Check for updates

esa ECOSPHERE

Application of lidar for critical endangered bird species conservation on the island of Kauai, Hawaii

Geoffrey A. Fricker,[1,2,3,†] Lisa H. Crampton,[4] Erica M. Gallerani,[4] Justin M. Hite,[4] Richard Inman,[3] and Thomas W. Gillespie[2]

[1]*Social Sciences Department, California Polytechnic University, San Luis Obispo, Building 47-13, San Luis Obispo, California 93407 USA*
[2]*Department of Geography, University of California Los Angeles, 1255 Bunche Hall,Box 951524, Los Angeles, California 90095 USA*
[3]*School of Geographical Sciences and Urban Planning, Arizona State University, PO Box 875302, Tempe, Arizona 85287 USA*
[4]*Kaua'i Forest Bird Recovery Project, Pacific Cooperative Studies Unit, PO Box 27, Hanapepe, Hawaii 96716 USA*

Citation: Fricker, G. A., L. H. Crampton, E. M. Gallerani, J. M. Hite, R. Inman, and T. W. Gillespie. 2021. Application of lidar for critical endangered bird species conservation on the island of Kauai, Hawaii. Ecosphere 12(6):e03554. 10.1002/ecs2.3554

Abstract. The Akikiki (*Oreomystis bairdi*) and Akekee (*Loxops caeruleirostris*) are two honeycreepers endemic to Kauai, Hawaii, that were listed as federally endangered in 2010. Both species are rare, little-studied, and occur in a remote, roadless area. We analyzed high-resolution airborne lidar data to identify forest structure and topography metrics associated with Akikiki and Akekee nest locations (88 for Akikiki and 22 for Akekee) and occurrences (3706 for Akikiki and 1581 for Akekee) from 2012 to 2017 on the Alakai Plateau to predict their distribution in unsurveyed areas. Akikiki and Akekee nested in areas with similar forest structure at 10 m resolution, but different maximum tree heights. Akikiki and Akekee foraged in areas with significantly different forest structure (maximum tree height, mean canopy height, relative heights) and topography (slope) based on occurrences. Elevation was consistently one of the most important metrics for predicting both species nest locations and occurrences across scales (10, 100, 250 m) and it appears that both species are at the upper limits of their elevational range. We estimate that the area of suitable nesting habitat for Akikiki is 17.59 km^2 while the area of suitable nesting habitat for Akekee is 11.10 km^2 at 10 m resolution. The Akikiki has a potential range of 38 km^2 while the Akekee has a range of 58 km^2 at 100 m resolution. We produce predictive nest and occurrence maps at 10 m and 100 m resolutions to spatially target conservation actions. Results suggest that if avian malaria cannot be controlled and both species populations do not stabilize over the coming years, translocation may be needed to insure their viability.

Key words: Akekee; Akikiki; discrete return airborne lidar; habitat associations; habitat suitability modeling; topography; vegetation structure.

Received 3 December 2020; accepted 16 December 2020; final version received 5 April 2021. Corresponding Editor: Debra P. C. Peters.

Copyright: © 2021 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail** africker@calpoly.edu

Introduction

Once a hotbed of avian biodiversity, Hawaii is now a global extinction epicenter. Sixty-eight percent of Hawaii's 109 endemic birds known from historic and subfossil records have already gone extinct (Reed et al. 2012). The situation on Kauai, the oldest of the main Hawaiian Islands, is particularly dire with five of Kauai's 13 historically known forest birds disappearing in the last 40 yrs (Reed et al. 2012, Paxton et al. 2018). Nonetheless, the island supports extremely high densities of endemic flora and fauna, including more single-island endemic passerine birds than

any other Hawaiian island (Paxton et al. 2016). Taking action to prevent additional extinctions is absolutely imperative.

Akikiki (*Oreomystis bairdi*) and Akekee (*Loxops caeruleirostris*) are two honeycreepers endemic to Kauai and listed as federally endangered in 2010. Akikiki and Akekee have declined dramatically to population sizes estimated at 468 (95% Confidence Interval [CI] 231–916) and 945 (95% CI 460–1547) individuals, respectively (Paxton et al. 2016). Akikiki's range contracted from 88 km^2 in 1973 to less than 25 km^2 in 2012, during which time their population decreased by 71% (Paxton et al. 2016). Akekee's range contracted from 127 km^2 to less than 50 km^2 over the previous decade, during which their population decreased by 98% (Paxton et al. 2016). Threats to these native species are many, but a leading cause of their decline is avian malaria carried by the invasive southern house mosquito (*Culex quinquefasciatus*). If these population trajectories continue, both species could go extinct within the next decade. Indeed, these population estimates make Akikiki one of the most endangered U.S. passerine species remaining in the wild and a top priority for the United States Fish and Wildlife Service (USFWS 2015).

Historically, Akikiki foraged on trunks, branches, and twigs of live and dead trees in sub-canopy shrubs and trees, such as koa (*Acacia koa*); however, their current range does not include koa forests (Foster et al. 2004, Paxton et al. 2016) as they have retreated to the refugia of the higher elevation ohia (*Metrosideros polymorpha*) forests. Large ohia (*M. polymorpha*) trees are especially important to Akikiki because they build nests just beneath the forest canopy near the trunk or on terminal branches (Foster et al. 2004, VanderWerf and Roberts 2008), often at heights near 9.2 m above the ground (Hammond et al. 2015). Adequate canopy structure is therefore critical to Akikiki survival and influences their current distribution. Previous work has shown that Akikiki occur in greater numbers in areas with tall and dense tree canopies (Behnke et al. 2016) and that their occupancy and density varied across their range: northwestern portions exhibited the lowest occupancy and densities while southeastern areas had higher occupancy and densities (Behnke et al. 2016, Paxton et al. 2016). This gradient corresponds positively with changes in elevation, precipitation, and vegetation metrics, including native shrub cover and canopy height (Behnke et al. 2016).

Akekee use their crossbills to pry open terminal ohia leaf buds to feed on invertebrate prey such as spiders, psyllids, and caterpillars (Lepson and Pratt 1997). They are canopy specialists whose occupancy has been positively correlated with mean canopy height and with maximum diameter at breast height of ohia trees (Behnke et al. 2016). Range contraction and occupancy follow the same geographic trend as Akikiki, although less pronounced; Akekee can still be found in the northwestern part of the plateau (Behnke et al. 2016, Paxton et al. 2016). Akekee are the highest arboreal-nesting bird in Kauai, nesting in the small branches in the canopy of ohia trees with nest heights near 11.1 m (Hammond et al. 2015).

Many aspects of these species' natural histories, distributions, and nest locations appear associated with topography (e.g., elevation and slope) and the three-dimensional structure of forests (e.g., canopy height and density, presence of large trees, and native shrub cover). However, their distributions span rugged, remote, and roadless terrain with high cloud cover, which has hampered assessments of their distribution, abundance, and habitat use. The need for remotely sensed observations of topography and forest structure to improve our understanding of their biology and to prioritize conservation efforts is clear.

High-resolution small footprint lidar is one such source of remote sensing capable of characterizing topography and forest structure (Garabedian et al. 2017, Bakx et al. 2019). Lidar, or light detection and ranging, is a form of remote sensing which uses laser light to measure variable distances to the Earth's surface and has many applications in forestry (Dubayah and Drake 2000). Small footprint (or discrete return) lidar may be ideal for quantifying attributes such as canopy height, understory structural variations, and topographical metrics in tropical forests (Fricker et al. 2015). Prior research has found that lidar observations closely matched field-collected vertical canopy profiles and leaf area index estimates in tropical forests (Tang et al. 2012). Moreover, metrics derived from lidar such as the vertical distribution of biomass, canopy

height, and canopy density have been used to predict avian richness, though these and other studies are often focused on North American and European temperate forests (Bakx et al. 2019). The use of lidar to quantify canopy structure in forest types such as ohia dominant, high elevation wet tropical forests has been minimal, at best (Bakx et al. 2019).

Over the past two decades, predictive habitat models, often in the form of species distribution modeling, have rapidly progressed to become an informative tool for identifying key areas for habitat conservation and management of imperiled species (Guisan and Zimmermann 2000, Franklin 2013). These predictive models of habitat are statistical models that relate the environmental conditions at locations where a species has been observed to locations where it has not been observed in order to predict habitat potential (often referred to as habitat suitability) at unobserved locations (Guisan and Zimmermann 2000). Unfortunately, locations where a species has not been observed are not always known or readily available, and true absence can be difficult to ascertain (MacKenzie et al. 2002, Elith and Leathwick 2009). This conundrum has contributed to the development of many so-called presence–background (PB) modeling methods that compare environmental conditions at locations where a species has been observed to environmental conditions characterizing the entire study area (background). These methods do not rely on locations where species are absent and have propelled software for PB data (e.g., Maxent; Phillips et al. 2006) to become primary tools for ecological research in recent years (Guillera-Arroita et al. 2015).

Identifying habitat suitability for Akikiki and Akekee on maps is essential to the prioritization of management actions. If a new area of highly suitable nesting habitat is identified then rat control, habitat restoration, fencing, mosquito abatement, and other conservation measures can be undertaken to protect that area. This information could also identify areas where future reintroductions or translocations can be undertaken to boost population sizes. Separately, this information can be used to refine population estimates, which are currently based only on a fraction of the area to which the surveys are extrapolated.

The objective of this study is to determine whether newly acquired high-resolution lidar data could elucidate changes in forest structure and topography relevant to the habitat suitability of these two endangered birds, as previous studies found that vegetation structure often becomes especially pertinent at small spatial scales (Bakx et al. 2019). Specifically, we sought to analyze lidar imagery to identify forest structure and topographic metrics associated with Akikiki and Akekee nest locations and occurrences and model their distributions. First, we hypothesized that nest locations and occurrences were associated with different canopy structure and topography metrics at three different scales to capture micro-habitat, habitat patches, and regional climate. Second, we model the distributions of both species and identify lidar metrics that are associated with their nest locations and occurrences. We hypothesize that elevation, canopy height, and canopy density best predict species' nest sites and occurrence (per Behnke et al. 2016). Third, we use the model outputs to predict the spatial distributions of both birds to unsurveyed areas on the Alakai Plateau and estimate the range of suitable nest and occurrence habitat. Combined with predictive habitat models, lidar observations may offer a useful method to quantify habitat for honeycreepers and other canopy dwelling species and allow managers to spatially target conservation measures.

Methods

Study area

The Alakai Plateau is located adjacent to the two highest peaks on the island of Kauai, Mount Waialeale, and Mount Kawaikini, which are near the center of the island and reach heights of 1569 and 1598 m above sea level, respectively (Scott et al. 1986, Foster et al. 2004). The Alakai Plateau receives approximately 11 m of annual precipitation each year, making it one of the wettest places on earth (Giambelluca et al. 2013). The high annual rainfall has eroded deep valleys with steep slopes around the relatively old (5.2 million years) Alakai Plateau. The Alakai Plateau is largely protected by the Alakai Wilderness Preserve managed by the Hawaii Division of Forestry and Wildlife (DOFAW); the remainder is in Forest Reserves also managed by DOFAW. It contains relatively homogeneous forests that do not have

statistically significant differences in maximum ohia diameter and canopy density; however, there are changes in forest profile, total shrub coverage, native shrub cover, mean canopy height, moss cover, total ground cover, and pig signs (Behnke et al. 2016). Hurricane Iniki hit Kauai in September 1992 and had a significant impact on forest structure below 1100 m (Harrington et al. 1997). Iniki was most powerful hurricane to hit the State of Hawaii; wind damage significantly impacted forest canopies on the islands and the resultant forest gaps provided ideal habitats for invasive non-native species such as Himalayan Ginger (*Hedychium gardnerianum*) to colonize these forests (Harrington et al. 1997).

Species nest and occurrence data

We used nest locations for Akikiki and Akekee collected from two primary study sites, Mohihi and Halepaakai, and one secondary site, Kawaikoi, from 2012 to 2017. Both Mohihi and Halepaakai are located on the Eastern side of the Alakai Plateau in well-known forest bird habitat and at high elevations (~1290 m and ~1300 m, respectively). From March to June, nests of both species were located by following adults exhibiting signs of breeding and nesting behavior (e.g., courtship feeding, copulation, food or nest material carries, aggression or defensiveness toward nest searchers, and cries of chicks, as described by Martin et al. 2016), for a total of 5116 person hours spent nest searching from 2012 to 2017. Upon finding nests, biologists in the field would record locations with a handheld Garmin Rino GPS. Nests, nest trees, and any information useful to determining nest stage were described. Nests of known pairs were monitored from at least 15 m away for at least 10 min every 2–5 d to determine reproductive activity, including incubation and chick-feeding behavior. Only active nests (i.e., in which eggs were laid) were included in analyses. During the same years, occurrence locations were recorded on a handheld GPS unit as close as possible to the locations of the birds themselves as individuals of these species were encountered during opportunistic encounters, nest searches, occupancy surveys, and variable circular plot (VCP) surveys during Hawaii Forest Bird Survey of 2012. Data associated with these locations (e.g., species, number of individuals, behavior exhibited, and type of observation) were recorded and later entered into a PostgreSQL database with a PostGIS connection to ArcGIS Desktop v10.4 (Fig. 1). While nests were associated with accurate geospatial data, occurrences were not always recorded at the exact location of an individual bird and are therefore less accurate.

In 2018, systematic bird surveys were undertaken across the Alakai Plateau along predetermined transects as part of the Hawaiian Forest Bird Survey (Foster et al. 2004, Paxton et al. 2016), and nest and area searching occurred as in previous years at the two primary field sites. Additionally, six Akekee nests and three Akikiki nests were discovered at a new site called Upper Upper Kawakoi (UUK). This site is on the eastern plateau but lies at a slightly lower elevation (~1250 m) than our two main sites. Field crew members spent a collective ~660 h at this new site during the nesting season of 2018, conducting area searches, following birds exhibiting breeding and nesting behavior and collecting GPS data for both occurrences and nests; however, no occupancy or VCP surveys were conducted at this site. Observations and nest locations from 2018 were withheld from predictive habitat modeling calibration and used to assess model accuracy. While precise location data for these endangered species cannot be shared publicly, data can be requested via the Kauai Forest Bird Recovery Project.

Multiscale approach

Ecologists widely recognize that the observed patterns of species traits cannot be explained at a single spatial scale and that patterns observed in communities at a one scale are often the result of interplay between various processes occurring at multiple scales (Menge and Olson 1990). Therefore, multiscale approaches to analyzing habitat relationships have gained traction in landscape ecology (Wiens 1989, McGarigal et al. 2016) and can be a useful approach for matching the scale of ecological processes with the patterns observed on a landscape.

We explored habitat associations for Akikiki and Akekee at three spatial scales using a multiscale framework with two separate approaches to identify differences between the two species in (1) preferred habitat characteristics and (2) spatial patterns of nest and sighting locations. In both approaches, we develop forest structure and sub-

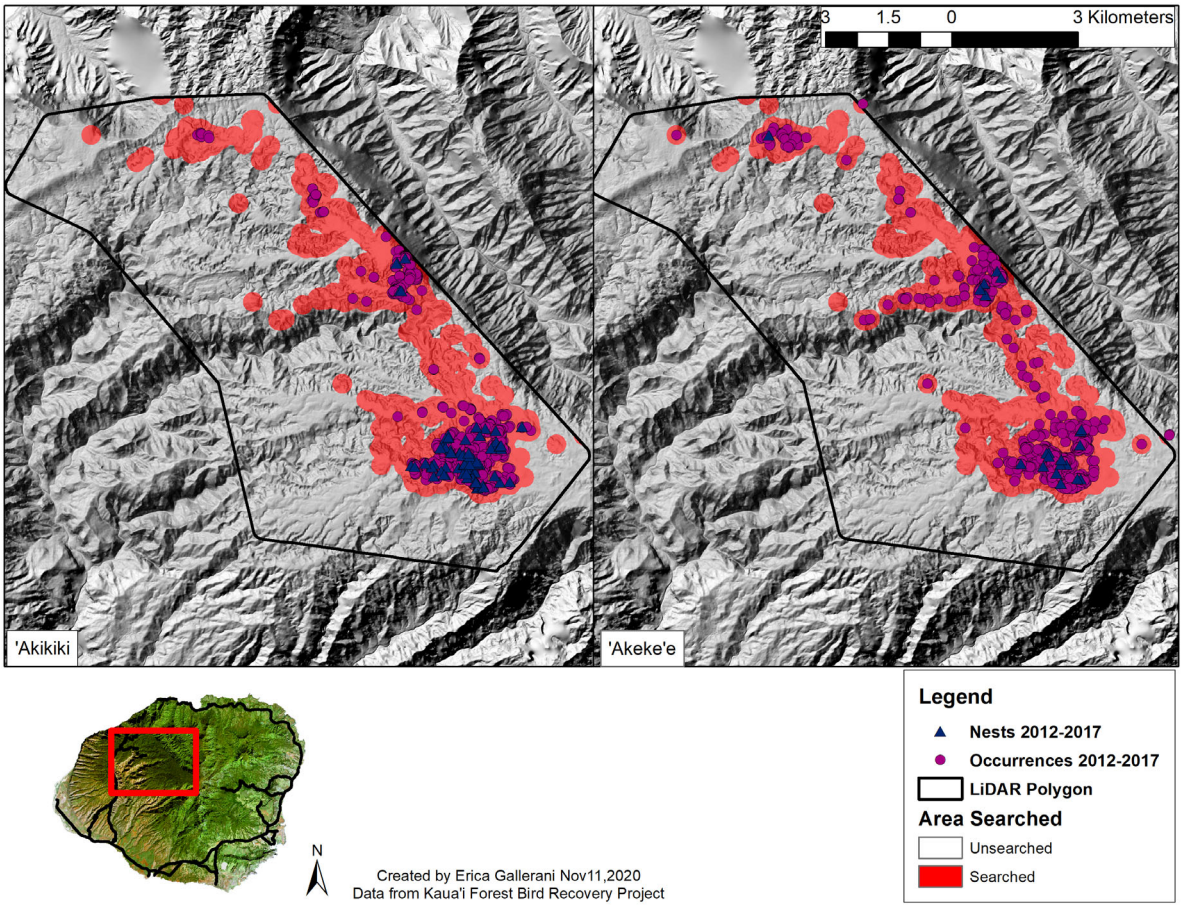

Fig. 1. Akikiki and Akekee nests and occurrences from 2012 through 2017 overlaid with the lidar footprint and a rough estimate of area searched vs. unsearched.

canopy topography metrics derived from lidar sampling to characterize habitat at 10 m (micro-habitat), 100 m (habitat patches), and 250 m (meso-habitat) scales. In the first approach, we characterize proximal habitat for each nesting site and each observation sighting at the three scales in order to compare differences between the two species. In the second approach, we develop habitat suitability models for both nesting sites and observations at each scale to explore differences in predicted habitat suitability between the two species across the Alakai Plateau.

Lidar metrics

We developed lidar metrics of forest structure and sub-canopy topography that were hypothesized to be important to species nest locations and distributions on the Alakai Plateau (Table 1). Lidar data were collected for a 69.5 km^2 area including the current range of both species over the Alakai Plateau from March 12 to March 14, 2017, using an ALIS-560 system mounted on a Robinson R44 helicopter. The ALIS-560 utilizes a full waveform Riegel scanner and provides an unlimited number of returns per pulse, and the average point density of the acquisition was greater than 30 points per square meter. We used Terrasolid software inside Bentley's Microstation platform to process the lidar data into a bare-earth digital terrain model (bare-earth DTM) and first-return digital surface model. Lidar metrics for forest structure and sub-canopy topography were then computed from the canopy surface model (CSM), the digital terrain model (DTM), and the difference between the two: the canopy height model (CHM), which characterizes the

Table 1. Lidar-derived forest structure and topography metrics at 10 m resolution (n = 753,666 pixels) from March 2017 over the Alakai Plateau, Kauai.

Lidar-derived metric	Value at 10 m
Forest structure	
Maximum canopy height (m)	65.0
Mean canopy height (m)	8.4
SD canopy height (m)	2.2
Mean canopy density (%)	76.1
SD canopy density (%)	17.1
Relative height (25, 50, 75, 90)	
Mean rh25 (m)	5.0
Mean rh50 (m)	6.3
Mean rh75 (m)	7.2
Mean rh90 (m)	7.7
Topography	
Maximum elevation (m)	1416.1
Mean elevation (m)	1178.8
Maximum slope (degrees)	89.4
Mean slope (degrees)	26.1
SD slope (degrees)	7.9
Mean TWI	2.5

Note: Abbreviations are SD, standard deviation; rh, relative height; TWI, topographic wetness index.

height of vegetation without the effect of topography (Fig. 2).

We developed nine metrics of forest structure and topography from lidar at 1 m spatial resolution across the Alakai Plateau; elevation, slope, topographic wetness index, canopy height, canopy density, and four relative height metrics. Each metric was summarized to characterize the environment immediately surrounding each nest and occurrence sighting to explore how each species differed with respect to forest structure, topography, and sub-canopy characteristics (Approach 1). All metrics were projected into Universal Transverse Mercator (UTM) Zone 4 North for subsequent spatial analyses.

Three metrics of canopy height (maximum canopy height, mean canopy height, and SD canopy height; Table 1) were calculated as the maximum, mean, and standard deviation of all 1 m^2 pixels of the CHM within a search window of 10×10 m (100 m^2; micro-habitat), 100×100 m (10,000 m^2; habitat patches), or 250×250 m (62,500 m^2; meso-habitat) centered around nesting sites and occurrences for each of the three spatial scales, respectively. We also developed metrics of relative height using a classified lidar point cloud computed with LAS tools (https://rapidlasso.com/lastools/) within ArcGIS Desktop 10.1. Lidar points classified as top of canopy were used to calculate the 25th, 50th, 75th, and 90th percentiles within each search window of their height above the ground (Drake et al. 2002, Dubayah et al. 2010, 2020). We use the 25th percentile value (rh25) to represent the height of understory vegetation. In these ecosystems, invasive understory plants, such as Himalayan Ginger (*Hedychium gardnerianum*), result in greater rh25 values than the native understory vegetation (Asner et al. 2008). The 75th percentile value (rh75) was used to represent the majority of overstory vegetation, while the 90th percentile value (rh90) is representative of forest biomass, similar to Lorey's Height, and is less sensitive to spurious outliers than maximum tree height (Yang et al. 2018).

Two metrics of canopy density (mean canopy density and SD canopy density; Table 1) were also calculated from the classified lidar point cloud of lidar points within each search window around nesting sites and bird occurrences. Mean canopy density was calculated by taking all points in the search area and using the ratio of all points divided by the number of all returns above a minimum height threshold (diameter at breast height = 1.37 m). If there is dense vegetation, the laser pulses will penetrate the canopy and create more returns compared to the number of points, whereas in areas with little or no vegetation, the number of points will be closer to the number of returns as each point will strike only one surface (the ground).

Six metrics of sub-canopy topography (maximum elevation, mean elevation, maximum slope, mean slope, SD slope, and TWI; Table 1, Appendix S1) were calculated using the bare-earth DTM ground model within each search window around nesting sites and bird sightings. Slope metrics are reported in degrees. Topographic Wetness Index (TWI) was used to quantify the amount of upslope contributing area draining through a specific DTM pixel weighted by the tangent of the slope (in radians; Fricker et al. 2015). A script to compute the TWI in ArcGIS can be found here: https://github.com/africker/Topographic-Wetness-Index.

Statistical analyses

All field and lidar variables were examined for a normal distribution with a one-sample Kolmogorov-Smirnov test. Some lidar metrics,

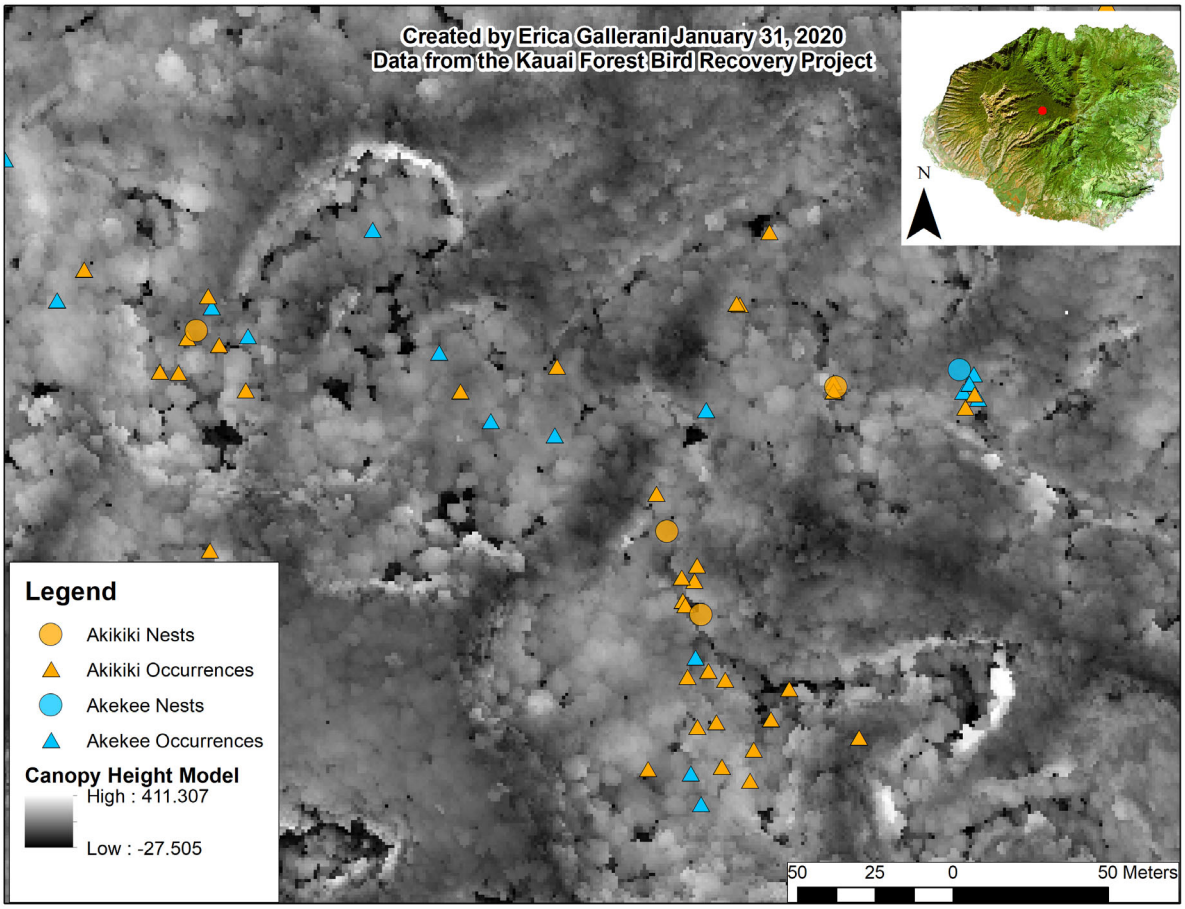

Fig. 2. Example of Akikiki and Akekee nest locations and occurrence data from 2012 to 2017, superimposed on 1 m lidar imagery.

specifically elevation, did not follow a normal distribution; thus, non-parametric tests were used for comparisons between lidar-derived forest structure and topography metrics for Akikiki and Akekee nest locations and occurrences. Intercorrelation of lidar-derived forest structure and topography metrics at 10, 100, and 250 m were examined using a spearman rank correlation (Appendix S2). Relative height metrics were highly correlated at 10 m with correlations declining at larger spatial resolution (100, 250 m). Studies quantifying the effects of collinearity as a source of uncertainty in MaxEnt model training found that the exclusion of highly correlated variables has little impact on model performance or predictions (Watling et al. 2015, Feng et al. 2019).

The variable diameter buffer around each nest and occurrence point was used as a location window to characterize the species' nest site preference and habitat (Approach 1). Mann-Whitney *U*-tests with Bonferroni-corrected *P* values were used to identify if there were significant differences in forest structure and topography between nests and occurrences of the Akikiki and Akekee at $\alpha = 0.05$ level of significance. This test identifies if there is evidence of distinct niches for nest tree locations and foraging areas between species or if there are overlaps in nest niche and habitat niche (Weisberg et al. 2014). We report mean and standard deviations of lidar-derived metrics for nests and occurrences for Akikiki and Akekee.

Predictive habitat modeling

MaxEnt version 3.3.4 k (Phillips et al. 2006) was used to create predictive habitat models for

the occurrence and nest locations from 2012 to 2017 for Akikiki and Akekee at 10-, 100-, and 250 m spatial resolutions (Approach 2). Feature types were limited to linear, product, or quadratic features to reduce model complexity as recommended for presence-only modeling (Hagar et al. 2020), and default options for background sampling were used. The nine metrics derived from 1 m lidar were used as environmental layer inputs for each model (canopy height, canopy density, elevation, slope, topographic wetness index, and four relative height metrics). Elevation is particularly relevant to the distribution of these species (Paxton et al. 2016) and a review of 50 avian species distribution models found that metrics related to canopy height and cover tend to effectively explain species distributions (Bakx et al. 2019). The nine metrics were resampled to 10 m, 100 m, and 250 m pixel sizes and run through the PrepareDataforMaxent tool for ArcGIS 10.1 (Dilts 2015).

To reduce effects of biased sampling caused by aggregated observations, we implement background weight correction with the FactorBiasOut algorithm (Dudík et al. 2005) and used bias grids created with the Kernel Density tool in ArcGIS for all nest and occurrence point datasets for both species at all three spatial scales. The bandwidth for each kernel was estimated using cross-validation to minimize mean-square error (Baddeley et al. 2015). The resulting kernel density rasters were linearly rescaled to one to 20, to give greater selection probability to areas with higher densities of observations (Elith et al. 2011). The rescaled kernel density rasters were then run through the same PrepareDataforMaxent10.0 tool for ArcGIS. This method relies on the knowledge of the biased sampling distribution, which in practice, is rarely known. However, because the biased observation dataset is a sample of the biased sampling distribution (i.e., the observations are sampled with the biased sampling distribution), it can be estimated when the observation dataset is large (Phillips et al. 2009).

Model accuracy and uncertainty were assessed with 100 replicates using the bootstrap resampling mode in MaxEnt. We report the mean area under the receiver operating characteristic curve score (AUC; Fielding and Bell 1997) across all replications, which for presence-only data, quantifies the probability that the model correctly ranks nest sites or observations higher than random background pixels (Radosavljevic and Anderson 2014). Mode uncertainty is reported as the standard deviation of habitat suitability values across all replications for any given cell, and we provide each of the parameters used for modeling (Appendix S3). We also report the contribution of each metric to the nest and occurrence model for Akikiki and Akekee using a jackknife test of variable contribution (Appendix S4). These tests of variable contribution indicate the relative importance of each variable by assessing the training gain of a model run with only a single variable compared to the training gain with all variables (Abolmaali et al. 2018). We estimate the range of both species for nest sites and occurrences by thresholding maps of predicted habitat suitability into presence and absence categories. Binary maps of presence and absence were created using a minimum training presence threshold (MTP; i.e., the minimum MaxEnt value at which each species' nests occurred). This threshold was applied because the species' locations are precise and accurate. Use of the MTP threshold results in areas identified to be at least as suitable as the species' present locations (Pearson et al. 2007). Finally, we assessed the accuracy of all models across each of the spatial scales using independent observations obtained in 2018. We mapped the 2018 nest and occurrences locations for both species over the model results and extracted the predicted probability of presence (mean, median, maximum, and minimum) for these locations at all three scales.

Results

Comparing nests and occurrences between species

We used 88 known nest locations for Akikiki and 22 nests for Akekee collected from 2012 to 2017. Akikiki nested in two tree species (*M. polymorpha*: 86 nests, *Cheirodendron* sp.: two nests), while Akekee nested only in *M. polymorpha*. The Mann-Whitney tests showed that at the 10 m spatial resolution, Akikiki preferred taller trees and canopies for nesting than Akekee, while Akekee preferred denser canopies with less heterogeneity in canopy density for nesting than Akikiki (Table 2). The topography metrics for both species' nest sites were similar except for maximum

Table 2. Akikiki (n = 83) and Akekee (n = 22) nest locations (10 m buffer) from 2012 to 2017, mean and standard deviation of lidar-derived forest structure and topography metrics, and results from Mann-Whitney U-tests and Bonferroni-corrected *P-values* (*P < 0.5).

Lidar-derived metric	Akikiki	Akekee	Mann-Whitney P	Bonferroni P
Forest structure				
Maximum tree height (m)	15.1 (2.9)	13.2 (2.3)	0.007	*
Mean canopy height (m)	10.9 (2.1)	9.7 (1.5)	0.014	
SD canopy height (m)	2.3 (1.0)	1.8 (0.9)	0.065	
Canopy density (%)	81.5 (9.0)	82.9 (9.2)	0.416	
SD canopy density (%)	15.8 (6.2)	15.6 (6.0)	0.862	
Relative height (25, 50, 75, 90)				
drh25	6.9 (1.7)	6.4 (1.5)	0.211	
rh50	8.6 (1.8)	7.8 (1.5)	0.084	
rh75	9.7 (1.9)	8.7 (1.5)	0.039	
rh90	10.3 (1.9)	9.2 (1.5)	0.017	
Topography				
Elevation (m)	1303.6 (34.8)	1297.4 (49.0)	0.618	
Maximum slope (degrees)	44.8 (15.4)	37.6 (14.6)	0.049	
Mean slope (degrees)	21.6 (9.7)	18.6 (10.1)	0.214	
Mean TWI	2.9 (0.7)	2.7 (0.6)	0.504	

slope, which suggests Akikiki prefers steeper slopes for nesting than Akekee (Table 2). However, only maximum tree height differed significantly between the two species' nest locations when corrected for multiple comparisons (Bonferroni correction), with no other significant differences in forest structure or topography (Table 2). There were no significant differences between the two species' nest locations for any forest structure or topography metrics at 100 m and 250 m resolutions (Appendix S5: Tables S1, S2).

We recorded 3706 occurrences for Akikiki and 1581 occurrences for Akekee from 2012 to 2017. The Mann-Whitney tests showed that at a 10 m spatial resolution, there were significant differences in maximum tree height, mean canopy height, and relative height values and maximum and mean slope (Table 3). Akikiki occur in areas

Table 3. Akikiki (n = 3706) and Akekee (n = 1137) occurrences (10 m buffer) from 2012 to 2017, mean and SD (in parentheses) of lidar-derived forest structure and topography metrics, and results from Mann-Whitney U-tests and Bonferroni-corrected P values (*P < 0.5, **P < 0.01).

Lidar-derived metric	Akikiki	Akekee	Mann-Whitney P	Bonferroni P
Forest structure				
Maximum tree height (m)	14.2 (2.8)	13.5 (2.8)	<0.001	**
Mean canopy height (m)	10.3 (2.1)	9.8 (2.2)	<0.001	**
SD canopy height (m)	1.9 (1.1)	2.0 (1.0)	0.060	
Canopy density (%)	82.4 (9.5)	81.4 (10.6)	0.901	
SD canopy density (%)	15.0 (6.3)	15.0 (6.5)	0.313	
Relative height (25, 50, 75, 90)				
rh25	6.7 (1.9)	6.3 (2.0)	<0.001	**
rh50	8.2 (2.0)	7.8 (2.1)	<0.001	**
rh75	9.2 (2.0)	8.7 (2.2)	<0.001	**
rh90	9.7 (2.0)	9.2 (2.2)	<0.001	**
Topography				
Elevation (m)	1304.5 (38.5)	1298.7 (50.6)	0.103	
Maximum slope (degrees)	41.0 (16.4)	38.9 (16.6)	0.001	*
Mean slope (degrees)	21.1 (10.9)	19.5 (11.0)	<0.001	**
Mean TWI	2.7 (0.8)	2.7 (0.8)	0.085	

with significantly taller individual trees, greater mean canopy heights, taller understory, and steeper slopes than Akekee. Akekee occur in areas with shorter canopies and lower understories than Akikiki. There were no significant differences between species' occurrences and forest structure or topography at 100 m and 250 m resolutions when corrected for multiple comparisons (Appendix S5: Tables S3, S4).

Predictions of nest and occurrences suitability

All nest location models in MaxEnt performed well for both Akikiki and Akekee with AUC values greater than 0.923 (Appendix S6: Table S1). The 10 m nest location models had the higher AUC values for Akikiki (AUC = 0.977) and Akekee (AUC = 0.968) than the 100 m (Akikiki = 0.971, Akekee = 0.946) and 250 m models (Akikiki = 0.959, Akekee = 0.923). At the 10 m resolution, slope (26%), elevation (16%), and relative height 25 (15%) contributed the most to Akekee nest locations while elevation (38%), relative height 90 (23%), and slope (10%) contributed the most to Akikiki nest distributions (Table 4, Fig. 3). Both species preferred to nest in areas with lower slopes, but at higher elevation, and with rh 90 greater than the landscape average (Table 4). At 100 m resolution, elevation (33%), canopy height (30%), and TWI (16%) contributed the most to the nest locations models for the Akekee while elevation (66%), relative height 75 (13%), and canopy height (7%) contributed the most for Akikiki nest locations model (Fig. 4). Again at this scale, both species preferred to nest in areas of higher elevation and taller canopy. Elevation and slope contributed the most for both species' nest location models at 250 m resolution and canopy height metrics generally decreased in importance from 10 m to 250 m resolution (Fig. 5).

All occurrence models in MaxEnt also performed well for both Akikiki and Akekee (AUC values >0.857; Appendix S6: Table S1). At 10 m resolution, elevation (44%), relative height 75 (20%), and slope (12%) contributed the most to Akekee occurrence distributions, while elevation (65%), canopy height (14%), and relative height 90 (12%) contributed the most to Akikiki occurrence distributions (Table 4). The direction of the relationship of elevation, slope, canopy height, and relative height 90 against the landscape average was the same as for nests at this scale for both species (Table 4). At 100 m resolution, elevation (54%), relative height 90 (10%), and relative height 75 (10%) contributed the most to the occurrence distribution models for the Akekee while elevation (78%) and relative height 75 (9%) contributed the most for Akikiki occurrence

Table 4. Percent contribution of lidar-derived forest structure and topography metrics for Akekee and Akikiki nest locations and occurrences at 10 m, 100 m, and 250 m resolution.

Species	Scale (m)	Canopy height	Canopy density	rh25	rh 50	rh 75	rh 90	Elev.	Slope	TWI
Nests										
Akekee	10	7.7	6.5	14.5	11.7	1.5	13.6	16.3	**25.8**†	2.5
	100	30.3	3.1	3.2	0.5	3.3	2	**32.8**	9.2†	15.5
	250	0.8	28.7	2.1	0.3	0.6	0.1	**32.8**	30.6†	4
Akikiki	10	9.1	5.7	0.3	6.3	5.3	22.5	**37.9**	10.3†	2.6
	100	7	1.6	1.6	2.1	13.2	1.4	**65.5**	5.9	1.7†
	250	0.4	5.4	1.9	0.7	0.7	0.4	**71.3**	17.2†	2†
Occurrences										
Akekee	10	11.5	3.5	0.4	3.1	19.5	6.1	**44.4**	11.3†	0.1
	100	2.4	7.3	2.6	0.8	9.6	10	**53.6**	8.8†	4.9
	250	1.8	**28.7**	16.4	4.3	1.8	1.7	26.5	9.4†	9.3†
Akikiki	10	13.8	0.5	0.1	0.4	7.4	11.5	**64.6**	0.8†	0.9
	100	1.7	2.6	1.2	1.3	8.7	4.9	**77.6**	0.9†	1.3†
	250	0.9	10.1	8.6	2	2.6	0.6	**64**	3.8†	7.2
Mean contribution		7.3	8.6	4.4	2.8	6.2	6.2	48.9	11.2	4.3

Notes: The highest percent contribution for each model is in boldface. Average contribution is for both nests and occurrences combined.

† Indicate metrics for which the variable mean is less than the mean of the landscape, all other variable means are greater than the mean of the landscape.

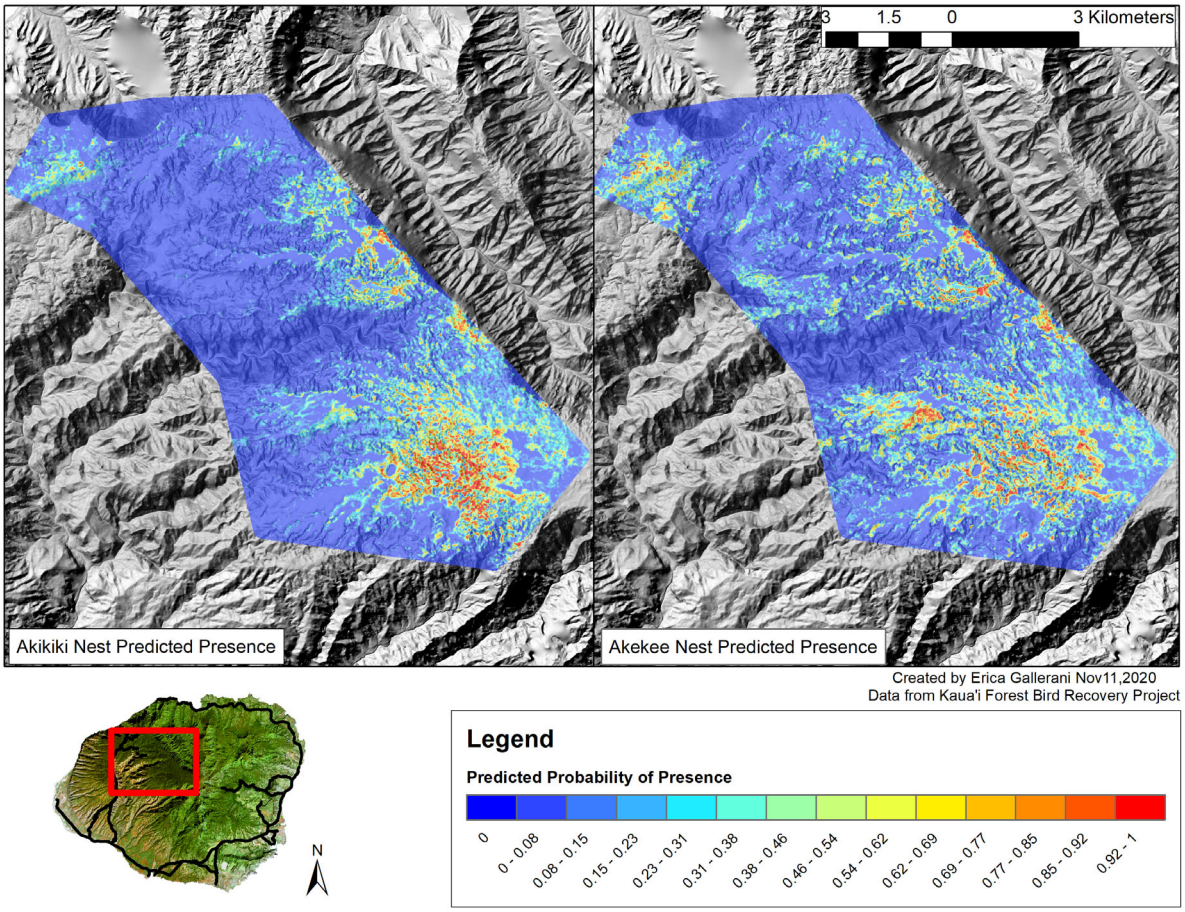

Fig. 3. Habitat suitability for Akikiki and Akekee based on nest locations data from 2012 to 2017 and 10 m lidar topography and structure metrics.

distribution model (Fig. 6). Elevation, canopy density, and slope contributed the most to species occurrences for both Akikiki and Akekee at 250 m resolution and the mean canopy height metrics contributed relatively little (>2%) to the model at this spatial resolution.

The independent observations from 2018 resulted in mean predicted probability of presence of 0.87 and 0.57 for Akikiki and Akekee nest locations at the 10 m scale, respectively (Table 5). At the 100 m scale, 2018 Akikiki and Akekee occurrences have a mean predicted probability of presence of 0.78 and 0.79, respectively (Table 5).

Species nesting and habitat ranges

Suitable nesting habitat for Akikiki was estimated to be 17.59 km^2 using a MTP threshold of 0.203, while Akekee resulted in 11.10 km^2 using a MTP threshold of 0.392 at the 10 m scale. The Akikiki has a potential range of 38.20 km^2 at 100 m resolution while the Akekee has a range of 57.57 km^2 at 100 m resolution (Appendix S6: Table S2). Nest and range sizes for the Akikiki decreased with increased pixel sizes (e.g., 100 m and 250 m). Nest range increased for the Akekee at 100 and 250 m and range sizes were similar across spatial resolutions (Table 6).

Discussion

Multiscale analysis

For our analysis of significant differences between Akikiki and Akekee niche space, we took insight from all spatial scales, as they all reported high AUC values (>0.857; Mandrekar 2010). However, managers should note that we

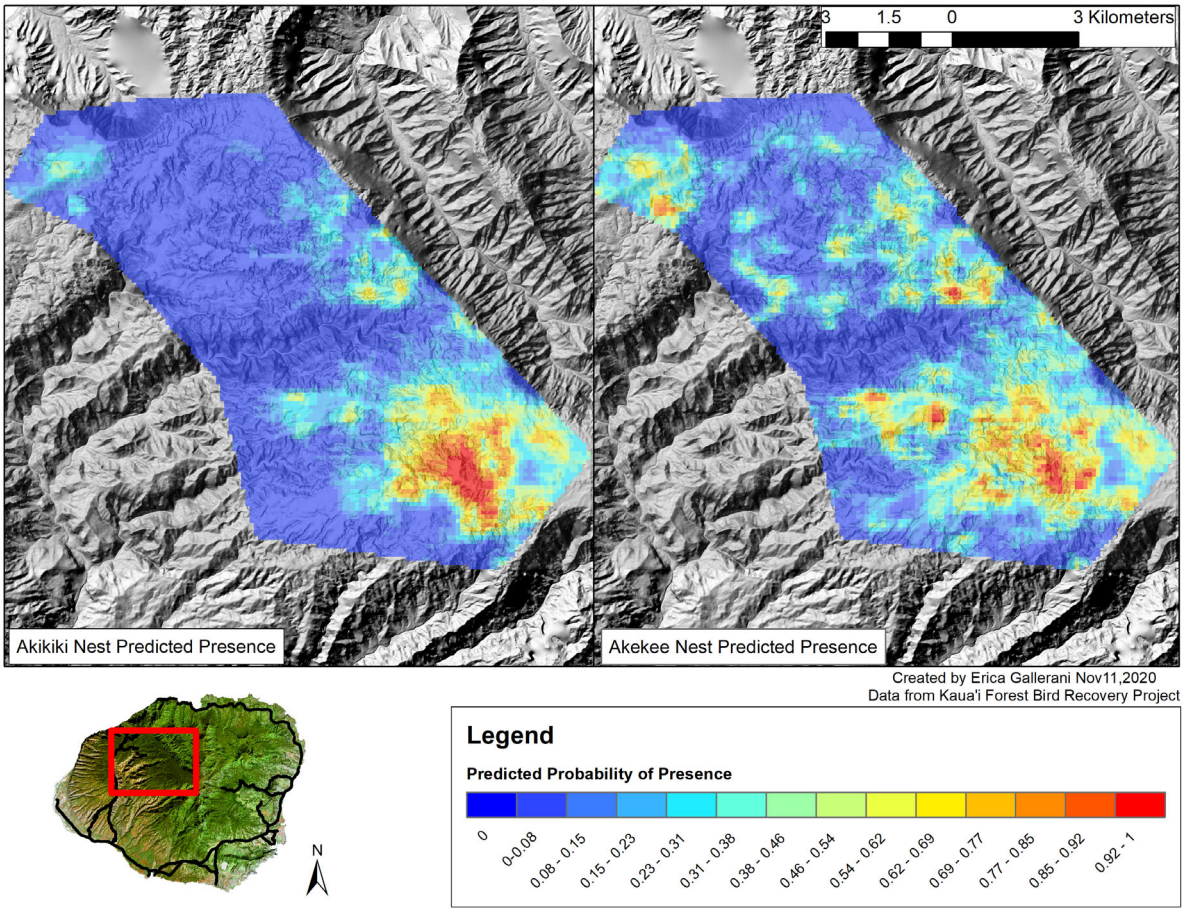

Fig. 4. Habitat suitability for Akikiki and Akekee based on nest locations data from 2012 to 2017 and 100 m lidar topography and structure metrics.

focus on mapping results from the 10 m scale for nests and the 100 m scale for occurrences, primarily due to the difference in quality between the two types of data. While nest data are highly accurate (within 10 m), occurrence data can be recorded several tens of meters away from the individual bird. When reporting AUC values, the 10 m scale performed better for nests for both species than the 100 m or 250 m scale. The 100 m scale performed better for occurrences for both species than the 10 m or 250 m scales (Appendix S6: Table S1). When looking at the predictive power of the models in regard to the excluded 2018 data, Akikiki nests had the highest mean, median, maximum, and minimum predicted probability of presence values at the 10 m scale. The results are less consistent across scale for Akekee, but, the sample size is much lower for this species than for Akikiki (9 and 22, respectively). However, from a management perspective our output maps accurately elucidate beneficial areas for nest searching for Akekee at the newly discovered UUK site (Fig. 7). Results were fairly consistent for 2018 occurrences, as the 100 m scale showed the highest mean, median, and maximum predicted probability of presence values when compared to the other scales (Table 5).

Akikiki and Akekee niche space

There were few significant differences in forest structure between Akikiki and Akekee nest locations across spatial resolutions (10, 100, 250 m), although across the landscape Akikiki appear to

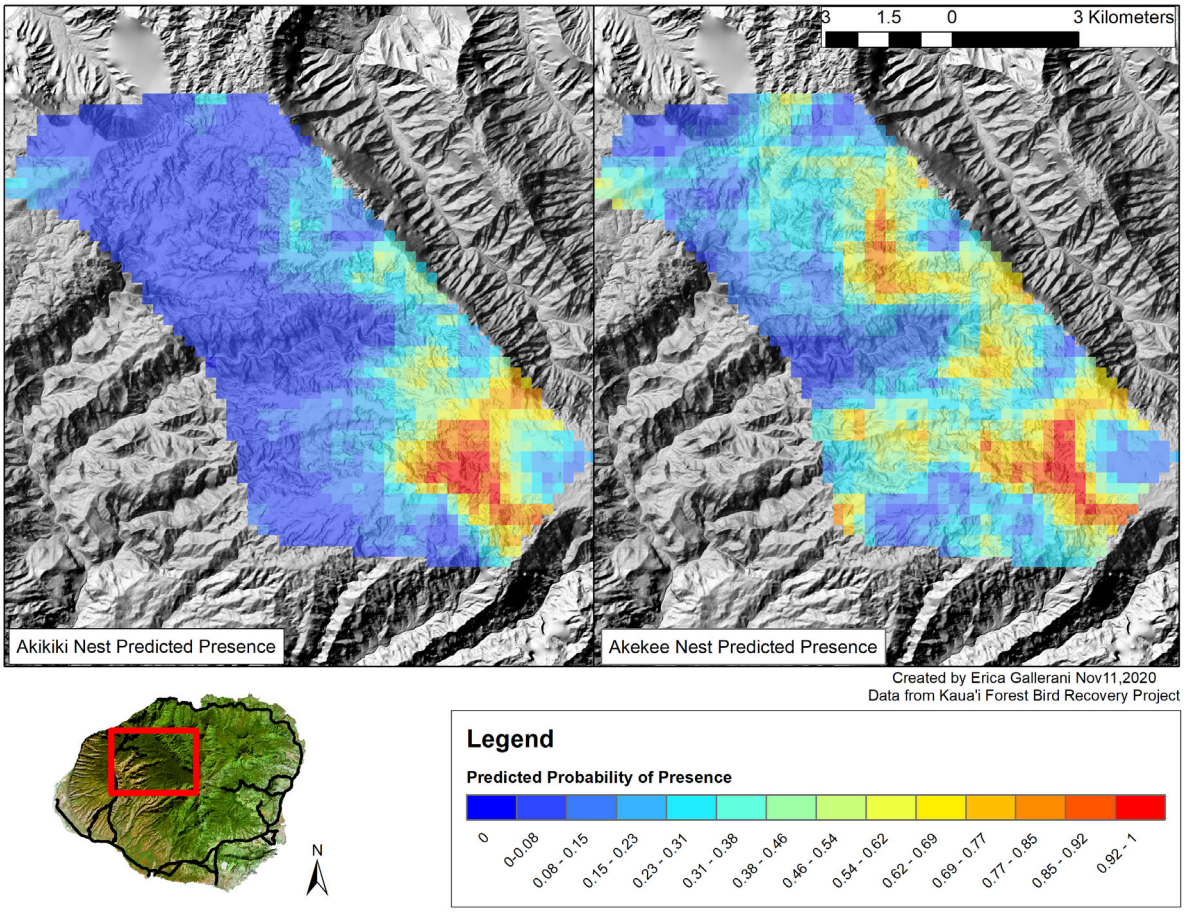

Fig. 5. Habitat suitability for Akikiki and Akekee based on nest locations data from 2012 to 2017 and 250 m lidar topography and structure metrics.

prefer taller individual trees and canopies for nesting than the Akekee at 10 m. This result contradicts most previous observations, which report Akikiki nesting in trees 8.0–9.6 m and Akekee nesting in trees 9.3–12.2 m in height (Lepson and Pratt 1997, Foster et al. 2000), although one Akikiki nest was found in a 12.5-m tree (VanderWerf and Roberts 2008). The topography of nest sites for both species was similar, but Akikiki prefers steeper maximum slopes for nesting locations at 10 m. This finding may reflect their tendency to nest over streams, which may be correlated with the greater tree height used by Akikiki in this study. Trees along streams are more protected from wind stress than trees in upland areas, and so attain greater heights. Also, lidar may measure tree height from the bottom of the stream to its crown if it is overhanging the stream, thus artificially increasing tree height. Although these differences were found to be statistically significant, they are not large in magnitude and therefore may not be biologically significant. A larger sample of field data may be necessary to determine if these slight changes are relevant to the birds' nest preferences.

Overall results suggest that both species currently nest in similar micro-habitats. VanderWerf and Roberts (2008) observed Akikiki nests in 2006 and noted that there were no other Akikiki nesting pairs within the vicinity indicating that Akikiki may not have overlapping territories or have high levels of interactions. Hammond et al. (2015) observed nearest neighbor Akikiki nest

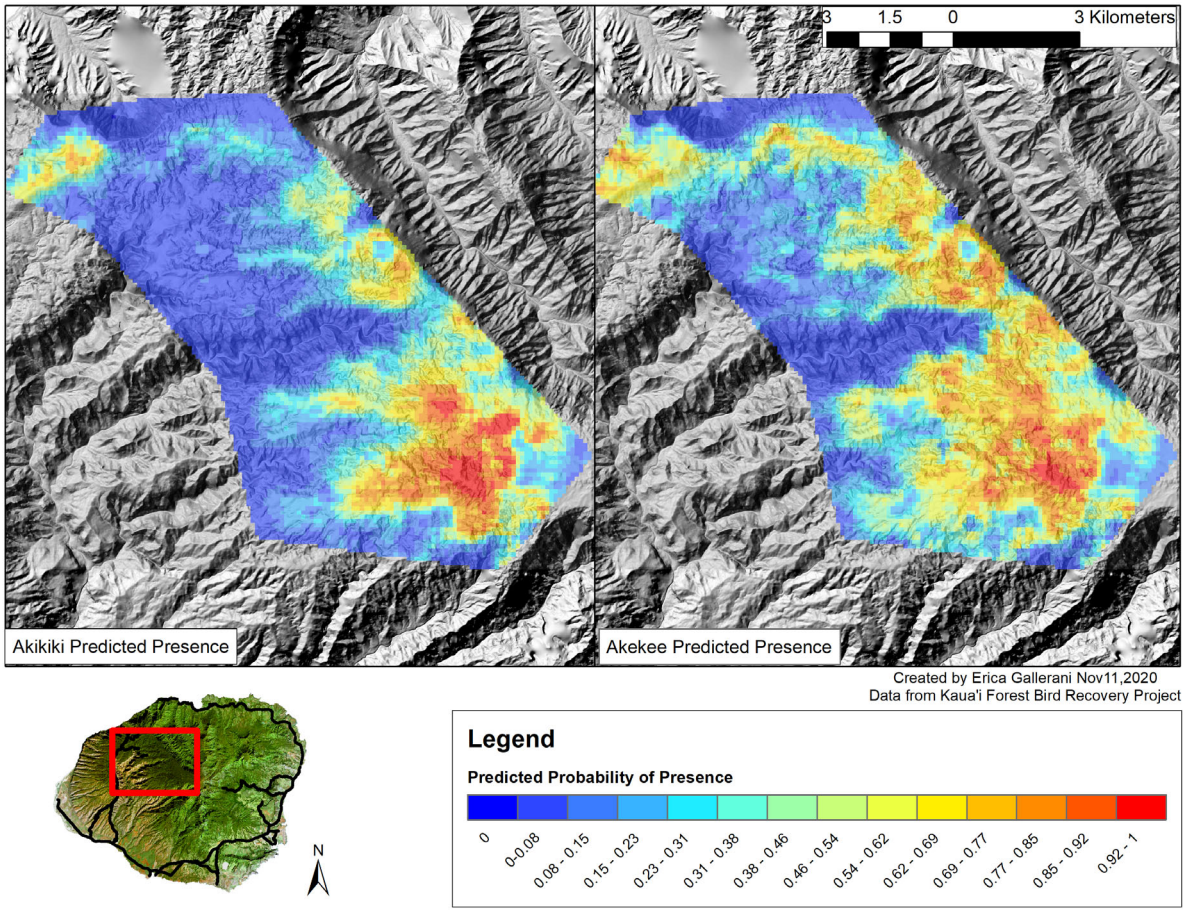

Fig. 6. Habitat suitability for Akikiki and Akekee based on occurrence data from 2012 to 2017 100 m lidar topography and structure metrics.

distance to be 268 ± 85 m supporting VanderWerf and Roberts (2008) findings for a single year. Our results using multi-years (2012–2017) indicate that there are overlaps between both species nest areas across years, with small mean distances recorded among nests found during these years. However, within years, both species, especially Akikiki, appear to defend nest sites and have larger between-nest distances.

There were significant differences in forest structure and topography metrics (slope) and species occurrence at 10 m resolution, suggesting that each species occupies different microhabitats. Akikiki occurred or foraged in areas with significantly taller individual trees, canopies, and understories than Akekee, reflecting Akikiki's known propensity for foraging in the understory on sub-canopy trees and the boles and branches of large trees (Foster et al. 2000). Akikiki also forage on steeper slopes than Akekee, perhaps because they forage near their nests over streams, whereas Akekee do not appear to be territorial. Behnke et al. (2016) found that Akikiki were absent from forests with canopies lower than 10 m in height, while Akekee persisted in lower canopies. However, we found that the Akikiki can occur in forests with canopy lower than 10 m across spatial resolutions; our results agree with Behnke et al. (2016) in that the Akekee can persist with a canopy lower than 10 m. High-resolution lidar metrics may discern micro-forest and topography metrics associated with habitat that are difficult to see or comparatively quantify in the field, especially with the point-quadrat method used by Behnke et al. (2016).

Table 5. The mean, maximum, minimum, and median predicted probability of presence values associated with 2018 nests and occurrence locations for both species (Akekee nests, n = 9; Akikiki nests, n = 22; Akekee occurrences, n = 510; Akikiki occurrences, n = 773).

Species	Scale (m)	Mean	Max	Min	Median
Nests					
Akekee	10	0.57	**0.97**	0.17	**0.59**
	100	**0.59**	0.93	0.28	0.54
	250	0.55	0.93	**0.36**	0.46
Akikiki	10	**0.87**	**1.00**	**0.50**	**0.96**
	100	0.82	0.99	0.13	0.90
	250	0.80	0.95	0.16	0.92
Occurrences					
Akekee	10	0.76	0.94	0.2	0.77
	100	**0.79**	**0.96**	0.17	**0.82**
	250	0.69	0.86	**0.27**	0.71
Akikiki	10	0.75	0.88	0.27	0.76
	100	**0.78**	**0.97**	0.31	**0.92**
	250	0.72	0.87	**0.35**	0.80

Note: The largest values are in boldface.

Lidar attributes associated with nest sites and occurrences

Both species' nest locations were strongly positively associated with elevation, canopy height, relative height 90 and 75, and negatively correlated with slope. Elevation was consistently associated across spatial resolutions with both species' nests. Even when controlling for sampling bias at high elevations with the factor bias out method, elevation continued to be the most important factor. The nesting range of both species in our study were between 1208 m and 1364 m, the highest forested areas on the island of Kauai, and no nests were observed below this elevation range. Although surveys were primarily undertaken above 1100 m, this finding clearly shows that both species occur at high elevations and are near the elevational limit of their range on Kauai. This may be due to avian malaria as prevalence of the disease in captured birds decreases above 1150 m elevation on Kauai (Atkinson et al. 2014; KFBRP, *unpublished data*). The area above 1200 m elevation and associated temperature threshold appear to be the native core habitat that is a driving force in the breeding success of Akikiki and Akekee, corroborating findings of Behnke et al. (2016) and Paxton et al. (2016).

After elevation, relative height 90, mean canopy height and slope were the most important metric for nests of both species at a 10 m resolution, with relative height 25 and relative height 50 also of importance for Akekee. The positive correlation with relative height 90 may reflect a selection for areas of increased vertical structure to reduce predation risk, especially from rats and owls (Jacobi et al. 1996, Pratt et al. 1997). Both species likely avoid the steepest areas of the Plateau because they are not covered in the large trees favored for nesting (Lepson and Pratt 1997, Foster et al. 2000, Hammond et al. 2015).

Elevation was also the most important metric for species occurrences across almost all spatial resolutions, again likely reflecting temperature and the distribution of avian malaria on the Plateau. Mean canopy height was an important metric for both species based on occurrences at 10 m resolution (Akikiki 12% and Akekee 14%) in our study, likely because of foraging preferences. Similarly, mean canopy height was present in nine of the top ten models for Akikiki and three of the top four models for Akekee according to Behnke et al. (2016). However, mean canopy height and relative height 90, which identifies large individual trees and associated biomass, were less important at 100 m and 250 m scales, suggesting that as pixel sizes increases, topographic features like elevation and slope become more important and vegetation structure becomes less important

Table 6. Minimum training presence threshold (MTP) for Akikiki and Akekee nests and occurrences and estimated range size across 10 m, 100 m, and 250 m pixel resolutions.

		10 m		100 m		250 m	
Species	Feature	MTP	Range (km^2)	MTP	Range (km^2)	MTP	Range (km^2)
Akikiki	Nests	0.20	17.59	0.35	13.09	0.30	15.94
	Occurrences	0.11	54.65	0.17	38.20	0.34	29.56
Akekee	Nests	0.39	11.10	0.18	38.48	0.30	36.50
	Occurrences	0.07	70.09	0.14	57.57	0.08	71.50

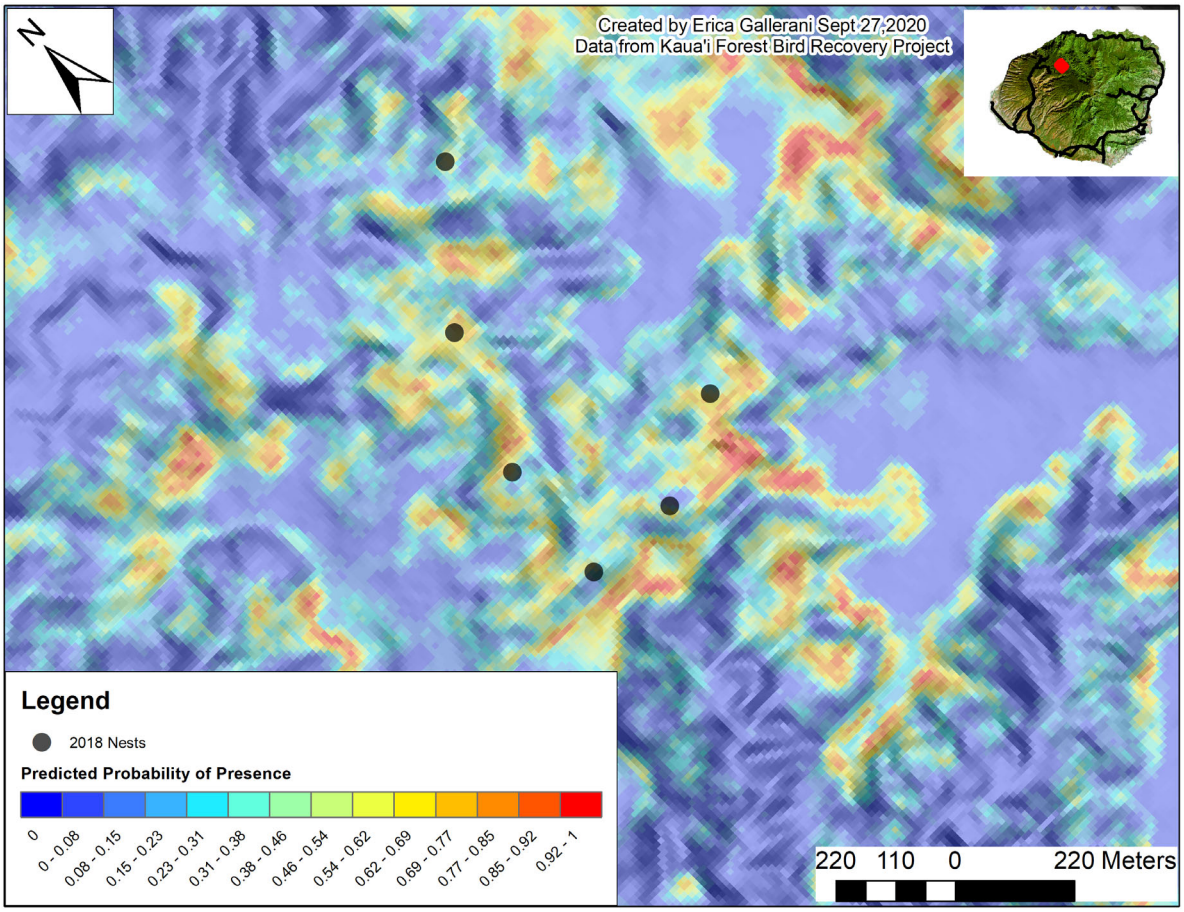

Fig. 7. Habitat suitability for Akekee nests based on occurrence data from 2012 to 2017 10 m lidar topography and structure metrics with 2018 Akekee nests from newly discovered Upper Upper Kawakoi (UUK) site.

in our study area. The decreasing importance of canopy metrics at 100 m and 250 m is likely due to the averaging or lower average canopies in larger pixels which results in the loss of information on taller trees.

Distribution maps and ranges

Estimation of species' breeding range using lidar may be a novel way to assess endangered species conservation status and trends in Hawaii, particularly for species that are difficult to survey due to their rarity or remote location. These nest models also identify potential areas where future nest surveys should be undertaken to confirm range estimates and inform conservation efforts for these species. Based on our models of nesting habitat at a 10 m resolution, we estimate that Akikiki have a breeding range of only 18 km^2 and Akekee have a breeding range of only 11 km^2. These ranges are considerably smaller than the area over which these species are predicted to occur and are particularly striking for Akekee, usually thought to have a bigger range than Akikiki (Paxton et al. 2016). This discrepancy may be a result of the smaller sample sizes used in Akekee nest models and the choice of threshold value. The minimum nest value used in generating the threshold for Akekee was from a 2014 nest in an area modeled as having a 0.392 probability of being suitable for nesting; for Akikiki, it was from a 2012 nest that occurred in an area modeled as having a 0.203 probability of being suitable for nesting. Despite intensive nest searching in that area from 2015 to 2018, no other nests have been found (J.M. Hite, *personal observation*), and thus, it may no longer be suitable for

nesting. If we use a value of 0.358 (more like the Akekee minimum value), we estimate the Akikiki breeding range at 9.8 km^2, which is more consistent with other range estimates for these two species.

Akikiki once occurred in the lowlands of Kauai (Burney et al. 2001) and the IUCN currently reports that its estimated extent of occurrence (EEO, which is based on the minimum convex polygon around all known or inferred occurrences) is 120 km^2 (IUCN 2018), but based on survey data, its actual range had contracted to less than 25 km^2 in 2012 (Paxton et al. 2016). Based on 2012 survey data, the Akekee range has contracted from the inferred original range of 127 km^2 to less than 50 km^2 (Scott et al. 1986, Paxton et al. 2016) and the IUCN reports an EOO of only 5 km^2 (IUCN 2018). We estimate that the Akikiki has a potential range of 38 km^2 and the Akekee has a range of 58 km^2 at a 100 m resolution based on 2012–2017 data. Both estimates are larger (30 km^2 for Akikiki and 20 km^2 for Akekee) than Paxton et al. (2016) perhaps due to the use of data from multi-years instead of a single year and differences in survey methods. The Paxton et al. (2016) estimates are based on 8-min counts conducted once at each of several hundred survey locations at elevations >1000 m on Kauai. The habitat modeling reported here is based on several thousand observations of each species over five years from a few study sites extrapolated to the larger Alakai Plateau based on habitat characteristics. The Paxton et al. (2016) estimates may more accurately reflect the area of occupancy given current small population sizes and the effects of malaria, whereas our estimates may represent the area of potentially suitable habitat available to these species once malaria is addressed and populations start to recover. Regardless, both sets of estimates suggest that the Akekee forages in a larger area than the Akikiki, partly because they follow the phenology of ohia leafing. Furthermore, both estimates show that current IUCN EEOs dramatically overestimate the current range of the Akikiki and underestimate the range of the Akekee (IUCN 2018).

Uncertainty

Major sources of uncertainty in habitat suitability modeling include comprehensiveness and quality of presence data, model domain, algorithm choice, and variable collinearity (Watling et al. 2015). In terms of these sources of uncertainty, strengths of our particular models lie in the most comprehensive dataset of occurrences and nests available for both species over several years, biological expertise as input for variable selection, and compensation for biased sampling distribution. However, while our model domain consists of historically suitable habitat for both species, there are areas included that are no longer suitable due to invasive disease and land cover change. The model domain can influence model performance as it determines the selection of pseudo-absences. When pseudo-absences are selected from beyond the geographical range of a species, the resulting model has high discriminatory power but is less informative (Acevedo et al. 2012). However, one of the best approaches to choosing a model domain is to use biological information relating to dispersal capacity and historical range of the species, as we have done (Acevedo et al. 2012). In some cases, our analysis used highly collinear variables (Appendix S2). Studies that systematically analyze the sources of uncertainty in habitat suitability modeling have found that algorithm choice and quality and comprehensiveness of presence data have the largest effect on model performance (Dormann et al. 2008, Watling et al. 2015). When compared to algorithm selection, both variable collinearity and model domain had little to no impact on model performance (Watling et al. 2015). To quantify uncertainty in our models, we provide standard deviation maps from our bootstrapped replicates (Appendix S7). In the future, multiple modeling algorithms, including presence–absence modeling, should be tested to determine suitable habitat.

Management implications

Airborne lidar can quantify endangered species nest locations, compare nest sites between species, and identify three-dimensional vegetation and topography metrics associated with endangered species' nests, thus informing management actions. Although few studies to date have correlated large samples of endangered nest locations and lidar in the wild (García-Feced et al. 2011, Weisberg et al. 2014, Barnes et al. 2016, Hagar et al. 2020), airborne lidar analyses

for nest location and preference should be more common in the future. In Kauai, predictive maps of nest locations should be systematically visited in the field to identify new nest sites to confirm our models and to protect with management actions. Many native bird species have high nest site fidelity and nest sites thus should be revisited annually (Hammond et al. 2015; KFBRP, *unpublished data*). Nest searching should be conducted in conjunction with further systematic surveys on the Alakai Plateau based on our predictive occurrence maps.

Results clearly show the importance of elevation for both species nest sites and occurrences, presenting a difficult management problem given climate change and the low elevation of Kauai. If malaria cannot be controlled and both species populations do not stabilize over the coming years, translocation may be needed to insure their viability. Indeed, translocations experiments to Maui and Hawaii islands, both higher in elevation, are being explored as a future management option (Paxton et al. 2018). Comparative lidar surveys over Maui and Hawaii could be used to identify if they have similar nesting sites attributes (canopy height, maximum height, canopy density) as Kauai and could be used to identify potential introduction sites (Fortini et al. 2015); we (L.H. Crampton, G.A. Fricker, E.M. Gallerani) are currently involved such a process for a site on Maui. However, clearly mosquitos and avian malaria will need to be controlled for long-term persistence of these species and Kauai appears to be an ideal location to test novel mosquito eradication methods because it contains such a high diversity of endangered bird species in a relatively small and isolated area.

Actions should be taken to maintain canopy height (10 m) and large trees (14 m). Although no current human development threatens the area, forest damage from hurricanes and rapid ohia death is always a possibility in the future (Camp et al. 2019). Both species nest in trees that average 10 m tall and if a significant disturbance occurs this would have short term impacts on potential nesting sites. Conservation managers should consider silvicultural practices that promote native forest structure within these species' historic ranges to ensure habitat remains once the threat of avian malaria is reduced.

Future research

Species distribution models have advanced to a point that they should be created for all native and non-native birds in Kauai. A stratified random and/or grid-based cell system could be used to promote the presence/absence modeling in the future. Sound-based automated recording systems are being explored to overcome some of the difficulties of sampling presence/absence on steep slopes or rugged terrain over the course of a year. Future distribution modeling should include climatic metrics of temperature (mean, minimum, maximum), precipitation, wind speed, and solar radiations available at a 250 m pixel resolution (Giambelluca et al. 2014) and remote sensing metrics such as NDVI from Landsat (30 m) or MODIS (250 m) to estimate productivity and heterogeneity on Kauai (Fricker et al. 2015). These metrics can also be combined with airborne or spaceborne lidar metrics to produce species distributions at 30 m and 250 m resolution over the Alakai Plateau. However, since elevation was clearly the most important factor in determining Akikiki and Akekee distributions, comparative lidar data are needed above 1000 m on Maui and the Big Island to identify if there are nest trees of similar composition and structure (e.g., maximum 14 m, mean tree height 10 m) and slope (Paxton et al. 2018). The recent and ongoing collection of spaceborne lidar data from the Global Ecosystem Dynamics Investigation (GEDI) will make that type of inter-island analysis possible (Dubayah et al. 2020). Additionally, future modeling should incorporate multiscale optimization in order to more robustly analyze the responsiveness of habitat preferences to scale (McGarigal et al. 2016). Monitoring rat and mosquito ranges will also be important to identify overlaps with nest locations and occurrences from this study in the future.

Conclusions

We identified 88 nests locations and 3607 occurrence locations for the Akikiki and 22 nest locations and 1581 occurrence locations for the Akekee from 2012 to 2017 on the Alakai Plateau, Kauai. Discrete return airborne lidar shows that the Akikiki and Akekee nest in forests with similar structure but with different maximum tree heights at a 10 m resolution. Akikiki and Akekee forage in

areas with significantly different forest structure (maximum tree height, mean canopy height, relative heights) and topography (slope) at a 10 m resolution. Elevation was consistently the most important metric for predicting both species nest locations and occurrences across spatial scales, and it appears both species are near the limit of their elevational range and translocation programs to Maui or Hawaii should be considered. However, significant relationships with forest structure metrics underscore the importance of maintaining habitat for these two species so that they can persist on Kauai and other islands once the threat of mosquito-borne disease is abated by landscape-level mosquito control. We estimate that Akikiki has a nesting range of 18 km^2 and potential range of 38 km^2 and Akekee has a nesting range of only 11 km^2 and potential range of 58 km^2. We produced predictive nest and occurrence maps at 10 m and 100 m resolution to spatially target conservation actions, such as predator control or fencing, in the future. We found that the finer scale models (10 m) were better predictors of nest locations while the moderate scale models (100 m) were better predictors for occurrences. However, 250 m scale models still performed well and are suitable for use in future analysis that includes coarser climate data.

Acknowledgments

All authors participated in the design of the study; LHC and TWG conceived of the study, LHC, JMH, and field technicians collected field data, GAF and EMG processed lidar and distribution maps; GAF, RI, TWG, and EMG analyzed the data, and all authors participated in writing of the manuscript. We thank Ryan Lam and Morgan Barnes for help with early distribution models and background research. We thank U.S Fish and Wildlife Service for a grant for high-resolution imagery and ongoing support to the Kauai Forest Bird Recovery Project (KFBRP) for field research. The Hawaii Department of Land and Natural Resources Division of Forestry and Wildlife with the Pacific Cooperative Studies Unit at the University of Hawaii Manoa also provided financial and logistical support to KFBRP.

Literature Cited

Abolmaali, S. M. R., M. Tarkesh, and H. Bashari. 2018. MaxEnt modeling for predicting suitable habitats and identifying the effects of climate change on a threatened species, *Daphne mucronata*, in central Iran. Ecological Informatics 43:116–123.

Acevedo, P., A. Jiménez-Valverde, J. M. Lobo, and R. Real. 2012. Delimiting the geographical background in species distribution modelling. Journal of Biogeography 39:1383–1390.

Asner, G. P., R. F. Hughes, P. M. Vitousek, D. E. Knapp, T. Kennedy-Bowdoin, J. Boardman, R. E. Martin, M. Eastwood, and R. O. Green. 2008. Invasive plants transform the three-dimensional structure of rain forests. Proceedings of the National Academy of Sciences of the United States of America 105:4519–4523.

Atkinson, C. T., R. B. Utzurrum, D. A. Lapointe, R. J. Camp, L. H. Crampton, J. T. Foster, and T. W. Giambelluca. 2014. Changing climate and the altitudinal range of avian malaria in the Hawaiian Islands – an ongoing conservation crisis on the island of Kaua'i. Global Change Biology 20:2426–2436.

Baddeley, A., E. Rubak, and R. Turner. 2015. Spatial point patterns: methodology and applications with R. Chapman and Hall/CRC, Boca Raton, Florida, USA.

Bakx, T. R. M., Z. Koma, A. C. Seijmonsbergen, and W. D. Kissling. 2019. Use and categorization of light detection and ranging vegetation metrics in avian diversity and species distribution research. Diversity and Distributions 25:1045–1059.

Barnes, K. W., K. Islam, and S. A. Auer. 2016. Integrating LIDAR-derived canopy structure into cerulean warbler habitat models. Journal of Wildlife Management 80:101–116.

Behnke, L. A. H., L. Pejchar, and L. H. Crampton. 2016. Occupancy and habitat use of the endangered Akikiki and Akekee on Kauai Island, Hawaii. Condor 118:148–158.

Burney, D. A., et al. 2001. Fossil evidence for a diverse biota from Kaua'i and its transformation since human arrival. Ecological Monographs 71:615–641.

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, Hawaii Island, USA. Condor 121:1–16.

Dilts, T. E. 2015. Prepare Rasters for Maxent tool for ArcGIS 10.1. University of Nevada Reno. http://www.arcgis.com/home/item.html?id=11bf7e689c92413f8d31933b3e1f56b1

Dormann, C. F., O. Purschke, J. R. Garcia Marquez, S. Lautenbach, and B. Schroder. 2008. Components of uncertainty in species distribution analysis: a case study of the great grey shrike. Ecology 89:3371–3386.

Drake, J. B., R. O. Dubayah, D. B. Clark, R. G. Knox, J. B. Blair, M. A. Hofton, R. L. Chazdon, J. F.

Weishampel, and S. Prince. 2002. Estimation of tropical forest structural characteristics, using large-footprint lidar. Remote Sensing of Environment 79:305–319.

Dubayah, R., et al. 2020. The Global Ecosystem Dynamics Investigation: high-resolution laser ranging of the Earth's forests and topography. Science of Remote Sensing 1:100002.

Dubayah, R. O., and J. B. Drake. 2000. Lidar Remote sensing for forestry. Journal of Forestry 98:44–46.

Dubayah, R. O., S. L. Sheldon, D. B. Clark, M. A. Hofton, J. B. Blair, G. C. Hurtt, and R. L. Chazdon. 2010. Estimation of tropical forest height and biomass dynamics using lidar remote sensing at la Selva, Costa Rica. Journal of Geophysical Research: Biogeosciences 115:1–17.

Dudík, M., S. Phillips, and R. E. Schapire. 2005. Correcting sample selection bias in maximum entropy density estimation. Advances in Neural Information Processing Systems 18:323–330.

Elith, J., and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics 40:677–697.

Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee, and C. J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 17:43–57.

Feng, X., D. S. Park, Y. Liang, R. Pandey, and M. Papeş. 2019. Collinearity in ecological niche modeling: confusions and challenges. Ecology and Evolution 9:10365–10376.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38–49.

Fortini, L. B., A. E. Vorsino, F. A. Amidon, E. H. Paxton, and J. D. Jacobi. 2015. Large-scale range collapse of Hawaiian forest birds under climate change and the need 21st century conservation options. PLOS ONE 10:e0140389.

Foster, J. T., J. M. Scott, and P. W. Sykes Jr. 2000. Akikiki (*Oreomystis bairdi*), version 2.0. *In* A. F. Poole and F. B. Gill, editors. The birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA. http://dx.doi.org/10.2173/bna.552

Foster, J. T., E. J. Tweed, R. J. Camp, B. L. Woodworth, C. D. Adler, and T. Telfer. 2004. Long-term population changes of native and introduced birds in the Alaka'i Swamp, Kaua'i. Conservation Biology 18:716–725.

Franklin, J. 2013. Species distribution models in conservation biogeography: developments and challenges. Diversity and Distributions 19:1217–1223.

Fricker, G. A., J. A. Wolf, S. S. Saatchi, and T. W. Gillespie. 2015. Predicting spatial variations of tree species richness in tropical forests from high-resolution remote sensing. Ecological Applications 25:1776–1789.

Garabedian, J. E., C. E. Moorman, M. Nils Peterson, and J. C. Kilgo. 2017. Use of LiDAR to define habitat thresholds for forest bird conservation. Forest Ecology and Management 399:24–36.

García-Feced, C., D. J. Tempel, and M. Kelly. 2011. LiDAR as a tool to characterize wildlife habitat: California spotted owl nesting habitat as an example. Journal of Forestry 109:436–443.

Giambelluca, T. W., et al. 2014. Evapotranspiration of Hawai'i. Final report submitted to the U.S. Army Corps of Engineers—Honolulu District, and the Commission on Water Resource Management, State of Hawai'i.

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 94:313–316.

Guillera-Arroita, G., J. J. Lahoz-Monfort, J. Elith, A. Gordon, H. Kujala, P. E. Lentini, M. A. Mccarthy, R. Tingley, and B. A. Wintle. 2015. Is my species distribution model fit for purpose? Matching data and models to applications. Global Ecology and Biogeography 24:276–292.

Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135:147–186.

Hagar, J. C., A. Yost, and P. K. Haggerty. 2020. Incorporating LiDAR metrics into a structure-based habitat model for a canopy-dwelling species. Remote Sensing of Environment 236:111499.

Hammond, R. L., L. H. Crampton, and J. T. Foster. 2015. Breeding biology of two endangered forest birds on the island of Kauai, Hawaii. Condor 117:31–40.

Harrington, R. A., J. H. Fownes, P. G. Scowcroft, and C. S. Vann. 1997. Impact of Hurricane Iniki on native Hawaiian Acacia koa forests: Damage and two-year recovery. Journal of Tropical Ecology 13:539–558.

IUCN. 2018. The IUCN red list of threatened species. Version 2018-2. http://www.iucn.redlist.org. Downloaded on 19 December 2018.

Jacobi, J. D., S. G. Fancy, J. G. Giffin, and J. M. Scott. 1996. Long-term population variability in the palila, an endangered Hawaiian honeycreeper. Pacific Science 50:363–370.

Lepson, J. K., and H. D. Pratt. 1997. Akeke'e (*Loxops caeruleirostris*), the birds of North America, 295. Cornell Lab of Ornithology, Ithaca, New York, USA.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, A. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

Mandrekar, J. N. 2010. Receiver operating characteristic curve in diagnostic test assessment. Journal of Thoracic Oncology 5:1315–1316.

Martin, T. E., G. R. Geupel, and F. Ornithology. 2016. Nest-monitoring plots: methods for locating nests and monitoring success (Métodos para localizar nidos y monitorear el éxito de estos). Wiley on behalf of Association of Field Ornithologists Stable 64:507–519.

McGarigal, K., H. Y. Wan, K. A. Zeller, B. C. Timm, and S. A. Cushman. 2016. Multi-scale habitat selection modeling: a review and outlook. Landscape Ecology 31:1161–1175.

Menge, B. A., and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community structure. Trends in Ecology & Evolution 5:52–57.

Paxton, E. H., R. J. Camp, P. M. Gorresen, L. H. Crampton, D. L. Leonard, and E. A. VanderWerf. 2016. Collapsing avian community on a Hawaiian island. Science Advances 2:e1600029.

Paxton, E. H., M. Laut, J. P. Vetter, and S. J. Kendall. 2018. Research and management priorities for Hawaiian forest birds. Condor 120:557–565.

Pearson, R. G., C. J. Raxworthy, M. Nakamura, and A. Townsend Peterson. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography 34:102–117.

Phillips, S. B., V. P. Aneja, D. Kang, and S. P. Arya. 2006. Modelling and analysis of the atmospheric nitrogen deposition in North Carolina. International Journal of Global Environmental Issues 6:231–252.

Phillips, S. J., M. Dudík, J. Elith, C. H. Graham, A. Lehmann, J. Leathwick, and S. Ferrier. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecological Applications 19:181–197.

Pratt, T. K., P. C. Banko, S. G. Fancy, G. D. Lindsey, and J. D. Jacobi. 1997. Status and management of the Palila, an endangered Hawaiian honeycreeper, 1987–1996. Pacific Conservation Biology 3:330–340.

Radosavljevic, A., and R. P. Anderson. 2014. Making better Maxent models of species distributions: complexity, overfitting and evaluation. Journal of Biogeography 41:629–643.

Reed, J. M., D. W. Desrochers, E. A. Vanderwerf, and J. M. Scott. 2012. Long-term persistence of Hawaii's endangered avifauna through conservation-reliant management. BioScience 62:881–892.

Scott, J. M., S. Mountainspring, F. L. Ramsey, and C. B. Kepler. 1986. Forest bird communities of the Hawaiian Islands: their dynamics, ecology, and conservation. Journal of Wildlife Management 53:860.

Tang, H., R. Dubayah, A. Swatantran, M. Hofton, S. Sheldon, D. B. Clark, and B. Blair. 2012. Retrieval of vertical LAI profiles over tropical rain forests using waveform Lidar at la Selva, Costa Rica. Remote Sensing of Environment 124:242–250.

U.S. Fish and Wildlife Service. 2015. Environmental Conservation Online System (ECOS): listed species believed or known to occur in Hawaii. https://ecos.fws.gov/ecp/report/species-listings-by-state?stateAbbrev=HI&stateName=Hawaii&statusCategory=Listed

VanderWerf, E. A., and P. K. Roberts. 2008. Foraging and nesting of the 'Akikiki or Kaua'i Creeper (*Oreomystis bairdi*). Wilson Journal of Ornithology 120:195–199.

Watling, J. I., L. A. Brandt, D. N. Bucklin, I. Fujisaki, F. J. Mazzotti, S. S. Romañach, and C. Speroterra. 2015. Performance metrics and variance partitioning reveal sources of uncertainty in species distribution models. Ecological Modelling 309–310:48–59.

Weisberg, P. J., T. E. Dilts, M. E. Becker, J. S. Young, D. C. Wong-Kone, W. E. Newton, and E. M. Ammon. 2014. Guild-specific responses of avian species richness to LiDAR-derived habitat heterogeneity. Acta Oecologica 59:72–83.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Yang, Y., S. S. Saatchi, L. Xu, Y. Yu, S. Choi, N. Phillips, R. Kennedy, M. Keller, Y. Knyazikhin, and R. B. Myneni. 2018. Post-drought decline of the Amazon carbon sink. Nature Communications 9:1–9.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3554/full