Chapter 9

Successful Biological Control of Glassy-Winged Sharpshooter, *Homalodisca vitripennis*, in Invaded Regions

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NON-TECHNICAL SUMMARY

Glassy-winged sharpshooter, *Homalodisca vitripennis* (Hemiptera: Cicadellidae), is an example of a U.S.-native insect that became a serious pest by invading new parts of the United States and other countries that lie beyond its native range. This pest has been accidentally moved into new areas through trade in live plants, which can carry its egg masses on the plants' leaves. In the absence of specialized egg parasitoids, *H. vitripennis* populations can reach extremely high densities. *Homalodisca vitripennis* is also problematic, in part, in native areas and parts of the invaded range, because of its ability to transmit subspecies of a xylem-limited bacterium, *Xylella fastidiosa*, which causes several lethal, scorch-like diseases in plants. The most infamous of these is Pierce's disease of grapes. In all invaded regions (i.e., California, French Polynesia, Hawaii, Cook Islands, and Easter Island), *H. vitripennis* has been successfully controlled through intentional or accidental introductions of the egg parasitoid *Cosmocomoidea ashmeadi*.

HISTORY OF INVASION AND NATURE OF PROBLEM

The Species Invasion

Glassy-winged sharpshooter, *Homalodisca vitripennis* (Hemiptera: Cicadellidae: Proconiini) (**Fig. 1**), formerly known as *H. coagulata*, is native to the southeastern United States and northeastern Mexico (Triapitsyn and Phillips, 2000). Sometime in the 1980s, *H. vitripennis* was accidentally introduced into southern California, most likely through trade in live ornamental plants from the southeast United States (i.e., intracontinental movement) (Sorensen and Gill, 1996; Blua et al., 1999). Following its introduction into California, this pest had high population growth, and these high-density populations potentially enabled further invasions into new areas. In 1999, *H. vitripennis* established in Tahiti and rapidly spread through French Polynesia (Grandgirard et al., 2000). It is likely *H. vitripennis* was introduced into Tahiti on nursery

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plants that originated from California. In 2004, *H. vitripennis* was recorded from Hawaii, and then from Easter Island and the Cook Islands in 2005 and 2007, respectively (Petit et al., 2008a; Rathe et al., 2015). In all instances, movement of live plants was the most likely conduit for long distance spread into new areas of the South Pacific. *Homalodisca vitripennis* eggs (**Fig. 2**) on the undersides of leaves were probably the life stage that was moved undetected into new areas (Petit et al., 2009). Long distance movement of adult *H. vitripennis* in the absence of host plant material via aircraft may also be possible, but the fitness of surviving females may be reduced by a lack of food and exposure to low temperatures in cargo storage areas (Rathe et al., 2015).

Figure 1. Adult glassy-winged sharpshooters, *Homalodisca vitripennis*, feeding on a citrus plant. (Mike Lewis, Center for Invasive Species Research, UC Riverside)

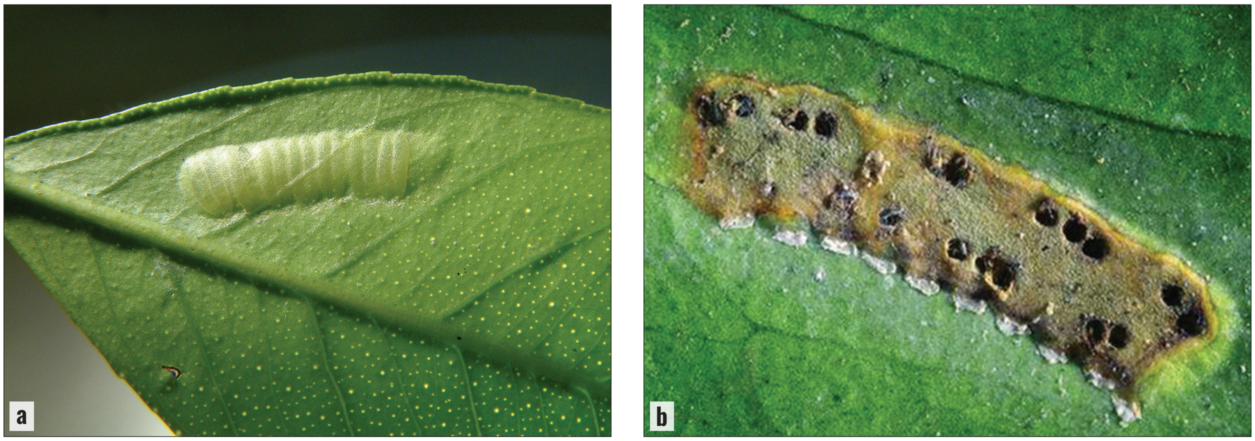

Figure 2. (a) *Homalodisca vitripennis* egg mass laid underneath the epidermis on the underside of a citrus leaf. An egg mass is comprised of individual eggs laid side by side. (b) *H. vitripennis* egg mass with emergence holes made by adult parasitoids that emerged from eggs. (a: Mike Lewis, Center for Invasive Species Research, UC Riverside; b: Regents, University of California)

Nature of the Problem

The damage *H. vitripennis* does, in both its native region and parts of its invaded range, is due primarily to its ability to transmit a xylem-limited bacterium, *Xylella fastidiosa*, of which at least five different subspecies have been identified (Baldi and La Porta, 2017). These subspecies may cause lethal diseases to some crops, urban ornamental plants, and native trees. Some well-known plant diseases that result from *X. fastidiosa* infection following *H. vitripennis* feeding include Pierce's disease of grapes, oleander leaf scorch, and similar maladies in liquidambar (**Fig. 3**), almonds, peaches, plums, and olives. Several of these diseases (e.g., olive leaf scorch) had not been observed prior to the establishment of *H. vitripennis* in California. This pest also increased the severity of existing *X. fastidiosa* problems in California, especially Pierce's disease in grapes. These outcomes were most likely the result of high *H. vitripennis* population densities and broad host range (Sicard et al., 2018). Fortunately, these diseases have not been observed following extra-continental invasion of *H. vitripennis* into the South Pacific as it appears that there were no sources of *X. fastidiosa*, despite the potential of imported plant species being present that could act as asymptomatic reservoirs of *X. fastidiosa*.

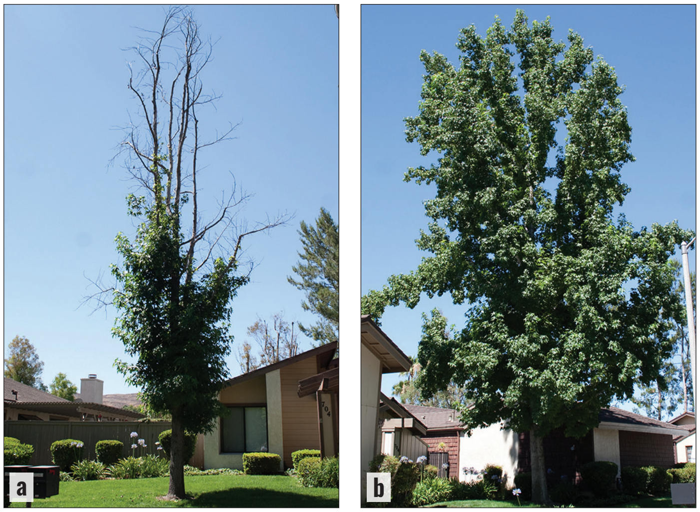

Figure 3. (a) Liquidambar tree in an urban area of southern California showing decline due to infection with *Xylella fastidiosa;* (b) a healthy liquidambar devoid of symptoms. (a,b: Mark Hoddle, UC Riverside)

It should also be noted that *X. fastidiosa* has invaded new regions (e.g., Italy [Sicard et al., 2018; Lindow, 2019]) independently of *H. vitripennis*.

Another problem with high densities of *H. vitripennis* nymphs and adults is that they are a significant public nuisance due to their production of copious amounts of watery waste that "rains" down from host trees such as crepe myrtle (*Lagerstroemia* spp.). Tree fruit productivity (e.g., of mangoes in French Polynesia) may decline under such heavy feeding pressure. Furthermore, adult insects are attracted to lights at night and readily fly in through open windows and doors, especially in tropical areas. Each morning there is a need to clean up and remove hundreds of dead insects from light fixtures, floors, tabletops, porches, etc. Another problem arises when adult *H. vitripennis* "buzz" people's heads when they are attracted to lights at night as the wing beat frequency can be very irritating to some people's hearing. Rarely, adult *H. vitripennis* may land on people and attempt to probe exposed skin, and "bites" of this nature are painful.

In French Polynesia, *H. vitripennis* may have had a significant negative impact on populations of native spiders. Laboratory and field studies indicated that *H. vitripennis* adults and nymphs were toxic to some species of native spiders that consumed them. The mechanism underlying this putative toxic effect is unknown but could have increased invasion severity in French Polynesia through the creation of natural enemy free space (Suttle and Hoddle, 2006).

WHY CONTROL THIS INVASIVE SPECIES?

Homalodisca vitripennis is a highly polyphagous species (Hoddle et al., 2003) that presents significant threats to perennial trees and vines growing in agricultural areas, urban landscapes, and native forests because of its ability to inoculate host plants with a pathogen, *X. fastidiosa*, which is potentially lethal. The economic losses resulting from *H. vitripennis*-vectored *X. fastidiosa* is estimated to be in the tens to hundreds of millions of dollars per year (Pilkington et al., 2005; Tumber et al., 2014). Reducing losses and minimizing disease incidence relies, in part, on reducing population densities of vectors such as *H. vitripennis* that spread the pathogen (Haviland et al., 2021). Vector control is necessary as negative impacts stem primarily when *H. vitripennis* reaches high densities on a diversity of host plants. Fortunately. *H. vitripennis* is not an efficient vector of *X. fastidiosa* and this provides opportunities for using biological control and other sustainable Integrated Pest Management (IPM) tools to reduce vector densities with concomitant decreases in incidence of *X. fastidiosa*-related diseases (Daugherty and Almeida, 2019).

During the initial phases of the *H. vitripennis* invasion in California, large populations of this pest lived in urban areas, from where they could invade neighboring agricultural production zones. Also, *H. vitripennis* adults can overwinter in organic perennial tree crops (e.g., organic citrus is an excellent overwintering host for *H. vitripennis*) or minimally managed farms (i.e., low-input IPM citrus), which can also be close to commercial vineyards. In spring, *H. vitripennis* can move from these overwintering areas into crops like grapes that are susceptible to Pierce's disease (Blua et al., 2005). Programs to protect grapes focus on vector-reduction through use of insecticides to deter *H. vitripennis* feeding (i.e., sub-lethal doses of systemic neonicotinoid insecticides) or to kill nymphs and adults. Area-wide management programs using insecticides can be effective in reducing the vector's density (Haviland et al., 2021). However, widespread insecticide applications may not be acceptable in urban areas, organic orchards or farms, or wilderness areas, and resistance development is also a significant concern (Byrne and Redak, 2021).

In urban areas in California, *H. vitripennis* can reach high densities because of high levels of host plant diversity, limited pest management, and year-round irrigation. As a result of feeding by *H. vitripennis* in urban areas, scorch-like mortality of oleanders, liquidambar trees, and olives —a phenomenon that used to be uncommon in California—increased significantly because of *X. fastidiosa* infections from *H. vitripennis* feeding. This cycle of infestation and urban tree mortality has significant economic costs, mainly due to the value of these large trees (i.e., tree appraisal values made by professional arborists for property valuations) and subsequent expenses for removing large dying or dead trees and replacing them. Area-wide insecticide treatments in urban areas for *H. vitripennis* control, however, are costly and unpopular with the public.

Similarly, massive spray programs are not feasible in wilderness areas where lower densities of *H. vitripennis* occur, as for example, in natural areas of French Polynesia (Petit et al., 2008a). This is particularly true for invaded islands of the South Pacific, especially French Polynesia, where natural areas are not only large but also extremely mountainous (Petit et al., 2008a). These obstacles to large-scale control can be overcome by using biological control instead of chemical control if a safe and effective natural enemy can be identified. For *H. vitripennis*, the egg parasitoid *Cosmocomoidea ashmeadi* (formerly known as *Gonatocerus ashmeadi*) (Hymenoptera: Mymaridae) (**Fig. 4**) is such a natural enemy. Its successful introduction has been very effective at reducing *H. vitripennis* populations in urban, agricultural, and wilderness areas in invaded regions (Grandgirard et al., 2008, 2009). Similar positive impacts in California were also attributable to *C. ashmeadi* (Gutierrez et al., 2011).

Figure 4. *Cosmocomoidea ashmeadi*, an egg parasitoid that parasitizes eggs of *Homalodisca vitripennis.* (Mike Lewis, Center for Invasive Species Research, UC Riverside)

THE ECOLOGY OF THE PROBLEM

Homalodisca vitripennis is much larger than the sharpshooters native to California (e.g., *Graphocephala atropunctata* [Cicadellini]), which can also transmit resident strains of *X. fastidiosa*, such as *X. fastidiosa* subsp. *fastidiosa* that causes Pierce's disease in grapes. The larger size of *H. vitripennis* allows it to feed on a wide range of woody hosts such as oleanders that were previously unsuitable for feeding by the native sharpshooters, thereby potentially inoculating new plant species with various subspecies of *X. fastidiosa*. Also, in comparison to native Californian sharpshooters, *H. vitripennis* can disperse further from point sources into crops (Haviland et al., 2021). The enhanced capabilities of this new vector have provided opportunities for subspecies of *X. fastidiosa* to exist together in the same host plant, a phenomenon that was likely uncommon in the absence of *H. vitripennis*. This co-occurrence, in turn, sets up opportunities for bacterial recombination events. Genetic changes resulting from recombination may result in bacterial subspecies that can cause infection and disease in new plant species (Nunney et al., 2012). Therefore, plant pathologists have recommended that steps be taken to minimize the likelihood of different *X. fastidiosa* subspecies being inoculated into the same host plants, to limit opportunities for new subspecies to arise through recombination events (Nunney et al., 2010).

Reducing vector densities is one way to reduce the rate and likelihood of such recombination events. In the absence of persistent spray programs, which have significant inherent problems such as non-target impacts and resistance development (Byrne and Redak, 2021), biological control provides an alternative approach to suppressing vector densities. When successful, biological control can help reduce not only vector densities but also the rates at which new *X. fastidiosa* subspecies arise because numbers of feeding *H. vitripennis* are reduced, which subsequently may also reduce grower reliance on insecticides for pest control as fewer plant disease-causing strains of *X. fastidiosa* are evolving.

PROJECT HISTORY THROUGH AGENT ESTABLISHMENT

Biological Control Efforts in California

Egg parasitoids of *H. vitripennis* occur in two hymenopteran families: Mymaridae (e.g., *Cosmocomoidea* [formerly *Gonatocerus*]) spp. and Trichogrammatidae (e.g., *Ufens* spp. [Al-Wahaibi et al., 2005]). *Cosmocomoidea ashmeadi* was accidentally introduced into California, likely through the unintentional movement of parasitized *H. vitripennis* egg masses on plants that originated from the home range of this pest (Vickerman et al., 2004). It is possible that *C. ashmeadi* established during the early phases of the *H. vitripennis* invasion, or it may have established before the *H. vitripennis* invasion by using the eggs of a native California Proconiini sharpshooter, *Homalodisca liturata* (formerly known as *H. lacerta*]) (Burks and Redak, 2003; Vickerman et al., 2004). Retroactive host specificity testing indicated that *C. ashmeadi* cannot parasitize native California sharpshooter species outside of the tribe Proconiini (Boyd and Hoddle, 2007).

As part of an importation biological control program targeting *H. vitripennis*, four species of egg parasitoids were introduced into California. Three of these parasitoids, *Cosmocomoidea fasciata* (a gregarious egg parasitoid formerly known as *Gonatocerus fasciatus*), *Cosmocomoidea triguttata* (a solitary egg parasitoid formerly known as *Gonatocerus triguttatus*), and *Cosmocomoidea morrilli* were sourced from the native range of *H. vitripennis* in the southeast United States (Triapitsyn and Phillips, 2000; Triapitsyn et al., 2003; Pilkington et al., 2005; Boyd and Hoddle, 2007). The fourth species, *Anagrus epos* (a gregarious, new association egg parasitoid) was imported from Minnesota (USA) where it attacks eggs of *Cuerna fenestella* (Hemiptera: Cicadellidae), a native, univoltine proconiine sharpshooter (Krugner et al., 2008). New association natural enemies (or neoclassical biological control agents) used in classical (or introduction) biological control are species that have no evolutionary association with the target pest but which have the ability to attack a novel host for food (e.g., a predator species) or as a reproductive host (e.g., a parasitoid species) (Hokkanen and Pimentel, 1989; Stenberg et al., 2021).

Table 1 summarizes releases of seven different parasitoid species into California for the biological control of *H. vitripennis*. Of these seven parasitoids, *C. triguttata* and *C. fasciata* failed to establish permanent populations in California, despite extensive releases and follow-up monitoring efforts (**Table 2**). For example, a total of 1,154,169 *C. triguttata* were released in California across 4,249 release sites from 2000 to 2013 (**Table 2**). A total of 617 field-collected *H. vitripennis* egg masses resulted in the rearing of 2,028 *C. triguttata* over the period 2000–2015. No field recoveries of this parasitoid have been made since 2015, and it is now assumed that this parasitoid has failed to establish in California (**Table 2**).

Similarly, *A. epos* likely did not establish in California. This may have been due, in part, to rearing difficulties because only 7,485 parasitoids were released over the period 2005–2009 across six counties: Fresno Co. (82 released), Kern Co. (3,538 released), Riverside Co. (2,050 released), Santa Clara Co. (390 released), Tulare Co. (658 released), and Ventura Co. (767 released).

Cosmocomoidea morrilli is native to the southeast United States and northeast Mexico, and the first record of *C. morrilli* in California was of specimens reared from an unidentified Prociniini egg mass (possibly *H. liturata*) in 1981 (Triapitsyn, 2006) before the establishment of *H. vitripennis*. It is uncertain if *C. morrilli* is native to California or whether it was accidentally introduced. This species was originally

Table 1. Total number of parasitoids released by species by year in California for biological control of *Homalodisca vitripennis*. Parasitoid releases were made primarily by the California Department of Food and Agriculture (CDFA).

PARASITOID SPECIES AND NUMBERS RELEASED								
Year	***C.* ashmeadi***	***C. morrilli***	***C. walkerjonesi***	***C. morgani***	***C. triguttata***	***C. fasciata***	***A.** epos***	***Ufens* sp.**
2000	0	0	0	0	1,440	0	0	0
2001	26,800	0	755	0	107,625	0	0	0
2002	36,598	0	27,195	0	215,442	3,498	0	0
2003	23,901	0	19,902	0	271,404	176,866	0	0
2004	23,666	0	8,836	0	78,536	88,540	0	0
2005	10,737	3,788	2,894	0	42,988	50,540	600	0
2006	12,437	45,122	0	0	42,833	30,850	3,882	0
2007	7,540	79,917	0	2,140	58,325	0	1,926	0
2008	79,865	97,171	0	16,114	89,162	0	1,077	0
2009	14,616	77,445	0	18,051	64,376	0	0	0
2010	8,438	86,490	0	29,941	75,876	0	0	0
2011	2,268	90,644	0	35,654	68,444	0	0	0
2012	3,811	26,635	0	19,374	19,093	0	0	0
2013	699	25,069	0	22,689	18,225	0	0	0
2014	586	17,946	0	29,222	0	0	0	0
2015	2,634	20,075	0	20,407	0	0	0	0
2016	4,570	24,157	0	17,049	0	0	0	0
2017	1,084	16,115	45	7,405	0	0	0	54
2018	12,673	12,517	14	15,998	0	0	0	855
2019	24,956	9,438	0	8,187	0	0	0	58
2020	18,016	8,612	0	6,191	0	0	0	0
2021***	10,939	9,800	0	4,659	0	0	0	0
Total	**269,643**	**650,941**	**59,641**	**253,081**	**1,153,769**	**350,294**	**7,485**	**967**

* *Cosmocomoidea*
** *Anagarus*
*** data available for *C. ashmeadi* through to the end of August

confused with the morphologically similar *Cosmocomoidea walkerjonesi* (see below), a parasitoid native to California but not recognized as a new species at the time. Molecular data and morphological traits have since been identified that separate *C. morrilli* and *C. walkerjonesi* (Triapitsyn, 2006). As part of the classical biological control program targeting *H. vitripenni*s, *C. morrilli* was intentionally introduced into California from Texas and Tamaulipas (Mexico) in 2001 (Morgan et al., 2002; Pilkington et al., 2005).

A second new association biological control agent, *Cosmocomoidea deleoni* (formerly known as *Gonatocerus deleoni*), was also considered for potential release and establishment in California. This natural enemy is a solitary egg parasitoid native to Argentina that was originally reared from eggs of *Tapajosa rubromarginata* (Cicadellidae: Proconiini). It was subjected to host range testing in quarantine (Lytle et al., 2012a), but it was found to be competitively inferior to *C. ashmeadi* (Irvin and Hoddle, 2011) and was not released. A third potential new association species, the trichogrammatid *Pseudoligosita plebeian*, was reared from *H. liturata* eggs collected in Mexico. It was studied but not released (Lytle et al., 2012b).

Table 2. Release and recovery data for two species of egg parasitoids—*Cosmocomoidea triguttata* (white) and *C. fasciata* (gray)—released in California for classical biological control of *Homalodisca vitripennis*. Releases and recovery surveys were made primarily by the California Department of Food and Agriculture (CDFA).

Year	**No. of release sites**		**No. of releases at site**		**Total no. parasitoids released**		**No. survey visits to release sites**		**No. GWSS egg masses recovered**		**No. parasitoids reared from GWSS eggs**		**No. of survey sites with parasitoid recoveries**	
	C. tri	***C. fasc***	***C. tri***	***C. fasc***	***C. tri***	***C. fasc***	***C. tri***	***C. fasc***	***C. tri***	***C. fasc***	***C. tri***	***C. fasc***	***C. tri***	***C. fasc***
2000	4	0	4	0	1,440	-	-	-	0	0	0	0	0	0
2001	42	0	137	0	107,625	0	-	-	1	0	10	0	1	0
2002	34	8	197	13	215,442	0	162	162	42	2	140	2	13	1
2003	46	38	527	332	271,404	3,498	312	317	34	2	182	10	15	1
2004	44	47	286	340	78,536	176,866	438	441	55	1	468	1	18	1
2005	67	57	200	244	42,988	88,540	428	430	13	0	36	0	5	0
2006	61	41	300	162	42,833	50,540	808	819	3	0	13	0	3	0
2007	65	0	270	0	58,325	30,850	982	985	121	0	425	0	21	0
2008	66	0	513	0	89,162	0	1,225	1,236	42	0	121	0	14	0
2009	65	0	380	0	64,376	0	1,246	1,247	20	0	82	0	9	0
2010	66	0	539	0	75,876	0	1,295	1,295	63	0	371	0	17	0
2011	65	0	546	0	68,444	0	1,268	1,268	28	0	157	0	9	0
2012	44	0	204	0	19,093	0	1,316	1,316	8	0	9	0	7	0
2013	41	0	146	0	18,225	0	1,043	1,043	3	0	3	0	3	0
2014	0	0	0	0	0	0	637	665	0	0	0	0	0	0
2015	0	0	0	0	0	0	570	661	1	0	11	0	0	0
2016	0	0	0	0	0	0	479	611	0	0	0	0	0	0
2017	0	0	0	0	0	0	0	528	0	0	0	0	0	0
2018	0	0	0	0	0	0	0	517	0	0	0	0	0	0
2019	0	0	0	0	0	0	0	494	0	0	0	0	0	0
2020	0	0	0	0	0	0	0	470	0	0	0	0	0	0
2021	0	0	0	0	0	0	0	346	0	0	0	0	0	0
Total	**710**	**191**	**4,249**	**1,091**	**1,153,769**	**350,294**	**12,209**	**14,851**	**434**	**5**	**2,028**	**13**	**135**	**3**

Two other species of parasitoids reared from *H. vitripennis* eggs collected in California that were subsequently mass reared and released for biological control of *H. vitripennis* included *Cosmocomoidea morgani* (possibly native to California [Triapitsyn, 2006]), and *C. walkerjonesi* (native to California [Triapitsyn, 2006]) (**Table 1**). Morphologically, *C. morgani* is more similar in appearance to some undescribed *Cosmocomoidea* species from Central America. Triapitsyn (2006) has speculated that *C. morgani* may not be native to California but may be an introduced species that established when *H. vitripennis* eggs masses were highly abundant. It is possible that *C. morgani* is native to California but simply was not detected before 2003 when it was reared for the first time. However, this seems unlikely (S. Triapitsyn, pers. comm.). Molecular studies may help determine the area of origin of *C. morgani*.

Biological Control Efforts in French Polynesia

Following the invasion and establishment in 1999 of *H. vitripennis* in Tahiti and Moorea (French Polynesia), surveys found very low levels of egg parasitism (<3%) by three local species of parasitoids (Grandgirard et al., 2007). These survey data strongly suggested that *H. vitripennis* was benefiting from natural enemy-free space and that the pest's high rate of population growth and rapid spread were due to natural enemy escape combined with a highly suitable climate that favored year-round reproduction. Consequently, the decision was made in 2004 to initiate an importation (= classical) biological control program with *C. ashmeadi* in French Polynesia, and a large-scale project was initiated with parasitoids from California (Grandgirard et al., 2008, 2009). Following the completion of studies that indicated an acceptably low level of risk to non-target parasitism, a total of 13,786 parasitoids were released at 27 sites on Tahiti between May and October of 2005 (Grandgirard et al., 2008). These releases resulted in rapid establishment, spread and impact, as described in the next section.

HOW WELL DID BIOLOGICAL CONTROL WORK?

In southern California, monitoring of *H. vitripennis* populations in non-sprayed citrus indicated that over the course of a 10-year period (2002–2012), *H. vitripennis* densities declined by >95%, and parasitism by *C. ashmeadi* was a likely cause (Banks et al., 2019) (**Fig. 5**). Densities of *H. vitripennis* in urban areas in California in 2022 now tend to be significantly lower compared to earlier levels. However, in some agricultural areas where insecticides have been consistently used to protect grapes from *H. vitripennis*-*X. fastidiosa*, pest populations remain unacceptably high (Byrne and Redak, 2021). This problem may be due, in part, to the development of insecticide resistance by *H. vitripennis* (Byrne and Redak, 2021), the damaging effects of the insecticides on natural enemies, including *C. ashmeadi*, and a very low tolerance threshold for the presence of this pest by grape growers.

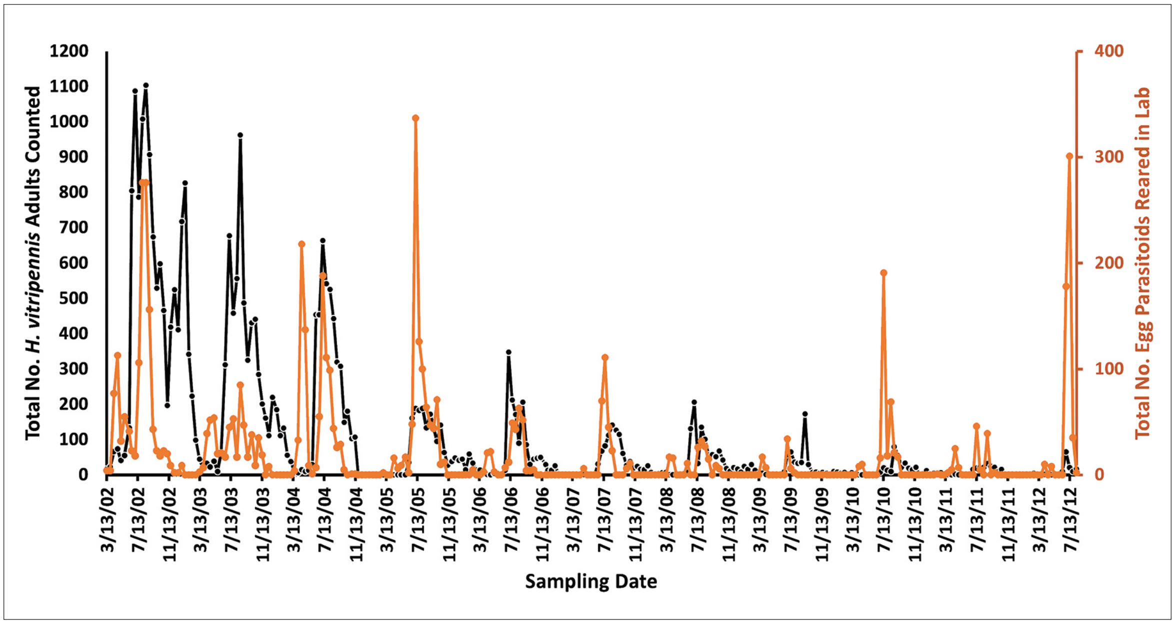

Figure 5. This chart shows an ~95% decline in *H. vitripennis* densities in non-treated lemons over the period 13 March 2002 to 8 August 2012 at Ag. Ops. UC Riverside, and the corresponding numbers of parasitoids reared from collected *H. vitripennis* egg masses that were found during timed visual searches of survey trees. (See Banks et al., 2019 for more details on field surveys and parasitoid rearing.)

In French Polynesia, the impact of *C. ashmeadi* on *H. vitripennis* population densities was extremely high and rapid. By December 2005, ~7 months after parasitoid releases began, parasitism of *H. vitripennis* egg masses averaged 80–100% in Tahiti and the neighboring island of Moorea. As a result of these high levels of egg parasitism, populations of *H. vitripennis* nymphs and adults decreased by more than 90% (Grandgirard et al., 2008, 2009).

This strong suppressive effect was later recorded across three additional archipelagos (Society, Austral, and Marquesas) in French Polynesia (Grandgirard et al., 2009). Interestingly, *C. ashmeadi* was not released into the Austral or Marquesas archipelagos; establishment of this parasitoid on these islands was likely due to the movement of parasitized *H. vitripennis* egg masses on plants being transported between islands (Petit et al., 2009). Similarly, for Hawaii, the Cook Islands, and Easter Island, *C. ashmeadi* was also moved inadvertently by people on plants, likely as parasitized *H. vitripennis* egg masses. Following the establishment (intentional or accidental) of *C. ashmeadi* in these new areas, *H. vitripennis* populations quickly declined to very low levels. Unfortunately, the impacts of *C. ashmeadi* across the Austral or Marquesas archipelagos in French Polynesia, Hawaii, and the Cook Islands have not been studied and deserve documentation. Similarly, for the islands of Tahiti and Moorea in French Polynesia, follow-up studies evaluating the long-term suppressive effect of *C. ashmeadi* on *H. vitripennis* populations are warranted.

BENEFITS OF BIOLOGICAL CONTROL OF *HOMALODISCA VITRIPENNIS*

Another significant but underappreciated consequence of elimination of *H. vitripennis* spread in the South Pacific region is that countries with significant agricultural enterprises (e.g., New Zealand, Australia, and Chile [Easter Island is a special territory of Chile]) were protected from invasion by this pest. The mechanism behind this protection was likely the substantial reductions in *H. vitripennis* densities in many areas due to biological control. There is also a high likelihood that when egg masses are accidentally transported into new areas, some eggs are parasitized by *C. ashmeadi*. In areas that receive parasitized *H. vitripennis* egg masses, the invader is less likely to establish because too few viable sharpshooters will be introduced to overcome the problem of failure to mate that arises as a small group of invaders spreads out randomly over a large area (Allee effect) (Petit et al., 2008b). Importantly, from a risk management perspective, the *C. ashmeadi* adults that emerge from *H. vitripennis* egg masses in areas where *H. vitripennis* invades but fails to establish are themselves unable to establish if suitable eggs for parasitism (i.e., Proconiini sharpshooter eggs) in receiving areas are not present.

Both New Zealand and Australia were sufficiently concerned about the invasion threat posed by *H. vitripennis* originating from infested islands in the South Pacific that proactive studies were undertaken to assess risks to native plants from *H. vitripennis*-*Xylella* (Rathe et al., 2014; Groenteman et al., 2015). A strong argument has been made that non-target impact assessments (i.e., host range and host specificity testing) should not be required for *C. ashmeadi* releases in New Zealand should *H. vitripennis* establish there because this natural enemy would pose little risk to New Zealand's native cicadellids, none of which are in the tribe Proconiini—the only group that is suitable for parasitism (Charles, 2012).

In southern California, especially urban areas, *H. vitripennis* populations are now very low, and it is rare to experience heavy levels *H. vitripennis* 'rain' (i.e., *H. vitripennis* excreta) falling from infested trees, even from highly preferred species like crepe myrtle. In agricultural areas, especially where insecticides tend to be applied frequently to protect grape cultivation, *H. vitripennis* is still considered a potential problem because of the risks it poses through the transmission of *X. fastidiosa*. The persistence of *H. vitripennis* in agricultural areas may also be due to reductions of natural enemy populations, including *C. ashmeadi*, because insecticides are accidentally killing these beneficial insects. Long-term, regular insecticide use is also driving resistance development in *H. vitripennis* in some major grape-growing areas (Byrne and Redak, 2021), and this phenomenon may exacerbate the risk this vector poses to commercial grape producers.

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