

Research Article

Community structure of shallow tropical reefs undergoing invasion by *Tubastraea* spp. in a Brazilian Marine Protected Area

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Abstract

Invasive sun corals (*Tubastraea* spp.) are spreading along the Brazilian coast where they compete for space with native species, produce chemical compounds with anti-fouling and anti-predation properties and modify community structure and function. The tropical rocky shores of the Ilha Grande Bay were the first to be invaded in the southwest Atlantic and the Tamoios Marine Protected Area (MPA) within the bay was directly in the path of the spread of *Tubastraea*. MPAs aim to conserve biodiversity, preventing habitat loss and fragmentation and maintain healthy ecosystems. As healthy communities might better resist invasion the aim of this study was to investigate to what extent the benthic communities of the MPA are resisting the invasion. Baseline data on the abundance of the invasive corals *Tubastraea* spp. and community structure (cover) were quantified at eight sites over six years. The benthic communities were dominated by multispecies algal turfs, the mat-forming zooantharian *Palythoa caribaeorum* and the red alga *Asparagopsis taxiformis* and fell into five community groups two of which contained *Tubastraea* spp. The number of invaded sites increased over time as did the abundance of *Tubastraea* spp. in the communities. *Tubastraea* spp. sequentially invaded the studied communities within the MPA independently of differing community compositions – i.e. they did not offer better biotic resistance than unprotected areas. This was facilitated by the patchy nature of the communities which allowed *Tubastraea* spp. to get a foothold by initially avoiding species such as *P. caribaeorum* which offer greater biological resistance. At one site a significant reduction in *Tubastraea* spp. was detected after mechanical control. We conclude that the MPA's status as a conservation unit was important to attract research and thus for establishing a baseline, quantifying change due to the invasion and focusing limited management resources, but not in providing significant biotic resistance to the invasion.

Key words: baseline, benthos, coral, rocky shore, Tamoios Ecological Station

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Introduction

Marine ecosystems are facing increasingly strong multiple-stressors. The coastal zone suffers intense degradation, as the coast concentrates activities that exert greatest pressure on coastal and marine areas (Maestro et al. 2019). One strategy that government agencies use to protect and conserve natural marine resources is the establishment of protected areas. Marine protected areas (MPAs) are geographically defined areas for the conservation of marine biodiversity and the maintenance of the community structure and functioning of the marine ecosystem (Keller et al. 2009; Claudet 2011; Watson et al. 2014). However, the objectives of an MPA have been expanded to encompass not only environmental, but also social and economic issues (Reuchlin-Hugenholtz and McKenzie 2015; Humphreys and Clark 2020). In the last few decades there has been an increase in the number and extension of protected areas around the world, emphasizing that protection is one of the most effective instruments to conserve biodiversity and resources, in addition to reducing human impact (Cifuentes et al. 2000; Maestro et al. 2019; Humphreys and Clark 2020). However, researchers have questioned how vulnerable MPAs are to the entry of non-native species (Iacarella et al. 2019) and their role as a barrier to the spread of such species (Occhipinti-Ambrogi and Savini 2003; Galil 2007) today is unclear (Giakoumi and Pey 2017).

Brazil has about 140 marine non-native species, 19 of which are invasive, causing significant change in native ecosystems (Teixeira and Creed 2020). Among them the sun corals *Tubastraea coccinea* Lesson, 1989 and *Tubastraea tagusensis* Wells, 1982, native to the Pacific (Creed et al. 2017a), were first reported in Brazil in the 1980s through fouling on oil / gas platforms, initially in Rio de Janeiro (Castro and Pires 2001; De Paula and Creed 2004; Creed et al. 2017a). They are now known to occur along 3,400 km of the Brazilian coastline from Ceará (Soares et al. 2016) to Santa Catarina (Barreiros et al. 2000; Capel 2012) on rocky and coral reefs and on artificial substrates (wrecks and vectors).

In addition to competing for space with native species (Creed 2006; De Paula 2007; Lages et al. 2010a, 2010b, 2011, 2012; Santos et al. 2013; Silva et al. 2017), the invasive corals *Tubastraea* spp. can cause tissue necrosis in other corals such as *Mussismilia hispida* (Creed 2006; De Paula 2007; Miranda et al. 2016), *Siderastrea stellata* and *Madracis decactis* (Miranda et al. 2016). *T. coccinea* and *T. tagusensis* also produce chemical compounds such as alkaloids (Maia et al. 2014a, b) with antifouling and anti-predation properties (Lages et al. 2010a, b; Lages et al. 2012; Santos et al. 2013). They can also modify community structure and function (Lages et al. 2011; Pires-Teixeira et al. 2021). These species also cause social and economic impacts by impacting fisheries resources (Mantelatto and Creed 2015), shipping and port installations (Creed et al. 2017a; Braga et al. 2021).

Ilha Grande, which is positioned to form the Ilha Grande Bay (IGB) region (Figure 1), is located in the south of the State of Rio de Janeiro, Brazil, was the first shoreline to be invaded by *Tubastraea* spp. in Brazil and has been most affected by the subsequent spread of *Tubastraea* spp. from Ilha Grande into the IGB (Silva et al. 2011, 2014; Creed et al. 2017a). These species have become highly abundant and widely distributed on the subtidal tropical rocky shores in the region (Creed et al. 2008; Lages et al. 2011; Silva et al. 2011, 2014), where they compete with native species (Creed 2006; Lages et al. 2010a, 2010b, 2011, 2012; De Paula et al. 2017; Guilhem et al. 2020) and change the community structure of the native communities (Lages et al. 2011; Mizrahi et al. 2017; De Paula et al. 2017). The Tamoios Ecological Station Marine Protected Area (MPA), located within the Ilha Grande Bay, Brazil, lies directly in the path of this invasion.

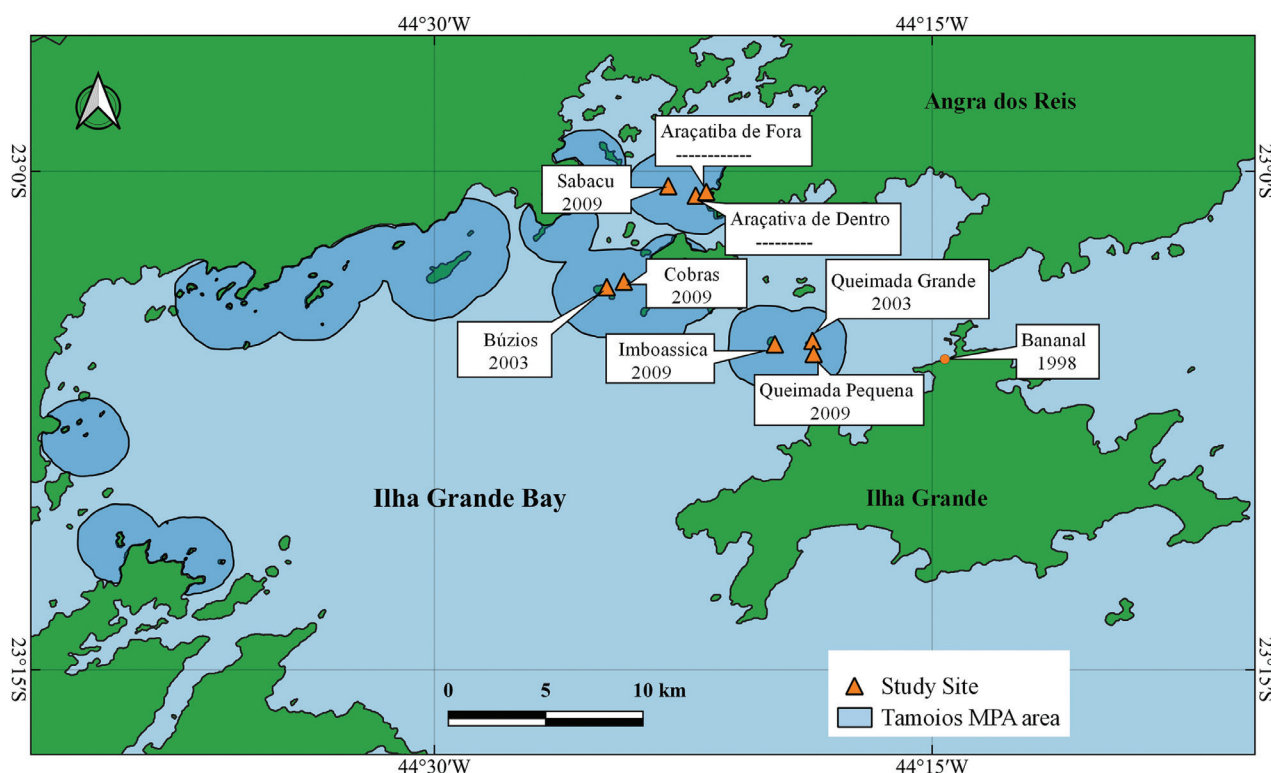


Figure 1. Map of the Ilha Grande Bay, Brazil, showing the Tamoios Marine Protected Area, eight study sites, first point of introduction into the region near Ilha Grande and the year *Tubastraea* was first detected at each location.

Although MPAs are fundamental for the conservation of biodiversity, preventing habitat loss and fragmentation (Rodrigues et al. 2004), they are not immune to invasions by non-native species, which can cause damage and threaten the conservation of these areas. The Tamoios MPA was directly in the path of the spread of *Tubastraea* and the two species were first recorded in the MPA in 2003 at Queimada Grande and Búzios Islands (De Oliveira Pires 2007; Creed et al. 2008) (Figure 1). These points are the closest inside the MPA to Ilha Grande, the first point of introduction in Brazil, ca 1998 (Silva et al. 2014; Creed et al. 2017a). Subsequently *Tubastraea* spp. expanded further into IGB and the MPA (Mantelatto et al. 2013; Silva et al. 2014; Gomes et al. 2015).

The aim of this study was to investigate to what extent the shallow tropical benthic rocky reef communities protected by the Tamoios MPA have resisted the invasion of *T. tagusensis* and *T. coccinea* and if they have changed their composition and community structure (cover abundance). Our hypotheses are that (1) densities and cover of *T. tagusensis* and *T. coccinea* increase over time within the MPA (6 years) and over space (eight sites) in the MPA; (2) the increasing dominance and ubiquity of *T. tagusensis* and *T. coccinea* within the MPA changes the community structure of native communities, regardless of the potentially enhanced resistance that protected ecosystems may be afforded by the MPA.

Materials and methods

This study was carried out at eight sites (islands) within the Tamoios Ecological Station Marine Protected Area, located within the Ilha Grande Bay, Brazil. The Tamoios MPA is a fully protected federal marine conservation area created by Decree n° 98.864 (Brasil 1990) as a mitigating measure for the construction and

operation of the Angra dos Reis nuclear power plants. Its aim is to preserve the island and marine ecosystems of IGB to allow background environmental monitoring of the region. It is formed of 29 discrete islands, islets and rocky reefs and respective 1 km radii of surrounding waters which total 5.7% of the surface area of IGB (Figure 1) (Brasil 2006). The MPA has an Ecological Station category which means that it must be wholly protected, with no visitation (including no take) apart from use for basic and applied research and development of education programs for conservation (Brazil 1981).

Sites were chosen based on different abundances of *Tubastraea* spp. previously determined by Silva et al. (2011): Queimada Grande (23°05'05.9"S, 44°18'36.2"W) and Queimada Pequena (23°05'29.6"S, 44°18'34.1"W), with high abundance; Cobras (23°03'19.0"S, 44°24'17.3"W) and Imboassica (23°05'12.2"S, 44°19'44.2"W) Islands, with medium abundance; Sabacu (23°00'26.6"S, 44°22'57.0"W) and Búzios (23°03'29.0"S, 44°24'48.2"W) Islands, with low abundance and Araçatiba de Fora (23°00'43.6"S, 44°22'07.3"W) and Araçatiba de Dentro (23°00'37.1"S, 44°21'48.2"W) Islands, where *Tubastraea* spp. were absent at the start of the study (Figure 1).

The benthic communities were sampled three times over a six year period (2011, 2012 and 2017, between May and July; periodicity was funding dependent) by SCUBA diving. At each site, concrete blocks were placed to permanently mark sample areas. The data were obtained using 50 m long transects parallel to the coast, at a depth of 2–6 m (where the highest abundance of *Tubastraea* spp. is found – De Paula and Creed 2005). A visual (quadrat) estimate method (sensu Mantelatto et al. 2018a) was used which is the standard method for community monitoring used by the Projeto Coral-Sol (Sun-Coral Project) and follows methods used by Oigman-Pszczol et al. (2004) and Lages et al. (2011) determined by Mantelatto et al. (2013) as best method for describing these communities. The community is sampled in 0.25 m² quadrats which are positioned at 30 randomly chosen points along each transect. The major space occupying sessile benthic taxons are quantified by two SCUBA divers who observe and score the taxon that occupies most space in each of 25 square subdivisions (0.10 × 0.10 m). The density of individuals or colonies of *T. tagusensis* and *T. coccinea* in each quadrat were also counted by divers.

The average densities (colonies.m⁻²) and cover (% abundance) of *Tubastraea* spp. were compared between different locations and years. The density data were square root- and cover arcsine-transformed means and compared with analysis of variance (ANOVA) and Tukey test using the SPSS 17.0 program for Windows (SPSS Inc.). The community's structures [as cover (%)] of major space occupying sessile benthic taxons were compared using mean cover values of taxa for n = 30 replicates for each site and time. To identify possible changes in the community structure caused by invading corals, invaded and non-invaded communities were compared. Univariate measures of species richness (*S*), diversity (Shannon-Wiener Index *H'*) and evenness (Pielou's index, *J'*) (Magurran 1988) were calculated and communities-times with *Tubastraea* spp. compared to those without using one-way ANOVAs. Community ordinations (non-metric multidimensional scaling analysis - MDS) and classifications (cluster analysis) were performed on Bray-Curtis similarity matrices derived from standardized and root fourth transformed community data. Similarity analyses (ANOSIMs) were carried out to test differences between groups and Similarity Percentage Analyses (SIMPERs) used to identify structuring taxa in community groups, especially from the point of view of the two invasive *Tubastraea* spp. The PRIMER program (6.1.13, Plymouth Routines in multivariate ecological research) was used for these analyses (Clarke and Gorley 2006).

Results

Density and cover of *Tubastraea* spp.

Over the six year period of the study the corals *Tubastraea* spp. were observed at six of the eight study sites but while they were present at Imboassica, Queimada Grande and Queimada Pequena over the whole study period they only appeared at Sabacu, Búzios and Cobras Island six years later (Figure 2). In general, the densities of *T. tagusensis* were higher than those of *T. coccinea* (means of 20.3 and 4.7 colonies.m⁻², respectively).

Density variation of *Tubastraea* spp. was observed to increase over the years. Mean colony density at the genus level (summing the two species together) was 19.5 colonies.m⁻² (SE = 8.8) in 2011, similar in 2012 (17.8 colonies.m⁻² ± 8.3) and increased to 23.8 colonies.m⁻² (± 9.2) in 2017. When comparing the species separately, *T. coccinea* increased between 2011 and 2012 (mean 0.95 and 7.2 colonies.m⁻² respectively) and somewhat by 2017 (to 5.9 colonies.m⁻²), while *T. tagusensis* density increase somewhat from 19.5 and 17.8 colonies.m⁻² in 2011 and 2012 to 23.7 colonies.m⁻² in 2017. For sites with *Tubastraea* spp., density varied significantly over time in a site specific manner for both species (Figure 2; ANOVA Time × Site interaction for *T. tagusensis* F = 1.92, p = 0.04; for *T. coccinea* F = 6.4 p < 0.001, data transformed (Y+0.5)^{1/2}).

When comparing the eight study sites, it was observed that Queimada Pequena (L8), Imboassica (L6) and Queimada Grande (L7) presented the highest average (± SE) densities of *Tubastraea* spp. (68 ± 13, 59 ± 6 and 28 ± 12 colonies.m⁻², respectively). *T. tagusensis* was observed in greater density in Queimada Pequena

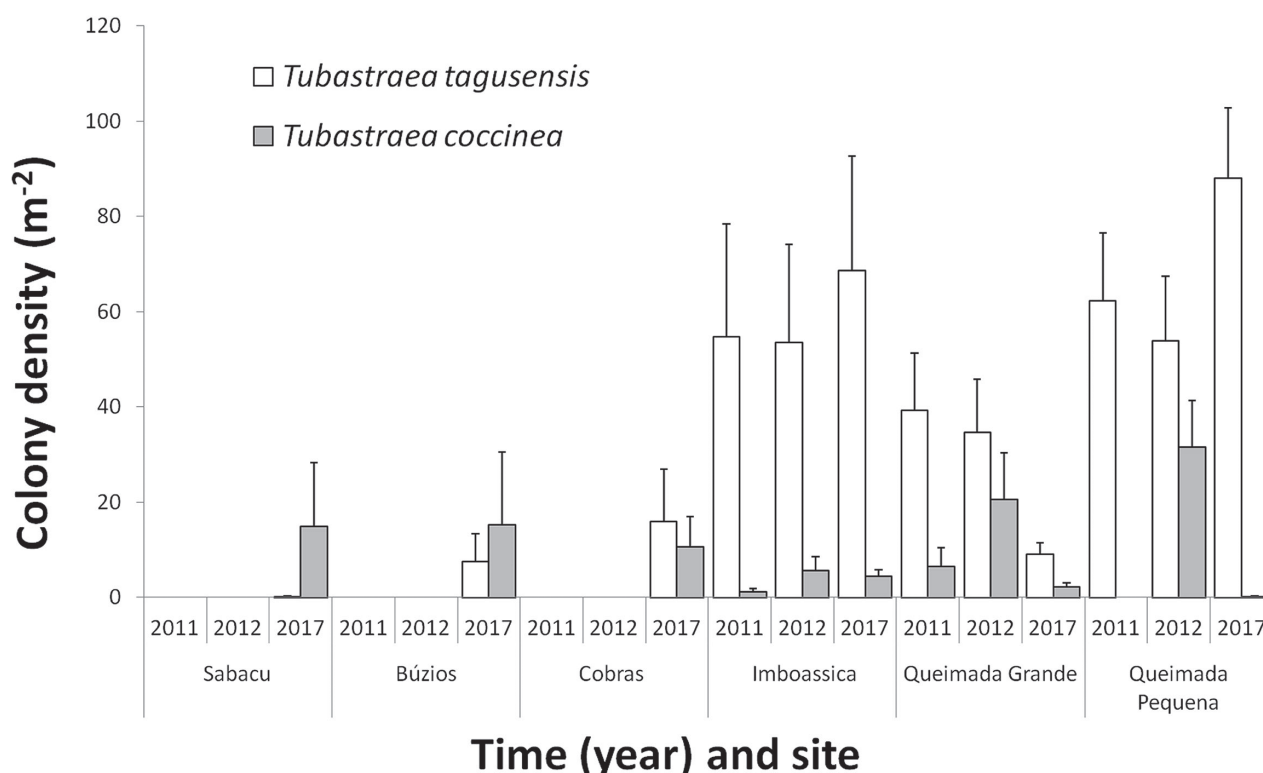


Figure 2. Abundance as colony density of the invasive corals *Tubastraea tagusensis* and *T. coccinea* in shallow subtidal tropical benthic rocky reef communities at eight study sites in the Tamoios Marine Protected Area, Ilha Grande Bay, Brazil over six years. Data are means and bars = Standard Error. Araçatiba de Dentro and Araçatiba de Fora are not shown as no colonies were found during the study period.

and Imboassica (average of 68 and 59 colonies.m² respectively). For *T. coccinea*, the highest densities were recorded in Queimada Pequena (L8) and Queimada Grande (L7) (10.5 and 9.7 colonies.m² respectively). It is worth noting that significant reductions in density occurred in Queimada Grande (L7) (2012 to 2017) from 21 to 2 colonies.m² for *T. coccinea* (ANOVA: $F = 7.93$, $p = 0.007$) and from 34 to 9 colonies.m² for *T. tagusensis* (ANOVA: $F = 5.59$, $p = 0.021$).

Despite the high densities of the invading corals *Tubastraea* spp. in the study sites, somewhat different results were observed for the percentage cover of these organisms (Figure 3). Using the cover method described above only four sites (Búzios, Imboassica, Queimada Grande and Queimada Pequena) presented percentage cover scores for *Tubastraea* spp. At Búzios cover was only scored in 2017 (Figure 3) while the other sites had cover of *Tubastraea* spp. at all survey times. Cover was quite low, usually less than 4% except for *T. tagusensis* at Queimada Pequena in 2017 (10.9%). For the sites with *Tubastraea* spp. cover varied significantly over time in a site specific manner for both species (Figure 3; ANOVA Time \times Site interaction for *T. tagusensis* $F = 6.42$, $p < 0.001$; for *T. coccinea* $F = 7.93$ $p = 0.007$, data arcsine transformed).

Benthic communities

We listed a total of 37 major space occupying taxa in the benthic communities of the Tamoios MPA during the study (Table 1; Suppl. material 1). Throughout the eight studied sites in the Tamoios MPA over half of shallow water benthos was covered by the multispecies algal turfs functional group (mean cover 54.9%), followed by the mat-forming zooantharian *Palythoa caribaeorum* (22.9%) the red alga *Asparagopsis taxiformis* (8.3%), the sponge *Desmapsamma anchorata* (3.2%) and the

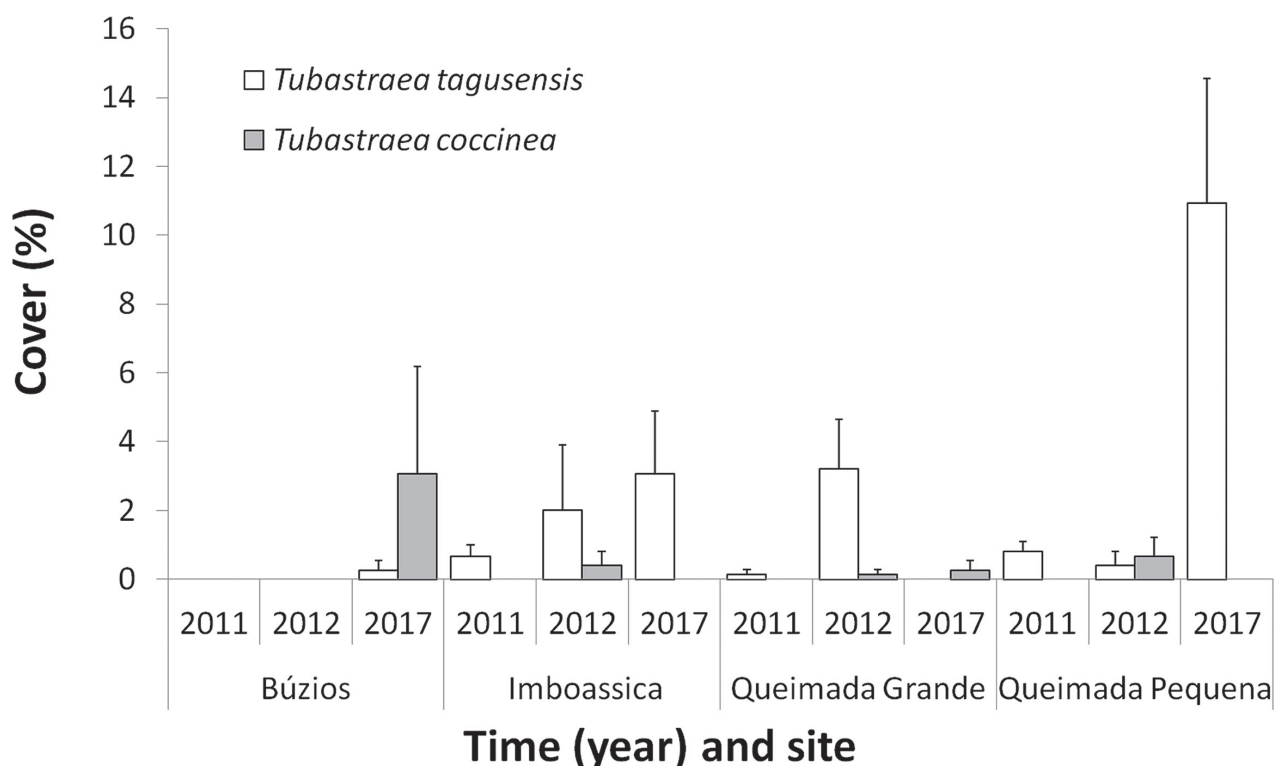


Figure 3. Abundance as cover (%) of the invasive corals *Tubastraea tagusensis* and *T. coccinea* in shallow subtidal tropical benthic rocky reef communities at eight study sites in the Tamoios Marine Protected Area, Ilha Grande Bay, Brazil over six years. Data are means and bars = Standard Error. Sabacu, Araçatiba de Dentro and Araçatiba de Fora are not shown as there were no cover scores found during the study period.

Table 1. List of taxa and mean cover (% \pm standard error) over six years at the eight study sites in the Tamoios Marine Protected Area, Ilha Grande Bay, Brazil.

Year	2011	2012	2017
Algae			
<i>Acanthophora spicifera</i> (M. Vahl) Børgesen, 1910	0.38 (\pm 0.41)	0 (\pm 0)	0 (\pm 0)
Crustose coralline algae	2.12 (\pm 1.48)	1.9 (\pm 0.62)	2.58 (\pm 1.28)
Turf-forming algae	56.96 (\pm 7.18)	60.76 (\pm 7.17)	47.04 (\pm 6.31)
<i>Asparagopsis taxiformis</i> (Delile) Trevisan de Saint-Léon, 1845	2.95 (\pm 1.45)	6.44 (\pm 4.43)	15.55 (\pm 4.48)
<i>Caulerpa racemosa</i> (Forsskål) J.Agardh, 1873	0.63 (\pm 0.39)	0.18 (\pm 0.13)	0.86 (\pm 0.48)
<i>Dictyota</i> sp.	0.35 (\pm 0.35)	0 (\pm 0)	0.8 (\pm 0.86)
<i>Dichotomaria marginata</i> (J.Ellis & Solander) Lamarck, 1816	0 (\pm 0)	0 (\pm 0)	0.47 (\pm 0.26)
<i>Laurencia</i> sp.	0.05 (\pm 0.05)	0 (\pm 0)	0 (\pm 0)
<i>Padina gymnospora</i> (Kützinger) Sonder, 1871	0.13 (\pm 0.09)	0.08 (\pm 0.06)	0.02 (\pm 0.02)
<i>Sargassum</i> sp.	3.08 (\pm 1.33)	0.13 (\pm 0.11)	1.07 (\pm 1.14)
Cnidaria			
<i>Astrangia rathbuni</i> Vaughan, 1906	0 (\pm 0)	0 (\pm 0)	0.07 (\pm 0.05)
<i>Carijoa riisei</i> (Duchassaing & Michelotti, 1860)	0.47 (\pm 0.4)	0.07 (\pm 0.05)	0.12 (\pm 0.08)
<i>Leptogorgia punicea</i> (Milne Edwards & Haime, 1857)	0 (\pm 0)	0 (\pm 0)	0.08 (\pm 0.09)
<i>Macrorhynchia philippina</i> Kirchenpauer, 1872	0.05 (\pm 0.04)	0.07 (\pm 0.04)	0.05 (\pm 0.05)
<i>Madracis decactis</i> (Lyman, 1859)	0 (\pm 0)	0.02 (\pm 0.02)	0 (\pm 0)
<i>Mussismilia hispida</i> (Verrill, 1901)	0.33 (\pm 0.11)	0.2 (\pm 0.09)	0.13 (\pm 0.09)
<i>Palythoa caribaeorum</i> Duchassaing & Michelotti, 1860	23.26 (\pm 8.05)	26.03 (\pm 8.58)	19.43 (\pm 8.22)
<i>Palythoa variabilis</i> (Duerden, 1898)	0 (\pm 0)	0 (\pm 0)	0.03 (\pm 0.04)
<i>Phyllactis praetexta</i> (Couthouy in Dana, 1846)	0 (\pm 0)	0.02 (\pm 0.02)	0.05 (\pm 0.04)
<i>Tubastraea coccinea</i> Lesson, 1830	0 (\pm 0)	0.15 (\pm 0.1)	0.42 (\pm 0.41)
<i>Tubastraea tagusensis</i> Wells, 1982	0.2 (\pm 0.13)	0.7 (\pm 0.46)	1.78 (\pm 1.45)
<i>Zoanthus sociatus</i> (Ellis, 1786)	1 (\pm 0.85)	0.55 (\pm 0.45)	1.12 (\pm 0.76)
Ectoprocta			
<i>Schizoporella</i> sp.	0.02 (\pm 0.02)	0 (\pm 0)	0.13 (\pm 0.11)
Porifera			
<i>Amphimedon viridis</i> Duchassaing & Michelotti, 1864	0.3 (\pm 0.18)	0.25 (\pm 0.19)	0.05 (\pm 0.04)
<i>Desmapsamma anchorata</i> (Carter, 1882)	5.32 (\pm 1.83)	1.27 (\pm 0.51)	2.94 (\pm 0.98)
<i>Dysidea etheria</i> de Laubenfels, 1936	0 (\pm 0)	0 (\pm 0)	0.12 (\pm 0.12)
<i>Haliclona</i> (<i>Soestella</i>) <i>caerulea</i> (Hechtel, 1965)	0.1 (\pm 0.09)	0 (\pm 0)	0 (\pm 0)
<i>Iotrochota arenosa</i> Rützler, Maldonado, Piantoni & Riesgo, 2007	1.54 (\pm 0.83)	0.7 (\pm 0.38)	2.49 (\pm 1.35)
<i>Mycale</i> (<i>Aegogropila</i>) <i>americana</i> van Soest, 1984	0 (\pm 0)	0 (\pm 0)	0.07 (\pm 0.07)
<i>Mycale</i> (<i>Zygomyscale</i>) <i>angulosa</i> (Duchassaing & Michelotti, 1864)	0 (\pm 0)	0 (\pm 0)	0.07 (\pm 0.06)
<i>Mycale</i> (<i>Carmia</i>) <i>magnirhaphidifera</i> van Soest, 1984	0 (\pm 0)	0 (\pm 0)	0.02 (\pm 0.02)
<i>Scopalina ruetzleri</i> (Wiedenmayer, 1977)	0 (\pm 0)	0 (\pm 0)	0.8 (\pm 0.49)
<i>Tedania</i> (<i>Tedania</i>) <i>ignis</i> (Duchassaing & Michelotti, 1864)	0.1 (\pm 0.11)	0.13 (\pm 0.14)	0.3 (\pm 0.2)
Urochordata			
<i>Didemnum</i> sp.	0 (\pm 0)	0.03 (\pm 0.02)	1.12 (\pm 0.7)
<i>Lissoclinum perforatum</i> (Giard, 1872)	0 (\pm 0)	0 (\pm 0)	0.02 (\pm 0.02)
<i>Phallusia nigra</i> Savigny, 1816	0.65 (\pm 0.29)	0.25 (\pm 0.23)	0.22 (\pm 0.23)
Echinodermata			
<i>Tropiometra carinata</i> (Lamarck, 1816)	0 (\pm 0)	0.07 (\pm 0.05)	0 (\pm 0)

incrusting calcareous algal functional group (2.2%); these five taxons represented more than 90% of the cover. The invasive coral *Tubastraea tagusensis* was the eighth most abundant taxon (0.9%) and *T. coccinea* was the eighteenth most abundant taxon overall (0.2%) (Table 1).

Overall mean richness of main space occupying benthic species was 10.5 species but this varied from 4 taxa (Cobras island in 2012) to 17 taxa (Queimada Grande in 2017) (Table 2). Overall mean diversity (Shannon-Wiener diversity index) of main space occupying benthic species was 1.14, but this also varied over time and space. Sabacu (2017), Araçatiba de Fora (2017) and Imboassica (2011) were most diverse and uniform, while Cobras island (2011 and 2012) and Araçatiba de Dentro (2012) had the least diverse and uniform communities (Table 2). When we compared richness, diversity and uniformity between communities-times with vs. without *Tubastraea* spp. ($n = 12$ for each level) all metrics were slightly higher in communities with *Tubastraea* spp. (mean richness = 10.8 vs. 10.2; diversity = 1.3 vs 1.0; uniformity = 0.53 vs. 0.44 but we found no significant differences (ANOVA, $n = 12$ for each level, $p = 0.531$, 0.108 and 0.062 respectively).

Table 2. Community structure metrics (species richness, Shannon-Wiener diversity index and Pielou uniformity index) over six years for shallow subtidal tropical benthic rocky reef communities at the eight study sites in the Tamoios Marine Protected Area, Ilha Grande Bay, Brazil.

Year	Richness			Diversity			Evenness		
	2011	2012	2017	2011	2012	2017	2011	2012	2017
Araçatiba de Dentro	10	12	12	0.80	1.18	1.68	0.35	0.48	0.68
Araçatiba de Fora	14	10	9	1.55	0.76	0.93	0.59	0.33	0.42
Sabacu	12	10	13	0.98	0.87	1.72	0.39	0.38	0.67
Búzios	11	9	12	1.46	0.94	1.41	0.61	0.43	0.57
Cobras	9	4	8	0.76	0.38	1.03	0.35	0.28	0.50
Imboassica	10	11	11	1.63	1.13	1.40	0.71	0.47	0.58
Queimada Grande	9	10	17	1.10	1.17	1.24	0.50	0.51	0.44
Queimada Pequena	8	8	13	0.94	0.76	1.51	0.45	0.37	0.59

In the analysis of multi-dimensional scaling it was possible to observe that at the 60% of similarity level there was an evident separation between communities with and without *Tubastraea* spp. (groups D and E with; A, B and C without; Figures 4a and b). The ANOSIM test detected a significant difference between communities-times with *Tubastraea* spp. presence vs. absence (ANOSIM, global $R = 0.372$, $p = 0.002$). ANOSIM did not detect significant differences between times (ANOSIM global $R = 0.078$, $p = 0.117$). Five community groups were formed at the 60% similarity level cut-off.

Using SIMPER (Suppl. material 2) it was possible to identify differences and similarities in species composition responsible for the groups. Group A (3 community samples) was characterized by turf-forming algae, *A. taxiformis*, *Phallusia nigra* and *D. anchorata*. This group differed from Group B (5 community samples) because in Group B *P. caribaeorum*, *Caulerpa racemosa* and *Sargassum* spp. were important community components whereas *P. nigra* was not. Group E, the largest group with 14 community samples, was characterized mainly by turf-forming algae, *P. caribaeorum*, *D. anchorata* and crustose coralline algae, differing from Group A because of greater cover of *P. caribaeorum* and crustose coralline algae and lesser cover of *A. taxiformis*. Group E differed from Group B mainly because *A. taxiformis*, *C. racemosa* and *Sargassum* spp. were not important components of Group E. Group C (a single community at Cobras in 2012) was characterized by

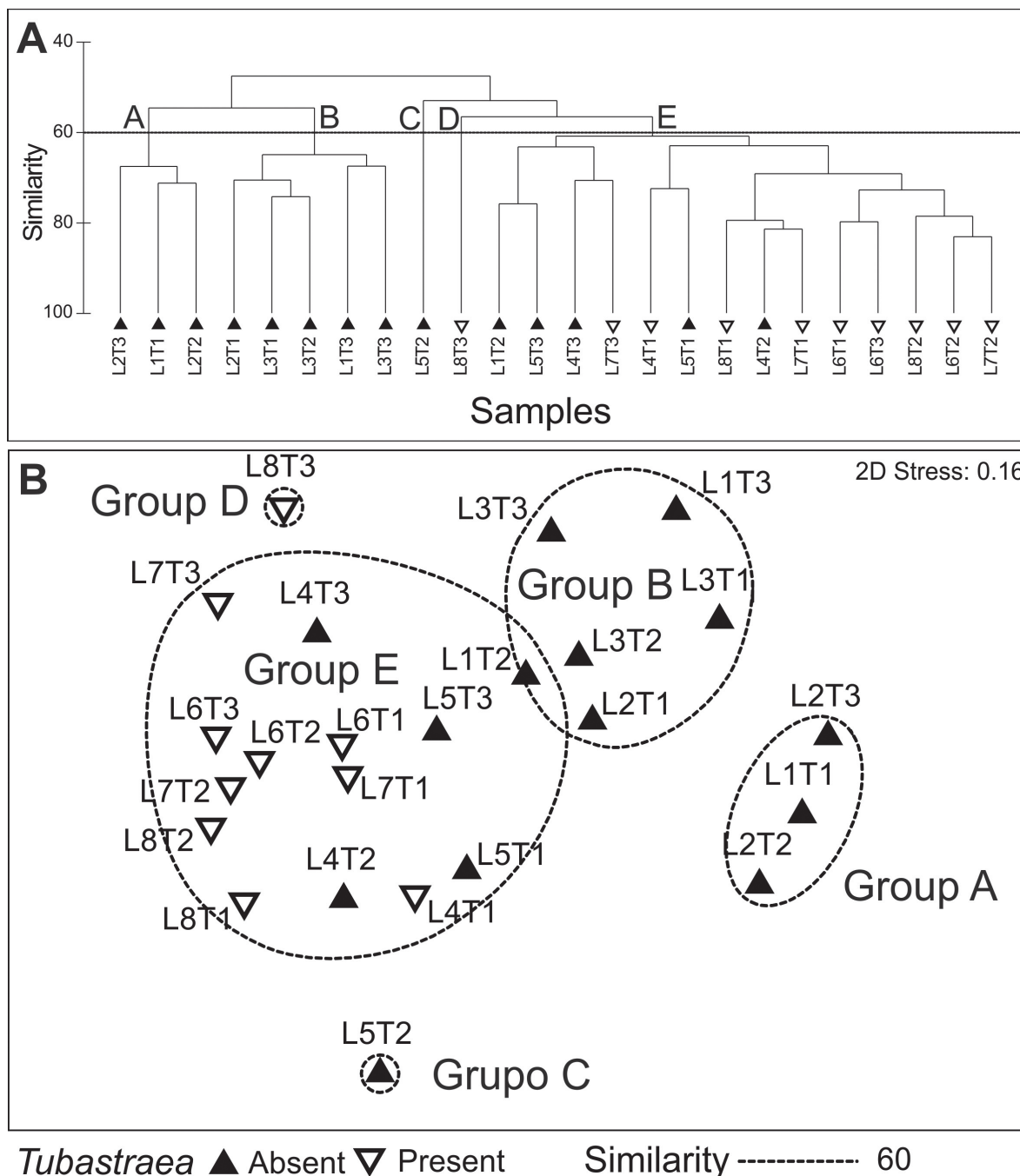


Figure 4. Classification and ordination of shallow subtidal tropical benthic rocky reef communities at eight study sites in the Tamoios Marine Protected Area, Ilha Grande Bay, Brazil over six years during invasion and range expansion by the the invasive corals *Tubastraea tagusensis* and *T. coccinea*. A) Cluster analysis with the 60% similarity cut-off for group formation; B) non-metric multidimensional scaling analysis showing Groups derived from the 60% cluster analysis cut-off. Analyses were performed on Bray-Curtis similarity matrices derived from standardized and fourth root transformed community data. Legend: L1 = Araçatiba de Fora, L2 = Araçatiba de Dentro, L3 = Sabacu, L4 = Búzios Island, L5 = Ilha das Cobras, L6 = Ilha de Imboassica, L7 = Ilha de Queimada Grande, L8 = Ilha de Queimada Pequena; T1 = 2011, T2 = 2012, T = 2017

near dominance of turf algae in that community (mean cover 90.1%). Group D was characterized by turf algae (58%) and high covers of crustose coralline algae (10%), *T. tagusensis* (11%) and *Iotrochota arenosa* (8.5%), as well as very low cover of *P. caribaeorum*. SIMPER identified that this group differed from the others largely due to the high cover of *T. tagusensis* (plus *I. arenosa* plus crustose coralline

algae when compared to Group A; minus *P. caribaeorum* when compared to Group E; plus *I. arenosa* minus *Sargassum* spp. when compared to Group B; plus *I. arenosa* when compared to Group C). Finally, with regard to the importance of *Tubastraea* spp. in Group E, it is important to note that neither species was one of the eight taxa which most contributed to characterize the group (90%). Furthermore *T. tagusensis* and *T. coccinea* were only the ninth and eighteenth most important taxa in their contribution to the dissimilarity between Groups A and E (respectively contributing 1.06% and 0.69%) and eleventh and eighteenth most important taxa in their contribution to the dissimilarity between Groups B and E (respectively contributing 4.04% and 2.19%) (Suppl. material 2).

Discussion

In this study we have provided baseline data on the abundance of the invasive corals *Tubastraea* spp. at eight locations within the Tamoios MPA during their ongoing invasion over a six year period. We have also described the main space occupying species that form the invaded shallow subtidal benthic rocky-reef communities as well as their change during the invasion. This is an important advance as reliable data on the distribution and abundance of the benthos in MPAs is essential to form a baseline, detect change and plan effective conservation strategies. Furthermore, under the invasion scenario, we also need to know the distribution and abundance of non-native species in order to assess spread dynamics, proportion how much change is due to the invasion and plan effective management actions (Mannino and Balistreri 2018).

In general, the densities of *T. tagusensis* were higher than those of *T. coccinea*. The earlier arrival, establishment and prevalence of *T. tagusensis* over *T. coccinea* has also previously been observed by Lages et al. (2011), Mantelatto et al. (2013), Silva et al. (2014) and Creed et al. (2021) and corroborated here. Differences in characteristics of the two species such as the reproductive biology, recruitment and survival rates, as well as the degree of chemical defense, determine this (Fenner and Banks 2004; Lages et al. 2010b; De Paula et al. 2014; Creed et al. 2021).

We found no significant overall difference in the community indices (richness, diversity and evenness). Using different invasive species, locations and communities (including *Tubastraea* spp. in the study region) Pires-Teixeira et al. (2021) demonstrated through diversity indices that the taxonomic diversity was lower in highly invaded rocky reef communities. Under certain scenarios increases in community indices can simply be a mathematical artifact of increasing richness (the insertion of the invasive species). Community indices are also sensitive to the stage of invasion and ecosystem engineering species such as *Tubastraea* spp. may provide novel microhabitats (Guilhem et al. 2020) and/or foster invasional meltdown (Vinagre et al. 2018; Tanasovici et al. 2020) which are further negative impacts hidden by the univariate statistics. Alternatively these differing results may reflect the processes behind the invasion paradox (Fridley et al. 2007), the co-occurrence of independent lines of support for both a negative and a positive relationship between native biodiversity and the invasions of non-native species.

The communities we described in the MPA are similar to those described throughout the region by others (Lages et al. 2011; Mantelatto et al. 2013; Koutsoukos et al. 2015; Mantelatto et al. 2020, 2022; Carneiro et al. 2021) and indeed are those typically expected for shallow subtidal rocky reefs on tropical shores in the southwest Atlantic (Aued et al. 2018; Mantelatto et al. 2018a). The turf algae are composed of a variety of species, mainly articulated coralline algae such as *Jania* sp. and *Hypnea* sp. and *Cladophora* sp. (Silva et al. 2017; Carneiro et al. 2021). This group of algae is characterized by resistance to physical disturbances

and herbivory (Hay 1981), which explains its high abundance on most studied rocky shores. The high abundance of *P. caribaeorum* in the communities is due to the fact that this cnidarian is considered to be a formidable competitor for space with other benthic organisms (Bastidas and Bone 1996; Mantelatto et al. 2018b; Guilhem et al. 2020; Carneiro et al. 2021; Soares et al. 2021). It grows by lateral extension and has one of the highest growth rates among the zoanthids (Suchanek and Green 1981) which allows for the rapid occupation of empty space on the shore. The sponges *D. anchorata* and *I. arenosa* also offer some biotic resistance to invasion by *Tubastraea* spp. as they are the main sponges that compete with the invasive coral (De Paula 2007; Meurer et al. 2010; Lages et al. 2012; Silva et al. 2017; Guilherme da Silva 2022). *I. arenosa* is considered to be the third most abundant sponge in the region (Castello-Branco and Menegola 2014).

It has been argued that one of the potential functions of MPAs is to provide resistance to the spread of non-native species (Shea and Chesson 2002). In order to invade a community a species must not only arrive but establish, grow and increase in abundance in the invaded community which depends on the opportunities that a particular invaded community provides for the invader (Shea and Chesson 2002). MPAs theoretically maintain healthier ecosystems with lower, and better managed human disturbance levels which in turn foster more mature communities. Mature communities should have more complete and efficient resource utilization, so they are less vulnerable to biological invasions (Shea and Chesson 2002; Guidetti et al. 2014). However as Mannino and Balistreri (2018) point out, despite there being plenty of information on other aspects of MPA's effectiveness, how they affect the invasion process has been little studied (Burfeind et al. 2013; Ardura et al. 2016; Giakoumi et al. 2016; Giakoumi and Pey 2017). It might be the case that MPAs are no more resistant to invasion than unprotected areas or may be even more susceptible, or this depends on the parameters used to assess communities (Cacabelos et al. 2020). For example propagule pressure may be enhanced by the placement of MPAs nearby pathways of introduction such as ports or harbors, and boat vector traffic and impacts may increase in the MPA due to increased tourism (Burfeind et al. 2013; Giakoumi and Pey 2017; Mannino and Balistreri 2018). The Tamoios MPA is fully protected with no visitation (including no take) which, at least on paper, should impede boat vector traffic and impacts, although it is nearby major shipping routes and ports (Silva et al. 2014).

We found no evidence that the communities we studied in the Tamoios MPA were any more resistant to invasion by *Tubastraea* spp. than unprotected locations. In fact the general trends indicated that in the region we are witnessing an ongoing range expansion by larvae being carried north and eastwards from the initial point of introduction at Ilha Grande circa 1998 (Figure 1), as has been demonstrated through extensive monitoring of the region by Silva et al (2011; 2014). In general terms the establishment of *Tubastraea* spp. in the MPA was sequential over space, with higher abundances at sites (Queimada Pequena and Queimada Grande) with a longer invasion history and/or nearer to Ilha Grande (Figure 1).

In the southwest Atlantic *P. caribaeorum* has been shown to offer some biotic resistance to both invasive soft (Mantelatto et al. 2018b) and hard corals (*Tubastraea* spp. – Luz and Kitahara 2017; Mantelatto et al. 2018a; Guilhem et al. 2020) as well as bivalves (Mendonça-Neto and Gama 2009) due to it preempting space and other features (Guilhem et al. 2020). However it is also true that there is substantial patchiness in the benthos as most variation in these shallow subtidal communities was determined by Carneiro et al. (2021) to be at their quadrat scale (supposedly ≈ 1 m scale). Furthermore, in an experimental study of the interaction of *Tubastraea* spp. and *P. caribaeorum* Guilhem et al. (2020) reported that it was

usual to find a standoff space between *T. tagusensis* and *P. caribaeorum* and this space was occupied by crustose coralline algae (40% of cases) and sponges (35%). Crustose coralline algae may enhance coral recruitment (e.g. Doropoulos et al. 2020; Silva et al. 2022) which may explain the positive association.

Considering the above observations a most likely scenario is that *Tubastraea* spp. sequentially invaded the studied communities within the MPA independently of differing community compositions – i.e. they did not offer better biotic resistance than unprotected areas. This was facilitated by the patchy nature of the communities which allowed *Tubastraea* spp. to get a foothold by initially avoiding species which offer greater biological resistance such as *P. caribaeorum*. Subsequently more resistant native species are slowly excluded by *Tubastraea* spp. as they grow to cover more area, create more contacts with native species and directly apply their physical and chemical defenses (Lages et al. 2010a; Santos et al. 2013). This scenario is corroborated by the fact that the invasion of *Tubastraea* spp. doesn't significantly change the niche space of invaded communities as *Tubastraea* spp. occupy a niche space similar to that already occupied by the native community of suspension feeders, sharing resources already consumed by the receptor community (L. Pires-Teixeira et al. pers. obs.).

Figure 1 presents the dates of first published records of *Tubastraea* spp. at each studied island in the MPA. It is interesting to note that there is a substantial delay between records of presence on each island (determined from De Paula and Creed 2004; Creed et al. 2008; Silva et al. 2011) and the quantitative appearance of the species in quadrats (either as individual colonies or occupying significant space). For example, although we know that *Tubastraea* spp. were already present in Búzios Island in 2003 and Cobras and Sabacu in 2009 we only quantitatively detected them in 2017. Furthermore, using our method, even in 2017 the abundances as percent cover at Cobras and Sabacu were so low as to not warrant scores as major space occupiers. We chose the study islands based on Silva et al. (2011), who used a semi-quantitative, more extensive monitoring method termed DAFOR which focuses only on the invaders. This method has been described and used quite often in Brazil as it is rapid and effective in determining presence over longer stretches of coastline (De Paula and Creed 2004; Creed et al. 2017b; Santos et al. 2019). However our sample locations on each island were haphazardly chosen (i.e. were not the same as those of Silva et al. (2011)). These observations suggest: 1) the scale of study is an important factor which should take into account along with the objectives and patchiness in the distribution of the invader and/or community; 2) the use of colony density and cover as descriptors of invasion in the community are complementary; 3) while the spread and establishment throughout the islands was quite fast (5–11 years) the invasion of the communities to levels where there was community change was slower (13–15 years). The complementary nature of the parameters colony density and cover corroborate previous studies of the invasion process that have demonstrated that during the establishment the colony density of *Tubastraea* spp. is initially high and cover low (many founding polyps and small colonies) but over time cover increases and colony density decreases (due to fusion and/or competition by overgrowth). This population dynamic is common for populations in the process of expansion, presented at the beginning of colonization with a high growth rate, followed by stabilization of the population size (Gotelli 2008). Regarding the timeline and detection it should also be noted that ideally sampling periodicity should be regular (2–3 years) which was not the case here (due to funding constraints).

Despite the perception that the communities within the Tamoios MPA didn't offer stronger biotic resistance than those unprotected ones, MPAs are recognized as important focal points and priority for management of biological invasions, especially

when resources are limited. As well as at Tamoios, a number of other MPAs (Ilha Anchieta State Park, Tupinambás Ecological Station, Laje de Santos Marine State Park, Arvoredo Marine Biological Reserve, Iguape Bay and Arraial do Cabo Marine Extraction Reserves) in Brazil have now been invaded by *Tubastraea* spp. (Creed et al. 2017a). The National Plan for the Prevention, Control and Monitoring of the Sun Coral in Brazil (IBAMA 2018) advocates action to consolidate management techniques and reduce the density of sun coral below acceptable limits in order to minimize impacts, especially in MPAs. In this regard it is important to note a significant decrease in the density of *Tubastraea* spp. at Queimada Grande in 2017. This was the result of mechanical control (see Creed et al. 2017b) of *Tubastraea* spp. which was undertaken at this site by the Sun-Coral Project team along with ESEC-Tamoios Technicians and volunteers in 2013. It was a demonstration action called Operation Eclipse (in reference to the common name sun corals) during which more than 12,200 colonies were removed (Gomes 2020). De Paula et al. (2017) and Creed et al. 2021 have shown that the removal of *Tubastraea* spp. from the benthic communities allows the structural and functional recovery of the native community and successful control of *Tubastraea* spp. is ongoing both in Brazil (Creed et al. 2021; Crivellaro et al. 2021; Savio et al. 2021) and the Gulf of Mexico (Precht et al. 2014).

The results presented here demonstrate the process of biological invasion of native tropical rocky reef communities by the invasive corals *Tubastraea* spp. in a MPA. At one site a significant reduction in *Tubastraea* spp. was detected after mechanical control. We therefore conclude that the MPA's status as a conservation unit was important to attract research and thus for establishing a baseline, quantifying change due to the invasion and focusing limited management resources, but not in providing significant biotic resistance to the invasion.

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Author's contribution

YCSFV – Investigation and data collection, data analysis and interpretation, writing – original draft and writing – review and editing; JCC – Research conceptualization, sample design and methodology, data analysis and interpretation, funding provision and writing – second draft, review and editing; BGF – Research conceptualization, sample design and methodology, data analysis and interpretation, funding provision and writing – review and editing.

Ethics and permits

All applicable international, national, and institutional guidelines for the care and use of animals were followed. ICMBio permits 16153-2 and 52613-1 and IBAMA Proc. N° 02001.003231 / 2014-02.

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Supplementary material 1

Mean percentage cover of each taxon per site and per time

Authors: Yollanda Carolina da Silva Ferreira Vançato, Joel Christopher Creed, Beatriz Grosso Fleury
 Data type: table (docx. file)

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Supplementary material 2

SIMPER analysis of community groups A–F

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 Data type: table (docx. file)

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