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SYNTHESIS

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The impact of rising temperatures on the prevalence of coral diseases and its predictability: A global meta-analysis

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Abstract

Coral reefs are under threat from disease as climate change alters environmental conditions. Rising temperatures exacerbate coral disease, but this relationship is likely complex as other factors also influence coral disease prevalence. To better understand this relationship, we meta-analytically examined 108 studies for changes in global coral disease over time alongside temperature, expressed using average summer sea surface temperature (SST) and cumulative heat stress as weekly sea surface temperature anomalies (WSSTAs). We found that both rising average summer SST and WSSTA were associated with global increases in the mean and variability in coral disease prevalence. Global coral disease prevalence tripled, reaching 9.92% in the 25 years examined, and the effect of 'year' became more stable (i.e. prevalence has lower variance over time), contrasting the effects of the two temperature stressors. Regional patterns diverged over time and differed in response to average summer SST. Our model predicted that, under the same trajectory, 76.8% of corals would be diseased globally by 2100, even assuming moderate average summer SST and WSSTA. These results highlight the need for urgent action to mitigate coral disease. Mitigating the impact of rising ocean temperatures on coral disease is a complex challenge requiring global discussion and further study.

KEYWORDS
climate change, coral reef, marine diseases, meta-analysis, sea surface temperature

INTRODUCTION

Host–pathogen–environment interactions over time, or 'disease dynamics', are now an integral part of understanding ecosystem function in the context of climate change (Altizer et al., 2013; Burge et al., 2014; Vega Thurber et al., 2020). Diseases can drastically alter the composition and resilience of communities, which has been documented across ecosystems and found to increase through time in many communities (Alvarez-Filip et al., 2022; Anderson et al., 2004; Burdon & Zhan, 2020; Burge et al., 2014; Estrada-Saldívar et al., 2020; Harvell

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et al., 2019; Ward & Lafferty, 2004). As increasing temperatures associated with climate change are a major driver of disease dynamics (Burge et al., 2014), climate change may expedite changes to biological communities by increasing the prevalence or severity of disease outbreaks (Aalto et al., 2020; Barris et al., 2018; Jones et al., 2021; Karvonen et al., 2010). For example, thermal extremes exert stress upon host immune systems and allow pathogens to emerge in new habitats, leading to higher disease rates (Burge & Hershberger, 2020; Byers, 2021; Harvell et al., 2007; Shields, 2019). Increasing temperatures may also change the timing or frequency of transmission periods, exposing vulnerable individuals to pathogens (Altizer et al., 2013). Furthermore, as temperature extremes are expected to increase in frequency, the time available for recovery after such events will be reduced, potentially contributing to the collapse of keystone species (Baker et al., 2008; Burge et al., 2014; Eakin et al., 2010). Alternatively, pathogens also have thermal limits, which may constrain their capacity to survive and reproduce, potentially restricting disease emergence or prevalence (Altizer et al., 2013; Byers, 2021). Therefore, understanding and predicting the impact of rising temperatures on disease dynamics is a challenging task and requires long-term global data on disease prevalence.

The sensitivity of different organisms to temperature-driven changes in disease dynamics can also depend on the type of ecosystem considered. Coral reefs are particularly sensitive to changes in sea surface temperature (SST), as shown by their susceptibility to bleaching (Glynn & D'Croz, 1990) and temperature-driven disease incidence (e.g. Bruno et al., 2007; Howells et al., 2020; Randazzo-Eisemann et al., 2022; Tracy et al., 2019; Walton et al., 2018). However, despite predictive models suggesting an upward trend in coral disease prevalence (e.g. Maynard et al., 2015; Walton et al., 2018), pathogen thermal limits and other factors may constrain coral disease increases (Altizer et al., 2013; Byers, 2021). Additionally, temperature fluctuations, such as heatwave events, experienced throughout life (i.e. a coral's 'thermal life history') contribute to increasing the range of temperatures corals can tolerate, thus enhancing the ability to resist disease (Palumbi et al., 2014; Randall et al., 2014; Thomas et al., 2018; Ward et al., 2007). Therefore, thermal impacts on coral disease dynamics are highly complex.

Extrinsic and intrinsic factors other than temperature can also alter coral disease dynamics. For example, human activity (e.g. commercial overexploitation of marine ecosystems), water flow and pollution have all been shown to influence coral disease (Lamb et al., 2014; Page et al., 2019; van de Water et al., 2015). Reef ecosystems with lower coral cover have displayed lower levels of disease prevalence, which is likely driven by limited pathogen transfer between such disparate individuals (Bruno et al., 2007; Caldwell et al., 2018; Dobbelaere et al., 2020; Zvuloni et al., 2015). Coral species with relatively slower population turnover rates exhibit higher levels of disease (Yakob & Mumby, 2011), hinting that species with a higher individual replacement rate may be less susceptible to disease. Concurrently, some coral populations appear more resistant to disease (Mydlarz et al., 2010), potentially due to differences in coral species assemblages, life histories and environments (e.g. González-Barrios et al., 2021; Williams et al., 2021; Williamson et al., 2022). Therefore, there are likely to be regional differences in coral populations. Finally, the assessment of thermally driven coral disease dynamics becomes even more complex over long time periods as the extrinsic human-induced factors are likely to concurrently increase over time (e.g. Lamb et al., 2014; Randazzo-Eisemann et al., 2022; Renzi et al., 2022; van de Water et al., 2015).

Progressing deterioration of coral communities and their key significance to marine life call for an urgent assessment of the expected magnitude and spatiotemporal trends of climate change-driven disease prevalence in corals. To do this, we conducted a global meta-analysis of disease prevalence over time in stony corals. We quantified the magnitude of the increase in coral disease prevalence over the last 40 years to determine the extent to which increases in average sea surface temperature (SST) and cumulative heat stress (as Weekly Sea Surface Temperature Anomaly—WSSTA) correlate with coral disease prevalence. Additionally, we determined how prevalence is likely to change independently of local rising temperatures—i.e., if factors other than temperature contribute to coral disease prevalence. Finally, we examined the global distribution of coral diseases to identify whether regional characteristics account for some of the variations in coral disease prevalence of each ocean basin. This study marks the first compilation and analysis of coral disease surveys alongside SST records on a global scale to better understand how climate change continues to impact coral reef ecosystems. While coral reefs remain complex and diverse systems, deepening our understanding of global projections of coral disease dynamics will assist in developing effective conservation efforts with the intent of slowing or preventing the rise in coral diseases and maintaining the health and stability of these ecological and economical assets.

METHODS

Reporting guideline

We reported our study following PRISMA EcoEvo guidelines (O'Dea et al., 2021). Our PRISMA diagram of literature search and screening (Figure S1), as well as our PRISMA EcoEvo checklist, are available as Supplementary Materials. We also followed a systematic

review method for literature search and selection, including piloting, benchmarking, and error checking (Foo et al., 2021).

Literature search and screening

We conducted literature searches in Scopus and Web of Science databases in July 2020 using the piloted search string (Table S1). Our search string contained terms related to stony corals, disease and climate change-induced temperature change. We tested the sensitivity of our search strategy against a set of 13 benchmark papers (Table S2). These search strings identified 3065 papers from Web of Science, and 963 papers from Scopus (Figure S1). Besides searching the databases, we used two key reviews of the coral disease research (Montilla et al., 2019; Sokolow, 2009) to perform additional backward and forward reference searches. We used Rayyan (Ouzzani et al., 2016) to screen all 3689 unique bibliographic records.

We screened the literature collection in two stages: abstract screening and full-text screening. At both stages, we used prepiloted decision trees (Figures S2 and S3) representing our selection criteria described below. Two reviewers (SB and PP) independently screened 150 randomly selected records to test the decision trees, yielding a 93% agreement rate between reviewers for abstract screening and 100% for the full-text screening stage. One reviewer (SB) then screened all remaining records. This process resulted in 158 papers selected for data extraction (Table S3). After filtering and cleaning, our final data set encompassed 108 papers for meta-analysis. Papers excluded during the full-text screening stage and their reason for exclusion can be found in Table S4.

Selection criteria

We included studies based on six criteria. First, studies needed to have provided in situ empirical benthic survey data of coral disease, as surveys are a common method used for identifying coral and reef conditions. Second, surveys must have been on a natural reef (i.e. studied reefs were subject to natural environmental conditions). Third, surveys must have examined stony corals. Fourth, studies must have reported coral disease prevalence and relevant descriptive statistics (e.g. average or median of % prevalence) and sample size (number of assessed sample plots) for calculating effect sizes. Fifth, studies must have reported the year the survey was conducted. Sixth, studies must have been available in English (see more on this criterion in Discussion).

For consistency, we excluded studies that did not use transects, quadrats or circle plots as the benthic survey collection method during data extraction (i.e. we excluded papers that used timed swims to survey reefs). We excluded these survey methods as quantifying the benthic area examined was unreliable or not possible to decipher from the paper, and study area was necessary for weighing each effect size (i.e. for conducting a weighted/formal meta-analysis).

Our second criterion excluded papers that examined corals from nurseries, laboratories, or other nonwild populations. However, we included studies conducted on corals from restoration efforts because these reefs do not differ from wild reefs in their exposure to environmental stressors (Afiq-Rosli et al., 2017; Monty et al., 2006; Rinkevich, 2014). In contrast, nurseries or other coral-growing facilities are generally protected from predators and other stressors, which could influence disease prevalence (Casey et al., 2014). Additionally, some reefs exist solely because of restoration efforts, such as the *Acropora cervicornis* populations in the Florida Keys (Miller et al., 2014), and excluding these would limit data coverage.

For the third criterion, we classified stony corals as reef-building corals with hard, calcareous skeletons. We focused specifically on stony corals for their ecological importance as habitat builders. Stony corals are also vital to coastal communities as they support both local economy and shore protection (Cesar & van Beukering, 2004). This criterion excluded papers which solely examined soft corals such as Alcyonacea since these corals differ from stony corals in which diseases they can acquire (Willis et al., 2004).

Included studies needed to have reported disease prevalence values as a percentage (or proportion), as per the fourth criterion. We define disease prevalence following Rogers (2010). Briefly, disease is typically associated with bacterial infection, discoloration of the tissue, and/or tissue loss. Discoloration and/or loss of tissue are the main identifiable signs used as evidence of disease presence in stony corals (Aeby et al., 2011; Raymundo et al., 2008; Rogers, 2010; Work & Aeby, 2011) and are used across the literature within benthic surveys to report coral disease prevalence. Thus, we used visual identification of disease signs as the primary reported method for identifying disease prevalence. Disease prevalence is a community-level metric, usually presented as the percentage/proportion of the coral community that displays symptoms (Rogers, 2010). Studies typically report overall disease prevalence across all stony coral taxa in the community, prevalence within the dominant taxa, and/or prevalence within the disease-impacted taxa on the reef. Prevalence differs from disease severity which measures disease progression rate within infected individuals (Rogers, 2010). While severity is an important metric for understanding how diseases will change with climate change, we did not examine it in this study and instead focus solely on prevalence as we found few studies consistently reporting severity during our pilot literature search. We also excluded measurements reported as 'bleaching' to disentangle colony-wide coral

bleaching from coral disease signs (Rogers, 2010). When corals bleach, they eject their symbiotic zooxanthellae, which does not meet our definition of disease.

Our fifth criterion required included papers to report the year(s) in which coral reef surveys were conducted. It was necessary for disease prevalence to be reported per year, even if the study examined a reef over many years. If multiple years were included in one prevalence metric, we determined that the effects of temperature would not be properly attributed to the prevalence observed. In cases where multiple years were conflated in one prevalence metric or the year was missing altogether, the paper was excluded.

In total, we excluded 889 papers based on study type (i.e. not an in situ survey on a natural reef population). We excluded 1910 papers as the study organism was not a stony coral. We excluded another 715 papers on the basis of being unrelated to disease or not including our examined prevalence metrics. We excluded 32 papers as the year of data collection was either missing or confounded such that we could not isolate the desired prevalence metric and matching year. Lastly, 25 papers from the literature search were not in English, and we thus excluded them too.

Data extraction and coding

We used the proportion of disease prevalence as the effect size in this study as such proportion would represent a measure of coral disease across the surveyed community. We incorporated the sampling error of this effect size through the sample area size, which we calculated using the number of sample plots and the area of each plot. While sampling error would typically be calculated from the sample size (in this case, individual coral count), the previous literature suggests that in situ coral counts can be unreliable for certain species (Rogers, 2010). Thus, we utilized sample area size as disease prevalence is a community-level measurement (Rogers, 2010). We extracted the disease prevalence percentage, plot sample size (number of plots) and area of sample plots from the main text, tables, figures or supplementary materials of the included literature. When prevalence was reported in a figure, we used the R (version 4.1.3; R Core Team, 2021; RStudio Team, 2021) package, metaDigitise (version 1.0.1; Pick et al., 2019), to digitally extract and estimate values from a screenshot of the figure. Each effect size represents disease prevalence at a location for a particular year. Some included studies examined certain drivers of coral disease (e.g. pollution and tourism.; Jones et al., 2012; Lamb et al., 2014) across different sites and/or years. We extracted these effect sizes in the same way as those without a documented driving factor as we expect that all effect sizes have varying levels of external driving factors, which could be accounted for in the model. Additionally, some studies report disease prevalence for more than one location, more than one year, or more than one disease type. In these cases, these were extracted as separate effect sizes to allow for analyses of external potentially influencing factors (moderators). The lead author (SB) extracted all effect sizes and moderators, some of which were checked and assisted by the other authors (ML, PP, SD and SN).

In addition to our effect size statistic (% prevalence) and its weighting variable (sampling area), we collected data (i.e. moderators) in two different ways. First, we directly gathered five variables from the included articles: (1) survey year (if conducted in the transition into a new year—for example, the survey began in December and ended in January—we presented data as data collected in separate years—that is, the prevalence of December and January separately—if able to do so; otherwise, we only utilized the year in which the survey started), (2) survey month(s), (3) the number of diseases identified during the survey encompassed in each effect size, (4) survey method (i.e. what type of transect/sample plot was used to map out a survey area) and (5) survey location (latitude and longitude; if not reported in the article, coordinates were estimated in Google Maps based on information provided in the papers such as figures/maps).

Second, we obtained three more variables using three types of external sources. These three variables are: (1) survey region (based on Hoegh-Guldberg et al., 2017 and Kleypas et al., 2008), (2) average summertime sea surface temperature (SST) in the summer prior to sampling in °C and (3) the weekly sea surface temperature anomaly (WSSTA) measure for the sampling period in °C-weeks. The last two were calculated from SST databases available online, which are detailed below.

Survey locations were initially classified into 10 regional locations (East Pacific, Caribbean/Atlantic, West Indian, Central Indian, Middle East, Southeast Asia, Australia, Melanesia, Micronesia and Polynesia) based on Kleypas et al. (2008) and six regional locations (Western Pacific, Eastern Pacific, Caribbean & Gulf of Mexico, Western Indian Ocean, Eastern Indian Ocean, and Coral Triangle & Southeast Asia) based on Hoegh-Guldberg et al. (2017). However, due to small sample sizes in some locations, we aggregated study locations during data analysis into three ocean basins: Atlantic, Pacific and Indian.

To analyse the effect of temperature on coral disease, we used two measures of temperature relevant to coral disease—SST and WSSTA (e.g. Bruno et al., 2007; Randall & Van Woesik, 2017). We used the average SST of the summer prior to sampling to investigate the influence of local average temperature change on disease prevalence. WSSTA measures the cumulative effect of anomalously high temperatures over a 52-week period and is thus used for identifying the influence of persisting anomalously high temperatures on disease prevalence (Bruno et al., 2007). While other metrics have been used to investigate heat stress on corals (e.g. degree heating

week, hot snap and cold snap—all usually reported with fine, that is day-to-day, resolution), WSSTA better corresponds to the yearly resolution of the extracted disease prevalence data. We also wanted to examine the global change in coral disease prevalence as a whole (i.e. not specific to any one disease), and metrics such as hot snap and cold snap require a finer geographical scale. They are also disease-specific as some diseases may be influenced by decreasing temperatures as opposed to increasing (Caldwell et al., 2016). We incorporated average summer SST of the year prior to sampling to potentially reveal insights into the possible existence of a time lag in disease symptom appearance (Caldwell et al., 2020; Heron et al., 2010; Maynard et al., 2011; Rudolf & Antonovics, 2005). As average summer SST may contain a period of several months until sampling, in cases where average summer SST correlates more strongly with disease prevalence than WSSTA, it may be likely that a time lag occurred before disease symptom appearance in that effect size. Additionally, the sampling dates reported in studies were heterogenous, making it difficult to identify an objective time to calculate a gradual SST change. We found it most parsimonious to use the previous year's summer. Neither of these temperature metrics correlate significantly with Year, suggesting these represent the impact of local temperature stress (Figure S4) and that global climate warming is still closely tied within the Year metric.

These two measures (average summer SST and WSSTA) were each obtained using different databases. We utilized a database from the National Oceanic and Atmospheric Administration Physical Sciences Laboratory online collection of gridded climate datasets to calculate average SST metrics during the summer months of the sampling year (Hirahara et al., 2014). We selected the COBE-SST2 dataset which included monthly SST means from January 1850 to December 2019 on a 1.0-degree latitude × 1.0-degree longitude global grid. Calculation of WSSTA was based on a database accessed through the Copernicus Climate Change Service (Lopez, 2019). We selected the 'Sea surface temperature daily data from 1981 to present derived from satellite observations' data set, compiled by The European Space Agency and Sea Surface Temperature Climate Change Initiative, which included daily SST measurements from January 1981 to the present day on a 0.05-degree latitude × 0.05-degree longitude global grid, for its long history and high-resolution (Lopez, 2019). The higher resolution enabled us to more accurately calculate the cumulative heat stress that forms the WSSTA measure.

Average summer SST included average temperatures from June, July and August for northern hemisphere surveys and December, January and February for southern hemisphere surveys. Our decision to use temperature data from the summer prior to the sampling period stemmed from the evidence that a time lag occurs between anomalously high temperatures and visual signs of disease emergence (Caldwell et al., 2020; Heron et al., 2010; Maynard et al., 2011; Rudolf & Antonovics, 2005). If the year of sampling was used to calculate average SST, there would be concern that these temperatures would not truly correlate with the sampled disease if a time lag does occur.

WSSTA was calculated as the sum of positive deviations in weekly temperature averages from a threshold temperature over the 52-week period prior to disease surveys (Bruno et al., 2007). We set this threshold as 1°C greater than the maximum average monthly temperature in the 1981–1992 period (this period is commonly referred to in thermal stress calculations as 'long-term climatology;' Figure S5). 1°C warmer than 'long-term climatology' is the temperature at which corals start to experience thermal stress (Glynn & D'Croz, 1990). These thermal stress temperatures above the threshold during a 52-week window are summed together to produce the WSSTA value in units of '°C-weeks' representing the accumulation of weekly heat stress in the previous year-to-date period (Skirving et al., 2020).

We visually detail the data extraction and coding process in Figure S6 in Supplementary Materials. A list of extracted variables including additional variables, which we did not use in our analyses, and their descriptions are available in Table S5.

Statistical analysis

We analysed disease prevalence (proportion) weighted by the natural logarithm of sampling area (m^2), using a Bayesian zero-inflated generalized linear mixed-effects model (GLMM) with the beta-distribution family and without assuming homoscedasticity (i.e. explicitly modelling heteroscedasticity). By weighting the model by the natural logarithm of sampling area, the weight is determined from the data itself, and thus proportional to the effect sizes as the effect size is a community-level metric. This model was implemented in the R package *brms* (version 2.17.0; Bürkner, 2017, 2018). The beta distribution allowed us to model proportion data without underlying count data, and the zero-inflated distribution dealt with the presence of zeros, which cannot be formally modelled under a beta-family GLMM. This GLMM used a logit link function (i.e. values are on a logistic curve) for the main (beta distribution, denoted as 'mu') and zero-inflated (Bernoulli distribution, denoted as 'zi') parts while the log link function was used to model the precision (log-normal distribution, denoted as 'phi'), which represents the degree of heteroscedasticity.

Our GLMM included the following five fixed effects: (1) weekly sea surface temperature anomaly (WSSTA), (2) average summer sea surface temperature (SST), (3) year at the start of the survey, (4) ocean (i.e. Pacific, Atlantic and Indian) and (5) the number of diseases identified. All the continuous variables were scaled for interpretability

(Schielzeth, 2010). The model also had the following four random effects: (1) site identity (unique locations; 199 levels), (2) paper identity (108 levels), (3) season at the start of the survey, adjusted for hemisphere (4 levels), and (4) method of data collection (i.e. belt transects, quadrats, belt and quadrat, circle plots and line transects; 5 levels). The first two random effects deal with nonindependence among effect sizes. This GLMM also incorporated the correction for zero-inflation (zi) and precision (phi) described above, which were modelled using the three key predictors: WSSTA, SST, and Year. This GLMM constituted our base model that provided a globally pooled estimate of disease prevalence.

From this model, we created seven more models by adding interactions between the three continuous variables (WSSTA, SST and Year) and the categorical variable, Ocean (i.e. WSSTA*Ocean, SST*Ocean, and Year*Ocean; single interaction, pairs of interactions, or all interactions). These models were compared using elpd (expected log point-wise predicted density) with the loo_compare function in the *loo* package (version 2.5.1; Vehtari et al., 2020; Table S6). Regional differences (ocean main effect and interactions) were expressed as contrasts between the reference level (Atlantic Ocean) and other levels (Pacific and Indian Oceans) as 'ocean' was the only fixed effect not on a continuous scale. All the models (base model and all interaction models) were run with the default prior, iteration = 30,000, and warm-up = 28,000 with two chains. In all the models, MCMC chains were converged ($R < 1.001$ where 1 indicates perfect convergence and is the smallest value; Gelman & Rubin, 1992) and mixed, which gave us an effective posterior sample size of over 1000 for all the parameters. We considered regression coefficients statistically significant if 95% credible intervals did not overlap with zero.

Since magnitude cannot be identified when relationships are nonlinear, we examined whether the rates of change in disease prevalence were significantly different between the maxima and minima (i.e. the extreme values) for each predictor that had a non-linear relationship with coral disease prevalence. We conducted this comparison using the emtrends function of the *emmeans* package (version 1.7.3; Lenth, 2022). Predictions using our model are further complicated by the fact that the year effect will inevitably contain the effects of the global trend in rising temperatures. Therefore, it is impossible to separate the time trend from the global warming trend completely. Our predictions into the future should always be seen as projecting the prevalence along the current (a linear 'business-as-usual') global warming trajectory. In this context, the average SST predictor should be seen as the finer and more local effect of temperatures captured at a smaller spatial scale.

We reported results in terms of the regression coefficient (b) that describes: (1) the changes in disease prevalence with the respective factor examined (WSSTA, average summer SST, or Year) in the mu part of the model, (2) the changes in the incidence of zero diseases in the zi part of the model and (3) the changes in residual variance (i.e. heteroscedasticity) in the phi part of the model. All three components (beta distribution: mu, zero inflation: zi, and precision: phi) were presented through the regression coefficients in their respective scales (mu and zi on the logit scale while phi in the log scale). Model predictions (as in figures) and projections, however, were back-transformed to be presented in their natural scales for ease of interpretation. Ocean interactions were presented in contrast between the Atlantic Ocean estimates and either the Indian or Pacific Ocean estimates as 'ocean' was the only fixed effect not on a continuous scale.

RESULTS

Characteristics of disease surveys and literature

Our data set comprised 108 papers, which yielded 918 effect sizes. A visual summary of the literature screening is presented as a PRISMA diagram (Figure S1). Included papers are listed in Table S3. Excluded papers from full-text screening and their reason for exclusion are listed in Table S4. Our data included coral surveys conducted between 1992 and 2018. About half of the data collected was surveyed in the Atlantic Ocean (50.5% of effect sizes), with fewer surveys from the Pacific Ocean (35.1%) and Indian Ocean (14.4%) (Figure 1a). Most surveys began during summer months: 48.1% of effect sizes in the northern hemisphere, and 38.7% in the southern hemisphere (Figure 1b). The most surveyed disease was White Syndrome (30.4%), followed closely by Black Band Disease (30.0%) and Yellow Band Disease (22.3%) (Table S7). Many studies reported disease prevalence per disease identified (78.5%), but some papers did not split disease prevalence into measures of a single disease and present an aggregated disease prevalence for all diseases identified (21.5%, Figure 1c). For information regarding the coral species examined and effect size distribution for each fixed factor, see supplementary information (Figure S7, Supplementary Materials).

The effect of average summer sea surface temperature (SST)

In our base model without interactions with Ocean (i.e., region), a rise in average summer SST predicted a nonlinear increase in coral disease prevalence (Figure 2a,b). The rates of increase were significantly different between the two extreme measured temperatures, 25°C and 32°C ($b_{[25^\circ C - 32^\circ C]} = 0.03$; b is the difference in regression

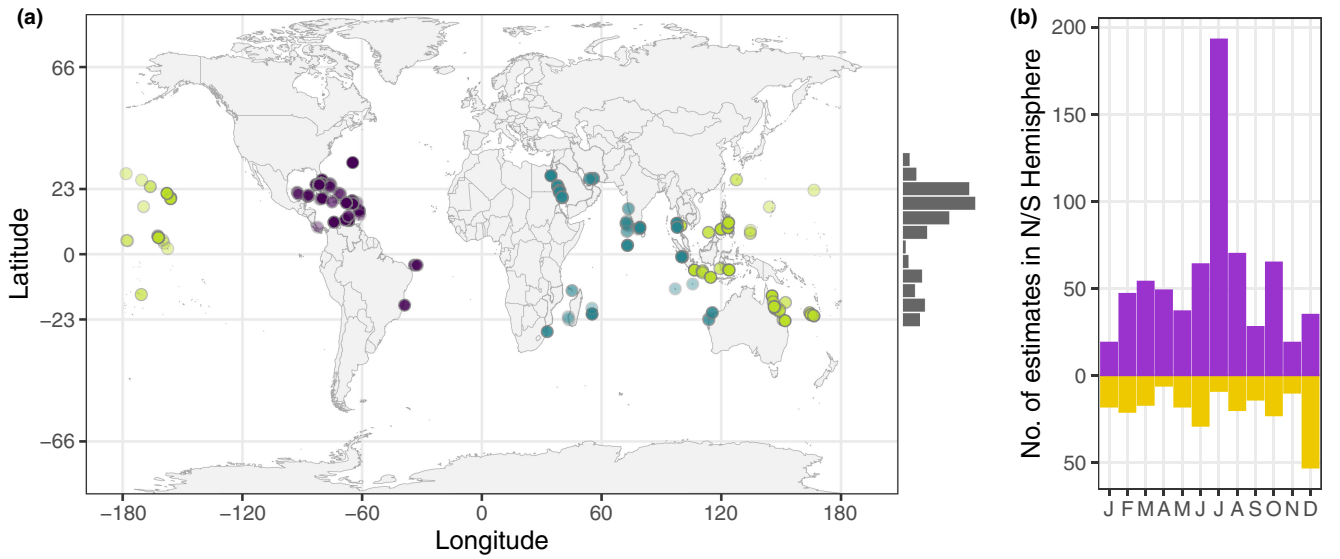

FIGURE 1 Data characteristics. (a) Map of survey locations. Atlantic Ocean surveys in dark purple, Indian Ocean surveys in teal blue, and Pacific Ocean surveys in yellow-green. Point transparency correlates with the number of effect sizes collected from that location. Histogram along right side of graph depicts the number of effect sizes within that latitude. (b) Number of effect sizes from surveys started within each month. Northern Hemisphere (incorporates 73.9% of total effect sizes) bars are coloured in purple. Southern Hemisphere (incorporates 26.1% of total effect sizes) bars are coloured in gold.

coefficients on the logit scale [logit] where zero corresponds to 50%; 95% credible interval, CI = 0.009–0.05; Figure 2c; Figure S8a). Our base (no interaction) model showed that this increase consisted of three parts: (1) a significant increase in non-zero (beta distributed – mu) disease prevalence observations (i.e. more instances of coral observed with signs of disease; $b_{[SST]} = 0.28$ [logit], 95% CI = 0.21–0.35; Figure 3a), (2) a significant, but weaker, increase in zero disease prevalence observations (i.e. more instances of coral observed without any signs of disease – zi; $b = 0.13$ [logit], 95% CI = 0.08–0.19; Figure 3b), and (3) a significant decrease in precision for disease prevalence (i.e. disease prevalence became less predictable as SST increased – phi; $b = -0.25$ on the log scale [log] where zero on the log scale corresponds to 1, 95% CI = −0.27 to −0.22; Figure 3c). Note that phi, which was modelled to vary, is analogous to the inverse of the 'residual variance', which is fixed in a conventional model, and other variance components (Paper ID, Season, Site ID, and Transect Type) from our base model are found in Table S8.

The effect of weekly sea surface temperature anomaly (WSSTA)

Our base model showed that increasing WSSTA predicted a nonlinear increase in disease prevalence (Figure 2d,e) with the rates of increase significantly different between the two extreme WSSTA values, 0.4°C-weeks and 4.3°C-weeks ($b_{[0.4\,^{\circ}\text{C-weeks} - 4.3\,^{\circ}\text{C-weeks}]} = 0.002$ [logit]; 95% credible interval, CI = 0.001–0.004; Figure 2f, Figure S8b). In the base model, this increase consisted of three parts: (1) a significant increase in non-zero disease prevalence observations ($b = 0.2$ [logit], 95% CI = 0.16–0.23; Figure 3d), (2) a significant decrease in zero disease prevalence observations (i.e. fewer instances of coral observed without any signs of disease; $b = -0.17$ [logit], 95% CI = −0.24 to −0.11; Figure 3e), and (3) a significant decrease in precision for disease prevalence (i.e. disease prevalence became less predictable as WSSTAs increased; $b = -0.24$ [log], 95% CI = −0.26 to −0.22; Figure 3f).

Trends over year

In our base model, over the period of 1992 and 2018, coral disease prevalence increased nonlinearly (Figure 2g,h) with the rates of increase significantly different between 1992 and 2018 ($b_{[1992–2018]} = 0.02$ [logit]; 95% CI = 0.004–0.03; Figure 2i, Figure S8c). This increase was accompanied by: (1) a significant increase in nonzero disease prevalence observations ($b = 0.25$ [logit], 95% CI = 0.19–0.31; Figure 3g), (2) a nonsignificant decrease in zero disease prevalence observations (i.e., fewer instances of coral observed without any signs of disease; $b = -0.03$ [logit], 95% CI = −0.08 to 0.02; Figure 3h) and (3) a significant increase in precision for disease prevalence (i.e. disease prevalence became more stable or predictable over time; $b = 0.31$ [log], 95% CI = 0.28–0.34; Figure 3i). When predicting future estimates of coral disease, the year model predicted 76.8% disease prevalence (95% CI = 53.2%–92.9%), given average summer SST and WSSTA remain at their means (28.6°C and 2.08°C-weeks, respectively).

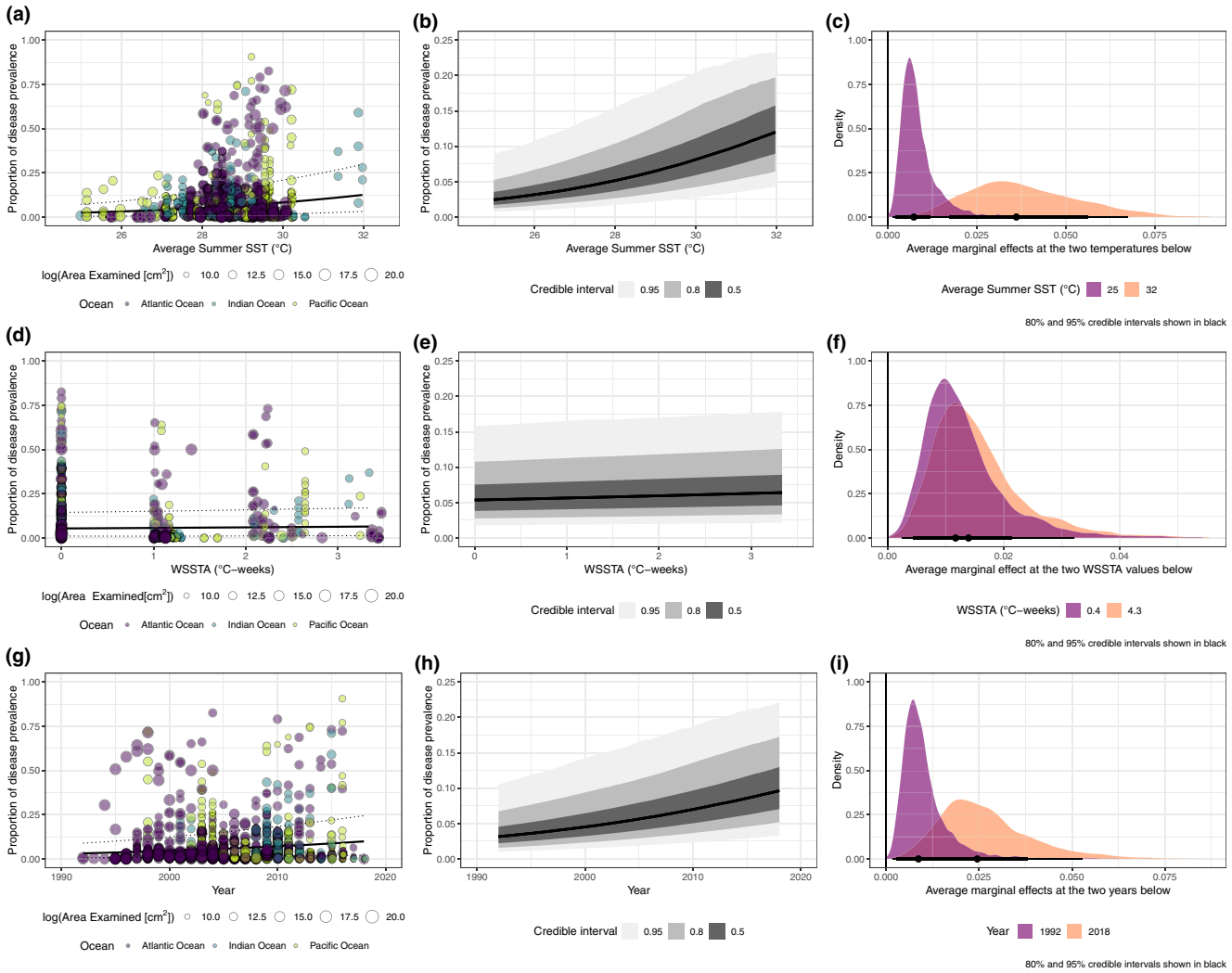

FIGURE 2 Changes in disease prevalence of a coral community over the three factors: average summer sea surface temperature (SST) in °C, weekly sea surface temperature anomaly (WSSTA) in °C-weeks, and Year. (a), (d), and (g): Observed values of disease prevalence. Datapoint size relative to sample area size (weight). Atlantic Ocean coloured in dark purple, Indian Ocean coloured in teal blue, and Pacific Ocean coloured in yellow-green. Black trend line depicts observed change in global disease prevalence. Dotted trend lines depict 95% credible intervals. (b), (e), and (h): Predicted values of disease prevalence for global dataset. Credible intervals shown: 50% (darkest), 80% (middle), and 95% (lightest) credibility. (c), (f), and (i): marginal effects of disease prevalence. Minimum values of each variable coloured in maroon. Maximum values of each variable coloured in orange. Credible intervals coloured in black: thick line represents 80% credibility and thinner line represents 95% credibility.

Regional differences

To test for regional differences, we conducted model selection among models that included interactions between the three oceans (Ocean: Pacific, Atlantic, Indian) and our three key predictors (average summer sea surface temperature—SST, weekly sea surface temperature anomaly – WSSTA, and Year). The best-fitting interaction model contained interactions between Ocean and average summer SST, and Ocean and Year (Table S6; for the variance components of this model, see Table S9). In this model, the difference between the slopes of these three oceans for average summer SST were significant for Atlantic-Pacific and Indian-Pacific interactions ($b_{[\text{Atlantic-Pacific}]}=0.25$ [logit]; 95% CI = 0.05–0.43; $b_{[\text{Indian-Pacific}]}=0.3$; 95% CI = 0.02–0.56; Figure S9a), but differences were nonsignificant for the Atlantic-Indian interaction ($b_{[\text{Atlantic-Indian}]}=-0.05$; 95% CI = −0.28 to 0.16; Figure S9a). The difference between slopes among these three oceans for Year were also significantly different for the Indian-Pacific and Atlantic-Pacific interactions ($b_{[\text{Indian-Pacific}]}=-0.62$; 95% CI = −1.11 to −0.14; $b_{[\text{Atlantic-Pacific}]}=-0.24$; 95% CI = −0.49 to −0.02; Figure S9b) and were non-significant for the Atlantic-Indian interaction ($b_{[\text{Atlantic-Indian}]}=0.38$; 95% CI = −0.06 to 0.82; Figure S9b). Yet, the three regions showed similar patterns in disease prevalence in relation to the three predictors (average summer SST, WSSTA, and year), except for the disease prevalence observed through time in the Indian Ocean (Figure 4).

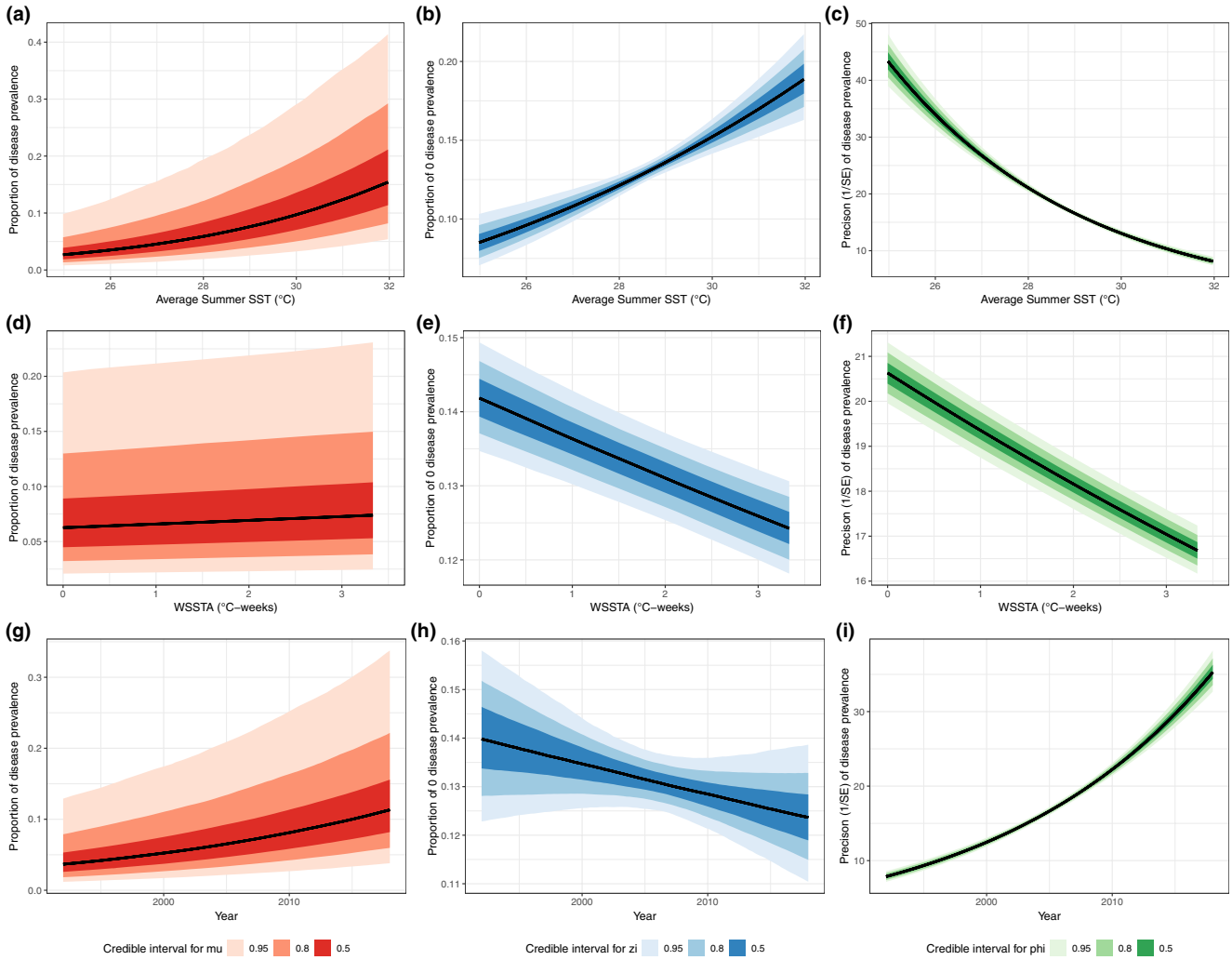

FIGURE 3 Global disease prevalence prediction depicted three ways. Rows distinguish variables: (a), (b), and (c) denote average summer sea surface temperature (SST) in °C; (d), (e), and (f) denote weekly sea surface temperature anomaly (WSSTA) in °C-weeks; and (g), (h), and (i) denote year. Credible intervals displayed for each represent 50% (darkest), 80% (middle), and 95% (lightest) credibility. Note that axes limits differ across all plots to best display the observed trends. (a), (d), and (g): Predicted proportion of non-zero disease prevalence within a coral community, that is omitting effect sizes of 0% disease prevalence (mu). Plots coloured in red. (b), (e), and (h): Predicted proportion of instances of 0% observed disease prevalence in a coral community (zi). Plots coloured in blue. (c), (f), and (i): Precision of coral community disease prevalence (phi). Plots coloured in green.

DISCUSSION

We conducted the first-ever global meta-analysis to quantify long-term trends in the magnitude of coral disease prevalence and determine the extent to which sea surface temperature (SST) or other factors influence coral disease prevalence. Average summer SST, Weekly Sea Surface Temperature Anomaly (WSSTA) and Year all significantly positively correlated with coral disease prevalence. We also newly discovered that these variables significantly influenced the predictability of disease prevalence (Figure 3). In addition, the Pacific Ocean significantly differed from the Atlantic and Indian Oceans regarding the effects of average summer SST and Year, although the directional patterns were consistent across different regions, with one exception (Indian Ocean disease prevalence showed a non-significant declining trend with Year; Figure 4). Below, we discuss the three key moderators (average summer SST, WSSTA, and Year) in turn and further elucidate the regional differences.

Seemingly contradictory effects of average summer SST

We found that coral disease prevalence increased with rising average summer SST (Figure 2, Figure S10a). Such a pattern was to be expected, as numerous studies have supported this trend (e.g., Bruno et al., 2007; Hazraty-Kari et al., 2021; Howells et al., 2020; Walton et al., 2018). In fact, when isolating the effect of these rising local summer temperatures, we expect coral disease to more than double by 2100 (19.6%, 95% CI = 5.5%–41.1%; compared to 2018: 9.92%, CI = 2.08%–24.5%). However, the

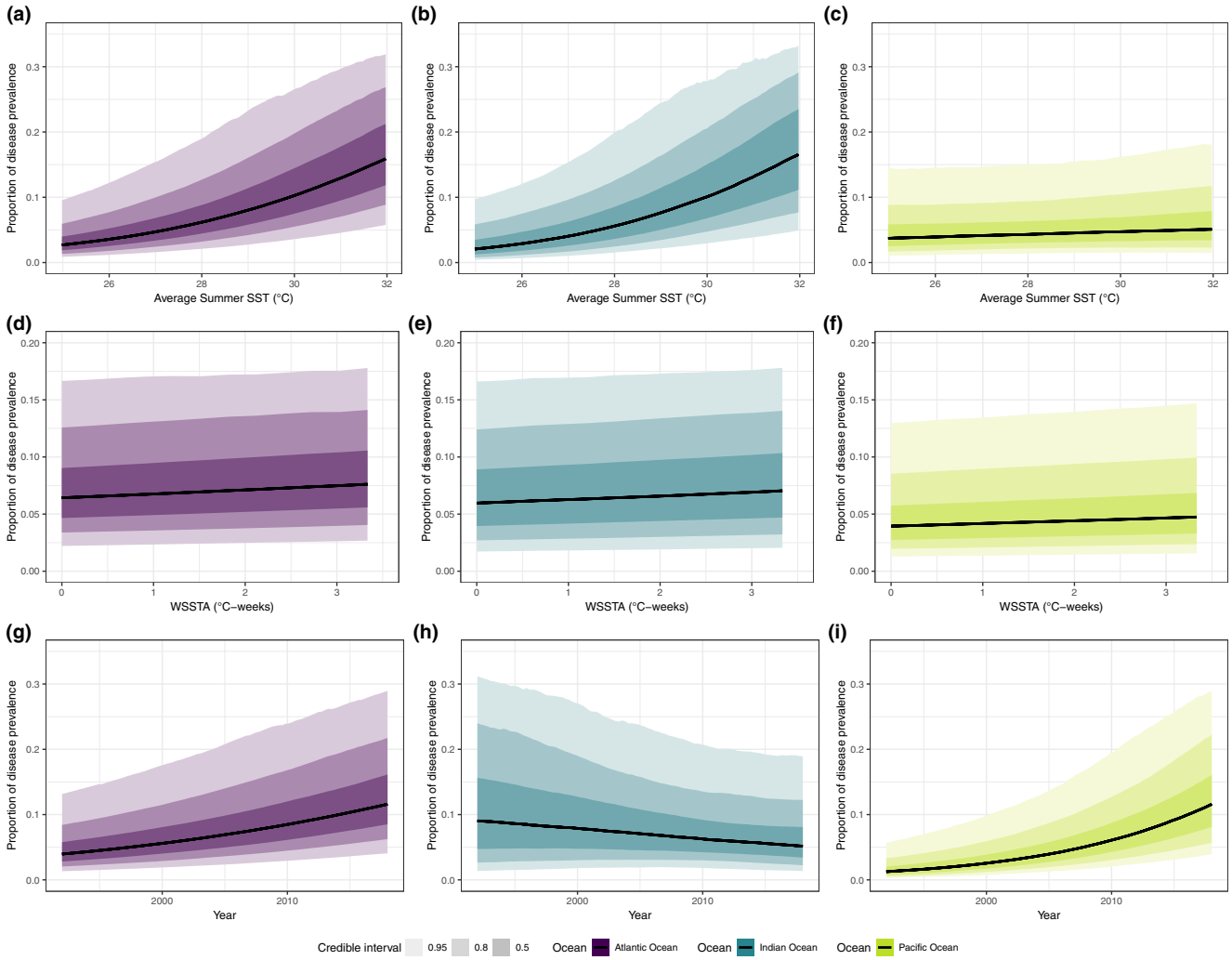

FIGURE 4 Three oceans' predicted non-zero values (mu) of disease prevalence (community-level) per fixed variable. Colours distinguish oceans: Atlantic Ocean in dark purple (a, d, and g), Indian Ocean in teal blue (b, e, and h), and Pacific Ocean in yellow-green (c, f, and i). Rows distinguish metrics: (a), (b), and (c) denote predicted disease prevalence as average summer sea surface temperature (SST) increases in °C; (d), (e), and (f) denote predicted disease prevalence as weekly sea surface temperature anomaly (WSSTA) increases in °C-weeks; (g), (h), and (i) denote predicted disease prevalence through time. Credible intervals displayed represent 50% (darkest), 80% (middle), and 95% (lightest) credibility.

prevalence of apparently healthy corals (no observed disease; zero-inflated component of the model; Figure 3) also increased with increasing average summer SST. This rise in healthy corals with increased SST directly contradicts previous literature (e.g., Walton et al., 2018).

There were hundreds, if not thousands, of coral species included in our global meta-analysis. Each species may react to changes in average summer SST differently, which might account for an increase in zero-disease (i.e. 'healthy') observations. While such observations do not negate the prediction of the overall increase in coral disease with rising summer SSTs, it is important to consider the different responses and resistance capacities to thermal stress among coral species (Drury, 2020; Guest et al., 2012; McClanahan et al., 2020). For example, reefs in the Persian-Arabian Gulf experience high temperatures and larger temperature variability (Camp et al., 2018). As the reefs in the Persian-Arabian Gulf are younger, they are hypothesized to be more able to withstand the current extremes of their environment (Camp et al., 2018). Through these varied responses to thermal stress, these coral species may dominate the observations of zero disease prevalence in future surveys.

We further found greater variability in disease prevalence with increasing average summer SST (Figure 3, Figure S10b). Such an increase in variability has never been formerly reported before, yet this can be explained by varying responses by different coral species, as with the rise in disease-free corals observed. In addition, coral reefs are complex habitats, and there is substantial variation in bleaching and heat stress responses that occur within and between reefs during bleaching events (Ainsworth et al., 2021; Fordyce et al., 2021; Page et al., 2019). A rise in disease prevalence variation with increasing average summer SST indicates that it will be more difficult to predict disease prevalence as average

summer SST rises. As a result, we may underestimate the severity of rising local SST on coral disease and fail to act within the available timeframe to conserve coral reefs.

The harmful effects of heat stress (WSSTA)

Our model suggested that as WSSTA (i.e. annually accumulated heat stress) increases, disease prevalence increases and the fraction of corals observed without disease symptoms decreases (Figure 3e). Therefore, increasing WSSTA was associated with higher rates of disease overall, which indicates heat stress is likely linked with coral disease. This is consistent with a study conducted by Bruno et al. (2007) where they found that annually accumulated heat stress was significantly correlated with an increase in white syndrome. However, Bruno et al. (2007) noted that high coral cover influenced disease prevalence associated with WSSTA. While we were unable to determine coral cover across all effect sizes, since we also found WSSTA correlates with high coral disease, our data was most likely collected using densely populated samples.

The identified increase in coral disease prevalence with WSSTA in the current study is consistent with previous studies of coral disease and heat stress (Aeby et al., 2021; Eakin et al., 2010). As coral disease appears highly correlated to accumulated heat stress, without mitigation, it is likely that high disease prevalence will yield greater coral mortality. We also found disease prevalence becomes more variable (i.e., precision decreased; Figure 3f, Figure S10). The increasing variability of disease occurrence with rising WSSTA, as with average summer SST, highlights once again the difficulty in predicting disease prevalence.

Coral disease through time

We predicted that coral disease prevalence will increase in future years (Figure 2) with consistently most corals bearing visible symptoms of disease (Figure 3I). By 2100, our model predicts 76.8% of corals in reefs will be infected globally (95% CI = 53.2%–92.9%; Figure S11a), provided that WSSTA and average summer SST do not exceed their averages (2.08°C-weeks and 28.6°C, respectively). This prediction represents the IPCC 'business as usual' RCP 8.5 climate projection (IPCC, 2022; Riahi et al., 2011). As local temperature stressors (i.e. WSSTA and average summer SST) increase, we expect even greater disease prevalence in reefs. For example, if average summer SST reaches 32.0°C, we predict 80.5% (95% CI = 64.4%–92.4%) disease in 2100 (Logan et al., 2014).

Our model predicted a consistent increase in coral disease occurrence even after accounting for the detrimental effects of rising temperatures in the form of WSSTA and average summer SST (Figure 3, Figure S10). In particular, predictions of later years at the mean temperature conditions yield a greater change in coral disease prevalence than predictions in the same year at higher temperature conditions. This latter prediction clearly reflects that additional factors, other than the two thermal conditions we examined, are at play in driving coral disease worldwide. Although we could not account for all additional factors explicitly in our models due to data gaps and the heterogenous nature of reporting other potentially important variables, the year effect provides a rough proxy of their combined effect as these factors are expected to increase with time. Some of the most commonly examined factors, apart from thermal factors, include ocean acidification (Prada et al., 2017), pollution (Redding et al., 2013), and anthropogenic damage due to, for example intrusive tourism practices (Lamb et al., 2014). Our synthesis clearly emphasizes a need for more disclosure of accompanying stressor variables and calls for the standardization of disease prevalence and stressor reporting. Future studies should strive to scrutinize these stressors such that specific influences can be identified and mitigated.

Differences and similarities among the oceans

Overall directional patterns of coral diseases across the three oceans were largely similar concerning the three variables: average summer SST, WSSTA, and Year (Figure 4), except for the interaction between coral disease and year in the Indian Ocean. This consistency is most likely because temperature rises have occurred globally with all oceans intaking heat-increasing radiation (Cheng et al., 2019). However, year and average summer SST, rather than thermal stress (WSSTA), are the variables that seem to be driving regional differences (Figure 4). While all oceans can expect an increase in disease prevalence concerning rising summer SST, the Pacific Ocean is predicted to experience the slowest and steadiest increase in disease prevalence (Figure 4c). In contrast, the Pacific Ocean is predicted to experience a more severe increase in disease prevalence than the Indian or Atlantic Oceans, independently from the two temperature-related conditions (Figure 4h,i). With the exception of the decline in coral disease predicted through time in the Indian Ocean (which is predicted with a wider confidence margin), the predicted trends of coral disease across oceans closely mirror the global predictions (Figure S11).

Several factors may underlie these regional differences in the effect of our three moderators on coral disease prevalence. Within each region, coral species are found in varying abundances and diversity. Coral species differ in heat tolerance ranges (e.g. Hoegh-Guldberg et al., 2007) and in symbionts that could aid in thermal tolerance (Santoro et al., 2021). As stress induced by factors other

than temperature (e.g., acidification, pollutants) can lower immune response (Harvell et al., 2007), differences in stress resistance may contribute to observed differences in disease dynamics between oceans. Additionally, the stressors themselves are heterogeneous spatially, as many of these stressors (e.g. pollutants, overfishing and tourism) are anthropogenic (Vega Thurber et al., 2020). The predicted rise in coral disease in the Pacific Ocean over time (independently from temperature) suggests that factors unrelated to temperature, such as tourism and acidification, most likely heavily influence coral disease in this region.

Limitations and recommendations

Our analysis represents the first systematic synthesis of global coral disease data. Firstly, the available global datasets for coral disease are sparse, both temporally and geographically (i.e. these data are highly concentrated to particular reefs, especially in the Caribbean area of the Atlantic Ocean), potentially creating biased predictions for certain years and locations. Of note, we included studies which were investigating a particular driver of disease (e.g. pollution and tourism.; Jones et al., 2012; Lamb et al., 2014), which could also influence our predictions as some effect sizes experienced additional stressors besides temperature. The included studies also differ in their species composition per disease prevalence metric, which could affect our predictions as species may differ in their disease susceptibility (Díaz & Madin, 2011; Gintert et al., 2019). Second, we focussed solely on publications in English due to logistic limitations. While our literature sample size is large, assessing more regions (given coral reefs are in developing nations) and including as many languages as possible in future reviews would aid in accurately describing the state of knowledge and incorporate a more global representation of data. Other languages make up 35% of literature in similar fields (Amano et al., 2016) and recent reports suggest non-English literature does augment environmental data in a non-negligible way (Amano et al., 2023; Pottier et al., 2022). Moreover, we also excluded grey literature, such as government reports. However, the inclusion of grey literature can create potential bias in the data from the lack of rigorous assessment of research quality (Bostrom-Einarsson et al., 2020). As such, this seeming limitation may have improved the quality of data synthesized in our study, which can be tested in future analyses.

Our synthesis has revealed four improvements that future primary studies could adopt to increase the relevance, visibility and comparability of their data. First, comparative studies would benefit from the complete adoption of standardized methodologies. Belt transects are the most common collection method within the literature of the past four decades (Teague et al., 2022). Second, prevalence reported per disease will also aid in data comparison, as most diseases are visually distinct and known to be linked to different drivers (e.g. water pollution and black band disease, heat stress and white syndrome; Teague et al., 2022; Weil & Rogers, 2011; Willis et al., 2004). Third, reporting the abundance of corals per site alongside disease percentages would allow researchers to better conduct meta-analyses, as it is necessary to distinguish between data collected from a reef with many individuals (i.e., high live cover) and a reef with few individuals (i.e. poor cover; Jameson et al., 2001). Fourth, there is a need for more research across a greater range of locations to ensure a more geographically robust understanding of coral disease. The Caribbean is highly studied as it was impacted by disease during the past four decades and has a high research presence in the region (Morais et al., 2022), whereas little data exist for many Indian Ocean reefs. We expect these improvements to enable better comparisons for systematic reviews to understand global trends and drivers of coral disease.

In conclusion, as coral disease is expected to rise in future years (76.8% of corals diseased by 2100), it is imperative to identify drivers of coral disease. We present these predictions as a most conservative worst-case scenario (i.e. the increasing trend in global temperature will not worsen, but it will not improve) to highlight this complex topic. While we recognize our study does not account for many other interactions also likely at play, our study is the first step towards paving the way for policymakers to develop effective mitigation strategies specific to these risks in their respective regions. Our meta-analysis highlights the devastating impacts of rising temperatures on coral reefs and the dire need for swift action to mitigate climate change.

AUTHOR CONTRIBUTIONS

Samantha Burke, Patrice Pottier, Tracy Ainsworth, Malgorzata Lagisz, Szymon M. Drobniak and Shinichi Nakagawa were involved in conceptualisation, methodology and writing—review and editing. Samantha Burke, Szymon M. Drobniak and Shinichi Nakagawa were involved in formal analysis. Samantha Burke, Patrice Pottier, Malgorzata Lagisz, Szymon M. Drobniak and Shinichi Nakagawa were involved in investigation and data curation. Samantha Burke, Patrice Pottier, Szymon M. Drobniak and Shinichi Nakagawa were involved in visualization. Samantha Burke was involved in writing—original draft and project administration. Szymon M. Drobniak and Shinichi Nakagawa were involved in supervision. All authors gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

Authors have no competing interests to declare.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14266.

DATA AVAILABILITY STATEMENT

Data compiled during the main study are available in a GitHub repository (https://github.com/sburke-unsw/CoralDiseaseMetaAnalysis). Data are stored in .csv format with a meta-data table in the Supplementary Materials. Code generated in this study is provided as an html file and is also available in the GitHub repository as .R or .Rmd files.

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REFERENCES

Aalto, E.A., Lafferty, K.D., Sokolow, S.H., Grewelle, R.E., Ben-Horin, T., Boch, C.A. et al. (2020) Models with environmental drivers offer a plausible mechanism for the rapid spread of infectious disease outbreaks in marine organisms. *Scientific Reports*, 10, 5975. Available from: https://doi.org/10.1038/s41598-020-62118-4

Aeby, G.S., Shore, A., Jensen, T., Ziegler, M., Work, T. & Voolstra, C.R. (2021) A comparative baseline of coral disease in three regions along the Saudi Arabian coast of the Central Red Sea. *PLoS One*, 16, e0246854. Available from: https://doi.org/10.1371/journal.pone.0246854

Aeby, G.S., Williams, G.J., Franklin, E.C., Kenyon, J., Cox, E.F., Coles, S. et al. (2011) Patterns of coral disease across the Hawaiian archipelago: relating disease to environment. *PLoS One*, 6, e20370. Available from: https://doi.org/10.1371/journal.pone.0020370

Afiq-Rosli, L., Taira, D., Loke, H.X., Toh, T.C., Toh, K.B., Ng, C.S.L. et al. (2017) *In situ* nurseries enhance coral transplant growth in sedimented waters. *Marine Biology Research*, 13, 878–887. Available from: https://doi.org/10.1080/17451000.2017.1307988

Ainsworth, T.D., Leggat, W., Silliman, B.R., Lantz, C.A., Bergman, J.L., Fordyce, A.J. et al. (2021) Rebuilding relationships on coral reefs: coral bleaching knowledge-sharing to aid adaptation planning for reef users: bleaching emergence on reefs demonstrates the need to consider reef scale and accessibility when preparing for, and responding to, coral bleaching. *BioEssays*, 43, e2100048. Available from: https://doi.org/10.1002/bies.202100048

Altizer, S., Ostfeld, R.S., Johnson, P.T.J., Kutz, S. & Harvell, C.D. (2013) Climate change and infectious diseases: from evidence to a predictive framework. *Science*, 341, 514–519. Available from: https://doi.org/10.1126/science.1239401

Alvarez-Filip, L., González-Barrios, F.J., Pérez-Cervantes, E., Molina-Hernández, A. & Estrada-Saldívar, N. (2022) Stony coral tissue loss disease decimated Caribbean coral populations and reshaped reef functionality. *Communications Biology*, 5, 440. Available from: https://doi.org/10.1038/s42003-022-03398-6

Amano, T., Berdejo-Espinola, V., Akasaka, M., de Andrade Junior, M., Blaise, N., Checco, J. et al. (2023) The role of non-English-language science in informing national biodiversity assessments. *Social and Behavioral Sciences*. Available from: https://doi.org/10.1038/s41893-023-01087-8

Amano, T., González-Varo, J.P. & Sutherland, W.J. (2016) Languages are still a major barrier to global science. *PLoS Biology*, 14, e2000933. Available from: https://doi.org/10.1371/journal.pbio.2000933

Anderson, P.K., Cunningham, A.A., Patel, N.G., Morales, F.J., Epstein, P.R. & Daszak, P. (2004) Emerging infectious diseases of plants: pathogen pollution, climate change and agrotechnology drivers. *Trends in Ecology & Evolution*, 19, 535–544. Available from: https://doi.org/10.1016/j.tree.2004.07.021

Baker, A.C., Glynn, P.W. & Riegl, B. (2008) Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. *Estuarine, Coastal and Shelf Science*, 80, 435–471. Available from: https://doi.org/10.1016/j.ecss.2008.09.003

Barris, B.N., Shields, J.D., Small, H.J., Huchin-Mian, J.P., O'Leary, P., Shawver, J.V. et al. (2018) Laboratory studies on the effect of temperature on epizootic shell disease in the American lobster, *Homarus americanus*. *Bulletin of Marine Science*, 94, 887–902. Available from: https://doi.org/10.5343/bms.2017.1148

Bostrom-Einarsson, L., Babcock, R.C., Bayraktarov, E., Ceccarelli, D., Cook, N., Ferse, S.C.A. et al. (2020) Coral restoration - a systematic review of current methods, successes, failures and future directions. *PLoS One*, 15, e0226631. Available from: https://doi.org/10.1371/journal.pone.0226631

Bruno, J.F., Selig, E.R., Casey, K.S., Page, C.A., Willis, B.L., Harvell, C.D. et al. (2007) Thermal stress and coral cover as drivers of coral disease outbreaks. *PLoS Biology*, 5, e124. Available from: https://doi.org/10.1371/journal.pbio.0050124

Burdon, J.J. & Zhan, J. (2020) Climate change and disease in plant communities. *PLoS Biology*, 18, e3000949. Available from: https://doi.org/10.1371/journal.pbio.3000949

Burge, C.A. & Hershberger, P.K. (2020) Climate change can drive marine diseases. In: Behringer, D.C., Lafferty, K.D. & Silliman, B.R. (Eds). *Marine disease ecology*. Oxford: Oxford University Press, pp. 83–94. Available from: https://doi.org/10.1093/oso/9780198821632.003.0005

Burge, C.A., Mark Eakin, C., Friedman, C.S., Froelich, B., Hershberger, P.K., Hofmann, E.E. et al. (2014) Climate change influences on marine infectious diseases: implications for management and society. *Annual Review of Marine Science*, 6, 249–277. Available from: https://doi.org/10.1146/annurev-marine-010213-135029

Bürkner, P.-C. (2017) brms: an *R* package for Bayesian multilevel models using *Stan*. *Journal of Statistical Software*, 80. Available from: https://doi.org/10.18637/jss.v080.i01

Bürkner, P.-C. (2018) Advanced Bayesian multilevel modeling with the R package brms. *The R Journal*, 10, 395. Available from: https://doi.org/10.32614/RJ-2018-017

Byers, J.E. (2021) Marine parasites and disease in the era of global climate change. *Annual Review of Marine Science*, 13, 397–420. Available from: https://doi.org/10.1146/annurev-marine-031920-100429

Caldwell, J., Heron, S., Eakin, C. & Donahue, M. (2016) Satellite SST-based coral disease outbreak predictions for the Hawaiian archipelago. *Remote Sensing*, 8, 93. Available from: https://doi.org/10.3390/rs8020093

Caldwell, J.M., Aeby, G., Heron, S.F. & Donahue, M.J. (2020) Case-control design identifies ecological drivers of endemic coral diseases. *Scientific Reports*, 10, 2831. Available from: https://doi.org/10.1038/s41598-020-59688-8

Caldwell, J.M., Donahue, M.J. & Harvell, C.D. (2018) Host size and proximity to diseased neighbours drive the spread of a coral disease outbreak in Hawai'i. *Proceedings of the Royal Society B: Biological Sciences*, 285, 20172265. Available from: https://doi.org/10.1098/rspb.2017.2265

Camp, E.F., Schoepf, V., Mumby, P.J., Hardtke, L.A., Rodolfo-Metalpa, R., Smith, D.J. et al. (2018) The future of coral reefs subject to rapid climate change: lessons from natural extreme environments. *Frontiers in Marine Science*, 5, 4. Available from: https://doi.org/10.3389/fmars.2018.00004

Casey, J.M., Ainsworth, T.D., Choat, J.H. & Connolly, S.R. (2014) Farming behaviour of reef fishes increases the prevalence of coral disease associated microbes and black band disease. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20141032. Available from: https://doi.org/10.1098/rspb.2014.1032

Cesar, H.S.J. & van Beukering, P.J.H. (2004) Economic valuation of the coral reefs of Hawai'i. *Pacific Science*, 58, 231–242.

Cheng, L., Zhu, J., Abraham, J., Trenberth, K.E., Fasullo, J.T., Zhang, B. et al. (2019) 2018 continues record global ocean warming. *Advances in Atmospheric Sciences*, 36, 249–252. Available from: https://doi.org/10.1007/s00376-019-8276-x

Díaz, M. & Madin, J. (2011) Macroecological relationships between coral species' traits and disease potential. *Coral Reefs*, 30, 73–84. Available from: https://doi.org/10.1007/s00338-010-0668-4

Dobbelaere, T., Muller, E.M., Gramer, L.J., Holstein, D.M. & Hanert, E. (2020) Coupled Epidemio-hydrodynamic modeling to understand the spread of a deadly coral disease in Florida. *Frontiers in Marine Science*, 7, 591881. Available from: https://doi.org/10.3389/fmars.2020.591881

Drury, C. (2020) Resilience in reef-building corals: the ecological and evolutionary importance of the host response to thermal stress. *Molecular Ecology*, 29, 448–465. Available from: https://doi.org/10.1111/mec.15337

Eakin, C.M., Morgan, J.A., Heron, S.F., Smith, T.B., Liu, G., Alvarez-Filip, L. et al. (2010) Caribbean corals in crisis: record thermal stress, bleaching, and mortality in 2005. *PLoS One*, 5, e13969. Available from: https://doi.org/10.1371/journal.pone.0013969

Estrada-Saldívar, N., Molina-Hernández, A., Pérez-Cervantes, E., Medellín-Maldonado, F., González-Barrios, F.J. & Alvarez-Filip, L. (2020) Reef-scale impacts of the stony coral tissue loss disease outbreak. *Coral Reefs*, 39, 861–866. Available from: https://doi.org/10.1007/s00338-020-01949-z

Foo, Y.Z., O'Dea, R.E., Koricheva, J., Nakagawa, S. & Lagisz, M. (2021) A practical guide to question formation, systematic searching and study screening for literature reviews in ecology and evolution. *Methods in Ecology and Evolution*, 12, 1705–1720. Available from: https://doi.org/10.1111/2041-210X.13654

Fordyce, A.J., Ainsworth, T.D., Page, C.E., Bergman, J.L., Lantz, C.A. & Leggat, W. (2021) Microalgal blooms in the skeletons of bleached corals during the 2020 bleaching event on Heron Island, Australia. *Marine and Freshwater Research*, 72, 1689–1694. Available from: https://doi.org/10.1071/MF21050

Gelman, A. & Rubin, D.B. (1992) Inference from iterative simulation using multiple sequences. *Statistical Science*, 7, 457–472.

Gintert, B.E., Precht, W.F., Fura, R., Rogers, K., Rice, M., Precht, L.L. et al. (2019) Regional coral disease outbreak overwhelms impacts from a local dredge project. *Environmental Monitoring and Assessment*, 191, 630. Available from: https://doi.org/10.1007/s10661-019-7767-7

Glynn, P.W. & D'Croz, L. (1990) Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality. *Coral Reefs*, 8, 181–191. Available from: https://doi.org/10.1007/BF00265009

González-Barrios, F.J., Cabral-Tena, R.A. & Alvarez-Filip, L. (2021) Recovery disparity between coral cover and the physical functionality of reefs with impaired coral assemblages. *Global Change Biology*, 27, 640–651. Available from: https://doi.org/10.1111/gcb.15431

Guest, J.R., Baird, A.H., Maynard, J.A., Muttaqin, E., Edwards, A.J., Campbell, S.J. et al. (2012) Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. *PLoS One*, 7, e33353. Available from: https://doi.org/10.1371/journal.pone.0033353

Harvell, C.D., Montecino-Latorre, D., Caldwell, J.M., Burt, J.M., Bosley, K., Keller, A. et al. (2019) Disease epidemic and a marine heat wave are associated with the continental-scale collapse of a pivotal predator (*Pycnopodia helianthoides*). *Science Advances*, 5, eaau7042. Available from: https://doi.org/10.1126/sciadv.aau7042

Harvell, D., Jordán-Dahlgren, E., Merkel, S., Rosenberg, E., Raymundo, L., Smith, G. et al. (2007) Coral disease, environmental drivers, and the balance between coral and microbial associates. *Oceanography*, 20, 172–195. Available from: https://doi.org/10.5670/oceanog.2007.91

Hazraty-Kari, S., Tavakoli-Kolour, P., Das, R.R., Farhadi, M., Barkhordari-Ahmadi, A., Yahyavi, M. et al. (2021) Baseline assessment of coral diseases in an environmentally extreme environment of the northern Persian gulf. *Marine Pollution Bulletin*, 171, 112707. Available from: https://doi.org/10.1016/j.marpolbul.2021.112707

Heron, S.F., Willis, B.L., Skirving, W.J., Eakin, C.M., Page, C.A. & Miller, I.R. (2010) Summer hot snaps and winter conditions: modelling white syndrome outbreaks on great barrier reef corals. *PLoS One*, 5, e12210. Available from: https://doi.org/10.1371/journal.pone.0012210

Hirahara, S., Ishii, M. & Fukuda, Y. (2014) Centennial-Scale Sea surface temperature analysis and its uncertainty. *Journal of Climate*, 27, 57–75. Available from: https://doi.org/10.1175/JCLI-D-12-00837.1

Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E. et al. (2007) Coral reefs under rapid climate change and ocean acidification. *Science*, 318, 1737–1742. Available from: 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. Available from: https://doi.org/10.3389/fmars.2017.00158

Howells, E.J., Vaughan, G.O., Work, T.M., Burt, J.A. & Abrego, D. (2020) Annual outbreaks of coral disease coincide with extreme seasonal warming. *Coral Reefs*, 39, 771–781. Available from: https://doi.org/10.1007/s00338-020-01946-2

IPCC. (2019) *IPCC special report on the ocean and cryosphere in a changing climate* [Pörtner, H.-O., Roberts, D.C., Masson-Delmotte, V., Zhai, P., Tignor, M., Poloczanska, E. et al. (Eds.)]. Cambridge, UK, New York, NY: Cambridge University Press, pp. 755. Available from: https://doi.org/10.1017/9781009157964

Jameson, S., Erdmann, M., Karr, J. & Potts, K. (2001) Charting a course toward diagnostic monitoring: a continuing review of coral reef

attributes and a research strategy for creating coral reef indexes of biotic integrity. *Bulletin of Marine Science*, 69, 701–744.

Jones, N.P., Kabay, L., Semon Lunz, K. & Gilliam, D.S. (2021) Temperature stress and disease drives the extirpation of the threatened pillar coral, Dendrogyra cylindrus, in Southeast Florida. *Scientific Reports*, 11, 14113. Available from: https://doi.org/10.1038/s41598-021-93111-0

Jones, R., Johnson, R., Noyes, T. & Parsons, R. (2012) Spatial and temporal patterns of coral black band disease in relation to a major sewage outfall. *Marine Ecology Progress Series*, 462, 79–92. Available from: https://doi.org/10.3354/meps09815

Karvonen, A., Rintamäki, P., Jokela, J. & Valtonen, E.T. (2010) Increasing water temperature and disease risks in aquatic systems: climate change increases the risk of some, but not all, diseases. *International Journal for Parasitology*, 40, 1483–1488. Available from: https://doi.org/10.1016/j.ijpara.2010.04.015

Kleypas, J.A., Danabasoglu, G. & Lough, J.M. (2008) Potential role of the ocean thermostat in determining regional differences in coral reef bleaching events. *Geophysical Research Letters*, 35, L03613. Available from: https://doi.org/10.1029/2007GL032257

Lamb, J.B., True, J.D., Piromvaragorn, S. & Willis, B.L. (2014) Scuba diving damage and intensity of tourist activities increases coral disease prevalence. *Biological Conservation*, 178, 88–96. Available from: https://doi.org/10.1016/j.biocon.2014.06.027

Lenth, R. (2022). emmeans: estimated marginal means, aka least-squares means.

Logan, C.A., Dunne, J.P., Eakin, C.M. & Donner, S.D. (2014) Incorporating adaptive responses into future projections of coral bleaching. *Global Change Biology*, 20, 125–139. Available from: https://doi.org/10.1111/gcb.12390

Lopez, A. (2019) Sea surface temperature daily data from 1981 to present derived from satellite observations. https://doi.org/10.24381/CDS.CF608234

Maynard, J., van Hooidonk, R., Eakin, C.M., Puotinen, M., Garren, M., Williams, G. et al. (2015) Projections of climate conditions that increase coral disease susceptibility and pathogen abundance and virulence. *Nature Climate Change*, 5, 688–694. Available from: https://doi.org/10.1038/nclimate2625

Maynard, J.A., Anthony, K.R.N., Harvell, C.D., Burgman, M.A., Beeden, R., Sweatman, H. et al. (2011) Predicting outbreaks of a climate-driven coral disease in the great barrier reef. *Coral Reefs*, 30, 485–495. Available from: https://doi.org/10.1007/s00338-010-0708-0

McClanahan, T., Darling, E., Maina, J., Muthiga, N., D'agata, S., Leblond, J. et al. (2020) Highly variable taxa-specific coral bleaching responses to thermal stresses. *Marine Ecology Progress Series*, 648, 135–151. Available from: https://doi.org/10.3354/meps13402

Miller, M.W., Lohr, K.E., Cameron, C.M., Williams, D.E. & Peters, E.C. (2014) Disease dynamics and potential mitigation among restored and wild staghorn coral, *Acropora cervicornis*. *PeerJ*, 2, e541. Available from: https://doi.org/10.7717/peerj.541

Montilla, L.M., Ascanio, A., Verde, A. & Croquer, A. (2019) Systematic review and meta-analysis of 50 years of coral disease research visualized through the scope of network theory. *PeerJ*, 2019, e7041. Available from: https://doi.org/10.7717/peerj.7041

Monty, J.A., Gilliam, D.S., Banks, K., Stout, D.K. & Dodge, R.E. (2006) Coral of opportunity survivorship and the use of coral nurseries in coral reef restoration. *Marine & Environmental Sciences Faculty Proceedings, Presentations, Speeches, Lectures*, 31.

Morais, J., Cardoso, A.P.L.R. & Santos, B.A. (2022) A global synthesis of the current knowledge on the taxonomic and geographic distribution of major coral diseases. *Environmental Advances*, 8, 100231. Available from: https://doi.org/10.1016/j.envadv.2022.100231

Mydlarz, L.D., McGinty, E.S. & Harvell, C.D. (2010) What are the physiological and immunological responses of coral to climate warming and disease? *The Journal of Experimental Biology*, 213, 934–945. Available from: https://doi.org/10.1242/jeb.037580

O'Dea, R.E., Lagisz, M., Jennions, M.D., Koricheva, J., Noble, D.W.A., Parker, T.H. et al. (2021) Preferred reporting items for systematic reviews and meta-analyses in ecology and evolutionary biology: a PRISMA extension. *Biological Reviews*, 96, 1695–1722. Available from: https://doi.org/10.1111/brv.12721

Ouzzani, M., Hammady, H., Fedorowicz, Z. & Elmagarmid, A. (2016) Rayyan—a web and mobile app for systematic reviews. *Systematic Reviews*, 5, 210. Available from: https://doi.org/10.1186/s13643-016-0384-4

Page, C.E., Leggat, W., Heron, S.F., Choukroun, S.M., Lloyd, J. & Ainsworth, T.D. (2019) Seeking resistance in coral reef ecosystems: the interplay of biophysical factors and bleaching resistance under a changing climate: the interplay of a Reef's biophysical factors can mitigate the coral bleaching response. *BioEssays*, 41, 1800226. Available from: https://doi.org/10.1002/bies.201800226

Palumbi, S.R., Barshis, D.J., Traylor-Knowles, N. & Bay, R.A. (2014) Mechanisms of reef coral resistance to future climate change. *Science*, 344, 895–898. Available from: https://doi.org/10.1126/science.1251336

Pick, J.L., Nakagawa, S. & Noble, D.W.A. (2019) Reproducible, flexible and high-throughput data extraction from primary literature: the metaDigitise R package. *Evolutionary Biology*, 10, 426–431. Available from: https://doi.org/10.1111/2041-210X.13118

Pottier, P., Lin, H.-Y., Oh, R.R.Y., Pollo, P., Rivera-Villanueva, A.N., Valdebenito, J.O. et al. (2022) A comprehensive database of amphibian heat tolerance. *Scientific Data*, 9, 600. Available from: https://doi.org/10.1038/s41597-022-01704-9

Prada, F., Caroselli, E., Mengoli, S., Brizi, L., Fantazzini, P., Capaccioni, B. et al. (2017) Ocean warming and acidification synergistically increase coral mortality. *Scientific Reports*, 7, 40842. Available from: https://doi.org/10.1038/srep40842

R Core Team. (2021) *R: a language and environment for statistical computing*.

Randall, C.J., Jordan-Garza, A.G., Muller, E.M. & van Woesik, R. (2014) Relationships between the history of thermal stress and the relative risk of diseases of Caribbean corals. *Ecology*, 95, 1981–1994. Available from: https://doi.org/10.1890/13-0774.1

Randall, C.J. & Van Woesik, R. (2017) Some coral diseases track climate oscillations in the Caribbean. *Scientific Reports*, 7, 5719. Available from: https://doi.org/10.1038/s41598-017-05763-6

Randazzo-Eisemann, Á., Garza-Pérez, J.R. & Figueroa-Zavala, B. (2022) The role of coral diseases in the flattening of a Caribbean coral reef over 23 years. *Marine Pollution Bulletin*, 181, 113855. Available from: https://doi.org/10.1016/j.marpolbul.2022.113855

Raymundo, L., Work, T., Bruckner, A. & Willis, B. (2008). A decision tree for describing coral lesions in the field. In: Raymundo, L.J., Couch, C.S. & Harvell, C.D. (Eds.) *Coral Disease Handbook: guidelines for assessment monitoring and management*. St. Lucia: Coral Reef Targeted Research and Capacity Building For Management Program, pp. 17–32.

Redding, J.E., Myers-Miller, R.L., Baker, D.M., Fogel, M., Raymundo, L.J. & Kim, K. (2013) Link between sewage-derived nitrogen pollution and coral disease severity in Guam. *Marine Pollution Bulletin*, 73, 57–63. Available from: https://doi.org/10.1016/j.marpolbul.2013.06.002

Renzi, J.J., Shaver, E.C., Burkepile, D.E. & Silliman, B.R. (2022) The role of predators in coral disease dynamics. *Coral Reefs*, 41, 405–422. Available from: https://doi.org/10.1007/s00338-022-02219-w

Riahi, K., Rao, S., Krey, V., Cho, C., Chirkov, V., Fischer, G. et al. (2011) RCP 8.5—a scenario of comparatively high greenhouse gas emissions. *Climatic Change*, 109, 33–57. Available from: https://doi.org/10.1007/s10584-011-0149-y

Rinkevich, B. (2014) Rebuilding coral reefs: does active reef restoration lead to sustainable reefs? *Current Opinion in Environment Sustainability*, 7, 28–36. Available from: https://doi.org/10.1016/j.cosust.2013.11.018

Rogers, C.S. (2010) Words matter: recommendations for clarifying coral disease nomenclature and terminology. *Diseases of Aquatic Organisms*, 91, 167–175. Available from: https://doi.org/10.3354/dao02261

RStudio Team. (2021) *RStudio: integrated development environment for R*. Boston, MA: RStudio, PBC.

Rudolf, V.H.W. & Antonovics, J. (2005) Species coexistence and pathogens with frequency-dependent transmission. *The American Naturalist*, 166, 112–118. Available from: https://doi.org/10.1086/430674

Santoro, E.P., Borges, R.M., Espinoza, J.L., Freire, M., Messias, C.S.M.A., Villela, H.D.M. et al. (2021) Coral microbiome manipulation elicits metabolic and genetic restructuring to mitigate heat stress and evade mortality. *Science Advances*, 7, eabg3088. Available from: https://doi.org/10.1126/sciadv.abg3088

Schielzeth, H. (2010) Simple means to improve the interpretability of regression coefficients: interpretation of regression coefficients. *Methods in Ecology and Evolution*, 1, 103–113. Available from: https://doi.org/10.1111/j.2041-210X.2010.00012.x

Shields, J.D. (2019) Climate change enhances disease processes in crustaceans: case studies in lobsters, crabs, and shrimps. *Journal of Crustacean Biology*, 39, 673–683. Available from: https://doi.org/10.1093/jcbiol/ruz072

Skirving, W., Marsh, B., De La Cour, J., Liu, G., Harris, A., Maturi, E. et al. (2020) CoralTemp and the coral reef watch coral bleaching heat stress product suite version 3.1. *Remote Sensing*, 12, 3856. Available from: https://doi.org/10.3390/rs12233856

Sokolow, S. (2009) Effects of a changing climate on the dynamics of coral infectious disease: a review of the evidence. *Diseases of Aquatic Organisms*, 87, 5–18. Available from: https://doi.org/10.3354/dao02099

Teague, J., Megson-Smith, D.A., Allen, M.J., Day, J.C.C. & Scott, T.B. (2022) A review of current and new optical techniques for coral monitoring. *Oceans*, 3, 30–45. Available from: https://doi.org/10.3390/oceans3010003

Thomas, L., Rose, N.H., Bay, R.A., López, E.H., Morikawa, M.K., Ruiz-Jones, L. et al. (2018) Mechanisms of thermal tolerance in reef-building corals across a fine-grained environmental mosaic: lessons from Ofu, American Samoa. *Frontiers in Marine Science*, 4, 434. Available from: https://doi.org/10.3389/fmars.2017.00434

Tracy, A.M., Pielmeier, M.L., Yoshioka, R.M., Heron, S.F. & Harvell, C.D. (2019) Increases and decreases in marine disease reports in an era of global change. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20191718. Available from: https://doi.org/10.1098/rspb.2019.1718

van de Water, J.A.J.M., Lamb, J.B., van Oppen, M.J.H., Willis, B.L. & Bourne, D.G. (2015) Comparative immune responses of corals to stressors associated with offshore reef-based tourist platforms. *Conservation Physiology*, 3, cov032. Available from: https://doi.org/10.1093/conphys/cov032

Vega Thurber, R., Mydlarz, L.D., Brandt, M., Harvell, D., Weil, E., Raymundo, L. et al. (2020) Deciphering coral disease dynamics: integrating host, microbiome, and the changing environment. *Frontiers in Ecology and Evolution*, 8, 575927. Available from: https://doi.org/10.3389/fevo.2020.575927

Vehtari, A., Gabry, J., Magnusson, M., Yao, Y., Bürkner, P., Paananen, T. et al. (2020) loo: efficient leave-one-out cross-validation and WAIC for Bayesian models. R package.

Walton, C.J., Hayes, N.K. & Gilliam, D.S. (2018) Impacts of a regional, multi-year, multi-species coral disease outbreak in Southeast Florida. *Frontiers in Marine Science*, 5, 323. Available from: https://doi.org/10.3389/fmars.2018.00323

Ward, J., Kim, K. & Harvell, C. (2007) Temperature affects coral disease resistance and pathogen growth. *Marine Ecology Progress Series*, 329, 115–121. Available from: https://doi.org/10.3354/meps329115

Ward, J.R. & Lafferty, K.D. (2004) The elusive baseline of marine disease: are diseases in ocean ecosystems increasing? *PLoS Biology*, 2, e120. Available from: https://doi.org/10.1371/journal.pbio.0020120

Weil, E. & Rogers, C.S. (2011) Coral reef diseases in the Atlantic-Caribbean. In: Dubinsky, Z. & Stambler, N. (Eds.) *Coral reefs: an ecosystem in transition*. Netherlands, Dordrecht: Springer, pp. 465–491. Available from: https://doi.org/10.1007/978-94-007-0114-4_27

Williams, S.D., Walter, C.S. & Muller, E.M. (2021) Fine scale temporal and spatial dynamics of the stony coral tissue loss disease outbreak within the lower Florida keys. *Frontiers in Marine Science*, 8, 631776. Available from: https://doi.org/10.3389/fmars.2021.631776

Williamson, O.M., Dennison, C.E., O'Neil, K.L. & Baker, A.C. (2022) Susceptibility of Caribbean brain coral recruits to stony coral tissue loss disease (SCTLD). *Frontiers in Marine Science*, 9, 821165. Available from: https://doi.org/10.3389/fmars.2022.821165

Willis, B.L., Page, C.A. & Dinsdale, E.A. (2004) Coral disease on the great barrier reef. In: Rosenberg, E. & Loya, Y. (Eds.) *Coral health and disease*. Berlin Heidelberg, Berlin, Heidelberg: Springer, pp. 69–104. Available from: https://doi.org/10.1007/978-3-662-06414-6_3

Work, T.M. & Aeby, G.S. (2011) Pathology of tissue loss (white syndrome) in Acropora sp. corals from the Central Pacific. *Journal of Invertebrate Pathology*, 107, 127–131. Available from: https://doi.org/10.1016/j.jip.2011.03.009

Yakob, L. & Mumby, P.J. (2011) Climate change induces demographic resistance to disease in novel coral assemblages. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 1967–1969. Available from: https://doi.org/10.1073/pnas.1015443108

Zvuloni, A., Artzy-Randrup, Y., Katriel, G., Loya, Y. & Stone, L. (2015) Modeling the impact of white-plague coral disease in climate change scenarios. *PLoS Computational Biology*, 11, e1004151. Available from: https://doi.org/10.1371/journal.pcbi.1004151

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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