

Multi-scale remote sensing-based landscape epidemiology of the spread of rapid 'Ōhi'a Death in Hawai'i

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ABSTRACT

Fungal pathogens of the genus *Ceratocystis* recently introduced to the Island of Hawai'i have killed hundreds of thousands of native 'Ōhi'a trees, an ecologically and culturally important keystone species. Symptoms of the associated disease, Rapid 'Ōhi'a Death (ROD), have been found to be easily detectable with high resolution imaging spectroscopy. We used wall-to-wall maps of affected 'Ōhi'a canopy built in four consecutive years (2016–2019) to analyze how changes in the distribution and density of browning canopy detections over this time period corresponded to environmental drivers at two spatial scales. Island-wide we found 256,387 brown crowns across the 4-year period. The total amount of affected forest area nearly doubled from 66,972.2 ha in 2016 to 121,464.7 ha in 2019, cumulatively representing 42.5% of the 264,372 ha of forest area observed at least once in the study. However, most browning activity was concentrated in 18 hotspots totaling approximately 29,836 ha with brown crown densities as high as 26 ha⁻¹. Using Random Forest (RF) models, we assessed the correspondence between 32 mapped environmental variables and measures of ROD spread calculated at 1-year time steps on a 300 m × 300 m grid across the island. We found that modelled probability of regional infection, or "susceptibility", was dominated by distance to existing infection at the start of a time step; increasing distance from 0 to 600 m decreased susceptibility from 0.8 to 0.3. Other important factors – tree cover, average windspeeds, and LiDAR-derived 3-d crown exposure – were 4–10 times less important to the model. In a second RF model we studied regional infection "severity", measured as detection density in first year of infection. In contrast to susceptibility, the severity model was significantly affected by numerous factors including windspeed metrics, canopy height and exposure as well as most weather and climate metrics related to water regime. Severity model predictions were less dominated by proximity to existing infection. In a separate regional analysis at 2 m resolution we found that taller trees were more prone to infection, and that trees on younger "historic" lava flows (i.e., substrates < 230 years old) showed slight but significantly lower infection rates than immediately adjacent older substrates. Our results document the extent and severity of 'Ōhi'a mortality across Hawai'i Island and provides insight into factors that appear to affect the spread of ROD; this information will inform management efforts to lessen the spread and impact of the disease on all the Hawaiian Islands.

1. Introduction

Biotic forest disturbances have been increasing globally as trade activity has rapidly increased transport and introduction of pests and pathogens to new regions (Faulkner et al., 2020; Seidl et al., 2011; Sikes et al., 2018) and these disturbances are expected to accelerate as an effect of climate change (Chapman, 2012; Seidl et al., 2011). Among disturbances, pests and pathogens may be among the most impactful, both ecologically and economically (Dale et al., 2001; Schelhaas et al., 2003; Vitousek et al., 1997). Forest degradation caused by such

disturbances has been deemed catastrophic (Lovett et al., 2016; Schelhaas et al., 2003) because it can rapidly alter species composition, forest structure, and ecological function over large regions (Evimer and Likens, 2010; Loo, 2009; Simberloff, 2011; Vitousek et al., 1997). However, collective and cumulative damage from such events is rarely quantified, even though it can sum to enormous ecological and economic loss (Anderson-Teixeira et al., 2020).

Despite the magnitude of their consequences, pathogen outbreaks have received a comparatively small share of research focus at the landscape level relative to other types of forest disturbance (Castello

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et al., 1995; Ireland and Kriticos, 2019; Loo, 2009). Although basic mechanisms of a disease caused by a particular pathogen may be well understood via laboratory investigations and small-scale field studies, such ex-situ experimentation rarely leads to understanding how these mechanisms scale to affect large regions (Eviner and Likens, 2010; Preston et al., 2016). There are numerous studies exploring and optimizing pathogen species distribution modelling approaches; these have most often focused on optimization of survey and detection efforts rather than on developing fundamental understanding of pathogen behavior in the wild (Ireland and Kriticos, 2019; Parnell et al., 2014). As a result, relatively little is known about how such pathogens interact with landscapes on larger scales (Lundquist and Klopfenstein, 2001). More landscape-scale epidemiology studies are critically needed, as they could fill the knowledge gap between small-scale studies and realized disturbance severity and extent and lead to insights of how best to slow or prevent the spread of destructive plant diseases (Holdenrieder et al., 2004; Plantegenest et al., 2007).

Due to the range of scales involved, landscape epidemiology studies can prove challenging (Parnell et al., 2014). A common approach has been to model suitability based on field-measured disease severity at locations with confirmed pathogen presence against mapped environmental factors. This has been done successfully in multiple locations around the world using various model forms at regional to global scales (Meentemeyer et al., 2011; Requena-Mullor et al., 2020; Watt et al., 2021). However, field surveys of disease severity are limited by cost, time, and accessibility, and they often rely on positive detection in convenient locations. As a result, they often lack true absence data, which can lead to model inaccuracies (Václavík and Meentemeyer, 2009). Thus field-based epidemiology studies, while useful for coarse assessments of environmental response, may lack the accuracy and statistical power to resolve high-resolution dynamics between a pathogen, its host, and the local environment. A viable pathway to remedy such limitations is to use remote sensing for detection of tree diseases, which can allow for a nearly complete census limited only by disease detectability (Vicent and Blasco, 2017). Remote sensing approaches and technologies have been applied to document patterns and dynamics of forest diseases such as Sudden Oak Death (He et al., 2019; Liu et al., 2006), Chestnut Blight (Marques et al., 2019), Emerald Ash Borer (Pontius et al., 2008), White Pine Needle Damage (Meneghini et al., 2022), as well as bark beetle damage (Bright et al., 2014; Tane et al., 2018), but such studies did not explicitly address and explore potential factors that may have been responsible for increasing pest or disease spread.

In approximately 2010, ‘Ōhi’a (*Metrosideros polymorpha*) trees on Hawai’i Island began to experience unusually high rates of mortality (Loope, 2016); noticeable increases in mortality initially occurred in the Puna District in the southeastern corner of Hawai’i Island. High levels of mortality were subsequently determined to be due to a newly identified disease termed Rapid ‘Ōhi’a Death or ROD (Keith et al., 2015). ‘Ōhi’a mortality of any sort is a cause for concern because of the tree’s foundational role as a native habitat-generating species (Mueller-Dombois and Fosberg, 2013). An estimated 303 million ‘Ōhi’a trees, representing 16 million Mg of aboveground carbon, currently exist on Hawai’i Island; collectively they account for 38% of all trees and 52% of all above-ground forest carbon on the island (Owen et al., 2022). ROD is caused by two distinct species in the genus *Ceratocystis*, a group of pathogenic fungi known to damage and kill a wide variety of woody plant species around the world (Hughes et al., 2020). *C. lukuohia*, a vascular wilt fungus, is the more virulent of the two species and the main cause of ‘Ōhi’a stand-level mortality. *C. huliohia* is a canker pathogen that is less virulent to ‘Ōhi’a and is associated with smaller-scale, localized mortality events (Barnes et al., 2018; Fortini et al., 2019; Loope, 2016). Ongoing genetic studies are determining that *C. lukuohia* is a recent introduction (i.e., 2 to 3 decades) to Hawai’i, while *C. huliohia* has likely been present for a much longer period (i.e., > 100 years). Both diseases manifest as interruption of water movement through a tree’s xylem; symptoms occur rapidly and

present as asymmetrical browning and wilting of the crown followed by mortality (Barnes et al., 2018). The relatively ephemeral (i.e., weeks to months) and striking reddish-brown canopy color stage is unique to ROD infection (Asner et al., 2018; Perroy et al., 2020). In general, ‘Ōhi’a trees of a given stand succumb to fungal infection in a haphazard pattern. Stands in which confirmed *C. lukuohia* infected trees occur exhibit mean annual mortality rates of ca. 10% compared to background rates of ca. 1%. Mortality rates are highly variable; some stands experienced annual mortality rates as high as 44% (i.e., complete stand mortality in < 3 years), while other stands containing trees killed by *C. lukuohia* exhibited no further mortality (R.F. Hughes, unpub. data).

As part of ongoing efforts to reduce spread of ROD on Hawai’i Island (Fortini et al., 2019), the Global Airborne Observatory (Asner et al., 2012), formerly the Carnegie Airborne Observatory, developed maps of tree crowns expressing ROD symptoms annually over four years (2016–2019) using laser-guided imaging spectroscopy (Asner et al., 2017). Maps were generated at 2 m resolution by pairing two computational machine learning methods (Vaughn et al., 2018), and they identify the location of individual tree crowns expressing ROD symptoms at the time of data acquisition. Having multiple timesteps of mapping afforded the unique opportunity to track the spread of this disease at high resolution both spatially and temporally. In this study we related between-timestep movement of likely ROD infections to a suite of climatic, topographic, geologic, vegetative, and other factors at multiple scales to discern patterns in the data. In so doing, we sought to answer three questions: 1) What were the levels, patterns, and dynamics of the Rapid ‘Ōhi’a Death across Hawai’i Island during the 4-year monitoring period of our study? 2) What factors are associated with occurrence and rate of spread of *C. lukuohia* across diverse landscapes of Hawai’i Island? and 3) Can relationships between these influential factors and rates of ‘Ōhi’a canopy browning inform us about the behavior of *C. lukuohia* in this landscape-scale system?

2. Methods

2.1. Study site

The island of Hawai’i contains a uniquely diverse set of environmental conditions within a relatively small area of just over one million ha (i.e., 10,430 km²). Elevations range from sea level to 4,207 m at the top of Mauna Kea, the tallest of five volcanoes on the island. The tropical latitude, strong geological features and consistent northeasterly trade winds create strong gradients in both average annual precipitation, which ranges from 204 to 7,629 mm (Giambelluca et al., 2013), and average annual temperature, which ranges from 4 to 24 °C (Giambelluca et al., 2014). These environments occur across a matrix of different soil development stages created by the mix of active and dormant volcanoes ranging from a few years in age to approximately one million years (Vitousek, 2004). Despite this variation, the extreme isolation of the Hawaiian Islands has limited natural introduction of new species, and overstory composition is generally limited to relatively few endemic species. Of the endemic tree species in Hawai’i, ‘Ōhi’a is by far the most dominant, occurring as the primary overstory component within nearly all forested land across all stretches of the island (Owen et al., 2022).

2.2. Browning ‘Ōhi’a canopy maps

The root source of data used in this study consisted of four maps of brown ‘Ōhi’a canopies, one for each of four consecutive years, that were each developed following an established spectral detection (Asner et al., 2018) and modelling (Vaughn et al., 2018) approach. In brief, this approach incorporated data from two paired instruments aboard the Global Airborne Observatory (GAO): 1) 2 m resolution orthorectified 214-band visible-to-shortwave infrared (VSWIR) imaging spectroscopy reflectance data covering the spectral range 350 nm–2,500 nm and 2) LiDAR-derived top-of-canopy surface height (TCH) models at 1 m

resolution. These data were collected and processed annually for four consecutive years by the GAO with data collection flights occurring during January 2016, June–July 2017, January 2018, and January 2019 (Fig. 1). Total mapped area varied by year, with 674,055 ha in 2016, 515,430 ha in 2017, 310,653 ha in 2018 (significantly less due to time and budget constraints), and 541,980 ha in 2019.

Two machine learning classifier models, one a support vector machine and the other a gradient boosted regression trees model, were each fit to training data built with spectral data falling into three distinct classes: 1) leafless branch canopy, 2) ROD-infected browning ‘Ōhi’a canopy, and 3) healthy vegetation canopy of any species. The training dataset representing examples of each of these classes was built by identifying individual tree crowns on the ground and in the imagery.

Each model fit was evaluated using a 10-fold cross validation approach, with the entire dataset split into 10 groups. Model predictions produced values between 0 and 1 that indicated likelihood of the observed spectrum representing browning ‘Ōhi’a canopy. We defined a simple decision rule to combine the two models’ predictions under the assumption that both models would be unlikely to produce false positives for the same pixels. A likelihood threshold of 0.65 was used to identify individual $2\text{ m} \times 2\text{ m}$ map pixels as browning ‘Ōhi’a canopy or not. This methodology produced a brown canopy sensitivity of 86.9% and very high precision of 97.4%. Once fit statistics were computed, each model was fit once more to the full training dataset for prediction. The models were updated each year with additional training sample data to address feedback from field checks, and the final model was retroactively



Fig. 1. Detection density maps for Hawai'i Island from each of the four GAO coverage campaigns, January 2016 (a), June–July 2017 (b), January 2018 (c), and January 2019 (d), with regions of higher map uncertainty masked out (shown in blue-filled polygons). Background imagery from Google Earth. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

applied to mapped reflectance data for each year.

Raw data maps were then filtered in multiple ways. First, we set a lower limit on canopy height considered in this analysis by masking all pixels with a TCH model height < 1.5 m above ground. Second, we grouped clusters of positive detection pixels that touched either by face or corner into individual affected “crowns”. It was rare for neighboring trees to be in a browning state simultaneously, so this seemed a reasonable assumption. Pixels making up clusters of < 2 pixels in total area were converted to “not brown” in final browning canopy maps used in all following analyses. This was done to further limit the influence of any remaining false positive detections, which often took the form of singleton positive detection pixels.

For each year, the final yearly browning ‘Ōhi’a canopy map became a $2\text{ m} \times 2\text{ m}$ map for the entire mapped area of the island of Hawai’i where each pixel represented one of four mutually exclusive states: 0) unmapped, 1) mapped and < 1.5 m above ground elevation, 2) mapped vegetation ≥ 1.5 m above ground not identified as browning ‘Ōhi’a, and 3) mapped browning ‘Ōhi’a ≥ 1.5 m above ground. Pixels in state 3 were considered positive detections of ROD and pixels in state 2 or 3 were considered “forested” for summary purposes. We also kept the cluster I.D. of each pixel in state 3 in these maps, and for each such cluster we recorded a centroid location to represent a single brown tree crown. Thus, we could investigate spread and distribution of ROD either as affected canopy area or as affected number of crowns, depending on the analysis. Certain regions in each of the annual maps exhibited higher temporaneous density that was more uniformly spread and not observed in following years. Because we were uncertain about the validity of these detections—possibly caused by light scattering from volcanic emissions not removed during atmospheric correction of the imagery, or canopy browning from other causes—we removed these regions from consideration for the affected year (Fig. 1) prior to all analyses.

2.3. Analysis overview

This study consisted of multiple investigations, each designed to answer a different question. In a first phase, we performed a statistical summary of annual infection rates across the island by looking at differences in count and density of brown crowns within and across the annual maps. Next, we performed a pair of coarse island-scale epidemiological analyses looking for environmental influences of two measures of ROD spread: Regional susceptibility to infection, and disease severity in recently infected regions. Finally, we performed a finer-resolution regional-scale analysis of the influence of canopy height, crown exposure, and substrate age on the likelihood of infection across all four years of mapping. We describe each of these in detail below.

2.4. Infection rate summary

Regarding infection rate, we first computed both the total number of individual affected crowns (as clusters) and the average density of these crowns relative to the total forested area mapped each year. Total number of crowns was simply the number of pixel clusters identified in the browning ‘Ōhi’a maps, while total forested area was computed by counting the number of forested pixels (state 2 or 3 as defined above) and multiplying by pixel area to obtain a spatial value (ha).

We next detected and delineated hotspots of browning activity throughout the study period by first computing the density of browning crowns each year. To compute density in a spatial manner, we aggregated the detected brown crown point data into a grid of $300\text{ m} \times 300\text{ m}$ (150×150 pixel), 9 ha regions covering the island. From preliminary analysis, we found this grid size maintained minimal within-region variation of forest structural traits while simultaneously maintaining fidelity to spatial patterns observable in the brown tree maps. The total number of detected brown crowns (as clusters) was summed for each 9 ha grid cell and scaled to a density (ha^{-1}) by dividing over the amount of forested area of each grid cell. For each grid cell, we computed average

and maximum brown crown density across the years it was mapped, producing a 300 m-resolution raster map of each of the two statistics. These maps were smoothed using a gaussian kernel with sigma 1.5, and we built a mask to identify all grid cells with an average annualized density of more than 1.0 crowns ha^{-1} and a maximum density of > 2.0 crowns ha^{-1} . The boundary of each contiguous region meeting these conditions was transformed into a polygon, and these polygons were divided into named groups based on place names near to their locality within the island. Average brown crown density was computed for each hotspot by averaging the pixels of the 300 m-resolution raster map of annualized density that fell within each hotspot boundary. Similarly, maximum brown crown density was computed for each hotspot by taking the maximum value of the 300 m-resolution raster map of maximum density within each hotspot boundary.

2.5. Island-scale analyses

A pair of island-scale analyses were performed to link patterns observed within several environmental factors with patterns in the spread of ROD around the island. Two different metrics of ROD spread were modelled using computational machine learning tools against mapped environmental, topographic, climatic, and anthropogenic factors. The basic unit of sampled data for each of these analyses was the browning canopy area in the form of a density value. This was computed on the same $300\text{ m} \times 300\text{ m}$ grid used for the infection rate summary analysis as the number of affected pixels—essentially summing affected crown sizes—within the cell to retrieve an area of affected ‘Ōhi’a canopy in units of pixels. This value was divided by the number of forested ha in the grid cell to retrieve a density as pixel detections ha^{-1} . A 9 ha grid cell was marked “infected” for a given year if the detection density was > 0 . These analyses considered the state of each grid cell across one-year timesteps, and the three potential timesteps (2016–2017, 2017–2018, and 2018–2019) were considered independent for the purpose of computing the measures of spread.

2.5.1. Measures of spread

The first measure of spread was designed to capture long-distance expansion of ROD disease. We only considered grid cells which were uninfected at the start of a given timestep in this analysis. Thus, once a grid cell became infected, it was not incorporated into the dataset for any remaining timesteps. For all such grid cell-timestep observations, we created a binary variable labeled “Initial” that was given a value of “1” if the grid cell was initially infected during the timestep (i.e., end of timestep detection density was > 0) and a value of “0” otherwise (i.e., end of timestep density remained zero). We used this binary dataset to model the probability of a grid cell becoming initially infected, i.e. $P(\text{Initial} = 1)$, which we termed “Susceptibility”. Across the GAO map coverage, we observed 30,896 occurrences of a grid cell exhibiting initial browning during one of the three timesteps. Of the grid cells that never exhibited brown crown density > 0 , we randomly selected an equal number of these grid cell-timestep observations to balance out the modelling dataset (i.e., $N_{\text{total}} = 61,792$).

The second measure of spread was designed to capture local rate of dispersion of *C. lukuhia* within a given region after that region had been initially exposed to the pathogen. In this analysis we considered only the 30,896 grid cell observations that became infected during a timestep, i.e. those exhibiting an Initial value of “1”. This way the amount of time for ROD to disperse through the area is theoretically limited to < 1 year because initial infection occurred during the timestep. For each recently infected grid cell, the amount of affected tree crown area would be a reasonable quantitative indicator of rate of spread. For this reason, the detection density at the end of the timestep was used to quantify “Severity”, or how quickly *C. lukuhia*-induced mortality occurred at local scales. The term severity is often used to mean the magnitude of disease symptom expression in a single tree. This term then translates well here because for most observable ROD infections, the entire tree

succumbs rather suddenly, and summed affected crown area is an appropriate measure of the average disease severity among trees in the region.

2.5.2. Island-scale driving factors

We evaluated a suite of 32 potential driving factors collected from various sources (Appendix S1 – Table S1). The first factor, “Distance from Nearest Infection”, was computed from the same gridded GAO brown tree density maps used to compute Initial and Severity values. This factor was computed for each observation using the distance to the nearest previously infected (i.e., brown crown density > 0 at timestep start) grid cell for each timestep. As such, the models could both quantify and adjust for spatial clustering inherent to infectious diseases.

Several factors in our list were derived from standard GAO LiDAR and VSWIR data products (Asner et al., 2012). We used the LiDAR-derived 1 m resolution ground elevation map, averaged to the same 9 ha grid used for brown tree density maps, to compute “Elevation” and “Slope”. Terrain aspect relative to the predominant trade wind direction from the Northeast was incorporated as “Northeastness”, a transformation to represent terrain aspect as a positive absolute angular difference from Southeast direction scaled such that a minimum of 0 occurs with Southwest aspects and a maximum of 1.0 occurs with Northeast aspects (Appendix S1). Using a LiDAR-derived 1 m resolution raster model of tree canopy top-of-surface height (TCH) above ground, we computed “Canopy Height” as the average TCH map value for each 9 ha grid cell. From the same TCH map, we computed “Tree Cover” as the proportion of 1 m-resolution LiDAR vegetation height surface pixels exhibiting a canopy height > 1.5 m above the modelled ground surface. Since one of the ways in which *C. lukuohia* is thought to colonize tree wounds resulting from wind-caused branch and stem breakage (Hughes et al., 2020), wind events have been hypothesized to be contributing causes of long-distance spread. Thus, we used TCH maps to create multiple metrics of directional tree crown exposure based on the high-resolution 3-dimensional tree crown heights relative to neighboring crowns (Appendix S1). In this way, we computed “Southern Crown Exposure” and “Northern Crown Exposure”. A directionless value, “Total Exposure”, was also computed as the sum of grid cell level exposures in all four cardinal directions.

Remaining potential driving factors were collected and adapted from various other sources. “Substrate Age” of each grid cell was obtained from a vector map of best-estimate flow ages across the Hawaiian islands (Sherrod et al., 2007); age of each grid cell was extracted from the flow map at the center point of each grid cell. Where age was provided as a range (e.g., 400 to 750 years old), the center point of the range was used. Weather and climate variables (Giambelluca et al., 2014) included “Average Rainfall”, “Cloud Frequency”, “Relative Humidity”, “Solar Radiation”, “Vapor Pressure Deficit”, and “Evapotranspiration”. We used modelled hourly estimates of windspeed (Michalakos et al., 2001) at 6 km resolution to compute 1) “Annual Average Windspeed” (i.e., overall average across all hourly maps for a given timestep) 2) “Maximum Daily Average Windspeed” (i.e. maximum daily average during a timestep), and 3) “Maximum Hourly Windspeed”, (i.e. the highest value among all hourly maps for a given timestep), for each grid cell during each timestep between GAO flights. Much of the island is receiving less annual rainfall than was typical decades to a century ago. To quantify drought severity and duration, we created five rainfall anomaly metrics that integrate annual differences between mapped yearly annual rainfall values and the computed average mapped amount from a baseline period at the beginning of the observations (Appendix S1). The first of these was “100-Year Rainfall Anomaly”, previously computed (Barbosa and Asner, 2017) to measure prolonged drought using modelled monthly maps of rainfall from 1920 to 2012 (Giambelluca et al., 2013). We used the same methodology to compute anomaly metrics at four additional time scales: “5-Year Rainfall Anomaly”, “10-Year Rainfall Anomaly”, “20-Year Rainfall Anomaly”, and “30-Year Rainfall Anomaly” (Appendix S1).

We used spatially explicit parameters of fire behavior (Rollins, 2009) that included estimations of percent occurrence of three classes of fire severity for each region based on disturbance models and an assumed fire regime: “Proportion of Low Intensity Fire”, “Proportion of Mixed Intensity Fire”, and “Proportion of Stand Replacement Intensity Fire”. Spatially explicit estimates of “Fire Return Interval” were also employed. We used a vegetation species composition map derived from satellite data (Gon et al., 2006) to create an indicator variable as to whether the vegetation classification for a given grid cell contained only ‘Ōhi’a, “pure ‘Ōhi’a”, as well as a variable indicating whether there was detected presence of “non-native” species in the overstory. We employed GIS layers indicating roads and streams (Perennial Streams, 2014; Roads – Hawaii County, 2014) to create maps of distance to nearest recorded road and distance to nearest mapped perennial stream.

2.5.3. Random forest analyses

We used data from maps of the various island-scale driving factors to model both island-scale mortality spread metrics, that is, Susceptibility and Severity, using Random Forest Machine Learning (RF) models (Appendix S1). RF models are flexible, non-parametric models with built-in defenses against overfitting, and they are straightforward to fit to large, complex datasets such as those used in this study. We fit the “Initial” variable—an indicator of whether or not a grid cell began showing brown crowns for the first time in a given timestep—using a RF classifier model. This model produces a continuous value for Susceptibility that is the predicted probability of initial infection between 0 and 1. We assessed model performance using a threshold to divide predictions for each grid cell into two predicted classes: Initial = 0 for Susceptibility values < 0.5, and Initial = 1 for Susceptibility values ≥ 0.5. The Severity variable—the count of infections in newly-affected grid cells—was modelled using an RF regressor model. This model directly estimates the continuous Severity value as the predicted detection density for a grid cell at the end of the time step. More details about these models can be found in Appendix S1.

An optimization algorithm was used with cross-validation to obtain optimal model settings in each case (Appendix S1). Relationships of Susceptibility and Severity values with individual input factors were evaluated using partial dependence plots (PDPs) which portray marginal averages in the response variables across the range of a given input factor (Appendix S1). The importance of each input factor to each model was computed using a procedure where values of an input parameter were randomly permuted, and statistics of model predictions under this permutation were compared to those of the unaltered dataset (Appendix S1).

2.6. Regional-scale analysis

This analysis also allowed us to quantitatively test and understand patterns observed in the field that 1) there were fewer ROD-affected trees on younger lava substrates compared to surrounding forests on older lava substrates, and 2) taller trees appeared more prone to ROD infection and mortality. However, because trees on younger substrates exhibited height distributions that were weighted more toward shorter trees than older substrates, a complex modeling approach was needed to have the statistical power test for significant differences in browning rates between the substrates. In addition, tree height is related to quantities of tree exposure and this would also need to be accounted for. Thus, we performed an extended analysis at a finer spatial scale using rates of browning determined at the pixel level from the annual 2 m × 2 m browning canopy maps.

We focused this analysis on a selection of recent lava flows and adjacent older lava flows occurring on Mauna Loa and Kilauea volcanoes (Fig. 2), and we used the annual 2 m × 2 m pixel maps of detected browning ‘Ōhi’a. Six sites of similar-aged flows occurring in “historic” time periods (i.e., 1700 AD to present) were selected across the southern and eastern sectors of Hawai’i Island. The average individual lava flow

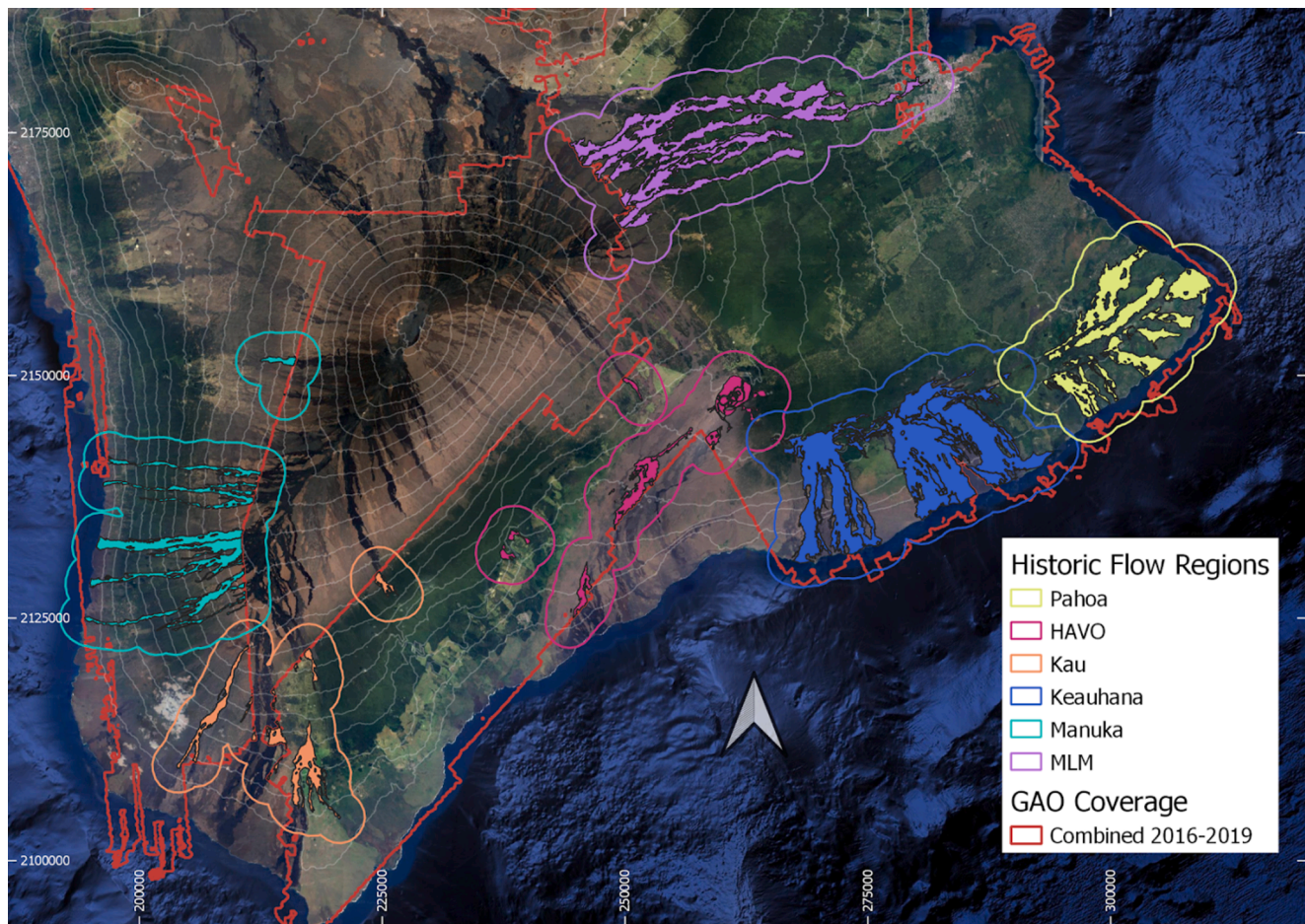


Fig. 2. Location of the “historic” flows (i.e., those < 230 in age) used in the 2 m resolution analysis of effects of tree height and substrate age on brown tree detection rates. Six separate regions were based on location and environmental similarity. Solid-colored regions are historic flows with their adjacent buffer areas within 2.5 km outlined in solid lines of the same color. Background Imagery from Google Earth.

area was 416.3 km² size, and all flows totaled 2497.9 km². Regarding each site, we identified an adjacent 2.5 km buffer area consisting of relatively older lava flows immediately surrounding the historic flow perimeter of the site (Fig. 2).

We collected data for all vegetated 2 m × 2 m pixels within each of the sites from the 2016 GAO brown tree map that were not classified as brown and that exhibited a height above ground > 1.5 m (determined by LiDAR-derived TCH values defined above). Any pixels subsequently classified as brown across any of the three remaining timesteps (2017, 2018, 2019) were marked as “browned”, and those that did not were marked as “unbrowned”. We used the ratio of count of browned pixels to total pixel count within each site and substrate age to quantify site-level differences in browning rates (Appendix S1 – Table S2). We used chi-squared tests to check for significant differences between levels of browning in historic flow areas compared to their corresponding older buffer environments.

We used logistic regression to model probability of an individual pixel browning while incorporating the interacting effects of substrate age, individual ‘Ōhi’a tree height, and surrounding canopy height. We created balanced training data by limiting the number of browned pixels to 10,000 for each combination of site and substrate, and we randomly selected an equivalent number of unbrowned pixels from the same combination (Appendix S1 – Table S2). For each selected pixel, we recorded: 1) the site to which the pixel belonged, 2) the substrate age (Age) categorized as “Historic” or “Buffer”, 3) the average canopy height (CanopyHt) computed from the LiDAR TCH map across all pixels within a 50 m by 50 m square centered on the selected pixel, and 4) the height

above (HtAbove) this average canopy height value as determined from the TCH map for each given pixel—a measure of upper crown wind exposure. The logistic model incorporating these 4 terms was built in a backwards stepwise manner, starting with a full model including all independent terms along with their two- and three-way interactions. At each iteration we retained all terms that were individually significant (i.e., p-value ≤ 0.05) or were part of an interaction term that was significant, and we iterated this process until all terms met these conditions. We initially tested a random term for “Site”, but it did not significantly reduce model variance and thus was not included in the analysis. We used R programming language to construct and analyze the models (R Core Development Team, 2012).

3. Results

3.1. Island-scale analyses

3.1.1. General trends

Throughout the four yearly episodes of airborne survey, 736,443 ha of Hawai’i Island was mapped at least once. Of this mapped area, 285,613 ha were “forested” (i.e. had a LiDAR-measured canopy height greater than 1.5 m), and total forested area with rapidly browning ‘Ōhi’a crowns grew significantly from 66,972 ha in 2016 to 121,464 ha in 2019, nearly doubling in number (Table 1). While the total amount of affected area grew rapidly, the number of brown crowns detected within a given time period actually declined from > 75,000 in 2016 to < 60,000 in 2018 and 2019 (Table 1). The average density of these crowns also

Table 1

Salient parameter values of each sample year's browning 'Ōhi'a canopy maps. Mapped area is the total land area covered over which spectrometer data was collected. Forested area is the amount of area exhibiting canopy heights > 1.5 m (as modelled with LiDAR data). Detected crowns consisted of clusters of two or more 2 m × 2 m pixels predicted to be browning 'Ōhi'a canopy. Affected forest area was the amount of forested area within 300 m × 300 m (9 ha) grid cells containing detected brown crowns. Cumulative affected area was the area of the union of affected regional area from all years up to the current year. Density was the number of detected crowns divided by total mapped forested area.

Statistic	Measurement Year			
	2016	2017	2018	2019
Mapped Area (ha)	674,055	515,430	310,653	541,980
Forested Area (ha)	227,354	245,635	173,477	264,372
Detected Crowns	76,577	63,024	58,147	58,639
Affected Forest Area (ha)	66972.2	89565.8	70961.5	81172.9
Cumulative Affected (ha)	66972.2	97799.6	109910.8	121464.7
Density (crowns ha ⁻¹)	1.143	0.703	0.819	0.722

declined from 1.14 crowns ha⁻¹ in 2016 to 0.703 crowns ha⁻¹ in 2017 and stabilized to between 0.70 and 0.82 crowns ha⁻¹ for the remainder of the study. Despite declines in density from the 2016 value, no significant trend was detected; a fitted regression exhibited a negative slope, but was not significantly different from 0 ($p = 0.274$). Although the 2017 average density value was based on data collected in June-July instead of January and was the lowest of all the years' values, it did not differ significantly from the average of the other years ($t = -0.753$, p -value = 0.5301). In total, we detected ca. 256,000 newly browned 'Ōhi'a crowns during the four years sampling episodes. The average density, weighted by the annual measured affected areas, was 0.83 brown crowns ha⁻¹ over the four-year period.

Brown crown density values were fairly low in most affected areas; only approximately one third (32.5%) of the affected area across all years exhibited a crown density greater than 1.0 crowns ha⁻¹, and we found that the spatial distribution of grid cells exhibiting high brown crown density values was concentrated into 18 hotspot regions across the island (Table 2, Fig. 3). The areal extent of these hotspot regions ranged from 89 ha at K'au Makai on the western flank of Mauna Loa volcano in the southern region of Hawai'i Island (i.e., Hotspot 7, Table 2) to 5,224 ha in the Hilo Forest Reserve region upslope of the city of Hilo

Table 2

Hotspot regions identified in the browning 'Ōhi'a detection maps. These regions were observed to exhibit high annualized rate of brown 'Ōhi'a crown density, measured as detected brown crowns ha⁻¹ over the four annual episodes of data coverage.

Hotspot	Region	Mapped (ha)	Forested (ha)	Avg. Density (crowns ha ⁻¹)	Max. Density (crowns ha ⁻¹)
1	Hilo Forest Reserve	5224.2	3463.7	1.25	8.06
2	Hilo	1531.0	1125.5	1.96	11.33
3	Hōnaunau	4362.3	2639.3	1.28	9.22
4	Kahuku	2847.5	2387.4	1.20	7.19
5	Kapāpala	853.3	450.6	1.25	5.39
6	Ka'u	3693.7	2748.5	2.10	13.85
7	Ka'u Makai	89.4	59.8	1.01	2.16
8	Ka'u Mauka	2381.3	1916.4	1.30	5.74
9	Keahou	664.5	358.3	0.95	3.33
10	Manukā	768.0	115.5	0.98	3.74
11	Pāhoa	1749.5	772.9	2.45	26.00
12	Palani	209.2	71.8	1.73	5.05
13	Pu'u Maka'ala	1521.7	1244.1	1.09	6.91
14	Pu'u Uau	119.4	59.0	1.21	4.99
15	South Kona	220.1	91.3	0.84	6.44
16	Stainback	307.9	213.9	1.99	7.09
17	Volcano	2388.8	1646.1	1.51	7.05
18	Waiākea	904.4	503.0	0.99	5.06

(i.e., Hotspot 1). Average annual densities ranged from <1.0 crowns ha⁻¹ at Keahou, Manukā, and Waiākea regions (i.e., Hotspots 9, 10, and 18) to > 2.0 crowns ha⁻¹ at Ka'u and Pāhoa regions (Hotspots 6 and 11). Maximum crown densities within these hotspots were much more variable, ranging from 3.3 in the Keahou hotspot to 26.0 crowns ha⁻¹ in the Pāhoa region (Hotspot 11).

3.1.2. Susceptibility model

The total classification accuracy value of the Susceptibility model fit under a five-fold cross-validation procedure was 0.732 (Gini = 0.624, Kappa = 0.464); that is, 73% of all predictions of whether 30,896 grid-cell-timestep observations initially browned during a timestep were correct. The model was somewhat more effective in correctly identifying grid cells that did initially brown than identifying those that did not (76% and 71%, respectively; Appendix S1 – Fig. S1a).

Very few input factors proved important to Susceptibility model predictions. Using a threshold of 0.005, meaning the model accuracy was reduced by 0.5% or more when a given factor was converted to noise via permutations, only 5 of the 32 factors were identified as important (Fig. 4). Exhibiting an importance value of 0.08, the parameter "distance from nearest detection" was by far the most important factor. This meant that the largest contributing factor to the Susceptibility model was simply how close a grid cell was to currently infected and dying 'Ōhi'a crowns. The partial dependence plot for this factor shows predicted Susceptibility decreasing rapidly from 0.8 for a grid cell immediately adjacent to an infected neighbor to 0.3 for a grid cell more than 600 m from an infected neighbor (Fig. 5a).

Additional factors were also important to the Susceptibility model, albeit to a lesser degree than "distance from nearest detection". Maximum hourly windspeed, i.e., the fastest one-hour average modelled windspeed in a given grid cell during the timestep, exhibited an importance value of 0.02 (Fig. 4). However, and contrary to expectations, maximum hourly windspeed was negatively correlated with Susceptibility, meaning that uninfected grid cells with higher average windspeeds exhibited a smaller probability of containing brown crowns at the end of the timestep (i.e., 0.65 at 6 m s⁻¹ versus 0.45 at 8 m s⁻¹; Fig. 5b). Tree cover was the third most important factor in the model, exhibiting an importance value of 0.008 (Fig. 4). Tree cover was positively associated with Susceptibility, and this relationship exhibited a sigmoidal shape (Fig. 5c); increasing density of tree-sized vegetation was associated with a greater probability that a given grid cell would brown initially, up to a cover value close to canopy closure (i.e., ca. 90%). Regarding grid cell aggregated crown exposure metrics, total crown exposure and southern crown exposure were also significantly important to the model; both exhibited importance values of 0.006 (Fig. 4). Each of these metrics were positively associated with Susceptibility, and their partial dependency plot trends exhibited a maximum exposure value at which increasing exposure had little or no effect (Fig. 5c-e). Thus, grid cells with a greater horizontally exposed surface area were more likely to exhibit brown crowns for the first time during a timestep. No other factors proved important to the model at a threshold of 0.005. We applied the Susceptibility RF model to all grid cells using input factor data from the last timestep (2019) to create maps of modelled Susceptibility values for the grid cells in 2020 (Fig. 6a). Regions of high probability of initial browning (i.e., > 0.5) were widespread throughout most of the windward forested regions of Mauna Kea and Kilaua Volcanoes, as well as both windward and leeward sides of Mauna Loa. Influences of both distance to the nearest brown canopy pixel detection and tree cover were evident in the distribution of high Susceptibility values; regions surrounding noted existing hotspots all received high predicted values, and patterns that visually matched the tree cover map were observable across the island. Despite a gradual increase in occurrence of brown crowns observed on the eastern flank of Kohala volcano (i.e., the peninsula on the northern end of the island), the modelled probability of initial browning remained relatively low in this region.

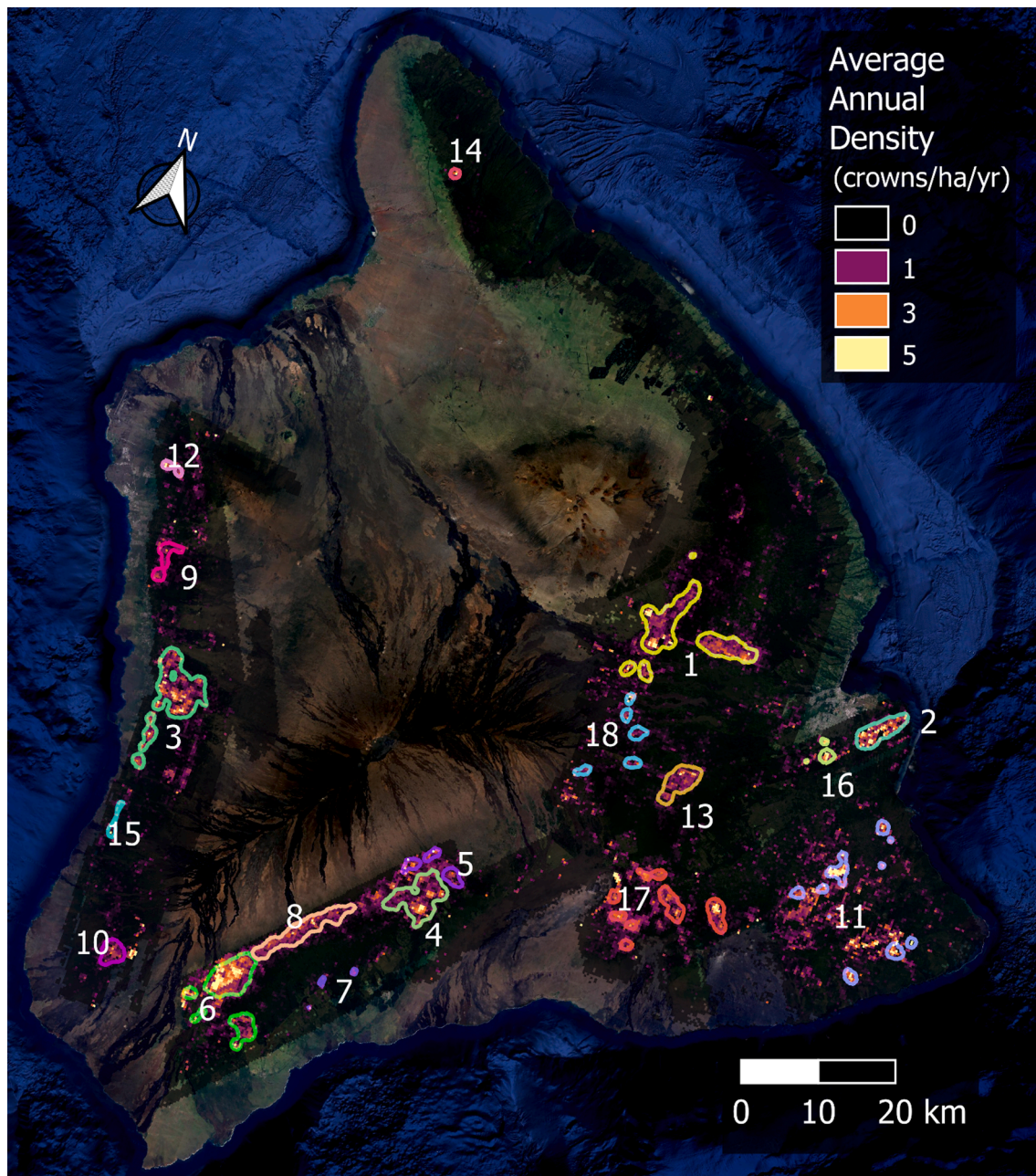


Fig. 3. Outlined hotspot regions of ROD activity where averaged brown crown density was > 1 crowns ha^{-1} and maximum density was > 2 crowns ha^{-1} during at least one measurement. The number labels correspond to the regions listed in Table 2. Hotspots were discovered across the distribution of ‘Ōhi’a within the island. Background imagery from Google Earth.

3.1.3. Severity model

The RF model for Severity exhibited a cross-validation R^2 value of 0.55. The model tended to overestimate extremely low Severity values, i. e., those grid cells with detection densities < 1.0 new detections ha^{-1} (Appendix S1 – Fig. S1b). However, model predictions were more consistently correlated with higher Severity values (Appendix S1 – Fig. S1b). In contrast to the Susceptibility model, many factors contributing to brown canopy occurrence were significantly important to the model of Severity (Fig. 7). In fact, nearly all factors were important using an importance value threshold of 0.025, or about 5% of the original model R^2 value, excepting those associated with fire regime (i. e., the proportion of low, moderate, and stand-replacement fires and return intervals) and canopy vegetation indicators (i. e., “pure ‘Ōhi’a” and “introduced”). As with Susceptibility analyses, distance from nearest detection was the most important factor, exhibiting an importance

value of 0.193 (Fig. 7; not comparable across the two island scale models because importance is computed from different fit statistics). Thus, newly affected regions closer to a source of the contagion were predicted to experience increased rates of new infections. However, the marginal change in this rate with distance was not as drastic as for the Susceptibility model; predicted Severity dropped from 3.4 to 2.2 detections ha^{-1} at 0 m and 1,000 m, respectively (Fig. 8c).

All LiDAR-derived measures of vegetation structure were important to the Severity model. Tree cover and Tree Height were both important and positively related to Severity, meaning that taller/denser stands were more prone to rapid increases in canopy browning (Fig. 8b, d). Substrate age was also important; soils younger than 1,000 years exhibited higher predicted Severity values than older substrates (Fig. 8c), although the values for the subset of historic flows (i. e., 1700 CE to present) ran counter to this finding (Fig. S3, Appendix). Total

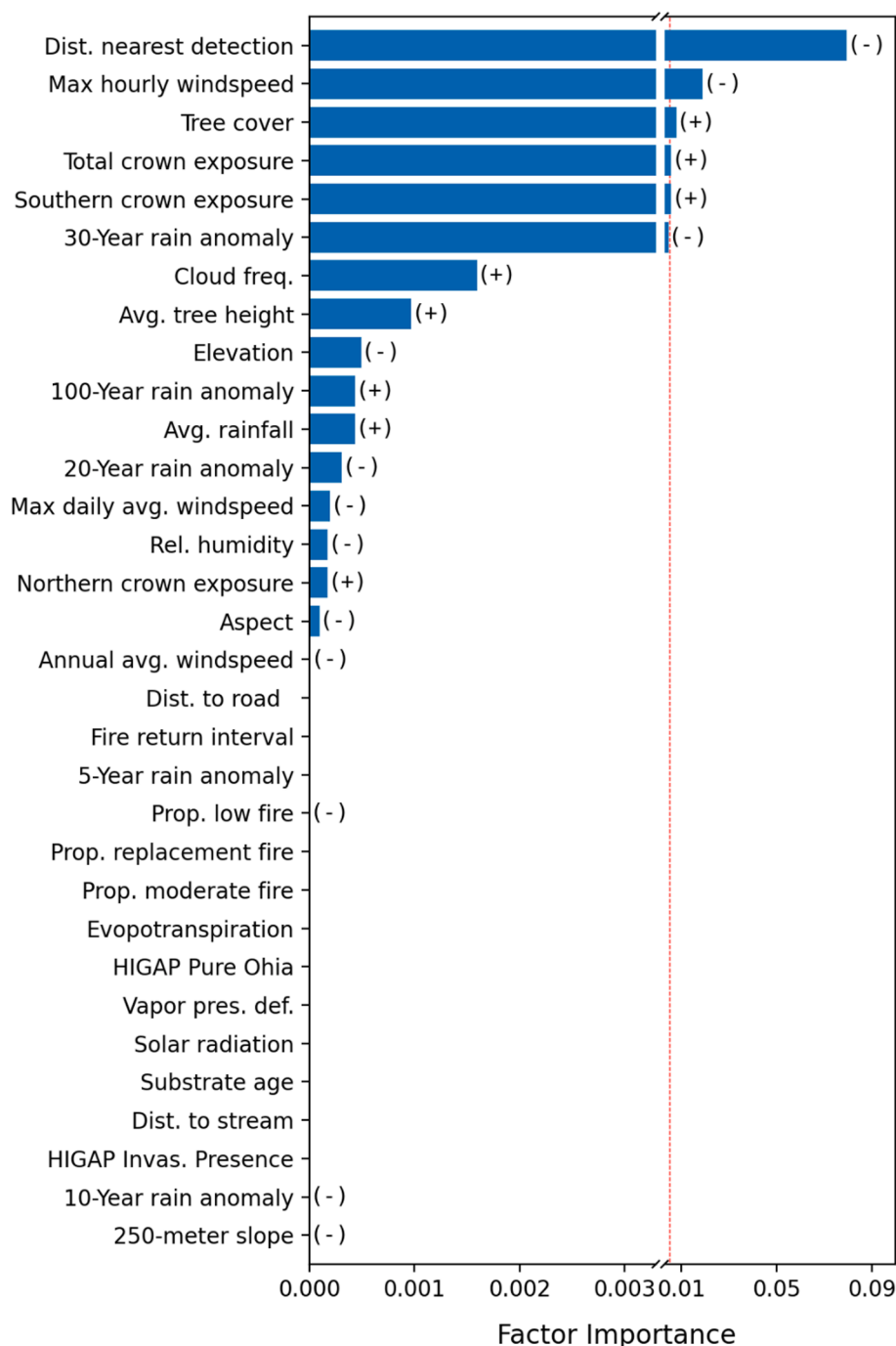


Fig. 4. Feature importance (permutation-based reduction in overall accuracy) values for the Susceptibility model of long-distance spread. The sign of the slope from the PDP plot data for each factor is shown to indicate whether changes in the factor are associated with an increase or decrease in probability of initial browning, Susceptibility. Factors with no sign may have a parabolic relationship with Susceptibility. The red line indicates the threshold value (0.005) used in the manuscript for deciphering important variables. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

exposure, northern exposure, and southern exposure were all important, indicating that increased crown exposure was associated with higher predicted Severity (Fig. 7). All terrain variables were also significantly important to the model (Fig. 7). Severity responded negatively to elevation and slope, meaning lower elevations and flatter slopes experienced higher rates of local spread. The negative effect of Northeastern exposure (i.e., expressed as northeastness) on Severity (i.e., aspect relative to NE direction) indicated that southwest-facing slopes exhibited higher predicted Severity (Fig. 7). Likewise, distance to road and distance to stream were both negatively correlated with Severity, indicating regions closer to roads or streams exhibited marginally higher predicted Severity.

Climate metrics were all important to the Severity model, and those related to wind and rainfall exhibited the greatest importance values.

The three average windspeed metrics (maximum hourly windspeed, maximum daily average windspeed, and annual average windspeed) were all highly important; Severity decreased markedly with increasing windspeed, with a slight increase occurring upon reaching a minimum (Fig. 9). Thus, regions exposed to moderate average windspeeds exhibited the lowest rates of brown canopy spread overall, but rates of brown canopy spread were highest in regions with low average windspeeds. Average rainfall was the third most important variable to the model. Drier regions, i.e., those receiving less than an average of 2,500 mm annual precipitation, experienced 25% higher Severity than wetter sites. However, among the wettest regions with > 2,500 mm of annual rainfall, there was a relatively small positive response to rainfall (Appendix S1 – Fig. S2a). The model also showed a parabolic response to other factors that helped define the moisture and temperature regime for

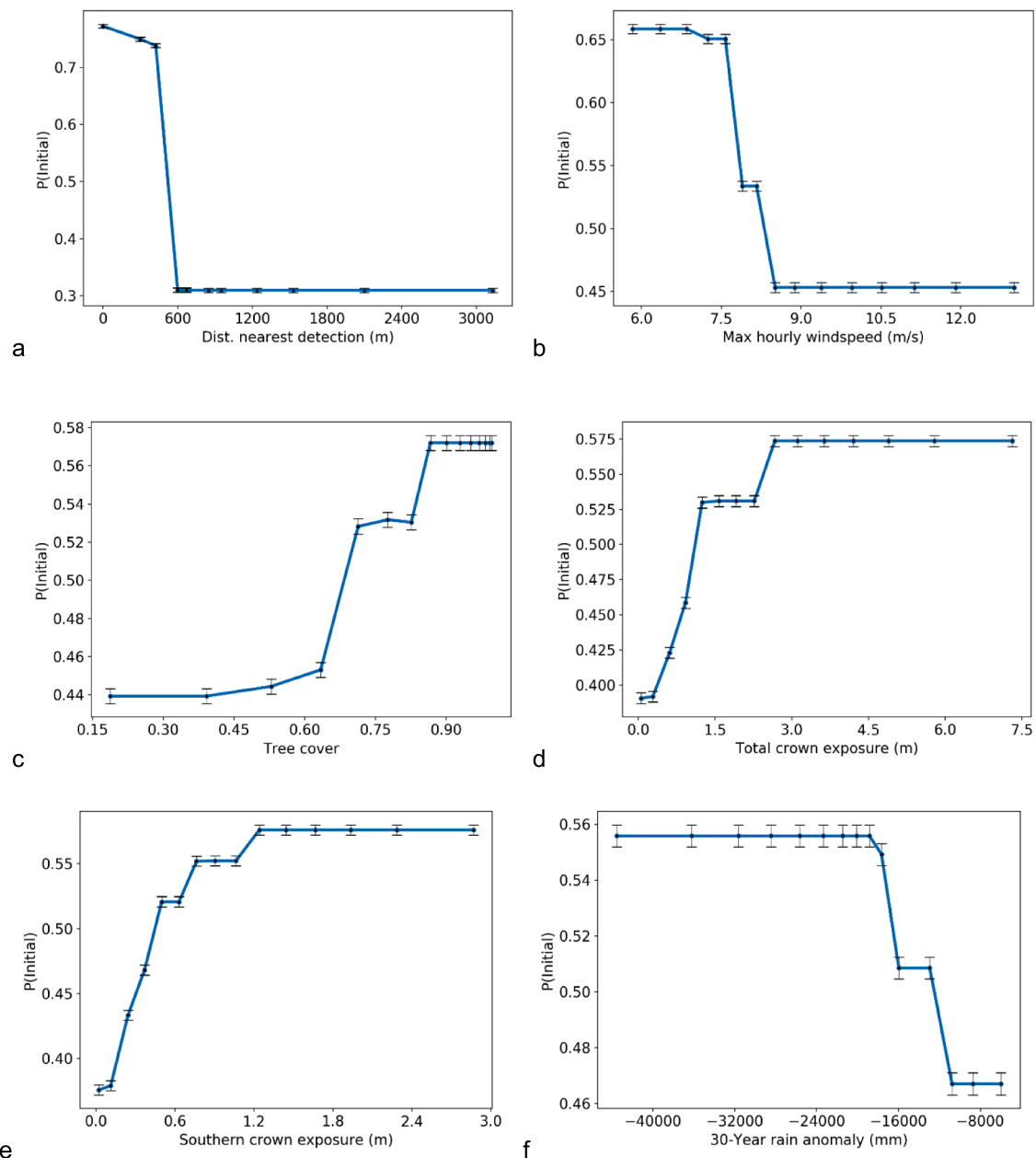


Fig. 5. Partial dependence plots for important variables from the Susceptibility (as $P(\text{Initial})$) Random Forest model in order of importance: (a) Distance to Nearest Detection, (b) Maximum Hourly Windspeed, (c) Tree Cover, (d) Total Crown Exposure, (e) Southern Crown Exposure, and (f) 30-year Rainfall Anomaly. Error bars indicate 95% confidence intervals around the mean.

a site: vapor pressure deficit, relative humidity, and cloud frequency (Appendix S1 – Fig. S2b-d). A similar parabolic response was seen for evapotranspiration. In general, regions with extremely wet or dry climates exhibited higher rates of brown canopy spread than regions with more mild climates.

Drought metrics were also important to the Severity model, and predicted Severity decreased with increasing values of each drought metric (i.e., 5-, 10-, 20-, 30-, and 100-year rainfall anomaly; Fig. 10). Since large negative values of these metrics indicate more severe drought conditions, this implies that regions undergoing extended drought conditions experienced higher rates of spread of ROD symptoms.

3.2. Regional-scale analysis

Historic lava flow areas exhibited a lower occurrence of brown

canopy pixels than surrounding regions of older substrate. Across all six studied regions, the average proportion of pixels that browned during the study period was 55.9% higher in the surrounding buffer regions compared to adjacent historic flows. Regarding individual sites, proportional differences between buffer and historic flows were highly variable, ranging from 30.4% lower in the Pāhoā region to 294% higher in the region of Hawai'i Volcanoes National Park (Appendix S1 – Table S2, Fig. S3).

The logistic regression model designed to compare the two substrate ages in the context of differing tree height distribution exhibited a fit with an R^2 of 0.10. While this would normally be considered a poor fit, individual crown infection was an extremely stochastic event, and capturing 10% of this variation was sufficient to identify trends. Six of the model terms were significant (using $\alpha = 0.05$) or were a component of a significant interaction term (Table 3). An intercept term for “Age” in the logistic regression model, which defined the average

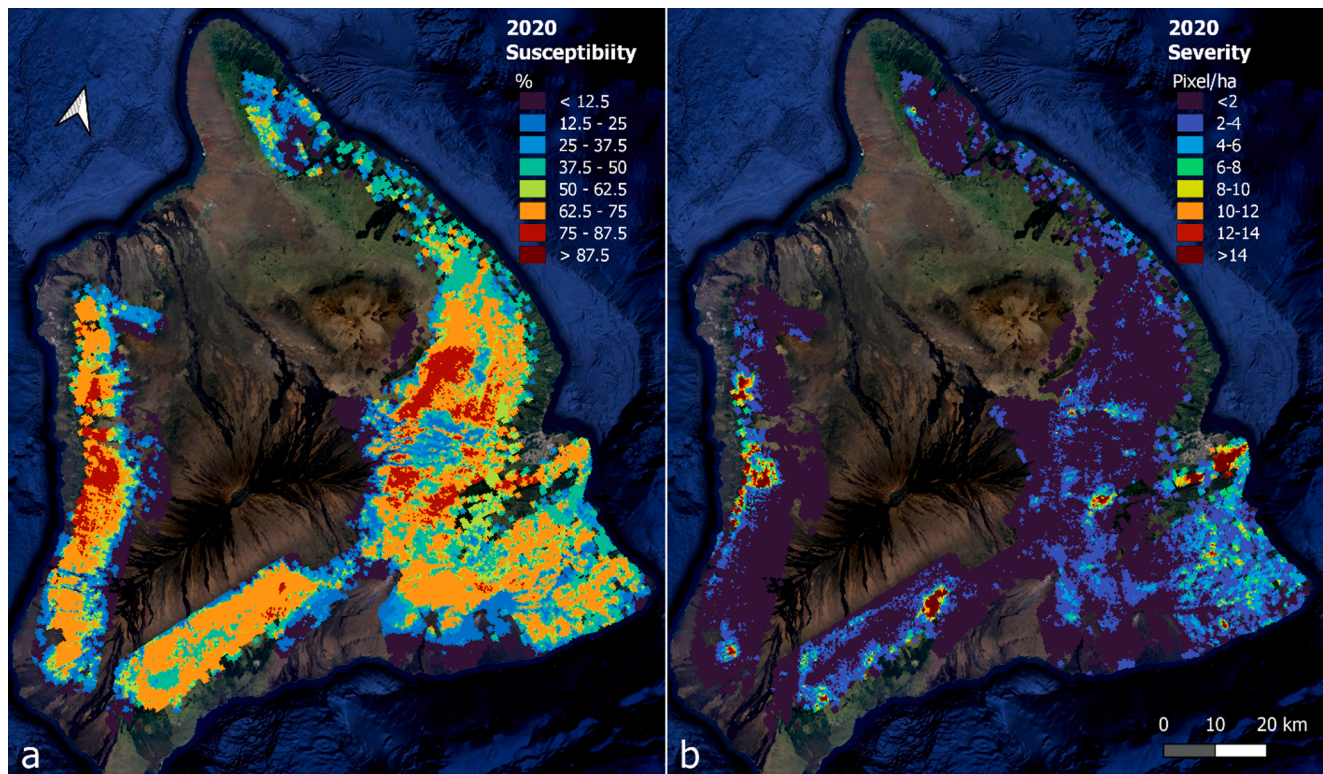


Fig. 6. Random Forest machine learning model projections forward from the last GAO observation (2019) for the two measures of spread (a) Susceptibility, i.e. modelled probability of grid cell becoming “infected” by having positive detections of browning ‘Ōhi’a for the first time and (b) Severity (number of new detections ha^{-1} in newly-infected grid cells). Background imagery from Google Earth.

probability difference between historic substrates and surrounding older substrates, was not significant ($p = 0.06$). Thus, we perceived no direct difference in browning probability detected between the two sets of substrate ages (i.e., historic flows and older buffer flows). However, differences were found between the two substrates in how browning rates correlate with individual tree and canopy height.

The model term defining the effect of average canopy height (CanopyHt) on pixel browning probability was significant ($p < 0.01$), and the positive slope coefficient of 0.16 indicated that predicted probability of browning increased with increasing canopy height. Thus, trees in taller forests were more likely to experience browning. Similarly, the height of an individual pixel above surrounding canopy (HtAbove) was also a significant predictor of browning probability ($p < 0.01$) with a positive slope of 0.04, meaning that increased exposure of the upper crown of a tree was linked with higher chance of that crown browning during the study period.

Additionally, the interaction term between CanopyHt and HtAbove the surrounding canopy was significant ($p < 0.01$) with small negative slope of -0.0192 . This indicated that the probability of crown browning within a pixel situated at a given height above the surrounding canopy was slightly lower in taller canopies than for shorter canopies (seen as curvature of lines in [Appendix S1 – Fig. S4a-b](#)). A significant interaction term ($p = 0.002$) of -0.0192 for Age and CanopyHt indicated that the positive slope between browning probability and CanopyHt was less steep in Historic substrates. In other words, browning rates are less affected by average canopy height in historic substrates ([Appendix S1 – Fig. S4a-b](#)).

4. Discussion

Over the course of the four years of this study, results indicated that ‘Ōhi’a tree crowns expressing the symptoms of ROD were well-distributed across much of Hawai’i Island. In total, we identified over

250,000 mapped individual crowns as potential diseased and dying trees. The cumulative total affected region containing such crowns nearly doubled from 66,972.2 ha in 2016 to 121,464.7 ha in 2019, which exemplified a disease still in a phase of rapid expansion. We found that approximately a third of this spread was concentrated in 18 continuously growing hotspots, some of which expanded up to several thousands of hectares. These numbers might seem small in magnitude compared to larger forest disturbances which have exceeded tens of millions of hectares and on the order of tens to hundreds of millions of individual trees ([Asner et al., 2016](#); [Cobb et al., 2020](#); [Fettig et al., 2022](#)). However, when viewed in terms of Hawai’i Island’s correspondingly small forested land base and the paramount ecological and cultural importance of this particular native tree species, the scope of ‘Ōhi’a mortality documented here represents an alarming increase. In our identified hotspots, We detected as many as 26 browning crowns ha^{-1} . Such values certainly indicate an annual mortality rate substantially lower than the average 28% reported by ([Mortenson et al., 2016](#)). However, the earlier survey was based on small and highly localized field inventory plots that would have included trees that died from ROD prior to sampling rather than just those that were currently undergoing canopy browning. Given the short duration of the browning phase, these two estimates might be more in line, and such rates in the context of a relatively small and highly important native forest land base were striking and cause for concern.

As we tracked trees expressing symptoms of Rapid ‘Ōhi’a Death’ (ROD) across time in our island-scale analyses, we found limited linkages between spread of the pathogen and various environmental factors. The Random Forest model of Susceptibility, or the likelihood of new regions getting infected, fit with a relatively moderate 73% accuracy, indicating that environmental factors were not strong determinants of infection, and that chance still played a major role. Similar to the Susceptibility model, in the regional scale analysis of pixel browning rate, the logistic regression model fit with an R^2 of only 0.10. Thus, even

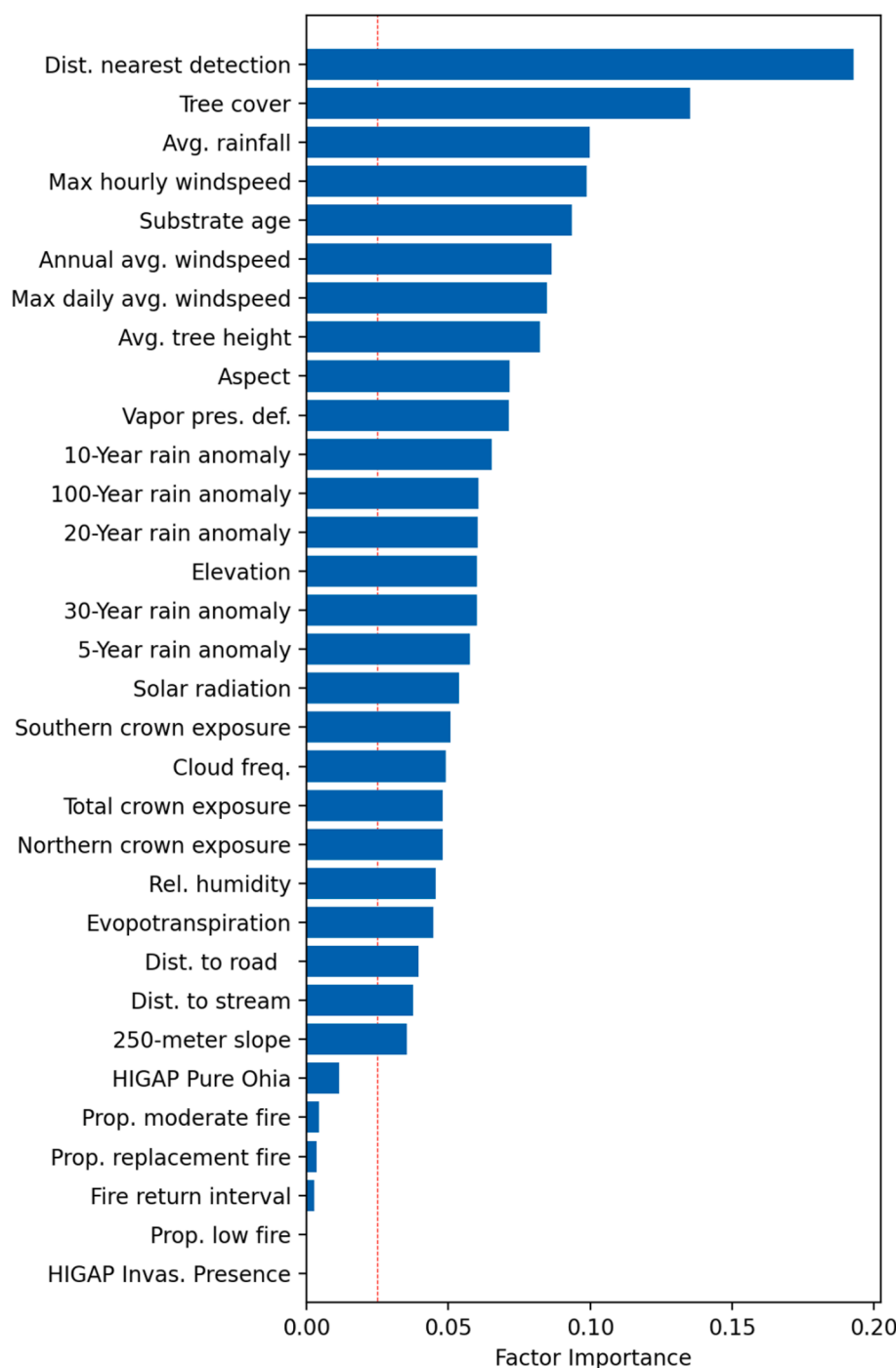


Fig. 7. Feature importance (permutation-based reduction in R^2) values for the Severity model. The sign of the slope from the PDP plot data for each factor is shown to indicate whether changes in the factor are associated with an increase or decrease in Severity. Factors with no sign may have a parabolic relationship with Severity. The red line indicates the threshold value (0.025) used in the manuscript for deciphering important variables. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

though a signal could be found among pixel browning rates in response to environment, 90% of the variation was considered simply random chance. These results were not surprising, given the binomial nature of the data and the number of random events necessary for even a single infection to occur. This predominant influence of chance was quantitatively expressed by the high importance of “Distance from nearest detection” in both RF models. Taken together with the corresponding importance of “Tree cover” in both models, this suggests that the majority of spread, both within and between individual grid cells, had less to do with particular environmental factors than with proximity and the size and abundance of the host population. Indeed, a proximity of less than 600 m to existing infections (i.e., two grid cells away) increased the probability of ROD encroachment from 30% to 75% (Fig. 5a). Likewise,

an increase in tree cover from 90% to 100% increased the predicted number of detections ha^{-1} from less than 2.6 to more than 3.5, representing an increase of 35%. The fact that susceptibility was not predicted by other environmental variables may be a function of the importance of high wind events such as Hurricane Iselle which impacted Hawai'i Island in 2014 and coincided with marked increases in *Ceratocystis*-induced 'Ōhi'a mortality. Such high-wind storm events simultaneously would have been able to spread large amounts of inoculum and injure/wound high numbers of trees allowing inoculum entry to those damaged trees to infect and eventually kill them (Cannon et al., 2022).

Despite the low relative importance of other environmental drivers to these models, they did capture several significant patterns in the island-scale Susceptibility and regional-scale pixel browning rate data.

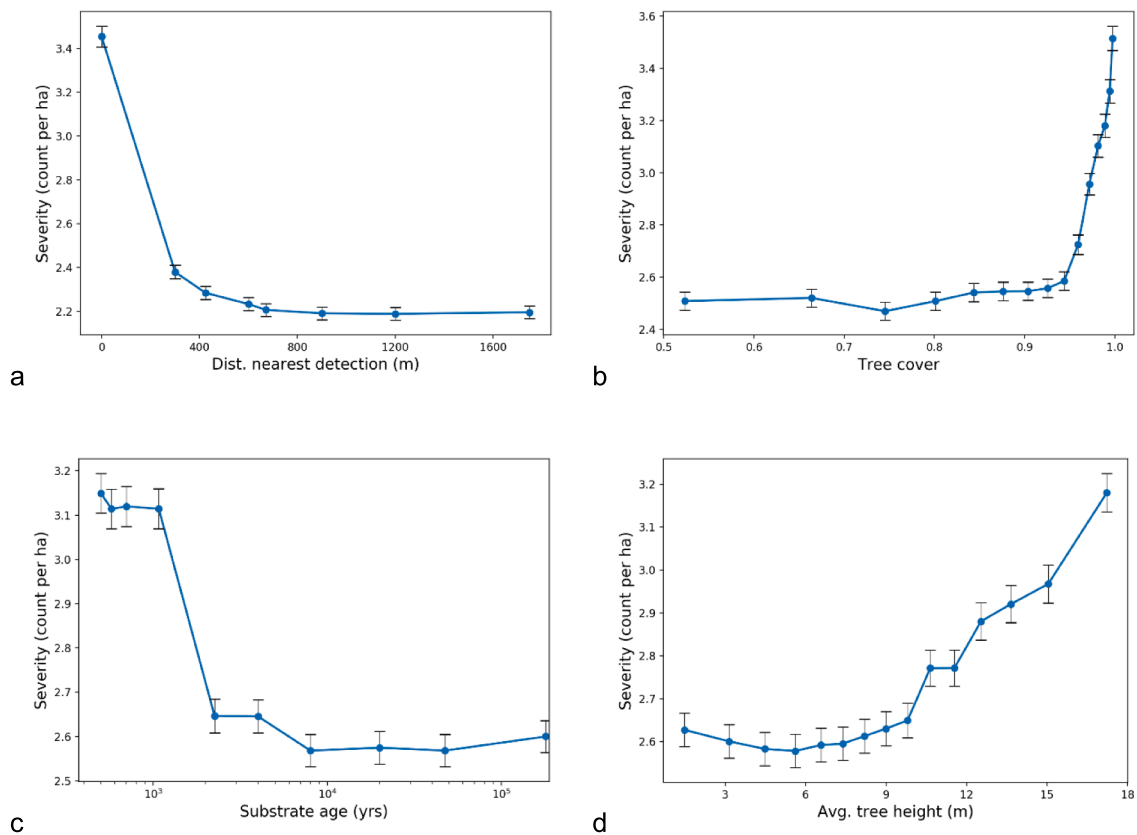


Fig. 8. Partial dependence plots for important variables from the Severity Random Forest model in order of importance: (a) Distance to Nearest Detection, (b) Tree Cover, (c) Volcanic Substrate Age, and (d) Average Tree Height. Error bars indicate 95% confidence intervals around the mean.

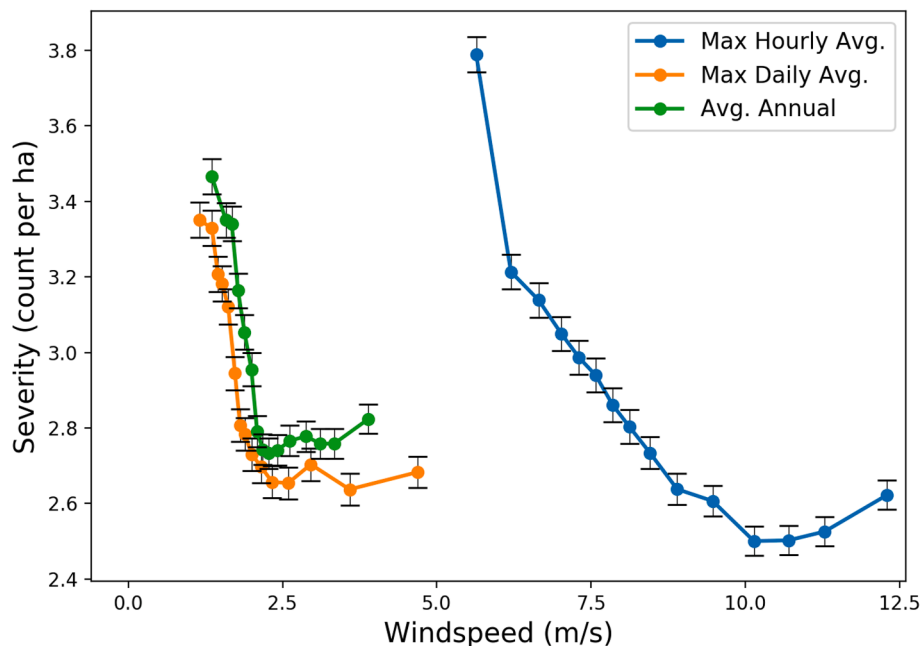


Fig. 9. Partial dependence plots for the three windspeed variables in the Severity Random Forest model. Error bars indicate 95% confidence intervals around the mean. The model found a decrease in Severity with increasing windspeed.

In general, increased exposure was strongly linked to spread of infection by the ROD pathogen (i.e., *C. lukuohia*) into previously unaffected areas. Crown exposure had a positive effect on both the predicted Susceptibility in the island-scale analysis (via southern and total crown exposure;

Fig. 5d,e) and on the modelled probability of a pixel browning in the regional analysis (via the “HtAbove” variable; Table 3). These results suggest a strong influence of wind (Cannon et al., 2022; Roy et al., 2020; Roy et al., 2019). Prior studies demonstrated the primary vehicle

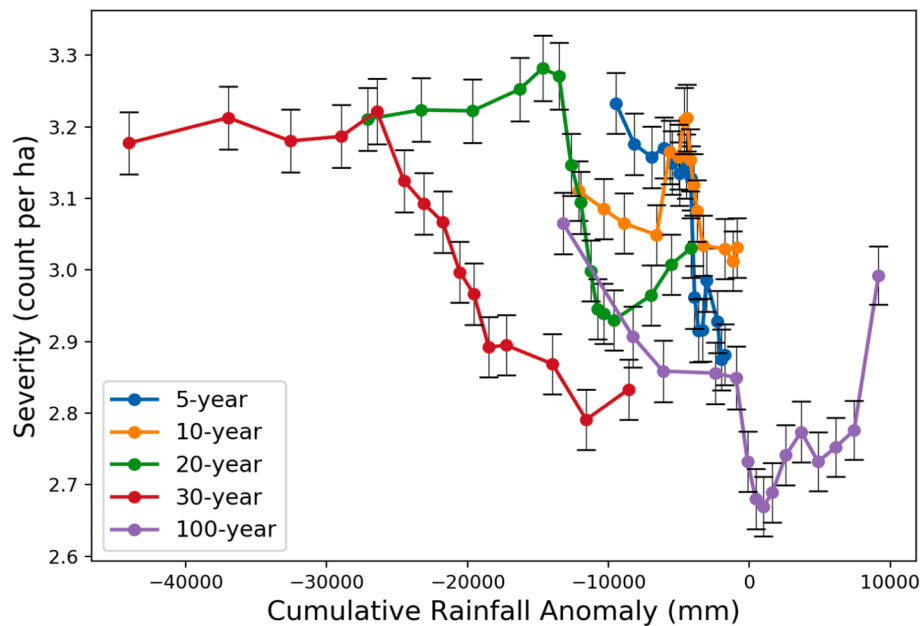


Fig. 10. Partial dependence plots from the Severity Random Forest model for 5-year, 10-year, 20-year, 30-year, and 100-year rainfall anomaly. Error bars indicate 95% confidence intervals around the mean.

Table 3

Coefficient estimates from logistic regression for 2 m pixel-level analysis of average canopy height (CanopyHt) and individual tree height above its surrounding canopy (HtAbove), a measure of crown exposure, within the context of differing lava substrate ages.

Term	Estimate	Std. Error	Z	P-value
Intercept	-1.4628	0.0495	-29.526	<0.00001
Age [Historic - Buffer]	0.1364	0.0722	1.888	0.05905
CanopyHt	0.1607	0.0044	36.858	<0.00001
Age:CanopyHt	-0.0192	0.0062	-3.092	0.00199
HtAbove	0.0401	0.0080	5.019	<0.00001
CanopyHt × HtAbove	-0.0019	0.0006	-3.226	0.00126

Ceratocystis inoculum to be ambrosia beetle boring dust impregnated with fungal spores of the pathogen (Roy et al., 2020; Roy et al., 2019), and wind transport has been hypothesized as a primary agent of long-distance transport of spore-laden beetle boring dust (Cannon et al., 2022). However, in contradiction to theories about the importance of wind transport, modelled windspeed average variables used in the models reported here were associated with decreases in both Susceptibility (32% reduction with average hourly maximum; Fig. 5b) and Severity (35% reduction; Fig. 9), indicating that windier regions were associated with lower brown canopy values. The mechanism for these contradictory findings is unclear, but several potential explanations could be tested in future research. First, modelled windspeeds are averaged, and as such they do not provide information concerning gust speeds or how windspeeds are moderated by tree canopy (Aylor, 1990). A more mechanistic explanation is that trees in regions with higher average windspeed might have developed stronger branches more robust to breakage in wind events. Alternatively, higher windspeeds might be associated with drier tree surfaces, reducing the chances for spores to adhere.

Several environmental factors that proved important to the Severity model were associated with climate and weather, with rainfall and drought metrics being the most influential. Higher average rainfall was associated with a decrease in predicted Severity (19% reduction; Appendix S1, Fig. S2), as were drought metrics computed at all time scales ranging from 5-year to 100-year (1% to 13% reduction for sites with less cumulative drought; Fig. 10). A similar pattern was found for relative

humidity (10% reduction on wetter sites; Appendix S1, Fig. S2). Taken together, these findings suggested that water stress might increase the propensity of ‘Ōhi’a trees to succumb to *C. lukuohia* infection. This finding seems contrary to frequent findings that higher humidity and rainfall are associated with increased activity in several fungal diseases (Bulman et al., 2016; Keane, 2000; Meentemeyer et al., 2004; Romero et al., 2022). In fact this association is so foundational that rainfall and humidity are used as main driving variables in a popular climatic niche model (Kriticos et al., 2015). However, a positive correlation with water stress has been found for fungal tree diseases (Requena-Mullor et al., 2020; Schoeneweiss, 1978). Such a link would likely be very mechanistic in nature and might have less to do with fungal survival than tree susceptibility. For example, drought-induced high water potential might exacerbate the impediment of water flow in the xylem caused during colonization by *C. lukuohia* (Barnes et al., 2018). Drought conditions may also lead to increased likelihood of breaks and splits from wind events, and such factors have been known to reduce tree resistance to bark beetles (Kolb et al., 2019; McDowell et al., 2008). Recently, direct spectral measurements of leaf water content have been used to successfully identify ‘Ōhi’a crowns that would later brown and succumb to the disease (Weingarten et al., 2021). Alternatively, ‘Ōhi’a tree- and stand-level response to extreme and/or prolonged drought may manifest in symptoms (e.g., canopy leaf browning) very similar to those expressed by ‘Ōhi’a trees infected by *C. lukuohia*. Because positive determination of *C. lukuohia* infection can only be affirmed by molecular tests or culturing of the fungal pathogen from tissue samples of brown crown trees, some browning ‘Ōhi’a crowns detected during our analyses may be attributed to drought rather than *C. lukuohia* infection.

Results presented here documenting the predominance of local spread and impact of Rapid ‘Ōhi’a Death provide evidence supporting the utility of protecting such forests from feral ungulate damage. Root-to-root transmission of inoculum of *Ceratocystis* species has been demonstrated in other tree species elsewhere (Harrington, 2013; Juzwik et al., 2011; Panconesi, 1999), and viable inoculum has been detected in soils of infected stands (Heller and Keith, 2018; Yelenik et al., 2020). However, the idiosyncratic “hop-scotch” pattern of *Ceratocystis* infection of ‘Ōhi’a stands (i.e., trees adjacent to infected trees are often not infected themselves) strongly suggests that ‘Ōhi’a tree root-to-root infection is not occurring. Rather, manifestation of localized or

clustered canopy browning is likely best explained by the effects of wind or feral ungulates. This assertion is supported by previous research showing that forests where feral ungulates are abundant and active exhibit 2 to 69 times higher rates of *Ceratocystis*-induced mortality compared to forests where ungulates have been excluded (Perroy et al., 2021). Feral ungulates wounding the roots and/or trunks of 'Ōhi'a trees as they travel and forage within forests would explain the hotspot patterns observed in our results; such wounding can be both acute and extensive where feral ungulates are abundant (Hess, 2016). This would not explain the less frequent events of long-distance spread of ROD seen across the island, which are more likely to be caused by high wind events. While little can be done to prevent wind moving inoculum long distances, it is certainly possible to significantly reduce chronic wounding events (i.e., feral ungulate damage to 'Ōhi'a trees and stands) through installation of fencing, and removal of feral ungulates.

Results indicating lower probabilities of crown browning of 'Ōhi'a trees growing on historical lava flows (i.e., flows < 240 ybp) relative to those growing on older surrounding lava flows agree with findings of ongoing field plot-based investigations that lower rates of *Ceratocystis*-induced annual mortality of 'Ōhi'a occur in forest stands on very young lava flows compared those on adjacent, older lava flows (Hughes, 2022). The mechanisms determining these patterns are not well understood, but they may provide hope for anticipated 'Ōhi'a forest restoration. Results from ongoing field plot-based investigations indicate that smaller-stature 'Ōhi'a stands (i.e., stands with trees averaging < 20 cm in diameter) exhibit average annual mortality rates that are less than half those expressed by older, larger stature 'Ōhi'a stands (Hughes, 2022). This finding that younger, smaller trees are less likely to succumb to Rapid 'Ōhi'a Death very much supports the logic behind efforts to replant 'Ōhi'a seedlings and saplings even in forest stands that have experienced extensive *Ceratocystis*-induced mortality. However, substrate differences were upheld even as tree size differences (as height) were at least partially accounted for in the model, suggesting that other factors might be a play as well. For example, historic flows are typically characterized by extremely rough, rocky, uneven terrain that lack appreciable amounts of soil, which represents poor habitat for feral ungulates. As a consequence, 'Ōhi'a stands growing on historic flows may elude chronic ungulate-induced wounding that other stands experience growing on older lava substrates that offer more suitable habitat to large populations of feral ungulates. Regardless of the mechanism, young individuals, particularly if they are protected from chronic-wounding, are highly likely to survive in the face of Rapid 'Ōhi'a Death and perpetuate 'Ōhi'a-dominated forests into Hawai'i's future.

Several methodological decisions were made during the course of this study to meet the time and scale demands necessary to map individual browning crowns across Hawai'i Island. Time and budget constraints relating to the expense of airborne surveying limited us to physically covering each region of the island once per year. Thus, all observations of crown status in this study represented only snapshots of potentially very dynamic processes, and as a consequence, we could not assess temporal patterns of ROD activity that naturally occur throughout the changing seasons. However, browning crown densities measured within our 2017 coverage were not significantly different from measurements taken in January of 2018 or 2019, lending some confidence that strong seasonality had little effect on the results. As we initiated mapping in 2016, we might have only captured the very end of an extensive ROD mortality event across the Puna District of Hawaii Island which began several years earlier (Mortenson et al., 2016). This may have limited our understanding of Susceptibility and Severity processes, since any previously affected areas in this region were ignored even if they were highly prone to infection and high rates of local spread. Although we could not quantify to what extent this influenced the results, it would likely depend on the range of values of the input factors that were found in the already affected regions of Puna and how these values compared to other regions of Hawai'i Island. We were also limited by the resolution and scale of many of the factors considered in the

Susceptibility and Severity analyses, and we may have missed correlations that might exist along finer gradients than we could include in the analysis. This may include factors such as tree phenotypes that might differentially respond to the pathogen (Cordell et al., 1998; Stenlid and Oliva, 2016), local biodiversity changes that might hinder spread (Ennos, 2014), and the presence or absence of ungulates believed to be vectors of spread or causes of wounding (Perroy et al., 2021), among others. Future work might use processes described here to expand analyses to include such additional factors.

In this work we demonstrated the potential for high resolution remote sensing-based maps of forest tree diseases to aid in discovery and understanding of patterns of spread in response to the environmental landscape. In doing so we quantitatively described in high resolution the full extent of damage from *Ceratocystis*-induced Rapid 'Ōhi'a Death across the island of Hawai'i. Our results showed the majority of 'Ōhi'a forests on Hawai'i Island to be highly susceptible to ROD. We found that increased distance from already-infected regions led to rapid decreases in predicted susceptibility and lower post-infection brown crown densities, evidence that vectors of local spread likely play a larger role in the realized expression of ROD symptoms across the island. However, the secondary influence of tree crown exposure at coarse and fine scales in increased infection rates indicated that wind-carried inoculum is responsible for a significant amount of spread. We found evidence that climate and weather variables, especially those affecting water balance, had some influence in the spread in ROD during the study period. These relationships should guide managers toward locations that could be more prone to future hotspot activity, and this was demonstrated by mapping the model predictions for the whole island in the future. As of now, *C. lukuohia*, the most virulent strain on Hawai'i, has only been found on one other island, Kaua'i, and its impact has been relatively localized to date. However, we anticipate the patterns we've documented here will help inform land managers should more extensive and impactful *Ceratocystis*-induced ROD infestations reach the other Hawaiian Islands (Cannon et al., 2022; Heller et al., 2019). Managers with an understanding of where ROD-induced mortality will be most severe can better plan mitigation efforts to minimize losses of this keystone tree species, and, in doing so, they might be able to prevent further downstream ecological declines across the many species supported by 'Ōhi'a (Camp et al., 2019; Mueller-Dombois and Fosberg, 2013).

CRediT authorship contribution statement

Nicholas R. Vaughn: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Writing – original draft, Writing – review & editing, Project administration. **R. Flint Hughes:** Conceptualization, Methodology, Investigation, Writing – review & editing. **Gregory P. Asner:** Conceptualization, Methodology, Investigation, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.120983>.

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