



Spatio-temporal dynamics of the threatened elkhorn coral *Acropora palmata*: Implications for conservation

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Abstract

Aim: Species distribution models (SDMs) can be useful for predicting spatial dynamics. For species vulnerable to climate change, much attention has focused on predicting the future range of occurrence. However, predicted range changes provide little information about the potential impacts on population structure. Here, we develop and apply an SDM approach that incorporates population demography of a threatened coral species (U.S. Endangered Species Act) and aim to provide guidance for conservation efforts. We additionally use projected climate change scenarios to predict the potential future range of occurrence and spatial population structure.

Location: U.S. Virgin Islands, United States.

Methods: We applied process-based dynamic range models to jointly model the spatio-temporal population dynamics and spatial habitat suitability of the threatened elkhorn coral *Acropora palmata* in the U.S. Virgin Islands. The approach integrates information from multiple data sources under a hierarchical Bayesian framework. The models connect two components: (1) a niche model that correlates environmental predictors with demographic rates and (2) a size-structured population model that describes local population dynamics and dispersal.

Results: The model predicts that, under scenarios of elevated sea surface temperature and significant wave height, (a) *A. palmata* will occur at only a small proportion of its potential habitat (water depth \leq 20 m) and (b) population structure of the colony will shift from larger towards smaller size classes.

Main conclusions: For *A. palmata*, restricted geographic range and smaller colony sizes, as predicted by the models, would limit future population success. In general, the inclusion of demographic structure into a population range model provides critical information for conservation or restoration efforts in the context of climate change.

KEYWORDS

Acropora palmata, elkhorn coral, endangered species, hierarchical Bayesian modelling, process-based model, species distribution modelling

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1 | INTRODUCTION

With the increasing effects of climate change on populations, forecasting species' distribution and abundance in response to changing environmental conditions is urgently required for guiding conservation efforts. This is especially critical for species that have become rare (Thomas, 2010). Species distribution models (SDMs; Guisan & Zimmermann, 2000) are statistical tools that predict potential distribution into novel environmental space based on the observed relationship between environmental features and species occurrence (i.e., presence or absence); such models have been widely used to inform conservation and management planning (e.g., Barrett, Nibbelink, & Maerz, 2014; Franklin, 2013; Lawler, Wiersma, & Huettmann, 2011). The majority of these studies base conservation priorities on changes in the predicted distribution range of species occurrence from correlative SDMs under different climate scenarios (e.g., Carvalho, Brito, Crespo, & Possingham, 2010; Summers, Bryan, Crossman, & Meyer, 2012; Triviño, Cabeza, Thuiller, Hickler, & Araújo, 2013). This approach relies on an assumption that locations with high environmental suitability tend to maintain a species' presence and high local abundance, minimizing potential impacts of climate change. However, evidence has shown that environmental suitability and local abundance may not be directly related (Gomes et al., 2018; Pearce & Ferrier, 2001; Weber, Stevens, Diniz-Filho, & Grelle, 2017) and that changes in predicted distribution range based solely on correlative environment–occurrence relationships may not account for potential effects on population dynamics, migration limitations and underlying dispersal processes. This suggests a need to incorporate underlying population dynamics and dispersal processes into SDM approaches to assess the impacts of environmental changes on species distribution and populations.

Attempts to model spatio-temporal abundance distributions face two main challenges. First, correlative SDMs are based on an assumption that species distributions are in equilibrium with current habitats, such that species occur in all, and only in, the habitable area, and that the current distribution range reflects a stable abundance–environment relationship over time and space (Guisan & Thuiller, 2005). However, the equilibrium assumption is questionable for most, if not all, populations impacted by changing environments. For example, species may not adjust rapidly, but rather show a time-lagged response in distribution and abundance to shifting geographic location of suitable habitat (Araújo & Pearson, 2005; Nogués-Bravo, 2009; Svenning & Skov, 2004). This can result in species being absent from optimal habitats and lead to confounding predictions (Zurell, Jeltsch, Dormann, & Schröder, 2009). Furthermore, many traditional correlative SDMs assume species occurrence or abundance observations are spatio-temporally independent (Guisan & Thuiller, 2005). However, in real-world scenarios, spatio-temporal autocorrelation is common, as the probability of occurrence or abundance often tends to be more similar in the neighbourhood than in distant locations due to distance-related biotic processes such as dispersal or reproduction (endogenous autocorrelation; Bahn, Krohn, & O'Connor, 2008;

Kissling & Carl, 2008; Thorson et al., 2015). For mitigating the potential biases, many studies have identified the need to incorporate dynamic mechanisms into SDMs, including dispersal and demography (Ehrlén & Morris, 2015; Franklin, 2010; García-Valdés, Zavala, Araujo, & Purves, 2013).

The second major modelling challenge is that reliable predictions require a sufficient sample size. Small sample size may decrease model performance when predicting distribution range (Wisz et al., 2008). In general, the number of observations should be sufficiently larger than the number of predictors included in the models to make robust inferences (Breiner, Guisan, Bergamini, & Nobis, 2015; Harrell, Lee, & Mark, 1996). However, spatio-temporal information on abundance and demography is often more limited than records of occurrence, especially for threatened species. One way to address this issue is to use a modelling approach that allows integration of information from diverse sources, such as different data types and prior knowledge from literature or expert opinions (Kuhnert, Martin, & Griffiths, 2010; Martin et al., 2012). As the existing SDMs are mostly restricted to one type of response variable (e.g., presence–absence, presence-only or abundance), flexible analytical tools that enable data integration have the potential to improve inference by making full use of available information (Plard, Fay, Kéry, Cohas, & Schaub, 2019).

To address the aforementioned challenges, recent SDM studies have developed Bayesian inferential and process-based approaches. Bayesian inference provides a formal mechanism for synthesizing multiple sources of information in one statistical framework. It can allow information from diverse sources to contribute to model parameterization, through assigning informative prior distributions reflecting current knowledge, and integrating multiple types of observations when constructing the likelihood model (Martin et al., 2012; McCarthy & Masters, 2005; Morris, Vesk, McCarthy, Bunyavejchewin, & Baker, 2015). Consequently, Bayesian applications in the field of ecology have been rapidly increasing over the past two decades (Hooten & Hobbs, 2015). In particular, the ability to improve inference for data-poor species has been demonstrated in recent studies (Hamer et al., 2016; LeBauer, Wang, Richter, Davidson, & Dietze, 2013; Pardo et al., 2016).

Process-based SDMs predict abundance and distribution range based on relationships between environmental conditions and underlying physiological constraints (Kearney & Porter, 2009) or demographic processes. For instance, Pagel and Schurr (2012) proposed process-based dynamic range models (DRMs) that predict abundance dynamics and range shifts based on vital rates shaped by environmental features and dispersal rates. By modelling vital rates as functions of environmental predictors, a DRM incorporates a dispersal kernel and a density-dependent population model capable of representing biotic characteristics of the focal species. This integration of models enables accounting for time-lagged response to environmental changes and spatio-temporal dependency that arises from population dynamics and dispersal (Ehrlén & Morris, 2015; Marion et al., 2012) and also has the advantage of being able to

simultaneously estimate habitat suitability, dispersal and demographic rates that may vary in response to a changing environment (García-Valdés et al., 2013). Therefore, this approach is particularly applicable for predicting abundance changes driven by dynamic processes (Zurell et al., 2016). However, the applications of DRMs to date have been focused on simulation data with few applications (e.g., Osada, Kuriyama, Asada, Yokomizo, & Miyashita, 2019) on field observations.

In this study, we extend process-based DRMs by incorporating a size-structured population model under a hierarchical Bayesian framework and apply the model to field observations of the threatened elkhorn coral *Acropora palmata*, a species highly sensitive to climate change (IUCN, 2017). The relative rarity and low population size of this species offer analytic challenges; however, there is an urgent management need for forecasts of changes in distribution range and abundance under projected climate change scenarios. Previous *A. palmata* population modelling efforts for Caribbean locations did not incorporate spatial distribution (Vardi, Williams, & Sandin, 2012; Williams & Miller, 2012), and previous efforts to spatially delineate potential habitat for Caribbean *Acropora* species largely focused on bathymetric water depth as a static predictor and did not incorporate population dynamics (Wirt, Hallock, Palandro, & Daly, 2013; Wirt, Hallock, Palandro, & Lunz, 2015).

With the model presented in this study, we aim to provide guidance for future conservation and research efforts. Specifically, our goals are to (a) predict current spatial distribution range and abundance; (b) predict future distribution and abundance under projected climate change scenarios; and (c) identify key knowledge gaps to help focus future data collection.

2 | METHODS

2.1 | Study species

The elkhorn coral *Acropora palmata* is a branching, reef-building species that inhabits shallow tropical Caribbean reefs. This coral species was once abundant in the Caribbean, but is currently rare due to massive population declines over the past few decades that have been linked to climate change (Eakin et al., 2010). *A. palmata* is currently listed as “threatened” under the US Endangered Species Act (Federal Register, 2006) and “Critically Endangered” on the IUCN Red List of threatened Species (IUCN, 2017). For *A. palmata*, sexual reproduction (in which gametes are released into the water column, fertilize and settle on benthic substrate after a planktonic period) appears to have limited success, and asexual reproduction is currently considered to be the dominant source of recruitment (Williams, Miller, & Baums, 2014). *A. palmata* colonies can reproduce asexually through fragmentation, in which branches that break off after a physical disturbance (e.g., wave energy) can reattach to the substrate and grow into a new colony (Highsmith, 1982).

2.2 | Study area and data

The study area included the shallow waters (water depth ≤ 20 m) off St. Thomas, St. John and St. Croix, U.S. Virgin Islands (USVI) in the Caribbean (Figure 1). *A. palmata* observations were compiled from multiple field sampling efforts during 2013–2015 (Appendix S1). The observations (1,193 field observations in total; see *Initialization* for details) contain two types of data: presence–absence and demographic records that include counts and size of colonies within 30-m² sampling plots.

Potential habitat of *A. palmata* colonies was defined as shallow water (water depth ≤ 20 m) with mapped benthic habitats classified as hard bottom, aggregate reef, patch reef, pavement, bedrock, or scattered coral and rock in St. Croix, St. Thomas and St. John, USVI. The overall distribution prediction grid (50 m \times 50 m cell resolution) for *A. palmata* occurrences was restricted to shallow water along the USVI coasts across the surveyed and projected years (Table 1). Bathymetric water depth, mean summer sea surface temperature (SST) and maximum significant wave height were selected as environmental predictors based on their relevance to population dynamics of *A. palmata* and a preliminary test on model performance (Appendix S1).

2.3 | Model framework

We aimed to estimate the spatio-temporal dynamics of abundance and demographic structure of *A. palmata* colonies within the study area across all years in the observation period and under projected climate change conditions. To account for the influence of environmental characteristics on local abundance and demographic dynamics, we adopted the general framework of DRMs (Pagel & Schurr, 2012). In this framework, a latent population process is constructed on a spatially explicit grid, in which the local colony in each grid cell is associated with neighbourhood cells via fragment dispersal (i.e., fragments moved to neighbourhood cells by waves) on distance-dependent rates, based on the assumption that larval dispersal is negligible (Williams et al., 2014). Because the size of coral colonies influences their contribution to population recruitment (Hughes, 1984), we constructed a size-structured population model for this analysis, instead of the size-aggregated Ricker model proposed in the original DRMs. We implemented the model in a hierarchical Bayesian framework, consisting of a process model, data model and parameter model (see Figure 2 for an overview).

2.4 | Process model

The process model describes the latent stochastic population process using a size-structured population model with discrete time steps (Buckland, Newman, Thomas, & Koesters, 2004). Here, we built upon the size-structured population model proposed by Vardi et al. (2012) for *A. palmata*. The model quantifies demographic

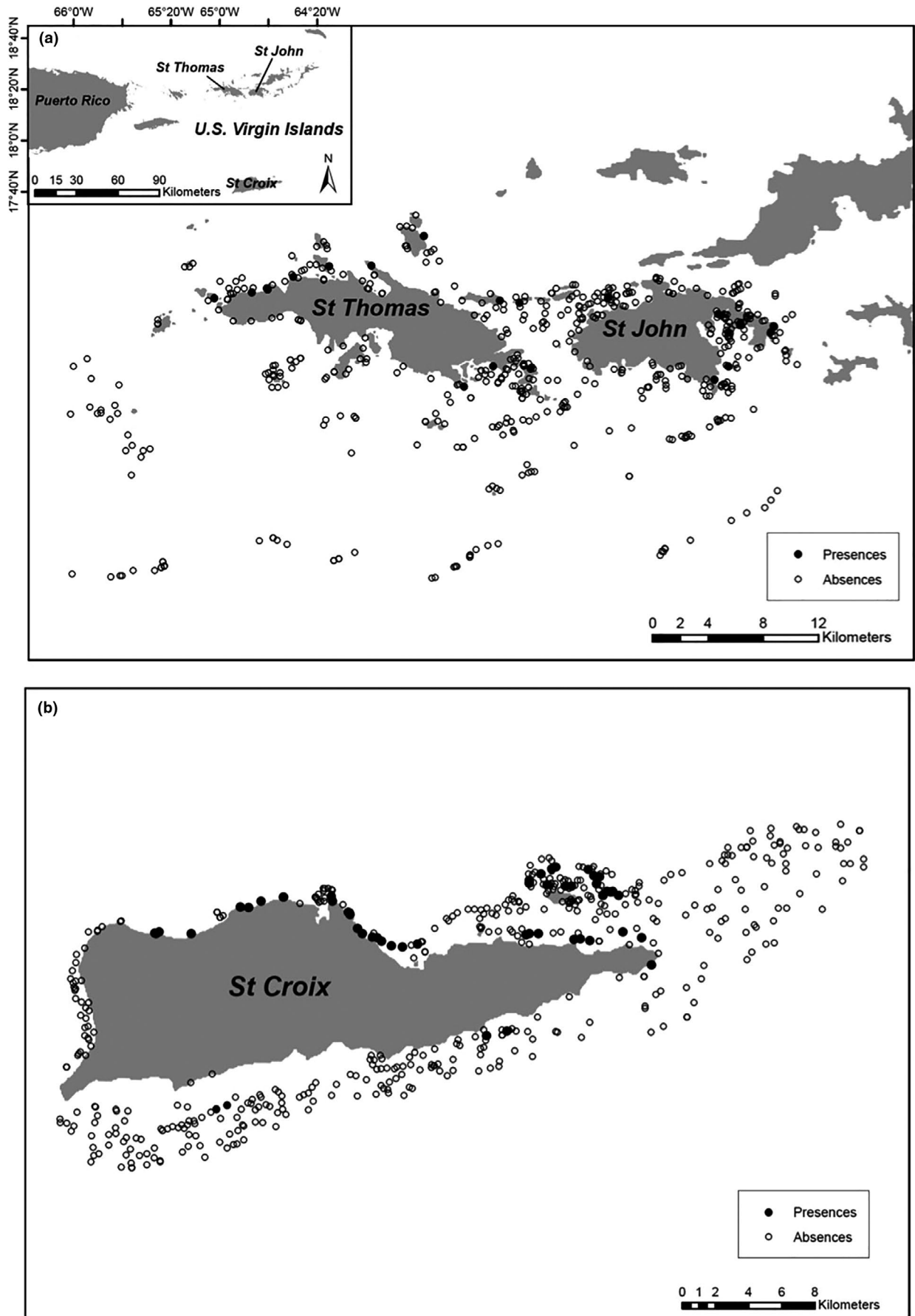


FIGURE 1 Location of the U.S. Virgin Islands in the Caribbean (inset) and presence (filled circles) and absence (open circles) observations of the Atlantic elkhorn coral *Acropora palmata* in (a) St. Thomas and St. John and (b) St. Croix in 2013–2015

TABLE 1 Proportion of total shallow water (water depth ≤ 20 m; PSW) with predicted *Acropora palmata* occurrences, proportion of occurrence sites in shallow water with predicted abundant colonies (density ≥ 3 colonies plot $^{-1}$; PSA) and the maximum predicted density (D_{\max}) in the survey years (2013–2015) and projected years (2035 and 2055)

	St. Croix					St. Thomas and St. John				
	2013	2014	2015	2035	2055	2013	2014	2015	2035	2055
PSW (%)	8.40 (14.9)	8.40 (10.66)	8.45 (10.73)	10.08 [10.11–10.05]	10.89 [11.04–10.73]	6.03 (13.45)	6.03 (8.64)	6.03 (11.27)	5.16 [5.16–5.17]	4.77 [4.76–4.78]
PSA (%)	1.11	1.12	1.39	2.37 [2.39–2.37]	2.61 [2.72–2.51]	0.51	0.51	0.46	0.34 [0.36–0.34]	0.36 [0.39–0.34]
D_{\max} (colonies)	4.24	3.71	3.75	5.04 [4.78–5.14]	5.65 [5.76–5.55]	3.22	3.96	4.04	3.72 [3.75–3.7]	3.43 [3.55–3.31]

Note: Proportion of occurrence sites within potential habitats, defined as shallow water with habitable benthic structure (see Appendix S5 for details), in survey years are provided in the brackets. Sensitivity of PSW, PSA and D_{\max} to projected climate change scenario, assessed using -25% and $+25\%$ of assumed climate change scenario, is provided in the square brackets.

dynamics as transitions among four size classes: (1) young recruits with rapid growth rate (size < 100 cm 2); (2) colonies with a low probability of asexual reproduction via fragmentation due to a lack of long branches (size between 100 cm 2 and 900 cm 2); (3) colonies with longer branches and a higher asexual fecundity (size between 900 cm 2 and $4,000$ cm 2); and (4) colonies with high asexual reproduction (size $\geq 4,000$ cm 2 ; Vardi et al., 2012).

Within each year t (from the start to the end), the local population dynamic in each grid cell i consists of three stochastic subprocesses: survival, transition between demographic stages and fragmentation (described below). These first-order Markov processes define $\mathbf{N}_{i,t-1}$, a vector describing the number of colonies in each size class. Then, the conditional expectation for the true, unobserved abundance in each size class is:

$$E[\mathbf{N}_{i,t}|\mathbf{N}_{i,t-1}] = \mathbf{S}_{i,t} \left(\mathbf{A}_{i,t} \mathbf{N}_{i,t-1} + (1 - jTOTO \sum P_{disp,ij}) \mathbf{F}_{i,t} \mathbf{N}_{i,t-1} + jTOTO \sum P_{disp,ij} \mathbf{F}_{i,t} \mathbf{N}_{i,t-1} \right), \quad (1)$$

in which $E[\mathbf{N}_{i,t}|\mathbf{N}_{i,t-1}]$ is the expected number of colonies in each size class in grid cell i in year t , $P_{disp,ij}$ and $P_{disp,ji}$ are distance-dependent dispersal kernels from cell i to j and cell j to i , respectively, and $\mathbf{S}_{i,t}$, $\mathbf{A}_{i,t}$ and $\mathbf{F}_{i,t}$ are transition matrices describing survival, transitions between difference size classes and reproduction through fragmentation, respectively (detailed below).

The survival matrix $\mathbf{S}_{i,t}$ defines the probability that individuals in each size class survive from year $t - 1$ to t . For each size class j , we assume that the survival of individuals is a binomial process with a survival rate $(1 - \phi_j)$, where ϕ_j is a size class-specific mortality rate.

The (k, j) entry in transition matrix $\mathbf{A}_{i,t}$ represents the probability that individuals in size class j transition to size class k . In each year t , individuals in each size class j are assumed to be able to grow, shrink or stay the same size with transition rates $g_{ij,k,t}$, $s_{ij,k,t}$ and $l_{ij,t}$, respectively. As the growth of individuals requires space, the transition rate $g_{ij,k,t}$ is assumed to be density-dependent and decrease exponentially with total abundance calculated after applying local survival at a rate of competition intensity b . The transition rates are also assumed to vary across space and time, and depend on the environmental condition in grid cell i in year t . To incorporate influence of environmental condition, the transition rates for growth $g_{ij,k,t}$ and shrinkage $s_{ij,k,t}$ are weighted by a habitat suitability weighting function $h_{i,t}$. The transition matrix $\mathbf{A}_{i,t}$ is therefore:

$$\mathbf{A}_{i,t} = \begin{bmatrix} l_{i,1,t} & s_{i,2,1,t} & s_{i,3,1,t} & s_{i,4,1,t} \\ g_{i,1,2,t} & l_{i,2,t} & s_{i,3,2,t} & s_{i,4,1,t} \\ g_{i,1,3,t} & g_{i,2,3,t} & l_{i,3,t} & s_{i,4,3,t} \\ g_{i,1,4,t} & g_{i,2,4,t} & g_{i,3,4,t} & l_{i,4,t} \end{bmatrix}, \quad (2)$$

where

$$g_{ij,k,t} = \bar{g}_{j,k} h_{i,t} e^{-bN_{i,t}}, \quad (3)$$

$$s_{ij,k,t} = \bar{s}_{j,k} (1 - h_{i,t}). \quad (4)$$

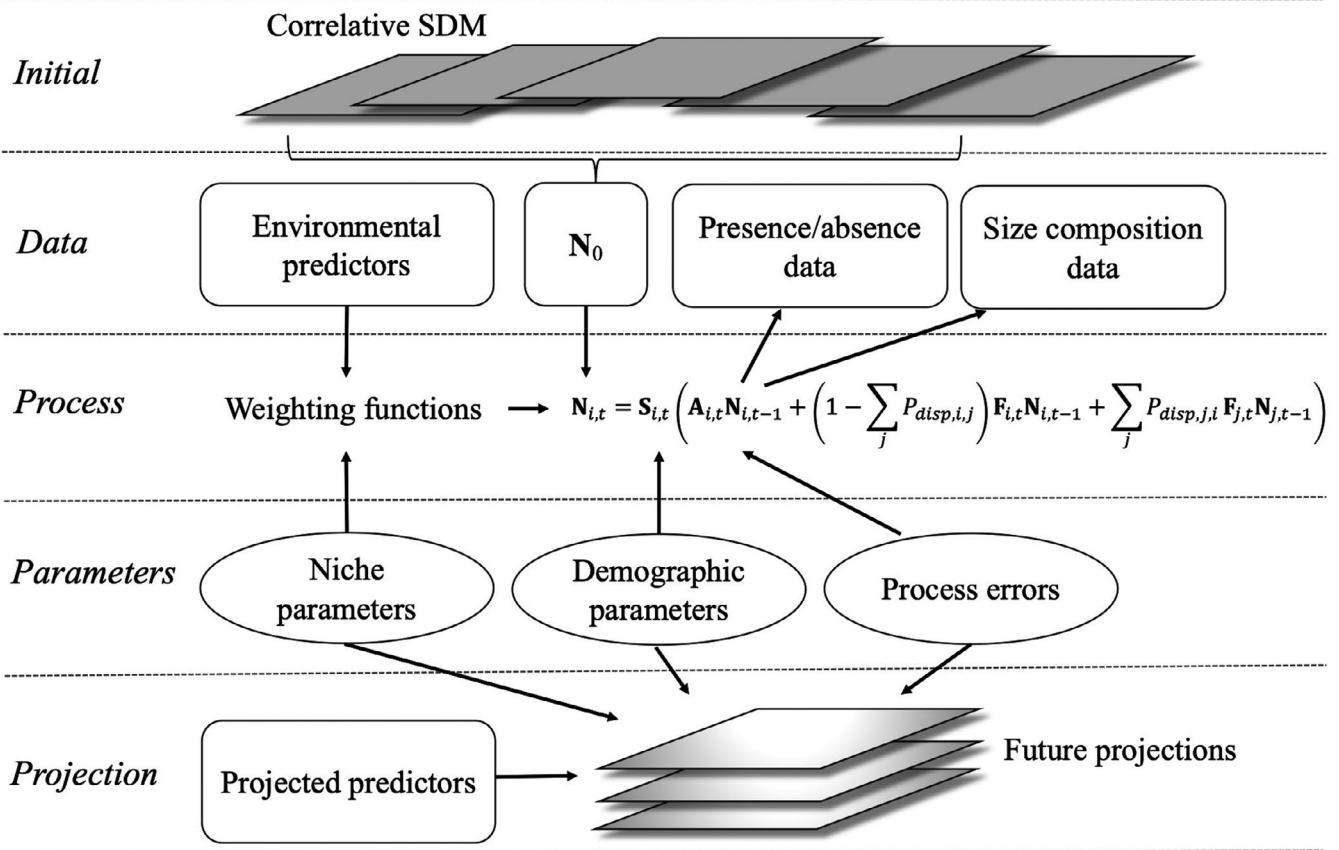


FIGURE 2 Modelling framework. The local population dynamics ($\mathbf{N}_{i,t}$) in each grid cell i within each year t is described by a size-structured population model, which consists of three stochastic subprocesses: survival ($S_{i,t}$), transition between demographic stages ($A_{i,t}$) and fragmentation ($F_{i,t}$), and the demographic rates in the subprocesses are shaped by environmental predictors and niche parameters via weight functions. Colony abundance at the initial year (\mathbf{N}_0) is estimated from an average of 10 predictions generated by the correlative SDM with the best model performance. Samples draw from posterior distributions of estimated parameters and projected environmental predictors were used for simulating future distributions and population dynamics of elkhorn coral *Acropora palmata*. The diagram was modified from Pagel and Schurr (2012)

Here $\bar{g}_{j,k}$ and $\bar{s}_{j,k}$ are parameters representing the basal transition rates before accounting for habitat suitability or density dependence, and $i_{i,t}$ refers to the probability of staying the same size. The competition intensity b is fixed to a low, constant value (0.01) for this model because intraspecific competition within the study population is expected to be unlikely given the low observation rate (where the species is present, it averages 1–2 colonies per 30-m² sample plot). The habitat suitability weighting parameter $h_{i,t}$ represents how suitable the environmental condition for growth of *A. palmata* in grid cell i is in year t , which was modelled as a truncated normal random variable bounded between 0 and 1 with $\mu_{h,i,t}$ given by a probabilistic niche model (Williams, Anandanadesan, & Purves, 2010; Zurell et al., 2016):

$$p(\mathbf{h}|\beta_1, \beta_2, C_1, C_2, \sigma_h) = tN_{[0,1]}(\mathbf{h}|\mu_h, \sigma_h^2) \quad (5)$$

$$\text{with } \mu_{h,i,t} = \exp \left\{ - \left(\frac{D_i - \beta_1}{C_1} \right)^2 - \left(\frac{T_{i,t} - \beta_2}{C_2} \right)^2 \right\}. \quad (6)$$

Here, σ_h accounts for unexplained variation in habitat suitability, D_i is temporally invariant water depth, and $T_{i,t}$ is mean summer SST in grid cell i in year t . The habitat preference of the species is described by parameters for the optimal niche position, β_1 and β_2 , and relative niche widths, C_1 and C_2 , with respect to water depth and mean summer SST.

The (k, j) entry in fragmentation matrix $F_{i,t}$ represents the probability that individuals in size class j generate fragments in size class k , which describes the asexual reproduction dominant in *A. palmata* recruitments. The fragmentation rates $f_{i,j,k,t}$ are assumed to vary spatio-temporally and depend on the maximum significant wave height in grid cell i in year t (Lirman, 2000), which was represented by wave action weighting function $w_{i,t}$. The fragmentation matrix $F_{i,t}$ is therefore as follows:

$$F_{i,t} = \begin{bmatrix} 0 & 0 & f_{i,3,1,t} & f_{i,4,1,t} \\ 0 & 0 & f_{i,3,2,t} & f_{i,4,2,t} \\ 0 & 0 & 0 & f_{i,4,3,t} \\ 0 & 0 & 0 & 0 \end{bmatrix}, \quad (7)$$

where

$$\bar{f}_{i,j,k,t} = \bar{f}_{j,k} w_{i,t}, \quad (8)$$

in which $\bar{f}_{j,k}$ is the unweighted fragmentation rate for generating fragments one or two size classes smaller than the original size. We modelled the wave action weighting parameter $w_{i,t}$ as a nonlinear relationship between fragmentation rate and maximum wave height, as waves may sweep fragments away and hinder fragment attachment, particularly strong waves caused by extreme weather such as severe storms and hurricanes (Vardi et al., 2012). The fragmentation weighting parameter $w_{i,t}$ was therefore modelled as:

$$p(\mathbf{w} | \beta_3, C_3, \sigma_w) = N(\mathbf{w} | \mu_w, \sigma_w^2) \quad (9)$$

$$\text{with } \mu_{w,i,t} = \exp \left\{ - \left(\frac{H_{i,t} - \beta_3}{C_3} \right)^2 \right\} \quad (10)$$

Here, σ_w accounts for process error in the fragmentation weighting model, $H_{i,t}$ is the maximum significant wave height in grid cell i in year t , and mean fragmentation rates peak at the wave height β_3 with scale parameter C_3 .

As coral fragments are known to be dispersed by waves up to several metres and the dispersal distance depends on fragment size and weight (Wulff, 1985), we assumed that fragments of size classes 1 and 2 disperse over both short (dispersal within a grid cell) and long (dispersal to a different grid cell), distances but fragments of larger size classes only disperse over short distances. The probability for long- and short-distance dispersal to occur was estimated using an area-to-area exponential dispersal kernel $P_{\text{disp},i,j}$ (Chipperfield, Holland, Dytham, Thomas, & Hovestadt, 2011), which approximates the transition probability to move from the area of grid cell i to the area of grid cell j , with mean dispersal distance of one grid cell. The post-dispersal number of colonies in each size class of $\mathbf{N}_{i,t}$ in focal cell i can therefore be estimated by summation of the post-transition abundance, number of fragments that disperse short distance within cell i and long distance from all neighbourhood cells j .

The process model is as follows:

$$p(\mathbf{N} | \mathbf{N}_0, b, \phi, \mathbf{h}, \mathbf{w}, \mathbf{g}, \mathbf{s}, \mathbf{f}, \sigma_p) = \prod_i \prod_t \text{Poisson} - \log \text{normal}(\mathbf{N}_{i,t} | E[\mathbf{N}_{i,t} | \mathbf{N}_{i,t-1}], \sigma_p^2),$$

where σ_p accounts for unexplained variation in demographic dynamics, partitioned by a Poisson–lognormal mixture distribution, \mathbf{N}_0 is the initial population state, $E[\mathbf{N}_{i,t} | \mathbf{N}_{i,t-1}]$ is the expected abundance defined in Equation (1), and \mathbf{N} is the estimated spatio-temporal abundance matrix across years. To partition the process error, Equation (11) was assumed to follow a Poisson distribution with mean $\lambda_{i,t}$, where $\log(\lambda_{i,t}) \sim N(E[\mathbf{N}_{i,t} | \mathbf{N}_{i,t-1}], \sigma_p^2)$. It is worth noting that the initial population state \mathbf{N}_0 could be estimated jointly with the model parameters of interest to allow for further flexibility in modelling the dynamic process; however, we estimated \mathbf{N}_0 independently (see Appendix S2) for the sake of parsimony and owing to the insensitivity of predicted density distributions to initial population structure (see Appendix S3).

2.5 | Data and parameter models

The data model associates latent total abundance $N_{i,t}$ and the size structure of the population $\pi_{d,i,t}$ in cell i at the end of year t with the two sources of observations: presence–absence $y_{p,i,t}$ and abundances of size classes $y_{d,i,t}$. The likelihood of size structure observations is given by the probability of observing $y_{d,i,t}$ colonies in size classes from total number of colonies observed with latent proportions of size classes $\pi_{d,i,t}$ from the process model, defined as

$$\pi_{d,i,t} = \left[(n_{1,i,t} / \sum_{j=1}^4 n_{j,i,t}), (n_{2,i,t} / \sum_{j=1}^4 n_{j,i,t}), (n_{3,i,t} / \sum_{j=1}^4 n_{j,i,t}), (n_{4,i,t} / \sum_{j=1}^4 n_{j,i,t}) \right]$$

, in which $n_{j,i,t}$ is the number of colonies in size class j , following a multinomial distribution. For presence–absence observations, the likelihood is given by the probability of at least one out of $N_{i,t}$ colonies to occur, in which the probability of observation increases with total abundance and was defined as $\psi_{i,t} = 1 - (1 - \pi_p)^{N_{i,t}}$, following a Bernoulli distribution with a per-colony detection probability π_p assumed to be high and follow Beta ($a = 10, b = 90$; see Pagel & Schurr, 2012, for further details of parameter values). Thus, the likelihood of the full data model is thus given by:

$$p(\mathbf{y}_p, \mathbf{y}_d | \mathbf{N}, \pi_p) = \Theta \prod \text{Multinomial}(\mathbf{y}_{d,i,t} | \pi_{d,i,t}) \times \Omega \prod \text{Bernoulli}(y_{p,i,t} | \psi_{i,t})$$

where Θ and Ω denote the subset of sites and years with demographic and presence–absence observations.

The Bayesian approach allowed us to build on prior information where available. Medium to strong informative priors based on literature were used for most parameters. Weakly informative priors were used for errors σ_p , σ_w and σ_p . Two niche parameters (β_1 and β_2) were fixed. Thus, the model had 17 parameters that were estimated in a Bayesian framework, including mortality rates (ϕ_1, ϕ_2, ϕ_3 and ϕ_4), basal transition rates for growth (g_1 and g_2), shrinkage (s_1 and s_2) and fragmentation (f_{SC3} and f_{SC4}), niche parameters (β_3, C_1, C_2 and C_3) and process errors (σ_p, σ_w and σ_p). The posterior samples from the estimated parameters were drawn to compute the 2D state variable $\mathbf{N}_{i,t}$ and used subsequently for simulations of abundance (see Section 2.8, Supporting Information and Appendix S4 for details).

2.6 | Bayesian estimation

DRMs were fitted to the data using the Differential Evolution Markov Chain sampler (ter Braak & Vuurgt, 2008), an efficient adaptive Markov chain Monte Carlo (MCMC) sampling method, with two independent chains each run in parallel with random starting values drawn from prior distributions of estimated parameters for 600,000 iterations, of which the first 350,000 samples were discarded as “burn-in.” Convergence of the chains was accessed using the Gelman–Rubin diagnostic (Gelman & Rubin, 1992) and visual inspection of the chain histories, and model fit was accessed using posterior predictive checks with Bayesian p -values calculated by comparing the discrepancy between observed data in each iteration

and predicted data conditional on the model being correct. The Bayesian MCMC estimation and convergence tests were implemented using package “BayesianTools” (Hartig, Minunno, & Paul, 2017) in R 3.4.3 (R Core Team, 2017).

2.7 | Initialization

We compiled 1,193 field observations of *A. palmata* from 2013 to 2015, including 75 presences, 1,087 absences and 31 sites with colony size measures (including 21 colonies in size class 1, 63 colonies in size class 2, 13 colonies in size class 3 and 47 colonies in size class 4). Of those, 620 observations from 2013 were used for initial population state estimation and 573 observations were included in the data model of DRM.

2.8 | Model projection

We predicted spatial distributions of *A. palmata* colonies under both current (2013–2015) and projected future (2016–2055) climate scenarios based on the posterior distributions obtained from Bayesian MCMC estimation. In the projected future climate scenarios, we assumed SST will increase at a rate of $0.19^{\circ}\text{C decade}^{-1}$, estimated from eleven global climate models (GCMs) downscaled for the eastern Caribbean Sea based on the Representative Concentration Pathway (RCP) 6.0 scenario (Flato et al., 2013; IPCC, 2012; Kibler, Tester, Kunkel, Moore, & Litaker, 2015). We further assumed significant wave height will increase 0.03 m/year , based on a 30-year

wave hindcast from 1979 to 2008 in the Caribbean Sea (Appendini, Torres-Freyermuth, Salles, López-González, & Mendoza, 2014). To quantify prediction uncertainty, we drew 500 sets of parameter samples from the posterior distributions and, for each set, simulated the spatio-temporal population dynamic model to generate abundance estimates within each grid cell (571,388 grid cells in total) for each year, from 2014 to 2055. We quantified predictions and uncertainty using the mean and standard deviation of the 500 simulated predicted density distributions for each year between 2014 and 2055. To assess the sensitivity of predicted distribution range and abundance to the assumed climate scenario, the simulations were also carried out using $\pm 25\%$ of the assumed SST and significant wave height increase rates.

3 | RESULTS

3.1 | Spatial distribution

The model predicted that occurrences of *A. palmata* were limited to a subset of potential habitat. In St Croix, coral colonies were predicted to occur at only 8.40%–10.89% of shallow water (water depth $\leq 20\text{ m}$) and 10.66%–14.90% of potential habitats within the study region (Figure 3). In St. Thomas and St. John, the predicted species occurrences were sparser, in part influenced by spatial gaps in nearshore wave data; the proportion of shallow water and of potential habitats with predicted species occurrences was 4.77%–6.03% and 8.64%–13.45% (Figure 4). The low percentages of species occurrences in both regions indicated that *A. palmata* occupied only

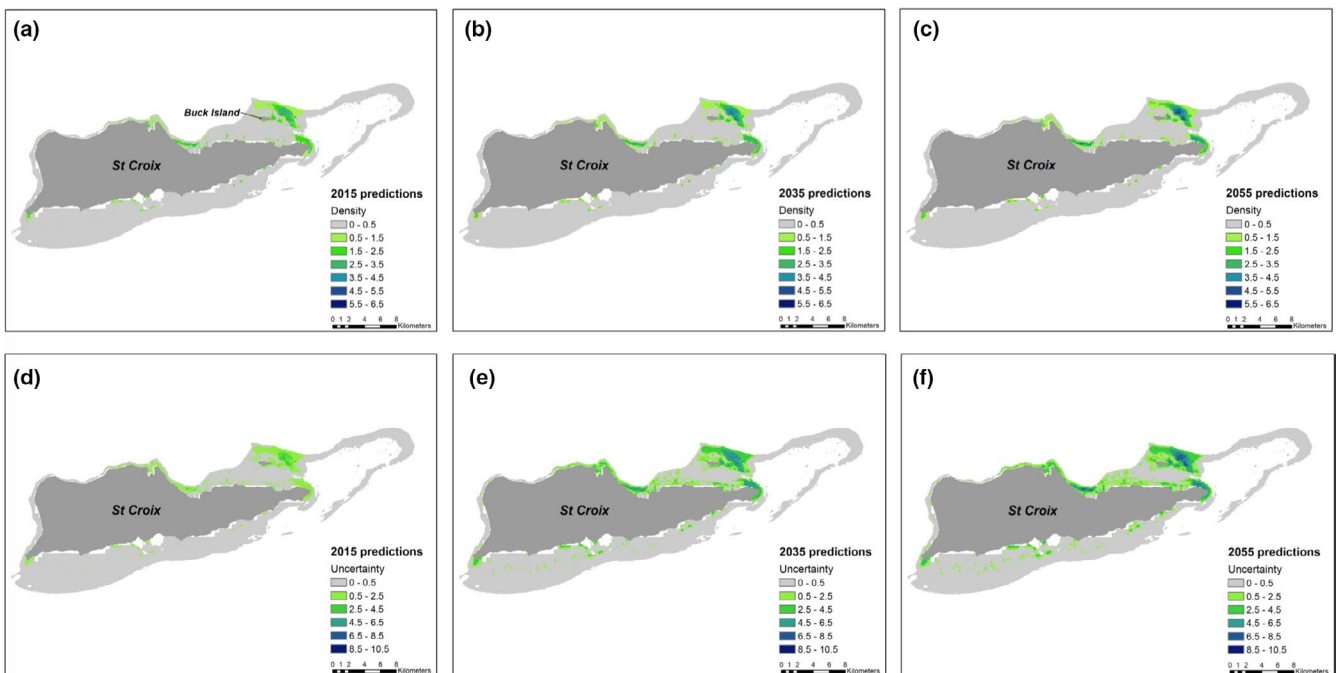


FIGURE 3 Predicted distribution of (a–c) mean density (colonies plot^{-1}) and the (d–f) associated uncertainty (standard deviation) of *Acropora palmata* colonies in St Croix in 2015, 2035 and 2055. Dark grey represents land, and light grey represents area with *A. palmata* predicted to be absent

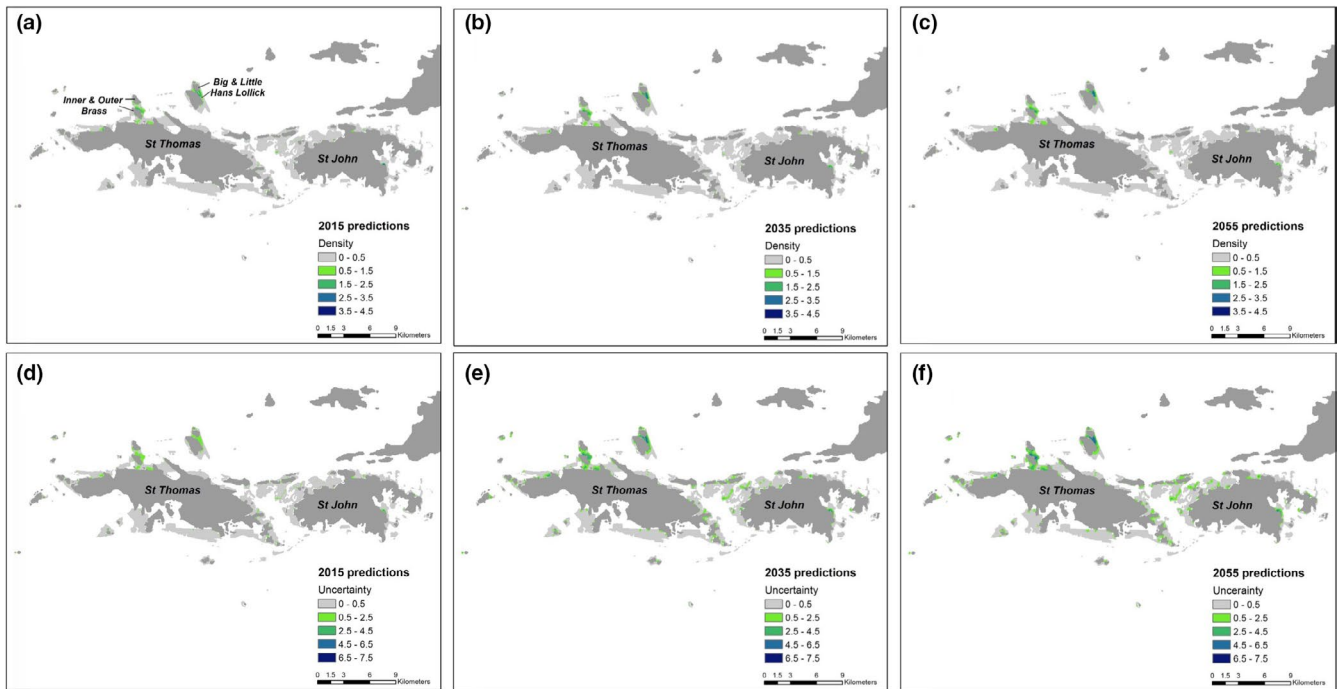


FIGURE 4 Predicted distribution of (a–c) mean density (colonies plot⁻¹) and the (d–f) associated uncertainty (standard deviation) of *Acropora palmata* colonies in St. Thomas and St. John in 2015, 2035 and 2055. Dark grey represents land, and light grey represents area with *A. palmata* predicted to be absent

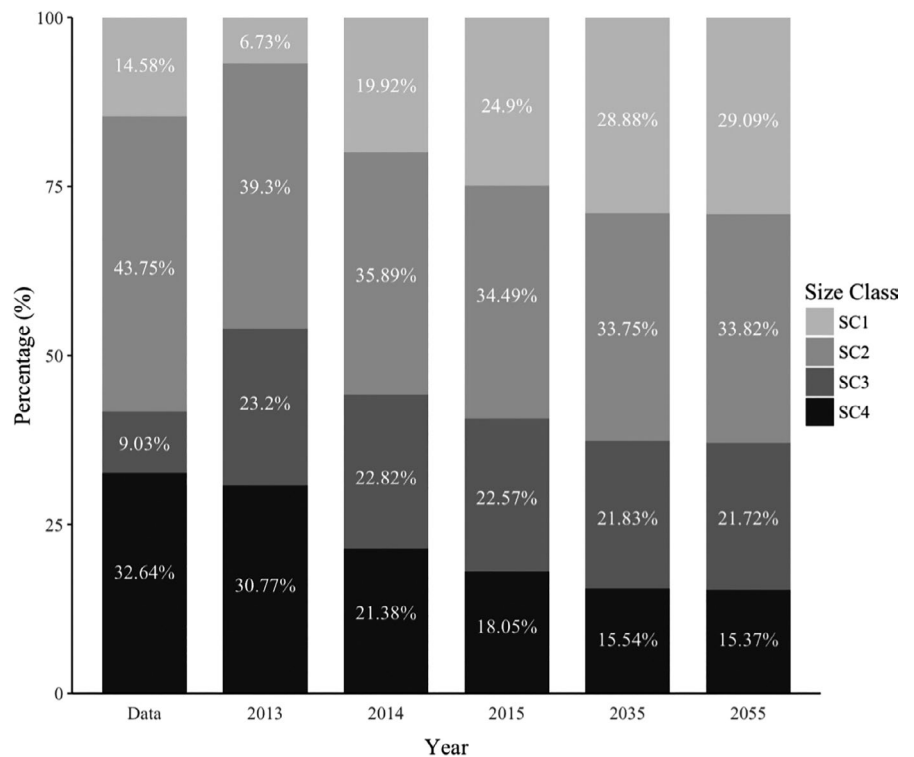


FIGURE 5 The proportional size class distribution of *Acropora palmata* colonies from observations and predictions for each year in St. Thomas, St. John and St Croix, U.S. Virgin Islands (USVI)

parts of its potential habitat, and this percentage will likely remain low into the future.

Despite the small changes shown in distribution range in both survey years (2013–2015) and projected years (2035 and 2055), the density of total *A. palmata* colonies was predicted to increase

regionally in St Croix. Within the predicted distributional range, coral colonies were expected to be relatively abundant at the north and east coasts of St. Croix and the north coast of Buck Island. The proportions of sites with high predicted density (≥ 3 colonies plot⁻¹) increased slightly from 1.11% to 2.61%, and the maximum predicted

density increased from 3.71 to 5.65 colonies plot⁻¹ from 2014 to 2055 (Figure 3, Table 1). In St. Thomas and St. John, where sites predicted to hold relatively abundant colonies are mainly between Big and Little Hans Lollik and Inner and Outer Brass, no detectable trend was found in the proportions of occurrence sites with high predicted density (ranged between 0.51% and 0.34%) across all years, but the maximum predicted density increased slightly from 3.22 and 4.04 colonies plot⁻¹ in the survey years and decreased from 3.72 to 3.43 in the projected years (Figure 4, Table 1). However, it is worth noting that an increase in prediction uncertainty with projection years, as well as with local total density, was found in both regions (Figures 3c,f and 4c,f).

Although the model predicted a small increase in distribution range and maximum local density, it also predicted a shift in size structure from larger towards smaller sizes. Compared to the size class distribution in 2013, the distribution in 2055 showed a 15.40% decline in size class 4 colonies and a 22.36% increase in size class 1 colonies (Figure 5).

3.2 | Parameter estimation

The convergence diagnostics indicated that each parameter estimated in the DRMs had achieved a convergence after burn-in ($\hat{R} \leq 1.2$), and the posterior predictive check showed no evidence of lack of model fit (Bayesian p -value = .533). The niche parameters captured *A. palmata*'s habitat preference for shallow and warm water with intermediate wave exposure (Table 2, Figure 6a). The estimated posterior median of water depth tolerance C_1 and temperature tolerance

C_2 from DRM was 15.19 m and 2.12°C, with 95% Bayesian credible interval (BCI₉₅) 12.89–17.34 m and 0.16–5.40°C, respectively, indicating that the species mainly occurred and had higher growth rates in the shallow water within a narrow range of summer mean SST around the assumed optimal value of 28°C. For the habitat preference on wave exposure, the estimated posterior median of optimal maximum wave height and wave tolerance was 1.80 m [BCI₉₅ = (0.32, 3.36)] and 1.44 m [BCI₉₅ = (0.11, 4.51)], suggesting the fragmentation of coral colonies was enhanced by intermediate wave exposure.

For larger size classes, the estimates of demographic parameters (mortality, shrinkage and fragmentation rates) were larger and more variable than the priors (Table 2, Figure 6b). The estimated posterior median of mortality rate for colonies in size class 3 and 4 was 0.16 [BCI₉₅ = (0.007, 0.50)] and 0.14 [BCI₉₅ = (0.004, 0.49)], suggesting a high mortality among large colonies. In addition to the high mortality, the estimated posterior median of basal transition rates for shrinking down one or multiple size classes was 0.18 [BCI₉₅ = (0.012, 0.58)] and 0.21 [BCI₉₅ = (0.015, 0.67)], suggesting a high probability for coral colonies to shrink, even in habitable environments. Higher estimated values with greater variation were also found for fragmentation rates. The estimated posterior median of fragmentation rates for size class 3 and size class 4 colonies was 0.40 [BCI₉₅ = (0.029, 0.89)] and 0.43 [BCI₉₅ = (0.087, 0.84)]. The estimates of process error σ_h (median = 3.34) and σ_w (median = 2.23) showed that there was unexplained variance in the habitat suitability and fragmentation weights (Equations 5 and 8), even with plausible estimates of niche parameters, suggesting the variation in demographic parameter estimation presumably comes from omitted processes or predictor variables.

	Prior mean	Mean	Median	SD	2.5%BCI	97.5%BCI
ϕ_1	0.25	0.26	0.21	0.20	0.007	0.79
ϕ_2	0.17	0.10	0.08	0.08	0.005	0.28
ϕ_3	0.056	0.19	0.16	0.14	0.007	0.50
ϕ_4	0.032	0.17	0.14	0.14	0.004	0.49
g_1	0.15	0.23	0.20	0.15	0.018	0.62
g_2	0.005	0.20	0.19	0.14	0.008	0.54
s_1	0.09	0.20	0.18	0.14	0.012	0.58
s_2	0.01	0.26	0.21	0.19	0.015	0.67
f_{sc3}	0.05	0.41	0.40	0.23	0.029	0.89
f_{sc4}	0.21	0.44	0.43	0.19	0.087	0.84
β_3	1.21	1.81	1.80	0.76	0.316	3.36
C_1	15	15.19	15.19	1.11	12.89	17.34
C_2	1	2.27	2.12	1.47	0.161	5.40
C_3	1	1.65	1.44	1.13	0.111	4.51
σ_h	100	3.34	3.34	2.64	0.176	9.72
σ_w	100	2.95	2.23	2.60	0.245	10.67
σ_p	100	0.47	0.41	0.35	0.019	1.39

TABLE 2 Prior mean and posterior distributions of the parameters of the dynamic range models

Note: See Table S2 for the full parameter and prior distribution description. Abbreviation: BCI, Bayesian credible interval.

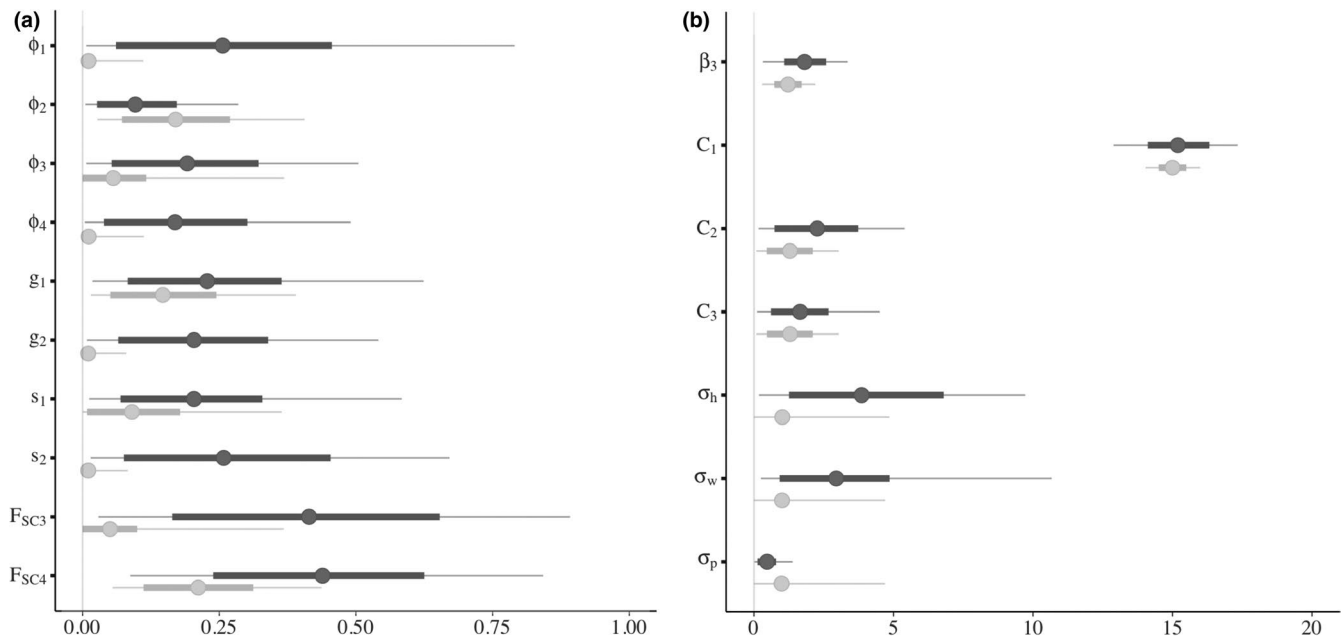


FIGURE 6 Posterior (dark grey) and prior (light grey) distributions of (a) niche and error parameters and (b) demographic parameters, where thin lines represent 95% Bayesian credible intervals, thick lines represent 68% Bayesian credible intervals, and grey circles are posterior means of the distributions. See Table S2 for the full parameter descriptions

4 | DISCUSSION

4.1 | Spatial distribution and population dynamics

Incorporating dynamic processes, such as demographic dynamics and dispersal, into SDMs is critical for species threatened by rapid environmental change. In the light of the dramatic loss of Caribbean coral populations over the past three decades (Aronson & Precht, 2001; Bruckner, 2002; IUCN, 2017), research on *A. palmata* spatial distribution and population dynamics has been surprisingly limited, perhaps due to the challenges of collecting data on a threatened species. Through the use of process-based DRMs that integrate information from diverse sources in a Bayesian framework, we have demonstrated the potential to predict the spatio-temporal distribution of *A. palmata* abundance at a regional scale.

In general, our predictions showed that *A. palmata* distributions were restricted to shallow water with intermediate wave exposure, and the occupancy of potential habitat was low. In St. Croix, *A. palmata* colonies were expected to be locally abundant at the north coasts of Buck Island (Figure 3), which is consistent with the relative higher coral density found at the same region in a field survey (Mayor, Rogers, & Hillis-Starr, 2006).

Our results also suggested that, with an increase in wave disturbance, a shift from large towards small colony sizes occurred in survey years, and this shrinkage is likely to continue into the future (Figure 5). This decline in *A. palmata* colony size has been documented in St. John (Roth, Muller, & van Woosik, 2013), Florida Keys (Porter et al., 2012) and the Mesoamerican Reef (Rodríguez-Martínez, Banaszak, McField, Beltran-Torres, & Alvarez-Filip, 2014). Decline in *A. palmata* size structure has negative implications not

only for population stability, but also for reef complexity and ecosystem services. First, smaller *Acroporid* corals may have reduced fecundity, both sexual and asexual (Hughes et al., 2000; Vardi et al., 2012). Second, smaller corals are more susceptible to stressors such as bleaching (Loya et al., 2001). Third, smaller coral leads to reduced structural complexity of coral reefs (“reef flattening”), which compromises the habitat suitability for corals and other reef-associated species, reducing biodiversity and ecosystem function (Alvarez-Filip, Dulvy, Gill, Côté, & Watkinson, 2009). Thus, it is crucial for models to account for size structure in addition to abundance when assessing the population status of *A. palmata* population.

4.2 | Conservation implications

Here, we projected that the decline in *A. palmata* populations is likely to continue in the absence of new additions to the population through either sexual reproduction or restoration efforts. To mitigate the rapid decline in the wild populations of corals, restoration efforts over the past decades have focused on outplanting coral colonies grown in nurseries. However, with limited quantitative data on the species’ distribution and population dynamics, these efforts have relied on local knowledge, and the level of restoration success has been variable (Young, Schopmeyer, & Lirman, 2012). Recent evidence (Forrester, Ferguson, O’Connell-Rodwell, & Jarecki, 2014; Young et al., 2012) and the first systematic, science-based guideline to restoration (Johnson, Lusic, & Bartels, 2011) both suggest that priority should be given to selecting larger transplanted fragments and sites with existing populations to enhance sexual recruitments. Our model’s predicted shift towards smaller sizes of *A. palmata*

population underscores the need to select preferentially larger coral fragments for outplanting. In addition, our results show relatively high predicted *A. palmata* density in the north and east coasts of St. Croix, north coasts of Buck Island, and area between Big and Little Hans Lollok and Inner and Outer Brass (Figures 3 and 4). The predicted high densities indicate strong potential for these areas to continue as potential habitat.

4.3 | Sources of uncertainty

Acropora palmata, as a rare species, has limited data available for long-term prediction. Despite the relatively precise estimates of niche parameters, the wide credible intervals of demographic parameters suggested that demographic process were poorly informed by the data, even when the uncertainty from density dependence was restricted. Data limitations are not surprising for a rare species; however, this does spotlight a potential drawback of process-based SDMs; that is, the key processes need to be explicitly described in the models, and uncertainty caused by omitted components can be difficult to identify (Beale & Lennon, 2012; Ehrlén & Morris, 2015). Indeed, in addition to environmental suitability for colony growth, *A. palmata* colonies have also been found to be influenced by other stressors, such as intense and frequent storms (Lirman, 2000), disease outbreak and predation from the corallivorous snail (*Coralliophila abbreviata*; Williams & Miller, 2012). With the data currently available, our SDM could not explicitly incorporate those processes, but below we suggest approaches for future model development.

Storm intensity and frequency are known to be influential in shaping demographic process and can affect *A. palmata* colonies in two competing ways: mild storms may increase colony abundance via fragmentation, but strong and consecutive waves caused by severe storms may prevent fragments from successfully reattaching to the substrate and may raise mortality rates (Lirman, 2000; Vardi et al., 2012). In this study, we considered the effect of the projected increase of wave energy on fragmentation, but not on colony mortality, because quantitative relationships between storm or wave intensity and mortality remain unpredictable. Future work could incorporate more detailed storm effects on mortality by associating mortality parameters (ϕ_i) with storm-specific wave data.

In addition to storm effects on mortality, diseases are also widely recognized as one of the major threats to *A. palmata* colonies in the Caribbean (Williams & Miller, 2012). Currently, the mechanisms that lead to disease outbreak are still largely unclear, but the risk of disease outbreak has been associated with thermal stress and colony density (Lentz, Blackburn, & Curtis, 2011; Muller & van Woessik, 2014; Patterson et al., 2002). Corallivorous snail predation, as another major stressor not included in the models, has been found more likely to occur in high-density sites (Grober-Dunsmore, Bonito, & Frazer, 2006), suggesting a density-dependent relationship. For further model development, we suggest linking dynamics of disease outbreaks or snail predation with the density-dependent parameter b .

Although the four size classes applied in this study were determined based on details of the biology and life history of *A. palmata*, our use of a matrix population model assumes artificial, discrete size classes, which may lead to imprecision in demographic parameter estimation as the variability among colonies within each size class was ignored. For further model improvement, population models capable of accommodating continuous state variables, such as integral projection models (Merow et al., 2014), should be considered as an important future research direction.

4.4 | Process-based SDMs in practice

Given the potential for climate change-driven influences on wildlife populations, process-based SDMs, which consider mechanisms underlying species distribution in addition to static occurrence–environment relationships, have been recommended for improving our understanding of the ongoing and future impacts (Evans, Merow, Record, McMahon, & Enquist, 2016). However, the applications of process-based SDMs to real-world scenarios remain relatively rare, presumably because of their computational intensity and high data requirements (Osada et al., 2019). Indeed, in this study, in addition to computation time (here 24 hr on average for 6,000 MCMC iterations), finding an adequate balance of model complexity was a major challenge. An ideal level of model complexity for the process of interest may depend on the information about the parameters depicting the process from the data in hand. Even with a seemingly sufficient amount of data collected with precision, inference could still be challenging if the data do not capture the focal process fully. To ensure that the spatial and temporal scales of current or future sampling are appropriate for the process of interest, Peacock, Krkošek, Lewis, and Lele (2017) suggested evaluating parameter estimability under simulated scenarios with different sampling designs using data cloning, a statistical tool that maximizes cloned likelihood with Bayesian machinery (Lele, Dennis, & Lutscher, 2007). Comparing the variances of parameter estimates in those simulated results could help improve estimability for the complex ecological process by providing guidance on study design for current or future data collection. Additionally, in a review on recent development in the field of SDMs, Dormann et al. (2012) suggested further developments of an accuracy–complexity return curve, which describes gain in model accuracy over complexity, for process-based SDMs as a potential tool for facilitating decisions on adequate levels of model complexity. In agreement with both Dormann et al. (2012) and Peacock et al. (2017), we highlight the need for developing a sophisticated framework to optimize SDM complexity in a way that balances tractability with predictive performance in combination with evaluations of statistical estimability for the ecological process investigated.

Despite offering a methodological advance in modelling species distribution and the potential future changes of *A. palmata* populations, limitations remain in this study. Constrained by the practical challenges of collecting underwater observations for a rare species, our results are based on field data with a limited

time span. As the future projections were inferred from model extrapolations, prediction bias can increase with the projection time if the limited observations fail to represent the fundamental spatio-temporal dynamics of *A. palmata* populations (Guisan & Thuiller, 2005). Extrapolating beyond observed data is a risk in any modelling endeavour that attempts to do so, particularly when attempting to forecast into the future. In the face of uncertainties inherent in projecting with future climate scenarios using species distribution modelling techniques, Bell and Schlaepfer (2016) highlight the importance of incorporating ecological mechanisms constraining species occurrences into statistical frameworks. In agreement with Bell and Schlaepfer (2016), we thus introduced informative priors with laboratory and empirical support into our models and suggest this approach as a basis for advancing the development of species distribution models.

5 | CONCLUSIONS

While the established quantitative framework assessing species vulnerability to climate change focuses mainly on range changes in species occurrence (Crossman, Bryan, & Summers, 2012; Summers et al., 2012), our study highlights the importance of also considering abundance and demographic dynamics. For species such as *A. palmata*, range changes alone may not well represent the true vulnerability and can yield misleading results. In the case of *A. palmata*, our predictions showed that there can be large changes in population structure even with relatively small changes in abundance and range. Given the uncertainty that arose in demographic parameter estimation, we recognize that demographic information about *A. palmata* remains limited, even when knowledge from diverse sources was integrated. We therefore suggest that more effort be placed on collecting population data and investigating relationships between stressors and demographic processes. Although challenges remain and further model development, as well as field validation, is encouraged, the predictions of this study provide information on the current and future status of the threatened coral species, *A. palmata*.

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PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13143>.

DATA AVAILABILITY STATEMENT

All predictive maps generated for this study are available as raster grids from the Pangaea database: <https://issues.pangaea.de/browses/PDI-19463>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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BIOSKETCH

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