



Priority effects, environmental filtering and neutral coexistence explain large- to small-scale distribution of invasive sun corals in the SW Atlantic

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ABSTRACT: Two sun coral species, *Tubastraea tagusensis* and *T. coccinea*, have successfully colonized reef habitats along the Southwest Atlantic. However, their invasive biology has been largely addressed without considering species-specific distribution patterns. Here, we assessed the distribution and abundance of *Tubastraea* spp. at vertical rocky reef sites within a number of islands along 120 km of coastline off the northern coast of São Paulo State, Brazil, to (1) investigate possible mechanisms underlying the invasion dynamics in the region, (2) test species-specific distributions according to a key environmental filter (depth), and (3) examine within-patch patterns to assess whether competition, niche-based or neutral processes are best candidates to modulate local species coexistence. Sun corals were found in the great majority of the studied locations, and the probability of finding them at any given reef site was estimated to be 0.54. There was substantial species segregation across locations, consistent with primary priority effects. Within locations, results suggest environmental filtering, with *T. coccinea* apparently advantaged in more hydrodynamic environments just below the surf zone. At sun coral patches with extensive co-occurrence of *T. tagusensis* and *T. coccinea*, the presence of each species can be, remarkably, modeled as an independent event, suggesting neutral coexistence. The spread of sun corals is an ongoing and increasingly invasive process that may be explained by the enemy-release hypothesis and the lack of negative interactions between *Tubastraea* species. The stochastic nature of small-scale distributions sets an additional challenge to predict (and thus control) sun coral invasion.

KEY WORDS: Biological invasions · Interspecific competition · Resource partitioning · Patch dynamics

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1. INTRODUCTION

At large spatial scales, environmental forces are often considered responsible for marine invertebrate recruitment regulation and, consequently, benthic community structure (Thorson 1950, McCulloch & Shanks 2003). On the other hand, the effects of bio-

logical factors, such as the outcomes of species interactions and the supply of suitable habitat and food resources, typically operate at smaller spatial scales (Barbosa et al. 2016), as found in the complex patch dynamics of natural reef systems. Some corals can typically select smooth habitat patches (such as those delimited by encrusting coralline algae) as settle-

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ment grounds (Harrington et al. 2004, Tebben et al. 2015, Mizrahi et al. 2017), potentially leading to a clustered distribution of individual colonies and positive associations at spatial scales in the order of 10s of cm. Conversely, interspecific interference competition may cause reduced growth (Sammarco et al. 1983, Tanner 1997), damage (Lapid et al. 2004, Hennessey & Sammarco 2014), partial mortality, or total smothering of the lower-ranked species (Idjadi & Karlson 2007), ultimately leading to spatial segregation (i.e. negative spatial associations) of interacting corals. Moreover, species that share the same competitive abilities, dispersal potential and average fitness can coexist in a neutral model (Chesson 2000), where species distribution may follow a random pattern. The model of neutral coexistence (Hubbell 1997, Chesson 2000) was conceived for species that share the same trophic level and are similar in size and general morphology, so that they could be pooled into a single functional group (Amarasekare 2003, Adler et al. 2007, Shinen & Navarrete 2010).

Of all possible networks of species interactions, competition among dominant species may shape whole benthic ecosystems (Menge 1976, Lubchenco 1980), especially among invasive species that may potentially monopolize and drastically change the physical structure of vast reef extensions (Lages et al. 2011, Silva et al. 2019). Sun corals, *Tubastraea coccinea* Lesson, 1829, and its congener *T. tagusensis* Wells, 1982, are invasive species in the Atlantic Basin (e.g. Ferreira 2003, de Paula & Creed 2004, Fenner & Banks 2004, Silva et al. 2011). These azooxanthellate scleractinian corals were first reported in Southeast Brazil in the late 1980s (Castro & Pires 2001) and have expanded to numerous sites along a 3500 km stretch of the Brazilian coastline (Lopes 2009, Silva et al. 2011, Creed et al. 2017, de Oliveira Soares et al. 2018), imposing a generalized threat to several native species (Barbosa et al. 2019a, Silva et al. 2019). In some localities, sun corals have become extremely abundant, with more than 1000 colonies m^{-2} (de Paula & Creed 2005) and colony population density rising at rates of up to 76% per year (Lages et al. 2011).

Both sun coral species exhibit several characteristics that may have contributed to their successful invasion. They present high colony growth rates ($302\text{ mm}^2\text{ yr}^{-1}$; Vermeij 2006), early maturation (Glynn et al. 2008) and high regeneration capacity (Luz et al. 2018). Adult colonies have the ability to reproduce sexually and asexually (Campbell 1983, Capel et al. 2014, 2017), and their larvae can metamorphose into planktonic polyps, which may enhance their dispersal potential (Mizrahi et al. 2014,

Barbosa et al. 2019b). There is evidence of their competitive dominance over native corals (Creed 2006, dos Santos et al. 2013, Barbosa et al. 2019a) and zoantharians (Luz & Kitahara 2017) and their capacity to inhibit recruitment of other species through negative allelopathic interactions (Lages et al. 2006, 2010). Additionally, sun corals can cope with substantial environmental change (Lenz et al. 2011) and are largely free of predation pressure at the invaded area (Lages et al. 2010, Moreira & Creed 2012), with reports restricted to attacks of the fireworm *Hermodice carunculata* (Sampaio et al. 2012). The traits described above have likely contributed to their present-day generalized dominance at sites where colonization was first recorded around a decade ago (e.g. Búzios Island, SP, Brazil; Mantelatto et al. 2011).

Sun corals are also known to inflict tissue necrosis and reduced growth upon contact with native corals (Creed 2006, dos Santos et al. 2013, Barbosa et al. 2019a), but interactions between *T. tagusensis* and *T. coccinea* have, to our knowledge, never been tested. Hennessey & Sammarco (2014) examined contact interactions between *T. coccinea* and the congener *T. micranthus* in the Gulf of Mexico and found no evidence of aggression or competitive interactions, concluding that these species recognized each other as 'self'. At some invaded sites, *T. tagusensis* and *T. coccinea* almost saturate space over patch sizes ranging in length from several 10s to a few 100 m, especially on vertical walls, where the 2 species frequently co-occur (da Silva et al. 2014, Silva et al. 2019). On vertical walls along homogenous rocky reef habitats, colonies of the 2 species are often found intermingled within distinctive 'sun-coral patches' (Fig. 1A). More rarely, and usually at more fragmented reef habitats such as boulders and man-made structures, these species may segregate within patches, forming clusters of considerable area (Fig. 1B). Understanding the distribution patterns of these co-occurring species at relevant spatial scales is a first step to frame more specific hypotheses on the nature of the interactions between them, as well as mechanisms of resource partitioning, which are largely unknown.

Some indirect evidence on difference in habitat use among sun coral species, based on morphology and potential thermal niche, can be used as starting points. Compared to *T. tagusensis*, *T. coccinea* coral-lites are shorter and colonies are flatter and have a larger basal encrusting area (Mangelli & Creed 2012, de Paula et al. 2014), which could eventually render an advantage at habitats more directly exposed to wave forces (Mantelatto 2012). Living close to the surface also requires tolerance to higher tempera-

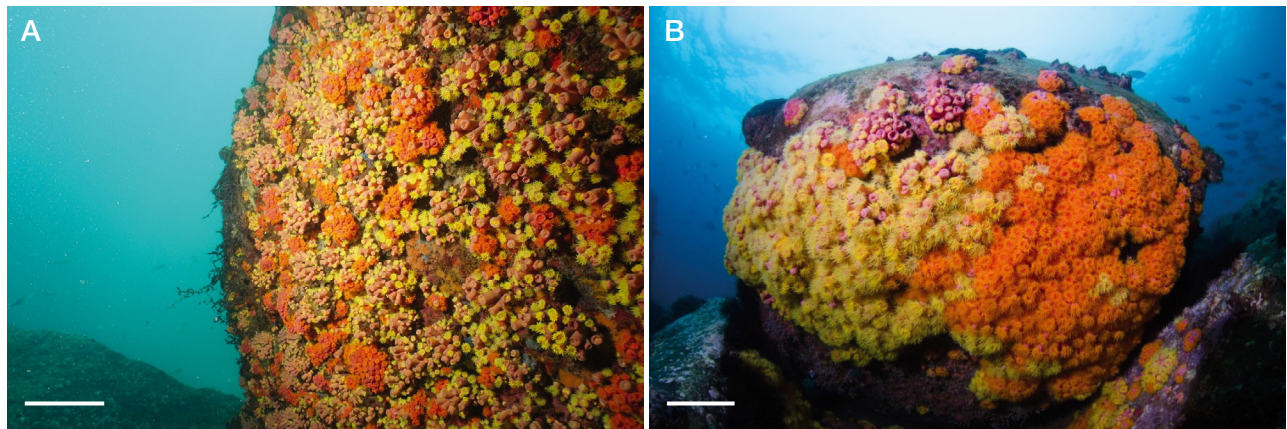


Fig. 1. Within-patch distribution patterns of yellow (*Tubastraea tagusensis*) and orange (*T. coccinea*) sun corals in (A) typical main-reef vertical walls, and (B) less-common fragmented boulder habitats. Scale bars = 10 cm. Photo credits: (A) Marcelo V. Kitahara and (B) Leo Francini

tures. The temperature regimes at native geographic ranges further suggest an advantage of *T. coccinea* at shallow reef habitats, as this species is thought to be originally widespread over the warm tropical Indo-Pacific Ocean. On the other hand, *T. tagusensis* was restricted to the Galapagos Islands, where historical average temperatures range from 20.9 to just 25.1°C at the surface (Puerto Villamil, Western Galapagos; www.seatemperature.org). There are apparently no constraints of localized low temperature at depth, since both species have been found well below 40 m at native sites (Wells 1982, Cairns 1994). Thus, it is plausible to predict that *T. coccinea* would tend to occupy shallow, warmer and more turbulent reef habitats, while *T. tagusensis* would be displaced to deeper, less turbulent and cooler reef areas. We are not aware of any studies to date that have investigated species-specific depth distributions at locations where both sun corals co-occur.

Owing to their invasive potential, sun corals can monopolize and drastically change the physical structure of vast reef extensions (Lages et al. 2011, Silva et al. 2019). Understanding the interaction outcomes between the 2 *Tubastraea* species is of paramount importance to predict the state of invaded reefs and assess the likelihood of colonization of still unaffected locations in the long run. Here, we examined the co-occurrence of *T. tagusensis* and *T. coccinea* at several different spatial scales to identify possible ecological processes, from long-distance dispersal to local competition and resource partitioning, which may determine these species' distributions in the SW Atlantic. Namely, we mapped and quantified the abundance of invasive sun corals at coastal islands off the central and northern coasts of São Paulo State, Brazil, encompassing 120 km of linear

coastline. At more local scales, we tested whether depth distributions are compatible with predictions based on colony morphology and potential thermal niche and whether species associations at the patch level support niche-related processes (e.g. interspecific competition and differences in species fitness, patterns of resource exploitation) or, alternatively, a neutral coexistence ruled by stochastic processes.

2. MATERIALS AND METHODS

2.1. Field work

The distributions and abundances of *Tubastraea* spp. at coastal island habitats off the central and northern coasts of São Paulo State, were surveyed through snorkeling and scuba diving from May to September 2018. We restricted this study to uniform, nearly vertical reef walls, which is the most frequent insular reef habitat in the study region. Nine locations were sampled, encompassing a coastline length ranging from 2 to 8 km and distributed over 5 islands of different sizes and 2 rocky islets. The small islands (Vitória, Búzios, Toque-toque and Montão de Trigo) and the 2 rocky islets (Laje de Santos and Farol do Moleque) were each considered as single locations. Three different locations were sampled at the larger São Sebastião Island (Fig. 2). The study area is located in the subtropical/warm-temperate Southwestern Atlantic Ecoregion (Spalding et al. 2007) and prone to extensive sub-surface thermal stratification during summer due to the coastward intrusion of the cold and saline South Atlantic Coastal Water (Castro et al. 2008). Within each location, 2 snorkeling divers searched for sun coral colonies at 5 evenly spaced

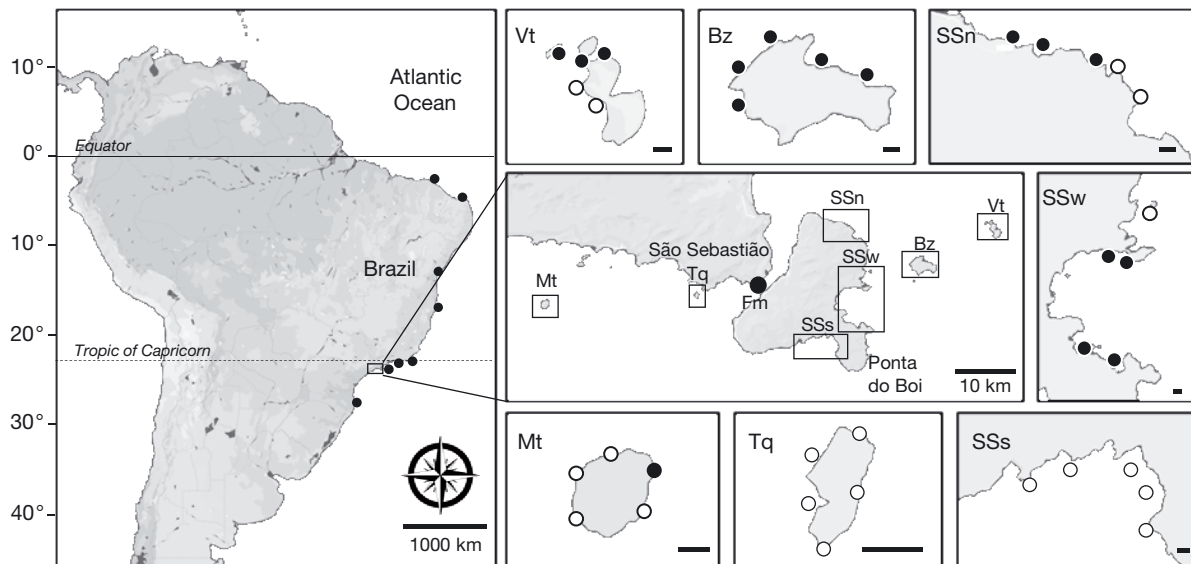


Fig. 2. Localities where invasive sun corals have been reported in Brazil (left, black dots) and the coastline of the study region, encompassing island habitats off São Sebastião (centre). Clockwise, close detail of study locations: Vitória (Vt), Búzios (Bz), São Sebastião Island north (SSn), São Sebastião Island west (SSw), São Sebastião Island south (SSs), Toque-toque (Tq), and Montão de Trigo (Mt). Black and white dots indicate sites where sun corals were present and absent, respectively. Details for Farol do Moleque (Fm) are not shown, as sampling was restricted to a single site in this location. Scale bars = 500 m

150 m coastlines (hereafter 'sites') for approximately 10 min, and classified their abundance into 6 categories (Table 1). At any given site where abundance was assigned Category 3 (very common) or higher, scuba-diver surveys were undertaken to estimate the percent cover of both species at 3 different depth intervals, encompassing most reef habitat available in these islands, and contrasting thermal regimes (Braga et al. 2017): 2–4 m (shallow), 6–8 m (mid), and 10–12 m (deep). At each depth, twenty 0.5×0.5 m photoquadrats at haphazard positions within sun coral patches were taken. The minimum spacing between positions was 1 m. At Montão de Trigo, sampling was restricted to the 2 shallowest levels, as sun corals were found only in sites with maximum reef depths of 9 m. At the 2 rocky islets Laje de Santos and Farol do Moleque (Fig. 2), access was only possible to a single random site (Category 3 and 2, respectively). At Laje de Santos, the boulders inhabited by

sun corals do not reach the surface, therefore the percent cover estimates were only obtained at mid and deep strata. Snorkeling at multiple sites was not possible at this location and, therefore, overall cover was not estimated.

2.2. Image analyses

Within-patch abundance was quantified for whole-quadrat digital images using the point-count method (100 points over a grid). Because we were also interested in small-scale association patterns between sun coral species, we verified their presence in non-overlapping sub-quadrats, 4 for each image, of sizes 10×10 , 15×15 , 20×20 and 25×25 cm. Besides their color (yellow tentacles for *T. tagusensis* and orange tentacles for *T. coccinea*), sun coral species could also be distinguished by

Table 1. Frequency categories used for a rapid assessment of the abundance of sun corals (*Tubastraea* spp.) at island reef sites off São Sebastião, SP, Brazil

| Category | Description |
|---------------|--|
| 0 Absent | No sun coral colonies observed |
| 1 Occasional | Mostly single isolated colonies. Aggregations over 1 m^2 (= patches) are rare and thin (<10 % cover) |
| 2 Common | High-density patches (>10 %) present but not frequent (less than 5) |
| 3 Very common | High density patches frequent (10 or more) |
| 4 Abundant | Uniform cover, frequently 50 % or more, over large reef extensions (>10 m) |
| 5 Dominant | Most vertical substrates dominated by sun corals. Cover frequently reached saturation (90–100 %) |

corallite shape (short in *T. coccinea* and elongated in *T. tagusensis*), confirming the *in situ* diagnoses from Mantelatto (2012).

2.3. Statistical analyses

Overall abundance of sun corals (both species combined) among locations that could be fully sampled was compared using a 1-way ANOVA on raw data, as variances were homogeneous (Cochran's $C = 0.3485$, $p > 0.05$). Depth distributions were tested using 2-way mixed-model GLMs in which 'depth' and 'location' were considered fixed and random factors, respectively. A significant interaction term 'depth \times location' would indicate spatial inconsistencies of any eventual depth trends. Separate analyses were run for *T. tagusensis* (raw data) and *T. coccinea* (arcsine transformed to meet homoscedasticity), because the only 2 locations with presence at all depth intervals were not the same for the 2 species. For both overall sun coral abundance and species-specific depth distributions, the SNK procedure was used for *a posteriori* pairwise comparisons. The GMAV5 software (Underwood & Chapman 1997) was used for these analyses.

Differences in the relative abundance of sun coral species across sites were clear-cut (see Section 3) and no statistical analyses were needed to test them. Species associations that could indicate, for instance, aggregation at favorable habitat conditions (positive)

or interspecific competition (negative) at the whole-quadrat scale (50×50 cm) were tested using Pearson correlation coefficients based on the percentage cover of the 2 species. At the smaller within-quadrat scales (from 10×10 to 25×25 cm sub-quadrats), presence/absence data were drawn instead, and the frequency of units with (1) no coral species, (2) *T. tagusensis* only, (3) *T. coccinea* only, and (4) both species together, were recorded. Observed frequencies were then contrasted with frequencies generated from null models assuming the occurrence of the 2 species as independent events. Departures from expected frequencies were tested using a G-test, with degrees of freedom corrected for an intrinsic hypothesis based on observations (i.e. the proportion of units containing *T. tagusensis* and *T. coccinea*). These analyses were performed in Statistica v.13 (TIBCO Software 2018).

3. RESULTS

3.1. Overall sun coral abundance

Invasive sun corals were present at 7 out of 9 sampled locations (Fig. 2), and 20 out of the 37 sites visited (Fig. 3A). Therefore, it is more likely (54%) to find sun corals at any single site within the study region than not to find them. When present, the most frequent abundance category was 'very common' (Category 3; Fig. 3A), suggesting that the formation of high-density patches may be relatively fast after

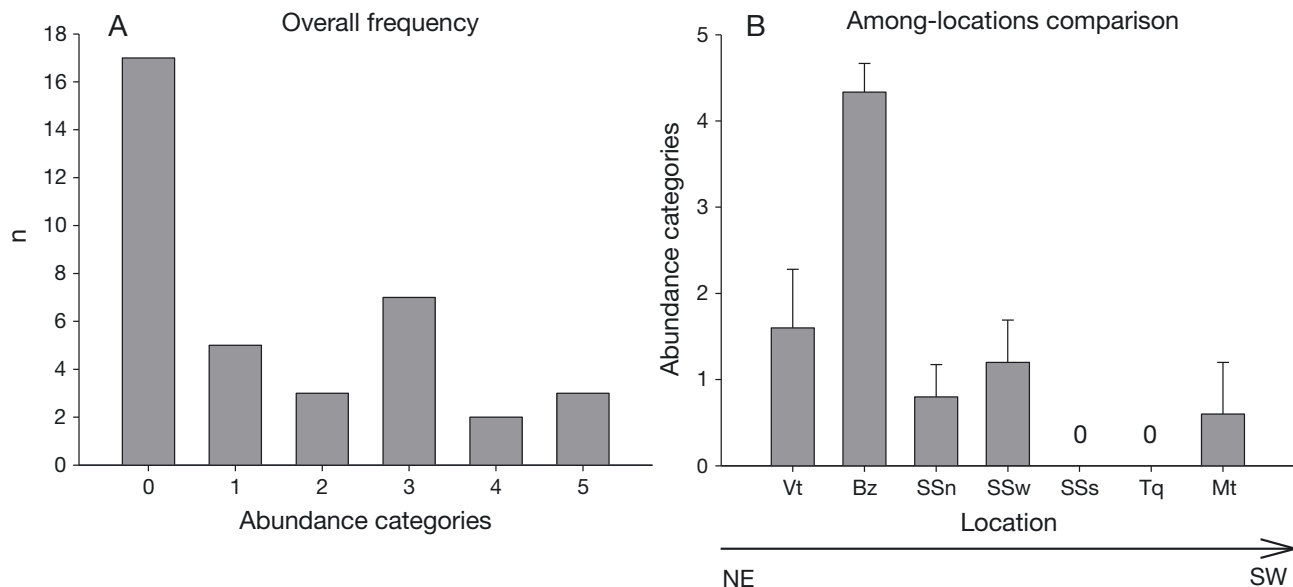


Fig. 3. (A) Overall frequency of sun coral abundance categories (sites pooled across locations; see Table 1 for category descriptions), and (B) abundance comparison among locations. Error bars show +1SE. Vitória (Vt), Búzios (Bz), São Sebastião Island north (SSn), São Sebastião Island west (SSw), São Sebastião Island south (SSs), Toque-toque (Tq), and Montão de Trigo (Mt)

colonization. The comparison among locations that could be fully sampled ($n = 5$ sites; $F_{4,20} = 10.4$, $p = 0.0001$) showed no clear geographic trend (north-east to southwest), with the abundance at Búzios being much higher than at all other sites where sun corals were present (Fig. 3B; $p < 0.01$). It is, however, important to note that at all 3 sites west of Ponta do Boi (Fig. 2), sun corals were either absent (São Sebastião Island south and Toque-toque) or occasional (Montão de Trigo; Fig. 3B).

3.2. Species-specific depth distributions

There was a clear overall segregation of sun-coral species across studied locations (Fig. 4). The relative abundance of *T. tagusensis* was higher at Vitória and Búzios, while *T. coccinea* clearly prevailed at São Sebastião Island west and Laje de

Santos, where no *T. tagusensis* colonies were observed. Depth distribution patterns were tested at locations where both species were found at all depth strata, making orthogonal analyses possible. These were Vitória and Búzios for *T. tagusensis*, and Vitória and São Sebastião Island west for *T. coccinea* (Fig. 4). For both species, the depth \times location interaction term was statistically significant, indicating that depth distributions were not consistent between locations (*T. tagusensis*, $F_{2,114} = 9.0$, $p = 0.0002$; *T. coccinea*, $F_{2,114} = 30.7$, $p < 0.0001$). *T. tagusensis* tend to be more abundant at deeper reef habitats, but with peak abundance varying from deep (Vitória) to mid (Búzios) strata ($p < 0.01$). Likewise, *T. coccinea* rather occupy shallower habitats, and higher cover estimates were observed at either shallow (Vitória) or mid depth (São Sebastião Island west, $p < 0.01$; Fig. 4). No other pairwise comparisons were significant.

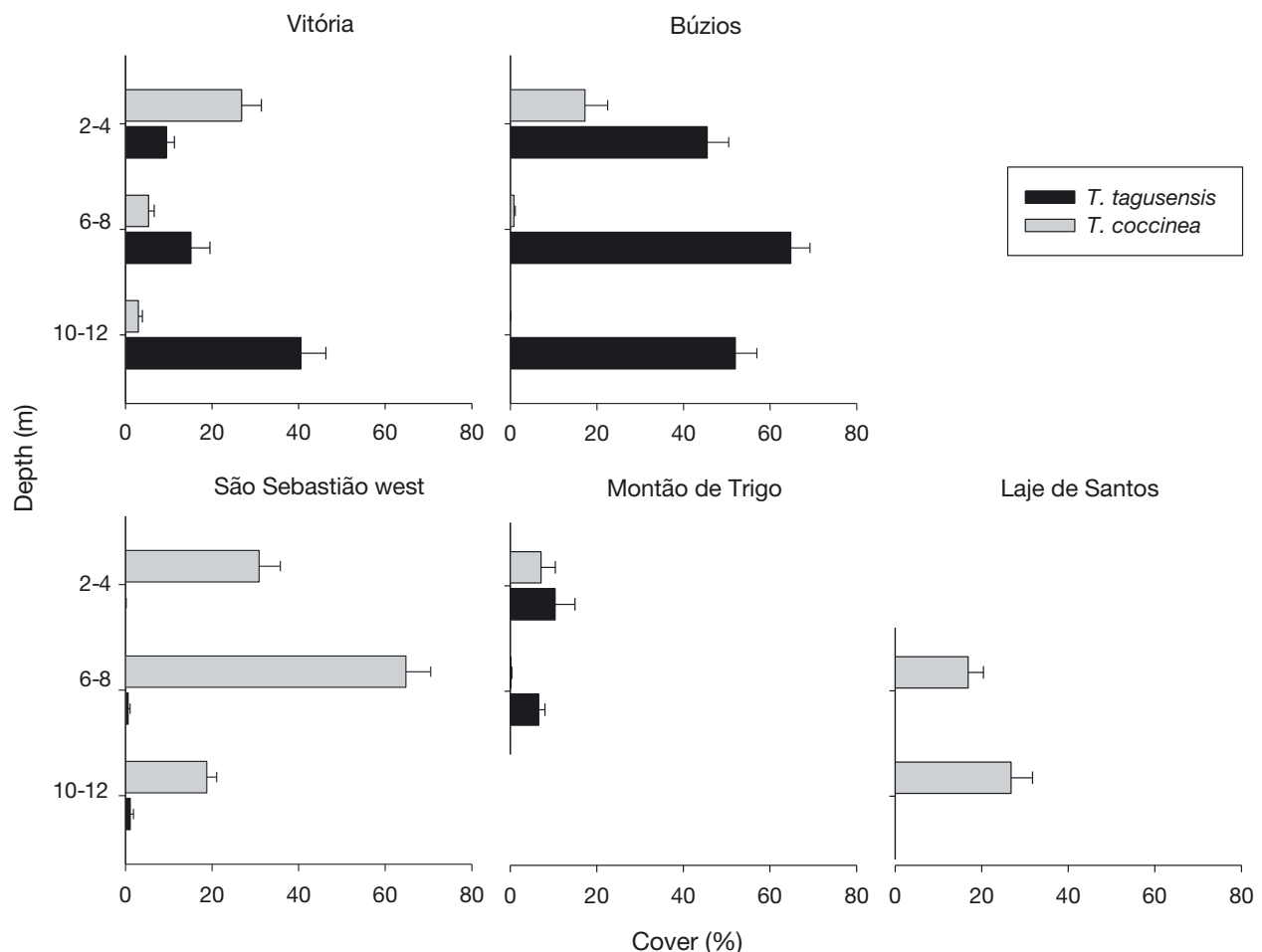


Fig. 4. Species-specific depth distributions at sites where the abundance of sun corals ranged from very common (Category 3; see Table 1) to dominant (Category 5). Potential habitat for sun corals was absent in the deep and the shallow reef at Montão de Trigo and Laje de Santos, respectively. Error bars show +1SE

3.3. Species co-occurrences

We restricted analyses to depth strata, within locations, where average sun coral cover was $\geq 20\%$ and the presence of both species was not negligible ($>3\%$), i.e. Vitória shallow, mid and deep, and Búzios shallow (Fig. 4). Based on percent cover estimates, no apparent patterns of species associations, either positive or negative, were observed at the whole-quadrat scale in all cases (Pearson correlation coefficients, $0.045 < r < 0.326$; $0.161 < p < 0.851$; Fig. 5). Independent species co-occurrences were also supported by analyses of presence-absence data at smaller scales, from 10×10 to 25×25 cm (Fig. 6). Observed frequencies of sub-quadrate with no sun corals, with only a single species (either *T. tagusensis* or *T. coccinea*), and with both species, remarkably followed the expected frequencies based on null models, assuming that the presence of *T. tagusensis* and *T. coccinea* are independent events. Negligible departures from expectations were the rule across depth strata within locations and sub-quadrate size ($0.05 < G < 2.07$; $0.151 < p < 0.957$; Fig. 6). Therefore, there is no sign of association, either positive or negative, between the occurrences of these species. Notably, we could discard sampling artifacts owing to species exclusion even at the smallest scale (10×10 cm). Such an effect would lead to higher frequencies of single-species and lower frequencies of 2-species counts compared to expectations, which was not the case.

4. DISCUSSION

Our results suggest that several factors operating at different spatial scales modulate the distribution of sun-coral species off the northern and central coasts of São Paulo State, Brazil. *Tubastraea coccinea* and *T. tagusensis* are largely segregated both among islands, separated by 10s of km, and within islands, across depth strata. However, at small spatial scales ranging from 10s of cm to a few meters, apparently neutral patch-dynamics result in pattern-less distributions for both species, suggesting that contact and allelopathic interactions between any 2 coral colonies—belonging to the same or to different species—are essentially

equal. These findings shed some light on the possible mechanisms underlying the distribution of sun coral species and may contribute to current conservation planning aimed at restraining their invasion in the region.

Strong segregation among islands coupled to the generalized potential for space monopolization suggest that the 2 sun-coral species are equally invasive, and that first arrivals at the onset of the invasive process, i.e. a priority effect through niche preemption (Fukami 2015, Vieira et al. 2018a), determine the share of the 2 species in advanced stages. As observed in other non-indigenous species (Johnston et al. 2009), sun corals may also become dominant because they recruit at far higher rates compared to native species (Lages et al. 2011, da Silva et al. 2014). The fact that islands dominated by the 2 sun-coral species are found at opposite sides of Ponta do Boi (Fig. 2) suggests that at least 2 different larval pools are effectively seeding adult populations over the sampled area. However, transport mechanisms connecting neighboring islands and propagule pressure (e.g. Caley et al. 1996, Barbosa et al. 2016) seem insufficient to explain the reef occupancy rates observed at a number of sites in the region (Silva et al. 2011, Creed et al. 2017). The very low genetic variation of sun-coral species along the SW Atlantic (Capel et al. 2017, 2019) strongly suggests that devel-

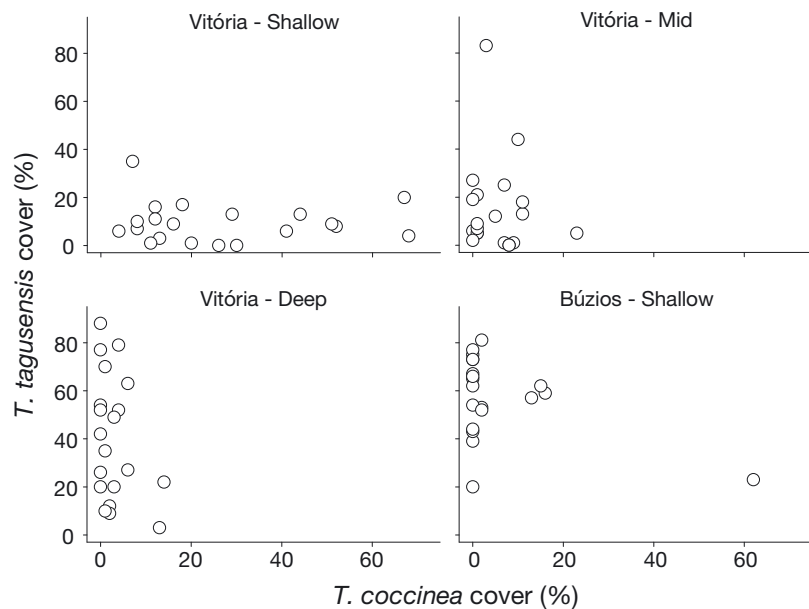


Fig. 5. Scatterplots showing the absence of any linear relationships between whole-plot (50×50 cm, $N = 20$) abundances of *Tubastraea tagusensis* and *T. coccinea* at Vitória (all depths) and Búzios (shallow reef), where average sun coral cover was 20% or more, and the presence of both species was not negligible ($>3\%$)

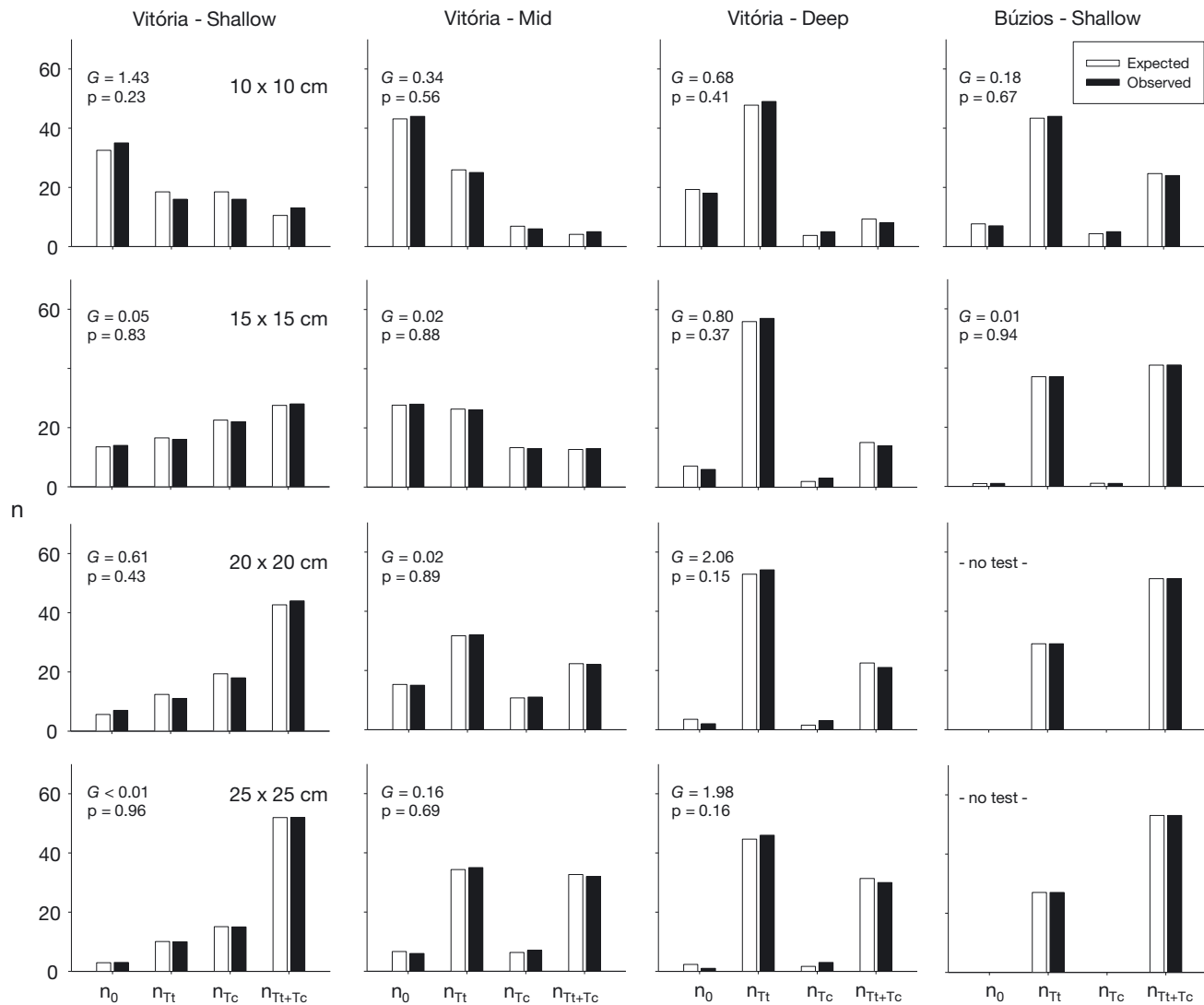


Fig. 6. Small-scale within-plot species co-occurrences at the locations examined in Fig. 5 (from 10 × 10 to 25 × 25 cm subquadrats; N = 80 in each case). In all cases, observed frequency distributions remarkably approximate the expected distributions based on chance alone, considering the presence of the 2 sun corals as independent events. The presence-absence categories on the x-axes correspond to the absence of both species (n_0), presence of *Tubastraea tagusensis* only (n_{Tt}), presence of *T. coccinea* only (n_{Tc}), and presence of both species (n_{Tt+Tc})

oping colonies from first recruitment events have largely propagated through asexual means, including polyp bail-out (Capel et al. 2014) and colony fragmentation (Luz et al. 2018). The faster the spread over the reef, the more likely that priority effects will build up (Vieira et al. 2018a,b). Here, we argue that an unbalanced pool of sun-coral recruits will result in an unequal sun-coral cover in later stages of the colonization process. Because the 2 species are invasive, the identity of sun corals would not at first glance seem to be a major issue for conservation policies. However, priority effects may not only give an advantage for the pioneering coral species but also modulate the identity and abundance of other spe-

cies' recruits and therefore patterns of further community assembly (Vieira et al. 2018a, Silva et al. 2019). In heavily invaded reefs, fouling species other than sun corals may be restrained to marginal cover and, therefore, their identity and relative abundance would become less relevant. However, the joint effects of *Tubastraea* spp. on the mobile invertebrate fauna are profound, with impacts on invertivore reef fishes (Miranda et al. 2018, Silva et al. 2019). Teasing apart the effects of *T. tagusensis* and *T. coccinea* in the assembly of mobile invertebrate populations would allow more accurate predictions of the impact of sun corals along the SW Atlantic invaded range.

Supporting earlier predictions, sun-coral species were also unequally distributed across depth strata. When sharing substantial reef space, as in Vitória, Búzios and Montão de Trigo, *T. coccinea* became more abundant in the shallow reef, and *T. tagusensis* reached higher reef cover at the mid and deep strata; a pattern consistent with species-specific functional morphology (Mangelli & Creed 2012). Moreover, more balanced species abundances were observed at shallow strata of reefs dominated by *T. tagusensis* (Vitória and Búzios), suggesting that *T. coccinea* does have an advantage at more turbulent (or thermally vulnerable) environments, just below the surf zone. This same reasoning would explain why *T. tagusensis* was present at mid and deep but not at the shallow depth stratum in São Sebastião Island west, where *T. coccinea* is the most abundant species. Apart from being better anchored to the substrate as a result of its larger encrusting base, more compacted colony morphology and shorter corallites allow *T. coccinea* to more efficiently dissipate wave forces and turbulence that frequently occur in the shallow reef. Aligned to our findings, Sammarco et al. (2013) verified that the average depth of *T. coccinea* was generally lower than the average depth of *T. micranthus* (a more branching species) at oil platforms in the Gulf of Mexico, where both species are also invasive. Remarkably, however, these species are able to colonize much deeper areas than reported in the present study, especially *T. micranthus*, which was observed at depths of up to 138 m (Sammarco et al. 2013). This is of great concern, as eradication or control of sun coral populations at depths beyond conventional scuba diving limits would be extremely challenging. In our study region, low-accessibility substrates that are potential sun-coral habitat, especially for *T. tagusensis*, are not limited to gas and oil platform pillars and pipes, but also include natural hard bottoms such as rhodolith beds (Amado-Filho et al. 2017).

The seemingly higher success of *T. coccinea* at shallow depths and of *T. tagusensis* at deeper depths may allow extensive co-occurrence between the 2 species at the site scale. Interactions between colonies of the 2 species, within sun-coral patches and mostly at shallow depth (≤ 4 m), could eventually reduce coexistence at this smaller scale, but this is not supported by our results. Although reported as being very strong competitors against other fouling invertebrates and macroalgae, particularly against native scleractinian corals (Creed 2006, dos Santos et al. 2013, Barbosa et al. 2019a) and zoantharians (Luz & Kitahara 2017) and causing extensive tissue necro-

sis and partial mortality, within-patch distributions of sun-coral colonies reject any spatial segregation patterns between the 2 species that could result from negative interactions between them so far. Thus, we accept at this stage the conclusions of Hennessey & Sammarco (2014) on *T. coccinea* and *T. micranthus*, i.e. that co-occurring sun corals are very closely related species that do not perceive each other as a threat. As such, one could alternatively expect that *T. tagusensis* and *T. coccinea* would share the same resources and exhibit very close habitat preferences within the mosaic-kind reef environment, usually very patchy at scales of only a few 10s of cm, or smaller (Gratwicke & Speight 2005, Boström et al. 2011). Namely, we would expect a positive trend in the scatterplots of Fig. 5, or a higher-than-expected frequency of plots with both species in Fig. 6, which were also not observed. Unlike closely related barnacle species, which exhibit wide niche overlap and cluster together in intertidal rocky shores of central Chile (Shinen & Navarrete 2014), or congeneric limpets that graze on similar food items and segregate at small spatial scales (Aguilera et al. 2013), the spatial distributions of invasive *T. coccinea* and *T. tagusensis* are surprisingly best described by null models assuming that the occurrences of these species are independent events (Fig. 6). Without proper testing through manipulative experiments, the spatial analyses carried out in this study do not sustain any clear niche-related hypotheses (e.g. competition, resource partitioning, facilitation), but rather suggest a case of neutral coexistence, where fitness, competitive ability, and dispersal potential are so similar that one species is unable to exclude the other (Hubbell 1997, Chesson 2000, Adler et al. 2007).

Our results showing the high likelihood of sun corals of invading any given reef habitat, their tendency to become dominant species—covering large fractions of reef space—and the similar invasive potential of both *Tubastraea* species further indicate this is an ongoing and increasingly invasive process. Here, we contend that priority effects play a major role in determining the relative abundance of sun-coral species at the larger spatial scale tested in this study (among locations), but tracking the development of colonies after experimental clearings would be needed to confirm this hypothesis. Further advances in understanding sun-coral spread should also consider the processes controlling the dynamics of these species' populations over the SW Atlantic, and whether they might be different from those taking place on their native ranges. For instance, in their original habitats, sun corals are predated by

the nudibranch *Phestilla melanobranchia* (Robertson 1970, Yiu et al. 2021), and in the tropical Eastern Pacific by the gastropod snail *Epidendrium billeanum* (Rodríguez-Villalobos et al. 2016), while studies to date at the SW Atlantic invaded sites have failed to identify any predator (Lages et al. 2010, Moreira & Creed 2012, Tanasovici et al. 2022), or any equal or superior competitor (Hennessey & Sammarco 2014, Sammarco et al. 2015), such as other hard corals, capable of regulating *T. coccinea* and *T. tagusensis* abundances. As such, besides the numerous intrinsic attributes contributing to their invasive potential, (e.g. high growth rates, sexual and asexual reproduction, high regenerative capacity), the evident success of sun corals in the SW Atlantic could be also explained by the 'enemy-release hypothesis' (Keane & Crawley 2002), which predicts that invasive species will grow faster than native ones when released from the strong predation and competition pressure they face in their original distribution range. Under these conditions, any interactions between the 2 *Tubastraea* species would largely dictate the structure and dynamics of vertical reef walls and down-facing sides of overhangs where sun-coral domination is more common. The possibility that competition for resources does not take place between *Tubastraea* species, and that their local co-occurrence is determined by stochastic neutral-like processes, reinforces the now common understanding that managing invading sun corals is a challenging and laborious task and that outcomes of removals, although positive (Savio et al. 2021), are difficult to predict in the long run.

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