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ORIGINAL PAPER

# Spatial variation in the dynamics and synchrony of coral reef communities in the US Virgin Islands

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**Abstract**
Most tropical coral reefs are experiencing declining coral cover, yet interpretation of this generality is tempered by spatial variation in coral cover among reefs separated over 20–200 km. This study addresses such landscape scale variation in coral reefs at 12 sites (7–10 m depth) around St. John (18° 18´ 37.04 N, 63° 43´ 23.17 W) and St. Thomas (18° 20´ 43.57 N, 65° 55´ 13.88 W), US Virgin Islands. Surveys completed from 2011 to 2021 were used to test for spatial variation in community dynamics among islands, shores, and sites. Community synchrony (φ) was used to evaluate portfolio effects in mediating changes in coral communities. From 2011 to 2021, changes in benthic communities differed among sites and times (i.e., there were site × year interactions), and, while coral cover declined at 11 sites, the decline was 2.6-fold faster around St. Thomas than St. John. The loss of coral cover was driven by multiple taxa that differed among sites, thus revealing asynchronous responses to prevailing conditions. Asynchrony suggests that coral communities at some of the sites have the capacity to exploit portfolio effects to modulate stability, yet these effects did not prevent declines in coral cover that reflect island-scale phenomena. In the US Virgin Islands, coral death is overwhelming the capacity for resilience of coral communities that historically may have benefitted from portfolio effects. Until coral assemblages are depleted through taxonomic extirpation, maintenance of the assemblage composition retains the possibility that increased resilience might emerge if environmental challenges can be alleviated.

**Keywords** Scleractinia · Long term · Asynchrony · Portfolio effects

## Introduction

Coral reefs in the twenty-first century differ from those described by ecologists in the twentieth century (e.g., Goreau 1959; Loya 1972), notably through large reductions in the population sizes of scleractinian corals (Bruno and Selig 2007; Schutte et al. 2010; Hughes et al. 2019). Even though corals may have constructed the framework upon which many reefs are built (Stoddart 1969; Allemand et al. 2011), extant communities often are dominated by taxa other than scleractinians (Norström et al. 2009; Pawlik and McMurray 2020). Nonetheless, these depleted coral communities are being described with unprecedented resolution to show that coral reefs are threatened (Veron et al. 2009; Hoegh-Guldberg et al. 2018). Evidence for this trend comes from widespread examples of reefs where stony corals and fishes have become rare, macroalgae are highly abundant, net community calcification is depressed, and overall, there is a poor prognosis for a reversal of these trends (Hoegh-Guldberg et al. 2007, 2018; Veron et al. 2009; Eyre et al. 2018).

Most contemporary descriptions of coral reefs underscore the severity of the crisis they face (e.g., Hoegh-Guldberg et al. 2018), which includes the high likelihood that the evolutionary survival of some corals will be impaired in a future of multiple stressors (Carpenter et al. 2008). While these assertions reflect ecological reality on some well-studied reefs (Edmunds 2013; Cinner et al. 2016), they overlook the high degree of spatial variation that characterizes coral reefs at almost every scale of investigation (Graham et al. 2015;

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Holbrook et al. 2018). Even while coral cover is declining worldwide (Eddy et al. 2021), this has occurred in concert with variation in coral dynamics among quadrats on individual reefs (Jackson 1991), differences in coral cover among sites separated by a few kilometers (Connell et al. 1997), and coral recruitment that can be high on one reef, but depressed on an adjacent reef (Glassom et al. 2006; Edmunds 2021). Such variation is a defining feature of this ecosystem, and it arises from the unique aspects of individual reefs (e.g., orientation and exposure), the spatio-temporal mosaic of disturbances to which they are exposed, and stochastic events (Karlson and Hurd 1993; Rogers 1993). Fifty years ago, however, there were more reefs with high versus low coral cover (Eddy et al. 2021), and the prevailing opinion was that damaged reefs would recover (Pearson 1981). Now, reefs with relatively high coral cover are unusual (Thomson and Frisch 2010; Steneck et al. 2019), and are thought to have high ecological value as "oases" or "bright spots" (Cinner et al. 2016; Guest et al. 2018; Sully et al. 2022) or, when representing larger areas, as bioclimatic units (BCUs) (Hoegh-Guldberg et al. 2018). Within these areas, corals are good candidates for protection, and could serve as a source of propagules to promote reef recovery at a larger spatial scale (Hoegh-Guldberg et al. 2018).

Understanding of the significance of spatial variation in coral community structure has expanded in the last decade, in part through an appreciation of the role of genetic connectivity among reefs (Kool et al. 2011; Holstein et al. 2014) within a metacommunity (sensu Leibold et al. 2004), as well as the extinction risks associated with rarity (Hull et al. 2015). Portfolio effect theory (Schindler et al. 2015) enriches the interpretation of spatial variation by addressing taxa that respond in dissimilar ways to common conditions in different locations. If these locations exchange genetic material, for example, through the dispersal of larvae, then the potential is created for population decline in one location to be slowed through larval subsidies from another locations, although the reverse may also be true (i.e., population growth might be slowed through larval loss to a location serving as a larval sink). The probability of such exchanges is dependent in part, on ocean currents, the distance between locations, spawning periodicity, the extent to which reefs are self-seeded versus supplied with larvae from distant sources, and coupling of phenotypes to environmental conditions (Marshall et al. 2010; Holstein et al. 2014; Kough and Paris 2015). Current thinking views the reliance of coral populations on larvae from local (i.e., self-seeded) versus distant locations as variable over time (Black et al. 1991; Wood et al. 2014; Kough and Paris 2015; Hock et al. 2019), but probably more dependent on local versus distant recruitment than once was thought (Figueiredo et al. 2013). The exchange of coral larvae among populations within a metacommunity in which portfolio effects are featured would be expected to promote community stability (Thibaut and Connolly 2013).

The coral reefs of the US Virgin Islands provide an interesting system for the exploration of spatial variation in community structure, because many accessible reef sites occur over local and landscape scales (i.e., ≤ 200 km [Mittelbach et al. 2001]), and across gradients of exposure (e.g., north and south shores), protection (i.e., within the VI National Park [Rogers et al. 2008]), and human population density (e.g., St. Thomas versus St. John). Moreover, some of these reefs are among the best studied in US waters (reviewed in Rogers et al. 2008; see also Ennis et al. 2020), which provides a detailed spatio-temporal context (dating from the late 1950s (Kumpf and Randall 1961)) to this study. Eleven of the 12 sites described in the present paper were first sampled in 2011 (Edmunds 2013, 2014, 2019; Edmunds et al. 2015) to test the generality of trends in benthic community structure described from 25 years of sampling on the south coast of St. John. The 12 sites were used in an orthogonal design crossing 2 islands and 2 shores to reveal 4 outcomes: (1) coral reef and coral community structure differed among sites, but not among shores or islands, (2) coral cover was 1.9-fold higher around St. Thomas versus St. John, (3) site variation differed among coral genera, and (4) octocorals were more provincial than scleractinians.

In 2011, scleractinian cover varied from 2.7% (in St. John at the Pooled Random Sites, hereafter PRS*) to 20.2% (Flat Cay, St. Thomas), and the differences among sites extended to octocorals, which varied in density from 0.95 ± 0.17 colonies 0.25 $m^{-2}$ (Flat Cay) to 5.86 ± 0.57 colonies 0.25 $m^{-2}$ (Waterlemon Cay, St. John). St. John and St. Thomas are only ~ 3.5 km apart, and their reefs are connected by westward flowing offshore seawater (at ca. 25–30 cm $s^{-1}$ [Richardson 2005]) that is characterized by slow flow (~ 3.4 cm $s^{-1}$) on the fringing reefs and occasional flow reversals (Horst and Edmunds 2010) providing opportunities for connectivity from western to eastern sites. Connectivity between the north and south shores is likely to be restricted by limited seawater movement between shores, although it remains possible through Pilsbury Sound that separates St. John and St. Thomas (Cherubin and Garavelli 2016). For these closely spaced reefs, there is theoretical and empirical evidence that corals are genetically connected (Holstein et al. 2014; Serrano et al. 2016; Gallery et al. 2021), and it is reasonable to consider the present sites as part of a metacommunity (sensu Leibold et al. 2004) that can serve as both sources and sinks for pelagic larvae. Coral reef community dynamics are unlikely to be independent among sites scattered around St. John and St. Thomas.

The earlier study (Edmunds 2014) of the present sites tested for implications of spatial variation in community state, and did not test for comparable variation in community dynamics, or the functional implications thereof (e.g., portfolio effects (Schindler et al. 2015)). The present study focuses on the rates at which communities have changed at the same 12 sites that were sampled in 2011, and results from 2011, 2015, 2019 (3 sites only), and 2021 are used to test three hypotheses: (1) coral reef community dynamics are heterogeneous among sites, in part because, (2) coral cover and coral community composition have changed in dissimilar ways among sites, with these dissimilarities, (3) modulated by changes in coral community synchrony (φ, the extent to which taxa change abundance in the same way (Thibaut and Connolly 2013). Quantifying φ at a site scale allowed a test for changes in φ over time, and provided insight into the role of portfolio effects (Thibaut and Connolly 2013; Schindler et al. 2015) in mediating site-level variation in community structure. Quantifying φ among sites and over time, evaluated the capacity for spatial insurance (Loreau et al. 2021) to mediate changes in community structure at the scale of shores and islands.

## Materials and methods

Sampling was accomplished photographically using digital cameras on a frame that held the camera perpendicular to the reef to record 0.5 × 0.5 m photoquadrats. Photographs were taken with a Nikon D90 camera in 2011 (12.3 MP, fitted with a Nikkor DX 18–70 lens), a Nikon D7000 in 2015 (16.2 MP, fitted with a Nikkor DX 18–70 lens), and a Nikon D810 in 2015–2021 (36.3 MP, fitted with a Nikkor FX 18–35 lens). Cameras were fitted with two strobes (Nikon SB105) and the pictures provided a resolution of objects > 5 mm diameter.

Two sampling regimes were employed. First, sampling in the core area of the time-series project (1992–present on the south shore of St. John) took place between White Point and Cabritte Horn (1.3 km apart, Fig. 1), and sampled six permanently marked sites (five at 9 m depth, one at 7 m depth) that were randomly selected in 1992. Along one 40 m transect at each site, photoquadrats were recorded at 40 positions that were randomized annually. Each sampling generated ~ 240 photoquadrats from which 40 were drawn randomly to characterize the fringing reefs along this stretch of shore (hereafter referred to as the Pooled Random Sites, PRS*) and support a balanced statistical contrast with the other 11 sites (described below). Sampling at the core sites in July/August 2011, 2015, 2019, and 2020 are used in the present analysis. Although the core sites were sampled in August 2020, they are contrasted with the January 2021 sampling of the other sites and considered together as “2021 sampling”.

In 2011, the sampling included 11 additional sites at 10 m depth that were scattered around St. John and St. Thomas to provide a contrast of shores ($n = 3$ sites shore$^{-1}$) and islands ($n = 6$ sites island$^{-1}$). These sites were selected haphazardly to sample fringing reefs at a landscape scale commensurate with the linear distance occupied by St. John and St. Thomas (~ 40 km). Logistical constraints prevented permanent marking of the sites, but they were relocated using GPS and landscape and seascape features. It, therefore, was possible to revisit the sites over time, but identical areas of reef were not sampled on each occasion. Sampling of the sites around both islands and their shores occurred in June 2011, June 2015, August 2019 (two sites on the south shore of St. John), and January 2021.

Coral reef benthic community structure was analyzed using CoralNet software (Beijbom et al. 2015) with manual annotation of 200 dots randomly located on each image, and the results were expressed as percentage cover. Analyses resolved scleractinians to the lowest taxonomic level possible, macroalgae (mostly *Dictyota*, *Lobophora, Padina, Sargassum*, *Halimeda*, and peyssonellid algal crust), and crustose coralline algae, algal turf, and bare space combined (CTB), because they could not reliably be distinguished in photoquadrats. Scleractinians subsequently were pooled to *Orbicella* spp., *Montastraea cavernosa*, *Agaricia* spp., *Colpophyllia natans*, *Pseudiploria* spp., *Diploria* spp., *Meandrina* sp., *Porites* spp., *Siderastrea* spp, and “other” corals.

### Statistical analyses

To explore the variability in coral reef community structure among 12 sites (Hypothesis 1), the mean covers (± SE) of coral (pooled taxa), macroalgae, and CTB were visualized in bar graphs by year, with descriptive statistics calculated from raw data. To test for differences among times, sites, shores, and islands, a partly nested ANOVA was used in which islands and shores were fixed effects, site was nested in shores and island, and time (2011, 2015, and 2021) was treated as a within plot (i.e., site) effect; percentage cover data were arcsine transformed. The statistical assumptions of normality and homoscedasticity were evaluated through examination of residuals; 2019 was excluded from the analysis as only three sites were sampled in this year. To evaluate rates of change in coral cover over time, cover (pooled among taxa and arcsine transformed) was regressed on time using quadrats as replicates; 2019 was included in these analyses at sites where sampling was conducted in this year. ANCOVA was used to test for differences in slopes of cover on time among the main effect of sites, with post hoc analyses (after Zar 2010) to test for differences among pairs of sites. Rates of change in cover by site (on a percentage scale) also were compared among site/shore combinations (using a Kruskal–Wallis test) and between islands (Mann–Whitney U test). Non-parametric analyses were used to compare rates of change in cover by site (i.e., the slopes of the regression lines), because the small sample sizes and their uncertain

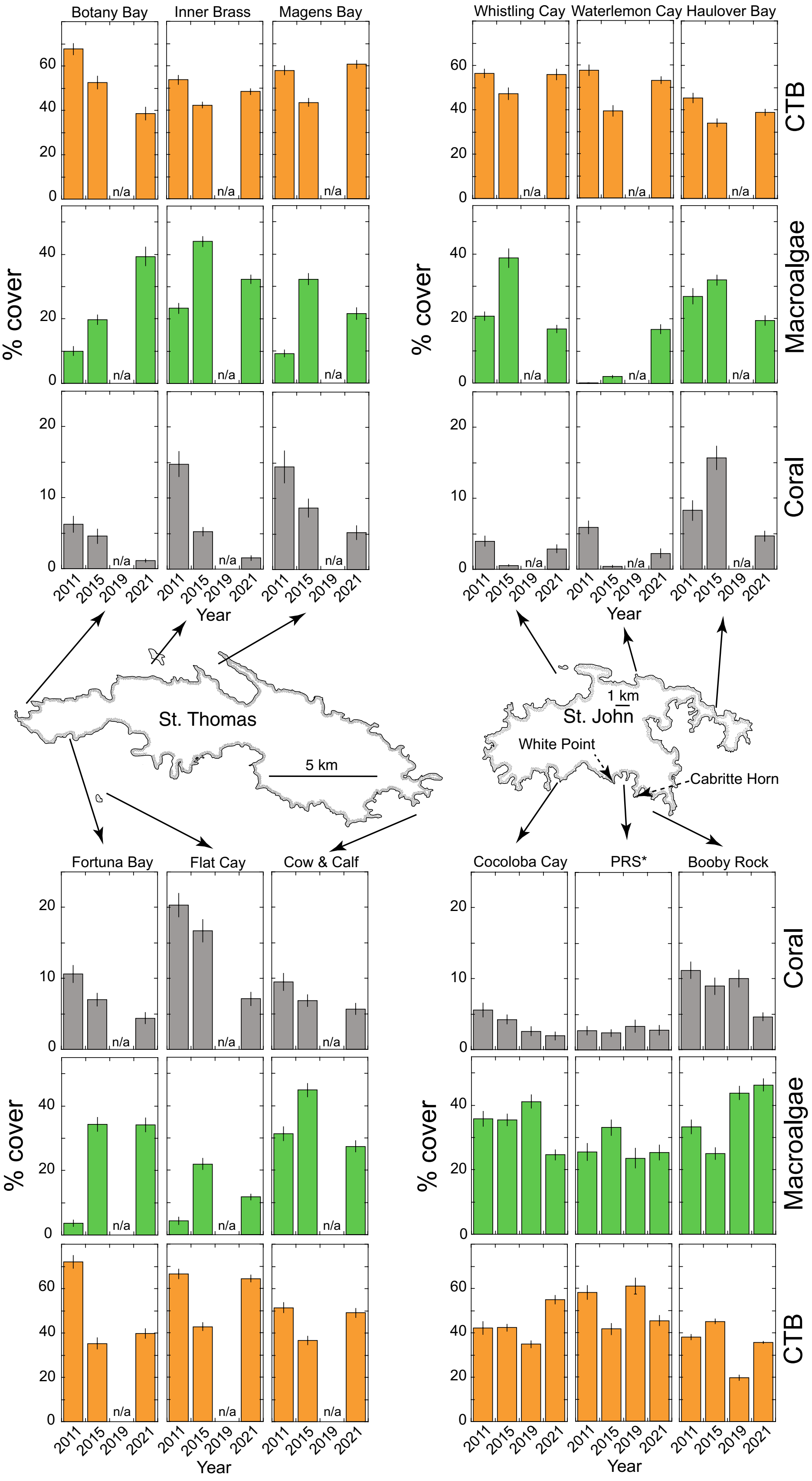

**Fig. 1** Coral reef community structure at twelve sites (7–10-m depth) around St. John (18° 18′ 37.04 N, 63° 43′ 23.17 W) and St. Thomas (18° 20′ 43.57 N, 65° 55′ 13.88 W) that were surveyed in 2011, 2015, 2019 (3 sites only), and 2021. Mean ± SE (n ~ 40 quadrats sampling$^{-1}$, based on untransformed data) shown for crustose coralline algae, algal turf, and bare space (combined, CTB, orange), macroalgae (green), and stony corals (gray). n/a = data not collected. PRS* was composed of data randomly subsampled from sites located between White Point and Cabritte Horn (dashed arrows on St. John)

variance structures. Univariate analyses were completed using Systat 13 (Systat Software, Inc, San Jose, CA).

The test for heterogeneous coral community dynamics among sites was accomplished separately by island and shore, with data visualized using two-dimensional ordination by non-metric multidimensional scaling (NMDS), with similarity profile analyses (SIMPROF) to test for significant differences over time. Ordinations were prepared using mean coral cover by taxon as calculated from arcsine-transformed data, and the back-transformed, mean values were square root transformed (to address analytical biases created by extreme values) before preparing resemblance matrices using Bray Curtis dissimilarities. Ordinations and SIMPROF analyses were completed using Primer 6 software (Clarke and Gorley 2006)).

Synchrony among taxa in changes in cover over time was calculated (Eq. 1) by site using the index φ (after Thibaut and Connolly 2013):

$$\varphi = \frac{v_n^c}{\left(\Sigma_i \sqrt{v_n^s(i,i)}\right)^2}, \tag{1}$$

where $v_n^c$ is the variance of the total community abundance for a community consisting of n species, and $v_n^s(i,i)$ is the variance over time of the *i*th species (*s*).

Phi scales from 0, when all taxa change in different ways over time (i.e., they are asynchronous), to 1, when all taxa change in the same way over time (i.e., they are synchronous) and was calculated by site over two periods, first from 2011 to 2015, then from 2015 to 2021. Synchrony among sites also was calculated over the same two periods (2011–2015 and 2015–2021) using the change in cover by taxon as the dependent variable in Eq. 1 and a matrix of all possible site combinations (e.g., Haulover Bay versus Waterlemon for 2011–2015, Haulover Bay versus Booby Rock for 2011–2015, etc.).

## Results

Mean (± SE) cover of the dominant space holders varied among all combinations of sites and years, ranging from 0.4 ± < 0.1% (Waterlemon in 2015) to 20.2 ± 1.6% (Flat Cay in 2011) for coral, from 0.1 ± 0.4% (Waterlemon in 2011) to 46.3 ± 1.9% (Booby Rock in 2021) for macroalgae, and from 19.8 ± 1.1% (Booby Rock in 2019) to 72.0 ± 2.9% (Fortuna Bay in 2011) for CTB (Fig. 1). The range in values among sites was broadly similar within each year, with coral varying from 2.7 ± 0.6% (PRS*) to 20.2 ± 1.6% (Flat Cay) in 2011, from 0.4 ± 0.1% (Waterlemon Cay) to 16.7 ± 1.6% (Flat Cay) in 2015, and from 0.6 ± 0.1% (Whistling Cay) to 7.12 ± 0.9 (Flat Cay) in 2021; macroalgae varied from 0.1 ± < 0.01% (Waterlemon Cay) to 35.8 ± 2.3% (Cocoloba Cay) in 2011, from 2.1 ± 0.4% (Waterlemon Cay) to 44.8 ± 2.2% (Cow and Calf) in 2015, and from 11.7 ± 1.0% (Flat Cay) to 46.3 ± 1.9% (Booby Rock) in 2021; CTB varied from 38.1 ± 2.4 (Booby Rock) to 72.0 ± 2.9% (Fortuna Bay) in 2011, from 34.0 ± 1.8% (Haulover Bay) to 55.9 ± 2.4% (Whistling Cay) in 2015, and from 35.7 ± 1.6% (Booby Rock) to 64.4 ± 1.6% (Flat Cay) in 2021. All three components of the coral reef community structure (i.e., coral, macroalgae, and CTB) differed among sites ($P < 0.001$), with the differences among sites varying among years ($P < 0.001$); none differed between islands and shores, and they were unaffected by the interaction of these two main effects ($P \geq 0.120$) (Table S1).

Coral cover (arcsine transformed) was linearly and negatively related to time at 11 of 12 sites (not at PRS*) (Fig. 2, Table 1). Overall the slopes of these relationships varied among sites (ANCOVA, F(10,1369) = 3.784, $P < 0.001$), although differences among pairs of sites could not be resolved by post hoc contrasts (for arcsine-transformed values, P > 0.05). On a percentage scale, coral cover declined at between -0.202% $y^{-1}$ (Waterlemon Cay) and -1.375% $y^{-1}$ (Flat Cay), and while the slopes did not differ among the four shore/island combinations (H = 5.051, $P = 0.168$), the decline was faster around St. Thomas than St. John (U = 32.0, $P = 0.025$) (Fig. 3).

Two-dimensional ordinations based on coral cover by taxon revealed changes in the taxonomic composition, with the rates and causes of the variation differing among shores/islands, and sometimes among sites within a shore (Fig. 4). Since the ordinations were independently generated by shore/island, the spatial distribution of samplings is not quantitatively comparable among shores/islands. Nevertheless, the vectors reveal the influence of the dominant coral taxa in determining the similarity between samplings for each site by shore, thereby showing that variation within each shore/island was caused by different taxa. On the south shore of St. Thomas, for example, the temporal differences at the three sites were driven by a reduced abundance of *Siderastrea*, with Flat Cay differing from the other two sites due to a greater abundance of *Porites* and *Orbicella*. In contrast, on the north shore of St. Thomas, the temporal changes at the three sites were caused by different taxa (e.g., a reduction in *Orbicella* at Inner Brass versus a reduction *Pseudodiploria* at the other two sites), with Botany Bay and Inner Brass differing between 2015 and 2021 through a reduced abundance of *Montastraea cavernosa*.

A larger number of taxa caused changes in coral community structure around St. John than St. Thomas. On the south shore of St. John, Booby Rock differed from the other two sites through a greater abundance of *Agaricia, Diploria* and *Orbicella*, and on the north shore, Haulover Bay differed from the other two sites through a greater abundance of *Porites*. On the south shore, relatively large changes in

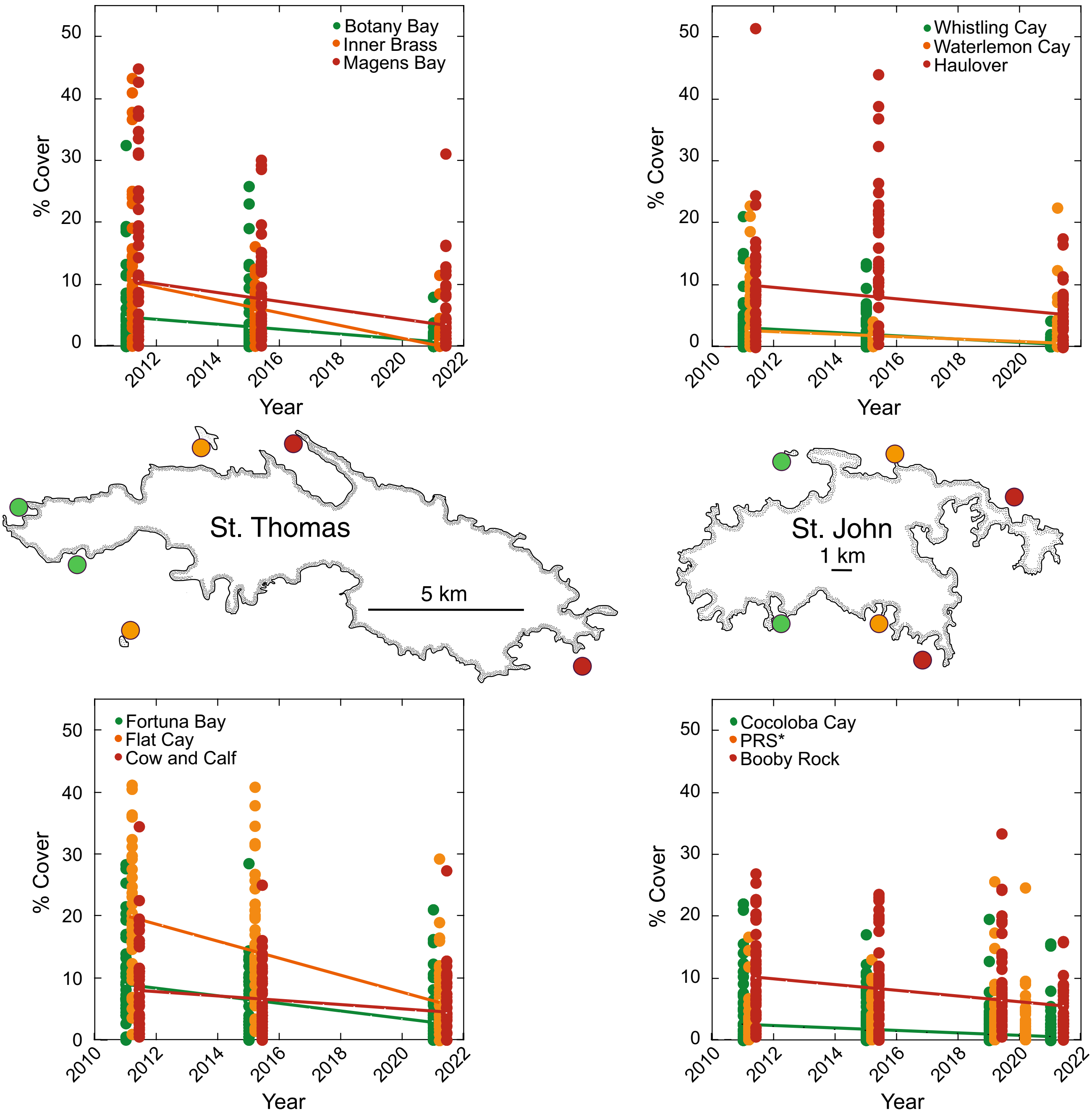

**Fig. 2** Change in coral cover (pooled among taxa) over time at 12 sites scattered between the north and south shores of St. John and St. Thomas. Color coded by sites, with data plotted by quadrats ($n = \sim 40$ site$^{-1}$ sampling$^{-1}$) and offset on the abscissa for clarity. Best fit linear regressions (Table 1) fitted to arcsine-transformed data and displayed on untransformed axes

coral community structure at PRS* and Booby Rock were caused by a reduced abundance of *Siderastrea*, whereas the coral community at Cocoloba Cay changed relatively little in taxonomic composition. On the north shore, the most striking changes at Waterlemon Cay and Whistling Key were caused by samplings in 2015 and 2021 (respectively) when coral cover was low (≤ 0.3%), whereas at Haulover Bay, the taxonomic composition changed relatively little.

SIMPROF analyses of coral community structure revealed significantly different clusters of sampling years at three of the four site/shore combinations. On the north shore of St. Thomas, the communities sampled in 2021 differed from communities sampled in previous years, although Magens Bay in 2021 differed from Botany Bay and Inner Brass in 2021, and Inner Brass in 2011 was more similar to Magens Bay in 2021 than to the other sites

**Table 1** Linear regression analyses of coral cover on time using quadrats as replicates and arcsine-transformed data

| Island | Shore | Site | Regression statistics | Slope % $y^{-1}$ |
|---|---|---|---|---|
| St. John | North shore | Whistling Cay | $F = 36.412$, $df = 1{,}118$, $P < 0.001$ | − 0.281 |
| | | Waterlemon Cay | $F = 11.099$, $df = 1{,}122$, $P = 0.001$ | − 0.202 |
| | | Haulover Bay | $F = 6.538$, $df = 1{,}119$, $P = 0.012$ | − 0.459 |
| | South shore | Cocoloba Cay | $F = 20.320$, $df = 1{,}155$, $P < 0.001$ | − 0.327 |
| | | PRS* | $F = 0.198$, $df = 1{,}158$, $P = 0.657$ | 0 |
| | | Booby Rock | $F = 11.033$, $df = 1{,}157$, $P = 0.001$ | − 0.458 |
| St. Thomas | North shore | Botany Bay | $F = 23.639$, $df = 1{,}118$, $P < 0.001$ | − 0.392 |
| | | Inner Brass | $F = 92.761$, $df = 1{,}117$, $P < 0.001$ | − 1.019 |
| | | Magens Bay | $F = 13.736$, $df = 1{,}116$, $P < 0.001$ | − 0.699 |
| | South shore | Fortuna Bay | $F = 23.059$, $df = 1{,}115$, $P < 0.001$ | − 0.603 |
| | | Flat Cay | $F = 49.320$, $df = 1{,}116$, $P < 0.001$ | − 1.374 |
| | | Cow and Calf | $F = 7.659$, $df = 1{,}116$, $P = 0.007$ | − 0.345 |

Slopes are reported on a percentage scale following back-transformation of predicted cover values by year

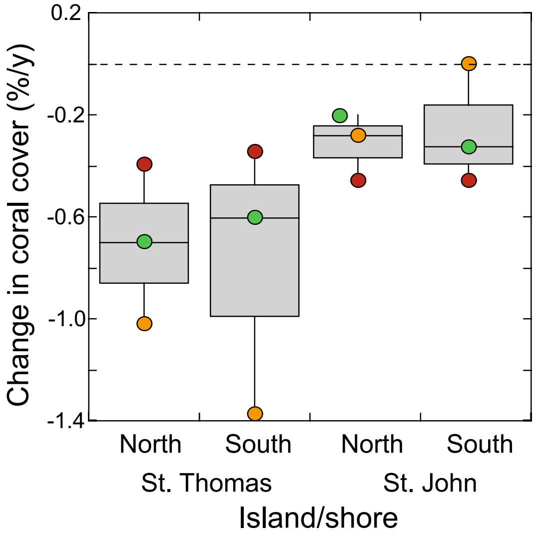

**Fig. 3** Box plots (boxes display medians and interquartile ranges) showing changes in coral cover over time (% $y^{-1}$, slopes of regression lines, Table 1) by shore and island; symbols color coded as in Fig. 2

and samplings in 2011 and 2015. On the north shore of St. John, two of the three communities sampled in 2021 were unique from other communities sampled over the study, and on the south shore of St. John, the community at Booby Rock remained different from the communities sampled at PRS* and Cocoloba Cay, although the community sampled in 2021 at Booby Rock differed from the community sampled at this site in 2011, 2015 and 2019. On the south shore of St. Thomas, the changes in community structure did not sum to statistically significant changes in community structure. The extent to which coral communities changed over time at the four site/shore combinations is clear when the relative abundances are averaged among sites within each shore (Fig. S1). In this format, the decline in abundance of *Montastraea cavernosa*, and the increase in abundance of *Porites*, is striking.

Phi summarizes the extent to which the changes in abundance of each coral taxon were synchronous over the scale to which the analyses were applied. Within each site/shore combination, from 2011 to 2015, φ varied from 0.053 (PRS*) to 1.000 (Waterlemon Cay), showing that changes in cover were synchronous at some sites, and asynchronous at others. The same was true over the second period (i.e., 2015–2021), when φ ranged from 0.030 (Magens Bay) to 1.000 (Whistling Cay, Inner Brass, and Cocoloba Cay). There was a trend at three of the four site/shore combinations for φ to increase over 2015–2021 relative to 2011–2015 (Fig. 5), but overall, φ did not differ between periods (pooled by shores and islands, $U = 2.351$, $P = 0.125$). When φ was recalculated to consider synchrony between all pairs of sites, over 2011–2015, it varied from 0.026 (Magens Bay versus Flat Cay) to 0.945 (Fortuna Bay versus Whistling Cay), and over 2015–2019, it varied from 0.020 (Magens Bay versus Cow and Calf) to 0.945 (Inner Brass versus Whistling Cay); φ did not differ between periods ($U = 1.772$, $P = 0.183$).

## Discussion

Spatial variation in community structure is deeply rooted in ecological descriptions of coral reefs extending from the 1960s (Goreau 1959; Stoddart 1963) to the present (Graham et al. 2015; Moritz et al. 2021). It is unsurprising, therefore, that the coral reef crisis is expressed to varying degrees on different reefs, with a few functioning as oases with respect to high coral cover (Cinner et al. 2016; Guest et al. 2018). On the Great Barrier Reef, for example, northern reefs were depleted of coral through bleaching, while southern reefs remained relatively unaffected (Hughes et al. 2019). Throughout the Caribbean in 2011, mean coral cover ranged

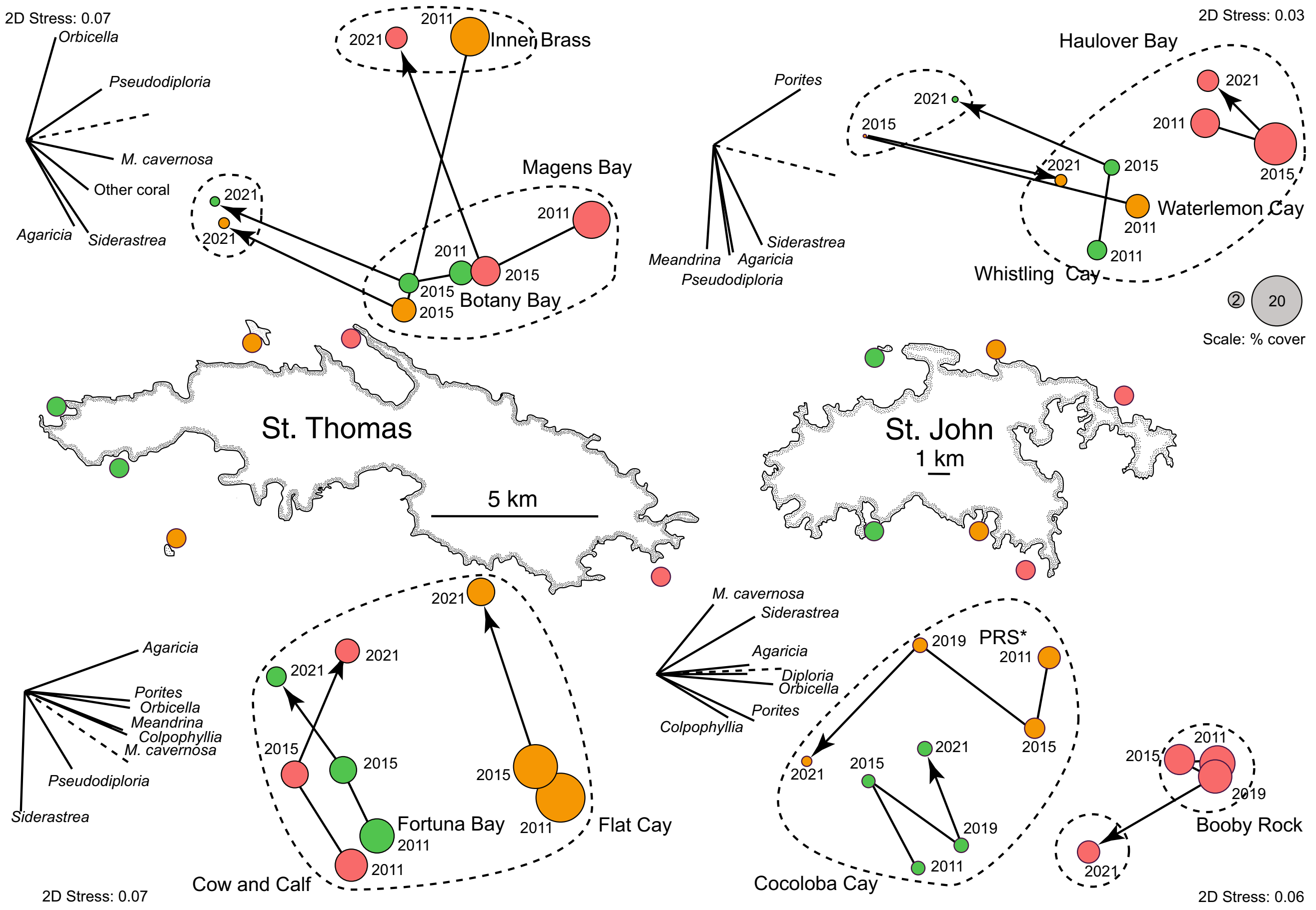

**Fig. 4** Two-dimensional ordinations by NMDS of variation in coral community structure among years by shore and islands. Four separate analyses were conducted for each shore/island using mean coral cover (calculated from arcsine-transformed data; *Montastrae cavernosa*, *Orbicella* spp. *Agaricia* spp. *Colpophyllia*, *Pseudodiploria* spp., *Diploria* spp., *Meandrina* spp., *Porites* spp., *Siderastrea* spp., and other corals), using resemblance matrices calculate using Bray Curtis dissimilarities with square root transformed data. Circles scaled to overall coral cover and colored red (eastern), orange (central) and green (western). Vectors show association (as Pearson correlations, filtered to exclude values $<0.6$) of each dependent variable (i.e., cover by coral taxon) with NMDS axes; straight dashed line indicate $r=1.0$. Dashed boundaries constrain samplings within each shore/island that are not significantly different (SIMPROF, $P>0.05$)

from 4% (Antigua and Barbuda) to 53% (Flower Garden Banks, USA) (Jackson et al. 2014), and in the Seychelles in the same year, it ranged from 10 to 48% at 21 sites (Graham et al. 2015). The aforementioned effects can reflect dissimilar community dynamics involving the rate of change of cover of benthic taxa, and sometimes, different trajectories of change (Connell et al. 1997; Holbrook et al. 2018). Reefs in the Seychelles provide good examples of these effects, with those studied by Graham et al. (2015) following contrasting trajectories after bleaching in 1998: 12 regained coral cover, and 9 transitioned to macroalgal dominance. The present study contributes to this literature by using results from a decade-long study in the US Virgin Islands to test three hypotheses and reveal: (1) among-site variation in community structure, that (2) is associated with community dynamics differing among sites, with coral cover declining faster around St. Thomas than St. John, and (3) variable synchrony in coral population fluctuations, with low values indicating the potential for portfolio effects to modulate stabilization of community dynamics (Thibaut and Connolly 2013). Under the environmental and biological conditions that have characterized the study reefs over the last decade, the inferred benefits of portfolio effects have not been realized for the study reefs (i.e., their coral cover has declined).

Since sampling the present sites in 2011, coral reefs in the US Virgin Islands have been exposed to several large disturbances including two hurricanes in September 2017 (Edmunds 2019), bleaching in late 2019 (Ennis et al. 2020), and an outbreak of stony coral tissue loss disease (SCTLD) that was first reported in St. Thomas in January 2019 (Costa et al. 2021; Brandt et al. 2021). Together with a spectrum of ongoing chronic disturbances including other coral diseases (Rogers 2009), sedimentation, runoff, and coastal pollution (Ennis et al. 2016, Oliver et al. 2018), these events have been

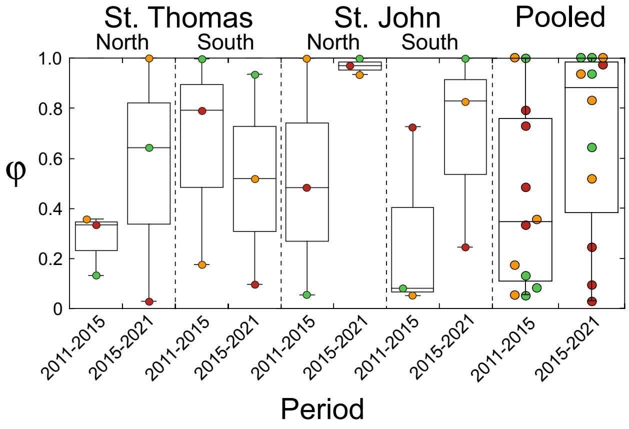

**Fig. 5** Community synchrony (φ) for reef corals in the US Virgin Islands over 2011–2015 and 2015–2021 at three sites (color coded as in Fig. 2, red = eastern, orange = central, green = western) on each of the north and south shores of St. John and St. Thomas. Analyses based on mean coral cover by taxon (9 taxa and other) as determined from arcsine-transformed values; Pooled = both islands and all shores

associated with a decline in coral cover around St. John and St. Thomas (Edmunds 2013, 2019; Ennis et al. 2020; Brandt et al. 2021). It is surprising, however, that broad aspects of the coral reef community structure (e.g., cover of coral, macroalgae, and CTB (Table S1)) did not vary between islands or shores, across differing human populations, conservation efforts, and environmental conditions. St. Thomas, for example, has a larger human population than St. John (51,634 versus 4,170 in 2010, respectively (www.census.gov), coastal pollution in several localities (Ennis et al. 2016; Oliver et al. 2018) and only small marine protected areas (MPAs), notably relative to the 2,286 ha of marine resources in the Virgin Islands National Park, and the 1,096 ha in the Virgin Islands Coral Reef National Monument (Rogers et al. 2008). Furthermore, the marine environments on the north and south shores of both islands differ in several ways, for example, with the north shore of St. John characterized by cooler seawater, greater chlorophyll concentrations (mg $m^{-3}$), and lower wave exposure (as J $m^{-3}$) than the south shore (Cunning et al. 2017).

Across these gradients, benthic reef communities on shallow reefs differed among sites, and coral cover declined more rapidly around St. Thomas compared to St. John. The site effects suggest that these reef communities were more strongly affected by conditions varying over a scale of kilometers (i.e., site scale) than over local or landscape scales (i.e., 20–200 km (Mittelbach et al. 2001)). This inference has implications for the management of coral reefs in the US Virgin Islands, because it suggests there may be opportunities to tailor management decisions to individual sites to achieve specific outcomes. For example, site-specific management could by tailored to increase coral cover, protect select taxa, safeguard recruitment hotspots (Edmunds 2021), or promote diversity in small populations that could enhance community stability (Abbott et al. 2017). While the slower rates of coral loss around St. John versus St. Thomas appear to implicate the MPAs around St. John (Rogers et al. 2008) as causal factors in reducing declines in coral cover, this conclusion is premature given the prominence of other factors that provide parsimonious explanations for the trend. Rather than being a product of MPAs alone, the slower rate of coral loss around St. John probably reflect multiples factors combining the consequences of MPAs with historical precedence (i.e., coral cover was considerably higher around St. Thomas than St. John in 2011) (Fig. 1, see also Edmunds 2014), enhanced anthropogenic stressors in the coastal waters of St. Thomas (Ennis et al. 2016; Oliver et al. 2018), and the arrival of SCTLD on the reefs of St. Thomas prior to St. John (Costa et al. 2021; Brandt et al. 2021).

The differences among sites in the rates at which coral cover declined from 2011 to 2021 extend to variation among sites in the overall coral reef community structure (i.e., coral, macroalgae, and CTB), as well as the diverse ways in which coral genera contributed to the changes in coral cover at each site. These effects are revealed by the two-dimensional ordinations prepared by shore for the coral communities with genus resolution (Fig. 4), which display the extent to which sites differed within shores/islands, as well as the discordant taxonomic drivers of change. Changes on the south shore of St. Thomas, for instance, as well as at two of three sites on the south shore of St. John, were associated by declining abundances of *Siderastrea*, while changes on the north shore of St. Thomas were associated with declining abundance of *Montastraea*, or increasing abundances of *Orbicella*.

The causes of the contrasts in coral community dynamics at multiple sites around St. John and St. Thomas currently are unclear, but they are inconsistent with an origin in the different environmental conditions on the north and south shores of the two islands (Cunning et al. 2017), or coastal pollution along the south shore of St. Thomas (Ennis et al. 2016; Oliver et al. 2018). The effects are expressed among sites separated by 2.3–37.6 km, which represents a local-to-landscape scale (sensu Mittelbach et al. 2001) over which variation in coral reef communities is common on shallow coral reefs (Edmunds and Bruno 1996; Graham et al. 2015; Moritz et al. 2021). Around St. Thomas and St. John, however, the spatial variation in coral community structure now is exhibited across a low and narrow range of mean coral covers (e.g., 2.7–20.2% in 2011, and 0.6–7.1% in 2021) (cf Edmunds and Bruno 1996; Graham et al. 2015; Moritz et al. 2021). Against this backdrop, there are two compelling hypotheses to account for the present site effects. First, that they reflect interactions of biological processes (i.e., affecting the abundance of coral genera, macroalgae, and CTB) and physical environmental conditions expressed on the scale of sites, and second, that they reflect historical legacies of the taxa dominating the shallow reefs at each sites when the study began.

Testing of these hypotheses is not currently possible, and in the future, is likely to be challenging. To test the first hypothesis, descriptions of environmental conditions and the functional biology of the relevant taxa will be required for multiple sites and across multiple years. Acquiring such data is likely to be a valuable endeavor, but the apparent similarity of the marine habitats at each site does not provide a compelling reason to expect the analyses will explain the patterns described herein. The second hypothesis is consistent with priority effects (Shulman et al. 1983; Almany 2003; Fukami 2015) that determine which taxa dominate select locations based on their time of arrival to suitable substrata (Connell and Slatyer 1977; Fukami 2015). Testing of this hypothesis will require monitoring over a period that probably will need to be substantially longer than 10 years to capture the effects of multiple disturbances, and might be successfully approached through genetic analyses (Beger et al. 2014). Such approaches might, for example, be able to use genetic structuring of coral hosts to test for patterns attributed to a historic and large recruitment event (as might occur through priority effects following a disturbance) versus gradual recruitment over years–decades.

Regardless of the mechanisms causing coral reef communities to differ in state and rate of change among sites around the US Virgin Islands, the outcome may have important implications with respect to community stability (sensu Connell and Slatyer 1977) on a landscape scale. Community synchrony (φ) describes the extent to which taxa in that community change in abundance in similar ways (Thibaut and Connolly 2013), and in the present case, it varied from complete synchrony at some sites ($\varphi = 1$) to near full asynchrony at others (φ trending to 0). Although φ tended to increase from 2011–2015 to 2015–2021, this effect was not statistically significant and, moreover, when φ was used to consider synchrony between sites, there was no evidence that φ changed over the study. Phi has utility in revealing the potential for portfolio effects (Thibaut and Connolly 2013) in species assemblages, where a high potential (low values of φ) can confer community stability (Thibaut and Connolly 2013) by spreading the risks of negative responses to environmental conditions among taxa. Inspection of the present trends in φ, therefore, support three inferences: (1) sites with low φ over 2015–2021 may be characterized by coral assemblages that are more resistant to future disturbances, (2) sites with high φ over 2015–2021 may have coral assemblages more susceptible to future disturbances, and (3) sites that show a strong increase in φ from 2011–2015 to 2015–2021 are of concern, because coral community stability in these locations appears to have deteriorated. The veracity of these inferences can be tested through further monitoring of these reef communities, but it is notable that coral cover declined at 11 of the present sites over 2011–2021, regardless of the degree of community synchrony. It is possible, therefore, that the relationship between stability and synchrony (i.e., portfolio effects) has been degraded by low abundances (i.e., coral cover of $\leq 7\%$ in 2021) under directional environmental change (Abbott et al. 2017).

The present sites initially were located haphazardly and were repeatedly surveyed using GPS and geographic features to relocate the sites. For each survey, reefs were sampled along a constant isobath using photoquadrats that were randomly placed along transects. The sites were not permanently marked, and large-scale sampling was achieved by trading precision of site relocation against capacity to visit multiple sites separated by as much as 37 km. The results cannot achieve the temporal resolution of repeated sampling of fixed plots (Green 1993; Van der Meer 1997), as used in the Territorial Coral Reef Monitoring Program of the US Virgin Islands (Ennis et al. 2020), and the sampling conducted between White Point and Cabritte Horn (Edmunds 2013) that the present study was designed to augment. As a result, temporal variation is not entirely independent of spatial relocation, with this effect strongest at sites with heterogeneous reef communities and less precise site relocation; these effects were realized at four sites. Sampling favored an *Orbicella*-dominated portion of the reef at Haulover Bay in 2015 (but not in 2011 or 2021) and at Inner Brass in 2011 (but not in 2015 or 2021), and sampling at Waterlemon Cay and Whistling Cay favored areas of low coral cover in 2015 (but not in 2011 or 2021). Such discrepancies are inherent in random or haphazard sampling of unmarked transects (but stratified by depth) (e.g., Aronson et al. 2005; Smith et al. 2008), and they can be mitigated through replication (e.g., multiple quadrats, transects, or sites). Nevertheless, repeated sampling at unmarked sites requires caution in interpreting abundance that vary among sampling times.

## Summary

This study reveals heterogeneity in coral reef community structure that affects both state (i.e., condition at one time) and dynamics (i.e., the rate of change). Spatial variation in community state corroborates trends reported for these sites in 2011 (Edmunds 2014; Edmunds et al. 2015), as well as for other sites throughout the Virgin Islands (Ennis et al. 2020). The site-dependent dynamics augment previous analyses (Edmunds 2014) to show with coarse resolution (i.e., coral cover) that the reefs are responding in the same way but at different rates to conditions that presumably are common to the region (e.g., seawater temperature and the outbreak of SCTLD). However, coral cover has declined twice as fast around St. Thomas compared to St. John, thus implicating island-scale effects as causes of coral mortality. Some of these island-scale effects probably represent the emergent properties of multiple coral taxa responding in different ways to similar environmental conditions at multiple sites. While these patterns are indicative of portfolio effects (Schindler et al. 2015), which have great ecological interest because of their capacity to promote community stability (Thibaut and Connolly 2013; Schindler et al. 2015), this potential does not seem to have prevented the decline of coral abundance around St. Thomas and St. John.

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**Author contributions** PJE designed, implemented and analyzed the study and completed the first draft of the manuscript; PJE and TBS collaborated on interpreting the data, developing the summary statements, and editing the final manuscript.

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**Data availability** The data for this project are hosted at http://www.bco-dmo.org/dataset/872285 and can be accessed using https://doi.org/10.26008/1912/bco-dmo.872285.1.

## Declarations

**Conflict of interest** The authors declare they have conflict of interests.

**Human and animal rights** All applicable international, national, and/or institutional guidelines for the care and use of animals were followed (no animals were manipulated or sampled in this research). Research was completed under research permits issued through the Virgin Islands National Park (VIIS-2021_SCI-0001).

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