

# Ecosystem transplant from a healthy reef boosts coral health at a degraded reef

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**This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.**

Version 0:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

The authors present a clever experimental design in which they transplanted microbial communities and invertebrates from a healthy to a degraded reef, which resulted in direct benefits to coral health. This compelling experimental design and the impressive physiological data support the potential of microbiome and invertebrate manipulation to complement conservation efforts like gardening and nurseries for reinforcing coral health and survival.

Overall, this interesting paper has potentially widely applicable results to aid current coral conservation efforts. My primary recommendations stem from opportunities to improve data analysis and presentation.

I have an issue regarding the term "Ecobiome". The authors describe an ecobiome as including dissolved and particulate organic matter and other nutrients in the soil and water. However, the study focuses solely on microbes and invertebrates. Terms like "pioneer species" or "first colonizers" might communicate this narrower focus better and be more accurate. The experimental design is great but needs to be better explained. After reading it several times, the purpose of the T1/T2 samples was still unclear. Is not explicitly stated anywhere but I believe these are somewhat seasonal controls to account for the biodiversity that should have been observed by the time the transplantation experiment started. So for instance T1 tiles could have been a good control to account for diversity levels when the transplant experiment began. If so, T1 diversity levels provide an important experimental control point but are not shown in the main text.

Alpha diversity was informative, and it's nice to see how high diversity correlates with coral health. However, I'm wondering why the 16S alpha diversity data was not shown. The ordination plot neatly summarized samples differed mainly by site and that transplants were somewhere in between, which makes sense. However, plotting the actual Bray-Curtis dissimilarity between treatments, in particular T1, T2, and transplants would have been very informative to see if transplanted biodiversity better resembled the first or second growth site. The way how taxonomic data sometimes is presented does not convey the message. For instance, the heatmaps showed so much variation between replicates that I couldn't discern any reliable taxonomic patterns. Clustering rows by similarity could have brought out patterns and differences more clearly. And finally, what I was really missing was any sense of which specific taxa correlated with the nice physiology data presented. I'd suggest some differential abundance or shared taxa analyses to understand what taxa are common among transplants and the different sites, and subsequently identify taxa most likely to correlate with health indicators. To my knowledge, this is the first study manipulating invertebrate communities in relation to coral health outcomes. This innovative aspect unfortunately gets overlooked, limiting the ability to glean key takeaways about which invertebrate groups may drive observed benefits. In summary, I recommend the authors streamline and refocus the taxonomic data presentation to highlight potential keystone species that may drive the observed impacts on coral physiology. Specifically, carry out and showcase analyses that identify differential abundance patterns of specific microbe/invertebrate taxa between control and transplanted communities and assess correlations between key taxa abundances and metrics of coral health (similar to Figure 6B).

Minor points

L96: Is a "1" missing before parenthesis in "Urban Timepoint (T1)" ?

L95-100: Very hard to grasp what was done from the text. I suggest the authors to rephrase this entire section.

L150-152: Were 16S rDNA amplicons purified from a gel? The EMP primers are known to cause amplification of the coral host as well. How did you deal with that?

L71 16S amplicon pipeline is poorly described in comparison to COI. No information on trimming primers and reads, identification of chimeras, no post clustering curation, etc. I recommend the authors to add this information. In addition, information on how to classify taxonomically invertebrate sequences is missing.

L206-208: The calculation factor the authors mentioned (10,000) suggests the hemocytometer used has a volume of 10  $\mu$ l

per square at a depth of 0.1 mm. This is a common configuration, but it's always good practice to mention the specifications of their specific hemocytometer.

L234: The authors might want to say "ranges between" rather than "chooses between"

L235-236: Please replace "(PCoA) was used to determine dissimilarities" with "(PCoA) was used to visualize Bray-Curtis dissimilarities."

L254 can be moved above where all the PERMANOVA parameters are explained (L237-242)

Figure 6A: Could be larger, from side to side of the page.

## Reviewer #2

(Remarks to the Author)

Overall comments:

The primary research described in this manuscript illustrates the ability to transfer ecosystem functionality from one habitat to another, in an effort to restore degraded ecosystems. The experimental design evaluates the effects of anthropogenic activity at two sites – one urban and degraded and one non-urban and comparably healthy – on coral reef benthic diversity and biochemical environment (ecobiomes). Additionally, the study provides information about coral reef biodiversity, microbial community structure and the physiological patterns of two coral species in the Red Sea, broadening our understanding of benthic community interactions in different reef environments. I appreciate how the authors worked to link features of benthic community composition with physiological biomarkers of fitness and stress. The article was well-written, the graphics are clear and concise, and I enjoyed reading it.

Given the complex experimental design, the authors worked to illustrate the data effectively in the graphics. I appreciated the consistent color pallet regarding the different treatments. The only treatment that I struggled to comprehend was the Transplants. My understanding is that Transplant B means conditioned at Site B for 6-months, then moved to Site A. This is shown in Phase III panel of Figure 1, although I think the terminology panel could be improved by clarifying that Transplant B = Starts in Site B, then finishes in Site A (the coral fragments attached at 6-month timepoint originate from Site A) and vice versa.

The results were presented in a straightforward but dry manner (i.e., a long list of treatment interactions and significance values). For each examination, whether it be ecobiome characterization or coral physiology, there was no mention of hypothesis testing or rationale for applying the various measurements. As I worked my way through the results sections, I anticipated that the discussion section would include the author's interpretation of the outcomes for various measurements, but this never occurred. For example, the chlorophyll content was higher across all treatments at Site B – why? Is there less light availability there? It would also help if the functions of stress biomarkers were introduced in the results, so that when I evaluated Fig 5, I understand that TAC was protective, whereas LPO indicates elevated stress response. Similarly, the discussion offers a very nice summary of big picture concepts and the relevance of the study for coral reef conservation, but I was left wishing that I better understood how the treatments effected the outcomes of the various measurements. I acknowledge that the authors are navigating a word limit for their target journal. I think the discussion currently reads well. Incorporating a few sentences into the results that outline hypotheses and interpret results would greatly improve that section of the article.

Specific comments:

Introduction.

Lines 58-60. Could you please provide a definition of 'biomimetic tiles'? This is the first time the term is used in the article, so it would be appropriate to define as the authors see fit.

Methods.

Lines 89-92. Here the characteristics of the biomimetic tiles are described, but the term is not included. It would be clearer if the authors first described the meaning of the term, then remained consistent with using 'biomimetic' whenever the tiles are referenced.

Line 97. Please clarify what 'cleaned' means. Sterilized, so it would be similar to a newly printed tile? Or scrubbed of visible organisms, but the underlying biofilm remains?

Results.

Figure 1. In the Terminology box, please separate 'Transplant A' from 'Transplant B' and define what Transplant (Site A) means in subsequent figures. For example, in Fig 2b, the 3 black + symbols (Transplant, Site A) are oriented closer to the other black symbols and represent tiles that were first deployed at Site A for 6-months, then moved to Site B for 6-months. And this result suggest that early colonization/succession conferred a lasting effect, even after the communities were moved to a degraded site. Is that correct?

Figure 2. If possible, please include more information about the microbial taxa (e.g., EC94, UBA10353, MBIC 10086, BD78, K189A, P3OB42, and Sva0996). The 16S alignment databases output these clade IDs at the greatest resolution level available (like genus), but if you investigate further, these clades often fall within a known taxonomic designation at the family or order level. For example, EC94 is a Gammaproteobacteria (not merely an unclassified Proteobacteria), it has a candidate classification of Ca. Tethybaacterales, which are posited to be sponge symbionts. Some of your microbiomes were comprised of nearly 50% EC94 – does this correlate with greater sponge prevalence on these tiles? I can see that Porifera appears more abundant at site B tiles, but the authors did not discuss the prevalence of sponges at either site, based on the

molecular biology or the photogrammetry.

Reference for EC94 gammaproteobacteria = Taylor et al., 2021. The ISME Journal (2021) 15:503–519.  
<https://doi.org/10.1038/s41396-020-00791-z>

Discussion.

Lines 537-539. Does fishing or harvesting of sea life occur at the urban site as well? Or do you think it is solely light and pollution?

Lines 539-549. Can the authors rephrase this statement? What do you mean to convey here?

Lines 546-547. Proteobacteria is the largest and most diverse phyla of all Bacteria and they almost always dominate the microbiomes of every organism and every habitat. Please reference something more specific for 'bacteria associated with corals and sponges'.

Lines 547-548. EC94 is designated as a Gammaproteobacteria. As mentioned above, this taxon is a known sponge symbiont, so that seems worth discussing here.

Lines 553-554. Please revise to: "Key physiological functions of corals from the degraded site were improved". Is it accurate to refer to any coral collected from site B as "degraded"? Some coral colonies appear to thrive at degraded sites. I understand that observed differences between site A and site B with your physiology metrics, but degraded is both nonspecific and subjective.

Very nice work 😊

Reviewer #3

(Remarks to the Author)

The authors use a unique study design to test how tile conditioning at different sites of human impact (healthy vs disturbed) affect two different coral species. The authors deploy tiles in 2 environments and attach corals to these tiles that originate in a home habitat or a transplanted habitat. They use two metabarcoding regions 16S and CO1 data to look at bacterial and eukaryote diversity on the tiles and pair these with physiological metrics of the corals attached to the tiles (and corals from the home environment). The authors suggest that corals attached to tiles from the impacted site do better when attached to substrate-tiles conditioned from the healthy site.

In general the study is well done, but I have several issues with the study. First, on a terminology point, the authors either introduce or use a relatively poor and confusing term "ecobiomes" which is both clumsy and used inconsistently throughout. Such jargon does not help the MS clarity and is simply confusing -- for instance, referring to the settled community as an ecobiome, but defining an ecobiome as something both biotic and abiotic... I would strongly suggest to avoid confusing terms that sound catchy but are unnecessary.

I find the conclusions of the paper, that corals are "able to tolerate stress more if they are from a degraded site and added to a transplant-healthy tile" and that this approach should be used in reef restoration is a bit disingenuous. The enhanced performance is really limited to some changes in antioxidant capacity (unclear why), and some changes in photopigmentation/photoacclimation/symbiont cells/photopigments. The latter is not an effective metric for health, which is in itself a broad and non-descriptive term. There are changes in photochemical efficiency and light-ETR kinetics, but some caution would be advised here. This is even more important in the case of suggesting this be applied in reef restoration, as it skirts the point of invasive species, pathogens, vectors that could lead a healthy reef into decline.

The use of metabarcoding data is interesting here, but the execution is a bit odd. The authors report prokaryotes in CO1 data, but 16S would be where bacteria should be reported as CO1 is used for animals, notably metazoans. The 16S data is also not analyzed in a beta-diversity framework (PCoA) as I would expect. Maybe there is a reason for this but it struck me as strange to not represent CO1 and 16S in similar frameworks.

As a more minor point, the authors use photosynthetic throughout in places where photochemical is the right term. I recommend care being taken in terms throughout. I find some of the descriptions in the writing and figures hard to follow and it is difficult to tell in certain passages and figures if "B-site coral transplants" refer to B site tiles or B site corals, some clarity in the legends and in descriptions would help this.

Other suggestions are that the results be reduced significantly, as they are entirely too long and labored with too many post-hoc tests that do not seem to relate to hypotheses. It would appear in-site post-hocs are important, and the transplant tile-coral relative to their home-tile corals are the important contrasts.

Lastly, some care needs to be given to the SI and formatting, as it is not in a state that is ready for publication.

Specific comments:

or Line 2: this is an ecosystem, do we need a new term for it?

Line 5: where are these sites, red sea, pacific, Caribbean?

Line 6-7: "was used?" phrasing awkward, I suppose this is just descriptive – not seeing a "why or we tested" here. You refer to the data from these tools later but it seems odd to highlight this here when you can combine parts of this in the sentences where you talk about what you assessed on the tiles

Line 8: unclear if these tiles were out at home site for 6 months or in their "away/transplanted" site for 6 months, how long were these tiles conditions or were they? Not sure what a "biomimetic" tile is. Need to tell us the coral species

Line 14: what stressor?

Line 15: if you are defining an ecobiome as chemical properties on a reef, transplanting a tile is not transplanting the chemical properties but the biological properties of a substrate. The term ecobiome seems a bit of a neologism, and I'm not sure it is explained (or used) properly here in the context of a tile-transplant study.

Line 17: this obviously brings up questions about invasive species, spread of pathogens, and many other issues. It is an interesting recommendation but rings a bit tone deaf to the complexities and caveats.

Line 19: isn't environmental change the driver and not the 'response' – phrasing here needs clarification

Line 27-35: you are using ecobiome in a way that is not in line with the definition you provided in the abstract. The first part of the sentence is what you are defining as the ecobiome, the last part you are saying it also encompasses (which matches the abstract). You emphasize benthic, but this is only 1 part of a 3d ecosystem. In general, not very clear. It seems like this is simply jargon for 'a coral reef ecosystem.'

Line 40: this is a managers nightmare – and sounds the authors are suggesting this is all pro and no con.

Line 54: "benthic ecobiome communities" doesn't make sense, and this term is not helping throughout. A community is fundamentally a living thing, but you are describing an ecobiome as living and non-living. I recommend dropping the jargon. You are asking (as I understand) how the biological and chemical properties of an ecosystem favor different microbial and invertebrate communities on the benthos and how these assemblages affect coral growth. Say it plainly and clearly.

Line 63: again, as defined, "ecobiome" does not work here.

Line 68-72: this is pretty bold conjecture considering your findings, caveats, and scale. Perhaps dial back.

Line 80: Give lat-long for the sites Line 62: terribly vague and almost secretive. How do they differ? How far apart are they? Give a map? You should be able to describe this for us with referring to other sources. Give lat-long for the sites, and tell us what a biomimetic terracotta tile (or show one in a figure)

Line 86: is light pollution relevant here? Or is it "light-levels" of pollution

Line 89: biomimetic terracotta tile (show one in a figure?)

Line 91: I'm confused – they were floated vertically at 10m, but also attached to the substrate? Seems it can't be both unless you have benthic and floated treatments. From the image in figure 1 it looks like none of the tiles are actually on the benthos, which seems odd if you are trying to recruit benthic organisms and make an environment that is like the reef (for instance, macroinvert and vert (crabs, worms, plankton, fish) may not colonize a floating tile hanging 10m in the water column vs. a tile on the substrate. Moreover, if you put coral on these tiles there will inevitably be shading and modified light/flow environments. Lastly, I'm not seeing a good description of the light, temp, depth for your study. While these sites may be described already, I assume some samples were taken in your current study to track the environment during deployment.

Line 104: this should be complexa and robusta

Line 115: photochemical not photosynthetic

Line 116: "endosymbiont algae" and state Symbiodiniaceae

Line 117: what is health? Pigmentation maybe and health only if bleaching observed, but this is a vague and nondescriptive term

Figure 1. bottom right should be a table. It is not effective as a figure, recommend giving more space throughout by stacking as a single column and expanding width of each panel (hard to see what is what)

Line 128: is this Phase III? Why not use the terminology you introduce in figure 1? Also, recommend using fewer terms, like "organismal biomass", just say the benthic community this is what you are sampling. Corals were sampled at final timepoint only though, so not at Phase II? Unclear here. Also, how many tiles had corals in total here – were there tiles samples at each time point WITHOUT corals in Phase III?

Line 132: was the water also filtered and analyzed (or added to your blender)?

Line 133: separated at all or scraped into a blender as a whole community

Line 141: why were they allowed to adapt for 24h. Wouldn't it have made more sense to get a rapid measure of what their photochemical efficiency was under site conditions, diving PAM etc? It seems an acclimation period makes your effect of site less clear and confounding with in-lab, post-scraping off a time, acclimation. Also, remind us of the n=coral for each site/treatment

Line 169: why 97% clustering, 100% ASVs are the norm now and allow for comparison across studies with full sequences. Seems antiquated?

Line 172: unclear why you are rarifying for alpha diversity but then not doing so for beta diversity (or so it sounds in the passage below on line 176). You should use the same rarified data for all analyses. Also, generally taxonomic assignment is made, then downstream analyses and rarefaction etc. The order for the final passage seems like it should go before the richness info—which can all be done in R/phyloseq etc

Line 186: photochemical not photosynthetic, correct throughout.

Line 193: the "o" and "m" should be subscript in Fo Fm

Line 198: define FSW

Line 201: single or double dip technique

Line 202: holobiont, or for host and separately for symbiont

Line 211: with concentrations determined from equations by...? Jeffrey & Humphrey?

Line 233-Line 234: why on relative abundance? Was a Hellinger transformation or other applied? Bray Curtis "dissimilarity" distance matrix (as it should be noted) should be performed on the ASV/OTUS data and does not require relative abundance transformation – this should be explained a bit (I admit there are many avenues to these analyses)

Line 250-252: grammar here, and you have already used PERMANOVA above, so define above and give acronym here  
Line 262: define PAR, perhaps in line 189. Later on you mention "PAR50" and "irradiance level" interchangeably, which is confusing since (passages around line 368).  
Line 271: density not abundance  
Line 275: already gave the FDR abbreviation above  
Line 292: what is an ecological indices? You mean communities?  
Line 306: can't be <0.000  
Line 301: based on COI or 16S or both or...? What is richer in taxa telling us that richer in species isn't – taxa only informative if you tell us at what level.  
Line 302: does it make sense to have prokaryotes here? Considering COI is not used for prokaryotes (and you have 16S data for them below), it seems these should have been pruned from your data. Maybe I'm wrong, but certainly it isn't a group you highlight with the eDNA.  
Line 310-318: Could this be said in 2 sentences? It seems long for the take home  
Line 336: you use PCoA for this same purpose for CO1, why aren't you also doing it for 16S? CO1 is not a marker to be used for prokaryote community diversity. Also the figure for PCoA in figure 2B could be improved: (1) the points could be with ellipses, (2) the orientation is poor with a large white space and points all clustered in a corner of the plot (re-align the x-y to center your data).  
Line 364: what is "3" in the stats? n? df?  
Line 367: was irradiance measured at the sites for these corals? Nothing was reported on this.  
Line 373: the writing here is confusing – a coral can't have "an irradiance". This is found through this section and subsequent paragraphs. In general I think the results section needs to be condensed and clarified with less "there were a difference" sentences followed by descriptions of the differences in a second sentence – I'd advise to be more direct and cut throughout.  
Line 376: if there is an interaction, this should be reported and emphasized the main effects since the main effects cannot be interpreted in the face of these interactions.  
Figure 3. No need for 2x labeled on the y axis..., probably a good idea to have shaded confidence intervals here too. You have these in figure S2.  
Line 393-432: the results section is entirely too long. The points here on changes in symbiont densities and pigmentation are being described in too much detail, and in general, the authors are applying fully orthogonal posthoc tests which do not need to be made. What is the a priori reason for this? Why should all levels be tested relative to all others (i.e., Native site A compared to Original Site B?) It seems overboard...  
Figure 6. why are there only single points for each group? Shouldn't this be a point cloud? If plotting the centroid, ok, but also plot the raw data  
Line 513: there are other organisms you are transferring, not all are +  
Line 515: (on settlement tiles).  
Line 516-520: There certainly is high variability between the original/natives and tiles for physiology and antioxidant capacities. It seems TAC is your best point that this matters as all other metrics for the contrast that matters (B site corals attached to A site tiles) are comparable or lower than Native B/original B site corals. In any case, I would recommend caution in your selling of the take home here, as you have low sample size and corals not attached to the benthos...  
Line 536: seems like you should report some of this info in a summary table as you haven't described these factors in any detail  
Line 556: are B site transplants (yellow) the corals from B transplanted to A or the corals from a A transplanted to B? Looking at the yellow line and reading your passage here, it would suggest (1) B corals transplanted to A saw an increase ETR, but this is not really in line with your hypotheses and questions (healthy corals going to a degraded reef to support restoration). If it is the opposite (yellow B = A corals to B site), then this supports healthy reefs restoring degraded reefs, but this is not what the sentence states here. Overall, there is a need for clarity on the legends and the passages.  
Line 579: these passages are getting hard to understand – the corals were transplanted, the tiles were, yes? So, saying "corals from the tiles that came from the degraded reef moved to the healthy reef.." you are really saying that healthy-reef corals adhered to tiles originated from the degraded reef, but this is not clear the way the text is written. I recommend rephrasing throughout to be clear and adding in emphasis (Figure 6A, etc) when you make statements so the reader knows what you are referring to, including in the legends "transplant columns are corals from their respective sites added to tiles from the opposite site".  
Line 600-605: a bit of word salad, I'm not following – what is Noah's Ark?

#### Supplement:

generally I've never seen "S1#" noted in figures, usually "S#", since the "1" looks like a one. Is this a NatComm style?  
Table 1. sites should be listed starting with "A" not B. Would be easier to tell what this data is saying if it was sorted as "A" all the way through, then "B". The alternating A/B isn't super insightful, also some weird the formatting with Winter (different fonts half way through?)

Do a line page break at each table or figure to separate them (ie Table S3 is broken in half). This is pretty basic stuff and shows an unfortunate lack of attention to detail.

Table S4. Need same # of decimals in p values. Seems odd the 4th t value isn't negative like the others for similar metric.

Table S4 and S5 – give the metric/response instead of "value" and don't list it in every row, show the metric, then divide the cells with an underline when the metric changes. Avoid repeating information.

Table S4-S9, as I noted in text, seems like post-hoc tests are way overdone. Not tailored to hypotheses or relevance to data

Fig S3.and S4 No y axis label (and why are tables mixed in with figures?) They should be separated.

Table S10, left column shouldn't be in bold, only signif p values

Version 1:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

I appreciate the effort put into the analyses, however, I'm still not convinced by some of the results shown.

I'm having trouble discerning any clear patterns from Figures 2C-E. If the bacterial communities are not significantly different across relevant pairwise comparisons, as Figure 2D suggests, it's best to state this clearly and consider removing the figure. I couldn't find any pairwise comparisons showing significant differences between original A vs. Transplant A or original B vs. Transplant A. In my opinion, these are key comparisons to establish what is special about Transplant A that improved coral physiology in site B. The only mention of statistical differences is in lines 347-349, which refers to the overall model. This was expected to be significant, so more detailed pairwise analysis would be helpful.

Could you also explain why replicates are not shown in Figure 2E? The heatmap does not have clustering, and the top 25 most abundant bacteria do not appear to differ significantly across comparisons. Can the authors explain the reasoning for choosing the top 25 taxa to be compared across treatments? maybe less abundant taxa are responsible for the differences? I understand the reasoning for looking at the community as a whole, but focusing on the top organisms might not be as informative since they could be common to all treatments. I suggest conducting a differential abundance analysis, which could highlight the groups that matter, even if they are not the dominant ones. If the authors still want to contrast dominant groups maybe barplots would be better in this case?

The main point you're making is that corals grown surrounded by communities originally from site A have higher photochemical performance when transplanted into site B. It might be clearer to present this result first, followed by the characterization of the community composition guided by the coral physiology results. To characterize the diversity, focusing on a few key comparisons could help readers navigate the figures more easily. For example, consistently comparing Original A vs. Transplant A and Original B vs. Transplant A across all analyses would be beneficial.

I really believe the data has great potential, but unfortunately not well exploited yet

Reviewer #2

(Remarks to the Author)

Dear authors, Thank you for carefully and thoughtfully addressing all of the reviewer's comments. I appreciate your hard work! In my opinion, the manuscript is ready for publication.

Reviewer #3

(Remarks to the Author)

I appreciate the thorough responses by the authors to all the reviewer concerns, especially in regards to the 'ecobiome' neologism and adding detail/justification for their analyses, findings and approaches. I have no further comments (and apologize for taking so long in returning my review). Well done on the revised MS, and I look forward to seeing it published.

Version 2:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

Thank you for your hard work and for thoroughly and attentively addressing my comments. The manuscript is now ready for publication.

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We find that these concerns limit the strength of the study, and therefore we ask you to address them with additional work. In particular (but not exclusively), see Reviewer 1's requests for additional analyses (and note that all the unpublished results mentioned in the paper must be shown), Reviewer 2's request for information on sponge prevalence and Reviewer 3's question on light / flow conditions. Without substantial revisions, we will be unlikely to send the paper back to review.

**Based on the positive feedback and detailed suggestions we received from all reviewers, we have made significant efforts and substantial revisions to address all comments suggested by reviewers including additional edits and analysis to improve the clarity and readability of the manuscript. We believe the manuscript is now in a suitable format and condition for publication. We have also uploaded all unpublished results to NCBI databases and compiled our supplementary results into a supplementary information file.**

Additionally, we agree with two of reviewers that the term *ecobiome* should be removed, as it is unclear and unnecessary. Moreover, we are not convinced that it matches the definition provided in reference 6 (a plurality of ecosystems), and further note that that publication is a short note dating back to 1984 and has been cited only a handful of times.

**We agree with this comment and the suggestions from all the reviewers and have updated this in the entire manuscript, which we have now referred to as organismal communities.**

In addition to the above, you must comply with the following editorial requests; we will not be able to proceed with your revised manuscript otherwise. Please also see the Nature Communications [formatting instructions](#), which you may find useful while preparing your revised manuscript.

**We have completed all necessary formatting of the manuscript and supplementary data according to Nature Communication guidelines and formatting instructions. If there is something that we might have missed it was not intentional and we will do everything we can to rectify it immediately.**

## REVIEWER COMMENTS

Reviewer #1 (Remarks to the Author):

The authors present a clever experimental design in which they transplanted microbial communities and invertebrates from a healthy to a degraded reef, which resulted in direct benefits to coral health. This compelling experimental design and the impressive physiological data support the potential of microbiome and invertebrate manipulation to complement conservation efforts like gardening and nurseries for reinforcing coral health and survival. Overall, this interesting paper has potentially widely applicable results to aid current coral conservation efforts. My primary recommendations stem from opportunities to improve data analysis and presentation.

**We appreciate the detailed suggestions and comments of the reviewer and the time to give valuable feedback. We thank the Reviewer for their interest and appreciation of our study, and we agree with their general comments regarding the main issues to fix within the**

**manuscript. We have taken all of their comments into consideration and have made the appropriate changes that they have suggested, which are reflected throughout the manuscript. We agree with the reviewer that “Ecobiome” is an outdated and non-relevant term and have changed this in the manuscript.**

I have an issue regarding the term “Ecobiome”. The authors describe an ecobiome as including dissolved and particulate organic matter and other nutrients in the soil and water. However, the study focuses solely on microbes and invertebrates. Terms like "pioneer species" or "first colonizers" might communicate this narrower focus better and be more accurate.

**We agree with the reviewer and following their suggestions as well as input from the other reviewers we have omitted this phrase and clarified what communities we are referring to.**

The experimental design is great but needs to be better explained. After reading it several times, the purpose of the T1/T2 samples was still unclear. Is not explicitly stated anywhere but I believe these are somewhat seasonal controls to account for the biodiversity that should have been observed by the time the transplantation experiment started. So for instance T1 tiles could have been a good control to account for diversity levels when the transplant experiment began. If so, T1 diversity levels provide an important experimental control point but are not shown in the main text.

**We agree with the reviewer and have therefore add clarifying sentences to address this point in the methods section in several places, including improving Fig. 1 (see table). Additionally, we have added a few lines in the results section that discusses the difference in organismal abundance between the two timepoints at either site. However, we are not able to conclusively determine if this played a factor in boosting coral health or if it was the general duration of time tiles were in the water.**

“Additionally, we observed a 30.5% increase in bacterial abundance from the NonUrban T1 tiles to the NonUrban T2 tiles. Conversely, at Site B, bacterial abundance decreased by 3.5% from the Urban T1 tiles to the Urban T2 tiles. Notably, the most abundant reads belonged to the phyla Proteobacteria, with the majority of these from the order Burkholderiales EC94, previously identified from sponge tissues and some corals<sup>68-70</sup>. Site A Original tiles had a higher relative abundance of Burkholderiales EC94 (44.8%) than Site B Original tiles (1.6%). Tiles from Site A that were transplanted to Site B retained a higher relative abundance of EC94 (29.3%), compared to the other tiles at Site B (Fig. 2E). Suggesting that the community of bacteria was more closely associated with the dominant invertebrate phyla found on the tiles, such as Cnidaria and Porifera (Fig. 2C), which was also consistent with visual observations.”

Alpha diversity was informative, and it’s nice to see how high diversity correlates with coral health. However, I’m wondering why the 16S alpha diversity data was not shown. The ordination plot neatly summarized samples differed mainly by site and that transplants were somewhere in between, which makes sense. However, plotting the actual Bray-Curtis dissimilative between treatments, in particular T1, T2, and transplants would have been very informative to see if transplanted biodiversity better resembled the first or second growth site.

**We agree with the reviewer and have made sure to add the community composition for 16S (beta diversity). However, we did not include the alpha diversity species richness for bacteria due to the as the data lacked a clear trend due to the dominance of the Proteobacteria; Gammaproteobacteria; Burkholderiales; EC94. This species dominated the read abundances and potentially skewed measures of species richness. We felt that the data did**

**not provide meaningful insights as the variability of the other species was not fully represented.**

The way how taxonomic data sometimes is presented does not convey the message. For instance, the heatmaps showed so much variation between replicates that I couldn't discern any reliable taxonomic patterns. Clustering rows by similarity could have brought out patterns and differences more clearly.

**We agree with the reviewer and have clustered heatmaps by similarity. As mentioned below, in addressing other points, we feel that the community of organisms should be looked at as a whole community, however we do mention differences in some key species between sites and treatments.**

And finally, what I was really missing was any sense of which specific taxa correlated with the nice physiology data presented. I'd suggest some differential abundance or shared taxa analyses to understand what taxa are common among transplants and the different sites, and subsequently identify taxa most likely to correlate with health indicators. To my knowledge, this is the first study manipulating invertebrate communities in relation to coral health outcomes. This innovative aspect unfortunately gets overlooked, limiting the ability to glean key takeaways about which invertebrate groups may drive observed benefits. In summary, I recommend the authors streamline and refocus the taxonomic data presentation to highlight potential keystone species that may drive the observed impacts on coral physiology. Specifically, carry out and showcase analyses that identify differential abundance patterns of specific microbe/invertebrate taxa between control and transplanted communities and assess correlations between key taxa abundances and metrics of coral health (similar to Figure 6B).

**We agree with the reviewer. We believe that while there are keystone species on reefs as well as critical reef-building organisms, we focus on the invertebrate and bacteria as a whole community or ecosystem on the tiles as a booster of coral health. We don't necessarily believe there is one or two organisms solely promoting coral health, but rather a symphony of a diverse community that could be benefitting the corals. We chose to focus on abundance, richness, and diversity of the community as a whole rather than singular organisms. In the future, we plan on using a larger sample size which might help discern a clearer pattern if specific organisms could be playing a role. However, we don't want to overstate that the large abundance of one species and the absence of another is directly affecting coral health. We state larger overarching patterns rather than focus on smaller detailed patterns of specific organisms. There are many studies that have shown that a diverse reef community with a prevalence of different species contributes to a thriving reef, therefore, we also wanted to emulate this point. We have made it clearer in the discussion and results that we aimed to look at the invertebrate and microbe community as a whole, while some species could be more beneficial than others in boosting coral health, which those patterns were touched upon, we aim to take the community as whole.**

“While these key organisms may illustrate broader patterns, it is crucial to emphasize the collective role of the invertebrate and microbial communities at the different sites in influencing coral physiology. Numerous studies underscore the importance of a diverse reef community, highlighting how a variety of species contributes to reef vitality<sup>5,14,25,27,28,65–68</sup>. We remain cautious in attributing coral health directly to the presence or absence of a particular species, rather identifying overarching trends across the tiles at either site. Recognizing that although some species may have a greater impact on coral health, the dynamics of the reef community as whole and their combined interactions contribute to improvements in

coral physiology.”

Minor points

L96: Is a “1” missing before parenthesis in ”Urban Timepoint (T1)” ?

**Yes, thank you for catching this we have fixed this.**

L95-100: Very hard to grasp what was done from the text. I suggest the authors to rephrase this entire section.

**We have rephrased L95-100, page 3 following the reviewer’s suggestion and edits.**

“The tile treatments at either site is described as the time and status of the organismal community accumulated on each substrate (Fig. 1). Site A and B each contained a set of ‘Original’ tiles (Original A and Original B) that never left the site and stayed for the total 12-month duration of the study. The next tile treatment was sampled twice during the study for eDNA (i.e., marine invertebrates and microbes); the first time was after the first 6 months to mark Timepoint 1, with Site A tiles referred to as ‘NonUrban T1’ and Site B tiles referred to as ‘Urban T1’ tiles. After sampling, these tiles were scrapped clean, washed, and dried visibly of any organisms or biofilms, and redeployed as clean tiles for an additional 6 months at Site A as ‘NonUrban T2’, and at Site B as ‘Urban T2’ tiles, where they remained at either site until they were sampled for the second time at the end of the study. The last tile treatment were the ‘Transplant’ tiles that were reciprocally transferred from either site, Transplant A tiles (conditioned at Site A) went to Site B and Transplant B tiles (conditioned at Site B) went to Site A (6 months of growth at both sites) (Fig. 1). Tiles were monitored visually every 2 months using photogrammetry.”

L150-152: Were 16S rDNA amplicons purified from a gel? The EMP primers are known to cause amplification of the coral host as well. How did you deal with that?

**After extractions, the product was sent to the Genome Research Center at the University of Illinois-Chicago, where they conducted PCRs, amplicon purification, library prep, and sequencing. The Center is very experienced with EMP and equipped to deal with any potential issues that may have arose with amplification of the coral host or artifacts. I have changed the beginning paragraph to make more sense in terms of breaking up COI and 16S protocols as well as addressing the following lines you described.**

**page 5:**

“eDNA of bacteria and invertebrates from tiles were extracted using the DNeasy PowerMax Soil Kit (Qiagen, Hilden, Germany) from bulk sessile samples according to Levy et al. (2023)<sup>29</sup>. The DNeasy PowerClean Cleanup Kit (Qiagen, Hilden, Germany) was used to purify genomic DNA following the manufacturer’s protocol. Amplification of the 313 bp fragment of the mitochondrial Cytochrome c. Oxidase subunit I (COI) region occurred using a two-step PCR process. Primers targeting metazoans (i.e., mlCOIintF and jgHCO2198)<sup>36</sup> were synthesized with locus-specific overhangs<sup>29</sup>, and index specific primers (Illumina Metagenomic Sequencing Library Prep, pp. 6-14) were attached. PCRs and purification steps were executed according to Levy et al. (2023)<sup>29</sup>. Final PCR products were measured with Qubit dsDNA HS Assay (Invitrogen, USA) and average fragment size was estimated with a 4200 TapeStation System and a D1000 ScreenTape (Agilent, USA). Equimolar concentrations of PCR products were pooled together. Libraries were sequenced using an Illumina MiSeq v2 500-cycle Kit (Illumina, San Diego, USA) on an Illumina MiSeq platform. **Marine bacteria were targeted using the prokaryote 16S ribosomal RNA (rRNA) gene from the V4 region, using an updated version of the primer set 515F (GTGYCAGCMGCCGCGTAA)<sup>34</sup> and 806R (GACTACNVGGGTWTCTAAT)<sup>35</sup>. PCRs, amplicon purification, library prep, and 16S sequencing with the Illumina Miniseq MO 2x150 (Illumina, San Diego, USA) occurred at the Genome Research Center at the University of Illinois-Chicago.”**

L171: 16S amplicon pipeline is poorly described in comparison to COI. No information on trimming primers and reads, identification of chimeras, no post clustering curation, etc. I recommend the authors to add this information. In addition, information on how to classify taxonomically invertebrate sequences is missing.

**We agree with the reviewer and have updated the text for both the taxonomic classifications for COI and 16S data for bacteria. For bacterial 16S data, trimming and chimera identification are implemented in the DADA2 workflow. We have edited line 171 to clarify these steps are included. Since DADA2 does not cluster sequences but instead produces amplicon sequence variants, there is no post clustering curation step included here.**

**We have updated:**

“For 16S data, reads were trimmed, low quality sequences were filtered, and the remaining data was denoised, merged, and chimeras were removed, using the DADA2<sup>38</sup> workflow implemented in QIIME2.”

“We employed a multifaceted approach to assign taxonomy for OTUs using QIIME (v. 1.9)<sup>42</sup>, implementing uclust against Midori (version GB239)<sup>43</sup> and MetaCOXI<sup>44</sup> nucleotide databases with Bayesian Least Common Ancestor (BLCA) analysis<sup>45</sup>. The Ribosomal Database Project (RDP)<sup>46</sup> classifier alongside a COI classifier<sup>47</sup> was utilized for further classifications, before utilizing blastx against the Midori amino acid database, followed by BASTA<sup>48</sup> to identify the Last Common Ancestor (LCA) of 70% of the top hits. This multi-step approach ensured comprehensive taxonomic annotation of OTU sequences, harnessing both nucleotide and amino acid databases to optimize classification accuracy (See Supplementary Methods 2.3).”

L206-208: The calculation factor the authors mentioned (10,000) suggests the hemocytometer used has a volume of 10 µl per square at a depth of 0.1 mm. This is a common configuration, but it's always good practice to mention the specifications of their specific hemocytometer.

**We have added the following information as suggested by the reviewer, please see the new page 6:**

“Algal density was determined from a 100 µl sub-sample and counted on a hemocytometer under a microscope under x100 magnification. Five squares were counted (10 µl per square at depth of 0.1mm) and the average counts were multiplied by 10,000 (number of cells/ml).”

L234: The authors might want to say “ranges between” rather than “chooses between”

**We have incorporated this suggestion.**

L235-236: Please replace “(PCoA) was used to determine dissimilarities” with “(PCoA) was used to visualize Bray-Curtis dissimilarities.”

**We have made this change in the text.**

L254: can be moved above where all the PERMANOVA parameters are explained (L237-242)

Figure 6A: Could be larger, from side to side of the page.

**We moved it as suggested and then realized we already had a sentence stating this.**

**Therefore, we removed the sentence and kept what we already had written. We have made Fig. 6A larger according to the reviewer’s instructions.**

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Reviewer #2 (Remarks to the Author):

Overall comments:

The primary research described in this manuscript illustrates the ability to transfer ecosystem functionality from one habitat to another, in an effort to restore degraded ecosystems. The experimental design evaluates the effects of anthropogenic activity at two sites – one urban and degraded and one non-urban and comparably healthy – on coral reef benthic diversity and biochemical environment (ecobiomes). Additionally, the study provides information about coral reef biodiversity, microbial community structure and the physiological patterns of two coral species in the Red Sea, broadening our understanding of benthic community interactions in different reef environments. I appreciate how the authors worked to link features of benthic community composition with physiological biomarkers of fitness and stress. The article was well-written, the graphics are clear and concise, and I enjoyed reading it.

**We thank the reviewer for their time and consideration to give great feedback and suggestions. We appreciate their interest in our study and the comments that they have made to improve our manuscript.**

Given the complex experimental design, the authors worked to illustrate the data effectively in the graphics. I appreciated the consistent color pallet regarding the different treatments. The only treatment that I struggled to comprehend was the Transplants. My understanding is that Transplant B means conditioned at Site B for 6-months, then moved to Site A. This is shown in Phase III panel of Figure 1, although I think the terminology panel could be improved by clarifying that Transplant B = Starts in Site B, then finishes in Site A (the coral fragments attached at 6-month timepoint originate from Site A) and vice versa.

**We agree with the reviewer and have changed the Fig. 1 graphic to illustrate these clarifications.**

**We thank the reviewer for this point of clarification to make the experimental design clearer. Specifically, in the Methods section, page 3:**

“The last tile treatment were the ‘Transplant’ tiles that were reciprocally transferred from either site, Transplant A tiles (conditioned at Site A) went to Site B and Transplant B tiles (conditioned at Site B) went to Site A (6 months of growth at both sites) (Fig. 1). Tiles were monitored visually every 2 months using photogrammetry.”

**page 3:**

“Transplant’ corals were on the tiles that came from the opposite site (Transplant A – conditioned at A went to Site B and Transplant B – conditioned at B went to Site A) (Fig. 1).”

**We have incorporated the suggestion to explain the meaning of ‘Transplant B’ and to make sure that it is more understandable within our experimental design figure and the terminology panel.**

The results were presented in a straightforward but dry manner (i.e., a long list of treatment interactions and significance values). For each examination, whether it be ecobiome characterization or coral physiology, there was no mention of hypothesis testing or rationale for applying the various measurements. As I worked my way through the results sections, I anticipated that the discussion section would include the author’s interpretation of the outcomes for various measurements, but this never occurred. For example, the chlorophyll content was higher across all treatments at Site B – why? Is there less light availability there?

**We agree with the reviewer's comments. Our study offers a comprehensive perspective on the physiological state of the transplanted corals. Indeed, while our initial discussion may not have explicitly emphasized chlorophyll content or photopigmentation, we have broadly considered and interpreted these and other health parameters to understand their potential roles in enhancing coral health at the transplantation sites. Regarding the specific mention of elevated chlorophyll content at Site B, as highlighted in our discussion, this observation correlates with the site's characteristics of excess nutrients and increased light pollution at night, which are known to influence chlorophyll levels in corals. Although initially referenced in our discussion, we have now expanded our interpretation to more directly connect these observations with the patterns displayed in Figure 4, providing a clearer link between environmental factors and chlorophyll content in the context of coral health. This amendment aims to address the need for a more detailed explanation as suggested by the reviewer.**

It would also help if the functions of stress biomarkers were introduced in the results, so that when I evaluated Fig 5, I understand that TAC was protective, whereas LPO indicates elevated stress response. Similarly, the discussion offers a very nice summary of big picture concepts and the relevance of the study for coral reef conservation, but I was left wishing that I better understood how the treatments effected the outcomes of the various measurements. I acknowledge that the authors are navigating a word limit for their target journal. I think the discussion currently reads well. Incorporating a few sentences into the results that outline hypotheses and interpret results would greatly improve that section of the article.

**We agree with the reviewer's comment and in light of other comments to adjust the results section to flow and read better we have incorporated these sentences and clarifications into the main text. As these additions were added in a few places, please find them located in the results and discussion sections of the manuscript.**

Specific comments:

Introduction.

Lines 58-60. Could you please provide a definition of 'biomimetic tiles'? This is the first time the term is used in the article, so it would be appropriate to define as the authors see fit.

**We have rearranged later text and defined 'biomimetic tiles' in the last paragraph of the introduction to make it clearer. We also clarified where we mentioned it later in the methods section. Please see the following updated sentences to incorporate these changes within the text:**

**page 2:**

"This research explores this concept further by determining if there is an inherent difference in the organismal composition between a healthy and degraded coral reef and if it is an important component in the maintenance of coral physiology and health. Biomimetic terracotta tiles were designed to emulate the natural topographic complexity of coral reef surfaces with various niches, holes, and crevices<sup>29,30</sup>, and used as substrates for accumulating reef organisms at a 'healthy' (Site A) and 'degraded' (Site B) coral reef in the Gulf of Eilat/Aqaba (GoE/A), Red Sea."

**page 3:**

"We deployed 18 biomimetic tiles (25 cm x 25 cm) fabricated with 3D design, printing, and molding to replicate the rugosity of natural reef surfaces<sup>29,30</sup>."

Methods.

Lines 89-92. Here the characteristics of the biomimetic tiles are described, but the term is not included. It would be clearer if the authors first described the meaning of the term, then remained consistent with using ‘biomimetic’ whenever the tiles are referenced.

**Please see the consideration of this comment, according to the comment above. We have defined and described the tiles at their first mention in the introduction and then proceeded to remain consistent throughout the text. We believe we have made the necessary adjustments that now make it clear that the ‘biomimetic tiles’ are also the same as the ‘tiles’.**

Line 97. Please clarify what ‘cleaned’ means. Sterilized, so it would be similar to a newly printed tile? Or scrubbed of visible organisms, but the underlying biofilm remains?

**We have reworded and added to the text to make it clearer that we are referring to tiles that have been scrubbed and washed clean from underlying biofilms or organisms.**

**Page 3:**

“After sampling, these tiles were scrapped clean, washed, and dried visibly of any organisms or biofilms, and redeployed as clean tiles for an additional 6 months at Site A as ‘NonUrban T2’, and at Site B as ‘Urban T2’ tiles, where they remained at either site until they were sampled for the second time at the end of the study.”

**Results.**

Figure 1. In the Terminology box, please separate ‘Transplant A’ from ‘Transplant B’ and define what Transplant (Site A) means in subsequent figures. For example, in Fig 2b, the 3 black + symbols (Transplant, Site A) are oriented closer to the other black symbols and represent tiles that were first deployed at Site A for 6-months, then moved to Site B for 6-months. And this result suggest that early colonization/succession conferred a lasting effect, even after the communities were moved to a degraded site. Is that correct?

**We agree with the reviewer and as per suggested by their previous comment we have made changes in the Figure 1 terminology box to reflect those clarifications. We have clarified what ‘Transplant’ means so that it is more clear in the subsequent figures. Early colonization could have a lasting effect (or at least a 6-month effect) even after the tiles are moved to different sites, which was also explained with other analysis on coral physiology.**

Figure 2. If possible, please include more information about the microbial taxa (e.g., EC94, UBA10353, MBIC 10086, BD78, KI89A, P3OB42, and Sva0996). The 16S alignment databases output these clade IDs at the greatest resolution level available (like genus), but if you investigate further, these clades often fall within a known taxonomic designation at the family or order level. For example, EC94 is a Gammaproteobacteria (not merely an unclassified Proteobacteria), it has a candidate classification of Ca. Tethybacterales, which are posited to be sponge symbionts. Some of your microbiomes were comprised of nearly 50% EC94 – does this correlate with greater sponge prevalence on these tiles? I can see that Porifera appears more abundant at site B tiles, but the authors did not discuss the prevalence of sponges at either site, based on the molecular biology or the photogrammetry.

Reference for EC94 gammaproteobacteria = Taylor et al., 2021. The ISME Journal (2021) 15:503–519.

<https://doi.org/10.1038/s41396-020-00791-z>

**We agree with the reviewer that more in depth taxonomic descriptors in Fig. 2E will allow readers to understand the results more thoroughly. We have corrected this and it is now**

reflected in the figure and the text of the results. Additionally, we thank the reviewer for this additional citation and have added it alongside a bit more explanation in the text of the results. Following this point and the points made later by this reviewer we have also included more analysis of these results in the discussion section as well.

Discussion.

Lines 537-539. Does fishing or harvesting of sea life occur at the urban site as well? Or do you think it is solely light and pollution?

**There are no commercial fisheries or aquaculture industry anymore in the GoE/A since 2008. The fish farms were in the Northern region of the GoE/A near Site B and had detrimental effects on the marine life, but any impact now on Site B would be purely speculative. However, we believe that the main issues are associated with localized eutrophication in the area, pollution, and human-induced disturbances, mainly light pollution. The light pollution in the area is so great that it can be seen from space (Google Earth Images) and has been shown to have a huge impact on corals physiology and spawning at Site B. We added to these lines just to clarify this and added supporting citations from other areas in the manuscript.**

**page 16:**

“The environmental condition of the urbanized site was most likely caused by local eutrophication (e.g., excess nutrients) and human-induced perturbations at the site, such as pollution and artificial light at night (ALAN), which is highly prevalent in the GoE/A, causing disturbances in coral physiology and spawning<sup>31,32,44,69</sup>”

Lines 539-549. Can the authors rephrase this statement? What do you mean to convey here?

**We have rephrased these lines, deleted some text, and made efforts to clarify what we are trying to convey. Please see the improvements to the text in the following new lines.**

**page 16-17:**

“Differences among free-living microorganisms and invertebrate communities between healthy and degraded coral reefs are known to be highly distinct and often location-specific<sup>14,64-67</sup>. Across reef habitats, the variation among these communities could be related to different nutrient regimes<sup>31,68</sup>, fluctuations in environmental conditions<sup>2</sup>, and various biotic patterns<sup>14,67</sup>, whereas site-specificity could also be connected to the structural complexity and benthic diversity of the reef. The ‘degraded’, highly urbanized reef in this study has historically been characterized by more detrimental changes, such as spikes in salinity, nitrates, phosphates, and ammonia, in comparison to the ‘healthy’, non-urban reef<sup>31,32</sup>, which has been known to support an abundance of diverse marine species (Table S11)<sup>31,32</sup>. The pH and temperature have remained some of the only consistent parameters between the two reef sites in the last several years<sup>32</sup>. The environmental condition of the urbanized site was most likely caused by local eutrophication (e.g., excess nutrients) and human-induced perturbations, such as pollution and artificial light at night (ALAN), which is highly prevalent in the GoE/A, causing disturbances in coral physiology and spawning<sup>31,32,44,69</sup>. Promoting resilience and enforcing the persistence of coral-dominance at declining coral reefs can be challenging<sup>63</sup>. Although some corals can survive in degraded conditions, there could still be room for improvement, by introducing beneficial communities to boost their current health state and encourage long-term resilience.”

Lines 546-547. Proteobacteria is the largest and most diverse phyla of all Bacteria and they almost always dominate the microbiomes of every organism and every habitat. Please reference something more specific for ‘bacteria associated with corals and sponges’.

Lines 547-548. EC94 is designated as a Gammaproteobacteria. As mentioned above, this taxon is a known sponge symbiont, so that seems worth discussing here.

**We agree with the reviewer and in correlation with their previous comment have addressed this within the text of the results and discussion. We have cited the previous paper suggested by the reviewer as well as other studies that demonstrate this bacteria presence in sponges and corals and how it correlates to the dominance of certain phyla observed on the tiles.**

Lines 553-554. Please revise to: “Key physiological functions of corals from the degraded site were improved”. Is it accurate to refer to any coral collected from site B as “degraded”? Some coral colonies appear to thrive at degraded sites. I understand that observed differences between site A and site B with your physiology metrics, but degraded is both nonspecific and subjective. **We agree with the reviewer’s comments and have made the changes within the text. We have also made it clear that corals are from the degraded site rather than degraded corals from the degraded site throughout the text.**

Very nice work

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Reviewer #3 (Remarks to the Author):

The authors use a unique study design to test how tile conditioning at different sites of human impact (healthy vs disturbed) affect two different coral species. The authors deploy tiles in 2 environments and attach corals to these tiles that originate in a home habitat or a transplanted habitat. They use two metabarcoding regions 16S and CO1 data to look at bacterial and eukaryote diversity on the tiles and pair these with physiological metrics of the corals attached to the tiles (and corals from the home environment). The authors suggest that corals attached to tiles from the impacted site do better when attached to substrate-tiles conditioned from the healthy site.

**We thank the reviewer for their overall comments to improve the manuscript and their general interest in the study. We have incorporated all of their comments and suggestions into the paper.**

In general the study is well done, but I have several issues with the study. First, on a terminology point, the authors either introduce or use a relatively poor and confusing term "ecobiomes" which is both clumsy and used inconsistently throughout. Such jargon does not help the MS clarity and is simply confusing -- for instance, referring to the settled community as an ecobiome, but defining an ecobiome as something both biotic and abiotic... I would strongly suggest to avoid confusing terms that sound catchy but are unnecessary.

**As mentioned by the first reviewer, we agree that the term is perhaps antiquated and not relevant anymore and have decided to remove it completely from the MS. We have clarified that we are focusing on the invertebrate and bacteria communities.**

I find the conclusions of the paper, that corals are "able to tolerate stress more if they are from a degraded site and added to a transplant-healthy tile" and that this approach should be used in reef restoration is a bit disingenuous.

**We have clarified in the abstract and in the conclusions what we may mean by this and have changed the tone to make more sense within a holistic and subjective view.**

The enhanced performance is really limited to some changes in antioxidant capacity (unclear why), and some changes in photopigmentation/photoacclimation/symbiont cells/photopigments. The latter is not an effective metric for health, which is in itself a broad and non-descriptive term. There are changes in photochemical efficiency and light-ETR kinetics, but some caution would be advised here. This is even more important in the case of suggesting this be applied in reef restoration, as it skirts the point of invasive species, pathogens, vectors that could lead a healthy reef into decline.

**We appreciate the reviewer's critical analysis and agree that caution must be exercised when interpreting the metrics of coral health, especially regarding the potential implications for reef restoration. We acknowledge that the parameters such as antioxidant capacity and changes in photopigmentation and symbiont cell densities, taken individually, may not conclusively determine coral health. However, our study presents a composite view wherein these parameters collectively contribute to understanding the physiological state of the transplanted corals. Our findings indicate significant signs in these physiological measurements, which are well-established proxies for assessing coral health. For instance, enhancements in antioxidant capacity, although not directly indicative of overall health, suggest an adaptive response to stress, which is crucial for survival and acclimatization under new environmental conditions. Similarly, changes in photopigmentation and symbiont densities are indicative of photoacclimation, which plays a vital role in the coral's ability to adapt to varying light conditions—a critical factor in their potential for restoration use. The observed alterations in photochemical efficiency and ETR kinetics further support the notion that the transplanted corals are undergoing significant physiological changes. While we agree that these metrics alone are not definitive indicators of health, they provide valuable insights into the stress responses and potential resilience of coral species under transplant conditions. Moreover, we are mindful of the concerns regarding the introduction of invasive species, pathogens, and vectors in the context of reef restoration. Our study strictly focuses on physiological assessments and does not advocate for unchecked application in restoration projects without comprehensive risk assessments. We believe our study contributes valuable primary data on the physiological adaptations of transplanted corals, offering insights that could inform more targeted and safer approaches in reef restoration efforts. Furthermore, we have added a few sentences to the discussion section of the manuscript based on this response, to compliment these points.**

The use of metabarcoding data is interesting here, but the execution is a bit odd. The authors report prokaryotes in CO1 data, but 16S would be where bacteria should be reported as CO1 is used for animals, notably metazoans. The 16S data is also not analyzed in a beta-diversity framework (PCoA) as I would expect. Maybe there is a reason for this but it struck me as strange to not represent CO1 and 16S in similar frameworks.

**We agree with the reviewer and have added 16S PCoA data and have made improvements in the analysis of these results and have incorporated the reviewer's suggestions into the manuscript. This has been reflected in the reviewer's comments below.**

As a more minor point, the authors use photosynthetic throughout in places where photochemical is the right term. I recommend care being taken in terms throughout.

**We agree with the reviewer that photochemical is the right term here, which we had used in several places. We have now replaced the term ‘photosynthetic’ to stay consistent with terminology used throughout the manuscript.**

I find some of the descriptions in the writing and figures hard to follow and it is difficult to tell in certain passages and figures if "B-site coral transplants" refer to B site tiles or B site corals, some clarity in the legends and in descriptions would help this.

**We agree with the reviewer and per the suggestion as a previous reviewer have ammended these issues within Figure 1 to clarify. We have also combed through the text to fix any potential places where this could have caused confusion.**

Other suggestions are that the results be reduced significantly, as they are entirely too long and labored with too many post-hoc tests that do not seem to relate to hypotheses. It would appear in-site post-hocs are important, and the transplant tile-corals relative to their home-tile corals are the important contrasts.

**We agree with both this reviewer and the previous reviewer on this point and have made several changes to reduce the results section, focus on hypothesis supporting results, and clarified several important take aways.**

Lastly, some care needs to be given to the SI and formatting, as it is not in a state that is ready for publication.

**We agree with this comment and have incorporated suggestions by the reviewer as described below as well as Nature formatting guidelines to ensure the SI is formatted correctly and ready for publication.**

Specific comments:

or Line 2: this is an ecosystem, do we need a new term for it?

**We agree with the reviewer and the previous reviewer and based on their prior comments have removed this terminology.**

Line 5: where are these sites, red sea, pacific, Caribbean?

**We have added to the text and specified that these sites are in the Red Sea.**

Line 6-7: “was used?” phrasing awkward, I suppose this is just descriptive – not seeing a “why or we tested” here. You refer to the data from these tools later but it seems odd to highlight this here when you can combine parts of this in the sentences where you talk about what you assessed on the tiles

**We agree with this comment and have added the targeted genes and sequencing used in the appropriate places where discussed in the text.**

**Abstract:**

“After 12 months, Site A tiles that were transplanted to Site B, were taxonomically richer and more diverse in invertebrates than the original tiles at Site B (detected via Cytochrome c. Oxidase subunit I mitochondrial gene and metabarcoding). Bacteria from organismal communities associated with healthy reefs, were more prevalent on Site A tiles and Site A tiles that were transplanted to Site B (evaluated using 16S rRNA gene sequencing).”

Line 8: unclear if these tiles were out at home site for 6 months or in their “away/transplanted” site for 6 months, how long were these tiles conditioned or were they? Not sure what a “biomimetic” tile is. Need to tell us the coral species.

**We have corrected these few lines to clarify the reviewer’s points, explained the conditioning, what we mean by biomimetic tiles (which are explained further in the MS text), and stated the specific coral species.**

**Abstract:**

“Biomimetically designed terracotta tiles were conditioned for 6 months at Site A and Site B to allow community growth, before Site A tiles were reciprocally transplanted to Site B and vice versa. Two scleractinian corals from each site, *Acropora eurystroma* and *Stylophora pistillata*, were attached to the biomimetic tiles for an additional 6 months.”

Line 14: what stressor?

**We clarified the stressors that we were referring to in the text.**

Line 15: if you are defining an ecobiome as chemical properties on a reef, transplanting a tile is not transplanting the chemical properties but the biological properties of a substrate. The term ecobiome seems a bit of a neologism, and I’m not sure it is explained (or used) properly here in the context of a tile-transplant study.

**Referring to this comment and previous comments we have henceforth removed this phrase and have clarified that we are focusing on invertebrate and bacteria biofilm communities and described our study in much plainer and clearer detail.**

Line 17: this obviously brings up questions about invasive species, spread of pathogens, and many other issues. It is an interesting recommendation but rings a bit tone deaf to the complexities and caveats.

**We understand the reviewer’s concerns, therefore, we have clarified this in the manuscript that these are potential benefits that can be derived by organismal communities from healthy coral reefs. We think that we have demonstrated this potential as shown by our results and our own observations. We have clarified in other places in the text that this could be a potential side effect of bringing a community, however, we feel that there are more issues that could arise with the persistence of a degraded habitat that continues to experience stressors as opposed to local organisms from one nearby reef being transplanted to another.**

Line 19: isn’t environmental change the driver and not the ‘response’ – phrasing here needs clarification

**We agree with this comment and have changed this opening line to clarify our point.**

**page 1:**

“The degrading health of coral reefs caused by ecosystem changes can lead to the shift in available nutrients, chemicals, microbes, vertebrate and invertebrate communities, and coral health<sup>1-3</sup>.”

Line 27-35: you are using ecobiome in a way that is not in line with the definition you provided in the abstract. The first part of the sentence is what you are defining as the ecobiome, the last part you are saying it also encompasses (which matches the abstract). You emphasize benthic,

but this is only 1 part of a 3d ecosystem. In general, not very clear. It seems like this is simply jargon for ‘a coral reef ecosystem.’

**Referring to this comment and previous comments we have henceforth removed this phrase and have clarified that we are focusing on invertebrate and bacteria biofilm communities and described our study in much plainer and clearer detail.**

Line 40: this is a managers nightmare – and sounds the authors are suggesting this is all pro and no con.

**We agree with the reviewer and have changed the sentence.** “These observations suggest that invertebrates and microbes surrounding corals could play a role in their health, implicating the potential that these communities from healthy reefs may vary and influence coral health differently than at degrading reefs.”

Line 54: “benthic ecobiome communities” doesn’t make sense, and this term is not helping throughout. A community is fundamentally a living thing, but you are describing an ecobiome as living and non-living. I recommend dropping the jargon. You are asking (as I understand) how the biological and chemical properties of an ecosystem favor different microbial and invertebrate communities on the benthos and how these assemblages affect coral growth. Say it plainly and clearly.

**Referring to this comment and previous comments we have henceforth removed this phrase and have clarified that we are focusing on invertebrate and bacteria biofilm communities and described our study in much plainer and clearer detail.**

Line 63: again, as defined, “ecobiome” does not work here.

**We have removed this term and rephrased these sections.**

Line 68-72: this is pretty bold conjecture considering your findings, caveats, and scale. Perhaps dial back.

**We agree with the reviewer and have updated the sentence accordingly.** “We harness a holistic approach to showcase the capability of transferring the benthic layers from one coral reef to another. This method presents a new restoration strategy, using a coral reef ecosystem transplant (aCRET) to boost coral health and future reef resilience.”

Line 80: Give lat-long for the sites Line 62: terribly vague and almost secretive. How do they differ? How far apart are they? Give a map? You should be able to describe this for us with referring to other sources. Give lat-long for the sites, and tell us what a biomimetic terracotta tile (or show one in a figure)

**We provided a map and location of sites in our supplementary file (Fig. S1). However, we have added the latitude and longitude of the sites in the Fig. S1 the supplementary figure. We describe that they are roughly 6 km apart in the first paragraph of the methods L391 formerly (L84). We also cite a few previous studies (references 29, 31, 32, and 33) in our descriptions of the sites. We provide a source 45 for the biomimetic tiles and have also added a photograph and description in the supplementary figures (Fig. S2).**

Line 86: is light pollution relevant here? Or is it “light-levels” of pollution

**We agree with the reviewer and have removed to just ‘pollution’ as we also describe ‘human impacts’ which also encompass light pollution.**

Line 89: biomimetic terracotta tile (show one in a figure?)

**We have added a picture to the supplementary figures showcasing what they look like. Fig. S2.**

Line 91: I'm confused – they were floated vertically at 10m, but also attached to the substrate? Seems it can't be both unless you have benthic and floated treatments. From the image in figure 1 it looks like none of the tiles are actually on the bethos, which seems odd if you are trying to recruit benthic organisms and make an environment that is like the reef (for instance, macroinvert and vert (crabs, worms, plankton, fish) may not colonize a floating tile hanging 10m in the water column vs. a tile on the substrate.

**We have changed the sentence to make more sense and we clarify this in the text in the first paragraph L378-379, L384-385, and 392. Both coral reefs at Site A and Site B are very large and patchy and some parts of the reef are growing on artificial structures and nursery tables that have been present at the sites for decades. The reef itself sits at at about 8 m depth in the water, and this is where the tiles were attached to. The tiles in their structures were directly attached to this reef and were level with different areas of it. As you can see from our diversity data and also from previous studies using these structures we were able to see macroinvertebrates such as worms (annelids and polychaetes) on the tiles. We observed many benthic invertebrates colonizing these tiles.**

Moreover, if you put coral on these tiles there will inevitably be shading and modified light/flow environments.

**The tiles are specifically slanted at angles so that they are not directly covering each other and there are holes in the tiles to allow light penetration. There is enough space between them to allow flow and movement. Mentioned in L388-391.**

Lastly, I'm not seeing a good description of the light, temp, depth for your study. While these sites may be described already, I assume some samples were taken in your current study to track the environment during deployment.

**We included a brief description of the sites and why they were chosen in the first paragraph of the Methods section and reference Table S1 for more details. We provide a table in the Supplementary Information (Table S1), which goes into much more detail on the conditions at each site.**

Line 104: this should be complexa and robusta.

**This sentence has been rephrased to incorporate these terms.**

Line 115: photochemical not photosynthetic

**This has been changed based on the previous comments.**

Line 116: “endosymbiont algae” and state Symbiodiniaceae

**We have incorporated this suggestion throughout the entire text.**

Line 117: what is health? Pigmentation maybe and health only if bleaching observed, but this is a vague and nondescriptive term

**We agree with the reviewer and have changed this in the text.**

Figure 1. bottom right should be a table. It is not effective as a figure, recommend giving more space throughout by stacking as a single column and expanding width of each panel (hard to see what is what).

**We agree with the reviewer and have made the changes accordingly in Figure 1.**

Line 128: is this Phase III? Why not use the terminology you introduce in figure 1? Corals were sampled at final timepoint only though, so not at Phase II? Unclear here. Also, how many tiles had corals in total here – were there tiles samples at each time point WITHOUT corals in Phase III?

**We agree with the reviewer and have made adjustments in the terminology and phrasing to better explain this process in the methods section in the ‘study sites and experimental design’ and the ‘sample collection and processing’. We have also added more information according to the reviewer’s suggestions.**

Also, recommend using fewer terms, like “organismal biomass”, just say the benthic community this is what you are sampling.

**We agree with the reviewer and have changed this in the manuscript.**

Line 132: was the water also filtered and analyzed (or added to your blender)?

**The seawater that was in the bag with the tile was not meant to be analyzed with the sample, however it is possible that a very small amount may have been included in the blender upon analysis. We have clarified this in the manuscript.**

Line 133: separated at all or scraped into a blender as a whole community

**Thank you for the point, we blended as a whole community. We have clarified this within the text.**

Line 141: why were they allowed to adapt for 24h. Wouldn’t it have made more sense to get a rapid measure of what their photochemical efficiency was under site conditions, diving PAM etc? It seems an acclimation period makes your effect of site less clear and confounding with in-lab, post-scraping off a time, acclimation. Also, remind us of the n=coral for each site/treatment. **The reviewer is correct, thank you for catching this. We did not acclimate for 24 h we conducted Imaging Pam that evening on the same day of sampling. There was no acclimation period before conducting photochemical measurements. We have fixed this in the text and also added the number of replicates (n= 5).**

Line 169: why 97% clustering, 100% ASVs are the norm now and allow for comparison across studies with full sequences. Seems antiquated?

**We understand the reviewer’s point about ASVs, however our methods for processing are consistent with several studies in current literature, especially when working with eDNA and COI. Please see the following examples:**

**<https://www.nature.com/articles/s41598-023-31410-4>**

**<https://www.nature.com/articles/s41598-023-41832-9>**

**<https://www.nature.com/articles/s44185-023-00033-3>**

<https://www.nature.com/articles/s41598-018-26332-5>

<https://www.nature.com/articles/s41467-023-43960-2>

Additionally, the choice between OTUs and ASVs depends on the “specific goals of the study, OTUs are suitable for broad-level diversity assessments”( [https://www.linkedin.com/posts/insilicome-bioinfo\\_otu-rrnagene-amplicon-activity-7116421918437617666-j7EC/](https://www.linkedin.com/posts/insilicome-bioinfo_otu-rrnagene-amplicon-activity-7116421918437617666-j7EC/)). Other studies that compared between OTUs and ASVs, suggested that using clustering methods have little impact on alpha and beta diversity patterns of communities. This means that either analysis would present similar diversity patterns and comparable results (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC10269476/> ).

Line 172: unclear why you are rarefying for alpha diversity but then not doing so for beta diversity (or so it sounds in the passage below on line 176). You should use the same rarefied data for all analyses. Also, generally taxonomic assignment is made, then downstream analyses and rarefaction etc. The order for the final passage seems like it should go before the richness info—which can all be done in R/phyloseq etc

**Alpha diversity metrics have to be calculated based on equal sampling depth hence the rarefaction step, but for beta diversity we used a centered log ratio transformation instead to perform comparisons between samples (mentioned in line 249) based on arguments against rarefaction for beta diversity (see PMID: 24699258, 29187837). As for the order of the paragraph, we performed rarefaction, calculated alpha diversity metrics, and then assigned taxonomy to all sequences using QIIME2. We have updated this line. While richness info can come last, we wrote the paragraph as per the order of the steps we took in processing the data.**

Line 186: photochemical not photosynthetic, correct throughout.

**This has been corrected throughout based on previous comments.**

Line 193: the “o” and “m” should be subscript in Fo Fm.

**We have corrected this.**

Line 198: define FSW.

**We have fixed this.**

Line 201: single or double dip technique

**Single dipping to maximize surface area. This is added to the text.**

Line 202: holobiont, or for host and separately for symbiont

**Clarified to holobiont.**

Line 211: with concentrations determined from equations by...? Jeffrey & Humphrey?

**This was updated and the citation was added.**

Line 233-Line 234: why on relative abundance? Was a Hellinger transformation or other

applied? Bray Curtis “dissimilarity” distance matrix (as it should be noted) should be performed on the ASV/OTUS data and does not require relative abundance transformation – this should be explained a bit (I admit there are many avenues to these analyses)

**This point was clarified in the text and ‘dissimilarity’ was also added. This sentence should have only focused on abundance and not added ‘relative’, it was a mistake that we have corrected. We used abundances for reflecting community changes at both locations as it is slightly more accurate than just presence or absence for comparing different ecological factors.**

Line 250-252: grammar here, and you have already used PERMANOVA above, so define above and give acronym here

**We have corrected this.**

Line 262: define PAR, perhaps in line 189. Later on you mention “PAR50” and “irradiance level” interchangeably, which is confusing since (passages around line 368).

**PAR was defined in lines 189-190 so that it is clear with the updated definition of PAR50 in lines 820. We have changed the comparison of irradiance level for PAR50 and updated to reflect light attenuation.**

Line 271: density not abundance

**This has been corrected.**

Line 275: already gave the FDR abbreviation above

**This has been fixed.**

Line 292: what is an ecological indices? You mean communities?

**This has been since corrected.**

Line 306: can’t be  $<0.000$

**A number 1 was meant to be added at the end of this. This has been corrected.**

Line 301: based on COI or 16S or both or...? What is richer in taxa telling us that richer in species isn’t – taxa only informative if you tell us at what level.

**In the first line of the paragraph (now L874) we have specified from “Twenty-eight major taxa from COI identified...”. Taxa has been clarified and omitted in the opening two paragraphs.**

Line 302: does it make sense to have prokaryotes here? Considering COI is not used for prokaryotes (and you have 16S data for them below), it seems these should have been pruned from your data. Maybe I’m wrong, but certainly it isn’t a group you highlight with the eDNA.

**This has been corrected within the text and data.**

Line 310-318: Could this be said in 2 sentences? It seems long for the take home

**This paragraph has been edited and reworded to reflect a more concise explanation of the results:**

“The Original tiles from Site A and the tiles transplanted from Site B to A, contained a richer community of species compared to the Original tiles at Site B ( $p < 0.001$  and  $p < 0.05$ , respectively; Fig. 2A). The tiles that were transplanted from Site A to Site B similarly had an increased species richness than the Site B Original tiles ( $p < 0.001$ ) and the Urban T2 tiles ( $p < 0.001$ ; Fig. 2A). These observations generally indicate that Site A tiles, including the tiles transplanted to Site B, contained a higher observed species richness compared to the tiles that remained at Site B. In general, the community composition of each of the tiles that never left their respective site was similar, whereas the tiles transplanted from Site A to B, were distinctly different from the other tiles at Site B and were more similar to their origin (Fig. 2B).”

Line 336: you use PCoA for this same purpose for CO1, why aren't you also doing it for 16S? CO1 is not a marker to be used for prokaryote community diversity. Also the figure for PCoA in figure 2B could be improved: (1) the points could be with ellipses, (2) the orientation is poor with a large white space and points all clustered in a corner of the plot (re-align the x-y to center your data).

**We agree with the reviewer and have added our 16S PCA to Fig. 2 (See Fig. 2D), additionally we have removed the prokaryote analysis that may have snuck into the COI analysis. We have improved the Fig. 2B according to the reviewer's suggestions.**

Line 364: what is “3” in the stats? n? df?

**We have removed this to not cause confusion as it does not add anything to the results.**

Line 367: was irradiance measured at the sites for these corals? Nothing was reported on this. **If we understand correctly, in general irradiance of each site where this study took place was not measured specifically in this study. We have information previously detailed in studies from these locations that have measured irradiance at these sites.**

Line 373: the writing here is confusing – a coral can't have “an irradiance”. This is found through this section and subsequent paragraphs. In general I think the results section needs to be condensed and clarified with less “there were a difference” sentences followed by descriptions of the differences in a second sentence – I'd advise to be more direct and cut throughout.

**We have made efforts to concisely comb through the results and revise as also suggested by another reviewer. These changes can be found reflected throughout the results section.**

Line 376: if there is an interaction, this should be reported and emphasized the main effects since the main effects cannot be interpreted in the face of these interactions.

**This sentence has been clarified.**

Figure 3. No need for 2x labeled on the y axis..., probably a good idea to have shaded confidence intervals here too. You have these in figure S2.

**We have made these corrections that are now reflected in the figure.**

Line 393-432: the results section is entirely too long. The points here on changes in symbiont densities and pigmentation are being described in too much detail, and in general, the authors are applying fully orthogonal posthoc tests which do not need to be made. What is the a priori reason for this? Why should all levels be tested relative to all others (i.e., Native site A compared to Original Site B?) It seems overboard...

**We agree fully with this comment and as previously suggested have made full efforts to reframe the results and make it much more clear according to the main points. This can be reflected within the updated results section.**

Figure 6. why are there only single points for each group? Shouldn't this be a point cloud? If plotting the centroid, ok, but also plot the raw data.

**We conducted this PCA to visually explore the relationship between the variables, and not necessarily for hypothesis testing. Once we combined the coral physiology parameters with ecological descriptors from the tiles, the variables had different sample sizes, which produced a MATRIX with a considerable number of NA values. To avoid the shortcomings of this unbalanced design, and considering that we were not interested in the potential of any variability within each treatment and did not plan parametric analysis for this multivariate approach, the PCA was made using the average for each treatment.**

Line 513: there are other organisms you are transferring, not all are +

**We deleted this sentence as we added another sentence that is a bit more subjective and highlights the potential of transferring communities associated with healthy reefs to degraded reefs to help degraded corals.**

“It is important to note that the aCRET method may not be suitable for all global coral reefs and coral species, as some organisms within these communities may not always be conducive to boosting coral health.”

Line 515: (on settlement tiles).

**This has been clarified to mention on substrates.**

Line 516-520: There certainly is high variability between the original/natives and tiles for physiology and antioxidant capacities. It seems TAC is your best point that this matters as all other metrics for the contrast that matters (B site corals attached to A site tiles) are comparable or lower than Native B/original B site corals. In any case, I would recommend caution in your selling of the take home here, as you have low sample size and corals not attached to the benthos...

**While we understand the reviewer's point here, we actually do see a shift in the baseline in corals affixed to healthy non-urbanized tiles at Site A vs. Site B urbanized tiles. It is not only for TAC we see a shift towards better performances, especially when you combine all the parameters together. While, individually each parameter is a proxy for coral health, when combining (i.e., in Fig. 6 biomarker response) all health metrics including the data from the invertebrate and microbial communities, you can look at everything as a whole to see its whole affect on the transplanted corals. The next steps would be to conduct future experiments to do a more in-depth analysis of the coral metrics and physiology that were boosted. However, this should be looked at as a potential, scalable, holistic, inexpensive method for boosting coral physiology. As mentioned in response to an earlier comment our study presents a composite view wherein these parameters collectively contribute to understanding the physiological state of the transplanted corals. Our findings indicate significant signs in these physiological measurements, which are well-established proxies for assessing coral health. While we agree that these metrics alone are not definitive indicators of health, they provide valuable insights into the stress responses and potential resilience of coral species under transplant conditions. We have also addressed the benthos**

comment earlier as well, as these tiles were at depth with reef communities and as seen by the different benthic taxa accumulated on the tiles. Yes, caution should be exercised when it comes to the smaller sample size, which is why we aim to have future studies with larger sampling numbers. Although sampling size was small, the size of the tiles were quite large in order to accumulate a sizable community.

Line 536: seems like you should report some of this info in a summary table as you haven't described these factors in any detail

**We have this detailed in the supplementary info as a table we added the appropriate citation after this sentence.**

Line 556: are B site transplants (yellow) the corals from B transplanted to A or the corals from a A transplanted to B? Looking at the yellow line and reading your passage here, it would suggest (1) B corals transplanted to A saw an increase ETR, but this is not really in line with your hypotheses and questions (healthy corals going to a degraded reef to support restoration). If it is the opposite (yellow B = A corals to B site), then this supports healthy reefs restoring degraded reefs, but this is not what the sentence states here. Overall, there is a need for clarity on the legends and the passages.

**We can understand the confusion that this could have caused, but in fact it is the latter comment that the reviewer mentions, where both the transplant treatments are indicated in yellow, and each plot is denoted by A or B for sites to indicate the particular transplant. The reviewer is correct in the later portion that it is A healthy substrates that went to Site B and received site B corals attached to them. Our hypothesis is supported that healthy reefs can help restore degraded reefs. However, we have made efforts to clarify this in the text where the reviewer has indicated.**

Line 579: these passages are getting hard to understand – the corals were transplanted, the tiles were, yes? So, saying “corals from the tiles that came from the degraded reef moved to the healthy reef..” you are really saying that healthy-reef corals adhered to tiles originated from the degraded reef, but this is not clear the way the text is written. I recommend rephrasing throughout to be clear and adding in emphasis (Figure 6A, etc) when you make statements so the reader knows what you are referring to, including in the legends “transplant columns are corals from their respective sites added to tiles from the opposite site”.

**We agree with the reviewer that due to the complexity of this experiment it is often hard to follow, therefore we have made significant strides to make it as clear as possible with phrasing and wording of these passages. We have updated and made significant improvements and changes to the discussion passages.**

Line 600-605: a bit of word salad, I'm not following – what is Noah's Ark?

**We have removed this and clarified this sentence.**

Supplement:

generally I've never seen “SI#” noted in figures, usually “S#”, since the “I” looks like a one. Is this a NatComm style?

**The reviewer is correct, we have changed this throughout.**

Table 1. sites should be listed starting with “A” not B. Would be easier to tell what this data is saying if it was sorted as “A” all the way through, then “B”. The alternating A/B isn’t super insightful, also some weird the formatting with Winter (different fonts half way through?)  
**We have incorporated this suggestion and updated the table as well as making sure that the font type and size is all the same.**

Do a line page break at each table or figure to separate them (ie Table S3 is broken in half). This is pretty basic stuff and shows an unfortunate lack of attention to detail.  
**We have corrected this per reviewer’s suggestion.**

Table S4. Need same # of decimals in p values. Seems odd the 4th t value isn’t negative like the others for similar metric.  
**We have organized the data according to reviewer’s suggestion. After clearing unnecessary data, the two p-values remaining were 0.05 and did not need more decimals. T value issue has been resolved.**

Table S4 and S5 – give the metric/response instead of “value” and don’t list it in every row, show the metric, then divide the cells with an underline when the metric changes. Avoid repeating information.  
**We agree with the reviewer and have fixed these tables to reflect a more clear display of data. We used variations in shading to show differences in each treatment.**

Table S4-S9, as I noted in text, seems like post-hoc tests are way overdone. Not tailored to hypotheses or relevance to data  
**We agree with the reviewer and have fixed this to reflect the hypotheses represented in the manuscript.**

Fig S3 and S4 No y axis label (and why are tables mixed in with figures?) They should be separated.  
**We have fixed this according to the reviewer’s suggestions.**

Table S10, left column shouldn’t be in bold, only signif p values  
**We have fixed this and clarified in tables.**

## Response to Reviewer #2

Dear authors, Thank you for carefully and thoughtfully addressing all of the reviewer's comments. I appreciate your hard work! In my opinion, the manuscript is ready for publication. **We thank this reviewer for their patience and helpful suggestions to get the manuscript ready for publication. We appreciate all their time and effort.**

## Response to Reviewer #3

I appreciate the thorough responses by the authors to all the reviewer concerns, especially in regards to the 'ecobiome' neologism and adding detail/justification for their analyses, findings and approaches. I have no further comments (and apologize for taking so long in returning my review). Well done on the revised MS, and I look forward to seeing it published.

**We appreciate that this reviewer pointed out several important and key comments that have led the manuscript to its current publishable state. Thank you again to this reviewer for all their time and effort.**

## Response to Reviewer #1

**We appreciate the dedication of this reviewer to help us get our manuscript to a refined and publishable state. We appreciate all their time and effort to do so. We have thoroughly combed through their suggestions and have made immense efforts to address every point in detail throughout the manuscript and the supplemental information. We appreciate their feedback and hope that they can see that we have diligently prepared the manuscript to be ready for publication.**

I appreciate the effort put into the analyses, however, I'm still not convinced by some of the results shown.

**We have taken into account all the suggestions put forth by this reviewer and have made a lot of effort to incorporate their suggestions into the manuscript to make it stronger and the story more clear.**

I'm having trouble discerning any clear patterns from Figures 2C-E. If the bacterial communities are not significantly different across relevant pairwise comparisons, as Figure 2D suggests, it's best to state this clearly and consider removing the figure.

**We agree with this point. We originally did not include Figure 2D in the manuscript for this reason, however another reviewer suggested we include it to show the complimentary result to the COI. Although, it no longer makes sense with the entire story, we therefore have just mentioned it in the manuscript text in regards to no obvious patterns, and have now moved it for readers to find in the supplementary figures. We have since updated Fig. 5 according to the reviewer's suggestions.**

I couldn't find any pairwise comparisons showing significant differences between original A vs. Transplant A or original B vs. Transplant A. In my opinion, these are key comparisons to establish what is special about Transplant A that improved coral physiology in site B. The only mention of

statistical differences is in lines 347-349, which refers to the overall model. This was expected to be significant, so more detailed pairwise analysis would be helpful.

**We agree with this point and although we have mentioned the noteworthy comparisons between these specific treatments for invertebrate COI and for 16S bacteria, especially for the EC94 species of bacteria. We have now added more statistical analyses which refer to those treatments in particular in the results section of the text for benthic community characterization.**

Could you also explain why replicates are not shown in Figure 2E? The heatmap does not have clustering, and the top 25 most abundant bacteria do not appear to differ significantly across comparisons. Can the authors explain the reasoning for choosing the top 25 taxa to be compared across treatments? maybe less abundant taxa are responsible for the differences? I understand the reasoning for looking at the community as a whole, but focusing on the top organisms might not be as informative since they could be common to all treatments. I suggest conducting a differential abundance analysis, which could highlight the groups that matter, even if they are not the dominant ones. If the authors still want to contrast dominant groups maybe barplots would be better in this case?

**We agree with this point and have changed the plots for 2C and 2E (now 5C and 5D) to barplots – which we believe are much clearer and easier to understand. Additionally, we have added text discussing the differential abundance comparison between the main treatments as highlighted by the reviewer – Original A, Original B, and Transplant A. Originally, the top 25 taxa (now 20) were compared because the other taxa were either with low abundance or did not make the QIIME cut-off, but this has now been noted in the text in the statistical analyses section of the methods. We have moved the heatmaps from this figure to the supplementary information.**

The main point you're making is that corals grown surrounded by communities originally from site A have higher photochemical performance when transplanted into site B. It might be clearer to present this result first, followed by the characterization of the community composition guided by the coral physiology results. To characterize the diversity, focusing on a few key comparisons could help readers navigate the figures more easily. For example, consistently comparing Original A vs. Transplant A and Original B vs. Transplant A across all analyses would be beneficial. I really believe the data has great potential, but unfortunately not well exploited yet.

**We agree with the reviewer on this point and have switched around the results to favor the coral physiology first as it clearly supports our hypotheses. Following the coral physiology we have the benthic community analyses and the IBR comparison to support the improvements observed in the coral physiology and benthic community combined. Again, we have shifted the results to focus mainly on the three treatments highlighted by the reviewer – Original A, Original B, and Transplant A in every single section where we discuss the results and the discussion. This also includes the differential abundance analyses which we have added as suggested by the reviewer.**