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RESEARCH

Biophysical drivers of coral reef community structure across a tropical benthic seascape

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Abstract Coral reefs are global biodiversity hotspots, important for ocean health and providing ecosystem services for thousands of species (including humans). Coral benthic communities form the structural basis of these ecosystems, influencing ecological processes and ecosystem functions. For thousands of years, coral benthic communities have been driven by naturally occurring properties of the environment, which we refer to as biophysical drivers. However, as humans increasingly encroach on and alter coastal marine ecosystems, anthropogenic conditions may override biophysical drivers, making it challenging to identify the sources of changes in community composition and consequent ecosystem functioning. Here, we use multivariate analyses to demonstrate that bathymetric slope (surface steepness) and intercardinal bearing, a proxy for wind and wave exposure, are significant drivers of benthic composition across Tetiaroa, French Polynesia, a remote coral atoll where the influences of biophysical conditions have not been previously investigated. Distance-based redundancy analysis concluded that together, these biophysical variables explained 66.02% of the variance in benthic community composition. Determining the most important drivers of benthic community composition in this area of minimal human influence provides baseline data for natural coral reef ecosystems. This information will help us understand and predict coral reef community responses to changing environmental conditions and guide conservation and restoration efforts of this ecologically important atoll.

Keywords Coral atoll · Biophysical drivers · Benthic community composition · Tropical coral reef · Spatial variation

Introduction

Coral reefs are important marine ecosystems for their role in maintaining overall ocean health and providing ecosystem services depended on by over 500 million people worldwide (Reid et al. 2005; Hicks 2011; Sobha, Vibija, and Fahima, 2023). Coral reefs are global biodiversity hotspots, with over 700 described coral species that provide food and habitat for a diverse range of other taxa, including single-celled organisms, algae, crustaceans, and fish (Moberg and Folke 1999; Sobha, Vibija and Fahima, 2023). Coral benthic communities provide the foundation for coral reef ecosystems, with Scleractinian (hard) corals representing keystone species that establish the reef framework (Darling et al. 2017; Dishon et al. 2020). Since the 1950s, the global coverage of Scleractinian coral has reduced by over 50%, and coral reef ecosystems are experiencing declines in health and size driven by multiple interacting stressors (Ban, Graham, and Connolly, 2014; Eddy et al. 2021). However, biophysical

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drivers have historically set the natural boundaries of coral reef ecosystem structure and function (Williams et al. 2019).

Biophysical drivers are properties of the environment dictated by geological and physical drivers such as topography (comprising factors like depth, slope, and structural complexity) through a cascade of influences (Aronson and Precht 2016; Jouffray et al. 2019; Williams et al. 2019). For example, topographic features such as oceanic ridges that influence gyres have been found to subsequently drive upwelling and constrain reef development along continental West coasts (Birkeland 1997; Hubbard 1997; Aronson and Precht 2016; Sonnewald, Reeve and Lguensat, 2023). However, the relative influences of these drivers vary between geographies and at different spatial and temporal scales, creating enormous diversity both within and across coral reefs globally. Biophysical drivers shape unique foundational coral communities by filtering for well-adapted species, which in turn determine the structure of entire coral reef ecosystems (I. D. Williams et al. 2015a, b; Heenan et al. 2016; Robinson et al. 2018; Kubicek et al. 2019). The influence of foundational benthic species is a result of the traits they possess, called functional traits, that often have a significant influence on fitness and the surrounding environment and play vital roles in ecosystem function. Subsequently, identifying relationships between environmental conditions and coral reef benthic communities, and monitoring shifts in community composition over time, could be highly informative in understanding current and future ecosystem changes, and their functioning in response to environmental change (Murdoch 2007). Community composition and resulting functional traits can link environmental conditions and ecosystem functions. However, growing anthropogenic stressors, including fishing, pollution, and climate change, are causing abnormal environmental changes to which coral reefs are negatively responding (Hughes et al. 2017). This anthropogenic influence can override biophysical factors and compromise our ability to identify the sources of changes in community composition and consequent ecosystem functioning (G. J. Williams et al. 2015a, b). Yet remote coral reefs currently experience limited anthropogenic influence relative to other coral reef ecosystems globally and, therefore, provide optimal opportunities to explore natural relationships between ecosystem structure and environmental conditions. By collecting data on various biophysical factors and benthic coral community composition from sites across Tetiaroa and applying a multivariate statistical approach, we address the question: Which biophysical drivers best explain the spatial variation in benthic community composition? We expect the benthic community structure to represent characteristics of a healthy coral reef ecosystem, particularly exhibiting high levels of diversity and heterogeneity due to minimal direct anthropogenic disturbance in the region. The results provide an understanding of the biophysical drivers that shape Tetiaroa's unique coral reef ecosystem, that can inform future management strategies.

Methods

Study site

We evaluated the strength of biophysical drivers on benthic community composition in Tetiaroa (149.5666°W, 17.0164°S), a coral atoll in Te Ao Mā'ohi (French Polynesia, Fig. 1). Located in the Windward group of the Society Islands, roughly 55 km north of Tahiti, Tetiaroa is a 34 km^2 atoll comprising twelve islets (hereafter, motu) and a broad central lagoon. Positioned in the Southeast Trade Winds zone, the atoll experiences a wet, tropical climate. East-southeast (ESE) winds prevail for 70–80% of the year and are generally strongest from April to October, the southern hemisphere's winter months (Collin et al. 2014; Jeanson et al. 2014). From November to February, ocean swells shift, originating instead from the north-northwest (NNW). The tidal range is relatively small, at less than 0.5 m (Jeanson et al. 2014).

Tetiaroa atoll's unique cultural history, from a secondary residence for the Tahitian King to private ownership, has afforded the atoll only a small resident population who support restricted tourism and development (Collin et al. 2014). Tetiaroa also remains central to French Polynesian culture, with many traditional customs upheld, including rāhui—restricting resource use such as fishing (Tetiaroa Society 2016). The most impactful human modifications on the atoll have been coconut palm plantations, a frequent mark of human habitation on tropical islands (McCauley et al. 2012), and repeated introductions of invasive rats (*Rattus rattus, R. exulans*) (Russell, Faulquier and Tonione, 2011a). In addition, invasive rat presence has fluctuated in frequency, severity, and location across Tetiaroa (Russel et al., 2011b). Rat invasions are known to have cascading influences on coastal marine ecosystems, particularly coral reefs, through their detrimental effects on island seabird populations (Steibl et al. 2024) and associated nutrient cycles (Graham et al. 2018). With regards to intensive human development and modification, disturbances here are minimal compared to similar locations, yet the atoll remains accessible. Additionally, under the stewardship of the Tetiaroa Society, the atoll's community is dedicated to its conservation and preservation.

Ecological field surveys

Ecological field surveys were conducted at 12 sites distributed around the atoll from November 6–14, 2021, to characterize the benthic community composition (Figs. 1 and 2). Four replicate 30-m transects were performed at each

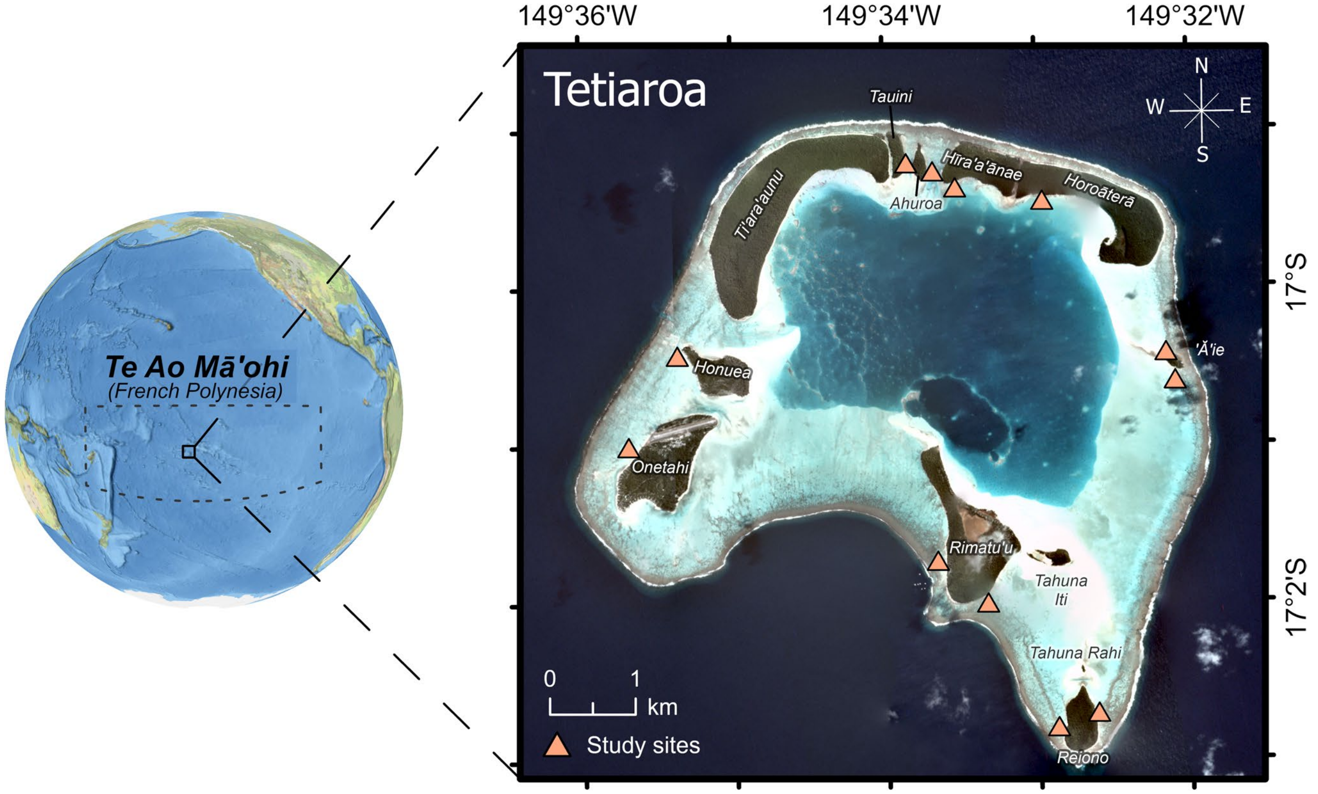

Fig. 1 Location of study sites within Tetiaroa, Te Ao Mā'ohi (French Polynesia). Satellite imagery: Pléiades © CNES 2022, Distribution AIRBUS DS, tous droits réservés. Usage commercial interdit

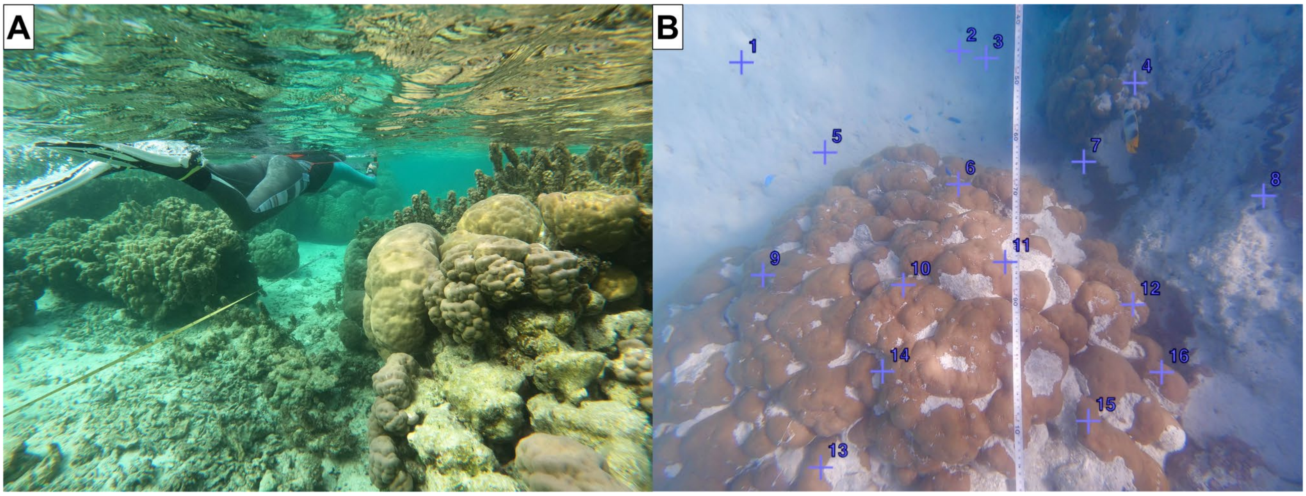

Fig. 2 **A** Scientist conducting a benthic video transect using a handheld frame mounted with a GoPro Hero camera and two down-facing laser pointers. **B** Example of a still image extracted from a 30-m transect video overlaid with 16 points for annotation generated via the CoralNet software

site, spaced at least 10-m apart, totaling 48 transects. Sites were haphazardly selected within sufficiently large and deep (0.2–2.5 m) reef patches at nine motu, with two sites positioned on either side of 'Ă'ie, Rimatu'u, and Reiono to represent reefs exposed to and protected from the dominant ESE swells. A snorkeler swam along the 30-m transect at each site, holding a handheld frame with a GoPro camera and two laser pointers (Fig. 2). Videos were recorded using standard settings on a GoPro Hero7, except for four transects at Rimatu'u, which used a GoPro Hero9. The videos were used to characterize the coral reef benthic community structure across study sites.

Benthic data processing

Percent benthic cover estimation

Still benthic images were extracted at 4-s intervals from each 30-m transect video survey using the VLC media player software. From each video survey, 18–24 high-quality images were isolated and checked to prevent overlap and ensure that the transect tape and benthos were visible. The resulting 1006 images and their metadata were then uploaded to CoralNet (v1.0), an open-access reef image analysis platform (Lamirand et al., 2022). During image extraction, a library of hard coral species and morphotypes was created to support subsequent image analysis. This library guided label selection for the CoralNet project label set, which included coral genera, species where possible, morphology, and other biotic (e.g., crustose coralline algae (CCA), turf algae, macroalgae) and abiotic (e.g., pavement, sand, rock) substrates (Supplementary Table 1). Using CoralNet's stratified random point generation method, 16 points were overlaid on each image. The EfficientNet feature extractor, with a 95% confidence threshold, provided suggested annotations. Each point was manually checked, and the annotation was confirmed to ensure accuracy and consistency.

Following image annotation, percent cover data and the associated metadata were exported from CoralNet. Cover data were then averaged at the site level across all images for the four transects at each site. Points identified as transect tape were removed. Live benthic substrates other than hard coral, CCA, macroalgae, and turf were combined into a general "Live benthos" category. This resulted in a dataset containing the site-level percent coverages of 18 benthic cover types. Data preparation and subsequent analyses were conducted using R (v4.3.0) in an RStudio desktop environment (v2024.4.2.764; Posit team 2024; R Core Team 2024) unless otherwise noted.

Biophysical data

To assess the influence of seafloor topography and relative land-sea positioning on benthic community composition, we calculated the mean depth, slope, slope of slope, and offshore distance across the 30-m transects conducted at each site. These data were derived from a 30-cm resolution light detection and ranging (LiDAR) dataset generated over Tetiaroa in May 2017, funded by the Island Digital Ecosystem Avatars (IDEA) program (Davies et al. 2016; Gruen et al. 2017; Ural, Gruen and Kocaman, 2019). To account for the potential delivery of allochthonous seabird-derived nutrients to each site, we also obtained nitrogen stable isotope records (reported as δ values for the ratio of ^{15}N:^{14}N (δ^{15}N)) from a concurrent study conducted in Tetiaroa atoll (Benkwitt et al. 2025). δ^{15}N serves as a proxy for seabird nutrient inputs, reflecting the elevated ^{15}N content in guano from pelagic-feeding seabirds, which has been shown to fuel the growth and productivity of corals and reef-associated algae (Graham et al. 2018; Benkwitt, Wilson and Graham, 2019; Benkwitt et al. 2023). Site-level δ^{15}N values were calculated as the mean of δ^{15}N values from *Turbinaria ornata* macroalgae samples collected within a 200-m buffer of the benthic survey transects. Finally, to address potential variations stemming from the sampling position relative to the greater atoll and consequent exposure to the prevailing Southeast Trade Winds, each site was assigned an intercardinal bearing value (e.g., ESE, WNW) derived from 45° angles originating from the atoll center (149.5666°W, 17.0164°S). Apart from intercardinal bearing, which was assigned using RStudio, biogeophysical variables were computed using ArcGIS Pro (v3.1.0, Esri Inc 2023) via a suite of geoprocessing tools in the ModelBuilder visual programming language (Table 1).

Statistical analyses

Cleveland dot plots were initially used to identify potential outliers in the five biophysical variables under consideration. To check for multicollinearity among these explanatory variables, which can inflate parameter estimates and undermine model accuracy if not addressed, Pearson's pairwise correlation coefficients (r) were calculated and visualized using the packages *stats* (v4.3.0, R Core Team 2024) and *corrplot* (v0.92, Wei et al., 2021). Applying a threshold of $r = 0.7$, the correlation matrix revealed that the LiDAR-derived metrics of slope and slope of slope demonstrated a strong positive correlation. The slope variable was retained due to its critical role in influencing light availability, sediment transport, water flow, and its substantial contribution to structural complexity—a key factor in determining coral reef community composition (Sheppard 1982; Kahng et al. 2010; Pittman and Brown 2011; Borland et al. 2021). Additionally, slope showed a lower overall correlation with other biophysical predictors. Consequently, the slope of slope metric was excluded from subsequent analyses.

Benthic cover data were log (x + 1)-transformed to reduce the effect of asymmetrical data distribution and then used as an input to a principal components analysis (PCA). PCA is a method for reducing dimensionality by identifying the 'principal components' (i.e., orthogonal axes) that best capture the variance in the matrix of site-level benthic compositions (James et al. 2021). This ordination method was chosen because it aligned with our aim of understanding how biophysical factors contribute to the variation in the benthic community. PCA uses raw data to produce the outcome principle components, potentially highlighting more meaningful

Table 1 Explanatory variables considered for use in the analysis of benthic community structure. Continuous variable values were averaged across the four replicate 30 m transects at each site to produce site-level means for subsequent analysis

Variable	Unit	Description	Technique
Depth	Meters (m)	Water depth (i.e., bathymetry)	LiDAR (see Gruen et al. 2017; Ural, Gruen and Kocaman, 2019)
Slope	Degrees (°)	Rate of maximum change in depth (i.e., surface steepness)	Slope (ArcGIS Pro Spatial Analyst Toolbox)
Slope of slope	Degrees of degrees (°)	Rate of maximum change in the slope (i.e., surface complexity)	Slope (ArcGIS Pro Spatial Analyst Toolbox)
Offshore distance	Meters (m)	Distance from the nearest point on the adjacent motu coastline to the transect	Generate Near Table (ArcGIS Pro Analysis Toolbox)
δ^{15}N signature	Per mil (‰)	δ values for the ratio of ^{15}N:^{14}N in macroalgae within 200-m of the transect. Used as a proxy for seabird nutrient enrichment	Stable isotope ratio mass spectrometry (see Graham et al. 2018)
Intercardinal bearing	Categorical factor	Location of the transect relative to the center of the atoll (e.g., SSE, NNW), assigned using 45° angles	Manual assignment using R

relationships and increasing interpretation ease and accuracy relative to other ordination methods, where raw data must be transformed into a distance matrix. PCA was conducted using the prcomp() function from the *stats* package. Covariate data were then converted into significant correlation vectors (factor for the Intercardinal bearing) using the envfit() function with 999 permutations from the package *vegan* (Oksanen et al., 2024), and combined with PCA plots to visualize relationships between patterns of variation within the underlying benthic community dataset and our biophysical predictors (Lange et al. 2021). A distance-based redundancy analysis (dbRDA) was applied to the benthic cover data following Legendre and Gallagher (2001) to evaluate how well the biophysical predictors explained the community dissimilarities observed in the PCA. The dbRDA, performed using the capscale() function in the *vegan* package, was constrained by the vectors depth, slope, distance from shore, and δ^{15}N signatures, as well as the factor intercardinal bearing. The distance method was set to "bray," which converted the data to a Bray–Curtis dissimilarity matrix before dbRDA. To prevent distortion due to negative eigenvalues and improve relationship stability and interpretability, the square roots of dissimilarities were used in dbRDA (Legendre and Anderson 1999). Once the initial model had been tested for statistical significance, backward selection (James et al. 2021) was applied using the *vegan* ordistep() function to identify the biophysical variables that best explain the variation in the underlying matrix. This determines the best model through a stepwise algorithm using the Akaike information criterion (AIC).

Results and discussion

Benthic community diversity varied across sites, with a maximum of 15 benthic cover types recorded at Honuea and a minimum of 10 benthic cover types found at both 'Ă'ie and Reiono, irrespective of motu side (Fig. 3). Sand was the dominant benthic habitat type, with an average percent cover of 36.61% (± 16.37 SD) across all sites in Tetiaroa Atoll. Notably, sand had the highest site-level percent cover average of any benthic cover type, reaching 68% at Honuea. In contrast, *Pavona varians* had the lowest average percent cover at just 0.01% (± 0.04). Aside from sand, the only other benthic classes with an average atoll-wide percent cover exceeding 1% were pavement (12.82 ± 6.75), rubble (12.44 ± 8.48), *Porites* massive/submassive (11.06 ± 5.60), sand/rubble (9.56 ± 4.00), turf (9.14 ± 4.43), and macroalgae (4.28 ± 4.00).

According to the PCA, the biophysical variables with a statistically significant influence on the spatial variation of Tetiaroa's benthic community composition included depth ($p = 0.008$, $R^2 = 0.07$), slope ($p = 0.003$, $R^2 = 0.09$), offshore distance ($p = 0.002$, $R^2 = 0.08$), and, marginally, intercardinal bearing ($p = 0.06$, $R^2 = 0.31$) (Supplementary Fig. 1). Following dbRDA analysis and backward selection, the most meaningful and parsimonious model identified included only slope ($p = 0.008$) and intercardinal bearing ($p = 0.001$), which together explained 66% of the variance in benthic community composition (Fig. 4A). Slope influences other variables, including structural complexity, irradiance, and sedimentation, altering site conditions and benthic communities (Sheppard 1982; Kahng et al. 2010). For example, a site on a steep slope is subjected to more downwelling sediment, reducing the likelihood of coral larval settlement and increasing disturbance frequency (Kahng et al. 2010).

In Tetiaroa, the Southeast Trade Winds generate a dominant ocean swell prevailing from ESE for most of the year (Fig. 4C). The dbRDA plot visualized sites according to (dis)similarities in benthic community composition and displayed similar spatial patterns to actual site geographic

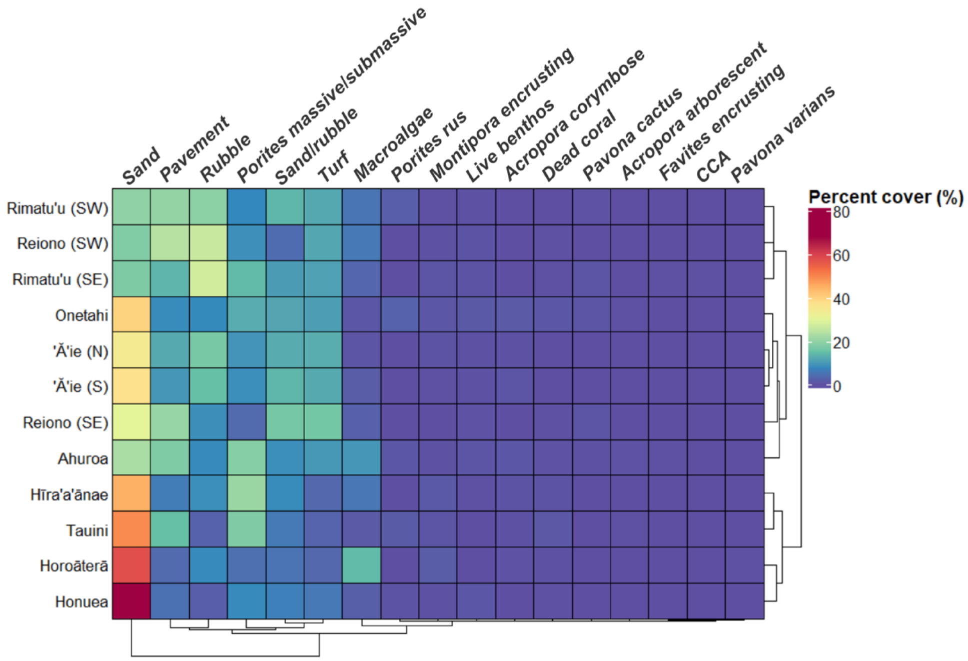

Fig. 3 Heatmap displaying the percent cover (%) of each benthic cover type across various sites, produced using the *ComplexHeatmap* R package (Gu 2022). Percent cover is represented by a gradient from cool to warm tones, where higher values correspond to warmer tones. Dendrograms indicate the hierarchical clustering of rows (sites) and columns (benthic types) based on the similarity of their percent cover values. The sand/rubble benthic type represents sandy bottoms interspersed with scattered dead or unstable coral rubble, where neither sand nor rubble was clearly dominant in the annotated images. Abbreviations: CCA = crustose coralline algae, N = north, S = south, SW = southwest, SE = southeast

locations, particularly regarding motu on the Eastern side of the atoll (Fig. 4). Easterly intercardinal bearing is a common covariate of the clustered sites on this side of the atoll (green circles); therefore, considering our results alongside contextual information such as wind regime, we suggest intercardinal bearing as an unintentional but appropriate proxy for wave/wind exposure of a site.

Rubble, turf, and pavement had the most negative contributions to dbRDA axis (CAP1). Consequently, these benthic cover types are most abundant at sites with low CAP1 values (Supplementary Fig. 2). Conversely, sand and *Montipora* encrusting species had more positive contributions, indicating that these types are less abundant at sites with low CAP1 values. For CAP2, macroalgae and rubble contributed most positively, while *Porites rus* contributed most negatively. The highest macroalgal cover was observed at Ahuroa, Hīra'a'ānae, and Horoāterā (Fig. 3). The positive contribution of macroalgae to CAP2 in Supplementary Fig. 2 positions the benthic group close to these sites in the top half of the plot, corresponding to high CAP2 values. These findings align with those from Page-Albins et al. (2012), who recorded the highest abundances of turf and macroalgae at sites with intermediate-low wave exposure in Pearl and Hermes Atoll, Northwestern Hawaiian Islands. These results may also provide insights into fish communities across Tetiaroa, where high macroalgal cover could indicate lower abundances of certain herbivorous fish groups, such as browsers that feed predominantly on macroalgae (Heenan et al. 2016). Specifically, these results may suggest variations in herbivore behavior across an exposure gradient, consistent with Karkarey et al. (2020), who found lower per capita bite rates in exposed reefs compared to sheltered ones due to environmental filtering.

By investigating the relationships between benthic communities and environmental conditions, we provide valuable insights into the coral reef community structure and potential dynamics of Tetiaroa's unique atoll system. Our finding that intercardinal bearing, linked to wind and wave exposure, significantly influences reef dynamics across Tetiaroa is consistent with several key studies that have identified wave energy and exposure as crucial factors in shaping coral reef benthic community composition (G. J. Williams et al. 2015a, b; Robinson et al. 2018; Ceccarelli et al. 2020; Lange et al. 2021). Additionally, our research extends the findings of these earlier studies that focused on outer and forereefs by highlighting the substantial impact of wind and wave exposure on coral benthic community structure not only seaward, but also inside the reef crest.

As human populations expand, particularly in coastal areas, we increasingly interact with coral reef ecosystems to an extent that may override biophysical factors, subsequently altering species assemblages and, thus, ecosystem structure and function (Williams and Graham 2019; Williams et al. 2019). To separate the influences of natural and anthropogenic drivers, previous studies have focused their work on remote coral reefs as they currently experience limited anthropogenic influence relative to other coral reef ecosystems globally (G. J. Williams et al. 2015a, b). Tetiaroa Atoll presents a unique opportunity for this as its small human population makes the practicalities of data collection far less challenging. This human presence has brought some disturbances in the form of monocropping and non-native species

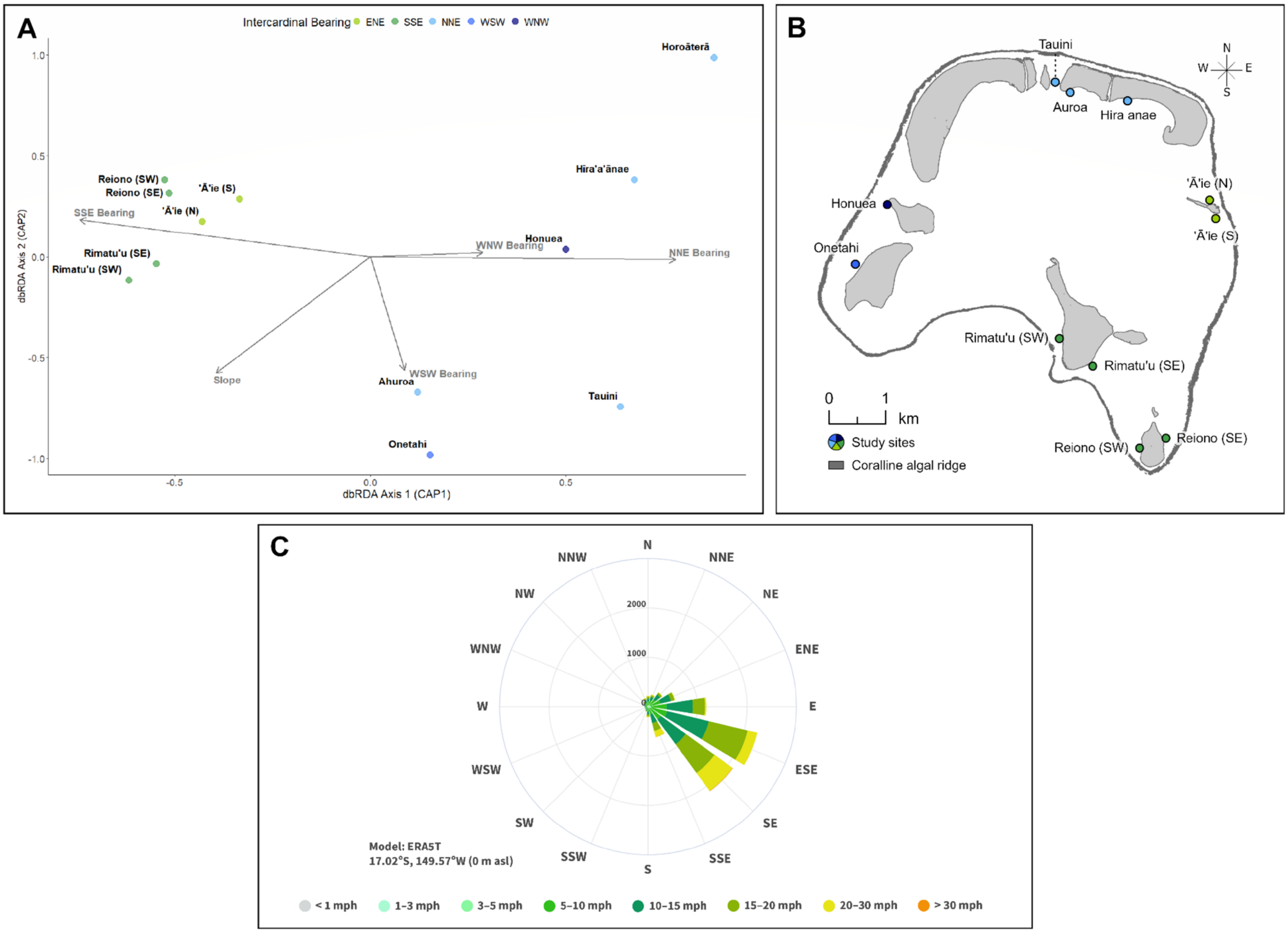

Fig. 4 **A** Distance-based Redundancy Analysis (dbRDA) biplot displaying (dis)similarities in benthic community composition among the sites. Sites are colored according to intercardinal bearing, where ENE = east-northeast, SSE = south-southeast, NNE = north-northeast, WSW = west-southwest, and WNW = west-northwest. The gray arrows represent the extent to which the vector (depth) and factor (intercardinal bearing direction) drive differences in benthic community composition between the sites. **B** Map of the study sites within Tetiaroa, French Polynesia, shaded according to their intercardinal bearing as represented in panel A. **C** Wind rose diagram displaying the number of hours per year for which the wind blows from the indicated direction, according to the ERA5T model. The location, size, and color of the shaded regions on the plot represent the direction, magnitude, and speed of wind conditions. The wind rose plot was generated using www.meteoblue.com (CC BY-NC)

introductions; however, in terms of intensive development and activity, the atoll is minimally disturbed relative to others. Nonetheless, even without the more common anthropogenic disturbances (e.g. fishing, pollution), climate change affects all coral reefs, regardless of location. For example, bleaching events and cyclones have frequently hit the Society Islands' coral reefs, including Tetiaroa, within the last 50 years (Adjeroud et al. 2005). Therefore, all 'baseline' data must come with the caveat that no coral reefs are now truly pristine, and we must utilize the few remaining places on earth where the ecosystems have not experienced intensive, direct anthropogenic disturbances.

Despite the importance of baseline data for coral reef ecosystems, each reef will experience unique combinations and relative influences of drivers, producing the observed global diversity of coral reef ecosystems (I. D. Williams et al. 2015a, b; Heenan et al. 2016). This is clear from our findings that suggest an average ~ 58% of the benthos across Tetiaroa is sand and rubble and, therefore, unsuitable for coral growth. These findings were unexpected, considering Tetiaroa's position in a well-known Indo-Pacific coral reef hotspot. Nevertheless, our findings still provide valuable insights into the influence of biophysical drivers in these ecosystems, as they play a role in forming (un)suitable benthos for coral growth and drive the resultant coral reef ecosystem structure and benthic community. Additionally, these findings remain applicable to other coral reef ecosystems, having identified prevailing coral species in an area where biogeophysical conditions appear to favor alternative benthic substrates and taxa. Tetiaroa's hard coral community has also recently been identified as highly resilient, harboring functional traits that promote tolerance to disturbance (Hills et al., in prep). Through this study, we also build an understanding of the drivers of (un)suitable habitat for coral growth, which could be developed through extended investigations into Tetiaroa's benthic habitat types specifically.

Further research is needed on the biophysical drivers of benthic community composition in Tetiaroa to build upon our preliminary findings. For example, investigating the effect of wind and wave exposure with a specific metric should be a priority, considering the profound influence of intercardinal bearing emerging in this study. Potential methods include the sourcing of wave energy data from the global Wave Watch III (Tolman et al., 2014) by Robinson et al. (2018) or the use of models to determine wave exposure based on wind speed, direction, and fetch length (Lange et al. 2021). The influence of wind on surface water movement is known as a causal mechanism of upwellings, that have been identified also as drivers of benthic community structure of tropical coral reefs (Spring and Williams 2023). Other, more detailed hydrodynamic variables and spatial pattern metrics could be included to capture the importance of ocean-atoll interactions in driving the patterns of benthic community composition within the atoll. At the scale of the entire atoll system, the openness of the system to the ocean can be assessed by calculating the hydrodynamic aperture, a unique marine and atoll-specific spatial pattern metric (Andréfouët et al. 2001; Wedding et al. 2011). Hydrodynamic aperture sums the width of openings in atoll carbonate rims, quantifying the system's openness to biological exchange and biophysical forcings from outside the outer reef crest (Andréfouët et al. 2001). Calculating the hydrodynamic aperture for specific segments of the reef crest could be an interesting addition to the predictor variables explored in this study, as aperture or distance from openings will influence conditions experienced at sites across the lagoon, particularly wave energy and nutrient availability. Future analysis of taxonomic and trait compositions should also be carried out, as the roles of traits in coral reef ecosystems lay the foundations for coral reef functioning, thus determining the relative influence of biophysical drivers on ecosystem- and atoll-wide function in addition to site-level community composition. Understanding the effect of biophysical drivers on community trait composition also has implications for estimating reef recovery potential and can be incorporated into future management and restoration plans that are tailored to unique atolls (Ceccarelli et al. 2020; Lange et al. 2021). This provides information to guide efforts in promoting or limiting natural biophysical coupling dependent on specific biophysical influences, building coral reef resilience to site-specific changes.

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Author contributions RAW, CEB, HEE, and LMW conceived and designed the research. RAW, KM, CEB, HEE, PP, MW, TS, and LMW conducted the field data collection. RAW, SH, CES, and PP analyzed the data. RAW, SH, CES, and PP wrote the manuscript. All authors read and approved the manuscript.s

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Data availability LiDAR data were generated by the Island Digital Ecosystems Avatars (IDEA) program. The code and datasets required to run these analyses are available online in the following GitHub repository: https://github.com/SashaHills/Tetiaroa_Benthic_Community_Composition.git.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval No collection of or testing on living organisms was performed in this study. All field protocols complied with the obligations of the Convention on Biological Diversity (CBD) and were approved by the competent authorities.

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