

The evolving threat of Rapid ‘Ōhi’a Death (ROD) to Hawai‘i’s native ecosystems and rare plant species

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ARTICLE INFO

Keywords:

‘Ōhi’a

Metrosideros polymorpha

Ceratocystis lukuohia

Rapid ‘Ōhi’a Death (ROD)

Hawai‘i

ABSTRACT

Hawai‘i’s most widespread native tree, ‘Ōhi’a lehua (*Metrosideros polymorpha*), has been dying across large areas of Hawai‘i Island mainly due to two fungal pathogens (*Ceratocystis lukuohia* and *Ceratocystis huliohia*) that cause a disease collectively known as Rapid ‘Ōhi’a Death (ROD). Here we examine patterns of positive detections of *C. lukuohia* as it has been linked to the larger mortality events across Hawai‘i Island. Our analysis compares the environmental range of *C. lukuohia* and its spread over time through the known climatic range and distribution of ‘Ōhi’a. Analyses show this fungal pathogen generally encompassed the core, but not the extremes of the climatic range of ‘Ōhi’a. We further modeled the potential distribution of *C. lukuohia* across the Hawaiian Archipelago to estimate the risk of ROD to other islands. Given the potential for *C. lukuohia* to alter the structure of ‘Ōhi’a dominated forests, we used our projected potential distribution of *C. lukuohia* to assess the risk of ROD to threatened and endangered plant species across Hawai‘i. Many native plants are likely vulnerable to these types of large ‘Ōhi’a mortality events: of 234 endangered native plant species considered, 147 (62.8%) have more than half of their range within current and expanding *C. lukuohia* suitable areas. We also found evidence that protecting habitat by fencing out introduced feral ungulates reduces the prevalence of the disease likely by reducing physical damage caused by these animals to ‘Ōhi’a trees, a precondition for *Ceratocystis* infection. Given the ongoing spread of *C. lukuohia*, we developed a dynamic web portal to host our results online, where models and analyses are updated with new lab-confirmed detections to provide managers with a useful tool to help monitor and assess the risk of *C. lukuohia* as it continues to spread.

1. Introduction

‘Ōhi’a lehua (*Metrosideros polymorpha* Gaudich.) is a keystone species and the most biologically and culturally significant native tree in the tropical forests of the Hawaiian Islands in terms of community succession, forest structure, and ecosystem function (Friday and Herbert, 2006; Mueller-Dombois et al., 2013; Ziegler, 2002). Additionally, ‘Ōhi’a forests provide primary habitat for most native plant and animal species (Eldredge and Evenhuis, 2003; Pratt et al., 2009), and they provide a strong cultural link between native Hawaiian culture and the local environment (Luiz, 2017; Mueller-Dombois et al.,

2013). ‘Ōhi’a is dominant in wet and moist forests but is common in dry forests as well, inhabiting areas anywhere from sea level to 2800 m in elevation (Mueller-Dombois and Fosberg, 1998) and areas receiving 950–7200 mm annual precipitation. On the island of Hawai‘i ‘Ōhi’a-dominated forests account for 250,000 ha of the land cover. Another 100,000 ha of ‘Ōhi’a forests occur on the other main Hawaiian Islands (Jacobi et al., 2017). Overall, ‘Ōhi’a trees account for more than 80% of the biomass of native forests (Loope, 2016) and about 50% of the basal area of woody plants across the archipelago (FIA database phase 2; <https://www.fia.fs.fed.us/tools-data/>) (Smith, 2002).

Widespread ‘Ōhi’a mortality in the Hawaiian Islands has been

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<https://doi.org/10.1016/j.foreco.2019.06.025>

Received 2 February 2019; Received in revised form 13 June 2019; Accepted 14 June 2019

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documented several times in modern history. The earliest record of distressed ‘ōhi’a stands was noted in the early 1900s in wet forests found on eastern Maui (Lyon, 1909). Various episodes of ‘ōhi’a dieback and forest decline have been documented since (Mueller-Dombois, 1985, 1983), including a widespread canopy dieback in the 1970s that covered approximately 25,000 ha on windward Hawai‘i Island (Jacobi et al., 1988). Two forms of dieback were recognized to occur more rapidly during that event, and they had dramatic landscape impacts on wet, mesic, and dry forests (Jacobi, 1993). While disease is usually the suspect in dieback cases, in this case abiotic or environmental factors were determined to be the primary factors in forest decline and biotic factors (e.g., insects and fungal pathogens) were considered secondary factors (Mertelmeier et al., 2019; Mueller-Dombois, 1985).

More recently, ‘ōhi’a forests have experienced events of high and rapid mortality termed Rapid ‘Ōhi’a Death (ROD). Average annual ‘ōhi’a mortality rates within ROD areas may be as high as 28% and indicate that heavily impacted ‘ōhi’a forests may be dominated by non-native species in the near future (Mortenson et al., 2016). Two recently described fungi, *Ceratocystis lukuohia* I. Barnes, T.C. Harr. & L.M. Keith and *Ceratocystis huliohia* I. Barnes, T.C. Harr. & L.M. Keith have been identified as the main causal agents for this ROD pattern of mortality (Barnes et al., 2018; Keith et al., 2015). Both species cause browning foliage followed by rapid tree mortality as fungal growth blocks transport of water and sugar throughout the vascular system (Barnes et al., 2018; Loope, 2016). *C. lukuohia* is now identified as the main cause of stand-level mortality events, whereas *C. huliohia* is thought to be associated with smaller, more localized mortality events. Reports of ROD-related mortality escalated in 2012, and widespread symptoms of canopy browning became visibly noticeable in 2014 (Stone, 2017). The initial detections of stand-level mortality and *Ceratocystis* came from low elevation, wet forests on the eastern corner of Hawai‘i Island (Mortenson et al., 2016). From there the disease spread west and southwest and reached higher elevations and the west side of the island by 2015 (data shown at <http://hawaiirodresearch.org>). Comprehensive remote sensing surveys of ‘ōhi’a forests identified 44,000 ROD symptomatic dead trees in 2017 on the island of Hawai‘i (Vaughn et al., 2018). Recently, the State of Hawai‘i has mapped more than 60,000 ha of ROD-symptomatic ‘ōhi’a forests.

Given the high tree mortality attributed to these previously unknown *Ceratocystis* species, it is important to determine the potential distribution as well as possible environmental constraints to its rapid spread to understand risks to other areas across the Hawaiian archipelago. Past research has explored local stand level impacts of ROD (Mortenson et al., 2016; Mueller-Dombois et al., 2013) and landscape-level patterns of ‘ōhi’a mortality (Asner et al., 2018; Vaughn et al., 2018). While stand level studies are critical to identify dynamics of infection and recovery, they do not in themselves offer assessment of wider landscape level risk. Likewise, although research exploring patterns of ‘ōhi’a mortality has been invaluable given its spatial coverage, it cannot yet differentiate *Ceratocystis*-related mortality from other possible causal agents of ‘ōhi’a mortality such as natural causes, ‘ōhi’a-dieback, or other diseases. In this research, we focused on examining

patterns of the distribution of lab-confirmed detections of *C. lukuohia* across Hawai‘i Island. The objectives were to explore the environmental limits of *C. lukuohia*, determine the spatial pattern of its spread, and examine the risk of spread throughout the main Hawaiian Islands that harbor rare plant species which are the focus of conservation efforts in Hawai‘i. Given the ongoing spread of *C. lukuohia*, we expect more ‘ōhi’a forests to be impacted by the disease. In response, we encapsulated most analyses into a dynamic web portal that updates results of new lab-confirmed *Ceratocystis* detections to provide managers and other decision-makers with real-time information regarding the status of Rapid ‘Ōhi’a Death across the state.

2. Methods

The USDA Pacific Basin Agricultural Research Center has developed a molecular diagnostic tool that uses isolated DNA directly from infected wood (Heller and Keith, 2018; Keith et al., 2015) to test for the presence of *C. lukuohia* and *C. huliohia* in samples collected from ‘ōhi’a trees showing ROD symptoms in the field. This tool uses real-time PCR protocols for fungal DNA detection to distinguish between the two pathogens. Of the more than 3400 georeferenced samples collected on Hawai‘i Island, 1199 trees (35%) were positive for *Ceratocystis*. Of those positive samples, 723 were classified as *C. lukuohia*, 263 were classified as *C. huliohia*, and 213 were not identified at the species level. The other 2216 samples (65%) were characterized as “non-detected” (*Ceratocystis* DNA was not identified in the collected samples).

For our analyses, this complete dataset was thinned to reduce biases in sampling that could impact analyses and model projections. This was necessary because in some *C. lukuohia*-infested stands, multiple symptomatic and nearby trees were tested leading to multiple sample results from identical environments. These repeat tests essentially represent the same information about the potential environmental association of the pathogen. To thin the dataset and remove these pseudo-replicates, we screened the data by first grouping all samples that occurred within each 500 m-sized raster grid (the resolution of our climate datasets). Then across all samples collected within each grid, we identified all unique combinations of environmental conditions based on other factors considered in our analysis and described below (mean annual temperature, mean annual precipitation, vegetation type and substrate age). Lastly, the thinning procedure selected a single sample from each unique combination of environmental conditions within each grid. To do this, a positive sample was picked if any of the repeat samples were positive (indicating that at this given location and associated environmental conditions, *C. lukuohia* can occur), or a negative sample was picked if otherwise all environmentally similar samples were non-detections. This thinned the original dataset of 3425 samples to 849 samples (212 positive *C. lukuohia* samples) (Fig. 1).

While our analysis focuses on the sampling and detections found on Hawai‘i, as of December 2018, the first detection of *C. lukuohia* was found on Kaua‘i. We acknowledge this new detection but it was not included in our analysis as we used all available lab data collected through November of 2018 for our analysis to produce our results at the

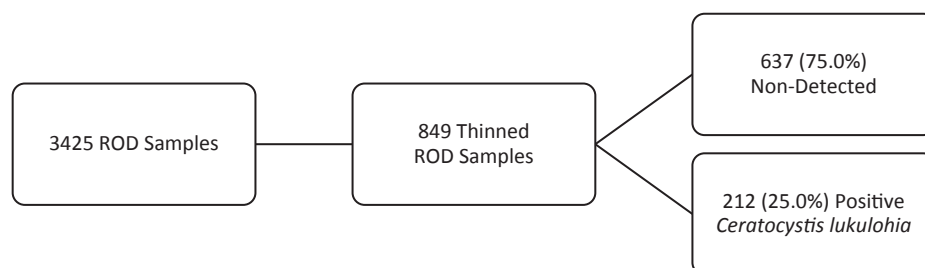


Fig. 1. Number of collected samples on Hawai‘i Island. Samples were collected by multiple partners and then processed to determine which *Ceratocystis* species was present (if any) by the USDA Agricultural Research Service.

time of this publication. Our dynamic web portal described below will include this and other updates to *C. lukuohia* distribution.

2.1. Exploring the environmental range of *C. lukuohia*

Using the thinned dataset described above, we considered sample locations with respect to several environmental variables to determine potential environmental limits of *C. lukuohia*. Positive and non-detected samples were tabulated by land cover type (Jacobi et al., 2017), biogeographic region, substrate type, and substrate age (Price et al., 2012), and rainfall and precipitation (Giambelluca et al., 2014). Substrate age and type were considered in this analysis as they are associated with differences in soil development and consequently vegetation differences (Kitayama and Mueller-Dombois, 1995).

For each of the variables above, we examined pathogen prevalence rates (i.e., the number of positive detections versus total number of samples) across environmental gradients and landscape classes. Additionally, for continuous climatic variables we used sample dates to characterize expansion of the environmental range of *C. lukuohia* over time within the context of 'ōhi'a forest environmental range. We opted for this relatively simple approach as opposed to a multivariate logistic approach that would require a broader sampling across multivariate space to properly describe absence of the pathogen. Lab tested samples were nearly always only collected from symptomatic and nearby trees, meaning they do not entirely represent disease-free areas across Hawai'i Island.

Mortenson et al. (2016) hypothesized that wounds to 'ōhi'a stems and roots caused by domestic and feral ungulates such as cattle, goats, sheep, and pigs can serve as entry points for *C. lukuohia*. With that in mind, we also compared *C. lukuohia* detections within and outside fenced areas that have been established across Hawai'i Island to reduce feral ungulate populations; we did this in order to evaluate whether exclusion of ungulates is associated with reduced prevalence of *Ceratomyx* infections. For this analysis we simply tallied samples collected within and outside existing fences based on Hawai'i State maps. We did not attempt to qualify which fenced areas were completely ungulate-free, as that information is not consistently available across the numerous fenced areas on Hawai'i, but instead assumed fencing in most cases is associated with substantially lower density of invasive ungulate abundance.

2.2. Modeling *C. lukuohia* distribution across the Hawaiian Islands

To determine the potential threat of *C. lukuohia* for forests on all of the main Hawaiian Islands, we created a species distribution model to identify the areas that *C. lukuohia* could potentially occupy on other neighboring islands based on current confirmed *Ceratomyx* locations from Hawai'i Island.

We used the same thinned data points described above for the distribution model of *C. lukuohia* to reduce sampling effort bias as SDM methods may invariably conflate high spatial sampling density with high site suitability (Araújo and Guisan, 2006; Wintle and Bardos, 2006). Because samples did not represent the full range of environmental conditions of disease-free forests as samples were nearly always collected for symptomatic trees, in addition to the positive *C. lukuohia* and non-detected samples selection, another 1000 randomly generated background points were also used to model the current distribution of *C. lukuohia* on Hawai'i Island.

We used MaxEnt (Phillips et al., 2006) to predict the distribution of *C. lukuohia* and ROD symptomatic trees based on bioclimatic variables that describe the main temperature and precipitation gradients across the Hawaiian archipelago. Minimum temperature at coldest month (BIO6) and mean annual precipitation (BIO12) were selected as our model predictors. This choice reflected the relatively clear pattern of disease prevalence across the wide temperature and rainfall gradients present across the archipelago, and their low collinearity. MaxEnt

compares the projected geographic distribution of occurrence points based on selected environmental predictors to a null distribution using the same predictors.

We used a receiver operating characteristic area under the curve (ROC AUC) score to determine diagnostic ability and evaluate the effectiveness of our model. ROC AUC scores typically vary between 0 and 1 and can be interpreted as the probability of the model to discern between non-detections and positive disease detections based on the predictors used. Thus, a model with a score of 0.5 is no better than a coin flip, and a model with a score of 1 is perfect in terms of accuracy. These models were projected across the main Hawaiian Islands to show the potential distribution of *C. lukuohia* beyond Hawai'i Island. This estimate likely does not describe the full potential range of *C. lukuohia* since this pathogen continues to spread across the landscape. Rather, the goal of this analysis is to describe *C. lukuohia*'s current distribution on Hawai'i Island and to evaluate potential impacts on the rest of the archipelago. This projected potential range of *C. lukuohia* is updated on the online portal with new data as it becomes available to continually update the projected risk of ROD archipelago-wide.

2.3. Potential vulnerability of Hawaiian plant species to *C. lukuohia*

While there is no known direct risk of *C. lukuohia* infecting other native plant species, other native Hawaiian plants are likely indirectly threatened by ROD. Given the dominance of 'ōhi'a in native Hawaiian forests and how many current threatened and endangered plants rely on 'ōhi'a for habitat structure (Ziegler, 2002), large changes to 'ōhi'a dominated forests are likely to have impacts on co-existing native species. Past research has documented large stand-level 'ōhi'a mortality events that substantially alter the structure of these forests (Mortenson et al., 2016). Furthermore, ROD-related 'ōhi'a mortality poses opportunities for invasive plant establishment and native species displacement (Boehmer et al., 2013; Jacobi et al., 1983). Hence, using previously developed range maps for Hawaiian plants (Price et al., 2012), we assessed the risk of ROD to other listed Threatened or Endangered plants by the US Fish and Wildlife Service that may be indirectly impacted by changes in habitat structure due to increased 'ōhi'a mortality. To do this we calculated the percentage of overlap area of these 234 selected plants within the projected distribution of *C. lukuohia* to determine which plants may be most vulnerable to the spread of *C. lukuohia* on Hawai'i Island specifically, and the Hawaiian Archipelago as a whole.

3. Results

Our results focus on *C. lukuohia* due to its role in large stand-level mortality events; figures in the live portal (see below) contain results for both *Ceratomyx* species.

As of now, *C. lukuohia* positive trees generally occupy the hotter (t -test: $t = 5.5$, $p < 0.001$) and wetter (t -test: $t = 9.8$, $p < 0.001$) portions of 'ōhi'a distribution compared to non-detected samples. While *C. lukuohia* has reached the higher limits of the mean temperatures of 'ōhi'a distribution early in its spread, its lower mean annual temperature limit of 13.6 °C has not changed over the last year (with few detections below 15 °C), and remains well above the 8 °C 'ōhi'a minimum mean annual temperature limit (Fig. 2). When further analyzing pathogen prevalence along the temperature gradient considering available temperature datasets, prevalence showed a strong relationship to mean annual temperature (0.65) but even higher and clear correlation to minimum temperature of coldest month (0.893; Fig. 3). Interestingly, prevalence was also strongly (but negatively) correlated to temperature variability metrics including temperature seasonality (-0.966) and temperature annual range (-0.972 ; Appendix A1).

Regarding mean annual precipitation, *C. lukuohia* occupies nearly the driest and wettest parts of the known 'ōhi'a distribution. *C. lukuohia* quickly spread to wet portions of the 'ōhi'a range before 2016 (i.e.,

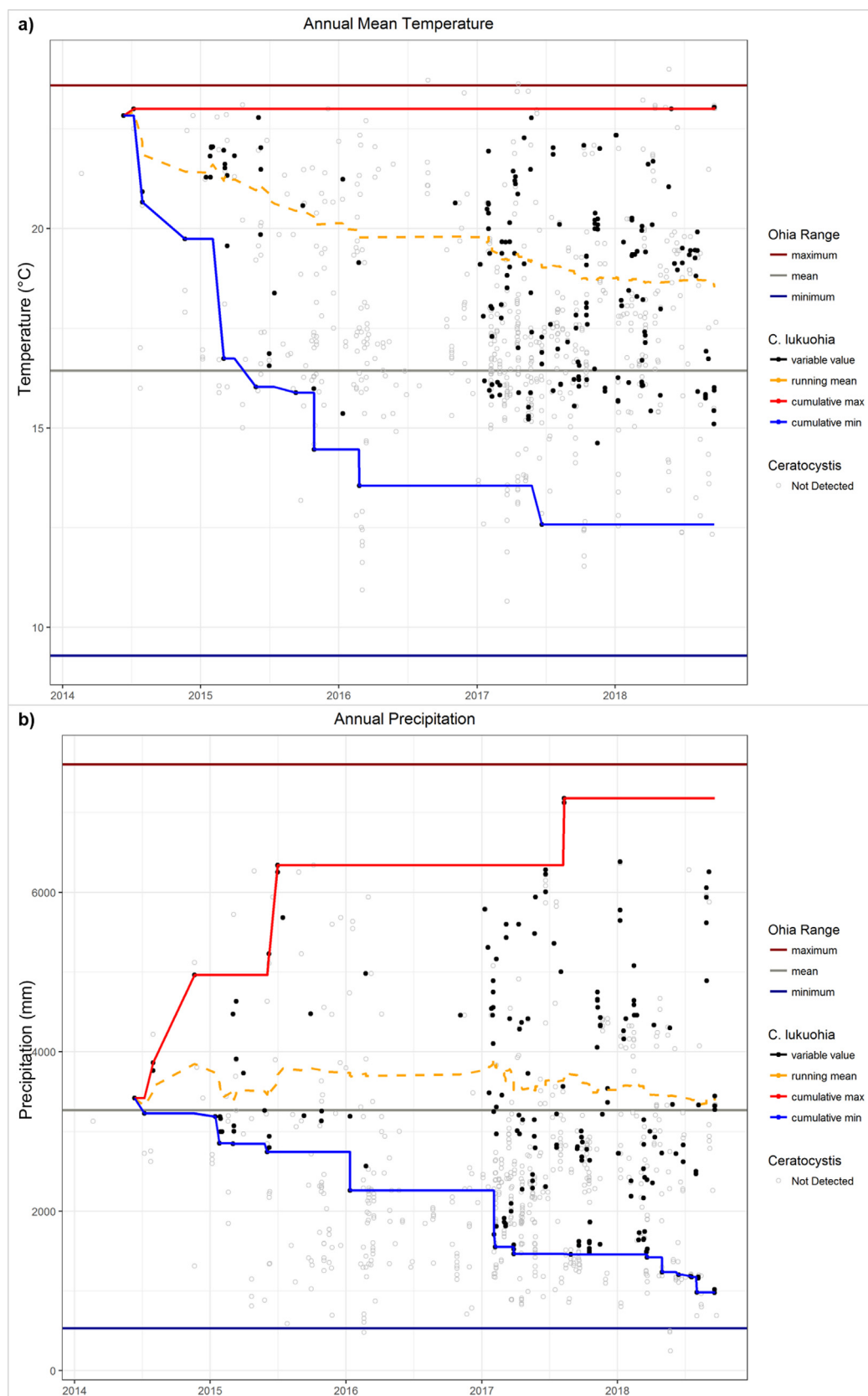


Fig. 2. Bioclimatic ranges of *C. lukuohia*. The distribution of (a) annual mean temperature (°C), and (b) annual mean precipitation (mm) variables for *C. lukuohia* on Hawai'i Island compared to the environmental ranges of 'ōhi'a.

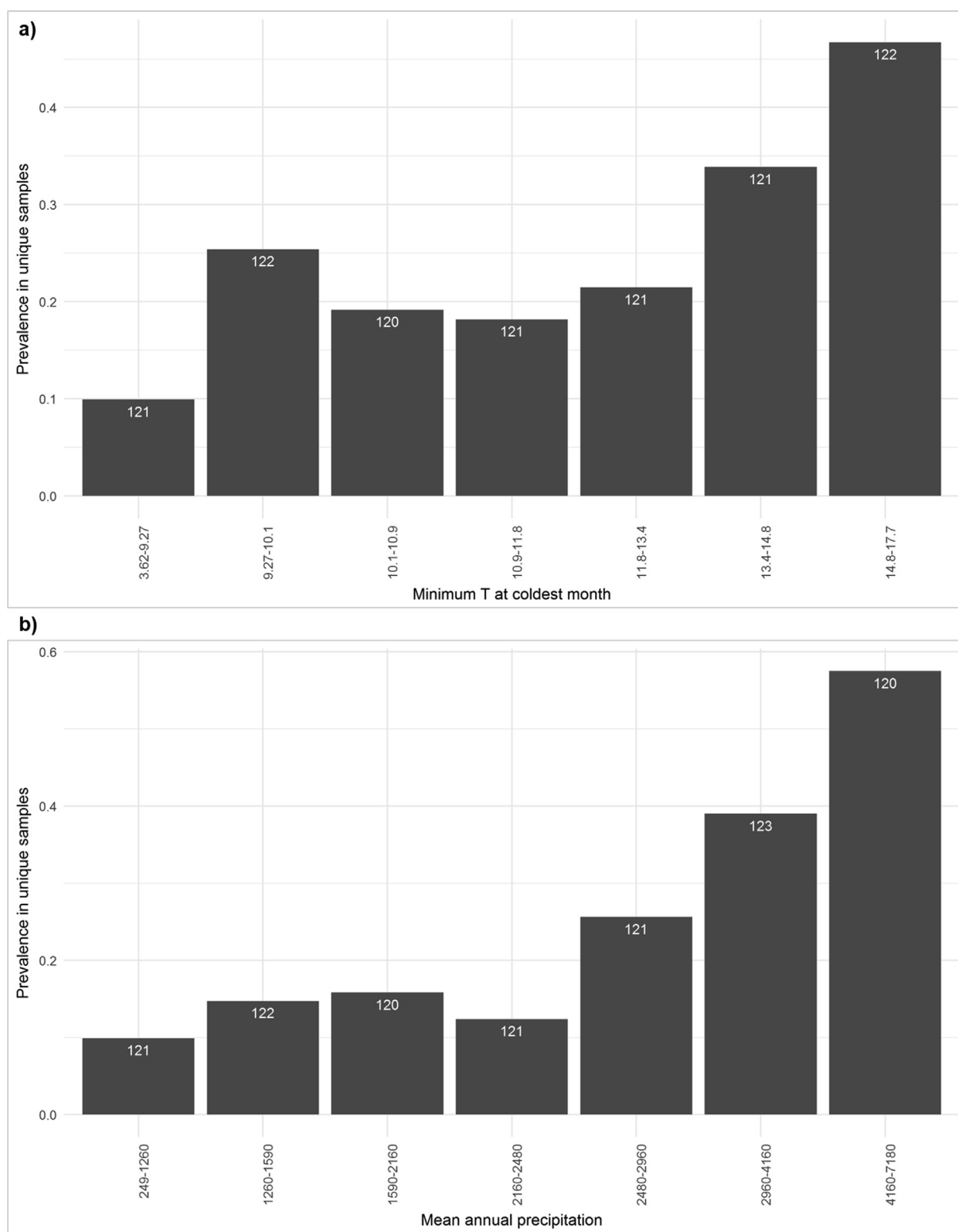


Fig. 3. *C. lukuohia* prevalence along Hawai'i Island climatic gradients. The prevalence of (a) minimum temperature of the coldest month (°C), and (b) annual mean precipitation (mm). To minimize bias in sampling along gradients, size of bins were selected to yield an equivalent number of environmentally unique samples (number displayed on top of each bar). Similar graphs for other variables included in Appendix A1.

windward slopes of Mauna Kea), and has expanded into wetter forests since late 2017 (Fig. 2). However, examining pathogen prevalence along the rainfall gradient, a clear correlation of increased pathogen prevalence with increased mean annual rainfall emerged (0.962 correlation; Fig. 3). Unlike temperature-related variables, no precipitation seasonality based variables yielded as consistent and monotonic trends

compared to means-based precipitation metrics. However, precipitation seasonality was showed a clear curvilinear relationship to pathogen prevalence (Appendix A1).

With regards to landcover type, most *C. lukuohia* prevalence patterns followed the precipitation patterns described above. *C. lukuohia* prevalence was highest across all wet plant communities (Appendix

A1).

Prevalence of *C. lukuohia* varied more erratically with respect to the wide substrate type, substrate age gradient and biogeographic regions across Hawai'i Island, which suggest that these factors may not be impacting patterns of 'ōhi'a disease and mortality across the landscape (Appendix A1). With respect to samples collected within and outside fenced areas, we found that 258 of the samples collected were from trees located in fenced areas. Of these samples, 21 tested positive for *C. lukuohia*, representing an 8.1% prevalence rate. In contrast, 191 of 591 samples tested positive for *C. lukuohia* in unfenced areas, equivalent to a 32.3% prevalence rate for the disease. Based on a binomial distribution, the probability of drawing only 21 out of 258 positive tests under the unfenced prevalence rate of 24.9% is $< 1.6 \times 10^{-20}$; this suggests a highly significant difference in disease prevalence within fenced areas compared to outside fenced areas. Furthermore, to ensure this pattern did not result from fenced areas being primarily in areas that are less environmentally suitable to the disease, we performed a post-hoc logistic regression on *C. lukuohia* detections based on mean annual temperature and precipitation, and fencing status that showed fencing to be a highly significant factor ($p < 0.0002$) associated with lower pathogen detections even when considering other important environmental covariates.

3.1. Modeled *C. lukuohia* distribution

We projected the modeled distribution of *C. lukuohia* across the Hawaiian Islands to identify where this pathogen could potentially expand based on minimum temperature of coldest month and mean annual precipitation (Fig. 4). Given a ROC score of 0.847 which is indicative of high accuracy, our model appears to have effectively discerned the difference between unique presence and absence points. Given the strong decreasing pattern of *C. lukuohia* prevalence with respect to temperature seasonality, we attempted to create models which included temperature seasonality variables as well. However, model

performance did not substantially improve so we opted to keep the simpler two variable model. The windward sides of the main Hawaiian Islands offer areas of high suitability for *C. lukuohia*. These projections highlight potential areas where *C. lukuohia* could spread on all of the main Hawaiian Islands. While our model projects the potential range that *C. lukuohia* could spread into, it does not take into account the methods by which this pathogen may be spread (i.e., beetle frass, human contact, ungulate wounding, etc.) which could affect its ability to reach some of these new areas. While our model projections give us an estimation of areas that are potentially vulnerable to the spread of *C. lukuohia*, the actual range of this pathogen has yet to be fully realized given the unfinished dispersal of the pathogen. We expect our projected model results to evolve to better represent the full niche as more data becomes available and can be readily incorporated into our modeling methods. The modeled results were also clipped to the current distribution of 'ōhi'a forests (Fig. A2). However, limiting the mapped distribution to areas identified as 'ōhi'a forests excludes other areas where 'ōhi'a was not mapped but is present in low abundance. Nonetheless, these projections highlight 'ōhi'a-dominated areas that fall outside suitable areas for *C. lukuohia* based on its current distribution, such as the Southern Waianae range on O'ahu and the upper Alakai bog in Kaua'i. However, if *Ceratocystis* continues to spread, additional 'ōhi'a-dominated areas may fall within high *C. lukuohia* suitability areas.

3.2. Ecosystem impacts and plant vulnerability

On Hawai'i Island, 38 species listed as threatened or endangered by the U.S. Fish and Wildlife, 13 of which are in endemic genera, overlapped with some portion of the current projected range of *C. lukuohia* (Fig. 5); six of these rare species' distributions overlapped by more than 95% of the modeled range of *C. lukuohia*.

Across the Hawaiian Archipelago, 215 of the threatened or endangered plant species exhibited some overlap with projected distributions of *C. lukuohia* statewide (Table A3). Of the 234 endangered

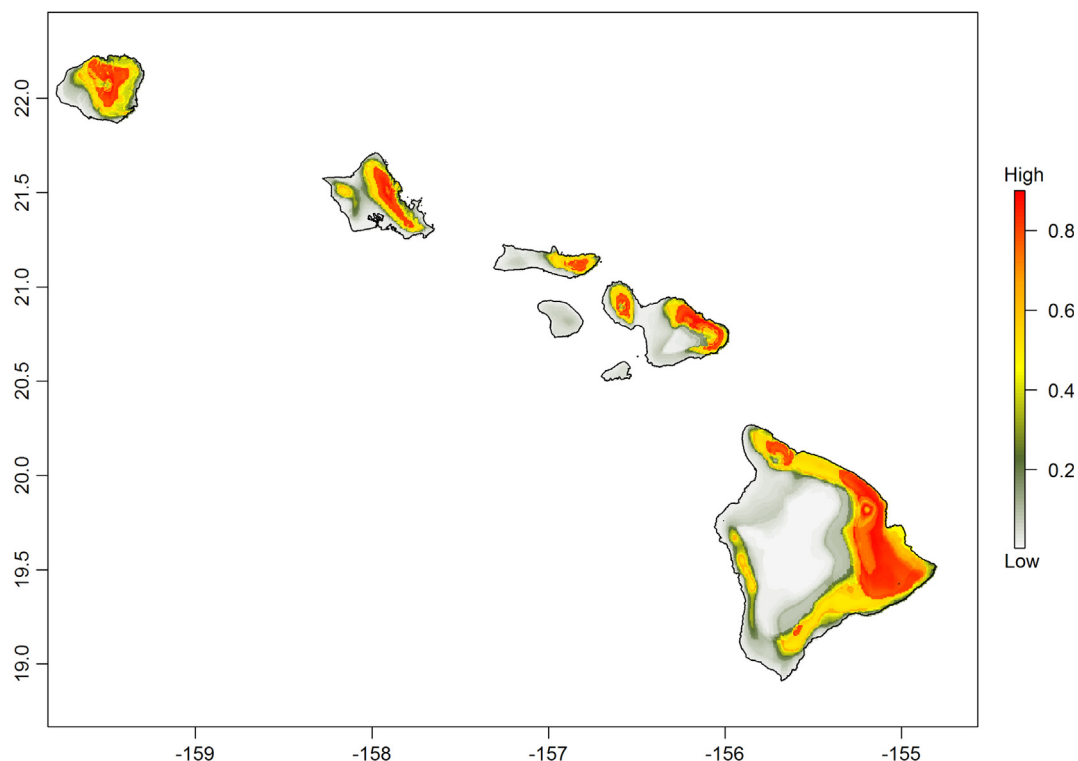


Fig. 4. Projected suitability for *C. lukuohia* across the main Hawaiian Islands under current climatic conditions. Areas in red indicate areas of higher suitability for *C. lukuohia* to spread and establish on other islands. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

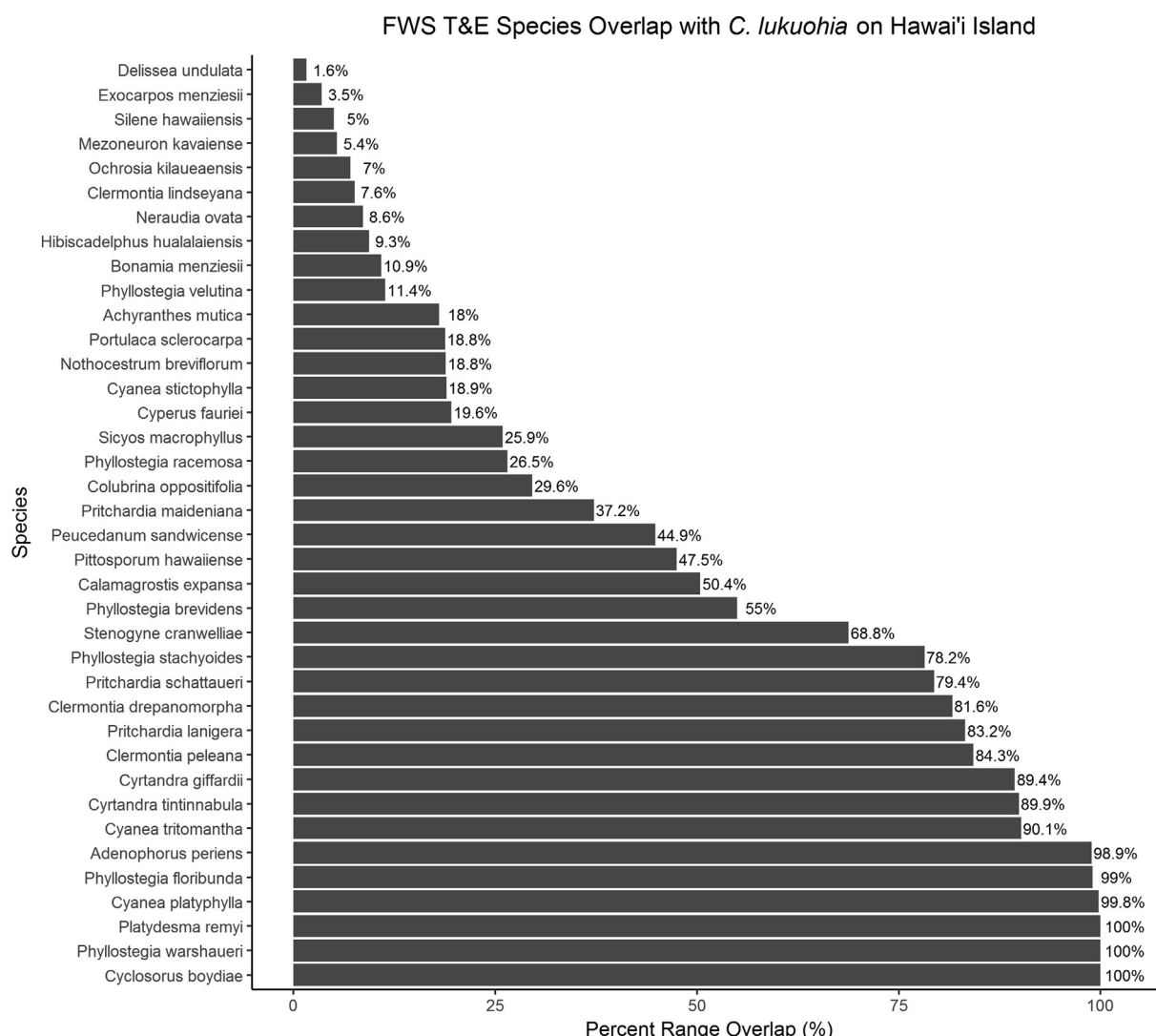


Fig. 5. Potential impact of *C. lukuohia* on listed Threatened or Endangered Species on Hawai'i Island. The overlap of US FWS threatened or endangered species ranges with the current distribution of ROD. Percentages indicate the spatial overlap in plant species distribution within the modeled projections of *C. lukuohia* on Hawai'i Island.

native plant species analyzed, 147 (62.82%) exhibited more than half of their modeled range within current and potentially expanding *C. lukuohia* suitable areas across the Hawaiian Islands. Of these, 135 are species that occur outside of Hawai'i Island and 35 of these species have their range entirely encompassed within the projected distribution of *C. lukuohia*.

4. Discussion

Other research has either proposed or employed similar methodologies and techniques to assess the ecological risk and environmental associations of pathogens based on the distributional patterns of lab-confirmed samples. Similar studies have focused on sudden oak death (*Phytophthora ramorum* Werres, De Cock & Man in't Veld) in the United States (Lione et al., 2017; Meentemeyer et al., 2015), and *Heterobasidion irregulare* Garbelotto & Ostrosina (Gonthier et al., 2012) and *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz & Hosoya (Dal Maso, 2014) in Europe. Early detection and risk models for these pathogens as well as *Ceratocystis* are important components in implementing effective control strategies to contain their spread. As the use of assays has proven to be pivotal in diagnosing invasive pathogens in previous studies (Sillo et al., 2018; Tomlinson and Boonham, 2015; Tomlinson et al., 2010), they have also been implemented for early detection

purposes in the case of identifying different species of *Ceratocystis* (Heller and Keith, 2018; Keith et al., 2015). The speed at which ROD appears to be spreading presents an urgent need for these rapid detection methodologies so that the changing risks associated with ROD can be identified and addressed in a timely manner.

Recent aerial surveys of 'ōhi'a mortality across Hawai'i Island, as well as plot level studies, indicate that mortality of ROD symptomatic trees threaten to substantially alter 'ōhi'a dominated forests (Asner et al., 2018; Vaughn et al., 2018; Mortenson et al., 2016). While previous and ongoing LiDAR, helicopter, and drone-based surveys have focused on mapping ROD symptomatic trees, a major challenge has been that these symptoms may arise from either diseases caused by *Ceratocystis* species or drought or possibly other causes. Our work differs from these past and ongoing efforts by focusing exclusively on lab-confirmed and species-specific distributional patterns, environmental associations, and broader ecological risks.

Gaps in sampling related to our ability to access ROD-symptomatic trees across the landscape likely resulted in biases in our analyses. Sampling of symptomatic trees has been focused on areas of greater accessibility in terms of landowner access, distance, and terrain, resulting in few samples from potentially undisturbed remote areas. To that extent, areas that have not been sampled may not necessarily represent areas that are free of *Ceratocystis*. Sampling also tended to be

concentrated in specific areas of interest, such as important conservation areas, which often led to clumping of samples that likely under-represents spatial variability of conditions under which *Ceratocystis* can occur. With that in mind, we have attempted to minimize the impact of the differential sampling across the landscape by only considering environmentally unique samples and by looking primarily at *C. lukuohia* prevalence rates which are not directly impacted by differential sampling intensity across the landscape. Yet, it is still possible that some of the prevalence patterns we observed are partially due to differences in sampling effort across the landscape. Nevertheless, the strong prevalence gradients we observed with respect to climate are unlikely to be entirely driven by sampling distribution. For temperature, for instance, we could expect a similar pattern of temperature-dependent prevalence if sampling for the fungal pathogen was relatively homogeneous across the entire temperature gradient while the pathogen was still expanding its range from higher temperature areas to lower temperature areas over time. This would have led to multiple non-detections at lower temperature areas early on when in fact *C. lukuohia* had not yet reached those areas. However, looking at the average temperature of samples across time, it is clear that as this pathogen expanded in range from high to low temperatures, the climatic distribution of sampling shifted as well (Fig. A4), partially reinforcing that the prevalence patterns we observed are at least partly related to biology, and not just sampling.

Our analyses showed that while *C. lukuohia* generally occupies the core climatic range of 'ōhi'a forests for most bioclimatic variables, some range extremes of 'ōhi'a appear to be beyond the climatic range of *C. lukuohia*, based on our current knowledge of its distribution. While *C. lukuohia* was found in forests from young to old substrates and across all regions of Hawai'i Island, *Ceratocystis* prevalence is currently highest in wet windward forests on Hawai'i Island. It exhibited a climatic range that occupies areas expressing warmer annual temperatures that are moderately wet, but it is not yet found in colder and wetter extremes of 'ōhi'a's range. However, the frequency of 'ōhi'a trees in the lower temperature environments within these native forests is low. On one hand, the range of annual temperature *C. lukuohia* can occupy has changed little since early detections and prevalence seems to be strongly correlated with temperature, suggesting a potential deceleration of *C. lukuohia* spread into colder habitat zones. On the other hand, *C. lukuohia* has a clear preference to wetter habitats with prevalence being strongly correlated with rainfall. This means that while there have been no detections on the wettest parts of 'ōhi'a's range, eventual spread to those areas may be particularly damaging. This is worrisome as the wettest parts of 'ōhi'a's range, on the windward slopes of Mauna Kea, are particularly difficult to access and have been little sampled.

That the majority of Hawaiian threatened and endangered plant species are found within 'ōhi'a forests emphasizes the importance of minimizing the spread of this pathogen on Hawai'i Island and keeping *C. lukuohia* from becoming established on the other Hawaiian Islands. *C. lukuohia* threatens not only 'ōhi'a trees directly, but stands to potentially affect other plant species whose habitat could be altered by widespread 'ōhi'a mortality. Across the archipelago, 35 endemic species have their current range entirely within the projected potential range of *C. lukuohia*. Death of 'ōhi'a canopy trees, whether from *Ceratocystis* or other causes, also allows accelerated establishment of invasive plants into Hawaiian forests, which could result in greater long-term ecological impacts (Boehmer et al., 2013; Jacobi et al., 1983). Now that *C. lukuohia* has been discovered on Kaua'i, the possibility of its spread and the threat it poses to native plant species on other islands has now become a reality.

Given the recent nature of Hawai'i's *C. lukuohia* outbreak, an overall prevalence rate of 25% across unique samples is substantial given the many factors that may lead to false negative results. First, because field sampling protocols were not well developed during the early phases of the outbreak, dead trees were sampled that may have not exhibited a consistent set of ROD symptoms. Second, sample location and timing for individual trees can result in false negatives where the fungus,

although in the tree, is undetected. For trees just recently infected, a false negative may result if the inoculation point is far enough away from the location on the tree sampled, for example at the point of a broken branch high in the crown of the tree. On the other hand, wood from old dead trees is difficult to test for presence of the fungus, whether by culturing techniques or by qPCR. To further complicate the issue, timing-dependent detection seems species-specific where *C. huliohia* causes internal cankers with well-defined borders that enlarge slowly whereas *C. lukuohia* moves more quickly within the infected tree. Consequently, as response to identified symptomatic trees quickens, sampling methods improve, and lab testing methodologies become more sensitive, there is the possibility that *Ceratocystis* mortality will be found to be a much wider problem than currently estimated. In fact, areas of ROD-symptomatic trees recently identified by aerial surveys were quickly sampled and consequently lead to higher detection rates for both *Ceratocystis* species.

4.1. Management tools and implications

That an estimated large number of native threatened and endangered plants are potentially vulnerable to ROD-driven habitat degradation and the results that suggest ungulate removal reduces *Ceratocystis* prevalence further suggest that some of the primary tools such as fencing that are already used to manage invasive threats in Hawai'i are also critically important tools to minimize the impact of ROD. Enhanced biosecurity to contain ROD impacts to Hawai'i Island is already well-recognized, with the State limiting the transport of 'ōhi'a wood, plant parts, and soil from Hawai'i Island to other islands. Most agencies working in 'ōhi'a forests have also substantially strengthened sanitation protocols and transportation restrictions for field staff, equipment, and vehicles within and across islands. However, similar measures are still practically nonexistent for the wider public. If fencing indeed minimizes *Ceratocystis* spread as our relatively simple analysis indicates (and has been preliminarily corroborated by ongoing airborne-based ROD mapping efforts) (R.F. Hughes, personal communication), *Ceratocystis*-induced ROD may prove to be yet another important rationale for boosting efforts in fencing to help with ungulate control across the state. This is only one of many identified detrimental ungulate impacts on native ecosystems that already include direct damage and herbivory, direct habitat degradation, spread of invasive competitors, and creating sites suitable for vectors of avian disease (Stone and Loope, 1987; Wehr et al., 2018).

While *C. lukuohia* related 'ōhi'a mortality is of critical concern to many land managers given the dynamic risk this disease poses to Hawaiian forests, understanding the larger picture of this pathogen and its spread has been a challenge. Monitoring the possible changes in environmental range and the resulting risk to other islands is important given the fact that the spread of *C. lukuohia* is ongoing and poses a real threat to 'ōhi'a across the Hawaiian Archipelago. To that aim, we have incorporated our analysis methodology and results into an active web-portal that automatically updates projected distribution maps and habitat characteristics as more lab-confirmed data is made available online at <http://hawaiirodresearch.org>. Given the dynamic nature of how *Ceratocystis* spreads across Hawaiian forests, we anticipate that distributional patterns of ROD and habitat parameters described here will change and more 'ōhi'a forests across the state will be impacted. Due to the sensitivity of the spatial data on Hawai'i that may affect the land-owners at the sampled collection sites, the exact spatial location of the positive points is located somewhere within the larger radius of the points displayed online via the portal. Development of this online portal will provide access for scientists, managers, and the general public to view the most recent information on ROD as new field surveys and lab analyses are completed.

4.2. Knowledge gaps

This study provides modeled distribution and habitat information that can be used to support a more detailed predictive risk assessment analysis of the potential threat that *C. lukuohia*, or ROD in general, poses to the main Hawaiian Islands. Our resulting distribution model highlights areas most susceptible to the spread of *C. lukuohia* across the wider Hawaiian landscape if this disease spreads across the archipelago. Nevertheless, this analysis does not replace the more challenging work to identify the likely complex mechanisms that drive the spread and environmental limits of 'ōhi'a diseases caused by *Ceratocystis*. These are likely to include the complex interactions between spore viability and the abundance and strength of multiple possible vectors such as insects, ungulates, humans, and wind.

Our focus on *C. lukuohia* is not intended to disregard other potential factors contributing to landscape-level 'ōhi'a mortality beyond the two *Ceratocystis* pathogens already identified as culprits to ROD symptoms. Of the 609 trees that were described at the time of sampling as displaying ROD-like symptoms, 315 (51.7%) returned non-detected results for either *C. lukuohia* or *C. huliohia*. 'Ōhi'a dieback, such as what occurred on Hawai'i Island in the 1970s (Mueller-Dombois, 1985) and myrtle rust (*Austropuccinia psidii* G. Winter.) are other known causal agents of large 'ōhi'a mortality events (Uchida et al., 2006). In fact, the apparent deviations in *C. lukuohia* prevalence across the landscape indicate a comprehensive examination of causes of 'ōhi'a mortality is warranted.

Acknowledgements

We thank the multiple people and agencies responsible for ROD sample collection and testing. These include Kyson Dunn, Nainoa Goo, Kalena Shiroma, and Edward Bufil, among others. We thank Wade Heller, Eva Brill, Blaine Luiz, and Lionel Sugiyama for their invaluable technical assistance. We also thank Rob Hamnett and Kyle Harper for helping organize the field sample and lab datasets. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.06.025>.

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