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11 **Title**: Extreme temperature events will drive coral decline in the Coral Triangle

12

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25

26 **Abstract**

27 In light of rapid environmental change, quantifying the contribution of regional- and local-scale drivers of coral  
28 persistence is necessary to characterize fully the resilience of coral reef systems. To assess multiscale responses to  
29 thermal perturbation of corals in the Coral Triangle (CT), we developed a spatially explicit metacommunity model  
30 with coral-algal competition, including seasonal larval dispersal and external spatio-temporal forcing. We tested  
31 coral sensitivity in 2083 reefs across the CT region and surrounding areas under potential future temperature  
32 regimes, with and without interannual climate variability, exploring a range of 0.5 to 2.0°C overall increase in  
33 temperature in the system by 2054. We found that among future projections, reef survival probability and mean  
34 percent coral cover over time were largely determined by the presence or absence of interannual sea surface  
35 temperature (SST) extremes as well as absolute temperature increase. Overall, reefs that experienced SST time  
36 series that were filtered to remove interannual variability had approximately double the chance of survival than  
37 reefs subjected to unfiltered SST. By the end of the forecast period, the inclusion of thermal anomalies was  
38 equivalent to an increase of at least 0.5°C in SST projections without anomalies. Change in percent coral cover  
39 varied widely across the region within temperature scenarios, with some reefs experiencing local extinction while  
40 others remaining relatively unchanged. Sink strength and current thermal stress threshold were found to be  
41 significant drivers of these patterns, highlighting the importance of processes that underlie larval connectivity and  
42 bleaching sensitivity in coral networks.

43

44 **Introduction**

45 The Coral Triangle (CT) region in the Indo-Pacific has long been recognized as the epicenter of coral  
46 diversity with over 500 species of stony coral (Veron et al., 2009). These reefs serve as direct providers of  
47 livelihoods for over 100 million people in coastal communities, yet the CT is also one of the most threatened reef  
48 systems in the world (Burke, Reynter, Spalding, & Perry, 2011). Local stressors such as overfishing, and watershed-  
49 based pollution are widely recognized as factors contributing to loss of coral cover. At the global scale, climate  
50 change is driving an increase in sea surface temperature (SST) and an associated frequency of mass coral bleaching  
51 and mortality events in the region (Donner, Skirving, Little, Oppenheimer, & Hoegh-Gulberg, 2005; Kleypas,

52 Castruccio, Curchitser, & McLeod, 2015). Widespread coral mortality has negative cascading effects throughout  
53 the reef ecosystem and the people that rely on them for food and income (Bruno & Bertness, 2001). Some  
54 consequences of coral decline include the loss of structural complexity that living coral maintains, decreases in the  
55 diversity and abundance of fish species (Graham et al., 2006), and reduced reef ecosystem services such as coastal  
56 protection from storms (Beck et al., 2018).

57 Like many areas in the world, increasing sea surface temperatures and bleaching frequency have been  
58 documented in the Coral Triangle (Bruno & Selig, 2007; McLeod et al., 2010). Across the region, a SST warming of  
59 roughly 0.1-0.2°C per year has been reported (Peñaflor, Skirving, Strong, Heron, & David, 2009). However, the  
60 area's complicated bathymetry and oceanography maintain spatially diverse micro-climates in terms of  
61 temperature and turbidity (Kleypas, Castruccio, Curchitser, & McLeod, 2015), and these differences could  
62 ostensibly lead to a wide range of reef-scale biological responses to climate-related stressors, namely warming  
63 waters that trigger coral bleaching events. Indeed, coral cover in the Indo-Pacific region is in active decline.  
64 Between 1997 and 2003, an alarming 3,000+ km<sup>2</sup> of coral cover per year is estimated to have been lost across the  
65 broader Indo-Pacific region (Bruno & Selig, 2007). More recent assessments report continued degradation in the  
66 Indo-Pacific and surrounding areas: the Great Barrier Reef (GBR) lost approximately 50% of hard coral cover  
67 between 1985 and 2012 (De'ath, Fabricius, Sweatman, & Puotinen, 2012) and experienced a 30% decline from  
68 March to November during the 2016 bleaching event (Hughes, Kerry, et al., 2018), while coral cover in the  
69 Philippines declined by about one third during the last decade (Licuanan, Robles, & Reyes, 2019). Additionally,  
70 climate anomalies such as those experienced during El Niño-Southern Oscillation events are known to trigger  
71 regional-scale mass bleaching events in the CT (Kleypas, Castruccio, Curchitser, & McLeod, 2015). While climate  
72 variability is a crucial factor in determining the susceptibility of corals to thermal stress, particularly in subsequent  
73 mass bleaching events (Boylan & Kleypas, 2008; Donner, 2011; Guest et al., 2012; McClanahan & Maina, 2003;  
74 Thompson & van Woesik, 2009), we have yet to fully understand the relative contribution of climate anomalies  
75 and rising mean temperatures to the persistence of coral metapopulations.

76 It is critical that the spatio-temporal response of CT reefs to thermal stress be characterized, with  
77 particular consideration towards the heterogeneous yet interconnected nature of these reefs. The recovery of  
78 coral and fish populations is an active and promising area of study, with several researchers suggesting that  
79 connectivity through larval dispersal could facilitate the population regrowth of reef organisms in areas where they  
80 have become relatively depleted (Cruz & Harrison, 2017; Hock et al., 2017). Recent marine larval dispersal studies  
81 that couple ocean circulation models and Lagrangian particle tracking simulations have elucidated patterns of  
82 connectivity over a range of spatial scales for several species (including Beger et al., 2015; Cowen, Paris, &  
83 Srinivasan, 2006; Cowen, Lwiza, Sponaugle, Paris, & Olson, 2000; Thompson et al., 2018; Villarino et al., 2018;  
84 Watson et al., 2011) as well as physical barriers that prevent larval exchange across subpopulations (Thompson et

85 al., 2018; Wood et al., 2016); these results support mechanisms for empirically observed patterns in species  
86 distributions and population structure (Berkley, Kendall, Mitarai, & Siegel, 2010; Galindo, Olson, & Palumbi, 2006;  
87 Galindo et al., 2010; Kool, Paris, Andréfouët, & Cowen, 2010; Kool, Paris, Barber, & Cowen, 2011). However, few  
88 studies have linked these connectivity patterns to broader community dynamics such as the competition for space  
89 between corals and macroalgae (but see Melbourne-Thomas et al. 2011; Melbourne-Thomas et al. 2011; Watson  
90 et al. 2011).

91 The competitive outcomes within the reef benthos have broad ecological implications. In particular, the  
92 interactions among coral, macroalgae, and herbivores on reefs can theoretically determine the potential for  
93 recovery from a coral-depauperate to a coral-dominated state (Mumby, Hastings, & Edwards, 2007). Furthermore,  
94 at least some reefs are thought to exhibit alternative stable states (Baskett, Fabina, & Gross, 2014; Blackwood &  
95 Hastings, 2011; Fung, Seymour, & Johnson, 2011; Mumby et al., 2007) meaning that trajectories can evolve  
96 towards either coral- or macroalgal-dominance depending on initial conditions. Larval recruitment, even when  
97 occurring seasonally, can have a significant impact on such dynamics (McManus, Watson, Vasconcelos, & Levin,  
98 2019). In light of these potential interactions, it is necessary to simultaneously consider multiple processes, namely  
99 within-patch competition and regional-scale larval dispersal, when assessing the potential impact of climate  
100 change on a reef system.

101 To explore the possible nonlinear and multiscale response of coral reefs in the Coral Triangle and its  
102 surrounding areas to climate change, we developed a metacommunity model based on an idealized system of  
103 reefs in a spatially realistic connectivity network. The metacommunity model tracks changes in coral and  
104 macroalgae populations on reef patches that result from competition for space between coral and macroalgae, as  
105 well as coral recruitment via larval exchange among reef patches within the connectivity network. The seasonal  
106 exchange of coral larvae among patches was modeled with a semi-empirical connectivity dataset generated from  
107 an ocean circulation model of the CT based on observed spawning patterns of a model coral found throughout the  
108 region (*Acropora millepora*). The effects of thermal stress on coral populations were simulated by directly linking  
109 coral mortality to heat stress under four different temperature increase scenarios: 0.5°C, 1.0°C, 1.5°C and 2.0°C  
110 over a period of 47 years. Finally, the role of interannual temperature variability on coral persistence was  
111 determined by comparing results among simulations that incorporate SST time series without interannual SST  
112 variance ('filtered' scenarios) and those with baseline, unfiltered SST ('unfiltered' scenarios).

## 113 **Materials and methods**

### 114 *CT-ROMS*

115 An implementation of the Regional Ocean Modeling System for the Coral Triangle, CT-ROMS, was used to  
116 simulate ocean circulation and SST for a 47-year hindcast from 1960-2007 (Castruccio, Curchitser, & Kleypas,

117 2013). CT-ROMS has a 5-km horizontal grid resolution with 50 vertical terrain-following levels. The full CT-ROMS  
 118 hindcast was for 50 years, with the first 3 years considered as spinup for the model to reach a dynamical balance.  
 119 The model domain spans 95°E-170°E and 25°S-25°N and is set to maximize coverage of reefs within the region  
 120 (Figure 1). Boundary conditions for the hindcast are based on the Simple Ocean Data Assimilation (Carton & Giese,  
 121 2008) and Modern Era-Retrospective Analysis for Research Applications (MERRA) analysis (Rienecker et al., 2011).  
 122 Tides in CT-ROMS are explicitly solved, and comparisons between observed and model-generated temperature  
 123 and ocean circulation patterns show high agreement (Castruccio et al., 2013). When evaluated against the  
 124 satellite-derived Coral Reef Temperature Anomaly Database (Selig, Casey, & Bruno, 2010), CT-ROMS SST outputs  
 125 accurately captured both means and variability. The root-mean-square (RMS) errors between observed and model  
 126 SST values were generally less than 1°C, with a mean RMS error for the entire domain of 0.7°C (Castruccio et al.,  
 127 2013). For the present study, we incorporated both SST and ocean current velocity fields from the CT-ROMS 1960-  
 128 2007 hindcast into a novel coral reef metacommunity model to simulate the ecological implications of different  
 129 temperature increase scenarios across the Coral Triangle.

### 130 *Metacommunity model*

131 We developed a discrete-time and spatially explicit form of a well-studied coral-algal competition model  
 132 (Elmhirst, Connolly, & Hughes, 2009; Fung, Seymour, & Johnson, 2011; Mumby, Hastings, & Edwards, 2007) that  
 133 incorporates a pulsed, annual week-long coral reproductive event (McManus, Watson, Vasconcelos & Levin, 2019)  
 134 during April of every year. To calculate the rate at which coral area is added during the recruitment period at site  $i$   
 135 during year  $y$  ( $l_i^y$ ), we have

$$136 \quad l_i^y = \frac{\delta}{A_i} \sum_{t=120j}^{127} \sum_{j=1}^J f A_j C_j(t) \mathbf{D}_{ij}^y \quad (1)$$

137 where  $t$  is time in days,  $J$  is the total number of reefs ( $J = 2083$ ),  $\delta$  is the size per individual of a coral recruit and  $A_i$   
 138 is the total amount of reef area (i.e. colonizable hard bottom) area at site  $i$ . The number of coral larvae produced  
 139 at each site  $j$  is  $f A_j C_j$ , where  $f$  is the effective fecundity or the number of viable larvae produced per unit area of  
 140 coral and  $C_j$  is the fractional coral cover at  $j$  (See Table S1 for a summary of parameter values and definitions).  
 141 Multiplying this term by  $\mathbf{D}_{ij}^y$  from the potential connectivity matrix (described below) gives the number of larvae  
 142 that reach site  $i$  from site  $j$  during year  $y$ . This quantity is summed across all sources for each destination or sink  
 143 site (including self-recruitment), which is further summed across the seven reproductive days. On a daily time-  
 144 scale, larval recruitment is “on” during the first week of April and “off” at all other times of the year to  
 145 approximate the spring spawning period for *A. millepora* (Baird, Guest, & Willis, 2009). If we let  $\text{mod}(a,b)$  be the  
 146 remainder of the division of  $a$  by  $b$ , larval recruitment during the first week of April can be written as  $l_i(t) = l_i^{(t)}$  if  
 147  $120 \leq \text{mod}(t,365) \leq 127$  and  $l_i(t) = 0$  during the rest of the year. This recruitment is scaled by the amount of

148 coral cover at the source site and the free space available in the destination site. Note that we do not implement  
 149 an explicit relationship between coral adult abundance and larval supply at any particular patch. Instead, we set an  
 150 effective fecundity wherein larvae are either retained in the same reef, exported to other sites or lost from the  
 151 network based on potential connectivity. In our simulations, the same set of connectivity matrices are used for  
 152 both the hindcast and the forecast, ignoring any changes in ocean circulation patterns. This is a reasonable  
 153 assumption, given that differences between hindcast and future ocean circulation projections and resulting  
 154 connectivity patterns are relatively small (Thompson et al., 2018).

155 In addition to natural coral death  $\mu_0$  (i.e., mortality that is unrelated to bleaching), additional coral  
 156 mortality due to bleaching,  $\mu_b$ , was incorporated as a function of  $DHW$  and a factor  $\eta$  that scales  $DHW$  to  
 157 bleaching stress. Since the relationship between  $DHW$  and coral mortality has yet to be fully characterized (but  
 158 see Welle et al., 2017), a linear relationship was assumed for coral death due to bleaching:

$$159 \quad \mu_b(w) = \eta \text{ DHW}_i(w) \quad (2)$$

160 To capture the effects of rapid algae colonization after a bleaching event (Diaz-Pulido & McCook, 2002;  
 161 Glynn, 1993), a term for constant, low-level external recruitment of algae  $\varphi$  was included sensu Elmhirst et al.  
 162 (2009).

163 The full system with coral  $C_i(t)$  and macroalgal  $M_i(t)$  cover on site  $i$  on day  $t$  is then

$$164 \quad \Delta C_i(t) = rC_i(t)F_i(t) + l_i(t)F_i(t) - (\mu_0 + \mu_b)C_i(t) \quad (3)$$

$$165 \quad \Delta M_i(t) = \gamma M_i(t)F_i(t) + aC_i(t)M_i(t) + \varphi F_i(t) - g(C_i(t))M_i(t) \quad (4)$$

166 Where  $\Delta$  is the change from day  $t$  to day  $t+1$ ,  $r$  is the coral rate of growth,  $\gamma$  is the macroalgal rate of growth, and  
 167  $F_i(t)$ , free space, is equivalent to  $1 - C_i(t) - M_i(t)$ . We used a convex form for macroalgal grazing with respect  
 168 to coral cover (McManus, Watson, Vasconcelos & Levin et al., 2019) such that  $g(C_i(t)) = g_0 + (g_1 - g_0)(C_i(t))^2$ .  
 169 Here,  $r$  is the coral rate of growth,  $\gamma$  is the macroalgal rate of growth,  $g_0$  is the baseline grazing rate when  $C = 0$   
 170 and  $g_1$  is the maximum grazing rate when  $C = 1$ .

171 The goal of this study is to provide a conservative estimate of the relative effects of thermal stress  
 172 magnitude and interannual variability on corals by assessing the potential sensitivity of a reef system to increasing  
 173 temperatures. In order to focus on this stressor, we made several simplifying assumptions regarding the system.  
 174 First, with the exception of total reef area, all sites are homogeneous with regards to the various rates occurring  
 175 within a reef patch such as grazing, coral growth and macroalgal growth. In reality, sites within our study region  
 176 vary greatly in terms of the benthic composition and the multitude of organisms that each reef patch supports.  
 177 Second, our metacommunity model lacks larval dynamics (Connolly & Baird, 2010) such that we assume perfect

178 survival of coral larvae; larval mortality is implicit in the effective fecundity term (Table S1). Third, we do not  
179 consider size-specific mortality of corals that would disproportionately affect smaller recruits compared to larger  
180 adult colonies (Hughes & Jackson, 1980). Finally, while we recognize that phase shifts from coral-macroalgal  
181 dominance are rare in the Indo-Pacific (Roff & Mumby, 2012), we note that although our framework allows algae  
182 to “take over” when coral cover declines from bleaching mortality, there is also capacity for coral recovery if  
183 thermal stress is reduced and/or recruitment is sufficiently high.

#### 184 *Potential connectivity*

185 Potential connectivity matrices (**D**) based on CT-ROMS current velocity fields from 1960-2007 (from  
186 Thompson et al., 2018) were used in the metacommunity simulations. These larval dispersal probabilities were  
187 calculated based solely on hydrodynamics (Mitarai, Siegel, Watson, Dong, & McWilliams, 2009; Watson et al.,  
188 2010) for the hindcast with TRACMASS (Döös, Kjellsson, & Jönsson, 2013), an offline Lagrangian particle tracking  
189 routine that follows the trajectory of particles from Eulerian velocity fields generated by CT-ROMS. For  
190 computational simplicity, grid cells were binned into groups of 8 x 8, producing a total of 2947 sites (each cell is 25  
191 km<sup>2</sup> on average; each grouping is ~1600 km<sup>2</sup>). Reef areas for each group were then calculated based on the Global  
192 Distribution of Coral Reefs (IMaRs-USF, 2010). Spring particle release was simulated from reefs across the CT for  
193 the hindcast period with a 10-day pelagic larval duration (i.e. larvae spend 10 days in the water before settlement).  
194 This is well within the empirically-measured survival window for a typical reef-building coral species found in the  
195 Indo-Pacific (Connolly & Baird, 2010). In this study, sites were considered only if they contained nonzero reef area,  
196 reducing the number of locations to 2083. We also completed a second set of simulations using coral connectivity  
197 calculated with a pelagic larval duration of 30 days (see Figures S1-S5). In total, a set of 47 potential connectivity  
198 matrices **D** of size 2083 x 2083 were utilized from Thompson et al. (2018), one for every year of the hindcast  
199 simulation (1960-2007). Characteristics of these potential connectivity matrices are described in detail elsewhere  
200 (Kleypas, Castruccio, Curchitser, & McLeod, 2015; Thompson et al., 2018; Thompson et al., 2014). To isolate the  
201 effects of absolute temperature increase and interannual variability, we used the same potential connectivity  
202 matrices for all hindcast and forecast scenarios.

#### 203 *Sea surface temperatures*

204 To test the effects of interannual SST variability on coral reef dynamics, future warming for the 2007-2054  
205 time period was simulated by generating an **unfiltered** (including interannual climate variability) and **filtered**  
206 (interannual climate variability removed – see below) set of SST time series. These unfiltered and filtered SSTs over  
207 time included increases of 0.5°C, 1.0°C, 1.5°C and 2.0°C over a period of 47 years, for a total of eight forecast  
208 scenarios (see examples in top rows of Figures 2A and 2B). These temperature increases are within the range of  
209 uncertainty produced by CMIP5 temperature forecast models for the region by 2050 (Field et al., 2014; Scott,

210 Alexander, Murray, Swales, & Eischeid, 2016). For example, the CMIP5 multi-model ensemble for the Sulu-Celebes  
211 Sea regions exhibits an average warming of  $\sim 1.0^{\circ}\text{C}$  from 2007 to 2050, while some models predict an increase of  
212 greater than  $3.0^{\circ}\text{C}$  (Figure S6).

213 For this study, we generated weekly SST time series forecasts by imposing a linear increase on the CT-  
214 ROMS detrended 1960-2007 time series ( $SST_0$ ), with and without application of a band-stop filter. These unfiltered  
215 (with interannual variability) and filtered (without interannual variability) SST forecast time series were then  
216 incorporated in the metacommunity simulations. First, hindcast SST data ( $SST_H$ ) were detrended using linear least-  
217 squares fitting. This reduced variability at the lowest decadal frequencies ( $<1$  cycle/7 years) and guaranteed  
218 continuity in the transition from hindcast to forecast temperatures. Second, future SST time series were generated  
219 by imposing a linear increase on the detrended hindcast,  $SST_0$ . The slope of increase for each scenario was  
220 calculated by taking the overall  $\Delta = \{0.5, 1.0, 1.5, 2.0\}^{\circ}\text{C}$  and dividing by the number of weeks, giving the slope  
221 for scenario  $x$  as  $m_x = \Delta_x / w_{\text{tot}}$ . The new temperature for scenario  $x$ , at site  $i$  and time in weeks,  $w$ , was computed  
222 as

$$223 \quad SST_{x,i}(w) = SST_{0,i}(w) + m_{x,i} w \quad (5)$$

224 Finally, to examine the effect of interannual SST variability on coral reef communities, a band-stop filter  
225 that reduced variance between approximately 1 cycle/7 years and 1 cycle/1.25 years was applied to the hindcast  
226 and forecast SSTs to create a set of temperature time series without extreme values (see Figures S8-S10 for power  
227 spectral density plots at representative sites). This method preserved annual, sub-annual and long-term trends ( $>7$   
228 year periodicity) while removing interannual variability that is associated with El Niño and La Niña events (top rows  
229 in Figure 2A and 2B).

### 230 *Degree heating weeks*

231 As a metric of thermal stress, the degree heating weeks (DHWs;  $^{\circ}\text{C}$ -weeks) experienced at each site over  
232 time were calculated for both filtered and unfiltered SST time-series (second rows in Figure 2A and 2B). Following  
233 Kleypas et al. (2015) and Kleypas et al. (2016), the thermal stress threshold (TST) was calculated at each location  
234 by computing the standard deviation ( $\sigma$ ) of the annual mean monthly maxima ( $MMM$ ) from 1960 to 1980. This  
235 climatology was chosen to avoid recent large-scale bleaching years (Kleypas et al., 2015). The TST at site  $i$  is  
236 therefore  $TST_i = MMM_i + 2.5\sigma_i$  (Donner, 2011). The DHW time series at each site and for each scenario was  
237 computed by summing the excess in temperatures that surpass the local TST across a 12-week period. In general,  
238 4-8 DHW, 8-12 DHW, and  $>12$  DHW are linked to mild, moderate, and severe bleaching, respectively (Kleypas,  
239 Castruccio, Curchitser, & McLeod, 2015).

### 240 *Simulations*



241 Parameters that allowed for alternative coral- and algal-dominated states were chosen for all simulations;  
242 all reefs were set with equivalent parameters except for the area (see Supplemental Information for parameter  
243 values and sources). Simulations were run at a daily time step in three parts: the spinup, hindcast, and forecast.  
244 During spinup, reefs were initialized in a high coral cover state, such that  $C_0 = 0.99$  and  $M_0 = 0.01$ . Reefs were  
245 initialized in this state since our aim was to detect the sensitivity of sites to temperature-driven mortality. In other  
246 words, a relatively high baseline facilitated our ability to detect and quantify coral decline. During the spinup, the  
247 system was solved until it reached equilibrium ( $t=18,614$  days) using the first year's potential connectivity  $\mathbf{D}^1$  and  
248 no mortality due to bleaching  $\mu_b = 0$ . The final coral and macroalgal values at the end of the spinup were then  
249 used as the initial conditions for the 1960-2007 hindcast scenarios with unfiltered (interannual variation preserved)  
250 and filtered (interannual variation removed) SSTs, run with time-varying dispersal  $\mathbf{D}$  and coral mortality due to  
251 bleaching based on DHW. Values at the end of the hindcasts served as initial conditions for the four unfiltered and  
252 four filtered SST forecast scenarios. Note that mortality due to coral bleaching is calculated at the daily time step  
253 while DHW was updated on a weekly basis (i.e., mortality due to bleaching was constant every day for one week).  
254 While the modified SST time series were used to compute weekly DHW based on each scenario, unmodified  
255 hindcast potential connectivity matrices were used for the future projections. Using hindcast connectivity  
256 preserved the effects of interannual to decadal scale processes such as El Niño and Pacific Decadal Variability on  
257 larval dispersal, although we note that current models disagree on how these systems may change in the future, if  
258 at all (Wang, Deser, Yu, DiNezio, & Clement, 2017). Furthermore, previous work found no significant changes in  
259 connectivity between hindcast and future simulations (Thompson et al., 2018).

#### 260 *Reef survival analysis and recruitment*

261 To elucidate the drivers of coral decline, a Cox Proportional Hazard (PH) regression (Cox, 1972) was  
262 performed on the probability of reef collapse during the forecast. Here, reef collapse is defined as reaching a  
263 fractional coral cover of 0.1 or less. The Cox PH is a statistical model commonly used in medical studies to  
264 determine the effects of different factors on an outcome such as the survival or death of a patient. This model  
265 produces hazard rates that quantify the relative risk attributed to a particular covariate; here, we are interested in  
266 factors that either increase or decrease the probability of reef collapse. The significance of each of the following  
267 three covariates was tested: TST, sink strength, and unfiltered vs. filtered SST (with and without interannual  
268 variability, respectively). Sink strength was computed by summing the probabilities of larvae arriving to each site  
269 from all sources for each year, excluding self-recruitment; mean sink strength is simply the average of these  
270 probabilities across the 47-year hindcast period (Thompson et al., 2018; Thompson et al., 2014). The 'filtered vs.  
271 unfiltered SST' covariate represents the risk of reef collapse with filtered SST relative to the unfiltered SST  
272 category. Reefs that had reached 0.1 coral cover by the end of the hindcast (described below) were excluded from  
273 the analysis. These excluded sites occurred along the Indochinese peninsula, Sumatra, Sulawesi and the Banda Sea

274 (Figure S6). Since the factors we explore in this model are time-varying, we used a time-stratified approach  
275 wherein separate Cox analyses was performed during set time windows (Dekker, De Mutsert, Van Dijk, Zoccali, &  
276 Jager, 2008). This generated hazard rates of factors during the time periods 2007-2027 (T1), 2027-2041 (T2) and  
277 2041-2054 (T3) denoting early, middle and late forecast periods, respectively.

278 Finally, a set SST simulations with only self-recruitment (i.e. zeros on the non-diagonal entries of **D**) were  
279 performed to assess the effects of connectivity and recruitment on coral persistence. The total yearly recruitment  
280 was calculated by summing across the week-long reproductive period in the metacommunity simulation and then  
281 scaled by the average reef area (160 km<sup>2</sup>) to provide a relative measure. This 'total relative recruitment' metric is  
282 interpreted as the number of average-sized sites that experienced full recruitment (i.e., empty sites that were  
283 completely filled by newly settled coral).

## 284 **Results**

### 285 *Coral and algal cover*

286 Overall, average percent coral cover across the region exhibited faster decline under forecasts with  
287 greater temperature increase and the inclusion of interannual SST variability (unfiltered SST) (Figure 3). Algal cover,  
288 on the other hand, exhibited the opposite pattern. Fractional coral cover at the end of the hindcast period was  
289 relatively high across the CT, with a mean ( $\pm 1$  standard deviation) of 0.79 ( $\pm 0.23$ ) and 0.90 ( $\pm 0.13$ ) for simulations  
290 that included (unfiltered) and excluded SST variance (filtered), respectively. At the end of the hindcast, 3.3% of  
291 reefs in the unfiltered scenario (N=69) and 0.19% of reefs in the filtered scenario (N=4) had a coral cover of 0.1 and  
292 less. The fraction of CT reefs with 0.1 coral cover and less at the end of the forecast increased with the severity of  
293 the SST scenario and ranged from 46.3% (N=962) to 93.4% (N=1945) in the unfiltered simulations and from 15.9%  
294 (N=331) to 71.9% (N=1498) in the filtered simulations (Figure 4). The distribution of collapse times, however, was  
295 very broad for the scenarios with smaller temperature increase: some reefs collapsed only after 10 years while  
296 others survived past 2057. As temperatures increased towards the maximum warming scenario of 2.0°C, half of  
297 the reefs collapsed by 2030, irrespective of the temperature filter. At the end of the temperature increase  
298 simulations, filtered scenarios without interannual SST variability had between 3 and 37 times the number of reefs  
299 in the highest fractional coral cover category (0.9-1.0) relative to the scenarios that preserved climate variation  
300 (Figure 4). By the end of all eight forecast scenarios, unfiltered simulations consistently had a larger proportion of  
301 the reef network in the lowest coral cover category (0-0.1).

302 Fractional algal cover typically increased as coral cover decreased (Figure 3). At the end of the hindcast,  
303 87.8% of reefs in the unfiltered scenario (N=1829) and 97.6% of reefs in the unfiltered scenario (N=2033) had an  
304 algal cover of 0.1 or less (Figure S12-A). In the 2.0°C-increase simulation, reefs with algal cover of 0.8 and above

305 represented 83.0% (N=1728) and 55.6% (N=1158) of the unfiltered and filtered network, respectively (Figure S12-  
306 E).

### 307 *Reef survival*

308 For the following analyses, a reef ‘survives’ if its fractional cover is 0.1 or higher at the end of the forecast  
309 period. Higher values of TST and mean sink strength were associated with a higher probability of reef survival for  
310 the duration of the simulation (Table 1, Figure 5). These effects were weakest in the first time period and strongest  
311 in the last, where a 1-unit increase in TST and scaled mean sink strength resulted in a risk reduction of  
312 approximately 82% and 89%, respectively. Reefs in scenarios with filtered SST had higher survival probability  
313 relative to unfiltered simulations (Table 1). As with TST and sink strength, this protective effect was greatest in the  
314 third time period, where the filtered SST regime resulted in an approximately 50% decrease in the risk of reef  
315 collapse relative to unfiltered SST (Table 1).

316 For the same magnitude of temperature increase, reefs in the filtered SST scenario had consistently  
317 higher survival (i.e. staying above a coral cover of 0.1) throughout the simulation than the unfiltered version;  
318 during earlier time periods, reefs in filtered runs exhibited less decline than reefs in scenarios with less overall  
319 warming, highlighting how interannual SST variability can have stronger effects than long-term increases in  
320 temperature. Across the warming scenarios, reefs that experienced filtered SST had a 54% chance of survival for  
321 the duration of the simulation while reefs subjected to unfiltered SST had a 27% chance of survival (Figure 5A). For  
322 reefs in unfiltered and filtered scenarios, respectively, the probabilities of surviving through the end of the  
323 simulation were 55% and 84% (0.5°C), 30% and 63% (1.0°C), 16% and 41% (1.5°C), and, 7.0% and 28.0% (2.0°C)  
324 (Figure 5B). By the end of 2050, when collapse was underway in all scenarios, including interannual variation in  
325 temperature had an effect comparable to a 0.5°C - to 1.0°C-increase over 47 years in overall trend.

326 **Table 1. Relative hazards<sup>1</sup> for reef collapse covariates among simulated Coral Triangle reefs across three time**  
327 **periods: 2007-2027 (T1), 2027-2041 (T2) and 2041-2054 (T3).**

Time period	TST (°C) (95% CI)	Scaled mean sink strength <sup>2</sup> (95% CI)	Filtered SST relative to unfiltered SST (95% CI)
T1	0.54 (0.51, 0.57)	0.82 (0.78, 0.86)	0.30 (0.28, 0.33)
T2	0.65 (0.62, 0.68)	0.87 (0.84, 0.90)	0.45 (0.42, 0.48)
T3	0.70 (0.66, 0.73)	0.89 (0.86, 0.93)	0.50 (0.46, 0.53)

328

329 <sup>1</sup>For continuous variables, the relative hazard or hazard ratio is the relative risk of reef collapse associated  
330 with a 1-unit increase of the variable. A relative hazard of less than one indicates that the variable exerts a  
331 protective effect while a relative hazard greater than one is associated with greater risk of reef collapse.  
332 For the filtered SST categorical variable (interannual variability removed), this is the risk of reef collapse  
333 relative to the unfiltered SST category (interannual variability preserved).

334 <sup>2</sup>For ease of interpretation, results are shown for scaled values such that a 1-unit increase is equivalent to  
335 1 standard deviation (SD) where sink strength SD = 0.31.

336

### 337 *Recruitment and spatial patterns*

338 In the metacommunity model, recruitment is affected by coral cover at source sites, available free space  
339 at sink sites, and the potential connectivity linking sources and sinks. At a particular site, for example, recruitment  
340 may be low because of reduced coral cover at source sites combined with low potential connectivity values among  
341 the focal site and its source sites. Furthermore, recruitment may also be low if the focal site has no available free  
342 space, either due to high coral cover, algal cover or a combination of both. Assuming sufficient larval supply, coral  
343 mortality from increasing SST should lead to an increase in free space that facilitates coral recruitment across the  
344 network. Total relative recruitment, defined as the number of average-sized reefs that experience coral  
345 settlement, was greater in simulations with normal connectivity compared to those with only self-connections by  
346 up to a factor of 6 (Figure 6). At the beginning of the forecasts with normal recruitment, unfiltered simulations  
347 exhibited higher relative recruitment, while filtered simulations had higher recruitment during later periods.  
348 Normal recruitment generally reached a maximum at a later time period in the filtered scenarios relative to the  
349 unfiltered simulations; this time lag was ~15 years in the 0.5°C scenario and decreased to ~5 years in the 2.0°C  
350 scenario. In the 0.5°C-, 1.0°C- and 1.5°C-increase scenarios, there were two recruitment peaks in the normal and  
351 self-recruitment time series with unfiltered SST due to free space becoming available as corals decline. In the 0.5°C  
352 and 1.0°C scenarios, recruitment is similarly high among filtered and unfiltered simulations during the last 24  
353 years, from ~2030-2054 (Figure 6a). In the 0.5°C and 1.0°C and 1.5°C forecasts with only self-recruitment,  
354 unfiltered simulations started with higher recruitment in the first ~20 years, were equivalent to filtered simulations  
355 during the intermediate period, and increased again towards the end of the time series. In the 2.0°C scenario with  
356 self-recruitment only, recruitment in the unfiltered scenario ultimately dropped below that of the filtered  
357 simulations during the last two years (Figure 6b).

358 Reliance on external recruitment was quantified by taking the difference in coral cover between  
359 simulations with interdependent connectivity and those with only self-recruitment, representing independent  
360 reefs. In the unfiltered scenarios, sites in the Indochinese peninsula, central Philippines, Micronesia, Flores Sea,

361 Celebes Sea and Solomon Islands were the most reliant on external recruitment (i.e. with the largest difference in  
362 coral cover:  $N=521$ ,  $\geq 75^{\text{th}}$  percentile) at the end of both 2027 and 2054 (Figures S14 and S15). Reefs in the northern  
363 Philippines and Sumatra had the highest reliance in 2027 while those in the Halmahera Sea were most reliant on  
364 external recruitment in 2054. In general, these results are consistent across all temperature increase scenarios and  
365 between unfiltered and filtered simulations. A notable difference is that while sites in the GBR and the Solomon  
366 Sea were heavily reliant on external recruitment in 2027 during the 1.0°C, 1.5°C and 2.0°C- filtered scenarios, these  
367 areas were strongly dependent on larval input in both 2027 and 2054 in the 0.5°C-increase scenario. Overall, there  
368 is more temporal separation in external recruitment dependence in the filtered compared to unfiltered  
369 simulations, such that sites that were maximally reliant in 2027 were less likely to remain so by 2054.

370 Reefs in the eastern Philippines, Sumatra, northern Borneo, the Flores Sea, and the Banda Sea were the  
371 most sensitive to thermal stress and experienced major declines during the two mildest forecasts, the 0.5°C and  
372 1.0°C scenarios, with filtered SST (Figure 7). Sites in Micronesia, the central Philippines, the Solomon Islands and  
373 Papua New Guinea were of intermediate sensitivity and collapsed by the end of all other forecasts (but not in the  
374 0.5°C and 1.0°C filtered SST scenarios). Finally, reefs in the GBR, northern Australia, northern Philippines and  
375 eastern Micronesia were least sensitive and at least some sites within these areas maintained coral cover above  
376 0.1 even under the more severe scenarios.

## 377 Discussion

378 This study combines a metacommunity model of coral-algal competition with seasonal larval dispersal and  
379 temperature output from biophysical simulations to elucidate the drivers of coral decline across a spatially realistic  
380 network. We find that coral population persistence under rising temperatures varies greatly across the Coral  
381 Triangle and its surrounding reefs both among and within forecast scenarios. These spatial patterns are driven by a  
382 combination of processes relating to temperature and larval connectivity. Our results suggest that interannual SST  
383 variability during climate change are a major determinant of coral decline and can exacerbate the effects of  
384 increasing temperatures on coral reef metacommunities at the regional scale. The effects of these thermal  
385 anomalies are relatively strong during initial time periods and are effectively equivalent to a 0.5°C - to 1.0°C-  
386 increase in SST time series without anomalies. In contrast, higher values of sink strength and thermal stress  
387 threshold confer a protective effect on reefs at the local scale.

388 Forecast simulations with SST time series that were filtered to remove interannual variability exhibit  
389 higher mean coral cover than their unfiltered counterparts throughout the simulation (Figure 3), highlighting the  
390 detrimental effects of extreme temperatures on coral persistence. These results are in line with those from a  
391 recent study that illustrated how temperature extremes during climate change can drive decline in large marine  
392 ecosystems (Pershing et al., 2019). In addition to differences in coral cover, excluding SST anomalies delays the

393 onset of collapse for coral populations, facilitating higher reef survival (Figure 5). This effect is most pronounced in  
394 scenarios with lower temperature increase, suggesting that extreme phases of ENSO are a major driver of coral  
395 decline when warming is intermediate and a secondary driver under greater overall thermal stress in strong  
396 warming scenarios. In fact, recent work has noted a temporal shift from rare bleaching events before 1980, to an  
397 intermediate period from 1980 to 2000 associated with El Niño-driven bleaching on a global scale, and to bleaching  
398 that regularly occurs outside of El Niño conditions in the last 20 years (Hughes et al., 2018). Depending on the  
399 magnitude of temperature increase, policies that aim to limit overall warming based on averages alone may be  
400 insufficient to prevent regional coral decline if the frequency of El Niño events increases with the global mean  
401 temperature (Hoegh-Guldberg, Jacob, & Taylor, 2018; Wang et al., 2017). Nonetheless, there is still considerable  
402 uncertainty in the response of El Niño frequency and intensity to warming (e.g. An & Choi, 2015; Guilyardi et al.,  
403 2012; Kim & Yu, 2012; Watanabe et al., 2012). Policies based on temperature recoil, i.e., allowing for overshoot of  
404 warming and relying on future carbon capture technology deployment to decrease temperatures (Tavoni &  
405 Socolow, 2013), may have limited impact on coral preservation.

406 Coral populations in the CT exhibited differential susceptibility to thermal stress (Figure 7). Since  
407 parameters across sites were equivalent except for area, these results are driven by heterogeneities in connectivity  
408 and local SSTs. Reefs in the eastern Philippines, the Banda Sea, and Sumatra were most vulnerable in our  
409 simulations, exhibiting collapse during the filtered 0.5°C scenario. Other studies have noted the potential  
410 susceptibility of the Philippines (Peñaflor et al., 2009) and Banda Sea (McLeod et al., 2010) to future bleaching in  
411 terms of historic and present-day warming trend, as well from projected thermal stress increase (Donner et al.,  
412 2005). Conversely, sites in the GBR, northern Australia and the Solomon Sea were relatively resilient, avoiding reef  
413 collapse under most warming conditions. However, we note that recent bleaching events led to high mortality of  
414 GBR corals in 2016 and 2017 (Hughes, Kerry, Connolly, et al., 2019), highlighting the effects that extreme warming  
415 conditions can have on sites that are considered resilient in our modeling results. Interestingly, our patterns of  
416 decline in the GBR (see Figures 7A.3 and 7A.4) are relatively similar to those of a recent modeling study focused on  
417 this area: northern and southern quarters of the GBR were less vulnerable to projected global stressors under RCP  
418 2.6 and 8.5 when compared to the rest of the region (Wolff, Mumby, Devlin, & Anthony, 2018). In general, reefs  
419 that exhibited the fastest decline seem to have low to intermediate values of both TST and sink strength, while  
420 areas that avoided decline had at least some reefs with high values of one or the other (Figure S18).

421 The importance of network contributions to coral recruitment is underscored by our comparison of  
422 simulations with normal connectivity and only self-connections. We see significantly higher recruitment with  
423 normal connectivity, though both normal and self-connectivity exhibit two visible peaks in the less severe warming  
424 scenarios (0.5 °C- and 1.0 °C-increase) (Figure 6). During the first peak in ~2020, there is still enough coral cover to  
425 fill the open space created by the initial decline. During the second peak in ~2045, coral cover has severely

426 declined such that the production of coral recruits is insufficient to fill available space. Unfiltered simulations had  
427 generally higher recruitment at the beginning of the forecasts since mortality (and thus open space) was higher;  
428 this pattern flipped towards the end of the simulation since scenarios without interannual SST variability typically  
429 had higher coral persistence by this point. While recruitment over time is clearly driven by temperature, the spatial  
430 patterns of recruitment over time are driven by both temperature increase and connectivity. In general, sites that  
431 benefit most from external recruitment by the end of the forecast (Figures S14 and S15) are also particularly  
432 susceptible to coral decline (Figure 7). This implies that there is higher vulnerability to regional-scale disturbance at  
433 locations that rely heavily on external recruitment.

434 In this study, we calculated TST (bleaching thresholds) based on a fixed climatological window, from 1960  
435 to 1980, implying that corals have no ability to adaptively respond. Because DHW is computed based on TST, this  
436 assumption likely overestimates the risk of coral decline on our simulated reefs and in that regard, our results can  
437 be considered a worst-case scenario. In fact, a modeling study projecting future coral bleaching (Logan, Dunne,  
438 Eakin, & Donner, 2014) found that calculations based on the previous 60 years (a rolling window that approximates  
439 genetic adaptation) decreased predicted bleaching frequencies by up to 80 percent when compared to calculations  
440 based on a static window. Furthermore, there is evidence that temperature variability is beneficial to coral TST:  
441 past exposure to a greater range of temperatures may lead to increased thermotolerance in some coral species  
442 (Bay & Palumbi, 2017; Carilli, Donner, & Hartmann, 2012; Mayfield, Chan, Putnam, Chen, & Fan, 2012; Putnam,  
443 Barott, Ainsworth, & Gates, 2017; Rivest, Comeau, & Cornwall, 2017) and coral communities as a whole  
444 (Ainsworth et al., 2016; Donner, 2011; Donner & Carilli, 2019; Guest et al., 2012; Hughes, Kerry, Connolly, et al.,  
445 2019; McClanahan & Maina, 2003; Sully et al., 2019; Thompson & van Woessik, 2009).

446 Precisely quantifying thermal tolerance is further complicated by the contribution of both environmental  
447 and genetic components (Bay, Rose, Logan, & Palumbi, 2017; Camp, Schoepf, & Suggett, 2018; Dixon et al., 2015;  
448 Torda et al., 2017); these mechanisms are also likely to be influenced by connectivity patterns (Kleypas et al.,  
449 2016). A natural extension of our study would be to recalculate TST and DHW based on different assumptions  
450 regarding coral adaptive capacity as a proxy for genetic adaptation, community shifts, and larval dispersal to see  
451 how coral decline in the CT would be subsequently altered relative to our current results. We believe that the main  
452 effects of doing so would be reduced decline at the network scale and spatial differences at specific predicted  
453 vulnerable and resilient sites. Another important caveat of the present study is that it is based on the dynamics of  
454 a single species, *A. millepora*, which is thought to be particularly sensitive to thermal stress because of its colony  
455 growth form and tissue thickness (Loya, Sakai, Nakano, & Woessik, 2001). Incorporating the response of other  
456 species or entire coral communities with different parameterizations for competitiveness, fecundity and other life  
457 history factors could lead to different conclusions.

458 In this work, we find that thermal stress and larval connectivity interact to shape the resilience of  
459 individual reefs to changes in temperature on a spatially realistic network. This study is not intended to predict the  
460 true series of events that will occur in the extended CT region. This is partly because localized anthropogenic  
461 effects that strongly affect reef resilience such as fishing, pollution, etc. are beyond the scope of this study. For  
462 example, our simulations do not capture the back-to-back GBR mass bleaching events (Hughes, Kerry, Connolly, et  
463 al., 2019) and predict high coral cover for that region. We also exclude processes such as larval dynamics (Connolly  
464 & Baird, 2010) and size-specific coral mortality (Hughes & Jackson, 1980) that would likely lead to faster coral  
465 decline in the model results, since recruitment would be reduced due to the addition of pre- and post-settlement  
466 mortality in newly settled corals. Finally, we note that in the absence of recruitment, our parameter set  
467 implemented on a single-reef system leads to coral- and algal-dominated alternative stable states where algae may  
468 “take over” once coral cover dips below a threshold (i.e., due to increased mortality). Other parameter values or  
469 certain levels of coral recruitment could lead to coral-dominated, algal-dominated or coexistence systems that  
470 exhibit different trajectory patterns. For example, a coral-dominated system may lead to slower coral cover decline  
471 overall since algae competition is not a significant source of mortality. Coral may also recover in an algal-  
472 dominated system in the presence of sufficient coral recruitment (McManus et al., 2019). Due to the heterogeneity  
473 of reefs in this network in terms of SST and area, such changes in parameterization could have counterintuitive  
474 effects that are beyond the scope of this study.

475 Our results imply that thermal stress and larval connectivity play significant roles in determining coral  
476 persistence of reefs in the CT. Any management recommendations should incorporate both of these processes,  
477 although the particular conservation goals dictate the most appropriate actions (Beger et al., 2015). For example,  
478 marine protected areas (MPAs) could encompass reefs that are predicted to experience relatively low thermal  
479 stress, yet these sites could become vulnerable if their larval source reefs continue to decline. Similarly, if the aim  
480 is to protect the most vulnerable reefs, preserving areas that supply larvae to those reefs may be insufficient (Hock  
481 et al., 2017), particularly under scenarios that lead to increases in the number of DHWs experienced. Future  
482 research should involve simulations which implement MPAs across a reef network (Melbourne-Thomas et al.,  
483 2011) to test the efficacy of various strategies such as those based on network centrality metrics and outgoing and  
484 incoming larval connections (Kininmonth et al., 2019). Building on the results presented here, such studies will be  
485 critical for identifying management strategies to ensure the persistence of coral reefs in the CT region under  
486 continued ocean warming.

#### 487 **Figure Legends**

488 **Figure 1.** Map of the Coral Triangle (CT) and surrounding areas. The CT-ROMS domain is within the gray box while  
489 reef sites are shown in blue. The dashed red line shows the official delineation of the CT (Veron et al. 2009) [Colour  
490 figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].



491 **Figure 2.** Response of coral cover to unfiltered (interannual variability preserved) (A) and filtered (interannual  
492 variability removed) (B) temperature scenarios. Sea surface temperatures, degree heating weeks, and percent  
493 coral cover over time for the hindcast and future projection scenarios at site 1806 located in the central Philippines  
494 (see Figure S7 for exact location) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

495 **Figure 3.** Fractional coral and algal cover over time for the hindcast, 1.0 °C- and 2.0 °C-increase scenarios for  
496 filtered and unfiltered SST simulations. Darker lines represent mean trajectory values across the network while  
497 lighter lines are individual trajectories from ten randomly selected reefs [Colour figure can be viewed at  
498 [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

499 **Figure 4.** Histograms comparing the final fractional coral cover across the CT for unfiltered (black) and filtered  
500 (hatched light gray) SST increase scenarios. Overlap of unfiltered and filtered results are shown in hatched medium  
501 gray.

502 **Figure 5.** Kaplan-Meier survival curves comparing reef survival across time for simulations between (A) all filtered  
503 and unfiltered SST scenarios and (B) across all eight SST scenarios. Note that reef 'death' is defined as reaching 0.1  
504 coral cover [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

505 **Figure 6.** Total relative recruitment over time showing (a) network and self-recruitment and (b) self-recruitment  
506 only. Results are normalized using the average reef size (160 km<sup>2</sup>), such that relative recruitment is equivalent to  
507 the number of average-sized reefs that are covered by newly settled coral. Each point is summed across the  
508 network and over the week-long recruitment period. Filled circles represent unfiltered scenarios while open circles  
509 are filtered scenarios; blue points represent simulations with interdependent, network recruitment, while yellow  
510 points experienced only self-recruitment, where reefs are independent of one another. Note the difference in  
511 scale between panels (a) and (b) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

512 **Figure 7.** Change in percent coral cover from the start of the hindcast to the final year of the 0.5 °C-, 1.0 °C-, 1.5 °C-  
513 and 2.0°C-increase scenarios for (A) unfiltered and (B) filtered SST [Colour figure can be viewed at  
514 [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

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#### 527 **Data Sharing and Accessibility**

528 The data that support the findings of this study are available from the corresponding author upon request.

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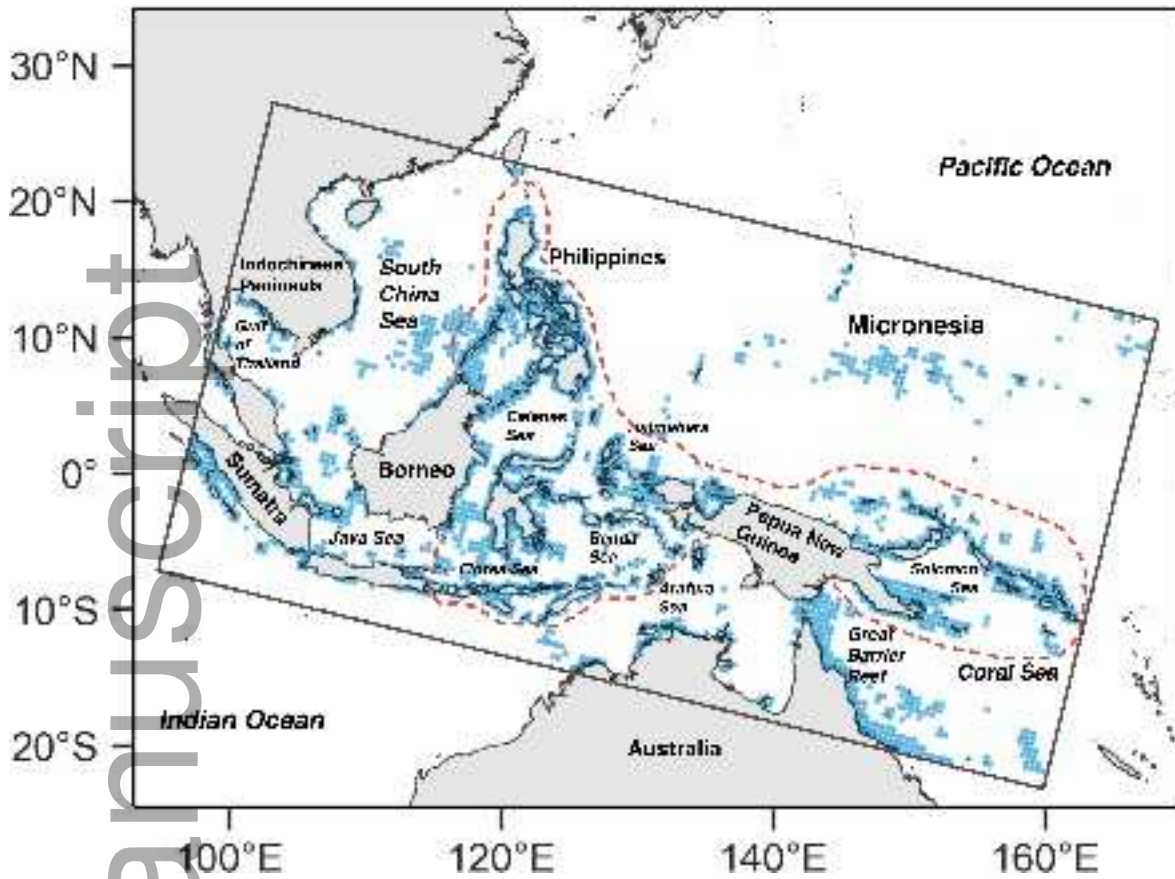
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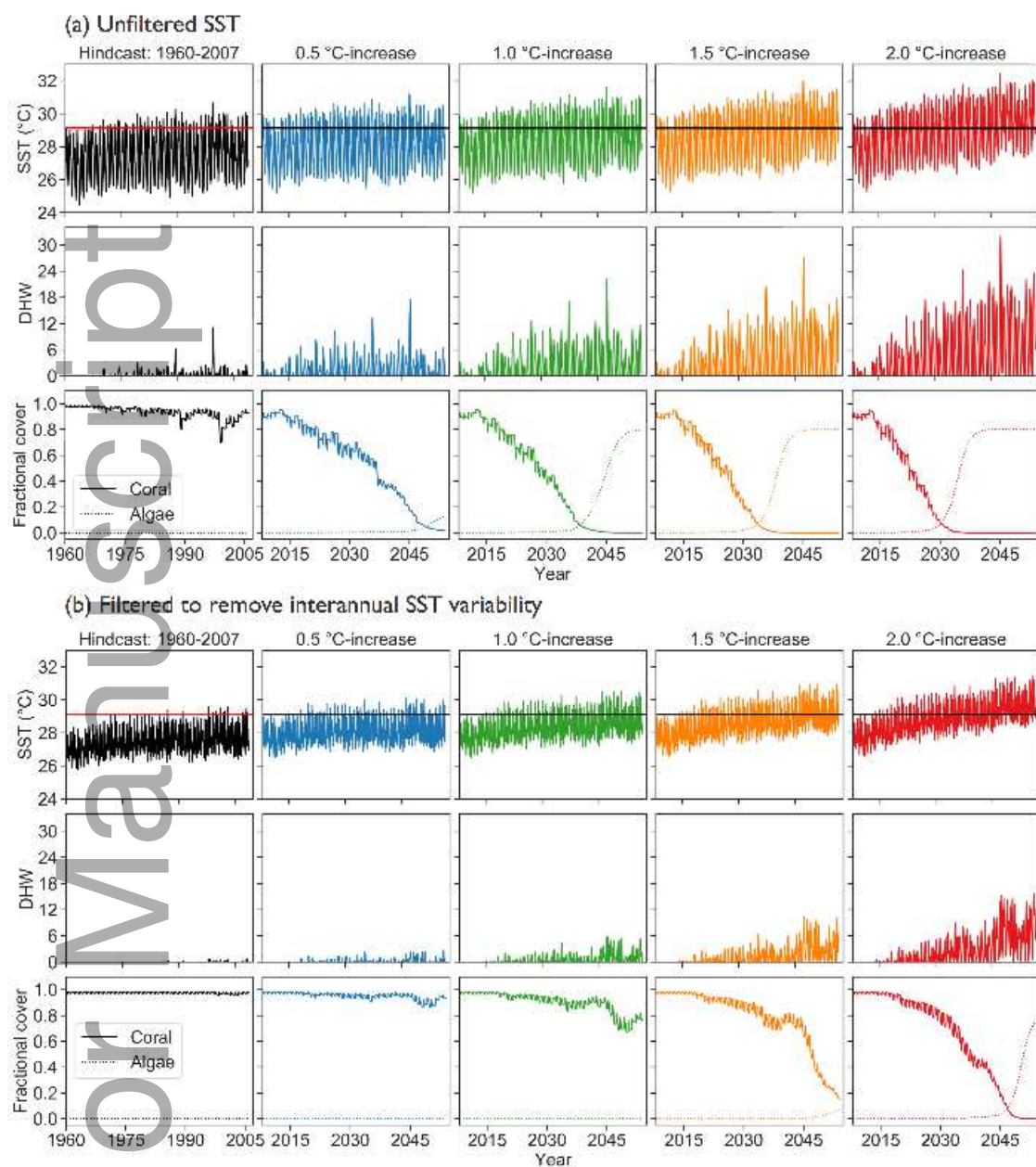
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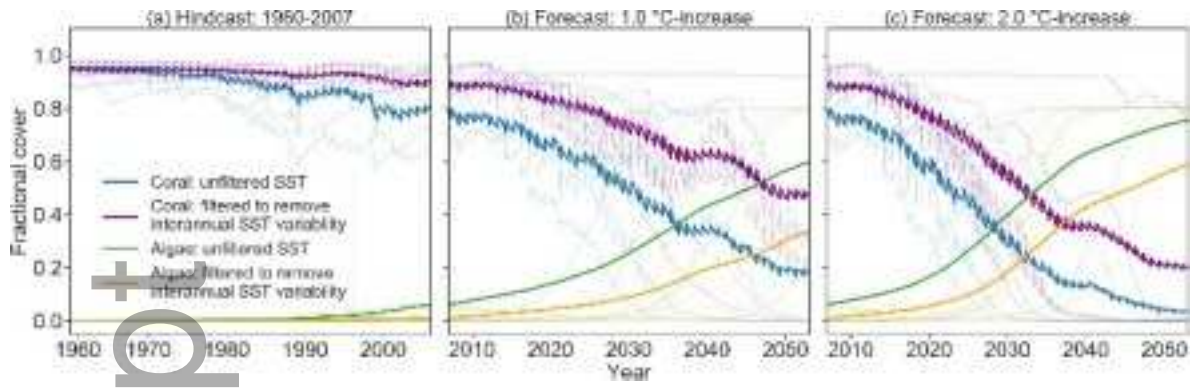
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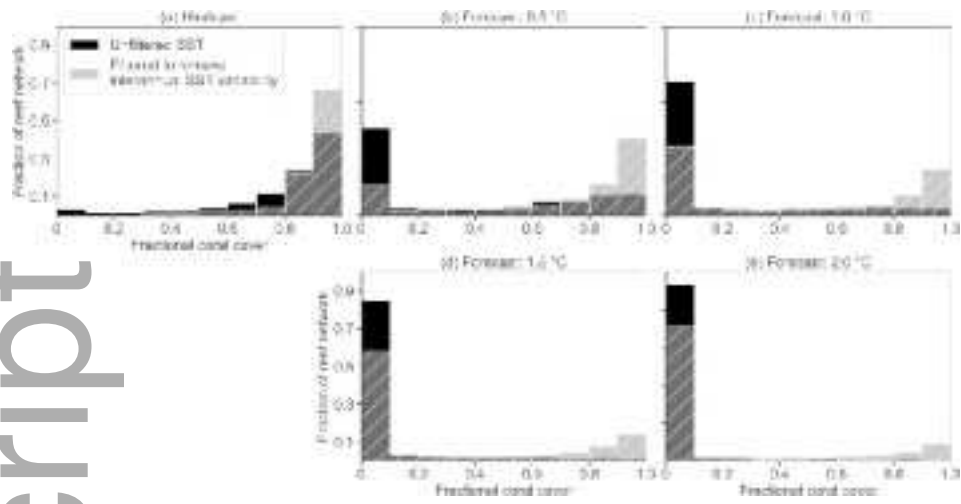
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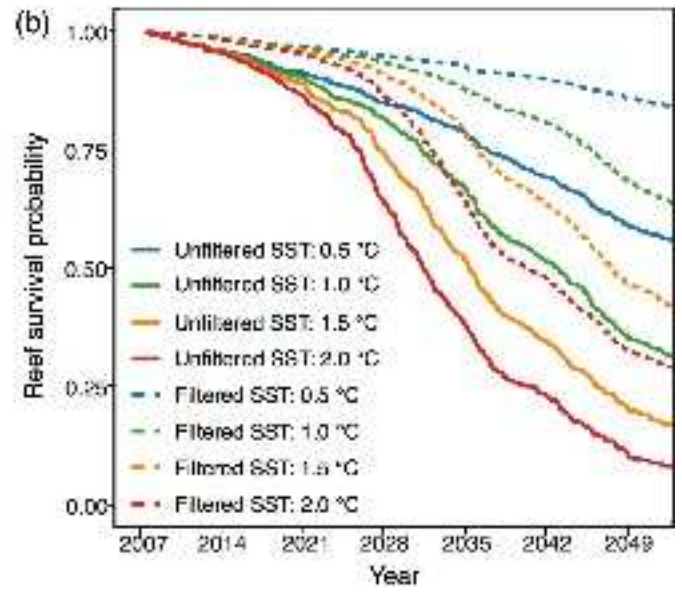
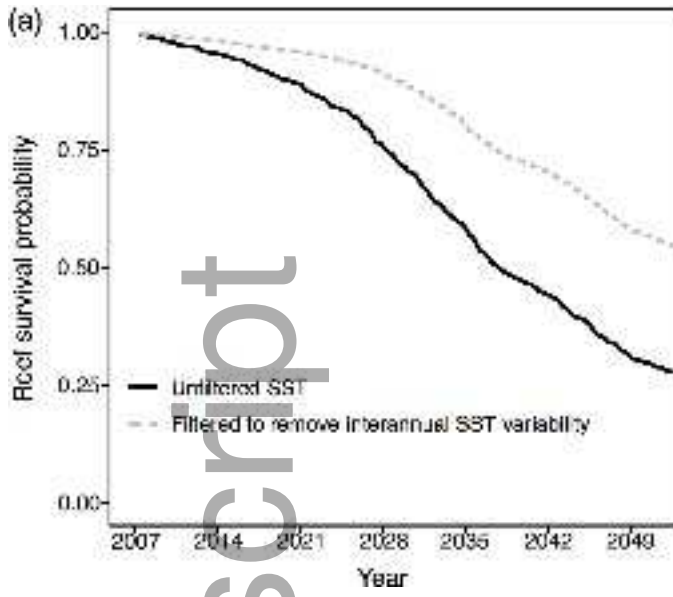
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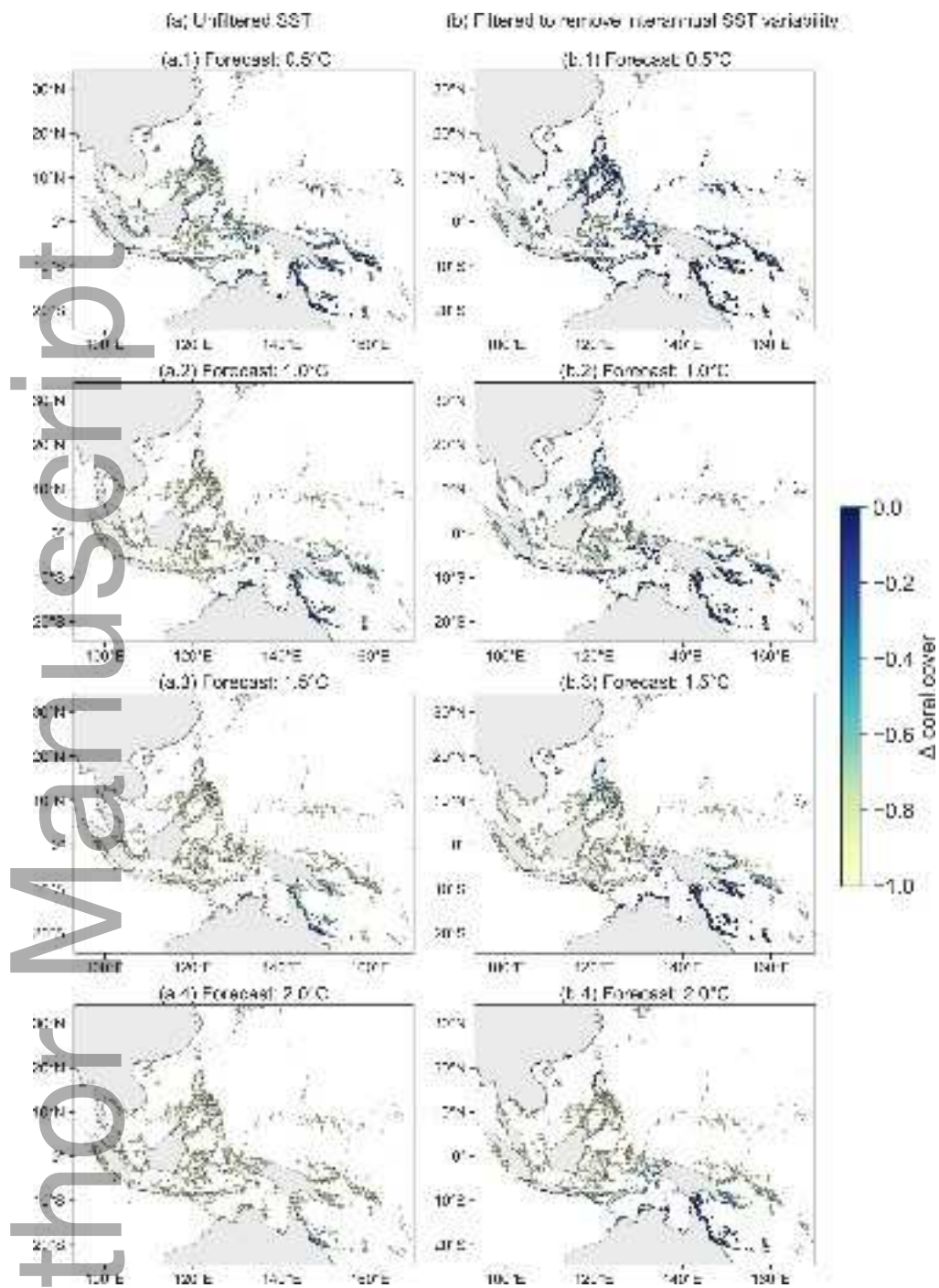


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