

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



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ABSTRACT

Pests or pathogens that affect trees have the potential to fundamentally alter forest composition, structure and function. Throughout the last six years, large areas of otherwise healthy 'ōhi'a (*Metrosideros polymorpha*) trees have been dying rapidly (typically within weeks) in lowland tropical wet forest on Hawai'i Island, USA. This mortality is quite distinct from previous well-documented 'ōhi'a dieback episodes driven by cohort senescence. *Ceratocystis fimbriata* was identified and routinely found associated with rapidly dying individuals of 'ōhi'a, Hawai'i's most widespread native tree. Pathogenicity of this fungus was proven and *M. polymorpha* was recorded as a new host for *C. fimbriata*. Mortality of 'ōhi'a at this scale is of great concern as the understory in these forests is often occupied by invasive non-native plants capable of severely limiting 'ōhi'a regeneration. Imagery of 'ōhi'a mortality obtained in 2012 revealed large expanses of greater than expected mortality (i.e., $\geq 10\%$) across 1600 ha. By 2014 'ōhi'a mortality levels $\geq 10\%$ had spread to 6403 ha, or 30% of total area classified as 'ōhi'a in our study area. Further, levels of 'ōhi'a mortality in field plots established within the study region averaged 39%, and mortality levels were comparable across size classes and forest compositions. Results from a subset of field plots re-inventoried one year after plot establishment revealed average annual 'ōhi'a mortality rates of 24% and 28% based on basal area and stem density measures, respectively; mortality rates were as high as 47% in some field plots. The dearth of 'ōhi'a seedling recruitment and characteristic understory dominance of non-native species documented within our research plots, coupled with the lethality of *C. fimbriata* to 'ōhi'a, suggest that these forests likely will be dominated by non-native species in the future.

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1. Introduction

Pests or pathogens that affect trees have the potential to fundamentally alter forest composition, structure and function as readily as fire, deforestation, development, and invasive plant species (Hicke et al., 2012). Globally, disease damage is likely exacerbated by ongoing climate change (Allen et al., 2010). Where diseases affect natural forests, they can have a profound impact on habitat

quality as well as local, regional, and global biodiversity (Hicke et al., 2012; Shearer et al., 2009; Chakraborty et al., 2008). Notable examples of significant pathogen-induced forest mortality include Sudden Oak Death caused by *Phytophthora ramorum* (Rizzo and Garbelotto, 2003), chestnut blight caused by *Cryphonectria parasitica* (Orwig, 2002) and Dutch elm disease caused by *Ophiostoma* spp. (Walters, 1992).

'Ōhi'a lehua (*Metrosideros polymorpha*) is arguably Hawai'i's most widespread and culturally significant native tree (Friday and Herbert, 2006; Mueller-Dombois and Fosberg, 1998). Approximately 50 species of *Metrosideros* occur worldwide, primarily in

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South Pacific island countries, as well as New Zealand and the Philippines. In Hawai'i, 'ōhi'a habitat extends from sea level to tree line at 2800 m, across surface substrates of all ages, and moisture gradients ranging from dry forests to wet forests, where it is dominant (Mueller-Dombois and Fosberg, 1998). Collectively, 'ōhi'a dominated forests occupy ca. 350,000 ha across the Hawaiian archipelago, with 250,000 ha of that total found on Hawaii Island, and the remaining 100,000 found on the other main Hawaiian Islands combined (Gon et al., 2006). Since arriving in Hawai'i four million years ago (Percy et al., 2008), it has succeeded as a generalist, colonizing habitats in almost every environment across the archipelago. Considering all the forested areas including Hawai'i Island, 'ōhi'a trees account for approximately 50% of the basal area and 50% of all the stems found within those forests (<http://apps.fs.fed.us/fiadb-downloads>). As a result, 'ōhi'a forests provide habitat for most of the 35 native forest bird species in Hawaii, 21 of which are threatened or endangered (Mitchell et al., 2005), most of the over 900 species of endemic vascular plants (Wagner et al., 1999), and many of the 5000 endemic species of insects (Miller and Eldredge, 1996). In addition, 'ōhi'a-dominated forests protect most of the critical watersheds for Hawai'i's citizens across the entire state (Hosmer, 1911).

Prior to human contact, the range of 'ōhi'a forests across the main Hawaiian Islands was much broader than it is today; land conversion (forest to agriculture and/or grazing lands), fire, development, and non-native feral ungulates and widespread invasive plant species establishment have reduced the distribution of 'ōhi'a forest substantially (Cuddihy and Stone, 1990). As the dominant tree species of the majority of forest communities in Hawai'i, 'ōhi'a trees bear substantial Hawaiian cultural significance. The tree itself was and is considered the physical embodiment of Kū, one of the four principal Hawaiian deities. 'Ōhi'a wood was incorporated into the two most sacred structures of heiau (temples) of governance in Hawai'i: the ki'iakua (god figures) and the lele (offering platform). 'Ōhi'a was a fundamental material for dwellings, tools, weapons, religious structures, food preparation implements and containers. Foliage and flowers continue to be critical components of many of the most valued lei, and tender parts of flowers, foliage and roots have been used in herbal medicine. Prevalent and easily recognized in ecosystems from sea level to tree-line, numerous 'ōlelo no'eau (wise and poetical Hawaiian sayings) refer to 'ōhi'a trees as positive symbols of strength, sanctity, and beauty (Gon, 2012).

During the last six years, many landowners in the Puna district of Hawai'i Island have reported, to the University of Hawai'i agricultural extension services, the rapid death (i.e., days to weeks) of previously healthy 'ōhi'a trees of all size classes, resulting in localized to extensive stands of predominantly dead 'ōhi'a trees. A similar phenomenon characterized as landscape-scale 'ōhi'a dieback was observed and thoroughly investigated in the 1970 s and 1980 s (Boehmer et al., 2013; Hodges et al., 1986; Mueller-Dombois, 1987; Mueller-Dombois et al., 2013). A variety of causes were associated with these previous 'ōhi'a dieback episodes including pathogens such as *Phytophthora cinnamomi* and *Armillaria mellea*, and an insect pest, the 'ōhi'a borer (*Plagithmysus bilineatus*) (Hodges et al., 1986). Overall, the chief underlying cause was determined to be cohort senescence, or age-driven mortality of even aged stands of 'ōhi'a that was generally triggered by any number of stressors (Mueller-Dombois et al., 2013). Cohort senescence is not uncommon for 'ōhi'a stands to experience since they often exhibit widespread and synchronous establishment on recently formed lava substrates; stages of senescence are relatively synchronous as well (Mueller-Dombois et al., 2013). Recently observed mortality of 'ōhi'a individuals and whole stands was unique because it occurred in areas that had not experienced classic 'ōhi'a dieback as documented in previous dieback research (Jacobi personal communication) and because affected trees were

dying so rapidly. The manner in which trees died was also unique—typically with a branch, fork or tree completely dying before its neighbor showed signs of stress (Fig. 1). In addition, rapid 'ōhi'a death occurred in and around areas of direct human influence (e.g., homes, gardens, road construction) as well as areas with little or no direct human influence (e.g., inaccessible wet tropical forest stands far from roads or homes).

In 2014, during exploratory fungal sampling, *Ceratocystis fimbriata* was isolated from dying 'ōhi'a in an area of recent widespread 'ōhi'a mortality. Keith et al. (2015) fulfilled Koch's postulates and showed that a particular strain of *C. fimbriata* is pathogenic to 'ōhi'a. Elsewhere, *Ceratocystis* species cause wilt diseases of crops and plantation tree species also planted widely in Hawai'i; these include sweet potato, coffee, mango, *Eucalyptus*, and *Acacia* (Roux et al., 2000). However, there are only records of *C. fimbriata* causing disease on sweet potato, syngonium, taro, Tongan yam and African tulip in Hawai'i (Browne and Matsuura, 1941).

In order to begin to address the ecological ramifications of this new disease to Hawai'i's dominant native tree, we posed the following questions: To date, how much area of 'ōhi'a-dominated forest has experienced *C. fimbriata*-induced mortality? What is the rate of spread of this disease in areas that we have detected it in? What are the forest dynamics in areas affected by the disease? Do certain size classes of 'ōhi'a succumb to the disease more readily than others? At what rate are 'ōhi'a trees dying and do mortality rates differ greatly among different stands? To address these questions, we used remotely-sensed imagery to estimate the distribution of *C. fimbriata*-induced mortality and the change in that distribution between 2012 and 2014. We also measured forest stand composition, structure, and the degree of tree mortality in a series of forest plots established throughout areas experiencing



Fig. 1. A typical 'ōhi'a experiencing symptoms of *Ceratocystis fimbriata* infection in the Puna and South Hilo Districts of Hawai'i Island. Tree exhibits one healthy, living branch and one dead branch, a common characteristic of infected trees.

the disease. We repeated these measurements in a subset of our forest plots after one year to determine annual rates of tree mortality, occurrence of 'ōhi'a seedling recruitment, and any other changes in forest composition or structure over time.

2. Methods

2.1. Study region

Our study region included the Puna District and the southern portion of the South Hilo District of Hawai'i Island, USA (Figs. 2 and 3). The forests of this region are classified as lowland wet tropical forest (Zimmerman et al., 2008). Remotely-sensed imagery was used to map 'ōhi'a mortality across all landownership, and forest monitoring plots were located both on State of Hawai'i managed forest reserves (i.e. Malama Ki, Nānāwale, Keauohana and Waiākea) and in small, privately owned forests. Collectively, the forest reserves constitute some of the least altered lowland wet forest in Hawai'i (Mueller-Dombois and Fosberg, 1998; Hughes and Denslow, 2005; Hughes et al., 2014) as much of this forest type in the districts have been urbanized or converted to agriculture (Cuddihy and Stone, 1990). Primary succession in this region typically manifests as colonization of young, barren lava substrates by a single cohort stand of 'ōhi'a trees, which grow as a monotypic forest stand during the first 100–200 years (Atkinson, 1970; Mueller-Dombois and Fosberg, 1998; Hughes et al., 2014). Species diversity and structural complexity increase as additional native

tree species (e.g., *Diospyros sandwicensis*, *Psychotria hawaiiensis*, *Psydrax odorata*, and *Pandanus tectorius*) establish under mature 'ōhi'a overstory canopies throughout subsequent centuries of succession (i.e., 200–700 years) (Wagner et al., 1999; Zimmerman et al., 2008). Declines in 'ōhi'a basal area and stem density often occur as dominance by mid-to-late successional species increases (Atkinson, 1970; Zimmerman et al., 2008).

Native vegetation is still found across much of the study region, although significant portions are now occupied or dominated by nonnative tree and shrub species, particularly in the understory (Cavaleri, 2014; Hughes et al., 2014; Schulten et al., 2014). Non-native understory species commonly encountered in the study area include *Psidium cattleianum* (strawberry guava), *Clidemia hirta* and *Melastoma candidum* (Zimmerman et al., 2008). Other non-native species in the region were purposefully introduced during nonnative tree planting efforts that took place across Hawai'i throughout the 1900 s (Nelson, 1965); these include *Falcataria moluccana*, *Casuarina equisetifolia* and *Eucalyptus robusta* (Little and Skolmen, 1989).

Mean annual temperature (MAT) of the study area was 23.8 °C, and mean annual precipitation (MAP) ranged from 2600 mm/year near the coast to 4700 mm/year at elevations approaching 550 m elevation (Giambelluca et al., 2013). The range of elevations and rainfall amounts are typical of 'ōhi'a forests (Friday and Herbert, 2006). Rainfall for the period 2011–2014 was slightly less than typical, with precipitation being between 60% and 90% of normal average as recorded at stations in Hilo, Pahoa, Kapoho, Keauohana, and Glenwood, all locations adjacent or inside of the affected areas.

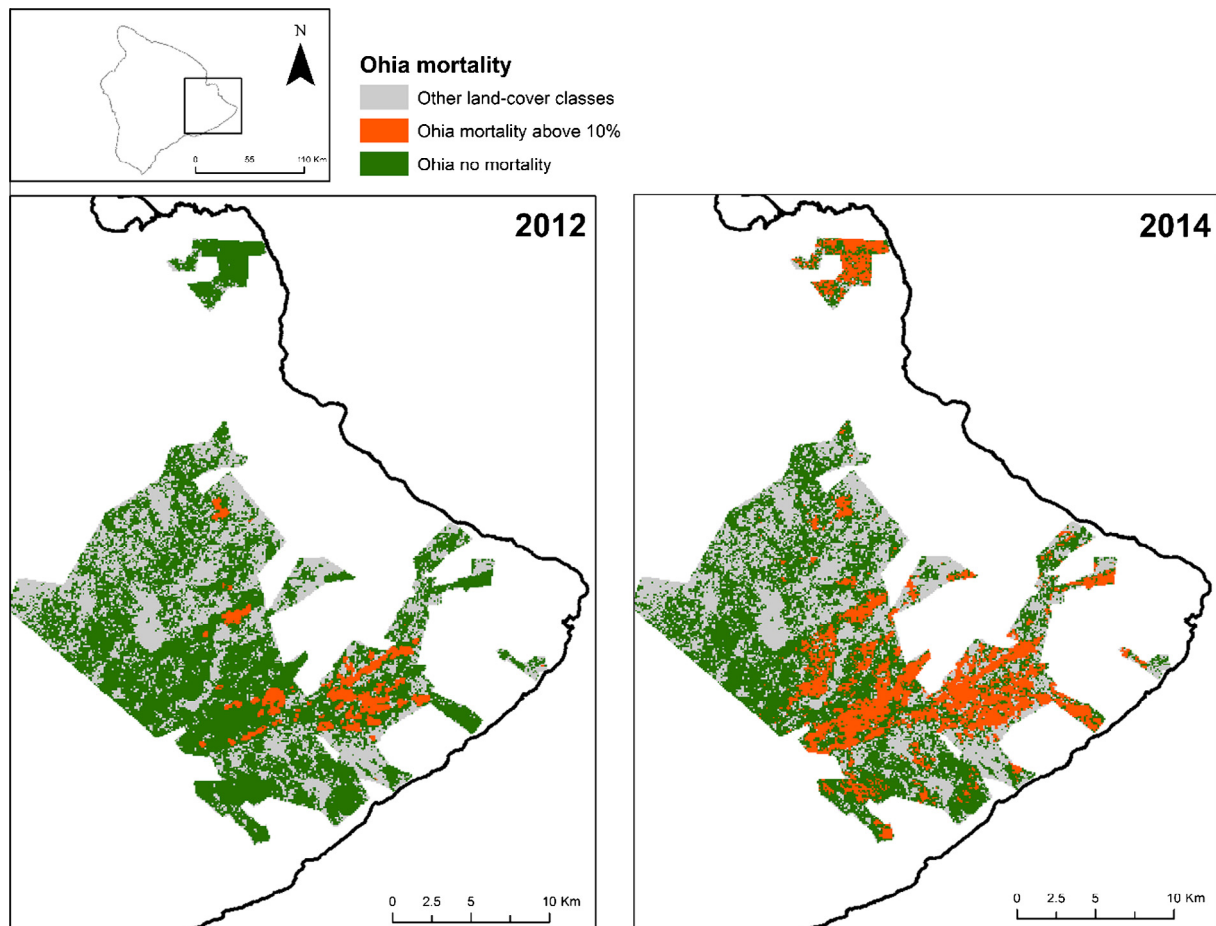


Fig. 2. Change in spatial distribution of 'ōhi'a mortality $\geq 10\%$ from 2012 to 2014 (using remotely sensed images) in the Puna and southern South Hilo Districts of Hawai'i Island.

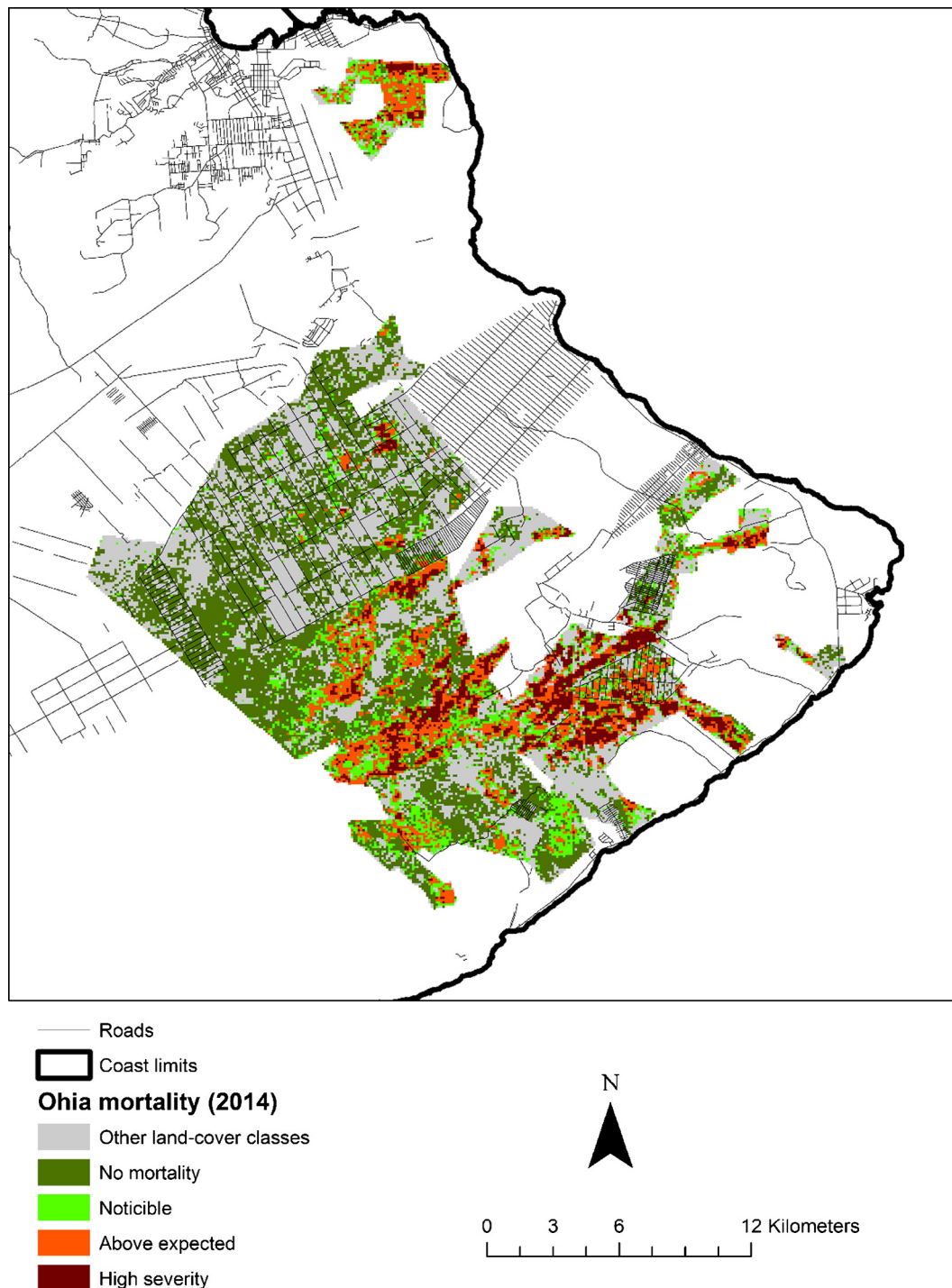


Fig. 3. Distribution of 'ōhi'a mortality across the Puna and southern South Hilo Districts of Hawai'i Island determined from remotely sensed images collected in 2014.

The lower rainfall would not be expected to cause significant mortality due to drought stress, though, as 'ōhi'a forests can occur in areas receiving as little as 400 mm precipitation annually. Extremely wet 'ōhi'a forests receive 6300 mm. Soils across the region formed on lava flows emanating from the lower east rift zone of the active Kilauea volcano, and substrate ages vary from <1 year to ca. 1500 years before present (Moore and Trusdell, 1991). Soils are typically histosols consisting of soil organic matter overlaying relatively unweathered lava. Andisols formed on volcanic ash substrates derived from explosive events also occur in limited quantity across the study region (Moore and Trusdell, 1991). Differences in the composition and structure of forests between young substrates

(i.e., <400 YBP) and older substrates (i.e., >400 YBP), which typically contained larger trees, were readily apparent on the ground and in remotely sensed imagery (Hughes et al., 2014). All the soils in the affected area were very young, having developed over the last few centuries. *C. fimbriata* has not yet reached areas of the island with older, deeply weathered soils.

2.2. Initial investigation and assessment

Mean annual temperature (MAT), mean annual precipitation (MAP) and soil types were determined for the areas examined. In early 2013 we conducted a preliminary inventory of recent 'ōhi'a

mortality along all roads in the lower (elevation) Puna district. This was followed by helicopter flights over the same region in the fall of 2013. Because 'ōhi'a trees died rapidly in our study, leaves turned brown at the same time creating an obvious indicator of recent mortality. However, as wind events capable of removing leaves were variable, fine branches were used as indicators of recent mortality as they typically remain for at least two years. We generated an initial estimate of the spatial distribution of recent 'ōhi'a mortality based on these efforts. This distribution layer was combined with layers of spatially explicit MAP, roads and residential development, and geologic features such as lava flow boundaries and fault zones in ArcGIS (ESRI Inc., Redlands, CA, USA).

2.3. Spatial distribution and temporal change of 'ōhi'a mortality

Using aerial photographs from February 2012 at 15 cm of spatial resolution (Pictometry International Inc. Henrietta, New York, USA), we mapped 'ōhi'a mortality within an area of 33,133 ha. Prior to mapping, an extensive visual training in areal signature of dead and live 'ōhi'a, based on its color, size and shape, was performed on known 'ōhi'a/non-'ōhi'a locations throughout the Puna district. Subsequently, the imagery was partitioned into 100 × 100 m grid cells, and we visually inspected the imagery within each grid cell to assign three classes: "Non 'Ōhi'a Forest", "'Ōhi'a no mortality", and "'Ōhi'a mortality ≥10%". In 2013 we were not aware of the potential large extent of this novel 'ōhi'a disease (*C. fimbriata*), and as such, our field validation data were restricted to the three above-mentioned classes. "Non 'Ōhi'a Forest" class refers to all other land cover types, such as urban areas and agricultural lands. The "'Ōhi'a no mortality" class includes forest stands where 'ōhi'a dead trees were not found. The third class, "'Ōhi'a forest mortality ≥10%", includes forest stands where 'ōhi'a dead trees represent ≥10% of each 100 × 100 m grid cell. We assessed the 2012 map accuracy using 34 field validation points collected in 2013, when the study commenced (estimates of how forest conditions would have appeared in 2012 were generated), and computing the Cohen's Kappa coefficient (Congalton, 1991) and overall disagreement (see details in Pontius and Millones, 2011; Pontius and Santacruz, 2014). The overall disagreement is the sum of the quantity disagreement (amount of disagreement between reference and classification data) and the allocation disagreement (amount of disagreement between reference and classification data that is due to the less than optimal match in the spatial allocation of the categories, given the proportions of the categories). We calculated these accuracy metrics using a contingency table. Although the number of field validation points is restricted, mapping errors may be minimized by the high spatial resolution of the images, our extensive effort in classifying the imagery, and the low diversity of canopy species found in the study area.

We re-evaluated 'ōhi'a mortality, across the same region in 2014 using World View-2 satellite imagery (8-band multispectral data) at a 50 cm spatial resolution collected in March of that year. In 2014, our field data indicated that patch sizes and severity of 'ōhi'a mortality within forest stands had greatly intensified, and at this time we examined and quantified gradients of mortality severity. As such, the 2014 imagery was also partitioned into 100 m × 100 m grid cells, and each grid cell was evaluated and assigned an 'ōhi'a mortality severity rating to provide collective estimates of the distribution and severity of 'ōhi'a mortality across the study region (Oblinger et al., 2012). 'Ōhi'a mortality in all grid cells was visually classified; i.e., each grid cell was manually examined to determine whether 'ōhi'a was present in the cell and, if so, what percentage were dead. Cells were classified as high severity (≥50% of 'ōhi'a dead), above expected (10–49.9% of 'ōhi'a dead), noticeable (0.1–9.9% 'ōhi'a dead) and no 'ōhi'a mortality. The areal

extent of 'ōhi'a forest in our study region was obtained from state HIGAP GIS layers (USGS 2001). For 2014 imagery, we carried out ground verification in 40 points randomly selected along roadsides and classified in the field regarding 'ōhi'a mortality severity and 'ōhi'a forest type. These field assessments were applied to our 'ōhi'a mortality mapping layers to produce a contingency table that included the classes: high, above-expected, noticeable, 'ōhi'a forest-no mortality, non 'ōhi'a forest. To perform a temporal comparison between 2012 and 2014, we also reclassified the 2014 map into three classes: "non 'ōhi'a Forest", "'ōhi'a no mortality", and "'ōhi'a mortality ≥10%". We then calculated Cohen's Kappa coefficient, quantity disagreement, allocation disagreement, and overall disagreement (Pontius and Millones, 2011; Pontius and Santacruz, 2014) to assess map accuracy for all map categories. In both 2012 and 2014 maps, we defined 'ōhi'a mortality based on dead trees from any potential cause, such as senescence, weather events or anthropogenic influence. As such, it's probable that some 'ōhi'a mortality in our study region was not due to *C. fimbriata*. Finally, we calculated the total temporal change in area of 'ōhi'a mortality ≥10% by overlapping the 2012 and 2014 maps.

2.4. 'Ōhi'a mortality monitoring plots

We established an initial set of monitoring plots ($n = 9$) in areas of recent 'ōhi'a mortality or adjacent to such areas in the lower Puna district during January and February of 2014; plots were established to document both recent and future 'ōhi'a mortality. Plot location were selected to capture variety with regard to abundance of non-native species, composition, stem density, proximity to anthropogenic activities, and prior recent 'ōhi'a mortality levels. These plots were re-inventoried in the winter of 2015 to document 'ōhi'a mortality rates, and a new set of monitoring plots was established at this time as well. A new set of plots ($n = 9$) were established where *C. fimbriata* infection of 'ōhi'a trees was confirmed in order to document future 'ōhi'a mortality and stand changes, rather than document past 'ōhi'a mortality. Data from this second set of monitoring plots was not included in analyses of 'ōhi'a mortality rates. Many of the second set of monitoring plots were established in the South Hilo district, which lies north of the lower Puna district, because *C. fimbriata* infection had been confirmed in these areas at the time of 2014 plot establishment. All plots were separated by ≥100 m.

Sampling and measurements were conducted on GPS fixed-radius 18 m, permanently monumented, circular plots, with 6 m radius co-located subplots to measure invasive species presence/abundance and 'ōhi'a regeneration (all seedlings ≥15 cm in height inventoried). A vegetation profile was conducted on a 6 m radius subplot within each plot to provide an ocular estimation of percent cover and mean height by species (see USDA Forest Service, 2013). Each tree ≥1.5 cm DBH encountered in the plot was tallied, and its species identity, DBH, crown position [i.e. open grown, dominant, co-dominant, suppressed, overtopped (USDA Forest Service, 2013)], and status (live or dead) were recorded. The presence of *C. fimbriata* in 'ōhi'a trees undergoing mortality was confirmed by analysis of wood samples of symptomatic trees (e.g., attached intact brown leaves on selected limbs or the entire canopy) located within 200 m of all monitoring plot locations. Pathogen presence was confirmed in each wood sample via analysis at the USDA, Agricultural Research Service, Pacific Basin Agricultural Research Center (PBARC), Hawai'i, USA, using techniques described by Keith et al. (2015).

2.5. Statistical analysis of 'ōhi'a mortality monitoring plots

A generalized linear mixed model analysis was executed in order to calculate the probability of individual 'ōhi'a trees being

dead using a cubic polynomial of the natural log of DBH size, after accounting for the variation in mortality among plots (SAS, SAS Institute Inc. Cary, NC, USA). Annual mortality rates were calculated as a simple percentage of 'ōhi'a stems ≥ 1.5 cm DBH live in 2014 that were dead in 2015 (re-inventoried at same time of year). We also calculated 2014–2015 mortality by% basal area lost (dead). Spearman rank order correlation tests ($P \leq 0.05$) of *P. cattleianum* abundance and basal area on arcsine-transformed 'ōhi'a mortality rate (winter 2014 to winter 2015) were conducted for each plot (SigmaPlot, Systat Software Inc. Chicago, IL, USA).

3. Results

3.1. Spatial distribution of 'ōhi'a mortality

Analysis of remotely-sensed imagery indicated that areas exhibiting substantial 'ōhi'a tree mortality (i.e., $\geq 10\%$ of 'ōhi'a trees dead) increased from 1600 ha in 2012 to 6403 ha in 2014. This increase represented 30% of the total area classified as 'ōhi'a forest in our study region in winter 2014 (Fig. 2). We highlight that the classification of 'ōhi'a mortality $\geq 10\%$ includes a large range of mortality, mainly in the 2014 mapping (see Fig. 3). High severity mortality ($\geq 50\%$ of 'ōhi'a trees dead) was found in 11% of the total

area classified as 'ōhi'a forest in our study region in winter 2014 (Table 1 and Fig. 3). An additional 3824 ha exhibited noticeable (visible mortality $< 10\%$) 'ōhi'a mortality (Table 1 and Fig. 3). Taken together, 47% of area classified as 'ōhi'a forest in our study region exhibited visible 'ōhi'a mortality. The 2014 imagery showed recent 'ōhi'a mortality occurring in the South Hilo district (Fig. 2), where it had not been present in the 2012 imagery. The 2012 mapping showed an overall disagreement of 12% (quantity disagreement of 10%; allocation disagreement of 2%, and kappa of 0.77). The 2014 mapping showed different accuracies as we performed classification using three (Fig. 2) or five classes (Fig. 3). Using three classes, the 2014 map showed an overall disagreement of 18% (quantity disagreement of 8%; allocation disagreement of 10%, and kappa of 0.76). Using five classes the 2014 map showed an overall disagreement of 30% (quantity disagreement of 10%; allocation disagreement of 20%, and kappa of 0.61). While analyzing remotely sensed data, we observed a trend that most 'ōhi'a mortality documented in this study occurred primarily on lava flows aged 400–750 year before present (YBP). Additionally, our preliminary ground inventory revealed mortality of many 'ōhi'a trees growing on areas of lava flows < 400 YBP that were adjacent to ≥ 400 YBP flows.

3.2. Stand characteristics

'Ōhi'a was the dominant native woody species in all of the 18 forest plots; on average, it comprised $58\% \pm 7\%$ of total native stem density (≥ 1.5 cm DBH) (i.e., stems ha^{-1}) and $89\% \pm 2\%$ of total native tree basal area (≥ 1.5 cm DBH) (i.e., $\text{m}^2 \text{ha}^{-1}$) (Table 2). In contrast, the two next most common native trees, *P. hawaiiensis* (kopiko) and *D. sandwicensis* (lama) collectively accounted for an average of $38\% \pm 7\%$ of total native stem density and $8\% \pm 3\%$ of total native basal area (Table 2). *P. cattleianum*, the most common non-native woody species across our study plots, exhibited values that were on average 35% of the average total native woody basal

Table 1
'Ōhi'a mortality severity mapped from 2014 World View II satellite imagery.

	Hectares	% of 'ōhi'a forest in study area
High severity mortality (red in Fig. 3) $\geq 50\%$ 'ōhi'a dead	2419	11.2%
Above expected mortality (orange in Fig. 3) 10–49.9% 'ōhi'a dead	3984	18.5%
Noticeable mortality (Light green in Fig. 3) 0.1–9.9% 'ōhi'a dead	3824	17.7%
'Ōhi'a forest, no mortality (green in Fig. 3)	11,341	52.6%

Table 2
Stem density (stems ha^{-1}), basal area (BA, $\text{m}^2 \text{ha}^{-1}$), and percent mortality of native trees species and a common non-native tree (*Psidium cattleianum*), as well as native and non-native shrub percent cover in forest plots established in Hawaiian forests undergoing Rapid 'Ōhi'a Death across the Puna and South Hilo Districts of Hawai'i Island.

	Elevation	Substrate age	‘Ōhi’a		<i>Psychotria hawaiiensis</i>		<i>Diospyros sandwicensis</i>		All native trees		<i>Psidium cattleianum</i>		Native shrub cover	Non-native shrub cover	‘Ōhi’a mortality 2014–2015	
Plot	(m)	(YBP)	Density	BA	Density	BA	Density	BA	Density	BA	Density	BA	%	%	(% of stems)	(% of BA)
<i>Established 2014</i>																
1	312	400–750	904	39.9	88	0.7	0	0.0	1100	42.7	3979	15.4	0	6	50%	49%
2	160	750–1500	305	13.7	0	0.0	0	0.0	305	13.7	0	0.0	65	20	42%	35%
3	291	400–750	560	38.7	49	0.5	0	0.0	609	39.2	12,556	41.5	0	0	46%	54%
4	287	400–750	747	22.6	0	0.0	0	0.0	747	22.6	7692	29.5	0	10	25%	7%
5	274	400–750	599	34.5	167	1.1	128	2.3	894	37.9	11,671	27.8	0	4	13%	8%
6	285	400–750	462	62.4	855	3.9	0	0.0	1434	68.7	0	0.0	4	68	23%	9%
7	232	400–750	422	42.6	236	2.8	275	2.3	933	47.7	7339	18.6	0	0	3%	3%
8	185	400–750	1700	40.6	5109	12.2	0	0.0	6808	52.9	5924	6.5	0	89	25%	29%
9	179	400–750	275	23.9	20	0.1	29	0.1	432	27.0	0	0.0	3	95	^a	^a
<i>Established 2015</i>																
10	284	400–750	1238	44.9	108	0.6	0	0.0	1444	47.2	15,650	30.5	3	0		
11	253	750–1500	973	14.3	20	0.0	20	0.2	1022	14.7	7692	12.4	83	9		
12	299	750–1500	314	29.7	10	0.2	0	0.0	403	31.9	265	0.7	90	9		
13	321	750–1500	403	20.8	69	0.3	0	0.0	501	21.9	1149	3.5	95	4		
14	342	750–1500	255	19.1	20	0.6	0	0.0	305	22.1	88	0.2	96	2		
15	398	750–1500	737	38.4	324	1.0	0	0.0	1385	45.0	3979	10.3	1	19		
16	240	200–400	894	14.4	20	0.1	0	0.0	914	14.5	0	0.0	99	0		
17	242	400–750	88	21.5	334	8.3	432	8.1	865	38.0	7604	8.1	4	3		
18	112	200–400	2004	10.3	0	0.0	0	0.0	2004	10.3	3360	1.3	65	5		
Mean			715.5	29.6	412.6	1.8	49.1	0.7	1228.0	33.2	4941.7	11.4	33.8	19.1		

^a Nearly 100% of 'Ōhi'a trees were dead at installation; data from plot 9 was not included in annual mortality rate calculations.

area, and stem density values that were five times greater average total native stem densities (Table 2).

All 'ōhi'a size classes exhibited substantial levels of mortality prior to the measurement of each plot (Fig. 4). On average, $39\% \pm 7\%$ of 'ōhi'a stem density, and $39\% \pm 7\%$ of 'ōhi'a basal area, had died in plots at the time of initial plot establishment in 2014 and 2015 (Table 3). In contrast, *P. hawaiiensis*, a common native understory tree, exhibited only 7% mortality at the time of plot installation (data not shown). Less common native species, *Mysine lessertiana* and *D. sandwicensis*, did not exhibit higher than expected mortality (i.e., $\geq 10\%$ dead), and less than 1% of the non-native *P. cattleianum* stems inventoried exhibited mortality (data not shown).

3.3. 'Ōhi'a mortality rates from 2014 to 2015

Between 2014 and 2015, annual mortality rates of 'ōhi'a in re-inventoried monitoring plots averaged $28\% \pm 6\%$ when expressed as a percentage of total stems, and $24\% \pm 7\%$ when expressed as a percentage of total basal area (Table 2). Mortality rates varied among individual plots; stem density and basal area

values were as high as 50% and 54%, respectively, and as low as 3% in each case (Table 3). We did not include plot # 9 in this portion of our analysis because virtually all 'ōhi'a trees within the plot had suffered *Ceratocystis*-induced mortality prior to plot establishment (Table 3). The lack of clear *C. fimbriata*-free areas prohibited the successful use of controls within our study region, although we had an annual (stem and basal area) mortality rate of 3% on plot 7 [our only plot that showed no evidence of decline from 2014 to 2015 (despite testing positive for *C. fimbriata*.)] (Table 3).

3.4. 'Ōhi'a regeneration, invasive species pressure and vegetative composition

We encountered only 13 'ōhi'a seedlings across the 18 monitoring plots (1.8 ha), and 11 of those 13 seedlings were located in a single monitoring plot that exhibited high native species diversity and minimal recent 'ōhi'a mortality (Table 2). Further, we found no correlation between *P. cattleianum* stem density ($r_s = 0.285$, $P = 0.434$) or basal area ($r_s = 0.119$, $P = 0.742$) and 'ōhi'a mortality rate (high P values in Spearman rank order correlation tests indicate no correlation). Total shrub cover averaged $53\% \pm 10\%$ for

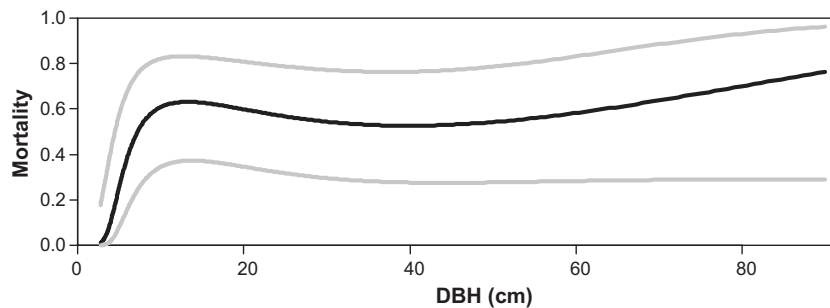


Fig. 4. A generalized linear mixed model showing the probability of all individual 'ōhi'a trees encountered in field monitoring plots being dead, after accounting for the variation in mortality among plots.

Table 3

Stem density, basal are, and percentage mortality of 'ōhi'a in trees encountered in forest monitoring plots located within areas experiencing Rapid 'Ōhi'a Death across the Puna and South Hilo Districts Hawai'i Island, USA.

Plot #	'Ōhi'a density (stems ha ⁻¹)				Mortality at installment (% of stems)	'Ōhi'a BA (m ² ha ⁻¹)				Mortality at installment (% of BA)	Mortality	
	2014	2014	2015	2015		2014	2014	2015	2015		2014–2015	
	Live	Dead	Live	Dead		Live	Dead	Live	Dead		(% of stems)	(% of BA)
<i>Installed 2014</i>												
1	157	747	79	825	83%	8.8	31.1	4.5	35.4	78%	50%	49%
2	236	69	138	167	23%	9.6	4.1	6.2	7.5	30%	42%	35%
3	275	285	147	413	51%	18.1	20.5	8.2	30.4	53%	46%	54%
4	118	629	89	658	84%	3.7	18.9	3.5	19.1	83%	25%	7%
5	452	147	393	206	25%	27.0	7.5	24.7	9.8	22%	13%	8%
6	128	334	99	363	72%	18.3	44.2	16.7	45.8	71%	23%	9%
7	383	39	373	49	9%	40.1	2.5	39	3.6	6%	3%	3%
8	815	884	609	1090	52%	16.0	24.6	11.2	29.4	61%	25%	29%
9	10	265	10	265	96%	0.05	23.9	0.05	23.9	99.8%	^a	^a
<i>Installed 2015</i>												
Mean ± S.E.											28% ± 6%	24% ± 7%
10	–	–	737	501	40%	–	–	38.1	6.8	15%	–	–
11	–	–	776	196	20%	–	–	12.5	1.8	13%	–	–
12	–	–	275	39	13%	–	–	27.7	2.0	7%	–	–
13	–	–	324	79	20%	–	–	17.3	3.5	17%	–	–
14	–	–	138	118	46%	–	–	7.6	11.5	60%	–	–
15	–	–	540	196	27%	–	–	31.4	7.1	18%	–	–
16	–	–	776	118	13%	–	–	12.0	2.5	17%	–	–
17	–	–	79	10	11%	–	–	17.9	3.6	17%	–	–
18	–	–	1768	236	12%	–	–	7.3	2.9	29%	–	–
Mean ± S.E.					39 ± 7%					39 ± 7%		

^a Plot containing primarily dead 'ōhi'a at installment; data from plot 9 was not included in annual mortality rate calculations.

all plots, and non-native shrub cover averaged $19\% \pm 7\%$. Common species included the native fern, *Dicranopteris linearis* (uluhe) whose cover averaged 33% across all plots, and non-native shrubs, *C. hirta* and *M. candidum*, whose cover averaged 7% and 4% across all plots, respectively (data not shown).

4. Discussion

Our results document a pronounced stand- and landscape-scale manifestation of *Ceratocystis*-induced mortality (commonly referred to as Rapid 'Ōhi'a Death, or ROD in Hawai'i). This current widespread 'Ōhi'a mortality has occurred in an entirely different region than past 'Ōhi'a dieback events (Mueller-Dombois et al., 2013), and our results indicate that *C. fimbriata*, a primary pathogen of 'Ōhi'a, is widespread across current affected areas and present in or adjacent to our plots (Keith et al., 2015). Our results clearly documented *Ceratocystis*-induced mortality of 'Ōhi'a across all size classes and competitive position (i.e. levels of suppression or dominance). This pattern is quite distinct from the cohort senescence/dieback phenomenon described by Mueller-Dombois et al. (2013) where mortality occurred in older trees. Keith et al. (2015) demonstrated *C. fimbriata* to be consistently lethal to 'Ōhi'a seedlings and saplings growing in ideal conditions of laboratory growth chambers. Furthermore, *P. cattleianum* abundance (and basal area) was not correlated with 'Ōhi'a mortality rates, suggesting that competition from invasive, non-native species was not a predisposing factor for *C. fimbriata*-induced mortality. Further, no other co-occurring species in our plots exhibited elevated levels of mortality or symptoms of *C. fimbriata* infection.

Our results clearly illustrate the dominance of 'Ōhi'a with regard to composition and structure, of the native wet lowland forests of the Puna District of Hawai'i Island. That 'Ōhi'a trees accounted for 72% of total native tree density and 91% of total native basal area in forest plots measured here is in close agreement with prior studies conducted in the same region. Across a series of forest types in lowland wet forests of Hawaii, Atkinson (1970) concluded that succession to 'Ōhi'a dominated forest was the most general trend. Hughes et al. (2014) documented dominance of 'Ōhi'a stands using LiDAR data across an inventory of 1300 ha of native forests varying widely with respect to forest age as well as substrate age and type (i.e., pāhoehoe or a'ā lava). Zimmerman et al. (2008) characterized species composition and forest structure in plots totaling 9 ha of sampling area across forest stands that varied by lava age and type. They noted that although 'Ōhi'a was clearly the most dominant native tree on both young and old lava substrates sampled in their study, very little 'Ōhi'a seedling recruitment was observed, and non-native invasive species – notably *P. cattleianum* and *M. candidum* – were dominant understory components beneath 'Ōhi'a overstory canopies, particularly on substrates >300 years in age (Zimmerman et al., 2008). These authors concluded, along with Hughes et al. (2014) and Atkinson (1970) that widespread mortality of 'Ōhi'a trees by whatever means will very likely transform these forests from native dominated to non-native dominated. As such, the current phenomenon of *Ceratocystis*-induced 'Ōhi'a mortality is of utmost concern because it both hastens the loss of the compositional, structural, and functional component of these native forests and paves the way for dominance of invasive, non-native plant species across large expanses of these wet lowland forest ecosystems. The potential loss of 'Ōhi'a is crucial, not just because of its dominance in these lowland forests, but because of its dominance throughout the complete history of these lowland forests, and its dominance across the Hawaiian landscape.

Because we mapped mortality of all dead 'Ōhi'a trees, regardless of cause in our study area, it's inevitable that some 'Ōhi'a individuals in our study area have died from anthropogenic or natural

causes other than *C. fimbriata*. The pathogenic rust fungus *Puccinia psidii* has also become more widespread in 'Ōhi'a across Hawai'i (Uchida et al., 2006), yet it does not appear capable of killing mature trees (Silva et al., 2014), although the disease does kill 'Ōhi'a seedlings in some locations within our study region. Our accuracy assessment for 2012 and 2014 imagery mapping indicate substantial agreement with field data (Landis and Koch, 1977; Congalton, 1991; Pontius and Millones, 2011), suggesting some error may be present in our mapping of 'Ōhi'a mortality. However, the increase in area affected and severity of 'Ōhi'a mortality is undeniable as both plot and remote sensing data indicated similar levels of disease spread.

Due to its extreme ecological and cultural importance as a native Hawaiian species, previous episodes of 'Ōhi'a forest decline on Hawai'i Island have been studied in depth (Mueller-Dombois et al., 2013). Following nearly 40 years of research, cohort senescence was identified as the chief determinant of landscape level 'Ōhi'a dieback (Mueller-Dombois et al., 2013). Boehmer et al. (2013) recently noted greater 'Ōhi'a regeneration in areas having experienced cohort senescence compared to areas that had not experienced cohort senescence. Such findings suggest an overall stable long-term 'Ōhi'a population despite the occurrence of past severe dieback episodes (Hodges et al., 1986). However, none of these past dieback episodes has been driven by disease or insect outbreaks (Hodges et al., 1986) and none has occurred in areas of high non-native plant abundance seen in our study region (Zimmerman et al., 2008; Mascaro et al., 2008; Cavaleri, 2014).

Extensive *C. fimbriata*-induced mortality in natural forest systems is rare. The few documented cases elsewhere in the world include mortality of the riparian species *Platanus orientalis* in Greece (Ocasio-Morales et al., 2007) and mortality of *Prosopis cineraria* and *Dalbergia sissoo* in Oman and Pakistan (Al Adawi et al., 2013; Poussio et al., 2010). Mortality levels as high as 80% along canal banks and 40% along roads were reported in investigations of *D. sissoo* decline in Pakistan (Bajwa et al., 2003), although other pathogens such as *Fusarium solani* and *P. cinnamomi* were found to be present in addition to *C. fimbriata* s.l. (Poussio et al., 2010). In Greece, *C. fimbriata*-caused mortality of *P. orientalis* occurred primarily along streams and rivers and was limited to a 400 km² area (Ocasio-Morales et al., 2007). *C. fimbriata*-induced mortality has also been documented in aspen trees (*Populus tremuloides*) throughout USA and Canada, but with substantially lower mortality rates than we documented in 'Ōhi'a (Hinds, 1972). In most of the aforementioned cases, spread of *C. fimbriata* via root grafting was hypothesized (Ocasio-Morales et al., 2007). Root contact may offer a mechanism for spread of *C. fimbriata* in Hawai'i as well; spread via waterways may not be as important, as our study region lacks perennial streams and rivers. With consistent mechanical injury lacking in the natural forest, wounding via wind or animal could also offer a mechanism of spread. There has been no documentation of a new invasive insect in the area but spread through native insects such as *P. bilineatus* remains a possibility. *C. fimbriata* was confirmed in numerous dead and dying 'Ōhi'a across all ages of lava flows in the region by winter 2015 (L. Keith, personal communication), yet, based on coarse flow age maps, the majority of documented recent 'Ōhi'a mortality in this study occurred on lava flows aged 400–750 YBP. Additionally, we consistently observed this pattern in the field, and suggest it may offer clues about potential contributing factors or *C. fimbriata* vectors, yet we were unable to test it to a level of satisfactory robustness. Further, our results documented 'Ōhi'a mortality as occurring both in areas near human influence as well as in areas away from direct human contact.

Rates of annual mortality at the stand level and rates of increase in the spread of mortality at the landscape-scale reported here were greater than other instances of *C. fimbriata* induced mortality

anywhere in the world (Bajwa et al., 2003; Poussio et al., 2010; Ocasio-Morales et al., 2007). Though a thorough estimate of 'ōhi'a background mortality is lacking, annual background mortality in tropical wet rainforest globally was considered to be <5% by Lugo and Scatena (1996), considerably lower than the annual rates we report. Furthermore, in 2004 Hughes and Denslow (2005) found 97% of total 'ōhi'a basal area to be live during their study in healthy 'ōhi'a forest in the Puna District. We were unable to establish control plots as no suitable locations in our study area were clearly *C. fimbriata* free. The comprehensive 'ōhi'a mortality we are currently observing in Hawai'i appears comparable to the introduced Dutch elm disease and chestnut blight on the US mainland. Over half the elm trees in the northern US have succumbed to Dutch elm disease (Stack et al., 2011), and the chestnut blight killed an estimated 3.5 billion American chestnut trees in the eastern U.S. between 1904 and 1940 (Raupp et al., 2006). Given results from this study, it is not unreasonable to expect analogous levels of *Ceratocystis*-induced 'ōhi'a mortality over time in Hawai'i.

Although *C. fimbriata*-induced mortality has not been documented in naturally occurring wet forests of the tropics to the extent documented here, numerous studies document *C. fimbriata*-induced mortality in plantation settings around the world. Plantations of *E. grandis* in South America, Africa and Australia have experienced severe *Ceratocystis* mortality (Roux et al., 2000; Barnes et al., 2003). *Ceratocystis* species have had devastating effects on *Acacia mearnsii* in South Africa (Roux and Wingfield, 2009). Recently, *Ceratocystis* has caused wilt symptoms and rapid mortality in *Acacia mangium* plantations across much of Indonesia and Vietnam (Tarigan et al., 2011; Thu et al., 2012). In Vietnam, annual mortality rates were 5–7% in plantations (Thu et al., 2012), values lower than annual 'ōhi'a mortality rates reported here. *Ceratocystis fagacearum*-induced oak wilt disease is now present across 24 U.S. states (Juzwik et al., 2011). *Ceratocystis* spp. infection in plantations often enters individual trees through wounds generated by pruning or other mechanical damage. Additionally, spores of many *Ceratocystis* species survive for extended periods in soil and can be spread via movement of contaminated soil (Marin et al., 2003).

Increases in the extent of 'ōhi'a mortality (defined as $\geq 10\%$ mortality of 'ōhi'a), coupled with a high rate of annual 'ōhi'a mortality, indicate that *C. fimbriata* induced mortality occurs quickly and spreads rapidly. Mean annual plot mortality rates from 2014 to 2015 suggest that 'ōhi'a mortality may be nearly eliminated in as little as four years in particular areas. These mortality rates are substantially higher than the 5.4% annual mortality rate noted by McPherson et al. (2010) for *Notholithocarpus densiflorus* experiencing Sudden Oak Death (SOD) in California, a disease which has killed more than >5 million trees along the coasts of Washington and Oregon over the last 20 years (Frankel and Palmieri, 2014). In addition, the failure of 'ōhi'a seedling recruitment and characteristic understory dominance of non-native species documented within our research plots, coupled with the lethality of *C. fimbriata* to 'ōhi'a (Keith et al., 2015), suggest that these forests will be dominated by non-native species in the future. On a more positive note, 'ōhi'a exhibits a high degree of genetic variability (Stacy et al., 2014) which may give some 'ōhi'a individuals predisposition to survive *C. fimbriata* in a manner similar to survivorship exhibited by *Quercus agrifolia* individuals exposed to *Ceratocystis fagacearum* infection (Dodd et al., 2005). Such patterns remain to be seen.

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