Founders predict trait evolution and population performance after evolutionary rescue in the red flour beetle

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ABSTRACT

Evolutionary rescue helps populations survive environmental change, but the phenotypic and demographic factors associated with rescue dynamics and its long-term effects remain unclear. We experimentally evolved 10 wild-collected 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 trait 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, population dynamics during rescue were uncorrelated both with ancestral trait distributions and post-rescue adaptation. Our results support prior work showing founders as key predictors of adaptation, and highlight the role of founder traits for long-term adaptation and trait evolution following evolutionary rescue.

SIGNIFICANCE STATEMENT

Understanding how populations adapt to sudden environmental change is vital given accelerating biodiversity declines, the rise of antimicrobial resistance and climate change. This study charts evolutionary rescue — where rapid adaptation prevents extinction — in flour beetles, across 70 generations. Using >10,000 census points and measuring fitness in ancestors, their first-generation offspring and in the evolved lines, we show that larval development rate is the strongest correlate of long-term population success across diverse wild-collected populations. Surprisingly, the effect of ancestral variation is dynamic and disassociated from finer-grained details of the rescue. All populations show highly parallel evolutionary rescue patterns, with convergent evolution in key traits. These findings have direct implications for predicting species' survival after environmental change, ranging from conservation to pest and pathogen management.

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). 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.* 2009; 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). 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). Thus, despite the large body of work on this topic, some important gaps remain in our empirical understanding of evolutionary rescue.

First, evolutionary rescue is often framed as a binary phenomenon: populations either go extinct or are rescued. Thus, most studies focus on factors that influence the probability of successful rescue, when mean absolute fitness (which initially declines in the new environment) increases beyond 1 via adaptive evolution (Gomulkiewicz & Holt 1995; Bell 2012; Gomulkiewicz & Shaw 2013; Orr & Unckless 2014; Carlson et al 2014; Bell 2017; Osmond et al 2020). However, the detailed demographic changes during rescue, and longer-term consequences of the rescue process, have received relatively little attention (but see Agashe et al 2011; Orr & Unckless 2014; Olazcuaga et al 2023). For instance, the frequency of rare adaptive alleles and the waiting time to sample new beneficial mutations should influence the bottleneck period after the initial population crash, the slope of the population size rebound, and how much variation is retained (Gomulkiewicz & Holt 1995; Bell 2012; Gomulkiewicz & Shaw 2013; Orr & Unckless 2014; Carlson et al 2014; Bell 2017). These processes should depend on the mean and variance in founder traits (which determine the response to selection during rescue), and the outcomes may in turn influence population performance after rescue. But empirically, we do not know what demographic factors and traits determine population size during and after successful rescue, and whether the speed or the magnitude of adaptation during successful rescue predicts subsequent population dynamics and fate. This knowledge is critical for effective applications of rescue, particularly in conservation. However, because most studies of

evolutionary rescue focus on short-term binary outcomes, these questions remain unanswered.

Second, the phenotypic drivers of evolutionary rescue and subsequent population performance are not always understood or predictable, and yet are vitally important to understand rescue (Chevin & Bridle 2025). The broadly beneficial role of founding genetic diversity in rescue (Barrett & Schluter 2008; Agashe 2009; Agashe *et al.* 2011; Lachapelle & Bell 2012; Ramsayer *et al.* 2013; Stewart *et al.* 2017) is driven by genetic variation which contributes to phenotypic traits that increase survival and reproduction in the new environment (Orr 2005, 2009), and that are therefore directly visible to selection (Hendry 2017). Prior experiments suggest that even in populations with high initial diversity, only some founder traits may contribute to rescue and adult population size after recovery (Agashe *et al.* 2011). But exactly which traits of founding individuals are relevant for the initial rate of population decline or the speed of evolutionary rescue, and how long do these effects persist?

Answering these questions is difficult for several reasons. Selection may simultaneously act on multiple phenotypic traits in the new environment, which may also interact with each other, e.g., via genetic correlations (Walsh & Blows 2009; Gomulkiewicz & Houle 2009). Trait distributions can change during rescue as selection pressures change, or due to demographic and genetic stochasticity imposed by rapid initial population decline in the new environment (Carlson *et al.* 2014; Gomulkiewicz & Holt 1995). For instance, high mortality in the new environment can immediately and strongly change trait distributions (Ciotti & Planes 2019). Finally, trait distributions and population dynamics can be influenced by plasticity ("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; Chevin & Bridle 2025) and carry-over (e.g., maternal) effects of founder individuals (Beckerman *et al.* 2002; Plaistow & Benton 2009; Savković *et al.* 2016; Stuligross & Williams 2021). For instance, short-term population dynamics in the red flour beetle *Tribolium castaneum* depend on both the past resource in which colonizing individuals developed, and the newly colonized resource (Van Allen & Rudolf 2013). Therefore, identifying which founder phenotypes are critical for evolutionary rescue and later population performance requires the measurement of several trait distributions during

and after 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.

We used laboratory experimental evolution in a harsh novel resource (corn flour), founding each line with one of ten wild-collected populations of the red flour beetle *Tribolium castaneum* with high fitness in their ancestral wheat flour environment (Fig. 1). We first confirmed that these ancestral populations had distinct distributions of several fitness-related traits, allowing the possibility of divergent outcomes during rescue and long-term adaptation. We then collected complete census data from each evolving line for 70 generation cycles (280 weeks, or 5 years and 4 months), propagated in an overlapping (rather than discrete) generation design. We observed successful evolutionary rescue in nearly all populations within ~20 generations, allowing us to monitor the impacts of ancestral traits for ~50 generations after rescue. Using our census data, we tested (a) which founder traits may have driven specific demographic events during evolutionary rescue (e.g., the decline, bottleneck and recovery phases) (b) which traits predicted long term population performance (population size and stability), and (c) whether and which trait distributions changed after one generation in corn flour and after 70 generations. Although we use the term ‘founders’, our work is relevant not only in the context of colonization of new habitats, but also *in situ* environmental change. We identify specific fitness components with surprisingly far-reaching effects on long term population performance, with potential applications for predicting population fate in the wild (Gomulkiewicz & Shaw 2013).

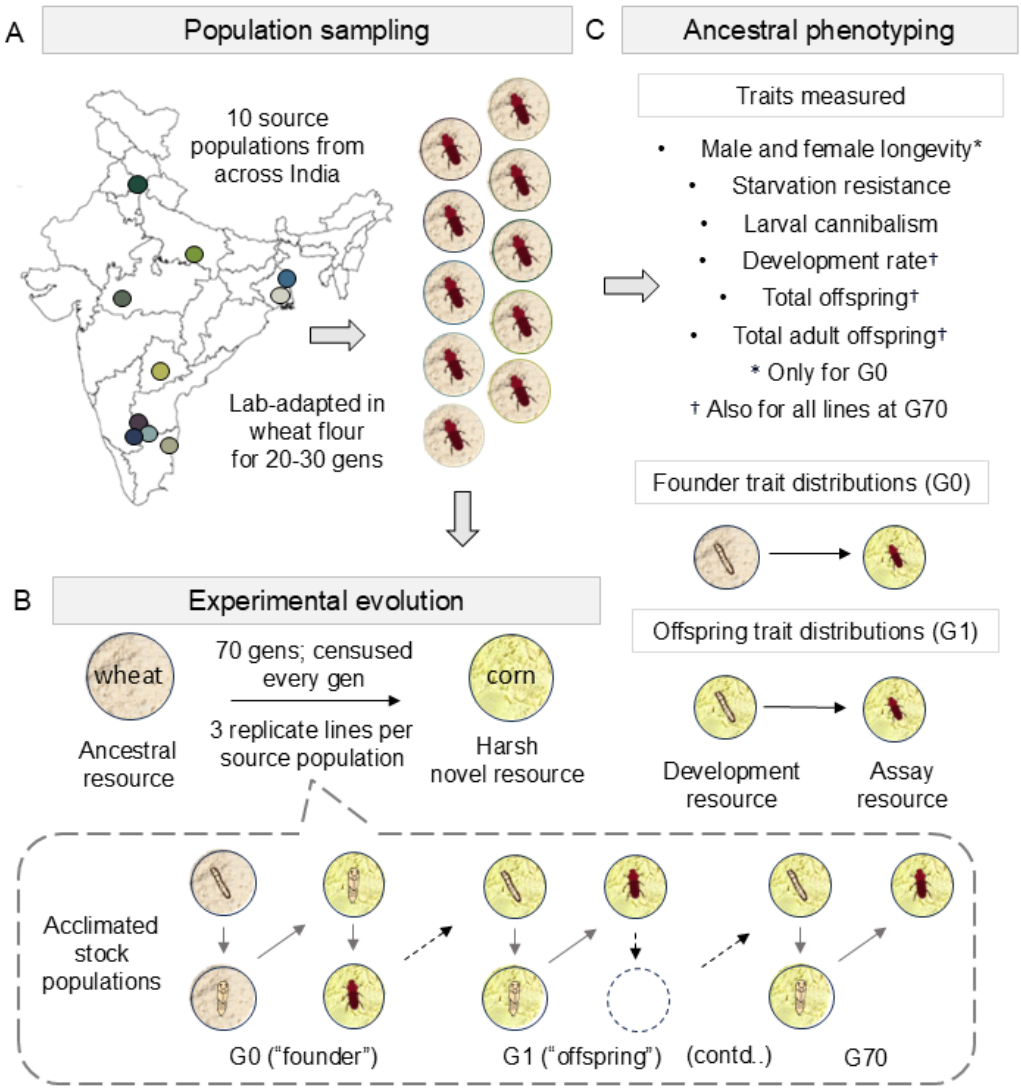

Figure 1. Schematic of the experimental design. (A) Population sampling and lab acclimation. Ten source populations were collected from across the Indian mainland (map: Survey of India), brought into the lab and acclimated to lab conditions in wheat flour (ancestral resource) for 20-30 generations. (B) 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). (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 (generation 0, G0), and the other mimicking their immediate offspring that developed in corn (G1). We also measured three of these traits indicated by our results (see 'Results') in all evolved lines at generation cycle 70.

RESULTS

Source populations had distinct ancestral trait distributions

We first measured founder phenotypes for the ten ancestral populations collected from eight different locations around India (Fig. S1). To capture the phenotypic trait distribution of the founders, we used wheat-developed individuals exposed to corn for the first time, which mimicked the founders' developmental environment. We focused on several traits relevant for flour beetle fitness, broadly affecting survival (adult longevity and starvation resistance), reproduction (total offspring, and total adult offspring) and other aspects of fitness that indirectly contribute to survival, reproduction or both (larval cannibalism and offspring development rate). Source populations were phenotypically distinct for all measured traits, except total adult offspring produced per female (Fig. 2; see Table S1 for full statistical report). The differences were substantial, with adults in some populations living for ~1.5 days longer than others under starvation, and females from some populations producing four times as many total offspring as others. In the slowest-developing populations, only ~3% of offspring pupated within the experimental window (4 weeks), compared to ~42% in the fastest-developing populations. Given these ecologically relevant differences across source population trait distributions, we expected to find divergent adaptive trajectories during rescue and subsequent trait evolution in corn. For instance, offspring development rate (hereafter 'development rate') and total offspring are important traits that directly affect population size. These traits were most strongly affected by source population identity (Table S1), suggesting that they could drive variation in population performance during the early stages of rescue and adaptation.

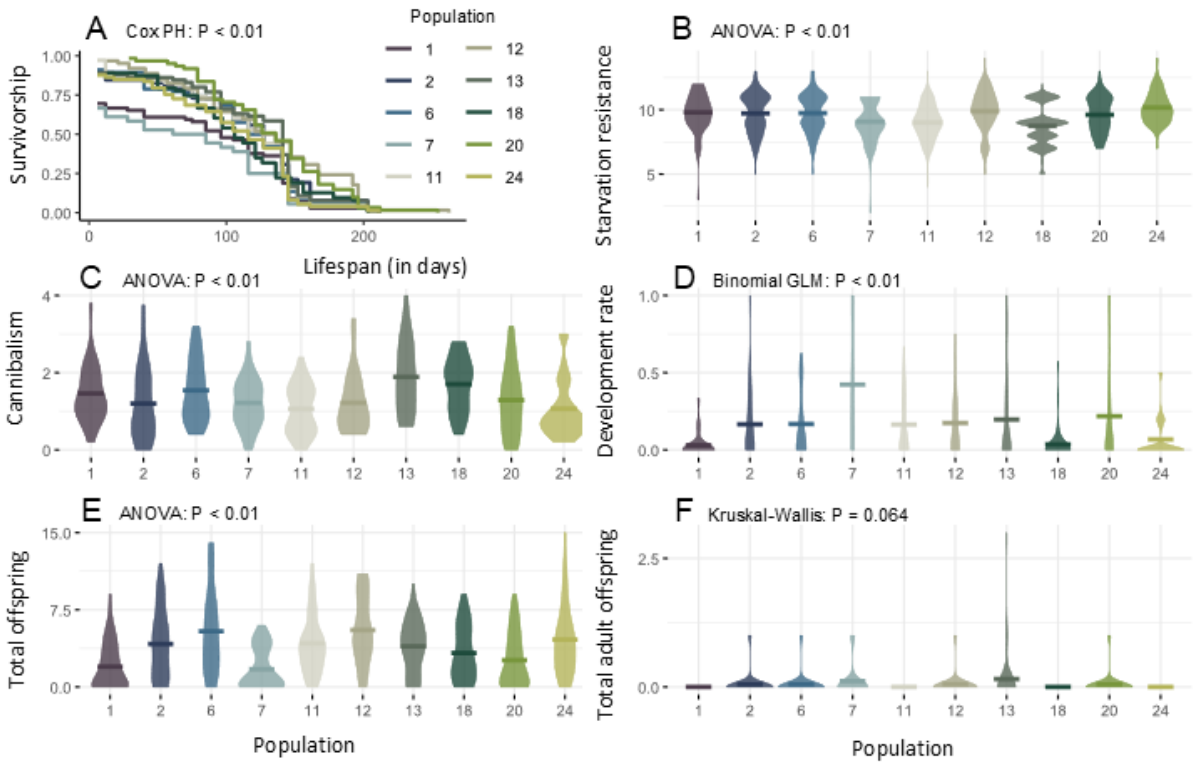

Figure 2. Variation in ancestral phenotypic traits across the ten source populations. Phenotypic trait distributions for each source population for different fitness-related traits (panels A-F). Solid lines inside the violin plots represent distribution means for different populations. (A) Beetle longevity (in days, males and females equally represented; N = 60-80 individuals/population) represented as Kaplan-Meier survivorship curves (B) Starvation resistance (in days, n = 48 pupae per population); (C) Per-capita larval cannibalism (eggs consumed/larvae, n = 25 per population), (D) Offspring development rate (proportion of pupated or eclosed individuals, n = 25-40 females per population) and (E–F) measures of reproductive fitness per female (n = 25-40 females per population), (E) Number of total offspring, and (F) Number of adult offspring. Founder starvation resistance assays for population 13 (panel B) were lost to an accident. One extreme data point is not shown in panel E (population 12, 42 total offspring) for ease of visualization, but is included in the reported statistics. We used different tests to assess whether source population had a significant impact on founder trait distributions – these varied by trait and are reported directly in the relevant panels. See Table S1 for summary statistics and Methods for trait assay details.

Most populations were rescued, but overall performance varied during adaptation to corn

All evolving lines adapted to corn flour in a strikingly parallel manner, with dynamics during the first 20 transfers (~20 continuous transfers) consistent with the classic U-shaped curve associated with evolutionary rescue (Fig. 3A-B). On average, populations showed a strong initial decline with ~15 dead adults/transfer for the first 5-6 transfers, then settled into a demographic bottleneck of ~12 adults for several generations (hereafter 'bottleneck') before rebounding at a rate of ~25 adults/transfer for a few generations. Surprisingly, only one population went extinct, but this enabled us to focus on testing the detailed dynamics and drivers of successful rescue.

We observed several signatures of adaptation – a gradual increase in both population size (Fig. S2A-B, Table S2) and stability over time (Fig. S2C-D, Table S3), with the average number of larvae staying consistent after ~40 transfers, possibly indicating that the populations were close to the habitat carrying capacity soon after rescue. Despite the broad parallelism in the overall dynamics across independently evolving lineages, average population size varied significantly across source population identity for much of the experiment, for both life stages (Fig. 3C; Table S4). Adult population size broadly converged across source populations after generation 40, but this was not so for larvae (Table S4). In contrast, population stability did not vary by source population identity at any time (Fig. 3D, Table S5). Further, the performance rank order of individual selection lines was weakly consistent (over time) during rescue (until transfer bin 2, or ~ generation 20; Table S6), after which bin-to-bin performance correlations strengthened, supporting the overall impact of source population identity on population performance.

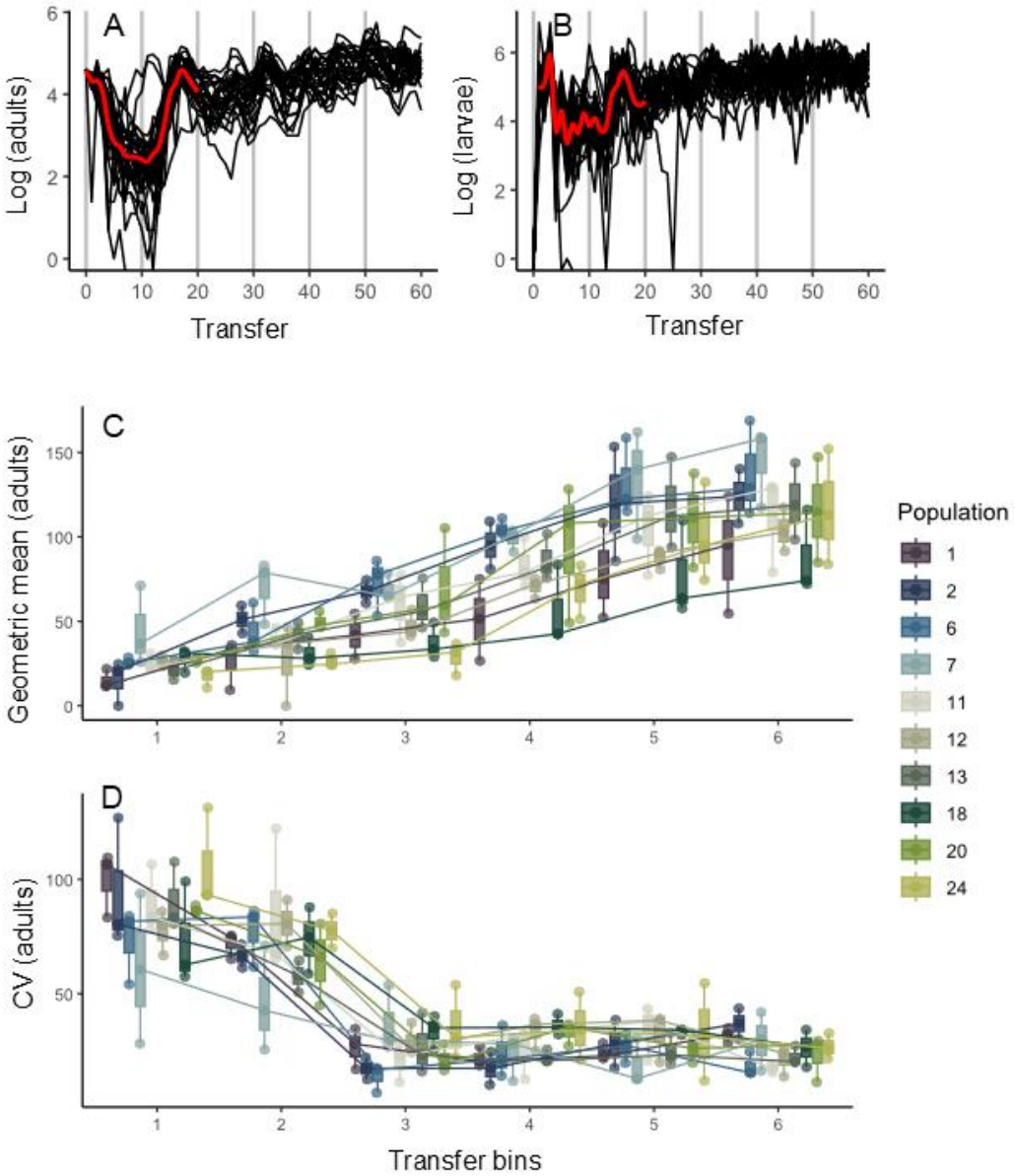

Figure 3. Overall demographic trends observed in corn-adapting lines. Time series of lines adapting to corn flour for (A) adults and (B) larvae, plotted on a natural log scale. The smoothed red curve (using loess) helps visualize the hallmark U-shaped curve of evolutionary rescue. Vertical grey lines represent transfer bins (10 transfers per bin). (C) Average population size and (D) coefficient of variation (inverse of stability) across the adult time series for each transfer bin, for triplicates of each source population (three data points per boxplot; source populations are indicated by different colours). See Tables S4-S5 for ANOVA statistics of population performance across source populations.

Population performance is most strongly associated with founder development rate

If specific traits drove differential population performance during and after rescue (Fig. 3C), we would see (a) significantly differentiated phenotypes across source populations (already reported above), and (b) a correlation between population performance and specific phenotypic trait values for founders. An initial principal component analysis showed that the first two principal components accounted for only 53% of the variance in the ancestral trait values. Therefore, we used original trait values to test for 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 correction, we found two traits that were strongly positively correlated with both adult and larval population size (Fig. 4A-B) for several tens of generations during adaptation — offspring development rate and female longevity (Fig. 4C). Aligning with our initial prediction, the strongest and longest-term association was between population size and the mean and variance of development rate for founding individuals. These were positively correlated with average population size throughout the experiment (Fig. 4C, Spearman's rho ranging from 0.41–0.67, all coloured squares have $p < 0.05$). Interestingly, the strength of both these correlations decreased during evolution (reducing from 0.67 to 0.41 (mean), and 0.71 to 0.41 (variance) from transfer bin 2 to 6). Mean female longevity in corn also stood out as a potential predictor of population performance, being strongly and positively correlated with the average number of larvae in the second half of our experiment (Spearman's rho values ranging from 0.4–0.64).

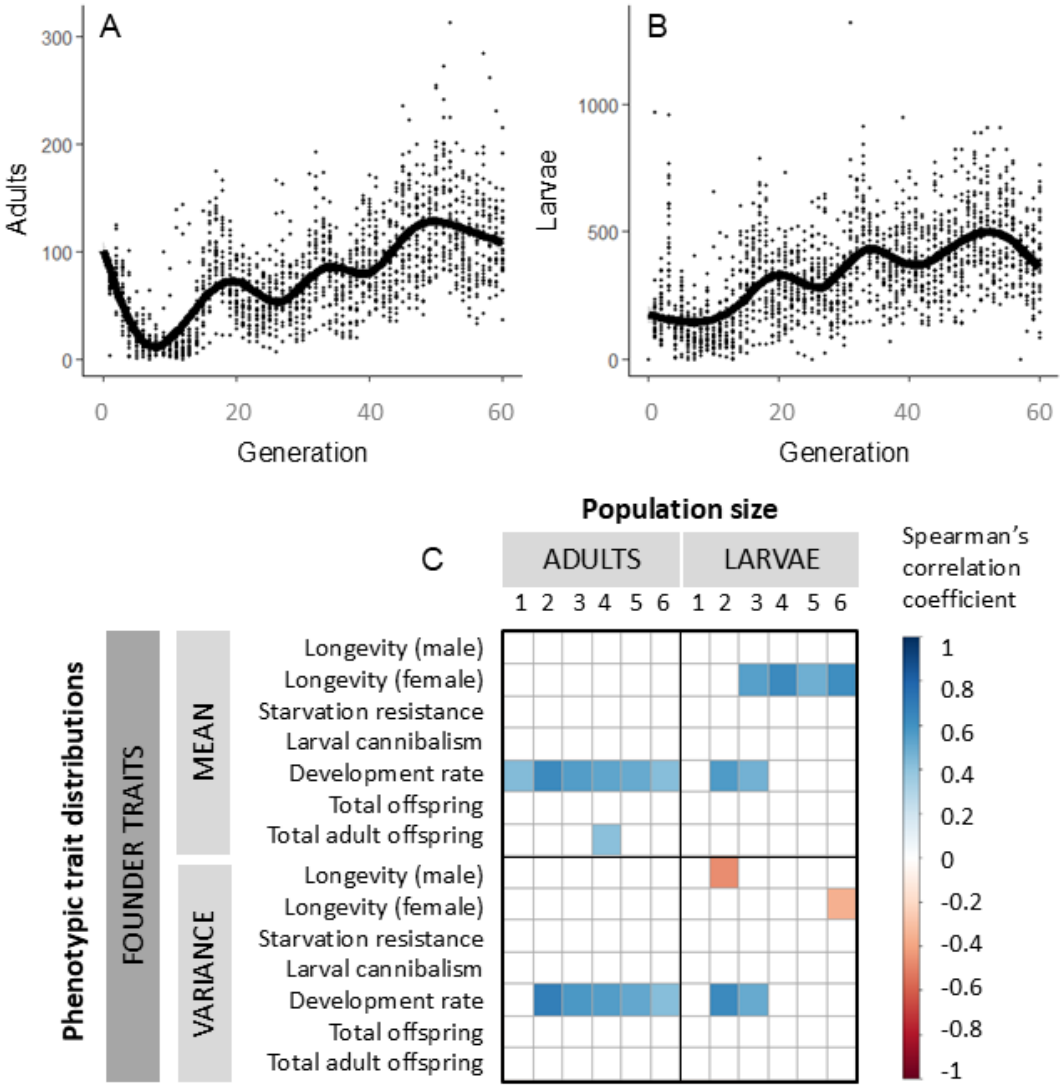

Figure 4. Ancestral phenotypic correlations for founder trait distributions with population size over time. Time series of (A) adults and (B) larvae combined across populations and replicates for visual reference. Black curves in both panels represent a smoothed fit of all data points per time point.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

Founder traits do not predict specific features of population dynamics during or after rescue, and rescue demography does not predict later population performance

Since most of our tested lines underwent successful evolutionary rescue, we focused on across-line variation in the demographic decline, bottleneck and recovery during successful rescue. Given the surprising long-term association of ancestral trait variation with population performance for up to several tens of generations, we also assessed whether founder traits influenced demographic declines and rebounds following rescue. Doing so helped us disentangle two possibilities – (a) founder traits drove population dynamics only during rescue, after which population ranks stayed consistent, leading to apparent (indirect) long-term correlations between founder traits and population performance, and (b) ancestral phenotypic variation directly drove population performance throughout the experiment, via continued trait evolution, eco-evolutionary feedbacks or changing trait correlations. The second possibility could additionally explain the appearance of ancestral trait correlations with population size after 20 generations of evolution (e.g., as observed for female longevity).

In contrast to our results with the 10-transfer bins (Fig. 4), we observed almost no correlations between ancestral traits and specific features of population dynamics during and after rescue (Fig. 5; individual piecewise fits shown in Fig. S3). The only significant correlations after correcting for multiple comparisons involved total offspring and female longevity. For instance, the first and third recovery started later in populations with higher mean total offspring (Spearman's rho=0.53 and 0.31 respectively, both $P < 0.05$). The start of the third recovery also correlated negatively with variance in female longevity in corn (Spearman's rho=-0.534, $P < 0.05$). Importantly, the rates and timings of specific rescue demographic events also did not correlate with post-rescue demographic events (Fig. S4). For instance, contrary to our expectation, populations that declined more slowly or recovered faster from the bottleneck did not consistently perform better than other populations.

Overall, these results suggest that while specific ancestral trait values had broad and consistent effects on population dynamics during corn adaptation across lines, they had weak predictive power with respect to specific demographic changes during and

327 after rescue. Further, specific demographic phases during the evolutionary rescue
328 itself were poor predictors of long-term population dynamics.
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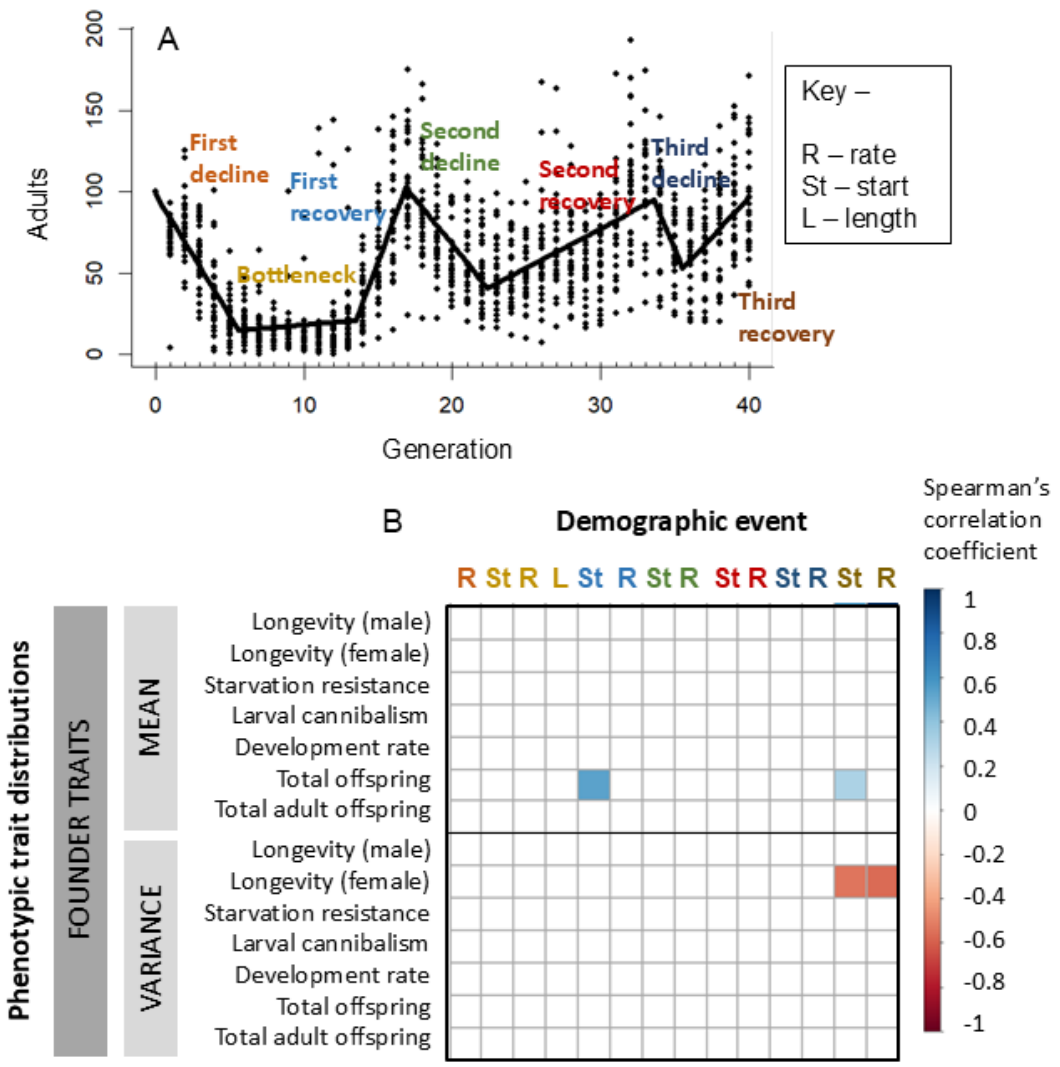

330
331 **Figure 5. Ancestral phenotypic correlations for founder trait distributions with**
332 **individual demographic parameters over time.** (A) Time series of the adult
333 population size, with the fitted global model combined across populations and
334 replicates for visual reference, highlighting our identification of individual demographic
335 events during and after the initial rescue. (B) Matrices showing significant correlations
336 corrected for multiple comparisons (blue – positive, red - negative) between the
337 individual demographic events with ancestral phenotypic traits (means or variances),
338 computed across lines. Only statistically significant Spearman's rho correlation
339 coefficients after correction for multiple comparisons are shown. 'Rates' are extracted

slopes from models fit individually to each evolved line; 'Starts' indicate the fitted breakpoint where one event ends and the other begins; and 'Length' refers to the bottleneck length preceding the rescue event.

Single-generation trait distribution shifts are typically adaptive but have poor predictive power for rescue and later dynamics

Given strong selection in the new corn habitat, we expected to find immediate and large changes in trait distributions within a single generation, which could influence population dynamics. Hence, we measured all the founder traits reported above (except longevity, due to the exceptionally long duration of this assay) for individuals approximating the first generation of each population. To do this, we allowed wheat-developed stock females to oviposit in corn (mimicking founders), and then measured phenotypes for the resulting corn-developed adults (mimicking the 1st-generation offspring of the founders).

Strikingly, all measured trait distributions changed significantly after a single generation in corn, with four of five traits showing adaptive shifts (Fig. S5; Table S7; note significant resource x source population interactions). Corn-reared (generation 1) females produced on average ~1 more adult offspring than wheat-reared founders (all populations combined, GLM, total adult offspring ~ development resource, $p<0.001$). These offspring also developed faster ($p_{\text{development resource}} <0.001$), even after accounting for offspring density in the assay plate (binomial GLM, proportion of pupae or adults at week 4 ~ development resource x density, $p_{\text{development resource}} < 0.01$, other p values > 0.05). In contrast, average lifespan under starvation decreased in generation 1 compared to founders. Finally, larvae produced in generation 1 did not show higher cannibalism, which is adaptive in stressful environments (Via 1999). Notably, ancestral fitness in wheat was a poor predictor of immediate fitness in corn: the relative fitness values of founder vs. generation 1 beetles from a given population were not correlated for any of the measured traits (Spearman correlation ranks in Table S8, Fig. S6). In summary, development rate and the number of offspring (both total and adult) changed adaptively within a single generation in corn.

373 Given the broadly adaptive trait distributions in generation 1 individuals, we expected
374 to find strong correlations with rescue dynamics and longer-term population
375 performance. However, the variance in reproductive fitness at generation 1 was
376 positively correlated with both adult and larval population size for 2-3 transfer bins only
377 towards the end of our experiment, after ~30 generations of no correlation (Fig. S7;
378 Spearman's rho estimates ranging from 0.42–0.61). Other traits showed sporadic (also
379 late) correlations (Fig. S7). Like founder traits, generation 1 traits were also typically
380 uncorrelated with detailed population dynamics during and after evolutionary rescue
381 (Fig. S8). Thus, despite adaptive shifts in key traits such as offspring development rate
382 and total offspring (Fig. S5), trait distributions after one generation in corn had poor
383 predictive power for population performance during rescue, but showed some
384 correlations with overall population performance in the later phase of population
385 growth.
386
387 **Development rate and reproductive fitness increased across 70 generations**
388
389 Our correlative analyses above indicated a major role for development rate in
390 mediating adaptation to corn (Fig. 4). To directly test this, we measured development
391 rate for each evolved line after ~70 generations of evolution. Since total offspring and
392 total adult offspring were also correlated with average population size (albeit at a later
393 stage), we report them below as well. All three traits had increased significantly at
394 generation 70, relative to both the founding individuals and generation 1 (Fig. 6A;
395 Table S9). Beetle offspring in the evolved lines were overall 11 times and 4 times more
396 likely to have successfully pupated in 4 weeks (i.e. had higher offspring development
397 rate) relative to the (founding) wheat-developed ancestors and (generation 1) corn-
398 developed individuals (top panel in Fig. 6A; Table S9). Further, females from evolved
399 lines produced ~4 more offspring (at all life stages) in corn relative to their wheat-
400 developed ancestors, with a corresponding increase of ~2 adult offspring (middle and
401 bottom panels in Fig. 6A respectively; Table S9). However, the evolved development
402 rate was not correlated with the ancestral development rate (Spearman's rank
403 correlation coefficient with founder and generation 1 development rate = 0.24 and
404 0.20; $p > 0.05$ for both), nor with population performance in the last 20 generations
405 (Spearman's rank correlations corrected for multiple comparisons, $p>0.05$).
406 Interestingly, populations that recovered faster during rescue (rate of first recovery in

407 Fig. 5A) had lower variance in evolved development rate after more than 50
408 generations (Fig. S9), indicating that rapid rescue may erode trait variation in the long
409 term.
410
411 Finally, linear discriminant analysis revealed clear separation between the phenotypic
412 space occupied by founders, generation 1, and generation 70 populations based on
413 the measured traits shown in Fig. 6A (Fig. 6B; PERMANOVA using Bray-Curtis
414 distance, $F = 51.243$, $R^2 = 0.69$, $p = 0.001$). A linear discriminant analysis of only the
415 evolved trait distributions (at generation 70) did not indicate clustering by ancestral
416 source population (Fig. 6C; PERMANOVA using Bray-Curtis distance, $F = 1.6123$, R^2
417 $= 0.056$, $p = 0.192$). Thus, the strong effect of source population identity on long-term
418 population dynamics did not shape evolved values of adaptive traits.

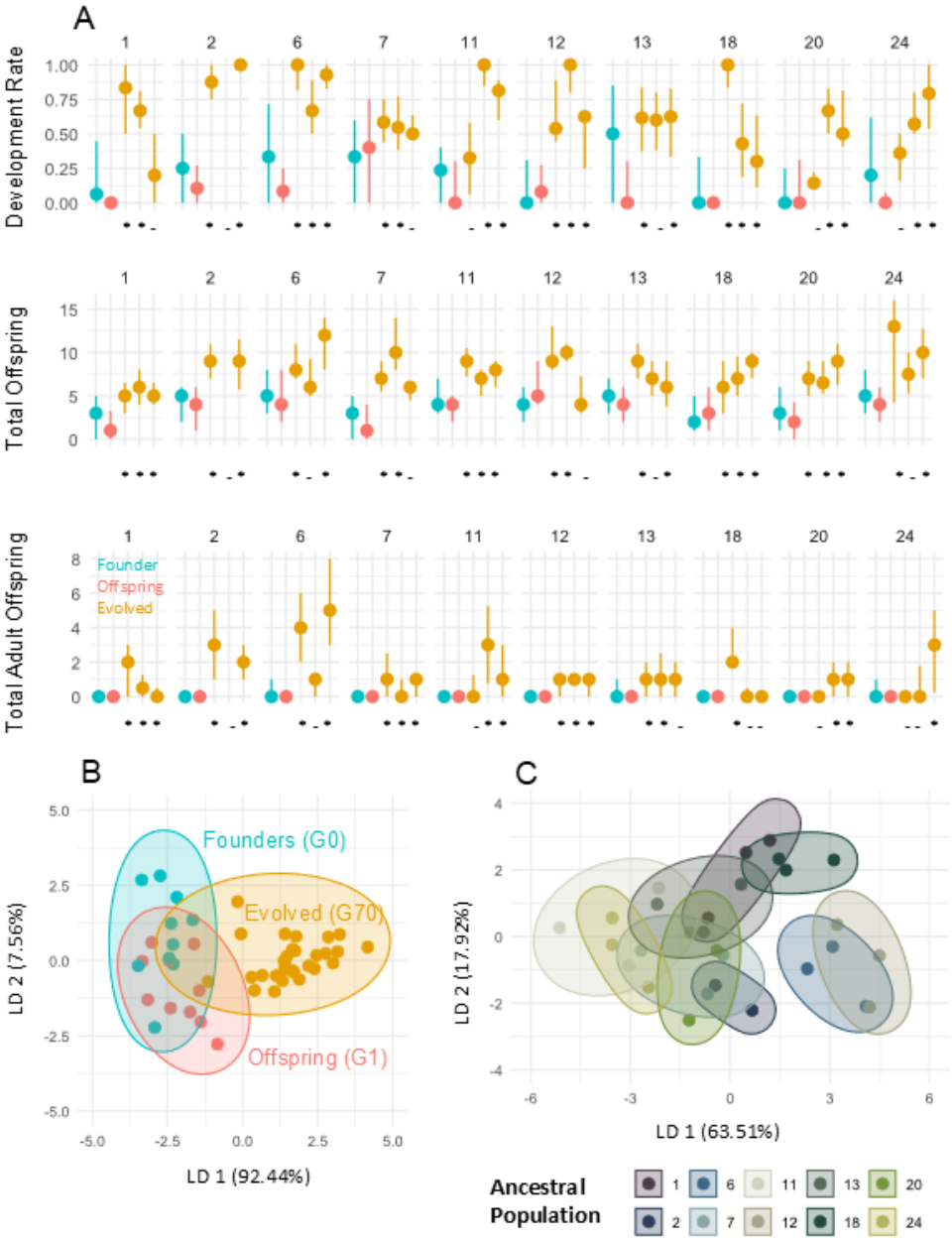

Figure 6. Ancestral and evolved development rate and reproductive fitness after 70 generation cycles of evolution. (A) The y-axes of the top, middle and bottom row of panels show development rate, total offspring and total adult offspring, respectively, for different populations. The x-axis shows trait 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 founders and offspring are identical to that in Fig. 2 and Fig. S5, replotted here for easy comparison. All significant differences are

429 reported in Table S9 (between the evolved traits vs. the founder and offspring traits).
430 Significant differences are represented as asterisks below each evolved trait
431 distribution relative to the red offspring distribution within a panel; dashes indicate non-
432 significant comparisons. Comparisons between the blue founder and red offspring
433 distributions are shown in Fig. S5. Sample sizes per distribution range from 25 to 40
434 females. (B, C) Plots show the first two linear discriminants that group population
435 phenotypes based on (B) ancestral founder and offspring traits or for populations
436 evolved in corn for 70 generations (triplicate lines per source population), or (C) source
437 population identity (see legend) for evolved traits. Data ellipses around the points are
438 to visually highlight groupings only.
439
440 **DISCUSSION**
441
442 We used comprehensive census data for 60 transfers (~60 generations) of
443 experimental evolution in a harsh novel environment to determine which founding traits
444 drove population dynamics during and after evolutionary rescue. Evolutionary rescue
445 occurred within ~20 transfers, leading to large parallel increases in population size and
446 stability. Development rate of founder offspring stood out as a strong and consistent
447 driver of adaptation, with mean and variance in this trait being positively correlated
448 with population performance (average population size). This trait also showed the
449 highest initial variation between source populations compared to other fitness-related
450 traits, potentially indicating past divergent selection. Development rate also increased
451 dramatically within a single generation of exposure to corn (potentially reflecting both
452 selective and plasticity effects), as well as over 70 generations of evolution. Finally,
453 the negative association between the speed of evolutionary rescue and the variance
454 in evolved development rate indicates surprisingly long-term potential effects of rescue
455 dynamics on trait evolution. Our results complement prior work showing faster
456 development rate associated with evolutionary rescue and adaptation to corn, along
457 with other traits such as larval preference for corn and fecundity (Agashe 2011). A
458 meta-analysis of arthropod studies further shows that juvenile development rate is
459 especially important for thermal adaptation (Pawar et al 2024), suggesting that this
460 trait may facilitate insect adaptation in several contexts. We also found a strong effect
461 of female longevity on population size, likely reflecting increased lifetime reproductive
462 output per female under the continuous generation cycles maintained in our

experiment. Thus, our study provides an empirical example 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 the detailed population dynamics during and after rescue, 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 results also indicate that the role of ancestral trait variation is dynamic. For instance, the impact of ancestral development rate was strongest during rescue and declined afterwards, during which correlations between population performance and other traits emerged. Therefore, we suggest that development rate was under selection more strongly in the early generations of the experiments, whereas other traits — such as reproductive fitness (offspring per female) — faced such selection later. Indeed, despite evidence suggesting strong selection on development rate and its role in driving adaptation, the evolved development rate at generation 70 was not correlated with late population performance. Nonetheless, it is possible that population performance at any given time may be strongly correlated with contemporaneous development rate. Overall, we suggest that distinct selection pressures likely operated across the course of the experiment, driving different correlations between various traits and population performance over time.

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 generation 1, 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 generally linking 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. In the end, it remains unclear what factors determined the speed and dynamics of evolutionary rescue in our study. Prior work also found that founding genetic diversity was not a good predictor of the rate of initial population decline, although it was strongly associated with the probability and magnitude of rescue in flour beetles (Agashe et al 2011). Interestingly, in our current work, 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.

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. The parallelism may be driven by strong initial maladaptation, evident from 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). Parallel adaptation in such cases is likely driven by a few large effect beneficial alleles (Oliveira & Campos 2024; Osmond *et al.* 2020), since the declining strength of selection in shrinking populations is unlikely to allow fixation of small-effect alleles during rescue (Otto & Whitlock 1997). An 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 (Szukala *et al.* 2022) 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 (Rivas *et al.* 2018; James *et al.* 2021; Yeaman 2022). Yet another possibility is that some of the parallel dynamics — in particular, the second population decline — may have resulted from environmental forcing, e.g., changes in the texture of the corn flour used to impose selection (see Methods). However, since the correlation of performance with development rate remains consistent before and after this event, this seems unlikely to strongly alter the primary underlying evolutionary processes. 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. 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 starvation resistance. This pattern echoes findings from reciprocal transplant studies with plants: environmentally induced phenotypes (as in our ‘offspring’ generation 1) 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

565 (mimicking, e.g., individuals that completed their larval development elsewhere, then
566 dispersed to a new resource patch) vs. their offspring (the first generation to complete
567 their entire development in the new resource) were differentially correlated with
568 population performance. *A priori*, we expected that performance in the new habitat
569 would correlate more strongly with offspring trait distributions because these should
570 be more relevant to the rescue event (in the new habitat) than the founder trait
571 distributions. On the contrary, we observe a strong and long-lasting impact of founder
572 traits (offspring development rate and female longevity), and only a late impact of
573 offspring traits (reproductive fitness). Although we are not aware of other comparable
574 experimental studies, prior analyses broadly examining the impact of parental effects
575 on population dynamics and adaptation have also typically found moderate to strong
576 parental impacts under diverse experimental conditions (Beckerman *et al.* 2002;
577 Plaistow & Benton 2009; Savković *et al.* 2016; Stuligross & Williams 2021). Our results
578 thus complement these prior studies and demonstrate the importance of parental
579 effects on adaptation. We see very strong correlations between population
580 performance and offspring trait values appearing as late as after ~40 generations of
581 evolution. We suggest that this may be because these phenotypic traits have weaker
582 effects on initial performance in corn, impacting population performance only after
583 rescue (also known as delayed life-history effects, or carry over effects) (O'Connor *et*
584 *al.* 2014). Delayed life history effects are not rare (Beckerman *et al.* 2002; Helle *et al.*
585 2012; Mugabo *et al.* 2010; Searcy *et al.* 2014), but the magnitude of the time lag that
586 we observed (~40 generations) is much higher than documented earlier. Note that the
587 lines were propagated in overlapping generations, so many founding individuals likely
588 lived beyond the 1st generation cycle and presumably continued producing offspring
589 across multiple transfers. However, the lag cannot be explained by exceptionally long-
590 lived founders: 40 generations corresponds to ~1100 days, far exceeding the lifespan
591 of any founder individual from any population in our dataset (~270 days).
592
593 The surprisingly low frequency of extinction in our populations (1 in 30) begs the
594 question of whether our populations underwent evolutionary rescue or simply
595 adaptation. We believe the dynamics indeed represent evolutionary rescue, for the
596 following reasons. One of the hallmarks of evolutionary rescue is a U-shaped curve in
597 population size over time, which is very clearly observed in our census data. Prior work
598 has reported U-shaped trajectories consistent specifically with evolutionary rescue of

599 *T. castaneum* populations experimentally evolved in corn flour (Agashe 2009; Agashe
600 *et al.* 2011; Hufbauer *et al.* 2015). All these studies reported multiple extinctions in
601 lines adapting to corn flour, suggesting that, in general, *T. castaneum* is strongly
602 challenged by corn (Via 1991). Populations in our study reached a median bottleneck
603 population size of 12 adults (± 5.17 SD), which is consistent with the bottleneck sizes
604 reached in prior work where extinction was common (Agashe *et al.* 2011). It is likely
605 that since our populations were wild-collected, they had greater genetic diversity
606 (compared to the laboratory-inbred lines used in prior work), potentially reducing
607 extinction probability. It is also likely that the maintenance of continuous generations
608 in our experiment (which allowed adults to reproduce for a long time) buffered
609 populations against extinction. This would also explain how offspring phenotypic
610 variation was preserved in the population for as long as 40 generations, allowing for a
611 late, but strong, impact on population performance. If true, this suggests that species
612 that reproduce continuously may show counter-intuitive adaptive trajectories during
613 and after rescue, as observed in our study. We suggest more empirical work
614 comparing discrete vs continuously reproducing populations or species for a more
615 nuanced understanding of rescue.
616
617 In summary, we utilized comprehensive datasets for a wide array of ancestral fitness-
618 relevant phenotypic traits and a 70 generation long experimental evolution system to
619 establish a central role for source population identity during and after evolutionary
620 rescue. Further, we identified founder development rate and female longevity as key
621 contributors to rescue, with most populations showing large adaptive shifts in
622 development rate within a generation as well as across 70 generations in corn. While
623 several studies have examined different aspects of our work in isolation, we were able
624 to study all of them together in a single experimental system. Many more empirical
625 studies with diverse species and methods are needed to catch up with the burgeoning
626 theory in the rescue literature, and also to assess the generalizability of our findings.
627 Nonetheless, our study already has several implications for our ability to predict
628 evolutionary change in several contexts (Wortel *et al.* 2023). Our results suggest that
629 some pest populations may be especially difficult to eradicate because fast juvenile
630 development may allow rapid evolutionary rescue under stressors such as novel
631 suboptimal resources or pesticides, facilitating convergence on fitness peaks.
632 Conversely, local populations with a high intrinsic capacity for rapid adaptation under

633 stress (e.g., with high development rates and reproductive fitness) may be best suited
634 for species conservation via re-introduction efforts. Our results also indicate that
635 detailed information on rescue dynamics may not be necessary to predict future
636 evolution, although much more work is needed to rigorously test this idea. Together
637 with a growing body of related work, we hope that our study will aid the prediction of
638 evolutionary responses to climate change and other anthropogenic stressors (Urban
639 *et al.* 2024).
640
641 **METHODS**
642
643 **Collection and maintenance of** source population**s and selection lines**
644
645 We used 10 wild-collected populations of *T. castaneum* from different locations in India
646 (50-100 individuals per source population, Fig. S1) and established large laboratory
647 stocks of these populations in plastic boxes (diameter 21 cm, height 8.5 cm) with holes
648 in the lid for ventilation. To propagate stocks, we allowed ~2000 adults (1-2 weeks
649 post-eclosion) to oviposit in ~750g whole wheat flour for 7 days, following a discrete
650 generation cycle, after which we allowed offspring to develop for ~28 days. This regime
651 ensured at least 2000 individuals every generation, facilitating maintenance of genetic
652 diversity. Stocks were acclimatized to laboratory conditions in dark Percival incubators
653 at 32°C (±1°C) for 2-3 years (~20-30 generations) prior to initiating the selection lines.
654 Note that populations are not numbered consecutively – they correspond with
655 laboratory IDs.
656
657 To study evolutionary rescue, we used a highly suboptimal novel resource, corn flour.
658 *T. castaneum* populations established in corn show low population growth rates
659 (Szűcs *et al.* 2014), and are often driven to extinction (Agashe 2009). We established
660 a total of 30 experimental lines in corn (10 source populations x 3 replicates each; Fig.
661 1) founded with 100 pupae each from the respective source population stocks, which
662 have a typical sex ratio of 1:1. In contrast with the stock maintenance, we propagated
663 the selection lines in overlapping generations. We initiated lines in a staggered manner
664 over 6 months, so that the three replicates of each source population were started on
665 different days. We maintained all lines in 50 g (±0.5 g) corn flour in plastic boxes (6.7
666 cm diameter) with small holes in the lid for ventilation. We purchased flour from the

667 same supplier throughout and documented any changes in the texture of the corn (Fig.
668 S10). To kill any prior pest infestations, new flour packets were sterilized by freezing
669 at –80°C for 24 hours. We maintained the lines in incubators as above.
670
671 Every 28 days (± 1 day) — corresponding to the average development time from egg
672 to pupae in corn (i.e., the approximate generation time) — we replenished the resource
673 by transferring populations to fresh flour. At each transfer, we censused all life stages
674 except eggs (i.e., we counted dead and living larvae, pupae and adults), by sifting the
675 contents of the box through meshes of different pore sizes (600-μm and 710-μm;
676 Daigger), and discarding dead individuals. Eggs typically take ~48 hours to hatch, so
677 all eggs laid 2-3 days prior to the census were discarded along with the used flour. We
678 heat-sterilized all equipment for a minimum of 10 minutes at 65°C to prevent cross-
679 contamination.
680
681 **Assessing population performance**
682
683 One line (replicate 2 of source population 2) went extinct within 5 generations and was
684 excluded from all further analyses. We also excluded census data between
685 generations 60-70 from subsequent analysis since we encountered many COVID19-
686 related disruptions to the workflow during this time. We evaluated the overall
687 population performance for each selection line from the census data for adults and
688 larvae (the most abundant life-stages in the lines) by calculating the geometric and
689 harmonic mean population size. The former is a natural scale for population size since
690 populations grow multiplicatively, and the latter is an approximate estimate of effective
691 population size (Rice 2004) and accounts for population size fluctuations (Vucetich *et*
692 *al.* 1997). Additionally, we estimated population stability by quantifying population size
693 oscillations using the coefficient of variation (CV). We split the dynamics (and
694 calculations) into bins of ten successive transfers (i.e., transfers 1–10, 11–20, till
695 generation 60) and evaluated population performance (average size and CV) per bin
696 to minimize autocorrelation effects. The harmonic and geometric means were strongly
697 correlated for both adults and larvae (Pearson's correlation > 0.99, Fig. S11), so we
698 only report geometric means throughout. In addition, as a direct assay of adaptation
699 we measured two important traits in each evolved line, as described in the next
700 section.

701

702 **Measuring fitness-related phenotypic traits**

703

704 We assayed the ten source populations for five fitness-related traits: adult longevity
705 (lifespan after eclosion with access to food), adult starvation resistance (lifespan after
706 eclosion without food), larval cannibalism (number of eggs cannibalized per larva per
707 day), offspring development rate (proportion of eggs that developed to the pupal or
708 adult stage in 4 weeks, hereafter 'development rate'), and a snapshot of adult
709 reproductive fitness (viable offspring produced per female – either total, or those that
710 developed to adulthood) (Fig. 1; Fig. S12; SI methods). Our measures of reproductive
711 fitness are defined this way to contrast with other phenotypes directly related to
712 survival (adult longevity and starvation resistance), and other traits that are indirectly
713 linked to either survival, reproduction, or both (cannibalism and offspring development
714 rate). Our snapshot reproductive fitness measures implicitly include female fecundity,
715 egg hatchability and survival to late larval stages within the assay, but we do not
716 measure each of these individually.

717

718 To mimic founder trait distributions ('G0', hereafter 'founder phenotypes'), we allowed
719 individuals from each of the 10 ancestral populations to develop in wheat, and then
720 transferred them to corn to measure the phenotypes. We also used a proxy for the
721 phenotypic distributions of the first generation of individuals that developed in corn
722 ('G1', i.e., the offspring of the founders, hereafter 'offspring phenotypes' or 'generation
723 1 phenotypes'), by measuring all the above phenotypes for stock individuals whose
724 parents developed in wheat but reproduced in corn, leading to the test individuals
725 developing in corn too). Doing so allowed us to test the relative importance of the
726 phenotypic distributions of the founders versus their offspring (with different
727 development resources), giving us more insight into potential disconnects between
728 ancestral variation and population dynamics. Finally, to test a hypothesis that arose
729 during data analysis (discussed in Results), we re-measured two traits (development
730 rate and reproductive fitness) after ~70 generations of evolution of each population
731 (hereafter 'evolved phenotypes'). We did this by deriving smaller sub-lines from the
732 evolving lines, which we then measured (SI methods).

733

734 **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. To clarify, we use ‘bottleneck’ to only refer to the period of consistently low population sizes after the initial decline and before the first recovery (see Fig. 5). 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 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.

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