

RESEARCH ARTICLE

Local-scale distribution and habitat filtering of annelids in a subtropical estuary

Gabriel P. da Silva¹ , Ricardo C. Álvarez² , Fabricius M.C.B. Domingos³ and Maikon Di Domenico⁴

¹Programa de Pós-Graduação em Zoologia, Departamento de Zoologia, Universidade Federal do Paraná. Caixa Postal 19020, 81531-980 Curitiba, PR, Brazil.

²Departamento de Invertebrados, Museu Nacional, Universidade Federal do Rio de Janeiro. Quinta da Boa Vista, São Cristóvão, 20940-040 Rio de Janeiro, RJ, Brazil.

³Departamento de Zoologia, Setor de Ciências Biológicas, Universidade Federal do Paraná. Caixa Postal 19020, 81531-980 Curitiba, PR, Brazil.

⁴Laboratório de Ecologia Marinha, Centro de Estudos do Mar, Universidade Federal do Paraná. Avenida Beira-mar, 83255-000 Pontal do Paraná, PR, Brazil.

Corresponding author: Gabriel P. da Silva (gabriel dpaula.silva@gmail.com)

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ABSTRACT. Recording the small-scale distribution of organisms in changing environments is crucial for understanding local ecological patterns. We surveyed annelids from mangroves across different estuarine environments (open areas as unstable environments; control and closed areas as more stable environments) and habitats (vegetated, non-vegetated, and transitional zones) at Ararapira Inlet, Guaraqueçaba, Paraná, Brazil. During spring and autumn, we collected 288 samples using a corer, with a 0.5 mm mesh to separate fauna from sediment. We identified 937 individuals across 33 species, 18 families, and 28 genera, with Nereididae being the most represented family. The nereidid species *Laeonereis acuta* and *Nereis oligohalina* were the most abundant, with 254 and 149 individuals, respectively. Regarding endemism, 17 species are native and eight are non-indigenous, while information is lacking for seven. Our Linear Mixed Model showed that both abundance and species richness were generally lower in Control and Open areas, as well as in vegetated habitats, with positive interactions between area and vegetated habitats. The Control area exhibited higher Shannon diversity and evenness, while Simpson diversity was higher in the closed area. The transitional zone had the highest richness (23 taxa), followed by the non-vegetated habitat (19) and the vegetated habitat (14). Differences in Shannon and Simpson diversity were observed among areas, with the most established environments displaying the highest diversity. Microphage was the dominant feeding mode, with 15 taxa (46%), followed by omnivory with ten (30%), and macrophage with eight (24%). We conclude that the species respond to a complex combination of spatial scale and environment type, reinforcing the need to consider multiple ecological drivers when analyzing community structure.

KEYWORDS. Checklist, macrofauna, mangrove, polychaeta, spatial scale.

INTRODUCTION

Mangrove ecosystems are among the most structurally complex coastal habitats, providing highly heterogeneous environments that sustain diverse faunal assemblages (Schaeffer-Novelli et al. 1990). Such environmental heterogeneity creates a mosaic of microhabitats that influences how species are distributed at small spatial scales, reflecting

differences in functional requirements, life-history strategies, and morphological adaptations (Stein et al. 2014, Van Son et al. 2014). The structure and functional traits of annelids in mangroves depend on the spatial scale (Freitas and Pagliosa 2020). Understanding how this fine-scale variation shapes community composition is essential to interpret the structure and functioning of mangrove ecosystems (Stein et al. 2014, Van Son et al. 2014).

Environmental processes act at multiple spatial scales and influence the structure and function of marine macrofauna communities (Freitas and Pagliosa 2020). As global-scale biodiversity loss in coastal habitats advances, understanding how benthic community diversity responds to environmental change is essential (Rodil et al. 2021). The southern hemisphere harbors a higher diversity of polychaete species, many of which are endemic (Pamungkas et al. 2021). Investigating local-scale distribution across different spatial scales provides essential information to understand biodiversity changes related to environmental variations of conservation concern (Chave 2013, Pincebourde et al. 2016).

There is a known relationship between macrofauna diversity and gradients of environmental complexity (Rodil et al. 2021). Mangrove invertebrates often show zonation patterns, colonizing a variety of micro-environments (Nagelkerken et al. 2008), and the presence of vegetated habitats in mangroves influences the local-scale distribution of macrofauna (dos Santos et al. 2024). As such, annelids can serve as environmental indicators of ecosystem health, particularly because of their sensitivity to degradation and pollution (Giangrande et al. 2005, Dean 2008) and their rapid response to environmental changes (Elías et al. 2021). Nonetheless, assessing biodiversity changes over seasons or following environmental disturbances is not a trivial task (Magurran 2021). Hence, investigating the local-scale distribution patterns of macrofaunal biodiversity can provide valuable insights into the functioning of mangrove environments (Quiroz-Martínez et al. 2021) and serve as a baseline for studying future environmental issues.

Annelida is one of the most diverse animal groups, with representatives from terrestrial, freshwater, and marine environments (Capa and Hutchings 2021). These animals are the predominant group in terms of abundance in soft-bottom substrates (Nagelkerken et al. 2008), exhibit a high degree of diversification, and possess complex functional traits (Freitas and Pagliosa 2020). The number of known species in the group is steadily increasing, primarily due to recent taxonomic revisions that have led to the discovery of new species (Capa and Hutchings 2021). Studies on benthic ecology and the taxonomy of marine annelids in Brazil date back to the 1960s (Lana et al. 2017). According to Amaral et al. (2022), about 1,343 species of polychaetes are currently known to occur in the country, spanning 463 genera and 76 families. Among members of macrofaunal communities, annelids are one of the most common taxa, exhibiting relatively high species richness and dominant abundance, comprising more than half of soft-bottom communities

(Quiroz-Martínez et al. 2021). They also display a high diversity of feeding types (Jumars et al. 2015) and functional traits (Faulwetter et al. 2014).

The most recent checklist of polychaetes from Paraná state included collections from Paranaguá and Guaratuba bays and samples from shallow bottoms on the northern continental shelf of the state, recording 44 families, 164 genera, and 259 species (Lana et al. 2006). Despite the historical efforts of numerous researchers who contributed to the inventory of species in the state (e.g., Lana et al. 2006), the Ararapira Inlet remained unexplored. This vast inlet is a dynamic estuary with periodic landscape changes (Angulo et al. 2019).

Given the pronounced geomorphological and hydrological shifts recently observed in the Ararapira Inlet, establishing a baseline inventory of its benthic fauna is essential. This study provides the first assessment of local-scale species distribution in the region, generating baseline data to detect potential spatial trends and future changes in mangrove ecosystem structure and function.

MATERIAL AND METHODS

Study area

The Ararapira Inlet is located between the states of Paraná and São Paulo, in the municipality of Guaraqueçaba (Fig. 1), forming part of the Cananéia-Paranaguá Estuarine Complex (Italiani et al. 2020). It spans approximately 16 km, with an average width of 400 m (Angulo et al. 2009). Over the last few years, a significant landscape change has impacted the local habitats: a new inlet opened in August 2018, and the older inlet closed in 2019 (Angulo et al. 2019).

Sampling and identification

We sampled the Ararapira Inlet during two seasons (Spring – October 2023 and Autumn – April 2024) in unconsolidated mangrove sediments and sandy beach substrates using a PVC corer (20 cm height × 15 cm diameter). Sampling was carried out across three areas (50 × 50 m each) representing a disturbance gradient: Closed inlet (area undergoing stabilization), control (ecologically stable area with minimal landscape changes), and Open inlet (unstable area under intense hydrodynamic influence).

Within each area, we established three habitats representing a vegetation gradient from mangrove to bare sand: vegetated (V) (mangrove forest, with salt marshes also present in the Closed inlet), transition zone (TZ) (interface between vegetated and bare areas), and non-vegetated (NV) (mud or sand flats).

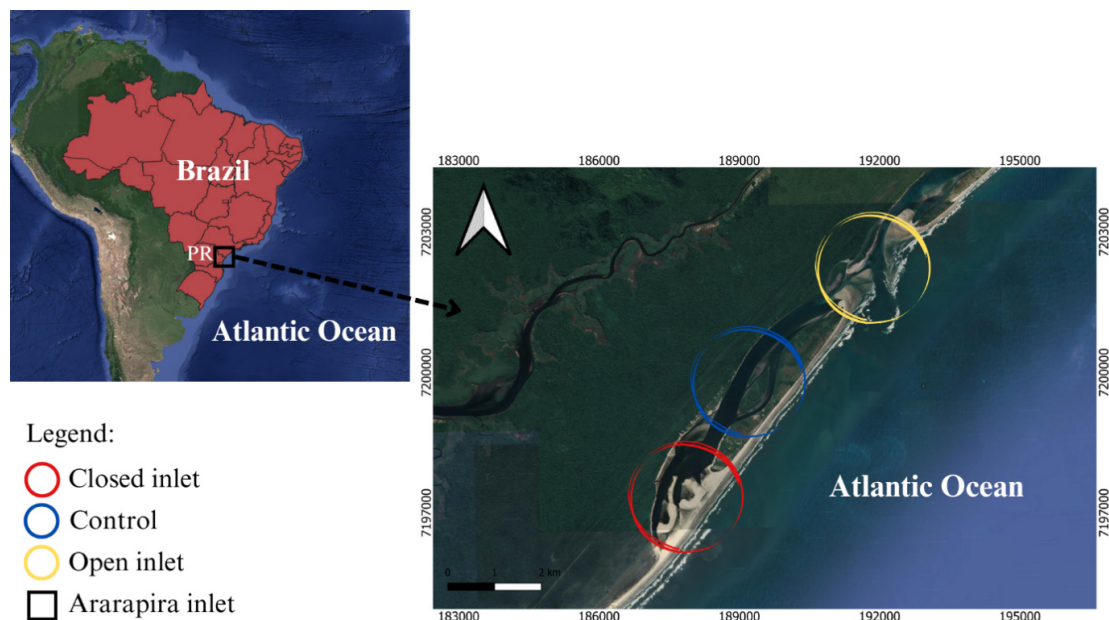


Figure 1. Ararapira Inlet, Paraná, Brazil. The three different sampling areas are shown: Closed inlet (red), Control area (blue) that remained relatively unchanged during the dynamic landscape events, and the Open inlet (yellow), which appeared in 2018.

In each habitat, four 1×1 m quadrats were randomly placed, and four random sampling units were collected within each quadrat, totaling 16 samples per habitat and 48 samples per area. This design resulted in 144 samples per season (288 in total). All samples were stored in plastic bags and sieved through a 0.5 mm mesh to separate the fauna from the sediment.

We anesthetized the annelids with isotonic magnesium chloride, fixed them in 3.7% formaldehyde, and then transferred them to 70% ethanol. For identification, a stereomicroscope and a Primo Star microscope (Zeiss) were used. Families and genera were initially identified based on Amaral and Nonato (1996), and more recent literature was used for detailed identifications (e.g., Conde-Vela and Salazar-Vallejo 2015, Wilson et al. 2023).

Species identification was performed by checking specialized taxonomic literature. Temporary glycerol slides were prepared to observe the morphology of parapodia and chaetae. We followed the most recent Annelida phylogenetic classification (Rouse et al. 2022) and adhered to the nomenclature in the World Register of Marine Species (WoRMS 2025). The dataset follows the Darwin Core format (Table S1). For feeding types, we followed Jumars et al. (2015), considering Microphage (MICRO), Macrophage (MACRO), and Omnivore (OMN). We conducted a literature review on the

Brazilian distribution of each taxon recorded in the area and added new records for Paraná state. Their invasive status in Brazil was categorized as Native (N), Non-Indigenous Species (NIS), or Cryptogenic (C) based on Lopes (2009), Rocha et al. (2013), and Teixeira and Creed (2020).

Data analysis

We used R version 4.3.3 (R Core Team 2024) to analyze the data. Diversity was estimated using Simpson's and Shannon's indices. Pielou's evenness was also calculated for each area. Hill numbers represent the effective diversity of a biological community; this approach unifies different diversity indices within a single framework modulated by a sensitivity parameter (q). A rarefaction curve was built using the vegan package.

We used linear mixed-effects models (LMM) to evaluate the effects of area (Closed, Control, and Open inlet) and habitat (vegetated, transition zone, and non-vegetated) on annelid abundance and species richness across seasons (spring and autumn). Separate models were fitted for each season to account for potential seasonal differences in community structure. Both area and habitat were included as fixed factors, as well as their interaction (area $\times$ habitat). The sampling design included four quadrats per habitat within each area; therefore, quadrat ID nested within habitat and area was included as a

random factor to account for the hierarchical structure and potential non-independence of observations. The models were fitted using the restricted maximum likelihood (REML) method with the lmer function from the lme4 package (Bates et al. 2015). Model assumptions of normality and homoscedasticity were verified by inspecting residual plots. The general model structure was richness ~ area * habitat + (1 | quadrat nested), and abundance ~ area * habitat + (1 | quadrat nested) for each season. Significant effects were further explored using post-hoc pairwise comparisons with estimated marginal means (emmeans package; Lenth et al. 2025), adjusted using Tukey's method. Estimates are interpreted relative to the reference levels (Closed area; Non-vegetated habitat).

RESULTS

We recorded 937 individuals in total, classified into 18 families, 28 genera, and 33 species (Table 1). Within Polychaeta, the subclasses Errantia and Sedentaria had similar species richness (52% and 48%, respectively). We also identified annelids from other groups, including three Sipuncula morphospecies and one Magelonidae species. Nereididae was the family with the highest species richness, with five taxa across five genera. Spionidae, Orbiniidae, and Capitellidae had the second-highest species richness, with three species each, distributed in three genera. Onuphidae had two species distributed in a single genus. The least representative families were Serpulidae, Magelonidae, Melinnidae, Eunicidae, Lumbrineridae, Terebellidae, Oeonidae, Cirratulidae, Goniadidae, Pilargidae, Nephtyidae, Sternaspidae, and Phyllodocidae, each with only one species.

The most abundant species were the nereidids *Laeoneis acuta* and *Nereis oligohalina*, with 254 and 149 individuals, respectively (Table 1, Fig. 2A). The higher abundance of *L. acuta* compared to other polychaetes also occurred during spring. Most of the recorded taxa are microphages (15 taxa, 46%), 10 taxa (30%) are omnivores, and eight taxa (24%) are macrophages. In the present study, omnivores represent the second-highest richness, followed by macrophage annelids (carnivores or herbivores).

Of the 33 recorded taxa, 11 species are new records for the state of Paraná: *Aglaophamus fabrun*, *Marphysa sebastiana*, *M. formosa*, *Lumbrineris cruzensis*, *Arabella aracaensis*, *Diopatra marinae*, *D. hannelorae*, *Timarete ceciliae*, *Leitoscoloplos cf. fragilis*, *Namalycastis lanai*, and *Terebella lesliae*. Some of these species were expected to occur in the state of Paraná, as they are recorded in the neighboring states of São Paulo and Santa Catarina (Table 1).

The total richness was similar among areas: control with 22 species, Open inlet with 20, and Closed inlet with 18 species (Fig. 2C). Rarefaction and extrapolation curves did not reach an asymptote, indicating that species richness in the areas is higher than what was sampled, despite the extensive sampling effort (Fig. 2C). The clear exception is the Closed inlet, where the curve indicates that sampling covered most of the area's diversity (Fig. 2C).

Regarding diversity indices, the Shannon index was higher in the Control area (2.15), while the Simpson index was higher in the closed area (0.83). Pielou's evenness was higher in the closed area (0.73). The diversity profile showed that the Closed inlet had higher evenness than the other areas (Fig. 2B).

Species richness was considerably lower during autumn (Fig. 3). Of the 33 recorded species, 16 were sampled in this season, whereas 32 were sampled during spring. The sampling period with the highest abundance was spring, with 588 individuals, while during autumn only 349 individuals were recorded.

The main effects of area, habitat, and their interactions on annelid abundance and species richness are summarized in Table 2 (full results in Table S2). Linear mixed models (LMM) revealed that both abundance and species richness were generally lower in Control and Open areas, and in vegetated habitats. Positive interactions between area and vegetated habitats, however, led to higher abundance and richness in specific combinations. Seasonal differences were observed: in spring, declines were more pronounced in vegetated habitats, whereas in autumn, abundance increased in the transition zone. These patterns indicate that habitat type and spatial modifications jointly shape community structure.

DISCUSSION

Ararapira Inlet annelids' responses differ among seasons, areas, and habitats. During spring, higher abundances were generally observed in the transition zone and vegetated habitats, depending on the area. Vegetated environments increase macroinvertebrate diversity compared to non-vegetated habitats (Qiu et al. 2019, Dos Santos et al. 2024). Besides vegetation, transitional habitats influence ecological processes (Fagan et al. 2003) and increase diversity (Wimp and Murphy 2021). Similar trends have been reported in previous studies, which suggest that seasonal dynamics can influence species composition and abundance, particularly in ecosystems exposed to environmental fluctuations (Amorim et al. 2020, Medeiros et al. 2022).

Table 1. List of species recorded at Ararapira Inlet. Feeding type: Macrophage (MACRO), Microphage (MICRO), and Omnivore (OMN). Habitat: Vegetated (V), Transition zone (TZ), and Non-Vegetated (NV). Status: Natural (N), Non-indigenous (NIS), and Cryptogenic (C). Distribution in Brazilian states: Pará (PA), Maranhão (MA), Piauí (PI), Ceará (CE), Rio Grande do Norte (RN), Paraíba (PB), Pernambuco (PE), Alagoas (AL), Sergipe (SE), Bahia (BA), Espírito Santo (ES), Rio de Janeiro (RJ), São Paulo (SP), Paraná (PR), Santa Catarina (SC), Rio Grande do Sul (RS). First record at Paraná State (*).

Taxon	Abundance	Feeding type	Habitat	Sampling period	Invasive Status	Distribution in Brazilian states
Subclass Errantia						
Phyllodocidae Örsted, 1843						
<i>Paranaitis chitinos</i> Oliveira, Eibye-Jacobsen & Lana, 2018	1	MACRO	TZ	S	N	RJ, PR
Nephtyidae Grube, 1850						
<i>Aglaophamus fabrun</i> Franco & Rizzo, 2016	1	MACRO	NV	S	N	RJ, PR*
Pilargidae Saint-Joseph, 1899						
<i>Sigambra grubii</i> Müller, 1858	62	OMN	V/TZ/NV	S, A	N	PA, MA, CE, PB, PE, SE, BA, ES, RJ, SP, PR, SC, RS
Nereididae Blainville, 1818						
<i>Alitta succinea</i> (Leuckart, 1847)	2	OMN	NV	S, A	NIS	PA, MA, PI, CE, RN, SE, BA, ES, RJ, SP, PR, SC, RS
<i>Nereis oligohalina</i> (Rioja, 1946)	149	OMN	V/TZ/NV	S, A	NIS	PA, MA, RN, AL, BA, ES, SP, PR, SC
<i>Perinereis anderssoni</i> Kinberg, 1865	48	OMN	V/TZ	S, A	N	PA, MA, PI, CE, RN, PB, PE, AL, BA, ES, RJ, SP, PR, SC, RS
<i>Laonereis acuta</i> (Treadwell, 1923)	254	OMN	V/TZ/NV	S, A	N	PA, PB, BA, SP, PR, SC, RS
<i>Namalycastis lanai</i> Alves, Glasby, Paiva & Santos, 2024	2	OMN	V	S	N	RJ, PR*, SC
Goniadidae Kinberg, 1866						
<i>Glycinde multident</i> Müller, 1858	43	MACRO	V/TZ/NV	S, A	N	MA, CE, SE, BA, RJ, SP, PR, SC, RS
Eunicidae Berthold, 1827						
<i>Marphysa sebastiana</i> Steiner & Amaral, 2000	2	OMN	TZ/NV	S	N	RJ, SP, PR*
<i>Marphysa formosa</i> Steiner & Amaral, 2000	1	OMN	TZ	A	N	SP, PR*
Onuphidae Kinberg, 1865						
<i>Diopatra marinae</i> Steiner & Amaral in Seixas et al., 2020	1	OMN	TZ	S	N	RN, PB, BA, ES, SP, PR*
<i>Diopatra hannelorae</i> Steiner & Amaral in Seixas et al., 2020	1	OMN	NV	S	N	SP, PR*, SC, RS
Lumbrineridae Schmarda, 1861						
<i>Lumbrineris cruzensis</i> Hartman, 1944	2	MACRO	TZ	S	NIS	ES, RJ, SP, PR*
Oeononidae Kinberg, 1865						
<i>Arabella aracaensis</i> Steiner & Amaral, 2009	63	MACRO	V/TZ/NV	S, A	N	SP, PR*
Subclass Sedentaria						
Cirratulidae Ryckholt, 1851						
<i>Timarete ceciliae</i> Magalhães, Seixas, Paiva & Elías, 2014	55	MICRO	V/TZ	S	N	BA, ES, PR*
Sternaspidae (Carus, 1863)						
<i>Sternaspis</i> sp.	1	MICRO	NV	S	-	Present study
Spionidae Grube, 1850						
<i>Dispio remanei</i> Friedrich, 1956	5	MICRO	V/NV	S, A	NIS	CE, RJ, SP, PR, SC
<i>Polydora cornuta</i> Bosc, 1802	10	MICRO	V/TZ/NV	S, A	NIS	ES, RJ, SP, PR
<i>Spiophanes duplex</i> (Chamberlin, 1919)	3	MICRO	NV	S	NIS	CE, BA, ES, RJ, SP, PR, SC, RS
Capitellidae Grube, 1862						
<i>Mediomastus californiensis</i> Hartman, 1944	92	MICRO	V/TZ/NV	S, A	NIS	PA, RJ, SP, PR, SC
<i>Heteromastus filiformis</i> (Claparède, 1864)	51	MICRO	V/TZ/NV	S, A	C	CE, AL, RJ, SP, PR, RS
<i>Capitella neoaciculata</i> Silva & Seixas, 2017	20	MICRO	V/TZ	S, A	N	PA, PE, BA, RJ, SP, PR
Orbiniidae Hartman, 1942						
<i>Leodamas</i> sp.	5	MACRO	NV	S, A	-	Present study
<i>Leitoscoloplos</i> cf. <i>fragilis</i> (Verrill, 1873)	2	MACRO	NV	S	NIS	RJ, SP, PR*
<i>Scoloplos</i> sp.	1	MACRO	NV	S	-	Present study
Terebellidae Johnston, 1846						
<i>Terebella leslieae</i> Santos, Nogueira, Fukuda & Christoffersen, 2010	4	MICRO	TZ	S	N	RN, PR*
Melinnidae Chamberlin, 1919						
<i>Isolda pulchella</i> Müller in Grube, 1858	47	MICRO	V/TZ	S, A	N	MA, PI, SE, ES, RJ, SP, PR, SC
Serpulidae Rafinesque, 1815						
<i>Hydroides</i> sp.	1	MICRO	TZ	S	-	Present study
Class Oweniida						
Magelonidae Cunningham & Ramage, 1888						
<i>Magelona papillicornis</i> F. Müller, 1858	5	MICRO	TZ/NV	S, A	N	MA, PI, SE, RJ, SP, PR, SC,
<i>Sipuncula</i> sp. 1	1	MICRO	TZ	S	-	Present study
<i>Sipuncula</i> sp. 2	1	MICRO	TZ	S	-	Present study
<i>Sipuncula</i> sp. 3	1	MICRO	TZ	S	-	Present study

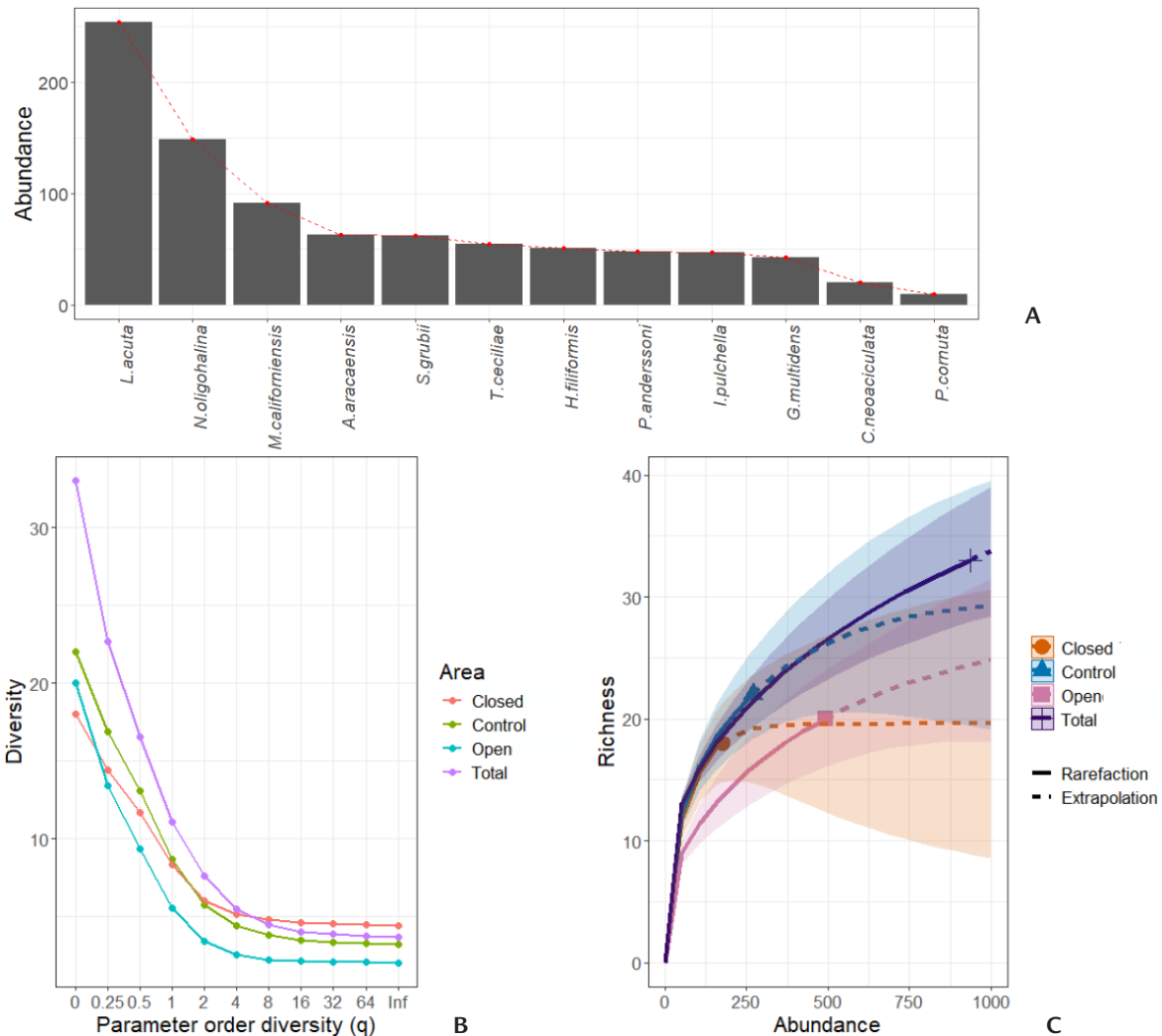


Figure 2. (A) Total abundance of the 12 most abundant recorded species; (B) Diversity profile by Hill's number among areas and total; (C) Rarefaction and extrapolation curve of each area and the total.

Habitat changes are the primary drivers of biodiversity loss (Swan et al. 2022). Regarding environmental changes at Ararapira Inlet, annelids' responses to habitat change have led to reduced biodiversity (Singer et al. 2023, Gammal et al. 2023). Ecosystems facing multiple stressors are vulnerable to cascading environmental changes, leading to a decline in annelid diversity (Gammal et al. 2023). The diversity response among species and environments is crucial to resilience for ecosystem reorganization (Elmqvist et al. 2003) and ecological stability (Ross et al. 2023).

Corroborating our results, *Laonereis acuta* and *Nereis oligohalina* are the most abundant species in estuarine environments from the southeastern Brazilian coast

(Omena and Amaral 2001, Sampieri et al. 2021). This is not surprising given that Nereididae is one of the most numerous and common families of polychaetes in the world (Wilson et al. 2023). Nereidids such as *Namalycaeus lanai* were recorded in high abundance in environments at early ecological succession stages (Alves et al. 2024). The differences observed between the areas in this study may indicate that the region is currently at a moderate stage of restoration five years after the inlet opening. Similar to other nereidid species, *Perinereis anderssoni* has a fast growth rate and a short lifespan (around one year) (Peixoto et al. 2018). According to Jumars et al. (2015), nereidids are deposit-feeding polychaetes, mostly omnivorous, and their

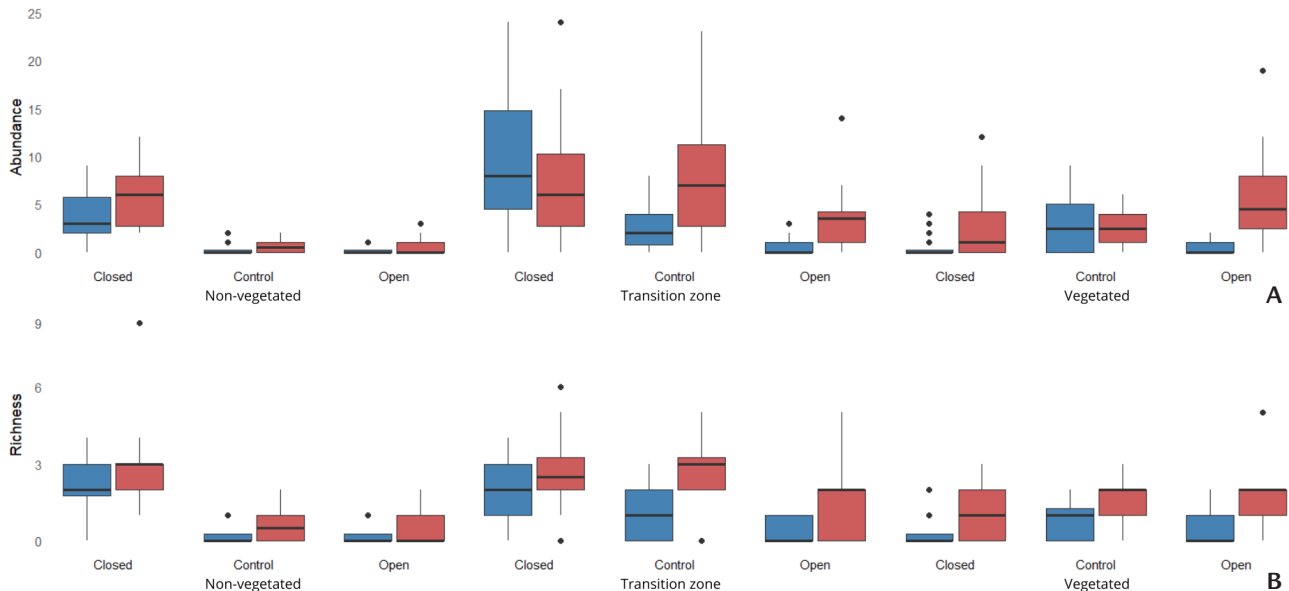


Figure 3. (A) Abundance of annelids at the Ararapira Inlet. The boxplots show median abundance and richness at each collected area (Closed, Control, and Open), within the three habitats (non-vegetated, transition zone, and vegetated), and across the two seasons (Autumn in blue, and Spring in red), and (B) Richness.

Table 2. Estimated effects, standard errors (SE), and t values from linear mixed models (LMMs) for species abundance and richness across areas and habitats by season. Estimates are relative to reference levels (closed area; non-vegetated habitat). Direction of effect indicated by arrows: ↑ increase, ↓ decrease, ≈ tendency. Post-hoc pairwise comparisons (Tukey-adjusted) were used to interpret significant differences.

Season	Response	Main factor/interaction	Estimate	Std. Error	t value	Main effect
Spring	Abundance	Area (Control)	-5.44	1.80	-3.02	↓ Lower abundance in Control area (vs Closed)
Spring	Abundance	Area (Open)	-5.44	1.80	-3.02	↓ Lower abundance in Open area (vs Closed)
Spring	Abundance	Habitat (Vegetated)	-3.19	1.80	-1.77	↓ Tendency toward lower abundance in vegetated habitat (vs Non-vegetated)
Spring	Abundance	Area × Habitat (Vegetated)	+5.19–8.06	2.54	2.04–3.17	↑ Combined positive effect
Autumn	Abundance	Area (Control/Open)	-3.56	1.46	≈ -2.46	↓ Lower abundance in modified areas (vs Closed)
Autumn	Abundance	Habitat (Transition zone)	+6.06	1.46	4.15	↑ Higher abundance in transition zone (vs Non-vegetated)
Autumn	Abundance	Habitat (Vegetated)	-3.25	1.46	-2.22	↓ Lower in vegetated habitat (vs Non-vegetated)
Autumn	Abundance	Area × Habitat (Vegetated)	+3.56–6.13	2.07	1.72–2.96	↑ Positive interactions
Spring	Richness	Area (Control/Open)	-2.38	0.45	-5.30	↓ Lower richness in Control/Open areas (vs Closed)
Spring	Richness	Habitat (Vegetated)	-1.75	0.45	-3.91	↓ Lower in vegetated habitat (vs Non-vegetated)
Spring	Richness	Area × Habitat (Vegetated)	+2.81	0.63	4.44	↑ Higher in area × vegetated combination
Autumn	Richness	Area (Control/Open)	-2.00	0.37	-5.46	↓ Lower richness in modified areas (vs Closed)
Autumn	Richness	Habitat (Vegetated)	-1.94	0.37	-5.29	↓ Lower in vegetated habitat (vs Non-vegetated)

feeding strategies are closely linked to mobility and habitat type. The relationship between motility and feeding mode is a well-established pattern in annelids, as there are no completely sessile macrophage feeders, and most microphagous species act as suspension feeders, consuming fine suspended particles (Fauchald and Jumars 1979, Jumars et al. 2015). Omnivory is particularly common among members of Nereididae, Eunicidae, and Onuphidae. In our study, habitats with greater structural complexity, such as vegetated and

transition zones, supported a higher diversity of feeding modes. In contrast, non-vegetated areas were dominated by more mobile species, a pattern consistent with observations that motile and small-bodied annelids prevail in muddy sediments, while sandy environments harbor species with more heterogeneous traits (Otegui et al. 2016).

Some species, such as *N. oligohalina*, showed seasonal differences in our study. Seasonal variations in population density and biomass of *N. oligohalina* have been attributed

to the seasonal fluctuation of salt marshes, which regulate the species' reproductive strategies (Pagliosa and Lana 2000). Because our sampling was conducted near salt marshes, the high abundance of these species in the present study may also be attributed to seasonal fluctuations, with a predominance in the spring season. Additional studies replicating both sampled seasons may help explain the variations observed between spring and autumn. Similarly, populations of *L. acuta* increased in density in late summer and were reduced to their minimum in spring (López-Gappa et al. 2001). This difference in *L. acuta* abundance across seasons between studies may be related to the species' adaptive responses to environmental changes in Ararapira Inlet. Although Sampieri et al. (2021) explored the molecular diversity of *Laonereis*, and Conde-Vela (2021) explored the morphological diversity, an integrative study of *Laonereis* along the southwestern Atlantic is still lacking.

On the other hand, the less abundant species were *Diopatra marinae*, *D. hannelorae*, *Hydroides* sp., *Scoloplos* sp., *Sternaspis* sp., *Paranaitis chitinoso*, *Aglaophamus fabrum*, and *Marphysa formosa*, with only one individual each. Many of the above-mentioned species are omnivores. *Diopatra marinae* was found in syntopy with another congener in Bahia, and it is believed that this generalist behavior prevents competitive exclusion, allowing the co-occurrence of similar species (Seixas et al. 2020). *Marphysa formosa* feeds only on algae and builds its fragile sandy tubes among them (Pardo and Amaral 2006).

Before the discovery that *Diopatra cuprea* (Bosc, 1802) comprised four species in Brazil, including *D. marinae* and *D. hannelorae* (Seixas et al. 2020), the cosmopolitan *Diopatra cuprea* was considered vulnerable due to a drastic reduction in abundance in southern and southwestern Brazil (ICMBio 2018). Therefore, *D. marinae* and *D. hannelorae* are expected to be included in future lists of threatened species. Since the Ararapira Inlet is well preserved and inhabited only by a small traditional fishing community, the low abundance in this locality is not necessarily attributed to the factors mentioned above; thus, other factors must be considered to explain their low abundance in the studied area, which are beyond the scope of this study.

These results highlight the complex interactive influence of environmental factors on species abundance, suggesting that the effects of habitat, area, and season do not act in isolation but rather interact to structure biological communities (Table 2). Species richness responds non-additively to the combination of habitat, area, and season, and is particularly influenced by interactions among these factors. These results were observed in other studies, in which different processes

act on the structure of the annelid community, such as seasonal changes, especially in ecosystems subject to environmental variations (Amorim et al. 2020, Medeiros et al. 2022).

In addition to spatial and temporal factors, natural environmental changes that disrupt Ararapira Inlet environments also explain the annelid diversity recorded in our study. The intermediate disturbance hypothesis (IDH) suggests that peak species diversity occurs at intermediate-scale disturbances (Moi et al. 2020), which vary in disturbance-induced spatial and temporal changes in resources and environmental conditions (Roxburgh et al. 2004). However, this hypothesis has received criticism, as the relationship between disturbances and species diversity is generally not unimodal (Fox et al. 2013, Moi et al. 2020).

The composition of annelid assemblages changes between vegetated and non-vegetated environments, with a decrease in the density of dominant species and an increase in rare species in less complex environments (Checon et al. 2017). The higher diversity of annelids recorded in the vegetated habitats can be explained by the presence of seagrass (Barrio-Froján et al. 2006, Henseler et al. 2019). In addition to the transition zone habitat, mangrove structural complexity promotes taxonomic diversity, as evidenced by greater diversity in vegetated than in non-vegetated habitats (Delfan et al. 2021). This higher diversity in vegetated habitats can be related to the number of niches and food density (Barrio-Froján et al. 2006) and structural complexity (Henseler et al. 2019). In the present study, the transition zone habitat had a higher richness than the other two habitats. One possible explanation that warrants further investigation is that this habitat concentrates species adapted to both non-vegetated and vegetated habitats.

Concerning endemism, 17 species are native to Brazil, eight are non-indigenous, and seven lack information because we could only identify them to the genus level. About 292 polychaete species have been recorded as non-indigenous worldwide (Çinar 2013), belonging to families such as Spionidae, Serpulidae, Sabellidae, and Nereididae, which ranked highest in non-indigenous species richness (Alvarez-Aguilar et al. 2022). In this study, we recorded a high number of non-indigenous species, considering that the study area is part of an environmental protection area, with the Superagui National Park, Cardoso Island State Park, and Guaraqueçaba Environmental Protection Area surrounding the location, and has a low human population density. This high number can result in environmental impacts (Lovel et al. 2006), altering community structure and food webs (Alvarez-Aguilar et al. 2022). Some common non-indigenous species occurring in

Brazil (Radashevsky 2005, Ferreira et al. 2024) were recorded in the Ararapira Inlet, such as the nereidid *Alitta succinea* and the spionid *Polydora cornuta*. This high number of species may be related to port activities near the study area.

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Author Contributions

GPS: Conceptualization, Data Curation, Formal analysis, Investigation, Methodology, Writing–Original draft.

RCA: Data curation, Investigation, Supervision, Writing-review & editing.

FM CBD, MDD: Data curation, Formal analysis, Investigation, Methodology, Conceptualization, Investigation, Methodology, Supervision, Writing-review & editing.

Competing Interests

The authors have declared that no competing interests exist.

Data Availability Statement

Datasets generated or analyzed in this study are available from the corresponding author on reasonable request.

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Ethical Statement

This study did not involve live vertebrate animals and therefore did not require approval by an ethics committee. Field sampling was conducted under ICMBio permit number 90360-1.

AI Statement

No artificial intelligence tools were used in the preparation of this manuscript.

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Supplementary material 1

Table S1. Dataset following the DarwinCore format. Collected animals are deposited in the Museu Nacional, MN/UFRJ* (currently, without the registration number), while the rest** will be deposited in collections at USP and UNICAMP.

Authors: Gabriel P. da Silva; Ricardo C. Álvarez

Data type: Species data

Supplementary material 2

Table S2. Linear mixed models result by seasons, areas and habitats.

Authors: Gabriel P. da Silva

Data type: Data analysis.

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