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ORIGINAL PAPER

Invasion dynamics of the glassy-winged sharpshooter *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae) in French Polynesia

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Abstract The glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar) [formerly *Homalodisca coagulata* (Say)] (Hemiptera: Cicadellidae), has recently emerged as a serious invasive pest. From its natural range in the southeast USA and northeast Mexico, it invaded successively California (late 1980s), French Polynesia (1999), Hawaii (2004), and recently Easter Island (2005) inadvertently through the transportation of infested plants. In French Polynesia, *H. vitripennis* has reached impressive densities becoming an important pest threatening agriculture, native biodiversity, as well as being a major social nuisance. Since 1999, *H. vitripennis* spread rapidly from Tahiti to neighboring islands, colonizing most of the archipelagos of French Polynesia. In this paper, we present the results of surveys of *H. vitripennis* populations from 15 islands of French Polynesia and use these data to investigate the invasion dynamics and colonization processes of this pest in a tropical climate. We found *H. vitripennis* present in 10 islands with two new records confirmed. Our analyses suggest that: (1) *H. vitripennis* abundance is strongly associated with urbanization, with highest pest densities found in the most developed coastal areas of infested islands, (2) *H. vitripennis* may exhibit an Allee effect during the early phase of an invasion, and (3) the invasion dynamics of *H. vitripennis* conform to a stratified dispersal model marked by rapid long-distance human-mediated movement.

Keywords Allee effect · Stratified diffusion · Urbanization · Expansion range

Introduction

The glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar) [formerly *Homalodisca coagulata* (Say) (Takiya et al. 2006)] (Hemiptera: Cicadellidae) is native to the southeast USA and northeast Mexico (Triapitsyn and Phillips 2000). It has significant invasive potential with strong flight capabilities, and long-lived adults capable of feeding on a wide range of host plants. Furthermore, this species often lacks natural enemies outside its native range, and its egg masses (possibly the most important invasion propagule) are difficult to locate on the undersides of leaves thereby escaping attention when plants are

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examined before relocating to new areas (Hoddle et al. 2003). *Homalodisca vitripennis* invaded California in the late 1980s (Sorensen and Gill 1996) and climate modeling suggests that many other areas of the world are highly vulnerable to invasion (Hoddle 2004). Indeed, *H. vitripennis* has now successfully established in areas outside of California as predicted by modeling, notably: French Polynesia in 1999 (Secretariat of the Pacific Community 2002), Hawaii in 2004 (Hoover 2004), and Easter Island in 2005 (Sandra Ide personal communication 2005).

The arrival of *H. vitripennis* in Tahiti and the problems resulting from this biological invasion have been described in detail elsewhere (Grandgirard et al. 2006). In the study presented here, we present data on the expansion of *H. vitripennis* from the founding population in Tahiti throughout the rest of French Polynesia. Understanding the population dynamics of this invasion is important to: (1) forecast pest establishment in tropical areas and refine early detection methods; (2) predict where *H. vitripennis* could further expand its range; (3) help streamline biological and other control programs through an understanding of environmental factors that permit unrestricted population growth and spread; and (4) provide 'before' data to assess the impact of control, such as the impact of biological control programs after natural enemies are established.

Spread of *H. vitripennis* in French Polynesia

Within seven years of its first detection on the island of Tahiti (Society Islands), *H. vitripennis* rapidly spread throughout French Polynesia. In the Society Islands, *H. vitripennis* was officially recorded on Moorea (17 km from Tahiti) and Raiatea (220 km from Tahiti) in September 2001, on Huahine (175 km from Tahiti) in June 2003, and on Bora Bora (260 km from Tahiti) in December 2003 (Rural Development Service of French Polinesia, unpublished data). *Homalodisca vitripennis* was recorded in Nuku Hiva in the Marquesas (1500 km from Tahiti) in September 2004 and was found in Tubuai (568 km from Tahiti) and Rurutu in the Australs (572 km from Tahiti) in January 2005 (Rural Development Service of French Polynesia, unpublished data). The serious threat to trading partners of an enormous density of *H. vitripennis* in French Polynesia was confirmed when *H. vitripennis* successfully invaded Easter Island in 2005 (4050 km from Tahiti). The invasion of Easter Island almost certainly originated from Tahiti because French Polynesia is the only country infected with *H. vitripennis* that has direct flights to Easter Island.

To control *H. vitripennis* populations in Tahiti and to limit the threat to neighboring countries and trading partners, a classical biological control program targeting *H. vitripennis* was launched in 2004 as a joint effort between the University of California (Riverside and Berkeley campuses through the UCB Gump Station in Moorea, French Polynesia) and French Polynesia's Department of Agriculture. After non-target risk assessments indicated an acceptably low risk to native cicadellid (leafhopper) species, the egg parasitoid, *Gonatocerus ashmeadi* Girault (Hymenoptera: Mymaridae), was released at two experimental sites in May 2005 in the north of Tahiti (Grandgirard et al. 2007). Here we present data on the distribution and density of *H. vitripennis* before *G. ashmeadi* was established and caused the rapid and catastrophic collapse of the target pest population. We use these population census data to investigate the invasion dynamics of *H. vitripennis* in tropical regions.

Bio-invasion population dynamics

The 'natural laboratory' setting of island archipelagos such as those of French Polynesia provides an opportunity to address fundamental scientific issues regarding biological invasions (Gillespie and Roderick 2002). How introduced species spread through a new geographic range, is one of the most important applied problems in ecology (Elton 1958; Kot et al. 1996). The invasion of numerous islands in French Polynesia by *H. vitripennis* permits an assessment of the spread dynamics and colonization processes of an insect pest. Questions of interest include: what are the suitable environmental conditions for the establishment of this pest? Can spread be described with a simple diffusion model? Which factors will favor or constrain propagation?

Estimation of the probability of establishment represents a major challenge in invasion biology (Sakai et al. 2001). An important component affecting establishment of a species is the Allee effect

(Allee 1931; Courchamp et al. 1999). An Allee effect is defined as "a positive relationship between any component of fitness of a species and density of conspecifics" (Stephens et al. 1999). This implies that an individual of a species that exhibits an Allee effect will have a decrease in some aspect of its fitness when conspecific density is low (i.e., underpopulation can make it hard to find mates or reduce the ability to withstand heavy mortality) (Allee 1938; Berec et al. 2001; Gascoigne and Lipcius 2004; Taylor and Hastings 2005). An Allee effect can strongly influence the early stages of an invasion by setting minimum population sizes that must be exceeded to overcome debilitating stochastic events before permanent establishment and spread of a sexually reproducing population is possible (Liebhold and Bascompte 2003). Thus, biological agents that are introduced to control an invasive species may be more likely to curb range expansion if the invasive target is suffering an Allee effect (Taylor and Hastings 2005). Typically, invader population dynamics are studied in detail after establishment, when population sizes are large enough to cause measurable damage. However, important population dynamics events occur at the beginning of an invasion when population sizes are small and difficult to monitor and measure (Leung et al. 2004). The invasion of French Polynesia by the sexually reproducing *H. vitripennis* occurred relatively recently, and its spread and population growth over widely dispersed islands presented a range of invasion stages amenable to simultaneous investigation.

The magnitude of the initial geographic expansion of a population is affected by localized diffusion as individuals radiate from the source population. In later phases, spread is accelerated by the proliferation of 'secondary source populations' created by long-distance migrants, which might be assisted intentionally or unintentionally by human-mediated transportation (Andow et al. 1990). Hengeveld (1989) proposed calling such a diffusion process "stratified diffusion" characterized by localized short distance movement by invaders punctuated by rapid long-distance human-assisted dispersal. This type of stratified dispersal is common for many invasive organisms and has been described in detail for invasive insects (Sharov and Liebhold 1998; Suarez et al. 2001; Gilbert et al. 2003). Long-distance dispersal is likely of great consequence in agricultural and urban landscapes where human-aided transport is possible and often associated with industries supporting these artificial and highly managed ecosystems (Fagan et al. 2002). For example, Mack (1981) demonstrated that railroad networks were critical to the spread of cheat grass in the western United States. Ehler (1998) made similar arguments concerning the spread of spotted alfalfa aphids paralleling major trucking routes in California (USA). Long-distance dispersal abilities of *H. vitripennis*, (i.e., human-aided dispersal), is a critical component to the invasion dynamics of this pest and must be considered for development of successful management plans aiming to retard future spread. The geographical make up of French Polynesia permits an investigation of *H. vitripennis* diffusion dynamics across varied and widely separated islands and island groups. This discontinuous land system makes it easy to separate natural dispersion within an island from long-distance human dispersion between islands.

To aid understanding of factors affecting the invasion success of *H. vitripennis* in French Polynesia three questions were investigated in this study. First, is *H. vitripennis* density associated with urban residential areas which have high diversity and concentrations of well-maintained exotic plants? Second, does *H. vitripennis* establishment in a new location exhibit an Allee effect? Third, does the spread of *H. vitripennis* in French Polynesia conform to a stratified dispersal process combining rapid long-distance movement and local diffusion?

Materials and methods

Sampling for *Homalodisca vitripennis*

Invasion of French Polynesia by *H. vitripennis* occurred around 1999, and its initial spread was not monitored carefully before this study commenced in 2005. Therefore, it was not possible to study directly the establishment and diffusion of the pest on the earliest and most heavily infested islands of Tahiti and Moorea. However, dates of first detection of *H. vitripennis* for infested islands are known, hence it is possible to chronologically track the invasion history of *H. vitripennis* by comparing its abundance and distribution from one island to another. The distribution and density of *H. vitripennis* on each island was observed and compared to the recorded invasion date. Thus, it was possible to infer progressive changes in infestation levels with time since invasion was first detected.

We surveyed populations of *H. vitripennis* on 15 islands of three French Polynesian Archipelagoes. Invasion dates for the islands were based on "official" records (with date of colonization based on first detection of *H. vitripennis* by French Polynesian government scientists) or "unofficial" records (where our surveys detected small localized populations indicative of a recent invasion). Seven islands in the Society Islands Archipelago were sampled for *H. vitripennis*: Moorea June 9 2005; Tahiti June 15 2005; Bora Bora June 24 2005; Raiatea June 28 2005; Tahaa June 30 2005; Huahine July 1 2005, and Maupiti December 22 2006. In the Marquesas Islands Archipelago, five islands were surveyed: Nuku Hiva November 22 2005; Ua Pou November 25 2005; Ua Huka November 30 2005, and Tahuata December 2 2005. Finally, three islands were sampled in the Austral Islands Archipelago: Raivavae January 16 2006; Tubuai January 19 2006 and Rurutu January 23 2006.

On each island, 25–50 geographical sites were sampled. Survey sites were <1 km (in major towns) to a maximum of 10 km (around the coast) apart. Distances between sampling sites were influenced by the size of major towns and the island itself. Ten sites were surveyed in and around the main city of each island, 20 sites around coastal areas, and 10 inland, either in valleys or at altitude on steep interior mountains. The sampling plan was designed to provide information that would enable the construction of a representative map of *H. vitripennis* population distributions and densities for surveyed islands.

Sampling sites were categorized into three classes based upon their level of urbanization. U1 zones are "fully urbanized" areas. These included the main cities on each island which often contained the main communication points (i.e., seaport and airport). Vegetation in U1 was almost exclusively exotic annuals including grasses, and perennial ornamental trees and shrubs. U2 zones were designated as "semi-urbanized" areas. These included small villages or residential areas predominantly in coastal areas of the islands. Vegetation in U2 zones consisted primarily of ornamental trees, grasses, vegetables, and agricultural plants (e.g., coconut, mango, papaya, and citrus trees). U3 zones were "non-urbanized areas". They are deserted natural areas with no human structures within 2 km. Vegetation was comprised of native flora and exotic invasive plants.

The same species of plants were sampled at each sampling site on all surveyed islands to facilitate meaningful data comparisons across sites and between islands. The commonly planted exotic ornamental shrub, *Hibiscus rosasinensis* (Aute) (Malvaceae), was chosen as the major host plant for surveys because: (1) this plant is commonly used as hedge, and is easily found all over French Polynesia; (2) it is the second most common plant on a list of 72 host plant species from which *H. vitripennis* has been collected from in Florida (the home range of this pest) (Hoddle et al. 2003); and (3) *H. rosasinensis* is a preferred host plant for *H. vitripennis* in French Polynesia (Petit pers. observation). Sampling for *H. vitripennis* was conducted in U1 and U2 on *H. rosasinensis* hedges approximately 3 m high and at least 5 m long in areas that received full sun. The phenology of the hedge was an important indicator of quality for *H. vitripennis* and always had flowers and abundant young stems between 50 cm and 1 m of length, a preferred feeding site for *H. vitripennis*. *Hibiscus rosasinensis* hedges were sampled over a 1 min interval by sweep netting young stems with a large insect sweep net. In U3 areas, there were often no hedges in the wilderness areas or on tops of mountains, so *Metrosideros* sp. was the host plant sampled in the absence of *H. rosasinensis* in these zones. All motile stages of *H. vitripennis* caught in the sweep net were extracted with an insect aspirator. The numbers of adults and nymphs collected were recorded separately. There was obviously a minimum density below which a *H. vitripennis* population could not be detected with this sampling technique. Hence, the apparent absence of the pest at a study site did not necessarily mean that the pest was absent in the area being surveyed. Nevertheless, the multiplicity of sites sampled in a given area provided a robust indication as to whether *H. vitripennis* was either present or absent and a relative measure of population density for comparison across islands.

Data analysis

To determine whether the "urbanization" effect affected *H. vitripennis* abundance, we performed a one-way ANOVA on the mean number of *H. vitripennis* motiles collected from sampling for each island surveyed for each level of urbanization. Significant differences between mean numbers of *H. vitripennis* for each urbanization class were separated using Tukey's Studentized range test at the 0.05 level of significance. We used the same analysis to determine the effect of time from the first detection of *H. vitripennis* populations on pest abundance across different islands. These quantitative analyses between islands were conducted only for the Society Islands, because they were monitored simultaneously over the same season and have very similar climate and geography.

Results

Homalodisca vitripennis was found in 10 of the 15 islands surveyed in French Polynesia (Table 1). The islands of Hiva Oa, Ua Huka, Ua Pou, Tahuata (Marquesas Islands Archipelago) and Raivavae (Austral Islands Archipelago) were free from *H. vitripennis* at the time surveys were conducted. The pest was found for the first time in Tahaa and Maupiti (both in the Society Islands Archipelago) during this study. In Maupiti and Rurutu (Austral Islands Archipelago [sampled in January 2006]), measures of *H. vitripennis* abundance were significantly depressed because the egg parasitoid *Gonatocerus ashmeadi* Girault (Hymenoptera: Mymaridae) that had been released for the biological control of *H. vitripennis* in Tahiti had become widespread on these two islands following its self-introduction and had achieved high levels of parasitism (Petit in prep.). Consequently, census data from Maupiti and Rurutu were omitted from analyses because of the effect of *G. ashmeadi* on *H. vitripennis* population densities. Likewise, *G. ashmeadi* was introduced into Tahiti (May 2005) before this study was conducted. However, due to the relatively large size of this island, the dispersion and impact of the parasitoid was extremely limited in June 2005, and its impact on *H. vitripennis* was not obvious at the sites monitored. Hence, *H. vitripennis* abundance data for Tahiti were used in analyses despite *G. ashmeadi* being on the island.

Survey results indicated that *H. vitripennis* nymph abundance was a more reliable measure than adult abundance for determining pest distribution and population size (Table 1). On average, sweep net sampling indicated that nymph densities were generally more than 10 times higher than adult densities. These results suggest that *H. vitripennis* is easier to detect in the nymphal stage when pest abundance is low, possibly because this life stage cannot fly whereas adults readily fly and jump away at the slightest disturbance. Further, the greater reliability of nymph density data most likely results from the fact that nymphs are native to the host plant sampled or immediately surrounding plants. Consequently, estimates of nymph abundance were used in analyses.

Significant differences in pest abundance were found among the different classes of urbanization

Table 1 Mean number (±s.e.) of *Homalodisca vitripennis* nymphs and adults collected per minute of sampling in urbanized (U1), semi-urbanized (U2), or non-urbanized (U3) area on eight islands of French Polynesia

Island	Nymph			Adult		
	U1	U2	U3	U1	U2	U3
Tahiti	170.0 ± 17.5 (10) a	84.9 ± 7.3 (30) b	2.5 ± 0.9 (14) c	16 ± 2.4 (10) a	8.5 ± 0.9 (30) b	0 (14) c
Moorea	107.8 ± 13.9 (10) a	75.1 ± 7.9 (16) a	4.5 ± 0.5 (6) b	22.4 ± 9 (10) a	8.4 ± 1.5 (16) a	1.5 ± 0.5 (2) a
Raiatea	57 ± 5.3 (10) a	2.3 ± 0.6 (20) b	0.1 ± 0.1 (8) b	3.7 ± 0.9 (10) a	0.8 ± 0.2 (20) b	0.4 ± 0.3 (8) b
Huahine	16.6 ± 3.4 (10) a	2.8 ± 1.0 (16) b	0.3 ± 0.2 (10) b	4 ± 0.9 (10) a	0.9 ± 0.4 (16) b	0 (10) b
Bora Bora	14.6 ± 1.5 (8) a	1.9 ± 0.5 (22) b	0 (2) b	4.0 ± 0.9 (8) a	0.4 ± 0.2 (22) b	0.5 ± 0.5 (2) b
Tahaa	7 ± 1.9 (4) a	0.9 ± 0.5 (12) b	0.1 ± 0.1 (8) b	3.2 ± 1 (4) a	0.5 ± 0.4 (12) b	0.6 ± 0.1 (8) b
Nuku Hiva	41.6 ± 8.2 (10) a	1.5 ± 0.9 (8) b	0 ± 0 (10) b	2.5 ± 0.6 (10) a	0 ± 0 (8) b	0 ± 0 (10) b
Tubuai	10.3 ± 2.2 (14) a	0.9 ± 0.5 (20) b	0 ± 0 (10) b	0.6 ± 0.2 (14) a	0.1 ± 0.1 (20) b	0 ± 0 (10) b

The number of sites sampled is indicated for each area within brackets. For each island, different letters indicate that the GWSS abundance (either nymph or adult) is significantly different between urbanized areas ($P < 0.05$)

Table 2 The effect of urbanization on *Homalodisca vitripennis* nymph and adult abundance

Island	Nymph			Adult		
	F	df	*P*	*F*	df	*P*
Tahiti	57.461	2; 51	0.0001	32.955	2; 51	0.0001
Moorea	7.152	2; 25	0.003	2.364	2; 25	0.115 (n.s.)
Raiatea	150.94	2; 35	0.0001	11.532	2; 35	0.0001
Huahine	16.894	2; 33	0.0001	15.094	2; 33	0.0001
Bora Bora	65.344	2; 29	0.0001	16.060	2; 29	0.0001
Tahaa	17.914	2; 21	0.0001	4.958	2; 21	0.017
Nuku Hiva	22.077	2; 25	0.0001	13.045	2; 25	0.0001
Tubuai	13.637	2; 31	0.0001	5.581	2; 31	0.009

(Table 2). On Tahiti, nymph abundance was significantly higher in the main city Papeete, intermediate in semi-urbanized areas, and low in non-urbanized areas that consisted primarily of native undisturbed flora (Table 1). This pattern was repeated on the nearby island of Moorea. Nymph abundance was significantly higher in urbanized (U1) and semi-urbanized areas (U2) than in non-urbanized areas (U3) (Table 1). Finally, on Raiatea, Huahine, Bora Bora, Tahaa, Nuku Hiva, and Tubuai, nymph abundance was highest in urbanized areas when compared to other sites sampled on these islands (Table 1). This pattern of pest abundance was also observed with *H. vitripennis* adults on each island, except for Moorea, where no significant differences across the three urbanization zones were observed (Table 1).

Within the Society Islands, we explored the link between abundance and infestation duration using nymph abundance data in urbanized areas only, because density data from these areas showed obvious contrasts. Significant differences in the mean number of nymphs sampled was found to exist between islands ($F = 34.824$; df = 5, 206; $P = 0.0001$). Significantly more *H. vitripennis* nymphs were found in Tahiti, intermediate numbers in Moorea, fewer in Raiatea, with the fewest nymphs being found in Huahine, Bora Bora, and Tahaa (Fig. 1). Therefore *H. vitripennis* abundance would appear to be strongly correlated with infestation duration with recently infested islands having lower pest densities than islands with longer periods of *H. vitripennis* inhabitation. The invasion sequence of an island by *H. vitripennis* begins with an initial establishment phase with low population growth and spread over the interval year 0 to year 3. This phase is followed by an exponential expansion stage during year 3 to year 6 of the invasion. Thus, the invasion dynamics of *H. vitripennis* throughout the Society Islands shows a non-linear pattern (Fig. 1).

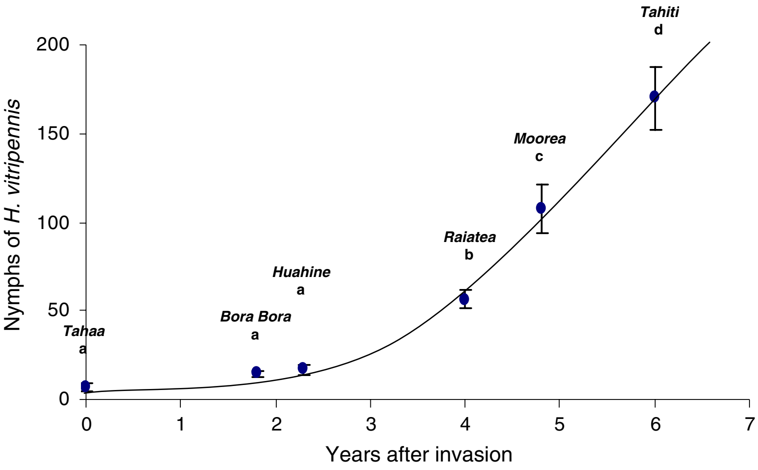

Fig. 1 Mean number of *Homalodisca vitripennis* nymphs (±s.e.) collected per 1 min of sweep net sampling in the urbanized area (U1) of each infested island in the Society Island Archipelago related to the time after the invasion was first recorded. Islands with different letters are significantly different ($P < 0.05$)

Chronological distribution and abundance maps for *H. vitripennis* on Tubuai, Nuku Hiva, Raiatea, and Tahiti illustrate the invasion dynamics of this pest following successful incursion (Figs. 2–5). Infestation of *H. vitripennis* on Tubuai (Austral Islands Archipelago) was very recent when surveys for this study were conducted. Small incipient populations of the pest were discovered in January 2005 in Mataura, the main city on Tubuai. In January 2006, *H. vitripennis* had not spread appreciably to other areas of the island, and the major infestation nucleus was still the city of Mataura with populations extending towards the airport. No specimens were detected in the semi-urbanized areas on the south end of Tubuai (Fig. 2). *Homalodisca vitripennis* abundance data for Tubuai mirrors the abundance curve for the Society Islands, with an average of 10 nymphs being collected per minute of sampling 1 year after the invasion of the pest was recorded (Fig. 1). Hence, the difference of climate between Australs (mean year round temperature = 21°C) and Society Islands (mean year round temperature = 25°C) seems to have had no obvious effect on the early invasion success of *H. vitripennis*. The same infestation pattern was observed on Tahaa in the Society Islands Archipelago with seven *H. vitripennis* nymphs collected per minute of sampling in the main city Haamene, and an absence of the pest on the rest of the island (Table 1).

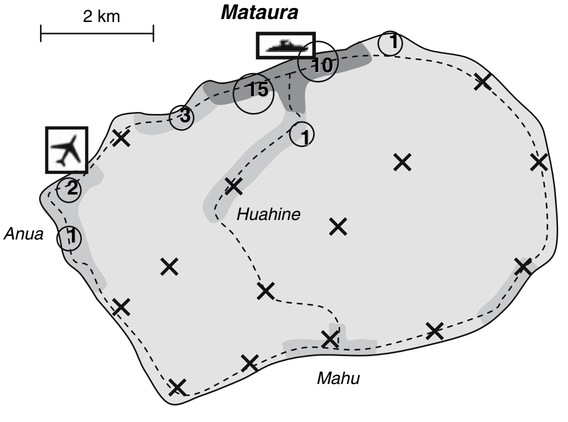

Fig. 2 Mean number of *Homalodisca vitripennis* nymphs per 1 min of sweep net sampling in Tubuai (Austral Islands Archipelago). Each point is the mean of two sampling sites (10 sites in urbanized areas); a cross indicates that no *H. vitripennis* were collected. Dark grey patches are urbanized areas, grey patches are semi-urbanized areas, and light grey are non-urbanized areas

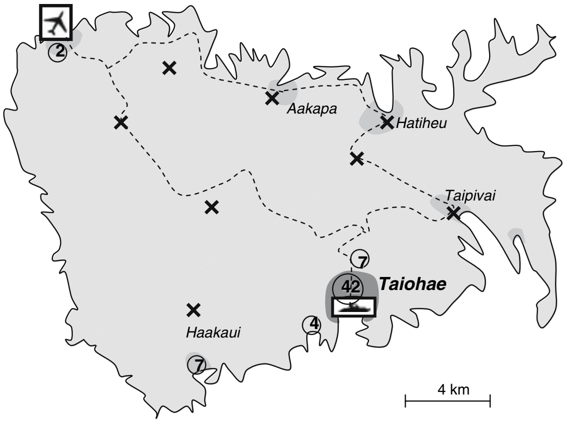

Fig. 3 Mean number of *Homalodisca vitripennis* nymphs per 1 min of sweep net sampling in Nuku Hiva (Marquesas Islands Archipelago). Each point is the mean of two sampling sites (10 sites in urbanized areas); a cross indicates that no *H. vitripennis* were collected. Dark grey patches are urbanized areas, grey patches are semi-urbanized areas, and light grey are non-urbanized areas

On Nuku Hiva (Marquesas Islands Archipelago) in November 2005, the *H. vitripennis* infestation was slightly more advanced than in Tubuai. As observed in Tubuai, the pest population in Nuku Hiva was mainly concentrated in the main city Taiohae and its surrounding area with an average of 42 nymphs being collected per minute of sampling (Fig. 3). However, two small populations of *H. vitripennis* were detected in Haakaui valley on the west side of the island and at the airport on the north side (respectively, 10 and 30 km from the main population and both categorized as U2). Numerous villages sampled on the east and north sides of Nuku Hiva were pest free. Because the invasion was recent and human movement into these remote areas is extremely difficult requiring four-wheel drive vehicles or boats, and often roads are impassable because regular rainfall causes dirt roads to become quagmires, movement of plants infested with *H. vitripennis* has most likely been slowed significantly.

The abundance of *H. vitripennis* on Nuku Hiva was inconsistent with predictions based on the spread dynamic model for the Society Islands (Fig. 1). In Taiohae, the main city on Nuku Hiva, 1.2 years after the invasion, the average number of *H. vitripennis* nymphs caught per minute of sampling was 42, and was higher than the theoretical value estimated from the model (around 10 nymphs per minute) in Fig. 1.

Three scenarios could explain this observation: (1) surveying was conducted during the wet season in Marquesas (versus dry season in Society Islands) and nymph captures could have been biased because of the time of year the survey was conducted; (2) the generally warmer climate in the Marquesas Islands (mean year round temperature = 27°C) compared to Societies (mean year round temperature = 25°C) could have enhanced *H. vitripennis* population proliferation; and (3) the pest could have arrived some time before its official detection in September 2004.

On Raiatea, in the main city of Uturoa (Fig. 4), an average of 56 *H. vitripennis* nymphs per minute of sampling were detected. At this density, *H. vitripennis* was entering the expansion phase of the spread dynamic model (Fig. 1). Unlike islands that had been infested earlier than Raiatea (e.g., Tubuai and Nuku Hiva), the *H. vitripennis* infestation on Raiatea was widespread over the entire island with *H. vitripennis* populations being found in every semi-urbanized area (U2). However, at the time of surveying, the pest was still largely concentrated in the main city of Uturoa. Subpopulations found outside of the main city never exceeded seven nymphs per minute of sampling, and pest populations were absent at several coastal sites on the island (Fig. 4).

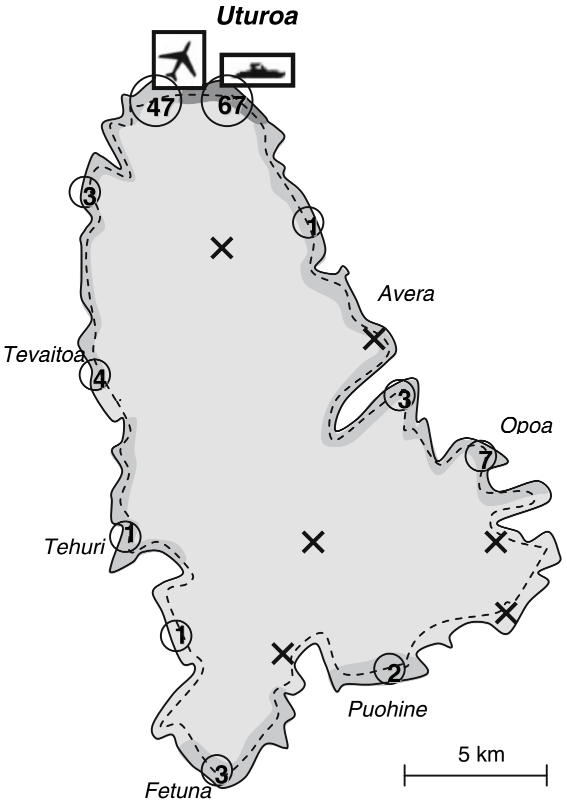

Fig. 4 Mean number of *Homalodisca vitripennis* nymphs per 1 min of sweep net sampling in Raiatea (Society Islands Archipelago). Each point is the mean of two sampling sites (10 sites in urbanized areas); a cross indicates that no *H. vitripennis* were collected. Dark grey patches are urbanized areas, grey patches are semi-urbanized areas, and light grey are non-urbanized areas

On the islands of Bora Bora and Huahine, the invasion situation was at an intermediate stage. Like Raiatea, *H. vitripennis* was concentrated in the two main cities, Vaitape and Fare, respectively, and had begun to spread from these epicenters onto the rest of the island. However, general *H. vitripennis* abundance was significantly lower than in Raiatea (Fig. 1), with an average of 17 nymphs per minute of sampling being detected in Fare, and 15 nymphs per minute in Vaitape.

Tahiti is the most densely inhabited island in French Polynesia. All the coastal areas of the island are urbanized except for the most southern part on the peninsula known as Tahiti-iti. Abundance of *H. vitripennis* in Tahiti was extremely high when surveys were conducted. The density observed in the main city of Papeete was the highest density observed in all of French Polynesia with an average of 170 *H. vitripennis* nymphs being caught in 1 minute of sweep net sampling (Fig. 5; Table 1). In the abundant semi-urbanized areas around the island, *H. vitripennis* densities were lower, but still very high compared to other infested islands in French Polynesia (Table 1). Unlike infested islands in the early stages of colonization by *H. vitripennis*, pest populations in Tahiti's coastal areas are relatively uniform with little contrast between urbanized and semi-urbanized areas. However, sampling of the rugged mountains and relatively uninhabited inland areas on Tahiti clearly indicated that *H. vitripennis* populations were very low with an average of two nymphs being caught per minute of sampling and in 42% of U3 sites a complete absence of the pest was recorded.

In nearby Moorea, dense populations of *H. vitripennis* were observed in September 2001, indicating the pest was certainly well established on this island before its official detection. The close proximity between Tahiti and Moorea (17 km distance) and the numerous daily commercial and public exchanges between the two islands via plane and ferry made it

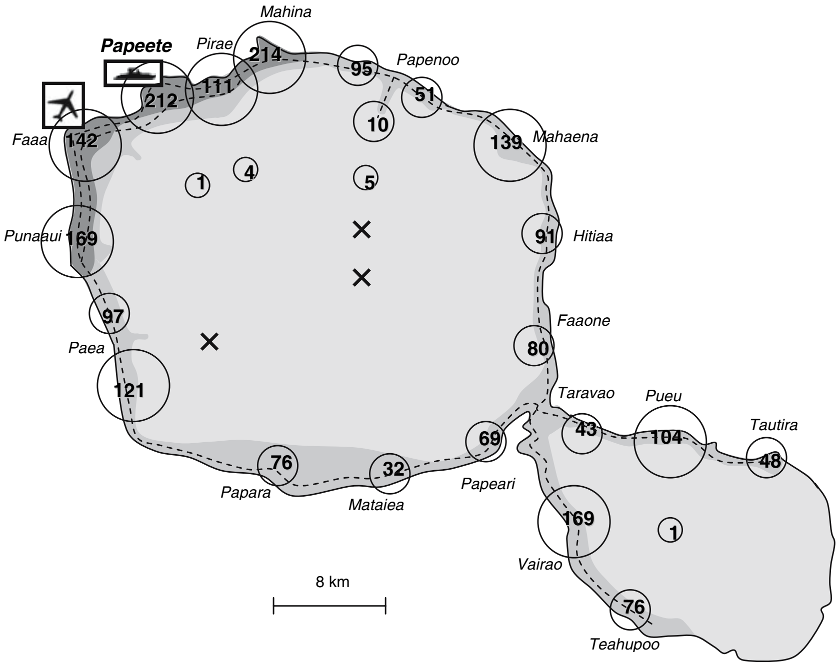

Fig. 5 Mean number of *Homalodisca vitripennis* nymphs per 1 min of sweep net sampling in Tahiti (Society Islands Archipelago). Each point is the mean of two sampling sites (10 sites in urbanized areas); a cross indicates that no *H. vitripennis* were collected. Dark grey patches are urbanized areas, grey patches are semi-urbanized areas, and light grey are non-urbanized areas

possible for *H. vitripennis* to be moved quickly on infested plant material from Tahiti to Moorea. Therefore, we speculate that populations had likely been building for at least 1 year before its official detection and that September 2000 was the probable arrival of *H. vitripennis* in Moorea. Distribution of *H. vitripennis* on Moorea was similar to that observed for Tahiti. The overall abundance of *H. vitripennis* in urbanized areas was lower than in Tahiti at an average of 108 nymphs per minute of sampling, but still remarkably high. *Homalodisca vitripennis* density was uniform in coastal areas of Moorea and no significant differences between U1 and U2 areas in Moorea were detected (Table 1). This result may be due to the fact that there is no main town on this island and numerous communication points and villages are distributed around the coastal area of the island making it likely that multiple infestation points occurred on Moorea.

Discussion

Understanding factors affecting the spread of an invasive pest is a critical element in invasion biology. The relatively recent invasion of French Polynesia by *H. vitripennis* and spread of this pest between major island groups and then dispersion within an island group has afforded an excellent and unique opportunity to determine factors affecting the pattern of spread and subsequent population growth of this insect pest.

Urbanization effect

Our results have demonstrated that *H. vitripennis* abundance in French Polynesia is strongly associated with urbanization, with highest pest densities being found in the most developed coastal areas of infested islands. Two possible explanations for this finding are that: (1) urbanized areas offer an extremely suitable environment for pest establishment and proliferation because of the high variety of host plant species (mainly exotic species) and densities of well maintained plants that are pruned, fertilized, and watered which promotes succulent growth ideal for year round feeding and oviposition (Daane et al. 2004), and (2) human activity (i.e., movement of plants and contaminated cargo and vessels) significantly increases the likelihood of pest introduction. Highly populated areas are characterized by high transit of people, cars, planes, trucks, and boats, all of which can be used to deliberately move plant material while simultaneously and unintentionally moving unwanted pest species such as *H. vitripennis* (Gilbert et al. 2004). Papeete, the major urban area in Tahiti, was the first area infested by *H. vitripennis* in French Polynesia probably because it is the international communication center and economic and tourist hub of the country. As *H. vitripennis* expanded its range in French Polynesia, the main communication points such as seaports and airports were epicenters for incipient populations. These entry points are located in highly urbanized areas with high floral diversity which most likely eased barriers to establishment. Additionally, urban areas may act as sinks for *H. vitripennis* as adults of this pest are strongly attracted to lights at night. The Society Islands are home to 86% of the French Polynesian population, Tuamotus 7%, the Marquesas 4%, and the Australs 3%. Consequently, it is not surprising that first detection of *H. vitripennis* on an island was strongly related to the number of inhabitants and subsequent inbound traffic flow. From the initial colonization of Tahiti (current population, 132,000), *H. vitripennis* first spread to the nearest Society Island, Moorea (14,600), then onto Raiatea (11,100), Huahine (5,700), Bora Bora (7,200), Tahaa (4,800), and finally onto Maupiti (1,100).

Allee effect and *H. vitripennis* invasion

An Allee effect is the positive relation between the population density of a species and its per capita growth rate (Stephens et al. 1999). An Allee effect may explain population expansion that is non-linear: a long period of slow growth occurs because of low population densities which can adversely affect survivorship and reproductive rates. Once the population overcomes a critical minimum density threshold, the population increases rapidly and the growth rate accelerates towards its carrying capacity (Arim et al. 2006). The population growth pattern observed for *H. vitripennis* throughout French Polynesia was non-linear. The population growth curve over time for infested islands showed a lag period of approximately 3 years followed by an explosive rate of population growth. The population growth characteristics of *H. vitripennis* across islands in varying stages of colonization seem consistent with that expected under the influence of an Allee effect.

Allee effects may also provide an explanation for lack of range expansion of a species, even when suitable habitats are nearby. Invasions succeed because individuals that disperse beyond the current range limits are able to establish viable populations (Keitt et al. 2001). Once new sites are colonized and the population is robust it can produce propagules that sustain the wave of advancement (Arim et al. 2006). Hence, below a critical threshold density, negative growth rates lead to propagation failure and generate stable range limits for populations (Keitt et al. 2001; Wilson et al. 1996). Consequently, many species showing an Allee effect have a relatively clustered distribution with many low abundance sites and few hot spots of high local abundance (Brown et al. 1995). This situation has been observed in French Polynesia for *H. vitripennis*. For example, islands experiencing the early stages of an incursion by *H. vitripennis* exhibited an obvious clustered population distribution with high density epicenters in the main cities, and multiple satellite sites with substantially lower pest abundance on the island. On the island of Nuku Hiva (Marquesas Islands Archipelago), the major city Taiohae is immediately surrounded by suitable habitat for *H. vitripennis*. Additionally, small villages on the east and north side of Nuku Hiva have sufficient suitable vegetation to sustain pest populations. However, *H. vitripennis* currently resides almost exclusively in Taiohae, probably because the maturing population has not generated enough propagules to maintain the wave of invasion from this focal point enabling it to overcome Allee effects that could result from low population numbers (e.g., as in mate finding). Conversely, on islands, such as Tahiti and Moorea, that have been infested longer than 5 years the Allee threshold has been overcome as robust populations of *H. vitripennis* are well established in multiple locations which are capable of producing abundant propagules for colonizing new areas. Interestingly, the coastal areas of Tahiti and Moorea have been extensively colonized by *H. vitripennis*. In direct contrast, the undeveloped interior areas of these two islands characterized by native vegetation and high altitude terrain have extremely rare *H. vitripennis* infestations characterized by low density populations.

Stratified diffusion and *H. vitripennis* invasion

Stratified diffusion of an invasive species combines two movement events: (1) rapid long-distance transport (often human mediated) and (2) local diffusion around the point of infestation. At the beginning of an invasion process, a few propagules invade a given locale and form an isolated colony which expands its range gradually via diffusion from the point source (Shigesada et al. 1995). The long-distance movement of *H. vitripennis* in French Polynesia has been mediated unintentionally by humans. Because of the rapidity of the invasion of the 10 currently infested islands that are located throughout the vastly distant island groups of French Polynesia, it is highly unlikely that storm activity was responsible for long distance spread of motile stages. Long-distance human-mediated dispersion of *H. vitripennis* has most likely occurred via egg masses introduced to new locations on ornamental or agricultural plants either shipped legally or smuggled illegally between infested and uninfested islands. Movement of egg masses on plants between islands poses the biggest risk of successful long-distance dispersion because plants under human care will be well looked after ensuring that egg masses will survive and a healthy host is available when nymphs emerge. The removal of stochastic events eliminating these small populations is further lessened if the infested plant is planted in a garden with lots of other healthy plants that are suitable for feeding and reproduction.

Adult *H. vitripennis* also pose an invasion risk as adults are frequently found alive inside air planes that move between islands. However, the adult stage is likely not the most high risk invasive propagule. If the adult stage was the main source of propagule pressure, the airport zone of infested islands would exhibit the largest pest populations. However, in Bora Bora and Maupiti, the airport is located on a motu (a small offshore coral island adjacent the main island), and these airport motus are not contaminated by *H. vitripennis*, whereas the main islands are infested. In Nuku Hiva, the pest population at the airport is extremely small, while the main pest nucleus is located in the main city of Taiohae. Therefore, *H. vitripennis* adults may not tolerate transit stress inside aircraft, they may be unable to find mates once in a new area, or too few plants of a suitable condition for feeding and breeding at airports impose a substantial barrier to establishment. Grandgirard et al. (2006) noted that continued spread of *H. vitripennis* in French Polynesia is probably due to insufficient domestic quarantine measures to prevent new invasions between archipelagoes within the country.

The second component of stratified dispersion is local diffusion when an incipient colony becomes well established and begins to expand naturally. The natural diffusion of *H. vitripennis* in French Polynesia appears to be rather slow, compared to human-mediated dispersion. One year after the invasion was detected in Tubuai, for example, *H. vitripennis* had not spread more than 5 km from Mataura. In Nuku Hiva, approximately the same rate of spread was observed around Taiohae. Moreover, this rate is certainly over estimated since it is hard to separate natural diffusion from short-distance (<5 km) human-mediated dispersion.

Conclusions

Three phases of *H. vitripennis* invasion in French Polynesia can be determined from this study: (1) Initially (1 year after invasion, e.g., Tahaa) the invasive population is confined to urbanized areas, population densities are low (<15 nymphs sampled in 1 min), and there is a conspicuous absence of the pest on the rest of the island. (2) An invasion of intermediate duration (2–4 years after pest arrival, e.g., Raiatea) is characterized by widespread distribution around coastal areas and large differences in population densities between urbanized and semi-urbanized areas. Pest density in urbanized areas is characterized by <50 nymphs per minute of sampling. (3) Finally, invasive populations after approximately 5 years (e.g., Tahiti) reach high density (>100 nymphs per minute of sampling) with uniform abundance between urbanized and semi-urbanized areas and very low pest abundance (<5 nymphs per minute of sampling) in undeveloped interior areas. Human activities (transportation and urbanization) are the key factors influencing *H. vitripennis* distribution and abundance in French Polynesia. Human-mediated long-distance dispersal events have had major consequences for the invasion ecology of *H. vitripennis* and enforcement of stricter regulations preventing plant movement between islands is needed to greatly reduce the spread of this pest throughout the South Pacific.

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