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Calcareous defence structures of prey mediate the effects of predation and biotic resistance towards the tropics

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Abstract

Aims: The importance of biotic interactions in creating and maintaining diversity is expected to increase towards low latitudes. However, the way in which predation affects diversity can depend on how predators mediate competitive interactions and also on defensive traits of prey. Here, we assessed the role of physical defences of prey to escape predation and how the importance of predation on community structure and diversity changes across latitude.

Location: Six sites, in three regions distributed across 45 degrees of latitude in the Atlantic Ocean: a tropical region in Angola, a subtropical region in Brazil and a temperate region in Wales, UK.

Methods: We manipulated predation on marine sessile communities, using exclusion cages and assessed community parameters, including their susceptibility to biological invasion during early and advanced succession.

Results: Predation was more intense in the tropics and in advanced communities suggesting that predation effects increase through time. In the tropical region, predators reduced the number of co-occurring species and beta diversity, limited the occurrence of exotic species and promoted a change in the identity of the dominant organisms, replacing soft-bodied organisms with calcified animals. In the subtropical region, predation promoted a similar trait-mediated change in the identity of dominant prey, although it was not strong enough to affect diversity and did not prevent bioinvasion. In the temperate region, other processes than predation seem to drive the community organization and resistance to invasion.

Main conclusions: Our results support both Biotic Interaction and Biotic Resistance Hypotheses, showing that the importance of predation to biodiversity increases towards the tropics. In addition, where predation is intense, morphological traits of prey drive the final structure and dominance in the community. Our results suggest that physical defences are the main traits preventing predation, perhaps explaining why calcified organisms are among the most common invasive species in coastal habitats.

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KEYWORDS

alien species, Atlantic Ocean, beta diversity, Biotic Interaction Hypothesis, diversity, fouling communities, functional traits, latitude, structural defences

1 | INTRODUCTION

The Biotic Interaction Hypothesis (BIH) predicts that the importance of biotic interactions in determining diversity increases from high to low latitudes (Freestone, Osman, Ruiz, & Torchin, 2011; Roslin et al., 2017; Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009). Over both evolutionary and ecological time-scales, these interactions are considered to promote diversity by speciation and support coexistence by niche compression (Usinowicz et al., 2017), while physical conditions and historical enrichment from the regional pool of species are thought to drive diversity at high latitudes (Freestone & Osman, 2011). Because biotic interactions can locally control diversity in tropical communities, they could be less susceptible to biological invasion than communities from temperate zones (Biotic Resistance Hypothesis—BRH) (Elton, 1958; Kimbro, Cheng, & Grosholz, 2013; Levine, Adler, & Yelenik, 2004).

Although the BIH is seen as a general rule to explain diversity patterns at a global scale, being supported by several lines of evidence (Schemske et al., 2009), its validity has been questioned (Moles & Ollerton, 2016; Moles et al., 2011), since the studies investigating the intensity and importance of biotic interactions along the latitudinal gradient have shown contrasting results with positive (Freestone et al., 2011; Kremer & Rocha, 2016; Longo, Hay, Ferreira, & Floeter, 2019), negative (Chen, Hemmings, Chen, & Moles, 2017) or no general correlation (Cheng, Ruiz, Altieri, & Torchin, 2019; Lavender, Dafforn, Bishop, & Johnston, 2017; Poore et al., 2012) between latitude and the importance of interactions. However, the number of studies investigating the BIH hypothesis is limited and the discussion is far from being closed. Therefore, instead of seeing it as a non-valid hypothesis, or even as a zombie idea (Moles & Ollerton, 2016), it is more useful to investigate when the hypothesis does and does not apply and which processes may modulate biotic effects with latitude.

Intense predation can disrupt competition, thus promoting coexistence (Chase et al., 2002; Menge & Sutherland, 1976) and increasing diversity (Schemske, 2009; Schemske et al., 2009). For example, positive effects of predation on diversity can take place when predators feed on dominant competitors and prey communities show a transitive competitive hierarchy with a trade-off between competitive ability and predation resistance, as experimentally demonstrated by Connell (1961). However, this is one of the many possible scenarios regarding the combined effects of predation and competition on diversity (Chase et al., 2002). The diversity of scenarios may explain the lack of agreement observed in empirical studies regarding the effects of biotic interactions on diversity across latitudes (Freestone et al., 2011; Lavender et al., 2017; Roslin et al., 2017). Alternatively, intense predation, directed at rare species (Almany & Webster,

2004; Spiller & Schoener, 1998), or at a subset of species regardless of their competitive ability, would result in an opposite pattern, preventing coexistence and decreasing diversity by allowing stronger competitors to dominate. Therefore, depending on the nature of the interactions, competition and predation can affect the importance of each other (Chase et al., 2002), with the predominant interaction in a given scenario promoting or limiting diversity (Chesson & Kuang, 2008). This scenario becomes even more complex, considering that propagule pressure can modulate the effects of competition and predation (Cheng et al., 2019), and may also vary biogeographically (Cheng et al., 2019; Connolly, Menge, & Roughgarden, 2001; Godoy, Rueda, & Hawkins, 2015).

Further reasons for the inconsistent relationship between latitude and intensity of predation are that the impact of consumption is unlikely to be identical for all groups within the prey community (Lavender et al., 2017; Vieira, Duarte, & Dias, 2012). Predators can completely remove a subset of species but in turn may enhance the likelihood of coexistence among a set of functionally similar prey species (Oricchio, Flores, & Dias, 2016; Vieira et al., 2012). Under these circumstances, predation does not increase total diversity (Oricchio, Flores, et al., 2016) but affects only specific phylogenetic or functional groups (Lavender et al., 2017), ultimately driving relative abundance and species composition, but not species richness (Osman & Whitlatch, 2004). Thus, characterizing geographic patterns in functional traits involved in biotic interactions can help us to better predict the consequences of predation in distinct regions (Schemske et al., 2009).

In the marine environment, the few studies approaching this subject show an increasing importance of predation controlling diversity (Freestone et al., 2011) and exotic species (Freestone, Ruiz, & Torchin, 2013; Kremer & Rocha, 2016) towards low latitudes, as predicted by the BIH. However, in some cases, intense predation structuring sessile communities and controlling exotic species is also observed in temperate areas (Cheng et al., 2019; Giachetti, Battin, Bortolus, Tatian, & Schwindt, 2019; Simkanin, Dower, Filip, Jamieson, & Therriault, 2013), when considering benthic predators instead of fishes. Biotic Interaction Hypothesis predictions are only valid for a specific functional group of organisms also in other cases (Lavender et al., 2017). Since behavioural traits that help prey to escape predation are restricted in sessile organisms following recruitment (Hughes, 2005; Jackson, 1977), these species are usually chemically or structurally defended, with most soft-bodied animals often considered chemically defended (Pawlik, 1993, 2000). However, growing evidence suggests that soft-bodied animals are the main prey of large predators in sessile communities and that physical defences are the main trait providing escape from predation (Oricchio, Flores, et al., 2016; Osman &

Whitlatch, 2004; Vieira, Dias, & Flores, 2016; Vieira et al., 2012). Here, we experimentally assessed if predation can explain the latitudinal variation in diversity and resistance to invasion of marine sessile communities from the Atlantic Ocean in the tropical Coast of Angola, the subtropical coast of Brazil and the temperate region of Wales, UK. Biotic interactions can interplay in complex ways to determine diversity, depending on species identity, ontogenetic stages and escape mechanisms of prey. Thus, besides analysing alpha and beta diversity, we also explored the importance of functional traits regarding the ability of prey to escape predation, in order to better explain the latitudinal variation in predation effects in sessile communities during two distinct successional stages. We expected that predation would be more intense in the tropics and regardless of latitude, directed towards soft-bodied animals.

2 | METHODS

2.1 | Study system

Marine sessile organisms have been used over the last decades to answer general questions in ecology (Connell, 1961, 1978; Paine,

1966) as they are abundant and pervasive in the shallow subtidal zones of coastal regions worldwide and their rapid colonization and growth allow the implementation of relatively short-term experiments. Sessile fouling assemblages are composed of a variety of taxa, including sponges, hydroids, corals, anemones, polychaetes, oysters, mussels, barnacles and bryozoans, encompassing distinct functional traits regarding feeding habitats, reproduction, life-form and defence (Freestone & Osman, 2011; Freestone et al., 2011; Russ, 1982).

2.2 | Consumer effects across latitude

Both macro- and micro-predators prey on sessile organisms, mainly during early stages of succession (Osman & Whitlatch, 2004), but the importance of each predator changes according to the sessile taxa and locality (Freestone et al., 2011; Lidgard, 2008; Oricchio, Flores, et al., 2016). While fish are among the most common predators of ascidians (Oricchio, Pastro, et al., 2016; G. Russ, 1980), small crabs, flatworms and gastropods can exert strong predation on bryozoans (Lidgard, 2008). Most of the predation events we observed in the subtropical and tropical regions during the experiment maintenance

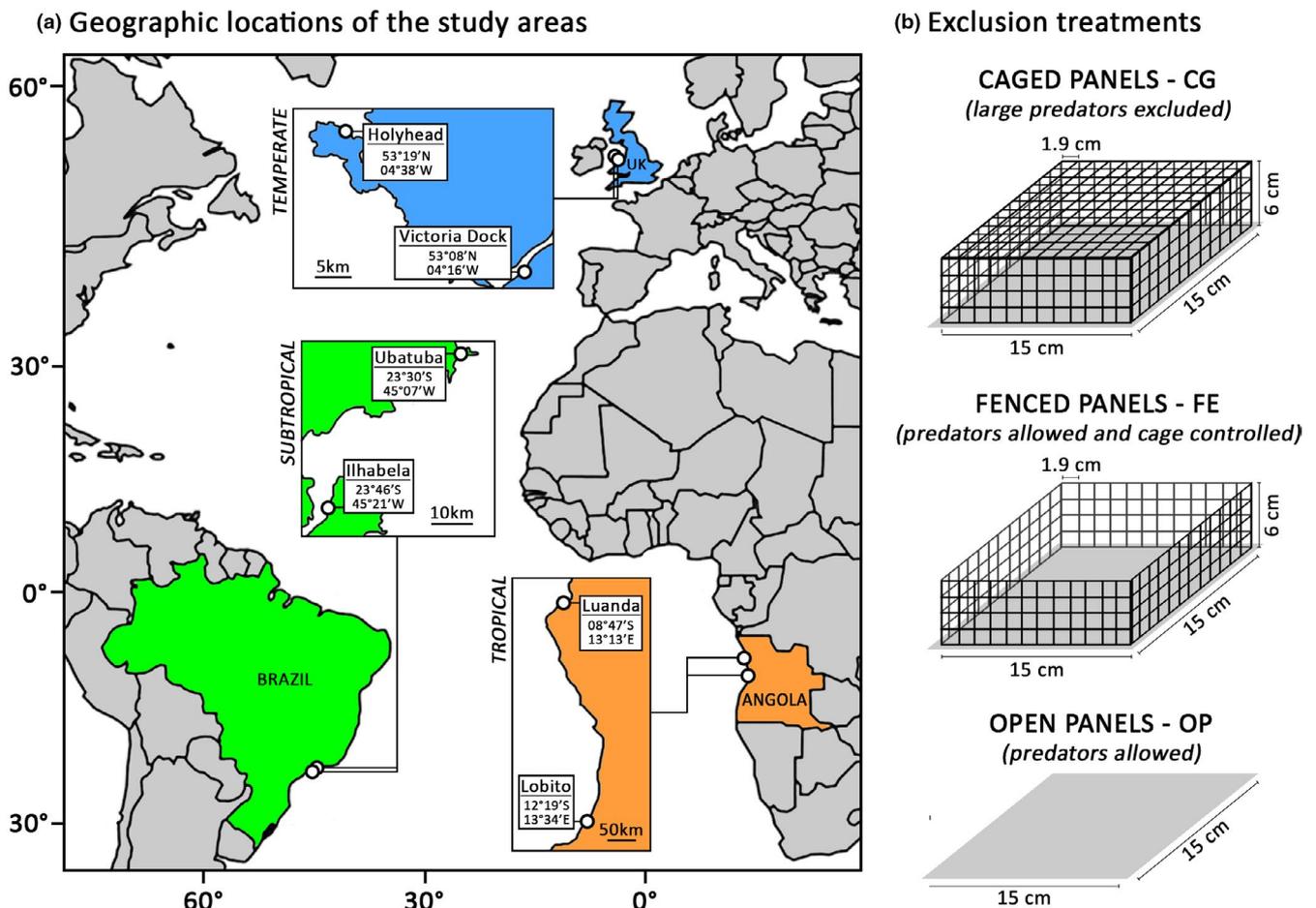


FIGURE 1 Sampling sites and experimental design. (a) Geographical location of the six sampling sites in the three continents; (b) Exclusion treatments: caged, fenced and open panels

were caused by large generalist fish, as demonstrated by Oricchio, Pastro, et al. (2016) for the subtropical region studied here. We observed no predation events in the temperate region.

To assess the importance of predation in determining patterns of diversity (Biotic Interaction Hypothesis) and community resistance to invasion (Biotic Resistance Hypothesis) across latitude, we conducted a large-scale experiment in three distinct regions of the Atlantic Ocean spanning three continents and 45 degrees of latitude. In each region, we selected two recreational marinas with similar conditions and no freshwater input. The experiment was conducted during the summer period in each region to account for seasonality in recruitment; thus, experiments were conducted at different times over the period between July 2016 and April 2017. The experiment was performed in the United Kingdom (a temperate region), in Holyhead Marina (53°19'N; 4°38'W) and Victoria Dock (53°08'N; 4°16'W) from July to October 2016; on the subtropical coast of Brazil, in the Ubatuba late Clube (23°30'S; 45°07'W) and in the Yacht Club of Ilhabela (23°46'S; 45°21'W) from December 2016 to March 2017, and on the tropical coast of Angola, in Clube Naval de Luanda (08°47'S; 13°13'E) and Clube Náutico de Lobito (12°19'S; 13°34'E), from January to April 2017 (Figure 1).

At each site, we suspended 48 horizontally oriented PVC panels (15 × 15 × 0.4 cm) at 2 m depth with a roughened surface facing down and with a minimum distance of 1 m from each other. The panels were equally assigned to three distinct treatments ($n = 8$ for each treatment and successional stage): "Caged communities" were protected against all large predators by a plastic mesh cage (15 cm side, 6 cm height, 1.9 cm mesh); "Fenced communities" developed in panels covered by an open cage with the same dimensions of full cages but lacking the top part, which controlled for hydrodynamic changes that may occur within the caged treatment, but ensured access to all predators; "Open communities" developed in panels with full access to predators but no cage material (Figure 1).

After 1 month (early succession), half of the panels in each treatment were retrieved, photographed to evaluate species coverage and preserved in 70% ethanol. Three months after experimental set-up, when most of the panels were completely colonized (advanced succession), the remainder of the panels were retrieved in an identical manner to the 1-month panels. For logistical reasons, we were not able to collect the 1-month panels from one site in the tropical region (Lobito).

All sessile species present in the 10 × 10 cm central region of the panels were identified to the lowest taxonomic level possible using a dissecting microscope. The border of the panels (5 cm) was not used to avoid manipulation artefacts. All identified species were classified according to their invasive status (i.e. exotic, native or cryptogenic) following Minchin, Cook, and Clark (2013) for the temperate region, Dias, Rocha, Lotufo, and Kremer (2013), Marques et al. (2013), Rocha et al. (2013), Kremer and Rocha (2016) for the subtropical region and Pestana, Dias, and Marques (2017) for the tropical region. From the pictures, we quantified the

relative cover of species as a proxy of abundance using the CPCe image analysis software with a grid of 100 intersections (Kohler & Gill, 2006).

2.3 | Statistical procedures

As we did not sample communities from Lobito after 1 month, we analysed the number of species (alpha diversity) and the number of exotic species among treatments and across regions separately for early (1 month) and advanced (3 months) communities. We used a Levene test to assess variance homogeneity across levels of fixed factors, while normality was assessed through visual inspection of residuals. Except for species richness after 1 m, that showed small departures from homoscedasticity, for all the other richness variables, variance was homogeneous ($p > .05$). Visual inspection of residuals of 1 m species richness showed small variance differences across sites, so we decided to use a parametric test. For early development data, we used a two-way ANOVA on log-transformed data, in which sites (5 levels) and predation treatments (3 levels) were fixed factors. For advanced data, when all marinas were sampled, we compared the total number of species and the number of exotic species among regions and across predation treatments (3 levels) using mixed-effects analyses of variance on log-transformed data because errors were normally distributed (Quinn & Keough, 2002). Region (temperate, subtropical and tropical) and treatment were fixed factors, and sites (2 levels) a random factor nested in region. For both early and advanced data, relevant pairwise comparisons were performed using the Tukey tests.

Also, in order to assess the importance of structural versus non-structural defence types on prey resistance against predation, we compared the percentage of soft-bodied species, soft-bodied exotic species and covered area occupied by soft-bodied organisms across regions and predation treatment levels using ANOVA (as above). Bivalves, barnacles, calcified polychaetes (serpulids) and encrusting bryozoans were classified as hard-bodied organisms, while solitary and colonial ascidians, non-calcified polychaetes, hydroids, scyphistomae, encrusting sponges and ciliophorans were classified as soft-bodied organisms. Because all arborescent bryozoans present in our panels were non-calcified (e.g. *Amathia* spp.) or lightly calcified species (e.g. *Bugula neritina*), they were grouped with soft-bodied organisms.

We expected that predation would limit not only the number of species per sample and the type of defence, but also species variation among replicates (Beta diversity). Thus, for each successional stage and site, we produced a distance matrix among samples using the classic Raup-Crick metric modified by Chase, Kraft, Smith, Vellend, and Inouye (2011) using R 3.1.0 (R Development Core Team). In this method, the probability of species being drawn from the species pool (gamma diversity for each site) is proportional to its among-site occupancy taking into account the differences in species richness among replicates. We then used the betadisper function with 999 permutations in the vegan package

(Oksanen et al., 2019) to evaluate the multivariate homogeneity of treatment dispersions (PERMDISP) (Anderson, Ellingsen, & McArdle, 2006). Pairwise comparisons were performed with the Tukey tests. Beta diversity was represented as the average distance to centroid by treatment level.

To examine the effects of predation on community structure across regions, we classified the species from the three regions into the following morpho-functional groups: solitary ascidians, colonial ascidians, calcified polychaetes, non-calcified polychaetes, hydroids, scyphistomae, calcified encrusting bryozoans, arborescent bryozoans, barnacles, encrusting sponges, ciliophorans, bivalves. Then, we used the abundance of all functional groups as response variables to build a resemblance matrix using Bray–Curtis distance and performed a PERMANOVA test with 999 permutations (Anderson, 2001), following the same models described for richness comparisons, independently for early and advanced communities. Post hoc pairwise comparisons were used to further examine significant sources of variation, and the SIMPER procedure was used to identify the relevant taxa responsible for among-group differences.

3 | RESULTS

Predation only affected species number in tropical communities, but played a different role depending on the stage of community succession (Table 1). Initially (1-month colonization) predation increased diversity; caged panels held fewer species than open or fenced panels (Tukey $p < .05$). After 3 months, we found a general negative effect of predation on species richness across regions. However, differences among caged and fenced/open communities in subtropical and temperate regions were absent, while predation in the tropics reduced the species number by 50% (marginally non-significant Treatment \times Region interaction $p = .065$). Within sites, open and fenced communities always had similar total and exotic richness, showing no procedural artefact. Predation reduced the proportion of soft-bodied species in the tropical region in both 1-month and 3-month communities and also in one of the subtropical sites (Ilhabela) after 1 month (Figure 2, Table 1).

Considering colonization by exotic species, although not testing the region effect (see methods), we observed that after 1 month, tropical and subtropical communities held more exotic species than temperate ones (Tukey, $p < .05$), regardless of predation regime (Figure 3, Table 2). However, after 3 months, we found a significant Treatment \times Region interaction, where predation reduced the number of exotic species in the tropical (Tukey $p < .05$) but not in subtropical or temperate communities (Figure 3, Table 2). While predation did not affect the richness of exotic species in the tropical region after 1 month, it reduced the proportion of soft-bodied exotic species (relative to all exotics). For 3-month-old communities, we found a Predation \times Site(Region) effect. Predation only reduced the proportion of soft-bodied exotic species in one of the tropical sites (Luanda), while in the other (Lobito) we observed a non-significant tendency in the same direction (Tukey, $p > .05$). No

effect of predation on the proportion of soft-bodied exotic species was observed for subtropical and temperate regions (Figure 3, Table 2).

After 1 month, predation did not affect community composition (beta diversity), but a procedural artefact was observed at one of the temperate sites (Holyhead), where communities from fenced panels attained lower beta diversity than fenced and also caged communities (Figure S1, Table 3). However, for 3-month-old communities, we found no artefact and predation reduced species variation in the Tropical region (average distance to centroid in caged communities was 7.4 and 3.0 times larger than that for predated communities in LO and LU, respectively), driving communities to a more homogeneous composition (Figure S2, Table 3).

Predation affected community structure in both tropical and subtropical communities, but not in temperate ones (Figure S3). For 1-month and 3-month-old communities in both tropical and subtropical regions, predation reduced the area occupied by arborescent bryozoans and solitary and colonial ascidians, promoting the occurrence of encrusting bryozoans (SIMPER analysis; Tables S1 and S2). However, for both successional stages fenced communities from Luanda (tropical) and Ubatuba (subtropical), although being more similar to open than to caged communities (SIMPER analysis; Tables S1 and S2), statistically differed from both treatment levels suggesting a methodological artefact that was caused by a higher abundance of colonial ascidians and arborescent bryozoans in fenced than in open panels (Figure 4, Table 4). The same treatment artefact was observed in the tropical and subtropical regions for the area occupied by soft-bodied organisms after 1 month. After 3 months, tropical and subtropical caged communities were dominated by soft-bodied organisms, while communities from open and caged treatments were dominated by calcified organisms. One of the subtropical sites (Ubatuba) again showed an intermediate proportion of soft-bodied organisms in fenced communities suggesting an artefact (Figure 4, Table 4; SIMPER analysis; Tables S1 and S2).

4 | DISCUSSION

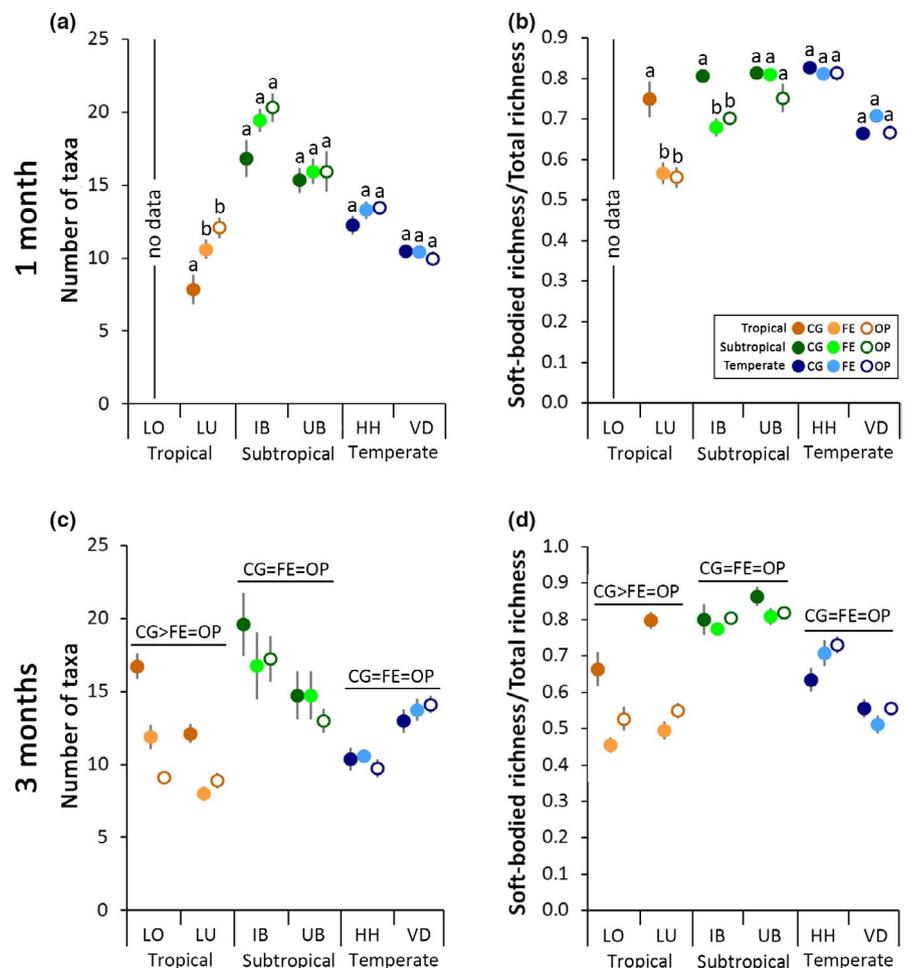
The results obtained here corroborate both the Biotic Interaction and Biotic Resistance Hypotheses: even considering the distinct biogeographical histories among the studied regions, predation in tropical sites controlled several dimensions of diversity, reducing both alpha and beta diversity, determining the identity of dominant species and reducing the number of non-native species. These outcomes occurred mainly after 3 months, suggesting that the effects of predation develop through community succession. Long-term studies (Jenkins & Uya, 2016) would help us to understand if the magnitude of such effects remains or are diluted by the interference of other process that takes place through succession (e.g. positive feedbacks for predator density or increase of available refuges provided by habitat complexity). In the subtropical region, predation only determined the relative abundance of species but not alpha/beta diversity, while in communities from the temperate zone, processes other

TABLE 1 Summary results of ANOVA for total taxa richness and for the proportion of soft-bodied taxa related to total taxa

Source	Total taxa richness				Soft-bodied taxa/Total taxa			
	df	MS	F	p	df	MS	F	p
1 month								
Site	4	0.334	54.8	<.001	4	0.149	41.1	<.001
Treatment	2	0.049	8.2	<.001	2	0.061	16.9	<.001
T × S	8	0.006	2.7	.010	8	0.022	6.0	<.001
Error	103				103	0.004		
3 months								
Region	2	0.378	3.0	.195	2	0.710	6.70	.0783
Treatment	2	0.118	9.0	.016	2	0.102	9.27	.0146
T × R	4	0.052	4.0	.065	4	0.095	8.64	.0115
Site (R)	3	0.128	15.0	<.001	3	0.106	17.67	<.001
T × S (R)	6	0.013	1.6	.167	6	0.011	1.83	.0981
Error	121	0.008			121	0.006		

Note: For 1-month communities, comparisons were performed considering caged, fenced and open treatments in Luanda, Ilhabela, Ubatuba, Holyhead and Victoria Dock. For 3-month communities, comparisons were performed considering caged, fenced and open panels in Luanda and Lobito sites nested into Tropical region, Ilhabela and Ubatuba sites nested into Subtropical region, and Holyhead and Victoria Dock sites nested into Temperate region. Bold *p*-values stand for significant effects ($p < .05$).

FIGURE 2 Effects of predation on richness. Mean (\pm SE) taxa richness (a and c) and proportion of soft-bodied taxa related to total taxa (b and d) on caged (CG—dark grey), fenced (FE—light grey) and open (OP—white) panels in Tropical (Lobito—LO and Luanda—LU), Subtropical (Ilhabela—IB and Ubatuba—UB) and Temperate (Holyhead—HH and Victoria Dock—VC) regions after 1 month (top) and 3 months (bottom) of succession. For comparisons among treatments within each site (a and b), the same letter stands for no significant differences. Differences among treatments within each site (a and b) and within each region (c and d) are based on Tukey's HSD tests with $p < .05$



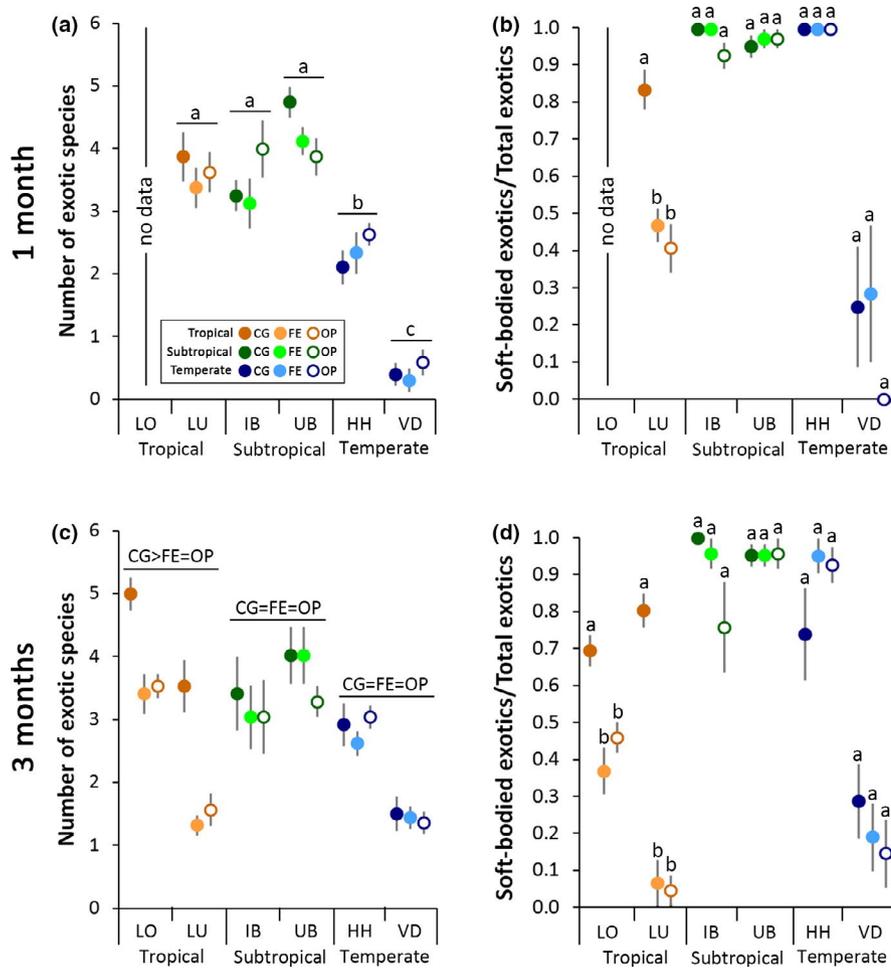


FIGURE 3 Effects of predation on exotic species. Mean (\pm SE) exotic species richness (a and b) and proportion of soft-bodied exotic species related to total exotic species (b and d) on caged (CG—dark grey), fenced (FE—light grey) and open (OP—white) panels in Tropical (Lobito—LO and Luanda—LU), Subtropical (Ilhabela—IB and Ubatuba—UB) and Temperate (Holyhead—HH and Victoria Dock—VC) regions after 1 month (top) and 3 months (bottom) of succession. For comparisons among sites (a) and treatments within each site (b and d), the same letter stands for no significant differences. Differences among sites (a), treatments within each region (c) and treatments within each region (c) are based on Tukey's HSD tests with $p < .05$

Source	Exotic richness				Soft-bodied exotics/Total exotics			
	df	MS	F	p	df	MS	F	p
1 month								
Site	4	51.6	72.4	<.001	4	2.93	83.1	<.001
Treatment	2	0.9	1.2	.300	2	0.22	6.1	.003
T × S	8	0.9	1.3	.240	3	0.11	3.0	.005
Error	103	0.7			103	0.04		
3 months								
Region	2	22.6	0.9	.479	2	3.45	1.9	.296
Treatment	2	10.2	23.5	.001	2	0.53	3.2	.116
T × R	4	4.7	10.9	.007	4	0.47	2.8	.126
Site (R)	3	23.8	24.1	<.001	3	1.84	51.1	<.001
T × S (R)	6	0.4	0.44	.851	6	0.17	4.7	<.001
Error	121	1.0			121	0.04		

Note: For 1-month communities, comparisons were performed considering caged, fenced and open treatments in Luanda, Ilhabela, Ubatuba, Holyhead and Victoria Dock. For 3-month communities, comparisons were performed considering caged, fenced and open panels in Luanda and Lobito sites nested into Tropical region, Ilhabela and Ubatuba sites nested into Subtropical region, and Holyhead and Victoria Dock sites nested into Temperate region. Bold p -values stand for significant effects ($p < .05$).

TABLE 2 Summary results of ANOVA for exotic species richness and for the proportion of soft-bodied exotic species related to total exotic species

TABLE 3 Summary results of PERMDISP for Raup-Crick dissimilarity among treatment levels (caged, fenced and open) in Lobito and Luanda (Tropical), Ilhabela and Ubatuba (Subtropical), and Holyhead and Victoria Dock (Temperate) for 1-month and 3-month communities

Region/Site	Source	1 month				3 months				
		df	MS	F	p	df	MS	F	p	
Tropical	Lobito	Treatment	no data				2	0.190	35.16	<.001
		Error					21	0.005		
	Luanda	Treatment	2	0.019	2.70	.090	2	0.210	74.76	<.001
		Error	21	0.007			21	0.002		
Subtropical	Ilhabela	Treatment	2	0.043	5.19	.014	2	0.001	0.04	.956
		Error	21	0.008			19	0.019		
	Ubatuba	Treatment	2	0.002	0.39	.676	2	0.039	3.81	.039
		Error	21	0.005			21	0.010		
Temperate	Holyhead	Treatment	2	0.124	11.96	<.001	2	0.030	2.15	.143
		Error	21	0.010			21	0.014		
	Victoria Dock	Treatment	2	0.018	1.99	.164	2	0.004	0.34	.712
		Error	19	0.009			19	0.012		

Note: No data were obtained for Lobito after 1 m. Bold *p*-values stand for significant effects ($p < .01$ for 1-month analyses and $p < .008$ for 3-month analyses after Bonferroni correction for multiple comparisons).

than biotic interactions, such as regional enrichment (Freestone et al., 2011) and habitat formation (Leclerc & Viard, 2018), are more likely to drive the diversity of communities. When we observed a procedural artefact, it was caused mainly by the recruitment of colonial ascidians and arborescent bryozoans on fences and secondary colonial growth to the sampling panels, which did not happen in open communities. However, even when we detected artefacts, the structure of the community was very similar between fenced and open communities and distinct from caged communities. In all sites where predation played a significant structuring role, it was clear that physical defences against predation were key. Generalist fish are among the most important predators in tropical regions, and even in subtropical regions, where they can be responsible for up to 83% of the predation events in a sessile community, removing mainly soft-bodied animals (Oricchio, Pastro, et al., 2016). This was evident in the pre-dated communities (i.e. fenced and open communities) from both tropical and subtropical regions where the assemblages present were characterized by organisms with mineralized protective apparatuses.

Predation is usually described as one of the main drivers of diversity. It can mediate competitive interactions by reducing resource monopolization exerted by strong competitors and then promoting diversity. Most of the evidence corroborating this idea comes from temperate regions and are based on two premises: (a) predation must be directed at dominant species and intense enough to reduce resource monopolization, but not to completely remove species from the community; and (b) there is a trade-off between competitive ability and resistance to predation. In the tropical region studied here, predation seems to be directed mainly at the dominant soft-bodied organisms as observed previously in marine fouling communities (Osman & Whitlatch, 2004; Vieira et al., 2012). However, in contrast to premise 1, predation was strong enough to

remove some of the main prey from the community, reducing diversity in the tropics. An additional factor to consider is the overall richness of fouling communities among study regions. In our study, temperate sites supported 38 morpho-species of sessile organisms, subtropical sites 90 morpho-species, while in the tropical coast of Angola, only 43 morpho-species were reported. Such differences in the regional species pool may help to explain why the same action of predation in the tropics and subtropics (removal of soft-bodied organisms), resulted in a different effect on diversity, with the tropics showing a lower chance of species replacement, and hence diversity maintenance, when compared to the subtropics.

In the subtropical region, predator and prey communities are diverse and predation is intense (Oricchio, Pastro, et al., 2016). Thus, there is the same expectation of a strong effect of predation on diversity. However, in the subtropics, predation only promoted replacement of dominant soft-bodied organisms by calcified bryozoans, which can also monopolize space in the way that colonial ascidians do when free from predators. Thus, in both pre-dated and predator-free scenarios from the subtropical region studied here, there is a transient scenario, alternating between two states of very hierarchical communities with always one species being able to occupy most of the available substrate, restricting the occurrence of poor competitors (Oricchio, Pastro, et al., 2016) and so refuting premise 2 (trade-off between competitive ability and resistance to predation). For both the subtropical and temperate regions, we found no evidence of predation driving species richness and for the temperate region there was no effect on community organization. Our results corroborate the few empirical studies showing that the importance of predation for diversity increases as we move from high to low latitudes (Freestone et al., 2011, 2013), contrasting to Lavender et al. (2017) that reported no obvious latitudinal pattern in Australia, where predation effects were restricted to a functional group of

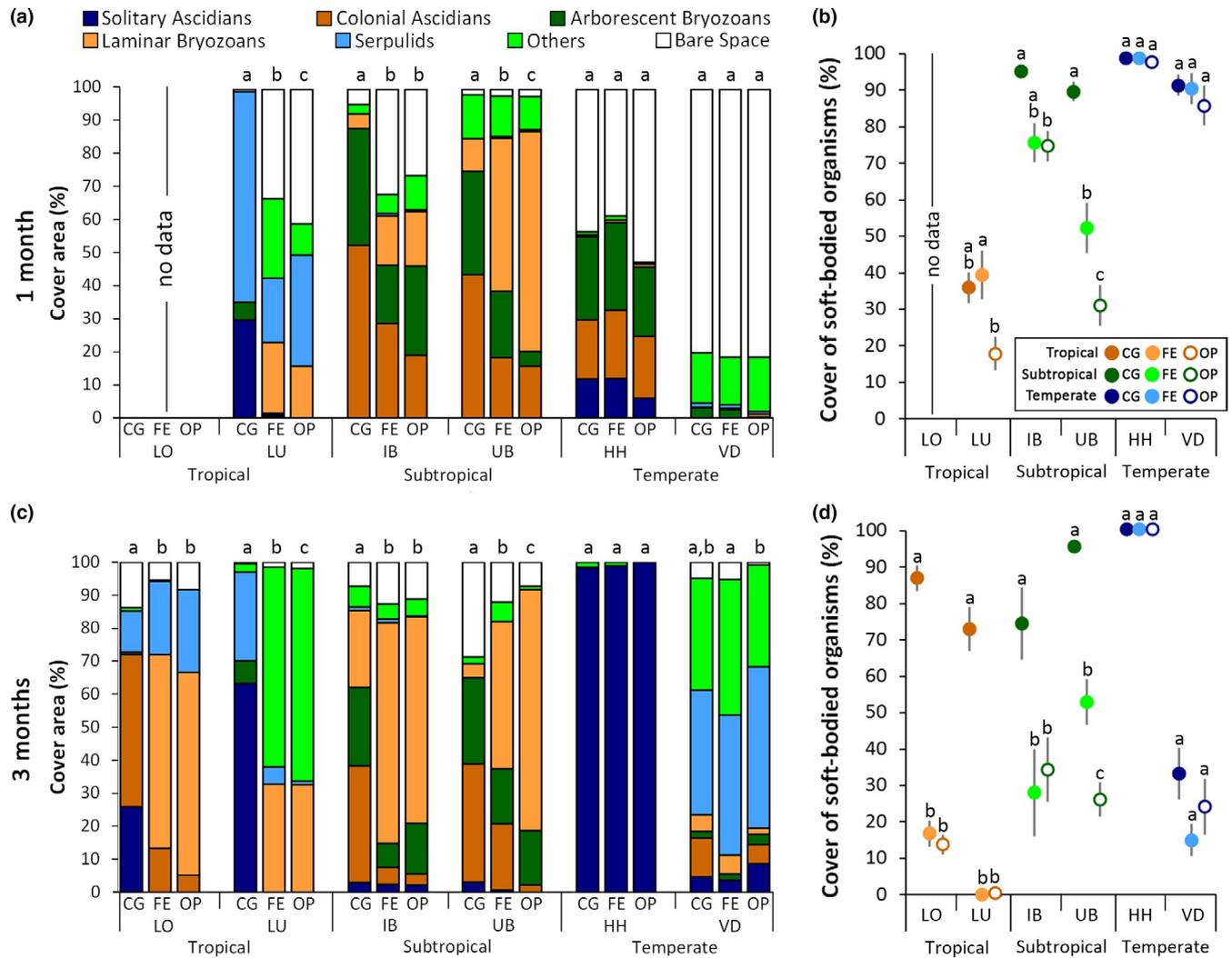


FIGURE 4 Effects of predation on the cover of major groups. Mean cover area of main taxonomic groups (solitary ascidians, colonial ascidians, arborescent bryozoans, laminar bryozoans, serpulids and others—bivalves, ciliophores, barnacles, hydroids, non-calcified polychaetes, scyphistomae and sponges) (a and c) and mean (\pm SE) percentage coverage of soft-bodied taxa (b and d) on caged (CG), fenced (FE) and open (OP) panels in Tropical (Lobito—LO and Luanda—LU), Subtropical (Ilhabela—IB and Ubatuba—UB) and Temperate (Holyhead—HH and Victoria Dock—VC) regions after 1 month (top) and 3 months (bottom) of succession. For comparisons among treatments within each site, different letters stand for significant differences based on pairwise test after PERMANOVA (a and c) and Tukey's HSD tests (b and d) with $p < .05$

prey. Besides, the lack of importance of biotic interaction in temperate zones has been corroborated by similar studies in the North Atlantic Ocean (Freestone & Osman, 2011) and the Mediterranean (Leclerc & Viard, 2018).

In our study, predation reduced the success of exotic species to invade communities in the tropics but not in high latitudes of the eastern Atlantic coast. Our results reinforce previous studies that observed the same pattern in the north (Freestone et al., 2013) and south (Kremer & Rocha, 2016) western Atlantic for fouling marine systems. As expected by biotic acceptance theory (Fridley et al., 2007; Stohlgren, Jarnevic, Chong, & Evangelista, 2006), when we found a native exotic richness relationship (NERR), it was positive in both local (for most sites from early and advanced communities) and global (only for early communities) scale (data not shown). As biotic resistance refers to several distinct processes including competition

and predation, the positive NERR reinforces the importance of predation to control bioinvasion, once species richness seems to be linked to how “good” is the environment, and not to competition, at least during the studied period. Then, in polar and temperate regions, abiotic resistance can play a more important part, as the pool of species able to cope with harsh conditions are more limited than in the tropics (de Rivera, Steves, Fofonoff, Hines, & Ruiz, 2011; Ruiz, Fofonoff, Carlton, Wonham, & Hines, 2000). While the abiotic resistance in temperate regions is prone to be weakened by global changes on a long-term basis (Mahanes & Sorte, 2019; Ruiz et al., 2000), the biotic resistance to invasion in tropical communities is already being threatened by the severe reduction in the diversity and abundance of fish promoted by human activities, such as overfishing and habitat degradation (Coleman & Williams, 2002; Llope et al., 2011). Reduction in predatory fish, allied to less restrictive physical

TABLE 4 Summary results of PERMANOVA for community structure and ANOVA for the percentage coverage area of soft-bodied organisms related to total coverage area

Source	Community structure				Soft-bodied coverage/Total coverage			
	df	MS	Pseudo-F	p	df	MS	F	p
1 month								
Site	4	48,877	120.4	.001	4	17,166	120.0	<.001
Treatment	2	8,172	20.1	.001	2	4,332	30.2	<.001
T × S	8	2,447	6.0	.001	8	1,265	8.8	<.001
Error	102	406			102	143		
3 months								
Region	2	59,756	1.8	.084	2	10,781	0.47	.663
Treatment	2	19,640	9.3	.005	2	27,892	52.61	<.001
T × R	4	7,540	3.6	.017	4	5,654	10.67	.007
Site (R)	3	32,609	78.8	.001	2	22,826	103.80	<.001
T × S (R)	6	2,124	5.13	.001	6	530	2.41	.031
Error	119	414			119	220		

Note: For 1-month communities, comparisons were performed considering caged, fenced and open treatments in Luanda, Ilhabela, Ubatuba, Holyhead and Victoria Dock. For 3-month communities, comparisons were performed considering caged, fenced and open panels in Luanda and Lobito sites nested into Tropical region, Ilhabela and Ubatuba sites nested into Subtropical region, and Holyhead and Victoria Dock sites nested into Temperate region. Bold *p*-values stand for significant effects ($p < .05$).

conditions in the tropics can help to explain the larger number of exotic species in tropical than in temperate sites in ours and other studies (Freestone et al., 2013; Kremer & Rocha, 2016).

A number of empirical studies have investigated latitudinal variation in the importance of biotic interaction for diversity, but few have considered the functional traits modulating variation in predation. Such investigations may provide insight into observed variation across studies. We show that the proportion of substrate monopolized by organisms with external structural defences was always higher than 70% in pre-dated communities from both tropical and subtropical regions. Dominant defended taxa included the calcified cryptogenic bryozoan *Schizoporela errata* (both tropics and subtropics), and the exotic serpulid *Hydroides elegans* (tropics only). In contrast, communities protected against predation were dominated by soft-bodied, mainly colonial organisms such as didemnid ascidians and lightly calcified arborescent bryozoans. The high success of some bryozoans, barnacles and serpulid worms as invasive species, as evidenced for North America (Ruiz et al., 2000), may be mediated by the calcified shield that prevents predation. In contrast, soft-bodied organisms such as ascidians and sponges are believed to escape predation mainly by the production or assimilation of chemical defences, although, several studies show that colonial ascidians are heavily consumed by fish (Oricchio, Flores, et al., 2016; Oricchio, Pastro, et al., 2016; Osman & Whitlatch, 2004; Vieira et al., 2012), including introduced species (Freestone et al., 2013; Jurgens, Freestone, Ruiz, & Torchin, 2017; Kremer & Rocha, 2016). Instead, strategies to avoid predation by non-calcified organisms may rely on escape in time, with colonial animals being able to asexually regrow after predation when colony tissue is partially damaged (Hiebert,

Vieira, Dias, Tiozzo, & Brown, 2019; Jackson, 1977; Jackson & Coates, 1986). The strategy of escape from predation in time may also explain why, in subtropical regions, predation does not reduce diversity. While rare ascidians are promptly removed by predators and replaced by calcified bryozoans, the ascidian species that dominate in predation-free panels are usually found in pre-dated communities but in very small densities. Thus, predation in the subtropics does not affect the number of species but mediates the use of resources among functionally distinct organisms.

Our results contribute to increase the generality of the BRH and, to a lesser extent, the BIH. We also highlight that some of the discrepancies between the expected effects of predation on diversity across latitudes may lie in not considering important features that may mediate the outcome of predation, such as functional traits of prey communities. Functional traits related to resistance against predators may not only modulate general predation effects on diversity but may also contribute to a better understanding of why some groups are more successful in invading new habitats even when predation is intense, such as in the tropics. Our work focused on only one trait, but results could already provide mechanistic insight into geographic variation in predation effects. We consider that the use of additional functional traits, such as growth form, reproductive strategy and behavioural response, will contribute to understand when and why the BIH and BRH hypotheses are not a general rule. Additionally, some questions related to processes taking place in the subtropics, that probably diverge from the tropics, have emerged. Manipulations considering variables not addressed in our study, such as the extent of regional species pool and propagule pressure, intensity of

predation and the importance of regrowth strategies of soft-bodied colonial organisms will shed some light on how predation affects diversity globally.

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DATA AVAILABILITY STATEMENT

The authors agree to store and share the data supporting results in Dryad upon acceptance of the article as described in the author guidelines.

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BIOSKETCH

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SUPPORTING INFORMATION

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

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