nature portfolio

Peer Review File

The Oak and the Reed: Two Environmental Response Strategies in Corals from Pacific Islands

Web links to the author's journal account have been redacted from the decision letters as indicated to maintain confidentiality

4th Jan 23

Dear Professor Furla,

Your manuscript titled "The Oak and the Reed: Two Environmental Response Strategies in Corals from Pacific Islands" has now been seen by 3 reviewers, whose comments are appended below. You will see that they find your work of some potential interest. However, they have raised quite substantial concerns that must be addressed. In light of these comments, we cannot accept the manuscript for publication, but would be interested in considering a revised version that fully addresses these serious concerns.

We hope you will find the reviewers' comments useful as you decide how to proceed. Should additional work allow you to address these criticisms, we would be happy to look at a substantially revised manuscript. If you choose to take up this option, please either highlight all changes in the manuscript text file, or provide a list of the changes to the manuscript with your responses to the reviewers.

We would be interested in considering a revised manuscript if it can provide compelling new and biologically relevant insights into coral phenotypes across broad geographical scales. To achieve this, we require that your manuscript provides clear hypotheses that contextualise the knowledge gap being addressed and thus the contribution that your findings offer. While descriptive studies are useful, the a priori reasoning behind why these analyses were chosen should be made explicit to the reader. Please also clarify for the reader why the biomarkers you have chosen help us better understand the responses of these corals to environmental differences beyond other existing response metrics. You should also demonstrate that your analyses were not affected by seasonal variation between sampling periods. We also encourage you to improve the quality of the data presentation to enhance the impact of your paper.

Please bear in mind that we will be reluctant to approach the reviewers again in the absence of substantial revisions.

If the revision process takes significantly longer than three months, we will 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.

We understand that due to the current global situation, the time required for revision may be longer than usual. We would appreciate it if you could keep us informed about an estimated timescale for resubmission, to facilitate our planning. Of course, if you are unable to estimate, we are happy to accommodate necessary extensions nevertheless.

We are committed to providing a fair and constructive peer-review process. Please do not 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 reviewers' comments with a list of your changes to the manuscript text (which should be in a separate document to any cover letter) and any completed checklist:

[link redacted]

** This url links to your confidential home page and associated information about manuscripts you may have submitted or be reviewing for us. If you wish to forward this email to co-authors, please delete the link to your homepage first **

Please do not hesitate to contact us if you have any questions or would like to discuss the required revisions further. Thank you for the opportunity to review your work.

Best regards,

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EDITORIAL POLICIES AND FORMAT

If you decide to resubmit your paper, please ensure that your manuscript complies with our editorial policies and complete and upload the checklist below as a Related Manuscript file type with the revised article:

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For your information, you can find some guidance regarding format requirements summarized on the following checklist:(https://www.nature.com/documents/commsj-phys-style-formatting-checklist-article.pdf) and formatting guide (https://www.nature.com/documents/commsj-phys-style-formatting-guide-accept.pdf).

REVIEWER COMMENTS:

Reviewer #1 (Remarks to the Author):

Overall;

This manuscript presents data on two different coral genera (at least 3 species within each genus) and their phenotypes over a large transect spanning islands across the Pacific Ocean from Panama to Guam. Phenotypes were composed of multiple biomarkers including animal biomass, symbiont biomass, protein carbonylation, protein ubiquitination and antioxidant capacity. The researchers used non-parametric statistics to determine that biomarkers significantly varied across species and

across islands. I applaud the authors for having a large dataset with interesting trends, the geographic scope is amazing.

However, I'm a little confused about the hypothesis you are testing. The way this manuscript reads it seems like you are just fishing for significant interactions between corals and a ton of different variables. This data mining approach will guarantee you will find significant relationships even though they might not be biologically relevant or novel. For instance, you found significant differences in phenotypes among species and among islands. But isn't that expected? Is your null hypothesis that there is no structure across space? This seems unlikely for the biomarkers of any organism terrestrial or marine. The same being true for the hypothesis that Pocillopora and Porites respond with the same phenotypes to environmental conditions, there is plenty of previous literature to show that this is not true. I do think this manuscript is a valuable contribution to our understanding of coral phenotype across broad geographical scales, but I think that the questions here need to be more explicit, probably through careful editing of the writing.

I am very concerned about a confounding factor: Are your coral samples are collected during a single time point? How representative of an individuals biology did you capture in your snap shot when you sampled the corals. Also are all of the islands surveyed during a similar time period? I know that you covered a huge spatial distance but don't you think that the timing of sampling might be a confounding variable in your analysis of the biomarkers. For instance, in your results for carbonyl content (line 184), you found a unique signature for the central islands, is this due to season sampled? I don't see any mention of the timing of your sampling or how you might have controlled for this confounding factor. If you sampled Panama in July and Guam in February these are two very different seasons even in the tropics!

I am concerned that this confounding factor stemming from your methods might be driving the results you present here. I think these issues need to be directly addressed in the text of the manuscript. You should discuss the limitations and advantages of your approach. Be clear with your reader, I want to know what you found but also understand the caveats of your data. Additionally on line 567 you should state which island was visited during which month, instead of saying that the sites were evaluated from July 2016 to Feb 2017. Be explicit here that will help to make the limits of your data more transparent.

Specific Comments

Introduction
Line 148. You have two commas here.

Results
In this section you talk a lot about the differences among the species within the genus. But you have buried this data in the supplemental material, I would like to see it. I am very interested in this variance among the species and considering the extent of your discussion here it is not clear why you are not showing these data.
Line 164. I don't see any indication of different species on Figure 1. Do you mean between genera? Since you are comparing more than two sites you should replace between with among.

Discussion

Overall, the discussion is very long. It is so long that I got distracted from the message. I think the clarity of your manuscript would really benefit from some careful editing of this section to really highlight your results and their impact on our understanding of coral biology. For instance, the paragraph starting on line 343 is not wrong but really just provides background to your study, I don't read a lot of your data in this paragraph, except maybe the last sentence, couldn't you delete most of this and move the last sentence to the paragraph above?

Your title and conclusions highlight your comparison between oaks and reeds (which I do think is illustrative), why haven't you incorporated that into your whole discussion? I see multiple places in your discussion where you are comparing the biology of Pocillopora and Porites where this comparison would be appropriate to mention.

Line 317-318. This sentence doesn't make sense. Edit for clarity

Line 354. Sure protein ubiquitination is a cellular process even in healthy cells, so I guess I'm not totally surprised that it's not terribly informative. But this is interesting since other studies have found it to be important. I think this paragraph could be 50% as long and still as informative, we don't need a review of all the cellular processes that ubiquitination does!

Line 422. I think you mean to say "for" instead of "of"

Line 432. Again this paragraph reads really long. Could you shave off 50% to make your message clearer?

Line 447. This whole section of writing is saying that you found no impact on phenotype… this could be much shorter.

Line 472. This is really interesting to me. And I think it might have something to do with coral longevity. So Pocillopora respond to recent events, and typically they are short lived (10-20years). I think of Pocillopora corals as weedy, spring up fast and survive stress events through multiple generations, and also don't live long. However Porites are linked to long term past climate and they are long lived (20-100's of years). How could a Pocillopora coral reveal any information about past climate events if they were not alive then? I think this paragraph would be a good place to talk about longevity and also include your oak vs reed comparison. This seems pretty central to your results, that these two genera have different traits that support their different life history strategies (think R vs. K selection). And they have different evolutionary histories too, Pocillopora being from the robust clade and Porites belonging to the complex clade. But be careful here, your results support this idea but you are not the first to propose it! I think an informative approach here would be to consider the literature that takes a trait based approach. Have you read: A trait based approach to advance coral reef science, by Madin et al., 2016 TREE 31: 419-428. Or Darling et al., 2012. Evaluating life-history strategies of reef corals from specific traits. Ecology Letters 15:1378-1386. This paper lumps corals into 4 basic
"strategies", how do your oak and reed fit into this framework? I think a better synthesis of this literature would help to put your research into the proper context.

Line 488. Ok so your biomarkers show a signal of past SST anomalies. This is something of an ascertainment bias. You are measuring antioxidant responses that we know are modified by temperature. And you found a signal of temperature in your measurements of these biomarkers. Do

you see how it would be hard to find anything else? I think a frank discussion of the biomarkers you selected and how those might bias your findings towards temperature stress would be important to include here.
But the fact that some of the biomarkers are tracking other environmental conditions is interesting, and you discuss this in the following paragraphs.

Acknowledgements
Line 717. This sentence ends abruptly, I'm not sure what you are trying to say here, maybe you typed the beginning of this sentence twice?

Figures
Figure 3. I'm sorry but I can't figure out what you are trying to communicate with this figure. Why is this important, does it convey critical information for your reader to understand phenotypes in these corals? Maybe a map would be more visually clear?

Table 3. What type of Porites are these. You have species names in parenthesis for Pocillopora above, but nothing for the Porites. I understand species delimitations are fraught in Porites but I can't tell from this table if you are referring to branching, sub-massive, or massive growth forms. Something here about the species/morphologies would help to clarify the types of Porites you were sampling.

Table 2, Figure 5 and 6. Can you replace the codes (R_Cli_029) with the actual variable. Right now it is really difficult to determine which variable you are displaying because your reader does not know these codes. I think this will go a long way in making these tables and figures clearer.

Figure 6. So after digging into your supplemental data I found that H_Cli_13 and H_Cli_15 are measuring SST anomaly, but one is max and one is standard deviation. I understand that you can have multiple variables that co vary in your analysis, but by presenting these two variables in your figure, you are suggesting to your reader they are different. And only after considerable time hunting through your supplemental material did I find that they are actually very related to each other. I'm not sure the best approach here (this is actually my favorite figure), but I think it will be important to be transparent about what these variables are to your reader, certainly writing the actual variable on the figure (as mentioned above) will help, but it is worth thinking about what you are presenting here and how to best deliver your message to the reader.

Supplemental Materials
I think being transparent with your data analysis is really important. Your supplemental figures are good and really helpful. I am stuck on Table S9. Here you have a bunch of different environmental variables. Many of them are historic, which I assume means that you found these on some sort of database. For instance, H_Cli_013 is Sea Surface Temperature anomaly, max per day (If I am interpreting your table correctly). Where did this data come from? I don't see any information in the methods or supplemental materials on how/where you got this data from. On line 650 you explain the procedure for these variables, and cite another paper on Biorxiv, and in that manuscript I found the databases and procedures used. I think 2-3 summary sentences after line 650 would go a long ways to making your environmental data analysis more transparent. I understand that your Biorxiv manuscript has all the details but I don't think many of your readers are going to bother with that link. I do think your methods could summarize the procedure so your reader at least has some idea of where these data originated from, and if the reader wanted more information they could track

down the Biorxiv manuscript.

I hope this review was helpful. Dr. Ritson-Williams

Reviewer #2 (Remarks to the Author):

Two Environmental Response Strategies The Oak and the Reed: Two Environmental Response Strategies in Corals from Pacific Islands by Barbara Porro,☖ & Thamilla Zamoum☖, Didier Forcioli, Eric Gilson Adrien Poquet, Eugenio Di Franco, Stéphanie Barnay-Verdier Fabien Lombard, Christian R.Voolstra, Benjamin C.C. Hume, Pierre E. Galand Clémentine Moulin, Emilie Boissin, Guillaume BourdinGuillaume Iwankow, Julie Poulain, Sarah Romac, Sylvain Agostini, Bernard Banaigs, Emmanuel Boss, Chris Bowler, Colomban de Vargas, Eric Douville, Michel Flores, Stéphane Pesant, Stéphanie Reynaud Matthew B. Sullivan, Shinichi Sunagawa, Olivier P. Thomas, Romain Troublé, Rebecca Vega Thurber, Patrick Wincker, Didier Zoccola Serge Planes, Denis Allemand Eric Röttinger, # and Paola Furla.

Overview: Authors evaluated 5 biomarkers including symbiont density, tissue biomass, protein ubiquitin, carbonylation, and antioxidant capacity in two genera of corals (Porites and Pocillopora) from the Eastern and Western Pacific. They related these findings to SNP profiles, symbiont ITS clusters, microbiome 16S clusters, and physical environmental variables. They then run all the results from these analyses (8 species and 2 genera of corals, 11 islands, Y and Z numbers of 16S and SNP clusters, and 101 environmental variables giving at least 5 * 8 *11 *101 * Y * Z or ~ 44000 different combinations that are run through a variety of statistical algorithms to yield a series of PCA and box plots with various parameters statistically significant or not. More importantly, why is this study important? Two main points in the abstract: "We show that corals, even if they share the same habitat and experience the same environmental perturbations, do not display the same strategies of environmental response." This seems self evident simply by examining the morphology of different species of corals. How are these analyses really shedding additional meaningful light on this issue? "Overall, this study sets the scientific and methodological foundation for future integrative studies that aim at understanding differential response strategies deployed by coral reefs to cope with environmental change and facilitating coral reef management and conservation projects all over the world." How, exactly can these results realistically be useful to coral reef managers? For instance, are managers going to be depending on things like carbonylation of proteins or ubiquitin levels to guide management of coral reefs? This paper reads like an unfocused fishing expedition looking for a question to answer. There might be some useful data lurking somewhere in this MS, but the presentation and analysis certainly does not make this evident.

Results

Lines 171-174: I don't understand what you mean by significant diversity or lack thereof. For instance, for Fig. S1, there are significant differences in parameters between Pocillopora species as well as Porites for all parameters. Is that not significant diversity?

Lines 175-183: I'm not clear why you are highlighting symbiont biomass in particular. Looking at Figure 2, there are significant differences for all parameters, islands, and genera. Perhaps condense everything to that one sentence.

Lines 188-190: Again, not sure how that statement jives with what's on Fig 1D or S1D. There are significant differences among lineages and islands/genera.

Lines 188-193: As above, vague statements that do not jive with figures. In box plots, different letters above a box indicate statistically significant differences.

Line 222: Do you mean different from the other islands?

Lines 222-224: "The Pocillopora species..." This sentence makes no sense. Different species will inherently have different phenotypes regardless of what analyses you use.

Line 226: What do you mean by punctually different?

Figure 1. I'm not understanding here how you disentangle species from islands as a statistical effect. Clearly, Figure 1 shows differences in parameters between islands and differences between species (Fig S1). So is the islands differences a function of islands or islandsXspecies? Were the same species of Pocillopora/Porites sampled for each island?

Methods:

Line 580: Proteins being extracted here are from the entire coral (endoliths, endosymbionts, animal tissues), not just the animal tissues, so "animal cytosoluble protein extracts" is not correct.

Line 596: I think here you mean to say you centrifuged sample, counted symbionts in sediment and quantified protein in supernatant, correct?

LIne 605-613: The anti-mouse antibody....from what animal did it originate? If you quantified the protein in your NaOH homogenate, why stain with amido black? You said earlier you dot blotted 3 and 0.5 ug of protein, so you must have calculated this from your Bradford assay no? Also why did you do different amounts of protein for each coral genus? For standardizing [protein] on dot blot, one normally does a standard curve of serially diluted known concentration of protein standard stained with amido black or coomassie blue ato relativize density of experimental dot. I assume you did a conjugate control to make sure your secondary antibody was not tagging the dot blot?

Lines 618-620: rabbit was primary antibody, but what was animal origin of secondary antibody?

Line 684: What function?

Lines 693-708: Given the non-independence of the comparisons here, how do you account for false discovery rate (see https://pubmed.ncbi.nlm.nih.gov/24831050/) as example.

Figure S1: What are the species of corals?

Reviewer #3 (Remarks to the Author):

The manuscript reveals original and relevant work for the coral field by combining data from abiotic and biotic factors to assess how the physiological plasticity of two coral species are mediated by environmental alterations. The findings were however, limited to two coral species in specific locations in the Pacific Ocean. The manuscript is very good but it has 'limitations' that should be better acknowledged/ discussed along the text.

I pointed a few suggestions in the manuscript pdf. Please see below for additional observations:

-Please review the use of the word 'biomarker' throughout the manuscript text and figures. In many cases I believe that the word 'proxy' or 'parameter' would be more appropriate. Pls better embase why coral and symbiont biomass are good biomarkers for inferring about coral phenotypic plasticity. It was first stated on L119, but refs. 16 and 29 are not specific for that. Another example on L327-330 - you mention coral trophic state, which can be inferred, for instance from fatty acid analysis (see Mies et al 2018 on Coral Reefs), which would then be a better biomarker for trophic state than just host/symbiont biomasses. Another example of what I mean can be seen on fig 4 - origin island was a parameter for your analysis, but it is not a biomarker.

-Pls add stats to your figs 1 and S1 so that we can better visualize the differences discussed in the text. Since you mentioned fig S1 a lot while presenting your results, maybe you could bring it to the main text or combine it into fig S1 - the main findings presented in these two figures could be combined.

-I'd remove tables containing only stats numbers for the supplementary material.

-L68: 'Climate' is not an environmental parameter. Pls rephrase here and be more specific about which parameters you used.

- Please be consistent in the way you present references throughout the manuscript. They should follow the journal recommendations (see example highlighted/comment in L90). Also, please exclude 'see for review' that appears multiple times when you referred a study throughout the manuscript.

-Please check manuscript writing structure (example L148).

-L116: Pls be more specific explaining which 'biological processes' you meant here and add references.

-L153: It would be good to have here at the introduction which parameters from your study were monitored to assess the corals phenotypic plasticity.

-L196-198: Please be more specific when sayin 'low' (L196) and put a number to state how low so that the comparisons you make are more clear. Check that throughout your results.

-L245-246: Please use more specific terms and state what you actually monitored to make that statement instead of using 'perception of the environment'.

-L303-304: You have a nice manuscript and good findings, but your findings are limited to 2 coral spp. in specific locations of the Pacific Ocean, therefore it cannot be generalized.

-L361-L366: Pls rephrase these sentences and avoid inaccurate terms. Always be precise when you can. You justify a 'less decipherable profile' based on physiological proxies that have not been measured in your study. Pls further discuss that.

-L526-529:Pls further discuss how these findings contribute to project biodiversity response to climate change. I don't think you can make broad statements with limited findings.

L533-534: I'm not sure what it's meant by 'the oak and the reed' - please avoid inaccurate quotes.

The Oak and the Reed: Two Environmental Response Strategies in Corals from Pacific Islands

Barbara Porro[1,2,3,4☖] & Thamilla Zamoum[1,2,3☖], Didier Forcioli[1,2,3], Eric Gilson[1,2,3,5], Adrien Poquet[1,2,3], Eugenio Di Franco[1,2,3], Stéphanie Barnay-Verdier[1,2,3,6], Fabien Lombard[7,8,9], Christian R. Voolstra[10], Benjamin C.C. Hume[10], Pierre E. Galand[8,11], Clémentine Moulin[12], Emilie Boissin[13], Guillaume Bourdin[7,14], Guillaume Iwankow[13], Julie Poulain[15], Sarah Romac[16], Sylvain Agostini[17], Bernard Banaigs[13], Emmanuel Boss[14], Chris Bowler[18], Colomban de Vargas[16], Eric Douville[19], Michel Flores[20], Stéphane Pesant[21], Stéphanie Reynaud[2,22], Matthew B. Sullivan[23], Shinichi Sunagawa[24], Olivier P. Thomas[25], Romain Troublé[12], Rebecca Vega Thurber[26], Patrick Wincker[15], Didier Zoccola[2,22], Serge Planes[13], Denis Allemand[2,22], Eric Röttinger[1,2,3,#] and Paola Furla[1,2,3,#,*]

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ABSTRACT

Coral reefs are severely threatened by global and local environmental changes. However, susceptibility to perturbations and subsequent mortality varies among coral species. In the present study, thanks to the unprecedented large TARA Pacific Expedition datasets, we tested the contribution of genetic or environmental causes to coral's phenotypic response in *Pocillopora* spp. and *Porites* spp., two emblematic coral species complexes that were sampled in sympatry at a large ecological scale throughout the Pacific Ocean. Coral phenotype signatures have been assessed by a multi-biomarker approach consisting in the analysis of animal and symbiont

biomasses, protein carbonylation, protein ubiquitination and total antioxidant capacities. This approach allowed the determination of a range of phenotypes in both species complexes reflecting discrete physiological states.

Although this approach determined a similarly strong anticorrelation in both genera between the intracellular redox state (protein carbonylation and total antioxidant capacity) and the animal as well as the symbiont biomasses, the two species complexes showed a diverse extent of phenotypic plasticity. *Pocillopora* spp. harboured a greater phenotypic plasticity responding to a large variety of environmental parameters (such as climate, nutrient richness, phosphate accumulation and the carbonate chemistry of the reefs), while *Porites* spp. exhibited more robust phenotypes partially influenced by coral host genetics, but mainly influenced by past climate events. We show that corals, even if they share the same habitat and experience the same environmental perturbations, do not display the same strategies of environmental response. Overall, this study sets the scientific and methodological foundation for future integrative studies that aim at understanding differential response strategies deployed by coral reefs to cope with environmental change and facilitating coral reef management and conservation projects all over the world.

INTRODUCTION

Climate change is expected to significantly increase the occurrence of cold and warm ocean sea-surface temperature extremes [1,2] that have already been well documented in the Pacific Ocean [3,4]. Accentuated by direct anthropogenic stressors due to local pollution and overfishing, climate change will have devastating consequences on marine organisms. Among them, reef-building corals are highly vulnerable to environmental changes, experiencing repeated mass coral bleaching (loss of the intracellular photosynthetic protist symbionts belonging to the Symbiodiniaceae

family), which have already led to substantial coral mortalities over large spatial scales [2].

However, susceptibility to environmental changes, and subsequent mortality, vary among coral species [5,6], but also within species (Loya et al. 2001). Consequently, survivor species will play a key role for coral reef resilience in a changing climate [7]. This difference in response to the environment has been attributed variously to different factors as, for example, the host genetic background [8–10], specific holobiont composition (the combination of different host species with one or multiple Symbiodiniaceae and bacterial lineages) [11–14], nutrient supply [15–17], ocean deoxygenation [18,19], and/or preconditioning to past repeated environmental changes [20–22]. However, the contribution of each of these factors to the coral's phenotypic response, and to what extent this is conserved within a coral genus or within diverse scleractinian corals living in a broad range of environmental conditions, remains unclear.

In corals, the phenotypic response is an unconstrained notion mainly due to their intrinsically morphological plasticity linked to environment-induced skeleton changes, see for review[23] and to their photoacclimation capacity that induced significant colour changes by modifying their cellular pigments and/or their symbiont population contents, see for review [24,25]. As corals can strongly depend on the high-energy products of their algal symbionts, those acclimation processes are essential for the trophic equilibrium in the oligotrophic waters where those organisms are largely distributed [26]. In addition, environmental perturbations (especially variations in temperature and UV radiation) induce in extreme cases bleached coral phenotypes which reflect symbiotic homeostasis breakdown, see for recent review[27]. To prevent bleaching, corals could then have (i) specific host-symbiont genotypes as specific adaptation to local environment, or (ii) display a large spectrum of phenotypic

plasticity. The latter allows the emergence of diverse physiological states from a unique genotype, in response to the environmental variation.

Several studies performed under controlled laboratory conditions and/or in field studies have identified biomarkers as indicators of the biological processes that take place during the symbiosis breakdown. These are proposed to be used as a signature of unhealthy physiological states, see for review[28]. Among them, biomarkers of the trophic coral state, as defined by the polyp tissue and/or the hosted symbiont biomasses, have been linked to coral sensitivity to environmental perturbations and reflected the existing nutrient intake by the coral, see for review[29,16]. Additional biochemical biomarkers, linked to modification of the intracellular redox state (*e.g.* protein carbonylation, oxidative scavenging capacities) or a more general damage signature as the ubiquitinated protein content, were validated in several studies measuring imbalances between reactive oxygen species (ROS) overproduction and antioxidant defences during environmental stress *e.g.*[30–38]. Accordingly, one consequence of this imbalance was the disruption of the cnidarian-Symbiodiniaceae association. However, to what extent the diverse biomarker signatures reflect an inherited and genotypically fixed character or diverse coral response to specific environmental factors is not clear. ~~In addition,~~ the heterogeneous nature of the reef environment makes it complex to identify the specific parameters that affect coral phenotypes.

In the present study, we took advantage of the large coral sampling performed at an unprecedented ecological scale throughout the Pacific Ocean during the TARA PACIFIC expedition 2016-2018[39]. We analysed 321 colonies from 11 islands across East-West and South-North gradients from the coasts of Panama to Micronesia and assessed the biological response to the environment of two emblematic coral-species complexes with different morphologies and lifestyles, *Pocillopora* spp. and *Porites* spp. *Pocillopora* spp. are branched corals, fast-growing and with moderate lifespan

(some decades [40,41]). *Pocillopora* spp. display flexibility towards Symbiodiniaceae, with the ability to harbour diverse species of *Symbiodinium*, *Cladocopium* or *Durisdinium* genera [42–47]. In contrast, even if they are found in sympatry with *Pocillopora* spp., *Porites* spp. display several different characteristics. *Porites* spp. are massive corals, with slow growth and long lifespan (several centuries [41,48]), with a strict symbiont fidelity to the genus *Cladocopium*, specifically with subclade C15 in the Indo-Pacific [42,13].

During the TARA PACIFIC expedition, visually healthy colonies of the two species complexes were sampled,, in the same sites but across a large diversity of habitats, enabling us to assess whether common or complementary/divergent strategies are deployed by the two genera to cope with environmental variations. Thus, by taking advantage of the multidisciplinary efforts of the TARA Pacific consortium and the diversity of available datasets (especially environmental and metagenomic data and analyses, see [49,50], we assessed the phenotypic plasticity in these two species complexes in response to environmental variations and determined to what extent these diverse physiological traits reflect genetic (of the coral host and its symbionts) and/or environmental correlations.

RESULTS

Distinct coral biomarker profiles across the Pacific Ocean

To obtain a physiological/phenotype profiling of *Porites* and *Pocillopora* colonies collected in reefs of different Pacific Ocean islands, we measured five different biomarkers revealing diverse trophic (animal and symbiont biomasses) and redox states (protein carbonylation and ubiquitination and TOSC). The comparison of the different biomarkers across the 11 islands and in the two genera, revealed an heterogeneous pattern either between species or between sites (Fig. 1).

For *Pocillopora*, animal biomass was high in the first three islands and then declined with a minimal mean in Moorea island which presented around three times less proteins compared to eastern colonies or to Guam (Fig. 1A). For *Porites*, we observed an East-West gradient with an eightfold reduction comparing colonies from Las Perlas and Guam colonies (Fig. 1A). Thanks to the identification of 5 species within the *Pocillopora* and 3 species in the *Porites* sampled coral [51], we could hence compare the specificity of the phenotype within each genus. Here, the animal biomass showed no significant diversity between the *Pocillopora* species, however, the three *Porites* species identified in our sampling presented a species-specific significant pattern of protein content (Fig. S1A).

Symbiont biomass normalised per milligram of protein was highest in Eastern Pacific for *Pocillopora* colonies (specifically for colonies from Panama islands, Las Perlas and Coiba) and lowest in Niue and Samoa islands (10- to 20-fold lower respectively; Fig.1B). *Porites* colonies harboured a more homogenous symbiont biomass even if Niue showed a lower symbiont content (Fig. 1B). Similar trends were observed following a tissue surface normalisation (Fig. 1C). The comparison of symbiont biomass in respect to host lineages show a higher symbiont content of *Pocillopora* species 4 (highly distributed in Eastern Pacific) and in *Porites* species 3 (present in the Central Pacific) (Fig. S1B and Fig. S1C).

For both species complexes, carbonyl content was higher in the three central islands of the transect, Moorea, Aitutaki and Niue (Fig. 1D). For example, in these three islands, the coral colonies of *Pocillopora* and *Porites* respectively presented carbonyl content means of 2 to 8 fold higher than the colonies from the East Pacific Ocean. The comparison of carbonyl content in respect to host lineages show no significant diversity between the *Pocillopora* species, however, the *Porites* species 2 (present in Central Pacific) had higher carbonyl content (Fig. S1D).

Concerning protein ubiquitination biomarker, the analyses show in *Pocillopora* a specific high content of ubiquitinated proteins in Gambier with an important variance between the sampled colonies (Fig. 1E). Although less pronounced, an increase in protein ubiquitination was also observed in *Porites* colonies from Gambier (Fig. 1E). No genetic link was observed for this marker for both species complexes (Fig. S1E).

For *Pocillopora*, TOSC was low in the two Panama islands and at Easter and Guam islands. TOSC was however maximal at Aitutaki, with around 20 times more antioxidant capacities in the colonies sampled at this island (Fig. 1F). For *Porites*, TOSC values were more homogenous with a slight increase along the transect line (Guam colonies presented a sevenfold increase of TOSC compared to Las Perlas). The comparison of TOSC in respect to host lineages revealed a species specific reduced amount of TOSC on *Pocillopora* species 4 and *Porites* species 1 (Fig. S1F), which should however be mitigated by an heterogeneity of species distribution along the transect.

Island- and species-specific coral phenotypic signatures

We then used a multimarker approach using the five biomarkers to establish phenotype signatures for each colony and compared them in respect to the genus, species and the islands of origin. A first permanova analysis testing the genus affiliation shows that the two sampled genera displayed different phenotypic profiles (p-value=0.0001) with a greater phenotypic dispersion of *Pocillopora* phenotype than *Porites* (p-value=0.001) visualisable in the Fig. S2 and Table S1. We have therefore analysed more in detail the *Pocillopora* and *Porites* signatures independently, using PCAs and PERMANOVA tests. The PCA of *Pocillopora* biomarker signatures revealed gradual distribution of the phenotypes along the first axis (Fig. 2A) mostly driven by both biomasses and carbonyls (Fig. 2B; Table S2). For *Porites*, the phenotypes were less spread into the PCA space but more homogeneously between the two first axes

(Fig. 2C) explained by a stronger independence between animal biomass and symbiont biomass (Fig. 2D; Table S2) than with *Pocillopora*.

The statistical partition of the phenotypic signatures by geographic origin or by coral species, has been tested for both genera by PERMANOVA (Table 1). For *Pocillopora*, the corals from the eastern and the western islands displayed phenotypes statistically different from the other corals (Fig. 3A and Table S3). The *Pocillopora* species 4 and 5 grouped different phenotypes from the other species (Fig 3B and Table S4), which was correlated with the spatial distribution of these species. The *Porites* phenotypes were less structured by geographical regions, but some islands were punctually different from others (Fig. 3C and Table S5), and only the species 3 had statistically different phenotypes from the two other species (Fig. 3D and Table S6). The corals from central Pacific islands presented more similar phenotype signatures if compared with other regions (Fig. 3A, C and Tables S2 and S5).

To test the influence of the island or species origins but also the associated microorganism diversity (testing separately the Symbiodiniaceae and the microbiome diversities), we performed a variation partition analysis. To avoid any bias, we considered only coral colonies from islands containing more than one coral species per genus. The analysis confirmed a main effect of the geographical origin on the variance of the diverse phenotypic signature for *Pocillopora* (Fig. 4A) and *Porites* (Fig. 4B). For *Porites*, the coral species seemed to be an additional explanatory factor. A complementary Mantel's test within each species did not reveal any correlation between the genetic distance and the coral phenotype (Fig. S3). On the other hand, microorganism diversity composition was a marginal driver of the coral phenotypes.

Differing coral sensitivities to environmental conditions

Because the phenotypes of both genera were demonstrated to be influenced mainly by the geographical origin of the corals, we explored the correlations between

biomarkers and environmental variables to identify putative drivers. Using sPLS, we identified clusters based on similarity of response for biomarkers and environmental variables and observed that the two coral genera did not have the same perception of their environment.

For *Pocillopora*, the 20% of environmental variables most correlated with the studied biomarkers (20 variables) were included in all environmental categories (for details see Material and Methods section) and structured in two clusters (Fig. 5A, Table 2). Among the first cluster, we identified three biological variables (C_Bio_086, C_Bio_092, C_Bio_094; corresponding respectively to high content on chlorophyll, nanoplankton and total Eukaryotes analysed in the seawater); five physico-chemistry variables measured the sampling days (C_Phy_081, C_Phy_090, C_Phy_099, C_Phy_100 and C_Phy_101 (corresponding respectively to high oxygen, turbidity, pH, silica content and sun exposure duration, Table 2); three climate variables (the sea surface temperature of the sampling day (C_Cli_084) but also to recent cold temperature anomaly (R_Cli_045) and past cold sea surface temperature anomalies (H_Cli_009). Among the second cluster of variables, we identified one dynamism variable (the sea surface height (C_Dyn_077), three contemporary physico-chemistry variables (C_Phy_083, C_Phy_096, C_Phy_098, corresponding respectively to high carbon dioxide content, total alkalinity, phosphate concentration) and three historical climate variables (H_Cli_013, H_Cli_015, H_Cli_029, H_Cli_071; corresponding to high intensity of sea surface temperature deviations, recent heatwaves episodes and short recovery time after recent cold waves). In *Pocillopora*, all those variables displayed strong correlation (between -0.66 to 0.57) with the biomarker data, with the exception of protein ubiquitination whose correlations never reached the 0.3 fixed threshold. For all correlated environmental variables, two main biomarker clusters are also observed showing anti-correlation between TOSC and carbonyl biomarkers *versus* animal and symbiont biomass biomarkers.

On the other hand for *Porites*, the 20% most correlated environmental variables with the biomarkers (34 variables), belonged mainly on historical climatological variables and were more weakly correlated (around -0.55 and 0.5, Fig. 5B) than what we observed in *Pocillopora*. In Porites, the most correlated variables were clustered in three groups (Fig.5B and Table 2). A first cluster grouped the sea surface height (C_Dyn_077) and historical seawater temperature anomalies linked to minimal recorded seawater temperature (H_Cli_001), cold waves (in frequency and duration, respectively H_Cli_060, H_Cli_065,) but also to the recovery time after heat wave (H_Cli_043, H_Cli_044). In the second cluster, we identified biomarkers correlation with three physico-chemistry variables (corresponding to high oxygen, turbidity and sun exposure duration; C_Phy_081, C_Phy_090, and C_Phy_101) and 11 historical climate variables depicting recurrent past and recent seawater cold temperature anomalies (H_Cli_047, H_Cli_048, R_Cli_049, H_Cli_052, H_Cli_073) and strong past fluctuation of seawater temperatures (H_Cli_004, H_Cli_012, H_Cli_013, H_Cli_014, H_Cli_015, H_Cli_019). Finally a third cluster grouped only climate variables linked with past and recent heat waves events (H_Cli_020, H_Cli_021, H_Cli_025, H_Cli_026, H_Cli_027, H_Cli_028, R_Cli_029, H_Cli_030, H_Cli_031, H_Cli_032, H_Cli_033, H_Cli_035, H_Cli_037, H_Cli_039). In *Porites*, we also observed anti-correlation between TOSC and carbonyl biomarkers *versus* animal biomass. However, contrasting with *Pocillopora* results, animal and symbiont biomasses did not correlate in the same way with the variables. In addition, even when the protein ubiquitination of *Porites* spp. passed the sPLS filters and showed correlations with the environment variables, the correlation values were far weaker.

Although the strength of the correlations between biomarkers and environmental variables and the type of environmental variables mostly depended on the genus, 7 environmental variables were common to *Pocillopora* and *Porites* (Fig. 6A) and concerned the sun exposition duration (C_Phy_101) and O_2 concentration (C_Phy_081), frequence of recent (R_Cli_029) and historical sea temperature

anomalies (C_Cli_013, C_Cli_015), the sea surface height (C_Dyn_077), and the turbidity (C_Phy_090). Comparing the correlation pattern of each biomarker (Fig. 6B to 6E and Table S7), the animal biomass appeared to be the biomarker that responded most similarly in *Pocillopora* and *Porites*.

DISCUSSION

The aim of the present study was to understand the environmental response of corals co-occuring in the Pacific Ocean and their ability to respond to specific local environments. Central to our approach was the use of physiological biomarkers to establish the coral phenotypic signatures and an holistic integration of those signatures with explanatory variables collected during the TARA PACIFIC expedition. This integrative approach allows the determination of diverse phenotypes in both species complexes, reflecting discrete physiological states. ~~In addition~~, we found that corals sharing the same habitat and experiencing the same environmental perturbations do not have the same strategy of environmental response. *Pocillopora* ssp harboured a greater phenotypic plasticity responding to a large variety of environmental parameters while *Porites* ssp exhibited more stable phenotypes mainly influenced by past climate events.

Biomarker approach allows the identification of specific physiological states in natural population of corals

The use of the five different biomarkers, never used together at such large species and geographic scales, allows to determine the phenotypic profiling of coral colonies. The analysis of the diverse phenotypes corroborated in both genera a significant and strong anticorrelation between the animal biomass, and to a lesser extent the symbiotic biomass, with the redox state. A coral with thick tissue and high symbiont

density hence presents a low redox state with little oxidative damage and little activation of antioxidant defences.

Previous studies have observed that variations of coral tissue thickness could be both species-specific and related to seasonality, geography or environmental perturbations [52–55]. In addition, variations in coral tissue thickness are considered to reflect the trophic state of the colony or, in other word, the "nutritional value" of an environment [52]. This could be obtained by modulation in carbon intake by heterotrophy (from living prey) or autotrophy (from carbon symbiont translocation) [56,57]. In addition, Thornhill et al.[58] observed that corals with high tissue thickness have higher survival rates after bleaching.

In parallel, symbiont density can also vary in respect to (i) Symbiodiniaceae lineages, or (ii) coral host lineages, but also (iii) in response to the environmental conditions in order to maintain the optimal autotrophic balance [29,59]. Leaving aside the bleached state, which reflects a well-defined unhealthy condition and has not been the focus of this study (as only visually coloured colonies have been deliberately sampled), variations in symbiotic content may reflect successful accommodation of the mutualistic relationship in response to the environment. In addition, optimal symbiont densities are also known to vary with coral tissue thickness as, in a certain limit, an indicator of a good nutritional condition [60]. Taking into account those considerations, our results suggest that coral colonies with high animal and symbiont biomasses present a resistant phenotype, less susceptible to stressors.

The redox baseline of corals can reflect specific host or symbiont specificities [61,62] and/or, as in other biological systems, environmental perturbations that are responsible for ROS overproduction in coral tissues, which in turn activates antioxidant systems preventing cellular damages. However, under severe stress, antioxidant defences might not be able to scavenge all ROS leading to oxidative damage and metabolic dysfunction, see for review on coral [63]. The extended ability

of coral to activate antioxidant capacities and/or to eliminate oxidised cellular compounds (as carbonylated proteins) can then be considered as a crucial point that allows corals to respond to the environment [64]. Associated with high biomasses, a low redox state could then reflect a healthy physiological status not challenged by any exogenous stressors.

The contribution of the protein ubiquitination biomarker is less resolutive at the scale of the entire transect. However, it reveals some specific colony/island phenotypic signatures as the ubiquitinated protein accumulation in *Pocillopora* colonies sampled in Gambier and in *Porites* colonies sampled in Ducie, but without any strong correlations with other biomarkers or environmental factors. In corals, protein ubiquitination has been linked to thermal stress in the field [30,31] or in laboratory-controlled conditions [35,65,66] and associated to tissue thickness decrease, bleaching process and high redox state. The incongruency here observed is however not surprising since the ubiquitination profile could also be linked not only to damaged proteins degradation in stress conditions but also to many other cellular processes in normal physiological conditions (including intracellular trafficking, inflammatory signalling, regulation of protein–protein interactions, high protein turnover during increased metabolism…), leading to a less decipherable profile. For example, in coral inoculated with pathogenic bacteria, Wright et al. [67] observed a protein ubiquitination upregulation in the more susceptible corals suggesting a crucial role of ubiquitin pathway in the immune response. It is then interesting to note that in Gambier and Ducie, the coral colonies presented some of the lowest bacterial diversity[68], suggesting an additional indicator of weakness of these reefs by a general bacterial dysbiosis as demonstrated in the experimental work of Santoro et al.[69]. Assuredly, our work points out that further efforts should be made to identify the drivers that lead to the diverse ubiquitination signature in order to gain a better insight into the biochemical coral response.

Both coral genera exhibit differentiation in phenotypes along the transect

In our study, we observed a graduation of phenotypes significantly linked to the island origin for *Pocillopora* spp. and for the island origin and the species belongings for *Porites* spp..

The analysis of *Pocillopora* samples showed that the Eastern Pacific Ocean colonies (from Las Perlas and Coiba) had a strong phenotypic differentiation with high biomasses and low redox status, in contrast with Central Pacific (especially Niue and Samoa), where colonies harboured low biomasses and high redox state (Fig. 1 and Fig. 3A). In the other islands, the corals harboured intermediate phenotypes defined by diverse biomarker signatures. In addition, species-specific signatures have been observed within *Pocillopora* species complex with species 4 (identified as *P. grandis* synonym of *P. eydouxi* [51]; Table 3) highly differentiated from all other species. On the other hand, *P. meandrina* and *P. verrucosa* (species 2 and 3 respectively, Table 3) displayed undifferentiated phenotypes wherever they have been sampled. As all Las Perlas and Coiba analysed colonies belonged to *P. grandis*, it is tempting to attribute a species-specific phenotype to *P. grandis* as a resultant of environmental selection pressure experienced in this area accompanied by low dispersion and strongly genetic isolation as demonstrated for other *Pocillopora* species [70]. However, the few *P. grandis* colonies analysed outside the Eastern Pacific (species 4 in Gambier and Moorea islands) show a phenotype closer to the other species present on the same island than to the colonies of *P. grandis* from Eastern Pacific (Fig. 2A). The absence of a genetic link in *Pocillopora* spp. is also confirmed by the insignificant explanation of variance by species assignment (Fig. 4A) and the lack of phenotype-genetic correlation with the observed phenotypes (Fig. S3). In conclusion, the geography and then the environmental characteristics are the main factors structuring the *Pocillopora* physiological status with a large phenotypic plasticity reflecting the diversity of the colonised habitats.

Porites spp. phenotypes were assuredly less structured with less diverse phenotypes, but some phenotypic peculiarities have been found along the transect. Among them, as observed in *Pocillopora*, the Las Perlas *Porites* colonies harboured a physiological status with high animal biomass and low redox state. Again, this specific phenotype is not linked to the unique genetic lineage sampled in Las Perlas (species 1 attributed to species K1[51], Table 3) as in Malpelo, the same lineage displayed different phenotypic signatures. Finally, a strong phenotypic species specificity has been found in species 3 (attributed to species K3[51], Table 3) largely spread from Easter Island to Guam, which demonstrated for this species a strong capacity of phenotypic homeostasis independently to the habitat diversity. Therefore, our work depicts a complex structuring of the physiological status in *Porites*, shaped not only by the environment but also by a genetic component.

Corals from East and Central Pacific islands possessed distinct common phenotypes

While *Pocillopora* and *Porites* species show different strategies of environmental response, we observed some convergence in phenotypes specifically in Las Perlas and Coiba samplings. These samplings were performed in the two largest marine protected areas of Panama (the Coiba National Park and the Archipiélago de Las Perla), both inscribed from 2004 in the UNESCO World Heritage List of Natural Sites. The reasons of this protection are due to the presence of biodiversity hotspots, including the presence of endemic, rare, and endangered species, but also to the presence of extreme environmental disturbances, from short-term variability in sea temperature and seasonal upwelling to long-term temperature excursions accompanying El Niño/La Niña episodes [71]. The convergent phenotypes here observed in the two genera, could then be attributed to the success of the ecosystem protection and/or to the result of the coral survival due to repetitive perturbation episodes, suggesting that this specific physiological status (high biomasses and low

redox state) are signal of low susceptibility (or high capacity for survival) to local perturbations.

The Niué and Upolu islands are two Central Pacific islands analysed during the transect in which both coral genera showed some phenotypic specificities. Few data are available concerning the health status of the Niue coral reefs, but a recent report underlined a low coral coverage (from 3 to almost 38 %) with coral communities that remain under stress from recurrent storms and coral bleaching [72]. In Upolu (an island belonging to the Independent State of Samoa), a survey carried out during the TARA Pacific expedition [73], also highlighted an extreme fragility of its reef, harbouring in some sites an extremely low coral coverage (<1%). In those environmental contexts, the *Pocillopora* phenotype (cumulating low biomasses and high redox state) observed in Niue and Upolu confirms the presence of coral colonies with a fragile physiological state. In the light of climate predictions for the coming years, our observations could then constitute a strong argument to reinforce coral conservation in suffering reefs. Indeed, stronger marine protected area policy, as set up in Las Perlas and Coiba, can reduce the direct anthropogenic pressure, mitigating the impact of the more difficult to control climate change.

Symbiodiniaceae and bacterial compositions do not distinguish coral phenotypes

In both species complexes, no influence of the Symbiodiniaceae and bacterial compositions was detected as explanatory factors of the diverse phenotypes (excepted for few highly ubiquitinated colonies as discussed previously). However, previous studies working with some focal coral populations and reefs have highlighted that low bacterial diversity may function as indicators of a less resilient status of the reef [69]. It is plausible that the differences in our findings stem from our field approach, as the analysis of colonies under natural and non-extreme conditions

456 reveals various stable physiological states well adapted to their environment and
457 therefore without any signs of dysbiosis.

458 Furthermore, it has been shown that different Symbiodiniaceae taxa harbour diverse
459 antioxidants which may provide different thermo- and oxidative tolerance to the
460 holobiont [74,62]. Among them, the symbionts belonging to *Durisdinium* spp. possess
461 greater thermal tolerance and it is often identified in warm water or in post-bleached
462 colonies [75]. Indeed, *Pocillopora* colonies harbouring *Durisdinium* were found in the
463 most equatorial warm water (as Panama Islands and Guam) but did not share a unique
464 phenotype, which implies two hypotheses: (i) *Pocillopora-Durusdinium* couple can
465 harbour diverse warm adapted/acclimatised phenotypes; (ii) this couple in warm
466 water cannot be systematically an acclimatisation sign of the holobiont but reflect the
467 opportunistic capacity of *Durusdinium* to prolifer in warm water. The latter hypothesis
468 is supported by experiments on symbiotic model cnidarians which have shown that
469 hosts harbouring *Durusdinium* can be unproductive and highly stressed [76].

470 Phenotype signatures of the two coral genera were differently linked to the
471 environment.

472 Our results show that the characteristics of the environment experienced by the
473 colonies at the time of sampling, but also the past climatic events, shape the coral
474 phenotypes of both genera. Nevertheless, *Pocillopora* phenotypes were linked with
475 a large diversity of contemporary environmental factors including biological, physico-
476 chemical, dynamism and climate variables, while *Porites* was mainly only linked to the
477 past climate. The phenotypic responses show few convergences but also many
478 peculiarities between the two genera that have been summed up in table 2.

479 Extreme past and recent cold anomalies (in intensity, duration and frequency) seem
480 to fragilize the *Pocillopora* and *Porites* phenotypes that systematically presented low
481 biomass and high redox state (Table 2). Even if, in the context of global ocean

warming, the impact of heat waves on coral reefs was strongly documented, several studies highlighted the impact of severe cold waves on corals, demonstrating even a stronger effect as well as on modulation of gene expressions [77], than on bleaching or mortality susceptibility [78]. The strong common correlation with sea surface height can also be linked to strong cold upwelled waves reaching the reefs that can increase coral susceptibility [79].

In contrast, the frequency of recent or past SST anomalies (including heat and cold waves) was among the strongest explanatory factors that correlated equally in both species complexes with almost all biomarkers and leading to colonies with low redox state and high biomasses. This link reinforces the statement that recurrent exposures to SST anomalies play an important role in coral acclimatisation [80], reducing the cost of stress response (*i.e.* low redox state) and enhancing coral tissue reserves (*i.e.* high animal biomass). Our results were also in accordance with Hackerott et al. [81] conclusions that stressed the importance of the past climate and especially repeated marine heat and cold waves in the coral sensitivity of massive corals, like Poritidae. This hormesis phenomenon can also explain the overall more stable phenotypes observed in *Porites* ssp.. All together, those data mitigated the prediction of coral reef sensitivity to climate change at least for the two studied species complexes.

In addition, *Porites* spp. and *Pocillopora* spp. shared similar responses to turbidity, light exposure duration and oxygen (Fig.6 and Table 2). The positive correlation between those factors and the animal biomass low redox state revealed an important weight of the nutrient-enriched water in the trophic state of the corals. Several studies have demonstrated that naturally turbid coral reefs exhibit high coral cover with fast-growing coral species [82–84]. Indeed, an increase of suspended particulate matter and light exposure can very likely favour the nutrition state of the corals, thus enhancing their mixotrophic nutrition. This is even more notable in *Pocillopora* phenotypes that are strongly and positively linked with the seawater richness in zoo- and

phytoplankton, suggesting that *Pocillopora* spp. are able to adjust the autotrophic/heterotrophic balance in response to the environment variability with the capacity to maintain or even increase their energy reserves. In addition, some studies have already linked large polyps phenotypes with increased dependence on heterotrophy and stress resistance [85,56,57,86]. We can therefore suggest that this capacity of trophic modulation could explain the extended distribution of *Pocillopora* genus in the Pacific Ocean and its stress resistance.

Finally, our work highlighted a sensitivity of *Pocillopora* colonies to phosphate pollution and acidification. Indeed, phosphate accumulation in the environment was associated with high redox state and small polyps with low symbiont density confirming the sensitivity of *Pocillopora* physiology to this pollutant. Phosphate contamination (mainly due to eutrophication through addition of fertilisers) negatively affects coral traits as skeleton production, reproduction and symbiont photosynthesis [87] but can also provoke increased DNA damages and lipid peroxidation [88]. Finally, carbonate chemistry also exhibited a link with the *Pocillopora* phenotypes harbouring high redox state and low biomass. Branched corals, as the Pocilloporidae, are very sensitive to acidification that provokes a decrease in growth and/or increase in skeletal porosity, see for review[89] but also oxidative stress response [90,91]. The peculiar sensitivity of *Pocillopora* spp. to those environmental factors demonstrates that evaluating coral phenotype across multiple genus/species is vital for projecting biodiversity responses to climate change.

Conclusion

In this work, by comparing the phenotypic signatures of species complexes from the widespread *Pocillopora* and *Porites* genera, we highlighted two different strategies of environmental response that could be synthesised as "the Oak and the Reed" strategies. Indeed, those two species complexes respond to the environment by a

535 contrasting gradient of phenotypic plasticity. *Porites* spp. exhibited more robust
536 phenotypes partially correlated to their genetics and their geographic distribution
537 and strongly shaped by past climatic events. This reduced plasticity is consistent with
538 *Porites* lineages being 'generalists' to a wide range of habitats but potentially limiting,
539 like in an oak, their rapid response to drastic rapid environmental changes. In contrast,
540 *Pocillopora* spp. exhibit a larger phenotypic plasticity strongly influenced by the
541 climate but also by the nutrient richness, the pollution and the carbonate chemistry
542 of the reefs, demonstrating a larger capacity for physiological modulations to cope
543 with global changes. This evidence suggests that, under severe environmental
544 changes, *Pocillopora* spp. would have, like a reed, an extended ability to rapidly
545 modify its physiology (*i.e.* activating antioxidant capacities) allowing it to be resilient
546 to stress while the massive *Porites* spp. studied here, is largely resistant to
547 disturbances by an investment in homeostasis regulation. This interpretation is in line
548 with the finding of *Pocillopora* species showing stronger genetic linkage to the
549 environment than the generalist *Porites* species, which exhibit a broad physiological
550 tolerance that is not very spatially adapted [51].

551 This unique study describing for the first time the extent of coral phenotypic plasticity
552 at an ecological scale never studied before, has important implications in the context
553 of monitoring and management of coral reefs. Indeed, it shows unequivocally that
554 natural populations of corals sharing the same habitat can have diverse responses
555 that are influenced by different environmental parameters. In addition, it helps to
556 highlight the importance of protection efforts in marine protected areas to several
557 coral reef species. Those data would constitute critical elements to be taken into
558 account in predictive ecosystem models especially in the context of climate change.
559 Consequently, it is apparent that the differential coral responses require a global
560 integrative approach to assess past and present contexts of coral reefs development,
561 and hence increase our understanding and our perspectives for coral management
562 and conservation projects.

MATERIAL & METHODS

Unless otherwise specified, all chemicals were obtained from Merck (France).

Animal sampling

Coral colonies of *Pocillopora* spp. and *Porites* spp. [51] were sampled between July 2016 and February 2017 across the Pacific Ocean during the TARA Pacific expedition (see Table S8 for sampling sites and GPS coordinates). They have been sampled according to UNCLOS and CITES permits (see supplementary Text S1) and to the sampling protocol described in Lombard et al.[49]. Briefly, 40 g of coral fragments from 155 *Pocillopora* spp. colonies and 166 *Porites* spp. colonies were sampled from 11 islands (but unfortunately *Pocillopora* samples from Malpelo island have been lost during the shipping), in at least three different sites at around 5 metres depth, and frozen on board in liquid nitrogen. The fragments remained then stored at -20 °C until analysed. The time before freezing varied in respect to the distance between the Tara Goelette and the sampling site, we performed a preliminary and complementary experiment to assess any artifactual results due to the freezing time lag (Supplementary Material and Methods and Fig. S4).

Phenotypic biomarkers assays

Proteins extraction: For each coral sample, a fragment of about 10 g was mechanically grinded to powder with a Qiagen Tissue LyserII at 25HZ for 10 sec. Soluble cytoplasmic protein were extracted by resuspending the obtained powder in a hypo-osmotic lysis buffer consisting of 25 mM 2-[4-(2-hydroxyethyl)piperazin-1-yl]ethanesulfonic acid (HEPES), 5 mM MgCl2, 5 mM 4-dithiothreitol (DTT), 5 mM ethylenediaminetetraaceticacid (EDTA), 2 mM phenylmethylsulfonylfluoride (PMSF), protease inhibitor cocktail (1 µl/ml) and anti-phosphatase (10 µl/ml) at pH 7.5 (ThermoScientific). Lysates were centrifuged at 12000×g for 5min, and only the

supernatant was recovered containing the animal cytosoluble protein extracts. All extraction steps were performed under constant cooling. The Bradford protocol was followed to determine supernatant protein concentration using bovine serum albumin (BSA) solution (2mg/ml) as standard [92].

Animal and Symbiont biomasses: To assess animal and symbiont biomasses, subsamples (~1 cm^2) of the individual coral fragments were incubated in 4 M sodium hydroxide solution for 1h to 3h [93]. Following the NaOH incubation, the supernatants were used for Symbiobiodiniaceae cell counting using the improved Neubauer hemocytometer and for animal protein concentration by Bradford protein assay. The surface area of the remaining coral fragments was then measured using aluminium foil technique [94]. Animal biomass was expressed in mg of protein per cm^2, and symbiont biomass was expressed in number of cells per mg of protein and per cm^2.

Protein ubiquitination: Ubiquitinated proteins were assayed by dot-blotting 3 µg of *Pocillopora* protein samples and 0.5 µg of *Porites* protein samples on nitrocellulose membranes following Haas & Bright [95]. The membranes were blocked in 5% Milk in PBS-Tween (0.05%) overnight and then incubated with primary antibody (1:1000; mouse mono- and polyubiquitinylated conjugate recombinant, Enzo Life science) and (HRP)-conjugated anti-mouse antibody (1:5000; Bio-Rad) as secondary antibodies. HRP signals were visualised using chemiluminescent substrates (Immobilon classico, Merck) and acquired using a FusionSolo imaging system (Vilber). Levels of spot density were measured using image analysis system G:Box (SynGene). To monitor and quantify the amount of protein actually blotted, the membranes were stained with an amidoblack solution. Amounts of ubiquitinated protein were finally expressed as arbitrary units (AU) per milligrams of protein after complementary normalisation with 1 µg of a unique *Anemonia viridis* standard protein extract blotted in each membrane.

Protein Carbonylation: Carbonylated protein contents were measured using ELISA assay followed by spectrophotometric quantification according to Buss et al.[96]. A total of 0.5 mg/ml of protein were derivatized using dinitrophenylhydrazine (DNP) solution (10 mM in 6 M guanidine hydrochloride and 0.5 M potassium phosphate, pH 2.5). Antibody against DNP component (1:2000) was used as primary antibody and an anti-rabbit IgG peroxidase conjugate (1:3000) was used for detection as secondary antibody. A standard curve of reduced and oxidised BSA was included in each microplate. Derivatized proteins were finally revealed by incubation of the microplate with a solution containing o-phenylenediamine (0.6 mg/ml) and hydrogen peroxide (1:2500) in 50 mM Na_2HPO_4 plus 24 mM citric acid. Absorbances were read at 490 nm by spectrophotometer (Safas, Monaco). Carbonyl contents were expressed as nanomoles per mg of protein.

Antioxidant Capacity: The total antioxidant capacities of protein samples were tested with the total oxidant scavenging capacity (TOSC) assay according to Naguib [97], with modifications allowing measurement in black 96-well microplates (96-wells Grener Bio-One). Protein extracts were diluted in a 75 mM phosphate buffer (pH 7.0) to obtain protein concentrations in the reactive medium between 0.01 and 0.045 mg/mL. The fluorescence signal was obtained by the oxidation of the fluorescent probe (180 nM; 6-carboxylfluorescein) by the peroxyl radical generator (36 mM AAPH (2,2'-azobis (2- amidinopropane) dihydrochloride), and Trolox (6-hydroxy-2,5,7,8-tetramethyl-1-chroman-2-carboxylic acid; 20 µM) was used as antioxidant calibrator for the assay. The fluorescence decay was measured by spectrofluorometer (Safas, Monaco) at an excitation/emission wavelength of 520/495 nm every two minutes for a total duration of 1h. Relative antioxidant activities of protein samples were measured by comparison with Trolox standard and results are reported as µmol Trolox equivalents/mg.

TARA Pacific metadata

To explore the relationships between the measured phenotype data and the genetics and the associated microorganism diversity from the samples and the environment variables from the sampled sites, we used metadata from the TARA Pacific consortium (Table 3). The coral species identification was performed on genome wide markers by Hume et al.[51] and sequencing of divergent genomic fragments[98] and resulted in 5 different identified species within the *Pocillopora* genus and 3 species within the *Porites* genus. For the coral associated microorganisms, on the one hand, we used the Symbiodiniaceae symbiont composition identified by the analysis of ribosomal nuclear ITS2 [99]. Concerning the microbiome, we used the bacterial diversity obtained thanks to ribosomal 16S for bacterial microbiome [68]. Finally, we also considered 101 contemporary (abbreviated to C), recent (R) and historical (H) environmental variables collected during the TARA Pacific expedition [49]. All the environmental variables were classified in four variables categories: Biological, Climate, Dynamism, or Physico-chemical (abbreviated to Bio, Cli, Dyn and Phy respectively). The complete code-names of the environmental variables used in the present study are available in the table S9.

Phenotypic analysis

The phenotypic signature from *Pocillopora* and *Porites*' colonies were analysed through the pipeline summarised in the figure S5.

Data visualisation and exploration

The specific distribution of variance by biomarker was displayed as boxplots by islands or coral species which were generated with the ggplot2 v3.3.5 R package [100]. The integrative phenotypic signal, combining the different biomarkers, was visualised by PCA with a comparison either between the two genera or within a given genus

665 and displaying island or species belonging, with FactoMineR v2.4 package [101] and
666 factoextra v1.0.7 [102].

667 *Statistical analysis*

668 Statistical pipelines and figures were made with R v4.1.1 [103].

669 *Global variation of biomarkers through the Pacific Ocean*: Biomarker by biomarker,
670 distributions were compared by island or by species with Kruskall-Wallis' test and a
671 Dunn's test as post-hoc when necessary with the dunn.test v1.3.5 package [104], after
672 filtering individuals with missing data. Because of the complementary and the
673 eventual redundancy of some of the biomarkers used, we tested their correlation with
674 the Kendall's tau before using all the biomarkers into the integrative phenotypic
675 signal (Fig. S6). We hence conserved all of them except the symbiont biomass
676 reported by the surface of tissue.

677 *Identification of putative drivers of coral phenotypic responses*: The comparison
678 between the coral genera, or among the islands and the coral species of a whole
679 phenotypic signature was tested with a PERMANOVA (vegan 2.5-7[105] and
680 pairwiseAdonis v0.4[106] packages using Bray-Curtis distance). This last analysis was run
681 3 times to ensure the repeatability of the outputs. To limit the number of false positive
682 comparisons in the pairwise analyses, we applied a false discovery rate correction
683 using the method described by Benjamini & Hochberg [107], implemented in the
684 function. The comparison at the coral genus scale was completed with a test of
685 homogeneity of dispersion with *betadisper* function in vegan v2.5-7 [105]. To estimate
686 the influence of the origin island, coral species belonging or the symbiotic diversity
687 of coral, the percentage of explained variance by each was measured with
688 variancePartition v1.23.4 package [108]. We considered only coral colonies from islands
689 containing more than one coral species per genus to limit bias (*i.e.* 87 *Pocillopora*
690 colonies and 96 *Porites* colonies). An additional analysis was performed within coral

691 species to determine a possible correlation between phenotypic and genetic
692 distances (Mantel's tests computed with the package vegan v2.5-7[105]).

693 *Biomarkers and environment variables correlation:* The influence of the environment
694 on the phenotypic signal was assessed using 101 environmental variables. To identify
695 correlations among the biomarkers and environmental variables, an sPLS (sparse
696 Partial Least Squares) analysis was performed (mixOmics v6.17.29 package[109]). The
697 sPLS analysis allowed us to model multiple correlated response variables, considering
698 the biomarkers as multiple responses and the environmental variables as multiple
699 predictors of the coral phenotypes. Briefly, the values (from biomarkers and
700 environmental data) were first turned into absolute values and then transformed with
701 BoxCox transformation (caret v6.0-90 [110]) tending toward normal distribution. The
702 correlation among the predictor variables (here the environmental data) and the
703 response variables (here the biomarkers) was measured in regression mode. Only
704 20% of the most correlated variables for the two components of the analysis were
705 retained, *i.e.* a maximum of 20 for each component. We also added a correlation
706 coefficient cut-off of 0.3 to highlight the strongest correlations. Then the common
707 environmental variables between *Pocillopora* spp. and *Porites* spp. were identified
708 with ggvenn v0.1.9 [111] and compared for each biomarker.

709 DATA AVAILABILITY

710 Data generated during the study are available in the public repository
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The authors declare no competing interests.

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REFERENCES

1. Johnson, N. A. *et al.* Integrative taxonomy resolves taxonomic uncertainty for freshwater mussels being considered for protection under the U.S. Endangered Species Act. *Sci. Rep.* **8**, 15892 (2018).
2. Cooley, S. *et al.* Oceans and Coastal Ecosystems and their Services. in *IPCC AR6 WGII* (Cambridge University Press, 2022).
3. Bulgin, C. E., Merchant, C. J. & Ferreira, D. Tendencies, variability and persistence of sea surface temperature anomalies. *Sci. Rep.* **10**, 7986 (2020).
4. Alexander, M. A., Shin, S.-I. & Battisti, D. S. The Influence of the Trend, Basin Interactions, and Ocean Dynamics on Tropical Ocean Prediction. *Geophys. Res. Lett.* **49**, e2021GL096120 (2022).
5. Muir, P. R., Marshall, P. A., Abdulla, A. & Aguirre, J. D. Species identity and depth predict bleaching severity in reef-building corals: shall the deep inherit the reef? *Proc. R. Soc. B Biol. Sci.* **284**, 20171551 (2017).
6. McClanahan, T. R. *et al.* Large geographic variability in the resistance of corals to thermal stress. *Glob. Ecol. Biogeogr.* **29**, 2229–2247 (2020).
7. Hoegh-Guldberg, O., Kennedy, E. V., Beyer, H. L., McClennen, C. & Possingham, H. P. Securing a Long-term Future for Coral Reefs. *Trends Ecol. Evol.* **33**, 936–944 (2018).
8. Barshis, D. J. *et al.* Protein expression and genetic structure of the coral Porites lobata in an environmentally extreme Samoan back reef: does host genotype limit phenotypic plasticity? *Mol. Ecol.* **19**, 1705–1720 (2010).
9. Polato, N. R., Altman, N. S. & Baums, I. B. Variation in the transcriptional response of threatened coral larvae to elevated temperatures. *Mol. Ecol.* **22**, 1366–1382 (2013).
10. Pinzón C. Jorge H., Beach-Letendre Joshuah, Weil Ernesto, & Mydlarz Laura D. Relationship between Phylogeny and Immunity Suggests Older Caribbean Coral Lineages Are More Resistant to Disease. *PLOS ONE* **9**, e104787 (2014).
11. Thinesh, T., Meenatchi, R., Jose, P. A., Kiran, G. S. & Selvin, J. Differential bleaching and recovery pattern of southeast Indian coral reef to 2016 global mass bleaching event: Occurrence of stress-tolerant symbiont Durusdinium (Clade D) in corals of Palk Bay. *Mar. Pollut. Bull.* **145**, 287–294 (2019).
12. Williams, S. D. & Patterson, M. R. Resistance and robustness of the global coral–symbiont network. *Ecology* **101**, e02990 (2020).
13. Forsman, Z. H., Ritson-Williams, R., Tisthammer, K. H., Knapp, I. S. S. & Toonen, R. J. Host-symbiont coevolution, cryptic structure, and bleaching susceptibility, in a coral species complex (Scleractinia; Poritidae). *Sci. Rep.* **10**, 16995 (2020).
14. Vega-Thurber, R. *et al.* Deciphering Coral Disease Dynamics: Integrating Host, Microbiome, and the Changing Environment. *Front. Ecol. Evol.* **8**, (2020).
15. Wiedenmann, J. *et al.* Nutrient enrichment can increase the susceptibility of reef corals to bleaching. *Nat. Clim. Change* **3**, 160–164 (2012).

16. Morris, L. A., Voolstra, C. R., Quigley, K. M., Bourne, D. G. & Bay, L. K. Nutrient Availability and Metabolism Affect the Stability of Coral–Symbiodiniaceae Symbioses. *Trends Microbiol.* **27**, 678–689 (2019).
17. DeCarlo, T. M. *et al.* Nutrient-supplying ocean currents modulate coral bleaching susceptibility. *Sci. Adv.* **6**, eabc5493 (2020).
18. Alderdice, R. *et al.* Divergent expression of hypoxia response systems under deoxygenation in reef-forming corals aligns with bleaching susceptibility. *Glob. Change Biol.* **27**, 312–326 (2021).
19. Altieri, A. H., Johnson, M. D., Swaminathan, S. D., Nelson, H. R. & Gedan, K. B. Resilience of Tropical Ecosystems to Ocean Deoxygenation. *Trends Ecol. Evol.* **36**, 227–238 (2021).
20. Grottoli, A. G. *et al.* The cumulative impact of annual coral bleaching can turn some coral species winners into losers. *Glob. Change Biol.* **20**, 3823–3833 (2014).
21. Sully, S., Burkepile, D. E., Donovan, M. K., Hodgson, G. & van Woesik, R. A global analysis of coral bleaching over the past two decades. *Nat. Commun.* **10**, 1264 (2019).
22. McClanahan, T. R. *et al.* Temperature patterns and mechanisms influencing coral bleaching during the 2016 El Niño. *Nat. Clim. Change* **9**, 845–851 (2019).
23. Todd, P. A. Morphological plasticity in scleractinian corals. *Biol. Rev.* **83**, 315–337 (2008).
24. Anthony, K. R. & Hoegh-Guldberg, O. Kinetics of photoacclimation in corals. *Oecologia* **134**, 23–31 (2003).
25. Iluz, D. & Dubinsky, Z. Coral photobiology: new light on old views. *Zoology* **118**, 71–78 (2015).
26. Muscatine, L., R. McCloskey, L. & E. Marian, R. Estimating the daily contribution of carbon from zooxanthellae to coral animal respiration1. *Limnol. Oceanogr.* **26**, 601–611 (1981).
27. Suggett, D. J. & Smith, D. J. Coral bleaching patterns are the outcome of complex biological and environmental networking. *Glob. Change Biol.* **26**, 68–79 (2020).
28. Parkinson, J. E. *et al.* Molecular tools for coral reef restoration: Beyond biomarker discovery. *Conserv. Lett.* **13**, e12687 (2020).
29. Davy, S. K., Allemand, D. & Weis, V. M. Cell Biology of Cnidarian-Dinoflagellate Symbiosis. *Microbiol. Mol. Biol. Rev.* **76**, 229–261 (2012).
30. Brown, B., Dunne, R., Goodson, M. & Douglas, A. Experience shapes the susceptibility of a reef coral to bleaching. *Coral Reefs* **21**, 119–126 (2002).
31. Downs, C. A. *et al.* Oxidative stress and seasonal coral bleaching. *Free Radic. Biol. Med.* **33**, 533–543 (2002).
32. Lesser, M. P. & Farrell, J. H. Exposure to solar radiation increases damage to both host tissues and algal symbionts of corals during thermal stress. *Coral Reefs* **23**, 367–377 (2004).
33. Richier, S. *et al.* Oxidative stress and apoptotic events during thermal stress in

the symbiotic sea anemone, *Anemonia viridis*. *FEBS J.* **273**, 4186–4198 (2006).
34. Richier, S. *et al.* Depth-dependant response to light of the reef building coral, Pocillopora verrucosa: Implication of oxidative stress. *J. Exp. Mar. Biol. Ecol.* **357**, 48–56 (2008).
35. Pey, A., Zamoum, T., Allemand, D., Furla, P. & Merle, P.-L. Depth-dependant thermotolerance of the symbiotic Mediterranean gorgonian Eunicella singularis: Evidence from cellular stress markers. *J. Exp. Mar. Biol. Ecol.* **404**, 73–78 (2011).
36. Krueger, T. *et al.* Differential coral bleaching—Contrasting the activity and response of enzymatic antioxidants in symbiotic partners under thermal stress. *Comp. Biochem. Physiol. A. Mol. Integr. Physiol.* **190**, 15–25 (2015).
37. Dias, M. *et al.* Oxidative stress on scleractinian coral fragments following exposure to high temperature and low salinity. *Ecol. Indic.* **107**, 105586 (2019).
38. Marangoni, L. F. de B. *et al.* Peroxynitrite Generation and Increased Heterotrophic Capacity Are Linked to the Disruption of the Coral–Dinoflagellate Symbiosis in a Scleractinian and Hydrocoral Species. *Microorganisms* **7**, 426 (2019).
39. Planes, S. *et al.* The Tara Pacific expedition-A pan-ecosystemic approach of the '-omics' complexity of coral reef holobionts across the Pacific Ocean. *PLoS Biol.* **17**, e3000483 (2019).
40. Darling, E. S., Alvarez-Filip, L., Oliver, T. A., McClanahan, T. R. & Côté, I. M. Evaluating life-history strategies of reef corals from species traits. *Ecol. Lett.* **15**, 1378–1386 (2012).
41. Bythell, J. C., Brown, B. E. & Kirkwood, T. B. L. Do reef corals age? *Biol. Rev.* **93**, 1192–1202 (2018).
42. Stat, M., Pochon, X., Cowie, R. O. M. & Gates, R. D. Specificity in communities of Symbiodinium in corals from Johnston Atoll. *Mar. Ecol. Prog. Ser.* **386**, 83–96 (2009).
43. Cunning, R., Glynn, P. W. & Baker, A. C. Flexible associations between Pocillopora corals and Symbiodinium limit utility of symbiosis ecology in defining species. *Coral Reefs* **32**, 795–801 (2013).
44. Ziegler, M., Roder, C., Büchel, C. & Voolstra, C. R. Niche acclimatization in Red Sea corals is dependent on flexibility of host-symbiont association. *Mar. Ecol. Prog. Ser.* **533**, 149–161 (2015).
45. Rouzé, H., Lecellier, G., Pochon, X., Torda, G. & Berteaux-Lecellier, V. Unique quantitative Symbiodiniaceae signature of coral colonies revealed through spatio-temporal survey in Moorea. *Sci. Rep.* **9**, 1–11 (2019).
46. Turnham, K. E., Wham, D. C., Sampayo, E. & LaJeunesse, T. C. Mutualistic microalgae co-diversify with reef corals that acquire symbionts during egg development. *ISME J.* **15**, 3271–3285 (2021).
47. Armstrong, E. J. *et al.* Transcriptomic plasticity and symbiont shuffling underpin Pocillopora acclimatization across heat-stress regimes in the Pacific Ocean. 2021.11.12.468330 (2021) doi:https://doi.org/10.1101/2021.11.12.468330.

48. Smith, A. *et al.* Field measurements of a massive Porites coral at Goolboodi (Orpheus Island), Great Barrier Reef. *Sci. Rep.* **11**, 15334 (2021).
49. Lombard, F. *et al.* Open science resources from the Tara Pacific expedition across coral reef and surface ocean ecosystems. 2022.05.25.493210 (2022) doi:10.1101/2022.05.25.493210.
50. Belser, C. *et al.* Integrative omics framework for characterization of coral reef ecosystems from the Tara Pacific expedition. Preprint at https://doi.org/10.48550/arXiv.2207.02475 (2022).
51. Hume, B. C. C. *et al.* Disparate patterns of genetic divergence in three widespread corals across a pan-Pacific environmental gradient highlights species-specific adaptation trajectories. (2022) doi:https://doi.org/10.1101/2022.10.13.512013.
52. Barnes, D. J. & Lough, J. M. Systematic variations in the depth of skeleton occupied by coral tissue in massive colonies of Porites from the Great barrier reef. *J. Exp. Mar. Biol. Ecol.* **159**, 113–128 (1992).
53. Fitt, W. K. *et al.* Response of two species of Indo-Pacific corals, Porites cylindrica and Stylophora pistillata, to short-term thermal stress: The host does matter in determining the tolerance of corals to bleaching. *J. Exp. Mar. Biol. Ecol.* **373**, 102–110 (2009).
54. Grottoli, A. G., Rodrigues, L. J. & Palardy, J. E. Heterotrophic plasticity and resilience in bleached corals. *Nature* **440**, 1186–1189 (2006).
55. Qin, Z., Yu, K., Liang, Y., Chen, B. & Huang, X. Latitudinal variation in reef coral tissue thickness in the South China Sea: Potential linkage with coral tolerance to environmental stress. *Sci. Total Environ.* **711**, 134610 (2020).
56. Houlbrèque, F. & Ferrier-Pagès, C. Heterotrophy in Tropical Scleractinian Corals. *Biol. Rev.* **84**, 1–17 (2009).
57. Levas, S. J., Grottoli, A. G., Hughes, A., Osburn, C. L. & Matsui, Y. Physiological and Biogeochemical Traits of Bleaching and Recovery in the Mounding Species of Coral Porites lobata: Implications for Resilience in Mounding Corals. *PLOS ONE* **8**, e63267 (2013).
58. Thornhill, D. J. *et al.* A Connection between Colony Biomass and Death in Caribbean Reef-Building Corals. *PLOS ONE* **6**, e29535 (2011).
59. Tivey, T. R., Parkinson, J. E. & Weis, V. M. Host and Symbiont Cell Cycle Coordination Is Mediated by Symbiotic State, Nutrition, and Partner Identity in a Model Cnidarian-Dinoflagellate Symbiosis. *mBio* **11**, e02626-19, /mbio/11/2/mBio.02626-19.atom (2020).
60. Wooldridge, S. A. Excess seawater nutrients, enlarged algal symbiont densities and bleaching sensitive reef locations: 1. Identifying thresholds of concern for the Great Barrier Reef, Australia. *Mar. Pollut. Bull.* **152**, 107667 (2020).
61. Richier, S., Furla, P., Plantivaux, A., Merle, P.-L. & Allemand, D. Symbiosis-induced adaptation to oxidative stress. *J. Exp. Biol.* **208**, 277–285 (2005).
62. Krueger, T. *et al.* Antioxidant plasticity and thermal sensitivity in four types of

Symbiodinium sp. *J. Phycol.* **50**, 1035–1047 (2014).
63. Baird, A. H., Guest, J. R. & Willis, B. L. Systematic and Biogeographical Patterns in the Reproductive Biology of Scleractinian Corals. *Annu. Rev. Ecol. Evol. Syst.* **40**, 551–571 (2009).
64. Finkel, T. & Holbrook, N. J. Oxidants, oxidative stress and the biology of ageing. *Nature* **408**, 239–247 (2000).
65. Ezzat, L., Merle, P.-L., Furla, P., Buttler, A. & Ferrier-Pagès, C. The Response of the Mediterranean Gorgonian Eunicella singularis to Thermal Stress Is Independent of Its Nutritional Regime. *PLOS ONE* **8**, e64370 (2013).
66. Zhou, Z. *et al.* Suppression of NF-κB signal pathway by NLRC3-like protein in stony coral Acropora aculeus under heat stress. *Fish Shellfish Immunol.* **67**, 322–330 (2017).
67. Wright, R. M. *et al.* Intraspecific differences in molecular stress responses and coral pathobiome contribute to mortality under bacterial challenge in Acropora millepora. *Sci. Rep.* **7**, 2609 (2017).
68. Galand, P. E. *et al.* Diversity of the Pacific Ocean coral reef microbiome. *Ref NCOMMS-22-40279-T* (2022).
69. Santoro, E. P. *et al.* Coral microbiome manipulation elicits metabolic and genetic restructuring to mitigate heat stress and evade mortality. *Sci. Adv.* **7**, eabg3088 (2021).
70. Combosch, D. J. & Vollmer, S. V. Population Genetics of an Ecosystem-Defining Reef Coral Pocillopora damicornis in the Tropical Eastern Pacific. *PLOS ONE* **6**, e21200 (2011).
71. Glynn, P. W., Manzello, D. P. & Enochs, I. C. *Coral Reefs of the Eastern Tropical Pacific: Persistence and Loss in a Dynamic Environment*. (Springer, 2016).
72. Bosserelle, P. *et al. Niue marine ecological surveys, 2016 and 2017; available on https://doi.org/10.1101/2021.11.12.468330*. https://apo.org.au/node/228031 (2018).
73. Ziegler, M. *et al.* Status of coral reefs of Upolu (Independent State of Samoa) in the South West Pacific and recommendations to promote resilience and recovery of coastal ecosystems. *Mar. Pollut. Bull.* **129**, 392–398 (2018).
74. McGinty, E. S., Pieczonka, J. & Mydlarz, L. D. Variations in Reactive Oxygen Release and Antioxidant Activity in Multiple Symbiodinium Types in Response to Elevated Temperature. *Microb. Ecol.* **64**, 1000–1007 (2012).
75. Berkelmans, R. & Oppen, M. J. H. van. The role of zooxanthellae in the thermal tolerance of corals: a 'nugget of hope' for coral reefs in an era of climate change. *Proc. R. Soc. Lond. B Biol. Sci.* **273**, 2305–2312 (2006).
76. Matthews, J. L. *et al.* Partner switching and metabolic flux in a model cnidarian–dinoflagellate symbiosis. *Proc. R. Soc. B Biol. Sci.* **285**, 20182336 (2018).
77. Wuitchik, D. M. *et al.* Characterizing environmental stress responses of aposymbiotic *Astrangia poculata* to divergent thermal challenges. *Mol. Ecol.* **30**, 5064–5079 (2021).

78. Saxby, T., Dennison, W. C. & Hoegh-Guldberg, O. Photosynthetic responses of the coral Montipora digitata to cold temperature stress. *Mar. Ecol. Prog. Ser.* **248**, 85–97 (2003).
79. DeCarlo, T. M. & Harrison, H. B. An enigmatic decoupling between heat stress and coral bleaching on the Great Barrier Reef. *PeerJ* **7**, e7473 (2019).
80. Ip, J. C.-H., Zhang, Y., Xie, J. Y., Yeung, Y. H. & Qiu, J.-W. Comparative transcriptomics of two coral holobionts collected during the 2017 El Niño heat wave reveal differential stress response mechanisms. *Mar. Pollut. Bull.* **182**, 114017 (2022).
81. Hackerott, S., Martell, H. A. & Eirin-Lopez, J. M. Coral environmental memory: causes, mechanisms, and consequences for future reefs. *Trends Ecol. Evol.* **36**, 1011–1023 (2021).
82. Browne, N. K., Smithers, S. G. & Perry, C. T. Coral reefs of the turbid inner-shelf of the Great Barrier Reef, Australia: An environmental and geomorphic perspective on their occurrence, composition and growth. *Earth-Sci. Rev.* **115**, 1–20 (2012).
83. Browne, N. K., Precht, E., Last, K. S. & Todd, P. A. Photo-physiological costs associated with acute sediment stress events in three near-shore turbid water corals. *Mar. Ecol. Prog. Ser.* **502**, 129–143 (2014).
84. Morgan, K. M., Perry, C. T., Smithers, S. G., Johnson, J. A. & Daniell, J. J. Evidence of extensive reef development and high coral cover in nearshore environments: implications for understanding coral adaptation in turbid settings. *Sci. Rep.* **6**, 29616 (2016).
85. Alamaru, A., Loya, Y., Brokovich, E., Yam, R. & Shemesh, A. Carbon and nitrogen utilization in two species of Red Sea corals along a depth gradient: Insights from stable isotope analysis of total organic material and lipids. *Geochim. Cosmochim. Acta* **73**, 5333–5342 (2009).
86. Conti-Jerpe, I. E. *et al.* Trophic strategy and bleaching resistance in reef-building corals. *Sci. Adv.* **6**, eaaz5443 (2020).
87. Dunn, J. G., Sammarco, P. W. & LaFleur, G. Effects of phosphate on growth and skeletal density in the scleractinian coral Acropora muricata: A controlled experimental approach. *J. Exp. Mar. Biol. Ecol.* **411**, 34–44 (2012).
88. Kteifan, M., Wahsha, M. & Al-Horani, F. A. Assessing stress response of Stylophora pistillata towards oil and phosphate pollution in the Gulf of Aqaba, using molecular and biochemical markers. *Chem. Ecol.* **33**, 281–294 (2017).
89. Allemand, D. & Osborn, D. Ocean acidification impacts on coral reefs: From sciences to solutions. *Reg. Stud. Mar. Sci.* **28**, 100558 (2019).
90. Soriano-Santiago, O. S., Liñán-Cabello, M. A., Delgadillo-Nuño, M. A., Ortega-Ortiz, C. & Cuevas-Venegas, S. Physiological responses to oxidative stress associated with pH variations in host tissue and zooxanthellae of hermatypic coral Pocillopora capitata. *Mar. Freshw. Behav. Physiol.* **46**, 275–286 (2013).
91. Luz, D. C. *et al.* Oxidative stress in the hydrocoral Millepora alcicornis exposed

to CO2-driven seawater acidification. *Coral Reefs* **37**, 571–579 (2018).
92. Jackson, A. P. A reconciliation analysis of host switching in plant-fungal symbioses. *Evolution* **58**, 1909–1923 (2004).
93. Zamoum, T. & Furla, P. Symbiodinium isolation by NaOH treatment. *J. Exp. Biol.* **215**, 3875–3880 (2012).
94. Hoegh-Guldberg, O. A method for determining the surface area of corals. *Coral Reefs* **7**, 113–116 (1988).
95. Haas, A. L. & Bright, P. M. The immunochemical detection and quantitation of intracellular ubiquitin-protein conjugates. *J. Biol. Chem.* **260**, 12464–12473 (1985).
96. Buss, H., Chan, T. P., Sluis, K. B., Domigan, N. M. & Winterbourn, C. C. Protein Carbonyl Measurement by a Sensitive ELISA Method. *Free Radic. Biol. Med.* **23**, 361–366 (1997).
97. Naguib, Y. M. A. A Fluorometric Method for Measurement of Oxygen Radical-Scavenging Activity of Water-Soluble Antioxidants. *Anal. Biochem.* **284**, 93–98 (2000).
98. Deshuraud, R. *et al.* From genome wide SNPs to genomic islands of differentiation: the quest for species diagnostic markers in two scleractinian corals, *Pocillopora* and *Porites*. (2022) doi:https://doi.org/10.1101/2022.10.21.513203.
99. Hume, B. C. C. *et al.* Tara Pacific ITS2 Symbiodiniaceae data release version 1. (2020) doi:10.5281/zenodo.4061797.
100. Wickham, H. ggplot2: Elegant Graphics for Data Analysis *R package version 3.3.5*. (Springer, 2016).
101. Lê, S., Josse, J. & Husson, F. **FactoMineR**: An *R* Package for Multivariate Analysis. *J. Stat. Softw.* **25**, 1–18 (2008).
102. Kassambara, A. & Mundt, F. factoextra: Extract and Visualize the Results of Multivariate Data Analyses. (2020).
103. R Core Team. R: A Language and Environment for Statistical Computing. (2022).
104. Dinno, A. dunn.test: Dunn's Test of Multiple Comparisons Using Rank Sums. R package version 1.3.5. (2017).
105. Oksanen, J. *et al.* vegan: Community Ecology Package. R package version 2.5-7. (2020).
106. Martinez Arbizu, P. pairwiseAdonis. R package version 0.4. (2021).
107. Benjamini, Y. & Hochberg, Y. Controlling false discovery rate: A practical and powerful approach to multiple testing. *J. R. Soc. Ser. B* **57**, 289–300 (1995).
108. Hoffman, G. E. & Schadt, E. E. variancePartition: interpreting drivers of variation in complex gene expression studies. *BMC Bioinformatics* **17**, 483 (2016).
109. Rohart, F., Gautier, B., Singh, A. & Cao, K.-A. L. mixOmics: An R package for 'omics feature selection and multiple data integration. *PLOS Comput. Biol.* **13**, e1005752 (2017).
110. Kuhn, M. caret: Classification and Regression Training. (2021).

111. Yan, L. ggvenn: Draw Venn Diagram by 'ggplot2'. R package version 0.1.9. (2021).

TABLES

Table 1: Phenotypes partitioning PERMANOVA test

	Df	Sums of Squares	Mean Squares	F Model	R2	Pr(>F)
Pocillopora						
Species	4	7.494	1.8735	14.212	0.27171	5.00E-05
Islands	9	3.7204	0.41338	3.1359	0.13489	5.00E-05
Species x Islands	5	1.0751	0.21502	1.6311	0.03898	0.067
Residuals	116	15.2917	0.13182		0.55442	
Total	134	27.5812			1	
Porites						
Species	2	3.0816	1.54082	20.0167	0.19312	1.00E-04
Islands	10	2.3537	0.23537	3.0576	0.1475	0.0002
Species x Islands	6	0.6689	0.11148	1.4482	0.04192	0.1404
Residuals	128	9.853	0.07698		0.61747	
Total	146	15.9572			1	

Table 2: Summary of the association between coral phenotypes and environments

Genera	Seawater Variables	Environments	Coral Phenotypic Signatures
Pocillopora	**C_Dyn_077**, C_Phy_083, C_Phy_096, C_Phy_098, H_Cli_009, R_Cli_045, C_Cli_084,	-· **Upwelling (Sea Surface Height)** -· Acidification (Carbon dioxide, pH, Alkalinity) -· Pollution (Inorganic Phosphate) -· Climate anomalies (Severe Past and Recent Cold Anomalies)	> High Redox state > Low Biomasses
	C_Bio_086, C_Bio_092, C_Bio_094, **C_Phy_081**, **C_Phy_090**, C_Phy_099, C_Phy_100, **C_Phy_101**, **H_Cli_013**, **H_Cli_015**, **R_Cli_029**, H_Cli_071	-· Phyto- and Zooplankton richness (Chlorophyll, Nanophytoplankton, TotalEukaryot,**Turbidity (KD_{490}),** Biogenic Silica ($SiOH_4$), **Oxygen, Sun**) -· Climate anomalies **(sea surface temperature deviation, Recent Heatwaves,** Past Heat Anomalies, Short resilient time after cold waves)	> Low Redox state > High Biomasses
Porites	**C_Dyn_077,** H_Cli_001, H_Cli_043, H_Cli_044, H_Cli_060, H_Cli_065	-· **Upwelling (Sea Surface Height)** -· Severe Cold Past Anomalies (maximal frequency of cold anomalies, maximal length of cold days, minimal SST)	> High Redox state > Low Animal Biomass
	C_Phy_081, C_Phy_090, C_Phy_101, H_Cli_004, H_Cli_012, **H_Cli_013,** H_Cli_014, **H_Cli_015,** H_Cli_019, H_Cli_047, H_Cli_048, R_Cli_049, H_Cli_052, H_Cli_073	-· Nutrient richness **(Turbidity (KD_{490}), Oxygen, Sun)** -· Climate anomalies (recurrent Past and Recent Cold Anomalies and high fluctuation of seawater temperature)	> low Redox state > High Animal Biomasses
	H_Cli_020, H_Cli_021, H_Cli_025, H_Cli_026, H_Cli_027, H_Cli_028, **R_Cli_029**, H_Cli_030, H_Cli_031, H_Cli_032, H_Cli_033, H_Cli_035, H_Cli_037, H_Cli_039,	-· **Recent** and past heat waves	> low Redox state > High Symbiont Biomasses

In bold, the environmental variables displaying same correlation for Pocillopora's and Porites' biomarkers

Table 3: Metadata from TARA Pacific consortium used in the present study

Dataset	Origin	Terms and abbreviations used	References
Pocillopora species	Species delimitation based on SNPs genotyping	species 1 (*P. effusa*) species 2 (*P. meandrina*) species 3 (*P. verrucosa*) species 4 (*P. grandis*) species 5 (P. SSH5_pver)	Hume et al. (2022)[51] Deshuraud et al.(2022)[9]
Porites species	Species delimitation based on SNPs genotyping	species 1 (K1) species 2 (K2) species 3 (K3)	
Symbiont composition	Symbiodiniaceae diversity characterised by ribosomal nuclear ITS2	10 Pocillopora's ITS2 Clusters 11 *Porites*' ITS2 Clusters	Hume et al. (2020)[99]
Bacterial Microbiome composition	Bacterial microbiome defined on ribosomal 16S marker	5 *Pocillopora*'s 16S clusters 7 *Porites*' 16S clusters	Galand et al. (2022)[68]
Environmental data	Biological (Bio), physico-chemical (Phy), hydrodynamical (Dyn) and climate (Cli) data collected during the TARA Pacific expedition Historical climate data recovered since 2002 to more recent past	101 historical (H), recent (R) or contextual (C) variables	Lombard et al. (2022)[49]

FIGURES

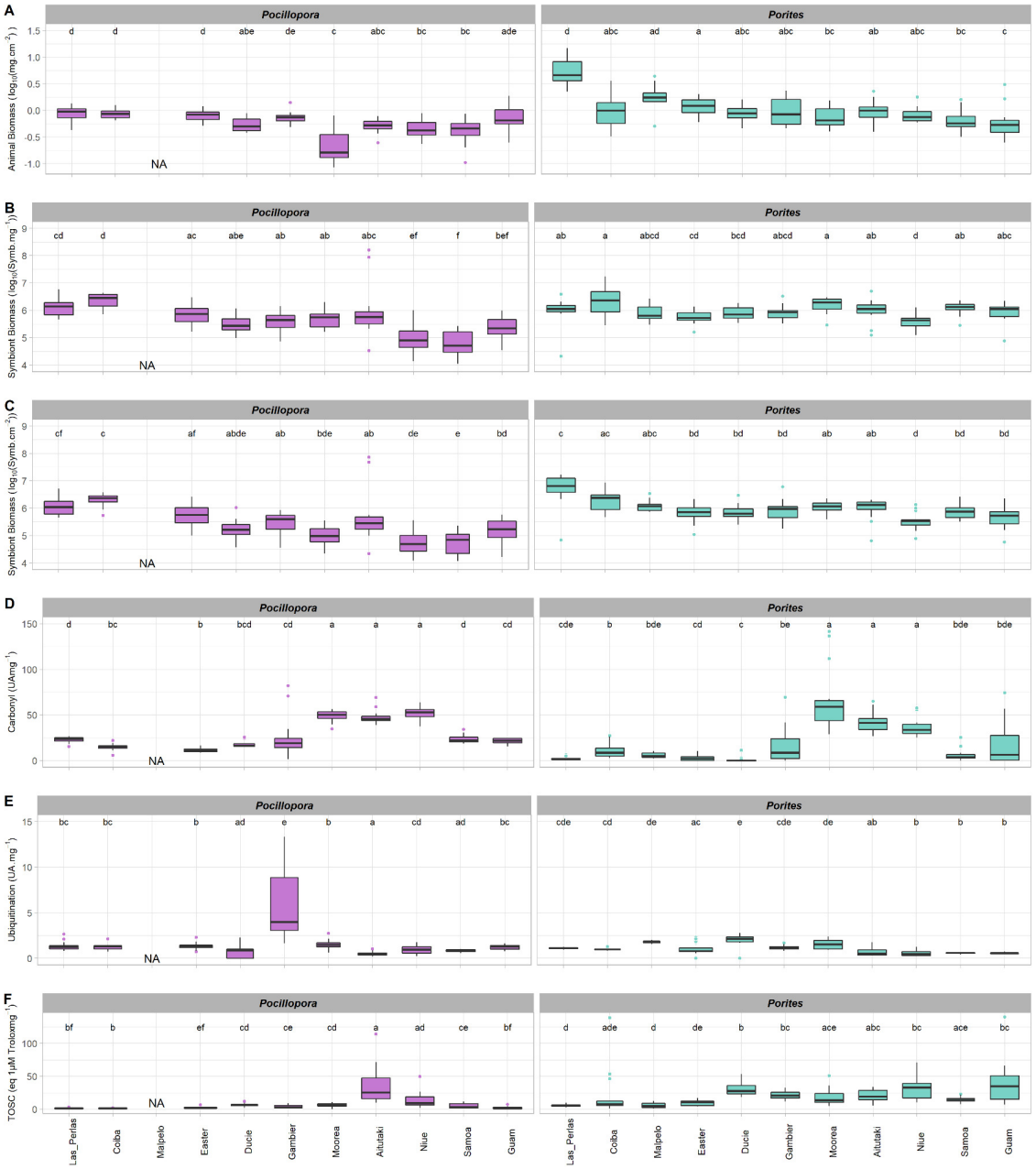

Figure 1 : Biomarker assays of coral colonies sampled in Pacific islands.
Variability of the biomarkers measured in *Pocilllopora* (purple-pink) and *Porites (*cyan*)* genera and in function of sampled islands. **(A)** Animal biomass assay; **(B)** Symbiont biomass assay (normalised by mg of protein); **(C)** Symbiont biomass assay (normalised by cm^2); **(D)** Protein carbonylation; **(E)** Protein ubiquitination; **(F)** Antioxidant capacity. Similar responses are tagged by the same letter on the top of the graph.

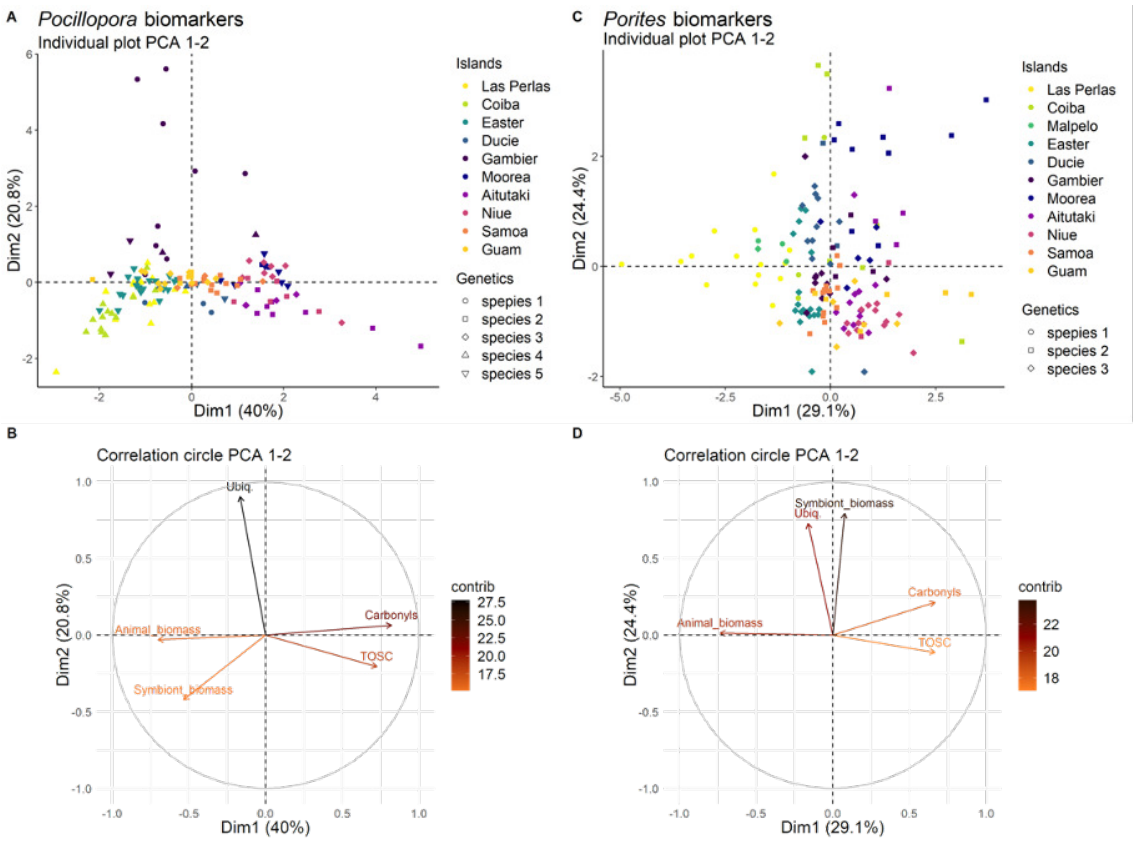

Figure 2: Phenotypic signatures of *Pocillopora* and *Porites* colonies

PCA on biomarkers data from *Pocillopora* spp. **(A,B)** and *Porites* spp. **(C,D)**. The dispersion of the phenotypic signatures (defined by the five measured biomarkers) are shown in **A** and **C**, where the colours represent the island origin, and the shapes represent the species. The importance of each biomarker explaining the PCA distribution of data is shown with correlation circles in **C** and **D**, where the colour scale is the contribution of each biomarker to the plotted PCA dimensions.

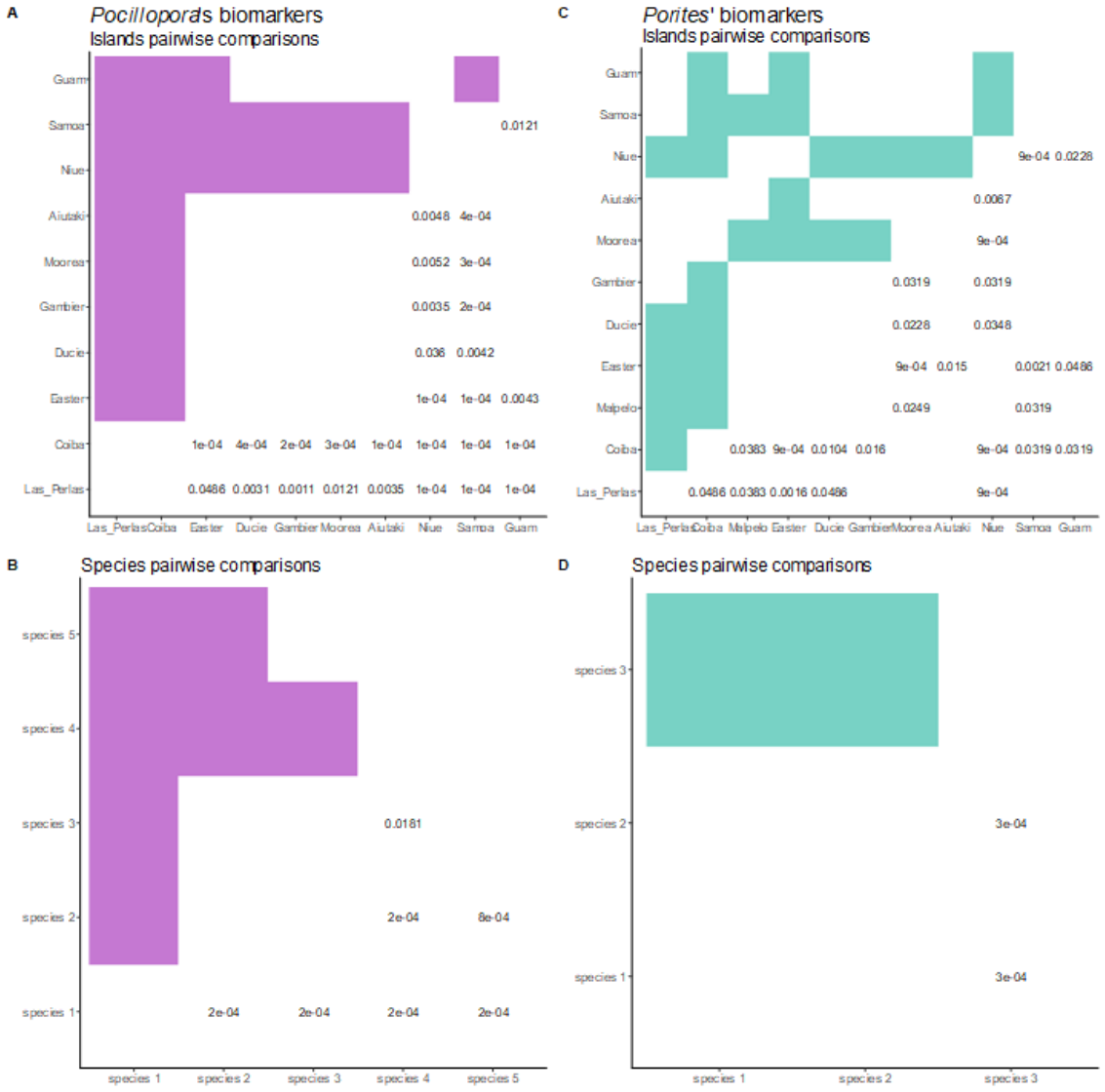

Figure 3: Statistical analysis of phenotypic signature partitioning of *Pocillopora* and *Porites* colonies. Graphical representation of pairwise PERMANOVAs for *Pocillopora*'s phenotypic signatures (purple-pink) **(A,B)** and *Porites* (cyan) **(C,D)**, according to the geographical origin of colonies **(A,C)** or to the species **(B,D)**. Coloured cases indicate statistically significant pairwise differences and the numeric p-value is displayed below the diagonal.

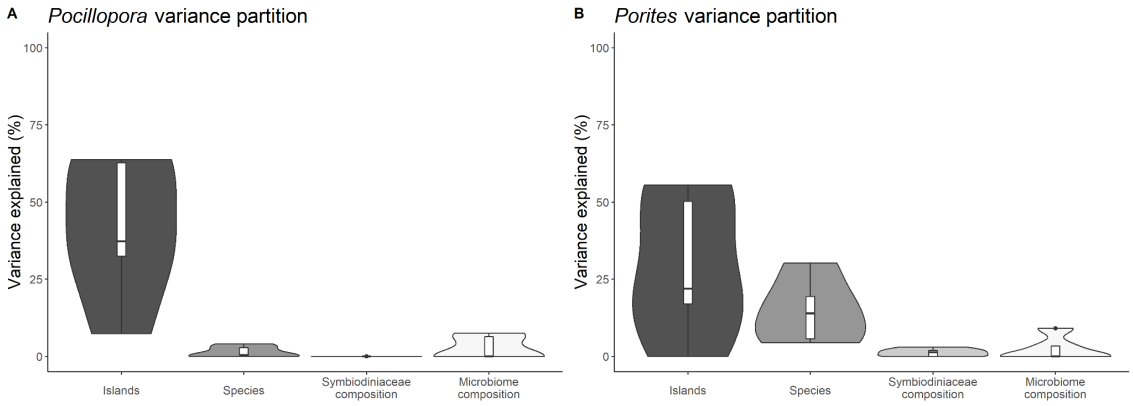

Figure 4: Variance partition of *Pocillopora* and *Porites* phenotypic signatures

Proportion of the variance explained by the different partitions of the phenotypic signature (defined by the five measured biomarkers): origin island (black), host species (grey), Symbiodiniaceae composition (light grey) or the microbiome composition (white) for *Pocillopora* and *Porites* colonies (**A** and **B** respectively).

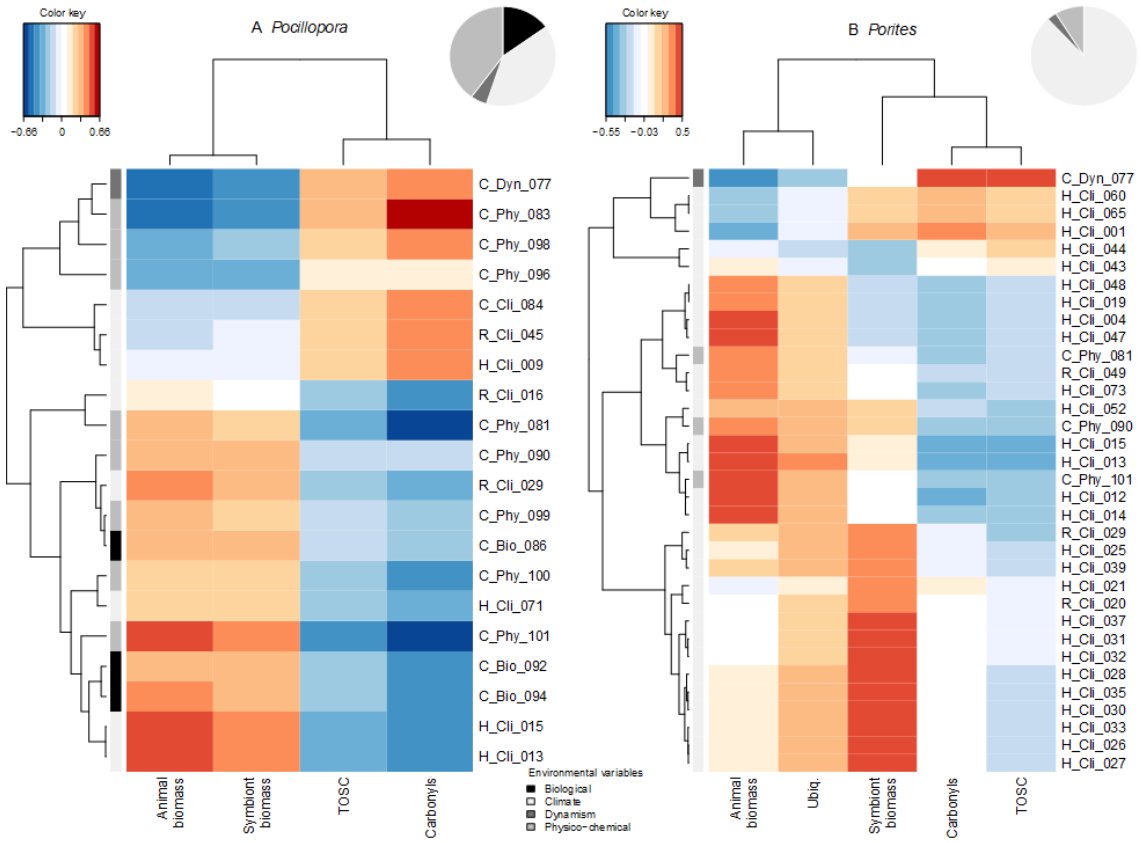

Figure 5: Sparse partial least squares (sPLS) regression of the coral biomarkers and the environment variables

Correlations among *Pocillopora* (A) or *Porites* (B) biomarkers and the environment data are represented with a classification of the environmental data by grey shades and with 3-letters code (from darker to lighter : Biological data (Bio); Hydro- and Aerodynamics data (Dyn); Physico-chemical data (Phy); and Climatic data (Cli)). In addition, environmental data are also identified as historical (H), recent (R) and contemporary to the sampling (C). The corresponding original variable names are available in Table S9. The correlation coefficient values are given by the colour key displayed in the top left and only biomarkers or environmental variables with an absolute coefficient value higher than 0.3 are displayed (leaving the lower values blank). In the top right are represented by pie-charts the proportion of environmental variables correlated with at least one biomarker.

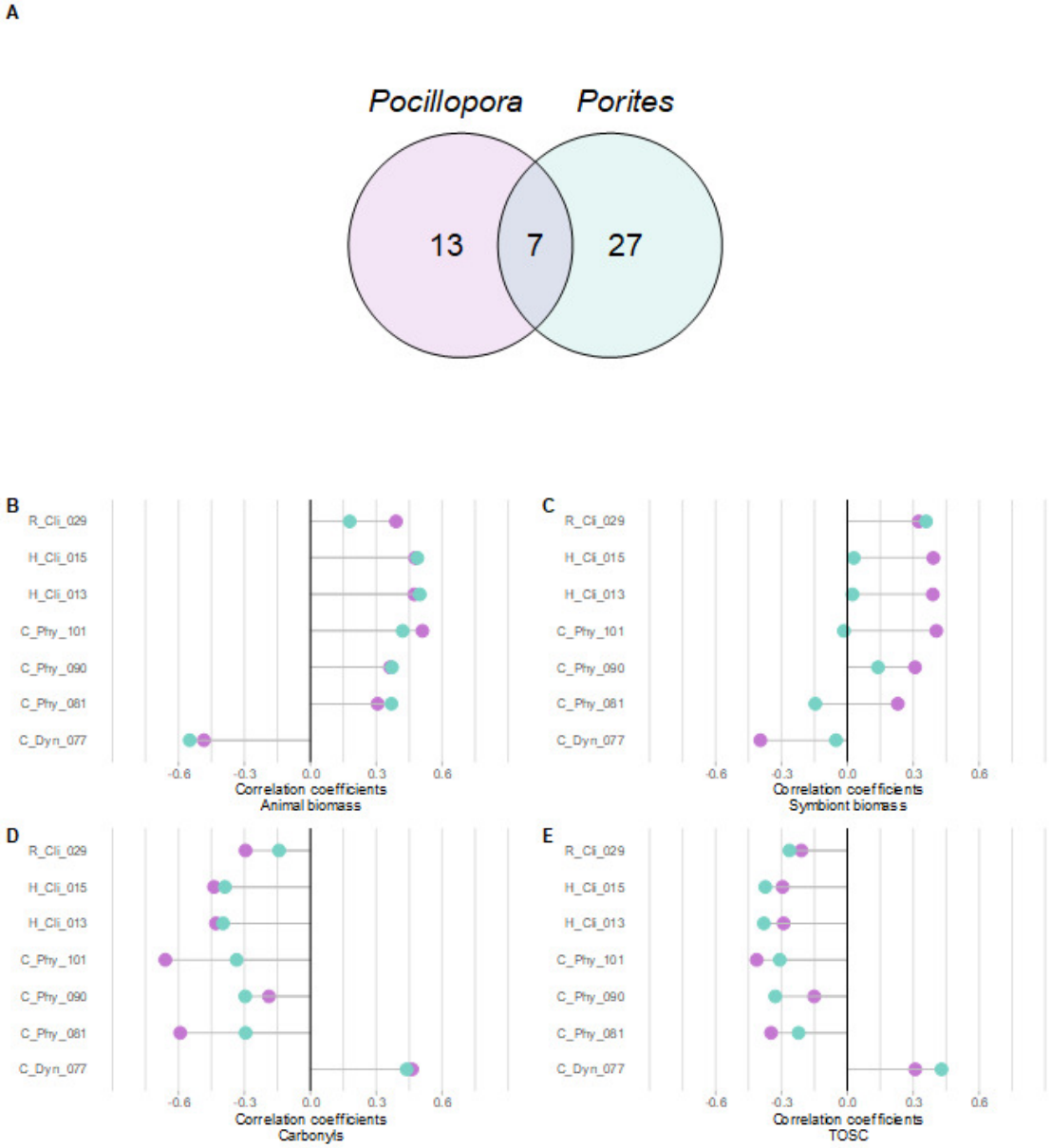

Figure 6: Comparison of the environmental response among the two genera

Number of common and private environmental variables with a correlation coefficient higher than 0.3 for at least one biomarker in *Pocillopora* (purple-pink) or *Porites* (cyan) **(A)**. Details of the correlations between *Pocillopora* and *Porites*' biomarkers with common environmental variables: Animal biomass **(B)**, Symbiont biomass **(C)**, Protein carbonylation **(D)** and Antioxidant capacity **(E)**.

The Oak and the Reed: Two Environmental Response Strategies in Corals from Pacific Islands

Porro & Zamoum et al.

REBUTTAL

We are extremely grateful for the careful reading of our manuscript and the insightful comments and suggestions of the three reviewers that allowed us to improve our manuscript considerably.

We provide here a specific response (in blue) to the reviewers' comments (in black) with the list of changes made to the manuscript. In addition a new version of the manuscript has been submitted in a format where all changes are indicated using change tracking. A second version is also provided without any editing marks.

The line positions mentioned below correspond to the version of the revised manuscript with edition marks.

Point-by-point response to the reviewers' comments

Reviewer #1

Overall;
This manuscript presents data on two different coral genera (at least 3 species within each genus) and their phenotypes over a large transect spanning islands across the Pacific Ocean from Panama to Guam. Phenotypes were composed of multiple biomarkers including animal biomass, symbiont biomass, protein carbonylation, protein ubiquitination and antioxidant capacity. The researchers used non-parametric statistics to determine that biomarkers significantly varied across species and across islands. I applaud the authors for having a large dataset with interesting trends, the geographic scope is amazing.

We thank you for recognizing the importance of this transdisciplinary work, which required significant human and technological efforts. In particular, we would like to thank Dr. Ritson-Williams for the excellent review that allowed us to identify the weaknesses and strengths of our manuscript and to present this substantially revised version.

However, I'm a little confused about the hypothesis you are testing. The way this manuscript reads it seems like you are just fishing for significant interactions between corals and a ton of different variables. This data mining approach will guarantee you will find significant relationships even though they might not be biologically relevant or novel. For instance, you found significant differences in phenotypes among species and among islands. But isn't that expected? Is your null hypothesis that there is no

structure across space? This seems unlikely for the biomarkers of any organism terrestrial or marine. The same being true for the hypothesis that *Pocillopora* and Porites respond with the same phenotypes to environmental conditions, there is plenty of previous literature to show that this is not true. I do think this manuscript is a valuable contribution to our understanding of coral phenotype across broad geographical scales, but I think that the questions here need to be more explicit, probably through careful editing of the writing.

We thank the reviewer for these comments and we have substantially modified the manuscript to be more explicit about the paper objective and hypotheses tested. This has been done by better contextualising the work and rephrasing the outstanding issues and thus the targeted hypotheses. This is particularly visible in the introduction section (specifically in lines 88-102, 112-14 and 156-171) and in the thorough all discussion section.

Briefly, in our work we questioned whether visually healthy colonies from reef-building corals, sampled concomitantly in a wide range of habitats, showed common or divergent phenotypic signatures in response to identical environmental variations.

To answer, we tested those two hypotheses:

1) The use of multiple quantifiable physiological biomarkers is relevant to define a variety of phenotypic signatures in visually healthy colonies.
2) The physiological responses of the two species complexes (that may vary from one genus to the other) are correlated to the same/similar environmental variables"

It is true that it was entirely predictable to see differences in phenotypes between these two species complexes given their life history traits, but it seems to us that it was not predictable to establish whether or not their physiological phenotypes would evolve in the same way in response to the environment. Finally, although it has often been suggested that as a long-lived species, *Porites* is more thermotolerant, our results seem to suggest that this definition may be reductive facing rapid and drastic environmental changes. Therefore the 'weedy' and plastic *Pocillopora* species may allow faster adaptive processes to take place.

I am very concerned about a confounding factor: Are your coral samples are collected during a single time point? How representative of an individuals biology did you capture in your snap shot when you sampled the corals. Also are all of the islands surveyed during a similar time period? I know that you covered a huge spatial distance but don't you think that the timing of sampling might be a confounding variable in your analysis of the biomarkers. For instance, in your results for carbonyl content (line 184), you found a unique signature for the central islands, is this due to season sampled? I don't see any mention of the timing of your sampling or how you might have controlled for this confounding factor. If you sampled Panama in July and Guam in February these are two very different seasons even in the tropics!
I am concerned that this confounding factor stemming from your methods might be driving the results you present here. I think these issues need to be directly addressed in the text of the manuscript. You should discuss the limitations and advantages of your approach. Be clear with your reader, I want to know what you found but also understand the caveats of your data. Additionally on line 567 you should state which island was visited during which month, instead of saying that the sites were evaluated from July 2016 to Feb 2017. Be explicit here that will help to make the limits of your data more transparent.

We thank the reviewer for raising this point. The coral samples were not collected in a single time point but during the TARA PACIFIC expedition. Islands 1 to 10 were sampled between mid-July 2016 and

early December 2016 so over 6 months while the eleventh island GUAM was sampled 2 months later (end of January 2017). This information is in the related manuscript Lombard et al. 2023, but we agree that the information should be recalled here. It is now noted in Table S9.

Furthermore, we strongly agree that seasonality could impact the phenotype of corals, in particular for symbiont density, tissue thickness and redox, which are known to vary with the seasons. We are also aware that, as the expedition spans several seasons, it is difficult to disentangle the effect of season from the geographical effect. Therefore, we placed great importance on correlation with contemporary environmental factors and possible temperature anomalies encountered along the way. The result that *Pocillopora* phenotypes are correlated with several contextual environmental variables, including sea surface temperature (C_Cli_084), might suggest a link with seasonality. However, if we restrict our comparison of island phenotypes to islands sampled on a reduced time scale (e.g. one month), we still find significant differences. For example, the phenotypes of the *Pocillopora* colonies of Moorea and Aiututaki are different from those of Niue and Samoa even though sampling was carried out in less than a month (Figure 4, Table S8 and specific rebuttal figure here below including month of sampling in the map). On the other hand, the similarity of Easter *Pocillopora* phenotypes to the ones from Aitutaki is also observed over different months (September-November) and even different seasons (winter and spring). Nevertheless, the influence of seasonality on the phenotypes of *Pocillopora* spp. colonies sampled in remote islands and at different time scales remains an open question. With the analysis of the full TARA Pacific dataset, we will be able to answer this question because we have resampled the same colonies at different times (seasons and years) and also to have a larger sample with more seasonal replicates. Unfortunately, these samples and results are not yet available.

For *Porites*, it seems clear that, given the small differences in phenotypes observed among the islands, sampling time and seasonality do not influence the phenotype of the colonies (Figure 4 and specific rebuttal figure here below including month of sampling in the map). Furthermore, SPLs analyses show a lack of response of *Porites* colony phenotypes to contemporary markers but rather to historical climatic anomalies, reinforcing the absence of environment fluctuation influences over the year.

In the former version of the manuscrit, we did not address this aspect in our manuscript but we agree with the reviewer that it is a point to be addressed and discussed. We have now addressed this point in the discussion Lines 454- 488 and 533-538.

Rebuttal Figure: Phenotypic signatures of *Pocillopora* and *Porites* colonies. Modified Fig 4 including months of sampling in the map.

Distribution of phenotypic signatures across the corals (purple-pink: *Pocillopora;* cyan: Porites) and the islands. The phenotypic signature by biomarker is represented by scaled average values (from grey: the minimum value; to genus colour: the maximum value) used here as an illustrative "barcode" phenotypic signature. The letters associated to the barcodes are the groups of statistical significance based on pairwise PERMANOVAs (Tables S3 and S5 for island comparisons; Tables S4 and S6 for species comparisons within *Pocillopora* and *Porites* genera respectively). Same letter indicates no significant statistical difference.

Specific Comments

Introduction

Line 148. You have two commas here.

The paragraph has been totally rewritten.

Results

In this section you talk a lot about the differences among the species within the genus. But you have buried this data in the supplemental material, I would like to see it. I am very interested in this variance among the species and considering the extent of your discussion here it is not clear why you are not showing these data.

Line 164. I don't see any indication of different species on Figure 1. Do you mean between genera? Since you are comparing more than two sites you should replace between with among.

We fully agree with the reviewer. We have moved Figure 1S into the main text as Figure 2 and changed the sentence to "Comparison of the different biomarkers across the 11 islands and within the two

genera revealed a heterogeneous pattern both between islands and between species (Fig. 1 and 2)" (Line 178).

Discussion

Overall, the discussion is very long. It is so long that I got distracted from the message. I think the clarity of your manuscript would really benefit from some careful editing of this section to really highlight your results and their impact on our understanding of coral biology. For instance, the paragraph starting on line 343 is not wrong but really just provides background to your study, I don't read a lot of your data in this paragraph, except maybe the last sentence, couldn't you delete most of this and move the last sentence to the paragraph above?

We agree with the reviewer and have made considerable efforts to reduce the overall discussion. Specifically, we have reduced this paragraph by eliminating some of the general state of the art on coral biology or moving it to a more appropriate introductory session. This session is now significantly reduced (line 339-400)

Your title and conclusions highlight your comparison between oaks and reeds (which I do think is illustrative), why haven't you incorporated that into your whole discussion? I see multiple places in your discussion where you are comparing the biology of *Pocillopora* and *Porites* where this comparison would be appropriate to mention.

We totally agree with the reviewer that this comparison should be raised throughout the discussion and not just in the conclusion. The discussion has thus changed significantly to introduce this comparison in the different sections.

Line 317-318. This sentence doesn't make sense. Edit for clarity

The sentence has been modified as follows: "In this study, we validated the use of five different biomarkers, never before used together at such large species and geographic scales, to determine the phenotypic profiling of coral colonies" (line 339).

Line 354. Sure protein ubiquitination is a cellular process even in healthy cells, so I guess I'm not totally surprised that it's not terribly informative. But this is interesting since other studies have found it to be important. I think this paragraph could be 50% as long and still as informative, we don't need a review of all the cellular processes that ubiquitination does!

We agree, the paragraph has been significantly reduced (lines 386-400).

Line 422. I think you mean to say "for" instead of "of"

Correct, we changed.

Line 432. Again this paragraph reads really long. Could you shave off 50% to make your message clearer?

We agree, the paragraph has been significantly reduced (lines 520-549) even if, in respect to comment on seasonality influence we have added to sentences.

Line 447. This whole section of writing is saying that you found no impact on phenotype… this could be much shorter.

We agree with the reduction of the whole discussion but we think it is important to argue more when the results do not fit the classical statement: variance in diversity of the microbiome and/or specific Symbiodiniaceae in response to the environment. Therefore, we have moderately reduced this paragraph (about 20%; lines 552-599).

Line 472. This is really interesting to me. And I think it might have something to do with coral longevity. So Pocillopora respond to recent events, and typically they are short lived (10-20years). I think of Pocillopora corals as weedy, spring up fast and survive stress events through multiple generations, and also don't live long. However Porites are linked to long term past climate and they are long lived (20-100's of years). How could a Pocillopora coral reveal any information about past climate events if they were not alive then? I think this paragraph would be a good place to talk about longevity and also include your oak vs reed comparison. This seems pretty central to your results, that these two genera have different traits that support their different life history strategies (think R vs. K selection). And they have different evolutionary histories too, Pocillopora being from the robust clade and Porites belonging to the complex clade. But be careful here, your results support this idea but you are not the first to propose it! I think an informative approach here would be to consider the literature that takes a trait based approach. Have you read: A trait based approach to advance coral reef science, by Madin et al., 2016 TREE 31: 419-428. Or Darling et al., 2012. Evaluating life-history strategies of reef corals from specific traits. Ecology Letters 15:1378-1386. This paper lumps corals into 4 basic "strategies", how do your oak and reed fit into this framework? I think a better synthesis of this literature would help to put your research into the proper context.

We warmly thank Dr. Ritson-Williams for his comments and we have fully followed your advice by incorporating the comparison between 'weedy' and 'stress-tolerant' species in the introduction (lines 91-102) and including the discussion of their specific life history characteristics (lines 489-502). In addition, we also contextualised our study with the article by Madin et al. (2016), which highlighted the need for a quantitative approach to understanding/resolving and predicting the ability of corals to cope with rapid environmental change.

The aspect of longevity is certainly an explanatory feature of life history that could explain the different stress response strategies. With a short generation time, the *Pocillopora* species could respond more quickly to environmental selection pressure. Selection on past generations could have shaped the genetic composition (and hence the phenotypic response) of the colonies found today in different islands with different environmental histories. In contrast, *Porites* species seem to have invested in homeostatic mechanisms that allow them to maintain a robust and less plastic phenotype.

The reviewer also raises the point that we have tested the correlation of *Pocillopora* phenotypes with historical variables that they may not have experienced because of their short lifespan. This is not entirely correct as, it is important to point out, the historical climate variables used here covered a minimum of 52 weeks (R_Cli: recent climate variables) and a maximum of the last 14 years (H_Cli: Historical climate), a scale where we could reasonably suggest that colonies of both complex species were present. The information is better clarified in the materials and methods (lines 830,832; see other point raised by the reviewer below).

Line 488. Ok so your biomarkers show a signal of past SST anomalies. This is something of an ascertainment bias. You are measuring antioxidant responses that we know are modified by temperature. And you found a signal of temperature in your measurements of these biomarkers. Do you see how it would be hard to find anything else? I think a frank discussion of the biomarkers you selected and how those might bias your findings towards temperature stress would be important to include here. But the fact that some of the biomarkers are tracking other environmental conditions is interesting, and you discuss this in the following paragraphs.

We agree with the reviewer's comments and this point is now raised in lines 619-626. Not only redox biomarkers but also biomass biomarkers are known to be sensitive to thermal stress and have been, most of the time, linked to the unhealthy state of the coral such as the bleached state.

However, as stated in the manuscript, we avoided sampling bleached colonies to avoid obvious considerations. Thus, the variability of these biological biomarkers in visually healthy colonies at this geographic scale was less predictable. In addition, there is a limited and sometimes conflicting literature on the biological response of corals to other environmental variables. We then agreed that the correlations identified may have an impact on our scientific community.

Acknowledgements
Line 717. This sentence ends abruptly, I'm not sure what you are trying to say here, maybe you typed the beginning of this sentence twice?

Correct, we modified.

Figures
Figure 3. I'm sorry but I can't figure out what you are trying to communicate with this figure. Why is this important, does it convey critical information for your reader to understand phenotypes in these corals? Maybe a map would be more visually clear?

Figure 3 (now Figure 4) has been completely redesigned retaining the information about the PERMANOVA statistical analysis. In addition, a "barcode" of the phenotype signature (by island and by species) have also been plotted on the maps. We warmly thank the reviewer for this suggestion that allows us to produce a graphical abstract-figure much more pertinent and readable.

Table 3. What type of Porites are these. You have species names in parenthesis for Pocillopora above, but nothing for the Porites. I understand species delimitations are fraught in Porites but I can't tell from this table if you are referring to branching, sub-massive, or massive growth forms. Something here about the species/morphologies would help to clarify the types of Porites you were sampling.

All the *Porites* colonies sampled were massive. As the referee pointed out, at the present state of knowledge, assigning species names to *Porites* genetic lineages is not straightforward and this point is extensively discussed in the paper by Hume et al. (2022) dealing with the same colonies. However, the species delimitation analysis proved that the *Porites* colonies studied here belong to different species that 'look' like *Porites lobata* but are significantly more divergent. To be consistent with Hume et al. (2022), we have chosen to maintain this nomenclature in the table but simplified our figures with the name (species 1, 2, etc).

We have now clarified this in the manuscript, added information on the massive morphotype of the sampled *Porites* in the introduction (lines 147-155) and in the M&M (line 723). In addition, in the supplementary materials, we included a distribution map of the lineages (Figure S5).

Table 2, Figure 5 and 6. Can you replace the codes (R_Cli_029) with the actual variable. Right now it is really difficult to determine which variable you are displaying because your reader does not know these codes. I think this will go a long way in making these tables and figures clearer.

See the answer proposed for figure 6 (next section).

Figure 6. So after digging into your supplemental data I found that H_Cli_13 and H_Cli_15 are measuring SST anomaly, but one is max and one is standard deviation. I understand that you can have multiple variables that co vary in your analysis, but by presenting these two variables in your figure, you are suggesting to your reader they are different. And only after considerable time hunting through your

supplemental material did I find that they are actually very related to each other. I'm not sure the best approach here (this is actually my favorite figure), but I think it will be important to be transparent about what these variables are to your reader, certainly writing the actual variable on the figure (as mentioned above) will help, but it is worth thinking about what you are presenting here and how to best deliver your message to the reader.

Thank you for your suggestion. First of all we added the reference to the table S9 in the legend of the figure 5 (now Fig. 6) to avoid wasting time to find correspondences. Then, we tried to add the names of the variables but that did not efficiently improve the visualisation of the correlations. We hence propose to add symbols to point out the type of the environmental variables in accordance with the global summary displayed in the table 2 in the figures 5 and 6 (now Fig. 6 et 7 respectively); and for the figure 6 (now Fig. 7), we added the variables names in the legend. The variables pointed out are: "Nutrition", "Upwelling", "Acidification", "Pollution", "Warm Anomalies", "Cold Anomalies and Temperature Fluctuations" and "Sea Surface Temperature"

Supplemental Materials

I think being transparent with your data analysis is really important. Your supplemental figures are good and really helpful. I am stuck on Table S9. Here you have a bunch of different environmental variables. Many of them are historic, which I assume means that you found these on some sort of database. For instance, H_Cli_013 is Sea Surface Temperature anomaly, max per day (If I am interpreting your table correctly). Where did this data come from? I don't see any information in the methods or supplemental materials on how/where you got this data from. On line 650 you explain the procedure for these variables, and cite another paper on Biorxiv, and in that manuscript I found the databases and procedures used. I think 2-3 summary sentences after line 650 would go a long ways to making your environmental data analysis more transparent. I understand that your Biorxiv manuscript has all the details but I don't think many of your readers are going to bother with that link. I do think your methods could summarize the procedure so your reader at least has some idea of where these data originated from, and if the reader wanted more information they could track down the Biorxiv manuscript.

We agree with the reviewer that juggling several articles to understand our manuscript is not easy and we agree with him on the need to add information on the provenance of metadata. In lines 812-836 we have included those information.

Reviewer #2 (Remarks to the Author):

Overview: Authors evaluated 5 biomarkers including symbiont density, tissue biomass, protein ubiquitin, carbonylation, and antioxidant capacity in two genera of corals (Porites and Pocillopora) from the Eastern and Western Pacific. They related these findings to SNP profiles, symbiont ITS clusters, microbiome 16S clusters, and physical environmental variables. They then run all the results from these analyses (8 species and 2 genera of corals, 11 islands, Y and Z numbers of 16S and SNP clusters, and 101 environmental variables giving at least 5 * 8 *11 *101 * Y * Z or ~ 44000 different combinations that are run through a variety of statistical algorithms to yield a series of PCA and box plots with various parameters statistically significant or not.

We thank the referee for underlining the amount of work that has been put into this manuscript and with his questions for helping us to improve it.

More importantly, why is this study important? Two main points in the abstract: "We show that corals, even if they share the same habitat and experience the same environmental perturbations, do not display the same strategies of environmental response." This seems self evident simply by examining the morphology of different species of corals. How are these analyses really shedding additional meaningful light on this issue?

With the question "Why this study is important", the reviewer certainly wants to show us that the objectives and hypotheses of the manuscript were not clear. To this end we have made a substantial effort to re-contextualise and re-write the objectives in the introduction and also considerably rework the discussion.

Briefly, in our work we wanted to test whether it was relevant to use macroscopic (easier to measure) and cellular (more sensitive but more difficult to measure) markers to define a variety of phenotypes much more diverse that the subdivision in branched, massive or encrusting. We also wanted to test whether the resolution of the different phenotypes was sufficiently high to differentiate the different stress response strategies of these corals.

Of course, it has already been observed that morphotypes of corals, such as branching and massive corals, often have specific life-traits that often lead to their being subdivided into weedy/competitive and stress tolerant species respectively (Darling et al. 2012; Hackerott et al. 2021), as if the former were automatically losers and the latter winners. Except that their large morphological plasticity makes it sometimes difficult to recognise the species and that it seems very simplistic to define the coral responses to the environment on the basis of morphological traits alone. Moreover, the very fact that they are present and in visually good health in contrasting environments makes us wonder whether there really is a winning or losing strategy.

In this work thanks to the used quantitative physiological biomarkers, we have then compared the cellular phenotypic plasticity between and within these two species complexes in order to clarify their tissular/cellular/molecular plasticity. Focusing also on the associated microorganism (Symbiodiniaceae and bacteria), we then explored in a more holistic way, the putative strategies of response to the environment. In addition, we tried to understand the role of genetics and environment both geographically and in terms of quantitative variables on the definition of these phenotypes.

"Overall, this study sets the scientific and methodological foundation for future integrative studies that aim at understanding differential response strategies deployed by coral reefs to cope with environmental change and facilitating coral reef management and conservation projects all over the world." How, exactly can these results realistically be useful to coral reef managers? For instance, are managers going to be depending on things like carbonylation of proteins or ubiquitin levels to guide management of coral reefs?

Through these questions, the reviewer does not seem convinced of the importance of this study for applied coral reef management. Nevertheless, we argue that such studies can be important for two main reasons:

1) Understanding the sensitivities of reef corals to an environment that can change gradually or rapidly. In the context of management/restoration projects, the choice could be between a reed, which is more sensitive to local disturbances, but whose growth and fecundity allow rapid restocking, and an oak, which is less sensitive to local disturbances, but which will have a slower structuring impact.

2) Highlighting that easy to measure biomarkers as biomass measurements (animal and/or algal) are sufficiently discriminating to reassess the physiological status of some reef corals.

We agree that these arguments have not been presented clearly in the manuscript and we have therefore made a substantive effort to argue in the conclusion of the paper (line 708-717).

This paper reads like an unfocused fishing expedition looking for a question to answer. There might be some useful data lurking somewhere in this MS, but the presentation and analysis certainly does not make this evident.

As explained above, we have modified the manuscript to make the questions and assumptions more explicit.

Results

Lines 171-174: I don't understand what you mean by significant diversity or lack thereof. For instance, for Fig. S1, there are significant differences in parameters between Pocillopora species as well as Porites for all parameters. Is that not significant diversity?

We clarified the sentence by : "Figure 2A shows that despite some significant differences among *Pocillopora* species, no species-specific animal biomass signature was identified. In contrast, all three *Porites* species identified in our sample showed a significant species-specific pattern for animal protein content." (line 187).

Lines 175-183: I'm not clear why you are highlighting symbiont biomass in particular. Looking at Figure 2, there are significant differences for all parameters, islands, and genera. Perhaps condense everything to that one sentence.

In the result session, we described independently the trend of the five biomarkers, with no emphasis on one of those. We started by animal biomass, the symbiont biomass and so on. We described their trend in respect to the island origin (Figure 1) and to the species belonging (Figure 1S, now Figure 2).

Lines 188-190: Again, not sure how that statement jives with what's on Fig 1D or S1D. There are significant differences among lineages and islands/genera.

We clarified the sentence by : "The comparison of carbonyl content in respect to host lineages (Figure 2D) show that despite differences among the *Pocillopora* species, non species-specific response on carbonyl was measured. Contrastingly, the Porites species 2 (present in Central Pacific) had higher carbonyl content than the other two Porites species." (line 207)

Lines 188-193: As above, vague statements that do not jive with figures. In box plots, different letters above a box indicate statistically significant differences.

Yes, the box plots in the figure translates the statistical differences among the islands (Fig1) or the species (Fig2) tested by Kruskall-wallis test followed by a Dunn's test post-hoc. Fig1E shows that there

are differences among the islands-ubiquitin signature but none of the island (except Gambier) has an ubiquitin specific signature.

To gain in clarity and precision we modified the text : "With regard to the protein ubiquitination biomarker, the analyses show a high specific content of ubiquitinated proteins in *Pocillopora from* Gambier, with a median more than 3-time higher than elsewhere and with a significant variance among the sampled colonies (Fig. 1E). Although less pronounced, a low specific amount of ubiquitinated proteins was also observed in Porites colonies from Niue, Samoa and Guam (Fig. 1E). No species specificity was observed for this marker within either species complexes (Fig. 2E)." (line 211).

Line 222: Do you mean different from the other islands?

Correct. We modified it.

Lines 222-224: "The Pocillopora species..." This sentence makes no sense. Different species will inherently have different phenotypes regardless of what analyses you use.
As introduced in line (ex-205), the phenotypes are described on the basis of a signature that integrates the 5 biomarkers analysed. On this basis, we performed a multivariate analysis (PERMANOVA) to compare the phenotypes of the species among them and among the islands. The phenotype signatures are now much more visible in figure 4, where a "barcode" of the phenotype signature (by island and by species) has been plotted on the maps associated with the PERMANOVA results. It turns out that some species have converging phenotypes and are therefore not significantly different. This is the case of *Pocillopora* species 2 and 3 which show a non-significantly different phenotype (wherever they were sampled).

In a more general context, vicariant species may have lost inter fecundity because of genome divergence in isolation, and not because of divergent adaptation to different environments. Such species could still display the same phenotypic response to the environment, if this response is not involved in their divergence.

Line 226: What do you mean by punctually different?

Thanks to the PERMANOVAs, we pointed out a patchy pattern of phenotypic difference/similarity for *Porites* corals. The pairwise comparisons highlighted on-off examples of differentiation and neither a clear geographical gradient nor regional partition. We propose to rephrase as : "but few islands appeared as one-off pairwise differentiation (as Niué or Coiba; Fig. 4 and Table S5)." (Now Line 249).

Figure 1. I'm not understanding here how you disentangle species from islands as a statistical effect. Clearly, Figure 1 shows differences in parameters between islands and differences between species (Fig S1). So is the islands differences a function of islands or islandsXspecies? Were the same species of Pocillopora/Porites sampled for each island?

To clarify the distribution of the different species across the Pacific Ocean, we added a map, now the Figure S5. Considering the possible effect of factor interaction, we tested by PERMANOVA the partition into species (i), or into islands (ii) and finally speciesXinteraction (iii). Because the interaction of the two partitioning factors (species and islands) was not statistically significant neither for *Pocillopora* nor for *Porites* colonies, we went deeper to the pairwise comparisons but analysing independently species and islands. These results were presented in the Table 1 for the global test, and after in the Tables 3, 4, 5 and 6 for the pairwise comparisons.

Methods:
Line 580: Proteins being extracted here are from the entire coral (endoliths, endosymbionts, animal tissues), not just the animal tissues, so "animal cytosoluble protein extracts" is not correct.

We modified by “cytosoluble protein extracts”

Line 596: I think here you mean to say you centrifuged sample, counted symbionts in sediment and quantified protein in supernatant, correct?

Not exactly. Because of their resistance to NAOH treatment, we can use the lysate to count symbionts without centrifugation. The same lysate was used in the Bradford assay to determine the animal biomass. Preliminary data showed that the mg of protein from the symbionts was negligible in the total lysate.

Line 605-613: The anti-mouse antibody....from what animal did it originate?

It was Goat anti-mouse IgG peroxidase conjugate. This information is now added line 780.

If you quantified the protein in your NaOH homogenate, why stain with amido black?

The amido black staining is used to ensure that we do not bias our results because of possible pipetting errors or incomplete protein deposition on the blot membrane.

You said earlier you dot blotted 3 and 0.5 ug of protein, so you must have calculated this from your Bradford assay no? Also why did you do different amounts of protein for each coral genus?

The Dot Blot method is very sensitive to protein overload. Due to the intrinsic molecular composition of each genus/species, the blot must be optimised. In this context, for each coral genus/species, preliminary analyses using a range of protein concentrations were performed to determine the optimal amounts of protein to be blotted. In all cases, the results were accurately normalised to the amount of protein blotted (and thanks to amido black methods).

For standardizing [protein] on dot blot, one normally does a standard curve of serially diluted known concentration of protein standard stained with amido black or coomassie blue ato relativize density of experimental dot.

Absolutely. To ensure comparison of the blotted membranes, further standardisation was carried out with "a range of known stained protein concentrations in each membrane". These known proteins were derived from a single protein extraction from the sea anemone *Anemonia viridis*. The extraction was performed once at the start of the assays and frozen as multiple aliquots to avoid degradation due to freeze/thaw cycles). The standard curve included a range of 0.5 to 4 µg of this protein extract. This information is now clarified in the Materials and Methods, line XX.

I assume you did a conjugate control to make sure your secondary antibody was not tagging the dot blot?

Yes, this is a routine preliminary experiment for all the immunodetection work we do in the laboratory.

Lines 618-620: rabbit was the primary antibody, but what was the animal origin of the secondary antibody?

It was Goat anti-rabbit IgG peroxidase conjugate. This information is now added to line 784.

Line 684: What function?

The adonis function. We implemented this information in the text.

Lines 693-708: Given the non-independence of the comparisons here, how do you account for false discovery rate (see https://pubmed.ncbi.nlm.nih.gov/24831050/) as example.

For all other multiple tests, we indeed performed an fdr correction as described in the “Material and Method” section (using the method described by Benjamini & Hochber [Benjamini, Y. & Hochberg, Y.

Controlling false discovery rate: A practical and powerful approach to multiple testing. J. R. Soc. Ser. B 57, 289–300 (1995)]). Considering specifically the sPLS analysis which is pointed out, it is designed to deal with multicollinear variables and noise. Basically, the filters we used to only conserve the most correlated variables (20 variables for each component and a correlation coefficient higher than 0.3) are the common filters we found in the literature to identify the strongest correlations between biomarker and environmental data [Ingham et al. Microbiome (2019) 7:13; https://doi.org/10.1186/s40168-019-0745-z]. To clarify, we completed the sentence as "The sPLS analysis, designed to treat multicolinear variables and noise, allowed us to model multiple correlated response variables, considering the biomarkers as multiple responses and the environmental variables as multiple predictors of the coral phenotypes."(line 482).

Figure S1: What are the species of corals?

The coral species are presented in the table 3 of the material and methods. However, as the material and method are presented at the end of the manuscript, we propose, for the sake of clarity, to refer to the table 3 in the legend of the Figure 2.

Reviewer #3 (Remarks to the Author):

The manuscript reveals original and relevant work for the coral field by combining data from abiotic and biotic factors to assess how the physiological plasticity of two coral species are mediated by environmental alterations. The findings were however, limited to two coral species in specific locations in the Pacific Ocean. The manuscript is very good but it has 'limitations' that should be better acknowledged/ discussed along the text.

We thank the reviewer for recognizing the originality and importance of this work. We totally agree that we cannot raise conclusions or generality for all reef corals. It is clearly not our wish. However, we provided new insights on two species complexes including in total 8 species (5 Pocilloporids and 3 Poritids).

I pointed a few suggestions in the manuscript pdf. Please see below for additional observations:

We thank the reviewer for his suggestions, all of which we have taken into account.

Please review the use of the word 'biomarker' throughout the manuscript text and figures. In many cases I believe that the word 'proxy' or 'parameter' would be more appropriate.

We agree with the reviewer that the 'biomarkers', 'proxy',' predictor', 'parameters', 'variables' are confusing terms that should be stated from the beginning. In the manuscript we used biomarkers to refer to quantifiable biological indicators. Due to the knowledge of the biological processes in which they are involved, these biomarkers are then considered as proxy/indicator/predictor of these processes. In our work we have then used these multi-biomarkers approaches to define coral phenotypes, interpreting them as a variety of physiological states from fragile (with low biomasses and high redox state) to healthy (with high biomasses and low redox state). In addition, we used environmental parameters to refer to environmental variables measured in the surrounding water.

To stay consistent with these choices of terminology, we have reviewed the manuscript in accordance.

Pls better embase why coral and symbiont biomass are good biomarkers for inferring about coral phenotypic plasticity. It was first stated on L119, but refs. 16 and 29 are not specific for that.

We agree that we didn't use appropriate references. We changed the references in the sentence as followed: "Among them, biomarkers of the trophic coral state, as polyp tissue thickness and/or the hosted symbiont density, have been linked to coral sensitivity to environmental perturbations and reflected the existing nutrient intake by the coral (Fitt et al. 2009; Grottoli et al. 2006; Qin et al. 2020; Wooldridge 2020)" (line 130).

Another example on L327-330 - you mention coral trophic state, which can be inferred, for instance from fatty acid analysis (see Mies et al 2018 on Coral Reefs), which would then be a better biomarker for trophic state than just host/symbiont biomasses.

We deeply agree that fatty acid or even cholesterol analyses would have been a better predictor of the trophic state than the animal and symbiont biomasses variations. However, we have been forced to use a minimum of coral fragments for all analyses. Indeed, this approach allowed us to use only 1 cm^2 of coral to obtain these two biomarkers. In the future, the TARA Pacific Consortium will carry out a metabolomic analysis of all these samples, which will allow us to establish the fatty acid content of the samples and to corroborate or not our results.

Another example of what I mean can be seen on fig 4 - origin island was a parameter for your analysis, but it is not a biomarker.

We totally agree. Even if we did not use the 'biomarker' term to define the diverse partitioning factors presented in figure 4, (now figure 5) we rephrase the legend for sake of clarity.

"Figure 5: Variance partition of Pocillopora and Porites phenotypic signatures
Proportion of the variance explained by the different partitions of the phenotypic signature (defined by the five measured biomarkers). The partitions are island of origin (black), host species (grey), Symbiodiniaceae composition (light grey) or the microbiome composition (white) for Pocillopora and Porites colonies (A and B respectively)."

-Pls add stats to your figs 1 and S1 so that we can better visualize the differences discussed in the text. Since you mentioned fig S1 a lot while presenting your results, maybe you could bring it to the main text or combine it into fig S1 - the main findings presented in these two figures could be combined.

The stats were already in the figs 1 and S1 but we omitted to specifically explain in the legend the statistical tests used. It is now added in the legend. In addition, in line with the comments of the reviewers 1 and 2, we have moved Figure S1 into the body of the manuscript. It now becomes Figure 2.

-I'd remove tables containing only stats numbers for the supplementary material.

Because of the comment of the reviewer #2, we propose to keep the table 1 in the body of the manuscript.

-L68: 'Climate' is not an environmental parameter. Pls rephrase here and be more specific about which parameters you used.

We agree, we modified "climate" by "temperature anomalies".

- Please be consistent in the way you present references throughout the manuscript. They should follow the journal recommendations (see example highlighted/comment in L90). Also, please exclude 'see for review' that appears multiple times when you referred a study throughout the manuscript.

We have corrected the ref citation throughout the manuscript as advised.

-Please check manuscript writing structure (example L148).

We fixed it.

-L116: Pls be more specific explaining which 'biological processes' you meant here and add references.

We have modified the sentence and the two following paragraphs (paragraphs lines 112 and line 128), introducing references to justify the use of the biomarkers analyzed in this work.

-L153: It would be good to have here at the introduction which parameters from your study were monitored to assess the corals phenotypic plasticity.

We agree and deeply modify all the paragraph introducing the studied parameters (lines 161).

-L196-198: Please be more specific when sayin 'low' (L196) and put a number to state how low so that the comparisons you make are more clear. Check that throughout your results.

We modified the sentences as follows: "For *Pocillopora*, the colonies from the two Panama islands and Easter and Guam islands had the lowest TOSC values. Contrastingly, Aitutaki colonies harboured maximal TOSC values, with around 20 times more antioxidant capacities" (Line 218).

-L245-246: Please use more specific terms and state what you actually monitored to make that statement instead of using 'perception of the environment'.

We agree and modified the sentence as followed: "Using sPLS, we identified clusters based on similar correlations between biomarker data and environmental variables, and found that the two coral genera did not show the same clustering" (line 268).

-L303-304: You have a nice manuscript and good findings, but your findings are limited to 2 coral spp. in specific locations of the Pacific Ocean, therefore it cannot be generalized.

Totally agree. However, the paragraph has been substantially modified and this statement is no longer present (line 328).

-L361-L366: Pls rephrase these sentences and avoid inaccurate terms. Always be precise when you can. You justify a 'less decipherable profile' based on physiological proxies that have not been measured in your study. Pls further discuss that.

We agree that it is the ubiquitination profile that is more difficult to decipher. We then rephrased as follows: "The incongruency here observed is however not surprising since the ubiquitination profile could also be linked not only to damaged proteins degradation under stress conditions but also to other cellular processes in normal physiological conditions. Therefore, the ubiquitination profile remains more difficult to decipher."(line 389).

-L526-529:Pls further discuss how these findings contribute to project biodiversity response to climate change. I don't think you can make broad statements with limited findings.

We agree. We have deleted this sentence

L533-534: I'm not sure what it's meant by 'the oak and the reed' - please avoid inaccurate quotes.

Thanks to your comment and the comments of the reviewer 1, we deeply modified the discussion to make this comparison more justifiable and convincing.

30th May 23

Dear Professor Furla,

Your manuscript titled "The Oak and the Reed: Two Environmental Response Strategies in Corals from Pacific Islands" has now been seen by our reviewers, whose comments appear below. In light of their advice I am 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 Reviewer #3. 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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REVIEWERS' COMMENTS:

Reviewer #1 (Remarks to the Author):

I think the authors have done a great job of addressing the reviewer comments. Congratulations on a nice manuscript that promises to advance our understanding of coral genotype by phenotype interactions across broad spatial scales.

Raphael Ritson-Williams

Reviewer #3 (Remarks to the Author):

The authors made edits that considerably improved the quality of the manuscript following the reviewers' comments and suggestions. However, there are a few points I believe that still need to be improved before it can be published. I've split my feedback in overall and specific comments.

Overall:

Along with some of the suggestions made by #Reviewer 1 and a few comments I had before – the general writing of the manuscript still needs improvement in the sense that sentences can be

shortened and written in a more direct form for presenting a clearer message. Also, unspecific terms should be avoided and the nomenclature along the manuscript should be more consistent. E.g., 1) I see no need for the abstract being presented as two paragraphs – it should only contain the main interesting results findings and the relevance of them (see more in specific comments); 2) I'd rather stick with "coral genus", instead of varying it along the MS, which only makes it more confusing. You used "coral species complex'' at different parts of the MS, as well as "coral genus'' /(L101) "coral genera" (L153) – please be consistent; 3) L65 "robust" phenotypes – what do you mean by that? It's more valid to be precise about what you meant by a "robust" phenotype (e.g., unchanged physiological traits?) rather than using the adjective vaguely; 4) introduction paragraphs starting at L103 and L118 are both talking about biomarkers, and they could be combined and shortened into a single paragraph (for note, I used the marked version of the MS).

One of the most outstanding characteristics of the study is the great spatial scale of sampling across the Pacific and this could be better highlighted in the abstract and overall, in the MS. Whereas, the limitations of it should be better addressed from the abstract to the discussion, especially regarding the seasonal variability of the sampling. L68-69 mentions that the study "sets the scientific and methodological foundation for future integrative studies", but haven't those methods been applied in previous studies before? Therefore, I don't think this MS "sets the foundation", but it rather validates what has been previously proposed over an extent geographical area for two coral genera.

Specific:

L52: Based on your findings "and", instead of "or" seems more appropriate. Also, "environmental conditions" instead of "environmental causes".
L61: I don't understand what you mean by a "diverse extent" of phenotypic plasticity, please rephrase it.
L68: You do not seem to have measured environmental "responses", but, instead, phenotype variation according to environmental conditions. Please rephrase sentence appropriately.
L144-146: I thought the samples were not all collected at the same time across the different geographic locations. Pls make this sentence shorter and clearer and clarify the "sampled concomitantly".
L155-157: Did you mean environmental parameters, for "environmental variables"? It's not clear what you're referring to as "putative explanatory variables". Pls be consistent along the MS. L509 you used "environmental factors". L618 you used "environmental measurements".
L171: According to the stats I see variation, but I cannot see a gradient across the spatial distribution of your points (Fig. 1a).
The addition of Fig.2 considered improved the presentation of the results, but instead of having both Figs. 1 and 2 with the same title, you could highlight that Fig.1 shows the spatial variation among your coral genus, whereas Fig.2 shows phenotypic variation and species specificity within each genus. Also, Figures would be "cleaner" without variation in host surface area (Figs 1c and 2c). As you mention in L183-185, host protein content is a more precise value, which has been used in most previous studies and your further stats and conclusions are ONLY based on that, so I don't think presenting data of host surface area adds much value for the MS. Similarly, Figs 3 and 4 had the same title but they are not presenting the same information. You could state what they are showing in the title.
L174-175: where do you present data for animal protein content? Do you mean coral host biomass? Be consistent and precise along MS.
L246: "environmental parameters" would suit the MS better than "environmental variables". Have a

look at that along the text.
The link with “past environmental parameters” (L305) for the conclusions regarding Pocillopora spp. Is not clear to me along the text and you mention it a few times (L386-387). It would be interesting to highlight which one of your biomarkers show, for instance, indications of SST, which would then link it to past environmental variations. Most important, you should acknowledge the limitations of your study - the physiological traits indicated those past events, but the actual abiotic data regarding that was not collected/ measured in your study. Although you explained that in the methods section L617-621 you could add a sentence in the MS text to clarify that.
L399: I like the integration of your MS findings with the Oak and the Reed parable, but in this sentence the final comparison with oak trees seems a bit out of context.
Overall nice improvement in your discussion and better integration of the Oak and the Reed metaphor in your conclusion!
L516-525: “Finally” indicates you’re jumping to the final msg of your MS, but then lots of other information were added L519-525. I believe the content should be rephrased and the ending of your conclusion should present a clear “take home msg” of your MS.

The Oak and the Reed: Two Environmental Response Strategies in Corals from Pacific Islands

Porro & Zamoum et al.

REBUTTAL MANUSCRIPT VERSION

COMMSENV-22-1162A

We thank the reviewer #3 for the last comments and suggestions that allowed us to finalise our manuscript.

We provide here a specific response (in blue) to the reviewer's comments (in black) with the list of changes made to the manuscript.

Point-by-point response to the reviewer #3 comments

Reviewer #3

The authors made edits that considerably improved the quality of the manuscript following the reviewers' comments and suggestions. However, there are a few points I believe that still need to be improved before it can be published. I've split my feedback in overall and specific comments.

We would like to thank reviewer n°3 for acknowledging the improvement of the manuscript which benefits from his contributions, as well as the other two reviewers.

We finalised the last version of the manuscrit, taking into account all his final comments.

Overall:

Along with some of the suggestions made by #Reviewer 1 and a few comments I had before – the general writing of the manuscript still needs improvement in the sense that sentences can be shortened and written in a more direct form for presenting a clearer message. Also, unspecific terms should be avoided and the nomenclature along the manuscript should be more consistent.

1) I see no need for the abstract being presented as two paragraphs – it should only contain the main interesting results findings and the relevance of them (see more in specific comments);

In accordance with this comment and the editorial rules, the abstract has been shortened and now consists of a single paragraph.

2) I'd rather stick with "coral genus", instead of varying it along the MS, which only makes it more confusing. You used "coral species complex'' at different parts of the MS, as well as "coral genus'' /(L101) "coral genera" (L153) – please be consistent;

For the sake of consistency, we have simplified the manuscript by using coral genus (singular, if we were referring specifically to the genus Pocillopora or Porites) or coral genera (plural, if we were referring specifically to the two genera Pocillopora or Porites). We limited the use of "coral species complex" once in the introductory session when we presented the biological models for this study, which consisted of various cryptic species belonging to both genera.

3) L65 "robust" phenotypes – what do you mean by that? It's more valid to be precise about what you meant by a "robust" phenotype (e.g., unchanged physiological traits?) rather than using the adjective vaguely;

The term "robust phenotype" is now defined in the first part of the discussion as follow: "Porites exhibited more robust phenotypes (with limited changes in physiological traits) mainly influenced by past climate events while Pocillopora harboured a greater phenotypic plasticity responding to a large variety of environmental variable."

4) introduction paragraphs starting at L103 and L118 are both talking about biomarkers, and they could be combined and shortened into a single paragraph (for note, I used the marked version of the MS).

We have combined and shortened this paragraph.

One of the most outstanding characteristics of the study is the great spatial scale of sampling across the Pacific and this could be better highlighted in the abstract and overall, in the MS. Whereas, the limitations of it should be better addressed from the abstract to the discussion, especially regarding the seasonal variability of the sampling.

An entire paragraph was devoted to the discussion of a putative seasonal effect (pasted here below)

> "As the coral sampling has been performed during the Tara Pacific expedition within a 6-month frame, it is also possible to point the impact of time of sampling as a confounding factor. From July 2016 (Panama Islands) to January 2017 (Guam), the expedition spanned several seasons, making it difficult to distinguish the seasonal from the geographical effect. However, if we restrict our comparison of island phenotypes to islands sampled on a reduced time scale, we still find statistically significant differences. For example, the phenotypes of the *Pocillopora* colonies of Moorea and Aitutaki were different from those of Niue and Samoa (Figure 4) even though sampling was carried out in less than a month within the same season (between November 6th to December 3rd, Table S8). On the other hand, the similarity of Easter *Pocillopora* phenotypes to the ones from Aitutaki was also observed over different months (September to November) which correspond to seasonal changes (from winter to spring). Nevertheless, to definitively unravel the impact of the seasons on an expedition involving the collection of samples in time and space, it will be necessary in the future to carry out additional studies resampling the same colonies at different times (seasons and years) and also to have a larger geographical sampling with more seasonal replicates."

In addition we added the temporal scale in the abstract: "In this study, we tested the contribution of genetic and environmental conditions to coral's phenotypic response in Pocillopora spp. and Porites spp. sampled together at a large ecological and temporal scale throughout the Pacific Ocean."

L68-69 mentions that the study "sets the scientific and methodological foundation for future integrative studies", but haven't those methods been applied in previous studies before? Therefore, I don't think this MS "sets the foundation", but it rather validates what has been previously proposed over an extent geographical area for two coral genera.

We agree and have deleted this sentence from the abstract.

Specific:

L52: Based on your findings "and", instead of "or" seems more appropriate. Also, "environmental conditions" instead of "environmental causes".

We agree and have amended the text accordingly.

L61: I don't understand what you mean by a "diverse extent" of phenotypic plasticity, please rephrase it. AND L68: You do not seem to have measured environmental "responses", but, instead, phenotype variation according to environmental conditions. Please rephrase sentence appropriately.

We deeply modified the last part of the abstract, replacing it by the sentence: "In conclusion, co-located coral species display different phenotypic response strategies that are influenced by different environmental conditions."

144-146: I thought the samples were not all collected at the same time across the different geographic locations. Pls make this sentence shorter and clearer and clarify the "sampled concomitantly".

Correct, we have clarified the sentence by "In the present study, we questioned whether visually healthy colonies, from two reef-building corals, co-located in a same wide range of habitats, showed common or divergent phenotypic signatures in response to identical environmental variations."

L155-157: Did you mean environmental parameters, for "environmental variables"? It's not clear what you're referring to as "putative explanatory variables". Pls be consistent along the MS. L509 you used "environmental factors". L618 you used "environmental measurements".

To be consistent throughout the manuscript, as well as with the work and manuscript from which the data originated, Lombard et al. 2023, we homogenised the term by "environmental variables". Indeed, we used all the contextual and historical measurements collected by Lombard and colleagues for a large set of environmental entities and we used them to evaluate, by statistical methods, putative causes of the coral biomarker signatures.

L171: According to the stats I see variation, but I cannot see a gradient across the spatial distribution of your points (Fig. 1a).

We agree and have modified the sentence: "For Porites, we observed an 8-fold reduction comparing colonies from Las Perlas to Guam colonies (Fig. 1aA)"

The addition of Fig.2 considered improved the presentation of the results, but instead of having both Figs. 1 and 2 with the same title, you could highlight that Fig.1 shows the spatial variation among your coral genus, whereas Fig.2 shows phenotypic variation and species specificity within each genus. Also, Figures would be "cleaner" without variation in host surface area (Figs 1c and 2c). As you mention in L183-185, host protein content is a more precise value, which has been used in most previous studies and your further stats and conclusions are ONLY based on that, so I don't think presenting data of host surface area adds much value for the MS.

We agree and have modified the figure 2 and 3 moving the data presentation normalised per coral surface area in the supplementary session, now edit figure S1.

Similarly, Figs 3 and 4 had the same title but they are not presenting the same information. You could state what they are showing in the title.

Correct, we are sorry for this mistake. The figures 3 and 4 have now appropriated and specific titles.

L174-175: where do you present data for animal protein content? Do you mean coral host biomass? Be consistent and precise along MS.

We modified the "animal protein content" by " animal biomass".

L246: "environmental parameters" would suit the MS better than "environmental variables". Have a look at that along the text.

To be consistent with the manuscript and work where the data come from (Lombard et al. 2023), we have homogenised the term "environmental variables" throughout the text.

The link with "past environmental parameters" (L305) for the conclusions regarding Pocillopora spp. Is not clear to me along the text and you mention it a few times (L386-387). It would be interesting to highlight which one of your biomarkers show, for instance, indications of SST, which would then link it to past environmental variations.

For both genera, the correlations between the biomarkers signature and the past environmental parameters were detailed in the result session. To better highlight which biomarker is correlated within the two environmental clusters, we completed the sentence with some details (here below in blue).

> "For *Pocillopora*, the 20 variables most correlated with the studied biomarkers were (...) structured in two clusters (Fig. 6aA, Table 2). Among the first cluster, characterised by strong correlation with antioxidant capacity and protein carbonylation, we identified (...) three climate variables (the sea surface temperature of the sampling day, recent cold temperature anomaly and past cold sea surface temperature anomalies, respectively C_Cli_084, R_Cli_045 and H_Cli_009). Among the second cluster, characterised by strong biomasses and low redox state, we identified (...) three historical climate variables (H_Cli_013, H_Cli_015, H_Cli_029, H_Cli_071; corresponding to high intensity of sea surface temperature deviations, recent heatwaves episodes and short recovery time after recent cold waves)."

Most important, you should acknowledge the limitations of your study - the physiological traits indicated those past events, but the actual abiotic data regarding that was not collected/ measured in your study. Although you explained that in the methods section L617-621 you could add a sentence in the MS text to clarify that.

We agree and we modified the sentence at the beginning of the paragraph "Differing coral sensitivities to environmental condition as follow:

> "Because the phenotypes of both genera were demonstrated to be influenced mainly by the geographical origin of the corals, we identified putative drivers by exploring the correlations between biomarkers and several environmental variables, collected during the Tara Pacific expedition or recovered by historical temperature data extracted from satellite imagery (see details in material and methods)."

L399: I like the integration of your MS findings with the Oak and the Reed parable, but in this sentence the final comparison with oak trees seems a bit out of context.

We deleted this final comparison.

Overall nice improvement in your discussion and better integration of the Oak and the Reed metaphor in your conclusion!

Thanks.

L516-525: "Finally" indicates you're jumping to the final msg of your MS, but then lots of other information were added L519-525. I believe the content should be rephrased and the ending of your conclusion should present a clear "take home msg" of your MS.

We agree. This last part of the conclusion has been shortened to go straight to the main message:

> "This shows unequivocally that natural populations of corals sharing the same habitat can have diverse responses that are influenced by different environmental parameters. It also allows for a reconsideration of the subdivision into loser and winner species, suggesting that it may not be the largest and strongest species of today that will be the most resilient tomorrow."