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Host preferences of non-native *Acalolepta aesthetica* (Coleoptera: Cerambycidae) on the Island of Hawai‘i

Helen R. Sofaer[1] | **Blake J. Miles**[2] | **Jorden A. Zarders**[2,3] | **Ellen J. Dunkle**[2] | **Renee L. Corpuz**[3] | **Sheina B. Sim**[3] | **Robert W. Peck**[2]

[1]U.S. Geological Survey, Pacific Island Ecosystems Research Center, Hawaii National Park, Hawaii, USA

[2]Hawai‘i Cooperative Studies Unit, University of Hawai‘i at Hilo, Hilo, Hawaii, USA

[3]Daniel K. Inouye U.S. Pacific Basin Agricultural Research Center, USDA Agricultural Research Service, Hilo, Hawaii, USA

Correspondence
Helen R. Sofaer, U.S. Geological Survey, Pacific Island Ecosystems Research Center, Hawaii National Park, HI 96718, USA.
Email: hsofaer@usgs.gov

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Abstract

1. Understanding the host preferences of non-native polyphagous insects is a key step in anticipating their impacts.
2. We apply a technique from wildlife ecology, a resource selection function, to quantify the host preferences of *Acalolepta aesthetica* Olliff (Coleoptera: Cerambycidae: Lamiinae) in its non-native range on the Island of Hawai‘i. We then visually surveyed its preferred host to map its distributional extent and conducted laboratory no-choice tests to assess risks to common native woody species.
3. The preferred host of *A. aesthetica* was the state tree, *Aleurites moluccanus* (L.) Willd., the kukui (or candlenut). Cacao (*Theobroma cacao* L.) was the second most preferred host. Infestations were also observed in *Citrus* species, *Artocarpus altilis* (Parkinson) Fosberg (‘ulu or breadfruit) and *Persea americana* Mill. (avocado), but preferences among these taxa were statistically indistinguishable.
4. *Acalolepta aesthetica* females oviposited on all tested species in no-choice trials, but larvae growing within ‘ōhi‘a (*Metrosideros polymorpha* Gaudich.) and koa (*Acacia koa* A. Gray) died. It therefore poses a low risk to these two tree species, which are foundational to Hawaiian native forests. *Acalolepta aesthetica* was able to complete its development within ‘ōlapa (*Cheirodendron trigynum* (Gaudich.) A. Heller), which could be monitored if the distribution of *A. aesthetica* spreads to native forests.
5. The host species preferred by *A. aesthetica* are highly valued for agricultural, horticultural and cultural uses. Developing monitoring and management techniques for this cerambycid and employing strong biosecurity could prevent human-mediated spread and limit negative impacts to other Hawaiian Islands, the U.S. mainland, and the world.

KEYWORDS
Cerambycidae, host preferences, host testing, resource selection

[Correction added on 20 February 2026, after first online publication: The copyright line was changed.]

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INTRODUCTION

One quarter of newly established non-native species have no previous history of introduction and establishment outside their native range (Seebens et al., 2018), and it can be difficult to anticipate whether and how these new non-native species may impact a recipient ecological system. When a new non-native species is detected, risk assessments consider species' taxonomy, natural and life history traits, and climate and habitat associations to guide management responses (Daehler et al., 2004). Species belonging to taxonomic groups containing harmful invaders have a higher risk of becoming harmful themselves (Buonaiuto et al., 2023). For insect pests, host breadth and preferences dictate plant-insect interactions to shape the impacts of a species in its invaded range; phylogenetic relationships between plant hosts present in the native and non-native range help predict whether an insect will become invasive (Gilbert et al., 2012; Mech et al., 2019). Most phytophagous insects are specialists, and the degree to which insects generalize on multiple host plants varies across taxonomic groups and between feeding guilds (Forister et al., 2015; Šenfeldová et al., 2024). Where potential host breadth is wide or unknown, studies that quantify host preferences and impacts in the newly invaded range can inform monitoring and management (Straw et al., 2015).

Cerambycid beetles (Coleoptera: Cerambycidae) represent a taxonomically and ecologically diverse group of phytophagous insects, comprising nearly 35,000 described species globally (Rossa & Goczał, 2021). The diet of adults can be varied within and among species and generally includes pollen, nectar, foliage, fruit, bark and sap exudates (Haack, 2017). Larvae typically develop within branches, stems and roots of herbaceous and woody host plants, and many consume one or more bark, phloem, cambium, xylem or heartwood tissue types (Linsley, 1959). Larvae may be restricted to a single host species (monophagous) or may be able to develop in a variety of plant species (polyphagous) (Hanks, 1999). The choice of host condition at the time of oviposition tends to follow cerambycid phylogenetic relationships (e.g., subfamily) and includes healthy, stressed, dying or dead plants (Hanks, 1999).

Cerambycids play an integral role in ecosystem dynamics (Edmonds & Eglitis, 1989) and can be indicators of biodiversity (Holland, 2007; Karpiński et al., 2021). However, several species have become serious agricultural or forestry pests within and beyond their native ranges. These pest species often form novel associations with hosts (Meng et al., 2015; Paine et al., 2011) and may experience fewer natural enemies when established outside their native range (Keane & Crawley, 2002). The concealed nature of their larval stage facilitates inadvertent transport in live trees, unprocessed timber, finished wood products, or wood packaging material and contributes to difficulties detecting them during biosecurity screenings (Haack et al., 2010; Hu et al., 2009). Cerambycid larval development time is influenced by the nutritional value of their food and by temperature and ranges from several months to several years (Haack & Slansky, 1987; Keena & Moore, 2010; Wang et al., 2002), potentially allowing some species to survive long periods of time stowed away during global transport. Invasive cerambycids such as Asian longhorn beetle (*Anoplophora glabripennis*), Eucalyptus longhorn borer (*Phoracantha semipunctata*), citrus longhorn beetle (*Anoplophora chinensis*) and red-necked longhorn beetle (*Aromia bungii*) are particularly destructive and have resulted in considerable costs to mitigate their impacts (Haack et al., 2010; Horrocks et al., 2024; Paine et al., 2011).

A longhorn beetle, *Acalolepta aesthetica* Olliff (Lamiinae), has recently become established on the Island of Hawai'i and appears to be a threat to a wide range of plants of agricultural, horticultural and cultural importance (Hawai'i Department of Agriculture, 2020). *Acalolepta aesthetica* is native to eastern Queensland and New South Wales, Australia (GBIF Secretariat, 2023). To our knowledge, the Island of Hawai'i is the only location where this species is currently established outside of its native range. *Acalolepta aesthetica* was first detected in the Puna District of the Island of Hawai'i in 2009 (Matsunaga & Chun, 2018), and by 2020 had been documented across much of the Puna District and near the town of Hilo in the South Hilo District (Conant, 2013; Curbelo, 2020; Hawai'i Department of Agriculture, 2020; Matsunaga et al., 2019). A genetic analysis found a single mitochondrial haplotype in all sequenced individuals, suggesting that the invasion arose from offspring of a single female (Curbelo, 2020). Known or probable host plants include at least 13 species within 8 orders and 11 families (Hawai'i Department of Agriculture, 2020). Although there are no reports of *A. aesthetica* infesting native Hawaiian plants, it is possible this species could become a pest of native trees, further stressing native forests following the profound impact imparted by Rapid 'Ōhi'a Death (Cannon et al., 2022).

Here, we extend knowledge of *A. aesthetica* host use by quantifying its host preferences in the field. Specifically, we used a resource selection function to analyse host use relative to host availability within infested properties. Resource selection functions are a widely used approach in wildlife ecology (Manly et al., 2002) and have the potential to be a useful tool for understanding insect host preferences. For insect pests, these models can be used to estimate preferences among host species by contrasting infested hosts with nearby uninfested individuals that were available as potential hosts. After estimating host preferences, we conducted roadside surveys of the most preferred host, illustrating how knowledge of host preferences can be used to characterize and monitor an invader's distribution. Finally, we conducted a lab study to evaluate whether *A. aesthetica* would oviposit on and develop within native woody species, including those important to upland native forests that it has not yet encountered because its known invaded range is currently restricted to lowland areas. Our study highlights the risks *A. aesthetica* poses to Pacific island socio-ecological systems and provides a foundation for studies of impacts and management options.

METHODS

Host preferences

Visual surveys for signs of *A. aesthetica* infestation were conducted on private properties in the Puna and South Hilo districts of the Island of Hawai'i with landowner consent between October 2020 and September 2021 (Figure 1; Miles, 2022). Properties were generally small (≤1 acre or 0.4 ha) residential parcels, as well as small orchards.

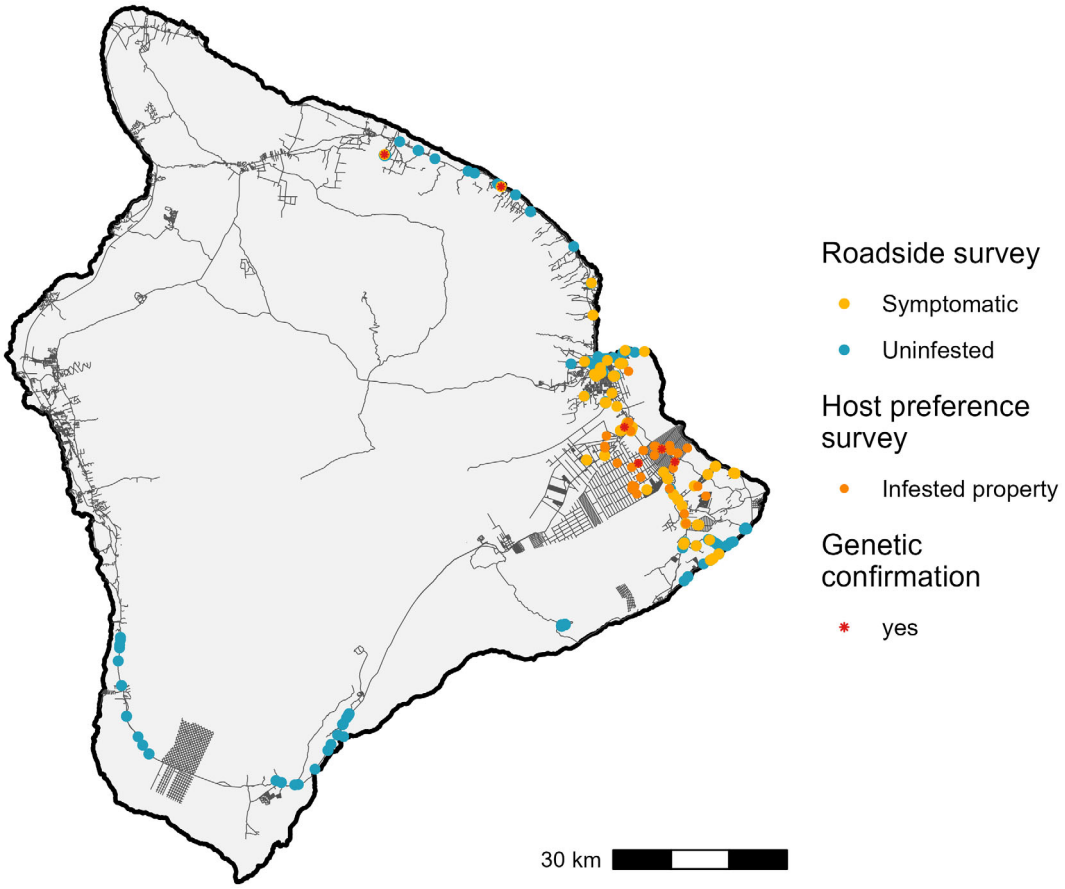


FIGURE 1 Locations on the Island of Hawai'i where plants were surveyed for *Acalolepta aesthetica*. Roads are shown in grey lines, such that grey blocks represent areas with a dense road network.

On each property, all woody trees were visually searched for signs of *A. aesthetica* infestation including sap and/or frass (a mixture of wood shavings and excrement) emerging from trunks or branches and exit holes (Figure 2a). Of 43 visited properties, 35 contained one or more trees with signs of *A. aesthetica* infestation. This high rate of infestation may be because property owners who had noticed symptomatic trees were more likely to connect with our team and agree to surveys. For each surveyed tree, we recorded the plant species, visually estimated basal diameter (cm) and noted the signs of infestation (frass, sap and exit holes). When properties contained multiple trees similar in size, such as in small orchards, a single row of data was collected to represent a group of individuals with a common infestation status and a common basal diameter. In the analysis, these were each treated as individuals with the same characteristics by using a weight variable in model estimation. We collected frass or larval samples from tree species that were not already documented as *A. aesthetica* hosts and used polymerase chain reaction (PCR) with species-specific primers diagnostic to the *A. aesthetica* CO1 sequence to confirm the infestation was caused by *A. aesthetica*. A genetic sample was collected from symptomatic individuals of six different plant species at four sites. An additional frass sample was collected from an 'ōhi'a (*Metrosideros polymorpha* (Gaudich.)) tree; the symptoms of this tree were not typical of *A. aesthetica* infestation (e.g., no sap was present).

A nucleic acid extraction was performed on the larval samples using the NucleoMag Tissue kit (Macherey-Nagel Inc., Allentown, PA, USA) and the frass samples using the DNeasy Plant Pro Kit (Qiagen, Germantown, MD, USA). Once DNA was isolated, PCR was performed using a reaction made of 12.5 μL Q5 Hot Start High-Fidelity Master Mix (New England Biolabs, Ipswich, MA, USA), 0.5 μL of 10 μM of each of the forward and reverse primer, 1 ng of isolated DNA and nuclease-free water to a total volume of 25 μL. Species-specific primers were designed around a 594 bp segment of the mitochondrial CO1 region for the species (NCBI GenBank accession: MT946709.1; Figure S1). The nucleotide sequences for the forward and reverse primers used were F-GAAC TTGGATCTCCCGGATCT and R-GGCACCAGCTAATACAGGTAGAG respectively. These sequences were selected due to variation in the area when compared to other Cerambycidae species found on the Island of Hawai'i such as the monkey pod round-headed longhorn beetle *Xystrocera globosa* (Olivier), the plumeria borer *Lagocheirus undatus* (Voet) and the sequence of closely related Cerambycidae from NCBI (Figure S2). This resulted in an expected fragment size of 498 bp. The cycling conditions used for the PCR were initial denaturation: 98°C for 30 s, 34 cycles of 98°C for 10 s, 59°C for 10 s, 72°C for 10 s and final extension of 72°C for 2 min. All PCR for the unknown samples were tested in quadruplicate and run concurrently with positive and negative controls. All PCR products were visualized on a 1% agarose gel with a 100 bp standard. A

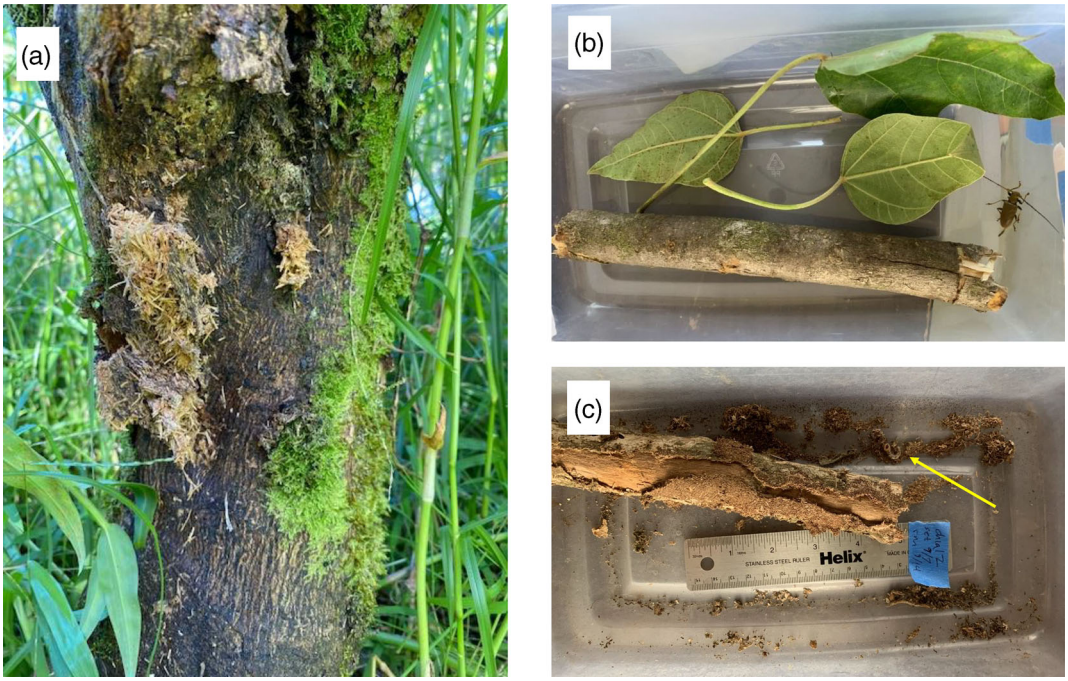


FIGURE 2 (a) Signs of *Acalolepta aesthetica* infestation in a kukui (*Aleurites moluccanus*) tree. (b) No-choice oviposition trials were conducted in the lab by placing a female in a bin with a piece of a cut branch from a focal species. Leaves of kukui or ʻulu were provided for feeding. (c) Larvae did not survive well in ʻōhiʻa (*Metrosideros polymorpha*). This picture shows the largest larva (see yellow arrow), which had fed on the bark of an ʻōhiʻa branch but did not burrow into the branch as was typically seen in the host species within which it was able to complete its life cycle. This larva died after falling out of the branch. Photos by (a) JAZ and (b, c) HRS.

QLB positive identification was determined if an amplicon (PCR product) about 500 bp in size was produced in at least one of the four test reactions.

We analysed the host preferences of *A. aesthetica* based on a use-availability study design. Analyses can estimate relative preferences by contrasting habitats that are used with habitats that are available but unused. Much of the literature on resource selection functions applies and evaluates this tool in the context of individuals' presence points, and a key methodological decision is how to sample from nearby environments to define available habitat (Northrup et al., 2022). In our study, we applied a use-availability analysis at the scale of individual trees, such that when a property had one or more infested trees, we assumed that the other trees on the property were also available to a female *A. aesthetica* that was selecting oviposition sites. Therefore, we included trees without symptoms of infestation located within the 35 properties containing at least one infested tree. We used this framework to analyse which tree species were preferred by *A. aesthetica*. As is common for use-availability designs (Johnson et al., 2006), we analysed our data using logistic regression. Our response variable was whether or not each individual tree was infested. To estimate which species were preferred as hosts, we included plant species for which we had sampled at least 15 individuals and that were found to be infested on at least two properties. Our model included fixed effects of tree species and basal diameter. We included a random effect of property on the intercept to account for different infestation severity among properties and the lack of independence between sampled trees on a single property. We fit the model using the glmmTMB package (Brooks et al., 2017) in R (R Core Team, 2024), using a binomial family and a logit link function, and assessed model diagnostics with the DHARMa package (Hartig, 2022). Post hoc tests based on Tukey's adjustment for multiple comparisons were conducted to test for differences in preferences among all pairs of evaluated host taxa and were implemented via the multcomp package in R (Hothorn et al., 2008). We present our results by displaying the estimated odds ratios, obtained by exponentiating the regression coefficients, which reflect the odds of infestation in each studied species relative to kukui. Values less than 1 indicate that a species was less preferred as a host than kukui. The tidyverse (Wickham et al., 2019) and sf (Pebesma, 2018) packages were used for data management and plotting.

Distribution

After establishing that kukui (*Aleurites moluccanus* (L.) Willd.; candlenut) trees were preferred hosts (refer to results), we conducted roadside surveys to approximate the spatial extent of *A. aesthetica*'s distribution, with an emphasis on lowland habitats on the eastern side of the Island of Hawaiʻi. Visual surveys using binoculars were conducted of kukui along roads between 24 March 2021 and 19 October 2023, looking for frass and/or sap extruding from trees. Trees were generally assumed to have been planted for their horticultural value, as individuals were largely single individuals or a sequence of several individuals that occurred in managed areas including roadsides, road medians, urban parks and parking lots. An exception was a large grove of kukui along Chain of Craters Road within Hawaiʻi Volcanoes

National Park in which 100 trees were surveyed on a single date. Each tree was recorded as having an infestation detected or not. Trees across the study were revisited as time allowed, and we recorded whether an active infestation was detected at each visit.

Host testing

We conducted no-choice trials to assess whether gravid female *A. aesthetica* would oviposit on, and larvae develop within, four abundant and ecologically important native tree species: ʻōhiʻa (*Metrosideros polymorpha*), koa (*Acacia koa* A. Gray), ʻōlapa (*Cheirodendron trigynum* (Gaudich.) A. Heller) and kāwaʻu (*Ilex anomala* Hook. & Arn.). Female *A. aesthetica* used in the trials were collected as adults from kukui in the field ($n = 5$) or reared in the lab from previous trials of oviposition and growth ($n = 10$). Prior to starting the trials, lab-reared females were individually placed into a 6-qt (5.7 L) plastic storage bin ($13 \times 8 \times 5$ in [$33.0 \times 20.3 \times 12.7$ cm]; Sterlite Corp., Townsend, MA; used in all aspects of the laboratory portion of this study) with one adult male *A. aesthetica* for about one week to allow time to mate. Adults were fed with leaves and small branches (too small to act as oviposition substrate) of kukui or ʻulu (*Artocarpus altilis* (Parkinson) Fosberg; breadfruit; an alternative preferred host, refer to results). Wild-caught females were confirmed to be gravid at the time of capture by observing oviposition on kukui. Oviposition trials were then conducted by individually placing mated females into plastic bins containing a small, freshly cut branch (~1.25–6 cm in diameter) of one of the four tested native plant species, along with several kukui leaves for food (Figure 2b). After approximately 7 days, the female *A. aesthetica* and the kukui leaves were removed from the bins, and the branches observed over time for extruded frass indicative of larvae hatching from the egg and beginning development. If no frass was observed, then the branches were closely examined for the presence of dead, unhatched eggs. We also noted the presence of oviposition scars, but only counted observed eggs and larvae as confirmed oviposition because females prepared locations for oviposition without laying an egg. We confirmed that each female was gravid and reproductively active throughout each trial by placing each female in a bin containing kukui branches for about 7 days before and after trials and searching the branches for evidence of oviposition. We included data from oviposition trials for which the female oviposited during the focal trial or was known to have oviposited both before and after the focal trial.

For oviposition trials that resulted in *A. aesthetica* larvae becoming established, we tracked larval survival to evaluate if they could complete development in cut branches of the four focal native tree species, and development was similarly tracked within kukui as a control. We generally selected one larva from each branch from the oviposition trials to assess for continued development. Each larva was left to develop in each branch for about two months (mean ± SD duration in a branch: 60 ± 22 days), and then transferred to a fresh branch of the same species. During transfers we split the branch open (generally using a small hatchet), removed the larva, weighed it and measured the width of its head capsule using a digital calliper (Husky 6 in. 3-Mode Digital Fractional Caliper Model #1467H). Larvae that were harmed during extraction were excluded from the study of development. The larva was then inserted into the end of a fresh branch of the same host species by gently guiding the larva headfirst into a pre-drilled hole slightly larger and deeper than the larva.

This study was conducted during July 2021 to November 2023 in an insectary kept under ambient conditions (i.e., without air conditioning or heating) at the U.S. Department of Agriculture (USDA) Agricultural Research Service facility, Hilo, HI. We summarized the proportion of oviposition trials for each focal species that resulted in an egg laid, as well as whether we observed completion of the life cycle.

RESULTS

Host preferences

Seven plant species met our inclusion criteria of having a minimum of 15 surveyed trees and two or more properties on which the species was infested (Table S1). These species were: kukui, ʻulu, trumpet tree (*Cecropia obtusifolia* Bertol.), citrus (*Citrus* spp.), croton (*Codiaeum variegatum* (L.) Rumph. ex A. Juss.), avocado (*Persea americana* Mill.) and cacao (*Theobroma cacao* L.). Kukui and ʻulu are Polynesian-introduced species with important cultural and agricultural uses. Trumpet tree was introduced by the 1920s for reforestation purposes and has become a widespread invasive species (Hawaii-Pacific Weed Risk Assessment, 2008). Citrus trees are non-native and widely planted, and we grouped all species of this genus together as non-fruiting individuals may not be reliably visually identified to the species level. Croton is a non-native ornamental plant commonly used in landscaping, which has been rated as having low invasion risk by the Hawaii-Pacific Weed Risk Assessment (Hawaii-Pacific Weed Risk Assessment, 2002). Avocado is non-native to the Hawaiian Islands and commonly planted for its fruits; we grouped all varieties together. Cacao is planted for chocolate production, and five surveyed properties had 30 or more cacao individuals, with two properties that had over 300 individuals. Of note, we sampled a total of 256 individual ʻōhiʻa trees across 19 sites and found that none of them were infested by *A. aesthetica*. In one instance, frass from an ʻōhiʻa tree was collected and confirmed to not contain *A. aesthetica* DNA. All frass samples from other tree species (*C. obtusifolia*, *Clusia rosea* Jacq., *Eriobotrya japonica* (Thunb.) Lindl., *Myristica fragrans* Houtt., *Picea* sp., *Psidium* sp.) collected for genetic confirmation returned a positive detection for *A. aesthetica* sequences.

Our analysis of host plant use versus availability showed that kukui was most preferred out of all analysed species (Figure 3). Cacao was the second-most preferred species and was approximately one-third as likely to be infested as kukui (exponentiated estimate ± SE: 0.322 ± 0.113, $z = -3.22$, $p = 0.001$). Post hoc tests showed that cacao was significantly preferred over citrus, ʻulu, trumpet tree, croton and avocado (Table 2). The latter species had widely overlapping confidence intervals and were estimated to have similar rates of infestation by *A. aesthetica*, with the exception that citrus was found to be

significantly preferred over avocado (Table 2). Larger host individuals were significantly more likely to be infested by *A. aesthetica* (exponentiated estimate ± SE: 1.05 ± 0.012, $z = 3.99$, $p < 0.001$).

Distribution

Roadside surveys documented kukui with signs of *A. aesthetica* infestation in the Puna District and north to the town of Honoka'a (Figure 1). Of 684 trees surveyed within this range, 218 were found to have symptoms of infestation in one or more surveys. None of the trees in the large grove within Hawai'i Volcanoes National Park had symptoms of infestation. Symptomatic trees were detected from the coast to 622 meters in elevation. A repeat visit to most surveyed trees found instances where trees that had previously shown signs of infestation no longer had symptoms of an active infestation, including in some cases where pruning was evident; in other cases, infested trees had been cut down (Figure S3).

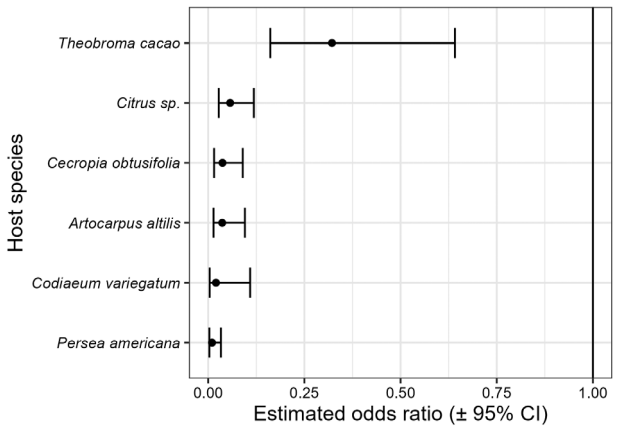


FIGURE 3 Host preferences are plotted relative to kukui (*Aleurites moluccanus*), which was estimated to be significantly preferred over other evaluated hosts. The odds ratio is the probability of infestation of a focal species divided by the probability of infestation of kukui. Infestation of kukui has an odds ratio of one (represented by the vertical line). Cacao (*Theobroma cacao*) was approximately one-third as likely to be infested as kukui and was significantly preferred over other evaluated hosts.

Host testing

No-choice oviposition trials revealed that *A. aesthetica* would oviposit on all the plant species evaluated (Table 1). The highest oviposition rate was observed in kukui (in 90% of 48 trials at least one egg was laid), the control species. High oviposition rates were also observed in 'ōlapa (83% of 12 trials) and kāwa'u (75% of 8 trials). In each of these three plant species, larvae developed in cut branches of the host species through pupation. However, the single larva that pupated within kāwa'u died as a pupa, whereas three individuals emerged as adults from 'ōlapa. These results confirm that *A. aesthetica* could complete its lifecycle on 'ōlapa and show limited evidence for the ability to develop within kāwa'u. We observed lower oviposition rates in 'ōhi'a (38% of 8 trials) and koa (30% of 10 trials). For each of these two species, fresh frass produced by early instar larvae was observed in two of the three trials in which oviposition was observed. However, none of these larvae survived. In the trial of 'ōhi'a in which the larva survived the longest (for three months), it was observed feeding on bark and did not tunnel into the wood; the larva fell out of the branch and died (Figure 2c).

The mean (± 1 SD) lifespan of female *A. aesthetica* reared in the lab and used in oviposition trials was 153 ± 33 days (maximum 201 days; the maximum observed lifespan of a wild-caught female was 131 days).

Data from this study has been made publicly available (Sofaer et al., 2025).

DISCUSSION

The preferred host of *A. aesthetica* is kukui, the state tree in the Hawaiian Islands. Kukui has great cultural value and has declined in its geographical extent and abundance (Lincoln et al., 2021). Additional species of agricultural and cultural importance are also used as hosts; our estimates show that cacao is the second-most preferred species, and 'ulu, citrus and avocado are also readily infested. After identifying kukui as the preferred host species, we surveyed kukui trees and found *A. aesthetica* occurs across much of the lowland eastern portion of the Island of Hawai'i. No-choice host tests revealed that *A. aesthetica* will oviposit on all tested native species and can

TABLE 1 Summary of oviposition trial results.

Host species	Number of oviposition trials	Number of females	Proportion of trials with oviposition	Final life stage observed
Aleurites moluccanus	48	14	0.9	Adult
Cheirodendron trigynum	12	12	0.83	Adult
Ilex anomala	8	8	0.75	Pupa
Metrosideros polymorpha	8	8	0.38	Larva
Acacia koa	10	10	0.3	Larva

Note: *Acalolepta aesthetica* females would oviposit on all tested species in no-choice trials, but oviposition rates were lower for *Metrosideros polymorpha* and *Acacia koa*; in these species, all individuals that hatched died as larvae. We observed growth until pupation in *Ilex anomala*, whereas individuals were able to complete their life cycle and emerge as adults in *Cheirodendron trigynum* as well as in our control species, *Aleurites moluccanus*.

TABLE 2 Results from post hoc tests of pairwise differences in the probability of *Acalolepta aesthetica* infestation across host species.

Contrast	Estimate	Standard error	*z* statistic	Adjusted *p*-value
Artocarpus altilis—*Aleurites moluccanus*	−3.31	0.49	−6.74	<0.0001
Cecropia obtusifolia—*Aleurites moluccanus*	−3.29	0.45	−7.3	<0.0001
Citrus sp.—*Aleurites moluccanus*	−2.86	0.37	−7.66	<0.0001
Codiaeum variegatum—*Aleurites moluccanus*	−3.9	0.86	−4.54	0.0001
Persea americana—*Aleurites moluccanus*	−4.61	0.61	−7.55	<0.0001
Theobroma cacao—*Aleurites moluccanus*	−1.13	0.35	−3.22	0.0189
Cecropia obtusifolia—*Artocarpus altilis*	0.02	0.5	0.04	1
Citrus sp.—*Artocarpus altilis*	0.45	0.47	0.97	0.956
Codiaeum variegatum—*Artocarpus altilis*	−0.59	0.92	−0.64	0.9948
Persea americana—*Artocarpus altilis*	−1.29	0.63	−2.06	0.351
Theobroma cacao—*Artocarpus altilis*	2.18	0.49	4.47	0.0002
Citrus sp.—*Cecropia obtusifolia*	0.43	0.39	1.1	0.9206
Codiaeum variegatum—*Cecropia obtusifolia*	−0.61	0.87	−0.7	0.9916
Persea americana—*Cecropia obtusifolia*	−1.31	0.57	−2.31	0.2161
Theobroma cacao—*Cecropia obtusifolia*	2.16	0.42	5.15	<0.0001
Codiaeum variegatum—*Citrus* sp.	−1.04	0.84	−1.24	0.8652
Persea americana—*Citrus* sp.	−1.74	0.56	−3.12	0.0262
Theobroma cacao—*Citrus* sp.	1.73	0.34	5.15	<0.0001
Persea americana—*Codiaeum variegatum*	−0.71	0.97	−0.73	0.9894
Theobroma cacao—*Codiaeum variegatum*	2.77	0.85	3.27	0.0162
Theobroma cacao—*Persea americana*	3.47	0.62	5.62	<0.0001

Note: Positive estimates indicate that the first species listed in the contrast was more preferred, and the statistical significance can be assessed based on the *p*-values, which incorporate Tukey's adjustments for multiple comparisons.

complete its life cycle within cut sections of ʻōlapa branches. It appears to pose low risk to native ʻōhiʻa and koa trees because infestations were not observed in the field for ʻōhiʻa (the beetle's range does not yet overlap that of koa), and *A. aesthetica* failed to develop in cut branches of both tree species.

Our study of host preferences found kukui had the highest infestation rates of any host species surveyed; one or more kukui trees were infested on 19 of the 21 properties where kukui was found, and 58% of individual trees on these properties had signs of infestation (Table S1). Kukui is not a novel host for *A. aesthetica*, as in Australia an adult *A. aesthetica* specimen in the Forestry Service collection of Biosecurity was reared out of kukui; the only other documented host record from Australian museum specimens was from *Agathis robusta* (J. Matsunaga, Hawaiʻi Department of Land and Natural Resources, written communication, 2024). Observations of *A. aesthetica* using kukui on the Island of Hawaiʻi support previous studies indicating non-native plants can be important hosts in the non-native range of phytophagous insects (Šenfeldová et al., 2024). Other *Acalolepta* species in Australia are also known to use *Theobroma* and *Artocarpus* species as hosts (Slipinski & Escalona, 2013), aligning with prior studies showing that phylogenetic relationships can help predict host use (Gougherty & Davies, 2021; Uden et al., 2023).

Preferences for high-value agricultural and horticultural host plants create the potential for substantial economic and socio-ecological impacts of *A. aesthetica*. The physiological impacts on different tree species are not expected to align directly with host preferences, as some host tree species may be better able to respond, survive, and maintain productivity under infestation (Baldwin & Preston, 1999). For example, the small diameter of cacao trees could make their vascular systems and structural integrity more susceptible to impacts of gallery excavation during *A. aesthetica* larval feeding and development compared to larger tree species like kukui. In addition, cultural, subsistence and economic impacts depend on the uses of each host tree. For kukui, its status as the Hawaiian state tree reflects its numerous uses for horticultural plantings, light and fuel, traditional medicine and lei ornamentation, among others (Lincoln et al., 2021). Cacao is the basis of a growing industry in the Hawaiian Islands that includes cacao production, chocolate making and associated agrotourism (Galt, 2020). Citrus trees are widely cultivated in yards and gardens (Ebesu & Evans, 2008). ʻUlu production and consumption are being revitalized in the Hawaiian Islands, and ʻulu fruits are a staple food central to agroforestry across the Pacific, underscoring the potential for strong negative impacts if *A. aesthetica* spreads elsewhere in the Pacific (Ragone, 2006). Residential avocado growing is widespread across the Hawaiian Islands, and commercial growers face recent challenges from other pests and diseases (Hawaiʻi Department of Agriculture, 2024). Understanding the degree to which *A. aesthetica* attacks stressed versus healthy individual trees and

assessing impacts on each host species are next steps for predicting and preventing declines in agricultural productivity (Haack et al., 2017). Preventing human-mediated spread to new locations through containment and management can help limit the geographic extent of these impacts.

Our use of resource selection functions applied a tool common in wildlife ecology (Manly et al., 2002) to the study of insect host preferences. This approach contrasts habitat (here, a host tree) that is used compared to what is available for use. Our study included only trees on properties that contained at least one infested tree, and so assumed that all trees on the property were available to a female *A. aesthetica* selecting an oviposition site. We considered this a valid assumption because the surveyed properties were small, typically with interspersed individuals of different tree species. Our analysis was limited to tree species that had a sufficient sample size; although this was based on statistical power, it led to a focus on widely planted and highly valued tree species. However, tree species that were not present on the surveyed properties, or not sufficiently abundant, were not assessed in this study and the degree to which they constitute suitable and preferred hosts is unknown. The analysis of host preferences guided our distributional surveys, which focused on the species we found to be most preferred, the kukui tree. Repeated surveys found a relatively slow rate of new infestations over time and revealed instances of both an apparent end to active infestation (in some cases with evidence of pruning) and also tree death (Figure S3). We expect that most kukui surveyed were intentionally planted, given that we largely surveyed landscaped areas, and without knowledge of their management histories we cannot infer impacts of untreated infestations or the efficacy of management. In addition to selectively pruning branches infested with *A. aesthetica*, the entomopathogenic nematode *Heterorhabditis indica* Poinar, Karunakar and David is being tested as a biological control agent for this pest (Big Island Invasive Species Committee, 2025).

Because of its wide host breadth, it is feasible that *A. aesthetica* may attack native Hawaiian plant species, with impacts that may be difficult to predict. However, our work indicates *A. aesthetica* is unlikely to impact the most abundant and widespread native tree in the Hawaiian Islands, the ʻōhiʻa. During host preference surveys, over 250 individual ʻōhiʻa trees were surveyed on infested properties, and none showed signs of *A. aesthetica* infestation. This result corroborates the fact that ʻōhiʻa has not been reported as a host of this beetle (Hawaiʻi Department of Agriculture, 2020) despite the high prevalence of ʻōhiʻa trees in the Puna District where the invasion is centred. No-choice trials found that female *A. aesthetica* would oviposit on each of the four native plant species offered, and although our sample sizes were small, none of the larvae survived in ʻōhiʻa or koa. In particular, the larva that developed the furthest in ʻōhiʻa fed on the bark and cambium and did not consume the harder inner wood (Figure 2c). In contrast, larvae developing on preferred hosts typically developed under the bark for a time and then tunnelled into the heartwood. Our findings therefore reinforce the poor suitability of ʻōhiʻa wood for *A. aesthetica* and align with research on other cerambycid species in which oviposition has been observed on a wider range of species than those within which larvae have completed development (Haack et al., 2010). The ability of *A. aesthetica* to develop within kāwaʻu is uncertain due to our small sample size. Because we did document that *A. aesthetica* can complete its life cycle within ʻōlapa, this species could be a candidate for monitoring potential spread and impacts in native forest.

We conducted visual surveys to analyse preferences at the scale of individual trees and to assess distributional patterns because standard lures used for monitoring cerambycids have not been found to be effective for *A. aesthetica* (Collignon et al., 2019). Our surveys were based on external signs of infestation, including frass, sap and exit holes (Figure 2a). However, there may have been undetected infestations, particularly in tall trees. Other cerambycid species can also attack the same hosts, raising the potential for false positives in which signs of infestation are wrongly attributed to *A. aesthetica*. To minimize the risk of false positives in our host preference study, we collected frass from trees that had not yet been confirmed as hosts and used genetic tools to confirm these infestations could be attributed to *A. aesthetica*. Similarly, genetic confirmation was used to test frass from the kukui trees found farthest to the north on the Island of Hawaiʻi (Figure 1).

The negative impacts of *A. aesthetica* (Hawaiʻi Department of Agriculture, 2020), and its broad host preferences, exemplify the benefits of strong biosecurity programmes to help prevent spread to other Hawaiian Islands, other Pacific islands, the U.S. mainland, and worldwide. Strong biosecurity programmes are guided by the relative risks posed by different organisms and pathways of invasion, which can be assessed via approaches including pest risk analysis (Devorshak, 2012), pathway analysis (Leung et al., 2014), horizon scanning (Lieurance et al., 2023) and sentinel plantings (Eschen et al., 2019). Cerambycid beetles have a high risk of human-mediated long-distance spread, particularly within wood, including wood packaging and wood products, or in and on live plants (Eyre & Haack, 2017). The host species most frequently attacked by *A. aesthetica* are valued agricultural and horticultural species, and further study could assess how host condition affects preferences, quantify impacts of infestation, and test management treatments. Development of effective lures could provide early detection and monitoring tools to enable a more nuanced understanding of distributional extent and rate of spread. Our study shows how resource selection functions can provide a field-based assessment of a new non-native insect's host preferences that can guide distributional assessments, as well as efforts to quantify socio-ecological impacts.

AUTHOR CONTRIBUTIONS

Helen R. Sofaer: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; visualization; writing – original draft. **Blake J. Miles:** Formal analysis; investigation; writing – review and editing. **Jorden A. Zarders:** Data curation; investigation; methodology; writing – review and editing. **Ellen J. Dunkle:** Data curation; investigation; writing – review and editing. **Renee L. Corpuz:** Investigation; writing – review and editing.

Sheina B. Sim: Formal analysis; funding acquisition; methodology; writing – review and editing. **Robert W. Peck:** Conceptualization; investigation; methodology; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are published (Sofaer et al., 2025; https://doi.org/10.5066/P13TORTW).

ORCID

Helen R. Sofaer https://orcid.org/0000-0002-9450-5223

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SUPPORTING INFORMATION

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

Table S1. Survey and infestation information for the focal plant species included in the analysis of *Acalolepta aesthetica* host preferences. For each species, we report the number of sites (properties) at which the host species was sampled, the number of sites at which the host species was found infested, the number of individuals that were sampled, the number of individuals that were infested and the proportion of individuals that were infested. Counts of sites and individuals include only those at sites that had at least one infested individual of any species ($n = 35$ sites); uninfested sites were not included in the analysis as we did not assume that these individuals were encountered by *Acalolepta aesthetica* and available for infestation.

Figure S1. Partial CO1 sequence for *Acalolepta aesthetica* and primer sequences used for the species-specific PCR used to identify beetle DNA from frass.

Figure S2. CO1 sequences from QLB larvae and adult and alignment to *Xystrocera globosa*, *Lagocheirus undatus*, *Anoplophora glabripennis* (AB439154.1), *Anoplophora chinensis* (AB439191.1), *Arhopalus* sp. (KY357781.1), *Monochamus saltuarius* (JN087435.1), *Acalolepta* sp. (MK704500.1), *Acalolepta grossescapus* (FJ559016.1) and *Acalolepta formosana* (FJ559004.1).

Figure S3. Results from revisiting kukui (*Aleurites moluccanus*) trees, visualized according the status (uninfested or infested) of the tree on the prior visit and the time elapsed since that visit. A longer duration between surveys was not associated with a higher likelihood of becoming infested, but note that this visualization does not account for the distance to the nearest infested tree. Some individuals that were previously recorded as infested no longer showed signs of an active infestation during the subsequent visit; whether these trees were pruned or treated is unknown. In rare instances, a previously infested tree was recorded as cut down or dead on the subsequent visit.

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