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Journal

Population Ecology, 57(1)

ISSN

1438-3896

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Publication Date

2015

DOI

10.1007/s10144-014-0451-4

Peer reviewed

Allee effects and population regulation: a test for biotic resistance against an invasive leafroller by resident parasitoids

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Received: 24 June 2013 / Accepted: 14 August 2014 / Published online: 14 September 2014
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Abstract Resident natural enemies can impact invasive species by causing Allee effects, leading to a reduction in establishment success of small founder populations, or by regulating or merely suppressing the abundance of established populations. *Epiphyas postvittana*, the Light Brown Apple Moth, an invasive leafroller in California, has been found to be attacked by a large assemblage of resident parasitoids that cause relatively high rates of parasitism. Over a 4-year period, we measured the abundance and per capita growth rates of four *E. postvittana* populations in California and determined parasitism rates. We found that at two of the sites, parasitism caused a component Allee effect, a reduction in individual survivorship at lower *E. postvittana* population densities, although it did not translate into a demographic Allee effect, an impact on per capita population growth rates at low densities. Instead, *E. postvittana* populations at all four sites exhibited strong compensatory density feedback throughout the entire range of densities observed at each site. As we found no evidence for a negative relationship between per capita population growth rates and parasitism rates, we concluded that resident parasitoids were unable to regulate *E. postvittana* populations in California. Despite a lack of evidence for

regulation or a demographic Allee effect, the impact of resident parasitoids on *E. postvittana* populations is substantial and demonstrates significant biotic resistance against this new invader.

Keywords Density feedback · *Epiphyas postvittana* · *Meteorus ictericus* · Population growth rates

Introduction

With the increase of globalization, the introduction of exotic species into new regions has become a worldwide threat to biodiversity, ecosystem function and agricultural production (Mack et al. 2000; Ricciardi 2007). Although the majority of introduced exotic species remain low in abundance and ecological or economic significance (Ricciardi and Cohen 2007), some become invasive in the introduced region, exhibiting numerical dominance and a rapid rate of spread (Levine et al. 2004; Pyšek and Richardson 2006). Numerous factors can influence the success of invasion, including propagule pressure, abiotic conditions, biotic traits of exotic species, and composition and structure of resident communities (Catford et al. 2009; Davis 2009; Simberloff 2009). The role of the resident community in slowing down or preventing invasions forms the basis of the biotic resistance hypothesis, which suggests that predation from or competition with members of the recipient community can reduce the success of invasion (Elton 1958; Maron and Vilà 2001; Carlsson et al. 2011; Dumont et al. 2011).

Biotic resistance has been particularly well studied in the context of herbivory by vertebrates and insects on invasive plants (Colautti et al. 2004; Levine et al. 2004; Liu and Stiling 2006; reviewed by Maron and Vilà 2001), and

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predation in aquatic and marine environments (Torchin et al. 2003; Carlsson et al. 2011; Dumont et al. 2011). In contrast, there have been few studies on invasive herbivores and their natural enemies. Moreover, biotic resistance is commonly inferred from measurements of natural enemy richness and impact, i.e., numbers of natural enemy species and the mortality or damage they inflict on invasive populations (e.g., Mitchell and Power 2003; Torchin et al. 2003; Carlsson et al. 2011; reviewed by Levine et al. 2004). Yet, a higher richness of natural enemies does not necessarily translate to greater impact, and the net effect of mortality on population growth rates can vary significantly depending on the life history strategy of the invader (Maron and Vilà 2001) and how mortality at a particular life stage influences population growth (McEvoy and Coombs 1999; Mills 2005; Raghu et al. 2006). Studies of natural enemy impacts on invaders need a greater focus on population-level effects rather than individual responses (Halpern and Underwood 2006), and only recently have matrix population models been used to integrate individual responses into population growth rates (Schutzenhofer et al. 2009). These population level studies provide the most unequivocal evidence for or against the biotic resistance hypothesis. However, such detailed or long-term studies are scarce and thus enemy resistance remains a controversial hypothesis with short-term observational and experimental studies that both support and refute the importance of predation as a biotic interaction that influences the success of invasion.

A necessary but not sufficient condition for natural enemies to be able to play a decisive role in regulating the population growth rate of an invasive species is that they must induce compensatory density feedback (Herrando-Pérez et al. 2012a), such that there is a decrease in the per capita growth rate of the host with increasing population size (Hassell 2000; Seitz et al. 2001; Murdoch et al. 2003). In contrast, if small invasive populations suffer higher proportional mortality from natural enemies than larger populations, this can generate depensatory density feedback (Herrando-Pérez et al. 2012a) in which case the top-down effect is destabilizing rather than regulating and is known as an Allee effect (Allee 1931; Liebhold and Bascompte 2003; Courchamp et al. 2008; Kramer et al. 2009). Interest in Allee effects has surged in the last decade as a key aspect of invasion biology that can potentially limit the establishment or facilitate the eradication of new exotic species (Taylor and Hastings 2005; Tobin et al. 2011). Allee effects can either be measured as reductions in individual fitness parameters, such as survival or mate finding, at lower densities (component Allee effects), or as reductions in per capita population growth rates at lower densities (demographic or ensemble Allee effects (Herrando-Pérez et al. 2012b), integrating the effects of all

component feedbacks (compensatory and depensatory) on demographic rates (Herrando-Pérez et al. 2012b). In theory, demographic Allee effects have the potential to limit the establishment success of invaders (Drake and Lodge 2006) or to reduce the risk and rate of spread of invaders (Lewis and Kareiva 1993). In the absence of compensatory or depensatory density feedback, however, natural enemy-induced mortality can still play an important role in the dynamics of invasive species by suppressing their abundance below the carrying capacity for the environment (Rohde 2006; Schmickl and Karsai 2010).

In the present study, over a 4 year period, we monitored the population densities and parasitism rates of Light Brown Apple Moth, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae), as an invasive species in California. *Epiphyas postvittana* is a tortricid leafroller native to South Eastern Australia that was first discovered in California in 2006. Larvae of this species are highly polyphagous and feed on 545 known plant species in 363 genera and 121 families (Brockerhoff et al. 2011). In a previous study, Bürgi and Mills (2014) documented the parasitoid assemblage of *E. postvittana* in California and found that it did not differ from the assemblage in its native range with respect to richness, level of specialization, and parasitism rates. In the absence of any evidence for enemy release in California, there is the possibility for significant biotic resistance to the *E. postvittana* invasion from the resident parasitoid community. Therefore, our specific objectives in this study were to address the following three questions regarding *E. postvittana* populations in California: (1) does per capita survivorship from parasitism provide evidence of a component Allee effect?, (2) does the per capita population growth rate of *E. postvittana* populations provide evidence of compensatory or depensatory density feedback, indicating the potential for regulation or demographic Allee effects?, and (3) is parasitism responsible for compensatory density feedback in *E. postvittana* population growth rates?

Materials and methods

Sampling sites

Epiphyas postvittana populations were monitored at two sites in Golden Gate Park in San Francisco (37°45'59.12"N, 122°29'14.19"W referred to as SF1, and 37°45'54.31"N, 122°30'10.66"W referred to as SF2) and two urban sites in Santa Cruz (36°57'21.28"N, 122°2'15.39"W referred to as SC1, and 36°58'49.05"N, 121°54'32.11"W referred to as SC2). At the SF1 site, *E. postvittana* was sampled on Australian tea tree (*Leptospermum laevigatum*) which had been planted only a few years prior to the beginning of the study in 2008, ranged

from 1 to 2 m in height, and were irrigated regularly in summer. At the SF2 site, a population was sampled on Australian tea tree plants that were much older (50+ years) with heights of up to 3.5 m. *Epiphyas postvittana* was sampled from small groups (patch diameters ranging from 2 to 4 m) of ornamental manzanita plants (*Arctostaphylos densiflora*) up to 0.5 m high at the SC1 site, which was located on a mulched road median in a suburban neighborhood. Manzanita was also sampled at the SC2 site where plants were 1.5 m high and formed a continuous 20 m long hedge surrounding a large parking lot. These sites were selected for regular sampling because, as noted by Geier and Briese (1980), in Australia extensive and virtually continuous infestations of *E. postvittana* are observed only in very specialized habitats such as suburban gardens and horticultural crops. These sites were thought to have had some of the longest established populations of *E. postvittana* in California based on initial numbers of adults collected in a pheromone-based trapping survey (USDA-APHIS 2012). The host plant species selected in each of the two locations were those that most consistently supported *E. postvittana* populations of sufficient abundance to allow destructive sampling. While *E. postvittana* was present on other host plant species in both locations, populations occurred only seasonally or were too small to allow effective sampling.

Epiphyas postvittana sampling and per capita population growth rate

From May 2008 until June 2010, sites were visited at 2-week intervals from April to October and at 4-week intervals from November to March. From July 2010 until July 2012 sites were visited three (SF) and four (SC) times per year. These periods had been identified as having the highest proportional representation of 4–6th instar larvae in the age structure of *E. postvittana* populations that have three (SF) and four (SC) overlapping generations throughout the year in California (Bürge et al. 2011). As no larval parasitoids of tortricid hosts complete their development in the earlier instars (Mills 1994), sampling during times with highest proportional representation of 4th to 6th instar larvae allowed us to best estimate parasitism levels in the field. The timing of the sample periods varied slightly among years, with dates at SC sites being February 1–8 (early spring), May 10–17 (late spring), July 23–August 19 (summer), September 23–28 (fall) and at SF sites March 29–April 9 (spring), July 12–August 10 (summer), October 5–14 (fall). Sampling at site SC1 was terminated in August 2011 when plants were removed, and did not start until January 2009 at site SC2 as it was a replacement for a previously sampled site where the *E. postvittana* population proved to be too low to be adequately monitored.

To sample *E. postvittana* populations, 5-min counts of visible leafrolls were conducted on each of 22 Australian tea tree plants at SF1 and SF2, and on 22 manzanita plants at SC1 and 15 manzanita plants at SC2. At SF1, initially the number of leafrolls on whole plants were counted, requiring approximately 7 min to complete, but the sampling was switched to timed 5 min counts on 10 April 2009. In addition, the number of plants sampled at SC1 was reduced to 16 after a severe pruning event in October 2008.

At all four sites, 50 leafrolls were collected from additional non-sample plants on each sampling occasion. At SC1 we observed an obvious initial gradient in larval population densities and therefore collected 100 leafrolls from different plants throughout the sampling area. Leafrolls were brought back to the laboratory and carefully opened to determine occupancy by larvae and pupae. Proportional occupancy was determined as the number of individuals per leafroll (from 50 leafrolls, or 100 for SC1), which could exceed 1 at times because of double or triple occupancy of leafrolls. Larvae were reared to adults on a bean-based diet (Cunningham 2007) in 96 ml plastic cups (Solo Cup Company, Highland Park, IL) under constant conditions at 21 °C, 70–85 % RH and a 16:8 h L:D photoperiod. In July 2011, we changed the diet used to rear the *E. postvittana* larvae to *Pectinophora gossypiella* (Saunders) diet provided by the USDA-APHIS Pink Bollworm Rearing Facility located in Phoenix, Arizona (Bartlett and Wolf 1985).

The timed leafroll counts were then multiplied by the proportional occupancy and divided by 5 or 7 min to get a standardized measure of *E. postvittana* population density N (mean number of *E. postvittana* per minute) for each plant sampled at all sites. For each sampling site, per capita population growth rate on sampling date t was calculated as $\ln[N(t + 646 \text{ dd})/N(t)]$, since one *E. postvittana* generation from egg to an adult female that has laid 50 % of her eggs takes 646 degree days (dd), as found by Gutierrez et al. (2010) in a re-analysis of data from a laboratory study in Australia (Danthanarayana 1975). In an earlier study we confirmed that a 646 dd generation time provided a good match to the seasonal patterns of voltinism in field populations of *E. postvittana* in California (Bürge et al. 2011). When time ($t + 646 \text{ dd}$) did not coincide with an actual sampling date, but rather fell between sampling dates, population abundance was estimated by linear interpolation using the two bracketing sampling dates.

Parasitoid species and parasitism rates

Cups containing field-collected *E. postvittana* larvae were checked weekly for *E. postvittana* pupae and parasitoid cocoons. Pupae were removed from cups and kept in 33 ml plastic vials in groups of up to 5 pupae where parasitoid or

moth emergence was monitored. After emergence, the identity of *E. postvittana* 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. Parasitism rates (as proportions) for primary larval and pupal parasitoids combined were estimated from the number of hosts parasitized (by either larval or pupal parasitoids) divided by the total number of host individuals collected on each occasion at each sampling site. We were unable to estimate parasitism rates in the more usual way (number of hosts parasitized divided by number of emerging moths plus parasitoids) due to some missing data on moth emergence. As there was consistent larval mortality (approximately 30 %) of *E. postvittana* during laboratory rearing, however, this may have led to an underestimation of parasitism rates since our method of calculation assumes that dead host larvae were not parasitized. All hyperparasitoids were found to be solitary species, and so hyperparasitism rates (as proportions) were estimated as the total number of hyperparasitoid individuals emerged divided by the total number of primary parasitoid cocoons collected. The relative frequency of parasitoid species at each sampling site was estimated as the number of host individuals parasitized by a particular parasitoid species divided by the total number of hosts parasitized.

Data analysis

All analyses were conducted using generalized additive mixed models (GAMMs, package “mgcv”) and R statistical software (R Development Core Team 2012). The use of GAMMs with non-parametric smoothing (function *s()*) allowed us to capture nonlinearities in the shape of the relationships between dependent and explanatory variables without having to select a particular parametric form. GAMMs also allowed us to take into account temporal pseudoreplication within each field site through repeated sampling, in the form of an exponential correlation (function *corExp(form = ~degree days)*) between sample dates that decreased exponentially with increasing temporal distance as represented by the number of degree days between them. Estimated degrees of freedom (*edf*), the degrees of freedom used to fit the smoothing function, varied for each explanatory variable and these results are presented separately for each model. The error distribution and link function for each model varied according to the measurement variable used, as indicated below. Since GAMMs cannot produce log likelihood estimates, parameter significance is presented as values for non-significant and significant parameters obtained from the full and reduced models respectively.

To assess whether parasitism caused a component Allee effect in *E. postvittana* populations, we tested for a positive relationship between per capita survivorship from parasitism (1–proportional parasitism rate for larval and pupal parasitoids combined) and *E. postvittana* population density separately for each sampling site, using GAMMs with a binomial error distribution and logit link.

As an assessment of evidence for compensatory or depensatory density feedback within *E. postvittana* populations, we examined the relationship between per capita population growth rate and *E. postvittana* population density separately for each sampling site, since plant species, plant age and local environmental conditions varied considerably between sites.

A positive relationship at low *E. postvittana* densities would suggest depensatory density feedback and hence a demographic Allee effect, while a negative relationship at higher *E. postvittana* densities would indicate compensatory density feedback and the potential for population regulation. To further assess whether parasitism could have the potential to regulate *E. postvittana* populations at each sampling site, we tested for a negative relationship between per capita population growth rate and parasitism rate. The effects of both parasitism and population density on per capita population growth rates of *E. postvittana* were tested simultaneously as explanatory variables in a single GAMM for each sampling site with a Gaussian error distribution and identity link.

Results

Epiphyas postvittana densities, parasitoid species and parasitism rates

For the period from May 2008 to July 2012 a total of 6222 *E. postvittana* individuals were collected and 994 parasitoids reared from the four sites sampled. Maximum *E. postvittana* densities per sampling date, averaged over all plants sampled, ranged from 111 *E. postvittana* counts per minute at SF1, to 60 and 61 at SC1 and SC2, and 16 at SF2 (Fig. 1). The total number of primary parasitoid species recorded was 16, and of hyperparasitoid species was six. The overall mean proportion of hosts parasitized was highest for the SF2 site at 0.35, lowest for the SC1 site at 0.03 and intermediate for SF1 (0.32) and SC2 (0.22). The dominant parasitoid in this study was *Meteorus ictericus* Nees, accounting for 51 % of total parasitism for all four sites combined, while the second most abundant parasitoid was *Enytus eureka* (Ashmead), which contributed 34 % to the total parasitism. Parasitoid species and their relative frequency at each site are given in

Fig. 1 Population density (mean number of occupied leafrolls per minute per plant) of *Epiphyas postvittana* (LBAM) at two sites in both San Francisco (SF) and Santa Cruz (SC), California (*upper line graph*) and parasitism rates (*lower bar graph*) from 2008 to 2012. Note the differences in axis scale between sites

Table 1 Relative frequency of the resident parasitoids reared from *Epiphyas postvittana* at two sites in both San Francisco (SF) and Santa Cruz (SC)

SF1		SF2		SC1		SC2	
<i>Enytus eureka</i>	49.7 %	<i>M. ictericus</i>	50.6 %	<i>M. ictericus</i>	51.0 %	<i>M. ictericus</i>	62.3 %
<i>Meteorus ictericus</i>	43.8 %	<i>E. eureka</i>	43.7 %	<i>E. eureka</i>	13.7 %	<i>Hormius</i> sp.	12.6 %
Unidentified parasitoids	2.0 %	Unidentified parasitoids	2.0 %	<i>Pediobius ni</i>	11.7 %	<i>G. franciscana</i>	8.9 %
<i>Campoplex</i> sp.	1.0 %	<i>Campoplex</i> sp.	1.5 %	<i>C. hesperus</i>	7.9 %	<i>Ischnus inquisitorius</i>	6.8 %
<i>Exochus nigripalpus</i>	1.0 %	<i>Centeterus</i> sp.	1.0 %	<i>Nemorilla pyste</i>	4.9 %	Unidentified parasitoids	4.7 %
<i>Coccygomimus hesperus</i>	0.7 %	<i>Apanteles</i> sp.	0.5 %	<i>Hormius</i> sp.	2.9 %	<i>E. eureka</i>	2.6 %
<i>Centeterus</i> sp.	0.3 %	<i>Hormius</i> sp.	0.5 %	Unidentified tachinid sp.	2.9 %	<i>P. ni</i>	1.1 %
<i>Glypta franciscana</i>	0.3 %	<i>G. franciscana</i>	0.2 %	<i>Brachymeria ovata</i>	2.0 %	<i>C. hesperus</i>	0.5 %
<i>Hormius</i> sp.	0.3 %			Unidentified parasitoids	2.0 %	<i>E. nigripalpus</i>	0.5 %
<i>Itoplectis quadricingulata</i>	0.3 %						
Unidentified tachinid sp.	0.3 %			<i>Actia interrupta</i>	1.0 %		

Table 1. Rates of hyperparasitism were 0.31 (SF1), 0.23 (SF2), 0.00 (SC1) and 0.13 (SC2). Hyperparasitoid species were *Gelis* sp1, *Gelis* sp2, *Scambus* sp., *Mesochorus* sp. and unidentified spp, with *Gelis* sp1 being the most dominant hyperparasitoid accounting for 67 % of the total hyperparasitism. Hyperparasitism of *M. ictericus* was 0.16 for all sites combined compared to 0.77 for *E. eureka* and 0.07 on other parasitoid species.

Per capita survivorship from parasitism as a component Allee effect

The relationship between per capita survivorship from parasitism and *E. postvittana* population density at each sampling site was used to test for component Allee effects. These relationships were non-significant at the sites SF2 ($edf = 1$, $df = 44$, $t = 0.62$, $P = 0.54$) and SC1 ($edf = 1$,

Fig. 2 Relationship between per capita survivorship from parasitism and population density (mean number of occupied leafrolls per minute per plant) of *Epiphyas postvittana* (LBAM) at two sites in both San Francisco (SF) and Santa Cruz (SC), California, as estimated with GAMMs. Models are fitted for the two sites with significant effects of population density

$df = 46$, $t = 0.23$, $P = 0.82$), but were significantly positive at the sites SF1 ($edf = 1$, $df = 48$, $t = 2.04$, $P = 0.047$) and SC2 ($edf = 1$, $df = 37$, $t = 3.13$, $P = 0.003$) (Fig. 2), with the latter thus being consistent with component Allee effects.

Compensatory or depensatory density feedback

To determine whether *E. postvittana* population growth rates exhibited compensatory or depensatory density feedback, indicating the potential for regulation or a demographic Allee effect, we examined the relationship between per capita population growth rate and *E. postvittana* population density. There was a strong nonlinear decline in per capita population growth rate with increasing *E. postvittana* population density, over the entire range of densities observed, that was highly significant at all four sampling sites (Fig. 3; Table 2). The absence of a positive relationship between population growth rate and population density at the lowest population densities confirmed the absence of any demographic Allee effects, while the negative relationship with increasing *E. postvittana* population density indicated strong compensatory density feedback. At all sampling sites, per capita population growth rates became negative at modest *E. postvittana* population densities and were estimated to be zero,

representing the carrying capacity, at mean densities of 11.3, 6.8, 18.2 and 13.2 occupied leafrolls per minute for the sites SF1, SF2, SC1 and SC2 respectively.

To determine whether the compensatory density feedback could have been driven by parasitism as a potential regulating factor in *E. postvittana* populations, we examined the relationship between per capita population growth rate and parasitism rate at each sampling site. None of these relationships proved to be significant at any of the four sampling sites (Fig. 4; Table 2), suggesting that greater rates of parasitism did not influence per capita population growth rates and that resident parasitoids did not regulate *E. postvittana* populations.

Discussion

From this study, we found that although *E. postvittana* in California experienced a parasitism-induced component Allee effect at two of the four sampling sites, these component effects on survivorship from parasitism did not translate into demographic Allee effects at any of the sampling sites. We also found evidence for strong compensatory density feedback among *E. postvittana* populations at all four sampling sites, and that this was not caused by parasitoids as parasitism did not have any influence on

Fig. 3 Relationship between per capita population growth rates of *Epiphyas postvittana* (LBAM) and mean population density (mean number of occupied leafrolls per minute per plant) at two sites in both San Francisco (SF) and Santa Cruz (SC), California, as estimated and fitted with GAMMs

Table 2 GAMM models for the relationship between per capita population growth rates of *Epiphyas postvittana* at two sites in both San Francisco (SF) and Santa Cruz (SC)

Site	Predictor	edf	df	t	P
SF1	Density	7.52	46	7.52	<0.001
	Parasitism	1.00	45	0.25	0.81
SF2	Density	2.23	44	5.24	<0.001
	Parasitism	1.00	43	0.51	0.61
SC1	Density	3.15	45	3.47	0.001
	Parasitism	1.00	44	0.72	0.48
SC2	Density	3.77	36	3.69	<0.001
	Parasitism	1.00	35	0.79	0.43

California and mean population density and parasitism rate, with estimated degrees of freedom (edf) for the smoothing terms, degrees of freedom (df) and parameter significance

per capita population growth rates. Nonetheless, we found that parasitism rates from the species-rich assemblage of resident parasitoids were unusually high, especially in spring and late summer, indicating substantial biotic resistance.

The relationship between per capita survivorship from parasitism and population density was not significant for two of the sites, but positive for the other two sites, suggesting that at least some populations of *E. postvittana* in California experience increased survivorship with population density representing a component Allee effect (Stephens et al. 1999). In the context of the different steps in the invasion process, if a component Allee effect from

parasitism also generates a demographic Allee effect, it has the potential to impact small founder populations, preventing them from becoming established (Drake and Lodge 2006; Liebhold and Tobin 2008). While it is not uncommon for predators to induce component Allee effects (Gascoigne and Lipcius 2004; Angulo et al. 2007; Kramer et al. 2009; Kramer and Drake 2010), they only occasionally translate into demographic Allee effects (Angulo et al. 2007) due to the complex interaction of density feedbacks and density-independent factors acting on individual fitness (Gascoigne and Lipcius 2004). Similarly, for *E. postvittana* in California the component Allee effects from parasitism did not translate into demographic Allee effects, as per capita population growth rates did not show any evidence of an increase over the lowest range of population densities observed.

Surprisingly, we found that *E. postvittana* populations in California were influenced by compensatory density feedback at all four sampling sites, suggesting the potential for strong regulation. From life table studies of *E. postvittana* in Australia, Danthanarayana (1983) found that egg and 1st instar larval mortality were key factors in the dynamics of populations on apple trees and associated understory weeds. He identified arthropod predation as the most important source of mortality at all life stages, and that loss of potential fecundity, a factor that increased with larval density, also had an important influence on the egg stage. Since parasitism did not appear to influence per capita population growth rates of *E. postvittana* at any of the sample sites in California, other factors, such as generalist

Fig. 4 Lack of relationship between per capita population growth rates of *Epiphyas postvittana* and proportional parasitism rates at two sites in both San Francisco (SF) and Santa Cruz (SC), California, as estimated with GAMMs (see Table 2 for further details)

arthropod predation (Berryman 2002), and loss of potential fecundity either through food limitation or crowding (Snell et al. 2001; Rotem and Agrawal 2003), or through induced plant defenses (Karban and Baldwin 1997; Underwood 2000; Kessler et al. 2012) may have been responsible for the compensatory density feedback.

While generalist predators such as earwigs, spiders, and beetles have been observed to attack *E. postvittana* in its introduced range (Hogg et al. 2013), they are usually unable to generate strong responses due to a lack of aggregative or reproductive numerical responses to prey densities (Symondson et al. 2002; Gascoigne and Lipcius 2004), unless the prey species constitutes a major component of the total available prey (Symondson et al. 2002). Egg parasitism of *E. postvittana* by *Trichogramma fasciatum* and *T. platneri* was found to average 51 and 47 % from March to November 2009 and 2010 at the SC1 site (Roltsch et al. 2011), and has been recorded to be as high as 84 % in late summer (Wang et al. 2012). However, egg parasitism is typically rather lower earlier in the season, and more importantly, Roltsch et al. (2010) and Roltsch et al. (2011) found that *E. postvittana* eggs on *L. laevigatum*, the plant monitored at the two SF sampling sites in our study, were very rarely parasitized. We can therefore exclude egg parasitism as the main driver of the compensatory density feedback, at least for the two SF sites. Nonetheless, these unusually high parasitism rates by

Trichogramma species could make an important contribution to the suppression of *E. postvittana* populations in California.

Another factor often found to contribute to compensatory density feedback is crowding or food limitation (Snell et al. 2001; Rotem and Agrawal 2003). However, in our study the density feedback was strongest at the lowest *E. postvittana* densities (less than 20 individuals per minute per plant) and at these low densities no obvious crowding or food limitation was observed in the field. This suggests that the most likely explanation for the compensatory density feedback at such low densities is induced plant defense, which can theoretically influence herbivore population growth rates (Edelstein-Keshet and Rausher 1989; Underwood 1999; Abbott et al. 2008), and has experimentally been shown to lead to compensatory reductions in larval growth rate (Underwood 2010), per capita fecundity (Sarfranz et al. 2013) and population growth rate with increasing herbivore density (Underwood and Rausher 2002). Similarly, Kaplan and Denno (2007) highlighted the importance of indirect effects via induced defenses rather than direct reduction of resources via defoliation in mediating interspecific competition among insect herbivores. The difference in host plants between our study on ornamentals in California and the apple orchard study by Danthanarayana (1983) in Australia may also be responsible for differences in the importance of induced plant

defenses for the dynamics of *E. postvittana* in these two studies. Although none of these potential explanatory factors were included in our study of *E. postvittana* populations in California, both induced plant defense and egg parasitism deserve greater attention in the future.

While parasitism by resident parasitoids showed no evidence of being able to regulate *E. postvittana* populations in California, parasitism rates did reach high levels in spring and late summer, particularly at the two sampling sites in San Francisco. Thus parasitism of *E. postvittana* populations undoubtedly contributes to the suppression of their population abundance. Since the host plants and sampling sites in our study were specifically chosen to provide consistent populations of *E. postvittana* of sufficient abundance to withstand destructive sampling, it is also possible that they represented exceptions in comparison with lower density populations at other locations and on other host plants. Whether these lower density populations are regulated by parasitoids or other factors remains unknown, but nonetheless, they provide further support for the importance of biotic resistance in suppressing the abundance of *E. postvittana* in California. In addition, continued monitoring throughout the later stages of the invasion process may reveal changes in the relative importance of the factors that have a regulatory influence on *E. postvittana* populations.

We conclude that despite the lack of enemy release and high parasitism rates observed for *E. postvittana* in California, the biotic resistance provided by resident larval and pupal parasitoids did not exhibit the characteristics needed to regulate *E. postvittana* populations. Further investigation will be needed to elucidate the extent to which biotic resistance from resident natural enemies can delay the spread and limit the impact of this newly established leafroller in California. In addition, further studies are needed to better address population-level effects of biotic resistance in invasive populations in order to more fully understand the complex interactions among factors that influence the success or failure of exotic invasions. *Epiphyas postvittana* in California represents an unusual case of an exotic insect herbivore that has met far greater resistance from resident parasitoids than is typical for accidentally introduced insect herbivores. While this resistance appeared to suppress rather than regulate *E. postvittana* abundance in California it deserves to be investigated further in combination with the observed compensatory density feedback as factors potentially limiting the invasiveness of *E. postvittana* in North America.

Acknowledgments This research was supported by funding from USDA-APHIS and the California Department of Food and Agriculture. We thank numerous taxonomists that helped identify the parasitoids, including John Luhman (University of Minnesota), James O'Hara (Invertebrate Biodiversity, Agriculture and Agri-Food

Canada), and John Heraty (UC Riverside). We also thank Wayne Sousa for his helpful comments on an earlier version of this manuscript.

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