

Delaying conservation at heatwave hotspots can undermine long-term eco-evolutionary benefits

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Article

Keywords: Thermal evolution, resilience, climate change, coral bleaching, marine reserves, restoration

Posted Date: October 13th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-10195380/v1>

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Additional Declarations: There is **NO** Competing Interest.

Abstract

In a rapidly warming climate, species persistence will increasingly depend on thermal evolution. Yet how evolution-informed conservation should harness spatial gradients of heatwave-driven selection remains unclear. Here, we extend an eco-evolutionary metapopulation model of reef-building corals to incorporate marine heatwaves, manageable recurrent non-climatic disturbances, and two conservation interventions: local protection and restoration. Prioritising efforts toward heatwave-exposed "hotspot" populations consistently generated the greatest evolutionary gains in heat tolerance, but strategies for improving coral abundance (coverage) were context dependent. Under a 2°C Paris Agreement scenario, protecting thermal refugia and restoring hotspots were optimal strategies for improving coverage. However, under a more plausible 3°C scenario, restoring refugia maximised near-term coverage gains whereas targeting hotspots delivered greatest long-term benefits. This fundamental time-dependent trade-off in conservation outcomes suggests potential for portfolio approaches or adaptive management that alters spatial prioritisations strategically over time. However, further simulations show neither such approach could recover both near- and long-term coral coverage benefits, likely because evolutionary adaptation is gradual and cumulative, becoming increasingly important as warming intensifies. Investing heavily in heatwave-exposed locations among the most vulnerable to degradation could be politically challenging, but rapidly implementing such evolution-informed spatial conservation is critical, as delays can curtail long-term evolutionary and ecological outcomes.

Introduction

As anthropogenic global warming accelerates¹, species conservation must move from recognising contemporary evolution is widespread to actively designing strategies to harness this potential². Intensifying marine heatwaves are driving mass coral bleaching and mortality across the world's coral reefs, with some coral populations already facing functional extinction^{3,4}. Population persistence throughout and beyond the 21st century will increasingly depend on the evolution of heat tolerance beyond current ranges^{5,6}. Heat tolerance is highly variable within and among coral populations and sufficiently heritable to support significant evolutionary responses to selection⁷⁻⁹. While some reefs already show evidence of increased heat tolerance¹⁰⁻¹², with contemporary thermal evolution likely underway^{13,14}, natural adaptation rates could be insufficient to maintain population persistence if warming is too fast^{9,15}. Global warming mitigation remains essential, but alongside this, local conservation strategies that incorporate evolutionary theory are urgently needed to support long-term population persistence¹⁶.

Local actions can facilitate coral resistance, recovery, and adaptation by reducing non-climatic disturbances. This can be achieved through protection measures such as improving water quality through sewage treatment, reducing sedimentation from deforestation, or preventing coral predator outbreaks¹⁷⁻¹⁹. However, where natural recovery is insufficient, active reef restoration or rehabilitation can help, for instance substrate stabilisation, substrate addition, coral seeding, and coral out-planting

can support recovery at historically blast-fished reefs^{20,21}. Because most reef-building corals disperse widely as larvae, such local conservation actions are expected to generate system-wide benefits across interconnected metapopulations.

Heatwave exposure varies across reef seascapes, from large-scale gradients spanning thousands of kilometres (e.g., Australia's Great Barrier Reef) to local gradients of tens to hundreds of kilometres that are often within regional or national jurisdictions (e.g., the Bahamas or Palau)^{7,22,23}. This spatial heterogeneity creates predictable variations in selective pressure that could be leveraged in conservation planning. Portfolio approaches have been proposed to spread risk amid uncertainty regarding coral's adaptive potential^{24–26}. Yet, as empirical and genomic evidence uncovers patterns of adaptive variation, more strategic spatial prioritisations become possible¹⁶. For example, heat-exposed 'hotspot' reefs may harbour heat-adapted genotypes and act as sources of adaptive variation across seascapes^{8,13}, whereas 'thermal refugia' may sustain higher coral abundance (measured as coverage) due to lower heat exposure, which could help maintain population size and genetic diversity¹⁵. Previous work suggests that management should prioritise survival and reproduction at hotter reefs, while facilitating recruitment and settlement at colder reefs^{5,16}. How these contrasting roles interact with simulated conservation actions to shape eco-evolutionary outcomes under different warming scenarios remains largely untested.

Here, we extend a spatially realistic eco-evolutionary metapopulation model of acroporid corals, ReefMod-PALAU, to incorporate both heatwave-driven coral bleaching mortality and recurring, non-thermal manageable disturbances (Fig. 1a). This allows us to develop spatial conservation strategies that either protect reefs from manageable stressors or restore damaged reefs to instigate recovery amidst otherwise variable levels of natural recruitment (Fig. 1b-c). The model has been validated on independent long-term monitoring datasets and has projected future coral declines and thermal evolution for the remote Pacific reef system of Palau⁹. Acroporids are speciose in the Indo-Pacific and a major contributor to reef functioning and maintaining ecosystem services²⁷, but also highly susceptible to heat stress. We evaluate alternative spatial strategies for local management, testing whether the prioritisation of hotspots, thermal refugia, random reef portfolios, hotspot-refuge 50:50 portfolios, or time-varying approaches can enhance eco-evolutionary outcomes more effectively (Fig. 1d-f). System-wide benefits of management arise through larval dispersal between targeted reefs and other locations in the wider meta-population. We quantify system-wide effects on coral coverage and heat tolerance—a coral's ability to survive heatwave stress—through time (1985–2100) and under contrasting emissions scenarios. We also test their robustness through a suite of sensitivity analyses related to disturbance regimes, larval connectivity, and coral life history strategies.

Results

Heatwave Exposure and Counterfactual Trajectories

We first explored spatial patterns in the historical exposure of Palau's reefs to past heatwaves using 36 years of satellite data on cumulative heatwave stress²⁸ (units: °C-weeks, 1985–2020). Distinct heat stress regimes emerge across the 95 reefs comprising ReefMod-PALAU given their past exposure to major heatwaves (those exceeding an average of 4°C-weeks), with individual reef exposure varying by up to 2°C-weeks (Fig. 2a). As an illustration of the differential impacts of spatial variations in heat stress regimes, we simulated a hypothetical heatwave reaching an average of 8°C-weeks across Palau's reefs. This translated into substantial variability in selective pressure, with coral mortality ranging from 34% to 66% among reefs (Fig. 2b).

Under future (2021–2100) counterfactual trajectories without reef management, thermal refugia consistently maintained higher levels of coral coverage than hotspot reefs by up to an additional 10% absolute coverage (Fig. 2c-d). Because populations became depleted through time, this corresponded to ~25% higher relative coverage in refugia during the mid–late 21st century (Fig. S1a-b). In contrast, stronger selective pressure at hotspots accelerated local thermal evolution, resulting in up to 0.14°C-weeks higher mean heat tolerance despite identical initial heat tolerance distributions (Fig. S1c). By the end of the 21st century, a clear spatial gradient had emerged: refugia exhibited up to 8% higher absolute coral coverage, whereas hotspots showed higher mean heat tolerance of up to 0.5°C-weeks (Fig. 2e–f). Thus, even in the absence of management, spatial variation in heat stress generated divergent eco-evolutionary trajectories across the seascape. Notably end-of-century coral coverage was approximately four times higher in the Paris Agreement scenario with warming limited to ~2°C (Shared Socioeconomic Pathway SSP1-2.6; Fig. 2e) compared to the more likely emissions scenario SSP2-4.5 that reaches ~3°C warming (Fig. 2f).

Prioritising Hotspots versus Thermal Refugia

We then compared a purely hotspot-focussed versus a purely thermal refuge-focussed approach to management, simulating the full protection or restoration of all reefs residing in these thermal regimes (*i.e.*, one-third of reefs in the system). We focus on difference (delta) values ($\Delta X = X_{\text{Hotspot}} - X_{\text{Refugia}}$) in both coral coverage and heat tolerance to compare the efficacy of managing hotspots ($\Delta X > 0$) versus thermal refugia ($\Delta X < 0$), with the management objective being to maximise both abundance and thermal tolerance (Fig. 3a). While enhancing coverage can support population turnover and resilience, enhancing heat tolerance through evolution can help ensure long-term persistence, and thus delivery of critical ecosystem services. Compared to the unmanaged counterfactual, all management scenarios increased system-wide absolute coral coverage by up to 4–5% and 1–1.5% for SSP1-2.6 and SSP2-4.5, respectively, and promoted heat tolerance by up to 0.8°C-weeks (Fig. S2). However, the spatial prioritisation of actions shaped the balance between demographic and evolutionary gains. Targeting hotspots rather than thermal refugia consistently accelerated the system-wide evolution of heat tolerance, producing relative gains of up to 0.13°C-weeks, which can equate to an additional 2–3% chance of heatwave survival (Fig. 3b). In contrast, effects on system-wide coral coverage were more variable (-0.4 to +0.5% absolute coverage) and were dependent on emissions scenarios, time horizons, and management type (Fig. 3b).

Notably though, these effects on heat tolerance and coral coverage were more striking for a system with a stronger spatial gradient in DHW exposure (see below), as noted for other reef systems²⁹. Further, in any individual simulation, the local benefits of management at target locations were up to an additional 20% absolute coral coverage for protection and up to an additional 5% absolute coral coverage for restoration (Fig. S3).

For a management strategy focusing on protection against non-thermal disturbances, greater coral coverage benefits were primarily achieved by prioritising thermal refugia rather than hotspots (Fig. 3b, left panels). Under SSP1-2.6, system-wide absolute coral coverage was up to 0.4% lower when protecting hotspots. But under SSP2-4.5, this disadvantage persisted through most of the 21st century, reducing over time and becoming almost negligible or even changing sign by the 2090s. These patterns reflect the inherently higher carrying capacity of thermal refugia (Fig. 2c–d), which amplifies demographic returns to protection.

For restoration strategies, spatial trade-offs were more strongly time dependent (Fig. 3b, right panels). Under SSP1-2.6, targeting hotspots consistently produced higher absolute coral coverage gains after the 2030s, reaching +0.5% by the 2090s. But under SSP2-4.5, targeting refugia yielded clearly superior near-term absolute coverage outcomes (*i.e.*, in the 2050s; +0.2%), whereas targeting hotspots delivered greater end-of-century absolute coverage gains (+0.4%). This time-dependent switch is associated with the fact that heat-driven mortality is reduced by targeting restoration at hotspots rather than refugia (Fig. S4a) and that heatwave stress becomes increasingly severe compared to levels of tolerance toward the latter half of the 21st century (Fig. S5). Thus, under higher emissions (SSP2-4.5), restoring hotspots enhanced long-term coral coverage outcomes at the cost of smaller near-term gains.

All patterns were robust to an alternative larval dispersal structure designed to reflect a larger reef system such as the Great Barrier Reef (Fig. S6), characterised by strong declines in dispersal strength with distance, with hotspots and thermal refugia only weakly connected through intermediate stepping stone reefs^{5,30}. As in our previous results, targeting hotspots maximised heat tolerance evolution across all warming and management scenarios, and under SSP2-4.5, improved end-of-century coral coverage at the expense of potential near-term coverage gains (Fig. S7).

The true variability in heatwave exposure across reefs is substantially higher than that estimated from 5 km spatial resolution satellite datasets. For example, Moore Reef on the Great Barrier Reef is an order of magnitude smaller than Palau yet high resolution models predict the spatial gradient in heatwave exposure to be twice that of Palau ($\sim 4\text{--}5^\circ\text{C-weeks}$)²⁹. To test sensitivity to this potential underestimation, we reran spatial conservation scenarios under amplified DHW gradients, up to five times the native regime (*i.e.*, $\sim 10^\circ\text{C-weeks}$, Fig. 3c–d). Optimal conservation prioritisations based on heatwave exposure remained robust (Fig. 3e), with coverage and heat tolerance benefits increasing with greater spatial DHW heterogeneity. Under a five-fold stronger DHW gradient, restoring hotspots rather than refugia yielded an additional $\sim 2\%$ system-wide coral coverage by 2100 under SSP2-4.5, equivalent to an additional $\sim 50\%$ in relative gains (Fig. S8–9). In this scenario, heat tolerance benefits extended up

to 1.12°C-weeks, which can equate to additional 20% in the chance of colonies surviving heatwaves (Fig. 3b).

Spatial Portfolios and Time-varying Strategies

Time-varying strategies that initially prioritise refugia before shifting to hotspots later in the century could, in principle, be optimal under SSP2-4.5 given the time-dependent benefits observed for hotspot- and refugia-focussed restoration strategies (Fig. 3b). Likewise, spatially fixed random reef portfolios or a 50:50 portfolio (i.e., the top 50% of hotspots and the top 50% of refugia) could achieve similar outcomes. To test this, we compared a new suite of simulations to the hotspot-only strategy. Negative delta values ($X_{\text{Other Strategy}} - X_{\text{Hotspot}}$) indicate greater system-wide benefits from a hotspot-focused restoration strategy, whereas positive delta values indicate greater benefits from the alternative strategy.

Despite our expectation, hotspot-focussed restoration remained the most effective strategy for promoting heat tolerance evolution and maximising end-of-century coral coverage across the system (Fig. 4a, Fig. S10). Likewise, neither the time-varying strategies nor random or 50:50 portfolios improved near-term (2050s) coral coverage beyond gains achieved by exclusively targeting thermal refugia (Fig. 4a). For strategies that shift from refugia to hotspots over time, end-of-century outcomes fell between those of the hotspot-only and refuge-only strategies, following a sigmoidal pattern: earlier transitions increasingly resembled hotspot-only strategies, whereas later transitions converged on refuge-only strategies (Fig. 4b-c). Thus, temporal switching redistributed rather than resolved the trade-off between near- and long-term outcomes. Near-term coral coverage was maximised by refuge-focussed restoration, and neither delayed transitions toward hotspots nor spatial portfolio approaches improved this outcome. These results were robust to other coral growth forms, as seen from simulations parameterised with the slower coral growth rates and higher heat tolerances of massive corals such as *Porites lobata* (Fig. S11).

Sensitivity to Non-Thermal Disturbance Regime

Results were robust to the frequency and spatial extent of manageable non-thermal disturbances. Across return times, ranging from once every six years to once every sixteen years, protecting refugia rather than hotspots consistently maximised coral coverage for most of the 21st century (Fig. S12). Under SSP2-4.5, restoration strategies continued to exhibit the time-dependent trade-off between near- and long-term coverage gains, and hotspot-focused restoration consistently maximised end-of-century coverage benefits, with this pattern being less profound but still present for protection strategies (Fig. S11). The mean trajectory across all these tested disturbance frequencies closely matched the once-per-decade regime presented in the main text, indicating our central conclusions are robust to assumptions of disturbance periodicity. These same patterns held true for an alternative disturbance extent scenario where simulated non-thermal disturbances were spatially less widespread, but disturbance years

occurred more frequently but with overall mortality equivalent to the once-per-decade system-wide regime (Fig. S13).

Discussion

Our study demonstrates that strategically designed local management can improve local and system-wide eco-evolutionary outcomes, and that a reef's heatwave exposure fundamentally shapes its role within the wider metapopulation. However, optimal spatial prioritisations are context dependent, varying with emissions scenarios, time horizon, and management type. Under the higher emissions scenario SSP2-4.5 (3°C of warming by 2100), we identified a previously unrecognised dichotomy: targeting restoration efforts at hotspot reefs maximises end-of-century coral coverage and thermal evolution yet can reduce potential coral coverage gains over the coming 2–3 decades relative to refuge-focused or spatial portfolio approaches. Thus, strategies that best promote long-term evolutionary rescue may constrain short-term demographic gains.

Local Reef Management has Time-varying Benefits

Guidance on integrating evolutionary principles into spatial coral conservation has largely been derived from theory developed for latitudinal-scale systems spanning strong temperature gradients (20–30°C), where hotter and cooler reefs are linked by intermediate stepping stone reefs^{5,26,31}. From this framework, management at warmer reefs has been recommended to prioritise survival and reproduction, while at cooler reefs the focus should be on supporting natural recruitment and restoration¹⁶. We build on this work, extending theory to smaller seascapes that differ more in cumulative heat exposure than mean ambient temperature and add important time-varying insights relevant to reef systems of all scales, although this may not hold if coral growth rates covary with thermal regimes.

Protection strategies to enhance coral survival are inherently associated with trade-offs between coral coverage and thermal tolerance. Our findings support past recommendations that protecting hotspot reefs can enhance heat tolerance evolution¹⁶, but highlight a cost of this strategy: associated reductions in near-term system-wide coral coverage benefits. Targeting protection efforts like marine reserves instead toward thermal refugia allows for improved coral coverage benefits, because these reefs have a higher carrying capacity for corals owing to their inherent lower heatwave exposure (Fig. 2c-d), as noted for the Great Barrier Reef¹⁵. If future heatwave stress can be mitigated through reduced greenhouse gas emissions, then protection efforts that prioritise the ecology and demography of coral populations (*i.e.*, targeting thermal refugia) could take precedence over those supporting thermal evolution (*i.e.*, targeting hotspots). However, this balance of priorities can invert under the higher warming trajectory the climate system is currently headed towards.

Our simulations show clearly that, under high emissions leading to global warming of 3°C this century, focussing restoration efforts—and to a weaker extent protection efforts—at hotspot reefs is comparatively a better way to improve long-term eco-evolutionary outcomes. However, the time-

dependency of system-wide benefits and disbenefits of hotspot-focussed conservation is an important finding of our investigation. This updates two recent global strategies for reef conservation. On the one hand, the 50 Reefs Initiative has recommended focussing on climate refugia, locations that avoid climatic stress, as these can repopulate degraded reefs in the event of the climate stabilising³². But on the other hand, evolutionary theory has shown that a focus on hot reefs rather than cold reefs can better support evolutionary adaptation¹⁶. While there is a strong case to update our definition of refugia types to diversify the portfolio of conservation targets²⁵, we show that benefits of any spatially fixed approach to reef management can be time varying. We show that short-term reductions in the extent of conservation benefits can pay dividends in the long-term, and that spatially directed rather than bet-hedging random portfolio approaches to conservation can improve outcomes. The time horizon managers choose for desired conservation benefits will shape the spatial strategies that are most suitable.

Assisted Evolution Could Alter Outcomes

Our study focusses on a standard approach to restoration, where the heat tolerance of out-planted corals is equivalent to that of their wild conspecifics. However, novel assisted evolution interventions are now being considered that could supplement traditional restoration approaches with genotypes that have enhanced tolerance to future climatic stress³³. Such interventions include assisted migration and assisted gene flow within and beyond a species range and actions to enhance fitness-related traits, for instance, through selective breeding or other manipulations^{33,34}. The optimal spatial configuration of assisted evolution interventions across heat stress regimes does not necessarily follow the outcomes of our present study, highlighting an important new direction for research and development. While our results show that coral out-planting could improve eco-evolutionary outcomes by focussing on hotspots, it is plausible that out-planting coral colonies with enhanced heat tolerance could be more effective at thermal refugia¹⁶, where native corals have experienced less selective pressure. Mixed strategies to reef management that combine assisted evolution, traditional restoration, and protection efforts among others could yield non-additive, interactive effects. Such emergent dynamics would have the potential to alter optimal spatial prioritisations, and so this area should be a priority for future research.

Scale, Life History and Genetic Considerations

The scale of evolution-informed reef management, the coral taxa targeted, and the genetic background of target populations will be important factors shaping future adaptive outcomes under warming. These are explained in full detail in Supplementary Text S1 and summarised briefly here. Our analyses focus primarily on the combined local and spillover benefits expected from large-scale reef management^{16,22,35,36}. While the scale of our modelled scenarios limits direct interpretation of absolute gains in coral cover and heat tolerance, the relative performance of alternative strategies and the importance of spatial heatwave gradients are robust. Local benefits of small-scale actions, while not the

focus of our study, are also important, particularly for high value sites of social, cultural, and economic importance. The benefits of spatial prioritisation across heatwave gradients could be further amplified by incorporating larval connectivity regimes, for instance by targeting strong source reefs that can improve downstream benefits¹⁶. While our results are primarily for acroporid corals and outcomes were robust to a slower-growing coral parameterisation, future work should better resolve how species diversity, life-history strategy, reproductive mode, and dispersal influence eco-evolutionary dynamics. Notably, our framework models heat tolerance as a quantitative genetic trait and does not explicitly incorporate allele dynamics, genetic drift, effective population size, symbiont evolution, or gene-by-environment interactions^{37–41}. These factors could have important implications for adaptive responses to warming, particularly when comparing coral populations that still retain large effective population sizes, such as in the Pacific⁴², to those suffering severe declines and erosion of genetic diversity, as in the Caribbean³.

Conclusions

In a rapidly warming world, conservation must shift from recognising the potential for contemporary evolution² toward harnessing and enhancing it instead. We show that optimal conservation strategies to support population size may differ from those that support thermal evolution, and these strategies may change over time. For species whose persistence under climate change is likely to rely on evolutionary rescue, then near-term declines may be unavoidable⁴³. Strategic conservation efforts may have to incur near-term reductions in potential eco-evolutionary benefits and demographic stability and accept that investments may need to be prioritised at heat-exposed and thus degradation-prone locations in order to support long-term evolutionary adaptation and population persistence. Yet, investments in stress-prone locations are likely to be confronting and a difficult ‘sell’, delivering relatively poor benefits on coral abundance in the near- to mid-term. The legitimacy of such strategies will depend, in part, on the robustness of results like ours across an even greater diversity of systems.

Methods

Eco-evolutionary Metapopulation Model Development

ReefMod-PALAU is an agent-based eco-evolutionary metapopulation model of corymbose *Acropora* corals in the remote Pacific coral reef system of Palau⁹. The model simulates coral demography, larval dispersal among reefs, bleaching mortality from marine heatwaves and the evolution of heat tolerance (Supplementary Text S2). The model builds on a significant body of evolutionary and demographic work on Palauan *Acropora*^{44–49}, has been validated on independent long-term monitoring datasets and has projected future coral declines and thermal evolution⁹. We extend ReefMod-PALAU to incorporate recurring, manageable non-thermal disturbances that increase coral mortality (Fig. 1a), which can be represented by stressors such as water quality decline, coral predator outbreaks, or destructive fishing.

These non-thermal disturbances were applied stochastically across reefs, testing for robustness through sensitivity analyses based on disturbance severity, frequency and extent (Supplementary Text S3).

Gradients in Heatwave Exposure

The heatwave exposure of each reef from 1985 to 2100 was based on sea surface temperature (SST) data from satellites for the historical burn-in period and from an ensemble of five Global Climate Models (GCMs) for the future projection, as in previous work⁹. The 5 km CoralTemp v3.1 dataset was used due to improved local accuracy compared to higher spatial resolution alternatives⁵⁰. Cumulative heat stress was quantified in terms of annual maximum Degree Heating Weeks (DHW, units: °C-weeks), a measure of the intensity and duration of heatwaves and the primer driver of mass coral bleaching and mortality events^{51–53}. We evaluated two Shared Socioeconomic Pathway (SSP) emissions scenarios: a Paris Agreement scenario of reduced carbon emissions with 21st century warming limited to 2°C (SSP1-2.6), and a more-likely higher emissions scenario given current policies reaching ~ 3°C warming (SSP2-4.5). ‘Native’ heat stress regimes were based on the consistent DHW patterns among reefs over past major heatwaves (> 4°C-weeks), with DHW exposure varying by ~ 2°C-weeks among reefs. To assess the influence of stronger DHW gradients which are known to exist over sub-kilometre spatial scales²⁹, we prepared alternate DHW timeseries with up to fivefold greater DHW gradients. Further details of cumulative heat stress derivation, global climate model selection, and heat stress regimes quantification are provided in the Supplementary Text S4 and S5.

Simulated Reef Management

We simulated two types of local reef management applied from 2025 to 2100: protection, which removes manageable non-thermal disturbances from selected reefs; and restoration, which involves out-planting corals using locally sourced broodstock without altering heat tolerance (parameterisation in Supplementary Text S6). We compared two primary spatial strategies targeting either all hotspot reefs (top tercile of past heatwave exposure), or all thermal refugia (bottom tercile of past heatwave exposure). For portfolio strategies we evaluated a random reef portfolio (targeting an equivalent number of randomly chosen reefs) and a 50:50 portfolio (the top 50% of hotspots alongside the top 50% of refugia). We also tested spatiotemporal strategies that transitioned over time from thermal refugia (that support higher coral coverage) to hotspots (that exhibit stronger selective pressure). Specifically, we tested the influence of delays in the timing of the spatial transition based on six different transition decades using logistic generalised linear models (from 2030s to 2080s). The performance of management strategies was evaluated relative to a no-management counterfactual by tracking system-wide coral coverage and mean heat tolerance through time. We compared outcomes across the 21st century with a focus on the near term, 25–35 years after management commencement (2050s), and the long term, 65–75 years after management commencement (2090s).

Sensitivity Analyses

As mentioned above, we performed sensitivity analyses on periodicity and spatial extent of non-thermal disturbance regimes to understand the robustness of eco-evolutionary response patterns among

contrasting management strategies (Supplementary Text S3). Further, to assess the generality of our findings beyond Palau's highly connected reef system, we also evaluated outcomes under an alternative dispersal structure representing larger reef systems where heat stress regimes are weakly connected via stepping stone reefs^{5,30}. This was achieved by applying a dispersal-by-distance function to Palau's connectivity matrices, reducing the magnitude of among-regime connections (Fig. S6). To assess the generality of our *Acropora*-based findings to other morphological groups of corals, we reran a full series of simulations (counterfactual and fixed conservation strategies) for a model with colony growth rates and initial heat tolerance parameterised in line with large massives such as *Porites lobata*, following Bozec *et al.* 2022⁵⁴.

Declarations

Conflicts of Interest

The authors have no conflicts of interest.

Funding

This work was supported by the Coral R&D Accelerator Platform (CORDAP) grant CORALADAPT to PJM (CAP-2022-1196), and a UKRI Natural Environment Research Council (NERC) Independent Research Fellowship to LL (UKRI4057).

Acknowledgements

We are grateful to our partners in Palau for their enduring support of our research, from the Palau International Coral Reef Center, The Nature Conservancy, Micronesia and Polynesia, and the Palau Automated Land and Resource Information System Office. We also thank the CORALADAPT team members who contributed to constructive conversations during this work, including James R Guest, and Adriana Humanes, as well as other colleagues, including Maria Beger and Cynthia Riginos.

Data Availability Statement

Processed datasets for this study and R code (version 4.0.2) used to analyse eco-evolutionary model results are freely available on Zenodo at <https://doi.org/10.5281/zenodo.20392804>. The MATLAB code (R2024a) to run the eco-evolutionary model is accessible on the lead author's GitHub profile at https://github.com/liamlachs/REEFMOD-PALAU_v2.1, with a stable version archived on Zenodo at <https://doi.org/10.5281/zenodo.20528898> (visible for review here at this temporary link).

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Figures

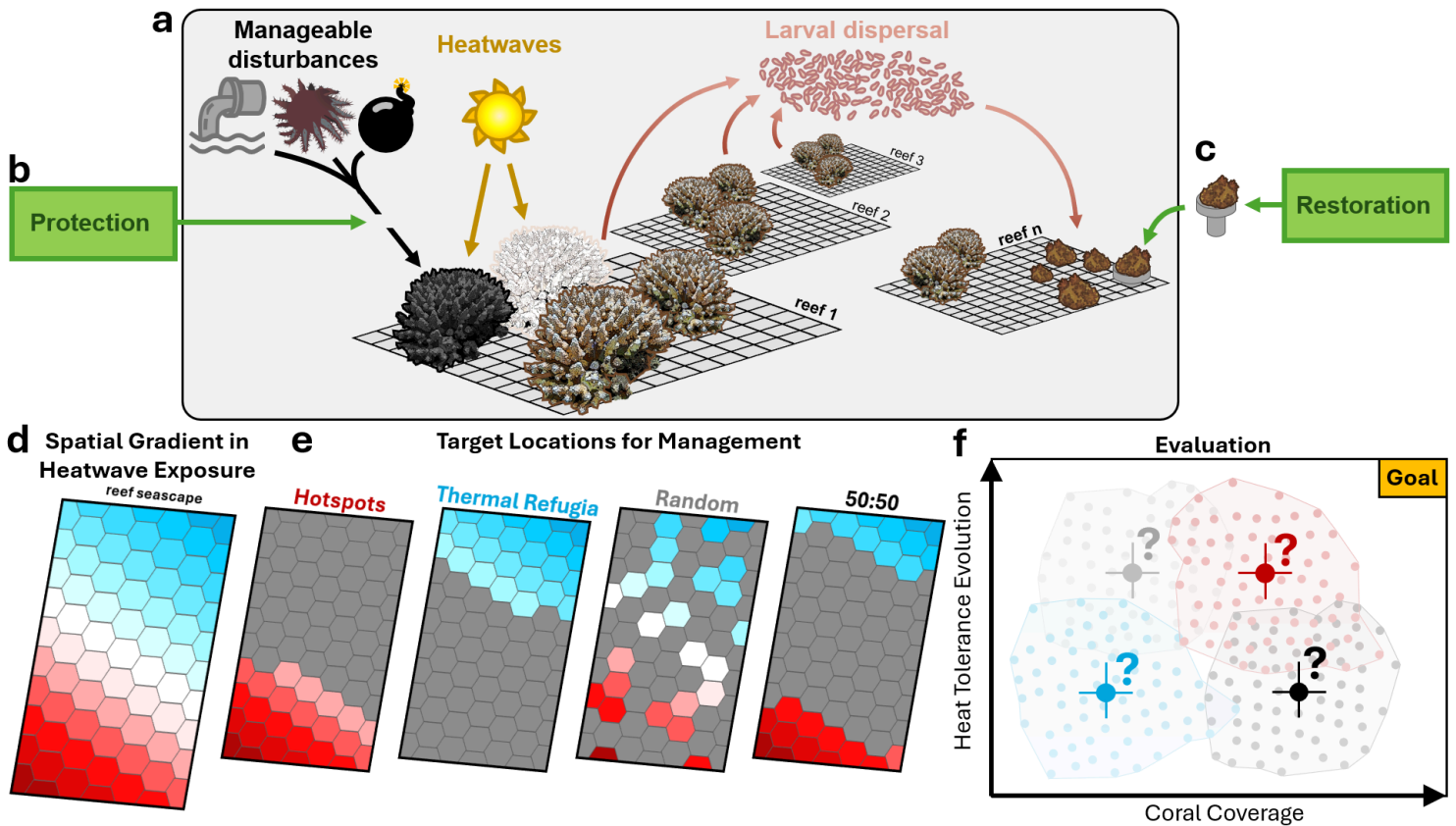


Figure 1

Conceptual overview and comparative approach in coral simulations. (a) An eco-evolutionary metapopulation model with individual *Acropora* corals located on spatially explicit reef units (20×20 cells of 1 m^2). Individual corals grow, reproduce, and are subject to heatwave-induced bleaching mortality, as well as mortality due to natural causes (background mortality) and manageable non-thermal disturbances. Coral larval dispersal through oceanographic currents drives semi-stochastic recruitment among reef units. As a heritable trait, coral heat tolerance can evolve in response to heatwave-induced selective pressure. Non-thermal disturbances occur stochastically on a recurring basis due to unspecified drivers (e.g., reduced water quality, coral predator outbreaks, or blast fishing). (b-c) Spatial management can focus on protecting reefs by removing manageable disturbances or restoring reefs through coral out-planting. (d) Reef units (hexagons) exist across a spatial continuum of heatwave exposure. (e) Different spatial management strategies are tested in which target reefs are selected based on their cumulative heat stress regimes. (f) The optimal management strategy would consistently maximise both heat tolerance evolution and coral coverage benefits.

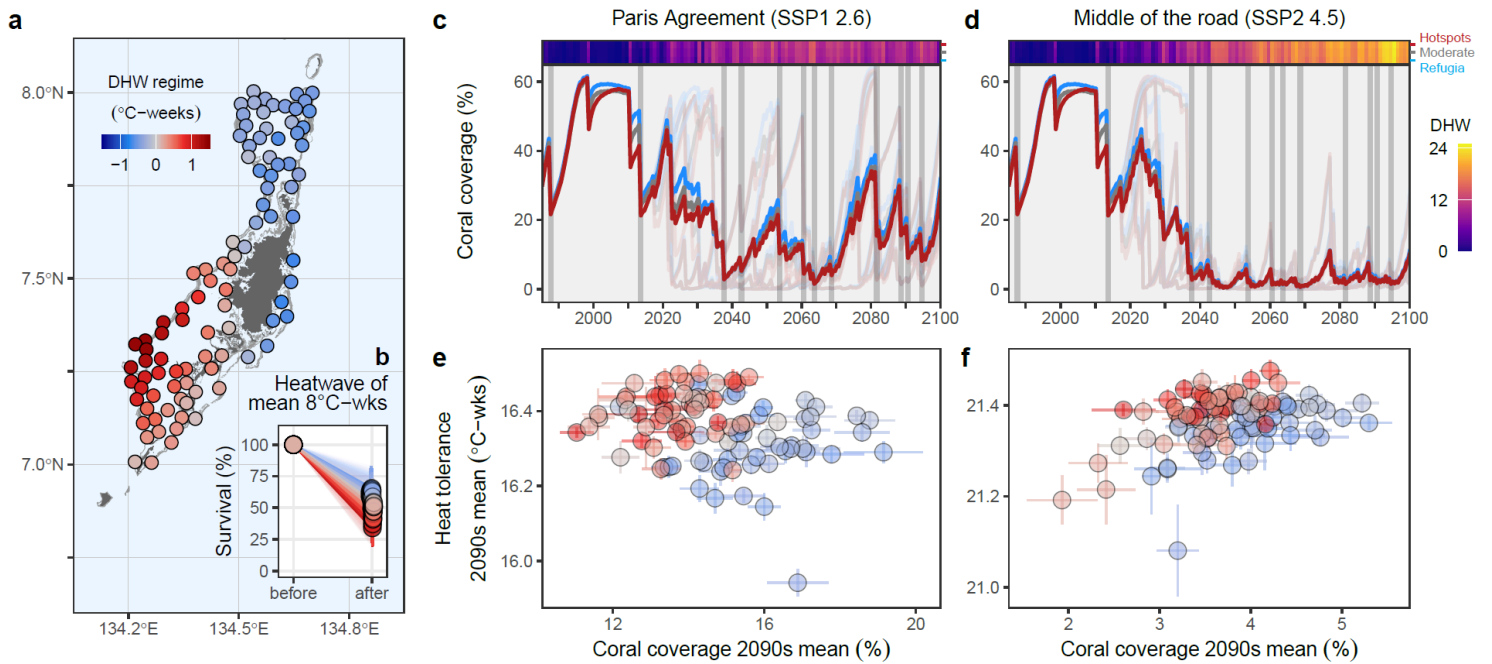


Figure 2

Heatwave exposure and eco-evolutionary trajectories in the absence of local conservation. (a) Map of historical heatwave exposure regimes by reef (circles), showing cumulative heat stress (DHW, blue-to-red colour) relative to the Palau-wide mean for all past heatwaves exceeding 4 °C-weeks, marking locations of land (dark grey) and reef (light grey). (b) Coral survival through a simulated heatwave with spatial DHW variability equal to historic DHW regimes and a Palau-wide mean of 8 °C-weeks (colour as in a), showing mean survival (points) and range (error bars) from 1000 random simulations. (c-d) Projections of coral coverage for hotspots (red), thermally moderate reefs (grey) and thermal refugia (blue) under past (1985-2020) and future (2021-2100) heat stress projected by five global climate models (GCMs) following two Shared Socioeconomic Pathways (SSPs) of greenhouse gas emissions (c: SSP1-2.6, d: SSP2-4.5). Pale trajectories indicate individual GCM simulations while bold trajectories indicate the GCM ensemble mean. Coral dynamics were simulated in response to unmanaged once-per-decade non-thermal disturbances (vertical grey lines) and downscaled heatwave projections (purple-to-orange colour bar) varying by heat stress regime. (e-f) Final levels of coral coverage and heat tolerance of each reef in the 2090s (e: SSP1-2.6, f: SSP2-4.5), showing reef heat stress regimes (colour as in a) and the GCM ensemble mean (point) and standard error (error bars).

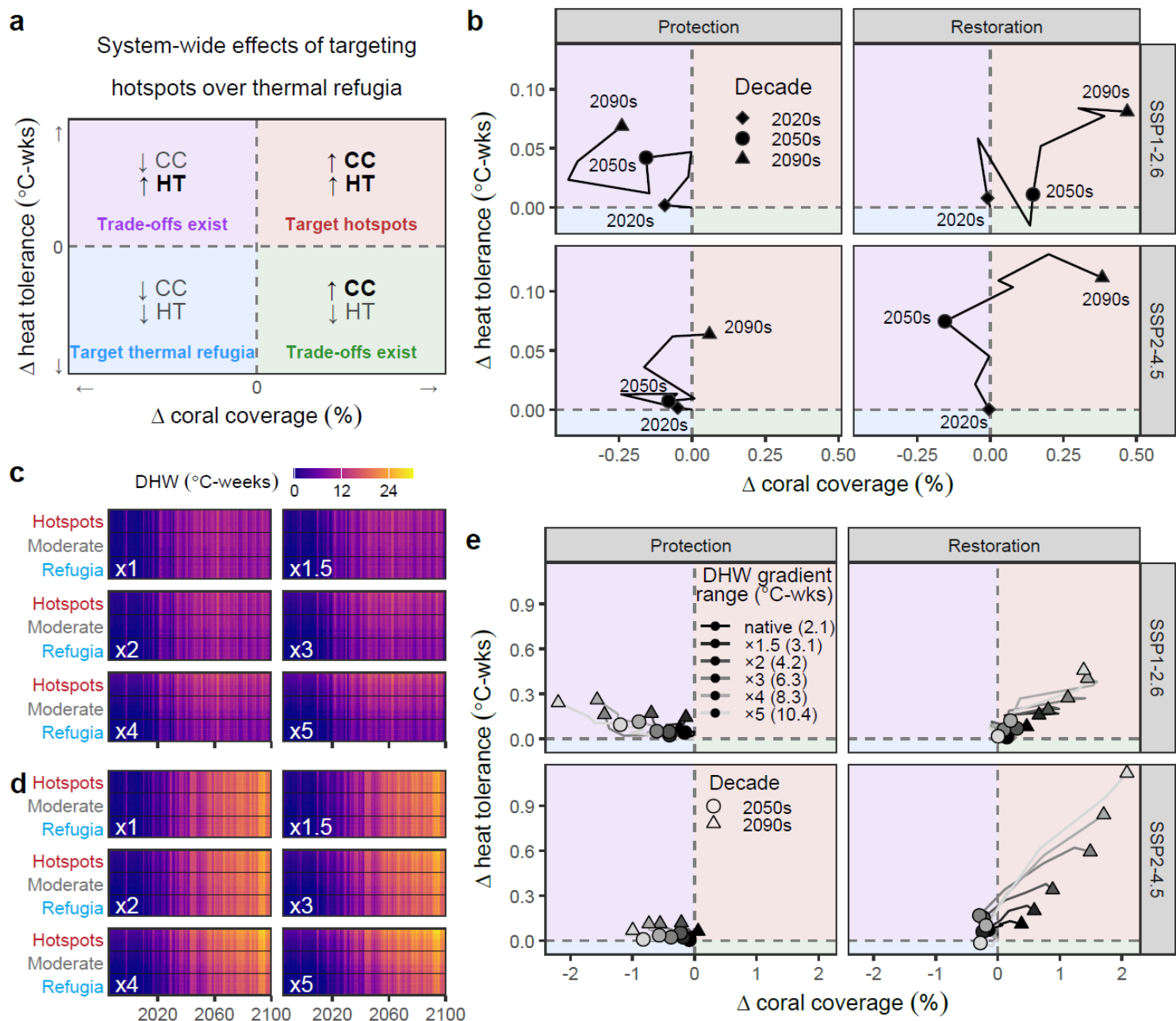


Figure 3

Comparison of the system-wide benefits of targeting management actions at hotspot reefs versus a baseline of targeting thermal refugia. (a) Conceptual diagram for interpreting delta values ($\Delta X = X_{\text{Hotspot}} - X_{\text{Refugia}}$). If results fall in the top right quadrant, for example, then managing at hotspots rather than thermal refugia improves system-wide coral coverage (CC) and heat tolerance (HT), suggesting targeting hotspots is a better strategy. In comparison, results that fall in the top left quadrant indicate that targeting hotspots reduces system-wide coverage gains but increase heat tolerance gains, indicating there are trade-offs associated to spatial management decisions. (b) Decadal Palau-wide timeseries (black lines), showing the difference in mean coral coverage and mean heat tolerance between hotspot-focussed and refuge-focussed management. Results are given for protection (left panels) and restoration (right panels) strategies in two Shared Socioeconomic Pathways (SSPs). (c-d) DHW

timeseries among reefs ordered in the y-axis by DHW anomaly under the different DHW gradient strength (x1-x5) under SSP1-2.6 (c) and SSP2-4.5 (d). (e) System-wide outcomes of hotspot-focussed versus refuge-focussed management depending on the strength of spatial DHW gradients (x1-x5 showing range of DHW anomalies among reefs in brackets, grey shading). Decadal means (for b and e) are computed across the full global climate model ensemble with 10 independent random seed simulations, highlighting the decades: 2020s (diamonds) 2050s (circles) and 2090s (triangles).

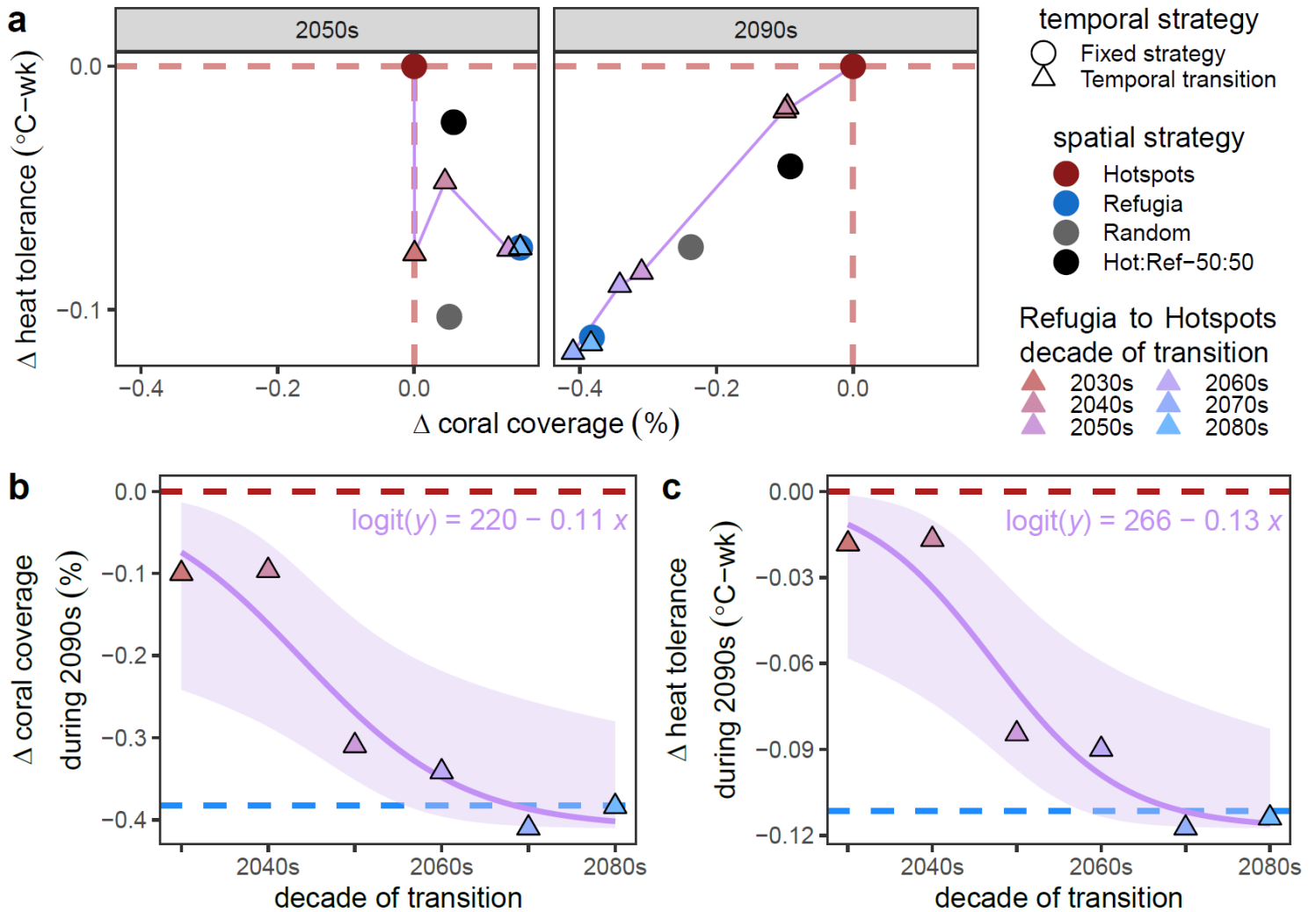


Figure 4

Comparison of spatial and spatiotemporal approaches to restoration under the higher emissions SSP2-4.5 scenario. Here, all strategies are shown relative to the hotspot only approach. Temporally fixed strategies targeted hotspots (red, c.f. Fig. 3), thermal refugia (blue, c.f. Fig. 3), random reef portfolios (grey), or 50:50 hotspot:refuge portfolios (black) independently, while temporally shifting strategies had restoration efforts first focusing on thermal refugia, before gradually transitioning to hotspots over a single decade period between the 2030s and 2080s (pale red-purple-blue points). These spatiotemporal strategies test the ability to address the near-term losses resulting from targeting restoration at hotspots rather than thermal refugia in SSP2-4.5 (c.f. Fig. 3b). (a) Comparison of each restoration strategy relative

to a purely hotspot reef-focussed approach ($\Delta X = X_{\text{Other Strategy}} - X_{\text{Hotspot}}$) in terms of coral coverage and heat tolerance, shown as the decadal mean in the 2050s (left) and 2090s (right). **(b-c)** The influence of transition delay for the temporally shifting strategy, showing mean coral coverage **(b)** and heat tolerance **(c)** in the 2090s as a function of the decade in which restoration switches from targeting hotspots to targeting thermal refugia. Model fit of logistic regression among each spatiotemporal strategy (pale red-purple-blue points) is given as the mean (purple line) and 95% CIs (purple shading). Decadal means are computed across the full global climate model ensemble with 10 independent random seed simulations.

Supplementary Files

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