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RESEARCH ARTICLE

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A framework for identifying and characterising coral reef "oases" against a backdrop of degradation

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Abstract

1. Human activities have led to widespread ecological decline; however, the severity of degradation is spatially heterogeneous due to some locations resisting, escaping, or rebounding from disturbances.
2. We developed a framework for identifying oases within coral reef regions using long-term monitoring data. We calculated standardised estimates of coral cover (z-scores) to distinguish sites that deviated positively from regional means. We also used the coefficient of variation (CV) of coral cover to quantify how oases varied temporally, and to distinguish among types of oases. We estimated "coral calcification capacity" (CCC), a measure of the coral community's ability to produce calcium carbonate structures and tested for an association between this metric and z-scores of coral cover.
3. We illustrated our z-score approach within a modelling framework by extracting z-scores and CVs from simulated data based on four generalized trajectories of coral cover. We then applied the approach to time-series data from long-term reef monitoring programmes in four focal regions in the Pacific (the main Hawaiian Islands and Mo'orea, French Polynesia) and western Atlantic (the Florida Keys and St. John, US Virgin Islands). Among the 123 sites analysed, 38 had positive z-scores for median coral cover and were categorised as oases.
4. *Synthesis and applications*. Our framework provides ecosystem managers with a valuable tool for conservation by identifying "oases" within degraded areas. By

evaluating trajectories of change in state (e.g., coral cover) among oases, our approach may help in identifying the mechanisms responsible for spatial variability in ecosystem condition. Increased mechanistic understanding can guide whether management of a particular location should emphasise protection, mitigation or restoration. Analysis of the empirical data suggest that the majority of our coral reef oases originated by either escaping or resisting disturbances, although some sites showed a high capacity for recovery, while others were candidates for restoration. Finally, our measure of reef condition (i.e., median *z*-scores of coral cover) correlated positively with coral calcification capacity suggesting that our approach identified oases that are also exceptional for one critical component of ecological function.

KEYWORDS

climate change, coral reef, decline, disturbance, oases, recovery, resilience, spatial variability

1 | INTRODUCTION

Human activities are impacting ecosystems by modifying environmental conditions and natural disturbance regimes over multiple spatial scales (Haberl et al., 2007; Halpern et al., 2008). As a result, ecosystems have experienced declines in species abundances, changes in diversity and compromised ecological function (Doney et al., 2012; Hansen, Stehman, & Potapov, 2010). Marine ecosystems are no exception. For example, coral cover has declined at three quarters of the reefs monitored in the Caribbean (Jackson, Donovan, Cramer, & Lam, 2014), and an estimated one-third of global mangrove and seagrass habitat has been lost (Richards & Friess, 2016; Waycott et al., 2009). Nonetheless, the severity of ecosystem degradation is not spatially homogeneous, and it is common to find locations that remain in, or return to, relatively good condition, despite ongoing disturbances (Davis, Pavlova, Thompson, & Sunnucks, 2013; Turner & Corlett, 1996). Identifying cases in which individuals or communities perform better than their neighbours, despite being at equal risk, is common in public health and medical fields (e.g., Hilborn, 2007; Sternin, Sternin, & Marsh, 1997). Similar approaches have become popular in ecology as they may identify areas that can be prioritised for conservation, and can provide insights into ecosystem characteristics that confer resilience (Cinner et al., 2016; O'Leary et al., 2017).

Most tropical coral reefs are increasingly under threat from local- (e.g., overfishing, coastal development) or global-scale (e.g., climate change) disturbances (Hughes et al., 2017). In many cases, impacts are reported as changes in average coral cover summarised across multiple sites, time periods, and spatial scales (i.e., 100s–1,000s km^2; e.g., De'ath, Fabricius, Sweatman, & Puotinen, 2012; Jackson et al., 2014). Although most regions with coral reefs have recently experienced declines in coral cover (Hughes et al., 2017), many regional-scale studies reveal individual sites that have not declined in coral cover, or those where cover has recovered rapidly (e.g., Gilmour, Smith, Heyward, Baird, & Pratchett, 2013; Graham, Jennings, MacNeil, Mouillot, & Wilson, 2015; Guest et al., 2016; Idjadi et al., 2006; Roff et al., 2014). Reefs that avoid the declines in coral cover experienced by their neighbours have been referred to as "oases" (Lirman et al., 2011) and may represent areas of considerable conservation interest.

The total cover of living corals is the most widely used metric of coral-reef condition, and long-term descriptions of this state variable are available from numerous locations worldwide (e.g., Adam, Burkepile, Ruttenberg, & Paddack, 2015; De'ath et al., 2012; Rodgers, Jokiel, Brown, Hau, & Sparks, 2015; Ruzicka et al., 2013). Large decreases in coral cover lead to decreased habitat complexity and calcium carbonate production and consequently a reef's functional ability to provide habitat and shoreline protection (Perry et al., 2015). As coral cover is a dynamic state variable that can fluctuate considerably over time (e.g., Adam et al., 2015; Gilmour et al., 2013), methods to identify ecologically meaningful spatial variation in reef condition and function are likely to be improved by incorporating a measure of temporal variability.

Here, we develop a methodological framework for identifying ecosystem oases, using coral reefs as an example, based on spatio-temporal variability in coral cover. We use the term "oasis" to describe reef sites that stand out due to their ability to escape, resist, or rebound from disturbances. First we illustrate this method using simulated data parameterised to represent four trajectories representing common patterns of temporal change in coral cover observed over the last three decades (e.g., Adam et al., 2015; De'ath et al., 2012; Guest et al., 2016; Idjadi et al., 2006; Jackson et al., 2014; Ruzicka et al., 2013). We then explore the utility of our method by identifying potential oasis sites using the percentage cover of live coral measured at 123 reef sites from four focal regions over decadal time scales. We test the hypothesis that reef oases (as defined above) have functional significance for the production and maintenance of reef structure by evaluating the relationship between standardised coral cover and coral calcification capacity (CCC). Finally, we evaluate the trajectories of change exhibited by oases and speculate about the mechanisms underpinning their ability to persist, while neighbouring sites become degraded. Our goal is to provide a framework that will assist ecosystem managers and conservation biologists to identify the most (and least) promising sites within ecosystems where long-term data are available.

2 | MATERIALS AND METHODS

2.1 | Defining, quantifying and identifying oases

We conceptualised an oasis as a site that has exhibited consistently higher coral cover relative to sites within a defined focal region. A site is defined here as a fixed location at 10–100 m^2 scale within a reef habitat, depth range, or area of shoreline that has been surveyed over at least a decade. "Consistently" (as defined here), refers to the proportion of occasions over which coral cover at each site remained above its regional mean value, with region referring to adjacent reefs on a scale of 10–100s of km. To examine variation in coral cover among sites and identify oases within focal regions, coral cover was standardized on a z-score scale relative to the mean coral cover of all sites surveyed within a given year within focal regions. Z-scores are used in a variety of biological applications to identify how far, and in what direction (positive vs. negative), a measured value deviates from the population mean, and they are expressed in units of standard deviation (*SD*) (Wang & Chen, 2012). Z-scores for a population have a mean of zero and a *SD* of one and are dimensionless, being obtained by dividing the difference between individual value (x) and the population mean (μ), by the population *SD* (σ):

$$z_{ijt} = \frac{(x_{ijt} - \mu_{jt})}{\sigma_{jt}}$$

where x_{ijt} = mean coral cover of site i in region j at year t, μ_{jt} = mean coral cover in region j at year t averaged across sites in that focal region and σ_{jt} = the *SD* of coral cover in region j at year t, taken across sites in that region. Note that the calculation of z-scores does not require any assumption about the shape of the underlying distribution of coral cover.

Z-scores were first calculated for each year at each site, relative to all sites in the region in that same year. The median z-score for each site was then calculated across all years. Median z-score, rather than mean z-score, was used to measure a site's performance, because medians are less sensitive to anomalous years in which large changes in coral cover occur. Using this approach, a site can only obtain a high median z-score by having consistently high coral cover, relative to other sites in the same region.

We used the coefficient of variation (CV) of coral cover to quantify temporal variation in coral cover within each site and across years:

$$\text{CV} = (\sigma / \mu) \times 100$$

where σ is the *SD* for coral cover for each site across years and μ is the mean coral cover for each site across years. A measure of temporal variability was included because a variety of coral cover trajectories (e.g., decline followed by recovery, phase shift with no recovery, etc.) can potentially produce positive z-scores. Examining CV as well as z-scores, therefore, provides a method to distinguish between sites that exhibit relatively stable coral cover over time from sites that oscillate or undergo shifts between high and low coral cover.

2.2 | Numerical simulations of coral-cover dynamics

Simulations were carried out to evaluate a wide range of empirical possibilities and to capture the behaviour of coral-cover dynamics based on four predetermined model scenarios. These were considered as representative of trajectories observed from long-term monitoring of reefs and included: (a) linear trends (i.e., where coral cover declines or increases linearly over time; e.g., De'ath et al., 2012; Jackson et al., 2014); (b) nonlinear oscillations (i.e., where coral cover undergoes cycles of decline followed by recovery; e.g., Gilmour et al., 2013; Idjadi et al., 2006); (c) phase shifts (i.e., where coral cover declines suddenly and remains low; e.g., Hughes et al., 2017); and (d) long-term stability (i.e., where coral cover varies from year to year, but does not increase or decrease significantly over time; Rodgers et al., 2015; Ruzicka et al., 2013).

For each scenario, we generated 30 random values for coral cover for a 30-year time series. The model parameters were chosen to return values of coral cover between 0% and 65% with a normal distribution and range that are representative of contemporary coral cover data from the Caribbean and Indo-West Pacific (e.g., De'ath et al., 2012; Gilmour et al., 2013; Guest et al., 2016; Idjadi et al., 2006; Jackson et al., 2014; Rodgers et al., 2015). A normal distribution can generate values that are outside the domain of the response variable (i.e., coral cover values between 0% and 100%), therefore, when coral cover simulations returned negative values, they were replaced with zero (coral cover values never exceeded 100% in our simulations). Detailed descriptions of the simulation steps, along with the parameter values and statistical distributions used to initialize the random number generation, are provided in the Supporting Information Appendix S1. After simulating 100 time series for each scenario, we calculated the median z-score and temporal variability (CV) of coral cover for each simulation and examined the results graphically (Figure 1). Photographic examples in Figure 1a illustrate and compare a typical degraded site (left photo) with an oasis site (right photo). Each simulation in Figure 1b is analogous to a "site" (as defined above) in a single, larger focal region. In Figure 1b, each point represents the median z-score (x-axis) and CV (y-axis) for a single simulated time series. Colours identify the four trajectories of change that were used to define the simulations. To aid comparison between a single point in Figure 1b to its corresponding time series in Figure 1c, the plot is divided into cells representing eight possibilities (1–8) for reef condition (median z-score of coral cover; x-axis) and temporal stability (CV; y-axis). Cells 1–4 represent the most temporally variable simulated sites (CV ≥50%), and cells 5–8 represent

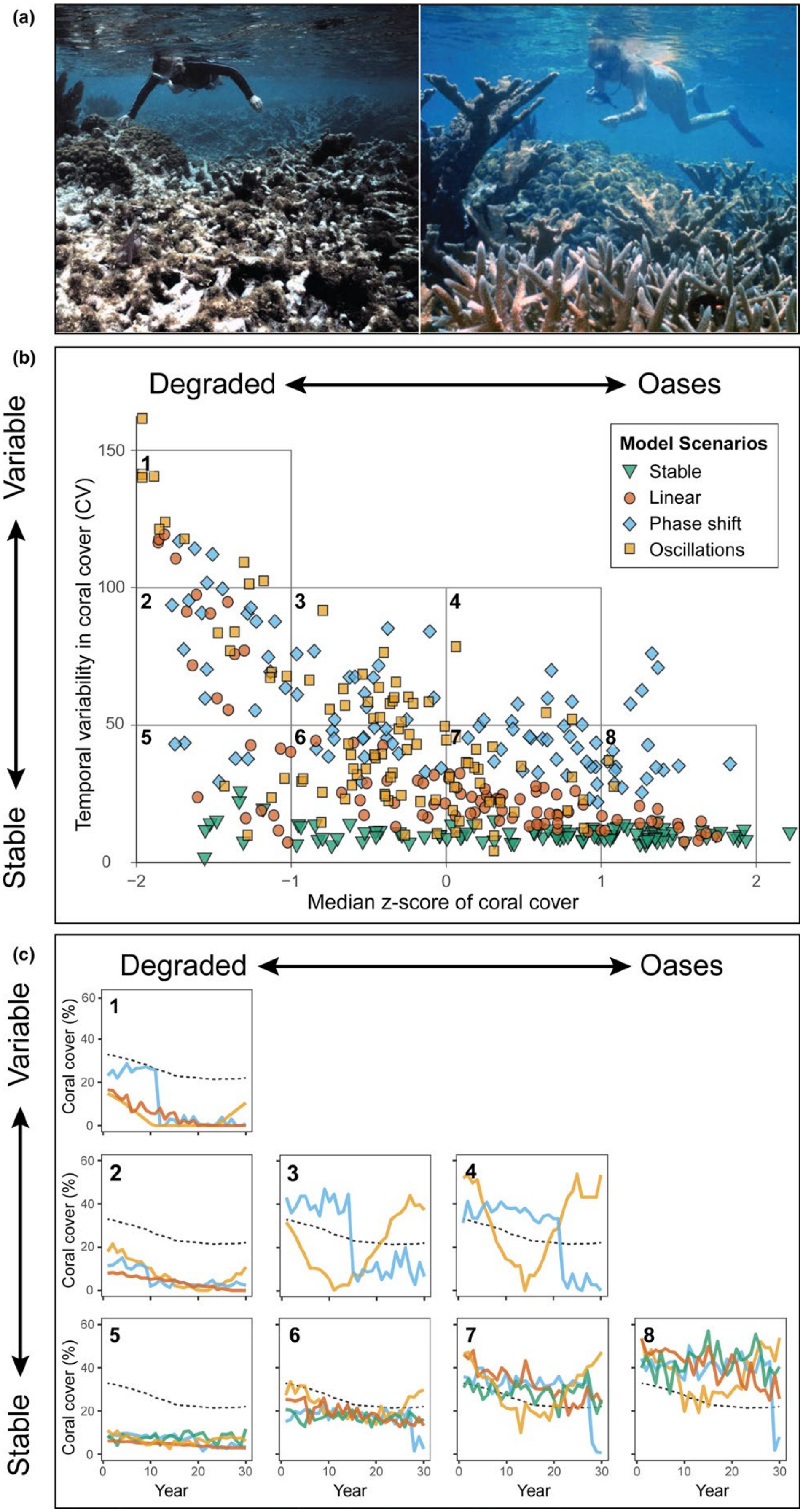
(a)
(b)
Degraded
Oases
Variable
Stable
Model Scenarios
Stable
Linear
Phase shift
Oscillations
Temporal variability in coral cover (CV)
Median z-score of coral cover
1
2
3
4
5
6
7
8
0
50
100
150
−2
−1
0
1
2
(c)
Degraded
Oases
Variable
Stable
Coral cover (%)
Year
0
10
20
30
40
60

FIGURE 1 Results of simulations showing outcomes for model scenarios of long-term change in percent coral cover. (a) Two photographs from E.A. Shinn's photographic time series at Grecian Rocks reef in the Florida Keys (USGS Data Release: https:/ doi.org/10.5066/F7S46QWR), illustrating degraded and oasis reefs identified in (b) and (c). In (b), each point represents the median *z*-score (*x*-axis) and coefficient of variation (*y*-axis) for a single simulated time-series, with colours representing four scenarios of differing changes in coral cover corresponding to linear changes, oscillating changes, phase shifts from high- to low- cover, and stable cover (colours with same coding in b and c). The plot is divided arbitrarily into cells representing eight possibilities (1–8) for reef condition along a spectrum from degraded to oasis status that incorporates relative standardised coral cover (*z*-score) and temporal stability. The plot contains 100 simulations for each scenario. Time series plots and frequency distributions of *z*-scores of all simulations are in Supporting Information Figures S1 and S2 in Appendix S1. In (c), coral cover from a single haphazardly selected simulation from each scenario is plotted against time within each of the eight cells shown in (b). The dashed line in each plot is the overall mean coral cover for all simulated sites across time. See methods and Supporting Information Appendix S1 for a detailed description of how this figure was derived

the least temporally variable simulated sites (CV ≤51%). In Figure 1c, coral cover from a single haphazardly selected simulation from each scenario is plotted against time within each of the eight cells shown in Figure 1b. The objective of this plot is to show the trajectories of coral cover that could produce the distribution of scores in Figure 1b.

2.3 | Examination of empirical coral-cover data from four focal regions

To apply our approach to empirical data, we used public domain, long-term coral cover data from four focal regions in the Pacific (main Hawaiian Islands and Mo'orea, French Polynesia) and western Atlantic (Florida Keys and St. John, US Virgin Islands) representing spatial scales ranging from ~80 to 17,000 km^2 (Supporting Information Table S1, Guest et al., 2018). We chose focal regions with different disturbance regimes because they provided a wide range of benthic change trajectories upon which to test our framework. Surveys were carried out at fixed sites between 1992 and 2015. Survey durations differed among focal regions and ranged from 11 years at Mo'orea to 24 years at St. John. Multiple fixed sites (defined here as distinct areas of reef surveyed within a defined reef habitat, depth range, or area of shoreline) were surveyed repeatedly (annually or every few years) in each focal region. To capture a variety of disturbance events (e.g., El Niño events, major storms, etc.), only sites with surveys extending over a decade or more and with at least three surveys during that period were used. Each focal region has experienced disturbances including overfishing, disease outbreaks, thermal stress, pollution, invasive species, predator outbreaks and major storms (Adam et al., 2015; Edmunds, 2002; Jokiel & Brown, 2004; Ruzicka et al., 2013; see Supporting Information Appendix S2 for detailed description of disturbance histories for each focal region).

For each site, mean coral cover was calculated across all surveyed transects, quadrats or stations (dependent on the sampling design for each project) within each year. The locations of fixed quadrats, transects or stations within sites were randomly or haphazardly selected, except for two sites in St. John (Tektite 1 and Yawzi 1) which were selected based on their high coral cover in 1987. (See Supporting Information Appendix S3 for descriptions of benthic survey methods for each focal location).

Thresholds for determining whether a median *z*-score is significantly greater than zero will depend on the particular spatial and temporal distribution of coral cover within the focal region, therefore, median *z*-scores suggest how unusual the coral cover is at a given site relative to the other sites within the same focal region. We identified all sites with positive median *z*-scores (and thus above-average coral cover in more than half of the sampled years) as potential oases. As an additional filter, if a site had been surveyed only three times within the monitoring period and if that site had declined in coral cover by the end of the study, it was not counted as an oasis, even if the overall median *z*-score was positive.

2.4 | Examination of the relationship between *z*-scores for coral cover and CCC

We calculated a scalar estimate of CCC for 121 of the study sites (two sites from St. John were omitted because data on coral community structure were not available) to evaluate whether this metric of ecological function associated with median *z*-scores of coral cover. To calculate CCC for each site, calcification rates of reef scleractinian and hydrozoan (*Millepora*) taxa were estimated as the product of published skeletal linear-extension rates, coral densities, and a growth form adjustment factor (sensu Morgan & Kench, 2012). The growth form adjustment factor accounts for the empty space created by branching, digitate or columnar morphologies versus massive or encrusting morphologies (Morgan & Kench, 2012; Supporting Information Table S2–S4). Direct measures of the three-dimensional surface area (i.e., rugosity) were not available for the sites used in the present study, therefore coral calcification rates were multiplied by the planar percentage cover for each coral taxon and for each year of study following Perry et al. (2012). As a result, the CCC approach used here assumes the reef is a flat, planar surface, and thus, will underestimate actual calcification capacity. We examined the relationship between median *z*-scores for coral cover (independent variable) and median CCC (kg $CaCO_3$ m^{-2} y^{-1}; dependent variable) within each region using Model I linear regressions after testing that residuals in the linear model were normally distributed.

3 | RESULTS

3.1 | Numerical simulations of coral-cover dynamics

The scatter plot of median *z*-score (*x*-axis) and CV (*y*-axis) of coral cover for the 400 simulated sites (Figure 1b), showed that the stable coral-cover scenario only occurred in the lower row of the plot (cells 5–8) where CV scores were <50%. Simulated sites with oscillating or

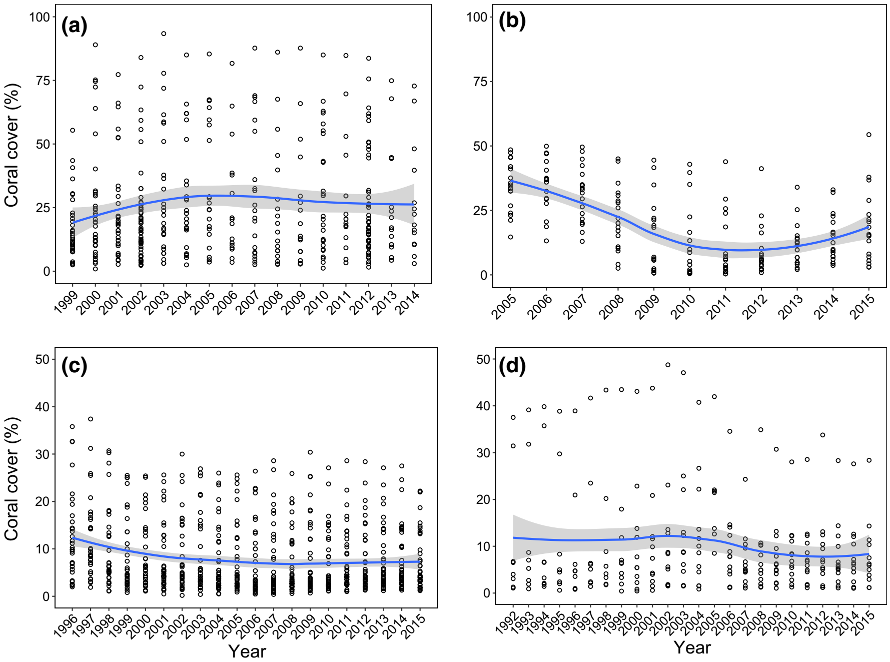

FIGURE 2 Long-term changes in coral cover, and within region-among site variation, in: (a) the main Hawaiian Islands (n = 52 sites, 16 years), (b) Mo'orea (n = 18 sites, 11 years), (c) the Florida Keys (n = 40 sites, 20 years), and (d) St. John, U.S. Virgin Islands (n = 13 sites, 24 years). Points represent average coral cover of replicate sites surveyed in each year within each focal region. The fitted lines (LOESS curve) show the smoothed change in coral cover for the region, while the points show empirical data by site and year, averaged across replicates used in the original studies (e.g., quadrats, transects, etc.). Note different scales on y-axis and timeline on the x-axis [Colour figure can be viewed at wileyonlinelibrary.com]

phase-shifted coral cover also occurred in the cells representing low temporal variability (i.e., cells 5–8) when the oscillations were less extreme or when a phase shift from high to low coral cover occurred later in the simulation period (e.g., see Figure 1b, cells 7 and 8). With the input parameters of our simulation, we observed no points within the upper right quadrant of our plot, indicating that it was not possible for a site to be both highly variable and to maintain a high z-score. Simulated oases (i.e., sites with positive median z-scores for coral cover) were found in cells 4, 7 and 8 (Figure 1b,c), but the majority had low CVs (<50%; Figure 1b,c, cells 7 and 8). However, there were some oases that had high CVs (>50%) indicative of oscillating and phase-shifted scenarios (Figure 1b,c, cell 4).

3.2 | Examination of coral-cover data from four focal regions

Mean coral cover (averaged across sites and within years, ±*SE*) increased from 17.2 ± 2.1% in 1999 to 27.2 ± 5.8% in 2014 in the main Hawaiian Islands, but it declined from 12.6 ± 1.6% in 1996 to 6.8 ± 0.9% in 2015 in the Florida Keys, from 11.5 ± 5.1% in 1992 to 8.0 ± 2.0% in 2015 in St. John, and from 34.5 ± 2.3% in 2005 to 18.5 ± 3.3% in 2015 in Mo'orea (Figure 2, Supporting Information Appendix S4). Within each focal region, mean annual coral cover (±*SD*), varied among sites (Figure 2) and ranged from 2.6 ± 1.0% to 84.0 ± 5.4% in the main seven Hawaiian Islands, from 8.7 ± 6.1% to 40.7 ± 4.9% in Mo'orea, from 1.0 ± 0.5% to 26.5 ± 2.7% in the Florida Keys and from 1.4 ± 0.6% to 37.0 ± 6.9% in St. John. Median z-scores of coral cover ranged from −1.08 to +2.42 for the main Hawaiian Islands, −0.82 to +1.87 for Mo'orea, −0.96 to +2.50 for the Florida Keys and from −0.81 to +2.63 for St. John (Figures 3 and 4).

Among our 123 study sites, 38 (31%) were identified as oases based on positive median z-scores of coral cover (ranging from +0.02 to +2.63; Figures 3 and 4). Oases had coral cover ranging from ~11% to ~84% (Supporting Information Table S1, Figures S3–S10 in Appendix S4). In general, the empirically defined oases exhibited patterns of temporal change in coral cover consistent with the simulations. For example, three of the four focal regions (the main Hawaiian Islands, the Florida Keys and St. John) had a high proportion (≥80%) of oases with low temporal variability (CV ≤50%), with Mo'orea being the exception where the majority of oases (63%) had high temporal variability (CV ≥50%; Figure 4a). The oasis sites with low CV were typical of the stable and linear-change scenarios described by the simulations. Examples of stable oasis sites from the empirical data include Molokini 13 in Maui, West Washer Women in the Florida Keys, and Tektite 1 in St. John (Figure 4b). Overall, only 13% of oases had high temporal variability (i.e., CV scores ≥50%) with mean coral cover values at these sites ranging from ~15% to 31% (Supporting Information Table S1, Figures S3–S10 in Appendix S4). These sites were characterised by periods of time with coral cover both above and below the average for the region. In some cases, temporally variable oases underwent declines followed by a marked recovery, for example, site LTER1 Outer 10 in Mo'orea and Moku o Lo'e 2 in O'ahu, thereby exhibiting the oscillating scenario in the simulations (Figure 4b; Supporting Information Figures S6 and S7 in Appendix S4). In other cases, oasis sites had relatively high coral cover for long periods of time followed by rapid decline without recovery, for example, Admiral Reef in the Florida Keys (Figure 4b; Supporting Information Figures S4 and S5 in Appendix S4), similar to the phase-shift scenario in the simulations.

3.3 | Examination of the relationship between coral-cover z-scores and CCC

Median CCC (pooled across years) ranged among sites from ~0.2 to ~22.8 kg $CaCO_3\ m^{-2}\ y^{-1}$ for the main Hawaiian Islands, ~0.4

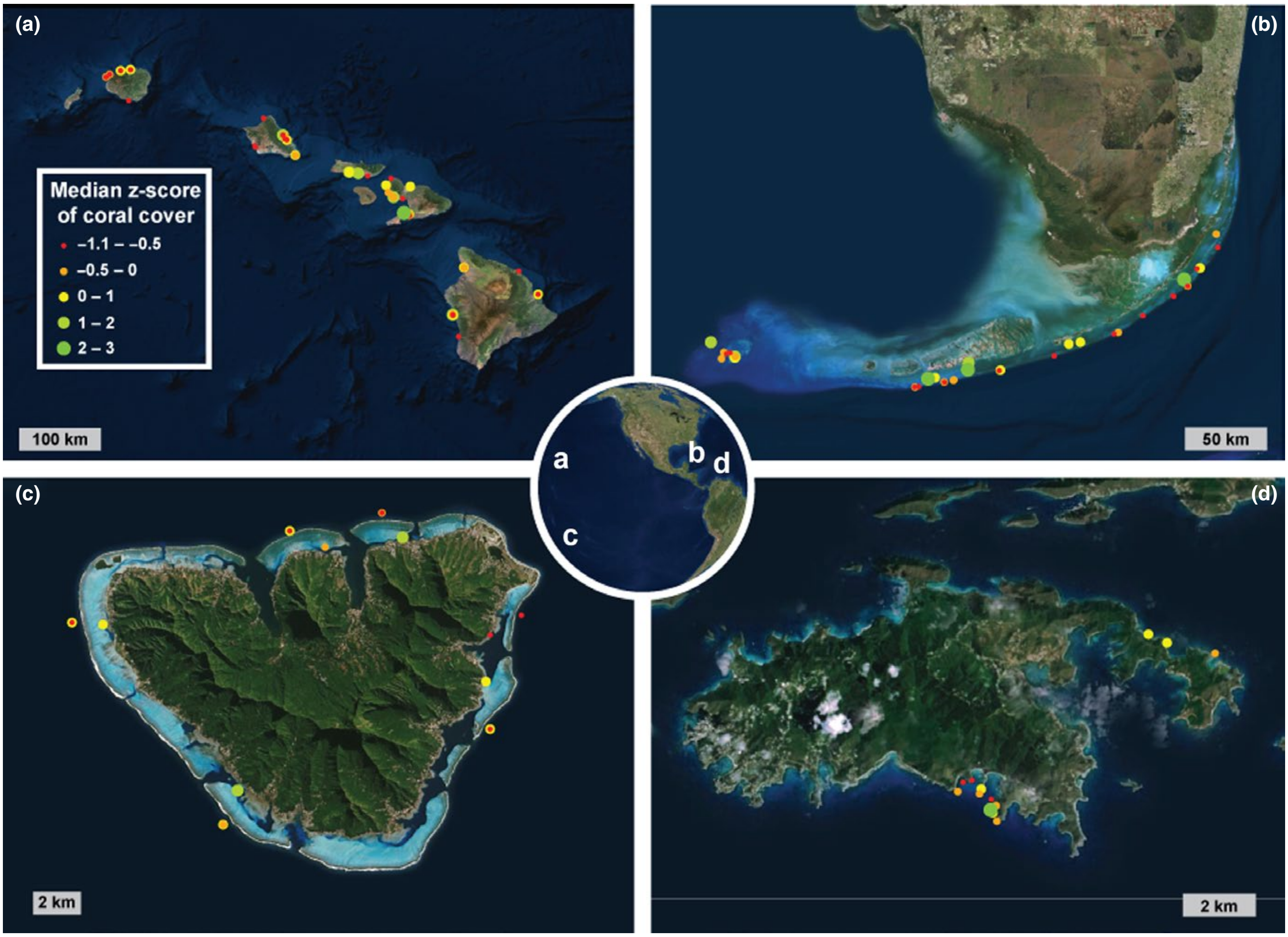

FIGURE 3 Maps showing the four focal regions used for this study: (a) main Hawaiian Islands, (b) Florida Keys, (c) Mo'orea, French Polynesia, and (d) St. John, US Virgin Islands. Circles marking sites are colour coded and sized based on their median *z*-scores, with increasing diameters of symbols denoting increasing median *z*-scores. Image credits: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, GIS user community

to ~5.4 kg m^{-2} y^{-1} for Mo'orea, ~0.2 to ~3.5 kg m^{-2} y^{-1} for the Florida Keys, and ~0.1 to ~1.9 kg m^{-2} y^{-1} for St. John (Supporting Information Table S4). Although CCC varied widely between locations, there was a significant positive relationship between median *z*-score of coral cover and CCC for all four focal locations (Figure 5). Among focal locations, variation in median *z*-scores of coral cover explained 79%–87% of the variation in CCC (Figure 5).

4 | DISCUSSION

There are several mechanisms that can allow coral cover to persist at relatively high levels when disturbances degrade neighbouring reefs. Firstly, oases could exist in a physical setting that is more likely to escape damage because they are in deeper water, in areas outside of storm tracks or where upwelling provides cooling (e.g., Riegl & Piller, 2003). Secondly, oases could possess biological or ecological characteristics that allow them to resist damage affecting nearby reefs, for example, because their fauna is acclimatised or adapted to certain disturbance events (e.g., Brown & Cossins, 2011). Finally, oases may rebound rapidly following disturbances because key ecological processes remain intact, for example herbivory and coral recruitment (e.g., Gilmour et al., 2013; Graham et al., 2015). We hypothesise therefore that oases identified using the framework described here can be characterized based on their coral cover trajectories, environmental conditions and disturbance histories, as follows: (a) *resistant* oases that are able to tolerate disturbances without losing coral cover due to specific traits of the corals at that site; (b) *escape* oases that have so far avoided major disturbances observed at neighbouring sites due to the physical and environmental characteristics of the site; (c) *rebound* oases that are capable of recovering rapidly from disturbances due to a range of physical, biological and ecological processes; and (d) *phase-shifted* oases, that have high coral cover for long periods of time, but that have recently declined rapidly. This final category appears counterintuitive, but as we argue below, some sites that have maintained high cover historically may be targets for restoration under certain circumstances. Escape and resistant oases are likely to exhibit lower CVs and high

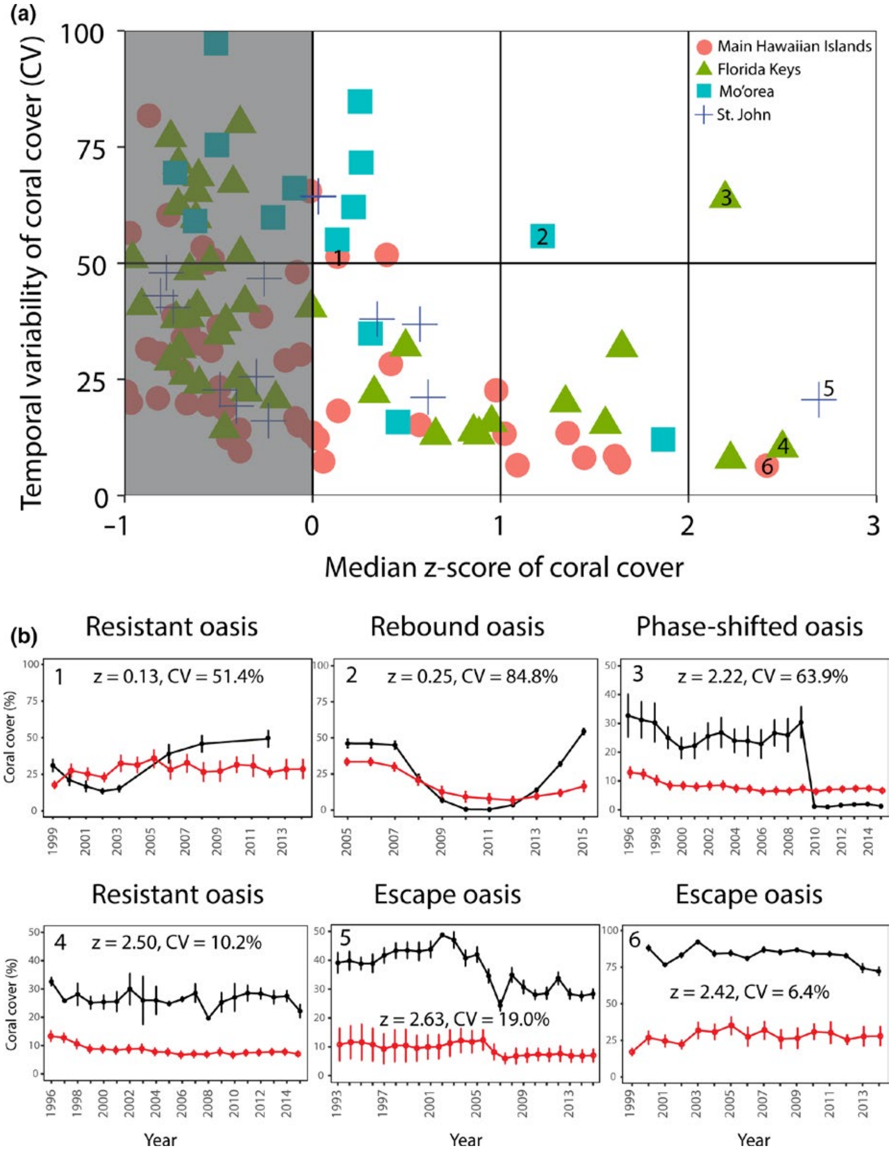

FIGURE 4 (a) Scatter plot displaying relationships between standardized coral cover (median *z*-scores) and variability in coral cover (coefficient of variation) for study sites identified as oases within each focal region for (red circles) main Hawaiian Islands, (blue squares) Mo'orea, (green triangles) Florida Keys and (blue crosses) St. John, U.S. Virgin Islands (based on data in Figure 2). See legend for Figure 1 for interpretation. (b) Examples of coral-cover trajectories from selected oasis sites: (1) Moku o Lo'e 2, (2) LTER1 Outer 10, (3) Admiral, (4) West Washer Women, (5) Tektite 1 and (6) Molokini 13. Black lines show mean coral cover for the site and the red line is overall mean coral cover for the region. Error bars show ± *SE*. Site labels indicate the point in the scatter plot in (a) for reference. Labels above each site indicate suggested categorisation of each oasis type (see Section 4 for explanation)

positive median *z*-scores, whereas rebound and phase-shifted oases are likely to exhibit higher CVs and lower positive median *z*-scores. This framework is important from a management perspective, as it prompts consideration of stability, resistance, or recovery of coral community structure within a historical context when assigning a measure of quality to individual sites within ecosystems (Mumby, Chollett, Bozec, & Wolff, 2014).

In this study, potential escape oases include Molokini Crater (Maui, main Hawaiian Islands) and the Tektite site at 14-m depth in St. John, as both are relatively protected from storms and experience relatively low levels of land-based influences (Edmunds, 2002; Rodgers et al., 2015; Rogers, McLain, & Tobias, 1991). Potentially resistant oases include several patch reefs in the Florida Keys (e.g., West Washer Women, Western Head, Jaap Reef) as they occur in areas with high variability in turbidity and temperature that may have favoured higher tolerance to acute thermal anomalies (Lirman et al., 2011; Ruzicka et al., 2013). Potential rebound oases, include an outer fore-reef site in Mo'orea at 10-m depth (LTER1 Outer 10 m), as this site had ~47% coral cover in 2005, <1% in 2010 (due to predation by *Acanthaster planci* and Cyclone Oli in 2010), but ~54% in 2015. Similarly, one shallow site (2-m depth) on O'ahu (Moku o Lo'e, in Kāne'ohe Bay, main Hawaiian Islands) increased in coral cover from 16% in 2001 to 49% in 2012. Kāne'ohe Bay has a long history of anthropogenic disturbances, but coral cover appears to recover when localised disturbances are effectively managed (Bahr, Jokiel, & Toonen, 2015). The history of this site suggests it possesses properties of both resistant and rebound oases. Potential phase shifted oases include Admiral in the Florida Keys, as this site declined from relatively high to low coral cover without recovery following a rare cold-water event in 2010 (Lirman et al., 2011). Considering that this site maintained average coral cover ≥21% for at least 15 years prior to 2010, it seems likely that typical environmental conditions there may still be suitable for coral growth and survival. If so, we suggest that Admiral may be a potentially strong candidate for targeted coral restoration (e.g., Lirman & Schopmeyer, 2016; see Figure 4b for examples of coral cover trajectories).

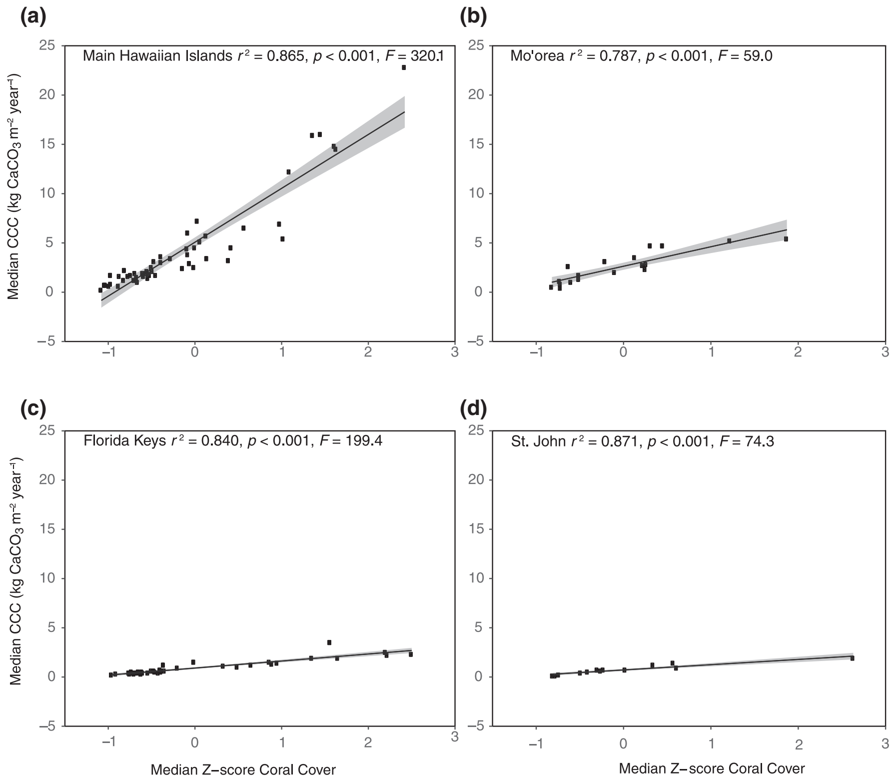

FIGURE 5 Scatter plots showing the relationship between median *z*-scores of coral cover and coral calcification capacity (CCC; kg $CaCO_3$ m^{-2} y^{-1}) for study sites within each focal region for (a) main Hawaiian Islands, (b) Mo'orea, (c) Florida Keys and (d) St. John, U.S. Virgin Islands. Fitted lines are Model I, least-squares linear regressions for predicted carbonate production. r^2 values and significance levels for the relationship are shown for each plot

There is ample evidence supporting the role of physical and biological drivers in determining ecosystem state of coral reefs (e.g., Graham et al., 2015). Nonetheless, it is possible that some oases exist because they have been spared from disturbance by chance alone. These "lucky" oases differ from escape oases as they do not possess any specific physical characteristics that reduce the likelihood of being disturbed. If it is the case that ecosystem state on reefs is determined more by stochasticity than by mechanistic drivers, then conservation planning will need to include as wide a range of reefs as possible to mitigate against this uncertainty (Webster et al., 2017).

While coral cover is an excellent proxy for reef condition, changes in coral cover alone cannot capture the full spectrum of changes that have negatively affected coral reefs in the last few decades. For example, shifts in taxonomic community structure also occur following disturbances and these may result in changes in reef function (Kuffner & Toth, 2016). Such shifts, described as "recovery without resilience", have been documented on a number of reefs in the Indo-West Pacific (e.g., Berumen & Pratchett, 2006). Both the total cover of corals and community composition play a role in determining CCC. It is conceivable, therefore, that a site dominated by slow growing taxa, could exhibit low CCC and vice versa, a site with lower cover of fast growing taxa could exhibit relatively high CCC. It is encouraging therefore that the generally higher CCC observed for oases in this study suggests a greater potential to maintain positive net coral reef-carbonate production relative to their neighbours. It is worth noting, however, that low rates of CCC for oases in the two Caribbean focal regions (e.g., max CCC St. John 1.9 kg m^{-2} y^{-1}, Florida Keys 3.5 kg m^{-2} y^{-1}) suggest that net carbonate production budgets for these sites may be close to zero once the additional factors, such as bioerosion and $CaCO_3$ dissolution, are taken into account (Perry et al., 2012).

Due to uncertainties about future environmental conditions, non-oasis sites that have historically performed poorly may improve and some oases will decline if they pass a tipping point (Hughes et al., 2017). We suggest, therefore, that our framework be used within adaptive networks of protected areas that also consider diversity, connectivity, metapopulation conservation and risk mitigation (Webster et al., 2017). There is considerable uncertainty about reef futures due to global change, however, combining detailed disturbance histories with our approach could lessen this uncertainty. The presence of oases in some locations does not advocate complacency about the severity of the crisis facing most of the world's coral reefs. Only concerted action to manage human disturbances at a local level and tackle carbon emissions globally will secure a future for tropical reefs. Nonetheless, we hope that our study will further efforts to identify similar "oases" in other ecosystems (e.g., tropical forests) and to improve our understanding of the mechanistic drivers underlying persistence of these sites in the face of global scale degradation.

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AUTHORS' CONTRIBUTIONS

All authors contributed to the conceptualisation of this study. J.R.G., P.J.E., R.D.G. and I.B.K. wrote the manuscript. R.E. produced the numerical simulations. T.A.C. and A.J.A. produced the calculations of coral-community calcification capacity. All authors read and edited the final draft of the manuscript.

DATA ACCESSIBILITY

Data available via USGS data release https://doi.org/10.5066/f78w3c7w (Guest et al. 2018).

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