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Species associations and community structure in an oceanic elasmobranch assemblage

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ABSTRACT: Elasmobranch assemblages support marine ecosystem health by regulating populations, transferring nutrients across habitats, and sustaining high-level consumers. Shifts in elasmobranch assemblages can reshape ecosystem dynamics through direct and indirect species associations. Here, we analyzed a 26 yr underwater visual survey dataset from Cocos Island National Park in the Eastern Tropical Pacific to examine community-level temporal shifts in the island's elasmobranch assemblage. We studied 13 species, analyzing changes in network strength, diversity indices, and species associations. We show a shift from a sparse, low-richness network in the early 1990s to a more densely connected assemblage by 2014. The elasmobranch assemblage showed 2 seasonal sub-communities: migratory oceanic species in the wet season and resident coastal species in the dry season. Scalloped hammerhead *Sphyrna lewini* and whitetip reef sharks *Triaenodon obesus* were the main contributors to year-to-year diversity changes. Significant association model outputs showed mostly negative associations, suggesting that predator—prey dynamics and intraguild competition are taking place in Cocos Island. We inferred 3 types of association patterns: (1) competition, when negative associations were possibly caused by competitive interactions rather than predator—prey dynamics; (2) predation, inferred when prey abundances were negatively associated with predator covariates; and (3) environmental preference, where shared or opposing thermal or seasonal habitat patterns explained positive or negative associations, respectively. Our findings advance understanding of the evolving Cocos Island elasmobranch community structure and network dynamics. Our study also provides a framework for examining the mechanisms driving interspecific associations in similar marine ecosystems.

KEY WORDS: Interspecific interactions · Competition · Network analysis · Predation · Marine ecology · Eastern Tropical Pacific · Ecological modeling · Cocos Island

1. INTRODUCTION

Marine ecosystems are shaped by complex biotic interactions, where processes like diel migrations and seasonal shifts influence species' behavioral and physiological responses to their predators, prey, and competitors (Lear et al. 2021) as well as affecting ecosystem structure (Carrier et al. 2012). However, evaluating competitive, predatory, and ecologically driven species interactions is challenging due to logistical and methodological constraints, especially for large marine predators whose interactions may occur infrequently and across large space and time scales. Additionally, species interactions are complex on their own, occurring through direct pathways such as predation and indirect mechanisms like com-

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petitive and associative processes (Twining et al. 2025). Ecosystem models and network analysis have emerged as powerful tools for capturing relevant ecological properties such as competitive interactions (Russo et al. 2022), intraguild predation, and spatial segregation (van Zinnicq Bergmann et al. 2024). Despite the nuanced process of factoring species interactions into management models, biologically appropriate ecological models that factor species abundance-related associations can provide valuable insights into ecosystem dynamics and population shifts (Twining et al. 2025) and provide better tools for mitigating economic impacts for local and international stakeholders (Ferretti et al. 2020).

As top and meso-predators, elasmobranchs influence how other species use marine habitats through both direct predator—prey interactions and indirect effects mediated by competition (Flowers et al. 2021, Dedman et al. 2024). For example, a study in Western Australia demonstrated behaviorally mediated niche shifts from suitable foraging grounds caused by the arrival of tiger sharks *Galeocerdo cuvier* driven by densities of dugongs *Dugong dugon* (Dill et al. 2003). The increase in dugong presence during summer attracted tiger sharks to the area, indirectly displacing bottlenose dolphins *Tursiops aduncus*, who avoided attractive foraging grounds in response to the increased predation risk by tiger sharks. Similarly, a study of 6 shark species in the Gulf of Mexico found evidence of intraguild competition and predator—prey interactions primarily mediated by bull sharks *Carcharhinus leucas* (Lear et al. 2021). Smaller species, such as blacktip sharks *C. limbatus*, showed habitat shifts following the diel patterns of larger competitors and predatory sharks. Batoid species also influence the marine community by altering predator distribution and driving changes in benthic ecosystems through predation of benthonic species (Flowers et al. 2021). For example, Ajemian et al. (2012) found that changes in the abundance and size of spotted eagle rays *Aetobatus narinari* in Bermuda can result in shifts in the density of their preferred mollusk prey. The authors suggested that moderate impacts on restoration programs caused by an increased number of spotted eagle rays underscore the need for further species-association focused studies.

The Eastern Tropical Pacific (ETP) is a vast ecoregion that extends along the Pacific Coast from southern Mexico to northern Peru, hosting a diverse community of co-occurring elasmobranch species (Navia et al. 2024). Cocos Island National Park (hereafter Cocos Island) is unique within the ETP for its systematic long-term monitoring of elasmobranch communities. Cocos Island was established in 1978, and its marine protected area expanded from 5 km^2 in 1984 to its current 54 844 km^2, playing a vital role in Costa Rica's cultural, economic, and natural heritage (Casto-Campos 2022). Despite its small size of 28.8 km^2, Cocos Island is globally recognized for its rich biodiversity, serving as a critical hotspot (Moreno et al. 2021) for marine endangered species and migratory macropredators (Nalesso et al. 2019, Klimley et al. 2022). However, the elasmobranch community at Cocos Island has undergone population shifts beyond the expected seasonal variability in the area during recent years. White et al. (2015) observed changes in elasmobranch population dynamics in shallow waters, driven by both climatic and oceanographic factors. The authors noted that although environmental conditions were important for most elasmobranch species, others were increasing in number regardless of yearly variations in temperature and productivity. Osgood et al. (2021) further addressed the changes in the Cocos elasmobranch community by suggesting that acute temperature anomalies may be pushing more mobile and migratory species, such as scalloped hammerheads *Sphyrna lewini*, away from the island. Saltzman & White (2023) revealed that the abundance of common filter-feeders, such as the mobula rays *Mobula* spp., at Cocos Island is moderately influenced by temperature shifts, only vaguely associated with primary productivity.

Recent studies suggest that competition and niche partitioning may play a role in shaping elasmobranch assemblages in the ETP (Estupiñán-Montaño et al. 2018, 2024). However, research on competition, niche partitioning, and network connectivity within the ETP predator populations remains limited. The diversity and long-term monitoring programs at Cocos Island make it a unique case study for evaluating elasmobranch network dynamics and ecological associations. Recent evidence suggests that migratory species such as scalloped hammerheads experience behaviorally mediated niche compression in the presence of larger predators and competitors in Cocos Island (Espinoza et al. 2024), yet the broader impacts of predator and competitor exclusion on community structure are not well understood. Saltzman et al. (2024) examined the changes in Cocos Island marine communities caused by the arrival or establishment of large predators such as Galapagos *Carcharhinus galapagensis* and tiger sharks that were uncommon or absent in the 1990s. The arrival (or return) of large predators to Cocos Island may reflect the combined effects of local marine protection and intensified fishing in unprotected oceanic regions in the ETP (Espinoza et al. 2020). As such, Cocos Island represents a unique model for understanding community shifts in the ETP and other elasmobranch communities facing similar challenges. Further analysis of species associations and network dynamics may improve our understanding of the ecological processes shaping elasmobranch communities.

In this study, we investigated temporal shifts in network structure and diversity within the elasmobranch community of Cocos Island, Costa Rica. We also analyzed species associations to elucidate potential associative interactions and intraguild competition in Cocos Island. Our specific objectives were as follows: (1) evaluate changes in the ecological network and biodiversity of the Cocos Island elasmobranch community using a long-term database (1993–2019). Given the shifts in the Cocos Island elasmobranch community, we hypothesize that these changes will be reflected in the network and biodiversity metrics of the community. (2) Determine how seasonal variation, environmental variables, and species associations affect elasmobranch abundance in Cocos Island using hierarchical models. Since different species show different responses to environmental variables and the presence of large predators seems to affect the presence and abundance of other elasmobranchs, we hypothesize that seasonality and species associations will affect the abundance of some species. (3) Infer potential interspecific associations in the Cocos Island elasmobranch community using our hierarchical model outputs. Given the range of strategies elasmobranchs have developed to partition their resources and the narrow trophic niches they often occupy, we hypothesize that the abundance and community shifts of less dominant and migratory species would be most affected by the relative abundance of competing or dominant species.

2. MATERIALS AND METHODS

Cocos Island National Park (5° 31′ 8″ N, 87° 4′ 18″ W) is a small (28.8 km^2), uninhabited island located 550 km off Costa Rica. Cocos Island experiences 2 seasons: wet, from June to November, and dry, from December to May. The island is a hotspot for marine biodiversity due to its isolation, complex geomorphology, and the influence of several sea currents (Garrison 2006). Cocos Island is a tropical marine environment, with sea surface temperatures ranging from 24 to 30°C, and it experiences thermal anomalies such as El Niño Southern Oscillation (ENSO), caused by the strengthening and weakening of oceanic currents (Osgood et al. 2021). Being a National Park, Cocos Island is an attractive site for wildlife tourism, with several companies taking more than 1900 tourists on diving trips to the island during the year (Moreno et al. 2021). The 54 844 km^2 marine protected area around Cocos Island is a no-take zone, where only research, tourism, and sustenance activities are allowed. Despite the flourishing tourism industry on the island and its long-standing status as a protected national park, illegal fishing activities and proper law enforcement remain the main conservation challenges for the area (Casto-Campos 2022).

We analyzed 35 706 citizen science underwater visual censuses (UVCs) collected between 1993 and 2019 by 53 experienced diving guides from the Undersea Hunter Group (www.underseahunter.com) across 17 distinct dive locations, grouped into 13 sites within the 54 844 km^2 marine protected area of Cocos Island (Fig. 1). We merged sites within 1 km of each other, resulting in inter-site distances ranging from approximately 1 to 41 km (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/meps15053_supp.pdf). UVCs occurred within sites relatively close to one another; therefore, we accounted for observations

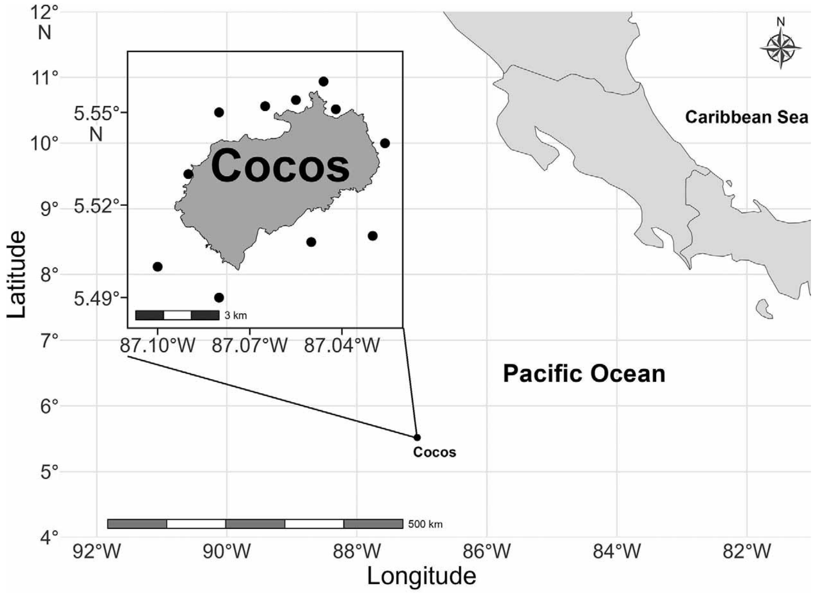

Fig. 1. Study site: Cocos Island, Costa Rica. Inset plot shows the actual contour of Cocos Island and its coordinates. Points show the approximate location of dive sites. See Fig. S1 for dive site names

among all sites by merging observations of all sites around Cocos Island. Given the large size and mobility of elasmobranchs at Cocos Island, we pooled species counts across sites to maintain biological relevance. All sampled sites were within the limits of the marine protected area of Cocos Island. We retained site-level resolution for network analyses where spatial variation may be important. When multiple divers recorded the same species on a given day, we averaged counts across observers. Divers collected sea water column temperature using their dive computer and estimated visibility in meters on site. Average dive time was approximately 40 min, with depth ranging from 25 to 32 m, remaining consistent over time for each site despite not being standardized as scientific UVCs. Divers used a standardized data sheet to record abundance estimates of 12 elasmobranch species (Table S1), of which 7 are listed as important pelagic species in the latest management plan for Cocos Island. Eagle rays, marbled rays *Taeniurops meyeni*, and whitetip reef sharks *Triaenodon obesus* were present year-round and therefore we considered them resident species of Cocos Island (Fig. S2); we considered the rest as migratory species for the purposes of this study. Additionally, we included sea turtles *Chelonia* spp. in our analysis due to their role as prey for large shark species. Blacktip *Carcharhinus limbatus*, Galapagos *C. galapaguensis*, and tiger sharks *Galeocerdo cuvier* were initially recorded only as observational notes, with systematic counts introduced after 2003 (Fig. S2). We only used UVCs records collected by experienced dive guides trained with photographic guides as an additional effort to standardize the quality of our citizen-science database and reduce misidentification of morphologically similar species of sharks. We grouped all the easily confounded species from the genus *Mobula* into a single category. We attempted to further reduce error by including visibility as a covariate and the total number of dives in a day as an offset term (Kéry & Schaub 2012).

2.1. Network analysis

We examined the ecological network of the elasmobranch community in Cocos Island from 1993 to 2019 using indirect network analysis. We built separate networks for each year and season. We separated years into seasons to account for the natural variation in Cocos Island during the wet (June—November) and dry (December—May) seasons. Thus, we ended with a separate network for each year—season combination (e.g. dry 1993, wet 1993, dry 1994, etc.). We represented each species as nodes in our network, with node size showing species abundance. Lines between nodes or 'edges' show species associations within the same period. We measured changes in the Cocos Island elasmobranch network across each season—year combination by using a simplified version of the network strength metric described by Barrat et al. (2004), calculated as:

$$\text{Strength} = \sum_{j=1}^{N} a_{ij} w_{ij} \quad (1)$$

where a_{ij} is the node degree or number of reciprocal connections of each species node i to other nodes j, with a maximum value of 24 (12 other species) for network N; w_{ij} is the edge weight, representing the number of co-occurrences on the same day between 2 species for each species pair ij. We show edge weights as the relative line thickness in network figures.

We used the 'iGraph' package (Csárdi & Nepusz 2006) in R programming version 4.4.1 (R Core Team 2016) to construct and visualize networks. We then evaluated significant changes in network metrics across years and seasons using linear regression models, with network strength as the response value and year and season as explanatory variables (Table S2). Additionally, we analyzed network metrics at each of the 13 most frequently visited dive sites around Cocos Island (Fig. S1). For each site, we built separate networks by season and year, allowing us to identify local deviations from the island-wide network patterns.

2.2. Diversity analysis

We used the 'vegan' package (Oksanen et al. 2022) in R to perform diversity and similarity analyses. We calculated the Hill-transformed Shannon diversity index at yearly and monthly scales to assess temporal changes in species diversity. The Hill index accounts for both species richness and evenness, expressing diversity as the effective number of species (Chao et al. 2014). We then modeled diversity over time using linear regressions with Hill values as the response variable and year or month as predictors (Table S2).

We used Bray-Curtis dissimilarity matrices to quantify differences in species composition with years and months as sampling units. We applied an analysis of similarities (ANOSIM) to our dissimilarity matrices to test for significant temporal shifts. We performed a similarity percentage (SIMPER) analysis on the Bray-Curtis dissimilarity matrices to identify the relative contribution of each species to dissimilarity between paired years (Clarke 1993).

2.3. Interactive association models

Our network and diversity analysis examined interspecific interactions as a function of the joint presence of elasmobranch species. Although informative, indirect network analysis does not account for how a species' occurrence and abundance relate to those of other species. Therefore, we also analyzed our data with hierarchical regression models ('interactive association models') using a Bayesian framework. We grouped data by week to make this analysis computationally tractable.

We performed our analysis with the package 'r2jags' (Su & Yajima 2024), interfacing the R coding language with JAGS, a Bayesian analysis software (Plummer 2017). We ran 10 000 iterations with a 1000-iteration burn-in and 3 chains to obtain model convergence (Zuur et al. 2009). We did not apply thinning to our models since it is computationally inefficient and unnecessary for ecological models (Link & Eaton 2012). Before running our models, we applied a correlation analysis among our model covariates (each species, year, week, sea surface temperature, and visibility) and merged covariates over the acceptable correlation cutoff of 0.7 (Dormann et al. 2013). We built separate models for each independent species with diffuse priors as slope and intercept terms, and environmental variables as well as the abundance of every other species as covariates. We considered the effect of a covariate significant if the 95% credible interval did not cross zero, indicating a consistent result across posterior samples (McElreath 2015).

We interpreted significant associations between the response variable and species covariates as indicators of potential species interactions. While species correlations are not evidence of causation, we propose that they offer theoretical support for ecological relationships that future studies could validate. We categorized associations into 3 types: (1) competition; encompassing direct and indirect ecological interactions (Twining et al. 2025). We inferred competition when species were negatively correlated, and no direct evidence exists of predator–prey interactions. We attempt to provide supporting literature examples for potential interference or indirect intra-guild competition. (2) Predation; defined as predator–prey interactions, including avoidance behavior. We identified predation when prey abundances were negatively associated with predator covariates, or when predator associations increased due to prey presence. Intraguild predation can drive spatial segregation and refuge use by prey (van Zinnicq Bergmann et al. 2024), making negative associations a potential indicator of predator–prey dynamics. (3) Environmental preferences; defined as positive correlations between species sharing similar thermal or seasonal niches or negative correlations among species with contrasting preferences. We based our inferences on patterns observed in previous studies at Cocos Island (Osgood et al. 2021, Saltzman & White 2023).

We modeled species abundance through a negative binomial distribution expressed as a Poisson model with a diffuse overdispersion term, ε, and diffuse priors for each covariate. We chose this distribution to address the overdispersion caused by the contrasts between counts for rare and abundant species (Zuur et al. 2009). The base equation for this model was:

$$\text{Counts}_i \sim \text{Poisson}\left(\lambda_i\right) \tag{2}$$

where λ_i represents the expected counts during the ith week, according to the following equation:

$$\begin{aligned}\log\left(\lambda_i\right) = \alpha + \beta_{\text{week}} \times \text{WeekCyclic}_i + \beta_{\text{visibility}} \times \\ \text{Visibility}_i + \beta_T \times T_i + \beta_{\text{Year}} \times \text{Year}_i + \\ \beta_j \times \text{Count}_{ji} + \log\left(\text{offset}_i\right)\end{aligned} \tag{3}$$

We transformed weeks using a sin–cosine cyclic transformation to account for seasonal variation, representing them as 'WeekCyclic' in our models. We chose to only include water temperature (T) and visibility as environmental variables since they have previously been demonstrated to have an impact on the relative abundance of elasmobranchs in the area (White et al. 2015, Osgood et al. 2021). We included the counts of other species as covariates in the model through a log link function in λ_i for each ith weekly observation for each j species, where offset_i equals the number of dives performed for each ith week; α and β are the slope and intercept terms, respectively.

We built separate logistic binomial models for blacktips, eagle rays, and manta rays due to their low abundance as:

$$\text{Counts}_i \sim \text{Bernouli}\left(\rho_i\right) \tag{4}$$

We used a logit link function instead of a log link; otherwise, the model equation followed the same formulation as the overdispersed Poisson.

We evaluated model convergence by inspecting posterior trace plots and comparing simulated samples from the posterior distribution against observed species counts. We evaluated our model sensitivity to species covariate removal by excluding turtles as a predictor, checking for significant changes in model outputs. We evaluated temporal sensitivity by fitting a model using the last 5 yr and comparing model outputs.

3. RESULTS

3.1. Network analysis

Our analysis showed that the elasmobranch network in Cocos Island shifted over time from fewer interactions in both seasons (prior to 2006) towards a more interconnected community (after 2006, more noticeable in recent years) (Fig. 2). Network strength increased significantly over time and during the wet season with the lowest mean (±SD) strength being 19.4 ± 4.36 in the 1997 dry season, and the highest being 142.34 ± 16.43 in the 2014 wet season (R^2 = 0.65, *t*-test: df = 50, $p < 0.001$; Table S2). More species co-occurred in recent years and during the wet season, resulting in a reciprocal network where species pairs had a similar degree value (maximum connections between nodes of 24, for reciprocal connections between the 12 other species).

Site-by-site analysis followed a similar but more variable pattern, with most sites following the same yearly and seasonal trends (Fig. S3). Four sites (Manuelita, SharkfinRock, Silverado, and SubmergedRock) differed from the observed network patterns, showing either a decrease in network strength over time or a lack of seasonal differentiation in network strength.

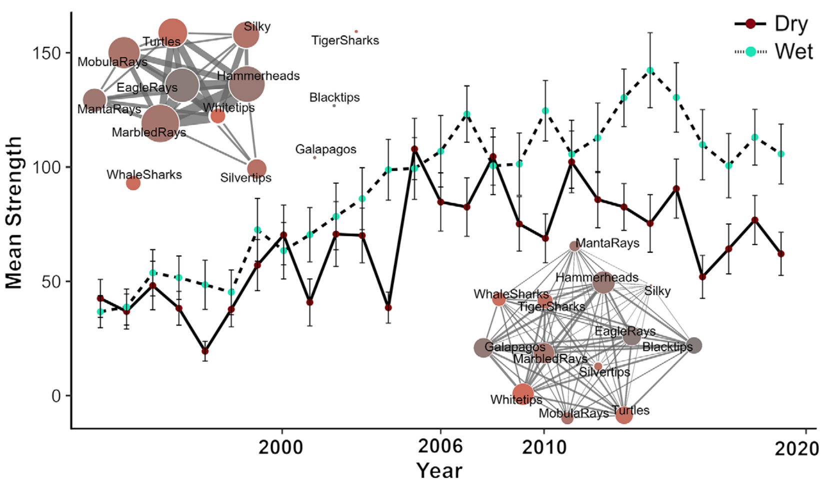

Fig. 2. Network dynamics through time in the Cocos Island elasmobranch community. Mean network strength is represented by lines for the dry and wet seasons; whiskers: ±SD. Neural networks plots show the most representative networks. Left: 1997 dry season, least interconnected; right: 2014 wet season, most interconnected. Node size (relative abundance) and edge thickness (association frequency) are scaled within each year for visualization and are not directly comparable across years

3.2. Diversity analysis

Annual Hill diversity ranged from 2.26 to 3.09, with a slight but non-significant increase in diversity after 2003 due to the arrival and increased abundance of blacktip, Galapagos, and tiger sharks over time (Fig. 3a). We observed the lowest diversity in 1998 and the highest in 2006. We did not find any significant variations in monthly species diversity, with Hill values ranging from 2.6 in March to 2.84 in November (Fig. S4).

ANOSIM results supported the network statistics, as we observed a strong and significant separation in community composition between consecutive years (ANOSIM, R = 0.32, $p < 0.001$) with lower mean dissimilarity values from 2006 onwards. Dissimilarity percentages ranged between 25 and 55% (Fig. 3b). The monthly variation showed a weak but significant level of separation in community composition (ANOSIM, R = 0.06, $p < 0.001$). Monthly dissimilarity percentages ranged between 35% (October) and 42% (April) (Fig. S5).

SIMPER analysis identified 3 species as the primary contributors to dissimilarity: scalloped hammerhead sharks, whitetip reef sharks, and marbled rays (Fig. 3c). Scalloped hammerheads were the dominant contributors to dissimilarity in most years (303 out of 351 pairs of years), with their contribution ranging from 9.9 to 64.32% of between-year dissimilarity. Whitetip reef sharks followed (48 pairs of years), contributing between 7.6 and 64%, whereas marbled rays consistently contributed the least among the top 3 species, with a range of 0.13 to 13.34%.

3.3. Interactive association models

The correlation analysis for our models showed no covariates with correlation values beyond the 0.7 or −0.7 collinearity cutoff with another covariate (Fig. S6). Excluding non-biological covariates, the highest correlation value observed between species counts was 0.48 (between marbled rays and whitetips), and the lowest correlation value was −0.17 (between Galapagos and whitetip reef sharks).

All models converged with relatively accurate predictions for mean occurrences of the species studied. We observed the highest differences

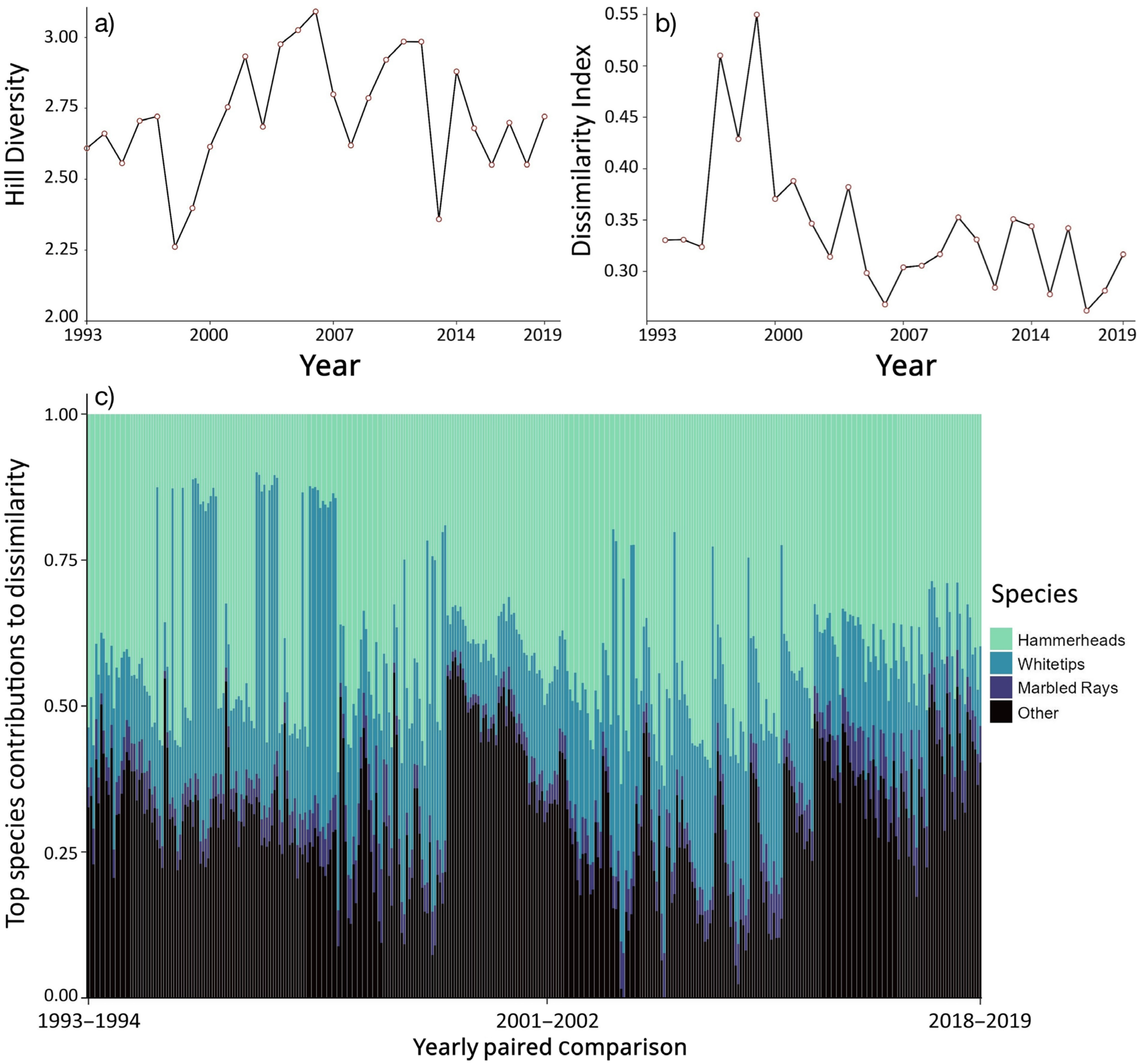

Fig. 3. Temporal analysis of species diversity and community composition in the elasmobranch community of Cocos Island. (a) Yearly Hill diversity index, with each point representing average diversity for a given year over the study period. (b) Bray-Curtis dissimilarity percentages between consecutive years. (c) Contribution of the top 3 species (scalloped hammerheads, whitetip reef sharks, and marbled rays) to the overall dissimilarity, determined by SIMPER analysis. The *x*-axis shows each paired year in ascending order, with the first vertical bar representing the dissimilarity between 1993 and 1994, followed by 1993 against 1995, and so on

between observed and predicted counts for scalloped hammerhead and whitetip reef sharks, the most abundant species (Fig. S7). We observed lower predictive power for the more abundant species, as expected due to the high number of individuals during certain periods of time. Errors were relatively small, with average weekly differences between observed and modelled abundances ranging from −2.5 to 5 individuals.

Model outputs remained largely unchanged when excluding turtles as a covariate, demonstrating the robustness of our approach (Fig. S8). However, time variability and sample size influenced the 2014–2019 models, where overall trends remained consistent but some species interactions lost statistical significance (Fig. S9). Notably, no significant associations switched from positive to negative or vice versa (Table S3).

In total, 8 out of the 13 species studied showed a significant declining trend in abundance, with only 3 species showing a positive trend (Table 1, Fig. 4). Temperature had a significantly negative effect on 6 species, with eagle rays being the only species positively associated with an increase in temperature. Visibility had a weak but significant negative effect on Galapagos and whitetip reef sharks. Seasonal variation, represented as the cyclic week of the year, had a significantly negative effect (decrease in occurrence during certain seasons) for scalloped hammerheads, silky sharks, and whale sharks, and a positive effect for mobulas, Galapagos, tiger and whitetip reef sharks.

We found 55 significant associations between species, 32 of which were negative associations (Fig. 4). We show detailed model covariates, including non-significant results, in Table S4. We observed the strongest negative associations between silvertip reef sharks and tiger sharks (mean ± SD: −0.39 ± 0.09), tiger sharks and marbled rays (−0.35 ± 0.11), and turtles and tiger sharks (−0.29 ± 0.05). We observed the strongest positive effects between eagle rays and silky sharks (0.44 ± 0.21), eagle rays and silvertips (0.43 ± 0.22), and blacktips and Galapagos sharks (0.43 ± 0.11).

4. DISCUSSION

We used a novel combination of network analysis, diversity metrics, and ecological modeling to provide an evaluation of elasmobranch community dynamics in the ETP. Our results corroborate past work on the continued decline of several key elasmobranch species (Fig. 4). Recent studies suggest that Cocos Island's elasmobranch community is undergoing a shift in species composition (White et al. 2015, Espinoza et al. 2020). Potential drivers of community change include the increasing frequency of sea surface temperature anomalies (Osgood et al. 2021, Saltzman & White 2023), the continued decline of the most abundant elasmobranch species, and the arrival of new predators and competitors to the system (Espinoza et al. 2024, Saltzman et al. 2024).

Our diversity and network analysis suggests that changes in the Cocos Island elasmobranch community are driven by complex ecological processes in addition to the previously reported declines in species abundances. Notably, the primary contributors to yearly dissimilarity remain the most abundant yet rapidly declining species: scalloped hammerhead sharks, whitetip reef sharks, and marbled rays. Scalloped hammerhead sharks are migratory animals, frequenting Cocos

Table 1. Significant species interactions. Abiotic predictors: number of significant effects for the species among our week, visibility, water temperature, and year covariates; predictor species: count of significant species covariate effects. Inferred associations show the number of significant interactions attributed to each hypothesized species interaction (competition, environmental preference, predation). We only accounted for significant effects (95% credible interval for posterior distribution did not cross zero)

Species	Common name	Population	Abiotic predictors	Predictor species	Inferred associations: Competition	Environmental	Predation
Carcharhinus limbatus	Blacktips	Increase	1	3	0	3	0
Aetobatus narinari	Eagle rays	Stable	1	5	0	3	2
Carcharhinus galapagensis	Galapagos	Increase	4	8	0	5	3
Sphyrna lewini	Hammerheads	Decrease	3	4	0	4	0
Mobula birostris	Manta rays	Decrease	1	3	0	3	0
Taeniurops meyeni	Marbled rays	Decrease	2	8	0	4	4
Mobula spp.	Mobula rays	Decrease	3	2	0	1	1
Carcharhinus falciformis	Silky	Decrease	2	4	0	4	0
Carcharhinus albimarginatus	Silvertips	Decrease	1	2	1	1	0
Galeocerdo cuvier	Tiger sharks	Increase	2	4	1	1	2
Chelonia spp.	Turtles	Decrease	2	7	0	4	3
Rhincodon typus	Whale sharks	Stable	1	2	0	2	0
Triaenodon obesus	Whitetip reef sharks	Decrease	4	7	0	6	1

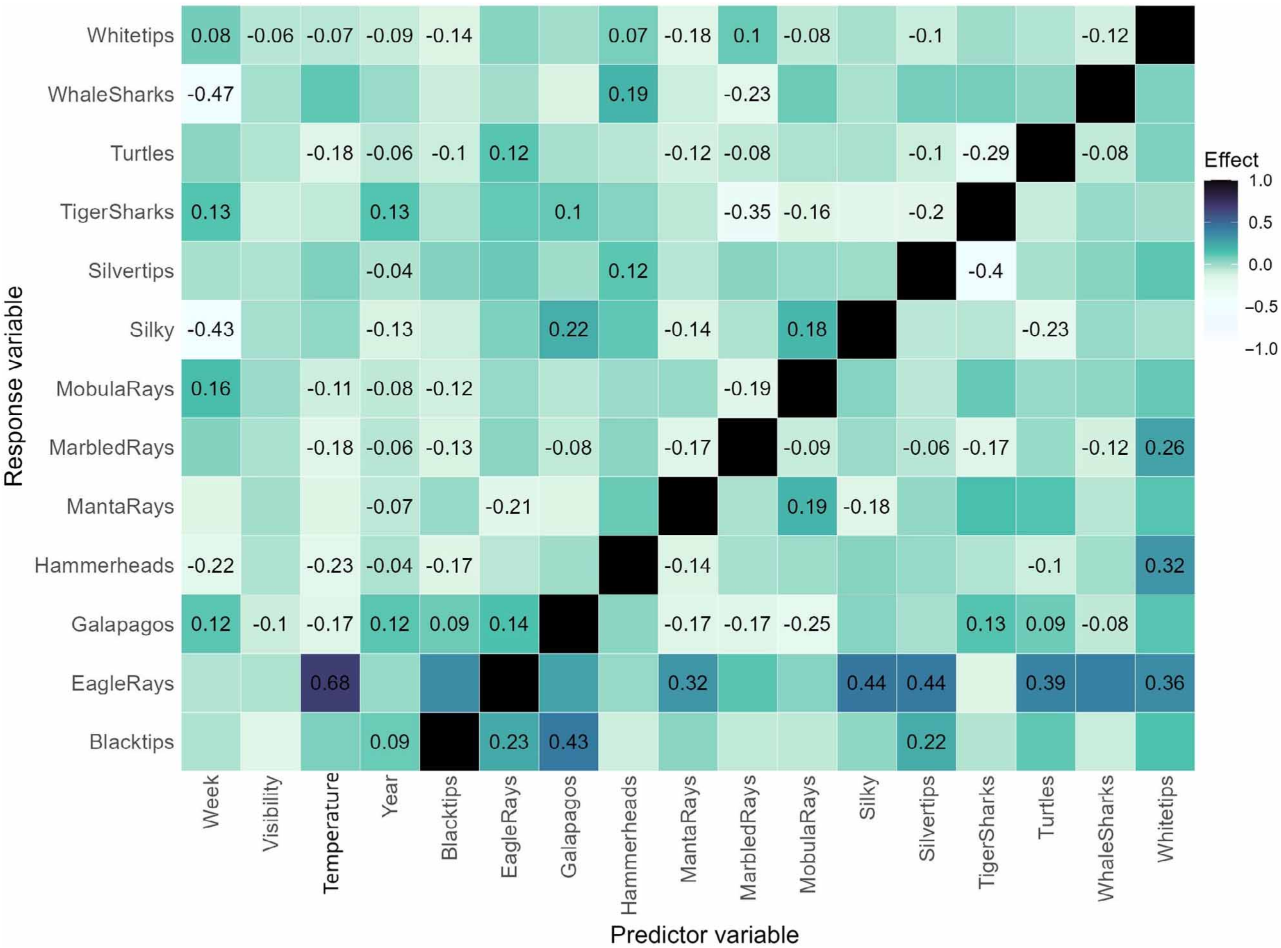

Fig. 4. Visualization of results from Bayesian models. Colors represent the mean posterior estimates of the Bayesian beta coefficients from each species interaction model. Response variables are shown on the *y*-axis; predictor variables are on the *x*-axis. Note that values are not mirrored due to the asymmetric nature of interactions. Darker colors: positive effects; lighter colors: negative effects. Cells with numbers highlight significant effects (95% credible interval for posterior distribution did not cross zero)

during the wet season and using the island as a navigational point for their long oceanic migrations across the ETP (Nalesso et al. 2019). Yearly variations in scalloped hammerhead shark abundance caused by their migration patterns and relatively high abundance explain their position as a dominant species in terms of community composition. Whitetip reef sharks and marbled rays are year-long residents who dominate the community when seasonal species leave Cocos Island (Garrison 2006).

Recent studies have shown the importance of Cocos Island for migratory species, which typically increase in abundance and diversity during the wet season (Nalesso et al. 2019, Espinoza et al. 2020, 2024, Klimley et al. 2022). The establishment of several oceanic marine protected areas (MPAs) in the central ETP has increased the abundance of large predators in non-take coastal and oceanic areas, with small predator competitors being displaced to unprotected fishing areas (Espinoza et al. 2020). Our results further corroborate this pattern by showing an increase in network strength caused by the arrival of the migratory blacktip, Galapagos and tiger sharks to the area, and their increased numbers during the wet season. Peaks in network strength during the dry season of 2006 may have been caused by the arrival or return of blacktip, Galapagos, and tiger sharks to Cocos Island. Adult predatory sharks may be changing their spatial patterns around the island, moving from coastal 'nursery' sites, and expanding their movements and space use into the typical diving sites (Espinoza et al. 2024). We acknowledge that the shift to systematic data recording from presence−absence records of the 3 newcomer species might have influenced the increased network strength. However, we believe the change in methodology was a direct result of the increase in diversity and network connectivity in the elasmobranch community, and not the other way around.

Our observations suggest that the elasmobranch assemblage in Cocos Island is divided into 2 temporally distinct sub-communities, with strong differences in community composition showing after 2006. The asymptote in network strength after 2014 may suggest that the community has reached a new stability point. Frelat et al. (2022) observed a similar shift in network composition caused by changes in predator abundances in the North Sea. The authors mention that although trophic networks remained unchanged on a large spatial scale, local processes caused a noticeable shift in the long-term community composition. This is similar to how our diversity metrics could not capture the monthly variation in diversity, inconsequential at the large multi-species scale of the ETP, but network analysis reveals that local structure is shaped by resident species during the dry season and by more seasonal species during the wet season in Cocos Island.

4.1. Competition

We inferred that the negative effect of one species' abundance on another's abundance could be evidence of potentially competitive associations, where predation is unlikely or infrequent between associated species, but intraguild predation could be occurring with shared prey items. Our observations should be considered with caution, as the lack of evidence for direct predation in Cocos Island and our model outputs are not enough evidence to rule out that correlative rather than causational effects are at play here. Our results suggest that competition may be occurring between tiger sharks and silvertip sharks, probably driven by spatial and ecological overlaps (Espinoza et al. 2024). Even when other large sharks, such as silvertips, are not regularly preyed upon by tiger sharks, exploitative competition for shared prey items may be taking place in the waters around the island (White et al. 2015). Both shark species were significant negative predictors for marble rays, a potentially shared prey (Garrison 2006), which, along with other benthic prey items, may be causing intraguild competition for resources between silvertip and tiger sharks. Additionally, both species were significant negative predictors of sea turtle abundance. Our model cannot determine whether turtles actively avoid large sharks or whether their presence reduces silvertip encounters by indirectly attracting tiger sharks. Agonistic interactions between predatory sharks have been reported in areas such as New Caledonia, where silvertip sharks ignored highly attractive food sources in the presence of tiger sharks (Clua et al. 2013). Future studies in the ETP can attempt to capture direct evidence of our theorized competitive associations through methods already in use in the area that are capable of demonstrating trophic overlap, such as stomach content and stable isotope analysis (Estupiñán-Montaño et al. 2018), as well as remote underwater video methods (Espinoza et al. 2020).

4.2. Predation

Blacktip sharks are known to feed on rays in Cocos (Garrison 2006) and occasionally prey on mobulids in the ETP (Estupiñán-Montaño et al. 2018), which may explain the negative associations between the species we observed in our models. Galapagos and silvertip sharks are large predators also known to feed on rays at Cocos Island (Garrison 2006). The negative association between Galapagos sharks, silvertip sharks, and marbled rays suggests that either direct predation or predator avoidance is at play. Tiger shark presence correlated with lower turtle abundance, an expected result given the known predator—prey dynamic between tiger sharks and turtles in the area (Heithaus 2001, Saltzman et al. 2024). Blacktips and silvertips were negative predictors of whitetip abundance. Although direct predation of whitetips by blacktips or silvertips has not been documented, previous studies at Cocos Island suggest that larger predators may opportunistically prey on smaller whitetips (White et al. 2015). Fear of potential predators is a powerful driver of behavior-mediated responses, leading to local changes in the distribution of marine species and driving prey and competitors away from otherwise attractive habitats (Wirsing et al. 2008). Our results are not direct evidence of predation, but predator avoidance processes may play a part in the inverse association we observed between whitetip, blacktip, and silvertip sharks.

4.3. Environmental preferences

We found significant associations between species that could not be linked to predatory mechanisms or intraguild competition. We advise caution when interpreting our results, however, since unobserved ecological processes and unknown interactions with other species may be behind the observed association patterns. Highly mobile predators such as blacktip, Galapagos, and tiger sharks showed positive correlations, possibly reflecting shared habitat preferences (Hoffmayer & Parsons 2003, Papastamatiou et al. 2006, Estupiñán-Montaño et al. 2018). Previous studies identified the arrival of blacktip, Galapagos, and tiger sharks as potential drivers of community shifts at Cocos Island (White et al. 2015, Espinoza et al. 2024), likely influenced by fishing (Burns et al. 2023, Worm et al. 2024) and climate change (Osgood et al. 2021). Large species of predatory sharks are known to share spatial resources despite the presence of potential competitors (van Zinnicq Bergmann et al. 2024). We cannot confirm that resource overlap and competitor tolerance operate the same way at the island scale, but our models suggest that some degree of spatial and trophic overlap driven by environmental preferences may be occurring in Cocos Island. We found a negative association between blacktips and scalloped hammerheads. Although large blacktips can prey on juvenile hammerheads (Castro 1996), this is unlikely at Cocos Island, where hammerheads are primarily adults. Similarly, while great hammerheads *Sphyrna mokarran* are known to prey on blacktips (Doan & Kajiura 2020), there is no evidence of frequent predation of blacktips by the other large shark species at Cocos Island. Instead, the contrasting ecological strategies of blacktips and scalloped hammerheads likely explain their negative association. Scalloped hammerheads are mostly nocturnal pelagic squid feeders, typically seen schooling or at cleaning stations, whereas blacktips feed on coastal waters, primarily on fish and rays (Garrison 2006, Espinoza et al. 2024).

Our model outputs reinforced previous findings about the importance of seasonal variations in temperature for batoid species (Saltzman & White 2023), since mobulids and eagle rays co-occurred with species sharing environmental preferences such as silky sharks. Eagle rays showed a positive correlation with turtles but a negative correlation with manta rays, possibly indicating habitat partitioning or differences in thermal or seasonal preferences (Rastoin-Laplane et al. 2023). Marbled rays' association with whitetip reef sharks and mobulas may have been caused by the known habitat preferences of the species in Cocos (Garrison 2006). However, the reason for the negative correlation between marbled rays, turtles, and whale sharks is more nuanced. Marbled rays are abundant year-round residents at Cocos, while turtles and whale sharks are migratory species with very different ecological characteristics that may play a role in the observed negative associations. Similarly, mobula rays were negatively associated with coastal predators such as Galapagos, tiger, and whitetip reef sharks, and positively correlated with oceanic species like silky sharks and manta rays, supporting previous findings about shared habitat preferences (Saltzman & White 2023). However, determining if causation rather than correlation is driving the negative association of marbled rays and mobulas with non-predatory, non-competitor species is beyond the scope of this study.

4.4. Conclusions and future work

Our analysis evaluated interspecific interactions within the elasmobranch community at Cocos Island but omitted other species in the ecosystem. The individual models we used provide interpretable results relevant to our research questions, yet more complex methodological frameworks, such as joint species distribution models or matrix-based time series models (Ovaskainen et al. 2017), could better account for indirect effects and trophic web interactions. Implementing specialized analysis using currently available data would require either a more systematic sampling approach or additional methodological adjustments that are outside the focus of this work. We addressed the limitations associated with sampling effort in our study by implementing offset terms in our models and averaging species counts — methods often used to work around sampling limitations for modeling (Kéry & Schaub 2012). We additionally addressed human error by using only experienced dive guide surveys and incorporating visibility. Visibility was a significant predictor of species occurrence for Galapagos and whitetip reef sharks. While whitetip sharks are abundant, easily identifiable, and relatively sedentary organisms, Galapagos sharks can be easily confounded with the more abundant silky shark. Therefore, we advise caution when interpreting our results for Galapagos sharks. Additionally, only 19 out of 59 biological predictors across our interactive models remained significant when rerunning our models using only the last 5 yr of data (Fig. S9). The small subset of significant effects likely reflects the challenge of detecting subtle species interactions within a limited dataset, a problem overcome in the complete model by the uniquely long series of data collected from Cocos Island. Community shifts may be indicators of broader ecological restructuring rather than methodological issues, and are a phenomenon commonly observed in dynamic ecological networks (Landi et al. 2018). Future work could explore differences in community metrics and network dynamics between historical and recent datasets to further assess how the Cocos Island community is changing. We hope that the results of this study can serve as a stepping stone towards integrating multi-species frameworks in ecological modeling, providing a more comprehensive understanding of community dynamics for the effective management and conservation of marine ecosystems.

Data availability. Data used for this study belongs to the Undersea Hunter Group (www.underseahunter.com). and are available from the corresponding author upon request. Annotated code can be reviewed and branched from our GitHub repository at https://github.com/Miguelbirostris/CocosElasmoNetwork2025.

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