ORIGINAL CONTRIBUTION





Abundance of Coffee berry borer in feral, abandoned and managed coffee on Hawaii Island

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Abstract

Coffee berry borer (Hypothenemus hampei Ferrari), the most damaging insect pest of coffee worldwide, was first detected on Hawaii Island in 2010. Poorly managed, abandoned and feral coffee sites on the island have since been thought to harbour coffee berry borer (CBB) populations, which then negatively impact neighbouring coffee farms. In the present study, we sought to quantify CBB abundance in these sites, which vary in management intensity and vegetation structure and diversity. We collected data on trap catch as a measure of CBB flight activity, fruit production and fruit infestation by CBB in eight well-managed farms and sites that were either poorly managed, abandoned or feral (wild) coffee. Sites were sampled bi-weekly over a period of 2 years from 2016 to 2017. We found that CBB flight activity was significantly higher in poorly managed sites relative to abandoned and feral sites, but was not significantly different from well-managed sites. Coffee production in well-managed farms was significantly higher than in abandoned and feral sites, but was not significantly different from poorly managed farms. CBB infestation in poorly managed sites was significantly higher than that observed in well-managed, abandoned and feral sites. We estimated an average load of 11-25 CBB per branch at poorly managed sites, compared to 3-9 per branch at well-managed sites, 1-16 per branch at abandoned sites and 1-3 per branch at feral sites. Our findings suggest that poorly managed sites should be prioritized for implementation of CBB control measures as part of a landscape-level integrated pest management (IPM) programme.

KEYWORDS

Coffea arabica, crop production, fruit infestation, integrated pest management, pest reservoir, trap catch

1 | INTRODUCTION

Coffee (*Coffea* spp., Rubiaceae) is the most important agricultural commodity in more than 70 countries in the humid tropics (Jaramillo, Borgemeister, & Baker, 2006). In the last three decades, worldwide

production of coffee has increased by 45% (ICO, 2020) via higher yielding varieties, high-density plantings, heavy applications of fertilizers and mechanized harvesting (Baker, Jackson, & Murphy, 2002). These increases in production are driven by growing demand, especially in new markets (USDA FAS, 2019). For continued growth

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in production and yield, pest management in coffee will be essential, and this increasingly must be attained with reduced reliance on chemical control (Watts & Williamson, 2015).

Although coffee has many insect pests (e.g., root-knot nematode Meloidogyne spp., black twig borer Xylosandrus compactus) and diseases (e.g., coffee leaf rust Hemileia vastatrix, coffee berry blotch Cercospora coffeicola), the coffee berry borer Hypothenemus hampei Ferrari (Coleoptera: Curculionidae) is widely considered the most damaging insect to coffee crops worldwide (Damon, 2000; Jaramillo et al., 2006; Vega, 2015). Adult females bore into the coffee fruit, where they build galleries in the seed (bean) and lay eggs. The offspring develop inside the coffee seed where they feed on the endosperm tissue. Male and female siblings mate, and the males remain in the fruit while the mated females leave and search out a new fruit in which to lay their eggs. Coffee berry borer (CBB) affects both the yield and quality of coffee, causing serious economic losses in all coffee-growing regions of the world (Le Pelley, 1968). Additionally, because the CBB completes its entire life cycle inside the coffee fruit, the females are only vulnerable to pesticide sprays when they are out in search of new fruits to infest, making this pest extremely difficult to control.

Hawaii has a relatively small coffee industry (24.6 million pounds of coffee cherry produced in the 2017-2018 season, USDA-NASS, 2018) but commands premium prices on the world specialty market due to its unique origin and high quality (Kinro, 2003). In 2010, the arrival of CBB dramatically changed Hawaii's coffee industry (Burbano, Wright, Bright, & Vega, 2011). The pest rapidly spread across Hawaii Island (~2,400 ha in coffee production; Teuber, 2010) and was later detected on the neighbouring islands of Oahu (2014) and Maui (2016). Both the yield and quality of coffee produced in Hawaii has decreased due to CBB, with significant declines in "Extra Fancy" and "Fancy" grades of coffee (Aristizábal, Bustillo, & Arthurs, 2016; Aristizábal et al., 2017). The CBB invasion has also resulted in increased production costs due to the need to conduct labour intensive control measures such as end-of-season strip picking of all fruits remaining on the trees and regular applications of the entomopathogenic fungus Beauveria bassiana (Aristizábal et al. 2016, 2017). For the crop years 2011/12 and 2012/13, the estimated economy-wide impact of CBB in Hawaii was a \$12.7 M loss in crop value, a \$25.7 M loss in sales, a \$7.6 M loss in household earnings and a loss of more than 380 jobs (Leung, Kawabata, & Nakamoto, 2014).

Since the arrival of CBB in Hawaii, it has been widely suggested that feral (wild) coffee, abandoned farms and poorly managed farms serve as reservoirs for this pest, and can contribute to infestation in nearby farms (Messing, 2012; Aristizábal et al. 2016; Woodill, Nakamoto, Kawabata, & Leung, 2017). However, no published research exists to our knowledge that quantifies the extent to which these different sites harbour CBB across the coffee-growing land-scape in Hawaii. The objective of this study was to examine CBB flight activity, fruit production and fruit infestation by CBB in well-managed coffee farms and compare it with that found in poorly managed, abandoned and feral sites over two growing seasons

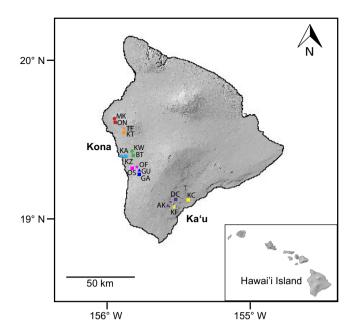


FIGURE 1 Location of study sites in the Kona and Ka'u districts of Hawaii Island (see Table 1 for further details). Adjacent sites are coded as the same colour: squares represent well-managed farms, triangles represent poorly managed farms, circles represent abandoned farms, and stars represent feral coffee sites. Inset map shows the position of Hawaii Island within the Hawaiian archipelago

TABLE 1 Description of sites studied in 2016 and/or 2017 in the major coffee-growing regions of Hawaii Island

		Elevation		
Site	District	(m)	Site type	Year
KC	Ka'u	279	Well-managed	2017
KF	Ka'u	298	Feral	2017
ON	Kona	296	Well-managed	2016
MK	Kona	300	Abandoned	2016
KZ	Kona	302	Well-managed	2016, 2017
KA	Kona	282	Abandoned	2016, 2017
KT	Kona	407	Well-managed	2016, 2017
TF	Kona	421	Feral	2016, 2017
OS	Kona	430	Well-managed	2016
OF	Kona	472	Feral	2016, 2017
GA	Kona	480	Well-managed	2017
GU	Kona	475	Poorly managed	2016, 2017
DC	Ka'u	597	Well-managed	2017
AK	Ka'u	553	Poorly managed	2017
ВТ	Kona	607	Well-managed	2017
KW	Kona	601	Abandoned	2017

(2016–2017) on Hawaii Island in order to improve area-wide integrated pest management (IPM) strategies for this economically important pest.

2 | MATERIALS AND METHODS

2.1 | Study sites

Six well-managed coffee farms located in the Kona district of Hawaii Island were selected for the study in 2016 (Figure 1, Table 1). Two additional well-managed farms in the Ka'u district of Hawaii Island were added to the study in 2017 (Figure 1, Table 1). We considered "well-managed" farms as those that conducted active management for coffee production, including regular pruning, fertilizing, weed management, pesticide sprays for CBB (B. bassiana and/or pyrethrinbased pesticides), cherry harvesting and end-of-season strip picking (Figure 2A). In general, well-managed farms were subject to management interventions multiple times per month. To limit confounding factors due to environmental conditions, we selected a site adjacent to or at a similar elevation to each well-managed coffee farm that was classified as one of the following: a poorly managed farm, an abandoned farm or feral coffee. Farms classified as "poorly managed" were not actively managed aside from mowing the grass and/ or cutting vegetation around coffee trees (Figure 2B); these particular sites were not used for coffee production during our study (i.e. were not harvested). Farms considered "abandoned" received no management for at least 2 years prior to the initiation of the study



FIGURE 2 Examples of site types studied: Well-managed farm (a), poorly managed farm (b), abandoned farm (c) and feral coffee (d). Note differences in shade, vegetation structure and diversity, and fruit production

(Figure 2C). Sites designated as "feral" were forested areas that had coffee plants growing wild in the understory (Figure 2D). In 2017, two of the well-managed farms (ON, OS) and one abandoned site (MK) in Kona were sold and replaced with the following sites in Kona: BT, GA and KW (Figure 1, Table 1). Each study site was approximately 1–2 ha in size. All well-managed and poorly managed farms grew coffee in full sun (Figure 2A,B); abandoned farms had few to no trees and were overgrown with tall grass, sometimes head-high (Figure 2C); feral coffee grew in densely forested areas with generally low levels of sunlight (Figure 2D). All coffee plants were *C. arabica* var. *typica*, with the single exception being farm KC which had primarily *C. arabica* var. *catuai* planted. Figure 3 shows a generalized overview of coffee plant phenology on Hawaii Island, along with the recommended timing of CBB management practices (see Kawabata, Nakamoto, & Curtiss, 2015).

2.2 | CBB flight activity

To investigate CBB flight activity, red funnel traps (CIRAD, Montpellier, France) were randomly distributed within each site, with the number of traps used dependant on the size of the site (3–5 traps for small sites 1–1.4 ha in size, 6–9 traps for large sites 1.5–2 ha in size). Traps were hung on stakes and positioned ~1 m above the ground. Each trap was equipped with 40 ml of a 3:1 methanol:ethanol lure placed in semi-permeable plastic bags, and a collection cup filled with an aqueous kill solution of propylene glycol (Figure 4A; see additional details in Johnson, Hollingsworth, Fortna, Aristizábal, & Manoukis, 2018). Traps were checked bi-weekly throughout the year, and the contents collected in 70% ethanol. Lures were refilled as needed, and kill solutions were replaced bi-weekly. In the laboratory, CBB were separated from all other insects and counted under a light microscope (Leica Microsystems GmbH).

2.3 | Fruit production and infestation

From March-December, coffee plants were assessed bi-weekly for fruit production and CBB infestation. Tree sampling followed the methods used in Johnson et al. (2018). Briefly, sampling grids were first established to ensure an even distribution of sampling of trees throughout each site. The number of trees sampled depended upon the size of the study area (8-15 trees sampled at small sites, 18-25 trees sampled at large sites). Sampling grids were not established at feral sites due to fewer trees available; at these sites, all coffee trees that could be found were sampled (8-12 trees). To assess fruit production, a single branch was randomly selected at chest height from each tree and the number of infestable fruits (green to ripe fruits that were pea-size and larger) were counted (Figure 4B). Given that dried coffee fruits (raisins) are known reservoirs of CBB (Johnson, Fortna, Hollingsworth, & Manoukis, 2019), we also counted the number of raisins on each branch. CBB infestation was assessed by examining green fruits for an entrance hole in the central disc (Figure 4C). Given

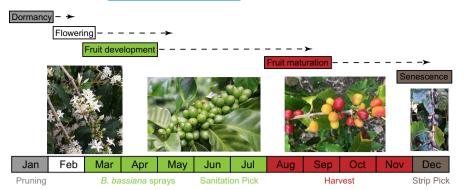


FIGURE 3 Coffee plant phenological stages generalized for Hawaii Island. Management practices currently recommended for coffee berry borer (CBB) under an integrated pest management (IPM) strategy are also included for reference

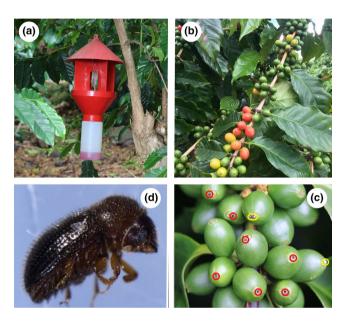


FIGURE 4 Variables examined in the present study, including (a) trap catch as a measure of flight activity, (b) fruit production (fruit per branch), (c) fruit infestation (red circles indicate coffee berry borer [CBB] infested fruits, and yellow circles show infested fruits with signs of white *Beauveria bassiana* fungus) and (d) coffee berry borer (CBB) loads

that ripe and over-ripe fruits were continuously harvested throughout the season on well-managed farms, only green fruits were included in our infestation assessment. When present, 1–3 infested green fruits were collected from each branch and stored at 14°C. Infested fruits were dissected within 24 hr under a dissecting microscope at 30–50× (Leica, Microsystems GmbH). We recorded the number of fruits in which the founding female was in the AB position (i.e., has commenced boring into the fruit but has not entered the endosperm) but was absent due to mortality or disturbance. This was done in order to accurately estimate the number of infested green fruits per branch that had the founding female present (Section 2.4).

2.4 | Estimation of CBB load per branch

Given that we did not track the total CBB population per infested green fruit, we calculated a conservative estimate for CBB load per branch based on adult CBB in green fruits only (assuming that each fruit had only a single founding female; Figure 4D), and a high estimate based on the adult CBB in green fruits plus the total CBB population (all life stages) in infested tree raisins (Johnson & Fortna et al.. 2019 for additional details on calculation). The mean CBB load per branch was calculated for each of the four site types using the following variables: G = mean number of green fruits/branch; I = meanproportion of infested green fruits or raisins/branch; P = meanproportion of infested green fruits/branch with founding female present; R = mean number of raisins/branch; C = the total CBB population per infested raisin; and S = the mean proportion of surviving CBB per raisin. The mean proportion of infested raisins (0.70), mean population per infested raisin (20 CBB) and mean survivorship per raisin (0.88) were taken from estimates by Johnson & Fortna et al. (2019) for tree raisins on Hawaii Island. The average CBB load per branch for the conservative estimate (CL) was as follows: CL = P $(G \times I)$. The average CBB load per branch for the high estimate (HL)was as follows: $HL = CL + (R \times I) \times (C \times S)$.

2.5 | Data analysis

We used generalized linear mixed models (GLMM) to determine whether site type (feral, abandoned, poorly managed and well-managed) was a good predictor of: (a) CBB flight activity, (b) fruit production and (c) fruit infestation by CBB. We ran three separate GLMMs, each having one of the three continuous variables as a response (trap catch, fruit production and fruit infestation). Each analysis included site type (four levels as categorical variables) as a fixed effect predictor. To control for random differences among sites, elevations (three levels as categorical variables: low [200-350 m], mid [351-500 m] and high [501-650 m]), years (two levels as categorical variables) and sampling dates (treated as repeated measures) were included as random effects. The GLMMs with fruit production and flight activity as responses were built using a Poisson distribution, while the GLMM with fruit infestation as a response was run using a binomial distribution. GLMMs and model comparisons using likelihood ratio tests were implemented in the package lme4 v. 1.1-19 (Bates, Machler, Bolker, & Walker, 2015) in R v. 3.5.0 (R Core Development Team, 2018). If site type was found to be a significant predictor in any of the GLMM analyses, post hoc tests (pairwise Tukey contrasts) were conducted in the package multcomp v. 1.4-13 (Hothorn, Bretz, & Westfall, 2008) in R.

3 | RESULTS

3.1 | CBB flight activity

Site type was a significant predictor of CBB flight activity as measured by trap catch according to the GLMM results ($X^2 = 20.18$, df = 3, p < .001). Multiple comparisons of means with Tukey contrasts across all sites/sampling dates showed that trap catch was significantly higher in poorly managed farms (mean \pm 1 SE; 91.40 \pm 42.11 CBB/trap/day) compared to feral (3.34 \pm 2.49 CBB/trap/day) and abandoned sites (0.17 \pm 0.17 CBB/trap/day), but was not significantly different from well-managed farms (29.40 ± 9.87 CBB/trap/ day) (Table 2; Figure 5A). Trap catch was also significantly higher in well-managed compared to feral sites, but there was no difference between abandoned and feral sites (Table 2; Figure 5A). While trap catch remained low year-round in abandoned sites, the main peak in flight activity for well-managed, poorly managed and feral sites was observed from March to May during both years (Figure 5B). A second smaller peak was observed in well-managed and poorly managed sites during the end of the season from late October to December for both years (Figure 5B).

3.2 | Fruit production

We found a significant effect of site type on fruit production ($X^2=11.19, df=3, p=.011$). Tukey contrasts showed that fruit production across all sites/sampling dates was significantly higher in well-managed farms (26.94 ± 2.92 fruits/branch) compared to abandoned (8.66 ± 2.03 fruits/branch) and feral sites (7.78 ± 3.38 fruits/branch) (Table 2; Figure 6A). Fruit production was not significantly different between poorly managed (19.56 ± 10.50 fruits/branch) and well-managed farms, or between poorly managed, abandoned and feral sites (Table 2; Figure 6A). For all site types, fruit production peaked from June to October (Figure 6B). Lastly, the mean number of raisins per branch was lowest at feral sites (0.13 raisins/branch) and well-managed farms (0.48 raisins/branch), while abandoned (1.22 raisins/branch) and poorly managed sites (1.13 raisins/branch) had similarly high numbers.

3.3 | Fruit infestation by CBB

We found a significant effect of site type on fruit infestation by CBB ($X^2 = 55.33$, df = 3, p < 0.001). Tukey contrasts showed that poorly managed farms had a significantly higher mean percentage of infested fruits ($62.97 \pm 0.77\%$) compared to feral ($17.89 \pm 2.06\%$), well-managed ($12.49 \pm 2.81\%$) and abandoned sites ($8.85 \pm 8.41\%$) (Table 2; Figure 7A). Fruit infestation was not significantly different

TABLE 2 Generalized linear mixed model estimates for fruit production, trap catch and fruit infestation as explained by site type (well-managed, poorly managed, abandoned and feral)

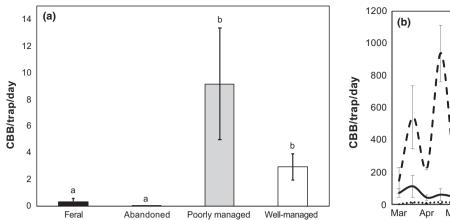
pe (well-managed, poorly managed, abandoned and feral)					
	Tukey contrasts				
Model variable	Estimate	SE	z-ratio	p-value	
Trap catch					
Feral vs. abandoned	1.697	1.200	1.414	.481	
Poorly managed vs. abandoned	5.700	1.179	4.835	***	
Well-managed vs. abandoned	4.149	.952	4.360	***	
Poorly managed vs. feral	4.003	.992	4.037	***	
Well-managed vs. feral	2.453	.845	2.904	*	
Well-managed vs. poorly managed	-1.551	.870	-1.782	.273	
Fruit production					
Feral vs. abandoned	-0.109	.437	0.249	.994	
Poorly managed vs. abandoned	0.498	.466	1.068	.705	
Well-managed vs. abandoned	1.096	.386	2.839	*	
Poorly managed vs. feral	0.607	.436	1.391	.501	
Well-managed vs. feral	1.204	.349	3.449	**	
Well-managed vs. poorly managed	0.598	.385	1.551	.402	
Infestation					
Feral vs. abandoned	1.129	.801	1.410	.483	
Poorly managed vs. abandoned	4.117	.793	5.188	***	
Well-managed vs. abandoned	0.056	.831	0.067	1.000	
Poorly managed vs. feral	2.987	.485	6.162	***	
Well-managed vs. feral	-1.073	.545	-1.970	.192	
Well-managed vs. poorly managed	-4.060	.533	-7.613	***	

^{*}Significant at p < .05,

between well-managed, abandoned or feral sites (Table 2; Figure 7A). Well-managed and abandoned sites exhibited a similar pattern of infestation over time, peaking at the beginning and end of the season (Figure 7B). In contrast, infestation in feral sites peaked from August to September and then decreased, while infestation in poorly managed farms increased throughout the season and peaked at an average of 95% infestation in December (Figure 7B). Across all sampling dates, the average percentage of infested fruits with CBB missing

^{**}Significant at p < .01,

^{***}Significant at p < .001.



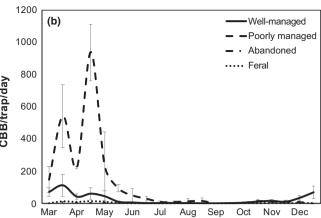
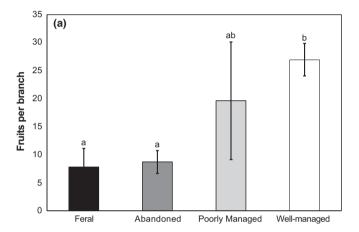


FIGURE 5 Mean (±SE) trap catch across the entire growing season on Hawaii Island (a) and mean (±SE) trap catch for each month (b). Trap catch is reported as the mean number of coffee berry borer (CBB) caught per trap per day. Lowercase letters represent significant differences in the means. Data is combined for 2016 and 2017



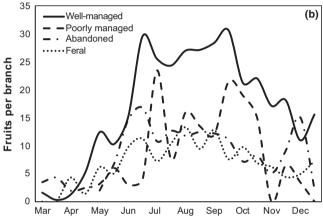


FIGURE 6 Mean (±SE) fruit production across the entire growing season on Hawaii Island (a) and mean fruit production for each month (b). Fruit production is reported as the mean number of fruits per branch. Lowercase letters represent significant differences in the means. Data from 2016 and 2017 are combined

in the AB position (i.e., boring was initiated but the founding female evacuated the fruit prior to entering the endosperm) was 13.02% in well-managed farms, 12.92% in abandoned sites, 6.59% in poorly managed sites and 6.13% in feral sites.

3.4 | CBB load estimates

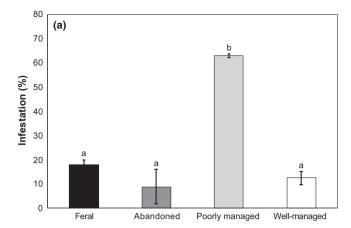
We estimate that the mean CBB load per branch across all sites/sampling dates was highest in poorly managed farms (11.45–25.37 CBB/branch) followed by well-managed farms (2.93–8.84 CBB/branch), abandoned farms (0.67–15.70 CBB/branch) and feral sites (1.31–2.91 CBB/branch).

4 | DISCUSSION

We compared CBB flight activity, fruit production and fruit infestation in well-managed coffee farms with poorly managed, abandoned

and feral coffee sites on Hawaii Island to determine the abundance of CBB in these sites that vary considerably in terms of management intensity. Across all sites and sampling dates, fruit production was highest in well-managed and poorly managed farms, while CBB flight activity and fruit infestation were highest in poorly managed farms. Our results suggest that poorly managed farms are the largest source of CBB on Hawaii Island compared with the other three site types studied, and therefore, these sites should be the focus of control measures to avoid spillover of the pest to neighbouring farms.

The four site types studied here differed in vegetation structure and density, and this likely contributed to differences in CBB flight activity, fruit production and fruit infestation. Feral coffee sites in Hawaii are comprised of a mix of older trees that were planted and abandoned decades ago, and younger trees from volunteer seedlings. Goto and Fukunaga (1986) surveyed the Hawaiian Islands and found more than three million feral trees persisting on ~5,361 acres in the Kona and Ka'u districts alone. These feral sites are characterized by high shade and diverse assemblages of plant species, both in the canopy and understory. In contrast, sites that were abandoned



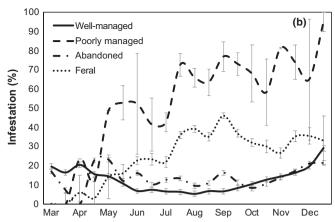


FIGURE 7 Percent (±SE) fruit infestation across the entire growing season on Hawaii Island (a) and mean (±SE) fruit infestation for each month (b). Infestation is reported as the mean percentage of fruits that had at least one coffee berry borer (CBB) entrance hole (i.e., at least one adult female). Lowercase letters represent significant differences in the means. Data are combined for 2016 and 2017

more recently (i.e., within the last 5 years) had higher light environments with few to no trees, and a high density of weeds and tall grasses surrounding coffee plants. We posit that the dense vegetation in feral and abandoned sites (trees/shrubs and tall grasses/ weeds, respectively) may serve as a natural barrier to CBB flight, explaining the low trap catch and fruit infestation found in both site types. This is in line with an earlier study by Teodoro, Klein, Reist, and Tscharntke (2009) that found lower CBB densities at sites that were more diverse and complex in terms of vegetation. Additionally, the low fruit production seen in feral sites is likely the result of high shade; reduced coffee yields under shade were also reported by Soto-Pinto, Perfecto, & Caballero-Nieto (2002).

The large range in CBB load (1–16/branch) estimated for abandoned sites reflects variation in fruit production and subsequent raisin load at these sites, which will depend on environmental conditions and how long the site has been abandoned. Extreme environmental conditions (high temperatures and low water availability) will limit fruit production in abandoned sites, and the CBB load will continue to diminish the longer a site is out of production and the reservoir of raisins has decreased. We noted that abandoned sites also suffered high coffee plant mortality, likely due to the long periods of drought that characterize the Kona coffee-growing region.

Fruit infestation by CBB in poorly managed farms averaged 63% across all farms/sampling dates. By the end of the harvest season in December, poorly managed farms reached an average of 95% infestation. Such a high level of infestation has generally not been reported in other coffee-growing regions, with infestation typically ranging from >1% up to 35% (Soto-Pinto et al. 2002; Benevides, Bustillo, Cárdenas, Montoya, 2003; Bosselman et al., 2009; Larsen & Philpott, 2010; Jaramillo et al., 2013). However, in Puerto Rico Mariño et al. (2017) reported that of 214 sites surveyed in 2014, the average infestation was 20% and ranged from 1%–95%. These authors suggested that the reasons for such high infestation included little to no management at the majority of sites, high cost and low availability of labour to conduct management and a lack of natural enemies.

The factors mentioned by Mariño et al. (2017) are directly translatable to the situation in Hawaii, where the cost of production and labour is high, labour to conduct management practices such as sanitation and frequent harvesting is difficult to secure, and natural enemies are largely absent (with the exception of flat bark beetles; see Follett et al., 2016). Many of these issues are due to the relatively recent introduction of CBB to the islands. In the present study, we found that for the eight well-managed farms that implemented multiple forms of CBB control, infestation levels averaged 13% (range = 2%-27%) throughout the season. This was significantly lower than that observed in poorly managed farms and highlights the importance of good farm management practices for the control of CBB.

Our findings also suggest that even if a well-managed farm is adjacent to a poorly managed farm with high levels of infestation, it is possible to maintain relatively low CBB populations throughout the season by implementing sanitation, pesticide applications early in the season, and frequent harvesting (see Figure 3; Kawabata et al. 2015). The sites that were neighbouring the poorly managed farms examined here kept infestation levels below 20% despite being adjacent to an area with high pest pressure. Although we did not examine CBB movement between sites, it is likely that females are able to migrate at least short distances between sites as conditions change in suitability. For example, we observed a massive increase in CBB flight activity and infestation at one feral site when the vegetation surrounding coffee trees were removed and fruit production subsequently increased. It is likely that CBB migrated from surrounding coffee farms and feral sites into this area once it became easier to access. This suggests that the use of physical barriers (i.e., exclusion netting) or border crops that are densely planted could inhibit the migration of CBB between sites and therefore minimize costs and labour needed to deal with the continuous influx of CBB from poorly managed sites into well-managed farms. Future research is needed to determine the height and distance that CBB are able to fly, and if their movement patterns change throughout the year depending on coffee plant phenology and differences in land use.

Poorly managed coffee farms represent a considerable challenge for landscape-level control of CBB due to the combination of high fruit production (and subsequently high numbers of raisins), ease of accessibility to fruits (as evidenced by high flight activity) and (by definition) lack of management resulting in high CBB loads and infestation rates. Reducing CBB abundance in poorly managed farms may be achieved by several different strategies, depending on the landowner or growers ultimate goals for a given site. If the aim is to transition a poorly managed site to a well-managed farm a comprehensive management strategy is needed, including pruning by block, spraying Beauveria bassiana early in the growing season, increasing the frequency with which coffee cherry is harvested, and conducting end-of-season strip picking (Kawabata et al. 2015; Aristizábal et al. 2016, 2017). Poorly managed farms would also be ideal sites for releasing natural predators such as parasitoid wasps and flat bark beetles. If comprehensive management is not possible and the landowner/grower is not relying on the coffee plants as a source of income, options include either stumping the coffee plants which will eliminate production for ~1 year, or halting mowing and weed management around coffee plants such that the vegetation may act as a natural barrier to CBB flight and infestation of any remaining berries. Lastly, if the ultimate goal for a given site is to convert the land to other uses, we recommend removing coffee plants as soon as possible to limit any negative impacts to neighbouring operations.

The present study is the first to our knowledge that has quantified and compared CBB abundance in well-managed, poorly managed, abandoned and feral coffee sites, and thus assessed the potential of these sites to act as population reservoirs for CBB. The information presented here suggests that fruit production is highest in well-managed sites, but that poorly managed sites have the potential for similarly high levels of fruit production. In addition, we found that CBB flight activity and fruit infestation were higher in poorly managed sites relative to well-managed, abandoned and feral sites. Together, these data suggest that poorly managed sites harbour higher CBB loads than well-managed, abandoned and feral coffee sites and thus should be priorities for landscape-level IPM programmes seeking to manage this economically important pest.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

MAJ and NCM conceived the research, collected data and wrote the manuscript. MAJ analysed data and conducted statistical analyses. NCM secured funding. All authors read and approved the manuscript.

DATA AVAILABILITY STATEMENT

Data collected in this study are available upon reasonable request to the first author.

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