REPORT

Ocean warming can help zoanthids outcompete branching hydrocorals

Bruno Charnaux Lonzetti[1] · Edson Aparecido Vieira[1] · Guilherme Ortigara Longo[1]

Abstract Although coral–algae competition is more widely and frequently studied, invertebrates are also major coral competitors, potentially influencing reef structural complexity. Ocean warming can affect the outcome of coral–algae interactions, but its effect on the competition between corals and other invertebrates is poorly understood. In Southwestern Atlantic reefs, the branching hydrocoral *Millepora alcicornis* provides important structural complexity but is commonly in contact with the zoanthid *Palythoa caribaeorum*. Considering that *P. caribaeorum* is an efficient competitor that is likely to be more resistant to future ocean warming, the potential replacement of *M. alcicornis* by this zoanthid could reduce reef structural complexity and diversity. We combined field and laboratory experiments to investigate the mechanisms of this hydrocoral–zoanthid interaction, including the role of allelochemicals, to understand the response of *M. alcicornis* to contact by *P. caribaeorum*, and the impact of increasing temperatures on this interaction. Contact with *P. caribaeorum* caused more damage to *M. alcicornis* than the physical control under current temperature (27 °C), both in field and laboratory experiments, but the damaged area recovered within 10 days. Under simulated warming (30 °C) filamentous algae colonized the damaged area,

impairing the recovery of *M. alcicornis*. Contact with *P. caribaeorum* chemical extract under current temperature caused more damage to *M. alcicornis* than its control but caused similar damage under warming conditions. These results highlight that warming increased *M. alcicornis* susceptibility to any physical contact and reduced its recovery potential, indicating that it may be outcompeted and overgrown by *P. caribaeorum* as the ocean warms.

Keywords Coral competition · Climate change · Allelochemicals · Structural complexity · Reef flattening

Introduction

Reefs harbor a great diversity associated with the structural complexity created by corals and other species that provide habitat, refuge, and food, resulting in a complex network of interactions that sustain diversity (Moberg and Folke 1999). Such complexity is mostly supported by branching corals (Graham and Nash 2013) and generates a great variety of microhabitats, positively affecting reef diversity (Alvarez-Filip et al. 2009; Rogers et al. 2014; Darling et al. 2017). Therefore, the reduction of coral cover can affect the functioning and maintenance of these systems (Bozec et al. 2015). While ∼ 40% of Indo-Pacific corals are considered branched (*i.e.,* branching, corymbose, digitate, and/or tabular), this proportion is reduced to ∼ 23% in the Caribbean and to ∼ 14% in the Southwestern Atlantic (Mies et al. 2020). In addition to scleractinian corals, hydrocorals of the genus *Millepora*, that also form branches and plates, can play a major role in adding structural complexity to reefs in the Pacific (*e.g., Millepora platyphylla*; Lewis et al. 2006), Caribbean (*e.g., Millepora complanata*; Nagelkerken & Nagelkerken 2004), and in the

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Southwestern Atlantic, where reef complexity provided by branching morphology rely mostly on a single species, *Millepora alcicornis*, (Leão et al. 2003; Coni et al. 2013; Leal et al. 2013). Even though the decline of scleractinian corals has caused *Millepora* to become more conspicuous in some Caribbean sites (Cramer et al. 2021), increasing their role in providing structural complexity, these hydrocorals have also experienced high mortality after massive bleaching events (Nagelkerken & Nagelkerken 2004; Ferreira et al. 2021) and the consequences of these losses to reef complexity are often overlooked.

Like other benthic organisms, corals and hydrocorals depend on space availability and on their ability to compete for this resource (Jackson 1977) as they are frequently in contact with a variety of organisms, especially macroalgae that is considered a major threat to coral health (Jompa and McCook 2003a; Longo and Hay 2015). Contacts with algae lead to physically and/or chemically mediated competitive interactions that can destabilize the coral's microbiome (Pratte et al. 2018) and cause coral bleaching and necrosis in the affected area (Rasher and Hay 2010), coral death and subsequent overgrowth by the competitor (Diaz-Pulido et al. 2009), often enhancing algal dominance and reducing diversity (Hughes et al. 2007). In addition to algae, invertebrates can also place significant competitive pressure on corals and may even overcome algae as the major competitive threat to corals, leading to loss of structural complexity and diversity (Cruz et al. 2015, 2016; Roth et al. 2018).

Southwestern Atlantic reefs are dominated by algal turfs and macroalgae (Aued et al. 2018) which are often in contact with the dominant massive corals without causing much harm (Grillo et al. 2018). In contrast, zoanthids have outcompeted corals and caused a phase shift from coral to zoanthid dominance in some of these reefs (Cruz et al. 2015, 2016). The zoanthid *Palythoa caribaeorum*, for instance, is common in the Western Atlantic, often dominating shallow reefs due to its high tolerance to variable environmental conditions (Sebens 1982), including a predicted high tolerance to future ocean warming (Durante et al. 2018). Besides, *P. caribaeorum* is one of the most important coral competitors in Southwestern Atlantic (Grillo et al. 2018) likely by using allelochemicals upon contact (Suchanek and Green 1981; Bastidas and Bone 1996; Almeida Saá et al. 2020). In a region where reefs have a relatively low coral cover (Aued et al. 2018) and low functional redundancy of branching corals (Coni et al. 2013; Mies et al. 2020), such as the Southwestern Atlantic, the dominance of a strong competitor like *P. caribaeorum* may pose an important threat to reef diversity.

Future temperature in the South Atlantic Ocean is projected to increase 3 °C by 2100 under the high greenhouse gas emission scenario (Barros et al. 2014), which may disrupt corals' symbioses with dinoflagellates causing coral bleaching and potentially mortality (Hughes et al. 2018; Bleuel et al. 2021). Additionally, the loss of symbionts can indirectly affect corals' ability to compete because thermally stressed corals may have less energy to allocate to competitive interactions (Johnston et al. 2020). In contrast, increased temperatures enhanced growth rates of *P. caribaeorum* when competing against the invasive sun coral *Tubastraea coccinea* (Almeida Saá et al. 2020). Under ocean warming scenarios, Southwestern Atlantic corals are predicted to become more prone to bleaching (Bleuel et al. 2021) and as a consequence more vulnerable to harsh competitors such as the zoanthid *P. caribaeorum*. Although hydrocorals within the genus *Millepora* are often considered good competitors due to their ability to rapidly colonize different substrates and expand their habitat (Dubé et al. 2019; Cramer et al. 2021), recent thermal-stress events have caused great damage and mortality, particularly to *M. alcicornis* (Ferreira et al. 2021), suggesting their competitive ability will decline with warming. If *P. caribaeorum* overgrows *M. alcicornis* in a warmer South Atlantic, it could cause major reef flattening and diversity loss (Alvarez-Filip et al. 2009; Graham and Nash 2013; Rogers et al. 2014; Bozec et al. 2015).

The hydrocoral *M. alcicornis* and the zoanthid *P. caribaeorum* co-occur throughout the tropical Western Atlantic ($\sim$ 30°N to $\sim$ 23°S and $\sim$ 30°N to $\sim$ 27°S, respectively), sharing the upper zone of shallow reefs (Sebens 1982; Lewis 2006; Aued et al. 2018) and commonly competing for space, with *P. caribaeorum* often overgrowing *M. alcicornis* (Fig. 1). We investigated this competitive interaction between *M. alcicornis* and *P. caribaeorum* under current temperature and simulated warming predicted for 2100 (Barros et al. 2014). We experimentally tested in the field and in the laboratory: (i) the effect of *P. caribaeorum* direct contact on *M. alcicornis* tissue; (ii) the recovery of *M alcicornis´* damaged tissue; (iii) how ocean warming will modulate the outcome of this interaction; and (iv) if *P. caribaeorum* chemical compounds play a role in the interaction in current and future temperatures. We expected: (i) direct contact with *P. caribaeorum* to cause tissue damage on *M. alcicornis*; (ii) better tissue recovery under current temperature than under warmer temperature; (iii) direct contact to cause greater damage under warmer temperature; and (iv) this interaction to be chemically mediated regardless of the temperature.

Fig. 1 Study system and organisms. Shallow patchy reef system of Rio do Fogo, Northeast Brazil (5°12′34.4''S 35°21′46.4''W; top); the hydrocoral *Millepora alcicornis* (*Ma*; photograph by J. Bleuel) and the zoanthid *Palythoa caribaeorum* (*Pc*) (center), and the competitive interaction between them (bottom). Arrows in the bottom panel indicate bleached areas of *M. alcicornis* previously in contact with *P. caribaeorum*
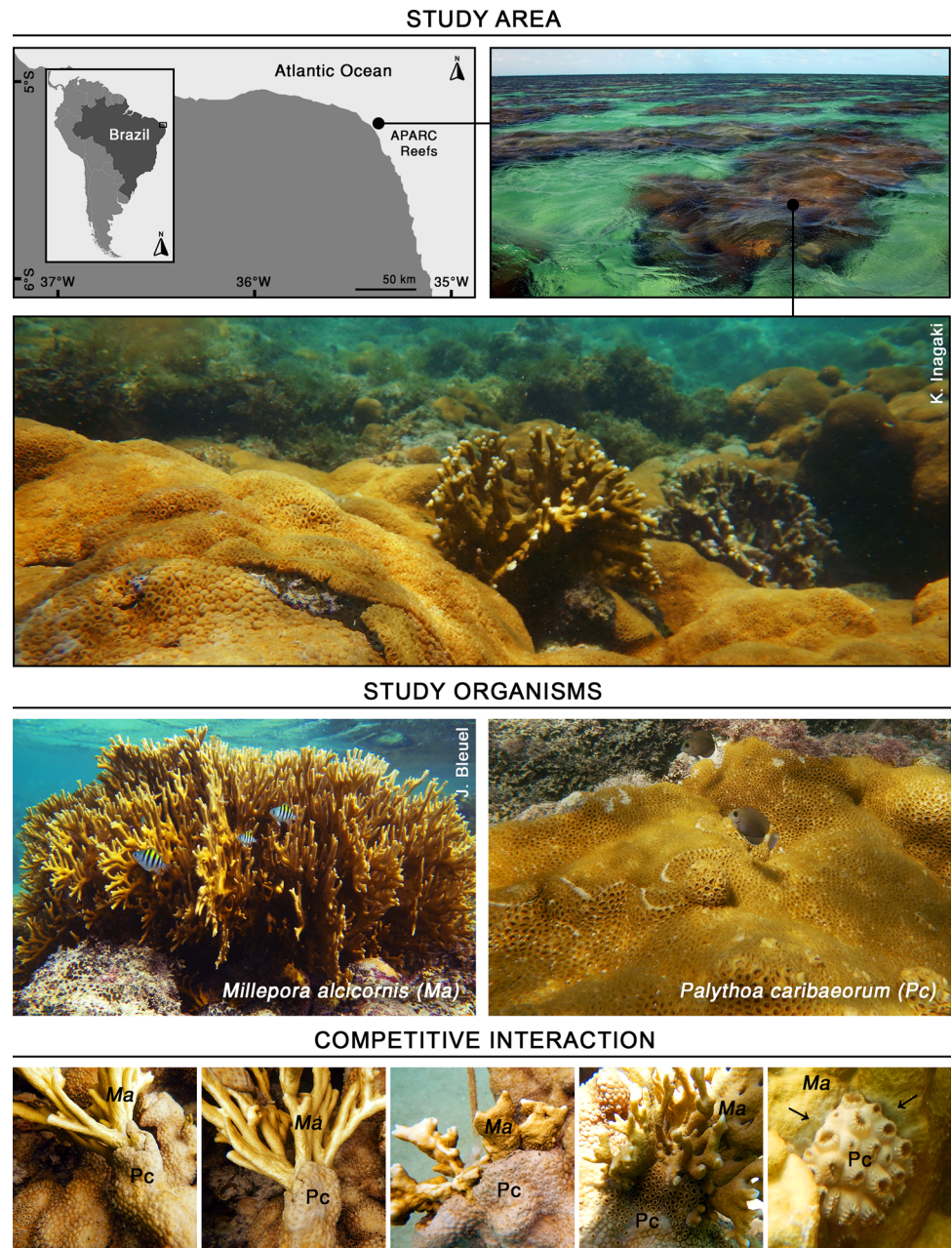
Materials and methods

Study site and system

We conducted this study in a shallow patchy reef located six kilometers from the coastline in Northeast Brazil (APARC—Área de Proteção Ambiental dos Recifes de Corais; 5°12′34.4″S, 35°21′46.4″W; Fig. 1). These reefs are dominated by algal turfs, coralline algae, massive corals (mostly *Siderastrea stellata* and *Porites astreoides*), one branching hydrocoral (*Millepora alcicornis*), and zoanthids (mostly *Palythoa caribaeorum*) (Aued et al. 2018; Roos et al. 2019). Unlike Pacific and Caribbean reefs, branching corals are scarce in Brazilian reefs and the hydrocoral *M. alcicornis* is the main branching species contributing to increasing structural complexity, providing habitat, refuge, breeding sites, and even food for various fish and benthic organisms (Leão et al. 2003; Coni et al. 2013; Leal et al. 2013).

We haphazardly assessed 42 colonies of *M. alcicornis* by photographing their bases to evaluate the frequency of colonies in contact with different organisms and the percentage of colony border (linear length) in contact with each organism. We found that 30% of the surveyed colonies were in contact with *P. caribaeorum*, representing ∼ 20% of its border contact, while other contacting

organisms were mostly algal turfs that are considered less harmful (Jompa and McCook 2003b). In order to understand the outcomes and mechanisms of this competitive interaction, we used a field experiment simulating the contact between *M. alcicornis* and *P. caribaeorum* and chemical assays to investigate the potential role of allelochemicals in this competitive interaction. Because ocean warming can compromise coral's competitive ability (Johnston et al. 2020), we repeated the same field experiment in the laboratory under similar temperature observed in the field (27 °C) and under the predicted warming scenario (30 °C). We used the rationale that if laboratory experiments under current temperatures (27 °C) produced similar outcomes to those observed in the field (27 °C), then the experimental setup would be appropriate to investigate warming effects in the laboratory (30 °C). Our rationale was confirmed, so the details on field and laboratory experiments are presented in the sections below.

Simulated contact between *Millepora alcicornis* and *Palythoa caribaeorum*

We tested the response of *M. alcicornis* to physical competition with *P. caribaeorum* in the field by collecting three 6–8 cm healthy fragments of 20 M. *alcicornis* colonies ($n = 60$), with no signs of bleaching, epibionts, or bioeroders and attaching them to stainless steel nails on the reef substrate (Online Resource Fig. S1). Our experimental design included three treatments ($n = 20$ fragments per treatment): (1) a *P. caribaeorum* contact treatment in which *M. alcicornis* fragments were placed in direct contact with a live fragment of *P. caribaeorum* (5 cm^2, *P. caribaeorum* polyps facing the *M. alcicornis* surface); (2) an inert *P. caribaeorum* mimic contact treatment in which *M. alcicornis* fragments were placed in contact with a kitchen sponge (5 cm^2, free of antimicrobial agents to avoid effects on coral microbiota); and (3) a manipulative control in which *M. alcicornis* fragments were not subjected to any contact. The manipulative control ensured any tissue damage or loss observed during our experiment was not caused by overall conditions or from the fragment detachment from the colony. The contact with an inert *P. caribaeorum* mimic was used to assess if the observed tissue damage or loss could be attributed solely to a physical effect of *P. caribaeorum*, with no chemical or biological mechanism associated (sensu Rasher & Hay 2010). Placing *P. caribaeorum* polyps directly facing *M. alcicornis* was the closest simulation of the natural competition in which *P. caribaeorum* contacts *M. alcicornis* with the polyp and gradually overgrows it after the death of *M. alcicornis* tissue (authors observation). Contact treatments were gently attached to *M. alcicornis* fragments using a cable tie (Online Resource Fig. S1). We also held 5

cm^2 fragments of *P. caribaeorum* attached to stainless steel nails with a cable tie adjacent to each replicate group as another manipulative control for *P. caribaeorum*. All *P. caribaeorum* control fragments survived, and there was no obvious color variation during the study that could indicate *P. caribaeorum* was perishing or adding any artifact to our experiment (Online Resource Table S1).

We took scaled photographs of the contacted area after 1, 3, and 13 days of contact introduction to assess *M. alcicornis* health (damage extent in cm^2, and L*a*b* color space; see 'Assessment of *M. alcicornis* tissue condition'). On day 1, the contact treatment was removed, a photograph was taken, and the contact reestablished with the same *P. caribaeorum* or mimic. On day 3, the contact treatment was removed, and a photograph was taken without treatment reestablishment. After 13 days, photographs were taken to assess damage duration and recovery.

We performed the same experiment in the laboratory under different temperature conditions (mimicking current field and future warming conditions) to test if ocean warming would modulate the outcome of contact competition. We took six healthy fragments (6–8 cm) from another 11 M. *alcicornis* colonies in the field ($n = 66$) and transported them from the study site to the laboratory (approximately three hours of transportation) under seawater within aerated cooler containers. In the laboratory, we gently glued them to squared plastic bases with cyanoacrylate-based glue (*Super Glue by Loctite®*) and evenly distributed the fragments (at least 10 cm apart; $n = 33$, 3 fragments of each colony) in two identical tanks (80 × 50 × 25 cm; length × width × height; 100 L in volume). Each tank was a closed seawater recirculating system with physical, biological, and chemical filtration in individual sumps (60 × 30 × 60 cm; length × width × height; 108 L in volume), and in proper lighting and temperature conditions calibrated based on field data that we measured every 15 min for three months with the HOBO Pendant® MX2202 data logger. Average light measurements in the field were 4606 lx ± 327 SE, which we converted to photosynthetic active radiation (PAR) by multiplying it by 0.0195 (sensu Thimijan and Heins 1983; Li-Cor 2008) reaching 90 μmol s-1 m-2 (PAR), and average temperature was 27 °C. We used the same HOBO Pendant® MX2202 data logger to calibrate the light conditions in the laboratory, reaching 4606 lx that converted to PAR using the constant related to our light equipment (0.017; sensu Thimijan and Heins 1983; Li-Cor 2008) represented 80 μmol s-1 m-2 (PAR). We also set a 12-h photoperiod with gradual dawn (only red and blue lights were on between 05:30 and 06:00, and the white light was activated at 06:00) and dusk. White light was off at 17:30 h, only red and blue lights were on between 17:30 and 18:00, and all lights were of at 18:00. We let the

hydrocoral fragments acclimate to the laboratory tanks for 15 days with the water temperature at 27 °C (field average) manually controlled in the two tanks. We controlled the lighting and the water temperature in the laboratory tanks every 15 min for the entire duration of the acclimation and experiment with the HOBO Pendant® MX2202 data logger. We did not feed the hydrocoral fragments either during the acclimation or the experiment, as most of the hydrocorals nutrition in general comes from the photosynthesis of the associated dinoflagellates (Gattuso et al. 1999; Furla et al. 2000). We also based our decision not to feed the hydrocoral fragments on a study that found that the growth of *M. alcicornis* was not impacted by the absence of feed in a setup similar to ours and for a much longer duration (Oliveira et al. 2008). For the experiment, we set the temperature in one tank at 27 °C (current field condition) and in the other at 30 °C (projection for 2100; Barros et al. 2014). We measured salinity and pH along the experiment with a salinity refractometer and a pH meter, respectively. Salinity and pH in both temperature treatments of the experiment remained comparable to field values (tanks: 35-42 ppm and pH 8.1–8.5; field: 35–40 ppm and pH 8–8.5) and did not differ between tanks (salinity test: t = 1.26, df = 20, p = 0.221; pH test: t = 1.69, df = 12, p = 0.116). Following the same setup used in the field experiment, in each tank, we assigned 11 M. *alcicornis* fragments to a *P. caribaeorum* contact treatment, 11 to an inert mimic contact treatment, and left the final 11 under no contact treatment working as a manipulation control.

We are aware that having one tank per temperature treatment formally generates pseudo-replicates (Underwood 1997). However, (1) data collection was focused on short-term measures of damaged area and color change exclusively at the point of contact and did not include systemic attributes such as growth and calcification rates; (2) the manipulative *M. alcicornis* controls remained healthy and consistently different from contact treatments under both temperatures throughout the study (see color data in the Results section), decreasing the possibility of significant effects of water-soluble compounds in *M. alcicornis* response to contact; (3) the six fragments of *P. caribaeorum* used as manipulative controls in each tank survived and had no obvious color variation during the experiment that could indicate *P. caribaeorum* was adding any artifact to influence the measured outcomes (Online Resource Table S1); (4) if there were any effects of soluble compounds of *P. caribaeorum* on the measured attributes of all *M. alcicornis* fragments within the same tank, it would probably override any effect related to the contact, which was not the case in this study (see Results); (5) the outcomes of our laboratory experiment mimicking the current conditions (27 °C) followed those observed in the field experiment, suggesting there was no interference

among contact treatments within the same tank; and (6) our experimental setup consisted of 33 fragments of *M. alcicornis,* between 6 and 8 cm in height at least 10 cm apart from each other and 11 fragments of *P. caribaeorum,* ($\sim 2 \times 2$ cm) randomly interspaced in a 80×50 cm surface (length x width), immersed in ~ 200 L of circulating water (adding the tank and sump capacities). Such a small biomass of *M. alcicornis* and *P. caribaeorum* in a high volume of water going through filtration would minimize potential effects of water-soluble compounds released either by the *M. alcicornis* or the *P. caribaeorum* that could systemically affect the results. Therefore, we used the fragments as true replicates considering the logistical constrains of having tank replicates (see Brown et al. 2002; López et al. 2021 for similar approaches regarding pseudo-replication).

As in the field experiment, we assessed the health of the coral fragments by measuring the damage extent and color space (see '*Assessment of M. alcicornis tissue condition*') in scaled photographs of the contact area after 1, 3, 5, 13, and 23 days after contact was initiated. On the first assessment, the contact was removed, a photograph was taken, and the same contact was reestablished. On day 3, we removed the contact to assess *M. alcicornis* health and did not reestablish the contact to assess recovery on the days 5, 13, and 23 using the same procedures described above.

Effects of surface allelochemicals of *Palythoa caribaeorum* on *Millepora alcicornis*

We investigated whether competition between *P. caribaeorum* and *M. alcicornis* is primarily driven by mechanical damage caused by tissue abrasion on *M. alcicornis* when in direct physical contact with *P. caribaeorum*, or if it could be mediated by chemical damage caused by allelochemicals of *P. caribaeorum*. To verify this, we exposed *M. alcicornis* to gel pads containing lipid-soluble compounds extracted from the surface of *P. caribaeorum*. First, we collected four pieces of *P. caribaeorum* (16 cm^2) from the same reef area and depth in which we performed the physical contact experiment and transported them in cooler containers with aerated seawater to perform the chemical extractions in the laboratory. Allelopathic compounds that mediate competitive interactions are typically found on the surface of an organism rather than in deeper tissues (Steinberg and Nys 2002; Nylund et al. 2007). We therefore adapted a method used for algae using hexane as a solvent, which, when applied for only 30 s, allows for the extraction of lipid-soluble metabolites from the surface of cells, without penetrating wet cells or causing lysis (de Nys et al. 1998; Rasher and Hay 2010). Therefore, this approach only extracts lipid-soluble metabolites from the

surface, rather than obtaining whole-cell extracts (Longo and Hay 2017). For each of the four *P. caribaeorum* pieces, we drained most of the seawater from *P. caribaeorum* surface, by positioning them vertically and gently agitating them up and down for 60 s. We then positioned each fragment above the wide and rounded opening (5 cm diameter) of a jar filled with 50 ml of hexane, ensuring polyps faced the solvent. With the *P. caribaeorum* fragment pressed against the jar opening to avoid hexane leakage, we turned the recipient upside down and gently stirred it in a circular horizontal motion for 30 s, ensuring polyps where in contact with hexane. The resulting solution was subjected to separation in a rotary evaporator at a 30 °C water bath. After the first round of evaporation, we transferred the resulting extract to a smaller recipient, resuspended any remaining extract in the flask with 15 ml of hexane, transferred it to the smaller recipient containing the extract, and performed a second round of hexane evaporation. We repeated this process for four *P. caribaeorum* fragments and mixed all the extracts, resuspending the resulted mixture with 4 mL of hexane (1 ml for each fragment extract). Extractions were performed within 10 h of sample collection.

To create gel pads with *P. caribaeorum* extract, we first homogenized 0.196 g of Phytagel™ (Sigma-Aldrich, USA) into 9.5 ml of water and then microwave heated the solution for 10 s. Right after heating, we added 1 ml of *P. caribaeorum* final extract, mixing it vigorously for homogenization. Quickly, to avoid solidification, the solution was poured on a strips-cut form containing a fine mesh bellow, letting it to dry. The solid gel-mesh strips were cut into small rectangles (1.0 × 2.0 × 0.3 cm; length × width × height). We followed the same procedure for control gels but added 1 ml of hexane instead of *P. caribaeorum* extract (sensu Longo and Hay 2017). In the field, we selected 20 M. *alcicornis* colonies and gently attached one extract and one control gel pad to different branches of the given colony using cable ties (Online Resource Fig. S1). We assessed the treatments' effects by evaluating color space after 24 h by taking pictures of the contact areas using the camera flash and black background to standardize light conditions. Damage area was not quantified for the chemical assay because the gel pad was considerably smaller than *P. caribaeorum* fragments or inert mimic used in the contact experiments, and the time span of 24 h produced only punctual damage.

We repeated this experiment in the laboratory simulating current and future temperatures to test if the effects of surface allelochemicals could be modulated by increased temperatures. We cleaned the laboratory tanks before this experiment, with neutral detergent and running water, as they were the same used in the previous laboratory experiment. We measured the lighting and temperature in

the tanks every 15 min for the entire duration of the experiment using the same HOBO sensors used in the previous experiments. Extracts were obtained as described above and we collected four fragments of 20 colonies of *M. alcicornis* following the same procedures used in the laboratory experiment simulating contacts with *P. caribaeorum*. We gently attached the extract and control gel pads to the fragments at 27 °C ($n = 40$, two of each colony) and 30 °C ($n = 40$, two of each colony) tanks using cable ties (Online Resource Fig. 1) and evaluated the color space of the damaged area after 24 h by taking pictures of the contact areas, following the same procedure described above.

Given the short duration of the chemical experiments, we did not use uncontacted fragments as a control but compared uncontacted areas of the experimental branches between treatments (chemical and temperature), using this comparison as a control in both field and laboratory experiments. The color of uncontacted areas of experimental branches did not vary between the chemical or temperature treatments, compared separately for the field and the laboratory experiments (Online Source Table S2), indicating that the color differences observed at the point of contact were related to the chemical treatment itself, not to the previous health condition of replicates or manipulation effects.

Assessment of *M. alcicornis* tissue condition

To estimate the damage extent caused by the contact with *P. caribaeorum* and its mimic on *M. alcicornis* fragments, we measured the damaged area (cm^2–size scaled by a ruler in the frame) by processing the photographs in the software IMAGEJ v.1.52a (Schneider et al. 2012). We estimated the color of the damage on *M. alcicornis* fragments by treatment analyzing photographs with Adobe Photoshop® mean blur tool, extracting the L*a*b* color space information (León et al. 2006). This color space consists of one parameter for lightness (L*), and two for color gradients, one ranging from green to red (a*) and the other from blue to yellow (b*). The higher the values, the lighter (L*), redder (a*), and more yellow (b*) the color. In biological terms, higher values for lightness represent brighter colors (bleaching) and lower values for a* and b* represent less healthy coral colors (necrosis or overgrowth).

Data analyses

In order to compare the size (cm^2) of damaged areas on *M. alcicornis* among contact treatments, we used repeated measure ANOVAs. In the field experiment simulating natural contacts, the predictors were the type of contact (fixed, three levels: *P. caribaeorum*, inert mimic, and

control), time (repeated, three levels: 1, 3, and 13 days), and the interaction between them. In the laboratory experiments simulating natural contacts, the predictors were the type of contact (fixed, three levels: *P. caribaeorum*, inert mimic, and control), temperature (fixed, two levels: 27 °C and 30 °C), time (repeated, five levels: 1, 3, 5, 13, and 23 days), and the interaction among them. In case of significant effects for any factor or interaction in the amin test, multiple comparisons were qualitatively performed by visual interpretation (Quinn and Keough 2002). Overall data were normal in each level of within-subject factor, and sphericity was attained by applying Greenhouse–Geisser correction when ε is smaller than 0.75. We conducted all univariate analyses on the software Systat 12®.

We used multivariate approaches to compare color information of the damaged area between treatments based on PERMANOVAs performed with 999 permutations on Euclidean resemblance matrices built with the normalized color parameters (L*, a*, and b*) as response variables (Anderson 2001). We additionally conducted SIMPER analyses for significant effect to obtain the color components that most contributed to the observed differences (Clarke 1993). Homogeneity of dispersion was evaluated with PERMDISP (Anderson 2001) comparing levels of the main factors with 999 permutations. We found deviations from the dispersion assumptions for some of the factors in our models (Online Resource Table S3), and we discuss our results in the light of these deviations. We plotted treatment groups and vectors for color parameters with PCA ordinations. For the field experiment simulating natural contacts, we used a PERMANOVA to test the effects of the type of contact (fixed, two levels: *P. caribaeorum* and inert mimic), time (fixed, three levels: 1, 3, and 13 days), and the interaction between them on the color space of the contact area. For the laboratory experiment, the predictors were type of contact (fixed, two levels: *P. caribaeorum* and inert mimic), temperature (fixed, two levels: 27 °C and 30 °C), time (fixed, five levels: 1, 3, 5, 13, and 23 days), and the interaction among them. For the chemical assays in the field, the predictors were type of contact (fixed, two levels: extract and control gels), and for the chemical assay conducted in the laboratory type of contact (fixed, two levels: extract and control gels), temperature (fixed, two levels: 27 °C and 30 °C), and the interaction between them. In case of significant effects, the default pairwise comparison tests for PERMANOVA in the analytical software were performed. We performed PERMANOVA, SIMPER and PERMDISP analyses on PRIMER 6 (Clarke and Gorley 2006) and PCAs using the package 'vegan' (Oksanen et al. 2008) and 'ggplot2' (Wickham 2016) in R software (R Core Team 2019).

Results

Simulated contact between *Millepora alcicornis* and *Palythoa caribaeorum*

In the field experiment, *P. caribaeorum* damaged an area of *M. alcicornis* 1.6 times larger than the area damaged by its mimic (Table 1, Fig. 2). The extent of the damage caused by *P. caribaeorum* and its mimic peaked after the first day of contact, stabilized until the third day when the contact was removed and started recovering with a reduction to about half of the area by the 13th day (Fig. 2a). We found evidence of significant dispersion in the factor 'treatment' in our multivariate model (Online Resource Table S3). However, the color of the damage caused by *P. caribaeorum* and the mimic was always different from the uncontacted control fragments, and between contact treatments after 1 and 3 days (Table 2, Figs. 2b, 3), corroborating our inference that the treatment differences are not entirely driven by differences in dispersion. While the control fragments showed a natural darker, redder, and yellower color (lower L* and higher a* and b* parameters, respectively), the area damaged by *P. caribaeorum* and the mimic was lighter, greener, and bluer (higher L* and lower a* and b* parameters, respectively), indicating that any contact imposed some harm to *M. alcicornis* (Online Resource Fig. S2; Figs. 2b, 3). However, the area damaged by *P. caribaeorum* was even lighter, bluer, and greener than the mimic by the first and third day (Online Resource Fig. S2; Figs. 2b, 3), suggesting a more intense effect of the living fragments of *P. caribaeorum* than the one caused by the inert mimic. By the day 13, the area damaged by both contacts did not differ in color, explaining the interaction (Table 2) and suggesting a recovery after the *P. caribaeorum* fragment removal after the third day.

When we simulated these contacts in the laboratory, the damage extension depended on a combination of temperature, contact, and time (Table 1; Fig. 2a). Similar to what we observed in the field, after one day of contact, *P. caribaeorum* caused more damage than its mimic at 27 °C. Both contacts damaged a similar area under 30 °C, which was comparable to the area damaged by *P. caribaeorum* in the field. On day 3, the damaged area increased regardless of the contact or temperature treatment. Following contact removal on day 3, temperature treatments started to diverge, with treatments under 27 °C showing a reduction in damage extension (recovery), while the damaged area remained stable for treatments under 30 °C (no recovery). *M. alcicornis* under 30 °C had damaged areas ∼ 1.6 and ∼ 2.0 times larger than *M. alcicornis* under 27 °C at the 13th and 23rd days, respectively. By the end of the experiment, 41% of the *M. alcicornis* fragments under

Table 1 Results of the repeated measure ANOVAs comparing the damaged area (cm^2) of *Millepora alcicornis* resulting from the simulated contact (*Palythoa caribaeorum* X inert mimic). The field experiment tested the effects of the simulated contact under current natural conditions and the treatment comparisons were performed through time (1, 3, and 13 days)

Source	Field experiment (*Greenhouse–Geisser ε – 0.84*)				Laboratory experiment (*Greenhouse–Geisser ε – 0.69*)			
	DF	MS	F	*P*	DF	MS	F	*P*
Between subjects								
Contact	1	79.27	8.48	**0.006**	1	6.03	0.56	0.458
Temperature	–	–	–	–	1	53.86	5.01	**0.031**
Cont. × Temp	–	–	–	–	1	9.38	0.87	0.356
Error	38	9.35			40	10.75		
Within subjects								
Time	2	47.37	21.78	**< 0.001**	4	43.08	44.56	**< 0.001**
Time × Cont	2	4.61	2.12	0.130	4	0.27	0.28	0.825
Time × Temp	–	–	–	–	4	7.70	7.97	**< 0.001**
Time × Cont × Temp	–	–	–	–	4	3.61	3.73	**0.016**
Error	76	2.18			160	0.97		

The laboratory experiment consisted in testing the effects of the simulated contacts under a warming simulation, testing for the effects of contact treatment and temperature (27 °C × 30 °C) through time (1, 3, 5, 13, and 23 days). Bold *P*-values stand for significant effects

30 °C (two in contact with the mimic and seven by *P. caribaeorum*, all from different genotypes) had their damaged area partially colonized by filamentous algae, which indicates a joint effect of temperature and *P. caribaeorum* weakening *M. alcicornis* recovery potential (Fig. 3). Differences in the color profile of damaged areas also depended on the interaction among temperature, contact, and time (Table 2, Fig. 2b). As observed in the field experiment, the color of areas in contact with *P. caribaeorum* and mimic was always different from uncontacted control fragments in the laboratory, but differences between *P. caribaeorum* and mimic treatments could be observed only under 27 °C (Table 2; Figs. 2b, 3). We found evidence of significant dispersion in the factor 'time' in our multivariate model (Online Resource Table S3). However, the clear separation of centroids through time also reinforces the validity of our inferences (see Fig. 2). Control fragments showed an overall natural darker, redder, and yellower color (lower L* and higher a* and b* parameters, respectively) when compared to the two contact treatments (Online Resource Fig. S3; Figs. 2b, 3). Under 27 °C, *P. caribaeorum* caused a damage with an overall lighter, greener, and bluer color than the area damaged by the mimic (Online Resource Fig. S3; Fig. 3), indicating a larger effect caused by the living *P. caribaeorum* fragment than contact with the inert mimic, as observed in the field experiment. Under 30 °C, no color difference was observed between *P. caribaeorum* and mimic damages, suggesting that temperature effects may overcome the effects of physical contact. The interaction with 'time' is probably related to the contact treatments sometimes exhibiting a darker color (lower L*) than the

uncontacted control fragments under 27 °C but never under 30 °C. We did not observe any signs of damage on *P. caribaeorum* from contacting *M. alcicornis* either in the field or in the laboratory experiments.

Effects of surface allelochemicals of *Palythoa caribaeorum* on *Millepora alcicornis*

In the field, contacts with the extract and the control gels resulted in a similar pattern to that observed in the simulated contact experiments. Contacts with extract gel resulted in lighter, greener, and yellower areas (higher L*, lower a* and higher b*, respectively) in comparison with areas in contact with the control gel (Table 3; Figs. 2c, 3; Online Resource Fig. S3), indicating that *P. caribaeorum* damage observed in the contact experiments was chemically mediated. In the laboratory, extract and control gels caused damages with similar color regardless of temperature, but damaged areas of *M. alcicornis* under 30 °C were lighter, redder, and yellower (higher L*, a* and b*, respectively) than those under 27 °C (Table 3; Figs. 2, 3; Online Resource Fig. S3), suggesting that temperature overcome any chemical effect. We found evidence of significant dispersion in the factor 'treatment' in our multivariate model (Online Resource Table S3). This deviation from the assumption of homogeneity of multivariate dispersion does not affect our inferences here, because there was no significant effect of 'treatment' or its interaction with 'temperature' in the PERMANOVA.

Fig. 2 Effects of the simulated competition between the hydrocoral *Millepora alcicornis* and the zoanthid *Palythoa caribaeorum* under current conditions (field experiments; left) and a warming scenario (laboratory; right). Mean (± SE) damaged area (top) of *M. alcicornis* in contact with *P. caribaeorum* and inert mimics. PCA ordinations considering the color space determined by the parameters *L**, *a**, and *b** for the damaged area by the simulated contact treatments (center), and chemical assay treatments (bottom) after 24 h. The transparent polygons in the PCAs represent the area comprised within the replicate points; thin black arrows are the color parameters vectors; and thick colored arrows indicate the temporal trajectories of the centroids
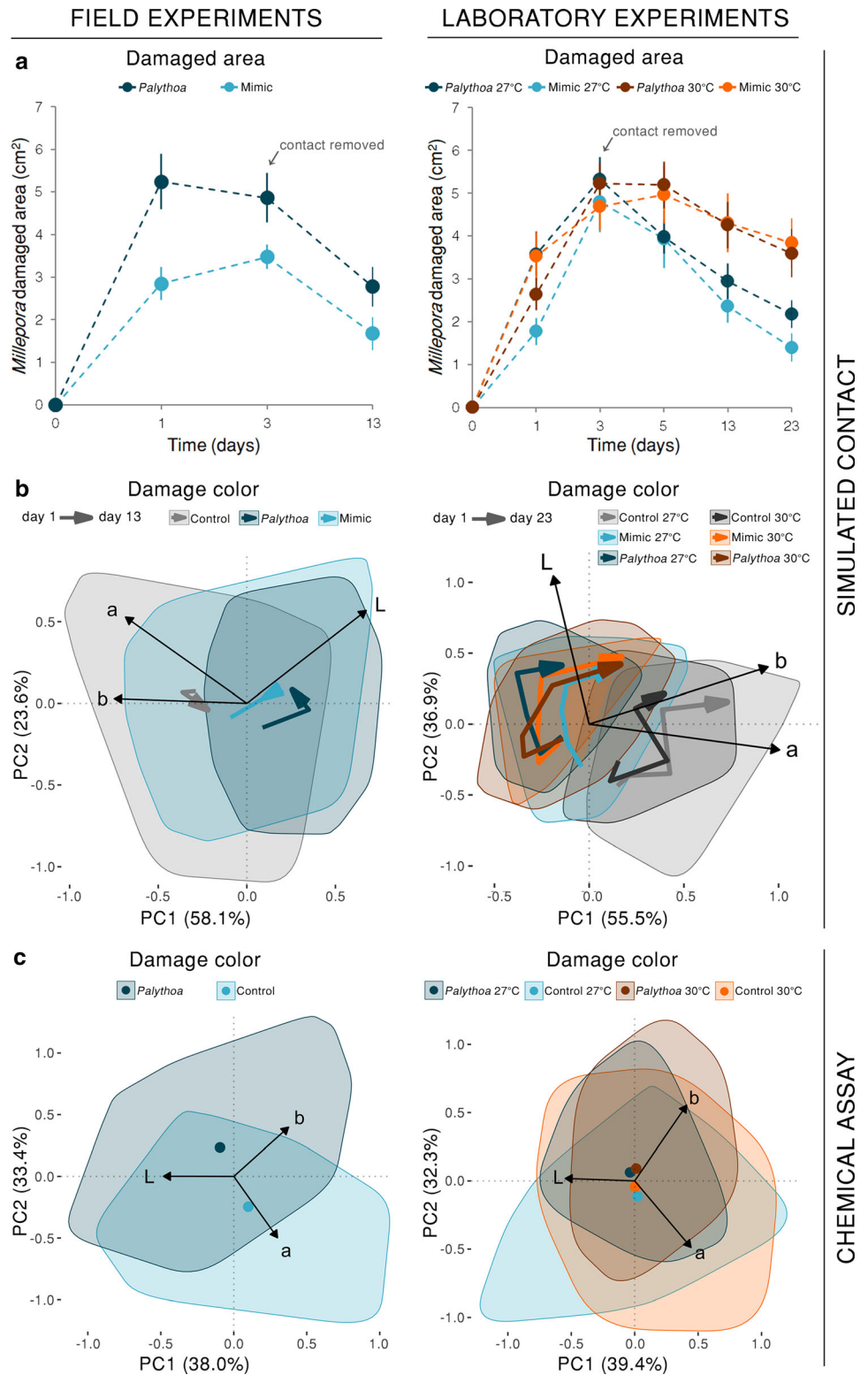
Table 2 Results of PERMANOVAs comparing the color space (considering the parameters L*, a* and b*) of the damaged area of *Millepora alcicornis* resulting from the simulated contact treatments (*Palythoa caribaeorum* X mimic X uncontacted control)

Source	Field experiment				Laboratory experiment			
	DF	MS	Pseudo-F	P	DF	MS	Pseudo-F	P
Contact	2	64.00	30.91	**0.010**	2	179.83	258.90	**0.001**
Temperature	–	–	–	–	1	5.85	8.43	**0.001**
Time	2	16.36	7.90	**0.001**	4	82.47	118.73	**0.001**
Cont. × Temp	–	–	–	–	2	8.38	12.06	**0.001**
Time × Cont	4	4.78	2.31	**0.022**	8	4.47	6.44	**0.001**
Time × Temp	–	–	–	–	4	2.11	3.04	**0.002**
Time × Cont × Temp	–	–	–	–	8	2.86	4.12	**0.001**
Error	168	2.07			300	0.70		

The field experiment tested the effects of the simulated contact under current natural conditions and the treatment comparisons were performed through time (1, 3, and 13 days). The laboratory experiment consisted in testing the effects of the simulated contacts under a warming simulation, testing for the effects of contact treatment and temperature (27 °C X 30 °C) through time (1, 3, 5, 13, and 23 days). Bold p-values stand for significant effects. For pairwise comparisons (footnote), P—*P. caribaeorum* fragment, M—inert mimic, C—uncontacted control, ns—non-significant, *P < 0.05, **P < 0.01

Pairwise comparisons: Field experiment – *Day 1*: PxM[*], PxC[**], MxC[**], *Day 3*: PxM[*], PxC[**], MxC[**], *Day 13*: PxM[ns], PxC[**], MxC[**]; Laboratory experiment – *27 °C*: *Day 1*: PxM[**], PxC[**], MxC[**], *Day 3*: PxM[*], PxC[**], MxC[**], *Day 5*: PxM[**], PxC[**], MxC[**], *Day 13*: PxM[**], PxC[**], MxC[**], *Day 23*: PxM[**], PxC[**], MxC[**]; *30 °C*: *Day 1*: PxM[ns], PxC[**], MxC[**], *Day 3*: PxM[ns], PxC[**], MxC[**], *Day 5*: PxM[ns], PxC[**], MxC[**], *Day 13*: PxM[ns], PxC[**], MxC[**], *Day 23*: PxM[ns], PxC[**], MxC[**]

Discussion

We found that the zoanthid *Palythoa caribaeorum* may be a superior competitor to the hydrocoral *Millepora alcicornis* by using both physical and chemical mechanisms. Under warming conditions, any physical contact will be harmful to *M. alcicornis* and limit its recovery capacity, threatening the role of this species in providing structural complexity in Western Atlantic reefs. The zoanthid *P. caribaeorum* is known for its high competitive ability, tolerance to warming, and low palatability (Gleibs et al. 1995; Francini-Filho and Moura 2010; Almeida Saá et al. 2020). In contrast, the competitive ability of hydrocorals within the genus *Millepora* is more related to its ability to colonize and grow fast (Dubé et al. 2019; Cramer et al. 2021). However, recent thermal stress events have greatly affected *M. alcicornis* populations (Ferreira et al. 2021). As oceans warm, *P. caribaeorum* will maintain its distribution in the tropics (Durante et al. 2018) and will continue to co-occur with *M. alcicornis*, which will likely be more vulnerable to competition with this zoanthid because of its poor response to thermal stress events. Therefore, the competitive interactions between them may lead to reduced structural complexity and diversity in the future, particularly in Brazilian reefs where *P. caribaeorum* is abundant (Aued et al. 2018) and *M. alcicornis* is the main species contributing to structural complexity through its branching morphology (Leão et al. 2003; Mies et al. 2020). If warming increases the susceptibility of corals and hydrocorals to competition while favoring competitors like *P.*

caribaeorum, this could affect other reefs in the Western Atlantic, including the Caribbean, threatening ecosystem diversity and function.

Ocean warming can weaken corals through bleaching and decrease their competitive ability against other organisms (Johnston et al. 2020). As thermosensitive organisms, corals can have their symbioses with dinoflagellates disrupted by warming (Hughes et al. 2018), which is expected to become more frequent and intense under future climate changes scenarios (Barros et al. 2014; Hughes et al. 2018; Bleuel et al. 2021). Additionally, climate change could enhance the competitive ability of some organisms, making them superior competitors in warmed and acidified oceans. For instance, elevated temperatures combined with the presence of a competitor led *P. caribaeorum* to higher growth rates (Almeida Saá et al. 2020), while elevated CO_2 concentrations increased mortality and decreased the health of the coral *Acropora intermedia* when contacted by macroalgae (Diaz-Pulido et al. 2011; Del Monaco et al. 2017). The damage caused by *P. caribaeorum* on *M. alcicornis* under warming was larger than under current temperature, resulting in differences in the color of the contacted areas when compared to the area contacted by the mimic, indicating an unhealthier state. It is worth noting that *P. caribaeorum* did not show any damage from contacting *M. alcicornis* in any of our experiments. These results combined indicate that *M. alcicornis* became more vulnerable when in contact with *P. caribaeorum*. Although we did not test if warming enhanced the competitive ability of *P. caribaeorum,* we observed a greater vulnerability of
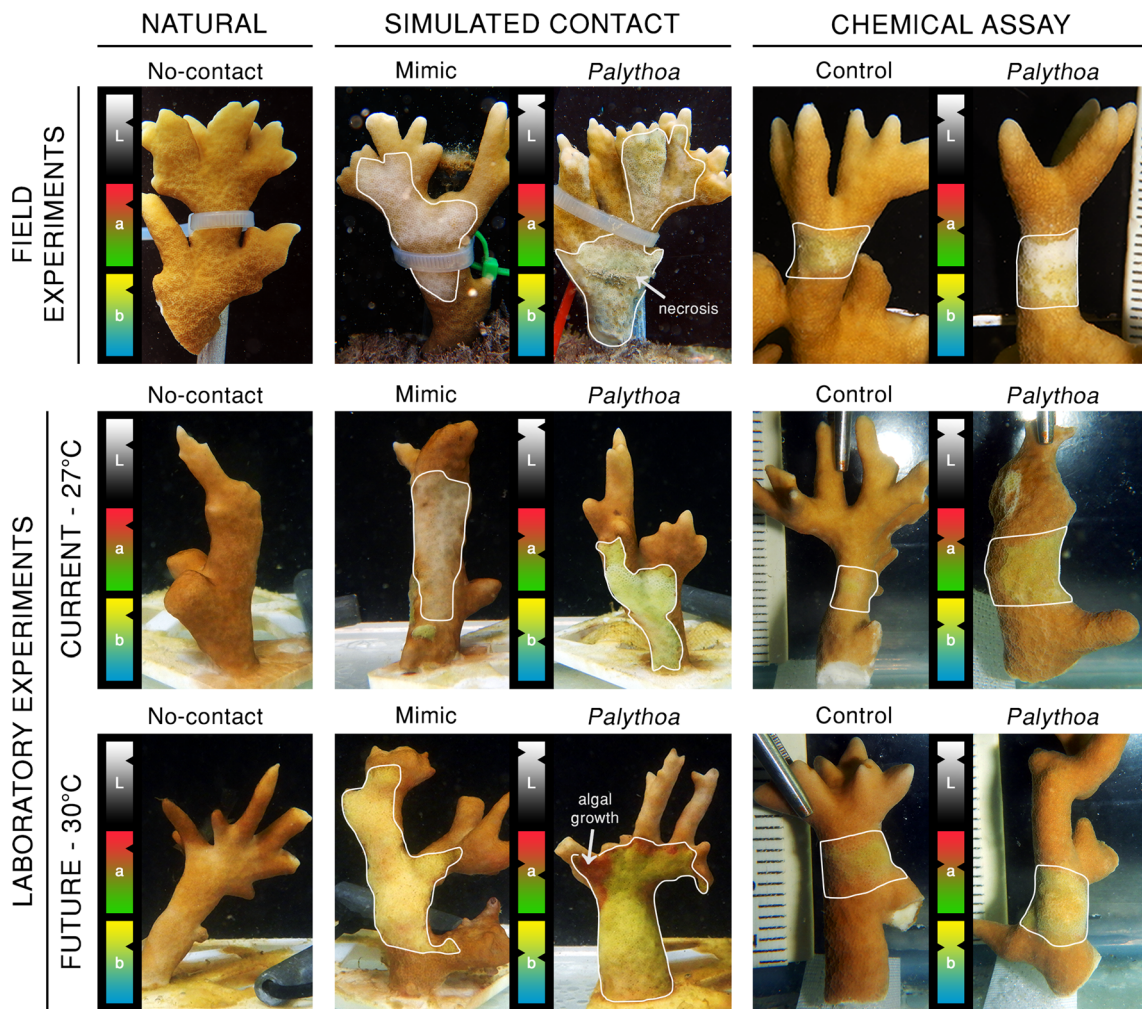
Fig. 3 Color characterization (*L**, *a**, and *b** parameters) of the damages caused by the zoanthid *Palythoa caribaeorum* on the hydrocoral *Millepora alcicornis* in the simulated contact experiment (center) and chemical assay (right) under current conditions (field experiment; top) and warming simulation (center and bottom) when compared to healthy not-contacted *M. alcicornis* fragments (left). The area in contact with the treatment is delineated in white, while necrosis (top) and algal growth (bottom) are indicated by white arrows. For each representative image, the correspondent color parameter values are indicated in the side color scale by black arrows

Table 3 Results of PERMANOVAs comparing the color space (considering the parameters L*, a* and b*) of the damaged area of *Millepora alcicornis* resulting from the chemical assay (*Palythoa caribaeorum* extract X control) after 24 h

Source	Field experiment				Laboratory experiment			
	DF	MS	Pseudo-F	*P*	DF	MS	Pseudo-F	*P*
Contact	1	11.05	3.96	**0.014**	1	2.57	0.86	0.487
Temperature	–	–	–	–	1	7.66	2.57	**0.040**
Cont. × Temp	–	–	–	–	1	0.30	0.01	0.968
Error	39	2.79			74	2.98		

The field experiment tested the chemical effects under current natural conditions. The laboratory experiment consisted in testing the chemical effects under a warming simulation and testing temperature effects (27 °C X 30 °C). Bold *P*-values stand for significant effects

M. alcicornis under warming because it was able to recover from contact damage under current temperatures, both in the field and in the laboratory experiments, but not under warming simulations (30 °C). Additionally, algae overgrew some *M. alcicornis* fragments under elevated temperature, which did not occur under current temperature.

These results suggest two major threats to *M. alcicornis*: (1) Any kind of physical contact will result in damage to *M. alcicornis* in warming conditions, and (2) competitive damage could indirectly enhance algal overgrowth in warmer conditions, preventing the hydrocoral recovery. Even though our warming experiment mimicked an acute and short-term thermal stress (less than 30 days), it still impaired recovery and led to algal colonization in the damaged areas under 30 °C. This scenario may become even worse as thermal anomalies are predicted to increase in frequency, severity, and duration in the near future (Oliver et al. 2019).

The surface allelochemicals of *P. caribaeorum* seem to be relevant in mediating contact competition with *M. alcicornis* under the current temperature, based on our field experiment. The role of chemical compounds on the competitive interactions of zoanthids has been discussed in studies with other *Millepora* species (Suchanek and Green 1981) and among zoanthids in intertidal systems (Rabelo et al. 2013), but the mechanisms that trigger the responses to these chemical compounds remain unclear. For example, the contact with *P. caribaeorum* and its surface allelochemicals may alter *M. alcicornis* microbiome and lead to damage. For coral–algae interactions, allelopathic compounds reduce the diversity of the coral microbiome, often affecting coral physiology and causing bleaching in the contact areas (Pratte et al. 2018). These altered microbiomes could induce coral disease, bleaching, and tissue loss (Pratte et al. 2018), which may be the case we observed with the extracts of the zoanthid *P. caribaeorum* in contact with the hydrocoral *M. alcicornis*. We did not observe clear allelochemical effects in our laboratory experiment, regardless of the temperature treatment, which could indicate that the effects of allelochemicals may be magnified under natural and more variable field conditions (*e.g.,* tides, turbidity, shading by clouds) in comparison with more stable laboratory conditions. It also suggests that temperature effects overcome the damage caused by allelochemicals, which is supported by the outcomes of our contact experiment where temperature effects were stronger than the effects of contact type (*P. caribaeorum* or inert mimic). This reinforces our inferences that weakened *M. alcicornis* may lose any competitive interaction under warming, regardless of the mechanism mediating the competition (*i.e.,* chemical, physical, or both).

Despite the importance of chemical and microbial activity in inflicting damage, coral competitors also use other mechanisms such as overgrowing and shading (Jompa and McCook 2003a). The threat posed by *Palythoa caribaeorum* on *M. alcicornis* may rely on chemical effects and changes on microbiota promoted by direct contact, but also on overgrowing strategies (Suchanek and Green 1981). Sponges can also use allelochemicals to prevent overgrowth by other sponges and ascidians (Engel & Pawlik 2000). However, opportunistic macroalgae can dominate degraded reefs and even outcompete sponges by growing much faster (González-Rivero et al. 2016). The zoanthid *P. caribaeorum* also grows fast and can overgrow competitors (Almeida Saá et al. 2020) using lateral aggression against species within the genus *Millepora* (Suchanek and Green 1981). The time span of our study did not allow us to report overgrowth, but it was common to find *M. alcicornis* reduced in size due to *P. caribaeorum* overgrowth in the field (Fig. 1). Therefore, *P. caribaeorum* may be one of the major natural drivers of reef complexity loss in the Southwestern Atlantic by outcompeting the hydrocoral *M. alcicornis* and potentially other corals. Some reefs in eastern Brazil have experienced a dominance shift from hard corals to the zoanthid *P.* cf. *variabilis* (Cruz et al. 2015). Similarly, dominance shift from hard to soft corals was documented in Seychelles in the Indian Ocean (Stobart et al. 2005) and in St. John in the Caribbean (Lasker et al. 2020). A critical difference among these events is that dominance shifts toward more encrusting organisms, such as *P.* cf. *variabilis* (Cruz et al. 2015) or *P. caribaeorum*, may lead to more significant declines in structural complexity than shifts to larger structurally complex gorgonians as observed in the Caribbean (Lasker et al. 2020). Therefore, a potential overgrowth of hard branching organisms such as *M. alcicornis* by encrusting organisms like *P. caribaeorum* may have severe consequences to reef complexity and diversity. These dominance shifts are likely to intensify with ocean warming, potentially altering species composition on coral reefs in the future.

Dominance shifts in reef ecosystems can be indirectly modulated by other interactions, such as grazing and predation (González-Rivero et al. 2011). Grazing herbivores can mediate coral–algae competition by favoring corals, with macroalgae competing with corals even becoming more vulnerable to herbivory (Rasher and Hay 2014; Longo and Hay 2015). In the Pacific, the macroalga *Galaxaura filamentosa* was more palatable to herbivorous fishes when previously competing with the coral *Porites cylindrica* (Rasher and Hay 2014), suggesting suppression of anti-herbivore chemical defenses. Similarly, in the Caribbean, the macroalga *Halimeda opuntia* in contact with the coral *Agaricia tenuifolia* was more palatable to the sea urchin *Diadema antillarum*, with no differences in the nutritional value in comparison with free living macroalgae, suggesting a downregulation of anti-herbivore chemical defenses (Longo and Hay 2015). A modeling study also indicated that low predation rates are critical to enable sponge dominance in Caribbean reefs (González-Rivero et al. 2011). In the case of *P. caribaeorum*, there is no evidence that predation controls its abundance (Suchanek

and Green 1981). In fact, *P. caribaeorum* is generally unpalatable to most predators and predation occurs sparsely (Francini-Filho and Moura 2010), though evidence suggests that egg-bearing polyps could be more targeted due to the benefits of ingesting higher nutritional value from the eggs overcoming its defenses (Longo et al. 2012). Therefore, it is unlikely that the competitive interaction between *P. caribaeorum* and corals will be attenuated by predation, especially in the warmer future when most fish feeding interactions on the benthos are predicted to decrease in intensity along the Western Atlantic (Inagaki et al. 2020).

Our results indicate that the zoanthid *P. caribaeorum* may outcompete the hydrocoral *M. alcicornis* under warming because increased temperatures make hydrocorals more susceptible to competition. If this is a general phenomenon for corals and considering that *P. caribaeorum* is conspicuous and widespread in the Western Atlantic, corals in this region may be at risk of being overgrown and replaced by this zoanthid under warming conditions. Predicting the future of reefs demands approaches that go beyond single species responses to climate change to include how climate change may affect species interactions. Understanding changes in competitive interactions and their outcomes is critical to predicting changes in ecosystem functioning and the services provided by coral reefs.

Declarations

Conflict of interest The author declare that they have no conflict of interest.

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