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PRIMARY RESEARCH PAPER

The response of fish functional guilds to environmental and spatial processes in a Neotropical coastal lagoon

Raiana Lima · **Francisco Gerson Araújo** · **Luciano Neves dos Santos**

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Abstract The degree to which environmental and spatial processes influence functional guilds in spatially structured coastal lagoons remains underexplored, yet this knowledge is critical for improving transferability of ecological models across different locations. We aimed to explore the response of estuarine use (EUFG) and trophic functional guilds (TFG) to environmental and spatial processes in a Neotropical coastal lagoon in southeastern Brazil. Analyses showed that EUFG were slightly more responsive to environmental and spatial processes than TFG, with 38% of their variation primarily influenced by salinity and spatial variables. In contrast, TFG showed a weaker response, with 30% of variation explained driven by depth, salinity, and transparency. The proportion of explained variation in both guild types, although moderate, suggests that additional factors, such as unmeasured environmental variables or biotic interactions, likely play a significant role in driving community assembly. Our results highlight the context-dependent nature of functional guild classification, as different guilds capture distinct ecological signals depending on the ecosystem and the proxies used to represent ecological processes. Thus, the selection of appropriate proxies is crucial, as is identifying ecologically equivalent windows, which could enhance the transferability of findings between coastal lagoons and other spatially structured ecosystems.

Keywords Functional guilds · Spatial autocorrelation · Induced spatial dependence · Variance partitioning · Spatial structures

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R. Lima (✉) · L. N. dos Santos
Theoretical and Applied Ichthyology Laboratory, Department of Ecology and Marine Resources, Federal University of the State Rio de Janeiro, Av. Pasteur, 458, Rio de Janeiro, RJ 22290-240, Brazil
e-mail: limaraiana@edu.unirio.br

L. N. dos Santos
e-mail: luciano.santos@unirio.br

F. G. Araújo
Fish Ecology Laboratory, Department of Animal Biology, Federal Rural University of Rio de Janeiro, BR 465, Km 7, Seropédica, RJ 23851-930, Brazil
e-mail: gerson@ufrrj.br

Introduction

Coastal lagoons are shallow, transitional environments at the interface of land and sea, whose unique hydrology results from the interplay between freshwater inputs and seawater exchanges (Knoppers & Kjerfve, 1999; Pérez-Ruzafa et al., 2011). These ecosystems play a crucial role in sustaining biodiversity and act as nursery, reproductive, and feeding grounds for many fish species across various life stages (Elliott et al., 2007; Esteves et al., 2008; Erzini et al., 2022). This ecological importance is recognized globally, from Mediterranean lagoons in Europe (Verdiell-Cubedo et al., 2013; Mignucci et al., 2023) to subtropical and temperate lagoons in Mexico (Moreno-Pérez et al., 2024) and Argentina (Bruno et al., 2013). Despite varying geomorphology, these systems are universally influenced by similar ecological drivers, such as salinity gradients, habitat complexity, and hydrological connectivity, which structure fish communities across biogeographic and climatic regions (Franco et al., 2006; Velázquez-Velázquez et al., 2008; Alsaffar et al., 2020; Fraley et al., 2021). Understanding the role that each of these drivers plays in community structuring is essential for ensuring the maintenance of these ecosystems and the fisheries they support (Pérez-Ruzafa & Marcos, 2012).

Functional guilds have become a widely used approach in ecological studies to investigate community structure and ecosystem functioning across diverse ecosystems (Franco et al., 2008), including mangroves on the Persian Gulf (Raeisbahrami et al., 2023) and streams in the USA (Hoeinghaus et al., 2001), highlighting its broad applicability. Estuarine use and trophic functional guilds, for instance, are particularly relevant because they provide robust insights into the species' ecological roles and interactions within estuarine ecosystems (Elliott et al., 2007). The first classifies species based on physiological tolerance to environmental variation and migratory patterns throughout their life cycles, while the latter reflects feeding strategies and may reveal potential mechanisms for reducing competition or optimizing resource consumption (Elliott et al., 2007). This approach is useful because it complements traditional taxonomic approaches by revealing underlying ecological processes that drive community shifts across time and space (Lin et al., 2017). Although widely used to investigate questions related to habitat loss (Mohseni et al., 2003), ecosystem health (Welcomme et al., 2006), and trophic state (Cruz et al., 2018), the response of functional guilds to environmental and spatial processes remains underexplored. This knowledge gap is particularly evident in systems characterized by strong environmental and spatial gradients, such as coastal lagoons. A better understanding of how guilds respond to these processes is important to improve transferability between locations and generalization of ecological models.

In coastal lagoons, the interaction between freshwater and seawater often results in pronounced spatial gradients, such as variations in salinity, depth, and temperature, which drive community patterns worldwide (Mouchet et al., 2012; Franco et al., 2019; Santos et al., 2023). Salinity is a key environmental filter in coastal lagoons because it segregates species based on osmoregulatory adaptations, while depth and temperature are more directly related to habitat suitability and seasonal migrations (Pombo et al., 2005; Sosa-López et al., 2007; Telesh & Khlebovich, 2010; Day et al., 2013). Due to their spatial complexity and varying environmental conditions, coastal lagoons serve as ideal systems for studying ecological processes and the responses of biological communities to environmental gradients. Since fishes exhibit diverse dispersal strategies and environmental preferences, their distribution patterns are shaped by both environmental and spatial processes and regulated by species-specific functional traits (Comte & Olden, 2018; Franco et al., 2021). Nevertheless, the extent to which environmental factors and spatial processes affect functional guilds in environments with pronounced spatial gradients remains poorly investigated.

Spatial structuring in aquatic ecosystems can significantly affect species distributions, yet its influence on functional guild composition is underexplored. While fish community structure is known to be influenced by both habitat characteristics and spatial configuration, with factors like ocean connectivity and habitat arrangement within a seascape regulating dispersal patterns and species interactions (Ricart et al., 2018), the specific role of spatial structures is still unclear. Spatial structures can emerge from processes like dispersal limitation, environmental gradients, and biotic interactions (Borcard et al., 2011), all of which have been documented in coastal lagoons globally – from competition influencing species distribution in the Acquatina lagoon, Italy (Maci & Basset, 2009) to salinity-driven patterns in the Terminos lagoon, Mexico (Paz-Ríos et al., 2023). Those processes can generate two distinct forms of spatial structure: induced spatial dependence, which occurs when species distributions reflect the spatially structured environmental variables; and spatial autocorrelation, which results from species-driven processes, such as dispersal constraints, competition, and predation (Legendre &

Legendre, 1998; Borcard et al., 2011). However, relatively few studies explicitly account for both induced spatial dependence and spatial autocorrelation or attempt to disentangle their relative contributions to community assembly—a necessary step for advancing beyond pattern description toward a process-based understanding of species distributions (Wagner & Fortin, 2005). Addressing this gap requires systems that exhibit pronounced environmental and spatial gradients, conditions met by the Saquarema lagoon, located in southeastern Brazil, where riverine input and a permanent sea connection establish a strong marine-estuarine gradient.

The Saquarema lagoon offers an ideal setting to investigate the response of functional guilds to ecological processes and the drivers of fish community patterns in spatially structured coastal systems. The lagoon maintains a direct, though occasionally restricted, connection to the sea via the Barra Franca channel, which remained open during the study period, allowing for continuous seawater exchange and supporting a pronounced marine–estuarine gradient, *i.e.*, salinity, transparency, and oxygen increase, while water temperature decreases from the inner to the outermost areas of the lagoon. This environmental configuration makes the Saquarema lagoon an ideal system for testing the efficiency of functional guilds in spatially structured environments. Understanding which guilds provide better insights into fish community structure in estuarine ecosystems and the mechanisms governing their distribution will be crucial for improving ecological models and guiding conservation strategies not only locally but also across different biogeographic regions.

Therefore, this study aims to (a) assess the response of estuarine use and trophic functional guilds to environmental and spatial processes, identifying which provides a better understanding of community assembly in spatially structured coastal lagoons and (b) investigate the influence of spatial structuring on the functional distribution of fish species, distinguishing between the effects of spatial autocorrelation and induced spatial dependence. Given the well-documented connection between environmental conditions and fish community assembly in coastal lagoons—systems often characterized by strong environmental gradients (González Castro et al., 2009; Selfati et al., 2019; Franco et al., 2021)—we hypothesize that estuarine use functional guilds will be more responsive to environmental variables, while trophic guilds will be more influenced by spatial processes, reflecting dispersal constraints and resource availability. We anticipate that the effects of induced spatial dependence will be more pronounced in estuarine use guilds, as species distributions are largely dictated by salinity gradients and habitat preferences. On the other hand, we expect spatial autocorrelation will be more prominent in trophic guilds, as species interactions (*e.g.*, competition and predation), resource availability, and dispersal limitation may lead to aggregated spatial patterns (Borda-de-Água et al., 2012).

Material and methods

Study area

Saquarema lagoon (22º54'S–42º33'W) is located along the coast of the State of Rio de Janeiro, Brazil (Fig. 1). Covering an area of approximately 21.2 km^2, it is composed of four large, interconnected water bodies: Urussanga (12.6 km^2), Jardim (2 km^2), Boqueirão (0.6 km^2), and Fora (6.0 km^2) (Azevedo, 2005). The lagoon has an average depth of 1.0 m and receives freshwater input from six rivers: Mato Grosso, Tinguí, Jundiá, Seco, Padre, and Bacaxá (Azevedo, 2005). It is considered a "choked" lagoon due to its restricted connection to the sea during some periods of the year and its single connection channel, which is long, narrow, and silted on some occasions (Kjerfve, 1994). Average salinity in the lagoon ranges from 16 to 40, and water renewal time for 50% of the volume in the Urussanga and Fora lagoons is 23 and 6 days, respectively (Knoppers et al., 1991; Franco et al., 2019). The climate of the region, according to the Köppen-Geiger classification, is Aw (tropical with dry summer), with seasonal patterns of rainfall and an average annual temperature of 25 ºC (Carmouze et al., 1991; Alvares et al., 2013; Valadão et al., 2020). During the spring and summer seasons, the Fora lagoon receives cold, nutrient-rich waters from the upwelling of the South Atlantic Central Water (SACW) (Erbas et al., 2021).

Data collection and processing

Samplings were performed every two months from September 2017 to July 2019. Nine sampling sites

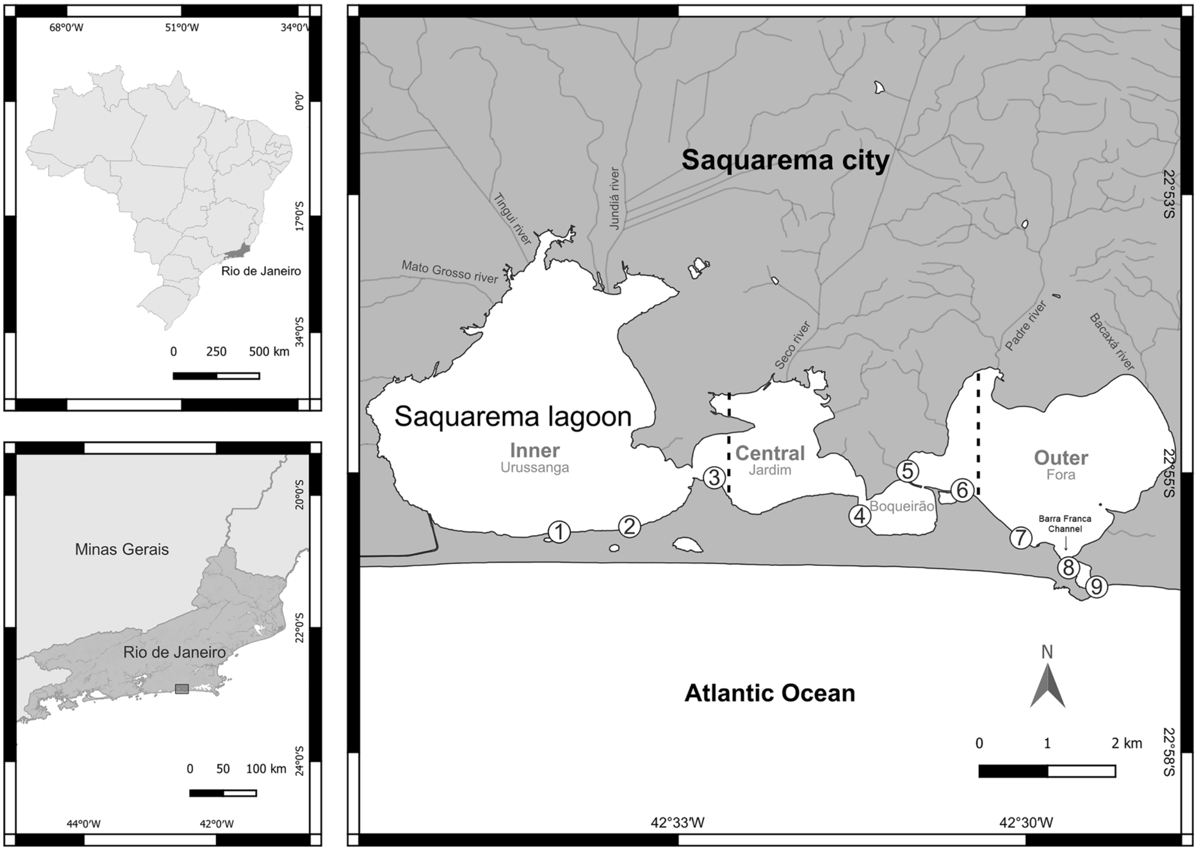

Fig. 1 Geographic location of Saquarema Lagoon, showing three zones (inner, central, and outer) and nine sampling sites distributed across the lagoon according to their proximity to the connecting channel (Barra Franca Channel)

Table 1 Estuarine use and trophic functional guilds and their definitions (adapted from Elliot et al., 2007 and Potter et al., 2015)

Functional guilds	Term	Description
Estuarine use	Marine stragglers	Species that spawn at sea and usually enter estuaries in low numbers
	Marine migrants	Species that spawn at sea and enter estuaries in large numbers and particularly as juveniles
	Estuarine	Species that complete their life cycles within the estuary
	Semi-anadromous	Species whose spawning occurs from the sea and extends only to the upper part of the estuary, not into fresh water
	Freshwater	Freshwater species found in moderate or low numbers in estuaries
Trophic	Zooplanktivores	Feed predominantly on zooplankton
	Zoobenthivores	Feed predominantly on invertebrates associated with substratum
	Detritivores	Feed predominantly on detritos
	Herbivores	Graze predominantly on living macroalgal and macrophyte material or phytoplankton
	Omnivores	Feed predominantly on filamentous algae, macrophytes, epifauna, and infauna
	Piscivores	Feed predominantly on finfish
	Opportunists	Feed on such a diverse range of food that cannot be assigned to one of the guilds above

were strategically distributed across the lagoon, covering three distinct zones defined by their proximity to the connecting channel, namely the inner (*i.e.*, furthest zone from the channel), central (*i.e.*, intermediate zone), and outer (*i.e.*, closest zone to the channel) zones. At each site, sampling was carried out in three replicates ($N = 3$) and fish were collected using a beach seine net (20 m width × 1.5 m height; 7 mm mesh size) during daylight hours from 0900 to 1700 h. Samplings took place on the beach shore, with the net deployed perpendicular to the shoreline at a distance of 20 m to the shore, and equipped with 20 m of hauling ropes, effectively covering an approximate sampled area of 400 m^2. Standardized sampling efforts were performed by two people, one at each end of the rope, with each sampling lasting, on average, 10 min. During each sampling event, 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 transparency-to-depth ratio) were measured with a Secchi disk. During data processing the average of the three replicates per site was calculated to address pseudoreplication, resulting in one value per site. To categorize the samples according to rainfall conditions, we used monthly rainfall data (mm) from the National Institute of Meteorology (INMET). We adopted a 60 mm threshold to differentiate the months; a standard criterion derived from the Köppen-Geiger classification system to define a dry month in tropical climates. Thus, sampling months with precipitation above 60 mm were classified as 'wet months' (jan/18, mar/18, may/18, nov/18, mar/19, and may/19), while those with precipitation below 60 mm were classified as 'dry months' (sep/17, nov/17, jul/18, jan/19, and jul/19).

We used marine fish identification manuals (Figueiredo & Menezes, 1978, 1980, 2000; Menezes & Figueiredo, 1980, 1985) and consulted relevant recent literature to identify the captured specimens. Taxonomic classification and nomenclature were checked and updated according to Eschmeyer's Catalog of Fishes: Genera, Species, References (Fricke et al., 2023) and Eschmeyer's Catalog of Fishes: Genera/Species by Family/Subfamily (Fricke et al., 2023). After taxonomic identification, each specimen was weighed using a precision scale (0.001 g) and measured (TL—total length in mm). Species were then classified into estuarine use and trophic functional guilds according to their environmental preferences and feeding behaviors, following the guild classification proposed by Elliot et al. (2007) and Potter et al. (2015) (Table 1). These two guilds were selected because they are among the most widely used functional guilds in ecological studies because they effectively capture species' functional roles and habitat dependencies and have been successfully used to analyze fish community structure and ecosystem functioning, particularly in the context of estuarine ecosystems and fish community dynamics (Franco et al., 2008; Cruz et al., 2018; Favero et al., 2019; Franco et al., 2021). These guilds are directly tied to key ecological processes, such as resource partitioning, trophic interactions, and habitat connectivity, which makes them particularly relevant to estuarine studies. Prior to guild classification, to prevent biases in our analyses and the functional guild classification due to ontogenetic changes, we used the total length of individuals at the first maturation (L50) available on FishBase (Froese & Pauly, 2023) to categorize species into juveniles ($TL < L50$) and/or adults ($TL \geq L50$) life stages (Online Resource Table 1).

Statistical analysis

We performed a Principal Coordinate of Neighbourhood Matrix analysis (PCNM; Borcard & Legendre, 2002; Dray et al., 2006) to generate spatial variables based on the geographical coordinates (latitude and longitude) of each sampling site. During this step, we used the "distm" function from the "geosphere" package v1.5–18 (Hijmans et al., 2022) to create the distance matrix based on the Haversine great-circle distance and performed the PCNM analysis using the "pcnm" function from the "vegan" v2.6–4 package (Oksanen et al., 2022). The PCNM eigenvectors represent a spectral decomposition of the distance matrix, capturing all spatial scales present in the sampling design and revealing the underlying spatial processes structuring the community (Dray et al., 2006). Only PCNM eigenvectors with positive eigenvalues were selected (Borcard & Legendre, 2002). To identify the role of each PCNM and the spatial process that they may represent, we performed Pearson correlation tests between the PCNM eigenvectors and two distance measures: the distance from each sampling site to the mouth of the connecting channel and the distances to the mouths of the six rivers flowing into the lagoon. Additionally, we performed Spearman correlation tests between the PCNM eigenvectors and (i) the abundance of estuarine use guilds and (ii) the biomass of trophic guilds. Both correlation analyses were performed using the "cor" function from the "stats" v.4.3.0 package (R Core Team, 2023).

We performed a Principal Component Analysis (PCA) to ordinate the samples according to spatial predictors and environmental variables (centered and standardized data of transparency, temperature, salinity, depth, pH, and dissolved oxygen) using the "rda" function from the "vegan" package. To identify the best subset of PCNM eigenvectors to be included in the analysis, we used the "envfit" function, which fits supplementary variables on ordination scores through multiple regression and assesses the significance of each variable (*i.e.*, PCNM eigenvectors) by using a permutation test. We used the function "PCAsignificance" available in the "BiodiversityR" v2.15–2 (Kindt, 2017) to estimate the number of significant axes using the broken stick criterion. We applied a two-way Permutational Analysis of Variance (PERMANOVA; Anderson, 2001) to the scores of the first two PCA axes to test for significant differences between zones and rainfall conditions (wet vs. dry), as well as for their interaction. The PERMANOVA based on Euclidian distance and 9999 permutations was performed using the "adonis" function from the "vegan" package (Anderson, 2017). Whenever significant differences or interactions were detected, pairwise tests were applied using the "pairwise.adonis" function from the "pairwiseAdonis" v0.4.1 package (Martinez, 2020).

To assess collinearity among predictors, we performed the Pearson correlation test and calculated the Variance Inflation Factor (VIF) for each environmental variable, using the "cor" function from the "stats" package and the "multicol" function from the "fuzzySim" v4.9.9 package (Zuur et al., 2010; Barbosa 2023). All variables showed Pearson's $|r|$ values below 0.7 and VIF values below 3 (Zuur et al., 2010; Online Resource Tables 2 and 3), indicating acceptable levels of collinearity, and were therefore included in the subsequent analyses.

We performed a Redundancy Analysis (RDA) to explore the relationships between environmental variables, spatial predictors, and the abundance of estuarine use functional guilds as well as the biomass of trophic guilds. The analysis was conducted using the "rda" function from the "vegan" package. Prior to RDA, abundance and biomass data were Hellinger transformed to address the double-zero problem in ordination analyses (Rao, 1995; Legendre & Gallagher, 2001). Environmental variables were centered and standardized to a mean of zero and a standard deviation of one. The most important spatial and environmental predictors were selected by the "forward selection" method (Blanchet et al., 2008), using the "ordiR2step" function from the "vegan" package. This step helped identify the best subset of PCNMs and environmental variables that significantly contributed to improving the model's predictive power. The "forward selection" was only performed when the global model was significant (all variables included in the model), to avoid biased variable selection (Blanchet et al., 2008). We tested the significance of the RDA models and their axes through an Analysis of Variance (ANOVA; Legendre et al., 2011) using the "anova.cca" function from the "vegan" package.

We performed a Variance partitioning analysis to determine how much variation in the abundance and biomass of guilds was explained by environmental variables, spatial predictors (PCNM eigenvectors), using the "varpart" function in the "vegan" package. This analysis allows us to partition the total percentage of variation explained by an RDA into unique contributions from the environment and space, as well as their shared contribution (Borcard et al., 1992). We tested the significance of the environmental and spatial fractions by performing an ANOVA using the "anova.cca" function. It is worth noting that during the adjustment process, negative r^2 values may arise. All statistical analyses were carried out in R software version 4.4.6 (R Core Team, 2023) via RStudio (RStudio Team, 2020).

Results

Correlation between PCNM vectors and distance matrices

The Pearson correlation revealed that PCNM1 was strongly negatively correlated with the distance from the connecting channel ($r = -0.94$), as well as with the distances from the Padre and Bacaxá rivers ($r = -0.80$ and $r = -0.94$, respectively), both located

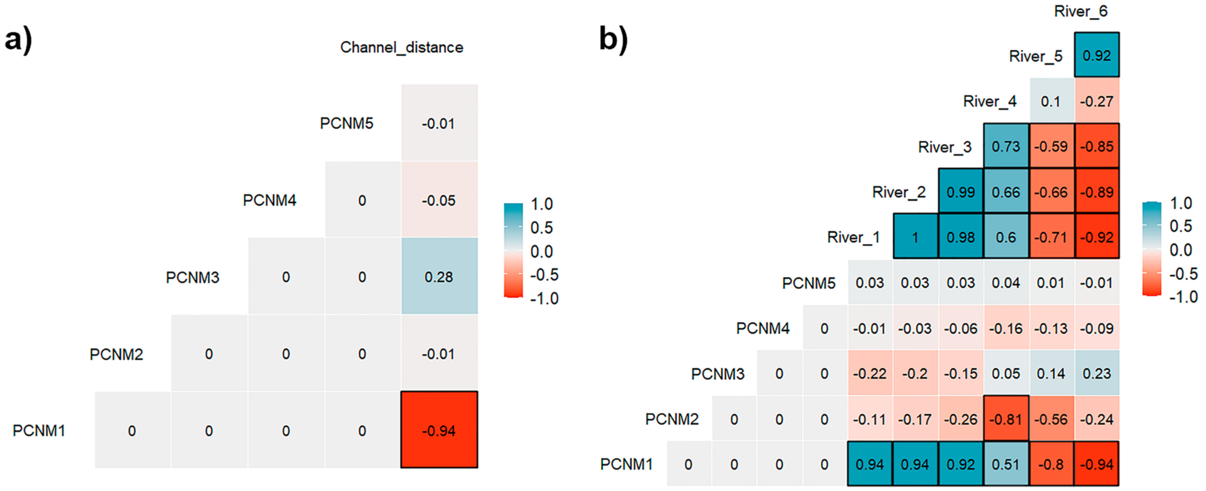

Fig. 2 Plots of the Pearson's correlations between PCNM eigenvectors with the distance to the connecting channel (**a**) and the six main rivers (**b**). Significant correlations are highlighted with a black square ($P < 0.05$). Color gradients (from red to blue) represent negative and positive correlations, respectively. The strength of correlations is represented by the correlation coefficient. Rivers 1, 2, and 3 refer to Mato Grosso, Tingui, and Jundiá rivers; River 4 refers to Seco river; Rivers 5 and 6 refer to Padre and Bacaxá rivers

in the outer zone. This indicates that as the distance to the channel and the outer zone increases, the influence of the spatial process represented by PCNM1 decreases (Fig. 2a and b). Thus, PCNM1 could serve as a proxy for processes associated with a marine-estuarine gradient, primarily mediated by the connecting channel. On the other hand, PCNM2 showed a strong negative correlation with the distance from Seco river ($r = -0.81$), while PCNM1 showed a moderate positive correlation with the same river ($r = 0.51$). These findings suggest that the influence of the spatial process represented by PCNM1 increases with the distance from Seco river, located in the central zone, whereas the influence of PCNM2 decreases.

Environmental variables

The first two PCA axes jointly explained 59.1% of the total variance, with Axis 1 accounting for 40.7% (eigenvalue = 3.66) and Axis 2 accounting for 18.4% (eigenvalue = 1.65) of the data variance (Fig. 3). PCNMs 1, 3, and 4 were selected as the best spatial predictors to be included in the analysis ($p = 0.001$, $p = 0.01$, $p = 0.02$, respectively). PCA axis 1 primarily captured spatial variation, with samples ordinated based on temperature and pH. Samples from the inner zone were predominantly distributed on the left side of the diagram, correlating with higher values of temperature ($r = -0.47$) and pH ($r = -0.48$), while outer zone samples displayed an opposite pattern. PCA axis 2 ordinated samples based on depth and transparency. Samples positively correlated with higher depth values ($r = 0.68$) clustered in the upper side of the diagram, while those correlated with higher transparency ($r = -0.55$) were primarily distributed in the lower part. Samples from the central zone were scattered across the diagram and overlapped with those from the inner and outer zones, suggesting that they share similar environmental conditions with the other zones. No variation was observed between rainfall conditions (wet vs. dry). These findings were further supported by PERMANOVA analysis performed on the first two PCA axes scores (Table 2).

Guilds, space, and environmental variables

The RDA used to explore the relationship between estuarine use functional guilds and spatial/environmental variables identified salinity, depth, and PCNM1 as the key drivers of these relationships (Fig. 4). Four variables—dissolved oxygen, pH, and PCNMs 3 and 4—were excluded from the RDA during the forward selection procedure. The first two RDA axes jointly explained 41% of the total

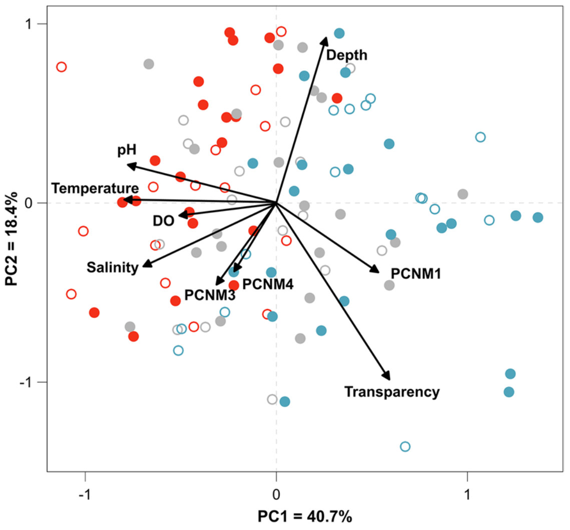

Fig. 3 Ordination diagram (biplot) of the zones and rainfall conditions (wet vs. dry) according to the principal components analysis (PCA) performed on the environmental variables and the selected PCNM eigenvectors. Samples were labeled by zones (red = inner zone; gray = central zone; blue = outer zone) and rainfall conditions (● = wet months; ○ = dry months)

variance (ANOVA, $F = 8.89$; $p = 0.001$), with RDA axis 1 (36.1%; eigenvalue = 0.11; ANOVA, $F = 63.34$; $p = 0.001$) splitting guilds based on salinity. Higher abundance of the estuarine guild was positively correlated with higher salinity values ($r = 0.59$), while the semi-anadromous guild displayed the opposite trend. RDA axis 2 (4.9%; eigenvalue = 0.01; ANOVA, $F = 8.68$; $p = 0.1$) split guilds based on PCNM5 and dissolved oxygen, with higher abundance of the marine migrant guild negatively correlated with PCNM5 ($r = -0.54$).

Table 2 Results of the PERMANOVA analysis and the pairwise test performed on the scores of the PCA axes by zones, rainfall conditions (wet vs. dry), and interaction between both

PERMANOVA		PC1	PC2	Pairwise
Zones	*F*	34.79	1.95	I≠C; I≠O; C≠O
	p	**0.0001**	0.14	
Rainfall conditions	*F*	1.09	0.44	–
	p	0.30	0.49	
Interaction	*F*	0.02	0.45	–
	p	0.97	0.63	

I inner zone, *C* central zone, *O* outer zone

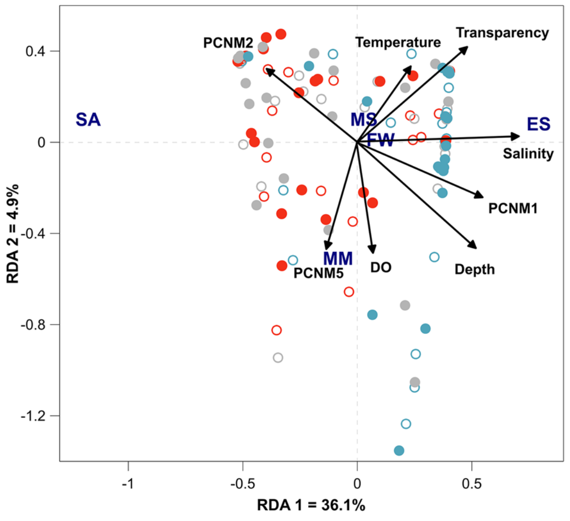

Fig. 4 Ordination diagram (triplot) of the zones and rainfall conditions (wet vs. dry) according to the redundancy analysis (RDA) performed on the Hellinger-transformed abundance of estuarine use functional guilds, environmental variables, and the PCNM eigenvectors selected by the forward selection. Samples were labeled by zones (red = inner zone; gray = central zone; blue = outer zone) and rainfall conditions (● = wet months; ○ = dry months). Estuarine use functional guilds: *MS* marine stragglers; *MM* marine migrants; *ES* estuarine species; *SA* semi-anadromous; *FW* freshwater. Environmental variables coding: *DO* dissolved oxygen

For trophic functional guilds, temperature, depth, salinity, and transparency were the main drivers of the relationship between these guilds and spatial/environmental variables (Fig. 5). Three variables—pH, dissolved oxygen, and PCNM 5—were excluded during the forward selection procedure. The first two RDA axes jointly explained 31.8% of the total variance (ANOVA, $F = 6.61$; $p = 0.001$), with RDA axis 1 (22.6%; eigenvalue = 0.06; ANOVA, $F = 34.69$; $p = 0.001$) splitting guilds based on depth, salinity, and transparency. Higher biomass of the opportunist guild was positively correlated with depth ($r = 0.53$). RDA axis 2 (9.2%; eigenvalue = 0.02; ANOVA, $F = 14.09$; $p = 0.01$) was negatively correlated with temperature ($r = -0.74$), and most of the guilds were clustered in the center of the diagram, showing no clear correlation with any environmental or spatial predictors.

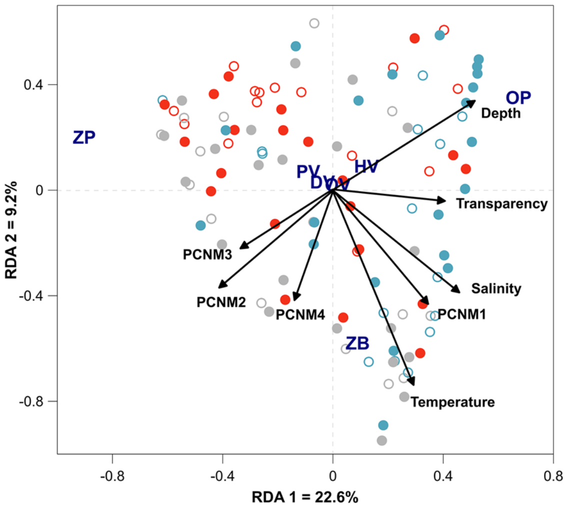

Fig. 5 Ordination diagram (triplot) of the zones and rainfall conditions (wet vs. dry) according to the redundancy analysis (RDA) performed on the Hellinger-transformed biomass of trophic functional guilds, environmental variables, and the PCNM eigenvectors selected by the forward selection. Samples were labeled by zones (red = inner zone; gray = central zone; blue = outer zone) and rainfall conditions (● = wet months; ○ = dry months). Trophic functional guilds: *ZP* zooplanktivores; *DV* detritivores; *HV* herbivores; *OV* omnivores; *PV* piscivores; *ZB* zoobenthivores; *OP* opportunists

Variance partitioning

Variance partitioning analysis showed that environmental variables, spatial processes, and their interactions explained 38% of the total variation in the abundance of estuarine use functional guilds (Table 3). Environmental variables, both purely and spatially structured, explained approximately 32% of the variation. Twenty-one percent of the variation was attributed to purely environmental variables, while the shared fraction between environment and space (*i.e.*, induced spatial dependence) explained 11%. Six percent of the variation was uniquely explained by space (*i.e.*, spatial autocorrelation).

For the trophic functional guilds, the analysis showed that environmental variables, spatial processes, and their interactions explained a small amount of the variation accounting for 30% of the total variation (Table 3). Environmental variables, both purely and spatially structured, explained approximately 24% of the variation. Seventeen percent of the variation was attributed to purely environmental variables, while the shared fraction between environment and space explained 7%. Six percent of the variation was uniquely attributed to space.

Table 3 Results of the variance partitioning analysis performed on the output of the redundancy analysis (RDA) applied to the abundance and biomass of estuarine use (EUFG) and trophic functional guilds (TFG)

Variance partitioning	EUFG R^2	TFG R^2
Environment	0.21***	0.17***
Space	0.06**	0.06***
Shared	0.11	0.07
Residual	0.62	0.70

***0

**0.001

*0.01

Discussion

Our findings revealed that both environmental and spatial processes played a role in structuring functional guilds in the Saquarema lagoon, although their explanatory power was limited, highlighting the complexity of community dynamics in coastal ecosystems. While estuarine use functional guilds were slightly more responsive to environmental and spatial processes compared to trophic guilds, partially supporting our hypothesis, the moderate explained variation in both guild types suggests that additional drivers, such as unmeasured environmental variables, biotic interactions, or methodological constraints, may influence community assembly in coastal lagoons. These findings also suggest that the choice of functional guild may be context-dependent, as different guild classifications capture distinct ecological signals depending on the ecosystem and the proxies used to represent spatial and environmental processes. Some implications of our findings are further discussed below.

The predominance of environmental factors, particularly salinity, in structuring estuarine use guilds we found aligns with previous studies in coastal lagoons, where salinity gradients are a key determinant of species distributions (Akin et al., 2005; Franco et al., 2019, 2021). In addition, the role of induced spatial dependence we observed in structuring these guilds highlights the extent to which species distributions are also influenced by environmental gradients that inherently exhibit spatial structure, as outlined by Wagner & Fortin, 2005. While the proportion of explained variation we observed in both estuarine use and trophic guilds was moderate, it is consistent with values reported in similar ecological studies and reflects the complexity of estuarine and lagoon fish communities, which are driven by several interacting biotic and abiotic factors (Selleslagh & Amara, 2008; Camara et al., 2018; Franco et al., 2019; Camara et al., 2020). Such results highlight the challenges of modeling community assembly in dynamic and spatially heterogeneous systems and suggest that the choice of functional guilds based on performance may be context dependent, *i.e.*, influenced by the particular characteristics of the ecosystem and the ecological processes operating within it.

Context dependence, as described by Catford et al. (2022), refers to ecological relationships that vary in strength or direction depending on the specific conditions under which they are observed. In our study, the unexplained variation not captured by environmental or spatial predictors could be attributed to apparent context dependence (Catford et al., 2022). Apparent context dependence can arise from several sources, including confounding factors (*e.g.*, unmeasured variables like nutrient availability or habitat complexity), statistical inference issues (*e.g.*, low statistical power or measurement errors), or methodological differences (*e.g.*, variations in how functional guilds were defined or measured). These sources of variation could also explain the slightly lower response we observed in trophic guilds, which are likely more sensitive to unmeasured variables like resource availability and species interactions.

Previous research has shown that species–habitat relationships vary depending on environmental and spatial factors, making generalizations across different ecosystems challenging (Igulu et al., 2014; Ricart et al., 2018; Bradley et al., 2019). For instance, estuarine use guilds, which are closely tied to physiological adaptations (*e.g.*, salinity tolerance) and migration patterns (Elliot et al., 2007), may be more effective in systems with pronounced environmental gradients, as observed in the Saquarema lagoon. In contrast, trophic guilds, which reflect resource availability and species interactions (Elliot et al., 2007), may be more informative in systems where additional ecological factors, such as dispersal limitation or biotic interactions, which were not explicitly considered in our study, play a stronger role. The limitations of generalizing functional guild classifications highlight the need for further refinement and suggest that their response may also vary depending on the proxies used and the scale of analysis.

Our findings also emphasize the importance of selecting appropriate proxies to quantify environmental and spatial processes. The response of functional guilds to these processes likely depends on the specific proxies used to quantify spatial structure, as well as the environmental gradients present in the system, capturing different aspects of species distributions and community structuring (Bradley et al., 2020). This highlights the importance of carefully selecting spatial frameworks tailored to the ecological question at hand and to establish ecologically equivalent windows, *i.e.*, ranges of similarity in key predictors between ecosystems, to determine when findings are transferable (Bradley et al., 2020). Additionally, incorporating other functional guilds, such as reproductive and dispersal guilds, can provide further insights into the processes driving community assembly (Troia & Gido, 2015).

A key limitation of our study is that we only considered two functional guild types, which may not fully capture the ecological complexity of fish communities and potentially overlook other functional aspects that could refine our understanding of fish community dynamics. Future studies should consider including additional guilds, such as those based on reproductive strategies or habitat preferences, as well as incorporating broader environmental and spatial datasets, to better capture the complexity of these ecosystems. Additionally, expanding the study to other aquatic ecosystems, such as freshwater lakes or marine environments, could also help determine the generalizability of our findings. A broader comparison across systems with different hydrological and spatial configurations would further clarify whether the observed patterns hold across diverse contexts.

Conclusion

In conclusion, while salinity and induced spatial dependence emerged as important drivers, particularly for estuarine use guilds, the limited explanatory power of our analyses reveals the complexity of the ecological processes structuring functional guilds within coastal lagoons, emphasizing the context-dependent nature of the relationships we observe. Overall, our findings suggest that additional factors such as unmeasured environmental variables, biotic interactions, and methodological choices may be at play and significantly influence guild response. Additionally, the choice of proxies used to represent ecological processes is critical, as they alter the interpretation of community dynamics and may depend on the ecological equivalence of the study system, *i.e.*, where habitats in different locations may function similarly if they share key predictors, thereby enhancing the transferability of ecological models. By identifying the ecologically equivalent windows for different systems, future research could improve the transferability of findings across coastal lagoons and other spatially structured ecosystems. Adopting such an approach would enable a more comprehensive understanding of coastal lagoons while improving the predictive power of ecological models. Only by addressing these gaps can we advance our knowledge on the drivers of community patterns in dynamic coastal environments.

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Author contributions Raiana Lima contributed toward conceptualization, investigation, data curation, formal analysis, software, visualization, and writing—original draft. Francisco Gerson Araújo contributed toward conceptualization, project administration, funding acquisition, and methodology. Luciano Neves dos Santos contributed toward conceptualization, funding acquisition, resources, methodology, investigation, validation, supervision, and writing—review & editing.

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Data availability All relevant data are available in the paper and its Supplementary Information. Additional data is available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no competing interests.

Ethical 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.

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