Functional Ecology | BRITISH ECOLOGICAL SOCIETY

Morphological traits can track coral reef responses to the Anthropocene

Kyle J. A. Zawada[1,2] | Joshua S. Madin[3] | Andrew H. Baird[4] | Tom C. L. Bridge[4,5] | Maria Dornelas[1]

[1]Centre for Biological Diversity, Scottish Oceans Institute, University of St. Andrews, St. Andrews, UK

[2]Department of Biological Sciences, Macquarie University, Sydney, New South Wales, Australia

[3]Hawai'i Institute of Marine Biology, University of Hawai'i at Manoa, Kaneohe, Hawai'i

[4]Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland, Australia

[5]Biodiversity and Geosciences Program, Museum of Tropical Queensland, Queensland Museum Network, Townsville, Queensland, Australia

Correspondence
Kyle J. A. Zawada
Email: kz28@st-andrews.ac.uk

Abstract

1. Susceptibility to human-driven environmental changes is mediated by species traits. Therefore, identifying traits that predict organism performance, ecosystem function and response to changes in environmental conditions can help forecast how ecosystems are responding to the Anthropocene.
2. Morphology dictates how organisms interact with their environment and other organisms, partially determining the environmental and biological contexts in which they are successful. Morphology is important for autogenic ecosystem engineering organisms, such as reef-building corals, because it determines the shape of the structures they create and by extension the communities they support.
3. Here, we present six morphological traits that capture variation in volume compactness, surface complexity and top-heaviness. With support from the literature, we propose causal links between morphology and a performance–function–response framework.
4. To illustrate these concepts, we combine 3D scanning and coral survey data to predict morphological traits from in situ colonies. We present a case study that examines how assemblage-scale morphological traits have responded to two cyclones and the 2016 mass bleaching event—two phenomena predicted to increase in severity in the Anthropocene—and discuss how these changes may impact ecosystem function.
5. The morphological traits outlined here offer a generalised and hypothesis-driven approach to tracking how reefs respond to the Anthropocene. The ability to predict these traits from field data and the increasing use of photogrammetry makes them readily applicable across broad spatiotemporal scales.

KEYWORDS
Anthropocene, coral reef, cyclones, disturbances, functional traits, morphology, performance traits, response traits

1 | INTRODUCTION

Ecosystem engineers are organisms which facilitate the presence of other species by modifying the environment. Understanding how ecosystem engineers respond to human activity is important given their fundamental role in ecosystems and the intensification of anthropogenic activity (Steffen, Broadgate, Deutsch, Gaffney, & Ludwig, 2015). Some traits of ecosystem engineers determine their performance, the effects they have on the environment and how they response to anthropogenic activity. Identifying traits that are

both measurable across different taxa and are linked to multiple biological and ecological processes should help establish causal pathways between anthropogenic activity and changes in ecosystem function. Here, we propose six morphological traits in reef-building corals, a diverse set of ecosystem engineers that are under increasing pressure from anthropogenic activity. We outline how these traits map to organism performance, ecosystem function and response to changing conditions and disturbances. We then provide a case study linking morphological traits to assemblage-scale responses to two cyclones and a mass bleaching event and discuss these results and approach in the context of increasing anthropogenic activity.

Many ecosystem engineers are niche constructors: organisms that significantly modify their environment in ways that improve their fitness (Laland, Matthews, & Feldman, 2016), with humans arguably the most prevalent and successful niche constructors on the planet. Human niche construction is now so extensive that many argue that the planet has entered a new geological era, the Anthropocene, defined by human activities becoming significant geological forces (Crutzen, 2006). Ecosystem engineers can also modify the availability of niches for other organisms (Stachowicz, 2001). The difference between ecosystem engineers and niche constructors is whether the modifications an organism has on the environment translates to changes in selection pressures that influence evolutionary processes; if it does, then it is a niche constructor (Laland et al., 2016). Similarly, processes associated with the Anthropocene will likely result in changes in selection pressures for many ecosystem engineers, requiring their evolution if they are to persist and potentially changing their capacity to act as ecosystem engineers.

We propose that the traits of ecosystem engineers can be linked to three fundamental processes that shape the maintenance and functioning of ecosystems: (a) organism "performance," (b) ecosystem "function" and (c) "response" to changing environmental conditions and to disturbances. "Performance" is defined here as any process that affects the organism itself, in terms of its ability to obtain and retain resources, competitive ability and demography. While the definition of "function" in a trait context is still up for debate (Bellwood, Streit, Brandl, & Tebbett, 2019; Violle et al., 2007), we define "function" here as the biological, geochemical and physical processes occurring within an ecosystem that determine the presence and abundance of other organisms. "Response" is defined here as the effects of external processes, such as changing environmental conditions or acute disturbance events, on the assemblage. Together, these form a performance–function–response (PFR) framework that can be unified via traits that covary with each process simultaneously.

The PFR framework unifies previous classifications of traits. Specifically, traits can be classified as being response and/or effect traits, where a response trait determines how organisms respond to change and an effect trait determines how an organism affects ecosystem processes (Suding et al., 2008). In parallel, the functional trait framework links traits to organism performance (Violle et al., 2007). The PFR framework unifies these ideas and focusses on traits that covary across multiple processes, for example, identifying traits linked

to both disturbance susceptibility and ecosystem function. Including organism performance can determine how organisms with traits that make them susceptible to a disturbance may also facilitate their subsequent recovery due to rapid growth and reproduction. This can then be used to identify which "responses" are part of an assemblage's adaptive strategy (i.e. long-term history of disturbance and recovery) and which are not (i.e. anthropogenically forced changes outside of adaptive histories). Further, a performance–function trait link may help indicate how rapidly ecosystem functions recover following disturbance: A trait associated with rapid growth may return to pre-disturbance levels faster than a trait that covaries with slower growth, along with any ecosystem functions associated with that trait.

Reef-building corals are one of the most well-known ecosystem engineers on Earth, providing habitat for a large number and diversity of organisms (Bell & Galzin, 1984; Jones & Syms, 1998), yet they are also increasingly affected by human activity (Hughes et al., 2017; Norström et al., 2016), through exposure to a broad range of novel ecosystem drivers (Williams et al., 2019). Many processes that determine the success of corals, and the ecosystem functions they provide, are linked to colony morphology. From a performance perspective, morphology has been linked to competitive ability (Connell et al., 2004; Precoda, Allen, Grant, & Madin, 2017), distribution along environmental gradients (Chappell, 1980; Done, 2011; Gove et al., 2015) and demographic processes such as growth, reproduction and survival (Álvarez-Noriega et al., 2016; Dornelas, Madin, Baird, & Connolly, 2017; Madin, Baird, Dornelas, & Connolly, 2014). Corals are well-established ecosystem engineers, building and maintaining the reef structure (Rasser & Riegl, 2002), providing direct and indirect habitat (Bell & Galzin, 1984) and changing local abiotic conditions (Richardson, Graham, Pratchett, & Hoey, 2017). As autogenic engineers, their morphology directly or indirectly modulates ecosystem function. Corals are also susceptible to disturbances associated with the Anthropocene, such as cyclones and thermal anomalies (Hughes, Anderson, et al., 2018; Loya et al., 2001; Madin & Connolly, 2006; Marshall & Baird, 2000; Massel & Done, 1993), in addition to longer term changes such as ocean acidification (Chan & Connolly, 2013), that threaten to compromise their capacity to build and maintain the reef framework (Perry & Alvarez-Filip, 2018), as well as many other ecosystem functions (Woodhead, Hicks, Norström, Williams, & Graham, 2019). In many cases, morphology covaries with susceptibility to disturbances. For example, the bleaching response of corals is partially dependant on their morphology, resulting in assemblage-scale shifts in functional traits (Hughes, Kerry, et al., 2018). These characteristics make reef-building corals a high-profile and pressing candidate system for exploring the PFR framework via morphological traits.

As we progress further into the Anthropocene, many ecosystems will increasingly be exposed to conditions outside of their adaptive histories. Ecosystem engineers, and the communities that rely on them, will likely respond to these changes in some form. Understanding and predicting these responses is difficult due to high taxonomic and spatiotemporal diversity that requires

large sampling effort to obtain sufficient data for each species, in addition to the challenge of surveying the large number of rare species in most communities (McGill et al., 2007). Identifying shared traits that covary and are expected to be causally linked with multiple processes simultaneously is one method to deal with the complexity of the problem. Here, we outline the PFR framework for reef-building scleractinian corals, an important group of ecosystem engineering organisms, focussing on morphological traits. We present six morphological traits that represent three axes of morphological variation in shape and outline how morphology maps across variation in performance, function and response, with support from the literature. We then explore changes in assemblage-scale traits with long-term coral survey data that captured two cyclones and the 2016 mass bleaching event to highlight the benefits provided by our approach. The aim of this study was to provide a quantitative and readily understandable approach to tracking reef futures as we progress further into the Anthropocene.

2 | MORPHOLOGICAL TRAITS LINKED TO PERFORMANCE, FUNCTION AND RESPONSE IN CORALS

Surface area, volume and planar area are commonly used morphological traits in corals. Surface area is important because most of the coral biomass is located at the surface and is where the coral interacts with the environment (Johannes & Wiebe, 1970), though live tissue can penetrate a few millimetres into the skeleton in some species (Edmunds & Gates, 2002). Most of the colony volume is non-living aragonite skeleton that requires a large proportion of the colony's energy to produce (Osinga et al., 2011). Planar area is the

two-dimensional area of a colony when viewed from above and is a low-cost measure of colony size commonly used in field studies, and recent work has shown that planar area and growth form can estimate surface area and volume accurately (House et al., 2018). However, these traits alone cannot capture how surface area and volume are distributed. For example, the adaptive benefits of a tabular morphology (i.e. top-heavy, thin plates with many small branches), such as shading out competitors and fast horizontal growth, cannot be described by surface area or volume in isolation.

Recently, we used three-dimensional laser scans of coral skeletons to measure morphological variation in coral (Zawada, Dornelas, & Madin, 2019). We outlined three axes of variation in shape: volume compactness, surface complexity and top-heaviness, with each axis represented by two traits. We also measured three size traits, volume, surface area and planar area (Table 1). Below, we outline how colony shape explains variation in performance, function and response processes, with support from the literature. We concentrate on colony shape here; however, the size of the colony will likely influence the effects of colony shape in many cases.

2.1 | Volume compactness

Volume compactness captures a gradient from "massive," boulder-like shapes to a variety of more intricate shapes such as tabular and "arborescent" branching colonies (Figure 1). Volume compactness is captured by two shape variables. The first, sphericity, is calculated using the surface area of the colony and the surface area of a sphere with the same volume as the colony. A sphere is the most compact shape possible in three dimensions, and so the ratio between the surface area of the sphere and the colony acts as a measure for volume compactness. Convexity is the second compactness variable, which is calculated by dividing the volume of the convex hull

TABLE 1 Four morphological axes of variation in corals represented by 11 traits

Morphological axis	Morphological trait	Description	Formula
Volume compactness	Sphericity	The ratio of the surface area of a sphere with the same volume as the object (O_{VOL}) and the surface area of the object (O_{SA})	$S = \dfrac{\pi^{1/3}(6O_{VOL})^{2/3}}{O_{SA}}$
	Convexity	The ratio of the volume of the object (O_{VOL}) and the volume of the convex hull around the object (C_{VOL})	$C = O_{VOL}/C_{VOL}$
Surface complexity	Fractal dimension	The slope of the number of boxes at size S that contain part of the object (N^S) and the size of the boxes (S)	$FD = \dfrac{\Delta \log N^S}{\Delta \log S}$
	Packing	The ratio of the surface area of the object (O_{SA}) and the surface area of the convex hull around the object (C_{SA})	$P = O_{SA}/C_{SA}$
Top-heaviness	First moment of surface area	The total surface area of the object (O_{SA}) multiplied by vertical distance from the objects lowest point (H). When comparing objects, each object should be scaled to a standard volume to remove size-related differences	$V_{SA} = \int_{H=0}^{H^{max}} O_{SA} H$
	First moment of volume	The total volume of the object (O_{VOL}) multiplied by vertical distance from the objects lowest point (H). When comparing objects, each object should be scaled to a standard volume to remove size-related differences	$V_{VOL} = \int_{H=0}^{H^{max}} O_{VOL} H$
Size	Volume	The total volume of the object	
	Surface area	The total surface area of the object	
	Planar area	The 2D projected area of the object when viewed from above	

of the colony (the smallest possible, completely convex shape that encloses the colony) by the volume of the colony. The convex hull of an object can be calculated on 3D coordinates using the quick-hull algorithm (Barber, Dobkin, & Huhdanpaa, 1996). Sphericity can be calculated from surface area and volume estimated from three-dimensional or non-three-dimensional methods (e.g. wax dipping, photogrammetry, laser scanning), whereas convexity requires a three-dimensional model of the colony (e.g. from photogrammetry, laser scanning).

For ecological performance, lower compactness relates to a "boom-and-bust" growth strategy, where colonies grow faster (Gladfelter, Monahan, & Gladfelter, 1978), but are more likely to
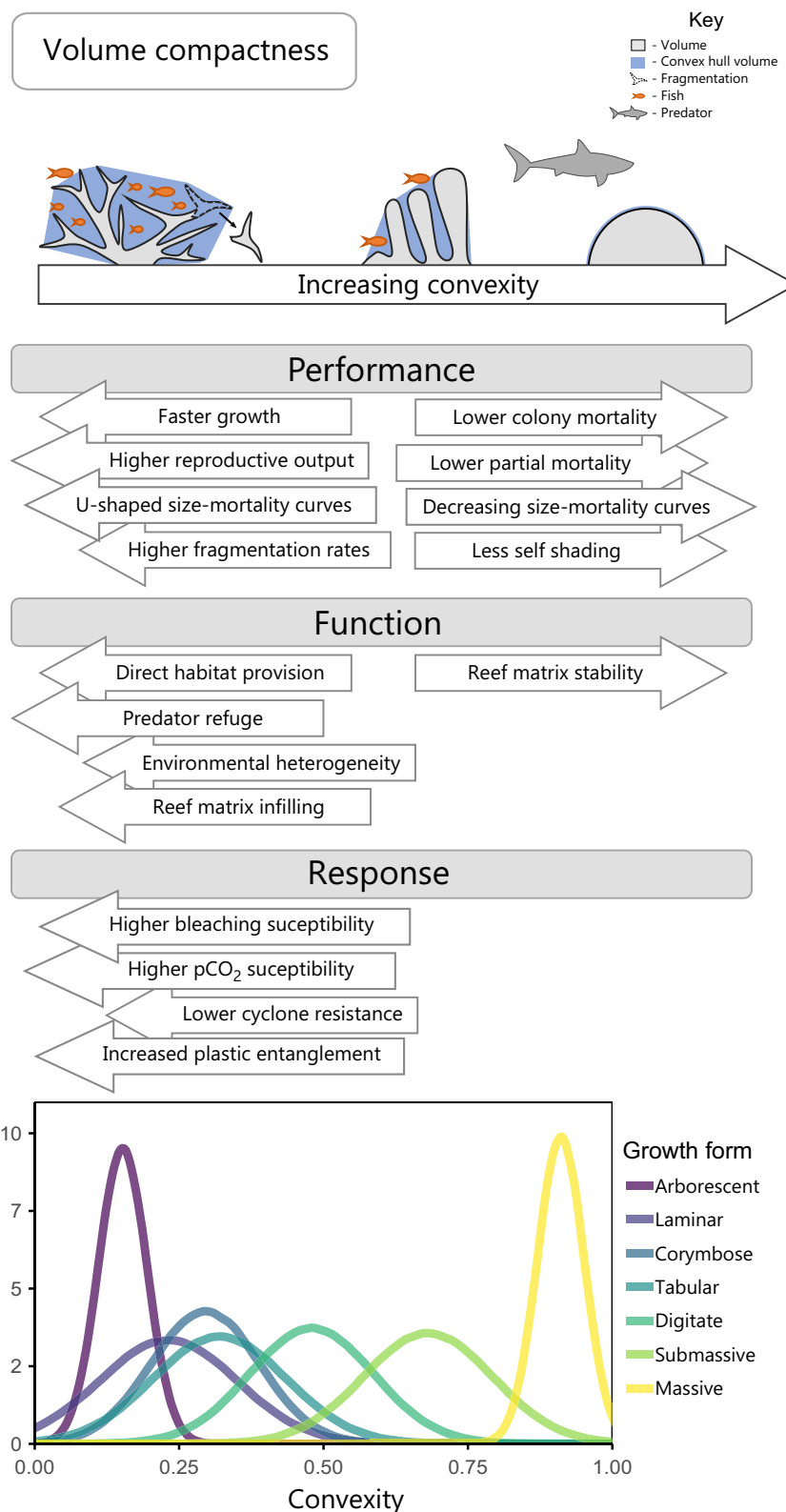

FIGURE 1 A conceptual figure outlining what variation in volume compactness means for (organism) performance, (ecosystem) function and response (to disturbances and changing conditions). While both sphericity and convexity capture variation in volume compactness, convexity is used here for clarity. Convexity is calculated by dividing the volume of the colony (or any other object) by the volume of the convex hull. The more compact a colony is, the less unoccupied space within the colony there is. The bottom panel shows the resampled distribution of convexity values using the mean and standard deviation for seven growth forms based on high-resolution laser-scanned colonies (Zawada et al., 2019), providing empirical support for the distribution of growth forms along a continuous trait axis
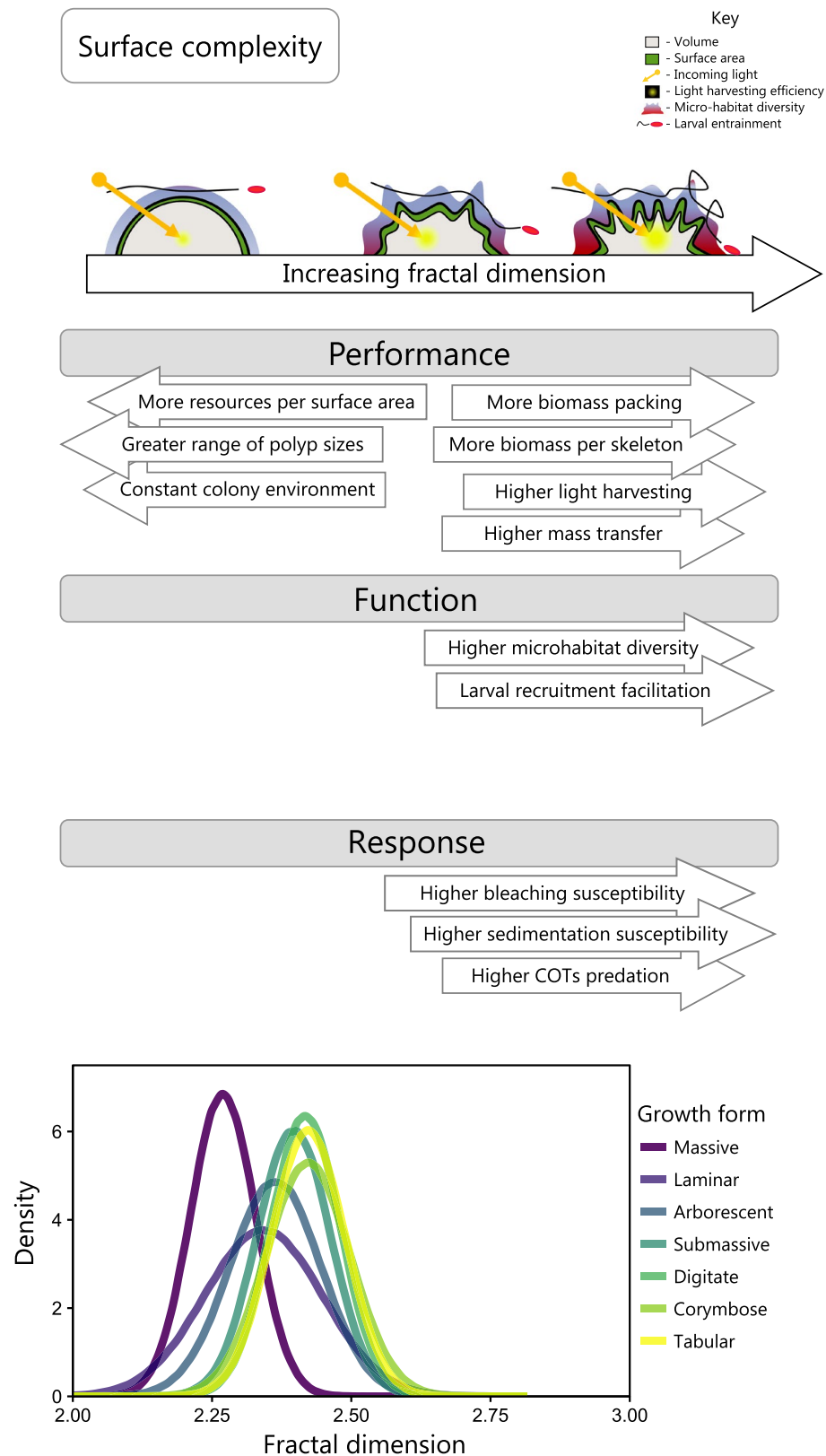
FIGURE 2 A conceptual figure outlining what variation in surface complexity means for (organism) performance, (ecosystem) function and response (to disturbances and changing conditions). While both packing and fractal dimension capture variation in surface complexity, fractal dimension is used here for clarity. Fractal dimension can be visualised as how much colony surface area there is per unit volume; the more convoluted the colony surface is, the more surface area is packed within local space. The bottom panel shows the distribution of fractal dimension values using the resampled mean and standard deviation for seven growth forms based on high-resolution laser-scanned colonies (Zawada et al., 2019), providing empirical support for the distribution of growth forms along a continuous trait axis

partially break (Lirman, 2000), resulting in higher growth variability (Dornelas et al., 2017). Compact colonies have lower colony mortality rates which decrease with colony size; however, less compact colonies have higher mortality rates and U-shaped size–mortality relationships (Madin et al., 2014). Furthermore, branch openness (a similar metric to volume compactness) has been linked to self-shading which may reduce light resources for shaded tissues (Kaniewska, Anthony, & Hoegh-Guldberg, 2008; Kim & Lasker, 1998). Additionally, while fragmentation is a source of partial mortality, it is also a mechanism for asexual reproduction where fragments reattach to the reef (Highsmith, 1982; Karlson, 1986), providing an alternative way to increase population size (Smith & Hughes, 1999; Tunnicliffe, 1981). Sexual reproductive output also tends to be higher in species with lower compactness (Álvarez-Noriega et al., 2016).

In terms of ecosystem function, sturdier and more compact colonies produce longer-lasting structures for reef-building and less compact branching corals fill in the gaps as rubble when they fragment (Rasser & Riegl, 2002). Less compact colonies also create a diversity of niches and microhabitats for other organisms such as fishes and invertebrates (Almany, 2004; Darling et al., 2017; Friedlander & Parrish, 1998, 1998; Graham & Nash, 2013), with smaller bodied fishes associated with less compact colonies (Alvarez-Filip, Gill, & Dulvy, 2011), which provide a refuge from predators (Wilson et al., 2008).

From a response perspective, colonies with low compactness are more susceptible to cyclone damage (Madin & Connolly, 2006) and heat-induced bleaching compared to more compact colonies (Lirman, 2000; Loya et al., 2001; Marshall & Baird, 2000). A gradient from structurally complex to boulder-dominated community structure has also been correlated with increasing pCO_2 levels linked to ocean acidification (Fabricius et al., 2011), suggesting another morphology–response link that may be driven by variation in compactness. "Spikier" morphologies also trap more plastic debris, which is linked to disease and tissue damage (Lamb et al., 2018).

2.2 | Surface complexity

Variation in surface complexity captures a gradient from smoother surfaced colonies, such as the massives and plate-like "laminar" growth forms, to growth forms with complex and convoluted surfaces, such as the closed-branching "corymbose" and tabular growth forms (Figure 2). Surface complexity is represented by two shape variables. Fractal dimension is calculated using the "cube counting" algorithm, a 3D version of the box counting method (Sarkar & Chaudhuri, 1994). A completely flat surface has a fractal dimension close to 2 (as it effectively occupies two dimensions), whereas as a surface becomes more convoluted and fills the 3D space, fractal dimension approaches 3 (i.e. the 2D surface is packed into 3D space). Packing captures whether the surface area of the colony is packed within the bulk of the colony volume (packing higher than 1) or distributed away from the bulk of the colony volume (packing lower than 1), with completely convex colonies having packing equal to

1. Packing is calculated by dividing the convex hull surface area by the colony surface area. Both fractal dimension and packing require three-dimensional models to be estimated (e.g. from photogrammetry, laser scans).

Surface complexity captures a range of trade-offs related to performance. High complexity maximises biomass within a local space but increases self-shading (Wangpraseurt, Larkum, Ralph, & Kühl, 2012), where low complexity spreads biomass out resulting in more resources (e.g. light, nutrients) per unit of biomass. Higher surface complexity has been linked to increased light harvesting efficiency (Enríquez, Méndez, Hoegh-Guldberg, & Iglesias-Prieto, 2017; Wangpraseurt et al., 2014), with species changing surface complexity depending on light availability (Hoogenboom, Connolly, & Anthony, 2008). Colonies with smoother surfaces have more space available for larger polyps, where convoluted surfaces restrict polyp size ranges. Higher complexity has also been linked to increased nutrient uptake in high water flow conditions (Thomas & Atkinson, 1997), potentially facilitating faster growth rates.

Surface complexity also relates to variation in ecosystem function. Colonies with higher surface complexity create diverse environmental conditions (such as light and water flow) both nearby and within the colony itself (Chamberlain & Graus, 1975; Wangpraseurt et al., 2012), broadening the available niches for other organisms. Microstructural surface complexity can also increase larval recruitment of corals by causing water turbulence (Hata et al., 2017), which may include the larvae of other species as well, providing they are not eaten by the colony as they pass through (Fabricius & Metzner, 2004).

From a response perspective, high surface complexity has been linked to higher sedimentation resistance (Stafford-Smith & Ormond, 1992) and crown of thorns prey preference (Pratchett, 2007). Higher surface complexity is also linked to increased heat-induced bleaching susceptibility (Marcelino et al., 2013), possibly as a negative side effect of the increased light harvesting efficiency or respiration rates interacting with higher temperatures (Jokiel & Coles, 1990; Wangpraseurt et al., 2014).

2.3 | Top-heaviness

Top-heaviness captures how colony surface area and volume are distributed vertically, capturing a gradient from encrusting and massive, to laminar and tabular colonies (Figure 3). Like surface complexity, the variation within some growth forms overlap due to all colonies "starting from the bottom" when they first settle on the reef. Top-heaviness is represented by the first moment of volume and first moment of surface area and is calculated by integrating the volume and surface area of the colony by the vertical distance from the attachment point. In both cases, the colony is scaled to a set volume to remove the effect of colony size. Both top-heaviness variables require three-dimensional data to be estimated (e.g. photogrammetry, laser scans).

Variation in top-heaviness has a number of trade-offs relating to organism performance. Top-heavy colonies have higher whole colony mortality (Madin et al., 2014) but lower benthic competition
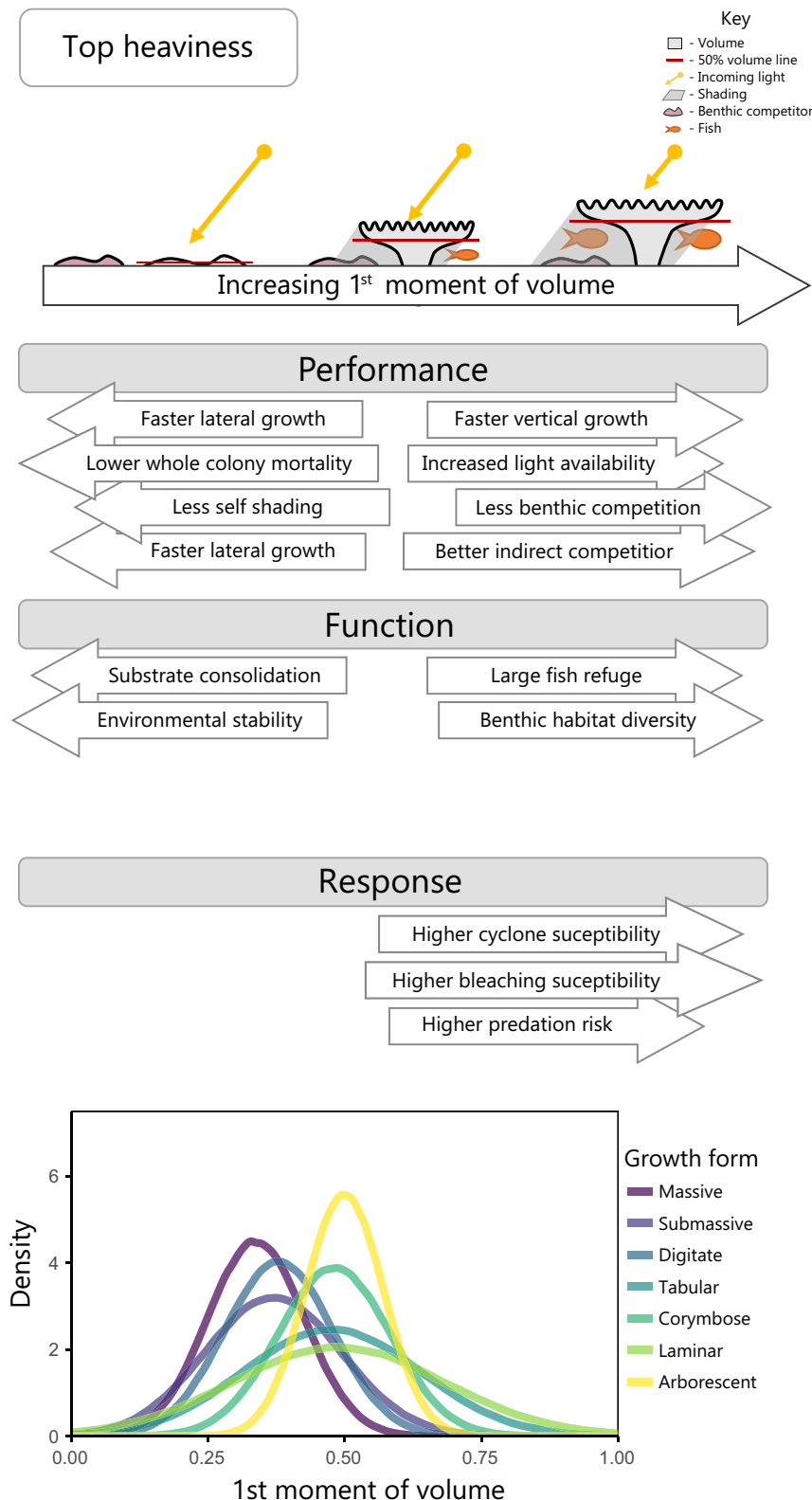
FIGURE 3 A conceptual figure outlining what variation in top-heaviness as a continuous morphological trait means for (organism) performance, (ecosystem) function and response (to disturbances and changing conditions). While the first moments of both volume and surface area capture variation in top-heaviness, the first moment of volume is used here for clarity. The first moment of volume can be visualised by thinking of the vertical distance from the base of the colony to the 50% volume line that splits the colonies volume into two equal halves. The longer this distance, the more top-heavy a colony is. The bottom panel shows the distribution of first moment of volume values using the resampled mean and standard deviation for seven growth forms based on high-resolution laser-scanned colonies (Zawada et al., 2019), providing empirical support for the distribution of growth forms along a continuous trait axis

(Precoda et al., 2017) and increased access to resources (Stimson, 1985) compared to bottom-heavy colonies.

Top-heavy colonies have a competitive advantage as they can shade-out and therefore reduce the growth and recruitment of neighbours by intercepting light (Baird & Hughes, 2000; Stimson, 1985), but are susceptible to high wave energy events that can dislodge them. Lower lying, encrusting forms allow for rapid horizontal expansion, operating as an escape strategy from superior benthic competitors (Jackson, 1979). This also allows lower lying colonies to reduce whole colony mortality likelihood by spreading biomass over

the substrate compared to colonies that grow up from a smaller area; however, the rate of benthic-associated partial mortality is higher in lower lying colonies (Meesters, Wesseling, & Bak, 1996).

From an ecosystem function perspective, colonies that are top-heavy provide habitat directly by creating open spaces underneath them that can shelter organisms such as large fishes (Kerry & Bellwood, 2015) and indirectly by shading the benthos, creating variation in abiotic conditions. Bottom-heavy encrusters may help consolidate the reef framework by calcifying over rubble and other benthic organisms, and lower lying colonies provide stable conditions for other organisms such as burrowing invertebrates and colonisers to occupy.

From a response perspective, top-heavy colonies are more susceptible to dislodgement from large wave forces due to lever effects and smaller attachment areas (Gove et al., 2015; Madin & Connolly, 2006), especially during cyclones. Being higher in the water column and exposed to higher light levels may also increase heat-induced bleaching susceptibility. Being higher in the water column also makes colonies easier targets for predators (e.g., crown of thorns) and increases contact with debris compared to lower lying and less accessible colonies.

3 | CASE STUDY: CORAL COMMUNITY RESPONSES TO DISTURBANCES VIA MORPHOLOGICAL TRAITS

Volume compactness, surface complexity and top-heaviness can be used to identify causal links to performance, function and response processes across multiple growth forms and species. Furthermore, many of the traits outlined here can be estimated accurately using planar area and growth form. Therefore, it is possible to estimate these traits from coral survey data and subsequently track how assemblage-scale trait composition vary spatially, temporally and in response to disturbances.

3.1 | Methodology

To retrospectively test some of the concepts outlined here, we estimated convexity, fractal dimension and the first moment of surface area for coral colonies surveyed across multiple sites and years. Field data were collected at Lizard Island, Australia, and consisted of line intercept transect (LIT) surveys of the benthic community focussing on scleractinian coral colonies, where a colony was defined as a contiguous live surface of coral. Data were collected over eight campaigns across 21 sites and a timespan of 22 years, recording 2,960 colonies from 181 species representing a broad spatial, temporal and taxonomic sample (Madin et al., 2018) Two cyclones in 2014 and 2015 and the 2016 mass bleaching event occurred during the data collection period.

Previously, we collected high-resolution scan data of coral skeletons to quantify colony shape (Zawada et al., 2019). The laser scan dataset consisted of 153 coral skeletons from museum collections that covered seven major growth forms and over three

orders of magnitude in size, representing a broad subsample of coral morphological variation. The six shape and three size traits (Table 1) were calculated for each colony in the laser scan dataset. These data were used to build models to predict the six shape variables, surface area and volume using growth form and planar area. Predicted R^2 (pR^2) values for the models were used to assess model suitability for each trait (see Supporting Information). Volume, surface area, sphericity, convexity, packing, fractal dimension and the first moment of surface area were moderately to well predicted (pR^2 = 0.89, pR^2 = 0.95, pR^2 = 0.88, pR^2 = 0.86, pR^2 = 0.51, pR^2 = 0.54, pR^2 = 0.74, respectively). The first moment of volume was poorly predicted (pR^2 = 0.13) and was not explored further. This approach allowed us to retrospectively estimate continuous morphological traits from survey data without measuring colony morphology in situ.

Using growth form and estimated planar area from the survey data, we predicted morphological traits using the models developed from the laser scan dataset. For the survey data, growth form was either recorded as part of the original dataset or was estimated using the typical growth form for a species using the coral traits database (Madin et al., 2016). Some growth forms in the survey data were not in the laser scan dataset (e.g. bottlebrush, encrusting) and were therefore excluded from the analysis: Of the 2,960 colonies recorded in total, 708 were excluded from further analysis. Planar area was estimated for each colony in the survey data using the intercept length of the colony as the radius in the formula for calculating the area of a circle. This method of planar area estimation is likely to underestimate due to the higher likelihood of the transect intercepting colony edges compared to the centre; however, relative size differences between colonies are preserved overall on average.

We tracked how the average volume compactness (represented by convexity), surface complexity (represented by fractal dimension) and top-heaviness (represented by the first moment of surface area) of coral assemblages responded to disturbances, as well as how the position and variation of the multitrait morphospace changed over time. Changes in coral cover and the weighted average of each trait were examined, with traits weighted by intercept as larger colonies contribute more to the habitat compared to smaller ones. Changes in the position and variation of the multitrait morphospace through time were explored via principal components analysis (PCA). We ran the PCA using the estimated morphological traits of colonies in the LIT dataset for the five sites that had data from 2011 prior to disturbances through to 2017 one year following the bleaching event (marked with an "*" in Figure 3). Each trait was scaled and centred to weight each variable equally in the analysis. We then grouped the data by year and added 95th percentile data ellipses around the PC axis scores, where the data ellipses were calculated using the variance–covariance matrix between the two PC axis scores and assuming a bivariate normal distribution. To quantify the changes in mean and variance, we ran a PERMANOVA and beta dispersion analysis, respectively, using the 2011 and 2017 data (via the "adonis" and "betadisper" functions from the R package "vegan" (Oksanen et al., 2015).
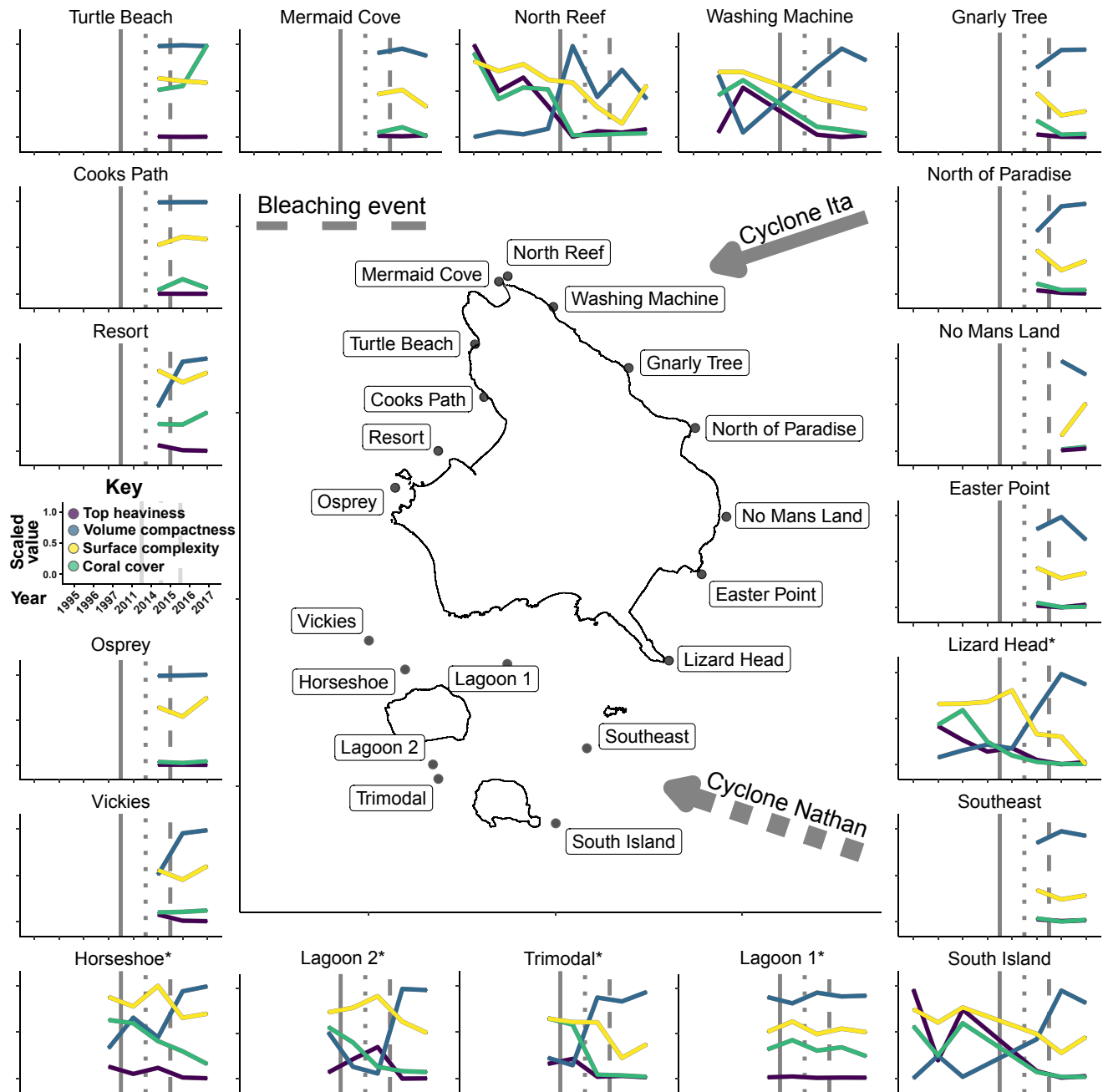
FIGURE 4 Changes in average morphological trait values of coral communities for 19 sites around Lizard Island, Australia, in response to disturbances. Vertical bars in outer panels and arrows on map indicate disturbances; solid, Cyclone Ita, a category 4 cyclone that struck the north-east of the island in 2014; dotted, Cyclone Nathan, a category 4 cyclone that struck the south-east of the island in 2015; and dashed, the 2016 mass bleaching event. Each morphological trait value is the weighted average for the coral community at each site for a given year, with colonies weighted by transect intercept length. Blue, volume compactness, measured as convexity, with higher convexity indicating more compact (massive) colonies and lower convexity indicating less compact (branching) species; yellow, surface complexity, measured as the fractal dimension of a colony, with higher values indicating that the surface of the colony is packed within space and lower values indicating the surface is smoother and more uniformly distributed; purple, top-heaviness, measured as the first moment of surface area, with higher values indicating that more of the surface is located vertically away from the substrate; green, live coral cover. Each variable was rescaled from 0 to 1 to allow them to be plotted simultaneously on a single axis. Note the general tendency for average volume compactness to be higher post-disturbance, suggesting a shift from more complex, branching morphologies to less complex, more massive ones. Sites marked with an "*" were used in the morphospace analyses

3.2 | Results

The morphological traits of coral assemblages around Lizard Island changed following two cyclones and the mass bleaching event (Figure 4). For the sites surveyed before the disturbances (North Reef, Washing Machine, Lizard Head and South Island), volume compactness, surface complexity and top-heaviness were mostly consistent among sites and across years, with low compactness and high surface complexity overall. Top-heaviness was more variable depending on site, decreasing at North Reef. Coral cover fluctuated and slightly decreased in some sites.

The effects of the cyclones were localised. In 2014, Cyclone Ita (solid arrow/break line) primarily effected the exposed northern sites, with the assemblage at North Reef shifting towards high compactness and lower top-heaviness. Coral cover at North Reef also dropped following the cyclone. In contrast, the southern sites with data available (Trimodal, Lagoon 1, Lagoon 2, Horseshoe, and Lizard Head) were mostly unaffected. In 2015, Cyclone Nathan (dotted arrow/break line) primarily effected sites facing south-east, with the assemblages at Lizard Head and Trimodal shifting towards high compactness and low top-heaviness. Coral cover at these sites was also reduced following the cyclone.

While the effects of the two cyclones varied among sites, the effect of 2016 mass bleaching event (dashed break line) was uniform around the island. Assemblages with high compactness were mostly unaffected with no change in coral cover; however, assemblages with low to intermediate–high compactness shifted towards high compactness following the bleaching event along with reduced cover. Overall, surface complexity and top-heaviness also decreased following the bleaching event. One-year post-bleaching most sites were yet to show signs of recovery to pre-disturbance conditions with a few exceptions (e.g. North Reef), and coral cover remained low (except for Turtle Beach and Resort). In general, over the course of the survey period, the average morphology of coral assemblages on Lizard Island has shifted from lower compactness, higher surface complexity and higher top-heaviness, towards higher compactness, lower surface complexity and lower top-heaviness.

The position and extent of the morphospace of the coral assemblage at Lizard Island has changed over time in response to disturbances (Figure 5). The mean position of the morphospace shifted between 2011 and 2017 (PERMANOVA: $F = 88.3$, $DF = (1,464)$**, $p < 0.001$) towards higher compactness and lower top-heaviness, with surface complexity remaining similar. The largest shift occurred between 2014 and 2015 following Cyclone Nathan, likely due to most of the sites being exposed to the cyclone; however, directly after and 1 year following the bleaching, compactness and top-heaviness continued to shift. The variation in the morphospace was reduced between 2011 and 2017 (ANOVA: $F = 22.2$, $DF = (1,464)$, $p < 0.0001$), mainly along the compactness and top-heaviness axes.

4 | DISCUSSION

The morphological traits of coral assemblages shifted in response to a series of disturbances, becoming less structurally complex and diverse. It is well established that that disturbances reduce habitat complexity which impacts the broader ecosystem (Alvarez-Filip, Dulvy, Gill, Côté, & Watkinson, 2009; Graham & Nash, 2013). However, establishing cause and effect from disturbance to reduced habitat complexity to changes to the ecosystem is difficult when using species, which may encompass multiple morphologies, or qualitative descriptions such as growth forms. For example, it is possible to correlate the loss of arborescent and branching growth forms following a disturbance with a subsequent shift in fish assemblage structure, but such approaches cannot identify the underlying mechanisms responsible for the observed shifts. For example, Hughes, Kerry, et al. (2018) detected shifts in assemblage structure and functional traits of coral assemblages on the Great Barrier Reef following bleaching and highlighted morphology as a key factor for both bleaching susceptibility and ecosystem function. Our approach provides targeted quantitative traits that explain why these changes are occurring; namely, that susceptibility to heat-induced bleaching is causally linked to a colonies' volume compactness and surface complexity. Therefore, when an acute heating event occurs, colonies with low compactness/high surface complexity are disproportionately affected compared to other colonies resulting in a shift in assemblage structure.

By establishing a links between the effects of disturbances on the functional composition of coral assemblages, we can start to predict the effects of these shifts at the community and habitat scale and consequently their consequences for ecosystem function. For example, organisms that rely on the microenvironments and niches resulting from high surface complexity and low volume compactness may become less abundant (Graham & Nash, 2013). A similar effect is expected in macroalgal assemblages, where complex canopy-forming macroalgae share functional similarities to complex corals, and is also expected to decrease in abundance in the Anthropocene (Fulton et al., 2019). While measuring morphology in macroalgae is much more difficult than for corals, if possible, we may expect morphological traits such as convexity to capture similar links to ecosystem function across taxonomic groups. The shift towards high compactness may correlate with a reduced capacity for reef-matrix infilling in the long term if populations of low compactness species do not recover (Rasser & Riegl, 2002), though cyclone-driven fragmentation is a source of rubble for infilling. The loss of top-heavy colonies may also result in reduced cover for larger fishes and less environmental variability via shading (Kerry & Bellwood, 2015). Additionally, larval recruitment may be reduced through the loss of colonies with high surface complexity that can entrain larvae and therefore facilitate settlement (Hata et al., 2017). The reduction in the spread of trait values should correlate with an overall reduction in habitat and functional diversity, resulting in reduced taxonomic and functional diversity of reef-associated species (Richardson et al., 2017). Tracking these traits over time distils the dynamics of multiple species into a few key measures that provide an overview of the assemblage and functioning of the ecosystem.

Examining traits across the PFR framework can determine how assemblages and communities respond to anthropogenic activities
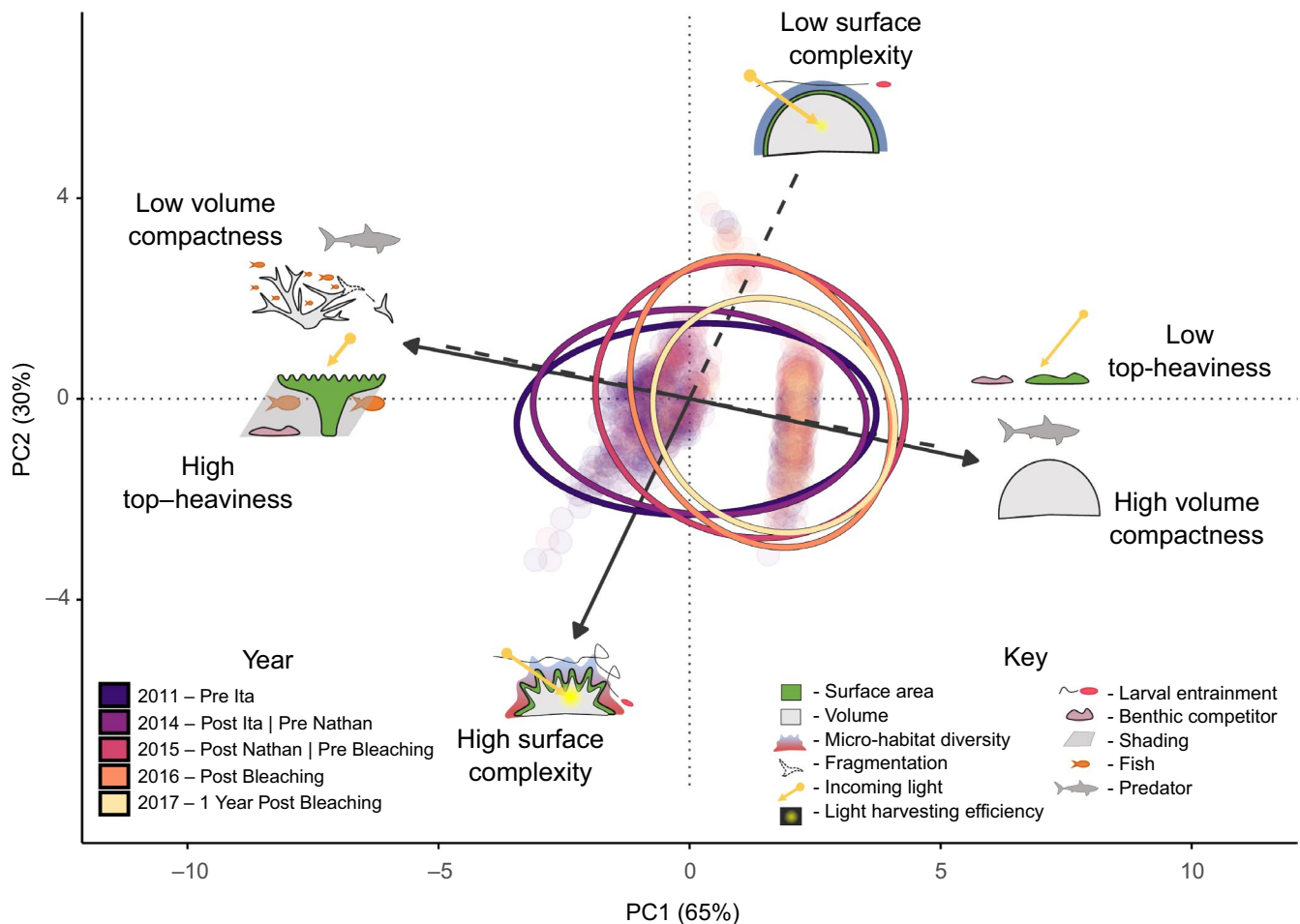
FIGURE 5 Changes in coral assemblage morphospace from five sites on Lizard Island, Australia, in response to two cyclones and the 2016 mass bleaching event. Morphospaces generated via principal components analysis using morphological traits estimated from planar area and growth form. Volume compactness measured as convexity, with higher convexity indicating more compact (massive) colonies and lower convexity indicating less compact (branching) species; surface complexity measured as the fractal dimension of a colony, with higher values indicating that the surface of the colony is packed within space and lower values indicating the surface is smoother and more uniformly distributed; top-heaviness measured as the first moment of surface area, with higher values indicating that more of the surface is situated vertically away from the substrate. Ellipses are 95th percentile data ellipses generated from a variance–covariance matrix and assuming a normal distribution for each axis. The banding of the points is due to the morphological traits being predicted from size and growth form models, and so each band represents the variation of shape within a growth form. Note how, over time and in response to multiple disturbances, the position and extent of the assemblage morphospace at Lizard Island has shifted towards less complex morphologies with less morphological diversity and towards reduced habitat complexity

and their capacity for recovery. Specifically, low compactness colonies are also associated with faster growth, reproduction via fragmentation and higher sexual reproductive output (Álvarez-Noriega et al., 2016; Dornelas et al., 2017; Highsmith, 1982), and so any ecosystem functions related to low compactness may return faster as populations recover. This is an alternative to taxonomic-based approaches: It is entirely possible that the trait composition of an assemblage returns over time, while species composition (i.e. beta diversity) remains markedly different (Fukami, Bezemer, Mortimer, & Putten, 2005). However, anthropogenic activity may change the frequency and intensity of disturbance events and cause longer term changes to the environment (Hoegh-Guldberg et al., 2007; Wilkinson, 1999), compromising the recovery of ecosystem function in the long term. If a change in trait composition due to disturbance

or changing conditions is detected, for example by tracking mean trait values, but the assemblage returns to the previous state over time, then we can infer that recovery, at least from a trait perspective, has occurred. Conversely, even if the assemblage shows signs of return to a previous trait composition, disturbances recurring before full recovery or traits remaining changed even over long periods of time may be indicative of Anthropogenically forced changes outside of the adaptive histories of corals.

Discussion of these traits is moot if they are prohibitively expensive or logistically difficult to obtain. The ability to predict informative traits from easily measured variables such as growth form and planar area, and the increasing use and availability of underwater photogrammetry for obtaining 3D models of in situ colonies, makes them readily available to be incorporated into research and

monitoring programmes. Monitoring teams would only need to obtain planar area measurements and be trained to distinguish growth forms (a much easier task than species identification) to be able to obtain an overview of a key trait such as volume compactness, and researchers can quantify these traits over time and along gradients through photogrammetry, possibly paring this with fish survey data or quantitative measures of ecosystem function. Directly measuring morphological traits should be undertaken when possible; however, we encourage the use of these predictive models to supplement research and monitoring programmes (see Data Accessibility section).

Given the current trajectory of the Anthropocene, there will continue to be impacts on coral reefs and many other ecosystems worldwide. Morphological traits can predict the observed differences in colony susceptibility to disturbances and responses to human activity by linking variation in organism performance, ecosystem function and response to disturbances and changing conditions, making them suitable for establishing causal links between anthropogenic change and long-lasting changes in reef ecosystems.

ACKNOWLEDGEMENTS

CONFLICTS OF INTEREST

The authors have no conflict of interests to declare.

AUTHOR CONTRIBUTIONS

K.J.A.Z., M.D. and J.S.M. developed the main ideas and structure of the paper. K.J.A.Z. wrote the first draft, ran the analyses and prepared the figures. M.D. and J.S.M. contributed to writing of the manuscript and gave feedback throughout. All authors contributed to collecting the data for the case study. A.H.B. and T.C.L.B. commented on the final draft and revised manuscript.

DATA AVAILABILITY

R Scripts are available on GitHub: github.com/Kylezx1/MorphoStratsHabitatBuildersAnthro.

Line intercept transect data available from figshare. https://doi.org/10.6084/m9.figshare.8115677.

Morphological traits data available from figshare. https://doi.org/10.6084/m9.figshare.8115674.

Predictive models are available in RDS format from figshare. https://doi.org/10.6084/m9.figshare.8115692.

ORCID

Kyle J. A. Zawada (iD) https://orcid.org/0000-0002-4587-8138

Joshua S. Madin (iD) https://orcid.org/0000-0002-5005-6227

Andrew H. Baird (iD) http://orcid.org/0000-0001-8504-4077

Tom C. L. Bridge (iD) https://orcid.org/0000-0003-3951-284X

Maria Dornelas (iD) https://orcid.org/0000-0003-2077-7055

REFERENCES

Almany, G. R. (2004). Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. *Oecologia*, *141*(1), 105–113. https://doi.org/10.1007/s00442-004-1617-0

Alvarez-Filip, L., Dulvy, N. K., Gill, J. A., Côté, I. M., & Watkinson, A. R. (2009). Flattening of Caribbean coral reefs: Region-wide declines in architectural complexity. *Proceedings of the Royal Society of London B: Biological Sciences*, *276*(1669), 3019–3025. https://doi.org/10.1098/rspb.2009.0339

Alvarez-Filip, L., Gill, J. A., & Dulvy, N. K. (2011). Complex reef architecture supports more small-bodied fishes and longer food chains on Caribbean reefs. *Ecosphere*, *2*(10), 1–17. https://doi.org/10.1890/ES11-00185.1

Álvarez-Noriega, M., Baird, A. H., Dornelas, M., Madin, J. S., Cumbo, V. R., & Connolly, S. R. (2016). Fecundity and the demographic strategies of coral morphologies. *Ecology*, *97*(12), 3485–3493. https://doi.org/10.1002/ecy.1588

Baird, A. H., & Hughes, T. P. (2000). Competitive dominance by tabular corals: An experimental analysis of recruitment and survival of understorey assemblages. *Journal of Experimental Marine Biology and Ecology*, *251*(1), 117–132. https://doi.org/10.1016/S0022-0981(00)00209-4

Barber, C. B., Dobkin, D. P., & Huhdanpaa, H. (1996). The Quickhull algorithm for convex hulls. *ACM Transactions on Mathematical Software*, *22*(4), 469–483. https://doi.org/10.1145/235815.235821

Bell, J., & Galzin, R. (1984). Influence of live coral cover on coral-reef fish communities. *Marine Ecology Progress Series*, *15*, 265–274. https://doi.org/10.3354/meps015265

Bellwood, D. R., Streit, R. P., Brandl, S. J., & Tebbett, S. B. (2019). The meaning of the term 'function' in ecology: A coral reef perspective. *Functional Ecology*. https://doi.org/10.1111/1365-2435.13265

Chamberlain, J. A. Jr, & Graus, R. R. (1975). Water flow and hydromechanical adaptations of branched reef corals. *Bulletin of Marine Science*, *25*(1), 112–125.

Chan, N. C. S., & Connolly, S. R. (2013). Sensitivity of coral calcification to ocean acidification: A meta-analysis. *Global Change Biology*, *19*(1), 282–290. https://doi.org/10.1111/gcb.12011

Chappell, J. (1980). Coral morphology, diversity and reef growth. *Nature*, *286*(5770), 249–252. https://doi.org/10.1038/286249a0

Connell, J. H., Hughes, T. P., Wallace, C. C., Tanner, J. E., Harms, K. E., & Kerr, A. M. (2004). A long-term study of competition and diversity of corals. *Ecological Monographs*, *74*(2), 179–210. https://doi.org/10.1890/02-4043

Crutzen, P. J. (2006). The "Anthropocene". In E. Ehlers, & T. Krafft (Eds.), *Earth system science in the anthropocene* (pp. 13–18). Berlin, Heidelberg: Springer.

Darling, E. S., Graham, N. A. J., Januchowski-Hartley, F. A., Nash, K. L., Pratchett, M. S., & Wilson, S. K. (2017). Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs*, *36*(2), 561–575. https://doi.org/10.1007/s00338-017-1539-z

Done, T. (2011). Corals: Environmental controls on growth. In D. Hopely (Ed.), *Encyclopedia of modern coral reefs: Structure, form and process* (pp. 281–293). Dordrecht, The Netherlands: Springer.

Dornelas, M., Madin, J. S., Baird, A. H., & Connolly, S. R. (2017). Allometric growth in reef-building corals. *Proceedings of the Royal Society of London B: Biological Sciences*, *284*(1851), 20170053. https://doi.org/10.1098/rspb.2017.0053

Edmunds, P. J., & Gates, R. D. (2002). Normalizing physiological data for scleractinian corals. *Coral Reefs*, *21*, 193–197. https://doi.org/10.1007/s00338-002-0214-0

Enríquez, S., Méndez, E. R., Hoegh-Guldberg, O., & Iglesias-Prieto, R. (2017). Key functional role of the optical properties of coral skeletons in coral ecology and evolution. *Proceedings of the Royal Society of London B: Biological Sciences*, *284*(1853), 20161667. https://doi.org/10.1098/rspb.2016.1667

Fabricius, K. E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De'ath, G., ... Lough, J. M. (2011). Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. *Nature Climate Change*, *1*(3), 165–169. https://doi.org/10.1038/nclimate1122

Fabricius, K. E., & Metzner, J. (2004). Scleractinian walls of mouths: Predation on coral larvae by corals. *Coral Reefs*, *23*(2), 245–248. https://doi.org/10.1007/s00338-004-0386-x

Friedlander, A. M., & Parrish, J. D. (1998). Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology*, *224*(1), 1–30. https://doi.org/10.1016/S0022-0981(97)00164-0

Fukami, T., Bezemer, T. M., Mortimer, S. R., & van der Putten, W. H. (2005). Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters*, *8*(12), 1283–1290. https://doi.org/10.1111/j.1461-0248.2005.00829.x

Fulton, C. J., Abesamis, R. A., Berkström, C., Depczynski, M., Graham, N. A. J., Holmes, T. H., ... Wilson, S. K. (2019). Form and function of tropical macroalgal reefs in the Anthropocene. *Functional Ecology*, *33*, 989–999. https://doi.org/10.1111/1365-2435.13282

Gladfelter, E. H., Monahan, R. K., & Gladfelter, W. B. (1978). Growth rates of five reef-building corals in the Northeastern Caribbean. *Bulletin of Marine Science*, *28*(4), 728–734.

Gove, J. M., Williams, G. J., McManus, M. A., Clark, S. J., Ehses, J. S., & Wedding, L. M. (2015). Coral reef benthic regimes exhibit non-linear threshold responses to natural physical drivers. *Marine Ecology Progress Series*, *522*, 33–48. https://doi.org/10.3354/meps11118

Graham, N. A. J., & Nash, K. L. (2013). The importance of structural complexity in coral reef ecosystems. *Coral Reefs*, *32*(2), 315–326. https://doi.org/10.1007/s00338-012-0984-y

Hata, T., Madin, J. S., Cumbo, V. R., Denny, M., Figueiredo, J., Harii, S., ... Baird, A. H. (2017). Coral larvae are poor swimmers and require fine-scale reef structure to settle. *Scientific Reports*, *7*(1), 2249. https://doi.org/10.1038/s41598-017-02402-y

Highsmith, R. (1982). Reproduction by fragmentation in corals. *Marine Ecology Progress Series*, *7*, 207–226. https://doi.org/10.3354/meps007207

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., ... Hatziolos, M. E. (2007). Coral reefs under rapid climate change and ocean acidification. *Science*, *318*(5857), 1737–1742. https://doi.org/10.1126/science.1152509

Hoogenboom, M. O., Connolly, S. R., & Anthony, K. R. N. (2008). Interactions between morphological and physiological plasticity optimize energy acquisition in corals. *Ecology*, *89*(4), 1144–1154. https://doi.org/10.1890/07-1272.1

House, J. E., Brambilla, V., Bidaut, L. M., Christie, A. P., Pizarro, O., Madin, J. S., & Dornelas, M. (2018). Moving to 3D: Relationships between coral planar area, surface area and volume. *PeerJ*, *6*, e4280. https://doi.org/10.7717/peerj.4280

Hughes, T. P., Anderson, K. D., Connolly, S. R., Heron, S. F., Kerry, J. T., Lough, J. M., ... Wilson, S. K. (2018). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science*, *359*(6371), 80–83. https://doi.org/10.1126/science.aan8048

Hughes, T. P., Barnes, M. L., Bellwood, D. R., Cinner, J. E., Cumming, G. S., Jackson, J. B. C., ... Scheffer, M. (2017). Coral reefs in the Anthropocene. *Nature*, *546*(7656), 82–90. https://doi.org/10.1038/nature22901

Hughes, T. P., Kerry, J. T., Baird, A. H., Connolly, S. R., Dietzel, A., Eakin, C. M., ... Torda, G. (2018). Global warming transforms coral reef assemblages. *Nature*, *556*(7702), 492. https://doi.org/10.1038/s41586-018-0041-2

Jackson, J. B. C. (1979). Morphological strategies of sessile animals. In G. Larwood & B. R. Rosen (Eds.), *Biology and systematics of colonial animals* (pp. 499–555). New York, NY: Academic Press.

Johannes, R. E., & Wiebe, W. J. (1970). Method for determination of coral tissue biomass and composition. *Limnology and Oceanography*, *15*(5), 822–824. https://doi.org/10.4319/lo.1970.15.5.0822

Jokiel, P. L., & Coles, S. L. (1990). Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. *Coral Reefs*, *8*(4), 155–162. https://doi.org/10.1007/bf00265006

Jones, G. P., & Syms, C. (1998). Disturbance, habitat structure and the ecology of fishes on coral reefs. *Austral Ecology*, *23*(3), 287–297. https://doi.org/10.1111/j.1442-9993.1998.tb00733.x

Kaniewska, P., Anthony, K. R. N., & Hoegh-Guldberg, O. (2008). Variation in colony geometry modulates internal light levels in branching corals, *Acropora humilis* and *Stylophora pistillata*. *Marine Biology*, *155*(6), 649–660. https://doi.org/10.1007/s00227-008-1061-5

Karlson, R. H. (1986). Disturbance, colonial fragmentation, and size-dependent life history variation in two coral reef cnidarians. *Marine Ecology Progress Series*, *28*(3), 245–249.

Kerry, J. T., & Bellwood, D. R. (2015). Do tabular corals constitute keystone structures for fishes on coral reefs? *Coral Reefs*, *34*(1), 41–50. https://doi.org/10.1007/s00338-014-1232-4

Kim, K., & Lasker, H. R. (1998). Allometry of resource capture in colonial cnidarians and constraints on modular growth. *Functional Ecology*, *12*(4), 646–654. https://doi.org/10.1046/j.1365-2435.1998.00228.x

Laland, K., Matthews, B., & Feldman, M. W. (2016). An introduction to niche construction theory. *Evolutionary Ecology*, *30*(2), 191–202. https://doi.org/10.1007/s10682-016-9821-z

Lamb, J. B., Willis, B. L., Fiorenza, E. A., Couch, C. S., Howard, R., Rader, D. N., ... Harvell, C. D. (2018). Plastic waste associated with disease on coral reefs. *Science*, *359*(6374), 460–462. https://doi.org/10.1126/science.aar3320

Lirman, D. (2000). Fragmentation in the branching coral *Acropora palmata* (Lamarck): Growth, survivorship, and reproduction of colonies and fragments. *Journal of Experimental Marine Biology and Ecology*, *251*(1), 41–57. https://doi.org/10.1016/S0022-0981(00)00205-7

Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H., & van Woesik, R. (2001). Coral bleaching: The winners and the losers. *Ecology Letters*, *4*(2), 122–131. https://doi.org/10.1046/j.1461-0248.2001.00203.x

Madin, J. S., Baird, A. H., Bridge, T. C. L., Connolly, S. R., Zawada, K. J. A., & Dornelas, M. (2018). Cumulative effects of cyclones and bleaching on coral cover and species richness at Lizard Island. *Marine Ecology Progress Series*, *604*, 263–268. https://doi.org/10.3354/meps12735

Madin, J. S., Baird, A. H., Dornelas, M., & Connolly, S. R. (2014). Mechanical vulnerability explains size-dependent mortality of reef corals. *Ecology Letters*, *17*(8), 1008–1015. https://doi.org/10.1111/ele.12306

Madin, J. S., & Connolly, S. R. (2006). Ecological consequences of major hydrodynamic disturbances on coral reefs. *Nature*, *444*(7118), 477–480. https://doi.org/10.1038/nature05328

Madin, J. S., Hoogenboom, M. O., Connolly, S. R., Darling, E. S., Falster, D. S., Huang, D., ... Baird, A. H. (2016). A trait-based approach to advance coral reef science. *Trends in Ecology & Evolution*, *31*(6), 419–428. https://doi.org/10.1016/j.tree.2016.02.012

Marcelino, L. A., Westneat, M. W., Stoyneva, V., Henss, J., Rogers, J. D., Radosevich, A., ... Backman, V. (2013). Modulation of

light-enhancement to symbiotic algae by light-scattering in corals and evolutionary trends in bleaching. *PLoS ONE*, *8*(4), e61492. https://doi.org/10.1371/journal.pone.0061492

Marshall, P. A., & Baird, A. H. (2000). Bleaching of corals on the Great Barrier Reef: Differential susceptibilities among taxa. *Coral Reefs*, *19*(2), 155–163. https://doi.org/10.1007/s003380000086

Massel, S. R., & Done, T. J. (1993). Effects of cyclone waves on massive coral assemblages on the Great Barrier Reef: Meteorology, hydrodynamics and demography. *Coral Reefs*, *12*(3–4), 153–166. https://doi.org/10.1007/BF00334475

McGill, B. J., Etienne, R. S., Gray, J. S., Alonso, D., Anderson, M. J., Benecha, H. K., ... White, E. P. (2007). Species abundance distributions: Moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters*, *10*(10), 995–1015. https://doi.org/10.1111/j.1461-0248.2007.01094.x

Meesters, E. H., Wesseling, I., & Bak, R. P. M. (1996). Partial mortality in three species of reef-building corals and the relation with colony morphology. *Bulletin of Marine Science*, *58*(3), 838–852.

Norström, A. V., Nyström, M., Jouffray, J.-B., Folke, C., Graham, N. A. J., Moberg, F., ... Williams, G. J. (2016). Guiding coral reef futures in the Anthropocene. *Frontiers in Ecology and the Environment*, *14*(9), 490–498. https://doi.org/10.1002/fee.1427

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., Ohara, R. B., ... Wagner, H. (2015). *Package 'vegan.'* Community Ecology Package, Version, 2(9).

Osinga, R., Schutter, M., Griffioen, B., Wijffels, R. H., Verreth, J. A. J., Shafir, S., ... Lavorano, S. (2011). The biology and economics of coral growth. *Marine Biotechnology*, *13*(4), 658–671. https://doi.org/10.1007/s10126-011-9382-7

Perry, C. T., & Alvarez-Filip, L. (2018). Changing geo-ecological functions of coral reefs in the Anthropocene. *Functional Ecology*, *33*, 976–988. https://doi.org/10.1111/1365-2435.13247

Pratchett, M. S. (2007). Feeding preferences of *Acanthaster planci* (Echinodermata: Asteroidea) under controlled conditions of food availability. *Pacific Science*, *61*(1), 113–120. https://doi.org/10.1353/psc.2007.0011

Precoda, K., Allen, A. P., Grant, L., & Madin, J. S. (2017). Using traits to assess nontransitivity of interactions among coral species. *The American Naturalist*, *190*(3), 420–429. https://doi.org/10.1086/692758

Rasser, M., & Riegl, B. (2002). Holocene coral reef rubble and its binding agents. *Coral Reefs*, *21*(1), 57–72. https://doi.org/10.1007/s00338-001-0206-5

Richardson, L. E., Graham, N. A. J., Pratchett, M. S., & Hoey, A. S. (2017). Structural complexity mediates functional structure of reef fish assemblages among coral habitats. *Environmental Biology of Fishes*, *100*(3), 193–207. https://doi.org/10.1007/s10641-016-0571-0

Sarkar, N., & Chaudhuri, B. B. (1994). An efficient differential box-counting approach to compute fractal dimension of image. *IEEE Transactions on Systems, Man, and Cybernetics*, *24*(1), 115–120. https://doi.org/10.1109/21.259692

Smith, L. D., & Hughes, T. P. (1999). An experimental assessment of survival, re-attachment and fecundity of coral fragments. *Journal of Experimental Marine Biology and Ecology*, *235*(1), 147–164. https://doi.org/10.1016/S0022-0981(98)00178-6

Stachowicz, J. J. (2001). Mutualism, facilitation, and the structure of ecological communities. *BioScience*, *51*(3), 235–246. https://doi.org/10.1641/0006-3568(2001)051[0235:MFATSO]2.0.CO;2

Stafford-Smith, M. G., & Ormond, R. F. G. (1992). Sediment-rejection mechanisms of 42 species of Australian scleractinian corals. *Marine and Freshwater Research*, *43*(4), 683–705. https://doi.org/10.1071/mf9920683

Steffen, W., Broadgate, W., Deutsch, L., Gaffney, O., & Ludwig, C. (2015). The trajectory of the Anthropocene: The great acceleration. *The Anthropocene Review*, *2*(1), 81–98. https://doi.org/10.1177/2053019614564785

Stimson, J. (1985). The effect of shading by the table coral *Acropora hyacinthus* on understory corals. *Ecology*, *66*(1), 40–53. https://doi.org/10.2307/1941305

Suding, K. N., Lavorel, S., Chapin, F. S., Cornelissen, J. H. C., Díaz, S., Garnier, E., ... Navas, M.-L. (2008). Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Global Change Biology*, *14*(5), 1125–1140. https://doi.org/10.1111/j.1365-2486.2008.01557.x

Thomas, F. I. M., & Atkinson, M. J. (1997). Ammonium uptake by coral reefs: Effects of water velocity and surface roughness on mass transfer. *Limnology and Oceanography*, *42*(1), 81–88. https://doi.org/10.4319/lo.1997.42.1.0081

Tunnicliffe, V. (1981). Breakage and propagation of the stony coral *Acropora cervicornis*. *Proceedings of the National Academy of Sciences*, *78*(4), 2427–2431. https://doi.org/10.1073/pnas.78.4.2427

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional!. *Oikos*, *116*(5), 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Wangpraseurt, D., Larkum, A. W. D., Franklin, J., Szabó, M., Ralph, P. J., & Kühl, M. (2014). Lateral light transfer ensures efficient resource distribution in symbiont-bearing corals. *Journal of Experimental Biology*, *217*(4), 489–498. https://doi.org/10.1242/jeb.091116

Wangpraseurt, D., Larkum, A. W. D., Ralph, P. J., & Kühl, M. (2012). Light gradients and optical microniches in coral tissues. *Frontiers in Microbiology*, *3*, 1–9. https://doi.org/10.3389/fmicb.2012.00316

Wilkinson, C. R. (1999). Global and local threats to coral reef functioning and existence: Review and predictions. *Marine and Freshwater Research*, *50*(8), 867. https://doi.org/10.1071/MF99121

Williams, G. J., Graham, N. A. J., Jouffray, J.-B., Norström, A. V., Nyström, M., Gove, J. M., ... Wedding, L. M. (2019). Coral reef ecology in the Anthropocene. *Functional Ecology*, *33*, 1014–1022. https://doi.org/10.1111/1365-2435.13290

Wilson, S. K., Burgess, S. C., Cheal, A. J., Emslie, M., Fisher, R., Miller, I., ... Sweatman, H. P. A. (2008). Habitat utilization by coral reef fish: Implications for specialists vs. generalists in a changing environment. *Journal of Animal Ecology*, *77*(2), 220–228. https://doi.org/10.1111/j.1365-2656.2007.01341.x

Woodhead, A. J., Hicks, C. C., Norström, A. V., Williams, G. J., & Graham, N. A. J. (2019). Coral reef ecosystem services in the Anthropocene. *Functional Ecology*, *33*, 1023–1034. https://doi.org/10.1111/1365-2435.13331

Zawada, K. J. A., Dornelas, M., & Madin, J. S. (2019). Quantifying coral morphology. *BioRxiv*, 553453. https://doi.org/10.1101/553453

SUPPORTING INFORMATION

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