

A rapidly closing window for coral persistence under global warming

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This manuscript has been previously reviewed at another journal. This document only contains information relating to versions considered at Nature Communications.

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

Version 0:

Reviewer comments:

Reviewer #2

(Remarks to the Author)

I thank the authors for their revised manuscript, which reasonably addresses all of the major comments I raised in my first review. I have some remaining suggestions, but they are all fairly minor. I think the revised manuscript is very good and, as mentioned in my first review, the incorporation of climate-related uncertainty is a particular strength of this study. Other research groups in the coral reef modelling space have much to learn from this. I would therefore recommend this paper to the editor for publication, subject to consideration of these minor comments.

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L40: I'm still not completely happy with the phrase "Future resilient reefs were mostly found in bleaching refugia" because I still think it could be misinterpreted by non-scientists as an empirical observation/prediction. This is less important for the main text, but very important for the abstract. I would prefer phrasing along the lines of "Our simulations predict that bleaching refugia may host the most resilient reefs under future climate change, as well as reefs with a greater diversity of thermal phenotypes".

L226-230: I still think this sentence would benefit from rephrasing (I think it is now less clear than the original version). Something along the lines of "Thus, while we may naïvely expect reefs to continue to shift towards a more stress-tolerant community, our simulations present a more complex picture due to the interacting effects of demography, connectivity, thermal tolerance, and rates of adaptation".

L321-322: The distributions for mean heat tolerance (between barrens and hubs, dotted vs solid in fig. 6b) are much more distinct than the distributions for coral cover (between barrens and hubs, dotted vs solid in fig. 5b), yet the former is described as "comparable distributions" while L284-286 instead draw attention to the differences in the latter. Do these figures not imply that the effect of connectivity on adaptation is greater than the effect on coral cover?

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L705-706: Perhaps rephrase to "Parameters controlling the impact of cyclones and CoTS have relatively limited effect on coral cover."

Extended Data Fig. 1: I would consider adding transparency to the individual reef coral cover trajectories (or plotting a 2D histogram of states rather than individual lines). In its current form, there are too many lines to tell what the density of trajectories are at different levels of coral cover.

Extended Data Fig. 12: I'm not sure what the point of this figure is! The density of points is too high to be useful (as above) but I can't see any convincing correlation by eye, certainly not a linear correlation that would warrant the linear best-fit (?) lines. The highest levels of coral cover appear with intermediate levels of larval supply, so I wonder if this is just a trivial consequence of the fact that most reefs have intermediate levels of larval supply (and there are therefore more extreme values for reefs with intermediate levels of larval supply).

Extended Data Fig. 13: I think the figure is fine, but I wonder if it might be more useful to plot the relative difference in coral cover rather than the absolute difference in coral cover (or to just plot the mean coral cover with a shaded region spanning the low and high values, a bit like Extended Data Fig. 9).

(Remarks on code availability)

Reviewer #3

(Remarks to the Author)

The authors have done a very solid job dealing with these comments. The treatment of adaptation in particular is a great improvement, and will be much clearer to readers. Overall, the writing is now much clearer, with substantial improvements following each comment about clarity.

I will write separate assessments of my own comments (R#3), and those of R#4.

R # 3

I had two main comments on the last version of this manuscript.

Critique 1 (Evolutionary Model): I worried that the model underestimated the natural variability of heat tolerance among coral species, particularly because each "morphological group" actually represents multiple species. I therefore suggested that the authors present wider within-group variation (ideally reflecting empirical evidence) to strengthen confidence in the evolutionary assumptions of the study.

Critique 2 (Validation & Uncertainty): I was concerned that the current validation relied too heavily on visual comparisons, and may have overestimated the model's predictive accuracy. I recommended a formal assessment of forecast error (e.g., comparing decadal predictions to actual observations) and pointed out that the model appears to "know" when disturbances happen in hindsight, which would not be possible in forecasts.

On the first point, I don't believe the authors have addressed my comment in their review. They say: "The variability in heat tolerance within a group was derived from experimental observations (Humanes et al. 2022) of a single population (*Acropora digitifera*) under simulated heat stress." This means they are using empirical estimates of within-population variation in heat tolerance (i.e., a study of a 102 individuals of *A. digitifera* from Palau) to model between-species variation (e.g., the differences among and within all large massive coral species). This would be like looking at the weight variation within adult humans in Australia, and using it to model the weight variation among all apes. I think this will substantially underestimate the potential of corals to adapt to heat stress.

On the second point, I think the authors have done a good job at reporting the predictive skill of their model. I also agree with the previous comments of the first and fourth reviewers, and appreciate that the authors now report the uncertainty associated with all their predictions. However, their report the uncertainty in different ways throughout the paper, which is confusing.

I have three recommendations going forward, sticking to my two main critiques:

(1) The modelled variability in heat tolerance among the groups (I believe "a group" can contain species from different families) be considerably larger than the variation observed within a single population of a single species.

(2) The authors follow standard procedure and report 95% confidence bounds throughout the manuscript, rather than inter-quartile ranges or $\pm$ SD. IQRs are a strange choice, because (by definition) as many predictions fall outside those bounds, as fall within them. Both inter-quartile ranges and $\pm$ SD feel like they're chosen to under-emphasise the variation.

(3) The parameter sensitivity analysis is a great idea, but needs to be more global. The goal here is to estimate the effects of uncertainty, which affects all, not just one, of the parameters. Marginal sensitivity analyses are only useful for reporting the relative impact of the different parameters. Sensitivity analyses should therefore be global, rather than marginal. That is, in your sensitivity analysis the authors should vary all parameters by $\pm$ 20% from their default values, not just one at a time. I think if you run 100 or so simulations, with each simulation varying all parameters by 20%, and show the results, this will be enough to get a feel for how the uncertainties will interact.

R # 4

I have one minor comment and one major comment about the revisions following the comments of R#4.

MINOR COMMENT

Concerning the final comment from the last round of R4. The authors rewrote this section to say:

“Thus, management strategies for adaptation that encompass multiple thermal environments can be flexible and unconstrained by patterns of larval supply.”

I would qualify this statement by saying “our model indicates that ..”.

MAJOR COMMENT: VALIDATION

The authors have undertaken a range of validation exercises to determine the extent to which we can be confident in the model predictions. I appreciate all the efforts.

What a reader will want to know is how accurate the forecast is. The authors primary claim is that: “We forecast a rapid coral decline [from 39% in 2023 to 14% in 2040] before mid-century regardless of emissions scenario”. The model in question has a large number of parameters and assumptions (e.g., the functional forms of the interactions, the groupings of coral species, etc). We know these are inaccurate, but we don't know how inaccurate, and we can't measure most of them. The best way to evaluate this prediction is therefore a hindcast validation, which the authors have the data to support.

The current validation initialises the model in 2008, and predicts coral cover at a reef level (which is then aggregated to subregion, and then the whole GBR) between 2009 and 2023. This is a reasonable test, across a decent time-frame (15 years) that is comparable to the primary predictions.

I would like to see this validation changed in several ways. First, we should evaluate the inaccuracy after 10 or so years. The authors calculate the “difference between the predicted and observed mean coral cover for each available year between 2009 and 2023”, but this averages across short-term forecasts and decadal-scale forecasts. The error will likely be smaller in 2009 (only one year after initialisation) than in 2023 (more than a decade after initialisation). Since the primary claims of the paper are about predictions 15 years in the future, we should evaluate and validate with decadal predictions. That is, initialise the model at 2008, and evaluate at 2018; initialise it at 2009, evaluate it at 2019, etc.

Second, the error statistics cannot be symmetric (not least because coral cover is a bounded variable). The errors (e.g., in the caption to Extended Fig 5, at Line 95 of the main text) give symmetric standard deviations. These should be asymmetric 95% intervals.

Third, the validation assumes that the modeller knows the dates and locations of key disturbance events on the GBR – primarily bleaching events and tropical cyclones. Of course, these are not known in advance, only in hindcasts. To get a better feel for how much uncertainty there is in the forecasts, we need to know what these hindcasts would say about 15 year predictions when disturbance events are not known with certainty. I appreciate that the authors addressed this issue in the previous review, but I didn't buy their response.

To explain why, consider where the authors address the validation results in the main text. “The comparison with monitoring data indicates a credible reconstruction of the past mean coral cover trajectory, with model errors – defined as the annual differences between predictions and observations – being evenly distributed and having a mean difference of -0.3% ($SD=\pm 4.7\%$).”

What they're saying here is that “Our hindcast validation made predictions that turned out to be within 5% of the true coral cover. Thus, when we say cover will drop to 14% by 2040, we can be confident that the real value will be between 9% and 19%. Both of these are a lot lower than the current value of 39%.”

(Remarks on code availability)

Reviewer #5

(Remarks to the Author)

Bozec and colleagues present an elegant study where they model eco-evolutionary dynamics across the Great Barrier Reef under different climate change scenarios, taking into account multiple variables related to demographics, environment, larval connectivity, different stressors (heatwaves, CoT outbreaks, storms), and intrinsic features of corals (e.g., heat tolerance).

The article is well written and has gone through a first round of reviews. In my opinion, the authors have done a great job in addressing all the concerns raised by the former reviewers, especially when it comes to clarifying reliability of the model and cautious interpretation of their findings.

The modeling work is impressive, the assumptions and parameters appear reasonable to me and have been clearly outlined. The results are highly relevant for the current environmental crisis coral reefs are facing. In my opinion, the article is ready for publication as it is.

(Remarks on code availability)

It appears to me that all code needed to reproduce the study have been made available and is well documented. I did not install and run the code.

Version 1:

Reviewer comments:

Reviewer #2

(Remarks to the Author)

I thank the authors for this second revision, and their thoughtful responses to my comments, and those of the other reviewers. I would make one final recommendation, namely to change "recovery is possible" (L25, abstract) to "recovery is possible this century", since the simulations end in 2100 and therefore cannot rule out the possibility of a recovery beyond 2100 for warming $>2^{\circ}\text{C}$ (coral cover reaches a non-zero minimum around 2080 under SSP2-4.5, so could conceivably recover after 2100). Apart from this, as far as I am concerned, the manuscript is ready for publication.

(Remarks on code availability)

Reviewer #3

(Remarks to the Author)

I thank the authors for engaging so thoroughly with my comments and suggestions, and for making so many revisions and running so many additional analyses.

While there are still parts of the paper that I do not 100% agree with, I do not represent the entire field, and the changes made acknowledge the challenges in a model of this complexity.

My one response (and this is for the purposes of dialogue, not further revision) is that while the bounds on HT are important and are indeed wide, the initial distribution will place considerable constraints on future evolution. Specifically, narrow initial distributions may mean wide bounds have no effect on future dynamics.

(Remarks on code availability)

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A rapidly closing window for coral persistence under global warming

We would like to thank the three referees for their careful read of the revised manuscript and their constructive feedback. In this second revision, we ran additional analyses, edited the text, refined two of the main figures and added four figures in the Supplementary Information to account for all comments raised by the referees.

Reviewer #2 (Remarks to the Author):

I thank the authors for their revised manuscript, which reasonably addresses all of the major comments I raised in my first review. I have some remaining suggestions, but they are all fairly minor. I think the revised manuscript is very good and, as mentioned in my first review, the incorporation of climate-related uncertainty is a particular strength of this study. Other research groups in the coral reef modelling space have much to learn from this. I would therefore recommend this paper to the editor for publication, subject to consideration of these minor comments.

We sincerely thank the Reviewer for their thoughtful evaluation and constructive comments on both the initial and revised versions of the manuscript. All remaining suggestions have been thoroughly addressed through appropriate revisions, as detailed below.

General: I can't find details for how CoTS and cyclones affected the coral population dynamics. I see that this is described in Bozec et al. (2021), but it should be described quantitatively (in brief) in the methods.

We have expanded the general description of the model to include a brief overview of how CoTS outbreaks and cyclones affect corals, with reference to the original published model for a comprehensive description of the related mechanisms:

Methods, L425: The model captures the major acute stressors responsible for widespread coral mortality across the GBR (Bozec et al. 2022): temperature-induced mass coral bleaching (detailed below), tropical cyclones, and outbreaks of the coral-eating crown-of-thorns starfish (*Acanthaster* spp., CoTS). Cyclone-induced coral mortality is taxa- and colony-size specific, with mortality rates predicted based on cyclone intensity (Saffir-Simpson scale). CoTS-induced mortality is taxa-specific, with fast-growing corals more susceptible. CoTS outbreaks are simulated using an age-structured metapopulation model, and coral mortality is determined CoTS abundance at a reef, calculated using CoTS age-specific consumption rates. Additional stressors include reduced water quality (suspended sediment), which hinders coral recruitment, and loose coral debris generated by acute disturbances, which hinders survival of recruits, jointly impeding coral recovery.

L40: I'm still not completely happy with the phrase "Future resilient reefs were mostly found in bleaching refugia" because I still think it could be misinterpreted by non-scientists as an empirical observation/prediction. This is less important for the main text, but very important for the abstract. I would prefer phrasing along the lines of "Our simulations predict that bleaching refugia may host the most resilient reefs under future climate change, as well as reefs with a greater diversity of thermal phenotypes".

We have re-formulated this sentence in the abstract as "Our simulations show that resilient reefs are primarily found in bleaching refugia", which clearly states that our findings are based on simulations while staying within the tight word limits of the journal. The new abstract is reproduced below:

Abstract: Coral reefs are increasingly threatened by marine heatwaves causing widespread coral bleaching and mortality. Projections of future heatwaves inform decision-making, but the interaction between disturbance refugia, coral life-history traits and capacity to adapt is key to forecasting coral persistence. Here, we simulate coral eco-evolutionary dynamics across 3,800 reefs of Australia's Great Barrier Reef under current climate projections. We forecast a rapid coral decline by mid-century under all emissions scenarios, with further decline under the most likely warming trajectory. However,

recovery is possible if warming remains below 2°C, allowing thermal adaptation to keep pace. Our simulations show that resilient reefs are primarily found in bleaching refugia, which also support a greater diversity of thermal phenotypes. While cool-adapted corals disperse to warm spots, we found no evidence of ‘gene swamping’ undermining thermal adaptation. Our findings highlight that management opportunities exist to promote adaptation in thermal refugia and warm spots, but emphasise that curbing global warming by 2050 is critical for coral persistence.

L226-230: I still think this sentence would benefit from rephrasing (I think it is now less clear than the original version). Something along the lines of “Thus, while we may naïvely expect reefs to continue to shift towards a more stress-tolerant community, our simulations present a more complex picture due to the interacting effects of demography, connectivity, thermal tolerance, and rates of adaptation”.

We have re-phrased this sentence as follow:

Results, Lxxx: Thus, while it can be expected that reefs will eventually be dominated by the most stress heat-tolerant taxa^{3,5,37}, our simulations present a more nuanced picture of future taxonomic composition emergent from the interactive effects of coral demography, connectivity, thermal tolerance and rates of adaptation, which have not yet been teased apart^{41,42}.

L321-322: The distributions for mean heat tolerance (between barrens and hubs, dotted vs solid in fig. 6b) are much more distinct than the distributions for coral cover (between barrens and hubs, dotted vs solid in fig. 5b), yet the former is described as “comparable distributions” while L284-286 instead draw attention to the differences in the latter. Do these figures not imply that the effect of connectivity on adaptation is greater than the effect on coral cover?

To address this point, we have redrawn the reef distributions for coral cover (Fig. 5b-c) and mean heat tolerance (Fig. 6a-b) to more clearly demonstrate how variation in heat stress exposure (thermal refugia vs. warm spots) and external supply of coral larvae (larval barrens vs. hubs) influence reef states and adaptation by 2050 and 2100. To reduce the influence of confounding factors unrelated to recent heat exposure or larval supply, we excluded reefs affected by reduced water quality (inshore reefs) and those affected by cyclones within the 5 years prior to 2050 and 2100. This filtering enhances the contrast among reef distributions (see revised Fig. 5 and 6 below) and allows for cleared interpretation of ecological/adaptive responses that are more directly attributable to recent thermal stress and larval supply.

In terms of coral cover, Fig. 5c reveals consistent and marked differences between larval barrens and hubs, with higher coral cover in larval hubs across all SSP scenarios – except under SSP3-7.0 in 2100, where extreme heat stress suppresses coral recovery, even in reefs receiving the highest larval input. For mean heat tolerance, Fig. 6b shows that reef distributions in 2050 are largely similar between larval barrens and hubs across all SSPs. By 2100, slight differences emerge, with larval hubs supporting higher proportions of heat-tolerant corals, contrary to the expectation that external larval supply would hinder adaptation by introducing maladapted larvae from cooler reefs. Therefore, we conclude that connectivity does not exert a clear influence on local adaptation. We revised the text to clarify the influence of external larval supply on future coral cover and heat tolerance. To further support our conclusions, we also provide a new figure (Supplementary Fig. 13) showing the distribution of coral cover and mean heat tolerance grouped by increasing deciles of external larval supply (see below).

Results, Lxxx: By defining larval barrens and larval hubs as the lower 10th vs. upper 90th percentiles of the annual external larval supply, respectively, we observe that higher coral cover is more commonly achieved in larval hubs across all warming scenarios (Fig. 5c). This suggests that external larval supply functions as a form of demographic rescue, which is consistent with previous findings using large-scale connectivity^{38,39,44}. Moreover, focusing on warm spots reveals that reefs with greater access to external larvae tend to fare better than those with reduced upstream connections, even in the face of high bleaching mortality (Supplementary Fig. 13a). Yet, the ability of larval dispersal to support predictably benefit coral populations diminishes under higher GHG emissions, particularly towards the end of the century. The disruption to reef state becomes so patchy and severe that larval supply is ~~driven~~

increasingly influenced by local retention and sporadic larval dispersions occasional dispersal from upstream reefs that retain enough adult corals.

Results, Lxxx: Lastly, we note that larval barrens and hubs display fairly similar comparable distributions of mean heat tolerance, particularly by mid-century (Fig. 6b, Supplementary Fig. S13b). Although While one might expect that larval connectivity might be expected to impede could hinder thermal adaptation with the arrival of by introducing maladapted, cooler phenotypes dispersing from thermal refugia⁴⁵, our simulations indicate that larval supply has no apparent influence on local adaptation in the mid-term. By the end of the century, larval hubs tend to support slightly higher proportions of heat-tolerant phenotypes, likely due to the influence of upstream reefs that still maintain functional reproductive populations – those that have successfully adapted to warming. However, with the majority of coral populations severely depleted by this time, the potential for genetic rescue through larval connectivity seems to offer limited benefits in the long term.

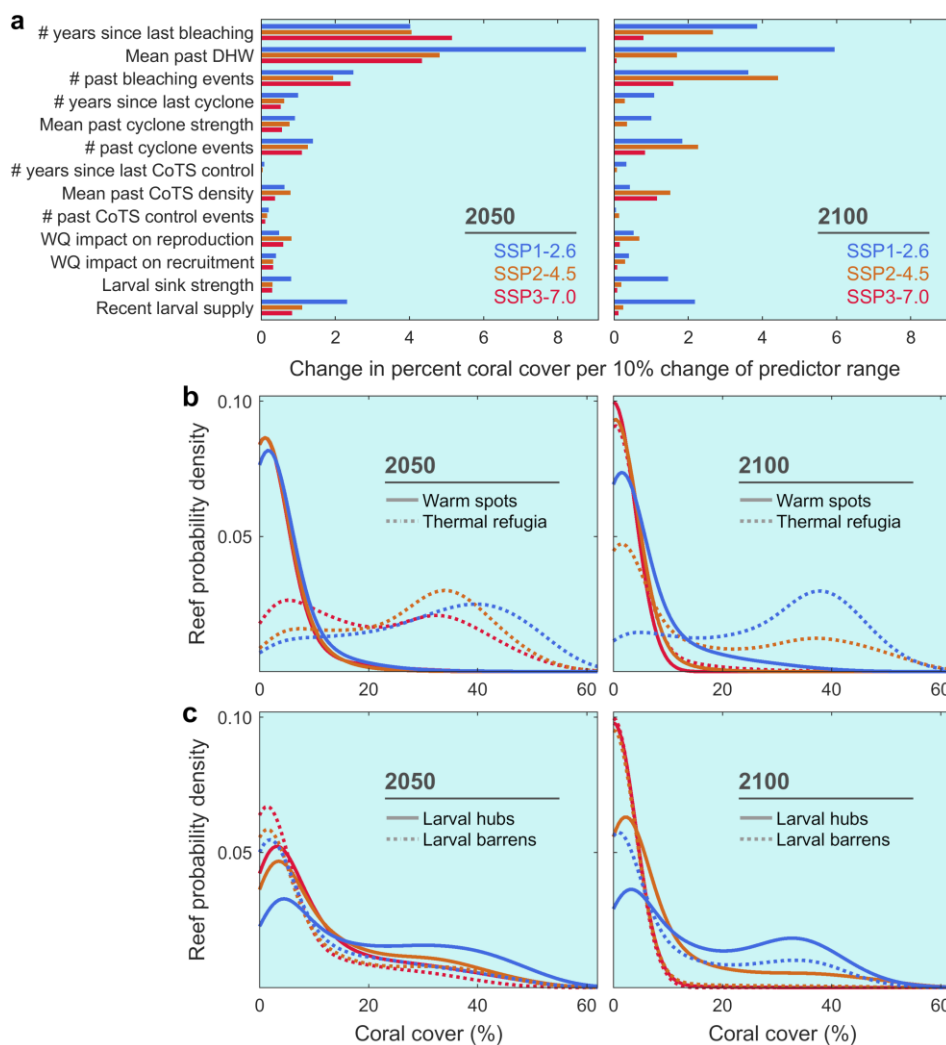


Fig. 5. Drivers of future coral persistence under plausible global warming. **a** Factors associated with healthier reef outcomes under SSP1-2.6, SSP2-4.5, and SSP3-7.0 for both mid-century (left) and end-century (right) based on predictions of statistical linear models. The influence of each predictor (Supplementary Table 2) is measured by the change in coral cover (as percentage points) for a 10% change of the predictor within its range. The final row represents external larval supply (i.e., excluding local larval retention). CoTS: crown-of-thorns starfish (*Acanthaster* spp.); WQ: water quality. **b–c** Probability (kernel) density distribution of reefs based on heat sensitive coral cover across thermal (**b**, warm spots and thermal refugia) and larval

supply (c, larval hubs and larval barrens) regimes, excluding reefs impacted by reduced water quality and cyclones in the preceding five years. Thermal and larval supply regimes are defined, respectively, as those reefs below the 10th or above the 90th percentile for annual DHW and annual amount of external larval supply. Reefs in thermal refugia (i.e., exposed to lowest thermal stress) and in larval hubs (i.e., exposed to highest larval supply) exhibit higher levels of coral cover compared to warm spots and larval barrens. Thermal environments and larval connectivity were calculated as the average heat stress and larval supply experienced in the preceding five years. Larval supply excludes local retention and only captures larvae from external source reefs. Colours of SSPs as in a.

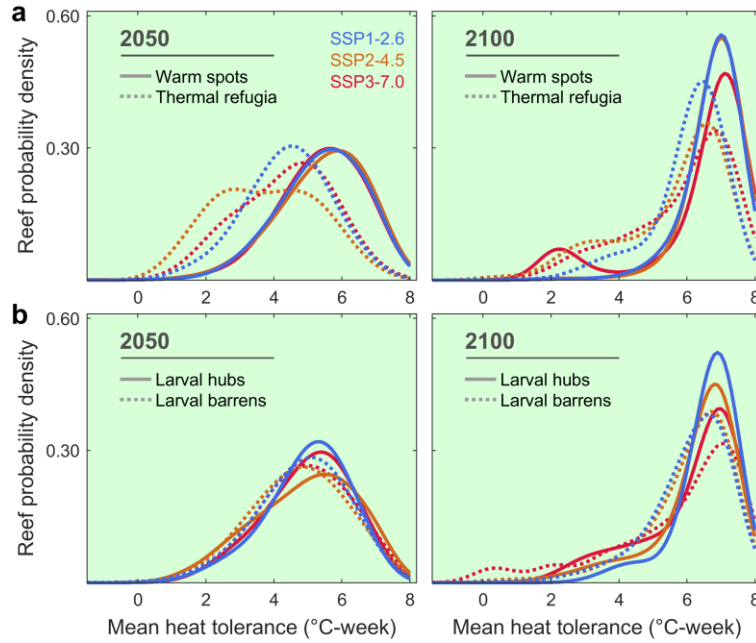
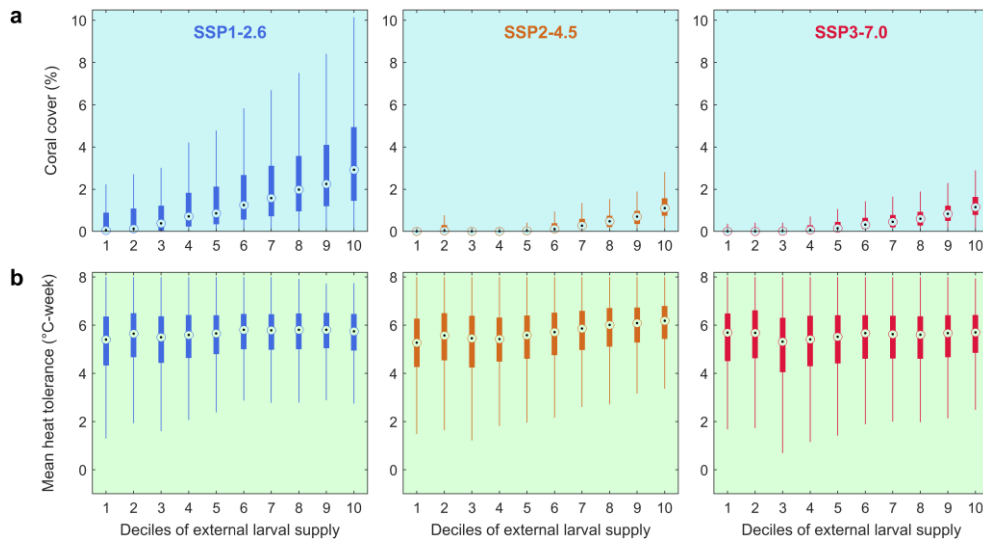


Fig. 6. Influence of thermal refugia and larval supply and coral adaptation. a–b Reef density distribution of mean heat tolerance of heat sensitive coral taxa across thermal (a) and larval supply (b) regimes (see definition in Fig. 5 legend) for both mid-century (left) and end-century (right). Heat tolerance is defined as the relative accumulated heat stress ($\pm$ °C-week) a coral colony can withstand compared to the present-day mean response of its taxonomic group (0 °C-week). Recurrent heatwaves progressively shift the mean tolerance on a reef by selecting corals with the highest heat tolerance (within biological limits set to ± 8 °C-week) over multiple generations. Reefs in thermal refugia slow down the evolution of heat tolerance yet support a greater diversity of heat tolerance values; warm spots achieve greater heat tolerance values at the price of reduced population sizes and lower phenotypic diversity.



Supplementary Fig. 13. Distribution of (a) total percent cover and (b) mean heat tolerance of thermally-sensitive coral groups (all acroporids + pocilloporids) predicted in 2050 across warm spots grouped by increasing deciles of external larval supply (i.e., larvae supplied by upstream reefs). External larval supply (larva.m-2) on each reef was averaged over the last five years. As in Fig. 5 & 6, warm spots are defined as reefs in the top decile of mean DHW calculated over the preceding five years. Inshore reefs (subject to reduced water quality) and reefs affected by cyclones during this period were excluded to maintain focus heat stress exposure. Boxes and whiskers defined as in Fig. 1 legend.

L695: The smaller Δ coral cover with increased warming is at least partially just because the baseline coral cover is lower, so the same relative difference in coral cover results in a smaller absolute difference in coral cover. I think the sensitivity analysis adds credibility to the study, but I am not convinced by the statement that the influence of these parameters “diminishes as warming intensifies”, at least not on the basis of Extended Data Fig. 13.

We fully agree with the reviewer, and as detailed in our response below, we now provide a figure showing the influence of each parameter as relative changes to the baseline coral cover. The text of this section was revised accordingly, such that the influence of each parameter on predicted coral cover is now described both in absolute and relative terms. Specifically, this statement was re-written as:

Methods, Lxxx: Among recovery-related parameters, colony growth and maximum settler density had the strongest effects, causing up to $\pm 35\%$ variation in mean coral cover – equivalent to ± 5 percentage points under SSP1-2.6, and less than 2 percentage points under higher warming, when mean coral cover drops below 10%.

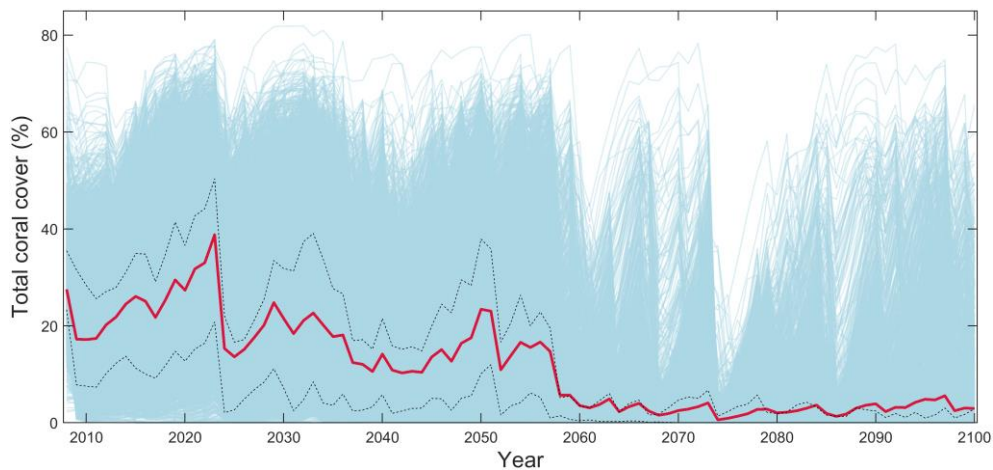
L705-706: Perhaps rephrase to “Parameters controlling the impact of cyclones and CoTS have relatively limited effect on coral cover.”

We thank the reviewer for highlighting the repetition of the word “impact”. This was re-phrased as follow:

Methods, Lxxx: Parameters controlling the impact magnitude of cyclones and CoTS had marginal effects.

Extended Data Fig. 1: I would consider adding transparency to the individual reef coral cover trajectories (or plotting a 2D histogram of states rather than individual lines). In its current form, there are too many lines to tell what the density of trajectories are at different levels of coral cover.

To enhance the visualisation of the variability in coral trajectories obtained under the selected scenario, we included the 25th and 75th percentile ranges of coral cover across all simulated reefs. Note that the coral trajectories shown reflect a single realisation out of 940 simulated coral futures. This figure is not intended to quantify variability, but to illustrate how spatial and temporal heterogeneity in disturbance impacts can lead to markedly different trajectories among reefs. The new figure (Fig. S1c) is shown below:



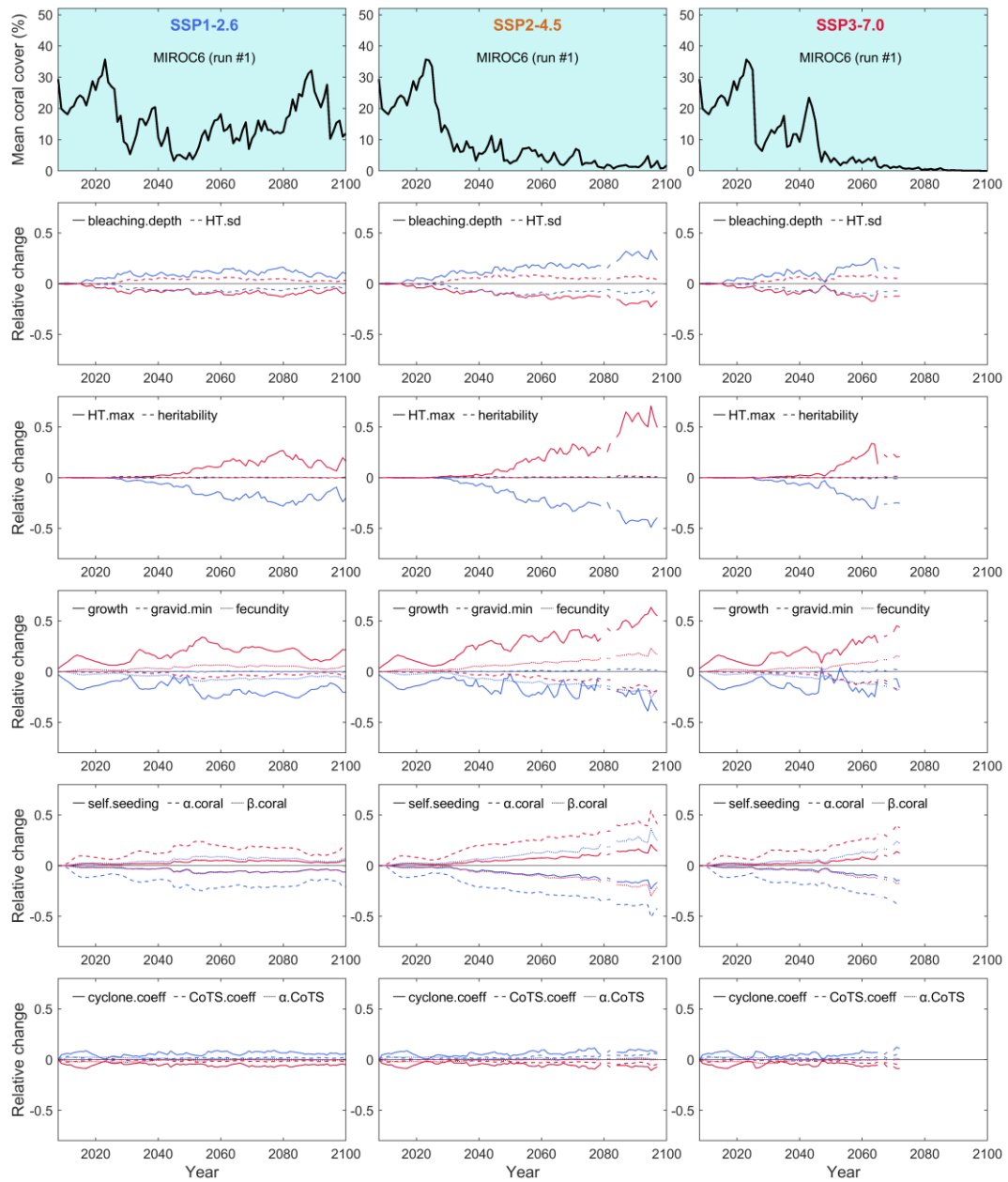
Supplementary Fig. S1c: [A single realisation of the combined hindcast and forecast projections of total coral cover across the GBR, illustrating the variability of coral cover trajectories among individual reefs \(blue lines, \$n=3,806\$ \). The red line indicates the average coral cover weighted by the area of each reef. The dashed lines represent the 25th and 75th percentiles of the yearly distribution of coral cover across all simulated reefs. Forecast projections were derived from one scenario of future cyclones and one scenario of future heat stress derived from the climate model CNRM-ESM2-1 under SSP2-4.5.](#)

Extended Data Fig. 12: I'm not sure what the point of this figure is! The density of points is too high to be useful (as above) but I can't see any convincing correlation by eye, certainly not a linear correlation that would warrant the linear best-fit (?) lines. The highest levels of coral cover appear with intermediate levels of larval supply, so I wonder if this is just a trivial consequence of the fact that most reefs have intermediate levels of larval supply (and there are therefore more extreme values for reefs with intermediate levels of larval supply).

[This is a fair point, and as mentioned in our response above, we have entirely revised this figure to now show the distribution of coral cover in warm spots, organised by increasing deciles of external larval supply \(Fig. S12a\). This new representation more clearly illustrates that higher levels of coral cover are found in locations that receive greater input of external larvae.](#)

Extended Data Fig. 13: I think the figure is fine, but I wonder if it might be more useful to plot the relative difference in coral cover rather than the absolute difference in coral cover (or to just plot the mean coral cover with a shaded region spanning the low and high values, a bit like Extended Data Fig. 9).

[We agree with the reviewer and have added a figure \(Supplementary Fig. 15\) displaying the influence of each parameter in terms of relative differences in coral cover:](#)



Supplementary Fig. 15. Model sensitivity to key input parameters as in Supplementary Fig. 14, this time measured as relative change in the GBR mean coral cover compared to the baseline simulation. Relative change was calculated as $(CC_{\pm 20\%} - CC_{\text{base}})/CC_{\text{base}}$, where a single parameter is varied by $\pm 20\%$ from its default value (blue: -20% ; red: $+20\%$), while all other parameters remain at their default values. Relative change was not calculated when the baseline GBR mean coral cover (CC_{base}) was below 1% , as such values can yield disproportionately large relative differences that are not informative at very low coral cover levels.

We also chose to keep the original figure displaying the absolute differences in mean coral cover, as it offers important complementary insight. Specifically, while relative changes are informative, their practical relevance depends on the underlying baseline. For instance, a 30% increase from a baseline of 1% coral cover represents only a 0.3 percentage point gain – insufficient to meaningfully alter our conclusions. Absolute values are therefore critical for interpreting the significance of parameter variation in the context of the predictions, especially across different warming scenarios where coral cover may be severely diminished.

The text in the Methods section was revised to reflect this new evaluation of parameter influence in both relative and absolute terms. Additionally, as requested by Reviewer #3, we have added a global sensitivity analysis to assess each parameter in the context of interactions with others:

Methods, Lxxx6: We assessed the sensitivity of future coral cover predictions to the input parameters that most strongly influence the key processes driving eco-evolutionary dynamics and resilience of corals: susceptibility to heat stress, thermal adaptation, recovery potential, larval supply and susceptibility to cyclones and CoTS outbreaks. As a result, 13 parameters were selected (Supplementary Table 3) and two sensitivity analyses were performed.

First, we varied each parameter independently by $\pm 20\%$ while holding the others constant, simulating a single scenario of future cyclones under three warming projections (SSP1-2.6, SSP2-4.5, SSP3-7.0) of the MIROC-6 climate model. The impact of the change in each parameter was assessed in terms of both absolute (Supplementary Fig. 14) and relative (Supplementary Fig. 15) differences in projected GBR mean coral cover. Among recovery-related parameters, colony growth and maximum settler density had the strongest effects, causing up to $\pm 35\%$ variation in mean coral cover – equivalent to ± 5 percentage points under SSP1-2.6, and less than 2 percentage points under higher warming, when mean coral cover drops below 10%. Variations in the limits of heat tolerance caused up to $\pm 30\%$ change in the mean coral cover after mid-century, with broader limits (± 9.6 °C-weeks) improving coral cover up to $\sim 5\%$ percentage points under SSP1-2.6. In contrast, changes in the heritability of heat tolerance had minimal impacts. Variations in depth-attenuation of DHW and the spread (standard deviation) of naive heat tolerance led to $\pm 20\%$ variation ($\pm 2.5\%$ percentage points under SSP1-2.6). Parameters controlling the magnitude impacts of cyclones and CoTS had marginal effects.

Second, a global sensitivity analysis was conducted to assess the influence of each parameter in the context of interactions with others. Here, 100 simulations of the same SSP1-2.6 scenario were run, randomly sampling all parameters from uniform distributions within their $\pm 20\%$ range. Parameter influence was captured by fitting a linear model to the resulting relative changes in GBR mean coral cover ($n = 100$ predictions) extracted at different time points (Supplementary Fig. 16). Colony growth and maximum settler density remained the most influential parameters throughout the century, with mean effects up to $\pm 25\%$ and $\pm 16\%$, respectively. The influence of heat tolerance limits increased over time, reaching $\pm 17\%$ by the end of century. Depth-attenuation of DHW and the spread of naive heat tolerance had mean effects up to $\pm 9\%$. Notably, cyclone impact magnitude had a substantial effect ($\pm 18\%$) – undetected in the first analysis – suggesting significant interactions with other parameters.

Reviewer #3 (Remarks to the Author):

The authors have done a very solid job dealing with these comments. The treatment of adaptation in particular is a great improvement, and will be much clearer to readers. Overall, the writing is now much clearer, with substantial improvements following each comment about clarity.

I will write separate assessments of my own comments (R#3), and those of R#4.

We appreciate the reviewer's recognition of the improvements made to the paper, many of which were guided by their initial evaluation and constructive feedback. We have addressed their remaining concerns with careful consideration, providing additional analyses and information where appropriate.

R#3

I had two main comments on the last version of this manuscript.

Critique 1 (Evolutionary Model): I worried that the model underestimated the natural variability of heat tolerance among coral species, particularly because each "morphological group" actually represents multiple species. I therefore suggested that the authors present wider within-group variation (ideally reflecting empirical evidence) to strengthen confidence in the evolutionary assumptions of the study.

Critique 2 (Validation & Uncertainty): I was concerned that the current validation relied too heavily on visual comparisons, and may have overestimated the model's predictive accuracy. I recommended a formal

assessment of forecast error (e.g., comparing decadal predictions to actual observations) and pointed out that the model appears to “know” when disturbances happen in hindsight, which would not be possible in forecasts.

On the first point, I don’t believe the authors have addressed my comment in their review. They say: “The variability in heat tolerance within a group was derived from experimental observations (Humanes et al. 2022) of a single population (*Acropora digitifera*) under simulated heat stress.” This means they are using empirical estimates of within-population variation in heat tolerance (i.e., a study of a 102 individuals of *A. digitifera* from Palau) to model between-species variation (e.g., the differences among and within all large massive coral species). This would be like looking at the weight variation within adult humans in Australia, and using it to model the weight variation among all apes. I think this will substantially underestimate the potential of corals to adapt to heat stress.

We appreciate the Reviewer’s concern given the importance of this parameterisation. However, there is an important clarification to make regarding this concern: in our previous response, we explained that the full variability of heat tolerance (HT) within a group is influenced by the imposed bounds (min and max) on our modelled HT values. The experimentally-derived HT distribution of *Acropora digitifera* provided by Humanes et al. (2022) is currently the only one available to parameterise our model of heat tolerance. Yet, this distribution is used only at initialisation, such that all coral groups start with the same distribution of relative heat tolerance (i.e., relative to the naive bleaching susceptibility of the group). Importantly, as the simulation progresses, HT distributions quickly change due to bleaching and reproduction. Therefore, the key factor in driving the variability of HT phenotypes is the imposed bounding limits rather than the initial HT distribution derived from *A. digitifera*, which is confirmed by the sensitivity analyses.

We acknowledge the challenge of extrapolating the variability in heat tolerance from one species to a multi-species group, and agree with the Reviewer that for multiple species this variability is most likely wider. This is why we broadened the bounding limits: HT ranges from -8 to $+8^{\circ}\text{C-week}$, compared to $-6/+6^{\circ}\text{C-week}$ for *Acropora digitifera* (corresponding to the 1st and 99th percentiles of the observed distribution). As a result, we are modeling a greater variability of HT than observed in the single species, which would capture some between-species variations. While we could have expanded the bounds further, doing so without empirical data (ie, similar to that available for *A. digitifera*) could risk overestimating this variability within a group, therefore overestimating the scope for thermal adaptation.

We have carefully revised the main text and supplementary text to address the Reviewer’s concern. First, in the Methods section, we have clarified the text regarding the HT bounding limits and improved our justification for the extrapolation of the variability of heat tolerance for a multi-species group:

Methods, Lxxx: Because a normal distribution has tails extending to infinity, negative and positive limits to HT ($\pm\text{HTmax}$) are required to avoid creating unrealistic heat tolerance values. ~~A conservative range would set limits to the bottom and top 1% of the empirical distribution, which correspond approximately to -6 and $+6^{\circ}\text{C-week}$, respectively (Extended Data Fig. 3b). A range based on the 1st and 99th percentiles of the observed distribution in Humanes et al. (2022) would set bounding limits to approximately -6 and $+6^{\circ}\text{C-week}$ (Supplementary Fig. 3b). Yet, this distribution is derived from experimental data gathered for a single species with a limited number of individuals. When extrapolating to multiple taxa, it is reasonable to assume a wider range of heat tolerance values. We extended this range by 2°C-week on either side of the original distribution (i.e., $|\text{HTmax}| = 8^{\circ}\text{C-week}$) considering that: (i) this distribution draws from experimental data gathered for a single species; a broader range of HT values can be legitimately assumed when inferring for multiple taxa; (ii) extreme thermal phenotypes might emerge from complex interactions among mechanisms of selection, acclimation and genetic mutations, to capture some additional level of variability among species within a modeled group. Due to the lack of empirical data on heat tolerance for other coral taxa – comparable to the values reported in Humanes et al. (2022) – there is significant uncertainty in extrapolating heat tolerance variability across multiple species. Furthermore, extreme thermal phenotypes could emerge in the future from the complex interactions among mechanisms of selection, acclimation and genetic mutations. As additional data become available for a broader range of taxa and our understanding of adaptive mechanisms progresses, it will become possible to more accurately represent the potential range of heat tolerance values.~~

We have also revised the paragraph describing the limitations of the model in the Discussion, to clarify that the range of variations in heat tolerance was extended above the limits inferred from the empirical data of a single species:

Discussion, Lxxx: Our model incorporates key components of natural selection: trait variation, survival of individuals with advantageous traits, and transgenerational inheritance of trait values. Although ~~While~~ our parameterisation allows bleaching sensitivity to vary among taxa (Supplementary Fig. 2c)⁴⁰, we note that the variation amongst thermal phenotypes, the foundation upon which natural selection operates, was parameterised from one of the more sensitive coral taxa (*Acropora* spp.)- as this was the most comprehensive data available¹⁹. We expanded the limits of heat tolerance within each modelled group to account for the variability conferred by multiple species. However, the lack of data for other taxa introduces additional uncertainty to these limits, which significantly influences eco-evolutionary projections (Supplementary Fig. 14-16). ~~Specifically, we set an upper limit on heat tolerance which has a notable influence on eco-evolutionary predictions (Extended Data Fig. 13). Hence, it is unclear how~~ the scope for thermal adaptation varies across taxa and much remains to be understood about the mechanisms of adaptation itself^{47,48}. Specifically, ~~Moreover,~~ our model does not account for other life history traits that may be affected by rising temperatures⁴⁹ or by the strengthening of thermal resistance⁵⁰, nor does it capture the evolutionary response of symbiont populations to warming, which influence coral growth and heat tolerance⁵¹.

We have revised the section of model assumptions, limitations and their implications in the supplementary text to clarify our assumptions and potential implications:

Supplementary Notes – Model assumptions and limitations, and their implications, Lxxx: Heat tolerance (HT) of coral individuals is defined relative to the mean bleaching susceptibility of the group at initialisation, with HT=0 °C-week conferring the bleaching mortality representative of the group. In all coral groups, HT phenotypes are created at initialisation by sampling from a normal distribution of mean 0 °C-week and standard deviation 2.5 °C-week following empirical observations obtained on a single acroporid population (*Acropora digitifera*) from a shallow outer reef crest of Palau¹⁵. In the absence of similar data on other coral populations, we assumed this distribution to be representative of the present-day (i.e., at the start of simulation in 2008) variability of heat tolerance within each modelled coral group. As the simulation progresses, changes to the HT distributions emerge under the combined effect of bleaching mortality and reproduction, but are constrained within bounding limits (HTmax). HT bounding limits of -6 / +6 °C-week would give a representative range of the observed variability of heat tolerance in *Acropora digitifera* (corresponding to the 1st and 99th percentiles of the observed distribution). We extended this range to -8 / +8 °C-week to account for some likely additional variability between species within the coral groups. This may be conservative, with potential to underestimate adaptation, but expanding the bounds further would risk overestimating the scope for adaptation through natural selection.

Given the lack of quantitative data on the variability of heat tolerance for other species, it is currently impossible to characterise directly this variability within a group. However, we can partially assess our predicted responses to bleaching with in situ observations of heat stress impacts (Fig. 1d, Supplementary Fig. 8). While these surveys rarely detail species-specific responses, other examples include reports of 95% mortality for *Acropora* corals after the 2024 mass bleaching at 2 m depth under 14.6°C-week heat stress in the Southern GBR (Byrne et al. 2025). Similarly, at Scott Reef (Western Australia), 85% *Acropora* mortality was reported at 9 m depth in response to 13.3°C-week after the 1998 heatwave (Gilmour et al. 2013). Under similar conditions of depth and heat stress exposure, our model would predict, respectively, 98% and 87% mortality across the three acroporid groups (if not previously exposed to bleaching). The fact that the model did not predict 100% mortality, and instead showed some survival, suggests that we do not under-represent the variability of heat tolerance within these groups. We added this point in the supplementary text:

Supplementary Notes – Model assumptions and limitations, and their implications, Lxxx: Given the lack of empirical data for other species, it is currently impossible to directly characterise the variability of heat tolerance within a group. Therefore, we rely on comparisons with in situ observations

[for testing our predicted responses to bleaching. Surveys in the Southern GBR \(Byrne et al. 2025\) have reported 95% mortality for *Acropora* after the 2024 mass bleaching at 2 m depth under 14.6°C-week heat stress. Similarly, at Scott Reef \(Western Australia\), 85% *Acropora* mortality was reported at 9 m depth in response to 13.3°C-week after the 1998 heatwave \(Gilmour et al. 2013\). Under similar conditions of depth and heat stress exposure, our model would predict, respectively, 98% and 87% mortality across the three acroporid groups, if not previously exposed to bleaching. This alignment suggests that our model provides a reliable representation of the present-day variability of heat tolerance within these groups.](#)

On the second point, I think the authors have done a good job at reporting the predictive skill of their model. I also agree with the previous comments of the first and fourth reviewers, and appreciate that the authors now report the uncertainty associated with all their predictions. However, they report the uncertainty in different ways throughout the paper, which is confusing.

I have three recommendations going forward, sticking to my two main critiques:

(1) The modelled variability in heat tolerance among the groups (I believe “a group” can contain species from different families) be considerably larger than the variation observed within a single population of a single species.

[Please see our response and revisions above. Current data on inter-individual heat tolerance, expressed as deviations in °C-week around the mean population response to heat stress, is limited to just one species. Yet as explained, we are modeling a greater variability of heat tolerance than observed in this species by expanding the bounding limits of heat tolerance. Without data from other taxa, we cannot determine whether the resulting range of heat tolerance per coral group is underestimated or overestimated. We maintain that the best approach is to acknowledge these limitations, the assumptions we have made, and clearly communicate their potential implications for our projections, which we have done.](#)

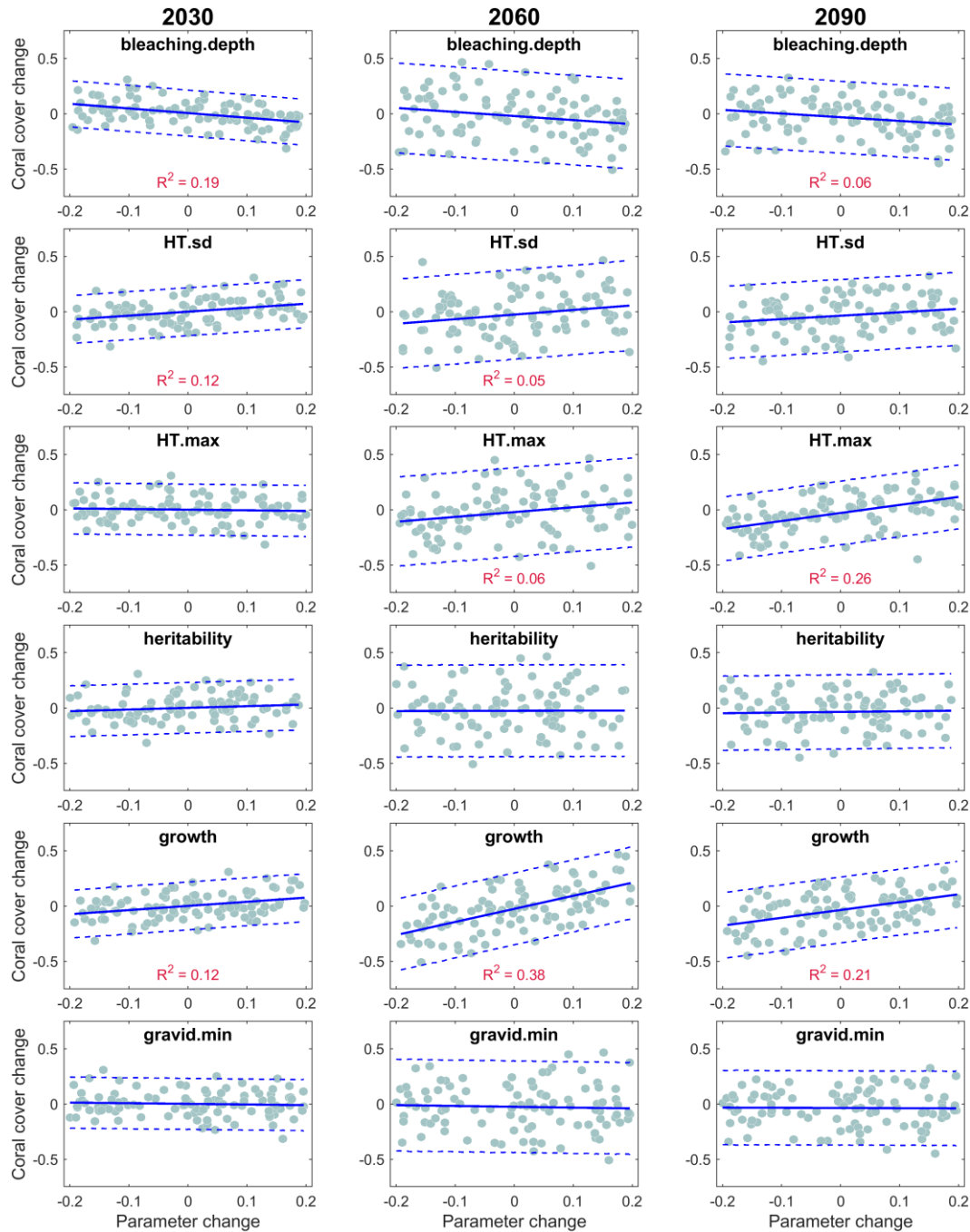
(2) The authors follow standard procedure and report 95% confidence bounds throughout the manuscript, rather than inter-quartile ranges or +/- SD. IQRs are a strange choice, because (by definition) as many predictions fall outside those bounds, as fall within them. Both inter-quartile ranges and +/- SD feel like they're chosen to under-emphasise the variation.

[It was not our intention to under-emphasise the variation, rather to aid ease of interpretation for the reader. In response, we have modified all figures and statistics relating to the projections of coral cover, and now consistently report mean values with 95% prediction intervals.](#)

(3) The parameter sensitivity analysis is a great idea, but needs to be more global. The goal here is to estimate the effects of uncertainty, which affects all, not just one, of the parameters. Marginal sensitivity analyses are only useful for reporting the relative impact of the different parameters. Sensitivity analyses should therefore be global, rather than marginal. That is, in your sensitivity analysis the authors should vary all parameters by +/- 20% from their default values, not just one at a time. I think if you run 100 or so simulations, with each simulation varying all parameters by 20%, and show the results, this will be enough to get a feel for how the uncertainties will interact.

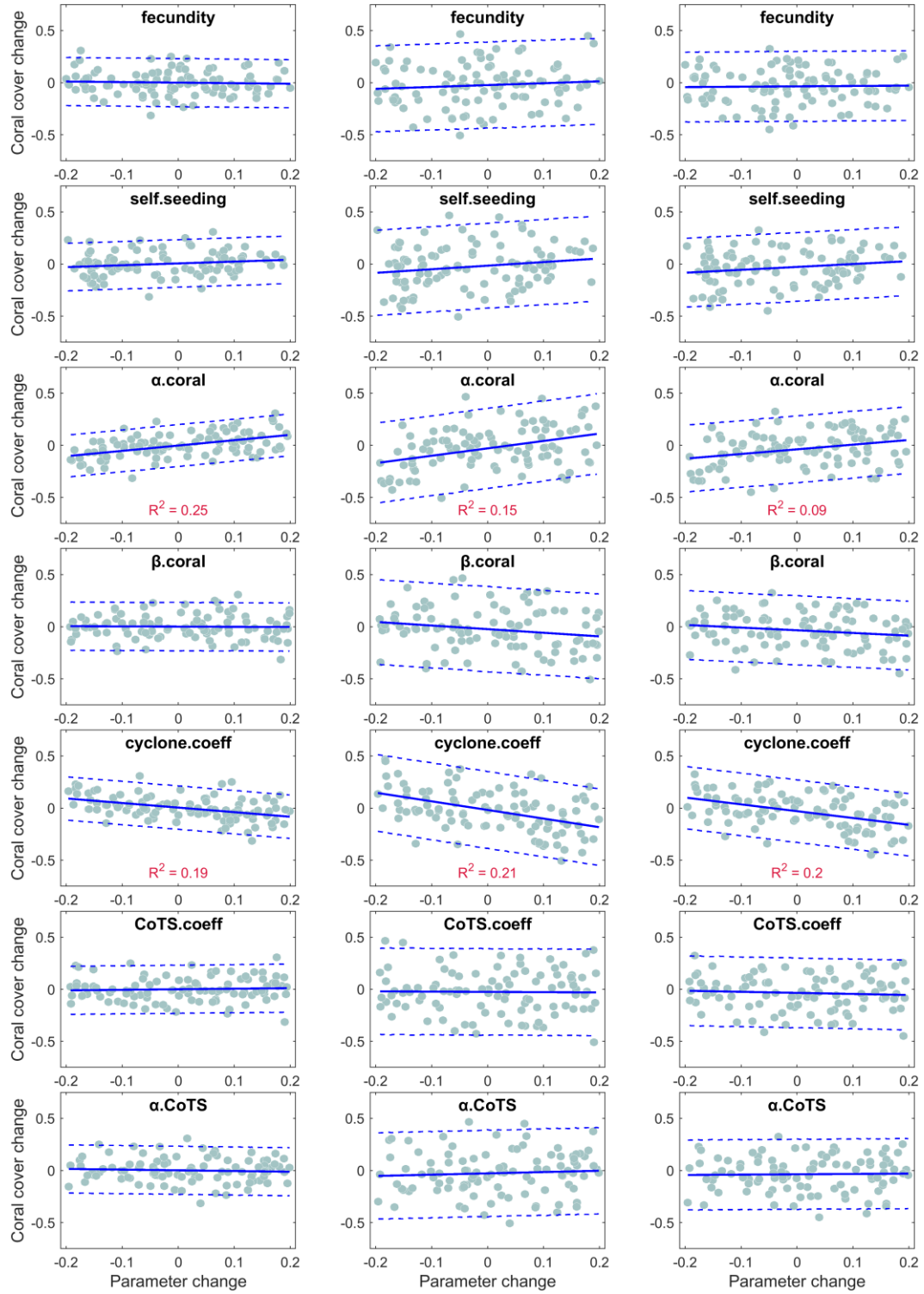
[We agree and have performed a global sensitivity analysis \(GSA\) to complement the marginal sensitivity analysis. As requested, we simulated 100 runs of the model with all parameters sampled at random from a uniform distribution between -20% and +20% of their current value. We examined the resulting effects at different points in time \(2030, 2060 and 2090\), expressed as relative changes in the GBR mean coral cover. We fitted a linear model to the predicted changes in response to the variations in parameter values, and estimated the mean effect of each parameter at the -20% and +20% end points. Results are shown in a new figure \(Supplementary Figure 16\). Note that we kept the first analysis \(marginal sensitivity analysis\), extended to include the effects of parameter variations measured as relative changes in mean coral cover \(as requested by Reviewer #2\), as both provide complementary insights to the GSA. As a result, the Method section was extended with the following paragraph:](#)

Methods, Lxxx: Second, a global sensitivity analysis was conducted to assess the influence of each parameter in the context of interactions with others. Here, 100 simulations of the same SSP1-2.6 scenario were run, randomly sampling all parameters from uniform distributions within their $\pm 20\%$ range. Parameter influence was captured by fitting a linear model to the resulting relative changes in GBR mean coral cover ($n = 100$ predictions) extracted at different time points (Supplementary Fig. 16). Colony growth and maximum settler density remained the most influential parameters throughout the century, with mean effects up to $\pm 25\%$ and $\pm 16\%$, respectively. The influence of heat tolerance limits increased over time, reaching $\pm 17\%$ by the end of century. Depth-attenuation of DHW and the spread of naive heat tolerance had mean effects up to $\pm 9\%$. Notably, cyclone impact magnitude had a substantial effect ($\pm 18\%$) – undetected in the first analysis – suggesting significant interactions with other parameters.



Supplementary Fig. 16. Results of the global sensitivity analysis, showing the relative change in the GBR mean coral cover obtained after random perturbations of each parameters within -20% and $+20\%$ of their

default value. Here, 100 simulations of one scenario of cyclones and future warming (run #1 of SSP1-2.6 projected by the MIROC-6 climate model – see Supplementary Fig. 14 & 15) were run with all parameters sampled at random from a uniform distribution. Relative change was calculated for each simulation i (dots) at different time points t (left to right: 2030, 2060, 2090) as $(CC_{i,t} - CC_{base,t})/CC_{base,t}$. Blue lines and dashed lines indicate, respectively, the linear fit and 95% prediction interval. The associated R^2 is provided in red when above 0.05.



Supplementary Fig. 16 (continued).

R#4

I have one minor comment and one major comment about the revisions following the comments of R#4.

MINOR COMMENT

Concerning the final comment from the last round of R4. The authors rewrote this section to say: “Thus, management strategies for adaptation that encompass multiple thermal environments can be flexible and unconstrained by patterns of larval supply.”

I would qualify this statement by saying “our model indicates that ..”.

We modified this statement as suggested by the Reviewer:

Discussion, Lxxx: Thus, our model projections indicate that management strategies for adaptation that encompass multiple thermal environments can be flexible and unconstrained by patterns of larval supply.

MAJOR COMMENT: VALIDATION

The authors have undertaken a range of validation exercises to determine the extent to which we can be confident in the model predictions. I appreciate all the efforts.

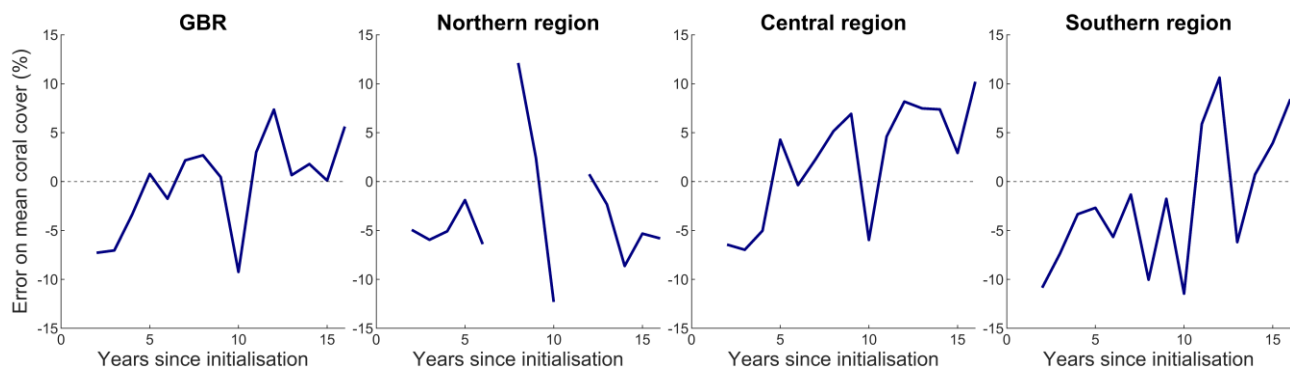
What a reader will want to know is how accurate the forecast is. The authors primary claim is that: “We forecast a rapid coral decline [from 39% in 2023 to 14% in 2040] before mid-century regardless of emissions scenario”. The model in question has a large number of parameters and assumptions (e.g., the functional forms of the interactions, the groupings of coral species, etc). We know these are inaccurate, but we don’t know how inaccurate, and we can’t measure most of them. The best way to evaluate this prediction is therefore a hindcast validation, which the authors have the data to support.

The current validation initialises the model in 2008, and predicts coral cover at a reef level (which is then aggregated to subregion, and then the whole GBR) between 2009 and 2023. This is a reasonable test, across a decent time-frame (15 years) that is comparable to the primary predictions.

I would like to see this validation changed in several ways. First, we should evaluate the inaccuracy after 10 or so years. The authors calculate the “difference between the predicted and observed mean coral cover for each available year between 2009 and 2023”, but this averages across short-term forecasts and decadal-scale forecasts. The error will likely be smaller in 2009 (only one year after initialisation) than in 2023 (more than a decade after initialisation). Since the primary claims of the paper are about predictions 15 years in the future, we should evaluate and validate with decadal predictions. That is, initialise the model at 2008, and evaluate at 2018; initialise it at 2009, evaluate it at 2019, etc.

We appreciate the approach suggested by the reviewer and understand its rationale. However, we believe there are inherent limitations – potentially irreducible – in quantifying the accuracy of coral cover predictions across the GBR, and this for any ecosystem model. A key distinction lies between the difficulty of reconstructing the physical environment of the recent, including disturbances, and secondarily the ability to simulate accurate responses in coral dynamics. Yet, reconstructing past exposures to acute disturbances at individual reef scales, across a seascape of 2,300 km, is an impossible task: accurate data do not exist at the required spatial resolution (1-10 km). We note that the largest discrepancies between observations and predictions are primarily driven by erroneous predictions of past cyclone exposures. This is particularly the case in 2009 (see Supplementary Figs. 5-6-7), contrary to the expectation that model errors would be smaller one year after initialisation. Here, significant damage of Tropical Cyclone Hamish was predicted based on the distance between reefs and the cyclone track, yet many of the real reefs escaped damage. Inversely, some of the real reefs experienced cyclone impacts despite being located beyond the expected damage radius from the cyclone’s track. While such misrepresentations of the physical environment have implications for the reconstruction of coral cover trajectories, they do not invalidate the assumptions that underpin the simulation of coral demographics and adaptation. In fact, a precise evaluation of accuracy in reconstructing coral cover would aim to validate the reconstruction of the physical environment, more than the modelled ecological processes.

In response to the Reviewer’s concern regarding the potential for model predictions to increasingly diverge from observations over time since model initialisation in 2008, we have added a figure (new Supplementary Fig. 6) that demonstrates that model errors do not exhibit a consistent temporal trend but are instead distributed relatively evenly across the hindcast period:



Supplementary Fig. 6. Annual model errors, calculated as the difference between predicted and observed mean coral cover (as shown in Supplementary Fig. 5), for each year following model initialisation in 2008 (which is excluded from the analysis). Errors were not computed when fewer than 5 reef observations were available, which occurred only in the Northern region. These discrepancies reveal persistent differences between model predictions and observations of coral cover throughout the hindcast period. Some of the largest discrepancies occurred in 2009, one year after initialisation, primarily due to incorrect estimates of reef-specific exposure to Tropical Cyclone Hamish. While such inaccuracies in environmental forcing affect the reconstruction of coral cover trajectories, they do not compromise the core assumptions underlying the simulation of coral demographics and adaptive responses.

Reference to this new figure was added in the main text as follow:

Results, LXXX. The comparison with monitoring data indicates a credible reconstruction of the past trajectory of mean coral cover trajectory (Supplementary Fig. 5), with model errors – defined as the annual differences between predictions and observations – being evenly distributed over time (Supplementary Fig. 6) and having a mean difference value of -0.3% percentage points ($SD = \pm 4.7\%$, 95% central interval: -9.3 – 7.5%).

In addition, we feel it important to re-state the objective of our study, which is about exploring possible futures for GBR corals, not reconstructing their recent trajectories – the purpose of a previous publication (Bozec et al. 2022). Reviewers #3 and #4 had concerns about the predictive capacity of the model, while acknowledging the challenges inherent to this exercise. In response, we have provided extensive analyses showing how the model performs in (1) reconstructing regional trends on the GBR (Supplementary Fig. 5), (2) reconstructing individual reef trajectories at local scales (Supplementary Fig. 7) and (3) hindcasting recent impacts of past bleaching events on the GBR (Supplementary Fig. 8). While presented as supplementary material, these analyses offer valuable insights on the model’s ability to simulate realistic dynamics of coral populations.

Although we acknowledge that the ecological hindcast is not perfect, we are confident that our approach provides a transparent and detailed validation of the reconstructed coral dynamics. Making such a complex ecosystem model accurate at multiple scales is an immense challenge, and even with relatively good accuracy, there will inevitably be some misalignment with observations. Importantly, while the primary source of model inaccuracies for hindcasting lies in the difficulty of predicting past disturbances, we firmly believe this is not a problem for future projections, because we cannot predict where, when and with what intensity future cyclone and bleaching events will occur in the future. This is the reason why we are

projecting coral dynamics under multiple scenarios of warming and cyclones (940 possible scenarios), which accounts for this uncertainty and enables us to explore a range of potential future outcomes.

Second, the error statistics cannot be symmetric (not least because coral cover is a bounded variable). The errors (e.g., in the caption to Extended Fig 5, at Line 95 of the main text) give symmetric standard deviations. These should be asymmetric 95% intervals.

Good point. Instead of reporting the standard deviation of the mean annual error between model predictions and observations of the GBR mean coral cover, we now provide the 95% central interval of the distribution of annual model errors, which reflects their asymmetry around the reported mean values. We revised the main text as follows:

Results, Lxxx: The comparison with monitoring data indicates a credible reconstruction of the past trajectory of mean coral cover trajectory (Supplementary Fig. 5), with model errors – defined as the annual differences between predictions and observations – being evenly distributed over time (Supplementary Fig. 6) and having a mean difference value of -0.3% percentage points (SD = ± 4.7% 95% central interval: -9.3–7.5%).

We also revised the legend of Supplementary Fig. 5 to reflect this change in estimating the variability of model errors:

Supplementary Fig. 5: (...) An annual model error was calculated as the difference between the predicted and observed mean coral cover for each available year between 2009 and 2023 (excluding the 2008 observations that were used to initialise the simulated reefs), resulting in a mean annual error of -0.3% (95% central interval: -9.3–7.5%), -3.3% (-12.6–12.3%), +2.3% (-7.0–10.6%) and -2.1% (-11.6–10.8%) for the GBR-wide, northern, central and southern reconstructions, respectively.

Third, the validation assumes that the modeller knows the dates and locations of key disturbance events on the GBR – primarily bleaching events and tropical cyclones. Of course, these are not known in advance, only in hindcasts. To get a better feel for how much uncertainty there is in the forecasts, we need to know what these hindcasts would say about 15 year predictions when disturbance events are not known with certainty. I appreciate that the authors addressed this issue in the previous review, but I didn't buy their response.

To explain why, consider where the authors address the validation results in the main text. "The comparison with monitoring data indicates a credible reconstruction of the past mean coral cover trajectory, with model errors – defined as the annual differences between predictions and observations – being evenly distributed and having a mean difference of -0.3% (SD=± 4.7%)."

What they're saying here is that "Our hindcast validation made predictions that turned out to be within 5% of the true coral cover. Thus, when we say cover will drop to 14% by 2040, we can be confident that the real value will be between 9% and 19%. Both of these are a lot lower than the current value of 39%."

We believe that the reviewer may be misinterpreting our statement. First, we have calculated the errors between model predictions and observations because the reviewer requested them. Our original statement about the model providing a credible reconstruction of past coral trajectories implied that we can trust the capacity of the model to simulate realistic coral dynamics and trends. This is different from accuracy in predicting coral cover at a particular point in time (e.g. in line with weather forecast).

Second, we are not making any inference of future uncertainty based on the errors made by the model in predicting the past. The uncertainty in future coral dynamics arises from the simulation of 940 future scenarios of random bleaching and cyclone events across 3,806 reefs. This variability allows us to capture the potential range of future reef states, on the basis that the model confidently predicts the ecological impacts of a specific disturbance of a given intensity, which is confirmed by the accuracy of coral reconstructions obtained for the reefs that were effectively impacted in the past (Supplementary Fig. 7). Here, the fact that the model did not predict the right ecological response because the reef was actually not exposed, or inversely, because it was exposed while it was not supposed to be, has no influence on the

quality of future predictions. The crucial factors for uncertainty in our projections are twofold: first, whether the modelled disturbance regimes of the future are realistic – this forecast is provided by an ensemble of 10 different climate models, and we are not aware of any other method for projecting temperatures into the future; and second, whether coral demographics and evolutionary dynamics are appropriately simulated in response to these disturbances – we believe they are, as demonstrated by our hindcast reconstruction, despite inevitable inaccuracies in estimating past exposure to disturbances. These are the elements that determine the robustness of our future projections, not past discrepancies.

In response to this comment, we have included a statement in the main text clarifying that the model errors observed during hindcast reconstructions do not affect its ability to project future coral dynamics, as long as these projections are based on multiple scenarios of stochastic bleaching and cyclones.

Results, LXXX: Coral cover reconstructions at individual-reef scales performed reasonably well (Supplementary Fig. 7), despite the challenge with model errors primarily arising from the difficulty of hindcasting patchy disturbances at high resolution, especially the damaging waves produced by cyclones^{20,26,27}. However, these discrepancies reflect the accuracy of the hindcast only and do not constrain future uncertainty, provided it is captured by stochastic disturbance scenarios and the model's representation of coral responses to specified disturbance intensities.

Reviewer #5 (Remarks to the Author):

Bozec and colleagues present an elegant study where they model eco-evolutionary dynamics across the Great Barrier Reef under different climate change scenarios, taking into account multiple variables related to demographics, environment, larval connectivity, different stressors (heatwaves, CoT outbreaks, storms), and intrinsic features of corals (e.g., heat tolerance).

The article is well written and has gone through a first round of reviews. In my opinion, the authors have done a great job in addressing all the concerns raised by the former reviewers, especially when it comes to clarifying reliability of the model and cautious interpretation of their findings.

The modeling work is impressive, the assumptions and parameters appear reasonable to me and have been clearly outlined. The results are highly relevant for the current environmental crisis coral reefs are facing. In my opinion, the article is ready for publication as it is.

We appreciate the Reviewer taking the time to evaluate our study and for their positive comments.

Reviewer #5 (Remarks on code availability):

It appears to me that all code needed to reproduce the study have been made available and is well documented. I did not install and run the code.

A rapidly closing window for coral persistence under global warming

Reviewer #2 (Remarks to the Author):

I thank the authors for this second revision, and their thoughtful responses to my comments, and those of the other reviewers. I would make one final recommendation, namely to change “recovery is possible” (L25, abstract) to “recovery is possible this century”, since the simulations end in 2100 and therefore cannot rule out the possibility of a recovery beyond 2100 for warming >2C (coral cover reaches a non-zero minimum around 2080 under SSP2-4.5, so could conceivably recover after 2100). Apart from this, as far as I am concerned, the manuscript is ready for publication.

We have re-formulated the sentence in the abstract following the recommendation made by Reviewer #2:

Abstract: However, recovery is possible this century if warming remains below 2°C, allowing thermal adaptation to keep pace.

Due to 200-word abstract limit, we reverted the second sentence to its earlier, clearer version. Although reviewers raised no concerns about this sentence, we had previously shortened it - mistakenly assuming a 150-word limit - which reduced its clarity:

Abstract: Global analyses of projected ~~Projections of future~~ heatwaves can inform decision-making, but forecasting the interactions between disturbance refugia, coral life histories and capacity to adapt is key for guiding strategic management of ~~to forecasting~~ coral persistence.

Reviewer #3 (Remarks to the Author):

I thank the authors for engaging so thoroughly with my comments and suggestions, and for making so many revisions and running so many additional analyses.

While there are still parts of the paper that I do not 100% agree with, I do not represent the entire field, and the changes made acknowledge the challenges in a model of this complexity.

My one response (and this is for the purposes of dialogue, not further revision) is that while the bounds on HT are important and are indeed wide, the initial distribution will place considerable constraints on future evolution. Specifically, narrow initial distributions may mean wide bounds have no effect on future dynamics.

We appreciate the Reviewer’s final comment and hope our work will encourage further discussion and research on the variability of heat tolerance among corals. While our sensitivity analysis showed that the bounds of heat tolerance have a stronger impact on model projections than the breadth of the initial distribution of heat tolerance, we agree that the latter still influences the projected evolutionary dynamics, as we acknowledged in the section about model assumptions and limitations.