

# Evolution of life history and dispersal traits during the range expansion of a biological control agent

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## Abstract

Evolutionary theory predicts that the process of range expansion will lead to differences between core and edge populations in life-history and dispersal traits. Selection and genetic drift can influence reproductive ability, while spatial sorting by dispersal ability can increase dispersal at the edge. However, the context individuals experience (e.g., population density and mating status) also impacts dispersal behavior. We evaluated theoretical predictions for evolution of reproductive life-history and dispersal traits using the range expansion of a biological control agent, *Diorhabda carinulata*, or northern tamarisk beetle. We found divergence between core and edge populations in fecundity, age at first reproduction, and female body mass. We also show that density and mating status influence dispersal and that dispersal increases at the edge of the range under some conditions. We find support for most predictions about evolution during range expansion, even across a heterogeneous environment, especially when the ecological context is considered.

## 1. Introduction

Ecological and evolutionary processes acting during range expansion (Bowler & Benton, 2005; Kokko & López-Sepulcre, 2006; Kubisch et al., 2014) are key to understanding the spread of invasive species (Hastings et al., 2005), potential success of biological control agents (Szűcs et al., 2019), and the ability of threatened species to track recent climate change (Mustin et al., 2009). The landscapes encountered by range expanding populations represent novel selective environments (Brown et al., 2013; Van Petegem et al., 2016), and simultaneously, the expansion itself can be a catalyst for evolution through spatial sorting and founder effects (Phillips et al., 2010b; Shine et al., 2011). Thus, range expansion can result in evolved differences in reproductive life-history and dispersal traits between populations at the core of the range and the edge of the expansion front (Peischl et al., 2013; Phillips, 2015; Simmons & Thomas, 2004).

The effect of range expansion on reproductive life-history traits, such as fecundity and age at first reproduction, depends upon whether selection or non-adaptive evolutionary processes are dominant at the expansion front (Phillips et al., 2010b). Selection is hypothesized to differ between core and edge due to differences in density (Burton et al., 2010; Fronhofer & Altermatt, 2015). Stable, high-density populations at the core generally exhibit density-dependent growth, where selection favors competitive ability (Phillips et al., 2010b). At the expansion front, population densities are low and competition is relaxed, so populations generally exhibit density-independent growth (Altwegg et al., 2013; Burton et al., 2010) and selection favors

high fecundity and early reproduction (**Fig. 1A**, solid arrow) (Brommer et al., 2002; Phillips et al., 2010b). However, edge populations may be so small that genetic drift can overwhelm selection, and deleterious alleles may ‘surf’ the wave of expansion during repeated founder events (Klopfstein et al., 2006). When these non-adaptive processes are dominant, edge populations may experience reduced fitness, or expansion load, relative to the core (**Fig. 1A**, dashed arrow) (Peischl et al., 2013; Peischl & Excoffier, 2015; Travis et al., 2007). Additionally, fecundity at the edge may be reduced relative to the core due to trade-offs between dispersal, reproduction, and competitive ability (Burton et al., 2010; Fronhofer & Altermatt, 2015; Phillips et al., 2010b).

Range expansion theory predicts that populations at the expanding edge will evolve increased dispersal ability relative to populations at the core through the process of spatial sorting (Phillips et al., 2008; Shine et al., 2011; Travis & Dytham, 2002). Spatial sorting occurs as individuals with greater dispersal ability are more likely to arrive at the range edge and disperse to new territory, resulting in populations at the expanding edge being a non-random selection of better dispersers. Since dispersal ability is heritable in many species (Saastamoinen et al., 2018), this gradient is further reinforced by spatially assortative mating among individuals at the edge. Despite strong evidence for spatial sorting (Berthouly-Salazar et al., 2012; Hill et al., 2011; Lombaert et al., 2014; Merwin, 2019; Monty & Mahy, 2010; e.g. Phillips et al., 2006, 2010a), some factors may inhibit or weaken evolutionary shifts in dispersal between core and edge. For example, adaptation to novel environments could slow expansion speed and reduce spatial selection on dispersal (Andrade-Restrepo et al., 2019; Hillaert et al., 2015). Additionally, species that are unlikely to disperse from low-density patches may be less likely to evolve increased dispersal ability at the edge of the range expansion (Fronhofer, Gut, et al., 2017; Travis & Dytham, 2002).

Dispersal is a multi-faceted behavior that involves individual choices about whether and how far to move. Dispersal may be informed by intraspecific interactions such as the presence of relatives and population density (Bitume et al., 2013; Endriss et al., 2019), and factors internal to the organism such as body condition, sex, or mating status (**Fig. 1B**) (Clobert et al., 2009; Schumacher et al., 1997). For many species, high population density can signal strong intraspecific competition, which may increase emigration (positive density-dependence) (Altwegg et al., 2013). Alternatively, species for which the benefit of living near conspecifics (e.g. mate availability, predator avoidance, reduced Allee effects) outweigh the cost of competition (Bowler & Benton, 2005) may decrease dispersal at high population densities (negative density-dependence). During range expansion, spatial selection increases dispersal even when population density is low, so density-dependent dispersal that is less strongly positive, or even negative, may evolve at the range edge (**Fig. 1B**, dashed line) (De Bona et al., 2019; Fronhofer, Nitsche, et al., 2017; Travis et al., 2009).

Mating status may also influence dispersal decisions for sexually reproducing species that can disperse before and after mating (Clobert et al., 2009; Li & Kokko, 2019; Schumacher et al., 1997). Mated individuals may show positive density-dependent dispersal to reduce competition and reproduce in a low density environment where offspring might have a better chance of survival (**Fig. 1B**, right), while unmated individuals may show negative density-dependent dispersal to increase the chances of finding a mate (**Fig. 1B**, left) (Clobert et al., 2009).

We can infer the relative dominance of evolutionary processes during a natural range expansion by evaluating the patterns of key reproductive life-history and dispersal traits across the range. We use the naturally replicated range expansion of an introduced biological control agent (hereafter, biocontrol agent) and examine patterns in life-history and dispersal traits to evaluate drivers of evolutionary change in range expansions in natural populations. This contributes to a growing literature testing range expansion theory on natural populations (Phillips et al., 2006, 2010a; Wolz et al., 2020) and is the first test we know of in a modern biocontrol agent (Szűcs et al., 2019). Understanding the evolutionary dynamics of biocontrol agents is of particular interest for predicting future spread and improving efficacy and safety across the range of a target pest species (Stahlke et al., 2021; Szűcs et al., 2019; Van Klinken & Edwards, 2002; Wright & Bennett, 2018).

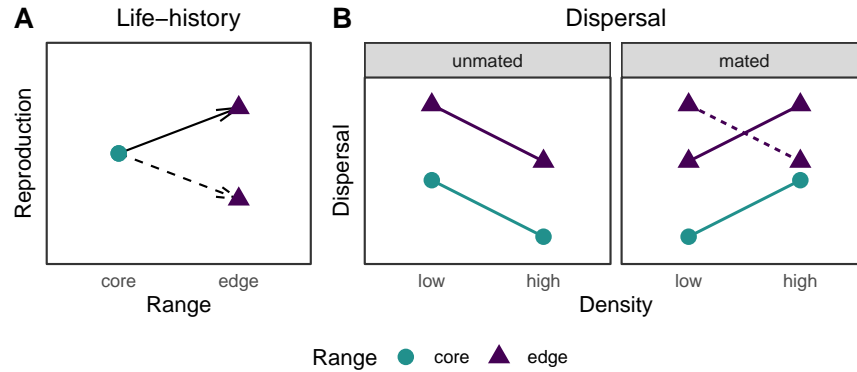


Figure 1: Reproductive life-history traits in edge populations may increase due to selection at low densities (A, solid line) or decrease due to expansion load (A, dashed line) compared to core. Dispersal is predicted to be informed by density and mating status and evolve upwards at the range edge (B). Density-dependence may also evolve at the edge (B, dashed line).

**Figure 1** summarizes how we evaluate evolutionary processes occurring during range expansion. Specifically, an increase in reproductive output of individuals from the edge relative to the core supports selection at low densities as the dominant process, while decreased reproductive output of edge individuals supports expansion load or trade-offs as the dominant process (**Fig. 1A**). Increased dispersal among individuals from the edge indicates that spatial sorting is acting during this range expansion (**Fig. 1B**), while if dispersal does not change between core and edge, other factors, such as adaptation to the new environment, may be limiting the opportunity for spatial sorting. We also expect that individuals' dispersal choices will be influenced by the contexts they experience, specifically density and mating status (**Fig. 1B**). If density-dependence has evolved during the range expansion, we predict that dispersal will be less positively or negatively density-dependent for mated individuals from the range edge (**Fig. 1B**, dashed line). We use a common garden to evaluate the patterns of evolution of early fecundity, age at first reproduction, body mass, and dispersal of eight populations of the biocontrol agent *Diorhabda carinulata*, collected from the core and edge of its range in the western US.

## 2. Materials and methods

*Diorhabda carinulata*, the northern tamarisk beetle, was released in 2001 into the western United States for the biological control of invasive riparian shrubs in the genus *Tamarix*, or saltcedar or tamarisk (DeLoach et al., 2003). Beetles have dispersed southward from a few initial release sites (**Fig. 2**) (D. W. Bean et al., 2012) following remote riparian corridors, which likely represent independent dispersal pathways. The *D. carinulata* range expansion provides an excellent study system for testing the predictions of range expansion theory because original release sites are known and the range expansion has been monitored (D. Bean & Dudley, 2018).

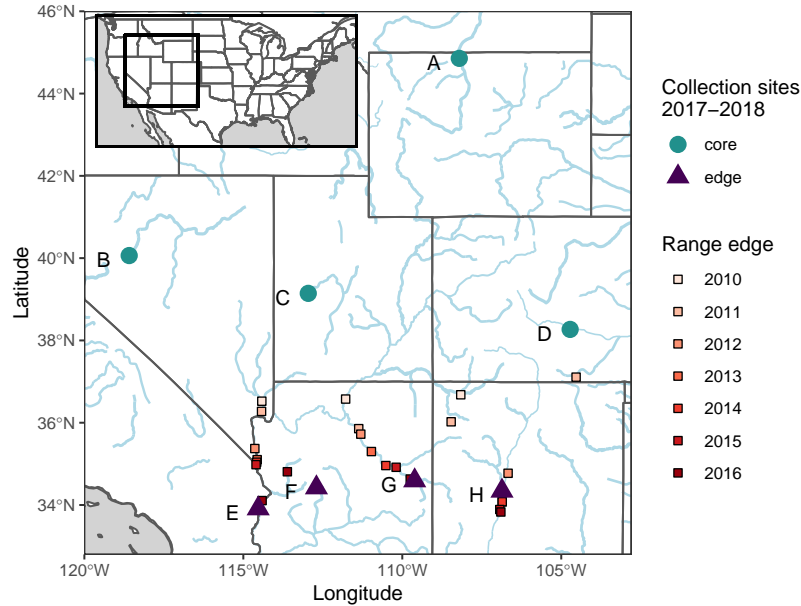


Figure 2: *D. carinulata* range expansion along river corridors (squares show edge locations each year and were jittered to show overlapping points), and collection sites at the core and edge (circles and triangles). Letters correspond to Table S1. Range edge data are from the RiversEdge West Tamarisk Beetle Distribution Map, available at: <https://arcg.is/1izOPW0>.

Eight collections of *D. carinulata* were made from across the introduced range of the species. Four collections were from well-established original introduction sites in the north of the range and represent the range core. Another four collections were from the newly established southern edge of the range (Fig. 2, Table S1). One edge population (H in Fig. 2 and Table S1) was collected slightly behind the probable edge in 2017 in order to avoid other *Diorhabda* species that were moving northward and overlapping the *D. carinulata* range (Ozsoy et al., 2019). Two populations (one core and one edge) were collected Fall 2017 and the first lab generations were put into reproductive diapause to reduce the number of lab generations before the start of the experiment. All other populations were collected in Summer 2018 and cultured in the lab for one generation to standardize maternal environment effects prior to starting experiments. All insects were reared in growth chambers under reproductive conditions (D. W. Bean, Wang, et al., 2007), with a 16h/8h light/dark cycle and 25°C/20°C day/night temperatures and were fed fresh tamarisk as needed.

## Life-history

Newly emerged adult females of the second lab generation were weighed before feeding and reared individually thereafter in 0.24 L plastic containers with mesh lids. Three days after eclosion, each female was paired with a male from the same population of about the same age and allowed to mate for 24 hours before the male was removed. Presence of eggs in each container was assessed daily. All eggs that were laid on the first day of oviposition were counted to provide a measure of early fecundity and the age at first reproduction in days was recorded. Individuals that had not oviposited within seven days of emergence were recorded as non-layers (Lewis et al., 2003). We collected mass and egg count data from 130 core and 140 edge female *D. carinulata*, and age at first reproduction from 104 core and 118 edge females.

## Dispersal

Dispersal ability was measured for only male *D. carinulata* since, in the field, males have been observed dispersing first and using pheromones to attract mixed-sex aggregations of reproductive adults (Cossé et al., 2005). After emergence as adults, males were randomly assigned to density and mating treatments. Males assigned to the mated treatment were paired with a female from the same population for 24 hours. The males were thereafter reared in 0.24 L plastic containers with mesh lids in groups of five (high density) or alone (low density). All males in each high-density container were of the same mating treatment. All containers received the same surplus amount of fresh tamarisk, regardless of how many beetles were in the container. Male beetles were between 6 and 23 days after eclosion and were weighed on the day of the dispersal trial.

We assessed dispersal of male beetles using tethered flight mills (reviewed in Minter et al., 2018), similar in design to Maes et al. (2014) (Appendix S1). Each beetle was given one hour to take any number of flights on a flight mill. Each individual was between 6 and 23 days post-eclosion for its flight trial. Data from each trial was converted into four dispersal elements: occurrence of at least one flight, number of flights, total flight distance, and average flight speed (Appendix S2). Each dispersal element has different biological relevance (Stevens et al., 2013; Tung et al., 2017). Occurrence of flight and number of flights measure the probability and frequency of movement from the local patch. Total distance and average speed measure how far individuals disperse, after initiation. Spatial sorting may act on any one or combination of these elements. We collected dispersal data from 279 core males and 311 edge males, with 65 to 81 males in each density-mating treatment combination and at least 15 from each population. Average speed was calculated for 231 core and 266 edge males that took at least one flight, with 56 to 71 males in each density-mating treatment combination.

## Statistical Analyses

The three life-history traits of female body mass, fecundity over 24 hours, and age at first reproduction were analyzed both individually and with a multivariate analysis of variance (MANOVA). In the MANOVA, only individuals that produced eggs during the experiment were included, since they were the only complete observations. The three life-history traits were the response variables, and range (core or edge), population, and eclosion date were fixed effects.

Mass of female beetles at adult emergence was analyzed individually with a linear mixed model, with range as a fixed effect and population of origin as a random effect.

Since some females (17%) did not lay eggs within 10 days, the data on the numbers of eggs were split into two datasets, one including the number of eggs for laying individuals, and the other including the binary response (laying or non-laying) for all individuals, to assess whether probability of laying and fecundity differed between core and edge populations. To account for overdispersion, a negative-binomial mixed model was fit to the count data (excluding non-laying individuals) using the glmmTMB package version 1.0.2.1 (Brooks et al., 2017) with range, mass, and age at first reproduction as fixed effects and population as a random effect. A logistic mixed model was fit with the glmmTMB package to the binary dataset with range and mass as fixed effects and population as a random effect. Age at first reproduction could not be included as a covariate due to convergence issues.

Age at first reproduction was analyzed for individuals that reproduced during the experiment using a Conway-Maxwell Poisson mixed model which accounts for under-dispersion in this dataset (Brooks et al., 2019), with range and mass as fixed effects and population as a random effect. We complemented this analysis with a Kaplan-Meier survival analysis, which accounts for censoring of individuals that either did not reproduce during the experiment or died before reproducing. Since covariates and random effects cannot be added in Kaplan-Meier survival analyses, the analysis was run twice, once with population as the predictor to visualize the spread among populations and again with range as the predictor to estimate the total effect of range.

Mass of male beetles at the time of the dispersal trial was analyzed with a linear mixed model, with range,

rearing density (low or high), mating status (unmated or mated), and interactions between those factors as fixed effects, age at time of weighing as a fixed covariate, and population as a random effect.

Each of the four dispersal elements (occurrence of flight, number of flights, total distance, and average speed) were analyzed separately. We chose not to do multivariate analyses on the dispersal traits since all but one variable was highly zero-inflated and skewed, which violates assumptions of multivariate tests such as MANOVA, and univariate tests could better incorporate sampling design and environmental covariates during the trials, which greatly improve model fit. For each dispersal element, the same factors were included. Range, density, mating status, and all interactions were fixed effects. Mass at the time of dispersal trial, age, mill friction (Appendix S1), and temperature were fixed covariates. Population and trial date were random effects.

The occurrence of at least one flight was analyzed with a binomial model with the packages lme4 version 1.1-26 (Bates et al., 2015) and lmerTest version 3.1-3 (Kuznetsova et al., 2017). The number of flights during the 1-hour trail was analyzed using both a negative binomial and a Poisson mixed model with the glmmTMB package. QQ plots of model residuals and residual vs. fitted plots from the DHARMA package version 0.3.3.0 were used to assess model fit (Hartig, 2020). The negative binomial mixed model best met assumptions of normality of residuals and was chosen as the final model. Total distance was a count of revolutions of the flight mill and thus a discrete variable. Six models were fit for total distance: a linear mixed model on log-transformed distance, a negative binomial mixed model, a generalized Poisson model (commonly used for highly right skewed data with a high frequency of low counts (Brooks et al., 2019; Joe & Zhu, 2005)), and a zero-inflated version of each of those, using the glmmTMB package. Based on the same residual diagnostics as above, the zero-inflated generalized Poisson model best met assumptions of normality of residuals and was chosen as the final model. Average speed during the 1-hr trial included only trials in which the beetle made at least one flight and was analyzed with a linear mixed model using lme4 and lmerTest.

In all dispersal models, the three-way interaction was dropped from the model if it was not statistically significant. Post hoc comparison of means was done with the emmeans package version 1.5.4 (Lenth, 2020). All analyses were done in R version 3.6.2 (R Core Team, 2018).

### 3. Results

#### Life-History

The MANOVA showed statistically significant differences in reproductive life-history traits between core and edge, populations, and eclosion dates (range: Pillai-Bartlett statistic=0.093,  $p < 0.001$ ; population: Pillai-Bartlett statistic=0.133,  $p = 0.046$ ; eclosion date: Pillai-Bartlett statistic=0.359,  $p < 0.001$ ). Across all three traits, reproduction increased about 7% at the edge compared to core.

In the univariate analysis, mass of females at adult emergence ranged from 6.5 to 14.7 mg. Females from the edge of the range were larger than females from the core on average (core mass=9.65 mg SE=0.163; edge mass=10.30 mg SE=0.160;  $F = 8.04$ ,  $p = 0.030$ ; **Fig. 3A**).

The number of eggs from the first day of reproduction ranged from 0 to 30. The proportion of beetles laying eggs during the study did not differ between the core and edge (core proportion=0.813, edge proportion=0.845,  $c^2 = 0.46$ ,  $p = 0.499$ ). Of those that oviposited during the study, edge beetles tended to be more fecund (core eggs=10.9, SE=0.40; edge eggs=12.0, SE=0.40;  $c^2 = 3.39$ ,  $p = 0.067$ ; **Fig. 3B**). Age at first reproduction was not a predictor of the number of eggs laid ( $c^2 = 0.01$ ,  $p = 0.916$ ), but larger females laid more eggs ( $c^2 = 5.79$ ,  $p = 0.016$ ).

Age at first reproduction ranged from three to seven days after adult emergence. From the regression analysis, edge beetles tended to reproduce earlier than core beetles (core age=5.51 days, SE=0.11; edge age=5.24

days,  $SE=0.10$ ;  $c^2=3.64$ ,  $p=0.058$ ; **Fig. 3C**). Mass at emergence was not a predictor of age at first reproduction ( $c^2=1.92$ ,  $p=0.166$ ). Results were similar in the Kaplan-Meier survival analysis. Median age at first reproduction was 5 days (95% CI: 5, 6) for edge and 6 days (95% CI: 6, 6) for core (Fig. 3D). The log-rank test for differences in survival curves indicated marginal differences between core and edge ( $c^2=3.8$ ,  $p=0.051$ ).

The mass of males at the time of the dispersal trial (thus, after feeding *ad libitum*) ranged from 6.9 to 19.3 mg. There was no difference in mass of males between core and edge populations ( $F=0.67$ ,  $p=0.445$ ). Older beetles weighed more than younger beetles ( $F=46.55$ ,  $p<0.001$ ) and males reared at high density weighed more than those reared at low density (high mass=12.2 mg,  $SE=0.134$ ; low mass=11.8 mg,  $SE=0.135$ ;  $F=15.09$ ,  $p<0.001$ ).

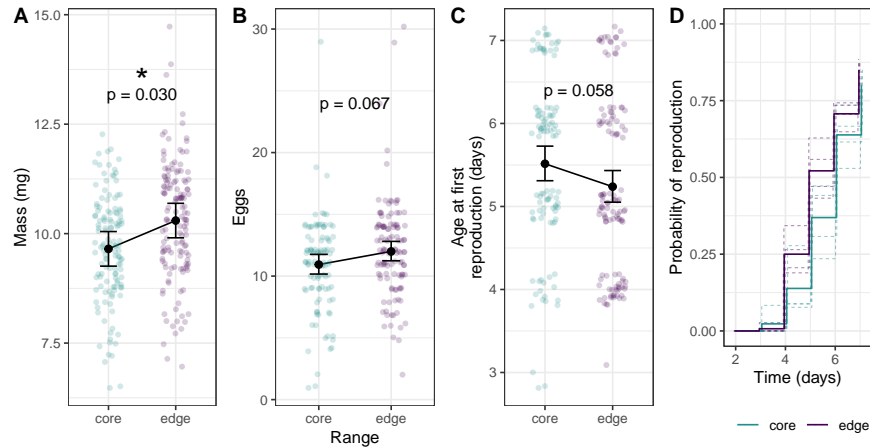


Figure 3: Means and 95% confidence intervals of the life-history traits of female body mass (**A**), 24-hr fecundity (**B**), and age at first reproduction, analyzed with regression (**C**) and Kaplan-Meier survival analysis (**D**). Observations from laying individuals only are shown in **B-C** and are jittered to show individual points. In **D**, solid lines represent means of core and edge only and dashed lines are each population.

## Dispersal

All four dispersal elements were positively correlated with each other (Spearman rank-order correlation, all pairwise  $p$ -values  $< 0.05$ ). In the statistical models, the three-way interaction between range, density, and mate status was not statistically significant in any model, so it was removed from all models. Results for covariates and random effects are in Table S2.

During the dispersal trials, 84.2% of all beetles took at least one flight. For occurrence of flight, the interaction between mating status and range was statistically significant ( $c^2=4.14$ ,  $p$ -value=0.042), indicating unmated edge beetles were more likely to fly than unmated core beetles (core probability=0.84, edge probability=0.93;  $z=-2.309$ ,  $p=0.021$ ), but there was no difference for mated beetles (core probability=0.86, edge probability=0.84;  $z=0.356$ ,  $p=0.722$ ; **Fig. 4A**). The interaction between density and mate status was close to statistical significance ( $c^2=3.01$ ,  $p=0.083$ ), such that unmated beetles tended to fly more than mated beetles at low density, but there was no difference between mated and unmated at high density (Fig. S2A).

The number of flights during the 1-hr trial ranged from 0 to 13 (median=2). The interaction between density and range was statistically significant ( $c^2=4.93$ ,  $p=0.026$ ), indicating at low density, edge beetles took more flights than core beetles (core flights=1.68,  $SE=0.15$ ; edge flights=2.13,  $SE=0.17$ ;  $t=-2.064$ ,  $p=0.040$ ), but there was no difference at high density (core flights=2.03,  $SE=0.16$ ; edge flights=1.93,  $SE=0.15$ ;  $t=0.490$ ,  $p=0.625$ ; **Fig. 4B**). The interaction between density and mate status was close to statistical significance,

demonstrating that unmated beetles tended to take more flights than mated beetles at low density and the opposite at high density ( $c^2=3.48$ ,  $p=0.062$ ) (Fig. S2B).

Individuals flew up to 2.3 km (median=8 m), during the 1-hr trial. The interaction between density and mate status was statistically significant in the final model, such that unmated beetles flew further than mated beetles at low density, but the opposite at high density ( $c^2=6.13$ ,  $p=0.013$ ; **Fig. 4C**). The range main effect was also close to statistical significance, indicating edge beetles tended to fly further than core beetles (core distance=59.6 m, SE=10.01; edge distance=69.5, SE=11.45;  $c^2=2.998$ ,  $p=0.083$ ).

Average flight speed ranged from 0.138 m/s to 0.914 m/s, and did not differ by range, density, mate status or their interactions (Fig. S2C).

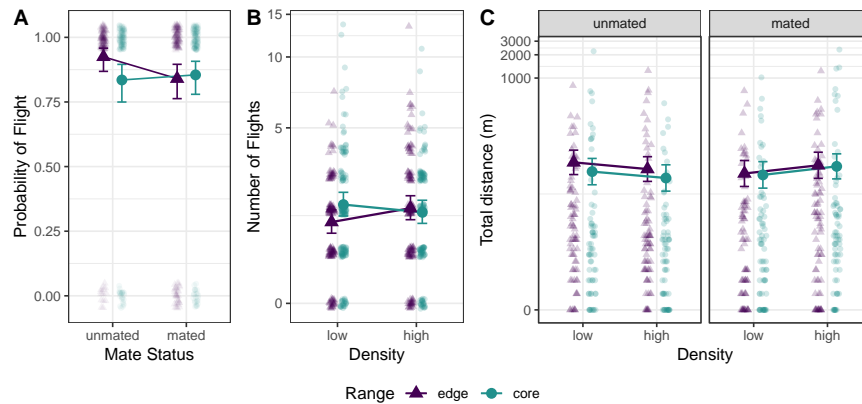


Figure 4: Means and 95% confidence intervals of dispersal elements. Mating status-dependent dispersal evolved from core to edge for probability of flight (**A**), and density-dependent dispersal evolved from core to edge for number of flights (**B**). Flight distance is informed by mating status and density (**C**). Observations have been jittered to show individual points. Note log-scale y-axis in **B** and **C**.

## 4. Discussion

Theory predicts that both life-history and dispersal traits will evolve during range expansion (Peischl et al., 2015; Peischl & Excoffier, 2015; e.g. Phillips et al., 2010b; Shine et al., 2011), with different evolutionary processes driving distinct patterns of evolution. It is unclear how well theoretical predictions hold up in complex natural systems including biocontrol agents, and which evolutionary processes appear to drive trait changes across range expansions (Szűcs et al., 2019). We studied the recent range expansion of the biocontrol agent *D. carinulata* in the western US and infer the dominant evolutionary processes acting during the range expansion by comparing populations at the core and edge of the range.

We found selection at low densities to be the dominant process over expansion load driving evolution of reproductive life-history traits at the edge of the range. Females from the edge laid on average one more egg than those from the core on the first day of reproduction. If this difference persists throughout the multi-week lifespan of adults, it could sum to a substantial difference in fitness between core and edge individuals. Although we were not able to measure lifespan or lifetime fecundity in this study, previous studies of *D. carinulata* indicate that early fecundity is a good predictor of lifetime fecundity (Bitume et al., 2017). We used mass as an additional gauge of fecundity, since insect body size is often related to egg production and how many eggs females can carry (Berger et al., 2012). We found this association between mass and fecundity to hold in *D. carinulata* and that individuals from the edge were larger than those from the core.



Age at first reproduction is an often-overlooked trait that can be just as important for fitness as fecundity itself, since reproducing earlier can increase the total time available for an individual to reproduce and early offspring often have an advantage over later offspring because there are fewer other offspring to compete with (Stearns, 1976). Developing faster and reproducing earlier can also allow more generations per year, which might allow acceleration of the range expansion from edge populations of *D. carinulata*, which are also less constrained by cold temperatures in the winter (Jamison et al., 2018). Early fecundity, mass of females, and age at first reproduction all indicate that selection has increased reproductive capacity at the edge of the range expansion. While the effect sizes are small for each individual trait, when viewed together, this provides strong evidence for a shift in reproductive life-history traits over about 15 years.

We did not find evidence of increased genetic load in edge populations relative to core populations. Genetic diversity has been retained along one *D. carinulata* expansion front (Stahlke et al., 2021), which may have contributed to rapid evolution of diapause induction timing (D. W. Bean et al., 2012). *D. carinulata* tends to aggregate (D. W. Bean, Wang, et al., 2007; Cossé et al., 2005), which may allow it to maintain high enough population sizes on the range edge to reduce the consequences of serial founder events and gene surfing inherent in range expansion. Populations of *Diorhabda* might also maintain high genetic variation since they were collected from multiple source populations and population sizes were deliberately large to avoid reducing variation that could increase establishment in the field (Stahlke et al., 2021; Szűcs et al., 2017).

Dispersal is an inherently and notoriously variable trait (Bowler & Benton, 2005) and we found this to be true for *D. carinulata*, even when measuring dispersal in a controlled lab environment. Accounting for the density and mating context of dispersal decisions in our experiments allowed us to observe evolution between core and edge more clearly and form hypotheses about the mechanisms behind the patterns we see. The occurrence of flight was affected by mating status along the range expansion such that unmated beetles from the edge flew more than those from the core. This implies that the response to mating has evolved between core and edge. This could be due to low mate availability in edge environments, so males on the edge are more likely to need to disperse before finding a mate. For the number of flights, dispersal became negatively density-dependent at the edge, such that the number of flights increased in low density environments compared to core, while staying about the same in high density environments. This implies that the response to density has evolved during range expansion. This could be due to selection for increased dispersal at range edges at low density, as predicted by theory (De Bona et al., 2019; Fronhofer, Nitsche, et al., 2017; Travis et al., 2009).

Edge beetles flew further than core beetles across all density and mating treatments, and density and mating status interacted as predicted by condition-dependent dispersal theory. Unlike with occurrence of flight and number of flights, the relationship of distance with mating status and density did not change over the range, but we do find a weak signature of spatial sorting of dispersal ability. In this species, spatial sorting might primarily act on occurrence or frequency of flights rather than flight distance or speed if most dispersal flights driving the range expansion are comprised of multiple frequent flights to catch air currents, instead of long-distance flights. Future studies will be needed to explore the nature of dispersal in this species and how spatial sorting acts on different dispersal elements in natural systems.

The effect of spatial sorting in the range expansion of *D. carinulata* system could be small because of maladaptation to novel environments on the edge of the range expansion that slow down range expansion and reduce assortative mating between dispersive individuals at the edge (Andrade-Restrepo et al., 2019; Hillaert et al., 2015). Early in its range expansion, *D. carinulata* was maladapted to photoperiod cues (D. W. Bean et al., 2012; D. W. Bean, Dudley, et al., 2007) and possibly higher summer temperatures in southern latitudes (Herrera et al., 2005). Adaptation to photoperiod has limited the rate of southern range expansion in this beetle and thus may reduce the effect of spatial sorting of dispersal. Despite this, our results suggest that spatial processes during range expansion may be important to natural range expansions even over heterogeneous environments.

In many species, dispersal evolves along with suites of traits, called dispersal syndromes (Ronce & Clobert,

2012), and in some cases, many life-history traits may correlate well with dispersal (Stevens et al., 2013). Trade-offs between dispersal and reproductive ability are widely hypothesized to be present due to allocation of finite resources (Bonte & Doherty, 2017; Stearns, 1989) though support for such trade-offs during range expansion is mixed (e.g. Hughes et al., 2003; Jan et al., 2019; Kelehear & Shine, 2020; Tabassum & Leishman, 2018; Therry et al., 2015). In the *D. carinulata* range expansions, we do not see evidence of a trade-off between dispersal and life-history traits, though we were unable to measure all traits within the same individuals. We measured dispersal in male *D. carinulata*, but there are many reasons for dispersal to differ between the sexes (reviewed in Li & Kokko, 2019). There may also be trade-offs between other traits, such as lifespan or immune system development or function (reviewed in Chuang & Peterson, 2016).

Long-term success of the *Tamarix-Diorhabda* biocontrol program requires *D. carinulata* to continue its spread to cover the range of the target weed and to adapt to new environments. Our results contribute further evidence of sufficient genetic variation for adaptive evolution to occur. We show an increase in both reproductive output and dispersal ability at the edge and low genetic load, which may enable an accelerating expansion front and will likely contribute to the establishment and persistence of *D. carinulata* populations at the edge (Phillips et al., 2010a). Evolution of these traits and others previously studied (e.g. D. W. Bean et al., 2012; Stahlke et al., 2021) suggests that there is sufficient genetic variation for populations to continue to adapt to novel environments during the expansion. As the first test of evolutionary theory of range expansions in a modern biocontrol agent, we show that these theoretical predictions can be applied to range expansions across heterogeneous environments, especially when the ecological context of individuals is included. We may expect to find selection at low densities to be the dominant evolutionary process over expansion load and for spatial sorting to act on other biocontrol agents that share many characteristics with *D. carinulata* (e.g. Bartelt et al., 2008; Muller-Scharer et al., 2014). Our results suggest that evolutionary processes impacting range expansions of natural populations can act simultaneously with adaptation to environmental gradients.

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