

Article

Temporal Diversity Shifts in Subtidal *Tubastraea*-Invaded Rocky Shores of Arraial do Cabo Bay, Southeastern Brazil

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Abstract

Invasive species can alter community composition and ecosystem functioning. In the subtidal rocky shores of Arraial do Cabo Bay, southeastern Brazil, the invasive coral *Tubastraea* spp. has established populations, raising concerns about long-term impacts on native benthic communities. This study investigates temporal shifts in β -diversity across 44 fixed plots containing *Tubastraea* spp., monitored over 383 days. Underwater photographic surveys and multivariate analyses identified nine distinct benthic community types, each forming mosaic structures of sessile organisms. Temporal β -diversity analyses revealed that only the group characterized by *Tubastraea*, crustose calcareous algae and the zoantharian *Palythoa caribaeorum* showed significant differences between species gains and losses over time, suggesting temporal-scale dependency. Key contributors to community dissimilarity included *P. caribaeorum*, crustose calcareous algae, turf, the sponge genus *Darwinella*, and *Tubastraea*. This study highlights the importance of considering both spatial and temporal heterogeneity when assessing the ecological impact of marine invasive species. Our findings underscore the need for multi-scale monitoring to fully understand the dynamics of tropical subtidal ecosystems under biological invasion. While numerous studies report a correlation between *Tubastraea* abundance and shifts in ecological diversity, this relationship may be weak, as critical drivers such as the complexity of community organization are rarely accounted for.

Keywords: benthic communities; hard-bottom; β -diversity; spatial heterogeneity



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1. Introduction

Mosaic structures in subtidal hard-bottom rocky shore environments refer to the spatial arrangement of patches that collectively influence ecological processes and biodiversity. At any given time and location, these benthic communities typically comprise a mosaic of patches at different successional stages, each supporting distinct species compositions and abundances. Dynamic patchiness, even in seemingly uniform habitats, may emerge from biological processes such as stochastic recruitment and spatially heterogeneous foraging behavior, including grazing and predation [1]. This spatial and temporal heterogeneity plays a key role in sustaining species diversity. The mosaic configuration observed in these subtidal benthic communities results from a combination of factors, including disturbance,

spatial competition among neighboring elements, differences in life history traits, colonization ability, and low biotic resistance [2–6]. Compared to the intertidal zone, the subtidal domain supports a much richer array of species, albeit in less accessible habitats [7].

High-diversity ecosystems are supposed to be more resistant to invaders, when compared to low-diversity ones, according to the Biotic Resistance Hypothesis [8]. The primary hypotheses describing the relationship between native species richness and ecosystem invasibility are opposing and scale-dependent, a conflict known as the Invasion Paradox [9]. The Biotic Resistance Hypothesis (BRH), proposed by Charles Elton in 1958 [10,11], posits that high native species diversity enhances ecosystem resistance [11–13], as niche competition leads to more complete resource use, preventing the establishment of new species [13]. This negative relationship is most frequently observed at fine spatial scales [9]. In contrast, the Biotic Acceptance Hypothesis (or Biodiversity Increases Invasibility Hypothesis) [9,12] argues that species-rich areas, or “diversity hotspots,” also act as hotspots for exotic species [9,13]. This positive correlation pattern, often observed at broad spatial scales [9,14], is driven by extrinsic factors such as habitat heterogeneity, high resource availability, or favorable environmental conditions, which benefit both native and exotic species [9,13,14]. The introduction of non-native species into marine environments can trigger profound alterations in community structure and ecosystem functioning, with cascading effects that reverberate throughout the food web and biogeochemical cycles [15]. The introduction or addition of species and the dislodgement or exclusion of the native species are main effects of biological invasions on diversity [16]. A significant proportion of marine non-indigenous species in Brazil is associated with subtidal habitats [7].

In Brazil, the genus *Tubastraea* (Cnidaria, Anthozoa, Scleractinia) has been intensively studied since its first report in Northern Rio de Janeiro State in the late 1980s, and it was suggested that colonies were accidentally transported by oil platforms [17]. Species from this genus are the first scleractinian corals introduced in the Southwestern Atlantic [18]. In recent years, studies have been conducted to resolve the taxonomic complexities within the genus *Tubastraea* along the Brazilian coast, aiming to clarify species boundaries and better understand their distribution [19–21]. Some studies in Brazil have suggested that the introduction of the invasive *Tubastraea* in Brazilian waters represents a significant threat to the region’s marine biodiversity, particularly impacting benthic communities [22]. Research on the transformation of rocky shores driven by *Tubastraea* invasion implicitly reflects alterations in both community diversity and species composition [23–30].

Temporal β -diversity is a temporal variation in community composition at a locality between two or more points in time [31]. Ecological processes operate at a variety of time scales [32]. On shorter temporal scales, temporal β -diversity might show rapid shifts in community composition, as species may temporarily relocate or adapt to changing environmental conditions (e.g., disturbances such as rough sea conditions, human interventions, or seasonal changes). This could reflect high turnover in species but may not immediately indicate long-term change in biodiversity. Over longer temporal periods, temporal β -diversity would capture more persistent changes and trends. This could reveal more significant shifts in community structure, as longer-term environmental factors (e.g., climate change, habitat degradation, or invasive species) accumulate, leading to local extinctions and permanent shifts in community structure. Long-term data would reflect more substantial and irreversible changes in diversity. Compared to spatial β -diversity, temporal β -diversity has received significantly less attention [33].

Understanding ecological phenomena requires observation across multiple temporal scales, this study aims to investigate changes in the diversity of benthic communities on hard substrates associated with the presence of the non-native coral *Tubastraea* spp. These potential effects were assessed across different temporal scales. The central hypothesis

is that communities associated with *Tubastraea* undergo shifts in diversity and that such changes can be detected at multiple temporal scales, reflecting the influence of different ecological processes over time.

2. Method

2.1. Study Area

The Cabo Frio region on the southeast Brazilian coast is renowned for its unique coastal–oceanic system, shaped by a shift in coastline orientation and the influence of shelf break topography, which intensifies interactions between coastal and oceanic processes [34]. This dynamic system is particularly active during the summer months, when favorable wind conditions drive frequent and sustained coastal upwelling, resulting in a sharp contrast between water masses. Non-upwelling periods are characterized by warm waters, with temperatures above 21 °C and low nutrient concentrations, while upwelling events transport colder, nutrient-rich waters to the surface, lowering temperatures below 18 °C, sometimes as low as 13 °C, and significantly increasing nitrate and phosphate levels [35]. This constant interplay between temperature variability, nutrient availability, and seasonal cycles highlights the ecological significance of the Cabo Frio upwelling system, which plays a crucial role in structuring local communities and shaping coastal marine ecosystems.

Study sites along the rocky shores at Enseada dos Cardeiros, Ilha dos Porcos, Enseada do Anequim, Pedra Vermelha, and Fenda de Nossa Senhora were selected for monitoring fixed plots (Figure 1). All sites are located within the same bay system and are subjected to similar disturbance regimes.

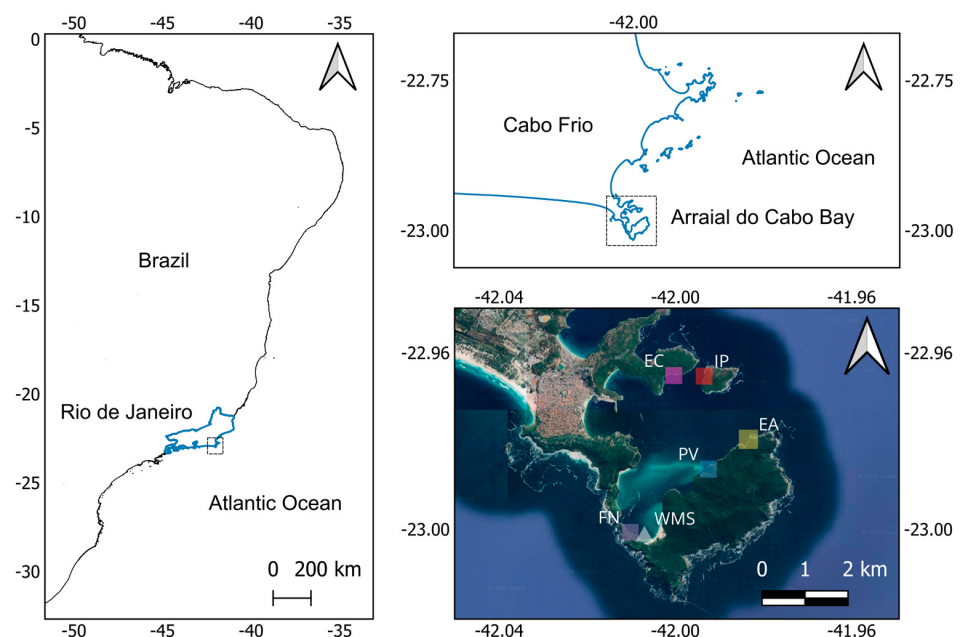


Figure 1. Map illustrating the position of sites within Arraial do Cabo Bay, located in southeastern Brazil. Sites: EC = Enseada dos Cardeiros (N = 8 plots); IP = Ilha dos Porcos (N = 10); EA = Enseada do Anequim (N = 8); PV = Pedra Vermelha (N = 8); FN = Fenda de Nossa Senhora (N = 10); and WMS = Aqualink.

2.2. Seasonal Upwelling and Temperature Dynamics in Cabo Frio

Due to the occurrence of upwelling, which impacts the dynamics of the benthic community in the region, the temperature was monitored throughout the study. Temperature data were obtained from the water monitoring system Aqualink (available at <https://aqualink.org/sites/1187>, accessed on 31 December 2024) whose sensor is positioned at approximately 6 m depth at the bay close to the FNS site.

2.3. Biological Sampling

Fifty fixed plots were initially established on vertical rock surfaces (90°) colonized by the non-native coral *Tubastraea*, targeting an established sample [36], using an underwater rotary hammer drill (Nemo SDS Rotary Hammer). These plots were distributed within a 20 m area from the rocky shore at depths ranging from 4 to 8 m. Forty-four plots were sampled due to the loss of 6 during the experiment. The substantial number of replicates provides high statistical power to detect even subtle effects of *Tubastraea* and offers a robust estimate of the associated uncertainty, strengthening the inference of causal relationships. Targeted plot locations reduce the variability among plots and therefore provide better statistical power for detecting changes in abundances over time [36]. A digital camera Canon PowerShot G7X Mark II in a waterproof case Meikon 40m was attached to a 15 cm × 15 cm aluminum square frame equipped with artificial lighting (LED Dive Lights AL1300XWP, Bigblue, Goleta, CA, USA). The images were cropped following the screws used in the fixed plots as the reference. In the software CPCe 4.1 [37], the percent cover of mosaic elements was estimated in cropped images by a point intercept technique. Biological sampling focused exclusively on sessile benthic organisms. The number of grid points, consisting of rows and columns, was determined such that each point represented an area of 1 cm². Mosaic elements representing unique, distinct and discrete states were determined (Table 1). Samplings were carried out from 23 November 2023 to 10 December 2024. Although sampling was initially planned to occur monthly, with an interval of approximately 30 days between samples, sea conditions occasionally made it impossible to adhere to this schedule. In addition to the initial sampling conducted on day zero, subsequent resampling was carried out on days 26, 60, 96, 154, 182, 210, 245, 280, 315, 355, and 383.

2.4. Data Analysis

Initially, fixed plots representing the same communities at time zero (day 0) were identified. This allowed for the definition of replicates of the same ‘age,’ each supporting distinct community compositions. Prior to analysis, arcsine transformation was applied for percent coverage data [38,39]. Hierarchical cluster analysis was used to establish the affinities between survey fixed plots that are likely to represent similar communities along the coasts of Arraial do Cabo Bay. Hierarchical cluster analysis was performed using the Bray–Curtis distance [40] and UPGMA method. Cophenetic correlation coefficients lower than 0.7 indicate the inadequacy of the cluster method [41]. The Permutational Multivariate Analysis of Variance using distance matrices under the reduced model was applied, restricting permutations within the repeated measures of each fixed plot, and significance was determined with 999 permutations, when applicable. The function `pairwise_permanova.R` (`vegan::adonis`) was used to perform pairwise PERMANOVA analyses, allowing for statistical comparisons between groups based on community dissimilarities. The Similarity Percentages SIMPER analysis [42] was applied to identify species that contributed to differences between groups, based on Bray–Curtis dissimilarities calculated from untransformed community data. Multivariate analyses were implemented with the R package *vegan* 2.7-1 [43].

The temporal β -diversity index or TBI [44], which quantifies changes in community composition between two time points and can be further divided into species gains and losses, was calculated for each community identified in the dendrogram. The relative abundance data were transformed using the arcsine method [38]. The percentage difference dissimilarity D (method Bray–Curtis distance) was applied to quantify community dissimilarities. Dissimilarities were partitioned into losses and gains; B is the unscaled sum of species losses and C is the unscaled sum of species gains between initial (zero days) and

each resampling (see the Section 2.3). Temporal β -diversity analyses were implemented with the R package *adespatial* 0.3-28 [45].

Table 1. Mosaic elements recorded during the study period. The taxonomic classification followed the information available in the World Register of Marine Species [46].

Mosaic Elements	Phylum/Division	Detail
Algal turf		Low layer of algae
<i>Codium spongiosum</i> Harvey, 1855	Chlorophyta	Ulvophyceae (Class)
Filamentous algae	Ochrophyta	Ectocarpaceae (Family)
<i>Dictyota menstrualis</i> (Hoyt) Schnetter, Hörning & Weber-Peukert, 1987	Ochrophyta	Dictyotaceae (Family)
<i>Dictyota mertensii</i> (C.Martius) Kützinger, 1859	Ochrophyta	Dictyotaceae (Family)
<i>Padina gymnospora</i> (Kützinger) Sonder, 1871	Ochrophyta	Dictyotaceae (Family)
<i>Sargassum</i> spp.	Ochrophyta	Fucales (Order)
Articulate calcareous algae	Rhodophyta	<i>Amphiroa</i> and <i>Jania</i> (Genus)
Ceramiales (Order)	Rhodophyta	Florideophyceae (Class)
Crustose calcareous algae	Rhodophyta	Florideophyceae (Class)
<i>Gelidium</i> spp.	Rhodophyta	Florideophyceae (Class)
<i>Peyssonnelia</i> spp.	Rhodophyta	Florideophyceae (Class)
<i>Plocamium brasiliense</i> (Greville) M.Howe & W.R.Taylor, 1931	Rhodophyta	Florideophyceae (Class)
<i>Amphimedon viridis</i> Duchassaing & Michelotti, 1864	Porifera	Demospongiae (Class)
<i>Aplysina fulva</i> (Pallas, 1766)	Porifera	Demospongiae (Class)
<i>Darwinella</i> spp.	Porifera	Demospongiae (Class)
<i>Dysidea etheria</i> de Laubenfels, 1936	Porifera	Demospongiae (Class)
Poecilosclerida (Order)	Porifera	Demospongiae (Class)
<i>Scopalina ruetzleri</i> (Wiedenmayer, 1977)	Porifera	Demospongiae (Class)
<i>Stelletta beae</i> Hajdu & Carvalho, 2003	Porifera	Demospongiae (Class)
<i>Astrangia rathbuni</i> Vaughan, 1906	Cnidaria	Scleractinia (Order)
<i>Chromonephthea braziliensis</i> van Ofwegen, 2005	Cnidaria	Malacalcyonacea (Order)
Hydroid	Cnidaria	Hydrozoa (Class)
<i>Palythoa caribaeorum</i> Duchassaing & Michelotti, 1860	Cnidaria	Zoantharia (Order)
<i>Tubastraea</i> spp.	Cnidaria	Scleractinia (Order)
<i>Perna perna</i> (Linnaeus, 1758)	Mollusca	Mytilida (Class)
Tubicolous polychaete	Annelida	Polychaeta (Class)
Cirripecta	Arthropoda	Crustacea (Subphylum)
<i>Bugula neritina</i> (Linnaeus, 1758)	Bryozoa	Cheilostomatida (Order)
<i>Schizoporella errata</i> (Waters, 1878)	Bryozoa	Cheilostomatida (Order)
<i>Steginoporella buskii</i> Harmer, 1900	Bryozoa	Cheilostomatida (Order)
<i>Virididentula dentata</i> (Lamouroux, 1816)	Bryozoa	Cheilostomatida (Order)
<i>Didemnum</i> spp.	Chordata	Ascidacea (Class)
<i>Diplosoma</i> spp.	Chordata	Ascidacea (Class)
<i>Symplegma rubra</i> Monniot C., 1972	Chordata	Ascidacea (Class)

3. Results

Across all plots and sampling periods, 36 distinct and mutually exclusive mosaic elements were recorded (Table 1). Filamentous algae were represented by the family Ectocarpaceae (Class Phaeophyceae). Tubicolous polychaetes were present but remained unidentified at the species level. Cirripectes were represented by the barnacles *Megabalanus coccopoma*, *Amphibalanus amphitrite*, and *Balanus trigonus*. The genus *Didemnum* was primarily represented by *Didemnum perlucidum*, along with *D. ligulum*, *D. rodriguezi*, and *D. granulatum*. Hydroids included *Macrorhynchia philipina*, *Pennaria disticha*, and members of the family Aglaopheniidae. The *Tubastraea* element in the table does not distinguish species or morphotype; we consider the genus. Turf communities were composed mainly of associations between macroalgae, hydroids, and sediments. The genus *Sargassum* was

represented by *Sargassum furcatum* and *Sargassum cymosum*. Two species of the genus *Darwinella* were the most common sponges on the coasts of Arraial do Cabo, although the identification at species level was not feasible. The order Poecilosclerida included *Guitarra sepia*, *Tedania ignis*, and *Mycale microsigmatosa*. Articulate calcareous algae were represented by *Jania adhaerens* and *Amphiroa beauvoisii*. Crustose calcareous algae recorded in Arraial do Cabo comprised nine species, predominantly from the families Corallinaceae and Hapalidiaceae. Additionally, patches of the order Ceramiales and the genus *Gelidium* occasionally dominated the environment. The genus *Peyssonnelia* was represented by *Peyssonnelia boudouresquei*, *P. capensis*, and *P. valentini*.

Cluster analysis revealed nine (9) distinct groups representing of sessile benthic communities (Figure 2A), generated by a cut-off at 46.2% dissimilarity. The cophenetic correlation coefficient was 0.78, indicating the adequacy of the cluster. Mosaic elements exhibiting up to 5% coverage are presented in Figure 2B, with their mean values and standard deviations detailed as follows: red group: *Schizoporella errata* (62.7% $\pm$ 22.4%), crustose calcareous algae (25.0% $\pm$ 35.4%), and *Tubastraea* (12.3% $\pm$ 12.9%); blue group: Poecilosclerida (62.5%), turfs (25.0%), *Darwinella* (9.4%), and *Tubastraea* (3.1%); green group (N = 2): *Palythoa caribaeorum* (32.0% $\pm$ 18.7%), *Darwinella* (31.6% $\pm$ 37.9%), turfs (19.1% $\pm$ 26.9%), and *Tubastraea* (17.4% $\pm$ 7.8%); purple cluster (N = 16): *Darwinella* (40.7% $\pm$ 17.3%), *Tubastraea* (17.0% $\pm$ 7.8%), Ceramiales (12.2% $\pm$ 13.8%), crustose calcareous algae (11.8% $\pm$ 9.3%), and turfs (10.9% $\pm$ 8.9%); orange group: turfs (29.0% $\pm$ 16.7%), Ceramiales (25.9% $\pm$ 14.9%), *Tubastraea* (19.5% $\pm$ 7.5%), crustose calcareous algae (12.0% $\pm$ 6.0%), and *Didemnum* (6.0% $\pm$ 15.4%); yellow group: *Tubastraea* (19.9% $\pm$ 9.1%), crustose calcareous algae (19.6% $\pm$ 10.2%), *Palythoa caribaeorum* (18.3% $\pm$ 16.1%), turfs (15.5% $\pm$ 12.0%), Ceramiales (6.1% $\pm$ 7.0%), Cirripedia (5.8% $\pm$ 5.2%), and *Darwinella* (5.5% $\pm$ 10.5%); brown group: *Schizoporella errata* (26.2%), *Darwinella* (21.4%), *Sargassum* (11.9%), *Dictyota mertensii* (10.7%), turfs (8.3%), *Tubastraea* (8.3%), Ceramiales (6.0%), and *Peyssonnelia* (6.0%); pink group: articulate calcareous algae (46.7%), Ceramiales (25.0%), turfs (10.0%), *Tubastraea* (6.7%), and hydroid (5.0%); gray group: Ceramiales (19.8% $\pm$ 13.8%), *Dictyota mertensii* (17.3% $\pm$ 23.5%), *Dictyota menstrualis* (15.4% $\pm$ 9.4%), *Tubastraea* (8.8% $\pm$ 3.5%), turfs (8.6% $\pm$ 5.7%), *Sargassum* (6.5% $\pm$ 13.8%), articulate calcareous algae (6.5% $\pm$ 4.1%), and crustose calcareous algae (6.6% $\pm$ 3.8%).

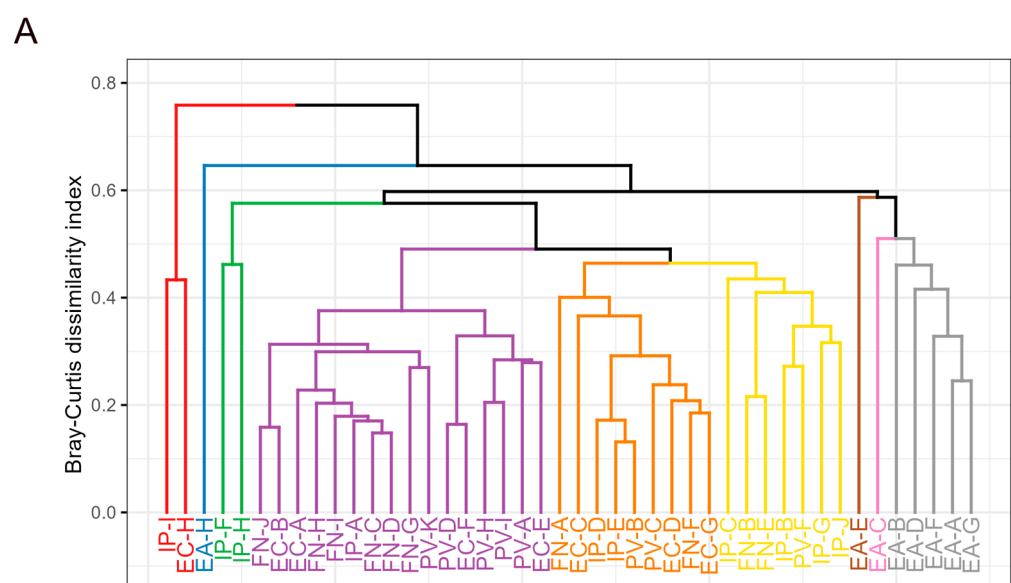


Figure 2. Cont.

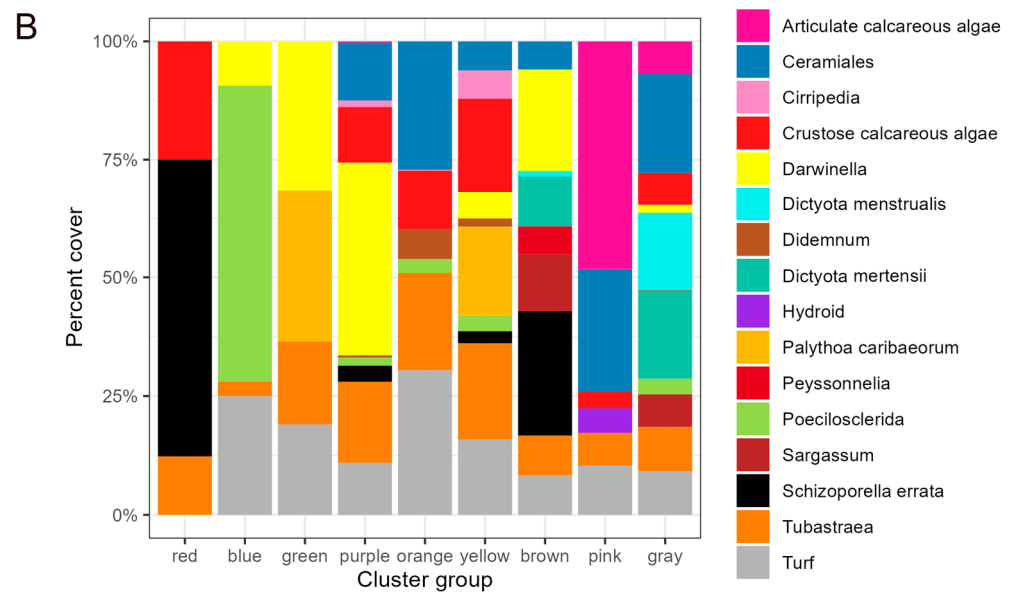


Figure 2. Dendrogram from a hierarchical cluster analysis shows the groups formed by study plots based on biotic data assessed with the Bray–Curtis distance and UPGMA linkage method (A). Most abundant mosaic elements (>5% percent cover) characterize the groups formed in the hierarchical cluster analysis (B).

The mean values of the TBI statistics calculated for each group were plotted, in comparison with the survey carried out at time zero with all successive surveys (Table 2). For groups consisting of a single sample (blue, brown, and pink groups), the calculated values were displayed. In contrast, for groups with multiple samples (purple, orange, yellow and gray groups), the displayed values represented the mean losses, gains, and dissimilarity. The dissimilarities (D) that measure the temporal β -diversity for a community show variation at different time scales. The highest dissimilarity value (62.4%) was observed in the blue group when comparing day 0 to day 96, whereas the lowest dissimilarity (8.3%) occurred in the green group between day 0 and day 26. The greatest variations in dissimilarity across temporal scales were observed in the following groups: pink (39%, with the highest dissimilarity between days 0 and 96, and the lowest between days 0 and 26), red (33%, 0–383 highest and 0–26 lowest), blue (37%, 0–96 highest and 0–383 lowest), brown (31%, 0–355 highest and 0–26 lowest), gray (27%, 0–245 highest and 0–26 lowest), orange (26%, 0–383 highest and 0–26 lowest), green (23%, 0–154 highest and 0–26 lowest), purple (22%, 0–355 highest and 0–26 lowest), and yellow (14%, 0–315 highest and 0–26 lowest). The difference between species gains (C) and losses (B) was assessed using a permutational paired t-test for the purple, orange, yellow and gray groups composed of three or more fixed plots. Significant differences between species gains and species losses were detected in the yellow group (Table 2) at days 154 (mean(C-B) = -0.0589 , Stat = -3.2605 , p .perm = 0.033), 182 (mean(C-B) = -0.0736 , Stat = -5.6440 , p .perm = 0.017), 210 (mean(C-B) = -0.0770 , Stat = -3.748 , p .perm = 0.03), 280 (mean(C-B) = -0.0541 , Stat = -2.9097 , p .perm = 0.04) and 315 (mean(C-B) = -0.0397 , Stat = 3.0862, p .perm = 0.034), indicating loss at all temporal scales (Table 3). The community represented by the yellow group exhibited a significant difference across sampling times, as indicated by the permutation test for adonis under a reduced model for repeated measures in fixed plots (Df = 11, Sum of Squares = 0.7505, R^2 = 0.0926, F = 0.6607, p = 0.001). Pairwise tests revealed significant differences at days 280 (Df = 1, Sum of Squares = 0.1075, R^2 = 0.09989, F = 1.3317, p = 0.04688), 315 (Df = 1, Sum of Squares = 0.12283, R^2 = 0.09462, F = 1.2542, p = 0.03125), and 383 (Df = 1, Sum of Squares = 0.1056, R^2 = 0.0930, F = 1.2297, p = 0.0625). The mosaic elements that contributed most to the differences between day 0 and subsequent resampling dates were *Palythoa*

caribaeorum, crustose calcareous algae, turf, *Tubastraea* spp., *Darwinella*, and *Ceramiales* (Table 3). *Palythoa caribaeorum* exhibited increased relative abundance in all comparisons where significant differences in pairwise tests were detected between day 0 and subsequent resampling dates. Regarding the temperature data presented in Figure 3, the period between 182 and 280 days showed no evidence of upwelling events.

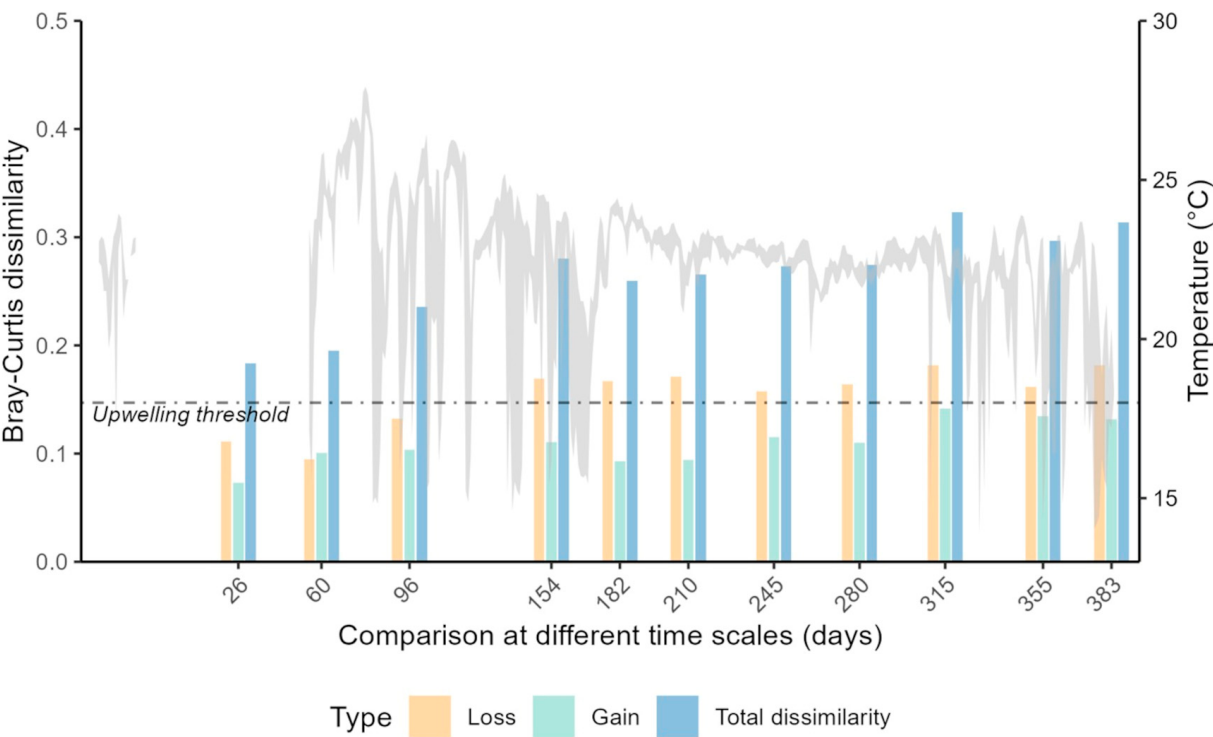


Figure 3. Temporal β -diversity of the benthic community in Arraial do Cabo Bay for the yellow group. The calculated components include species gain, loss, and dissimilarity between the initial time point (day 0) and each subsequent resampling event (e.g., day 0 vs. day 26, day 0 vs. day 60, etc.). Daily minimum and maximum seawater temperatures, retrieved from the Aqualink water monitoring system, are shown in gray. The dot-dashed horizontal line indicates the threshold temperature (18 °C) used to distinguish the presence of upwelling water masses.

Table 2. The dissimilarities (D) and *p*-values associated with the tests of significance of the distances between day 0 and each subsequent resampling event (e.g., day 0 vs. day 26, day 0 vs. day 60, etc.), for 9 communities (red, blue, green, purple, orange, yellow, brown, pink and gray). Bold *p*-values indicate statistically significant differences between groups in PERMANOVA analysis.

		Red	Blue	Green	Purple	Orange	Yellow	Brown	Pink	Gray				
		D	D	D	D	<i>p</i> -Values	D	<i>p</i> -Values	D	D	D	D	<i>p</i> -Values	
Temporal escale	0–26	21%	34%	8%	11%	0.97	14%	0.77	18%	0.08	16%	14%	20%	0.61
	0–60	26%	28%	24%	16%	0.97	21%	0.51	20%	0.79	27%	22%	27%	0.19
	0–96	37%	62%	25%	20%	0.86	33%	0.09	24%	0.10	37%	53%	36%	0.72
	0–154	41%	51%	32%	27%	0.63	38%	0.11	28%	0.03	36%	40%	39%	0.18
	0–182	31%	32%	23%	28%	0.41	35%	0.54	26%	0.02	41%	37%	37%	0.80
	0–210	34%	54%	29%	27%	0.83	38%	0.71	27%	0.03	32%	48%	47%	0.75
	0–245	47%	43%	26%	29%	0.29	38%	0.70	27%	0.08	45%	43%	46%	0.36
	0–280	42%	35%	16%	29%	0.93	39%	0.76	27%	0.04	37%	40%	46%	0.87
	0–315	47%	51%	24%	32%	0.80	33%	0.69	32%	0.03	45%	35%	35%	0.88
	0–355	50%	31%	23%	32%	0.93	39%	0.88	30%	0.18	48%	33%	36%	0.82
	0–383	54%	25%	20%	32%	0.73	40%	0.49	31%	0.06	41%	40%	34%	0.38

Table 3. Relative abundance (RA) of the mosaic elements of the yellow group community that contributed to differences between day zero and resampling events on days 154, 182, 210, 280, 315, 355, and 383. Contribution (C) of the most influential mosaic elements to the dissimilarity between resampling events. Arrows indicate increases (↑) and decreases (↓) in relative abundance between day zero and at resampling events. The contribution cut-off was set at 80%.

Mosaic Elements	Zero RA	154 RA C	182 RA C	210 RA C	280 RA C	315 RA C	355 RA C	383 RA C
<i>Palythoa caribaeorum</i>	18% ↑	22% 21% -	22% 21% ↑	20% 21% ↑	21% 22% ↑	21% 19% ↓	20% 22% ↑	20% 24%
Crustose calcareous algae	20% ↑	29% 17% ↑	29% 19% ↑	31% 18% -	20% 15% ↓	14% 13% ↑	22% 15% -	20% 15%
Turfs	16% ↓	12% 14% ↑	18% 15% ↓	11% 14% ↑	22% 15% ↓	12% 12% ↓	8% 10% ↓	13% 10%
<i>Tubastraea</i> spp.	20% ↓	19% 11% ↓	19% 11% ↑	21% 11% ↓	19% 11% -	20% 10% ↓	19% 10% -	20% 11%
<i>Darwinella</i>	5% -	5% 9% -	5% 9% ↑	7% 10% ↑	7% 10% ↑	6% 10% ↑	7% 10% ↑	8% 12%
Ceramiales	6% -	6% 7% ↓	2% 6% ↓	3% 7% ↓	1% 6% ↑	10% 10% ↑	9% 12% ↑	8% 11%
Cirripectida	6% ↓	1% 6%						
Poecilosclerida	3%			↑	7% 7% ↑	8% 7% ↑	8% 8% ↑	7% 8%

4. Discussion

The alarming rate of compositional changes demands thorough scientific investigation, as understanding this phenomenon is crucial for developing effective conservation strategies and management approaches. These findings carry particular significance for policymakers who depend on expert ecological assessments. The introduction of non-native species produces divergent ecological outcomes: diversity may increase when invaders occupy previously vacant niches without displacing native species, or diversity may decrease when invasive species compete with and ultimately exclude native taxa.

An analysis of 44 fixed plots, controlling topographic variation, which plays a key role in shaping benthic community structure, and assuming uniform exposure to the seasonal upwelling-driven environmental stress characteristic of the Cabo Frio region, identified nine distinct benthic communities. Regarding the spatial structure of the communities, it was observed that samples tended to be more similar between different sites than within the same site. For instance, the community identified as purple comprised fixed plots from multiple locations, including Fenda de Nossa Senhora, Enseada dos Cardeiros, Ilha dos Porcos, and Pedra Vermelha, with *Darwinella* spp. representing the main organism within this group. In contrast, some communities appeared to be site-specific. The gray community, for example, was exclusively associated with fixed plots from Enseada do Anequim, with *Dictyota* spp. as the main organism within this group. Three other communities, blue, brown, and pink, were represented by a single fixed plot each, suggesting highly localized or unique community structures. The blue community was characterized mainly by sponges of the order Poecilosclerida, the brown community by the bryozoan *Schizoporella errata* and the sponge *Darwinella* spp., and the pink community by articulate calcareous algae. The yellow community, which showed significant differences in β -diversity analyses, included samples from Ilha dos Porcos, Fenda de Nossa Senhora, and Pedra Vermelha, and was characterized primarily by crustose calcareous algae and *Tubastraea*, indicating a broader but still distinct distribution.

A central concern in ecology is understanding the spatial patterns of ecological structures. The data presented here, at particular spatial scales of resolution, support the interpretation that these subtidal rocky shores are organized as a mosaic of successional states representing multiple stable points [47]. Sgrott Sauer Machado et al. [48], in a study conducted at Praia Rasa in the Cabo Frio region, close to the area investigated in the present study, described the benthic community in the lower intertidal zone as exhibiting a markedly patchy spatial structure. The nine groups identified from the observer's perspec-

tive reveal spatial heterogeneity on rocky shores and suggest, from the perspective of the multispecies ecological entity, that such heterogeneity results from the interaction between spatial scales relevant to the persistence of the ecological entity within the environment. Accordingly, functional heterogeneity, a concept that refers to the perception or response of the ecological entity, which in this context consists of multispecies patches, is not the same for different groups of organisms inhabiting the same environment, as the processes affecting these groups operate at different temporal or spatial scales [32].

The variations observed in the communities identified as yellow in the present study can be explained based on the roles played by key species within these communities. *Palythoa caribaeorum* contributed most to the dissimilarity observed between resampling events. The ecological success of *P. caribaeorum* can be attributed to its well-documented competitive strategies, which include both physical mechanisms, such as overtopping, and chemical defenses that inhibit the settlement or persistence of other organisms [49]. In ref. [28], lower temperatures associated with upwelling events were shown to reduce the growth rates of *Palythoa caribaeorum* in Ilha Grande Bay, Rio de Janeiro, Brazil. In ref. [50], physical interactions initiated by *Tubastraea coccinea* did not negatively affect *Palythoa caribaeorum*, but instead imposed increased metabolic costs on the former and stimulated enhanced growth in the latter, ultimately resulting in the overgrowth of the non-native. In ref. [28], *P. caribaeorum* was capable of overgrowing *Tubastraea tagusensis*, although a competitive stalemate was noted with *T. coccinea*. In the same area as the present study [51], reported instances of non-geniculate coralline algae, contextualized here as crustose calcareous algae, overgrowing and causing the death of living non-native *Tubastraea* spp. Turf or epilithic algal matrix is a substrate rich in macroalgae, invertebrates, and microbiota, serving as a key foraging ground and primary food source for numerous tropical fish and invertebrate species [52,53]. *Darwinella* is a common sponge found at several sites in Arraial do Cabo; however, the factors driving its distributional patterns remain unclear. Calderon et al. [54] suggest that spatial distribution may be influenced by competition for space between algae and *Darwinella*, a process likely mediated by the sea urchin *Echinometra lucunter*. The trend of decreasing relative abundance of Ceramiales after a period of multiple upwelling events and its subsequent increase following a period without upwelling coincides with observations reported before by [55], who relate that, in the Cabo Frio region, the reproductive period of algae from the order Ceramiales appears to be closely linked to the seasonal rise in surface water temperatures typically observed during the winter months.

Other elements of the mosaic found on the rocky shores of Arraial do Cabo play important roles in the maintenance of benthic communities over time, with some being closely linked to the oceanographic process. The benthic community, dominated by corticated foliose macroalgae, primarily *Dictyota menstrualis*, *Dictyota mertensii*, and species of the genus *Sargassum*, was represented mainly by the gray group, with additional representation in the brown group. Studies by [35,56] demonstrate that variations in the relative abundance and size of these macroalgae are strongly correlated with the seasonal upwelling regime characteristic of the Cabo Frio region. Refs. [56,57] further highlight that upwelling events, in particular, can drive rapid shifts in ecological dominance within these communities. Sponges and the encrusting bryozoan *Schizoporella errata* are commonly reported in advanced stages of succession and are considered excellent interference competitors because of their ability to exclude other species [58,59]. The non-native encrusting bryozoan *Schizoporella errata* was present in the red, brown, purple, and blue groups. The dynamics observed in the yellow and green groups highlight the competitive dominance of *Palythoa caribaeorum* within the benthic community.

The hypothesis that communities associated with *Tubastraea* undergo shifts in diversity was tested across nine *Tubastraea*-associated community types, revealing that one exhibited differences between gains and losses that were dependent on the temporal scale of observation. The results indicate that rocky shore environments with subtidal community patch mosaic structures exhibit distinct ecological dynamics, suggesting that broad generalizations are inadequate for assessing changes in diversity. Previous studies have documented changes in tropical rocky shores associated with *Tubastraea* spp., implicitly addressing shifts in community diversity and composition [23–30]. One of the earliest assessments by [23] reported that the presence of *Tubastraea* spp. initially increased richness and diversity, but predicted a subsequent decline as competitive interactions intensified. Later, ref. [24] suggested an indirect negative impact on diversity in mussel beds, as the removal of *Perna perna* facilitated the establishment of the invasive corals. Ref. [25] showed that invaded reef areas supported lower abundance and diversity of native corals. Through a removal experiment, ref. [26] demonstrated that excluding *Tubastraea* spp. promoted the recovery of native diversity. Ref. [28] indicated that competition with *Palythoa caribaeorum* may reduce biodiversity in shallow benthic communities. In artificial substrates, ref. [29] found no significant reduction in total richness, although native taxa were replaced by non-native species. Finally, ref. [30] confirmed that invaded communities exhibit lower taxonomic and functional diversity, reinforcing the pattern of higher diversity in non-invaded areas. To date, most of these studies have been conducted on rocky shore environments. Invasive corals can indirectly compromise reef ecosystem structure and diversity, exemplified by [27]’s finding that they diminish functional diversity via reduced fish–benthos interactions. Brazilian reefs may exhibit low resistance to alien coral impacts, due to their relatively low species richness and high endemism, which may facilitate the establishment of *Tubastraea* spp.

Several of the studies discussed in our review employed or referred to alpha diversity in their analyses or discussions. Ref. [23] explicitly calculated alpha diversity metrics, including species richness (S), the Shannon–Wiener diversity index (H'), and Pielou’s evenness index (J'). Similarly, ref. [30] applied taxonomic diversity indices (alpha diversity metrics), such as Simpson’s index ($1-\text{Lambda}$), Margalef’s richness index (d), Shannon (H'), Fisher’s alpha, and Pielou’s evenness (J'), in addition to referring to “taxon richness.” Ref. [29] assessed the richness of both sessile and mobile benthic communities in their study. Ref. [25] did not directly calculate these indices; they highlighted the “lower species richness” of Brazilian coral reefs as a factor contributing to their low resistance to the impacts of alien corals. Studies often compare invaded and non-invaded communities, which can indirectly suggest differences in species composition between habitats; this approach does not explicitly assess beta diversity. In fact, none of the reviewed articles calculated a standardized index of beta diversity. Although comparisons between areas may imply compositional dissimilarity, they fall short of directly quantifying beta diversity or examining its relationship with *Tubastraea* presence while accounting for habitat heterogeneity.

The findings of this study underscore the importance of both the timing and methodology used to assess diversity, as well as the need for a comprehensive understanding of the ecological processes that generate and maintain hard-substrate communities on rocky shores. Our multivariate descriptive approach was sufficient to reveal the context-dependent nature of invasion impacts, future studies could greatly benefit from employing variance-partitioning frameworks, such as mixed-effects models or multivariate path analysis, to quantitatively disentangle the contributions of specific biotic (e.g., competition with *Palythoa*) and abiotic drivers on community turnover. While numerous studies report a correlation between *Tubastraea* abundance and lower ecological diversity, this relationship

may be weak, as critical drivers such as habitat complexity, anthropogenic influences or type communities are rarely accounted for. Therefore, while our results point to differential susceptibility among community patches, rigorously defining ‘degradation-prone’ states remains a goal for future research. Our study underscores the importance of moving beyond uniform management strategies to account for this inherent patch-level variability on rocky shores.

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