

Predictive modeling of coral distribution and abundance in the Hawaiian Islands

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ABSTRACT: This study developed species distribution models (SDMs) of the 6 dominant Hawaiian coral species (*Montipora capitata*, *Montipora flabellata*, *Montipora patula*, *Pocillopora meandrina*, *Porites compressa*, and *Porites lobata*) around the main Hawaiian Islands (MHI). To construct the SDMs, we used boosted regression tree (BRT) models to investigate relationships between the abundance (i.e. benthic cover) of each species with a set of environmental variables for the time period from 2000 to 2009. Mean significant wave height and maximum significant wave height were the most influential variables explaining coral abundance in the Hawaiian Islands. The BRT models also identified relationships between coral cover and island age, depth, downwelled irradiance, rugosity, slope, and aspect. The rank order of coral abundance (from highest to lowest) for the MHI was *Porites lobata*, *M. patula*, *Pocillopora meandrina*, *M. capitata*, *Porites compressa*, and *M. flabellata*. Mean coral cover predicted for each species was relatively low ($\leq 5\%$) at each island and for the entire MHI except for *Porites lobata* around Hawaii (11%). The areas of highest predicted coral cover summed for the 6 species were Kaneohe Bay on Oahu; the wave-sheltered reefs of Molokai, Lanai, Maui, and Kahoolawe; and the Kohala coast of Hawaii. Regional-scale characterizations of coral species from these SDMs provide a framework for spatially explicit population modeling and ecological inputs to marine spatial planning of Hawaiian coral reef ecosystems.

KEY WORDS: Coral · Species distribution · Modeling · Benthic cover · Boosted regression trees · Hawaiian Islands

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INTRODUCTION

Coral reefs are an ecosystem in transition (Dubinsky & Stambler 2011). As reefs transform over the next century, the ability to understand the magnitude and composition of coral community changes depends upon the accuracy and resolution of the biological characterization of reef ecosystems. Scleractinian corals are the foundation species of tropical and subtropical reefs, yet information to evaluate their status is deficient. For example, only 5 of 845 coral species had sufficient species-specific population trend data to recently evaluate their extinction risk using the associated IUCN Red List criteria (Carpenter et al. 2008). Remote sensing technology has

enabled global- and regional-scale mapping of shallow coral reefs (Spalding et al. 2001, Mumby et al. 2004), yet the sensors only allow interpretation of habitats (e.g. patch reef, fore reef) or functional groups (e.g. coral, algae, sand) and cannot differentiate between individual species (Mumby et al. 2004, Goodman & Ustin 2007). Field surveys can provide information at a species level, but are often limited to a small set of geographic locations. As a method to integrate the strengths of the different approaches to improve the biological characterization of reefs, species distribution models (SDMs) can incorporate field observations and environmental covariates from observational, remotely sensed, or model data into statistical models that predict macroecological-scale,

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spatially continuous distributions of coral species (Guisan & Thuiller 2005, Austin 2007, Elith & Leathwick 2009).

Widely utilized for modeling species in many ecosystems (Elith & Leathwick 2009, Ready et al. 2010, Robinson et al. 2011), SDMs have less frequently been applied to coral reef species but have been used to predict distributions of biological functional groups and habitat types (Garza-Pérez et al. 2004, Guinotte et al. 2006, Chollett & Mumby 2012) and coral reef community metrics (Harborne et al. 2006, Pittman et al. 2009, Knudby et al. 2010). SDMs are constructed by building a representation of the realized species niche and extrapolating the niche requirements into geographical space (Guisan et al. 2007, Elith & Leathwick 2009, Peterson et al. 2011). Comparative analysis of population condition and geographic distribution across a range of temporal and spatial scales are possible with SDMs (Guisan et al. 2007, Elith & Leathwick 2009, Peterson et al. 2011).

Coral species distributions are influenced by a number of environmental factors such as wave energy, benthic geomorphology, and turbidity. In the Hawaiian Islands, disturbance from waves is the primary factor that structures coral communities (Dollar 1982, Grigg 1983, Engels et al. 2004, Jokiel et al. 2004, Storlazzi et al. 2005). Dollar (1982) found a vertical zonation of coral species dominance, from shallow to deep, of a *Pocillopora meandrina* boulder zone, *Porites lobata* reef bench zone, and *Porites compressa* structured by wave energy and storm frequency. In addition to wave height and direction, Jokiel et al. (2004) identified depth, rugosity, geological island age, and organic sediment content (an indicator of turbid, low light environments) as significant factors that structure Hawaiian coral communities. Although these studies identified significant environmental factors for Hawaiian reefs, no prior studies have systematically examined the influence of these factors on the distribution and abundance of coral species across the entire seascape of shallow reefs in the main Hawaiian Islands (MHI).

In order to evaluate the contribution of environmental drivers to Hawaiian corals, we developed species distribution models for the benthic cover of the 6 most common coral species (*Montipora capitata*, *M. flabellata*, *M. patula*, *Porites compressa*, *P. lobata*, *Pocillopora meandrina*) around the MHI. To construct the SDMs, we use boosted regression trees (BRT), an efficient, ensemble method for fitting statistical models of species response variables (e.g. benthic cover) from environmental predictor variables (Elith et al. 2006, Elith et al. 2008). We integrate field surveys for

corals with environmental data of wave exposure, benthic geomorphology, and downwelled irradiance from 2000 to 2009 to predict species distribution and abundance. Using the BRTs, we identify optimal models for each species from a set of model runs that explore the best model parameters to minimize predictive deviance (Elith et al. 2008). We discuss the geographic distributions and benthic cover patterns of the coral species and the set of environmental factors most prominently used by the models to construct the distributions.

MATERIALS AND METHODS

Study area

The study area included the shallow seafloor (0 to 30 m depth) around the 8 MHI. The Hawaiian archipelago encompasses a group of volcanic islands and atolls that span 2500 km in the central north Pacific Ocean (Fig. 1, Fletcher et al. 2008). The geography of these volcanic islands is characterized by prominent coastal capes and headlands that demarcate coastal exposures to different climate and ocean conditions (Fig. 1). The north coasts of Kauai, Oahu, and Maui are exposed to large northern hemisphere winter swells (≥ 7 m), while southern hemisphere storms produce waves (3 to 5 m) along Hawaiian south shores in summer (Fletcher et al. 2008). The eastern or windward side of the islands experience consistent easterly tradewinds (10 to 20 knots) that generate steady wind-driven waves (1 m; Fletcher et al. 2008). There are only 2 large, natural semi-enclosed waters bodies in the MHI, Pearl Harbor and Kaneohe Bay on Oahu (Fig. 1). Coral reefs are found around the coasts and embayments of all islands (Battista et al. 2007).

Coral species benthic cover observations

We compiled a benthic cover database of 6 Hawaiian coral species (*Montipora capitata*, *M. flabellata*, *M. patula*, *Pocillopora meandrina*, *Porites compressa*, *Porites lobata*) from scientific research and monitoring programs of the University of Hawaii (Brown et al. 2004, Jokiel et al. 2004), National Park Service (Brown et al. 2007) and NOAA Coral Reef Ecosystem Division (www.pifsc.noaa.gov/cred) as well as research project data archived in the National Oceanographic Data Center (www.nodc.noaa.gov). Our database included 37 710 total benthic cover observations from 2000 to 2009, of the 6 coral species around the MHI (Fig. 1,

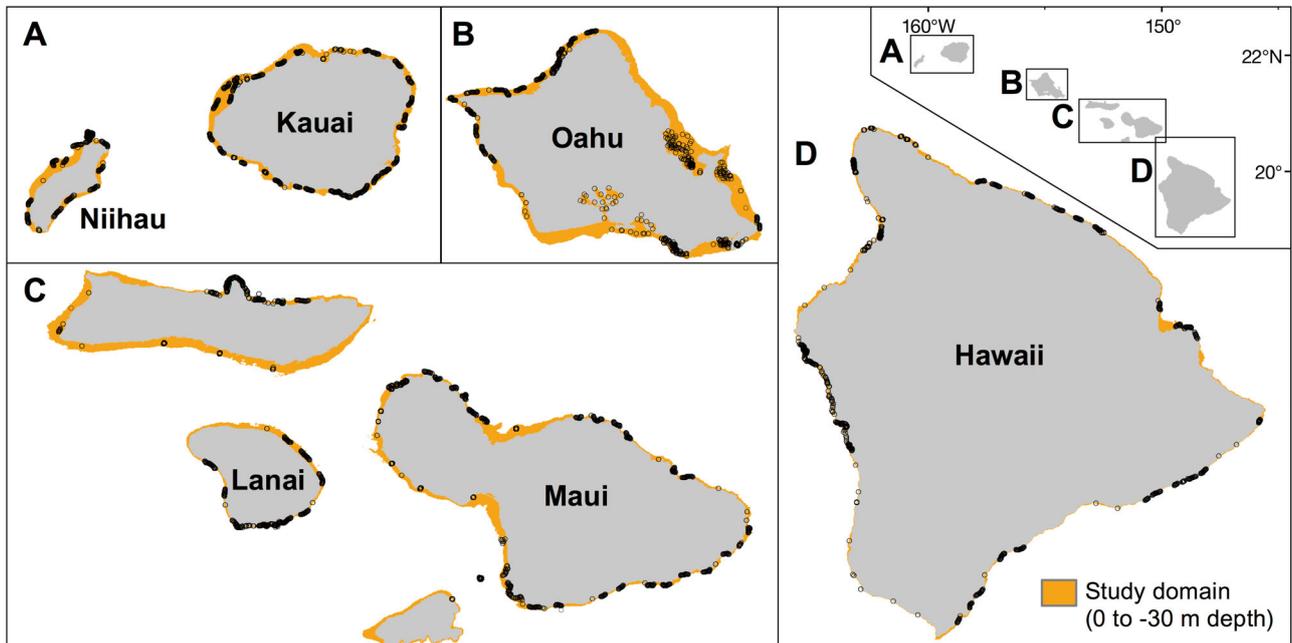


Fig. 1. Location of the Hawaiian Archipelago in the central North Pacific Ocean (inset) and the 8 main Hawaiian Islands (MHI) with benthic cover field observations for coral species (open circles) compiled from 2000 to 2009. The study area (orange) extends throughout the shallow, coastal waters (0 to 30 m depth)

Table 1. Number and range of benthic cover (%) from observations and model grid cells for 6 coral species around the main Hawaiian Islands (MHI). Grid cell cover values were computed from a survey area-weighted mean average of observations within that cell

Species	Field observations		Model grid cells	
	N	Cover range (%)	N	Cover range (%)
<i>Montipora capitata</i>	4580	0–80.7	1190	0–58.0
<i>Montipora flabellata</i>	4555	0–54.2	1192	0–29.9
<i>Montipora patula</i>	4555	0–72.0	1193	0–72.0
<i>Pocillopora meandrina</i>	4580	0–39.7	1190	0–32.9
<i>Porites compressa</i>	14 860	0–100.0	5611	0–94.0
<i>Porites lobata</i>	4580	0–85.7	1190	0–73.6

Table 2. Summary statistics of environmental covariates. na = not available, mya = million years ago

Variable	Mean	SD	Range	Unit
Aspect	182.4	107.0	0.0–360.0	°
Depth	–13.3	8.8	–30.0–0.0	m
Island age	na	na	<0.5–5.0	mya
Max. significant wave height	3.0	1.5	0.00–8.3	m
Mean significant wave height	1.1	0.4	0.00–4.3	m
Downwelled irradiance	0.4	0.2	0.0–1.0	Proportion
Rugosity	1.002	0.013	1.0–2.5	Ratio
Sandbottom	0.21	0.38	0.0–1.0	Proportion
Slope	1.7	1.7	0–14.4	°

Table 1). Survey methods included *in situ* diver observations and interpreted photo-quadrats for survey areas ranging from 0.25 to 25 m². Using the location information provided with each survey, we mapped benthic cover observations for each coral species as vector point features. Vector points were converted to raster grids using a survey area-weighted mean of coral cover for each grid cell in ArcGIS (v. 9.3.1, ESRI). The number of grid cells with data on benthic cover ranged from 1190 to 5611 (Table 1). Each grid was georectified and matched to the extent of a 50 m resolution base analysis grid. No significant correlations were observed between sampled area within a grid cell and species cover.

Environmental data layers

We utilized 9 environmental covariate data layers for the statistical modeling (Table 2). Digital files for all environmental data layers were georectified to a base analysis grid of 477

795 cells (approximately 1194 km²) that covered the extent of the study domain in ArcGIS (v. 9.3.1, ESRI) and geoprocessed using scripts in Python (www.python.org). Data manipulation for coral surveys and environmental variables was performed using base functions in R (v. 2.14, R Development Core Team). Detailed figures (Figs. S1–S32) of the environmental data layers for the Hawaiian Islands are in the Supplement at www.int-res.com/articles/suppl/m481p121_supp.pdf.

A bathymetry synthesis for the MHI (Hawaii Mapping Research Group 2011) provided depth data for the majority of the study domain. The horizontal resolution of the bathymetry synthesis was approximately 50 m (~0.0005°). For cells that contained no bathymetric data, depths recorded from NOAA National Geodetic Survey soundings and coral reef survey observations were used to fill gaps where possible. After gap filling with empirical depth observations, we used an iterative nearest neighbor method, in an 8-cell neighborhood, to calculate depth for no data cells using the average depth of the neighborhood to create a no gaps bathymetry file. This method was used for approximately 2.7% of the study grid cells.

We derived 3 measures of benthic geomorphology (slope, aspect, and rugosity) from the bathymetry data layer. Bathymetric slope was the steepest angle, measured in degrees, of a plane defined for a depth grid cell and its surrounding 8 neighbors. Bathymetric aspect was the steepest downslope direction, measured in compass degrees (0° to 360°) of a plane defined by the slope grid cell and its 8 surrounding neighbors. Bathymetric rugosity was the ratio between the surface area and the planimetric area of the depth grid cell and its 8 surrounding neighbors.

Sandbottom habitat areas were converted from digital polygon features delineated from interpreted satellite imagery (Battista et al. 2007) to 5 m resolution raster grids. Sandbottom included sand, mud, and silt habitats. Sandbottom habitat raster cells (at 5 m resolution) were summed within the cells of the basemap grid (at ~50 m resolution) to derive a sandbottom proportion (scale of 0 to 1) data layer. Sandbottom cells with a value of 1 were not included in the analysis.

From a SWAN hindcast model (v40.51, SWAN Team 2006) forced with spectral wave data from WAVEWATCH III (WW3 v3.14, Tolman 2009) for every 6 h during January 2000 to December 2009, we obtained parametric wave data for the Hawaiian Islands. Maximum significant wave height, max. H_s , and mean significant wave height, mean H_s , were es-

timated for the 10 yr period at a grid resolution of 0.005 degrees (for Oahu and Kauai) or 0.01 degrees (for Maui Nui and Hawaii) which was resampled to 0.0005 degrees using an 8-cell nearest neighbor interpolation algorithm on mean values. Results were validated from a comparison of computed and measured H_s values at NOAA/NDBC Buoys 51201 and 51202 which demonstrated good overall correlation ($r = 0.9$) with a slight underestimate in modeled H_s values (Arinaga & Cheung 2012). Interpolated max. H_s values also corresponded well with an independent study of modeled wave heights (at grid resolutions of 40 m) for large NW storms around Hanalei Bay along the north coast of Kauai (Hoeke et al. 2011).

Downwelled irradiance was modeled using the Beer-Lambert law in the form: $E_d(Z) = E_d(0^-)e^{-K_d Z}$, where $E_d(Z)$ is the downwelled irradiance at depth Z determined from the bathymetry data layer, $E_d(0^-)$ is the irradiance just below the sea surface, and K_d is the diffuse attenuation coefficient (Kirk 1994). Diffuse attenuation coefficient (K_d) for PAR (photosynthetically active radiation, 400 to 700 nm) values were 0.054 for coastal waters greater than 10 m depth, 0.212 for coastal waters shallower than 10 m, and 0.273 for waters of semi-enclosed embayments including Kaneohe Bay, Pearl Harbor, and Keehi Lagoon on Oahu (Connolly et al. 1999, Isoun et al. 2003, Jacobson 2005). A digital file of downwelled irradiance [$E_d(Z) / E_d(0^-)$] was calculated as the proportion of downwelled irradiance at depth Z from the bathymetry data file to the irradiance just below the surface (Grigg 2006).

We assigned a categorical variable called 'island age' to each 50 m grid cell that represented the geological age of the nearest island group estimated using the K-Ar radiometric dating method (Clague & Dalrymple 1994). The 8 islands (and associated age ranges) were represented by 4 categories: Kauai (5 mya), Oahu (2.5 to 3.5 mya), Maui Nui (1 to 2 mya), and Hawaii (<0.5 mya). The Kauai category included Kauai and Niihau while the Maui category represented Maui, Molokai, Lanai, and Kahoolawe. For convenience, the Maui category is referred to as 'Maui Nui' throughout the study which reflects the shared geological origin of the group of 4 islands (Fletcher et al. 2008). Oahu and Hawaii categories did not include additional islands.

Statistical modeling

BRT models were constructed for each coral species cover using the routines *gbm* (generalized boosted

regression models) v1.6–32 (Ridgeway 2012) and *gbm.step* (Elith et al. 2008) in the R statistical program v2.14 (R Development Core Team, www.r-project.org). BRT models combine regression trees that fit environmental predictors to response variables with a boosting algorithm that assembles an ensemble of trees in an additive, stage-wise fashion (Hastie et al. 2001, Elith et al. 2008). Within the BRT models, 3 terms were used to optimize predictive performance: tree complexity, learning rate, and bag-fraction. Tree complexity (*tc*) determined the number of nodes in a tree that should reflect the true interaction order on the response being modeled, although this is often unknown, and learning rate (*lr*) was used to shrink the contribution of each tree as it is added to the model (Elith et al. 2008). The bag-fraction determined the proportion of data to be selected at each step and, therefore, the model stochasticity (Elith et al. 2008). For each species, the BRT model training dataset was a one-time random selection of 70% of the original total dataset of model grid cells (Table 1). The remaining 30% was held out for independent validation of each optimal BRT model. We determined optimal settings for these parameters by examining the cross-validation deviance over *tc* values 1–5, *lr* values of 0.05, 0.01 and 0.005, and bag fractions of 0.5 and 0.75. All possible combinations were run, with the optimal number of trees in each case being determined by *gbm.step* (Elith et al. 2008). Each model run included 10-fold cross-validation using training datasets. The combination of the 3 parameter settings with the lowest cross-validation deviance was then selected to produce the optimal BRT model for each species fit with the entire training dataset (Elith et al. 2008). Finally, the deviance of the optimal model was evaluated on the test (30%) dataset. All models were run with arc-sine transformed measures of cover which were treated as a Gaussian (normal) response distribution (Read et al. 2008, 2011). For the final BRT models, the relative contribution of each predictor was based on the number of times the variable was selected for splitting, weighted by the squared improvement to the model as a result of each split, and averaged over all trees (Friedman & Meulman 2003, Elith et al. 2008). Partial dependency plots were used for interpretation and to quantify the relationship between each predictor variable and response variable, after accounting for the average effect of all other predictor variables in the model. We used *gbm.interactions* (Elith et al. 2008) to quantify interaction effects between predictors. The relative strength of interaction fitted by BRT was quantified by the residual variance from a linear model, and the value indicates the rela-

tive degree of departure from a purely additive effect, with zero indicating no interaction effects fitted (Elith et al. 2008). We defined a threshold interaction value and reported the interactions with values ≥ 0.1 .

RESULTS

The final BRT models predicted the geographic distributions of benthic cover of the 6 dominant coral species for the MHI (Fig. 2). Model settings for the final BRT models ranged from 1350 to 4500 trees, a tree complexity of 4 or 5, a learning rate of 0.01 or 0.005, and a bag fraction of 0.75 (Table 3). Model cross-validation deviances ranged from 0.009 to 0.021 and deviances on the test dataset were between 0.002 and 0.026 (Table 3). Max. H_s and mean H_s were consistently the most important variables to explain the benthic cover of the 6 dominant coral species in Hawaii with varying levels of secondary contributions from island age, aspect, depth, rugosity, slope, and downwelled irradiance to particular species (Table 4, Figs. S33–S36 in the Supplement at www.int-res.com/articles/suppl/m481p121_supp.pdf).

Benthic cover of the 3 *Montipora* species was most influenced by max. H_s , mean H_s , and bathymetric aspect (Table 4) with *M. flabellata* found in the highest wave energy environments, *M. patula* in intermediate wave environments, and *M. capitata* in low wave environments along north-east coastlines (Fig. 2a,c). *Pocillopora meandrina* cover was predicted to be highest in areas of high max H_s , mean H_s , and steep slopes (Fig. 2d, Table 4). Models predicted the highest benthic cover for *Porites compressa* in areas with low max. H_s and mean H_s with an interaction of 1.27 between max. H_s and mean H_s (Fig. 2e, Table 4). *Porites lobata* cover was most strongly influenced by the island variable with highest cover at Hawaii and declining toward Kauai. Max. H_s and mean H_s were strong secondary predictors for *P. lobata* cover (Fig. 2f, Table 4). Generally, highest coral abundances were predicted around Hawaii with a gradually declining gradient of cover toward the northwest across island groups of increasing age, as well as a shift from *Porites* spp. to *Montipora* spp. community dominance (Fig. 3).

Coral cover predicted for each species was relatively low (under 5%) at each island and for the entire MHI except for *Porites lobata* around Hawaii (Fig. 3). *P. lobata* had the highest predicted coral cover at Niihau (2.2%), Molokai (3.3%), Maui (4.1%), Lanai (5.5%), Kahoolawe (5.2%), and Hawaii (11.1%) while *Montipora patula* had the highest

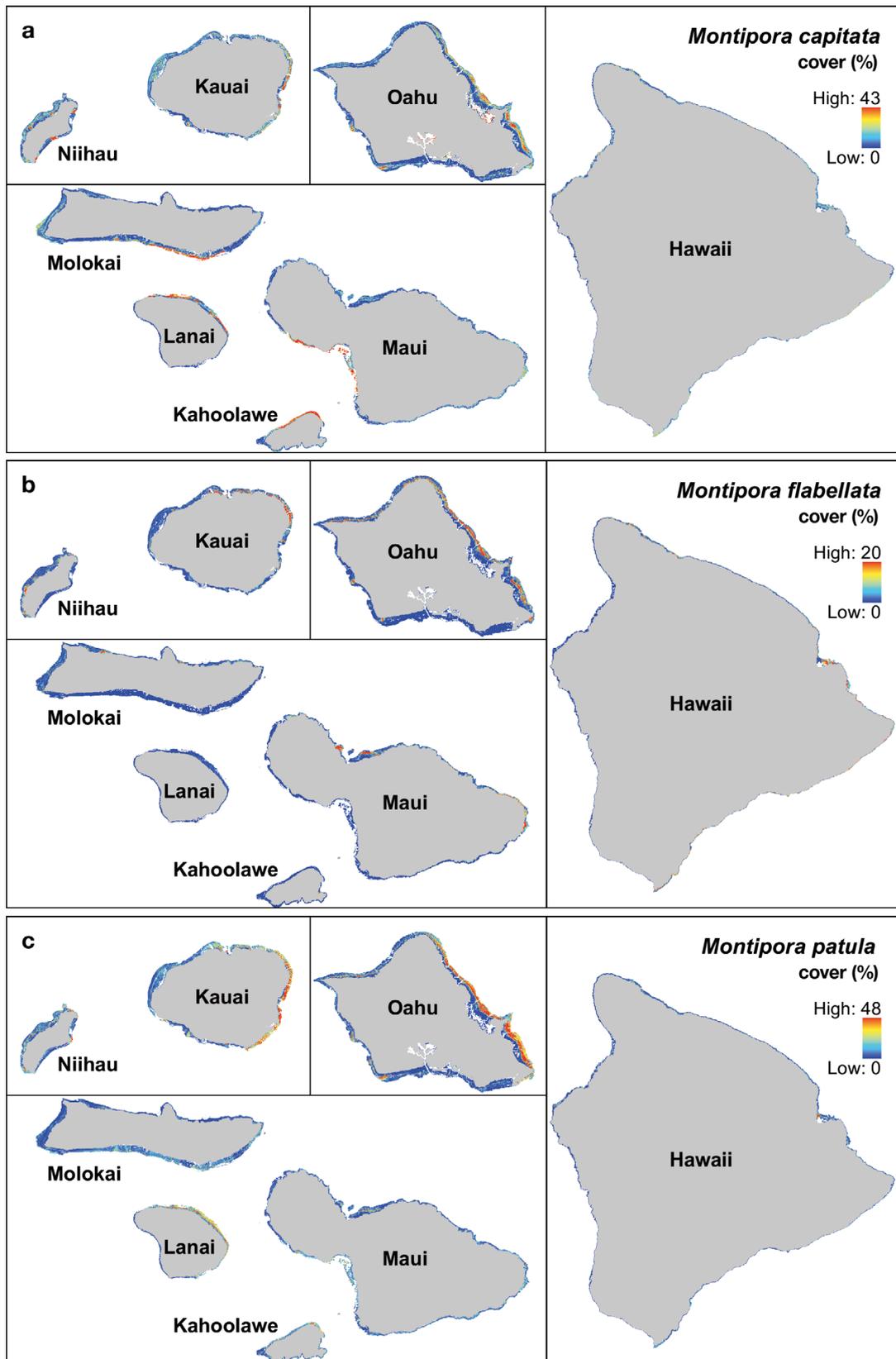


Fig. 2. (Above and facing page.) Model-predicted coral cover (%) for (a) *Montipora capitata*, (b) *M. flabellata*, (c) *M. patula*, (d) *Pocillopora meandrina*, (e) *Porites compressa*, and (f) *Porites lobata* around the MHI

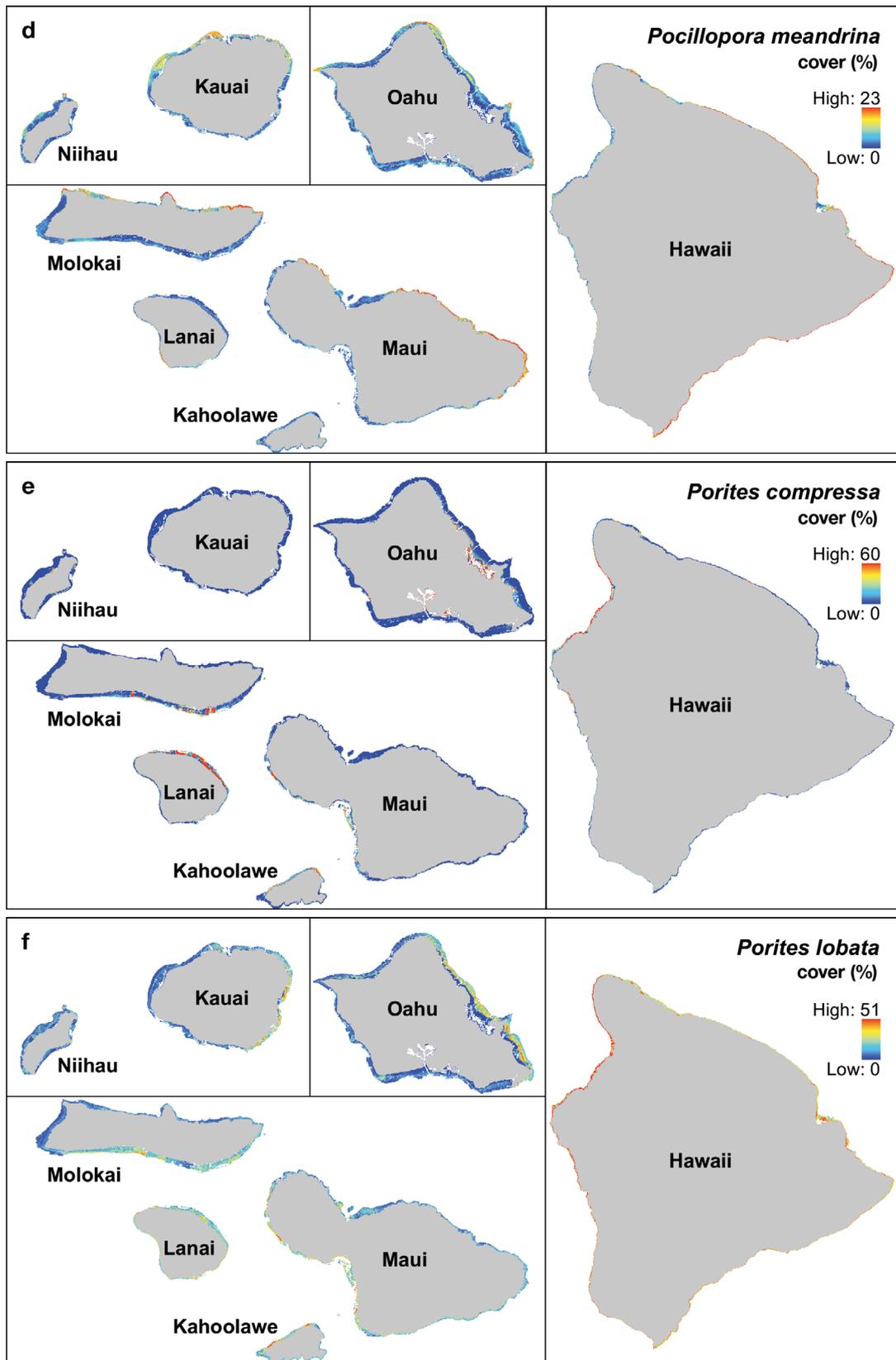


Fig. 2 (continued)

Table 3. Model settings and cross-validation deviance of final BRT models for benthic cover of *Montipora capitata*, *M. flabellata*, *M. patula*, *Pocillopora meandrina*, *Porites compressa*, and *Porites lobata* around the MHI. Model settings include the number of trees (nt), tree complexity (tc), and learning rate (lr). Bag fraction was 0.75 for each model. Cross-validation deviance (cv dev) with \pm SE, and deviance of evaluation observations (eval cv)

	nt	tc	lr	cv dev	eval cv
<i>Montipora capitata</i>	2550	5	0.01	0.011 \pm 0.001	0.012
<i>M. flabellata</i>	1450	4	0.01	0.002 \pm 0	0.002
<i>M. patula</i>	4050	5	0.005	0.011 \pm 0.001	0.010
<i>Pocillopora meandrina</i>	3400	4	0.005	0.009 \pm 0.001	0.011
<i>Porites compressa</i>	2550	5	0.01	0.010 \pm 0.001	0.010
<i>Porites lobata</i>	1350	5	0.01	0.021 \pm 0.001	0.026

Table 4. Relative contribution of environmental variables to BRT models of *Montipora capitata* (Mcap), *M. flabellata* (Mfla), *M. patula* (Mpat), *Pocillopora meandrina* (Pmea), *Porites compressa* (Pcom), and *Porites lobata* (Plob). Environmental variables: H_s : mean and maximum significant wave height (m); Island age (mya); aspect ($^\circ$); depth (m); rugosity (surface/planar area); slope ($^\circ$); downwelled irradiance [$E_d(Z)/E_d(0^-)$]; sandbottom (proportion)

	Mcap	Mfla	Mpat	Pmea	Pcom	Plob
Mean H_s	25.5	26.7	18.7	21.2	33.5	14.5
Max. H_s	17.4	22.2	16.4	17.8	20.7	14.7
Island age	2.7	3.8	11.3	3.5	6.8	28.6
Aspect	14.7	17.1	14.4	11.5	3.2	9.0
Depth (m)	9.8	8.6	10.3	8.6	10.8	9.6
Rugosity	6.9	11.4	7.4	13.7	8.5	6.1
Slope	7.0	4.3	8.2	11.4	4.0	8.0
Downwelled irradiance	10.4	4.8	9.6	3.1	6.5	6.9
Sandbottom	5.5	1.2	3.7	3.1	6.1	2.6

cover around Kauai (3.3%) and Oahu (3.0%) (Fig. 3). The rank order of abundance (from highest to lowest with coral cover in parenthesis) for the entire MHI was *P. lobata* (4.4%), *M. patula* (2.2%), *Pocillopora meandrina* (1.44%), *M. capitata* (1.40%), *Porites compressa* (0.8%), and *M. flabellata* (0.3%). No island had the same rank order of abundance as the overall MHI order, but Molokai and Maui were most similar to the MHI. Notable divergences from the MHI rank order were *Porites compressa* with the 2nd and 3rd highest cover at Lanai and Hawaii, respectively, and *Pocillopora meandrina* with the second highest cover around Maui and Hawaii (Fig. 3).

Predicted total coral cover from a summation of the 6 species varied between a low of 7.5% (Niihau and

Molokai) to 18.4% with an overall mean of 10.5% for the MHI. Kaneohe Bay on Oahu; the wave-sheltered area of Maui Nui that includes reefs of Molokai, Lanai, Maui, and Kahoolawe; and the Kohala coast of Hawaii were predicted as areas of the highest total coral cover summed for the 6 species (Fig. 4). Mean island coral cover ranged between 2 and 26% with the highest cover around Lanai and Hawaii and the lowest at Niihau and Kauai.

DISCUSSION

Using BRT models, we developed continuous spatial distribution maps of the benthic cover for the dominant 6 Hawaiian coral species around the MHI. The BRT models identified the most important sets of environmental variables for each species (Table 4). Mean coral cover for each species and species rank abundance by island and the entire MHI were calculated from final BRT model predicted coral covers (Figs. 3 & 4).

Wave exposure or wave energy has been identified as the primary factor influencing the distribution, zonation, and composition of Hawaiian coral reefs (Dollar 1982, Grigg 1983, Engels et al. 2004, Jokiel et al. 2004, Storlazzi et al. 2005). In the present study, both max. H_s and mean H_s were consistently the most important variables to explain the benthic cover of Hawaiian coral species (Table 4). This result suggests a synergistic effect between the typical, daily wave conditions and periodic high energy wave events from storms in structuring coral communities around the Hawaiian Islands (Dollar 1982, Grigg 1983). Other environmental variables contributing greater than 10% relative importance to BRT models were island age, aspect, depth, rugosity, slope, and downwelled irradiance, relationships which were also reported by Jokiel et al. (2004).

Predicted cover for *Pocillopora meandrina* was highest in shallow, high-wave energy environments along the north coasts and headlands of Kauai, Oahu, and Maui and the entire coastline of Hawaii (Fig. 2d). These areas are commonly characterized by shallow, basalt boulder habitats with steep slope, high rugosity, and high wave-energy (Jokiel et al. 2004, Battista et al. 2007). Although significant wave height is a surface observation, its predictive capacity for coral species abundance seems promising, and appears to perform similarly to other wave-related metrics such as near-bottom shear stress (Storlazzi et al. 2005) or wave exposure (Chollett & Mumby 2012).

Of the 3 *Montipora* species, *M. capitata* appears the most broadly adaptable to a range of habitats

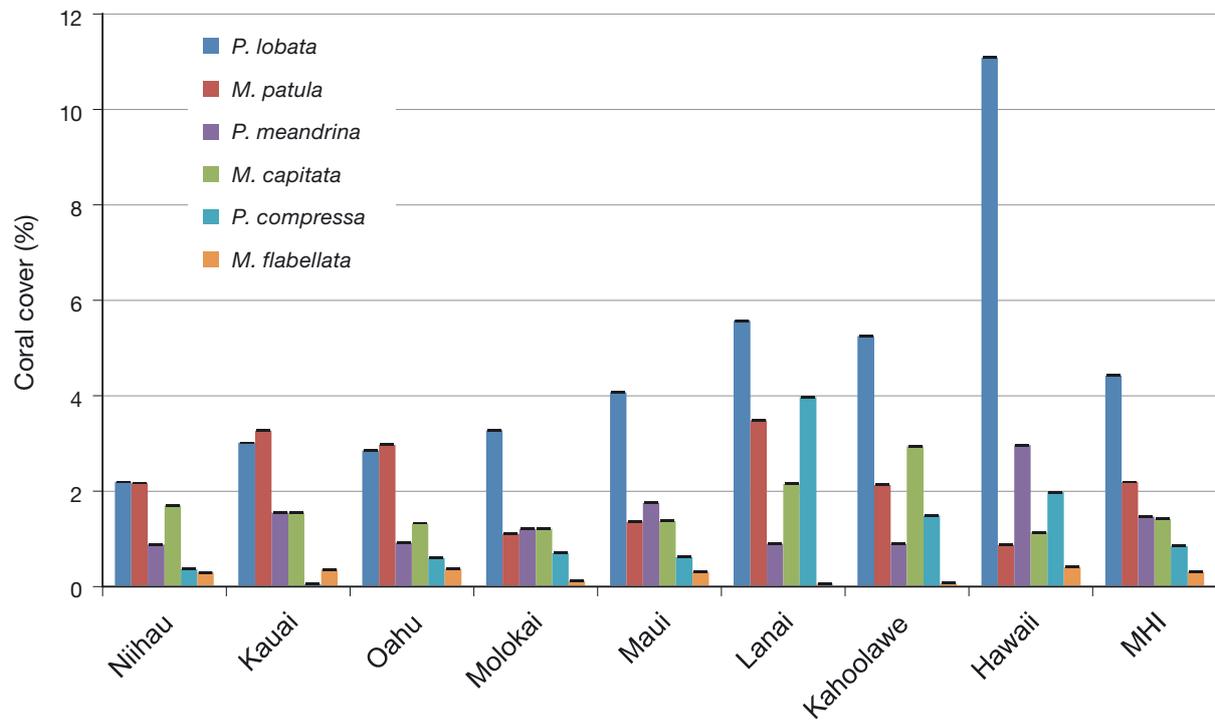


Fig. 3. Mean benthic cover (%) \pm SE (black bars on the tops of the distributions) of 6 coral species (see Table 4 for full taxonomic names) predicted from final boosted regression tree (BRT) models for each Hawaiian island and the entire MHI

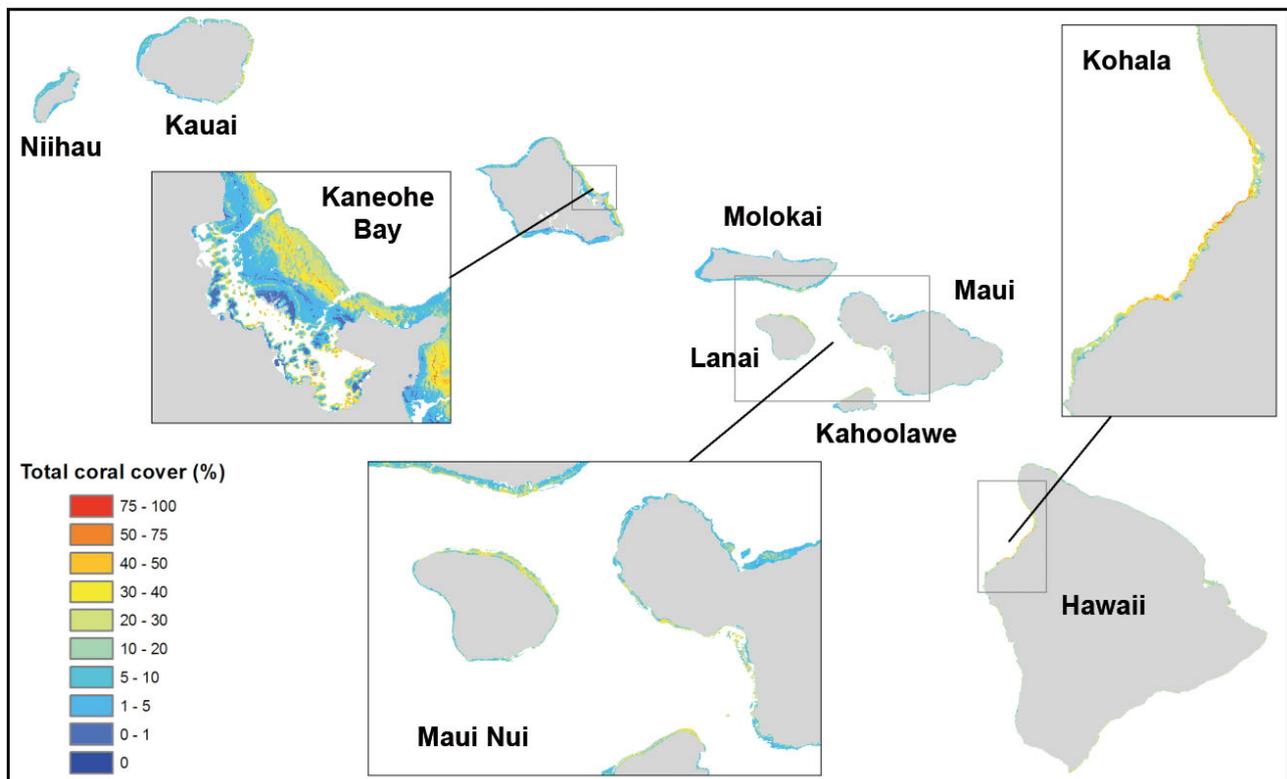


Fig. 4. Geographic map of summed total cover for 6 coral species predicted from BRT models for the MHI

since it is predicted to occur both along fore reefs as well as in quiescent environments such as Kaneohe Bay on Oahu (Fig. 2a). The ability of *M. capitata* to occupy such diverse habitats may be due to the extreme phenotypic plasticity that the species exhibits (Forsman et al. 2010). For example, a single colony of *M. capitata* may possess sections that are laminar, encrusting, or branching (Forsman et al. 2010). *M. patula* and *M. flabellata* were predicted to occur in higher wave environments than *M. capitata*. Highest predicted cover for *M. patula* and *M. flabellata* was along the east coasts of Kauai and Oahu and wave-sheltered areas of Maui Nui (Fig. 2b,c). Both species are endemic to Hawaii and currently under review for listing as threatened or endangered species under the US Endangered Species Act (Brainard et al. 2011). The present study represents the most comprehensive distribution and abundance information available for these 2 species and should be used to inform ongoing conservation efforts.

Porites compressa cover dominated low wave-energy environments that are typically shallow, nearshore habitats with turbid waters from sediment resuspension and watershed inputs (Hunter & Evans 1995, Coles et al. 1997, Jokiel 2006). High *P. compressa* cover was also predicted for wave-sheltered coasts of Maui Nui and deeper waters (>10 m) around Hawaii, an observation reported by Dollar (1982, our Fig. 2e). At intermediate wave energies (1 to 3 m max H_s), *Porites lobata* was predicted to be the dominant coral (Fig. 2f) and was the most abundant coral species in the MHI (Fig. 3). Island age was also a strong positive factor for *P. lobata* with high benthic cover occurring around the youngest island, Hawaii (<0.5 mya).

In general, coral cover was predicted to be highest in primarily wave-sheltered coastlines and embayments. High coral cover locations were predicted throughout the islands, but reefs with highest cover were concentrated in Kaneohe Bay on Oahu, the wave-sheltered areas of Maui Nui, and along the west coast of Hawaii (Fig. 4). These areas have varying benthic geomorphology and levels of downwelled irradiance but share similar low wave energy characteristics. Previously, the Engels et al. (2004) model of modern coral zonation for the Hawaiian Islands related the occurrence of highest total coral cover to low wave-energy environments. Storlazzi et al. (2005) also observed the highest total coral cover along sections of the Molokai coastline with the lowest wave-induced near bed shear stress. These studies correspond well with the predicted results from our BRT models.

Rank order of coral species abundance differed slightly from prior studies. We found the rank order (from highest to lowest) to be *Porites lobata*, *Montipora patula*, *Pocillopora meandrina*, *M. capitata*, *Porites compressa*, and *M. flabellata*. From a survey of the southwest coasts of Kauai, Oahu, Maui, and Hawaii, Grigg (1983) found the rank order of abundance for the 6 coral species in the present study as *Porites lobata*, *P. compressa*, *M. capitata*, *Pocillopora meandrina*, *M. patula*, and *M. flabellata*. Jokiel et al. (2004) surveyed 60 monitoring locations throughout the MHI and observed a similar rank order of abundance (and coral cover) of *Porites lobata* (6.1%), *P. compressa* (4.5%), *M. capitata* (3.9%), *M. patula* (2.7%), *Pocillopora meandrina* (2.4%), and *M. flabellata* (0.7%). Compared to Grigg (1983) and Jokiel et al. (2004), our study found *Porites compressa* to be relatively less abundant overall and *M. patula* more abundant than *M. capitata*.

The BRT models provided strong results for the predicted cover of the 6 coral species (Table 3), but the inclusion of additional environmental variables and a more comprehensive geographic distribution of field samples should lead to better model performance and more accurate cover predictions. For example, finer grain bathymetry data (<10 m cell size) could improve the predictive power of modeled bottom complexity (such as found in Jokiel et al. 2004), but were not available for the entire study domain. Furthermore, significant wave heights are a surface measurement. Wave environments at the sea floor are more accurately characterized by bottom water velocity (Lowe et al. 2009) or near bed shear stress (Storlazzi et al. 2005), which may be 2 potential variables for future study. A better representation of downwelled irradiance would incorporate the absolute surface irradiance instead of a relative metric which assumes similar surface levels throughout the study domain.

Species observations compiled for this study were collected throughout the MHI (Fig. 1). Although most areas were well sampled, several locations had high sample clusters which may bias model results towards the characteristics of those areas. In addition, Kahoolawe, south Molokai, north Lanai, and northeast Oahu were undersampled and we suggest future coral surveys to focus on these areas. In the absence of acquiring additional samples, future studies could include a spatially explicit term to address potential spatial autocorrelation in the models (Latimer et al. 2006) or select subsets of the existing datasets by geographic location to achieve area proportional sampling between islands (Jiménez-Valverde et al. 2009) to mitigate spatial sampling bias.

Regional-scale characterizations of coral species from SDMs provide the framework for spatially explicit ecosystem modeling and marine spatial planning of coral reefs (Franklin et al. 2003, Crowder & Norse 2008, Klein et al. 2010). SDMs of coral species are critically useful since species respond differentially to thermal stressors (Guest et al. 2012) and coral diseases (Williams et al. 2010, Aeby et al. 2011), while studies of total coral cover alone overlook changes in reef composition and species dominance. Data from coral SDMs can be incorporated into spatial optimization exercises for marine conservation (Leathwick et al. 2008) or for geographically explicit threat assessments to reefs (Selkoe et al. 2009, Burke et al. 2011). The geographic characterization of coral reefs would benefit greatly from the improved coral distribution and abundance information generated from SDMs.

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