



# Estimating the potential for coral adaptation to global warming across the Indo-West Pacific

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## Abstract

The potential of reef-building corals to adapt to increasing sea-surface temperatures is often debated but has rarely been comprehensively modeled on a region-wide scale. We used individual-based simulations to model adaptation to warming in a coral metapopulation comprising 680 reefs and representing the whole of the Central Indo-West Pacific. Encouragingly, some reefs—most notably Vietnam, Japan, Taiwan, New Caledonia and the southern half of the Great Barrier Reef—exhibited high capacity for adaptation and, in our model, maintained coral cover even under a rapid “business-as-usual” warming scenario throughout the modeled period (200 years). Higher resilience of these reefs was observed under all tested parameter settings except the models prohibiting selection and/or migration during warming. At the same time, the majority of reefs in the region tended to collapse within the first 100 years of warming. The adaptive potential (odds of maintaining high coral cover) of a given reef could be predicted based on two metrics: the reef’s present-day temperature, and the proportion of recruits immigrating from warmer locations. The latter metric explains the most variation in adaptive potential, and significantly correlates with actual coral cover changes observed throughout the region between the 1970s and the early 2000s. These findings will help prioritize coral conservation efforts and plan assisted gene flow interventions to boost the adaptive potential of specific coral populations.

## KEYWORDS

adaptation, assisted gene flow, climate change, individual-based modeling, metapopulation

## 1 | INTRODUCTION

The world has been warming at an unprecedented rate for the past half century (IPCC, 2014). This brings about major ecological changes (Parmesan, 2006), among which the worldwide decline of coral reefs is one of the most alarming (Hoegh-Guldberg et al., 2007). Several highly cited publications have asserted that natural evolution is too slow to allow corals to adapt to global warming (Hoegh-Guldberg, 1999; Hoegh-Guldberg et al., 2007; Hoegh-Guldberg, Poloczanska, Skirving, & Dove, 2017); however, this view is debatable. The scenario envisioned in those papers involves the origin and spread of

entirely novel adaptive mutations (Orr, 2005). This would indeed be slow, as well as difficult to predict without knowledge of such elusive parameters as mutation rate, number of potentially adaptive loci, and mutational effect size. However, the first-order evolutionary response in natural populations rarely involves new mutations; instead, it is based on adaptive alleles pre-existing in a population as part of standing genetic variation (Barrett & Schluter, 2008; Hermisson & Pennings, 2005; Savolainen, Lascoux, & Merilä, 2013). This mode of adaptation can be very rapid (Campbell-Staton et al., 2017; Lescak et al., 2015). In a metapopulation in which a species is distributed across multiple locally adapted sub-populations, there

is also a possibility of rapid adaptation via immigration, redistributing adaptive alleles among populations (Garant, Forde, & Hendry, 2007; Whiteley, Fitzpatrick, Funk, & Tallmon, 2015). Several recent papers have argued that this particular mode of adaptation is likely to be of major importance for reef-building corals as they adapt to warming (Bay, Rose, Logan, & Palumbi, 2017; Kleypas et al., 2016; Matz, Treml, Aglyamova, & Bay, 2018). Indeed, all coral species exist across a considerable gradient of temperatures while genetically adapting to local thermal conditions (Bay & Palumbi, 2014; Dixon et al., 2015; Palumbi, Barshis, Traylor-Knowles, & Bay, 2014) and exchanging migrants over very long distances (Ayre & Hughes, 2004; Baums, Miller, & Hellberg, 2005; Matz et al., 2018; Romero-Torres, Treml, Acosta, & Paz-García, 2018), which appears to set the stage perfectly for immigration-based adaptation (Matz et al., 2018; Torda et al., 2017).

Here, we aimed to identify factors affecting corals' potential to adapt to warming across the central Indo-West Pacific, the ocean region where the majority of the world's coral reefs are found. We have recast our earlier individual-based model of metapopulation adaptation (Matz et al., 2018) as a non-Wright-Fisher model, which is better suited to modeling ecological processes (Haller & Messer, 2019), and extended it from five locations on the Great Barrier Reef to 680 reefs representing the whole oceanic region. The new model was parameterized with the number of populations, reef habitat sizes, and connectivity pattern expected for a reef-building coral of the genus *Acropora* (Treml et al., 2012; Treml, Roberts, Halpin, Possingham, & Riginos, 2015). Our model included a period of long-term adaptation to temperatures fluctuating around a location-specific mean, followed by the onset of location-specific warming as predicted under different scenarios: representative concentration pathways (RCP) 4.5, which assumes reduction of greenhouse gas emissions and stabilization of the greenhouse effect by 2100, and RCP 8.5, which represents rapid warming under "business-as-usual" conditions (Figure S1; Hurrell et al., 2013). We have also explored the influence of juvenile mortality rate, genetic parameters affecting the efficiency of selection (environmental noise, width of the fitness function), and the amount of non-neutral genetic variation (number of quantitative trait loci [QTL], mutation rate, and mutation effect size). In addition, we have modeled the effects of (a) disabling new mutations, (b) disabling migration, (c) disabling selection, and (d) disabling both migration and selection during the warming period. We have then compared our results to the actual coral cover changes observed throughout the region by the early 2000s (Bruno & Selig, 2007).

## 2 | MATERIALS AND METHODS

### 2.1 | Non-Wright-Fisher model

Our model was written as a non-Wright-Fisher model in version 3.3 of the SLiM forward genetic simulation framework (Haller & Messer, 2019). Compared to our earlier model (Matz et al., 2018), this new

non-Wright-Fisher formulation made it possible to model the statistic that is the most meaningful for coral ecology—coral cover—as a proportion of the available carrying capacity occupied. The model outputs (per population) a set of metrics: mean phenotype, mean fitness, number of segregating QTL mutations, standard deviation of breeding value, mean age of adults, number of adults, and adult mortality in the last generation. The model code reads the habitat sizes, migration matrix, and environmental settings from external files, while the major population-genetic parameters (see next paragraph) are supplied as external arguments. This makes the model easy to repurpose for many metapopulation-evolution scenarios.

### 2.2 | Main run parameter settings

In the main run of our model we used conservative settings both in terms of the amount of mutational variation and factors affecting the efficiency of selection. We assumed 100 additive QTLs affecting an individual's thermal optimum, with new mutations having subtle effects following the distribution  $N(0^\circ\text{C}, 0.03^\circ\text{C})$ . The genetically determined thermal optimum (breeding value) of an individual was calculated as the sum of the effects of all QTLs, and the actual phenotype was then computed by adding a random value drawn from  $N(0^\circ\text{C}, 0.5^\circ\text{C})$  to model environmental noise resulting in imperfect heritability. We then computed the fitness of each individual relative to the fitness of a hypothetical individual with a phenotype perfectly matching its environment, based on the difference between the individual's phenotype and the environmental temperature at its location (the temperatures were centered around the prewarming mean across all modeled locations). We used a Gaussian fitness function following the shape of the normal distribution  $N(0, 1)$  rescaled to a maximum of 1, which implies that an individual's fitness would drop by about 40% if its phenotype were mismatched with the local temperature by  $1^\circ\text{C}$ . This setting is realistic and most likely conservative, as we have discussed previously (Matz et al., 2018).

### 2.3 | Reproduction and age-related mortality

Each *Acropora* individual produces  $10^5$ – $10^6$  eggs per yearly spawning event, but the vast majority of these offspring die as larvae or very young recruits without giving rise to a new colony. We assumed that each adult coral produces just a single surviving recruit per year, and that recruit still had only a 50% chance of survival in its first year compared to an adult of the same phenotype. Second year juveniles had 75% of the adult survival rate, and in the third year the surviving corals became reproducing adults (Baria, dela Cruz, Villanueva, & Guest, 2012), with their individual-specific survival rate equal to their relative fitness calculated as described in the previous paragraph. These settings resulted in an average adult coral age, prior to warming, of approximately 10 years, which is reasonable for fast-growing acroporids.

## 2.4 | Habitat size and genetic variation

We assumed that the smallest reefs (completely enclosed within a single  $10 \times 10$  km cell on the map) could contain 100 corals, and larger reefs had more carrying capacity, proportionally to the number of  $10 \times 10$  km cells they occupied (up to 20,000 corals per reef). While these numbers are on par with genetic estimates of effective population sizes (Matz et al., 2018), they are much lower than census sizes. We kept our population sizes low to keep the model conservative (i.e., limiting for adaptation) and also faster-running, but compensated for this by assuming a mutation rate on the upper boundary of values reported in the literature,  $10^{-5}$  per QTL per generation (Barton & Turelli, 1989). This compensation is reasonable since (in the absence of selection and migration) the amount of genetic variation in a population depends on the product of population size and mutation rate.

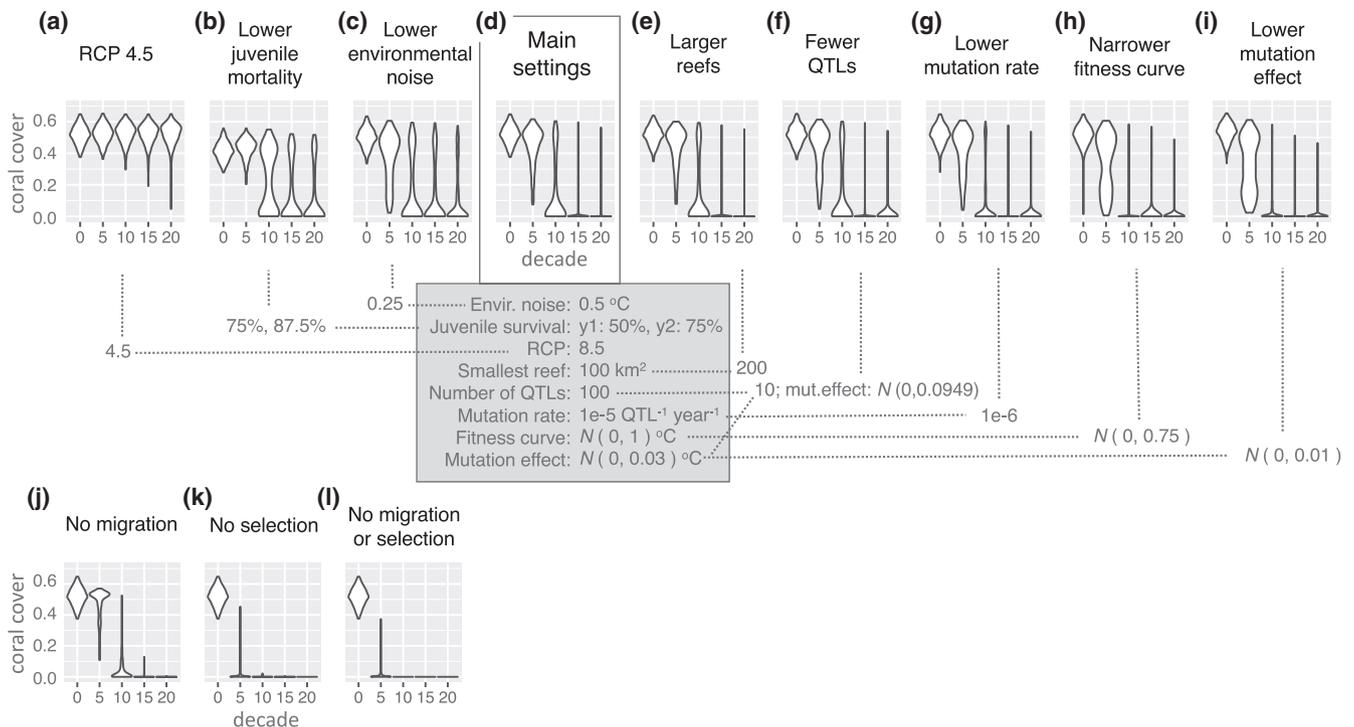
## 2.5 | Environment

Location-specific temperatures were based on the mean yearly temperature at each location (Figure 2a) during the genetic equilibration

period (see below), after which warming was imposed with the location-specific rates predicted under either RCP 4.5 or RCP 8.5 (Figure S1; Hurrell et al., 2013). We explored three models of short-term temperature variation (to which long-term warming was added): constant, fluctuating as a sine wave with a period of 5 years and amplitude of  $0.5^\circ\text{C}$  to approximate El Niño cycles (Quinn, Taylor, & Crowley, 1993), and random temporally uncorrelated fluctuations with an amplitude drawn from a normal distribution using the standard deviation of temperatures empirically observed at each location. These three environmental models yielded nearly identical results, and so all the figures presented here correspond to the sinusoidal model.

## 2.6 | Parameter variations

For each parameter we tried a different setting in addition to the setting in the “main run,” summarized in Figure 1. In the “Low juvenile mortality” scenario, first year recruits had a 75% survival rate in the first year and an 87.5% survival rate in the second year, compared to adults (as opposed to 50% and 75% in the main run). The “Lower environmental noise” scenario had a smaller random

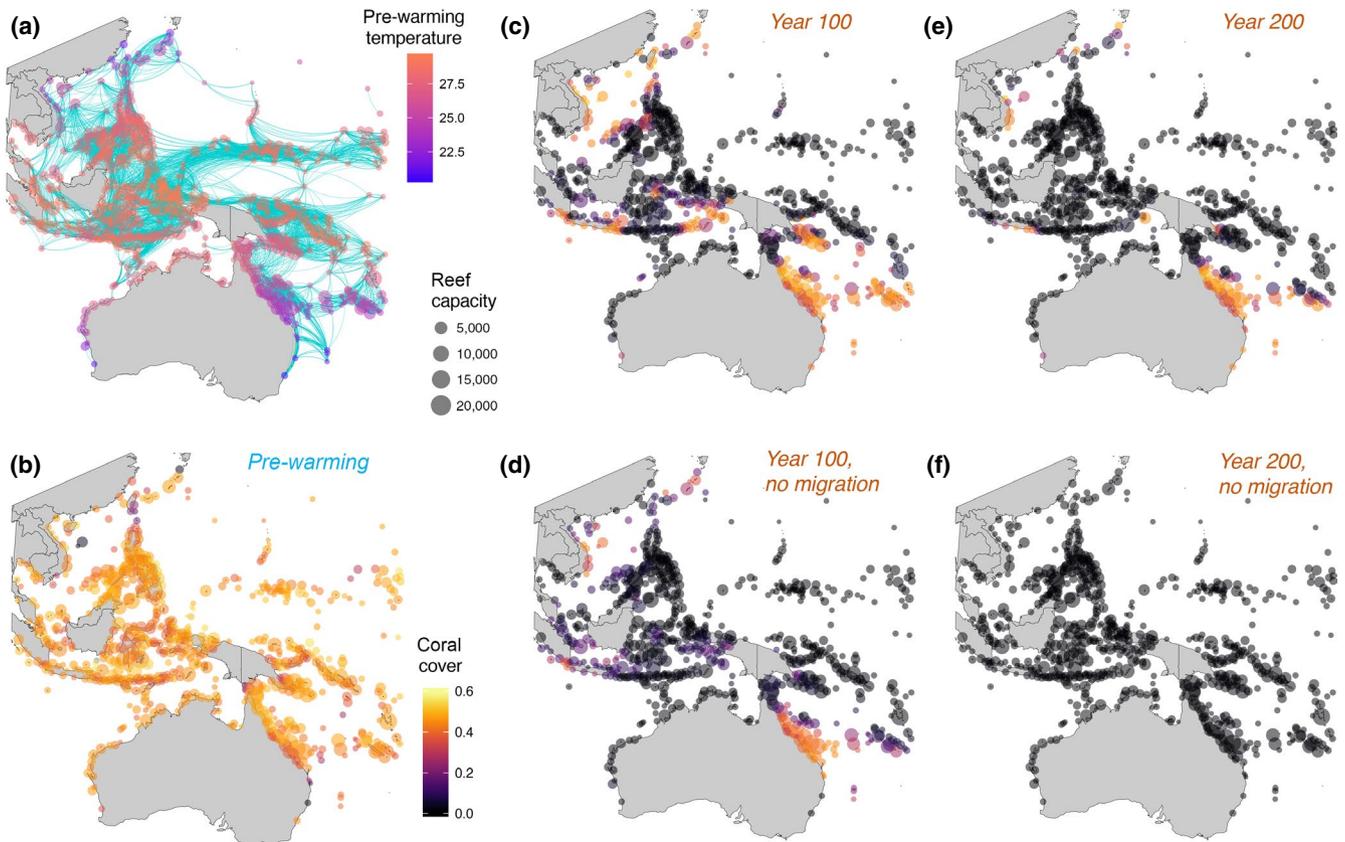


**FIGURE 1** Coral cover changes in response to warming under different parameter settings. On all panels, the x-axis is decade since the start of warming; the y-axis is coral cover (proportion of carrying capacity occupied by adult corals). The shapes are violin plots (rotated kernel density plots, mirrored on each side of the x-value) excluding ten top and ten bottom values. Panels in the top row represent model runs with different parameter settings, arranged from highest to lowest reef persistence under warming. Each alternative scenario is different from the “main settings” in a single parameter indicated under the panels, except the “Fewer QTLs” scenario which had fewer QTLs and also elevated mutation effect to preserve the amount of mutational genetic variation. Panels in the lower row represent the three “null” models, where migration (j), selection (k), or both migration and selection (l) were switched off during the warming period. The “no new mutations during warming” scenario is not shown here because its results are indistinguishable from those from the main run of the model (d, see Section 3). RCP, representative concentration pathways

value (0.25°C) added to the breeding value when computing phenotype. The “Fewer QTLs” scenario involved 10 QTLs (instead of 100) with roughly threefold higher possible mutational effects; i.e., drawn from  $N(0^\circ\text{C}, 0.0949^\circ\text{C})$  instead of  $N(0^\circ\text{C}, 0.03^\circ\text{C})$ . This adjustment of the mutation effect size was done to preserve the average variance of the breeding value introduced by mutations per zygote per generation:  $2N_q\mu\sigma^2$ , where  $N_q$  is the number of QTLs,  $\mu$  is the per-locus mutation rate, and  $\sigma$  is the standard deviation of mutational effect at each locus (the factor of 2 is for diploidy). The “Narrower fitness function” scenario implied that the fitness of an individual would drop by ~60% (instead of ~40%) when its phenotype mismatched the environment by 1°C. The “Lower mutation rate” scenario used a tenfold lower rate, and the “Lower mutation effect” scenario drew effect sizes from  $N(0^\circ\text{C}, 0.01^\circ\text{C})$ , threefold lower than in the main run. Habitat sizes in the “Larger reefs” scenario were twofold larger. Under the “no mutation during warming” scenario, mutation rate was set to zero at the onset of warming. Finally, under “no selection during warming” scenarios, once the warming began phenotypes of all individuals within each sub-population were randomly shuffled in each generation, which prevented selection from favoring specific genotypes.

## 2.7 | Migration

The movement of individuals among sub-populations of *Acropora* was estimated using our biophysical model of larval dispersal for the Indo-Pacific (Trembl et al., 2012, 2015). This model incorporates hydrodynamic data (1/12° & daily resolution for 1992–2012), coral reef habitat maps (Schlitzer, 2018), and biological parameters for coral larvae. In this model, dispersing larvae were represented by (a) the coral spawning time following two summer full moons; (b) the larval settlement window, from 6 to 60 days (maximum larval duration; Connolly & Baird, 2010); (c) the daily larval mortality (5%; Connolly & Baird, 2010); and (d) larvae being passive and distributed in the top 10 m of the ocean. In this model, larvae are moved throughout the seascape following spawning using an efficient and fourth-order-accurate advective transport scheme (Smolarkiewicz, 1983). A detailed model description and sensitivity analysis is available in Trembl et al. (2012). The results from the dispersal simulations were used to create a long-term average forward transition matrix quantifying the likelihood that larvae spawned at a source reef survive and settle to all potential reef sites (including the natal source patch); this is the migration matrix used here (Figure 2a; Figure S2). Under the “no migration



**FIGURE 2** Spatial structure of the model and variation in coral cover (proportion of occupied carrying capacity) across reefs during warming. Sizes of points on all panels indicate habitat size at each location. (a) Pre-warming temperatures and migration patterns. Migration (cyan arcs) is to be read clockwise to infer direction; arc line widths correspond to 0.1%–1%, 1%–10%, and 10%–100% probability of migration. (b) Prewarming coral cover. (c, d) Coral cover after 100 years of warming under the main settings (c) and under the scenario in which migration was set to zero during warming (d). (e, f) Same as (c) and (d) but after 200 years of warming [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

during warming” scenarios, all the offspring were retained within the natal population during the warming period.

## 2.8 | Genetic equilibration

To rapidly achieve genetic equilibrium, our model used the same stepwise procedure as the original model (Matz et al., 2018). Specifically, the first 2,000 years were run with population sizes 25-fold smaller but mutation rate 25-fold higher than target values, followed by 2,000 years of tenfold smaller population sizes and tenfold higher mutation rate. The remaining years were run at the target population sizes and mutation rates; warming began at year 5,500. In this way, the product of population size and mutation rate is constant throughout the simulation, but the genetic equilibrium is approached substantially faster due to the smaller population size at the beginning of the simulation. We have confirmed that the genetic variation stays constant in the last 200 years preceding warming, so the adaptation to warming starts from a state of genetic equilibrium.

## 2.9 | Model runs and calculation of adaptive potential

The analysis focused on the 400 year window centered on the start of warming. All scenarios were run four times with different random seeds; the decadal averages for each run were averaged among runs. The coral cover per site was computed as the number of adults divided by the carrying capacity of the site. Adaptive potential of a reef was calculated using a binomial model, as the odds of the reef's decline below 50% of its prewarming coral cover. We used a binomial model because the response of individual reefs to warming was largely binary, i.e., either strong decline or almost no decline (see Section 3).

## 2.10 | Matching with actual reef survey data

Bruno and Selig (2007) have compiled coral surveys across the Indo-Pacific from the 1970s to early 2000s, to quantify region-wide coral cover changes. To match the locations of surveyed and simulated reefs, we clustered all reefs into groups within a distance corresponding to one degree of latitude (111 km) from each other, and selected clusters that (a) contained both simulated and real reefs, (b) contained real reefs surveyed >15 years apart, and (c) contained a reef survey completed after 2000. All the real reef data within each cluster were then used to compute a regression coefficient of coral cover against year. Essentially, this analysis treats all surveys of reefs within a local cluster as replicate surveys of the same reef (very few individual reefs were actually surveyed repeatedly over a long period). These “real-change” regression coefficients were correlated to factors predicting adaptive potential in our model, or, in another

analysis, to the modeled coral cover changes. Predictor values or responses were averaged across reefs within the same cluster.

## 3 | RESULTS

### 3.1 | General trends across parameter settings

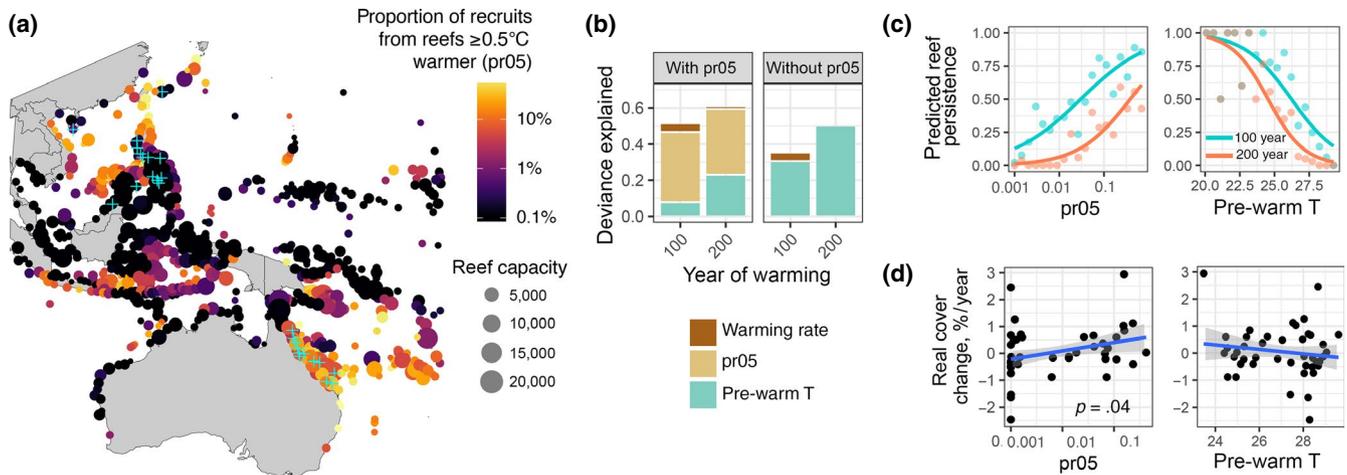
Prior to warming, adult coral cover at each site stabilized at similar levels across most models (Figure 1), indicating that populations were similarly successful at local adaptation irrespective of most parameter settings. The cover was slightly lower under a narrower fitness curve, which is explained by lower mean population fitness under this setting (even if perfectly adapted, due to environmental noise), and under lower juvenile mortality, which leads to a smaller proportion of adults in each population.

Coral cover declines during warming were broadly similar across parameter settings, with the notable exceptions of slower warming (RCP 4.5; Figure 1a; Figure S1a) under which the majority of reefs remained unaffected, and runs where selection was switched off during warming, which led to rapid reef collapse (Figure 1k,l; Video S1). Under all other scenarios, which assumed a “business-as-usual” warming rate (RCP 8.5; Figure S1b), reef responses were largely binary: reefs either collapsed or maintained coral cover close to pre-warming levels, which resulted in bimodal density curves of coral cover across reefs (e.g., Figure 1b–i). Lower juvenile mortality (Figure 1b) resulted in a substantially higher proportion of reefs maintaining coral cover compared to all other runs for RCP 8.5. In all other cases, the majority of reefs collapsed by the tenth decade of warming, and yet some reefs maintained their cover until the end of the modeled period (20 decades). Notably, when migration was set to zero during warming (Figure 1j), reefs declined only slightly more in the first 10 decades, but then collapsed faster and more completely than in any other scenario except the scenarios without selection (see also Figure 2c–f; Video S1).

Warming also resulted in an increase in magnitude of coral cover response to thermal fluctuations, i.e., more severe coral mortality episodes in response to heat waves (Figure S3; this can also be seen in Videos S1 and S2 as intensifying pulses of darker color). This result supports the observation from our previous model (Matz et al., 2018).

### 3.2 | Spatial variation in reef responses

The spatial pattern of reef responses to warming was qualitatively similar across all tested parameter settings, varying mostly in intensity (Figure 2c,e; Video S2), except when selection was switched off during warming, which led to rapid reef collapse region-wide (Video S1). Encouragingly, across different parameter settings we have observed that reefs located in the Northwest and Southeast parts of the modeled region remained largely unaffected (Figure 2c,e). When migration was switched off during warming, these reefs still



**FIGURE 3** Predictors of reef's adaptive potential in the first 100 years of warming ("main settings" scenario). (a) Map of pr05, the proportion of recruits immigrating from reefs that are at least 0.5°C warmer. Note the similarity of this pattern to the pattern of coral cover after 100 years of warming (Figure 2c). The locations for which actual long-term coral cover data were available (Bruno & Selig, 2007) are marked by cyan crosses. (b) Proportion of deviance explained by different predictors (binomial GLM: log-odds of reef maintaining >50% of original cover). Analysis on the right panel uses the same data as the left panel but does not include pr05 as a predictor. All predictors are significant at  $p < .05$  in at least one of the tests. (c) Relationship between major predictors of adaptive potential (pr05 and prewarming temperature) and reef resilience after 100 and 200 years of warming (proportion of reefs maintaining their cover). Values shown are computed for 20 bins of predictor value (34 reefs per bin). Lines are binomial GLM fits. (d) Correlation between predictors of adaptive potential and actual coral cover change over 15 years across the turn of the century, based on data from Bruno and Selig (2007). Lines are linear regressions, gray areas are 95% confidence intervals of the linear fits. Only the correlation with pr05 is statistically significant [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

exhibited resilience during the first 100 years (Figure 2d) but collapsed by year 200 (Figure 2f). Notably, switching off new mutations during warming had no effect whatsoever on the spatial pattern of reef resilience. Switching off selection as well as migration resulted in complete collapse of all reefs by year 100 (Figure 1k).

### 3.3 | Predictors of adaptive potential

Three factors emerged as significant predictors of adaptive potential (odds of coral cover staying above 50% of its prewarming state): reef-specific warming rate, prewarming temperature, and a metric we call pr05: the proportion of recruits that come from locations that are at least 0.5°C warmer (Figure 3a). The pr05 metric reflects the chance that a reef will receive heat-tolerance alleles through immigration, and accounts for the most deviance: 39% after 100 years and 36% after 200 years of warming (Figure 3b). The next-best predictor—prewarming temperature—accounts for 8% of deviance in addition to pr05 after 100 years of warming, or 31% of deviance on its own (it is correlated with pr05, Figure S4a). After 200 years of warming, prewarming temperature accounts for 23% of deviance in addition to pr05, or for 50% of deviance on its own.

The influx of immigrants from warmer reefs is expected to interfere with local adaptation during the prewarming period (Ronce & Kirkpatrick, 2001). However, we only see a negative relationship between pr05 and prewarming coral cover at very high levels of pr05, when warmer-location immigrants comprised more than 10% of the total recruit pool (Figure S4b).

Finally, we have found pr05 to significantly correlate with the actual coral cover changes observed throughout the region (Bruno & Selig, 2007; Figure 3d). At the same time, there was no significant correlation between real and modeled cover changes either at 50 or 100 years of simulated warming (Figure S5). This is not surprising, since our model is designed to explore the variation in adaptive potential among reefs while deliberately ignoring all other factors relevant for coral survival, as we discuss below. Nevertheless, it appears that our model did help to identify pr05 as an important environmental predictor of coral resilience.

## 4 | DISCUSSION

The world is already about 50 years into the warming scenario that we model (IPCC, 2014). Will corals be able to track global warming with evolutionary adaptation? Yes and no. As long as we are willing to assume that coral populations are genetically adapted to their local thermal regimes (Bay & Palumbi, 2014; Dixon et al., 2015; Palumbi et al., 2014), our results indicate that evolution, powered by migration and selection for optimal genotypes, will play a major role in reef survival (Figure 1; Video S1). Encouragingly, some reefs are predicted to be able to efficiently adapt for a very long time, most notably the reefs at the latitudinal range edge: the Mid- and Southern Great Barrier Reef, New Caledonia, Vietnam, Taiwan, and Japan (Figure 2c,d). These reefs lasted throughout the whole modeled period (200 years) even under rapid warming (RCP 8.5 scenario; Figure 2d). The same reefs lost their long-term resilience in the absence of migration (Figure 2f) and even more so in the absence of

selection (Figure 1k,l; Video S1). Conversely, their resilience was maintained in the absence of new mutations during the warming period. Taken together, these observations indicate that long-term resilience of these reefs relies on natural selection favoring heat-tolerance alleles that existed in the metapopulation prior to warming, which are exchanged between populations via migration. Indeed, the connectivity pattern (Figure 2a) suggests that resilient reefs are major downstream accumulation sites for genetic variation, while their elevated  $pr05$  (Figure 3a) confirms that they receive a large proportion of immigrants from warmer reefs. Moreover, the fact that in the no-migration model reef resilience was not strongly affected in the first 100 years (Figures 1j and 2e) indicates that during the initial warming period the resilience is supported predominantly by selection on genetic variants that have already arrived into populations by the start of warming, and only later do reefs become dependent on introgression of additional variants. Notably, these results differ from our previous model (Matz et al., 2018): there, prohibiting migration immediately led to rapid decline in downstream populations, while new mutations were the main fuel for long-term adaptation. This is most likely due to the fact that the new model is much larger in scale and is also based on the non-Wright-Fisher algorithm with overlapping generations. Both of these factors would lead to higher standing genetic variation, which could support an initial adaptive response independent of migration as well as longer-term adaptation independent of new mutations.

At the same time, the majority of reefs, especially those that are already warm and do not receive immigrants from yet warmer places, are highly prone to declines due to warming (Figure 2c,e; Video S2). Under the “business-as-usual” RCP 8.5 scenario (Figure S1b) the majority of reefs near the equator and in Western Australia go extinct within the first 100 years (Figure 2c). Slower warming under the RCP 4.5 scenario (Figure S1a) greatly offsets these declines (Figure 1a). Reef declines are also less prominent under the lower juvenile mortality setting (Figure 2a; Video S2), possibly for a similar reason to the high reef persistence under RCP 4.5: lower juvenile mortality resulted in younger average age of populations, which implies faster population turnover relative to the warming rate and might therefore be analogous to slower warming.

It is important to emphasize that our model is an abstraction designed for one purpose only: to reveal variation in adaptive potential among reefs and identify its environmental predictors. It is not a model of reality, because it assumes that adaptive potential is the only factor relevant for reef persistence. It does not attempt to account for a variety of other factors that influence reef health, such as change in migration rates with warming (Munday et al., 2009), competition with algae (McCook, Jompa, & Diaz-Pulido, 2001), disease (Bruno et al., 2007), ocean acidification (Hoegh-Guldberg et al., 2007), or transition of some coral predator to devastating boom-and-bust population cycles, as happened with the crown-of-thorns starfish (Kayal et al., 2012). Corals must adapt to all these challenges at the same time, and although there is an indication that such multi-dimensional adaptation might be possible in the short-term (Wright et al., 2019), the long-term outcome remains uncertain.

We also do not account for the increase in storm severity with climate change (Emanuel, 2005), which is already a major destructive force for many Indo-Pacific reefs (De'ath, Fabricius, Sweatman, & Puotinen, 2012). It is also important to note that for corals that mature and grow slower than the acroporids modeled here adaptation would be progressively unlikely, since slower population turnover rate would impair adaptation just as much as higher rate of warming. All this means that even the most genetically resilient reefs (according to our model) are still vulnerable to climate change. Although in theory they might be able to evolve rapidly enough, they remain prone to all the other sources of mortality to which global warming contributes. Essentially, then, our model provides a best-case scenario that can be used as a baseline to test for the role of other factors in reef decline.

Should we consider helping corals evolve? For marine creatures like corals, which have huge census sizes, produce on the order of a million offspring each year, and undergo natural hybridization between species that spawn together, natural evolution will likely be more efficient than any lab-based effort because of vast standing genetic variation combined with the opportunity for very strong selection in nature. Still, our results suggest one intervention that might help: facilitating genetic influx from warmer locations, to raise the local  $pr05$ . This type of intervention is called “assisted migration” (Haller, Mazzucco, & Dieckmann, 2013) or “assisted gene flow” (Aitken & Whitlock, 2013), and would make particular sense on reefs that do not receive any natural immigrants from warmer locations. Using cryopreserved sperm from warmer reefs to fertilize local eggs and outplanting the juveniles would introduce otherwise inaccessible adaptive alleles while capitalizing on local maternal effects (Baums et al., 2019). While earlier works have proposed similar interventions (Dixon et al., 2015; Kleypas et al., 2016; Matz et al., 2018), our current results suggest the scale on which it has to be done. While even a small increase in  $pr05$  already lowers the risk of reef decline (Figure 3c), the most tangible effects are observed when  $pr05$  is on the order of several percent or higher. This means that one would have to outplant warm-adapted recruits in numbers approaching 1%–5% of total natural recruitment, which may or may not be realistic depending on the coral species and the ocean basin. Our model can be used to estimate the efficiency of such efforts on specific reefs.

All that said, by far the most helpful thing that we could do for coral reefs would be to curb greenhouse gas emissions to push the global warming trajectory closer to the RCP 4.5 scenario. According to the model presented here, only slowing down the warming rate would ensure that the majority of coral reefs would retain enough adaptive potential to escape extinction.

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#### DATA AVAILABILITY STATEMENT

The model code, input files, model results, and scripts to recreate all analyses and figures are available at [https://github.com/z0on/CoralTriangle\\_SLiM\\_model](https://github.com/z0on/CoralTriangle_SLiM_model). The HYCOM+NCODA Ocean Reanalysis results are available at <http://hycom.org>.

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#### REFERENCES

- Aitken, S. N., & Whitlock, M. C. (2013). Assisted gene flow to facilitate local adaptation to climate change. *Annual Review of Ecology, Evolution, and Systematics*, 44(1), 367–388. <https://doi.org/10.1146/annurev-ecolsys-110512-135747>
- Ayre, D. J., & Hughes, T. P. (2004). Climate change, genotypic diversity and gene flow in reef-building corals. *Ecology Letters*, 7(4), 273–278. <https://doi.org/10.1111/j.1461-0248.2004.00585.x>
- Baria, M. V. B., dela Cruz, D. W., Villanueva, R. D., & Guest, J. R. (2012). Spawning of three-year-old *Acropora millepora* corals reared from larvae in northwestern Philippines. *Bulletin of Marine Science*, 88(1), 61–62. <https://doi.org/10.5343/bms.2011.1075>
- Barrett, R. D. H., & Schluter, D. (2008). Adaptation from standing genetic variation. *Trends in Ecology & Evolution*, 23(1), 38–44. <https://doi.org/10.1016/j.tree.2007.09.008>
- Barton, N. H., & Turelli, M. (1989). Evolutionary quantitative genetics: How little do we know? *Annual Review of Genetics*, 23(1), 337–370. <https://doi.org/10.1146/annurev.ge.23.120189.002005>
- Baums, I. B., Baker, A. C., Davies, S. W., Grottoli, A. G., Kenkel, C. D., Kitchen, S. A., ... Shantz, A. A. (2019). Considerations for maximizing the adaptive potential of restored coral populations in the western Atlantic. *Ecological Applications*, 29, e01978. <https://doi.org/10.1002/eap.1978>
- Baums, I. B., Miller, M. W., & Hellberg, M. E. (2005). Regionally isolated populations of an imperiled Caribbean coral, *Acropora palmata*. *Molecular Ecology*, 14(5), 1377–1390. <https://doi.org/10.1111/j.1365-294X.2005.02489.x>
- Bay, R. A., & Palumbi, S. R. (2014). Multilocus adaptation associated with heat resistance in reef-building corals. *Current Biology*, 24(24), 2952–2956. <https://doi.org/10.1016/j.cub.2014.10.044>
- Bay, R. A., Rose, N. H., Logan, C. A., & Palumbi, S. R. (2017). Genomic models predict successful coral adaptation if future ocean warming rates are reduced. *Science Advances*, 3(11), e1701413. <https://doi.org/10.1126/sciadv.1701413>
- Bruno, J. F., & Selig, E. R. (2007). Regional decline of coral cover in the Indo-Pacific: Timing, extent, and subregional comparisons. *PLoS ONE*, 2(8), e711. <https://doi.org/10.1371/journal.pone.0000711>
- Bruno, J. F., Selig, E. R., Casey, K. S., Page, C. A., Willis, B. L., Harvell, C. D., ... Melendy, A. M. (2007). Thermal stress and coral cover as drivers of coral disease outbreaks. *PLoS Biology*, 5(6), 1220–1227. <https://doi.org/10.1371/journal.pbio.0050124>
- Campbell-Staton, S. C., Cheviron, Z. A., Rochette, N., Catchen, J., Losos, J. B., & Edwards, S. V. (2017). Winter storms drive rapid phenotypic, regulatory, and genomic shifts in the green anole lizard. *Science*, 357(6350), 495–498. <https://doi.org/10.1126/science.aam5512>
- Connolly, S. R., & Baird, A. H. (2010). Estimating dispersal potential for marine larvae: Dynamic models applied to scleractinian corals. *Ecology*, 91(12), 3572–3583. <https://doi.org/10.1890/10-0143.1>
- De'ath, G., Fabricius, K. E., Sweatman, H., & Puotinen, M. (2012). The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences of the United States of America*, 109(44), 17995–17999. <https://doi.org/10.1073/pnas.1208909109>
- Dixon, G. B., Davies, S. W., Aglyamova, G. V., Meyer, E., Bay, L. K., & Matz, M. V. (2015). Genomic determinants of coral heat tolerance across latitudes. *Science*, 348(6242), 1460–1462. <https://doi.org/10.1126/science.1261224>
- Emanuel, K. (2005). Increasing destructiveness of tropical cyclones over the past 30 years. *Nature*, 436(7051), 686–688. <https://doi.org/10.1038/nature03906>
- Garant, D., Forde, S. E., & Hendry, A. P. (2007). The multifarious effects of dispersal and gene flow on contemporary adaptation. *Functional Ecology*, 21(3), 434–443. <https://doi.org/10.1111/j.1365-2435.2006.01228.x>
- Haller, B. C., Mazzucco, R., & Dieckmann, U. (2013). Evolutionary branching in complex landscapes. *The American Naturalist*, 182(4), E127–E141. <https://doi.org/10.1086/671907>
- Haller, B. C., & Messer, P. W. (2019). SLiM 3: Forward genetic simulations beyond the Wright–Fisher model. *Molecular Biology and Evolution*, 36(3), 632–637. <https://doi.org/10.1093/molbev/msy228>
- Hermisson, J., & Pennings, P. S. (2005). Soft sweeps: Molecular population genetics of adaptation from standing genetic variation. *Genetics*, 169(4), 2335–2352. <https://doi.org/10.1534/genetics.104.036947>
- Hoegh-Guldberg, O. (1999). Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research*, 50(8), 839–866. <https://doi.org/10.1071/MF99078>
- Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., ... Hatzitolos, M. E. (2007). Coral reefs under rapid climate change and ocean acidification. *Science*, 318(5857), 1737–1742. <https://doi.org/10.1126/science.1152509>
- Hoegh-Guldberg, O., Poloczanska, E. S., Skirving, W., & Dove, S. (2017). Coral reef ecosystems under climate change and ocean acidification. *Frontiers in Marine Science*, 4, 158. <https://doi.org/10.3389/fmars.2017.00158>
- Hurrell, J. W., Holland, M. M., Gent, P. R., Ghan, S., Kay, J. E., Kushner, P. J., ... Marshall, S. (2013). The community earth system model: A framework for collaborative research. *Bulletin of the American Meteorological Society*, 94(9), 1339–1360. <https://doi.org/10.1175/BAMS-D-12-00121.1>
- IPCC. (2014). Climate change 2014: Synthesis report. In Core Writing Team, R. K. Pachauri, & L. A. Meyer (Eds.), *Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change*. Geneva, Switzerland: IPCC. 151 pp.
- Kayal, M., Vercelloni, J., de Loma, T. L., Bosserelle, P., Chancerelle, Y., Geoffroy, S., ... Adjeroud, M. (2012). Predator crown-of-thorns starfish (*Acanthaster planci*) outbreak, mass mortality of corals, and cascading effects on reef fish and benthic communities. *PLoS ONE*, 7(10), e47363. <https://doi.org/10.1371/journal.pone.0047363>
- Kleypas, J. A., Thompson, D. M., Castruccio, F. S., Curchitser, E. N., Pinsky, M., & Watson, J. R. (2016). Larval connectivity across temperature gradients and its potential effect on heat tolerance in coral populations. *Global Change Biology*, 22(11), 3539–3549. <https://doi.org/10.1111/gcb.13347>
- Lescak, E. A., Bassham, S. L., Catchen, J., Gelmond, O., Sherbick, M. L., von Hippel, F. A., & Cresko, W. A. (2015). Evolution of stickleback in 50 years on earthquake-uplifted islands. *Proceedings of the National Academy of Sciences of the United States of America*, 112(52), E7204–E7212. <https://doi.org/10.1073/pnas.1512020112>
- Matz, M. V., Trembl, E. A., Aglyamova, G. V., & Bay, L. K. (2018). Potential and limits for rapid genetic adaptation to warming in a Great Barrier

- Reef coral. *PLOS Genetics*, 14(4), e1007220. <https://doi.org/10.1371/journal.pgen.1007220>
- McCook, L. J., Jompa, J., & Diaz-Pulido, G. (2001). Competition between corals and algae on coral reefs: A review of evidence and mechanisms. *Coral Reefs*, 19(4), 400–417. <https://doi.org/10.1007/s003380000129>
- Munday, P. L., Leis, J. M., Lough, J. M., Paris, C. B., Kingsford, M. J., Berumen, M. L., & Lambrechts, J. (2009). Climate change and coral reef connectivity. *Coral Reefs*, 28(2), 379–395. <https://doi.org/10.1007/s00338-008-0461-9>
- Orr, H. A. (2005). The genetic theory of adaptation: A brief history. *Nature Reviews Genetics*, 6(2), 119–127. <https://doi.org/10.1038/nrg1523>
- Palumbi, S. R., Barshis, D. J., Traylor-Knowles, N., & Bay, R. A. (2014). Mechanisms of reef coral resistance to future climate change. *Science*, 344(6186), 895–898. <https://doi.org/10.1126/science.1251336>
- Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics*, 37, 637–669. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>
- Quinn, T. M., Taylor, F. W., & Crowley, T. J. (1993). A 173 year stable isotope record from a tropical south pacific coral. *Quaternary Science Reviews*, 12(6), 407–418. [https://doi.org/10.1016/S0277-3791\(05\)80005-8](https://doi.org/10.1016/S0277-3791(05)80005-8)
- Romero-Torres, M., Trembl, E. A., Acosta, A., & Paz-García, D. A. (2018). The Eastern Tropical Pacific coral population connectivity and the role of the Eastern Pacific Barrier. *Scientific Reports*, 8(1), 9354. <https://doi.org/10.1038/s41598-018-27644-2>
- Ronce, O., & Kirkpatrick, M. (2001). When sources become sinks: Migrational meltdown in heterogeneous habitats. *Evolution*, 55(8), 1520–1531. <https://doi.org/10.1111/j.0014-3820.2001.tb00672.x>
- Savolainen, O., Lascoux, M., & Merilä, J. (2013). Ecological genomics of local adaptation. *Nature Reviews Genetics*, 14(11), 807–820. <https://doi.org/10.1038/nrg3522>
- Schlitzer, R. (2018). *Ocean data view*. Retrieved from <http://data.unep-wcmc.org/datasets/1>
- Smolarkiewicz, P. K. (1983). A simple positive definite advection scheme with small implicit diffusion. *Monthly Weather Review*, 111(3), 479–486. [https://doi.org/10.1175/1520-0493\(1983\)111<0479:ASPDA S>2.0.CO;2](https://doi.org/10.1175/1520-0493(1983)111<0479:ASPDA S>2.0.CO;2)
- Torda, G., Donelson, J. M., Aranda, M., Barshis, D. J., Bay, L., Berumen, M. L., ... Munday, P. L. (2017). Rapid adaptive responses to climate change in corals. *Nature Climate Change*, 7(9), 627–636. [10.1038/nclimate3374](https://doi.org/10.1038/nclimate3374)
- Trembl, E. A., Roberts, J. J., Chao, Y., Halpin, P. N., Possingham, H. P., & Riginos, C. (2012). Reproductive output and duration of the pelagic larval stage determine seascape-wide connectivity of marine populations. *Integrative and Comparative Biology*, 52(4), 525–537. <https://doi.org/10.1093/icb/ics101>
- Trembl, E. A., Roberts, J., Halpin, P. N., Possingham, H. P., & Riginos, C. (2015). The emergent geography of biophysical dispersal barriers across the Indo-West Pacific. *Diversity and Distributions*, 21(4), 465–476. <https://doi.org/10.1111/ddi.12307>
- Whiteley, A. R., Fitzpatrick, S. W., Funk, W. C., & Tallmon, D. A. (2015). Genetic rescue to the rescue. *Trends in Ecology & Evolution*, 30(1), 42–49. <https://doi.org/10.1016/j.tree.2014.10.009>
- Wright, R. M., Mera, H., Kenkel, C. D., Nayfa, M., Bay, L. K., & Matz, M. V. (2019). Positive genetic associations among fitness traits support evolvability of a reef-building coral under multiple stressors. *Global Change Biology*, 25(10), 3294–3304. <https://doi.org/10.1111/gcb.14764>

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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