

ARTICLE

Early detection of a tree pathogen using airborne remote sensing

Erin Weingarten^{1,2} | Roberta E. Martin^{1,2}  | Richard Flint Hughes³ |
Nicholas R. Vaughn¹  | Ethan Shafron¹ | Gregory P. Asner¹ 

¹Center for Global Discovery and Conservation Science, Arizona State University, Tempe, Arizona, USA

²School of Geographical Sciences and Urban Planning, Arizona State University, Tempe, Arizona, USA

³Institute of Pacific Islands Forestry, USDA Forest Service, Hilo, Hawaii, USA

Correspondence

Roberta E. Martin

Email: roberta.martin@asu.edu

Funding information

USDA, Forest Service, Grant/Award Number: FP00020713; State of Hawai'i Department of Land and Natural Resources (DLNR)

Handling Editor: Nancy Glenn

Abstract

Native forests of Hawai'i Island are experiencing an ecological crisis in the form of Rapid 'Ōhi'a Death (ROD), a recently characterized disease caused by two fungal pathogens in the genus *Ceratocystis*. Since approximately 2010, this disease has caused extensive mortality of Hawai'i's keystone endemic tree, known as 'ōhi'a (*Metrosideros polymorpha*). Visible symptoms of ROD include rapid browning of canopy leaves, followed by death of the tree within weeks. This quick progression leading to tree mortality makes early detection critical to understanding where the disease will move at a timescale feasible for controlling the disease. We used repeat laser-guided imaging spectroscopy (LGIS) of forests on Hawai'i Island collected by the Global Airborne Observatory (GAO) in 2018 and 2019 to derive maps of foliar trait indices previously found to be important in distinguishing between ROD-infected and healthy 'ōhi'a canopies. Data from these maps were used to develop a prognostic indicator of tree stress prior to the visible onset of browning. We identified canopies that were green in 2018, but became brown in 2019 (defined as "to become brown"; TBB), and a corresponding set of canopies that remained green. The data mapped in 2018 showed separability of foliar trait indices between TBB and green 'ōhi'a, indicating early detection of canopy stress prior to the onset of ROD. Overall, a combination of linear and non-linear analyses revealed canopy water content (CWC), foliar tannins, leaf mass per area (LMA), phenols, cellulose, and non-structural carbohydrates (NSC) are primary drivers of the prognostic spectral capability which collectively result in strong consistent changes in leaf spectral reflectance in the near-infrared (700–1300 nm) and shortwave-infrared regions (1300–2500 nm). Results provide insight into the underlying foliar traits that are indicative of physiological responses of *M. polymorpha* trees infected with *Ceratocystis* and suggest that imaging spectroscopy is an effective tool for identifying trees likely to succumb to ROD prior to the onset of visible symptoms.

KEYWORDS

canopy chemistry, *Ceratocystis*, Global Airborne Observatory, Hawai'i Island, imaging spectroscopy, *Metrosideros polymorpha*, 'ōhi'a, Rapid 'Ōhi'a Death

INTRODUCTION

Metrosideros polymorpha (common name: ‘ōhi‘a) is the keystone tree species of Hawaiian forests and comprises the majority of remaining native forest canopy (Dawson et al., 1990). The range of ‘ōhi‘a is extremely broad, inhabiting areas from sea level to 2500 m in elevation, dominating wet forests while also being common to dominant in dry forests (Friday & Herbert, 2006; Mueller-Dombois & Fosberg, 1998). The habitat these endemic trees provide is crucial to fauna and flora in Hawaiian forest (Dawson et al., 1990; Pratt & Jacobi, 2009). ‘Ōhi‘a is the first species to colonize new lava fields and is largely responsible for successional processes that lead to the diverse closed-canopy native forests (Friday & Herbert, 2006; Stemmermann, 1983).

Over the past decade, ‘ōhi‘a stands have experienced abnormally high rates of mortality (Loope et al., 2016). In 2010, a new disease, coined Rapid ‘Ōhi‘a Death (ROD), was noted in ‘ōhi‘a stands present across eastern portions of Hawai‘i Island (Camp et al., 2019; Keith et al., 2015). The disease was determined to be caused by two distinct species in the pathogenic fungal genus *Ceratocystis*: the vascular wilt fungus, *Ceratocystis lukuohia*, and the canker pathogen, *Ceratocystis huliohia* (Barnes et al., 2018; Keith et al., 2015). *Ceratocystis lukuohia* is the main cause of stand-level mortality events, while *C. huliohia* is associated with smaller-scale, localized mortality events (Barnes et al., 2018; Fortini et al., 2019; Loope et al., 2016). Distinct from other previously documented landscape-scale ‘ōhi‘a dieback events (Jacobi, 1983; Mueller-Dombois, 1980; Mueller-Dombois et al., 2013), ROD occurs as *C. lukuohia* or *C. huliohia* spores enter and colonize the vascular tissue of the tree and interrupt water flow through the xylem (Barnes et al., 2018; Mortenson et al., 2016). Visible symptoms occur rapidly and are characterized by asymmetrical browning and wilting of the canopy followed by tree death in weeks (Barnes et al., 2018; Mortenson et al., 2016). This brown stage is noticeable and relatively unique to ROD infection (Asner et al., 2018; Perroy et al., 2020). The disease caused by ROD is especially alarming owing to its current unpredictability and capacity for swift mortality of ‘ōhi‘a trees and stands. ‘Ōhi‘a trees in a given stand appear to die in a haphazard pattern, across all size and age classes with an average annual mortality rate of about 10%, though some stands experience rates as high as 42% (Vaughn et al., 2018; R. F. Hughes *personal communication*). These rates are much higher than other tree diseases (Loope et al., 2016). The loss of ‘ōhi‘a from forests will accelerate the establishment of invasive plants in Hawaiian forests and will degrade watersheds (Boehmer et al., 2013; Fortini et al., 2019; Jacobi, 1983).

Current research on the disease is focused on understanding the ROD infection across Hawai‘i Island and how to slow its spread. Maps of brown canopies have been created for the island (Vaughn et al., 2018), but by the time an ‘ōhi‘a canopy turns brown, it is too late to save the tree. Detecting visually asymptomatic canopies is essential to understanding where the disease will move at a timescale feasible for controlling the disease. Methods of detecting plant pathogens and complex biological signals and processes have utilized imaging spectroscopy for crop tree disease detection (Calderón et al., 2015; López-López et al., 2016; Zarco-Tejada et al., 2018), species identification from leaf reflectance (Cavender-Bares et al., 2016), changes in physiological function and water status (Barnes et al., 2017), and detection of plant pathogens for managing forest ecosystem threats (Fallon et al., 2020). Access to ROD-infected trees across the island remains a challenge due to the range of ‘ōhi‘a over many thousands of hectares of remote forest often located on private property, making crowns difficult to reach on foot. Remote sensing is a particularly useful tool owing to its ability to monitor and map large areas of land in very fine detail (Asner & Martin, 2016). While unmanned aerial vehicles are quick to deploy and offer detailed high-resolution imagery (Perroy et al., 2020), they are limited to mapping small areas at a time and are not permitted over certain federal and most private lands. Additionally, helicopter surveys are limited by the ability of the human eye to spot brown canopies at a distance, by a lack of spatial accuracy, and expense of flight time. Data from Earth-orbiting satellites are readily available, but these data are too spatially and spectrally coarse to pinpoint individual browning trees. The Global Airborne Observatory (GAO; Asner et al., 2012), which employs sensors in a fixed-wing airplane, is uniquely able to fill this gap with its ability to collect laser-guided imaging spectroscopy (LGIS) data.

Laser-guided imaging spectroscopy data are derived from the fusion of imaging spectroscopy data from a visible-to-shortwave infrared (VSWIR) imaging spectrometer to three-dimensional information provided by a boresight-aligned light detection and ranging (LiDAR) scanner (Asner et al., 2012), allowing for the precise spatial position of each spectrum to be known. This type of imaging spectroscopy utilizes contiguous high-spectral-resolution measurements of reflected solar radiation spanning 427 channels in the 400–2500 nm wavelength region in 5 nm increments to estimate canopy traits, such as water, nutrient, and defense compounds (Asner et al., 2017; Kokaly et al., 2009; Ollinger, 2011), which allow for the detection of changes in foliar chemistry. Asner et al. (2018) demonstrated that ROD infection exhibits distinct spectra at leaf and canopy scales and defined a spectral signature to map ‘ōhi‘a trees likely infected by ROD and that the leaf-level spectral differences

were related to underlying foliar chemical differences. Foliage from healthy canopies had higher LMA and higher concentrations of chemical traits important for growth, including chlorophyll (Chl), non-structural carbohydrates (NSC), and leaf water content (LWC). Green canopy leaves also contained higher levels of phenols and tannins, while brown leaves had higher concentrations of carbon (C) and recalcitrant compounds such as cellulose. These leaf traits are associated with structure and defense. Using the canopy spectral signature, Vaughn et al. (2018) applied the full VSWIR reflectance spectrum collected from airborne data and a machine learning algorithm to map the browning canopies around Hawai'i Island with accuracies of 86% and higher. These were essential first steps, but to adequately contain the spread of ROD, we need to understand when and where the disease will spread prior to browning of the canopies as well as identifying possible foliar traits that underpin the spectral differences that may, in turn, be indicative of the physiological response of the trees.

Given the significant differences in foliar chemistry exhibited between leaves from green and visibly brown state canopies (Asner et al., 2018), our goal was to determine if there is a detectable spectral and related chemical signal prior to visible browning in 'ōhi'a at the canopy scale. We hypothesized that the spectral signature and modeled indices of foliar traits of canopies that eventually succumb to the disease and turn brown (hereafter, defined as "to become brown" or TBB) would differ significantly from those of healthy canopies. Moreover, we expected to detect this signal in ROD-infected trees as differences in both the spectral signature and the foliar traits previously established by Asner et al. (2018) as the canopy-based signature for ROD. As LGIS measurements detect and express changes in foliar chemistry, we endeavor to use this knowledge to develop an understanding of the relationship between spectral reflectance and underpinning foliar chemical traits associated with the TBB canopy state. Analyzing traits individually, we predicted the modeled canopy's chemical trait indices associated with light capture and growth (i.e., Chl and LWC) would decrease, and those linked with defense (i.e., phenols and cellulose) would increase due to an increase in stress before completely succumbing to the disease (turning visibly brown). However, multiple non-linear interactions among foliar chemicals may eventually explain the differences in canopy states and their associated canopy reflectance spectra. Ultimately, by extracting remotely sensed spectra and related modeled chemistry data from 'ōhi'a canopies, we present a method for creating a diagnostic measure of canopy stress prior to the onset of visible symptoms. Results will support the development of the mapping this signal, which is crucial information to prevent future spread of ROD.

METHODS

Our study utilized 2018 and 2019 airborne LGIS data collected from across Hawai'i Island (Figure 1) to evaluate the potential for detecting spectral and underlying foliar chemical trait differences between green canopies and those that were visibly green in 2018 but were TBB in 2019 (Figure 2a,b). The separability between green canopies and those that would become brown was evaluated using VSWIR spectra covering 400–2500 nm in 5-nm contiguous wavebands (Figure 3). To provide insight into the underlying chemical properties of the spectral separability, we calculated indices for 11 foliar traits known to be indicative of ROD (Asner et al., 2018) using chemometric models derived from forests in Northern Borneo (Martin et al., 2018). Although the range of values in modeled canopy-level trait were comparable to those measured and modeled in the leaf-level studies of green and brown 'ōhi'a leaves conducted by Asner et al. (2018), the absolute values were shifted. For this reason, we chose to use chemical indices. Machine learning was then used on both the canopy reflectance and canopy foliar trait datasets to evaluate the potential for modeling and eventually mapping this early warning signal of the disease.

Imaging spectroscopy data

We used canopy-level LGIS data collected by the GAO in January of 2018 and 2019 to evaluate spectrochemical differences between green 'ōhi'a canopies and canopies that were visibly green in 2018 but became brown (TBB) in 2019. The GAO data are collected with co-aligned instruments: a VSWIR imaging spectrometer and a dual-channel airborne LiDAR scanner, allowing for the simultaneous spatio-temporal fusion of the data (Asner et al., 2012). This enables computation of the precise 3-D location of the spectrometer data with very high precision that is essential in order to mask canopy gaps and shadows. Canopy mask is responsible for the intra- and inter-canopy shadowing, and identifying regions of short or absent canopies that can contaminate the spectral signal. During each flight campaign (in 2018 and 2019), LGIS data were collected over forested areas throughout the island. During flight, the aircraft's speed was maintained within 10% of the 60 m s⁻¹ nominal air speed and within 200 m of the nominal planned elevation of 2000 m above ground level. The LiDAR was operated at an effective pulse frequency of 200 kHz, a scan frequency of 34 Hz, 30 percent overlap, and field-of-view of 38 degrees to match the 34-degree field of view of the VSWIR after clipping 2 degrees from the scan edges. These settings yielded a mean density of 3.3 pulses m⁻².

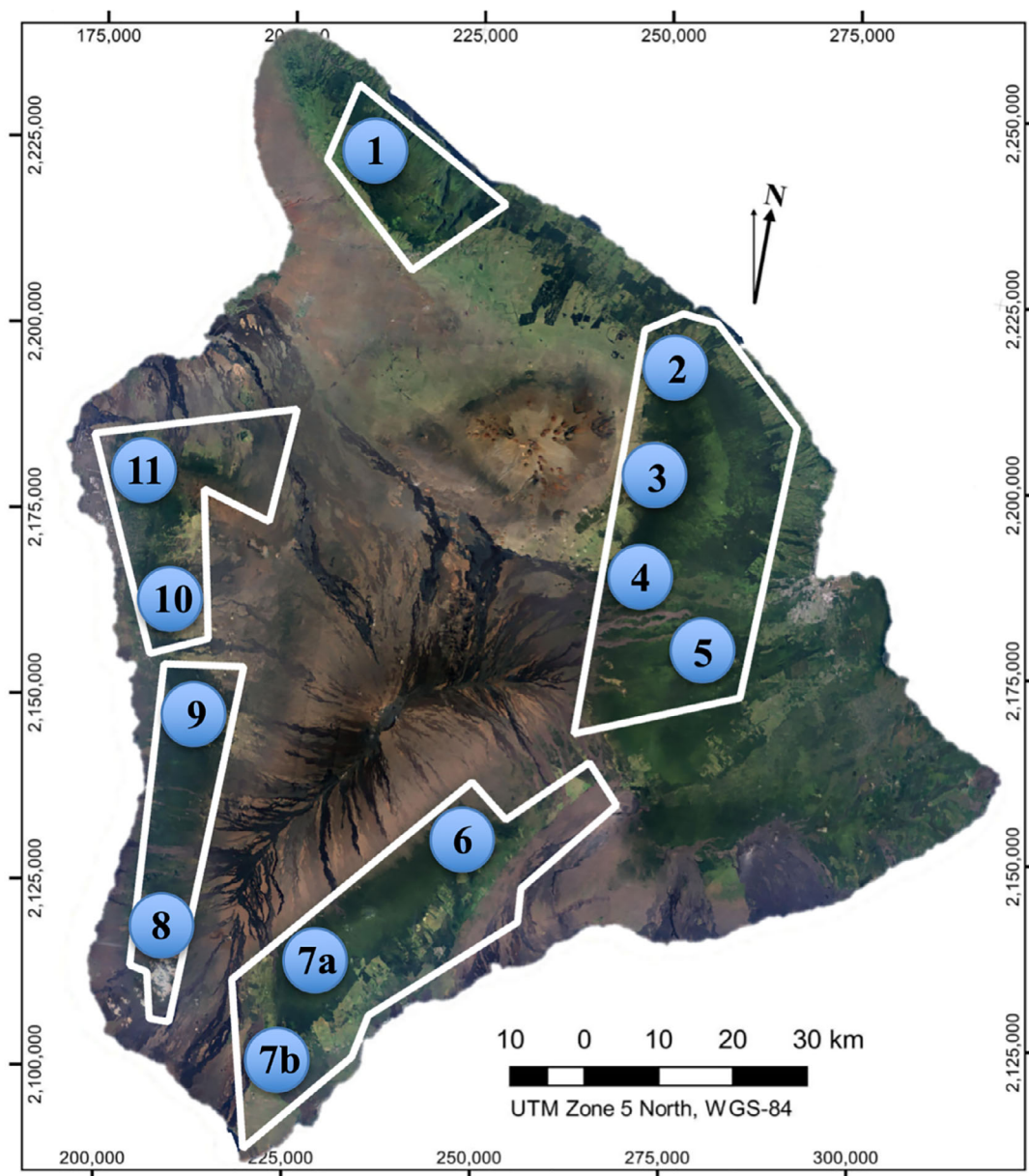


FIGURE 1 Map denoting the 11 regional groupings of hand delineated “to become brown” (TBB) in 2019 and green ‘ōhi’a canopies distributed across Hawai‘i Island. Each regional grouping contains 60 TBB and 60 green ‘ōhi’a canopies except for group 7 which is split in half. White polygons indicate 2018 Global Airborne Observatory (GAO) flight line data. Background imagery is from Google, DigitalGlobe (2017)

and a VSWIR resolution of 2 m. The VSWIR data were collected in 427 channels between 350 and 2485 nm at 5 nm increments (full-width at half max).

The VSWIR radiance data were averaged by neighboring pairs to 10 nm to improve the signal-to-noise, yielding a final dataset of 214 bands. These data were atmospherically corrected to surface reflectance using the ACORN-6LX model (Imspec LLC) and computed observation angles and elevation with an iterative procedure applied to each flight line to set the aerosol optical parameter using the visibility parameter as well as

minimize the cross-track brightness (Colgan et al., 2012; Vaughn et al., 2018).

The LiDAR point cloud data were processed to 1-m resolution digital surface maps of ground elevation, canopy surface elevation, and canopy surface height above ground using the LAStools software suite (Rapidlasso GmbH). The canopy surface data were combined with the time of day to precisely identify pixels that represent canopy locations within the unshaded and unobstructed view of the VSWIR spectrometer (Asner et al., 2012). A minimum top of canopy height threshold of 1.5 m was

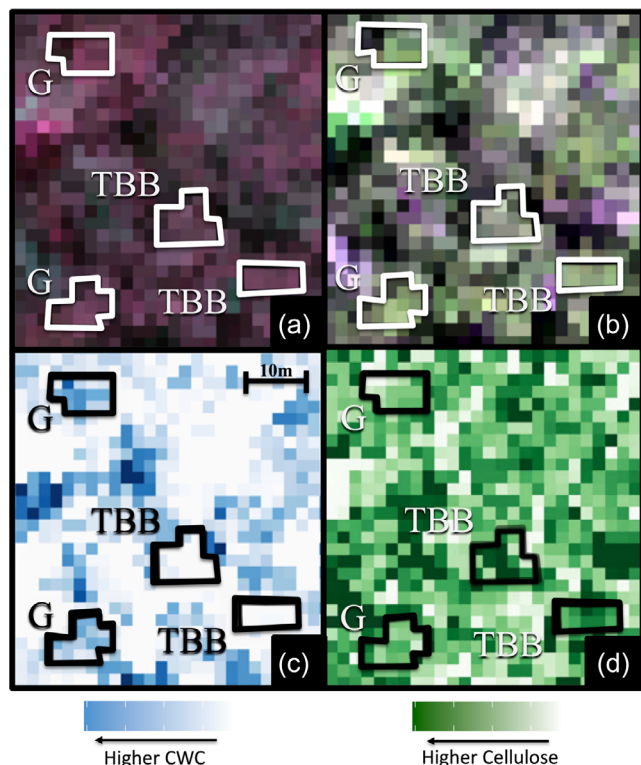


FIGURE 2 Sample foliar trait imagery containing “to become brown” (TBB) in 2019 and green ‘ōhi‘a canopies. Imaging spectroscopy data were collected in 2018 by the Global Airborne Observatory (GAO). (a) Color infrared (CIR), (b) red, green, and blue colors (RGB), (c) canopy water content (CWC) ($L m^{-2}$), and (d) cellulose (%)

applied to the imagery to remove bare ground and short non-forest vegetation such as exposed grass cover. To ensure that we mapped only live canopies, we used maps of 2018 brown and dead trees, created by Vaughn et al. (2018) to mask out 2018 brown and dead tree pixels. Finally, to remove pixels of low leaf area and non-foliated canopy, we used a threshold for Normalized Difference Vegetation Index (NDVI). In tropical forests, NDVI thresholds of 0.75–0.80 have been used to ensure the inclusion of highly foliated canopies (Asner, Anderson, et al., 2015; Asner, Martin, et al., 2015; Martin et al., 2018). The ‘ōhi‘a canopies tend to have lower overall NDVIs, due to foliar pubescence and lower overall nutrient concentrations than other species (Cordell et al., 2001a; Vitousek et al., 1992). Moreover, we did not want to eliminate the crowns that could have potentially a lower NDVI due to disease. Therefore, for this study, a conservative threshold of 0.50 was selected after examining the distribution of NDVI values in the pixels (Appendix S1: Figure S1). Spectra with abnormally low reflectance values $<10\%$ at 800 nm were also removed.

Prior to analysis, bands in the range of atmospheric water absorption and noisy ends of the spectrum were

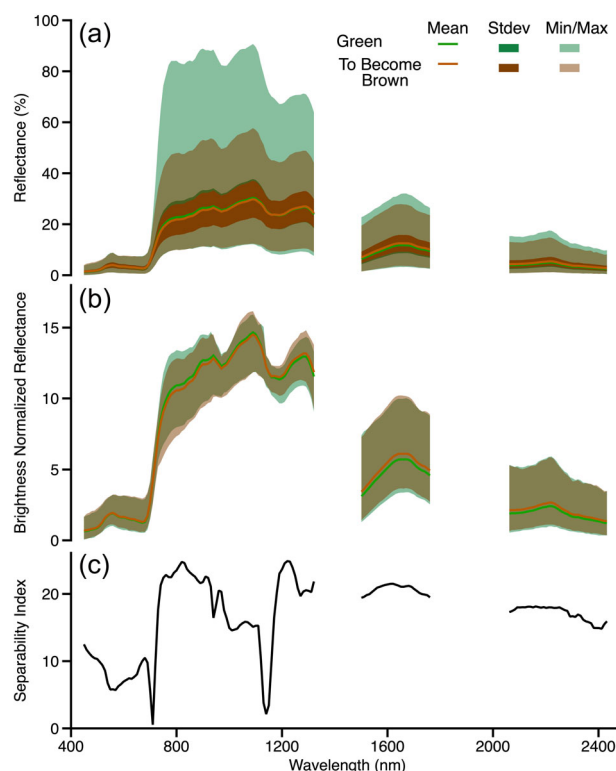


FIGURE 3 Variation between reflectance for $n = 7984$ green and $n = 5530$ “to become brown” (TBB) ‘ōhi‘a pixels across Hawai‘i Island are shown for (a) original spectra, (b) brightness-normalized (BN) spectra, and (c) spectral separability index (SSI) of BN spectra

removed leaving wavelengths of 440–1320, 1500–1760, and 2040–2440 nm and cross-spectrum brightness normalization (BN) was applied to each trimmed spectrum (pixel) so that the magnitude (Euclidean norm) of each brightness-normalized spectrum was 1.0, using the formula:

$$\vec{v}_n = \frac{\vec{v}_r}{|\vec{v}_r|},$$

where $\vec{v}_r$ is the original reflectance spectrum as a vector and $\vec{v}_n$ is the brightness-normalized reflectance spectrum. The process BN follows minimizes differences in observed brightness in reflectance data due to canopy leaf orientation and depth, and has been found to improve chemical retrievals using airborne imaging spectroscopy (Asner, Anderson, et al., 2015; Asner, Martin, et al., 2015; Feilhauer et al., 2010).

Canopy spectral evaluation

We measured the degree of separation between green and brown leaves and canopy spectra using a spectral

separability index (SSI) of the brightness-normalized spectra (Somers & Asner, 2013). This wavelength-level measure indicates the importance of each wavelength in distinguishing between two classes. The SSI was calculated for each wavelength using the equation:

$$SSI = \frac{|\mu_{\lambda\text{green}} - \mu_{\lambda\text{brown}}|}{s_{\lambda\text{green}} + s_{\lambda\text{brown}}},$$

where $\mu_{\lambda\text{class}}$ is the mean reflectance value at a given wavelength, and $s_{\lambda\text{class}}$ is the standard deviation of the wavelength within the given leaf or canopy class. Evaluating the separability of the spectra between classes can reveal spectral regions associated with known leaf or structural traits that most strongly differ between the TBB and green classes.

Foliar trait indices

Indices of 11 foliar traits known to be indicative of ROD (Asner et al., 2018) were mapped to the 2018 filtered GAO data. Partial least squares regression (PLSR) between airborne reflectance and field foliar trait samples were used to generate the chemometric trait models for the mapped traits (Martin et al., 2018). Chemometric models summarize the information of the data and select optimal measurements to provide relevant chemical information. These models were developed and validated using airborne spectral and foliar trait data from prior investigations in Sabah, Malaysia, that span the range of trait values found in Hawaiian forests (Martin et al., 2018). Most modeled canopy trait values were similar to the lab-measured values from ‘ōhi‘a leaves (Asner & Martin, 2016), although we still used the mapped traits as indices (Balzotti et al., 2016; Balzotti & Asner, 2017) to assess relative differences between canopy status rather than precise chemical values and the full VSWIR reflectance spectra to understand the signals we observed. The 11 traits were selected because they were previously found to be important for distinguishing between leaves from ROD-infected and healthy ‘ōhi‘a canopies (Asner et al., 2018). Moreover, they are important for explaining the fundamental ecological processes of forest growth and defense. Traits pertaining to light capture and growth included LMA, nitrogen (N), LWC, NSC, and Chl. Carbon (C), defense phenols, tannins, lignin, and cellulose were selected because they relate to chemical and structural defense. Canopy water content is an indicator of the physiological status of tree and an integrated measure of both LWC and leaf area index (LAI). It is also responsive to leaf and tree canopy stress (Asner et al., 2016; Martin et al., 2018).

The foliar trait index map for CWC, expressed as the vertically integrated total amount of liquid water in the canopy foliage in L m^{-2} (Asner et al., 2016), was modeled from LGIS reflectance data and derived from the spectral absorption features centered at 980 and 1160 nm (Asner et al., 2016; Gao & Goetz, 1990). The application of the Sabah chemometric model to Hawaiian forests resulted in a negative shift in nitrogen values. The values of N were scaled to give a minimum value of 0.01. Foliar nitrogen is being used as a relative index to understand the underlying chemical contributions to the spectral differences in canopies stemming from ROD infection, not to assess the absolute nutrient status of leaves, and in this context scaling the value of N does not impact the general analysis of traits (Balzotti et al., 2016; Balzotti & Asner, 2017).

Canopy selection

We selected regions of high forest cover dominated by ‘ōhi‘a with confirmed ROD cases imaged in 2018 by the GAO for the study (Figure 1). These regions span a range of elevation and climatic conditions (Giambelluca et al., 2013; Sherrod et al., 2007; Table 1). A map of brown trees generated from 2019 GAO imagery was used to identify canopies that were visibly green in 2018 but became brown in 2019 (defined as TBB). We identified green canopies in proximity to TBB canopies using color infrared (CIR; Figure 2a) and red, green, blue colors (RGB; Figure 2b) imagery from 2018 and 2019. Ultimately, our sample size contained 660 TBB and 660 adjacent green ‘ōhi‘a canopies in 11 local groupings across Hawai‘i Island (Figure 1). For each grouping, a subset of green and TBB canopies were verified in the field to confirm that the trees were ‘ōhi‘a. After filtering the pixels within each canopy for brightness normalization, NDVI, shade, and minimum height, we ended with 13,514 total pixels, partitioned as 5530 TBB and 7984 green pixels. The median was 9 pixels per canopy, though a few canopies contained as many as 59 pixels. These large canopies likely contained many indistinguishable crowns due to large areas of contiguous browning in the same height class (Appendix S1: Figure S2). In these cases, all pixels were included. All image data were assessed in QGIS software (QGIS Development Team, 2018).

Statistical analyses

Pixel values of foliar trait index data were averaged to the canopy level to examine differences between TBB and green canopies across Hawai‘i Island. Wilcoxon-signed

rank t tests, which are non-parametric and do not assume normality, were used to determine whether there were significant differences between TBB and green canopies in terms of individual foliar trait indices across the island and between regional groupings. To account for differences between environmental variables and foliar trait indices, nested ANOVA tests were conducted by nesting canopy status within region, which determined the differences between TBB and green ‘ōhi‘a canopies within each region. This approach allowed us to account for environmental effects while looking for differences in canopy status (Table 1). Pearson’s correlations were used to examine linear relationships among foliar traits within green and TBB canopies as they varied across the landscape. To understand differences in the multivariate linear partitioning of variation among chemical traits in green and TBB canopies, we conducted a principal components analysis (PCA) with 11 foliar traits at the canopy

level. Bartlett’s test of sphericity was performed to check for significance. Relative contributions of principal components were calculated to explain the linear proportional importance of the foliar traits. All statistical analyses were performed using R version 1.2.1335 (R Core Team, 2013).

Modeling

A Gradient-Boosting Machine (GBM) classification model was used to identify the differences in non-linear foliar trait combinations between green and TBB ‘ōhi‘a pixels across all the regions in the dataset. A GBM model generates an ensemble of decision trees using an iterative procedure where at each successive iteration, a decision tree is fit to the remaining residuals from the previous iteration. This process is known as “boosting” (Elith

TABLE 1 Environmental descriptions including mean values for substrate age, mean annual precipitation (MAP), mean annual temperature (MAT), and elevation of each regional grouping across Hawai‘i Island

Group	Description	Substrate age (years)	MAP (mm)	MAT (°C)	Elevation (m)
1	East of Kahua/Ponoholo Ranch, North of Pu‘u O Umi, and south of Kohala Forest Reserve	50, 190,000	103 (97–111)	16 (15–17)	1143 (1082–1190)
2	Most are in Hilo Forest Reserve with some canopies in Hakalau Forest National Wildlife refuge and Laupāhoehoe Natural Area Reserve	8000, 47,500	145 (100–195)	15 (12–17)	1226 (809–1635)
3	Hakalau Forest National Wildlife Refuge	47,500	151 (91–267)	13 (11–15)	1531 (1119–1899)
4	West of Hilo Watershed Forest Reserve	47,500, 60,750	101 (98–110)	13 (13–13)	1542 (1510–1590)
5	Split between Upper Waiākea Forest Reserve and Pu‘u Maka‘ala Natural area reserve	500, 8000	233 (215–252)	15 (15–16)	1102 (1009–1135)
6	Most all in Ka‘ū Forest Reserve. One canopy in Kapāpala Cooperative Game Management area and a few canopies in Kapāpala Forest Reserve. These canopies were specifically selected across an elevation gradient	1075	86 (77–91)	14 (11–17)	1470 (1029–1966)
7a	Most in Kau Forest reserve and a few in Hawai‘i Volcanoes National Park Kahuku Ranch Cooperative Nene sanctuary	1075, 20,000	92 (88–96)	13 (12–14)	1738 (1621–1825)
7b	Mostly in Ka‘ū Forest Reserve and a few just outside in Pāhala	2250, 20,000	96 (76–110)	18 (17–20)	734 (585–894)
8	Mostly in Manuka Natural Area Reserve and a few in Kona Hema Preserve	1075, 2250	39 (38–39)	18 (17–20)	862 (779–957)
9	Mostly west of Hakalau Forest National Wildlife Refuge and a few canopies inside the refuge	2250	54 (46–63)	20 (19–22)	530 (381–658)
10	South of Wai‘aha Springs Forest Reserve in Honua‘ula	700, 8000	48 (46–52)	21 (18–23)	633 (480–729)
11	Split between Honua‘ula Reserve Forest and in Kalaoa	2250, 4000	48 (38–59)	18 (15–22)	984 (759–1392)

Note: The range of values is given in parentheses.

et al., 2008; Friedman, 2001). Such models incorporate both bias and variance reductions, distinguishing them from other decision-tree based approaches such as Random Forest (RF), which are focused on variance reduction (Breiman, 2001; Pavlov, 2019). The GBM model was employed in order to incorporate non-linear interactions between features while being robust to multicollinearity (Friedman, 2001; Mason et al., 1999).

Although the number of canopies for both classes was identical, the number of valid pixels for green canopies was higher than those of TBB canopies. To create a balanced dataset of TBB and green pixels for the model, we randomly drew 5530 green pixels without replacement from the 7984 available. To avoid under-representing smaller canopies, we first selected 1 pixel from each of the 660 canopies and then filled the remaining samples from all unselected pixels without regard to canopy membership. The model was run at the pixel level to properly capture variation among pixels within individual TBB and green ‘ōhi‘a canopies. The final model of 11 foliar chemical trait indices included $n = 5530$ green and $n = 5530$ TBB pixels distributed across Hawai‘i Island, and represented $n = 660$ green and $n = 660$ TBB canopies. Optimal model hyper-parameters were identified using a grid search technique, checking every unique set of hyper-parameters in a 144-stage grid built from candidate values of the number of estimators, maximum depth, and learning rate of the classifier (Vaughn et al., 2018). Ten-fold cross-validation was performed on each set of parameters with a 90/10 train test split in each fold to get the true positive, true negative, false positive, and false negative counts for each of the 144 models. All model training was done using the package Scikit-Learn for Python (Varoquaux et al., 2015). The final set of parameters was selected that maximized the overall recall of predictions made in the 10-fold cross-validation procedure. Recall, which balances accuracy and precision is given by the equation below:

$$\text{recall} = \frac{\text{true positives}}{\text{true positives} + \text{false negatives}}.$$

While the subsequent classified data were binary, GBM models output prediction probabilities, and a threshold value, T , should be specified to assign a true or false value to each prediction. The default value is 0.5. To view how the classification results change as we adjusted T , we computed a receiver operating characteristic (ROC) curve. This curve plotted the optimal model’s true positive rate against the false-positive rate over 1000 unique values of T to illustrate the diagnostic ability of a binary classifier. As the threshold values increase, both true positives and false positives increase. Therefore, analysis of the ROC curve

provides a measure of model performance across a range of possible threshold values (Fawcett, 2006).

We calculated permutation importance and partial dependence plots (PDPs) from the gradient-boosting models to understand the relationship between foliar traits and the predicted browning probability. Permutation importance describes a decrease in the score when the values of a feature are randomly permuted prior to model application. Partial dependence plots demonstrate the marginal change in our model’s predicted probability of TBB as we increase the value of a single feature between its 5th and 95th percentile, all others being set to their respective means (Friedman, 2001).

RESULTS

There were quantifiable differences between TBB in 2019 and green ‘ōhi‘a canopies on Hawai‘i Island (Table 2). Across the regional groupings with differing environmental conditions, the variance was observed among reflectance spectra and foliar trait values (Appendix S1: Table S6). Even with this variation, two gradient-boosting machine models predicted classes with moderately high accuracy across a large environmental gradient (Table 3).

Early signs of Rapid ‘Ōhi‘a Death in canopies

In the true-color imagery of 2018, TBB and green ‘ōhi‘a canopies appeared identical based on visual assessment (Figure 2a,b). But spectrally, TBB canopies in Hawaiian forests exhibited remotely sensed foliar chemical and reflectance differences that were distinct from their green counterparts (Figure 2c,d, and 3).

Green and TBB ‘ōhi‘a canopy reflectance spectra (Figure 3a,b) overall had similar shapes, though their slight differences in scattering and reflectance features (Figure 3c) match our hypotheses based on differences between green and brown ‘ōhi‘a spectra (Asner et al., 2018). Brightness normalization reduced the overall variability of green and TBB canopy spectra and increased the reflectance values in the near-infrared relative to the remainder of the spectrum (Figure 3b). The green-leaf values followed the classic pattern with a local spectral reflectance peak at 550 nm, strong absorption near 680 nm, increased brightness in the near-infrared (700–1300 nm), and strong absorption in the shortwave-infrared (1300–2500 nm). The highest spectral separability between the canopy states was located in the shortwave-infrared (>1300 nm) wavelength range, which is associated with differences in cellulose and NSC, as

TABLE 2 Means and standard deviations (in parentheses) of foliar traits for green ($n = 660$) and “to become brown” (TBB; $n = 660$) ‘ōhi‘a canopies

Trait	Green ‘ōhi‘a ($n = 660$)		TBB ‘ōhi‘a ($n = 660$)	
	Mean	Range	Mean	Range
Light capture and growth				
CWC (L m^{-2})**	2.57 (0.39)	1.34–4.06	2.40 (0.38)	1.20–3.61
LWC (%)**	53.8 (3.7)	41.1–61.2	53.1 (4.5)	38.4–60.9
LMA (g m^{-2})**	198.4 (25.5)	125.2–284.7	193.5 (23.6)	121.6–268.9
Nitrogen (%)	1.02 (0.27)	0.28–2.34	1.00 (0.27)	0.17–1.8
Chlorophyll (mg g^{-1})**	4.23 (0.84)	1.91–6.89	4.05 (0.95)	1.48–6.88
NSC (%)*	53.9 (5.0)	33.8–66.5	54.5 (5.0)	35.4–67.4
Structure and defense				
Phenols (mg g^{-1})**	122.2 (17.3)	62.7–163.7	127.6 (15.8)	79.9–200.6
Tannins (mg g^{-1})	98.2 (10.9)	65.1–122.3	98.2 (12.3)	57.2–141.8
Carbon (%)	51.4 (1.2)	46.0–55.0	51.4 (1.3)	47.5–54.9
Cellulose (%)*	13.8 (2.2)	7.5–20.7	14.1 (2.6)	5.2–22.0
Lignin (%)	21.1 (4.7)	7.6–37.9	20.9 (5.2)	5.9–41.2

Note: For each trait, an asterisk (*) indicates significant differences between group means (Wilcoxon t tests, $*p < 0.05$, $**p < 0.0001$). Abbreviations: CWC, canopy water content; LMA, leaf mass per area; LWC, leaf water content; NSC, non-structural carbohydrates.

TABLE 3 Confusion matrix results from the cross-validation procedure of the optimal fit of the two gradient-boosting machine (GBM) models at a default classification of 0.5. A GBM included the spectral data (400–2500 nm) another contained the 11 foliar trait indices from a balanced dataset of green and “to become brown” (TBB) ‘ōhi‘a pixels ($n = 11,060$) distributed across Hawai‘i Island

	Predicted			Recall	Precision	Cohen’s Kappa
	Observed	Green	TBB			
Spectral data	Green	4120	1410	0.75	0.75	0.493
	Brown	1393	4137			
Foliar traits	Green	3998	1532	0.72	0.72	0.441
	Brown	1512	4018			

well as water concentrations between green and TBB canopy states (Figure 3b,c). In the visible wavelengths, there is spectral separability in the 680–780 nm wavelength range, which is associated with differences in phenols and Chl (Figure 3c). Moreover, we see separability around 940 nm, associated with water features. Maximum spectral separability at the canopy level was achieved using brightness-normalized reflectance spectra from the airborne imaging spectrometer data (Figure 3c).

Mapped canopy foliar indices varied across the island (Table 2; Appendix S1: Figure S3, Table S5) and within regional groupings (Table 1; Appendix S1: Table S6). Compared to single traits, average canopy indices for LMA, Chl, LWC, and CWC were higher in green canopies, whereas phenols and cellulose were higher in TBB canopies (Table 2). Differences between canopy status within regional groupings (e.g., regions 9–11) were not always apparent (Appendix S1: Table S6), probably due

to the more rapid nature of disease takeover in certain areas. When chemical separations were observed, the differences between TBB and green canopies were clearly depicted in the remotely sensed maps of foliar traits, such as with higher CWC in green canopies and higher cellulose in TBB canopies (Figure 2c,d). Total percentages of N and C and concentrations of tannins and lignins of canopies did not differ between green and TBB canopies (Table 2). At the pixel level, all traits except cellulose and lignin differed between the TBB and green ‘ōhi‘a (Appendix S1: Table S1, Figure S4).

Principal component (PC) analysis revealed linear combinations of foliar traits produced multiple axes of variation in green and TBB canopies (Figure 4; Appendix S1: Table S2). Nearly 50% of the variation was found in the first two PCs (Figure 4), but seven PCs were needed to account for 95% of the variation. The first two principal components (PC1 and PC2) explained 27% and

23% of the variation in green and 32% and 24% in TBB ‘ōhi‘a canopies, respectively (Figure 4; Appendix S1: Table S2). Variation in the first axis for green canopies was largely explained by N and LMA, which were also negatively correlated ($r = -0.79$ and -0.81 in green and TBB canopies, respectively; Appendix S1: Figure S5, Table S4), while variation in the second axis was dominated by NSC and lignin. Both NSC and lignin were also negatively correlated within green ($r = -0.76$) and TBB canopies ($r = -0.70$; Appendix S1: Table S4). Variation in the first axis in TBB canopies was dominated by LWC and to a lesser extent, cellulose, while the variation in PC2 was more evenly distributed among LMA, nitrogen, and lignin (Figure 4; Appendix S1: Table S3). Noticeable differences between TBB and green canopies were found on axis three (PC3; Appendix S1: Table S3). Tannins, Chl, and CWC values of green canopies explained variation of the PC3, while tannins and less so Chl explained variation in TBB canopies.

Modeling an early-stage disease signal

The GBM model with full VSWIR reflectance spectrum accurately classified 75% of TBB and green training

pixels. The GBM with 11 foliar trait indices accurately classified 72% of TBB and green training pixels. Optimal parameter values for the full VSWIR spectrum exhibited a learning rate of 0.05, a maximum tree depth of seven, and an assembly of 5000 decision trees. Optimal parameter values for the foliar trait index GBM exhibited a learning rate of 0.02, a maximum tree depth of eight, and an assembly of 2500 decision trees. Both GBMs were conservative during training, with many more false-negatives than false-positives occurring in the TBB class. For the full reflectance model, recall, precision, and f1 values were each 75% and the Cohen’s Kappa value was 0.493. For the model with 11 foliar trait indices, recall, precision, and f1 values were each 72% and the Cohen’s Kappa value was 0.441 (Table 3). For the full VSWIR model, as we varied the probability threshold for binary classification 0–1, the true positive rate of the model increased sharply from zero to approximately 40% before gradually increasing to approximately 92% as the false positive rate reached 50% (Appendix S1: Figure S6a). For the trait model, as we varied the probability threshold for binary classification 0–1, the true positive rate of the model increased sharply from zero to approximately 35% before gradually increasing to approximately 90% as the false positive rate reached 50% (Appendix S1:

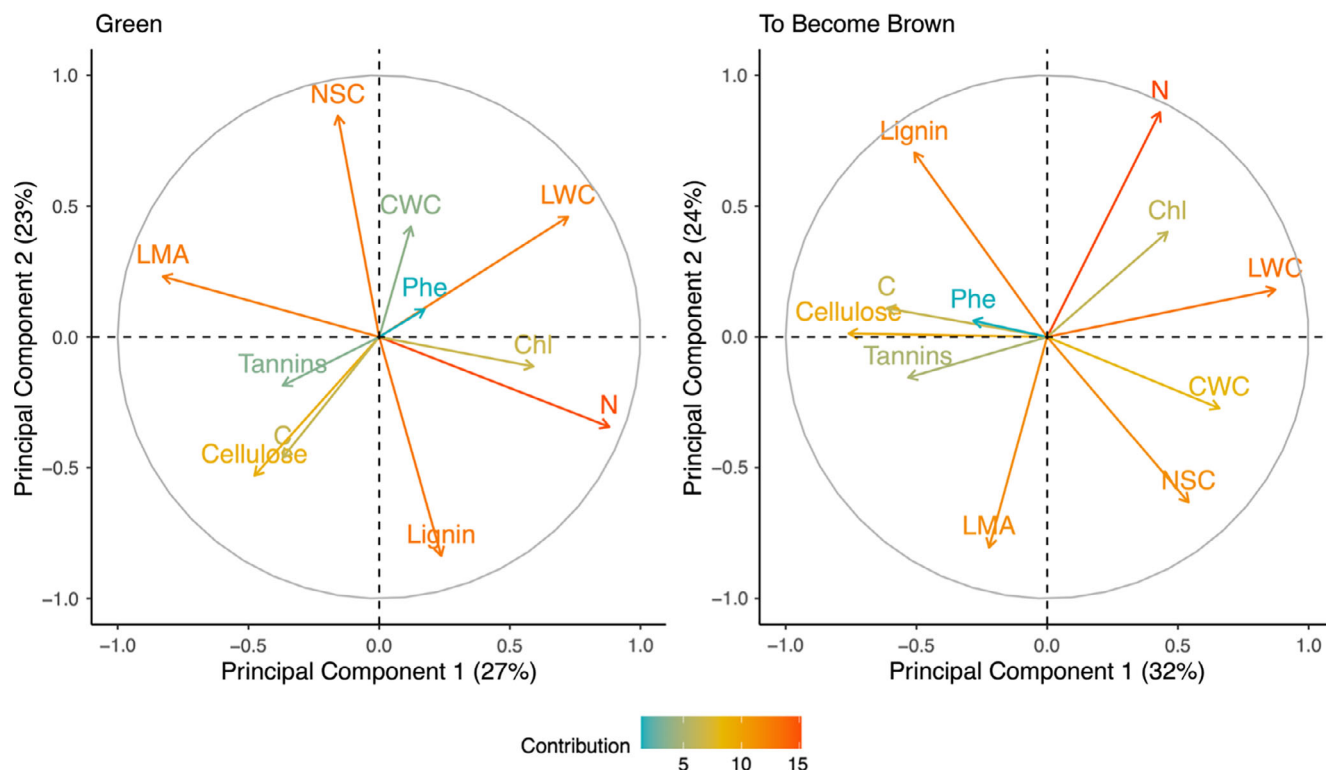


FIGURE 4 Principal component analysis (PCA) of the 11 foliar trait indices for “to become brown” (TBB; $n = 660$) and green ($n = 660$) ‘ōhi‘a canopies distributed across Hawai‘i Island. Foliar traits are colored by overall percent contribution. Canopy water content (CWC, L m^{-2}), leaf water content (LWC, %), leaf mass per area (LMA, g m^{-2}), nitrogen (%), chlorophyll (Chl, mg g^{-1}), non-structural carbohydrates (NSC, %), phenols (Phe, mg g^{-1}), tannins (mg g^{-1}), carbon (%), cellulose (%), lignin (%)

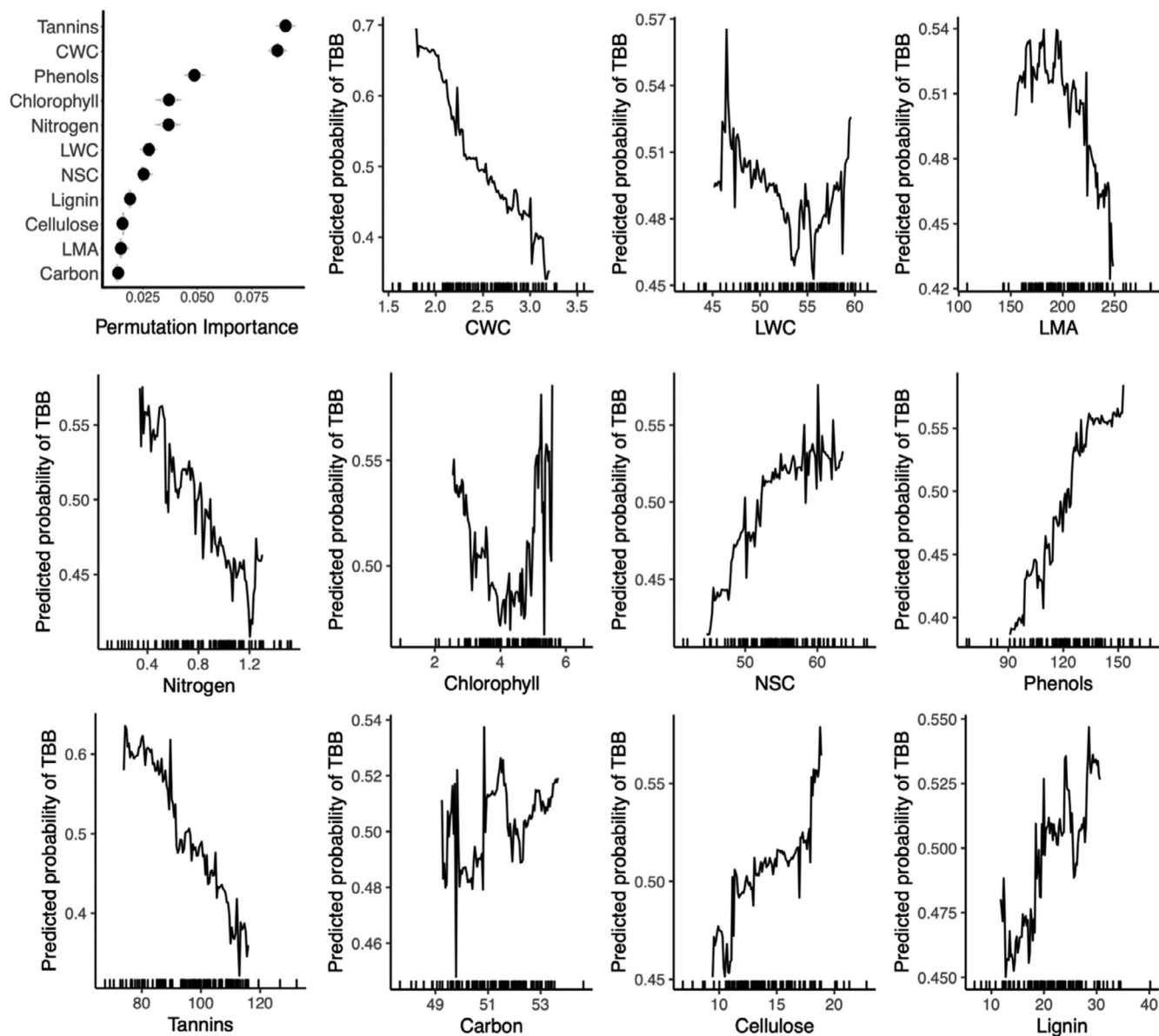


FIGURE 5 Permutation (variable) importance (top left) for the 11 foliar trait indices from a balanced dataset of green and “to become brown” (TBB) ‘ōhi‘a pixels ($n = 11,060$) distributed across Hawai‘i Island. The median and 95% confidence intervals are displayed. Permutation importance was computed by measuring the reduction in accuracy of the trained gradient-boosting machine (GBM) model after permuting each feature randomly 10 times with the entire dataset. The remaining plots are partial dependence plots (PDPs) of browning probability displaying 100 random samples from the balanced dataset for the 11 foliar traits indices. Probabilities were also calculated from 10-fold cross-validation in the GBM. The rug plots display the 100 random samples. Canopy water content (CWC, $L\ m^{-2}$), leaf water content (LWC, %), leaf mass per area (LMA, $g\ m^{-2}$), nitrogen (%), chlorophyll (Chl, $mg\ g^{-1}$), non-structural carbohydrates (NSC, %), phenols ($mg\ g^{-1}$), tannins ($mg\ g^{-1}$), carbon (%), cellulose (%), lignin (%)

Figure S6b). As shown by an area under the curve (AUC) of 0.83 (full VSWIR GBM) and 0.81 (foliar traits GBM), the models were superior to chance at detecting differences between classes (Appendix S1: Figure S6). Ambiguous pixels were more likely to be misclassified as green than TBB (Table 3).

Permutation feature importance results from the non-linear, multivariate GBM showed tannins to be most important in predicting canopy status, followed closely

by CWC (Figure 5). Although tannins were not significantly different between conditions of canopies when tested individually, these results indicate the importance of their variation in combination with other traits. While tannins and CWC exerted the largest effect for model differentiation of green and TBB pixels relative to other traits, all traits had high confidence in the median of permutation feature importance with small deviations indicating they all collectively contributed to the separation

of canopy conditions. The PDPs derived from the GBM were used to explore how different foliar trait indices influence the probability of a canopy being TBB (Figure 5). These depict the functional relationship between input variables and predictions. Partial dependence plots did not highlight specific non-linear interactions between the prediction variables, but rather displayed average response of probability of being a TBB canopy across all predictor variables as a function of the variable being examined. Nitrogen, CWC, LMA, and tannins expressed strong negative linear trends with TBB probability. Conversely, phenols, lignin, cellulose, and NSC demonstrated a positive relationship with TBB probability, though the expressed relationship for cellulose and NSC were more curvilinear. Both Chl and LWC exhibited a concave parabolic relationship with TBB probability, though the actual change in TBB value across the range of these traits was minimal. Carbon did not show a discernable pattern in the PDPs (Figure 5).

DISCUSSION

The canopy reflectance spectra and foliar trait indices mapped from GAO LGIS revealed quantitative differences between TBB and green ‘ōhi‘a canopies, despite the lack of visible brown symptoms when first measured in 2018. While the green and TBB canopies were visually inseparable in the 2018 imagery, we found a characteristic difference in leaf traits that affected the reflection of electromagnetic radiation in a way only observable with imaging spectroscopy (Asner, 1998). Reflectance spectra displayed distinct separability across nearly all wavelengths with the greatest differences found in the NIR and SWIR regions (Figure 3c) indicative of subtle differences in water content, nitrogen, and relative distribution of carbon compounds associated with a structure (lignin and cellulose) and defense (phenols and tannins). The strength of this browning signal was evidenced by consistency in the chemical separability of green and TBB ‘ōhi‘a trees both at pixel and canopy levels, further demonstrating the potential utility in using hyperspectral imagery for spatially explicit vegetative pathogenesis forecasting.

Principal components analysis revealed subtle variations in the combination of foliar traits that distinguished green canopies from TBB canopies, pointing toward possible physiological responses. The two axes of variation in PCA addressed strategies for growth and carbon use within ‘ōhi‘a canopies. In PCA’s of both green canopies and TBB canopies, linear combinations of LWC and cellulose were arranged between the first two components in an orthogonal manner relative to NSC, LMA, lignin,

and nitrogen. This pattern indicated independent function. Changes in LWC and NSC values are indicative of shorter-term stress, while changes in cellulose, lignin, and LMA values are indicative of longer-term carbon investments (Klein et al., 2014). However, differences between TBB and green canopies were demonstrated through traits such as tannins, which split importance with Chl in green canopies, but dominate PC3 in TBB canopies (Appendix S1: Table S3). These differences in proportioning of foliar chemical trait indices between TBB and green canopies are consistent with stress response in trees (Klein et al., 2014). In response to *Ceratocystis* infection, ‘ōhi‘a canopies may be producing tyloses, gels, and gums to limit spore movement, which could alter concentrations of foliar traits including tannins and lignins (Yadeta & Thomma, 2013). Additionally, CWC and lignin, both important for describing the chemical signature of green canopies, are of limited importance in the chemical signature of TBB canopies. Such changes to canopy chemistry were consistent with foliar responses to drought following cavitation of xylem and could be responsible for causing differences in distributions of foliar traits (McDowell et al., 2008).

By utilizing foliar chemicals detected by high-fidelity measurements of the full electromagnetic spectrum, we demonstrated the first results to detect and model a signal of infection prior to visible browning. Prior to this study, Perroy et al. (2020) used a spectroradiometer to measure four vegetation indices in the visible and near-infrared (VNIR) spectrum including cellulose absorption index (CAI), moisture stress index (MSI), photochemical reflective index (PRI), and NDVI. While CAI and MSI showed promise, the VNIR portion of the spectrum was deemed insufficient for the early detection of ROD infection. Several foliar trait indices estimated from our spectrometer incorporate information from the shortwave region of the VSWIR spectrum (Martin et al., 2018). This added information is essential for predicting this early detection signal because when restricted to the VNIR range, the ability to predict canopy chemical traits is greatly reduced (Asner et al., 2011). Thus, our modeling analyses revealed important spectral signals that would otherwise go undetected.

Spectral and underpinning chemical differences between TBB and green canopies were detected by the GBM across a very broad environmental gradient (381–1966 m) within a single species. This result is important, because, while there is only one species of ‘ōhi‘a on Hawai‘i Island, canopies express great morphological variation due to environmental factors such as precipitation levels (Cordell et al., 1998; Kitayama et al., 1997; Stemmermann, 1983), temperature (Drake, 1993; Sakishima, 2015), light availability (Burton &

Mueller-Dombois, 1984; Cordell et al., 1998; Morrison & Stacy, 2014), and soil age (Cordell et al., 2001b; Treseder & Vitousek, 2001).

Prior studies have combined hyperspectral data collected by spectroradiometers with modeling approaches for the early detection of forest fungal pathogens. Abdulridha et al. (2016) used neural networks to detect laurel wilt from a lab spectroradiometer (400–950 nm), though they were most successful when leaves displayed visible symptoms. Heim et al. (2019) employed random forest modeling with data collected by a field spectroradiometer (350–2500 nm) to detect myrtle rust. Fallon et al. (2020) also used a field spectroradiometer (400–2400 nm) and employed partial least squares discriminant analyses to detect oak wilt. Such studies demonstrate that multivariate modeling can reveal variance in data and identify spectral signatures associated with healthy and diseased states of canopies, and that early detection is most successful when the full spectrum is utilized. Our results documented commonalities in spectral reflectance and foliar chemical changes expressed in TBB ‘ōhi‘a canopies across diverse environmental gradients and ‘ōhi‘a leaf morphology. Our findings suggest that a spectral-chemical signature of TBB trees can be mapped across Hawai‘i Island, and they advance the idea that spectral-chemical signatures for operational mapping with imaging spectroscopy can be implemented.

As we intended to detect differences in canopy signal between ROD impacted and healthy ‘ōhi‘a, we selected canopies in locations of confirmed ROD outbreaks. Although we call canopies TBB rather than “future ROD canopies,” we are reasonably confident that canopy browning was caused by ROD (i.e., infected by the fungal pathogen, *Ceratocystis*). Rapid ‘ōhi‘a death commonly undergoes rapid symptom progression whereby tree canopies change from green to brown in weeks to months (Barnes et al., 2018; Mortenson et al., 2016). This often rapid and extensive brown-leaf state generated by ROD is unique in ‘ōhi‘a and distinct from other ‘ōhi‘a death or dieback events (Jacobi, 1983; McDowell et al., 2008; Mueller-Dombois, 1980; Mueller-Dombois et al., 2013). Therefore, by detecting a difference in spectral and chemical signals between green and TBB canopies in areas of known ROD infection, we suggest that trees are either stressed prior to showing visible symptoms and succumbing to the disease or that certain crowns and stands are more susceptible to ROD than others. While the abrupt onset of visible symptoms is the result of trees reaching a “tipping point,” where the xylem is blocked, water and nutrient flow stops, and wilt and browning occur (Barnes et al., 2018; Hughes et al., 2020; Mortenson et al., 2016), it is possible the tree had been infected with the *Ceratocystis* disease for an extended period. Although

we cannot yet confirm that our results provide a definitive signal for ROD-induced browning, this study shows that early detection of canopy browning, presumably from ROD is possible. In this study, our approach to use LGIS allows us to detect differences before symptoms are visible to the human eyes; thus, putting management a step ahead of the disease.

The mortality of ‘ōhi‘a from ROD has spread well beyond initial areas of infection of the Puna District of Hawai‘i Island documented by Mortenson et al. (2016). It now occurs on each of the five main volcanoes of Hawai‘i Island (Camp et al., 2019; Vaughn et al., 2018). Increasing our ability to promptly detect and understand the movement of the disease is essential. Early detection of ROD will allow us to determine the most vulnerable regions to browning and properly inform management regarding the allocation of resources to reduce damage and prevent spread (Loope et al., 2016). In this study, we demonstrated the ability to use canopy chemistry to develop a prognostic indicator of tree stress prior to the visible onset of browning. Ultimately, we show a technique for landscape-scale imaging spectroscopy modeling and propose future mapping to be possible and applied to other pathogens. These results are extremely promising for aiding in the conservation efforts of reducing the impact of ROD.

ACKNOWLEDGMENTS

This study was funded by the State of Hawai‘i Department of Land and Natural Resources (DLNR) and USDA Forest Service (FP0020713). The Global Airborne Observatory is made possible by support provided by private foundations, visionary individuals, and Arizona State University.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Martin et al., 2021) are available in Figshare: <https://doi.org/10.6084/m9.figshare.15019443>.

ORCID

Roberta E. Martin  <https://orcid.org/0000-0003-3509-8530>

Nicholas R. Vaughn  <https://orcid.org/0000-0003-0428-2909>

Gregory P. Asner  <https://orcid.org/0000-0001-7893-6421>

REFERENCES

- Abdulridha, J., R. Ehsani, and A. De Castro. 2016. “Detection and Differentiation Between Laurel Wilt Disease, Phytophthora Disease, and Salinity Damage Using a Hyperspectral Sensing Technique.” *Agriculture (Switzerland)* 6(4): 56.

- Asner, G.P. 1998. "Biophysical and Biochemical Sources of Variability in Canopy Reflectance." *Remote Sensing of Environment* 64(3): 234–53.
- Asner, G.P., C.B. Anderson, R.E. Martin, R. Tupayachi, D.E. Knapp, and F. Sinca. 2015. "Landscape Biogeochemistry Reflected in Shifting Distributions of Chemical Traits in the Amazon Forest Canopy." *Nature Geoscience* 8(7): 567–73.
- Asner, G.P., P.G. Brodrick, C.B. Anderson, N. Vaughn, D.E. Knapp, and R.E. Martin. 2016. "Progressive Forest Canopy Water Loss During the 2012–2015 California Drought." *Proceedings of the National Academy of Sciences of the United States of America* 113(2): E249–55.
- Asner, G.P., D.E. Knapp, J. Boardman, R.O. Green, T. Kennedy-Bowdoin, M. Eastwood, R.E. Martin, C. Anderson, and C.B. Field. 2012. "Carnegie Airborne Observatory-2: Increasing Science Data Dimensionality via High-Fidelity Multi-Sensor Fusion." *Remote Sensing of Environment* 124: 454–65.
- Asner, G.P., and R.E. Martin. 2016. "Spectranomics: Emerging Science and Conservation Opportunities at the Interface of Biodiversity and Remote Sensing." *Global Ecology and Conservation* 8: 212–9.
- Asner, G.P., R.E. Martin, C.B. Anderson, and D.E. Knapp. 2015. "Quantifying Forest Canopy Traits: Imaging Spectroscopy Versus Field Survey." *Remote Sensing of Environment* 158: 15–27.
- Asner, G.P., R.E. Martin, C.B. Anderson, K. Kryston, N. Vaughn, D.E. Knapp, L.P. Bentley, et al. 2017. "Scale Dependence of Canopy Trait Distributions Along a Tropical Forest Elevation Gradient." *New Phytologist* 214(3): 973–88.
- Asner, G.P., R.E. Martin, L.M. Keith, W.P. Heller, M.A. Hughes, N. R. Vaughn, R.F. Hughes, and C. Balzotti. 2018. "A Spectral Mapping Signature for the Rapid Ohia Death (ROD) Pathogen in Hawaiian Forests." *Remote Sensing* 10(3): 404.
- Asner, G.P., R.E. Martin, D.E. Knapp, R. Tupayachi, C. Anderson, L. Carranza, P. Martinez, M. Houcheime, F. Sinca, and P. Weiss. 2011. "Spectroscopy of Canopy Chemicals in Humid Tropical Forests." *Remote Sensing of Environment* 115(12): 3587–98.
- Balzotti, C.S., and G.P. Asner. 2017. "Biotic and Abiotic Controls over Canopy Function and Structure in Humid Hawaiian Forests." *Ecosystems* 21: 331–48.
- Balzotti, C.S., G.P. Asner, P.G. Taylor, C.C. Cleveland, R. Cole, R.E. Martin, M. Nasto, B.B. Osborne, S. Porder, and A.R. Townsend. 2016. "Environmental Controls on Canopy Foliar Nitrogen Distributions in a Neotropical Lowland Forest." *Ecological Applications* 26(8): 2451–64.
- Barnes, M.L., D.D. Breshears, D.J. Law, W.J.D. van Leeuwen, R.K. Monson, A.C. Fojtik, G.A. Barron-Gafford, and D.J.P. Moore. 2017. "Beyond Greenness: Detecting Temporal Changes in Photosynthetic Capacity with Hyperspectral Reflectance Data." *PLoS One* 12: 1–17.
- Barnes, I., A. Fourie, M.J. Wingfield, T.C. Harrington, D.L. McNew, L.S. Sugiyama, B.C. Luiz, W.P. Heller, and L.M. Keith. 2018. "New Ceratocystis Species Associated with Rapid Death of *Metrosideros polymorpha* in Hawai'i." *Persoonia: Molecular Phylogeny and Evolution of Fungi* 40: 154–81.
- Boehmer, H.J., H.H. Wagner, J.D. Jacobi, G.C. Gerrish, and D. Mueller-Dombois. 2013. "Rebuilding after Collapse: Evidence for Long-Term Cohort Dynamics in the Native Hawaiian Rain Forest." *Journal of Vegetation Science* 24(4): 639–50.
- Breiman, L. 2001. "Random Forests." *Machine Learning* 45(1): 5–32.
- Burton, P.J., and D. Mueller-Dombois. 1984. "Response of *Metrosideros polymorpha* Seedlings to Experimental Canopy Opening." *Ecology* 65(3): 779–91.
- Calderón, R., J.A. Navas-Cortés, and P.J. Zarco-Tejada. 2015. "Early Detection and Quantification of Verticillium Wilt in Olive Using Hyperspectral and Thermal Imagery over Large Areas." *Remote Sensing* 7(5): 5584–610.
- Camp, R.J., D.A. LaPointe, P.J. Hart, D.E. Sedgwick, and L.K. Canale. 2019. "Large-Scale Tree Mortality from Rapid Ohia Death Negatively Influences Avifauna in Lower Puna, Hawai'i Island, USA." *The Condor* 121(2): 1–16.
- Cavender-Bares, J., J.E. Meireles, J.J. Couture, M.A. Kaproth, C.C. Kingdon, A. Singh, S.P. Serbin, A. Center, E. Zuniga, and G. Pilz. 2016. "Associations of Leaf Spectra with Genetic and Phylogenetic Variation in Oaks: Prospects for Remote Detection of Biodiversity." *Remote Sensing* 8(3): 221.
- Colgan, M.S., C.A. Baldeck, J.B. Féret, and G.P. Asner. 2012. "Mapping Savanna Tree Species at Ecosystem Scales Using Support Vector Machine Classification and BRDF Correction on Airborne Hyperspectral and LiDAR Data." *Remote Sensing* 4(11): 3462–80.
- Cordell, S., G. Goldstein, F.C. Meinzer, and P.M. Vitousek. 2001a. "Morphological and Physiological Adjustment to N and P Fertilization in Nutrient-Limited *Metrosideros polymorpha* Canopy Trees in Hawai'i." *Tree Physiology* 21(1): 43–50.
- Cordell, S., G. Goldstein, F.C. Meinzer, and P.M. Vitousek. 2001b. "Regulation of Leaf Life-Span and Nutrient-Use Efficiency of *Metrosideros polymorpha* Trees at Two Extremes of a Long Chronosequence in Hawai'i." *Oecologia* 127(2): 198–206.
- Cordell, S., G. Goldstein, D. Mueller-Dombois, D. Webb, and P.M. Vitousek. 1998. "Physiological and Morphological Variation in *Metrosideros polymorpha*, a Dominant Hawaiian Tree Species, along an Altitudinal Gradient: The Role of Phenotypic Plasticity." *Oecologia* 113: 188–96.
- Dawson, J.W., L. Stemmerman, W.L. Wagner, D.R. Herbst, and S. H. Sohmer. 1990. *Manual of the Flowering Plants of Hawaii*, 964–70. Honolulu, HI: Bernice P. Bishop Museum.
- Drake, D.R. 1993. "Germination Requirements of *Metrosideros polymorpha*, the Dominant Tree of Hawaiian Lava Flows and Rain Forests." *Biotropica* 25: 461–7.
- Elith, J., J.R. Leathwick, and T. Hastie. 2008. "A Working Guide to Boosted Regression Trees." *Journal of Animal Ecology* 77(4): 802–13.
- Fallon, B., A. Yang, C. Lapadat, I. Armour, J. Juzwik, R.A. Montgomery, and J. Cavender-Bares. 2020. "Spectral Differentiation of Oak Wilt from Foliar Fungal Disease and Drought is Correlated with Physiological Changes." *Tree Physiology* 40(3): 377–90.
- Fawcett, T. 2006. "An Introduction to ROC Analysis." *Pattern Recognition Letters* 27(8): 861–74.
- Feilhauer, H., G.P. Asner, R.E. Martin, and S. Schmidtlein. 2010. "Brightness-Normalized Partial Least Squares Regression for Hyperspectral Data." *Journal of Quantitative Spectroscopy and Radiative Transfer* 111(12–13): 1947–57.
- Fortini, L.B., L.R. Kaiser, L.M. Keith, J. Price, R.F. Hughes, J.D. Jacobi, and J.B. Friday. 2019. "The Evolving Threat of Rapid 'Ōhi 'a Death (ROD) to Hawai'i's Native Ecosystems and Rare Plant Species." *Forest Ecology and Management* 448: 376–85.

- Friday, J.B., and D.A. Herbert. 2006. "Metrosideros polymorpha ('ōhi'a lehua)." In *Species Profiles for Pacific Island Agroforestry*, edited by C.R. Elevitch, 1–27. Hōlualoa, Hawai'i: Permanent Agriculture Resources (PAR). <http://www.traditionaltree.org>.
- Friedman, J.H. 2001. "Greedy Function Approximation: A Gradient Boosting Machine." *Annals of Statistics* 29(5): 1189–232.
- Gao, B., and A.F.H. Goetz. 1990. "Column Atmospheric Water Vapor and Vegetation Liquid Water Retrievals from Airborne Imaging Spectrometer Data." *Journal of Geophysical Research: Atmospheres* 95(D4): 3549–64.
- Giambelluca, T.W., Q. Chen, A.G. Frazier, J.P. Price, Y.-L. Chen, P.-S. Chu, J.K. Eischeid, and D.M. Delparte. 2013. "Online Rainfall Atlas of Hawai'i." *Bulletin of the American Meteorological Society* 94(3): 313–6.
- Heim, R.H.J., I.J. Wright, A.P. Allen, I. Geedicke, and J. Oldeland. 2019. "Developing a Spectral Disease Index for Myrtle Rust (*Austropuccinia psidii*)." *Plant Pathology* 68(4): 738–45.
- Hughes, M.A., J. Juzwik, T.C. Harrington, and L.M. Keith. 2020. "Pathogenicity, Symptom Development, and Colonization of *Metrosideros polymorpha* by *Ceratocystis lukuohia*." *Plant Disease* 104(8): 2233–41.
- Jacobi, J.D. 1983. "Metrosideros Dieback in Hawai'i: A Comparison of Adjacent Dieback and Non-dieback Rain Forest Stands." *New Zealand Journal of Ecology* 6: 79–97.
- Keith, L.M., R.F. Hughes, L.S. Sugiyama, W.P. Heller, B.C. Bushe, and J.B. Friday. 2015. "First Report of *Ceratocystis* Wilt on 'Ōhi'a (*Metrosideros polymorpha*)." *Plant Disease* 99(9): 1276.
- Kitayama, K., R. Pattison, S. Cordell, D. Webb, and D. Mueller-Dombois. 1997. "Ecological and Genetic Implications of Foliar Polymorphism in *Metrosideros polymorpha* Gaud. (Myrtaceae) in a Habitat Matrix on Mauna Loa, Hawai'i." *Annals of Botany* 80(4): 491–7.
- Klein, T., G. Hoch, D. Yakir, and C. Körner. 2014. "Drought Stress, Growth and Nonstructural Carbohydrate Dynamics of Pine Trees in a Semi-Arid Forest." *Tree Physiology* 34(9): 981–92.
- Kokaly, R.F., G.P. Asner, S.V. Ollinger, M.E. Martin, and C.A. Wessman. 2009. "Characterizing Canopy Biochemistry from Imaging Spectroscopy and its Application to Ecosystem Studies." *Remote Sensing of Environment* 113: S78–91.
- Loope, L., F. Hughes, L. Keith, T. Harrington, R. Hauff, J.B. Friday, C. Ewing, G. Bennett, P. Cannon, and C. Atkinson. 2016. *Guidance Document for Rapid Ohia Death: Background for the 2017–2019 ROD Strategic Response Plan*. Honolulu, HI: University of Hawaii: College of Tropical Agriculture and Human Resources.
- López-López, M., R. Calderón, V. González-Dugo, P.J. Zarco-Tejada, and E. Fereres. 2016. "Early Detection and Quantification of Almond Red Leaf Blotch Using High-Resolution Hyperspectral and Thermal Imagery." *Remote Sensing* 8(4): 276.
- Martin, R.E., G.P. Asner, E. Francis, A. Ambrose, W. Baxter, A.J. Das, N.R. Vaughn, T. Paz-Kagan, T. Dawson, and K. Nydick. 2018. "Remote Measurement of Canopy Water Content in Giant Sequoias (*Sequoiadendron giganteum*) During Drought." *Forest Ecology and Management* 419: 279–90.
- Martin, R.E., K. Chadwick, P.G. Brodrick, L. Carranza-Jimenez, N. R. Vaughn, and G.P. Asner. 2018. "An Approach for Foliar Trait Retrieval from Airborne Imaging Spectroscopy of Tropical Forests." *Remote Sensing* 10(2): 199.
- Martin, Roberta E., Erin Weingarten, R. Flint Hughes, Nicholas R. Vaughn, Ethan Shafron, Gregory P. Asner. 2021. "Data_Weingarten_et al_2021." Figshare, data set. <https://doi.org/10.6084/m9.figshare.15019443.v1>
- Mason, L., J. Baxter, P.L. Bartlett, and M.R. Frea. 1999. "Boosting Algorithms as Gradient Descent." *Advances in Neural Information Processing Systems* 12: 512–8.
- McDowell, N., W.T. Pockman, C.D. Allen, D.D. Breshears, N. Cobb, T. Kolb, J. Plaut, J. Sperry, A. West, and D.G. Williams. 2008. "Mechanisms of Plant Survival and Mortality During Drought: Why Do some Plants Survive while Others Succumb to Drought?" *New Phytologist* 178(4): 719–39.
- Morrison, K.R., and E.A. Stacy. 2014. "Intraspecific Divergence and Evolution of a Life-History Trade-off along a Successional Gradient in Hawaii's *Metrosideros polymorpha*." *Journal of Evolutionary Biology* 27(6): 1192–204.
- Mortenson, L.A., R. Flint Hughes, J.B. Friday, L.M. Keith, J. M. Barbosa, N.J. Friday, Z. Liu, and T.G. Sowards. 2016. "Assessing Spatial Distribution, Stand Impacts and Rate of *Ceratocystis fimbriata* Induced 'ōhi'a (*Metrosideros polymorpha*) Mortality in a Tropical Wet Forest, Hawai'i Island, USA." *Forest Ecology and Management* 377: 83–92.
- Mueller-Dombois, D. 1980. "The 'ōhi'a Dieback Phenomenon in the Hawaiian Rain Forest." In *The Recovery Process in Damaged Ecosystems*, edited by J. Cairns, Jr., 153–61. Ann Arbor, MI: Ann Arbor Science Publishers.
- Mueller-Dombois, D., and F.R. Fosberg. 1998. "Northern Polynesia: The Hawaiian Archipelago." In *Vegetation of the Tropical Pacific Islands*, edited by D. Mueller-Dombois and F.R. Fosberg, 461–77. New York, NY: Springer.
- Mueller-Dombois, D., J.D. Jacobi, H.J. Boehmer, and J.P. Price. 2013. *'Ōhi'a Lehua Rainforest: Born among Hawaiian Volcanoes, Evolved in Isolation: The Story of a Dynamic Ecosystem with Relevance to Forests Worldwide*. Honolulu, HI: Friends of the Joseph Rock Herbarium.
- Ollinger, S.V. 2011. "Sources of Variability in Canopy Reflectance and the Convergent Properties of Plants." *New Phytologist* 189(2): 375–94.
- Pavlov, Y. L. 2019. "Random Forests." *Random Forests*, 1–122.
- Perroy, R.L., M. Hughes, L.M. Keith, E. Collier, T. Sullivan, and G. Low. 2020. "Examining the Utility of Visible Near-Infrared and Optical Remote Sensing for the Early Detection of Rapid 'Ōhi'a Death." *Remote Sensing* 12(11): 1846.
- Pratt, L. W., and J. D. Jacobi. 2009. "Loss, Degradation, and Persistence of Habitats." In *Conservation Biology of Hawaiian Forest Birds, Implications for Island Avifauna*, edited by T. K. Pratt, C.T. Atkinson, P.C. Banko, B.L. Woodworth, and J.D. Jacobi, 137–58. New Haven, CT: Yale University Press.
- QGIS Development Team. 2018. *QGIS Geographic Information System*. Open Source. Gossau: Geospatial Foundation Project.
- R Core Team. 2013. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. <http://www.R-project.org/>
- Sakishima, T. 2015. *Local Adaptation of the Hawaiian Endemic Tree (Metrosideros polymorpha) across a Long Elevation Gradient*. Hilo, HI: University of Hawai'i.
- Sherrod, B. D. R., J. M. Sinton, S. E. Watkins, K. M. Brunt, and U.S. Geological Survey. 2007. "Geologic Map of the State of Hawai'i." USGS Open File Report, 2007–1089.

- Somers, B., and G.P. Asner. 2013. "Mapping Tropical Rainforest Canopies Using Multi-Temporal Spaceborne Imaging Spectroscopy." In *Proceedings. SPIE 8887, Remote Sensing for Agriculture, Ecosystems, and Hydrology XV* 888704.
- Somers, B., M. Zortea, A. Plaza, and G.P. Asner. 2012. "Automated Extraction of Image-Based Endmember Bundles for Improved Spectral Unmixing." *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing* 5(2): 396–408.
- Stemmermann, L. 1983. "Ecological Studies of Hawai'ian *Metrosideros* in a Successional Context." *Pacific Science* 37: 361–73.
- Treseder, K.K., and P.M. Vitousek. 2001. "Potential Ecosystem-Level Effects of Genetic Variation among Populations of *Metrosideros polymorpha* from a Soil Fertility Gradient in Hawai'i." *Oecologia* 126(2): 266–75.
- Varoquaux, G., L. Buitinck, G. Louppe, O. Grisel, F. Pedregosa, and A. Mueller. 2015. "Scikit-Learn." *GetMobile: Mobile Computing and Communications* 19(1): 29–33.
- Vaughn, N.R., G.P. Asner, P.G. Brodrick, R.E. Martin, J.W. Heckler, D.E. Knapp, and R.F. Hughes. 2018. "An Approach for High-Resolution Mapping of Hawaiian *Metrosideros* Forest Mortality Using Laser-Guided Imaging Spectroscopy." *Remote Sensing* 10(4): 1–17.
- Vitousek, P.M., G. Aplet, D. Turner, and J.J. Lockwood. 1992. "The Mauna Loa Environmental Matrix: Foliar and Soil Nutrients." *Oecologia* 89(3): 372–82.
- Yadeta, K., and B. Thomma. 2013. "The Xylem as Battleground for Plant Hosts and Vascular Wilt Pathogens." *Frontiers in Plant Science* 4: 97.
- Zarco-Tejada, P.J., C. Camino, P.S.A. Beck, R. Calderon, A. Hornero, R. Hernández-Clemente, T. Kattenborn, et al. 2018. "Previsual Symptoms of *Xylella fastidiosa* Infection Revealed in Spectral Plant-Trait Alterations." *Nature Plants* 4(7): 432–9.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Weingarten, Erin, Roberta E. Martin, Richard Flint Hughes, Nicholas R. Vaughn, Ethan Shafron, and Gregory P. Asner. 2022. "Early Detection of a Tree Pathogen Using Airborne Remote Sensing." *Ecological Applications* e2519. <https://doi.org/10.1002/eap.2519>