length preceding the rescue event is shown.

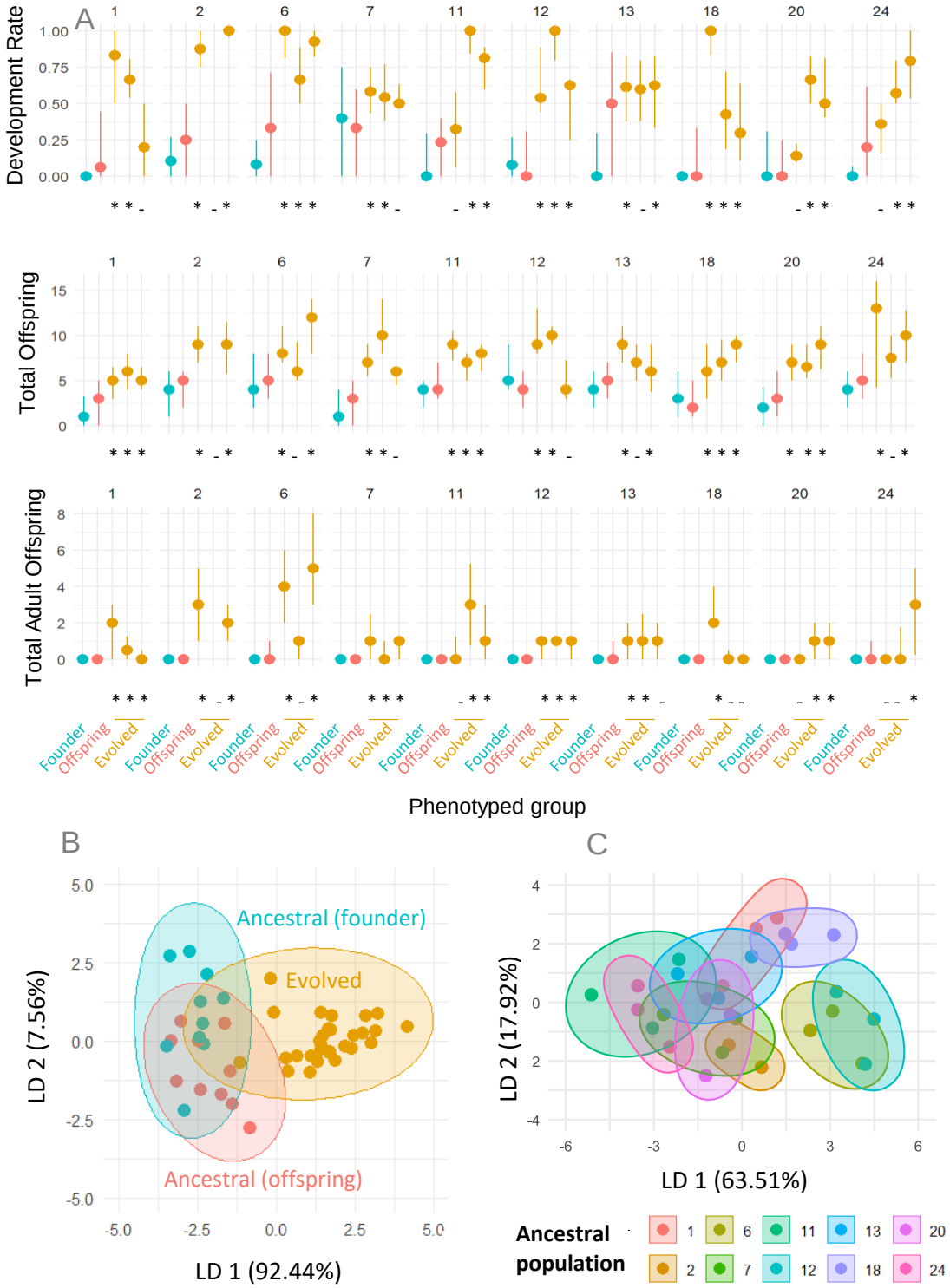

Figure 6. Ancestral and evolved development rate and reproductive fitness after 70 generation cycles of evolution. **(A)** The y-axes of the top, middle and bottom row of panels show development rate, total offspring and total adult offspring, respectively, for different populations. The x-axis shows trait values for ancestors developed in wheat (mimicking founding individuals; "founder", blue), ancestors developed in corn (mimicking first-generation offspring; "offspring", red); and three evolved replicates (yellow). Points indicate the median of the trait distribution and lines represent the interquartile range. Data shown for ancestors is identical to that in Figure 3, replotted here for easy comparison. Significant differences are reported in Table S11, and entire trait distributions are shown as violin plots in Figure S15. Sample sizes per distribution range from 25 to 40 females. **(B, C)** Plots show the first two linear discriminants that group population phenotypes based on **(B)** ancestral founder and offspring traits or for populations evolved in corn for 70 generations (triplicate lines per source population), or **(C)** source population identity (see legend) for evolved traits.

declined afterwards, during which correlations between population performance and other traits emerged. This may be because of a strong, early selective filter only for rapid development in corn, followed by a weaker filter for other traits at later stages of adaptation. We also found a strong effect of female longevity on population size, likely reflecting increased lifetime reproductive output per female under the continuous generation cycles maintained in our experiment. Taken together, these highlight the importance of maximizing the reproductive fitness of the population under rescue via multiple mechanisms (juvenile development rate and female lifetime reproduction). Thus, our study provides an empirical example of a set of specific traits consistently driving adaptation to a suboptimal habitat in populations founded by diverse source populations, across both single-generation and longer-term change. By using an extensive long-term dataset under controlled laboratory conditions and focusing on rescue dynamics, our work builds on prior studies demonstrating how adaptation is affected by intraspecific variation (Leites & Benito Garzón 2023), single-generation trait changes (Chevin & Hoffmann 2017), and both factors acting together (Grenier et al. 2016).

Our study justifies the broad focus on founding individuals for rescue, establishing the importance of founding trait variation for predicting broad aspects of adaptation (e.g., whether long-term adaptation occurs or not). However, we also find multiple disconnects between founding variation and the details of rescue as well as subsequent population dynamics, cautioning against complete reliance on founding traits for predicting finer-grained details (e.g., the time and rate of rescue). First, our results broadly support our hypothesis that the role of ancestral trait variation is dynamic. Based on the declining strengths of correlation with population size over time, we suggest that development rate was under selection more strongly in the early generations of the experiments, whereas other traits — such as reproductive fitness — faced such selection later. Secondly, in contrast to the consistent positive correlations with overall population performance, ancestral trait distributions were not at all associated with specific demographic events during or after evolutionary rescue. In fact, none of the factors we tested — mean or variance in founder traits, mean or variance in traits of the offspring, and demographic events during early stages of rescue — were correlated with any aspect of rescue dynamics. This was surprising because we had predicted rescue rate and bottleneck duration to be the primary demographic events driving overall population performance, especially given the large amount of research linking the importance of demographic processes to evolutionary rescue (Carlson et al. 2014; Hufbauer et al. 2015; Olazcuaga et al. 2023). Could this lack of association in our experiment arise because the rescue dynamics were too similar across populations? This is not the case: the length of the initial population size bottleneck ranged from 4 to 11 transfers across lines, and the slope of the subsequent recovery varied 18-fold across the fastest vs. slowest populations. Perhaps the populations were prone to high levels of demographic stochasticity during rescue, obscuring any effects of founder traits. However, it remains unclear what factors determined the speed and dynamics of evolutionary rescue in our study. Interestingly, early demographic events also did not correlate with later dynamics, suggesting that the rescue event itself (e.g., the bottleneck length or population size decline and recovery rates) did not contribute to shaping later dynamics. We speculate that this is because once rescue occurs, population dynamics are primarily driven by the strong negative density dependence typical of *T. castaneum*, which is relatively invariant across our source populations (Buddh et al. 2024). Further work on other species with different mechanisms of population regulation may reveal whether the lack of longer-term effects of rescue dynamics is a general outcome, or specific to the particular life history of each species. Regardless, our findings throw up new questions about the interactions between evolutionary rescue and longer-term adaptation.

Could the highly parallel phenotypic shifts and population dynamics that we observed tell us something about the underlying genetic changes? Parallel trait evolution is found frequently, with many potential mechanisms and underlying processes (Bolnick et al. 2018; Wortel et al. 2023). We discuss two possibilities, differentiated by their timescales. If the parallel adaptation happened due to rapid adaptation during rescue, the parallelism may be driven by strong initial maladaptation (evident by the large crash in population size). Such strong declines are broadly predicted to facilitate genetic and phenotypic parallelism (Oliveira & Campos 2024), especially for sexually reproducing species with high standing genetic variation (Burke et al. 2014; MacPherson & Nuismer 2017). The fixation of a few large effect beneficial alleles is more likely to underlie the parallelism (Oliveira & Campos 2024; Osmond et al. 2020), since the declining strength of selection in shrinking populations is unlikely to fix small-effect alleles during rescue (Otto & Whitlock 1997). The alternative possibility is that parallel phenotypic evolution occurred after rescue. Given the timescale of our experiment, traits in all populations could slowly approach the optimum or maximal possible values in corn, even with multiple different small-effect alleles being fixed. If we had measured trait values soon after rescue, we may have been able to differentiate between these two possibilities. Note that despite the broad phenotypic convergence, our populations may have adapted via distinct genetic pathways with different rates of adaptation, as observed in laboratory experimental populations founded with closely related yeast genotypes (Kryazhimskiy et al. 2014). This is more probable if the focal traits under selection are polygenic — likely true in this case — because initially different source populations could then more easily find

diverse genetic routes to the fitness optimum (Yeaman 2022). Finally, we speculate that the strong and parallel correlations between population performance and ancestral traits may reflect a major role for standing genetic variation rather than *de novo* mutations in driving adaptation in our study (Burke et al. 2014; MacPherson & Nuismer 2017). In general, standing genetic variation is known to facilitate evolutionary rescue (Agashe et al. 2011; Barrett & Schluter 2008; Gomulkiewicz & Holt 1995; Lachapelle & Bell 2012; Ramsayer et al. 2013; Vander Wal et al. 2013). Identifying the genetic basis of functional trait variation as well as adaptation in these populations will thus allow us to understand the mechanisms underlying the remarkably parallel trait evolution during rescue and beyond.

An important result from our work is the dramatic shift in trait distributions between founders and their offspring within a single generation, consistent across all 10 source populations. Although we cannot discern whether the trait changes reflect selective mortality or plasticity (or a combination of both), the shifts were clearly adaptive, with the sole exception of adult longevity. This echoes findings from plant reciprocal transplant studies: environmentally induced phenotypes (as in our 'offspring' cohort) typically align with the direction of locally adapted populations (Radersma et al. 2020). Adaptive plasticity can facilitate adaptive evolution on short time scales (Ghalambor et al. 2007), and previous work has discussed the helpful role of plasticity in 'buying time' for adaptive evolution to occur prior to evolutionary rescue (Chevin et al. 2013b; Harmon & Pfennig 2021). Importantly, trait distributions corresponding to the founder beetles (mimicking, e.g., individuals that completed their larval development elsewhere, then dispersed to a new resource patch) vs. their offspring (the first generation to complete their entire development in the new resource) were differentially correlated with population performance. *A priori*, we expected that performance in the new habitat would correlate most strongly with offspring trait distributions because these should be more relevant to the rescue event (in the new habitat) than the founder trait distributions. On the contrary, we observe a strong and long-lasting impact of founder traits (offspring development rate and female longevity), and only a sporadic and late impact of offspring traits (reproductive fitness). Although there are no other comparable experimental studies that we are aware of, prior analyses broadly examining the impact of parental effects on population dynamics and adaptation have also typically found moderate to strong parental impacts under diverse experimental conditions (Beckerman et al. 2002; Plaistow & Benton 2009; Savković et al. 2016; Stuligross & Williams 2021). Our results thus complement these prior studies and demonstrate further evidence for the importance of parental effects on adaptation. We consistently see very strong correlations with offspring trait values appearing as late as after ~40 generations of evolution, despite the trait distributions themselves being measured for individuals approximating only the first generation. We suggest that this may be because these phenotypic traits have weaker effects on performance in corn, impacting population performance only after rescue (also known as delayed life-history effects, or carry over effects) (O'Connor et al. 2014). Delayed life history effects are not rare (Beckerman et al. 2002; Helle et al. 2012; Mugabo et al. 2010; Searcy et al. 2014), but the magnitude of the time lag that we observed (~40 generations) is much higher than documented earlier. Note that the lag cannot be explained by exceptionally long-lived founders: 40 generations corresponds to ~1100 days, far exceeding the lifespan of any founder individual from any population in our dataset (~270 days).

The surprisingly low frequency of extinction in our populations (1 in 30) begs the question of whether our populations underwent evolutionary rescue or simply adaptation. We believe the dynamics indeed represent evolutionary rescue, for the following reasons. One of the hallmarks of evolutionary rescue is a U-shaped curve in population size over time, which is very clearly observed in our census data. Prior work has reported U-shaped trajectories consistent specifically with evolutionary rescue of *T. castaneum* populations experimentally evolved in corn flour (Agashe 2009; Agashe et al. 2011; Hufbauer et al. 2015). All these studies reported multiple extinctions in lines adapting to corn flour, suggesting that, in general, *T. castaneum* is strongly challenged by corn (Via 1991). Populations in our study reached a median bottleneck population size of 12 adults (± 5.17 SD), which is consistent with the bottleneck sizes reached in prior work (Agashe et al. 2011). It is likely that since our populations were wild-collected, they had greater genetic diversity (compared to the laboratory-inbred lines used in prior work), potentially reducing extinction probability. It is also likely that the maintenance of continuous generations in our experiment (which allowed adults to reproduce for a long time) buffered populations against extinction. This would also explain how offspring phenotypic variation was preserved in the population for as long as 40 generations, allowing for a late, but strong, impact on population performance. If true, this would suggest species that reproduce continuously mayshow counter-intuitive adaptive trajectories during and after rescue, as observed in our study. We suggest more empirical work comparing discrete vs continuously reproducing populations or species for a more nuanced understanding of rescue.

In summary, we utilized comprehensive datasets for a wide array of ancestral fitness-relevant phenotypic traits and a 70 generation long experimental evolution system to establish a central role for founding population identity during and after evolutionary rescue, suggesting that the current focus on founders for rescue studies is indeed helpful. Further, we were able to identify founder development rate and female longevity as key contributors to rescue. However, we find that phenotypic trait shifts can be quite staggering even within a single generation, cautioning against

generalized rescue predictions. While several studies have examined different aspects of our work in isolation, we were able to study all of them together in a single experimental system. Many more empirical studies with diverse species and methods are needed to catch up with the burgeoning theory in the rescue literature, and also to assess the generalizability of our findings. Nonetheless, our study already has several implications for our ability to predict evolutionary change in several contexts (Wortel et al. 2023). Our results suggest that some pest populations may be especially difficult to eradicate because of fast juvenile development that allows rapid evolutionary rescue under stressors such as novel suboptimal resources or pesticides, facilitating convergence on fitness peaks. Conversely, local populations with a high intrinsic capacity for rapid adaptation under stress (e.g., with high development rates and reproductive fitness) may be best suited for species conservation via re-introduction efforts. Our results also indicate that detailed information on rescue dynamics may not be necessary to predict future evolution, although much more work is needed to rigorously test this idea. Together with a growing body of related work, we hope that our study will aid the prediction of evolutionary responses to climate change and other anthropogenic stressors (Urban et al. 2024).

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