Region-wide temporal and spatial variation in Caribbean reef architecture: is coral cover the whole story?

LORENZO ALVAREZ-FILIP*†, ISABELLE M. CÔTÉ†, JENNIFER A. GILL*‡, ANDREW R. WATKINSON§ and NICHOLAS K. DULVY†

*Centre for Ecology, Evolution, and Conservation, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK, †Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada V5A 1S6, ‡Tyndall Centre for Climate Change Research, Norwich NR4 7TJ, UK, §School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK

Abstract

The architectural complexity of coral reefs is largely generated by reef-building corals, yet the effects of current regional-scale declines in coral cover on reef complexity are poorly understood. In particular, both the extent to which declines in coral cover lead to declines in complexity and the length of time it takes for reefs to collapse following coral mortality are unknown. Here we assess the extent of temporal and spatial covariation between coral cover and reef architectural complexity using a Caribbean-wide dataset of temporally replicated estimates spanning four decades. Both coral cover and architectural complexity have declined rapidly over time, with little evidence of a time-lag. However, annual rates of change in coral cover and complexity do not covary, and levels of complexity vary greatly among reefs with similar coral cover. These findings suggest that the stressors influencing Caribbean reefs are sufficiently severe and widespread to produce similar regional-scale declines in coral cover and reef complexity, even though reef architectural complexity is not a direct function of coral cover at local scales. Given that architectural complexity is not a simple function of coral cover, it is important that conservation monitoring and restoration give due consideration to both architecture and coral cover. This will help ensure that the ecosystem services supported by architectural complexity, such as nutrient recycling, dissipation of wave energy, fish production and diversity, are maintained and enhanced.

Keywords: climate change, ecosystem services, foundation species, habitat loss, reef degradation

Received 1 October 2010; revised version received 2 December 2010 and accepted 4 December 2010

Introduction

In some ecosystems, complex structural or functional attributes can be provided by a single taxon. For example, particular tree species within forests or kelp in temperate seas can provide shelter and living space for a wide variety of other species (Jones *et al.*, 1997). In addition, foundation species can underpin fundamental ecosystem processes such as productivity and nutrient cycling (Bruno & Bertness, 2001; Ellison *et al.*, 2005). In tropical shallow waters, hard corals increase the architectural heterogeneity of the seascape considerably, providing suitable habitat and microclimatic conditions for a myriad of species and contributing substantially to ecosystem dynamics (Hatcher, 1997). Loss of hard corals on reefs is therefore likely to have severe repercussions for associated biodiversity, ecosystem structure, function and stability.

Hard corals are increasingly threatened worldwide by direct and indirect effects of human activities (Pandolfi *et al.*, 2003; Carpenter *et al.*, 2008; Mora, 2008). As result, live coral cover has decreased rapidly on tropical reefs throughout the world (Gardner *et al.*, 2003; Bruno & Selig, 2007). However, many of the services that coral reefs provide to humans and other species are mediated not by the cover of live hard corals but by the three-dimensional architectural complexity of the underlying reef structure. For instance, reef complexity is strongly related to the availability of shelter and refugia, and consequently to fish and invertebrate richness, abundance and biomass (e.g. Idjadi & Edmunds, 2006; Wilson *et al.*, 2007). Reef architecture also plays a key role in providing additional important environmental services to humans such as coastal protection. Wave energy transmitted over reefs is significantly dissipated by the friction exerted by bottom roughness (Lugo-Fernandez *et al.*, 1998; Sheppard *et al.*, 2005).

Correspondence: Lorenzo Alvarez-Filip, Centre for Ecology, Evolution, and Conservation, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK, tel. + 44 1603 591346, fax + 44 1603 593901, e-mail: lalvarez@sfu.ca

Reductions in the architectural complexity of Caribbean reefs have also occurred in recent decades (Alvarez-Filip *et al.*, 2009), but the extent to which the declines in coral cover and reef complexity are directly linked will depend on the nature of the any relationship between coral cover and complexity, and extent of any time lag between the coral mortality and the subsequent erosion of coral skeletons. At large scales, direct relationships between changing coral cover and reef architecture have been suggested based on the aftermath of widespread coral mortality following mass bleaching events on some Indo-Pacific reefs (Wilson *et al.*, 2006; Pratchett *et al.*, 2008). 'Before-and-after' comparisons of reefs either side of the 1998 ENSO bleaching event show that declines in architectural complexity appeared to lag behind bleaching-induced coral mortality by more than 5 years (Graham *et al.*, 2007, 2008). In contrast, there is little evidence in the Caribbean of a region-wide lag in loss of reef complexity following declines in coral cover, but turning points in the regional trajectory of declining architectural complexity coincide closely with the loss of structurally complex *Acropora* corals in the late 1980s and with bleaching-induced coral mortality in 1998 (Aronson & Precht, 2006; Alvarez-Filip *et al.*, 2009). Consequently, fundamental questions regarding the exact nature of the relationship between coral cover and reef architecture, including the generality of a 5-year lagged response, remain unanswered.

Here we use a Caribbean-wide dataset of temporally replicated coral cover and reef architecture estimates that spans four decades to explore the regional covariance in coral cover and reef architectural complexity. First, we test whether the change in architectural complexity lags behind the change in live coral cover. Second, we then explore the relationships between the annual rates of change in coral cover and architectural complexity. Third, we examine the variation among individual sites in live coral cover and reef architecture across the region.

Material and methods

Data collation

We collated all available site-specific data on the percentage cover of live hard coral and associated architectural complexity for reefs within the wider Caribbean Basin. We focused on studies that used the rugosity index to describe reef architecture, as this is the most commonly used method for measuring reef complexity in the region (Alvarez-Filip *et al.*, 2009). The rugosity index of reef complexity is a descriptor of small-scale reef relief and thus the patterns reported here relate primarily to fine-scale architectural complexity. However, the positive correlations between fine-scale reef rugosity and reefscape-scale visual and remote sensing estimates of complexity reported in some studies (Kuffner *et al.*, 2007; Wilson *et al.*, 2007; Alvarez-Filip, 2010) suggest that larger-scale patterns of complexity may, to some degree, follow the patterns depicted at finer scales. Reef rugosity is less frequently measured than coral cover, thus we first searched for studies reporting rugosity of specific sites, and then from this dataset we selected all studies that also reported information on coral cover.

The database was compiled by searching online ISI Web of Science, Google Scholar and other relevant databases (e.g. Reefbase) for peer-reviewed and grey literature. We searched for pertinent papers in all issues of the journals *Coral Reefs*, *Bulletin of Marine Sciences*, *Atoll Research Bulletin*, *Caribbean Journal of Science* and in all *Proceedings of the International Coral Reef Symposium*. Additionally, we directly contacted scientists and site managers asking for any available data pertaining to their study sites. The search resulted in a total of 81 studies that includes 312 records from 139 reefs surveyed between 1977 and 2008 across the Caribbean. From this larger database, we identified 24 studies with repeated measures (i.e. data collected over more than 1 year; Fig. S1). This subset included 96 records reporting information for 37 reef sites between 1978 and 2004 (Table S1), and ranging in duration from 2 to 12 years (mean = 5.01 ± 3.41 SD years).

Time-lags in the loss of reef architecture

To test for a delayed response in architectural complexity to changing coral cover, we first used all available studies (repeated and unrepeated) to calculate regional annual averaged estimates of live coral cover and reef rugosity. We then calculated the coefficient of correlation between annual average coral cover and architectural complexity for lags of up to 15 years. This technique provides a broad overview of the temporal correlations between coral cover and architectural complexity. However, each iteration includes data from different sites and thus spatial variation in either coral cover or architectural complexity could reduce the strength of the correlation and the power to detect lags.

To address this potential problem we used two methods to test for lagged effects using only repeated-measures studies, in which both coral cover and architectural complexity measures were available for more than 1 year. First, the coefficients of correlation between coral cover and architectural complexity were calculated for lags of up to 4 years for each separate time series (only for those eight time series with at least 4 years of overlapping data) and the overall mean correlation coefficient for each lag was calculated (Fig. S2). Second, we calculated lagged-correlations between the matrices of coral cover and architectural complexity of all sites with coral cover and architectural complexity estimates for each specific lag (equivalent to a 'lagged' Mantel test). This method allowed us to explore lags of up to 6 years across at least 12 sites. Our finding was robust to the choice of method (see Figs 1d and S2), so we present only the findings from the analysis of all 37 time series, as they provide much greater spatial and temporal representation.
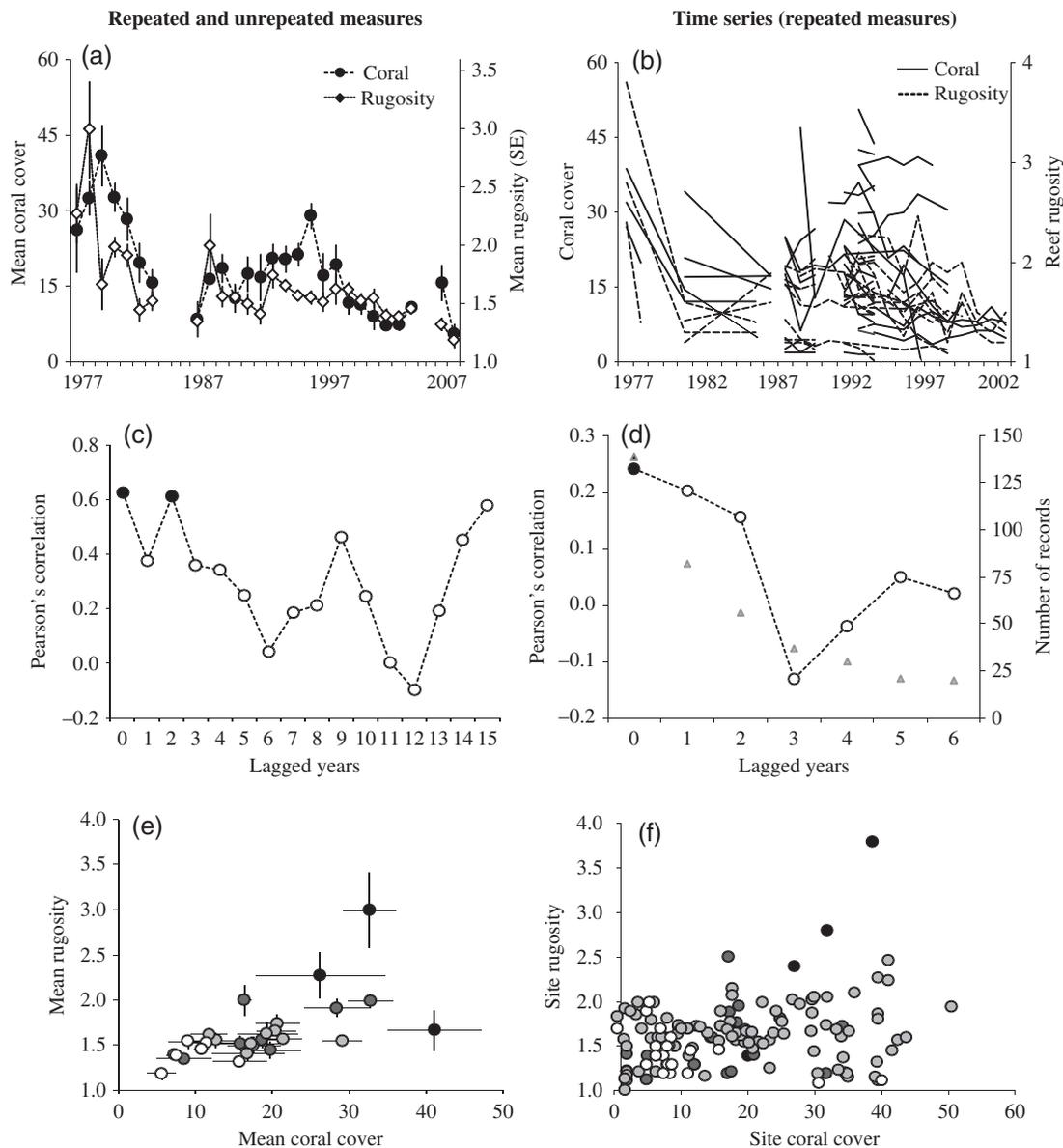
Repeated and unrepeated measures

Time series (repeated measures)

Fig. 1 Temporal relationships between coral cover and reef rugosity for Caribbean reef sites. Left panels are constructed with regional annual averaged (± SE) estimates of live coral cover and reef rugosity, showing (a) changes in mean coral cover and reef rugosity across the Caribbean from 1977 to 2008; (c) changes in Pearson correlation coefficients for lagged relationships between regional average live coral cover and reef rugosity for the same time period; and (e) the strongest correlation for lagged iterations (i.e. no-lag). Right panels are constructed with temporally replicated series, and show (b) live coral cover and reef rugosity for each of the 37 time series, (d) changes in Pearson's correlation coefficients for lagged relationships between live coral cover and reef rugosity on the same sites, in which each time series was lagged by one additional year in each iteration; and (f) the strongest correlation for those lagged iterations (i.e. no-lag). (b, e) Significant correlations, corrected for false discovery rates, are indicated with filled circles. The grey triangles in (b) indicate the number of records used in each iteration. (c, f) The decade that each estimate represents is indicated (black: 1970s, dark grey: 1980s, light grey: 1990s, white: 2000s).

In all analyses, the largest significant coefficient of correlation is considered as the best estimate of the number of years between the death of coral and a decline in architectural complexity. False discovery rates were used to correct for multiple tests (Benjamini & Hochberg, 1995).

Annual rates of change in coral cover and rugosity

To investigate the nature of the relationship between coral cover and reef architecture, we examined how annual region-wide changes in coral cover were related to the corresponding

annual change in architectural complexity between 1974 and 2004. Similar rates of change (and minimal lag) would indicate a strong direct relationship between coral cover and architectural complexity, whereas different rates of change would indicate that the relationship between the two is less direct and or potentially governed by different causal mechanisms. We used a weighted meta-analytic approach to estimate annual rates of change in live coral cover and reef architecture in the temporally replicated studies (Rosenberg *et al.*, 2000). The standardized effect size was the annual rate of change in coral cover and reef rugosity for each study, calculated as

$$\text{annual rate of change} = (\log End - \log Start)/d,$$

where *End* and *Start* represent the final and initial coral cover or reef rugosity of the time series, respectively, and *d* is the number of years elapsed between the two estimates. Calculating annual rates of change between the initial and final estimates for time series that both increase and decrease over time (see Fig. 1b) may not fully capture the overall change. We therefore performed a second analysis to calculate the annual rate of change from the average of the differences between each pair of years (note that some time series are not continuous) to produce site-specific estimates of change for coral cover and reef rugosity. Results from both analyses were very similar (see Figs 2 and S3), thus we only present findings from the first analysis, as this methodology has been previously used in studies of ecological change on coral reefs (Côté *et al.*, 2005; Paddack *et al.*, 2009) and its properties as an effect size have been thoroughly investigated (Côté *et al.*, 2005).

We weighted effect sizes using the natural logarithm of the total transect length surveyed (see also Mosqueira *et al.*, 2000; Côté *et al.*, 2001; Molloy *et al.*, 2008). Statistically significant effect sizes were identified by 95% bias-corrected bootstrapped confidence intervals (CI; generated from 9999 iterations) that did not encompass zero. The Q_M statistic was used to test for differences in rates of change in live coral cover and architectural complexity. A significant Q_M implies that there are differences in mean effect sizes among groups, but a nonsignificant Q_M does not preclude individual groups showing significant effect sizes (i.e. individual CIs that do not overlap zero). The meta-analyses were conducted in METAWIN Version 2.0 (Rosenberg *et al.*, 2000). Annual rates of change and confidence intervals are presented back-transformed to percentages to facilitate their interpretation.

Spatial relationships between coral cover and rugosity

Finally, we explored the variation in live coral cover and reef architecture among sites throughout the region using (i) all available data (i.e. repeated and unrepeated studies) and (ii) a smaller dataset of unrepeated measures (which avoids including more than one estimate per site). As both datasets provide very similar results (see Figs 3 and S4), we only present findings for all the available data because of the wider spatial and temporal representation. Preliminary analysis demonstrated that the variation in reef rugosity was unequal along the gradient of coral cover, so we used quantile regression to describe the relationship between coral cover and architectural complexity (Koenker & Bassett, 1978). Quantile regression differs from ordinary least squares regression in that it minimizes the sum of absolute values of residual errors around a specified quantile of the dependent variable, rather than just changes in the mean (Cade & Noon, 2003). Exploring the full range of quantile responses provides a more complete view of the relationship between variables than those captured by individual (median) quantile regression functions (Knight & Ackerly, 2002), hence we estimated the complete series of quantile regression functions from the 1st to the 99th quantile for the regional relationship between coral cover and reef architecture. Analyses were carried out in R and using the QUANTREG package (R, 2009).

Results

What is the time-lag between coral cover loss and reef architecture decline?

The annual mean estimates of coral cover and reef rugosity from sites throughout the Caribbean and the trajectories of individual time series both indicate declines in coral cover and architectural complexity over the last 30 years (Fig. 1a and b). However, there was little evidence for a time-lag of more than 2 years between the onset of a change in coral cover and a subsequent change in architectural complexity, either for sites throughout the region or for individual time series, (Figs 1c and d and S2). In all analyses, the strongest correlation between architectural complexity and coral cover was found when the data were unlagged (Figs 1e and f and S2). After correction for multiple tests, only the relationships with no lag and the 2-year lag of all sites were statistically significant ($\alpha = 0.05$, Tables S2 and S3). However, two relatively
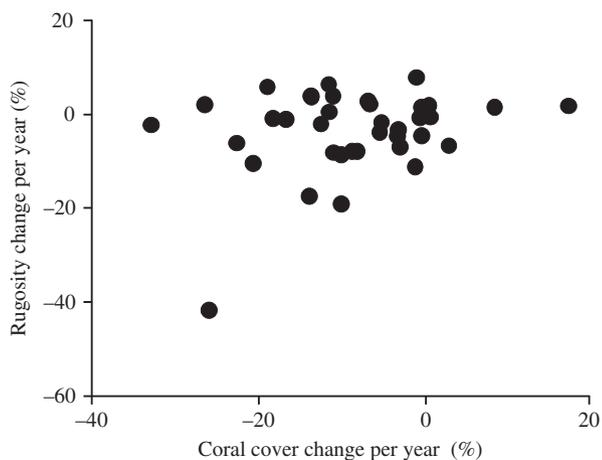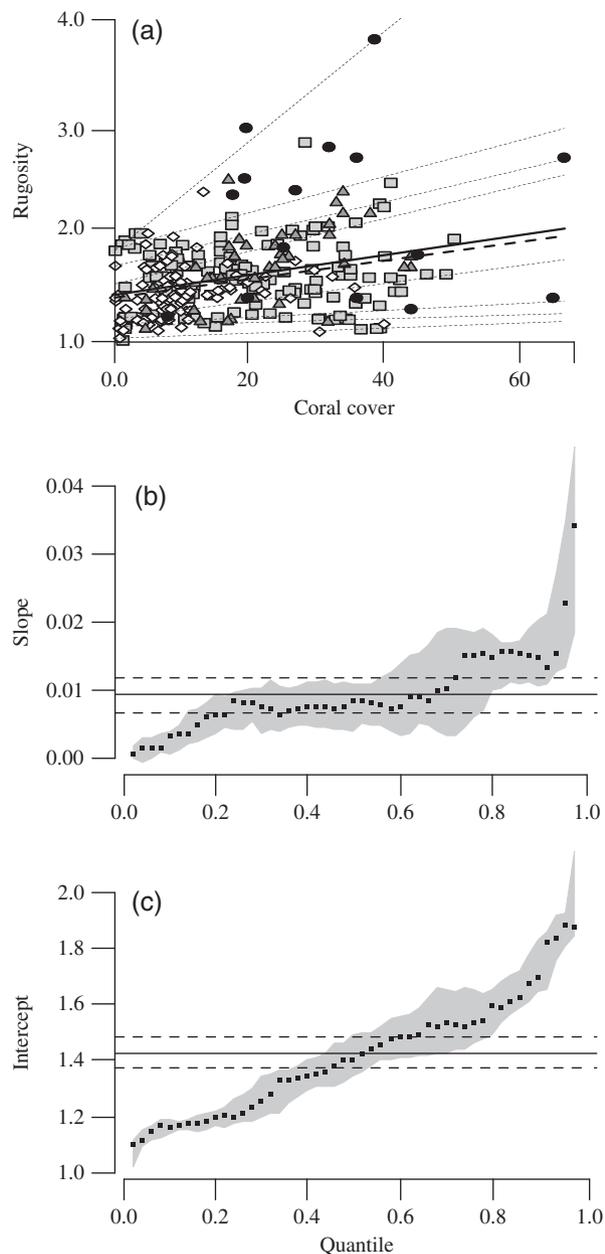

Fig. 2 The absence of a relationship between annual rates of change in live coral cover and architectural complexity on 37 reef sites across the Caribbean region ($R^2 = 0.07$, $P = 0.12$).

Fig. 3 (a) Relationship between coral cover and reef rugosity on 139 reef sites (323 surveys from 1977 to 2008) throughout the Caribbean. The decade in which each study was conducted is indicated (circles = 1970s, triangles = 1980s, squares = 1990s, diamonds = 2000s). Nine estimated quantile regression lines (0.01, 0.05, 0.1, 0.25, 0.5, 0.75, 0.9, 0.95, 0.99 quantile) are superimposed on the scatterplot; the median (0.5 quantile) is indicated with a black dashed line and the others are indicated with grey dotted lines. The least square estimate of the mean function is indicated by the black solid line ($R^2 = 0.11$, Slope = 0.009, $P < 0.001$). The (b) slopes and (c) intercepts of the quantile regressions are shown from the 0.01 quantile to the 0.99 quantile, with 90% confidence bands (grey shading), and the mean (solid line) ± 90% confidence intervals (dashed lines) from the ordinary least squares regression.

high correlation values also occur in the regional analysis at ~9 and 15 years (Fig. 1c), both of which are significant or marginally significant before the correction factors are applied (Table S2).

Are the rates of change in coral cover and reef architecture similar?

There is no consistent relationship between the annual rates of change in coral cover and annual changes in reef rugosity across the 37 sites with repeated measures (Fig. 2). The overall meta-analysis showed that both live coral cover and reef architecture have declined significantly (i.e. the confidence intervals do not encompass zero) but at different overall rates ($Q_M = 3.68$, $P = 0.054$). The annual rate of change in coral cover has been −8.6% (95% CI = −11.9% to −5.2%) whereas the annual change in rugosity has been −4.0% (95% CI = −7.8% to −1.3%).

Is reef architecture a function of coral cover?

Across 31 years and 139 reef sites throughout the Caribbean, architectural complexity varies greatly among sites with similar levels of coral cover (Fig. 3a). For example, the rugosity indices of reefs with 10% coral cover varies from 1.05 (i.e. relatively flat) to ~2.0 (i.e. moderately complex reefs) whereas, at 40% coral cover, rugosity ranges more widely from 1.05 to 3.5 (i.e. highly complex reefs; Fig. 3a). Quantile regression analyses indicated consistently positive relationships between coral cover and reef architecture, with steeper relationships for higher quantiles of architectural complexity (Fig. 3b). In the lower quantiles, rugosity is low across a wide range of coral cover estimates, indicating that reefs with relatively high coral cover may still be quite flat (Fig. 3b). By contrast, the steepest coral cover–architectural complexity relationships are associated with high rugosity even at the lowest levels of coral cover (Fig. 3b and c), with slopes of the highest quantiles lying far above the mean and 90% CI of the overall relationship (Fig. 3a and b). Thus, some reefs with lower coral cover may still have some level of architectural complexity.

Discussion

The region-wide decline in coral cover represents both an absolute loss and a reduction in the quality of reef habitat, but the implications of coral loss for reef architecture will depend on whether coral skeletons erode rapidly following coral mortality. Our findings indicate that, across the Caribbean, reductions in coral cover have been rapidly followed by the loss of architectural

complexity, despite variation among sites in the relationship between coral cover and architectural complexity and in their rates of change. This suggests that the scale, frequency and magnitude of stressors on Caribbean reefs have been sufficiently severe to cause declines in architectural complexity and live coral cover that are apparent at regional scales, despite small-scale variation in reef community composition and structure.

The trajectories of coral cover and architectural complexity are likely to be influenced by the scale, frequency and intensity of disturbances to reefs, and the degree to which drivers of change in coral cover and complexity co-occur in space and time. Events such as coral disease and bleaching can produce widespread coral mortality without immediately modifying the reef framework (beyond halting carbonate accretion; Glynn, 1997; Aronson & Precht, 2001; Sheppard *et al.*, 2002). By contrast, hurricanes and persistent direct human impacts can both kill coral and degrade underlying reef structures (Hughes, 1994; Hughes & Connell, 1999; Gardner *et al.*, 2005). In the Caribbean, drivers of both coral mortality and erosion have operated as virtually chronic pressures throughout the entire region in recent decades (Pandolfi *et al.*, 2003; Gardner *et al.*, 2005; Aronson & Precht, 2006; Mora, 2008). The similar timing and scale of the region-wide declines in coral cover and complexity are thus likely to be a consequence of these chronic pressures.

The absence of time-lags reported here may also be influenced by declines in coral cover and/or reef complexity that began some time before the onset of the time series. Declines in coral cover before the first year of our time series could influence subsequent declines in reef complexity during the first years of the time series, in which case longer periods of time may be needed to detect evidence of lags in reef erosion following coral mortality. The suggestion of high region-wide correlations between coral cover and architectural complexity after 9–15 years (Fig. 1c), suggests that there may be some evidence for lags in the erosion of architectural complexity on time-scales that may be expected for some biological disturbances, such as bleaching or diseases (Pratchett *et al.*, 2008). As these time series accumulate, so too will the power to evaluate the significance of these longer lags.

The rate of decline in Caribbean reef complexity over the last three decades may be influenced by the relative abundance of different coral morpho-functional types, which can vary in both structure and relative susceptibility to erosion following mortality. In the Caribbean, the largest changes in coral cover occurred as a result of the disease-induced die-off of acroporids in the late 1970s and early 1980s (Aronson & Precht, 2006; Schutte *et al.*, 2010). Before this the erect branching structures of

Acropora corals contributed disproportionately to reef complexity. Although the robust skeletons of *A. palmata* may have persisted longer than the fragile framework of *A. cervicornis* in some locations, the regional trends of declining coral cover and architectural complexity suggest that most dead *Acropora* were relatively rapidly broken down and eroded following mortality (Aronson & Precht, 2006; Alvarez-Filip *et al.*, 2009). In our study, similarly rapid annual rates of change of both coral cover and architectural complexity were apparent during the *Acropora* die-off period (1978–1985; coral cover $=-23.19$, bias-corrected 95% CI $=-2.73$ to -1.49; rugosity $=-27.03$, bias-corrected 95% CI $=-14.64$ to -9.57), suggesting a rapid response of architectural complexity to coral cover loss during this period. However, only three studies are available for these years, and therefore the temporal pattern of decline in reef complexity reported here refers primarily to the years since the demise of *Acropora*, in which Caribbean reefs have been dominated by a combination of massive and weedy corals.

The weak relationship between rates of change in coral cover and architectural complexity (Fig. 2) suggests that additional factors have influenced the response of reef complexity to the loss of coral cover. Caribbean coral communities have changed continuously since the mass mortality of acroporids. Important reef-building corals such as *Montastrea* have been declining throughout the region and stress-resistant coral species that contribute relatively little to the reef framework and architectural complexity have increasingly dominated Caribbean reefs (e.g. *Agaricia* and *Porites*; Hughes, 1994; Edmunds & Carpenter, 2001; Aronson *et al.*, 2002; Green *et al.*, 2008). Thus changes in coral composition leading to 'flatter' reef communities, together with possible changes in carbonate budgets as a consequence of higher amounts of bare substrata (Eakin, 1996; Glynn, 1997), can occur in the absence of declines in coral cover. Previous studies do indeed suggest that rates of loss of Caribbean reef architecture have remained high in recent years (Alvarez-Filip *et al.*, 2009), while coral loss has almost ceased (Schutte *et al.*, 2010).

For any given level of coral cover, reef rugosity can vary markedly (Fig. 3). Although variation in other reef organisms, such as sponges and soft corals, may contribute to local reef rugosity (e.g. Diaz & Rutzler, 2001; Halford *et al.*, 2004), it is likely that much of the variation in architectural complexity reflects different habitat types and variation in coral species assemblages (Chittaro, 2004; Alvarez-Filip, 2010). Coral identity may therefore be an important mediator of reef complexity and, consequently, the impact of coral loss on reef architecture will differ among sites, with sites domi-

nated by architecturally complex reef-building corals bearing the greatest losses in rugosity following coral mortality. Unfortunately, coral species composition and reef type were seldom reported in the studies included here, hence we could not explore their influence on patterns of change in architectural complexity.

The loss of architectural complexity following declines in coral cover in the Caribbean differs from the pattern reported in the Indo-Pacific region, where a lagged response in the aftermath of widespread coral mortality following mass bleaching events was apparent (Wilson *et al.*, 2006; Graham *et al.*, 2007, 2008; Pratchett *et al.*, 2008). However, these studies encompassed different temporal scales; our Caribbean analyses explore year-by-year changes throughout a multidecadal period of continual coral and reef architecture loss, whereas the Indo-Pacific studies spanned either side of a discrete catastrophic coral mortality event. In addition, there are important historical and ecological differences between these two regions that are likely to influence these processes, with Caribbean reefs typically having fewer coral species, less ecological redundancy and frequent hurricane impacts (Bellwood *et al.*, 2004; Briggs, 2005). To determine whether our findings can be broadly generalized would require similar longitudinal and spatial studies of Indo-Pacific reefs.

Architectural complexity is clearly not a simple function of coral cover. Therefore, to restore the ecosystem services that Caribbean reefs provide to other species, including humans, these two critical reef attributes may need to be considered separately and at different spatial scales. Much of coral reef conservation at present focuses on ecological management and control of the cover of coral and algae (Gardner *et al.*, 2003; Côté *et al.*, 2006; Bruno & Selig, 2007; Mumby *et al.*, 2007; Bruno *et al.*, 2009). However, restoring coral cover on reefs may not necessarily provide the architectural complexity that underpins important coral reef ecosystem services relating to nutrient recycling, dissipation of wave energy and fish production (Szmant, 1997; Lugo-Fernandez *et al.*, 1998; Sheppard *et al.*, 2005). Understanding the range of the biotic and abiotic drivers of architectural complexity may therefore provide an effective means of targeting reef management in relation to the services provided by different reef structures.

References

Alvarez-Filip L (2010) *Habitat complexity in coral reefs: patterns of degradation and consequences for biodiversity.* PhD thesis, University of East Anglia, Norwich, 124 pp.

Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 3019–3025.

Aronson RB, Macintyre IG, Precht WF, Murdoch TJT, Wapnick CM (2002) The expanding scale of species turnover events on coral reefs in Belize. *Ecological Monographs*, **72**, 233–249.

Aronson RB, Precht WF (2001) White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia*, **460**, 25–38.

Aronson RB, Precht WF (2006) Conservation, precaution, and Caribbean reefs. *Coral Reefs*, **25**, 441–450.

Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. *Nature*, **429**, 827–833.

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate – a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B – Methodological*, **57**, 289–300.

Briggs JC (2005) Coral reefs: conserving the evolutionary sources. *Biological Conservation*, **126**, 297–305.

Bruno JF, Bertness MD (2001) Habitat modification and facilitation in benthic marine communities. In *Marine Community Ecology* (eds Bertness MD, Gaines SD, Hay ME), pp. 201–218. Sinauer, Sunderland, MA.

Bruno JF, Selig EZ (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS One*, **2**, e711.

Bruno JF, Sweatman H, Precht WF, Selig ER, Schutte VGW (2009) Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology*, **90**, 1478–1484.

Cade BS, Noon BR (2003) A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment*, **1**, 412–420.

Carpenter KE, Abrar M, Aeby G *et al.* (2008) One-third of Reef-building Corals face elevated extinction risk from climate change and local impacts. *Science*, **321**, 560–563.

Chittaro PM (2004) Fish–habitat associations across multiple spatial scales. *Coral Reefs*, **23**, 235–244.

Côté IM, Gardner TA, Gill JA, Hutchinso DJ, Watkinson AR (2006) New approaches to estimating recent ecological changes on coral reefs. In *Coral Reef Conservation* (eds Côté IM, Reynolds DJ), pp. 293–313. Cambridge University Press, Cambridge, UK.

Côté IM, Gill JA, Gardner TA, Watkinson AR (2005) Measuring coral reef decline meta-analyses. *Philosophical Transactions of the Royal Society*, **360**, 385–395.

Côté IM, Mosqueira I, Reynolds JD (2001) Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. *Journal of Fish Biology*, **59**, 178–189.

Diaz MC, Rutzler K (2001) Sponge: an essential component of Caribbean coral reefs. *Bulletin of Marine Science*, **69**, 535–546.

Eakin CM (1996) Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982–1983 El Nino at Uva Island in the eastern Pacific. *Coral Reefs*, **15**, 109–119.

Edmunds PJ, Carpenter RC (2001) Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *Proceedings of the National Academy of Sciences*, **98**, 5067–5071.

Ellison AM, Bank MS, Clinton BD *et al.* (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment*, **3**, 479–486.

Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science*, **301**, 958–960.

Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2005) Hurricanes and Caribbean coral reefs: impacts, recovery patterns, and role in long-term decline. *Ecology*, **85**, 174–184.

Glynn PW (1997) Bioerosion and coral reef growth: a dynamic balance. In *Life and Death of Coral Reefs* (ed Birkeland CE), pp. 68–95. Chapman & Hall, New York.

Graham NAJ, Mcclanahan TR, Macneil MA *et al.* (2008) Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems. *PLoS One*, **3**, e3039.

Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Robinson J, Bijoux JP, Daw TM (2007) Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conservation Biology*, **21**, 1291–1300.

Green DH, Edmunds PJ, Carpenter RC (2008) Increasing relative abundance of *Porites astreoides* on Caribbean reefs mediated by an overall decline in coral cover. *Marine Ecology Progress Series*, **359**, 1–10.

Halford A, Cheal AJ, Ryan D, Williams DM (2004) Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. *Ecology*, **85**, 1892–1905.

Hatcher BG (1997) Coral reef ecosystems: how much greater is the whole than the sum of the parts? *Coral Reefs*, **16**, S77–S91.

Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, **256**, 1547–1551.

Hughes TP, Connell JH (1999) Multiple stressors on coral reefs: a long-term perspective. *Limnology and Oceanography*, **44**, 932–940.

Idjadi JA, Edmunds PJ (2006) Scleractinian corals as facilitators for other invertebrates on a Caribbean reef. *Marine Ecology Progress Series*, **319**, 117–127.

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, **78**, 1946–1957.

Knight CA, Ackerly DD (2002) Variation in nuclear DNA content across environmental gradients: a quantile regression analysis. *Ecology Letters*, **5**, 66–76.

Koenker R, Bassett G (1978) Regression quantiles. *Econometrica*, **46**, 33–50.

Kuffner IB, Brock JC, Grober-Dunsmore R, Bonito VE, Hickey TD, Wright CW (2007) Relationships between reef fish communities and remotely sensed rugosity measurements in Biscayne National Park, Florida, USA. *Environmental Biology of Fishes*, **78**, 71–82.

Lugo-Fernandez A, Roberts HH, Suhayda JN (1998) Wave transformations across a Caribbean fringing-barrier Coral Reef. *Continental Shelf Research*, **18**, 1099–1124.

Molloy PP, Reynolds JD, Gage MJG, Mosqueira L, Côté IM (2008) Links between sex change and fish densities in marine protected areas. *Biological Conservation*, **141**, 187–197.

Mora C (2008) A clear human footprint in the coral reefs of the Caribbean. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 767–773.

Mosqueira I, Côté IM, Jennings S, Reynolds JD (2000) Conservation benefits of marine reserves for fish populations. *Animal Conservation*, **3**, 321–332.

Mumby PJ, Hastings A, Edwards HJ (2007) Thresholds and the resilience of Caribbean coral reefs. *Nature*, **450**, 98–101.

Paddack MJ, Reynolds JD, Aguilar C *et al.* (2009) Recent region-wide declines in Caribbean Reef fish abundance. *Current Biology*, **19**, 590–595.

Pandolfi JM, Bradbury RH, Sala E *et al.* (2003) Global trajectories of the long-term decline of Coral Reef ecosystems. *Science*, **301**, 955–958.

Pratchett MS, Munday PL, Wilson SK *et al.* (2008) Effects of climate-induced coral bleaching on coral-reef-fishes ecological and economic consequences. *Oceanography and Marine Biology: An Annual Review*, **46**, 251–296.

R (2009) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rosenberg MS, Adams DC, Gurevitch J (2000) *MetaWin: Statistical Software for Meta-Analysis, Version 2.0*. Sinauer, Sunderland, MA.

Schutte VGW, Selig ER, Bruno JF (2010) Regional spatio-temporal trends in Caribbean coral reef benthic communities. *Marine Ecology Progress Series*, **402**, 115–122.

Sheppard C, Dixon DJ, Gourlay M, Sheppard A, Payet R (2005) Coral mortality increases wave energy reaching shores protected by reef flats: examples from the Seychelles. *Estuarine Coastal and Shelf Science*, **64**, 223–234.

Sheppard CRC, Spalding M, Bradshaw C, Wilson S (2002) Erosion vs. recovery of coral reefs after 1998 El Nino: Chagos reefs, Indian Ocean. *Ambio*, **31**, 40–48.

Szmant AM (1997) Nutrient effects on coral reefs: a hypothesis on the importance of topographic and trophic complexity to reef nutrient dynamics. *Proceedings of the 8th International Coral Reef Symposium*, **2**, 1527–1532.

Wilson SK, Graham NAJ, Polunin NVC (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine Biology*, **151**, 1069–1076.

Wilson SK, Graham NAJ, Pratchett MS, Jones GP, Polunin NVC (2006) Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology*, **12**, 2220–2234.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Regional distribution of reef sites with both live coral cover and rugosity data replicated over more than one year.

Figure S2. Pearson correlation coefficients for lagged relationships between live coral cover and reef rugosity on eight reef sites (grey circles). Black triangles represent the average across all time series.

Figure S3. Relationship between the averages ($\pm$ SE) of the annual rates of change in live coral cover and architectural complexity on 37 reef sites across the Caribbean region ($R^2 = 0.09$, $P = 0.08$). At each site, rates of change were calculated between each pair of years and then averaged to produce a site estimate of change for coral cover and reef rugusity.

Figure S4. (*a*) Relationship between coral cover and reef rugosity on 140 unreplicated reef surveys through the Caribbean from 1977 to 2008. The decade in which each study was conducted is indicated (circles = 1970s, triangles = 1980s, squares = 1990s, diamonds = 2000s). Nine estimated quantile regression lines (0.01, 0.05, 0.1, 0.25, 0.5, 0.75, 0.9, 0.95, 0.99 quantile) are superimposed on the scatterplot; the median (0.5 quantile) is indicated with a black dashed line and the others are indicated with grey dotted lines. The least square estimate of the mean function is indicated by the black solid line ($R^2 = 0.19$, Slope = 0.013, $P < 0.001$). The (*b*) slopes and (*c*) intercepts of the quantile regressions are shown from the 0.01 quantile to the 0.99 quantile, with 90% confidence bands (grey shading), and the mean (solid line) $\pm$ 90% confidence intervals (dashed lines) from the ordinary least squares regression.

Table S1. Supplementary site information of the time series reporting coral cover and reef rugosity for Caribbean reefs.

Table S2. Unadjusted and corrected (using false discovery rates) *P* values of the correlations between the regional average live coral cover and reef rugosity from 1978 to 2008, with time-lags ranging from 0 to 15 years.

Table S3. Unadjusted and corrected (using false discovery rates) *P* values of regional correlation between site-lagged live coral cover and reef rugosity, with time-lags ranging from 0 to 6 years.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.