REPORT

Physiological factors facilitating the persistence of *Pocillopora aliciae* and *Plesiastrea versipora* in temperate reefs of south-eastern Australia under ocean warming

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Abstract High-latitude reefs are suboptimal coral habitats, but such habitats are increasingly considered to be potential refugia from climate change for range-shifting coral reef species. Notably, tropical reef fish have been observed along the south-east coast of Australia, but their establishment on temperate rocky reefs is currently limited by winter minimum temperatures and other resource needs, such as structurally complex habitats typical of tropical reefs. Recent expansion of the branching subtropical coral *Pocillopora aliciae* in rocky reefs near Sydney (34° S) could diversify the architectural structure of temperate marine environments, thereby providing potential shelter for tropical reef taxa in warming seas. Here, we investigated whether future environmental conditions (*i.e.* temperature increase) can influence the dominance of the subtropical branching coral *P. aliciae* over the resident encrusting coral *Plesiastrea versipora* in coastal Sydney by characterising physiological (*e.g.* metabolic stability) and behavioural (*e.g.* interspecific competitive hierarchy) traits that contribute to their competitive fitness. Our results suggest that a metabolic response, mediated by sterol and lipid metabolic pathways and provision of antioxidants, allows *P. aliciae* to reduce cellular stress and withstand exposure to short-term increased temperature. Conversely, *P. versipora* was more susceptible to heat exposure with no metabolic mediation observed. While *P. versipora* displayed greater aggressive behaviour when in direct contact with *P. aliciae* under all temperature conditions, the superior physiological and metabolic flexibility under increased temperatures of *P. aliciae* suggests that this species will likely outperform *P. versipora* under future increased temperatures. Such contrasting responses to environmental change would facilitate shifts in coral community and functional composition that could support further tropicalisation of coastal New South Wales.

Keywords Temperate reef · Tropicalisation · Physiology · Behaviour · Metabolomics · Coral

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Introduction

Warming of the global oceans from climate change is causing marine species to extend their ranges poleward to stay within the bounds of their thermal optima (Cheung et al. 2012; Poloczanska et al. 2013; Vergés et al. 2014). Although high-latitude ecosystems represent suboptimal habitats for tropical reef-building corals (Order Scleractinia) as a result of lower aragonite saturation state and pronounced seasonality of temperature and light regimes (Sommer et al. 2018), they are increasingly recognised as potential refugia for

tropical reef species impacted by climate change, including scleractinian corals (Beger et al. 2014; Camp et al. 2018a, b). Indeed, marine tropical species have already migrated into cooler, higher latitude areas in response to climate change (Poloczanska et al. 2016), like for instance tropical reef fish and coral species in Australia (Baird et al. 2012; Booth and Sear 2018). Over 150 have been observed along the temperate coast of Sydney, Australia (34° S) since 2002, although only 20 have overwintered for at least one year (Booth et al. 2018). While overwinter survival of tropical fish is closely linked with minimum temperatures, other factors (*e.g.* increased habitat structural complexity provided by corals) may further contribute to the establishment of tropical fish communities on temperate reefs (Booth and Sear 2018).

Coastal waters of south-east Australia support diverse temperate reef ecosystems, which host several species of scleractinian corals including *Plesiastrea versipora*, an encrusting cosmopolitan species found in relatively high abundance in coastal Sydney (Madsen et al. 2014) and further south (Madin et al. 2015). No architecturally complex corals existed in Sydney, where seawater temperature ranges between 18.8 and 24.7 °C (2012–2022 monthly average), until the subtropical endemic branching coral *Pocillopora aliciae* (Schmidt-Roach et al. 2013) was recorded in 2013 (Booth and Sear 2018) and has since increased in abundance, with over 70% cover in some densely populated patches (Sommer unpublished). Recent projections of *P. aliciae* population structure under recurrent thermal stress scenarios suggest that this species is vulnerable to heat stress at the core of its range in the Solitary Islands Marine Park, New South Wales, Australia (30.3° S, 153.143° E) (Lachs et al. 2021), where seawater temperature normally ranges between 16.6 and 27.5 °C (Malcolm et al. 2011). Furthermore, the establishment of *P. aliciae* populations at higher latitudes appears to rely on larval supply from the subtropical populations, which renders the potential of temperate reefs as biodiversity refugia less likely (Cant et al. 2021). Indeed, recent work highlights the role of ocean currents in mediating poleward range extension of corals in eastern Australia, with lack of tropicalisation of coral assemblages in Solitary Islands Marine Park (30.3° S) between 1990 and 2014 linked to low larval connectivity with coral populations on the southern Great Barrier Reef (Mizerek et al. 2021). Nevertheless, patches of *P. aliciae* colonies (that can exceed 30 cm in diameter) are being increasingly observed in coastal Sydney (33.8° S, 151.305° E) and are predicted to further establish where strengthening of the East Australian Current is expected to accelerate tropicalisation of this habitat (Booth and Sear 2018). Development of a 3D reef structure attributed to the growth of branching corals could lead to an increase in benthic habitat complexity and, in turn, facilitate tropicalisation of reef fish communities along the Sydney coast.

A suite of abiotic and biotic factors has been proposed to limit the range extension of corals into high-latitude regions, many of which require further examination (Abrego et al. 2021). For a given coral species to expand its geographic range, environmental conditions at a new location must fall within temperature, light, aragonite saturation, dissolved oxygen, salinity, and nutrient availability tolerance limits (Yamano et al. 2011), and coral larvae must find the right type of symbionts and settlement cues (Abrego et al. 2021). In addition, the coral must be capable of surviving predation and interspecific competition for space within the native biological community (Preston et al. 2008). In tropical waters, the capacity of corals to thrive into less-optimal environments is usually associated with a shift in metabolic balance of the host coral and/or the algal endosymbionts (Family Symbiodiniaceae) to enhance stress tolerance (Camp et al. 2020; Roach et al. 2021). Such metabolic shifts can be associated with a fitness cost, such as a slower coral growth rate (Camp et al. 2017). An example of such metabolic shifts is presented by the adaptation of *Astrangia poculata* to locations with different thermal regimes, which is mediated by metabolic and physiological adjustments from the host associated with genetic population differentiation driven by adaptive loci (Aichelman et al. 2019; Aichelman and Barshis 2020). Aggressive interactions between coral species, such as the protrusion of mesenteric filaments to digest neighbouring colonies and the use of sweeper tentacles, may play a key role shaping the architecture and composition of certain reef communities (Einat and Nanette 2006), and environmental changes have been shown to alter the competitive hierarchy of coral-coral interactions (Johnston et al. 2020). Whether similar metabolic and competition hierarchy responses hold true for (sub)tropical coral taxa expanding into temperate habitats remains unexplored, but such an assessment will benefit model predictions of changing population dynamics and subtropical reef structure under future climate scenarios.

An example of the mechanisms enabling the persistence of corals at high latitude is provided by the Sydney population of *P. versipora*, which can subsist despite its isolation from other populations through high survival of reproductive stages and sporadic recruitment peaks (Precoda et al. 2018). Also, high-latitude corals can exhibit different susceptibility to thermal stress posed by climate change, as evidenced by distinct physiological responses not necessarily coupled with Symbiodiniaceae composition (Goyen et al. 2019). However, little is known about specific physiological and behavioural adaptations that allow coral species from lower latitudes to expand into, and persist in, high-latitude reef habitats, as well as the impacts of the colonisation upon the native temperate coral community. While a previous study has shown that *P. versipora* undergoes heat stress and bleaching at 26 °C in Sydney (Goyen et al. 2019), the upper

thermotolerance limit of the invasive *P. aliciae* remains untested. Therefore, it is uncertain which species will have a competitive advantage under future seawater warming at this location. To address this knowledge gap, we characterised and compared the physiological and metabolic responses of the subtropical *P. aliciae* colonising Sydney, and of the native *P. versipora*, under current and predicted sea surface temperature scenarios. We discuss our results in the context of the potential ecological implications of tropicalisation of temperate reef ecosystems.

Material and methods

Coral collection

In October 2019, ten fragments of each *P. aliciae* (~5 cm length) and *P. versipora* (~25 cm^2) were collected from separate coral colonies offshore of Manly Head and Cobblers Beach, Sydney, Australia, respectively (Fig. S1). Samples of *P. aliciae* were collected using pliers and those of *P. versipora* with hammer and chisel. Coral fragments were transported in aerated seawater back to aquaria facilities at the University of Technology Sydney (UTS). Aquaria setup and coral growth conditions are described in Method S1.

Heat exposure experiment

An experiment was conducted to determine the physiological responses of *P. aliciae* and *P. versipora* under ambient *versus* elevated temperature regimes. The experiment was designed following recommendations from the Coral Bleaching Research Coordination Network for short-term exposure to heat (Grottoli et al. 2021). The experimental setup is detailed in Method S2 and included five coral fragments of each species *per* treatment randomly arranged in four tanks (two for control and two for treatment). After a ten-day acclimation period at 20 ± 1 °C (similar to in situ temperature), the temperature was increased in the treatment tanks, while the remaining physicochemical properties (monitored daily; Method S2) were maintained at similar levels to controls (Table S1 and Fig. S2), with the exception of dissolved oxygen (DO) that exhibited a decline with increasing temperature due to the inverse relationship between temperature and DO solubility (Fig. S3). Corals in the treatment tanks were exposed to a temperature ramping of 1 °C daily over a five-day period up to a sustained temperature of 26 °C, *i.e.* the upper tolerance limit of *P. versipora* in Sydney (Goyen et al. 2019), and +3 °C of the average maximum monthly mean (MMM) for Sydney in October for the past 5 years calculated using the historical Sea Surface Temperatures data (available online from the Australian Government Bureau of Meteorology) for a further

six days to assess acute responses to heat. The surface seawater temperature for the south-eastern coast of Australia is predicted to increase up to 3 °C above the MMM temperature (to ~27°C in Sydney) between 2080 and 2100 (Bull et al. 2020). All corals were sampled for metabolic profiling and quantification of bleaching response at the end of the experiment.

Photobiology

A Diving-PAM fluorometer (Walz, Effeltrich, Germany) was used to monitor coral photosynthetic performance via daily measurements of the Photosystem II (PSII) maximum quantum yield (F_v/F_m) as described previously (Goyen et al. 2019). After verifying no significant tank effect in photophysiology ($F = 2.98$, $p > 0.12$), non-normal data were analysed using the Kruskal–Wallis test ($p < 0.05$, SPSS v. 20, IBM Corp.). Briefly, measurements were performed on each coral fragment within the first two hours of the photoperiod, at a fixed distance of 1 mm from the coral's surface (measuring light intensity 4, saturation pulse intensity 4, saturating width 0.6 s, damping 2, gain 1). Closed system respirometry was used to determine the ratio of gross photosynthesis to dark respiration (*P:R*) 1–2 days prior to sampling for metabolic profiling for 3 replicates *per* species and treatment, as described in Method S3. Effect of species and temperature treatment upon *P:R* was tested using a two-way ANOVA after confirming assumptions of normality and homoscedasticity using Levene's and Shapiro–Wilk tests, respectively; evaluation of *P:R* data was performed using IBM SPSS Statistics v26.

Competition experiments

Parallel experiments were used to determine whether the range-expanding *P. aliciae* showed a behavioural advantage over the local Sydney species *P. versipora* to compete for space under different temperature scenarios. Distinct coral fragments from each species (in addition to the 10 fragments *per* species for the heat exposure experiment) were used. A fragment of *P. aliciae* was placed next to one of *P. versipora*, ensuring surfaces of both coral fragments were in physical contact and 24 h footage (and photographs at start and end) were taken using a Dino-Lite AM4115T digital microscope and the software DinoXcope v1.25 (dinolite.us). This was repeated at three separate temperatures. The first two replicates were performed after two weeks of acclimation in the experimental setup (Videos S1 and S2). Another two replicates, one for control (Video S3) and one for treatment (Video S4), were carried out just before the temperature ramp. The last two replicates, one for control (Video S5) and one for treatment (Video S6), were performed during the sustained exposure to heat (D3 and D4). We considered

the recorded aggressive behaviour, in which one coral fragment ejects its mesenterial filaments to digest the tissue of the other, as the criterion to determine outcompetition.

Intracellular metabolite extraction and data analysis

Sample processing protocols for coral and symbiont fraction separation and intracellular metabolites extraction were adapted from Matthews et al. (2020); a summary can be found in Method S4. Concentrated samples were derivatised and analysed as *per* Matthews et al. (2018), and details are provided in Method S5. Unfortunately, one *P. aliciae* and one *P. versipora* control host samples were lost during GC–MS analysis due to an instrument malfunction. Relative metabolite concentrations of both the host and symbiont fractions between species and treatments were evaluated by principal component analyses (PCA). In addition, a permutational multivariate analysis of variance (PERMANOVA) was conducted using PRIMER v6.0 (PRIMER-E Ltd, UK) for both host and symbiont fractions on a Bray–Curtis dissimilarity matrix comprising a two-factor design (species and treatment), type III sum of squares, and 9,999 permutations under a reduced model. Significance Analysis of Microarrays (and Metabolites) [SAM; (Xia and Wishart 2011)] is considered robust for detecting differences between treatments with unequal small sample sizes and unequal variances in metabolomic datasets (Tusher et al. 2001; Yang et al. 2006). SAM was performed to identify metabolites in the coral host and symbiont fractions that varied according to temperature treatment within and between species. SAM significant metabolites were determined based on a False Discovery Rate (FDR)-corrected significance value ($p_{adj} < 0.05$).

Quantification of bleaching response

Symbiont cell densities were quantified from 500 μL aliquots of host slurry (Method S4) using an Improved Neubauer haemocytometer (Boeco, Germany), with 10 replicate cell counts *per* sample to a confidence interval of below 10%. Cell density was normalised to host protein content (Smart et al. 2010). Non-normal data were analysed using the Kruskal–Wallis test ($p < 0.05$, SPSS v. 20, IBM Corp.).

Symbiont chlorophyll a (Chl a) content was quantified after N, N-dimethylformamide (DMF) extraction in darkness over 48 h at 4 °C. Extracts were centrifuged (16,000 g for 5 min) and triplicate 200 μL aliquots were analysed in 96-well plates (UVStar, Greiner Bio-One GmbH, Germany) at 646.8, 663.8 and 750 nm, using a microplate reader (Enspire 2300, Perkin-Elmer, Waltham, MA, USA). Chl a concentration was determined after optical path-length correction (0.555 cm) using the equations of Porra et al. (1989).

Data were analysed using a one-way ANOVA ($p < 0.05$, SPSS v. 20, IBM Corp).

Symbiodiniaceae composition identification

Symbiont DNA was extracted and the Internal Transcribed Spacer 2 region (*ITS2*) amplified as *per* Ros et al. (2021) only from control samples of both coral species (Method S6). Samples were processed at the Australian Genome Research Facility (AGRF; Melbourne, Australia) using two-stage amplicon generation and *ITS2* sequencing on the Illumina MiSeq platform using a 600-cycle kit. To determine symbiont type *per* sample, demultiplexed read pairs were analysed using SymPortal (Hume et al. 2019).

Results

Thermal stress indicators

Various photophysiological and biomass parameters of the endosymbiotic Symbiodiniaceae were measured as a proxy for photosynthetic capacity of control *versus* heat-exposed *P. aliciae* and *P. versipora* (Table S2). As expected, symbiont cell density (Fig. 1a) was significantly reduced in *P. versipora* under increased temperatures (two-sided *t*-test, $t = 3.232$, $p = 0.012$), but did not differ significantly between control and heat conditions in *P. aliciae* (two-sided *t*-test, $t = 1.336$, $p = 0.229$). While changes in maximum quantum yield of PSII (F_v/F_m) were minimal at the last day of the experiment (D6) between conditions in *P. aliciae* (Tukey HSD, $p = 0.995$), it significantly decreased in colonies of *P. versipora* under increased temperatures (Tukey HSD, $p < 0.002$; Fig. 1c). F_v/F_m did not differ significantly between control condition of each species (Tukey HSD, $p = 0.998$). Chl a concentration *per* symbiont cell (Fig. 1b) was not significantly affected in response to increased temperatures in *P. aliciae* or *P. versipora* (two-sided *t*-test, $t = -0.170$ and $p = 0.869$, and $t = -0.323$ and $p = 0.755$, respectively).

The ratio of gross photosynthesis to dark respiration (*P:R*) was measured as a proxy of coral holobiont functional performance (Fig. 1d). While the average *P:R* was smaller for the heat condition (26 ˚C) in both species, the difference between conditions was more prominent in *P. aliciae* (average of 2.45 at 20 °C and 1.99 at 26 °C) than in *P. versipora* (average of 2.44 at 20 °C and 2.24 at 26 °C), driven by both an increase in *P* and a decrease in *R* (Fig. S4). Even so, there were no significant effects (two-way ANOVA) on *P:R* between treatments ($p = 0.15$) or species ($p = 0.57$), or for the interaction between treatment and species ($p = 0.53$), possibly due to the small sample sizes.

Fig. 1 Photophysiological and biomass measurements of Symbiodiniaceae symbionts. Symbiont cell density (cells mL^{-1}) **(a)** and chlorophyll a content ($\mu g \, cell^{-1} \, mL^{-1}$) **(b)** *per* species and condition. An asterisk (*) represents significant ($p \leq 0.05$) difference in the within-species comparison based on a Kruskal–Wallis test. **(c)** Daily maximum quantum yield of PSII (F_v/F_m) is shown as mean ± SEM of both coral species in the control and high-temperature (treatment) conditions ($n=5$) for the five days of temperature ramping (R1-5) and the six days of the experiment (D1-6). **(d)** Gross photosynthesis to dark respiration ratio (*P:R*) *per* species and condition ($n=3$). The mean for each instance is shown as a square with the corresponding condition colour. Grey lines connecting the condition means highlight the difference between species
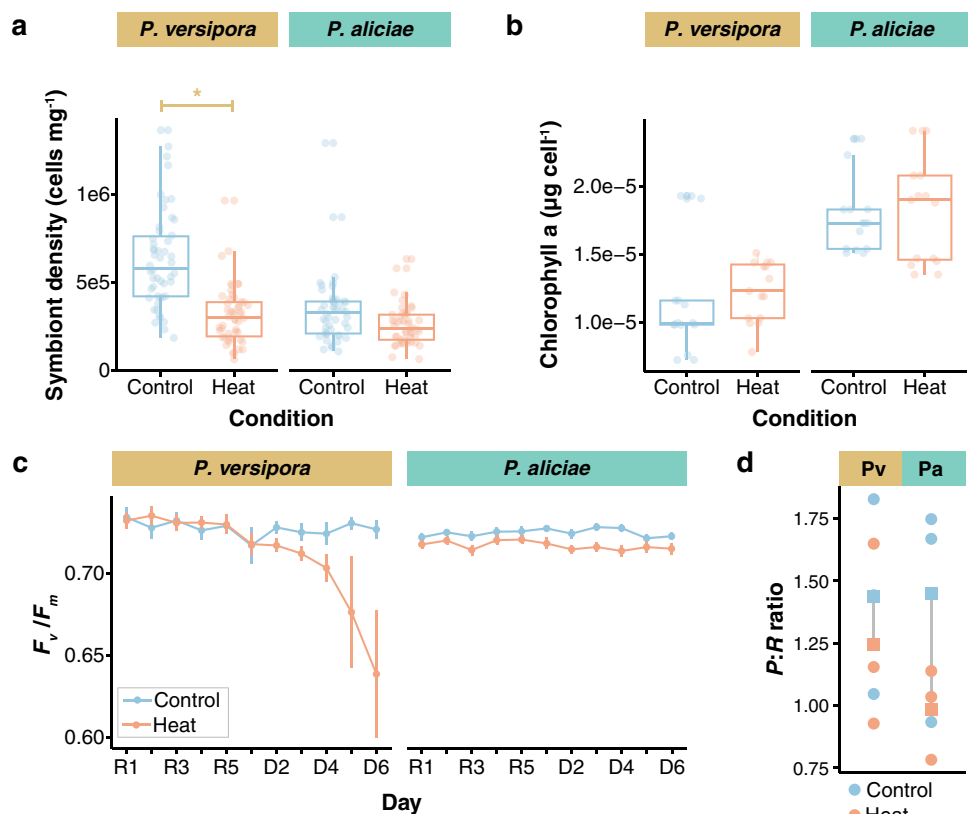
Host metabolite profiles

Non-targeted GC–MS analysis identified 54 metabolites in *P. aliciae* and *P. versipora* host tissues, including carbohydrates, amino acids, fatty acids, lipogenesis intermediates and organic acids (Table S3). PERMANOVA revealed no significance between the treatments when coral species were pooled, or for the species×treatment interaction ($p=0.77$; Table S4). PCA of the metabolite profiles revealed a slight separation between control and heat-treated *P. aliciae* samples along PC1 (42.6%; Fig. 2a). Within-species analysis (via SAM) revealed this was driven by a significant increase in relative abundance (SAM, $p_{adj} < 0.05$) of three metabolites under increased temperatures (Fig. 2b): campesterol (a sterol), stearic acid [C18:0] (a saturated fatty acid) and oleic acid [C18:1] (an unsaturated fatty acid). No metabolites significantly decreased in relative abundance for *P. aliciae* under heat. Meanwhile, no separation was revealed in the PCA between the *P. versipora* metabolite profiles from the two temperature conditions (Fig. 2c). Furthermore, SAM revealed no metabolites significantly differed between control and heat-treated samples of *P. versipora* (SAM, $p_{adj} > 0.05$; Fig. 2d). As such, *P. aliciae* appears to be undergoing a metabolic shift, while *P. versipora* is not.

The metabolite profiles of coral host tissues were significantly different between *P. aliciae* and *P. versipora*

species under both control and heat-treated conditions (PERMANOVA $p=0.0001$; Fig. 3 and Table S4). Under control conditions, PCA (Fig. 3a) revealed separation between the two coral species along PC1 (45.4%). Six metabolites differed significantly between species (SAM, $p_{adj} < 0.05$; Fig. 3b): fucosterol (a sterol) was more abundant in *P. aliciae* tissues, while cholesterol, ornithine, arginine, oleic acid [C18:1] and sucrose were more abundant in *P. versipora* tissues. Similarly, under raised heat PCA revealed a separation between *P. aliciae* and *P. versipora* metabolite profiles along PC1 (61.5%; Fig. 3c), driven by a higher relative abundance of fucosterol, inositol-1-phosphate and citric acid in *P. aliciae* (SAM, $p_{adj} < 0.05$; Fig. 3d). In *P. versipora*, most metabolites abundant under control conditions were no longer significantly different between the two species under heat, except for cholesterol, sucrose, and fructose (SAM, $p_{adj} < 0.01$).

Symbiont metabolite profiles

Symbiodiniaceae composition analysis (Fig. S5) revealed that *Cladocopium* sp. C75h (profile *C75h-C75i-C75g*) was the predominant symbiont in all five *P. aliciae* control samples, whereas the dominating symbiont in all *P. versipora* control samples was *Breviolum* sp. B18 (profile *B18-B18a*). Non-targeted GC–MS analysis identified 37

Fig. 2 Metabolite responses of coral hosts to heat. Top panels show PCA **(a)** and SAM **(b)** plots of the *Pocillopora aliciae* metabolite profiles under control conditions and heat. Bottom panels show the corresponding PCA **(c)** and SAM **(d)** plots for the *Plesiastrea versipora* hosts under both experimental conditions. Significant metabolites identified by SAM in **(d)** are shown according to the legend at the bottom
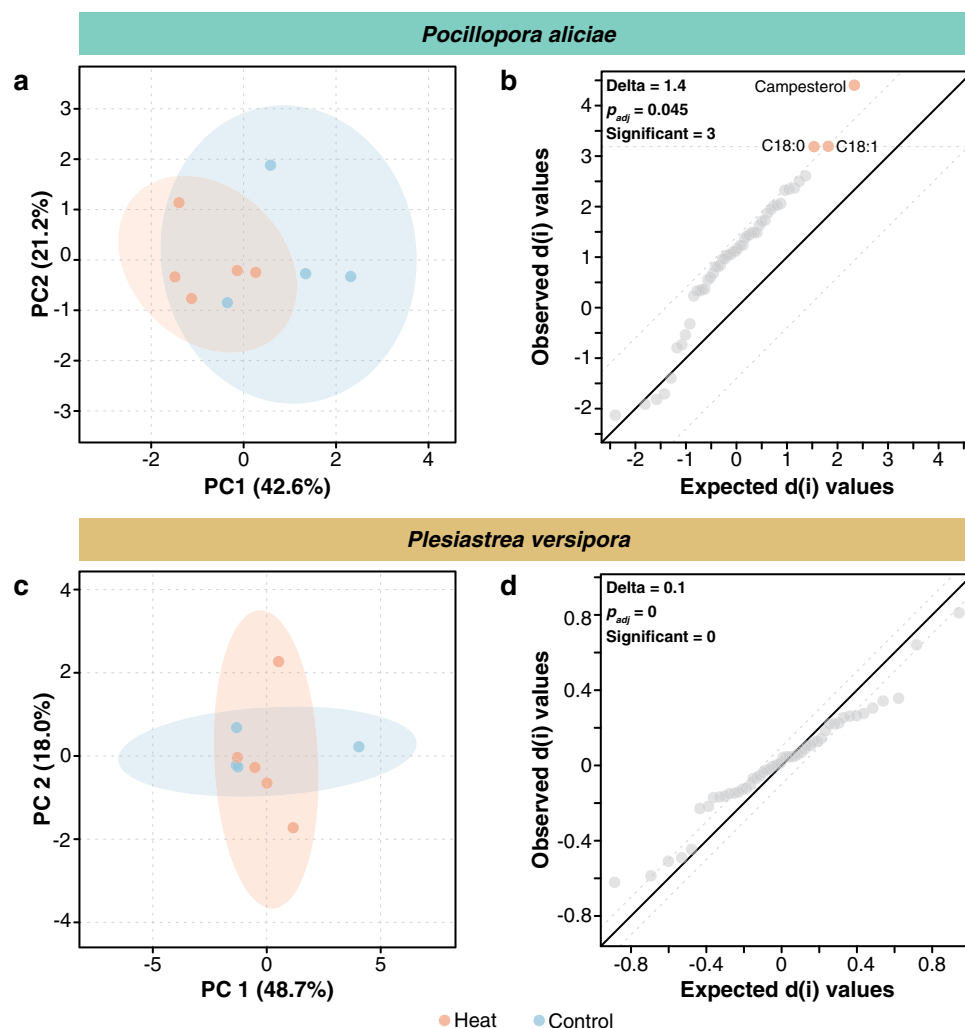

metabolites in *P. aliciae* and *P. versipora* symbionts, including carbohydrates, amino acids, fatty acids, lipogenesis intermediates and organic acids (Table S5). PERMANOVA (Table S4) revealed that symbiont metabolite profiles differed significantly between species ($p = 0.0001$), treatments ($p = 0.034$) and the interaction between species and treatment ($p = 0.007$). PCA of the symbiont metabolite profiles of *P. aliciae* under control and increased temperature exhibits a shift along both PC1 (57.6%) and PC2 (21.2%; Fig. 4a), which is driven by the significant increase of two metabolites (galactosylglycerol and myristic acid [C14:0]) in *P. aliciae* symbionts as response to raised temperatures (SAM, $p_{adj} < 0.01$; Fig. 4b). Meanwhile, no differences were found in the symbiont metabolite profiles of *P. versipora* between temperature treatments (SAM; Fig. 4c and d).

PCA revealed a separation along both axes (PC1 47.2%; PC2 29.1%) between the symbiont metabolite profiles of the two coral species under control conditions (Fig. 5a), which is consistent with the distinct dominant symbionts in each species (*Breviolum* sp. B18 in *P. versipora*

and *Cladocopium* sp. C15h in *P. aliciae*; Fig. S5). Nine metabolites significantly differed in relative abundance between the two coral species under control conditions (SAM, $p_{adj} < 0.05$; Fig. 5b): three sterols (ß-sitosterol, campesterol and fucosterol) were more abundant in *P. aliciae* symbionts, while mannitol, glucuronic acid, pyroglutamic acid, and the carbohydrates mannose, glucose, and arabinose, were more abundant in *P. versipora* symbionts. Substantial separation along PC1 was found between the symbiont metabolite profiles of the two coral species under heat exposure (Fig. 5c), of which 12 metabolites significantly differed ($p_{adj} < 0.05$; Fig. 5d). Campesterol and fucosterol were still more abundant in *P. aliciae* symbionts, along with inositol-1-phosphate, myo-inositol, gentibiose, glycerol, and an unsaturated fatty acid [C18:2]. In *P. versipora* symbionts, mannose and arabinose remained more abundant, while trehalose, eicosanoic acid [C20:0] and malic acid were more abundant under heat, and not in control conditions, compared to *P. aliciae* symbiont metabolite pools.

Fig. 3 Metabolite profile differences between host tissues of the two coral species. Top panels show PCA (**a**) and SAM (**b**) plots of the metabolite profiles from the host tissues of the two coral species under control conditions. Bottom panels show the corresponding PCA (**c**) and SAM (**d**) plots for the coral hosts under the heat treatment. Significant metabolites identified by SAM are shown in colour in (**b**) and (**d**) according to the legend at the bottom
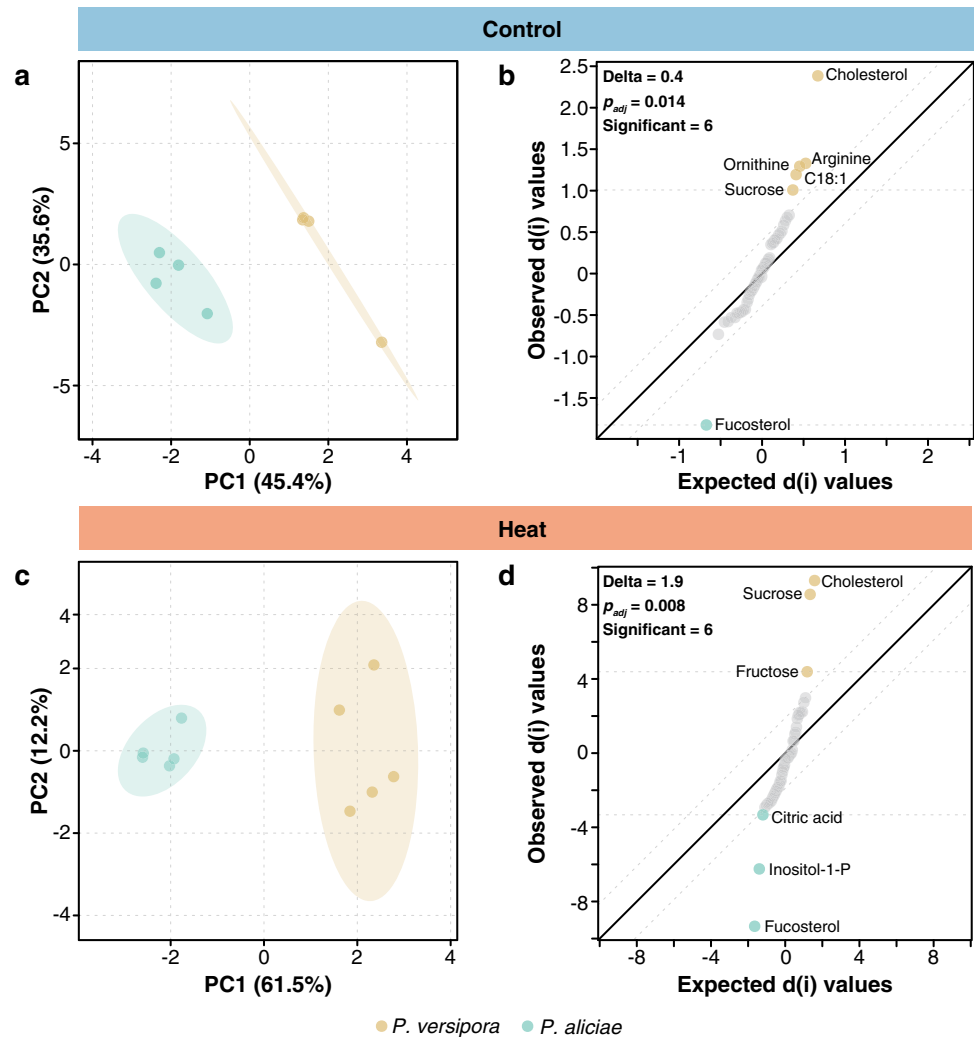
Interspecific competition

Simulated interspecific competition for space between *P. versipora* and *P. aliciae* was recorded at three time points: (i) during the acclimation period (Videos S1 and S2), (ii) immediately prior to the temperature ramp (Videos S3 and S4), and (iii) during the heat exposure experiment (Videos S5 and S6 for control and treatment tanks, respectively). In all instances, *P. versipora* extruded mesenteric filaments that digested tissue of *P. aliciae* in close proximity, causing a wound that exposed its skeleton. However, the tissue of *P. aliciae* exhibited more activity initially, notably polyp movement and extension, in the trials performed during the acclimation period. Overall, the interaction between both coral species followed a regular pattern, without evident differences between control and heat conditions, in which *P. versipora* always outcompeted *P. aliciae* (Fig. S6): soft tissue pulsed inflation and mesenterial filament projection in *P. versipora*, followed by tissue retraction and loss in *P. aliciae*, secretion of mucus that forms a barrier between the two

colonies, and finally retraction of mesenterial filaments by *P. versipora*. Although it is unclear which species secreted the mucus observed in the footage, it is likely a response from the immunocompromised tissues of *P. aliciae* (Bythell and Wild 2011).

Discussion

Unaltered photophysiology of *P. aliciae* under short-term heat exposure

We observed no significant changes in the photophysiology of *P. aliciae* under increased temperatures during this experiment. In contrast, *P. versipora* exhibited a typical bleaching response upon exposure to 26 °C, consisting of declines in both density and photochemical efficiency of algal symbionts, that has been reported previously (Goyen et al. 2019). This suggests that the subtropical endemic *P. aliciae* may be better adapted to acute seawater temperature

Fig. 4 Metabolite responses of symbionts to heat. Panels in the top show PCA **(a)** and SAM **(b)** plots of the *Pocillopora aliciae* symbionts metabolite profiles under control conditions and heat. Panels in the bottom show the corresponding PCA **(c)** and SAM **(d)** plots for the *Plesiastrea versipora* symbionts under both experimental conditions. Significant metabolites identified by SAM in **(d)** are shown in colour according to the legend at the bottom
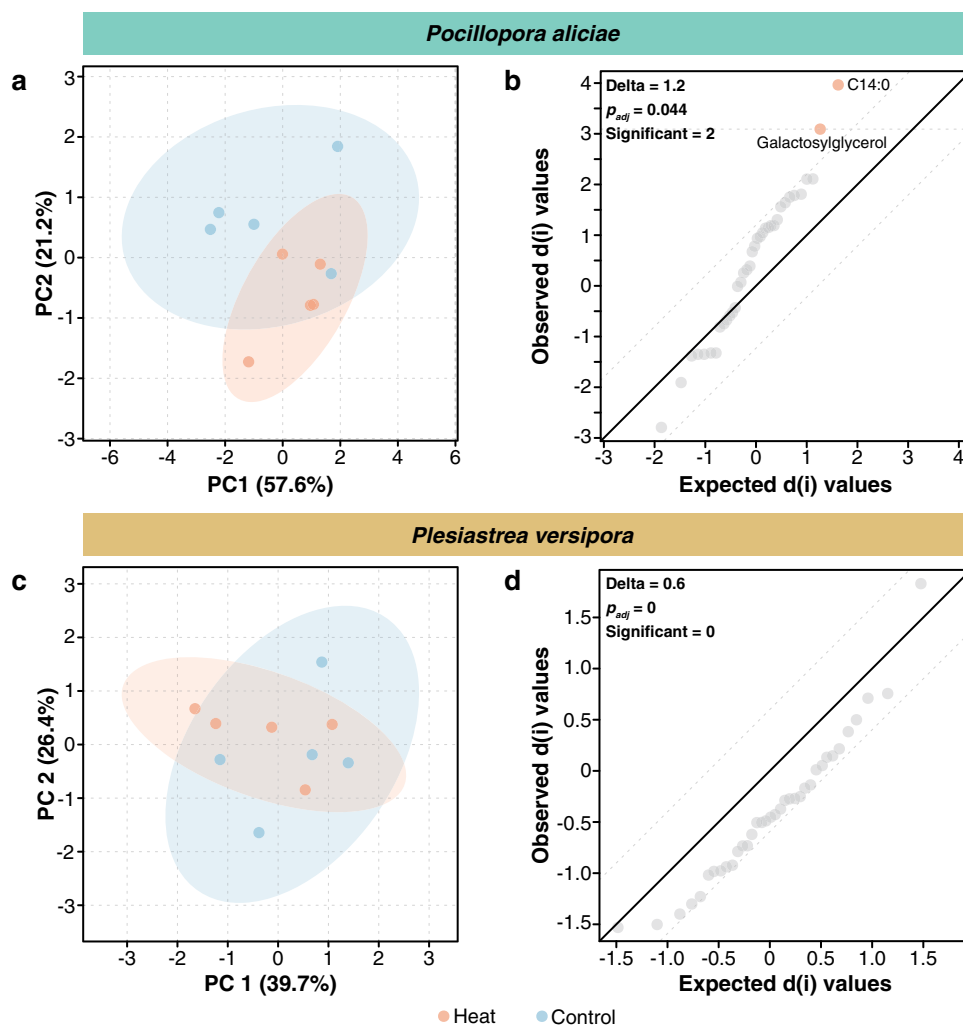

increases than, and therefore holds a competitive advantage over, the native *P. versipora* in coastal New South Wales (NSW), Australia. Such findings contradict the conventional notion that branching corals exhibit greater thermosensitivity compared to encrusting (and massive) corals (Loya et al. 2001). Differential responses in photobiology between coral species are inherently linked to functional diversity between Symbiodiniaceae species (Suggett et al. 2017; Camp et al. 2020; Ros et al. 2021). *P. versipora* exhibits the broadest latitudinal range of any scleractinian coral (Burgess et al. 2009), possibly because it associates with distinct symbiotic partners at different latitudes. Specifically, at lower latitudes (*e.g.* Orpheus Island, Great Barrier Reef), *P. versipora* typically associates with symbionts in an undescribed species of the genus *Cladocopium*, whereas at higher latitudes, *e.g.* NSW, *Breviolum* are usually the dominant endosymbionts (Rodriguez-Lanetty et al. 2001), notably the same type found in this study (*Breviolum* sp. B18) (Goyen et al. 2019). It has been hypothesised that such a pattern is explained by the distinct physiological capabilities of the algal symbionts as

a result of adaptation to different seawater temperatures, supporting the idea that flexible symbioses in corals can lead to extended phenotypes with adaptive potential (Parkinson and Baums 2014; Matthews et al. 2020). While the thermal stability of symbiosis that we report here for *P. aliciae* adult stages suggests a physiological capacity to facilitate further expansion into temperate reefs systems along the south-east Australian coast upon temperature increase, other studies have shown that juvenile stages of this species are susceptible to similar increases in seawater temperature (> 24 °C) at a lower latitude based on growth, survival and recruitment rates (Cant et al. 2021; Lachs et al. 2021). Surface seawater temperature for the south-eastern coast of Australia is predicted to increase up to 3 °C above the maximum monthly mean temperature (increased to ~ 27 °C at Sydney Harbour) between 2080 and 2100 according to the RCP8.5 scenario due to the intensification of the East Australian Current depending on local wind dynamics (Bull et al. 2020). Therefore, follow-up investigations regarding the effects of heat stress on recruitment for both species are essential to

Fig. 5 Metabolite profile differences between symbionts of the two coral species. Top panels show PCA (**a**) and SAM (**b**) plots of the metabolite profiles from symbiont cells of the two coral species under control conditions. Bottom panels show the corresponding PCA (**c**) and SAM (**d**) plots for the symbionts under the heat treatment. Significant metabolites identified by SAM in (**b**) and (**d**) are shown in colour according to the legend at the bottom
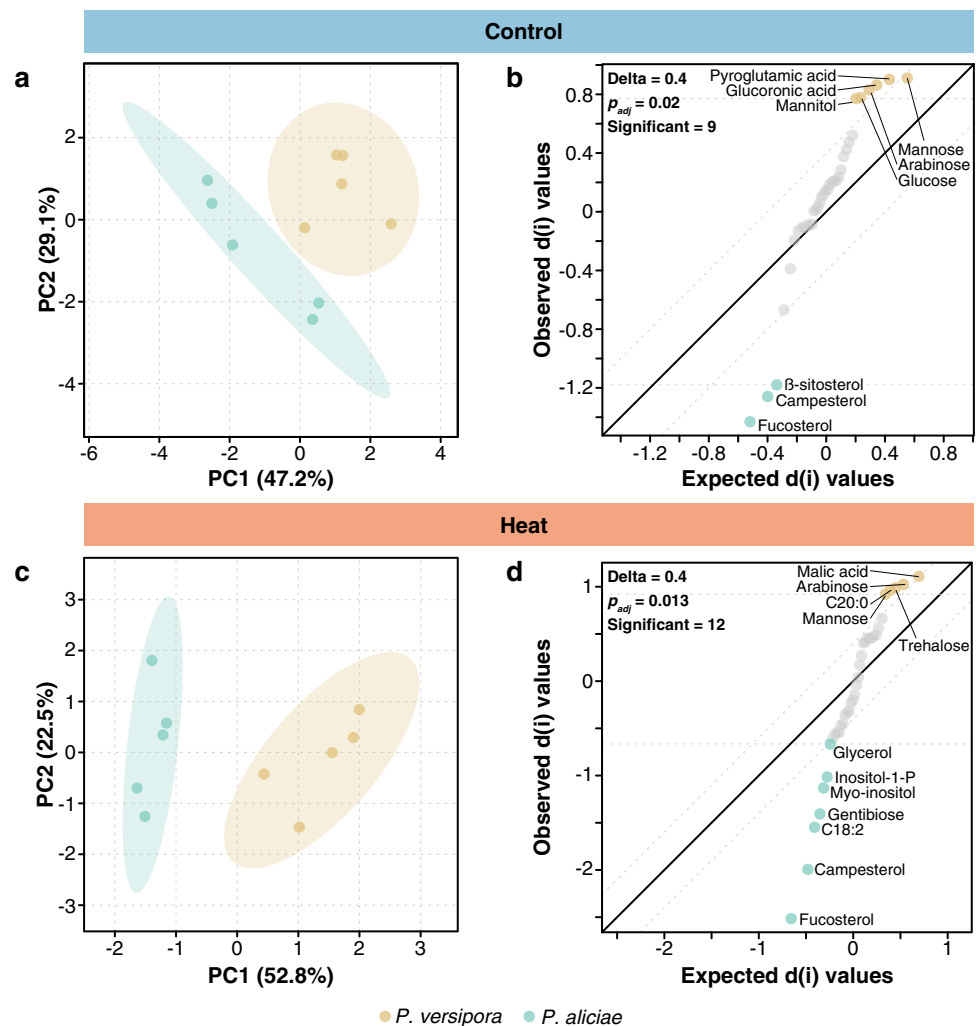
Species-specific metabolic responses to raised temperatures

Within-species response

The metabolic shift in *P. aliciae* in response to heat treatment involved an increase in free campesterol, two saturated fatty acids and a monounsaturated fatty acid in the host (Fig. 2b). Campesterol is produced only by Symbiodiniaceae and then translocated to the coral host (Treignier et al. 2009; Crandall et al. 2016). While knowledge of sterol metabolic pathways in cnidarians is lacking (Carreón-Palau et al. 2020), a heat-stress response in coral species of *Acropora* has been hypothesised to involve plant signalling hormones synthesised from the steroid-derivative campesterol (Hillyer et al. 2017). Therefore, the increased abundance of campesterol in *P. aliciae* host tissues is consistent with a concerted

metabolic response to heat between coral hosts and symbionts (Suggett and Smith 2020; Rädecker et al. 2021; Roach et al. 2021; Ros et al. 2021), which might be related to the higher photosynthetic rate observed under heat (Fig. S4).

Increased saturation of the cell lipid bilayer functions in thermal acclimation, directly and indirectly, by increasing stability and protecting it against damage by reactive oxygen species (Tchernov et al. 2004; Papina et al. 2007). In *P. aliciae,* we observed a significant increase in the abundance of pools of the saturated fatty acid stearic acid (C18:0) in the host tissues (as well as an increased abundance of monounsaturated oleic acid C18:1), and myristic acid (C14:0) in the symbiont cells (Figs. 2b and 4b). While our methods cannot distinguish whether these changes were associated with modifications to cell membranes, or other processes, increasing membrane saturation is energetically costly, and we also observed an increase in abundance of the lipogenesis intermediate galactosylglycerol in the *P. aliciae* symbionts (Fig. 4b). Previous studies propose that the increased abundance of lipid intermediates in response to heat stress and

bleaching of other coral species is likely implicated with the alteration of anabolic and catabolic pathways caused by energetic constraints (Hillyer et al. 2017, 2018). The breakdown of lipid stores as an alternative source of energy appears to be a common mechanism in the heat-stress response of scleractinians when the availability of photosynthetically derived metabolites is diminished, and our results suggest a similar response in *P. aliciae*, as supported by a heat-induced reduction of the respiration rate (Fig. S4). Overall, our results indicate that *P. aliciae* is capable of coping with short-term heat by a metabolic shift that might help maintain energy availability and potentially changes to membrane saturation that support symbiosis stability, which implies an adaptive advantage for the forecasted tropicalisation scenario.

Despite the photophysiological impairment in *P. versipora* under raised temperatures, neither the host nor the symbiont metabolite profiles revealed any metabolic responses to stress or adjustment to compensate for the decreased photosynthetic capacity (Figs. 2d and 4d). The lack of metabolic response in *P. versipora* suggests that either: (1) sampling occurred prior to observable metabolic shifts, (2) the drop in F_v/F_m and symbiont cell density remained within a normal physiological range, or (3) there are limited/no metabolic mechanisms to adjust for short-term thermal stress, *i.e.* host and symbionts lack cellular mechanisms for a quick response to bleaching-inducing conditions (*e.g.* increased antioxidant production, increased mobilisation of stored energy when photosynthesis-derived metabolism is reduced). While the first scenario is plausible, recent evidence suggests that decreased metabolic exchange precedes bleaching (Rädecker et al. 2021), and we were able to detect a reduction in F_v/F_m (~0.05). Support for the second possibility is given by the small reduction in F_v/F_m too, which was also variable across replicates (Fig. 1c). It has been proposed previously that *P. versipora* can adjust its metabolism to temperature changes that range within normal values for its distribution (10–21 °C) (Howe and Marshall 2001, 2002). Indeed, bleaching and metabolic shifts have been reported in *P. versipora* at 26 °C (Goyen et al. 2019), but those observations were done following a natural heat wave in Sydney Harbour that lasted several months, in which exposure to heat was more prolonged than in our experiment. However, the third alternative suggests that *P. versipora* does not possess cellular mechanisms necessary to withstand higher temperatures at this latitude, which is also supported by recent findings (Goyen et al. 2019). More specifically, *P. versipora* symbionts might not be able to enhance photosynthesis to maintain the nutritional exchange with the host (Fig. S4), but this is not conclusive given our low sample size and variability across replicates. Together, these observations affirm the competitive advantage of *P. aliciae* over *P. versipora* during acute heat exposure (*e.g.* when heat waves cause the seawater temperature to exceed the MMM), and may explain

the more recent establishment and growth of *P. aliciae* in Sydney given the recent heatwave-induced mass bleaching of *P. versipora* at this location (Goyen et al. 2019). However, it is important to note that fitness post-bleaching was not assessed for either coral species in this study, and therefore whether this competitive advantage holds true over longer timeframes requires further study–particularly given the documented quick and widespread recovery of *P. versipora* from the aforementioned bleaching event might represent a greater competitive advantage for this species.

Between-species response

Host and symbiont metabolism under control conditions and heat differed between *P. aliciae* and *P. versipora* (Fig. 6). Under control conditions, the *P. aliciae* holobiont exhibited generally more compounds related to sterol metabolism than that of *P. versipora*. While the role of sterols in corals remains unclear (Rosset et al. 2021), sterols and their derivatives function in regulating physiological membrane function, transmembrane signalling and immune responses, and in the cnidarian-dinoflagellate symbiosis. Genomic evidence suggests that the hosts rely on the symbionts for sterol supplies (Baumgarten et al. 2015), and sterol trafficking features in optimal host-symbiont pairings (Matthews et al. 2017). Thus, the relatively more active sterol metabolism in *P. aliciae* under control conditions may reflect interpartner signalling and homeostasis in this holobiont. Meanwhile, *P. versipora* showed more free simple sugars and intermediates of antioxidants and of the urea cycle (Figs. 4d and 6d). This might be explained by the symbiont species composition in *P. versipora* in this condition (Table 1) as nitrogen cycling within the coral-dinoflagellate symbiosis involves ammonium produced via the urea cycle (Wang and Douglas 1998; Grover et al. 2006). In turn, the increased activity of the urea cycle may enhance symbiont replication (Matthews et al. 2018). In addition, potential impacts of the host nutritional state and seasonal availability of inorganic nitrogen on nitrogen metabolism of *P. versipora* symbionts (Davy et al. 2006), which affect photosynthetic performance, need to be considered. The increased abundance of free carbohydrates could indicate an active turnover of energy derived from the tricarboxylic acid (TCA) cycle. The higher photosynthetic activity *per* host cell in *P. versipora* (Fig. 1) may also explain the higher levels of free carbohydrates and antioxidants in the host tissues of this coral.

Under heat (Fig. 6b), the higher abundance of the C20:0 fatty acid in *P. versipora* symbionts *versus P. aliciae* symbionts might be related to the activation of eicosanoids; these intercellular signalling compounds have been previously implicated in the stress response of cnidarians, also mediated by lipid signalling (Lõhelaid et al. 2015; Matthews et al. 2017). Inositol signalling has been identified as a signalling
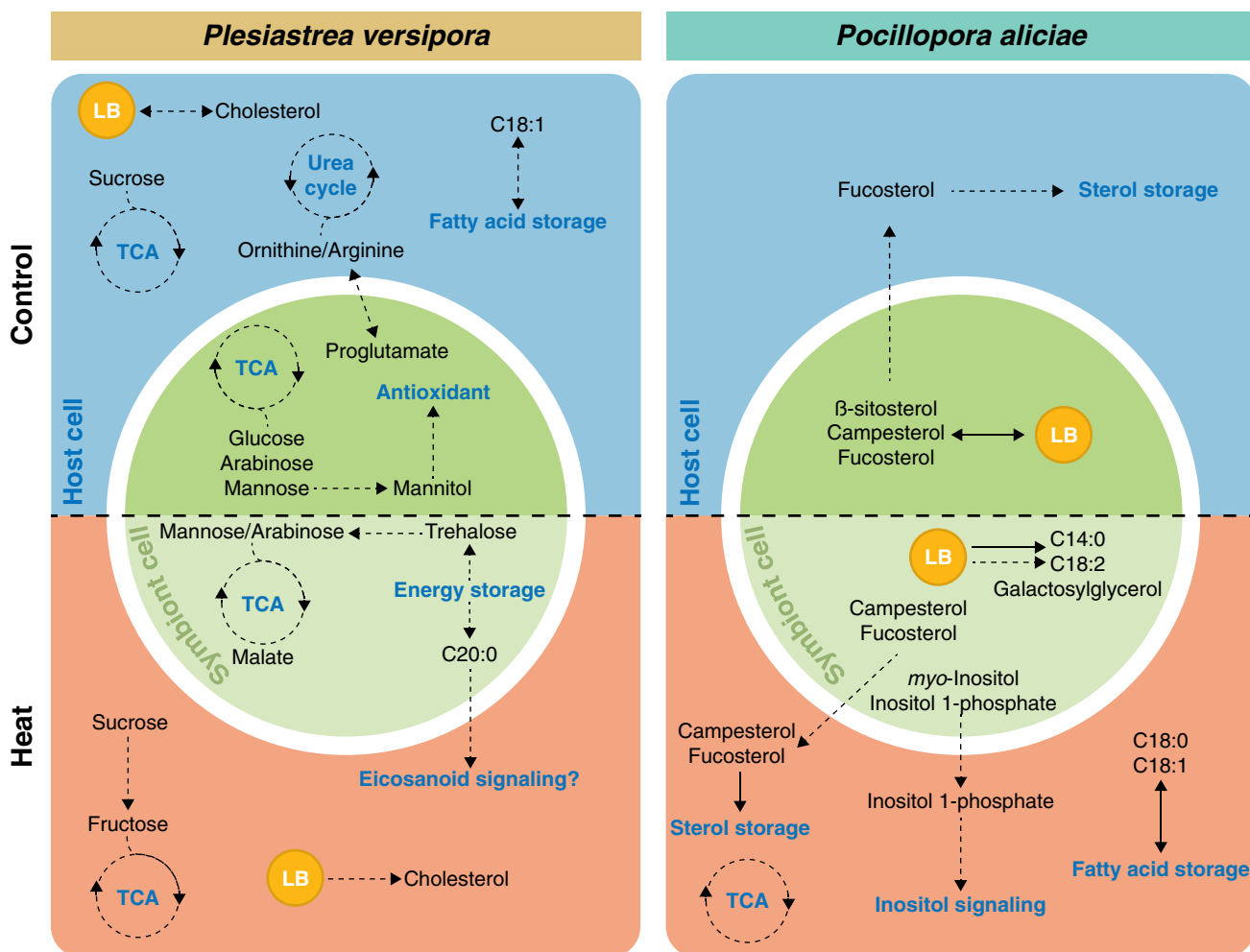
Fig. 6 Diagrammatic representation of the metabolic differences between *Plesiastrea versipora* and *Pocillopora aliciae* based on our analyses of response to heat within each species (continuous arrows) and on the interspecific differences observed in control and heat conditions (dashed arrows). TCA: tricarboxylic acid cycle, LB: lipid biosynthesis pathway

Table 1 Summary of the photophysiology measurements for *Plesiastrea versipora* and *Pocillopora aliciae* in response to increased temperature

Photophysiology indicator	*Plesiastrea versipora*		*Pocillopora aliciae*		Interspecific differences		Response to heat exposure	
	Control	Heat	Control	Heat	Control	Heat	Pv	Pa
Chl a	$1.16^{-5} \pm 2.03^{-6}$	$1.23^{-5} \pm 9.44^{-7}$	$1.79^{-5} \pm 1.40^{-6}$	$1.84^{-5} \pm 1.90^{-6}$	na	na	–	–
Symbiont density	$6.31^5 \pm 8.34^4$	$3.17^5 \pm 5.02^4$	$3.41^5 \pm 5.40^4$	$2.58^5 \pm 2.94^4$	na	na	↓	–
F_v/F_m	0.72 ± 0.001	0.72 ± 0.003	0.73 ± 0.004	0.62 ± 0.028	–	Pa	↓	–
P:R	1.44 ± 0.23	1.24 ± 0.21	1.45 ± 0.26	0.99 ± 0.11	–	–	–	–

Values are means ± standard error. Significant interspecific differences are shown for the two experimental conditions ('Control' and 'Heat'); the species with a higher value for the corresponding indicator and condition is mentioned either as 'Pv' (*Plesiastrea versipora*) or as 'Pa' (*Pocillopora aliciae*). Response to heat exposure is also shown for each species. A decrease in the indicator value under heat exposure is shown as an arrow pointing down (↓). Insignificant differences are represented by '–'. 'na' is given where analyses are not relevant

pathway commonly associated with stress response in corals, including bleaching (Hillyer et al. 2017, 2018), and is thought to be involved in the maintenance of a functional coral-dinoflagellate symbiosis (Matthews et al. 2017, 2018). Accordingly, this signalling pathway appears to be important for *P. aliciae* to maintain symbiosis and cell homeostasis under raised temperatures, as supported by the excess of several intermediates of this pathway in both host (Fig. 4d) and symbiont (Fig. 6d). Abundance of free sterols and C18:2 in *P. aliciae* symbionts under heat suggests either breakdown or enhanced division of these cells, but the lack of significant changes in *P. aliciae* symbiont density between the two experimental conditions (Fig. 2b) makes it impossible to ascertain which process dominated.

The higher abundance of free sugars in algal symbionts after heat exposure, such as that observed in *P. versipora* symbionts, has been linked to the production and mobilisation of photosynthates in synchrony with enhanced respiratory reactions for the generation of energy in the thermally stressed host (Hillyer et al. 2017). However, this notion disagrees with the reduction of respiration rate in *P. versipora* after exposure to heat (Fig. S4).

Potential implications of *P. versipora* and *P. aliciae* competition on future reef structure

Although outcomes of competition between coral species vary in time and space (Einat and Nanette 2006), our competition experiments suggest that *P. versipora* is capable of outcompeting *P. aliciae* in the race for space when in close contact, even under acute heat exposure. Our results suggest that the aggressive behaviour of *P. versipora* can prevent the establishment of *P. aliciae* in close proximity (although no direct competition has yet been observed in coastal NSW); however, increasing temperatures could change these dynamics as *P. versipora* colonies are lost. The faster growth rates of branching corals like *P. aliciae* (Pinzón et al. 2014; Pratchett et al. 2015) could lead to shading effects that would limit sunlight access to slower-growing encrusting *P. versipora* colonies, contributing further to its decimation primarily driven by increasing seawater temperature.

Although *P. aliciae* and *P. versipora* co-occur in coastal habitats in New South Wales (Sommer et al. 2014), there is currently no noticeable competition between the two species (Sommer's personal observation). In addition to competitive ability in close contact, the different life history traits and environmental tolerances of *P. aliciae* and *P. versipora* likely influence their distribution and abundance patterns in these marginal habitats (Sommer et al. 2017). For instance, brooding reproduction (Schmidt-Roach et al. 2013), rapid settlement and high self-recruitment of brooding species (Figueiredo et al. 2013), and fast growth rates (Harriott 1999) once established, make *P. aliciae* a good coloniser of new habitats

and it is likely that *P. aliciae* will establish in areas currently occupied by *P. versipora*. Altogether, our study suggests that future conditions may contribute to the further proliferation of *P. aliciae* over *P. versipora*. This could lead to a change in the architecture of coastal ecosystems in Sydney, shifting from predominantly encrusting corals to branching species.

Coastal NSW reef ecosystem as a refuge for tropical reef species from climate change

Previous studies suggest that high-latitude marine environments of East Australia have limited potential as refugia for the biodiversity of the Great Barrier Reef from climate change because of natural instability, anthropogenic perturbances and massive bleaching events of native coral communities (Lybolt et al. 2011; Goyen et al. 2019; Kim et al. 2019). However, such studies are generally limited to corals at subtropical latitudes and do not consider the tropicalisation of temperate marine ecosystems and the poleward range expansion of corals to temperate latitudes in East Australia (> 30° S). Our data suggest that the subtropical *P. aliciae* colonising the Sydney seaboard (34° S) can cope better under increased temperature at this location, and hence also under the raising temperatures during the process of tropicalisation, than the native species *P. versipora*. Although the settlement of *P. aliciae* in NSW coastal waters currently depends largely on larval recruitment from lower-latitude populations (Cant et al. 2021), which are under severe threat due to heat stress (Kim et al. 2019; Lachs et al. 2021), this might change as this brooder population becomes more established. Therefore, it is essential to determine whether the temperate *P. aliciae* population will be able to subsist from local recruitment only to confidently assess the possibility of *P. aliciae* further proliferating and, perhaps, even displacing native coral species, like *P. versipora*, as this reef ecosystem undergoes tropicalisation. A drastic increase in architectural complexity in the coastal NSW reef ecosystem would likely facilitate colonisation and establishment of other tropical and subtropical reef species, as it already provides habitat for coral reef fish (Booth and Sear 2018; Booth et al. 2018; Figueira and Booth 2010). Still, a stricter multipronged assessment (Kavousi and Keppel 2017) remains to be done to ascertain whether coastal waters of NSW have the potential to act as a refuge for subtropical and tropical reef species from climate change.

The ecological services and economic revenue of the Sydney marine environment makes it a very valuable ecosystem (Banks et al. 2016). In addition to the global threat to coral reefs posed by climate change, urbanisation in coastal NSW represents a major continuous threat through, for example, increased stormwater drainage inflow (Varkey et al. 2018) and habitat modification (Mayer-Pinto et al. 2015). Although

management strategies are already in place, we hope that the recognition of coastal NSW as a potential biodiversity refuge has a greater impact on its protection.

Declarations

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