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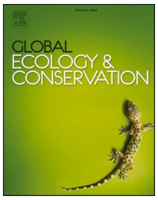

Spatial decoupling of α and β diversity suggest different management needs for coral reef fish along an extensive mid-oceanic ridge

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ABSTRACT

Understanding the underlying drivers of biodiversity is essential for conservation planning of large, connected seascapes. We tested how patterns in α and β components of species and functional diversity of coral reef fish (214, species, 23 families) varied along the extensive Chagos-Lakshadweep oceanic ridge (the largest chain of mid-oceanic atolls in the Indian Ocean) and evaluated geomorphological, environmental, and anthropogenic predictors of diversity patterns. α and β diversity (species and functional) showed contrasting patterns along the ridge; richness and α diversity decreased towards the north and were influenced by anthropogenic pressures, while β diversity increased towards the north, along environmental gradients and with geographic distance. Species β diversity was dominated by turnover (> 80%), while functional β diversity was dominated by nestedness (> 60%). Geographically distant reefs (> 2000 km apart) with high structural complexity were functionally similar, illustrating a ridge-wide capacity for reefs to maintain ecological structure and function despite significant differences in biodiversity. Low spatial congruence in different facets of biodiversity suggest differentiated management needs for reef fish communities along the Chagos-Lakshadweep ridge. Specifically, while a single large marine reserve may be effective for biodiversity conservation in the Chagos archipelago in the south, a network of several smaller conservation areas may be needed to confer resilience to densely populated and biologically differentiated reefs further north.

1. Introduction

Establishing the spatial distribution of biodiversity is a major requisite of conservation planning to confront the growing

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biodiversity crisis. Biodiversity is multifaceted, and its two main components - alpha (α) and beta (β), describe diversity at different scales. While α diversity describes the number and abundance of species, traits or genes within communities or habitats (Whittaker, 1972), β diversity measures variation in community composition among spatial units (Whittaker, 1972; Anderson et al., 2011) Where α diversity captures a static component of biodiversity, β diversity captures its more dynamic aspects, revealing information on connectivity patterns and mechanisms of regional biodiversity maintenance, essential for conservation planning (Socolar et al., 2016). Evaluating both components together help match diversity drivers with scale-appropriate conservation action.

β diversity is typically decomposed into 'turnover' and 'nestedness' components which hint at different mechanisms structuring assemblages. Turnover indicates the degree of simultaneous losses and gains of species or traits across locations, where nestedness indicates the degree to which species or traits at a location are a subset of richer locations (Baselga, 2010). Turnover reflects species/trait sorting due to competition, differential environmental tolerances, or historical events. In contrast, nestedness hints at selective extinction or colonisation of species/traits due to differential adaptive capacities or physical and historical barriers to dispersal (Qian et al., 2020). These β diversity components have important conservation implications. For instance, when nestedness prevails, prioritising few of the richest sites can be an optimal conservation strategy; high turnover would require conserving many more sites, not necessarily the richest ones (Bevilacqua and Terlizzi, 2020). Understanding relationships between β and α diversity can help manage dynamics of communities, including their stability and resilience potential (Devictor et al., 2010). Given the accelerating biodiversity crisis, we urgently need ecologically embedded conservation planning based on a multifaceted understanding of biodiversity across large regional scales.

Coral reef fishes are highly diverse, play fundamental roles in reef productivity, function, and resilience (MacNeil et al., 2015) and support extensive ecosystem services like fisheries (Woodhead et al., 2019). Drivers of reef fish biodiversity can vary between species and functional diversity, α and β components, and with scale. Typically, at larger spatial scales (continents), climatic, biogeographical factors and connectivity predict reef fish α diversity (Cowman and Bellwood, 2013). More regionally, disturbance history dominates α diversity (Pratchett et al., 2011). At reef-scales, geomorphic gradients in benthic condition and topographic complexity dominate, mediating habitat use and biotic interactions (MacNeil et al., 2009). This natural variation in species and functional diversity may be overridden by stressors from human habitation, fishing, and market pressures (Williams et al., 2015; Cinner et al., 2020). Fish species β diversity has been found to vary with reefscape area (Arias-González et al., 2008) and along steep environmental and latitudinal gradients (Rodríguez-Zaragoza et al., 2011), but little is known of patterns and drivers of reef fish functional β diversity (Bevilacqua and Terlizzi, 2020). Similarly, while nestedness and turnover vary in their contributions to total β diversity across elevation, precipitation, climate, and latitude gradients on land, far less is known from the sea (Bender et al., 2017; Loiseau et al., 2017; Bevilacqua and Terlizzi, 2020).

We explored patterns and predictors of multifaceted reef fish biodiversity in the Chagos-Lakshadweep Archipelagos, the largest chain of mid-oceanic atolls in the Indian Ocean. This extensive ridge provides a unique opportunity to understand how local and regional predictors interact and contribute to reef fish biodiversity across a substantial latitudinal gradient of geologically connected atolls. Using detailed ecological surveys from 54 sites across 14 atolls along 2500 km of the Chagos-Lakshadweep ridge, we evaluate 1) how different components of reef fish biodiversity and composition vary among the Lakshadweep, Maldives and Chagos Archipelagos, (2) turnover or nestedness contributions to total species and functional β diversity, (3) variation in species and functional trait composition and (4) the influence of anthropogenic, environmental and geomorphological factors in shaping diversity patterns. We expect α diversity to decline with reef condition and local anthropogenic influence and that species and functional composition would vary with distance: sites closer together being compositionally similar. Because increasing latitude typically represents stronger environmental contrasts, we expect species and functional β diversity to increase with latitude. Because processes generating β-diversity are complex and context dependent, we had no a-priori expectation of whether β-diversity was driven by nestedness or turnover.

2. Materials and methods

2.1. The Chagos-Lakshadweep Ridge

Chagos Archipelago (henceforth Chagos), Maldives and Lakshadweep Archipelago (henceforth Lakshadweep) form the largest chain of coral atolls in the Indian Ocean. The ridge has geomorphologically similar, low-lying atolls, extending across 20º latitude, and 3000 km, with distinct east-west gradients in bathymetry and wave exposure (Ben Avraham and Bunce, 1977). The ridge has biogeographically homogenous fish faunas but have different social, political, and historical contexts, and heterogenous resource use patterns (Appendix A1).

3. Sampling

3.1. Biodiversity surveys

We surveyed fish and benthic communities in Lakshadweep (RK, RA), Maldives (NAJG, KLN) and Chagos (NAJG, MSP) between 2010 and 2013. In all, 54 sites were surveyed on outer reef slopes (4–10 m depth) of 10 atolls across the ridge (Appendix A1). Spatial coverage was highest in Chagos (4 of 5 atolls) followed by Lakshadweep (9 of 13 atolls), with just one atoll (1 of 23 atolls) surveyed in Maldives. Fish communities were sampled with underwater visual censuses (UVCs) on 3–6 belt transects per site. 50 x 10 m (500 m^2) belt transects were used in Lakshadweep to survey all fishes. In Maldives and Chagos, larger, more mobile species were recorded in 50 x 5 m (250 m^2) belts, while site-attached pomacentrids were recorded on 50 x 2 m (100 m^2) belts. All surveyors had > 5 year's experience conducting fish UVCs; bias among experienced divers is among the smallest components of variation in fish counts (McClanahan et al., 2007). Divers recorded all observed fishes within the transect and estimated individual sizes (total length to the nearest cm). To minimize observer biases, we pooled sizes into 10 cm bins for analysis. We excluded all individuals < 7 cm, given difficulties in accurately surveying small cryptic fishes using UVC (Edgar et al., 2004). Elasmobranchs were also disregarded to avoid overestimating abundance of transitory predators that are poorly sampled using UVC (Samoilys and Carlos, 2000). We excluded 54 rare species with only 1 occurrence (singletons), which can disproportionately influence biodiversity indicators (Gaston, 1994). After all exclusions, we had 214 species from 23 families. To account for differences in transect area, we report abundance estimates at 100 m^2.

We assessed benthic condition using 3–6 replicate 50 m transects, estimating proportional cover of benthic organisms (e.g., corals) using point-intercept (100 uniformly spaced points) transects (Chagos and Maldives) or benthic photoquadrats (Lakshadweep). In Lakshadweep, photoquadrats (size=50 cm^2) were taken every 5 m along the 50 m transect. We placed a 10 cm^2 grid on the photoquadrat using ImageJ software and recorded the dominant substrate within each square. Proportional cover of benthic organisms across 5 photoquadrats was averaged for each transect. Both methods give similar estimates of benthic cover on reefs (Côté et al., 2005). Corals were identified to genus and classified into 'typical' growth forms (Veron, 2000): encrusting, branching, tabular, foliose, massive and submassive. We used percentage cover of branching and tabular corals (dead+live) per transect as a proxy for structural complexity, as these forms are known to be functionally important for fishes (Kerry and Bellwood, 2015). This index compared well (R^2 =0.68) with more standard, underwater visual estimates of structural complexity at 7 reefs (total transects = 28) in Chagos where both measures were available. All transect data were averaged to give site-level estimates for analysis.

3.2. *Selection of explanatory variables*

We collated data on two anthropogenic, two geomorphological and two environmental variables known to influence reef fish assemblages (Williams et al., 2015). Anthropogenic predictors chosen were human gravity and population density. Human population density was calculated as individuals per forereef area (km^2) in a 10 km radius around each site (indicative of direct and indirect anthropogenic pressures per reef area, Williams et al., 2015). Additionally, we used human gravity, an estimate of market-driven fishing pressure (Cinner et al., 2018), measured as human populations in the surrounding 500-km area divided by the squared travel time to the reef from the nearest population centre. Spatial data on population density was taken from the 'gridded population of the world dataset (UN Adjusted, v2)' for 2011 (CIESIN, 2018) and reef area was extracted from the 'global distribution of warm-water corals 2010' spatial layer (UNEP-WCMC et al., 2010). The human gravity layer is available from Cinner et al., 2018. The geomorphological predictors used were latitude and wave exposure. Latitude was used as a proxy for SST and rainfall that increase towards Chagos, and the frequency of seasonal tropical cyclones that increases towards Lakshadweep (Stoddart, 1973). Sites were coded as 'exposed' or 'sheltered' based on exposure to seasonal physical disturbance regimes which strongly impact these systems owing to the prominent south-west monsoon weather front in the north (Arthur et al., 2006) and south-east trade winds in the south (Ben Avraham and Bunce, 1977). We used percentage live coral cover and structural complexity (% cover of functionally important structural forms) as environmental predictors. Human gravity was highly correlated with latitude ($R^2 = 0.90$) and structural complexity ($R^2 = 0.60$) and was therefore dropped from further analysis.

3.3. *Statistical analysis*

3.3.1. *Reef fish functional space*

We characterised fish species based on five common functional traits: diet, mean observed body size, water column position, mobility and social grouping (Hadj-Hammou et al., 2021, Appendix B). We conducted a PCoA on a distance matrix computed from Gower's distances (Gower, 1971) between species pairs (Villéger et al., 2008). The first two axes of the PCoA explained ~60% of total variation in functional space and were used in the calculation of functional α and β diversity indices.

3.4. *Biodiversity indicators*

Species and functional α diversity: We standardized species assemblages based on relative sampling effort and sample completeness to a sample size of 500 individuals per transect (~92% completeness, Appendix C1) (Chao et al., 2014). We then estimated six indices of species and functional α diversity based on the unified framework of Hill numbers (Chao et al., 2014). Hill numbers ^qD are a mathematically unified family of diversity indices based on 'effective numbers of entities', differing among themselves only by an exponent q, which indicates their sensitivity to abundance. We calculated Hill numbers of taxonomic entities (species) and functional entities (i.e., species-pairs with unit distance estimated by Rao's quadratic entropy, Chiu and Chao, 2014) for $q = 0$, 1 and 2. Hill numbers when $q = 0$ represent species/functional richness with all species/functions having the same weight, $q= 1$ represents common species (evenness) or species/functions being weighted exactly for their abundance in the community (similar to Shannon Index), and $q = 2$ represents dominance (diversity) favouring abundant species/functions (similar to the Inverse-Simpson's Index). There are two advantages of using Hill numbers as compared to single diversity measures in this study. Firstly, because Hill numbers are based on 'effective numbers of unit entities', it allows a direct comparison between the species and functional aspects of diversity and secondly, it helps generate a 'diversity profile' (ie., a plot of Hill numbers ^qD as a continuous function of parameter q) which characterizes the species abundance distribution of an assemblage and provides complete information about its diversity (Chao et al., 2014). For instance, the shape of the curve conveys the evenness of a community; a perfectly even community is represented by a horizontal line (D does not change as q increases) and a highly uneven community is represented by a curve with an initial steep descent as q increases. We plot species and functional α diversity measures as diversity profiles with $q = 0,1,2$ (Fig. 1).

Species and functional β diversity: To analyse patterns in species and functional β diversity we used two complementary approaches. First, we calculated species β diversity using pairwise-site Sørensen coefficients (β_{sor}) based on species presence–absence data (Baselga, 2012; Baselga et al., 2017). Given that species turnover (β_{sim}) and nestedness (β_{sne}) combine to equal β diversity (dissimilarity), we further partitioned β_{sor} into these two additive components (Baselga, 2012). For functional β diversity, we used the two synthetic functional axes from the functional distance matrix calculated above (which explained ~60% of total functional variation in trait space) to estimate the functional overlap (overlap of convex hulls) between pairs of sites, together with species presence-absence data to calculate three pair-wise functional dissimilarity indices based on Sørensen coefficients (Villéger et al., 2013); β diversity ($F\beta_{sor}$), turnover ($F\beta_{sim}$), and nestedness ($F\beta_{sne}$). We first calculated average species and functional β diversity values for each site by computing the mean of pairwise comparisons between focal sites and the 53 remaining sites (Villéger et al., 2013). Second, to compare the relative contribution of turnover and nestedness components to total species and functional β diversity within each region, we calculated multisite, species and functional dissimilarities (Baselga, 2013; Villéger et al., 2013). Owing to computational limitations, we randomly selected 10 sites from each region to calculate functional multisite dissimilarity measures using the function *functional.beta.multi.* in *betapart* package. Additionally, we used nonmetric Multidimensional Scaling (NMDS) to illustrate the compositional separation among sites and regions based on $S\beta_{sor}$ and $F\beta_{sor}$.

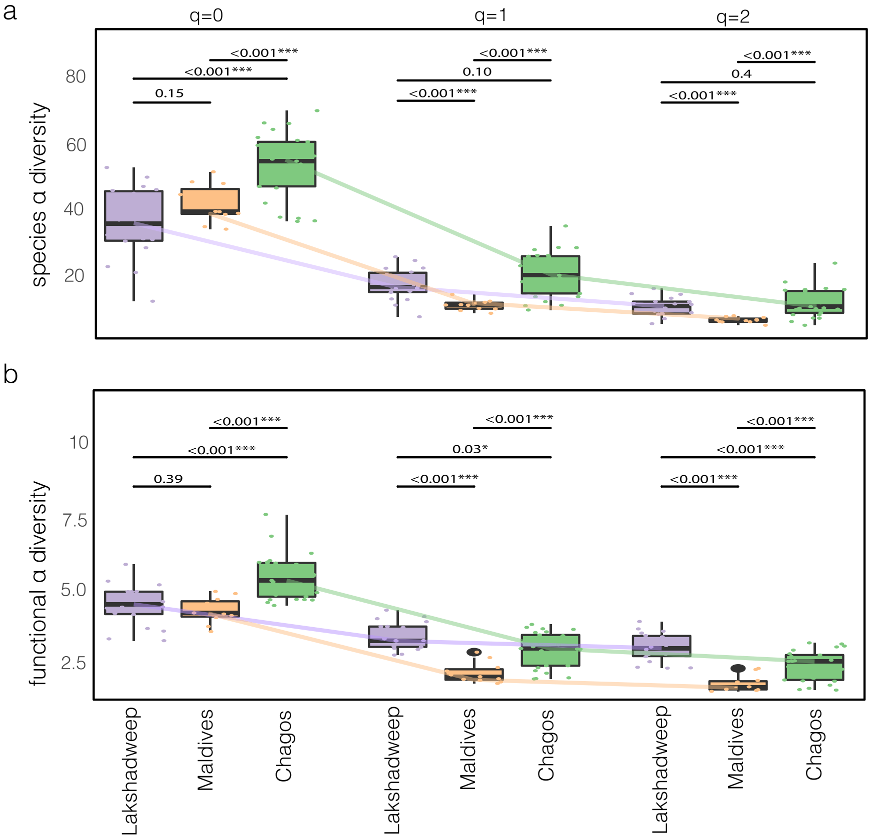

Fig. 1. Species and functional α diversity profiles in the Chagos, Maldives and Lakshadweep archipelagos based on the unified framework of Hill numbers (^{q}D) or the 'effective number of entities' needed for two assemblages to be considered equally abundant (Chao et al., 2014). For species Hill numbers (a) species are considered as unit entities, for functional hill numbers (b), the mean pairwise distance between two randomly selected individuals in a community (Rao quadratic entropy) is considered as a unit entity. Parameter 'q' represents reliance of the diversity measure on abundance of species/ traits in the assemblage, such that $q = 0$ represents species/functional richness, $q = 1$ represents the commonness of entities (i.e, species/functional evenness) and $q = 2$ represents dominance of entities (i.e, species and functional α diversity). The steepness of the diversity profile across values of 'q' indicates the degree of unevenness in the assemblage. Data presented as boxplots with points representing average site values (Lakshadweep: 18 sites, Maldives: 11 sites, Chagos: 25 sites). Asterix represent significantly different regions (using Wilcoxon rank sum test) with p values < 0.05 * ,< 0.01 ** ,< 0.001 *** .

3.5. Statistical modelling

To illustrate the differences between means of biodiversity indices between Lakshadweep, Maldives and Chagos, we used Wilcoxon rank sum tests.

We then used linear mixed effects models (LMEM) to compare the relative effects of anthropogenic (human population density), environmental (live coral cover, structural complexity) and geomorphological (wave exposure, latitude) predictors (as fixed effects), on various α diversity metrics. Atolls nested in regions (i.e, Lakshadweep, Maldives and Chagos) were used as random factors (to accounted for nested data structure and potential survey effects). The six indices of α diversity based on species and functional Hill numbers with $q = 0$ (richness), $q= 1$(Shannon Index) and $q = 2$ (Inverse Simpson Index) were used as response variables. Fixed effects were square root-transformed to account for skewness. Models were inspected for multicollinearity using Variance Inflation Factors (VIF< 2). We tested the full set of variables to facilitate comparing the impacts of different predictor variables across α diversity indices. We determined conditional and marginal R^2 following the method of Nakagawa and Schielzeth (2013) to estimate the explained variance of fixed and random effects in the LMEMs. We present effect sizes of fixed effects (i.e, standardized coefficients ± 95% CI, Fig. 4) and model estimates in Appendix D1. Standard diagnostics and visual inspections were conducted on model residuals.

Lastly, spatial patterns in species and functional β diversity ($S\beta_{sor}$ and $F\beta_{sor}$) were tested using a Generalised Dissimilarity Model (GDM, Fitzpatrick et al., 2013). GDM is a nonlinear extension of matrix regression for analysing and predicting patterns of compositional dissimilarity in relation to environmental gradients. GDMs apply a maximum likelihood estimation and flexible I-splines, to evaluate the effects of specific variables on between site dissimilarities. Specifically, the maximum height of each I-spline represents the relative importance of the variable on β diversity, while holding all other variables constant (Ferrier et al., 2007). All analysis were performed in R (R Development Core Team 2013, Appendix C.2 for list of R packages used).

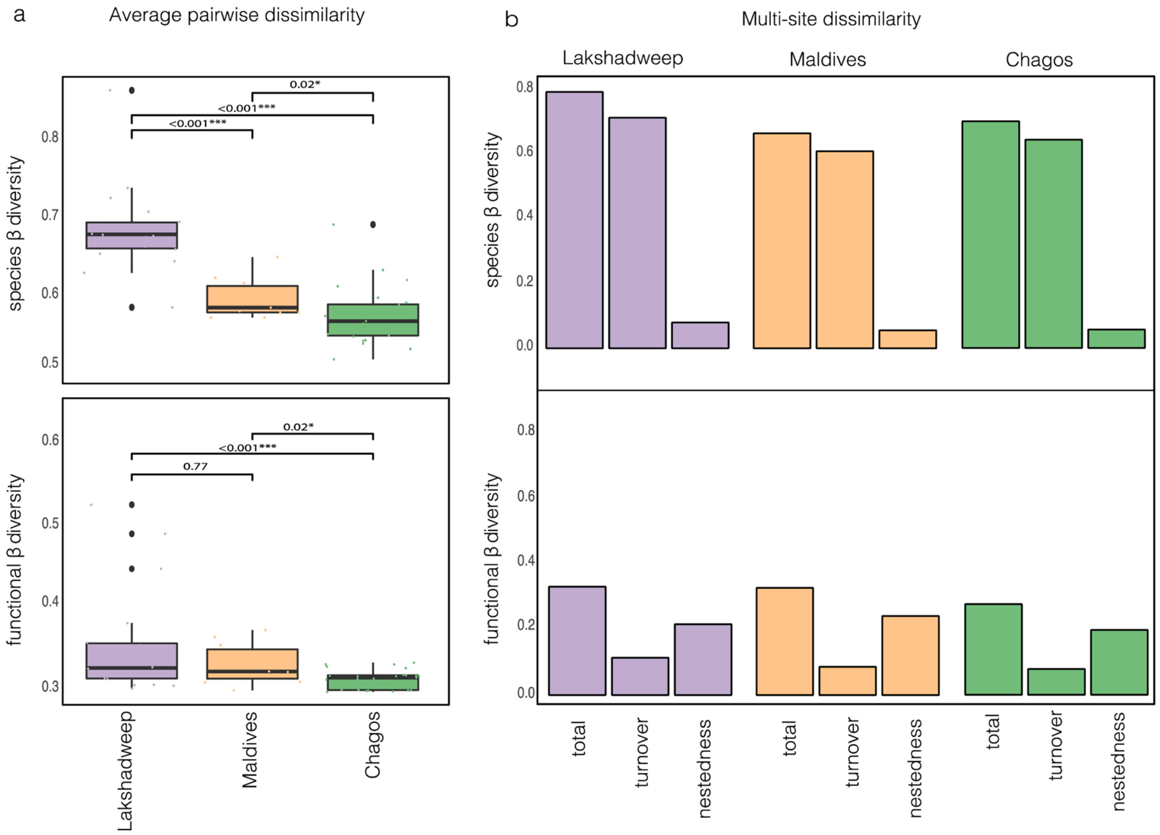

Fig. 2. Species and functional β diversity patterns across the ridge: a. Average pairwise species and functional dissimilarities (Sørensen dissimilarity) of sites in Chagos, Maldives and Lakshadweep. Points represent sites in different regions (Lakshadweep:18 sites, Maldives: 11 sites, Chagos: 25 sites). Asterix represent significantly different regions (using Wilcoxon rank sum tests) with p values < 0.05 * ,< 0.01 ** ,< 0.001 *** b. Multisite dissimilarity in Chagos, Maldives and Lakshadweep and the contribution of nestedness and turnover components to total species and functional β diversity (Sorensens dissimilarity).

4. Results

4.1. Variability in environmental and anthropogenic predictors

Human population density (humans density.km^2 of reef area) varied most in Lakshadweep, from Perumal Par (uninhabited), to Kavaratti atoll, with the highest population density across the dataset (1240 ± 206 SE individuals. reef km^2). In Chagos, Diego Garcia had low population density (92 individuals. reef km^2), while all other atolls were uninhabited. Huvadhoo atoll in Maldives had low population density (350 ± 42 SE individuals. reef km^2). Apart from Diego Garcia, all atolls in Chagos were no-take marine reserves, while atolls in Maldives and Lakshadweep were openly fished. Fishing pressure, estimated by the human gravity index was highest across Lakshadweep (52.66 ± 17.34 SE individuals/travel time^2), followed by Maldives (10.23 individuals/travel time^2) and lowest in Chagos (0 individuals/ travel time^2). Mean live coral cover was highest in Maldives (47.00% ± 1.40% SE), followed by Chagos (36.39% ± 3.40% SE) and Lakshadweep (32.33 ± 3.03% SE). Mean structural complexity was three times higher in Chagos (24.43% ± 4.70% SE) and Maldives (20.52% ± 1.69% SE) compared to Lakshadweep (7.21% ± 1.59%, Appendix A.2).

4.2. Patterns in species and functional α and β diversity

Species and functional richness ($q = 1$) of reef fish assemblages was highest in the south in Chagos, followed by Maldives and Lakshadweep to the north (Fig. 1.a,b). Interestingly species and functional eveness ($q = 1$) and diversity ($q = 2$) were lowest in Maldives among regions ($q = 1$ & 2, Fig. 1). Based on a shallower diversity profile, assemblages in Lakshadweep were functionally more even as compared to Chagos and Maldives (Fig. 1b), which appear to be dominated in abundance by large herbivores and small planktivores respectively (Fig. 3b). Contrary to patterns in α diversity, mean pairwise species and functional β diversity declined from

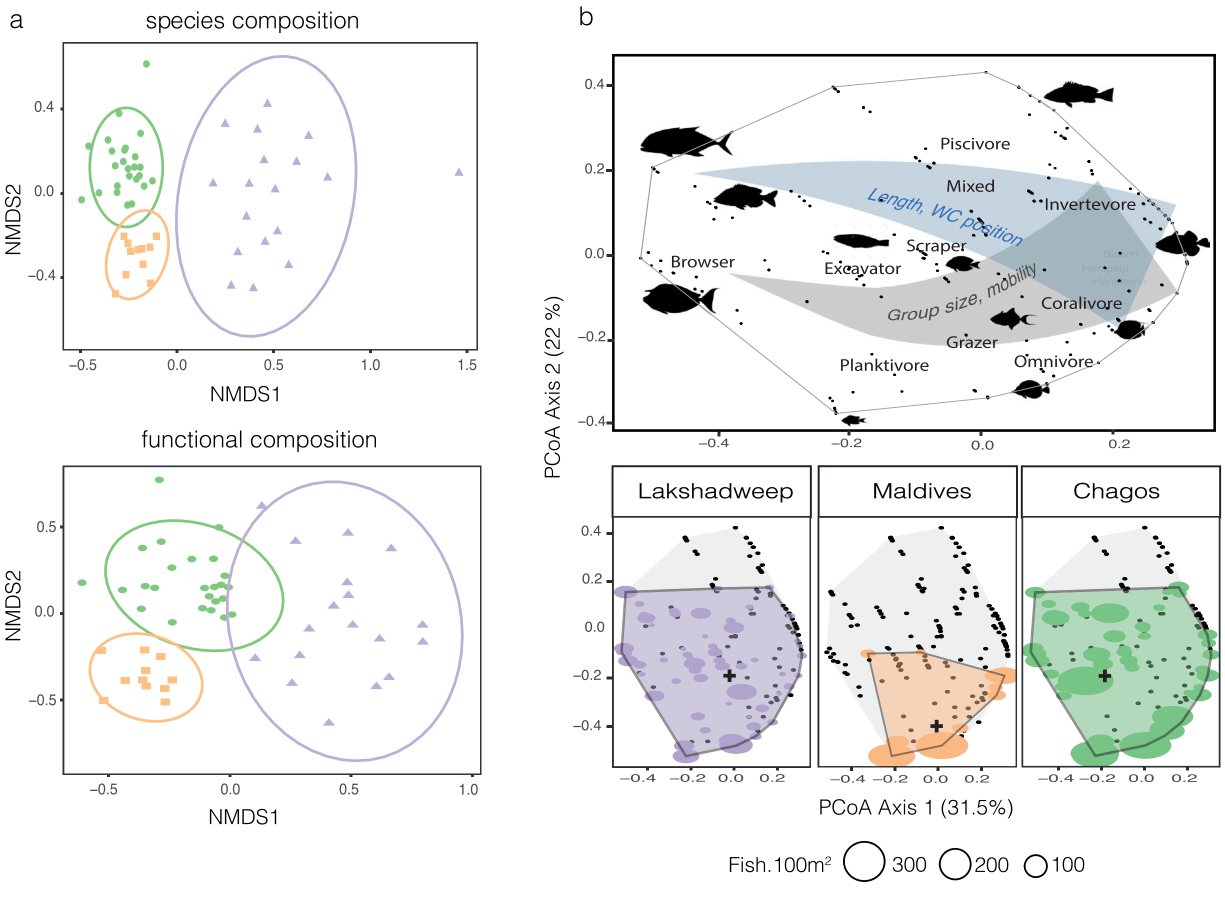

Fig. 3. Species and functional composition: a. Nonmetric multidimensional scaling (NMDS) plot based on Sorensens dissimilarities ($S\beta_{sor}$ and $F\beta_{sor}$) of species and functional assemblages in Lakshadweep (purple), Maldives (orange) and Chagos (green). The lines surrounding each region represent 95% confidence ellipsoids of weighted averages of NMDS scores for each region (stress< 0.18). b. Biplot of functional space as per a PCoA of Gowers distances based on five functional traits (Appendix S2). Species positions indicated by black dots. Commonly observed species are illustrated by their positions in functional space. Arrows indicate direction of increase in body size, water column position, group size and mobility. Trophic groups are indicated in black text. Coloured polygons represent the functional volume occupied by 80% of the most abundant species in the regions. + symbol indicates the centroid of the polygon.

north to south (i.e, from Lakshadweep to Chagos, Fig. 1 & 2). Across all regions, species β diversity was two times higher than functional β diversity (Fig. 2b). The turnover component accounted for most variation of overall species β diversity (>80%, Fig. 2b), while nestedness contributed to most variations of overall functional β diversity (>60%, Fig. 2b).

Species composition varied significantly between Chagos, Maldives and Lakshadweep (Fig. 3a). Interestingly, sites in Chagos and Lakshadweep, nearly 2000 km apart, were more similar in functional composition than sites in Maldives that were closer in proximity (Fig. 3a). The dominant fishes (species contributing to 80% of overall abundance, Fig. 3b coloured polygons) significantly differed in functional composition between regions; Huvadhoo atoll in Maldives was dominated by small-bodied, solitary, benthic, sedentary and low trophic-level species, particularly planktivores, with a mean body size of 8 cm (Fig. 3.b, Appendix B.4). In contrast, both Chagos and Lakshadweep were similar in composition and dominated in abundance by larger-bodied, mobile, benthopelagic fish predators and herbivorous browsers with a mean body size of 12 and 18 cm, respectively (Fig. 3.b, Appendix B.4).

4.3. *Predictors of differences in species and functional α and β diversity*

The relative influence of environmental, anthropogenic and geomorphological drivers differed among biodiversity indices. Anthropogenic pressure (human population density) significantly and negatively impacted species and functional α diversity components. Random atoll factors explained a significant variation in various α diversity indices (Appendix D1). In the GDM models, the percentage deviance explained by anthropogenic, environmental and geomorphological variables was higher for species β diversity (64.22%) than functional β diversity (23.20%). Species β diversity was largely explained by geographic distance between sites (23.16%), while structural complexity and human population density explained only 6–10% of model deviance (Table 1, Appendix D.2). Contrastingly, structural complexity explained maximum deviance in functional β diversity (35.46%), followed weakly by geographic distance (12.01%) and human population density (~ 6%, Table 1, Appendix D.2). Reef exposure had a weak (~1%), but significant effect on both species and functional β diversity.

5. Discussion

We explored how patterns in α and β components of coral reef fish species and functional diversity varied along the extensive Chagos-Lakshadweep ridge. There was a spatial mismatch between α and β components of species and functional diversity: specifically, while richness decreased, β diversity increased from south (Chagos) to north (Lakshadweep). All aspects of α diversity (species and functional) were negatively influenced by anthropogenic pressure, while β diversity (species and functional) varied with structural

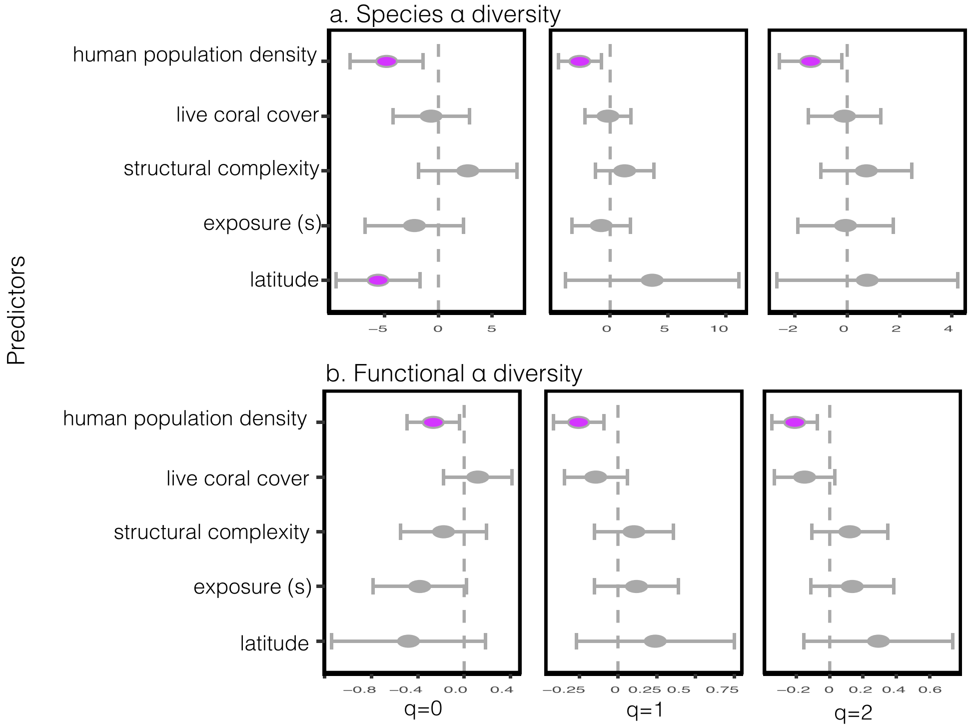

Fig. 4. Standardized estimates (mean ± 95% CI) of anthropogenic (human population density), environmental (live coral cover, structural complexity) and geomorphological (wave exposure, latitude) fixed effects in six α diversity indices – species and functional α diversity estimated by Hill numbers q= 0,1,2. Grey points indicate non-significance, purple and green coloured points indicate significant negative and positive effects respectively.

Table 1

A summary of the generalised dissimilarity modelling (GDM) results for species, and functional β diversity across the Chagos-Lakshadweep ridge. The significance of each variable is indicated in table.

	Species composition	Functional composition
GDM deviance	44.48	53.08
Explained deviance	64.23	23.20
Variable Importance (% deviance explained by predictors)		
Geographic distance	26.16[a]	12.01[b]
Human population density	6.84	6.17
Live coral cover	0.01	0.00
Structural complexity	10.17[a]	35.47[c]
Reef exposure	0.97[b]	0.49

The number of permutations for significance testing was n = 100.

[a] $p < 0.01$

[b] $p < 0.05$

[c] $p < 0.001$

complexity and geographic distance. Species β diversity was characterised by high species turnover, whereas functional β diversity was characterised by high nestedness, suggesting strong trait filtering of reef fish assemblages along the ridge. However, a remarkable similarity in fish assemblages between structurally complex reefs in Lakshadweep and Chagos that are 2000 km apart, illustrates the capacity of reefs to maintain ecosystem structure and function, suggesting that a prioritization of functional over species diversity may help confer resilience to reefs along the ridge. Low spatial congruence of α and β diversity, and complex patterns in the turnover and nestedness components of β diversity, highlight important dilemmas for spatial conservation against a rapidly shifting profile of human and environmental disturbances along the Chagos-Lakshadweep ridge.

From south (Chagos) to north (Lakshadweep), species and functional richness declined along the ridge linked to increasing human population density. However, patterns in species and functional evenness and α diversity were much more nuanced. As seen across Caribbean and Western Pacific reefs (Stallings, 2009, 2014), resource-use patterns and not merely human population density can significantly influence (species and functional) α diversity components of fish assemblages, overriding natural environmental patterns. In this study, this pattern was most evident in Huvadhoo atoll (Maldives), where species and functional α diversity and evenness were disproportionately lower than the more populated Lakshadweep. Specifically, reefs in Huvadhoo were dominated by small bodied, solitary, and sedentary planktivores and invertivores, with a very low abundance of large-bodied, mobile predators and herbivores which were characteristically different from sites in Chagos and Lakshadweep (Fig. 3b, Appendix B.4). This is a clear indicator of sustained reef fishing pressure in Maldives (Sattar et al., 2012; Martins et al., 2012), which has been low in the Lakshadweep prior to 2012 (Karkarey et al., 2014). Despite high live coral cover and structural complexity, the disproportionate impacts of anthropogenic pressures on the species and functional composition of reef fish assemblages in Maldives serve as a reminder of what unbridled fisheries and tourism development augur for the rest of the ridge. This is particularly important for functionally and taxonomically depauperate fish assemblages in Lakshadweep, where developmental and reef fishing pressures have steadily increased in recent years.

Where α diversity declined, β diversity (species and functional) increased from south to north along the ridge. Structural complexity emerged as a strong predictor of both species and functional β diversity, suggesting strong environmental filtering of fishes' traits.

One plausible explanation for this is the stronger effect of annual tropical cyclones that likely increases environmental heterogeneity towards the north of the ridge (Ben Avraham and Bunce, 1977). For example, the south-west monsoon creates high wave exposure on the western aspects of atolls for 5 months every year, strongly influencing patterns in habitat structural complexity in Lakshadweep (Arthur et al., 2006; Yadav et al., 2016). Interestingly, species β diversity was explained by high turnover in species composition, while functional β diversity was largely explained by nestedness, suggesting that replacement of species among sites does not necessarily reflect concomitant changes in fish functional space. Our study is in line with previous studies from the region that have documented strong trait-based filtering of herbivorous (Rathod et al., 2020), and piscivorous fish (Karkarey et al., 2014) along wave exposure gradients, despite species richness differences.

Species assemblages became more distinct with geographic distance however trait convergence was observed even among distant sites with comparable structural complexity. Convergence was observed along traits like large body size, home range size (sedentary and highly mobile species), watercolumn position (benthic and pelagic) and diet (piscivores, mixed-diet fish, invertivores and herbivorous grazers and browsers, Appendix B.4). These results have important implications for conservation along the extensive Chagos-Lakshadweep ridge, demonstrating that sites with high structural complexity could potentially be biodiversity hotspots along the ridge, capable of maintaining functional resilience even when species compositions differ.

5.1. *Conservation implications of biodiversity patterns*

Spatial discrepancies in α and β biodiversity indices present a dilemma for spatial conservation, specifically for the design and placement of marine reserves and the prioritization of species versus traits. β diversity dialectically interacts with α diversity as a result of community assembly through local and regional filters (Soininen et al., 2018). The regional species pool provides spatial insurance, which, via immigration and dispersal, may be important for sustaining local ecosystem functioning despite habitat disturbances (Loreau et al., 2003). Overall, Lakshadweep had lowest species and functional richness and highest species and functional β diversity.

There is potential for this high β diversity to compensate for the relatively low species richness in these locations by providing a diverse atoll-level pool of species exhibiting response diversity in the face of disturbance (Nash et al., 2016).

Discordant patterns of species turnover and functional nestedness reveal a further conservation dilemma, pitting species against traits in biodiversity conservation. Our results show that functions present in reefs with low structural complexity are subsets of reefs with high structural complexity. Prioritising reefs with high structure may thus be an optimal strategy to conserve a greater range of functions, not only within each jurisdiction, but across the ridge. However, for species, many different reefs need to be considered simultaneously to conserve the regional species pool, with turnover dominating species β diversity. Given the capacity for regional functional resilience and superior habitat condition (i.e., live coral cover and structural complexity) in Huvadhoo atoll in the Maldives, management actions that constrain fishing of larger-bodied, mobile herbivores and predators may increase their populations and expand the functional space occupied by these fish communities. Large MPAs in the uninhabited Chagos Archipelago are an exemplar, but may not be replicable or desirable where human densities are high. Here, other strategies for biodiversity conservation would be helpful, potentially providing larger ecological and more equitable conservation gains. Particularly, the highly biotically differentiated and depauperate assemblages of the Lakshadweep may need a more diverse strategy – one which incorporates a network of small conservation areas around sites with high structural complexity and measures that curb fishing pressures.

5.2. *Caveats and future directions*

Based on observational data alone, our study reveals interesting distributional patterns in reef fish diversity along the Chagos-Lakshadweep ridge. We acknowledge caveats that provide important directions for future research. Firstly, there is a need to study the effect of spatial scale on patterns and drivers of biodiversity change in this system. It is well known that predictors of reef fish diversity are scale dependent (Yeager et al., 2017). Secondly, our surveys were snapshots conducted at a relatively stable period in the ridge’s disturbance history; when benthic condition had significantly recovered 12–15 years after the 1998 mass-coral bleaching event and reef fishing pressures were relatively low in Lakshadweep. The Chagos-Lakshadweep ridge has undergone major shifts in environmental contexts in the last decade; particularly in the frequency and intensity of mass bleaching (Pisapia et al., 2019; Sheppard et al., 2020; Yadav et al., 2016) and an uptick of fishing pressures (R.K R.A, personal observations). Alarmingy, the frequency and track direction of tropical cyclones too is changing along the northern Indian Ocean in the last decade (Deshpande et al., 2021), with detrimental impacts on previously ‘sheltered’ coral reefs in Lakshadweep (Riyas et al., 2020). The loss of structural complexity from repeated mass-bleaching events and tropical cyclones suggests a reduced buffering of wave exposure and human pressures and raises concerns for fish biodiversity along the ridge in the future. Thirdly, Maldives was under-sampled in our dataset (low completeness, SAC not reaching an asymptote, Appendix C.1). While these sites provide a useful comparison for biodiversity at extremes of the environmental and anthropogenic gradient (high coral cover, high resource use), they do not necessarily represent Maldives as a whole. Inclusion of more atolls with gradients of human and environmental pressures would only strengthen our understanding of regional biodiversity patterns. Lastly, geomorphological, environmental, and anthropogenic gradients are highly correlated with latitude in this system. Future studies could use study designs that explicitly attempt to isolate key combinations of predictors.

6. Conclusions

The Convention of Biological Diversity has set targets for the protection of 30% of seas and oceans by 2030. In an effort to meet these targets, the Lakshadweep administration notified three large marine protected areas (to 685 sq km) in northern Lakshadweep in 2020. In contrast, the Maldives government has established 42 small MPAs (total area of 249.92 km^2) around popular dive sites and uninhabited atolls. While establishing MPAs are a positive forward step, the effectiveness of large no-take marine reserves is often limited in conserving biodiversity in areas of high human densities (Cinner et al., 2020). While issues around equity and justice strongly influence compliance and efficacy (Campbell and Gray, 2019), a part of the problem may be the narrow and static conceptualisations of biodiversity (specifically, richness, endemism, and habitat heterogeneity) that are still commonly used as proxies for biodiversity in marine reserve design (Mace, 2014). Our study provides the first large-scale (pan ridge) understanding of the patterns and relative predictors of multifaceted coral reef fish biodiversity along the extensive, geologically connected Chagos - Lakshadweep oceanic ridge. It forms an important baseline for biodiversity in a region facing a shifting profile of human-induced disturbances. We highlight low spatial congruence in different aspects of biodiversity – α and β components, and complex relationships between the nestedness and turnover components for species and functional β diversity, that need to be carefully monitored and considered for effective regional biodiversity conservation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability statement

Data from this MS are available upon request.

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Authorship Statement

Rucha Karkarey: Conceptualization, Formal analysis, Data curation, Investigation, Writing – original draft, Visualization, Project administration, Funding acquisition. **Rohan Arthur:** Conceptualization, Investigation, Writing – review & editing, Data curation, Project administration, Funding acquisition. **Kirsty. L. Nash:** Conceptualization, Investigation, Writing – review & editing. **Morgan. S. Pratchett:** Conceptualization, Investigation, Writing – review & editing. **Mahesh Sankaran:** Conceptualization, Writing – review & editing. **Nicholas. A. J. Graham:** Supervision, Conceptualization, Investigation, Methodology, Validation, Resources, Writing – review & editing, Data curation, Project administration, Funding acquisition.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02110.

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