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Do characteristics of pollinator-friendly gardens predict the diversity, abundance, and reproduction of butterflies?

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Abstract. 1. Pollinator declines have motivated efforts to plant nectar and host plants for butterflies and other pollinators, but whether gardens promote pollinator conservation requires further investigation.

2. We established garden plots to determine whether plant type (native vs. exotic) and weed maintenance (low or high) influence adult butterfly abundance and species richness, and the abundance and survival of immature stages of four species (monarch, queen, black swallowtail, and gulf fritillary). To assess how predator activity and mortality of immature stages might differ inside gardens compared to other suitable habitat patches, we compared caterpillar survival on sentinel host plants placed within and outside of plots.

3. The abundance and species richness of adult butterflies (all taxa) increased with the number of flowering plants per plot, but did not depend on plant type or weeding treatment. Exotic plots had greater adult monarch and gulf fritillary abundances, greater monarch and queen egg counts, and lower black swallowtail caterpillar counts relative to native plots.

4. The survival of immature stages (egg to instar 5) ranged from 2 to 13% and was similar across plots, except for gulf fritillary larvae, which had higher survival in exotic plots. Monarch caterpillar mortality risk was higher on sentinel plants placed inside plots, relative to those outside of plots.

5. This study suggests that garden plots attracted a diversity of adult butterflies and supported the reproduction of focal species. Given lower immature monarch survival within versus outside of plots, further work is needed to examine natural enemy pressure within pollinator gardens.

Key words. Black swallowtail, butterfly diversity, caterpillar survival, gulf fritillary, host plant selection, monarch, pollinator conservation, queen, weed management.

Introduction

Greater awareness of global-scale declines of insect pollinators has prompted nature enthusiasts to create gardens containing plants attractive to pollinators, with the potential benefit of providing resources to pollinators and promoting their conservation. Planting flowers as sources of nectar and pollen could provide food, counter habitat loss, and bolster pollinator populations by increasing connectivity between fragmented habitat patches (Goddard *et al.*, 2010; Vergnes *et al.*, 2012; Garbuzov & Ratnieks, 2014a). Gardens can also offer resources such as caterpillar host plants for butterflies and nesting sites for native bees (Cutting & Tallamy, 2015). There is some evidence to suggest that pollinator gardens could positively influence the abundance of pollinators and might mitigate the

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impact of habitat loss on biodiversity (Goddard *et al.*, 2010). At the same time, some studies indicate that gardens could serve as 'ecological traps' if they draw pollinators away from higher quality natural habitats or expose them to increased risk of predation, disease, or pesticides (Levy & Connor, 2004; Muratet & Fontaine, 2015; Pereira-Peixoto *et al.*, 2016). Gardens likely attract not only pollinators, but also their natural enemies, including vertebrate and invertebrate predators, parasitoids, and disease. The attraction of enemies might increase if pollinators themselves are aggregated in gardens, and could lead to higher mortality risk (i.e. lower pollinator survival) inside gardens compared to other habitats (Levy & Connor, 2004). Further efforts are therefore needed to explore how garden characteristics, such as plant selection and garden maintenance approaches, affect pollinator fecundity, abundance, diversity, and survival.

Plants selected for gardens can influence which pollinator species are attracted to these habitats (Smith *et al.*, 2006; Shackleton & Ratnieks, 2016). While plant choice depends on individual gardener preferences and access to information and resources, gardens in urban areas tend to be dominated by non-native plants and native cultivars selected for ornamental value, which can have mixed effects on pollinator fitness (McKinney, 2006; Harrison & Winfree, 2015). For example, cultivars and hybrids bred for prolific displays and attractiveness to humans, such as 'doubling' of petals, might offer reduced or less accessible floral rewards for some pollinators (Corbet *et al.*, 2001). Further, non-native plants lacking co-evolutionary history with native pollinators might decrease the plants' usefulness to certain species, particularly to specialist insects that utilise particular plant species as food for adults or larval stages, and that might select plants based on cues such as secondary compounds (Corbet *et al.*, 2001; Novotny & Basset, 2005). Alternatively, non-native plants might be less well defended against herbivory and might be more palatable and offer greater nutrition.

Evidence to date indicates that in planted gardens, native plant species (vs. exotics) are generally associated with greater pollinator abundance, and pollination activity (Fukase & Simons, 2016). For example, suburban gardens with only native plants were shown to have a higher diversity and abundance of caterpillars and birds compared to those with predominately non-native plants, and native plants were estimated to support three times as many butterfly and moth species than exotic plants (Burghardt *et al.*, 2009; Tallamy & Shropshire, 2009). Other studies suggest that pollinators show no foraging preference for exotic or native plants (Chrobock *et al.*, 2013; Garbuzov & Ratnieks, 2014a), as might occur if both plant types offer similar quantity and quality of nectar and pollen. While pollinator foraging preferences have received considerable attention, further work is needed to examine the influence of native versus exotic plants in attracting pollinators and supporting their survival and reproduction.

Homeowners manage garden habitats by weeding, tilling, irrigating, fertilising, and applying pesticides and herbicides (Robbins *et al.*, 2001). Gardening practices such as weeding can impact habitat complexity: a heavily weeded garden might have fewer refuge sites enabling escape from predators and parasitoids and might lack substrates needed for nesting (e.g. some aboveground nesting bees; Karban *et al.*, 2013). At the same time, a garden full of weeds (i.e. a complex habitat) might offer more hiding spots for natural enemies and thereby increase mortality rates (Langellotto & Denno, 2004). In addition, pollinator species that overwinter on standing dead vegetation, leaf litter, or other ground cover might be removed or destroyed during clearing events, which lowers adult abundance in the spring. Indeed, some grassland butterfly species are more abundant in fields with low-intensity (vs. high-intensity) mowing or grazing (Dover *et al.*, 2011; Stuhldreher & Fartmann, 2014). Experimental studies using standardised practices to replicate common practices are needed to examine the impacts of garden management.

In this study, we asked how plant species choice and garden maintenance practices affect butterflies as a highly visible group of pollinators that gardeners often seek to attract and support by planting caterpillar host plants and adult nectar sources (Breeze *et al.*, 2011). Throughout a growing season, we quantified the species richness of adult butterflies and the abundance of all butterfly life stages in experimental garden plots that varied in plant type (either native or exotic plants) and weed maintenance intensity (low or high). In addition, we examined the probability of eggs surviving to last larval stage (instar) for four focal butterfly species. Finally, to test whether survival might be lower inside gardens compared to other suitable habitat patches, for one species (monarch), we assessed the mortality risk of caterpillars on host plants located inside versus outside plots. Based on previously published work (Corbet *et al.*, 2001; Novotny & Basset, 2005; Tallamy & Shropshire, 2009), we predicted that native plant gardens would attract a greater diversity and abundance of butterflies and show evidence for greater reproductive activity (i.e. greater egg and caterpillar counts). We also expected to find higher diversity of butterflies and greater reproductive activity in gardens under low weed maintenance owing to increased habitat complexity. Finally, we predicted that the natural enemy communities (especially predators) might be attracted to garden plots due to higher adult butterfly activity, and thus, we expected higher caterpillar mortality risk inside compared to outside gardens.

Materials and Methods

Study site

The study was carried out at the Wormsloe Historic Site in Savannah, Georgia, USA (31.9647°N, 81.0706°W;

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Fig. 1), where we established experimental garden plots in Spring 2013. The 135-hectare site is located on an inshore coastal island and is dominated by forest habitat with open grass areas that are mowed every 1–2 weeks during the growing season. The immediate boundaries of the open grass areas consist of a mixed deciduous–pine forest, while the matrix on larger scale (i.e. within 1.5 km) consists of herbaceous wetlands, open water, and developed areas (Homer *et al.*, 2015). Climate in this area is humid subtropical, with long summers, mild winters, and low frequency of freezes. Based on the regional checklist of Butterflies and Moths of North America database (Lotts & Naberhaus, 2016), a total of 108 butterfly species have been sighted in this region (i.e. Chatham County, Georgia), and thus, this location is well suited for addressing our research goals.

Experimental design

A total of 12 experimental plots (7.6 m by 15.2 m) were established within the site's open grass areas. Plots were organised within three mowed grass areas (referred to as blocks hereafter) separated by approximately 250 m and arranged to receive equal amount of sun (Fig. 1). The mowed grassy areas generally lacked forbs. Within each block, plots were at least 20 m apart (but no more than 88 m apart) and were surrounded by mowed grass on all sides. Proximity of the plots resulted in a common adult butterfly pool for all plots: adult butterflies could readily move between plots and blocks. Plots were fenced (to a height of 2.3 m with 4.5 × 5 cm grid plastic mesh) to prevent deer herbivory and irrigated with an automatic system. Each plot contained a total of 128 individual plants selected from a set of 13 species, including nectar plants and lepidopteran host plants, with equal number of plants per species per plot (list of plant species is provided in Appendix S1: Table S1). Plants were arranged in an 8 by 16 matrix with randomly assigned positions. Within each block, we employed a 2-by-2 factorial design, where factors included plant type (native or exotic) and weed maintenance intensity (low or high).

Native plots contained plants native to Georgia, USA, with the exception of one species, Bronze fennel (*Foeniculum vulgare*), and exotic plots had plants not native to the United States (Appendix S1). *Foeniculum vulgare* was added to the native plots because soon after garden establishment, we noted that the black swallowtail (*Papilio polyxenes* Fabricius, 1775, Family: Papilionidae) did not appear to oviposit on the original native host plant species chosen. To maintain an equal number of species and plants across treatments, a second non-native black swallowtail host plant was also added to the exotic plots (Appendix S1). Plant choice was based on species known to tolerate sandy soil and full sun, availability from local nurseries in ample quantities, and either the presence of bright-coloured, nectar-producing flowers, or suitability as caterpillar host plant for one of four target species known to inhabit this area: black swallowtail, gulf fritillary (*Agraulis vanillae* Linnaeus, 1758, Family: Nymphalidae), queen (*Danaus gilippus* Cramer, 1776, Family: Nymphalidae), and monarch (*D. plexippus* Linnaeus, 1758, Family:

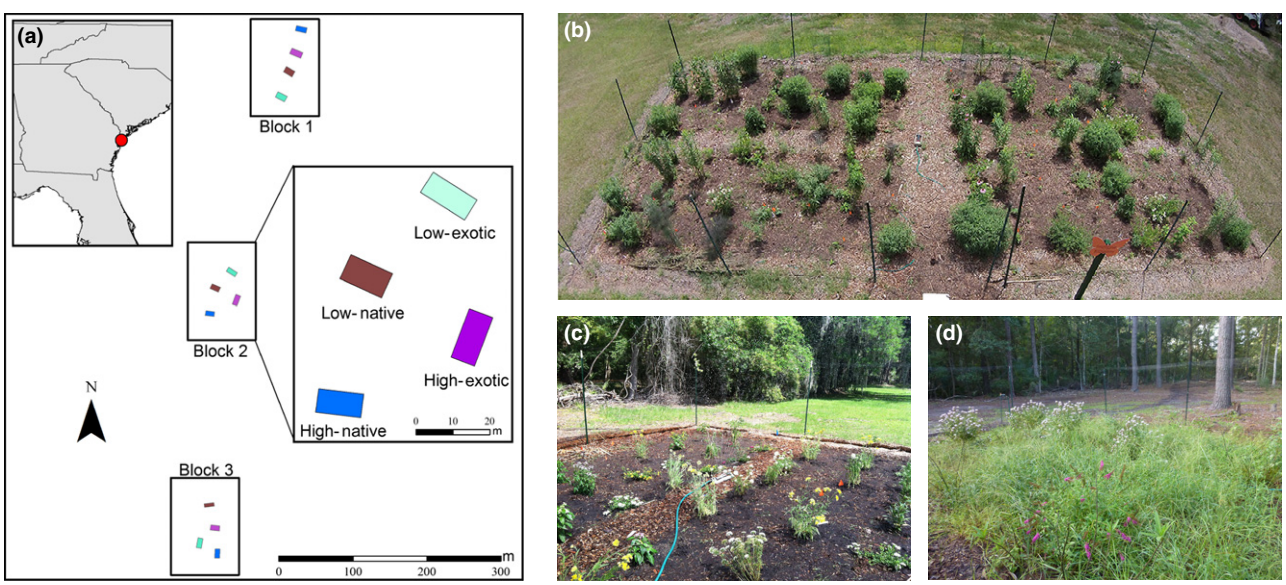

Fig. 1. (a) Location of study site near Savannah, Georgia, USA, and a schematic of the experimental layout at the site. Twelve plots (7.6 m by 15.2 m) are organised into three replicate blocks, and within each block, a two-by-two factorial design was employed, where factors included plant type (all native or all exotic plants) and weed maintenance (low or high). (b) Aerial photograph of a native plant species plot in May 2014. (c, d) Photographs of garden plots with (c) high and (d) low weed maintenance intensity.

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Nymphalidae). Each plot type had one host plant species for monarchs and queens (15 plants per plot), one host plant species for gulf fritillaries (five plants per plot), and two host plant species for black swallowtails (10 plants per species per plot). Caterpillar host plant species selected for the study did not include horticulture cultivars, hybrids, or varieties in order to provision butterflies with resources similar to those encountered in the wild. Host plants for the four focal butterfly species were absent in the areas surrounding the plots and study site (A. Majewska, pers. obs.). Thus, the plots most likely represent isolated habitat patches for the focal species, with adult butterflies attracted from other locations.

In May 2014, plots were weeded and mulch was applied. Weeding, which consisted of hand pulling, mechanical trimmers, and spot glyphosate application, was executed every other month in low maintenance and every other week in high maintenance plots. At the beginning of each month (with exception of May), before weeding of a plot, we estimated the per cent weed cover of each plot's total surface area, using 2D photograph images taken above the plots with an unmanned aerial vehicle (Drone, DJI Phantom1). Specifically, the per cent of area per plot occupied by plants that were not part of the study design was visually estimated from the photographs as 0, 1–25, 26–50, 51–75, or 76–100%. As the garden plots were established in areas previously maintained as grassy fields, weeds predominantly consisted of native and exotic grasses. On a monthly basis, we also recorded the number of individual plants that were actively flowering in each plot.

Adult butterfly diversity and abundance estimates

The number and species identity of each adult butterfly seen during a 7-min interval were recorded in each plot via a point count and a meandering walk. Because adult butterflies could readily move between proximate plots, we restricted count time to 7 min to minimise duplicate counting of the same individuals. Counts were made between 1000 and 1400 h, by standing within 5 m of a plot for 5 min, followed by an even paced walk on the central paths of the plot for 2 min to assure that butterflies hidden behind vegetation were counted. Each plot was observed at each sampling interval, and the order of plot observations was randomised. Species identification was aided by binoculars. Because we did not net the butterflies, it is possible that this method underestimated small butterfly species diversity, as these species are more difficult to spot from a distance. Previous studies showed strong positive correlations between a similar method, namely Pollard counts (Pollard & Yates, 1994), and species' abundance estimates based on capture–mark–recapture studies (Pollard, 1979). Owing to outside constraints, counts were performed from May to September between one and four times each month, with counts for all plots occurring on the same observational day and during clear weather with temperatures above 20°C. Monthly species richness per plot was calculated as the sum of species seen per plot per month, and the variation in frequency of counts was accounted for in statistical analyses described below. Because analyses of two other diversity measures (Simpson's index and Shannon–Weaver index) showed nearly identical results to analyses of species richness, we report only species richness results below. We estimated monthly abundance of all butterfly species collectively, and for each of the four target species separately, as the total number of individuals seen per plot per month. As before, variation in number of counts was accounted for in statistical analyses.

Egg and caterpillar counts

Caterpillar host plants were monitored weekly, at end of each week, from mid-May to early August 2014, and once a month in late August and late September 2014, for eggs and caterpillars of four focal species noted above. We randomly selected five plants per species per plot and scanned all leaf surfaces, stems, buds, and flowers for eggs and caterpillars of the target butterfly species. In a few cases, less than five plants were checked owing to unexpected deer herbivory. In another instance, due to observer error, additional plants were checked 1 week. Thus, the range of checked plants was 2–14 per target species per week, and we accounted for this variation in statistical analyses described below. We recorded separately the number of eggs, small larvae (instars 1–3), and large larvae (instars 4–5) per plant.

Egg survival estimates

During a 6-week period from mid-June to late July, we followed the fate of eggs on a subset of 2–5 marked caterpillar host plants per focal butterfly species per plot. Plants were marked with a unique identifier to survey the same plants. To estimate the proportion of eggs that survived to last stage of larval development, we followed Nail *et al.* (2015) by comparing the number of eggs on the marked plants 1 week, to the number of instar 5 larvae present on the same marked plants 2 weeks later (which accounts for the estimated time needed for larval development in the field, assuming a constant degree-day model and similar development time for each focal species). As lepidopteran rate of development is temperature dependent (Zalucki, 1982), this approach might underestimate survival, because some observations of instar 5 might be missing if development is faster than expected during a given observation period. It is also important to note that caterpillars can leave their natal host plant in search of other host plants. Data from one individual plant (exotic plot with high weed maintenance) were excluded because the instar 5 gulf fritillary larvae count exceeded the egg count recorded 2 weeks prior.

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Monarch sentinel plant experiment

We tested for differences in larval mortality by placing monarch caterpillars on sentinel host plants set within versus outside the plots in July 2014. Two potted swamp milkweed plants (*Asclepias incarnata*) were positioned inside each of the 12 plots, and at an additional 16 locations outside of the plots, between 5 and 700 m from the nearest plot. The outside-plot locations were within open grassy areas and at the forest edges of these open areas of the site, where the milkweed plants could naturally grow (although were not detected). Plants were glasshouse-grown and of equal age, height, and foliage. Caterpillars were the outcrossed grand-progeny of wild monarchs originally collected from St. Marks, Florida, USA, during the fall migration in October 2013. We placed 2–4 first-instar caterpillars (reflective of densities observed earlier in the season and synchronised to emergence date) on each plant and monitored their daily presence on plants until they reached instar 5. For each pair of plants, one was placed in a 2 l tub of water and Tanglefoot™ was applied to the rim of the pot to exclude non-flying natural enemies (predominantly ants); the second plant was placed directly on the ground. For plants placed outside of plots, we surrounded them with a 1-m-diameter netting fence (2.5 cm mesh and 1.5 m tall) to prevent deer herbivory. Plants were spaced so as to not contact each other or the netting. Upon completion of the experiment, all instar 5 caterpillars were collected, brought back to an onsite laboratory, and raised to emergence in individual 0.5 l containers to quantify parasitoid attack rate.

Statistical analyses

We used R programming software for statistical analyses (R Core Team, 2017). We first asked which factors predicted adult butterfly diversity and abundance (all taxa combined) per plot as response variables. Predictors in the model were plant type (exotic vs. native), weed maintenance (low vs. high), the two-way interaction, month (linear and quadratic terms to account for nonlinearity), and the number of flowering plants per plot. We included block (1, 2, or 3) as a random effect. As counts made during one observation interval might depend on the counts of previous observation interval, we added a first-order autoregressive component (AR1). Specifically, prior to analysis, we calculated the autoregressive term as the natural log of the count observed previous time step plus 1 [i.e. $\log_e$ (previous count +1)]. Counts for time steps prior to the start of data collection (i.e. before May 1) were assumed to be zero. To determine the most suitable probability distribution for the models, we used package *fitdistrplus* (Delignette-Muller *et al*., 2010). Based on the Cullen and Frey graphs (skewness–kurtosis plots) as well as goodness-of-fit statistics of response data, we used negative binomial errors for models of adult abundance, species richness, and egg and caterpillar counts data as response variables. All model fits were confirmed via quantile comparison plots of the residuals using *plotresid* function of *RVAideMemoire* package (Hervé, 2015). A lack of temporal autocorrelation in residuals was confirmed using *acf* and *pacf* functions of *forecast* package (Hyndman *et al*., 2017). We fitted generalised linear mixed-effects models (GLMM; *lme4* package; Bates *et al*., 2014) and used an offset to account for variation in the number of observations made each month. We repeated the GLMM analysis on adult abundance for each of the focal species (Table 1). Due to counts of adult queens equal to zero in June and July, month was included only as a linear term for this species to avoid overfitting.

Next, we assessed which factors predicted egg and caterpillar counts for each focal butterfly species. We tested the effects of plant type, weed maintenance, interaction between plant type and weed maintenance, the number of flowering plants per plot, and linear and quadratic terms of week of year. As before, block was included as a random effect and first-order autoregressive term (AR1) was added. Week of year was used in these models because the frequency of sampling varied over the season (e.g. weekly early season and biweekly late season). Owing to a high number of zeros in the egg and caterpillar count data, we employed the function *glmmadmb* (*glmmADMB* package; Skaug *et al*., 2011), with zero-inflated negative binomial error structure and log-link function to account for overdispersed data with an excess of zeros (Zuur *et al*., 2009; Bolker *et al*., 2012). To account for varying sampling effort, we used an offset equal to the log-transformed number of checked plants per plot. As queen eggs are indistinguishable from monarch eggs with a naked eye, we analysed egg count data for these two species together (although we note that given the low number of queen caterpillars relative to monarchs, the combined count was likely dominated by monarchs). The model for monarch larvae required Poisson error structure to avoid overfitting.

We also asked whether estimated egg survival to instar 5 for the focal species was predicted by plant type, weed maintenance, the interaction between plant type and weed maintenance, and the number of flowering plants per plot. We assessed differences in per plant egg survival probability of each of the four species separately via logistic regression models. Survival was modelled as a binary response equal to the survival and mortality totals of individuals during a 2-week monitoring period, with plant ID number, plot, and block set as random effects to account for repeated estimates from the same marked plants, plots, and blocks. To avoid overfitting, for monarch and queen egg survival models, we only included the random effect of plot, as all estimates were derived from unique plants. Given that caterpillars might move away from natal host plants and settle on other host plants, we repeated the analysis at the plot level, where survival was modelled as a binary response equal to the survival and mortality totals of individuals per plot during a 2-week monitoring period, with plot and block set as random

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Table 1. Summary of the most parsimonious models (after global selection) for the response variables of adult species richness, adult abundance (all taxa combined), adult abundance for each focal species, and egg and caterpillar abundance of four focal species (monarch, queen, gulf fritillary, black swallowtail). Independent variables tested were plant type, weed maintenance, the two-way interaction, time (both linear and quadratic effects), and the number of flowering plants. Time for models using adult data was month, and for egg and caterpillar data, week of year. Block was included as a random effect in all models, and we accounted for temporal autocorrelation among plots with first-order autoregressive term.

	Plant type (native)	Weed maintenance (low)	Plant type x weed maintenance	Time	Time^2	Number of flowering plants
Adult species richness	ns	ns	//	*** ↑	***	* ↑
Adult abundance						
All taxa	ns	ns	//	*** ↑	***	*** ↑
Monarch	***↓	ns	//	*** ↑	***	ns
Queen	ns	ns	//	//	//	//
Gulf fritillary	*↓	ns	*	*** ↑	***	//
Black swallowtail	ns	ns	//	*** ↑	***	//
Egg counts						
Monarch & Queen	* ↓	ns	//	//	//	//
Gulf fritillary	ns	ns	//	*↓	**	//
Black swallowtail	ns	ns	ns	*** ↑	***	//
Caterpillar counts						
Monarch	ns	ns	//	ns	ns	//
Queen	ns	ns	//	* ↑	ns	//
Gulf fritillary	ns	ns	//	ns	***	//
Black swallowtail	** ↑	ns	//	*** ↑	***	* ↑

Each row summarises a model for a different response variable. 'ns' represents a non-significant term, and '//' indicates that the variable was not included in the most parsimonious model. '↑' and '↓' represent a positive and negative significant effect for linear terms only, respectively, and asterisks denote the *P*-value, $*P < 0.05$, $**P < 0.01$; $***P < 0.001$. For full model results, see Appendix S2: Tables S1–S5.

effects to account for repeated estimates. Because the two approaches yielded nearly identical results, we only report on the results of plant level analyses.

For all analyses, we began with a full model and performed model selection using the function *dredge* (*MuMIn* package; Bartoń, 2017). Because we had *a priori* hypotheses regarding plant type and weed maintenance, and due to temporal autocorrelation of the data, plant type, weed maintenance, and the autoregressive term (AR1) were terms retained in all models, while other explanatory variables were run in all possible combinations. The model with lowest AICc was selected as the most parsimonious model (Table 1; Appendix S2: Tables S1–S5). Models within two AICc of the top model were considered having equivalent levels of support and therefore competitive (Burnham & Anderson, 2003). We present results for the single best model selected (lowest AICc) in the main text, and other competitive models are reported in Appendix S2: Tables S6–S9.

To examine predictors of monarch larval mortality on sentinel plants, we used a Cox proportional hazards model (*survival* package; Therneau & Lumley, 2017) with repeated events to estimate per plant differences in hazard rates, assuming that caterpillars placed on the same plant were not independent from each other. Specifically, we used time to caterpillar loss as the outcome and stratified on the event number (i.e. number of caterpillar disappearances). Explanatory variables included plant placement (whether the plant was inside or outside of a plot), terrestrial predator exclusion (whether the plant was treated to exclude terrestrial predators), and the log-transformed distance from nearest plot (the latter term was non-significant and excluded from further analysis). In a separate analysis, we examined data from plants placed within plots only and tested whether plant type and weed maintenance influenced survival. Due to unexpected deer herbivory on sentinel plants during the experiment, six plants placed within three plots were excluded from analyses.

Results

General results

We observed adult butterflies in all plots, totalling 312 adults over the course of the season, representing 22 species of Lepidoptera (see Appendix S1: Table S2 for the full species list; Table S3 for summary of focal species counts). Collectively, adult butterflies recorded at these plots captured 20% of all butterfly species recorded in Chatham County, Georgia (Lotts & Naberhaus, 2016). The six most abundant adult butterflies were the gulf fritillary (*A. vanillae,* 34.3%), monarch (*D. plexippus,* 27.9%), Palamedes swallowtail

(*Papilio palamedes* Drury, 1773, Family: Papilionidae 16.2%), queen (*D. gilippus,* 10.6%), cloudless sulphur (*Phoebis sennae* Linnaeus, 1758, Family: Pieridae 5.3%), and black swallowtail (*P. polyxenes,* 3%); collectively, these represented 97.3% of all individual butterflies observed in the plots and included our four focal species. Abundance and species richness of adults tended to increase over the course of the study and peaked in August (Fig. 2a).

Adult butterfly species richness

Plant type, weed maintenance, and the autoregressive term were retained for model selection and therefore are present in all most parsimonious models for adult butterflies. The most parsimonious model of adult butterfly species richness showed a significant influence of month (linear and quadratic terms; Table 1, $P < 0.001$), with butterfly species richness peaking in August (Fig. 2a) and showing a downward trend from August to September. The number of flowering plants was also included in the most parsimonious model for butterfly species richness and showed a positive effect (Fig. 2b; Appendix S2: Table S1; $z = 2.01$, $P < 0.05$). Plant type and weed maintenance were not significant predictors of adult butterfly species richness (Table 1; $P > 0.05$).

Adult butterfly abundance

The most parsimonious model of adult butterfly abundance for all taxa included month (both linear and squared terms) and the number of flowering plants (Fig. 2b; Table 1). Plant type and weed maintenance were not significant predictors of adult abundance. Adult abundance increased with time and both linear and nonlinear terms were significant (Fig. 2a; Table 1; $P < 0.001$). More adult butterflies were found in plots with a greater number of flowering plants (Fig. 2b; $z = 4.28$, $P < 0.001$).

Analyses of focal species adult abundances (tested separately) also showed nonlinear relationships with time: monarch, gulf fritillary, and black swallowtail abundances tended to peak at intermediate time points and decrease thereafter (both linear and quadratic time terms were significant; Table 1; $P < 0.001$). Monarch abundance showed a significant relationship with plant type, with more adult monarchs in exotic plots ($z = 2.83$, $P < 0.01$), and no relationship with weed maintenance (Table 1). Monarch abundance also increased with the number of flowering plants, although this effect was nearly significant ($z = 1.9$, $P = 0.058$). The best supported model of adult queen abundance included only plant type and weed maintenance, which were not significant predictors (Fig. 3; Table 1; $P > 0.05$). Similarly, plant type and weed maintenance were not significant predictors of adult black swallowtail abundance (Fig. 3). Model selection indicated that adult gulf fritillary abundance was predicted by plant type and the interaction between plant type and weed maintenance

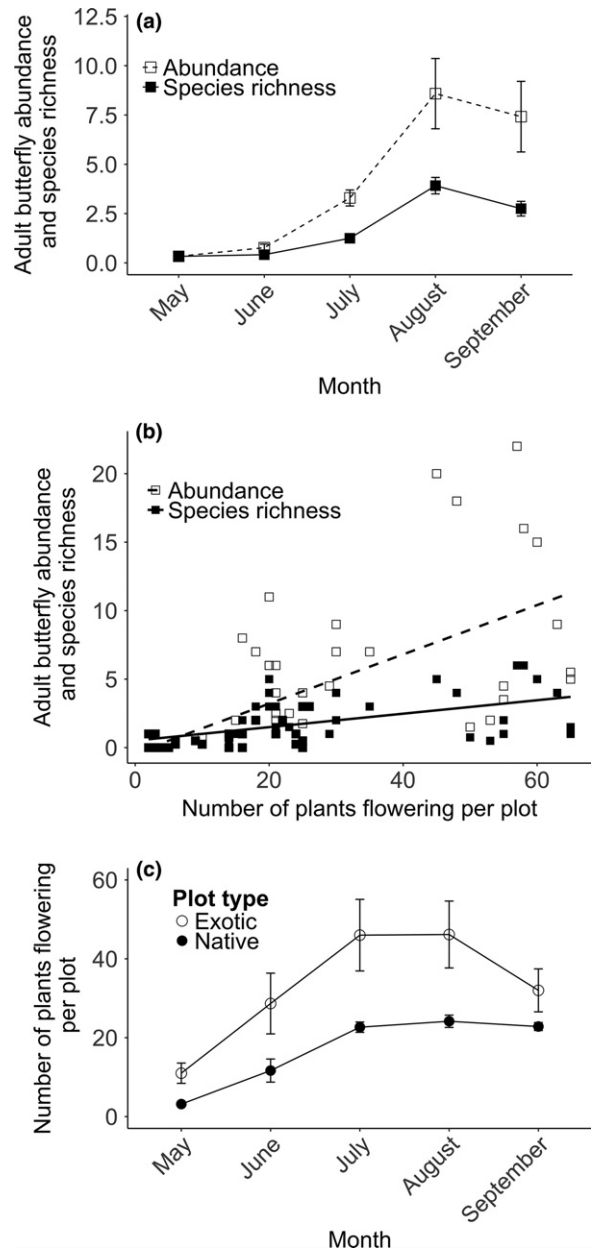

Fig. 2. Average monthly adult butterfly abundance (open squares) and species richness (closed squares), calculated as the sum of adult butterflies or number of species observed in a plot, divided by number of observation periods per month, for all plots (a) over time and (b) relative to number of flowering plants per plot. (b) Each point represents the number of adult butterflies or species richness observed in a plot and the corresponding number of flowering plants. Lines show the least-squares fit for abundance (dashed line) and species richness (solid line). (c) Mean number of flowering plants per month for exotic (open circles) and native (closed circles) garden plots. Error bars represent ± SE.

(Table 1; Fig. 3). More gulf fritillary adults were found in exotic plots ($z = 2.60$, $P < 0.01$), and the fewest adults were recorded in native plots with high weed maintenance

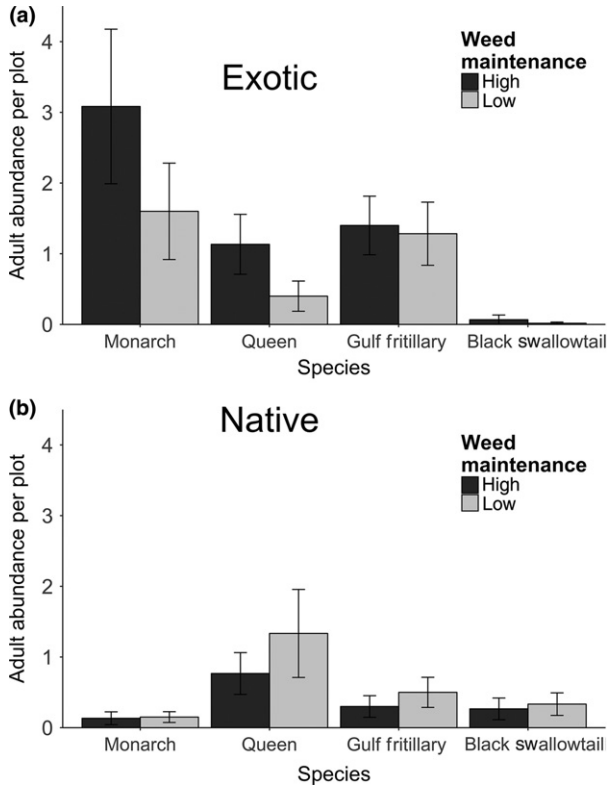

Fig. 3. Adult butterflies in garden plots. Mean adult butterfly abundance (number of butterflies per plot), grouped by weed maintenance regime for monarchs, queens, gulf fritillaries, and black swallowtails, in (a) native and (b) exotic plots. Dark bars represent high weed maintenance and grey bars represent low weed maintenance. Error bars are ± SE.

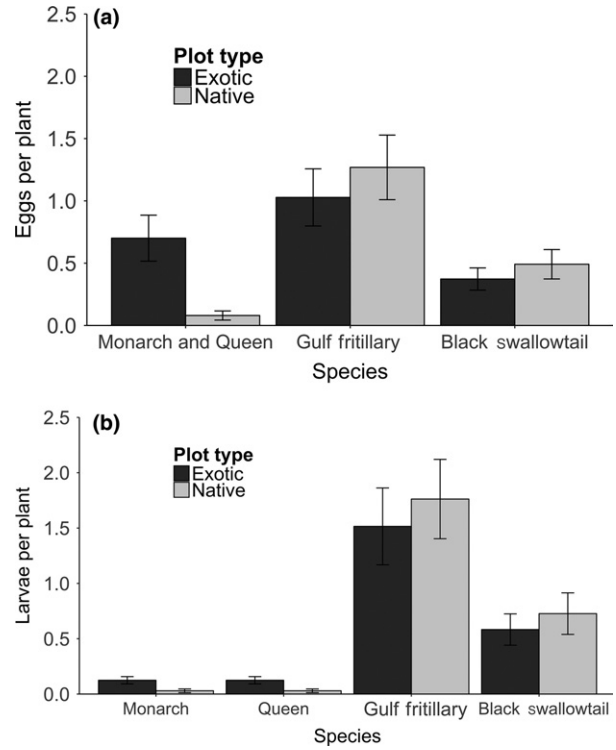

Fig. 4. Immature stages per plant in the garden plots. (a) Mean egg count for monarchs and queens combined, gulf fritillaries, and black swallowtails in relation to plot type (native or exotic). (b) Mean egg count for monarchs, queens, gulf fritillaries, and black swallowtails in relation to plot type. Dark bars represent exotic plots, and grey bars represent native plots. Error bars represent ± SE.

(Fig. 3; $z = 2.02$, $P < 0.05$). A follow-up analysis of gulf fritillary abundance that included the per cent weed cover per plot (in place of weed maintenance treatment) showed no significant main effect or interaction between plant type and weed cover ($z = 0.473$, $P = 0.64$).

Egg and caterpillar counts

A total of 2354 plant checks were performed, at which we found 1327 lepidopteran eggs and 1499 larvae of the four focal species (Appendix S1: Table S3). Pre-adult life stages (egg, caterpillar, and pupa) of each of the four focal species were present in all of the plots; however, we found no black swallowtail eggs or caterpillars on golden Alexander (*Zizia aurea*) in the native plots or on Queen Anne's lace (*Daucus carota*) in the exotic plots. Data from these two plant species were not included in the analyses.

Plant type, weed maintenance, and the autoregressive term were included in all of the most parsimonious egg and caterpillar count models. For monarch and queen egg counts, the most parsimonious model showed that plant type was a significant predictor, with higher numbers of monarch and queen eggs in exotic compared to native plots (Fig. 4a; Table 1; $z = 2.49$, $P < 0.05$). No other species' egg counts varied with plant type or weed maintenance (Table 1). Week of year (both linear and squared terms; Table 1) significantly predicted egg counts for gulf fritillaries. Black swallowtail egg and caterpillar counts also increased initially over time and then decreased, and both the linear and squared week of year terms were significant (Table 1; Appendix S1: Fig. S1). Black swallowtail caterpillar counts were further influenced by plant type, with higher quantities in native versus exotic plots (Fig. 4b; $z = 2.61$, $P < 0.01$) and by the number of flowering plants, such that greater counts were found in plots with more flowering plants (Table 1; $z = 2.16$, $P < 0.05$).

Egg survival within garden plots

The proportion of eggs surviving to larval instar 5 was 0.05 ± 0.04 for monarchs and queens ($n = 14$ plants), 0.13 ± 0.03 for gulf fritillaries ($n = 70$ plants), and 0.02 ± 0.01 for black swallowtails ($n = 56$ plants). Egg survival of monarchs and queens (analysed together) and black swallowtails was not predicted by plant type or weed maintenance, and no other tested variable was included in the most parsimonious model (Appendix S2: Table S5).

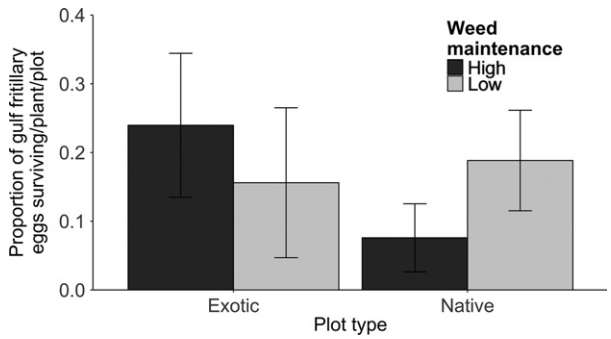

Fig. 5. Proportion of gulf fritillary eggs surviving to last larval development stage per plant grouped by plant type and weed maintenance. Total of $n = 13$ and 10 plants were followed in exotic plots with high and low maintenance, and $n = 28$ and 19 plants were followed in native plots with high and low maintenance, respectively. Error bars represent ± SE.

Gulf fritillary egg survival was influenced by plant type and the interaction between plant type and weed maintenance, with higher survival in exotic plots (Fig. 5; $z = 3.16$, $P < 0.01$), and higher than expected survival in plots with both exotic plants and high weed maintenance (Fig. 5; $z = 2.74$, $P < 0.01$; Appendix S2: Table S5). A follow-up analysis that included the per cent weed cover per plot showed the same relationship: highest survival in plots with exotic plants and lower weed cover ($z = 2.84$, $P < 0.01$).

Monarch sentinel plant experiment: outside vs. inside garden plots

Cox proportional hazard analysis of monarch caterpillar survival on sentinel plants showed a significant influence of plant placement (inside vs. outside plots) on the probability of mortality ($z = 2.73$, $P < 0.01$), while terrestrial predator exclusion had no effect ($z = 1.49$, $P = 0.14$). Specifically, mortality rate was 51% lower mortality on plants placed outside versus within garden plots (hazard ratio = 0.51, $n = 61$, 0.32–0.83; 95% CI). Model diagnostics using the scaled Schoenfeld residuals showed no violation of the proportional hazard assumptions for the model ($\chi^2 = 0.93$, $P = 0.63$). We also examined whether monarch caterpillar survival differed based on plant type and weed maintenance for plants placed within the plots, but neither of these variables predicted mortality risk (plant type: $z = 1.16$, $P = 0.25$; weed maintenance: $z = -0.11$, $P = 0.91$). All instar 5 caterpillars collected at the completion of the experiment survived to adulthood and no parasitoids were detected.

Discussion

Adult butterfly species richness and abundance

Our results showed that a high diversity of adult butterflies visited experimental garden plots, and that plot characteristics (here defined as native or exotic plants and low or high weed maintenance) did not strongly influence adult butterfly species richness or abundance. These results, combined with previous work on other pollinator species, indicate that pollinator response to garden practices is likely to be taxon-specific and that factors other than native versus exotic planting schemes might influence the diversity of pollinators found in gardens (e.g. Smith *et al.*, 2006). It is important to note that additional factors such as garden size, types of blooming plants, and the surrounding landscape characteristics, including degree of urbanisation, can also affect butterfly diversity (Di Mauro *et al.*, 2007; Bergerot *et al.*, 2010; Matteson & Langellotto, 2011). In a garden context, flower abundance has been shown to increase the species richness of various pollinators, including butterflies, bees, and wasps (Matteson & Langellotto, 2011; Pardee & Philpott, 2014; Quistberg *et al.*, 2016). Consistent with previous work, our study showed that the number of individual plants flowering at a given time predicted greater butterfly species richness.

Garden plot characteristics examined here did not predict differences in total adult butterfly abundance, counter to expectations that plots with native plants and more weeds would attract more butterflies. Many butterfly species are classified as nectar plant generalists (Scott, 1992) and therefore might not show preferences for nectar plant type. Our findings that a higher number of actively flowering plants predicted greater butterfly abundance agrees with a previous study on the cabbage white butterfly (*Pieris rapae*; Matteson & Langellotto, 2012), as well as studies on bees which were also more abundant in gardens with more plants in flower (Frankie *et al.*, 2005; Pardee & Philpott, 2014; Salisbury *et al.*, 2015). Other factors such as flower density and the size of floral displays, diversity of colours, chemical cues, nectar volume, and sugar concentration can affect insect attraction and activity (Bergerot *et al.*, 2010; Chrobock *et al.*, 2013), but were not measured here.

Analyses of the four focal butterfly species showed that more monarch and gulf fritillary adults were observed in plots with exotic plant species. The presence of highly attractive plant species with larger and brighter floral displays, such as butterfly bush (*Buddleia davidii*) present in the exotic plots, may have influenced monarch and gulf fritillary abundance (Corbet, 2000; Matteson & Langellotto, 2011). Also, exotic ornamentals tend to bloom over a longer duration (Garbuzov & Ratnieks, 2014b), a trend we observed in our study plots. One explanation for more monarchs in exotic plant plots could be their attraction to non-native tropical milkweed, *Asclepias curassavica*, used for nectar and as a caterpillar host plant. Male monarchs exhibit territorial behaviour during the breeding season and defend milkweed patches (Zalucki, 1993) and appeared to defend exotic plots more regularly in this study (A. Majewska, pers. obs.).

For gulf fritillary abundance, we further found a significant interaction between plant type and weed

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maintenance, with the greatest number of adults in plots with both exotic plants and fewer weeds. It is possible that nectar and host plants were more visible in the weeded plots or that the weeded plots offered fewer hiding places for predators. In addition to avian predators, invertebrate predators such as spiders, wasps, and praying mantids (seen in plots in this study) might be better hidden in gardens filled with weeds, causing butterflies to avoid these sites. Interestingly, gulf fritillary egg survival to the last stage of larval development was also highest in exotic plots with more intense weeding, suggesting that adults might be choosing to visit sites with lower predation risk. Assessments of adult survival in addition to measures of predator abundance and the characteristics of weedy gardens, however, are needed to further explore these mechanisms.

Egg and caterpillar abundance and survival

Butterfly egg and larval stages were found in all plot types examined, yet not all host plant species were equally used. Black swallowtail immature stages were not detected on two of the four available host plants, despite previous reports of use in other studies and butterfly garden guides (Erickson, 1975; Black *et al*., 2016). A particularly interesting pattern was noted for monarchs and queens, for which nine times as many eggs were laid on plants in exotic compared to native plots (Fig. 4a). This pattern might be caused by chemical features of the non-native tropical milkweed, which is heavily defended by a high diversity and concentration of cardenolide toxins, which monarch and queen caterpillars sequester, rendering them unpalatable to predators through early adulthood (Malcolm & Brower, 1989; Agrawal *et al*., 2015). Monarchs are known to oviposit on milkweeds with greater cardenolide concentrations (Roeske *et al*., 1976). By comparison, the native *A. incarnata* used in this study has low levels of cardenolides (Malcolm, 1991). Monarchs have also been shown to use cardenolides against infection by the specialist protozoan *Ophryocystis elektroscirrha*, with infected female monarchs preferentially laying eggs on *A. curassavica* versus less toxic milkweed species, and caterpillars that feed on more toxic milkweeds developing lower parasite loads as adults (Lefèvre *et al*., 2010; Lefevre *et al*., 2012; Sternberg *et al*., 2012). Thus, owing to its secondary compounds, *A. curassavica* might have received higher oviposition by monarchs over native *A. incarnata*, which likely contributed to the greater abundance of monarchs in exotic versus native plots.

In addition to greater secondary compounds, *A. curassavica* grew faster and taller than the native *A. incarnata* and flowered throughout the entire observation period, whereas *A. incarnata* grew more slowly, flowered mainly in July, and naturally senesced starting in mid-September. This lack of seasonality exhibited by the non-native milkweed when planted in mild climates has been linked to high prevalence of *O. elektroscirrha* by fostering year-round breeding behaviour in monarchs (Satterfield *et al*., 2015, 2016). Thus, while we show that *A. curassavica* is attractive to monarchs, planting this non-native milkweed within the United States has been discouraged owing to its lack of seasonality and contribution to elevated infection prevalence in monarchs inhabiting areas with mild winter climates (Satterfield *et al*., 2015, 2016).

Monarch and queen egg densities documented in our plots were relatively high compared to other sites (e.g. the Midwestern United States in mid-summer) monitored by citizen scientists through the Monarch Larva Monitoring Program (www.mlmp.org). At our site, monarch egg density averaged 0.39 eggs per plant (0.08 eggs per plant for native *A. incarnata* and 0.70 eggs per plant for non-native *A. curassavica*), and maximum egg densities at the end of the monitoring period were even higher (1.49 eggs per plant in September). By comparison, in the Midwestern United States, monarch egg densities are approximately ten times lower (0.043 eggs per plant during the peak summer breeding months; Nail *et al*., 2015). While high egg numbers might seem beneficial for conservation, greater egg and larval densities could lead to greater intraspecific competition among larvae and higher pressure from natural enemies such as predators, parasitoids, and disease (Altizer & de Roode, 2015; De Anda *et al*., 2015; Oberhauser *et al*., 2015). Indeed, the proportion of monarch and queen eggs surviving to last stage of larval development at our site was slightly lower (5%) than reported by citizen scientists (8%; Nail *et al*., 2015).

Weed maintenance and plant type did not influence egg survival probability of focal butterfly species in this study, with one exception: gulf fritillary immature survival was higher in exotic compared to native plots. In this case, the non-native *Passiflora* host plant used in this study might offer antipredator defences to gulf fritillaries, such as toxic secondary compounds used in caterpillar defence. Indeed, *Passiflora* spp. vary in their levels of toxic cyanogenic glycosides, which are accumulated by larvae of related *Heloconius* butterflies and used as defence against predators (Spencer, 1988; Hay-Roe & Nation, 2007). The significant interaction between plant type and weed maintenance on gulf fritillary immature survival could indicate complex interactions between plant chemistry and predator communities, and further work is needed to examine the causes of mortality and how those vary with garden traits.

The potential attraction of natural enemies to butterfly gardens was supported by our finding that monarch survival on sentinel milkweed plants was lower within (versus outside) of garden plots. Exclusion of terrestrial predators (most likely ants, spiders) did not influence mortality risk of monarch caterpillars, suggesting that flying invertebrates such as wasps, hemipterans or mantids, or small vertebrate predators such as passerine birds, might have caused most of the mortality (Oberhauser *et al*., 2015). Because sentinel plants outside of gardens were in mowed grassy habitat, the general lack of forbs in the surrounding plant community might have attracted fewer predators and increased caterpillar survival. Nonetheless, previous

work suggests that gardens can have altered predator communities and higher predation risk. For example, bird predation on all stages of cabbage butterflies (*Pieris rapae* and *P. brassicae*) was greater in gardens, whereas in an agricultural field, eggs and larvae were mainly preyed upon by arthropods (Baker, 1970). In another study, survival of eggs of the pipevine swallowtail (*Battus philenor*) was lower on caterpillar host plants in gardens than at sites where those plants occur naturally (Levy & Connor, 2004). On the other hand, Cutting and Tallamy (2015) showed no difference in survival of subadult stages of monarchs between gardens and natural sites. These mixed results point to the need for further work to identify predators and examine predation activity in gardens and other habitats utilised by butterflies for reproduction.

Concluding remarks

As pollinators continue to experience habitat loss, pollinator-friendly gardens could offer increasingly valuable breeding and foraging habitat for butterflies. Results of this study showed that a diverse assemblage of butterflies was attracted to all plots and that targeted butterflies used host plants in all plot types for reproduction. While we did not find differences in overall butterfly abundance and species richness between native and exotic plots, it is important to note that native plants have ecological value beyond serving as foraging resources to butterflies, such as local adaptation to regional climate and soil conditions. Further, native plants can support larger and more diverse arthropod communities, which might have cascading effects on multiple trophic levels (Burghardt & Tallamy, 2013). Unexpectedly, our work showed that monarch and gulf fritillary abundances were higher in exotic plant gardens, possibly owing to greater floral displays, and for monarchs, probably owing to more attractive host plant species. The lower survival of caterpillars within garden plots suggests that further study is needed to determine whether gardens offer a net benefit for butterfly conservation, or whether they might attract butterflies but produce fewer individuals than might otherwise be supported by natural habitats.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12286:

Appendix S1. Additional information on methods and general results of the study.

Appendix S2. Tables including full results of the most parsimonious models and ranking of competitive models.

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