Mar Biol (2016) 163:236
DOI 10.1007/s00227-016-3010-z

ORIGINAL PAPER

Geographic patterns of *Symbiodinium* diversity associated with the coral *Mussismilia hispida* (Cnidaria, Scleractinia) correlate with major reef regions in the Southwestern Atlantic Ocean

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Received: 12 December 2015 / Accepted: 6 October 2016

Abstract Shallow water reef-building corals associate with photosynthesizing dinoflagellates (*Symbiodinium* spp.) that may affect growth and resilience of their hosts. Understanding host–symbiont associations is critical for assessing the susceptibility of corals to climatic changes. Despite that, the diversity of *Symbiodinium* associated with corals from the Southwestern Atlantic Ocean is poorly known. Here, we describe diversity across major *Symbiodinium* clades associated with colonies of the endemic reef-building coral *Mussismilia hispida* (Verrill, 1902) along the Brazilian coast. By analyzing the 18S rDNA gene, we found that *M. hispida* associates with three clades of *Symbiodinium* (A, B and C). Moreover, the geographic distribution of host–symbiont associations is related to temperature and turbidity and closely follows previously recognized reef regions along the Brazilian coast. These results suggest that similar ecological processes are likely shaping both the reef communities and the host–symbiont associations over *M. hispida* distribution along the coast. Our study provides an advance in the understanding of symbiont diversity in a key reef-building coral. In addition, it contributes new insights for future investigations aiming at comprehending the factors determining *Symbiodinium* geographic distribution.

Introduction

Shallow water reef-building corals (Cnidaria, Scleractinia) associate with photosynthesizing dinoflagellates of the genus *Symbiodinium* Freudenthal, 1962 commonly known as zooxanthellae (Blackall et al. 2015). Several types of environmental disturbances may cause a substantial loss of symbionts from the hosts (coral bleaching), with potential mortality for the coral (Hoegh-Guldberg 1999; Jokiel and Brown 2004; Baker et al. 2008). Coral bleaching events have increased in scale, severity and frequency, mainly due to thermal anomalies in seawater surface temperatures during the last decades—rendering coral reefs as one of the ecosystems most threatened by climate change (Baker et al. 2008; Caldeira 2013; Frieler et al. 2013).

Currently, nine evolutionary lineages of *Symbiodinium* (clades or types A to I), each with many subgroups (subclades or subtypes), are recognized based on relatively conserved markers as the 18S and 28S rDNA to some of the chloroplast, as the cp23S, and more variable ones such as the psbA, ITS1, ITS2 rDNA and microsatellites (reviewed by Baker 2003; Coffroth and Santos 2005; Pochon and Gates 2010). While geographic patterns of host–*Symbiodinium* associations may occur along the distribution of some coral species, the environmental driving factors of

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Responsible Editor: S. Uticke.

Reviewed by B. Hume and Undisclosed experts.

Electronic supplementary material The online version of this article (doi:10.1007/s00227-016-3010-z) contains supplementary material, which is available to authorized users.

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Symbiodinium distribution may be different for each host species or symbiont type, despite being usually linked to variations in sea surface temperatures (Cooper et al. 2011; Tonk et al. 2013).

Many species of corals harbor multiple clades of *Symbiodinium*, and the symbiont composition may vary both within and/or between colonies depending on environmental conditions and geographic locations (Rowan et al. 1997; Baker 2003; Frade et al. 2008; Bongaerts et al. 2010; Stat et al. 2011). Accordingly, several studies have shown that *Symbiodinium* clades and sub-clades differ in their tolerance to prolonged environmental disturbances, such as thermal anomalies, and that tolerant groups may ensure their host's survival (Berkelmans and Van Oppen 2006; van Oppen et al. 2009; Cunning and Baker 2012; Howells et al. 2012). In addition to host factors (Weis 2010), the ability to harbor different *Symbiodinium* clades may provide an effective way to withstand severe and extended stressful conditions (Jones and Berkelmans 2011; Oliver and Palumbi 2011). Thus, understanding the taxonomic identity of the symbiotic partners and the flexibility in symbiotic interactions turns out to be an essential step to comprehend the susceptibility of a reef-building coral to climatic changes.

The Brazilian coastline extends for ~7400 km from 4°N to 34°S, with semiarid, tropical-humid and subtropical climates. The continental shelf is usually very narrow (~50 km in width), but particularly enlarged (~200 km in width) in the Abrolhos Bank (AB) region (17°S, 39°W). The Brazilian coast is under the influence of the South Equatorial Current that reaches the continental shelf between 11 and 15°S flowing northward as the North Brazil Current and southward as the Brazil Current (Ekau and Knoppers 1999). The Royal Charlotte Bank, the Abrolhos Bank and the Vitória-Trindade Seamount Chain (16–20°S) consist of topological barriers for the southward warm waters of the Brazil Current. South of this region, the coast is mainly affected by the upwelling regimes of the South Atlantic Central Water (Ekau and Knoppers 1999). On the basis of relatively similar scleractinian species composition, four major coral reef regions have been commonly recognized along the Brazilian coast: Northern, Northeastern, Eastern and Southern (Laborel 1970; Leão et al. 2003). While boundaries of the Northern region are, respectively, the Amazon River mouth (0°30′S) and Cabo de São Roque (5°29′S), the Northeastern region extends from Cabo de São Roque down to the São Francisco River mouth (10°30′S). South of these two regions, the Eastern region continues from São Francisco River to the Doce River mouth (19°S). Finally, the Southern region is located between the Doce River and the coast of Santa Catarina State (27°S) (Laborel 1970; Leão et al. 2003).

South Atlantic shallow water coral reefs are only found along the Brazilian coast, where they are commonly subjected to an active terrigenous sedimentation (Leão et al. 2003). Still, knowledge about the diversity of symbionts from the ~18 spp. of shallow water scleractinian corals in Brazil has been largely neglected. It has been mainly restricted to the report of *Symbiodinium* C associated with colonies of *Siderastrea stellata* Verrill, 1868 in João Pessoa, Northeastern Brazil (Costa et al. 2008), and the description of *Siderastrea* spp. harboring *Symbiodinium* C3, C46 and B5 in the state of Paraíba, and *Symbiodinium* C1 and C46 in the state of Bahia (Monteiro et al. 2013). Baker (Baker 2003) reported the presence of *Symbiodinium* C in the Abrolhos Bank (Bahia State) and clades A, B and C in southeastern Brazil, without reference to the identity of their coral hosts. Recently, Silva-Lima et al. (Silva-Lima et al. 2015) reported the presence of *Symbiodinium* C3 in 12 colonies (and *Symbiodinium* A4 in two of these colonies) of *Mussismilia braziliensis* from the Abrolhos Bank. They also found two colonies of *M. hispida*, from the Vitória-Trindade seamount chain, associated with *Symbiodinium* A4 and other two with *Symbiodinium* B19.

As one of the major reef builders, the endemic brain-coral genus *Mussismilia* Ortmann, 1890 (Mussidae) comprises three species endemic to Brazil, *M. hispida* (Verrill, 1902), *M. braziliensis* (Verrill, 1868) and *M. hartti* (Verrill, 1868). Recently, the allocation of *Favia leptophylla* (Verrill, 1868) within the genus *Mussismilia* has been proposed (Budd et al. 2012). Among shallow water reef-building corals from Brazil, *M. hispida* is the most widespread along the coast, thriving in the Brazilian highly turbid coastal waters. Encompassing a wide range of temperatures, *M. hispida* occurs from Maranhão to São Paulo States (0°–23°S; ~3200 km), where its subplocoid colonies usually grow in a spherical cap shape.

In this study, we describe for the first time the diversity of *Symbiodinium* associated with the reef-building coral *Mussismilia hispida* along 2700 km of its geographic distribution. By assessing the diversity of *Symbiodinium* associated with 298 colonies across almost the whole geographic distribution of the species, we aimed at understanding whether (1) *M. hispida* can associate with more than two clades (A and B) of *Symbiodinium*, (2) *Symbiodinium* clades vary between and within colonies in each sampling site, and (3) geographic patterns of symbiont distribution can be distinguished.

Materials and methods

Study sites

Colonies of *M. hispida* were sampled at 11 sites on the continental shelf and three oceanic islands across different depth ranges [Electronic Supplementary Material

(ESM) 1 and 2] along the four main biogeographic regions recognized:

1. *Northern region* Fortaleza (FZ), in Pedra da Risca do Meio Marine Park, a rocky submerged area where coral communities are poorly known (Soares et al. 2011);
2. *Northeastern region* Tamandaré Reefs (TE) and João Pessoa Reefs (JP) are comprised by three lines of elongated sandstone banks parallel to the coast in a growing complexity of columns fused on their tops; Oceanic islands: Atol das Rocas (AR), a small elliptical atoll formed primarily by coralline algae; Fernando de Noronha (FN), a small volcanic archipelago poorly covered by corals;
3. *Eastern region* Todos os Santos Bay in Salvador (SA) harbors shallow fringing coral reefs around Itaparica Island and some minor islands (Leão et al. 2003); in the Recife de Fora Marine Park, Porto Seguro (PS), a well-preserved coral reef bank can be found in water shallower than 20 m; the Abrolhos Bank (AB), which has been considered the largest and richest area of coral community in Southwestern Atlantic.
4. *Southern region* South of the Doce River, the region is characterized by a lack of coral reef complexes where rocky shores provide habitats for corals and numerous other invertebrates: Guarapari islands (GP), Armação dos Búzios (BZ), Arraial do Cabo (AC), Ilha Grande (IG) and Ilhabela (IB). Ilhabela is the closest site to the southernmost limit of the distribution of *M. hispida*. Oceanic island: Ilha da Trindade (TR), an island with rocky reefs covered mainly by coralline algae, and located in the volcanic Vitória-Trindade seamount chain.

The following permit numbers were issued by the Ministério do Meio Ambiente for sampling in Federal Conservation Units: TE, 32145-2; AB, 968-1; AC and IG, 26348-1 and 23938-1; AR, 29953-2; FN, 29687-4; FZ, JP, SA, GP, TR, 22387-2. Unnumbered permits for sampling in BZ and PS, at sites within Municipal Conservation Units, were issued by the "Prefeitura da Cidade de Armação dos Búzios" and the "Secretaria Municipal de Meio Ambiente de Porto Seguro," respectively.

Sampling material and DNA extraction

Samples (~1 g) from the top (superior portion) of 298 colonies of the brain-coral *M. hispida* were collected with a hammer and a leather punch (12 mm) and fixed in CHAOS solution (Fukami et al. 2004). Sampling was not made according to specific seasons or years and encompassed a range of 11 months up to 6 years (ESM1). We also sampled the border (lateral portion) in addition to the top of 20 colonies at two depth ranges (1–3 and 8–10 m) from three sites (016°24.037′S 038°59.316′W, 5 colonies, 1–2 m; 016°23.945′S 038°59.214′W, 5 colonies, 2–3 m; 016°25.343′S 038°59.336′W, 10 colonies, 8–10 m) at Recife de Fora Marine Park, Porto Seguro (PS). When sampling was carried at the same depth on multiple days, we easily distinguished sampled colonies from those that were not collected yet for their small but clearly visible mark on the top portion. Genomic DNA was extracted using a phenol/chloroform protocol. For that, 0.25 mL of CHAOS lysis-buffer was added to ~0.1 g of coral sample and kept at room temperature for at least five days. The lysate was then placed in a new tube with 0.25 mL of PEB (Phenol Extraction Buffer; 100 mM Tris pH 8.0, 10 mM EDTA, 1 % SDS) and 0.5 mL of phenol/chloroform (1:1). After centrifugation at 16,873 × g for 5 min, the aqueous phase was removed and re-extracted with 0.5 mL of phenol/chloroform (1:1) followed by centrifugation at $16{,}873\times g$ for 5 min. Nucleic acids were precipitated by adding an equal volume of cold 100 % isopropanol, and samples were incubated overnight at −20 °C. Finally, the pellet was washed in cold 70 % ethanol, dried in a vacuum centrifuge (Eppendorf) and resuspended in 0.05 mL of sterile ddH_2O with 1 % RNase (10 mg mL^{-1}). Quantity and quality of DNA extracts were assessed by using an Implen Spectrophotometer.

Symbiodinium-18S RFLP profiling

Fragments of the 18S rDNA (~1600 bp) were amplified by using the specific pairs of primers ss3Z and ss5Z (Rowan and Powers 1991b). Reaction mixtures (30 µL each) contained 1X PCR buffer (Promega), 200 µM dNTPs, 2.5 mM $MgCl_2$, 1 mg mL^{-1} bovine serum albumin, 0.5 µM each primer, 1U GoTaq polymerase (Promega), 4 ng template DNA and sterile ddH_2O to volume. Cycling conditions for the 18S rDNA: 5 min at 94 °C (1 cycle); 1 min at 94°, 1 min at 55 °C and 2:30 min at 72 °C (1 cycle); 1 min at 92 °C, 1 min at 55 °C and 2:30 min at 72 °C (29 cycles); final extension at 72 °C for 10 min. PCR products and a DNA ladder (GeneRuler 100 bp DNA Ladder Plus, Fermentas) were run on 1 % agarose gels in 0.5X TBE buffer that, after staining with ethidium bromide, were visualized under a UV transilluminator. Amplified products were digested with the restriction enzyme *Taq* I (Promega) in 20 µL reactions incubated at 65 °C overnight containing 4 µL PCR product, 1X enzyme buffer, 5U *Taq* I and sterile ddH2O to volume.

Symbiodinium clades were identified according to RFLP profiles described in the literature (Rowan and Powers 1991a) and profiles for DNA extracts from cultures of *Symbiodinium* clades A, B, C and D (common in the Atlantic Ocean; DNA extracts donated by Prof. Mark Warner, University of Delaware, USA). Also, resulting PCR products of 16 samples (including two samples of type C from *Mussismilia hartti*) comprising encountered RFLP profiles were purified with the GFX PCR and DNA Gel Band kit (GE Healthcare) and sequenced in both forward and reverse direction (ABI 3500). Sequences were manually edited (assembled and trimmed) using SeqMan (v 7.00, DNASTAR, Inc.) and deposited in GenBank (accession numbers KR092113-KR092128). To corroborate the identifications, a phylogenetic reconstruction analysis was performed with the partial 18S rDNA sequences generated in this study and sequences retrieved from GenBank (ESM 3). The dataset included partial sequences of *Symbiodinium* A, B, C, D, E and F (clades G, H and I were not found) in addition to *Prorocentrum micans*, *Gymnodinium catenatum* and *Protodinium simplex* that were used as outgroups for rooting purposes only. All reference sequences that had the closest matches to our sequences (with *e* values of 0.0, 100 % coverage and down to 99 % identity) were included in our analysis. We analyzed a total of 148 sequences (including the 16 sequences generated in this study). Sequences were aligned by MUSCLE, as selected through a customized version of AQUA (provided by Chris Creevey), a script for alignment algorithm comparisons including MUSCLE, PRANK, MAFFT and each refined by RASCAL (Muller et al. 2010). After manually trimming the ends and misaligned positions, we generated a final alignment of 1422 bp. We selected the model and performed maximum likelihood analyses using IQ-TREE v1.4.4 (Nguyen et al. 2015). According to the Akaike Information Criterion (AIC), the TIM2 + G4 was the best fitting model for the data with base frequencies of $A = 0.263$, $C = 0.190$, $G = 0.269$ and $T = 0.278$, and a gamma distribution shape parameter of 0.874. To efficiently explore the tree space, we performed eight ML tree searches (each with five replicates; 40 runs in total). We evaluated different values of perturbation strength and number of unsuccessful iterations to stop in each tree search. Ultrafast bootstrap support values were calculated with 1000 pseudoreplicates and 5000 iterations under maximum likelihood criteria (Minh et al. 2013). Chromatograms of sequences generated in this study, alignment, scripts and results of the phylogenetic analysis are deposited at https://github.com/npicciani/symbiodinium.

Oceanographic data and statistical analyses

Sea surface temperature (SST) monthly averages and Kd490 (diffuse attenuation coefficient at 490 nm, a proxy for turbidity) at 4 km spatial resolution were acquired from the Moderate Resolution Imaging Spectroradiometer on Aqua satellite (MODIS-Aqua), available from the NASA Ocean Biology Processing Group. Data were retrieved for all sampling locations from January 2004 to December 2014 (also available at https://github.com/npicciani/symbiodinium). For statistical analyses, we used the 10-year average of each monthly average retrieved from all MODIS-Aqua passes for each location. We assessed the relationship among *Symbiodinium* clades and environmental variables (SST and turbidity) through a distance-based redundancy analysis (db-RDA) (Legendre and Anderson 1999) using the Bray-Curtis similarity index based on clades frequency among samples in each site. In this analysis, a similarity matrix of distances was submitted to a Principal Coordinate Analysis (PCoA) followed by a Redundancy Analysis (RDA) of the principal coordinates obtained (Borcard et al. 2011). Since RDA performs a multivariate linear analysis, we conducted a prior analysis with both variables (SST and Kd) using both first- and second-degree explanatory variables. A test of significance of each variable using *ordistep* function (package vegan) rejected second-degree terms for both Kd and SST, $p > 0.05$). Therefore, the analysis was only carried out for first terms (linear relationship). The analyses were performed in the R 3.2.2 environment (R Core Team 2015) using the package *vegan* (Oksanen et al. 2015).

Results

Our analyses indicate that *Mussismilia hispida* may be associated with at least three clades of *Symbiodinium*: A, B and C (Fig. 1). Overall, *Symbiodinium* A was detected as the only dominant clade in half (51 %) of all colonies analyzed (298 samples). *Symbiodinium* B was found exclusively in 21 % of the colonies and occurred only in Southeastern Brazil. The third type, *Symbiodinium* C, was associated with 23 % of the colonies, which were all from the state of Bahia (SA, PS, AB). Co-occurrence of two clades of *Symbiodinium* on the top sample of a colony was found only in 4 % of all examined samples (*Symbiodinium* A and B; GP, BZ and IB). In the oceanic islands (AR, FN and TR; 25 % of total sampling), colonies were associated with only *Symbiodinium* A. *Symbiodinium* 18S rDNA sequences obtained were consistently assigned to the clades previously described as common in the Atlantic Ocean [A, B and C; Fig. 2; see Baker (2003)], therefore corroborating the identifications based on RFLP profiling. We found a total of three haplotypes among our 16 sequences. One of those haplotypes is distinct from all sequences publicly available on GenBank. Sequences from *Symbiodinium* B are notably close to each other forming a monophyletic group even though representing two localities (Ilhabela, Armação dos Búzios). All *Symbiodinium* A haplotypes are closely related to each other in a well-supported (94 % ultrafast bootstrap support) clade with other haplotypes mostly derived from non-coral hosts.

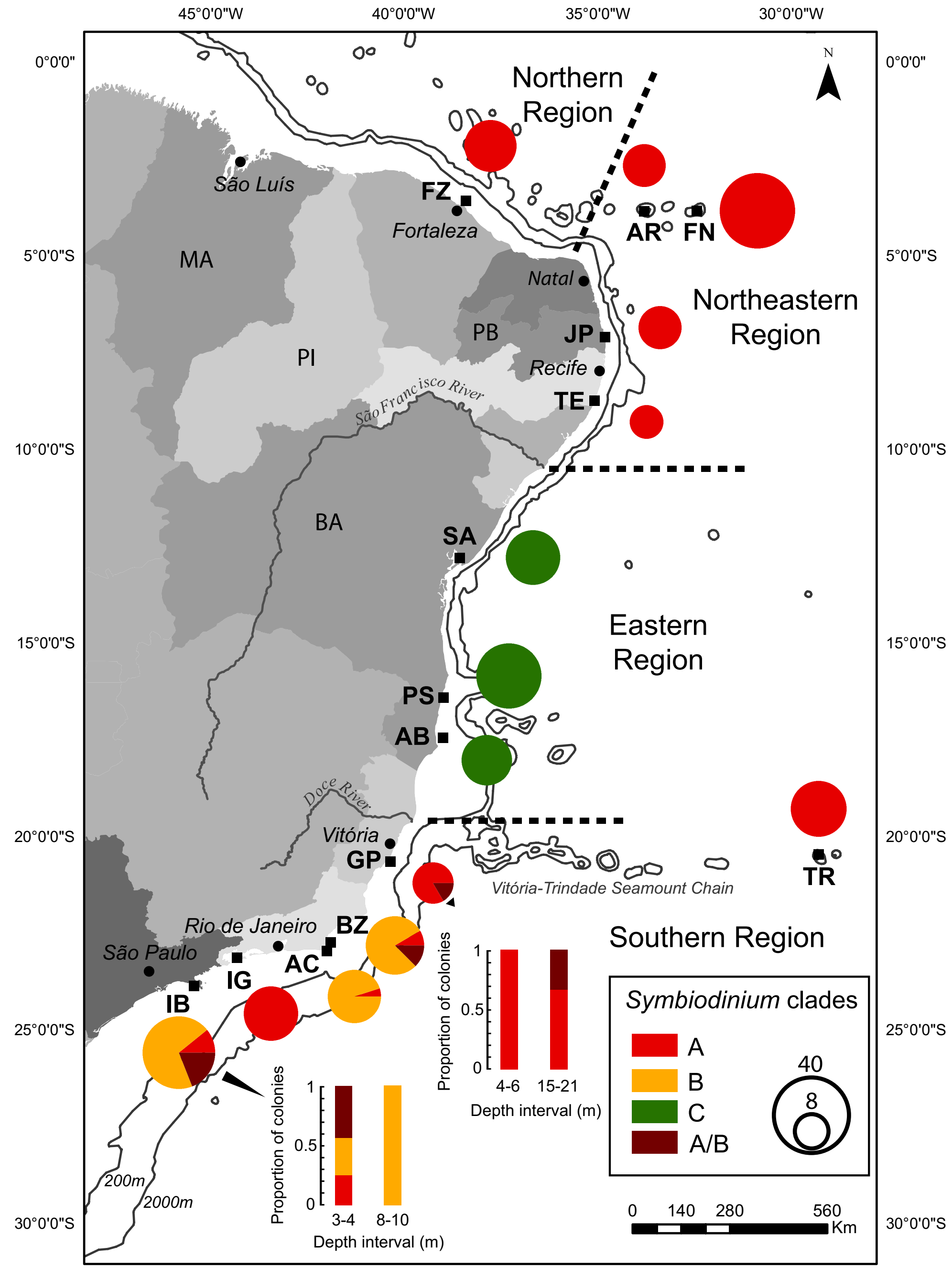

Fig. 1 *Symbiodinium* clades associated with the brain-coral *Mussismilia hispida* (Verrill, 1902) along the Brazilian coast. Abbreviations for collection sites (sampling depth) are as follows: FZ = Fortaleza (18–25 m), AR = Atol das Rocas (0–5 m), FN = Fernando de Noronha (1–25 m), JP = João Pessoa (2–8 m), TE = Tamandaré (1–4 m), SA = Salvador (6–12 m), PS = Porto Seguro (1–10 m), AB = Abrolhos Bank (two samples at ~4 m, other depths not recorded), TR = Ilha da Trindade (3–25 m), GP = Guarapari (4–21 m), BZ = Armação dos Búzios (1–5 m), AC = Arraial do Cabo (2–5 m), IG = Ilha Grande (1–6 m), IB = Ilhabela (3–10 m). MA, PI, PB and BA denote, respectively, states of Maranhão, Piauí, Paraíba and Bahia. Pie charts represent the relative proportion of *Symbiodinium* clades found at each site (A, B, C or A/B when clades A and B co-occurred in the same sample) with diameters proportional to the number of sampled colonies in each location. Bar charts denote the relative proportion of colonies in GP (4–6 m, $n = 4$; 15–21 m, $n = 6$) and IB (3–4 m, $n = 16$; 8–10 m, $n = 21$) with different *Symbiodinium* clades at two depth intervals at each site. The four major reef regions (Northern, Northeastern, Eastern and Southern) as recognized by Leão et al. (2003) are indicated

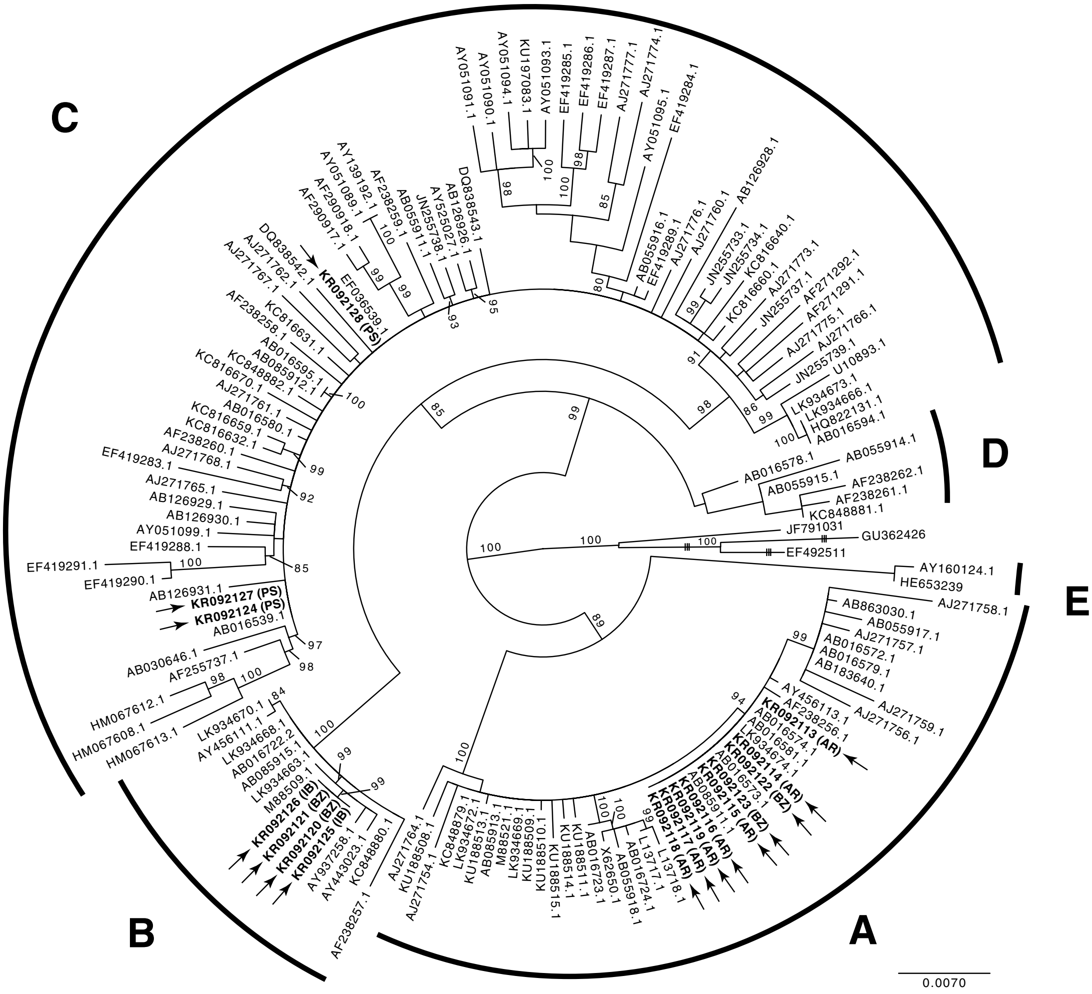

Fig. 2 Maximum likelihood (ML) tree of *Symbiodinium* 18S rDNA assembled dataset under TIM2 + G4 model. *Symbiodinium* clades A, B, C, E and F as indicated. Bold tip labels with arrows are sequences obtained in this study. BZ = Armação dos Búzios; IB = Ilhabela; PS = Porto Seguro; AR = Atol das Rocas. Scale bar denotes the estimated number of nucleotide substitutions per site. Ultrasfast bootstrap support values (>75) are shown at the nodes. Accession numbers are given at the tip labels. Information about the reference sequences used is presented on ESM 3. Outgroup branches were reduced a third in length as indicated by the three bars on each branch

Symbiont variation among colonies of *M. hispida* was observed in only four localities in Southeastern Brazil: Guarapari, Armação dos Búzios, Arraial do Cabo and Ilhabela (GP, BZ, AC and IB; Fig. 1). Colonies in these sites were associated with *Symbiodinium* A, B or both clades (A and B). Occurrence of *Symbiodinium* B (exclusively or co-occurring with *Symbiodinium* A in each colony) increased with depth at Guarapari and Ilhabela, and it was also found to be dominant in shallow depths (1–5 m) at Armação dos Búzios and Arraial do Cabo (Fig. 1). We found no within-colony variation in symbiont diversity at two distinct depth ranges (1–3 and 8–10 m) at Recife de Fora Marine Park (PS)—regardless of sampling the top or the border of colonies, only *Symbiodinium* C was detected.

The two db-RDA constrained axes explained 47 % of total variance (28 and 19 %, respectively), being both axes significant (pseudo-$F = 4.9629$; $p = 0.007$). Explanatory variables, temperature (SST, pseudo-$F = 4.96$; $p = 0.025$) and turbidity (Kd, pseudo-F=4.21; $p = 0.015$), were linearly related to *Symbiodinium* clades. The db-Rda analysis showed that *Symbiodinium* B, mostly found in Armação dos Búzios, Arraial do Cabo and Ilhabela, was negatively correlated with temperature (Fig. 3, $r = -0.99$), but not with turbidity ($r = 0.27$). *Symbiodinium* C, exclusively found in localities at the state of Bahia (SA, PS, AB), was positively correlated with turbidity ($r = 0.93$), but not with temperature ($r = 0.19$). On the other hand, *Symbiodinium* A, the most abundant symbiont, found along the Northern, Northeastern, Southern (GP and IG, only) regions and oceanic islands was negatively associated with turbidity ($r = -0.95$) and showed a weak but positive relationship with temperature ($r = 0.47$; Fig. 3).

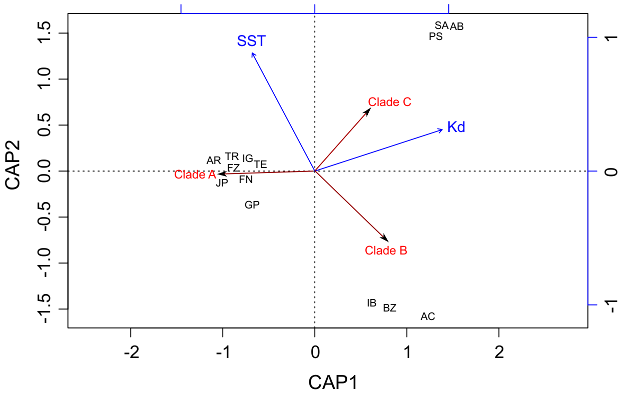

Fig. 3 Distance-based redundancy (RDA) analysis of *Symbiodinium* clades composition associated with *Mussismilia hispida* colonies among sites. SST = sea surface temperature monthly averages; Kd = diffuse attenuation coefficient at 490 nm, a proxy for turbidity. For sites abbreviations, see legend in Fig. 1

Discussion

Geographic patterns of host–*Symbiodinium* associations

Geographic boundaries of association patterns found in *M. hispida* closely correlate with the limits of major geographic areas used to describe the distribution of reef-building corals in Brazil as indicated in Fig. 1 (Laborel 1970; Leão et al. 2003). *Symbiodinium* A occurred in the Northern and Northeastern Areas, which together extend from the Amazon River mouth (0°30′S) to the São Francisco River mouth (10°30′S) (pattern one). *Symbiodinium* C was present in the Eastern Area, which extends south of the São Francisco River mouth until the Doce River mouth (19°40′S) (pattern two). Colonies with *Symbiodinium* A, B or both were found to occur in the Southern Area that comprises the region from the Doce River mouth to Santa Catarina State (27°30′S) (pattern three). These observations agree with previous reports from Baker (2003; see Fig. 3 and supplemental material), which indicate the exclusive presence of *Symbiodinium* C in the Abrolhos Bank (AB), and the presence of the clades A and B in the Southeastern region of Brazil (Rio de Janeiro and São Paulo States).

While reefs in the Northeastern Area are mostly patch or elongated bank reefs on a narrow continental shelf (~50 km) and very shallow waters (up to 10 m in depth), those in the Eastern Area show a great variety of forms. In the Eastern Area, reef structures may vary from fringing and bank reefs above beach rocks to isolated pinnacles that can rise from waters deeper than 20 m on a shelf that can reach ~200 km in width (Maida and Ferreira 1997; Leão et al. 2003). As described in previous studies, reef development decreases toward the São Francisco River mouth (Castro and Pires 2001), the largest river in Eastern Brazil, that acts as an ecological barrier. Its discharge rate of ~2850 m^3 s^{-1} seems to inhibit coral reef development up to Salvador, located north of the Eastern Area. The Eastern Area comprises not only the most complex coral reef structures but also the highest diversity of shallow water scleractinian species (~18 spp.) in the coast. No coral reef development and a noticeable impoverishment of coral fauna take place in the Southern Area (Laborel 1970; Castro and Pires 2001). An obvious interpretation of these correlated distribution patterns is that similar processes have been shaping both the composition of coral communities and the distribution of symbionts associated with *M. hispida* along the Brazilian coast. Overlapping distribution of the three host–*Symbiodinium* patterns with marine ecoregions recognized on the basis of "patterns of ocean circulation, coastal geomorphology, and distribution of major faunal populations" (Sullivan-Sealey and Bustamante 1999; Spalding et al. 2007) can also be distinguished. For instance, pattern one overlaps with the Northeastern Brazil ecoregion, while pattern two mostly overlaps with the Eastern Brazil ecoregion and pattern three with the Southeastern Brazil as defined by Sullivan-Sealey and Bustamante (1999). Taken together, these observations reinforce the suggestion that biogeographic processes determining the distribution of marine organisms along the coast are also influencing the distribution of *Symbiodinium* clades associated with *M. hispida*.

Our data agree with common reports of *Symbiodinium* A from shallow waters ranging from 0 to 5 m in depth with high irradiance conditions (Loh et al. 1998, 2001; LaJeunesse 2002). In Fortaleza, despite the greater depths of occurrence of the colonies (18–25 m), there is a large distance from the coast (~13 km) and clear waters up to 30 m in visibility (Soares et al. 2011), as observed in the three oceanic islands (AR, FN, TR). *Symbiodinium* A was found to be negatively correlated to turbidity and weakly associated with high temperatures (Fig. 3). The ability of lineages of *Symbiodinium* A to efficiently synthesize photoprotectors as mycosporine-like amino acids [MAAs; (Banaszak et al. 2000)] seems to allow them to mostly occupy shallow areas in marine environments. Also, *Symbiodinium* A was the only lineage found at the two extremes of *M. hispida*'s distribution. While physiological generalizations to the clade level are unsuitable, the group might encompass either a suite of closely related lineages with different abilities to thrive in highly distinct environments or a suite of lineages with high levels of phenotypic plasticity. Noticeably, *Symbiodinium* A haplotypes were closely related to other ones retrieved from non-coral hosts, which could be a result of a bias in sequence discovery towards non-coral hosts in this group.

Colonies of *M. hispida* were associated only with *Symbiodinium* C along the state of Bahia (~1000 km coastline), regardless of depth range (total range of 1–12 m). Additionally, *Symbiodinium* C was positively correlated to turbidity, as shown in the locations sampled in Bahia state (SA, PS, AB; Fig. 3). Although clade C was related to high level of sedimentation, *Symbiodinium* C comprises the most diverse group within the genus, with the highest number of known subclades and a wide variety of hosts (from sea anemones, corals, sponges and molluscs to foraminifera) (LaJeunesse et al. 2003; LaJeunesse 2005; Pochon and Pawlowski 2006). Many analyses support an extreme physiological variability within the group: some subclades can be better adapted to sun exposed regions and others to turbid conditions (Ulstrup and Van Oppen 2003; Van Oppen et al. 2005). Also supporting the variability within the group, *Symbiodinium* C has been found in association with corals occurring from shallow waters (Stat et al. 2011) down to 60–100 m in depth (Chan et al. 2009) and with antipatharians from 10 to 396 m (Wagner et al. 2011), both in Hawaiian waters. Despite the signal in our dataset showing *Symbiodinium* C positively associated with high-turbidity localities, the widely reported within-group variation could be associated with local environmental variations. For instance, only *Symbiodinium* C was found in the Abrolhos Bank despite highly significant variation in sedimentation rates (yearly average from 9 to 104 mg cm^{-2} day^{-1}) being reported for the three points we sampled (Pedra de Leste, Sebastião Gomes and Coroa Vermelha; ESM1) (Castro et al. 2012). An average sedimentation rate of ~ 200 mg cm^{-2} day^{-1} as found in several months in Sebastião Gomes by far exceeds the threshold known for heavy sedimentation stress (~ 10 mg cm^{-2} day^{-1}) in coral reefs (Rogers 1990). Also, only *Symbiodinium* C was detected both on top and border of colonies from shallow (1–3 m) and deep (8–10 m) waters at the three sampling sites in Recife de Fora Marine Park, Porto Seguro (ESM1). Our data reinforce the observation that some coral species do not display clade-level symbiont variation related to distinct ecological niches within colonies (Baker et al. 1997; Van Oppen et al. 2001; Ulstrup and Van Oppen 2003; Frade et al. 2008; Wicks et al. 2012). A differential distribution of subclades (not recognized in our study) of *Symbiodinium* C within colonies cannot be ruled out as these could be related to minor local variations.

Lineages of *Symbiodinium* B have been found associated with a high diversity of hosts, from anemones, hydrozoans and zoanthids to, more frequently, gorgonians, commonly in deeper regions (10–15 m). A shift in the association from *Symbiodinium* C to *Symbiodinium* B with increase in latitude has been observed in colonies of *Plesiastrea versipora* along the northeastern and southeastern coast of Australia (Rodriguez-Lanetty et al. 2001). The authors suggest that *Symbiodinium* B, commonly found in temperate regions, might be better adapted to low-light and low-temperature conditions (*cf.* Refs. Loh et al. 2001; Knowlton and Rohwer 2003; Garren et al. 2006). Colonies of *M. hispida* in the Southern region were associated with the same *Symbiodinium* B haplotype, which were negatively correlated to temperature. In this region, sea surface temperatures are usually low, varying from ~22 °C in the winter to ~25 °C in the summer (ESM 2). In particular, *Symbiodinium* B (exclusively or co-occurring with *Symbiodinium* A) was mostly found at higher depths and higher latitude, suggesting a temperature-driven spatial distribution in this region. The dominance of *Symbiodinium* B among colonies in shallow waters at Armação dos Búzios and Arraial do Cabo can be clearly explained by the effect of an intense upwelling of cold waters in this region. Upwelling of the South Atlantic Central Water (SACW) occurs on a regular basis, mainly due to the action of north-northeastern wind, but also because of the directional change of the coastline (Valentin 2001). Also in agreement with our results, the two colonies of *M. hispida* harboring *Symbiodinium* B19 in the Vitória-Trindade seamount chain were collected at high depths (45 and 60 m) in cold water conditions (Silva-Lima et al. 2015). In contrast, the other two colonies collected in the same area at a shallower depth (22 m) were associated with *Symbiodinium* A4 (Silva-Lima et al. 2015).

Would availability of *Symbiodinium* clades and/or population connectivity explain the patterns of symbiotic association?

A growing body of evidence has indicated that many corals have the ability to associate with multiple clades of *Symbiodinium* (Mieog et al. 2007; Silverstein et al. 2012) and that acquisition of these symbionts in early ontogenetic stages is apparently non-selective (Coffroth et al. 2001). Local availability and abundance of different symbionts may play an important role in determining host–*Symbiodinium* associations of adult colonies (Van Oppen et al. 2001; Ulstrup and Van Oppen 2003). Nevertheless, we consider it unlikely that local availability of clades plays a role on determining *Symbiodinium* associations found in *M. hispida*. This is because in the same three locations (SA, PS, AB), *Millepora alcicornis* associates with *Symbiodinium* clades A and B (A. Garrido and C. Zilberberg, unpublished data). Additionally, colonies of the massive corals *Siderastrea* spp. hosted *Symbiodinium* C and B in Paraíba, Northeastern Brazil (Costa et al. 2008; Monteiro et al. 2013). In Abrolhos, Silva-Lima et al. (Silva-Lima et al. 2015) reported the presence of *Symbiodinium* A4 in cultured samples of *M. braziliensis* symbionts. Even with the potential availability of other clades of *Symbiodinium*, *M. hispida* possessed *Symbiodinium* A in João Pessoa

(Paraíba) and *Symbiodinium* C in Salvador, Porto Seguro and Abrolhos as the dominant clades detected by PCR–RFLP. This observation indicates that different clades of symbionts proliferate in colonies of *M. hispida* at different locations.

The possibility that population-specific factors could be shaping the distribution of symbiotic associations is highly unlikely. A recent population genetic survey supports extensive connectivity among populations of *M. hispida* along the Northeastern and Eastern Brazilian coast, with no evident partition among those from the state of Bahia and JP, TE or GP (L. Peluso and C. Zilberberg, unpublished data). If population-driven factors were explaining the differences in host–symbiont associations, we would expect levels of connectivity among populations to reflect the patterns of association along the coast. Uncorrelated patterns of population structuring and symbiont distribution at the clade level would not support the hypothesis. Nonetheless, further comparative and experimental studies are necessary to better understand how population connectivity affects host–symbiont associations in *M. hispida*.

Conclusions

The occurrence of *Symbiodinium* A, B and C in colonies of *M. hispida* demonstrates its ability to associate with multiple clades of symbionts. This flexibility in symbiotic association potentially contributes to the extensive distribution of this species along the coast and oceanic islands. Geographic patterns of host–*Symbiodinium* associations in *M. hispida* follow previously recognized reef regions along the Brazilian coast suggesting that similar processes might have been structuring coral communities and symbiotic associations. Implications of *Symbiodinium* diversity for the susceptibility of the species to environmental disturbances need to be evaluated through further refined molecular studies and physiological experimental approaches. We maintain that understanding *Symbiodinium* diversity is critical to assess the resilience of Brazilian reef-building corals. Our current knowledge on *Symbiodinium* diversity and the components that may affect this interaction will benefit from future research on host–*Symbiodinium* interactions among Brazilian corals.

Acknowledgments We thank Dr. A. M. Solé-Cava (UFRJ) and Dr. M. Klautau (UFRJ) for laboratory facilities. Thomas Bell (UCSB) provided helpful assistance with compilation of MODIS-Aqua data. Dr. M. Warner (UD) generously supplied DNA extracts of *Symbiodinium* cultures. Dr. E. Calderon (Coral Vivo/MNRJ), C. Pereira (Coral Vivo), L. Lopes (Coral Vivo), A. Climério, J. Medeiros (CEBIMar), E. Honuma (CEBIMar) and J. Sebroeck (in memoriam, CEBIMar) provided assistance in field collections. Dr. T. Oakley (UCSB), colleagues of the Evolution Seminar (EV595/UCSB), L. Lima (IEAPM) and V. Tascheri (UFRJ) contributed with insightful comments on early versions of the manuscript. We thank the Brazilian Marine Biodiversity Network SISBIOTA-Mar (CNPq 563276/2010-0 and FAPESC 6308/2011-8, PI: S.R. Floeter) for collection of samples at PML, FZ, TE, SA, AR, FN and TR. Project BIOTA (FAPERJ E-26/110.015/2011, PI: PC Paiva), particularly, Dr. R. Ventura and Dr. F. Pitombo for collecting at IG, A. Garrido and L. Peluso for sampling in GP and Dr. F. Nunes for the JP samples. We also thank the Coral Vivo Research Network, sponsored by Petrobras through the program Petrobras Socioenvironmental and co-sponsored by Arraial D'Ajuda EcoParque, for financial and logistical support for field work, and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for a master fellowship to NP (process 130913/2011-1) and a research fellowship to PCP (process 303939/2014-1). We are thankful to the NASA Ocean Biology Processing Group for production and distribution of MODIS-Aqua satellite data.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest relevant to the subject of this article.

Animal rights statement Animals have been sampled and/or treated according to the national legislation, and all required permissions have been obtained.

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