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Establishment of *Psyllaephagus parvus* and *P. perplexans* as serendipitous biological control agents of Eucalyptus psyllids in southern California

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Abstract The free-living lemon gum psyllid, *Cryptoneossa triangula* Taylor, and the lerp-forming spotted gum psyllid, *Eucalyptolyma maideni* Froggatt (Hemiptera: Psyllidae) are invasive pests of eucalypts in California. In 2007, *Psyllaephagus parvus* Riek (Hymenoptera: Encyrtidae) was discovered parasitizing spotted gum psyllids and *Psyllaephagus perplexans* Cockerell was collected from lemon gum psyllids. While neither parasitoid species was purposely introduced, presence of the parasitoids was significantly associated with reduced intensity and duration of population peaks for both psyllid species. Spring peaks were reduced more than fall peaks. We estimated minimum rates of parasitism from the ratio of mummies to live nymphs. Higher parasitism was recorded in coastal than inland locations during the spring, while parasitism was similar for coastal and inland populations in the fall. Logistic regression models suggest parasitoids were the determining factor of psyllid population densities, although physical parameters, such as irrigation, may affect psyllid or parasitoid populations.

Keywords *Cryptoneossa triangular* · *Eucalyptolyma maideni* · *Psyllaephagus parvus* · *Psyllaephagus perplexans* · Psyllidae · Eucalyptus

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Introduction

Eucalyptus trees have been important components of the California landscape for 150 years (Doughty 2000). Eucalypts were initially imported for timber, but are currently used as ornamental landscape or windbreak species and can now be found in most California regions with suitable climates. Until 1984, eucalypts were free of both insect and disease pests. Since that time, however, a series of herbivorous insect species across at least four feeding guilds have invaded California and are now causing significant damage to many of the eucalypt species in the state (Gill 1998; Paine et al. 2011). Since eucalypts are planted widely in California and many trees are quite large, biological control programs offer the only economically and logistically feasible mechanism for controlling many of the invasive eucalyptus herbivores.

Psyllids are one of the feeding guilds that have been particularly destructive and have a widespread impact on eucalypts in California landscapes (Dahlsten et al.

2005). Many psyllids live and feed under starchy shelters, called lerps, constructed from excreted honeydew (Basden 1970). The accumulation of these lerps and honeydew on leaves and under infested trees creates a nuisance, while heavy infestations lead to defoliation, branch dieback and occasionally tree death (Paine et al. 2000). Infestations are highly visible due to the presence of lerps and sooty mold, creating cosmetic damage as well. As with a similarly visible pest, the ash whitefly, even moderate infestations may affect the quality of container-grown trees from nurseries (Bellows et al. 1990) and decrease the value of infested trees used for ornamental landscaping (Jetter et al. 1997).

Spotted gum psyllid *Eucalyptolyma maideni* Froggatt (Hemiptera: Psyllidae) was first observed in Orange County, California, USA in August 2000 colonizing the foliage of spotted gum *Corymbia* (*Eucalyptus*) *maculata* (Hook) Hill & Johnson and lemon gum *Corymbia* (*Eucalyptus*) *citriodora* (Hook) Hill & Johnson. Spotted gum psyllid has spread through many counties of California (Garrison and von Ellenreider 2003). The lerp of spotted gum psyllid is shaped like a feather, with many lateral ribs forming a narrowed, closed end at its inception and a larger, opened end as the lerp increases in size. Lerps typically reach 6 × 3 mm in width. Several nymphs may inhabit one lerp, and move freely in and out of lerps (Morgan 1984). A closely associated species, lemon gum psyllid *Cryptoneossa triangula* Taylor (Hemiptera: Psyllidae), appeared in California in 1995 (Gill 1998). Lemon gum psyllid does not construct a lerp itself, but uses the lerps of spotted gum psyllid for shelter. As such, lemon gum psyllid can occur in high numbers when spotted gum psyllid is present.

Through foreign exploration trips in Brisbane and Adelaide Australia, we identified *Psyllaephagus parvus* Riek (Hymenoptera: Encyrtidae) as a key biological control agent for spotted gum psyllid. The parasitoid was then imported from material collected in and near Adelaide Australia, and established at the University of California, Berkeley Quarantine Facility in 2004 and 2006. Non-target studies were begun for permit applications for field release to the Animal Plant Health Inspection Service (APHIS) of the US Department of Agriculture. However, prior to any field releases, field populations of spotted gum psyllid nymphs in southern California were found to already be attacked by *P. parvus*. Consequently, imported parasitoids from the quarantine colony were not released. Parasitized spotted gum psyllid nymphs were first observed in southern California in summer 2007 in Riverside, San Diego and Orange counties. In fact, two parasitoids were found attacking psyllids on spotted gum trees in southern California. *P. parvus* was discovered parasitizing spotted gum psyllid nymphs, while *Psyllaephagus perplexans* Cockerell (Hymenoptera: Encyrtidae) was collected from lemon gum psyllid nymphs.

Here, we describe population levels of the psyllids and their parasitoids. In preparation for the classical biological control program, directed against spotted gum psyllid, we had established long-term monitoring plots to develop base-line data. One plot was at a coastal location and another in the southern interior valley. These sites were established two years before parasitoids were detected. Following discovery of the parasitoids in field populations, we expanded the monitoring efforts with four additional sites, two coastal and two inland locations. All sites were monitored for three years after parasitoids were discovered. We discuss the impact of these parasitoids on spotted gum psyllid and lemon gum psyllid populations, factors that may impact parasitoid performance, and the relevance of these parasitoids to psyllid suppression in southern California.

Methods

Site characteristics

Long term monitoring sites were established in 2004 in one coastal and one inland location. Four additional sites were added after parasitoids were detected in 2007 (Table 1). Coastal sites were located in (1) Tustin (roadside landscaping), (2) Irvine (along a city bike path), and (3) San Diego (on the University of California San Diego campus). Inland sites were located in (1) Riverside (in a spotted gum eucalyptus plantation on the University of California Riverside's Agricultural Experiment Station), (2) Campus (on the University of California Riverside campus using established landscape plants) and (3) Redlands (in a business complex parking lot landscaped with eucalyptus). Ten trees were selected for monitoring at each site.

Table 1 Physical characteristics for long-term and post-parasitoid establishment psyllid monitoring sites in southern California

	T (°C) Jan/Jul[a]	Precipitation (cm)[b]	Location	Irrigation	Ground cover
Tustin[c]	20/29	35	33°44′37″N 117°46′48″W	Yes	Grass
Irvine	20/29	35	33°39′53″N 117°47′33″W	Yes	Litter
San Diego	19/27	30	32°52′22″N 117°13′58″W	No	Litter
Riverside[c]	19/34	27	33°57′52″N 117°19′54″W	No	Litter
Campus	19/34	27	33°58′15″N 117°19′31″W	Yes	Shrubs
Redlands	18/34	35	34°03′28″N 117°11′48″W	Yes	Shrubs

[a] Average daily maximum for January and July for each site (long term average from National Oceanic and Atmospheric Administration)

[b] Long term annual average (National Oceanic and Atmospheric Administration)

[c] Long-term monitoring plots, where psyllid populations were sampled before and after establishment of *Psyllaephagus* species

Adult psyllid populations at long term monitoring sites in Tustin and Riverside were tracked from summer 2004 through December 2009. Psyllid parasitoids for both spotted gum and lemon gum species were verified present at all sampling sites during the spring-summer in 2007. Monitoring in San Diego and Irvine began in spring 2007. Monitoring in Redlands and the Riverside Campus location began in spring 2008. Daily temperature, humidity and precipitation data were obtained from the University of California IPM Weather Database for sites in Tustin, Irvine, San Diego and Riverside. Weather data for Redlands were obtained from the San Bernardino County Water Resources Board.

Psyllid and parasitoid monitoring

Adult psyllid populations were monitored using one sticky trap in each selected tree. The traps consisted of a transparent 10 cm plastic disk (polypropylene deli container lid) coated with a thin layer of motor oil additive (STP® Oil Treatment) and clipped over a yellow background. Previous research has shown that adult female psyllid catch rates are correlated with nymph and egg densities on eucalyptus leaf samples, as well as activity periods of adult psyllids (Dahlsten et al. 2005). Trap samples were collected approximately weekly or biweekly throughout the study. Weekly samples were collected for periods and/or sites when there was high psyllid abundance. In the laboratory, all psyllid adults on each trap were counted and identified to species. Psyllid counts were calculated as psyllids per week per tree. Sticky traps were also monitored for the presence of adult parasitoids throughout the entire study period beginning in 2004.

In 2008 and 2009, leaf samples were collected every three weeks during the period of peak psyllid activity which occurs in spring and early summer. Additional samples were collected in fall 2008 and 2009. We collected foliar samples of 30 cm long branch tips at mid-crown height from two points spaced randomly around the tree canopy using a pole-pruner with an attached basket lined with a 125 liter trash bag attached below the pruner to catch cut foliage. Immediately after each cut, the trash bag was closed to minimize loss of insect fauna. Collected foliage was stored in an ultracold (−65°C) freezer in the laboratory. All psyllid nymphs and mummies on leaves were counted and identified. Early instars with no wing buds were grouped together (1st and 2nd instars). Wing buds on psyllids are typically visible from the 3rd instar. Older nymphs were identified to species (3rd–5th instars). Psyllid parasitoids primarily attack 3rd through 5th instars (Daane et al. 2005). Since both spotted gum psyllid and lemon gum psyllid occur under lerps, grouping by the youngest instar allowed for reasonable processing time while still providing full species identification for stages available for parasitoids.

We estimated a minimum rate of parasitism from the ratio of mummies to live nymphs. Rates of parasitism were calculated from the total number of older nymphs (wing buds present) and mummies for each psyllid species. Total nymph and mummy counts for all ten trees at each site were pooled in each sampling period to calculate rate of parasitism.

To investigate the impact of hyperparasitism we collected leaf samples from one coastal and one inland location in June 2010. Samples were bulk samples from multiple trees, estimated to include enough foliage to provide near 100 mummies of each parasitoid species. After collection, fresh leaves were examined and all mummies were removed using a hole punch to excise the mummy and leaf tissue it was attached to. All other insects were removed from the leaf disk, and the disks were placed in gelatin capsules and stored at room temperature until parasitoids emerged (2–3 weeks). Parasitoids were frozen in an ultracold (−65°C) freezer, and then identified by comparison to type specimens.

Additionally, leaf samples were taken in northern California to determine whether the parasitoids, *P. parvus* or *P. perplexans*, had dispersed from southern California. Two sites on the University of California Berkeley campus were searched monthly and sampled every 4–8 weeks from 2007 to 2010. Spotted and lemon gum eucalyptus are not as frequently planted in northern California, and fewer trees were available to sample at each site; two or three trees were sampled at each site. When lerps were observed, we collected foliar samples of 30 cm long branch tips at lower- and mid-crown heights, dependent on tree height, as described previously. Collected foliage was searched in the laboratory and the number of lerps with live 3rd–5th instar psyllids was recorded. Infested leaves were detached, placed in an emergence container, and held at 25 ± 2°C for emergence of adult parasitoids.

Statistical analysis

To evaluate the impact of parasitoids on psyllid populations, only adult trap catches from the long term sites at Riverside and Tustin were used. We compared the duration and intensity of psyllid population peaks before and after parasitoid establishment. Psyllid abundance was classified into four intensity levels. Classes were assigned based on areas of change in slope for a distribution graph for number of psyllid trapped in each sample. Trap catches below five females per week were considered non-peak. Peak intensity was classified as small (5–9 females per week), medium (10–14 females per week) or high (≥15 females per week). Intensity was calculated as the days above each abundance level during these peaks. Peak duration was the longest period when psyllid trap catches remained above five females per week for spring and fall each year. We compared average intensity and duration of population peaks for both psyllid species before and after parasitoid establishment.

We used a G-test (Sokal and Rohlf 1981) to see if peak duration or peak intensity differed before and after parasitoid establishment. We estimated normal periods of peak psyllid populations by comparing trap data from all our sites over the course of the study. Psyllid populations were likely to peak between February and July for spring and between October and December for fall. This gave a maximum range of 170 days for spring peaks and 90 days for fall peaks. Peak abundance levels were determined only for psyllids during these periods. G-tests for peak intensity had three df, and for peak duration had one df.

To investigate the relationship of psyllid abundance with environmental parameters and the presence of parasitoids, we built models using logistic regression (SAS Institute Inc. 2003) and used Akaike's Information Criterion, modified for small sample size (AIC_c; Burnham and Anderson 1998), to identify the best models for predicting psyllid populations. We chose logistic regression for model building because of the mix of categorical and continuous variables in our data set. Logistic regression evaluates the functional relationship between a discrete dependent variable and one or multiple independent variables that may be discrete or continuous. AIC incorporates the log-likelihood with a penalty for added parameters. This information-theoretic approach facilitated selecting a best model (lowest AIC) and ranked the remaining models (Burnham and Anderson 1998). The difference between the AIC score for the best model and each model with only one of the explanatory variables is an indication of the relative importance of each variable. Models within two AIC units of the best model have strong support while models more than ten AIC units from the best model have no support. We also report traditional goodness-of-fit measures for each model (Wald's χ^2, *P*).

Because of the seasonality of psyllid populations and occasional extreme peaks, psyllid abundance was skewed and had high variance. Therefore, we assigned female trap catches into a small number of abundance classes to reduce the variability. Classes were assigned in categories from low to high abundance as 0 = none, 1 = <5, 2 = <10, 3 = <15 and 4 = ≥15 females per week. Classes were assigned based on areas of change in slope for a distribution graph for number of psyllid trapped in each sample.

We constructed separate models for coastal and inland psyllid abundance for each psyllid species. Site parameters included total precipitation during each trap period and average daily maximum temperature and humidity for each trap period. Samples collected from 2004 through 2006 were scored as parasitoids absent while samples collected from 2007 through the duration of the study were scored as parasitoids present. Models for lemon gum psyllid included a variable for spotted gum abundance class.

Similar models were constructed for rates of parasitism and environmental factors for leaf samples. Data for regression models on rate of parasitism were from samples collected only during periods of high psyllid abundance. Precipitation was not included in these regressions because psyllid peak populations occurred during times of low rainfall in southern California. Data from the inland site at Redlands were not included because weather data were incomplete for that site.

Results

Characteristics at long term monitoring sites

Adult parasitoids were not observed on sticky traps until the spring peak in 2007. After adult parasitoids were observed on traps, the presence of mummies was verified at all sites. Adult parasitoids were present on sticky traps during psyllid population peaks from 2007 onwards.

Parasitoids reduced both the duration and intensity of the seasonal peaks in each psyllid species (Table 2). Peak intensity during the spring, measured as the distribution of days in each psyllid abundance class, was significantly different before and after parasitoid establishment for both inland and coastal populations for both psyllid species. Peak intensity during fall was also significantly decreased, but was less impacted than spring peaks, with spotted gum

Table 2 Average intensity and duration of spotted gum psyllid (SGP) and lemon gum psyllid (LGP) population peaks, showing abundance levels for days above low, medium and high psyllid abundance

	G_{adj} comparing before and after parasitoid					Days above abundance level (%)						Duration	
	SGP		LGP			SGP			LGP			SGP	LGP
	Intensity	Duration	Intensity	Duration		5+	10+	15+	5+	10+	15+		
Inland													
Spring	218.5**	199.9**	260.7**	207.2**	Before	70	38	25	85	77	63	138	163
					After	9	3	0	24	6	5	11	16
Fall	13.3*	4.8*	10.4*	2.2	Before	33	24	13	17	8	3	32	16
					After	19	11	2	7	0	0	14	7
Coastal													
Spring	35.3**	25.6**	62.3**	37.5**	Before	26	11	0	42	25	16	41	67
					After	5	1	1	10	0	0	7	14
Fall	8.1*	0.09	55.5**	18.2**	Before	30	13	10	58	37	11	28	57
					After	33	19	3	31	0	0	21	20

The range for spring peaks is 170 days and 90 days for fall peaks. Values are significantly different before and after parasitoid establishment at * $\alpha \leq 0.05$ and ** $\alpha \leq 0.001$

psyllid populations in coastal sites showing decreased intensity only for the highest abundance class for female trap catches.

Duration of spring peaks was significantly shorter after parasitoid establishment for both inland and coastal populations (Table 2). Spring peak duration for inland psyllid populations decreased by more than 90% after parasitoid establishment for both spotted gum and lemon gum psyllids. Spring peak duration decreased by 75% for coastal populations. Fall peak duration was less impacted by parasitoid establishment, and decreased only for spotted gum psyllid at the inland site, and for lemon gum psyllid at the coastal site.

Before the parasitoid was established, peak duration for both psyllid species during spring was three times longer at the inland site compared to the coastal site, and peak populations were also higher (Fig. 1). After parasitoid establishment, spring peak intensity and duration were more similar for the inland and coastal site. Fall peak intensity for spotted gum psyllid was similar for the inland and coastal site. Lemon gum psyllid peak duration during the fall was longer for the coastal site than for the inland site, and remained longer even after parasitoid establishment.

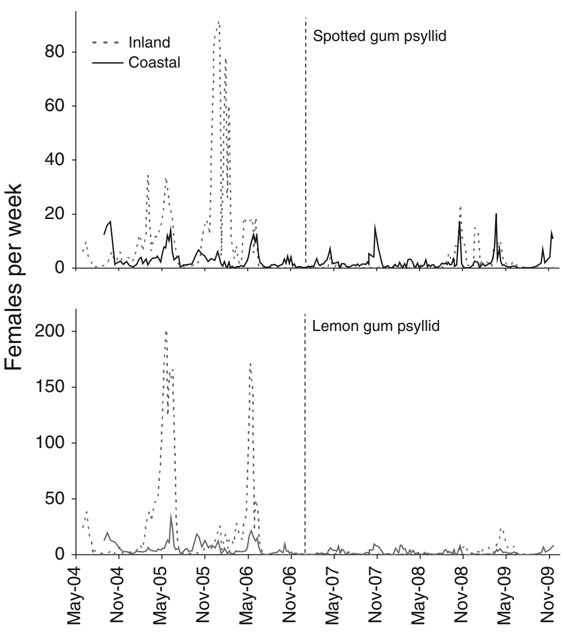

Fig. 1 Adult female trap catches at long term monitoring sites. Vertical dashed line indicates when parasitoids were detected in field populations

Regression models for long term monitoring sites

Trap catches of spotted gum females for both inland and coastal populations were best predicted by whether or not the parasitoids were present at the time of sampling (Table 3). No other factor was within ten AIC units of the best model for inland populations. Environmental factors had some support for predicting coastal spotted gum psyllid trap catches, but were greater than two AIC units away and did not generate models with a significant Wald's χ^2. The best models for predicting lemon gum psyllid trap catches for both coastal and inland sites included the abundance rank for spotted gum psyllids and the variable for parasitoid presence (Table 3). Spotted gum psyllid abundance alone also had some support for predicting lemon gum psyllid trap catches for

Table 3 Model results for predicting psyllid abundance at long term monitoring sites (inland $n = 229$, coastal $n = 228$)

Model	AIC_c	ΔAIC	Wald's χ^2	*P*
Inland: spotted gum				
Parasitoid present	608.9	0	28.6	<0.001
RH max	633.7	24.8	5.6	0.02
Precipitation	635.3	26.4	3.0	0.08
T max	637.7	28.8	1.0	0.32
Coastal: spotted gum				
Parasitoid present	285.5	0	6.8	0.01
T max	292.0	6.5	0.7	0.41
RH max	292.4	6.9	0.3	0.59
Precipitation	292.5	7.0	0.2	0.65
Inland: lemon gum				
Parasitoid + SGP	494.2	0	114.4	<0.001
SGP abundance class	502.1	7.9	111.6	<0.001
Parasitoid present	624.0	129.8	39.7	<0.001
RH max	648.1	153.9	18.1	<0.001
Precipitation	660.3	166.1	0.13	0.71
T max	665.9	171.7	0.53	0.47
Coastal: lemon gum				
Parasitoid + SGP	280.0	0	67.9	<0.001
SGP abundance class	300.7	20.7	57.2	<0.001
Parasitoid present	354.5	74.5	19.4	<0.001
Precipitation	375.3	95.3	0.02	0.90
T max	375.3	95.3	0.03	0.86
RH max	375.3	95.3	0.01	0.91

Models with one predictor variable had one df, models with two predictor variables had two df inland populations, but not coastal. None of the environmental parameters produced a model within ten AIC units of the best model for lemon gum psyllids.

Parasitoid performance

The average rate of minimum parasitism of spotted gum psyllid over all leaf samples collected was 13% for the coastal sites and 9% for the inland sites. Overall parasitism of lemon gum psyllid was 21% for the coastal site and 6% for the inland site. Parasitism of spotted gum psyllid was generally higher in the fall than in the spring for both coastal and inland sites (Fig. 2). Parasitism rates of lemon gum psyllid were consistent during both spring and fall for the coastal psyllid populations, but much lower in the spring than in the fall for inland sites.

There were no significant differences among the six sites for rate of parasitism of spotted gum psyllid in spring ($F_{5,71} = 2.8$, $P = 0.03$, no significant comparisons for Tukey's Studentized Range Test) although parasitism tended be lowest at the Redlands and Riverside locations (data not shown). During the spring, parasitism of lemon gum psyllid was higher for all three coastal sites compared to all three inland sites coastal sites ($F_{5,71} = 22.5$, $P < 0.001$). There were no significant differences in parasitism among sites for spotted gum ($F_{5,16} = 1.7$, $P = 0.19$) or lemon gum psyllid ($F_{5,16} = 0.9$, $P = 0.50$) during the fall.

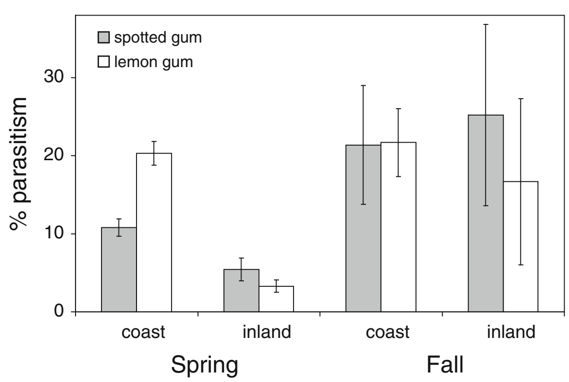

Fig. 2 Estimated minimum rate of parasitism of spotted gum and lemon gum psyllids after parasitoid establishment (mean and SE). Data combined for three coastal and three inland sites for each season. Spring had six and fall had three sampling periods

Regression models for predicting the rate of parasitism were constructed with data from leaf samples collected during typical spring and fall peaks. Parasitism of spotted gum psyllid from inland sites was best predicted by irrigation being present (Table 4). There was also strong support for seasonality, with parasitism being higher in the fall than in the spring. Parasitism of lemon gum psyllid at inland sites was best predicted by season, where parasitism was higher in the fall than in the spring. There was also some support for the model with humidity. The two predictors are correlated since humidity tended to be higher in the fall than in the spring at inland sites.

For coastal sites, parasitism of spotted gum psyllid was best predicted by season, although all models were within two AIC units of the best model (Table 4). Parasitism of lemon gum psyllid at coastal sites was best predicted by temperature, although all models were within two AIC units of the best model. However, no models for parasitism of spotted gum or

Table 4 Model results for predicting percentage parasitism

Model	AIC_c	ΔAIC	Wald's χ^2	*P*
Inland: spotted gum				
Irrigation	260.1	0	7.8	0.001
Season	261.2	1.1	6.8	0.01
T max	266.0	5.9	3.3	0.07
RH max	268.4	8.3	0.2	0.63
Coastal: spotted gum				
Season	381.4	0	0.3	0.26
RH max	382.2	0.8	0.5	0.47
T max	382.3	0.9	0.5	0.49
Irrigation	382.7	1.3	0.04	0.84
Inland: lemon gum				
Season	205.2	0	5.9	0.02
RH max	210.2	5.0	1.2	0.28
Irrigation	260.3	55.1	1.0	0.31
T max	260.8	55.6	0.6	0.43
Coastal: lemon gum				
T max	472.3	0	0.6	0.44
Irrigation	472.8	0.5	0.1	0.74
RH max	472.8	0.5	0.1	0.77
Season	472.9	0.6	0.01	0.94

Parasitism is calculated from pooled samples for each site and sampling date (inland $n = 32$, coastal $n = 53$, df for all regressions = 1) lemon gum psyllids at the coastal sites had a significant Wald's χ^2.

Hyperparasitism

We collected 81 spotted gum psyllid mummies from the coastal site and 212 from inland site. We had 141 and 71 mummies from lemon gum psyllids from coastal and inland sites, respectively. Approximately 40% of mummies failed to produce adult parasitoids and were excluded from hyperparasitism calculations. Wasps that did not match our two parasitoid species were preliminarily identified as probable hyperparasitoids by John Andrews (University of California Berkeley). Full identification will take some time due to poorly developed keys for Australian *Psyllaephagus* and many undescribed species. Hyperparasitism was higher for spotted gum psyllid than for lemon gum psyllid, but was similar for coastal and inland sites. For mummies that produced adult wasps, hyperparasitoids of spotted gum psyllid accounted for 35% (coastal) and 37% (inland) of all emerged adults. Hyperparasitoids of lemon gum psyllid accounted for 21% (coastal) and 14% (inland) of all emerged adults.

Northern California

Psyllid populations in northern California peaked later in the season, as compared with the southern California sites we monitored, with the most lerps and live psyllids collected from June through August. At collections during these peak periods, between 200 and 500 psyllids (material was not separated by species) were placed in emergence containers on each of 2–4 sampling periods per year. No parasitoids were reared from this material.

Discussion

We found that self-introduced parasitoids of spotted gum psyllid and lemon gum psyllid had a significant impact on the intensity and duration of seasonal peaks in psyllid populations in southern California. Psyllid peaks were reduced in both coastal and inland locations, but the effect was much greater for inland populations. Before parasitoid establishment, spring population peaks were much more severe at inland than coastal monitoring sites. After parasitoid establishment, parasitoid peaks were reduced in both locations, and were more similar for coastal and inland locations. Both spring and fall peaks were affected, but the effect was greater for spring populations.

For both coastal and inland populations, the presence of the parasitoid was the single greatest factor in predicting spotted gum psyllid populations. Lemon gum psyllid populations were also strongly associated with the presence of the parasitoids, but also associated with spotted gum psyllid abundance. Lemon gum psyllid uses the lerps of spotted gum psyllid, so this association was expected. While the presence of the parasitoid was by far the strongest factor for predicting psyllid populations for inland populations, models for the association of humidity and psyllid abundance also produced a significant regression. Inland psyllid populations tended to be higher during periods of higher humidity and moderate temperature. Coastal psyllid populations were not significantly associated with any of the environmental parameters we measured.

We examined factors associated with parasitoid performance during periods when psyllid populations were at their peaks. For both coastal and inland populations, rates of parasitism of spotted gum psyllid were higher in the fall than in the spring. However, neither temperature or humidity was significantly associated with rates of parasitism for spotted gum psyllid. Lemon gum parasitoids performed equally well in spring and fall for coastal locations. Inland locations had higher parasitism in the fall than in the spring. Inland California has warmer summers and cooler winters compared to the more mild coastal regions. Differences in parasitoid performance between coastal and inland locations are likely due to these climatic differences. Parasitoids of another eucalyptus pest, the red gum lerp psyllid *Glycaspis brimblecombei* Moore, also performed better in coastal locations compared to inland locations (Dahlsten et al. 2005). Rates of hyperparasitism were similar for coastal and inland sites, and are not likely contributing to the difference in parasitoid performance for coastal and inland locations.

For inland populations, parasitism was higher on sites where trees were irrigated. Irrigation did not affect parasitism for coastal populations. The reasons for this association cannot be conclusively determined from our study. Parasitoids may perform better in areas where spotted gum trees are irrigated because of differences in tree growth, which could affect leaf quality. Differences in leaf quality could impact parasitoids directly or indirectly through differences in psyllid performance. Irrigated inland sites also had shrubs and other ornamental plants near eucalyptus trees. Differences in landscaping complexity and nearby nectar sources could also influence parasitoid populations. We also note that spotted gum psyllid populations in northern California were not attacked by *P. parvus*, and yet remained at lower densities. While studies at these northern sites were limited, it was apparent that poor overwintering survival of the psyllid populations may have helped keep their numbers in check under the colder and wetter climate.

Biological control agents have been released for two other psyllid pests in California. The blue gum psyllid, *Ctenarytaina eucalypti* (Maskell) is considered successfully controlled by the parasitoid *Psyllaephagus pilosus* Noyes (Dahlsten et al. 1998). Parasitism rates of blue gum lerp psyllid were 50–100% the year after parasitoid release (Dahlsten et al. 1998; Paine et al. 2000). Moderate control of the red gum lerp psyllid has been achieved with the parasitoid *P. bliteus* (Daane et al. 2005; Dahlsten et al. 2005). The statewide average parasitism of red gum lerp psyllid was 22% (Dahlsten et al. 2005). This was sufficient impact to reduce defoliation and tree death of red gum eucalyptus. We calculated a minimum rate of parasitism for spotted gum psyllid and lemon gum psyllid near 20%. Most *Psyllaephagus* spp. are koinobiont (Dahlsten et al. 2005; McDaniel and Moran 1972; Patil et al. 1993). It is therefore likely that this study underestimates parasitism since it is based on apparent parasitism from the ratio of mummies to live nymphs. The duration of psyllid spring population peaks has been drastically reduced. We expect that this will also serve to limit tree death and defoliation for spotted gum and lemon gum eucalyptus.

The source of the two parasitic wasps discovered in California remains a question. In spite of continuous monitoring for adult parasitoids on sticky traps from 2004 onward, we did not detect parasitoids until 2007. There have been at least 16 invasive insect pests of eucalyptus introduced into California (Paine et al. 2011), all in the absence of natural enemies. All of the invasive psyllids have become established first in California and have been subsequently discovered in other eucalypt growing regions of the world (Paine et al. 2010). The only documented example of a eucalypt-feeding insect and its natural enemy establishing simultaneously occurred on the Isle of Man with the introduction of *C. eucalypti* accompanied by its parasitoid *P. pilosus* Noyes (Bennett 2005). It is important to note that *C. eucalypti* had been brought under complete biological control in California following the intentional introduction of *P. pilosus* almost a decade earlier (Dahlsten et al. 1998).

Lemon gum psyllid was present in California for more than a decade and spotted gum psyllid had been reported in southern California for at least seven years with no reports of natural enemies, despite extensive sampling across a broad geographic area (personal observation). In a single summer, the two parasitoids were collected in both inland and coastal locations in southern California. It is possible that they had been present since the psyllids had initially established, but their populations were at such low levels as to be undetectable. However, introductions of both herbivores and their natural enemies would imply that there had been a large initial population of psyllids introduced into the new environment (Lockwood et al. 2005; Von Holle and Simberloff 2005). Alternatively, there could have been repeated introductions of infested host material that included both the parasites and their hyperparasitoids.

A classical biological program directed against the spotted gum psyllid was in the final stages leading to release of a parasitoid from quarantine when that species was discovered preying on field populations of the psyllid. In addition, a second species of parasitoid not under consideration for release was discovered preying on the lemon gum psyllid. We had been systematically monitoring psyllid population sizes and temporal patterns of growth and decline for several years in preparation for natural enemy releases. Having the pre-release data has fortunately enabled us to evaluate the impact of the unanticipated appearance of the parasitoids on psyllid populations and the success of a serendipitous biological control program. Although not optimal because of the presence of hyperparasitoids in the community, psyllid populations were substantially reduced by the parasitoids. Whether the reductions will be enough to offset psyllid damage remains to be determined.

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