

Lack of enemy release for an invasive leafroller in California: temporal patterns and influence of host plant origin

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Abstract The enemy release hypothesis posits that the success of invasive species can be attributed to their escape from natural enemies. Invading hosts are expected to encounter an enemy assemblage consisting of fewer species, with lower representation of specialists, and to experience less mortality as a result. In this study, we examined parasitism of the Light Brown Apple Moth (LBAM), *Epiphyas postvittana* (Walker), in California, an exotic leafroller that is native to southeastern Australia. From 2008 to 2011 we monitored parasitoid species richness, representation of the more specialized koinobiont parasitoids, and parasitism rates of LBAM collected three times per year from four plant species of Australian origin and six plant species of non-Australian origin, at two locations in coastal California. We found the resident parasitoid assemblage of LBAM in California to have comparable levels of species richness, to have a similar representation of koinobionts versus idio-bionts, and to inflict similar parasitism rates as in its native range. The two dominant parasitoids were *Meteorus ictericus* (Braconidae) and *Enytus eureka* (Ichneumonidae). Parasitoid species richness varied with season and plant origin and decreased slowly, but significantly, over the 4 year period. Parasitism rates

were lowest in spring and highest on plants of Australian origin, but did not change with year. Hyperparasitism rates were higher on *E. eureka* (36.5 %) compared with *M. ictericus* and other parasitoids combined (3.3 %) and were highest on plants of Australian origin. We subsequently discuss the lack of both apparent enemy reduction and realized enemy release for LBAM in California and the unique finding that a shared plant origin enhanced the parasitism of this exotic leafroller by resident parasitoids.

Keywords *Epiphyas postvittana* · Parasitoid assemblage · *Enytus eureka* · *Meteorus ictericus* · Hyperparasitism

Introduction

Invasive species are among the major threats to biodiversity, displacing native species, posing risks to endangered species, and altering ecosystem functions (Ricciardi 2007; Vitousek et al. 1996). The economic costs of invasive species incurred annually by the United States through direct damage and management expenses, is estimated to be around 120 billion dollars (Pimentel et al. 2005). With such dramatic impacts on natural and agricultural ecosystems it is essential to understand the invasion process

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and the factors that can influence the invasiveness of alien species (Allendorf and Lundquist 2003; Davis 2009; Gurevitch et al. 2011).

One of the central concepts of invasion biology is the enemy release hypothesis (ERH) which posits that the success of invasive species can be attributed to their escape from natural enemies (Elton 1958; Keane and Crawley 2002; Liu and Stiling 2006; Mitchell and Power 2003). Enemy release can be assessed by either comparing the enemy assemblage of a host species in an invaded region to that in its native region (biogeographical comparison), or by making comparisons of enemy assemblages on closely related native and invasive hosts in the same community (community comparison) (Colautti et al. 2004). While enemy release applies to all groups of natural enemies, in this study we specifically focus on insect parasitoids. Parasitoids, as a group of natural enemies, are insects that develop on (ectoparasitoids) or in (endoparasitoids) the bodies of other insects, with endoparasitoids in particular sharing a strong coevolutionary relationship with their hosts (Quicke 1997). This, and the fact that they are often the dominant cause of mortality for phytophagous insect populations (Cornell and Hawkins 1995), makes them effective model organisms for the study of enemy release among phytophagous insect hosts.

The ERH is based on the observation that in the introduced range exotic host species are often attacked by a smaller number of resident enemy species than in the native range, representing an apparent enemy reduction, and that in most, but not all cases, apparent enemy reduction can also be accompanied by a reduction of the impact of resident enemies on exotic host populations, providing evidence of realized enemy release (Colautti et al. 2004; Mitchell and Power 2003; Torchin et al. 2003). In a biogeographical study comparing phytophagous insects as both natives and exotics, Cornell and Hawkins (1993) found that 68 % of the species showed much greater parasitoid species richness as natives and 94 % showed greater parasitism rates as natives, indicating that realized enemy release is somewhat more common among exotic phytophagous insects than apparent enemy reduction. Another aspect of the ERH is that enemy assemblages on exotic hosts are expected to have a greater representation of generalists than specialists (Keane and Crawley 2002) as resident specialists take longer to acquire the phenological, behavioral, or

ecological adaptations needed to successfully use a novel exotic host. The generalist versus specialist paradigm for parasitoid assemblages is often represented by the proportion of idiobionts versus koinobionts (Althoff 2003; Sheehan and Hawkins 1991). Idiobionts are parasitoids that typically kill or permanently paralyze their host at oviposition (Askew and Shaw 1986; Haeselbarth 1979). By preventing further host activity, idiobionts do not need to adapt to the host's physiology, which allows them to exploit a broader host range and to switch to novel hosts more easily. Koinobiont parasitoids, on the other hand, allow their hosts to continue to feed and develop after oviposition (Askew and Shaw 1986; Haeselbarth 1979). This latter mode of development requires a greater level of adaptation to a host than for idiobiont parasitoids, resulting in a smaller host range.

In the present study, we examined the parasitoid assemblage and parasitism rates of the light brown apple moth (LBAM) *Epiphyas postvittana* (Walker) as an invasive species in California. LBAM is a tortricid leafroller native to South Eastern Australia and was first discovered in California in 2006 (Brown et al. 2010). Larvae of this species are highly polyphagous and feed on 545 known plant species in 363 genera and 121 families (Brockhoff et al. 2011). Highly polyphagous exotic insect herbivores, like LBAM, are likely to be found on a variety of host plants in an introduced region that will differ in both origin and coevolutionary history with the herbivore, and consequently, will generate differences in the composition and activity of associated resident parasitoids. Similarly, we might also expect differences in parasitoid composition and activity between seasons and years (Le Corff et al. 2000). Our specific objective in this study was to evaluate parasitism of LBAM in California by resident parasitoids and to test three predictions of the ERH: (1) that the parasitoid assemblage should be less species rich in California than in its native range, (2) that parasitism rates should be lower in California than in its native home, and (3) that the parasitoid assemblage associated with LBAM in California should primarily be represented by idiobiont species. For each prediction we present data on parasitism of LBAM in California and we subsequently compare these data with previously published observations of parasitism of LBAM in Australia (biogeographical comparison) and with previously published observations of parasitism of related leafrollers in the western U.S. In addition, we assessed

the extent to which parasitoid species richness and parasitism rates of LBAM in California varied with host plant origin, year and season. To our knowledge, this is the first study to investigate the effect of a shared origin between an exotic herbivore and its host plants on the species richness and impact of resident enemies at the third trophic level.

Materials and methods

Sampling locations, sites, and dates

Light Brown Apple Moth populations were sampled at two locations, one in San Francisco county, referred to as SF, and another in Santa Cruz county, referred to as SC, with an aerial distance between them of 98 km. These two locations are thought to have had some of the longest established populations of LBAM in California based on initial numbers of adults collected in a pheromone-based trapping survey (USDA-APHIS 2011). At both locations, an extensive search for multiple sites was undertaken before the start of the project, resulting in 11 and 8 sites at SF and SC respectively. At the SF location, all sampling sites were located within Golden Gate Park, with a maximal aerial distance of 4.7 km between them. At SC, sampling sites were located in urban gardens, parking lots, or small county parks between Santa Cruz and Capitola, with a maximum aerial distance between them of 7.6 km. Sites consisted of a group of plants of the same species that supported LBAM populations that were consistent enough that they could be sampled at least 4 times during the study period. Seven plant species were sampled at the SF location, with numbers of sites and plant origin (A for Australian and O for other) for each species included in parentheses: *Leptospermum laevigatum* (3; A), *Melaleuca linariifolia* (1; A), *Agonis flexuosa* (1; A), *Mersine africana* (2; O), *Choisya ternata* (1; O), *Hypericum calycinum* cv. 'Hidcote' (2; O) and *Correa alba* (1; A). At the SC location three plant species were sampled: *Pittosporum tobira* (4; O), *Arctostaphylos densiflora* (3; O) and *Abelia x grandiflora* (1; O). To test for the effect of plant size on parasitoid species richness, the height of 10 random plants were measured at each site once at the end of the study period.

Egg masses of LBAM could not be found reliably and were not sampled for parasitism at any of the sites.

As no parasitoids of tortricid hosts complete their development in the earlier larval instars (Mills 1994), fourth to sixth instar larvae and pupae were sampled to allow maximum exposure of hosts to parasitism in the field before collection. Plants were sampled three times per year during periods that had been identified as having the highest proportional representation of 4–6th instar larvae in the age structure of LBAM populations that have 3–4 overlapping generations throughout the year in California (Bürge et al. 2011). Sampling was conducted from summer 2008 through fall 2011 and the timing of the three sample periods varied slightly between the two locations, May 18–30 (spring), July 09–27 (summer), and September 19 to October 20 (fall) for SF, and May 16–21 (spring), July 28–August 11 (summer), and September 25–October 17 (fall) for SC.

Parasitoid species richness, parasitism rates and hyperparasitism

Forty LBAM leafrolls occupied by fourth to sixth instar larvae, pupae or parasitoid cocoons were collected at each site and brought back to the laboratory on each sampling occasion. Groups of 12–15 larvae of the same instar were placed in 96 ml plastic cups (Solo Cup Company, Highland Park, IL) and were reared to adult on a bean-based diet (Cunningham 2007) under constant conditions at 21 °C, 70–85 % RH and a 16:8 h (L:D) photoperiod. Larval instars of the field-collected LBAM were determined from head capsule measurements (Danthanarayana 1975). Cups were checked weekly for LBAM pupae and parasitoid cocoons. Pupae were removed from cups and kept in 33 ml plastic vials in groups of up to five and after emergence the identity of LBAM adults was checked using Gilligan and Epstein (2009). Parasitoid cocoons were kept separately in 38 ml glass vials to await adult emergence. Adult parasitoids were identified to genus before obtaining species determinations from a series of taxonomic specialists.

The number of parasitoid species reared from field-collected leafrolls was used as a measure of parasitoid species richness. Parasitism rates for primary parasitoids, i.e. parasitoids that directly attack LBAM life stages, were estimated from the number of parasitized LBAM hosts in relation to the number of LBAM collected on each occasion at each site. As few host

pupae were obtained from the leafrolls sampled on each occasion (see Table 1), parasitism rates were not estimated separately for larvae and pupae of LBAM, but for the combined life stages sampled. Dividing the number of parasitized hosts by the number of LBAM collected provides a conservative estimate of parasitism as there was consistent mortality of LBAM larvae (~30 %) during laboratory rearing that could have differentially affected parasitized individuals. We used mean parasitism rates rather than maximum parasitism rates as peak parasitism rates from individual samples are frequently prone to bias (Van Driesche 1983).

As all hyperparasitoids, i.e. parasitoids that attack the primary parasitoids of LBAM, were found to be solitary species, hyperparasitism was estimated as the total number of hyperparasitoid individuals emerged divided by the total number of primary parasitoid cocoons collected.

Statistical analysis

All statistical analyses were conducted using R (R Development Core Team, version 2.15.0, 2012). For analyses of parasitoid species richness, parasitism rates and rates of hyperparasitism we used generalized linear mixed models with penalized quasi likelihood (glmmPQL in the package “MASS”) and either a Poisson (counts) or binomial (rates) error structure. For all of the models, year, season and plant origin were included as explanatory variables. Year was treated as a continuous variable, while season (spring, summer, fall) and plant origin (Australian, Other) were considered factors. To account for repeated measures at the same sites, site was included as a random factor and was nested within location (SF, SC). Significance values reported for the explanatory variables year, season and plant origin were obtained from the null model for factors with significance levels of $\alpha \leq 0.05$, or from reduced models for factors with significance levels of $\alpha > 0.05$. For categorical factors with more than two levels, non-significantly different levels were pooled. For the analysis of rates of hyperparasitism, the only interaction tested was the season by year interaction due to overparameterization of the model.

For the analysis of parasitoid species richness, sample size (number of parasitoid individuals) varied considerably between replicates due to large fluctuations in parasitism rates between plant species, year

Table 1 Mean proportional representation (\pm SE) of larvae and pupae per sampling date and location

Location	Summer 2008	Fall 2008	Spring 2009	Summer 2009	Fall 2009	Spring 2010	Summer 2010	Fall 2010	Spring 2011	Summer 2011	Fall 2011
SF (larvae)	1.00 (\pm NA)	0.94 (\pm 0.028)	0.97 (\pm 0.018)	0.99 (\pm 0.007)	0.91 (\pm 0.037)	0.93 (\pm 0.037)	0.95 (\pm 0.026)	0.98 (\pm 0.016)	0.87 (\pm 0.125)	0.97 (\pm 0.025)	1.00 (\pm 0.000)
SF (pupae)	0.00 (\pm NA)	0.06 (\pm 0.028)	0.03 (\pm 0.018)	0.01 (\pm 0.007)	0.09 (\pm 0.037)	0.07 (\pm 0.037)	0.05 (\pm 0.026)	0.02 (\pm 0.016)	0.13 (\pm 0.125)	0.03 (\pm 0.025)	0.00 (\pm 0.000)
SC (larvae)		0.73 (\pm 0.088)	0.98 (\pm 0.016)	0.93 (\pm 0.028)	0.89 (\pm 0.106)	0.96 (\pm 0.018)	1.00 (\pm 0.000)	0.71 (\pm 0.128)	0.95 (\pm 0.030)	1.00 (\pm 0.000)	1.00 (\pm 0.000)
SC (pupae)		0.27 (\pm 0.088)	0.02 (\pm 0.016)	0.07 (\pm 0.028)	0.11 (\pm 0.106)	0.04 (\pm 0.018)	0.00 (\pm 0.000)	0.29 (\pm 0.128)	0.05 (\pm 0.030)	0.00 (\pm 0.000)	0.00 (\pm 0.000)

and season (the 40 LBAM collected on each sampling date at each site produced between 0 and 40 parasitoid individuals). Species richness is known to exhibit a logarithmic relationship with sample size that can be approximated by a linear relationship at the lower end of the curve (Hawkins 1994). Visual inspection of the species accumulation curve confirmed that a linear approximation was adequate and we therefore included sample size (number of parasitoid individuals) as a covariate in the GLM analysis for parasitoid species richness (Hawkins 1994).

To further investigate the influence of variation among plant species on the accumulation of parasitoid species associated with LBAM in California, we created a matrix with all recorded parasitoid species represented as columns and the 11 plant species as rows. The cells of the matrix were filled with the total number of individuals of each parasitoid species collected on each plant species over the entire sampling period. We then randomly picked (with replacement) 50, 250 or 500 parasitoids from either a single plant or a combination of plants and recorded the number of parasitoid species contained in each sample of randomly chosen specimens. On *L. laevigatum*, for example, we had recorded seven different parasitoid species throughout the entire sampling period, ranging in abundance from 1 to 166 specimens. Randomly resampling *L. laevigatum* could therefore yield between one and seven parasitoid species. By increasing sample size from 50 to 250 and 500 we simulated an increase in sampling effort on a given number of plants. To test the effect of number of plant species sampled on number of parasitoid species recovered, we applied this resampling procedure to groups of plants with 1–11 plant species per group. Plant groups consisted of all possible combinations of plant species for each group size (i.e. groups with two plant species had all possible two species combinations out of 11 total species). As the number of possible plant species combinations varied with the number of plants resampled, the extent of resampling for levels with fewer combinations was increased to match the sampling effort of the level with the most combinations which was $252 (=10!/[5! \times (10 - 5)!])$. This analysis differs from a typical rarefaction analysis (Gotelli and Colwell 2001) in that the re-sampling was based on the pool of plant species in addition to the pool of parasitoid individuals.

We also tested for the dependence of cumulative parasitoid richness over the entire sampling period at

each site on plant size, and for the dependence of mean parasitism rates averaged over the entire study period at each site on plant size. We used generalized linear models with Poisson and binomial error structures, respectively, and quasi likelihood where necessary. In the model for cumulative parasitoid species richness we also included number of parasitoids collected as a covariate to account for the effect of sample size. Lastly, we tested the relationship between parasitism rates and parasitoid species richness, with data collected for each site at each sample date as replicates, using a generalized linear model with a binomial error structure, logit link and quasi likelihood. For all three models, model reduction and log likelihood ratio tests were used to assess the statistical significance of the individual factors at $\alpha = 0.05$.

Results

For the period from summer 2008 through fall 2011 a total of 2285 (SF) and 3592 (SC) LBAM individuals were collected and 976 (SF) and 864 (SC) parasitoids were reared from them. The proportional representation of larvae and pupae for each sampling date and location is shown in Table 1. Thirteen parasitoid species, belonging to four families and twelve genera, were reared from LBAM collected at both locations combined (Table 2). Eight were larval parasitoids, four were pupal parasitoids, and one was a larval-pupal parasitoid. All of the parasitoids are native to North America, with the exception of *Meteorus ictericus* that originates from the Palearctic region. The biological traits of each parasitoid species, their relative abundance, and their representation among the different host instars collected are provided in Table 2.

Meteorus ictericus, a solitary larval endoparasitoid, was found to be the numerically dominant parasitoid at all sites sampled and was responsible for 71.2 % of the total parasitism of LBAM. The second most abundant parasitoid, providing 16 % of the total parasitism, was the solitary larval endoparasitoid *Enytus eureka*. *Pediobius ni*, a gregarious pupal parasitoid, made a significant contribution to parasitism at the SC location (10.5 %), but was absent from the SF location, resulting in a 5 % contribution to total parasitism. Ranked fourth in their relative contribution to total parasitism (2.3 %) was a group of tachinid flies that consisted of three species, *Nemorilla pyste*, *Actia*

Table 2 The primary parasitoids of *Epiphyas postvittana* in California indicating life style (K: koinobiont, I: idiobiont), mode of parasitism (G: gregarious, S: solitary) relative frequency at each location, and representation from different host stages collected

Order	Family: Subfamily	Species	K/I	Mode of parasitism	Relative frequency (# collected) SF	Relative frequency (# collected) SC	Percent representation from host stages collected (4th, 5th, 6th, pupa) (%)
Hymenoptera	Braconidae: Meteorinae	<i>Meteorus ictericus</i> Nees	K	S	70.9 % (677)	74.4 % (633)	25.7, 41.3, 32.5, 0
Hymenoptera	Braconidae: Hormiinae	<i>Hormius</i> sp.	I	G	0 % (0)	0.1 % (1)	0, 0, 0, 0 (found only as cocoons)
Hymenoptera	Ichneumonidae: Campopleginae	<i>Enytus eureka</i> (Ashmead)	K	S	26.1 % (249)	5.1 % (44)	93.8, 0, 6.3, 0
Hymenoptera	Ichneumonidae: Banchinae	<i>Glypta franciscana</i> Dasch	K	S	1.2 % (12)	0.2 % (1)	16.7, 50, 33.3, 0
Hymenoptera	Ichneumonidae: Ichneumoninae	<i>Centeterus</i> sp.	I		0 % (0)	0.2 % (1)	0, 0, 0, 100
Hymenoptera	Ichneumonidae: Pimplinae	<i>Coccygominus hesperus</i> Townes	I	S	0.2 % (2)	0.8 % (7)	0, 0, 0, 100
Hymenoptera	Ichneumonidae: Cryptinae	<i>Ischnus inquisitorius</i> (Mueller)	K	S	0.2 % (2)	3.6 % (31)	0, 0, 0, 100
Hymenoptera	Ichneumonidae: Metopiinae	<i>Exochus nigripalpis</i> Thompson	K	S	0.6 % (6)	0.6 % (5)	0, 0, 16.7, 83.3
Hymenoptera	Ichneumonidae: Pimplinae	<i>Itopectis quadricingulata</i> (Provancher)	I	S	0.1 % (1)	0.1 % (1)	0 % , 0 % , 0 % , 100 %
Hymenoptera	Eulophidae: Entodontinae	<i>Pediobius ni</i> Peck	I	G	0 % (0)	10.7 % (91)	0, 0, 0, 100
Diptera	Tachinidae	<i>Actia interrupta</i> Curran	K	S	0.6 % (6)	4.2 % (36)	0, 23.1, 61.5, 15.4
		<i>Nemorilla pyste</i> (Walker)					
		Tachinid sp1					

interrupta, and one unidentified species; data on the relative contribution of each species were not collected. The fifth most important species was the larval-pupal parasitoid *Ischnus inquisitorius* accounting for 1.8 % of the total parasitism. Both the tachinids and *I. inquisitorius* were more significant at the SC location (4.2 and 3.6 %) than at the SF location (0.6 and 0.2 %). Only three of the parasitoid species found at the SC location, *P. ni*, *Centeterus* sp., and *Hormius* sp., were absent from the SF location, whereas all of the parasitoid species found at the SF location also occurred at the SC location. The generalist contribution to the primary parasitoid assemblage, as represented by the proportion of idiobionts, was 0.36.

Parasitoid species richness

Parasitoid species richness was significantly higher on plants with Australian origin ($t = 2.18$, $df = 15$, $P = 0.05$), significantly lower in spring compared with summer and fall combined ($t = 3.4$, $df = 100$, $P = 0.001$) and showed a significant, but slow, decrease with year ($t = 2.26$, $df = 100$, $P = 0.03$, Fig. 1). Sample size as a covariate was significant ($t = 3.46$, $df = 100$, $P < 0.001$). Cumulative parasitoid species richness over the

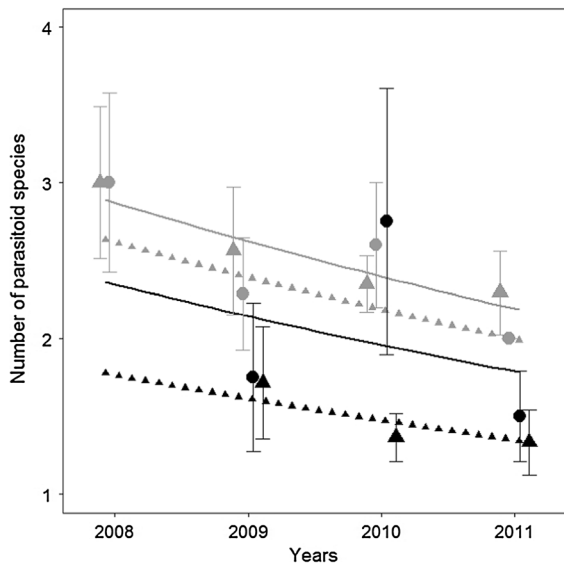


Fig. 1 Mean parasitoid species richness (+SE) of *Epiphyas postvittana* in California showing a significant decrease for year and significant differences at an $\alpha > 0.05$ level for season (grey symbols fall and summer combined, black symbols spring) and plant origin (circles and solid lines Australian origin, triangles and dashed lines Other origin). Symbols on the horizontal axis are staggered to reduce overlap

entire period did not show a significant relationship with plant size, which ranged from 0.36 to 3.18 m ($\chi^2 = 0.03$, $df = 1$, $P = 0.86$), but sample size as a covariate was significant ($\chi^2 = 4.13$, $df = 1$, $P = 0.04$).

Rarefaction curves for parasitoid species in relation to plant species richness produced logarithmic curves that showed the importance of plant species as well as parasitoid sample size on parasitoid species richness (Fig. 2). The curves indicate that a single plant species generates a statistical expectation of around three to five parasitoid species with little influence of sample size. However, when more plant species are considered the expected parasitoid richness asymptotes at about 5 species for the smaller sample size of 50, at almost 9 species for a sample size of 250 parasitoids, and about 11 species for a sample size of 500 parasitoid individuals collected.

Parasitism rates

Parasitism rates per site ranged from 0 to 100 % with an overall grand mean of 34.47 % (± 2.21). Parasitism

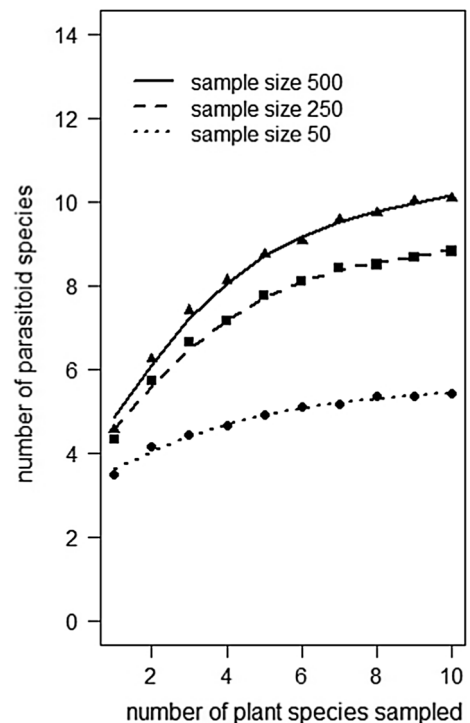


Fig. 2 The predicted relationship between number of plant species sampled and number of parasitoid species encountered for different sample sizes of parasitoid individuals collected from *Epiphyas postvittana*

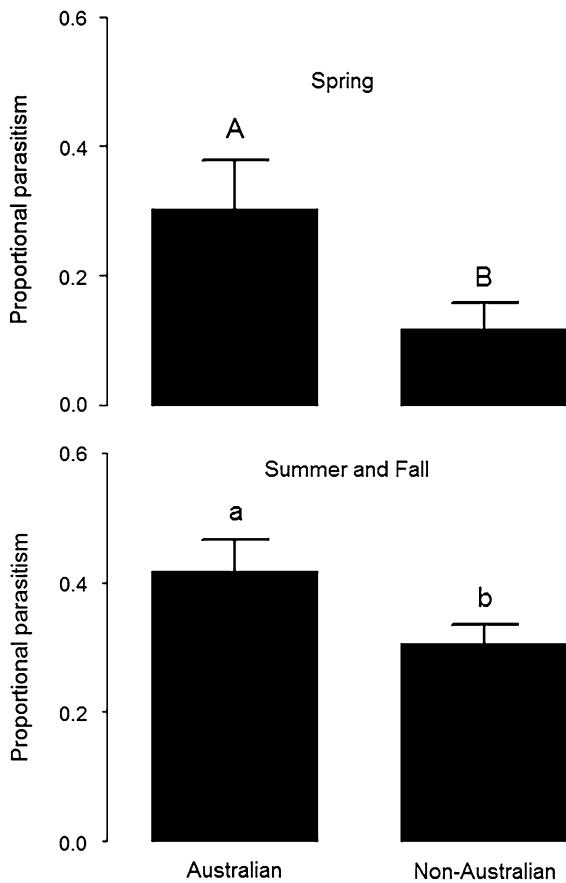


Fig. 3 Mean parasitism rates (+SE) of *Epiphyas postvittana* in California showing significant differences for season and plant origin. *Uppercase, lowercase and different letters* indicate statistical differences at an $\alpha > 0.05$ level

rates were significantly higher on plants of Australian origin ($t = 2.44$, $df = 15$, $P = 0.03$) and were significantly lower in spring compared with summer and fall combined ($t = 5.92$, $df = 108$, $P < 0.001$, Fig. 3).

There was no significant effect of year on parasitism rates ($t = 1.61$, $df = 108$, $P = 0.11$). When considering the dominant parasitoid *M. ictericus* alone, parasitism was not significantly higher on plants of Australian origin ($t = 1.48$, $df = 15$, $P = 0.16$), but was significantly lower in spring compared with summer and fall ($t = 4.62$, $df = 99$, $P < 0.001$) and increased significantly with year ($t = 2.07$, $df = 99$, $P = 0.04$). The relationship between mean parasitism rate and plant size was not significant ($F_{1,16} = 0.72$, $P = 0.41$), but the effect of parasitoid species richness on parasitism rates was significant ($\ln[y/1-y] = 0.24x - 1.54$; $F_{1,117} = 11.21$, $P = 0.001$), resulting in an estimated increase from 0.21 proportional parasitism for one parasitoid species to 0.47 for six parasitoid species.

Hyperparasitism

A total of 110 hyperparasitoid individuals were recovered from the collected cocoons consisting of 4 species and a group of unidentified Pteromalidae (Table 3). The dominant hyperparasitoid species, with 78.2 % of the total hyperparasitism, was *Gelis* sp1, a species that has wingless females and winged males. The second most abundant hyperparasitoid species was *Itopectis quadricingulata*, making up 10 % of the total hyperparasitism. The hyperparasitoid species and their relative frequency among primary parasitoid species are provided in Table 3. The overall rate of hyperparasitism was 8.96 % (± 1.46) for all parasitoid cocoons collected and varied significantly with primary parasitoid species, being lower for *M. ictericus* and “Other” parasitoids combined than for *E. eureka* ($t = 5.24$, $df = 171$, $P < 0.001$, Fig. 4). The

Table 3 The hyperparasitoids of *Epiphyas postvittana* in California indicating relative frequency at each location and representation from different primary parasitoid species collected

Order	Family: Subfamily	Species	Relative frequency (# collected) SF	Relative frequency (# collected) SC	Percent representation from <i>Meteorus</i> , <i>Enytus</i> , others (%)
Hymenoptera	Ichneumonidae: Pimplinae	<i>Itopectis quadricingulata</i>	8.5 % (8)	7.1 % (1)	44.4, 55.6, 0
Hymenoptera	Ichneumonidae: Cryptinae	<i>Gelis</i> sp1	80.9 % (76)	71.4 % (10)	10.6, 85.9, 3.5
Hymenoptera	Ichneumonidae: Cryptinae	<i>Gelis</i> sp2	6.4 % (6)	0 % (0)	0, 100, 0
Hymenoptera	Ichneumonidae: Mesoichorinae	<i>Mesochorus</i> sp.	2.1 % (2)	0 % (0)	0, 100, 0
Hymenoptera	Pteromalidae:	Unidentified spp.	2.1 % (2)	21.4 % (3)	33.3, 33.3, 33.3

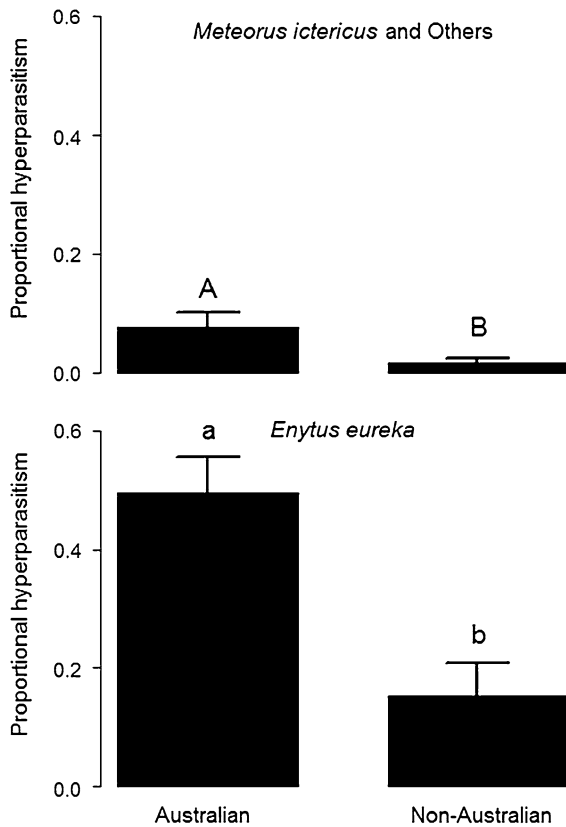


Fig. 4 Mean proportional hyperparasitism (+SE) of field-collected cocoons of primary parasitoids of *Epiphyas postvittana* in California showing significant differences for primary parasitoid species and plant origin. Uppercase, lowercase and different letters indicate statistical differences at an $\alpha > 0.05$ level

effect of plant origin was also significant, with hyperparasitism on plants of Australian origin being significantly higher ($t = 2.43$, $df = 16$, $P = 0.03$). We also found a marginally significant effect of season, with hyperparasitism in spring being significantly lower than in summer and fall combined ($t = 1.83$, $df = 171$, $P = 0.07$), while the effect of year was not significant ($t = 0.38$, $df = 170$, $P = 0.71$).

Discussion

Biogeographical and community comparisons of parasitoid species richness and specificity

The enemy release hypothesis (ERH) predicts that parasitoid assemblages on exotic hosts should have a reduced species richness with a high representation of

generalists, and limited parasitism pressure (Colautti et al. 2004; Liu and Stiling 2006; Roy et al. 2011; Torchin et al. 2003). In our study, in which we sampled fourth through sixth instar larvae and pupae of LBAM in coastal California, we found 13 species of primary parasitoids and 5 species of hyperparasitoids. In two other studies of parasitism of LBAM in California (Bürge et al. in prep; Wang et al. 2012), an additional two egg parasitoids (*Trichogramma fasciatum* (Perk.) and *T. platneri* Nagarkatti), four larval parasitoids (*Apanteles* sp., *Agrypon clandestinum* First., *Campoplex* sp., Tachinid sp2), one pupal parasitoid (*Brachymeria ovata* [Say]) and one hyperparasitoid (*Scambus* sp.) were found. This raises the total California parasitoid species to 20 primary and 6 hyperparasitoids. In southeastern Australia, the native range of LBAM, Paull and Austin (2006) found the hymenopteran parasitoid assemblage of host larvae and pupae to consist of a total of 17 primary parasitoids, 5 hyperparasitoids, and 3 species of unknown trophic level. From two other studies of LBAM parasitoids in Australia (Danthanarayana 1983; Geier and Briese 1981), two additional hymenopteran parasitoids and four tachinid parasitoids have been recorded, bringing the total number of primary parasitoid species to 23. This suggests a remarkable similarity in the species richness of primary and hyperparasitoids in California and Australia, with no overlap between parasitoid species found in the two regions. While these estimates of species richness are based on different levels of sampling effort in the two regions, and on ornamental plants in California versus crop plants in Australia, they provide an insightful comparison despite being an incomplete representation of the full parasitoid assemblage in either region.

A community comparison of the parasitoid assemblages of related native leafrollers in the western U.S. yielded results similar to the biogeographical comparison. In coastal California, Walker and Welter (2004) collected 227 larvae and pupae of *Argyrotaenia citrana* (Fern.) from apple orchards and recorded a total of 6 parasitoid species. From a survey in Washington state, LaGasa et al. (1999) reared 92 larvae and pupae of *Choristoneura rosaceana* (Harr.) recording 20 different parasitoid species. Another 4 year study in Washington state apple orchards showed that *Pandemis pyrusana* Kaerfott and *C. rosaceana* both supported a total of 6 different parasitoid species (Mullinix et al. 2011), whereas in

British Columbia apple orchards these leafrollers supported 8 and 18 parasitoid species respectively (Vakenti et al. 2001).

These biogeographical and community comparisons suggest that the parasitoid assemblage of LBAM in California is equally as rich as in its native range and as rich as the parasitoid assemblages from related native hosts in the western U.S., providing no evidence for apparent enemy reduction. For comparison, Cornell and Hawkins (1993) found that parasitoid species richness on exotic hosts was equal to or greater than that of the same species as native hosts in 28 out of 87 comparisons, which shows that a lack of apparent enemy release is not uncommon among exotic phytophagous insects. These types of comparisons should be made with caution, however, since the apparent species richness of a parasitoid assemblage is strongly dependent on sample size (Hawkins 1994).

In our study, we found 5 idiobionts and 8 koinobionts in the primary parasitoid assemblage of LBAM in California, suggesting that only about a third (0.38) of the species were generalists. The corresponding primary parasitoid assemblage of LBAM in its native Australia consisted of 9 idiobionts and 14 koinobionts and thus consists of a very similar proportion (0.39) of generalist species (Danthanarayana 1983; Geier and Briese 1981; Paull and Austin 2006). In contrast, however, for native leafrollers in the western U.S., Walker and Welter (2004) found that *A. citrana* was attacked exclusively by koinobionts and LaGasa et al. (1999) found the proportion of idiobionts in the parasitoid assemblage of *C. rosaceana* to be 0.15. While parasitoid species richness in invaded regions has been shown to reach levels similar to those in native regions within 10 years of introduction, Cornell and Hawkins (1993) estimated that the idiobiont to koinobiont ratio of an exotic host can take anywhere from 150 to 10,000 years to achieve the ratio represented in its native range. A potential factor contributing to the rapid accumulation of both parasitoid species richness and koinobiont species by LBAM in California could be the presence of many closely-related tortricids that act as a catalyst in the recruitment of more specialized parasitoids due to physiological and behavioral similarities between hosts (Harvey et al. 2012). Although the genus *Epiphyas* is restricted to Australia, California is home to numerous species in the tribe Archipini and a wealth of species within the subfamily Tortricinae (Powell

1964) all of which show the same larval leafrolling behavior as LBAM and appear to be associated with a high representation of koinobiont parasitoids. Use of the idiobiont/koinobiont dichotomy to represent different levels of host specialization among parasitoids was based on the finding that, on average, koinobiont parasitoids parasitize fewer host species than idiobiont parasitoids (Althoff 2003). While exceptions can certainly occur to this general rule (Althoff 2003; Mills 1992), it is nonetheless valuable as a broad categorization of the more generalist nature of parasitoids on invasive versus native hosts (Cornell and Hawkins 1993).

Our analysis of the influence of plant origin and temporal factors on variation in parasitism rates revealed that parasitoid species richness was higher on host plants of Australian origin compared with host plants from other origins (Fig. 1). In general, little is known about the effect of plant origin on parasitoid species richness. However (Engelkes and Mills 2013) found reduced performance of LBAM larvae on plants native to California compared with congeneric plants from other origins, some of which had been present in the native range of LBAM for at least four decades. If we assume that the Australian plants in the current study resulted in higher quality LBAM hosts than the plants from other origins, then parasitoid species richness would be correlated to host quality. One possible mechanism for such a linkage could be that parasitoids preferentially attacked the higher quality hosts on Australian plants. Alternatively, a shared history of LBAM with Australian plants could have led to a stronger herbivore-induced plant volatile response, and consequently to differential attraction of parasitoid species between plants from different origins. Parasitoid species richness also revealed a significant, but slow decrease in parasitoid species richness between years over the course of the study (Fig. 1). Most of the rarer parasitoid species were late larval or pupal parasitoids that could have been competitively displaced by the earlier-attacking and numerically-dominant parasitoids, such as *E. eureka* and *M. ictericus*, as they became more efficient at using LBAM as a novel exotic host. We also found that parasitoid species richness was significantly lower in spring compared with summer and fall combined. As most native tortricid species in California are univoltine and active in spring only (Powell 1964), LBAM may have become an important alternative

host for multivoltine parasitoid species later in the season. Furthermore, we found that in our study parasitoid species richness (or parasitism rates) did not increase with plant size. This is contrary to the competition theory by Askew (1980), which predicts that with increasing size and architectural complexity of host plants, the presence of more herbivores reduces competition among generalist parasitoids and permits greater species packing among parasitoid assemblages. The absence of any relationship between parasitoid species richness and plant size in both this and other studies (Mills 1993; Sheehan 1991; Stireman and Singer 2003) question the validity of competition theory in structuring parasitoid communities.

From our analysis of rarified estimates of parasitoid species richness we conclude that increasing the number of plant species sampled would be expected to have a greater impact on observed parasitoid species richness than increasing sample size. This not only helps to identify the best sampling strategy for parasitoids of polyphagous insect hosts, but also confirms the hypothesis that polyphagy of phytophagous insects is often linked with a higher parasitoid species richness (Sheehan 1994; Stireman and Singer 2002), although an earlier study did not find such a relationship (Hawkins and Lawton 1987).

Biogeographical and community comparisons of parasitism rates

Parasitism rates for LBAM from our study in California averaged 34 %. To obtain comparable estimates of parasitism from the life tables developed for LBAM in Australia by Danthanarayana (1983) we divided the number of individuals dying from parasitism in each life table by the number entering the second through fifth larval instar stage minus the number dying from removal or predation. The resulting parasitism rates from the five and 3 year study in two abandoned apple orchards in the Melbourne region ranged from 5 to 55 % and from 8 to 58 % per generation, with an overall average of 22 and 30 %, respectively. Similarly, for a community based comparison of native leafrollers in the western U.S., parasitism rates averaged 33.4 % (two most abundant parasitoid species only) for *A. citrana* in California (Walker and Welter 2004), 26 and 31 % for *P. pyrusana* and *C. rosaceana* respectively in Washington (Mullinix et al. 2011), and 28 % for *C. rosaceana* and *P. pyrusana*

combined in British Columbia (Cossentine et al. 2004). From this we conclude that LBAM in California experiences comparable or even slightly greater levels of parasitism than in its native region and similar levels of parasitism as native leafrollers in the western United States, and thus that there is no evidence of a realized enemy release for LBAM in California. For comparison, Cornell and Hawkins (1993) found that only 3 out of 52 exotic host species had the same or higher parasitism rates as in their native ranges, indicating that a lack of realized enemy release is much less common than a lack of apparent enemy reduction for exotic phytophagous insects. However, these results should be interpreted with caution, as parasitism rates are likely to vary with both host plant species and LBAM densities, and additional studies, measuring parasitism of LBAM in a wider range of habitats in both its native and introduced regions, are needed to verify these conclusions.

Our analysis of the influence of plant origin and temporal factors on variation in parasitism rates revealed that parasitism was higher on host plants of Australian origin compared with host plants from other origins for the full parasitoid assemblage, but not for *M. ictericus* alone. While variation in parasitism on different plant species has been documented previously (Barbosa et al. 2001; Lill et al. 2002), to our knowledge, no such an effect on parasitism of a shared origin between an exotic herbivore and its host plants has been documented before. Based on the assumption that host quality of LBAM on plants of Australian origin would be superior (Engelkes and Mills 2013), higher parasitism rates could have resulted from greater survivorship of parasitoids on hosts collected from Australian plants. Alternatively, the increased parasitism rates of LBAM on Australian plants could have been due to greater abundance of LBAM on plants of Australian origin, as in a separate study, we found parasitism of LBAM in California to exhibit negative density dependence in some cases (Bürgi et al., submitted). However, as we did not estimate host densities at each of the sample sites this cannot be confirmed. Yet, we also found that parasitism by *M. ictericus* alone did not vary significantly with host plant origin, indicating that increased parasitism rates on plants of Australian origin could have resulted from higher parasitoid species richness on those plants. We also found that parasitism rates were significantly lower in spring compared with summer and fall. While

seasonal patterns of parasitism have been found in several other studies (DeLoach 1983; Le Corff et al. 2000; Myers 1981; West 1985), in this case the pattern most likely reflects a dilution effect due to the availability of alternative native tortricid hosts which typically have only a single generation in spring (Powell 1964).

There was also a significant relationship between parasitism rate and parasitoid species richness of the LBAM hosts collected in our study. Other studies of the linkage between natural enemy richness and biological control have either found similar positive relationships (Snyder and Tylianakis 2012; Stireman and Singer 2003; Tylianakis et al. 2006), found no relationship at all (Rodríguez and Hawkins 2000; Straub and Snyder 2006), or even found a negative relationship (Finke and Denno 2004). The positive relationship found in our study suggests complementarity among the resident parasitoid species that have adopted LBAM as a suitable novel host and likely relates to the broad range of host life stages attacked and developmental strategies used by the individual species in this parasitoid assemblage.

Hyperparasitism

We recorded 6 hyperparasitoid species with an overall rate of hyperparasitism on field-collected primary parasitoid cocoons of 13.8 %, while Paull and Austin (2006) listed 5 species as hyperparasitoids of LBAM in Australia. Rates of hyperparasitism in California varied significantly with plant origin, being higher on plants of Australian origin compared with plants from other origins, reflecting the same pattern observed for parasitism rates by primary parasitoids. We also found that the rate of hyperparasitism was lower on *M. ictericus* and “Other” parasitoids combined compared with *E. eureka*. Although *M. ictericus* was 10 times more abundant than *E. eureka* it was hyperparasitized 12 times less frequently. An important difference between these two primary parasitoids is that hosts of *M. ictericus* stay alive until well after parasitoid cocoon formation and spin an additional layer of silk webbing around themselves and the parasitoid cocoon. From observations made in other studies, both the added silk webbing (Tanaka and Ohsaki 2006) and the presence of a live larva (Harvey et al. 2011) can deter hyperparasitism of primary parasitoid cocoons.

However, it remains to be determined to what extent this relative release from hyperparasitism contributed to the success of *M. ictericus* on LBAM in California.

Conclusion

Cornell and Hawkins (1993) found that only 3 out of 52 phytophagous insect species lacked both apparent enemy reduction and realized enemy release as exotics, and all three were Lepidoptera, the phytophagous insect order that supports the highest levels of parasitoid species richness (Hawkins and Lawton 1987). Our study provides evidence that LBAM adds a fourth species to this category. Whether the lack of enemy release from parasitoids for LBAM in California also extends to other groups of natural enemies, such as predators and pathogens, remains unknown. In general, however, the practice of biological control is based on the notion that populations of exotic invaders are not effectively suppressed by resident enemies, and we know of only one example of the successful biological control of an exotic pest by a native parasitoid species, the bayberry whitefly, *Parabemisia myricae* (Kuwana) in southern California (Rose and DeBach 1992). Nonetheless, practitioners of biological weed control continue to avoid the use of phytophagous control agents from taxonomic groups that support rich parasitoid assemblages in an effort to ensure that they benefit from realized enemy release (Paynter et al. 2010). During its invasion of California LBAM has met considerable resistance rather than release from resident parasitoids, and factors that might have facilitated this resistance include: (1) the occurrence of numerous native leafrollers that support a rich native parasitoid species pool in the invaded region (Powell 1964), (2) specialization among leafroller parasitoids that is based on the host feeding niche rather than host species (Mills 1992), and (3) overlapping host generations with all life stages present throughout the year allowing native parasitoids to avoid the limitations of temporal synchronization with suitable host life stages (Bürgi et al. 2011). Additionally, we found that plants from the same region of origin as LBAM further contributed to the lack of realized enemy release, although the generality of such a finding remains to be tested for a broader range of species.

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