

Comparative fitness of invasive and native populations of the potato psyllid (*Bactericera cockerelli*)

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Abstract

Two genetically distinct potato psyllid populations [*Bactericera cockerelli* (Sulc) (Homoptera: Psyllidae)] were identified in our previous study: native and invasive. The invasive population, ranging from Baja, Mexico to central California, was the result of a recent invasion, while the native population is endemic to Texas. The native (Texas) and invasive (California) populations were collected from tomato and pepper, respectively, and were examined on both hosts to test the comparative fitness of invasive populations. Our results indicated that on both plant hosts, psyllids from the native range demonstrated higher survivorship, a higher growth index, and shorter development times than the psyllids from invasive populations. The fecundity of the native-range psyllids also was significantly higher than that of invasive psyllids on tomato, but not on pepper. For the native population, host plant differences for all fitness measurements were not significant. However, within the invasive population, psyllids feeding on tomatoes showed consistently better survivorship and a higher growth index than those feeding on pepper, despite the decreased developmental time required on peppers. The LC_{50} values (concentrations causing 50% mortality) of both populations were determined for three pesticides. Resistance to two of these pesticides was found in the invasive population. Thus, the invasive quality of the California populations may be related to increased pesticide resistance. However, it is impossible to determine if the California population was preadapted to pesticide resistance, or if the resistance developed after the range expansion and is simply a contributing factor to maintaining the expansion.

Introduction

The EICA (evolution of increased competitive ability) hypothesis (Blossey & Notzold, 1995) states that invasive populations of a species are more robust (larger body size, developing faster, producing more offspring, living longer, etc.) than the population in the native range. This reportedly co-occurs with a loss in chemical defensive capability in plants. Although this hypothesis was originally developed for plants, the concept has been extended to include invasive insects such as the Argentine ant (Tsutsui et al., 2000). One proposed mechanism is that the genetic bottleneck usually associated with founding populations selects for individuals that are more robust (e.g., with increased fitness) in the invasive group as compared with the native population (see Willis & Orr, 1993). Cheverud & Routman (1996) and

Cheverud et al. (1999) demonstrated in mammals that epistasis during such bottlenecks could actually increase additive genetic variance. Such increased genetic variance would allow invasive populations to adapt more readily to changes associated with a new environment (Lee, 2002). In the case of Argentine ants, an alternative mechanism was observed. A genetic bottleneck reportedly limited variance in an invasive population, causing reduced intraspecific aggression between colonies, which resulted in the development of large, very successful 'super colonies' (Tsutsui et al., 2000; Tsutsui & Case, 2001). Regardless of the inherent mechanism, relatively few studies have collected the necessary genetic and fitness information from native and expansion ranges that demonstrate the population variability necessary to allow a test of this hypothesis for insects. Given the increased focus on invasive species in recent years (Lee, 2002), even studies that examine the fitness correlates of invasive insect species in both their native and

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introduced ranges are surprisingly rare, despite the potential insights that can be gained from such comparisons.

In the past 5 years, an invasive population of the potato psyllid [*Bactericera cockerelli* (Sulc) (Homoptera: Psyllidae)] on the south-western coast of North America (Liu & Trumble, 2004) has provided an opportunity to test the EICA hypothesis using a non-social insect. Large and damaging outbreaks have occurred in coastal California, USA, and Baja, Mexico (Liu & Trumble, 2004, 2005). Losses in California and Baja, on fresh market tomatoes have been extensive, reaching 80% yield reduction in 2001 in Baja and 50% losses in California (Liu et al., 2006). Damage has also been extensive on fresh market peppers, resulting in emergency exemptions for some pesticides (US EPA, 2005). This invasion has been unusual both for the duration of the infestation and for the extent of geographic range invaded.

Infestations in western North America by *B. cockerelli* have been historically rare. Although early reports stated that this pest was found only in the central portion of the continent during summer months (Utah, Colorado, and parts of Wyoming, USA; Richards, 1928), sporadic populations were reported in relatively small geographic areas within California during the 1930s and 1940s (Pletsch, 1947). These populations rarely persisted for more than a year or two before disappearing. Detailed analyses of typical annual migrations indicated the psyllids originate in southern Texas, USA and perhaps the extreme north-eastern portion of Mexico, move north on the warm monsoon winds from the Gulf of Mexico to New Mexico and Arizona, USA, and then extend their populations northward during the summer months within central North America nearly to the Canadian border (Wallis, 1946; Pletsch, 1947; Al-Jabar, 1999). Each year, the high summer temperatures in Arizona and New Mexico and the cold winter temperatures in central North America prevent survival, requiring populations to re-establish from their native range in southern Texas/north-eastern Mexico. No explanations have been provided describing how these insects unexpectedly reached the west coast of North America in 1999–2000.

Molecular analyses of the psyllid populations from the native range (southern Texas) and the invasive populations (western North America) demonstrated that the populations are genetically distinct based on cladistic analyses of ISSR marker and COI sequence data (Liu et al., 2006). Within central North America, psyllid populations ranging from Coahuila, Mexico to Colorado and Nebraska, USA are genetically similar. Similarly, the western North American populations from Baja, Mexico to Ventura Co., California also are genetically clustered (Liu et al., 2006). However, nothing is known regarding potential similarities or differences in the biology or fitness correlates of the two genetically and geographically distinct populations.

Materials and methods

Insects

Approximately 500 adults and nymphs collected from fresh market tomatoes in Weslaco City (Texas, USA) in June 2005 were used to establish a colony from the native host range. The invasive colony was established by collecting approximately 500 adults and nymphs from bell pepper plants in Ventura County (California, USA) in July 2005. Although the colonies were established from a subsample of the eastern population, the Texas population is considered representative of native populations because the Texas–Mexico border region is the source for annual northward migration (Pletsch, 1947). Our previous studies showed that populations from eastern Mexico, Colorado, and Nebraska are genetically quite similar (Liu et al., 2006). The Ventura population also represents a population subsample, but this is a centrally located population among the genetically similar invasive populations found on the west coast of North America (Liu et al., 2006).

Both colonies were maintained with thousands of individuals at 25 ± 1 °C and a photoperiod of L14:D10. Host plants were potatoes [*Solanum tuberosum* L. (Solanaceae); VanZyverden Russett, Meridian, MS, USA]. A plant genus other than *Lycopersicon* was chosen as the rearing host because Tavormina (1982) and Via (1984a,b) demonstrated that some insect species developed a preference for the host species from which they had been reared. Adults used in all tests were standardized by selection of insects with teneral coloration (light or pale green), indicating that they had emerged within the previous 2–3 days. Because oviposition does not occur within the first 3 days (Knowlton & James, 1931), selection of 2- to 3-day-old adults eliminated problems with oviposition status variability. Nymphal instar determination was made based on the maximum body width of the first to fifth nymphal instar (0.2, 0.3, 0.5, 0.7, and 1.1 mm, respectively), and the development of wing pads (Rowe & Knowlton, 1935; Pletsch, 1947).

Plants

All test plants were grown in 15 cm diameter pots with University of California mix (see Matkin & Chandler, 1957) and were fertilized three times weekly with the label rate of Miracle Gro nutrient solution (Scotts Company, OH, USA). All plants used were between 1 and 2 months of age with 5–10 fully expanded leaves, at the developmental stage achieved approximately 1 week after transplanting in the field. Although damage can occur at any time, young plants are particularly susceptible (Carter, 1950). Plants of similar size and vigor were used for all replications.

Two tomato cultivars of *Lycopersicon esculentum* Mill. (Solanaceae) (petoseed ‘yellow pear’, and sunseeds ‘shady

lady') were used. The 'yellow pear' cultivar is a variety commonly planted by consumers, and was shown to be a preferred tomato cultivar for psyllids in our previous studies (Liu & Trumble, 2004, 2005). This cultivar was employed for our psyllid fecundity, and growth and development tests. The cultivar 'shady lady' is a common commercial variety in California, and was one of the least preferred cultivars tested for psyllids (Liu & Trumble, 2004, 2005). This cultivar was chosen for tests of insecticide susceptibility. A common bell pepper cultivar [*Capsicum annuum* L. (Solanaceae); Novartis 'Taurus'] was used in all tests where pepper was required.

Fitness correlates

Body-size measurements. Body size is often used as a measure of fitness (Sokolovska et al., 2000; Braun et al., 2004). Adult size was measured under 12× magnification using the length of the body proper (from the front end of head to the abdomen tip). Five groups of 10 adults (five females and five males) from both the native and the invasive populations were measured. The adult size comparisons were made using analysis of variance (ANOVA) (StatView, 1998).

Fecundity. Newly emerged adults were held on fresh potato leaves in a Petri dish for 3 days. Ten adults (five females and five males) then were introduced into an opaque plastic container with a height of 37 cm and with a diameter of 45 cm with either two 'yellow pear' tomato or two 'Taurus' pepper plants. The adults were allowed to oviposit for 7 days, and the numbers of eggs were then counted. This study was conducted for both the invasive and the native psyllid populations, thereby creating four treatments. Each treatment was replicated five times.

Growth, development, and nymphal mortality. To compare the growth and development of both populations, tomato or pepper plants were placed in the opaque plastic container (as above), and psyllid adults were introduced and allowed to oviposit for 2 days. The numbers of eggs on each plant were counted, and 20–40 eggs were allowed to remain on each plant, because the test plants could sustain 40 nymphs' feeding until adult eclosion (Liu & Trumble, 2005). If more than 40 eggs were produced, excess numbers were removed to simplify tracking of individuals. Again, four treatments were conducted, including both the invasive and the native psyllid populations and both plant species. Each treatment was replicated nine to 12 times. All tests were conducted at 26 °C and a photoperiod of L14:D10. Treatment plants were randomly arranged on the shelves in the experimental chamber. Each replicate was monitored for mortality until the last nymph completed development to the adult stage.

Nymphal instar was examined daily, and the numbers of early-instar (including the first- and second-instar) nymphs, and late-instar (including the third- to fifth-instar) nymphs were recorded. As nymphs reached the third to fifth instar, treatments were checked twice daily for adult eclosion, allowing the calculation of a more accurate developmental time from egg to adult.

Pesticide-resistance trials. Because of the possibility that pesticide resistance could be providing a fitness advantage for the invasive population, we evaluated three pesticides selected for their use patterns on both populations. Chemicals and recommended rates included in the study were spinosad (Conserve 120 SC, Dow AgroSciences Inc., Indianapolis, IN, USA; 1.72 ml l⁻¹, applied with a hand sprayer), spiromesifen (Oberon 2 SC, Bayer CropScience LP, Research Triangle Park, NC, USA; 0.67 ml l⁻¹, applied with a hand sprayer), and imidacloprid (Admire 2 Flowable, Bayer Corporation, Kansas City, MO, USA; 0.94 ml l⁻¹, applied to the soil at 100 ml per pot). The test concentrations were 192 (equals 0.94 ml l⁻¹), 96, 48, 24, and 0 mg active ingredient (a.i.) l⁻¹ for imidacloprid, 160 (equals 0.67 ml l⁻¹), 80, 40, 20, and 0 mg (a.i.) l⁻¹ for spiromesifen, and 200 (equals 1.72 ml l⁻¹), 100, 50, 25, and 0 mg (a.i.) l⁻¹ for spinosad. All test insecticides except imidacloprid were sprayed until run-off; about 50 ml per plant. Spinosad and imidacloprid have been registered for at least 5 years, whereas spiromesifen was just registered in 2004. We hypothesized that spinosad and imidacloprid should show significant differences in activity between populations if pesticide susceptibilities were different. Spiromesifen was included as a positive control because this material has just been released in the USA, and invasive populations appeared in western North America before the material was approved for use.

To determine the LC₅₀ of insecticides for both psyllid populations, tomato plants (cultivar 'shady lady') were exposed to ovipositing adults. The plants and eggs were sprayed with spinosad or spiromesifen 3–4 days later. Imidacloprid was applied as a soil drench within 24 h after the oviposition of eggs to allow the chemical to distribute systemically. As in the tests of growth and development, 30–40 eggs were allowed to remain on each replicate (one plant per replicate). Survivorship was monitored until all nymphs had died, and only those eggs that hatched were used to calculate mortality. Each concentration of each treatment was replicated at least five times.

Statistical analyses

Insect development was characterized using the growth index (GI) introduced by Zhang et al. (1993). Growth index values were calculated as:

$$GI = \frac{\sum_{i=1}^{i_{\max}} [n_{(i)} \times i] + \sum_{i=1}^{i_{\max}} [n'_{(i)} \times (i-1)]}{N \times i_{\max}},$$

where i = developmental stage of the insects, $i_{\max} = 4$, the highest attainable stage of the insect at day 35 and $n_{(i)}$ = the number of insects alive at stage i , $n'_{(i)}$ = the number of insects dead at stage i , and N = the total number of insects tested. Stages were chosen as 1 = egg hatch, 2 = instars 1 + 2, 3 = instars 3 + 4 + 5, and 4 = adult. This index provides an indication of the developmental stage reached by the cohort of test insects at the completion of the test, with values approaching one indicating a large proportion reaching the adult stage and values near zero indicating few insects surviving beyond the first stage.

Due to the non-normal distribution of data, late-instar mortality data analyses were conducted with the Mann–Whitney U-test (StatView, 1998). All GI data and early-instar mortality data were transformed (square root of the arcsine) prior to analysis. Where appropriate (data were normal), survivorship, developmental time, and GI were analyzed by two-way ANOVA to identify interactions between geographic locations and hosts [PROC general linear model (GLM) procedure of SAS, 2002] ($P < 0.05$ level). In the two-way ANOVA, differences in means were assessed by the Tukey honestly significant difference (HSD) test controlling for overall experiment-wise error rates. The 'lsmeans' line in the PROC GLM two-way ANOVA was as follows: lsmeans location host location*host/stderr pdiff adjust = Tukey. This step calculates errors from three sources including location, host, and location*host; it also makes multiple mean comparisons adjusting with the Tukey test. The insecticide LC_{50} values and the relevant 95% fiducial limits were determined using Proc Probit procedure in SAS (2002). LC_{50} values were considered different significantly and indicative of resistance if the 95% fiducial limits of the LC_{50} values did not overlap (Khan & Morse, 1998; Liu et al., 2003).

Results

Body size

No differences were found between the mean adult body size of native-range psyllids (mean = 1.902 ± 0.026 mm) and that of the invasive populations mean = (1.870 ± 0.022 mm) (ANOVA, $P < 0.05$).

Survivorship

The survivorship of native psyllids was significantly higher than that of invasive psyllids on tomato as well as pepper (Figure 1). Within the native population, there were no differences in the egg to adult survivorship on pepper or on

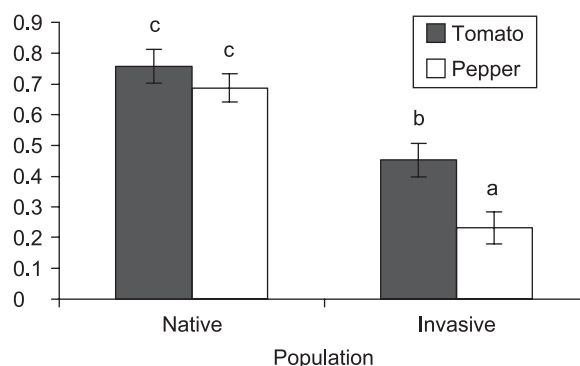


Figure 1 Comparisons of survivorship (mean $\pm$ SE) of native and invasive *Bactericera cockerelli* psyllids on tomato and pepper (different letters indicate significant differences, two-way ANOVA, $P < 0.05$).

tomato. Within the invasive population, overall survivorship on tomato was significantly higher than that on pepper ($F_{1,36} = 9.52$, $P < 0.004$; Figure 1).

Survivorship was also measured for early- vs. late-instar nymphs. On pepper, both native and invasive psyllids suffered more mortality during early instars than late instars (Figures 2 and 3). The early-instar nymphal mortality of invasive psyllids on pepper was significantly higher than all the other treatments ($F_{1,36} = 20.84$, $P < 0.001$; Figure 2). Early-instar invasive psyllids also suffered significantly higher mortality than native psyllids on tomato ($F_{1,36} = 38.42$, $P < 0.001$; Figure 2). For late-instar nymphal mortality, the only difference found was between native psyllids on pepper and invasive psyllids on tomato (Mann–Whitney U-test, $P < 0.05$; Figure 3).

Growth index

In between-population comparisons, the native psyllid's GI was significantly higher than the GI of invasive psyllids

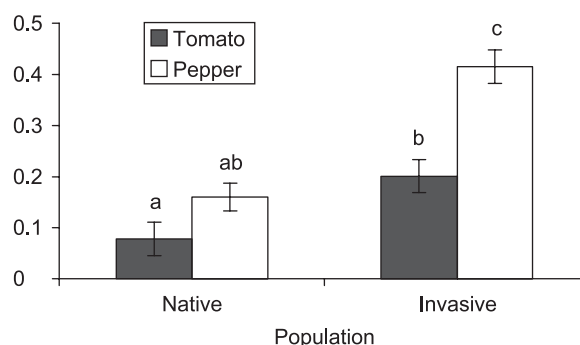


Figure 2 Comparisons of early-instar nymph mortality (mean $\pm$ SE) of native and invasive *Bactericera cockerelli* psyllids on tomato and pepper (different letters indicate significant differences, two-way ANOVA, $P < 0.05$).

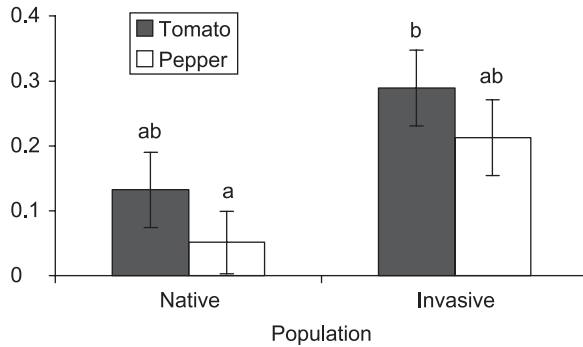


Figure 3 Comparisons of late-instar nymph mortality (mean $\pm$ SE) of native and invasive *Bactericera cockerelli* psyllids on tomato and pepper (different letters indicate significant differences, Mann–Whitney U-test, $P < 0.05$).

for either tomatoes or peppers ($F_{1,36} = 65.12$, $P < 0.0001$; Figure 4). For within-population comparisons, no difference was found between the native psyllid's GI on pepper and that on tomato. However, the GI of invasive psyllids on tomato was significantly higher than that on pepper ($F_{1,36} = 22.85$, $P < 0.0001$; Figure 4).

Fecundity and development time

The 7-day fecundity of psyllids from the native range was significantly higher than that of the invasive psyllids on tomato ($F_{1,16} = 4.91$, $P = 0.042$; Figure 5); no other differences in fecundity were observed. Similarly, the egg–adult developmental time was significantly longer for the invasive population than for the psyllids from the native range ($F_{1,16} = 58.31$, $P < 0.001$; Figure 6). Within the native population, there was no significant difference in developmental times between pepper and tomato (Figure 6). However, within the invasive population, significantly more time

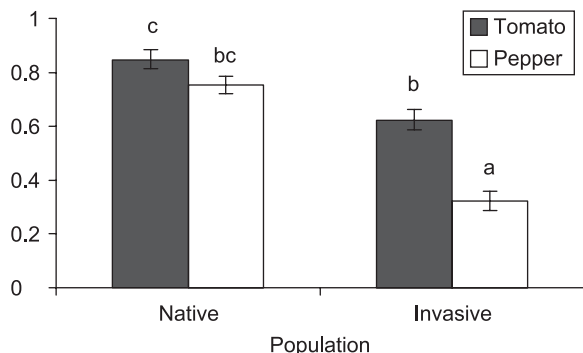


Figure 4 Comparisons of growth index (mean $\pm$ SE) of native and invasive *Bactericera cockerelli* psyllids on tomato and pepper (different letters indicate significant differences, two-way ANOVA, $P < 0.05$).

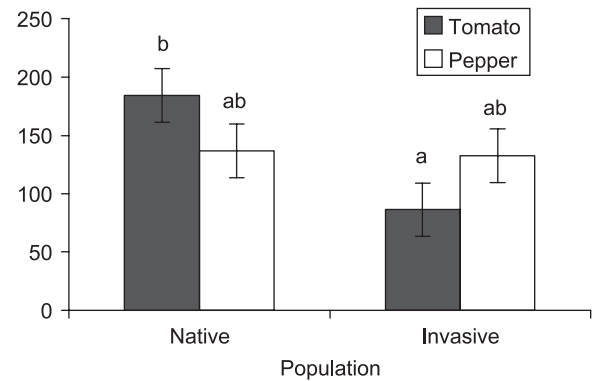


Figure 5 Comparisons of 7-day fecundity (mean $\pm$ SE) of native and invasive *Bactericera cockerelli* psyllids on tomato and pepper (different letters indicate significant differences, two-way ANOVA, $P < 0.05$).

was required for development on tomato than on pepper (Figure 6).

Pesticide susceptibility

Based on non-overlapping confidence intervals, the LC_{50} values for native (20.3 mg a.i. l^{-1}) and invasive psyllids (26.2 mg a.i. per l^{-1}) differed significantly for imidacloprid (Table 1). Similarly, for spinosad, the LC_{50} values for native populations (7.7 mg a.i. l^{-1}) and invasive populations (24.3 mg a.i. per l^{-1}) also differed significantly. The LC_{50} values for spiromesifen had overlapping 95% fiducial limits, and were therefore not considered different.

Discussion

The rapid growth rate of psyllids, their high fecundity, and the broad range of hosts they accept (Liu & Trumble, 2005, 2006) are characteristics common to successful colonists.

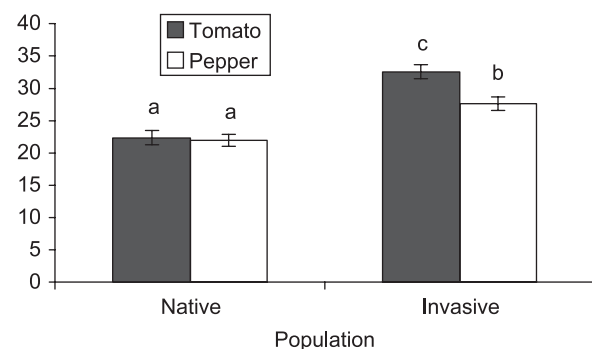


Figure 6 Comparisons of development time (mean $\pm$ SE) of native and invasive *Bactericera cockerelli* psyllids on tomato and pepper (different letters indicate significant differences, two-way ANOVA, $P < 0.05$).

Table 1 Comparison of toxicities of imidacloprid, spinosad, and spiromesifen to native (Texas) and invasive (California) psyllid populations

Insecticide	Location	Time period	No. of insects tested	LC ₅₀ (95% fiducial limits), mg a.i. l ⁻¹ (days)
Imidacloprid	Texas	10	870	20.318 (17.373–22.775)
Imidacloprid	California	10	750	26.189 (24.472–27.826)
Spinosad	Texas	10	870	7.669 (3.951–11.435)
Spinosad	California	10	750	24.320 (19.886–28.400)
Spiromesifen	Texas	10	870	15.489 (11.382–19.213)
Spiromesifen	California	10	750	25.149 (18.571–31.190)

Small body sizes and a high-carrying capacity of environment can lead to an increased possibility of successful establishment (Sakai et al., 2001 and references therein). Thus, *B. cockerelli* has the life-history characteristics necessary for completing the steps required for a successful introduction and subsequent invasion. These steps include the introduction of psyllids into a new habitat by airborne migration, initial colonization and successful establishment, and subsequent dispersal with secondary spread into new habitats (Sakai et al., 2001). However, both the native-range psyllids and the insects from the invasive population could reasonably be expected to maintain 'invasive' characteristics. The psyllids from the native populations in southern Texas migrate annually from crop plants to perennial desert vegetation in New Mexico, and then to potatoes and other crops as far north as Canada (Pletsch, 1947; Al-Jabar, 1999). Thus, our data suggest that they have maintained the ability to accept a wide variety of host plants and to generate large populations following repeated migration events.

Two distinct genetic processes commonly have been reported to produce ecological specialization in new environments: mutation accumulation and antagonistic pleiotropy (Cooper & Lenski, 2000) [but see also Lee (2002) for a discussion of additive genetic variance]. In mutation accumulation, mutations become fixed by genetic drift in genes that are not maintained by selection; adaptation to one environment and loss of adaptation to another are caused by different mutations. Antagonistic pleiotropy arises from trade-offs such that the mutations that are beneficial in one environment are detrimental in another. When organisms adapt genetically to one habitat, they may lose fitness in other habitats. This latter possibility may be the case in our study. The native-range psyllid population from Texas performed better than the invasive population on both tomato and pepper in terms of survivorship, growth index, and development time. These observations support the molecular characterization by Liu et al. (2006)

that indicated these geographically isolated populations are genetically distinct. Within the invasive population, there was some variability in performance across host plants. Even though the invasive psyllids were originally collected on pepper, they showed higher survivorship, and a larger GI on tomato than on pepper. However, development time was significantly longer on tomato. No such differences were evident for the psyllids from the native range, which is consistent with a gene pool providing broader adaptation across these host plants.

This study provides only a partial test of the EICA hypothesis. Potential changes in defensive capabilities of the insects were not measured. However, increases in growth and fitness in the invasive population were not evident as predicted by the EICA hypothesis. If the invasive population was not more robust than the native population, why then was the invasive population so successful on the west coast of North America? Although some biological control agents have been identified (mostly generalist predators), none have provided useful levels of suppression of *B. cockerelli* in the field (Al-Jabar, 1999). Therefore, exploitation of enemy-free space (as defined by Berdegue et al., 1996) does not appear to be a likely factor in the observed range expansion. One potential explanation would be an enhanced resistance to commonly applied pesticides.

The LC₅₀ values in Table 1 indicated that the invasive psyllids were less sensitive to two commonly used pesticides as compared to psyllids from the native range. Imidacloprid and spinosad are widely used in California, targeting psyllids and other sucking insects as well (CA Department of Pesticide Regulation, 2003). Similar data are not available in Texas (Texas Pesticide Information Network, 2001. http://www.pmac.net/PR_park_pesticides.pdf). Imidacloprid is a systemic, chloronicotinyl insecticide used for the control of insects that has been widely used for insect control on tomato and pepper for nearly 10 years. Field trials on peppers conducted by Kund et al. (2006) provided substantial evidence that the psyllid is not controlled by repeated

applications of imidacloprid in California, thus supporting the conclusion that resistance has developed. Spinosad is a secondary metabolite from the aerobic fermentation of *Saccharopolyspora spinosa* (a soil-dwelling bacterium) (McPherson et al., 2003), and has been similarly used on both crops for many years. Spiromesifen is a newly registered insecticide (2005 in California and Baja, Mexico) for psyllid suppression that is now used on tomato and pepper. This product belongs to a new chemical class of tetrone acids and has a mode of action classified as a lipid biosynthesis inhibitor (Liu, 2004 and references therein). Although recently registered throughout the USA and Mexico for psyllid suppression, no significant differences in resistance were observed. These observations are consistent with a range expansion through pesticide resistance. In addition, pesticide resistance has been shown in other insects to be associated with a physiological cost that can reduce biological measures of fitness as compared to a susceptible population (Follett et al., 1993; Chevillon et al., 1997; Foster et al., 1999). Therefore, we suspect that, at least in part, pesticide resistance is responsible for the range maintenance of *B. cockerelli* in western North America. However, there is no information available to verify that the psyllids that expanded into western North America were preadapted for pesticide resistance, or if the observed resistance developed after the range expansion had occurred. Additional studies will be needed to determine the possible role of adaptation to other environmental factors such as temperature and humidity in the range expansion of this insect. Nonetheless, we predict that the small size, rapid reproduction, pesticide resistance, and wide host range of this insect will facilitate expansion of its geographic range beyond North America.

This research also identified a larger evolutionary question. Specifically, why do the native populations undertake extensive northward migrations every year? The migrating populations die each year with the onset of cold weather and there are no reports that the offspring of the migrating individuals ever return to the endemic foci areas of southern Texas or north-eastern Mexico. Thus, what is driving these apparently suicidal northward migrations in the native population? Further studies will be necessary to determine why these migrations occur.

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