

ORIGINAL ARTICLE

Endemic island plant–herbivore interactions: Kamehameha butterfly (Nymphalidae) and Hawaiian Urticaceae

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Abstract

Insect–plant interactions are less well studied than other types of herbivory on islands, precluding a comprehensive understanding of the evolutionary ecology of these interactions. Declines in native island plants and insects call for urgent attention to characterize these species' interactions for their conservation and to better understand evolution in these unique, insular ecosystems. In Hawai'i, the Kamehameha butterfly (*Vanessa tameamea*) is one of only two native butterflies, and larvae are specialists on native urticaceous plants. Using a no-choice bioassay, we investigated performance of *V. tameamea* reared from egg hatching through eclosion on four native urticaceous host plants, *Boehmeria grandis*, *Pipturus albidus*, *Touchardia latifolia*, and *Touchardia oahuensis*, and one exotic urticaceous species, *Cecropia obtusifolia*. Performance varied significantly among the plant diets, with *V. tameamea* performing best on *P. albidus* and *T. oahuensis* among the performance metrics of survival, pupal and adult body mass, and development time. Larval responses to the exotic host plant *C. obtusifolia* varied among populations, with O'ahu caterpillars successfully completing development on it, but Hawai'i Island caterpillars rejecting it completely, suggesting a geographic mosaic for this novel species interaction. Characterization of a suite of nutritive and defensive plant traits revealed significant variability among plant species, but patterns did not align well with *V. tameamea* performance rankings, making it difficult to identify key drivers of host plant quality. Future work examining additional plant traits under natural conditions would provide new insights, contributing critical ecological information to conserve this charismatic island species.

KEYWORDS

caterpillar performance, coevolution, herbivory, host plant switching, leaf nutrients, phenolics, plant defense, Urticaceae

1 | INTRODUCTION

Tropical forests on continents typically harbor high species richness and intense plant–herbivore interactions (Coley & Barone, 1996). In contrast, tropical oceanic islands have relatively low species

richness, leading to predictions for weak species interactions on islands (Carlquist, 1974; Darwin, 1859; Elton, 1958). Presumed weak or absent plant–herbivore interactions on islands have led to the general prediction that island plants lack defenses as a consequence of relaxed selection pressure for defense production (Burns, 2019;

Krischik & Denno, 1983; Lonsdale, 1999). Indeed, studies have documented vulnerability to herbivory in island plants, but because most of these focused on introduced mammalian herbivores (Bowen & VanVuren, 1997; Moreira et al., 2021), they may not reflect island plant defenses evolved in response to native herbivores. Islands that have few or no mammalian herbivores host many other types of native herbivores, including insects, birds, tortoises, and land crabs, which can cause high levels of damage, alter community structure and assembly, and drive ecosystem dynamics on islands (Gibbs et al., 2010; James & Burney, 1997; O'Dowd & Lake, 1990). However, the declines and extirpations of native herbivores and their host plants on islands (Walther & Hume, 2016) make it challenging to characterize native island plant-herbivore interactions. Furthermore, while interactions between native plants and exotic herbivores have received considerable research attention on islands (Moreira et al., 2021), there are few studies of interactions between native herbivores and exotic plants. Considering the very high rates of exotic plant invasion to islands (Kueffer et al., 2010) and the relatively frequent use of exotic host plants by insect herbivores in continental systems (Forister & Wilson, 2013), it is likely that this interaction occurs on islands.

For new insights into island plant-herbivore interactions, studies that examine native and novel species interactions and that incorporate both putative defense traits and measures of herbivore performance are needed (Monroy & García-Verdugo, 2019; Moreira & Abdala-Roberts, 2022; Moreira et al., 2022; Tanentzap et al., 2011; Watts et al., 2011). As the most isolated archipelago in the world, the Hawaiian Islands offer compelling opportunities to examine plant-herbivore interactions in a famously disharmonic biota. Among the estimated 10,000 native insect species in Hawai'i, which diversified from approximately 350 to 400 colonization events (Eldridge & Miller, 1995; Hembry et al., 2021; Howarth & Mull, 1992), there are only two native butterflies, *Vanessa tameamea* (Eschscholtz 1821; Nymphalidae), the Kamehameha butterfly and state insect of Hawai'i, and *Udara blackburni* (Tuely 1928; Lycaenidae), Blackburn's blue butterfly (Riotte & Uchida, 1979; Williams, 1928). *Vanessa tameamea* inhabits montane and riparian native forests where its larvae are oligophagous specialist herbivores (Ali & Agrawal, 2012), feeding solely on the leaves of species in the family Urticaceae (Gorelick & Wielgus, 1968; Leeper, 1975; Riotte & Uchida, 1979; Swezey, 1954; Tabashnik et al., 1992; Williams, 1928). Little is known about *V. tameamea* preference and performance across host plants, but anecdotal observations suggest that larvae are most common on *Pipturus albidus*, or māmakī, a relatively fast-growing shrub to small tree that remains relatively common as a native mesic to wet forest species (Craven et al., 2018; Gorelick & Wielgus, 1968; Wagner et al., 1999). The butterfly's populations have declined in recent decades, and the species is now considered Vulnerable on the IUCN Red List (Gorelick & Wielgus, 1968; Tabashnik et al., 1992; Walker & Haines, 2022).

Urticaceae, commonly referred to as the nettle family, includes species defended by toxic stinging hairs (Hurley, 2000; Iwamoto et al., 2014; Levin, 1973; Mustafa et al., 2018). However, not all

urticaceous species possess this trait, and the majority of Hawaiian-represented genera fall within clades that generally lack stinging hairs, even in continental species (Kim et al., 2015; Wells et al., 2021; Wu et al., 2013). Furthermore, urticaceous stinging hairs have largely been implicated in defense against mammals (Iwamoto et al., 2014; Tuberville et al., 1996), so their relevance to defense against specialist insect herbivores remains unclear. More likely, other physical and chemical traits provide urticaceous species with defense against insects, such as leaf toughness, biomineralization, or secondary compounds (Awmack & Leather, 2002; Hanley et al., 2007; He et al., 2014; Salminen & Karonen, 2011).

To investigate *V. tameamea* performance across urticaceous host plants, we conducted a no-choice bioassay combined with plant trait analysis for four native urticaceous species, all documented host plants for larval *V. tameamea*, and one potential novel host plant, the exotic urticaceous species, *Cecropia obtusifolia* (Bertol.) (Table 1). Multiple exotic urticaceous species have established in Hawai'i (Imada, 2019; Staples & Herbst, 2005; Wagner et al., 2005), potentially serving as alternative host plants and contributing to *V. tameamea* conservation in areas where native hosts have declined, or never occurred. *Cecropia obtusifolia* is not a documented food source for wild larval *V. tameamea*, but it is naturalized on Kaua'i, O'ahu, and Hawai'i Island and is the only known exotic urticaceous species found to be abundant in forests where *V. tameamea* and the native host plants used in this study occur (Craven et al., 2018; Imada, 2019). *Cecropia obtusifolia* has large leaves, compared to several other naturalized exotic Urticaceae, providing *V. tameamea* with enough material for the caterpillar's characteristic folded-leaf shelter that it forms during the larval stage. Nonetheless, if *V. tameamea* is using the exotic *C. obtusifolia* during larval development, it is likely that this results in poor fitness as exotic host plants generally reduce herbivore fitness compared to native host plants with which the herbivores share an evolutionary history (Yoon & Read, 2016), although relaxed defenses in the invaded populations of *C. obtusifolia* (Blossey & Notzold, 1995) could also lead to the opposite prediction.

For insights into host plant quality, we investigated plant traits predicted to underly the palatability and nutritional quality for larval development (Table 2). Chemical defense was assessed as total phenolics and the proportion of total phenolics that oxidize under alkaline conditions, which target lepidopteran larvae (Anstett et al., 2019; Barbehenn et al., 2006; Moilanen & Salminen, 2008; Salminen & Karonen, 2011; Vihakas et al., 2015). Structural defense was examined via measures of leaf toughness (leaf mass per area and leaf thickness), and calcium concentration as an indicator of intracellular crystals that can reduce palatability and digestibility of plant tissues (Hanley et al., 2007; He et al., 2014; Mustafa et al., 2018). Because herbivore development is influenced by nutrient content and defenses (Kariyat & Portman, 2016), we also analyzed leaf nitrogen and phosphorus concentration. Butterfly performance was quantified as survival, growth (pupal and adult mass), and rate of development (duration of larval and pupal stages), providing a holistic understanding of fitness across the five host plant diets (Kariyat & Portman, 2016).

TABLE 1 Urticaceous species tested in the bioassay, including biogeographical variables relevant to their availability as host plants to *Vanessa tameamea*, and potential defense traits, such as the presence of latex, stinging hairs, and cystoliths (Friis, 1993; Imada, 2019; Wagner et al., 2016; Treiber et al., 2019). Whether these species have been observed host plants of *V. tameamea* is reported (Gorelick & Wielgus, 1968; Williams, 1928). IUCN Red List Assessments reflect the current abundances and stability of these plant species (Grave, 2020; Walsh in review; Rønsted, in review; Zamora, 2022).

	<i>Boehmeria grandis</i>	<i>Pipturus albidus</i>	<i>Touchardia latifolia</i>	<i>Touchardia oahuensis</i>	<i>Cecropia obtusifolia</i>
Origin	Endemic	Endemic	Endemic	Endemic	Exotic (native to Central and South America)
Distribution	All main Hawaiian Islands except Niʻihau and Kahoʻolawe				Kauaʻi, Oʻahu, and Hawaiʻi
IUCN Red List assessment	Not evaluated	Least concern	Vulnerable	Least concern	Least concern
Habitat	Mesic to wet forest				Pastures, low elevation wet forest
Growth form (height m)	Shrubs (1–2)				Shrubs or small trees (2–6)
Stinging hairs	No	No	No	No	No
Cystoliths	Yes	Yes	Yes	Yes	No
Reported <i>V. tameamea</i> host plant	Yes	Yes	Yes	Yes	No

TABLE 2 Plant functional traits quantified in the host plant species.

Leaf trait	Units	Predicted effects on herbivores
Leaf thickness (LT)	mm	–
Leaf mass per area (LMA)	g/m ²	–
Chlorophyll (SPAD)	unitless	+
Leaf carbon: nitrogen ratio (leaf C:N)	unitless	–
Leaf phosphorus content (leaf P)	mg/g	+
Leaf calcium content (leaf Ca)	mg/g	–
Total phenolics	mg/g	–
Proportion of oxidized phenolics	unitless	–

Note: Leaf chemical content was calculated on a dry-mass basis. Chlorophyll content was estimated using a SPAD meter, which reports relative units of light absorbance in the blue (400–500 nm) and red (600–700 nm) light regions. Predicted effects on caterpillar performance in bioassay range from traits that promote growth and survival (+) and those that reduce growth and survival (–), providing plant resistance.

This study provides the first rigorous characterization of performance of *V. tameamea* on its native urticaceous host plants, shedding light on endemic island plant–herbivore interactions and providing key insights for conservation of this iconic island butterfly. We predicted that: (i) performance of *V. tameamea* would be higher on native than exotic urticaceous host plants, reflecting their shared evolutionary history (Yoon & Read, 2016); (ii) *V. tameamea* performance would vary among the native plant diets, and (iii) urticaceous species with higher expression of defensive traits and lower concentrations of leaf nutrients would be associated with reduced *V. tameamea* performance.

2 | METHODS

2.1 | Study system

Caterpillars used in the bioassay were obtained from three *V. tameamea* colonies reared at the University of Hawaiʻi at Mānoa (UHM, Honolulu, Hawaiʻi), originating from founder butterflies collected on two separate mountain ranges on Oʻahu (Koʻolau and Waiʻānae) and one founder population from Hawaiʻi Island. The Koʻolau colony was founded from a single mated wild female collected in April 2014 and never augmented with additional wild individuals. The Waiʻānae colony was founded from several individuals collected in January 2015 and was periodically augmented with wild individuals. The third population came from two individuals collected in 2015 near Daniel K. Inouye Highway, Hawaiʻi Island (known locally as Saddle Road). Laboratory colonies were maintained on *P. albidus* because of its proximity to campus and ease of regular collection, but caterpillars used in the bioassay were started at the egg stage and so were naive to their given plant diet. Plant trait analyses for the five focal plant species (Table 1) were conducted using

samples collected from wild populations from one or two locations in the Ko'olau Mountains, the same sites from which bioassay leaf material was collected.

2.2 | Bioassay

To investigate *V.tameamea* performance across plant diets, we conducted a no-choice bioassay in Fall 2015 for four woody species native to Hawai'i (Table 1): *Boehmeria grandis* (Hook. & Arnott) A. Heller, *P.albidus* (Hook. & Arnott) A. Gray, *Touchardia latifolia* Gaud., and *T.oahuensis* T. Wells & A.K. Monro, formerly known as *Urera glabra* (Hook. & Arn.) Wedd.; and one exotic species, *C.obtusifolia*. These five species grow in the same mesic to wet forest habitat as *V.tameamea*, are more abundant than other Urticaceae, and are not federally endangered, allowing us to collect large amounts of leaves for this study from wild individuals without causing undue harm to sensitive plant populations.

Butterfly eggs were kept in containers without host plant material, and upon hatching, naive caterpillars were reared on a single species diet throughout their development. Each diet was fed to 15 replicate caterpillars per population, giving a total sample size of $N=225$ caterpillars (5 diets $\times$ 3 populations $\times$ 15 replicates). Undamaged, mature leaves fed to caterpillars were collected from randomly-selected, healthy, juvenile, and mature plants in wild populations in order to avoid overharvesting from individual plants. Leaves were rinsed and refrigerated until used, replenishing the stored leaves every 3–4 days to maintain freshness. Caterpillars were reared on benches with a 12L:12D light cycle to approximate the mean day length in Hawai'i in individual plastic ramekins, which were cleaned every 2 days when fresh leaf material was provided. Caterpillars were moved to larger ramekins at the fourth instar and remained there through eclosion. Position on the laboratory bench was shuffled daily to minimize potential light or microclimate effects.

Caterpillars were observed daily to record mortality and to track developmental stages, including hatching, pupation, and eclosion. Pupation was indicated by the presence of a hardened chrysalis, and eclosion was marked by the emergence of the adult butterfly from the chrysalis. Butterfly sex was recorded upon eclosion (Figure S1). The pupation period was highly conserved across host plant diets (11–13 days), so rate of development was estimated as the total duration (in days) between hatching and eclosion. In addition, performance was measured as total growth, estimated as pupal and adult mass. Adult butterfly mass was recorded 8–12 h after the butterfly had eclosed in order to minimize variance in adult weights due to hemolymph loss and expulsion of the meconium.

2.3 | Plant traits

To investigate traits potentially underlying variation in *V.tameamea* performance across the five species diets, leaf trait data were collected on unblemished leaves randomly sampled from 8 to 9 mature

individuals per species from up to two sites in the Ko'olau mountain range (Pali Lookout and Mānoa Cliff) over the course of 2 days in October 2016 (Table 2), following standard trait analysis protocols (Pérez-Harguindeguy et al., 2013). Before harvesting leaves in the field, chlorophyll content was measured using a chlorophyll meter (SPAD 502 Plus, Konica Minolta, Inc., Japan), and leaf thickness was measured using a 0.01 mm precision micrometer (Model 54–850/860, Fowler High Precision, Newton, Massachusetts), avoiding leaf veins. Leaves were then harvested and immediately stored on ice until returned to the laboratory, where digital photographs were taken to calculate leaf area using ImageJ (version 1.50i, Wayne Rasband, National Institutes of Health, USA). Leaves were then dried at 60°C to constant mass and weighed for calculation of leaf mass per area (LMA). Dried leaves were ground to analyze concentrations of carbon (C), nitrogen (N), phosphorus (P), and calcium (Ca) at the University of Hawai'i at Hilo Analytical Laboratory according to standard methods (Hue et al., 2000).

Total phenolics and the portion of phenolics that oxidize at pH 10 (as is found in caterpillar guts) were measured using spectrophotometry, following an established protocol (Kim et al., 2020; Salminen & Karonen, 2011). Full methods are available in Appendix S1. Briefly, dried leaves were ground and extracted with acetone/water, and the extracts were concentrated to water phase. The phenolics assays were done on a microplate reader (iMark, Bio-Rad Laboratories, Inc., Hercules, CA, USA). The oxidation was activated with sodium carbonate buffer. To determine the total phenolics before and after oxidation, the oxidized and untreated samples were incubated with 1N Folin-Ciocalteu reagent, and absorbance was measured at 730 nm and converted into gallic acid equivalents. The difference between the total phenolics and remaining total phenolics after oxidation corresponds to the concentration of phenolics that are oxidizable at pH 10.

2.4 | Data analysis

All analyses and figures were done in R 4.3.0 (R_Core_Team, 2023) using RStudio 2023.06.0+421 (Posit_team, 2023). Figures were produced using packages *ggplot2* and *ggbiplot* (Vu, 2011; Wickham, 2016).

Butterfly survival using a generalized linear model (GLM) with a binomial distribution (link = "logit") using the "glmer" function in the package *lme4* (Bates et al. 2015). Survival was based on $N=224$, because one caterpillar escaped during the study. There were six instances in which butterflies eclosed with severe deformities that prevented them from taking flight, which we treated as mortalities for the survival analysis and excluded from biomass analyses. Only the predictor main effects of diet and population were included in the survival analysis. Sex could not be included because we could not assign sex to caterpillars that died during development. Interactions were excluded when model assumptions were not met (i.e., convergence criteria).

The remaining bioassay performance metrics—adult mass, pupal mass, and total development time (hatching to eclosion)—were analyzed using model selection based on Akaike's information criterion (AIC) using the package *MuMIn* (Bartoń, 2023). For these analyses, data were used only for individuals that survived through eclosion

without deformities ($N=157$). Butterfly sex was determined post-eclosion based on sexually dimorphic wing color patterns (Figure S1). All response variables met linear model assumptions for normality of residuals and homogeneity of variance. Each performance metric was analyzed using an ANOVA, using the “lm” function in the package *stats* (R_Core_Team, 2023), that included fixed effects for diet (plant species), sex, and population (source site of butterflies). Population was treated as a fixed effect because the large biogeographical separation potentially resulted in genetic differentiation that could influence caterpillar performance in meaningful ways with respect to host plant species and to account for potential bottleneck effects from low numbers of founders per population. For significant diet effects, Tukey post hoc comparisons using the package *stats* were included to better understand pairwise differences in caterpillar performance on different host plant diets.

Due to the likelihood that plant traits covary, trait data were initially analyzed using multivariate analysis of variance (MANOVA) and PCA, using *dplyr* and *ggbiplot* packages, respectively (Vu, 2011; Wickham, 2016). To better understand variability among species for individual traits, the data were then analyzed using univariate mixed model ANOVAs using the “lme” function in *nlme* with plant species as a fixed effect and sample collection site as a random effect (Pinheiro et al., 2023; Pinheiro & Bates, 2000). To meet ANOVA assumptions, leaf C:N ratio, calcium, phosphorus, and total (initial) phenolics data were log-transformed. Data for the proportion of leaf phenolics that were oxidized were square-root transformed to meet ANOVA assumptions. Tukey post hoc comparisons were performed with the package *stats* to better understand pairwise comparisons in functional traits between plant species.

3 | RESULTS

3.1 | Survival

Vanessa tameamea survival was generally high (mean proportion = 0.70 ± 0.06 SE) but varied significantly among populations and by plant diets (Table 3, Figure 1). Among the native host plant species, butterfly survival was highest on *T. oahuensis* and lowest on

T. latifolia (Figure 1). First-instar larvae from the Saddle Road (Hawai'i Island) population did not accept the exotic *C. obtusifolia* as a food source and consequently, all caterpillars died, whereas both populations from O'ahu readily ate *C. obtusifolia* and had survival rates similar to those reared on native host plants (Figure 1).

3.2 | Butterfly performance

Butterfly performance, as assessed by pupal and adult mass, varied significantly among plant species diets, populations, and sex (Table 3, Figure 2). Diet significantly influenced both pupal and adult mass (Table 3), with consistent mass rankings among species (Figure 2). Pupal and adult mass were significantly lower for *V. tameamea* reared on the exotic *C. obtusifolia* and native *T. latifolia* compared to those reared on the native *B. grandis*, *P. albidus*, and *T. oahuensis*. As expected, pupal and adult mass differed significantly between sexes (Table 3, Figure S2), with females tending to be larger than males, although this depended to some degree on population (significant sex $\times$ population interactions, Figure S2). Population contributed significantly to pupal mass (Table 3), though these differences were small (Figure S3) and dissipated by the adult stage (Table 3).

Development time (days from hatching to eclosion) was also significantly affected by host plant diet (Table 3, Figure 2). The shortest time was on *P. albidus* leaves, suggesting that this species is the most nutritious or least well defended. In comparison, individuals reared on *B. grandis* reached eclosion significantly slower than those raised on other diets, taking more than 1 week longer to reach adulthood than those reared on *P. albidus*. Individuals reared on *T. latifolia*, *T. oahuensis*, and *C. obtusifolia* had intermediate developmental times (Figure 2). Although population also contributed to variability in development time (Table 3), differences were small (approximately 2 days) and unlikely to be biologically meaningful.

3.3 | Plant functional traits

As expected given their contributions to shared function, the eight plant functional traits assessed covaried significantly (MANOVA:

TABLE 3 Bioassay performance results, including survival ($N=224$), pupal and adult mass ($N=157$), and total development time (egg hatch through eclosion, $N=157$).

Predictor variable	Survival	Pupal mass (g)	Adult mass (g)	Development time (days)
Plant diet	$\chi^2 = 16.79^{**}$	$F_{4,147} = 16.054^{***}$	$F_{4,147} = 16.963^{***}$	$F_{4,149} = 77.573^{***}$
Population	$\chi^2 = 13.72^{**}$	$F_{2,147} = 5.758^{**}$	$F_{2,147} = 1.696$	$F_{2,149} = 15.618^{***}$
Sex	N/A	$F_{1,147} = 6.174^*$	$F_{1,147} = 8.979^{**}$	$F_{1,149} = 3.282$
Sex $\times$ population	N/A	$F_{2,147} = 6.068^{**}$	$F_{2,147} = 3.039^+$	N/A

Note: Performance metrics were analyzed with fixed effect ANOVA models that included three main effects: plant species diet, butterfly population, and sex. Sex $\times$ population interactions were included when significant, but interactions diet $\times$ population and diet $\times$ sex failed to converge and so were excluded from all models. Sex could not be determined in larval and pupal stages, and so was not included for analyses of survival. *F*-test (continuous response variables) or Wald chi-square joint test (binary response variable) statistics are reported, with significance shown as: *** $p < .0001$; ** $p < .01$; * $p < .05$; + $.06 < p < .05$.

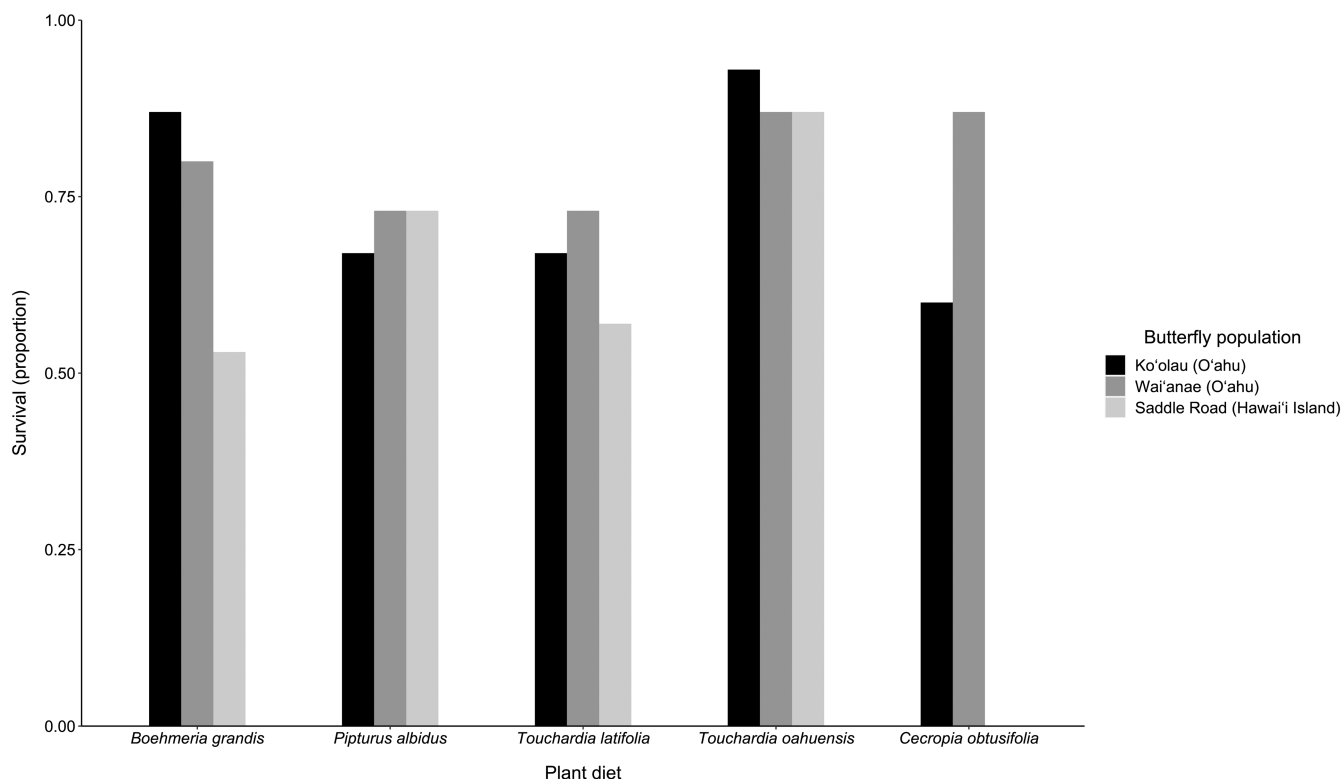


FIGURE 1 *Vanessa tameamea* survival reared on the five focal plant diets across two O'ahu populations (Ko'olau and Wai'anae) and one Hawai'i Island population (Saddle Road). Each bar represents % survival of $n = 15$ caterpillars, except for the Saddle Road population fed *Cecropia obtusifolia* ($n = 14$), none of which survived past the first instar.

Pillai's trace = 2.8338, $F_{(32,224)} = 17.009$, $p < .0001$). The three primary axes in principal component analysis together accounted for 74.2% of the trait variation (Table 4). The first axis (PC1) represents sclerophyll or leaf toughness, correlating with leaf thickness, LMA, and C:N ratio (Table 4). The second axis (PC2) represents a positive association between chlorophyll and total phenolics, which are negatively related to calcium content (PC2), and the third axis (PC3) represents covariance among LMA, chlorophyll, and % oxidized phenolics which are negatively correlated to phosphorus. Importantly, the four native species overlap considerably in multivariate trait space, while the exotic *C. obtusifolia* clearly separates from the native plant species (Figure 3).

The univariate analyses revealed that all traits varied significantly among plant species (Table 5, Figure 4). As indicators of nutritive quality, phosphorus content was highest in *T. oahuensis*, chlorophyll content was highest in *C. obtusifolia*, and C:N ratio was lowest in *T. oahuensis* (Figure 4), potentially indicating that *T. oahuensis* is the most nutritious diet for *V. tameamea* development. Indicators of sclerophyll that may reduce the palatability or digestibility of leaves include LMA, leaf thickness, and calcium (as a component of cystoliths), and these traits also vary significantly in complex patterns among plant species (Figure 4). Leaf thickness is greatest in *P. albidus* while LMA and calcium content are highest in *T. latifolia*, identifying these species as potentially more tough and less palatable for caterpillars. Finally, total phenolic content was far greater in *C. obtusifolia* and *B. grandis*, although these species had quite low proportion of

oxidized phenolics (Figure 4), and so the extent of chemical defense via phenolics remains unclear for these species.

4 | DISCUSSION

Native insect–plant interactions are less well studied than other types of herbivory on islands (Moreira et al., 2021), making these dynamics relatively unknown. Although dispersal to and colonization of islands is likely to be more common for insects than vertebrates (Whittaker & Fernandez-Palacios, 2007), island insect communities are highly disharmonic (Gillespie & Roderick, 2002; Hembry et al., 2013), making it difficult to predict the ecology of these interactions. For example, among the approximately 1000 species of Lepidoptera native to Hawai'i, only two are butterflies (Nishida, 2002; Rubinoff, 2017). The Kamehameha butterfly, *V. tameamea*, holds special cultural significance as the state insect, and recent and on-going declines in population sizes (Walker & Haines, 2022) call for urgent research characterizing the ecological conditions necessary to ensure its conservation. Using an approach that combined a no-choice bioassay with plant trait analysis, we detected significant variation among known and potential urticaceous host plants to support *V. tameamea* development.

Caterpillar performance varied among the five host plant diets, but the ranking of diet quality depended on performance metric. Survival was highest when caterpillars were reared on the native

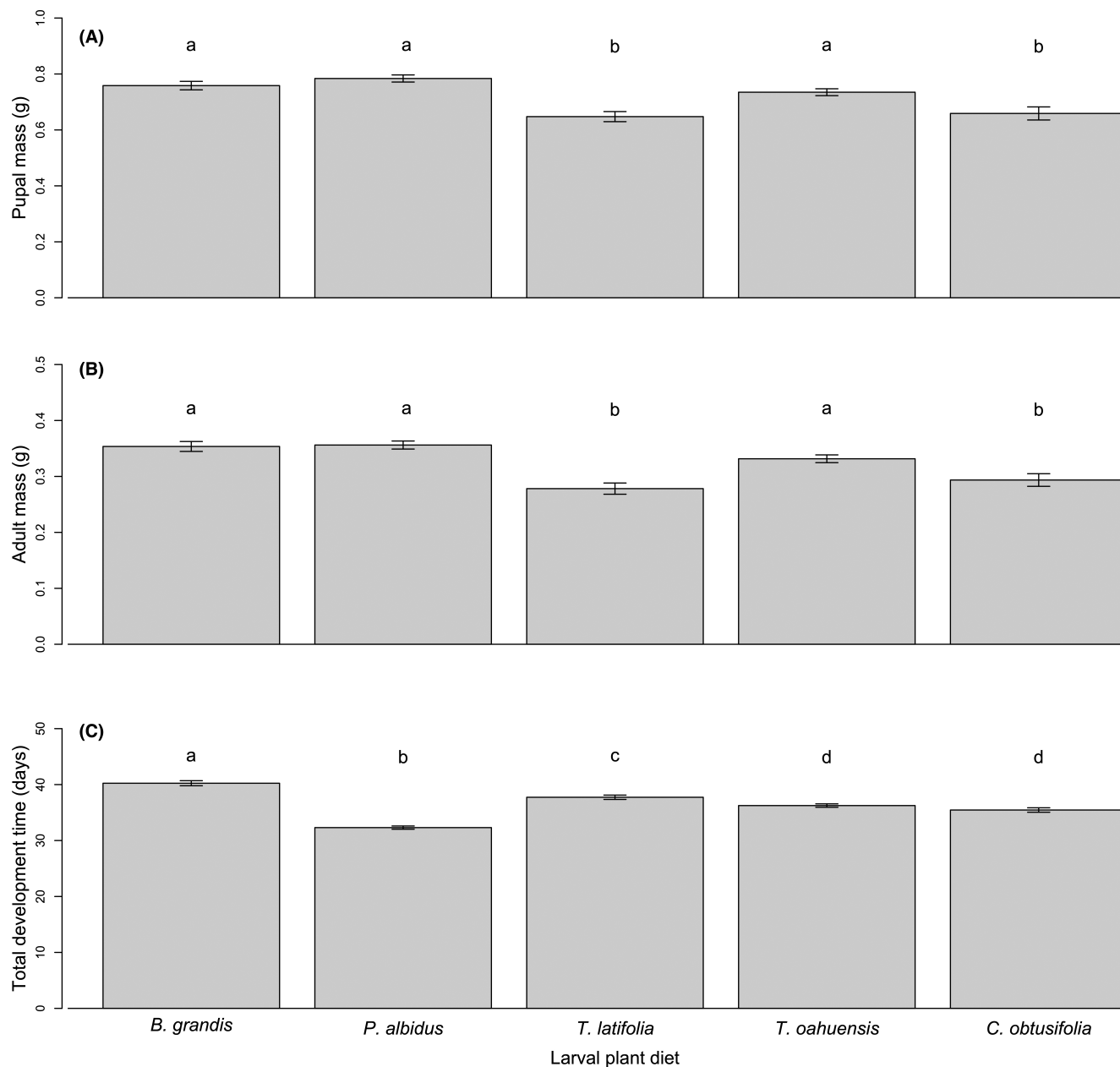


FIGURE 2 *Vanessa tameamea* performance when reared on the five focal plant diets, assessed as pupal mass (a), adult butterfly mass (b), and total development time (egg hatch to eclosion) (c). Bars are means ($\pm$ SE) for $n=22-40$, depending on survivorship. Tukey's HSD were used to infer significant ($p < .05$) pairwise differences, notated with different lower-case letters.

T. oahuensis, with survival on the other host plants also varying among *V. tameamea* populations. Notably, caterpillars from the Hawai'i Island population refused to feed on the exotic *C. obtusifolia* leaves, leading to complete mortality. Considering performance in terms of body mass, the native *T. latifolia* and exotic *C. obtusifolia* diets were the least favorable, leading to significantly smaller pupal and adult mass. The remaining three native host plant species appear to be equivalent for caterpillar development, leading to similar sizes of pupae and adults. Because larger butterflies tend to have greater fecundity (Honěk, 1993), this result suggests lower fitness for *V. tameamea* that develop on *T. latifolia* among the native host plants. Differential fecundity of *V. tameamea* among the host plant

diets could arise via variability in egg number or size (Awmack & Leather, 2002) and would require additional research extending into the offspring generation.

In contrast to the patterns for body size, performance assessed with respect to the rate of development produces a different conclusion. Caterpillars developed through eclosion significantly faster when reared on the native *P. albidus*, eclosing a full week later when reared on the native *B. grandis*, with intermediate rates detected among the other three plant diets. It has been predicted that longer larval periods increase predation risk (Benrey & Denno, 1997), though the relationship between development rate and predation has been difficult to detect given the complexity of

TABLE 4 Loading scores for plant traits included in PCA analysis of five focal host plant species.

Component	PC1	pc2	pc3
Total % of Variance	35.41	19.68	19.11
Trait loadings			
Leaf thickness	0.4655	-0.2114	-0.1949
LMA	0.2973	-0.2708	-0.5344
Chlorophyll	-0.1852	0.3268	-0.5953
C:N ratio	0.5136	0.0975	0.1705
Phosphorus	-0.4112	-0.1037	0.3180
Calcium	0.0927	-0.7219	0.1492
Total phenolics	0.3917	0.4692	0.1923
% Phenolics oxidized	-0.2564	-0.1164	-0.3642

plant-herbivore-predator interactions under natural conditions (Chen & Chen, 2018). In Hawai'i, predatory birds and arthropods are abundant in the forest ecosystems where *V.tameamea* occurs, though these predator communities have undergone dramatic shifts from native- to exotic-dominated composition in recent decades (Barton et al., 2021; Gruner, 2004, 2005). Despite the turn-over in species assemblages, it is likely that *V.tameamea* caterpillars have consistently experienced predation, emphasizing the importance of fast development time as an escape strategy.

Variability in performance on the different host plant species could play a role in *V.tameamea* population dynamics. Considering *V.tameamea* performance in terms of all performance metrics, the native species *P.albidus* and *T.oahuensis* emerge as the most favorable host plants, leading to high survival and producing among the heaviest adults in a significantly shorter time, thereby potentially supporting the most vigorous and stable populations. Although we cannot rule out the potential role of maternal effects from earlier generations being reared on *P.albidus* nor the potential effects of low population genetic variability within each population due to low founder numbers, this result resonates with field observations that larvae are most common on *P.albidus* (Gorelick & Wielgus, 1968; Tabashnik et al., 1992). *Pipturus albidus* was historically widespread and an abundant native urticaceous species (Wagner et al., 1999), but recent declines in *P.albidus* as well as the native *T.oahuensis*, the most suitable host plants as determined in our study, could be contributing to instability of *V.tameamea* population dynamics (Pauchard et al., 2009; Potter et al., 2023). Additional field research linking host plant abundance to *V.tameamea* oviposition behavior, caterpillar development, and eclosion rates is needed to clarify the role of host plant availability on the butterfly population dynamics.

Our bioassay results suggest that switching to the exotic *C.obtusifolia* as a host plant may be a feasible strategy for persistence for *V.tameamea* populations on O'ahu Island, supporting relatively high caterpillar performance in terms of survival and development rate. Novel host plant use is increasingly common among insect herbivores due to the global accumulation of exotic plants (Forister & Wilson, 2013), although there is a general tendency for herbivores

developing on exotic host plants to have lower fitness than when developing on their native host plants (Yoon & Read, 2016), a pattern corroborated by our results. Successful switching to a novel, exotic host plant depends on insect diet breadth, relatedness of the novel host plant to the herbivore's co-evolved host plants, and on the relative abundances and distributions of available host plants (Forister & Wilson, 2013). In addition to the performance data provided here, information about butterfly host-seeking behavior and oviposition preference are critical for understanding host plant use and the potential integration of novel species such as *C.obtusifolia* (Thompson & Pellmyr, 1991). To our knowledge, *V.tameamea* caterpillars have never been observed feeding on *C.obtusifolia* in the wild, suggesting that the plant may not possess oviposition cues for female butterflies despite being a suitable host for larvae on O'ahu. In some cases, oviposition onto unsuitable novel host plants can be considered "oviposition mistakes" when larvae fail to develop (Berenbaum, 1981; Davis & Cipollini, 2014). In our experiment, we observed 100% mortality of *V.tameamea* caterpillars from the Hawai'i Island population when reared on *C.obtusifolia*, suggesting that this interaction would represent an "oviposition mistake." Despite these maladaptive outcomes, insect herbivores may switch to novel, exotic host plants if availability drives the species interaction (Singer & Parmesan, 2019), and the genomics of host plant identification and use are providing new insights into these novel interactions (Simon et al., 2015). Distinct outcomes for interactions between *V.tameamea* caterpillars and the novel *C.obtusifolia* host plants between O'ahu and Hawai'i Island populations potentially indicate a mosaic of co-evolutionary dynamics, consistent with other species interactions that occur across heterogeneous and disjunct landscapes (Thompson, 1999).

To better understand why *V.tameamea* development varies among plant diets, we characterized a suite of nutritive and defensive leaf traits for the five urticaceous species used in the bioassay. As expected from global patterns of plant form and function, traits covaried significantly, likely due to shared function in ecophysiology and defense (Agrawal, 2020; Díaz et al., 2016). Inspection of the principal component analyses revealed some degree of species separation in multivariate trait space, especially for the exotic *C.obtusifolia*, which appears to be quite distinct from the native urticaceous species. Univariate analyses confirmed significant trait differences among species, revealing that *C.obtusifolia* differs particularly in leaf calcium concentration, with approximately 80% lower concentrations than the native urticaceous species. High leaf calcium concentration is an indicator of intracellular crystals that can reduce palatability and digestibility of plant tissues (Hanley et al., 2007; He et al., 2014; Mustafa et al., 2018), and calcium cystoliths are known to be common in urticaceous species (Friis, 1993). The high levels of calcium in the native urticaceous species could reflect selection pressure by *V.tameamea* or other native herbivores for defensive leaf crystals, which a specialist herbivore may nonetheless overcome, but it remains unclear why *C.obtusifolia*—with apparent lack of cystoliths—does not support higher larval performance. Patterns of leaf toughness and phenolics also fail to align with caterpillar

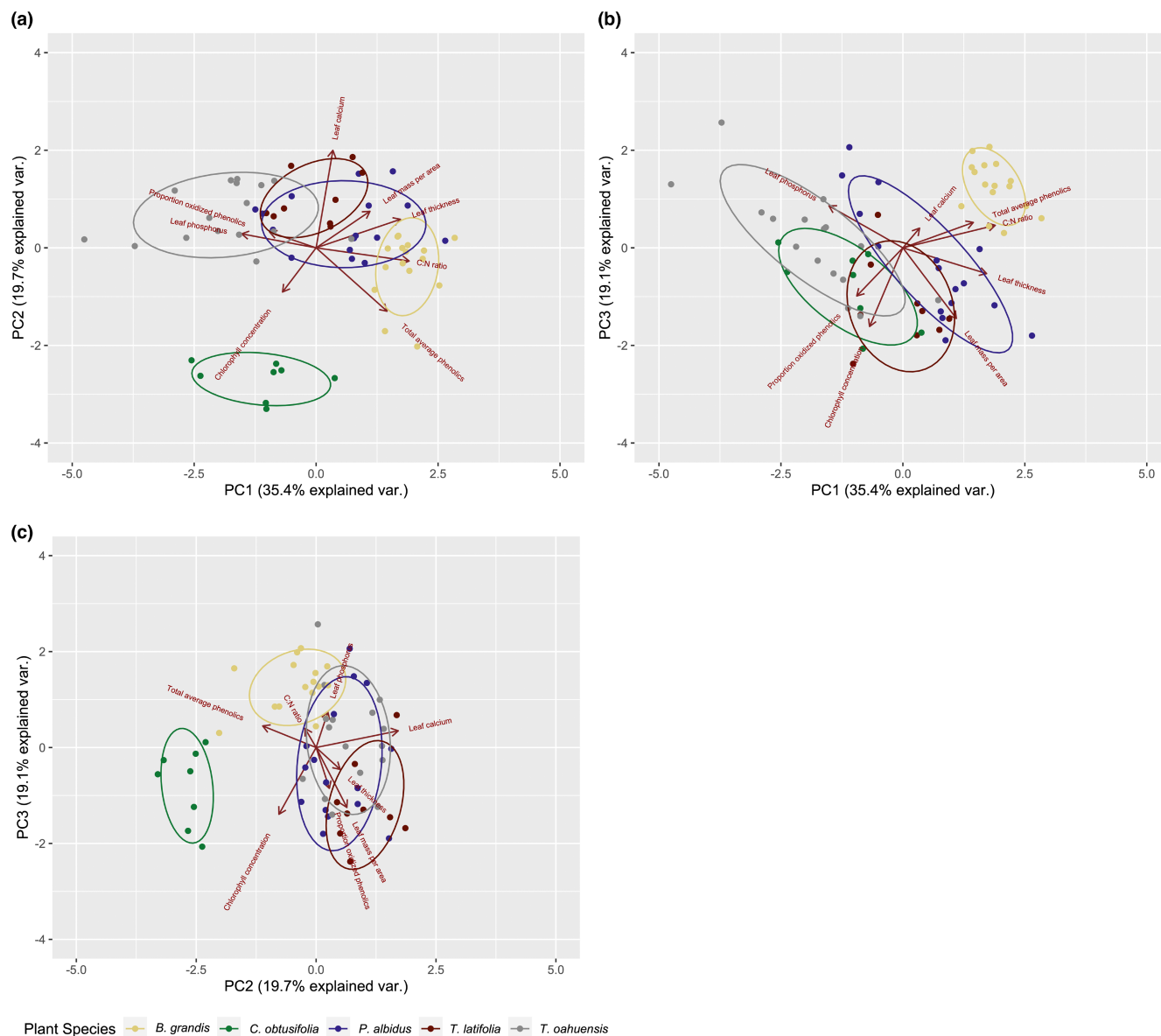


FIGURE 3 Principal component analysis (PCA) to investigate trait-based variation among the five focal plant species used in *Vanessa tameamea* bioassay. Trait abbreviations and units are reported in Table 2, and PCA variance components and trait loadings are reported in Table 4.

performance rankings on host plant species, suggesting a minor or negligible role in defense.

Because larval development may depend even more on nutritional quality than defenses of host plants (Awmack & Leather, 2002; Coley et al., 2006), we also measured leaf phosphorus, carbon, and nitrogen (C:N ratio) content. Better performance of *V. tameamea* on the native *T. oahuensis* may be linked to the plant's significantly higher leaf P and lower LMA. In contrast, no major patterns arise within the quantified leaf metrics as to why *V. tameamea* performed so well on the native *P. albidus*, suggesting other variables matter more for *V. tameamea* development than the traits measured here. Although we did not measure how quickly the caterpillars form protective shelters when given new leaves, relatively low performance on the native *T. latifolia* could be due to the very dense, coriaceous

TABLE 5 Leaf functional traits vary significantly among plant species, as indicated by *F*-tests.

Leaf trait	Species effect
Leaf thickness (LT)	$F_{4,59} = 35.06127^{***}$
Leaf mass per area (LMA)	$F_{4,59} = 4.3531^{**}$
Chlorophyll (SPAD)	$F_{4,59} = 24.3578^{***}$
Leaf carbon: nitrogen ratio (leaf C:N)	$F_{4,59} = 21.883^{***}$
Leaf phosphorus content (leaf P)	$F_{4,59} = 6.27106^{***}$
Leaf calcium content (leaf Ca)	$F_{4,59} = 68.1702^{***}$
Total phenolics	$F_{4,59} = 71.8480^{***}$
Proportion of oxidized phenolics	$F_{4,59} = 14.7733^{***}$

Note: Significance is shown as: $^{***}p < .0001$; $^{**}p < .01$; $^{*}p < .05$; $^{+}0.06 < p < .05$.

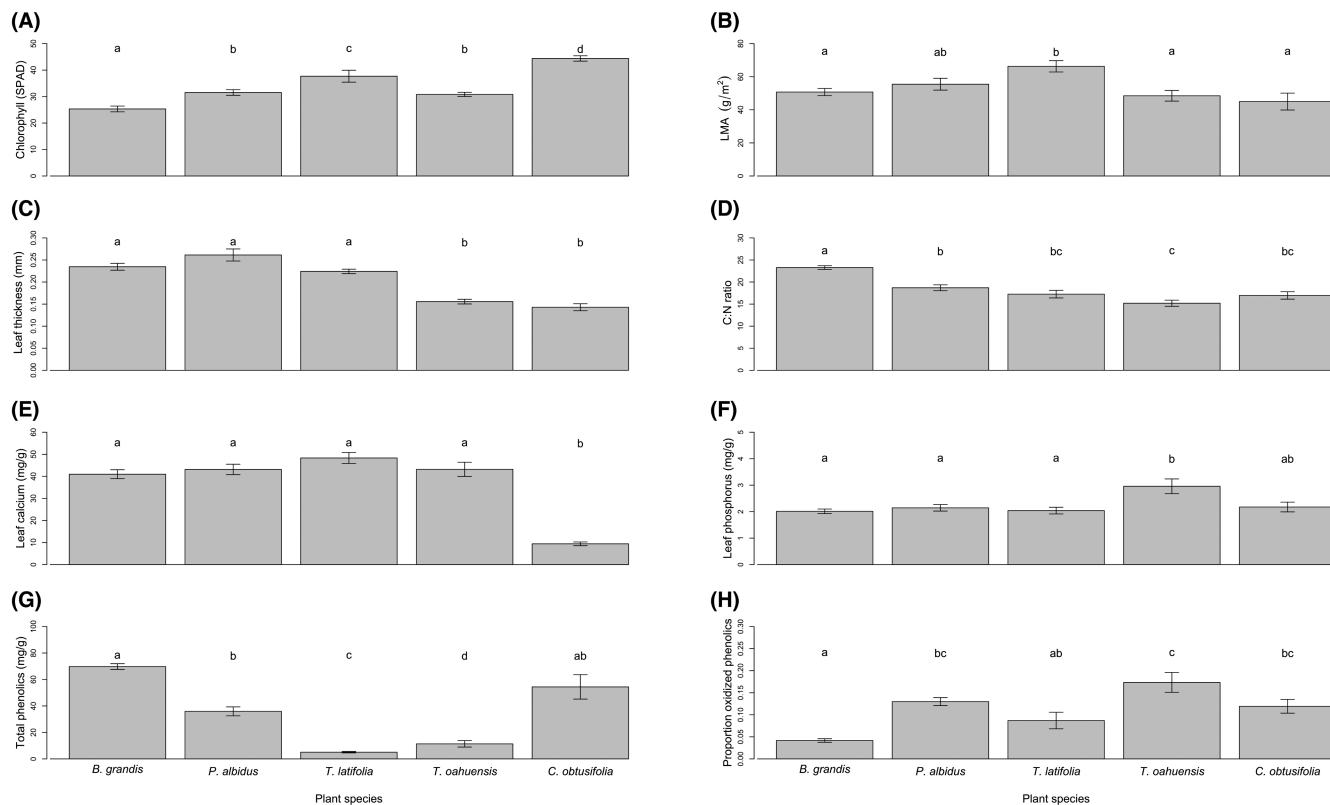


FIGURE 4 Plant functional trait variation among the five focal plant species. Bars are means ($\pm$ SE) for $n=8-16$, depending on number of individual wild plants sampled. Trait abbreviations and units are reported in Table 1. Tukey's HSD are used to infer significant ($p < .05$) pairwise differences, notated with different lower-case letters.

nature of its leaves (higher leaf LMA) compared to other plant diets used in the study if higher leaf LMA impedes development of the caterpillar due to the amount of time and energy it would take the caterpillar to form its protective leaf-fold shelter. Additional analyses that consider nutrient availability, not just content, and other secondary compounds may provide more insights into the factors driving variability in host plant quality. Quantifying tissue consumed may also be informative as compensatory feeding may contribute to high performance on host plant diets characterized by low nutritive content. Trials on intact plants under field conditions may be particularly informative, as laboratory bioassays with clipped plants may alter leaf traits or influence consumption rates in ways that obscure the major drivers of herbivore performance (Friberg & Wiklund, 2016). Field trials would also more definitively characterize trait-performance links through simultaneous measurements, an approach that we were unable to use because plant trait analyses were conducted 1 year after the bioassay due to logistical constraints.

This study provides the first detailed investigation into the native urticaceous host plants of Hawai'i's state insect, the Kamehameha butterfly. Using controlled conditions and carefully monitored development, we documented host plant suitability throughout the larval stages, pupation, and adult butterfly eclosion, providing a robust assessment of host plant quality throughout the butterfly life cycle. Importantly, the rankings of host plant suitability differed among life cycle stages, illustrating the value of characterizing the

entire life cycle. Specifically, larval/pupal survival was highest on *T. oahuensis*, growth in mass was equally high on *T. oahuensis*, *B. grandis*, and *P. albidus*, and rate of development was fastest on *P. albidus*. Despite measuring eight plant traits known to influence herbivore performance via defensive and nutritive activities, the plant traits driving variability in host plant quality remain unclear, identifying this as a key area for future research. Variability in host plant quality for *V. tameamea* is likely to contribute to population instability, although additional field research on natural populations is needed to confirm these dynamics. Conservation of *V. tameamea* may benefit from efforts to ensure the availability of the most favorable host plants, *P. albidus* and *T. oahuensis*, with potential insurance provided by non-native species such as *C. obtusifolia* that appear sufficient for successful eclosion of butterflies in at least part of their distribution.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to disclose.

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.866t1g1xb> (Barton & Bogner, 2024).

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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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