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Vegetation dynamics at the upper reaches of a tropical montane forest are driven by disturbance over the past 7300 years

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Abstract

We assessed tropical montane cloud forest (TMCF) sensitivity to natural disturbance by drought, fire, and dieback with a 7300-year-long paleorecord. We analyzed pollen assemblages, charcoal accumulation rates, and higher plant biomarker compounds (average chain length [ACL] of *n*-alkanes) in sediments from Waiʻānapanapa, a small lake near the upper forest limit and the mean trade wind inversion (TWI) in Hawaiʻi. The paleorecord of ACL suggests increased drought frequency and a lower TWI elevation from 2555–1323 cal yr B.P. and 606–334 cal yr B.P. Charcoal began to accumulate and a novel fire regime was initiated ca. 880 cal yr B.P., followed by a decreased fire return interval at ca. 550 cal yr B.P. Diebacks occurred at 2931, 2161, 1162, and 306 cal yr B.P., and two of these were independent of drought or fire. Pollen assemblages indicate that on average species composition changed only 2.8% per decade. These dynamics, though slight, were significantly associated with disturbance. The direction of species composition change varied with disturbance type. Drought was associated with significantly more vines and lianas; fire was associated with an increase in the tree fern *Sadleria* and indicators of open, disturbed landscapes at the expense of epiphytic ferns; whereas stand-scale dieback was associated with an increase in the tree fern *Cibotium*. Though this cloud forest was dynamic in response to past disturbance, it has recovered, suggesting a resilient TMCF with no evidence of state change in vegetation type (e.g., grassland or shrubland).

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Introduction

Natural disturbance is a central driver of forest patterns, processes, and dynamics (Pickett and White, 1985). It has been fairly well studied in temperate, boreal, and lowland tropical forest ecosystems, but little research has focused on the role of natural disturbance in tropical montane cloud forest (TMCFs). Overall, TMCFs are viewed as being slow to recover from disturbance because of very slow growth rates (Bruijnzeel et al., 2010). Understanding the role of disturbance in TMCFs is particularly important now because climate change can alter climate-driven disturbance regimes. These changes can in turn catalyze rapid ecological change (Turner, 2010) in an ecosystem considered vulnerable to climate variability (e.g., Loope and Giambelluca, 1998; Foster, 2001). The perception of a "fragile" TMCF suggests changes in natural disturbance characteristics may alter TMCF composition and structure, perhaps even heralding vegetation state changes and the loss of cloud forest area, with important implications for biodiversity and water resources.

The natural disturbance regime of any particular TMCF varies geographically, but may be characterized by windstorms and hurricanes, fire, volcanic eruptions, landslides, stand-scale dieback, and/or gap dynamics. Many of these disturbances are climate-driven. Hurricanes are themselves a weather phenomenon and paleorecords suggest that in the Caribbean hurricane frequency is modulated by sea surface temperature, El Niño–Southern Oscillation (ENSO), and the West African monsoon (Donnelly and Woodruff, 2007). Landslides are more frequent in regions with high rainfall and are often triggered by heavy rainfall events (Walker et al., 1996; Paolini et al., 2005). Stand-scale dieback can be caused by droughts or other strong climate fluctuations, or simply by the accumulated climate stress experienced by a cohort of trees (Mueller-Dombois, 1986; Werner, 1988; Dezzeo et al., 1997; Auclair, 1993; Fashing, 2004). A more frequent and severe fire regime can be generated by warming, drying, and increased climate variability (Martin and Fahey, 2006; Hemp, 2009). In fact, since the Last Glacial Maximum, fire activity and climate variability have shown a positive relationship in the Neotropics, as a result of insolation-driven changes in moisture (Power et al., 2010).

Understanding how changes in climate-driven disturbances influence the ecology and potential for vegetation state changes in TMCFs is important. But predicting how changes in the distur-

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bance regime will affect ecosystems is a complex challenge for tropical montane ecologists. We need long ecological records to elucidate the full range of variability in disturbance and to understand the ecological impacts of changes in disturbance characteristics (Whitlock et al., 2010). High-resolution paleoecological records can offer the needed long time scale and high temporal resolution to focus on the role of disturbance in ecosystems. Paleoecological data show that the biogeochemical consequences of disturbance are often short-lived, but there is a gradient from resistance to resilience to complete state change in ecosystem processes (McLauchlan et al., 2014). Often, vegetation type determines the nature and timing of biogeochemical response to disturbance (McLauchlan et al., 2014). Because vegetation type is such an important component of how systems recover from disturbance, understanding the sensitivity of species composition to disturbance, and the likelihood for vegetation state change, is an important research goal.

We provide long ecological records of species composition and natural disturbance in a TMCF in Hawai‘i that is now, and historically has been, largely free of anthropogenic disturbance. The natural disturbance regime for Hawaiian TMCFs includes volcanic activity (Sherrod et al., 2007), isolated landslides, gap dynamics (Kellner and Asner, 2009), stand-scale dieback (Mueller-Dombois, 1980), windstorms (rarely hurricane force), and El Niño–induced droughts (Crausbay et al., 2014). The role of fire in the natural disturbance regime is largely unknown (Smith and Tunison, 1992) and there is no clear evidence of fire in Hawaiian TMCFs today. Our paleorecords focus on three disturbance types—stand-scale dieback, drought, and fire. We characterize TMCF vegetation response to changes in disturbance to determine whether on long time scales this system was resistant, resilient, or experienced vegetation state changes.

Study Area

The main Hawaiian Islands are situated a few degrees below the Tropic of Cancer and are near the poleward edge of the Hadley Cell (Fig. 1, part a). As a result of this geography, high elevations in the Hawaiian Islands are under the influence of the trade wind inversion (TWI), which has a mean base height ranging from 2076 to 2255 m (Cao et al., 2007). The summit of Haleakalā volcano extends to 3055 m on the island of Maui (Fig. 1, part a). Wai‘ānapanapa is a small, shallow lake situated at 2100 m near the mean TWI on Haleakalā's windward face (Fig. 1, part b, 20º44′16.01″N, 156º7′23.88″W). The lake is among a string of lakes and bogs distributed along Haleakalā's northeast volcanic rift zone from 1450 to 2300 m elevation and sits within a collapsed cinder cone from a vent deposit dated at 50,000–140,000 years old (Sherrod et al., 2007). Wai‘ānapanapa is surrounded by cloud forest and sits very near the forest's upper limit (Fig. 2, parts a–b).

The climate of the study area is characterized by northeasterly trade winds, which bring orographic rainfall and clouds to windward areas below the TWI. Rainfall near the upper limit of cloud forest is ~5200 mm per year, relative humidity averages about 85%, and mean annual temperature is 10.7 °C (Crausbay, unpublished data).

The sharp upper limit of cloud forest abuts a subalpine shrubland at higher elevations (Crausbay and Hotchkiss, 2010). Forest line significantly limits many species' distributions (Crausbay and Hotchkiss, 2010). The cloud forest is dominated by *Metrosideros polymorpha* Gaudich (Myrtaceae), and above it the subalpine shrubland is dominated by *Leptecophylla tameiameiae* (Cham. and Schlecht.) C. M. Weiller (Ericaceae) and the tree fern *Sadleria cyatheoides* Kaulf. (Blechnaceae).

Humans arrived in the Hawaiian Islands only ca. 1200 years ago (Kirch, 2007). Neither Hawaiians (Burney et al., 1995) nor early Europeans utilized these upper TMCFs extensively and they have never been logged. As a result, the study area is largely free of human disturbance. A notable exception is the presence of feral non-native ungulates in the study area at various times since European contact. Alpine grasslands and subalpine shrublands above the TWI experienced the majority of ungulate influence. Here, the invasion of non-native plants with a temperate lineage followed the ungulates, and though there has been significant recovery of native plants following feral animal removal (Hughes et al., 2014), non-native plants still persist, especially in the alpine grassland. In contrast, the upper TMCF largely resisted invasion by non-native plants (Loope et al., 1992). Currently, the area from the alpine grassland to the upper montane forest is considered ungulate-free following an intensive fencing and eradication program.

Methods

SEDIMENT CORING AND CHRONOLOGY

We recovered a 7.1-m-long sediment sequence from Wai‘ānapanapa (1 m water depth) with a modified Livingstone piston corer. Upper sediments were collected with a 2- to 3-m-long, 7-cm-diameter polycarbonate tube fitted with a tennis-ball piston. We captured the sediment-water interface this way and subsampled the upper meter of sediment on site in 0.5-cm intervals. Deeper sediments were collected with a 1-m-long, 5-cm-diameter stainless steel barrel fitted to a Livingstone piston. Cores were extruded from the aluminum barrel and wrapped in plastic and aluminum foil and sealed in polyvinyl chloride (PVC) tubes. The tops of polycarbonate tubes were stuffed with floral foam to absorb excess water and pack the unconsolidated surface sediments to preserve the stratigraphy as cores were transported. Cores were sent to LacCore, the National Lacustrine Core Facility hosted by the Limnological Research Center at the University of Minnesota (Minneapolis, Minnesota), where they were split longitudinally into working and archived halves, photographed, and subjected to magnetic susceptibility analysis. The working halves of sediment cores were sliced into 0.5-cm intervals.

Dating control was provided by 14 accelerator mass spectrometer (AMS) ^{14}C measurements on terrestrial plant material, including leaves, stems, seeds, wood, and pollen/spore concentrates obtained with heavy liquid separation (Table 1). Radiocarbon dates were calibrated with IntCal09, converted to cal yr before present (B.P.), where "present" is 1950 C.E., and age-depth models were constructed using the Bayesian techniques in the P_Sequence algorithm in OxCal v4.1.7 software with $k = 1$ cm (Bronk Ramsey, 2009). A basal date was analyzed after most sampling, causing a difference in sampling resolution in the lower half of the core.

POLLEN

To reconstruct vegetation, we used 42 subsamples of 1 cm^3 of sediment on average every 13 cm to concentrate pollen/spores using standard techniques including acetolysis (Faegri and Iversen, 1989). Pollen was rarely sampled from the same centimeters as *n*-alkanes, because sediment requirements for *n*-alkanes left little sediment for additional sampling. Each pollen sample was processed at LacCore. Pollen/spore residues were mounted in sili-

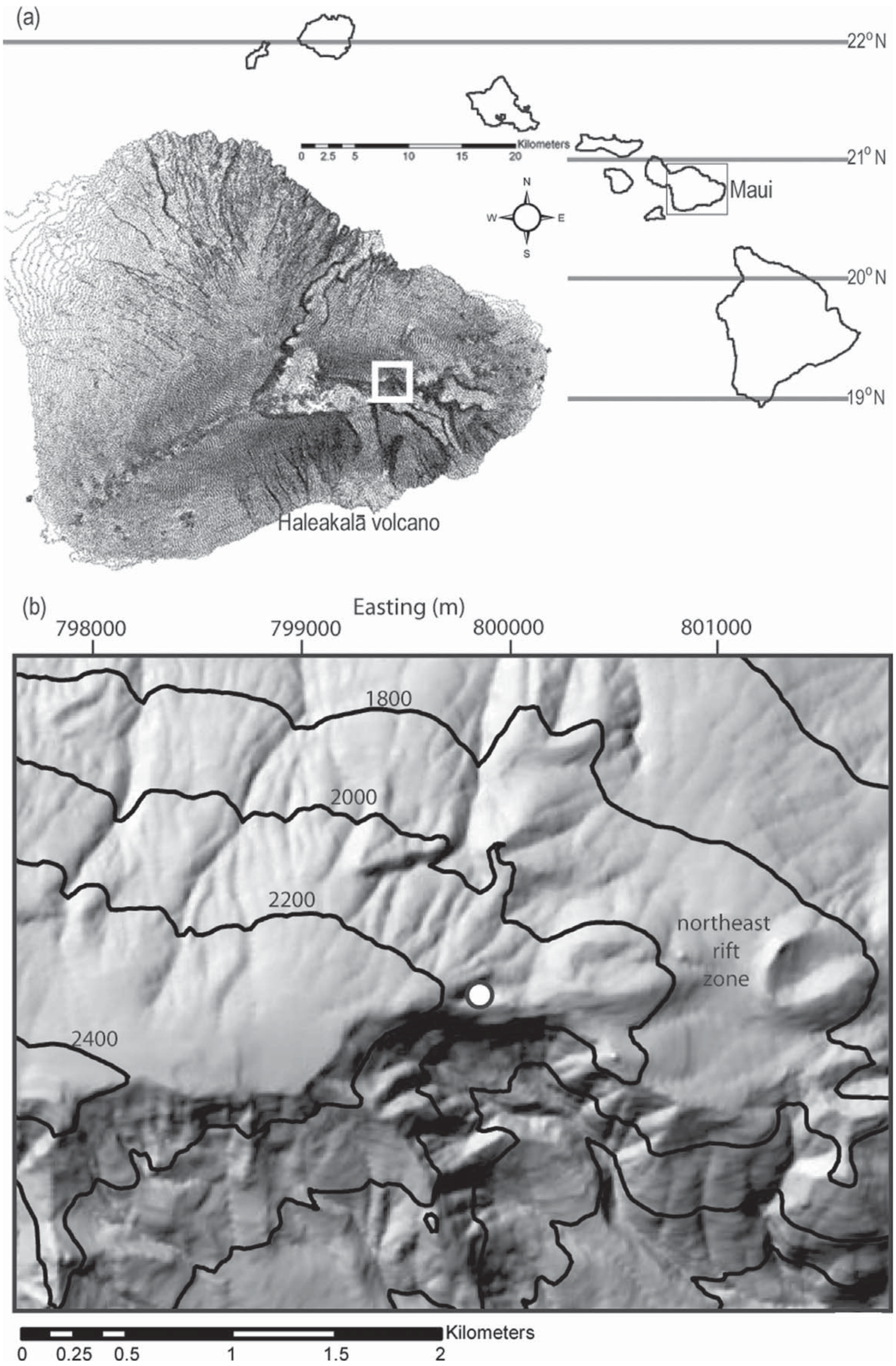

FIGURE 1. (a) Regional location of the study site on Haleakalā volcano, on the Hawaiian Island of Maui. (b) Location of Wai'ānapanapa within the northeast rift zone at high elevation on windward Haleakalā, with easting in meters from the UTM coordinate system (NAD83, UTM Zone 4).

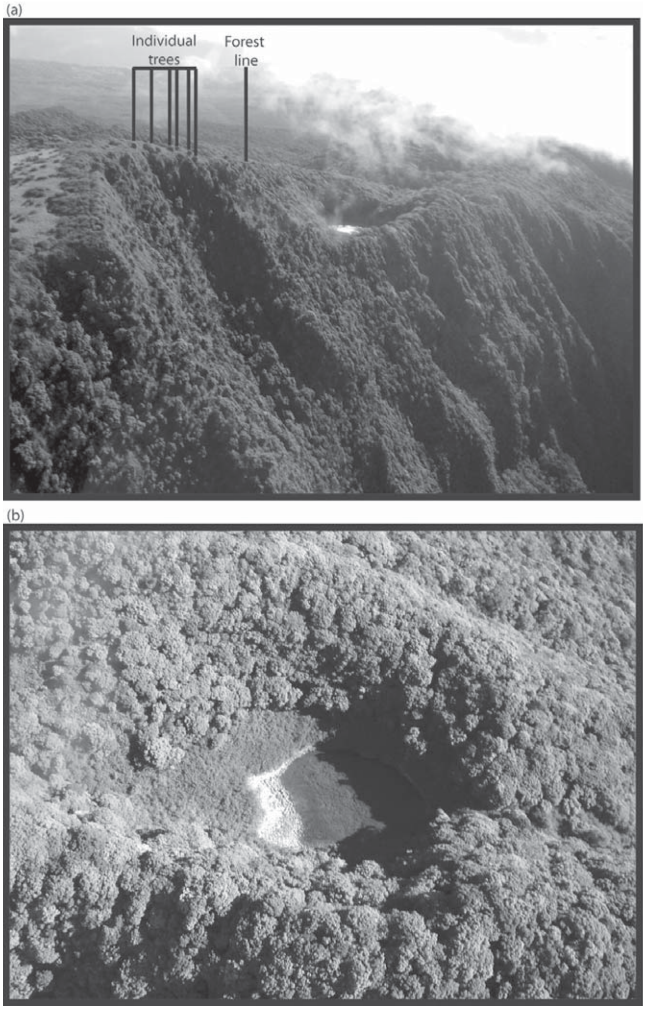

FIGURE 2. (a) Photograph of Wai'ānapanapa showing its position relative to the upper limit of cloud forest and (b) the dense cloud forest that surrounds the lake basin. Photo by Gregor Schuurman.

cone oil, and all pollen and fern spores were quantified at 400× and sometimes 1000× until we reached a sum of 500 pollen grains (excluding any fern spores). Counts averaged 630 pollen grains (range = 520 – 1068). Pollen and spore percentages were then calculated from raw counts after psilate monolete fern spores and wetland taxa (Poaceae, Cyperaceae, Tubuliflorae undifferentiated, *Plantago*) were excluded from the sum (after Crausbay and Hotchkiss, 2012).

BIOMARKERS

We reconstructed the drought regime with the abundance of sedimentary *n*-alkanes, calibrated by modern samples across an elevational gradient. The modern samples focused on two types of *Metrosideros polymorpha* leaves—a glabrous variety (var. *microphylla*) abundant at lower elevations in wetter areas and pubescent varieties (var. *polymorpha* and var. *incana*) abundant at higher elevations in drier areas. The modern leaf sites include (1) four pubescent and three glabrous sites taken along an elevational gradient from ~100 m to 2400 m a.s.l. on the windward, east slope of Mauna Loa volcano on the Island of Hawai'i (Kahmen et al., 2011), and (2) two pubescent sites near the modern TWI on the windward side of the island of Maui at 2040 m and 2090 m. Alkanes were analyzed on 27 samples, which included several *M. polymorpha* leaves from three trees at each of the nine sites. Since leaf wax composition was very similar among the replicates (three trees per site), we report only mean site average chain length (ACL) of *n*-alkanes here (standard deviations for the ACL ranged between 0.17 and 0.69, with a mean standard deviation of 0.41).

This modern library of *M. polymorpha n*-alkanes aids the interpretation of *n*-alkanes on samples from the sediment core. To measure sedimentary *n*-alkanes, we took 48 subsamples of 5 cm^3 of sediment on average every 11 cm. All alkanes were extracted in the organic geochemical laboratory at University of Potsdam, Germany, using an accelerated solvent extraction system (ASE 350, Dionex Corp., Sunnyvale, California, U.S.A.) to obtain total lipid extracts. Total lipid extracts were further separated using silica gel chromatography (solid phase extraction, SPE) into three fractions:

TABLE 1

Accelerator mass spectrometry ^{14}C ages from a sediment sequence from Wai'ānapanapa on the Hawaiian Island of Maui.

Lab ID	Depth (cm)	Material	$\delta^{13}C$ (‰)	^{14}C age (yrs)
UGAMS–7013	56.5	stem, moss	–28.2	140 ± 40
UGAMS–7015	129.8	Cyperaceae seeds	–26.0	460 ± 40
UGAMS–7018	196.8	*Metrosideros* leaf	–27.2	500 ± 40
UGAMS–5984	249.0	pollen, fern spores	–28.3	1560 ± 30
UGAMS–7016	347.3	wood	–28.3	1760 ± 40
UGAMS–7017	370.8	wood	–27.4	1860 ± 40
UGAMS–7019	382.0	wood	–28.6	1900 ± 40
UGAMS–7012	424.8	wood	–29.2	2170 ± 40
UGAMS–7011	453.8	wood	–28.4	2390 ± 40
UGAMS–7014	463.0	wood	–28.6	2550 ± 40
UGAMS–8789	491.6	pollen, fern spores	–27.2	2950 ± 30
UGAMS–8790	510.3	pollen, fern spores	–26.8	4720 ± 35
UGAMS–8168	546.3	pollen, fern spores	–27.7	6250 ± 25

hydrocarbons (containing the *n*-alkanes), alcohols, and fatty acids. The first fraction containing the *n*-alkanes were analyzed using an Agilent 7890A Gas Chromatograph (GC) with an Agilent 5975C mass spectrometric detector (MSD) to identify and with a flame ionization detector (FID) (Agilent Technologies, Palo Alto, California, U.S.A.) to quantify biomarkers; the other fractions were archived. A more detailed description of the *n*-alkane extraction procedure and GC-MSD/FID measurement is given elsewhere (Garcin et al., 2012). Peak areas of nC_{25} to nC_{33} alkanes were obtained from the FID detector trace for the calculation of the average chain length values.

CHARCOAL

We reconstructed the fire regime with a contiguous record of microscopic charcoal fragments. Influx of small fragments of charcoal records the occurrence of past fires and both theoretical and empirical studies demonstrate that charcoal >125 µm provides the best indication of local fires (methods reviewed in Whitlock and Larsen, 2002). We quantified charcoal particles >125 µm in contiguous 0.5-cm increments of the sediment core. For each sample, we processed 1 cm^3 of sediment by treating with hot 10% KOH, sieving, transferring material >125 µm to a petri dish, and "bleaching" the sample with 30% H_2O_2 in a drying oven at 60 °C for 24 hours. We counted charcoal particles at 60× magnification on a dissecting microscope.

DATA ANALYSIS—POLLEN

To assess overall stability of vegetation, we conducted rate-of-change analysis with the Sørensen distance metric, $2w/(a + b)$, where w is the sum of shared abundances and a and b are the sums of abundances in individual sample units, to quantify the dissimilarity between all adjacent pollen/spore spectra (McCune and Grace, 2002). We divided the resulting dissimilarity index, expressed as percentages where values range from 100% (no species in common) to 0% (identical species composition), by the number of years elapsed between samples (e.g., Cole, 1985; Gavin et al., 2013). This analysis was performed in PAST™ 2.17c (Hammer et al., 2001; can be accessed at http:folk.uio.no/ohammer/past).

To assess variation in vegetation community composition, pollen percentages were subjected to nonparametric multidimensional scaling (NMS). Runs started with six axes and a random starting configuration, with a maximum of 500 iterations, an instability criterion of 0.0000001, 250 runs with real data, and 250 randomized runs. Dimensionality was selected by comparing the final stress values among the best solutions for each dimensionality, beginning with two dimensions, and adding additional dimensions only if they reduced the final stress by 5% or more. Final stress was lower than that for 95% of the randomized runs (i.e., $P < 0.05$ for the Monte Carlo test). Axes are orthogonal and statistically independent. Variance explained was distributed among the primary axes by calculating the coefficient of determination (r^2) between distances in the ordination space and distances in the original space. Ordinations were based on a Sørensen distance matrix. Correlations between an individual taxon's abundance and axis scores were assessed with a Pearson's r. All of these analyses were performed in PC–ORD™ 6.0 (MjM Software Designs, Gleneden Beach, Oregon, U.S.A.).

DATA ANALYSIS—BIOMARKERS

We used peak areas of nC_{25} to nC_{33} alkanes for the calculation of the ACL index using the following equation:

$$\mathrm{ACL} = \Sigma n * area(C_n)\ \Sigma area(C_n)^{-1}, \qquad (1)$$

where n is number of carbon atoms of the alkane and $area(C_n)$ the appropriate area of the compound with n carbon atoms.

We compared the sedimentary paleorecord of ACL to the sediment surface sample, interpreted in a context of *n*-alkane concentration and ACL of modern *M. polymorpha* leaf samples. Drought is defined as a time period when samples frequently showed ACL lower than the sediment surface sample, because the site is currently situated at the modern mean TWI on a steep moisture gradient. These samples likely originated from a greater abundance of the pubescent *M. polymorpha* variety, suggesting drier conditions and a TWI below Wai'ānapanapa.

DATA ANALYSIS—CHARCOAL

We reconstructed local fire events and fire return interval by separating charcoal accumulation curves into a low frequency "background" component and a high frequency "peak" component. Charcoal concentration was first interpolated to the median sample interval of 2.5 years and smoothed using LOWESS with a window width of 300 years (Higuera et al., 2009). Peaks most likely to represent local fires were identified in CharAnalysis as $C_{peak} = C_{interpolated} - C_{background}$, with a locally defined threshold level with a 300-year window and a Gaussian mixture model that fits two overlapping distributions to the peak frequency distribution for the sediment core. Threshold values that identify a peak, and thus a fire event, were determined as a percentage of the noise distribution, with only peaks >99.9% of the noise distribution retained for peak analysis and calculation of fire return intervals. Peaks were discarded if the minimum charcoal particle count within 75 years of a peak had a >5% chance of coming from the same Poisson distribution as the maximum peak sample count. Peaks that passed both the threshold and the minimum count test were used to calculate fire return interval. We used the program CharAnalysis, written by P. E. Higuera and freely available at https://sites.google.com/site/charanalysis/. We compared charcoal accumulation rates from three periods of the Wai'ānapanapa record with a Kruskal-Wallis one-way analysis of variance (ANOVA) on ranks and conducted a pairwise multiple comparison procedure using Dunn's Method; all performed in SigmaPlot™ version 12.0 (Systat Software, San Jose, California).

DATA ANALYSIS—VEGETATION AND DISTURBANCE

To show the relationship between disturbance and vegetation, we first categorized each pollen sample based on evidence of fire (defined by charcoal), evidence of drought (defined by ACL), and evidence of dieback (defined by samples with <35% tree pollen and scores <–1.2 on axis 2, see Results). We quantified whether species composition was significantly different in samples associated with a particular type of disturbance (e.g., drought vs. no drought, fire vs. no fire, and dieback vs. no dieback), with a multiresponse permutation procedure (MRPP), a nonparametric method for testing multivariate differences among predefined groups. We used a Sørensen distance measure and a weighting option for each item in the group = $n(I)\ \mathrm{sum}(n(I))^{-1}$. MRPP provides a chance-corrected within-group agreement value, $A = 0$ when heterogeneity within groups equals expectation by chance; $A = 1$ when all items are identical within groups. We identified the taxa that were correlated with a particular disturbance type with Indicator Species Analysis (ISA) based on Dufrêne and

Legendre's (1997) method. We also identified species composition groups, independent of disturbance type, with hierarchical agglomerative clustering (flexible beta = –0.25 linkage method based on a quantitative Sørensen distance matrix, McCune and Grace, 2002) and stratigraphically unconstrained pollen assemblage data. To visualize the relationship between vegetation and disturbance, we overlaid these independently derived species composition groups on the ordination, along with disturbance ellipses. All of these analyses were performed in PC–ORD™ 6.0.

Results

LITHOLOGY AND CHRONOLOGY

The sediment sequence from Waiʻānapanapa is variable over its 7.1 m length. The basal ~30 cm of sediments consists of organic-rich diatomaceous silty tephra with a gradual transition to organic-rich diatomaceous silty clay (descriptions following Schnurrenberger et al., 2003). This diatomaceous silty clay is interrupted by a slump of sediment at 3.9–5.2 m depth which we removed from the age-depth model. The slump is characterized by a rocky (>1 cm), silty tephra accompanied by copious large pieces of wood and roots. We constrained the date of this slump with a radiocarbon date above and 20 cm below it (1900 ± 40 and 2170 ± 40 cal yr B.P., Fig. 3). The slump was likely caused by a landslide and is dated at 1850 cal yr B.P. (Fig. 3). The model shows the basin had a slow sedimentation rate for the first four millennia (from 7300 to 3200 cal yr B.P.), and after 3200 cal yr B.P., sedimentation rate increased (Fig. 3).

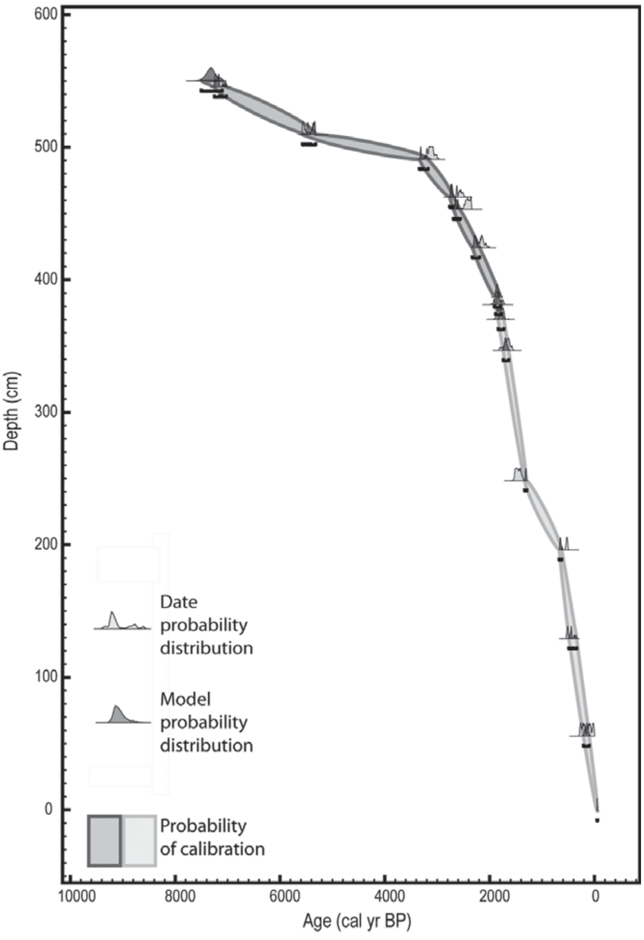

FIGURE 3. Age-depth model for Waiʻānapanapa at 2103 m on windward Haleakalā. Width of the color bands describes the degree of uncertainty in the model. Two shades of gray meet at the site of a slump, ~1850 cal yr BP, which was removed from the age-depth model. Models were created with OxCal v4.1.7 (Bronk Ramsey, 2009).

POLLEN ANALYSIS

Because of the strong change in sedimentation rate at ca. 3000 yr ago (Fig. 3), pollen samples are on average ~90 years apart from the present to 3000 yr ago and ~ 500 years apart from 3000–7300 yr ago (Appendix Fig. A1). The rate of change in species composition from sample to sample averaged 2.8% decade^{-1} (range 0.2 to 5.1), suggesting species composition was nearly identical between different adjacent samples. A non-metric multidimensional scaling ordination of all pollen assemblages over the past 7300 cal yr B.P. explained 93.2% of the variation in species composition with three axes, with the majority of variation (82.3%) on two axes (axis 1 = 54.5%, axis 2 = 27.8%; Fig. 4, parts a–b). Hierarchical cluster analysis identified four groups of pollen assemblages that were significantly different (MRPP, $A = 0.20$, $P = 0$, Fig. 4, parts a–b).

BIOMARKER ANALYSIS

The overall concentrations of *n*-alkanes from modern *M. polymorpha* leaves were significantly different between pubescent and glabrous varieties (mean = 77.8 and 259.1 μg g^{-1} dry weight, respectively). The ACL values of modern *M. polymorpha* leaves also clearly separated the pubescent and glabrous varieties, with values of pubescent varieties in higher elevation, drier sites averaging 26.92 (range 26.28–27.89) and values of glabrous varieties in lower elevation, wetter sites averaging 30.58 (range 30.44–30.78). Three of the four pubescent sites sit near the mean TWI, and their ACL averaged 26.83.

Because of the strong change in sedimentation rate at ca. 3000 yr ago (Fig. 3), *n*-alkane samples are on average ~70 years apart from the present to 3000 yr ago and ~650 years apart from 3000–7300 yr ago. Throughout the sediment core we found nC$_{25}$ to nC$_{33}$ alkanes to be the major constituents of the first SPE fraction. Average chain length values showed remarkable variability throughout the core, ranging from 26.89 to 30.32 (Fig. 4, part c). The ACL value for the surface of the sediment core was 28.07, suggesting this value represents the mean TWI in sedimentary ACL. This value is higher than the ACL from modern pubescent leaf samples near the TWI (26.83), likely because of the lower concentration of *n*-alkanes in pubescent varieties, relative to glabrous varieties, that are contributing to the sediment sample (the lake is surrounded by both pubescent [~80%] and glabrous [~ 20%] varieties today; Crausbay, unpublished data). The ACL was lower than the surface sample at various times from 2555–1323 cal yr B.P. and 606–334 cal yr B.P. (Fig. 4, part c), suggesting greater abundance of pubescent varieties and a TWI situated at an elevation below Waiʻānapanapa. We define these two periods as having an increased drought frequency. The lowest ACL value (26.89) in the record was observed at 425 cal yr B.P.

CHARCOAL ANALYSIS

The majority of this sediment sequence—from 7300 cal yr B.P. until ~880 cal yr B.P.—contained very few charcoal particles (range 0–4, median 0, Fig. 4, part d). Between ca. 880 and 500 cal

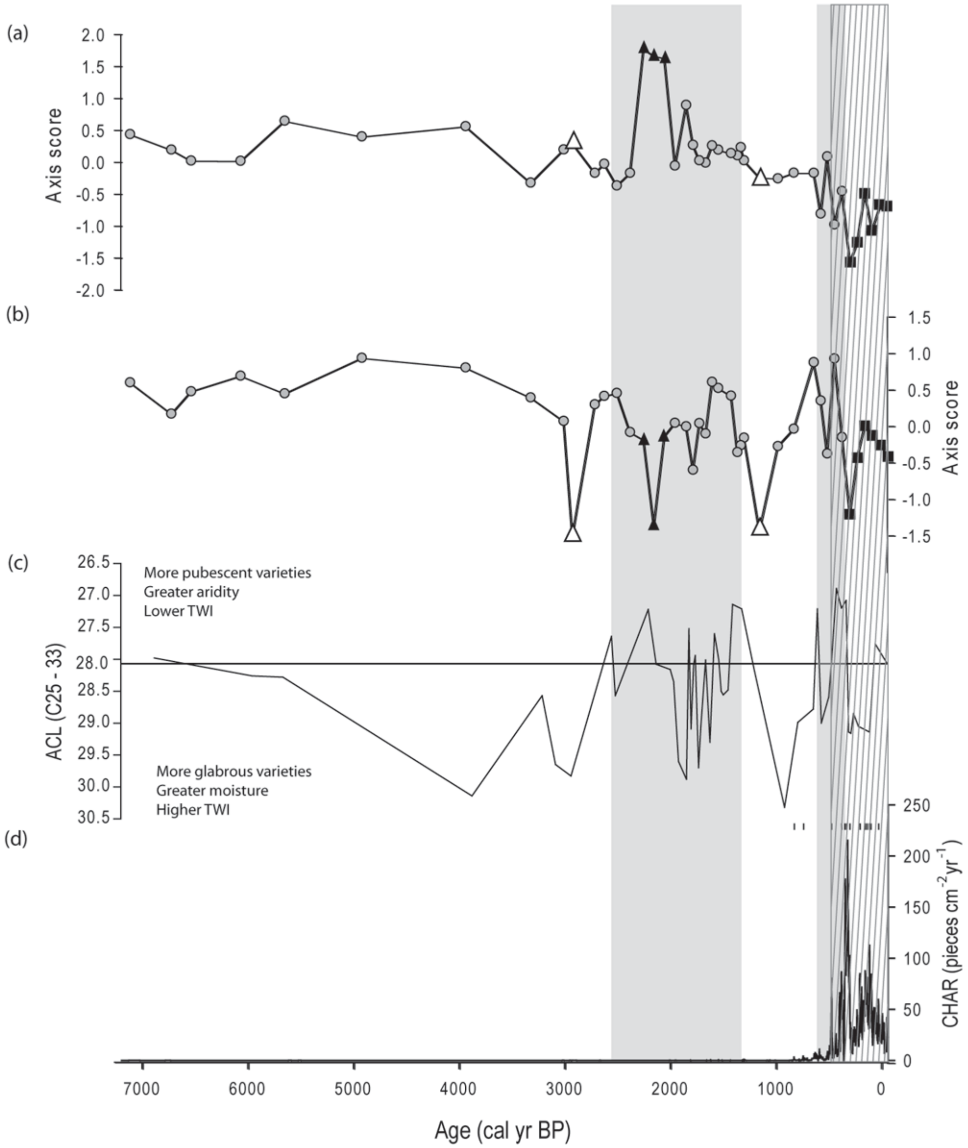

FIGURE 4. Changes over time in (a) axis 1, and (b) axis 2 of a nonmetric multidimensional scaling (NMS) ordination of pollen/spore assemblages from Wai'ānapanapa, which sit at the modern mean trade-wind inversion (TWI) on windward Haleakalā, Maui. In graphs a-b, the species composition group to which each sample is assigned is shown; gray circles = cluster group 1, white triangles = cluster group 2, black triangles = cluster group 3, and black squares = cluster group 4 (see Fig. 5, part d). (c) Average chain length (ACL) from leaf waxes over time from Wai'ānapanapa. A horizontal line is drawn at the surface sediment sample with ACL = 28.07. Samples above this line (lower ACL) suggest more pubescent M. polymorpha and a drier site, with a lower-elevation TWI; samples below the line (higher ACL) suggest more glabrous M. polymorpha and a wetter site, with a higher-elevation TWI. Time periods with increased drought frequency are shown with a gray background, in regions of the ACL paleorecord with repeated samples of ACL lower than the modern surface sample, and (d) charcoal accumulation rates from Wai'ānapanapa, with samples interpolated to 2.5-year intervals. Fires that meet the 99.9% threshold are indicated with vertical lines. Time of decreased fire return interval is highlighted with a hachured background.

yr B.P., charcoal particle accumulation rates averaged 1.64 pieces cm^{-2} yr^{-1} (range 0–11, Fig. 4, part d), with one small peak at 835 cal yr B.P. and one at 750 cal yr B.P., suggesting fire return intervals averaged about ~170 years (range 85–267). After ca. 500 cal yr B.P., charcoal accumulation averaged 39.05 pieces cm^{-2} yr^{-1} (range 0–215, Fig. 4, part d). Eleven peaks were identified between 500 and –55 cal yr B.P. (at 483, 388, 355, 340, 310, 213, 163, 145, 123, 110, and 38 cal yr B.P.), with large peaks of 190 and 143 pieces cm^{-2} yr^{-1} at 123 and 110 cal yr B.P. and very large peaks of 788 and 4717 pieces cm^{-2} yr^{-1} at 355 and 340 cal yr B.P. (Fig. 4, part d). Fire return intervals from 500 to –55 cal yr B.P. averaged about 44.5 years (range 13–97). Charcoal accumulation is significantly different between all three time periods (7300–880 cal yr B.P., 880–500 cal yr B.P., and 500 cal yr B.P. to the present; H = 2097.6, $P < 0.001$).

VEGETATION AND DISTURBANCE

Pollen assemblages themselves provided evidence for dieback. Axis 2 of the NMS ordination showed brief negative excursions (<–1.2, Fig. 4, part b), and a Pearson's correlation showed that negative positions on axis 2 had significantly lower abundance of pollen from the two most abundant trees in the TMCF today, *Metrosideros* and *Myrsine* (r = –0.65 and –0.67, respectively). The four samples that constitute these brief negative excursions on axis 2 have the lowest ranks for total tree pollen. We interpret these four samples as times of dieback. The three disturbance types—dieback, drought, and fire—were distinguished in an ordination of pollen assemblages (Fig. 5, parts a–c). Pollen assemblages were significantly different between samples associated with drought (MRPP, chance-corrected within-group agreement A = 0.02, P = 0.035), fire (MRPP, A = 0.06, P = 0.000001), and dieback (MRPP, A = 0.05, P = 0.00012). Some taxa were significantly associated with a particular disturbance type (Table 2). Species assemblage groups, determined independently of disturbance types in hierarchical cluster analysis, are clearly separated in ordination space and occur within the polygons defining different disturbance types (Fig. 5, part d). Group four was negative on axis 1 and is a subset of samples associated with fire from 452 cal yr B.P. to the present; group three was positive on axis 1 and is a subset of samples as-

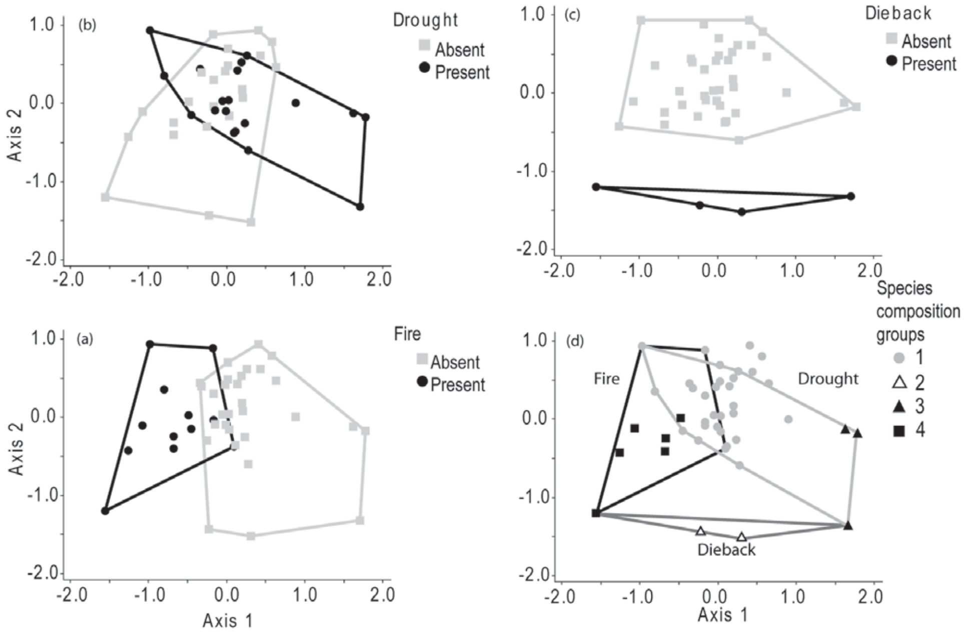

FIGURE 5. The two most important axes of a non-metric multidimensional scaling ordination of pollen assemblages from Wai'ānapanapa on east Maui, which show samples with evidence of (a) drought, (b) fire, and (c) dieback. (d) shows four species composition groups defined by a stratigraphically unconstrained cluster analysis (MRPP, A = 0.20, P = 0; also see Figs. 4, parts a and b) with polygons surrounding the three disturbance types. Axis 1 explains 54.5% of the variation in species composition, and axis 2 explains 27.8% (axis 3, not shown, explains 10.9%).

TABLE 2

Indicator species analysis showing pollen and spore types that are significantly ($P < 0.05$) more (+) or less (–) frequent/abundant in samples associated with each disturbance type. Pollen/spore assemblages are from a 7300 cal. yr BP record from Wai'ānapanapa near the upper limit of cloud forest on the Hawaiian Island of Maui.

Drought	Fire	Dieback
Lamiaceae +	*Fragaria* +	Grammitidaceae +
Rumex +	Chenopodiaceae +	*Cibotium* +
	Dicranopteris +	
	Sadleria +	
	Gunnera +	
	Hypolepis +	
	Grammitidaceae –	

sociated with drought from 2259–2061 cal yr B.P. (Fig. 5, part d). Group two was negative on axis 2 and defines dieback events in which total tree pollen percentages are <35% (Fig. 4, part b, and Fig. 5, part d, Appendix Fig. A1). These clear, brief negative excursions on axis 2 occurred at 2931, 2161, 1162, and 306 cal yr B.P.; 2161 and 306 cal yr B.P. both occur during periods with evidence for drought and 306 cal yr B.P. is coincident with evidence of a local fire at 310 cal yr B.P.; the events at 2931 and 1162 cal yr B.P. do not correspond with evidence of either fire or drought (Fig. 4 and Fig. 5, part d).

Discussion and Conclusions

DYNAMICS OF A TROPICAL MONTANE CLOUD FOREST

Species composition in this Hawaiian montane cloud forest was relatively stable over the past seven millennia, changing on average less than 3% every decade, with a maximum change rate of only up to 5% per decade. Dynamics in this TMCF over the past several millennia can be explained by three disturbances and their interactions—drought, fire, and dieback (Figs. 4 and 5). Drought frequency increased from ca. 2500 to 1300 cal yr B.P. and again from ca. 600 to 300 cal yr B.P. A novel fire regime began when the environment was becoming drier at ca. 880 cal yr B.P., whereas fires were entirely absent at this site for the previous ~7300 years. Fire return intervals then decreased dramatically during the latter drought period, beginning ca. 550 cal yr B.P. Evidence of widespread dieback events occurred on millennial time scales, suggesting diebacks are an inherent component of TMCF dynamics in Hawai'i and can occur with or without drought or fire. These disturbances and their interactions did not herald state changes, but were characterized by different abundances of vines, lianas, tree ferns, and disturbance-indicating taxa.

DROUGHT REGIME

Today in Hawai'i, the drought regime is driven partly by El Niño. These El Niño events dramatically reduce rainfall, especially in winter, by varying trade-wind strength, disrupting the development of subtropical cyclones and upper-level lows, and hindering the passage of mid-latitude frontal systems (Chu and Chen, 2005). Strong El Niño droughts also tend to lower the elevation of the TWI base height and increase aridity above its mean position (Cao et al., 2007; Crausbay et al., 2014). Recently, multiple high-resolution paleorecords of ENSO (Riedinger et al., 2002; Moy et al., 2002; Rein et al., 2005; Koutavas et al., 2006; Conroy et al., 2008) provide coherent evidence of maximum ENSO frequency, magnitude, and duration between ca. 2000 and 1000 yr ago, likely the highest ENSO event-frequency during the Holocene (Conroy et al., 2008). Biomarkers from Wai'ānapanapa suggest drought frequency increased and the TWI was at a lower elevation during this period. A nearby higher-elevation pollen record also suggests a drier environment after ca. 2200 cal yr B.P. (Burney et al., 1995). Together, these data suggest a lower TWI around this time of maximum El Niño frequency.

There is some evidence that El Niño–induced droughts are ecologically relevant in this Hawaiian TMCF because they may limit the cloud forest's upper elevation (Crausbay et al., 2014) and influence leaf phenology (Pau et al., 2010). However, understanding the influence of El Niño on TMCF species composition necessarily requires long ecological records. Soon after the drought regime began intensifying ca. 2500 years ago, pollen assemblages (axis 1) changed dramatically (at ca. 2260 years ago), and made positive excursions in ordination space (Fig. 4, part a). A dieback event peaked around this time at 2160 cal yr B.P., suggesting the interaction of drought and dieback caused one of the strongest changes this TMCF experienced in ~7300 years. This interaction of drought and dieback was associated with significantly more vines and lianas. *Rumex*—a pollen type likely representing the scandent liana *R. giganteus,* which is endemic to the Hawaiian Islands—appears for the first time since ca. 7300 cal yr B.P. at the onset of this ENSO-associated drought regime (ca. 2500 cal yr B.P.; see Appendix Fig. A1). Another pollen type—Lamiaceae, likely representing scandent and decumbent vines in the endemic genus *Stenogyne*—shows a strong, short-lived peak during the drought plus dieback centered on 2160 cal yr B.P. (see Appendix Fig. A1). Overall, these data suggest that this forest responded to increased drought frequency with dieback of some prominent cloud forest tree taxa and increases in vines and lianas. Recently, vines have increased in biomass in many lowland tropical forests. Although the driver is unknown, this widespread pattern may be the result of increasing aridity, disturbance, CO_2, and/or temperature (van der Heijden and Phillips, 2008; Schnitzer and Bongers, 2011). Our work suggests that increasing aridity is associated with increased abundance of vines and lianas. Recent work shows that vines reduce a forest's capacity to accumulate carbon (Schnitzer et al., in press), suggesting changes in the drought regime may alter C cycling in TMCFs. Nevertheless, this paleorecord shows that this TMCF was ultimately resilient to the drought frequency observed here, even during a time of peak El Niño frequency (e.g., Conroy et al., 2008).

FIRE REGIME

For the majority of this 7300 cal yr B.P. record from Waiʻānapanapa, there was a dearth of charcoal (Fig. 4, part d), suggesting no fires occurred in this area, agreeing with the general sentiment that upper TMCFs in Hawaiʻi rarely experience fire. However, the paleorecord shows that for the first time in several millennia, around 880 cal yr B.P., a novel fire regime with a long fire return interval began. The fire return interval decreased dramatically around 550 cal yr B.P., near the time when biomarkers show the lowest values (425 cal yr B.P.), suggestive of the most arid interval with the lowest-elevation TWI in the last 7300 years. This time period coincides with evidence of a positive phase of the Pacific Decadal Oscillation (PDO, 1450–1550 C.E.; MacDonald and Case, 2005) and a stronger Aleutian Low (AL, ca. 500 cal yr B.P.; Anderson et al., 2005), both of which promote drought in Hawaiʻi (Chu and Chen, 2005; Diaz and Giambelluca, 2012). The ignition source for fires in this novel fire regime is unknown and could be lightning, lava, or humans. These changes in the fire regime occurred several centuries after Polynesian arrival to the Hawaiian Islands. Sustained human activity in this high elevation area was largely absent at this time (Burney et al., 1995), suggesting a human ignition source is unlikely, but not impossible. Lava flows in this area are all significantly older than ca. 880 cal yr B.P. (Sherrod et al., 2006, 2007), suggesting lava is also an unlikely ignition source. Regardless, the fire regime intensified around the time of the lowest ACL in the record, suggesting that whatever the ignition source, drought—perhaps driven by the PDO or AL—played a role in intensifying this fire regime.

When the fire regime changed, pollen assemblages changed quickly, but in the opposite direction as the response to increased drought frequency (Figs. 4, parts a–b, and 5). After the fire regime began, spores from the epiphytic Grammitidaceae declined (Table 2). In addition, the herb *Fragaria chiloensis* and the endemic tree fern genus *Sadleria* increased in abundance (Table 2). Today, *Fragaria chiloensis* and one *Sadleria* species (*S. cyatheoides*) have their greatest abundance in dry-mesic subalpine shrublands. In addition, the Gleichenoid fern *Dicranopteris*, which often forms thickets following disturbance, increased in abundance. *Dicranopteris* is a non-polypod fern, part of a lineage that diversified well before angiosperms, and as a result has a unique foliar stoichiometry with particularly low calcium content (Amatangelo and Vitousek, 2008). Non-polypod ferns therefore have a capacity to alter the rate of nutrient cycling through calcium immobilization (Amatangelo and Vitousek, 2009). In addition, other disturbance indicators, including Chenopodiaceae and over-represented pollen and spore types, increased in abundance. These disturbance indicators were likely not growing on site, but became increasingly over-represented in pollen assemblages because of a more open forest increasing the frequency of longer pollen transport distances (e.g., Bunting et al., 2004). This change in the fire regime altered the understory community but did not affect the composition of cloud forest tree taxa over the long term, except for modest increases in the tree *Myrsine* at the onset of an intensified fire regime (Appendix Fig. A1). However, evidence for a dieback event (306 cal yr B.P.) was coincident with a fire event (310 cal yr B.P.) several centuries after the onset of the novel fire regime (Fig. 4, parts b and d). Over centuries, this record suggests these TMCF tree taxa are resilient to the ~45-year fire return interval observed in the paleorecord.

DIEBACK EVENTS

Today, *Metrosideros* is known to experience widespread stand-scale dieback events, associated with water-logging or a series of climatic perturbations that increasingly cause the collapse of larger even-aged forest segments (Mueller-Dombois, 1980; Akashi and Mueller-Dombois, 1995). Evidence for dieback—not only of *Metrosideros* but also of other cloud forest tree taxa—occurred four times in this record. Rapid negative excursions along axis 2 of the NMS ordination highlight the center of these dieback events (Fig. 4, part b). Each event can be characterized by rapid declines in tree pollen of some TMCF canopy species and a rise in pollen from the endemic tree fern *Cibotium*, another non-polypod fern with the potential to influence nutrient cycling rates. These dieback events occurred approximately every millennium and began well before human arrival to the islands. Dieback events likely occurred prior to the first dieback event we report here, at ca. 3000 cal yr B.P., but the sampling resolution of our pollen/spore record is too low before this time period to be sure. Overall, evidence for dieback in the record of pollen assemblages suggests diebacks are an inherent part of the ecology of Hawaiian TMCF forests, only sometimes associated with aridity or fire.

ISLAND TMCF STABILITY

This study suggests that over the long term, this island TMCF is resilient to changes in climate-driven disturbances. The ecosystem was in general fairly stable, with change in species composition averaging ~3% per decade from sample to sample, and changes in the disturbance regime likely drove these changes in species composition. Interestingly, these changes are generally focused in the understory, and there was no evidence of state changes (e.g., a switch to shrubland or grassland) in this system for over seven thousand years. These data are somewhat incongruous with the perception that island ecosystems in general, and TMCFs in particular, are sensitive to changes in climate or disturbance, particularly fire. Other island ecosystems have shown pronounced state changes over the Holocene, often in response to climate variability. In the Canary Islands, for example, a rapid shift in forest taxa occurred with a drier climate in the mid-Holocene (Nogué et al., 2013). In the more tropical island of Mauritius, rapid transitions in forest type were linked to climate events in the early Holocene as well as to internal forest dynamics (de Boer et al., 2013). Our research suggests a contrasting resilient island TMCF in the context of natural disturbance. In addition, non-native plant introductions and human-induced changes in fire frequency or intensity can dramatically alter species composition, or even perhaps cause the extinction of tree species on islands (de Nascimento et al., 2009; Connor et al., 2012). Although the introduction of non-native plants and animals has greatly affected other Hawaiian ecosystems (e.g., Yelenik and D'Antonio, 2013), the upper reaches of montane cloud forest, though dynamic, have an essentially natural origin.

CONCLUSIONS

The paleorecord from Waiʻānapanapa shows clearly the importance of natural disturbance to TMCF ecology, but also shows that this TMCF was resilient and experienced no vegetation state changes over the past 7300 years. Biogeochemical consequences of changes in disturbance are strongest when they are accompanied by a change in vegetation type, so our data suggest the range of disturbance observed in this paleorecord may have had little biogeochemical consequence. However, some of the disturbance-driven changes in species composition may influence biogeochemical cycling through (1) changes in the abundance of vines, which may alter a forest's ability to accumulate carbon (e.g., Schnitzer et al., in press) and (2) changes in the abundance of non-polypod ferns such as *Cibotium* or *Dicranopteris*, which may alter the rate of nutrient cycling (e.g., Amatangelo and Vitousek, 2009). Our research suggests this island TMCF has been resilient to the droughts and fire regimes of the past few millennia. However, TMCFs may cross ecological thresholds with more frequent/intense disturbance and experience state changes, promoting the loss of cloud forest area (e.g., Asbjornsen and Wickel, 2009). Understanding where this threshold is located for each TMCF is a research priority.

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APPENDIX

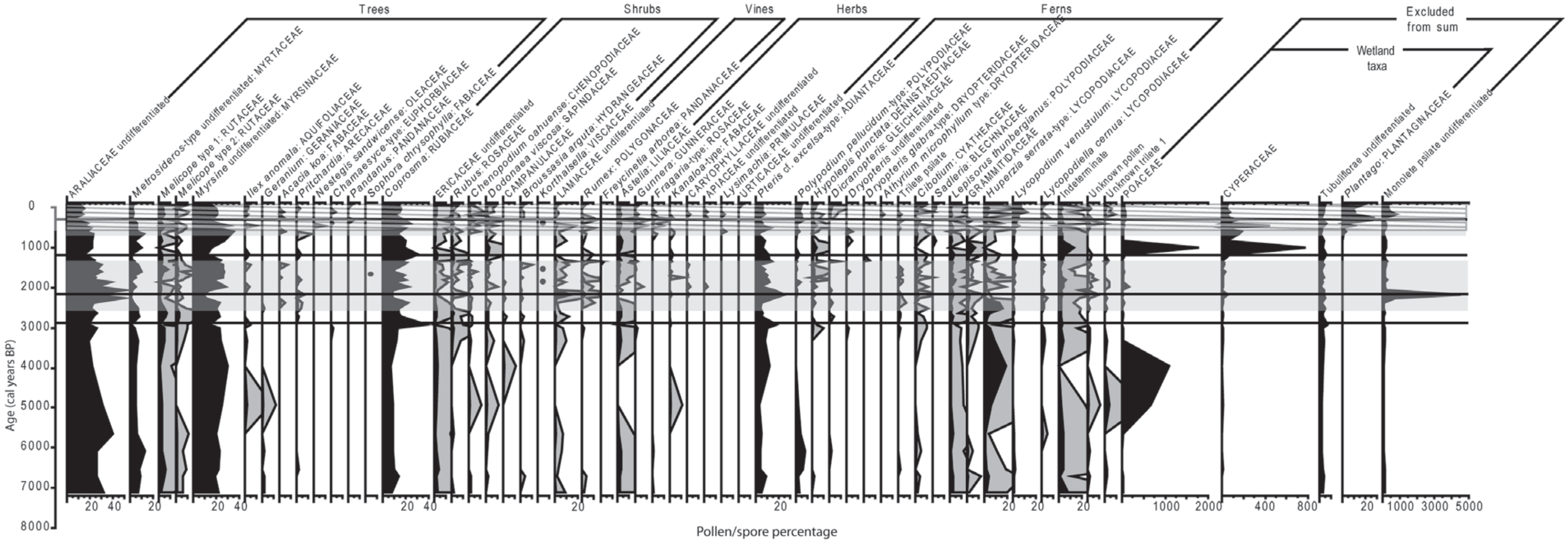

FIGURE A1. Pollen percentages over time from Wai‘ānapanapa at 2103 m on windward Haleakalā, east Maui. Exaggeration curves of 10% are shown in gray, and pollen types that never exceed 0.5% are shown as dots. Disturbance regimes are highlighted in horizontal bands; drought is gray, fire is hachured, and dieback events are horizontal black lines.