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Latitudinal patterns of species diversity on South American rocky shores: Local processes lead to contrasting trends in regional and local species diversity

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Abstract

Aim: We evaluated whether patterns of species diversity (α , β and γ) of rocky shore assemblages followed latitudinal gradients (i.e. LDGs) along the South American coasts, and tested hypotheses related to potential processes sustaining or disrupting the expected LDG pattern at various spatial scales.

Location: Coasts of South America.

Taxon: Macroalgae and sessile/slow-moving macrofauna on intertidal rocky shores.

Methods: We evaluated changes in species composition across 143 sites. The degree of replacement and loss of species at different spatial scales (i.e. coasts, regions and sites) were estimated to help distinguish among ecological, historical and evolutionary hypotheses for explaining LDGs. Furthermore, components of diversity and taxonomic distinctness were measured, and variability in these measures was decomposed using analysis of covariance. Finally, we examined relationships between diversity and a suite of environmental and anthropogenic variables to identify potential mechanisms that may be responsible for the reported spatial relationships.

Results: Species composition varied with latitude, and this variability was relatively consistent on both coasts. At all spatial scales, replacement of species was the dominant phenomenon (>95%), rather than loss in the total number of species (<5%). LDGs were strongly dependent on the diversity component and the spatial scale: generally, positive for regional β -diversity, negative for α -diversity and site β -diversity. Sea surface temperature (SST) was the variable that best explained patterns of diversity along both coasts (14%–22%), but other regional and local environmental variables associated with river discharges, upwelling, confluence of currents, tides and anthropogenic pressures also accounted for an important portion of variation (5%–14% each).

Main conclusions: Species diversity of South American rocky shores followed, with interruptions, LDGs. The trend of those LDGs, however, depended on the scale and metric used to describe diversity. It is proposed that patterns of LDGs at various scales are not the result of a single overarching process but are strongly influenced by local and regional processes. Although the most evident environmental gradient was the decrease in SST towards the south, it was demonstrated that regional and local environmental variables were also important for understanding the increase in regional β -diversity towards the tropics.

KEYWORDS

intertidal rocky shores, latitudinal diversity gradient, Macroecology, Southeast Pacific, Southern Caribbean, Southwestern Atlantic, spatial scales, species diversity

1 | INTRODUCTION

Latitudinal diversity gradients (LDGs), with species richness peaking near the equator and declining towards the poles, are one of the most commonly and well-documented large-scale biotic patterns in terrestrial ecosystems (Hillebrand, 2004; Kinlock et al., 2018; Willig, Kaufman, & Stevens, 2003). However, there are multiple examples where LDGs have not been found in marine systems (Rivadeneira, Thiel, González, & Haye, 2011; Valdovinos, Navarrete, & Marquet, 2003), or the relationship is far weaker than in terrestrial systems or inverse (Liuzzi, López Gappa, & Piriz, 2011; Saeedi, Dennis, & Costello, 2017; Santelices & Marquet, 1998), or the peak of species richness is not centred around the equator (Chaudhary, Saeedi, & Costello, 2016; Levinton & Mackie, 2013; Roy, Jablonski, Valentine, & Rosenberg, 1998). Furthermore, the shape and strength of the relationship often varies among basins or taxa (Astorga, Fernández, Boschi, & Lagos, 2003; Hummel et al., 2017; Macpherson, 2002) and can depend on the spatial scales examined (Willis & Whittaker, 2002). For instance, a large proportion of our knowledge on marine LDGs patterns comes from (1) studies based on meta-analyses of existing information rather than surveys using standardized methods (but see Navarrete, Lagos, & Ojeda, 2014; Rivadeneira, Navarrete, & Fernandez, 2002), (2) studies that focused solely on α -diversity and did not consider other components of diversity (but see Anderson, Tolimieri, & Millar, 2013; Navarrete et al., 2014) or (3) studies that focused on a specific taxonomic group (but see Bulleri et al., 2012).

Despite the myriad of studies describing LDGs, it is still unclear what drives these patterns (Brown, 2013) due to (1) the non-quantitative nature of existing hypotheses, (2) lack of integration among ecological and evolutionary hypotheses, (3) patterns of LDGs are concomitantly explained by different hypotheses and (4) intrinsic differences among ecosystems (Blowes et al., 2019; Brown, 2013; Pontarp et al., 2019). The many explanations that have been proposed fall into three broad categories of models, which are not necessarily exclusive, namely (a) ecological: processes operating over generational time-scales, such as ambient energy/productivity, environmental predictability/stability, interspecific interactions, niche breadth and spatial heterogeneity (Willig et al., 2003); (b) evolutionary: processes operating over geological time-scales that depend on the *time* for diversification, which on average have been longer in the tropics, where disruption of evolutionary processes owing to orogenic and glaciation cycles has been less important (Jablonski, Kaustuv, & Valentine, 2006) or (c) historical: processes also operating over geological time-scales but dependent on the *rate* of diversification, which is faster in the tropics since temperature may ultimately boost evolutionary rates (Mittelbach et al., 2007). Yet, before attempting to identify potential mechanisms underlying spatial and temporal patterns of diversity, those patterns that we are trying to explain must be clearly described (Underwood, Chapman, & Connell, 2000). Furthermore, and given that LDGs are not easily amenable to experimental manipulations (but see Cheng, Ruiz, Altieri, & Torchin, 2019 as a recent example), advancement in our

understanding of underlying causes mostly relies on our ability to improve the characterization of these patterns for different taxa, the biological attributes of the species and the characteristics of the environment they inhabit (e.g. Fernández, Astorga, Navarrete, Valdovinos, & Marquet, 2009). In this sense, rocky shores are ideal systems to study LDGs and their potential drivers because they (a) are easily accessible and sampling protocols have been standardized comprehensively; (b) encompass a terrestrial-marine gradient over relatively small distances; (c) have very diverse, abundant, macroscopic and sessile organisms belonging to various functional groups and (d) their natural history is generally well understood (Underwood, 2000).

Our specific goals in this paper were to test whether patterns of species diversity of rocky shore assemblages of South America (SA) (a) followed LDGs and (b) were consistent along the two oceanic coasts (i.e. Atlantic and Pacific). The simplest prediction was that, if evolutionary and historical processes operated in the same magnitude and direction, patterns of spatial variation in species diversity would be similar along the two coasts of SA independently of local and regional ecological processes. We also predicted that, if LDGs were produced by an environmental gradient related to latitude (i.e. temperature), then spatial variation of species diversity along the approximately 1,000 km of Southern Caribbean coast (which runs west to east and has essentially no latitudinal change) would be much lower than along similarly standardized segments of shore in any section of the Atlantic or Pacific coasts. Also, to test hypotheses derived from environmental models, we related the species composition of the intertidal rocky assemblages of SA with a suite of environmental and anthropogenic variables to examine potential mechanisms that may be responsible for spatial patterns. All of the above was done taking into consideration different components of diversity: α -, β - and γ -diversity, and incorporating three spatial scales: sites, regions and coasts, which allowed identifying potential processes responsible for observed patterns.

2 | MATERIALS AND METHODS

2.1 | Area of study

Surveys were done at a total of 143 rocky intertidal sites spanning 16 regions along each of the Pacific (50 sites) and Atlantic (62 sites) coasts of SA and one region along the Caribbean coast (31 sites) (Figure 1, Table S1). Arrangement of sites followed a hierarchically nested design that included five spatial scales: (a) coasts; (b) regions; (c) locations (haphazardly selected, separated by at least 5 km); (d) sites (haphazardly selected, separated by 500–2000 m) and (e) quadrats (0.25 m², $n = 10$ –30 depending on sites). Sampling was done during warm/dry seasons and spring tides, which did not occur at the same times in all regions. In addition, not all working groups were able to sample their sites during the same calendar year at the specific windows of time described above; consequently, sampling was

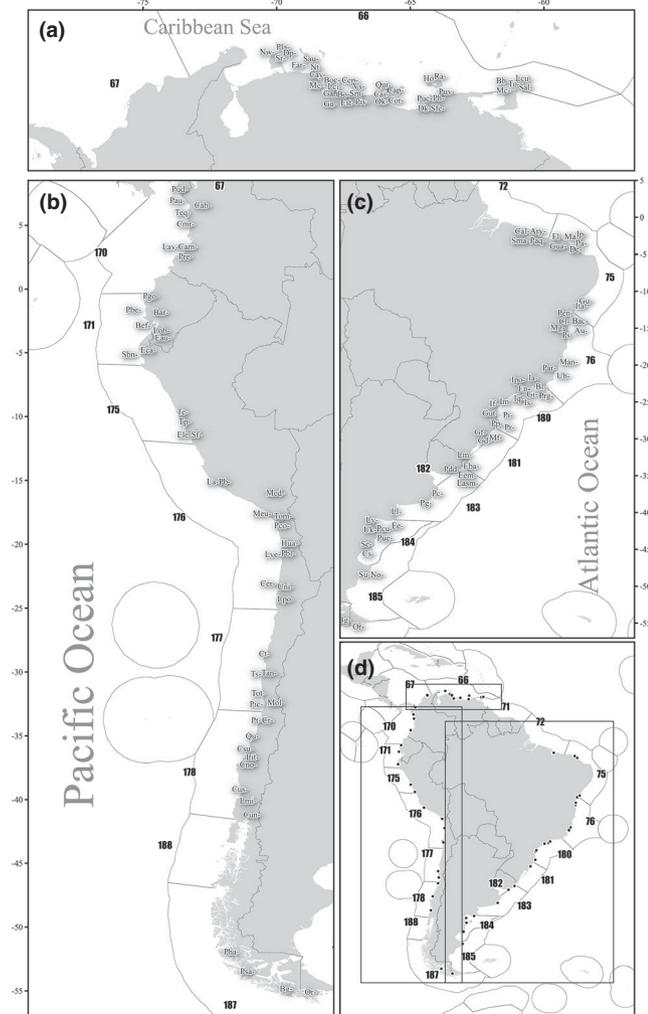


FIGURE 1 Sampling sites and locations along the South American coast. Rocky intertidal sites sampled along the (a) Caribbean Sea, (b) Pacific Ocean and (c) Atlantic Ocean. Locations and Regions (Spalding et al., 2007) are identified with black dots and bold numbers, respectively (d). Names and number of Regions are also listed in Table S1

completed between July 2010 and June 2012. Since the implementation of this sampling design depended on (a) the heterogeneous capabilities of the 27 working groups involved in this project and (b) accessibility and availability of sampling sites (i.e. rocky shores) in all 16 ecoregions; resulting sampling effort was not properly balanced at the scale of locations (number of locations per region ranged between 1 and 7). Consequently, all analyses were done only at the scales of regions and sites.

2.2 | Biological and environmental sampling

At each site, replicate quadrats were haphazardly located in two to three different intertidal strata defined according to tidal amplitude and known intertidal zonation of the regions (Milosavlitch et al., 2016), following the standardized NaGISA protocol (Cheng et al., 2019). Numbers of samples were defined on the basis of

species accumulation curves from pilot surveys done during 2009–2010. Pilot surveys were done in at least two sites per region, where 60 quadrats were sampled in two to three intertidal strata. Prior to data analyses, we confirmed that the selection of different sample sizes per site/region did not have an effect on our various estimations of diversity (Figure S1). Most identifications were made in the field, but in those cases when it was not possible to do so (some algae), back-up photographs were taken, and/or fauna specimens were collected for reference and sent to specialists for identification. All organisms were identified to the lowest possible taxonomic level (>95% to at least genus level). A data quality control protocol was applied at two different levels: within the specific working groups in each country/region and within the working group that centralized and compiled all datasets. All environmental data were derived from existing databases. In all, 21 environmental variables were examined to test for relationship with spatial variation of diversity. Variables were obtained for each sampling site from a variety of sources and categorized as ‘environmental’ or ‘anthropogenic’ (Table S2).

2.3 | Data analyses

2.3.1 | Latitudinal changes in species composition along coasts

The complete list of taxa considered in this study is available in Table S3. All analyses described below were done on presence/absence of taxa pooled over all samples from each site because it is well known that small quadrats represent only a small fraction of the species at a given site. After pooling, the Sorensen's similarity coefficient was estimated over each pair of sites to test for latitudinal changes in species composition along coasts by means of an ordered rank-based two-way nested ANOSIM, using the factors ‘coast’ (un-ordered with two levels: Pacific and Atlantic) and ‘region’ (an ordered factor from north to south and nested in ‘coast’). This analysis was not done for the Caribbean as there was only one region. Patterns of similarities were visualized with non-metric multidimensional scaling (nMDS). These analyses were done using the software PRIMER v7 (Clarke, Gorley, Somerfield, & Warwick, 2014). We also estimated the total dissimilarities between the Caribbean region, Atlantic and Pacific coasts, as well as between sites within each coast, and then decomposed those dissimilarities into two additive components that reflect two antithetic processes: (a) turnover of species, caused by replacement of species as a possible consequence of niche partitioning and (b) nestedness, caused by species loss along a gradient, which is a potential result of physiological constraints or dispersal capabilities of different species (Baselga, 2010, 2012). Making this decomposition is essential to discern between the processes that maintain patterns of species diversity among and within coasts. For this purpose, we used Baselga's framework, a conceptual approach widely discussed and validated in different biogeographical contexts (Baselga & Leprieur, 2015; Lu, Vasseur, & Jetz, 2019). This framework involves breaking down the β -diversity (Sorensen similarity)



into the equivalent of turnover (using as metric the Simpson's coefficient of similarities) and nestedness (using the Baselga's coefficient of nestedness). This analysis was done with the R package 'betapart' (Baselga & Orme, 2012).

2.3.2 | Latitudinal variation in components of species diversity along coasts and regions

γ -diversity and α -diversity were estimated as the total number of expected species per region and site, respectively, using the second-order Jackknife method (Chapman & Underwood, 2009). Preliminary analyses showed that Jackknife method gave similar results to Chao's. β -diversity, defined as 'the extent of change in community composition', can be estimated in several ways at different spatial scales (Anderson et al., 2011). We used multivariate dispersion as an estimator of average β -diversity for two spatial scales: (a) site and (b) region. For these, the Sorensen's similarity coefficient among each pair of samples was estimated, then the average distance of each sample of a site to the site centroid in the Sorensen space was calculated, as well as the average distance of each site centroid within the region centroid (Anderson et al., 2011). To identify LDGs in γ , α , site β -diversity and region β -diversity, the estimates were plotted against latitude. In addition, and since the Pacific and Atlantic coasts are at least six times longer than the Caribbean coast, estimators of α and site β -diversity were plotted over a standardized length of coast (i.e. 1,000 km). We also formally evaluated whether patterns of variation of these components of species diversity along the latitudinal gradient were consistent on both coasts. For this purpose, we used ANCOVA, with 'latitude' as the covariate, and 'coast' the main factor. When it was detected that the relationship was not linear, local polynomial regression was used instead. For these analyses, only the taxa identified to species or genus were considered (>95% of reported taxa).

In addition to the conventional measures of species diversity, we calculated the *Average taxonomic distinctness* (Δ^+) (Clarke & Warwick, 1998), using the software PRIMER v7 (Clarke et al., 2014). For these calculations, we assumed that the taxonomic trees were good surrogates of their phylogenetic relatedness and estimates were made separately for each phylum (Ellingsen, Clarke, Somerfield, & Warwick, 2005; Warwick & Somerfield, 2008). Average taxonomic distinctness (Δ^+) was complemented with estimations of variation in taxonomic distinctness (Λ^+) (Clarke & Warwick, 2001). Δ^+ is an estimator of taxonomic breadth of the sample, whereas Λ^+ can be used to describe the taxonomic structure of a sample (Clarke & Warwick, 2001). These estimators were used as proxies for the relative importance of ecological, evolutionary and historical processes in determining LDGs. As proposed by Rivadeneira et al. (2011), we interpreted that negative latitudinal relationships with Δ^+ were the result of high diversification rates near the equator, positive relations were the result of higher diversification towards temperate regions, while no relationship indicated that local ecological constraints (e.g. niche partitioning) have dominated over latitudinal processes.

2.3.3 | Species composition and environmental variables

The total variation among sites within each coast was partitioned using distance-based linear models to identify potential environmental drivers of species diversity patterns. After assessing collinearity, marginal tests for each variable were done using simple linear regression and the hypothesis of no relationship was tested using 9,999 permutations of raw data. Subsequently, linear models with multiple predictors were generated using all possible combinations of statistically significant predictor variables, from the simplest model (one variable) to the most complex (all variables), using as a criterion of choice the lowest value of the modified Akaike Information Criterion (AICc). These analyses were done using the routine DistLM in the software PERMANOVA (Anderson, Gorley, & Clarke, 2008).

3 | RESULTS

3.1 | Latitudinal changes in species composition along coasts

The composition of assemblages clearly differed across coasts (two-way ANOSIM, $R = 0.411$, $p < 0.001$) and varied with latitude on both coasts (two-way ANOSIM, $R^0 = 0.714$, $p < 0.001$). On the Pacific, sites from the Panama Bight and Guayaquil regions clearly differentiated from the rest of southern regions (Figure 2), whereas sites from Central Peru to Chilean Fjords were more similar, but still formed part of the latitude gradient (Figure 2). On the Atlantic, the Brazilian sites were distinct from sites of the southern cone, but these also followed a latitudinal pattern. However, the Amazonian sites did not conform to the same trend, being more similar to regions such as Rio Grande and SE Brazil despite these being the most tropical regions of this coast (Figure 2). The Caribbean sites were clearly separated from the oceanic coasts, being more similar, unsurprisingly, to the tropical regions of the Atlantic coast of SA than the Pacific (Figure 2, Table 1a). Even so, total dissimilarity between the Caribbean coast and the Atlantic coast was higher than expected (Table 1a), sharing only a small fraction of its species (~8% of taxa identified at the species level). This pattern was strengthened by including taxa identified to higher taxonomic resolutions (i.e. genera) (Table 1a). Analysis at the scale of sites within the Pacific and Atlantic coast showed that most (>90%) changes in species composition were due to turnover of species rather than nestedness (Table 1b), indicating that no gradual loss in the total number of species occurred along the latitudinal gradient and that changes were due largely to replacement of species.

3.2 | Latitudinal variation in components of species diversity along coasts and regions

Patterns of latitudinal variation of γ -diversity differed between oceans (Figure 3). In the Pacific, γ -diversity was highest in the Guayaquil region,

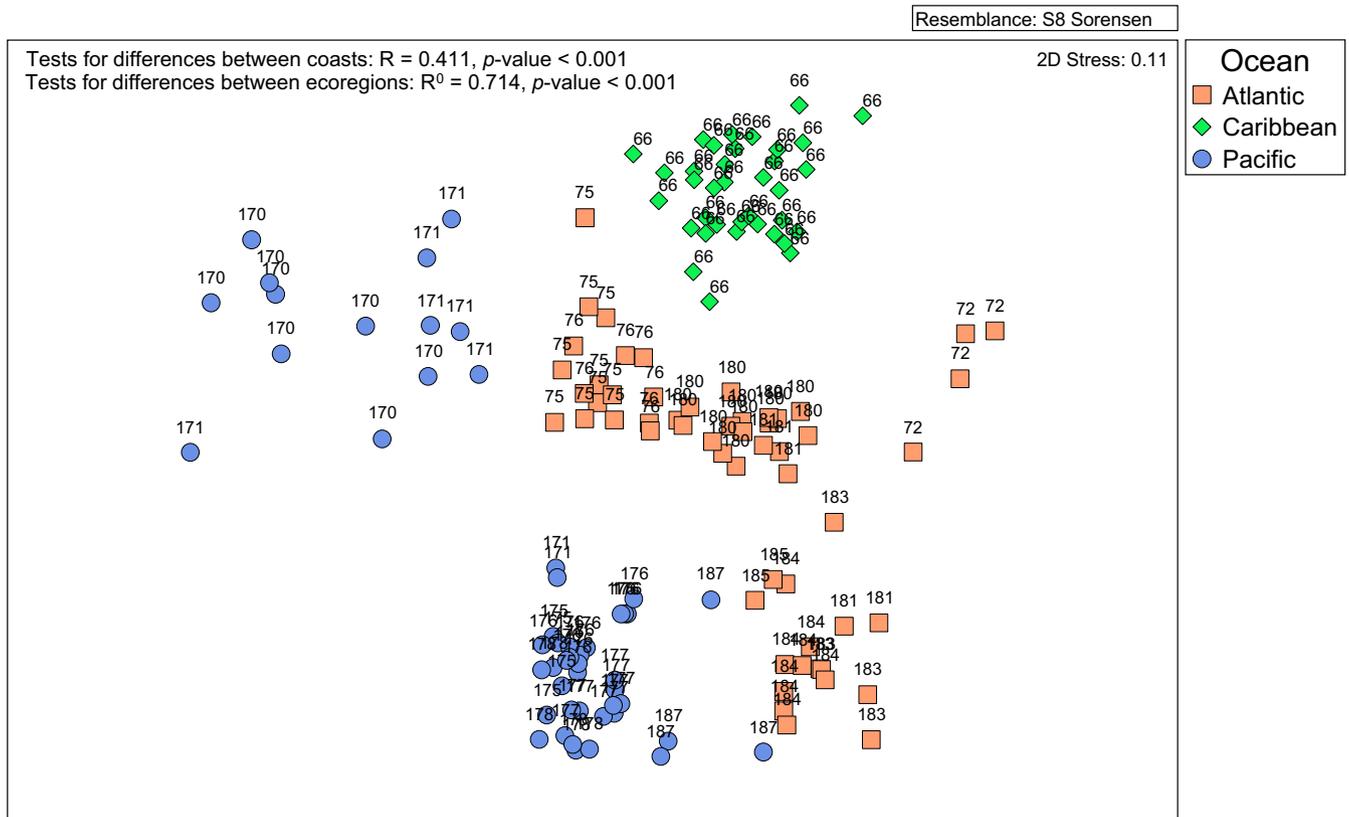


FIGURE 2 Non-metric multidimensional scaling (nMDS) of centroids of sites (based on Sorensen similarity matrix) across different Regions in the Atlantic and Pacific coasts of South America. Regions (numbers) are shown from north to south. Names and number of Regions are also listed in Table S1

TABLE 1 Total multi-site Sorensen dissimilarity and decomposition in turnover and nestedness components

a. Between Southern Caribbean and oceanic coasts						
South Caribbean	Atlantic		Pacific			
	All taxa	Species	All taxa	Species		
Total	0.88	0.85	0.98	0.98		
Turnover	0.81	0.69	0.97	0.96		
Nestedness	0.07	0.16	0.01	0.02		
b. Within each coast of South America						
	Atlantic		Pacific		South Caribbean	
	All taxa	Species	All taxa	Species	All taxa	Species
Total	0.97	0.97	0.96	0.96	0.95	0.93
Turnover	0.96	0.95	0.95	0.94	0.93	0.90
Nestedness	0.01	0.02	0.01	0.02	0.02	0.03
No of sites	58	58	49	49	36	36
No of taxa/species	484	276	400	286	240	88

Note: Analyses are presented for all taxa, regardless of the taxonomic resolution, and for those identified at the species level. Number of sites, taxa and species are shown.

whereas the two lowest values were found in the adjacent regions: the tropical Panama Bight and Central Peru regions. On the Atlantic, γ -diversity was highest at Eastern Brazil, with the smallest pool of

species observed in the Amazonia and Patagonian Shelves. Notably, the regional pool of species in the Caribbean region was as high as the richest regions from the Atlantic and Pacific oceans (Figure 3).

FIGURE 3 γ -diversity per region, estimated with second-order Jackknife method. Black portion of columns represents number of taxa identified at level of species, grey represents taxa identified at genus, white portion indicates not-observed species. Ecoregions according to Spalding et al. (2007)

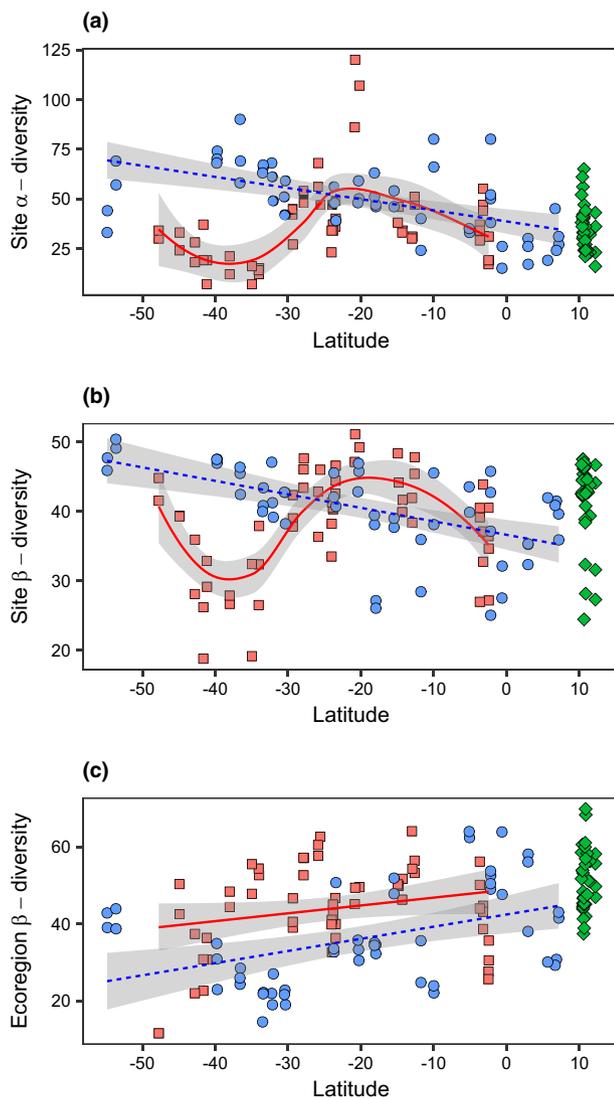
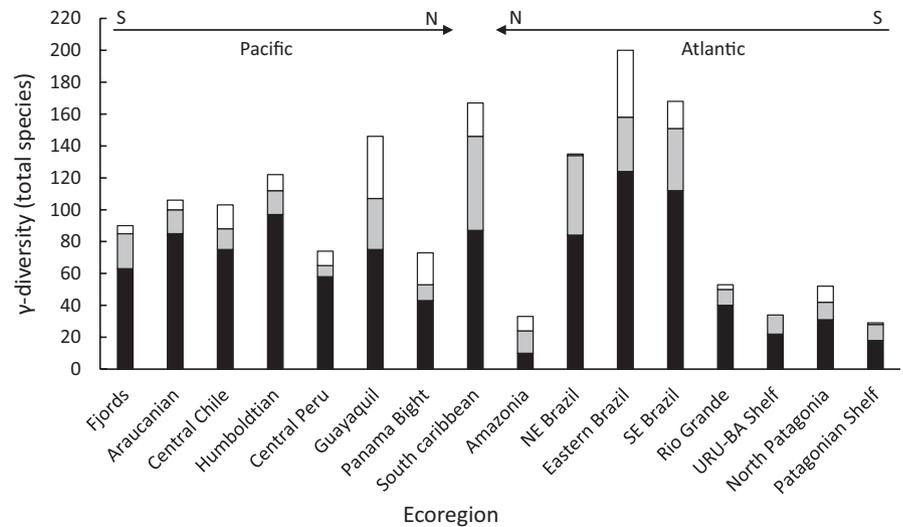


FIGURE 4 Relationships among latitude with α -diversity (a), site β -diversity (b) and region β -diversity (c) of rocky shore assemblages in the Atlantic (grey circles), Pacific (black squares) and Caribbean coasts (empty diamonds)

Patterns of spatial variation of α -diversity along the latitudinal gradient of SA were not the same in both oceans (Figure 4a). Along the Pacific coast, there was a relatively steady decline in the α -diversity from the southernmost end of the continent towards the equator, following a marked inverse latitudinal gradient of species richness (Figure 4a). In contrast, the number of species per site along the Atlantic coast did not follow a simple general pattern, with distinct trends apparent in different segments of the latitudinal gradient (Figure 4a). Across all subtropical and tropical regions (29°S and 10°N), the number of species per site showed a clear unimodal pattern, peaking at 20°S and decreasing to the south and north (Figure 4a). Further south, α -diversity followed a strong gradient, decreasing from the very south (47°S) towards latitude 32°S, which coincides with the biogeographical barrier of the La Plata River estuary mouth. Notably, the Caribbean coast showed large variation in α -diversity (between 18 and 71 species per site), despite the fact that all the sites on this coast were essentially at the same latitude but dispersed over 1,000 km (Figure 4a). Figure 4a also shows that variation in α -diversity was about three-quarters of the variation observed in the Pacific coast (between 18 and 90 species per site) and about half of the variation observed in the Atlantic coast (between 12 and 122 species per site) (Figure 4a). However, when α -diversity per site was compared over a standardized (i.e. 1,000 km) coast length (to account for differences in the lengths of the coasts that were sampled), variation was very similar on all three coasts of SA (Figure S2a) indicating the importance of spatial variability rather than latitude per se.

Site β -diversity showed similar trends to those of α -diversity on both oceanic coasts (Figure 4b). Along the Pacific coast, there was a clear linear inverse latitudinal gradient (Figure 4b), whereas along the Atlantic coast, the relationship was nonlinear and bimodal in shape, with peaks at 55°S and 20°S and lowest values near 40°S and 5°S. Interestingly, variation of β -diversity measures within sites along the Caribbean coast was within the same range as those described for standardized stretches (i.e. 1,000 km) of the oceanic coasts of SA (Figure S2b). Furthermore, we estimated that our sample coverage was well over 80% (Figure S3), which indicates that the number of species registered by each taxon and locality reflects very well the

diversity of species registered in each region. Consequently, we consider that the relationships of α - and β -diversity on both coasts reflect a natural property of the diversity along the continent rather than being an artefact caused by unbalanced sampling effort within each region (Ulrich et al., 2017).

Contrary to site β -diversity, variability among sites within regions (i.e. region β -diversity) increased linearly towards the tropics on the Atlantic and Pacific coasts (Figure 4c), and this occurred to a similar degree on both coasts (ANCOVA, interaction Latitude \times Ocean, $F = 0.58$, $p = .16$). Although the main factors in this analysis (i.e. latitude and coast) were statistically significant (Latitude $F = 10.67$, $p < .001$ and Ocean $F = 15.50$, $p < .001$), these two sources of variation explained only 27% of the entire variation (7% latitude, 20% coast). Most of the variation in β -diversity corresponded to the residual component (73%), which indicates intrinsic differences among sites within a region.

Latitudinal patterns of change in Δ^+ and Λ^+ differed among Phyla (Figure 5). For mollusks, Δ^+ values were constant along latitude although clearly higher in the Atlantic than in the Pacific (Table S4, ANCOVA for mollusks, covariate Latitude, $p > .05$), even when richness of mollusks was higher in the later. However, Λ^+ increased

towards temperate latitudes with the same slope on both oceanic coasts (Table S4, ANCOVA for mollusk, covariate Latitude, $p < .05$), with higher values for the Pacific compared to the Atlantic. Despite the small latitudinal range in the Caribbean, both Δ^+ and Λ^+ were as variables as on the Pacific and Atlantic coasts. For crustaceans, Δ^+ was positively related ($p < .05$) to latitude, with the same slope in the Atlantic and Pacific coast (Table S4). On the other hand, Λ^+ of crustaceans was not related to latitude and was similar, but variable, between coasts (Table S4, Figure 5b). As with mollusks, no clear relationship of Δ^+ of cnidarian with latitude was detected (Table S4), although Λ^+ was positively related to latitude, with the same slope on both coasts (Table S4, Figure 5b). On the other hand, Δ^+ for Ochrophyta (brown algae) and Rhodophyta (red algae) were inversely related with latitude, even when the number of species per site did not vary with latitude. Such change in Δ^+ was consistent along Atlantic and Pacific coasts. For Ochrophyta, the range of variability in Δ^+ in the Caribbean was considerably smaller than in the other two coasts, although comparable in magnitude. Conversely, Rhodophyta in the Caribbean tended to have lower values of Δ^+ but these were more variable than for sites from Atlantic and Pacific

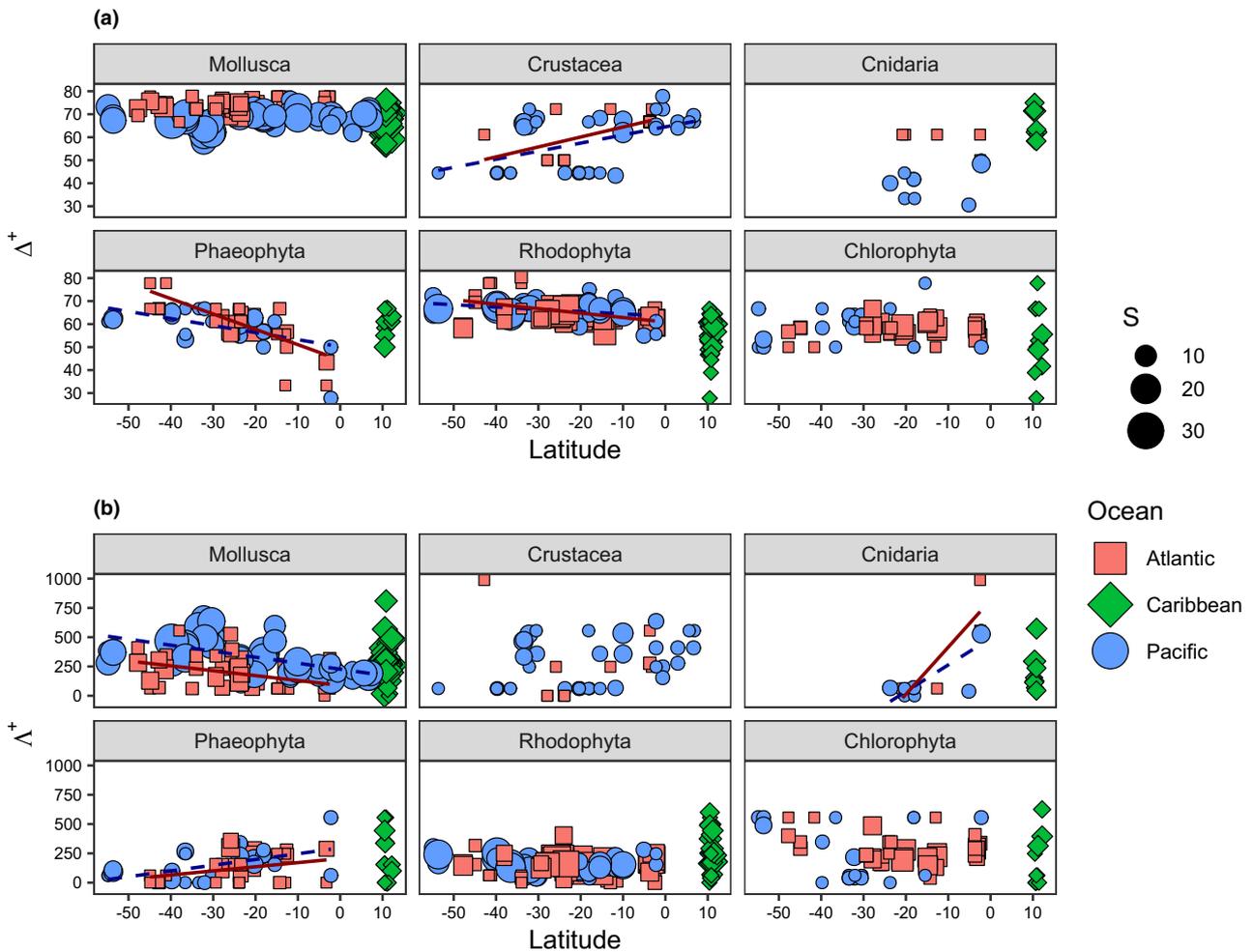


FIGURE 5 Average (Δ^+) and variation (Λ^+) in taxonomic distinctness of rocky shore assemblages for each Phylum between -60° and 10° along South American Coasts. Sizes of the symbols represent the number of species at each site. Lines represent the respective linear regression fitting

coasts. Finally, neither Δ^+ nor Λ^+ of Chlorophyta was related to latitude and did not differ between coasts.

3.3 | Species composition and environmental variables

The environmental variables that best explained patterns of variation of rocky shore assemblages along the SA coasts differed between oceans (Table 2). For the Pacific, around 55% of total variation in species composition was explained by 10 environmental variables. From these, the most important was the annual average sea surface temperature (SST). This variable alone explained 12% of total variation (i.e. $R^2 = 0.12$, Table 2) and was the variable with the highest correlation with latitude ($r = 0.96$, Table S5). Annual average chlorophyll a ($R^2 = 0.09$), pollution ($R^2 = 0.08$) and acidity ($R^2 = 0.08$) accounted

for the individual highest portions of explained variation. These four variables, together with nutrients, UV, annual anomalies of SST and annual anomalies of chlorophyll a were included in models with very small differences in their AICc values (<0.8).

For the Atlantic, about 52% of variability in species composition was explained by 10 variables. As in the Pacific, the most important variable was the annual average SST, accounting for 12% of total variability (Table 2), and again being highly correlated with latitude ($r = 0.96$, Table S5). Tide range was the second most important environmental variable ($R^2 = 0.10$), followed by nutrients and shipping ($R^2 = 0.07$ for both, Table 2). Other variables such as annual anomalies of SST, UV, population and inorganics accounted individually for 7%–9% of total variation. All these variables were positively correlated with latitude (Table S5).

On the Caribbean coast, up to 34% of the variation in species composition among sites was explained by environmental variables. Most of the best linear models included six variables, with annual tide

TABLE 2 Distance-based multivariate linear model analyses (DistLM) showing predictor variables that explained patterns of spatial variation of species composition along the Pacific, Atlantic and Caribbean coasts of South America

a. Marginal test								
Variable	Pacific		Variable	Atlantic		Variable	Caribbean	
	p value	R^2		p value	R^2		p value	R^2
SST_average	0.001	0.12	SST_average	0.001	0.12	Tide_range	0.001	0.09
Chl a _average	0.001	0.09	Tide_range	0.001	0.10	Chl a _desvest	0.001	0.09
Acid	0.001	0.08	SST_desvest	0.001	0.09	AC	0.001	0.09
ORP	0.001	0.08	Log(NUTC)	0.001	0.07	Chl a _average	0.001	0.08
Chl a _desvest	0.001	0.08	SH	0.001	0.07	UV	0.001	0.08
SST_desvest	0.002	0.06	AC	0.001	0.07	ORP	0.001	0.07
Tide_range	0.002	0.05	ORP	0.001	0.07	SH	0.001	0.07
UV	0.003	0.05	SST_anomalies	0.001	0.07	SST_desvest	0.002	0.06
Log(NUTC)	0.004	0.05	Chl a _average	0.001	0.06	SST_anomalies	0.001	0.06
INP	0.004	0.05	UV	0.001	0.06	Log(NUTC)	0.002	0.05
SH	0.007	0.04	Chl a _desvest	0.001	0.06	SST_average	0.005	0.05
SST_anomalies	0.016	0.04	INP	0.001	0.06	HUM	0.007	0.05
HUM	0.025	0.03	HUM	0.001	0.05	INP	0.013	0.05
Chla_anomalies	0.102	0.03	Chl a _anomalies	0.476	0.02	Chl a _anomalies	0.093	0.04
b. Overall best solutions								
Coast	AICc	R^2	No. Variables	Selections				
Pacific	409.40	0.55	10	SST_average, Chl a _average, AC, ORP, Chl a _desvest, Tide_range, UV, SH, SST_desvest, HUM, SST_anomalies				
Atlantic	454.11	0.52	10	SST_average, Tide_range, SST_desvest, Log(NUTC), SH, AC, SST_anomalies, Chl a _average, ORP				
Caribbean	290.86	0.34	6	Tide_range, Acid, Log(NUTC), INP, SST_desvest, SST_average				

Note: From 18 environmental variables, 7 were excluded from the analyses because collinearity (Pearson coefficient of correlation >0.8). Analyses include (a) marginal tests for each variable, presented in decreasing order of relevance based on the coefficient of determination R^2 and the associated p value obtained with 9,999 permutations; (b) model selection for the best combination of individual variables based on the lowest AICc value (i.e. modified Akaike Information Criterion). For each coast, the overall four best solutions are presented from highest R^2 to the lowest. Acronyms correspond to those in Table S2.

range the best correlated ($R^2 = 0.09$), followed by acidity ($R^2 = 0.09$) and nutrients ($R^2 = 0.18$). Unlike on the two oceanic coasts, SST in the Caribbean explained only a small portion of total variability in species composition ($R^2 = 0.06$).

4 | DISCUSSION

Despite differences in the composition of rocky shore assemblages between the Atlantic and Pacific coasts of SA, our general results were common to both coasts. Specifically, (a) latitudinal variation in species composition was driven primarily by species turnover, (b) LDGs in regional-scale species richness were similar (Figure 3) and (c) no LDGs in species richness occurred at the site scale (although patterns of latitudinal variation differed between coasts; Figure 4). In general, the structure and composition of assemblages associated with intertidal rocky shores of SA followed expectations derived from the Rigby Iken and Shirayama (2007) model of ecoregions, which states that latitudinal patterns of regional β -diversity are dominated by turnover (species replacement) rather than nestedness (species loss). On all three coasts, patterns of spatial distribution of diversity showed contrasting patterns of spatial distribution depending on the scale that was considered (regional versus site).

4.1 | Regional-scale species richness

The regional-scale LDGs observed on the Atlantic and Pacific coasts of SA were not monotonic. The analysis of discontinuities in these patterns suggests controls on regional species richness that likely interact with the alleged climate-related controls on evolutionary or historical diversification processes (Belanger et al., 2012).

In the Pacific, the highest estimates of γ -diversity occurred in the tropical Guayaquil ecoregion (Latitude: 0° – 6° S), followed by the Humboldtian ecoregion (12° S– 25° S). The Guayaquil ecoregion is the zone where the Panama and Humboldt currents converge, which promotes high biological diversity due to temperate and tropical species co-existing (Miloslavich et al., 2011). The Humboldtian ecoregion is under the influence of the southern Pacific upwelling system, which injects nutrients into surface waters leading to high primary production and diverse food webs (Thiel, Macaya, & Acuña, 2007). Conversely, the lowest estimates of γ -diversity occurred in the tropical ecoregions of Panama Bight and Central Perú. Aside from these regional diversity minima, there was a trend of increased γ -diversity from the southernmost ecoregions to Guayaquil.

In the Atlantic, two clear coastal segments can be differentiated: the first ranges from the Patagonian to the Rio Grande ecoregion (Latitudes: 30° S– 50° S), and the second ranges from the SE Brazil to the Amazonian ecoregion (Latitudes: 5° N– 20° S). In the first segment, γ -diversity was generally lower than in the second and varied little across ecoregions. In the second segment, γ -diversity shows a hump-shaped pattern, peaking at the Eastern Brazil ecoregion (Latitudes: 15° S– 25° S), which is under the influence of the Cabo Frio

upwelling (Coutinho et al., 2016). Decreases in γ -diversity towards the north and south of this second segment could be associated with the influence of two large estuarine systems (Amazon River and Los Patos Lagoon, respectively; see Cavalcante Morais & James, 2014; Coutinho et al., 2016) and/or the relative scarcity of rocky shores (Cavalcante Morais & James, 2014; Pellizzari, Vélez-Rubio, Cristine-Silva, & Carranza, 2016). Colonization and diversification in these coastlines could have also been limited due to increased environmental variability and/or the relative isolation of their rocky habitats, which could have limited dispersal across patches (Pellizzari et al., 2016).

4.2 | Local-scale species richness

Patterns of latitudinal variation in α -diversity did not conform to LDG predictions for the Atlantic or Pacific coasts, and generally differed between them. In the Pacific, we observed decreasing α -diversity with decreasing latitude—that is, an *inverse* LDG; see Rivadeneira et al. (2011). This is in line with previous findings on the latitudinal diversity of particular taxonomic groups (seaweeds, peracarid crustaceans) along the temperate Pacific coast (see Rivadeneira et al., 2011; Santelices & Marquet, 1998). Yet, our findings illustrate that an inverse latitudinal gradient of α -diversity in rocky shore assemblages extends into the tropical Pacific, which has not been previously reported.

In the Atlantic, we also observed an inverse latitudinal gradient of α -diversity, but from the southernmost end to 35° S. This is consistent with previous findings on macroalgae (Liuzzi et al., 2011) and points to the ubiquity of inverse latitudinal gradients along the temperate South American coasts (see also Rivadeneira et al., 2002; Rivadeneira et al., 2011; Santelices & Marquet, 1998; Valdovinos et al., 2003). In contrast, α -diversity showed a hump-shaped pattern from 35° S to the Equator, peaking at ca. 20° S latitude (like γ -diversity which peaked at the Eastern Brazil region). This further supports the existence of subequatorial peaks in marine diversity, as revealed by a recent meta-analysis (see Chaudhary et al., 2016).

Distinct mechanisms have been proposed to explain the inverse α -diversity gradients for particular taxa, including the Rapoport rule for algae (Santelices & Marquet, 1998), larval developmental modes for crustaceans and mollusks (Astorga et al., 2003; Fernández et al., 2009) and historical/evolutionary effects for peracarids (Rivadeneira et al., 2011). In agreement, our examination of taxonomic distinctness (Δ^+) revealed that latitudinal biodiversity patterns differ among taxa. Crustaceans showed greater Δ^+ towards the tropics (see also Astorga et al., 2003). In contrast, brown algae showed higher Δ^+ towards temperate zones, which matches global patterns of diversity for this group (see Keith, Kerswell, & Connolly, 2014), but higher levels of Δ^+ towards the tropics. This suggests a higher degree of diversification towards the south, but an increasing degree of speciation for some groups towards the tropics (e.g. Dictyotaceae). Unlike these taxa, mollusks and red algae (the most species-rich groups) showed a Δ^+ that remained invariant with latitude. The fact that taxonomic breadth (a proxy for



diversification) did not change with latitude along either coast provides evidence against historical and evolutionary models as primary drivers of latitudinal diversity patterns in these taxa.

Since different mechanisms seem to explain inverse LDGs for individual taxa, no general process can be postulated to explain the occurrence of inverse LDGs in the taxonomically broad assemblage studied here. As discussed below, the latitudinal patterns of rocky shore α -diversity documented here are likely shaped by the interplay of large-scale historical/evolutionary processes determining the regional species pool and local ecological factors driving species dispersal, colonization and survival.

4.3 | Regional and local controls on species richness

In the light of our findings, the diversity of South American rocky shore assemblages at the local scale can be viewed as being constrained by the regional species pool, but ultimately determined by small-scale and site-specific ecological processes (see also Keith et al., 2014; Rivadeneira et al., 2002). Here, the highest γ -diversity was observed in ecoregions influenced by the convergence of oceanic currents or upwelling systems (i.e. Guayaquil, Humboldtian, Eastern Brazil; see also Coutinho et al., 2016; Lara et al., 2019; Rivadeneira et al., 2015). Yet, site-scale β -diversity was also the highest in these ecoregions. This indicates high differentiation of assemblages among sites, possibly attributable to small-scale variations in ecological processes.

Two additional lines of evidence point to the importance of local processes in determining local-scale diversity across South American rocky shores. First, latitudinal variations in site-scale β -diversity are dominated by species turnover both in the Pacific and Atlantic coasts. This means that species replacement is even across sites located within the same ecoregion. Second, variations in α - and β -diversity were observed across sites of the Caribbean coast, despite their small latitudinal spread (less than 0.5°). Such variations (i.e. across sites in the Caribbean) were comparable to those across the oceanic coasts of SA, and also dominated by turnover. This implies that local factors can cause substantive variation in local assemblage composition even where larger-scale latitudinal controls (e.g. temperature gradients) are clearly negligible such as on the Caribbean coast, as found over similar spatial scales on Australasian rocky shores (Glasby, Gibson, & Cruz-Motta, 2017; Lloyd, Cruz-Motta, Glasby, Hutchings, & Gribben, 2020).

Our analyses of assemblage composition in relation to environmental variables shed light on possible controlling factors both at the regional and local scales. Significant, regional-scale factors included SST and chlorophyll *a* concentration. SST explained the highest amount of variation in local assemblage composition on both the Pacific and Atlantic coasts, which suggests a primary role of temperature in controlling species diversification and current distributions (see also Levinton & Mackie, 2013 for an example on fiddler crabs). On the other hand, Chlorophyll *a*, an indicator of primary production, was also a significant factor explaining variability in

biodiversity on all coasts, which supports the hypothesis that convergence of oceanic currents and upwelling systems promote high biological diversity at the regional scale (Miloslavich et al., 2011). But overall, and despite the influence of these two regional processes (temperature and primary productivity), an important part of the variation was explained by a large group of variables that included a combination of natural factors (e.g. tides and nutrients) and anthropogenic stressors, such as pollution, ship traffic and human population density. This was especially conspicuous in the Caribbean where there was no relationship with SST. Hence, it could be provisionally stated that temperature and primary production appear to shape the biodiversity of South American rocky shores at the regional scale, while local-scale variation in biodiversity is associated with human impacts and, possibly, other environmental variables not included in our analysis (e.g. local wave exposure, desiccation levels and rock properties).

4.4 | Concluding remarks

The regional structure and composition of South American rocky shore assemblages displayed positive LDGs along the Pacific and Atlantic coastlines. In contrast, local α -diversity tended to increase towards the south (i.e. negative LDGs). These opposing patterns indicate that regional β -diversity, which is higher towards the tropics, could offset the inverse latitudinal gradients of local species richness, leading to overall LDGs at the regional scale. The dominance of species turnover as a source of site-scale β -diversity, together with the relatively high variations in α -diversity along the Caribbean coast, indicates that local processes are important sources of variation in assemblage composition regardless of any large-scale and/or latitudinal controls. SST gradients and primary productivity hotspots (i.e. upwelling and convergence zones) account for significant variation in assemblage composition and are likely major influences on large-scale, evolutionary and historical diversification processes. Yet, a variety of local environmental factors also contribute to the compositional variation of local rocky shore assemblages (e.g. anthropogenic variables such as pollution, ship traffic and nearby human population density). This suggests that the analysis of species diversity patterns at continental scales cannot ignore small-scale ecological processes in the search of a robust, general understanding. As pointed out by Simberloff (2004), we should embrace the view that 'small-scale' ecology can be crucial for explaining many macroecological patterns, like those reported here.

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DATA AVAILABILITY STATEMENT

Detailed information about records and geographic distribution of each species is available online at OBIS (<http://ipt.iobis.org/carib-beanobis/resource?r=sarce-rockyshores>). Supplementary Table 1 contains the complete list of species and taxa used in this study.

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BIOSKETCH

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Author contributions: J.J.C.M and P.M. conceived the general idea and coordinate the research group (SARCE), and together with C.M., S.A.N., A.A.V.F, G.P. and F.B. designed the study. J.J.C.M and E.G. performed the analysis and led the writing of the manuscript. A.H.A and C.H. compiled and curated the dataset. F.B., S.A.N., R.D.S., T.M.G. and J.L.G. substantially contributed to the core versions of this manuscript. All authors commented and provided important inputs to the final versions of this manuscript. All authors, except C.M., T.M.G. and E.K.S., contributed with data.

SUPPORTING INFORMATION

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

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