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ORIGINAL ARTICLE

Strawberry guava invasion of a Hawaiian rainforest: Changing population patterns

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Abstract

Strawberry guava (waiawī, *Psidium cattleyanum* Sabine, Myrtaceae) is a small tree invasive on oceanic islands where it may alter forest ecosystem processes and community structure. To better understand the dynamics of its invasion in Hawaiian rainforests in anticipation of the release of a biocontrol agent, we measured growth and abundance of vertical stems ≥0.5 cm DBH for 16 years (2005–2020) in *Metrosideros-Cibotium* rainforest on windward Hawai'i Island. Specifically, we compared the growth and abundance of both shoots (originating from seed or from the root mat) and sprouts (originating above ground from established stems) in four replicate study sites. Mean stem density increased from 9562 stems/ha in 2005 to 26,595 stems/ha in 2020, the majority of which were stems <2 cm DBH. Early in the invasion, both density and per capita recruitment of shoots was greater than that of sprouts, but as overall stem density increased, sprout abundance and recruitment came to surpass that of shoots. Relative growth rates among small stems <2 cm DBH declined over time for both shoots and sprouts, but relative growth rates of sprouts were consistently greater than that of shoots after the first 3 years. The capacity of strawberry guava to recruit from both shoots and sprouts facilitates its invasion of rainforest, its persistence in the forest understory, and its response to canopy opening. Strawberry guava thus poses a considerable risk of stand replacement for Hawaiian rainforests. Stand management will require perpetual efforts to control both seed production and sprouting.

KEYWORDS
Hawaii, *Metrosideros* forest, Myrtaceae, *Psidium cattleyanum*, reproduction

1 | INTRODCTION

While mainland tropical rainforests are seen as resistant to the establishment and spread of non-native invasive species (Denslow & DeWalt, 2008), rainforests on oceanic islands are notably vulnerable (Barton et al., 2021; Carlquist, 1974; Denslow, 2003; Vitousek, 1986). Strawberry guava (*Psidium cattleyanum* O. Deg., Myrtaceae) is a small, shade-tolerant tree native to the Atlantic forests of Brazil and introduced to Hawai'i in 1825 (Nagata, 1985; Stone & Pratt, 1994). Its ability to invade tropical rainforests on oceanic islands is especially notable (Cronk & Fuller, 1995; Shimizu, 2006; Tng et al., 2016; Virah-Swamy et al., 2009). The tree has spread throughout the Hawaiian

Islands and across the Pacific and Indian Oceans (Richardson & Rejmánek, 2011) with significant impacts on the forests of Hawai'i (Smith, 1985), Mauritius (Cronk & Fuller, 1995), the Seychelles (Proença et al., 2022), and the Bonin islands (Shimizu, 2006) among others. Barton et al. (2021) estimate that it is the second most abundant species in the Hawaiian Islands where it occurs from sea level to 1500 m (Johnson, 2008) and in sites with <1250 to >7000 mm annual rainfall (Jacobi & Warshauer, 1992). Dense populations of strawberry guava in native rainforest alter such community and ecosystem processes as seedling establishment, forest structure, soil properties, litter fall, water movement, and the foraging of native birds and exotic pigs (Barbosa et al., 2016; Cordell et al., 2016; Enoki & Drake, 2017; Fortini et al., 2021; Harrington & Ewel, 1997; Ostertag et al., 2009; Rosam, 2015; Smith, 1985; Strauch et al., 2016; Takahashi et al., 2010; Vitousek, 1986). Its fleshy fruits are prized for food and, although not currently cultivated commercially, the species has attracted considerable research on the pharmaceutical and nutritional properties of fruits and foliage (e.g., Medina et al., 2011; Patel, 2012) and may attract commercial interest in the future. In lowland agricultural areas, the fallen fruits are hosts of fruit flies (Diptera: Tephritidae), a major pest of soft fruits such as papaya in Hawai'i (Vargas et al., 1990).

In Hawai'i, strawberry guava occurs in a diverse array of habitats but in natural areas it is found most commonly in wet *Metrosideros-Cibotium* and wet *Acacia koa-Metrosideros-Cibotium* forests (Wagner et al., 1999). Our objective here was to describe the population dynamics of guava in one such ecosystem at high priority for conservation. We report the structure and dynamics of a strawberry guava population invasion in wet *Metrosideros-Cibotium* rainforest on Hawai'i Island. To do so, we established replicate study plots in forests selected to represent this habitat which had similar initial densities of guava. In particular, we explored the contributions of two groups of recruits to the growth of the guava population in a rainforest environment: (1) rooted shoots originating from seed or from the root mat and (2) above-ground sprouts arising from established stems.

Using 16 years (2005–2020) of long-term plot measurements, we describe the growth of the population and changes in the relative abundances of strawberry guava stems arising from shoots or sprouts. Where invasive trees frequently establish via a strategy of gap capture (e.g., Daehler, 1998), strawberry guava may establish under closed canopy forest as well. Demographic studies of plant invasions can shed light on what makes invasive plants so successful and can be used to inform management (Horvitz et al., 2018; Jelbert et al., 2019; Sakai et al., 2001). This study was established to provide a better understanding of the roles of these two modes of recruitment in a population invading an otherwise intact rainforest in anticipation of the release of a biocontrol agent. *Tectococcus ovatus* Hempel (Homoptera: Eriococcidae) (Johnson, 2008) is a highly host-specific leaf-galling insect introduced from Brazil to Hawai'i in 2012. The expected impact of the agent is suppression of both vegetative sprouting and fruit production (Johnson, 2008). The results from this study will provide a baseline for better understanding of the relative impacts of *Tectococcus* on two important modes of reproduction of guava in Hawai'i. *Tectococcus* was released in 2017 and 2018 in the tree canopies at our study sites. As indicated by the amount of galling on fallen leaves, *Tectococcus* population levels remained low in 2020 but began to increase in 2021 (Johnson unpub. data). *Tectococcus* galls first began to appear on young plants in 2020. Thus, we do not believe that *Tectococcus* had a substantive impact on *Psidium* populations during the period of study (2005–2020).

2 | METHODS

2.1 | Sites

We measured guava stem diameters annually between 2005 and 2020 at each of four replicate study plots selected to represent early stages of strawberry guava invasions in intact *Metrosideros-Cibotium* rainforest on windward Hawai'i Island (Juvik & Juvik, 1998). Wet forests in Hawai'i are high priority conservation areas because of the biological diversity they harbor and their importance in the water economy of the islands (Jacobi & Warshauer, 1992; Tunison, 1992). Our study plots were established in the following conservation areas: Kahauale'a Natural Area Reserve (KAH, 19°10′N, 155°10′W), Pu'u Maka'ala Natural Area Reserve (MAK, 19°34′N, 155°11′W), Ola'a Forest Reserve (OLA, 19°27′N, 155°11′W), and Upper Waiakea Forest Reserve (WAI, 19°35′N, 155°12′W). All sites are at approximately 900 m elevation and distances between sites are 2–17 km. Estimated annual rainfall is 3000–4000 mm at OLA and KAH and 4000–5000 mm at WAI and MAK (Giambelluca et al., 1986). Projected mean annual temperature based on adiabatic lapse rates is 17–17.5°C for the elevation range of the four study sites (Giambelluca & Schroeder, 1998). All sites are on relatively young tholeiitic basalt lava flows that formed 200–1500 years BP (Wolfe & Morris, 1996). The forests resemble native lowland (100-1200 m elevation) wet forests with an ʻōhiʻa lehua (*Metrosideros polymorpha* Gaud) overstory and an understory dominated by tree fern (hāpuʻu, *Cibotium* spp.) as described by Gagne and Cuddihy (1999) and Juvik and Juvik (1998). All areas are under conservation protection by the State of Hawai'i.

2.2 | Species

Strawberry guava (waiawī, *Psidium cattleyanum* Sabine) is a small tree, 2–8 m tall. The yellow-fruited form (see Figure S1), dominant in the forests studied here, is one of three forms common across Hawai'i (Wagner et al., 1999) and occurring in similar habitats and differing in fruit color and shape. Nomenclature follows Royal Botanic Garden Kew "Plants of the World Online." Strawberry guava produces 2–3 cm diameter berries with multiple 5 mm long seeds (Wagner et al., 1999) via both sexual reproduction and apomixis. In the wet forests of Hawai'i, seeds germinate within a year and do not accumulate in a soil seed bank (Uowolo & Denslow, 2008). In Hawai'i, seeds are dispersed by birds, rodents, and pigs as well as humans.

Strawberry guava also reproduces vegetatively from both above-ground stems and from the root mat. For the purposes of this study, sprouts are defined as arising above-ground from established leaning or vertical stems. Such sprouts may overtake a leaning mother stem, obscuring the origin of older stems. Alternatively rooted shoots may arise via seed germination or directly from the root mat. In this study, we measured and tracked vertical stems standing more than 45 degrees from horizontal and greater than 0.5 cm DBH at breast height (measured at 1.37 m). The population thus contained both shoots, apparently originating from seed or roots, and sprouts, originating as branches from older shoots or sprouts. We were unable to distinguish root sprouts from seedlings non-destructively and thus identified stems with an obvious above-ground connection to a mother stem as sprouts; shoots arising from the soil with no obvious above-ground connection to an existing stem were assumed to have originated from seeds or roots. Huenneke and Vitousek (1990) working in forests in the same area found that the proportion of rooted stems arising from seeds versus from roots varied widely. Thus, our study population is narrowly defined as vertical stems arising directly from the soil (shoots) or vegetatively from previously established stems (sprouts); leaning stems were excluded.

2.3 | Surveys

At the start of the study (2005), all four sites had established populations of strawberry guava with a range of stem diameters represented. With one exception (OLA), we established one 0.25 ha plot at each site. The study plot at OLA, with an initially higher-density guava population, was 0.15 ha. All vertical stems at least 2 cm DBH were tagged in each plot and their diameters measured. In addition, we tagged and measured all vertical stems ≥0.5 cm DBH and <2 cm DBH in a stratified random set of 5 × 5 m subplots at each site (KAH: 6 subplots; MAK: 5 subplots; OLA: 5 subplots; WAI: 11 subplots). Diameter was re-measured annually, and new recruits tagged. Stems dying and leaning to less than 45 deg from horizontal were noted and not included in the study population going forward. The population of strawberry guava at each site reported here thus comprised only vertical stems.

2.4 | Analyses

We calculated basal area (BA) and yearly relative growth rates ($RGR = \log(BA_{t+1}/BA_t)$) based on basal area for individual stems. Density (stems/ha) was calculated from sample plots to allow comparisons among sites with different sample areas; estimates of total population density was based on the sum of the density of stems ≥2 cm DBH from the entire plot plus the estimate of density of small stems (≥0.5 cm DBH and <2 cm DBH) from the subplots. Thus, total estimated density comprised all vertical stems ≥0.5 cm DBH for each site. Total basal area per hectare was calculated similarly. Lambda ($N(t+1)/N(t)$) was calculated from total population densities. To better understand the pattern differences in shoots and sprouts, we focused on sources of variation among small stems <2 cm DBH, which comprised the majority of the population. Per capita annual recruitment and per capita stem death plus initial leaning of stems were calculated for both shoots and sprouts as a function of the total number of stems of all sizes present in the previous year at each site.

To determine whether lambda varied over time, we used linear mixed effects models using the lme() function in the nlme package (Pinheiro et al., 2023) in R (R Core Team, 2022). Year (coded as a factor) was the fixed effect, and site was the random effect. We accounted for temporal autocorrelation using AR1() auto correlation structure. We used a likelihood ratio test to assess whether the random effect of site was significant. To determine how shoots and sprouts differed over time in their densities, relative abundances, total basal area per ha, relative growth rates of stems <2 cm DBH, per capita recruitment, and per capita dying or leaning, we used linear mixed effects models using the lme() function in the nlme package. For all models, we included stem type (shoot, sprout), year, and the stem type × year interaction as fixed effects (with year coded as a factor) and site as a random effect. Additionally, for the relative growth rate model, we included a random effect of a stem ID nested within site. All models accounted for temporal autocorrelation using AR1() autocorrelation structure. When needed, we also accounted for heteroscedasticity by fitting different variances for each stem type in each year using varIdent(). Type III ANOVAs were run on the models to test significance of fixed effects. Post hoc tests were used to test for the difference between stem types in each year using the multcomp package (Hothorn et al., 2008). Marginal means and standard errors for plotting relative growth rates were calculated using the emmeans package (Lenth, 2023). ANOVA results are provided in the figure captions with additional information in Table S1.

2.5 | Age estimations

In addition, we estimated the ages of shoots in the population based on annual basal area increments. For this estimate, we pooled data from the shoots at all four study sites under the assumption that the sites were samples of a forest-wide population of strawberry guava. Only shoot growth was used in this estimate because sprout growth is in part dependent on the mother stem. Shoot growth rates vary as a function of DBH as well as a function of light availability and other microsite characteristics; thus, we used four estimates of annual growth increment to provide a range of age estimates. Excluding stems with zero or negative relative growth rates, we estimated smallest, largest, mean, and median basal area increments of shoots in 1 cm DBH size classes using data for the year 2019–2020. For the few stems larger than 12 cm DBH, we pooled data for all remaining large stems to estimate the increment. For each 1 cm growth ring and estimated annual basal area increment, we calculated the number of years a stem would take to reach the next size class. The total lapsed time to pass through size class 1 (0.5–2 cm DBH) through size class 21

(20–21 cm DBH) was an estimate of the years elapsed between the smallest and largest shoot size.

3 | RESULTS

3.1 | Population growth

Densities of strawberry guava in 2005 varied between a low of 2994 stems/ha (WAI) and 13,780 stems/ha (OLA). Populations increased at all 4 sites across 16 years of measurements (Figure 1). In 2020, population densities varied between 4030 stems/ha at WAI to 35,353 stems/ha at KAH. Annual population growth rates (lambda, Figure 2) were highly variable; differences were marginally significant among sites ($p = .075$) but not over years ($p = .921$). Sprouts and shoots differed in their pattern of change, however (Figure 3). Whereas sprout density increased over time, the growth in density of shoots flattened. During the first several years of the study, mean densities of shoots were marginally greater than that of sprouts, but not in the later years. Figure S2 shows this pattern was consistent across sites. At all sites, sprout density increased over time whereas shoot densities flattened or declined. The proportion of sprouts of all size classes in the population increased from a mean (SE) of 0.22 (0.02) in 2005 to 0.64 (0.02) in 2020.

Figure 4 illustrates the distribution of shoots and sprouts among size classes. Small size classes in both shoots and sprouts predominated (note the log scale on the y axis), but there were larger stems and more large stems among the shoots than among sprouts. Throughout the study period, stems <2 cm DBH comprised the majority (>80%) of the population (data from 2020 shown). The absence of shoots between 16 and 20 cm DBH suggests a hiatus in the establishment of new stems following the initial arrival of strawberry guava in the area. Total basal area per hectare of both sprouts and shoots increased over time at all sites (Figure 5). Total basal area of shoots was significantly greater than that of sprouts for all years up until 2018, reflecting the absence of large sprouts in the population. At the outset of the study, small shoots were predominant (Figure 6); as total stem density increased, however, the abundance of small shoots as a proportion of the total population declined and the relative abundance of small sprouts steadily increased. Across this time, there was no significant change in the abundance of small stems as a proportion of the total population.

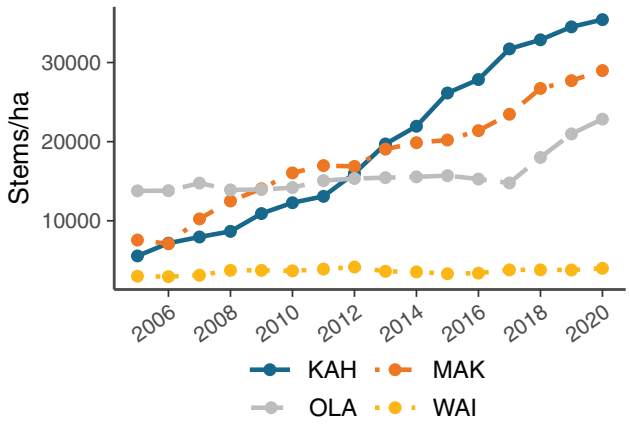

FIGURE 1 Density of vertical stems (sprouts and shoots combined) between 2005 and 2020 at each of four study sites.

3.2 | Stem growth

Relative growth rates (RGR, Figure S3) of both shoots (a) and sprouts (b) were more variable among small stems than among large stems (data from 2019 to 2020). Data from other years (not shown) showed similar patterns. Small stems exhibited the fastest relative growth rates as well as the slowest relative growth rates, including zero growth and shrinkage, some of which may be due to measurement error. For stems <2 cm DBH, mean relative growth rates of both shoots and sprouts declined over time (Figure 7) with growth rates of shoots declining more rapidly than that of sprouts. After the first few years, relative growth rates of sprouts were consistently greater than that of shoots.

3.3 | Recruits

Vertical and leaning shoots and sprouts all contribute new individuals to the population via both shoot and sprout production. Although sprout and shoot recruitment rate were initially similar, over time, per capita recruits of shoots declined and per capita recruits of sprouts increased (Figure 8), consistent with patterns of relative abundance and relative growth rates in the <2 cm DBH size class. Over this time, however, per capita recruits from all sources did not vary significantly.

3.4 | Death and leaning

Both death and leaning removed stems from the population of vertical stems. Although there were significant differences among years in per capita loss rate, variation among sites and years was high and there were no significant differences in per capita loss rates of shoots and sprouts (Figure 9).

3.5 | Age structure of shoots

In estimating the ages of the largest trees, we were limited by those shoots captured in the samples; larger and older trees elsewhere in the forest if present would support an earlier date of first establishment. Our estimates of the age of the largest stem varied widely (Table 1). An estimate of 485 years for slowest growing stems puts the shoot establishment more than 250 years before the introduction of the species to the islands and thus must be discounted. The largest shoots in our samples growing at maximum rates throughout their lives may be as young as 34 years old. Age estimates based on

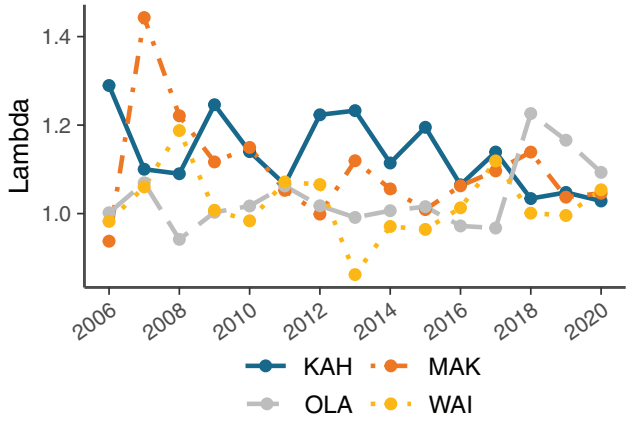

FIGURE 2 Annual population growth rates (lambda, N_{t+1}/N_t) at four study sites. Lambdas did not vary significantly over years (no significant fixed effect of year). A likelihood ratio test showed that the random effect of site was nearly significant ($\chi^2_1 = 2.07$, $p = .075$).

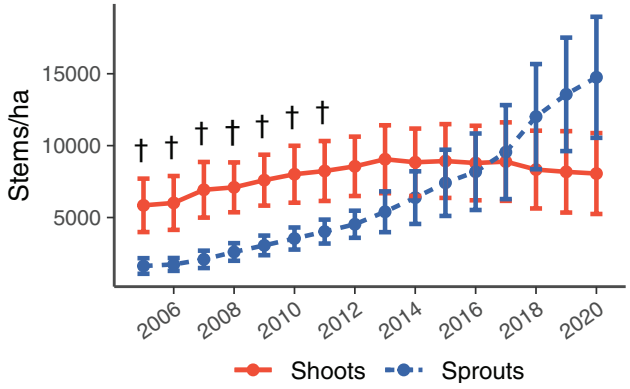

FIGURE 3 Mean (se) density of all vertical shoots and sprouts in four study sites. Differences due to year ($F_{15,93} = 2.663$, $p = .002$) and the interaction between year and stem type ($F_{15,93} = 1.895$, $p = .033$) were significant but not stem type. Crosses denote differences at $p = .1$ between shoots and sprouts for a given year based on post hoc tests.

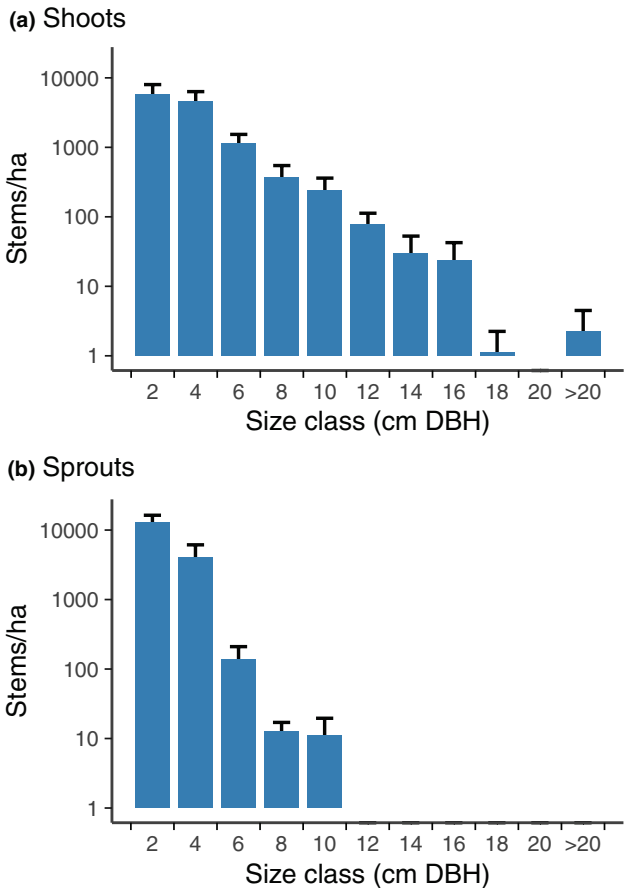

FIGURE 4 Densities of stems in 2-cm size classes of shoots (a) and sprouts (b). Data are means (se) of 2020 data for four sample sites. Upper limit of size class noted.

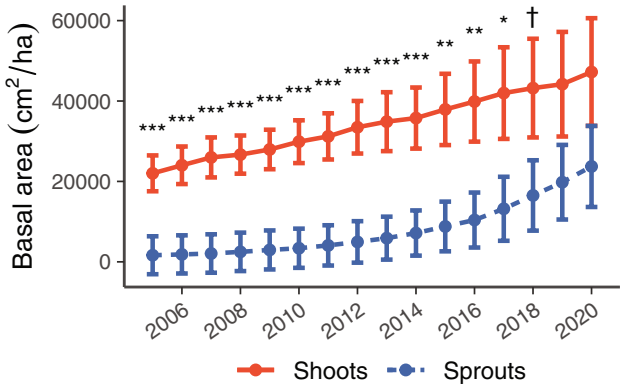

FIGURE 5 Total basal area (cm^2/ha) of vertical shoots and sprouts over time (means (se) of four study sites). Differences due to stem type ($F_{1,93} = 10.738$, $p = .0015$), year ($F_{15,93} = 12.296$. $p < .0001$), and the interaction between year and stem type ($F_{15,93} = 6.469$, $p < .0001$) were all significant. Asterisks denote significant differences between shoots and sprouts for a given year ($^{\dagger}p < .1$, $^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$).

mean and median growth rates were 86 and 92 years, respectively. Not included in this range is the time between germination and recruitment at the 0.5 cm DBH size, for which we have no estimate. There were few records of shoots larger than 12 cm DBH. Using the estimated time for a stem to grow from 16 to 20 cm DBH, the gap in the size frequency distribution of stems (Figure 4), we can suggest a time lag of 14–15 years between the first establishment of strawberry guava in this forest and the recruitment of new shoots from local reproduction. Our age estimates are rough and, in the absence of tree-ring counts, should be taken as approximations.

4 | DISCUSSION

Our data illustrate the pattern of increase in density of the yellow form of *Psidium cattleyanum* within *Metrosideros-Cibotium* rainforest habitat on windward Hawai'i Island and provide insight into factors contributing to the success of the invasion. Annual stem growth increments suggest that the oldest trees on our plots may be at least 30–90 years old. As in many introduced species (Bruno et al., 2005;

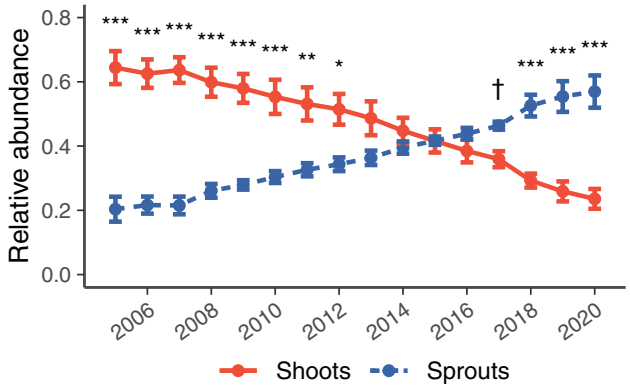

FIGURE 6 Change in the relative abundances of small (<2 cm DBH) shoots and sprouts as proportions of the total population (means (se) of 4 sites). Differences due to stem type ($F_{1,93}=4.861$, $p=.030$) and the interaction between stem type and year ($F_{15,93}=12.456$, $p<.0001$ were significant, but not year. Significant differences between stem types by year from post hoc tests are indicated by asterisks ($^{\dagger}p<.1$, $^{*}p<.05$, $^{**}p<.01$, $^{***}p<.001$).

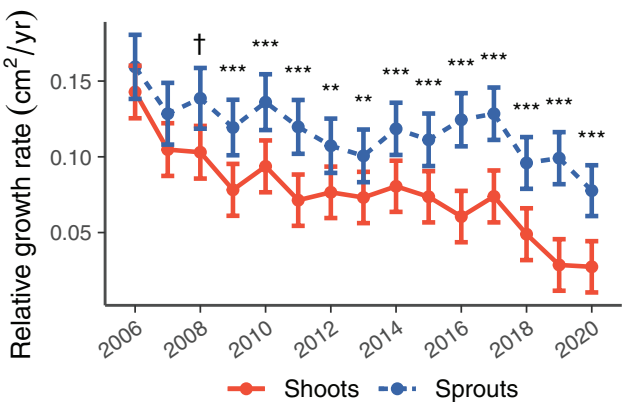

FIGURE 7 Relative growth rates of small (<2 cm DBH) shoots and sprouts (marginal means (se) of stems from four sites). Significant fixed effects included stem type ($F_{1,1766}=100.047$, $p<.0001$), year ($F_{14,7304}=25.914$, $p<.0001$), and the interaction between stem type and year ($F_{14,7304}=2.882$, $p<.001$). Asterisks denote a significant difference between shoots and sprouts for a given year ($^{\dagger}p<.1$, $^{*}p<.05$, $^{**}p<.01$, $^{***}p<.001$).

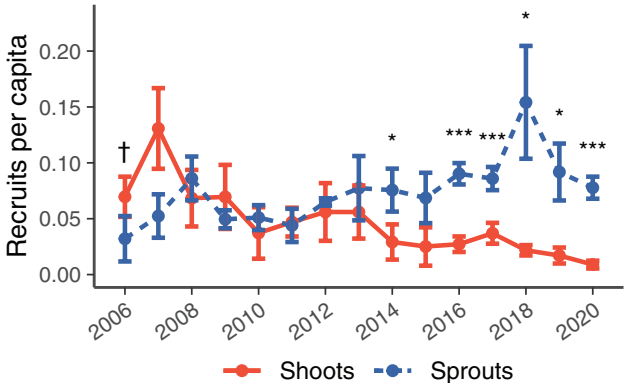

FIGURE 8 Per capita recruits of shoots and sprouts (means (se) of 4 sites). Differences due to stem type ($F_{1,87}=8.923$, $p=.0037$) and the year by stem type interaction ($F_{14,87}=3.001$, $p<.001$) but not year were significant. Asterisks denote significant differences between stem types for a given year.

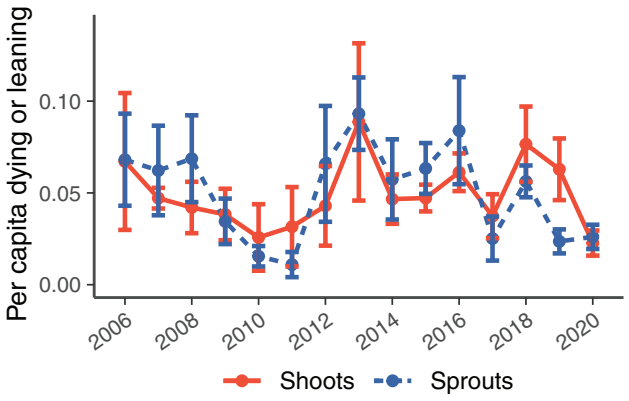

FIGURE 9 Per capita stems dying or initially leaning for shoots and sprouts (means (se) of 4 sites). Differences due to year ($F_{14,87}=2.224$, $p=.013$) were significant, but not stem type or the interaction between year and stem type.

Sakai et al., 2001), propagule supply and dispersal limitation appear to have resulted in a time lag between first appearance and the subsequent rapid growth of the population. Here, that time lag appears to be between 14 and 15 years. Canopy opening due to a major ʻōhiʻa (*Metrosideros*) dieback event in the 1960s and 1970s on windward Hawai'i Island (Hodges et al., 1986; Jacobi et al., 1988; Mueller-Dombois, 1987; Mueller-Dombois et al., 1977) may have facilitated the initial establishment of *P. cattleyanum* in the area. As those initial plants reached reproductive maturity, this local source of seeds contributed to the population growth described here. We see this process in the early dominance of shoots in our populations, in the fact that the largest stems are shoots, and in the contribution of shoots to the estimated total basal area/ha of the species. Using total basal area/ha as a proxy for the relative roles of shoots and sprouts in community and ecosystem processes, we see that early establishing shoots likely exert long-term impacts on the invaded community.

Although initial population expansion was driven by recruitment of shoots, as population density increased and understory light levels likely declined (e.g., Rosam, 2015), sprouts came to dominate recruitment and population growth. We see this shift in the decline of both absolute and relative abundances of shoots and the increase in both absolute and relative abundance of sprouts. We focused our analyses on the dynamics of small stems as their growth and survival were most likely to be affected by increasing population density and declining resource availability. Over time we saw a decline in relative growth rates of both small shoots and sprouts. However, the decline in growth rates of small shoots was significantly greater than that of small sprouts whose growth was subsidized by mother stems. This decline in growth rates of small shoots is consistent with the decline in per capita recruits among shoots in comparison with sprouts. Per capita losses of shoots and sprouts due to death and leaning did

TABLE 1 Estimated years for shoots to reach different sizes once they attain 0.5 cm DBH.

Lower bound	Upper bound	Mean increment	Median increment	Minimum increment	Maximum increment
≥0.5	<2	9	11	57	2
≥2.0	<3	17	20	87	3
≥3.0	<4	22	26	110	4
≥4.0	<5	27	31	132	6
≥5.0	<6	31	35	154	7
≥6.0	<7	35	39	176	9
≥7.0	<8	39	44	197	10
≥8.0	<9	43	49	218	12
≥9.0	<10	46	52	238	14
≥10.0	<11	50	55	258	16
≥11.0	<12	53	59	268	18
≥12.0	<13	56	61	284	19
≥13.0	<14	58	64	301	20
≥14.0	<15	61	67	320	22
≥15.0	<16	64	70	340	23
≥16.0	<17	67	73	361	25
≥17.0	<18	70	76	383	26
≥18.0	<19	74	80	406	28
≥19.0	<20	78	84	431	30
≥20.0	<21	81	88	457	32
≥21.0	<22	86	92	485	34

Note: We report the estimated time (years) to attain the upper DBH limit of the size class using four different estimates of annual basal area increments for each growth ring based on 2019–2020 data: the mean growth increment in the size class, the median growth increment, the minimum growth increment, and the maximum growth increment. Only positive growth increments were included. The first size class included stem ≥0.5 and <2 cm DBH; other DBH size classes are 1 cm.

not differ but appeared to be episodic across years, likely reflecting storm patterns and pig incursions. Thus, in our study sites, differences in recruitment and growth among shoots and sprouts appear to drive the increase in the relative abundance of sprouts and decline in abundance of shoots. Interestingly, neither per capita recruitment nor relative abundance of small stems of both sprouts and shoots taken together changed significantly across the years; rather the relative success of these two sources of new stems shifted over time.

ʻŌhiʻa-dominated forests are notable for their relatively open canopies (Barton et al., 2021), contributing to the vulnerability of these forests to the establishment and spread of naturalized species. The increase in density and total basal area of strawberry guava itself reduces light penetration and increases the volume of leaf litter. In her study of *Psidium*-invaded lowland forest on Hawaiʻi Island, Rosam (2015) found that understory light environments were heterogeneous in native forests but that both light availability and quality declined in *Psidium*-invaded forests. The increasing density of *Psidium* also contributes to heavy litter production and a dense root mat (e.g., Strauch et al., 2016; Weber, 2017). Foliage of strawberry guava has been shown to have allelopathic effects on in vitro seed germination trials (Hister et al., 2016), although the role of allelopathy in wet tropical environments may not be strong. Co-occurring species such as tree ferns (*Cibotium* spp) also contribute to low understory light levels, all of which likely adversely affected recruitment of shoots in comparison with that of sprouts.

Stems leaning as the result of tree and branch falls, wind, and pig foraging contribute to sprout initiation (Huenneke & Vitousek, 1990. Shimizu, 2006), although sprouts may also originate from non-leaning stems. Attachment to the mother stem provides access to resources from both a substantial root system and an advantageous crown position of larger mother stems. The importance of vegetative reproduction among successful woody invaders of forest habitats is well recognized (Daehler, 1998; Horvitz et al., 1998; Reichard & Hamilton, 1997; Sebert-Cuvillier et al., 2007). Sprouting allows self-perpetuation of stems following crown death—the persistence niche of Bond and Midgley (2001)—as well as a bank of saplings in the event of gap formation. Among tropical rainforest trees, sprouting is common among shade tolerant but not pioneer species (Bellingham et al., 1994; Everham III & Brokaw, 1996; Putz & Brokaw, 1989; Yih et al., 1989) and the ability of shade-tolerant tree seedlings and sprouts to take advantage of canopy opening due to tree and branch fall is a common pattern (Denslow, 1987; Lediuk et al., 2016; Sebert-Cuvillier et al., 2007; Shimizu, 2006; Webster et al., 2005).

This pattern is also characteristic of strawberry guava. Like many woody invaders, strawberry guava exhibits traits facilitating gap capture, such as effective dispersal and reproductive maturity at small stem sizes. Strawberry guava also exhibits shade tolerance, sprouting facility, and capacity for rapid growth in both open and closed canopy conditions which promote its spread and effective dominance of wet forests in Hawai'i (Daehler, 1998; Tng et al., 2016). The shift from shoot to sprout recruitment not only carries an advantage in the capture of gaps but also facilitates population expansion under intact and increasingly dense forest canopy. The consistency of recruitment across the changing environmental and community structures of these forests contributes to the robust population growth of the species.

Psidium cattleyanum is apomictic and polyploid (Tuler et al., 2017), enabling population establishment by single individuals, mitigating loss of genetic diversity arising from founder effects (Petit et al., 2004), and facilitating establishment in a wide range of habitats both in Hawai'i and in its native range (Simoes & Marques, 2007; Tuler et al., 2017). Similarly, ʻōhiʻa exhibits many growth forms enabling its occupancy of a wide range of habitats. Hawaiian landscapes are marked not only by variation in elevation, rainfall, and topography but also by the age, nutrient supply, and physical attributes of the lava substrates (Barton et al., 2021; Barbosa et al., 2016; Giambelluca & Schroeder, 1998; Hodges et al., 1986; Jacobi et al., 1988; Kitayama & Mueller-Dombois, 1995; Mueller-Dombois et al., 1977; Mueller-Dombois, 1987; Zimmerman et al., 2008). Such environmental variation across *Metrosideros-Cibotium* wet forests likely contributed to the variation in population growth among our four study sites.

As with strawberry guava shoots, seedling establishment of ʻōhiʻa declines with canopy closure and forest maturation. In contrast to strawberry guava, ʻōhiʻa requires substantial canopy opening for regeneration (Mueller-Dombois et al., 1977), often brought about by the senescence of even-aged cohorts (Loope & Giambelluca, 1998). The dominance and persistence of ʻōhiʻa in Hawai'i reflect both this cycle of canopy dieback and cohort establishment and the heterogeneity of growth forms and environmental tolerances within the species (Kitayama et al., 1997; Kitayama & Mueller-Dombois, 1995; Mueller-Dombois, 1987). Periodic canopy dieback, however, provides an opportunity for stand-altering invasion of strawberry guava which is able to persist and regenerate as the canopy closes (Barbosa et al., 2016; Cannon et al., 2022), displacing ʻōhiʻa regeneration and altering the ecosystem (Cordell et al., 2016; Drake, 1998; Tunison, 1992). In addition, widespread canopy death (Rapid ʻŌhiʻa Death), caused by recent invasion of the pathogen *Ceratocystis* spp., appears likely to further accelerate population growth of strawberry guava (Fortini et al., 2019; Mortenson et al., 2016).

Managers are faced with a daunting challenge in the management of *P. cattleyanum*. Both mechanical/chemical (Tunison, 1992) and biological (Johnson, 2008; Wikler et al., 2000) control methods are likely to open canopy and increase light to the understory. Although seed longevity in the soil is short and its presence in the seed bank scant (Uowolo & Denslow, 2008), *Psidium* is effectively dispersed by non-native birds and pigs (Barton et al., 2021, Wagner et al., 1999) to take advantage of canopy opening. The abundance of sprout production suggests a continuing increase in stem density even under shade following canopy closure. Moreover, stand-altering events including storms, droughts, and pathogens associated with climate change are likely to contribute to stand invasion (Diez et al., 2012). These factors emphasize the importance of ongoing vigilance in the control of guava in high priority natural areas.

Our data suggest that an effective biological control agent should target small stems in the understory as well as tree growth and fruit production. *Tectococcus* is expected to reduce fruiting as well as growth rates of plants in both overstory and understory. While effective control of invasive species via reduction in seed production and dispersal is difficult to attain (e.g., DeWalt et al., 2022), the possibility of *Tectococcus* impacts on growth rates of both sprouts and shoots holds promise for reduction in population growth rates. While *Tectococcus* likely had minimal impact on growth rates or recruitment of shoots or sprouts during the time reported here, we expect both to be affected as the agent population spreads from the canopy to the understory. The degree to which biocontrol agents and other stand-altering events affect the dynamics of strawberry guava population growth is the subject of continuing research at our study sites.

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CONFLICT OF INTEREST STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.dr7sqvb42.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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