Received: 2 September 2023 | Accepted: 18 July 2024

DOI: 10.1111/eea.13507

Entomologia Experimentalis et Applicata

ORIGINAL ARTICLE

Impacts of assisted migration: An introduced herbivore has short-term and long-term effects on its native host plant population

Nitin Ravikanthachari[1,2] | **Libby L. Burch**[1] | **Rachel E. Powell**[1] | **Danielle M. Scott**[1] | **Charlotte R. Wayne**[1] | **Kristjan Niitepõld**[1] | **Risa H. Rosenberg**[1,3] | **Carol L. Boggs**[1,2,4]

[1]Rocky Mountain Biological Laboratory, Crested Butte, Colorado, USA

[2]Department of Biological Sciences, University of South Carolina, Columbia, South Carolina, USA

[3]Världsnaturfonden WWF/WWF Stockholm, Solna, Sweden

[4]School of Earth, Ocean & Environment, University of South Carolina, Columbia, South Carolina, USA

Correspondence
Carol L. Boggs, School of Earth, Ocean & Environment, University of South Carolina, Columbia, SC 29208, USA.
Email: cboggs@seoe.sc.edu

Present address
Nitin Ravikanthachari, Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA

Libby L. Burch, Department of Pediatrics, University of California, San Francisco, CA 94158, USA

Rachel E. Powell, Tansley Team, Sheridan, CA 95681, USA

Danielle M. Scott, WorkRamp, San Francisco, CA 94107, USA

Charlotte R. Wayne, The Rockefeller University, New York, NY 10065, USA

Kristjan Niitepõld, The Finnish Science Centre Heureka, Vantaa, 01300, Finland

Funding information
Stanford University Vice Provost for Undergraduate Education

Abstract

Assisted migration consists of the introduction of a species to previously inhabited areas or to new suitable regions. Such introductions have been touted as a viable tool for conserving the earth's biodiversity. However, both the likely success of assisted migrations and the impacts on local communities are hotly debated. Empirical data on the local impacts of assisted migration are particularly lacking. We examined the short and long time-scale effects of herbivory on *Lonicera involucrata* (Richards) Banks ex. Spreng (Caprifoliaceae) after an introduction of *Euphydryas gillettii* Barnes (Lepidoptera: Nymphalidae, Melitaeini) to Gunnison County, Colorado, USA, via an assisted migration in 1977. The plant is the primary larval host plant for the butterfly. We quantified plant seed production, plant survival, and population stage structure in two sets of observational experiments. We found that herbivory by *E. gillettii* increased *L. involucrata* reproduction on an annual time scale, independent of plant size and local microhabitat characteristics. Over the time since the butterfly's introduction, herbivory by *E. gillettii* resulted in a plant population structure biased toward smaller plants in the butterfly introduction and satellite sites compared with sites without the butterfly. Our results highlight the importance of studying the effects of assisted migrations on native populations at different temporal scales. As assisted migration becomes an indispensable tool for species conservation, our work adds to the understanding of the multi-trophic impacts of assisted introductions on local populations and communities.

KEYWORDS
Caprifoliaceae, *Euphydryas gillettii*, introduced species, Lepidoptera, *Lonicera involucrata*, plant-herbivore interaction, population stage structure, reproductive success, seed production, species translocation

INTRODUCTION

Assisted migration is an increasingly advocated, although controversial, tool for species' conservation in the face of climate and land use change (Butt et al., 2020; Hällfors et al., 2016; Hewitt et al., 2011; McLaghlan et al., 2007). Assisted migration may take the form of species' re-introductions into habitats/communities where

the species recently went extinct, or of introductions into suitable unoccupied habitats/communities. In general, such suitable habitats and communities contain competitors, predators, prey, and host plants found in the native range of the introduced species, unlike most other anthropogenic species invasions for which the invader comes into a novel community. As a result of this difference in community composition, extrapolation from expectations from invasion biology for the effects of assisted migration on communities in the short and long term may be inaccurate.

Nonetheless, we do have evidence that species that are introduced via assisted migration or re-introduction disrupt food webs in their new community or, at a minimum, alter the life histories of their prey (Boyce, 2018). Both the predicted and actual impacts on communities, as well as the probability of success, are still subject to considerable debate (Novak et al., 2021; Pearson et al., 2022; Strayer, 2022; Timms et al., 2012). This debate results in part from a dearth of experimental evidence concerning the impacts of assisted translocations of animal species, as studies of attempted assisted migrations have focused strongly on plant species (Butt et al., 2020; Sáenz-Romero et al., 2021).

We can surmise the effect of introduced herbivorous insects on their host plants in their new location through general studies of plant responses to herbivory. These responses may include changes in resource allocation and life-history traits. However, the direction of these changes varies among plant species. For example, some plant species reduce allocation to reproduction under herbivory, in a presumed trade-off favoring survival (Doubleday & Cappuccino, 2011; Gruner & Norton, 2006; Rees & Paynter, 1997). Alternatively, other plant species increase their rate and amount of reproduction (Belovsky & Slade, 2000; Butler & Kielland, 2008). Many plant species correct for the effects of herbivores by increasing their growth rates in response to tissue damage (McNaughton, 1983; Oba et al., 2000). Alternatively, plants may respond by delaying senescence and increasing the allocation of carbon to reserves in roots for future use (Schwachtje et al., 2006). In general, using a meta-analysis Garcia and Eubanks (2019) showed that some form of overcompensation for insect herbivory was widespread across plant and herbivore families, plant growth form, and plant part on which herbivores fed.

These changes on an individual plant level can affect population structure and dynamics, sometimes radically altering stage structure and population size (Crawley, 1989). For example, reproduction at a younger age can result in plant populations with less total biomass and age structures biased toward younger ages (Belovsky & Slade, 2000; Jenkins et al., 2007). In the extreme case, plant populations could be eradicated or severely reduced locally, paralleling cases of successful biocontrol of non-native invasive plants by herbivores introduced from the plant's native region (Franks et al., 2006). However, this should only occur if the herbivore exerts very strong top-down control of the plant population elsewhere where they co-occur.

Here, we examine the effects of herbivory on *Lonicera involucrata* (Richards) Banks ex. Spreng (Caprifoliaceae) by the butterfly *Euphydryas gillettii* Barnes (Lepidoptera: Nymphalidae) after an assisted migration. We focus on the effects on plant reproduction, survival, and population size structure. The butterfly was introduced to our study area, which is 500 km southeast of its native range, in 1977 to test the hypothesis that empty niches exist due to dispersal constraints (Holdren & Ehrlich, 1981). We ask: what short-term effects does herbivory by *E. gillettii* have on seed production by *L. involucrata*? Does such herbivory translate into long-term impacts on the size or viability of the individual and on the stage structure of *L. involucrata* populations? Based on studies outlined above, we hypothesize that seed production will be altered due to changes in resource allocation in the short term due to herbivory by *E. gillettii* and that plant size or viability will decrease in the long term under herbivore pressure causing a change in the stage structure of the populations. Thus, we expect that the temporal scale of the study will be important. Conclusions drawn from the short-term study will differ from that of cumulative effects over the longer term.

MATERIALS AND METHODS

Study species

Lonicera involucrata is a perennial deciduous shrub native to northern and western North America. It inhabits moist open forests, between about 1800 and 3000 m asl. The shrub is rhizomatous, producing closely spaced ramets or shoots. It produces flowers and fruit annually, but little other information is available on its demography. In our study area, *L. involucrata* is commonly found in association with spruce, *Picea engelmannii* Parry ex. Englem., and willows, *Salix* spp. The plant is browsed by deer and elk but, to our knowledge had few, if any, insect herbivores prior to the introduction of *E. gillettii* to our study area.

Euphydryas gillettii is native to wet montane meadows in the Rocky Mountains, from British Columbia and Alberta, Canada, to Wyoming, USA (Williams, 1988). It is univoltine. The adult flight period lasts for 3–6 weeks starting in late June or early July. Females deposit eggs in clusters on the underside of *L. involucrata* leaves near the top of shoots (Bonebrake et al., 2010). The pre-diapause larvae form webs and feed on the parenchymal leaf tissues of *L. involucrata*. Pre-diapause larvae frequently decimate entire shoots (CL Boggs, pers. obs.). The vast majority of pre-diapause herbivory is on *L. involucrata*; eggs in our study site were found on an alternative host, *Valeriana occidentalis* A. Heller (Valerianaceae), in only 1 year between 1978 and 1989, and only once on one

plant since 2002 (unpubl. data). Fourth instar larvae diapause overwinter. Post-diapause larvae feed individually on *L. involucrata* or occasionally on *V. occidentalis* before pupating and eclosing as adults.

Our focal population of *E. gillettii* was introduced to a 1.75-ha site at the Rocky Mountain Biological Laboratory (RMBL) in Gunnison County, CO, USA (38°57′5″ N, 106°59′6″ W, 2912 m asl) in 1977 from Granite Creek, WY, USA (43°41′42″ N, 110°26′55″ W, 2130 m asl) (Holdren & Ehrlich, 1981). The introduction site is south of the native range but appeared to be suitable habitat. The introduced population fluctuated between 15 and 150 individuals for the next 25 years, then exploded to an estimated 3000 individuals in 2002 (Boggs et al., 2006). Since then, the population size has fluctuated over two orders of magnitude, from 65 to 9675 adult butterflies (unpubl. data). The geometric mean adult population density between 2002 and 2011 was 671 adults/ha.

Study sites

We studied the short-term effects of *E. gillettii* herbivory on *L. involucrata* at the original butterfly introduction site ("Main") at RMBL (Holdren & Ehrlich, 1981). We included an additional 0.75-ha site ("Avalanche"), located 0.6 km southeast of Main. Avalanche was naturally colonized by the butterfly in 2002 (Boggs et al., 2006).

To examine the long-term effects of larval herbivory on individual plants and plant population size structure, we chose three additional control sites near RMBL without *E. gillettii*. It was not feasible to simply use plants that had never been fed on within sites occupied by *E. gillettii*, as we lack a record of which plants had been fed on over the Years 1978–2011. Furthermore, plants not fed on would almost certainly have differed in microclimate, among other features, from plants that were fed on. Instead, we selected plants arbitrarily across sites with and without the butterfly. We aimed to choose sites without butterflies that were in proximity to sites with butterflies. All five study sites contained similar vegetation. Both the Main and Avalanche experimental sites consisted of east-facing meadows with beaver ponds and streams at the base of Gothic Mountain. The Avalanche site lacked the *P. engelmannii* trees present in the Main site, due to high avalanche activity. The three control sites without butterflies were Trail 401, Copper Creek, and North Main. The North Main site was on the same east-facing slope of Gothic Mountain as Main and Avalanche. Trail 401 and Copper Creek consisted of montane meadows, which were drier and at slightly higher elevation than the other three sites. Within each of these five sites, we randomly selected 2–4 10 × 10 m subsites, depending on the size of the site, with a total of seven subsites in the treatment and seven in the control sites. We recorded the coordinates and elevation of each of the 14 subsites using Google Earth (Figure 1).

Short-term effects of herbivory

Using forestry flagging and aluminum metal tags, we marked 78 *L. involucrata* individuals in Main and nine plants in Avalanche. For each plant, we recorded the number of *E. gillettii* larval webs present in early September 2004 as the larvae were entering diapause, along with evidence of herbivory by animals other than *E. gillettii*. We did not record herbivory in 2005. *L. involucrata* generally matures fruit prior to herbivory by pre-diapause *E. gillettii*. Additionally, the butterfly population size in Main crashed from 1682 adults in 2004 to 84 adults in 2005 (Boggs et al., 2006), such that post-diapause herbivory in 2005 was negligible.

We attempted to collect all ripe fruits from each marked plant in 2005 and counted the seeds set. Occasionally, seed dispersers collected the fruits before we did, as evidenced by scars on the base of the bracts. We had earlier recorded aborted fruits on each plant, so we could determine whether the scar represented aborted or dispersed fruits. For cases of missing fruits, we recorded the number missing and estimated total seed set by the plant based on the average for other fruits on that plant.

In 2004, we recorded plant parameters that are correlated with the likelihood of *E. gillettii* herbivory on *L. involucrata* (Bonebrake et al., 2010). These included exposure of the plant to sun (1 = morning [AM], 2 = afternoon [PM], 3 = both [AM + PM]), soil wetness in the first half of July and early September (1 = dry surface, 2 = moist surface, 3 = standing water), and presence or absence of *P. engelmannii* within 1 m of the plant. The index of soil wetness used in the analysis was the mean of the July and September values. In addition, we recorded measures of plant size: total number of shoots in 2004 and plant volume in 2004 and 2005. Plant volume was calculated as a rectangular cube, based on plant height, plant width and plant length measured with a measuring tape.

Long-term effects of herbivory

On July 6–8, 2011, we collected data on all *L. involucrata* individuals in each of the long-term study subsites. Using a tally-counter, we separately recorded the number of live and dead shoots on an individual plant. As *L. involucrata* has rhizomes, individual plants were denoted as shoot clusters that were located within 15 cm of each other.

We assigned each *L. involucrata* individual to a size class based on its live shoot count. Most plants with <10 live shoots had no dead shoots, and plants with <25 shoots typically were not flowering. Therefore, the first two size classes encompassed plants containing 1–10 and 11–25 live shoots. We arbitrarily delineated the next three size classes to include plants having 26–150, 151–500, and >500 live shoots.

We recorded instances of flowering, number of dead shoots, large mammal or insect herbivory, and whether the

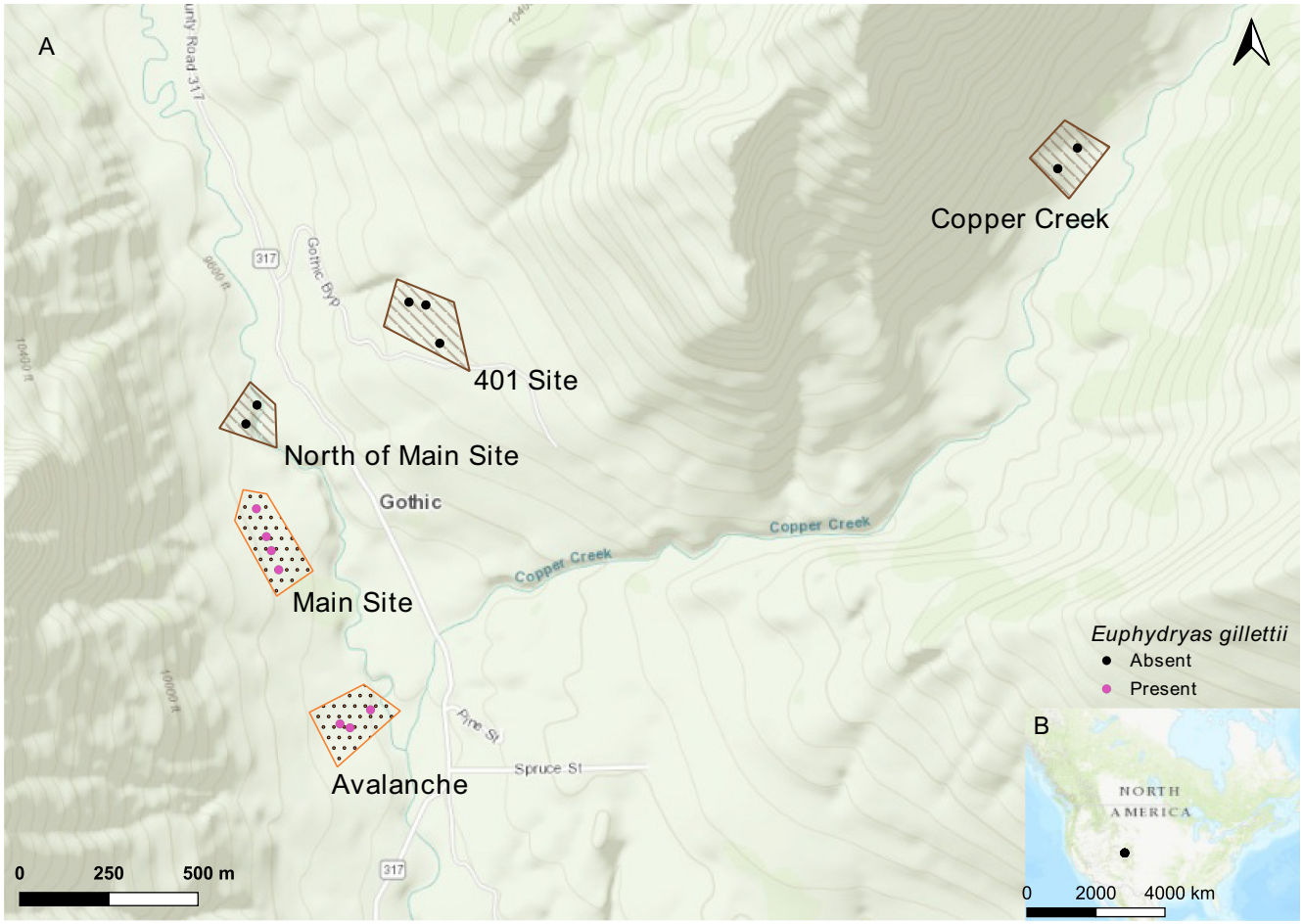

FIGURE 1 Map of the sites used in this study. (A) Main and Avalanche were experimental sites, North Main, Trail 401 and Copper Creek were control sites without butterflies present. (B) General location of the study area within America north of Mexico.

perimeter of the leaves was slightly reddened, indicating a pathogen infection. Based on the surrounding topography and the position and path of the sun, we assessed whether the plant received morning or afternoon sunlight. We classified the soil around each plant according to the soil wetness scale described above.

Using a measuring tape or stick, we recorded the standing height of each *L. involucrata* plant to the nearest centimeter. Additionally, we approximated the height of the tallest surrounding vegetation, excluding *P. engelmannii*, to the nearest 0.5 m. We estimated the percent cover of any vegetation within a meter that was taller than the *L. involucrata* individual and noted the presence and estimated height of any *P. engelmannii* within 1 m of the plant.

Statistical analysis

All analysis was carried out in R v.4.3.2 (R Core Team, 2020). To determine the short-term effects of herbivory on plant growth and reproduction, we constructed a piecewise structural equation model (SEM) using the psem function of piecewiseSEM package v.2.3.0 (Lefcheck, 2016). We chose piecewise SEM over the traditional variance–covariance-based SEM because piecewise SEM can fit generalized linear models to construct a single causal network. Our SEM included three component generalized linear models (GLM, paths) (Table 1; Figure 2). Path 1 included a Gaussian GLM with a log function with plant volume in 2005 as the dependent variable and the total number of shoots as the independent continuous variable. Path 2 included a Poisson GLM with a log function with the number of larval webs in 2004 as the dependent variable and the total number of shoots as the independent continuous variable. Path 3 included a Poisson GLM with a log function with the number of seeds in 2005 as the dependent variable with plant volume in 2005 and number of larval webs in 2004 as continuous independent variables. All models included the presence/absence of AM/PM sun, soil wetness index, and presence/absence of *P. engelmannii* as categorical independent variables. We additionally tested for multicollinearity among the predictor variables (Table S1) using the vif function from the car package v.3.1-2 (Fox et al., 2007). Our model also tested the correlation between total number of shoots in 2004 with number of seeds in 2005 and between number of larval webs in 2004 and plant volume in 2005. We

constructed multiple SEM paths and chose the model with the best global goodness of fit and the lowest Akaike information criterion (AIC) scores.

We used an ordinal Bayesian cumulative generalized linear mixed model using the brms function of the package brms v.2.21.0 (Bürkner, 2017) in R to determine the long-term effects of *E. gillettii* herbivory on *L. involucrata*. We specifically used a Bayesian approximation method to account for any multicollinearity among the dependent variables. We used the plant size class based on the number of live shoots in 2011 as the categorical dependent variable and the number of dead shoots in 2011 (as a measure of long-term herbivory) as a continuous independent variable, presence/absence of larval webs in 2011, number of flowers/plant, availability of sunlight (AM only, PM only or throughout the day), presence/absence of spruce, presence/absence of leaf redness, and presence (experimental)/absence (control) of *E. gillettii* as independent factor variables with site identity as the random effect. We calculated LOO (leave-one-out cross-validation) scores (Table S3) among all combinations to select the best model based on the highest elpd (expected log predictive density) score. As all subset models had comparable elpd scores, we selected the subset model with the fewest predictor variables as our final model.

TABLE 1 Paths of piecewise structural equation model that best explained factors affecting short-term plant growth and reproduction.

Path	Dependent variable	Independent variable
1	Plant volume in 2005	No. of shoots in 2004 + presence/absence of AM/PM sun + presence/absence of spruce
2	No. of larval webs	Total no. of shoots in 2004
3	No. of seeds in 2005	Total no. of shoots in 2004 + plant volume in 2005 + no. of larval webs in 2004 + presence/absence of AM/PM sun + presence/absence of spruce + soil wetness index

Note: Tests for correlations: No. of shoots in 2004 and no. of seeds in 2005; No. of larval webs in 2004 and plant volume in 2005.

RESULTS

Short-term effects of *E. gillettii* herbivory

Herbivory by animals other than *E. gillettii* was negligible. Of the 87 plants surveyed in 2004, eight had partial damage to one to six leaves, likely caused by other herbivores, with the mean number of leaves damaged being three. One plant lost five of its 66 shoots to vertebrate grazers. For context, the mean number of shoots per plant in 2004 was 64, with a range of 4–302, and each shoot contained over six leaves.

Our piecewise SEM model (Table 1; AIC = 43.87; Fisher's $C = 7.627$, $p = 0.47$, df = 8; Table S2 for model selection) indicated that herbivory by *E. gillettii* affected plant reproduction by increasing the number of seeds, while not affecting plant growth (Figure 2; Table 2). Our model revealed that plant volume in 2005 increased with an increase in the number of shoots, whereas presence/absence of either morning or afternoon sunlight, or presence of *P. engelmannii* were not significant contributors to plant growth (Figure 2; Table 2). The number of larval webs increased with an increase in the number of shoots (Figure 2; Table 2). The number of seeds in 2005 increased

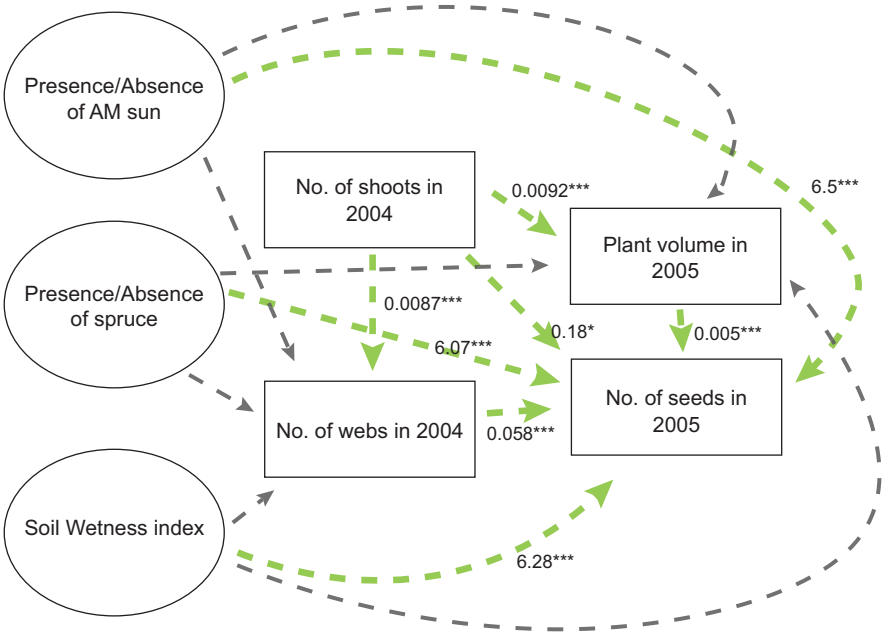

FIGURE 2 Piecewise structural equation model of factors affecting plant growth and reproduction. Values represent regression estimates of predictors. Green paths represent estimated positive significant links. Gray paths represent non-significant links in the model. *$0.01 < p < 0.05$, ***$p < 0.001$.

TABLE 2 Piecewise structural equation model regression estimates and *p*-values of factors affecting short-term plant growth and reproduction.

Response	Predictor	Estimate	SE	df	Critical value	*p*	Std. estimate
Plant volume 2005	(Intercept)	−0.46	0.16	76	−2.92	<0.001	0
	No. of shoots in 2004	0.01	6.0E-04	76	14.96	<<0.001	0.43
	Sun	-	-	2	1.98	0.15	-
	AM + PM sun	−0.26	0.11	76	−2.27	0.02	-
	PM only sun	−0.18	0.19	76	−0.94	0.35	-
	AM sun only	0.07	0.14	76	0.49	0.62	-
	Spruce	-	-	1	2.28	0.14	-
	Spruce present	−0.20	0.11	76	−1.76	0.08	-
	Spruce absent	−0.04	0.10	76	−0.45	0.66	-
No. of larval webs in 2004	(Intercept)	−0.65	0.17	79	−3.87	<0.001	0
	No. of shoots in 2004	0.008	0.001	79	7.59	<<0.001	-
No. of seeds in 2005	(Intercept)	6.32	0.02	72	362.04	<<0.001	0
	Plant volume 2005	0.44	0.003	72	132.72	<<0.001	-
	No. of larval webs in 2004	0.06	0.002	72	30.99	<<0.001	-
	Sun	-	-	2	7.09	<0.001	-
	PM sun only	5.15	0.02	Inf	264.49	<<0.001	-
	AM + PM sun	5.42	0.01	Inf	413.76	<<0.001	-
	AM sun only	6.50	0.02	Inf	430.70	<<0.001	-
	Spruce	-	-	1	7.83	0.006	-
	Spruce present	5.30	0.01	Inf	360.85	<<0.001	-
	Spruce absent	6.08	0.01	Inf	436.20	<<0.001	-
	Soil	-	-	3	2.78	0.047	
	Soil = moist/dry	5.37	0.01	Inf	386.57	<<0.001	-
	Soil = moist/standing water	5.49	0.04	Inf	122.27	<<0.001	-
	Soil = dry	5.61	0.01	Inf	412.78	<<0.001	-
	Soil = moist	6.29	0.01	Inf	701.64	<<0.001	-
No. of larval webs in 2004	Plant volume 2005	0.01	-	81	0.12	0.45	0.01
No. of shoots in 2004	No. of seeds in 2005	0.19	-	117	2.03	0.02	0.19

with an increase in plant volume in 2005 (Figure 2; Table 2) and with an increase in the number of webs in 2004 (Figure 2; Table 2). This indicated that herbivory stimulated seed production independent of plant size. Spruce, soil wetness index, and sunlight also had significant positive effects on the number of seeds, with plants receiving morning sun alone, growing in areas with moist soil and growing without spruce within 1 m producing significantly more seeds based on marginal means (Figure 2; Table 2). Our model also indicated that the number of shoots in 2004 and the number of seeds produced in 2005 were positively correlated (Table 2).

Long-term effects of *E. gillettii* herbivory

Long-term herbivory by *E. gillettii* is correlated with a decrease in the number of live shoots per plant in *L. involucrata* (Table 3; Figure 3; see Table S3 for model selection), indicating a change in the stage structure of the *L. involucrata* population. The average plant size class based on the number of live shoots was smaller in subsites with *E. gillettii* (Table 3; Figure 3). Average plant size class increased with herbivory by other animals, number of dead shoots, and the presence of flowers (Table 3; Figure 3). No other tested variable (presence of larval webs in 2011, sun exposure, presence of spruce, and presence of leaf redness) entered the model as significant factors.

DISCUSSION

In the short term, *L. involucrata* responded to *E. gillettii* herbivory by increasing the number of seeds produced in the next year. Over the longer term, the presence of *E. gillettii* significantly decreased the average number of live shoots

TABLE 3 Regression estimates, $\hat{R}$ (convergence statistic), bulk effective sample size (ESS), and tail ESS for the Bayesian cumulative mixed model of factors affecting the plant size class, which was based on the number of shoots.

	Estimate	SE	95% confidence interval	$\hat{R}$	Bulk ESS	Tail ESS
Intercept (class 1)	−0.10	0.64	−1.46 to 1.06	1.00	2273	2451
Intercept (class 2)	1.21	0.65	−0.14 to 2.45	1.00	2676	2355
Intercept (class 3)	4.74	0.75	3.26 to 6.26	1.00	2979	2843
Intercept (class 4)	8.32	1.22	6.09 to 10.85	1.00	3201	3330
Presence of other herbivory	0.83	0.43	0.00 to 1.68	1.00	4330	2700
No. of dead shoots	0.03	0.01	0.01 to 0.04	1.00	3279	2792
Presence of flowers	2.59	0.52	1.60 to 3.65	1.00	3527	2538
Presence of *Euphydryas gillettii*	−1.32	0.76	−3.00 to 0.14	1.00	1886	1818

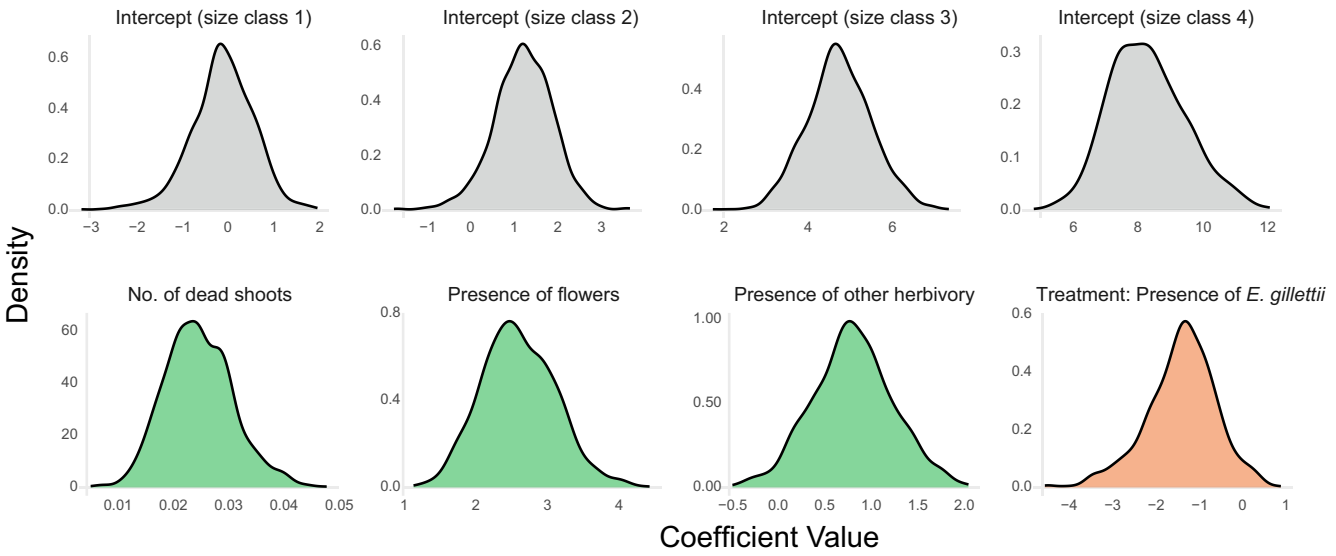

FIGURE 3 Bayesian posterior distributions of coefficients of predictors of plant size class based on the number of live shoots. Plots indicated in green represent significant factors that increase plant size class, whereas values indicated in orange represent significant factors that decrease plant size class. Gray plots indicate intercepts for each plant size class.

on a given *L. involucrata* individual, when compared to a control set of plants without exposure to herbivory by *E. gillettii*. The stage structure of *L. involucrata* with sustained *E. gillettii* herbivory was thus skewed toward smaller individuals.

Our results are consistent with studies indicating that some plants increase reproduction in response to herbivory (Belovsky & Slade, 2000; Butler & Kielland, 2008) rather than decreasing reproduction in an assumed trade-off with survival. Likewise, we found no evidence for compensatory growth in our long-term study. Given the correlation between plant size and seed production, it seems likely that *L. involucrata* seed production has been reduced on average over the years in sites with *E. gillettii*. Repeated local herbivory by *E. gillettii* is thus likely to result in changes in vital rates of both survival and fecundity, along with changes in stage structure, over time.

The contrast between short-term and long-term effects on *L. involucrata* fitness components also suggests that the temporal scale of a given study matters if we are to detect the effects of assisted migration. Our results support the suggestion that the effects of an introduction or invasion on community dynamics may differ between the acute and chronic phases of the invasion (Strayer et al., 2006). Thus, studies performed immediately after an assisted migration may yield results that differ from a similar analysis of population and community dynamics generations later (see also Boyce, 2018).

Oviposition preferences of female butterflies should also affect the longer-term impacts of *E. gillettii* on *L. involucrata* population structure and dynamics. Females lay clusters of 50–300 eggs on a single leaf, and show distinct preferences for oviposition plant characteristics, which may vary with summer temperature (Bonebrake et al., 2010). As a result, some plants (and leaves) receive

multiple egg clusters. However, the distribution of egg clusters is skewed toward one per plant, compared with a Poisson distribution (J. DuRant, L. Fisher, N. Shive & C. Boggs, ms in prep). The resulting stochastic and deterministic variation in the intensity of herbivory may affect the long-term dynamics and stage structure of the plant population.

Our experimental design had certain limitations. First, as noted in the methods, we were unable to implement a paired and highly replicated design. Nonetheless, we found no statistical anomalies due to the present design. Second, we focused on the individual-level ecological effects of the butterfly introduction on the plant. We did not explore changes in the broader community of species interacting with the plant or butterfly, nor did we consider adaptation of either partner. However, both types of effects are certainly feasible, even though *L. involucrata* is the native host plant of *E. gillettii* throughout the herbivore's range. Third, our study design did not incorporate variables to specifically test for the herbivore's absence from the control site, which could be influenced by factors influencing differences in plant growth and reproduction between the control sites and sites with *E. gillettii* or factors which we did not measure. Ongoing and future studies on factors driving changes in *E. gillettii* populations and movement will shed more light on factors that could influence habitat preference, if any. Finally, although we incorporated the effects of major abiotic (presence of sunlight, soil moisture, and sunburn) and biotic (herbivory by other organisms and presence of other plant species) drivers influencing plant life-history traits, other factors, both biotic and abiotic, that were not included in our analysis could result in differences seen in plant growth and reproduction. For example, differences in snow-melt timing (Francon et al., 2020), diversity of plant genotypes (Olanrewaju et al., 2021), and anthropogenic disturbances (Spicer et al., 2023) among sites could result in differences in plant growth and reproduction. Nonetheless, the results presented here still hold true as we identified that biotic factors, specifically that of herbivory by *E. gillettii* and not of major abiotic factors (sunlight and soil moisture) explained most of the variation seen in changes in plant reproduction and growth between habitats with and without *E. gillettii*.

In particular, the current population of *L. involucrata* had not experienced herbivory by *E. gillettii*, leaving open the possibility for coevolutionary responses. Interactions between herbivores and their host plants are mediated by long-term local coevolution creating selection mosaics of coevolutionary hotspots (where true reciprocal selection occurs) and coevolutionary cold spots (where reciprocal selection is absent) (Thompson, 1999, 2005). For example, longstanding herbivory by the North American beaver, *Castor canadensis* Kuhl, has resulted in the adaptation of resistance to herbivory by *Populus* spp. (Bailey & Schweitzer, 2010). Alternately, some herbivorous insects have evolved a tolerance to their host plant's toxins over time, making the plant more susceptible to further herbivory by the same species (Despres et al., 2007). Although we have no evidence for ongoing evolutionary changes in either plant or insect, this remains a possibility.

In the face of various forms of anthropogenic change, assisted migration to combat species loss will undoubtedly become increasingly relevant. Even though the *E. gillettii* population was not originally introduced to the Colorado site for conservation purposes, the extended observational record of this population provides valuable insights for those considering the use of assisted migration for biodiversity or conservation aims. Our research fills the gap in understanding the population-level short-term and long-term impacts of assisted migration on native resources.

AUTHOR CONTRIBUTIONS

Nitin Ravikanthachari: Formal analysis (lead); writing – review and editing (equal). **Libby L. Burch:** Conceptualization (supporting); investigation (equal); writing – original draft (equal). **Rachel E. Powell:** Conceptualization (supporting); investigation (equal); writing – original draft (equal). **Danielle M. Scott:** Conceptualization (supporting); investigation (equal); writing – original draft (equal). **Charlotte R. Wayne:** Conceptualization (supporting); investigation (equal); writing – original draft (equal). **Kristjan Niitepõld:** Conceptualization (supporting); investigation (equal); writing – review and editing (supporting). **Risa H. Rosenberg:** Conceptualization (supporting); investigation (equal); writing – review and editing (supporting). **Carol L. Boggs:** Conceptualization (lead); data curation (lead); funding acquisition (lead); investigation (equal); methodology (equal); project administration (lead); supervision (lead); writing – review and editing (lead).

ACKNOWLEDGMENTS

Many thanks to K. Tomalty, K. Stanford, N. Bonoff, T. Karasov, and C. Lemire for endless hours of seed counting and plant measurements, and to I. Enquist, for his tally-counting prowess. We thank the Bailey family for permission to work on their land, and Rocky Mountain Biological Laboratory for arranging USFS research permits. Funding came from Stanford University's Vice Provost for Undergraduate Education. E. LoPresti and two reviewers provided helpful comments on the manuscript. We acknowledge that this work was conducted on the ancestral homeland of the Uncompahgre (Tabeguache) Ute band.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available at https://doi.org/10.5061/dryad.sn02v6xdb.

ORCID

Carol L. Boggs https://orcid.org/0000-0001-7601-6277

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. VIF (Variance inflation factor) among predictor variables used in the construction of SEM investigating the short-term effects of *Euphydryas gillettii* herbivory on *Lonicera involucrata*.

Table S2. Model selection for the piecewise SEM for short-term effects of herbivory on *Lonicera involucrata*.

Table S3. LOO (Leave-One-Out Cross-Validation) scores for model selection for Bayesian CLMM to understand the effects of long-term herbivory on *Lonicera involucrata*.

How to cite this article: Ravikanthachari N, Burch LL, Powell RE, Scott DM, Wayne CR et al. (2024) Impacts of assisted migration: An introduced herbivore has short-term and long-term effects on its native host plant population. *Entomologia Experimentalis et Applicata, 00*: 1–10. https://doi.org/10.1111/eea.13507