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Spatial organisation and functional composition of benthic reef assemblages across a depth gradient in western Aldabra Atoll

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Introduction: Coral reefs face unprecedented structural reorganisation following climate-induced mass mortality. While net coral loss is well-documented, the resulting spatial arrangement of surviving communities remains understudied. This study characterises the spatial organisation, functional composition, and environmental drivers of benthic communities on the western seaward reefs of Aldabra Atoll, Seychelles, using data from 2022.

Methods: Using 300, high-resolution 1 m^2 video-still quadrats across two depth contours (8 m and 15 m), we integrated genus-level identification with life-history strategies (LHS) and substrate stability analysis.

Results: Our data revealed that the reefs were overwhelmingly dominated by stress-tolerant, massive corals, reflecting a resilient, post-disturbance state following historical thermal anomalies. However, multivariate dispersion (patchiness) significantly increased with depth highlighting the role of environmental filtering. We identified four spatial organisational “signatures” among organisms and abiotic features. Using the Variance-to-Mean Ratio (VMR), we identified a deterministic shift in spatial signatures: from shallow aggregated frameworks to deeper, fragmented nucleated patches. Statistical niche modelling confirmed that substrate stability acts as a physical bottleneck; *Isopora* spp. exhibited an extreme affinity for rock pavement, while *Goniopora* spp. dominated mobile rubble.

Discussion: Our results demonstrate that post-bleaching recovery in Aldabra is partly driven by niche-driven environmental filtering rather than purely stochastic neutral drift.

KEYWORDS
benthic reef community, post-bleaching, life-history strategies, multivariate dispersion, Variance-to-Mean Ratio (VMR), substrate stability, Western Indian Ocean

Introduction

Coral reefs are critical ecosystems, supporting an estimated 25% of all marine biodiversity and providing essential services to coastal communities worldwide (Souter et al., 2021). However, these systems face unprecedented threats from climate change-induced heatwaves that trigger widespread bleaching and mass mortality (Hughes et al., 2017; Morrison et al., 2019). Although research has extensively documented the resulting net losses in coral cover following disturbance events (GCRMN, 2016; Bahr et al., 2017; Eakin et al., 2019), quantifying mortality alone does not capture the structural and functional configuration of the surviving benthic community—a key determinant of future resilience (Darling et al., 2013; Bruno et al., 2019; Botté et al., 2022).

While standard long-term monitoring tracks longitudinal trends in benthic cover, it often lacks the resolution required to identify the precise spatial arrangement of surviving organisms (Rivera-Sosa et al., 2025). Although integrating high-resolution spatial data into temporal frameworks offers the most comprehensive dataset, resource constraints frequently dictate a trade-off between temporal frequency and spatial scale (Andréfouët et al., 2002; Hedley et al., 2016; Urbina-Barreto et al., 2021). Consequently, a high-resolution spatial snapshot provides a deep characterisation of the reef's physical architecture at a single point in time. Because corals are sessile, their coordinates represent the physical manifestation of cumulative recruitment, competition, and mortality over the preceding decade (Ford et al., 2021). Therefore, a spatial snapshot allows for the testing of fundamental ecological hypotheses which help determine whether community organisation is driven by deterministic environmental filtering or by random dispersal (Done, 1982; Simmons et al., 2022). For example, stochastic distribution patterns (e.g. via variance-to-mean analysis) can provide evidence for neutral theory (Hubbell, 1997); however, some research refutes this, showing that the high variability in coral community composition is better explained by environmental factors than by neutral drift (Dornelas et al., 2006).

The assembly of these post-disturbance communities is influenced by the functional traits of individual taxa, including growth form, reproductive mode, and skeletal density (Darling et al., 2013; Madin et al., 2016; Kayal et al., 2015; Helder et al., 2022). These traits dictate the competitive hierarchy and the relative rates of colonisation and extinction among species (Kayal et al., 2015; Watt-Pringle et al., 2022). Such demographic trade-offs manifest as distinct spatial signatures; for instance, high colonisation potential (typical of ruderal species such as weedy *Pocillopora* spp.) may lead to stochastic, widespread distributions via rapid larval dispersal, whereas competitive power (characteristic of 'K-strategists' or climax species such as competitive *Acropora* spp.) in stable environments often results in clustered, space-filling frameworks through aggressive lateral growth and shading (Baird and Hughes, 2000; George et al., 2021; Ford et al., 2021). A common framework for simplifying these traits is the categorisation of corals into life-history strategies: competitive, stress-tolerant, weedy, and generalist (Darling et al., 2012). Categorising species into these functional groups facilitates global comparisons and identifies the overarching 'ecosystem services', such as habitat provision via structural complexity, offered by a community (George et al., 2021; Darling et al., 2012).

These broad groupings are essential for assessing the general function and status of a reef or a wider region (Lawrence et al., 2025), revealing patterns of overall resilience and environmental filtering (Nyström, 2006; Carturan et al., 2018, Carturan et al., 2022). However, relying solely on functional classifications can obscure species- or genus-specific dispersion patterns reflecting specific life-history limits such as environmental responses, reproductive strategies and micro-habitat requirements (Sampayo et al., 2020; Page et al., 2024). For example, the genus *Acropora* is often broadly categorised by a competitive strategy, however, individual species within this group exhibit vastly different depth tolerances and light requirements, which dictate their specific spatial niche (Darling et al., 2012). These small-scale physiological tolerances contribute to local community assembly (Teo and Todd, 2018; Ayre and Hughes, 2000).

By analysing both large-scale functional groups and small-scale genus patterns, we can distinguish between the broad service provided by a reef and the underlying biological processes, such as niche-specific colonisation (Urbina-Barreto et al., 2021). Furthermore, this dual-level approach enables the quantification of functional redundancy (Clarke et al., 2006); it determines whether critical ecological services are supported by a diverse array of taxa or are vulnerable to the decline of a single genus (Bellwood et al., 2003). By mapping these distributions, we can separate broad-scale environmental filtering, where morphologies cluster in response to physical variables like wave energy, from finer-scale biological interactions or dispersal limitations that are only discernible through genus-specific spatial signatures (Ford et al., 2021).

The spatial success of a coral colony is determined by the synergy between its life-history traits and environmental filters, primarily depth and substrate stability (Ayre and Hughes, 2000). Depth dictates vertical zonation by modulating light attenuation and hydrodynamic energy (Williams et al., 2018). However, post-bleaching landscapes introduce further abiotic stressors, such as thermal stress and mechanical instability, that fragment coral populations (Kubicek et al., 2012). While deeper habitats may preserve three-dimensional complexity by buffering these stressors, shallow reefs often succumb to environmental volatility and can 'flatten' and form dispersed patches (Lawrence et al., 2025). Ultimately, the demographic success of a coral genus is not solely a function of its innate colonisation potential; it is mediated by the physical state of the benthos. The transition from stable reef frameworks to loose rubble inhibits recruitment and imposes a selective pressure (Carleton and Sammarco, 1987) that favours taxa capable of navigating mechanical instability or outcompeting algal colonisers (McCook et al., 2001; Arnold et al., 2010; Pulsford et al., 2016).

Aldabra Atoll, a UNESCO World Heritage site in the Seychelles, provides a unique location to examine these spatial signatures. As a remote system with minimal direct anthropogenic pressure, its reef structures primarily reflect the results of natural environmental filtering and recent climatic disturbances (Stoddart, 1971; Sheppard and Obura, 2005). Following the 2015/2016 global bleaching event, Aldabra's reefs experienced a sharp decline in live hard coral cover, dropping from a mean of 22.5% in 2014 to 10.4% in 2016 (Cerutti et al., 2020; Koester et al., 2020; Burt et al., 2025). By 2022, the system showed signs of variable recovery, with mean cover rebounding to 17.0% (Burt et al., 2025). However, these broad metrics do not explain specifically how different taxa have spatially organised in response to changed biotic conditions.

Broad temporal monitoring often overlooks fine-scale ecological shifts, therefore, this study prioritises high spatial resolution to uncover the underlying processes driving reef health. We quantify the spatial and functional organisation of benthic communities across the western reefs of Aldabra Atoll, in 2022, by integrating genus-level identification with functional classifications—specifically life-history strategies and morphology. Our primary aim is to decode the spatial signatures of historical recruitment and mortality. To achieve this, we first characterise taxonomic and functional composition across depth contours (8 m vs 15 m). Second, we evaluate how substrate stability, distinguishing between consolidated rock and mobile rubble, governs the occupancy and abundance of dominant coral genera. Finally, we model the micro-spatial organisation of benthic components at the 1 m^2 scale, employing multivariate dispersion and Variance-to-Mean Ratio (VMR) to determine if clustering patterns indicate functional redundancies or environmental filtering.

Methods

Data collection

Aldabra Atoll, the most southerly atoll of the outer islands of the Seychelles in the Indian Ocean (Figure 1), is one of the world's largest and most remote raised coral atolls (155 km^2 land; 196 km^2 lagoon). It was designated as Special Reserve under Seychelles' legislation in 1981 and inscribed as UNESCO World Heritage Site in 1982. Data were collected at three western outer reefs of Aldabra (ARM01, ARM06, ARM07; Figure 1) over five days in October 2022, as part of the Monaco Explorations Indian Ocean expedition. At each site, two 50 m straight-line video transects were conducted at distinct depths, one at 8 m and one at 15 m, representing the shallow reef and the deeper slope, respectively. Transects were positioned at least 200 m apart to minimise sampling overlap and ensure independent spatial observations. A GoPro Hero 8 was used to record video footage of transects at high-resolution (4K). The camera was oriented perpendicular to the seabed at a height of approximately 1 m distance above the benthos, capturing an area of approximately 1.5 m by 1.5 m.

Data processing

The fundamental sampling unit for this study was an approximately 1m by 1 m quadrat, extracted as a still frame image every 1m along each 50 m video transect. While the raw video frames captured an area of approximately 1.5 m by 1.5 m, the effective sampling area was standardised to approximately 1 m by 1 m quadrats for analysis. This reduction was achieved by applying a 250-pixel margin offset to the perimeter of each frame, a necessary step to eliminate edge-effect distortions and ensure that benthic classification was performed only on the highest-resolution, centre-aligned portion of the imagery. This resulted in 50 quadrat images per 50 m transect, totalling 300 quadrats across the six transects (Figure 2). To quantify benthic cover, we used CPCe (Coral Point Count with Excel extensions; Kohler and Gill, 2006) to apply a

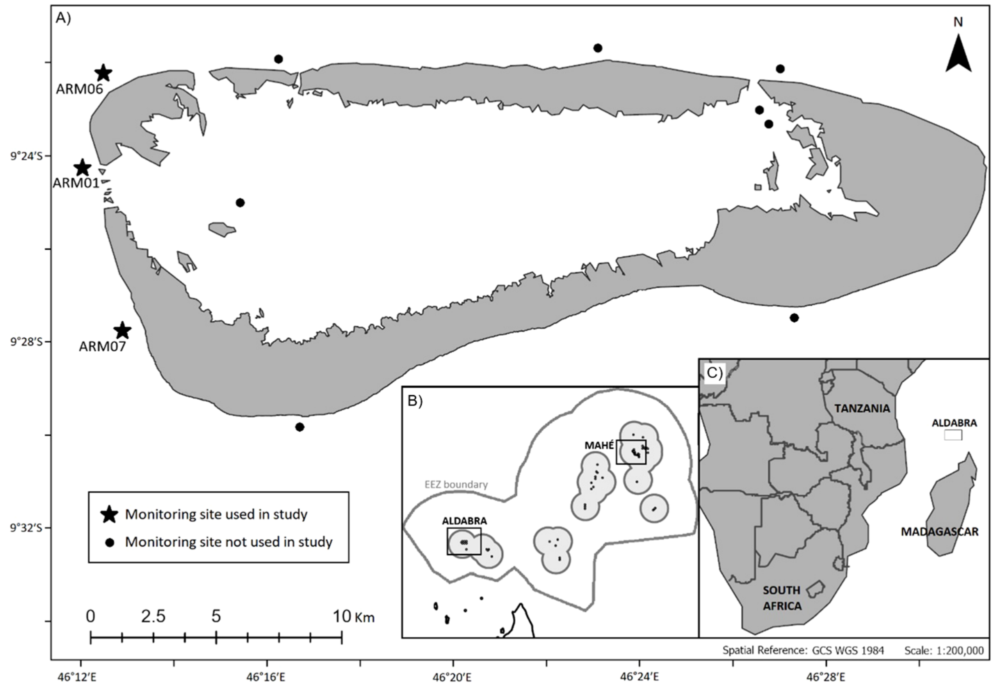

FIGURE 1
Monitoring sites around Aldabra Atoll, Seychelles, in the western Indian Ocean. **(A)** Aldabra Atoll with stars indicating three study monitoring sites (ARM06, ARM01, ARM07) and circles for non-study sites; **(B)** Aldabra and Mahé islands within Seychelles' EEZ boundary for regional context; **(C)** locates Aldabra relative to Madagascar, Tanzania, and South Africa. North arrow, coordinates, legend, and scale are included. Data sources for the creation of this map include Esri, TomTom, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors, the GIS User Community. TUBS (2025).

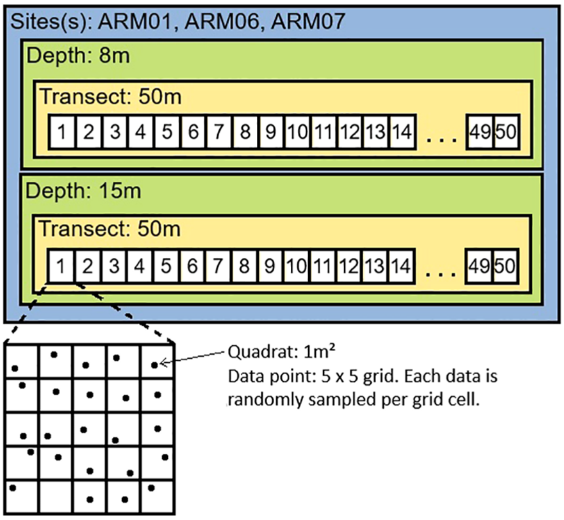

FIGURE 2
Nested, multi-scale sampling approach across three primary Sites (ARM01, ARM06, ARM07). Within each site, sampling is stratified by depth (8 m and 15 m). A single 50m Transect is established within each site/depth location to capture n=6 independent transects. Each 50m transect is divided into 50 contiguous $1m^2$ Quadrats, providing a high-resolution, continuous benthic landscape profile. Within each $1m^2$ quadrat, a systematic Point-Intercept method is used for benthic identification. A 5x5 grid is superimposed over the quadrat, creating 25 equally spaced cells. A single Data Point is sampled from a random position within each cell, resulting in 25 data points per quadrat and a total of 7,500 data points across the study (300 quadrats x 25 points).

stratified random sampling approach which divided each quadrat into a 5 x 5 grid, resulting in 25 data points per quadrat, resulting in a total of 7,500 data points across the study. Each data point was classified into one of nine benthic categories (Supplementary Figure 1), with hard corals identified to genus level (Lieske and Myers, 2004; Veron et al., 2016; Kelley, 2022), and subsequently assigned one of four functional life-history strategies (LHS) (stress-tolerant, generalist, competitive, weedy) following Darling et al., (2012, Darling et al., 2013, Darling et al., 2019). Coral genera were also each classified into one of five morphology categories (massive, branching, encrusting, free-living, submassive).

Data analysis

All data analysis was performed in R using R Studio (Posit team, 2025; R Core Team, 2025).

An overall description of the benthic community of the reefs in western Aldabra Atoll was conducted. Data preparation for this description involved the conversion of point-intercept counts from 300 quadrats into percentage cover values alongside standard error values (SE). Overall spatial composition and the fine-scale matrix of the reef were captured through continuous benthic landscape profiles, which mapped the distribution of major categories within each $1m^2$ quadrat along each 50m transect (Figure 3C). Absolute values of benthic groups were used to present the dominance of features (the frequency of occurrence among quadrats) against rarity (the total number of data point recorded across the data set) (Figure 3B). Hard corals were further split into genera and presented by growth morphology and coral life history strategies (LHS) to show the proportions of LHS and the taxonomic diversity of each LHS (Figure 3A).

To evaluate the drivers of community variation, multivariate community structure was analysed using Constrained Analysis of Principal Coordinates (CAP) based on a Bray-Curtis dissimilarity matrix. Prior to analysis, raw counts were square root transformed to reduce the influence of hyper-dominant taxa. The significance of site and depth as environmental constraints was evaluated using a permutational ANOVA, while taxonomic drivers with a correlation score exceeding 0.4 were highlighted as vectors to identify the specific organisms responsible for community shifts (Figure 3A). This was accompanied by a Beta-Dispersion analysis, which utilised a permutation test to compare the mean distance of quadrats to their depth-group centroids. If most quadrats had a low distance to the centroid, this would be indicative of reef uniformity, where, each 1 m^2 quadrat resembles the average of the site. Conversely, if the distances to the centroid are large, this indicates that quadrats are variable. One quadrat might consist of 100% rock pavement, another might be dominated by *Porites*, and a third might be covered by algae.

To gain further clarity about any potential effect of substrate stability on coral distribution and patterning, we evaluated the co-occurrence frequency of dominant coral genera against both stable rock pavement and loose substrates, rubble and sand, by performing a Monte Carlo Chi-squared test with 2000 simulations (Figure 4). Pearson residuals were used to identify high-fidelity ecological associations that deviated significantly from a random spatial distribution.

To quantify dispersion and determine whether the distribution of benthic features departed from randomness and help to describe the spatial organisation of the western Aldabra Atoll benthic communities, we calculated the Variance-to-Mean Ratio (VMR), a metric frequently used to detect regular, random, or aggregated spatial patterns in sessile marine assemblages (Endean et al., 1997). This metric assessed the structural arrangement of taxa and functional groups by comparing the variance in point-counts per image to the mean. A VMR of 1.0 represents a stochastic Poisson distribution (Neutral/Random), while values significantly exceeding 1.0 indicate clustered arrangements. Conversely, values below 1.0 suggest uniform distributions.

We partitioned each community group and genera into four spatial signature quadrants based on the intersection of clustering significance and the extent of occupancy (Table 1). The occupancy threshold was set at 80% (n = 40 quadrats) to represent the geometric saturation point, where a feature transitions from a disjointed patch to a persistent structural matrix. While statistical significance sits at approximately 1.35, a conservative clustering threshold of 1.5 VMR was adopted to distinguish high-intensity aggregations from sampling noise. This multi-level approach was applied across taxonomic hierarchies and extended to coral life-history strategies and growth morphologies (Supplementary Figure 2) to provide a comprehensive map of the spatial organisation within the western Aldabra reef system.

The statistical significance of these spatial patterns was determined through the application of a Chi-square (χ^2) test to the observed VMR. The test statistic was derived as the product of the VMR and the degrees of freedom (n - 1 = 49), corresponding to the

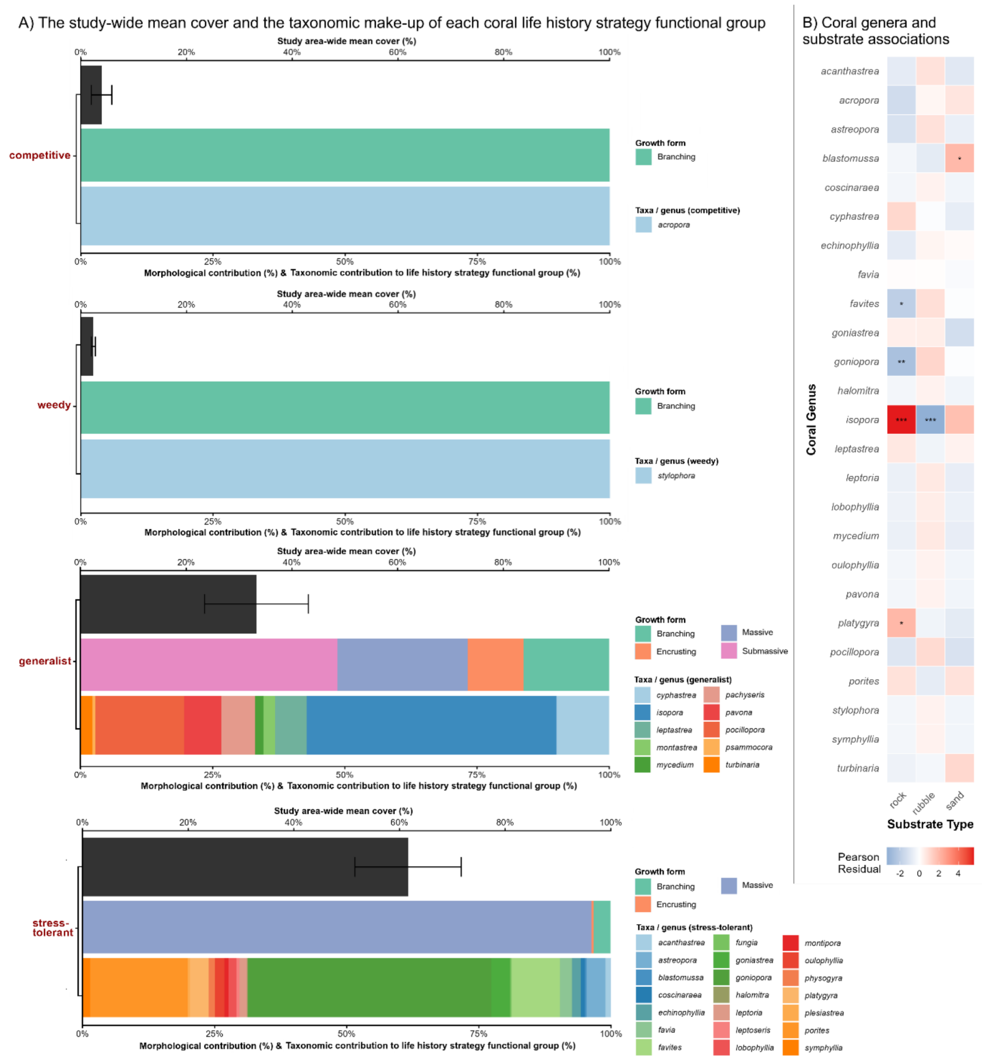

FIGURE 3

(A) Integrated functional and taxonomic profile of Aldabra coral communities. Top/grey bars represent the atoll-wide mean percentage cover for each life-history strategy (LHS), calculated across six independent 50m transects (n=6). Error bars denote Standard Error (SE). Bottom/coloured bars represent the proportional composition of morphologies and coral genera within each specific LHS pool, derived from all recorded occurrences across 300 quadrats. Direct visual comparison between the physical space a strategy occupies on the reef (regional dominance) and its morphological and taxonomic diversity. **(B)** Values represent Pearson residuals derived from a Chi-squared test of independence between dominant coral genera and substrate types. Asterisks (*) denote associations significantly deviating from random expectation ($p < 0.05$). Red cells indicate a positive "affinity" (taxa occur as neighbours to that substrate more often than expected within quadrats), while blue cells indicate "no affinity".

50 images sampled per transect. Observed clustering was deemed statistically significant where $p < 0.05$ when assessed against the χ^2 distribution. To maintain the integrity of our spatial classifications, we excluded rare taxa with fewer than six data points per transect. This minimum abundance threshold ensured that the identified spatial strategies represent consistent biological behaviours of the benthic community rather than statistical anomalies.

Results

Taxonomic and functional composition

The coral community across western Aldabra exhibited a highly skewed functional profile, dominated by stress-tolerant life-history strategies (61.62% ± 10.07; Mean ± SE, n=6) and generalist taxa (33.28% ± 9.83). In contrast, competitive (3.92% ± 1.94) and weedy (2.37% ± 0.38) strategies were negligible components of the total coral pool (Figures 3A, 5C). This functional signature was reflected in the reef's physical architecture: massive morphologies served as the primary structural unit (66.83% ± 9.77, Figure 3A), followed by submassive forms (27.25% ± 12.64), while branching corals accounted for less than 10% of the community. Notably, this morphological framework remained remarkably consistent across the depth gradient; massive corals occupied nearly identical proportions at 8 m (66.41% ± 16.81) and 15 m (67.25% ± 13.94).

Mean hard coral cover was consistent across the depth gradient, representing approximately one-quarter of the total benthos (24.40% ± 8.69 at 8 m and 24.96% ± 6.66 at 15 m; n=3 sites per depth). However, site-specific diagnostics revealed substantial local heterogeneity (Figure 5A); coral cover peaked at site ARM07 (41.68% ± 2.26 at 8 m), nearly

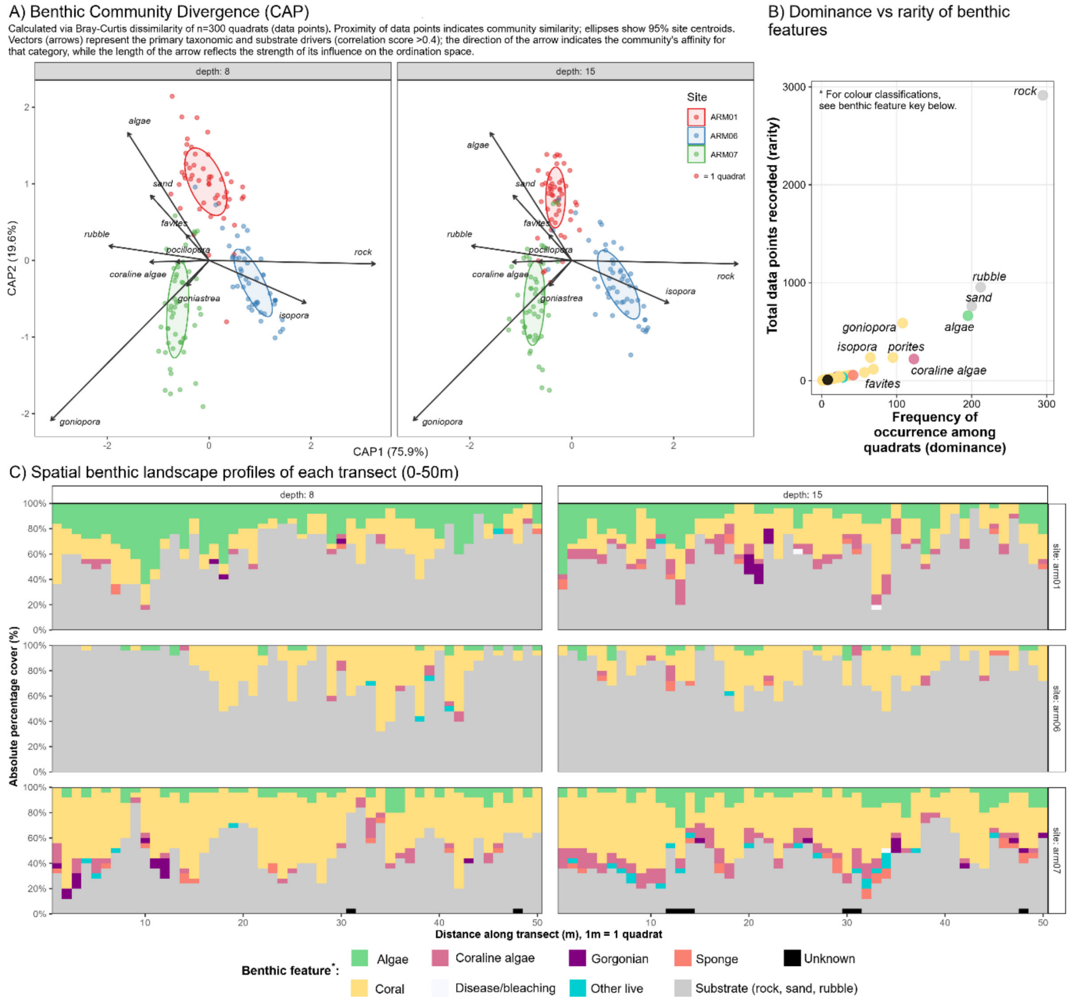

FIGURE 4

(A) Individual data points represent the community "fingerprint" of a single 1m^2 quadrat (n=50 per transect; N = 300 total). Proximity between points indicates high taxonomic and substrate similarity based on a square-root transformed Bray-Curtis dissimilarity matrix. The axes (CAP1 and CAP2) are constrained by the environmental predictors of Depth and Site, respectively, representing the linear combinations of benthic categories that best discriminate between the sampling groups. Ellipses denote the 95% confidence interval around the community centroid for each site; a larger ellipse area indicates higher beta-dispersion (patchiness) within that transect. Vectors (arrows) represent the primary taxonomic and substrate drivers (correlation score >0.4); the direction of the arrow indicates the community's affinity for that category, while the length of the arrow reflects the strength of its influence on the ordination space. **(B)** This scatter plot maps two scales of abundance: Frequency (x-axis; the number of quadrats out of 300 in which a taxon appears) and Dominance (y-axis; the total sum of data points across the entire study). Points are colour-coded by benthic category. Taxa in the top-right quadrant are common and abundant. Taxa in the bottom-left are infrequently encountered and low in cover. Points sitting higher on the y-axis but low on the x-axis represent features which are rare across the study area but form dense patches where they do occur. **(C)** Each discrete vertical bar represents a single 1m^2 quadrat (n=50 per transect). The height of the segments within each bar is determined by the 25-point intercept hits recorded per quadrat, scaled to 100% cover. Solid blocks of colour indicate areas of high mono-specific dominance, while rapidly shifting colours indicate patchiness.

triple the cover recorded at the same depth at ARM01 (14.16% ± 1.58). The abiotic landscape was defined by a stability gradient, with consolidated rock pavement serving as the primary foundation (63% ± 5.2 of the abiotic pool). Site ARM06 exhibited the highest stability (rock cover: 67.60% ± 3.14 at 8 m), while ARM07 displayed higher physical instability, with mobile rubble peaking at 18.42% ± 1.85 on the 15 m slope. Notably, Crustose Coralline Algae (CCA) cover followed a strong depth-dependent trend, increasing nearly threefold from 1.52 ± 0.63 at 8 m to 4.49% ± 1.83 at 15 m.

Taxonomic analysis identified *Goniopora* and *Porites* as the primary benthic "players" of western Aldabra. *Goniopora* provided the highest regional mean cover at 8 m (15.61% ± 8.94) where it reached a peak of 26.55% ± 2.13 at ARM07. In contrast, *Porites* maintained a more consistent presence across the dataset, though it was significantly more abundant at 8 m (11.41% ± 2.79) than at 15 m (8.10% ± 1.23). Beyond these, *Isopora* emerged as a critical site-specific dominant; at ARM06 (8 m), it reached 17.57% ± 2.00. As a generalist taxon, its dominance at ARM06 marks a localised departure from the stress-tolerant matrix found elsewhere. Regional algal cover averaged 8.84% ± 3.28 but was intensely localised; site ARM01 (8 m) recorded a macroalgal signal of 22.32% ± 1.85, which diminished at 15 m (13.92% ± 1.72). Conversely, at ARM06, algae remained a minor component (< 2%) across both depths, indicating that coral-algal competition is highly site-contingent.

Ecological Composition of Aldabra Reef Communities

A) Broad Benthic Categories

Unit of variance: n=50 quadrats (1m²) per transect. Error bars: mean ± SE.

B) Dominant Coral Genera

Top 10 genera. SE calculated from n=6 independent transects (regional certainty).

C) Coral Life History Strategies

Unit of variance: n=50 quadrats. Error bars (±SE) represent local functional variability.

Sampling Area: 300m² total (3 sites x 2 depths x 50m transects). All bars represent mean values.

FIGURE 5

Benthic community composition of the sampling area. **(A)** Broad categories, **(B)** dominant coral genera, and **(C)** life history strategies. Data represent mean % cover calculated from 7,500 points across 300 quadrats. Bars represent the mean, and error bars denote symmetrical standard error (± SE), reflecting spatial patchiness (n=50 quadrats per transect or n=6 transects across the sampling area). Colours represent depth strata: Salmon pink (8 m) and Teal (15 m).

Multivariate analysis (CAP) confirmed that benthic community structure was significantly influenced by the interaction of site and depth (Permutational ANOVA; $F_{3,296} = 34.42$, $p = 0.001$). These environmental constraints explained 25.87% of the total multivariate variance (Figure 4, 5B). Multivariate dispersion, describing community "patchiness", differed significantly between depth zones ($F_{1,298} = 4.66$, $p = 0.03$); the 15 m contour exhibited higher multivariate dispersion (0.402) than the 8 m contour (0.379), confirming greater spatial heterogeneity and a more fragmented benthic matrix in deeper habitats. Habitat association analysis identified that coral occupancy was non-randomly dictated by substrate stability ($\chi^2 = 95.08$, $p = 0.001$). Specifically, the generalist genus *Isopora* exhibited a high affinity for stable rock pavement (Residual = 5.60) and *Goniopora* demonstrated an association with mobile rubble habitats (Residual = 1.17), highlighting it as a primary coloniser of unstable post-disturbance substrates.

TABLE 1 The four derived spatial signatures of benthic organisms and groups alongside their corresponding VMR thresholds and occupancy thresholds.

Strategy	VMR threshold	Occupancy threshold	Ecological interpretation
Aggregated frameworks	Significant clustering (VMR >1.5)	High (> 80%)	Primary structural drivers; consistent but internally dense communities defining the reef matrix.
Nucleated patches	Significant clustering (VMR >1.5)	Restricted (< 80%)	Localised hotspots; taxa forming aggregations in response to specific micro-habitats or environmental refugia.
Homogeneous veneers	Non-significant clustering (VMR ~1.0)	High (> 80%)	Pervasive space-fillers; uniform distribution across the landscape, often limited by competitive exclusion.
Stochastic distributions	Non-significant clustering (p >= 0.05)	Restricted (< 80%)	Opportunistic components; presence driven by random dispersal or transient environmental conditions.

Spatial organisation ("spatial signatures")

The spatial organisation of the benthic groups and organisms at western Aldabra Atoll exhibited significant variability across sites and depths, as evidenced by the distinct distribution of taxa within the four spatial signature quadrants (Figure 6). While most benthic features were classified as stochastic distributions, characterised by low occupancy and distributions that did not deviate significantly from randomness (VMR ≈ 1, $p > 0.05$), the primary structural components of the reef matrix, such as algae, *Goniopora*, rock, and rubble, demonstrated significant clustering and high occupancy, effectively defining the aggregated framework of the system.

At site ARM01, the benthos was characterised by stochastic distributions and homogeneous veneers, where algal cover and submassive corals acted as pervasive space-fillers across both depths (8 m and 15 m). Goniopora at site ARM07 also emerged as a key structural driver, exhibiting high occupancy (> 80%) and significant clustering (VMR up to 2.13, $p < 0.001$). Exposed rock transitioned from an aggregated framework at ARM06 to a homogeneous veneer at ARM07; at the latter, it achieved nearly 100% occupancy with lower clustering intensity (VMR ≈ 1.06). This spatial uniformity at ARM07 corresponds with the high hard coral cover recorded at this site, where the consolidated area of calcium carbonate and bare rock provided a pervasive, evenly distributed foundation for colonisation.

In contrast, ARM06 was characterised by a high prevalence of nucleated patches, low occupancy but high clustering taxa, particularly within the substrate and coral categories. Here, localised growth was restricted by the extreme clustering of loose coral rubble. At 15 m, rubble exhibited the most extreme clustering recorded across the study (VMR = 10.2, $p < 0.001$), despite an occupancy of only 38%. This intense aggregation of rubble coincides with its identification as a primary driver of community variation in the CAP analysis (Figure 3A). Similarly, *Porites* and *Isopora* at this site functioned as nucleated patches; *Isopora* (8 m) showed a VMR of 2.86 ($p < 0.001$), aggregating into high-density "islands" of growth restricted by the availability of stable substrate.

Most coral genera were consistent across depth with their spatial signature. However, some genera showed depth-dependent shifts in their spatial configuration, moving from random to clustered arrangements with increasing depth. For instance, massive and submassive corals like *Goniastrea* and *Astreopora* only reached significance as clustered features in the deeper 15 m facets of ARM07. This depth-stratified clustering mirrors the higher multivariate dispersion (0.402) found at 15 m compared to 8 m, confirming greater spatial heterogeneity in deeper habitats. There were some genus specific exceptions to this rule, however; *Porites* at ARM01 and *Isopora* at ARM06 shifted from nucleated patches at 8 m into a stochastic distribution at 15 m.

The spatial signatures were strongly influenced by life-history strategies and growth morphologies (Supplementary Figure 2). Stress-tolerant taxa and massive morphologies demonstrated the most consistent structural presence, creating aggregated frameworks at 8 m in ARM07 (VMR = 1.60 and 1.51, respectively; $p < 0.05$). Functional aggregation was most intense at site ARM06, where stress-tolerant and generalist corals showed high clustering and 50% occupancy. Submassive morphologies (VMR = 2.84, $p < 0.001$) and stress-tolerant strategies (VMR = 3.87, $p < 0.001$) showed high clustering at 8 m, despite moderate occupancy levels. Morphological analysis further revealed that encrusting forms functioned as significant nucleated patches at ARM01 across both depths (VMR > 2.0, $p < 0.001$), while branching morphologies remained stochastic across all sites and depths.

At the 8 m shallow sites, the benthos is predominantly characterised by aggregated frameworks and nucleated patches with higher clustering, reflecting the intense environmental filtering of higher hydrodynamic energy and light availability that confines organisms to specific, stable substrates. In contrast, the deeper 15 m reef slopes exhibit a shift toward stochastic distributions and homogeneous veneers, accompanied by lower mean VMR values and increased multivariate dispersion.

Discussion

This study characterised the spatial arrangement and functional composition of the benthic communities in Aldabra Atoll's western seaward reefs in 2022. By integrating taxonomic and functional strategies with physical substrate stability, our findings reveal a community primarily shaped by site-specific environmental filtering, where depth significantly modulates community patchiness (multivariate dispersion). The system is overwhelmingly dominated by resilient, stress-tolerant massive corals that act as the primary structural architects. Community assembly driven in part by the capacity of specific taxa to form localised aggregations, which we

FIGURE 6
Spatial organisation "signatures" derived from the occupancy (dominance) vs clustering of organisms and substrate features of the benthic reef community in western Aldabra Atoll.

term spatial signatures, as either persistent frameworks or nucleated patches. While the dominance of certain corals correlates with substrate stability, unmeasured factors, such as larval supply, light attenuation, wave action and interspecific competition likely also influence this spatial organisation (Aston et al., 2019).

Explanations for this overwhelming dominance of stress-tolerant and generalist coral life history strategies can be explained by the two most abundant genera recorded in this study: *Goniopora* spp. and *Isopora* spp. *Goniopora* is a low lying, wide spread genus which produces small "polyp-balls" that detach upon reaching approximately 2 cm in diameter, allowing them to settle directly onto shifting substrates and grow into independent colonies (Rosen and Taylor, 1969). On a post-disturbance reef such as Aldabra, this combination of morphological and reproductive traits provides a competitive advantage over species that require consolidated, rigid frameworks.

Conversely, *Isopora palifera* exhibits high mechanical robustness, characterised by a low colony shape and wide basal attachment areas relative to its vertical mass making it resilient against high-velocity wave action (Madin et al., 2008). Following a disturbance, this morphology increases the survivorship of *Isopora* by enabling it to occupy open space and increase average colony size (Madin et al., 2008). While *I. palifera* may be outcompeted by faster-growing, delicate species under calm conditions, it holds a distinct ecological advantage during severe hydrodynamic events (Madin et al., 2008). Furthermore, it demonstrated atoll-wide resistance to heat stress, allowing it to thrive in stable, post-bleaching environments (Koester et al., 2020). Overall, these findings demonstrate how each coral group has capitalised upon a specific ecological niche, enabling them to resist recent perturbations and outcompete neighbours.

The dominance of stress-tolerant, slow-growing massive morphologies across both depth zones indicates a shift toward more resilient taxa following the 2015/2016 global bleaching event when branching corals were more abundant (Hughes et al., 2018b; Cerutti et al., 2020; Burt et al., 2025). The scarcity of competitive taxa suggests that the reefs are operating in a recovering state. While crustose coralline algae (CCA) cover remains sufficient for recruitment (Koester et al., 2021), the combination of thermal stress and unstable substrata limits the establishment of competitive coral taxa and thereby reducing community diversity (Arnold et al., 2010). This shift toward stress-tolerant species mirrors global post-bleaching patterns where resilient, slow-growing taxa prevail following repeated thermal anomalies (McClanahan et al., 2004; Sheppard and Obura, 2005; Hughes et al., 2018b; Morais et al., 2021; Tebbett et al., 2023; McCarthy et al., 2024).

Even where live coral cover is high, such as the transition to a homogeneous veneer of the genus *Goniopora* at site ARM07, lack of diversity among life history strategies represent may represent a loss of function and 3D complexity compared to historical branching frameworks (Darling et al., 2013). These massive colonies dissipate less hydrodynamic energy than the branching architects of climax reefs, but they nonetheless create a stable microhabitat that supports the wider community (Pomeroy et al., 2023; Summers and Donner, 2022).

As the intervals between bleaching events decrease the persistence of less diverse community configuration may become a permanent state (Hoegh-Guldberg et al., 2019). The life history strategy and morphological imbalance observed raises concerns that Aldabra's outer reefs may struggle to recover historical levels of structural complexity and function.

However, site-specific variation provides a more nuanced outlook for the atoll. Coral cover at ARM07 was nearly triple that of ARM01, suggesting that localised conditions or micro-refugia allow certain seaward areas to maintain higher densities despite regional thermal stress (Burt et al., 2025). Furthermore, Aldabra's overall resilience may be buffered by its stable lagoonal habitats, where branching Porites drive recovery (Koester et al., 2020), potentially offsetting the functional shifts observed on seaward slopes (Burt et al., 2025).

Our multi-scale spatial analysis refutes the absolute dominance of neutral drift (Dornelas et al., 2006). CAP analysis reveals that site and depth account for approximately 26% of community variation, indicating that environmental filtering influences community composition rather than random survivorship. Although Endean et al. (1997) documented regular spacing among massive corals on stable, continuous reef platforms, we find that ARM06 was characterised by nucleated patches, particularly for generalist *Isopora* and submassive morphologies, where growth was restricted by the extreme clustering of loose coral rubble (VMR = 10.2, representing significant overdispersion). Suggesting that physical substrate constraints can override biological spacing mechanisms. Across sites we see that site ARM06 In contrast, site ARM07 was characterised by aggregated frameworks that formed a dense protective matrix where stable substrate pervaded.

Across depths, the deeper 15 m reef slope exhibited higher multivariate dispersion and fragmented, heterogeneity in benthic community composition compared to the more continuous and homogeneous 8 m shallows. Spatial signature analysis revealed that benthic community configurations are largely governed by local environmental filters, with stable substrates promoting aggregated frameworks in the shallows, while unstable rubble fields restrict taxa into highly clustered nucleated patches. Meanwhile, deeper environments display a more dispersed, stochastic structure as climatic stress declines. This depth-dependent variation supports the Intermediate Disturbance Hypothesis, whereby reduced physical stress and varying environmental pressures or resource availability allow for a more disjointed, niche-diverse community to persist (Connell, 1978; Pedersen et al., 2019; Kramer et al., 2020). Conversely, broad-scale environmental filters constrain the establishment of competitive and weedy life histories, leaving them as sparse, stochastic components (VMR ≈ 1) of the benthos. As a result, biological drivers, such as space competition, are overridden by the abiotic constraints of the atoll.

Habitat association analyses confirm that occupancy for some coral genera is non-randomly structured by the underlying physical substrate, with taxa showing specialised affinities for either consolidated rock or mobile rubble. Specifically, among two dominant genera, the generalist genus *Isopora* showed a strong affinity for stable rock pavement, whereas the stress-tolerant *Goniopora* demonstrated an association with mobile rubble habitats—a pattern that may explain its success in this recovering, post-disturbance community. These fine-scale associations indicate that substrate instability acts as a critical post-disturbance environmental filter (Kubicek et al., 2012; Kenyon et al., 2023).

The preference of *Isopora* for consolidated pavement highlights its requirement for a firm foundation to sustain its space-filling morphology (Madin et al., 2008). The capacity of *Isopora palifera* to thrive on stable surfaces is further bolstered by the presence of Crustose Coralline Algae (CCA), which stabilise the reef framework and enhance coral larval settlement (Koester et al., 2020). Conversely, the persistence of *Goniopora* on unstable substrates suggests that massive frameworks can tolerate the shifting local hydrodynamics of rubble fields better than other taxa where mechanical instability inhibits recruitment and increases post-settlement mortality (McCook et al., 2001; Arnold et al., 2010).

For instance, *Goniopora stokesi* exhibits adaptations to unstable, sandy, or detrital calcareous substrates (Rosen and Taylor, 1969). The polyps of *G. stokesi* remain expanded during the day and project several millimetres beyond the calice, making them highly efficient at shedding sediment and avoiding burial (Rosen and Taylor, 1969).

The broader implication is that substrate type acts as a physical gatekeeper for community organisation. Taxa aggregate not necessarily due to biological facilitation, but because they are physically restricted to the few remaining patches of suitable settlement substrate in a fragmented landscape.

The observed reliance on a stress-tolerant and generalist genera, with notably low counts of competitive corals, creates a community at risk of functional redundancy, leaving the ecosystem vulnerable to future climatic anomalies (Bellwood et al., 2006; Carturan et al., 2022). However, Aldabra's status as a remote, protected reserve provides an important baseline for recovery without local anthropogenic pressures, facilitating resilience through protected demographic processes (Graham et al., 2020). Furthermore, the evolutionary history of *Acropora* spp. demonstrates an inherent capacity to rebound following major climatic disturbances, suggesting that coral lineages possess deep historical adaptability to large-scale perturbations (Mao et al., 2018). The insights from this study suggest that restoration interventions could be modified to mimic natural spatial signatures. Rather than employing uniform planting densities, conservation efforts could focus on establishing aggregated frameworks of massive, stress-tolerant taxa, such as *Goniopora* spp., to act as physical stabilisers before reintroducing more sensitive, branching species (Carleton and Sammarco, 1987; Page et al., 2024). Establishing these robust structural foundations will be critical for supporting the long-term persistence of Aldabra's reefs as climate pressures intensify.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

DL: Methodology, Conceptualization, Data curation, Investigation, Formal analysis, Writing – original draft. CH: Writing – review & editing, Conceptualization, Funding acquisition, Supervision, Project administration. AK: Project administration, Writing – review & editing. AB: Project administration, Writing – review & editing. HK: Funding acquisition, Conceptualization, Writing – review & editing, Project administration, Supervision. MB: Supervision, Project administration, Conceptualization, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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