

Losing a battle but winning the war: moving past preference–performance to understand native herbivore–novel host plant interactions

Leone M. Brown^{1,2} · Greg A. Breed³ · Paul M. Severns⁴ · Elizabeth E. Crone²

Received: 9 February 2016 / Accepted: 23 November 2016 / Published online: 2 December 2016
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Abstract Introduced plants can positively affect population viability by augmenting the diet of native herbivores, but can negatively affect populations if they are subpar or toxic resources. In organisms with complex life histories, such as insects specializing on host plants, the impacts of a novel host may differ across life stages, with divergent effects on population persistence. Most research on effects of novel hosts has focused on adult oviposition preference and larval performance, but adult preference may not optimize offspring performance, nor be indicative of host quality from a demographic perspective. We compared population growth rates of the *Baltimore checkerspot* butterfly, *Euphydryas phaeton*, on an introduced host, *Plantago lanceolata* (English plantain), and the native host *Chelone glabra* (white turtlehead). Contrary to the previous findings suggesting that *P. lanceolata* could be a population sink, we found higher population growth rates (λ) on the introduced than the native host, even though some component parameters of λ were higher on the native host. Our findings illustrate the importance of moving beyond preference–performance studies to integrate vital rates across all

life stages for evaluating herbivore–host plant relationships. Single measures of preference or performance are not sufficient proxies for overall host quality nor do they provide insights into longer term consequences of novel host plant use. In our system, in particular, *P. lanceolata* may buffer checkerspot populations when the native host is limiting, but high growth rates could lead to crashes over longer time scales.

Keywords Butterflies · Demography · Herbivores · Introduced species · Plant–insect interactions · Preference · Performance

Introduction

It goes without saying that introduced plants can affect native herbivores (reviewed by Bezemer et al. 2014). In some cases, non-native plants escape local herbivory, giving them a competitive advantage over native plants and limiting food availability for local herbivores (Blossey and Nötzold 1995; Carpenter and Cappuccino 2005; Rodgers and Stinson 2008; Wolfe 2002). Alternatively, introduced plants can supplement native food sources, providing additional resources that may facilitate range expansion or benefit herbivores if environmental conditions change (Graves and Shapiro 2003; Rodriguez 2006; Tepedino et al. 2008). The benefit of alternative food sources should depend on their quality, how preferred they are by native herbivores, and herbivore life history. A novel food source could be lower quality, but good enough from a demographic perspective if it allows the herbivore to maintain a population growth rate of λ greater than or equal to one. Alternatively, a higher quality food source might be associated with lower herbivore population growth rates if

Communicated by Roland A. Brandl.

✉ Leone M. Brown
leone.m.brown@gmail.com

¹ Odum School of Ecology, University of Georgia, 140 E. Green St, Athens, GA, USA

² Department of Biology, Tufts University, 163 Packard Ave, Medford, MA, USA

³ Institute of Arctic Biology, University of Alaska Fairbanks, 902 N. Koyukuk Dr, Fairbanks, AK, USA

⁴ Department of Botany and Plant Pathology, Oregon State University, 2082 Cordley Hall, Corvallis, OR, USA

herbivore patch occupancy is limited by immigration independent of habitat quality, or if quality varies temporally with environmental factors, such as fire or other seasonal changes (Boughton 1999, 2000; Pickens and Root 2008).

For a novel food source to become a major part of the diet of an herbivore without negatively impacting the herbivore population, it should, in theory, meet nutritional needs and optimize fitness (Emlen 1966; Schoener 1971; Sih and Christensen 2001). In organisms with complex life histories, such as insects, whether or not food choice optimizes fitness may not be immediately evident nor entirely under control of the feeding individual itself. For instance, if adult insects, which may or may not feed, oviposit on introduced plant species toxic to their larvae, the negative effect of these ‘lethal oviposition mistakes’ on larval development can create population sinks (Bowers and Schmitt 2013; Chew 1977; Courtney 1981; Graves and Shapiro 2003). Alternatively, if the herbivore is pre-adapted or able to quickly adapt to differences in chemistry between the native and introduced hosts (Keeler and Chew 2008; Singer et al. 2008; Strauss et al. 2006), the novel host may buffer the population against crashes, especially if the native host plant abundance is limited (Schlaepfer et al. 2011). Over evolutionary time, the host preferred by adults should be that which optimizes larval performance—the ‘preference–performance’ or ‘mother knows best’ hypothesis (Garcia-Robledo and Horvitz 2012; Gripenberg et al. 2010; Levins and MacArthur 1969; Thompson 1988). Although ‘preference–performance’ is more often the rule than the exception (Garcia-Robledo and Horvitz 2012; Gripenberg et al. 2010), some studies find that mothers are bad at choosing. For instance, positive effects of host plant choice on non-larval stages, such as adult survival, may dictate preference and lead to so-called ‘optimal bad motherhood’ (Garcia-Robledo and Horvitz 2012; Mayhew 2001; Scheirs et al. 2000).

Most research on the ecology and evolution of herbivore host plant use has focused on this ‘preference–performance’ axis (Bernays and Graham 1988; Garcia-Robledo and Horvitz 2012), neglecting the consequences of host plant use across the entire life cycle on population dynamics. Whether or not offspring survival is optimized, however, vital rates across life stages only need be high enough to maintain population persistence; hence, ‘optimal bad motherhood’ may not necessarily lead to population extinction. Previous researchers have encouraged and taken a demographic approach by measuring vital rates in herbivorous insects to understand major causes of mortality (e.g., Carey 2001; Cornell and Hawkins 1995, 1998). To our knowledge, however, only Garcia-Robledo and Horvitz (2011; laboratory-reared *Cephaloleia* beetles) have incorporated vital rates across the life cycle into population growth rates; they found broad support for the ‘mother

knows best’ hypothesis (i.e., oviposition preference matched larval performance), and positive but lower growth rates on a novel host. Outside of a controlled laboratory environment, however, population dynamics may be less predictable. In populations interspersed between patches of native and novel hosts, for instance, a non-optimal host could create a population sink or ecological trap (Bezemer et al. 2014; Pulliam 1988), but could also increase overall abundance through dispersal (Holt 1985).

Checkerspot butterflies are an increasingly well-documented example of a species that uses an introduced host plant. Several checkerspot species rely on host plants that contain iridoid glycosides sequestered by larvae to make them unpalatable to predators, including *Melitaea cinxia* in Europe, *Euphydryas phaeton* in the Eastern USA, and the subspecies *E. editha editha/bayensis* in California, *E. editha taylori* in the Pacific Northwest USA, and *E. editha monoensis* in Nevada (Kuussaari et al. 2004). In the mid-to-late 19th century, the introduction and range expansion in USA of the iridoid-containing *Plantago lanceolata* (English plantain; Cavers et al. 1980) led to its eventual co-option by several North American checkerspot species as a larval food source (Severns and Warren 2008; Singer et al. 2008; Stamp 1979). Among these species, there is apparent oviposition preference for the native host in *E. phaeton* (Bowers et al. 1992; G. A. Breed unpublished data), but preference toward *P. lanceolata* appears to have evolved in some populations of *E. editha monoensis* (Singer et al. 1993, 2008). Although threatened and endangered populations of *E. e. monoensis* and *E. e. taylori* both use *P. lanceolata*, inclusion of this broad-ranged host in their diet has not led to their recovery (Singer et al. 2008), though other factors likely caused their decline (e.g., the invasion of exotic grasses to *E.e. taylori* habitat, Severns and Warren 2008). *P. lanceolata* has been considered a lower quality food source for *E. phaeton* based on tests of oviposition preference and larval preference and performance (Bowers et al. 1992). Specifically, Bowers et al. (1992) showed that newly hatched pre-diapause larvae preferred the native *C. glabra* (white turtlehead) over the non-native *P. lanceolata*, and both pre- and post-diapause larvae had lower growth rates on *P. lanceolata* than *C. glabra*. *P. lanceolata* may also increase palatability of prey to predators (Bowers 1980). Thus, although some *E. phaeton* populations are reported to use *P. lanceolata* exclusively (Bowers et al. 1992; Stamp 1979), the use of this plant could be maladaptive at the individual level and a demographic sink at the population level.

In this paper, we investigate effects of the introduced *P. lanceolata* as an adopted host plant on population dynamics of *E. phaeton*, the *Baltimore checkerspot* butterfly. In some parts of its range, adults of *E. phaeton* oviposit on both the native host plant, *Chelone glabra*, and the introduced

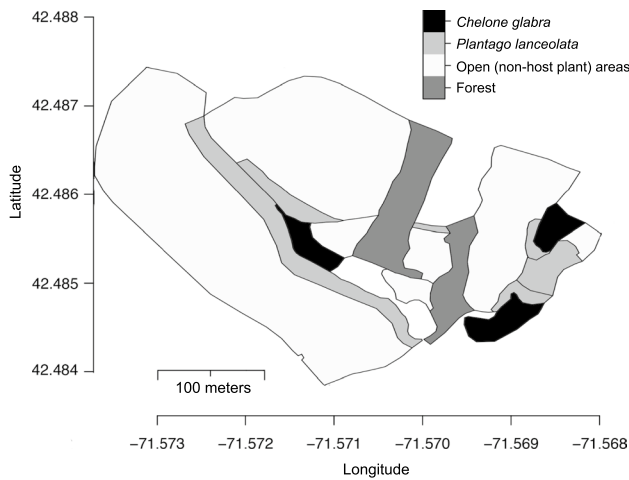


Fig. 1 Map of site and areas covered by *C. glabra* and *P. lanceolata*

P. lanceolata, but *P. lanceolata* has yet to be incorporated into the diet in other parts of *E. phaeton*'s range where both host plants exist in close proximity (Frye et al. 2013). In our study landscape (Harvard, MA, USA), *E. phaeton* uses both host plant species. Given that *P. lanceolata* has been reported to be lower quality and is not the preferred host plant for oviposition (Bowers et al. 1992; G. A. Breed unpublished data), we expected that use of *P. lanceolata* could either (1) negatively impact butterfly abundance by acting as a population sink, or (2) increase overall butterfly abundance, even if it is lower quality. We also expected that any negative (or positive) impacts on larval stages might be reflected in later life stages (Boggs and Freeman 2005). We measured vital rates of *E. phaeton* across its life cycle on both host plants to estimate host plant-specific population growth rates, and simultaneously monitored the population's actual growth over several years. We explore the implications of novel host plant use for population dynamics in a heterogeneous landscape by going beyond laboratory studies of preference–performance to integrate vital rates across the entire life cycle.

Materials and methods

We studied *E. phaeton* at a ~10.5 ha conservation site in the town of Harvard, MA, USA (species and site are described in Brown and Crone 2016). G. Breed, P. Severns, and E. Crone visited multiple sites in 2011 and chose this site for studying *E. phaeton*, because the population used both host plants, *C. glabra* and *P. lanceolata*, and the host plants occurred in relatively discrete spatial patches. The site contains ~2 ha of host plant cover, ~30% of which is the native host plant, *C. glabra*, and ~70% of which is the non-native English plantain, *P. lanceolata* (estimated by

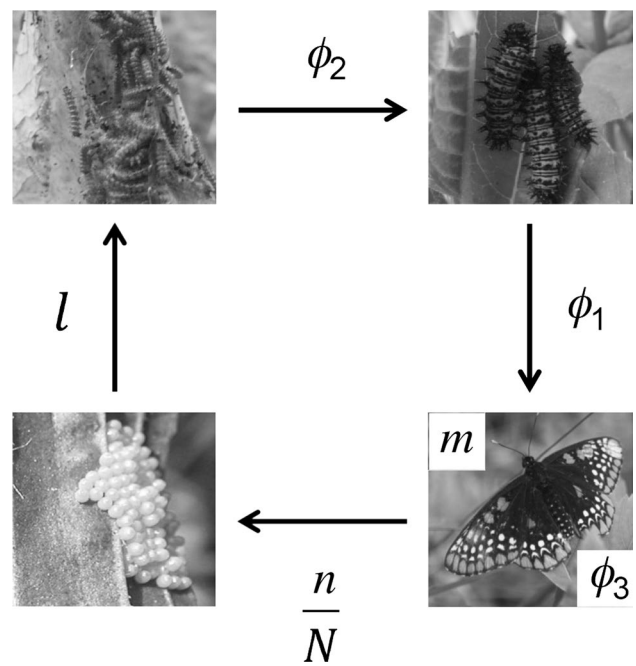


Fig. 2 Life cycle of *E. phaeton*, illustrating parameters used to estimate population growth rates: ϕ_1 post-diapause (spring) larval survival, ϕ_2 overwinter (fall to spring) survival, ϕ_3 adult female survival, m adult female mass, N adult female population size, n number of nests, and l number of pre-diapause (fall) larvae per nest

mapping areas containing host plants; Fig. 1). *E. phaeton* populations using *P. lanceolata* occur largely in agricultural landscapes, where mowing keeps other vegetation low enough for *P. lanceolata* to be available to *E. phaeton* adults, but can also destroy larval nests (Bowers and Richardson 2013). In 2012, G. Breed consulted with the site's land managers to change the timing of mowing to minimize impacts on late summer–early fall *E. phaeton* larvae on *P. lanceolata*, when pre-diapause (i.e., fall) larval nests are on host plants and the larvae have not yet dropped to the ground to overwinter (Stamp 1982). We collected data to estimate vital rates across the entire life cycle, including larval survival [post-diapause (spring) and overwinter survival], the number of nests laid and number of larvae per nest, adult female population size, adult female survival rate, and adult female mass (Fig. 2).

Larval survival

We measured post-diapause (i.e., spring) larval survival to eclosion as adults on each host plant by collecting individuals in the early spring 2012 and 2013 and rearing them in 60 × 60 cm insect enclosures set-up over unoccupied *C. glabra* or *P. lanceolata* (four post-diapause larvae in each of 10 *C. glabra* and 12 *P. lanceolata* enclosures in 2012, and five post-diapause larvae in each of 14 *C. glabra* and

14 *P. lanceolata* enclosures in 2013). In 2012, the population was very small and all larvae were originally found in host plant patches of *C. glabra*; enclosures depleted of host plant were removed from the study. In 2013, larvae were moved to enclosures from patches of both *C. glabra* and *P. lanceolata* in a crossed design, following Bowers et al.'s design for estimating larval survival in the laboratory (1992). Enclosures at risk of depletion were supplemented with the host plant over which they were placed (Appendix S1 in Brown and Crone 2016). We estimated overwinter survival from winter 2013 to spring 2014 on each host plant by setting up cages around inactive pre-diapause nests in mid-fall 2013 (9 *C. glabra* cages and 10 *P. lanceolata* cages), and counting and removing post-diapause larvae from cages in spring 2014 (Appendix S1 in Brown and Crone 2016).

Number of nests, nest size, and population-level oviposition preference

In the late summer/early fall of 2013 and 2014, we estimated the number of nests laid by adult females on *C. glabra* and *P. lanceolata* using a mark-resight study. We searched for nests on both host plants across the entire site on five occasions, marking newly sighted nests close to the ground with an inconspicuous tag, and recording resights of already marked nests. We estimated the number of pre-diapause larvae per nest in the late summer/early fall 2013 and 2014 by making a small opening in a portion of nests (63 in 2013, 92 in 2014) and counting the number of individuals in each nest to the nearest ten from 2 to 5 times (to minimize nest disturbance) over 5–10 occasions (Appendix S1 in Brown and Crone 2016). We inferred population-level oviposition preference for *C. glabra* or *P. lanceolata* by testing whether the proportion of nests found on each type of host plant differed from the proportion of area occupied by a given host at our site, i.e., ~0.3 for ~30% host plant cover of *C. glabra* (*C.g.*) and ~0.7 for ~70% of host plant cover of *P. lanceolata* (*P.l.*). We used the upper and lower confidence intervals (CIs) of the number of nests estimated to estimate upper and lower confidence intervals of the proportions (e.g., $C.g.^{uppCI} = C.g.^{uppCI} / (C.g.^{uppCI} + P.l.^{lowCI})$ and $C.g.^{lowCI} = C.g.^{lowCI} / (C.g.^{lowCI} + P.l.^{uppCI})$).

Female daily adult survival, population size, and individual mass

We used a capture-mark-recapture study of adult butterflies to estimate daily survival of females eclosed from *C. glabra* or *P. lanceolata* insect enclosures in 2012 and 2013, and to estimate population size of wild-caught adult females in 2012, 2013, and 2014 (adding adults eclosed from insect enclosures to final estimates; Table 1; Brown and Crone 2016). We

marked the wings of adults with a unique color combination of 3–5 dots using metallic gel pens, and surveyed the entire site for new individuals and recaptures several times per week from the late June until no more butterflies were observed in the field (mid-July to early August depending on the population size). As a proxy for fecundity, we used a digital scale to measure body mass of all adult females upon removal from insect enclosures in 2012 and 2013.

Host plant-specific population growth rates

We estimated demographic parameters for calculating host plant-specific population growth rates using generalized linear models and mixed-effects models (GLMs and GLMMs; e.g., including a random effect of enclosure to account for variation in microsite or other variables that might influence larval survival estimates), and methods for analyzing capture-mark-recapture/resight and unmarked population data (Table 1). From these models, we obtained the host plant-specific values for post-diapause survival, ϕ_1 , overwinter survival, ϕ_2 , larvae per nest, l , female adult mass, m , and female daily adult survival, ϕ_3 , and population-level values for the number of nests, n , and number of adult females, N . These parameters are included in the equations that follow.

We used parametric bootstrapping of host plant-specific and population-level parameters to estimate host plant-specific population growth rates as $\lambda = \phi_1 \times \phi_2 \times \frac{n}{N} \times l \times m^*$. Here, a value of $\lambda = 1$ indicates an annually stable (not growing or declining) population, $\lambda = 2$ indicates a population doubling annually, and $\lambda = 0.9$ indicates a population declining by 10% annually (see Gotelli 2001). In our formula, m^* is a body mass correction for n/N , assuming that fecundity is proportional to body mass (Wickman and Karlsson 1989), to allocate the proportion of total nests per adult relative to the body mass of adults reared on *C. glabra* (*C.g.*) versus *P. lanceolata* (*P.l.*), where $m_{C.g.}^* = \frac{2 \times m_{C.g.}}{m_{C.g.} + m_{P.l.}}$ and $m_{P.l.}^* = \frac{2 \times m_{P.l.}}{m_{C.g.} + m_{P.l.}}$. Given that post-diapause larval survival and the number of nests per adult varied across years, we estimated host plant-specific population growth rates (λ_{hp} , corresponding to parameters for *C. glabra* or *P. lanceolata*) as:

$$\lambda_{hp} = \left[\left(\phi_{1hp2012} \times \phi_{2hp} \times \frac{n_{2013}}{N_{2013}} \times l_{hp} \times m_{hp}^* \right) \times \left(\phi_{1hp2013} \times \phi_{2hp} \times \frac{n_{2014}}{N_{2014}} \times l_{hp} \times m_{hp}^* \right) \right]^{\frac{1}{2}}$$

The equation above distributes all nests equally among females reared on both hosts. Because adult survival differed somewhat among hosts (albeit non-significantly at the 0.05 level; see "Results"), an alternative assumption could be that oviposition probability is proportional to life span,

Table 1 Parameters used to calculate habitat-specific growth rates, and models for estimating parameters from data collected between 2012 and 2014

Parameter; dates collected	Statistical model	Means, standard errors, confidence intervals
		<i>Chelone glabra</i>
		<i>Plantago lanceolata</i>
Post-diapause (spring) larval survival, ϕ_1 ; spring 2012 and 2013	Binomial GLM with post-diapause host plant and year as factors: effect of enclosure location ($\chi^2 = 4.89$, $df = 1$, $P = 0.027$) and year ($\chi^2 = 17.16$, $df = 1$, $P = 3.434 \times 10^{-5}$); including larval origin (i.e., host plant from which larvae were collected) as a fixed effect or enclosure ID as a random effect in a GLMM did not improve model fit (Bates et al. 2014; Brown and Crone 2016)	2012 Logit-link mean (SE): -0.000 (0.316) 2012 Logit-link mean (SE): -0.423 (0.295) 2012 Back-transformed mean (95% CI): 0.500 (0.349–0.651) 2013 Logit-link mean (SE): 1.386 (0.299) 2013 Logit-link mean (SE): 0.588 (0.249) 2013 Back-transformed mean (95% CI): 0.800 (0.646–0.882) 2013 Back-transformed mean (95% CI): 0.643 (0.527–0.749)
Overwinter (fall to spring) larval survival, ϕ_2 ; fall 2013–spring 2014	Poisson GLMM with post-diapause larval count as response and offset of log-transformed pre-diapause nest count (Brown and Crone 2016); including enclosure ID as a random effect was a better fit to the than a Poisson GLM	Log-link mean (SE): -1.292 (0.288) Back-transformed mean (95% CI): 0.275 (0.147–0.492) Log-link mean (SE): -0.587 (0.265) Back-transformed mean (95% CI): 0.556 (0.318–0.971)
Adult female daily survival, ϕ_3 ; summer 2012 and 2013	CJS model implemented in R2jags, best model for estimating survival on both host plants included effect of year on recapture but not survival probability (recapture rate was higher in 2012 when the population was smaller; Kéry and Schaub 2012; Brown and Crone 2016)	Mean (SE, 95% CI): 0.780 (0.040, 0.697–0.853)
Adult female population size, N_t ; summer 2012, 2013 and 2014	Gross population estimates (N^* -hat) from POPAN module in Program MARK; in models for all years, recapture probability differed by capture occasion, entrance parameter was constant; in 2012 best model, survival declined linearly with time in best model; in 2013 and 2014 best models, survival was constant across time (White and Burnham 1999)	Means (SEs, 95% CIs) 2012: 45 (5, 36–57) + 20 females from insect enclosures = 65 total (wild caught + enclosure reared) 2013: 222 (30, 171–289) + 34 females from insect enclosures = 256 total (wild caught + enclosure reared) 2014: 1202 (95, 1030–1402) (all wild caught)
Adult female body mass, m_t ; summer 2012 and 2013	LM with weak effect of post-diapause larval host plant on adult mass ($\chi^2 = 2.83$, $df = 1$, $P = 0.092$); no effect of larval origin or year; including enclosure ID as a random factor in an LMM did not improve model fit (Bates et al. 2014)	Mean (SE, 95% CI): 0.304 (0.011, 0.282–0.326) Mean (SE, 95% CI): 0.309–0.347

Table 1 continued

Parameter; dates collected	Statistical model	Means, standard errors, confidence intervals
		<i>Plantago lanceolata</i>
Number of nests, n ; late summer 2013 and 2014	Closed population model with memory effects implemented in R2jags, where probability of finding a nest in time $t + 1$ differed if the nest was seen in time t (Kéry and Schaub 2012; Brown and Crone 2016)	2013 mean (SE, 95% CI): 50 (8, 40–70)
		2014 mean (SE, 95% CI): 248 (28, 203–313)
Number of pre-diapause (fall) larvae per nest, l ; late summer/early fall 2013 and 2014	Open population model, 'unmarked' pack-age in R, with 0 recruitment and constant dynamics; best model included varying detection by host plant and by year; including survival effect in model fit the data better than a closed model that only estimates abundance and detection (Fiske and Chandler 2011)	Log-link mean (SE): 4.96 (0.027)
		Back-transformed mean (95% CI): 143 (135–150)
		<i>Chelone glabra</i>
Number of nests, n ; late summer 2013 and 2014	Closed population model with memory effects implemented in R2jags, where probability of finding a nest in time $t + 1$ differed if the nest was seen in time t (Kéry and Schaub 2012; Brown and Crone 2016)	2013 mean (SE, 95% CI): 26 (1, 25–28)
		2014 mean (SE, 95% CI): 34 (4, 28–45)
Number of pre-diapause (fall) larvae per nest, l ; late summer/early fall 2013 and 2014	Open population model, 'unmarked' pack-age in R, with 0 recruitment and constant dynamics; best model included varying detection by host plant and by year; including survival effect in model fit the data better than a closed model that only estimates abundance and detection (Fiske and Chandler 2011)	Log-link mean (SE): 4.54 (0.033)
		Back-transformed mean (95% CI): 94 (88–100)

and thus increases with survival. Therefore, we estimated an alternative $\lambda_{C.g.}$ and $\lambda_{P.l.}$ by correcting for differences in survival of adult females reared on the two host plants. We converted daily survival rate into mean days (d) survived as $d_{C.g.} = \frac{1}{1-\phi_{3C.g.}}$ and $d_{P.l.} = \frac{1}{1-\phi_{3P.l.}}$, survival corrected for fecundity as $\phi_{3C.g.}^* = \frac{2 \times d}{d_{C.g.} + d_{P.l.}}$ and $\phi_{3P.l.}^* = \frac{2 \times d_{P.l.}}{d_{C.g.} + d_{P.l.}}$, and λ_{hp}^* as:

$$\lambda_{hp}^* = \left[\left(\phi_{1hp2012} \times \phi_{2hp} \times \frac{n_{2013}}{N_{2013}} \times l_{hp} \times m_{hp}^* \times \phi_{3hp}^* \right) \times \left(\phi_{1hp2013} \times \phi_{2hp} \times \frac{n_{2014}}{N_{2014}} \times l_{hp} \times m_{hp}^* \times \phi_{3hp}^* \right) \right]^{\frac{1}{2}}$$

We estimated confidence limits for host-specific population growth rates by parametric bootstrapping. To do so, we generated 10,000 values of each host plant-specific or population-level component of λ by sampling from a normal distribution with the mean and standard deviation of the transformed estimates (Table 1), and back-transforming these 10,000 values to calculate λ . We estimated means and confidence intervals for λ_{hp} and λ_{hp}^* from their respective 10,000 estimates.

We evaluated how respective differences in post-diapause larval survival, overwinter larval survival, number of larvae per nest, adult female mass, and adult survival on the native host plant, *C. glabra*, versus the non-native host plant, *P. lanceolata*, affected population growth rates. To do so, we recalculated λ values for the native host plant, *C. glabra*, by replacing each of the above vital rates on *C. glabra* in turn with the value estimated for *P. lanceolata* (i.e., a Life Table Response Analysis, LTRE; Caswell 2001). We did not do this for number of nests on *C. glabra* versus *P. lanceolata* per adult, since the total number of nests per adult was combined in our equations. For consistency, we evaluated the results of these substitutions for values of both λ (without including differences in adult survival) and λ^* (including differences in adult survival).

Results

Across life cycle stages, there were differences in the suitability of *C. glabra* versus *P. lanceolata* as inferred from demographic parameters: values for demographic parameters were higher on *C. glabra* for 2/6 of the parameters used to estimate host plant-specific λ , and higher on *P. lanceolata* for 3/6 of the parameters (Table 2).

Larval survival

Post-diapause larval survival was higher on *C. glabra* than *P. lanceolata* in 2012 and 2013 ($\chi^2 = 4.89$, $df = 1$,

Table 2 Most suitable host plant inferred from parameter estimates, i.e., the host plant conferring higher values of the specified parameter; ϕ_1 , ϕ_2 , ϕ_3 , m , and l were used to estimate λ on *C. glabra* and *P. lanceolata*

Parameter	Host plant
Post-diapause (spring) larval survival, ϕ_1	<i>C. glabra</i>
Overwinter (fall to spring) larval survival, ϕ_2	<i>P. lanceolata</i>
Adult female survival, ϕ_3	Neither (slightly higher on <i>P. lanceolata</i>)
Adult female mass, m	<i>C. glabra</i>
Pre-diapause (fall) larvae per nest, l	<i>P. lanceolata</i>
Proportion of nests relative to area occupied	<i>P. lanceolata</i>
Habitat-specific population growth rates, $\lambda_{C.g.}$ or $\lambda_{P.l}$	<i>P. lanceolata</i>

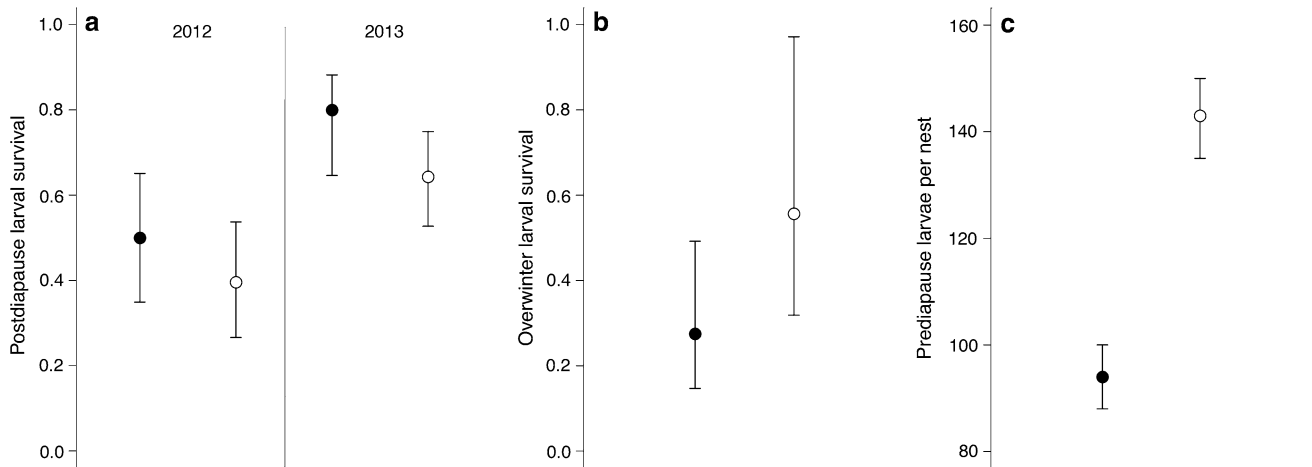


Fig. 3 Larval survival rates and number of larvae per nest on *C. glabra* (filled circles) and *P. lanceolata* (open circles): **a** post-diapause larval survival in 2012 and 2013, **b** overwinter larval survival, **c** mean number of larvae per nest. Error bars indicate 95% confidence intervals

$P = 0.027$) with an effect of year ($\chi^2 = 17.16$, $df = 1$, $P = 3.434 \times 10^{-5}$; Table 1; Fig. 3a); a model with a random effect of enclosure did not fit the data better than a model without random effects ($\Delta AIC = 2$), indicating a little difference in microsite between enclosures. Overwinter survival, on the other hand, was higher on *P. lanceolata* than on *C. glabra* ($\chi^2 = 3.25$, $df = 2$, $P = 0.071$; Table 1; Fig. 3b); a model with a random effect of enclosure was a better fit to the data than a model without the random effect ($\Delta AIC = 344$), indicating variation among microsites in estimates of overwinter survival beyond that attributed to host plant alone (among-site variance = 0.69).

Number of nests, nest size, and population-level oviposition preference

More nests were laid on *P. lanceolata* than *C. glabra* in both 2013 and 2014 (Table 1; Fig. 4a), and *P. lanceolata* nests contained more larvae than *C. glabra* nests (Table 1; Fig. 3c). In 2013, the proportion of nests on *P. lanceolata* versus *C. glabra* did not differ from the proportion of area covered by *P. lanceolata* and *C. glabra*, but in 2014, the

proportion of nests on *P. lanceolata* was higher than its proportion of land cover (Fig. 4b).

Female daily adult survival, population size, and individual mass

Daily survival of adult females did not differ based on their post-diapause host (*P. lanceolata* versus *C. glabra*; Table 1; Fig. 5a). Females that were reared during the post-diapause period in enclosures with *C. glabra* were larger in mass than females reared in enclosures with *P. lanceolata* ($\chi^2 = 2.83$, $df = 1$, $P = 0.092$; Table 1; Fig. 5b). The population size of adult females increased from 2012 to 2014 (Fig. 5c).

Host plant-specific population growth rates

Habitat-specific population growth rates, with and without adjusting for survival differences in fecundity, were higher on *P. lanceolata* than *C. glabra* (Fig. 6). The survival-fecundity adjustment exaggerated this difference, but did not qualitatively affect our conclusions about

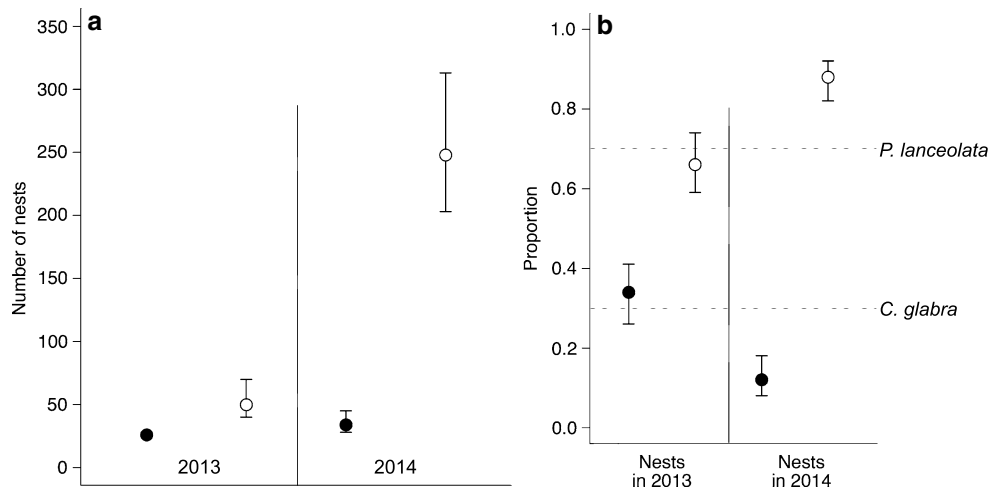


Fig. 4 Nests in *C. glabra* (filled circles) and *P. lanceolata* (open circles): **a** Total number of nests estimated in 2013 and 2014 on both host plants; **b** Proportion of nests found on *C. glabra* and *P. lanceo-*

lata in 2013 and 2014. Dashed lines indicate the proportion of the entire site covered by each host plant. Error bars indicate 95% confidence intervals

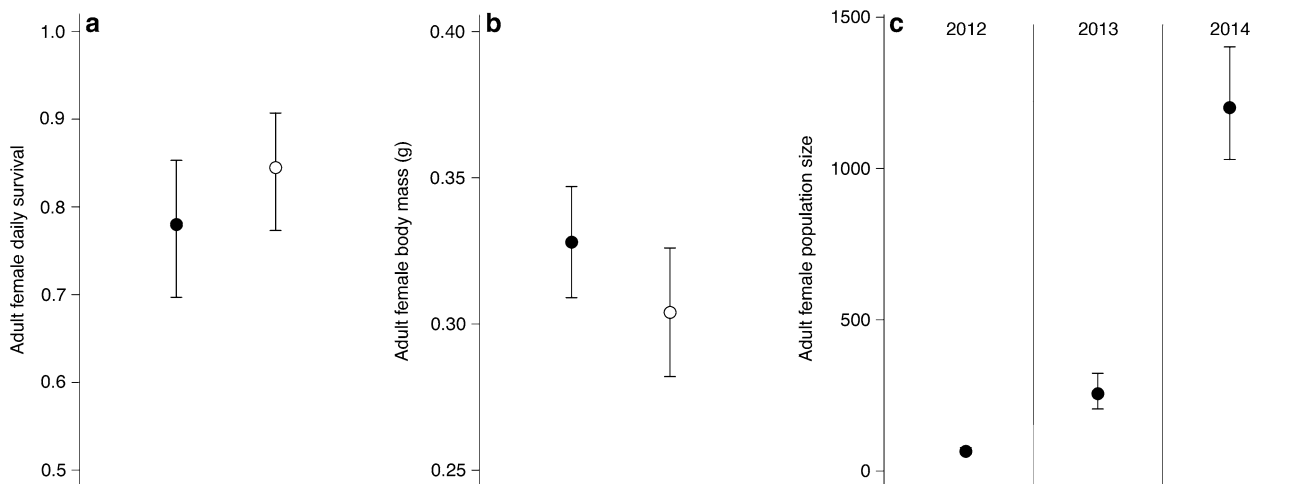


Fig. 5 Female adult **a** daily survival, **b** body mass on *C. glabra* (filled circles) and *P. lanceolata* (open circles), and **c** total female adult population size from 2012–2014. Error bars indicate 95% confidence intervals

host plant-specific population growth rates (Fig. 6). Estimated annual population growth rates were high, but broadly consistent with observed increases in population size during the study period (Fig. 5c). Replacing the value for overwinter survival on *C. glabra* with the value for overwinter survival on *P. lanceolata*, assuming that all other parameter values were those of *C. glabra* led to the greatest change in population growth rates relative to the same replacement for other vital rates for *C. glabra*; all other means fell within the confidence limits of the original population growth rate estimates for *C. glabra* (Fig. 7).

Discussion

Contrary to expectations, our findings suggest that *P. lanceolata* is neither maladaptive at the individual level, nor a population sink in the traditional sense. It has long been held that understanding herbivore host plant expansions requires understanding female oviposition preference and offspring performance (Janz and Nylin 2008), all of which had pointed to *C. glabra* being a superior host for *E. phaeon* prior to this study. Integrating vital rates across the entire life cycle in the wild, however, suggests that superiority in preference or performance at some stages and in

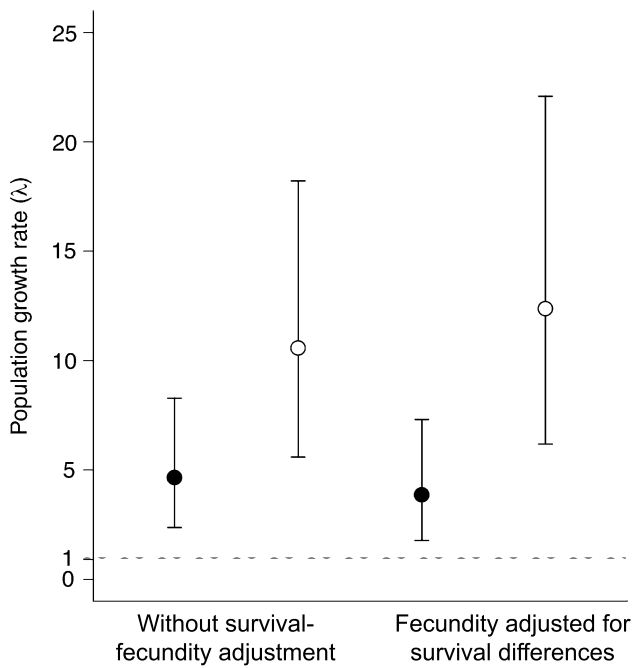


Fig. 6 Population growth rate on *C. glabra* (filled circles) and *P. lanceolata* (open circles) estimated without and with adjusting for survival differences in fecundity of adult females. Error bars indicate 95% confidence intervals

the lab does not necessarily lead to higher overall growth rates (Table 2), and yields insight into case studies where seemingly inferior novel hosts maintain populations in the wild (Forster and Wilson 2013).

It is plausible that *P. lanceolata* may, in fact, be a lower quality food source leading to lower individual fecundity

(Boggs and Ross 1993); we found lower survival of post-diapause larvae to eclosion and smaller masses (a proxy for fecundity) of adult females eclosed on *P. lanceolata*. These results correspond with previously documented lower larval growth rates and pupal masses in *E. phaeton* (Bowers et al. 1992), and are in accordance with a recent meta-analysis showing lower overall survival of larvae on exotic hosts (Yoon and Read 2016). Lower rates of post-diapause survival to eclosion and smaller female adult masses in our study, however, are countered by the larger pre-diapause nest size and the higher overwinter survival on *P. lanceolata*. Past studies have suggested that adult butterflies reared on *C. glabra* are more toxic (Bowers 1980). In our field populations, however, adult survival did not depend on larval host, and was marginally higher on *P. lanceolata*, the opposite direction of the expected difference in toxicity.

Our demographic study indicated that *E. phaeton* has high habitat-specific population growth rates on both the native *C. glabra* and the introduced *P. lanceolata*, but these were significantly higher on *P. lanceolata*. The high growth rates on *P. lanceolata* may be beneficial in the short term for rescuing declining populations across parts of *E. phaeton*'s range, but may have long-term costs. Both anecdotal reports by local naturalists and more formal scientific studies point to the vulnerability of checkerspot populations to crashes (Boggs et al. 2006; Stamp 1984; Williams 2012). In general, density dependence may be a cause of population crashes, especially if post-diapause larvae consume host plants more quickly than they can recover and adults then oviposit on unsuitable hosts (Bowers and Schmitt 2013). If populations cycle due to density dependence, host types that have higher population growth rates in the short term are also the most

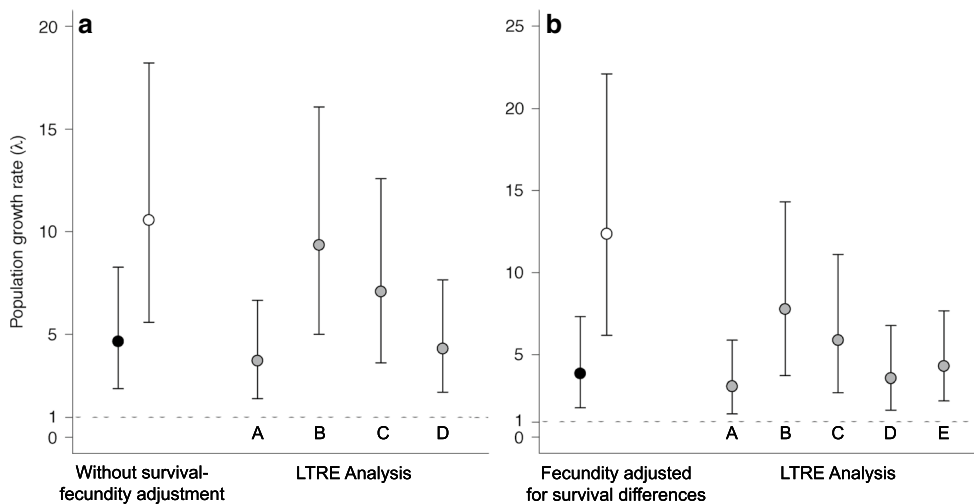


Fig. 7 Population growth rates on *C. glabra* (filled circles) and *P. lanceolata* (open circles) both **a** with and **b** without adult survival correction, followed by LTRE analysis where each *C. glabra* vital

rate was replaced, in turn, with the *P. lanceolata* value (grey circles) for *a* post-diapause survival, *b* overwinter survival, *c* number of larvae per nest, *d* female adult body mass, and *e* female adult survival

likely to crash. Larger populations may also be more vulnerable to parasitoids, a known threat to checkerspot populations (Lei and Hanski 1997; Stamp 1981).

Forister et al. (2009) propose a conceptual model with three potential ways in which a novel host can be incorporated into the diet of a native herbivore. From their conceptual model, we can ask: Is *P. lanceolata* chosen because of chemical similarity to *C. glabra*? Is *P. lanceolata* superior for some life stages?, and Is *P. lanceolata* used simply because its occurrence overlaps with locations of adult resources? We cannot rule out any of these possibilities, which may be why *P. lanceolata* appears to be such a suitable host. First, *P. lanceolata* is chemically similar to *C. glabra*, which is probably why it is accepted for oviposition and larval feeding in the first place. Both host plants contain iridoid glycosides and catapols (Bowers et al. 1992; Fuchs and Bowers 2004), and broadly speaking, butterflies may have lower preference for native hosts than previously believed (Yoon and Read 2016).

Second, our findings suggest that *P. lanceolata* is a superior host for pre-diapause larvae, but not for post-diapause larvae. Larger pre-diapause nests might reflect higher early instar pre-diapause survival on *P. lanceolata* (cf. Bowers et al. 1992), which we did not directly measure. Although larger pre-diapause nests should be subject to higher parasitism, *P. lanceolata* may actually buffer populations from parasitoids (Bowers and Richardson 2013; Van Nouhuys and Hanski 1999), making larger nests adaptive on *P. lanceolata* but not *C. glabra*. Overwinter survival was also marginally higher on the non-native host, and led to the largest difference in population growth rates in our sensitivity analysis. It is possible that pre-diapause and overwintering larvae benefit from the warmer, drier locations associated with *P. lanceolata* (which would also explain the effect of microsite in pre-but not post-diapause larval survival estimates), but post-diapause larvae do not. In our study, microsite conditions and host plant identity are inherently confounded; this distinction between laboratory-based studies and our field-based study reflects real covariance that occurs in nature. Finally, post-diapause larval survival may be higher on the native *C. glabra* if differences in secondary compounds between the two hosts affect post-diapause larval growth and survival to eclosion, or due to the higher efficiency with which late instar larvae can convert *C. glabra* to biomass relative to *P. lanceolata* (see Table 2 and Table 3 in Bowers et al. 1992).

Third, in our population, the choice of *P. lanceolata* for oviposition could result in part from overlap with nectar sources. While *C. glabra* at our site is located in wet areas with high density of ferns and sedges, the *P. lanceolata* habitat along the edges of these wetlands is replete with nectar plants where both males and females regularly feed (G. Breed, L. Brown, E. Crone, P. Severns, pers. obs.). The combination of the above factors, as well as shared

ancestry with European checkerspots that commonly use *P. lanceolata* (e.g., *Melitaea* and *Euphydryas* species; Wahlberg 2001), may have made it inevitable that *P. lanceolata* would be chosen as a novel host for *E. phaeton* populations. Given that post-diapause larval survival and individual oviposition preference are higher on *C. glabra*, however, it was not intuitive without integrating data from the entire life cycle that population growth rates would be higher on the novel than the native host plant.

Predicting the probability and consequences of novel host plant shifts requires not only knowing that a host plant is acceptable for oviposition and produces viable larvae, but also consideration of the relationship between host plant use (occupancy or utilization) and availability (Forister and Wilson 2013), and herbivore and host plant life history. Our study illustrates the importance of evaluating this relationship across both temporal and spatial scales in a univoltine butterfly on native and non-native perennial hosts. In 2013, it appeared that *E. phaeton* used both *P. lanceolata* and *C. glabra* in proportion to their availability on the landscape, yielding nearly equal rates of utilization. In 2014, when the adult female population size was nearly four times larger, *P. lanceolata* was utilized at a much higher rate relative to its proportional landscape availability. While the higher proportion of nests on *P. lanceolata* than *C. glabra* relative to area (i.e., higher utilization) in 2014 could reflect preference for the novel host that was only evident at larger population sizes, this pattern could also reflect higher preference for *P. lanceolata* habitat, in general, which contains an abundance of nectar plants. Higher utilization may also result from patch-specific host plant densities; preliminary data and field observations at our site suggest higher densities of *P. lanceolata* within host plant patches on the landscape (E. Crone, unpubl. data). This higher density would yield more oviposition sites within similar-sized areas, and could also explain higher rates of pre-diapause survival—if gregarious larvae which are unlikely to leave the nest can more easily find new food plants as a group, there should be less competition for food even if the overall quality is lower. It is worth noting that we did not measure quality per se, but the *P. lanceolata* at our site is in moist lowland areas surrounding the wetland and is subsequently relatively lush, which may contribute to its suitability as a food source (G. Breed, L. Brown, E. Crone, P. Severns, pers. obs.); it is unknown whether *P. lanceolata* from drier locations would be equally utilized. Finally, while our species is univoltine, its life history with post-diapause larvae of the previous generation feeding on the same year's host plants as pre-diapause larval stages of the next generation can lead to similar expectations as might be found in a multivoltine herbivore population feeding on annual plants (e.g., Fei et al. 2014). For instance, both Stamp (1984) and Bowers

and Schmitt (2013) documented that in very large populations, post-diapause larvae may deplete the host plant, leaving adult butterflies with limited resources for oviposition, and pre-diapause larvae with limited food resources. Variation in life history characteristics of both herbivore and host plants will inevitably influence the expected effect of the novel host plant on population dynamics.

The incorporation of novel food sources into the diet of native herbivores has implications for herbivore ecology, evolution, and conservation, and is especially relevant in dynamic landscapes associated with global change (Forister and Wilson 2013). In practice, examination of larval and adult preference and larval performance in the lab have laid a strong foundation on which to base our predictions about the evolution and impact of host plant shifts. Beyond the laboratory, both simpler and more complex approaches have been made to infer mechanisms leading to novel host plant use in globally altered landscapes (e.g., Pearse and Altermatt 2013; Singer and McBride 2010). However, to fully understand the consequences of novel host plant use where populations are at real risk of decline and extinction, we need to incorporate the entire life cycle, ideally in the wild, to determine how performance at individual life stages scales up to rates of population growth. Although many past researchers have called for integrating herbivore performance across the life cycle, few have done so. In our study and a previous laboratory-based study of tropical beetles (Garcia-Robledo and Horvitz 2011; the only previous study we know of to integrate host quality over the entire life cycle of a non-pest herbivore), some vital rates were superior on the native host, and others were superior on the novel host, indicating that no single vital rate is predictive of host quality. We expect that vital rates of different life stages may vary across hosts in other systems as well, and these should be considered before conclusions about host plant suitability are made. A shift from the traditional experiments to a more integrative view of systems may yield valuable insights into plant–herbivore ecology and evolution, and inform habitat restoration for declining populations.

Acknowledgements We thank the Conservation Commission of the town of Harvard, MA, for allowing us to use their land for our research. We also thank Aubrie James, Emma Sass, Natasha Tigeros, Norah Warchola, Ailene Ettinger, Lauren Redosh, Haley Coffman, Livia Baer-Bositis, Deane Bowers, Natalie Kerr, Dash Donnelly, Cheryl Schultz, Glenda Wardle, Michal Bodziewicz, and Rafal Zwolak for help with fieldwork. We are grateful to Richard Chandler for helpful advice regarding population models, and we are indebted to the Handling Editor and three anonymous reviewers for incredibly helpful comments and suggestions that greatly improved this manuscript. This work was supported by a National Science Foundation Award to LMB (DEB-1402287) and a Department of Defense SERDP Award to EEC (RC-2119), with additional support from Harvard Forest, Harvard University, and Tufts University.

Author contribution statement EEC, GAB, and PMS conceived the original ideas and designed and carried out fieldwork conducted in 2012. LMB and EEC designed and carried out fieldwork conducted in 2013 and 2014. LMB and EEC collated and analyzed all of the data and wrote the manuscript.

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