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Source: Journal of Economic Entomology, 108(1):252-258.

Published By: Entomological Society of America

URL: <http://www.bioone.org/doi/full/10.1093/jee/tou050>

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# *Diaphorina citri* (Hemiptera: Liviidae) Abundance in Puerto Rico Declines with Elevation

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J. Econ. Entomol. 108(1): 252–258 (2015); DOI: 10.1093/jee/tou050

**ABSTRACT** *Diaphorina citri* Kuwayama is the primary vector of Huanglongbing, the most devastating disease of citrus. *D. citri* populations in Puerto Rico were monitored with yellow sticky traps on citrus trees or other psyllid host plants at different elevations, ranging from 10 to 880 m above sea level. Trapping was conducted in March through May of 2013 and 2014 when psyllid populations usually are highest. Population levels of *D. citri*, based on the trapping data, varied among the sites, and there was a strong trend in both years for decreasing psyllid abundance with increased elevation based on the number of psyllids captured on traps and the proportion of trees shown to be infested. No psyllids were collected at an elevation of >600 m. Reduced populations at higher elevations could be a consequence of differences in temperature, air pressure, oxygen levels, ultraviolet light, or other factors alone or in combination. We discuss our results as they pertain to management of *D. citri* and Huanglongbing.

**KEY WORDS** Asian citrus psyllid, *Citrus*, elevation, Puerto Rico, Huanglongbing

## Introduction

Huanglongbing (HLB, citrus greening) is the most serious disease of citrus in the world (Bové 2006). The putative causal agents of HLB are phloem-limited bacteria identified as *Candidatus Liberibacter* spp. (Sechler et al. 2009, Tyler et al. 2009) and are vectored by the Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Liviidae), and the African citrus psyllid, *Trioza erythrae* (del Guercio) (Hemiptera: Triozidae) (Catling 1970, Halbert and Manjunath 2004, Hall et al. 2013). *D. citri* was first reported in Florida in 1998 (Halbert et al. 1998) and in Puerto Rico in 2001 (Halbert and Nuñez 2004). Huanglongbing attributed to *Candidatus Liberibacter asiaticus* was first reported in Florida in 2005 (Halbert 2005) and has been in Puerto Rico since at least 2007 (unpublished data).

No cure exists for HLB, but best management practices (Su et al 1986) include application of pesticides to control the vector (Su et al 1986, Bové 2006, Gottwald 2010, Hall and Gottwald 2011), roguing of infected trees (Su et al 1986, Gottwald 2010), and ensuring only disease-free trees are planted (Su et al 1986, Gottwald 2010). Increased frequency of pesticide applications has selected for Asian citrus psyllid populations that are resistant to some insecticides (Tiwari et al. 2011) and have reduced natural enemy populations, resulting in outbreaks of secondary pest problems (Dutcher 2007).

Psyllid populations are dependent on citrus flush for reproduction (Hall and Albrigo 2007, Sétamou et al. 2008) and, consequently, many growers apply pesticides at this time. Of the several flushes that develop each year in mature trees, the spring flush coincides with flowering, and beekeepers are reticent to bring hives near orchards that are being sprayed. Removal of infected trees has run into problems as well. Many infected trees may be asymptomatic and remain in the orchard as sources of inoculum because of the lengthy incubation period (Chiyaka et al. 2012). The costs of surveying for and removing infected trees are often too high for farmers to pursue aggressively (Spann et al. 2011).

Identifying the habitat restrictions of Asian citrus psyllids or of HLB would be useful in assessing the risk of these pests in new regions and for developing management strategies. There has been anecdotal evidence that *D. citri* is less abundant at higher elevations. For instance, a study monitoring psyllid abundance in Florida, Puerto Rico, and Texas using yellow sticky traps revealed negligible populations of psyllids ( $0.3 \pm 0.09$  adults per trap per 2wk) at a Puerto Rican site reportedly 686 m above sea level compared with  $2.8 \pm 0.6$  and  $3.0 \pm 0.9$  adults per trap per 2wk at locations 130 and 220 m above sea level, respectively (Flores et al. 2009). If, in fact, Asian citrus psyllid populations are suppressed at higher elevations, determining the reasons could lead to new management strategies for Asian citrus psyllid and HLB.

We measured Asian citrus psyllid population levels at different elevations where citrus is grown in Puerto Rico to determine potential patterns associated with elevation.

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## Materials and Methods

**Study Sites.** Seventeen sites were selected based on variations in elevation and accessibility (Fig. 1 and Table 1). Elevation was determined using topographical maps. Sites varied from commercial citrus farms to small family orchards or dooryard trees.

**Mayaguez 1.** This site was located at the U.S. Department of Agriculture (USDA)–Agricultural Research Services Tropical Agriculture Research Station in Mayaguez, Puerto Rico, and included an irregular planting (botanical garden style) of various Rutaceae, including *Citrus limon* (L.) Burman, *Murraya exotica* L., *Citrus reticulata* Blanco, *Swinglea glutinosa* (Blanco) Merrill, *Triphasia trifolia* (Burman) Percy Wilson. This site was studied only in 2013.

**Mayaguez 2.** This site was a medium-sized (approximately 100 trees) home orchard of *C. limon* and *C. reticulata*. This site was studied in both years of the study.

**Las Marias.** This site was a moderate-sized home orchard (approximately 0.25 ha) of *C. limon*, *C. reticulata*, and *Citrus sinensis* (L.) Osbeck planted on sloping terrain. The owners also had a hedge of *M. exotica* and a commercial *Citrus* seedling business. This site was studied in both years of the study.

**Adjuntas.** This site was a moderate-sized experimental orchard (approximately 0.5 ha) at the University of Puerto Rico Agricultural Experiment Station in Adjuntas, PR, and consisted of *C. reticulata*, *C. sinensis*, and chironja, a cross between *C. maxima* and *C. sinensis*, all planted on sloping terrain. This farm also cultivates coffee. This site was studied in both years of the study.

**Guanica.** This site was a moderate-sized commercial orchard (approximately 4 ha) of *C. limon* near plantings of papaya, red peppers, onions, and pumpkins. This site was only studied in 2013.

**Sabana Grande.** This site was a moderate-sized commercial orchard (approximately 0.5 ha) of *C. limon* near plantings of papaya, tomatoes, pineapples, bananas, and plantains. This site was studied only in 2013.

**Río Cañas.** This site was a home orchard, consisting of only five trees of *C. reticulata* and *C. limon* planted on sloping terrain. This site was studied only in 2013.

**Castañer.** This site was a row of citrus in a large commercial orchard (approximately 10 ha) with plantings of *C. aurantium* and *C. reticulata*. This farm also cultivates coffee, bananas, and avocados planted on a sloping terrain. This site was studied in 2013, but also was sampled for 2 wk in 2014.

**La Ceiba.** This was a small home garden consisting of *C. limon*, *Citrus paradisi* Macfadyen, *Berbera koenigii* (L.) Sprengel, and *C. aurantium* L. planted on a sloping terrain. This site was studied only in 2013.

**Portugues.** This site was a small home garden consisting of five trees, all *C. sinensis* intercropped with coffee and bananas on a sloping terrain. This site was studied only in 2013.

**Santa Isabel.** This site was a small commercial orchard (approximately 0.5 ha) of *C. limon*. The orchard was surrounded by bananas and mangoes. This site was studied only in 2014.

**Los Millonarios.** This site was a small home orchard consisting of *C. sinensis* interplanted with bananas and coffee on sloping terrain. This site was studied only in 2014.

**Rosario.** This site was a small home orchard of *C. limon* and *C. × sinensis* and also included a *Citrus* nursery. This site was studied only in 2014.

**Lajas.** This site is a small orchard of *C. limon* at the UPR Agricultural Experimental Station at Lajas, PR. The farm also has plantings of corn, Spanish lime, avocado, and mangoes. This site was studied only in 2014.

**Aguada.** This site is a moderate home orchard of *C. limon* planted on a sloping terrain. This site was studied only in 2014.

**Lares.** This site is a moderate commercial orchard of *C. aurantium* on a sloping land and interplanted with coffee. This site was studied only in 2014.

**Maricao.** This site is a large commercial farm (approximately 5 ha) of *C. aurantium* and *C. reticulata* on sloping terrain interplanted with bananas and coffee. This site was studied only in 2014.

**Monitoring Psyllid Populations.** Three yellow sticky traps (12.7 by 17.8 cm; Great Lakes IPM, Vestaburg, MI) were placed on randomly selected citrus trees and other Asian citrus psyllid host plants at the study sites in 2013 following the general procedures presented by Flores et al. (2009). Only one sticky trap per tree was used in 2014 because Asian citrus psyllid abundance in the first year was correlated between traps on the same tree ( $r$  ranged from 0.66 to 0.79;  $P < 0.0001$ ). Many sites used in 2013 were abandoned in 2014 because of pesticide use or too few fruit trees to sample. At most sites in each year, traps were placed on 10 trees. We deviated from this sample size at some locations either because there were not 10 trees at a site or we had interest in sampling  $>10$  trees: exceptions included Portugues (5 trees sampled), Río Cañas (5 trees sampled), Las Marias (15 trees sampled in 2014), Mayaguez 2 (15 trees sampled in 2014), Maricao (20 trees sampled), and Rosario (23 trees sampled). Traps were collected and replaced weekly. Collected traps were placed in gallon-size plastic bags, labeled with the site and date information, and returned to the laboratory to count psyllids. The total number of psyllids captured per tree per trapping period and the proportion of trees infested per trapping period were recorded for each site. Sampling was conducted in March through May each year, the timing coinciding with the beginning of the rainy season and flush of new growth on citrus trees at all sites. Previous data (Flores et al. 2009) indicated that psyllid populations were negligible in most orchards outside of this season and our personal observations support this. Visual searches we conducted for 1 mo during the study on at least 10 trees at Maricao, Adjuntas, and Los Millonarios to confirm that Asian citrus psyllid was not present at these sites.

**Mini-Survey for HLB.** In 2014, 10 trees were selected randomly from each of three low-elevation sites (Santa Isabel, Rosario, and Lajas) and each of



**Fig. 1.** Map of Puerto Rico showing sites where *D. citri* was sampled.

**Table 1.** Sites used in the study, including coordinates in decimal degrees and elevation in meters

Location	Latitude (dd)	Longitude (dd)	Elevation (m)	Years studied	Ten trees sampled for HLB
Mayaguez 1	18.20891	-67.13788	10	2013	
Guanica	17.97711	-66.89810	12	2013	
Lajas	18.03311	-67.07202	26	2014	Yes
Rosario	18.11932	-67.07728	34	2014	Yes
Mayaguez 2	18.24184	-67.13290	39	2013, 2014	
Santa Isabel	18.01617	-66.41492	47	2014	Yes
Sabana Grande	18.04165	-66.95258	48	2013	
Aguada	18.34614	-67.21362	70	2014	
La Ceiba	18.22015	-67.10920	161	2013	
Las Marias	18.24686	-66.98046	181	2013, 2014	
Rio Canas	18.24063	-67.05718	300	2013	
Lares	18.30264	-66.91034	341	2014	
Castaner	18.19765	-66.83041	459	2013	
Adjuntas	18.17314	-66.79780	580	2013, 2014	Yes
Millonarios	18.17906	-66.84486	614	2014	Yes
Portuguese	18.14103	-66.68061	648	2013	
Maricao	18.15184	-66.89087	880	2014	Yes

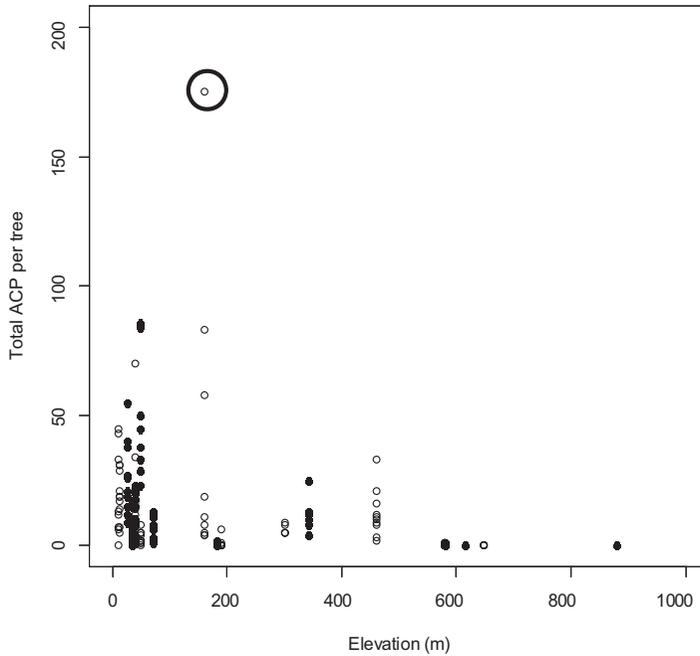
three high-elevation sites (Millonarios, Adjuntas, and Maricao). Five randomly selected leaves from around mid-canopy were collected from each tree and returned to the laboratory for testing. AmplifyRP Acceler8 kits for *Candidatus Liberibacter* (Agdia, Elkhart, and Indiana) were used to confirm infection by *Candidatus Liberibacter*.

**Analyses of Data.** The number of Asian citrus psyllids trapped on individual trees at each site was summed to provide the total number of Asian citrus psyllids trapped during the 9-wk sampling period for each tree. The total number of Asian citrus psyllids per tree was plotted against site elevation separately for 2013 (three traps per tree) and 2014 (one trap per tree). Because the total number of Asian citrus psyllids per tree was not normally distributed and violated assumptions of equal variance, we analyzed the association between total psyllids per tree and elevation using a Poisson regression, accounting for overdispersion. We also determined the proportion of trees at each elevation that had Asian citrus psyllid infestations; positive infestations were recorded if a tree had even a single psyllid recorded on it at any time during the study. The proportion of trees with Asian citrus psyllid infestations was plotted against elevation. We determined the Pearson's product-moment correlation coefficient ( $r$ ) for the relationship between the proportion of psyllid-infested trees and elevation and tested the hypothesis

that there is a relationship between elevation and the proportion of trees infested using Student's  $t$ -distribution ( $t$ ; Fisher 1915, R Core Team 2013). Proportion data were arcsine-transformed prior to analysis.

## Results

The number of adult *D. citri* captured on traps varied widely among sites and within sites (Fig. 2 and Table 2). The total number of Asian citrus psyllids captured per season varied from 0 (Los Millonarios, Maricao, and Portuguese) to 449 (Santa Isabel). No Asian citrus psyllid was trapped at any of the sites at elevations >600 m, nor did visual examinations of orchards reveal any psyllids (Fig. 2; Table 2). At some sites, Asian citrus psyllid abundance was low (only 1–10 individuals trapped during the season). Only two Asian citrus psyllids were trapped at the Adjuntas site in 2013 and only one was trapped in 2014. Only seven Asian citrus psyllids were trapped at the Las Marias site in 2013 and only nine were trapped in 2014. Few Asian citrus psyllids (30) were captured at the Sabana Grande site during the season. Poisson regression indicated that there was a significant association between the number of psyllids per tree at a site and elevation for both years (2013:  $F = 10.941$ ,  $df = 96$ ,  $P = 0.0013$ ; 2014:  $F = 51.779$ ,  $df = 131$ ,  $P = 4.301 \times 10^{-11}$ ). The proportion of trees with Asian citrus psyllids was negatively



**Fig. 2.** The total number of *D. citri* trapped per tree (psyllids on 13 by 18 cm yellow sticky cards) plotted against elevation (m). Open circles are data collected in 2013, closed circles are data collected in 2014. The circled value is from *B. koenigii*. Poisson regression analysis, accounting for overdispersion, indicated a significant association between total psyllids per tree and elevation for both years (2013:  $F = 10.941$ ,  $df = 96$ ,  $P = 0.0013$ ; 2014:  $F = 51.779$ ,  $df = 131$ ,  $P = 4.301 \times 10^{-11}$ ).

**Table 2.** The mean number of psyllids per trap per week at each site ( $\pm$ SEM) and the mean proportion of trees with Asian citrus psyllids ( $\pm$ SEM)

Site	Elevation (m)	Mean number of Asian citrus psyllids per trap per week $\pm$ SEM		Mean proportion of trees with Asian citrus psyllids $\pm$ SEM	
		2013	2014	2013	2014
Mayaguez 1	10	2.65 $\pm$ 0.35		0.69 $\pm$ 0.09	
Guanica	12	2.27 $\pm$ 0.27		0.83 $\pm$ 0.04	
Lajas	26		3.28 $\pm$ 0.436		0.92 $\pm$ 0.03
Rosario	34		0.44 $\pm$ 0.06		0.34 $\pm$ 0.04
Mayaguez 2	39	5.00 $\pm$ 1.07	1.21 $\pm$ 0.19	0.85 $\pm$ 0.05	0.52 $\pm$ 0.07
Santa Isabel	47		5.80 $\pm$ 0.79		0.79 $\pm$ 0.03
Sabana Grande	48	0.33 $\pm$ 0.64		0.20 $\pm$ 0.10	
Aguada	70		0.73 $\pm$ 0.15		0.45 $\pm$ 0.06
La Ceiba	161	4.19 $\pm$ 1.35		0.62 $\pm$ 0.07	
Las Marias	181	0.07 $\pm$ 0.03	0.07 $\pm$ 0.03	0.10 $\pm$ 0.03	0.09 $\pm$ 0.03
Rio Canas	300	0.89 $\pm$ 0.29		0.34 $\pm$ 0.11	
Lares	341		1.21 $\pm$ 0.13		0.62 $\pm$ 0.05
Castaner	459	1.39 $\pm$ 2.58		0.53 $\pm$ 0.10	
Adjuntas	580	0.02 $\pm$ 0.02	0.01 $\pm$ 0.01	0.03 $\pm$ 0.02	0.02 $\pm$ 0.02
Millonarios	614		0.00 $\pm$ 0.00		0.00 $\pm$ 0.00
Portuguese	648	0.00 $\pm$ 0.00		0.00 $\pm$ 0.00	
Maricao	880		0.00 $\pm$ 0.00		0.00 $\pm$ 0.00

Sites are arranged from lowest to highest elevation.

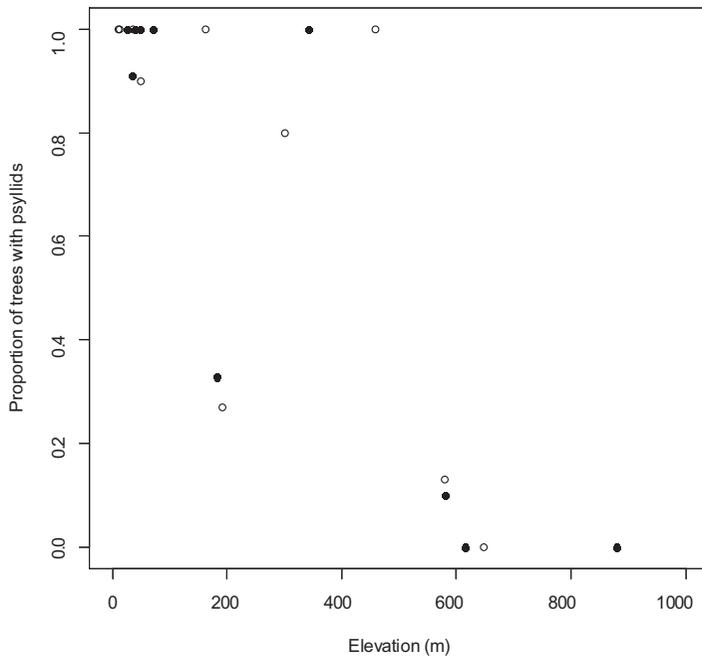
correlated with elevation and the effect was significant for both years of the study (Fig. 3; 2013:  $r^2 = 0.53$ ,  $t = -3.028$ ,  $df = 8$ ,  $P = 0.016$ ; 2014:  $r^2 = 0.751$ ,  $t = -4.91$ ,  $df = 8$ ,  $P = 0.001$ ).

Of the 30 trees surveyed for HLB at high elevation sites (Millonarios, Adjuntas, and Maricao, all at  $\geq 580$  m), none tested positive for the disease. At elevations of  $\leq 47$  m, 7 of the 10 trees from the Santa Isabel orchard tested positive, 3 of the 10 trees from the Lajas

site tested positive, and 1 of the 10 trees from the Rosario site tested positive.

**Discussion**

Plots of the mean number of adults captured per tree per week and of proportions of trees with adults visually revealed a negative relationship between Asian citrus psyllid abundance and elevation. No psyllids



**Fig. 3.** The overall proportion of sampled trees with *D. citri* at each site plotted against elevation (m). Open circles are data collected in 2013, closed circles are data collected in 2014. Pearson's product-moment correlation analyses on arcsine-transformed proportions indicated a significant negative relationship between the proportion of trees with *D. citri* populations and elevation for both years: 2013:  $r = -0.7308$ ,  $t = -3.0281$ ,  $df = 8$ ,  $P = 0.01636$ ; 2014:  $r = -0.8666$ ,  $t = -4.9126$ ,  $df = 8$ ,  $P = 0.0012$ . The correlation analysis was conducted on arcsine-transformed proportions, but untransformed data are presented.

were recorded at any sites >600 m. This is in contrast to a report by Flores et al. (2009), which indicated low populations of Asian citrus psyllids occurred at Adjuntas at an elevation of 648 m—this reported elevation was erroneous, as we studied the same trees at Adjuntas and confirmed the elevation to be 580 m. The elevation reported in the Flores et al. study was determined using a handheld GPS device that must have malfunctioned.

Asian citrus psyllid population levels according to our trapping data varied not only among sites at different elevations but also among sites at more similar elevations. At lower elevations where we might expect to have seen large numbers of Asian citrus psyllids on traps, sometimes relatively few Asian citrus psyllids were trapped. A number of factors may have contributed to differences in the number of adults captured at these sites, including the particular host plant species present, plant and Asian citrus psyllid management practices, and environmental conditions, of which, the latter can negatively or positively influence psyllid flight activity and the resulting capture rates of Asian citrus psyllids on sticky traps (Hall 2009). Data collected in 2013 included three anomalous groups of data that suggest strong influences of factors on Asian citrus psyllid abundance other than those associated with elevation. Two sites, the farm at Sabana Grande and the farm at Las Marias, had much lower Asian citrus psyllid populations (30 and 7 Asian citrus psyllids trapped, respectively) than we would expect, given their elevations (48 and 181 m, respectively). The farm at Sabana Grande

was sprayed aggressively with insecticides, and this probably accounts for the very low number of Asian citrus psyllids we trapped at the site. The owners of the Las Marias farm mentioned that they do not apply insecticides. If this is the case, some other factor(s) must have accounted for the low Asian citrus psyllid populations at this site. Possible explanations include increased shade (which would be expected to be less favorable for Asian citrus psyllid biology in addition to reducing Asian citrus psyllid flight activity); in fact, this location was surrounded by a dense forest. The La Ceiba site included one *B. koenigii* seedling and this seedling consistently had much higher numbers of Asian citrus psyllids than other citrus at this site or other sites (Fig. 2). The very high populations of Asian citrus psyllids we found on *B. koenigii* in 2013 are intriguing and suggest that this plant is either more attractive to Asian citrus psyllid or supports much higher populations of Asian citrus psyllid than the *Citrus* spp. and the *M. exotica* that we sampled. In a survey rating Asian citrus psyllid hosts according to colonization, Westbrook et al. (2011) found that *B. koenigii* was one of the most attractive hosts, but was not significantly more attractive than *M. exotica* and other citrus species. *B. koenigii* could be useful in Asian citrus psyllid monitoring programs as a sentinel plant or attractive odors from this host may be used to increase the attractiveness of current trapping devices.

Although there is a significant negative correlation between the proportion of trees infested with Asian citrus psyllid and elevation, this phenomenon seems to

come into effect between 500 and 600 m; correlation analysis conducted on the data <500 m fails to reject the null hypothesis that the true correlation is equal to 0, i.e., there is no relationship between elevation and proportion of trees infested with Asian citrus psyllid ( $t = -1.81$ ,  $df = 7$ ,  $P = 0.1127$  for 2013;  $t = -2.41$ ,  $df = 6$ ,  $P = 0.053$  for 2014). Similarly, conducting a Poisson regression analysis on the total number of Asian citrus psyllid per tree against elevation using only data from sites <500 m does not reveal significant differences in Asian citrus psyllid populations at any of these elevations for data collected in 2013 ( $df = 71$ ;  $P = 0.467$ ) and reduced the significance for 2014 ( $df = 91$ ;  $P = 0.042$ ). Studying Asian citrus psyllid populations at this range of elevations may more clearly elucidate the factor(s) responsible for the lower psyllid populations at higher elevations.

It is well established that most, if not all, organisms occupy specific geographical niches dictated by abiotic factors (e.g., temperature and rainfall) and by biotic factors (e.g., the presence of hosts, prey, predators, and competitors; Hesse et al. 1947). The responses of arthropods to changing environments along elevation gradients has been particularly well studied (Hodkinson 2005). Changes in elevation result in predictable changes in temperature (average atmospheric lapse rate is a decrease of 6.4°C for every 1,000 m increase in altitude; Anslow and Shawn 2002). The African citrus psyllid, *T. erytrae*, is restricted to cooler temperatures and is not found <500 m above sea level (Bové and Cassin 1968, cited in Catling 1969, 1970). *D. citri*, however, has long been known to occupy citrus orchards in warmer, lower elevation habitats (Catling 1970).

Being poikilothermic, the rate of development from egg to adult in Asian citrus psyllid is temperature-dependent (Liu and Tsai 2000), as is the intrinsic rate of increase for populations (Nava et al. 2010). We did not take temperature data at the sites and many of the sites do not have temperature data available. However, if we assume an average temperature lapse rate of 6.4°C for every increase of 1,000 m elevation (Anslow and Shawn 2002) and given an average annual temperature of 24°C at sea level in Puerto Rico, the average temperatures of our sites range from 18 to 24°C. Based on calculations from Nava et al. (2010), Asian citrus psyllids at 880-m elevation would take about two times as long to develop from egg to adult as Asian citrus psyllids at sea level. A prolonged period in the nymphal state increases the risk of being consumed by predators, particularly coccinellids, and parasitoids. If temperature is the factor keeping Asian citrus psyllid abundance low >600 m, climate change may increase the range at which Asian citrus psyllid can develop. The coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae), the most important pest of coffee worldwide, was restricted to elevations <1,500 m (Damon 2000), but infestations by this insect now have been observed above this threshold elevation, likely because of global increases in temperature (Jaramillo et al. 2009). Similarly, if temperature is responsible for the trend we see, it is important to keep in mind that

temperature at sea level varies with latitude. The effect we see may only be accurate for Puerto Rico.

Temperature is not the only factor that varies with elevation. There are also changes in factors such as short-wave radiation, partial pressure of respiratory gases, precipitation, oxygen content, and air pressure. The effects of these factors, alone and in combination, on Asian citrus psyllid populations and psyllid host plants, as they relate to elevation, deserve investigation. Short-wave radiation within the UV band tends to rise with increasing altitude (Blumthaler et al. 1997). Dáder et al. (2014) found that supplemental UV-A radiation affected plant chemistry and had different effects on aphids versus whiteflies. Hengxiao et al. (1999) found that plant chemistry was altered when pines were grown at different elevations. If any of these factors change citrus tree physiology or chemistry in such a way that psyllid development is drastically decreased or that the disease organisms are unable to develop, it is possible that these conditions may be induced in citrus trees at lower elevations as a form of therapy. Another practical implication for this study would be to put citrus nurseries >600 m, where numbers of *D. citri* are minimal to non-existent.

In conclusion, this study provides strong evidence that Asian citrus psyllid populations are negatively correlated with elevation, and suggests that the lower Asian citrus psyllid abundance at higher elevations results in lower HLB incidence.

### Acknowledgments

We thank Roberto Carrera-Martinez, Christian Millan-Hernandez, Laura Aponte, Jorge Ruiz, Veronica Rodriguez Rosas, Mabel Vega, Natanael Valentin, and Robert McPhail for their long days in the field and the laboratory. We also thank Susan Halbert and two anonymous reviewers for editing earlier versions of this manuscript, and we thank Zaid Abdo for statistical advice. This report presents the results of research only; mention of a proprietary product does not constitute an endorsement by the United States Department of Agriculture.

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Received 19 August 2014; accepted 21 November 2014.