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RESEARCH ARTICLE

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Regeneration of *Metrosideros polymorpha* forests in Hawaii after landscape-level canopy dieback

Linda Mertelmeyer[1] | James D. Jacobi[2] | Dieter Mueller-Dombois[3] | Kevin Brinck[4] | Hans Juergen Boehmer[5,6]

[1]Technical University of Munich, Munich, Germany

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

[3]Department of Botany, University of Hawaii at Manoa, Honolulu, Hawaii

[4]Hawaii Cooperative Studies Unit, University of Hawaii at Hilo, Hilo, Hawaii

[5]School of Geography, Earth Science and Environment (SGESE), University of the South Pacific (USP), Laucala Bay, Suva, Fiji Islands

[6]Institute for Applied Ecological Studies (IFANOS), Nuremberg, Germany

Correspondence
James D. Jacobi, Pacific Island Ecosystems Research Center, U.S. Geological Survey, Hawaii National Park, HI.
Email: jjacobi@usgs.gov

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Abstract

Questions: (a) Have *Metrosideros polymorpha* trees become re-established in Hawaiian forests previously impacted by canopy dieback in the 1970s? (b) Has canopy dieback expanded since the 1970s? (c) Can spatial patterns from this dieback be correlated with habitat factors to model future dieback in this area?

Study Site: An 83,603 ha study area on the eastern slopes of Mauna Loa and Mauna Kea volcanoes on the island of Hawaii, USA.

Methods: We analyzed very-high-resolution imagery to assess status of *Metrosideros polymorpha* forests across the eastern side of the island of Hawaii. We generated 1,170 virtual vegetation plots with a 100-m radius; 541 plots in areas mapped in 1977 with trees dead or mostly defoliated (dieback), and 629 plots in adjacent wet forest habitat, previously mapped as non-dieback condition. In each plot we estimated the frequency of *M. polymorpha* trees that were dead or mostly defoliated, and the frequency of trees with healthy crowns. These results were combined with habitat data to produce a spatial model depicting probability of canopy dieback within the study area.

Results: Seventy-nine percent of plots mapped in 1977 in dieback condition recovered their canopy and were now considered in non-dieback condition. Ninety-one percent of plots in previous non-dieback areas were found to still have a healthy *M. polymorpha* canopy in 2015. A spatial model allowed us to identify areas within the study area with high, medium, and low probability of experiencing this same type of canopy dieback in the future.

Conclusions: Most former dieback areas mapped within the study area in 1977 now show recovery of the tree canopy through growth of new cohorts of young *M. polymorpha* trees. This suggests these forest communities are resilient to this type of canopy loss and tree death so long as other factors do not disrupt the natural regeneration process.

KEYWORDS

canopy dieback, cohort senescence, forest decline, forest health, Hawaii, landscape-level analysis, *Metrosideros polymorpha*, ohia, recovery, regeneration, tree mortality, vegetation dynamics

1 | INTRODUCTION

Tree mortality and forest-decline events have been increasingly reported around the globe over the last decade (Allen, 2009; Allen et al., 2010; Boehmer, 2011; Brienen et al., 2015; Carnicer et al., 2011; Hartmann et al., 2018; Peng et al., 2011; van Mantgem et al., 2009; Williams et al., 2013), many of the studies with a focus on potential effects of climate change. However, tree and forest mortality have been of interest to researchers for decades, with some work on forest decline even reaching back to the early 1900s (Lewton-Brain, 1909; Lyon, 1909). Forest decline research has been conducted in Europe, North America, Hawaii, New Zealand, and Australia, and results included assessments of physical destruction and physiological decline caused by abiotic stress, pathogens, and tree demography (Breshears et al., 2005; Huettl & Mueller-Dombois, 1993; Mueller-Dombois, 1987; Mueller-Dombois, Jacobi, Boehmer, & Price, 2013).

The forests of the Pacific islands are considered fragile ecosystems with low resilience to perturbations (Keppel, Morrison, Meyer, & Boehmer, 2014), and highly susceptible to canopy dieback (Auclair, 1993; Huettl & Mueller-Dombois, 1993; Mueller-Dombois, 1987). Dieback is a special form of forest decline which affects only canopy trees and is known from many forest ecosystems (Aynekulu et al., 2011; Jane & Green, 1983; King & Neilson, 1992; Lawesson, 1988; Mueller-Dombois, 1988; Mueller-Dombois et al., 2013; Stewart, 1989; White, 1986). The term has been defined as “progressive dying back from the tips of twigs, branches or tops” (Ciesla & Donaubauer, 1994; Manion, 1981; Podger, 1981) which may lead to death of the tree. In this paper we focus on the response and dynamics of the native ohia (*Metrosideros polymorpha* Gaudich.) forest after a widespread canopy dieback event that occurred on the wet windward side of the island of Hawaii starting in the mid-1960s and continuing through the 1980s. This phenomenon has been referred as the 1970s ohia dieback (Burgan & Nelson, 1972; Hodges, Adee, Wood, & Doty, 1986; Jacobi, Gerrish, Mueller-Dombois, & Whiteaker, 1988; Mueller-Dombois & Krajina, 1968; Mueller-Dombois et al., 2013; Petteys, Burgan, & Nelson, 1975).

Metrosideros polymorpha is the most abundant tree species in the native wet and mesic forests throughout the main Hawaiian Islands (Mueller-Dombois & Fosberg, 1998; Mueller-Dombois et al., 2013; Wagner, Herbst, & Sohmer, 1999). Although *M. polymorpha* has many characteristics typical of a pioneer species (Burton & Mueller-Dombois, 1984), it dominates plant communities in Hawaii that range from sea level to tree-line, from very dry habitats on the leeward sides of the islands to extremely wet windward forests, and from young lava substrates on the island of Hawaii to habitats on very old soils on the island of Kauai (Mueller-Dombois et al., 2013).

1.1 | A brief overview of ohia dieback

There was a great deal of concern in the late 1960s and early 1970s about the future of *M. polymorpha* forests on the island of Hawaii as large areas on the wet eastern side of this island exhibited extensive defoliation and mortality of the dominant canopy-forming *M. polymorpha* trees (Burgan & Nelson, 1972; Mueller-Dombois, 1985; Petteys et al., 1975; Figure 1). A similar canopy dieback was documented in the Hawaiian Islands in the early 1900s in a wet forest on the northeast slope of Haleakala volcano on Maui Island (Lewton-Brain, 1909; Lyon, 1909; Mueller-Dombois, 2006). When Holt (1988) studied this area in the 1980s he found no signs of active canopy dieback and the vegetation in the site affected in the early 1900s had become a low-stature, open *M. polymorpha* community similar to “bog-formation and stand-reduction” stands described by Mueller-Dombois (1985).

Intact closed-canopy native forests in Hawaii provide many important ecological services, such as habitat for a multitude of species of endemic and indigenous plants and animals (Mueller-Dombois et al., 2013; Ziegler, 2002); they serve as the main vegetation cover layer for watersheds and help regulate water infiltration and surface flow beneath the tree canopy (Izuka et al., 2016; Safeeq & Fares, 2012); and are also an important carbon sink (Selmants, Giardina, Jacobi, & Zhiliang, 2017). Such services could be compromised by a decline or loss of the tree canopy, causing alarm for managers of these resources (Jacobi, 1993).

1.2 | Two research hypotheses

Canopy dieback on Hawaii island in the 1970s occurred over ~49,000 ha of *M. polymorpha* forest, half of which was characterized to be in heavy to severe dieback (i.e., >50% of the *M. polymorpha* canopy trees dead or mostly defoliated). The remaining 24,000 ha exhibited no canopy dieback or just slight-to-moderate dieback (<50% of the canopy trees dead or defoliated; Jacobi, 1990; Jacobi et al., 1988). Research initiated at that time focused on two different hypotheses to explain this extensive canopy dieback: (a) disease, and

FIGURE 1 Aerial view taken in 1978 of the *Metrosideros polymorpha* forest on the eastern side of the island of Hawaii showing *M. polymorpha* forest with heavy canopy dieback (foreground) and a dieback stand from the ground (inset photo). Healthy closed canopy *M. polymorpha* forests are seen in the central part of the photograph, as well as pasture on the right side, and Mauna Loa volcano in the background. Photographs by J. Jacobi and J. Boehmer (inset)

(b) natural succession, similar to the Maui dieback event in the early 1900s (Mueller-Dombois, 2006).

The disease hypothesis centered on the supposition that *M. polymorpha* trees were being killed by one or more non-native pathogens that were spreading across the landscape. The primary focus of this research was on the fungal pathogen *Phytophtora cinnamomi* (Bega, 1974; Kliejunas & Ko, 1973, 1976) that had been implicated in a widespread mortality of *Eucalyptus* trees in plantations of Western Australia (Newhook & Podger, 1972). Research on the natural succession hypothesis was initiated in 1976 to assess both the extent and ecological characteristics of the *M. polymorpha* forest impacted by canopy dieback relative to areas that did not exhibit dieback in this same forest zone (Mueller-Dombois, 1980; Mueller-Dombois, Jacobi, Cooray, & Balakrishnan, 1980). This study included (a) identifying spatial patterns and habitat characteristics of areas that were experiencing *M. polymorpha* dieback; (b) attempting to determine the cause and mechanisms related to the dieback; and (c) assessing the response of the vegetation, and particularly *M. polymorpha*, after most of the trees had died in an area. For this project five different types of *M. polymorpha* dieback were identified: wetland dieback, dryland dieback, *M. polymorpha* displacement dieback, gap-formation dieback, and bog-formation dieback (Mueller-Dombois et al., 2013), based on habitat characteristics and vegetation dynamics of the affected plant communities.

The results of spatial analyses of the 1970s dieback (Akashi & Mueller-Dombois, 1995; Jacobi, 1983; Mueller-Dombois, 1986; Mueller-Dombois et al., 1980) showed that the extent and spread of *M. polymorpha* dieback in this area, primarily on sites experiencing the wetland dieback type, appeared to be directly related to substrate age and type, and was also correlated with elevation and rainfall. The ecology and dynamics of the *M. polymorpha* dieback forest and potential mechanisms for the 1970s dieback event were summarized by Mueller-Dombois (1985) and Hodges et al. (1986). The consensus of both research efforts was that the dieback was not caused directly by introduced fungal pathogens. Instead it was the result of a natural sequence of *M. polymorpha* tree canopy development, followed by a relatively synchronous senescence and death or defoliation of the canopy (cohort senescence), possibly exacerbated by nutrient limitations. Fungal pathogens were considered secondary agents that subsequently invaded the weakened trees, but not a primary cause of the dieback.

During the 1970s, 25 permanent plots were established in both dieback and non-dieback sites within the study area to serve as the basis for a long-term study of the canopy trees and their associated plant communities in and adjacent to areas that had experienced heavy to severe *M. polymorpha* dieback (Mueller-Dombois et al., 1980). These vegetation plots have been monitored at irregular intervals between 1976 and 2003 to track changes in the status and growth of the *M. polymorpha* trees and associated vegetation over time (Jacobi, Gerrish, & Mueller-Dombois, 1983; Jacobi et al., 1988); the plots were last sampled in 2003 (Boehmer, Wagner, Jacobi, Gerrish, & Mueller-Dombois, 2013). The results from the plot monitoring suggested that many of the original dieback sites had shown strong recovery of the *M. polymorpha* tree canopy through recruitment of new trees which had started from seedlings that became established when the canopy was opened by dieback. Many of these seedlings were found to have grown into saplings and reproductively active trees over the 30+ years of the study (Boehmer et al., 2013).

1.3 | Need for a broader survey

It was not clear if the results of the dieback monitoring study, based on a small number of vegetation plots, truly represented the current condition of the *M. polymorpha* forest across the entire original dieback area. Therefore, a much larger study was conducted to assess the status of the *M. polymorpha* forests, in and adjacent to the areas that experienced canopy dieback in the 1970s, to evaluate the response of *M. polymorpha* to that dieback event. This new study was conducted by analyzing very-high-resolution aerial imagery to characterize the status of the tree canopy and understory vegetation throughout the region. Three specific questions were addressed in this study: (a) Are the results of the vegetation-plot analysis over time representative of that same pattern of *M. polymorpha* forest recovery across the larger landscape of the study area? (b) Has there been an expansion of *M. polymorpha* canopy dieback in this area since the 1970s? (c) Can the spatial patterns seen for the 1970s dieback event be correlated with selected habitat factors and used to model future canopy dieback in this area?

2 | DATA AND METHODS

2.1 | Study area and original data sets

The canopy dieback that impacted the *M. polymorpha* forests in the 1970s and early 1980s occurred primarily in wet forest habitat along the eastern side of the island of Hawaii, west and north of the city of Hilo (Appendix S1). An 83,603 ha study area in this region, that extends from ~300 to 1,800 m elevation, was selected by Mueller-Dombois (1983, 1985) to analyze the distribution and spread of this dieback event, and to evaluate the changes in the plant communities that were impacted by *M. polymorpha* canopy defoliation or death. Approximately 30% (25,076 ha) of the study area that was dominated by closed-canopy *M. polymorpha* forest was mapped by Jacobi (1989, 1990) as having heavy or severe canopy dieback (≥50% of the *M. polymorpha* tree canopy defoliated or dead) based on aerial imagery taken in 1977.

The study area lies on lava and volcanic ash substrates erupted from Kilauea, Mauna Loa, and Mauna Kea volcanoes that range in age from <200 years to >300,000 years since they were deposited, with the oldest areas generally found in the northern half of the study area (Sherrod, Sinton, Watkins, & Brunt, 2007). This large expanse of native forest occurs on the windward side of Hawaii Island that experiences northeast trade winds for more than 75% of the year. As a result, it is an area of relatively high annual rainfall that receives nearly 8,000 mm per year in the central part of the study area, and decreases to just over 2,200 mm per year at the upper elevations on its western side (Giambelluca et al., 2012; Appendix S2).

Between 1976 and 1980, 45 vegetation monitoring plots were established in this study area, in both active dieback stands and healthy *M. polymorpha* forests, to allow for monitoring changes in the structure and composition of the vegetation over time (Mueller-Dombois et al., 1980). Twenty-five of these plots have been resurveyed several times during the past 30 years (Boehmer et al., 2013) and 21 plots are located within the current study area (Appendix S1). The vegetation plots were 20 m × 20 m in size and trees of all species >5 m tall were permanently marked, with diameter measured at breast height (DBH), and assessed for crown foliage vigor using the five tree vigor classes described by Mueller-Dombois et al. (1980). *Metrosideros polymorpha* tree vigor classes included: (1) trees with fully foliated crowns; (2) trees with some defoliated branches, 10%–50% of the crown dead; (3) trees with most (≥50%) of the upper crown branches defoliated, but with some live adventitious branches growing along the trunk; (4) recently dead trees with many brown leaves and small branches, and most of the bark remaining on the trunk; and (5) dead trees that had only major branches remaining and most of the trunk without bark. Additionally, information was recorded on the abundance (count of individuals) of all woody species <5 m tall in subplots within the plot, as well as an estimate made of cover for all plant species within the plot in 1-m height classes. A detailed description of the field sampling and analysis methodologies can be found in earlier publications (Boehmer et al., 2013; Jacobi et al., 1983, 1988). A dieback index (DI) for each plot was calculated by dividing the sum of the number of *M. polymorpha* trees in vigor classes 3, 4, and 5 by the total number of *M. polymorpha* trees in each plot. Plots with a DI ≥50% were classified as being in dieback condition (DB); plots with DI <50% were classified as in non-dieback condition (NDB).

2.2 | New data collection and analysis methods

To assess the present status of the *M. polymorpha* forest canopy across the eastern side of the island of Hawaii we analyzed very-high-resolution imagery collected between 2008 and 2015 by Pictometry International (Pictometry International Corp., Rochester, NY, USA). The Pictometry (POL) imagery consists of three-band, true-color red-green-blue (RGB) digital photographs with ~60% overlap, taken from a fixed-wing aircraft. The images have a spatial resolution of ~20 cm (Appendix S3).

We used the random points tool in ArcMap (version 10, Environmental Systems Research Institute, Redlands, CA, USA) to generate 1,170 virtual sampling locations across the study area; 541 POL assessment plots were located in areas that had been mapped as being in heavy to severe dieback on the 1977 imagery (Jacobi, 1989, 1990), and 629 plots located in similar and adjacent forests in this same area, but mapped as being in non-dieback condition from the 1977 imagery (Appendix S4). The coordinates for these points were imported as a Keyhole Markup Language (KML) file into the POL Connect image viewer for analysis. A 100-m radius perimeter was established around each point location to mark the virtual plot boundary using the POL circle tool. These circular plots on the POL imagery were then used to assess the status of the *M. polymorpha* forest canopy condition, tree species composition, and understory condition at every sampled location. For each plot, we visually estimated the percent of *M. polymorpha* trees >5 m tall (measured using the POL height tool) that appeared to be dead or heavily defoliated (i.e., in vigor class 3, 4, or 5). If a plot had ≥50% of its *M. polymorpha* trees in this condition it was classified in dieback (DB); otherwise, it was classified as being in non-dieback (NDB) condition.

To calibrate our assessment process we also constructed POL plots around the locations for the 25 permanent plots that had been established in 1976, and then compared our new assessment of canopy dieback using POL imagery for these locations with status from the most recent ground-based resurvey of these plots that was conducted in 2003 (Boehmer et al., 2013). Additionally, we conducted a second analysis of 120 plots that were randomly selected from the 1,170 POL assessment plots to test the repeatability of using the Pictometry imagery to determine *M. polymorpha* canopy dieback status.

2.3 | Data analysis and spatial modeling

Changes in *M. polymorpha* dieback status and distribution were determined by comparing canopy status in 1977 with status in 2015, based on our assessment of the plot sites using the more recent POL imagery. This was done by calculating the percent of POL assessment plots within the mapped dieback and non-dieback areas from the 1977 photographs (Jacobi, 1989, 1990) that had changed their status to the other category (DB to NDB, or NDB to DB) in 2015, or did not change in status from the original survey (DB to DB, or NDB to NDB).

Several previously published reports and geographic information system (GIS) data layers were used to code additional information on site attributes for each plot using the spatial join tool in ArcMap. This information was used for an analysis of dieback and non-dieback habitat characteristics. These data sets included substrate age

TABLE 1 Summary of an accuracy assessment analysis comparing the dieback status for 25 field plots sampled in 2003 (Boehmer et al., 2013) with their dieback status as recorded from analyzing Pictometry very-high-resolution imagery taken in 2015

	Status in 2015			
Status[a] in 2003	DB	NDB	Row totals	Percent correct
DB	2	3	5	40
NDB	3	17	20	85
Column totals	5	20	25	
Percent correct	40	85		76

[a]Status: DB = >50% of *M. polymorpha* canopy trees dead or with more than 50% of their canopy defoliated. . NDB = <50% of *M. polymorpha* canopy trees dead or with more than 50% of their canopy defoliated.

(Sherrod et al., 2007), elevation from the U.S. Geological Survey's 10-m digital elevation model (DEM; U.S. Geological Survey, 2014), mean annual rainfall (Giambelluca et al., 2012), and substrate moisture zones (Price et al., 2012). The habitat data allowed us to develop a model to predict the probability of dieback occurring at a given point within the study area. We fit logistic regression models for the presence of dieback using elevation, rainfall, and effective soil moisture as potential predictors, along with all two-way interactions. We used the AIC statistic corrected for small sample size (AIC_c) to calculate relative model weights. Four models: elevation + moisture (39%), elevation + moisture and their interaction (33%), rainfall + elevation + moisture (16%), and rainfall + elevation + moisture plus the elevation–moisture interaction (12%) accounted for most of the model weight. Those four models were used to produce weighted predicted probabilities of dieback in 10 m × 10 m pixels in the study area. The results of this model were then projected across the study area using ArcMap 10.

3 | RESULTS

3.1 | Calibration of the Pictometry image assessment method

There was adequate spatial and spectral resolution in the POL imagery to recognize the current condition of *M. polymorpha* tree crowns in each plot. For our calibration set of 25 permanent plots that were sampled on the ground in 2003 by Boehmer et al. (2013), and then with the POL assessment in 2015, 19 plots showed no difference in DI with the two methods, three plots that Boehmer et al. measured as NDB were identified as DB plots using the Pictometry imagery, and another three plots that Boehmer et al. measured as DB were identified as NDB plots using the Pictometry imagery (Table 1). When we tested the repeatability of using Pictometry imagery to determine *M. polymorpha* canopy dieback status, we found 98 of the 120 plots were classified in NDB status in the full assessment and 91 were correctly classified as in NDB status with the second assessment (Table 2). Twenty-two of the plots were classified in DB status in the full assessment and 10 were correctly classified in DB status in the second assessment.

TABLE 2 Summary of the accuracy assessment analysis of dieback status for 120 randomly selected Pictometry (POL) assessment plots that were analyzed a second time

Original plot assessment status[a]	Reassessment plot status[a]			
	DB	NDB	Count	Percent correct
DB	10	12	22	45
NDB	7	91	98	93
Count	17	103	120	
Percent correct	59	88		84

[a]Status: DB = >50% of *M. polymorpha* canopy trees dead or with more than 50% of their canopy defoliated. . NDB = <50% of *M. polymorpha* canopy trees dead or with more than 50% of their canopy defoliated.

TABLE 3 Summary of dieback status of Pictometry (POL) assessment plots in 1977 as mapped by Jacobi (1989) and 2015 from the analysis of POL imagery

Plot type	Number of plots	Dieback status in 1977				Dieback status in 2015			
		Count DB	Percent DB	Count NDB	Percent NDB	Count DB	Percent DB	Count NDB	Percent NDB
DB 1977	541	541	100	0	0	112	21	429	79
NDB 1977	629	0	0	629	100	54	9	575	91
Total	1,170	541		629		166		1,004	

DB 1977 = POL assessment plots that were located in areas mapped by Jacobi (1089) as showing heavy to severe 'ohi'a canopy dieback in 1977. NDB 1977 = POL assessment plots that were located in areas mapped by Jacobi (1989) as showing slight or no 'ohi'a canopy dieback in 1977.

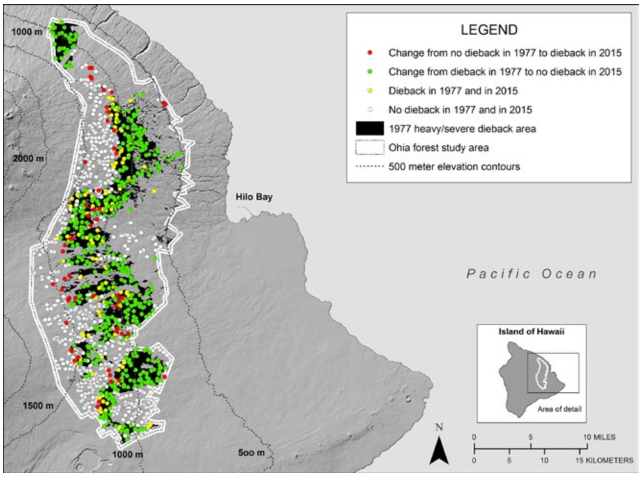

FIGURE 2 Map showing the *Metrosideros polymorpha* forest study area on the eastern side of the island of Hawaii with the area mapped as heavy or severe canopy dieback by Jacobi (1989) in 1977, and status of the *M. polymorpha* canopy at each of the Pictometry (POL) assessment plots

3.2 | Assessment of current canopy dieback status across the study area

All of the *M. polymorpha* forest mapped as being in dieback by Jacobi (1989) on the 1977 imagery had >50% of the trees with vigor class ≥3, indicating heavy to severe dieback at that time. Therefore, all 541 random POL assessment plots we allocated to this mapping stratum were in forest stands that were considered to have been in dieback condition when the Jacobi (1989, 1990) map was created. Likewise, all areas and their associated 629 random plots in adjacent forest areas that were not mapped as experiencing dieback within the study area on the 1977 imagery were considered to have been in non-dieback condition at that time, with most trees having a vigor class <3 (i.e., little or no dieback). In our current assessment of this area using the POL imagery, 79% of the plots in former heavy to severe dieback condition were found to have a young recovering tree canopy and were now considered to be in non-dieback condition. Just 21% of the plots originally found in the mapped dieback areas were still considered to be in heavy to severe dieback condition. For the part of the study area that was previously mapped in non-dieback condition, 91% of the POL assessment plots were found to have a healthy *M. polymorpha* canopy, and just 9% were considered now to be in dieback condition (Table 3, Figure 2).

3.3 | Relationship between canopy condition and selected habitat features

Assessment plots that were in canopy dieback status, either in 1977 or in 2015, showed some differences with plots in non-dieback status for several of the habitat variables that were analyzed (Table 4).

TABLE 4 Summary statistics for annual rainfall and elevation in meters for sites recorded as being in dieback status (DB) in either 1977 or 2015, or in non-dieback status (NDB) in 2015

Status	*N*	Mean	*SD*	Range	*t*	*p* Value
Annual rainfall[a]						
Dieback	595	5,300	1454	4,901	13.02	<0.001
Non-dieback	575	4,230	1355	4,429		
Elevation (m)[b]						
Dieback	595	1,074	185	1,076	−14.16	<0.001
Non-dieback	575	1,250	236	1,329		

[a]Annual rainfall from Hawaii Rainfall Atlas (Giambelluca et al., 2012). [b]Elevation from U.S. Geological Survey's 10-m digital elevation model (U.S. Geological Survey, 2014).

TABLE 5 Summary of substrate age across the study area and count of plot sites recorded as being in dieback status (DB) in either 1977 or 2015, or in non-dieback status (NDB) in 2015, for each substrate age group

Substrate age group	Substrate age range in years BP	Range midpoint	Count of DB plots	Count of NDB plots
1	<200	200	4	2
2	200–750	650	33	45
3	750–1,500	1,125	39	77
4	1,500–3,000	2,250	58	78
5	3,000–5,000	3,500	87	58
6	5,000–10,000	7,500	122	146
7	10,000–30,000	25,000	197	143
8	30,000–50,000	35,000	0	0
9	50,000–140,000	115,000	55	26

Plots that were classified as heavy to severe *M. polymorpha* dieback sites had on average a higher mean annual rainfall (5,300 mm) than plots in sites that did not experience canopy dieback (4,230 mmm), similar to results presented by Akashi and Mueller-Dombois (1995). Additionally, POL assessment plots classified as heavy to severe *M. polymorpha* canopy dieback sites were located at a lower average elevation (1,074 m) than plots found in sites that did not experience canopy dieback during this time (average of 1,250 m elevation). Although elevation and rainfall are often highly correlated, this is not fully the case on this windward side of the island of Hawaii where annual rainfall measured at sea level increases from 3,590 mm to nearly 8,000 mm at 900 m elevation, then decreases again to 2,000 mm at 1,850 m elevation (Giambelluca et al., 2012). Heavy to severe canopy dieback was found in plots on substrates that ranged from a mean range of 100 years to over 182,000 years BP (Table 5), but there generally was a larger number of plots with canopy dieback on the older substrates (>3,000 years), than was found on younger substrates.

The analysis of dieback status and habitat variables allowed us to develop a spatial model to depict the potential for *M. polymorpha* canopy dieback happening at a given site (Appendix S5). Three zones were identified on this map that represent areas that have low (<0.25 predicted probability of dieback), medium (0.25–0.50 predicted probability), or high (>0.50 predicted dieback) probability for the 1970s type of *M. polymorpha* canopy dieback occurring there sometime in the future. Most of the areas that were mapped as having heavy to severe canopy dieback in 1977, or those POL assessment plots that were originally mapped with a healthy *M. polymorpha* canopy but were identified as having canopy dieback on the recent POL imagery, fall within the high and medium-probability zones with this model (Figure 3). Several sites with POL assessment plots in currently healthy forest condition were located in areas that have either high or moderate probability of experiencing *M. polymorpha* canopy dieback in the future.

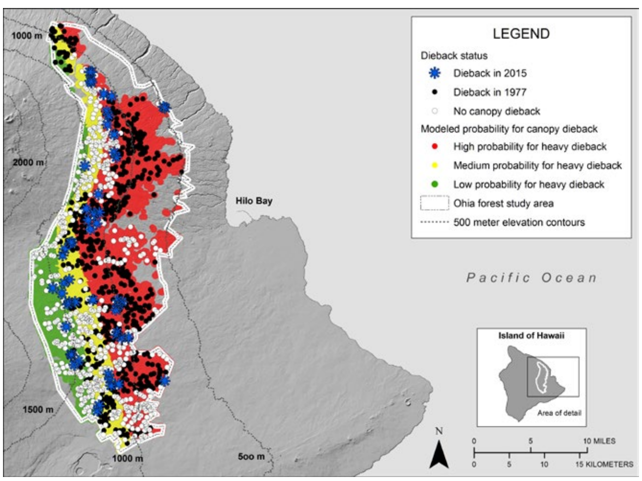

FIGURE 3 Map showing the *Metrosideros polymorpha* forest study area on the eastern side of the island of Hawaii with the modeled potential distribution of *M. polymorpha* canopy dieback and location of the Pictometry (POL) assessment plots recorded as showing canopy dieback status in either 1977 or 2015 or no canopy dieback at any time throughout the study

4 | DISCUSSION

4.1 | Recovery of the *M. polymorpha* canopy following dieback

Although it was concluded that the dieback event at its peak in the 1970s was a natural phenomenon that led to the synchronous defoliation and death of many of the *M. polymorpha* cohorts that dominated these forests (Hodges et al., 1986; Mueller-Dombois, 1985; Mueller-Dombois et al., 2013), there was still a concern that the native forest might not be able to recover to its former closed-canopy state. A slow or unnatural recovery could happen if other factors, such as aggressive non-native plant species invading the recently-opened understory vegetation, prevented *M. polymorpha* seedlings from becoming established (Boehmer et al., 2013; Jacobi et al., 1983). This scenario could seriously impact community dynamics, maintenance of native biodiversity, and watershed functions for the affected areas (Jacobi, 1993).

Our results indicate that the *M. polymorpha* canopy in 79% of the POL assessment plots in former dieback sites had recovered to the point that they were no longer considered to be dieback stands, and canopy dieback had just slightly expanded into areas that were formerly considered to be healthy (Figure 2; Table 3). All the plots in the previously mapped dieback sites in the very north of the study area show no dieback in the current assessment. Also, there appears to have been more recovery of the *M. polymorpha* forest in the lower elevation sites that had previously been mapped in dieback status. Most of the plots located at higher elevation than the previously mapped dieback zone have retained an intact *M. polymorpha* canopy over the past 40 years. The plots showing new canopy dieback in our 2015 assessment appear to be scattered across the entire middle portion of the study area but are mostly located adjacent to the originally mapped dieback units. The plots that were considered to have heavy to severe canopy dieback in both 1977 and 2015 were mainly found throughout the center of the previously mapped dieback zone (Figure 2). These results are consistent with the conclusions presented by Boehmer et al. (2013) that most of the former dieback areas mapped by Jacobi (1989) are now showing a clear recovery of their canopy as a result of the vigorous growth of new cohorts of young *M. polymorpha* trees that became established once the canopy was opened by the dieback event.

Because *M. polymorpha* is a shade-intolerant species (Burton & Mueller-Dombois, 1984), there are generally very few saplings and immature trees of this species in a closed-canopy forest. However, if the tree canopy is opened either locally, such as from a tree fall, or over larger landscapes, such as was seen with a widespread canopy dieback event in the 1970s, the site can be quickly colonized by *M. polymorpha*. Our long-term monitoring of the 1970s *M. polymorpha* study area has enabled us to identify a new closed canopy of maturing *M. polymorpha* trees, ranging in size from 5 m to 10 m tall, in most of our 25 long-term vegetation plots (Boehmer et al., 2013), as well as from our current assessment of hundreds of virtual POL assessment plots. These results suggest the *M. polymorpha* forest community in this area appears to be resilient to this type of canopy loss perturbation so long as other factors, such as invasive plant species, do not disrupt the natural succession process into a forest canopy.

4.2 | Potential for future *M. polymorpha* canopy death

The map showing the modeled potential distribution of *M. polymorpha* canopy dieback provides a way to identify other native *M. polymorpha* forest stands located in areas that may be susceptible to a similar canopy dieback sometime in the future. Specifically, several areas within the high probability zone for heavy canopy dieback were still found to have healthy *M. polymorpha* forest in our assessment of the POL plots (white dots in Figure 3). These include a zone in the southern-most portion of the study area, an area stretching eastward in the central part of the study area, and a small area in the high probability zone to the north. There are also many areas in the zone identified as having medium potential for heavy or severe dieback that still have a healthy *M. polymorpha* canopy. Based on the results of the various *M. polymorpha* dieback research studies that have been conducted since the 1970s, it is likely that some, if not all, of these forests may eventually also go into the canopy dieback stage at some time in the future. Our results suggest that many of these areas have the potential to recover their canopy again through the establishment of a new *M. polymorpha* cohort after the canopy has been opened. However, most of the areas in the zone identified as having low probability for heavy dieback are not expected be impacted by this same type of landscape-level canopy loss.

A new threat to the *M. polymorpha* forest has been recently identified. This phenomenon, called rapid ohia death (ROD), is characterized by a very quick death of a *M. polymorpha* tree which results in a distinctive canopy of brown, recently dead leaves (Mortenson et al., 2016). Trees with ROD symptoms can easily be seen on the ground and from the air and are being mapped using hyperspectral imagery and LiDAR (Vaughn et al., 2018). The primary factor believed to currently cause the rapid death in many of these recently dead *M. polymorpha* trees is the fungal pathogen, recently described as *Ceratocystis lukuohia* (Barnes et al., 2018), that had not been detected previously in Hawaii. A major effort is currently under way to inform the public about this new and expanding threat to the native *M. polymorpha* forests and to minimize the possibility of transporting *Ceratocystis* to other areas by vehicles, people working in contaminated areas, and by moving wood products (Rapid Ohia Death website, https://cms.ctahr.hawaii.edu/rod/HOME.aspx).

While it is likely that *Ceratocystis* may continue to expand its distribution and impacts on the *M. polymorpha* forest, both on the island of Hawaii, to which it is currently confined, and elsewhere across the state, other types of canopy dieback, such as seen during the 1970s, may also continue to impact *M. polymorpha* forests over time. The role of *M. polymorpha* as a dominant tree, particularly in most wet and mesic habitats across the main Hawaiian Islands, underscores the dramatic impact its loss would have on this forest ecosystem if most of the canopy trees were killed and not replaced. Regardless of the cause of *M. polymorpha* canopy death in an area, it will be prudent to continue monitoring to determine if there is adequate regeneration of *M. polymorpha*, as has been seen with the strong recovery of the *M. polymorpha* canopy on Hawaii Island since the 1970s. Additionally, it is important to find ways to minimize the accidental or intentional introduction and establishment of new pathogens and other invasive species into Hawaii that may either directly impact keystone species, such as *M. polymorpha*, and the forest recovery process following future episodes of tree canopy death.

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DATA ACCESSIBILITY

Tables containing the image assessment results, the accuracy assessment results, and locations with modeled potential distribution of canopy dieback are available from the U.S. Geological Survey's ScienceBase Catalog. These files and a shapefile of the study area can be accessed and downloaded at https://doi.org/10.5066/p97oso15.

ORCID

James D. Jacobi https://orcid.org/0000-0003-2313-7862

Kevin Brinck https://orcid.org/0000-0001-7581-2482

REFERENCES

Akashi, Y. & Mueller-Dombois, D. (1995). A landscape perspective of the Hawaiian rain forest dieback. *Journal of Vegetation Science*, *6*, 449–464. https://doi.org/10.2307/3236343

Allen, C. D. (2009). Climate-induced forest dieback: An escalating global phenomenon? *Unasylva*, *231/232*, 60, 43–49.

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., … Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, *259*, 660–684. https://doi.org/10.1016/j.foreco.2009.09.001

Auclair, A. N. D. (1993). Extreme climatic fluctuations as a cause of forest dieback in the Pacific Rim. *Water, Air, and Soil Pollution*, *66*, 207–229.

Aynekulu, E., Denich, M., Tsegaye, D., Aerts, R., Neuwirth, B., & Boehmer, H. (2011). Dieback affects forest structure in a dry Afromontane forest in northern Ethiopia. *Journal of Arid Environments*, *75*, 499–503. https://doi.org/10.1016/j.jaridenv.2010.12.013

Barnes, I., Fourie, A., Wingfield, M. J., Harrington, T. C., McNew, D. L., Sugiyama, L. S., … Keith, L. M. (2018). New *Ceratocystis* species associated with rapid death of *Metrosideros polymorpha* in Hawaiì. *Persoonia*, *40*, 154–181. https://doi.org/10.3767/persoonia.2018.40.07

Bega, R. V. (1974). *Phytophthora cinnamomi*: Its distribution and possible role in ohia decline on the island of Hawaii. *Plant Disease Reporter*, *58*, 1069–1073.

Boehmer, H. J. (2011). Vulnerability of tropical montane rain forest ecosystems due to climate change. In H. G. Brauch, Ú. O. Spring, C. Mesjasz, J. Grin, P. Kameri-Mbote, B. Chourou, … J. Birkmann (Eds.), *Coping with global environmental change, disasters and security* (pp. 789–802). New York, NY: Springer. https://doi.org/10.1007/978-3-642-17776-7

Boehmer, H. J., Wagner, H. H., Jacobi, J. D., Gerrish, G. C., & Mueller-Dombois, D. (2013). Rebuilding after collapse: evidence for long-term cohort dynamics in the native Hawaiian rain forest. *Journal of Vegetation Science*, *24*, 639–650. https://doi.org/10.1111/jvs.12000

Breshears, D. D., Cobb, N. S., Rich, P. M., Price, K. P., Allen, C. D., Balice, R. G., … Meyer, C. W. (2005). Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 15144–15148. https://doi.org/10.1073/pnas.0505734102

Brienen, R. J. W., Phillips, O. L., Feldpausch, T. R., Gloor, E., Baker, T. R., Lloyd, J., … Zagt, R. J. (2015). Long-term decline of the Amazon carbon sink. *Nature*, *519*, 344–348. https://doi.org/10.1038/nature14283

Burgan, R. E. & Nelson, R. E. (1972). *Decline of ohia lehua forests in Hawaii*. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station (USDA Forest Serv. Gen. Tech. Rep. PSW-3).

Burton, P. J. & Mueller-Dombois, D. (1984). Response of *Metrosideros polymorpha* seedlings to experimental canopy opening. *Ecology*, *65*, 779–791. https://doi.org/10.2307/1938050

Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sánchez, G., & Peñuelas, J. (2011). Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 1474–1478. https://doi.org/10.1073/pnas.1010070108

Ciesla, W. M. & Donaubauer, M. E. (1994). *Decline and dieback of trees and forests: A global overview*. Rome, Italy: Food and Agriculture Organization of the United Nations (FAO Forestry Paper 102).

Giambelluca, T. W., Chen, Q., Frazier, A. G., Price, J. P., Chen, Y.-L., Chu, P.-S., … Delparte, D. M. (2012). Online rainfall atlas of Hawai'i. *Bulletin of the American Meteorological Society*, *94*, 313–316. https://doi.org/10.1175/bams-d-11-00228.1

Hartmann, H., Schult, B., Sanders, T. G. M., McInnis-Ng, C., Boehmer, H. J., Allen, C. D., … Anderegg, W. R. L. (2018). Monitoring global tree mortality patterns and trends. Report from the VW symposium 'Crossing scales and disciplines to identify global trends of tree mortality as indicators of forest health'. *New Phytologist*, *217*, 984–987. https://doi.org/10.1111/nph.14988

Hodges, C. S., Adee, K. T., Wood, H., & Doty, R. D. (1986). *Decline of ohia (Metrosideros polymorpha) in Hawaii: a review*. Berkeley, CA: USDA Forest Service (Gen. Tech. Rep. PSW-86). https://doi.org/10.2737/psw-gtr-86

Holt, R. A. (1988). *The Maui forest trouble: Reassessment of an historic forest dieback*. Unpublished M.Sc. Thesis. Honolulu, HI: University of Hawaii.

Huettl, R. F. & Mueller-Dombois, D. (1993). *Forest decline in the Atlantic and Pacific region*. Berlin, Germany: Springer-Verlag. https://doi.org/10.1007/978-3-642-76995-5

Izuka, S. K., Engott, J. A., Rotzoll, K., Bassiouni, M., Johnson, A. G., Miller, L. D., & Mair, A. (2016). Volcanic aquifers of Hawai'i — Hydrogeology, water budgets, and conceptual models. *U.S. Geological Survey Scientific Investigations Report* 2015-5164.

Jacobi, J. D. (1983). *Metrosideros* dieback in Hawaii: A comparison of adjacent dieback and non-dieback rain forest stands. *New Zealand Journal of Ecology*, *6*, 79–97.

Jacobi, J. D. (1989). *Vegetation maps of the upland plant communities on the islands of Hawai'i, Maui, Moloka'i, and Lana'i*. Honolulu, HI: Cooperative National Park Resources Studies Unit, University of Hawaii, Department of Botany (Tech. Rep. 68).

Jacobi, J. D. (1990). *Distribution maps, ecological relationships, and status of native plant communities on the island of Hawai'i*. Unpublished Ph.D. dissertation. Honolulu, HI: University of Hawaii.

Jacobi, J. D. (1993). Distribution and dynamics of *Metrosideros* dieback on the island of Hawai'i: implications for management programs. In R. F. Huettl, & D. Mueller-Dombois (Eds.), *Forest decline in the Atlantic and Pacific Region* (pp. 236–242). Berlin, Germany: Springer-Verlag. https://doi.org/10.1007/978-3-642-76995-5

Jacobi, J. D., Gerrish, G., & Mueller-Dombois, D. (1983). 'Ohi'a dieback in Hawaii: Vegetation changes in permanent plots. *Pacific Science*, *37*, 327–337.

Jacobi, J. D., Gerrish, G., Mueller-Dombois, D., & Whiteaker, L. (1988). Stand-level dieback and *Metrosideros* regeneration in the montane rainforest of Hawai'i. *GeoJournal*, *17*, 193–200. https://doi.org/10.1007/bf02432922

Jane, G. T. & Green, T. G. A. (1983). Vegetation mortality in the Kaimai Ranges, North Island, New Zealand. *Pacific Science*, *37*, 385–389.

Keppel, G., Morrison, C., Meyer, J.-Y., & Boehmer, H. J. (2014). Isolated and vulnerable: the history and future of Pacific Island terrestrial biodiversity. *Pacific Conservation Biology*, *20*, 136–145. https://doi.org/10.1071/pc140136

King, G. A. & Neilson, R. P. (1992). The transient response of vegetation to climate change: A potential source of CO_2 to the atmosphere. *Water, Air, and Soil Pollution*, *64*, 365–383. https://doi.org/10.1007/bf00477111

Kliejunas, J. T. & Ko, W. H. (1973). Root rot of ohia (*Metrosideros collina* ssp. *polymorpha*) caused by *Phytophthora cinnamomi*. *Plant Disease Reporter*, *57*, 383–384.

Kliejunas, J. T. & Ko, W. H. (1976). Association of Phytophthora cinnamomi with ohia decline on the island of Hawaii. *Phytopathology*, *66*, 116–121. https://doi.org/10.1094/phyto-66-116

Lawesson, J. E. (1988). Stand-level dieback and regeneration of forests in the Galápagos Islands. *Vegetatio*, *77*, 87–93. https://doi.org/10.1007/bf00045754

Lewton-Brain, L. (1909). The Maui forest troubles. *Hawaiian Planters' Record*, *1*, 92–95.

Lyon, H. L. (1909). The forest disease on Maui. *Hawaiian Planters' Record*, *1*, 151–159.

Manion, P. D. (1981). *Tree disease concepts*. Englewood Cliffs, NJ: Prentice-Hall Inc.

Mortenson, L. A., Flint Hughes, R., Friday, J. B., Keith, L. M., Barbosa, J. M., Friday, N. J., … Sowards, T. G. (2016). Assessing spatial distribution, stand impacts and rate of *Ceratocystis fimbriata* induced 'ōhi'a (*Metrosideros polymorpha*) mortality in a tropical wet forest, Hawai'i Island, USA. *Forest Ecology and Management*, *377*, 83–92. https://doi.org/10.1016/j.foreco.2016.06.026

Mueller-Dombois, D. (1980). The ohia dieback phenomenon in the Hawaiian rain forest. In J. Cairns Jr (Ed.), *The recovery process in damaged ecosystems* (pp. 153–161). Ann Arbor, MI: Ann Arbor Science Publishers Inc.

Mueller-Dombois, D. (1983). Canopy dieback and successional processes in Pacific forests. *Pacific Science*, *37*, 317–325.

Mueller-Dombois, D. (1985). 'Ōhi'a dieback in Hawaii: 1984 synthesis and evaluation. *Pacific Science*, *39*, 150–170.

Mueller-Dombois, D. (1986). Perspectives for an etiology of stand-level dieback. *Annual Review of Ecology and Systematics*, *17*, 221–243. https://doi.org/10.1146/annurev.es.17.110186.001253

Mueller-Dombois, D. (1987). Natural dieback in forests. *BioScience*, *37*, 575–583. https://doi.org/10.2307/1310668

Mueller-Dombois, D. (1988). Canopy dieback and ecosystem processes in the Pacific area. In W. Greuter, & B. Zimmer (Eds.), *Proceedings of the XIV International Botanical Congress* (pp. 445–465). Koenigstein, Germany: Koeltz.

Mueller-Dombois, D. (2006). Long-term rain forest succession and landscape change in Hawai'i: The 'Maui Forest Trouble' revisited. *Journal of Vegetation Science*, *17*, 685–692. https://doi.org/10.1111/j.1654-1103.2006.tb02492.x

Mueller-Dombois, D. & Fosberg, F. R. (1998). *Vegetation of the tropical Pacific Islands*. New York, NY: Springer-Verlag. https://doi.org/10.1007/978-1-4419-8686-3

Mueller-Dombois, D., Jacobi, J. D., Boehmer, H. J., & Price, J. (2013). *'Ōhi'a Lehua rainforest: born among Hawaiian volcanoes, evolved in isolation: the story of a dynamic ecosystem with relevance to forests worldwide*. Honolulu, HI: Friends of the Joseph Rock Herbarium.

Mueller-Dombois, D., Jacobi, J. D., Cooray, R., & Balakrishnan, N. (1980). *'Ōhi'a Rain Forest Study: Ecological investigations of the 'ōhi'a dieback problem in Hawaii*. Honolulu, HI: Hawaii Agricultural Experiment Station, University of Hawaii.

Mueller-Dombois, D. & Krajina, V. J. (1968). Comparison of east-flank vegetations on Mauna Loa and Mauna Kea, Hawaii. In R. Misra & B. Copal (Eds.). *Proceedings of the Symposium on Recent Advances in Tropical Ecology, Vol. II* (pp. 508–520). Varansi, India: International Society for Tropical Ecology.

Newhook, F. J. & Podger, F. D. (1972). The role of *Phytophthora cinnamomi* in Australian and New Zealand forests. *Annual Review of Phytopathology*, *10*, 299–326. https://doi.org/10.1146/annurev.py.10.090172.001503

Peng, C., Ma, Z., Lei, X., Zhu, Q., Chen, H., Wang, W., … Zhou, X. (2011). A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change*, *1*, 467–471. https://doi.org/10.1038/nclimate1293

Petteys, E. Q. P., Burgan, R. E., & Nelson, R. E. (1975). *Ohia forest decline: its spread and severity in Hawaii*. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station.

Podger, F. (1981). Definition and diagnosis of diebacks. In K. M. Old, G. A. Kile, & C. P. Ohmart (Eds.), *Eucalypt diebacks in forests and woodlands* (pp. 1–8). Melbourne, Australia: CSIRO Publishing.

Price, J. P., Jacobi, J. D., Gon III, S. M., Matsuwaki, D., Mehrhoff, L., Wagner, W. L., … Rowe, B. (2012). *Mapping plant species ranges in the Hawaiian Islands — developing a methodology and associated GIS layers*. Reston, VI: U.S. Geological Survey Open-File Report 2012-1192.

Safeeq, M., & Fares, A. (2012). Hydrologic response of a Hawaiian watershed to future climate change scenarios. *Hydrological processes*, *26*, 2745–2764. https://doi.org/10.1002/hyp.8328

Selmants, P. C., Giardina, C. P., Jacobi, J. D., & Zhiliang, Z. (2017). *Baseline and projected future carbon storage and carbon fluxes in ecosystems of Hawai'i*. Menlo Park, CA: U.S. Geological Survey Professional Paper 1834. https://doi.org/10.3133/pp1834

Sherrod, D. R., Sinton, J. M., Watkins, S. E., & Brunt, K. M. (2007). *Geologic map of the State of Hawai'i*. Reston, VA: U.S. Geological Survey Open File Report 2007-1089.

Stewart, G. H. (1989). Ecological considerations of dieback in New Zealand's indigenous forests. *New Zealand Journal of Forestry Science*, *19*, 243–249.

U.S. Geological Survey (2014). *National elevation dataset (NED)*. Reston, VA: U.S. Geological Survey.

van Mantgem, P. J., Stephenson, N. L., Byrne, J. C., Daniels, L. D., Franklin, J. F., Fulé, P. Z., … Veblen, T. T. (2009). Widespread increase of tree mortality rates in the Western United States. *Science*, *323*, 521–524. https://doi.org/10.1126/science.1165000

Vaughn, N. R., Asner, G. P., Brodrick, P. G., Martin, R. E., Heckler, J. W., Knapp, D. E., & Hughes, R. F. (2018). An approach for high-resolution mapping of Hawaiian *Metrosideros* forest mortality using laser-guided imaging spectroscopy. *Remote Sensing*, *10*, 502. https://doi.org/10.3390/rs10040502

Wagner, W. L., Herbst, D. R., & Sohmer, S. H. (1999). *Manual of the flowering plants of Hawaii: Revised edition*. Honolulu, HI: University of Hawaii Press.

White, T. C. R. (1986). Weather, *Eucalyptus* dieback in New England, and a general hypothesis of the cause of dieback. Pacific Science, *40*, 58–78.

Williams, A. P., Allen, C. D., Macalady, A. K., Griffin, D., Woodhouse, C. A., Meko, D. M., … McDowell, N. G. (2013). Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change*, *3*, 292–297. https://doi.org/10.1038/nclimate1693

Ziegler, A. C. (2002). *Hawaiian natural history, ecology, and evolution*. Honolulu, HI: University of Hawaii Press.

SUPPORTING INFORMATION

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

Appendix S1 Map showing the study area on the eastern side of the island of Hawaii with the area mapped as heavy or severe canopy dieback in 1977, and location of the 25 permanent study plots established in the 1970s

Appendix S2 Map showing the study area, the area mapped as heavy or severe canopy dieback in 1977, and mean annual rainfall classes in mm

Appendix S3 Example of one of the canopy status assessment plots (yellow boundary) showing the detail of the young *M. polymorpha* tree canopy as seen on the Pictometry image taken in 2015 for an area that is recovering from canopy dieback in the 1970s

Appendix S4 Map showing the study area on the eastern side of the island of Hawaii with the area mapped as heavy or severe canopy dieback in 1977, and location of the image assessment plots used to assess current status of the *M. polymorpha* canopy

Appendix S5 Map showing the study area on the eastern side of the island of Hawaii with the area mapped as heavy or severe canopy dieback in 1977, and the modeled potential distribution of *M. polymorpha* canopy dieback based on habitat correlates with canopy dieback and non-dieback areas

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