Inter-specific relationships and their ecological role in an oceanic elasmobranch community

Miguel de Jesús Gómez García*[1], Remington J. Moll[2], Alex Hearn[3,4], Mario Espinoza[3,5,6], Easton R. White[1]

[1] Department of Biological Sciences, University of New Hampshire, Durham, New Hampshire, USA.
[2] Department of Natural Resources and the Environment, University of New Hampshire, Durham, New Hampshire, USA.
[3] MigraMar, Bodega Bay, CA 94923, USA.
[4] Universidad San Francisco de Quito USFQ/Galápagos Science Center, Quito, Ecuador
[5] Centro de Investigación en Ciencias del Mar y Limnología, Universidad de Costa Rica, San Pedro, San José 11501-2060, Costa Rica.
[6] Escuela de Biología, Universidad de Costa Rica, San Pedro, San José 11501-2060, Costa Rica.

*Correspondence author: miguel.gomezgarcia@unh.edu

- **Journal of Animal Ecology**

Abstract

Marine ecosystems support a diverse array of co-occurring species, whose presence and abundance influence the behavior, population dynamics, and distribution of interacting organisms. Elasmobranchs play a central role in marine ecological processes as top and meso-predators across various ecosystems. Previous work has shown that some elasmobranchs are key to ecosystem health and resilience, regulating communities through competitive, predatory, and territorial interactions. However, few studies have evaluated the effect of interspecific interactions on the abundance and diversity of individual populations in marine ecosystems, partly due to the difficulty of obtaining long-term data on species co-occurrence. Our objective was to analyze elasmobranch species co-occurrence in Cocos Island National Park in the Eastern Tropical Pacific and its effect in species abundance, diversity, and interactions within the community. We analyzed a 26-year underwater visual survey dataset through network statistics, diversity indices, and Bayesian species interaction models. Here we show that the elasmobranch community in early 1990s shifted from a sparse, low richness network to a more diverse, densely connected community in the late 2010s, with diversity peaking in 2006. We identified three types of species interactions within the elasmobranch community: competition, predation, and ecosystem preference. The Scalloped hammerhead (*Sphyrna lewini*) and Whitetip reef (*Triaenodon obesus*) sharks were the main contributors to year-to-year variations in diversity. In addition, most species had a negative relationship with the co-occurrence of other elasmobranchs, underscoring the importance of potential competitive and predatory interactions. Our findings offer valuable insights for marine conservation efforts, particularly for understanding how interspecific interactions and ecological processes influence ecosystem stability over time. Our study provides a framework for future research on species co-occurrences in marine ecosystems, emphasizing the need for integrated, interaction-focused models that can better predict ecosystem responses to threats like overfishing and environmental change.

Resumen

Los ecosistemas marinos sostienen un diverso conjunto de especies, cuya abundancia afecta el comportamiento, dinámica poblacional y distribución de los organismos con los que interactúan. Los elasmobranquios juegan un papel central en los procesos ecológicos marinos al ser meso-depredadores y depredadores tope en diversos ecosistemas. Estudios demuestran la importancia de los elasmobranquios para la salud y resiliencia de los ecosistemas, regulando a las comunidades marinas mediante procesos de competencia, depredación y territorialidad. No obstante, pocos estudios han evaluado el efecto que las interacciones interespecíficas ejercen sobre la abundancia y diversidad de las poblaciones en ecosistemas marinos, debido en parte a la difícil tarea de recolectar datos de coocurrencia de especies a largo plazo. Nuestro objetivo fue analizar la coocurrencia de elasmobranquios en el Parque Nacional Isla del Coco en el Pacífico Oriental Tropical, y su efecto en la abundancia, diversidad e interacciones de las especies en su comunidad marina. Analizamos 26 años de datos obtenidos de censos visuales submarinos a través de estadísticas de redes, índices de diversidad y modelos interactivos Bayesianos. Demostramos que la comunidad de elasmobranquios pasó de ser una red dispersa con riqueza más baja en los 1990s, a una comunidad más densamente conectada y diversa en los 2010s, con un poco de diversidad en 2006. Identificamos tres tipos de interacciones entre especies en la comunidad de elasmobranquios: competencia, depredación y preferencias ecosistémicas. Los tiburones martillo común (*Sphyrna lewini*) y puntas blancas de arrecife (*Triaenodon obesus*) fueron los principales contribuyentes a la variación anual de diversidad. Adicionalmente, la mayoría de las especies mostró una relación negativa con la coocurrencia de otras especies de elasmobranquios, resaltando la importancia de las potenciales interacciones competitivas y de depredación. Nuestros descubrimientos ofrecen una línea base para futuros estudios sobre la coocurrencia de especies en ecosistemas marinos, y enfatizan la necesidad de producir modelos integrados basados en interacciones para predecir de mejor manera la respuesta de los ecosistemas a amenazas como la sobrepesca y el cambio climático.

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 competitors (Lear et al., 2021) as well as ecosystem structure (Carrier et al., 2012). However, evaluating competitive, predatory and ecologically driven species interactions is challenging due to logistic 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 competition and predator mediated effects (Twining et al., 2024). Species co-occurrence models and indirect network analysis have emerged as a powerful tool for capturing relevant ecological properties such as tropic and competitive interactions (Russo et al., 2022). By evaluating the relationship between co-occurring species and community composition, we can indirectly provide evidence for complex ecological proses that shape species interactions and affect community resilience (Frank et al., 2005). Understanding the effects of species co-occurrence is crucial for evaluating the ecological health of systems providing services to stakeholders, and the economic stability of said ecosystem services (Frank et al., 2005). Similarly, local processes mediated by behavioral shifts, predation and competitive interactions have been shown to affect national and local stakeholders' economies (Dill et al., 2003; Gregr et al., 2020). Despite the nuanced process of factoring species interactions into management models, biologically appropriate ecological models that factor species abundance and co-occurrence can shed light over complex ecosystems (Twining et al., 2024), and provide better tools for mitigating economic impacts for local and international stakeholders (Ferretti et al., 2020; Frank et al., 2005).

As top predators and meso-predators, elasmobranchs play critical roles in regulating marine ecosystems through direct and indirect interactions with their prey and competitors (Dedman et al., 2024; Flowers et al., 2021; Lear et al., 2021). For example, A study in Western Australia demonstrated behaviorally mediated niche shifts in dugongs (Dugong dugon) following the arrival of tiger sharks (*Galeocerdo cuvier*) (Dill et al., 2003). The presence of tiger sharks also displaced non-prey competitors, such as dolphins, from otherwise attractive foraging areas. Similarly, a study of six shark species in the Gulf of Mexico revealed local changes mediated by diel patterns of site use by sharks, as well as evidence of larger species such as tiger and bull sharks (Carcharhinus leucas) excluding smaller species such as blacktip sharks (Carcharhinus limbatus) (Lear et al., 2021). Batoid species also play an important role in ecosystem function as meso-predators and benthic feeders (Flowers et al., 2021). Ajemian et al. (2012) evaluated the impacts of an increase in spotted eagle ray (*Aetobatus narinari*) population in Bermuda. Authors found shifts in preferred mollusk prey items according to eagle rays' size and prey density, suggesting moderate impacts on restoration programs caused by an increased number of rays, and underscoring the need for further interaction focused studies. Addressing gaps in the analysis of multi-species networks, predator co-occurrence, and competition-driven community shifts is crucial for understanding and managing complex marine systems (Hollowed et al., 2000; van Zinnicq Bergmann et al., 2022).

The Eastern Tropical Pacific (ETP), is a vast ecoregion which 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. As one of the world's oldest oceanic marine protected areas (MPAs), Cocos Island plays a vital role in Costa Rica's cultural, economic, and natural heritage (Salas et al., 2012). Despite its small size of 28.8 km2, Cocos Island is recognized globally for its rich biodiversity, serving as a critical hotspot (Moreno et al., 2021) for marine endangered species and migratory macropredators (Klimley et al., 2022; Nalesso et al., 2019). However, the elasmobranch community at Cocos Island has undergone population shifts beyond the expected seasonal variability in the area during recent years. For example, 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 species, others were increasing in number regardless of yearly variations. Osgood et al. (2021) further addressed the changes in Cocos elasmobranch community by suggesting that acute temperature anomalies may be pushing more mobile and migratory species away from the island. Abundant species, such as scalloped hammerhead sharks and mobula rays, exhibited strong but inconsistent responses to temperature changes, indicating the potential influence of additional, unidentified factors such as seasonal patterns and biotic interactions. Saltzman and White (2023) on the other hand, examined environmental and biological drivers of filter feeder abundance at Cocos Island, finding that while some species responded strongly to temperature shifts, other species were only vaguely associated with factors such as primary productivity. Thus, recent research on Cocos Island elasmobranch communities underscores the need to explore alternative sources of variation in both seasonal and yearly community dynamics.

Despite continued interest in Cocos Island as a case study for elasmobranch community processes, research on competition, niche partitioning, and network connectivity within its predator populations remains limited. While some studies highlight the role of competition and niche partitioning in the Eastern Tropical Pacific (Estupiñán-Montaño et al., 2017, 2024), the ecological and behavioral effects of species co-occurrence at Cocos Island remain largely unexplored. Evidence suggests that certain species experience behaviorally mediated niche compression in the presence of larger predators and competitors (Espinoza et al., 2024), yet the broader impacts of predator and competitor exclusion on community structure are not well understood. Notably, Saltzman et al (2024) examined the changes in Cocos Island marine communities caused by the arrival or establishment of large predators such as Galapagos and Tiger sharks that were relatively uncommon or absent in the 1990s. The authors reported a 43% decline in the relative abundance of migratory sea turtles, an effect likely driven by tiger shark predation, but accentuated due to illegal fishing and external migration-related mortality. Further analysis of predator co-occurrence and network dynamics is essential to better understand the ecological processes shaping Cocos Island's elasmobranch community.

In this study, we investigate the network structure and shifts in diversity of the elasmobranch community in Cocos Island, Costa Rica. We also analyzed the effects of elasmobranch species co-occurrence in Cocos Island and its effect within the community. We hypothesize our analysis will allow us to infer which species interactions are taking place, and if these interactions could be caused by competition between species, predation, or as a response to environmental preferences. Our specific objectives were to: 1) evaluate ecological network and biodiversity metrics using a long-term database (1993-2019) of the elasmobranch community; 2) assess changes in seasonal trends in the elasmobranch community of Cocos Island; and 3) determine the effect of including species interactions as a covariate in ecological models. Given the range of strategies elasmobranchs have developed for resource partitioning and the narrow trophic niches these organisms occupy, we hypothesized 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.

Materials and methods

Cocos Island National Park (N 05°31'08'', W 87°04' 18'') is a small (28.8 km^2) uninhabited Island located 550 km off Costa Rica. Cocos Island experiences two seasons, wet from June to November and dry from December to May. The Island is a hotspot for marine biodiversity thanks to its isolation, complex geomorphology and the influence of several sea currents (Garrison, 2006). Cocos Island is a tropical marine environment with waters ranging from 24 to 30 °C in sea surface temperature, and 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 to diving trips to the island most of the year (Moreno et al., 2021). Despite the flourishing tourism industry in the island and its long-standing status as a protected national park, illegal fishing activities and proper law enforcement remain as the main conservation challenges for the area (Arias et al., 2016).

We used underwater visual census data collected from 1993 to 2019 by experienced diving guides (n = 53) from the Undersea Hunter Group (underseahunter.com), resulting in a total of 35,706 dives at 17 sites around Cocos Island (Figure 1). This dataset is one of the largest and longest-running underwater visual censuses (UVC) for elasmobranchs (Osgood et al., 2021). Average dive time was approximately 40 minutes, 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 observed numbers of the most common elasmobranch species. Species were recorded as either the presence/absence or counts of 12 species of elasmobranchs including filter feeders, meso-predators and top-predators (Supplementary Table 1). We merged species of the genus Mobula in a single category due to their spatial and temporal overlap excluding manta rays (*Mobula birostris*). Additionally, we included sea turtles (*Chelonia spp.)* in our analysis due to their role as prey for large shark species. The database was manually reviewed to correct transcription errors. Blacktip (*Carcharhinus limbatus*), Galapagos (*Carcharhinus galapaguensis*), and tiger sharks (*Galeocerdo cuvier*) were initially recorded only as observational notes, with systematic counts introduced later (Supplementary Figure 1). While some human error (e.g., double counting) may have occurred, such bias remained consistent throughout the survey period. Models potentially affected by this issue account for it through offset terms. Although sampling could be considered a form of citizen science, all UVCs were conducted by experienced dive guides, ensuring high data quality. Sensitivity analyses were performed when needed, and the shift in data collection reflects changes in community composition at Cocos Island over time.

If more than one diver observed a species during a day, we averaged counts for that species across all involved divers. We used the total number of dives in a day as an offset term in our models to account for sampling effort (Kéry & Schaub, 2012). Visual censuses occurred within sites relatively close to one another (n=17); therefore, we accounted for observations amongst all sites by merging observations of all sites around Cocos Island (Supplementary figure 6). Site-by-site species counts were treated separately for analysis in which site variation could be important.

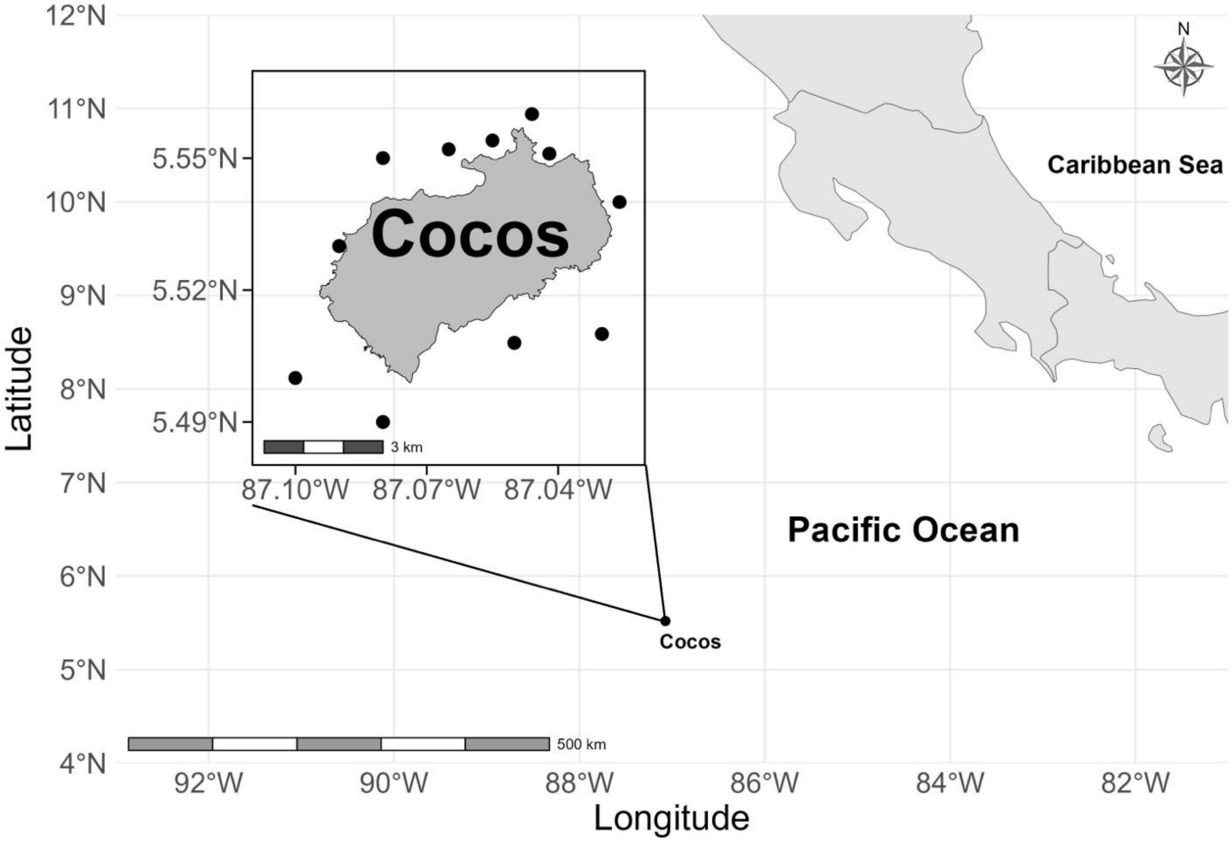

Figure 1. Study site: Cocos Island), Costa Rica (CR). The inset plot shows the actual contour of Cocos Island and its coordinates; points show the approximate location of dive sites.

Network Analysis

We conducted a network analysis to examine the inter-specific interactions of the elasmobranch community in Cocos Island from 1993 to 2019. Our analysis was based on species detection and non-detection data aggregated for each day. We represented species as nodes, node size as species abundance, and edges between nodes as the co-occurrence of species within the same period. We quantified the weight of each edge as the number of days when two species cooccurred within a given year. We then calculated network strength as the weighted number of connections between nodes. Finally, we built separate networks for each of the observed seasons in Cocos Island (wet from June to November and dry from December to May) to account for climatic and seasonal variability in the region for each year (for example, a network for the dry season in 1993, wet season in 1993, dry in 1994 and so on).

We used the iGraph (Csardi & Nepusz, 2006) package and its dependencies in the R programming environment (R Core Team, 2016) for statistical analysis and network construction. We performed centrality and betweenness analysis to identify key species within the network and highlight shifts in the community over time. We used this information to build graphical representations of the nodes and edges in the network. We tested significant changes in network metrics between years and seasons using simple linear regression models.

Additionally, we analyzed the variation in network metrics on a site-by-site basis amongst the 17 most popular dive sites around Cocos Island (Supplementary figure 6). We repeated the analysis according to the mean number of individual species detected on each site used by divers in Cocos Island looking for deviations to the general network patterns detected in Cocos Island as a whole, producing many individual networks for each site-season-year combination.

Diversity Analysis

We conducted diversity and similarity analyses using the vegan package (Oksanen et al., 2022) in R. We calculated the Hill transformed Shannon Diversity Index on a yearly and monthly basis for the study period, aiming to assess temporal changes in species diversity. This index provides a measure of species diversity by accounting for both species richness and evenness, presenting values as easily interpretable effective numbers of species. We analyzed the statistical significance of yearly and monthly variations in diversity by using simple linear regression models.

We calculated Bray-Curtis dissimilarity matrices to quantify differences in species composition over time for the entire dataset. We generated separate matrices for our data aggregated by year and season, allowing us to examine both annual and seasonal variation. We applied an Analysis of Similarities (ANOSIM) to these matrices to evaluate whether significant temporal changes in species composition occur across years and between months.

To further explore the drivers of community composition changes, we performed a Similarity Percentage (SIMPER) analysis on the Bray-Curtis dissimilarity matrices. This analysis identifies the contribution of individual species to the overall dissimilarity between groups of paired years, highlighting which species are the primary drivers of community change over time (Clarke, 1993).

Interactive Abundance Models

Our network and diversity analysis examined interspecific interactions as a function of the joint presence of elasmobranch species. Although useful, indirect network analysis does not consider how the occurrence of a species or group of species affects the abundance of the others. Therefore, we also analyzed our data with hierarchical regression models “Interactive Abundance 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, 2015) in R. This package interfaces the R coding language with JAGS, a Bayesian analysis software (Plummer, 2017). We ran 10,000 iterations with a 1,000 iteration burn-in and three chains to obtain model convergence (Zuur et al., 2008). 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 co-variates (each species, year, weeks, sea surface temperature and visibility, supplementary table 2) and merged covariates over the generally accepted 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). Although our output effects were correlative in nature, we will be referring to our species-to-species covariate effects as "interactions" for simplicity.

For most species, abundance was modeled through a negative binomial distribution expressed as a Poisson model with a diffuse over dispersion term ε and diffuse priors for each covariate. This distribution was chosen to address the over dispersion caused by the contrasts between counts for rare and abundant species (Zuur et al., 2008). The base equation for this model was:

$$\mathrm{Counts}_i \sim \mathrm{Poisson}(\lambda_i)$$

Where λ_i represents the expected counts during the *i*th week, according to the following equation:

$$\log(\lambda_i) = \alpha + \beta_{week} * WeekCyclic_i + \beta_{visibility} * \mathrm{Visibility}_i + \beta_{SST} * \mathrm{SST}_i + \beta_{Year} * Year_i + \beta_j * \mathrm{Count}_{ji} + \log(\mathrm{offset}_i)$$

Weeks represented as "WeekCyclic" were transformed using a sin-cosin cyclic transformation to account for seasonal variation. We chose to only include sea surface temperature (SST) and visibility as environmental variables since they have previously been demonstrated to have an impact on the relative abundance of elasmobranchs in the area (Osgood et al., 2021; White et al., 2015). We included the counts of other species as covariates in the model though a log link function in λi for each ith weekly observation for each j species, where $offset_i$ equals the number of dives performed for each ith week. α and βweek are the slope and intercept terms respectively.

Additional models were built for blacktips, eagle rays and manta rays, due to their low abundance. We recorded observations in these models as a binomial detection/non-detection variable, adjusting them to a logistic binomial model as:

$$\mathrm{Counts}_i \sim \mathrm{Bernouli}(\rho_i)$$

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

We re-ran our models while excluding turtles as a predictor checking for significant changes in model outputs to evaluate model sensitivity to species removal. Additionally. We re-ran the model using only the last 5 years of data to evaluate temporal variation and reduce-sampling sensitivity.

Results

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), forming a denser network (Figure 2). Network strength increased significantly over time and during the wet season (lowest mean strength of 19.4 + 4.36 SD in 1997 dry season, highest of 142.34 + 16.43 SD in 2014 wet season, p < 0.01, supplementary table 2). More species co-occurred in recent years and during the wet season, resulting in a reciprocal network where species pairs had a similar number of connections or “degree” (maximum of 24, for reciprocal connections between the 12 other species).

We generated a separate network (nodes and edges) for each year-season combination, but we chose to display only the two most representative networks as insets in Figure 2. The dry season of 1997 is shown as an example of the least interconnected network, while the wet season of 2014 represents the most interconnected network.

Network strength increased over time, with a marked rise after 2006 (Figure 2). In other words, species co-occurrences at Cocos Island became more frequent over the study period, peaking in the wet season of 2014. Prior to 2006, network strength remained relatively similar between seasons, but after this point, interactions became notably stronger during the wet season. The increased in network strength was mainly caused by the arrival and increased occurrence of blacktips, Galapagos and tiger sharks.

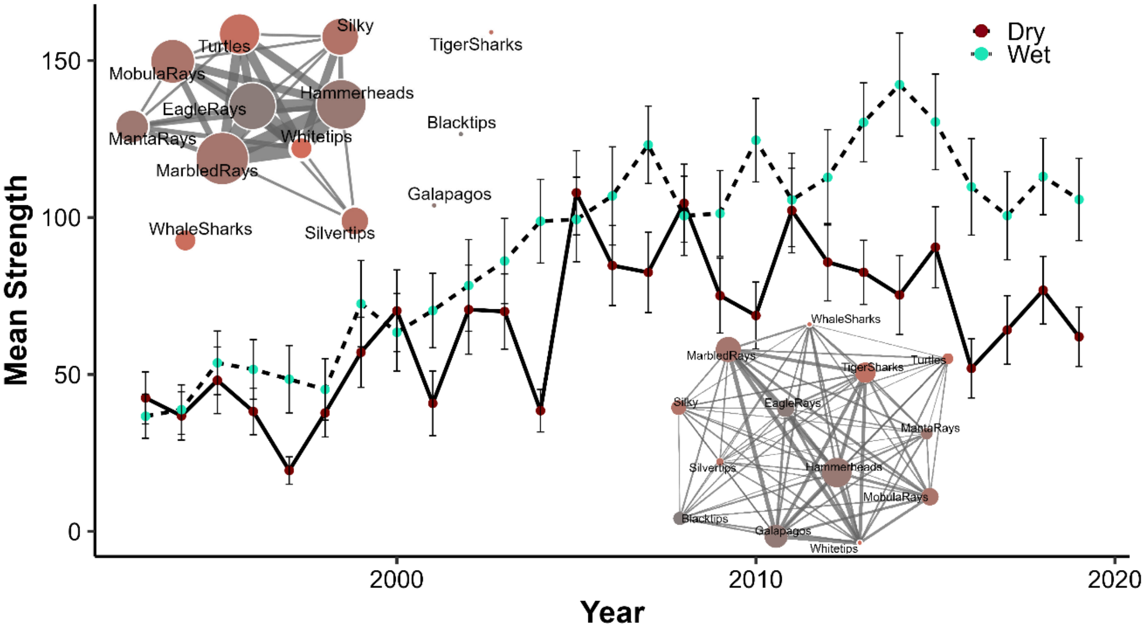

Figure 2. Network Dynamics through time in Cocos Island Elasmobranch community. Men network strength is represented by a solid line for the dry season and a dashed line for the wet season. Wisker represents standard deviation. Neural networks plots show the least interconnected network (1997, left) and the most interconnected network (2014, right). Each node (colored circles) represents a species in the network, size shows the species relative abundance. Lines between nodes (edges) represent species co-occurrence. Line thickness shows the relative edge weight or proportion of co-occurrence events.

Site by site analysis followed a very similar (if more variable) pattern, with most sites following the same yearly and seasonal trends (Supplementary figure 7). Four sites (Manuelita B, 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.

Diversity

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 blacktips, Galapagos and tiger sharks over time (Figure 3a). The lowest diversity was observed in 1998, while the highest occurred in 2006. We did not find any significant variations in monthly species diversity, with values ranging from 2.6 in March to 2.84 in November (Supplementary figure 2).

ANOSIM results supported the network statistics, as we observed a strong and significant separation in community composition between consecutive years (R = 0.32, p = 0.001) with lower mean dissimilarity values from 2006 onwards. Dissimilarity percentages ranged between 25% and 55% (Figure 4b). On the other hand, the monthly variation showed a weak but significant level of separation in community composition (R= 0.06, p=0.001). Peak dissimilarity was observed during April, descending towards its lowest point in October before increasing again (Supplementary Figure 3).

Finally, we identified three species as the primary contributors to dissimilarity within the community thanks to the SIMPER analysis: Scalloped hammerheads, Whitetip reef sharks, and Marbled rays (Figure 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 pair of years), contributing between 7.6% and 64%, whereas Marbled rays consistently contributed the least among the top three species, with a range of 0.13% to 13.34%.

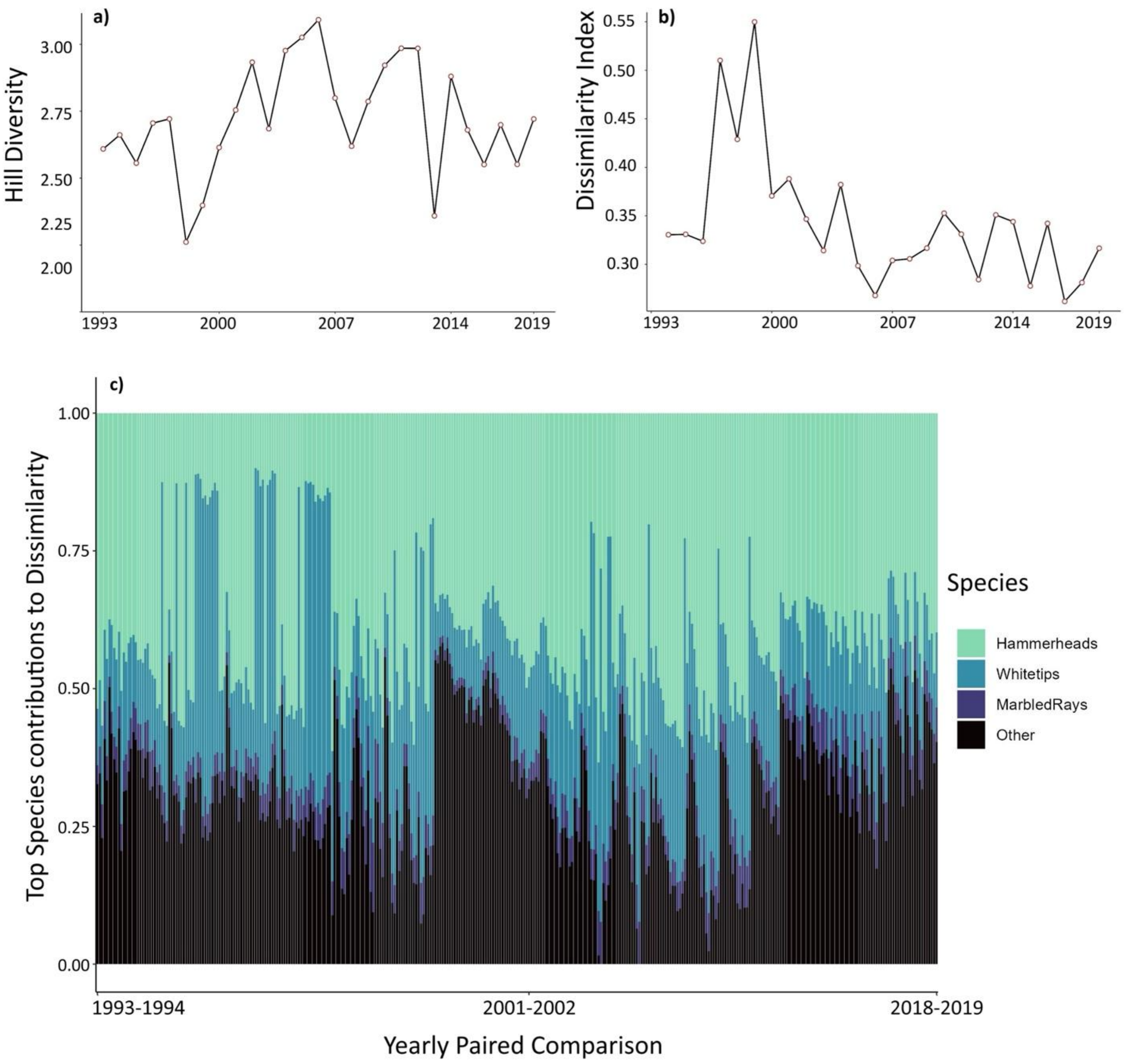

Figure 3. Temporal analysis of species diversity and community composition in the elasmobranch community of Cocos Island. Panel (a) shows the yearly Hill Diversity Index, with each point representing average diversity for a given year over the study period. Panel (b) displays the Bray-Curtis dissimilarity percentages between consecutive years. Panel (c) highlights the contribution of the top three species (Scalloped hammerheads “Hammerheads” light teal color, Whitetip reef sharlks “Whitetips” blue color, and Marbled rays, dark blue color) to the overall dissimilarity, as determined by SIMPER analysis. 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.

Interactive Abundance Models

The correlation analysis for our models shows no covariates with correlation values beyond the 0.7 or -0.7 collinearity cutoff with another covariate (Supplementary Figure 4). Excluding non-biological covariates, the highest correlation value observed between species counts was 0.48 (between Marbled rays and Whitetips), the lowest correlation value was of -0.17 (Between Galapagos and Whitetips).

All models converged with relatively accurate predictions for mean occurrences of the species studied, with the highest differences between observed and predicted abundances observed for scalloped hammerhead and whitetip reef sharks, the most abundant species (Supplementary Figure 5). The lower predictability observed for the more abundant species was expected due to the high number of individuals observed during certain periods of time. The errors, however, were relatively small, with average weekly differences ranging from -2.5 to 5 individuals.

Model outputs remained largely unchanged when excluding turtles as a covariate, demonstrating the robustness of our approach. However, time variability and sample size influenced the 2014–2019 models, where overall trends remained consistent, but some species interactions lost statistical significance. Notably, no significant species co-occurrence switched from positive to negative or vice versa. These results are provided in the supplementary material.

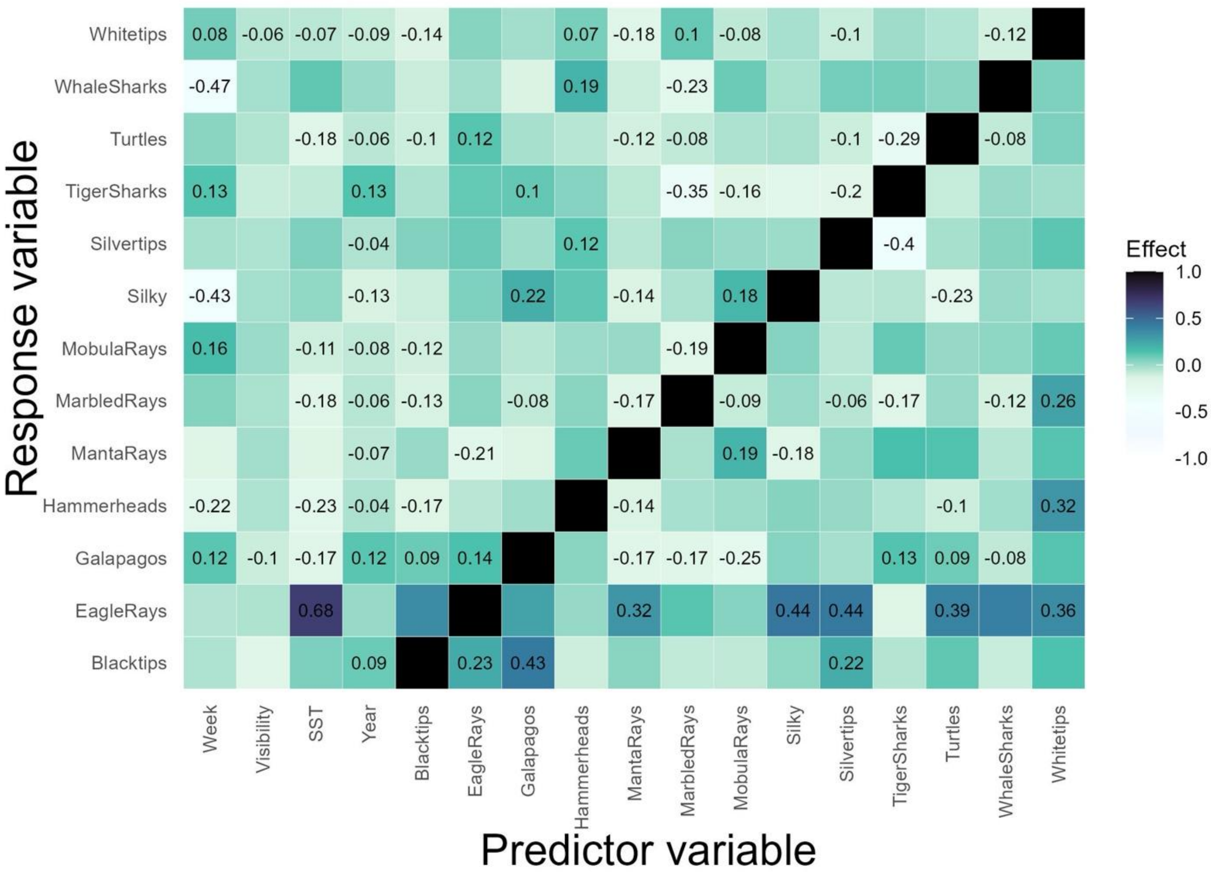

Figure 4. Visualization of results from Bayesian models. Colors represent the mean posterior estimates of the Bayesian beta coefficients from each species interaction model. Response variables are shown in the y axis, predictor variables are shown in the x axis. Note that values are not mirrored due to the asymmetric nature of interactions. Darker colors for positive effects, lighter colors for negative effects. Cells with numbers highlight significant effects (95% credible interval for posterior distribution did not cross zero did not cross 0).

Eight out of the 13 species studied showed a significant declining trend in abundance with only three species showing a positive trend (Table 1). Sea surface temperature had a significatively negative effect on the occurrence of six species, with Eagle rays being the only species positively influenced by an increase in temperature (Figure 4). Visibility had a weak but significant negative effect on Galapagos and Whitetips. Finally, 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 and Whale sharks, and a positive effect for Mobulas, Galapagos, Tiger and Whitetip reef sharks.

Regarding species interactions. Galapagos sharks, Marbled rays and Turtles were tied for the greatest number of significant interactions with eight each. In contrast, Mobula rays, Silvertip and Whale sharks were tied for the least significant interactions count with two each. As expected, most species interactions were negative (43 out of the 59). 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 (0.43 ± 0.11). The strongest negative effects were observed between Silvertips and Tiger sharks (-0.39 ± 0.09), Tiger sharks and Marbled rays (-0.35 ± 0.11), and Turtles and Tiger sharks (-0.29 ± 0.05).

Table I. Summary of significant species interactions. Coefficient shows the mean posterior beta coefficient for year as a predictor of species abundance, with NS showing non-significant effects. The abiotic predictors column show the number of significant effects for the species amongst our Week, Visibility, Sea Surface Temperature (SST) and Year covariates. Predictor species show the count of significant species covariate effects. Species interactions show the number of significant interactions attributed to each hypothesized species interaction. Only significant effects (95% credible interval for posterior distribution did not cross zero did not cross 0) are counted.

Species	Population	Coefficient	Abiotic predictors	Predictor species	Species interactions		
					Competition	Environmental	Predation
Blacktips	Increase	0.09	1	3	0	3	0
Eagle rays	Stable	NS	1	5	0	3	2
Galapagos	Increase	0.12	4	8	0	5	3
Hammerheads	Decrease	-0.04	3	4	0	4	0
Manta rays	Decrease	-0.07	1	3	0	3	0
Marbled rays	Decrease	-0.06	2	8	0	4	4
Mobula rays	Decrease	-0.08	3	2	0	1	1
Silky	Decrease	-0.13	2	4	0	4	0
Silvertips	Decrease	-0.04	1	2	1	1	0
Tiger sharks	Increase	0.13	2	4	1	1	2
Turtles	Decrease	-0.06	2	7	0	4	3
Whale sharks	Stable	NS	1	2	0	2	0
Whitetips	Decrease	-0.09	4	7	1	5	1

Discussion

Here we use a novel combination of network analysis, diversity metrics, and ecological modeling to provide an evaluation of elasmobranch community dynamics in the Eastern Tropical Pacific. Our results corroborate past work on the continued decline of several key elasmobranch species (Figure 4). Several recent studies suggest that Cocos Island's elasmobranch community is undergoing a shift in species composition(Espinoza et al., 2020; White et al., 2015). Potential drivers of these changes 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). We provide new insights into the observed changes in community composition by using indirect methods to evaluate species interaction and community processes.

Our diversity and network analysis suggest 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. In contrast, network strength, a key measure of community connectivity and resilience (Landi et al., 2018), has experienced significant changes in just a few decades. Peaks in network strength during the dry season of 2006 and the wet season of 2014 were most likely caused by the arrival of blacktips, Galapagos and tiger sharks, their increase in abundance and higher co-occurrence with other species. Nevertheless, the reduction in network strength after 2014 may suggest the community has reached a new stability point. Furthermore, we observed an inverse relationship in network strength between seasons, with higher network strength values during the wet period correlating with reduced network strength in the dry season. Our observations suggest that the community may have split into two temporally distinct sub-communities. The fact that diversity metrics did not capture this seasonal variation implies that, while most species can be encountered year-round, network structure is shaped by resident species during the dry season and by more seasonal species during the wet season. Next, we built on our work with diversity and network metrics by exploring potential interspecific interactions based on our interactive model outputs.

Competition

Competition encompasses both direct and indirect ecological interactions, including territoriality and interference over limited resources (Twining et al., 2024). We interpreted the negative effect of one species on another's abundance as evidence of potential competition, limited to species unlikely to have predator-prey relationships but sharing ecological or trophic niches. For example, while large blacktip sharks occasionally prey on neonate or juvenile scalloped hammerheads (Castro, 1996), such interactions are unlikely at Cocos Island, where hammerhead sharks are primarily adults. Furthermore, previous studies have reported competitive exclusion of blacktips by larger sharks such as great hammerheads (*Sphyrna mokarran*), bull sharks (*Carcharhinus leucas*) and tiger sharks (Doan & Kajiura, 2020; Lear et al., 2021) suggesting the negative interaction between blacktips and scalloped hammerheads is competitive in nature. Our results also suggest competition is occurring between tiger sharks and silvertip sharks, likely driven by spatial overlap or shared resource use (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 island (White et al., 2015). Competition for prey may explain the negative interaction between tiger sharks and silvertips, since both shark species were significant negative predictors for turtle and marble ray abundance. Such competitive exclusion events have also been reported in areas such as New Caledonia, where silvertip sharks ignored highly attractive food sources, such as whale carcasses, in the presence of tiger sharks (Clua et al., 2013). Competitive exclusion plays an important role in shaping the structure of predator communities (Condamine et al., 2019; Schoener, 1974) and should be considered in managing and evaluating shifting communities such as Cocos Island's elasmobranchs.

Predation

We determined the occurrence of potential predation (predator-prey interactions) when we observed either an increase in predator abundance associated with the presence of potential prey or a decline in prey species correlated with predator presence. Blacktip sharks frequently prey on mobulids in the Eastern Tropical Pacific (Estupiñán-Montaño et al., 2018), which may explain why blacktips were negative predictors for mobulas and marbled rays. These batoids are more pelagic species than marbled rays and much smaller than manta rays (Saltzman & White, 2023). Galapagos and silvertip sharks are large predators known to feed on rays at Cocos Island (Garrison, 2006) and could negatively affect marbled ray abundance, suggesting either direct predation or predator avoidance. As expected, tiger shark presence correlated with lower turtle abundance, aligning with studies that highlight turtles as a key component of tiger shark diets (Heithaus, 2001; Saltzman et al., 2024) . Despite being opportunistic predators, tiger sharks did not show significant predation effects for species other than turtles in our models. Instead, their presence negatively affected other top predators, suggesting that predation-driven changes in the Cocos Island community result not only from direct consumption but also from behavioral responses to predator presence. Potential behavioral effects were further highlighted by the negative correlation between silvertip and reef whitetip sharks. Although direct predation of whitetips by silvertips has not been documented, previous studies at Cocos Island suggest larger predators may opportunistically prey on smaller whitetips (White et al., 2015). The large number of potential predation interactions suggested by our results reflect the complexity of trophic dynamics and behaviorally mediated interactions in marine communities with multiple co-existing predators.

Environmental preferences

Finally, we inferred that some significant species co-occurrences may have been caused by environmental conditions based on previous studies (Osgood et al., 2021; Saltzman & White, 2023). Highly mobile predators such as blacktip, Galapagos, tiger, and silky sharks showed positive correlations, likely reflecting shared habitat preferences (Estupiñán-Montaño et al., 2018; Hoffmayer & Parsons, 2003; Papastamatiou et al., 2006). Previous studies identified the arrival of blacktip, Galapagos and tiger sharks as a potential driver of community shifts at Cocos Island (Espinoza et al., 2024; White et al., 2015), likely influenced by fishing (Burns et al., 2023; Worm et al., 2024) and climate change (Osgood et al., 2021). Batoid species also exhibited strong associations with environmental variables. Research on filter feeders at Cocos Island previously identified oceanographic conditions as key drivers of species composition (Saltzman & White, 2023). Model outputs reinforced this finding, as multiple batoid species co-occurred with specific environmental conditions rather than with competing sharks or predators. Eagle rays showed a positive correlation with turtles but a negative correlation with manta rays, possibly indicating habitat partitioning or differences in environmental tolerance. Warmer sea surface temperatures also influence eagle ray distributions, which may explain the observed patterns (Rastoin-Laplane et al., 2023). Marbled rays were positively associated with whitetip reef sharks but negatively associated with turtles, mobula rays, and whale sharks, suggesting a preference for coastal habitats over oceanic environments (Garrison, 2006). Similarly, mobula rays were negatively correlated with coastal predators such as Galapagos, tiger, marbled, and whitetip reef sharks, and positively correlated with oceanic species like silky sharks and manta rays, reinforcing shared habitat preferences and trophic niches (Saltzman & White, 2023). Our findings suggest that environmental preferences play a crucial role in structuring the elasmobranch community at Cocos Island, with species aggregating in response to environmental conditions rather than direct biotic interactions.

Study limitations and implications for management

Our analysis evaluated interspecific interactions within the elasmobranch community at Cocos Island but omitted other species in the ecosystem. Future research could implement joint species abundances as predictors, as well as other important functional groups in Cocos Island such as fish and other prey items to determine if more complex indirect relationships are also playing a role in shaping the community. The individual models we used provided 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. However, implementing more specialized analysis using currently available data would require either a more systematic sampling approach or additional methodological adjustments tailored, both of which fall beyond the scope of this study. 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). Our sensitivity analysis further highlighted structural considerations within our models. For example, only 19 out of 59 biological predictors across our interactive models remained significant when re-running our models using only the last 5 years of data (Supplementary figure 8). 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. These 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. In this study, we found that species co-occurrence data and indirect analytical methods have the potential to provide meaningful insights about inter species interactions. We hope our results work as a steppingstone 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.

Acknowledgements

We would like to thank the Undersea Hunter team for their data collection efforts over three decades. Barbara Spiecker, Ruscena Wiederholt, Nathan Furey, and members of the Quantitative Marine Ecology Lab contributed to earlier versions of this manuscript.

Data Availability

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

Bibliography

Ajemian, M. J., Powers, S. P., & Murdoch, T. J. T. (2012). Estimating the potential impacts of large mesopredators on benthic resources: Integrative assessment of spotted eagle ray foraging ecology in Bermuda. *PLoS ONE*, *7*(7). https://doi.org/10.1371/journal.pone.0040227

Arias, A., Pressey, R. L., Jones, R. E., Álvarez-Romero, J. G., & Cinner, J. E. (2016). Optimizing enforcement and compliance in offshore marine protected areas: A case study from Cocos Island, Costa Rica. *Oryx*, *50*(1), 18–26. https://doi.org/10.1017/S0030605314000337

Burns, E. S., Bradley, D., & Thomas, L. R. (2023). Global hotspots of shark interactions with industrial longline fisheries. *Frontiers in Marine Science*, *9*. https://doi.org/10.3389/fmars.2022.1062447

Carrier, J. C., Jusick, J. A., & Heithaus, M. R. (2012). *Biology of Sharks and Their Relatives.* (J. C. Carrier, J. A. Musick, & M. R. Heithaus, Eds.; Second Edi). CRC Press. https://doi.org/https://doi.org/10.1201/b11867

Castro, J. I. (1996). Biology of the blacktip shark, Carcharhinus limbatus, off the southeastern United States. *Bulletin of Marine Science*, *59*(3), 508–522.

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, *18*, 117–143.

Clua, E., Chauvet, C., Read, T., Werry, J. M., & Lee, S. Y. (2013). Behavioural patterns of a Tiger Shark (Galeocerdo cuvier) feeding aggregation at a blue whale carcass in Prony Bay, New Caledonia. *Marine and Freshwater Behaviour and Physiology*, *46*(1), 1–20. https://doi.org/10.1080/10236244.2013.773127

Condamine, F. L., Romieu, J., & Guinot, G. (2019). Climate cooling and clade competition likely drove the decline of lamniform sharks. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(41), 20584–20590. https://doi.org/10.1073/pnas.1902693116

Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal*, *Complex Sy*(1695). https://igraph.org

Dedman, S., Moxley, J. H., Papastamatiou, Y. P., Braccini, M., Caselle, J. E., Chapman, D. D., Cinner, J. E., Dillon, E. M., Dulvy, N. K., Dunn, R. E., Espinoza, M., Harborne, A. R., Harvey, E. S., Heupel, M. R., Huveneers, C., Graham, N. A. J., Ketchum, J. T., Klinard, N. V., Kock, A. A., … Heithaus, M. R. (2024). Ecological roles and importance of sharks in the Anthropocene Ocean. In *Science (New York, N.Y.)* (Vol. 385, Issue 6708, p. adl2362). https://doi.org/10.1126/science.adl2362

Dill, L. M., Heithaus, M. R., & Walters, C. J. (2003). Behaviorally mediated indirect interactions in marine communities and their conservation implications. *Ecology*, *84*(5), 1151–1157. https://doi.org/10.1890/0012-9658(2003)084[1151:BMIIIM]2.0.CO;2

Doan, M. D., & Kajiura, S. M. (2020). Adult blacktip sharks (Carcharhinus limbatus) use shallow water as a refuge from great hammerheads (Sphyrna mokarran). *Journal of Fish Biology*, *96*(6), 1530–1533. https://doi.org/10.1111/jfb.14342

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., Mcclean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Espinoza, M., Araya-Arce, T., Chaves-Zamora, I., Chinchilla, I., & Cambra, M. (2020). Monitoring elasmobranch assemblages in a data-poor country from the Eastern Tropical Pacific using baited remote underwater video stations. *Scientific Reports*, *10*(1). https://doi.org/10.1038/s41598-020-74282-8

Espinoza, M., Quesada-Perez, F., Madrigal-Mora, S., Naranjo-Elizondo, B., Clarke, T. M., & Cortés, J. (2024). A decade of submersible observations revealed temporal trends in elasmobranchs in a remote island of the Eastern Tropical Pacific Ocean. *Scientific Reports*, *14*(1). https://doi.org/10.1038/s41598-024-64157-7

Estupiñán-Montaño, C., Galván-Magaña, F., Tamburín, E., Sánchez-González, A., Villalobos-Ramírez, D. J., Murillo-Bohórquez, N., Bessudo-Lion, S., & Estupiñán-Ortiz, J. F. (2017). Trophic inference in two sympatric sharks, sphyrna lewini and carcharhinus falciformis (Elasmobranchii: Carcharhiniformes), based on stable isotope analysis at malpelo Island, Colombia. *Acta Ichthyologica et Piscatoria*, *47*(4), 357–364. https://doi.org/10.3750/AIEP/02177

Estupiñán-Montaño, C., Pacheco-Triviño, F., Cedeño-Figueroa, L. G., Galván-Magaña, F., & Estupiñán-Ortiz, J. F. (2018). Diet of three shark species in the Ecuadorian Pacific, Carcharhinus falciformis, Carcharhinus limbatus and Nasolamia velox. *Journal of the Marine Biological Association of the United Kingdom*, *98*(4), 927–935. https://doi.org/10.1017/S002531541600179X

Estupiñán-Montaño, C., Polo-Silva, C. J., Elorriaga-Verplancken, F. R., Sánchez-González, A., Zetina-Rejón, M. J., Delgado-Huertas, A., Rojas-Cundumí, J., & Galván-Magaña, F. (2024). Marine community trophic structure of Malpelo Island, Colombia from stable isotopes approach. *Journal of Marine Systems*, *244*(March 2023). https://doi.org/10.1016/j.jmarsys.2024.103973

Ferretti, F., Jacoby, D. M. P., Pfleger, M. O., White, T. D., Dent, F., Micheli, F., Rosenberg, A. A., Crowder, L. B., & Block, B. A. (2020). Shark fin trade bans and sustainable shark fisheries. *Conservation Letters*, *13*(3), 1–6. https://doi.org/10.1111/conl.12708

Flowers, K. I., Heithaus, M. R., & Papastamatiou, Y. P. (2021). Buried in the sand: Uncovering the ecological roles and importance of rays. *Fish and Fisheries*, *22*(1), 105–127. https://doi.org/10.1111/faf.12508

Frank, K. T., Petrie, B., Choi, J. S., & Leggett, W. C. (2005). Ecology: Trophic cascades in a formerly cod-dominated ecosystem. *Science*, *308*(5728), 1621–1623. https://doi.org/10.1126/science.1113075

Garrison, G. (2006). *Peces de la Isla del Coco* (G. Ginge, Ed.; 2nd ed.). INBio.

Gregr, E. J., Christensen, V., Nichol, L., Martone, R. G., Markel, R. W., Watson, J. C., Harley, C. D. G., Pakhomov, E. A., Shurin, J. B., & Chan, K. M. A. (2020). Cascading social-ecological costs and benefits triggered by a recovering keystone predator. *Science*, *368*(6496), 1243–1247. https://doi.org/10.1126/science.aay5342

Heithaus, M. R. (2001). The biology of tiger sharks, Galeocerdo cuvier, in Shark Bay, Western Australia: Sex ratio, size distribution, diet, and seasonal changes in catch rates. *Environmental Biology of Fishes*, *61*(1), 25–36. https://doi.org/10.1023/A:1011021210685

Hoffmayer, E. R., & Parsons, G. R. (2003). Food habits of three shark species from the Mississippi Sound in the northern Gulf of Mexico. *Southeastern Naturalist*, *2*(2), 271–280. https://doi.org/10.1656/1528-7092(2003)002[0271:FHOTSS]2.0.CO;2

Hollowed, A. B., Bax, N., Beamish, R., Collie, J., Fogarty, M., Livingston, P., Pope, J., & Rice, J. C. (2000). Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? *ICES Journal of Marine Science*, *57*(3), 707–719. https://doi.org/10.1006/jmsc.2000.0734

Kéry, M., & Schaub, M. (2012). *Bayesian Population Analysis using WinBUGS, A Hierarchical Perspective* (First). Elsevier. http://store.elsevier.com/Bayesian-Population-Analysis-using-WinBUGS/Marc-Kery/isbn-9780123870216/

Klimley, A. P., Arauz, R., Bessudo, S., Chávez, E. J., Chinacalle, N., Espinoza, E., Green, J., Hearn, A. R., Hoyos-Padilla, M. E., Nalesso, E., Ketchum, J. T., Fischer, C., Ladino, F., Shillinger, G., Soler, G., Steiner, T., & Peñaherrera-Palma, C. (2022). Studies of the movement ecology of sharks justify the existence and expansion of marine protected areas in the Eastern Pacific Ocean. *Environmental Biology of Fishes*, *105*(12), 2133–2153. https://doi.org/10.1007/s10641-021-01204-6

Landi, P., Minoarivelo, H. O., Brännström, Å., Hui, C., & Dieckmann, U. (2018). Complexity and stability of ecological networks: a review of the theory. *Population Ecology*, *60*(4), 319–345. https://doi.org/10.1007/s10144-018-0628-3

Lear, K. O., Whitney, N. M., Morris, J. J., & Gleiss, A. C. (2021). Temporal niche partitioning as a novel mechanism promoting co-existence of sympatric predators in marine systems. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1954). https://doi.org/10.1098/rspb.2021.0816

Link, W. A., & Eaton, M. J. (2012). On thinning of chains in MCMC. *Methods in Ecology and Evolution*, *3*(1), 112–115. https://doi.org/10.1111/j.2041-210X.2011.00131.x

Moreno, M. L., Jiménez, K., & Villalobos, C. (2021). Approximation of the benefits of socioeconomic activities in Cocos Island National Park and the effects of climate change. *Revista Interamericana de Ambiente y Turismo*, *17*(1), 14–26. https://doi.org/10.4067/s0718-235x2021000100014

Nalesso, E., Hearn, A., Sosa-Nishizaki, O., Steiner, T., Antoniou, A., Reid, A., Bessudo, S., Soler, G., Peter Klimley, A., Lara, F., Ketchum, J. T., & Arauz, R. (2019). Movements of scalloped hammerhead sharks (Sphyrna lewini) at Cocos Island, Costa Rica and between oceanic islands in the Eastern Tropical Pacific. *PLoS ONE*, *14*(3), 1–16. https://doi.org/10.1371/journal.pone.0213741

Navia, A. F., Alfaro-Shigueto, J., Ágreda-Arango, J., Areano, E., Avalos-Castillo, C., Bizzarro, J. J., Bustamante, C., Cevallos, A., Concha, F. J., Cruz-Escalona, V. H., Ebert, D. A., Espinoza, M., González-Leiva, A., Guzmán, H. M., Hearn, A., Hleap, J. S., Mangel, J. C., Mejía-Falla, P. A., Morales-Saldaña, J. M., … Vélez-Zuazo, X. (2024). Unveiling Macroecological Patterns of Elasmobranchs in the Eastern Pacific Ocean. *Journal of Biogeography*. https://doi.org/10.1111/jbi.15037

Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O’Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., … Weedon, J. (2022). *vegan: Community Ecology Package*. https://cran.r-project.org/package=vegan

Osgood, G. J., White, E. R., & Baum, J. K. (2021). Effects of climate-change-driven gradual and acute temperature changes on shark and ray species. *Journal of Animal Ecology*, *90*(11), 2547–2559. https://doi.org/10.1111/1365-2656.13560

Ovaskainen, O., Tikhonov, G., Dunson, D., Grøtan, V., Engen, S., Sæther, B. E., & Abrego, N. (2017). How are species interactions structured in species-rich communities? A new method for analysing time-series data. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1855). https://doi.org/10.1098/rspb.2017.0768

Papastamatiou, Y. P., Wetherbee, B. M., Lowe, C. G., & Crow, G. L. (2006). Distribution and diet of four species of carcharhinid shark in the Hawaiian Islands: Evidence for resource partitioning and competitive exclusion. *Marine Ecology Progress Series*, *320*, 239–251. https://doi.org/10.3354/meps320239

Plummer, M. (2017). *JAGS: Just another Gibbs sampler. Version 4.0.3 user manual.* https://people.stat.sc.edu/hansont/stat740/jags_user_manual.pdf

R Core Team. (2016). *R: A language and environment for statistical computing.* (3.3.3). R Foundation for Statistical Computing. https://www.r-project.org/

Rastoin-Laplane, E., Salinas-de-León, P., Goetze, J. S., Saunders, B. J., McKinley, S. J., Norris, C., Gosby, C., Mattingly, A., Garcia, R., & Harvey, E. S. (2023). Fluctuations of Galapagos mid-water and benthic reef fish populations during the 2015–16 ENSO. *Estuarine, Coastal and Shelf Science*, *294*. https://doi.org/10.1016/j.ecss.2023.108523

Russo, L., Casella, V., Marabotti, A., Jordán, F., Congestri, R., & D’Alelio, D. (2022). Trophic hierarchy in a marine community revealed by network analysis on co-occurrence data. *Food Webs*, *32*. https://doi.org/10.1016/j.fooweb.2022.e00246

Salas, E., Ross-Salazar, E., & Arias, A. (2012). *Diagnóstico de áreas marinas protegidas y áreas marinas para la pesca responsable en el Pacífico costarricense.* (E. Salas, E. Ross-Salazar, & A. Arias, Eds.). Fundación MarViva.

Saltzman, J., Hearn, A. R., Fuentes, M. M. P. B., Steiner, T., Arauz, R., Macdonald, C., Heidemeyer, M., & White, E. R. (2024). Multidecadal underwater surveys reveal declines in marine turtles. *Conservation Science and Practice*, *6*(11), 1–38. https://doi.org/10.1111/csp2.13249

Saltzman, J., & White, E. (2023). Determining the role of environmental covariates on planktivorous elasmobranch population trends within an isolated marine protected area. *Marine Ecology Progress Series*, *722*, 107–123. https://doi.org/10.3354/meps14435

Schoener, T. W. (1974). Competition and the form of habitat shift. *Theoretical Population Biology*, *6*(3), 265–307. https://doi.org/10.1016/0040-5809(74)90013-6

Su, Y., & Yajima, M. (2015). *R2jags: Using R to run "JAGS"* (R package version 0.7-1.1). https://github.com/suyusung/R2jags

Twining, J. P., Augustine, B. C., Royle, J. A., & Fuller, A. K. (2024). Abundance-mediated species interactions. *Ecology*. https://doi.org/10.1002/ecy.4468

van Zinnicq Bergmann, M. P. M., Guttridge, T. L., Smukall, M. J., Adams, V. M., Bond, M. E., Burke, P. J., Fuentes, M. M. P. B., Heinrich, D. D. U., Huveneers, C., Gruber, S. H., & Papastamatiou, Y. P. (2022). Using movement models and systematic conservation planning to inform marine protected area design for a multi-species predator community. *Biological Conservation*, *266*(April 2019), 109469. https://doi.org/10.1016/j.biocon.2022.109469

White, E. R., Myers, M. C., Flemming, J. M., & Baum, J. K. (2015). Shifting elasmobranch community assemblage at Cocos Island-an isolated marine protected area. *Conservation Biology*, *29*(4), 1186–1197. https://doi.org/10.1111/cobi.12478

Worm, B., Orofino, S., Burns, E. S., D'Costa, N. G., Feitosa, L. M., Palomares, M. L. D., Schiller, L., & Bradley, D. (2024). Global shark fishing mortality still rising despite widespread regulatory change. *Science*, *383*(6679), 225–230. https://doi.org/10.1126/science.adf8984

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2008). *Mixed Effects Models and Extensions in Ecology with R* (Third). Springer. https://doi.org/10.1007/978-0-387-87458-6