State of the State Tree: Historical and Modern Ecology of Kukui (Candlenut, *Aleurites moluccanus*) in Hawai'i

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State of the State Tree: Historical and Modern Ecology of Kukui (Candlenut, *Aleurites moluccanus*) in Hawai'i[1]

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Abstract: Kukui was an important element to indigenous Hawaiian agroforestry and retained some of its importance throughout Hawai'i's history. We examine the historical ecology and trends of kukui, including a review of the ethnobotany. We use current and historical remote imagery to map kukui canopy on the five largest Hawaiian Islands. Kukui is still widespread through the state, being a significant component in many novel low-land forests. However, kukui is declining, having lost an average of ~58% of total canopy cover over the last 70 years. Spatial trends suggest that kukui likely did not spread much following the large-scale shifts in Hawaiian socio-ecosystems that accompanied the arrival of colonial powers. We suggest that the footprint of kukui in Hawai'i closely approximates the extent of indigenous agroforestry and forest alteration.

Keywords: agroecology, agroforestry, *Aleurites*, candlenut, ecology, Hawai'i, kukui, *moluccanus*

Hawai'i is among the most ecological diverse places in the world, containing over two thirds of the Holdridge life zones (Asner et al. 2005) organized across ~16,600 km^2. The native ecology of the islands was leveraged for a range of agroecological strategies by Native Hawaiian cultivators (Lincoln and Vitousek 2017, Lincoln et al. 2018), which altered the ecological landscape in both intentional (e.g., cultivation) and unintentional (e.g., impact of introduced plants and animals) ways. The initial settlement of Hawai'i likely occurred in the 10th century (Kirch 2011, 2014, Athens et al. 2014) and the trajectory of Hawaiian crops and cropping systems therefore occurred for upwards of a millennium prior to European contact.

Our Polynesian ancestors introduced only a handful of plants to the Hawaiian Islands (Whistler 2009), most of which originated in southeastern Asia or nearby islands such as Borneo and Papua New Guinea. Hawai'i is among the last places settled in the vast Pacific Ocean and is one of the most isolated group of islands in the world; only the hardiest and most valuable crops made it to the end of the two-millennia process of island settlement by the Polynesian wayfinders. Among the crops that accompanied the Hawaiians-to-be was kukui (candlenut; *Aleurites moluccanus*). Kukui is a hardy, fast growing, and highly useful tree that would have been quickly spread wherever settlement occurred. In addition to being a core crop, kukui was an essential part of arboricultural and other agricultural systems (Handy and Handy 1972, Lincoln and Ladefoged 2014, Lincoln 2020*a*). As with other locations in the Pacific, it is thought that the conversion of native to novel forest ecosystems was an accumulated process that paralleled shifts in the sociopolitical state of

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the society (Dye and Sholin 2013, Quintus et al. 2019, Huebert and Allen 2020). In Hawai‘i, several forms of arboriculture manifested, including vast kukui-dominated forests that are described in several locations (Handy and Handy 1972, Lincoln 2020*a*). For instance, it is believed that a single kukui-dominated forest blanketed ~20,000 ha on the eastern slopes of Mauna Kea volcano (Lincoln 2020*a*). The consideration of such large-scale forest alteration by Native Hawaiians would greatly increase the presumed prehistoric human footprint on the islands (Ladefoged et al. 2009, Gon et al. 2018).

The shift in thinking and management that accompanied the arrival of, and eventual seizure of power by, colonial powers resulted in the erasure or abandonment of many Hawaiian agroecosystems and the diminishment of the associated crops (Chirico and Farley 2015, Kagawa-Viviani et al. 2018). Multiple forces such as those seen in other indigenous regions—including the depopulation of Native Hawaiians due to diseases, the overthrow of the Hawaiian Kingdom and the usurping of lands, and the dominant control of water and land tenure by foreign businesses—caused a massive shift in the tenure and management of Hawaiian ecosystems. However, in many cases the agricultural plants and animals were naturalized into the ecosystems and still persist today, playing various social and ecological roles.

Although the prominence of kukui diminished in the historical era, recognition of its importance remained. After the coming of the foreigners, kukui nut oil was shipped abroad in the mid-1800s, with as much as 10,000 gallons exported per year, representing about 10–15 ha of harvest out of an estimated 4,000–16,000 ha of kukui forests at the time (Wilcox and Thompson 1913). When Hawai‘i became a state in 1959 it was kukui that was proclaimed the state tree (HRS §5-8), taking the title from the coconut palm (*Cocos nucifera*) that had been proclaimed the official tree of the Territory of Hawai‘i in 1930. The preamble of the declaration states that "the multiplicity of its uses to the ancient Hawaiians for light, fuel, medicine, dye and ornament and its continued value to the people of modern Hawai‘i, as well as the distinctive beauty of its light green foliage which embellishes many of the slopes of our beloved mountains, causes the kukui tree to be especially treasured by the people of the Fiftieth State of the United States as an arboreal symbol of Hawai‘i."

Despite the acknowledgment of its importance, kukui remains vastly understudied in its historical and contemporary socioecological roles. In this article, we first provide a review of the ethnobotany and historical ecology of kukui in Hawai‘i, followed by an assessment of its ecological extent and trajectory using historical and contemporary imagery. We ask basic, but essential, ecological questions such as: how widespread was kukui in Hawaiian agroecosystems? and under the current socioecological regime is kukui expanding or contracting in its range? Answering such questions may illuminate aspects of traditional forest alteration and management of Native Hawaiian society, representing place-adapted socioecological knowledge developed over centuries of landscape interactions. Considerations of past and current distributions of kukui can help to inform management tradeoffs, such as those encompassed in biocultural (e.g., Kurashima et al. 2017, Chang et al. 2019) and ecosystem services (e.g., Mascaro et al. 2012), and what the future of Hawai‘i's state tree might be.

MATERIALS AND METHODS

Review of Kukui in Ancient Hawai‘i

English and Hawaiian language sources were used to generate a broad body of Hawaiian ethnobotanical knowledge regarding kukui usage and cultivation. In particular, Hawaiian language sources synthesized by the late Dr. Mary Kawena Pukui and published through the Bishop Museum were critical resources. Unfortunately, despite its detailed documentation and discussion, kukui appears sparsely in the historical literature, with only minimal treatment by Dr. Craighill Handy (Handy 1940, Handy and Handy 1972), David Malo (Malo 1903), Dr. Marion Kelly (Kelly 1983), and others. Previous reviews and research on

Hawaiian arboricultural adaptation (Lincoln and Ladefoged 2014, Lincoln and Vitousek 2017, Lincoln et al. 2018, Quintus et al. 2019, Lincoln 2020*a*) summarized resources on the extent and application of these systems in Hawai'i and also contributed to the foundation of the ethnohistorical review.

Remote Analysis of Kukui

Two methods were used for the remote sensing of kukui through high resolution satellite imagery. Using orthorectified World View 3 data we manually mapped candlenut trees in 1,750:1 zoom frames in ArcMap 10.1 (ESRI, Redlands, CA) in five regions of Hawai'i Island, creating a point feature for every candlenut canopy radius identified. Candlenut has a very distinct, silvery appearance on the landscape due to short downy hairs on the leaves that make it easy to identify. Verification of 1258 trees was conducted using (1) Google Street View for trees that were within the viewplane of paved roads ($n = 758$) or (2) ground verification ($n = 500$), with no false positives identified. Following manual mapping in select areas, we used a semi-automatic approach to map kukui across the five largest Hawaiian Islands from high spatial resolution satellite Worldview-2 imagery. The Worldview-2 imagery has eight spectral bands in the visual and infrared spectrum with 2 m spatial resolution. The images were collected in 2013 for Kauai, 2014 for Maui, 2016 for Moloka'i, 2016–2017 for Hawai'i Island, and 2017 for O'ahu. The approach started with a supervised classification followed by manual correction of the classification errors. For the supervised classification, we chose three vegetation classes—kukui, other forests, and pasture/grassland—and collected the corresponding training data. For the mapping of a single tree species such as kukui, it is often challenging to simultaneously minimize both (1) false positives (i.e., commission errors) and (2) missing true positives (i.e., omission errors). However, from the perspective of manual cleaning of classification errors, it is easier to remove false positives than add true positives. We therefore intentionally chose the other two broadly-defined non-kukui vegetation classes so that the automatic classification is overwhelmed by commission errors instead of omission errors. We used the classical maximum likelihood classifier (MLC) method in the ENVI (Harris Geospatial Solutions, Inc., Melbourne, FL) remote sensing software. After applying the MLC, we manually edited the map and corrected the classification errors in the ArcGIS software.

Spatial points were used to extract values from environmental and political layers for analyses. Spatial environmental layers were acquired from the Hawaii Rainfall Atlas (Giambelluca et al. 2013), the Hawaii Evapotranspiration Atlas (Giambelluca et al. 2014), and the Hawai'i State GIS Database (http://geoportal.hawaii.gov/). Attribute tables were exported and analyses were done in JMP Pro 14 (SAS Institute, Cary, NC).

Habitat Suitability Mapping

Using extracted environmental parameters from the mapping exercise above, a habitat suitability model was constructed using a fuzzy-set methodology adapted from Ramirez-Villegas et al. (2013), which uses linear interpolation to derive a suitability score of 0–100 on a per pixel basis for each environmental parameter considered using maximum and optimal habitat ranges; multiple parameters are combined using the minimum value of the sets that each cell location belongs to—a conservative approach based on the law of the minimum, in which crop yield is proportional to the most limiting condition to growth (Paris 1992, Bowen and Hollinger 2002). The model was constructed in R Studio using the same approach, parameters, and code as in Mausio et al. (2020). For the model parameters, the absolute value ranges for each environmental parameter was defined as the 99.9% quantiles associated with the mapped kukui; the optimal value ranges were considered to be the parameter values at the 90% quantiles.

Historical Imagery Assessment

We identified 20 areas for historical imagery analyses by manually outlining the distribution of remotely sensed kukui across the five islands and generating random point locations in ArcMap. For each site, historical aerial images were acquired in the ranges of 1950–1952, 1964–1966, and 1976–1979. Original images were sourced from the United States Geological Survey and the National Oceanic and Atmospheric Administration, and images were digitized at 600 dpi by the University of Hawai‘i at Mānoa Map Library. After images were acquired, three sites were deemed unusable due to either high cloud cover or low resolution. The remaining images were georeferenced in ArcMap 10.1 using a minimum of 25 control points of stable landscape features. Within the overlapping areas of the images, a 500-hectare polygon was generated representing a cloud free area and populated with 2,000 randomly generated points. For all images, the number of points that fell on a kukui were counted and recorded as a sampling proxy for total kukui canopy cover.

Data Integration

The various time periods explored in this article have different metrics, resolution, and accuracy. The ethnobotany allows us to make some informed estimations of the ancient demand for kukui oil, which can be converted into rough estimates of minimum acreage needed. For the historical era we pull on written estimations and anecdotal evidence from the earliest photos in Hawai‘i, and use extrapolations from the trends observed in the recent history to estimate cover in the past. Our quantitative analysis of imagery fills in the last 70 years into the present. We then discuss our interpretation of the patterns, informed by the general patterns of land-use history and the ecological behavior of kukui.

RESULTS

Ethnobotanical Uses of Kukui

Kukui was a critical tree in the Hawaiian agricultural economy prior to European contact (Abbott 1992, Lincoln 2009), as it was throughout many Pacific island groups. Although kukui was not a significant food source, a relish known as *‘inamona* was frequent in enlivening the Hawaiian diet. Kernels of the candlenuts were roasted and salted to yield a delicious condiment that tastes like toasted macadamia nuts (Abbott 1992). The nuts are a source of feed for both wild and domesticated pigs in ancient Hawai‘i, and extensive groves of kukui are associated with the feeding of *Kamapua‘a*, the mischievous hog god (Handy and Handy 1972).

The principle use of candlenut by kānaka ‘ōiwi (Native Hawaiians) was as a fuel source, with the oily nuts being burnt directly or used to extract the liquid oil. So universal was the application that the Hawaiian language words for lamp/light (*lama*) and candlenut (*kukui*) are occasionally used interchangeably. The simplest form of lamp, *kālī kukui*, consisted of candlenut kernels skewered on dry coconut leaflet midribs. Longer reeds were bound together and wrapped in ti (*Cordyline fruticosa*) leaves to prevent the kernels from burning too fast (Fornander 1920). Another disposable form was the *lama ‘ohe*, in which lengths of bamboo were filled with kukui kernels and burned, producing stronger light for a longer time but also a large amount of smoke and soot. More sophisticated were *pōho kukui*—stones hollowed to hold a reservoir of kukui oil; a wick made from cloth or cord could be used to create a bright burning candle. Similarly, cloth soaked in oil and tightly bound to poles created larger torches.

The oil was commonly applied to the skin in medicinal ointments or as a moisturizer and protection against the sun. The oil was used on material goods to aid in waterproofing, preservation, and aesthetics. *Kapa*, the common bark cloth of old, was often oiled with kukui oil to increase longevity and make the fabric softer and less abrasive against the skin. The oil reacts well with woods and provides a beautiful finish and sheen. For instance, the *‘ahakea* (*Bobea* spp.) wood is dull orange-brown but becomes dark gold when rubbed with kukui oil (Abbott 1992). Traditionally, kukui oil was the final finish on all parts of the canoe with frequent applications after “each use of the canoe” in order to maintain the waterproofing (Abbott 1992, p. 81).

The candlenut tree produces a range of dye colors but, more importantly, is rich in tannins that serve as a mordant to adhere color to materials. The Polynesian standard of brown is not common in Hawai'i but when used is made from the bark of the kukui tree while beige is derived from the immature fruits. The inner bark of the roots provides a red color used to dye fishnets to make them less visible to fish and to increase their longevity. However, the most common application of kukui was for black ink. Canoes, for instance, use a black paint known as *pā'ele* for decoration and preservation, which was made from a kukui charcoal base mixed with the juice from the inner bark of kukui roots, resulting in a paint resistant to abrasion and water (Abbott 1992). Similarly, highly permanent stamping of traditional cloth with a thick ink made from the coal of kukui nut shell and the oil was common. A similar application of this ink, sometimes made from charred kukui shell and sugarcane juice (Lincoln 2020*b*) is used for tattoos.

Kukui was a vital part of the medicinal cornucopia. The oil and sap of kukui can be a strong laxative, and in higher quantities serves as a total purge that is standard in the treatment process of many ailments. The sap is applied to heal mosquito bites, canker sores, and other small topical ailments as both a treatment and a sealant. For more massive sores and ulcers, a salve including the mashed roasted kukui nuts as the base is used. The leaves may be used to wrap areas of swelling, bruising, and minor sprains. For this application, bruised leaves can be placed against the skin, followed by wrapping with fresh leaves to seal the area. The oil is used to prevent scarring and stretch marks. Other applications include using the charcoal from the shell for sore throats (Abbott 1992), internal application to treat ear, nose, and throat disorders (Young et al. 2005), as well as more complicated recipes (Chun 1994).

As a physical resource, the lightweight wood is useful for small canoes or the 'ama (outrigger) of larger canoes, fishing floats, house timber, and other applications (Malo 1903). The hard nuts were commonly used to make children's toys such as whistles and spinning tops. The leaves, the delicate white flowers, and the polished nut shells are all used in lei making.

Some unique applications of kukui relate to fishing. One can apply the oil to the ocean surface to create a sheen and see into the shallow reefs better. Mashed candlenut and coconut may also be used to create a chum; dipping fishhooks and spearheads into the mixture help attract fish. Large amounts of the nuts and coconut fermented with seafood waste such as shrimp peels create an odorous oil that when added to a vegetarian chum serves to attract fish.

Kukui is the most commonly referenced mulch material in Hawaiian agriculture, followed by hau (*Hibiscus tiliaceus*), 'ama'u fern (*Sadleria* spp.), and sugarcane (Handy and Handy 1972, Winter et al. 2018). Kukui mulch was stamped into the mud of flooded terraces and used to fertilize rainfed gardens (Handy and Handy 1972). Taro grown with kukui mulch is often described as being the largest and most delicious, and the use of candlenut for soil development is documented in many areas across the state at different scales (Handy and Handy 1972, Lincoln 2020*a*).

Ancient Extent of Kukui in Hawai'i

The many uses of kukui in ancient Hawai'i suggests that, like many other Pacific Islands (Larrue et al. 2010), kukui would have been widespread. Sparse trees around homesteads and within a range of agricultural systems were likely common. Unfortunately, the tree does not receive much treatment in the consideration of Hawaiian agriculture. Handy (1940) provides only the following statement as to its cultivation:

> The kukui candlenut tree, which grows in dense groves in all wet gulches and valleys and in ancient groves on Molokai, Kauai, and Hawaii, was introduced into these islands by the ancestors of the Hawaiians. In Molokai, the famous grove is Lanikaula. Kau-hakake is the kukui grove in Moloaa on Kauai where grand old trees are still standing, survivors of a once great forest. In

> Kona, Hawaii, two famous groves are still remembered, named Ko-au-kukui-ula and Kukui-ala-inamona. Hamakua, Hawaii, once had a vast forest of kukui. (p. 195)

The extensive kukui forests are slightly expanded in the seminal work of Handy and Handy (1972):

> The broad slopes of the wet windward coast Hāmākua of Hawaiʻi between the abrupt eroded shore and the high forest . . . were, before the era early sugar plantations, completely covered by kukui forest. [] This is the area which in Hawaiian lore was known as the domain of Kamapuaʻa, in contra-distinction to the drier and lava-strewn areas . . . which was Peleʻs [volcano goddess] country. When the rain drenched forests covered these slopes of Hāmākua, undoubtedly great numbers of wild hogs roamed these forests, feeding on the kukui nut. In a kukui forest there were open glades called *pa kukui* in which taro was grown. (p. 231)

Recently, an analysis of remnant kukui trees on the eastern slopes of Mauna Kea on Hawaiʻi Island suggests that the kukui forests were extensive in the Hāmākua district, covering some 20,000 ha and extending up to approximately 700 m above sea level (Lincoln 2020*a*). While the cultivation of taro as the core staple of the Hawaiian people (Kagawa-Viviani et al. 2018, Winter et al. 2018) was the focus of the shifting cultivation system within the candlenut forests, the novel forests likely provided a substantial source of oil, timber, and pigs. Such management of entire ecosystem types for multiple physical and cultural services is a hallmark of Hawaiian land management (Winter et al. 2020).

In addition to such kukui forests, kukui was a part of many arboricultural systems. Agroforestry was particularly prevalent in areas that were too steep, too rocky, too infertile, or too salty for more intensive production systems, and was therefore common in colluvial areas, areas with very young soils, areas along the coast, and areas with excessive rainfall (Lincoln and Vitousek 2017). Valley walls provide an example of places that were often too steep to support intensive rainfed agriculture. If fertile, colluvial soils were sometimes worked to form rudimentary terraces, but often were established with semi-wild tree and shrub plantings that would provide necessary resources, seasonal products, and unmanaged reserves against disasters that might cause the loss of intensive systems nearby (Kirch 1977, Kurashima and Kirch 2011). The planting of breadfruit, in particular, is evidenced by dozens of historical and prehistorical references (e.g., Meilleur et al. 2004). These valley plantings accounted for the bulk of agricultural production in some areas and was a pivotal component to agriculture throughout the islands (Allen 2004, Kurashima and Kirch 2011). In the famous breadfruit grove of Kona, Hawaiʻi Island, testimonies indicated that kukui was interspersed (Lincoln and Ladefoged 2014) and in the Hilo district, Hawaiʻi Island, kukui appears to be an interspersed part of diversified arboricultural systems as well (Lincoln 2020*a*).

Very young, rocky areas with minimal soil were also largely converted to forms of arboriculture. Regions such as Kona and Puna, with landscapes dominated by very young (<10 ky) lava flows, are famous for their breadfruit, coconut, and pandanus groves (Meilleur et al. 2004, Lincoln and Ladefoged 2014). On these barren landscapes, enclosures, or *pā*, were composted with local organic waste and mixed with the small amounts of soils that could be excavated nearby to aid in appropriately rotting composts (Kalokuokamaile 1922, translated by M. K. Pukui). The beds would be prepared several months before the rainy season so that when the rains came the new soil would be at an optimal level of development. While a handful of these cultivation pits would commonly be located near households to compost local waste, within the novel or native forests "many times forty" of these pits would comprise of an agricultural field (Kalokuokamaile 1932, p. 2). When conducted with kukui, these *pā* enclosures were appropriately referred to as *pākukui*.

Current Distribution and Ecology of Kukui in Hawai'i

Contemporarily, Kukui was found in 28 of the 31 districts examined, with approximately 41.7 km^2 of kukui canopy distributed unevenly across the five islands surveyed (Figure 1). In total, kukui represented 0.26% of the total land area examined, but ranged up to 2.6% of the land area within the district of Ko'olau, Moloka'i (Table 1).

Across all islands, the distribution of environmental parameters represented by kukui trees was generated (Table 2). Most parameters were normal in their distribution (skewness −0.4 to 0.4), exceptions being soil pH and CEC that exhibited skewness values near 1. Overall, the maximum range of kukui observed in this study was generally greater than suggested by published environmental limitations to the growth (e.g., FAO 2007), however values defined by the 99.9%

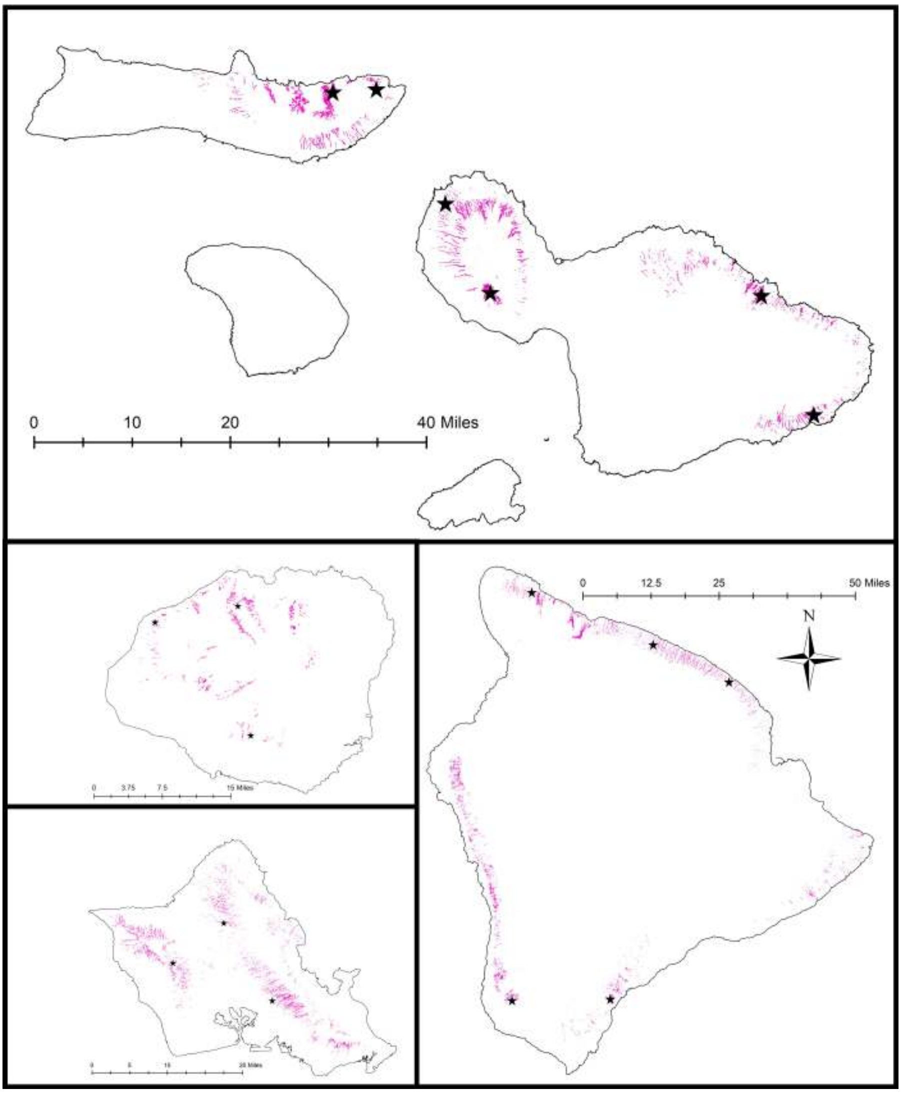

FIGURE 1. The remotely sensed extent of kukui crown canopy in Hawai'i. Polygons are outlined to enhance visibility making the total area look inflated. Stars represent the locations of the historical imagery analysis.

TABLE 1

Total Basal Area and the Percent Land Cover of Remotely Mapped Kukui on the Five Largest Hawaiian Islands

District	Island	Kukui Basal Area (m^2)	% Total Area
All	All	41,695,766	0.26
All	Hawai‘i	14,432,995	0.14
	Kauai	4,974,563	0.35
	Maui	8,785,213	0.47
	Moloka‘i	4,215,122	0.62
	Oahu	9,287,873	0.61
Hamakua	Hawai‘i	4,387,764	0.26
Hilo	Hawai‘i	924,774	0.05
Kau	Hawai‘i	2,185,752	0.08
Kohala	Hawai‘i	1,387,305	0.13
Kona	Hawai‘i	4,432,081	0.22
Puna	Hawai‘i	1,115,318	0.09
Halelea	Kauai	2,662,421	1.11
Kona	Kauai	1,689,006	0.24
Ko‘olau	Kauai	288	0.00
Napali	Kauai	467,456	1.16
Puna	Kauai	155,391	0.04
Hamakualoa	Maui	794,161	0.55
Hamakuapoko	Maui	147,709	0.20
Hāna	Maui	392,915	0.35
Honuaula	Maui	0	–
Kaanapali	Maui	2,116,686	1.39
Kahikinui	Maui	0	–
Kaupo	Maui	747,169	0.58
Kīpahulu	Maui	601,875	1.17
Ko‘olau	Maui	2,009,987	1.10
Kula	Maui	0	–
Lahaina	Maui	1,406,328	0.93
Peali Komohana	Maui	568,383	0.26
Kona	Moloka‘i	1,010,983	0.18
Ko‘olau	Moloka‘i	3,204,139	2.60
Ewa	Oahu	2,990,154	0.69
Kona	Oahu	1,701,451	0.97
Koolauloa	Oahu	715,295	0.36
Koolaupoko	Oahu	365,611	0.18
Waialua	Oahu	2,015,314	0.68
Waianae	Oahu	1,500,049	0.68

quantiles aligned well with published extents. Habitat suitability maps for kukui provide a quantified estimate of kukui habitat extent and quality across the archipelago (Figure 2).

Historical Trajectory of Kukui

Historical imagery was of sufficient quality for clear identification of kukui at 17 sites

TABLE 2

Summary Statistics for Select Environmental Parameters for All Kukui Tree Locations Mapped on the Five Largest Hawaiian Islands ($n = 465{,}212$)

	Mean	StDev	Minimum	Maximum	99.9% Quantiles		90% Quantiles	
Elevation (m)	316	168	0	1290	4	847	95	547
Air temperature (°C)	21.1	1.06	13.0	23.7	18.1	23.4	19.7	22.5
Rainfall (mm/yr)	2335	989	365	6030	677	5445	1075	3616
Water balance (mm/yr)[a]	−442	1153	−5440	4395	−3904	3142	−1764	1149
CEC (cmol/kg)	43	12	17	106	22	96	31	63
pH	5.5	0.9	4.0	7.8	4.0	7.6	4.6	7.0
Drainage class[b]	51	0.5	1	7	2	7	4	6

[a] Average annual rainfall minus average annual Penman-Monteith potential evaporation.
[b] NRCS ranging from 0 (excessively drained) to 7 (extremely poorly drained).

(Figure 3). Of the 17 sites, 16 indicated consistent loss of kukui canopy cover, with losses ranging from −24% to −91% from the early 1950s to present (Table 3). One site in the Manuka area of Hawai'i Island showed stable or slightly increasing kukui canopy cover (+5.7%). Across all sites and time periods, the percent remaining of kukui canopy was best fit ($P < .001$, $r^2 = 0.58$) by a logistic decay function:

$$= \frac{54{,}557{,}184}{1 + e^{0.01543*(Y+859.2644)}}$$

where Y is the time difference in years. A simple linear model of total kukui cover by site

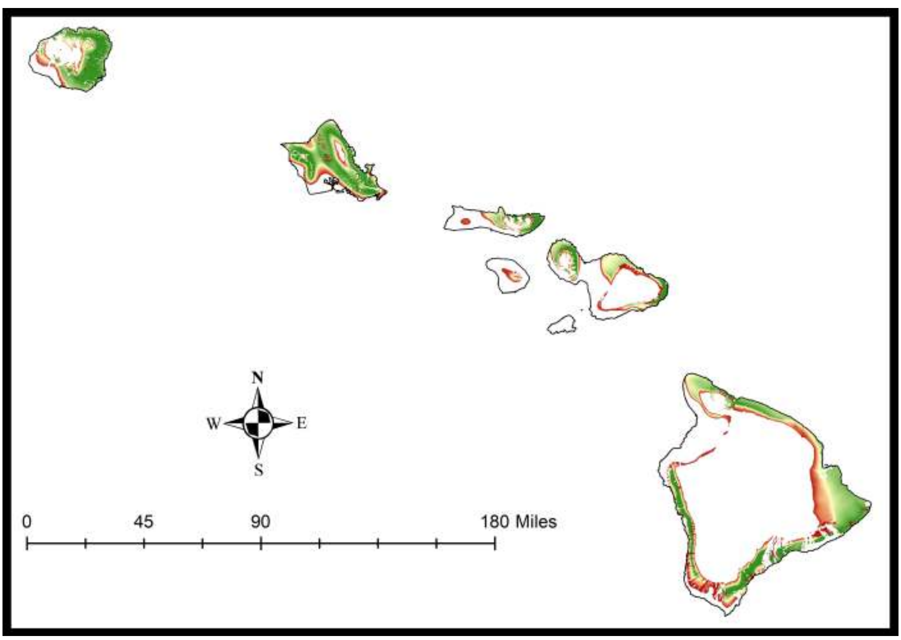

FIGURE 2. Modeled habitat suitability ranging from optimal (green), to moderate (yellow) to poor (red); white areas cannot support kukui.

TABLE 3

Historical Imagery Analysis of Kukui Cover for 17 Sites across Five Islands in Hawai'i

		1949–1954		1962–1965		1977–1978		2017		Linear Regression		Exponential Decay	
Location	Island	% Cover	% Change	% Cover	% Change	% Cover	% Change	% Cover	% Change	r^2	$P>$	r^2	$P>$
Makaha	Kauai	6.7	0	7.4	10.4	6.1	−9.0	4.2	−37.3	–	–	–	–
Haena	Kauai	11.5	0	6.8	−40.9	4.3	−62.6	2.5	−78.3	–		0.95	0.02
Waimea	Kauai	19.3	0	13.8	−28.5	10.3	−46.6	6.5	−66.3	–		0.99	0.01
Wahiawa	Oahu	9.3	0	8.3	−10.8	5.1	−45.2	1.0	−89.2	0.98	0.01	0.92	0.04
Waianae	Oahu	8.7	0	6.5	−25.3	5.3	−39.1	3.1	−64.4	–	–	1.00	0.00
Nuuanu	Oahu	16.6	0	12.5	−24.7	7.4	−55.4	2.3	−86.1	0.93	0.04	0.96	0.02
Wailau	Moloka'i	18	0	15.2	−15.6	13	−27.8	12.2	−32.2	–	–	0.94	0.03
Halawa	Moloka'i	15.4	0	10.6	−31.2	6.6	−57.1	1.4	−90.9	0.94	0.03	0.97	0.01
Kaanapali	Maui	15.3	0	12.6	−17.6	10.2	−33.3	3.9	−74.5	0.99	0.00	0.95	0.03
Olowalu	Maui	23	0	20.6	−10.4	18.5	−19.6	15	−34.8	0.94	0.03	0.98	0.01
Keanae	Maui	19.5	0	11	−43.6	10.5	−46.2	6.1	−68.7	–	–	0.94	0.03
Kīpahulu	Maui	5.7	0	44	−22.8	2.6	−54.4	3.5	−38.6	–	–	–	–
Kapaau	Hawai'i	4	0	3	−25.0	1.5	−62.5	0.5	−87.5	–	–	0.95	0.02
Honokaa	Hawai'i	2.6	0	2	−23.1	1.7	−34.6	1.4	−46.2	–	–	0.97	0.02
Laupahoehoe	Hawai'i	13.3	0	11.5	−13.5	6	−54.9	3.5	−73.7	–	–	0.89	0.05
Pahala	Hawai'i	8	0	4.6	−42.5	3.8	−52.5	6.1	−23.8	–	–	–	–
Manuka	Hawai'i	5.3	0	5.4	1.9	8.1	52.8	5.6	5.7	–	–	–	–
Average		**11.9**	**0.0**	**9.2**	**−21.4**	**7.1**	**−38.1**	**4.6**	**−58.0**	**0.20**	**0.00**	**0.22**	**0.00**

The percent change in the table is measured from the 1949–1954 imagery sources.

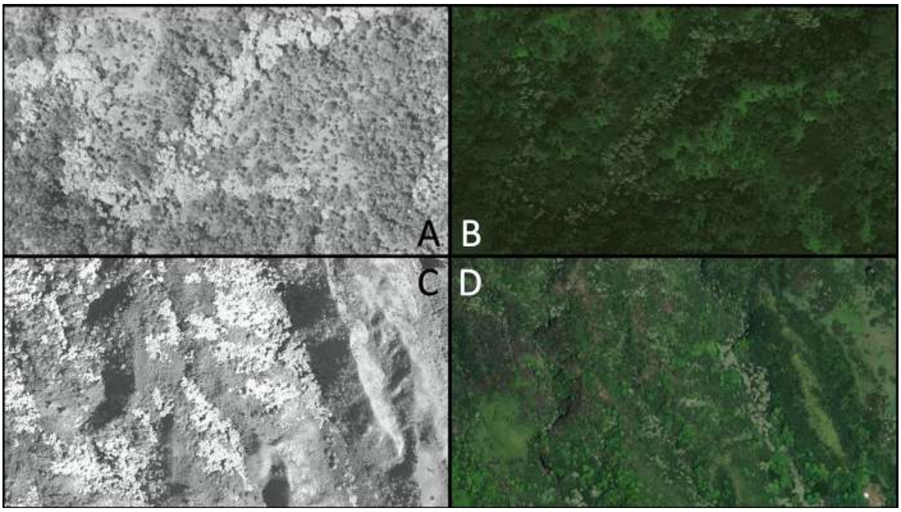

FIGURE 3. Examples comparing the 1950s imagery (left) to the modern imagery (right) in Wahiawa, O'ahu (*A*, *B*) and Kīpahulu, Maui (*C*, *D*).

provided very high prediction power ($P < .0001$, adj. $r^2 = 0.81$):

$$= 10.75 - Y * 0.105 + C_L$$

where Y is the time difference in years and C_L is a location specific constant.

DISCUSSION

The traditional importance of kukui as a resource and the historical significance of kukui on the landscape is clearly expressed by the language designating kukui as the state tree of Hawai'i. A review of traditional usage of kukui suggests the need for a substantive source of kukui oil in the past. If canoes and people were oiled almost daily, a massive supply of the nuts would have been needed. Any extrapolation from this literature is subject to substantial assumptions, from the number of people, to the amount of usage, and to the harvest rates. But by using generic production figures for kukui (200 trees per hectare and 90.7 kg/tree) and taking ranges of the unknowns we can begin to understand the magnitude of demand. Assuming a 100% harvest rate, ancient population estimates (400,000 to 800,000) and range of usage (1 to 8 fluid ounces per person per day), we calculate a range of ~240,000 to ~3,850,000 trees per year necessary to meet demand, equivalent to ~1,200 to ~19,500 ha of kukui. These numbers could balloon up very quickly if consumption of kukui oil was higher or if harvest rates were lower.

Other ethnobotanical applications, such as being a preferred composting material and having high medicinal value, would suggest that kukui was common within agricultural areas to ensure adequate access. This is in addition to more substantial roles in mixed arboricultural systems, which would have occupied a range of ecological niches (e.g., Kurashima and Kirch 2011, Lincoln and Ladefoged 2014), and novel kukui forests (e.g., Lincoln 2020*a*). Therefore, it can be considered that kukui was widespread in Hawai'i across much of its potential habitat but with considerable variation in planting densities, including as a dominant canopy species in novel kukui forests, a moderate part of mixed agroforestry systems, and a sparse part of fixed-field and home garden agricultural systems. The different starting points of kukui would have had different ecological trajectories once left untended, contributing to the current distribution visible on the landscape.

An assessment of historical imagery suggests that the cover of kukui has declined by ~58% over the last ~70 years following an exponential decay curve. Projecting the current kukui cover (4,170 ha) into the past utilizing the regressed exponential decay would suggest ~20,700 ha in 1910, which is higher than the estimates provided at the time (4,000–16,000 ha, Wilcox and Thompson 1913). Projecting back further to 1820 (an important year for social change, and arguably an approximate year initiating the rapid decline of traditional Hawaiian socioecosystems) would suggest ~84,000 ha, or approximately 5% of the land area. We argue that this figure is improbably high, but possible given that kukui cover is still >2.5% of the total land area in some districts today.

The decline of kukui was observed statewide. We observed in the historical photos that considerable loss was caused by human alteration of the environment such as urban expansion and clearing for agriculture, but also that much of the loss stems from shrinking patches of kukui in novel forest ecosystems. Even in remote locations rarely accessed by people, such as Wailau valley on the northern coast of Molokaʻi Island, kukui expressed consistent and substantial loss of cover (in this case over 30% in 70 years). In these remote cases, we believe that the decline has two potential explanations: (1) the pattern represents a point in the ecological succession that started when Hawaiians cultivation and forest management declined, or (2) kukui was in ecological equilibrium but new factors such as invasive plants, diseases and pests, and changing climate are reducing its ability to compete. We would suggest that the pattern we see on the landscape is largely a result of the natural succession occurring following the ceasing of large-scale encouragement of kukui on the landscape by the indigenous peoples, although new pressures such as invasive species may be exacerbating the decline.

There are several lines of evidence that support this hypothesis. Although we did not formally analyze the landscape-level extent of kukui in the historical images, we did examine the upper and lower elevational extents of the trees in the historical photos. In our approximation, the total extent of kukui did not change much, if at all, in the last 70 years. Rather, we only see a decline in the density of kukui across its extent. Furthermore, there are vast areas of highly suitable kukui habitat—according to the model developed in this article—that is devoid of kukui, most notably within the districts of Puna on Hawaiʻi Island and Hāna on Maui Island. Given that we do not witness a decrease in kukui extent, the unfilled kukui habitat would suggest both that (1) kukui was not initially established by Hawaiian cultivators everywhere it could grow, and (2) that kukui did not expand so much as to fill its entire ecological range.

Alternatively, kukui may not have expanded at all and only existed on the landscape as maintained by Hawaiian cultivation. If this is true it would suggest that (1) the extent of kukui on the landscape today represents a minimum extent of Hawaiian cultivation and forest management and (2) that there was an extraordinarily high cover of kukui in Hawaiian environments prior to 1800. Anecdotally, there are some pictures from the late 1800s and early 1900s that would suggest that kukui cover on the landscape was significantly higher than what we have analyzed for the 1950s, lending further support to our suggestion that kukui has largely been in a state of decline since the interruption of Hawaiian socioecosystem management.

The rate of loss of kukui canopy cover, while ~9% per decade, was likely not constant over the last 250 years since European contact. In our historical assessment, larger patches of kukui appeared to better maintain themselves over the past 70 years, while small patches have rapidly disappeared. Therefore, initial loss in kukui cover when large, monotypic patches likely existed may have been very low. Kukui is also considered very fast growing and potentially invasive in heavily disturbed environments (Wagner et al. 1990, Randall 2001, Swarbrick and Hart 2001, Krisnawati et al. 2011). Consequently, there may have been some expansion of kukui cover following the abandonment of cleared agricultural areas, serving as a pioneer canopy.

This is consistent with our historical analysis, where the only expansion of kukui canopy over time was observed in recently abandoned agricultural areas (mostly pastures). Over time, as secondary forest growth occurs, kukui may be less able to compete. This would be supported by kukui's relatively poor growth, performance, and form when growing in dense or shaded conditions (Krisnawati et al. 2011). It would also suggest that kukui would perform well ecologically in systems of shifting cultivation, such as are documented for Hawai'i (Lincoln 2020*a*).

In the mid-1800s to the mid-1900s large-scale loss of kukui cover must have occurred with the expansion of the plantations in Hawai'i. The legacy of this clearing can be clearly seen in the kukui distribution on the eastern and northern facing coasts of Hawai'i Island. Here, dense stands of kukui exist in virtually every little ravine and rivulet where heavy machinery was not able to access for the clearing and cultivating of plantation crops. Conversely, the flat lands between the depressions are devoid of kukui.

The large footprint of kukui, which we suggest is indicative of the extent of Hawaiian arboriculture or forest alteration, significantly alters the perspectives on pre-European Hawaiian agriculture and land management. Recent publications suggest that Hawaiians only directly altered ~3% of the landscape for the production of food and resources (Ladefoged et al. 2009, Gon et al. 2018, Kurashima et al. 2019). A rough calculation of the extent of land alteration indicated by kukui suggests a value of ~15%, or five times the level of land alteration presently presented. This perhaps makes sense, given that previous estimates primarily consider only plant-based foods (and specifically taro and sweet potato), excluding other production needs including fiber, timber, animal husbandry, and other resource needs and wants. To date, three forms of Hawaiian agriculture have been modeled (flooded, intensive rainfed, and colluvial systems; Ladefoged et al. 2009, Kurashima et al. 2019), but these assessments ignore a range of other agriculture forms (Lincoln and Vitousek 2017, Lincoln et al. 2018), including arboriculture and agroforestry. Yet, we know these types of systems played a crucial, and oftentimes dominant, role in Polynesian agriculture (Yen 1974, Kirch 1989, Huebert and Allen 2016, Quintus et al. 2019, Huebert and Allen 2020). That kukui provided multiple outputs (oil, timber and firewood, animal husbandry, mulch, medicine, etc.) and, as a tree crop, required minimal labor inputs could explain large-scale conversion of the landscape to kukui and companion species.

Despite historical declines, kukui is still a substantial component of a diverse range of ecosystems in Hawai'i. There are a number of areas where kukui is a major novel forest species, particularly along the floors and walls of large, remote river valleys. Kukui does well in mesic and wet habitats, but has populations in dry areas as well. Despite its prominent position in the past and current lowland ecology of Hawai'i, a Google Scholar search of the terms "Hawaii," "ecology," and "Aleurites" returns no relevant studies on the ecological roles facilitated by this early-introduced tree. A lack of study regarding the ecological roles kukui might play makes it difficult to discuss the effects of kukui decline.

CONCLUSION

Kukui was, and remains, an important ecological species in lowland novel forests in Hawai'i, but is declining due to human alteration of the landscape as well as an apparent lack of competitiveness in mature forests. As the use of many low-land forests becomes increasingly reduced, and new invasive species continue to claim land, kukui is a dwindling reminder of a time when the forests were actively managed for production and ecosystem services, and supported a thriving biocultural landscape. Perhaps it is indicative of our contemporary land management when the state of our state tree is one of substantial decline.

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