Oecologia (2013) 172:823–832
DOI 10.1007/s00442-012-2537-z

PLANT-ANIMAL INTERACTIONS - ORIGINAL RESEARCH

Fitness costs of butterfly oviposition on a lethal non-native plant in a mixed native and non-native plant community

Mifuyu Nakajima · Carol L. Boggs · Sallie Bailey · Jennifer Reithel · Timothy Paape

Received: 15 August 2012 / Accepted: 13 November 2012 / Published online: 20 December 2012
© Springer-Verlag Berlin Heidelberg 2012

Abstract Non-native plants may be unpalatable or toxic, but have oviposition cues similar to native plants used by insects. The herbivore will then oviposit on the plant, but the offspring will be unable to develop. While such instances have been described previously, the fitness costs at the population level in the wild due to the presence of the lethal host have not been quantified, for this or other related systems. We quantified the fitness cost in the field for the native butterfly *Pieris macdunnoughii* in the presence of the non-native crucifer *Thlaspi arvense*, based on the spatial distributions of host plants, female butterflies and eggs in the habitat and the survival of the larvae in the wild. We found that 2.9 % of eggs were laid on *T. arvense* on average, with a survival probability of 0, yielding a calculated fitness cost of 3.0 % (95 % confidence interval 1.7–3.6 %) due to the presence of the non-native in the plant community. Survival probability to the pre-pupal stage for eggs laid on two native crucifers averaged 1.6 % over 2 years. The magnitude of the fitness cost will vary temporally and spatially as a function of the relative abundance of the non-native plant. We propose that the fine-scale spatial structure of the plant community relative to the butterflies' dispersal ability, combined with the females' broad habitat use, contributes to the fitness costs associated with the non-native plant and the resulting evolutionary trap.

Keywords Brassicaceae · Evolutionary trap · Host mismatch · Larval survival · Pieridae

Communicated by Konrad Fiedler.

M. Nakajima (✉) · C. L. Boggs · S. Bailey
Department of Biology, Stanford University,
Stanford, CA 94305, USA
e-mail: mifuyunf@06.alumni.u-tokyo.ac.jp

M. Nakajima · C. L. Boggs · S. Bailey · J. Reithel · T. Paape
Rocky Mountain Biological Laboratory, P.O. Box 519,
Crested Butte, CO 81224, USA

Present Address:
S. Bailey
Forestry Commission, Silvan House, 231 Corstorphine Road,
Edinburgh EH12 7AT, UK

Present Address:
T. Paape
Institute of Evolutionary Biology and Environmental Studies,
University of Zurich, Winterthurstrasse 190,
8057 Zurich, Switzerland

Introduction

Biological invasions by non-native species are increasing worldwide as a result of the increasing pace of global human movement (Hulme 2009; McNeely 2006). New ecological interactions involving non-natives can alter the fitness of native species, influencing population dynamics and community structure of the invaded communities (e.g., Carlsson et al. 2009; Carroll 2007; Harvey et al. 2010; Mooney and Cleland 2001; Phillips and Shine 2004; Strauss et al. 2006). The ecological and evolutionary impact of a non-native may be particularly strong for systems in which the non-native species is closely related to a native species, with the potential to intrude into coevolved relationships within the community. Non-native species can create an "evolutionary trap" that confuses the native species through cues that are similar to its coevolved partner species, so that the native species no longer benefit from the species' interaction (Schlaepfer et al. 2005).

Such interactions involving coevolved native communities and non-native species have been reported for several butterfly and larval host plant systems, which were the original inspiration for studies of coevolution (Ehrlich and Raven 1964). Our study system is a good example. The native butterfly *Pieris macdunnoughii* (Lepidoptera, Pieridae; formerly *Pieris napi macdunnoughii* L.; Chew and Watt 2006) in Colorado, USA, oviposits on a non-native Eurasian plant *Thlaspi arvense* L. (Brassicaceae), despite the fact that the plant is lethal for young larvae (Chew 1974, 1975). The Pieridae likely coevolved with their larval hosts, members of the Brassicales (Wheat et al. 2007), thus developing detoxification mechanisms for the plant secondary compounds, glucosinolates, which are repellents for most herbivores. Wasteful oviposition on *T. arvense* by other pierids has also been reported (e.g., *P. occidentalis* and *P. protodice* in California, USA; Graves and Shapiro 2003). Other butterfly and non-native plant systems show similar mismatch (e.g., *Papilio zelicaon* and *Ammi visnaga*, reference in Graves and Shapiro 2003; *Pa. demoleus sthenelus* and *Citrus* sp., Straatman 1962; *Cressida cressida*, *Troides priamus richmondius*, and *Aristolochia elegans,* Straatman 1962; *Danaus plexippus* and *Vincetoxicum* spp., Casagrande and Dacey 2007; and *Anthanassa ardys*, *A. tulcis*, and *Hypoestes phyllostachya*, Feldman and Haber 1998).

Thus, oviposition on non-native, lethal hosts is common and has been cited as a good example of individual-level impacts of non-native species invasions (Lockwood et al. 2007). However, the overall proportion of offspring lost in the wild due to oviposition on lethal hosts has not been quantified and the impact of a deleterious host on fitness and hence on population dynamics of a native butterfly has not been assessed quantitatively.

Here, we estimate the loss of *P. macdunnoughii*'s offspring due to oviposition on a lethal, non-native plant, *T. arvense* in Colorado, as the product of oviposition and survival rates in the field. Our quantitative assessment of offspring loss in the wild due to *T. arvense* is based on the (1) spatial and temporal distribution of the native and non-native hosts in the field, (2) butterfly habitat occupancy and egg distribution, and (3) larval survival on *T. arvense* and native hosts, including the influence of micro-habitat on egg distribution and larval survival. Using these data, we estimated the fitness costs to the butterfly due to the presence of *T. arvense* in the community.

Materials and methods

Overview

The percentage loss of *P. macdunnoughii*'s offspring due to oviposition on the non-native, *T. arvense*, is calculated as [(Expected proportion of offspring lost due to oviposition on *T. arvense*/expected total proportion of offspring surviving from eggs) × 100]. We estimate this value as follows:

$$\begin{aligned}&[\text{Expected proportion of eggs oviposited on } T.\,arvense\\&\quad\times(\text{survival of eggs on the native hosts}\\&\quad-\text{survival of eggs on } T.\,arvense)/\\&(\text{expected proportion of eggs oviposited on } T.\,arvense\\&\quad\times\text{survival of eggs on } T.\,arvense\\&\quad+\text{expected proportion of eggs oviposited on the}\\&\quad\times\text{native hosts}\times\text{survival on the native hosts})]\times 100\end{aligned}\tag{1}$$

To estimate the proportion of eggs laid on the non-native plant, we first surveyed the availability of *T. arvense* and native hosts by mapping all host plants in the study area over 2 years. Second, to estimate the probability of *P. macdunnoughii* visiting each host plant species, we examined habitat use by adult female *P. macdunnoughii*. Third, we surveyed the distribution of eggs laid by female *P. macdunnoughii* among hosts in selected plots to look for a bias in host usage. Finally, we examined larval survival on *T. arvense* versus native hosts. Relative contributions from each host plant to the next generation equals the larval survival on the plant times the proportion of eggs on each plant. In all analyses, we included data on aridity and other micro-habitat attributes that may influence plant species composition, the butterfly's behavior, and larval survival (Janz et al. 2005 and references therein). We also recorded plant phenology, which may affect the larval survival (e.g., Cushman et al. 1994).

The confidence interval for the estimate of fitness loss was calculated by resampling all the data, except for the availability of *T. arvense* for which only one data point exists. To examine the effect of *T. arvense* availability on the estimate, we calculated the fitness loss with the abundance of *T. arvense* increased x times over that observed. The parameter x takes values from 1 to that where the fitness loss becomes 100 %, in increments of 0.0001. Note that this estimate assumes no change in the spatial pattern of native and non-native hosts. The change in the confidence interval under increasing *T. arvense* was also calculated by resampling all the data. The calculations were done with Mathematica 8.0.1 (Wolfram Research, IL, USA).

Study system

Our study site was the same as that of Chew (1975), at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Gunnison County, Colorado, USA (38°57′22.89″N,

106°59′18.23″W; elevation 2,885 m, 16 ha). *Pieris macdunnoughii* at the study site is mostly univoltine with an occasional partial second generation (Chew 1977). Adults emerge from pupal diapause after snowmelt between late May and mid-June. Females lay eggs singly, usually on the underside of the leaf. Chew (1975) confirmed four native crucifers as hosts at the study site in the mid-1970s: *Boechera* spp. (formerly *Arabis* spp.), *Cardamine cordifolia* A. Gray, *Draba aurea* Vahl ex Hornem., and *Descurainia incana* (Bernh. ex Fisch. & C.A. Mey.) Dorn. Hereafter "host plants" refers only to these four species plus *T. arvense*.

Thlaspi arvense was likely introduced to the study area in the mid- to late-1800s, when the area saw an influx of silver miners. The plant population is maintained by local soil disturbance from humans, domestic grazing stock, or wildlife. The inability to feed on *T. arvense* does not reflect changes in the host plant, as *T. arvense* from both Sweden (where the plant is native) and Colorado are toxic to Colorado *P. macdunnoughii* larvae (Boggs and Wiklund 2012). Both adult willingness to oviposit on *T. arvense* in the laboratory and inability of larvae to complete development on the plant in the laboratory have persisted to at least the mid-2000s (Boggs et al. 2012).

Habitat characterization

We derived insolation, aspect, and elevation from USGS Digital Elevation Model (DEM; US Geological Survey, Rocky Mountain Mapping Center, Denver, CO, USA) using the surface analyst function of ArcGIS Spatial Analyst (ESRI, Redlands, CA, USA) and combined these data with information on local hydrology from the RMBL database and aerial photos, again using ArcGIS Spatial Analyst. Based on these spatial data, we divided the study site into three levels of aridity (dry, intermediate, and wet).

Plant spatial distribution

In mid-July 2000, we recorded the location of all host plants in the entire study area. Four people searched for all visible host plants and recorded the periphery of each host plant patch using a GPS (GeoXT, Trimble, CA, USA). These data were converted to a raster file in which each cell (25 × 25 cm) contained the dominant host plant species or no hosts. Hereafter, we refer to the number of cells dominated by each host plant species as the "plant cover". We used a *G* test for each host species to test the null hypothesis that the proportion of each host species in each aridity category (dry, intermediate, or wet) equaled the proportion of habitat in each aridity category in the study area.

Plant annual phenology

The phenology of *Boechera* spp., *C. cordifolia*, *Dr. aurea*, and *T. arvense* was recorded in three patches for each host species from mid-July 2000. Since most *De. incana* were rosettes and not readily identifiable at time the phenology study started, we did not include it. However, *De. incana* is a late bloomer that is available for a long period during the flight season. Patches were chosen such that each patch (5.2–338.4 m^2) contained only one host genus. Where possible, one patch for each host plant was located in a dry, an intermediate, and a wet habitat. Distance among patches (24–590 m) was within the dispersal range of an individual *P. macdunnoughii* (see below). Every 3 days from June 23 to August 11, 2000, we estimated the number of host plants at each phenological stage (pre-flowering, flowering, seeding or senescent) in each patch. A 1-m^2 quadrat was placed randomly within the patch. The number of host plants at each phenological stage within that quadrat was counted and that number was multiplied by patch area to estimate the total plants in each phenological stage. We approximated the patch by a quadrilateral polygon and measured the four sides in order to calculate patch area.

Plant temporal distribution

To examine changes in host plant distribution across years, we chose ten patches (range 4–11 m^2 for natives, 17 m^2 for *T. arvense*), which were surveyed in July 2000 and included all host plants except *C. cordifolia.* This host was not included because its spatial distribution is more restricted than that of the other hosts and it is a perennial. Patches were distributed across habitat aridity categories. We recorded host abundance in these same patches in June–August 2002. Correlation between abundances in 2000 and 2002 were tested for each plant species surveyed.

P. macdunnoughii habitat occupancy

We examined habitat occupancy by adult female *P. macdunnoughii* in June–August 2000 at three sites (about 200 m^2 each) distributed among each of the three habitat aridity levels, for a total of nine sites. The sites were scattered over the survey area: the mean distance between patches was 242.8 m (SD = 134.3), with the minimum distance of 44 m. Working at 1- to 6-day intervals and for a constant daily time in each patch in sunny, calm weather, we caught adults and recorded sexes and locations. Using a fine-tipped marker, we marked the adults on the hind wing with numbers on first capture, or recorded the individual identifying marks for recaptures. For each patch, the total number of captures was divided by the number of survey visits to that patch to obtain catch per unit effort (CPUE).

Egg distribution in the field

We examined heterogeneity among host plants in the number of eggs per plant, as well as the heterogeneity in egg density among patches of each host plant species, in the context of the plant's physical attributes. The survey was conducted jointly with the host phenology survey described in "Plant spatial distribution" and "Plant annual phenology". At the time of each phenology survey, we searched 50 plants per patch for eggs. We used a multiple linear regression to find significant correlations between the number of eggs and the following factors: patch identity, host species, aridity level (dry, wet or intermediate), patch area (m^2), estimated total host abundance in the patch, host phenology (pre-flowering, flowering, seeding or senescent), abundance of hosts at the same phenological stage in the patch, and the interaction between plant species and aridity level. We first compared the Akaike's Information Criterion (AIC) values of linear regression models with all possible combinations of factors listed above, and defined the best model as the one with the smallest AIC. We then examined the significance of the factors in the best model by ANOVA. Statistical calculations and tests were all done in the statistical software R (v.2.10.1; R Development Core Team 2009).

Larval survival

We focused on larval survival on two native host species, *C. cordifolia* and *De. incana*, along with *T. arvense*. Work by Chew (1975) showed that larvae on the native *De. incana* had significantly faster development times than larvae on other native hosts. Additionally, *C. cordifolia* was the most abundant native host. Finally, these hosts are available over a large part of the season, reducing complications due to phenology. We conducted two types of larval survival surveys in the field for different purposes: (1) to examine the effect on larval survival and development rate of host plant species and phenology, and (2) to examine the effect on larval survival and development rate of plant height, density, and insolation. In both studies, due to low mobility of larvae (Bergman 1999; Chew 1977; Doak et al. 2006), we assume that larval disappearance without dying is negligible, and that observed larvae hatched from eggs on the plant on which the larva was found. We also assume that the probability of re-sighting eggs and larvae is 100 %. Unlike some other cases (e.g., *Coenonympha tullia nipisiquit* in New Brunswick, Canada; Sei and Porter 2003), the vegetation structure of our study site did not hinder re-location of eggs and larvae.

Survey I

In 2002, we randomly selected 15 plots of 1–10 m^2, containing *C. cordifolia*, *De. incana*, or *T. arvense*. Every 2–3 days from June 29 to August 1, new eggs and larvae found in the plots were numbered. The location and developmental stage of each individual larva was recorded, until the larva pupated or disappeared. The host plant species and its phenological stage (as defined in "Egg distribution in the field") were also recorded. We repeated the observation between June 25 and September 3, 2005 in six arbitrarily selected plots containing the host plants.

In order to increase sample size beyond that of eggs naturally laid in the wild, we also observed eggs laid by caged female *P. macdunnoughii* on host plants in the study site. Females were individually caged with an individual host plant in a study patch until oviposition, after which cages were removed, females released, and resulting eggs observed as above. We observed the larvae that hatched from eggs naturally found on the host plants (12, 1, and 7 in 2002 and 5, 14, and 0 in 2005 on *C. cordifolia*, *De. incana*, and *T. arvense*, respectively) as well as from eggs experimentally placed on the host plants (79, 96, and 9 in 2002 and 233, 117, and 97 in 2005 on *C. cordifolia*, *De. incana*, and *T. arvense*, respectively).

Larval survival to a given larval stage on each host species was estimated as the observed number of individuals at each developmental stage. Differences in larval survivorship curves between host species, i.e., *C. cordifolia*, *De. incana*, and *T. arvense*, and between years were tested by Peto and Peto's log-rank test (Pyke and Thompson 1986). The relationship between larval survival and phenology was tested by one-way ANOVA for 2002 data.

Survey II

In order to examine the effect of habitat variables on oviposition, we searched for eggs on at least 50 arbitrarily selected plants in each of the same 15 plots as above in 2002 ("Survey I"). We recorded resulting larval survival as above ("Survey I"), along with host plant species, plant height, density of surrounding host plants, surrounding ground cover, and insolation level (sun or shade). The density of surrounding plants was estimated using a 1-m^2 grid centered at the focal plant, and the ground cover was described as the proportion of ground covered by any plant species in the grid. All observations were done on eggs laid naturally by free-flying females in the field; no caged females were used. This allowed us to observe the fate of eggs on plants that female *P. macdunnoughii* preferred.

We developed generalized linear models with the last developmental stage observed (egg, 1st–5th instar or prepupal) as the dependent variable and all combinations of plant attributes listed above as independent variables. Parameter values were estimated using maximum likelihood. We compared the AIC of models with all

combinations of parameters using the function "glm" in R, and selected the model with the smallest AIC.

Fitness estimate and confidence interval

As we describe the details in "Results", the data we used to estimate the fitness loss were: (1) proportion of the total percent cover of all mustards that are *T. arvense* in aridity level *i*, (2) proportion of butterfly captured at aridity level *i*, and (3) survival of eggs to pre-pupae on the native hosts and on *T. arvense*. As we described above ("Overview"), we show how (1) affects the estimate by increasing the abundance of *T. arvense* in 2000 (i.e., the number of cells occupied by *T. arvense*) x times in all aridity levels with x from 1 in increments of 0.0001. To obtain the confidence interval for the estimate, we calculated the fitness loss (Eq. 1) from all the possible combinations of the data collected for (b) and (c).

For (2), the raw dataset consisted of butterfly's CPUE at three sites in each of three aridity levels. We picked one CPUE value from each aridity level and calculated the proportion of CPUE. We repeated it for all the possible combinations of CPUE values and obtained 27 resamples.

For (3), we had four data points for survival on native hosts (*C. cordifolia* and *De. aurea* in 2002 and 2005). We used the averages of all the possible combinations of data except for the case where the survivals on both native hosts are 0, i.e., larvae die out regardless of consuming *T. arvense* or not (see "Results" for details of the larval survival). Thus, we obtained three resamples of larval survival, and therefore $27 \times 3 = 81$ resamples of fitness loss in total.

Results

Habitat characterization

The distribution of habitat aridity across the study area is shown in Fig. 1a. Percentages of 25 × 25 cm cells in wet, intermediate, and dry habitat in the overall study area were 25.3, 60.8, and 13.8 %, respectively.

Plant spatial distribution

The distribution of each host species was uneven among aridity levels (Fig. 1a; *Boechera* spp., *C. cordifolia*, *De. incana*, *Dr. aurea*, and *T. arvense*, $G = 27{,}371.0$, 225,233.9, 21,484.6, 418.7, and 3,825.1, respectively, each with $df = 2$ and $P < 0.001$). *Cardamine cordifolia* was found in wet sites more often than expected based on site availability, whereas all other hosts were found more often in intermediate and dry sites (Fig. 1b). The host plants

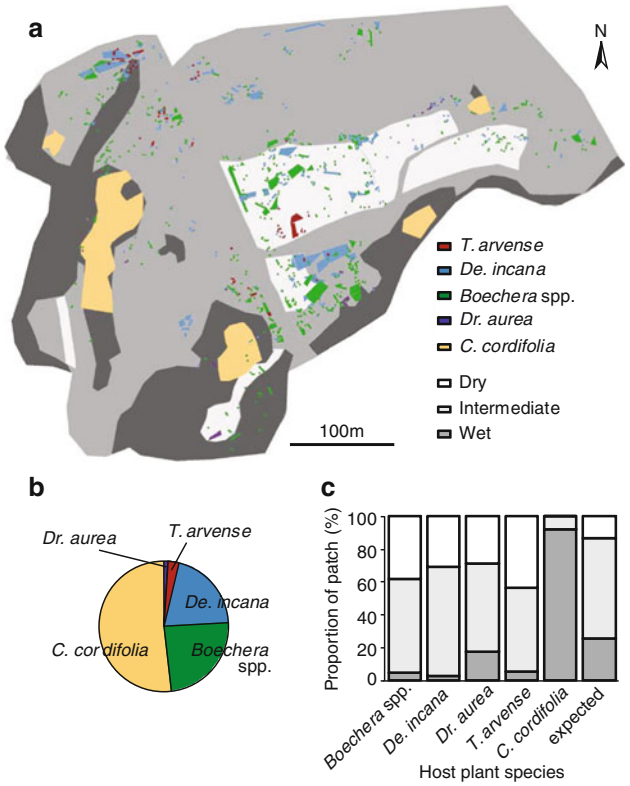

Fig. 1 Results of habitat survey in summer 2000. **a** Spatial distribution of aridity levels (wet, dry, and intermediate) and host plants (higher resolution available online). **b** Proportion of each host's cover to the total host cover. **c** Proportion of aridity levels at each plant's cover (*colors* are the same as **a**). *Expected* refers to the relative frequency in the whole study site

overall, including native species and *T. arvense*, occupied 8.3 % of the survey area. *Thlaspi arvense* constituted 2.7 % of total host cover (Fig. 1c).

Plant annual phenology

Plant phenological trajectory through the season was similar for *Boechera* spp., *Dr. aurea*, and *T. arvense*, whereas that of *C. cordifolia* differed (Fig. 2), paralleling the distribution among aridity levels.

Plant temporal distribution

Only the abundances of *Boechera* spp. in 2000 and 2002 were significantly correlated across years ($r = 0.65$, $df = 16$, $P = 0.02$; Fig. 3). The abundances of *De. incana* across years showed a weak correlation ($r = 0.46$, $df = 16$, $P = 0.09$). *Draba aurea*, *De. incana*, *T. arvense*, and *Boechera* spp. disappeared completely from 9, 6, 6, and 2 patches, respectively, out of 10 that were re-surveyed for each species in 2002. These data indicate substantial spatial turnover of host plants among years.

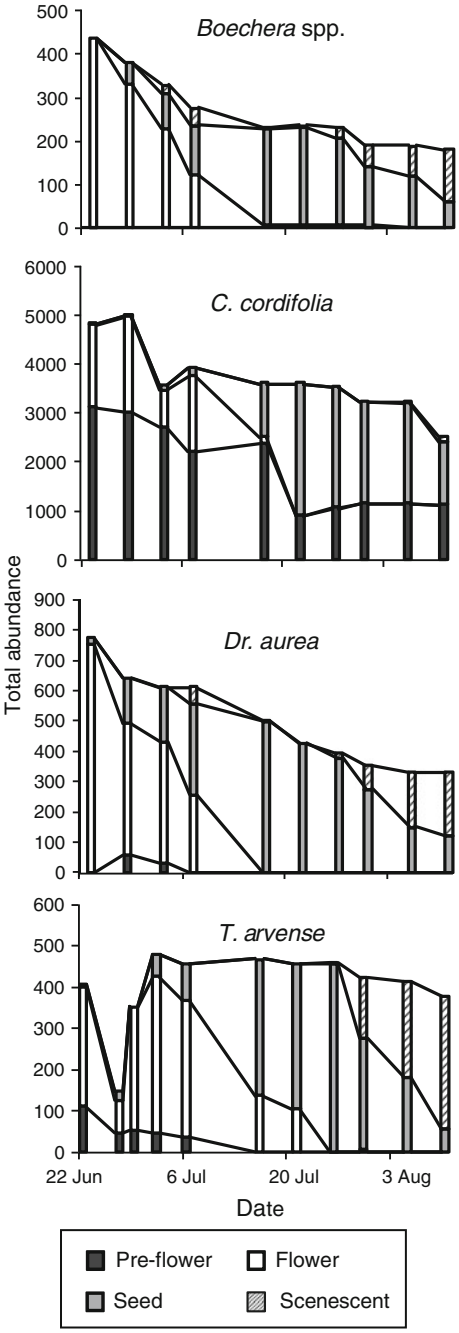

Fig. 2 The estimated plant abundances totaled for all patches of each host species at each phenological stage in summer 2000

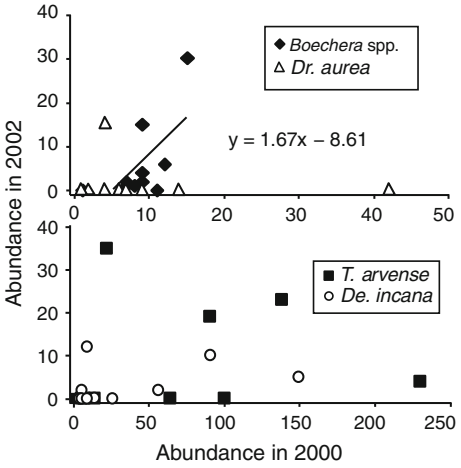

Fig. 3 Host plant abundances (number of individuals) in 2000 and 2002 for each patch. The *regression curve* and *equation* are shown only where significant (i.e., *Boechera* spp.)

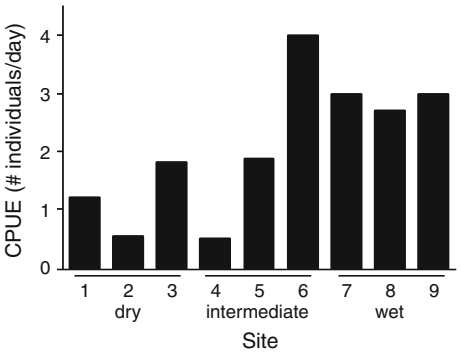

Fig. 4 Butterfly CPUE (catch per unit of effort) at each site at each aridity level (dry, wet or intermediate) in 2000

P. macdunnoughii habitat occupancy

The distributions of female butterfly CPUE among the sites were significantly different from homogenous ($n = 143$, $G = 28.2$, $df = 8$, $P < 0.001$). Female butterflies were caught more frequently in wetter sites (Fig. 4) and hence in sites dominated by *C. cordifolia* over the other hosts.

Overall distance moved on recapture (200.0 m ± 174.4 SD) did not differ from the mean distance between sites (242.8 m ± 134.3 SD; t test, $t = -1.14$, $df = 69$, $P = 0.26$). Therefore, our capture sites were close enough for *P. macdunnoughii* to move among all of them.

Egg distribution in the field

There was no significant difference in the number of eggs per plant found among the *T. arvense, C. cordifolia, Dr. aurea* or *Boechera* spp. (27 eggs and an estimated 48,979 plants across all the species, $\chi^2 = 4.4$, $df = 3$, $P = 0.22$; Table 1). The model that had the smallest AIC was [number of eggs = aridity level + intercept] (AIC = 48.9) but the effect of aridity level was not significant ($t = 1.4$, $P = 0.16$).

Larval survival

Survey I

None of the eggs on *T. arvense* survived to be observed as first instar larvae ($n = 16$) in 2002 or as second instar

Table 1 Patch description and the number of eggs found on 50 plants in each patch in 2000

Plant	*T. arvense*			*C. cordifolia*			*Dr. aurea*			*Boechera* spp.		
Aridity	Wet	Intermediate	Dry	Wet	Wet	Intermediate	Intermediate	Intermediate	Dry	Intermediate	Dry	Dry
Area (m^2)	5.85	20.48	299.50	43.25	200.50	5.23	26.53	33.95	60.39	338.38	147.88	81.75
No. of eggs	4	0	2	11	1	6	0	0	0	1	1	1
Total estimated no. of plants	535	402	3,471	4,040	25,385	7,507	1,055	1,595	2,316	1,425	773	475

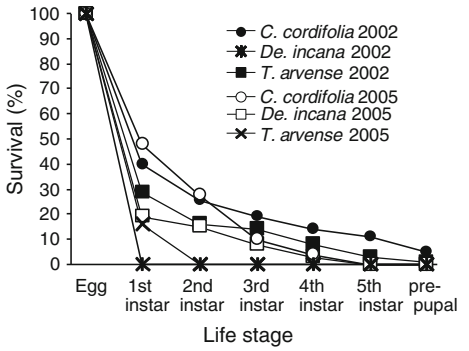

Fig. 5 Larval survival on *Cardamine cordifolia*, *Descurainia incana*, and *Thlaspi arvense* obtained from survey I in 2002 and 2005

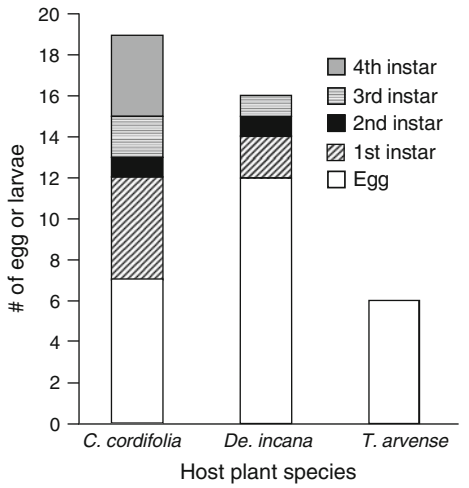

Fig. 6 Frequency of *Pieris macdunnoughii*'s final developmental stage observed on each host species in 2000 at survey II

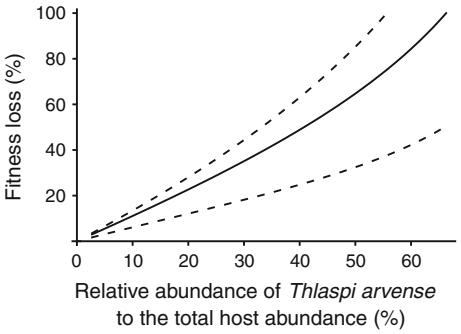

Fig. 7 Estimate of fitness loss (%) in *Pieris macdunnoughii* with increasing abundance of *Thlaspi arvense*. *Solid line* and the *dashed lines* show the estimate and the 95th and 5th percentiles of the fitness loss, respectively

larvae ($n = 97$) in 2005 (Fig. 5). In contrast, survival to pre-pupa on native host plants ranged from a high of 5.5 % on *C. cordifolia* in 2002 to a low of 0.0 % on both species in 2005, with a mean across all species and years of 1.6 % (5.5 and 1.0 % on *C. cordifolia* and *De. incana* in 2002, respectively, and no survival on either host in 2005; Fig. 5). Larval survivorship curves on *C. cordifolia* ($n = 91$) and *De. incana* ($n = 97$) were not significantly different in 2002 (LR = 0.6, $P = 0.44$) but were significantly different in 2005 (*C. cordifolia*: $n = 238$; *De. incana*: $n = 131$; LR = 13.2, $P = 0.0003$). Therefore, for 2002 data, we compared the survival on *T. arvense* with the average survival on these two native hosts combined. The larval survivorship curve on *T. arvense* was significantly different than on native hosts (LR = 50.8, $P < 0.001$). The larval survivorship curve on *T. arvense* was also significantly different from either of the two natives in 2005 (vs. *C. cordifolia*: LR = 276.3, $P < 10^{-6}$; vs. *De. incana*: LR = 67.4, $P < 10^{-6}$). There were no significant differences between years for any host species (*C. cordifolia*: LR = 0.84, $P = 0.36$; *De. incana*: LR = 2.38, $P = 0.12$; *T. arvense*: LR = 0.09, $P = 0.76$). Survival rate was not correlated with phenological state of the plant when the egg was laid (*C. cordifolia*: $F = 0.6$, $df = 2.31$, ns; *De. incana*: $F = 0.6$, $df = 1.27$, ns).

Survey II

The best model describing the effect of habitat factors on final larval stage reached by an egg or larva was [the final larval stage = plant height + plant species + plant density + intercept] (AIC = 86.9), but the only significant coefficient was plant species ($t = 4.5$, $P < 0.001$; plant height: $P = 0.10$, plant density: $P = 0.07$). When only eggs or larvae from free-flying females were considered,

larval survival was greatest on *C. cordifolia*, followed by *De. incana*, whereas none of the larvae on *T. arvense* reached 1st instar (Fig. 6).

Fitness estimates

Because the proportion of eggs laid on a given host species was independent of the local environmental factors that we investigated ("Egg distribution in the field"), we assume that the probability of finding eggs on *T. arvense* is proportional to the availability of *T. arvense*. Both plant availability and the butterfly's habitat occupancy were significantly related to habitat aridity ("Plant spatial distribution", "Plant annual phenology", and "*P. macdunnoughii* habitat occupancy", respectively). Therefore, we predict the proportion of eggs on *T. arvense* in relation to habitat aridity as follows:

Proportion of eggs on *T. arvense* $= \sum$ (proportion of percent cover of all mustards that are *T. arvense* in aridity level i $\times$ proportion of butterfly captured at aridity level i) $=$ $(0.003 \times 0.467) + (0.042 \times 0.342) + (0.068 \times 0.191) =$ 0.029, where $i =$ wet, intermediate, dry. Similar calculations for the native hosts yield estimated proportion of eggs on each host as 0.491 for *C. cordifolia*, 0.215 for *De. incana*, 0.253 for *Boechera* spp., and 0.012 for *Dr. aurea*.

As the larval survival in the calculation of fitness cost, we use the survival on the host plants obtained as described in "Larval survival, Survey II" because the larval survival was independent of host plant phenology and other microhabitat conditions. Since the larval survival on *T. arvense* was 0 % and the average survival on the native hosts was 1.6 %, the fitness cost at the population level due oviposition on *T. arvense* (Eq. 1) is $\{0.029\ (0.016 - 0)/[(0.029 \times 0) + (0.971 \times 0.016)]\} \times 100 = 3.0$ %.

The 95th, 50th, and 5th percentiles of the estimate were 3.6, 3.0, and 1.7 %, respectively. The fitness loss became 100 % when the abundance of *T. arvense* was increased by 70.4791 times from that in 2000, at which the total abundance of *T. arvense* became 66.3 % of the all host abundances (Fig. 7). The 95th and 5th percentiles of the fitness loss became 100 % when the abundance of *T. arvense* was increased by 44.9364 and 185.5612 times, that is to 55.6 and 83.8 % of the total host spatial coverage, respectively.

Discussion

We estimated the fitness cost of *P. macdunnoughii* eggs due to oviposition on *T. arvense* at our field site as 3.0 % (95 % confidence interval 1.7–3.6 %). We also showed the potential risk of *P. macdunnoughii*'s fitness loss with increase of *T. arvense* availability. To our knowledge, this is the first such estimation of fitness costs for field populations of herbivores in a community with a lethal host plant species. Given that *T. arvense* was not found directly adjacent to a native host species, and that first instar larvae have limited reserves to support wandering, it is unlikely that any disappearances resulted in successful encounters with a suitable host. Our data thus suggest that significant selection pressures operate on individuals within the population, either for avoiding oviposition or for overcoming larval feeding inhibition on the non-native host plant, given appropriate genetic variation and absence of constraints.

Eggs laid on *C. cordifolia* contributed an order of magnitude more individuals to the next generation than did eggs laid on *De. incana*, in spite of lower larval fitness on *C. cordifolia.* This finding highlights the fact that, in a mixed plant community, larval performance metrics by themselves do not reflect the relative contribution of host plant species to the next generation of herbivores. Rather, egg distribution patterns can strongly affect the outcome. This general phenomenon has also been observed in other butterflies (e.g., see Kuussaari et al. 2004 for a review in checkerspots) and is important to understanding the role of particular hosts within a community in population dynamics, and in some instances, extinction or conservation.

Among oviposition hosts, *T. arvense* ranked second among crucifers in proportion of eggs, behind *C. cordifolia*. This phenomenon is driven in part by the correlation between habitat affinities of the plants and female butterflies. The predominance of eggs on *C. cordifolia* is consistent with the significant tendency of female *P. macdunnoughii* to occupy wetter sites, and the observation that *C. cordifolia* was both dominant among host species in wet sites and had the highest total abundance among the all host plants. However, *T. arvense* is highly invasive (Warwick et al. 2002) and is found across all aridity classes within our study site. Females do use drier habitats, leading to a distribution of eggs across a broad range of native and the non-native host.

Our estimate of the egg loss due to oviposition on the non-native is the overall mean of multiple years. Larval fitness varied across two native hosts and 2 years. We documented variation among years in larval survival to the pre-pupal stage on the two native hosts in 2002 and 2005, with lower survival in 2005. Weather conditions could contribute to this difference between years, if cooler temperatures or less solar radiation slowed development times. It was cooler in 2005 than in 2002, although not unusually so (mean maximum temperature at Crested Butte, Colorado in July: 15.17 °C in 2002, 14.43 °C in 2005; Western Region Climate Center 2011, NOAA). Variation across years in location and abundance of hosts will lead to variation in the impact of *T. arvense* on the butterfly population. We found that the locations and abundance of hosts other than *Boechera* spp. changed across years (as does abundance of *C. cordifolia* in extreme and persistent drought

conditions, C. Boggs, personal observation), although we expect that hosts would consistently be found in the same or similar habitat aridity levels across time. This variation occurred in the absence of major changes in disturbance patterns within the site, and over a short time span relative to that of climate change. Such variation in spatial distribution may change the host availability and/or accessibility for the female *P. macdunnoughii*, and hence increase the temporal variability of egg distributions on host plants, including on *T. arvense.*

Such temporal and spatial variation may also contribute to the evolution or maintenance of oligophagy in *P. macdunnoughii*, which facilitates oviposition on *T. arvense*. For example, Logarzo et al. (2011) found that temporal and spatial absence of the preferred host of the cerambycidae *Apagomerella versicolor* likely contributed to the evolution of oligophagy in cooler areas of the species' range.

Our finding of significant fitness costs to oviposition mistakes on *T. arvense* raises the questions of why the butterflies continue to attempt to use the plant or why *T. arvense* constitutes an apparent evolutionary trap, at least 25 generations after the phenomenon was first documented by Chew (1975) and over 100 generations since the plant was introduced to the area. Oviposition choice involving *T. arvense* has a genetic component (Boggs et al. 2012). However, Rodman and Chew (1980) hypothesized that, in this system, the resemblance of the oviposition chemical cue, glucosinolate, of *T. arvense* to that of *De. incana* prevented *P. macdunnoughii* from avoiding *T. arvense*. In her laboratory rearing experiment, larval development on *De. incana* was the fastest among native hosts (Chew 1975), and we observed higher larval survival rates in the field on *De. incana* than on *C. cordifolia*. Therefore, selection on *P. macdunnoughii* for use of *De. incana* could have promoted oviposition on *T. arvense*.

Selection need not only operate on oviposition preference, but could also operate on larval willingness to feed. The apparent lack of evolutionary response seen in the *P. macdunnoughii* and *T. arvense* system contrasts sharply with the outcome of an Eurasian plant invasion in the habitat of *P. oleracea*, a close relative of *P. macdunnoughii*. *Pieris oleracea* in Massachusetts, USA, has begun to utilize its non-native host plant, garlic mustard (*Alliaria petiolata*) (Courant et al. 1994; Keeler and Chew 2008), which was lethal 30 years ago (Bowden 1971). This system could be an example of an "evolutionary hot spot", whereas our system is an "evolutionary cold spot" (Thompson 1994). Why one is hot and the other cold is still unclear, but may depend on levels of genetic variation and developmental constraint within the butterfly populations, which in turn depend on population history along with mutation rates. In addition, an increase in toxic host plant density and the resultant decrease in the butterfly's fitness might accelerate the evolution of oviposition preference or host utilization. The projection of our estimated fitness loss may then be altered. Understanding the mechanism underlying the butterfly's host preference and utilization would shed important light on the evolutionary and population dynamics in this system.

The system we have documented here shows the fitness cost of a resource species invading into a co-evolved consumer–resource system. The extent of the cost likely depends on the fact that the distribution of potential butterfly host plants is fine-grained, relative to the dispersal abilities of individual female butterflies. This idea is supported by the finding that habitat preference by both plant and butterfly are important determinants of the fitness cost. The spatial and temporal distribution of the resource will be important in shaping the ecological and evolutionary future of the population. The patterns of outcomes from a range of such distributions remain to be explored.

Acknowledgments This work conforms to the legal requirements of the USA. The authors thank J. Bowsher, A. Cathcart, E. Forwand, and R. Neill for field assistance, and T. Fukami, R. McCoy, W. Watt, A. Porter and an anonymous reviewer for comments on the manuscript. Funding came from the Stanford Vice Provost for Undergraduate Education's Biology Field Studies Program, NSF REU site grant DBI 9987953 to RMBL, and the Stanford University Center for Conservation Biology's Bing Fund.

Conflict of interest The authors declare that they have no conflict of interest.

References

Bergman KO (1999) Habitat utilization by *Lopinga achine* (Nymphalidae: Satyrinae) larvae and ovipositing females: implications for conservation. Biol Conserv 88:69–74

Boggs CL, Wiklund C (2012) When putative host plants invade: perfomance and heritability of performance of butterfly larvae in the native and non-native plant range (in preparation)

Boggs CL et al (2012) Introduced host and native herbivore: opportunities for evolution in the face of maladaptation (in preparation)

Bowden SR (1971) American white butterflies (Pieridae) and English food-plants. J Lepidopterists Soc 25:6–12

Carlsson NOL, Sarnelle O, Strayer DL (2009) Native predators and exotic prey—an acquired taste? Front Ecol Environ 7:525–532

Carroll SP (2007) Natives adapting to invasive species: ecology, genes and the sustainability of conservation. Ecol Res 22:892–901

Casagrande RA, Dacey JE (2007) Monarch butterfly oviposition on swallow-worts (*Vincetoxicum* spp.). Environ Entomol 36:631–636

Chew FS (1974) Strategies of food plant exploitation in a complex of oligophagous butterflies (Lepidoptera). PhD dissertation, Biology. Yale University, New Haven

Chew FS (1975) Coevolution of Pierid butterflies and their cruciferous foodplants 1. The relative quality of available resources. Oecologia 20:117–127

Chew FS (1977) Coevolution of Pierid butterflies and their cruciferous foodplants 2. Distribution of eggs on potential foodplants. Evolution 31:568–579

Chew FS, Watt WB (2006) The green-veined white (*Pieris napi* L.), its Pierine relatives, and the systematics dilemmas of divergent character sets (Lepidoptera, Pieridae). Biol J Linn Soc 88: 413–435

Courant AV, Holbrook AE, Van der Reijden ED, Chew FS (1994) Native pierine butterfly (Pieridae) adapting to naturalized crucifer? J Lepidopterists Soc 48:168–170

Cushman JH, Boggs CL, Weiss SB, Murphy DD, Harvey AW, Ehrlich PR (1994) Estimating female reproductive success of a threahened butterfly: influence of emergence time and hostplant phenology. Oecologia 99:194–200

Doak P, Kareiva P, Kingsolver J (2006) Fitness consequences of choosy oviposition for a time-limited butterfly. Ecology 87:395–408

Ehrlich PR, Raven PH (1964) Butterflies and plants: a study in colevolution. Evolution 18:586–608

Feldman TS, Haber WA (1998) Oviposition behavior, host plant use, and diet breadth of *Anthanassa* butterflies (Lepidoptera: Nymphalidae) using plants in the Acanthaceae in a Costa Rican community. Fl Entomol 81:396–406

Graves SD, Shapiro AM (2003) Exotics as host plants of the California butterfly fauna. Biol Conserv 110:413–433

Harvey JA, Bukovinszky T, van der Putten WH (2010) Interactions between invasive plants and insect herbivores: a plea for a multitrophic perspective. Biol Conserv 143:2251–2259

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. J Appl Ecol 46:10–18

Janz N, Bergstrom A, Johansson J (2005) Frequency dependence of host plant choice within and between patches: a large cage experiment. Evol Ecol 19:289–302

Keeler MS, Chew FS (2008) Escaping an evolutionary trap: preference and performance of a native insect on an exotic invasive host. Oecologia 156:559–568

Kuussaari M, van Houhuys S, Hellmann JJ, Singer MC (2004) Larval biology of checkerspots. In: Ehrlich PR, Hanski I (eds) On the wings of checkerspots: a model system for population biology. Oxford University Press, Oxford, pp 138–160

Lockwood JL, Hoopes M, Marchetti M (2007) Invasion ecology. Blackwell, Malden

Logarzo GA, Casalinuovo MA, Piccinali RV, Braun K, Hasson E (2011) Geographic host use variability and host range evolutionary dynamics in the phytophagous insect *Apagomerella versicolor* (Cerambycidae). Oecologia 165:387–402

McNeely JA (2006) As the world gets smaller, the chances of invasion grow. Euphytica 148:5–15

Mooney HA, Cleland EE (2001) The evolutionary impact of invasive species. Proc Natl Acad Sci USA 98:5446–5451

Phillips BL, Shine R (2004) Adapting to an invasive species: toxic cane toads induce morphological change in Australian snakes. Proc Natl Acad Sci USA 101:17150–17155

Pyke DA, Thompson JN (1986) Statistical analysis of survival and removal rate experiments. Ecology 67:240–245

R Development Core Team (2009) A language and environment for statistical computing, 2.3.0 edn. R Foundation for Statistical Computing, Vienna

Rodman JE, Chew FS (1980) Phytochemical correlates of herbivory in a community of native and naturalized Cruciferae. Biochem Syst Ecol 8:43–50

Schlaepfer MA, Sherman PW, Blossey B, Runge MC (2005) Introduced species as evolutionary traps. Ecol Lett 8:241–246

Sei M, Porter AH (2003) Microhabitat-specific early-larval survival of the maritime ringlet (*Coenonympha tullia nipisiquit*). Anim Conserv 6:55–61

Straatman R (1962) Note on certain Lepidoptera ovipositing on plants which are toxic to their larvae. J Lepidopterists Soc 16:99–103

Strauss SY, Lau JA, Carroll SP (2006) Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? Ecol Lett 9:357–374

Thompson JN (1994) The coevolutionary process. University of Chicago Press, Chicago

Warwick SI, Francis A, Susko DJ (2002) The biology of Canadian weeds 9. *Thlaspi arvense* L. (updated). Can J Plant Sci 82:803–823

Western Region Climate Center (2011) Monthly temperature listings. N Crested Butte, Colorado

Wheat CW, Vogel H, Wittstock U, Braby MF, Underwood D, Mitchell-Olds T (2007) The genetic basis of a plant-insect coevolutionary key innovation. Proc Natl Acad Sci USA 104:20427–20431