

Heat tolerance varies considerably across reef-building corals of the Great Barrier Reef

Corresponding Author: Ms Melissa Naugle

Attachments originally included by the reviewers as part of their assessment appear at the end of this file.

Version 0:

Decision Letter:

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Dear Ms Naugle,

Your manuscript titled "Environmental, host, and symbiont drivers of heat tolerance in a species complex of reef-building corals" has now been seen by 3 reviewers, and we include their comments at the end of this message. They find your work of interest, but some important points are raised. We are interested in the possibility of publishing your study in Communications Earth & Environment, but would like to consider your responses to these concerns and assess a revised manuscript before we make a final decision on publication.

We therefore invite you to revise and resubmit your manuscript, along with a point-by-point response that takes into account the points raised. In particular, we ask that you consider the point raised by Reviewer #3 regarding the potential role of symbiotic bacteria in the context of coral tolerance to environmental stressors. Please highlight all changes in the manuscript text file.

We are committed to providing a fair and constructive peer-review process. Please don't hesitate to contact us if you wish to discuss the revision in more detail.

Please use the following link to submit your revised manuscript, point-by-point response to the referees' comments (which should be in a separate document to any cover letter), a tracked-changes version of the manuscript (as a PDF file) and the completed checklist:

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We hope to receive your revised paper within six weeks; please let us know if you aren't able to submit it within this time so that we can discuss how best to proceed. If we don't hear from you, and the revision process takes significantly longer, we may close your file. In this event, we will still be happy to reconsider your paper at a later date, as long as nothing similar has been accepted for publication at Communications Earth & Environment or published elsewhere in the meantime.

Please do not hesitate to contact us if you have any questions or would like to discuss these revisions further. We look forward to seeing the revised manuscript and thank you for the opportunity to review your work.

Best regards,

Clare Davis, PhD
Senior Editor
Communications Earth & Environment

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REVIEWER COMMENTS:

Reviewer #1 (Remarks to the Author):

Summary: This paper examines the thermal thresholds of almost 600 *A. hyacinthus* coral colonies across the Great Barrier Reef. The authors quantify the contribution of a suite of drivers to thermal tolerance and retained performance metrics, finding significant evidence for local adaptation and substantial genetic variation across the reef system.

Major comments: This is a timely study and an important contribution towards elucidating coral adaptive capacity. The sampling effort is impressive in scope and I appreciate that the authors took the time to use more than one metric to quantify their focal process, namely the measurement of photochemical efficiency and NDVI to quantify heat tolerance. That the authors genetically identified symbiont community structure is a testament to the completeness of this work. Overall, the

scale- and metric-dependent findings of this paper with regards to heat tolerance variation is highly interesting and provides a baseline to design future studies in the field of coral reef adaptation.

The paper is very well written and polished. The presentation of results and contextualization of the findings is excellent. In my opinion, the paper is ready to be published as is.

I do have a suggested citation for the section where the authors discuss variation in Symbiodiniaceae communities (L387):

<https://royalsocietypublishing.org/doi/full/10.1098/rsos.212042>

Reviewer #2 (Remarks to the Author):

Naugle et al. present an incredible effort to characterize potential drivers of thermal tolerance in well-studied coral reef species complex. This is indeed one of a few direct assessments that exist in the coral bleaching and tolerance literature, exhibiting scientifically sound and strong experimental design, analyses, and conclusions and contributing a novel holistic understanding of bleaching variation along a large geographic gradient. The analyses are valid, detailed, and garner relative support through comparative modeling. There are minor issues, concerns, and/or questions regarding the methods and conclusions drawn that can be addressed via a minor revision of the current manuscript. Attached is a point-by-point comment for the authors to consider and address.

Reviewer #3 (Remarks to the Author):

Against the backdrop of global warming and intensified human activities, studying the heat tolerance characteristics and mechanisms of corals has become a hot topic in the field of coral reefs. However, the factors influencing the heat tolerance of corals are undoubtedly diverse. This article evaluates the heat tolerance characteristics of a coral species (*A. hyacinthus*) in the Great Barrier Reef based on environmental factors, symbiotic Symbiodiniaceae community, and host genome. The most valuable aspect of this article is the large and extensive sampling in the experiments, making it one of the largest studies to date on intra-species heat tolerance differences. Nevertheless, the article also has some shortcomings. The four heat tolerance indicators measured in the study (photosynthetic efficiency, chlorophyll content, etc.) seem somewhat forced, as there is actually not much research directly using these indicators to determine coral heat tolerance. If there were, providing relevant citations might have been more substantiated. Additionally, coral symbiotic bacteria should be the most abundant and active component in coral holobionts, a critical factor influencing coral host environmental tolerance, yet the article does not analyze this aspect. Furthermore, although the authors conducted coral genome sequencing, it appears that the genomic differences among samples were not carefully analyzed, and there was no thorough correlation analysis with factors such as coral heat tolerance, environmental differences, etc. Overall, the results obtained from the analysis in the article mostly align with past research findings and do not provide any innovative results. Therefore, I believe that the publication of this article should be reconsidered.

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Author Rebuttal letter:

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to thermal tolerance and retained performance metrics, finding significant evidence for local adaptation and substantial genetic variation across the reef system.

Major comments: This is a timely study and an important contribution towards elucidating coral adaptive capacity. The sampling effort is impressive in scope and I appreciate that the authors took the time to use more than one metric to quantify their focal process, namely the measurement of photochemical efficiency and NDVI to quantify heat tolerance. That the authors genetically identified symbiont community structure is a testament to the completeness of this work. Overall, the scale- and metric-dependent findings of this paper with regards to heat tolerance variation is highly interesting and provides a baseline to design future studies in the field of coral reef adaptation.

The paper is very well written and polished. The presentation of results and contextualization of the findings is excellent. In my opinion, the paper is ready to be published as is.

I do have a suggested citation for the section where the authors discuss variation in Symbiodiniaceae communities (L387):

<https://royalsocietypublishing.org/doi/full/10.1098/rsos.212042>

Thank you for these comments. We appreciate your suggested citation and have added it to support the statement on lines 386-388: "Inshore environments may exert unique selective pressure on Symbiodiniaceae communities due to higher temperatures, greater temperature or water variability, and/or increased turbidity (Cooper et al., 2011; de Souza et al., 2022; Matias et al., 2022; Tonk et al., 2013)"

Reviewer #2 (Remarks to the Author):

Naugle et al. present an incredible effort to characterize potential drivers of thermal tolerance in well-studied coral reef species complex. This is indeed one of a few direct assessments that exist in the coral bleaching and tolerance literature, exhibiting scientifically sound and strong experimental design, analyses, and conclusions and contributing a novel holistic understanding of bleaching variation along a large geographic gradient. The analyses are valid, detailed, and garner relative support through comparative modeling. There are minor issues, concerns, and/or questions regarding the methods and conclusions drawn that can be addressed via a minor revision of the current manuscript. Attached is a point-by-point comment for the authors to consider and address.

Thank you for your feedback and point-by-point comments. These have each been addressed below.

Introduction

Line 39-40. This statement should be supported by a reference if applicable.

We agree and have added a reference to line 40 to support this statement:

Riginos, C. et al. Cryptic species and hybridisation in corals: challenges and opportunities for conservation and restoration. *EcoEvoRxiv*. (2024).

Results

Table 1. Out of curiosity, why would ED50's have a greater variance than retained? Is predicted tolerance during heat stress more variable or uncertain (based on SE of calculation) than measured bleaching outcomes which are finite values?

We expect that ED50s have a greater variance for the reason you describe. Since ED50s are generated by a log-logistic model of the predicted temperature at which a 50% decline in the trait value occurs, there is some intrinsic error built into this value. In contrast, the retained value compares the measured difference between a trait at a control temperature (i.e., MMM) and high temperature stress (i.e. +9°C), without the need for a model-generated value. Further, the retained values are calculated per fragment (e.g., the difference between heat and control for each of the three replicates) and then averaged among those 3 values, while the ED50s are modeled using all three replicates for each temperature treatment, thereby not as explicitly accounting for differences among replicates.

Line 272-274. Similar to the question in Table 1, the results of greater ED variation within site and greater retained variation among sites are compelling to consider. Since most predictors were at site levels, yet ED metrics were more variable, are the authors confident in the ED results and conclusions drawn from them?

For both ED50 and retained metrics of NDVI, there was greater within-site variation compared to among-site variation. Conversely, for both ED50 and retained metrics of Fv/Fm, there was greater among-site variation than within-site variation. Since most predictors were at the site level, this has the effect of predictors not explaining variation in NDVI as well as Fv/Fm (seen as deviance explained in Fig 6). Yet, a moderate amount of NDVI variation is still explained by predictors, and NDVI follows latitudinal trends similarly to Fv/Fm, albeit not as strongly. We have confidence in the ED50 values which were generated from a fully replicated design (Figure 1B) and the greater variation in NDVI metrics at the colony level (i.e., within-site) raised in this comment is likely due to the later measurement of this trait after the accumulation of more thermal damage (i.e., 17 versus 10 hours after the start of the experiment) or a more variable holobiont response in NDVI versus symbiont response in Fv/Fm (lines 359-363).

Discussion

Lines 296-298 and 368-369. Fifer et al. 2021 () demonstrated that flow was an important influence on bleaching outcomes for *Acropora pulchra*. Do the authors have access to current data as a possible predictor? Additionally, microbial communities could also contribute to the unexplained variance but this is not discussed herein.

<https://doi.org/10.1111/mec.15869>

We agree that flow and microbial communities may affect heat tolerance or bleaching outcomes. We had access to eReefs flow data but chose not to include it due to the large spatial resolution (1km) where flow dynamics affecting the physiology of individuals or populations would occur on much smaller spatial scales. Further, *Acropora hyacinthus* typically occupies shallow, exposed, reef crest or flank habitats with high water flow. Still, it is possible that differences in water flow would affect heat tolerance among individuals. We have added the bolded portion to the statement on lines 372-374: “Although we accounted for thermal and nutrient variables along depth stratifications, there may be additional unmeasured microhabitat features such as water flow⁴⁷ that could affect within-reef heat tolerance.” We have also added a sentence to lines 406-407 to address the potential role of microbial communities: “Further, symbiotic bacteria are another component of the coral holobiont that may influence heat tolerance⁵³, but were not explored in this study”.

Lines 305-306. Does the “over 0.4°C” represent the mean difference in ED50 between N and S? See Somero 2010 for support of living near upper tolerance limits.

The 0.4°C represented a cutoff below the mean of the differences between ED50s and MMM at northern/inshore reefs vs. southern reefs. We have clarified this to instead state these mean differences between northern/inshore reefs vs. southern reefs for both Fv/Fm and ED50. This now reads with the bolded text and recommended citation: “*A. hyacinthus* on northern and inshore reefs had higher thermal thresholds (Fv/Fm and NDVI ED50s; Fig. 2A-B) but were living on average 0.6-0.8°C closer to those thresholds than those on southern reefs. These populations living near their upper thermal limits may have higher absolute thermal thresholds but less capacity to adapt to future warming⁴¹” (lines 305-309).

Line 307. Perhaps add “and by a higher tolerance in retained traits” after “summer maximum temperatures”. That result provides strong evidence of withstanding and/or recovering from bleaching.

Good suggestion; we agree on strengthening this statement. The sentence has been amended to: “While southern populations in this study exhibited lower absolute thermal thresholds, their greater distance from summer maximum temperatures and higher tolerance in retained traits indicates that they may be better positioned to persist through future warming, perhaps enhanced by gene flow of heat-adapted alleles from northern populations” (lines 309-313).

Line 316-317. After reviewing NOAA CRW's 5km products from 2021-2022, it appears as though most Northern sites were sampled during warm periods where DHW was closer to 4, and most Central and Southern sites (except Heron) were sampled during little to no DHW. First, the methods don't mention sampling colonies that were visually healthy or unbleached, if there was any colony-level paling, could or were the response metrics adjusted to reflect baseline stress? Second, could the southern populations be “better positioned to persist through future warming” as an effect of sampling these corals under no thermal stress versus the northern population experiencing localized thermal stress? Especially for the result on Lines 114-115, where Southern corals may have had more pigment/photochemical ability to begin with. Lines 357-359. See Nielsen et al. 2022 for a thorough investigation into the differences among traits measured across acute heat stress. Were the authors able to do hyperspectral imaging at the same time as PAM measurements? It would have been an interesting comparison or validation of metric-associated variance.

You raise some important points. We agree that baseline stress measured as DHW or visual paling during sampling may affect experimental heat stress responses, and explicitly tested this (Table S2; Fig. 6). You are correct in that northern GBR reefs were sampled under higher DHW (0.5-4 DHW), than southern GBR reefs (0-0.47 DHW) and this variation in DHW was found to be an important driver of heat tolerance (Fig. 6). Interestingly, when colonies were exposed to greater DHW at the time of sampling, they exhibited higher heat tolerance (i.e., greater Fv/Fm ED50 and greater retained NDVI; Fig 6). Thus, northern populations would have benefitted from this effect compared to southern populations. Consequently, there is no evidence to suggest that the effect of southern populations being better positioned through future warming is a trend strengthened by baseline stress during sampling.

We agree that timing of phenotypic measurements is an important consideration. Timing of measurements in this study was chosen due to logistics (i.e., Fv/Fm was measured at night to maintain dark adaptation in outdoor aquaria) and temporal effects on each trait from Nielsen et al., 2022 (i.e., NDVI declines were more apparent the following morning compared to Fv/Fm; see Fig. 2 in Nielsen et al. 2022). This is an important point that could be more explicitly stated. We have added the bolded text and the Nielsen et al 2022 citation to the following: “Here, thermal threshold variation in color paling (NDVI) was over 2.5 times more variable within sites compared to photochemistry (Fv/Fm). This may reflect the later measurement of this trait after the accumulation of more thermal damage (i.e., 17 versus 10 hours after the start of the experiment), or a more variable holobiont response in NDVI versus symbiont response in Fv/Fm. A later measurement of Fv/Fm may have produced more variable results as time-series Fv/Fm was shown to remain fairly consistent after an acute heat stress assay until 48 hours after the end of heat stress in *A. tenuis*48” (lines 363-366).

A “more variable holobiont response in NDVI versus symbiont response in Fv/Fm” should be elaborated upon, especially since host characteristics likely influence how light reaches symbiont cell’s light-harvesting complex (LHC). Since NDVI is captured after heat stress, perhaps it is a measure of the remaining symbiont species/community as opposed to the symbiont community’s photochemical response during acute stress, under the hypothesis that the in hospite community changes throughout bleaching and the measurements are capturing two different communities, which likely have differing photophysiology (chloroplast number, size, LHC size, etc.). I’m baffled yet enthralled by these results!

These are interesting points. We agree that heat stress can alter symbiont communities to accommodate more tolerant taxa either due to shuffling of existing genotypes or acquisition of novel genotypes from the environment. However, we do not expect substantial rearrangements to the Symbiodiniaceae community composition in our assays given that the majority of individual colonies hosted only a single type profile of *Cladocopium* (Fig. S5; lines 224-225), providing a lack of variation for symbiont shuffling (note that the ASVs in Fig. 5 predominantly reflect intragenomic variation; lines 217-219). Additionally, the 17-hour duration of our assays would be insufficient for the uptake and proliferation of novel genotypes from seawater (Van Oppen et al., 2011). Rather, we attribute the variable NDVI response to either the later timing of the measurement after the accumulation of thermal damage (17 vs 10 hours) or to the incorporation of both coral host and symbiont properties to NDVI where Fv/Fm is more purely a symbiont-related trait (lines 358-362).

Lines 368-369 and 631-634. Considering the sampling area within sites (<5km) and the resources used for temperature metrics, NOAA-CRW at 5km and eReefs at 1km scales, it seems likely that there might not be enough spatial resolution to determine within reef variation and this point should be discussed. Moreover, are any of the sites within 5km of one another, and why couldn’t eReefs be used for all temperature metrics?

This is an important point and one that we spent extensive time considering. No sites were within 5 km of one another (the closest two reefs were > 10 km apart), so NOAA-CRW resolution would provide distinct values at different reefs. NOAA-CRW was a preferred resource primarily due to its temporal range (1985-present) compared to eReefs (2014-present). This is why temperature metrics of finer-scale variability were computed from eReefs and measurements requiring some historical baseline (e.g., DHW-related metrics) were computed from NOAA-CRW. This justification is stated in the legend of Table S2 “Temperature variables of climatology, anomalies, and recent heat stress were calculated using CoralWatch data since they rely on DHW which corresponds to the historical MMM which is calculated using the CoralWatch dataset. Temperature metrics of variability were calculated using eReefs, which provides higher resolution recent temperature data.” To more explicitly state this in the main text, the bolded portion was added to the Methods: “Variables of climatology and thermal anomalies requiring a historical baseline were computed using CoralWatch which ranges from 1985 and has a 5 km resolution, while variables of warming rate and temperature variability requiring finer-scale resolution were computed using eReefs which ranges from 2014 and has a 1 km resolution (Table S2)” (lines 638-642).

Methods

Line 469. Since actual temperatures were not mentioned, +9°C MMM seems to be 37.7°C correct? (At least for NOAA-CRW 5km Northern GBR MMM of 28.7°C) That is quite high as acute tests go for Acroporids and I'm surprised retention could be calculated from this treatment. Did the resulting sample size decrease at all for these metrics?

Temperatures were listed as MMM +9°C because they varied due to the site MMM. These values are indeed quite high (e.g., close to 38°C on some Northern reefs) and were chosen to elicit a strong enough decline in measured phenotype to produce an ED50 curve (see Fig. 1D). Notably, the sample size did not decrease substantially in this treatment; there were only 4 cases where Fv/Fm yielded a 0, and no cases where NDVI yielded a 0. We also explored retained traits using the +6°C treatment, but this distribution was non-normal with some colonies generating values close to 1 (indicating no decline in performance, particularly for Fv/Fm).

Additionally, and perhaps this is why +9°C MMM didn't yield total necrosis, taking climatological MMM values as the baseline temperature might not be appropriate. How does the MMM compare with current summertime average temperatures? The world is much warmer than it was in the 1980 and 90's and using the full climatology may not be representative of current in situ temperatures.

We used a climatological baseline to provide a standardized reference across our sites and to enable comparison with independent studies (Evensen et al., 2023, 2021; Voolstra et al., 2020). Using MMM values was preferential over current summertime temperatures which are subject to bias due to inter-annual variation (i.e., over- and under-estimated baselines in warmer and cooler years, respectively). However, average summertime temperatures at all of our sites were within -0.9-1.2°C of the MMM in the year that the assays were performed. The MMM +9° treatment in our assays was designed to elicit a strong response (as discussed above). The majority of fragments at most reefs lost more than 75% of their pigmentation at 17 hours (i.e., NDVI; Fig. 2D), and our qualitative observations are that this continued to decline beyond this time-point (similar to Nielsen et al. 2022). This strong response included both bleaching and necrosis. As these responses are not distinguished by our trait measurements, we have added clarification in the Methods on lines 538-540: "This demonstrates that the NDVI trait captures the decline in chlorophyll that occurs with colour paling during the bleaching stress response, due to a loss of endosymbiont cells, their pigments, and/or tissue necrosis".

Figures

Figures 2, 5, and . I would appreciate a bold line or some demarcation to separate northern from southern sites (and maybe central as well) for visual reference for those who have not worked in GBR.

We agree and have now added a dashed line to Figures 2 and 5 with the amended caption for Figure 2 on lines 156-157: "The dashed line indicates the latitudinal divide between north-central sites (above dashed line) and southern sites (below dashed line)" and for Figure 5 on lines 254-255: "The dashed line indicates the latitudinal divide between north-central sites (left) and southern sites (right)"

Line 253. Were the authors intending to only describe inshore as yellow, it reads incomplete as the blue and green color representation was not included.

Thank you for pointing this out. We have revised the sentence on lines 253-254 to now state: "Shelf position (bottom row) is shown to visualize ITS2 sequence differences at inshore sites (yellow) versus mid-shelf (green) and offshore sites (blue)."

Supplemental

Linear Model Results. Although there is parsimony between the BRTs and linear models, the retention of genomic cluster, health chart, and light is interesting yet not discussed much in the text. Are these putative predictors not discussed because of their low R²? What do the authors make of these discrepancies?

Yes, these predictors in the single-metric linear models (Fig S9) had relatively low R² values in the linear models, only appeared for one trait each, and did not appear in the boosted regression trees. Further, some of these predictors held similar latitudinal trends as climatology and may simply co-vary with climatology, rather than explaining additional variation. For this reason, we have prioritized the BRTs in the main text and retained the linear models in the supplemental, even though they have limitations. For example, in the single-metric linear models, Light_PC1

was highly correlated with TempClimatology_PC1, and likely reflects the same trend. However, we note your original point and agree that the inclusion of host cluster and health chart in Fig S9 as well as the stepwise linear models (Table S6) are worthy of a mention in the main text. Thus, we have added to lines 278-281: "These results were supported by linear models which showed that the amount of variance explained by predictors and traits was largely consistent with BRTs, though these models tended to retain additional predictors including genetic cluster and coral health chart score (Fig. S9; Table S6)."

Figure S4. I would appreciate a comparison between natural and experimental bleaching results from North Direction. Do the response metrics have similar results among genomic clusters? It is still poorly understood whether these acute heat stress assays can recapitulate natural bleaching responses and this is an opportunity for such comparison. In text, the cluster performance comparison was discussed but it was not specified that these stemmed from two geographically separated populations.

We agree that it remains poorly understood how well acute heat stress assays represent natural bleaching responses. We believe that more research is needed to answer this question and have plans for a future study to directly address this. Unfortunately, we cannot directly compare response metrics among genomic clusters at North Direction to natural vs experimental bleaching. While both sets of samples are from the same geographic population, only the target cluster (group 1) is well-represented in the experimental results (46 of 53 colonies), providing insufficient replication (≤ 3 colonies for groups 2-4) to enable comparison with the natural bleaching samples (Fig. 4; Fig. S5).

Reviewer #3 (Remarks to the Author):

Against the backdrop of global warming and intensified human activities, studying the heat tolerance characteristics and mechanisms of corals has become a hot topic in the field of coral reefs. However, the factors influencing the heat tolerance of corals are undoubtedly diverse. This article evaluates the heat tolerance characteristics of a coral species (*A. hyacinthus*) in the Great Barrier Reef based on environmental factors, symbiotic Symbiodiniaceae community, and host genome. The most valuable aspect of this article is the large and extensive sampling in the experiments, making it one of the largest studies to date on intra-species heat tolerance differences. Nevertheless, the article also has some shortcomings. The four heat tolerance indicators measured in the study (photosynthetic efficiency, chlorophyll content, etc.) seem somewhat forced, as there is actually not much research directly using these indicators to determine coral heat tolerance. If there were, providing relevant citations might have been more substantiated. Additionally, coral symbiotic bacteria should be the most abundant and active component in coral holobionts, a critical factor influencing coral host environmental tolerance, yet the article does not analyze this aspect. Furthermore, although the authors conducted coral genome sequencing, it appears that the genomic differences among samples were not carefully analyzed, and there was no thorough correlation analysis with factors such as coral heat tolerance, environmental differences, etc. Overall, the results obtained from the analysis in the article mostly align with past research findings and do not provide any innovative results. Therefore, I believe that the publication of this article should be reconsidered.

Thank you for your feedback and recognition of our large-scale and extensive sampling of intraspecific variation in the heat tolerance of corals. However, we respectfully disagree with the perceived shortcomings in our manuscript and provide our reasoning below.

The heat tolerance indicators (metrics) measured in our study are the most widely used in coral heat tolerance research. This is because they capture key processes in the coral bleaching stress response, namely photochemical damage (Fv/Fm) and the loss of symbiont cells and/or their photosynthetic pigments from coral tissue (NDVI), in a non-invasive manner (i.e., using chlorophyll fluorescence and hyperspectral imagery). Fv/Fm is the standard metric used in acute heat stress assays to rank taxonomic, spatial, and temporal variation in coral heat tolerance (e.g., Barshis et al., 2018; Klepac et al., 2023; Nielsen et al., 2022) and allows our results to be compared to prior and future work. It is also routinely used in longer-term heat stress experiments (e.g. Schoepf et al., 2019) and occasionally in field-based studies (where measurements can be taken under dark adaptation; e.g. Kemp et al., 2014). NDVI is similar to other photographic measurements of bleaching (e.g., color intensity as in Winters et al., 2009) and directly relates to chlorophyll content (Figure S1; Leal et al., 2015; Rouse et al., 1974). As with Fv/Fm, photographic measurements of bleaching are routinely used in both experimental (e.g., Kenkel et al., 2013; Wright et al., 2019) and field (e.g., Chow et al., 2016) studies of variation in coral heat tolerance. Expressing both of these traits as retained values (e.g., Voolstra et al., 2020; Walker et al., 2022) and ED50 thresholds (Cunning et al., 2021; Evensen et al., 2022, 2021; Marzoni et al., 2023) is also consistent with previous work. However, as ED50 is a newer metric to express heat tolerance in corals, we have now added a citation in the Methods to

support its use (Evensen et al., 2021; line 548). We believe additional citations are not necessary to justify our heat stress measurements due to their widespread use and journal limitations on citations but we are willing to add these at the Editor's request.

We agree that symbiotic bacteria are an important component of the coral holobiont, yet their role in determining heat tolerance remains poorly understood and limited to a few correlative studies (reviewed in van Oppen and Nitschke, 2022). While measuring differences in symbiotic bacteria was outside the scope of this study, we now acknowledge their potential influence at lines 406-407 "Further, symbiotic bacteria are another component of the coral holobiont that may influence heat tolerance⁵³, but were not explored in this study".

We also entirely agree that host genomic differences are likely to play an important role in defining heat tolerance (lines 442-445). Our whole-genome sequencing data will be analyzed in detail to uncover associations with environmental gradients and coral phenotypes to develop genomic predictive models of coral heat tolerance. This does not fall within the scope of this study and will be thoroughly examined for a future genomics-focused manuscript. However, we included results on the genomic assignments of the coral host in the present study (Fig. 3,4) to account for variation in heat tolerance among cryptic taxa (see lines 65-77).

We present the largest-scale study of intraspecific variation in coral heat tolerance including almost 600 individuals of *A. hyacinthus* across the GBR. Some of our findings align with previous work affirming the strong influence of long-term and recent thermal history on coral heat tolerance. Yet, we also present novel results due to the extensive scope of our study. We reveal substantial variation in multiple heat tolerance traits from spatial scales of a few to 10s of meters (i.e., within reef) to 10s to 100s of kilometers (i.e., among reef). This variation has implications for how heat-tolerant corals are identified, protected, and restored. As an example, the results of this study have already been integrated into a restoration program to select parents for breeding trials to enhance tolerance traits in coral offspring. Further, our study is the first, to our knowledge, to simultaneously measure the effects of Symbiodiniaceae, host genetic cluster, and multiple environmental drivers on coral heat tolerance, enabling the relative importance of these factors to be directly compared.

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Version 1:

Decision Letter:

** Please ensure you delete the link to your author home page in this e-mail if you wish to forward it to your coauthors **

Dear Ms Naugle,

Your manuscript titled "Environmental, host, and symbiont drivers of heat tolerance in a species complex of reef-building corals" has now been seen by our reviewers, whose comments appear below. In light of their advice we are delighted to say that we are happy, in principle, to publish a suitably revised version in Communications Earth & Environment under the open access CC BY license (Creative Commons Attribution v4.0 International License).

We therefore invite you to revise your paper one last time to address the remaining concerns of our reviewers. At the same time we ask that you edit your manuscript to comply with our format requirements and to maximise the accessibility and therefore the impact of your work.

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Alice Drinkwater,
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REVIEWERS' COMMENTS:

Reviewer #1 (Remarks to the Author):

The authors have addressed all feedback thoroughly. I stand by my original view that the paper is an important contribution to the literature and should be published. I disagree with Reviewer 3's feedback regarding a lack of innovation, as this paper had extensive sampling and was able to highlight interesting scaled-dependent findings because of that. I also don't think there is enough evidence to support reviewer's claim that symbiotic bacteria play a more "active" role than symbiotic microalgae with regards to coral holobiont adaptive capacity.

Reviewer #2 (Remarks to the Author):

Thank you for your thoughtful responses to the questions, concerns, and suggestions in the rebuttal document and the modifications made to improve the manuscript. The manuscript can be accepted following very minor revisions. First, I noticed Figure S5 also needs to have the shelf position descriptions for blue and green colors. Second, although the authors confirmed that the sample sizes of genomic clusters 2-4 are too low to compare natural vs. experimental bleaching responses, $n=46$ colonies from Group 1 would be still interesting and valid to explore natural vs. experimental. Other attempts in the existing literature have much lower sample sizes than 46 colonies. Finally, although the experimental baseline MMM cannot be changed, it is worth considering that the *A. hyacinthus* colonies sampled are likely only one to two decades old, and climatological data dating back to 1985 is superfluous in this context. MMM is the highest-ranking predictor in ED50 BRT results, but these values incorporate temperatures that date further back than the corals' lifespan, how can we confidently understand the influence of MMM?

Reviewer #3 (Remarks to the Author):

The author has provided detailed answers and responses to the previous review comments. In response to the key issues, the author has presented scientific explanations and provided literature support for the author's viewpoints. I have no further comments.

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Author Rebuttal letter:

Melissa Naugle
National Marine Science Centre
Southern Cross University, Australia

Dear Reviewers,

Thank you for your time and feedback in reviewing this manuscript and providing us the opportunity to further strengthen it.

In response to the remaining minor comments from Reviewer 2:

We have added the shelf position descriptions to Figure S5.

We agree that a comparison between natural and experimental heat stress responses would be interesting, but unfortunately, the 46 colonies sampled for natural bleaching were different than the colonies sampled for the heat stress experiment. Thus, we are unable to make the comparison requested. We have revised the wording to clarify this in the methods: "Heat tolerance was evaluated in an additional 60 colonies within the *A. hyacinthus* complex at North Direction during a natural bleaching event in March 2021" (lines 445-446).

The CoralWatch maximum monthly mean (MMM), which incorporates temperatures since 1985, is a widely used metric of thermal climatology. It is used here and elsewhere to represent the influence of thermal history on current coral populations through multi-generational evolutionary processes and/or intra-generational acclimatization. In our initial collection of environmental variables, we also computed a modified MMM metric using eReefs temperature data, which incorporates temperatures from 2014. The CoralWatch MMM were highly correlated with eReefs MMM values in our dataset ($R = 0.98$, $p < 2.2e-16$) and was similarly predictive of heat tolerance. Since long- and short-term MMM were so highly correlated and with similar predictive ability, we prefer to use the CoralWatch MMM in our boosted regression tree (BRT) models since it is the more widely used metric.

Regards,
Melissa Naugle
Corresponding Author

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General Comments:

Introduction

Line 39-40. This statement should be supported by a reference if applicable.

Results

Table 1. Out of curiosity, why would ED50's have a greater variance than retained? Is predicted tolerance during heat stress more variable or uncertain (based on SE of calculation) than measured bleaching outcomes which are finite values?

Line 272-274. Similar to the question in Table 1, the results of greater ED variation within site and greater retained variation among sites are compelling to consider. Since most predictors were at site levels, yet ED metrics were more variable, are the authors confident in the ED results and conclusions drawn from them?

Discussion

Lines 296-298 and 368-369. Fifer et al. 2021 (<https://doi.org/10.1111/mec.15869>) demonstrated that flow was an important influence on bleaching outcomes for *Acropora pulchra*. Do the authors have access to current data as a possible predictor? Additionally, microbial communities could also contribute to the unexplained variance but this is not discussed herein.

Lines 305-306. Does the “over 0.4°C” represent the mean difference in ED50 between N and S? See Somero 2010 for support of living near upper tolerance limits.

Line 307. Perhaps add “and by a higher tolerance in retained traits” after “summer maximum temperatures”. That result provides strong evidence of withstanding and/or recovering from bleaching.

Line 316-317. After reviewing NOAA CRW's 5km products from 2021-2022, it appears as though most Northern sites were sampled during warm periods where DHW was closer to 4, and most Central and Southern sites (except Heron) were sampled during little to no DHW. First, the methods don't mention sampling colonies that were visually healthy or unbleached, if there was any colony-level paling, could or were the response metrics adjusted to reflect baseline stress? Second, could the southern populations be “better positioned to persist through future warming” as an effect of sampling these corals under no thermal stress versus the northern population experiencing localized thermal stress? Especially for the result on Lines 114-115, where Southern corals may have had more pigment/photochemical ability to begin with.

Lines 357-359. See Nielsen et al. 2022 for a thorough investigation into the differences among traits measured across acute heat stress. Were the authors able to do hyperspectral imaging at the same time as PAM measurements? It would have been an interesting comparison or validation of metric-associated variance.

A “more variable holobiont response in NVDI versus symbiont response in Fv/Fm” should be elaborated upon, especially since host characteristics likely influence how light reaches symbiont cell’s light-harvesting complex (LHC). Since NDVI is captured after heat stress, perhaps it is a measure of the remaining symbiont species/community as opposed to the symbiont community’s photochemical response during acute stress, under the hypothesis that the *in hospite* community changes throughout bleaching and the measurements are capturing two different communities, which likely have differing photophysiology (chloroplast number, size, LHC size, etc.). I’m baffled yet enthralled by these results!

Lines 368-369 and 631-634. Considering the sampling area within sites (<5km) and the resources used for temperature metrics, NOAA-CRW at 5km and eReefs at 1km scales, it seems likely that there might not be enough spatial resolution to determine within reef variation and this point should be discussed. Moreover, are any of the sites within 5km of one another, and why couldn’t eReefs be used for all temperature metrics?

Methods

Line 469. Since actual temperatures were not mentioned, +9°C MMM seems to be 37.7°C correct? (At least for NOAA-CRW 5km Northern GBR MMM of 28.7°C) That is quite high as acute tests go for Acroporids and I’m surprised retention could be calculated from this treatment. Did the resulting sample size decrease at all for these metrics?

Additionally, and perhaps this is why +9°C MMM didn’t yield total necrosis, taking climatological MMM values as the baseline temperature might not be appropriate. How does the MMM compare with current summertime average temperatures? The world is much warmer than it was in the 1980 and 90’s and using the full climatology may not be representative of current in situ temperatures.

Figures

Figures 2, 5, and . I would appreciate a bold line or some demarcation to separate northern from southern sites (and maybe central as well) for visual reference for those who have not worked in GBR.

Line 253. Were the authors intending to only describe inshore as yellow, it reads incomplete as the blue and green color representation was not included.

Supplemental

Linear Model Results. Although there is parsimony between the BRTs and linear models, the retention of genomic cluster, health chart, and light is interesting yet not discussed much in the text. Are these putative predictors not discussed because of their low R^2 ? What do the authors make of these discrepancies?

Figure S4. I would appreciate a comparison between natural and experimental bleaching results from North Direction. Do the response metrics have similar results among genomic clusters? It is still poorly understood whether these acute heat stress assays can recapitulate natural bleaching responses and this is an opportunity for such comparison. In text, the cluster performance comparison was discussed but it was not specified that these stemmed from two geographically separated populations.