



Predicted distribution of 'ua'u (Hawaiian petrel *Pterodroma sandwichensis*) nest sites on Haleakalā, Maui

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ABSTRACT: Haleakalā National Park and montane areas on east Maui, Hawaiian Archipelago, support critical nesting habitat for endangered 'ua'u Hawaiian petrel *Pterodroma sandwichensis*. Habitat loss, non-native predators, and damage by feral ungulates are limiting factors for ground-nesting petrels at Haleakalā and throughout Hawai'i. Because nesting habitats differ among the Hawaiian Islands, habitat distribution modeling for Hawaiian petrel has been island specific. Based on 2453 known nest site locations, we provide the first landscape-scale predictive model describing relative abundance and habitat available for nesting petrels throughout upper Haleakalā (1830 to 3055 m). We evaluated (principal components analyses and Pearson's correlation) 13 spatial landscape and climate predictor variables associated with nest sites and the background landscape followed by random forest modeling to predict nest site density. Six variables (elevation, slope, topographic position index at 2 scales, heat load index, presence-absence ash/cinder, and presence-absence vegetation) indicated nest sites occurred non-randomly throughout the central part of the summit and crater; greatest concentrations were predicted along the crater rim and a ridgeline extending southwest from the summit. Moderately high predicted density occurred in the northeastern and northern crater. Lower elevations to the north, west, and south flanks of Haleakalā had relatively fewer predicted nest sites. Although we focused on higher elevations on Haleakalā, there is no reason to suspect that conservation efforts would not be successful at lower elevations, provided nesting petrels were protected from invasive predators, grazing ungulates, and significant land alteration.

KEY WORDS: Gadfly petrel · Nesting habitat · Hawaiian petrel · Haleakalā · Habitat modeling · Random forest modeling · Conservation science

1. INTRODUCTION

Continuous human occupation and introduction of non-native mammals to the Hawaiian Islands has wrought dramatic landscape-level changes to island habitats and caused rapid loss of biodiversity (Munro

1944, Olson & James 1984, Reed et al. 2012). Today, many remaining native Hawaiian species occur in highly fragmented and inaccessible habitats (Pratt & Jacobi 2009). Available avian fossil and archaeological records indicate the widespread and plentiful occurrence of seabirds during the early period of

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human occupation (800 to 1000 yr ago; Kirch 2011, Rieth et al. 2011), including 'ua'u Hawaiian petrel *Pterodroma sandwichensis*, from low elevations near the ocean to high-elevation lava fields flanking volcanoes on Maui and Hawai'i (Olson & James 1982a,b, Moniz 1997). Hawaiian petrel is listed as endangered in the USA (US Fish and Wildlife Service 2016), by Hawai'i State (Hawai'i Revised Statutes §195D-4 n.d.) and internationally in the IUCN Red List of Threatened Species (BirdLife International 2018). Hawaiian petrels nest and are monitored on Kaua'i, Lāna'i, Maui, and Hawai'i.

Hawaiian petrel persists with appreciable conservation management almost exclusively in remote montane areas of the Hawaiian Islands (US Fish and Wildlife Service 2016, BirdLife International 2018). Although they once supported nesting petrels, and presence has been detected at low levels on Moloka'i (US Geological Survey & Maui Nui Seabird Recovery Program unpubl. data) and O'ahu, nesting on these islands has yet to be confirmed (Day & Cooper 2002, Young et al. 2019, Kubler-Dudgeon et al. 2020). Remaining Hawaiian petrel nesting habitat varies from brushy, low-land 'ōhi'a lehua *Metrosideros polymorpha*–uluhe fern *Dicranopteris linearis* forest on Lāna'i, to dense rainforest on Kaua'i, to xeric, largely barren, high-elevation (>2500 m) lava flows on Hawai'i, and older, high-elevation lava-flow and alpine shrubland habitats on Haleakalā, east Maui. Such island habitats are typical of other tropical and sub-tropical *Pterodroma* spp. (e.g. *P. phaeopygia*, *P. feae*, *P. desertas*, *P. madeira*, and *P. barau*) that mostly nest within earthen burrows, but also use rock crevices or caves when soil is not available (Cruz & Cruz 1990, Probst et al. 2000, Fjeldså et al. 2020). Because of the diversity among habitats on the different Hawaiian islands, predictive habitat modeling for Hawaiian petrel has been island specific (VanZandt et al. 2014, Troy et al. 2017). Such island-specific conservation information is required because Hawaiian petrel exhibits inter-island genetic variation, with petrels on Haleakalā displaying genetic isolation from those on neighboring Hawai'i and Lanai (Welch et al. 2012a). This is important because island-specific conservation management can increase specific sub-population growth to maintain internal recruitment and decrease the risks of catastrophic declines to philopatric populations that lack dispersal capability (Welch et al. 2012b).

Haleakalā (the eastern volcano of the Island of Maui) supports critical remaining nesting habitat for Hawaiian petrels and has the largest known breeding population throughout the Hawaiian Archipelago. Loss of habitat, predation by non-native pred-

tors, and habitat damage by feral ungulates are major limiting factors for ground-nesting Hawaiian petrels (Hodges & Nagata 2001, Raine et al. 2020). Additional impacts in Hawai'i are caused by habitat-altering invasive plants (VanZandt et al. 2014), grounding of birds associated with anthropogenic lights at night, and collisions of birds with utility lines and other structures (Travers et al. 2021). The primary management actions during the past several decades to increase Hawaiian petrel numbers on Haleakalā have focused on excluding feral ungulates (goats, pigs) with perimeter fencing to prevent habitat destruction and trampling of nest sites, and controlling invasive mammalian predators (rats, mongooses, and cats) using rodenticide and lethal trapping (Larson 1967, Hodges & Nagata 2001, Kaholoa'a et al. 2019, Kelsey et al. 2019).

Accurate spatial predictions of suitable nesting habitat and relative abundance are integral for informing monitoring and conservation strategies for Hawaiian petrels throughout the Hawaiian Islands (Troy et al. 2017), but these have yet to be developed for Haleakalā. Herein, we provide the first landscape-scale predictive model describing the relative abundance and most likely contemporary habitat available for nesting petrels throughout the upper elevations of Haleakalā. Specifically, our goals were to (1) assemble all available nest site location data, (2) evaluate a suite of environmental variables associated with known nest sites versus randomly located potential nest sites, and (3) predict and map potential suitable contemporary nesting habitat. Our results are intended to provide critical new information that can be used in the future to search more systematically for additional nest sites and to improve predictive models that can be used to evaluate the degree to which important conservation actions, including predator control and fencing, overlap with or enclose important nesting habitat, respectively.

2. MATERIALS AND METHODS

2.1. Hawaiian petrel nest sites and monitoring on Haleakalā

In 1954, Richardson & Woodside (1954) located and described 2 Hawaiian petrel nesting sites near the western floor of the crater within Haleakalā National Park (HALE; Fig. 1). Early efforts to locate and describe nest sites were extremely limited until the 1970s when Kjargaard (1978) increased the opportunistic search effort on foot by looking for sign

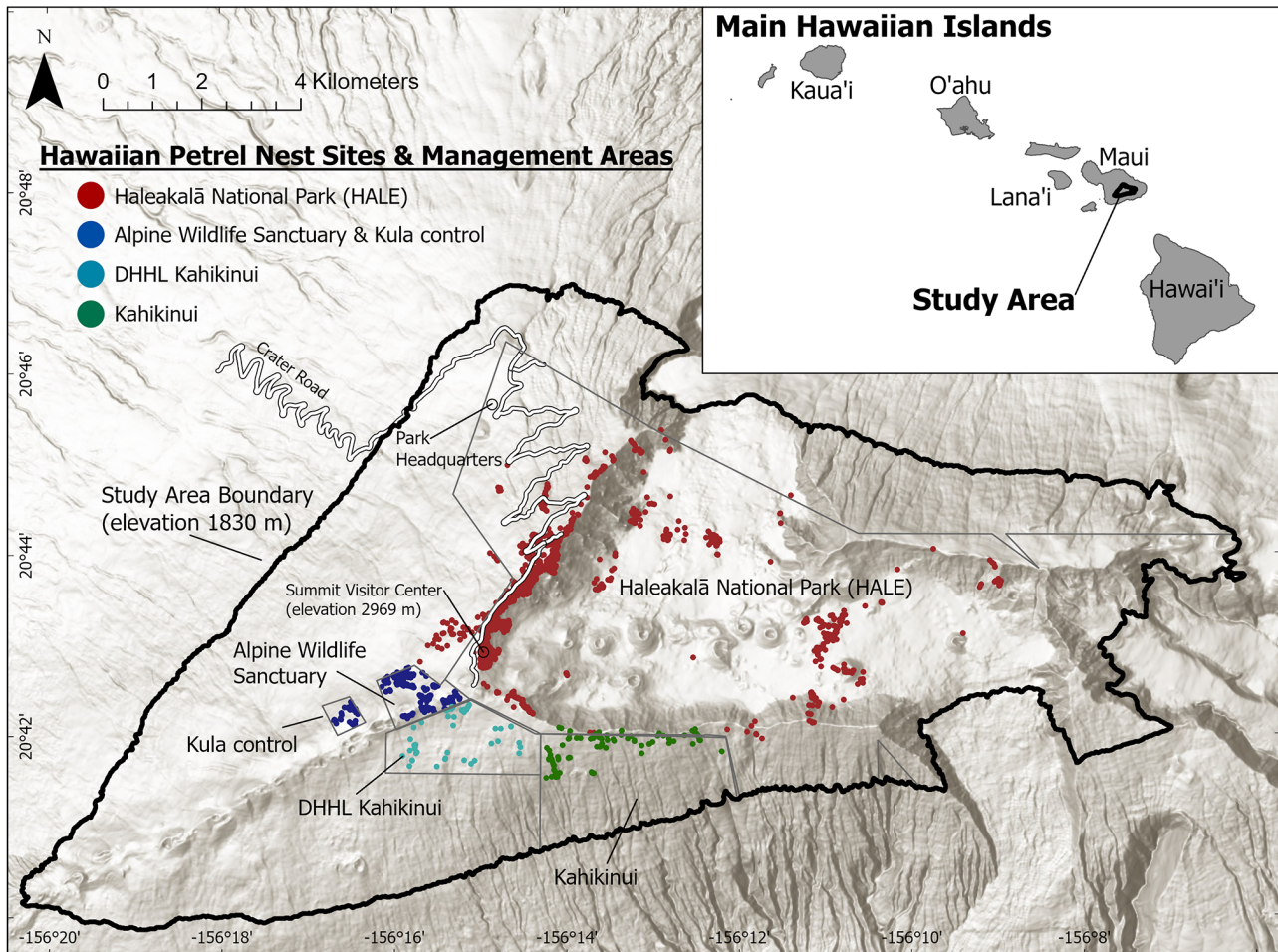


Fig. 1. Study area located on Haleakalā, east Maui delineated by the 1830 m contour (bold black line). Colored dots show Hawaiian petrel nest site locations according to sub-area jurisdictions

(guano, feathers, tracks) in accessible areas initiated by Larson (1967) and others during 1966 to 1971. Following Larson (1967), Simons (1985) contributed additional study of Hawaiian petrel breeding biology at HALE. Since 1988, opportunistic nest searching on foot and looking for petrel sign has occurred within HALE, along with annual monitoring of selected nest sites. Beginning in 1997, HALE staff used Global Positioning System (GPS) units to geolocate all known historic nest site locations and, by expanding opportunistic search efforts annually, have continually added new nest site locations when they are discovered.

More systematic searches for nest sites on Haleakalā adjacent to HALE were implemented in various management areas overseen by Hawai'i State Department of Land and Natural Resources Department of Forestry and Wildlife (DLNR-DOFAW) and the State Department of Hawaiian Homelands (DHHL; Table 1, Fig. 1). West of HALE, near the summit of the volcano, the Haleakalā High

Altitude Observatory has conducted astronomical research since 1958 and from 2011 to 2018, during construction of the Daniel K. Inouye Solar Telescope (DKIST), researchers conducted area-focused nest site searches, predator control, and nest monitoring within the fenced Alpine Wildlife Sanctuary (AWS) which encompasses the DKIST construction site and west of the AWS within an adjacent 'Kula control' site located in the DLNR-DOFAW Kula Forest Reserve (not shown; Chen et al. 2019; Table 1, Fig. 1). Beginning in 2011, south of HALE and the AWS, searches for nest sites have occurred in the upland area known as 'DHHL Kahikinui' to inform habitat planning and conservation associated with the Auwahi Wind Farm Project (Table 1, Fig. 1; Tetra Tech 2012). Since 2013, the Maui Nui Seabird Recovery Project (MNSRP) has searched for nest sites (with recorded effort) within 'Kahikinui' which includes lands managed by DLNR-DOFAW (Nakula Natural Area Reserve and Kahikinui Forest Reserves, not

Table 1. Study regions and Hawaiian petrel nest site counts from Haleakalā, east Maui. Areas of individual regions represent specific area searched in study above 1830 m elevation

Region	Area (ha)	Jurisdiction	Sampling	Nest sites
Haleakalā National Park (HALE)	7321	National Park Service	Opportunistic, targeted ^a	1877
Alpine Wildlife Sanctuary (AWS)/ Kula control site	210	DOFAW (Alpine Wildlife Sanctuary, Kula Forest Reserve, Kahikinui Forest Reserve)	Area-focused searches ^b	407
DHHL Kahikinui	366	Department of Hawaiian Homelands (Kahikinui Forest Project) ^c	Opportunistic, systematic searches ^d	68
Kahikinui	718	DOFAW (Kahikinui Forest Reserve, Nakula Natural Area Reserve)	Opportunistic, systematic searches ^e	101
			Nest sites for model input:	2453

^aR. Kaholoa'a unpubl. data (2020)
^bChen et al. (2019)
^c<https://dhhl.hawaii.gov/2022/12/06/new-plan-guides-kahikinui-forest-restoration/>
^dJ. Learned unpubl. data (2020)
^eTetra Tech (2012)

shown) and MNSRP has also searched for nest sites in the northern portions of the 'Kahikinui' area near the crater rim along the southern flank of HALE (Table 1, Fig. 1). Nest site searching and monitoring have continued annually to document changes in Hawaiian petrel presence and nesting abundance. In 2020, MNSRP in collaboration with HALE extended search efforts to the crater rim within the national park boundary (J. Learned unpubl. data 2021). From 2013 to 2021, 24.9% of the combined Natural Area Reserves above 1830 m elevation (1.79 km²) were exhaustively searched at least once annually to locate nest sites (MNSRP unpubl. data). This is equivalent to 1% of the total area evaluated herein. Although recent efforts in other areas to locate petrel nest sites have been aided by using scent-trained dogs (Aikman et al. 2001, Galase 2019, Bolton et al. 2021), search efforts on Haleakalā have been conducted on the ground by unaided human observers.

2.2. Study area and nest site locations

We delineated the study area (modeling domain) to be all land above 1830 m elevation on Haleakalā (163 km²), which included all known and recorded nest site locations through 2020. The modeling domain encompassed 4 study sub-areas where nest searching has occurred: HALE, Alpine Wildlife Sanctuary (AWS), DHHL, and Kahikinui (Table 1, Fig. 1). We combined burrow location datasets from the 4 study sub-areas and removed nest locations with

duplicate names and locations, nests with missing locations, and potential nests sites that were temporarily marked but later determined to not be nest sites. The final dataset used for predictive modeling contained 2453 unique nest site locations from the 4 study areas (Table 1). We counted the number of nest sites in 10 × 10 m grid cells across the modeling domain (to match the spatial resolution of predictor variables and modeling, see Sections 2.3 and 2.4) resulting in 1960 grid-cell locations containing nest site counts (dependent variable; range: 1 to 8 nest sites per grid cell).

2.3. Environmental predictors

We used spatially continuous predictor variables that quantified the landscape and were hypothesized to be important for describing Hawaiian petrel nesting habitat on Haleakalā (Table 2). To generate topographic variables, we obtained a 10 m resolution digital elevation model (DEM; US Geological Survey 2013) from which we derived slope, topographic position index (TPI; De Reu et al. 2013, Coates et al. 2020), surface roughness (Riley et al. 1999, Williams et al. 2009, Evans et al. 2014, Vorsino et al. 2014, Coates et al. 2020), and heat load index (HLI; McCune & Keon 2002, Evans et al. 2014). TPI quantifies the elevation of a location as higher (positive values), lower (negative values), or similar (values near zero) to the surrounding landscape at a given scale (Gallant 2000); this variable can represent small hills

Table 2. Spatial predictor variables used for modeling Hawaiian petrel nest site abundance and nesting habitat at Haleakalā, east Maui. All variables were re-sampled to a 10×10 m (100 m^2) grid cell resolution to match the variable with the greatest resolution (elevation). Variables in **bold italic** were used in the final model. TPI: topographic position index; HLI: heat load index; MGS: mean growing season; LOS: length of growing season

Category	Variable name	Scale	Type	Description	Native dataset, data type, resolution, source
Topography	Elevation	1 cell; 100 m^2	Continuous	Elevation (m) Topography	National Elevation Topography Dataset, raster, 10 m, US Geological Survey (2013)
	Slope	3×3 cells; 0.1 ha	Continuous	Maximum slope angle (degrees) between focal cell elevation and surrounding elevations (9-cell window)	
	TPI03	3×3 cells; 0.1 ha	Continuous	Topographic position index; (focal cell elevation) - MEAN(focal + neighborhood elevations)	
	TPI05	5×5 cells; 0.25 ha	Continuous		
	TPI10	10×10 cells; 1 ha	Continuous		
	TPI100	100×100 cells; 100 ha	Continuous		
	Rough03	3×3 cells; 0.1 ha	Continuous	Terrain roughness; square root of the average of the squared differences in elevation between the target center cell and neighborhood cells	
	Rough05	5×5 cells; 0.25 ha	Continuous		
	Rough10	10×10 cells; 1 ha	Continuous		
Rough100	100×100 cells; 100 ha	Continuous			
HLI	3×3 cells; 0.1 ha	Continuous	Predicted potential annual direct incident radiation based on slope, aspect (folded to SW = max, NE = min), and latitude		
Substrate	RockType	1 cell; 100 m^2	Categorical	Geologic rock type simplified to: Lava flows, Cinder and spatter, Sand and gravel, Ash (including tephra), Intrusion, Lithic debris	Geology of Hawai'i, shapefile, 15–50 m, Sherrod et al. (2007)
	Ash01	1 cell; 100 m^2	Binary	Geologic rock type simplified to: Not ash/cinder, Ash/cinder	
Vegetation	VegType	1 cell; 100 m^2	Categorical	Categories: Barren, Forest, Shrub, Grass/Herbaceous, Developed, with developed removed (converted to nearest neighbor)	LANDFIRE 2016 Existing Vegetation Type, raster, 30 m, LANDFIRE (2016)
	Veg01	1 cell; 100 m^2	Binary	Categories: Not vegetated, Vegetated, with developed removed (converted to nearest neighbor)	
	MGS	1 cell; 100 m^2	Continuous	Mean growing season NDVI value	USGS ARD Database, raster, 30 m, Dwyer et al. (2018)
	LOS	1 cell; 100 m^2	Continuous	Length of growing season	
Biophysical	Veg0Ash0	1 cell; 100 m^2	Binary	No vegetation or cinder/ash	LANDFIRE 2016/ Geology of Hawai'i
	Veg0Ash1	1 cell; 100 m^2	Binary	No vegetation, cinder/ash present	
	Veg1Ash0	1 cell; 100 m^2	Binary	Vegetation present, no cinder/ash	
	Veg1Ash1	1 cell; 100 m^2	Binary	Vegetation and cinder/ash present	
Climate	Rain	1 cell; 100 m^2	Continuous	Cumulative annual rainfall (mm)	Rainfall Atlas of Hawai'i, raster, 250 m, Giambelluca et al. (2013)
	Wind	1 cell; 100 m^2	Continuous	Mean annual wind speed (m s^{-1}) at 22:00 h local time	Evapotranspiration of Hawaii, raster, 250 m, Giambelluca et al. (2014)

and depressions (fine scales) or mountaintops/ridges and valley bottoms (large scales). Roughness is a measure of how variable elevations are in the surrounding landscape and is scale dependent. We evaluated TPI and roughness at 4 scales (0.1, 0.25, 1, and 100 ha, equivalent to 3, 5, 10, and 100 cell [10×10 m] neighborhoods; Table 2). HLI quantifies the potential annual direct incidental radiation based on slope, aspect, and latitude. We also included geological rock type (Sherrod et al. 2007) as a categorical variable (RockType) and as a binary class indicating the presence-absence of the cinder/ash rock type (Ash01; Table 2).

To generate biological variables, we included existing vegetation type (LANDFIRE 2016) as a categorical variable (VegType) and as a binary class to indicate vegetation presence-absence (Veg01; Table 2). We also included the 4 possible binary combinations of Veg01 and Ash01 as predictive layers, because nest sites (i.e. burrows) are not typically found in cinder/ash unless vegetation exists to provide soil cohesion. We derived an index of mean growing season (MGS) and length of growing season (LOS) from monthly estimates (2001–2018) of the Normalized Difference Vegetation Index (NDVI) acquired from the USGS Analysis Ready Data (Dwyer et al. 2018). Analysis Ready Data are produced from Landsat 4-8 satellite images that have been accurately georegistered, calibrated, and pre-processed (top of atmosphere and atmospheric correction). We included 2 spatially continuous climatic variables: cumulative annual rainfall (Rain; Giambelluca et al. 2013) and mean annual wind speed (Wind; Giambelluca et al. 2013; Table 2). The large area and complex topography at higher elevations on Haleakalā result in large zonal variability across the study area landscape for these 2 climatic variables.

We converted non-raster data sources (polygons of RockType and VegType) to 10 m resolution raster format. We resampled raster datasets with a native resolution coarser than the DEM (10 m) to 10 m by nearest neighbor (for categorical variables) or bilinear (for continuous variables) methods before generating derivative variables. We prepared and derived all variables using ArcGIS (ESRI) in Hawai'i Albers Equal Area Projection (EPSG 102007).

We evaluated (1) the degree to which the potential environmental predictor variables differentiated nest sites from background sites; and (2) correlations among predictor variables. Our selection of meaningful predictor variables was informed by first evaluating variables that contained redundant information. Evaluation consisted of 2 steps (see Supplement at

www.int-res.com/articles/suppl/n052p231_supp.pdf). First, we used principal components analysis (PCA) to visualize the interrelationships among the variables and evaluate the degree to which nest sites and background sites diverged along the PCA axes. Second, we generated a matrix of Pearson correlation coefficients (r) of pairwise relationships among the predictor variables and identified correlated pairs where $r \geq 0.70$ (~50% variation explained by the other variable).

2.4. Modeling to predict nest site distribution

We used random forests (RF; Breiman 2001) to predict the number of petrel nest sites per 100 m² (10×10 m cells). RF is a supervised machine learning modeling algorithm that extends the capabilities of classification and regression trees (CART; Olden et al. 2008) by recursively creating a very large number of trees from bootstrap sampling of the dataset. RF compares the predictions of each tree to the data not included in the bootstrap sample (the validation, or 'out-of-bag' sample), thereby creating numerous, internally cross-validated models. Unlike CART, trees are not 'pruned' but allowed to develop to their full extent. We calculated variable importance (VI) by randomly permuting the values of each predictor within each recursion and then recalculating the change in model performance. Because each recursion uses a different random subset of the response data and a different random subset of the predictor variables, it is considered an ensemble modeling procedure. The algorithm processes high-dimensional data very efficiently and avoids overfitting data. Furthermore, outliers and spatial autocorrelation have less influence on predicted values compared with parametric models, and complex, non-linear relationships are incorporated directly in the model. One of the principal criticisms of RF (and machine learning in general) for explanatory purposes is that regression coefficients and their measures of uncertainty are not calculated (Humphries & Huettmann 2018, Humphries et al. 2018). In addition, because individual trees cannot be examined, RF can be perceived as a black box. However, by acknowledging these criticisms and, more importantly, when prediction is specifically the goal, RF has been recognized as an effective and appropriate machine learning algorithm (Cutler et al. 2007, Crisci et al. 2012).

Input response data included the count of nest sites and predictor variable values within the 1960 grid cells (10×10 m) containing nest sites from the com-

binned datasets. Background data included predictor variable values extracted at 50 000 randomly selected cells from the full study area grid ($\sim 1.63 \times 10^6$ grid cells). Because nest site locations were mostly collected opportunistically, we assumed geographic sampling bias of environmental conditions was associated with individual nest sites. Geographic sampling bias occurs when areas are overrepresented due to relatively greater local sampling effort or when some of the environmental space suitable for a species is poorly represented (Kramer-Schadt et al. 2013, Fourcade et al. 2014). Landscape environmental parameters tend to be spatially autocorrelated and geographic bias will propagate environmental bias through a model. This can confound interpretation of model results, cause overfitting, and lead to poor model performance. ‘Spatial thinning’ can reduce the effects from sampling bias (Boria et al. 2014, Steen et al. 2021). Spatial thinning consists of filtering data in areas where response data are highly concentrated while retaining greater proportions of data in areas where concentrations are less (Aiello-Lammens et al. 2015). We used the *spThin* package in R (Aiello-Lammens et al. 2015) to generate 100 spatially thinned datasets with a nearest neighbor distance of 60 m between nest site locations. This resulted in 100 thinned sets of 542 to 548 grid cells.

We developed and evaluated models with the *randomForest* package in R (Liaw & Wiener 2002). Model development consisted of 3 steps. First, based on the PCA and Pearson’s correlation, we removed one of each pair of variables where $r > 0.70$. Second, we split each thinned dataset into training (75%) and test (25%) sets, then partitioned the training data with 10-fold cross-validation, with model runs ($N = 500$ per thinned set) for each partition k split into training (70%) and out-of-bag sets. Third, we tuned models in each thinned set to determine the total number of trees and optimal number of predictor variables to include at each split in the trees. Lastly, we conducted individual model runs with the remaining predictor variables and optimal variable numbers and splits in the trees.

Due to inter-relationships among elevation, wind, rain, and vegetation (based on PCA [Table S1, Fig. S1] and correlation [Table S2, Fig. S2]), we evaluated 4 candidate models (Table 3) to assess the degree to which model performance varied with different combinations of variables (see Supplement): Model 1 = Topography (Elevation, HLI, Slope, TPI03, TPI100) + Substrate (Ash01) + Vegetation (Veg01); Model 2 = Topography (Elevation, HLI, Slope, TPI03, TPI100) + Substrate (Ash01); Model 3 = Topography (Elevation,

Table 3. Mean square error (MSE) and pseudo- R^2 values in training and test datasets among 4 model groups of random forest models to predict Hawaiian petrel nest site relative abundance on Haleakalā, east Maui. Model 1 was selected as the final model. Predictor variables were associated with 4 categories (see Table 2): Topography, Substrate, Climate, and Vegetation. SE and lower and upper 95% confidence intervals (LCL and UCL) are shown

Model	Set	Estimate	SE	LCL	UCL
Model 1 = Topography (Elev, HLI, Slope, TPI03, TPI100) + Substrate (Ash01) + Vegetation (Veg01)					
MSE	Test	0.050	0.0001	0.049	0.050
	Train	0.052	0.0001	0.052	0.052
Pseudo- R^2	Test	0.206	0.0007	0.205	0.207
	Train	0.204	0.0007	0.202	0.205
Model 2 = Topography (Elev, HLI, Slope, TPI03, TPI100) + Substrate (Ash01)					
MSE	Test	0.052	0.0002	0.051	0.052
	Train	0.051	0.0002	0.051	0.051
Pseudo- R^2	Test	0.222	0.0008	0.220	0.223
	Train	0.215	0.0008	0.213	0.216
Model 3 = Topography (Elev, HLI, Slope, TPI03, TPI100) + Substrate (Ash01) + Vegetation (Veg01) + Climate (Wind)					
MSE	Test	0.051	0.0002	0.050	0.051
	Train	0.051	0.0002	0.051	0.052
Pseudo- R^2	Test	0.217	0.0008	0.215	0.218
	Train	0.217	0.0008	0.215	0.218
Model 4 = Topography ([NO Elevation], HLI, Slope, TPI03, TPI100) + Substrate (Ash01) + Vegetation (Veg01) + Climate (Wind, Rain)					
MSE	Test	0.051	0.0002	0.051	0.052
	Train	0.052	0.0002	0.052	0.052
Pseudo- R^2	Test	0.206	0.0007	0.205	0.207
	Train	0.204	0.0007	0.202	0.205

HLI, Slope, TPI03, TPI100) + Substrate (Ash01) + Vegetation (Veg01) + Climate (Wind); and Model 4 = Topography ([NO Elevation], HLI, Slope, TPI03, TPI100) + Substrate (Ash01) + Vegetation (Veg01) + Climate (Wind, Rain). We used 3 measures to evaluate performance within and between the models: (1) the stability of the model mean squared error (MSE) as the number of trees increased; (2) the MSE of the cross-validations; and (3) comparison of pseudo- R^2 values ($1 - [MSE/\sigma^2]$) between training and test sets with ordinary least square regression (see Supplement). We evaluated variable importance (VI) as the proportional increase in MSE when a variable was not included in the models (see Supplement).

Using our final selected model, predicted number of petrel nest sites per 100 m² cell were calculated by averaging predictions among thinned sets with pre-

cision estimated using 1 standard deviation (SD). We mapped predicted nest density (per 100 m²) and SD, and examined the distributions of predictor variable values for the background study area compared with those weighted by predicted nest density to describe the modeled results on the landscape and in habitat space.

3. RESULTS

3.1. Nest sites and model performance

The distribution of observed nest sites counted among the 100 m² cells was right skewed (Fig. 2): 82% of cells included single sites, with an additional 13% of cells having 2 sites; very few cells (~0.5%) had 5 to 8 nest sites (Fig. 2).

Overall, the 4 predictive models had similar, low MSE (≤ 0.05 ; Table 3), indicating models did not overfit the data and were consistent in model predicted values. Model 1 without climate and Model 2 without climate and vegetation required fewer (3 to 4) variables for splitting trees compared with the other 2 model groups (6 variables each). MSEs for all 4 models reached an asymptote at 3 variables per tree split. Beta regressions indicated MSEs for test data were less than those for training data, indicating that the model predicted well throughout the study area, but the differences in MSE between test and training data

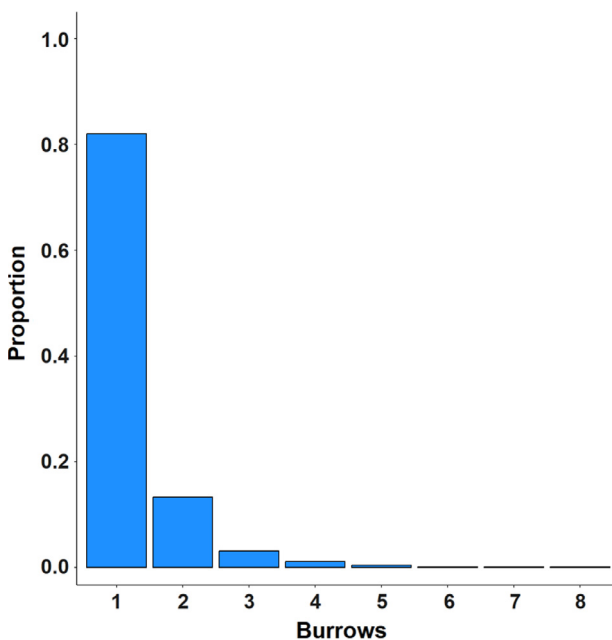


Fig. 2. Proportion of total occupied grid cells (1960 total) showing the number of Hawaiian petrel nest sites (N) per 100 m² grid cell on Haleakalā, east Maui

were greatest for Model 3 (mean difference in MSE of -0.19); for the remaining 3 models mean differences in MSE were less than -0.05 (Table S3). Overall, this reflects model consistency and accuracy.

The patterns for pseudo-R² were similar to those of MSE; ordinary least squares regression indicated negligible differences among training and test sets (Table 3). Because pseudo-R² values are not the same as R² values derived by least-squares estimation, values are only meaningful when compared with other pseudo-R² from models evaluating the same data (Table 3). Moreover, pseudo-R² values between 0.2 and 0.4 indicate very good model fit (McFadden 1974). Performance within models was reflected in performance between the models for both MSE and pseudo-R² with negligible differences in either measure among the 4 models. Thus, among the 4 models, pseudo-R² values indicated relatively good model fit for both training and test data (Table 3).

Absolute pairwise differences in predicted number of Hawaiian petrel nest sites within 10 × 10 m grid cells were similar among models, with 95 to 99% of the differences falling within a range of -0.4 to 0.3 nest sites per cell (Fig. S3); however, the range in differences did vary among the pairwise comparisons (Fig. S3). The greatest differences were between models with elevation (Models 1 to 3) and Model 4 without elevation (Fig. S3a,b,c), and the least differences were among models with elevation (Models 1 to 3) and without rain (Fig. S3d,e,f). When vegetation was paired with wind and rain (Model 4), there was little difference in number of predicted nest sites compared with when vegetation and climate (wind and rain) were excluded (Model 2) (Fig. S3b).

The ECDFs highlighted small percent differences in predicted number of nest sites among models (Fig. S4) and were consistent with results of the absolute differences (Fig. S3). The greatest differences in predicted number of nest sites occurred between the model without elevation (Model 4) and the model with elevation and without wind and rain (Model 1); differences approached 200% (Fig. S4a). The comparison between the model without elevation (Model 4) and the model without rain, wind, and vegetation (Model 2) approached percent differences of 50%, but 95 to 99% of differences were between ~5 and 10% (Fig. S4c). Percent differences among the other pairwise combinations also were small, with 95 to 99% ranging from 2 to 10% (Fig. S4b,d,e,f).

Although differences among models were not great, pairwise comparisons (Figs. S3 & S4) and VI (Fig. 3) revealed elevation (VI of ~35–45%) was the strongest predictor in models where it was present

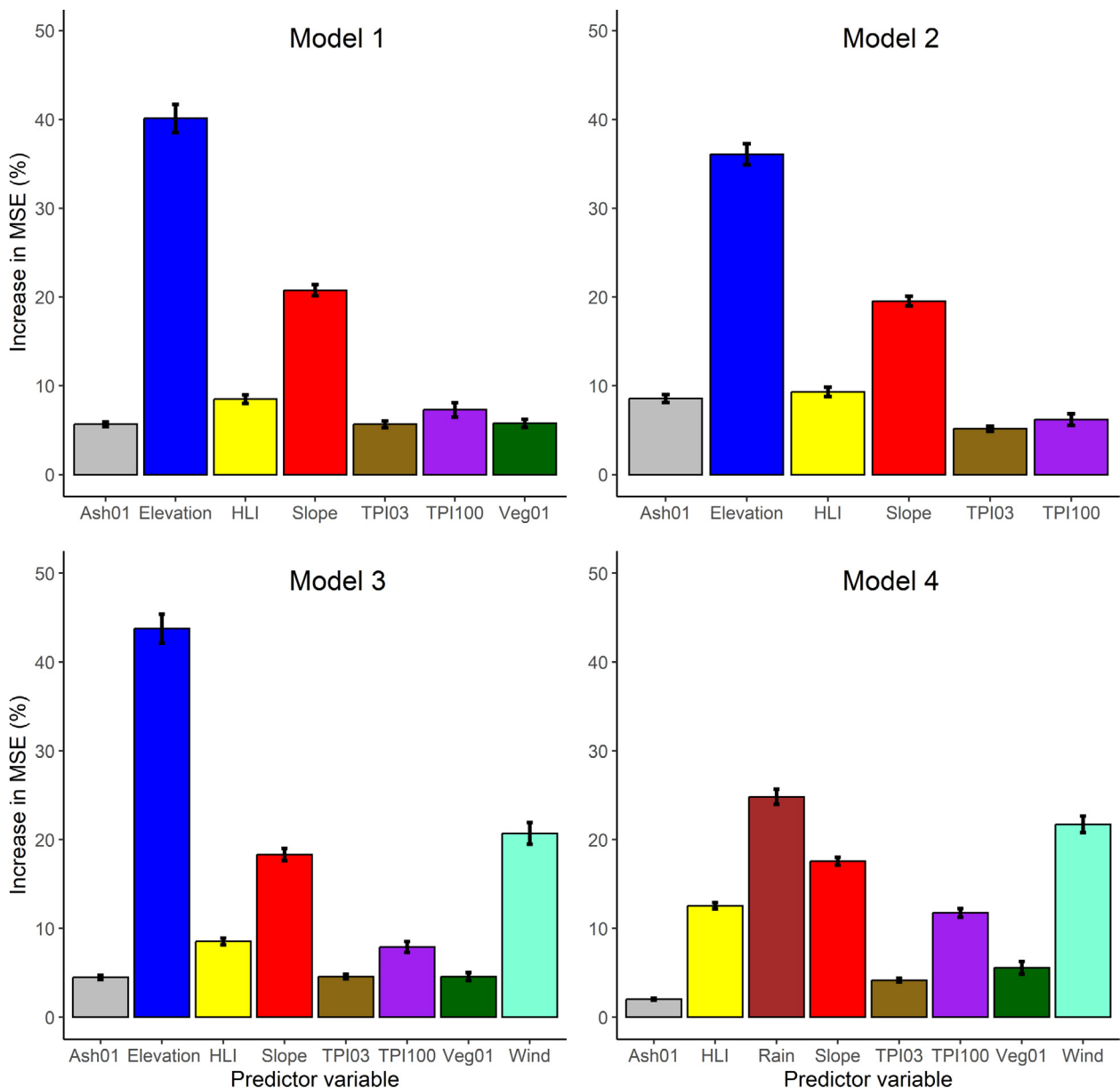


Fig. 3. Variable importance (VI) expressed as percent increase in MSE (mean \pm 95% CI) for 9 variables in 4 model groups used for prediction of the number of nest sites of Hawaiian petrels on Haleakalā, east Maui. Model 1: Topography (Elevation, Heat Load Index [HLI], Slope, Topographic Position Index [TPI03 and TPI100]) + Substrate (Ash01) + Vegetation (Veg01) was selected as the final model for nest site prediction. Variables in Models 1 to 4 and definitions of all predictor variables are given in Table 2

(Models 1 to 3; Fig. 3). In the absence of elevation, wind and rain were relatively less important, yet each accounted for $\sim 25\%$ variable importance (Fig. 3). In the model without elevation (Model 4; Fig. 3), the cumulative importance of rain and wind was similar to that of elevation in the other 3 models where elevation was included. Slope (VI of $\sim 20\%$) had the second highest VI among all models, except in the model without elevation (Model 4), where the values for rain and wind were greater (Fig. 3). HLI

had moderate importance (VI of $\sim 10\%$), particularly in the model group without elevation (Model 4; Fig. 3). The TPI03 and TPI100 had lower importance in Models 1 to 3 (VI of $<10\%$), and the binary variables Ash01 and Veg01 also showed lower importance in Models 3 and 4 (VI of $<10\%$).

Based on the collective patterns of MSE, pseudo- R^2 , absolute differences in predicted values, ECDFs, and large VI for elevation, we selected Model 1 (elevation, slope, HLI, TPI03, TPI100, the presence-

absence of cinder/ash [Ash01], and the presence-absence of vegetation [Veg01]) for predicting and mapping relative nest site abundance on Haleakalā.

3.2. Final model predictions

Predicted nest site abundance reflected the influence of the strongly right-skewed empirical distribution of observed number of nest sites (Fig. 2), with no values >2 nest sites per 100 m² (Fig. 4). The greatest concentrations of nest sites were predicted to be in a crescent along the crater rim from the northwest to southeast and straddling the ridgeline descending to

the southwest from the summit (Fig. 4). Other areas with moderately high predicted density included the relatively flat, eastern and northern interior of Haleakalā crater, particularly where cinder cones are not present (Fig. 4). A large proportion of area, especially the lower elevation flanks along all sides of Haleakalā, was predicted to have few nest sites (Fig. 4).

Inspection of the distributions of landscape parameter values (weighted by predicted nest density) and compared with background values revealed Model 1 predicted more nest sites at higher elevations (2100 to 2300 m and >2600 m; Fig. 5A) and in areas with slopes <10° and 35 to 45° compared to background (Fig. 5B). Nest sites were predicted more frequently where local topographic positions were similar to or slightly greater than the local mean (TPI03; Fig. 5C), and where landscape-scale topographic positions were greater than the landscape-scale mean (TPI100; Fig. 5D). Nest sites were predicted to be more abundant at slightly lower HLI values than background (Fig. 5E) and where vegetation was lacking compared with the background (Fig. 6C,D).

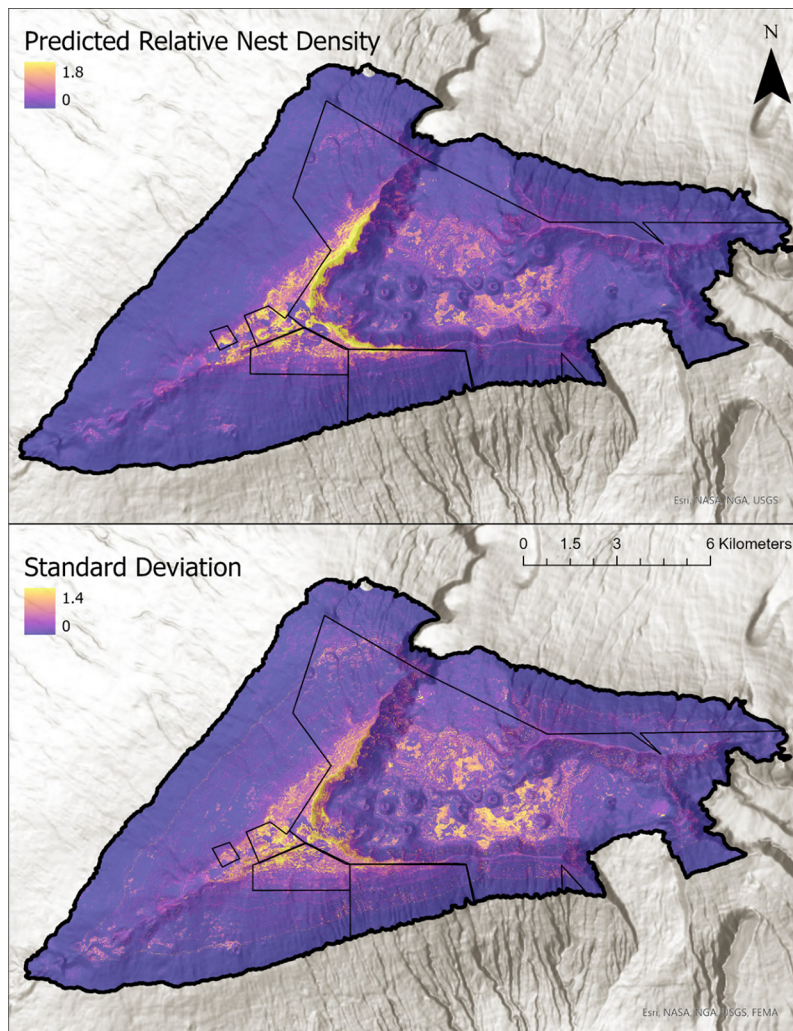


Fig. 4. Final predicted relative Hawaiian petrel nest site density (per 10 × 10 m grid cell; 100 m²; top) and SD (bottom) on Haleakalā, east Maui. Predictions were based on a random forest model (Model 1) that included elevation, slope, small-scale topographic position index (TPI03, 30 × 30 m), large-scale topographic position index (TPI100, 1000 × 1000 m), heat load index, presence of volcanic cinder/ash, and presence of vegetation (see Table 2 for description of predictor variables)

4. DISCUSSION

With 2453 Hawaiian petrel nest site locations recorded since 1954 on Haleakalā, east Maui, we developed a RF model to predict nest site locations per 100 m² throughout 163 km² of available, high-elevation habitat. Our model highlighted 2 important aspects about the nesting habitat on Haleakalā. First, nest sites were non-randomly distributed and aggregated with greater densities in higher, and more rugged and topographically variable areas of the volcano. Second, at the landscape scale, elevation, slope, and topographic variability were the main factors underlying predicted nest site locations, while substrate (i.e. presence-absence of volcanic cinder/ash) and presence-absence of vegetation were relatively less important (increase in MSE of ~6%) at the 10 m scale.

The clumped distribution of predicted nest sites could potentially re-

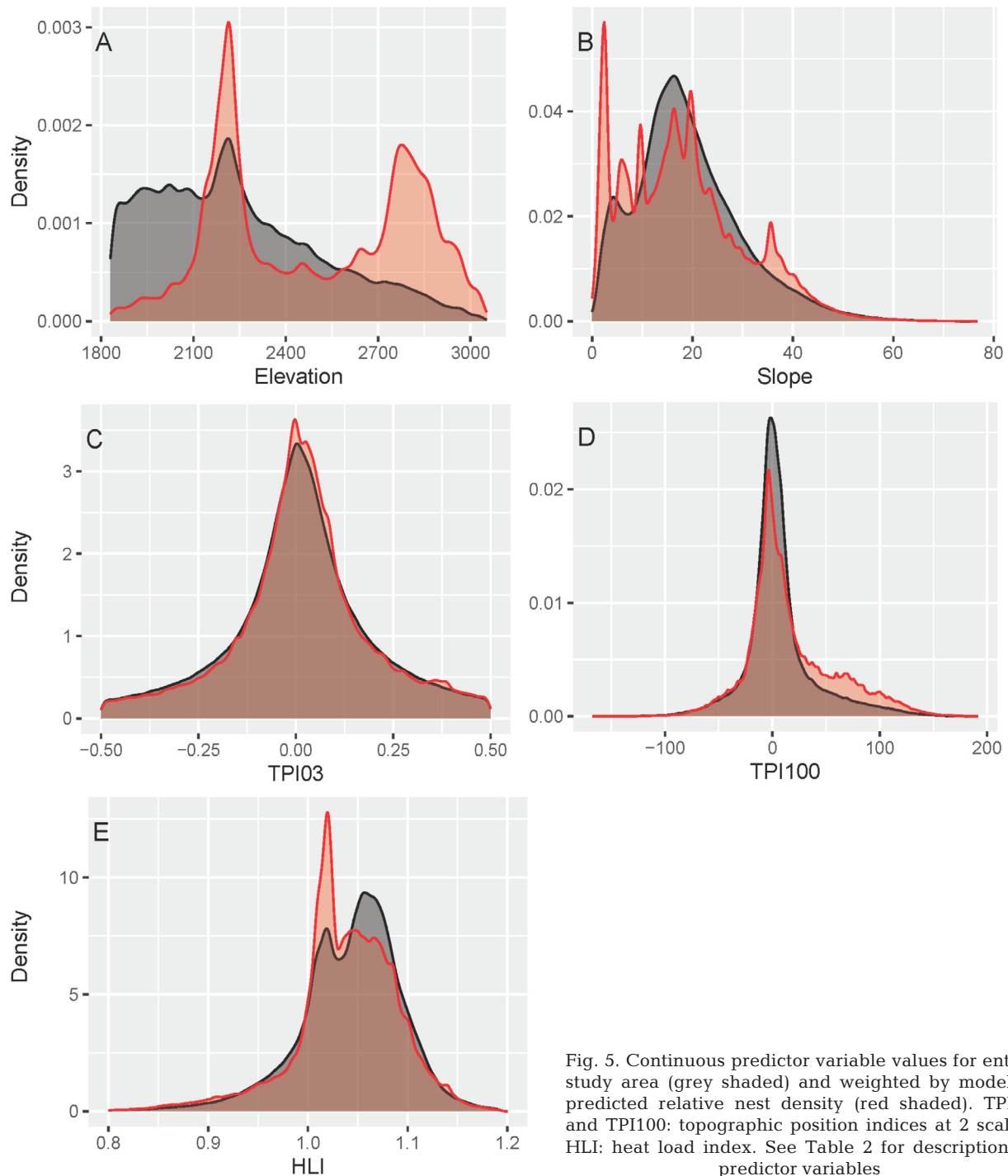


Fig. 5. Continuous predictor variable values for entire study area (grey shaded) and weighted by modeled predicted relative nest density (red shaded). TPI03 and TPI100: topographic position indices at 2 scales; HLI: heat load index. See Table 2 for description of predictor variables

sult from environmental filtering, legacy effects from predation and habitat alteration by non-native species, subsequent habitat protection and recovery (Hodges & Nagata 2001, Kelsey et al. 2019), and smaller-scale alpine volcanic geomorphology (Brandt et al. 1995). Environmental filtering is often expressed through habitat selection, and while the RF

model is not a habitat selection model per se, results indicated Hawaiian petrel nest sites occurred in areas with different habitat conditions compared with random background environmental conditions. Furthermore, the contemporary distribution reported here may result from certain legacy effects. For example, the densest areas of seabird colonies may

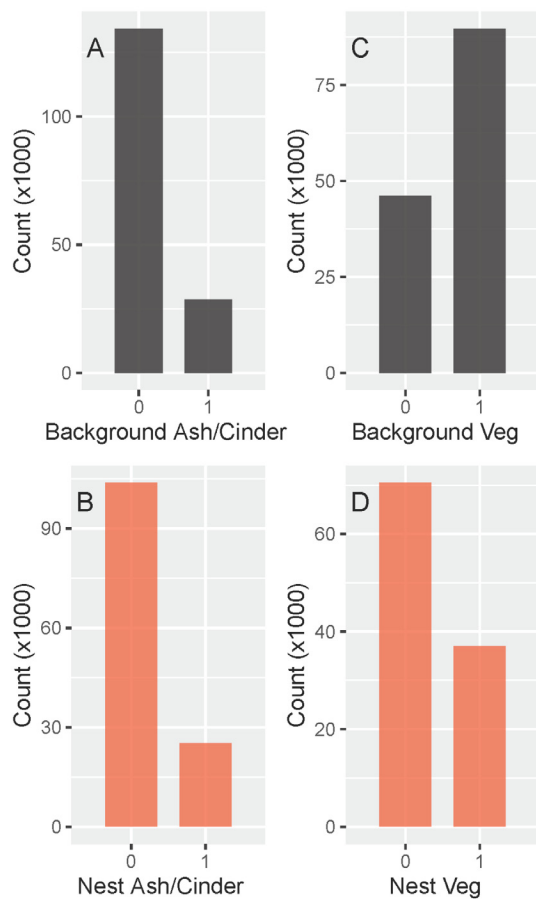


Fig. 6. Binary predictor variable values (presence = 1, absence = 0) for entire study area (grey) and weighted by modeled predicted relative nest site density (red)

be regulated in part by internal recruitment among strongly philopatric individuals as is typical of Procellariiformes (Warham 1990, Clark et al. 2019, Bird et al. 2022). Also, extreme environmental conditions (e.g. winter, aridity, and high elevation) at Haleakalā likely regulate invasive mammal populations and may result in similar dynamics as have been hypothesized for colonies of Hutton's shearwater *Puffinus huttoni* and sooty shearwater *Ardenna grisea* that have been shown to persist due to inverse, density-dependent predation (Lyver et al. 2000, Cuthbert 2002). More information about long-term burrow occupancy and recruitment would help us to understand possible density-dependent patterns associated with coloniality and spatial clustering of Hawaiian petrel nest sites at Haleakalā. Additionally, more information about the distribution and interaction among petrels with invasive mammals at Haleakalā would be beneficial for understanding spatial population dynamics associated with nest site distribution

while also helping to better understand the effects of predators and predator management efforts.

Predictor variables appeared to be ecologically meaningful measures of environmental conditions for predicting nest site distribution on Haleakalā. The patterns in spatial distribution of predicted nest sites may result in part from inherent scale-dependent patterns in geomorphology. Our RF model results were consistent with results from an analysis of Hawaiian petrel habitat selection that included a much smaller area focused on the west flank and crater rim of Haleakalā (Brandt et al. 1995). Our more spatially extensive results indicated slopes (30 m scale) $<10^\circ$ and 35 to 45° had more nest sites compared with the background. Slope $>45^\circ$ represents habitat that is dangerous or impossible to survey effectively and there likely are petrels nesting in inaccessible areas not well represented in our modeling. It is possible that flat areas in the crater floor have more soil available for petrels to excavate burrows (see locations in Fig. 1), or perhaps availability of nesting habitat is also influenced by additional landscape features (not measured in this study). Topographic position indices (TPI) at 2 scales (30 and 1000 m) were important; the first scale (30 m) includes small landforms such as ledges, fractured dikes, and large boulders, and the larger scale (1000 m) reflects larger variability in the landscape associated with lava channels, larger dikes, gullies, and ridges. Brandt et al. (1995) found nest sites were most likely to be located on steep slopes, under large rocks, and in the vicinity of shrubs. Presence of cinder/ash in our model was negatively related to predicted nest site density, consistent with Brandt et al. (1995), who pointed out that large areas near the summit composed of loose cinder and ash were not usable by petrels and likely do not support stable burrowing habitat. However, their results indicated that red-colored soil was more common than expected at nest sites. While it is not clear from Brandt et al. (1995) what color can be ascribed to cinder/ash, future model improvement might be possible by quantifying substrate color from high-resolution satellite imagery. More effort is needed to resolve potential nesting habitat throughout Haleakalā, where in the absence of excluded ungulates, petrels may now be able to excavate and maintain fragile earthen burrows (R. Kaholoa'a pers. obs.) more typical of Hawaiian petrel on other Hawaiian Islands and among gadfly petrels in general.

Mostly consistent with previous studies throughout Hawai'i, we found predicted nest sites on Haleakalā were associated with relatively high elevation and

steep, rocky, unvegetated habitat (Fig. 5). On Haleakalā, although impossible to determine for certainty, the importance of elevation as a predictor may in part reflect an artefact of the abandonment of formerly used lower elevation sites. On Lanaʻi and Kauaʻi burrows were found in lower elevation forests with a well-developed understory of ferns (VanZandt et al. 2014, Troy et al. 2017). On Lānaʻi, VanZandt et al. (2014) used logistic regression to model nest site parameters and stratified-random location parameters and found petrel nest locations at 600 to 1000 m were best described by greater slopes where understory was dominated by native vegetation with an open canopy. On forested montane areas of Kauaʻi, Troy et al. (2017) used similar presence/available logistic regressions and found petrel nest habitat suitability was best described by areas with greater mean annual wind speeds and in areas with greater slope and native vegetation cover. These patterns underscore the need to include such data as analyzed herein for Haleakalā together with nest sites data from multiple islands (Troy et al. 2017, Raine et al. 2021) to investigate linkages between Hawaiian petrel niche dimensions or habitat selection based on nest site characteristics. Although we did not quantify habitat parameters immediately surrounding nests at Haleakalā, such data do exist for subsets of the data analyzed herein (e.g. Kahikinui; J. Learned unpubl. data) and a standardized approach among the other jurisdictional areas on Haleakalā could provide better information to describe nest site requirements that can be used to inform conservation in the future.

The RF models were relatively consistent within and across model sets, especially regarding variable importance, lending confidence to their ability to predict accurate patterns in the present Hawaiian petrel nest site distribution on Haleakalā. Nevertheless, several caveats exist. First, nest sites were identified and located predominantly by opportunistic sampling, and even though spatially thinning the datasets helped reduce spatial sampling bias, our model predictions likely were influenced to some degree by the opportunistic nature of the original sampling in the field. Most importantly, biased effort focused more on areas where nests were more likely to occur, thus positively influencing predicted densities for specific habitat characteristics. Next, although our predictor variables were spatially continuous, ecologically sensible, and based broadly on prior studies (e.g. Brandt et al. 1995, VanZandt et al. 2014, Troy et al. 2017), we emphasize that our results are primarily predictive and not explanatory per se.

This was especially so for the substrate and vegetation variables, which had spatial scales that were relatively coarse compared with the size of a localized nest site area (i.e. a few m²), thus making it difficult to understand important smaller-scale habitat associations with nest sites. For example, Brandt et al. (1995) and Raine et al. (2021) reported clear selection for substrate and vegetation within a few meters of nest site sites on Haleakalā and Kauaʻi, respectively. Additionally, whereas our predictor variables represent biophysical components of the environment, additional potentially important biotic factors, including the occurrence or expected density of non-native predators and invasive plants, were not included. Although these factors can be important for predictive modelling, such spatially explicit data on biological and ecological interactions can be difficult to obtain (Giannini et al. 2013, Wisz et al. 2013). Nevertheless, we acknowledge future model performance may be enhanced by including such ecological interactions and other meaningful variables (Leach et al. 2016, Dormann et al. 2018).

Existing long-term data also offer the unique ability to evaluate the effects of climate change and climate variability on petrel reproductive output and recovery. Climate change and variation in ocean climate conditions can influence range expansion of predators (e.g. cats and mongooses), and survival and reproductive output among seabirds in Hawaiʻi and the subtropics (Waugh et al. 2015). Linking climatological variation with spatial patterns in occupancy could inform future management of threats associated with predators that may change with climate at Haleakalā. A logical step could be to conduct ecological niche factor analysis (Hirzel et al. 2002) to describe the degree of selection for specific habitat conditions (niche breadth). Similar steps have been suggested as important research priorities that can shed more light on understanding the relationships between environmental parameters and breeding success of ecologically similar Barau's petrel *Pterodroma barau* (Pinet et al. 2009).

5. CONCLUSIONS

Island-specific extirpations, low population size, and cumulative impacts from non-native species were among the main reasons Hawaiian petrel remains listed under the Endangered Species Act as endangered (US Fish and Wildlife Service 1967). Throughout the Hawaiian Islands, fossil evidence (Olson & James 1982b) and historical observations

(Munro 1955) indicate Hawaiian petrels once occurred across a large elevation gradient with variable biophysical conditions. The current range of Hawaiian petrel throughout Hawai'i is a relic of predation by rats, mongooses, feral cats, and feral pigs, and severe habitat alteration by feral goats, pigs, other ungulates, and invasive plants. It is possible that habitat conditions where nest sites have been described on Haleakalā may not reflect optimal biophysical habitat, but instead represent a narrower range of former nesting conditions that describe refugia from predation and habitat alteration. Yet, in its current state, Haleakalā remains one of the most significant nesting areas throughout the species' range. Our results provide critical new information to better evaluate breeding population size, to assess the degree to which predator control and fencing overlap with or enclose predicted habitat, and to identify areas that could be systematically targeted to locate additional unknown nest sites and improve predictive models in the future. Although this study focused on predicting nest site locations at higher elevations on Haleakalā, suitable nesting habitat might exist at lower elevations, provided nesting petrels are protected from invasive predators, grazing ungulates, and significant land alteration. Variation in ocean climate conditions, climate change and its influence on range-expansion of predators (e.g. cats and mongooses), recent efforts by the State of Hawai'i and federal agencies to increase renewable energy resources (including wind power), and new science infrastructure at Haleakalā may place additional stress on the species. Recently, conservation efforts in Hawai'i have targeted reintroduction and social attraction of extirpated species, such as Hawaiian petrel and 'a'o Newell's shearwater *Puffinus newelli* to protected, predator-proof nesting areas at lower elevations in the main Hawaiian Islands (e.g. Nihoku on Kaua'i and Kahakuloa-Makamaka'ole on west Maui; Young et al. 2018, Raine et al. 2023, VanderWerf et al. 2023). Our predicted nesting habitat can inform such efforts and help guide placement of additional ungulate fencing that could increase conservation easements and assist spatial management efforts for increased protection and invasive predator control to benefit nesting petrels. Lastly, although our initial predictive maps are useful for evaluating habitat extent in general, we caution they not be used to extrapolate true breeding pair abundance. Future evaluation of ongoing monitoring data incorporating breeding propensity and annual occupancy would help inform such an estimate of the breeding population at Haleakalā and surrounding high-elevation habitat on east Maui.

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