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Divergent drivers of richness–depth gradients among taxonomic groups

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Abstract Depth plays a crucial role in shaping marine biodiversity patterns, with species richness typically decreasing with depth. Despite extensive documentation of this pattern, the drivers of richness changes across depth remain unclear. Richness–depth patterns can arise from multiple proximate mechanisms acting simultaneously, such as changes in abundance, evenness, and the spatial aggregations of individuals. Using a unified framework, we examined variation in richness patterns and their underlying mechanisms in the northern Red Sea for fishes (down to ~150 m), Scleractinia, Octocorallia, and Porifera (down to ~45–70 m). Our results reveal taxa-specific richness responses. Overall, abundance changes emerged as the most consistent driver of richness variation with depth, although its direction and magnitude differed among taxa. Fish richness declined with depth, primarily driven by reduced abundance and lower evenness. In contrast, Porifera exhibited increased richness with depth, largely explained by higher abundances. Scleractinia richness peaked at 10 m and slowly declined with depth, similarly linked to changes in abundance. In contrast, Octocorallia showed a slight richness increase with depth, mainly due to higher evenness at greater depths, although gaps in

observations at intermediate depths may have obscured fine-scale peaks within the studied range. Increasing sampling scale (by combining sampling units) amplified these patterns. The results highlight the importance of understanding abundance gradients for richness, which may be overlooked when relying solely on cover-based estimates. The taxon-specific variability in richness–depth patterns challenges the conventional expectation of declining richness with depth, yet uncovers important commonality in the underlying mechanisms.

Keywords Depth gradient · Species richness · Fishes · Corals · Sponges · Measurement of biodiversity (MoB)

Introduction

One of the major endeavors in ecology is to explain biodiversity changes across environmental gradients such as latitude, elevation, and depth (Macarthur 1965; Gaston 2000; Dillon and Conway 2021). A clear understanding of these patterns is critical, as biodiversity hotspots should serve as priority areas for conservation efforts. However, both the richness trends and the underlying processes remain ambiguous (Rahbek 1995; Gaston 2000; Hagen 2023). Several factors contribute to this complexity, including the strong influence of scale on observed patterns, inherent differences among taxa, and variation in data collection methods (Levin 1992; Chase et al. 2018). Together, these factors hinder our ability to distinguish general ecological patterns from local idiosyncrasies and to disentangle multiple competing explanations for observed richness patterns (Roberts et al. 2019).

In the marine realm, depth is largely regarded as a major moderator of biodiversity, as increased depth often co-varies with reduced light availability, cooler temperatures, lower

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productivity, and greater environmental stability (Lalli and Parsons 1997; Bertness et al. 2001; Kahng et al. 2019). Indeed, species richness tends to decrease with increased depth (Tolimieri 2007; Pinheiro et al. 2023; Danovaro 2024). Yet, specific trends vary, from monotonous declines to peaks at various depths along the gradient (Huston 1985; Samaai et al. 2010; Pyle et al. 2019; Roberts et al. 2019b). For example, coral reef fish richness was shown to either monotonically decrease down to 150 m (Tolimieri 2007; Pinheiro et al. 2023; Danovaro 2024), or peak around 30 m before declining (Huston 1985; Pyle et al. 2019). Thus, how marine diversity changes with depth, and whether these patterns are consistent across major taxa, remains unclear.

While species richness trends are fundamentally driven by environmental gradients (ultimate drivers), patterns can arise through various changes in community structure (proximate drivers; Fig. 1). Thus, a decline in richness may result from lower overall abundance (Wright 1983), shifts in evenness (McGlinn et al. 2021), and increased intraspecific spatial aggregation (Veech et al. 2003; Blowes et al. 2017). These proximate drivers can act additively, oppositely, or synergistically to shape the overall richness pattern. Importantly, a single ultimate driver may influence different proximate drivers in different, and even opposed, ways. For example, higher primary productivity in shallow waters may increase richness by increasing overall abundance (Storch et al. 2018), while simultaneously reducing evenness by favoring a few dominant species (Huston 1994). Likewise,

depth-related changes in habitat structure or resource distribution may increase spatial aggregation, while also favoring dominant resource specialists, decreasing evenness and both reducing richness (Gartner et al. 2008). Understanding how different proximate drivers of community structure—abundance, evenness, and aggregation—change with depth can therefore provide deeper mechanistic insights into how environmental gradients shape species richness patterns.

Coral reefs are one of the most diverse ecosystems on earth (Knowlton 2001; Yuan et al. 2024), yet the drivers of biodiversity change over depth, from shallow water to deep, mesophotic reefs (~ 150 m), are not well established. Abundance often declines with depth but can also peak, remain stable, or increase (Jankowski et al. 2015; Scott et al. 2022). Similarly, evenness has also been reported to decrease, increase, or show no consistent change (Cleary et al. 2005; Jankowski et al. 2015). Lastly, while it is clear that many reef species exhibit aggregated distributions (Karlson et al. 2007), how spatial aggregation changes across depth gradients has received little attention. Part of the difficulty in making generalizations can be associated with differences in location and taxa examined. Thus, one way to overcome these limitations in inferring generalities necessitates the comparison of multiple groups within the same locality.

Biodiversity metrics are inherently scale dependent, changing nonlinearly with sampling effort and spatial grain (Chase et al. 2018). This scale dependence can alter not only the magnitude of observed patterns but also their

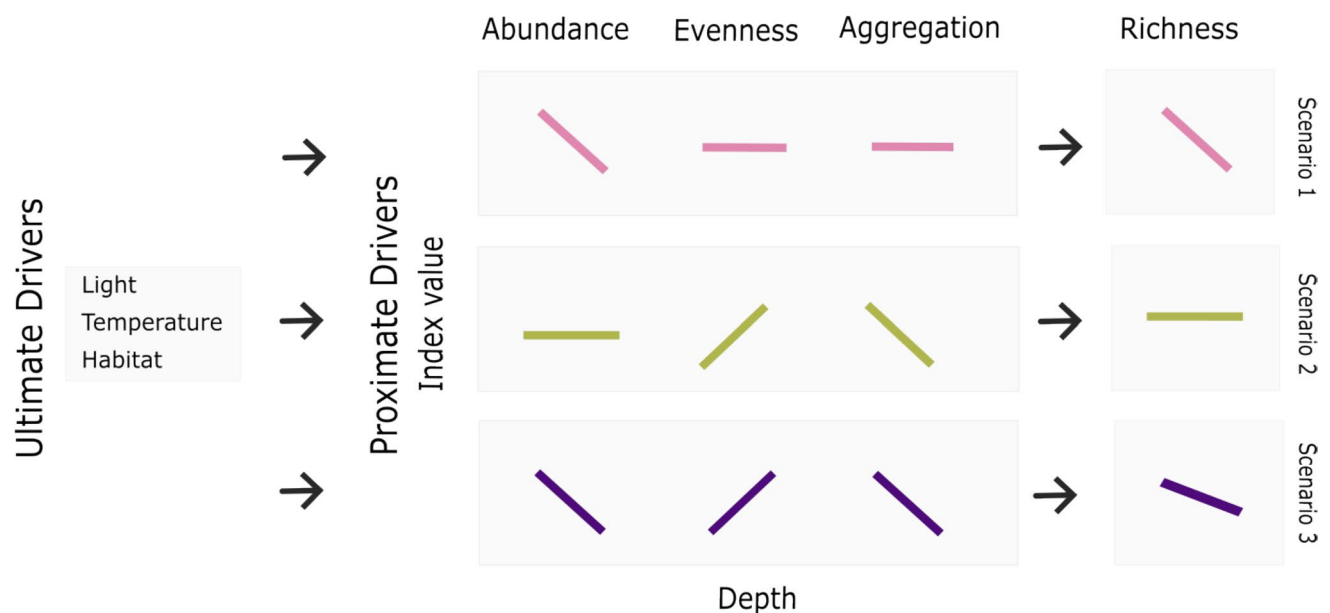


Fig. 1 Conceptual illustration of the way ultimate drivers influence species richness through changes in proximate drivers, such as abundance, evenness, and aggregation. Three hypothetical scenarios are shown: (1) Abundance declines with depth while evenness and aggregation remain stable, producing an abundance-driven richness

decline; (2) abundance is stable, but evenness increases and aggregation decreases with depth resulting in no net change in richness; and (3) all proximate drivers change with depth, with declining abundance, increasing evenness, and decreasing aggregation, together leading to a moderate richness decline

directionality (Scheiner et al. 2000; Whittaker et al. 2001; Blowes et al. 2019), consequently altering conclusions and interpretation (Blowes et al. 2020). Considering multiple scales is therefore essential for achieving a generalizable inference.

A recent framework offers a powerful lens for dissecting the proximate drivers of richness patterns along environmental gradients while accounting for scale-dependent effects (McGlinn et al. 2018, 2021). This framework decomposes the observed richness into distinct components related to overall abundance, evenness, and aggregation. This is achieved by constructing and comparing three key rarefaction curves—individual-based (IBR), spatial sample-based (sSBR), and non-spatial sample-based (nsSBR) rarefactions. Collectively, these rarefactions isolate the distinct contribution of each proximate driver to richness change (Blowes et al. 2020). Modeling these contributions against depth and contrasting them with null models can be used to test which components shape richness variation along the gradient and expose patterns that may otherwise remain hidden under traditional approaches (McGlinn et al. 2021). This method opens the door to deeper insights and allows for a more nuanced understanding of how species richness changes with depth.

In this study, we investigated species richness patterns along a continuous depth gradient in the northern Red Sea, from shallow waters down to 45–150 m. We compare four major taxonomic groups: fishes, Scleractinia, Octocorallia, and Porifera. Our goal was to identify the proximate mechanisms shaping these patterns by isolating changes in abundance, evenness, and intraspecific aggregations, and quantifying their contributions to richness. We addressed three central questions: (1) Do richness–depth patterns converge or diverge across taxonomic groups? (2) Do the proximate mechanisms driving richness change operate similarly across depths and taxa? (3) How does the sampling scale influence these patterns? Together, these questions aim to clarify the generality and context dependence of richness change with depth.

Materials and methods

Study sites

Our research was conducted on one of the northernmost coral reefs in the world, located at the northern tip of the Gulf of Aqaba, Red Sea (29.5581° N, 34.9482° E). The area features a steep bathymetric gradient, with coral reefs extending to depths of 150 m and forming an extensive mesophotic coral ecosystem (Loya 2004; Eyal et al. 2019).

The “Yam Ha-almogim” Marine Protected Area (MPA), established in 2009, spans the western coast of the Israeli

Gulf of Aqaba (29.509°N, 34.926°E) and restricts fishing and maritime transport. Two of our main sampling sites were situated within this MPA, approximately 200 m apart: the *Coral Beach (CB)* site (29.5044°N, 34.9192°E) that hosts a well-developed reef system, including a lagoon, reef flat, and a reef slope that extends into deeper waters (Loya 1972; Brokovich et al. 2008; Shlesinger et al. 2018), and the *Interuniversity Institute (IUI)* site (29.5019°N, 34.9175°E) that supports diverse reef communities along a steep slope reaching 70 m depth (Raijman-Nagar et al. 2024), but its shallow reefs are less developed (Shlesinger and Loya 2016). For Octocorallia, we also examined the *Oil Jetty (OJ)* site (29.5227°N, 34.9324°E), located outside the MPA. This site had been closed to the public for over 60 years and was reopened in 2017. The OJ area is characterized by scattered coral knolls interspersed with sand and seagrass, gradually transitioning into ancient, boulder-like mesophotic reefs (Raijman-Nagar et al. 2024). For fishes, the study area spanned the entire Israeli shelf of the Gulf of Aqaba (Fig. 2a), including the northern section (29.542°N, 34.967°E) with its gentle slopes and unconsolidated substrate. The differences between the unconsolidated habitat and the western section with coral reef-dominated consolidated habitat were later assessed as part of the sensitivity analyses (Fig. S1 and 2).

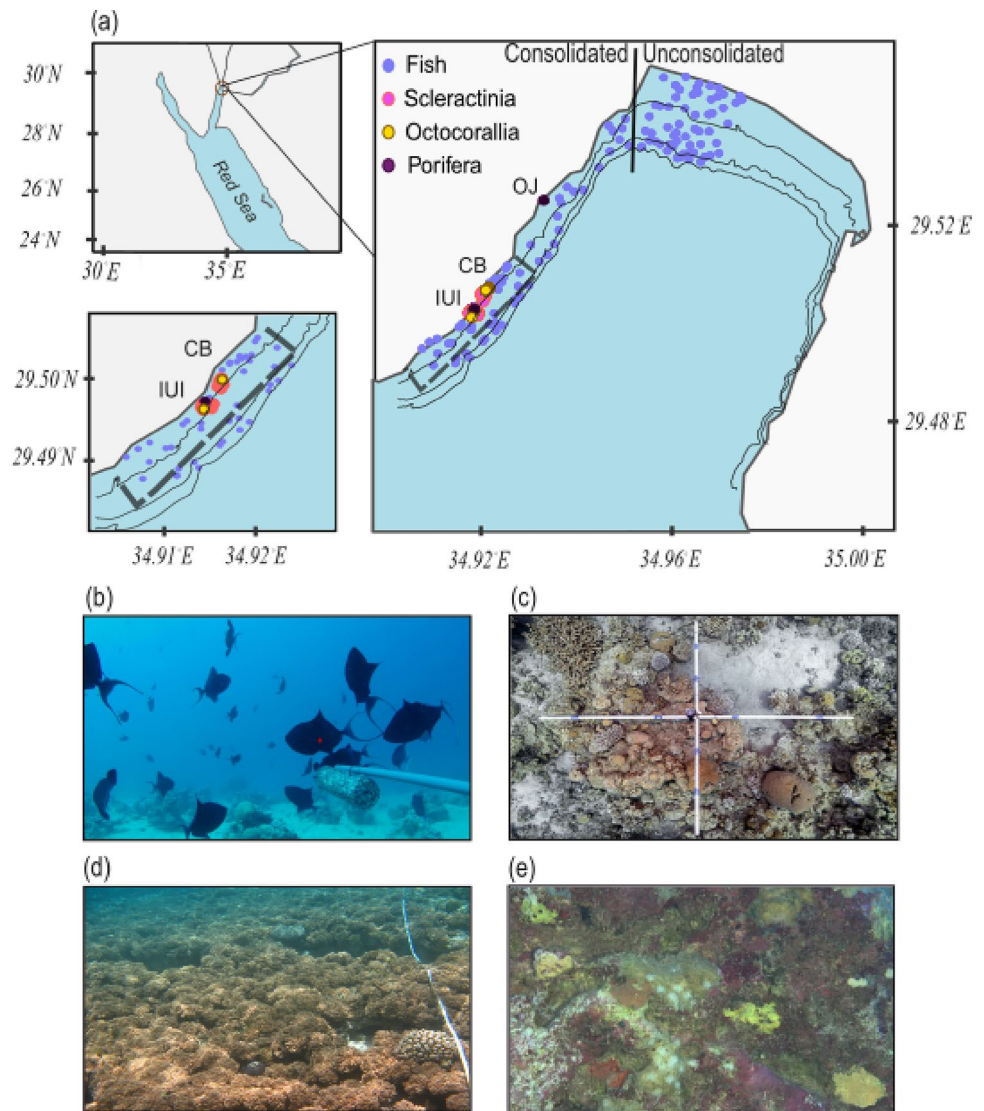
Sampling methods

Fishes, Scleractinia, Octocorallia, and Porifera communities were surveyed between 2018 and 2022 across an overall depth gradient of 0–150 m, but with taxa-specific depth limitations and with all taxa overlapping down to 45 m.

Fishes

Fish communities were surveyed between 2019 and 2022 using stereo-BRUVs, a non-intrusive method that minimizes observer bias and overcomes the spatial and temporal limitations of scuba-based surveys (Langlois et al. 2020; Chaikin and Belmaker 2026). Each deployment consisted of two cameras mounted on a steel frame with ~800 g of mashed anchovies as bait (Fig. 2b). Samples recorded 60-min videos, from which abundance was measured using the maximum number of individuals per species observed in a single frame across the entire video length (MaxN). This approach avoids overestimating abundance (Cappo et al. 2007). A total of 123 geo-referenced stereo-BRUVs deployments were conducted, covering depths of 8–149 m. In total, 3,632 individual fish were recorded, representing 173 species (Chaikin and Belmaker 2026).

Fig. 2 **a** Sampling locations by taxonomic group: fishes (blue), Scleractinia (pink), Octocorallia (yellow), and Porifera (purple). The protected area is marked by dashed lines, and the approximate border between the western-consolidated and northern-unconsolidated habitats in the fish data is marked with a solid line. Thin lines indicate 50-m depth contours. Panels **b–e** illustrate survey methods: Baited Remote Underwater stereo-Video systems (stereo-BRUVs, ~40 m²) for fishes, permanent reef plots (3 m²) for Scleractinia, belt transects (30 m²) for Octocorallia, and photo-quadrats (0.35 m²) for Porifera. OJ—oil jetty; CB—coral beach, IUI—Interuniversity Institute



Scleractinia

Scleractinian corals were surveyed in 2018 using *in situ* imaging during scuba dives (Fig. 2a, c). At each of two sites (IUI and CB), 3 m² permanently marked plots (i.e., samples) were established at six depths: 2, 5, 15, 30, 45, and 55 m (Shlesinger and Loya 2019; Shlesinger and van Woesik 2021). The plot size was selected as a practical compromise between maximizing sampling area and maintaining a feasible long-term monitoring program across six depth strata (2–55 m), which involved repeated technical dives, high-resolution imaging, and detailed image annotation. Each site–depth combination included five plots, yielding 60 plots in total. Plots were evenly spaced at approximately 15-m intervals within each depth, except at the IUI 5- and 45-m sites, where 30–50 m spacing was necessary because local bathymetry and extensive unconsolidated *Alveopora*-dominated habitat limited suitable consolidated reef for

establishing permanent plots. The plots were photographed, and all coral colonies > 2 mm were identified to the highest taxonomic level and counted using Adobe Photoshop CS6. Additional validation dives confirmed species identifications and collected reference specimens for taxa that could not be confidently identified from images alone. Voucher specimens were deposited in the Steinhardt Museum of Natural History (Tel Aviv University), bleached for skeletal examination, and compared with museum collections to verify species identity. Taxonomy followed WoRMS (2025), and only colonies identified to species level were retained for analysis (93% of colonies). In total, 8,352 individuals were recorded, representing 138 species.

Octocorallia

Octocorallia communities were surveyed in 2015 using visual censuses conducted along 10 × 1 m belt transects at two

sites (IUI and CB; Fig. 2a). Transects were photographed while scuba diving using a Canon G9 camera (Fig. 2d), with a measuring tape and a 1 m perpendicular rod used to define a consistent 1 × 1 m photographed area and provide scale (Shoham and Benayahu 2017). This sampling approach is consistent with widely used quantitative coral reef survey methods (e.g., NOAA NCRMP; Roberson et al 2014; Liberman et al. 2025). A total of 80 transects were performed across five depths: 1, 3, 35, 40, and 45 m (Shoham and Benayahu 2017). However, at one site (IUI), only the three deeper depths were sampled. On land, all visible octocoral colonies were identified to the highest possible taxonomic level (species or genus) and counted. In total, 3,886 colonies were recorded, representing 30 unique taxonomic units (25 species and 5 genera). Sample-level geo-referenced positions were not recorded, and transects were therefore treated as depth stratified but not spatially explicit.

Porifera

Porifera were surveyed between 2018 and 2020 at six depths: 5, 10, 20, 50, 60, and 70 m (Raijman-Nagar et al. 2024). For each combination of sites (IUI and OJ) (Fig. 2a) and depth, 30–35 photo-quadrats (each of 0.7 × 0.5 m) were performed, totaling 337 samples. Such quadrat size is commonly used in photo-quadrat-based benthic surveys and suitable for resolving reef community composition. In shallow water (5–20 m), photo-quadrats were taken ~ 1 m above the reef using a camera mounted on a tray with two video lights and two laser beams for scale, assuring images perpendicular to the surface (horizontal or vertical). At deeper depths (50–70 m), photo-quadrats were taken approximately 1 m above the seabed using a Remotely Operated Vehicle (ROV ECA-Robotics H800) equipped with an FHD camera, lights, and laser beams for scale. Photo-quadrats were captured at 10-m intervals, after the ROV's position was adjusted to the slope angle to ensure that the camera was aimed perpendicular to the reef. When possible and needed, specimens were collected during the survey to facilitate accurate identification. Within each photo-quadrat, all individuals were identified to the lowest possible taxonomic level or defined according to their morphology and referred to as “morphospecies.” In total, 992 individual porifera were recorded, belonging to 64 unique taxonomic units (21 species and 41 morphospecies). Georeferenced data were not collected, and transects were therefore treated as depth stratified but not spatially explicit.

Analyses

Data analyses consisted of two components: (1) direct depth patterns, describing how richness, abundance, evenness, and aggregation change with depth for each taxonomic group, estimating the direct responses of richness and its proximate

components to depth, and (2) proximate drivers effects on species richness, applying the MoB framework to identify how these components collectively drive the observed richness–depth patterns.

Direct depth patterns

To assess how community structure responds to the depth gradient, we calculated four diversity metrics—richness, abundance, evenness, and intraspecific aggregation—for each taxonomic group across its observed depth range.

Richness and abundance were directly calculated per sample for each group. *Evenness* was calculated using the *sigma* (σ) parameter, which estimates the variability in abundances among species (Bulmer 1974; Engen et al. 2002; Alroy 2025; Lazarus et al. 2025). Sigma was estimated using the Poisson lognormal distribution (PLN), where each sample is treated as a Poisson random sample from an underlying lognormal species abundance distribution with variance σ . Because higher σ values indicate greater variability—and therefore lower evenness—we present community evenness as the reciprocal ($1/\sigma$), so that larger values correspond directly to more even communities. Evenness was calculated for samples containing at least 3 species. *Intraspecific aggregation* was calculated using the standardized Morisita index of dispersion, which measures the degree to which individuals of each species are clustered across samples within depth layers (Morisita 1962; Krebs 1999). We retained only species with more than 10 individuals and present in at least two samples, and averaged index values across species. Index values < 0.5 indicate even distribution among plots, and > 0.5 reflects spatial aggregation. We also evaluated alternative approaches for quantifying aggregation, including Ives's J index, the negative binomial dispersion parameter (k), and the nonstandardized Morisita index, but these produced similar results. Since fish depth data were continuous and the analysis required repetitions within depth bins, we grouped the observations into 15-m depth bins.

Statistical analysis

To model the relationships between the diversity measures and depth, we used the ‘senlm’ package, which fits flexible nonlinear models suitable for capturing complex ecological patterns along environmental gradients (Anderson et al. 2022). To extract the mean response, we fitted all combinations of eight candidate mean functions—uniform, constant, Gaussian, mixed Gaussian, beta, sech, HOF, and modskurt—which represent a range of flat, unimodal, and skewed shapes suitable for capturing diverse ecological responses to depth. For the ‘counts’ data type (richness, abundance), we tested eight error distributions: Poisson, negative binomial (NB), zero-inflated Poisson (ZIP), zero-inflated NB (ZINB),

and their lognormal extensions (ZIPL, ZINBL, ZIPL.mu, ZINBL.mu) to account for possible overdispersion and zero-inflation. For the continuous evenness and aggregation indices, we applied a different set of error distributions: Gaussian, Tweedie, and various zero-inflated or gamma-based models (zig, zigl, zigl.mu, ziig, ziigl, ziigl.mu). For each response, we selected the best model from the 64 possible combinations using the corrected Akaike Information Criterion (AICc). Confidence intervals were computed using the *t*-distribution, with degrees of freedom equal to the number of parameters in each mean response model, reflecting the standard parametric approach for model-based estimates.

Proximate drivers effects on species richness

To explore the underlying proximate drivers effect on richness, we used the Measurement of Biodiversity (MoB) framework (Chase et al. 2018; McGlinn et al. 2018, 2021) implemented through the R package ‘mobr’ version 3.0.0 (McGlinn et al. 2018). MoB also accounts for differences in scale, here defined as the number of samples or the number of individuals accumulated. The full methodology is detailed in McGlinn et al. (2018) and outlined below are the key steps of the analysis as applied to our study.

The first step involved constructing three types of richness rarefaction curves: individual-based rarefaction (IBR), non-spatial sample-based rarefaction (nsSBR), and spatial sample-based rarefaction (sSBR). Each curve reflects different combinations of the three proximate drivers of richness, and by subtracting them, we can isolate the individual contribution of each component (McGlinn et al. 2021).

In the present analysis, we were interested in the effect of depth on richness, so we generated rarefaction curves separately for each depth bin (Fig. S3). The IBR curve was generated by randomly drawing *n* individuals from the total number of individuals (*N*) at a specific depth bin and recording the progressive accumulation of species. Its shape is determined solely by the species abundance distribution: In more even communities, species accumulate faster, whereas in uneven ones the curve rises more slowly. The nsSBR curve is built by randomly selecting *k* samples, with individuals redistributed among them while preserving the original sample-level density. Species accumulate faster when the number of individuals sampled is higher. This curve, therefore, integrates the combined effects of abundance and evenness on species accumulation. Finally, the sSBR curve retains spatial structure by accumulating samples according to their spatial proximity, thereby capturing the influence of all three community components—abundance, evenness, and spatial aggregation—on richness accumulation. Since calculating the aggregation effect demanded geo-referenced samples, we were only able to calculate it for the fishes and Scleractinian corals.

The second step involved subtracting the rarefaction curves for each depth to isolate the individual influence of each component: the effect of aggregation = sSBR – nsSBR, the effect of abundance = nsSBR – IBR, and the effect of evenness = IBR. These effects were then modeled against depth bins, with the slope representing the change in each component’s influence along the gradient. In the final step, we explored the effect of scale by assessing how the slopes of diversity components change with depth under varying sampling efforts. Additionally, randomization-based null models were applied to each component to test whether the observed relationships with depth differed from those expected under a null model. See McGlinn et al. (2018) for full methodological details.

Sensitivity tests We first applied all analyses to the full dataset (i.e., all depths and sites) and then repeated them on several data subsets to assess robustness under different constraints. These subsets included the shared depth range across taxa (≤ 55 m) and for each site separately. For fishes, we additionally separated observations by consolidated (western region) and unconsolidated (northern region) habitats to evaluate habitat effects. We also tested alternative binning schemes to examine their influence on aggregation estimates, and in addition to 15-m bins, we also tested bins of 10 m and 30 m. The observed patterns were consistent across bin sizes (Fig. S4 and 5).

We further applied several sensitivity tests specifically for the proximate drivers effects on species richness analyses. The ‘mobr’ package models linear relationships between the drivers’ effects and depth, which may not always hold. In some cases, a component can have contrasting effects across depth zones for instance, positive in shallow waters and negative in deeper areas. When such nonlinear patterns were evident, we conducted additional separated analyses for each depth segment. Additionally, in Octocorallia we evaluated how the sampling gap at intermediate depths influenced the MoB results by conducting an additional dichotomous analysis (i.e., shallow versus deep) alongside the continuous depth approach—since no difference was detected, we only show the continuous approach.

All statistical analyses and data visualization were performed in R version 4.4.2 (R Core Team 2024). Additionally, large language model assistance (ChatGPT; OpenAI) was used to support code development and debugging; all analyses, interpretations, and final text were performed and verified by the authors.

Results

Direct depth patterns

The four taxonomic groups exhibited distinct patterns of species richness, abundance, evenness, and intraspecific aggregation across depths (Fig. 3, Table S1). Fishes richness declined from 8 to 149 m, reaching a plateau at approximately 60 m, whereas Porifera richness increased monotonically from the surface to 60 m. Scleractinian coral richness peaked at ~10 m, with a sharp initial increase followed by a modest decline to 55 m. Octocorallia displayed little variation with depth, though gaps in observations between 4 and 34 m limited inference about potential hidden peaks within the studied range.

Site-specific analyses reinforced the overall richness trends, though its shape varied among sites. Due to limited data, Porifera and Octocorallia were analyzed only at one site each (IUI and CB, respectively), but both exhibited patterns similar to those observed in the main

analysis (Fig. S6). Fishes richness peaked in shallow waters (<20 m) in CB but not IUI, while Scleractinia richness increased with depth at CB but remained stable at IUI. For fishes, comparing the largely consolidated habitat (western region) with the largely unconsolidated habitat (northern region, Fig. S1) revealed declining richness in both habitats, yet richness was consistently higher—and its decline markedly sharper—in the consolidated habitat down to ~75 m, where both curves converged.

Abundance trends also varied among taxa (Fig. 3). Fishes abundance declined to ~60 m, with little change at greater depths. In contrast, Scleractinia and Porifera showed continuous increases in abundance with depth, while Octocorallia displayed no variation. Site-level patterns resembled the full data analysis with a few changes between the CB and IUI sites in Scleractinia and Octocorallia mostly in shallow waters (Fig. S6). The comparison between consolidated and unconsolidated habitats for fishes mirrored the richness results: higher fishes

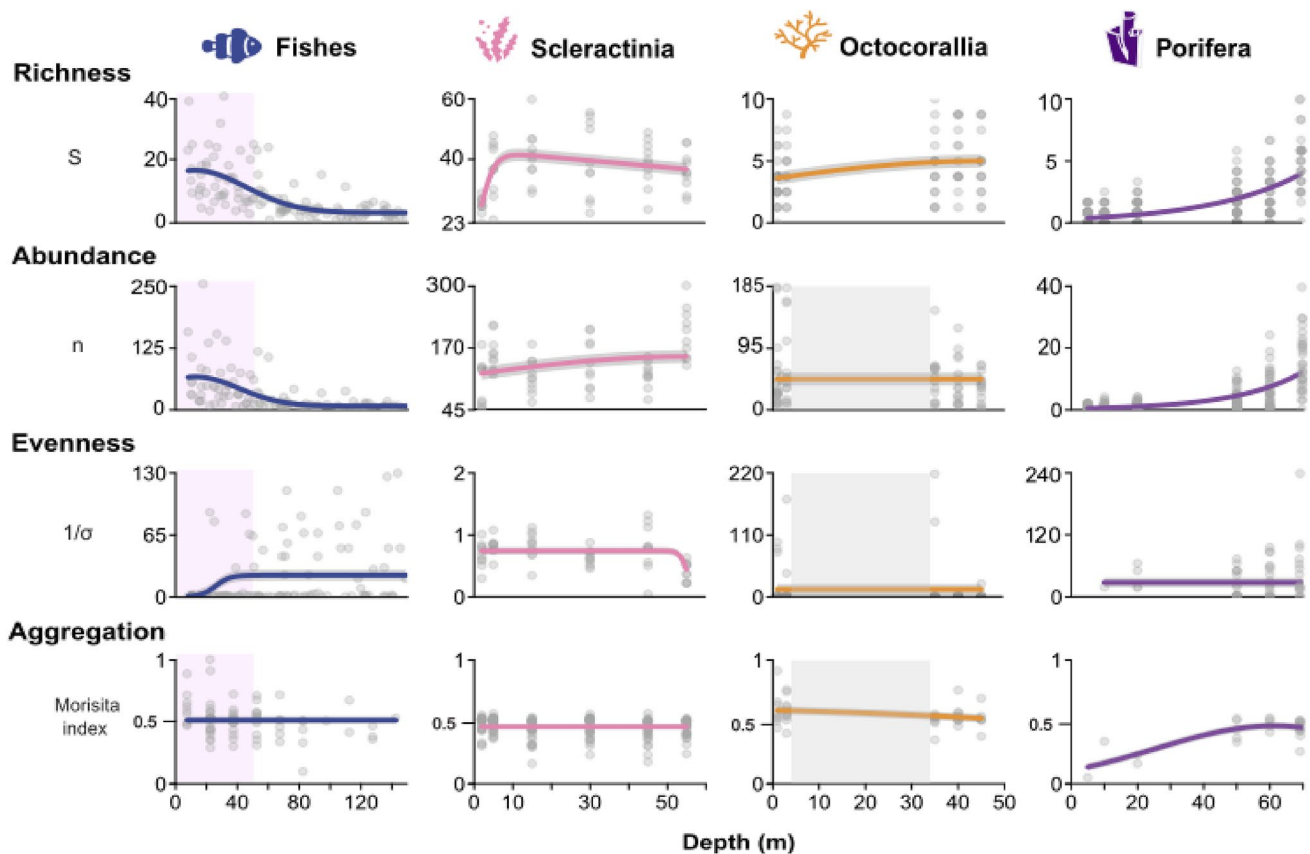


Fig. 3 Changes in richness and its proximate drivers along the depth gradient for the four taxonomic groups. Points show sample-level values, and fitted lines depict the best-supported model for each taxonomic combination. The shaded area for fishes indicates the common depth range (<55 m), while the shaded area for Octocorallia indicates

missing data between 4 and 34 m. Evenness was estimated using the inverse of the Poisson lognormal dispersion parameter (σ). Aggregation was quantified as the mean Morisita index across species, where values greater than 0.5 indicate aggregated spatial distributions

abundance and a steeper decline in the consolidated habitat down to ~75 m, where the curves converged (Fig. S1).

Evenness and aggregation exhibited generally weak depth-related patterns (Fig. 3). In fishes, evenness increased at shallow depths suggesting reduced dominance from intermediate depths onward. We present in Fig. 3 the model that supported stabilizing at deeper depth, while a Gaussian model that suggests a reduction in evenness in deeper depths received slightly higher support but visually appeared to produce severe interpolation error (Fig. S7). Comparisons between consolidated and unconsolidated habitats revealed a clear unimodal evenness pattern with depth for fishes in consolidated habitats, whereas no depth-related evenness trend was observed in unconsolidated habitats (Fig. S1). Thus, whether evenness decreases or remains stable at deeper depths remains somewhat unclear. Scleractinia, Octocorallia, and Porifera evenness showed little change with depth. Aggregation declined modestly in fishes, shifting from random toward more uniform distributions, while in Porifera it increased slightly from uniform toward random. No consistent aggregation patterns were detected for Scleractinia or Octocorallia. Site-specific analysis revealed inconsistencies with the flat trend in the main analysis, showing decrease with depth in the IUI site and a bimodal trend in the CB (Fig. S6).

To assess whether unequal depth coverage affected the results, we repeated the analyses using only the shared depth range (0–55 m; Fig. S8). Results were largely consistent with the main analysis and presented a clear unimodal trend for fishes evenness.

Proximate drivers effects on species richness

To investigate the proximate drivers underlying richness variation with depth, we applied a MoB analysis. The effects of these proximate drivers on richness varied among taxa and fluctuated in both magnitude and direction along the gradient (Fig. 4 and 5).

Abundance effect

The effect of abundance on species richness was generally strong, but the directionality in which abundance affects richness across depth varied among taxonomic groups (Fig. 4). In fishes, the effect was predominantly negative, indicating that richness declined with decreasing abundance along the depth gradient (Fig. 4a). The decline was significant, intensified with increasing sampling effort (Fig. 4a), and was consistent across both consolidated and unconsolidated habitats (Fig. S2). A similar negative effect with depth was observed in Octocorallia (Fig. 4c). However, the overall linear trend was weak and statistically insignificant across all scales (Fig. 4c). By contrast,

Scleractinia and Porifera displayed positive abundance effects with depth, indicating that greater abundance promoted higher richness in deeper zones (Fig. 4b, d). These patterns were scale dependent and strengthened with sampling effort, especially in Porifera (Fig. 4b, d). To assess potential nonlinear trends, we examined the trend for fishes before and after 60 m and found no clear change (Fig. S9). For Octocorallia, potential nonlinear patterns could not be formally evaluated due to no sampling coverage across intermediate depths.

Evenness effect

The effect of evenness on richness differed among taxa (Fig. 4). In fishes, it was consistently negative across depths and intensified with scale (Fig. 4e), suggesting that declining evenness with depth reduces richness. This pattern was also preserved in the habitat analysis, although it was less significant (Fig. S2). In contrast, Octocorallia showed a strong positive effect, where greater evenness at depth corresponded to higher richness, a pattern that also intensified with scale (Fig. 4g). For Scleractinia and Porifera, evenness effects remained weak across depths and close to zero across scales, except for a slight negative trend at small scales in Scleractinia (Fig. 4f, h). Potential mesophotic breakpoints in fishes evenness were detected around 37 m and 60 m. Rerunning the MoB analysis for fishes before and after the breakpoints revealed a positive and significant trend before 37 m, indicating that increased evenness with depth supports higher richness, whereas beyond this depth the trend reversed, indicating reduced richness due to lower evenness (Fig. S10). After 60 m, the change in evenness with depth was no longer significant (Fig. S9).

Aggregation effect

Intraspecific aggregation effects on richness were evaluated only for fishes and Scleractinia, for which geo-referenced data were available (Fig. 5). In fishes, the overall effect was positive, suggesting that high aggregations in shallow waters contributed negatively to richness (Fig. 5a). Yet this effect was indistinguishable from the null model across scales (Fig. 5a). Examining the trend before and after 37 m yielded a negative trend before 37 m and a positive trend deeper than 37 m, both scale dependent and significant (Fig. S10). These opposing trends likely produced the non-significant positive aggregation pattern in the full-range analysis (Fig. 5a) and suggest that aggregation reduces richness mostly at intermediate depths. In Scleractinia, aggregation contribution to richness was low (although there was a weak positive effect at very small scales) (Fig. 5b).

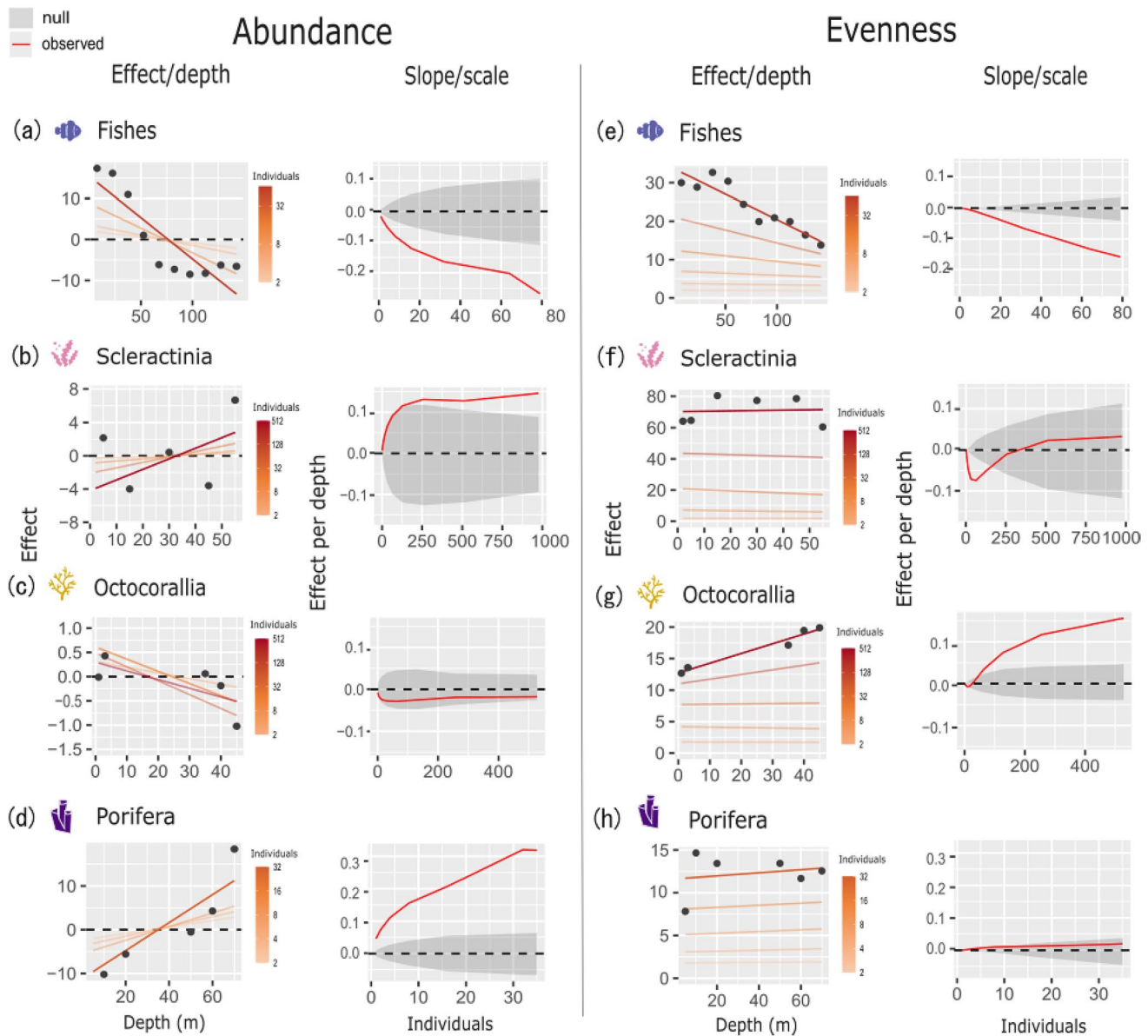


Fig. 4 Effects of abundance **a–d** and evenness **e–h** on species richness for four taxa (fishes), Scleractinia, Octocorallia, Porifera) across depth and sampling scales. Left panels show linear model fits of the drivers' effects against depth, with colors indicating the number of individuals, and black circles indicating effects at the highest scale. Effects are calculated as the difference between two rarefaction

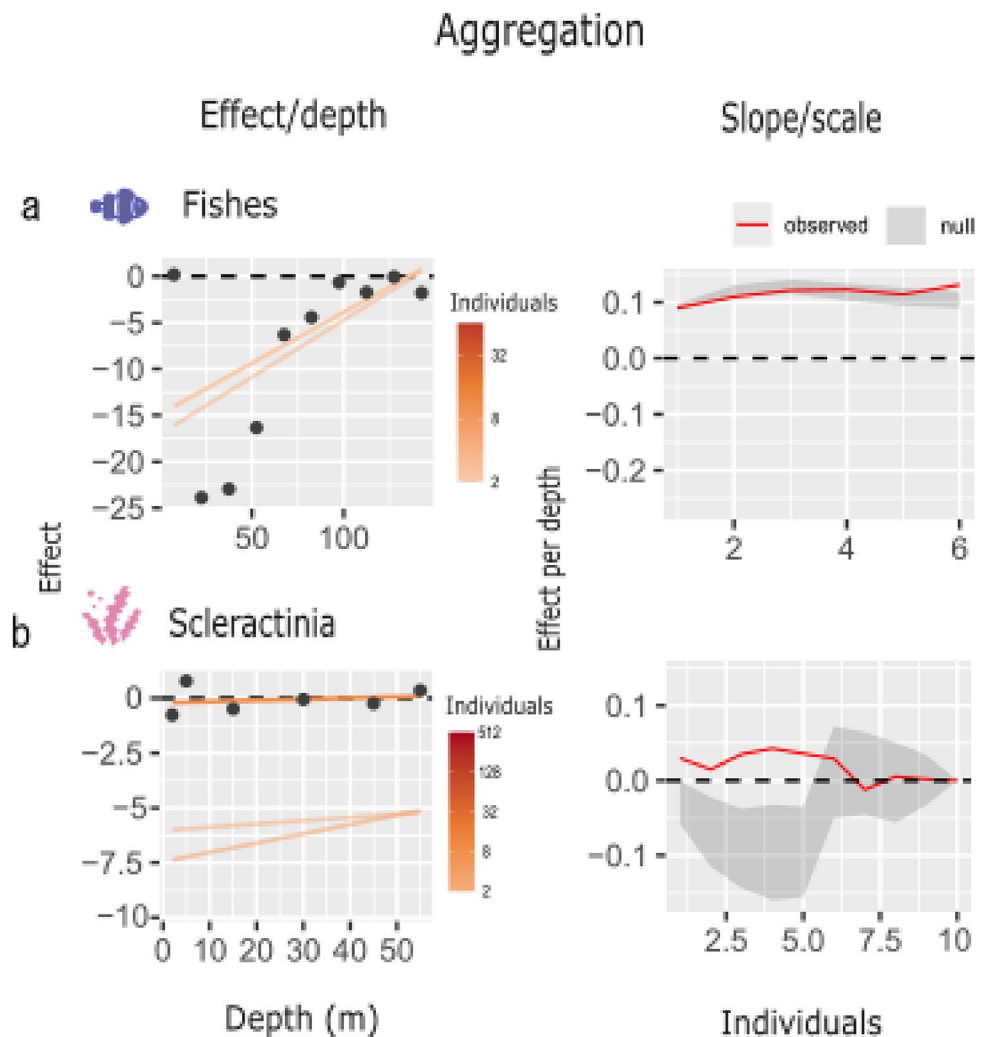
curves within each depth bin: Values of zero indicate no difference, whereas positive values denote that greater abundance or evenness or lower aggregations enhance richness. As evenness is directly represented by the IBR, the minimum value is zero. Right panels depict the slopes of the effect against depth across scales, with observed values (red) and 95% null-model confidence intervals (gray)

Discussion

It is well established that depth shapes marine biodiversity patterns (Danovaro 2024; Owens and Rahbek 2025). However, the exact patterns and the pathways through which richness–depth relationships arise are less understood. In this study, we examined depth-related changes in four different taxonomic groups from shallows to the upper mesophotic at the same geographical location, with data for

fishes extending to the lower mesophotic. We find a surprisingly divergent taxon-specific response to depth. Only fishes exhibited the widely expected decline in richness with depth, whereas Porifera showed a gradual increase, Scleractinia peaked in shallow waters, and Octocorallia displayed no consistent trend (Fig. 3). Our results reinforce previous observations of taxon-specific richness patterns along depth gradients, including gradual decrease in fishes (Lesser et al. 2019; Pinheiro et al. 2023), hump-shaped richness patterns

Fig. 5 Effect of conspecific aggregation on species richness along the depth gradient for fishes and Scleractinian corals, which contained sample-level spatial data. Left panels show linear model fit of the drivers effects against depth, colored by number of individuals, with black circles indicating effects at the highest scale. Right panels depict the slopes of the effect against depth across scales, with observed values (red) and 95% null-model confidence intervals (gray)



in Scleractinia and Octocorals (Bridge et al. 2012; Roberts et al. 2019a; Bell et al. 2019; Pérez-Rosales et al. 2022), and variable or weak depth-related trends in sponges (Bell et al. 2019). This variation suggests that richness–depth patterns are taxon specific which explains why no single consistent pattern of change in richness has emerged.

One of the most straightforward explanations for local-scale species richness variation across sites is the ‘more individuals hypothesis’ (Belmaker et al. 2007; Hurlbert and Jetz 2010; Storch et al. 2018). This hypothesis posits that communities with a greater number of individuals are more likely to harbor more species due to increased representation of the species pool, with differences in the number of individuals commonly attributed to variation in environmental factors (Srivastava and Lawton 1998; Gotelli and Colwell 2001). Indeed, in our data, abundance emerged as the most consistent, prominent driver for richness change over depth, closely tracking richness itself (Fig. 3 and 4). However, the direction of change of abundance with depth varied markedly among taxa (Fig. 4).

We found increased Porifera and Scleractinian coral abundances toward deeper waters (down to 70 m and 55 m, respectively), whereas fishes showed high abundances in the shallows that decreased down to 150 m (Fig. 3).

Multiple ultimate drivers may explain the shape of richness across depth, but they clearly must predominantly act on impacting gradients of abundance. Overall, abundance trends across taxa did not correspond to the commonly evoked depth-related environmental gradients—such as light or temperature—that typically show a monotonic change across depth (Lindfield et al. 2016; Tamir et al. 2019; Danovaro 2024). Thus, each taxa either responds differently to the same ultimate environmental drivers or is constrained by distinct drivers (Eyal et al. 2019; Kahng et al. 2019). These distinct drivers may include physical and ecological processes beyond light and temperature—such as hydrodynamic conditions, circulation patterns, and resource availability—which can shape abundance through their effects on larval transport, habitat connectivity, and

species interactions (Cowen et al. 2006; Brokovich et al. 2008; Wooster et al. 2017).

One possible ultimate driver for reduced abundance that operates predominantly within shallow waters is disturbance. Storms and other acute stressors, such as marine heat waves, can disproportionately impact sessile organisms in shallow waters, reducing their abundance and hence richness. Indeed, we find evidence for reduced abundance and richness for both Porifera and Scleractinia, while for fishes both abundance and richness remain high in shallow waters. This fits expectations, as mobile taxa may be able to largely evade shallow water disturbances and thus recover quickly (Connell 1978; Huston 1994). An example for this pattern was seen in the present studied location, where recovery following a severe storm was rapid for fishes but slow and site specific for *Scarlatianian* coral (Gavriel et al. 2023; Yuval et al. 2023; Oron et al. 2023).

We were able to uncover the strong relationship between abundance and richness, as this study uses abundance data for all taxa examined. However, for many benthic organisms, percent cover is a more common metric than individual counts (Murray et al. 2002; Edmunds and Riegl 2020). Percent cover and abundance capture different aspects of community structure and may vary in opposite directions: Numerous small individuals can yield high counts but little cover, while few large colonies may dominate yet produce low abundances (Barrera-Falcon et al. 2021). Indeed, the use of cover is important for understanding the ecological role of each group (González-Barrios et al. 2021). At the same time, abundance provides important information on demography with information on early life stages and fine-scale population structure and is better at detecting rare species (Luter et al. 2016; Zvuloni and Belmaker 2016; González-Barrios et al. 2021; Shlesinger and van Woesik 2021). Moreover, the MoB framework—which partitions the effects of the three proximate drivers of richness—explicitly requires count data (McGlenn et al. 2021). Consequently, using count data was essential for revealing how taxa richness responds to abundance across depth. Integrating standardized counts and cover data is thus critical for a more complete understanding of community changes along depth gradients.

Beyond changes in the number of individuals, changes in evenness also played a role in shaping richness patterns, especially for fishes and Octocorallia. Within the MoB framework, higher evenness always has a positive effect on richness, similar to the effect of abundance. However, the direction of the effect over depth was not consistent across groups: For fishes, lower evenness at greater depths was linked to reduced richness (Fig. 4e), while for Octocorallia, higher evenness with depth was associated with increased richness (Fig. 4f). Interestingly, changes in evenness derived from the sigma index (Fig. 3) did not always align with the effect of evenness on richness estimated by the MoB analysis

(Fig. 4), but similarities were sensitive to the exact model chosen in the direct analyses and the breakpoints examined within the MoB framework (Figs. S7, 9 and 10). Increased intraspecific aggregation generally reduces richness. Unfortunately, we were able to test this effect using the MoB framework only for two of the four taxa examined (Fig. 5). For these taxa, as well as in the direct analyses across all taxa (Fig. 3), depth-related changes in aggregation were weak, suggesting that aggregation plays a secondary role in shaping richness patterns relative to abundance.

Our conclusions apply only to the depths examined. For fishes only, where the depth examined was the widest (down to 150 m) we were additionally able to examine deeper water breakpoints in community structure, and ~60 m emerged as a clear breakpoint for richness, abundance, and evenness (Figs. 3, 4). This is consistent with previous studies identifying depth-related shifts around this depth across multiple mesophotic coral ecosystem taxa (Rocha et al. 2018; Lesser et al. 2019; Pinheiro et al. 2023). In a previous study in the Gulf of Aqaba, ~30 m was also identified as a transition zone between shallow and deeper fish assemblages (Brokovich et al. 2008). We similarly find such a transition for fishes, with lower evenness observed in shallow waters (< 37 m) potentially marking a reduction in schooling planktivores (Lesser et al. 2019; Siqueira et al. 2021; Pinheiro et al. 2023). However, such a transition was not found in the other taxa examined in the Gulf of Aqaba, suggesting this may be a fish-specific pattern.

We found meaningful differences when examining consolidated versus unconsolidated habitats for fishes (Fig. S1). On consolidated habitat, richness and abundance declined sharply from high values in shallow waters to low around ~75 m, whereas the unconsolidated habitat exhibited much lower initial richness and abundance and a more gradual decrease. These trends may be driven by greater habitat complexity and niche availability in coral reefs, leading to shallow water peaks in abundance and richness (Komyakova et al. 2013). However, in deeper waters richness and abundance converged to similar patterns in both habitats, possibly indicating common constraints. Overall, these differences highlight a strong influence of habitat type on diversity patterns in shallow waters, while suggesting that habitat imposes a weaker or more indirect influence at greater depths.

Several additional factors may influence the observed variation in richness patterns among taxa. One of them is the chosen depth range. A unimodal trend can appear as increase, decrease, or no trend depending on the studied range (Leathwick et al. 2006). Although taxa in our study were sampled across different depth extents (with most groups extending only into the upper mesophotic zone), the contrasting responses identified in the main analysis (Fig. 3) persisted within the shared depth range (0–55 m,

Fig. S8), indicating that these differences reflect genuine taxon-specific patterns rather than sampling extent artifacts. Scale—i.e., the grain (sampling unit size) and extent (overall surveyed area)—can strongly influence ecological inference (Chase et al. 2018; Fritsch et al. 2020). In our study, the MoB analysis allowed us to test how the direction of the proximate drivers (abundance, evenness, and aggregation) changes with grain by increasing the number of sampling units and individuals (Fig. 3). We found broadly consistent patterns when increasing the number of sampling units, typically with increased magnitude of effect (Fig. 3). We also varied the extent of our study area within the sensitivity analyses by focusing on particular sites and found that the differences among groups largely persisted across sites (Fig. S6). This further supports the conclusion that the taxa-specific trends are unlikely related to different sampling effort and methodology among taxa.

Overall, this study provides a novel perspective on richness–depth patterns by simultaneously examining multiple taxa across a broad depth gradient within the same location, enabling direct comparison of species richness patterns and their proximate drivers. We reveal substantial taxon-specific variability that challenges the conventional expectation of declining richness with depth. Our findings further show that abundance is the most consistent driver of richness change with depth, although the direction of abundance shifts with depth is strongly taxon dependent. This underscores the importance of understanding abundance dynamics, an aspect often obscured when relying solely on cover-based estimates for sessile taxa. Future work should build on these insights by linking environmental conditions to the proximate drivers: abundance, evenness, and aggregation, to elucidate how they jointly shape richness across depth.

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Author contributions ID conceptualized the research, analyzed the data, and wrote the original draft. SC, LN, ES, YB, OB, MI, and TS collected the data and reviewed the manuscript. JB conceptualized the project, provided guidance, and edited the manuscript.

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Data availability No datasets were generated or analyzed during the current study.

Declarations

Conflict of interest The authors declare that this study was conducted without any commercial or financial relationship that could be construed as a potential conflict of interest.

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