Evolution, 2026, **0(0)**, 1–12
https://doi.org/10.1093/evolut/qpag015
Advance access publication 30 January 2026
Original Article

Adaptation at the edge: patterns of local adaptation and genetic variation during a contemporary range expansion

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Abstract

During range expansion, differences can evolve between populations at the core and expanding edge of a range. Theory and experiments often focus on range expansions across uniform environments, but in nature, many range expansions occur over environmental gradients that present novel selection pressures. We study phenotypic evolution at the core and edge of a range expansion across a gradient, and the expression of genetic variation of core populations in novel environments. We focus on the timing of winter dormancy in a beetle (Diorhabda carinulata), expanding from northern areas with cold winters to southern areas with milder winters. Phenotypes of core populations are consistent with adaptation to northern environments and maladaptation to southern ones. However, phenotypes of edge populations vary, indicating potential adaptation to more variable conditions across the southern sites. Clear shifts in phenotype at the edge relative to the core suggest rapid evolution in response to southern climates. Heritability in a core population was high in a local environment but undetectable in a novel (edge) environment. These results show that core populations have adapted to their local environments, and that long-distance movement into novel environments may reduce heritable genetic variation on which selection can act, and thus hinder adaptation.

Keywords: heritability, evolvability, diapause, phenology, biological control, photoperiodism

Introduction

Understanding the factors that allow expansions of species' distributions is a major theme of ecology and evolutionary biology (Holt, 2003). Theory and model systems show that when an organism is introduced into a new location, and its range starts to expand from there, differences evolve between populations at the introduction origin, or core of a range, and those at the expanding front, or edge (Miller et al., 2020). These differences can arise due to processes internal to the populations, such as spatial sorting of better dispersers at the expanding edge (Shine et al., 2011; Travis & Dytham, 2002) and "surfing" of deleterious alleles leading to reduced fitness at the edge (expansion load; Peischl et al., 2015). Additionally, populations expanding their ranges are subject to external selection pressures, and when an expansion spans environmental or latitudinal gradients, core, and edge populations experience different environments, in which different traits or trait values may be advantageous (Colautti & Barrett, 2013). In this case, populations at the edge may need to adapt to the novel environment at the edge for range expansion to continue.

There is a strong body of research demonstrating adaptation to novel environments well after range expansion has occurred (e.g., Batz et al., 2020; Carbonell et al., 2021; Ittonen et al., 2022; Lancaster et al., 2015; Medley et al., 2019; Oduor et al., 2016; Urbanski et al., 2012). Such adaptation is thought to be crucial to successful range expansion (Colautti & Barrett, 2013), but empirical data on adaptation to environments at the front of active range expansions is scarce. Newly established expanding edge populations may exhibit phenotypes consistent with local adaptation to the new environment, populations may be incompletely adapted, or populations may be maladapted. Indeed, maladaptation to the local environments in the expanded range is not uncommon (Brady et al., 2019a, b; Ebeling et al., 2011; Ross et al., 2009; Zhao et al., 2013).

The key to adaptation is, of course, genetic variation. If there is ongoing migration from the core to the edge, maladaptive variation may overwhelm selection at the edge and

Received March 25, 2025; revisions received January 21, 2026; accepted January 23, 2026
Associate Editor: Yvonne Willi; Handling Editor: Jason Wolf

thereby prevent optimal adaptation to the local environment (Lenormand, 2002). However, the alternative of insufficient genetic variation can also constrain adaptation and range expansion. Populations at the edge may have reduced genetic variation due to repeated founder events during spread (e.g., Watts et al., 2010), which could also lead to maladaptation when expanding across an environmental gradient. The expression of genetic variation is particularly dependent on the environment for threshold traits, which show discrete character states underlain by quantitative trait variation, since small changes in the environment can cause large changes in phenotypes. Thus, insights into potential constraints on range expansion can be gained by focusing on trait variation at the core of the range, and how the expression of such variation is influenced by different environments encountered across latitudinal gradients.

In temperate climates, latitudinal gradients include a shifting range of winter conditions that organisms often persist through in a dormant state. The timing of dormancy is often under strong stabilizing selection because entering dormancy either earlier or later than optimal will decrease reproductive output and survival probability (Bean et al., 2007; Enriquez & Visser, 2023; Koštál, 2006). Latitudinal clines in the timing of dormancy are found in many taxa (Bradshaw & Holzapfel, 2001, 2007; Ittonen et al., 2022; Urbanski et al., 2012) and provide strong evidence of adaptation to distinct climates by latitude in animals (Hut et al., 2013; Tyukmaeva et al., 2011) and plants (Yang et al., 2021). Thus, during a range expansion across latitude in a seasonal environment, a main constraint will be whether populations can adapt to the seasonality of the new location (Bradshaw & Holzapfel, 2007; Chuine, 2010; Grevstad & Coop, 2015; Grevstad et al., 2022; Iler et al., 2021; Joschinski & Bonte, 2021; van Asch et al., 2007).

Here, we study an active range expansion across an environmental gradient in seasonality to understand the evolutionary shifts in phenology of populations at the expansion front relative to the range core. The northern tamarisk beetle (*Diorhabada carinulata*) was introduced to the United States for biological control of a widespread invasive riparian plant. The tamarisk beetle overwinters in a dormant state called diapause, which is triggered in the late summer when daylengths become shorter than a threshold daylength. Interestingly, the beetle was released across a wide latitudinal gradient but did not establish south of 38°N. Beetles introduced in the south likely entered diapause too early in the season and so burned through fat reserves early and could not successfully overwinter (Bean et al., 2007; Enriquez & Visser, 2023). After establishment in more northern areas, however, beetle populations successfully expanded southwards (Bean et al., 2012).

Here, we specifically ask (1) how populations from the recently colonized edge and from the core of the introduced range respond to daylength cues, (2) whether these responses are consistent with local adaptation, and (3) if exposure to novel environments shifts the expression of quantitative genetic variation, and thus may have influenced initial patterns of establishment of the beetle. We performed a reciprocal environment experiment with populations from across the range to assess local adaptation of diapause timing traits. To assess quantitative genetic variation, we measured heritability of the diapause traits in two environments. We expect that populations from core and edge will be adapted to the cues of their home environment and that novel environments may decrease the heritability of diapause traits, which could constrain adaptation during range expansion.

Materials and methods

Study system

The northern tamarisk beetle (*D. carinulata*: Coleoptera, Chrysomelidae, hereafter the tamarisk beetle or simply the beetle) is a specialist on the invasive woody shrub tamarisk (*Tamarix* spp.). Starting in 2001, tamarisk beetles originally from Fukang, China, and Chilik, Kazakhstan, were released as a biological control agent into the United States to help manage the shrub (Bean et al., 2007; Stahlke et al., 2022). The range expansion of the tamarisk beetle southward in the United States follows the target host, which grows along rivers, creating naturally separated expansion fronts that provide meaningful population replicates. Molecular genetic diversity has largely been maintained during the southward range expansion (Stahlke et al., 2022). Edge populations have evolved increased dispersal and fecundity relative to core populations, indicating both spatial sorting and selection at the edge (Clark et al., 2022).

Diapause in the tamarisk beetle is initiated in late summer or fall by a photoperiod cue, which is slightly influenced by temperature (Bean et al., 2007; Dalin et al., 2010). All life stages, from larva to adult, are sensitive to photoperiod and diapausing adult females resorb their reproductive organs and no longer lay eggs (Bean et al., 2007; Koštál, 2006). Mechanistically, individuals store information about photoperiod across several days and initiate diapause when a threshold has been reached (Takeda & Suzuki, 2022). Previous experiments on the tamarisk beetle have shown that adult females ceased oviposition 5–20 days after being placed in diapause-inducing daylengths, with fewer days required in shorter daylengths (Bean et al., 2007; Bean et al., 2007).

Insect collections and rearing

We collected at least 200 adult tamarisk beetles by hand from *Tamarix* spp. at each of eight sites, four in the northern (core) and four in the southern (edge) parts of the range in the United States (Table 1, Figure 1) in Fall 2017 and Spring 2018 (details of collections are in Clark et al., 2022). We chose original release sites from the biocontrol program as the northern core sites (Carruthers et al., 2008), and the southern expansion front for the southern edge sites. The populations at the southern edge had arrived within the previous year, except for population G (La Joya, New Mexico), which likely arrived 4 years prior to our collection, based on survey data (https://riversedgewest.org/documents/previous-annual-tamarisk-beetle-maps). We collected at the more established site G to avoid collecting a cryptic sibling species that was expanding northward within the same river system. To standardize the effects of maternal environment, beetles were maintained in bulk in growth chambers under reproductive conditions of 16/8 hr light/dark per day and 25/20 °C day/night and fed fresh tamarisk as needed for one generation.

Table 1. Location and climate of tamarisk beetle collection sites.

		Site	Lat.	Long.	Elevation (m)	Ave. annual cumulative degree (days)	Ave. first frost date	Day-length at first frost (hr)
North/core	A[1]	Lovell, Wyoming	44.856	−108.207	1115.35	1438	Oct. 2	11.73
	B	Humboldt, Nevada	40.063	−118.590	1189.62	1841	Sep. 30	11.87
	C[2]	Delta, Utah	39.144	−112.958	1386.43	1767	Oct. 8	11.54
	D[3]	Pueblo, Colorado	38.268	−104.721	1448.19	1990	Oct. 15	11.27
South/edge	E	Little Colorado River, Arizona	34.593	−109.611	1669.56	2043	Oct. 13	11.45
	F	Wickenburg, Arizona	34.422	−112.701	1204.74	3516	Nov. 18	10.32
	G	La Joya, New Mexico	34.342	−106.864	1433	2547	Oct. 29	10.91
	H[4]	Blythe, California	33.912	−114.533	96.9	4524	Dec. 12	9.94

Note. Elevation data are from USGS TNM Elevation Tool. Degree days were calculated by the phenology model for the tamarisk beetle at USPest.org with temperature thresholds of 11.1 and 36.7 °C, averaged for four to 10 years before collections (2008–2017), depending on availability of weather station data. First frost day was calculated as the first day after the summer with a daily low temperature at or below 0 °C and averaged for the same 10-year period. Daylength at first frost shows how the appropriate photoperiod cue for diapause will change based on latitude and winter onset. All temperature data were retrieved from the National Oceanic and Atmospheric Administration for the closest available station to the collection location. Sites indicated with superscripts were also sampled in Stahlke et al. (2022) with site codes from that paper as follows: [1] 1WY; [2] 34UT; [3] 2CO; [4] Near 12AZ.

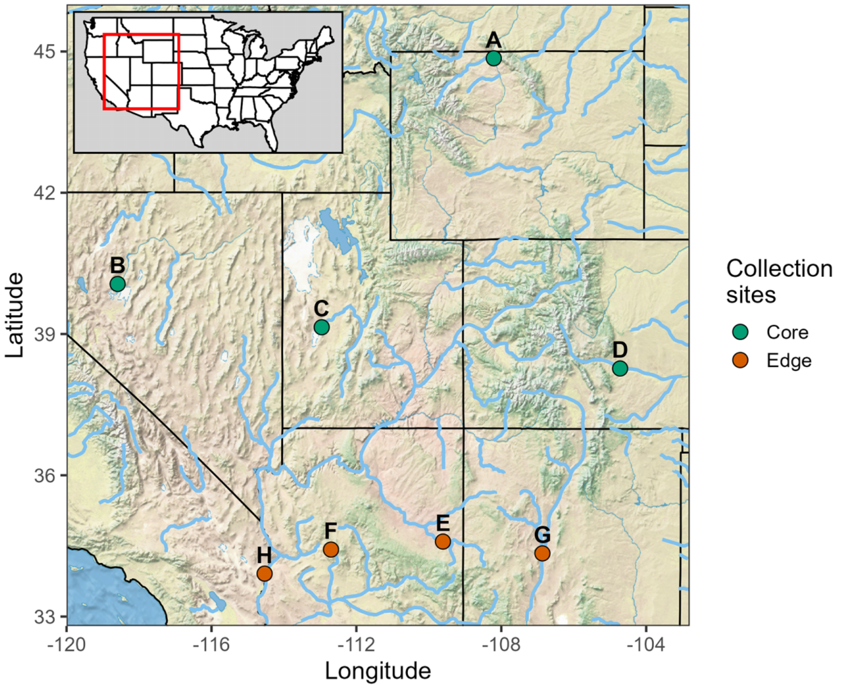

Figure 1. Collection sites for the tamarisk beetle in the western United States. Letters refer to Table 1. Core sites are original release sites of the tamarisk beetle. Edge sites were at the expanding range edge when collected. All sites were used to examine the pattern of local adaptation of diapause timing. Genetic variation of diapause timing was only measured for site C.

Reciprocal environment experiment

To quantify differences between populations in diapause responses (Question 1), we subjected adult female tamarisk beetles from all collection locations to two photoperiods simulated in growth chambers in the lab and tracked initiation of diapause. After eclosion as adults, randomly chosen adult females from the second lab generation were reared individually in 0.24 L plastic containers with mesh lids, at reproductive photoperiods (16 hr of light per day) and mated with at least one male from the same collection location. Thirteen to sixteen days post-adult emergence, females were switched to one of two treatments that represented diapause-inducing photoperiods that occur before winter conditions in the north (14:20 hr: min of light per day) or south (12:40 hr: min of light per day).

The daylength treatments were based on preliminary tests of critical daylength (daylength at which 50% of a population enters diapause) performed in 2017 (1 year prior to our collections, unpublished data, author). The 14:20 hr: min of light treatment is close to the critical daylength for the population in Delta, Utah (core site C) and occurs on July 27 at that site. The 12:40 hr: min of light treatment is close to the critical daylength of Topock Marsh, Arizona (near edge site H) and occurs on September 6 at that site. Containers of beetles were rotated between four total programmable growth chambers during the light period each day, keeping the daylength treatment experienced by each individual constant, to equalize growth chamber effects within treatments. Temperatures were warmer in the light period and cooler during the dark period to more closely mimic natural conditions, as in the standard rearing procedure above. The average temperature was 22.99 °C in the longer-daylength treatment and 22.64 °C in the shorter-daylength treatment.

Each day after the switch to diapause-inducing daylengths, we recorded whether each female laid any eggs in the previous 24 hr. When a female had not laid eggs in 7 consecutive days, that individual was scored as in diapause, starting from the first day with no eggs (Bean et al., 2007). Containers were inspected for eggs for 43 days, and females that were still laying eggs at that time were scored as reproductive (not in diapause). In our pilot experiments, there was no instance of a female that stopped oviposition for 7 consecutive days starting to lay eggs again, so we consider cessation of oviposition to be a reliable indicator that a female had started the process of entering diapause. We recorded two diapause responses for each female: diapause incidence (diapause initiated or not) and number of days to enter diapause after starting the assigned daylength treatment for those that entered diapause during the experiment. We measured an average of 33 and minimum of 10 females per population per treatment, for a total of 521 individuals, 71 of which died before the end of the experiment, precluding the measurement of diapause incidence and timing.

Reciprocal environment statistical analyses

We determined whether diapause responses have evolved from the core to the edge of the range expansion (Question 1) by analyzing differences between collection locations in both diapause incidence and days to diapause. For diapause incidence, we fit a Bayesian logistic regression with logit link function in which the proportion of beetles in diapause was predicted by beetle origin (core or edge), daylength treatment (northern or southern diapause-inducing daylengths), and their interaction as fixed effects and collection location (factor with eight levels) as a random effect. We used a Bayesian model for this analysis because, unlike similar frequentist models, it can estimate parameters in cases of complete separation (which happens when a predictor variable or combination of predictor variables perfectly predicts an outcome, which we see in our data as 100% of core individuals entered diapause in the short daylength treatment) (Gelman et al., 2008). We selected uninformative priors and obtained 3,000 post-warmup draws. To further examine how the proportion of beetles in diapause varied by collection site, we estimated the proportion of beetles in diapause from each collection site from the random effect in the same model.

We analyzed days to diapause responses with three main models: two negative binomial models (to account for overdispersion in the count data) and one survival regression model. We fit negative binomial models on, first, the complete dataset (including diapausing and non-diapausing individuals), and second, the subset of individuals that entered diapause. For the complete dataset, non-diapausing beetles were given a value of 43 days until diapause since this was the last day on which we collected data. Non-diapausing individuals represent biologically important variation within the data and assigning 43 days to these individuals is a conservative way to include them in the dataset, since these individuals will likely never enter diapause at the treatment daylengths. While including all samples slightly inflates estimates of mean days until diapause, it gives a more complete picture of differences in diapause responses across collection locations. Excluding non-diapausing samples more accurately estimates days until diapause for those that did enter diapause. In both negative binomial models, days until diapause were predicted by beetle origin (core or edge), daylength treatment, and their interaction as fixed effects with a log link function. Collection location was included as a random effect. The linear parameterization of the negative binomial (where variance increases linearly with the mean: $V = \mu(1+\varphi)$, where μ is the mean and φ is the dispersion parameter) was used in the model with all samples, and the quadratic parameterization (where variance increases quadratically with the mean: $V = \mu(1+\mu/\varphi)$) was used for the diapausing individuals subset, which minimized overdispersion for each model. To produce population-level estimates of days until diapause, we replaced beetle origin (north/core or south/edge) with collection location as a fixed effect in each negative binomial model.

Third, we analyzed days until diapause with a survival regression model. While this model has the benefit of accounting for censoring in the data (since not all individuals entered diapause and some individuals died before the end of the experiment), it assumes that non-diapausing individuals would eventually enter diapause, which is likely not a good assumption. We fit this model on data from all collection locations, and separately by collection location. Methods for this analysis are presented in the Supplemental Materials.

The logistic model was fit with the *brms* package (Bürkner, 2017), negative binomial models with the glmmTMB R package (Brooks et al., 2017), and survival models in the *survival* R package (Therneau, 2020). We used the DHARMa package (Hartig, 2024) to assess overdispersion and model fit with Q–Q and residual vs. fitted plots. Statistical significance of effects was determined with Wald chi-square tests in the *car* package (Fox & Weisberg, 2019) or by comparing the 95% credible interval to 0 in the case of the Bayesian model. Post-hoc tests of differences between marginal means were done using the *emmeans* package (Lenth, 2025).

Testing for local adaptation

After determining the diapause responses of each population to the daylength treatments, we assessed whether those responses are consistent with local adaptation (Question 2) based on the relationship between the treatment daylengths and critical daylength, and by examining whether diapause responses are associated with environmental gradients. Because our methods for measuring diapause timing did not include explicit fitness metrics, we use these two complementary analyses to evaluate whether the populations are likely locally adapted.

For a well-established population, the critical daylength is often considered to be the optimal diapause timing in that environment due to strong stabilizing selection on diapause timing (Chuine, 2010; Van Asch & Visser, 2007), so that diapause is neither too early in the season (reducing time for reproduction and increasing mortality during a longer diapause period) nor too late in the season (exposing individuals to lethal cold and starvation) (Bean et al., 2007; Enriquez & Visser, 2023; Koštál, 2006). If critical daylength is close to a treatment daylength, this indicates that the population is likely adapted to that environment. Since the treatment daylengths were chosen to be close to the critical daylengths of a northern core and a southern edge population, a good fit to the environment is indicated by about 50% of a population entering diapause. We expect that populations that are reasonably adapted to environments similar to the treatment will vary above and below 50% rather than being exactly 50%. We expect this because core and edge environments were each represented by only one treatment in our experiment, while our replicate core and edge populations were from different latitudes and elevations (within the core and within the edge regions). While varying around 50% in diapause supports adaptation, all individuals or no individuals from a population entering diapause are maladaptive for that environment. All in diapause indicates the population would enter diapause too early, while none in diapause indicates the population would enter diapause too late. For each population, we evaluated the proportion of individuals from each population entering diapause in each treatment using the logistic regression from above and compared the confidence intervals around the proportion in diapause to 50% to determine whether the population was likely adapted to that treatment.

We also looked for gradients in diapause responses that correlated with environmental variables, which is a common method to look for evidence of adaptation (Hut et al., 2013). Our choice of sites aimed to capture differences between core and edge, with real constraints on what could be sampled for both those types of sites (core only from original release sites, and edge from the most recently established locations possible). Thus, the sampled sites were not directly designed to test for clines across environmental variables. Despite this, our sites varied across several environmental variables, allowing an initial exploration of the role of the environment on evolution of diapause responses. We characterized the environment of each collection location with latitude, elevation, total annual cumulative growing degree days (11.1 °C lower threshold, 36.7 °C upper threshold), and day of first frost (Table 1) because all of these variables influence the length of the growing season and the optimal diapause timing. Because these variables are highly correlated across these eight sites, we performed a principal component analysis and used the resulting first axis (PC1) as the environmental variable in further analyses. We fit a linear mixed model in which days to diapause was predicted by PC1, the treatment daylength, and their interaction. Random intercepts were included for collection location. We included non-diapausing individuals, as above, by assigning 43 days to diapause.

Quantitative genetic variation

To understand how genetic variation in diapause timing and its expression may have influenced initial patterns of establishment and range expansion (Question 3), we measured genetic variation in days until diapause in a population at the origin of the expansion.

We focused on one collection site (site C, Delta, Utah) at the origin of the range expansion (Carruthers et al., 2008), which we collected in 2019 using the same methods as for the eight populations used above. The Delta population is considered to be well adapted to its location because the critical daylength has been stable for many years. We expect diapause trait means and variances of this population will be similar to when it was introduced in 2001, since diapause timing has not been under strong selection and the population has remained large (unpublished data, author). This site is especially relevant to the southward range expansion because the specific ecotype released in Delta has been shown to be the dominant ecotype of the range expansion to the south (Stahlke et al., 2022).

Heritability (h^2) and evolvability (I^A) are metrics useful for understanding the genetic variation available for evolution of phenotypic traits (Hansen et al., 2011; Houle, 1992; Lynch & Walsh, 1998). Heritability scales additive genetic variation by total phenotypic variation of a trait, while evolvability scales additive genetic variation by the mean value of the trait. Evolvability has been suggested to be the better measure of evolutionary potential, while heritability has been used historically, so we provide both (Hansen et al., 2011; Houle, 1992). Because heritability and evolvability are functions of the environment in which they are measured (Lynch & Walsh, 1998), we used two daylength regimes that simulated diapause-inducing daylengths from the northern (home) and southern (away) parts of the range. The light period was 13:55 hr: min in the northern treatment and 13:26 hr: min in the southern treatment. The northern treatment was slightly shorter than the critical daylength of the Delta population, which would induce diapause in about 80% of individuals, based on previous measurements of critical daylength (Bean et al., 2007). The southern treatment was the daylength that would induce diapause in all or nearly all individuals, and represents the critical daylength of tamarisk beetles living near Lake Mohave, Nevada, about 480 km south of Delta. The temperature was 28/20 °C lights-on/lights-off for both treatments. Interactions between temperature and daylength in diapause initiation have been shown to be minimal for this population (Dalin et al., 2010).

We used a paternal half-sibling breeding design (Lynch & Walsh, 1998, p. 554) to estimate genetic variance components of days until diapause in two parallel experiments, one for each of the two daylength environments. Thirty-nine sires (males) of the second lab generation were each mated to seven or eight randomly chosen dams (females). Eggs were collected from each dam and reared in full-sibling families. When larvae were third instars, density was standardized to 15 larvae per full-sibling family per 0.24 L container to reduce environmental variation that might obscure additive genetic variation. After mating with non-siblings, two females from each full-sibling family were split to be used in the two experiments, one for each daylength environment. Adult females were reared individually for 43 days, and days until diapause were measured as above. We excluded from the analysis the offspring from sires that did not produce enough offspring for at least two adults per treatment, resulting in 35 successful half-sib families, with between 2 and 8 dams per sire producing offspring (average 5). Days until diapause were measured on 180–185 female adult offspring per daylength treatment.

Analysis of genetic variation

Non-diapausing individuals were assigned a value of 43 days until diapause, a conservative approach, as described above for the analysis of the reciprocal environment data. Variance components were estimated using restricted maximum likelihood separately for each of the two experiments (i.e., each daylength), with sire as a random effect (Lynch &

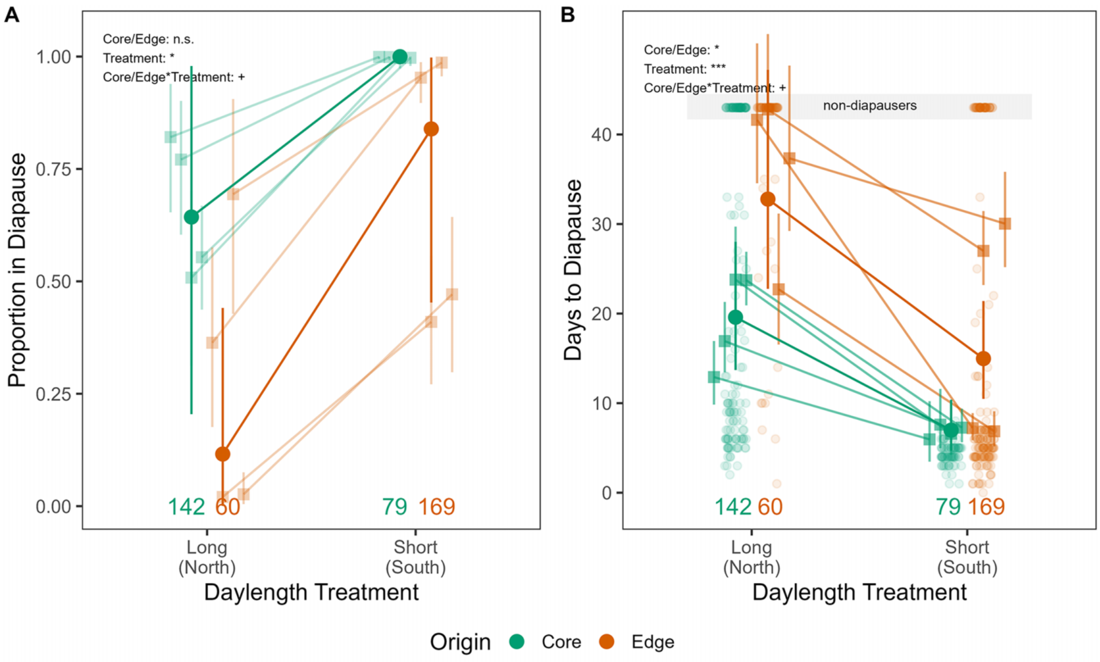

Figure 2. Model estimates of (A) proportion of individual *D. carinulata* in diapause and (B) days until diapause in northern and southern diapause-inducing daylength treatments. Circles indicate means of core/north and edge/south. Squares indicate means for individual core and edge populations. Statistical results presented are from core/edge model only. For (A), * indicates 95% CI does not overlap 0, and + indicates 90% CI does not overlap 0. For (B), *p*-values from Wald Chi-square tests are presented as follows: ***$p < .001$; **$p < .01$; *$p < .05$; + $p < .1$. Error bars are 95% credible intervals (A) or confidence intervals (B). In (B), points in the background indicate days until diapause for each individual measured and non-diapausing beetles are included at a value of 43 days to diapause.

Walsh, 1998). Variance due to dam and dominance variance are included in the error variance in this design (Lynch & Walsh, 1998, p. 554–555). Additive genetic variance is estimated as $V_A = 4 \times V_{sire}$ and total phenotypic variance as $V_P = V_{sire} + V_{resid}$ (Lynch & Walsh, 1998). Narrow-sense heritability (h^2) was calculated as $h^2 = V_A/V_P$. Evolvability (I_A), or the expected proportional change in a trait under a unit strength of selection, was calculated as $I_A = V_A/m^2$, where m is the trait mean (Hansen et al., 2011; Houle, 1992). Likelihood ratio tests were used to determine the significance of the sire variance component (V_{sire}). Standard error and confidence intervals around V_A, V_P, h^2, and I_A were calculated with a bootstrap method, following Houde and Pitcher (2016). In short, samples of sires were drawn from the observations with replacement up to the original sample size, and the variance components, heritability, and evolvability were calculated as above for each sample. A total of 1,000 random samples were drawn, and variance, standard error, and confidence intervals were calculated from the resulting distribution.

Analyses were performed in R version 4.5.1 (R Core Team, 2025). We describe our results using the language of "clarity" as proposed by Dushoff et al. (2019).

Results

Core and edge populations have diverged

The reciprocal environment experiment revealed differences between core and edge populations in diapause responses to the two daylength treatments, with edge populations requiring shorter daylengths to enter diapause, entering diapause less frequently, and taking longer to initiate diapause than core populations in the same daylength treatments. The two measurements of diapause responses, proportion in diapause and days until diapause, are strongly negatively correlated across all populations in both daylength treatments (−0.96 Pearson correlation coefficient) (Figure S1).

In the northern daylength environment (i.e., the critical daylength of one of the core populations), responses of beetles from the core and edge of the range diverged (Table S1), with 64% of individuals from the core entering diapause, compared to only 11% of individuals from the edge (post-hoc comparison of means odds ratio = 13.7, 95% highest posterior density (HPD) does not overlap 0) (Figure 2A). Similarly, core and edge populations diverged in the length of time to enter diapause in the northern daylength (Tables S2 and S3), with beetles from the core taking 10.7 days, and beetles from the edge taking 23.4 days ($Z = -3.24$, $p = .0012$) (Figure S2). When individuals that did not enter diapause were included in the averages, the pattern remains in the same direction (core = 19.6 days, edge = 32.8; $Z = -1.98$, $p = .0477$; Figure 2B). In the northern treatment, there is some variation between the collection locations in both the proportion and days to diapause in the northern daylength treatment (Figure 2, Figure S3).

In the southern daylength environment (near the critical daylength of an edge population), 99% of core beetles entered diapause, compared to only 84% of edge beetles (post-hoc comparison odds ratio = 863.1, 95% HPD does not overlap 0) (Figure 2A, Table S1). Additionally, core beetles entered diapause faster than edge beetles when non-diapausing beetles were included in averages (core = 7.0 days, edge = 15.0 days; $Z = -2.821$, $p = .0048$) (Figure 2B, Table S2). Considering only those that entered diapause,

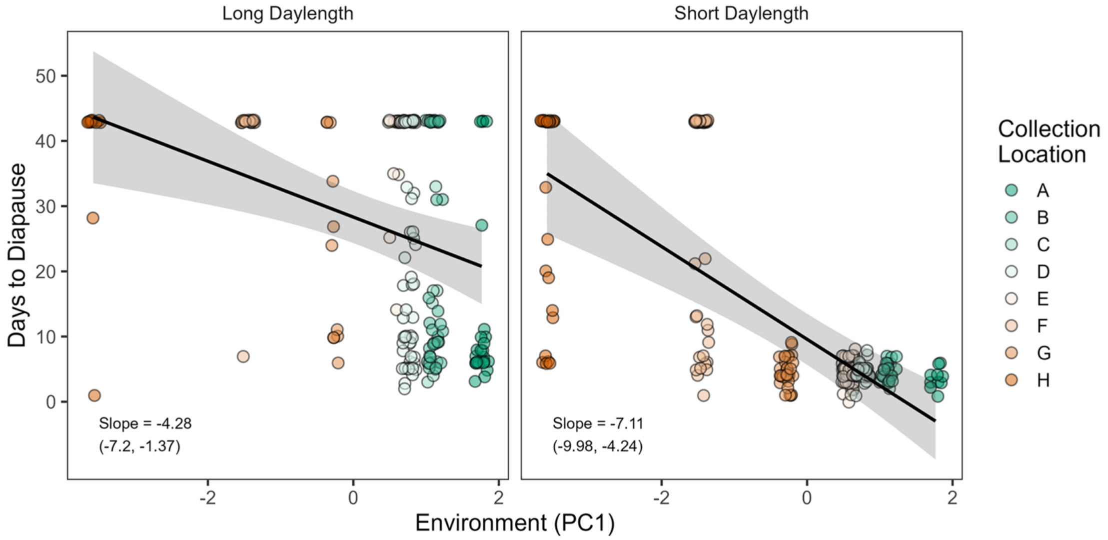

Figure 3. Associations between diapause responses and the environment of the collection sites. Points indicate the response of each individual in the experiment. The black line and shaded area indicate model predictions and 95% confidence interval, with slope and 95% confidence interval of the slope indicated at the bottom of each panel. Individuals that did not enter diapause were given a value of 43 days to diapause, as described in the methods. The environment is summarized with the first axis of a PCA with increasing scores corresponding to higher latitude, higher elevation, lower cumulative annual growing degree days, and earlier first frost day. PCA1 explained 77% of variation in these variables across these sites.

core beetles took 4.2 days to enter diapause, compared to 6.9 days for edge beetles ($Z = -2.342$, $p = .0192$) (Figure S2, Table S3). While there was very little variation in diapause responses between the core collection locations within the short-day treatment, the edge locations exhibited striking variation. Individuals from two edge locations had similar responses to the northern locations with nearly all individuals entering diapause, while very few individuals from the other two edge locations entered diapause (Figure 2, Figure S3). Results of the survival analysis showed similar patterns for both daylength treatments (Figure S4).

Populations are likely locally adapted

We use two lines of evidence to suggest that the differences we find between core and edge populations of *D. carinulata* are due to local adaptation to the environment across the range: (1) the relationship of responses to known population critical daylengths and (2) the correlation between responses and environmental gradients.

First, beetles from all four northern sites appear to be adapted to the northern environment, since they entered diapause in intermediate proportions, ranging from 51% to 82% for individual populations (Figure 2A, Figure S3A, Table S4). This is consistent with the treatment daylength being close to their critical daylength in the field, however with some variation between populations, which is expected, given different latitudes and elevations of collection sites within the core and edge regions. In particular, sites A and B appear to be adapted to enter diapause at a longer daylength (earlier in the year) than our treatment, given their high diapause proportions. Nearly complete diapause of core populations in the southern environment (99%, Figure 2A, Figure S3A, Table S4) indicates that northern populations are maladapted to the southern environment since individuals would diapause too early in the summer, reducing fitness. This is consistent with these beetles failing to establish at southern sites when they were first released for biological control (Bean et al., 2012).

Low diapause incidence of two edge populations in the northern treatment (~2%, Figure 2A, Figure S3A, Table S4) indicates that many individuals would be susceptible to winter freezes and are thus maladapted to the northern part of the range. However, two southern sites, sites E and G, appear to remain adapted to the northern daylength treatment, since 36%–70% entered diapause. In the southern daylength treatment, the four edge populations varied in their responses. Nearly all (95%–99%) individuals from sites E and G entered diapause in the southern environment treatment (like the northern beetles), while only 41%–47% of individuals from both sites F and H entered diapause (Figure 2A, Figure S3A, Table S4). This suggests differences in the biology of the populations, such that populations E and G are adapted to enter diapause at daylengths longer (earlier in the year) than the treatment, while sites F and H appear to be relatively adapted to the treatment daylength.

Second, we tested for clines in diapause traits with respect to site conditions to determine if the population divergence is likely due to local adaptation. The first PC axis of four environmental variables explained 77% of variation across the sites, with higher values on this axis corresponding to higher latitudes, higher elevation, lower annual degree days, and earlier first frost (Figure S5). We found a strong association between diapause timing and the environmental score (PC1) in both daylength treatments ($F_{6,43} = 23.23$, $p = .002$), with faster diapause initiation at sites with higher latitude, higher elevation, lower annual degree days, and earlier first frost (Figure 3). These clines suggest that variation in the environment, and specifically in the length of the growing season, is driving differences between the core and edge of the range, and that environmental variation within the core and edge is likely driving fine-scale adaptation of diapause timing across the range.

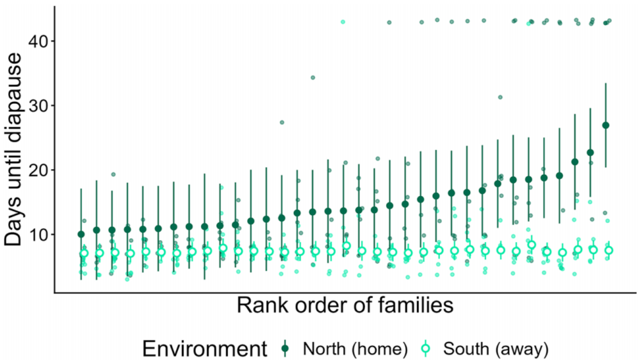

Figure 4. Variation in days until diapause among half-sibling families from site C in northern (home) and southern (away) daylength environments. Family estimates (95% CI) are ordered along the *x*-axis by increasing mean days until diapause in the home treatment. Background points show days until diapause for individuals in the northern and southern environments.

Through these analyses, we find that the pattern of diapause responses that we see across the range of the tamarisk beetle is likely the result of adaptation of diapause timing to local conditions, particularly the length of the growing season.

Genetic variance of days until diapause

We estimated variance components, heritability, and evolvability of days until diapause for individuals from northern core site C (Delta, Utah) in two daylength environments. Family means for days until diapause were more variable in the northern (home) environment, ranging from 10.5 to 27 days, than in the southern (away) environment, ranging from 6.9 to 8.4 days (where here we refer to home and away rather than north and south because only one core site was tested in the two environments; Figure 4). Genetic variance components strongly depended on the environment in which they were measured. Variance due to sire was highly statistically clear in the northern environment ($\mathrm{LRT}_1 = 10.95$, $p = .0009$), but not in the southern environment ($\mathrm{LRT}_1 = 0.41$, $p = .52$). Total phenotypic variance and additive genetic variance were reduced in the southern environment compared to the northern environment (Figure 5A, Table S5). Heritability of days until diapause was estimated at 0.74 (95% CI 0.13, 1.45) in the northern environment and 0.15 (95% CI 0, 0.58) in the southern environment (Figure 5B, Table S5). Evolvability of days until diapause was statistically clearly positive in the northern environment ($I_A = 0.50$ (0.08, 1.08)), but not clearly different from zero in the southern environment ($I_A = 0.04$ (0, 0.10), Figure 5C, Table S5).

Discussion

Local adaptation

We studied a range expansion of the tamarisk beetle across 10.9 degrees of latitude representing an environmental gradient from earlier to later onset of unfavorable winter conditions. In a striking example of rapid evolution, the newly established southern populations at the edge of the range expansion diverged in response to photoperiod from the northern core populations they originated from only 20–30 generations (10 years) prior. The differences between core and edge are genetically based, as revealed by the common garden design. Furthermore, we find that local populations respond to diapause-inducing light regimes in ways that would likely maintain higher mean fitness than non-local populations, and form clinal gradients associated with climate variables, suggesting local adaptation to environmental conditions across the range expansion.

Populations from the expanding edge were generally more variable in their diapause responses than those from the core of the range. While the four core sites have been established since 2001 (Carruthers et al., 2008), the four edge sites used in this study had arrived there within about a year of the time of collection. It may be that additional time would allow further adaptation to the seasonality of their locations. However, much of the variation among edge sites may be driven by differences in climate and seasonality of their local environments, such as timing and variability of winter onset, host plant senescence, and growing season length. Temperature in the fall may be one factor that is especially important in matching diapause timing with a local environment and weather in any particular year. In the tamarisk beetle, there is some evidence that diapause is delayed if temperatures are warm in the fall, especially in southern sites where winters are milder (Bean et al., 2007; Dalin et al., 2010). The role of temperature-sensitivity in diapause timing or the quality of the host plant as food has not been well explored in this system but doing so would further illuminate how adaptation and adaptive phenotypic plasticity facilitate establishment in novel environments (Dalin et al., 2010; Lankinen et al., 2013; Winterhalter & Mousseau, 2007). The outcome of selection in newly established range edges will depend on how long a population has been in an area, gene flow between populations, the strength of selection and heritable genetic variation in the new environment, and the role of adaptive plasticity at each location. Repeated sampling in these locations could provide additional insight into ongoing adaptation after colonization.

Quantitative genetic variation

We found substantial heritability and evolvability of days until diapause in core site C at a photoperiod near its critical photoperiod but not at a photoperiod representing a more southern environment. This shows that there is ample underlying genetic variation in diapause-related traits, in agreement with other studies of heritability of diapause (Erickson et al., 2020; Tanaka & Murata, 2017). Additionally, it shows that expression of this variation depends on the environment. In the southern environment, tamarisk beetles exhibited reduced variation overall, both additive and total phenotypic variation. Our results align with diapause being a threshold trait, which is a trait with discrete phenotypes (e.g., diapause and non-diapause) underlain by a continuous variable with a threshold (Roff, 1996; Tanaka & Murata, 2017). Because nearly all individuals reached the threshold for diapause induction in the southern environment, there was little variation in the trait and no heritability. This may help explain why early releases of the tamarisk beetle failed below 38°N but were able to establish there via dispersal more than a decade later. In the early releases, northern-adapted individuals mistimed diapause in southern locations by entering diapause too early (Bean et al., 2007), a response we still see in core populations subjected to the southern environ-

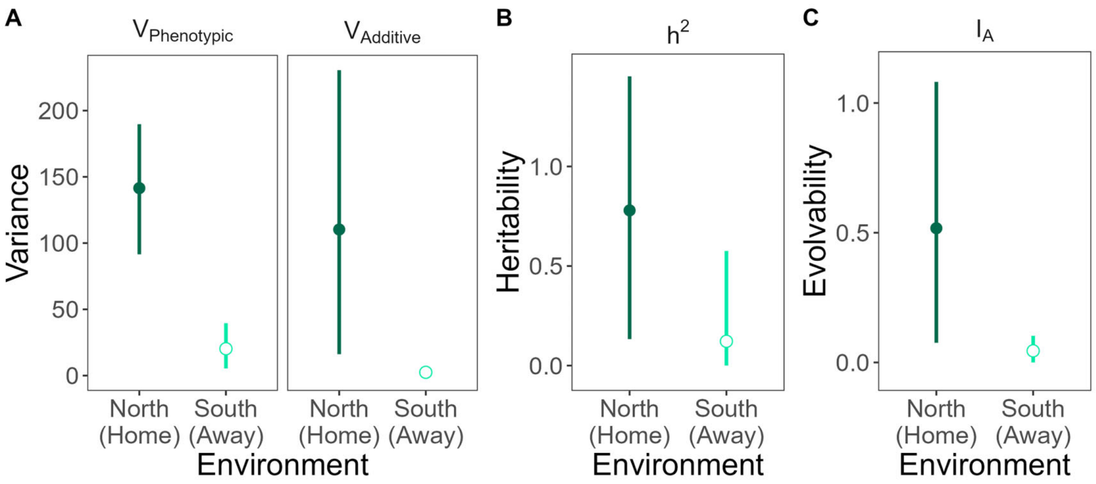

Figure 5. Estimates of components of genetic variation (bootstrap 95% CI) for days until diapause for females from core site C in two daylength environments, which are close to the critical daylength of the population (home), and shorter than the critical daylength (away). Some confidence intervals are not visible because they are smaller than the point. (A) Total phenotypic and additive genetic variation. (B) Heritability. (C) Evolvability.

ment in this study. However, the genetic variation that could have fueled adaptation of northern-adapted individuals and matched diapause initiation with the climate in the southern environment was not expressed in this environment. The high heritability and evolvability we observed when individuals were close to the home environment suggest that adaptation can be rapid, if the environmental gradient is gradual or movement across it is relatively slow so that heritability and evolvability can be maintained (Polechová & Barton, 2015). The tamarisk beetle's range expansion since about 2010 was enabled by evolution of diapause timing, with beetles initiating diapause at shorter daylengths at southern latitudes (Bean et al., 2012). That evolution was likely made possible by the maintenance of heritability of diapause timing during gradual movement southward, with few human translocations.

The trait days until diapause allowed us to measure individual variation in the developmental response to photoperiod. It might also provide information needed to determine the molecular basis of dormancy in insects. Despite the importance of photoperiodism in determining the response to changing environments (Bradshaw & Holzapfel, 2007; Emerson et al., 2009), the integration of photoperiod sensors, summation of photoperiod information, and hormonal signaling of diapause remain poorly understood (Saunders et al., 2004). Experimental work shows that the sum of information gained over several light cycles determines whether insects follow continuous development or switch to diapause (Saunders, 2002; Takeda & Suzuki, 2022). This may proceed like a molecular bucket filling with a molecule when days are short, with diapause initiated when the bucket fills up. Shorter days fill the bucket faster than longer days. Our findings suggest that photoperiod summation varies between individuals (e.g., variation in bucket size or rate of accumulation at different photoperiods), is heritable, and evolves. This information may provide additional insight into the molecular mechanism and evolution of the photoperiodic cue that is not evident from population-level critical daylength measurements. Future genomic studies may be able to use this trait to examine the genes that underlie individual variation in diapause timing.

Implications for range expansions

During the tamarisk beetle range expansion, dispersal ability has increased in edge populations compared to core populations, especially at low densities, and females from the edge are more fecund compared to those from the core (Clark et al., 2022), showing that spatial sorting, evolution of density-dependent dispersal, and selection on reproductive ability have occurred during this range expansion. Here, we show that adaptation to novel environments along a latitudinal gradient occurred alongside these spatial processes. Without evolution of diapause timing, the southward expansion likely could not have occurred, as indicated by failure of the initial introductions of the beetles to southern latitudes. Even with rapid evolution, modeling reveals that the need for diapause timing to evolve across the environmental gradient slowed the expansion southward relative to what it would have been had there been no latitudinal gradient (Benning et al., 2024), in alignment with findings of Hargreaves and Eckert (2014).

Our results suggest that introductions or human translocations of biological control agents or species of conservation concern to ecologically distinct sites done with good intentions may actually hinder adaptation and establishment if genetic variation is not expressed in those novel environments. Indeed, while more than 50% of biocontrol programs achieve some level of control (Hinz et al., 2020), many agents fail to establish after release (Heimpel & Mills, 2017; Schulz et al., 2019) and assisted migration of species facing human-caused climate change is also frequently unsuccessful (Butt et al., 2021; Schäfer et al., 2020). Many hypotheses to explain these failures focus on the role of ecological interactions between the agent and biotic or abiotic features of its environment, while others emphasize the role of depleted genetic variation and lack of adaptation (Forsman, 2014; Heimpel & Mills, 2017; Schäfer et al., 2020; Schulz et al., 2019). Our research reveals another alternative: underlying allelic variation may be adequate for selection to act on, but it may not be expressed as heritable trait variation in new environments after release. This may be especially evident in threshold traits, including some traits related to morphology, migration behavior, and life history (Roff, 1996). Here, we show that diapause timing is a highly heritable trait in local environments, but even a relatively small mismatch with the environment depleted the heritability of the trait. Studies of heritability and evolvability of ecologically important traits in the relevant environments prior to release may be beneficial in predicting both suitability for the environment and ability of an agent to adapt post-release.

The genetic paradox of invasions posits that introduced species will have low genetic variation because of small population sizes and repeated population bottlenecks (Dlugosch et al., 2015; Estoup et al., 2016). The paradox is, then, how do invasive species persist, expand their ranges, and ultimately thrive in introduced environments? Some have argued that for many invasions, the assumptions of the paradox are faulty—quantitative genetic diversity remains high after introduction, and that variation can be selected on to match the population with its introduced environment (Dlugosch & Parker, 2008; Estoup et al., 2016). For the tamarisk beetle in North America, we show that additive genetic variation for an ecologically important trait, diapause timing, remains high, and can evolve quickly. Biological control agents may particularly fall into this category, especially if multiple source populations are collected, and population sizes are maintained through quarantine and mass rearing (Szűcs et al., 2019).

As many species expand their ranges across environmental gradients, it is vital to understand the processes of local adaptation and maintenance of genetic variation in newly established habitats at the range edge. The appropriate timing of dormancy will be crucial for many species in temperate climates to persist in novel environments. For invasive species, biological control agents, and natural populations facing rapid environmental changes caused by climate change, understanding patterns of adaptation and expressed genetic variation will help to predict future movement and establishment in novel environments.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

Data and code supporting the results of this study are available at https://doi.org/10.5281/zenodo.18356646.

Author contributions

All authors contributed to conceiving and designing the study. E.I.C., A.R.S., and D.W.B. performed the field collections. E.I.C. performed the experiments and data analysis. E.I.C. wrote the initial draft of the manuscript. All authors contributed to editing and revision of the manuscript.

Funding

This research was supported by a USDA Agriculture and Food Research Initiative (AFRI) grant to R.A.H., E.V.B., D.W.B., and P.A.H. [grant number COLO-2016-09135], a USDA NIFA AFRI Predoctoral Fellowship to A.R.S. [grant number 2020-67034-31888], a USDA NIFA AFRI Predoctoral Fellowship to E.I.C. [grant number 2021-09368], and by the USDA NIFA [Hatch Project 1012868] to R.A.H.

Conflict of interest

The authors declare no conflicts of interest.

Acknowledgments

We gratefully acknowledge undergraduate research assistants Jenna Galvin, Tori Applehans, Itai Boneh, Sam Chaney, Maria Mango, and Katie Schneider..

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Received March 25, 2025; revisions received January 21, 2026; accepted January 23, 2026
Associate Editor: Yvonne Willi; Handling Editor: Jason Wolf