

***Erythrina sandwicensis* Demography and Spatial Patterns of *Erythrina* gall wasp,  
*Quadraticus erythrinae* Infestation in Waikoloa, Hawai'i**

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**Abstract:**

Hawai'i's tropical dry forests are unique and highly endangered ecosystems that are currently being degraded by human development and invasive species. The Wiliwili tree, *Erythrina sandwicensis* (Fabaceae), a dominant species in Hawaiian tropical dry forests is now critically threatened due to the destructive impacts of invasive species, in particular the *Erythrina* gall wasp, *Quadraticus erythrinae* (Hymenoptera: Eulophidae). Here, we investigated the spatial and size distribution patterns of *E. sandwicensis* and potential effects of *Q. erythrinae* on population demographics by surveying a 310 ha parcel of dry forest in Waikoloa, Hawai'i. This population of *E. sandwicensis* is comprised of 119 live trees, all of which are large adults that were spatially clumped to a radius of 400 meters.. In addition, the level of infestation of individual trees by *Q. erythrinae* was highly spatially autocorrelated, with the greatest correlation occurring within 100 m. Individual trees with higher gall wasp infestation had less tree leaf cover and a lower probability of seeds being present. The results of this study demonstrate that the largest population of *E. sandwicensis* on Hawai'i is currently threatened by an invasive insect that alters the ability of trees to photosynthesize and decreases reproductive output. The clumped distribution of individuals likely facilitates the spread of the gall wasp but may allow for spatially focused conservation efforts. Thus a greater understanding of the severity of

invasive species impacts on plant physiology and reproductive fitness is necessary for the proper management of *E. sandwicensis* and Hawaiian dry forest ecosystems.

### **Introduction:**

The tropical dry forests of Hawai'i are both home to over 25% of the endangered Hawaiian flora and represent a critically threatened habitat (Cabin et al. 2000). Due to deforestation, land development, invasion of nonnative plant species, fire, and grazing by nonnative ungulates, 90% of this ecosystem has been lost since the arrival of humans (Bruegmann 1996). Hawaiian dry forests are found on the leeward side of the islands and receive minimal annual rainfall, making these landscapes regions of low productivity dominated by slow growing flora (Clark et al. 2001, Cabin et al. 2002a). One important endemic dominant tree in the dry forest is the Wiliwili, *Erythrina sandwicensis* (Fabaceae). While the decline of this fragile ecosystem and the efficacy of various conservation strategies have been well documented during the past decade (Allen 2000, Cabin et al. 2000, Cabin et al. 2002a, Cabin et al. 2002b), there is a paucity of information on the demography of *Erythrina sandwicensis*.

*E. sandwicensis*, a member of the large pantropical genus *Erythrina*, is the dominant and only endemic *Erythrina* species in the Hawaiian Islands (Rock 1913, Wagner et al. 1999, Medeiros et al. 2008). This species exhibits a high degree of habitat specificity, being restricted to tropical dry forests below 600 meters in elevation and to substrates derived from 'a'a lava flows (Little and Skomen 1989). 'A'a is characterized by high viscosity basaltic lava that forms loose, rough lava blocks at it cools (Rowland & Walker 1990) and facilitates seed germination between the cracks in the lava. To inhabit this rough arid landscape, *E. sandwicensis* has developed an association with nitrogen fixing bacteria and is one of the few dry season

deciduous species (Little & Skolmen 1989, Wagner et al. 1999, Sprent & Parsons 2000). *E. sandwicensis* is also a culturally significant plant species in Hawai‘i and has been traditionally used for surfboards, canoes, and fishnet floats due to its low density wood (Little & Skolmen 1989). The brightly colored orange-red seeds and flowers were used for leis by Native Hawaiians (Medeiros et al. 2008). Due to its cultural significance and its status as one of the few remaining endemic tree species, significant effort has been allocated towards identifying isolated populations of *E. sandwicensis* across the Hawaiian Islands (D. Faucette pers. comm., Little & Skolmen 1989, Medeiros et al. 2008), but spatial and size distribution of this species has not been published.

Once one of the most common endemic tree species in Hawai‘i, *E. sandwicensis* populations have been reduced to small isolated groups due to a myriad of factors. The arrival of the African fountain grass *Pennisetum setaceum*, an invasive C<sub>4</sub> perennial bunch grass has resulted in numerous deleterious effects on dry forest ecosystem function (Litton et al. 2008). This fast growing grass thrives in high light, low moisture environments and has dramatically altered the fire regime in dry forest ecosystems (D'Antonio & Vitousek 1992, Blackmore & Vitousek 2000). Although there are no data on effects of fountain grass on *E. sandwicensis* growth and recruitment specifically, this invasive grass has been shown to affect other native dry forest trees (Cabin et al. 2000). Another major threat to native trees has been the grazing of feral ungulates (Cabin et al. 2000). Although *E. sandwicensis* was once believed to be protected from nonnative ungulates by the rough ‘a‘a landscape (Medeiros et al. 1984), feral goats have recently been observed stripping bark from mature trees and grazing on seedlings (D. Faucette pers. comm.). In addition to ungulate grazing, *E. sandwicensis* recruitment has also been recently threatened by the invasion of the bruchine chrysomelid beetle, *Specularius impressithorax*. This

species arrived to the Hawaiian Islands from Africa in January 2001 and has caused the loss of over two-thirds of the annual *E. sandwicensis* seed crop (Medeiros et al. 2008). Adult beetles oviposit eggs onto the seeds, after which the larvae bore into them rendering the seeds largely inviable (Samuelson & Medeiros 2006, Medeiros et al. 2008).

The major threat to *E. sandwicensis* is the *Erythrina* gall wasp, *Quadrastichus erythrinae*, which 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 transported to Hawai‘i from China (Gramling 2005). *Q. erythrinae* is widely distributed across Asia and the Pacific Islands, preferentially infecting species within the *Erythrina* genus (Kim et al. 2004). Female wasps inject eggs into newly emerged petioles, stems, shoots, flowers and seed pods, which results in tissue galling as the larvae develop (Kim et al. 2004). Fully developed adults emerge within 20 days and have a life expectancy of two to three days (Heu et al. 2006). In cases of heavy infestation, galling can result in substantial defoliation and in severe cases 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, accidental introduction on imported *Erythrina* trees (Gramling 2005, Uechi et al. 2007), or both. In an effort to manage the detrimental effects of this gall wasp on *Erythrina* spp., particularly the endemic *E. sandwicensis*, a variety of treatments have been employed such as insecticide application, release of hyperparasitoid wasps, and removal of infected tissue (Gramling 2005, Li 2006). However, given the speed at which this wasp has spread across the Hawaiian Islands and the devastating effects it has had on *Erythrina* populations, there have been no published studies of the spatial distribution of infestation within a population or the effects of this infestation on individual tree physiology.

In the present study we first measured size structure and spatial distribution of the *E. sandwicensis* population in Waikoloa, which represents the largest population on Hawai'i Island (D. Faucette *per. comm.*). Second, we asked if there were relationships between the level of infestation and both leaf cover and reproductive status of individual trees. Finally, we tested whether there was spatial patterning in gall wasp infestation through an analysis of spatial autocorrelation, a measure of the degree to which the level of infestation of neighboring trees influence individual tree infestation. This study will provide vital information on the demography and dynamics of infestation needed to implement informed management decisions.

## Methods

### *Site Description*

The study was carried out in the 310 ha Waikoloa Dry Forest Recovery Project (WDFRP) in Waikoloa Village, HI (206347E, 2204717 N UTM). Waikoloa Village is located on the west side of the island of Hawai'i at an elevation of 250-380 m. The mean annual precipitation and temperature at the site was XX mm and XX °C. The substrate at this site is almost entirely characterized by 'a'a lava flows between 1,500 and 5,000 years old (Wolfe & Morris 1996), although pāhoehoe (smooth lava) with intermittent 'a'a occurs at the southern end of the WDFRP. This open dry forest is composed of predominately three tree species: *E. sandwicensis* (Fig. 1), *P. pallida* (Kiawe), and *P. hawaiiensis* (Uhiuhi). The understory plant community is dominated by *P. setaceum*. Feral goats are present at the site. Previous conservation work at the site has included a complete census and mapping of the *E. sandwicensis* population in 2007.

There have been insecticide injections of Imidacloprid on a limited number of trees using Wedgle Direct-Inject (Arbor Systems, Omaha, NE), Sidewinder precision tree injector (Noosaville, QLD, Australia), and Arborjet Tree I.V. systems (Woburn, MA).

### *Data Collection*

GPS coordinates from the 2007 census were used to locate each live *E. sandwicensis* tree in the population.. At each tree we collected the following information: size (basal diameter measured at ground level), canopy cover, level of gall infestation, and the presence or absence of seeds. Based on visual inspection, each tree was placed into one of five canopy cover classes: (1) 1-9%, (2) 10-32%, (3) 33-65%, and (4) over 65% of total area. Canopy cover was based on visual inspection that assessed the presence of leaves on the branches, thus standardizing for number of branches present. To assess infestation, 20 terminal branches were haphazardly selected and the percentage of galled leaf tissue was visually assigned to one of four classes: (0) 0%, (1) 1-32%, (2) 33-65%, (3) over 65% galled (Fig. 2). For all analyses, the level of galling was computed for each tree as the mean of the infestation classes for the 20 branches.

### *Data Analysis*

The demographics of the *E. sandwicensis* population were characterized by determining the distributions of tree sizes and leaf covers and the frequency of seed production. The relationships among the individual parameters were tested using Pearson product-moment correlation (size and leaf cover), logistic regression (size and seeds) and  $\chi^2$  test (leaf cover and seeds). The distribution of infestation level across the entire population was determined. We then tested if infestation level was predicted by tree size and if infestation affected the leaf cover or reproduction using standard (leaf cover) and logistic (seeds) regressions. For the leaf cover regression, cover classes were converted to their corresponding mid-range value of percent coverage (*e.g.*, class one [1-9%] has a mid-range value of 5). All analyses were conducted using R (Team 2009).

To describe the spatial distribution of the population, we employed point process methods, in particular the pair correlation function (PCF) (see Stoyan & Penttinen 2000 for description and derivation). The PCF describes the probability of observing a pair of points distance  $r$  apart, scaled by the corresponding probability for a random (Poisson) distribution of points (Stoyan & Penttinen 2000). The shape of the PCF as a function of the distance  $r$  describes how the population is distributed in space. For any distance, a value of 1.0 indicates that the trees are randomly distributed, whereas values larger than 1.0 corresponds to aggregation and less than 1.0 indicates uniformity. The PCF for the *E. sandwicensis* population was calculated and compared with a null distribution of PCFs, generated by randomizing the positions of the trees 1000 times. The statistically significant difference of the empirical PCF from that under the null model (Poisson distribution of trees) was checked using a Monte Carlo simulation

procedure. These analyses were carried out using the package *spatstat* in R (Baddeley & Turner 2005).

We then determined if the infestation of *E. sandwicensis* trees was spatially autocorrelated using Moran's I statistic (Moran 1950). Once trees are grouped into a set based on the distance between trees, I is calculated as:

$$I = \frac{N \sum_i \sum_j w_{ij} (X_i - \bar{X})(X_j - \bar{X})}{\sum_i \sum_j w_{ij} \sum_i (X_i - \bar{X})^2}$$

where  $\bar{X}$  is the mean galling index of all the trees in the distance set,  $X_i$  and  $X_j$  are galling indices of two different trees in the distance set,  $N$  is the total number of trees in the distance set, and  $w_{ij}$  is the weighting based on the distance between trees. The weight was determined for each pair of trees in the distance set using

$$w_{ij} = \frac{d_{ij}}{\min(d_{ij})}$$

where  $d_{ij}$  is the distance between a pair of trees in the distance set.

We compared the empirical value of I to a null distribution of I values generated from 1000 Monte Carlo simulations to determine if there was significant spatial autocorrelation at that distance. To determine how spatial autocorrelation varies as distance between trees increases, we ran this analysis using trees 0-100m, 100-200m, 200-300m, 300-400m, 400-500m, 500-600m, 600-700m, 700-800m, 800-900m, and 900-1000m apart from each other. To factor out



any bias in spatial pattern of gall infestation due to the pesticide treatment, we ran these analyses on the residuals from a t-test grouped by treatment (injected or not-injected), rather than on the raw infestation data. This t-test was highly significant ( $t_{119} = -7.18$ ,  $p < 0.001$ ), and so running the analyses on the residuals to exclude the effect of injection on the spatial pattern is warranted. These analyses were run in the *spdep* package in R (Bivand 2009).

## Results

### *Population Demographics and Infestation*

The Waikoloa population of Wiliwili trees consists of 119 trees spread over 310 ha and consists of exclusively large adults only found on 'a'a lava flows. All trees were larger than 40 cm in basal diameter (min: 44.5, max: 118.4, mean: 75.4, SD: 16.3; Fig. 3). Table 1 shows the distribution of the trees by leaf cover category and how many trees in each category contained seeds. In total, 43 trees had visible seeds within the seed pods (36.1%; Table 1). In general, the fraction of trees with seeds is significantly different across the leaf cover categories ( $\chi^2 = 18.5$ ,  $p < 0.001$ ), which is driven by the trend toward more trees with seeds in higher leaf cover categories. Larger trees were not more likely to contain seeds (logistic regression,  $p = 0.25$ ). However, basal diameter and leaf cover were positively correlated ( $r = 0.284$ ,  $p = 0.002$ ).

All *E. sandwicensis* trees at Waikoloa were infested (Fig. 4). The mean infestation level was 1.56 (SD  $\pm$  0.59) and ranged from 0.25 to 2.75. Infestation level was not predicted by the size of individual trees ( $p = 0.134$ ). Increased infestation did, however, reduce tree leaf cover (regression coefficient = -30.9,  $p < 0.001$ , Fig. 5a) and reduce the probability that a tree had

seeds (odds ratio = 0.258,  $p < 0.001$ , Figure 5b). There was a strong shift in the proportion of trees with seeds at a galling index of approximately 1.0 (Fig. 5b). Nearly three-quarters of trees with a composite galling score less than or equal to 1.0 had seeds (17 of 23, 74%), whereas only one-quarter of trees with a composite galling score over 1.0 had seeds (26 of 96, 27%).

### *Spatial Distribution of Trees and Infestation*

Figure 4 shows the spatial distribution of *E. sandwicensis* trees in the Waikoloa population, and their respective infestation levels. The empirical *E. sandwicensis* PCF is considerably larger than the null envelope of PCFs (Fig. 6), a difference which is statistically significant (MC randomization,  $p = 0.002$ ), suggesting that the trees are more spatially aggregated than expected for a randomly distributed population. The empirical function appears to converge on the null envelope at approximately 400 m distance (Fig. 7).

Infestation of trees is highly spatially autocorrelated, and the strength of the autocorrelation decreases with increasing distance bin (Fig. 8). The highest autocorrelation occurred in the 0-100 m distance bin (Moran's  $I = 0.351$ ) The Moran's  $I$  was statistically different from the null distribution in the 0 100 m ( $p = 0.001$ ), 100 200 m ( $p = 0.003$ ), 200 300 m ( $p = 0.018$ ), 300 400 m ( $p = 0.014$ ), and 400 500 m ( $p = 0.019$ ) distance groups. The distance bins  $> 500$  m were all highly non-significant ( $p > 0.92$ ).

### **Discussion:**

The Waikoloa *E. sandwicensis* population is comprised primarily of large adults with a mean basal diameter of 75.4 cm, indicating that this population has not experienced any recent

successful recruitment events. Although seedlings were occasionally found directly under adult *E. sandwicensis* individuals, survival was effectively zero, apparently due to grazing by feral goats (D. Faucette, *pers. obs.*). Since feral goats first arrived in 1778 (Tomich 1969), there is high grazing pressure on seedlings, and the trees are known to grow slowly, it is unlikely that the individuals in the population are younger than 100 yrs old. It will be important to age these trees to determine the last major recruitment event and to gain an understanding of the conditions required for a viable population. The absence of recruitment presents a critical problem for the adaptive evolution of *E. sandwicensis* to the environmental challenges it now faces. Current research is underway to elucidate the degree of genetic variability in this population (B. Brand *pers. comm.*), even with a high degree of genetic variability, and thus the ability to evolve in response to disturbances, this population will not be able to adapt without active management. In absence of conservation efforts, not only will this population continue to experience the deleterious effects of various disturbances, but given its clumped distribution within the Hawaiian Islands, this population will also be threatened by inbreeding, which can lead to loss of genetic variation, reduced fitness, reduced survival of offspring and increased risk of extinction (Frankham 1995). Therefore, it will be imperative that attention be paid to promoting genetic diversity as a part of conservation efforts..

Consistent with previous studies, *E. sandwicensis* appears to be susceptible to *Q. erythrinae* infestation (Messing et al. 2008), which may have significant consequences for host physiology. Within the 310 ha study area, all 119 live individuals had some level of infestation. Furthermore, we observed a negative relationship between leaf cover and infestation. Due to the short-term nature of this study, it was not possible to follow each tree from new flushing through leaf maturation to quantify the level of defoliation caused by galling. This study was conducted

shortly following the emergence of new leaves and previous studies of *Erythrina* spp. have documented rapid galling and subsequent defoliation in the early stages of phenology. As a result, there is strong evidence that galling is directly related to leaf cover reduction. A significant loss of leaf cover one month following flushing will likely reduce the carbon gain through photosynthesis and subsequently reduce growth. Research is currently underway to assess the effect of galling on leaf properties that influence carbon gain, such as water use efficiency, photosynthetic capacity, and stomatal conductance (Thomas et al. in prep).

There was a strong positive correlation between leaf cover and presence of seeds. Although the mechanism linking reproduction and *Q. erythrinae* infestation is still unclear, due to loss of leaf cover and reduction in carbon gain, *E. sandwicensis* may be unable to allocate energy to reproduction, which requires large carbon investments (Lambers et al. 1998). Further investigations are needed to assess the role of *Q. erythrinae* in altering the reproductive capacity of *E. sandwicensis* populations. With only 36 % of the population reproductively active, it is also important to note that seed damage from *S. impressithorax* was observed, thus presenting a further threat to the reproductive fitness of the Waikoloa *E. sandwicensis* population.

Investigating the spatial distribution of a population provides vital information on dispersal patterns, how a species is affected by its surrounding resources, its reproductive biology, and potential patterns of disease or parasite transmission (Walde & Murdoch 1988, McCallum & Dobson 1995, Condit et al. 2000, Bleher & Bohning-Gaese 2001). The Waikoloa *E. sandwicensis* population demonstrated a non random clumped distribution to 400 meters. To date, there have been no studies of the dispersal agent and dispersal patterns of *E. sandwicensis* seeds, but seeds were originally suggested to be transported by Hawaiian honeycreepers (subfamily Drepanidinae) (Carlquist 1966). Although, with the loss of over half of the species in

this subfamily (Spiegel et al. 2006), it is unclear whether other bird families contribute to *E. sandwicensis* dispersal. During the present study, a large number of seeds were observed directly under the adult trees, which may indicate low rates of dispersal. The clumped distribution of *E. sandwicensis* presents several consequences for the future of this population. First, a larger proportion of seedlings will be grazed by feral ungulates within the densely populated region due to the optimal foraging hypothesis, which states that predators will maximize their energy intake while spending the least amount of time foraging as possible (MacArthur & Pianka 1966). With the widespread invasion of *P. setaceum* across the Hawaiian tropical dry forests, there is also a greater risk of fire killing a larger portion of the population.

The rapid dispersal of *Q. erythrinae* across the Hawaiian Islands has widely affected *Erythrina* spp., yet in the present study, infestation in the Waikoloa *E. sandwicensis* population was highly spatially autocorrelated to 500m. In other words, the level of infestation of an individual is dependent on the infestation level of the neighboring trees. Although the dispersal patterns and mechanisms underlying host choice are still unknown, there are several possible explanations for the observed spatial patterns of infestation. Similar to grazers, the optimal grazing hypothesis can also be applied to host-parasite interactions. The primary goal of parasites is to maximize the number of offspring that survive to reproductive maturity (Hubbard & Cook 1978). Therefore, *Q. erythrinae* may target the most densely populated regions to limit flight time between trees (Hubbard & Cook 1978, Walde & Murdoch 1988). Another possible explanation is that a larger proportion of the wasps stay near the tree on which they were born to decrease the time to oviposition (Walde & Murdoch 1988).

Although the clumped distribution of *E. sandwicensis* and its infestation by *Q. erythrinae* present several problems for the fate of the Waikoloa as well as other populations, they do

provide invaluable information for implementation of effective conservation efforts. First, to inhibit ungulate grazing of seedlings, fences should be erected around areas with a high density of trees. Such strategies will allow managers to protect a larger number of trees without fencing entire preserves. Second, current efforts to remove fountain grass should be focused on the southern densely populated region, as well as the trees that have lower infestation, higher leaf cover and higher fecundity. This will reduce the risk of loss of a large percentage of the population and protect those individuals that have shown increase resistance to infestation, as well as enhance recruitment by increasing available space. Finally, given the spatial autocorrelation of infestation, effort should be placed on eradicating *Q. erythrinae* from densely populated areas. Several techniques have been attempted, which have produced varying results. Due to the speed at which these wasps disperse, culling infected trees has proved ineffective (Gramling 2005).

In conclusion, this study contributes valuable information on the demography of one of the largest extant *E. sandwicensis* populations on the island of Hawai‘i. Demographic information is particularly important given the extreme pressure this population is under from multiple disturbances. This is also the first study that combines an investigation of the spatial patterns of *Q. erythrinae* infestation within an *E. sandwicensis* population and the effects of infestation on host physiology. The Waikoloa *E. sandwicensis* population is comprised solely of large adults, with no recruitment due primarily to ungulate grazing. *Q. erythrinae* infestation was variable across the population, but galling was present in all 119 trees. Without active management, this infestation could pose a significant threat to the survival of this population as it appears to affect leaf cover and reproductive output. *E. sandwicensis* is clumped in its distribution worldwide, across the Hawaiian Islands due to its fragmented habitat, and this study

provides evidence that this species is aggregated at the population level as well. *Q. erythrinae* infestation was also spatially autocorrelated in its distribution, indicating that the severity of infestation was affected by neighboring trees. While this clumped distribution poses several problems for the fate of this population, it may also improve effective allocation of conservation efforts to a larger portion of the population.

Table 1. Distribution of leaf cover and reproduction status of *Erythrina sandwicensis* at Waikoloa.

Leaf Cover Category	<u>1-9%</u>	<u>10-32%</u>	<u>33-65%</u>	<u>&gt;65%</u>	<u>Total</u>
Number of Total Trees	15	33	32	39	119
Number with Seeds	0	9	11	23	43





Figure 1. *Erythrina sandwicensis* tree in Waikoloa.



Figure 2. *Erythrina sandwicensis* leaves exhibiting four levels of *Quadraticus erythrinae* galling; a. (0) 0%, b. (1) 1-32%, c. (2) 33-65%, d. (3) over 65% galled.

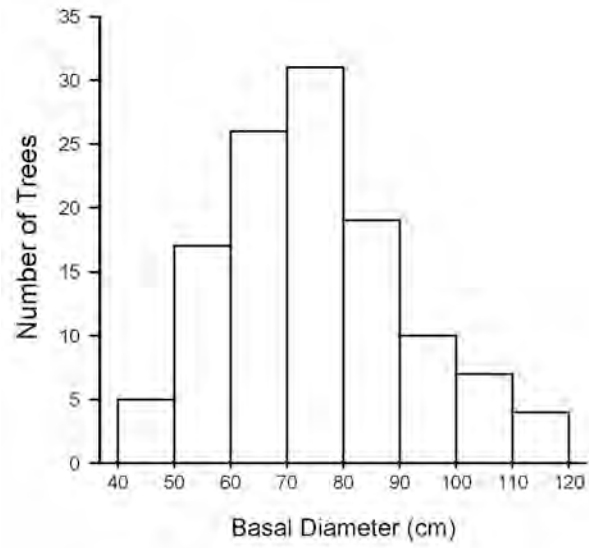


Figure 3. Distribution of individual tree basal diameters.

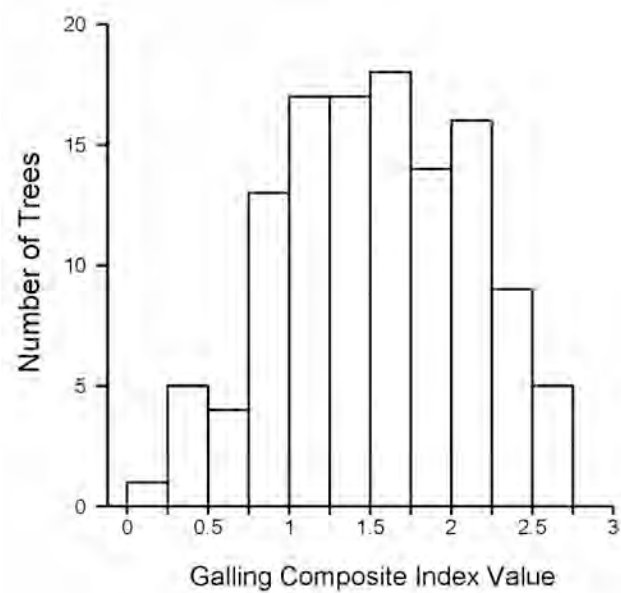


Figure 4. Distribution of infestation level (measured as the galling composite index value) across all 120 *E. sandwicensis* trees.

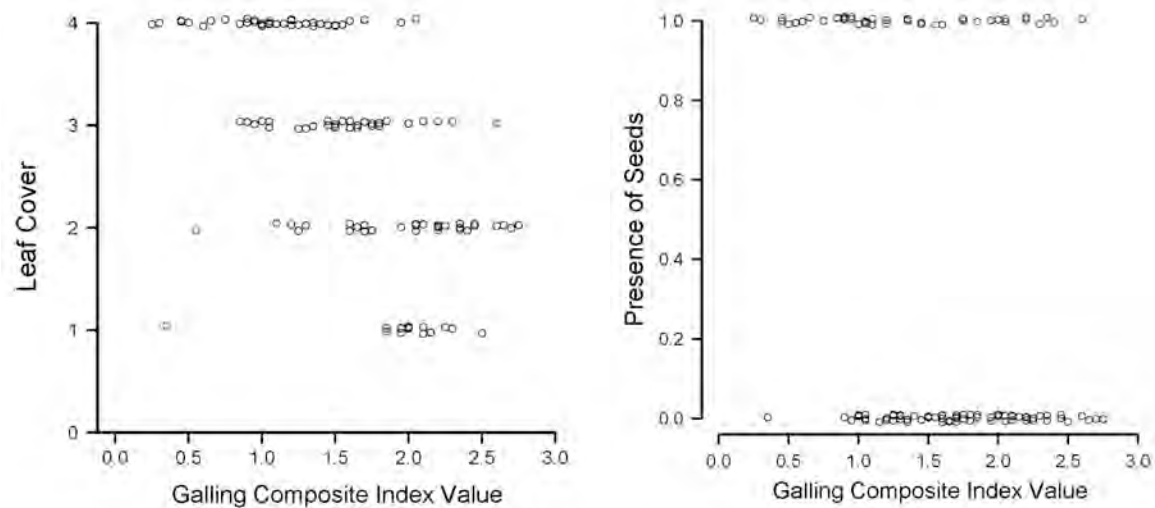


Figure 5. Relationship between gall infestation and (a) leaf cover or (b) presence of seeds for individual trees. Data were jittered on the y-axis in each graph to allow better visualization.

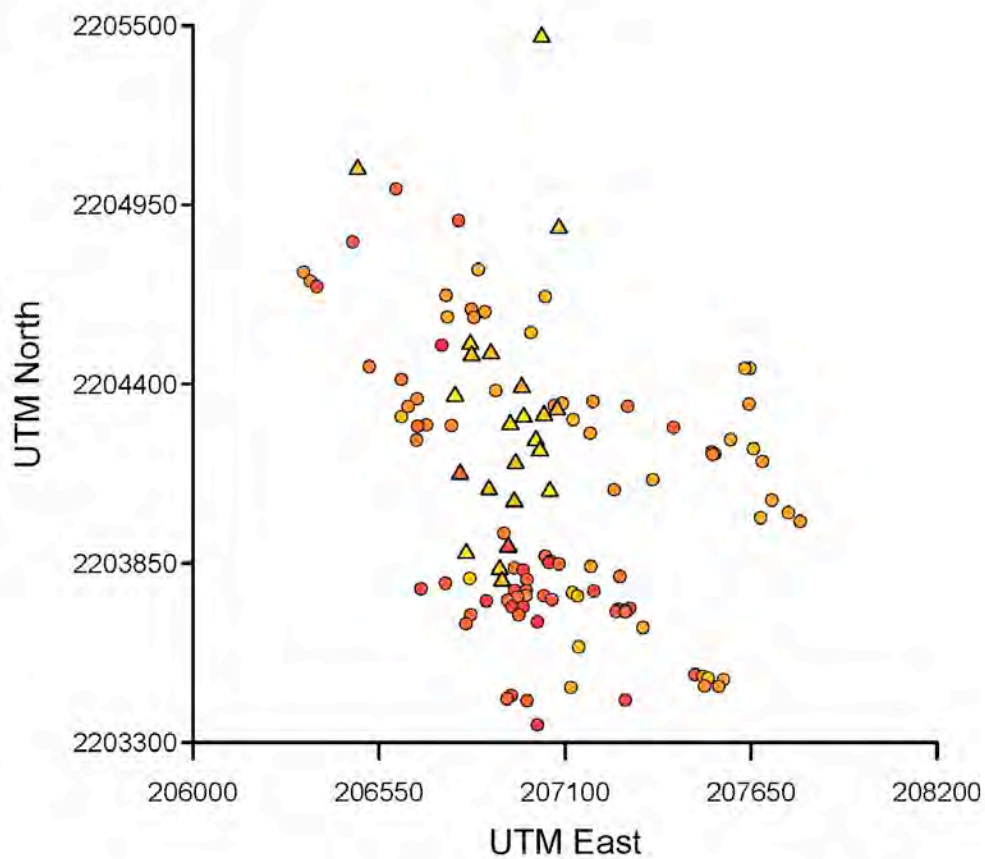


Figure 6. Spatial distribution of *E. sandwicensis* trees in the Waikoloa population. Each point represents a tree in the population. Circles are untreated trees, triangles are treated trees. Color scales with infestation level: yellow = low, orange = medium, red = high.

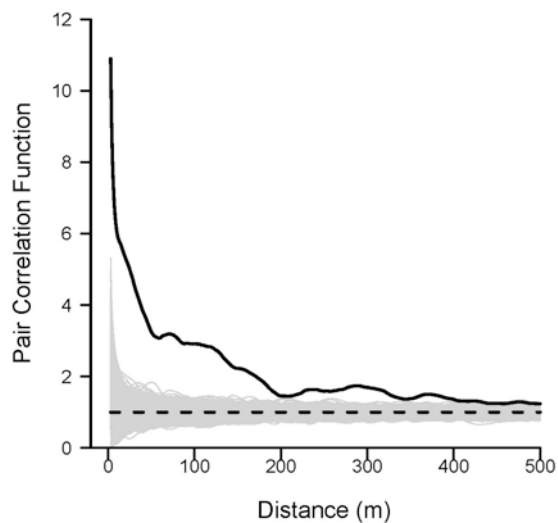


Figure 7. Pair correlation function of the *E. sandwicensis* population with respect to distance between trees. Empirical function (solid black line) is considerably greater than the expected null value (dashed black line) and the corresponding null envelope (grey area), indicating that the trees are more aggregated than expected by a Poisson distribution. The empirical function appears to converge upon the null model around 400 m distance.

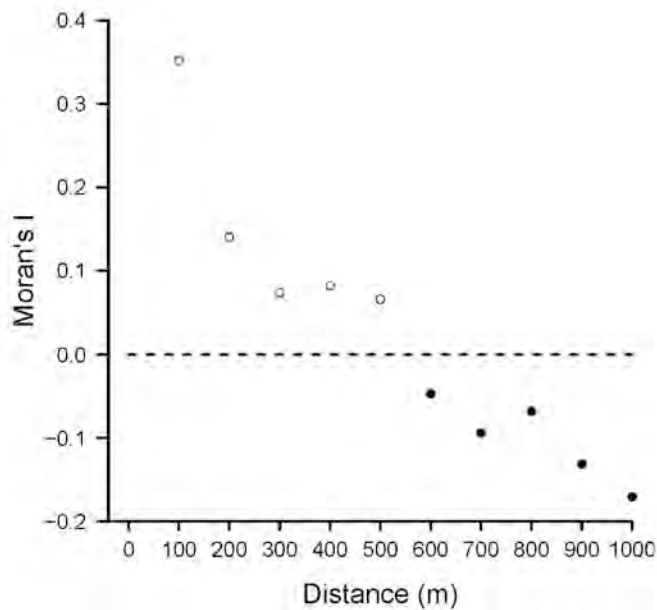


Figure 8. Spatial autocorrelation of infestation (measured by Moran's I) as a function of distance bin. Open circles are significantly different from the null distribution of I values; filled circles do not deviate statistically from the null distribution.

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