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CAUSES OF LATITUDINAL GRADIENTS IN SPECIES RICHNESS: A TEST WITH FISHES OF THE TROPICAL EASTERN PACIFIC

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Abstract. Recent advances in analytical methods and exploration of regional diversity patterns in greater depth than simple whole-fauna patterns may change our understanding of the determinants of latitudinal gradients in species richness. Using a comprehensive database on the geographical distributions of the large fauna of endemic shorefishes from the Tropical Eastern Pacific (TEP), we delineated latitudinal diversity gradients (LDGs) of species with different range sizes and assessed how the mid-domain effect, energy supply, environmental variability, and habitat availability predicted the various LDGs. We used statistical methods that account for spatial autocorrelation within each variable and consider collinearity among them. We found marked variation in LDGs among species with different range sizes: species with large ranges contributed the most to the convex form of the entire-fauna LDG while species with small ranges generated most deviations from that form. The mid-domain effect was the strongest determinant for the entire-fauna LDG, largely due to the strength of its effect on widespread species. Habitat variables were the best predictors for LDGs of small-range species but had no significant effects on the entire-fauna pattern. We found that any relationship between energy supply and LDGs likely is spurious and arises from statistical effects of (1) the marked spatial autocorrelation of the residuals in those relationships and (2) strong covariation between energy supply and the mid-domain effect, two factors that have never been analyzed together in marine studies (and seldom in terrestrial studies). There was no indication that environmental stability was an important LDG determinant at any level within the fauna. We found that latitudinal (Rapoport) trends in range size in this fauna arise as corollaries of the mid-domain effect. The disparate contributions of species with different range sizes to diversity patterns demonstrate the failure of traditional, whole-fauna LDGs to adequately represent all faunal components and their determinants, particularly those of small-range (and more threatened) species. We argue that, just as analyses of whole-fauna patterns within a region obscure variation in determinants among faunal components, analyses of patterns at transoceanic (multiregional) scales are likely to conceal important regional variation in determinants of diversity gradients.

Key words: diversity; energy/habitat/stability effects; fishes; geographic range; mid-domain effect; Rapoport's rule; spatial scale.

Introduction

Revealing the causes of geographical patterns in species richness has been a primary and longstanding goal in ecology (Darwin 1839, Wallace 1878). Interest in this problem has increased recently due to the accumulation of detailed information on the ranges, habitats, and biology of organisms and a desire to predict the responses of biodiversity to ongoing global changes in the environment, a necessary prediction if we are to design effective schemes for its conservation (Dayton 2003). While diversity patterns have become increasingly well documented, the development of adequate causal explanations for them remains one of the most significant challenges for ecologists (Rohde 1992, Gaston 2000, Willig et al. 2003). Of particular relevance are issues related to the use of appropriate analytical techniques (e.g., Lichstein et al. 2002, Graham 2003) and to whether patterns based on entire faunas or floras adequately represent all diversity components (e.g., Jetz and Rahbek 2002, Lennon et al. 2004). The importance of these issues presages a significant change in our current understanding of causes of diversity gradients.

Most tests of mechanisms driving species diversity have relied on standard analytical techniques. Unfortunately the outcomes of those techniques can be biased by two common attributes of ecological data: spatial autocorrelation, the lack of independence among geographic sampling units in a given variable (e.g., Lichstein et al. 2002), and multicollinearity, covariation among multiple predictive variables (e.g., Graham 2003). Spatial autocorrelation leads to underestimation of standard errors and strong inflation of Type I errors when traditional statistical methods are used (see ex-

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tended discussion in Lichstein et al. [2002]). Collinear variables, on the other hand, can reflect either true functional relationships or spurious correlations and can reduce (sometimes fatally so) the statistical power of true relationships in traditional statistical methods (Graham 2003). As used here multicollinearity refers to the covariation among variables surrogating different hypotheses and not the redundancy in variables that surrogate a single hypothesis. The commonness of multicollinearity and its disruptive effects on interpretation of the significance of single variables highlights the need for analyses that encompass all known major potential explanatory hypotheses. Despite the likelihood of effects of spatial autocorrelation and multicollinearity, few studies of diversity patterns have used statistical approaches that are available for dealing with these problems (see reviews in Lichstein et al. [2002], Graham [2003]).

Spatial patterns in species richness are traditionally appraised for entire faunas or floras (see discussions in Jetz and Rahbek [2002], Lennon et al. [2004]). However, it has recently been realized that these patterns fail to ''evenly represent'' all taxa, because the contribution each species makes to the overall pattern depends on the size of its geographic range (Jetz and Rahbek 2002, Lennon et al. 2004). Because such patterns are assembled by counting the total number of species found at each location, species with larger ranges will ''over-contribute'' to these patterns by being counted at many more locations than will species with small ranges. Such a disproportionate contribution can lead to biases in the presumed determinants of diversity patterns, particularly those affecting the diversity of small-range (and often more threatened) species (Jetz and Rahbek 2002, Lennon et al. 2004).

The seriousness of problems associated with the use of standard analytical methods for assessing diversity patterns and the uneven representation of species in whole-fauna patterns has emerged only relatively recently, and the effects of those problems remain largely untested. Indeed, to date only one study has comprehensively addressed issues arising from autocorrelation, multicollinearity, and the adequate representation of all species within an entire-fauna diversity pattern. Jetz and Rahbek (2002), who assessed all major known causal mechanisms relating to the diversity patterns of African birds, found that various analytical methods that controlled for autocorrelation and multicollinearity produced different results and that various causal factors had contrasting effects on species with different range sizes. Their results highlight the importance of these issues and the need for similar analyses in other systems. Here we extend their mode of analysis to a marine system, a regional fish fauna. Marine and terrestrial environments are very different, and fishes and birds have very different life history characteristics, ecologies, and dispersal capacities. Hence the mechanisms underlying the geography of their diversity may well be different. Our methods also extend on those used by Jetz and Rahbek (2002) by assessing patterns and effects of collinearity among explanatory variables and comparing the results produced by a more extensive set of statistical tests.

Comprehensive analyses that embrace all known potential causal mechanisms are essential not only because they deal with problems of multicollinearity, but also because no single mechanism appears to account adequately for such patterns (Rohde 1992, Gaston and Blackburn 2000, Willig et al. 2003). Most causation hypotheses for spatial patterns in species richness can be grouped into those dealing with energy supply (species richness increases with energy supply), environment stability (species richness increases with stability), habitat area (species richness increases with area), the Rapoport effect, and the mid-domain effect (see reviews in Gaston and Blackburn [2000], Willig et al. [2003]). The Rapoport effect maintains that gradients in species richness arise from a tendency for latitudinal range size to increase towards the poles in response to environmental variability (Rapoport's rule): while a mix of small-range (narrow environmental tolerance) and large-range (broad tolerance) species add to the diversity of stable low latitudes, only the latter subset can live at the more variable higher latitudes (Stevens 1989). The mid-domain hypothesis is a null model, which proposes that a ''nonbiological'' latitudinal gradient in species richness that features a peak in diversity in the center of a domain can arise from the random overlap of ranges between boundaries delineated by physiographic features and physiological tolerances (Colwell and Hurts 1994). Although the importance of the mid-domain effect on diversity patterns is a matter of ongoing debate (see Zapata et al. 2003, Colwell et al. 2004, Pimm and Brown 2004) the need for tests of that effect remains, most importantly in combination with other potential causal factors (Colwell et al. 2004, Pimm and Brown 2004).

In this paper we analyze the effects of range size on latitudinal diversity gradients (LDGs) in a fauna of a well-recognized, discrete biogeographical region and assess potential underlying causes for those patterns. We first examine how LDGs of species with different range sizes contribute to the LDG of the entire fauna and then assess how causal factors for those groups emerge in the analysis of the whole-fauna pattern. We use various statistical techniques designed to deal with spatial autocorrelation and multicollinearity. We also assess the extent to which the latitudinal trend in range size of the entire fauna conforms to Rapoport's rule. We use the substantial endemic shorefish fauna of the Tropical Eastern Pacific (TEP) as our focal fauna.

Methods

Region of study

The Tropical Eastern Pacific is perhaps the most isolated tropical marine region in the world (Glynn and

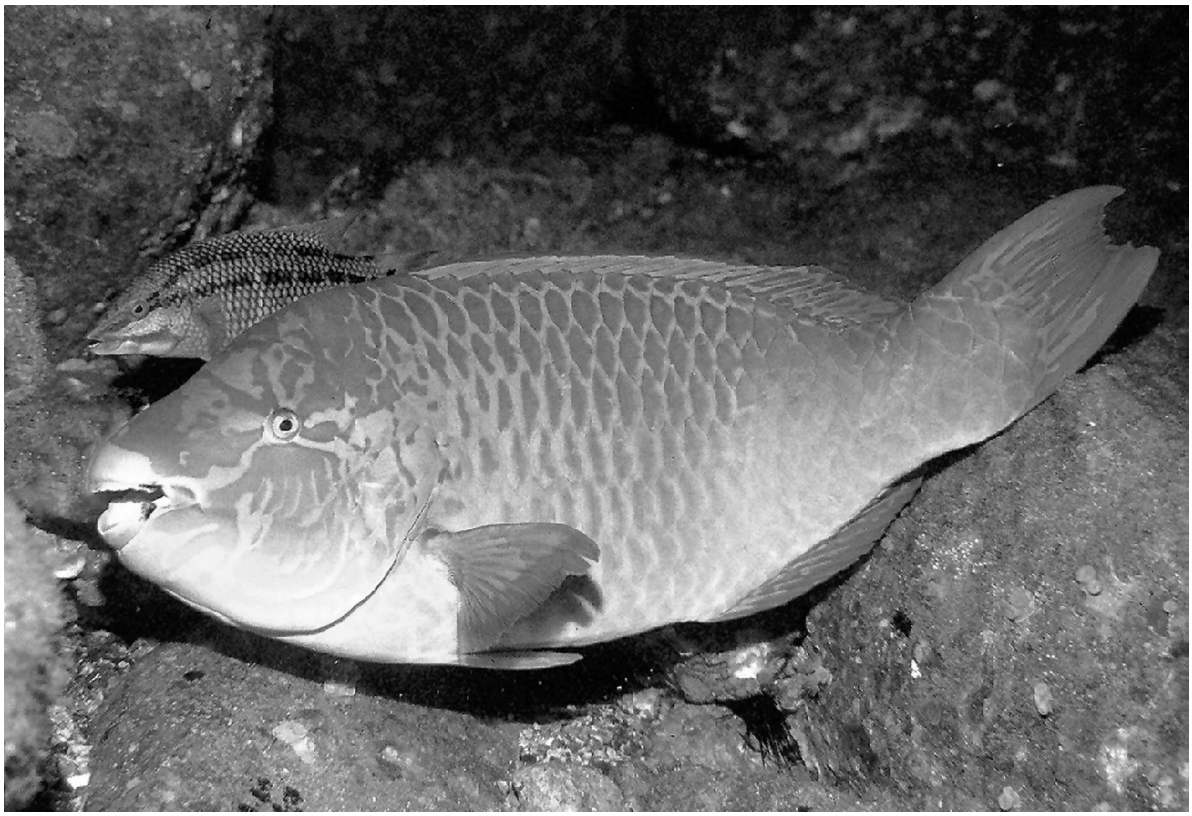

PLATE 1. The azure parrotfish (*Scarus compressus*), one of over 700 shore-fishes endemic to the Tropical Eastern Pacific, occurs throughout most of that region. Photo credit: G. R. Allen.

Ault 2000). About 73% of the ~1200 shorefish species found in this region are endemic to it (Robertson and Allen 2002; see Plate 1). Several potent barriers maintain the isolation of this regional biota. The Eastern Pacific Barrier, an uninterrupted ~5000 km wide stretch of deep ocean on the western side of the TEP, has largely isolated it from the mass of reefs of the central and western Pacific for as much as 65×10^6 yr (Grigg and Hey 1992). The Isthmus of Panama on the eastern side has totally isolated the TEP from the Caribbean for $\sim 3 \times 10^6$ yr (Coates and Obando 1996). The northern and southern limits of the TEP usually are considered to be at approximately 25° N (i.e., near the tip of the peninsula of Baja California) and 5° S (northern Peru). These represent the points at which cold equator-bound currents from California and Peru turn westward to the central Pacific (Glynn and Ault 2000, Robertson and Allen 2002). Strong disjunctions in the diversity of a wide variety of marine taxa at those turning points have been attributed to effects of adverse currents that preclude range expansion and to intolerance to drastic changes in temperature (Roy et al. 1998, Gaylord and Gaines 2000, Robertson and Allen 2002). However, a significant number of TEP fishes extend their ranges into the Gulf of California well beyond 25° N (Robertson and Allen 2002), because the Gulf is warmer than the outer coast of Baja and lacks currents likely to prevent species from spreading to higher latitudes. In addition, during El Niño events a huge surge of warm water moves across the central Pacific to the TEP and spreads north and south along the coast of the Americas well beyond 25° N and 5° S (Glynn and Ault 2000). During such events the ranges of many tropical fishes temporarily extend past those ''normal'' northern and southern limits (e.g., Chirichigno and Velez 1998, Lea and Rosenblatt 2000). Hence, for the present analysis we set the boundaries at 32° N (which includes the hard boundary of the northern edge of the Gulf of California) and 8° S. Those limits span the entire ranges of the great majority of species whose distributions are concentrated in the TEP.

The species database

Latitudinal diversity gradients were quantified as the sum of species overlapping their ranges in each 1° latitudinal band. Ranges were based on the endpoints of each species' distribution in the database in Robertson and Allen (2002), which includes the distributions of 1195 resident and vagrant shorefishes found in the TEP. These represent all known shallow-water (found in <100 m of water) shoreline fishes in that region, as

TABLE 1. Levels of spatial autocorrelation (as Moran's *I* coefficients) and collinearity (as coefficients of correlation) between pairs of possible determinants of the diversity of Tropical Eastern Pacific shorefishes.

Hypothesis and/or factor	Moran's *I* coefficient	Mean temperature	Chlorophyll *a*	Minimum temperature	Temperature, SD
Mid-domain effect	0.85*	0.96*	−0.22	0.84*	−0.76*
Mean temperature	0.81*		−0.29	0.88*	−0.77*
Chlorophyll *a*	0.53*			−0.48*	0.52*
Minimum temperature	0.90*				−0.96*
Temperature, SD	0.94*				
Bottom area <100 m	0.40*				
Coastline length	0.57*				
No. islands	0.60*				
Rapoport's effect (Stevens' method)	0.85*				

Notes: Moran's *I* coefficients of autocorrelation were calculated based on a spatial matrix that considers as neighbors the bands immediately above and below each latitudinal band, with only one neighbor for the southernmost and northernmost bands. Note that here Moran's *I* coefficients indicate the autocorrelation of the variable itself and not the autocorrelation of residuals of particular regressions. The latter are used to expose any violations of the assumption of independence of the residuals (as in Fig. 3). The mid-domain effect and latitudinal trends in range size (Rapoport's effect) were based on the entire fauna. Moran's *I* coefficient was not calculated for the midpoint method of quantifying Rapoport's effect because some of the outermost latitudinal bands lacked any range midpoints (see Fig. 1d). Asterisks indicate significant correlations at $P < 0.05$.

well as oceanic epipelagic species that enter the region's nearshore waters. We restricted our analysis to the 736 endemic species that live along the continental shore and whose ranges lie entirely between 32° N and 8° S. We excluded the following groups: species found only at oceanic islands in the TEP, the Revillagigedos, Clipperton, Cocos, Malpelo, and the Galápagos (because their distributions are affected by isolation and by environmental factors different from those on the mainland [cf. Leis 1986, Mora and Robertson 2005]); species whose ranges extend beyond the 32° N and 8° S boundaries (their supra-regional distributions suggest that they are largely unaffected by conditions in or constraints that define the TEP); trans-Pacific fishes that appear to have migrated to the TEP from elsewhere in the Pacific (see Robertson et al. 2004); species that are vagrants in the region (rather than having self-sustaining populations there); and a handful of species introduced from the Atlantic (e.g., migrants through the Panama Canal). We assess diversity patterns of the entire fauna and of species in four range-size categories: up to 10° of latitude, 11–20°, 21–30°, and 31–40°.

Potential determinants of diversity

Proposed determinants of LDGs that we investigated include the mid-domain effect; the Rapoport effect; energy input (using mean sea surface temperature and primary production as surrogates); environmental variability (using minimum and standard deviation in sea surface temperature as proxies); and habitat availability (using three features thereof: area of substrate <100 m deep, coastline length, and the number of coastal [non-oceanic] islands). Minimum temperature is a useful indicator of environmental variability because large areas of the TEP are affected by seasonal upwellings, which can produce mass die-offs of shorefishes and other organisms (Mora and Ospina 2002; D. R. Robertson, *personal observation*).

To construct a null model of the mid-domain effect we randomly allocated ranges of our set of species between the 32° N and 8° S boundaries of the TEP. For each species, its range was randomly placed, with equal probability, between the boundaries of the domain to the extent possible without placing either edge of its range beyond the limits of the domain (Colwell and Lees 2000). We then quantified species richness for each 1° interval of latitude as the total number of species whose ranges were included in that interval. Repetition of this randomization procedure 1000 times yielded a mean number of species per interval, which we considered as the expectation of the mid-domain effect. Traditional mid-domain models have been criticized for failing to account for the two-dimensionality of most species' ranges (Zapata et al. 2003). Our comparison is largely unaffected by this bias because the coastline of the TEP is relatively simple and straight and is longitudinally oriented, and we analyzed the ranges only of continental species. It is also important to note that we focus entirely on the endemic fauna to the TEP. We removed non-endemic species to reduce biases arising from their distributions having been affected by geographical and historical factors acting outside the TEP. Relative to the scale of the TEP, non-endemic species are widely distributed, and their removal did not affect the shape of the entire-fauna LDG (the coefficient of correlation between the LDGs with and without non-endemics was 0.99). Colwell et al. (2004) noted that removal of non-endemic species in previous studies led to only minor deviations from expectations of the mid-domain effect and concluded that studies based solely on endemic faunas are legitimate in their own right and could produce useful results.

TABLE 1. Extended.

Bottom area <100 m	Coastline length	No. islands	Rapoport's effect: Stevens' method	Rapoport's effect: Midpoint method
−0.09	−0.10	0.00	−0.35*	0.71*
0.00	−0.07	−0.04	−0.34*	0.77*
0.18	0.30	0.21	−0.13	−0.20
−0.06	−0.26	−0.08	−0.07	0.71*
0.17	0.38*	0.13	−0.04	−0.60*
	0.82*	0.71*	−0.44*	0.01
		0.79*	−0.56*	−0.12
			−0.60*	−0.10
				−0.07

Latitudinal (Rapoport) trends in mean range size for the entire fauna were quantified by (1) averaging the range size of all species present in a 1° latitudinal band (Stevens' method: Stevens [1989]); and (2) averaging the range size only of species whose range midpoints are in a particular band (the mid-point method: Rohde et al. [1993]). Rohde et al. (1993) developed the latter method because means from different latitudinal bands derived by Stevens' method lack statistical independence. To assess the Rapoport effect, we tested the prediction that tropical sites will have more species with smaller mean range size.

Environmental data for each latitudinal band were obtained as follows: Temperature data came from 17 yr of weekly satellite records of sea surface temperature provided by Reynolds Optimum Interpolation Weekly SST Analysis, for each 1° × 1° (latitude × longitude) along the eastern Pacific coast (*available online*).[4] As a measure of primary productivity we used the abundance of chlorophyll *a* in a 50 × 10 km transect oriented perpendicular to the coastline at each 1° interval. This was extrapolated from a color-coded satellite image of worldwide chlorophyll concentrations averaged over a 5-yr period (*available online*).[5] Area of substratum above 100 m depth, coastline length (of coastal island plus continental shorelines), and the number of coastal (non-oceanic) islands were obtained by digitizing nautical charts of the region (1:600 000–1:1 000 000 scales). We included all coastal islands larger than 0.1 km^2 that were clearly separated from the general direction of the shoreline (i.e., are not part of a sediment island system obscuring the mouth of an estuary or of fractal sediment island complexes within river deltas). In the TEP, most of the shallow bottom consists of sand and mud, while coastline length and the abundance of islands are better indicators of the availability of reef habitats and of habitat heterogeneity and patchiness.

[4] ⟨http://www.emc.ncep.noaa.gov/research/cmb/sst_analysis/OISST_ts.txt⟩

[5] ⟨http://seawifs.gsfc.nasa.gov/SEAWIFS/IMAGES/S19972742002120.L3m_CU_CHLO_SWREP4.gif⟩

Data analyses

The purpose of this research was to investigate whether LDGs of TEP shorefishes conform to predictions of various general diversity hypotheses. We first determined the levels of collinearity among independent variables and the extent of their spatial autocorrelation to assess how these problems are likely to affect relationships. Spatial autocorrelation was quantified using Moran's *I* coefficients of autocorrelation at intervals spanning the entire domain. To account for multicollinearity, we used a combination of single and multiple regression techniques as recommended by Graham (2003). These include single and multiple ordinary regressions, ridge regression analysis, and single and multiple spatial regressions. Principal component analyses were not useful in our case because highly collinear variables, surrogating different hypotheses (e.g., temperature and mid-domain; see Table 1), were part of the same principal components, which precluded their interpretation. Likewise structural equation modeling was of little use here as the knowledge of the hypothetical links among variables is still vague. To account for spatial autocorrelation, we used trend surface analysis (Legendre and Legendre 1998) and spatial regression models (Kaluzny et al. 1998, Lichstein et al. 2002) (see Appendix). The reliability of these methods was assessed by determining the levels of autocorrelation in their residuals using Moran's *I* coefficients of autocorrelation. Probability values for all single regressions were adjusted using the sequential Bonferroni method (Rice 1989).

RESULTS

The entire fish fauna of the TEP exhibits a strong latitudinal gradient in species richness (Fig. 1a). The number of species peaks near the center of the region and declines steadily towards its latitudinal limits. However, there are two areas in which richness levels exceed those in this gradient, between 8° and 10° N (Panama to Costa Rica) and between 23° and 29° N (the lower Gulf of California).

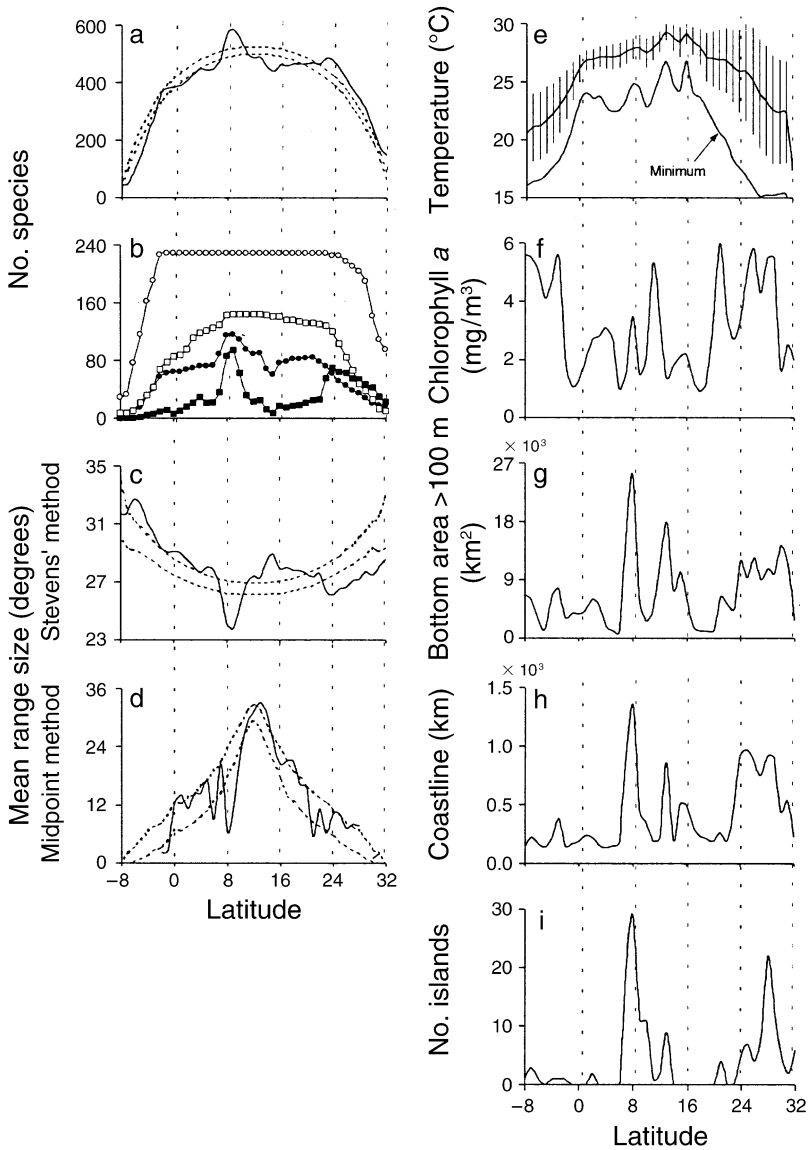

FIG. 1. Latitudinal patterns in the Tropical Eastern Pacific of species richness of (a) the total shorefish fauna and (b) different range-size groups: species with ranges up to 10° of latitude (closed squares, n = 208 species), 11°–20° (closed circles, n = 154 species), 21°–30° (open squares, n = 145 species), and 31°–40° (open circles, n = 229 species). The remaining panels show trends in (c, d) mean range size and (e–i) five potentially determinant environmental variables. Dotted lines represent the 95% confidence limits of the (a) richness and (c, d) mean range-size distributions generated by the mid-domain model. Error bars in panel (e) indicate ±SD.

Partitioning species into range-size categories highlights the disparate contributions made by these different groups to the LDG of the entire fauna. Despite there being a similar number of species in each range-size group (Fig. 1), the contribution of species records to the overall pattern increased as species' range size increased (Fig. 1b). Species in the smallest range group exhibited strong peaks of richness between 8° and 10° N and between 23° and 29° N, and relatively low diversity throughout the remainder of the domain (Fig. 1b). Species in the second smallest range-size group displayed a similar, although less extreme form of the smallest range group's pattern. Together the diversity gradients of these two small-range groups accounted for the departures (excesses and deficits) from a smooth gradient in the entire-fauna pattern. Species in the third largest range-size group displayed a fairly gradual cline from the center towards the edges of the TEP, while those with the largest ranges were, not surprisingly, uniformly distributed throughout the bulk of the region, except around its edges (Fig. 1b).

TABLE 2. Relationships between the species richness of Tropical Eastern Pacific shorefishes and different variables using different forms of regression analyses.

Variable	OSR	TSA	TSA(a)	TSA(b)	SSR	OMR	RRA	MSR
a) All species								
Multiple R^2						0.96*	0.88*	0.91*
Mid-domain effect	18.70*	23.12*	0.04	0.86	11.86*	6.03*	4.77*	6.81*
Mean temperature	12.82*	−0.05	0.00	0.81	−1.12	0.90	2.26*	−0.80
Chlorophyll *a*	−2.59	0.75	0.00	0.15	−0.67	−1.72	−0.87	−0.84
Minimum temperature	6.34*	−2.80*	0.02	0.49	−0.01	−2.10*	−0.31	0.72
Temperature, SD	−3.24*	2.38	0.01	0.20	−0.70	−0.79	0.46	−0.58
Bottom area <100 m	0.83	1.17	0.00	0.01	0.87	−0.12	−1.01	−0.87
Coastline length	1.66	2.80*	0.02	0.05	2.06	0.43	1.11	1.33
No. islands	1.31	2.63	0.02	0.03	2.42	1.93	1.54	0.80
Rapoport's effect								
Stevens' method	−8.57*							
Midpoint method	3.18*							
b) Range sizes up to 10° latitude								
Multiple R^2						0.72*	0.62*	0.56*
Mid-domain effect	1.57	1.67	0.05	0.01	1.41	0.01	1.31	1.12
Mean temperature	1.30	1.33	0.03	0.01	0.89	2.32*	1.00	−0.64
Chlorophyll *a*	0.37	0.50	0.00	0.00	−0.40	−0.98	−0.65	−1.01
Minimum temperature	−0.48	0.51	0.01	0.00	0.89	−2.43*	−1.05	0.52
Temperature, SD	1.75	0.04	0.00	0.07	0.23	−1.06	0.97	0.93
Bottom area <100 m	3.38*	2.80*	0.12	0.10	1.63	−0.57	−0.51	−0.62
Coastline length	6.37*	4.88*	0.28	0.23	2.82*	0.82	1.43	1.29
No. islands	5.54*	5.31*	0.31	0.13	2.50*	3.11*	2.65*	0.77
c) Range sizes between 11° and 20° latitude								
Multiple R^2						0.90*	0.84*	0.85*
Mid-domain effect	14.72*	−0.04	0.00	0.85	8.46*	1.73	2.74*	2.35*
Mean temperature	11.64*	−1.47	0.01	0.77	−0.20	2.29*	2.28*	0.00
Chlorophyll *a*	−3.00*	−0.24	0.00	0.19	−0.36	−0.41	−0.33	−0.49
Minimum temperature	8.91*	−0.76	0.00	0.67	2.01	−1.38	0.43	0.81
Temperature, SD	−5.3*	0.12	0.00	0.42	−1.81	−1.31	−0.57	−0.26
Bottom area <100 m	0.48	1.13	0.00	0.00	1.60	−0.76	−1.09	−0.80
Coastline length	0.67	1.41	0.01	0.01	2.28	−0.99	−0.03	0.25
No. islands	1.28	3.3*	0.03	0.01	3.20*	3.26*	2.47*	1.96*
d) Range sizes between 21° and 30° latitude								
Multiple R^2						0.97*	0.91*	0.94*
Mid-domain effect	29.70*	41.53*	0.00	0.96	14.60*	7.57*	4.87*	6.12*
Mean temperature	19.57*	−0.44	0.00	0.91	−0.81	1.01	3.03*	0.35
Chlorophyll *a*	−2.80*	−0.48	0.00	0.17	−0.80	−0.31	−0.10	−0.58
Minimum temperature	8.80*	−0.94	0.00	0.67	0.26	−2.26*	0.06	−0.56
Temperature, SD	−4.60*	−1.22	0.00	0.35	−1.90	−0.69	0.14	−0.97
Bottom area <100 m	0.26	−0.07	0.00	0.00	0.18	0.41	−0.77	0.32
Coastline length	0.63	−0.04	0.00	0.01	0.18	1.03	0.96	0.58
No. islands	0.28	−0.08	0.00	0.00	0.16	−1.45	−0.05	−0.55
e) Range sizes between 31° and 40° latitude								
Multiple R^2						0.95*	0.88*	0.92*
Mid-domain effect	24.21*	34.28*	0.20	0.74	16.47*	10.96*	7.12*	9.72*
Mean temperature	9.48*	10.49*	0.01	0.69	−1.89	0.32	1.31	−0.64
Chlorophyll *a*	−2.58	0.61	0.00	0.14	−0.50	−2.40*	−1.37	−0.14
Minimum temperature	5.28*	−1.70	0.02	0.40	−1.70	−0.95	−0.15	−0.26
Temperature, SD	−2.60	2.13	0.02	0.13	0.04	−0.54	0.32	−1.10
Bottom area <100 m	0.27	−0.50	0.00	0.00	−0.58	−0.01	−0.68	−1.29
Coastline length	1.19	0.67	0.00	0.03	0.49	0.28	0.73	1.01
No. islands	0.49	−0.32	0.00	0.01	0.81	0.61	0.47	0.25

Notes: For ordinary single regressions (OSR), trend surface analysis (TSA), single spatial regression (SSR), ordinary multiple regression (OMR), ridge regression analyses (RRA), and multiple spatial regression (MSR), *t* values are shown. Asterisks indicate statistically significant *t* values/correlations at $P < 0.05$ for the outcomes of multiple regressions and after sequential Bonferroni adjustments in the different single models. The *t* values for each predictor in TSA were obtained from ordinary multiple regression models containing the spatial trend and the predictor. The variance explained by the nonspatial environmental component, TSA(a), and the spatially structured environmental component, TSA(b), in TSA is also included (see Appendix for details). In TSA, the R^2 of the trends alone are as follows: (a) all species, 0.9; (b) range sizes up to 10° latitude, 0.28; (c) range sizes between 11° and 20° latitude, 0.87; (d) range sizes between 21° and 30° latitude, 0.98; range sizes between 31° and 40° latitude, 0.78.

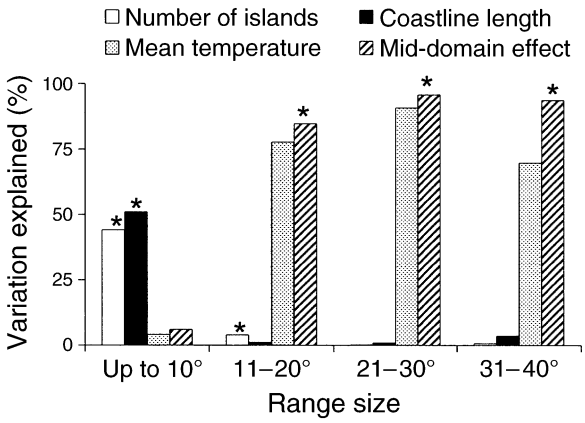

FIG. 2. Variation explained by the ''key'' causal factors of latitudinal gradients in species richness in the shorefish fauna of the Tropical Eastern Pacific. Asterisks indicate significant single spatial regressions.

Spatial variations in species richness expected by the mid-domain effect, as well as geographical variations in range size (Rapoport's rule) and environmental variables are shown in Fig. 1 (a–i). Standard single regression models identified the mid-domain effect and mean temperature as the best single predictors of the entire-fauna LDG (Table 2a). Individually, all variables except chlorophyll and habitat descriptors also were strong predictors of the entire-fauna LDG (Table 2a). However, there was a marked variation in the predictors of LDGs of species with different range sizes. The predictive effects of the mid-domain and temperature variables were weakest for the LDG of the smallest range group (Table 2b) and strong for the other groups (Table 2c–e, Fig. 2). In contrast, the relationship of LDGs to habitat features followed the reverse pattern: only the two small range categories showed any relationship with habitat variables (Table 2b–c), with the smallest range group showing by far the strongest effects (see Fig. 2).

Each of the predictive variables analyzed in this study displayed statistically significant and often strong spatial autocorrelation (Table 1, Fig. 3). Partitioning of the variance that each of them explained into spatial and nonspatial components in the trend surface analyses (Table 2) indicates that the effect of most of them is highly structured in space (column ''TSA(b)'' in Table 2). Only habitat variables had statistically significant effects that were independent of their spatial structure (column ''TSA(a)'' in Table 2), which reflected their relatively low levels of spatial autocorrelation (Table 1). Controlling for spatial autocorrelation by using trend surface analysis and spatial regression models showed that some standard single correlations were spurious. Of particular interest is the lack of significance for all temperature variables in almost all range-size categories (Table 2a–e). This is very likely due to the strong autocorrelation of temperature at all scales (Table 1, Fig. 3). We also found that spatial regression models were more effective than trend surface analyses at removing autocorrelation at all scales (e.g., compare Fig. 3d vs. c). This demonstrates that the former technique produces more reliable results, due to the violation of independence in the latter. The use of spatial regression models confirmed the importance of the mid-domain effect for widely distributed species (Table 2c–e) and of habitat variables for the two smallest range groups (Table 2b–e, Fig. 2). In contrast, this analysis found no relationship between habitat variables and the entire-fauna LDG (Table 2a). It is also important to note that these conclusions about contrasting effects of the mid-domain and habitat are robust against effects of collinearity because the mid-domain was not significantly collinear with any habitat variable (Table 1).

The different forms of multiple regressions that we used (ordinary multiple regression, ridge regression analysis, and multiple spatial regression) consistently supported the conclusions reached above about the importance of mid-domain effect and habitat variables on the different range-size LDGs, with one exception (Table 2). Among the three habitat variables island abundance had the most consistent effect on the two smallest range-size categories (Table 2). Only multiple spatial regression failed to indicate an effect of island abundance on the diversity of the smallest range group of species (Table 2b). This nonsignificant result evidently was due to covariation of island abundance with coastline length and bottom area (Table 1), because removal of the latter two variables from that model led to island abundance having a significant effect on the smallest

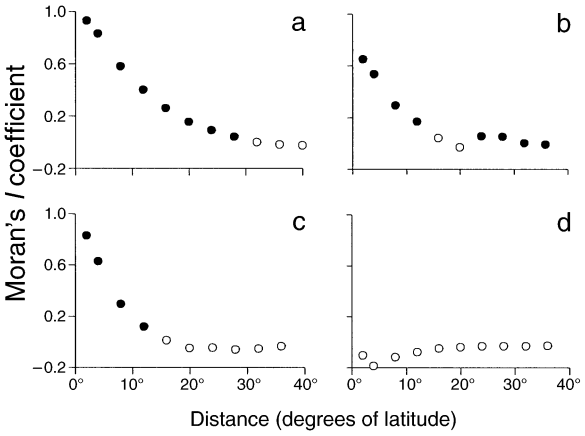

FIG. 3. Spatial correlograms for (a) all-species richness, (b) the residuals of an ordinary single-regression analysis between all-species richness and temperature (as an example), and the residuals of the same relationship in (c) a trend surface analysis and (d) a single spatial regression model. Key to symbols: filled circles, significant correlations; open circles, nonsignificant correlations. Under the null hypothesis of no spatial autocorrelation, Moran's $I = 0$. Spatial regression analyses were similarly reliable at removing autocorrelation in the residuals of the analyses of all other variables.

range LDG ($t = 2.49$, $P < 0.01$). Thus, island abundance is an adequate descriptor of habitat availability, with coastline length and bottom area being largely redundant.

The significance attached to mean and minimum temperature varied tremendously among the various multiple regression models (Table 2). This variation reflects complications due to multicollinearity among these temperature variables and between them and the mid-domain effect (Table 1). However, an important difference between the effects of mean and minimum temperature and those of habitat descriptors is that neither temperature variable (either separately or in combination) was significantly related to any LDG when spatial autocorrelation was accounted for in the single and multiple spatial regression models (see Table 2). This suggests that the high correlations between these temperature variables and diversity patterns shown by standard statistical methods are spurious effects that arise from the strong spatial signal in the distribution of temperature (Table 1, Fig. 3). None of the multiple regression models indicate that standard deviation in temperature (i.e., environmental variation) affects any LDG (Table 2). Only an ordinary multiple regression model supported an effect of chlorophyll (on the diversity of large-range species), an effect that disappeared when spatial autocorrelation was controlled for in the single- and multiple spatial regression models (see Table 2e).

Latitudinal variation in range size followed the pattern predicted by Rapoport's rule (mean range size increases with latitude) when ranges were averaged using Stevens' method but the opposite pattern when they were averaged using the mid-point method (Fig. 1c–d). As a result, while species richness and average range size were significantly correlated, Stevens' and the mid-point methods produced negative and positive correlations, respectively (Table 2a). To investigate how these opposite patterns in range size arise, we compared the two actual patterns with the latitudinal patterns of average range size produced by the mid-domain model, i.e., the pattern obtained when the actual ranges are randomly arranged between the region's boundaries. We found that the two actual latitudinal patterns of variation in mean range size conform well to opposite trends that arise from the mid-domain effect (Fig. 1c–d, Table 1).

Discussion

Many different hypotheses, including null models (the mid-domain effect), other patterns (the Rapoport effect), and environmental factors (e.g., energy, habitat, and stability) have been proposed (and vigorously contested) as causal for general latitudinal gradients in species richness (Willig et al. 2003). To date, however, few studies have attempted a comprehensive analysis of such factors for a regional fauna. In such an analysis we found that the mid-domain effect stands out as the best predictor of the overall diversity of shorefishes in the TEP (see also Connolly et al. [2003] and Mora et al. [2003] for Indo-Pacific reef fishes). This effect can be explained by the strong representation of large-range species in the overall pattern of species richness (Fig. 1b; and see Jetz and Rahbek [2002]) and a strong mid-domain effect on their distribution (Table 2c–e; and see Colwell and Lees [2000] and Zapata et al. [2003]). It is important to note that the TEP has specific geographic conditions that may facilitate the dominance of the mid-domain effect: the west coast of the Americas has a simple, unbroken coastline that may make it relatively easy for shorefishes to expand their ranges towards the boundaries of the TEP. If regional geography is important in this way then the mid-domain should have stronger causal effects in other tropical regions with similarly simple geographies (e.g., the east coast of Africa) than in geographically complex areas such as the Caribbean and west Pacific.

However, while the mid-domain effect and the form of the underlying geometric constraints in the TEP seem to affect the gradient in diversity of widely distributed species, this is not the case for narrowly distributed fishes in that region. For species with small ranges, we found that habitat variables were the best predictors of their diversity. Interestingly, none of these habitat variables was significantly related to the overall pattern of species richness pointing out the limitations of studies based on entire faunas or floras. In the TEP, the diversity of species with small ranges peaks at Panama/Costa Rica and the Gulf of California. Increased species richness in those two areas may have arisen in two ways. First, those two areas may represent ''centers of origin'' with habitat fragmentation and isolation producing high levels of speciation, an assumption that is supported by retentive hydrodynamic processes associated with islands (Mora and Sale 2002) and strong levels of genetic differentiation among populations of adjacent islands in one of those areas (Riginos and Victor 2001). Second, those areas may represent ''centers of accumulation,'' with high habitat and environmental diversity allowing them to support many species, including those that did not originate there under prevailing conditions.

Energy supply is argued to regulate the diversity of species by affecting rates of speciation (see Harmelin-Vivien 2002) and by limitations in its availability to species (Currie 1991, Roy et al. 1998, Macpherson 2002, Astorga et al. 2003). Our study, however, failed to support this hypothesis and showed that correlations between temperature and species richness can spuriously arise from statistical effects of (1) spatial autocorrelation in the distribution of temperature and (2) strong covariation between temperature and the mid-domain effect, two factors that have never been analyzed together in marine studies and seldom in terrestrial studies (Colwell et al. 2004). If the strong collinearity between the mid-domain pattern and temperature that we found in the TEP is widespread, then the effects

of energy on species richness may generally have been overestimated in previous studies. Another limitation of studies supporting the importance of temperature is associated with scale. Kerr and Packer (1997) found that the species richness/energy hypothesis may be more applicable to high latitudes, which have lower climatic energy levels than the energy-rich tropics. Hence, multiregional studies may yield significant temperature effects despite the existence of strong regional variation in the actions of temperature. This may explain why larger-scale studies of temperate plus Tropical Eastern Pacific invertebrates concluded that temperature does effect their LDGs (see Roy et al. 1998, Astorga et al. 2003), although those studies also need to be revisited to deal with statistical issues described above. A final concern regarding the energy/species hypothesis is its failure to explain why species richness rather than population densities should increase with energy supply (Currie 1991, Willig et al. 2003). In fact, microcosm experiments have suggested that, while increases in temperature do modify species abundances, they also reduce species richness, in some cases through competitive exclusion (Chapin et al. 1995, Petchey et al. 1999). This is the opposite effect to that expected from the energy/species-richness hypothesis.

Chlorophyll *a* is a useful alternative to mean temperature as a proxy for energy supply because it provides a measure of the general biological response to energy input and varies throughout the TEP in a quite different pattern to temperature. We found no relationships between diversity trends (of the entire fauna or any range-size subgroup) and chlorophyll levels with the use of methods fully controlling for spatial autocorrelation. This reinforces the conclusions from our temperature analyses that energy supply is not the primary determinant of diversity patterns within the TEP.

An alternative interpretation for the strong correlations between mean and minimum temperature and LDGs is that those variables surrogate domain boundaries (defined by physiological constraints implicit in the mid-domain effect) rather than energy supply. Evidence is accumulating that climate regimes influence species' distributions through species-specific thresholds in temperature tolerance (Hoffman and Parsons 1997, Gaston 2003, Thomas et al. 2004). Range expansions in many taxa brought about by recent global warming (review in Walther et al. [2002], Parmesan and Yohe [2003]) reveal the actions of such physiological tolerances to temperature on range limits. That temperature surrogates domain boundaries rather than energy supply could explain the high correlation between the mid-domain and temperature and the increasing effect of both on LDGs as range size increases: while temperature as a surrogate of geographical constraints certainly predicts such an increasing effect (Colwell and Lees 2000, Zapata et al. 2003), we are not aware of a rational explanation for why temperature as a surrogate of energy should affect LDGs of species with large ranges more than LDGs of those with small ranges.

Relative stability of environmental conditions may also affect gradients in species richness (e.g., Harmelin-Vivien 2002). The TEP is an extremely dynamic region, due not only to seasonal fluctuations in temperature, but, more importantly, to an abundance of strong seasonal upwellings and to frequent effects of the El Niño southern oscillation cycle, both of which affect large parts of the study region (Glynn and Ault 2000). Strong temperature fluctuations in the TEP arising from extreme upwelling and strong El Niños are associated with both local die-offs and extinctions (Thompson and Lehner 1976, Mora and Ospina 2001, 2002, Victor et al. 2001) and range extensions (Chirchigno and Velez 1998, Lea and Rosenblatt 2000, Victor et al. 2001) of shorefishes. Hence environmental variation might be expected to be an important controller of the geography of diversity in that region. We found no indications that that was the case for either the entire fauna or the different range-size subgroups. In the TEP, population recoveries by fishes are known to occur after mass mortalities due to extreme local temperature fluctuations (Grove 1985, Victor et al. 2001). Hence the strong potential for recolonization after such events greatly limits any effect of temporarily variable environments on LDGs.

The degree to which there is an increase in range size with latitude (Rapoport's rule) and the significance of such a pattern for the geography of species richness has been vigorously contested during the last two decades (Stevens 1989, Gaston et al. 1998, Jones et al. 2002). Among TEP shorefishes, we found that latitudinal distributions in range size followed this rule when we used Stevens' method, but exhibited the opposite trend when we used the mid-point method. Yet we also found that both trends emerge as corollaries of the mid-domain effect, rendering Rapoport patterns irrelevant, at least in the present case. However, such relationships are not universal among tropical shorefishes, as recent studies of Indo-Pacific reef fishes found no latitudinal pattern of variation in range size consistent with Rapoport's rule (Hughes et al. 2002, Jones et al. 2002), even though the species-richness distribution conformed to the mid-domain effect (Connolly et al. 2003, Mora et al. 2003).

Our appreciation of ecological patterns and processes depends on the spatial and temporal scales at which we choose to view them (Levin 1992). While there is a need to assess mechanisms at the scales at which they operate, such scales may be different from that at which patterns are viewed (Levin 1992). As a case in point, within the vast expanse of the Indo-Pacific, which typically is treated as an integrated whole by biogeographers (e.g., Hughes et al. 2002, Jones et al. 2002, Connolly et al. 2003, Mora et al. 2003), there are at least 13 major biogeographic barriers (Bellwood and Wainwright 2002). Those barriers set the limits of subre-

gions with different environmental regimes and geographic attributes and relatively distinctive faunas (Bellwood and Wainwright 2002). Thus diversity patterns at the scale of the entire Indo-Pacific emerge from the collective patterns of a large ensemble of smaller subregions. Assessing causal mechanisms for patterns at the Indo-Pacific scale while ignoring subregional variation in biodiversity and environmental and geographical attributes may well obscure important aspects of causality operating at smaller scales. Variation in the effects of different causal factors on regional LDGs is only to be expected given the tremendous variation in historical, geographic, and climatic conditions among such subregions. This highlights a major inadequacy in methods used to appraise causal mechanisms of global diversity patterns and draws attention to the need to perform future studies including comprehensive description of regional patterns and processes.

Searches for all-embracing explanations of the causes of geographic variation in species richness tend to assume that patterns and determinants of overall species richness are representative for most species. This paper provides the first assessment of that assumption for any marine taxon. As has been shown for birds (Jetz and Rahbek 2002, Lennon et al. 2004), we found that in fishes overall diversity patterns fail to adequately represent all faunal components, particularly species with small ranges. We also found strong contrasts among the predictors of diversity patterns for species with different range sizes, variation in predictors that was obscured in analyses based on the entire fauna. One implication of this result is that conservation strategies based on analyses of overall species richness are unlikely to alleviate threats to small-range species, which tend to be under higher risks of extinction (Hawkins et al. 2000, Jetz and Rahbek 2002).

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APPENDIX

A description of the methods used to account for spatial autocorrelation is available in ESA's Electronic Data Archive: *Ecological Archives* E086-095-A1.