Effectiveness of *Erythrina* gall wasp biocontrol and implications for the recovery of threatened Wiliwili trees (Fabaceae: *Erythrina sandwicensis*)¹

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BELL, R. C., A. BELMAKER, C. S. COUCH, K. M. MARCHETTO, J. L. SIMONIS, R. Q. THOMAS, J. P. SPARKS (Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853), J. M. BROWN (Department of Microbiology, Cornell University, Ithaca NY 14853), K. S. FRANCISCO, AND M. E. MANUEL (Tropical Conservation Biology and Environmental Science, University of Hawai'i at Hilo, Hawai'i, HI 96720). Effectiveness of *Erythrina* gall wasp biocontrol and implications for the recovery of threatened Wiliwili trees (Fabaceae: Erythrina sandwicensis). J. Torrey Bot. Soc. 140: 215-224. 2013.-Wiliwili (Erythrina sandwicensis), an endemic Hawaiian dry forest tree species, is threatened by an invasive gallforming wasp (Quadrastichus erythrinae) first detected in Hawai'i in 2005. Eurytoma erythrinae, a predator of Q. erythrinae from Tanzania, was selected as a biological control agent and was released at sites throughout the Hawaiian Islands. To assess the effectiveness of this biocontrol release, we measured the extent of damage attributable to Q. erythrinae wasps in 124 E. sandwicensis trees at the Waikoloa Village Dry Forest Recovery Project before (January, 2009) and after (January, 2011) the release of the parasitoid wasp at this site. Because host spatial distribution has important consequences for the establishment and success of natural enemies such as parasitoids, we took a spatially explicit approach to account for the potential spatial heterogeneity in E. sandwicensis. We observed an increase in galling damage across the population and 21 trees became completely defoliated between the two survey years. The distribution of E. sandwicensis across the landscape was highly clumped and tree-level change in galling damage showed a strong spatial signal. Erythrina sandwicensis recovery was non-random with respect to landscape indicating that individual response to the biocontrol agent and exogenous factors (e.g., drought) may have strong interactions with the invasion and persistence of the pest Q. erythrinae.

Key words: dry forest, Eurytoma erythrinae, Hawai'i, invasive species, parasitoid.

Tropical dry forests in Hawai'i host 25% of endangered Hawaiian flora and are a critically threatened ecosystem with only 5–10% percent of the historical distribution remaining across the Hawaiian Islands (Bruegmann 1996, Cabin et al. 2000). Hawaiian dry forests are located on the leeward side of the Hawaiian Islands, receive minimal annual rainfall, and are dominated by slow growing trees such as

Wiliwili (Erythrina sandwicensis, Degener) and Lama (Diospyros sandwicensis, Fosberg) (Cabin et al. 2000, Clark et al. 2001). The severe reduction in tropical dry forest habitat is attributed to deforestation, land development, invasive plant species, changes in fire regime, and introduced ungulate grazing (Bruegmann 1996). Though the decline of dry forests and the efficacy of various conservation strategies are well documented (Allen 2000, Cabin et al. 2000, Cabin et al. 2002a, Cabin et al. 2002b), dry forest species face considerable challenges to population recovery, even within protected and managed areas. One species in particular, the Wiliwili tree, E. sandwicensis, is under additional pressure due to an invasive gallforming wasp (*Quadrastichus ervthrinae*, Kim) first detected in Hawai'i in 2005 (Li 2006). Here we assess the efficacy of biocontrol in

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managing the *Q. erythrinae* outbreak in a large population of *E. sandwicensis* and focus on the possible influence of host tree distribution on that efficacy.

The Erythrina gall wasp, Q. erythrinae, was first observed on O'ahu in April 2005 and spread to neighboring islands over the following four months (Li 2006). This invasive species is believed to have originated in Africa (Messing et al. 2008), but was probably transported to Hawai'i from China (Gramling 2005) and is now widely distributed across Asia and the Pacific Islands where it infects species within the Erythrina genus (Kim et al. 2004). Tissue galling in Erythrina trees results from female Quadrastichus wasps ovipositing eggs into newly emerged petioles, stems, shoots, flowers, and seedpods (Kim et al. 2004). Fully developed adults emerge from the galled tissue within 20 days (Heu et al. 2006). In cases of heavy infestation, galling can result in substantial defoliation and in severe cases may cause tree death (Yang et al. 2004). Although the dispersal mechanisms of this wasp have not been studied, it has been suggested that Q. erythrinae are transported by wind or accidental introduction on imported Erythrina trees (Gramling 2005, Uechi et al. 2007).

In an effort to decrease the detrimental effects of this gall wasp on Erythrina, particularly the endemic E. sandwicensis, a variety of treatments have been tested (Gramling 2005, Li 2006) including insecticide application and infected tissue removal. These treatments have proved insufficient to address the large spatial scale of the Q. erythrinae infestation and do not provide lasting improvement. In an attempt to identify a permanent management solution, the Hawai'i Department of Agriculture, and the University of Hawai'i at Manoa College of Tropical Agriculture and Human Resources, identified and assessed the biological life history and host specificity of three potential biological control agents with origins in Africa. Eurytoma erythrinae (Gates and Delvare), a predator of Q. erythrinae from Tanzania, was selected as the candidate biological control agent (Reimer 2007). The potential efficacy of E. erythrinae is based on its larvae parasitizing Q. erythrinae larvae; females deposit a single egg into a gall of infected tissue where the larva feeds on the body fluids of its host (Reimer 2007). Since E. erythrinae were released starting in 2008 at

sites across the islands of Hawai'i, Maui, O'ahu, and Kaua'i, monitoring efforts have focused on focal trees near release sites and no published reports are available.

Erythrina sandwicensis is restricted to tropical dry forests below 600 m in elevation and to substrates derived from lava flows that are characterized by high viscosity basaltic lava that forms loose, rough blocks as it cools (Rowland and Walker 1990). These lava flows create a heterogeneous landscape (Vitousek et al. 1992) and thus individual E. sandwicensis trees are likely to be non-uniformly distributed across a particular flow. In many systems, the spatial distribution of a host has important consequences for the establishment and success of natural enemies such as parasitoids (Walde and Murdoch 1988) as well as the effectiveness of control agents (Fagan et al. 2002). Therefore, the uneven spatial distribution of E. sandwicensis likely has an effect on the distribution and severity of galling as well as the potential effectiveness of the biocontrol agent.

In the present study, we measured the extent of damage due to Q. erythrinae wasps in 124 E. sandwicensis trees at the Waikoloa Village Dry Forest Recovery Project before and after the release of the parasitoid wasp. In our analyses, we took a spatially explicit approach to account for the potential spatial heterogeneity in E. sandwicensis. If the parasitoid wasp was effective in controlling the Q. erythrinae outbreak at the study site, we expected to see a decrease in the degree of galling, an increase in canopy cover, and an increase in seed production after the release of the parasitoid wasp. If the spatial distribution of E. sandwicensis affected the distribution of galling and the establishment of the biocontrol agent, we expected that trees that are closer to each other would respond more similarly to each other compared to trees that are more distant.

Materials and Methods. We monitored a population of 124 *E. sandwicensis* trees in the Waikoloa Dry Forest Recovery Project (WDFRP) near Waikoloa Village, Hawai'i (19° 54′ 50″ N 155° 47′ 57″ W). *Erythrina sandwicensis* is a tropical deciduous tree species in which leaf-out coincides with rainfall. Censuses were conduced in January 2009 (coincident with the release of the gall wasp) and in January 2011 (two years after the release). Of the 124 trees in the population (all



FIG. 1. Categories of leaf galling on *Erythrina sandwicensis* caused by *Quadratichus erythrinae* wasps as follows: (A) 0% of leaves galled; (B) 1-32% of leaves galled; (C) 33-65% of leaves galled; (D) over 65% of leaves galled.

of which have precise GPS coordinates), 121 were alive in the 2009 census and we collected data from 120 of these trees in the 2011 census (one tree could not be located in 2011). In 2009 we measured the basal diameter of each tree. In both 2009 and 2011, we quantified canopy cover, galling severity, mortality, and the presence or absence of seeds for each tree in the population. Canopy cover was based on five simultaneous individual visual assessments of leaf abundance around the circumference of the tree in the following ordinal categories: (0) no leaves, (1) 1-32%, (2) 33-65%, and (3) over 66%. We determined the canopy cover of each tree in the two survey years by converting the observations into percentages (using the midrange value for categories 1-3) and taking the average of the five measurements. Leaf galling severity was measured haphazardly on 20 branch tips around the circumference of a tree canopy according to the following categories: (0) 0% of leaves galled, (1) 1-32%, (2) 33-65%, (3) over 66% galled (Fig. 1). We determined each tree's composite galling damage for the two survey years by converting the galling category measurements into percentages (using the midrange value for categories 1-3) and taking the average of the 20 measurements. Coverage categories were converted to midrange percentiles to avoid overweighting of zero values. Finally, we recorded the presence or absence of mature seedpods on trees to evaluate reproductive effort (all trees with seedpods present had several hundred mature seedpods). Trees with leaves present in 2009 that were completely defoliated in 2011 were not included in the galling analyses because we could not evaluate 2011 galling indices for these 21 trees. These same trees also did not have seeds in 2011; therefore they were also excluded from the seed analyses.

We first determined if galling damage levels had significantly changed between the two survey years. For all trees with leaves present in both years (n = 99), we used the two composite galling values to calculate the change in damage over time (2011 damage -2009 damage). Because the damage data do not conform to the assumptions of standard statistics (non-normal, bounded), we implemented a permutation test and used the median of the tree-level changes as our summary statistic for the population (Gotelli and Ellison 2004). We generated a null distribution of median change by randomizing each tree's data across the two years, calculating the change in damage for each tree, and then determining the median of the changes. We conducted 10,000 randomizations, which generated a distribution of median values that we would observe if there were no difference (positive or negative) between the two years. If our observed median falls outside the 95% probability density of the distribution, then the observed median change is statistically significant (Gotelli and Ellison 2004). A parallel approach was used to determine if tree-level canopy cover changed significantly between the two years.

We quantified the overall spatial distribution and degree of clumping of the tree population using the pair correlation function (PCF) with traditional kernel smoothing and iso-edge correction (Stoyan and Penttinen 2000). For all PCFs, a value of 1.0 is representative of a Poisson random distribution, a value larger than 1.0 indicates clumping, and values less than 1.0 indicate evenness. We generated the empirical PCF for E. sandwicensis using all 124 trees located in 2009 and defined the sampling area as a rectangle with boundaries set by the most extreme locations in the four cardinal directions and a buffer of 100 m. To determine whether 100 m was an appropriate buffer value for the population boundary, we verified the absence of trees within 100 m of the established boundaries. For the generation of the PCF, we used inter-point distances ranging from 0 to 1000 m (distances between the trees ranged from 3.16 to 2110.00 m; median 629.80 m). We compared the empirical PCF to a null distribution of 10,000 PCFs generated by randomizing the positions of the trees under a Poisson distribution using a Monte Carlo simulation procedure.

To determine if the spatial distribution of *E. sandwicensis* affected the distribution of galling

and the establishment of the biocontrol agent, we quantified whether trees that were closer to each other exhibited similar changes in galling damage between the two survey years (i.e., were they spatially autocorrelated). For this analysis, we quantified spatial autocorrelation using Moran's I statistic (Moran 1950) and used a neighborhood-based approach to determine how the autocorrelation varied as a function of the distance between trees. We binned trees into neighborhoods of sizes ranging from 10 to 1000 m (in 10 m increments) and determined the statistical significance of autocorrelation at each neighborhood size using Monte Carlo permutations.

To determine if tree size or the galling damage a tree experienced in 2009 predicted defoliation in 2011, we used a standard logistic regression with 2009 damage level and basal diameter as continuous predictor variables and presence or absence of canopy cover as a binary response. We used a parallel approach to determine whether size or the degree of galling in 2009 predicted the presence of seeds in 2011 (also a binary response). All statistics and programming were conducted in R (R Development Core Team 2011), using the spatstat (Baddeley and Turner 2005) and spdep (Bivand et al. 2011) packages for the spatial analyses.

Results. Population galling damage in 2011 (mean: 40.3%, median: 38.6%, SEM: 2.2%, n: 99) was higher than in 2009 (mean: 36.3%, median: 36.2%, SEM: 1.6%, n: 121), but there was substantial variation among trees in both years (Fig. 2). In 2009, galling damage ranged from 4.1% to 74.5% and from 3.3% to 83.0% in 2011. There was also large variation in the amount of galling damage experienced by an individual tree from year to year (Fig. 2): the median change was a 7.4% increase in damage, but ranged from a 56.2% decrease to a 55.7% increase. The observed increase in tree-level damage across the population was statistically significant by permutation test (P = 0.0125). Tree basal diameter, which ranged from 38.10 to 136.50 cm (mean = 73.37 ± 17.35 cm), was not a significant predictor of galling in either year or in the change in galling between years (P > 0.1). There was no significant change in tree-level canopy cover over the two-year period (permutation test, P = 0.081).

The average distance between *E. sandwicensis* trees in the Waikoloa population was



FIG. 2. Distributions of tree-level percent galling damage in 2009 (n = 121, top) and 2011 (n = 99, middle), and tree-level changes in percent damage (bottom). Grey bars in the 2009 data indicate trees that were completely defoliated in 2011. Arrow in the bottom panel shows the population median change in galling (7.4%).

660.60 m (range 3.16 to 2110.00 m, Fig. S1). The PCF analysis indicated this population exhibited a non-random, or clumped distribution (PCF > 1.0, P = 0.0002, Fig. S2) over a spatial scale relevant to the size of our study population (the empirical PCF converged to a random spatial distribution at 687 m). The tree-level change in galling damage also showed a strong spatial signal, with the trees in the center and eastern portions of the population declining, and trees in the southern and northwestern portions of the population improving (Fig. 3). The spatial autocorrelation analysis showed that trees closer to each other had a more similar change in galling between the two years than trees further apart (I = 0.2945, P = 0.0004). The neighborhoodbased analysis indicated that this pattern was significant up to distance of approximately 450 m between trees (Fig S3).

Twenty-one trees became completely defoliated between 2009 and 2011 (17.6%), and the damage level in 2009 was a significant predictor of which trees fell into this category (Odds-Ratio: 1.03, P = 0.033). In other words, trees with the maximum galling observed in 2009 (74.5% damage) were more than five times as likely to be completely defoliated in 2011 than trees with the minimum galling observed in 2009 (4.1% damage). Tree basal diameter was not a significant predictor of defoliation (P > 0.1).

Despite our measures of deterioration in tree condition (canopy cover and galling damage), a greater proportion of trees produced seeds in 2011 (67.5%) compared to 2009 (37.2%). The degree of galling experienced in 2009 was a significant predictor of which trees had seeds in 2011 (Odds-ratio: 0.27, P = 0.023, deviance explained = 5.8%) such that trees with the minimum galling observed in 2009 (4.1% damage) were approximately two times as likely to have seeds in 2011 than trees with the maximum galling observed in 2009 (74.5% damage). Tree basal diameter was not a significant predictor of seeds in 2011 (P > 0.1).

Discussion. Since the 2009 release of the parasitoid wasp at Waikoloa Village, galling severity of the E. sandwicensis population has increased significantly and more than 20 trees have become completely defoliated. Though the population median canopy cover was not significantly different between the two survey years, higher galling severity in 2009 was correlated with increased defoliation and a lower probability of having seeds in 2011, indicating that prolonged galling may have severe consequences for the viability of this population. Despite improvement in some individual trees and an increase in the proportion of trees producing seeds in 2011, the data for this population are inconsistent with media reports of widespread remediation of the Q. erythrinae outbreak across the Hawaiian Islands (Wianecki 2011).

The slight increase in *E. sandwicensis* galling severity at Waikoloa Village does not appear to be driven by limited dispersal of the biocontrol agent from release sites or low establishment success. We observed *Eurytoma* wasps in high abundance in trees at the study site indicating that the parasitoid population has persisted for at least two years since its introduction. Furthermore, the trees surrounding one documented release site (along



FIG. 3. Spatial distribution of trees and tree-specific changes in percent galling damage. Circles indicate trees that improved (decrease in percent damage), triangles indicate trees that declined (increase in percent damage), and the size of the points represents the magnitude of the change (larger points show stronger changes). The black line denotes the access road through the site.

the road, shown in Fig. 3) deteriorated in condition from 2009 to 2011. While these observations imply that the biocontrol agent *E. erythrinae* is not reducing the gall-forming *Q. erythrinae* population at this site, evidence that *E. erythrinae* galls at several long-term observation sites (Hawaii Department of Land and Natural Resources, 2011) suggests that there is a tangible impact of the biocontrol that may not be readily apparent at this population site.

Galling damage for *E. sandwicensis* at Waikoloa Village was not measured prior to 2009. Therefore, yearly increases in galling severity prior to the introduction of *E. erythrinae* are unknown. Our surveys indicate that galling severity was slightly greater (7%) in 2011 relative to 2009. However, it is possible that the parasitoid *E. erythrinae* curbed additional population growth in *Q. erythrinae*, and that the damage observed in the *E. sandwicensis* population could have increased by more than 7% without the introduction of *E. erythrinae*. Furthermore, while it appears that *E. erythrinae* are parasitizing a substantial proportion of *Q. erythrinae* galls, complete eradication of the pest over a very short time period is often not possible with biocontrol methods (Murdoch et al. 1985, Myers et al. 2000). Rather, in the long term *E. erythrinae* may decrease the population of *Q. erythrinae* to reach a low-density equilibrium between the two wasp species and consistently lower levels of galling in *E. sandwicensis*.

Environmental factors may also influence the effectiveness of biocontrol in this system. Studies in other long-lived tree species have shown that environmental stressors such as drought contribute to galling susceptibility (Pike et al. 2006) and that survival of gall forming insect populations is higher in xeric (drier) habitats (Fernandes and Price 1992). Leaf emergence in *Erythrina sandwicensis* occurs at a similar time each year and the date of emergence is often modulated by the onset of precipitation in the fall that varies in magnitude from year to year. Rainfall during the three months prior to our surveys (October through December) varied between the two survey years from 74 mm (prior to the 2009 survey) to 6 mm (prior to the 2011 survey) (www.wunderground.com). Despite this variation, all leaves were fully expanded and we did not observe any differences in average canopy cover between the two survey years suggesting that the trees were in similar stages of leaf-out. Total annual rainfall at Waikoloa Village has varied greatly over the past six years (2006-2011) from 79 mm (2010) to 396 mm (2006) and rainfall was much lower in 2008 through 2010 (ranging from 79 mm to 143 mm) compared to 2006 and 2007 (259 mm and 396 mm respectively) (www.wunderground. com). It is likely that water availability influences the susceptibility of E. sandwicensis to galling and if a significant interaction occurs between galling and water stress, the dry years from 2008 to 2010 likely diminished the success of the biocontrol agent.

This study suggests that there is considerable variation in the susceptibility of E. sandwicensis to Q. erythrinae (Fig. S3), which is non-randomly distributed in the population. Therefore, multiple factors such as differential water-stress across the landscape, or individual variation in resistance to Q. erythrinae, may influence susceptibility to galling and subsequent mortality. The endemic species of the Hawaiian Islands are especially susceptible to competition and exploitation by invasive species (Howarth and Ramsay 1991). Many organisms, including dozens of arthropod pests invade the islands every year (Beardsley 1979) and biocontrol methods to curb these invasions have been broadly implemented for more than a hundred years (Funasaki et al. 1988). This study highlights that distribution patterns, variation among individual trees in resistance to insect galling, and abiotic factors like rainfall may attenuate the success of a biocontrol agent and that only by monitoring at the population-level will we capture this variation and potentially improve estimates of species recovery (Delfosse 2005).

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Appendix



FIG. S1. Frequency histogram of pairwise distances between trees, which range from 3.16 to 2100.00 m (mean = 660.60 m, sd \pm 366.12 m). The arrow labeled 450 m indicates the maximum pairwise distance at which change in condition is positively spatially autocorrelated between trees (see Fig S3). The arrow labeled 687 m indicates the pairwise distance at which the spatial distribution between trees becomes random (see Fig S2).



FIG. S2. Pair correlation function for the *E. sandwicensis* spatial distribution using all 124 trees present in 2009. The solid black line is the empirical PCF generated by the actual data. The null expected value of 1.0 is the dashed line, which is surrounded by the 95% confidence envelope (grey area) generated from 10,000 Monte Carlo Simulations. The arrow points out the distance between trees (687 m) at which their spatial distribution becomes random (the empirical PCF did not statistically significantly differ from random).



FIG. S3. The strength of spatial autocorrelation in tree-specific changes in percent damage (as measured by Moran's I) as a function of neighborhood size (distance between trees). The null expected value of 0.0 is shown by the dashed line surrounded by the 95% confidence intervals generated by 10,000 Monte Carlo simulations. Filled points are statistically significantly different from random, open points are not. Overall, the recovery was significantly positively spatially correlated (I = 0.2945, P = 0.0004), and the positive autocorrelation holds over neighborhoods with radii less than *ca.* 450 m. In other words, trees within 450 m of each other tend to be more negatively correlated in terms of recovery than random.