


# Species-specific environmental preferences associated with a hump-shaped diversity/temperature relationship across tropical marine fish assemblages

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## Abstract

**Aim:** To identify key environmental factors associated with local fish species richness across a large tropical marine region.

**Location:** Wider Caribbean region.

**Methods:** Species richness estimates were based on a sightings database covering the wider Caribbean region. Environmental variables considered were distance to key habitats, habitat area, temperature, depth, salinity, nutrient concentration, as well as natural and anthropogenic disturbance. We test the significance of associations between these factors and species richness, establish the shape of these relationships and use spatial cross-validation to test the generality of these results. Species-specific environmental associations within these relationships were then tested.

**Results:** Five environmental variables showed significant associations with species richness, but only two, temperature and depth, proved robust to spatial cross-validation. Temperature was the best performing environmental predictor, showing a unimodal relationship with species richness and optimum temperatures consistent across analytical choices and data sets. Relationships between species richness and other environmental factors were also typically unimodal. Variation in species-specific temperature associations was significant within species richness gradients; with a higher number of species associated with optimal temperatures.

**Main conclusions:** Temperature represents the dominant environmental predictor of fish species richness identified by our study, showing a hump-shaped curve, peaking at around 27.4°C. This meant that the warmest sites within our study were not necessarily the most species rich. Variation in species thermal niches may play a key role in driving species richness gradients, with significant general positive trend for fish species to occur in locations exhibiting optimum sea surface temperatures.

## KEYWORDS

biodiversity, citizen science, coral reef, drivers of fish species richness, ecological sampling simulation, Reef Environmental Education Foundation, sampling bias, species richness estimators, The wider Caribbean Region

## 1 | INTRODUCTION

Identification of environmental factors associated with species richness can provide key insights into the ecological and evolutionary processes shaping life on Earth (Rahbek & Graves, 2001; Rosenzweig, 1995). While such relationships between species diversity and environmental factors are relatively well studied in terrestrial environments, they are often less understood in marine environments (Tittensor et al., 2010). Ecological studies covering spatial ranges that are functionally meaningful for the majority of species in the marine environment are often constrained by acquisition of relevant data due to inaccessibility and high cost (Holt, Rioja-Nieto, Aaron Mac Neil, Lupton, & Rahbek, 2013; Mora, Tittensor, & Myers, 2008).

Among biogeographical regions, spatial species richness patterns are ultimately the result of variation in the rates of speciation, extinction and dispersal (Mora, Chittaro, Sale, Kritzer, & Ludsins, 2003; Wiens & Donoghue, 2004). Within biogeographical regions, variation in species richness may be more due to variation in local conditions (Rahbek, 2005). Local habitat characteristics have been hypothesized to influence the number of species present within a community in a wide variety of ways. Firstly, community-level hypotheses focus on how local conditions influence the capacity of communities to support more organisms, with more favourable conditions, such as increased productivity (Mittelbach et al., 2001), area (Preston, 1960) or habitat heterogeneity (Kerr & Packer, 1997), hypothesized to support more organisms, and subsequently, more species. Alternatively, local environmental factors may be linked to species richness patterns due to variation in the environmental niches of species (Guisan & Rahbek, 2011), with locations experiencing conditions that are favourable to a greater number of species facilitating communities with higher species richness (Lortie et al., 2004). Identifying the shape of relationships between species richness and environmental predictors can be informative regarding potential mechanisms underlying these patterns (Evans, Greenwood, & Gaston, 2005).

In order to elucidate regional scale patterns and processes in species richness across local assemblages, extensive standardized survey data are required. This study is focused on shallow water marine fish communities across the Greater Caribbean and utilizes a SCUBA-based fish survey programme covering the region (REEF, 2011). Previous studies of marine fish species richness patterns across the Caribbean or wider Caribbean, have been conducted at scales coarser than that of local assemblages. Island-scale analysis of Caribbean marine fish demonstrated a classic positive species-area relationship, as well as a negative species richness relationship with productivity (chlorophyll-*a*) and/or geographical isolation (Sandin, Vermeij, & Hurlbert, 2008). A Census of Marine Life study of all Caribbean marine species found species richness to be higher in the Antilles and northern coast of South America, although sampling issues complicated interpretation of these patterns (Milosavlitch et al., 2010). Francisco-Ramos and Arias-González (2013) demonstrated that Caribbean marine fish assemblages tend to be more

homogeneous than expected by chance and that local species richness (alpha diversity) is a major driver of overall diversity (i.e. gamma diversity) across the Caribbean basin.

The biodiversity of tropical coastal fish assemblages has been well studied across wide variety of spatial extents and resolutions. At the largest spatial extents, there is little evidence to suggest that variation in environmental niches among species influences the richness of species assemblages. Conversely, biogeographical factors such as the mid-domain-effect, the influence of bounding constraints to species ranges (Connolly, Bellwood, & Hughes, 2003), evolutionary connectivity (Cowman & Bellwood, 2013; Mora et al., 2003) and general macroecological processes, in particular habitat area (Bellwood & Hughes, 2001; Parravicini et al., 2013), are well established. Key environmental factors have been linked to species richness patterns within marine regions, such as sea surface temperature, salinity and nitrate (Mellin, Bradshaw, Meekan, & Caley, 2010), habitat area and depth (Cornell & Karlson, 1996; Karlson & Cornell, 1998), and geographical isolation (Mellin, Ferraris, Galzin, Kulbicki, & Ponton, 2006; Sandin et al., 2008). While these factors include variables that can be linked to either interspecific variation in environmental affinities, general community-level processes, or both, lack of information regarding the shape of these species richness relationships and the potential for species-specific responses along these gradients, hinders interpretation regarding these underlying mechanisms.

In this study, we assess the capacity of a variety of potential environmental variables to predict species richness patterns, testing the shape of relationships shown by significant environmental predictors. We then establish the capacity of these relationships to predict species richness patterns in areas beyond those from which they were derived. Building on this analysis, we investigate species-specific responses across the identified environment/species richness gradients in order to consider the potential for interspecific variation in environmental affinities underlying these patterns.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

The wider Caribbean Region is part of the Tropical Western Atlantic and extends from Bermuda, southern Florida and the Gulf of Mexico throughout the Caribbean Sea to the northern coast of South America.

### 2.2 | Survey data and fish species richness estimates

Data on fish species were obtained from surveys conducted by volunteer SCUBA divers between 1st January 2000 and 31st December 2010, under the guidance of the Reef Environmental Education Foundation (REEF). During a survey, divers swim freely around in a dive site and record every observed fish species that can be confidently identified. The survey protocol is specifically



designed for volunteer data collectors and is effective in rapid assessment of both fish distribution and abundance (Schmitt, Sluka, & Sullivan-Sealey, 2002). It has also been demonstrated to produce data on species richness that are consistent with more standardized sampling protocols (Holt et al., 2013). Collected data also include geographical coordinates, habitat type and dive details (i.e. average depth and time). Habitat type was not recorded consistently within locations by observers and was, therefore, not included in any of our analyses (however, data on distance to key habitats were obtained from alternative sources and included in our analysis, see Environmental variables section below and Table 1). Surveys were classified, according to the experience of the volunteer, as either “expert” or “novice” surveys, with expert surveys being defined as those undertaken by observers who have completed over 35 surveys and two fish identification examinations. A comparable amount of training has been shown to result in survey data with precision that is within one percent of that of an experienced “control” diver (Darwall & Dulvy, 1996). The main results presented in this manuscript are based only on these “expert” data. A total of 38,454 surveys (41.3% of all surveys), were classified as “expert.”

Two major concerns regarding the reliability of such data sources are the variation in survey effort per site and the consistency of survey results between different observers. These factors can be expected to have an influence on the numbers of species recorded and we performed extensive exploratory analysis in order to identify the most effective means to address these issues (Appendix S1, Supporting information).

## 2.3 | Environmental variables

Environmental variables were chosen based on published literature (Table 1, Figure S2.3, Appendix S2, Supporting information). Values for the different environmental variables were extracted for each survey site location.

## 2.4 | Statistical analysis

Our analytical procedure was split into two main sections: (1) identification of significant environmental predictor of fish species richness and the shape of these relationships and (2) testing for the influence of species-specific responses along the relationships identified in section 1.

**TABLE 1** Environmental factors tested for their capacity to predict fish species richness within coastal communities throughout the wider Caribbean. For references, see (Appendix S4, Supporting Information)

Environmental factor	Potential influence on species richness	References	Data used & Source	Source
Temperature	i) By influencing species distributions due to interspecific variation in physiological tolerances ii) Indirectly through association with productivity	Sunday et al. (2011) Currie (1991), Rosenzweig (1995), Roy et al. (1998)	Mean annual sea surface temperature (SST) from 2000–2009, grid cell size = 1/12°, (°C)	Casey et al. (2010)
Salinity	By influencing species distributions due to interspecific variation in physiological tolerances	Lam et al. (2005)	Mean annual salinity from 2000–2009. Grid size 1°	Antonov et al. (2010)
Nitrate	Through association with productivity	Falkowski (1997), Macpherson (2002), Pennington et al. (2006)	Mean annual nitrate concentration from 2000–2009. Grid size 1°	Garcia et al. (2010)
Connectivity with seagrass beds or mangroves	Through association with productivity	Nagelkerken et al. (2001), Mumby et al. (2004), Harborne et al. (2006)	Km to nearest seagrass bed and km to nearest mangrove	UNEP-WCMC (2011) UNEP-WCMC (2005)
Isolation	Decreasing numbers of species in more isolated locations due to dispersal limitation	MacArthur & Wilson (1967), Sandin et al. (2008)	Km to nearest land	UNEP-WCMC (2011)
Anthropogenic disturbance	By altering natural environments at a rate beyond that which species can adapt	DeVantier et al. (2006), Mora et al. (2011)	Human population density within 25 km in 2005	CIESIN (2005)
Habitat area	Through influence on number of individuals, habitats or biogeographical regions	Preston (1960), Williams (1964), MacArthur & Wilson (1967), Connor & McCoy (1979), etc. Coral reef example: Bellwood and Hughes (2001)	Reef length	UNEP-WCMC & Centre, W.F. (2010)
Depth	Through association with productivity Through variation in physiological tolerances of species or in habitat forming species	Cornell and Karlson (2000) Baird et al. (2003)	Median reported diver depth	REEF (2011)

## 2.4.1 | Environmental species richness relationships

### Testing for environmental factors associated with fish species richness

The first analytical step was to identify environmental factors that were significantly associated with species richness, without constraining the shape of such relationships during this testing. The generalized additive model (GAM) methodology was selected for this purpose due to its capacity to describe simple and complex ecological response shapes (Elith et al., 2006) and its lack of requirement of a priori assumptions about the type of relationship being modelled. Initially, the potential contribution of individual variables was assessed by constructing a separate GAM for each environmental variable. The predictor with the highest percentage deviance explained (DE), DE being a pseudo  $R^2$  defined as  $1 - \frac{\text{residual deviance}}{\text{null deviance}}$ , was retained as the starting point for model building followed by a forward stepwise selection process:

1. Each of the remaining variables was added to the model separately and the variable producing the largest increase in DE was retained, provided this increase was more than 1%.
2. If the added variable was correlated with any other variable (Spearman's correlation  $>0.5$  &  $p < .05$ ), the correlated variable was not included in the further model building.
3. General cross-validation scores from GAMs and ANOVA with a  $\chi^2$ -test were used to compare models every time a new variable was added, in order to test for significant differences between the models.

Steps 1, 2 and 3 were repeated until all the environmental variables meeting the requirements were included in the model. Interactions between variables were not included in the analysis, in order to focus on the importance of each variable individually. Continuous predictors were smoothed using thin plate regression splines and the individual smoothing components were specified to a maximum of 4 degrees of freedom when fitting the models. As is typical with species richness data, a Poisson distribution with a log link function was applied to all GAM models. Site type (MPA or not MPA) was included in the model as a two level factor.

### Testing the shape of environmental species richness relationships

The second analytical step was to establish the most likely shapes of the species richness/environmental factor relationships for the significant factors identified in step 1. Three types of predictive model were tested: linear, quadratic and cubic, and the performance of each model was evaluated via the Akaike information criterion, corrected for small sample size (AICc), with the model returning the lowest AICc scores considered as being the best representation of the relationship between environmental predictor and fish species richness. The parameters for all models were estimated via a generalized least squares (GLS) approach in order to account for spatially variable error structure by allowing with variance to differ among

sub-regions of overall survey area defined by the REEF fish survey project, i.e. two digit region codes for the Tropical Western Atlantic, with 22 sub-regions in total (available at REEF, 2011).

### Model cross-validation

The final step in this part of the analysis was to cross-validate the relationships established in step two; in order to establish the generality of these relationships across different areas of our study region. This approach divided the data in half by first selecting a point within the overall survey region then selecting the nearest 50% of survey sites to that point (with these sites becoming the "testing data set"). Parameters for the best performing models identified by the previous analysis were then reevaluated using the data from the remaining 50% of survey sites (referred to as the "training data set"). The accuracy of models based on these revised parameters was evaluated via linear regression, using model estimates of species richness from the testing set as the explanatory variable and observed species richness as the dependent variable. Perfect models would be expected to return linear regressions with a slope of one (reflecting complete accuracy: a one-to-one relationship between predictions and original estimates) and  $R^2$  values of one (reflecting perfect precision) and an intercept of zero. The results from the spatial cross-validations were based on the  $R^2$ -values, slope intersects and slope coefficients from the 1,000 iterations.

## 2.4.2 | Testing for the influence of species-specific environmental associations along environmental species richness gradients

In order to investigate species-specific environmental associations, we calculated the mean environmental conditions across the sites where each species was recorded as being present. These averages were compared to null expectations calculating standardized effect sizes (SES):

$$SES = \frac{\text{obs} - \text{mean}(\text{null})}{\text{sd}(\text{null})}$$

Where obs = observed mean value and null = 1,000 randomly generated mean values. For this analysis, null values were generated for each species by randomly selecting the same number of occurrences as shown in the observed data, within the coarse distribution of each species (i.e. within the same REEF sub-regions used in the spatial GLS models above). The species-specific SES values, mean SES value across species and the variance in SES values across species were all compared to the distribution of null expectations produced by calculating SES values for each of the null runs; tested again in a two-tailed manner with SES values showing  $p < .05$  reported as "significant." If species environmental associations are related to species richness gradients, then a significant deviation in mean SES should be apparent, with more species associated with the optimal end of the gradient. If a species replacement occurs over an environmental gradient, then a significant increase in SES variance should be



apparent, as occurrence along the gradient will vary among species more than null expectations.

All statistical analyses and data simulation were performed using the R statistical software (R Development Core Team 2011) and utilizing the packages: "nlme" (Pinheiro, Bates, DebRoy, & Sarkar, 2014), "vegan" (Oksanen et al., 2015) and "mgcv" (Wood, 2011).

### 3 | RESULTS

A total of 962 survey sites, with a total of 317 species, were retained after the data selection criteria were applied to the data set. These sites were distributed across the wider Caribbean region, with species richness estimates varying from 23 to 222 (Figure 1). Three species were elasmobranchs and the remainder were teleosts, including 17 orders and 59 families (a full species list along with higher taxonomic information is attached as Appendix S3, Supporting information).

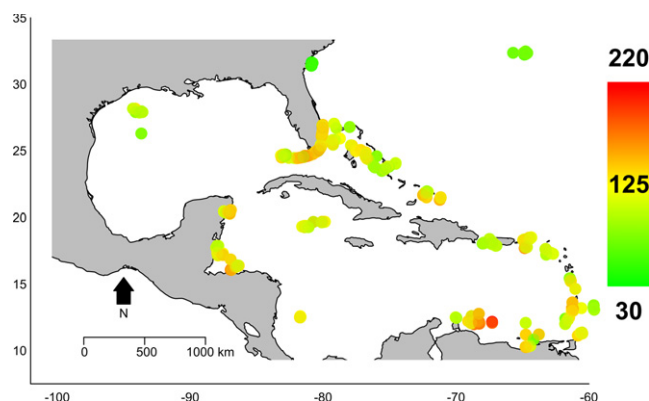
#### 3.1 | Environmental species richness relationships

##### 3.1.1 | Identification of environmental predictors

The environmental predictor selection procedures resulted in a GAM retaining five environmental variables (Figure 2) and a DE value of 41.8%. The variables "distance from reef to nearest land," "distance from reef to mangrove" and "distance from reef to sea grass bed" were all correlated with each other above the  $r = .5$  threshold and only the latter was included in the final model, since this was the first of these variables to be added during our stepwise process.

##### 3.1.2 | Shape of environmental species richness relationships

Of the five environmental predictors identified in part 1a, only "Distance to seagrass beds" was best described via a simple linear model



**FIGURE 1** Distribution of survey sites with associated fish species richness estimates within the wider Caribbean region, based on the jackknife second order estimator. Points plotted with semi-transparent colours [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

(Figure 3), based on the AICc criterion. For the remaining predictors, temperature and salinity were best described with cubic models, while nitrate and depth were best described with quadratic models. Species richness showed a unimodal relationship with sea surface temperature, salinity, nitrate and depth, peaking at 27.4°C, 36.0 ppm, 1.1  $\mu\text{M}$  and 12.1 m respectively (Figure 3). Increased distance to sea grass beds had a negative linear association with reef fish species richness (Figure 3).

##### 3.1.3 | Model validation

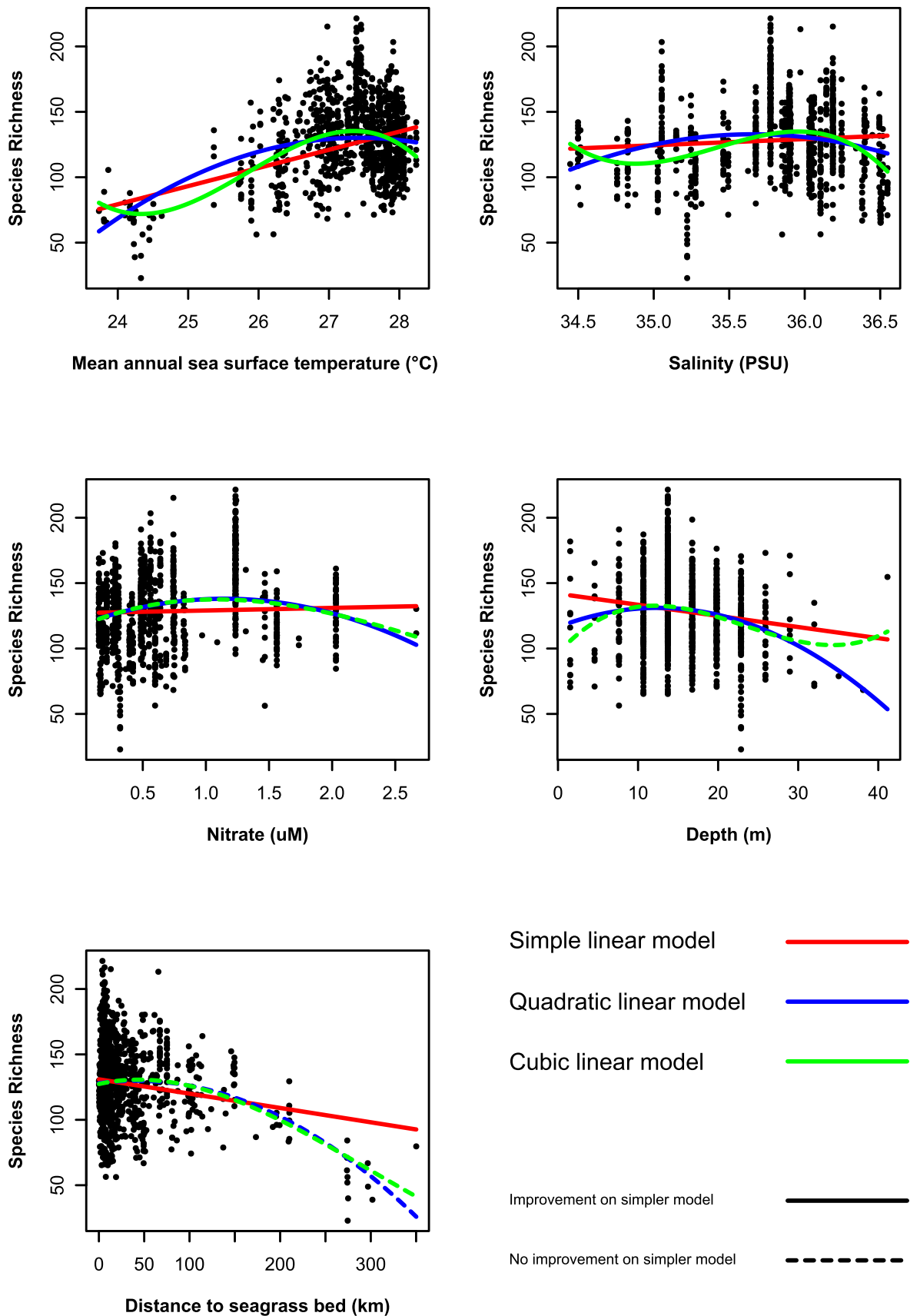
Sea surface temperature outperformed the other significant environmental predictors in our validation tests, with predicted versus actual species richness estimates showing a mean slope close to one (1.12), slopes from all validation runs being positive and significantly different to zero (mean slope  $p < .001$ ), intercepts that tended not to be significantly different from zero (mean intercept  $p = .11$ ) and a mean  $R^2$  value of 0.16 (Figure 3). The remaining predictors varied considerably in their validation performance according to these criteria (Figure 3), with only depth showing robust results for slopes and intercepts.

#### 3.2 | Species-specific environmental preferences along environmental species richness gradients

In light of the performance of the species richness/environmental models, the depth and temperature gradients were selected for this part of the analysis. Since depth and temperature both showed unimodal species richness/environment curves, the species-specific environmental preference analysis was split into two parts: the minimum to optimum part of the gradient (referred to as either the "cold" or "shallow" species richness gradient) and the optimum to maximum part of the gradient (referred to as either the "warm" or "deep" species richness gradient).

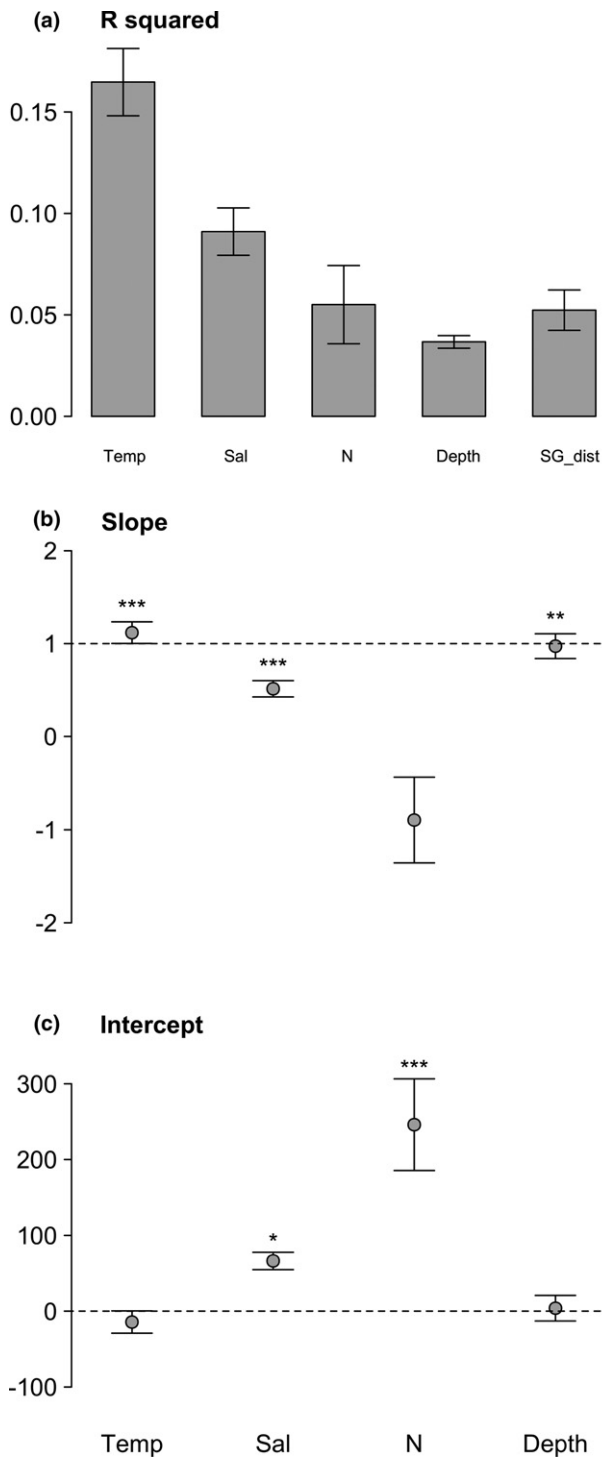
For temperature, within the cold species richness gradient, standardized effect size of mean species temperature of occurrence tended to be higher than null expectations (observed mean SES = 0.65,  $p < .001$ ) and also more variable than null expectations (observed variance SES = 14.69,  $p < .001$ ). A total of 164 species (from 293) showed significant SES values, 98 positive and 66 negative (Figure 4a). Within the warm species richness gradient, standardized effect size tended to be lower than null expectations (observed mean SES = -0.99,  $p < .001$ ) and, again, more variable than null expectations (observed SES variance = 8.18,  $p < .001$ ). A total of 102 species (from 271) showed significant SES values, 27 positive and 75 negative (Figure 4b). Forty-seven species were significantly associated with optimal temperatures in both the cold and warm species richness gradient analyses.

For depth, within the shallow species richness gradient, standardized effect size tended to be higher than null expectations (observed mean SES = 0.73,  $p < .001$ ) and more variable than null expectations (observed SES variance = 3.96,  $p < .001$ ). A total of 100 species (from 275) showed significant SES values, 72 positive and 28



**FIGURE 2** Linear, quadratic and cubic regressions of environmental predictors of fish species richness within the wider Caribbean region. Solid versus dashed lines indicates whether quadratic and cubic regression represents improvements over a simpler alternative (based on AICc comparisons) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]





**FIGURE 3** Results of linear model based spatial cross-validation tests of regression models produced for specific environmental fish species richness predictors within the wider Caribbean region: sea surface temperature (Temp), salinity (Sal), nitrate (N), distance to seagrass beds (SG\_dist) and median dive depth (depth). Robust models should return high (a)  $R^2$  values, (b) slopes that are close to a value of one and significantly different to zero, (c) intercepts that are not significantly different to zero. Statistical significance indicated by asterisks (\* =  $<.05$ , \*\* =  $<.01$  and \*\*\* =  $<.001$ ). Plots summarize the results of 1,000 iterations of spatial cross-validation tests, each based on geographically separating survey sites into two equal groups and attempting to predict the species richness of groups of sites using models calibrated with data from the other group. Bar heights and points reflect mean values across all iterations and error bars represent 95% confidence intervals. N.B. The “distance to seagrass beds” predictor performed so poorly regarding its slope and intercept values that it could not be plotting with the other results (mean values =  $-24.5$  and  $3279.1$  respectively)

## 4 | DISCUSSION

Temperature is the dominant factor associated with fish species richness within our analyses. Species richness is positively associated with sea surface temperature at temperatures below  $27.4^{\circ}\text{C}$ , and negatively associated with temperatures above this level. There was significant variation in species-specific thermal preferences along this temperature/species richness gradient, with many species significantly associated with optimal temperatures but fewer significantly associated with colder temperatures and particularly few associated with the warmest temperatures. Salinity, nitrate, depth and “distance to seagrass beds” were also significant predictors of fish species richness, however, only depth showed a robust performance to spatial cross-validation, suggesting that the results for the other predictors may not have general relevance.

The key differences between our results and the results of previous studies of marine species richness across the Caribbean region are that we have identified temperature to be a major factor associated with fish species richness (not previously reported within the region) and, unlike Sandin et al. (2008), we did not detect any species richness/area relationship. Inter-study differences in geographical resolution will certainly have contributed to these differences. It is, thus, possible that up-scaling the REEF data to broader, island-scale, units would produce results that are more similar to those of Sandin et al. (2008). Our results strongly suggest that local species richness does vary considerably across the region, even within islands. High diversity sites are clustered in the Dutch Antilles and the Florida Keys, but with fairly high levels of local variation. Low diversity sites are located in Bermuda, the Gulf of Mexico, Northern Florida and the Great Guana Cay (an islet in the Bahamas). These specific results show consistency with those of Sandin et al. (2008), where appropriate comparisons exist: Curacao (in the Dutch Antilles) is one of the more diverse islands, considering its size, and Bermuda is the least diverse of the islands in their study system. Miloslavich et al. (2010) did not record relatively high numbers of fish species in

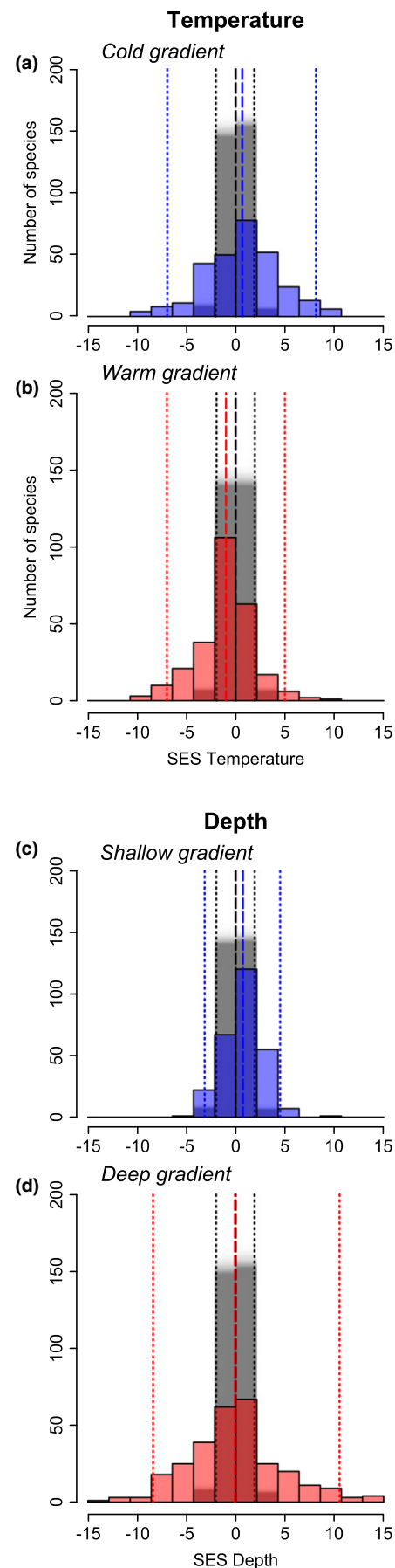
negative (Figure 4c). Within the deep species richness gradient, mean standardized effect size was not significantly different to null expectations (observed mean SES =  $-0.081$ ,  $p = .086$ ) but standardized effect sizes were more variable than null expectations (observed SES variance =  $22.72$ ,  $p < .001$ ). A total of 168 species (from 295) showed significant SES values, 74 positive and 94 negative (Figure 4d). Fourteen species were significantly associated with optimal depth in both the shallow and deep species richness gradient analyses.

**FIGURE 4** Species-specific standardized effect size (SES) analytical results for fish species environmental associations along temperature and depth species richness gradients, within the wider Caribbean region. Both of these environmental variables show a hump-shaped relationship with species richness therefore the temperature analysis was split: for temperature into (a) a gradient of increasing species richness from the minimum temperature to the optimum temperature and (b) a gradient of decreasing species richness from the optimum temperature to the maximum temperature; for depth into (c) a gradient of increasing species richness from the minimum depth to the optimum depth and (d) a gradient of decreasing species richness from the optimum depth to the maximum depth. Coloured semi-transparent bars give frequency of empirical SES values and grey semi-transparent bars give distribution of SES values produced by 1,000 null runs based on randomly selecting the observed number of sites of occurrence within the distribution of each species. See methods for further details [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

the Dutch Antilles but did, as in our study, demonstrate high levels of local variability in species totals within island systems.

Although temperature has previously been identified as a main factor associated with patterns of fish species richness in tropical marine regions at global spatial scales (Mellin et al., 2010; Parravicini et al., 2013), the shape of this relationship has not been demonstrated. Unimodal temperature/species richness relationships have been demonstrated in other marine systems (Adjou, Bendtsen, & Richardson, 2012; Irigoien, Huisman, & Harris, 2004) and have been linked with mechanisms associated with productivity (Rosenzweig, 1995). However, although temperature has been proposed as a proxy for energy input in tropical marine systems, the strength of any relationship between temperature and productivity remains to be established. Variation in species thermal tolerances also represents a potential explanation for the unimodal species richness temperature curve observed in our study and our species-specific environmental preference analysis suggests both high interspecific variation in thermal associations and a relatively high number of species associated with optimal temperatures. High water temperature (28.5–32°C) has been observed to influence the survival (Donelson, Munday, & McCormick, 2012), swimming abilities and metabolic performances (Johansen & Jones, 2011) of some coral reef fish as well as reduce growth of both juveniles and adults (Munday, Kingsford, O'Callaghan, & Donelson, 2008). Furthermore, marine fish distributions have been linked to their thermal tolerances (Sunday, Bates, & Dulvy, 2011) and certain reef fish species have been shown to be living at around their specific optimum temperatures (Rummer et al., 2014). Fish species richness could also be affected indirectly by temperature, via its influence on key habitat forming species (in particular corals), as habitat complexity has long been known to be associated with fish species richness in reef systems (Luckhurst & Luckhurst, 1978).

Above optimal temperatures, there are relatively few species that are associated with the warmest temperatures and the majority of species within communities at the warmest sites may represent a







nested subset of those at sites experiencing optimum temperatures. At the colder end of the temperature gradient (below the optimum temperature), species replacement appears to be more balanced (albeit still with the majority of species still associated with optimum temperatures), suggesting that there are more fish species adapted to the coldest part of the temperature gradient than to the warmest part. The more balanced nature of species temperature associations in this part of the species richness/temperature relationship suggests that interspecific variation in environmental tolerances is less likely to be influencing the observed species richness patterns in colder waters. As colder sites show lower levels of species richness, co-occurrence among the species associated with these temperatures is likely to be reduced at these sites, possibly due to reduced productivity or reduced habitat complexity. Alternative mechanisms that could result in such reduced co-occurrence are geographical isolation and ecological diversification.

Our study found four other significant environmental predictors of fish species richness: salinity, nitrate, depth and distance to key habitats, although all except for depth failed to accurately predict species richness patterns within our cross validation analysis. Unimodal relationships were again prevalent amongst these predictors, with potential mechanisms related to either productivity or physiological tolerances. The most robust of these variables, according to our spatial cross-validation test, was depth, which showed a unimodal relationship with species richness peaking around 12 m. Depth also showed significant species-specific responses along its gradient, in a manner fairly similar to temperature, with one part of the gradient (optimum depth to the deepest depth) a more balanced spread of species associations than while the other (the shallowest depth to the optimum depth), with relatively few species associated with the shallowest depths. The remaining significant environmental factors identified by our study appear to reflect only localized patterns, at best.

Of the factors shown to not be significant predictors of species richness in this study perhaps the most surprising might be habitat area (measured in this case as reef length), as this factor is a well-known predictor of species richness across a wide variety of ecological systems, including coral reef fish (Parravicini et al., 2013). This result may be a reflection of the fact that actual area sampled by divers is probably not closely related to overall reef area and will be roughly consistent between sites due to human limitations on dive times and swimming distances. Anthropogenic and natural disturbance can be expected to influence natural communities and have long been hypothesized to influence community species richness. Our results provide no support for these ideas but temporal studies may provide more relevant tests as they are not confounded by natural spatial patterns of species richness.

Caveats in terms of the interpretations and conclusions presented in this study include the fact that the availability of predictive environmental and biological data does not necessarily fully reflect all factors influencing species richness across our study system. Data for factors that are associated with species richness at very local

scales, such as habitat complexity, percentage coral cover, etc., are not currently available across the full geographical extent of this study. Broad-scale factors, such as meta-community dynamics, have the potential to influence species richness patterns (MacNeil et al., 2009) and, given the highly connected nature of marine populations within the Caribbean (Shulman & Bermingham, 1995), may represent a source of unexplained variation in this study. Furthermore, ecological surveys of such diverse communities are inevitably imprecise and our data standardization tests suggest that the level of error contained within site species richness estimates remains fairly high, in spite of our analytical optimization. In addition, neither evolutionary and historical factors (Keith, Baird, Hughes, Madin, & Connolly, 2013), nor biotic processes, e.g. co-existence or competition (Connolly & Moko, 2003; Cornell & Karlson, 2000), were considered within our study. Isolation over evolutionary time-scales has been suggested to be a critical factor shaping fish species richness patterns across the entire region of the Atlantic Ocean (Bender, Pie, Rezende, Mouillot, & Floeter, 2013; Floeter et al., 2008) but it is unclear whether such influences exist within our more limited study region. These potential sources of unexplained variation reduce expectations of the predictive power of the relationships established by the study.

This study demonstrates that temperature has a clear association with fish diversity and that present day temperature extremes may be sub-optimal for fish species richness. Without further evidence concerning the mechanisms underlying this hump-shaped temperature/species richness curve, predictions of the consequences of changing temperatures should be avoided. However, given the seriousness of predicted temperature increases, the identification of these mechanisms should be prioritized. Future work should seek to evaluate the link between temperature and ecosystem productivity in these systems, and seek to identify the geographical scale at which such productivity patterns typically sustain populations of fish and other marine species. The high levels of observed local variation in species richness estimates are suggestive of an influence of habitat-specific characteristics and obtaining relevant environmental data across a wide range of geographical scales represents another important research challenge to be addressed.

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## BIOSKETCH

All of the authors have present or past affiliations with the Center for Macroecology, Evolution and Climate, Copenhagen. The Center integrates terrestrial and marine research in a cross-disciplinary research program addressing fundamental questions on the origin, maintenance, conservation and future of life and biological diversity on Earth.

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