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Island biogeography of Caribbean coral reef fish

Stuart A. Sandin^{1*}, Mark J. A. Vermeij² and Allen H. Hurlbert^{3†}

¹Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, 9500 Gilman Drive, La Jolla, CA 92093-0202, USA, ²CARMABI Foundation, P.O. Box 2090, Piscaderabaai z/n, Willemstad, Curaçao, Netherlands Antilles, ³National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, 735 State St., Suite 300, Santa Barbara, CA 93101, USA

ABSTRACT

Aim The goal of our study was to test fundamental predictions of biogeographical theories in tropical reef fish assemblages, in particular relationships between fish species richness and island area, isolation and oceanographic variables (temperature and productivity) in the insular Caribbean. These analyses complement an analogous and more voluminous body of work from the tropical Indo-Pacific. The Caribbean is more limited in area with smaller inter-island distances than the Indo-Pacific, providing a unique context to consider fundamental processes likely to affect richness patterns of reef fish.

Location Caribbean Sea.

Methods We compiled a set of data describing reef-associated fish assemblages from 24 island nations across the Caribbean Sea, representing a wide range of isolation and varying in land area from 53 to 110,860 km². Regression-based analyses compared the univariate and combined effects of island-specific physical predictors on fish species richness.

Results We found that diversity of reef-associated fishes increases strongly with increasing island area and with decreasing isolation. Richness also increases with increasing nearshore productivity. Analyses of various subsets of the entire data set reveal the robustness of the richness data and biogeographical patterns.

Main conclusions Within the relatively small and densely packed Caribbean basin, fish species richness fits the classical species–area relationship. Richness also was related negatively to isolation, suggesting direct effects of dispersal limitation in community assembly. Because oceanic productivity was correlated with isolation, however, the related effects of system-wide productivity on richness cannot be disentangled. These results highlight fundamental mechanisms that underlie spatial patterns of biodiversity among Caribbean coral reefs, and which are probably also are functioning in the more widespread and heterogeneous reefs of the Indo-Pacific.

Keywords

Caribbean, coral reef, fish, island biogeography, isolation by distance, productivity, species–area relationship.

*Correspondence: Stuart A. Sandin, Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, 9500 Gilman Drive, La Jolla, CA 92093-0202, USA. E-mail: ssandin@ucsd.edu

†Present address: Department of Biology, University of North Carolina, Chapel Hill, NC 27599–3280, USA

INTRODUCTION

Understanding the biogeographical distribution of tropical reef species has long been a goal among marine ecologists. Proposed mechanisms that determine species distributions can be grouped broadly into two categories: (1) varying species diversity in response to varying environmental conditions, and (2) varying diversity due to varying patterns of dispersal among sites. The

first category is founded on principles of niche selection and suitability. Species-specific physiological limits can prevent the spread of individual populations to regions of extreme temperature (Burns, 1985; Floeter *et al.*, 2005; Mora & Robertson, 2005), turbidity (van Woesik & Done, 1997; Anthony & Connolly, 2004) and exposure to waves (Huston, 1985), among other environmental factors, thereby affecting membership in a local species assemblage. Species richness may also be determined by

the relative availability of critical habitat types (Fraser & Currie, 1996). For example, the diversity and abundance of coral reef species has been shown to increase with increased refuge availability (Caley & St. John, 1996; Gratwicke & Speight, 2005), proximity to nursery habitats (Nagelkerken *et al.*, 2001; Mumby *et al.*, 2004) or settlement habitat (Harrington *et al.*, 2004). Bellwood & Hughes (2001) demonstrated that much variation in biodiversity across Indo-Pacific coral reefs can be described simply by the amount of habitable area in the region (i.e. from island to archipelago scale).

Secondly, biogeographical distributions of species can be affected by patterns of dispersal across space. Paralleling the predictions of island biogeography theory (MacArthur & Wilson, 1967), Molles (1978) showed, on patch reef habitats, that fish richness declined with increasing distance from larger 'source' reefs and that fish richness increased with increasing patch reef area. At a much larger spatial scale, reef species richness has been shown to decrease with increasing distance from sources of historic biodiversity (Stehli & Wells, 1971; Mora *et al.*, 2003). Alternatively, geographical patterns of coral and fish richness can be described by models of random species range distributions within a geometrically constrained area, i.e. the mid-domain effect (MDE; Connolly *et al.*, 2003; Mora *et al.*, 2003; Bellwood *et al.*, 2005). However, successful colonization of distant islands has been linked to the length of species pelagic larval duration (PLD), with distant islands in the Indo-Pacific containing fish species with disproportionately long PLDs (Lester & Ruttenberg, 2005). Clearly, both dispersal dynamics and habitat availability directly affect the number of species found at any particular site.

To date, the majority of studies of reef species distributions have been conducted across biogeographical provinces, and principally across Indo-Pacific sites. A recent study by Floeter *et al.* (2008), however, highlights the varied biogeographical and evolutionary patterns typical of Atlantic reef fishes. Within the greater Atlantic region, the Caribbean Sea is home to a relatively diverse reef fish fauna that is compositionally distinct from neighbouring regions (Floeter *et al.*, 2008). However, the insular Caribbean appears to be well mixed on evolutionary time-scales, as evidenced by the low levels of genetic structure within multiple fish species (Shulman & Bermingham, 1995) and the relative paucity of range-restricted species within the basin (Robins, 1991). As such, the insular Caribbean offers a unique context for examining biogeographical patterns without the concerns of range limitations and geological history that underlie dominant models from the Indo-Pacific, e.g. length of PLD, the MDE or distance from sources of historic biodiversity. Instead, the factors determining the richness of a Caribbean island are more likely to be simple mechanisms, paralleling the founding predictions of island biogeography theory (MacArthur & Wilson, 1967). In particular, we may expect smaller islands to have relatively fewer species due to lower colonization rates and/or higher extinction rates compared with larger islands (Molles, 1978; Lawlor, 1986). Additionally, island isolation is expected to reduce equilibrium values of local richness by decreasing immigration rates (MacArthur & Wilson, 1967) and increasing extinction rates (Brown & Kodric-Brown, 1977). Here we investigate the effects

of habitat availability and degree of isolation in determining the richness of reef fish across islands in the Caribbean. We also assess the importance of two key environmental variables, temperature and productivity, which have been shown to explain a large fraction of the variance in both marine (e.g. Macpherson, 2002; Bellwood *et al.*, 2005) and terrestrial (e.g. Allen *et al.*, 2002; Hawkins *et al.*, 2003; Whittaker *et al.*, 2007) richness gradients.

METHODS

Macroecological patterns

We compiled data on species richness of the coral reef-associated fish assemblages from Caribbean island nations (Fig. 1). Data were compiled from the online resource FishBase (<http://www.fishbase.org/>, accessed April 2008; Froese & Pauly, 2008). We limited our data search to an exhaustive extraction from this resource alone, thereby minimizing the effects of variation in sampling protocols and data standards. The dominant sources in FishBase for the insular Caribbean include general field guides (e.g. Smith, 1997), region-specific checklists (e.g. Böhlke & Chaplin, 1993; Claro & Parenti, 2001) and taxon-specific surveys (e.g. Compagno, 1984; Whitehead, 1985), thereby providing collated species lists from efforts largely conducted from 1980 to the present.

Both the land area and the estimated area of reef habitat were compiled for each island nation from ReefBase (<http://www.reefbase.org/>, Oliver *et al.*, 2005). Island isolation was estimated using multiple metrics. The minimum distance of each island nation from the nearest large land mass (i.e. island > 5000 km² or mainland) was estimated using map measurements. Only four Caribbean islands exceed the threshold size of 5000 km²: Cuba, Hispaniola, Jamaica and Puerto Rico. Note that this definition is specific to islands, not the total land area of island nations, exceeding a particular threshold size, though the results are comparable using either definition. The distance of each island nation from the nearest large reef mass (i.e. island nation with reef area > 1000 km² or mainland, represented by the same islands above plus the reefs of Turks and Caicos and the Bahamas) was estimated similarly using map measurements. Three additional distance metrics were compiled, including the distances of each island nation from the nearest island (of similar or larger size), nearest island group and nearest mainland (collected from the United Nations Environment Programme (UNEP) Island Directory; <http://islands.unep.ch/isldir.htm>). All geographical data are presented in Table S1 in the Supporting Information.

For each island nation we quantified two oceanographic descriptors, mean annual sea surface temperature (SST) and ocean productivity. The SST data were collected at 4-km resolution as part of the AVHRR Pathfinder Version 5.0 SST Project, and represent mean annual values averaged over 1985–2001 (<http://www.nodc.noaa.gov/SatelliteData/pathfinder4km/userguide.html>). We used remotely sensed estimates of chlorophyll-*a* as a surrogate for oceanic productivity. Data were collected by the SeaWiFS sensor at a resolution of approximately 9 km and

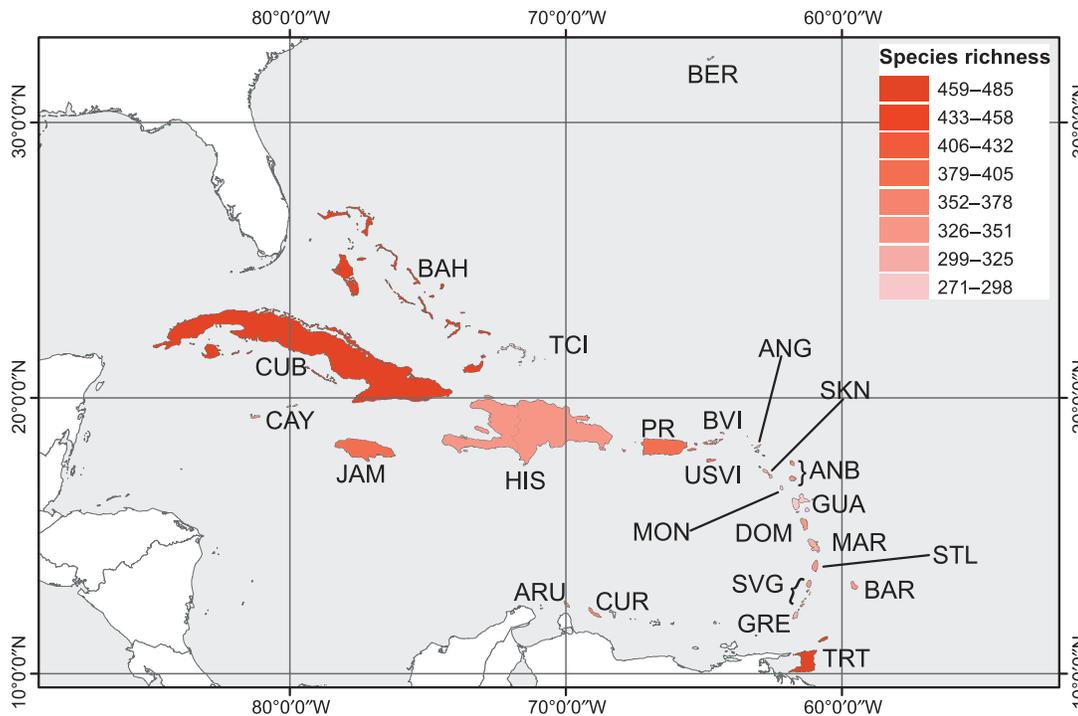


Figure 1 Patterns of species richness for Caribbean reef-associated fishes. Data are presented by the political unit of island nation, representing either single islands or collections of adjacent islands. Note the exception of Hispaniola which includes combined data from two nations sharing the same geographical island. Island abbreviations are as follows: ANB, Antigua and Barbuda; ANG, Anguilla; ARU, Aruba; BAH, Bahamas; BAR, Barbados; BER, Bermuda; BVI, British Virgin Islands; CAY, Cayman Islands; CUB, Cuba; CUR, Curaçao; DOM, Dominica; GRE, Grenada; GUA, Guadeloupe; HIS, Hispaniola; JAM, Jamaica; MAR, Martinique; MON, Montserrat; PR, Puerto Rico; SKN, St Kitts and Nevis; STL, St Lucia; SVG, St Vincent and the Grenadines; TRT, Trinidad and Tobago; TCI, Turks and Caicos Islands; USVI, US Virgin Islands.

reflect mean annual values in $\mu\text{g l}^{-1}$ averaged over 1998–2003 (<ftp://data.nodc.noaa.gov/pub/data.nodc/pathfinder/CoralAtlas/>). Temperature and chlorophyll data were averaged for each island over all data pixels whose centres fall within a 20-km buffer of land boundaries. While the two data sets differ in the length of time series, the use of temporal averaging allows us to characterize the mean oceanographic conditions experienced by island faunas independent of seasonal variation or temporal trends. It is this information on long-term averages that we expected to be most directly related to the faunal list-based richness data from FishBase.

Due to the limits of data availability we used political geographical units and not islands *per se*, and some island nations span multiple islands or fractions of islands. For the few examples of nations spanning multiple islands, the islands are adjacent and form a relatively contiguous reef area (e.g. Bahamas bank), thus the degrees of isolation are approximately equal across the archipelago. We excluded the one clear exception, the Netherlands Antilles, a nation comprising both Windward and Leeward islands that are more than 1000 km apart and for which island-by-island data were not available, with the exception of Curaçao. For the one case of nations sharing one island (i.e. Dominican Republic and Haiti), we lumped data to consider the geographical unit of Hispaniola. We ignored potential impacts of variable geological history across islands both within and

between island nations in order to maximize available data. As such, we assumed that the broad effects of habitat area and isolation would be stronger than potential variation caused by geological features in the region.

Data analyses

Prior to examining models of species richness, we examined the correlational structure present among our predictor variables using Pearson correlation coefficients. Next, we assessed the importance of island area, island isolation and oceanographic parameters on the species richness of fish faunas through regression-based approaches. For comparison of richness with island (and reef) area we \log_{10} transformed both richness and area data, thus testing for significant power-law relationships (Arrhenius, 1921). For the remaining correlation and regression analyses, all data were \log_{10} transformed prior to analyses to achieve statistical normality. Because we lacked clear a priori expectations of the best metric of island isolation, we used these analyses for exploratory model fitting rather than formal hypothesis testing.

To test the robustness of observed biogeographical patterns in the fish data, we repeated analyses on five subsets of data with putatively improved degrees of accuracy and lower potential bias than the entire data set. (1) *Island subset*: among Caribbean island nations, a subset have been host to disproportionately

Table 1 Pearson correlation coefficients among physical parameters from each island nation. All predictors were \log_{10} transformed.

	Land area (km ²)	Reef area (km ²)	Nearest large land (km)	Nearest large reef (km)	Ocean productivity ($\mu\text{g l}^{-1}$ chl- <i>a</i>)	Sea surface temperature (°C)
Land area	1					
Reef area	0.698*	1				
Nearest large land	-0.400	-0.112	1			
Nearest large reef	-0.441*	-0.206	0.971*	1		
Ocean productivity	0.374	0.088	-0.597*	-0.659*	1	
Sea surface temperature	0.367	0.037	-0.244	0.234	-0.090	1

*Statistically significant correlations ($r_{\text{crit}}(0.05, \text{d.f.} = 22) \geq |0.406|$).

extensive biogeographical sampling due to the presence of active field stations or intensive research effort. The subset of nine such sites is identified in Table S2. (2) *'Consensus' reef fish families*: in a comparison of Eocene and modern reef fish faunas, Bellwood (1996) identified 10 consensus families common to palaeontologically recent reef fish communities. Limitation of data sets to include only species from these families minimizes the potential error of including species that are habitat generalists and not obligate reef associates (e.g. serranids, lutjanids). (3) *Apparent reef fish*: 10 reef-associated fish families were identified based on their relative detectibility (e.g. large body size, diurnal habits, relative commonness), namely Acanthuridae, Balistidae, Chaetodontidae, Haemulidae, Labridae, Lutjanidae, Pomacentridae, Pomacentridae, Scaridae and Serranidae. Species from these families are unlikely to be undersampled due to cryptic behaviour (e.g. blennids, gobiids) or nocturnal habits (e.g. apogonids, holocentrids). The two remaining subsets are combinations of (1) with (2) and (3), as follows. (4) *Island/consensus subset*: species of consensus families from sites of high sampling effort [(1) \cap (2)]. (5) *Island/apparent subset*: species of apparent families from sites of high sampling effort [(1) \cap (3)].

The presence of strong positive spatial autocorrelation in both dependent and predictor variables can lead to spurious correlations and an overestimate of the degrees of freedom in regression analyses (Lennon, 2000). For all variables and for the residuals of regression models, we examined spatial correlograms by plotting Moran's *I* as a function of the distance between observations (Legendre & Legendre, 1998). Spatial autocorrelation in species richness over distances of several hundred kilometres was negligible, especially when examining the residuals of species richness after island area, isolation and environmental variables were taken into account (Figure S1). As such, we used traditional linear regression for all analyses.

RESULTS

Correlation analysis

Most predictor variables were strongly correlated with at least one other variable (Table 1). Land area and reef area were correlated across island nations, suggesting an approximate proportionality between emergent land and shallow, nearshore habitat used by

Table 2 Results of regression analyses for univariate models describing the number of fish species across island nations. All data (both response and predictors) were \log_{10} transformed for analyses and include 24 island nations.

Predictors	Model	Model	R^2	<i>F</i> -statistic	<i>P</i> -value
	intercept	slope			
IA	2.38	0.05	0.50	21.8	< 0.001
RA	2.44	0.04	0.15	4.0	0.059
NLL	2.77	-0.10	0.51	23.1	< 0.001
NLR	2.75	-0.10	0.48	20.0	< 0.001
OP	2.60	0.11	0.35	11.8	0.002
SST	0.43	1.47	0.07	1.7	0.206

IA, island area (km²); RA, reef area (km²); NLL, nearest large land (km); NLR, nearest large reef (km); OP, ocean productivity ($\mu\text{g l}^{-1}$ chlorophyll-*a*); SST, sea surface temperature (°C)

reef-building organisms. Additionally, pairwise comparisons of the five metrics of isolation revealed a high degree of correlation. Because of this high similarity across metrics, we limit reference here to only two: distance to nearest large (> 5000 km²) land mass and distance to nearest large (> 1000 km²) reef mass.

Both isolation metrics correlated negatively with land area and, more weakly, with reef area (Table 1). Additionally, both isolation metrics correlated negatively with ocean productivity, suggesting that more isolated islands receive fewer nutrient subsidies and support less phytoplanktonic productivity. Mean SST varied little across the island nations and was not strongly correlated with any of the other predictors (Table 1).

Macroecological patterns

The richness of reef-associated fish species ranged from 271 to 485 ($n = 24$; Table S2, Fig. 1). Fish species richness correlated strongly with island area (Table 2, Fig. 2a). Fish species richness correlated only marginally with reef area (Table 2). The discrepancy between results based on land area versus reef area was driven largely by data from Trinidad and Tobago, which has a disproportionately small reef area for total land area of the island nation (40 km² reef area, 5128 km² land area; Table S1).

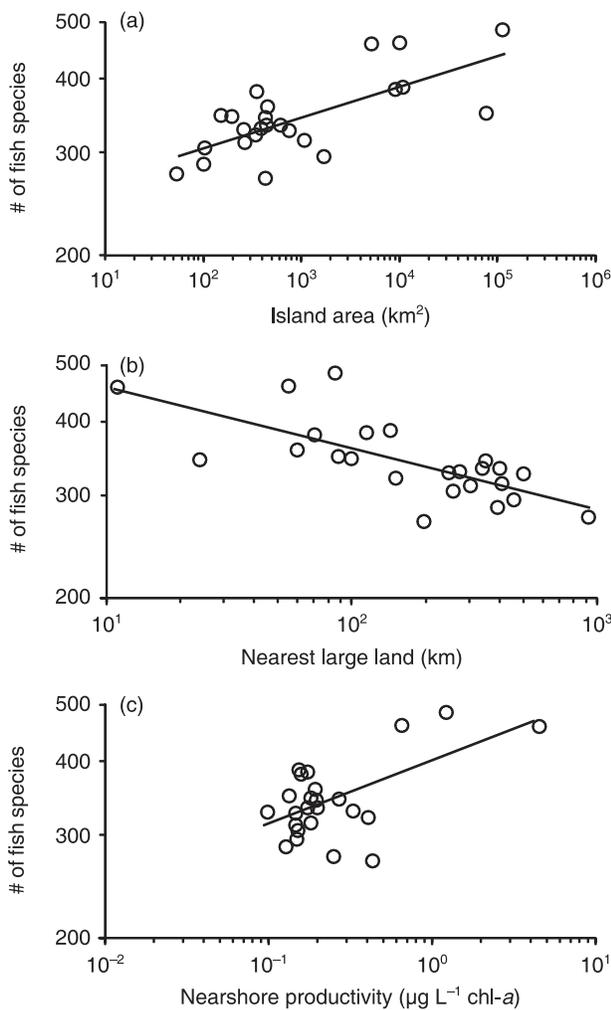


Figure 2 Biogeographical patterns of Caribbean coral reef fish richness. (a) Species–area relationship, relating richness to island area. (b) Species–isolation relationship, relating richness with distance to the nearest large land (i.e. island > 5000 km² or mainland). (c) Species–productivity relationship, relating richness to nearshore productivity (i.e. chlorophyll-*a* concentration within 20 km buffer). The lines describe the significant power-law relationships (note logarithmic transformation on both axes).

Eliminating this data point more than doubles the amount of variation explained by reef area.

Fish species richness was strongly, negatively related to the distance to nearest large island (Fig. 2b). The relationship with distance to nearest large reef was similarly strong (Table 2). Removal of the most isolated island nation in these data, Bermuda, did not affect these results appreciably, with regression *P*-values remaining < 0.001 for both metrics of isolation. Fish richness was positively related to ocean productivity as estimated by the nearshore concentration of chlorophyll-*a* (Fig. 2 c), but showed no relationship with mean annual SST (Table 2).

To evaluate models invoking the effects of multiple predictors on fish species richness, we conducted multiple regression analyses in an information theoretic-based model selection framework (Burnham & Anderson, 2002). We examined models that

Table 3 Multi-predictor model selection results. Models are ranked by a small sample correction to Akaike’s information criterion (AIC_c). Models with ΔAIC_c < 2 have substantial support (Burnham & Anderson, 2002).

Model	Adjusted <i>R</i> ²	AIC _c	ΔAIC _c
IA + NLL	0.69	-85.27	0.00
IA + NLL + OP	0.70	-83.97	1.30
IA + NLL + SST	0.68	-82.75	2.52
IA + NLR	0.64	-81.64	3.63
IA + NLL + OP + SST	0.68	-81.08	4.19
IA + NLR + OP	0.65	-80.25	5.02
IA + NLR + SST	0.63	-79.03	6.24
IA + NLR + OP + SST	0.63	-77.45	7.82
RA + NLL	0.57	-77.22	8.05
RA + NLL + OP	0.60	-77.08	8.19
RA + NLL + OP + SST	0.61	-76.26	9.01
RA + NLL + SST	0.56	-75.23	10.04
RA + NLR	0.50	-73.28	11.99
RA + NLR + OP	0.52	-72.81	12.46
RA + NLR + OP + SST	0.54	-72.37	12.90
RA + NLR + SST	0.49	-71.45	13.82

IA, island area (km²); RA, reef area (km²); NLL, nearest large land (km); NLR, nearest large reef (km); OP, ocean productivity (µg l⁻¹ chlorophyll-*a*); SST, sea surface temperature (°C)

included predictors for area, isolation and both, one or none of the oceanographic variables. As was evident from the univariate analyses, island area was superior to reef area and distance to nearest large land was a better measure of isolation than distance to nearest large reef (Table 3). The model with the greatest support based on the small sample-adjusted Akaike information criterion (AIC_c) was one invoking only these two island biogeographical variables [$\log_{10}(\text{spp}) = 2.59 + 0.04 \log_{10}(\text{area}) - 0.08 \log_{10}(\text{isol.})$, $F_{2,21} = 27.1$, $P < 0.001$, $R^2 = 0.69$]. However, a similar model that additionally included nearshore productivity also received a high level of support (ΔAIC_c = 1.30, Table 3). The strong negative correlation between productivity and isolation makes it difficult to disentangle their separate effects on richness. Both models explained more than two-thirds of the variation in fish species richness across island nations.

Repeating analyses on subsets of the total data set provided no evidence of systematic bias in the fish richness data. We conducted model competitions for five subsets of data controlling for possible biases in effort across island nations, reef specificity of species, species detectability and combinations thereof. Fish species richness consistently correlated positively with island area and ocean productivity, and negatively with isolation within each of these data subsets. Again, models invoking island area, distance to nearest large landmass and productivity tended to have the greatest support (Table S3).

DISCUSSION

Although much study of biogeographical distributions has been completed using data from Indo-Pacific coral reefs, comparatively

few studies have considered the distribution of reef-associated fishes across the Caribbean Sea. In this study we tested the importance of basic measures of habitat availability (estimated as reef or land area) and island remoteness in describing species richness across Caribbean island nations. Island biogeography theory predicts that species richness will increase with increasing habitat area and with decreasing distance from source communities (*sensu* MacArthur & Wilson, 1967). We found that these predictions were supported by data from insular Caribbean fish assemblages.

Clear relationships existed between fish richness and island area (positive) and degree of island isolation (negative). The effect of reef area on fish richness was also positive, but much weaker than the effect of island area. The major outlying datum was the disproportionately high fish species richness relative to reef area from Trinidad and Tobago (Tables S1 & S2). This island pair has little reef development relative to island size due to the large freshwater inputs from the nearby Orinoco River outflow (Spalding *et al.*, 2001; Rocha, 2003). Perhaps because of the paucity of reef development in the region, principally reef-associated species exploit less-preferred habitats (e.g. rocky reefs, seagrass beds) around the islands (Heck, 1979). If such facultative shifts of habitat are common, we may expect that island area (which correlates loosely with coastline and shallow shelf area) would better describe habitat availability, and thus species richness, than reef area. While reef area provides a reasonable measurement of habitat availability in most cases, island area potentially reflects both habitat availability and habitat diversity. That is, a larger island is more likely to contain mangroves, estuaries, seagrass beds and other habitats suitable for some reef-associated fishes compared with a smaller island with the same total reef area.

Regardless of the measure of habitat used, the functional relationship between log-transformed habitat area and fish richness is a power between 0.04 and 0.05 (Table 2). It is interesting to note that this power is appreciably smaller than the scaling exponents found across most other systems (*c.* 0.15–0.40, Drakare *et al.*, 2006). Low species–area exponents are expected when average range sizes are large with respect to the extent of analysis (Rosenzweig, 1995; Allen & White, 2003) as is the case in this system (Robins, 1991). Relative to the large number of terrestrial examples, there are few studies reporting species–area relationships in marine environments (Neigel, 2003), thus limiting meaningful comparison of these Caribbean data with those from other regions.

A recent study of global terrestrial island faunas found strong support for a model combining island biogeography theory with environmental variables (Kalmar & Currie, 2006). While we found clear evidence for the importance of area and isolation on the richness of insular Caribbean fish faunas, the support for an effect of nearshore productivity was more difficult to ascertain. This is due primarily to the fact that productivity and both measures of isolation were strongly correlated. Islands near larger land masses tended to have higher values of nearshore productivity, presumably due to some combination of increased allochthonous inputs from freshwater runoff and increased proximity to upwelling zones. Although productivity is a significant univariate predictor of species richness, variance partitioning

suggests that most of the variance it can explain in species richness can also be attributed to isolation (unique and shared variance components when island area is in the model: ocean productivity, $r_{OP}^2 = 0.015$; nearest large land, $r_{NLL}^2 = 0.114$; $r_{shared}^2 = 0.110$). Nevertheless, the model including productivity had a ΔAIC_c of only 1.3, suggesting that it shared substantial support alongside the pure island biogeographical model (Burnham & Anderson, 2002). Productivity could enhance species richness by increasing mean population sizes and thereby decreasing extinction rates (Wright, 1983; Srivastava & Lawton, 1998), by increasing the diversity of resource types and/or allowing a reduction in the mean niche breadth (Evans *et al.*, 2005), by allowing populations to recover more rapidly from disturbance (Huston, 1994) or by supporting an additional trophic level and thereby reducing the chance of competitive exclusion (Abrams, 1995). Much more work is needed to disentangle any of these potential effects of productivity from isolation in this system.

Temperature, while identified as an important predictor of species richness in a number of other broad-scale marine studies (e.g. Roy *et al.*, 1998; Macpherson, 2002; Bellwood *et al.*, 2005), explained very little variation in fish richness across the Caribbean basin. In large part this is due to the narrow range of temperatures found there relative to the two to three orders of magnitude variation in the other key predictors. Thus, while temperature may be an important variable at global scales, it is of little use here.

We have shown here that the species richness of reef-associated fish across the Caribbean demonstrates clear predictability and macroecological patterning. Islands that are larger, less isolated and with more productive waters support more diverse assemblages, suggesting the influence of both local and regional processes. These results also reinforce the notion that if marine protected areas are to preserve diversity, they must ensure both sufficient area and sufficient connectivity with potential source populations (Roberts, 1997; Carr, 2000). Through systematic compilation of more detailed taxonomic and habitat data within the Caribbean, there are opportunities to understand much more about how reef communities are structured. Especially critical toward our growing understanding is the compilation of parallel data sets for other reef taxa, for example including corals, algae, molluscs and others. These data remain challenging to compile due to the high amounts of regional morphological variability within species (especially in corals) and the lack of consistent taxonomic recording of these groups. However, this study reveals the importance of smaller tropical ocean basins (i.e. the Caribbean and Red Seas relative to the Indo-Pacific) as settings for illuminating patterns and processes structuring marine communities.

ACKNOWLEDGEMENTS

Special thanks are offered to Scott 'Dwerg' Hamilton, Walter Jetz and Jana McPherson for their insights, and to Julian Olden and two anonymous referees for improving this manuscript. This is DPS contribution no. 4.

REFERENCES

- Abrams, P.A. (1995) Monotonic or unimodal diversity–productivity gradients: what does competition theory predict? *Ecology*, **76**, 2019–2027.
- Allen, A.P. & White, E.P. (2003) Effects of range size on species–area relationships. *Evolutionary Ecology Research*, **5**, 493–499.
- Allen, A.P., Brown, J.H. & Gillooly, J.F. (2002) Global biodiversity, biochemical kinetics, and the energetic–equivalence rule. *Science*, **297**, 1545–1548.
- Anthony, K.R.N. & Connolly, S.R. (2004) Environmental limits to growth: physiological niche boundaries of corals along turbidity–light gradients. *Oecologia*, **141**, 373–384.
- Arrhenius, O. (1921) Species and area. *Journal of Ecology*, **9**, 95–99.
- Bellwood, D.R. (1996) The Eocene fishes of Monte Bolca: the earliest coral reef fish assemblage. *Coral Reefs*, **15**, 11–19.
- Bellwood, D.R. & Hughes, T.P. (2001) Regional-scale assembly rules and biodiversity of coral reefs. *Science*, **292**, 1532–1534.
- Bellwood, D.R., Hughes, T.P., Connolly, S.R. & Tanner, J. (2005) Environmental and geometric constraints on Indo-Pacific coral reef biodiversity. *Ecology Letters*, **8**, 643–651.
- Böhlke, J.E. & Chaplin, C.C.G. (1993) *Fishes of the Bahamas and adjacent tropical waters*, 2nd edn. University of Texas Press, Austin, TX.
- Brown, J.H. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, **58**, 445–449.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multi-model inference: a practical information-theoretic approach*. Springer, New York.
- Burns, T.P. (1985) Hard-coral distribution and cold-water disturbances in South Florida: variation with depth and location. *Coral Reefs*, **4**, 117–124.
- Caley, M.J. & St John, J. (1996) Refuge availability structures assemblages of tropical reef fishes. *Journal of Animal Ecology*, **65**, 414–428.
- Carr, M.H. (2000) Marine protected areas: challenges and opportunities for understanding and conserving coastal marine ecosystems. *Environmental Conservation*, **27**, 106–109.
- Claro, R. & Parenti, L.R. (2001) The marine ichthyofauna of Cuba. *Ecology of the marine fishes of Cuba* (ed. by R. Claro, K.C. Lindeman and L.R. Parenti), pp. 21–57. Smithsonian Institution Press, Washington, D.C.
- Compagno, L.J.V. (1984) FAO species catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2 – Carcharhiniformes. *FAO Fisheries Synopsis*, **125**, 251–655.
- Connolly, S.R., Bellwood, D.R. & Hughes, T.P. (2003) Indo-Pacific biodiversity of coral reefs: deviations from a mid-domain model. *Ecology*, **84**, 2178–2190.
- Drakare, S., Lennon, J.J. & Hillebrand, H. (2006) The imprint of the geographical, evolutionary and ecological context on species–area relationships. *Ecology Letters*, **9**, 215–227.
- Evans, K.L., Warren, P.H. & Gaston, K.J. (2005) Species–energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews*, **80**, 1–25.
- Floeter, S.R., Behrens, M.D., Ferreira, C.E.L., Paddock, M.J. & Horn, M.H. (2005) Geographical gradients of marine herbivorous fishes: patterns and processes. *Marine Biology*, **147**, 1435–1447.
- Floeter, S.R., Rocha, L.A., Robertson, D.R., Joyeux, J.C., Smith-Vaniz, W.F., Edwards, A.J., Barreiros, J.P., Ferreira, C.E.L., Gasparini, J.L., Brito, A., Falcón, J.M., Bowen, B.W. & Bernardi, G. (2008) Atlantic reef fish biogeography and evolution. *Journal of Biogeography*, **35**, 22–47.
- Fraser, R.H. & Currie, D.J. (1996) The species richness–energy hypothesis in a system where historical factors are thought to prevail: coral reefs. *The American Naturalist*, **148**, 138–159.
- Froese, R. & Pauly, D. (eds) (2008) *FishBase*, version 04/2008. Available at: <http://www.fishbase.org/>
- Gratwicke, B. & Speight, M.R. (2005) Effects of habitat complexity on Caribbean marine fish assemblages. *Marine Ecology Progress Series*, **292**, 301–310.
- Harrington, L.M., Fabricius, K., De'ath, G. & Negri, A. (2004) Recognition and selection of settlement substrata determine post-settlement survival in corals. *Ecology*, **85**, 3428–3437.
- Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.
- Heck, K.L., Jr (1979) Some determinants of the composition and abundance of motile macroinvertebrate species in tropical and temperate turtlegrass (*Thalassia testudinum*) meadows. *Journal of Biogeography*, **6**, 183–200.
- Huston, M.A. (1985) Patterns of species diversity on coral reefs. *Annual Review of Ecology and Systematics*, **16**, 149–177.
- Huston, M.A. (1994) *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, Cambridge.
- Kalmar, A. & Currie, D.J. (2006) A global model of island biogeography. *Global Ecology and Biogeography*, **15**, 72–81.
- Lawlor, T.E. (1986) Comparative biogeography of mammals on islands. *Biological Journal of the Linnean Society*, **28**, 99–125.
- Legendre, P. & Legendre, L. (1998) *Numerical ecology*, 2nd English edn. Elsevier Science, Amsterdam.
- Lennon, J.J. (2000) Red-shifts and red herrings in geographical ecology. *Ecography*, **23**, 101–113.
- Lester, S.E. & Ruttenberg, B.I. (2005) The relationship between pelagic larval duration and range size in tropical reef fishes: a synthetic analysis. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 585–591.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- Macpherson, E. (2002) Large-scale species–richness gradients in the Atlantic Ocean. *Proceedings of the Royal Society B: Biological Sciences*, **269**, 1715–1720.
- Molles, M.C., Jr (1978) Fish species diversity on model and natural reef patches: experimental insular biogeography. *Ecological Monographs*, **48**, 289–305.
- Mora, C. & Robertson, D.R. (2005) Factors shaping the range–size frequency distribution of the endemic fish fauna of the

- Tropical Eastern Pacific. *Journal of Biogeography*, **32**, 277–286.
- Mora, C., Chittaro, P.M., Sale, P.F., Kritzer, J.P. & Ludsin, S.A. (2003) Patterns and processes in reef fish diversity. *Nature*, **421**, 933–936.
- Mumby, P.J., Edwards, A.J., Arias-González, J.E., Lindeman, K.C., Blackwell, P.G., Gall, A., Gorczyńska, M.I., Harborne, A.R., Pescod, C.L., Renken, H., Wabnitz, C.C.C. & Llewellyn, G. (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature*, **427**, 533–536.
- Nagelkerken, I., Kleijnen, S., Klop, T., van den Brand, R.A.C.J., Cocheret de la Morinière, E. & van der Velde, G. (2001) Dependence of Caribbean reef fishes on mangroves and sea-grass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. *Marine Ecology Progress Series*, **214**, 225–235.
- Neigel, J.E. (2003) Species–area relationships and marine conservation. *Ecological Applications*, **13**, S138–S145.
- Oliver, J., Noordeloos, M., Yusuf, Y., Tan, M., Nayan, N., Foo, C. & Shahriyah, F. (2005) *ReefBase: a global information system on coral reefs*, version 10/2005. Available at: <http://www.reefbase.org/>
- Roberts, C.M. (1997) Connectivity and management of Caribbean coral reefs. *Science*, **278**, 1454–1457.
- Robins, C.R. (1991) Regional diversity among Caribbean fish species. *BioScience*, **41**, 458–459.
- Rocha, L.A. (2003) Patterns of distribution and processes of speciation in Brazilian reef fishes. *Journal of Biogeography*, **30**, 1161–1171.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Roy, K., Jablonski, D., Valentine, J.W. & Rosenberg, G. (1998) Marine latitudinal diversity gradients: tests of causal hypotheses. *Proceedings of the National Academy of Sciences USA*, **95**, 3699–3702.
- Shulman, M.J. & Bermingham, E. (1995) Early life histories, ocean currents, and the population genetics of Caribbean reef fishes. *Evolution*, **49**, 897–910.
- Smith, C.L. (1997) *National Audubon Society field guide to tropical marine fishes of the Caribbean, the Gulf of Mexico, Florida, the Bahamas, and Bermuda*. Alfred A. Knopf, New York, NY.
- Spalding, M.D., Ravilious, C., Green, E.P. (2001) *World atlas of coral reefs*. UNEP World Conservation Monitoring Centre, University of California, Berkeley.
- Srivastava, D.S. & Lawton, J.H. (1998) Why more productive sites have more species: an experimental test of theory using tree-hole communities. *The American Naturalist*, **152**, 510–529.
- Stehli, F.G., Wells, J.W. (1971) Diversity and age patterns in hermatypic corals. *Systematic Zoology*, **20**, 115–126.
- Whitehead, P.J.P. (1985) FAO species catalogue. Vol. 7. Clupeoid fishes of the world (suborder Clupeoidei). An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings. Part 1 – Chirocentridae, Clupeidae and Pristigasteridae. *FAO Fisheries Synopsis*, **125**, 1–303.
- Whittaker, R.J., Nogués-Bravo, D. & Araújo, M.B. (2007) Geographical gradients of species richness: a test of the water-energy conjecture of Hawkins *et al.* (2003) using European data for five taxa. *Global Ecology and Biogeography*, **16**, 76–89.
- van Woerik, R., Done, T.J. (1997) Coral communities and reef growth in the southern Great Barrier Reef. *Coral Reefs*, **16**, 103–115.
- Wright, D.H. (1983) Species–energy theory: an extension of species–area theory. *Oikos*, **41**, 496–506.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Maps and spatial correlograms for species richness and residuals.

Table S1 Geographical data for Caribbean island nations.

Table S2 Diversity of reef-associated fishes for Caribbean island nations.

Table S3 Model comparisons based on a small sample correction of the Akaike information criterion (AIC_c) for five different subsets of the data.

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BIOSKETCHES

Stuart Sandin is a marine ecologist with the Center for Marine Biodiversity and Conservation at Scripps Institution of Oceanography (La Jolla, CA, USA). His research focuses on the community ecology of marine systems, especially coral reefs.

Mark Vermeij is the scientific director of the CARMABI research station on Curaçao, Netherlands Antilles. His research interests include evolutionary and ecological dynamics of benthic marine organisms, with particular emphasis on corals, algae and, most recently, fishes.

Allen Hurlbert is broadly interested in macroecology, with specific research foci including both local- and global-scale patterns of species richness, turnover in species composition in space and time, the structure of species' geographical ranges and, occasionally, fish.

Editor: Julian Olden