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Limited spatial rescue potential for coral reefs lost to future climate warming

Ariel Greiner[1] | Marco Andrello[2] | Emily Darling[1,3] | Martin Krkošek[1] | Marie-Josée Fortin[1]

[1]Department of Ecology & Evolutionary Biology, University of Toronto, Toronto, Ontario, Canada

[2]Institute for the Study of Anthropic Impacts and Sustainability in the Marine Environment, National Research Council, CNR-IAS, Rome, Italy

[3]Marine Program, Wildlife Conservation Society, Bronx, New York, USA

Correspondence
Ariel Greiner, Department of Ecology & Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, ON M5S 3B2, Canada.
Email: ariel.greiner@mail.utoronto.ca

Abstract

Aim: The aim was to determine reef connectivity and future coral cover levels under global scenarios of coral bleaching loss and potential recovery.

Location: Global coral reefs.

Time period: Present-day to 2100.

Major taxa studied: Scleractinian coral.

Methods: We used a global coral larval dispersal model that describes population connectivity among reefs at a resolution of ⅙° × ⅙° (c. 18 km × 18 km) cells. To simulate different patterns of bleaching events, we ran three scenarios at different levels of coral reef habitat loss followed by a reseeding of coral larvae from surviving reefs to simulate recovery.

Results: We found a total of 604 distinct reef networks, but more than half of the world's reef cells are contained in six large coral reef networks (294–5,494 cells), whereas the rest form smaller networks. In the bleaching scenario where previously identified predicted climate refugia were maintained, initial connectivity was largely preserved even when 71% of global coral reef habitat was lost, but the relict reef cells were unable to reseed even 50% of former coral reef habitat because many of the relict reefs are in the same networks as each other. In scenarios where refugia were lost first or with random loss, less of the initial connectivity was maintained, but more widespread reseeding was possible because more reef cells within smaller networks were maintained.

Main conclusions: Our findings highlight the importance of maintaining functional coral reef habitat outside of predicted climate refugia to sustain connectivity globally, and suggest an important role for "stepping stone" reefs between the climate refugia. Without attention to these issues of habitat loss and connectivity, much of global coral reef habitat might not be reseeded without human intervention.

KEYWORDS
bleaching, climate change, coral reefs, larval dispersal, network theory, reseeding

1 | INTRODUCTION

Climate change is affecting ecosystems all over the world. Nevertheless, some patches of the same ecosystem are more sensitive to climate change owing to their location, species composition and habitat characteristics (Baumgartner et al., 2018; Kavousi & Keppel, 2018). This is a phenomenon observed in many ecosystems, including Mediterranean ecosystems (Klausmeyer & Shaw, 2009), wetland ecosystems (Sofaer et al., 2016) and coral reefs (Hughes, Anderson, et al., 2018). These differential impacts of climate change on different patches affect the potential of ecological processes to foster recovery of the more damaged patches. One particular ecological process that can foster recovery is dispersal. Some species can disperse from one patch to another to track their thermal niche and therefore ensure their persistence by accessing sufficient resources (Krosby et al., 2010). However, climate change can alter dispersal among patches by increasing the distance between patches (Gerber et al., 2014) (i.e., owing to patch loss or degradation), increasing larval development rate (Figueiredo et al., 2014; O'Connor et al., 2007) or by increasing the hostility of the matrix in between the patches, reducing the potential for source–sink dynamics or spatial rescue effects (Gotelli, 1991; Mouquet & Loreau, 2003).

Spatial rescue refers to the recovery of a patch owing to immigration of organisms from other patches. The consequences of damaging a particular patch depend on how many connections that particular patch has with other patches and the resulting disruption of the overall connectivity of patches in the region (Rubio et al., 2015). Thus, rescue potential can vary among the remaining configuration of functioning patches after loss or degradation owing to climate change, leading to different likelihoods of recovery or maintenance of functioning in patches of that ecosystem (Hughes et al., 2019; Thompson et al., 2017). As such, any assessment of the long-term survival of a patchy ecosystem in the face of anthropogenic change needs to consider the range of possible loss/degradation scenarios, their resultant patch configurations and the impacts on overall spatial rescue potential.

Coral reefs are one of the most diverse yet imperilled ecosystems on the planet and are a critical case study for understanding the impacts of climate change on future ecosystem functioning and persistence because they support hundreds of millions of people through economic or subsistence activities. Coral reef cover has been reduced owing to local impacts (overfishing, pollution and coastal development; Andrello et al., 2021) and climate change impacts. In recent years, coral populations world-wide have experienced major losses attributable to mass bleaching events caused by increased temperature stress (Hughes, Kerry, et al., 2018), such as the 2014–2017 bleaching event that degraded coral reefs worldwide, including, 29% of the Great Barrier Reef (GBR) (Hughes, Kerry, et al., 2018) and 68% of the Chagos Archipelago (Head et al., 2019). Models at both coarse (*c.* 1°×1°; *c.* 110km×110km) and fine (4 km×4 km) scales predict that 70–99% of reefs risk long-term degradation owing to bleaching by 2100 or earlier (Frieler et al., 2013; van Hooidonk et al., 2016). Climate change also leads to increased

disturbance from cyclones (Knutson et al., 2010) and stress from ocean acidification (Hoegh-Guldberg & Bruno, 2010), which add to the dire prognosis for reef persistence in the Anthropocene. Fortunately, there are some reefs that are located in climate refugia (i.e., habitats that are thought to provide long-term mitigation of environmental stressors, such as increased ocean temperature and acidification; Kavousi & Keppel, 2018). There has been much interest in identifying these reef climate refugia (Beyer et al., 2018; Kavousi & Keppel, 2018), because reefs in climate refugia might be able to act as sources of larvae for other reefs (Hoegh-Guldberg et al., 2018; Mumby et al., 2011) and re-populate (rescue) connected reefs that are not in refugia.

Spatial rescue relies on connectivity. Connectivity of coral reef species is made possible by the dispersal of pelagic larvae mediated by ocean currents (Sheppard et al., 2017). Connectivity among reefs is essential for population replenishment and has also been found to influence coral biogeography, genetic structure and population dynamics (Paris-Limouzy, 2011) and patterns in coral species richness (Veron, 1995). Ultimately, connectivity links reefs into larger networks, and metrics such as network size and the number of incoming and outgoing connections of a particular reef (i.e., node degree; Dale & Fortin, 2014) can characterize different patterns of connectivity. Several modelling studies of larval dispersal have provided predictions of coral reef connectivity for specific regions (e.g., GBR, Kininmonth et al., 2010; Indo-West Pacific, Treml et al., 2015) and globally (Wood et al., 2014), but these studies sought primarily to quantify the connectivity patterns, and the few studies that attempted to delineate distinct networks at large scales did not extend beyond a regional scale (Cowen et al., 2006; Holstein et al., 2014; Treml et al., 2008). Some studies have explored the effects of altering the connectivity among coral reefs and the effect that has on coral reef persistence (Hughes et al., 2019; Mumby & Hastings, 2008), but these studies focused on reefs in particular regions and did not incorporate future climate change scenarios. Other studies have explored the addition of substrate that facilitates coral recruitment to particular regions of the ocean floor to provide "stepping stones" (Saura et al., 2014) for coral larvae to settle on, grow on and then disperse from, in order to improve coral connectivity in those regions (Lee et al., 2018). More studies are needed to assess reef network configurations of the global coral reef system and the recovery potential of global coral reef habitat loss under future climate change scenarios, both of which are critical considerations for conservation and management of reefs. This study attempts to fill this gap.

During the Anthropocene, coral reef habitat will be lost, but it is important to understand which coral reef habitat will potentially be lost first, how this loss will affect the connectivity among remaining coral reef habitat and whether the remaining coral reef habitat will be able to rescue (reseed) the coral reef habitat that is lost. Projects such as the 50 Reefs initiative (Beyer et al., 2018) have given guidelines regarding which reefs might be located in climate refugia (Kavousi & Keppel, 2018) and thus persist during the Anthropocene, but we also need a better understanding of

what coral larval dispersal networks look like in the global coral reef system; specifically, which reefs are connected to which, how many distinct coral larval dispersal networks exist and how big these coral larval dispersal networks are.

Here, we model various levels of coral reef habitat loss under three scenarios meant to span a range of plausible loss scenarios (the predicted climatic survival scenario, the refuge-loss scenario and the random scenario; described in more detail in section 2.1) and evaluate the consequences of that loss for the future connectivity of coral reefs globally using network metrics. Then, based on the resulting configuration of coral reef habitat from each scenario at the highest level of loss, we assess the potential to reseed other reef areas based on hydrodynamic models of ocean currents (under an optimistic reseeding paradigm, described in section 2.5). Exploration of these three alternative loss scenarios and the reseeding potential of each at the highest level of loss will help to determine how coral reef connectivity might change during the Anthropocene, and thus help to inform conservation management plans.

2 | METHODS

To assess how the different scenarios and levels of coral reef habitat loss alter coral reef networks, we combine a model of global coral larval dispersal probabilities, modified from the global connectivity matrix calculated by Wood et al. (2014), with coral reef climate refugia predictions (calculated as "scores" for each reef cell by Beyer et al., 2018, which represent a combination of environmental variables weighted via expert solicitation; see section 2.2). The global connectivity matrix calculated by Wood et al. (2014) represents the dispersal of a generic broadcast-spawning scleractinian coral larva. We explore our questions at the level of the global coral reef system to understand the implications for coral reef connectivity of three scenarios of global coral reef habitat loss and their corresponding reseeding potential.

2.1 | Reef loss scenarios

We looked at one data-driven loss scenario informed by global models of climate refugia (Beyer et al., 2018) and two other scenarios, in order to explore a range of plausible loss scenarios at various different levels of global reef loss (explained below). Each scenario removed the same number of reef cells at each level of loss, but in different patterns associated with different mechanisms of exposure and sensitivity to climate change:

1. In the predicted climatic survival (PCS) scenario, at each level of loss, reef cells are removed in the order dictated by the revised version of the scores from the study by Beyer et al. (2018) (see section 2.2), whereby the lowest-scoring reefs (i.e., highest climate risk) are removed before reefs with higher scores (lower climate risk; i.e., climate refugia). This represents

the scenario whereby the Beyer et al. (2018) predicted climate refugia have the highest persistence of all coral reef habitat.

2. In the refuge-loss scenario, at each level of loss, reef cells are removed in the opposite order dictated by the revised Beyer et al. (2018) scores, whereby the highest scores are removed first. This represents a scenario where coral habitat in predicted climate refugia (Beyer et al., 2018) are lost first. This scenario is plausible, because these predicted climate refugia (Beyer et al., 2018) were defined as such in part because they have experienced low heat stress in the past and are therefore likely to be composed of coral species with a greater sensitivity to thermal stress (Darling et al., 2013). Therefore, if current refuges are exposed to extreme thermal stress, their coral communities would potentially be the most vulnerable to substantial loss and reorganization.

3. In the random scenario, at each level of loss, reef cells are removed at random. Two hundred thousand reef cell loss replicates are computed at each level of loss using a complete randomization procedure. This is intended to serve as a null or baseline scenario but is plausible because it reflects the possibility that risk of loss might be unrelated to climate refugia, potentially because non-climatic human pressures are similar in predicted climate refugia and in other reef cells (Andrello et al., 2021) or because extreme heat events that often result in bleaching are hard to predict (Hughes, Anderson, et al., 2018) or because of the large scale of the climate projections used by Beyer et al. (2018) when defining climate refugia (for more details, see section 2.2). Given that the size of the reef cells (i.e., ⅛° × ⅛°) is larger than c. 80% of temperature anomalies observed on coral reefs (Selig et al., 2010) and thus their loss represents a comparable or higher level of spatially aggregated loss owing to bleaching as is observed on reefs, we did not consider more spatially aggregated random loss patterns.

For all three scenarios, we simulated coral habitat loss corresponding to a potential bleaching event by removing reef cells from the global coral reef system (initially composed of 12,292 reef cells). To investigate different levels of coral reef habitat loss, we removed between 434 reef cells (i.e., c. 140,616 km² of coral reef habitat) and 8,680 reef cells (i.e., c. 2,812,320 km² of coral reef habitat). Removal of 434 reef cells simulated a severe bleaching event equivalent to the surface area of reef altered in 2016–2017 on the GBR (Hughes, Kerry, et al., 2018). Removal of 8,680 reef cells removed c. 71% of the original reef cells, a substantial loss of overall coral reef habitat, in line with long-term predictions of degradation (Frieler et al., 2013; van Hooidonk et al., 2016), resulting in a comparable reef surface area to that covered by the 61 reef bioclimatic units (BCUs) (27%) prioritized by Beyer et al. (2018) (see section 2.2). We chose to remove 71% of the original reef cells [following the pessimistic predictions of Frieler et al. (2013) and van Hooidonk et al. (2016), among others] because the level of resultant reef surface area was comparable to the BCUs prioritized by Beyer et al. (2018) that are now a conservation target of many global multi-million-dollar conservation initiatives (Bloomberg Philanthropies' Vibrant Oceans Initiative; Coral Reef Rescue Initiative; and Global Fund for Coral

Reefs) and because worst cases are important considerations when tasked with predicting future outcomes of climate change. For each level of coral reef habitat loss, we calculated network metrics (Supporting Information Table S1). For the random scenario, we computed 200,000 random replicates for each such level of coral reef habitat loss (similar ratio of cells to replicates as in the study by Watson et al., 2011); we then reported the average of each network metric value for each level of global coral reef habitat loss under the random scenario.

2.2 | Climate impact scores

Beyer et al. (2018) calculated climate refugia predictions (encompassed by "scores") for coral reefs using 30 data layers at a cell spatial resolution of .05°×.05° (54,596 reef cells of *c.* 5 km×5 km). These scores were designed to capture both how likely a particular reef cell was to survive climate warming (bleaching, cyclone risk; i.e., climate refugia potential) and its ability to reseed other reefs, using 28 climatic metrics and two connectivity metrics. Note that the climatic metrics were calculated at a variety of scales, with the thermal history and recent thermal condition metrics computed at a scale of .05°×.05° (*c.* 5 km×5 km) and the climate projection metrics derived from datasets at a 1°×1° scale, but then averaged within a 5.5° radius (Beyer et al., 2018). Using these scores, Beyer et al. (2018) prioritized reef BCUs (sets of spatially contiguous reef cells) for conservation (prioritized reef BCUs; 50 reefs).

  Here, for our study, we recalculated the scores from the study by Beyer et al. (2018) using only the data layers of past, present and future thermal impact and cyclone risk (i.e., the climatic metrics), while removing the connectivity metrics to obtain the "connectivity-less scores". The connectivity metrics were removed so that the order of removal was not influenced by the connectivity of particular patches, but solely by the local climatic refugia potential. This was crucial because our objective was to evaluate the consequences of local coral loss on subsequent connectivity and reseeding potential. Given that the connectivity of the global coral reef system (via Wood et al., 2014) is known only at a coarser resolution (i.e., reef cell size; ⅛°×⅛°, *c.* 18×18 km, for a total of 12,292 cells) we needed to recompute these connectivity-less scores at this coarser level to match the global coral larval dispersal probabilities determined by Wood et al. (2014). To do this, we assigned each Wood et al. (2014) reef cell the average of the connectivity-less scores that were contained within it [connectivity-less scores ranged from zero to one; the median score of a Wood et al. (2014) reef cell is .00344; and the median standard deviation in connectivity-less score within one Wood et al. (2014) reef cell is .00254] to obtain the "revised" Beyer et al. (2018) scores. This recomputation was performed to match the scale of the two datasets using ArcMap (v.10.4.1; ESRI, 2016), and all the remaining work was performed in R (v.3.5.3; R Core Team, 2019) (for more details, see Supporting Information Supplementary Material 1a).

2.3 | Potential and reference connectivity

The coral larval dispersal probabilities predicted by Wood et al. (2014) were based on a global coral reef cell connectivity matrix derived from a larval dispersal model [generated using the open-source connectivity modelling system (CMS) software; Paris et al. (2013)], in which every element of the matrix describes the probability of a larva moving from a source reef cell to a target reef cell. The connectivity matrix of Wood et al. (2014) included some extremely long-distance connections (>1,000 km). A comparative study on marine species world-wide (Manel et al., 2019) found that larval dispersal modelling studies led to predictions of larval dispersal distances that were much larger than estimates obtained from empirical analysis (<90 km; Carlon & Olson, 1993; Gilmour et al., 2009; Hughes et al., 2019; Sammarco & Andrews, 1988). Although empirical analysis might also be biased, the putative long-distance connections identified by larval dispersal models (potential connectivity) are probably overestimated by models that do not resolve small-scale hydrodynamics and do not account for larval behaviour (Bode et al., 2019; Manel et al., 2019). Manel et al. (2019) found that the median maximum empirically estimated dispersal distance for marine pelagic larvae was 42 km (median across 55 species; interquartile range 27–250 km). Therefore, we modified the connectivity matrix such that the mean Euclidean dispersal distance was 42 km (as opposed to 529 km in the connectivity matrix of Wood et al., 2014) by including only simulated larval dispersal probabilities >.033 (hereafter referred to as the "reference connectivity matrix"). We then performed a sensitivity test to explore how this threshold affected the results by repeating the analysis for different mean Euclidean dispersal distance thresholds, from 30 to 250 km (reflecting the interquartile range reported by Manel et al., 2019), in steps of 20 km to account for grid cell size (*c.* 18 km×18 km). The results described in the Results and Discussion sections were all generated from the reference connectivity matrix unless stated otherwise.

2.4 | Network metrics

We assessed how reef cell connectivity would change according to the three loss scenarios at various levels of global coral reef habitat loss by tracking four network metrics that summarized how the distribution of reef cell networks changed for the global coral reef system. Here, a network is defined as the set of nodes (hereafter, reef cells) that are all connected by dispersal (i.e., coral larval dispersal) directly and indirectly via intermediate steps and do not send or receive dispersers (i.e., larvae) to/from any other reef cells; the connections (edges) might be directed and asymmetric. This connectedness was determined by the existence of a connection between reef cells in the reference connectivity matrix described above (or those used for the sensitivity test). A network made up of one reef cell indicates a reef cell that does not send or receive larvae to/from other reef cells in the global coral reef

system, but might send larvae to itself and receive larvae from itself. Four network metrics were calculated for the global coral reef system: (1) the average node degree (the average number of incoming and outgoing connections any reef cell has to other reef cells); (2) the number of networks; (3) the geometric mean network size (calculated as the geometric mean number of cells in all of the networks in the global coral reef system); and (4) the average source strength (for more details of all the metrics, see Supporting Information Supplementary Material 1a; Table S1). The geometric mean network size was calculated instead of the mean or median network size because the network size distribution in the global coral reef system was found to be non-normal, with many small and many very large networks. Source strength is defined as the number of reef cells to which a particular reef cell can send larvae over many generations, including not only the direct connections but also higher-order connections (i.e., the out-neighbourhood size). The average source strength thus measures the average out-neighbourhood size across all of the reef cells in the global coral reef system. Thus, the higher the average source strength of the global coral reef system, the higher the potential of a particular reef cell (on average) to be a source of larvae for many other reef cells.

These network metrics were chosen because they help to define how connected the global coral reef system is as a whole, with a highly connected global coral reef system being one in which any particular reef cell is (on average) more likely to be able to send larvae to any other reef cell. Few, large networks, a high average node degree and a high average source strength would indicate a highly connected global coral reef system. Also, if the global coral reef system has a higher average node degree, it indicates that the reefs within the networks are highly connected and thus potentially better able to withstand the loss of single reef cells. Furthermore, a single reef cell is more likely to be influenced by reef cells that are far away from it if the global coral reef system has fewer, larger networks.

2.5 | Reseeding potential

Starting from the reef cells that remain after the highest level of loss (i.e., the relict reef cells) from each of the three scenarios, we estimated the potential for spatial rescue by reseeding of coral larvae from the relict reef cells to the lost reef cells, using the relevant connectivity matrix. Given that recovery after reseeding is a slow process (Hughes, Anderson, et al., 2018), we do not anticipate that reseeding will make a noticeable impact while reef degradation owing to climate change is ongoing at its current frequency/level, hence we chose to start the reseeding from the relict reef cells (i.e., the reef cells that remain after the highest level of loss) rather than the remaining reef cells from one of the lower levels of loss (for further justification of the relevance of this level of loss, see also rationale in section 2.1). Hence, we initialized each relict reef cell with 100 coral larvae and set the rest of the reef cells (i.e., the lost reef cells)

to have zero coral larvae to simulate severe mortality on degraded reef cells after bleaching (e.g., Hughes et al., 2019). We then multiplied the coral larval abundances in each reef cell by the reference connectivity matrix (or matrices with other mean dispersal distance thresholds, for the sensitivity test) to simulate one generation of dispersal, or one reseeding event. After this initial reseeding event, before each subsequent generation, each reef cell that had greater than zero abundance by the end of the previous generation was given 100 larvae (this was done to avoid having fractional larvae; the reseeding results are the same if this is not performed), and the reseeding process was repeated. This process was repeated 50 times to simulate 50 generations. We then quantified the number of reef cells that were reseeded at each generation and the number of generations before the number of reef cells reseeded plateaued. We also quantified the number of networks, geometric mean network size, average node degree and average source strength of the final, fully reseeded networks from each of the three scenarios (Supporting Information Table S2). We chose 50 generations, because this was found (through preliminary simulations) to ensure that the number of reef cells being reseeded plateaued, thus allowing us to assess the total number of reef cells possible to be reseeded from each remaining configuration of reef cells. This describes an optimistic reef cell reseeding paradigm, because it assumes that a small number of coral larvae of any species can successfully reseed any reef cell in the current global coral reef system.

3 | RESULTS

3.1 | Initial connectivity map

The initial global coral reef system is composed of 604 distinct networks of coral reef cells (Figure 1a). Most of the networks are very small (64% are formed by only one reef cell), whereas a few are very large (5,494 reef cells in the largest network; Figure 1c). The largest network of reef cells encompasses most of the reef cells in the GBR and the Coral Triangle, including the Philippines and Indonesia (Figure 1a). Other large networks each encompass reef cells off the coast of East Africa, the Red Sea and the Persian Gulf. The remainder of the Indo-Pacific reef cells make up smaller networks, such as the Hawaiian reef cells in four distinct networks. The reef cells in the Caribbean make up four large networks and a few smaller networks (Figure 1a). The distribution of network sizes is highly skewed, with most networks made up of fewer than five reef cells (Figure 1c). Reef cells around the world diverge dramatically in the number of reef cells to which they can send larvae (i.e., their ability to be sources of larvae; Figure 1b). The reef cells with the largest out-neighbourhoods (i.e., highest source strength) are those in the Philippines (c. 700 reef cells), followed by a few in the Northern region of the GBR (c. 370–540 cells) and some reef cells around Cuba (c. 400 cells). The median out-neighbourhood size is 47 reef cells, and the interquartile range is 12–124 reef cells for reef cells globally (Figure 1b). Unsurprisingly, reef cells

(a)

(b)

(c)

(d)
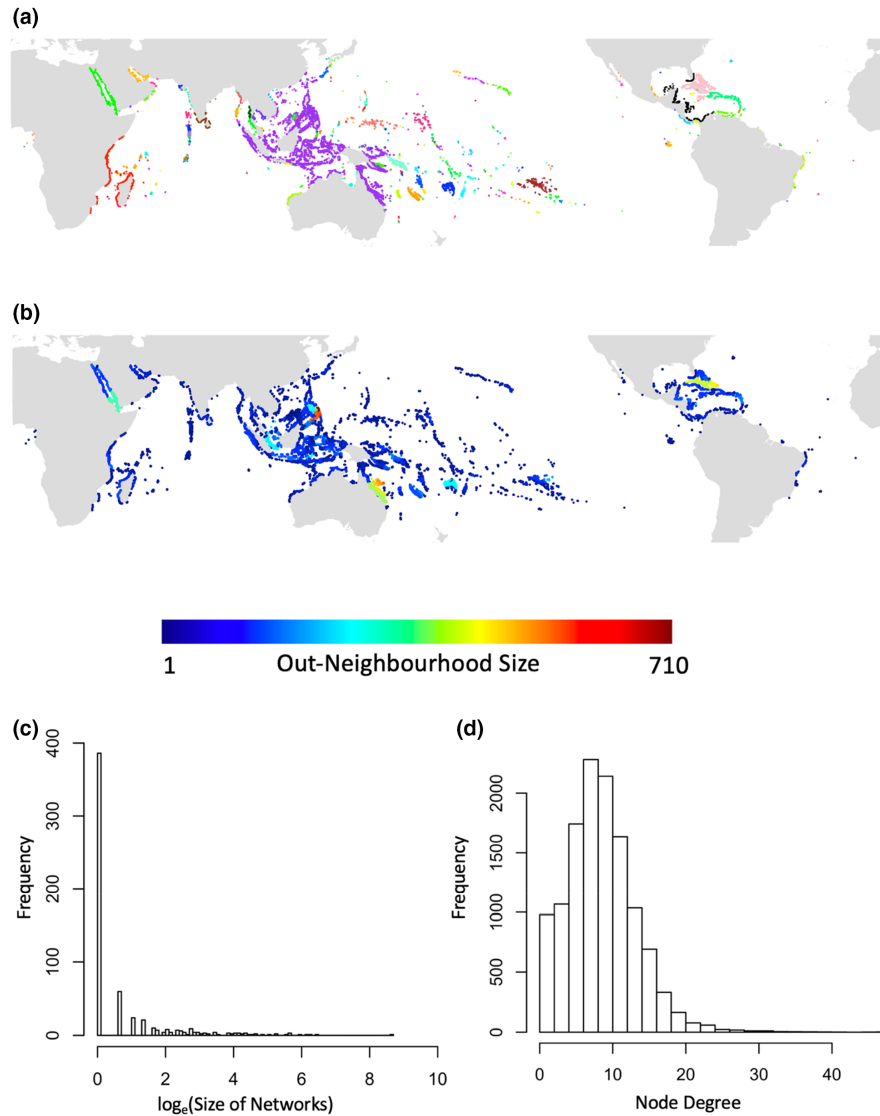
FIGURE 1 Initial coral reef connectivity of the global coral reef system. (a) Networks. Each reef cell is represented by a coloured dot on the map, and colours indicate network membership; some colours appear to repeat because there are more networks ($n = 604$) than there are distinguishable colours. However, an effort was made to ensure that similar-coloured networks did not appear near to each other; for example, the large purple network in the Indo-Pacific is one network. (b) Source strength. The colour of each reef cell indicates the total number of reef cells that can be reached through larval dispersal over multiple generations (i.e., out-neighbourhood size) from said reef cell. (c) Histogram of $\log_e$(size of networks) for initial reef networks. The x-axis shows the natural logarithm (log base e) of network size, hence the spike at zero represents all the networks composed of only one reef cell [because $\log_e(1) = 0$]. (d) Histogram of node degree for the initial set of reef cells. Only the results from the reference connectivity matrix are shown here. See the Supporting Information (Supplementary Material 1a) for description of metrics.

tend to have larger out-neighbourhoods if they are in regions with large numbers of reef cells. The median node degree (Figure 1d), or median number of incoming and outgoing connections of any particular reef cell, is nine (interquartile range: 6–12 connections). Median node degree and median out-neighbourhood size were calculated as node degree and out-neighbourhood size were not normally distributed.

3.2 | Scenarios of global coral reef habitat loss

The three different scenarios of loss had drastically different consequences for the connectivity of reef cells in the global coral reef system, particularly regarding the change in average node degree (average number of ingoing and outgoing connections from a node) and number of networks (Figures 2 and 3). As the level of loss increased, average node degree declined under both the random and refuge-loss scenarios, whereas it held relatively steady under the

PCS scenario (8.95–8.15; Figure 2a–c). The number of networks present declined as the level of loss increased under the PCS scenario, whereas it increased as the level of loss increased under the random scenario and increased until c. 50% of the reef cells remained (before declining) under the refuge-loss scenario (Figure 2d–f). At higher levels of loss, geometric mean network size doubled under the PCS scenario, increased slightly under the refuge-loss scenario and declined in the random scenario (Figure 2g–i). As the level of loss increased, average source strength fell steadily under the random and refuge-loss scenarios but plateaued initially before falling under the PCS scenario (Figure 2j–l). The average source strength at the highest level of loss was higher under the PCS scenario (30.9) than under the refuge-loss and random scenarios (19.9 and 3.3, respectively; Figure 2j–l). At most levels of loss (including the highest level of loss), the PCS scenario had the highest average node degree, geometric mean network size and average source strength and the fewest networks, implying that it has the highest overall connectivity of the three scenarios at most loss levels.
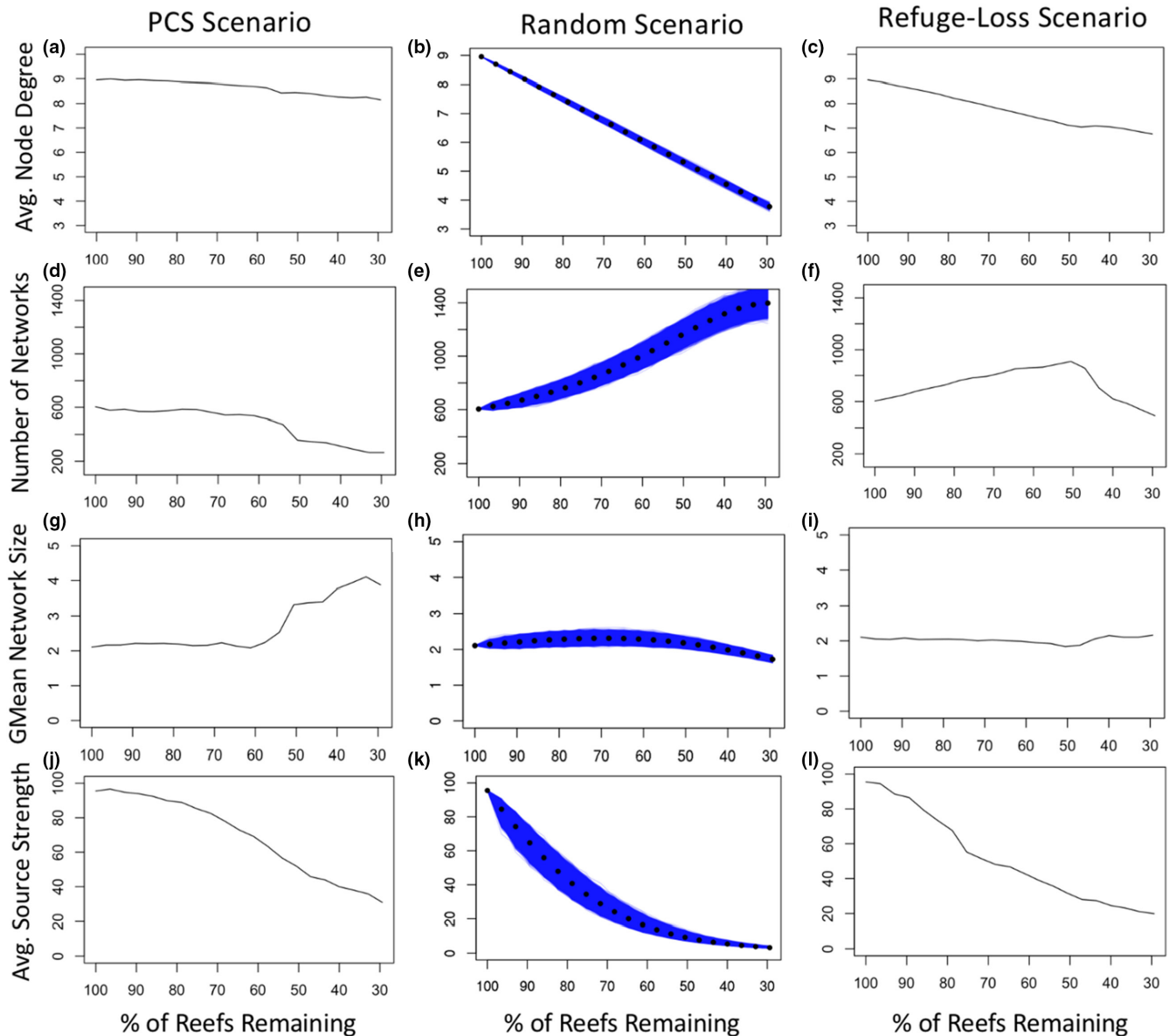
FIGURE 2 Changes in network metrics at different levels of loss. Each graph shows how a particular network metric [from top to bottom: average (Avg.) node degree, number of networks, geometric mean (GMean) network size and average source strength; see Supporting Information Supplementary Material 1a] changes as the level of loss increases according to each of the three scenarios. The line in the predicted climatic survival (PCS) scenario and refuge-loss scenario graphs shows how the network metric in question changes at different levels of loss under each scenario. Each blue line in the random scenario graphs represents the change in network metric for one of the 200,000 different random loss replicates (200,000 blue lines are drawn in each graph), and the black dots represent the mean value of the network metric across all 200,000 random loss replicates at that level of loss (i.e., at that percentage of reef remaining). Only the results from the reference connectivity matrix are shown here.

3.3 | Reseeding scenarios

Full reseeding of the present-day global coral reef habitat never occurred from the relict reef cells (i.e., the cells remaining at the highest level of loss) following each of the three scenarios (Figure 4). The relict reef cells under the random scenario were able to reseed the most reef cells (on average, but also independently), almost double that of the other scenarios. The number of reef cells reseeded under the PCS and refuge-loss scenarios was similar in comparison to the number reseeded under the random scenario (Figure 4d), but the

resultant reseeding under the PCS scenario was more geographically concentrated than that under the refuge-loss scenario (Figure 4a,c). The refuge-loss scenario reseeded most of the present-day global coral reef habitat, other than noticeable gaps around Rapa Nui (Easter Island), Indonesia, lower Persian Gulf, much of Eastern Africa and reef cells around India and Sri Lanka. The average connectivity (geometric mean network size, average node degree and average source strength) of the reseeded regions under the PCS scenario was higher than the average connectivity under the refuge-loss or random scenarios (Supporting Information Table S2), although the PCS scenario reseeded fewer reef

(a) Predicted Climatic Survival (PCS) Scenario
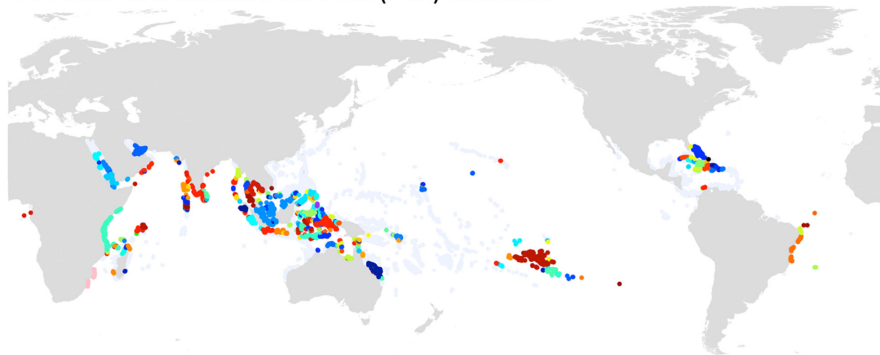
(b) Sample Random Scenario
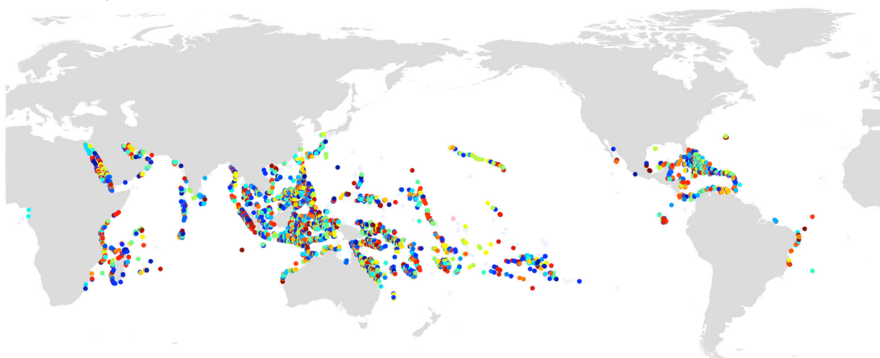
(c) Refuge-Loss Scenario
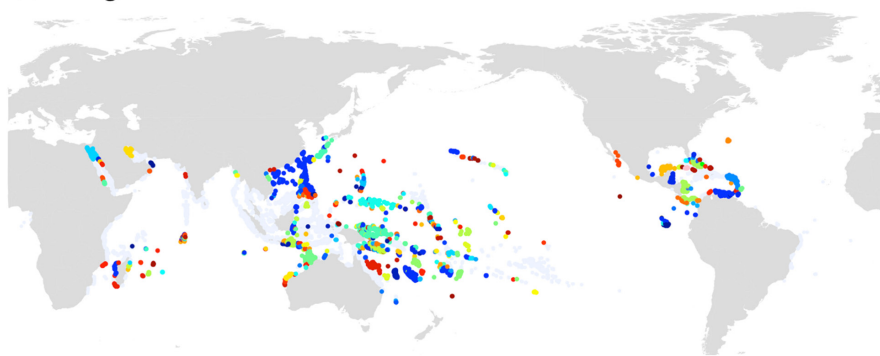
FIGURE 3 Distribution of networks at the highest level of loss. These maps show the relict reef cells (i.e., the reef cells that remain at the highest level of loss, shown in bright colours) under each different scenario and the reef cells that were lost (pale blue). Every relict reef cell of a particular network is coloured the same; lost reef cells are not coloured by network and are all coloured pale blue. Owing to the large number of networks represented on each map, care was taken not to have two colours repeat in the same area, but multiple distinct networks are represented using the same colour. Only one of the 200,000 resulting random global reef replicates at the highest level of loss under the random scenario is shown in panel (b). Only the results from the reference connectivity matrix are shown here.

cells (Figure 4d). The number of reef cells reseeded plateaued the fastest under the random scenario (median: nine generations; interquartile range: 8–10) and slowest under the PCS scenario (27 generations), and the refuge-loss scenario reseeded in 25 generations.

3.4 | Effect of mean dispersal distance threshold

The mean Euclidean dispersal distance used to screen the connectivity matrix affected the initial connectivity map, the loss scenarios and the reseeding potential of relict reef cells. At the largest dispersal distance tested (250 km), the global coral reef system comprised 15 networks: two large networks extending over most reef cells in the Indo-Pacific region and the Atlantic region, respectively, and accounting for 97.9% of reef cells, plus 13 smaller networks (Supporting Information Figure S1). Thus, like the initial networks of the reference connectivity matrix (Figure 1c), we saw a few large and many small

networks at higher mean dispersal distance thresholds (Supporting Information Figure S1b). As the mean dispersal distance threshold increased, the relict coral reef habitat (i.e., the coral reef habitat remaining at the highest level of loss) comprised fewer, larger networks (Supporting Information Figure S2a,b) made of more connected reef cells (higher average source strength and node degree; Supporting Information Figure S2c,d), as expected. As the mean dispersal distance threshold increased over 110 km, the average source strength of the relict reef cells under the random scenario became higher than that of the PCS scenario (Supporting Information Figure S2c), and the average node degree of the refuge-loss scenario became higher than that of the PCS scenario (Supporting Information Figure S2d). At all mean dispersal distance thresholds, the relict reef cells under the PCS scenario were in fewer, larger networks (Supporting Information Figure S2a,b). The percentage of reef cells reseeded in the three scenarios ranged from c. 40% at 30 km dispersal distance (PCS and refuge-loss scenarios) and >60% in the random scenario to c. 100% at >90 km

FIGURE 4 Results of reseeding. (a,c) These maps show the relict reef cells (i.e., the reef cells that remained after the highest level of loss) under the predicted climatic survival (PCS) scenario and the refuge-loss scenario, the reef cells that were able to be reseeded from the relict reefs ("reseeded reefs") and the reef cells that were never reseeded under that scenario ("not reseeded"). Each dot represents a reef cell. (b) This map shows the relict reef cells (i.e., the reef cells that remained following the highest level of loss) under a single random scenario replicate ("relict reefs"), the reef cells that were able to be reseeded from those relict reefs ("reseeded reefs") and the reef cells that were never reseeded under that scenario replicate ("not reseeded"). (d) This graph shows the percentage of initial reef cells (12,292 reef cells) that were reseeded in each of the three scenarios (PCS scenario, refuge-loss scenario and random scenario) after each time step during the reseeding process. The "random scenario" dotted line represents the mean number of reef cells reseeded at each time step, across all 200,000 random loss replicates (each starting from the relict reef cells of a different random loss replicate, shown in pink lines surrounding the dotted line). Only the results from the reference connectivity matrix are shown in this figure.

(a) Predicted Climatic Survival (PCS) Scenario
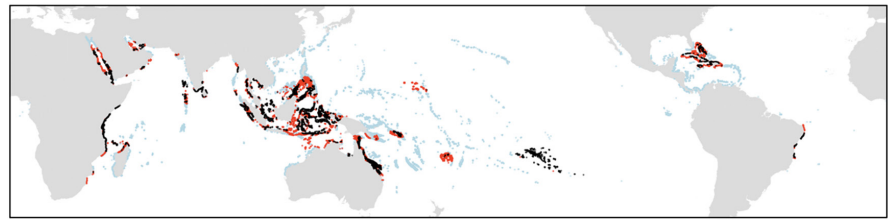
(b) Sample Random Scenario
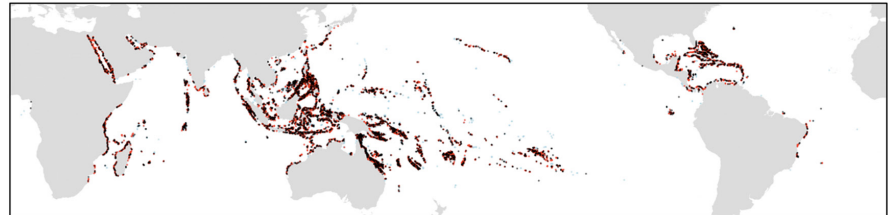
(c) Refuge-Loss Scenario
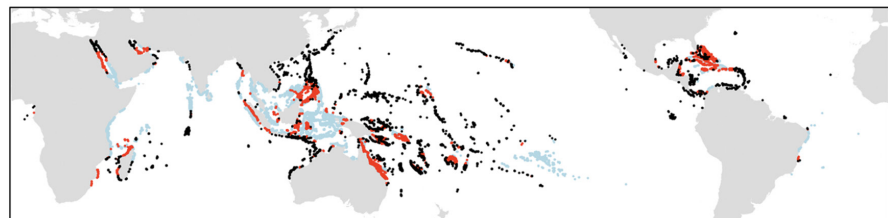
● Relict Reefs ● Reseeded Reefs ● Not Reseeded

(d) Percentage of Reefs Reseeded Over Time

Legend:
PCS Scenario
Refuge-Loss Scenario
Mean(Random Scenario)
Random Scenario
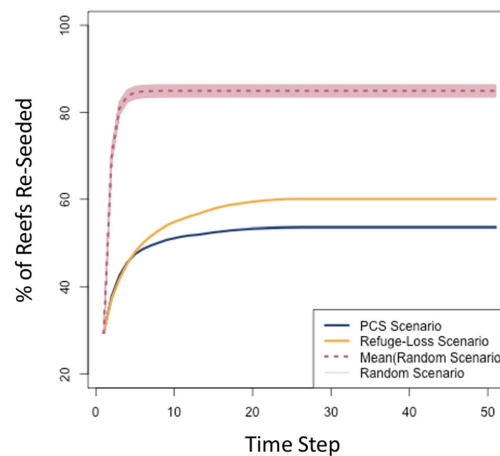
dispersal distances in the random scenario, *c.* 100% at >150 km dispersal distances in the refuge-loss scenario and approaching 100% at 250 km in the PCS scenario (Supporting Information Figure S3a). The ranking of the three scenarios did not change, with the refuge-loss scenario leading to a higher or equal number of reseeded reef cells than the PCS scenario at all mean dispersal distance thresholds tested (Supporting Information Figure S3a). Finally, larger mean dispersal distance thresholds allowed for reseeding of reef cells in less time in comparison to intermediate mean dispersal distance thresholds (Supporting Information Figure S3b).

4 | DISCUSSION

Our results from the reference connectivity matrix (i.e., mean dispersal distance threshold of 42 km) show that almost half of the world's reef cells are in one connectivity network, more than two-thirds are contained in 14 large networks, and the remaining one-third are in 590 smaller networks, illustrating the large disparities in world-wide reef cell connectivity. The observed networks are similar to those delineated by Cowen et al. (2006) (except no separation of the Panama–Colombia Gyre) and by Holstein et al. (2014)

(slightly more connected than that for the most fragmented species) in the Caribbean using biophysical models and preserve many of the similarities to empirical results of the connectivity matrix of Wood et al. (2014) (e.g., they reflect empirical findings reported by Ayre & Hughes, 2000; Kool et al., 2011). The three scenarios of loss and the various mean dispersal distance thresholds considered in the present study resulted in different patterns of future coral reef cell connectivity in the global coral reef system, emphasizing the importance of improving predictions of future coral cover loss and connectivity and adapting conservation plans accordingly. Furthermore, from the level of long-term degradation of global coral reef habitat anticipated by 2100 (Frieler et al., 2013; van Hooidonk et al., 2016), even under an optimistic reseeding paradigm, not all global coral reef habitat can be reseeded naturally, unless a very high mean dispersal distance threshold is assumed. Although future realized coral reef habitat loss will probably not follow any of these three scenarios precisely, these scenarios are intended to provide a general overview of possible global patterns of loss.

4.1 | Reef loss scenarios affect connectivity of relict reefs

Under the PCS scenario at the highest level of loss, most of the initial coral reef cell networks still exist (albeit, smaller), and the resulting connectivity is high, whereas under the other two scenarios, most of the initial coral reef cell networks are fragmented, and the overall connectivity is much lower at the highest level of loss (i.e., when only the relict reef cells remain). Thus, if the highest level of reef loss follows the random scenario or the refuge-loss scenario, conservation initiatives will need to account for altered patterns of connectivity. This underscores the importance of monitoring the spatial patterns of global bleaching events to inform predictions of how connectivity might change owing to coral reef habitat loss. Our finding that the PCS scenario (the scenario most informed by existing climate data) results in limited change to initial coral reef cell connectivity is encouraging, because it indicates that relatively large networks can be maintained (i.e., connectivity can remain high) despite the loss of coral reef habitat. However, we should not rely on the PCS scenario (or one similar to it) proving accurate, because we must acknowledge the inherent uncertainty in predicting future climatic conditions (Jones, 2000) and, by extension, climate refugia (Beyer et al., 2018). Our work emphasizes the importance of improving our understanding of how reefs are connected to each other and how those connections will change as coral reef habitat is lost, in order to inform expectations of post-bleaching recovery.

4.2 | Reseeding potential of the relict reefs

Under the PCS scenario, the relict global coral reef system had the highest geometric mean network size, node degree and source strength (Figures 2 and 3) but reseeded the lowest percentage of reef cells (54% of present-day reef cells; Figure 4) relative to the other two scenarios. The relict global coral reef system under the refuge-loss scenario and the random scenario had lower connectivity but were able to reseed more reef cells than the PCS scenario (Figure 4). This discrepancy arises because, in comparison to the other two scenarios, the relict reef cells under the PCS scenario are more likely to be in the same networks as each other, hence this higher source strength simply allows them to be better at reseeding each other. The above results assume a mean dispersal distance threshold of <110 km, above which the average source strength and average node degree of the relict reefs are not the highest under the PCS scenario (Supporting Information Figure S2); however, the PCS scenario is still the worst at reseeding at all mean dispersal distance thresholds (Supporting Information Figure S3a). Taking this network perspective thus illustrates the dangers of preserving only reefs in predicted climate refugia (Beyer et al., 2018), when many of said reefs happen to be in the same networks as each other. Reef prioritization should incorporate network membership and reseeding redundancy, in order that reefs that reseed many of the same reefs as other prioritized reefs are ranked lower than those that are able to reseed different reefs. The method used here to evaluate the reseeding potential of different scenarios could be applied to each reef (exploring a variety of thresholded connectivity matrices and considering various scenarios of reef degradation) as a metric of reseeding potential for use in reef prioritization decisions.

Although the random scenario resulted in the most reseeding from the relict reefs (Figure 4d; Supporting Information Figure S3a), this does not mean that reef prioritization schemes should ignore predicted climate refugia (such as those proposed by Beyer et al., 2018) and should instead choose reefs at random, because the reefs in the predicted climate refugia have the best chance of survival. The random scenario is the best at reseeding because the relict reef cells stemming from it belong to a larger number of networks than the relict reef cells from the other scenarios (and reseeding is possible only among reefs belonging to the same network), but this ignores the increased susceptibility of the average reef to climatic influences in comparison to reefs in predicted climate refugia (Beyer et al., 2018). Reefs outside of the predicted climate refugia (Beyer et al., 2018) are more likely to bleach and degrade and will thus be more challenging to conserve and are less likely to send out sufficient numbers of coral larvae. Instead, these results indicate the benefit of preserving the prioritized BCU reef cells (Beyer et al., 2018) in addition to selecting some other good source reefs (i.e., those with high source strength under the initial configuration; Figure 1b) to preserve reefs in the networks unreachable by larvae from the prioritized reef BCUs (Beyer et al., 2018) or the relict reef cells under the PCS scenario. Alternatively, "stepping stone" reefs could be created (Lee et al., 2018; Saura et al., 2014) to connect the networks without prioritized BCU reef cells or PCS scenario relict reef cells to the networks with said reef cells.

When the time to reseed is also considered, it becomes clear that natural reseeding is not likely to be a viable recovery method for coral reefs world-wide, because the recovery time is long in comparison to

the disturbance frequency of bleaching events. Under all three scenarios, in the reference connectivity matrix and at other mean dispersal distance thresholds, it takes several generations to reseed all reachable reef cells (Figure 4d; Supporting Information Figure S3b). Under the reference connectivity matrix, no set of relict reef cells under any of the three scenarios was able to reseed all present-day reef cells. The highest level of loss considered (29% of present-day reef cells remaining) is similar to the level of long-term degradation predicted by 2100 (Frieler et al., 2013; van Hooidonk et al., 2016) and the reef surface area assigned to prioritized reef BCUs by Beyer et al. (2018); therefore, this result cautions that natural reseeding from only 29% remaining reef cover is not likely to be a viable conservation strategy to preserve all reefs world-wide (considering the breadth of possibilities encompassed by the three scenarios). Also, the time between bleaching events on many reefs is now thought to be shorter than the shortest coral maturation time (10- to 15-year maturation time; Hughes, Anderson, et al., 2018), further limiting the potential success of natural reseeding. For higher mean dispersal distance thresholds [mean dispersal distance thresholds >90 km (random scenario) or >150 km (refuge-loss scenarios); Supporting Information Figure S3a], full reseeding is possible, but it still takes more than five generations at minimum. If each coral generation is ≥10–15 years, this implies that full reseeding will take many decades and might be possible only for coral species with longer than expected dispersal distances, and this is under an optimistic reseeding paradigm. Explicit coral growth time-scales and bleaching event frequencies should be incorporated into reseeding models to assess fully the extent to which natural coral reseeding is a practical rescue method for reefs around the world.

4.3 | Assessing the mean dispersal distance threshold

The connectivity of coral reefs in the global coral reef system is still surrounded by much uncertainty, but it is likely that the reference connectivity matrix (obtained with a mean dispersal distance of 42 km; Manel et al., 2019) is more representative of the dispersal potential of coral larvae than the higher mean dispersal distance thresholds assessed through our sensitivity test. Not much is known about realized dispersal distances of coral larvae; there are many laboratory-based studies that have measured coral pelagic larval duration and concluded that they have the potential to disperse very far because of large pelagic larval durations (e.g., 195–244 days, Graham et al., 2008; 103 days, Richmond, 1987), whereas others argue that small-scale ocean features, active larval behaviour (e.g., larval orientation, vertical migration) and settlement competency times that are far below pelagic larval duration estimates might lead to much smaller realized dispersal distances (Figueiredo et al., 2013; Sammarco & Andrews, 1988). However, from (1) the synthesis by Manel et al. (2019) of empirical studies of marine dispersal in general; (2) the findings of short (<90 km) dispersal distances from the few empirical studies of coral larval dispersal that have been performed

(Carlon & Olson, 1993; Gilmour et al., 2009; Hughes et al., 2019; Sammarco & Andrews, 1988); (3) the finding that coral reef fish larval dispersal distances tend to be in the range of tens of kilometres (Green et al., 2015); and (4) the fact that all larval dispersal distances are likely to shorten owing to climate change (O'Connor et al., 2007; Figueiredo et al., 2014; also see Hughes et al., 2019 for a realized example), it is likely that the results from the reference connectivity matrix might be more representative of the dispersal potential of coral larvae than the results from higher mean dispersal distance threshold connectivity matrices. If this is indeed the case, we should not expect full reseeding to occur from the expected long-term degradation predicted (Frieler et al., 2013; van Hooidonk et al., 2016), but coral species with longer dispersal distances might be expected to reseed higher proportions of their initial distributions. Future work is needed to determine dispersal distances of different coral species empirically to find out whether full reseeding of coral reefs will be possible from the long-term degradation predicted by 2100 (Frieler et al., 2013; van Hooidonk et al., 2016) and to gain a better understanding of the global coral reef system and how loss of coral reefs will impact coral reef connectivity.

4.4 | Caveats of global modelling and simulations

As with all simulation studies performed for the global coral reef system, there are many aspects of the present study that could be improved upon if more data were available. The coarse spatial resolution of the global grid, resulting from the coarse resolution of the connectivity matrix of Wood et al. (2014), limits our ability to interpret the results at finer spatial scales, because one reef cell could contain one or many distinct reefs. Using a grid with finer spatial resolution would probably not change connectivity and reseeding patterns at large scales much, but would allow for more specific, actionable interpretations of our results at small scales and would enable us to look at more realistic patterns of bleaching stress (instead of being limited by a grid cell size that is larger than *c.* 80% of temperature anomalies; Selig et al., 2010). In particular, if a global coral connectivity matrix with finer spatial resolution were developed, it would be worth exploring explicit temperature anomaly scenarios (varying size, magnitude, spatial aggregation, etc.).

Another caveat is that climate change is likely to change ocean current patterns (Hoegh-Guldberg & Bruno, 2010) and shorten the pelagic larval duration of many species (Figueiredo et al., 2014; O'Connor et al., 2007). It is unclear exactly how ocean current patterns will change (Hoegh-Guldberg & Bruno, 2010), only that they are predicted to do so and that the changes are likely to be region specific (Andrello et al., 2015; Coleman et al., 2017); therefore, it is hard to model how these changes will affect coral reef connectivity in general and the patterns that we observe here. Shortening the pelagic larval duration of species (Figueiredo et al., 2014; O'Connor et al., 2007) will likely reduce the average connectivity of coral reefs and might shrink the average network size (e.g., Andrello et al., 2015) and limit reseeding potential in the global coral reef system even

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BIOSKETCH

Ariel Greiner is a theoretical ecologist and conservation scientist interested in determining the best conservation strategies for conserving the ecosystems of the world. The main focus of the research team involved in this study is determining how best to incorporate coral reef dynamics and connectivity into spatial optimization models intended for conservation planning of networks of coral reefs.

SUPPORTING INFORMATION

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