ECOGRAPHY

Research

Spatial scaling properties of coral reef benthic communities

Helen V. Ford, Jamison M. Gove, Andrew J. Davies, Nicholas A. J. Graham, John R. Healey, Eric J. Conklin and Gareth J. Williams

H. V. Ford (https://orcid.org/0000-0002-9431-2982) ✉ (helen.ford@bangor.ac.uk) and G. J. Williams (https://orcid.org/0000-0001-7837-1619), School of Ocean Sciences, Bangor Univ., Anglesey, UK. – J. M. Gove, NOAA Pacific Islands Fisheries Science Centre, Honolulu, HI, USA. – A. J. Davies, Dept of Biological Sciences, Univ. of Rhode Island, Kingston, RI, USA. – N. A. J. Graham, Lancaster Environment Centre, Lancaster Univ.,UK. – J. R. Healey, School of Natural Sciences, Bangor Univ., Bangor, Gwynedd, UK. – E. J. Conklin, The Nature Conservancy, Honolulu, HI, USA.

Ecography
44: 188–198, 2021
doi: 10.1111/ecog.05331

Subject Editor: Gretta Pecl
Editor-in-Chief: Miguel Araújo
Accepted 28 September 2020

The spatial structure of ecological communities on tropical coral reefs across seascapes and geographies have historically been poorly understood. Here we addressed this for the first time using spatially expansive and thematically resolved benthic community data collected around five uninhabited central Pacific oceanic islands, spanning 6° latitude and 17° longitude. Using towed-diver digital image surveys over ~140 linear km of shallow (8–20 m depth) tropical reef, we highlight the autocorrelated nature of coral reef seascapes. Benthic functional groups and hard coral morphologies displayed significant spatial clustering (positive autocorrelation) up to kilometre-scales around all islands, in some instances dominating entire sections of coastline. The scale and strength of these autocorrelation patterns showed differences across geographies, but patterns were more similar between islands in closer proximity and of a similar size. For example, crustose coralline algae (CCA) were clustered up to scales of 0.3 km at neighbouring Howland and Baker Islands and macroalgae were spatially clustered at scales up to ~3 km at both neighbouring Kingman Reef and Palmyra Atoll. Of all the functional groups, macroalgae had the highest levels of spatial clustering across geographies at the finest resolution of our data (100 m). There were several cases where the upper scale at which benthic community members showed evidence of spatial clustering correlated highly with the upper scales at which concurrent gradients in physical environmental drivers were spatially clustered. These correlations were stronger for surface wave energy than subsurface temperature (regardless of benthic group) and turf algae and CCA had the closest alignments in scale with wave energy across functional groups and geographies. Our findings suggest such physical drivers not only limit or promote the abundance of various benthic competitors on coral reefs, but also play a key role in governing their spatial scaling properties across seascapes.

Keywords: autocorrelation, benthic ecology, coral morphology, physical drivers, scale, seascape

NORDIC SOCIETY OIKOS

www.ecography.org

Introduction

Patterns in nature are often highly scale dependent (Levin 1992). Conclusions drawn from observations at one scale may be inconsistent when observing at another scale. Scales of observation in ecology are often chosen for arbitrary, logistical or anthropocentric reasons and may not be appropriate for the target organism, system or process in question (Addicott et al. 1987, Wiens and Milne 1989, Boström et al. 2011). Such mismatches of scale can reduce our predictive capacity of ecosystem dynamics and lead to erroneous extrapolations over larger scales from spatially or temporally limited sampling observations (Hatcher et al. 1987, Schneider 2001). Despite this, observational scales in ecology have generally remained constrained and limit our understanding of the scaling of natural systems (Estes et al. 2018). By conducting ecological investigations at systematically varied scales, the dynamics of natural systems and how they vary as a function of scale can be properly quantified (Rahbek and Graves 2000, Nash et al. 2014).

Since the 1980s, ecology has benefitted from an advancement of concepts related to ecological pattern and scale, including the idea that biological spatial patterns emerge at characteristic scales in response to their environment (Wiens and Milne 1989, Levin 1992, Schneider 1994). The progression of 'landscape ecology' theory occurred alongside an increased diversity of field techniques, most notably remote sensing technology (Dungan et al. 2002, Wagner and Fortin 2005). These technologies greatly expanded scales of observation and enabled practical implications of landscape ecology to be used in ecosystem management (Lee et al. 2008, De Knegt et al. 2011, Jones et al. 2013). Progression of theory within the marine environment has been slower due to logistical constraints of collecting comparable data across scales (Kenny et al. 2003, Hinchey et al. 2008, D'Urban Jackson et al. 2020), but has nonetheless emerged to form the discipline of 'seascape ecology' (Pittman et al. 2011).

On tropical coral reefs, spatial scales of observation were greatly expanded by the onset of remote sensing technology, permitting their global-scale mapping to a coarse taxonomic resolution (Mumby et al. 1997, Hochberg and Atkinson 2003, Purkis 2018). More recently, in situ digital imaging techniques, such as structure-from-motion photogrammetry, have enabled us to study the spatial ecology of coral reef benthic communities at higher taxonomic resolutions (Edwards et al. 2017, Pedersen et al. 2019). Despite these important advances, such data re-introduce the issue of limited sampling extents and previous research has instead tended to focus on comparing spatial patterns across discrete hierarchical scales (Murdoch and Aronson 1999, Williams et al. 2015b). By combining high-resolution digital imagery with towed-diver surveys, recent research has started to reveal the spatial structure of coral reef benthic communities around entire tropical islands (Gove et al. 2015, Aston et al. 2019). These data present the opportunity to apply landscape ecological theory and spatial pattern metrics to the marine realm to explore ecological patterns and processes across scales (Wedding et al. 2011).

Spatial autocorrelation is a long-standing statistical technique within ecology (Legendre 1993, Cocu et al. 2005) that describes the similarity of a given variable at nearby locations as being greater or less than expected by chance (Fortin et al. 2016). It can be quantified over multiple scales to show how species, habitats and environmental variables are spatially structured. Environmental conditions can be spatially autocorrelated due to several factors, such as climate and geomorphologic processes, which in turn can drive the spatial autocorrelation patterns of ecological communities (Legendre 1993, Gobbi and Brambilla 2016).

The scale at which spatial autocorrelation is no longer present or changes from being clustered to over-dispersed can indicate a new process acting on biological variables (Zhang and Zhang 2011). Spatial autocorrelation has been used to quantify forest fragmentation (Zhang et al. 2009), optimise sampling protocols for marine macrobenthic invertebrate communities (Hamylton and Barnes 2018) and to relate spatial patterns of insect abundance to environmental gradients (Cocu et al. 2005). On coral reefs, indices of spatial autocorrelation have been used to quantify the spatial patterning of coral bleaching across scales of cm to 100s of m (Levy et al. 2018) and benthic communities up to kilometre-scales around the circumference of a single tropical island (Aston et al. 2019). Despite these recent efforts, our understanding of the patterns of spatial autocorrelation of coral reef communities across scales and geographies remains limited.

Here we quantify the spatial scaling properties of tropical benthic communities over ~140 linear km of reef around the circumference of five uninhabited coral reef islands. By processing thousands of in situ benthic images and using in situ and modelled environmental data, we employ a spatial metric to quantify the patterning of competing functional groups, hard coral morphologies and their suspected physical drivers across scales. Wave energy and subsurface variations in seawater temperature, indicative of intra-island gradients in upwelling (Gove et al. 2006, Aston et al. 2019), can limit or promote the abundance of different benthic groups around tropical islands, including different morphologies (growth forms) of reef-building corals (Williams et al. 2013, Gove et al. 2015). We therefore expect these physical drivers to play a role in the spatial ecology and spatial scaling of tropical benthic communities. Our study objectives were primarily to test whether the intra-island distributions of benthic communities differed from random and if so, up to what scales. We then asked how consistent these spatial scaling properties were across geographies and to what degree they correlated with the spatial scaling of concurrent gradients in physical drivers. Our study therefore establishes important baselines for the spatial ecology of coral reef benthic communities in a world where escalating human interactions with coral reefs (Norström et al. 2016, Hughes et al. 2017, Williams et al. 2019) are fundamentally altering their biological–environmental relationships (Williams et al. 2015a).

Methods

Study sites

Our study system consisted of five U.S.-affiliated coral reef islands and atolls (hereafter referred to as 'islands') spanning 6° latitude and 17° longitude in the central Pacific Ocean (Fig. 1): Jarvis Island, Palmyra Atoll, Kingman Reef (Line Islands Archipelago), Howland Island and Baker Island (U.S. Phoenix Islands). In 1974, Jarvis, Baker and Howland became U.S. National Wildlife Refuges. Kingman and Palmyra were afforded the same protection in 2001. All five islands were declared part of the Pacific Remote Islands Marine National Monument in 2009, further affirming their protected status. Throughout their history, these five islands have lacked permanent human populations and represent some of the most remote coral reef ecosystems on the planet. As such, they offer the opportunity to study the ecology and natural variation of coral reefs in the absence of confounding direct local human impacts (Williams et al. 2015a, Heenan et al. 2020), within a relatively similar oceanographic and climatic setting (Gove et al. 2013).

Benthic community digital surveys and spatial processing

Digital benthic images were collected around the circumference of each island using towed-diver surveys (Kenyon et al. 2006) in March to April 2008 as part of the National Oceanic and Atmospheric Administration's (NOAA) Pacific Island Fisheries Science Center's (PIFSC) Pacific Reef Assessment and Monitoring Program (RAMP). This survey year was chosen for the present study from the biennial/triennial surveys at each island spanning 2001 to the present due to: 1) representing 10 yr of recovery potential following the suspected mass coral bleaching in 1998, and 2) being prior to a bleaching event that affected the region in late 2009 to early 2010 (Williams et al. 2010, Vargas-Ángel et al. 2011). As such, this survey year provided the least disturbed benthic community spatial patterns within the time series. Divers manoeuvred a sub-surface instrumented board towed by a surface boat at ~3 km h^{-1} to target the 15 m depth contour around each island. The tow-board was equipped with a downward facing digital SLR camera (Canon EOS 10-D/50-D) and strobes, taking images every 15 s (equating to every ~15 m) from a height of ~1 m above the benthos. The average area of the benthos that each survey image captured using this technique was 10.9 m^2 (SE = 0.1 m^2, n = 700) (Kenyon et al. 2006).

Every alternate image was selected for subsequent analyses and images were filtered to only include those within a depth range of 8–20 m on the forereef habitat (reef slope facing the open ocean) of each island to ensure comparability with prior studies in the region (Gove et al. 2015, Williams et al. 2015a, Aston et al. 2019). We used the analysis software CoralNet (Beijbom et al. 2015) to overlay 10 points in a stratified-random design over each photo and identify the benthos below each as either: hard coral (to morphology), macroalgae, soft coral, crustose coralline algae, turf algae, other invertebrates (echinoderm, bivalve, zoanthid, anemone, corallimorph) and bare sand (for detailed descriptions of functional groups and coral morphologies see Supplementary material Appendix 1 Table A1, A2).

A global positioning system (GPS) aboard the boat time-stamped to the camera and a SeaBird™ Electronics (SBE) 39 subsurface pressure, temperature-depth recorder on the tow-board, combined with a layback algorithm (Kenyon et al. 2006), allowed each photograph to be georeferenced to the nearest ~3–5 m and depth referenced. For the few instances where depth data were missing, we used an interpolation based on inverse distance weighting using the Spatial Analyst tool in ArcGIS (ver. 10.7.1) and matched the missing depths to interpolated depth data from the same island area from surveys in 2006 and 2010. Each island's circumference was divided into a series of discrete, sequentially numbered grid cells (100 m wide) using a custom Python script (sensu Aston et al. 2019, <https://doi.org/10.5281/zenodo.1199350>); the number of grid cells around each island ranged from 77 to 340. Benthic image data were spatially joined to each grid cell and, to be included in further spatial analyses, grid cells had to contain ≥ 4 benthic images (sensu Aston et al. 2019). To help satisfy this prerequisite and maximise spatial coverage around each island, for those grid cells with < 4 images we revisited our initial filtering step (where we excluded every alternate image) and re-selected some images for processing. In total, we processed 6022 images across the five islands (Howland, 787; Baker, 838; Jarvis, 1107; Kingman, 1560; Palmyra, 1730) to calculate a mean cover value for each benthic variable per grid cell, with 77–96% of grid cells containing data around the five islands (Supplementary material Appendix 1 Table A3).

Quantifying physical drivers

We calculated surface wave power using a 3-h output at 50 km resolution from NOAA's Wave Watch III global model (WWIII; <http://polar.ncep.noaa.gov/waves>). Wave power (W m^{-1}) was calculated from significant wave height (H_s) and peak period (T_p), defined as:

$$WP = \frac{\rho g^2 T_p H_s^2}{64\pi}$$

where ρ is the density of seawater (1024 kg m^{-3}) and g is the acceleration of gravity (9.8 m s^{-2}). From this output, calculations using an incident wave swath method (sensu Aston et al. 2019) estimated the wave power at regularly spaced locations around each island, ranging from ~100–500 m depending on island size We calculated an integrated 10-yr average (1998–2008) in wave energy flux (kW h m^{-1}) for each location and used a 250 m radial buffer around each location to spatially join to the 100 m grid cells, averaging values within cells that contained multiple overlapping buffers.

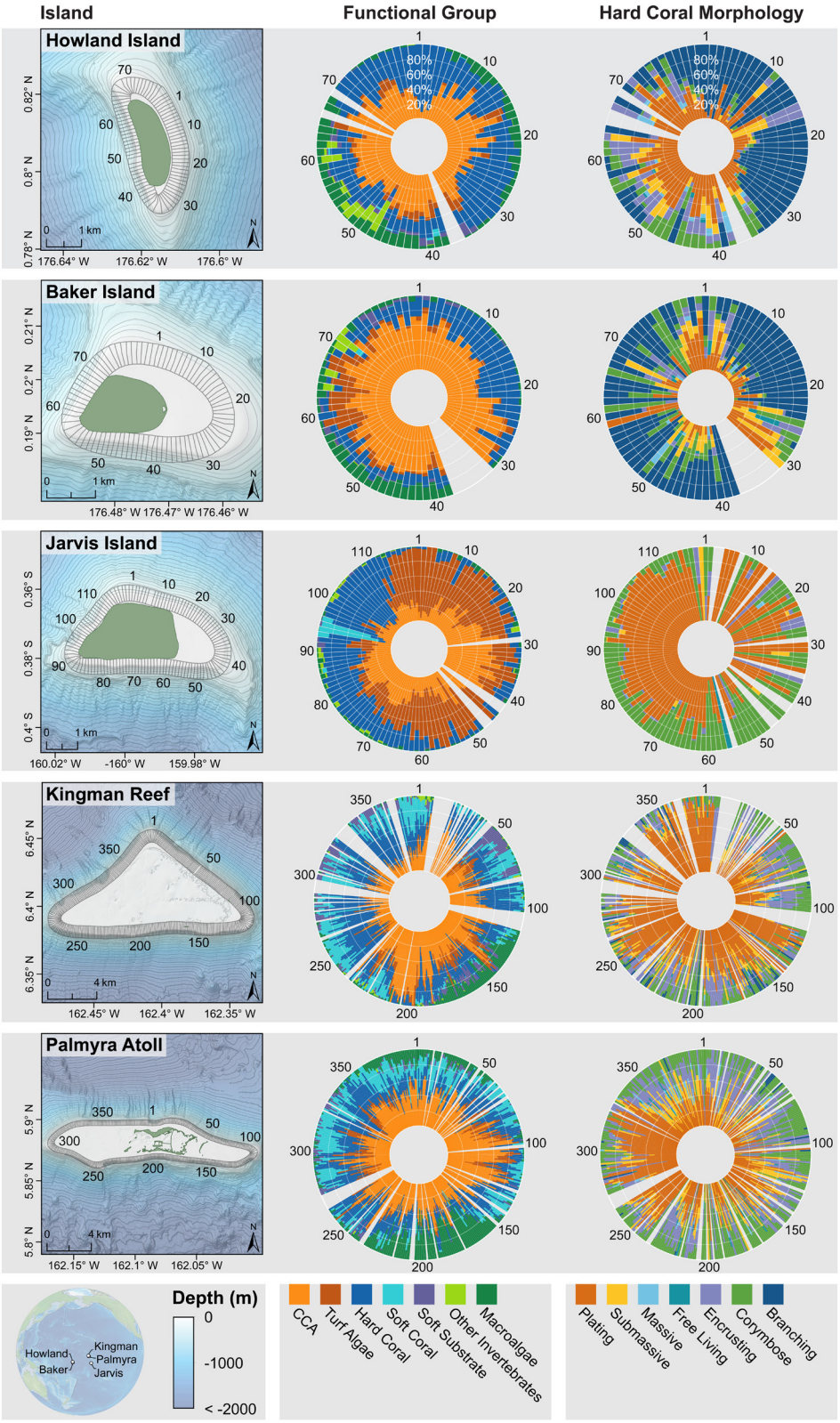

Figure 1. Spatial variations in percentage cover of coral reef benthic functional groups and dominant hard coral morphologies on the outer reef slopes (~15 m depth) of five uninhabited central Pacific islands collected via towed-diver digital image surveys in 2008 across ~140 linear km of reef (n = 6022 images). The white cells around each island are 100-m grid cells that overlap the towed-diver tracks and are used to spatially reference benthic images (their numbers start due north and correspond with those on the island rosette plots). Grey regions on the rosette plots represent missing data regions. The islands are ordered in increasing size top to bottom.

In situ seawater temperature was recorded during each towed-diver survey in 2008 using the SBE39 logger attached to the towboard (10 s sample rate, 0.002°C accuracy). Despite being a temporal snapshot, these in situ temperature data capture long-term intra-island gradients in sub-surface temperature that are indicative of localised upwelling (Gove et al. 2006). Like the benthic and wave data, we spatially joined the subsurface temperature data to each discrete island grid cell and calculated a mean value per cell.

Spatial statistics and sensitivity analyses

To quantify changes in the spatial autocorrelation of benthic communities and their physical drivers across scales, we used the Moran's I statistic (Moran 1950) within a custom-coded function (Aston et al. 2019) in the R programming language (R Core Team), and which we build upon here to allow the comparison of these patterns across islands. When calculating the Moran's I statistic for hard coral morphologies, we selected the two to three most abundant morphologies at each island. We defined the observed Moran's I value (OMI) as:

$$I = \frac{n}{S_0} \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} w_{i,j} \left(x_i - \bar{x}\right)\left(x_j - \bar{x}\right)}{\sum_{i=1}^{n} \left(x_i - \bar{x}\right)^2}$$

where n is the number of observations, $w_{i,j}$ is the matrix of weights according to the inverse Euclidean distance between observations, x_i is the observed value at location i, x_j is the observed value at location j, $\bar{x}$ is the mean value and S_0 is the sum of spatial weights. The spatial weights are defined as the inverse of the minimum distance, $d_{i,j}$, around the circumference of each island between locations i and j, as follows:

$$d_{i,j} = \min\left(\left(j - i\right), \left(n + i - j\right)\right)$$

$$w_{i,j} = \frac{1}{d_{i,j}} \text{ for } i \neq j, 0 \text{ otherwise}$$

A significant ($p < 0.05$) departure from an OMI value of zero (i.e. away from a random distribution) indicated that the spatial pattern of the variable in question at that scale was highly organised in space. Positive OMI values indicated positive autocorrelation (i.e. spatial clustering), while negative OMI values indicated negative autocorrelation (i.e. over-dispersion). We calculated the Moran's I statistic at the finest spatial resolution of the data (100 m grid cells), and then again in a moving window averaging process at increasing 100-m increments to a maximum scale of 4 km (limited by replication beyond that scale due to island size). Grid cells containing 'no data' (i.e. < four benthic images) were excluded from the moving window averaging process. As spatial patterns in nature can be anisotropic, at each scale we re-computed the Moran's I statistic and p-value for all possible 100 m grid cell starting locations of the moving window averaging process and iterating in both directions around the circumference of each island. We report the mean, maximum and minimum OMI value for each scale from this process and the scale at which the upper bound of p exceeded 0.05 (i.e. did not differ significantly from a random spatial distribution).

As the number of grid cells with 'no data' varied across islands (Fig. 1), we performed a series of sensitivity analyses to quantify the possible impact this might have on our comparison of spatial autocorrelation patterns. At Kingman, 21% of grid cells had 'no data' (81 out of 380). For the other islands, we assigned 'no data' values to grid cells at random until we reached the same ratio of missing data as Kingman, then repeated our moving window averaging process and recalculated the Moran's I statistic. We repeated this at each island 100 times, each time randomising the 'no data' grid cell locations. From the iterations, we calculated a mean resampled OMI and p-value and identified the smallest and largest scale at which $p \geq 0.05$ (Supplementary material Appendix 1 Fig. A1).

Results

The spatial scaling of coral reef benthic communities across geographies

The spatial distribution of benthic functional groups appeared non-random around the circumference of each island, with some groups dominating large expanses of coastlines for several km (Fig. 1). On occasion, these regions of spatial dominance showed consistencies between islands. For example, macroalgae was spatially clumped along the southeast coast of Kingman and the south coast of neighbouring Palmyra, reaching 11–46% cover over a 1.8 km stretch of coastline at Kingman and 25–68% along a 1.5 km stretch at Palmyra (Fig. 1). Different coral morphologies also exhibited non-random distributions, and again displayed discrete zones of spatial dominance along coastlines (Fig. 1). For example, plating coral peaked at 70% cover and dominated 1.2 km of Kingman's south coast, while branching coral cover dominated the northeast coast of neighbouring Howland and Baker for 1.1 km and 1.2 km, respectively (Fig. 1).

All benthic functional groups displayed strong evidence of spatial clustering (positive autocorrelation) around the circumference of each island, but the scale and strength of this autocorrelation differed between islands (Fig. 2). Around Howland, crustose coralline algae (CCA) and turf algae showed positive spatial autocorrelation at scales up to 0.3 km and CCA had similar spatial clustering at neighbouring Baker. Around Kingman, Jarvis and Baker, turf algae were spatially clustered across the seascape at scales of ~1 km. Macroalgae and hard corals displayed comparable scaling patterns at neighbouring Howland and Baker; both groups were spatially clustered at scales up to ~500 m at Howland

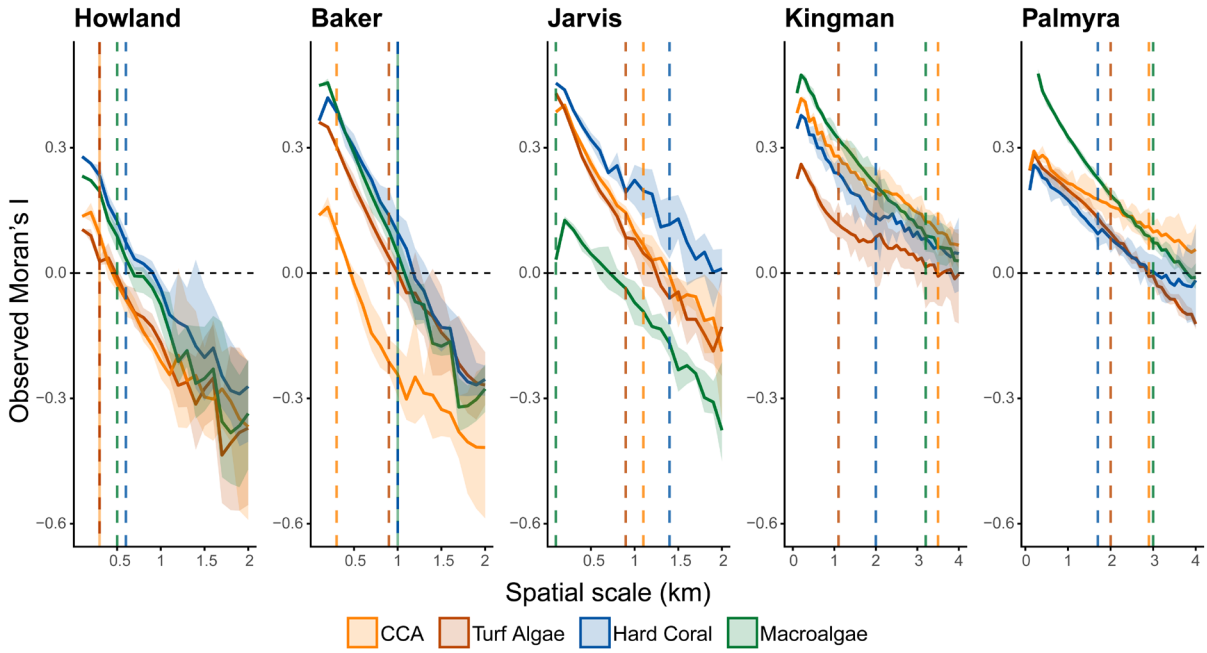

Figure 2. Patterns of spatial autocorrelation (solid coloured line) in the percentage cover of benthic functional groups at increasing 100-m scale increments around five uninhabited central Pacific islands. The observed Moran's I (OMI) value indicates a clustered distribution (+ve values), random distribution (0 value, horizontal dotted line) to increasingly dispersed (−ve values). The OMI is calculated for all possible starting points around each island and the range in these values for each scale is shown as the shaded region. The vertical dotted line shows the scale at which the OMI value is not significantly different from random for each benthic group ($p \geq 0.05$). CCA, crustose coralline algae.

and ~1 km at Baker. These inter-island spatial autocorrelation patterns were robust to variations in the number and spatial distribution of grid cells containing no data; the scales at which benthic functional groups significantly differed from random only changed by up to 100 m (Supplementary material Appendix 1 Fig. A1). Macroalgae were the most spatially clustered of any functional group at the finest resolution of our data (100 m), having a consistently high observed Moran's I index of ~0.4 around Baker, Kingman and Palmyra (Fig. 2). However, the spatial distribution of macroalgae at Jarvis did not differ from random at any scale, likely due to its low island-mean cover of 1.8% (almost three times lower than at Kingman, the island with the next lowest abundance).

Different coral morphologies also showed strong evidence of spatial clustering around the circumference of each island, with some consistencies in scaling between morphologies of the same type at different islands (Fig. 3). At neighbouring Howland and Baker, branching corals were spatially clustered up to scales of 700–800 m and followed a similar gradient in spatial autocorrelation across scales (Fig. 3). The scaling of encrusting corals was also similar between Kingman, Howland and Palmyra, being spatially clustered up to scales of 1.1–1.3 km (Fig. 3). Branching corals at Howland and Baker and plating corals at Jarvis had their highest degree of spatial clustering at the finest spatial resolution (100 m) (Fig. 3). In contrast, plating corals at other islands, as well as submassive, corymbose and encrusting coral morphologies, peaked in autocorrelation at a 200 m scale, suggesting a less clustered distribution at smaller spatial scales (Fig. 3).

Correlation between the spatial scaling properties of benthic communities and their physical drivers

There were cases where the upper scale of significant spatial clustering remained similar between benthic community members and the physical drivers. At the functional group resolution, this overall correlation was stronger for wave energy ($\rho = 0.73$) than for subsurface temperature ($\rho = 0.46$) as well as individually for any single benthic functional group ($\rho = 0.71$–0.93 for wave energy, 0.37–0.82 for subsurface temperature) (Fig. 4) (see Supplementary material Appendix 1 Fig. A2 for spatial autocorrelation patterns in wave energy and subsurface temperature across scales). There was also inter-island variability in this alignment. For example, around Baker, wave energy was spatially clustered up to scales of ~1 km and turf algae, macroalgae and hard coral were also clustered up to ~1 km. Around Kingman, subsurface temperature and turf algae were both spatially clustered up to ~1 km, while wave energy and hard coral cover were both clustered up to scales of ~2.4 km. In contrast, there was consistently poor alignment at Palmyra, with none of the upper scales of significant autocorrelation in the benthic functional groups closely resembling those of the physical drivers (Fig. 4).

The correlation between the upper scale at which there remained significant spatial autocorrelation in the benthos and physical drivers was not as strong for hard coral morphologies ($\rho = 0.50$ and 0.46 for wave energy and subsurface temperature, respectively). There was substantial variation across the different coral morphologies, with some showing closer

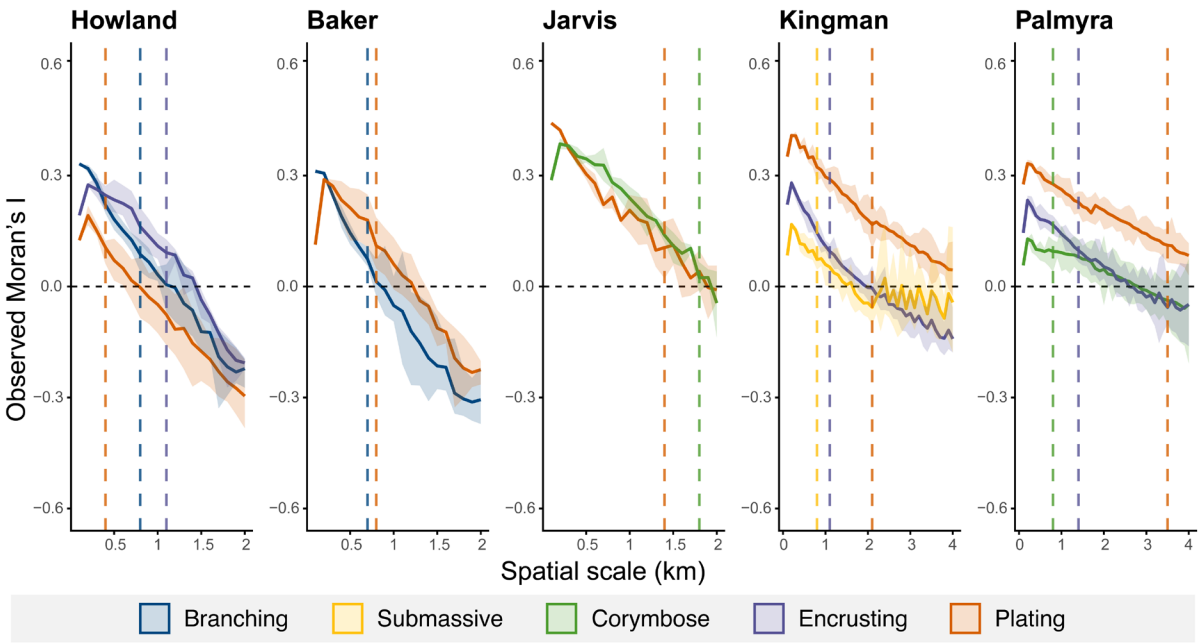

Figure 3. Patterns of spatial autocorrelation (solid coloured line) in the percentage cover of dominant hard coral morphologies at increasing 100-m scale increments around five uninhabited central Pacific islands. The observed Moran's I (OMI) value indicates a clustered distribution (+ve values), random distribution (0 value, horizontal dotted line) to increasingly dispersed (−ve values). The OMI is calculated for all possible starting points around each island and the range in these values for each scale is shown as the shaded region. The vertical dotted line shows the scale at which the OMI value is not significantly different from random for each benthic group ($p \geq 0.05$).

alignment to the physical drivers than others. For example, the spatial scaling of plating corals closely matched those of wave energy regardless of island, and some coral morphologies appeared to be more closely aligned at specific islands than others (Fig. 5). Encrusting corals around Howland were spatially clustered up to 1.1 km, exactly matching the spatial scaling of subsurface temperature and wave energy. At Jarvis, plating corals were clustered up to 1.4 km, similar to the spatial clustering exhibited by both subsurface temperature and wave energy (to within 200 m). Finally, at Kingman, encrusting and submassive corals and subsurface temperature were spatially clustered up to scales of ~1 km, while plating corals and wave energy were both clustered up to ~2 km scales (Fig. 5).

Discussion

The autocorrelated nature of coral reef seascapes

Our results show that coral reef benthic communities are naturally spatially clustered across tropical island seascapes, with individual groups in some cases dominating entire kilometre-sections of coastline (Fig. 1). Structural complexity of benthic assemblages can be influenced by the dominant functional group or coral morphology, which will have an effect on the spatial structure of reef-associated organisms, including fish communities (Alvarez-Filip et al. 2011, Richardson et al. 2017). Furthermore, these sections of dominance are evidence that 'ecotones' – discrete transition points between two communities or habitat types – exist around these tropical oceanic islands, which will likely have structuring effects on reef-associated organisms, akin to those of forest edges (Pfeifer et al. 2017) and coral reef-seagrass transition zones (Dorenbosch et al. 2005). Acknowledging the autocorrelated nature of coral reef benthic communities, may have important management implications. For example, larger patches dominated by hard coral of a structurally complex morphology with a seagrass-hard coral ecotone, may be more beneficial to maintain ecosystem structure and function. Such patterns of naturally occurring spatial autocorrelation should be considered in marine spatial planning and coral restoration efforts that may attempt to mimic the inherent spatial properties of coral reefs.

The spatial scaling patterns of benthic groups differed across geographies but had the common attribute of displaying positive spatial autocorrelation up to several kilometres of scale across all five study islands. Previously, Bradbury and Young (1983) found corals to be spatially clumped at 60-m scales across shallow reef flats and reef crests of the Great Barrier Reef in Australia. Edwards et al. (2017) also found most coral taxa were spatially clustered within 100 m^2 plots at 10 m depth on the outer reef slope of Palmyra Atoll, central Pacific (one of our study islands). We found the highest levels of positive autocorrelation in all benthic community members at our smallest spatial scales (100–200 m) around all five of our study islands. We therefore hypothesise that positive autocorrelation, particularly at smaller scales, is a common spatial attribute of corals and other benthic organisms across depths, reef habitats and geographies.

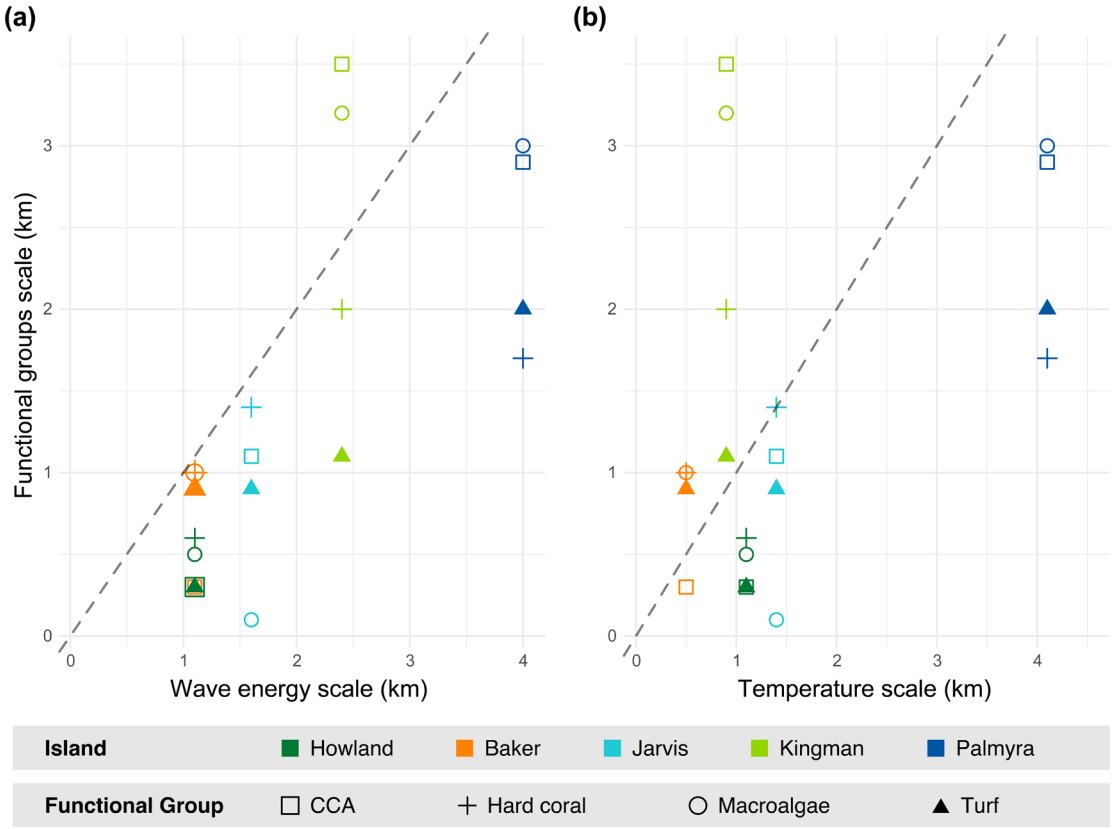

Figure 4. Correlation between the upper scale at which there remained significant spatial clustering in the benthic functional groups and physical drivers around five uninhabited central Pacific islands (diagonal dotted line is a 1:1 reference). Overall Spearman rank correlation coefficient (ρ) equaled 0.73 for wave energy and 0.46 for subsurface temperature. Correlation values for each individual benthic functional group and wave energy equaled: crustose coralline algae (CCA) = 0.81, turf algae = 0.93, hard coral = 0.71, macroalgae = 0.79), and for subsurface temperature equaled: CCA = 0.48, turf algae = 0.82, hard coral = 0.37, macroalgae = 0.47).

Drivers of coral reef benthic community seascapes

The non-random spatial dominance of benthic functional groups and hard coral morphologies around kilometre-sections of our five study islands likely exist, in part, because of concurrent gradients in the physical environment. Physical environmental drivers are key determinants of benthic community structure around oceanic islands, promoting or limiting the abundance of competitors particularly in the absence of local human impacts (Gove et al. 2015, Williams et al. 2015a). Howland, Baker and Jarvis have pronounced cross-island gradients in subsurface temperature, reflective of localised upwelling along their western coasts that results in the up-slope movement of deep, cold, nutrient-rich waters onto shallow reef communities (Gove et al. 2006, Tsuda et al. 2008, Aston et al. 2019). Algae can benefit from increased growth under high nutrient conditions on coral reefs (Littler et al. 1983, Miller et al. 1999), which may explain spatial clustering of turf algae and macroalgae along continuous kilometre-scale sections of Baker and Howland's western coasts, respectively. As well as benefiting algae, upwelling can enhance growth rates in reef-building corals (Diaz-Pulido and Garzón-Ferreira 2002, Edmunds and Leichter 2016) by providing heterotrophic energetic subsidies (Williams et al. 2018). In some cases, this can give corals a competitive advantage over algae and strong upwelling is thought to explain the kilometre-sections of hard coral dominance along the western coast of Jarvis (Aston et al. 2019).

Like competing benthic functional groups, individual hard coral morphologies displayed strong spatial clustering along kilometre-sections of the island coastlines that are also likely driven, in part, by gradients in physical drivers. Our results indicate that the high spatial clustering of hard coral along the western coast of Jarvis, a more wave-sheltered part of the island, is almost exclusively dominated by plating coral. Plating and branching corals are susceptible to breakage and dislodgement by high wave energy (Madin et al. 2014), whereas encrusting, digitate and massive coral morphologies are more wave-resistant and dominate in more wave-exposed areas (Gove et al. 2015). Branching corals also dominated sections of Howland and Baker's north-eastern to south-eastern coasts, which are sheltered from winter storm swells from the north–west (Mundy et al. 2010). In contrast, Palmyra's northern coast is exposed to north–west winter swells (Williams et al. 2013) and here we saw spatial clustering of more wave-tolerant encrusting and corymbose corals.

Benthic functional groups not only dominated kilometre-sections of island coastlines, but also showed non-random

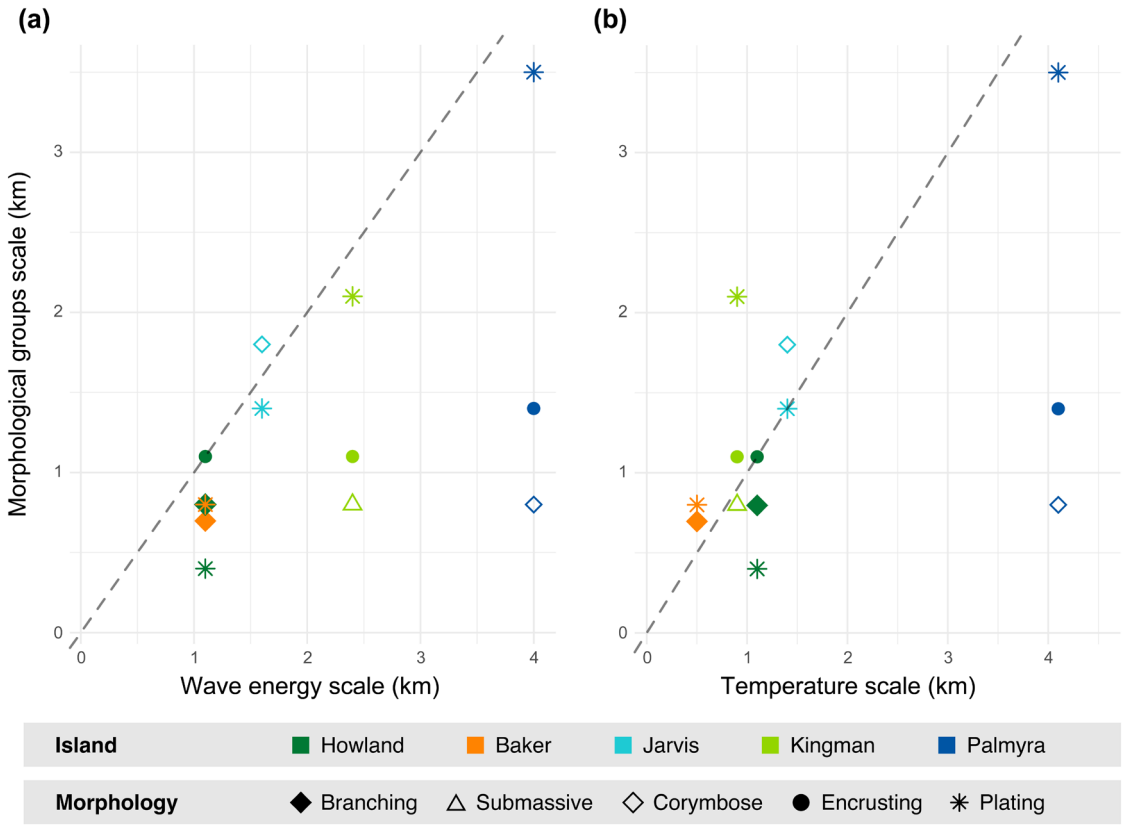

Figure 5. Correlation between the upper scale at which there remained significant spatial clustering in the dominant hard coral morphologies and physical drivers around five uninhabited central Pacific islands (diagonal dotted line is a 1:1 reference). Overall Spearman rank correlation coefficient (ρ) equaled 0.50 for wave energy and 0.46 for subsurface temperature. Note that unlike in Fig. 4, correlation values for individual morphologies are not calculated due to a lack of adequate replication across islands.

patterns of spatial clustering across scales (Fig. 2, 3). In some cases, the upper scale at which benthic functional groups were spatially clustered around islands closely correlated with the upper scale at which the physical drivers were spatially clustered (Fig. 4). This correlation was more evident with wave energy than subsurface temperature regardless of functional group. Across functional groups, the strongest correlations with the physical drivers were evident in turf algae and CCA. High wave energy often favours low-lying, wave-tolerant algae, such as turf and CCA and limits the dominance of larger upright macroalgae that, like some corals, are vulnerable to dislodgement (Page-Albins et al. 2012, Williams et al. 2013, Gove et al. 2015). Our findings suggest, that physical drivers on coral reefs not only limit or promote the abundance of individual benthic groups, but also play a key role in governing their spatial scaling properties across tropical seascapes.

The spatial scaling of coral reef benthic communities was more similar between islands closer in proximity and size. For example, at neighbouring Kingman and Palmyra (63 km apart), macroalgae were spatially structured up to ~3 km scales at both islands. At neighbouring Howland and Baker (69 km apart), CCA was spatially structured up to scales of 0.3 km at both islands. We hypothesise that these common benthic scaling patterns between closely situated islands reflect broader-scale autocorrelation in environmental conditions that exist across archipelagos, with islands in closer proximity exposed to similar surrounding environmental conditions (Gove et al. 2013). Kingman and Palmyra also have much larger total reef areas and longer coastlines, producing more expansive areas of reef slope of the same aspect, than at the other three islands (Gove et al. 2016). This may allow environmental homogeneity over greater linear extents, particularly with regards to incoming wave energy and could give rise to the large homogeneous zones of spatial dominance by single benthic functional groups and coral morphologies that we observe at Kingman and Palmyra. Smaller coastlines and total reef areas at Howland, Baker and Jarvis could explain why benthic functional groups here, only remained spatially clustered at smaller spatial scales.

Our results support the expectation that environmental drivers can cause ecological responses at larger spatial scales, while biotic factors drive smaller-scale patterns and processes (Legendre 1993). We found the upper bounds in scale at which the benthic and physical variables showed spatial clustering were highly correlated, suggesting that physical drivers set the upper spatial bounds in which benthic communities are spatially organised around tropical oceanic islands. At smaller spatial scales (100–200 m), we saw the highest degree of benthic community spatial clustering, which may be better explained by biotic factors. For example, the dominant

macroalgae around our study islands are calcifying *Halimeda* (Vroom et al. 2010, Williams et al. 2013) that reproduce asexually over short distances by fragmentation. This type of reproduction could explain the high degrees of macroalgal spatial clustering at scales of 100–200 m around Kingman, Palmyra, Howland and Baker. Similarly, the high spatial clustering of branching corals at smaller scales at Howland and Baker, could be explained by the branching corals all being fast-growing Acroporids that can also reproduce over short distances through fragmentation (Baird and Hughes 2000).

Conclusion

For the first time, we quantify the autocorrelated nature of coral reef seascapes across geographies in the absence of direct local human impacts. All major benthic functional groups and hard coral morphologies showed evidence of positive autocorrelation (spatial clustering) up to scales of 0.3–3.5 km around the circumference of five oceanic tropical islands. The scales across which benthic community members exhibited spatial structure and the strength of these autocorrelation patterns differed between islands but was more similar between islands closer in proximity and of a similar size. In some cases, benthic community spatial scaling was similar to the scaling of concurrent gradients in physical drivers, in particular wave energy. This suggests that physical drivers not only play a role in governing patterns of community abundance on tropical coral reefs, but also contribute to determining their spatial scaling properties across the seascape. How these patterns of biological autocorrelation change in response to changes in physical gradients, such as those that occur during environmental disturbance events, remains unknown and is an exciting avenue for future research.

Data availability statement

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.vq83bk3r1> (Ford et al. 2020).

Acknowledgements – We thank NOAA's Pacific Islands Fisheries Science Center (PIFSC) Ecosystem Sciences Division and the officers and crews of the NOAA ships Hi'ialakai and Oscar Elton Sette for coordinating and conducting all towed-diver surveys. We thank members of the Reef Systems Lab at Bangor University's School of Ocean Sciences for their collective advice towards project development, the NOAA internal review process and two anonymous reviewers for their helpful comments on the manuscript draft. We thank Amanda Dillon at Aline Design for help with figure formatting and Joey Lecky for his assistance in the creation of Figure 1.
Funding – HVF was supported by a Envision Doctoral Training Programme scholarship funded by the National Environment Research Council (NERC) of the UK and co-funding from The Nature Conservancy.
Author contributions – HVF and GJW conceived the study; HVF analysed the data with GJW, JMG and AJD; HVF wrote the manuscript with GJW. All authors contributed to the editing of the manuscript.

References

Addicott, J. F. et al. 1987. Ecological neighborhoods: scaling environmental patterns. – Oikos 49: 340–346.
Alvarez-Filip, L. et al. 2011. Complex reef architecture supports more small-bodied fishes and longer food chains on Caribbean reefs. – Ecosphere 2: 1–17.
Aston, E. A. et al. 2019. Scale-dependent spatial patterns in benthic communities around a tropical island seascape. – Ecography 42: 578–590.
Baird, A. H. and Hughes, T. P. 2000. Competitive dominance by tabular corals: an experimental analysis of recruitment and survival of understorey assemblages. – J. Exp. Mar. Biol. Ecol. 251: 117–132.
Beijbom, O. et al. 2015. Towards automated annotation of benthic survey images: variability of human experts and operational modes of automation. – PLoS One 10: e0130312.
Boström, C. et al. 2011. Seascape ecology of coastal biogenic habitats: advances, gaps and challenges. – Mar. Ecol. Prog. Ser. 427: 191–217.
Bradbury, R. and Young, P. 1983. Coral interactions and community structure: an analysis of spatial pattern. – Mar. Ecol. Prog. Ser. 11: 265–271.
Cocu, N. et al. 2005. Spatial autocorrelation as a tool for identifying the geographical patterns of aphid annual abundance. – Agric. For. Entomol. 7: 31–43.
D'Urban Jackson, T. et al. 2020. Three-dimensional digital mapping of ecosystems: a new era in spatial ecology. – Proc. R. Soc. B 287: 20192383.
De Knegt, H. J. et al. 2011. The spatial scaling of habitat selection by African elephants. – J. Anim. Ecol. 80: 270–281.
Diaz-Pulido, G. and Garzón-Ferreira, J. 2002. Seasonality in algal assemblages on upwelling-influenced coral reefs in the Colombian Caribbean. – Bot. Mar. 45: 284–292.
Dorenbosch, M. et al. 2005. Distribution of coral reef fishes along a coral reef-seagrass gradient: edge effects and habitat segregation. – Mar. Ecol. Prog. Ser. 299: 277–288.
Dungan, J. L. et al. 2002. A balanced view of scale in spatial statistical analysis. – Ecography 25: 626–640.
Edmunds, P. J. and Leichter, J. J. 2016. Spatial scale-dependent vertical zonation of coral reef community structure in French Polynesia. – Ecosphere 7: e01342.
Edwards, C. B. et al. 2017. Large-area imaging reveals biologically driven non-random spatial patterns of corals at a remote reef. – Coral Reefs 36: 1291–1305
Estes, L. et al. 2018. The spatial and temporal domains of modern ecology. – Nat. Ecol. Evol. 2: 819–826.
Ford, H. V. et al. 2020. Data from: Spatial scaling properties of coral reef benthic communities. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.vq83bk3r1>.
Fortin, M.-J. et al. 2016. Spatial analysis in ecology. – Wiley StatsRef: Statistics Reference Online. Wiley.
Gobbi, M. and Brambilla, M. 2016. Patterns of spatial autocorrelation in the distribution and diversity of carabid beetles and spiders along Alpine glacier forelands. – Ital. J. Zool. 83: 600–605.
Gove, J. M. et al. 2006. Temporal variability of current-driven upwelling at Jarvis Island. – J. Geophys. Res. 111: C12011.
Gove, J. M. et al. 2013. Quantifying climatological ranges and anomalies for Pacific coral reef ecosystems. – PLoS One 8: e61974.
Gove, J. M. et al. 2015. Coral reef benthic regimes exhibit nonlinear threshold responses to natural physical drivers. – Mar. Ecol. Prog. Ser. 522: 33–48.

Gove, J. M. et al. 2016. Near-island biological hotspots in barren ocean basins. – Nat. Comm. 7: 1–8.
Hamylton, S. M. and Barnes, R. S. K. 2018. The effect of sampling effort on spatial autocorrelation in macrobenthic intertidal invertebrates. – Hydrobiologia 811: 239–250.
Hatcher, B. G. et al. 1987. Scaling analysis of coral reef systems: an approach to problems of scale. – Coral Reefs 5: 171–181.
Heenan, A. et al. 2020. Natural variation in coral reef trophic structure across environmental gradients. – Front. Ecol. Environ. 18: 69–75.
Hinchey, E. K. et al. 2008. Preface: marine and coastal applications in landscape ecology. – Landsc. Ecol. 23: 1–5.
Hochberg, E. J. and Atkinson, M. J. 2003. Capabilities of remote sensors to classify coral, algae and sand as pure and mixed spectra. – Remote Sens. Environ. 85: 174–189.
Hughes, T. P. et al. 2017. Coral reefs in the Anthropocene. – Nature 546: 82–90.
Jones, K. B. et al. 2013. Informing landscape planning and design for sustaining ecosystem services from existing spatial patterns and knowledge. – Landsc. Ecol. 28: 1175–1192.
Kenny, A. et al. 2003. An overview of seabed-mapping technologies in the context of marine habitat classification. – ICES J. Mar. Sci. 60: 411–418.
Kenyon, J. C. et al. 2006. Towed-diver surveys, a method for mesoscale spatial assessment of benthic reef habitat: a case study at Midway Atoll in the Hawaiian Archipelago. – Coast. Manage. 34: 339–349.
Lee, M. F. et al. 2008. Remote sensing assessment of forest damage in relation to the 1996 strong typhoon Herb at Lienhuachi Experimental Forest, Taiwan. – For. Ecol. Manage. 255: 3297–3306.
Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? – Ecology 74: 1659–1673.
Levin, S. A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. – Ecology 73: 1943–1967.
Levy, J. et al. 2018. Assessing the spatial distribution of coral bleaching using small unmanned aerial systems. – Coral Reefs 37: 373–387.
Littler, M. M. et al. 1983. Evolutionary strategies in a tropical barrier reef system: functional-form groups of marine macroalgae. – J. Phycol. 19: 229–237.
Madin, J. S. et al. 2014. Mechanical vulnerability explains size-dependent mortality of reef corals. – Ecol. Lett. 17: 1008–1015.
Miller, M. W. et al. 1999. Effects of nutrients versus herbivores on reef algae: a new method for manipulating nutrients on coral reefs. – Limnol. Oceanogr. 44: 1847–1861.
Moran, P. A. P. 1950. Notes on continuous stochastic phenomena. – Biometrika 37: 17.
Mumby, P. J. et al. 1997. Coral reef habitat-mapping: how much detail can remote sensing provide? – Mar. Biol. 130: 193–202.
Mundy, B. C. et al. 2010. Inshore fishes of Howland Island, Baker Island, Jarvis Island, Palmyra Atoll and Kingman Reef. – Atoll Res. Bull. 585.
Murdoch, T. J. T. and Aronson, R. B. 1999. Scale-dependent spatial variability of coral assemblages along the Florida Reef Tract. – Coral Reefs 18: 341–351.
Nash, K. L. et al. 2014. Discontinuities, cross-scale patterns and the organization of ecosystems. – Ecology 95: 654–667.
Norström, A. V et al. 2016. Guiding coral reef futures in the Anthropocene. – Front. Ecol. Environ. 14: 490–498.
Page-Albins, K. N. et al. 2012. Patterns in benthic coral reef communities at Pearl and Hermes Atoll along a wave-exposure gradient. – Pacific Sci. 66: 481–496.
Pedersen, N. E. et al. 2019. The influence of habitat and adults on the spatial distribution of juvenile corals. – Ecography 42: 1703–1713.
Pfeifer, M. et al. 2017. Creation of forest edges has a global impact on forest vertebrates. – Nature 551: 187–191.
Pittman, S. J. et al. 2011. Practicing coastal seascape ecology. – Mar. Ecol. Prog. Ser. 427: 187–190.
Purkis, S. J. 2018. Remote sensing tropical coral reefs: the view from above. – Ann. Rev. Mar. Sci. 10: 149–168.
Rahbek, C. and Graves, G. R. 2000. Detection of macro-ecological patterns in South American hummingbirds is affected by spatial scale. – Proc. R. Soc. B 267: 2259–2265.
Richardson, L. E. et al. 2017. Structural complexity mediates functional structure of reef fish assemblages among coral habitats. – Environ. Biol. Fishes 100: 193–207.
Schneider, D. C. 1994. Quantitative ecology: spatial and temporal scaling. – Elsevier.
Schneider, D. C. 2001. The rise of the concept of scale in ecology. – Bioscience 51: 545–553.
Tsuda, R. T. et al. 2008. Additional marine benthic algae from Howland and Baker Islands, Central Pacific 1. – Pacific Sci. 62: 271–290.
Vargas-Ángel, B. et al. 2011. Severe, widespread El Niño-associated coral bleaching in the US Phoenix Islands. – Bull. Mar. Sci. 87: 623–638.
Vroom, P. S. et al. 2010. Marine biological community baselines in unimpacted tropical ecosystems: spatial and temporal analysis of reefs at Howland and Baker Islands. – Biodivers. Conserv. 19: 797–812.
Wagner, H. H. and Fortin, M.-J. 2005. Spatial analysis of landscapes: concepts and statistics. – Ecology 86: 1975–1987.
Wedding, L. M. et al. 2011. Quantifying seascape structure: extending terrestrial spatial pattern metrics to the marine realm. – Mar. Ecol. Prog. Ser. 427: 219–232.
Wiens, J. A. and Milne, B. T. 1989. Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. – Landsc. Ecol. 3: 87–96.
Williams, G. J. et al. 2010. Modeling patterns of coral bleaching at a remote Central Pacific atoll. – Mar. Pollut. Bull. 60: 1467–1476.
Williams, G. J. et al. 2013. Benthic communities at two remote Pacific coral reefs: effects of reef habitat, depth and wave energy gradients on spatial patterns. – PeerJ 1: e81.
Williams, G. J. et al. 2015a. Local human impacts decouple natural biophysical relationships on Pacific coral reefs. – Ecography 38: 751–761.
Williams, G. J. et al. 2018. Biophysical drivers of coral trophic depth zonation. – Mar. Biol. 165: 60.
Williams, G. J. et al. 2019. Coral reef ecology in the Anthropocene. – Funct. Ecol. 33: 1014–1022.
Williams, S. M. et al. 2015b. Hierarchical spatial patterns in Caribbean reef benthic assemblages. – J. Biogeogr. 42: 1327–1335.
Zhang, N. and Zhang, H. 2011. Scale variance analysis coupled with Moran's *I* scalogram to identify hierarchy and characteristic scale. – Int. J. Geogr. Inform. Sci. 25: 1525–1543.
Zhang, X. et al. 2009. NDVI spatial pattern and its differentiation on the Mongolian Plateau. – J. Geogr. Sci. 19: 403–415.