Estuarine, Coastal and Shelf Science 326 (2025) 109528

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Disentangling assembly processes: environmental and biotic filtering jointly drive lagoon fish co-occurrence patterns

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ARTICLE INFO

Keywords:
Assembly rules
Ichthyofauna
Joint species distribution models
Functional guilds
Environmental drivers
Species interactions

ABSTRACT

In coastal lagoons, fish community assembly is shaped by both environmental filters and biotic interactions, yet their relative importance remains unclear. In this study, we aimed to disentangle the primary drivers of fish community assembly in a tropical coastal lagoon. Additionally, we sought to identify shared or opposite environmental responses and potential biotic interactions that might help elucidate observed co-occurrence patterns. Results revealed that co-occurrence patterns in a tropical lagoon fish community are driven by a near-equal combination of these two processes, challenging the long-standing assumption that environmental filtering is the dominant driver in these systems. Using a joint species distribution model (JSDM) combined with functional guild classification and a literature survey, we found that 53% of co-occurrence patterns were driven by shared environmental responses, while 47% reflected residual correlations, potentially indicative of biotic interactions. Positive and negative associations were balanced, with correlations suggesting predator avoidance, schooling behavior, and possible competition. Our findings highlight that a pluralistic approach, accounting for both abiotic and biotic factors, is essential for a comprehensive understanding of community assembly. While many residual associations could not be confidently attributed to specific ecological processes due to limited trophic information, our results underscore the value of integrating species traits and ecological knowledge to interpret model outputs. We suggest that future research incorporate additional factors, such as indirect biotic interactions, seasonal effects, additional functional traits and environmental harshness, into the modelling of species distributions, particularly in disturbance-prone environments like coastal lagoons where the effects of environmental and biotic filtering can vary depending on environmental harshness.

1. Introduction

Understanding the processes shaping biological communities is a central goal in community ecology. The assembly rules framework establishes that after large-scale processes, such as speciation, migration, and dispersal, determine which species will be able to reach a specific region, environmental filters and biotic interactions will then shape the composition of a local community (Kneitel and Chase, 2004; Weiher and Keddy, 1999). Environmental filtering plays a major role in structuring fish communities in streams and coastal lagoons (Mouchet et al., 2013; Kirk et al., 2022), where environmental conditions select species based on their affinities, allowing co-existence through shared environmental responses (Keddy, 1992). However, in some aquatic ecosystems, biotic interactions can be equally important to community assembly, and can alter species coexistence patterns through predation, competition, parasitism, mutualism, and facilitation (biotic filtering; MacArthur and Levins, 1967; Wisz et al., 2013; Inoue et al., 2017; Astarloa et al., 2019). The influence of environmental and biotic filtering on species co-occurrence can also vary depending on environmental harshness (Soliveres et al., 2012; Long et al., 2015), specifically on the physiological stress imposed by wide salinity fluctuations in tropical systems (Kültz, 2015; Telesh and Khlebovich, 2010). Despite extensive research on these processes (Wisz et al., 2013; Asefa et al., 2017; Kirk et al., 2022), some questions remain about their relative contributions to community assembly in dynamic and heterogeneous ecosystems like coastal lagoons.

Coastal lagoons are transitional water bodies between fresh and saltwater that serve as nurseries, reproduction, and feeding grounds for

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https://doi.org/10.1016/j.ecss.2025.109528
Received 27 March 2025; Received in revised form 6 August 2025; Accepted 29 August 2025
Available online 1 September 2025
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fish species at different life stages and are crucial for sustaining fishery stocks worldwide (Vendel and Chaves, 2006; Elliott et al., 2007; Erzini et al., 2022). Their unique characteristics, including their transitory nature, strong environmental gradients and variable sea connectivity, make them ideal systems for studying community assembly processes. However, these same features also render coastal lagoons highly vulnerable to both natural and human-induced disturbances (Pérez-Ruzafa et al., 2011; de Wit, 2011). Given their ecological importance, such knowledge is essential for predicting species' responses to future environmental changes, for safeguarding these ecosystems and for developing effective fisheries management strategies (Pecuchet et al., 2016; Montanyès et al., 2023).

Historically, traditional methods for modelling the influence of environmental factors on species distributions, such as generalized linear models and multivariate ordination techniques (García-Baquero and Crujeiras, 2015; Nóbrega et al., 2019), often overlook potential dependencies between species, a fundamental aspect of community ecology. Failing to consider biotic interactions can result in an over simplistic view of community dynamics and lead to inaccurate assumptions about assembly processes and community structure (Boulangeat et al., 2012; Royan et al., 2016). Recently, joint species distribution models (JSDMs) have been developed, as an extension of traditional species distribution models (SDMs), to overcome this limitation by simultaneously modelling multiple species while assessing how environmental variables influence species co-occurrence (Pollock et al., 2014; Warton et al., 2015). This approach accounts for species co-occurrence by estimating residual correlations, *i.e.*, the component of species' occurrences that cannot be explained by the predictors included in the model, which may reflect other ecological processes, such as biotic interactions and/or unmeasured environmental variables (Pollock et al., 2014). However, interpreting these residuals and effectively distinguishing the effects of biotic interactions from unmeasured environmental variables remains challenging (Zurell et al., 2018). Because biotic interactions do not always manifest as clear, non-random co-occurrence patterns, ecologists often investigate co-occurrence patterns alongside species traits such as habitat selection and guild membership (Peres-Neto, 2004; Mouchet et al., 2013; Kohli et al., 2018).

Classifying species into functional guilds, based on their use of the environment and feeding preferences, provides valuable insights into the structure and functioning of estuarine ecosystems such as coastal lagoons (Elliott et al., 2007). While estuarine use functional guilds reflect species' migratory patterns and physiological adaptations, trophic guilds are related to feeding habits, interactions between species and may reflect strategies to avoid competition (Elliott et al., 2007). Thus, combining the guild approach with JSDMs can aid in the challenge of distinguishing biotic interactions from environmental responses, while also being a powerful tool for drawing inferences about co-occurrence patterns in complex, heterogeneous environments.

Previous studies have successfully applied JSDMs to disentangle the relative effects of environmental and biotic filters in ecological communities, identifying biotic interactions such as codominance in trees, heterospecific attraction in river birds, and schooling behavior in prey fish species (Pollock et al., 2014; Royan et al., 2016; Astarloa et al., 2019). However, despite their growing use in ecological research, the application of JSDMs to fish communities has been relatively limited (Astarloa et al., 2019; Haak et al., 2019; Wagner et al., 2020; Perrin et al., 2022; Roberts et al., 2022). Notably, to the best of our knowledge, no studies have yet employed this approach in coastal lagoons, leaving a critical gap in our understanding of community assembly processes in these ecosystems. Addressing this gap could substantially improve our understanding of the relative importance of assembly processes in structuring fish assemblages, ultimately enhancing theoretical ecology in estuarine and coastal science.

In this study, our overall aim was to disentangle the primary drivers of fish community assembly in a tropical coastal lagoon. To achieve this, we had three main objectives: a) to investigate non-random co-occurrence patterns; b) to partition these patterns into responses to environmental variables and/or potential interactions, quantifying their relative contributions, and c) to identify shared or opposite environmental responses and potential biotic interactions that could explain associations between fish species pairs, based on their functional guilds. Given the strong environmental gradients in coastal lagoons and the well-stablished role of environmental filtering in community assembly in these ecosystems (González Castro et al., 2009; Selfati et al., 2019; Santos et al., 2023), we hypothesized that environmental filtering would have a greater influence than biotic filtering on fish co-occurrence patterns in the lagoon. We predicted that: a) strong positive environmental correlations would be predominant among species within the same estuarine-use guilds, due to shared responses, and strong negative correlations would be predominant among species from different guilds due to different responses; and b) strong negative residual correlations would be predominant among species within the same trophic guilds as an indicative of competition.

2. Material and methods

2.1. Study area

Saquarema lagoon (22°54′S - 42°33′W) is situated in Saquarema city, along the eastern coast of Rio de Janeiro state, Brazil. Spanning approximately 21.2 km^2, the lagoon has an average depth of 1 m and receives freshwater input from six major rivers. Classified as a "choked" lagoon, it has limited connectivity to the sea at certain periods of the year through a single connection channel (Barra Franca channel), which is long, narrow, and silted on some occasions (Kjerfve, 1994). Salinity in the Saquarema lagoon ranges from 16 to 40, but overall euhaline conditions (salinity $>$30) are prevalent (Franco et al., 2019). The climate is tropical with a dry summer, featuring seasonal patterns in rainfall and an average annual temperature of 25 °C (Carmouze et al., 1991; Alvares et al., 2013; Valadão et al., 2020).

2.2. Data collection and processing

Sampling was conducted once every two months from September 2017 to July 2019 at nine sampling sites distributed across the lagoon's margins, covering three zones (*i.e.*, inner, middle, and outer). Sampled sites were shallow, marginal areas primarily characterized by soft, unvegetated bottoms composed of unconsolidated substrate (*i.e.*, sand and mud). Each site was sampled three times ($N = 27$ samples per campaign) using a beach seine net (20 m width x 1.5 m height; 7 mm mesh size) during the day, between 0900 and 1700 h. The net was positioned perpendicular to the shore and fitted with 20 m of hauling ropes, covering an approximate sampled area of 400 m^2. Standardized sampling efforts were performed by two people, one at each end of the rope, and lasted an average of 10 min. During samplings, water temperature (°C), pH, dissolved oxygen (mg/L), and salinity were measured with a multi-parameter probe (HANNA HI 9828). Depth (cm) and water transparency (cm), calculated as the water transparency/depth ratio), were measured with a Secchi disk. Monthly rainfall data (mm) was obtained from the National Institute of Meteorology (INMET).

We identified captured specimens using marine fish identification manuals (Figueiredo and Menezes, 1978, 1980, 2000; Menezes and Figueiredo, 1980, 1985) and relevant recent literature. Taxonomic classification and nomenclature were checked and updated according to Eschmeyer's Catalog of Fishes: Genera, Species, References (Fricke et al., 2023a) and Eschmeyer's Catalog of Fishes: Genera/Species by Family/Subfamily (Fricke et al., 2023b). After taxonomic identification, individuals were measured for total length (TL) in mm and total weight (TW) in grams using a precision scale (0.001 g).

2.3. Statistical analysis and ecological interpretation

We used a probabilistic modelling approach applied to a presence-absence data matrix to identify significant positive, negative, and random co-occurrence patterns between species pairs (Veech, 2013). This model, which is based on combinatorial analysis, calculates the likelihood of species co-occurring in random samples within a community. This approach improves the ability to detect false positive and false negative associations between species, while also correcting for biases in randomization processes (Veech, 2013). We stablished an alpha threshold of 0.05 and ran the analysis using the "cooccur" v1.3 package (Griffith et al., 2016).

To investigate the drivers of species co-occurrence patterns, we used a joint species distribution modelling approach (JSDM; Pollock et al., 2014) based on a hierarchical Bayesian framework. This method is valuable for exploring the underlying processes and mechanisms that drive community assembly. Environmental correlations in co-occurrence patterns can support the hypothesis that environmental filtering significantly influences community structure, while evidence of residual correlation could indicate that biotic interactions as the primary process, albeit the influence of unmeasured environmental covariates cannot be entirely ruled out (Börger and Nudds, 2014). Evidence of both environmental and residual correlation could support a pluralistic hypothesis of community structuring. However, if no significant associations are found, JSDM analysis can support the null hypothesis of random community organization. Further details on the JSDM approach are available in Pollock et al. (2014) and Warton et al. (2015).

We fitted the JSDM to a binary response variable (a presence-absence matrix of species by site) using a binomial probit regression, with seven environmental variables as predictors: water temperature, pH, dissolved oxygen, salinity, transparency, rainfall and depth. Prior to entering these variables into the model, we centred and standardized them to have a mean of zero and a standard deviation of one, ensuring comparability and reducing potential bias. We assessed collinearity among predictors by calculating the variance inflation factor (VIF) for the environmental variables (Zuur et al., 2010) using the "multicol" function in the "fuzzySim" v4.9.9 package (Barbosa, 2023). All variables had VIF value below 3, indicating acceptable collinearity levels, and were included in the model (Suppl. Material Table 1). Additionally, a random row effect was incorporated in the analysis to account for site-specific variability. We ran four chains with 300,000 iterations, with the first 30,000 discarded as burn in, and thinned the remaining samples by a factor of 10 to retain 27,000 samples for the analysis. We specified default priors for all model parameters. The model was fitted using the "jSDM" package v0.2.6 (Vieilledent and Clément, 2023), and correlation plots were built with the "corrplot" v0.92 package (Wei and Simko, 2021). Model convergence was assessed visually through diagnostic plots of the model key parameters and the Gelman-Rubin potential scale reduction factor (*i.e.*, R-hat <1.1; Gelman and Rubin, 1992). Statistical analyses were conducted using R software version 4.4.6 (R Core Team, 2023) via RStudio (RStudio Team, 2020).

To ecologically interpret pairwise species associations, we examined significant environmental and residual correlations using the methods proposed by D'Amen et al. (2017) and Astarloa et al. (2019) (Table 1). We assigned species to functional guilds based on the classification from Elliott et al. (2007) and Potter et al. (2015), which categorize species according to their environmental affinities (estuarine use functional guilds) and feeding preferences (trophic functional guilds) (Suppl. Material Table 2). Estuarine use functional guilds were: 1) Marine stragglers; 2) Marine migrants; 3) Estuarine; 4) Semi-anadromous; and 5) Freshwater. Trophic functional guilds were: 1) Zooplanktivores; 2) Detritivores; 3) Herbivores; 4) Omnivores; 5) Piscivores; 6) Zoobenthivores; and 7) Opportunists. A summary of the number of species per guild is available on Suppl. Material Table 3. To avoid biases in our analyses and in the classification into functional guilds due to ontogenetic changes, prior to guild classification, we categorized species into juveniles (TL $<$ L50), and/or adults (TL $\geq$ L50) based on their total length at first maturation (L50) available on FishBase (Froese and Pauly, 2023). The proportion of juveniles and adults per species is available on Suppl. Material Table 4.

Table 1

Ecological interpretation given to pairwise associations based on their environmental and residual correlations (adapted from D'Amen et al., 2017; Astarloa et al., 2019). Residual factors refer to biotic interactions or unmeasured environmental variables. Correlation coding: (−): significant negative correlation; (+): significant positive correlation; (0): no significant correlation.

Environmental correlation	Residual correlation	Ecological interpretation of pairwise associations	Meaning
0	+	Positive interactions	Species co-occurred more than expected due to residual factors (potential positive interactions)
–	+	Positive interactions despite different environmental response	Species co-occurred more than expected despite different responses to measured environmental variables (potential positive interactions)
+	+	Positive interactions and shared environmental responses	Species co-occurred more than expected due to shared responses to measured environmental variables and residual factors (potential positive interactions)
+	0	Shared environmental response	Species co-occurred more than expected due to shared responses to measured environmental variables
–	0	Different environmental respose	Species co-occurred less than expected due to measured environmental variables
–	–	Negative interactions and different environmental response	Species co-occurred less than expected due to measured environmental variables and residual factors (potential negative interactions)
+	–	Negative interactions despite shared environmental response	Species co-occurred less than expected despite shared responses to measured environmental variables (potential negative interactions)
0	–	Negative interactions	Species co-occurred less than expected due to residual factors (potential for negative interactions)
0	0	Random pair	Random association

We also conducted a literature survey on scientific papers focusing on describing species' diets, feeding behaviors, and species interactions. Given the high trophic plasticity of fish species across habitats (Timmerman et al., 2021), we initially restricted our search to studies conducted primarily on the Brazilian coast. However, due to limited records of interactions between fish and few studies characterizing species' diets, we expanded our search to global studies. Our goal with the guild classification and literature survey was to aid in the

Table 2
Residual correlation, species' trophic functional guild (TFG), ecological meaning of pairwise association, probable interaction type, amount of supporting evidence, reference of supporting evidence, methodology used in the source, and observations for identified biotic interaction. Trophic functional guilds (TFG): ZP = zooplanktivore; ZB = zoobenthivore; PV = piscivore; HV = herbivore; DV = detritivore; OV = omnivore. Codes: sp.1 = first species of the pair; sp.2 = second species of the pair. NA = Not Available. Acronyms can be found in Suppl. Material Table 2.

Pairs	Residual correlation	TFG sp.1	TFG sp.2	Ecological meaning of pairwise association	Probable interaction type	Evidence	Reference	Methodology	Observations
Alvul x Dirho	−0.42	ZB	ZB	Negative interactions	Competition/ Avoidance	NA	NA	NA	NA
Alvul x Sysco	−0.36	ZB	ZB	Negative interactions	Competition/ Avoidance	NA	NA	NA	NA
Anjan x Antri	−0.22	ZP	ZP	Negative interactions	Competition/ Avoidance	2	Silva et al., 2004; Araújo et al. (2008)	Inference based on space partitioning	Not diet studies
Antri x Braur	−0.19	ZP	ZP	Negative interactions	Competition/ Avoidance	NA	NA	NA	NA
Basop x Pocro	−0.23	ZB	ZB	Negative interactions	Competition/ Avoidance	NA	NA	NA	NA
Calat x Muliz	0.24	PV	HV	Positive interactions	Predation/ Aggregation	NA	NA	NA	NA
Calat x Odarg	0.33	PV	OP	Positive interactions	Predation/ Aggregation	NA	NA	NA	NA
Calat x Spgre	0.33	PV	ZB	Positive interactions	Predation/ Aggregation	NA	NA	NA	NA
Calat x Spspe	−0.55	PV	ZB	Negative interactions	Predator avoidance	NA	NA	NA	NA
Calat x Trfal	0.51	PV	ZB	Positive interactions	Predation/ Aggregation	NA	NA	NA	NA
Elsmi x Euarg	−0.53	PV	ZB	Negative interactions	Predator avoidance	2	Santos et al. (2020); Santos-Martínez and Arboleda (1993)	Stomach and intestinal content	Interaction found in Santa Marta, Colombia. Lowest taxonomic level of food items: Family
Elsmi x Mucur J	−0.63	PV	HV	Negative interactions	Predator avoidance	1	Santos-Martínez and Arboleda (1993)	Stomach content	Interaction found in Santa Marta, Colombia; Lowest taxonomic level of food items: Family
Elsmi x Opogl	−0.19	PV	DV	Negative interactions	Predator avoidance	NA	NA	NA	NA
Elsmi x Pocro	0.63	PV	ZB	Positive interactions	Predation/ Aggregation	1	Santos-Martínez and Arboleda (1993)	Stomach content	Interaction found in Santa Marta, Colombia. Lowest taxonomic level of food items: Family
Euarg x Poviv	−0.22	ZB	ZB	Negative interactions	Competition/ Avoidance	NA	NA	NA	NA
Haclu x Sabra	0.45	ZP	OV	Positive interactions	Schooling	1	Martins and Perez (2006)	Visual observation of schooling behavior	Not a diet study
Hyuni x Mucur J	−0.54	HV	HV	Negative interactions	Competition/ Avoidance	NA	NA	NA	NA
Hyuni x Olsau	−0.43	HV	PV	Negative interactions	Predator avoidance	NA	NA	NA	NA
Opogl x Phjan	−0.61	DV	DV	Negative interactions	Competition/ Avoidance	NA	NA	NA	NA

interpretation of residual correlations obtained from the JSDM (*i.e.*, probable biotic interactions) and to identify shared or different environmental responses and/or biotic interactions, such as predation, competition or mutualism, that could explain the association between species pairs. For instance, a negative residual correlation obtained from a JSDM between two species in the same trophic guild could suggest avoidance of interspecific competition, while a negative residual correlation between a predator and its potential prey may indicate prey decline or extinction due to predation, or avoidance behavior (Kneitel and Chase, 2004; Englund et al., 2009). Conversely, a positive residual correlation between predators and potential prey may point to predation (Freilich et al., 2018). Negative co-occurrence between non-predatory species from different trophic guilds might result from distinct environmental responses, whereas positive inter-guild co-occurrence may arise from shared environmental responses (Royan et al., 2016). Nevertheless, the challenge of attributing evidence of mutualism or competition to pairwise associations, along with a lack of precise information available in the literature regarding predator-prey interactions, led us to primarily focus on quantifying trophic evidence and inferring possible interactions based on guild membership.

3. Results

3.1. Co-occurrence patterns

Across all sampling campaigns, a total of 68 fish species were captured. Probabilistic modelling of species co-occurrence revealed positive (species co-occur significantly more than expected), negative (species co-occur significantly less than expected) and random species associations (observed of co-occurrence does not significantly differ from expected). From our presence-absence data matrix, we obtained a total of 2346 possible pairs. However, 1759 pairs were automatically

Table 3

Residual and environmental correlation, species' estuarine use (EUFG) and trophic functional guild (TFG), ecological meaning of pairwise association, probable interaction type, amount of supporting evidence, reference of supporting evidence, methodology used in the source, and observations for identified biotic interaction. Estuarine use functional guilds (EUFG): MS = marine stragglers; MM = marine migrants; ES = estuarine species; SA = semi-anadromous; FW = freshwater. Trophic functional guilds (TFG): ZP = zooplanktivore; ZB = zoobenthivore; PV = piscivore; HV = herbivore; DV = detritivore; OV = omnivore. Codes: sp.1 = first species of the pair; sp.2 = second species of the pair. NA = Not Available. Acronyms can be found in Suppl. Material Table 2.

Pairs	Residual correlation	Environmental correlation	TFG sp.1	TFG sp.2	EUFG sp.1	EUFG sp.2	Ecological meaning of pairwise association	Probable interaction type	Evidence	Reference	Methodology	Observations
Alvul x Mifur	−0.39	0.20	ZB	ZB	MS	MS	Negative interactions despite shared environmental response	Competition/ Avoidance	NA	NA	NA	NA
Alvul x Poviv	−0.27	−0.36	ZB	ZB	MS	FW	Negative interactions and different environmental response	Competition/ Avoidance	NA	NA	NA	NA
Anjan x Calat	−0.42	−0.43	ZP	PV	SA	MS	Negative interactions and different environmental response	Predator avoidance	1	Gonzalez et al. (2021)	Stomach content and stable isotope	Lowest taxonomic level of food items: Family
Anjan x Elsmi	0.52	0.63	ZP	PV	SA	MM	Positive interactions and shared environmental response	Predation/ Aggregation	NA	NA	NA	NA
Anlyo x Antri	0.82	−0.06	ZP	ZP	MS	MM	Positive interactions despite different environmental response	Aggregation	1	Félix et al., (2007)	Inference based on species co-occurrence	Not a diet study
Anlyo x Braur	−0.15	0.36	ZP	ZP	MS	MM	Negative interactions despite shared environmental response	Competition/ Avoidance	NA	NA	NA	NA
Anlyo x Elsmi	−0.47	0.26	ZP	PV	MS	MM	Negative interactions despite shared environmental response	Predator avoidance	NA	NA	NA	NA
Anlyo x Haclu	0.72	−0.41	ZP	ZP	MS	MM	Positive interactions despite different environmental response	Aggregation	1	Beets and LaPlace (1986)	Inference based on species co-occurrence	Not a diet study. Interaction found in the U.S. Virgin Islands
Antri x Elsmi	−0.45	−0.17	ZP	PV	MM	MM	Negative interactions and different environmental response	Predator avoidance	NA	NA	NA	NA
Antri x Euarg	0.26	0.22	ZP	ZB	MM	ES	Positive interactions and shared environmental response	Aggregation	1	Spach et al. (2004)	Inference based on species co-occurrence	Not a diet study
Antri x Opogl	0.33	0.28	ZP	ZB	MM	MS	Positive interactions and shared environmental response	Aggregation	1	Spach et al. (2004)	Inference based on species co-occurrence	Not a diet study
Basop x Ctbol	0.29	0.41	ZB	ZB	MS	ES	Positive interactions and shared environmental response	Aggregation	1	Macieira and Joyeux (2011)	Inference based on species co-occurrence	Not a diet study
Basop x Dirho	−0.56	−0.48	ZB	ZB	MS	ES	Negative interactions and different environmental response	Competition/ Avoidance	NA	NA	NA	NA
Basop x Elsmi	−0.44	−0.51	ZB	PV	MS	MM	Negative interactions and different environmental response	Predator avoidance	1	Santos et al. (2020)	Stomach and intestinal content	
Basop x Gooce	−0.52	−0.12	ZB	ZB	MS	MM	Negative interactions and different environmental response	Competition/ Avoidance	NA	NA	NA	NA
Braur x Calat	−0.36	−0.55	ZP	PV	MM	MS	Negative interactions and different environmental response	Predator avoidance	1	Gonzalez et al. (2021)	Stomach content and stable isotope	Lowest taxonomic level of food items: Family

(*continued on next page*)

Table 3 (*continued*)

Pairs	Residual correlation	Environmental correlation	TFG sp.1	TFG sp.2	EUFG sp.1	EUFG sp.2	Ecological meaning of pairwise association	Probable interaction type	Evidence	Reference	Methodology	Observations
Braur x Elsmi	0.59	0.61	ZP	PV	MM	MM	Positive interactions and shared environmental response	Predation/ Aggregation	NA	NA	NA	NA
Calat x Ceede	−0.33	−0.21	PV	HV	MS	MS	Negative interactions and different environmental response	Predator avoidance	1	Gonzalez et al. (2021)	Stomach content and stable isotope	Lowest taxonomic level of food items: Family
Calat x Gooce	−0.57	−0.33	PV	ZB	MS	MM	Negative interactions and different environmental response	Predator avoidance	1	Gonzalez et al. (2021)	Stomach content and stable isotope	Lowest taxonomic level of food items: Family
Calat x Sysco	−0.38	−0.47	PV	ZB	MS	MS	Negative interactions and different environmental response	Predator avoidance	NA	NA	NA	NA
Ceede x Hyuni	−0.42	−0.26	HV	HV	MS	MS	Negative interactions and different environmental response	Competition/ Avoidance	NA	NA	NA	NA
Ceede x Muliz	−0.41	−0.36	HV	HV	MS	MM	Negative interactions and different environmental response	Competition/ Avoidance	NA	NA	NA	NA
Ceede x Olsau	0.27	0.13	HV	PV	MS	MS	Positive interactions and shared environmental response	Predation/ Aggregation	NA	NA	NA	NA
Ctbol x Dirho	−0.44	−0.60	ZB	ZB	ES	ES	Negative interactions and different environmental response	Competition/ Avoidance	NA	NA	NA	NA
Ctbol x Elsmi	−0.36	−0.52	ZB	PV	ES	MM	Negative interactions and different environmental response	Predator avoidance	1	Santos et al. (2020)	Stomach and intestinal content	Lowest taxonomic level of food items: Family
Ctbol x Gooce	−0.18	−0.26	ZB	ZB	ES	MM	Negative interactions despite shared environmental response	Competition/ Avoidance	NA	NA	NA	NA
Ctbol x Mifur	−0.70	−0.21	ZB	ZB	ES	MS	Negative interactions and different environmental response	Competition/ Avoidance	NA	NA	NA	NA
Ctbol x Pocro	−0.42	−0.46	ZB	ZB	ES	MS	Negative interactions and different environmental response	Competition/ Avoidance	NA	NA	NA	NA
Diarg x Olsau	−0.23	−0.38	OV	PV	MS	MS	Negative interactions and different environmental response	Predator avoidance	NA	NA	NA	NA
Dirho x Spgre	−0.45	−0.38	ZB	ZB	ES	MS	Negative interactions and different environmental response	Competition/ Avoidance	NA	NA	NA	NA
Dirho x Spspe	−0.36	−0.52	ZB	ZB	ES	MS	Negative interactions and different environmental response	Competition/ Avoidance	NA	NA	NA	NA
Dirho x Trfal	−0.27	0.62	ZB	ZB	ES	MS	Negative interactions despite shared environmental response	Competition/ Avoidance	NA	NA	NA	NA
Elsmi x Gooce	0.42	0.55	PV	ZB	MM	MM	Positive interactions and shared environmental response	Predation/ Aggregation	NA	NA	NA	NA
Elsmi x Haclu	−0.35	−0.48	PV	ZP	MM	MM	Negative interactions and different environmental response	Predator avoidance	NA	NA	NA	NA

(*continued on next page*)

Table 3 (*continued*)

Pairs	Residual correlation	Environmental correlation	TFG sp.1	TFG sp.2	EUFG sp.1	EUFG sp.2	Ecological meaning of pairwise association	Probable interaction type	Evidence	Reference	Methodology	Observations
Elsmi x Hyuni	0.62	−0.21	PV	HV	MM	MS	Positive interactions and different environmental response	Predation/ Aggregation	NA	NA	NA	NA
Elsmi x Mifur	0.36	0.27	PV	ZB	MM	MS	Positive interactions and shared environmental response	Predation/ Aggregation	NA	NA	NA	NA
Elsmi x Muliz	0.42	−0.45	PV	HV	MM	MM	Positive interactions and different environmental response	Predation/ Aggregation	NA	NA	NA	NA
Elsmi x Olsau	−0.45	0.19	PV	PV	MM	MS	Negative interactions despite shared environmental response	Competition/ Avoidance	NA	NA	NA	NA
Elsmi x Sabra	−0.32	−0.32	PV	OV	MM	MM	Negative interactions and different environmental response	Predator avoidance	NA	NA	NA	NA
Elsmi x Spgre	−0.21	−0.07	PV	ZB	MM	MS	Negative interactions and different environmental response	Predator avoidance	NA	NA	NA	NA
Euarg x Pocro	−0.49	−0.30	ZB	ZB	ES	MS	Negative interactions and different environmental response	Competition/ Avoidance	NA	NA	NA	NA
Gooce x Spgre	−0.48	0.34	ZB	ZB	MM	MS	Negative interactions despite shared environmental response	Competition/ Avoidance	NA	NA	NA	NA
Gooce x Trfal	−0.53	0.33	ZB	ZB	MM	MS	Negative interactions despite shared environmental response	Competition/ Avoidance	NA	NA	NA	NA
Jelin x Olsau	−0.40	−0.13	OP	PV	ES	MS	Negative interactions and different environmental response	Predator avoidance	NA	NA	NA	NA
Muliz x Olsau	−0.57	−0.43	HV	PV	MM	MS	Negative interactions and different environmental response	Predator avoidance	1	Arceo-Carranza and Ciappa-Carrara (2015)	Stomach content	Interaction found in La Carbonera Lagoon (Yucatán, Mexico)
Spspe x Trfal	−0.47	−0.64	ZB	ZB	MS	MS	Negative interactions and different environmental response	Competition/ Avoidance	NA	NA	NA	NA

removed from the analysis due to their expected co-occurrence being <1, leaving 587 to be analyzed. We found that positive associations were more common than negative ones (Fig. 1). Among the analyzed pairs, 87 (14.8 %) exhibited co-occurrence patterns that significantly differed from random. Specifically, 60 pairs showed positive associations, while 27 showed negative associations. Five hundred (85.2 %) of pairwise associations were classified as random. The full list of all 587 analyzed pairs are provided in the Suppl. Material Table 5.

3.2. *Environmental variables vs. biotic interactions*

The output of the JSDM revealed a nearly equal contribution from environmental and biotic filtering, with a slightly higher proportion of co-occurrence among fish species attributed to their environmental responses (53 % of significant correlations) vs residual correlations (47 %) (Fig. 2). Our analysis identified 133 species pairs that exhibited purely environmental correlation (Suppl. Material Table 6). The contributions of shared (69 pairs) and different (64 pairs) environmental responses to environmental correlation between species were balanced. In contrast, 102 species pairs displayed purely residual correlation (Suppl. Material Table 7), with a similar balance between negative (54 pairs) and positive (48 pairs) interactions. Furthermore, 135 species pairs exhibited both significant environmental and residual correlations (Suppl. Material Table 8), primarily driven by negative interactions coupled with environmental responses (76 had negative interactions and (dis)similar environmental response vs. 59 pairs had positive interactions and (dis) similar environmental response) (Fig. 3).

We found a homogenous proportion of significant positive and negative correlations due to environmental response (134 positive vs. 133 negative), with approximately 26 % of these correlations ranging from moderate ($0.5 \leq |r| \leq 0.7$) to strong ($0.7 \leq |r| \leq 0.9$) (Fig. 1a). In contrast, the range of residual correlations was comparatively wider, with approximately 32 % of these correlations ranging from moderate to strong (Fig. 1b), and more frequently negative (106 positive vs. 130 negative).

3.3. *Ecological interpretation of associations*

When attributing an ecological meaning to the co-occurrence patterns, we found that the combined effects of environmental and biotic filtering accounted for the majority of the associations (Fig. 4), collectively explaining 75 % of the pairwise associations we observed. Individually, shared environmental responses accounted for 14 % of the associations, while different environmental responses accounted for 13 %. Negative interactions and negative interactions combined with different environmental responses each accounted for 11 % of the associations. Positive interactions and positive interactions combined with shared environmental responses accounted for 10 % and 9 % of the associations, respectively. Positive interactions despite different environmental responses and negative interactions despite shared environmental responses accounted for less than 10 % of the associations.

3.4. *Biotic interactions*

We identified potential biotic interactions among 65 species pairs, with 19 species pairs displaying purely residual correlations, driven

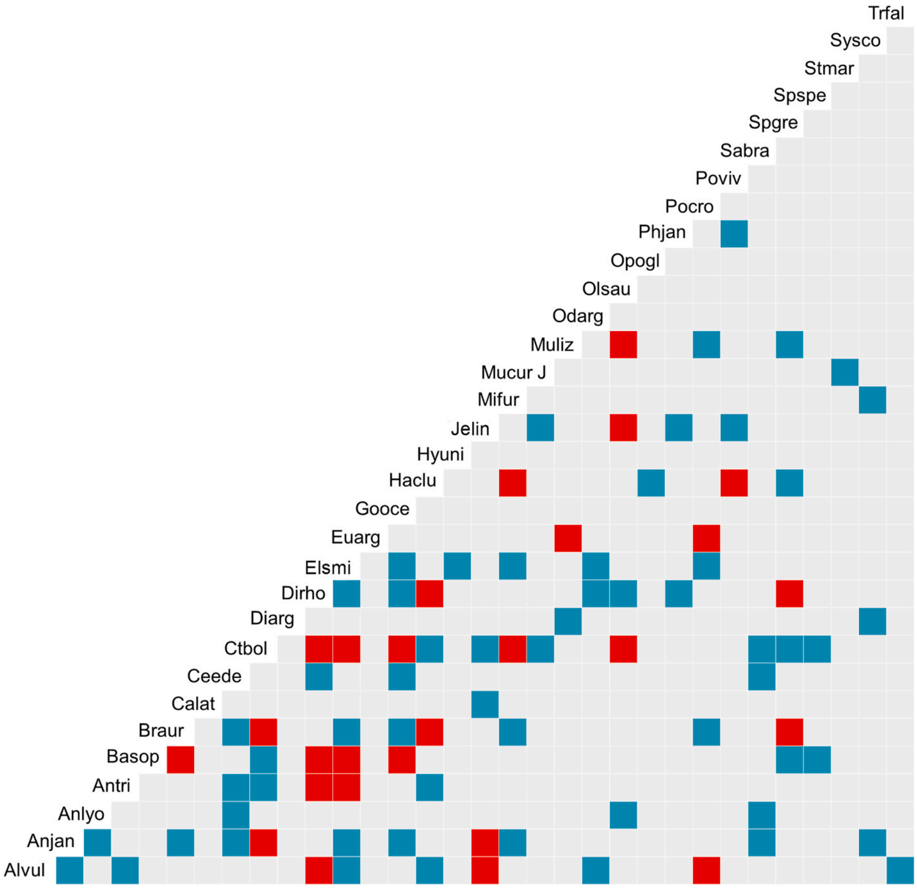

Fig. 1. Co-occurrence matrix visualization showing significant pairwise associations between 87 fish species calculated based on the probability model of species co-occurrence (Griffith et al., 2016), with an alpha threshold of 0.05. Significant positive associations are shown in blue and negative associations in red. Random associations are shown in grey. Acronyms can be found in Suppl. Material Table 2. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

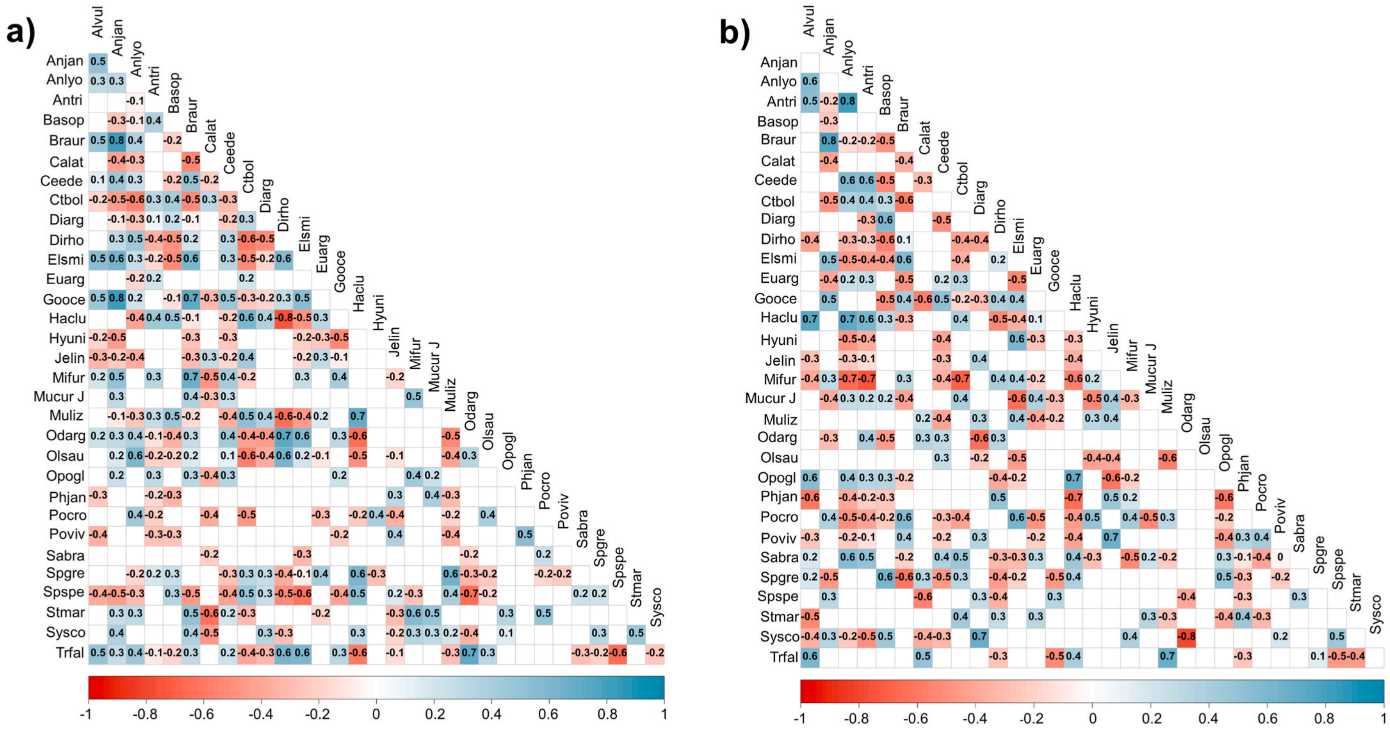

Fig. 2. Plots of the correlations between species due to environmental responses (**a**) and residual correlations (**b**) based on the joint species distribution model (JSDM). Only significant correlations, based on 95 % credible intervals, are shown. Color gradients (from red to blue) represent negative and positive correlations, respectively. The strength of correlations is represented by the correlation coefficient. Acronyms can be found in Suppl. Material Table 2. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

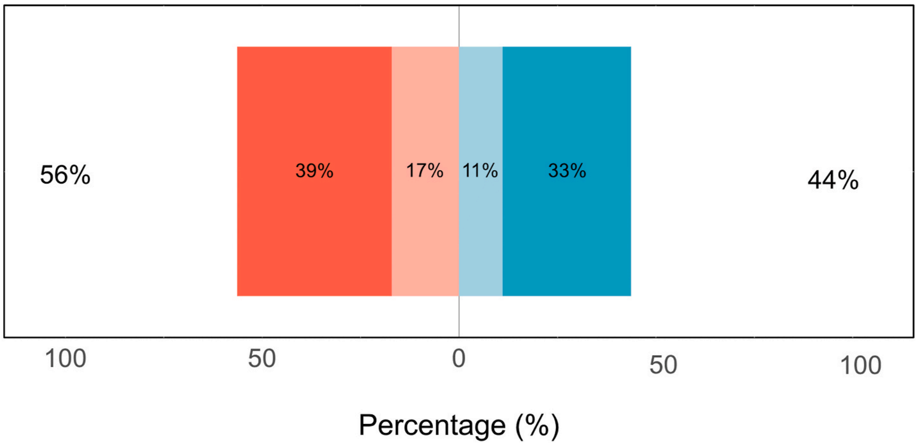

Fig. 3. Ecologically interpreted combined environmental and residual correlations displayed with their corresponding proportion. Color gradient (from red to blue) represent: negative interactions and different environmental response; negative interactions despite shared environmental response; positive interactions despite different environmental response; and positive interactions and shared environmental response, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

primarily by negative associations (13 negative vs. 6 positive) (Table 2). An additional 46 pairs exhibited both environmental and residual correlations, which were also primarily driven by negative associations (34 negative vs. 12 positive) (Table 3).

Our literature survey provided support for specific interaction types for 17 of these pairs (Tables 2 and 3). Evidence suggesting predator avoidance behavior was noted for nine pairs, including: *Elops smithi* and *Bathygobius soporator*; *E. smithi* and *Ctenogobius boleosoma*; *E. smithi* and *Eucinostomus argenteus*; *E. smithi* and *Mugil curema* (juvenile); *Caranx latus* and *Anchoa januaria*; *C. latus* and *Brevoortia aurea*; *C. latus* and *Cetengraulis edentulus*; *C. latus* and *Gobionellus oceanicus*; *Oligoplites saurus* and *Mugil liza*. Associations consistent with schooling or aggregation behaviors were identified in six pairs (Tables 2 and 3), such as: *Harengula clupeola* and *Sardinella brasiliensis*; *Anchoa lyolepis* and *Anchoa tricolor*; *A. lyolepis* and *H. clupeola; A. tricolor* and *E. argenteus; A. tricolor* and *Opisthonema oglinum*; *B. soporator* and *C. boleosoma*. Evidence suggesting predation/predator-prey aggregation and competition/competition avoidance behavior was found for two pairs: *E. smithi* and *Pogonias cromis*; *A. januaria* and *A. tricolor*, respectively.

4. Discussion

The dual influence of environmental conditions and species interactions on fish distributions is well-documented in aquatic systems

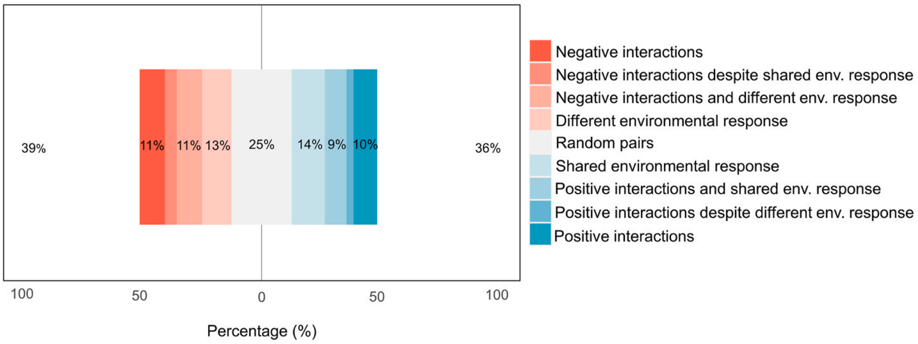

Fig. 4. Ecologically interpreted associations (explained in Table 1) displayed with their corresponding proportion (percentages smaller than 5 % are not shown). Color gradients (from red to blue) represent negative and positive associations, respectively. Random associations (no significant correlation) are displayed in the center of the figure. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

(Hanson et al., 2005; Radinger et al., 2019; Montanyès et al., 2023), yet their relative importance in shaping communities within coastal lagoons remains poorly investigated. Our study directly addresses this gap, revealing a near-equal contribution from environmental and biotic filtering to fish species co-occurrence patterns, thereby partially rejecting our initial hypothesis. This finding challenges the conventional assumption that environmental filtering is the primary driver of community assembly in coastal lagoons and aligns with emerging evidence from other taxa and aquatic systems (Inoue et al., 2017; Astarloa et al., 2019), underscoring the importance of taking both aspects into account to fully understand community structure. It also suggests that the dynamic nature of coastal lagoons promotes pluralistic sources for community assembly, thus, too simplistic hypotheses (*e.g.*, single-process dominance) may not be suited for these ecosystems and may overlook other factors that cause these processes to counterbalance each other, like salinity-driven stress.

The balanced contributions of environmental and biotic filtering in our study likely reflect the level of environmental harshness in the lagoon, specifically the physiological stress imposed by strong salinity fluctuations. Coastal lagoons typically exhibit varying salinity conditions, ranging from freshwater to hypersaline, which can act as an environmental filter or stressor (harsh condition), imposing physiological stress on species with different osmoregulatory mechanisms and limiting their occurrence in certain habitats (Kjerfve, 1986; Telesh and Khlebovich, 2010; Kültz, 2015; Franco et al., 2019). Harsh environmental conditions are known to influence species co-occurrence, leading to a shift in the relative importance of filtering processes along an environmental harshness gradient (Soliveres et al., 2012; Long et al., 2015). In this sense, Soliveres et al. (2012), drawing on the Stress Gradient Hypothesis, proposed eight scenarios to predict the effects of environmental and biotic filtering on species co-occurrence, while considering community phylogenetic patterns and the degree of environmental harshness. Based on the Soliveres et al. (2012) framework, a balanced contribution of environmental and biotic filtering is expected under less favorable conditions, where a random phylogenetic structure should be observed. Although we did not specifically address the extent of physiological stress experienced by fish species in the Saquarema lagoon due to salinity, the observed balance in filtering processes we observed is consistent with this theory.

Previous work by Franco et al. (2019) found that Saquarema lagoon supports higher species richness than neighboring lagoons (namely Araruama and Maricá lagoons). The lower species richness found in the other lagoons was primarily attributed to stressful salinity conditions that limited the number of species capable of thriving in their extreme conditions (Franco et al., 2019). Thus, environmental harshness imposed by salinity fluctuations could be causing the counterbalancing effect of environmental and biotic filtering we observed in the lagoon. In this sense, future studies should explicitly incorporate analyses of environmental harshness and phylogenetic patterns to better understand community assembly in coastal lagoons, which could offer more insights into species co-occurrence patterns.

Despite inherent limitations, JSDMs have been effective in detecting general patterns of co-occurrence linked to environmental filtering (Radinger et al., 2019), competition (Zurell et al., 2018), and facilitative mechanisms (Royan et al., 2016). In our study, the positive residual correlations we observed may partly reflect mutualistic associations resulting from aggregating and schooling behavior of species with similar diets. Long-stablished descriptions of schooling behavior and aggregation among pelagic fishes, including mixed schools among engraulids and clupeids, could explain some of the positive interactions detected in our analysis (Pitcher, 1986; Brehmer et al., 2007). Negative interactions, like the ones we observed between planktivorous species such as *Anchoa januaria* and *Anchoa tricolor*, may reflect strategies to avoid competition for food resources or space partitioning, as previously observed in the Sepetiba Bay, Southeastern Brazil, which allows coexistence and minimizes competition (Araújo et al., 2008; Silva et al., 2018).

Negative associations observed between piscivores and their potential preys could reflect predator avoidance behavior, which has been previously suggested for anchovies and herrings (Félix-Hackradt et al., 2010; Pichler et al., 2017). On the other hand, positive associations between predators and prey may indicate predation, based on the trophic evidence found in the literature, or aggregation behavior, with predators favoring areas with prey abundance (Hassell and May 1974; Stewart and Jones, 2001). The limited availability of trophic evidence, particularly the lack of studies identifying stomach contents at the species level, makes it difficult to determine which of these mechanisms best explain the observed associations. Furthermore, the differing movement ecology of the species must also be considered, as seasonal and ontogenetic movements are known to be important drivers of fish distribution in estuarine systems. Co-occurrence in our study is based on captures at the same locations across a two-year period and does not necessarily imply simultaneous interaction. For example, positive associations between mobile predators and more sedentary prey could reflect spatial tracking of resource availability, as adult fish regularly move into lagoons to use them as feeding grounds (Moreno-Pérez et al., 2024), while negative associations might result from prey avoidance of predator-dominated areas, a behavior documented for juvenile fish in turbid estuarine habitats (Ramos et al., 2016). We did not incorporate functional traits related to mobility, which could help elucidate these dynamics. We recommend future studies include such traits to improve the interpretation of residual co-occurrence patterns.

Interpreting biotic interactions from residual correlations in JSDMs is a powerful but challenging task. Residual correlations are influenced by the choice of environmental covariates and may capture not only true biotic interactions but also the effects of unmeasured environmental variables, indirect biotic interactions, or interactions modulated by environmental conditions, which could lead to erroneously attributing unexplained variation to biotic interactions (Hui, 2016; D'Amen et al., 2017; Ovaskainen and Abrego, 2020). As a result, residual correlations can lead to patterns that are statistically accurate but lack ecological support and should be interpreted with caution (Blanchet et al., 2020). In this sense, it is recommended to examine the results alongside additional sources of information, such as relevant literature. Our literature survey and the classification of species into functional guilds suggest that, while most environmental correlations reflected (dis)similar environmental responses, some of the residual correlations may not have reflected genuine biotic interactions.

The literature survey and functional guild analysis supported many inferred interactions; however, some associations remain speculative due to a lack of detailed trophic studies for many neotropical species. For instance, detailed diet information for key piscivores such as *Caranx latus* and *Centropomus undecimalis* is limited, as well as records of species interactions from the literature. Indeed, many species in our study lack documented interactions in literature, and, when available, diet studies often only identify prey at the family level. Furthermore, species interactions in Brazilian coastal systems remain poorly documented, and many inferences in our study were based on studies conducted in other countries or indirect methods, such as visual observations and stable isotope analysis (Martins and Perez, 2006; Gonzalez et al., 2021). This lack of taxonomic and ecological resolution constrains our ability to validate inferred associations and likely leads to underestimation of interactions. Although our results provide some insights into the complex interactions of the fish species in coastal lagoons, addressing this gap will require future studies that focus on detailed diet analyses and direct observation of species interactions in these systems. Such efforts would greatly strengthen the biological interpretation of JSDM results and clarify the role of biotic interactions in fish community assembly.

Several methodological considerations shape the interpretation of our results and highlight directions for future research. The most significant is that our analysis pooled data collected across two years without explicitly modeling seasonal effects. The probabilistic model of Veech (2013) is not designed for temporally structured data where the probability of occurrence for many species (*e.g.*, species arriving in seasonal recruitment pulses) is not constant. This temporal segregation can be misinterpreted as spatial avoidance by the model. The same limitation extends to our JSDM analysis, where unmodeled seasonality could act as a confounding factor in residual correlations. We chose to aggregate data as a necessary trade-off to achieve a robust sample size for the analyses. However, we believe that our multi-layered approach provides strong evidence to our findings. For instance, when the JSDM identifies a negative residual correlation between two species, and the literature confirms that the same two species are known competitors (*e.g.*, *Anchoa* space partitioning described by Araújo et al., 2008; Silva et al., 2018), the most parsimonious explanation is a genuine biotic interaction. Nevertheless, we strongly recommend that future studies with higher-frequency sampling incorporate seasonal effects directly into their models. Furthermore, our sampling was conducted with a beach seine, which is selective for smaller, nearshore species and likely underrepresents larger fishes (Franco et al., 2012). As such, our conclusions primarily apply to this component of the fish community.

Despite these limitations, multiple studies have shown that JSDMs can reliably detect species interactions based on occurrence data, thereby providing confidence in our results (Royan et al., 2016; Astarloa et al., 2019; Silva et al., 2023). We also sought to minimize confounding factors by incorporating only abiotic predictors with well-stablished influence on fish distributions. However, we acknowledge that a more comprehensive trait-based approach, with the inclusion of other functional traits beyond trophic and estuarine-use guilds, could provide deeper insights. Future research should incorporate morphological or physiological traits to offer a more mechanistic understanding of community assembly. Nonetheless, given the substantial amount of residual correlations observed, we suggest that future studies consider additional abiotic and biotic factors in order to properly investigate fish species co-occurrence patterns. These may include fine-scale habitat information, other physical and chemical variables, the degree of hydrological connectivity, behavioral traits, and interactions with other taxa.

Random co-occurrence patterns were prevalent in our analyses, and several potential reasons can explain why such patterns may be observed. Firstly, they can arise from the influence of multiple environmental factors, leading to both aggregated and segregated distribution patterns. On some occasions, contrasting assembly processes might offset one another, resulting in patterns of random co-occurrence (García-Baquero and Crujeiras, 2015). Furthermore, the use of presence/absence data in our JSDMs may contribute to random co-occurrence patterns as a consequence of imperfect detection of certain species, leading to false absences in the species presence/absence matrix (Tobler et al., 2019). Imperfect detection is another factor known to significantly impact the predictive accuracy of SDMs and can also affect the outcomes of JSDMs (Lahoz-Monfort et al., 2014; Tobler et al., 2019). To account for potential biases generated by imperfect detection, only data from locations that were sampled on multiple occasions were used in our analysis.

In conclusion, our study acknowledged the importance of environmental conditions in shaping fish communities within a coastal lagoon, while also contributing to the debate about the relevance of biotic interactions. The balanced influence of these processes in Saquarema lagoon challenges oversimplistic models of community structure based solely on abiotic gradients, suggesting that biotic interactions should not be underestimated. We also demonstrated the importance of considering additional factors, such as indirect biotic interactions and environmental harshness, in the modelling of species distributions, especially in disturbance-prone environments where the effects of environmental and biotic filtering may vary according to environmental harshness. While our JSDM approach revealed meaningful co-occurrence patterns, these must be interpreted in light of data limitations and validated with complementary sources. Despite limited evidence to support direct inferences about species interactions, our literature survey and species guilds classifications revealed both positive and negative interactions, including schooling, aggregation, competition, and predator avoidance behavior. Nonetheless, our results showed that detailed diet studies and a better understanding of species interactions is essential to move beyond statistical associations toward mechanistic explanations. Such studies could provide valuable support for results derived from Joint Species Distribution Models.

CRediT authorship contribution statement

Raiana Lima: Writing – original draft, Visualization, Software, Investigation, Formal analysis, Data curation. **Francisco Gerson Araújo:** Project administration, Methodology, Funding acquisition, Conceptualization. **Luciano Neves dos Santos:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Funding acquisition, Conceptualization.

Ethics approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This research was conducted under SISBIO Collection of Species Permit number 10707 issued by ICMBio, Brazilian Environmental Agency.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT-4 in order to check for spelling and grammar errors and improve the language of the manuscript. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Funding

This work was supported by the Fundo Brasileiro para a Biodiversidade – FUNBIO (grant to FGS, ref. 016/2017), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (research grant to LNS, ref. 315020/2021-0, and to FGA), Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) (research grant to LNS, E−26/200.489/2023, master's fellowship to RL, E−26/201.460/2023) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) (master's fellowship to RL).

Declaration of competing interest

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

Acknowledgments

We thank the Graduate Course in Neotropical Biodiversity (PPGBIO-UNIRIO), and people at the Laboratório de Ictiologia Teórica e Aplicada for providing logistic support. We also thank Fundo Brasileiro para a Biodiversidade (FUNBIO), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) and Universidade Federal do Estado do Rio de Janeiro (UNIRIO) for providing financial support.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2025.109528.

Data availability

Data is available from the corresponding author on reasonable request.

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