LETTERS
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Management for network diversity speeds evolutionary adaptation to climate change

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Ecosystems around the world are reorganizing due to climate change[1], motivating management responses to facilitate species persistence and maintain ecological functions. Spatial management actions are generally undertaken to relieve local stressors on populations and have recently been suggested as an approach to facilitate species range shifts, provide refugia and enhance resilience to climate change[2,3]. Efforts to identify which habitats to protect, however, typically assume that organisms do not evolve in response to shifting environmental conditions[4,5] despite growing evidence that rapid evolutionary responses occur under new selective regimes in the wild[6,7]. It is not clear whether conservation strategies would be different if evolutionary dynamics were considered during conservation planning. Here, we show that evolutionary responses fundamentally change recommendations for conservation actions. With spatially explicit simulations of a simple three-species coral reef ecosystem, we show that the preferred management strategies changed from those focusing on thermal refugia when evolutionary capacity was absent to those prioritizing trait and habitat diversity or high cover when adaptive evolution was possible. Prioritizing habitat diversity protects heat resistant populations and protects cooler refuges and the stepping stones between them. The protection of habitat heterogeneity and connectivity also produced substantially larger benefits outside reserves than refugia-based strategies, providing conservation planners an opportunity to facilitate adaptation to ongoing and unpredictable change.

Like many ecosystems globally, reef-building corals are acutely threatened by rising temperatures and other stressors[8,9], as shown by recent global bleaching events[10]. Predictions about the future of corals are generally grim (for example, refs. [11,12]), but there is growing recognition that corals have the capacity to adapt rapidly to changing climate[7,13,14]. Explicit consideration of such evolutionary potential may change recommendations for current management actions to foster long-term persistence[15].

Here we examined alternative conservation strategies for populations with different evolutionary capacities subject to ongoing climate warming. Adapting a generic eco-evolutionary and climate change model[16], we modelled coral communities arranged across a heterogeneous thermal landscape in which individual reefs have unique thermal environments. We simulated a coral reef network consisting of 60 equally sized reefs, arranged linearly so that each reef was connected via larval dispersal to directly adjacent reefs. Similar to previous coral models[17,18], we simulated population and evolutionary dynamics of three functional groups competing for space on each individual reef: two coral groups (one fast-growing with narrow thermal tolerance, one slow-growing with broad thermal tolerance) and macroalgae. Each reef had a unique temperature, which increased linearly along the reef in our primary analysis (hereafter, the 'gradual' thermal landscape). The population dynamics of each of the two coral groups over space (x) and time (t) was modelled as a function of the group's intrinsic rate of increase, its fitness at position x and time t, which depended on the optimal temperature of the group at position x compared to the ambient temperature, the genetic variance present in the population (V_i) and the dispersal rate (D_i). We assumed the slower growing, stress-tolerant coral group had a competitive advantage and that algae could overgrow corals. We modelled thermal tolerance as a quantitative trait dependent on many genes of small effect[14,19,20]. Our model is not intended to project real future coral cover, but rather to compare the relative cover achieved under different management strategies.

In each generation, dispersal carried trait genes to adjacent locations. Selection acted on these new trait distributions in each generation. We simulated climate change as an asymptotic increase in temperature of 3 °C over 150 years to a new steady-state. We modelled coral reef conservation by increasing algal mortality from its background rate (a random value between 0 and 0.3) to its maximum value (0.3) at specific locations chosen as protected areas, as would happen by protecting herbivorous fish or reducing nutrient inputs. Protected areas in the model thus benefit corals by reducing competition with macroalgae, as observed in the Caribbean[21].

To demonstrate that the model produces realistic dynamics and that evolution is important over ecologically relevant time scales, we examined model simulations of long-term coral cover across a range of dispersal rates and levels of additive genetic variance. Corals faced with long-term warming quickly became functionally extinct in the absence of any evolutionary capacity (that is, $V_i = 0$; Figs. 1 and 2a; Supplementary Fig. 1a), which is consistent with previous studies[17]. Functional extinction occurred even when 20% of the reef network was protected. With even modest evolutionary capacity (although less than the median estimates of physiological trait heritability[22]), corals were able to maintain high cover, particularly within protected areas (Figs. 1 and 2), suggesting that even a small amount of evolutionary adaptation can help maintain ecosystem functions[13,17].

We next explored three broad conservation approaches promoted in the literature that prioritize protecting reefs identified by either (1) thermal conditions, (2) current coral cover or (3) the

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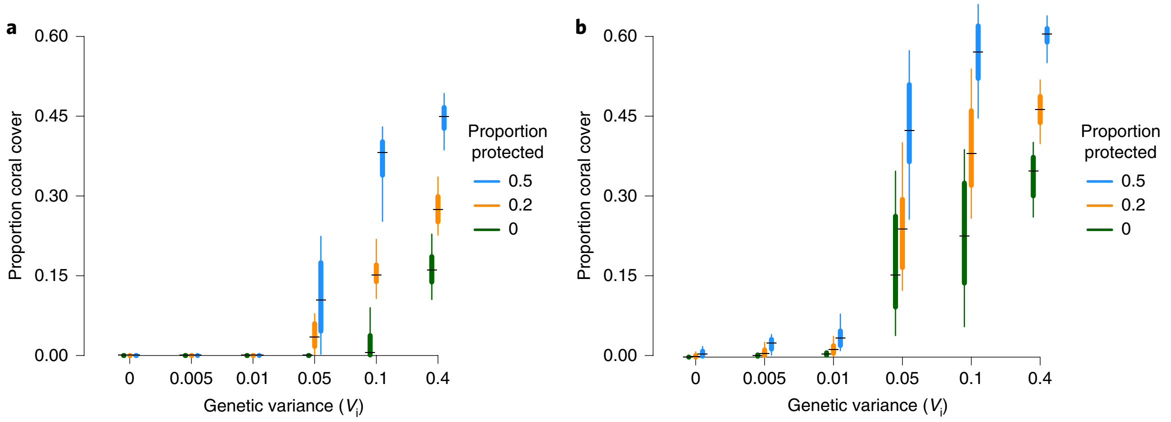

Fig. 1 | Evolutionary capacity improves long-term coral cover when faced with climate change. a,**b**, Bars represent average coral cover (across the reef network) at the end of simulations (500 years after onset of climate change) under scenarios of no dispersal (**a**) and high dispersal (**b**). Thick bars represent the interquartile range of average coral cover at each level of simulated genetic variance; thin lines represent 95% of the simulated results. Black bars represent the median coral cover values. Different colours represent different levels of protection across the reef network. Note that the *x* axis is not linear. Protected sites were selected at random for this analysis.

heterogeneity of traits and habitat conditions within the protected-area network (Table 1; Supplementary Fig. 2). The temperature-based strategies focused on sites expected to contain populations preadapted to future conditions ('hot reefs' strategy[23]) or on sites predicted to be suitable in the future ('cold reefs' strategy[24]). The cover-based strategies focused on either protecting sites currently holding large populations of desired species ('high cover' strategy) or on sites with the smallest populations ('low cover' strategy). The heterogeneity-based strategies focused on protecting habitat, trait or response diversities ('portfolio' and 'evenly spaced' strategies) or on protecting random sites across the network.

Three factors influenced the relative performance of different management strategies: adaptation potential, time-frame of reference and thermal landscape. Without evolutionary potential (that is, $V=0$), the strategy protecting cooler sites maintained highest coral cover amongst all strategies (Fig. 3c) but did not prevent functional extinction under climate change (Figs. 2a and 3c). With even small amounts of evolutionary capacity (that is, $V>0.05$), the cold reefs strategy was amongst the worst strategies for maintaining coral cover in the long run (Fig. 3c). This is particularly interesting because the cold reefs strategy is analogous to the widely suggested approach of protecting thermal refugia (for example, ref. [25]). Even with only a small amount of evolutionary capacity (that is, $V>0.05$), the most effective strategies were those protecting heterogeneity and those protecting the highest cover locations (Figs. 2 and 3c). Protecting only cold sites would require nearly double the amount of protected area to achieve the same conservation benefits as protecting locations across the thermal gradient (Fig. 3b). The evenly spaced strategy performed particularly well across all biological scenarios (Figs. 2 and 3c). This approach maintained corals with a diversity of trait values within reserves, providing more opportunities for retention of traits that matched the variable environmental conditions in unprotected reefs. Additionally, the evenly spaced strategy minimized the distance from any unprotected area to the nearest protected area, increasing the likelihood of adapted larvae reaching unprotected reefs.

The relative performance of strategies often changed between early transient periods and over the duration of the 500-year simulations. In a gradual thermal landscape, differences amongst conservation strategies were driven by rapid changes in traits, although differences in coral cover developed slowly (Fig. 2; Supplementary Fig. 3) and primarily outside protected areas in the long term (Fig. 2b,c). Heterogeneity strategies initially demonstrated intermediate performance before becoming among the best performing strategies over the long term.

Table 1 | Descriptions of protected-area selection strategies used in the analysis

Category	Strategy	Algorithm
Temperature	Hot reefs	Select the x% hottest reefs at the time of site selection
	Cold reefs	Select the x% coldest reefs at the time of site selection
	Hot and cold reefs	Select the $(x/2)$% hottest and the $(x/2)$% coldest reefs at the time of site selection
Cover	High cover	Select the x% of reefs with the highest coral cover at the time of site selection
	Low cover	Select the x% of reefs with the lowest coral cover at the time of site selection
Heterogeneity	Evenly spaced	Select x% of reefs, evenly spaced across the entire reef network
	Portfolio	Select the x% of reefs that maximize average coral cover while minimizing the temporal covariance in coral cover among reefs
	Random	Select x% of reefs at random

Sites are selected for management after a historical burn-in period with constant average temperature at each site. Climate change began simultaneously with site selection. Site management is assumed to increase the mortality of macroalgae (for example, through increased herbivory as a result of stricter fishing regulations).

A gradual thermal landscape imposes restrictive geography on some management strategies – for example, the hot reefs strategy protected only one end of the linear reef network. To dissociate the thermal and geographic features of management, we generated a randomized thermal landscape. In these simulations, the evenly spaced and random strategies again performed well but the temperature-based strategies (particularly the cold reefs strategy) performed better than when under gradual thermal landscape conditions (Fig. 2d). With a randomized thermal landscape,

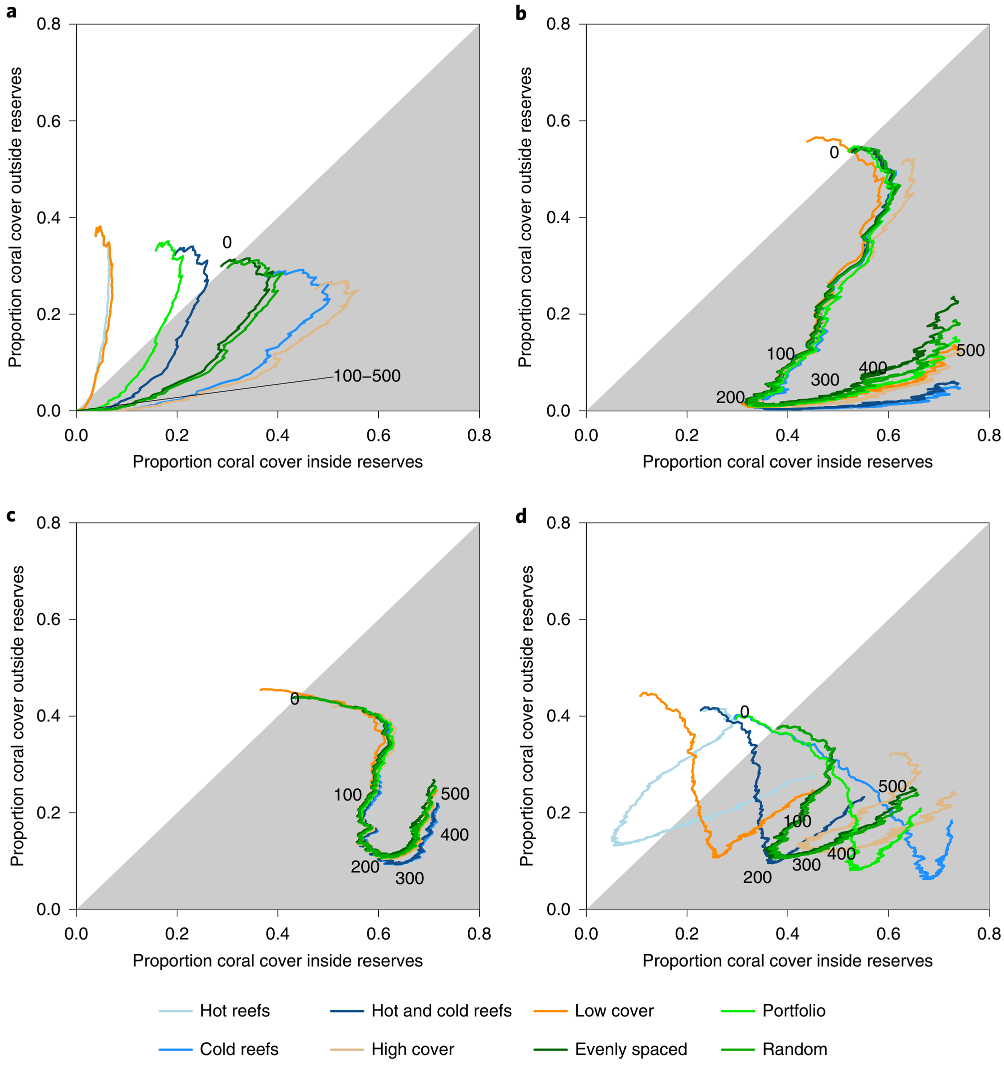

Fig. 2 | Average cover of corals inside protected reserves relative to outside protected reserves across the duration of simulations. a–d, All scenarios have 20% of the total reef network in protected areas. Lines show the trajectories of reefs through time as the median values across 100 stochastic model iterations. Numbers indicate number of years after the onset of climate change along each trajectory. Each panel represents a different biological (that is, level of additive genetic variation in coral populations $V = 0$ (no genetic variance; **a**), $V = 0.1$ (low genetic variance; **b**) or $V = 0.4$ (high genetic variance; **c**)) or physical (that is, thermal landscape arrangement (low genetic variance; **d**)) scenario. Line colours correspond to different spatial prioritization strategies. All results were produced with intermediate dispersal rates ($D = 0.001$).

traits from hot sites can quickly reach protected cold sites, which ultimately become suitable habitats for these hot-adapted traits. Reality lies somewhere between these two simulated thermal landscape arrangements, although limited evidence suggests reefs are generally linked to other reefs with similar thermal regimes[17,26], more similar to our gradual thermal landscape. Circumstances that put warm and cold reefs in close proximity might include cool upwelling zones in otherwise warm regions[22] or warm-water reefs that are distributed intermittently as a function of shallow water, restricted flow and daytime low tides[7]. Our model suggests that protecting connections between such disparate habitats is highly beneficial[15].

The success of evenly spaced and random protective strategies reflects the importance of maintaining trait heterogeneity across the landscape during demographic collapses predicted over the next 100 years (Fig. 2). In effect, conserved hot reefs served as important sources of preadapted corals, conserved cold reefs served as future habitats of these corals and intermediate reefs were key stepping stones. Protecting all three types of habitats results in a de facto three-part conservation strategy of protecting current populations adapted to future conditions, protecting climate refugia as locations of future populations and maintaining ecosystem connectivity. Coral populations declined to very low levels of cover outside reserves but when trait diversity was maintained across the landscape, evolutionary rescue led to increased total cover outside and inside reserves. This rescue is a consequence of a greater match between trait and environmental conditions throughout the landscape[27]. Our model of ecosystem change probably represents the best-case scenario for temperature-based strategies because it is driven by a known single stressor (that is, temperature), and yet the temperature-based approaches still performed poorly relative to heterogeneity-based strategies. In a more realistic scenario where populations respond to multiple (potentially unknown) stressors, strategies predicting ecological responses and prescribing management from models are even less likely to perform well[28,29] and will require extensive data collection and analysis, thereby delaying implementation of conservation actions. Alternatively, the robust performance of the evenly spaced and random strategies across realistic biological scenarios

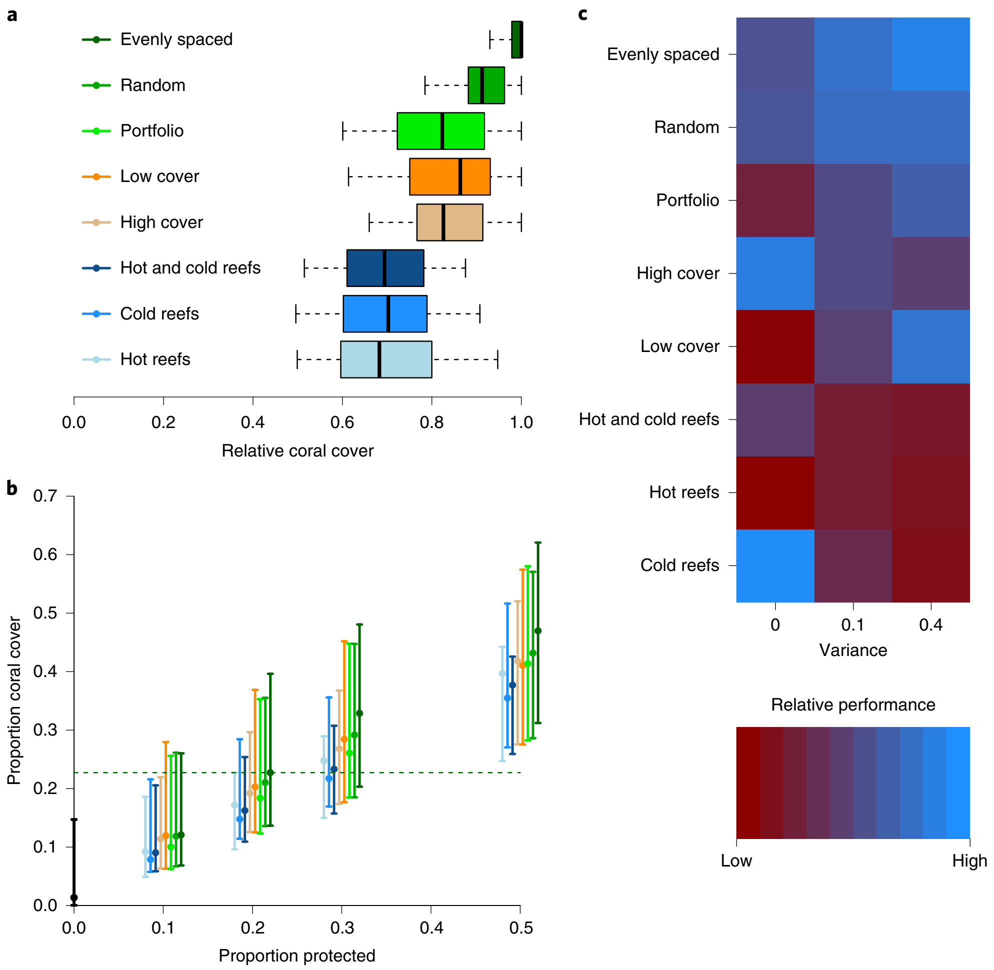

Fig. 3 | The presence of evolution alters which conservation strategies perform best. a–c, When additive genetic variation is present, protected-area heterogeneity strategies perform better than temperature-based strategies, even at lower levels of protection. **a**, Coral cover relative to the best performing strategy within each stochastic iteration of the simulation model for each local management strategy. Thick lines represent the median relative coral cover, the box represents the interquartile range and the whiskers cover all points that fall within the 95% simulation intervals. These results represent the scenario with intermediate additive genetic variance ($V=0.1$) and dispersal ($D=0.001$). **b**, Coral cover at year 500 for different proportions of the reef network within protected areas and spatial prioritization strategies. Points represent the median coral cover value across all simulations at intermediate dispersal ($D=0.001$) and genetic variance ($V=0.1$) values. Error bars indicate the 90% simulation intervals. The dashed horizontal line represents the median coral cover using the evenly spaced strategy at proportional protection of 0.2, which is greater than the median coral cover under the cold strategy at proportional protection of 0.3. **c**, Relative performance of different protection strategies (as defined in **b**) across a range of evolutionary capacities, with intermediate dispersal rates.

suggests scientific uncertainties need not delay conservation actions for protecting diversity.

Although spatial conservation planning theory calls for maintaining the ecological and evolutionary processes that support ecosystem structure and function (for example, refs. [28,30]), much contemporary literature focuses on identifying and protecting climate refugia (for example, ref. [25]). Here we show that ignoring the potential for evolutionary adaptation can lead to selection of inferior conservation strategies over the long term. Our simulations suggest that a narrow focus on climate refugia will sacrifice genetic diversity critical to the evolution of traits needed to persist under new climates. Maintaining trait and habitat diversity across landscapes and through time will provide the greatest number of opportunities for species to adapt[28], either through gene flow or in situ adaptation. In the absence of genetic information, trait and habitat diversity are likely to be useful proxies. Focusing on spatial and temporal heterogeneity has the advantage of not requiring excessive data collection to parameterize models to generate predictions of future states. Diversifying strategies can be applied to conservation actions immediately across a range of marine and terrestrial threatened ecosystems by ensuring that spatial management networks are designed to include a heterogeneous network of demographically connected locations with different environmental and biological conditions driving local adaptation. Prompt action can provide ecosystems experiencing rapid change with a chance to successfully adapt and maintain functions in an uncertain future.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of code and data availability and associated accession codes are available at https://doi.org/10.1038/s41558-019-0518-5.

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Author contributions

T.E.W., D.E.S., M.A.C., M.S.W. and M.L.P. conceived the study. T.E.W., D.E.S., M.A.C., M.S.W., S.R.P., P.J.M., T.E.E. and M.L.P. designed the experiments. T.E.W. developed the models and ran the analyses. T.E.W., D.E.S., M.A.C., M.S.W., S.R.P., P.J.M., T.E.E. and M.L.P. interpreted the results. T.E.W., D.E.S., M.A.C., M.S.W., S.R.P., P.J.M., T.E.E. and M.L.P. wrote and/or substantively revised the manuscript.

Additional information

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Methods

Simulated ecosystem. We simulated a coral reef network consisting of 60 equally sized individual reefs in a linear arrangement. Each reef had a unique temperature, which increased linearly along the reef. The complex physical structure of coral reef ecosystems is generated by scleractinian corals, which compete for suitable substrate with other corals and macroalgae. The shifting competitive balance due to changing conditions on reefs can drive these systems to either coral-dominated or macroalgal-dominated states[15,17]. Similar to previous studies[17,18], we simulated the dynamics of three functional groups of biota: two coral groups and a group representing macroalgae. The coral groups were: (1) a fast-growing group with narrow temperature tolerances and (2) a slow-growing group with broader thermal tolerances. We chose to model two coral and one macroalgal 'species' for computational simplicity in order to maintain focus on the relative performance of alternative management strategies and for consistency with previous coral reef community models. We note that in the original model[16], species differed primarily in their optimal temperature (z_i), whereas our three species differed in other axes (particularly growth rate and width of the temperature response), which allowed coexistence in a given location. Limiting the system to only two coral and one macroalgal species provides for a more tractable case study of a complex system with multiple dynamic conditions (that is, local temperatures changes, local management strategy). By simplifying the ecosystem under examination, we are better able to focus on the effects of thermal change and spatial management design, while still accounting for critical ecological interactions. Additionally, this is a common community structure used to model reef community response to change, both in evolutionary[17,31] and non-evolutionary[32] settings. Although this approach underplays the full diversity of corals within reef ecosystems, it captures two of the prominent functional groups of corals found on reefs globally[33].

Population dynamics. Species' persistence is influenced by the suitability of their environment, interactions with other species and their ability to adapt to changes in their environment (evolutionarily, through plasticity or through dispersal). Traditional analyses of species responses to environmental change have focused on habitat suitability and dispersal because evolutionary processes were considered to operate at time-scales too long to be important under rapid climate change. However, as rapid evolution in response to changing environments is increasingly recognized[6,34], eco-evolutionary approaches provide a powerful avenue for examining the potential responses of species to future climate change by incorporating each of these processes[16,35,36].

Using a simulation modelling approach adapted from ref. [16], we track the population and evolutionary dynamics of the three functional groups. The population and trait dynamics of the two coral groups, N_1 and N_2, in location x and time t are modelled as:

$$\frac{\mathrm{d}N_i(x,t)}{\mathrm{d}t} = g_i(x,t)N_i(x,t) + \frac{1}{2}V_i\frac{\partial^2 g_i(x,t)}{\partial z^2}\bigg|\, z = z_i(x,t)\, N_i(x,t) + D_i\frac{\partial^2 N_i(x,t)}{\partial x^2} \tag{1a}$$

$$\frac{\mathrm{d}z_i(x,t)}{\mathrm{d}t} = q_i V_i\frac{\partial g_i(x,t)}{\partial z}\bigg|\, z = z_i(x,t) + D_i\left(\frac{\partial^2 z_i(x,t)}{\partial x^2} + 2\frac{\partial \log N_i(x,t)}{\partial x}\frac{\partial z_i(x,t)}{\partial x}\right) \tag{1b}$$

$$q_i(x,t) = \max\left(0, 1 - \frac{N_{\min}}{\max(N_{\min}, 2N_i(x,t))}\right) \tag{1c}$$

where $N_i(x,t)$ is the abundance (proportional reef coverage) of coral group i at location x and time t, $g_i(x,t)$ is the fitness, V_i is the genetic variance, $z_i(x,t)$ is the trait (that is, optimum temperature for growth), D_i is the dispersal rate and q reduces evolutionary rates at extremely low population abundances where $N_{\min} = 10^{-6}$. This approach to modelling genetic variance assumes that thermal tolerance is polygenic and controlled by many genes of small effect[37]. Local dispersal is a function of the densities of a species in the site of interest x, as well as those sites immediately adjacent to it in both directions (final term in equation (1a)). Fitness was modelled as:

$$g_i(x,t) = r_i(x,t)\left(1 - \sum_{I}\alpha_{i,j}N_i(x,t)\right) - m_i(x,t) \tag{2}$$

$$m_i(x,t) = \begin{cases} \mu & T(x,t) < z_i(x,t) \\ 1 - \exp\left(\frac{-(T - z_i(x,t))^2}{w_i^2}\right) & T(x,t) > z_i(x,t) \end{cases} \tag{3}$$

$$r_i(x,t) = \frac{r_{\max,\,i}}{\sqrt{2\pi w_i^2}}\exp\left(\frac{-(T(x,t) - z_i(x,t))^2}{w_i^2}\right) \tag{4}$$

where $r_i(x,t)$ is the growth rate, α is a matrix of group competition coefficients, $m_i(x,t)$ is mortality, μ is the base mortality, $T(x,t)$ is the current temperature, w_i is the thermal tolerance breadth and $r_{\max,i}$ scales the growth rate function (Supplementary Tables 1 and 2). This formulation of mortality differs from the model used in ref. [16] by the addition of temperature and trait effects on mortality when temperature is higher than the optimal population temperature $z_i(x,t)$. Our formulation results in an asymmetric population growth response to changing temperatures, with greater reductions in population growth at temperatures above the optimal temperature of the population rather than below. Ectotherms commonly demonstrate physiological performance curves of this shape[38], making them particularly susceptible to increasing temperatures under climate change[39].

We assumed that the slow-growing, stress-tolerant coral had a competitive advantage over the fast-growing coral (modelled with $\alpha_{1,2}$ in equation (2); Supplementary Table 1; refs. [31,40]). We also assumed that the coral groups had thermal optima at the local mean temperature at the start of the simulations (that is, $z_i(x,0) = T(x,0)$). Starting densities for all functional groups were drawn from a uniform distribution between 0 and 0.25 for each reef in the network.

The presence of alternative phases has been documented for some Caribbean coral reefs where reefs switch between states of high (low) cover of scleractinian corals with low (high) macroalgal cover[32,41] in response to changes in grazing pressure, although other stressors might result in similar outcomes[42]. Macroalgae were modelled similarly to corals, except they were assumed to have constant growth rates (that is, insensitive to temperature) and mortality rates $m_A \approx U(0,0.3)$. As such, the second term of equation (1a) does not apply, nor do equations (1b), (1c), (3) or (4). Instead:

$$\frac{dN_A(x,t)}{dt} = g_A(x,t)N_A(x,t) + D_A\frac{\partial^2 N_A(x,t)}{\partial x^2} \tag{5}$$

$$m_A(x,t) = \begin{cases} U(0,0.3) & x \text{ outside Protected Area} \\ 0.3 & x \text{ inside Protected Area} \end{cases} \tag{6}$$

$$r_A(x,t) = r_{\max,A} \tag{7}$$

where equation (5) r1a), equation (6) replaces equation (3), and equation (7) replaces equation (4). Coral growth rate ($r_{\max,A}$; Supplementary Table 1) was selected to provide realistic community dynamics under steady-state conditions. Although it appears substantially slower than coral growth rate scalars, coral growth rates are further scaled by thermal conditions, generating a maximum macroalgal growth rate higher than the maximum growth rates of corals. Additionally, we assume that macroalgae can overgrow corals ($\alpha < 1$). Despite these disadvantages, corals are able to maintain or increase cover due to lower mortality rates than macroalgae when corals are well adapted to their thermal environment. This is particularly true in locations selected for protection, in which $m_A(x,t) = 0.3$; where A identifies parameters for macroalgae dynamics.

Macroalgae are assumed to be temperature insensitive across the ranges of temperatures explored in these simulations. This is a common simplifying assumption in coral reef models incorporating macroalgal dynamics[17,42]. Marine macroalgal communities have not been as intensively studied as coral communities, and although there is growing knowledge of how individual species may respond to increased temperatures[43], there is limited information regarding how macroalgal communities as a whole may respond to climate change. Furthermore, it has been suggested that climate change is unlikely to result in direct changes to macroalgal mortality rates, but instead to indirectly impact macroalgae dynamics through community shifts and changing species interactions (for example, reduced competition from declining coral cover[44]). Due to these uncertainties and in order to maintain a simple ecological community consistent with previous research on coral-macroalgal-climate dynamics, we modelled macroalgal dynamics as responding only to predation (through changes in mortality) and competition for space.

Dispersal rates and genetic variance are uncertain parameters across the landscape. As such, we simulated across a range of values for each parameter to reveal trends that are robust to parameter values. We simulated three levels of dispersal rate, including no ($D = 0$), intermediate ($D = 0.001$) and high ($D = 0.01$) dispersal rates (Supplementary Table 2). For the analysis of which prioritization strategies are robust to parameter uncertainty, we simulated no ($V = 0$), intermediate ($V = 0.1$) and high ($V = 0.4$) levels of genetic variance (similar to values in ref. [45]). For the analysis of the role of evolution in allowing the persistence of corals, we included values between the no and intermediate values of genetic variance ($V = 0.001$, 0.005, 0.01, 0.05; Supplementary Table 2) to investigate the presence of any threshold values of genetic variance required for successful adaptation. Both coral groups were given the same dispersal and genetic variance values in each simulation.

Climate conditions. Simulations were initially run with constant mean temperatures to allow starting conditions to unfold. Climate change was then simulated as an asymptotic increase in temperature of 3 °C across approximately 150 years to a new steady-state. This represents warming near the upper end of predicted future values[46,47]. The ability for evolutionary adaptation to maintain coral cover in our model is therefore encouraging.

Because temperature varies amongst years and climate change will not occur in a smooth fashion, spatially autocorrelated stochastic thermal anomalies were included throughout the simulations. Temperature changed annually, either with stochastic anomalies or directionally plus stochastic anomalies. Annual stochastic anomalies were spatially correlated such that reefs in closer proximity had more similar anomalies than more distant reefs. A network-wide anomaly was randomly drawn and then a spatially autocorrelated anomaly was added to individual sites. This resulted in hot (or cold) years for the entire reef network, but the anomalies for some groups of reefs were hotter (or colder) than others in any given year.

Prioritization of management. Concurrent with the onset of climate change, managed areas were selected according to different prioritization strategies. Designation of a location as a managed area caused the mortality rate of macroalgae to change from $m_A \approx U(0,0.3)$ to $m_A = 0.3$ (similar to unfished reefs in ref. [26]). Thus, more empty space was opened for colonization by coral species. In practical terms, this could be caused by standard local management actions, such as increasing herbivory on a reef or reducing nutrient pollution. Although this would reduce macroalgal growth rate, rather than increasing mortality, the community level impacts would be similar. For each simulation, a set percentage of the reef network was managed (0–50% of individual reefs).

Prioritization strategies fell into three general categories: temperature-based, cover-based and heterogeneity-based (Table 1). Managing areas that are either expected to contain populations preadapted to anticipated future conditions (our 'hot reefs' strategy[23]) or sites that are predicted to not experience substantial environmental change or become suitable in the future (our 'cold reefs' strategy) are commonly suggested spatial conservation strategies[48]. Protecting sites that currently hold large populations of desired species (our 'high cover' strategy) has also been suggested, as they may have greater genetic diversity and are better able to withstand demographic shocks brought on by climate change[49]. Alternatively, strategies focusing on sites with small populations (our 'low cover' strategy) have been suggested for management or protection, either via restoration or rehabilitation of habitat conditions in degraded sites to increase regional habitat quality[50], or for harbouring adaptive alleles in the surviving individuals[51]. Other researchers suggest protecting habitat, trait or response diversities (our 'portfolio' and 'evenly spaced' strategies), arguing that such strategies provide more options for ecosystems to adapt to uncertain future conditions[28,52]. The gradual thermal gradient of the simulated reefs causes the evenly spaced strategy to sample universally in both physical and trait space as well as in minimizing the distance between unprotected and protected areas. In contrast, the temperature-based strategies concentrate management at either end of the reef network.

One hundred stochastic iterations were run for our primary analyses of each combination of dispersal rate, genetic variance, reef management level and prioritization strategy. The performance of the different prioritization strategies was compared by average coral cover across the reef network (as an indicator of ecosystem function) and relative coral cover within a stochastic run. Relative performance was measured as coral cover under each strategy divided by the highest coral cover amongst all strategies within each iteration. Within each stochastic model run, simulations of all prioritization strategies experienced the same starting conditions and temperature anomalies, making comparisons between prioritization strategies meaningful. For comparisons of relative coral cover, the average coral cover of each strategy was divided by the maximum average coral cover amongst all strategies within that stochastic iteration. The best performing strategy thus had a relative coral cover of 1, with all other strategies falling between 0 and 1.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The simulated datasets generated during this study are available from https://github.com/pinskylab/ecoevo_coral.

Code availability

The R code used to generate the simulated datasets is available from https://github.com/pinskylab/ecoevo_coral.

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Software and code

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Data collection	All simulation models were run in the R Statistical Programming Environment. Custom code is available from the corresponding author upon request.
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Study description	Eco-evolutionary simulation models of coral reef communities were run under different biological conditions and subjected to changing climatic conditions. Thermal tolerance traits were allowed to evolve through both genetic drift and natural selection. We examined the performance of multiple potential spatial conservation strategies across a 500-year simulation period.
Research sample	Modeled coral reef communities comprised of three functional groups (i.e., a fast-growing, temperature sensitive coral, a slow-growing stress-resistant coral, and macroalgae) on a linear reef network comprised of 60 simulated reefs with unique thermal conditions.
Sampling strategy	The percent cover of all functional groups and the thermal tolerance traits of the coral groups were monitored at each time step for 500-years.
Data collection	Data were generated from an eco-evolutionary simulation model in the R Statistical Programming Environment.
Timing and spatial scale	Simulations were run to describe 500-years of changing environmental, ecological, and evolutionary conditions across the simulated 60 reef linear networks.
Data exclusions	None of the simulated data were excluded from the analysis.
Reproducibility	The study is very reproducible, as no sample data were used and all simulation model code is available from the corresponding author upon request.
Randomization	Annual thermal anomalies were randomly drawn and the same thermal anomalies were applied to all spatial conservation strategies.
Blinding	No blinding, not applicable.

Did the study involve field work? ☐ Yes ☒ No

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