Revealing the drivers of taxonomic and functional diversity of nearshore fish assemblages: Implications for conservation priorities

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Abstract
Aim: Understanding patterns and drivers of biodiversity are essential towards developing effective conservation strategies for shallow marine habitats broadly. However, little is known about the natural and anthropogenic factors that structure fish biodiversity of sandy beaches, one of the largest and most socio-economically valuable nearshore habitats due to their endemic fauna, economic importance and cultural relevance. Here, we investigated how environmental variables and urbanization affect taxonomic and functional diversity of nearshore fish assemblages to provide general biodiversity patterns that can serve as baseline information for management plans when considering conservation prioritization.

Location: Southeast Brazil.

Methods: We surveyed fish communities at 77 sites along 150 km of coastline with different natural features and degrees of human influence using a combination of seine nets and surf-BRUVS. We used generalized additive models (GAMs) to investigate the influence of environmental variables and urbanization on taxonomic and functional diversity of resident fish assemblages.

Main results: We found that significant breaker wave height was the most important environmental variable in explaining the taxonomic and functional diversity of fish assemblages. The effects of increasing wave height were mostly negative, except for piscivorous fishes, which were most abundant at high energy sites, and for benthic and zoobenthivorous species, which were most abundant at sites with intermediate wave exposure. The latter species were also associated with higher chlorophyll-a contributing to increased taxonomic richness and abundance. Further, anthropogenic impacts generally reduced diversity, with highest diversity only observed at the most pristine sites.

Main conclusions: Our results demonstrate that both natural environmental variation and human activities structure the fish assemblages of sandy beach surf zones,
1 | INTRODUCTION

Understanding spatial patterns in biodiversity and the processes that shape them is a critical step towards the design and implementation of effective conservation strategies for marine ecosystems, particularly in coastal zones where people and the sea meet. Sandy beaches occupy one third of the world’s ice-free coastline (Luijendijk et al., 2018) and provide important ecosystem services such as tourism and recreational economies (Defeo et al., 2009) and function as important nurseries (Lombardi et al., 2014), foraging sites (Tatematsu et al., 2014) and spawning grounds (Hirose & Kawaguchi, 1998; Lasiak, 1986) for fishes. Many of the fish species found near sandy beaches occupy surf zones only during their juvenile stages before migrating to adjacent ecosystems. Therefore, surf zones are fundamental habitats that contribute to the successful development and recruitment of adult populations of commercially important species and ultimately support 40– 60% of coastal fisheries (Gillanders et al., 2003). Potential changes in fish diversity of sandy beach surf zones may consequently have serious ecological and economic and social implications. Nearshore and artisanal fisheries are still very important for many communities, either for subsistence or for the local economy (Begossi et al., 2011), and ensuring the sustainability of this activity is of great socio-economic relevance.

Sandy beaches face increasing pressures from urbanization (e.g. construction on the sand, urban runoff) and climate-related environmental changes (e.g. erosion, storminess) on both the terrestrial and marine sides (Schlacher et al., 2007). These pressures are expected to strongly modify the beach environment and resident biodiversity, likely compromising the key ecosystem services noted above. To safeguard beach biodiversity and services, it is necessary to analyse the main drivers of local biodiversity. Understanding how changes in the environment act on the local species can provide essential information to construct tools that support conservation and can help mitigate or even reverse these impacts. Despite their high intrinsic value, research in conservation and management of sandy beaches remains one of the most limited and further rarely considers maintaining adequate ecosystem functioning (Nel et al., 2014). This knowledge gap is even more critical when we consider the current state of knowledge of surf zone fishes, which has rarely integrated observations across diverse morphodynamic and anthropogenic conditions (Olds et al., 2018).

The composition of surf zone fish assemblages can be influenced by several environmental factors such as beach exposure (Borland et al., 2017; Nakane et al., 2013) and freshwater input (Aráujo et al., 2002, Pessanha & Araújo, 2003). Surf zone assemblages may also be exposed to multiple stressors linked to human activities, such as urbanization, tourism and fishing (Costa et al., 2017a). However, the identification of these combined effects on surf zone fishes have gone largely unexplored with focus instead on fish communities in other adjacent aquatic environments such as rivers (Tejerina-Garro et al., 2005), estuaries (Yabsley et al., 2020) and reefs (Taira et al., 2018).

More recently, studies have begun to explore the functional consequences of human impacts on natural communities through the use of organismal traits (Villéger et al., 2010). By estimating the diversity of organismal traits, or functional diversity (FD), it is possible to understand how species respond to and modify their environments given their characteristics (traits). This approach therefore provides a more mechanistic understanding of how biodiversity is structured in response to changes in biological and physical–chemical drivers and how changes in species influence the functioning of ecosystems (Gagic et al., 2015; Petchey & Gaston, 2006). Decreases in FD reduce the potential of communities to respond to changing environmental conditions in marine (Mouillot et al., 2011) and terrestrial ecosystems (Cadotte et al., 2011; Flynn et al., 2011). Sandy beaches are one of the most vulnerable coastal systems, as prior evidence suggests that few species fulfil key functional roles and may also be the least able to withstand eventual disturbances (Azevedo et al., 2017). Most decision-making processes, however, have been based on species, habitat or socioeconomic metrics (D’Agata et al., 2014; Mouillot et al., 2011), and FD is often left out of management and conservation assessments (Laikre et al., 2016; von der Heyden, 2017).

To address these various knowledge gaps, we investigated how a combination of environmental variables and urbanization affect fish taxonomic and functional diversity of nearshore fish assemblages by sampling 77 sandy beach sites across the southeastern Brazilian coast with different natural features and degrees of urbanization. This approach delivers a more comprehensive picture of the fish diversity at these sites across a gradient of impacts, which together can provide general biodiversity patterns that can serve as baseline information for management plans when considering conservation prioritization.

KEYWORDS
anthropogenic effects, ichthyofauna, integrated coastal management, sandy beach, surf-BRUVS, urbanization
2 METHODS

2.1 Study area

This study was performed in 77 sites along 27 sandy beaches on the North Coast of the state of São Paulo, Southeast Brazil. Our sampling sites (Figure 1) stretched over 150 km of coastline and included most beach types, from reflective to dissipative beaches (McLachlan et al., 2018) and from nearly pristine to highly urbanized beaches.

2.2 Sampling and processing

Each beach was divided into three sites parallel to the beach edge: two close to the endpoints of the beach and one at the middle of the beach. These sites were established to account for the considerable spatial variation in abiotic features along a single beach, such as degree of exposure and beach slope. Surf fish assemblages may display high spatial (e.g. depth) and temporal (e.g. tide, season) variability (Olds et al., 2018); therefore, we conducted surveys only during high-tide, around midday of spring tides during 3 mo of the austral autumn of 2018 (i.e. when the impact of coastal tourism is lower and in order to avoid drastic changes in the fish assemblage caused by seasonal changes and the entry of cold fronts, which are more common in winter (Pianca et al., 2010)) and at similar depths (1–1.5 m) at each site.

Fish biodiversity was sampled using a combination of two methods: surf-BRUVS and beach seine nets, since synergistic use allows more accurate estimates of total fish diversity (Shah Esmaeili et al., 2021). Surf-BRUVS consist of a GoPro 6+ © Camera attached to a 10 kg weight and equipped with a bag containing 500 g of selected bait (Sardinella brasiliensis) approximately 0.5 m in front of the camera (Vargas-Fonseca et al., 2016). At each site, two surf-BRUVS were placed 100 m apart. Each BRUV recorded fish for one hour and fishes were identified and counted using the standard Max N statistic (Murphy & Jenkins, 2010).

Seine sampling was done 60 minutes after the video recording using a beach seine net of 20 m wide, 2.6 m high with 5 mm mesh and a 2 m high, 4 m long funnel. Two hauls were performed per site for approximately 20 m parallel to the shore (approximately 400 m² for each haul). Fishes were sorted, counted and conserved for further identification to species level in the laboratory. For each site, richness was based on the number of species combining both methods, while for abundance only the highest number of individuals registered between the two methods was considered, thereby eliminating double counts.

For environmental variables, we measured chlorophyll-a (μg/L), significant breaker wave height (cm), beach slope (tan β), distance to and size of the nearest river mouth (m) for each site. Sediment mean grain size was also evaluated based on five sediment samples that were collected along the beach profile using a 5-cm wide cylindrical corer, up to 20-cm deep. Samples were sieved into twelve granulometric fractions, and the mean calculated using the formulae provided by Folk and Ward (1957). However, this variable was not included in further analyses due to the strong correlation with beach slope. Samples for chlorophyll-a were collected using a 1-L dark bottle of both bottom and superficial water and filtered through GF/F filters (25 mm diameter, 0.7 μm pore size). Chl-a was determined spectrophotometrically in acetone extracts before and after acidification (Strickland & Parsons, 1972) and total phytoplankton biomass (μg/L) estimated according to Lorenzen’s (1967) equation. Beach slope was determined by across-shore profiling of the supralittoral to the surf zone at each site (Emery, 1961). River influence was estimated for each site by calculating the over-water distance to and width of the closest river mouth using satellite images (CNES/Airbus, Maxar Technologies) obtained from Google Earth software. In beaches without a river, the distance between sampling sites and the nearest river was replaced by an arbitrarily large value equal to four times the longest distance.

FIGURE 1 Study area on the North coast of São Paulo, 77 sites (symbols) along 27 sandy beaches in the municipality of São Sebastião, Caraguatatuba and Ubatuba.
connecting a site and river within the same beach, a modification of the approach proposed by Borcard and Legendre (2002) for meta-community studies. The width of the closest river mouth was considered null in beaches without a river. Significant breaker wave height was measured as the average breaking height of 1/3 of the highest waves registered of 20 consecutive waves (McLachlan et al., 2018), evaluated after the end of fish sampling.

Urbanization was estimated by attributing values from 0 (absence) to 5 (highest level) to each of the following variables: (1) Proximity to urban centres, (2) buildings on the sand (i.e., those located within the beach perimeter), (3) beach cleaning (i.e., periodicity of beach cleaning by public agencies), (4) solid waste on the sand, (5) vehicle traffic on the sand and (6) frequency of visitors. An ‘urbanization index’ (González et al., 2014), was then calculated as the mean across these five categories, ranging from “0” (least urbanized) to “5” (highest urbanization). Scoring for these indicators was defined either in situ (averaging the scores from three observers, to avoid individual bias) and/or with information provided by local authorities (e.g., beach cleaning, frequency of visitors).

2.3 Data analysis

We collected data on species functional traits from literature and online databases (FishBase) and compiled a species-by-traits matrix that comprised 4 traits with 14 modalities that are directly linked to ecosystem processes (association: solitary or schooling; water column feeding position: benthic, demersal, pelagic, surface; diet: detritivorous, phyto- and zooplanktivorous, zoobenthivorous or piscivorous; median length $L_{med}$: 5–20, 20–40 or >40 cm) (Laureto et al., 2015; Mouchet et al., 2013; Mouillot et al., 2007; Somerfield et al., 2008; Stuart-Smith et al., 2013).

Then, we calculated five metrics of functional diversity: number of singular species, functional richness (FRic), functional dispersion (FDis), functional evenness (Feve) and community-weighted mean trait value (CWM). The number of singular species is related to the number of functionally unique species in each community. If all species are functionally different (i.e., occupy completely orthogonal functional states), the number of functionally singular species will be identical to the total number of species ( Laliberté et al., 2015).

FRic, FDis and Feve are complementary and describe the distribution of species and their abundances within the functional space (Mouchet et al., 2010). FRic estimates the total volume of multivariate functional space occupied by a given species assemblage and can be used as a proxy of the range of functional traits represented in an assemblage (Mouchet et al., 2010). Feve represents the regularity of the distribution of species abundances in the functional space, with low Feve indicating that some niches have a reduced number of individuals performing those functions (Mason et al., 2005; Mouchet et al., 2010). FDis refers to the mean distance of all species in a given assemblage from the centre of the functional space weighted by their abundances, with low functional dispersion suggesting a convergence of individuals and/or functional traits in multivariate trait space. CWMs summarize the average value of each individual trait within a community (Garnier et al., 2004) and were used here to identify responses of individual traits that contribute to the multivariate indices. These analyses were conducted in the R environment (R Development Core Team, 2013) using the function ‘fd’ of the FD package (Laliberté et al., 2015).

We used the ‘gam’ function of the R package mgcv (Wood, 2012) to run generalized additive models (GAMs) to investigate the relationship between environmental variables and urbanization, and taxonomic (i.e., species richness and abundance) and functional diversity of fish assemblages. Data were log10-transformed and models were checked for homogeneity of variance and normality of errors. As no substantial deviations were found, we fit all models to a Gaussian distribution. Variables were checked for multicollinearity using the variance inflation factor (VIF) using VIF >2 as a cut-off value (Zuur et al., 2010), and for concurrury using the largest (worst) value >0.7 as a cut-off. We accounted for the presence of spatial structure including latitude and longitude of sampling sites as a smoothed, interaction term in the model (Wood, 2006).

Models best predicting taxonomic and functional diversity of fishes were selected using an information theory approach (Burnham & Anderson, 2002). First, models were run comprising all combinations of predictors without interactions. Then, we ranked multiple models using sample-size corrected Akaike information criteria (AICc) and excluded models with $\Delta$AICc $>$ 4. The relative importance of each variable was then estimated as the sum of the Akaikc weights (AICcw) over all of the models in which the variable appears from the model averaging (Burnham & Anderson, 2002). We considered only predictors with a probability greater than 50% (i.e. sum of the AICcw >0.5) as important. Relationships between selected response variables and predictors were analysed through the graphical output of GAMs. All analyses were conducted in the R environment (R Development Core Team, 2013) using the mgcv (Wood, 2012), MuMln (Barton & Barton, 2015), vegan (Oksanen et al., 2013) and (Laliberté et al., 2015) packages.

3 RESULTS

3.1 Environmental characteristics

The environmental characterization performed at each sampling site reinforced the wide range of natural features and degrees of urbanization investigated in this study. Significant breaker wave height ranged from 3.86 to 160 cm (mean $\pm$ SD: 56.04 $\pm$ 35.42), chlorophyll- a concentration ranged from 0.92 to 81.1 $\mu$g/L (mean $\pm$ SD: 5.79 $\pm$ 35.81), the slope ranged from 0.008 to 0.12 (mean $\pm$ SD: 0.051 $\pm$ 0.028) and average grain size from 1.252 to 3.46 $\phi$ (mean $\pm$ SD: 2.37 $\pm$ 0.552). Sampled sites also differed in regard to river influence, with the width of the nearest river ranging from 0 to 280 m (mean $\pm$ SD: 45.55 $\pm$ 55.90) and the distance to the nearest river between 18 and 39,480 m (mean $\pm$ SD: 12377.7 $\pm$ 18026.51). Finally, sampling sites included almost pristine (UI =0.38) as well as highly urbanized beaches (UI =4.17) (mean $\pm$ SD: 2.27 $\pm$ 0.87).
A complete characterization of the sampling sites can be found in Table S2 and in the rug plots in Figures 2, 3 and 4.

### 3.2 | Richness and Abundance

A total of 8766 fishes was sampled across all beaches, belonging to 64 species and 26 families (Table S1), with the white sea catfish *Genidens barbus* (Lacepede, 1803) and the false herring *Harengula clupeola* (Cuvier, 1829) being the most abundant species. Based on our application of GAMs, breaker wave height, chlorophyll-a and urbanization were the most important variables predicting species richness and abundance (Table 1; Figure 5). Fish species richness was higher at sites with lower wave height (AICcw = 1.00; Figure 2a), higher chlorophyll-a levels (AICcw = 0.92; Figure 2b) and lower urbanization (AICcw = 0.52; Figure 2c). The final model explained 41.8% of the deviance in the number of fish species. Similarly, fish abundance was higher at sites with lower waves (AICcw = 1.00; Figure 2d) and lower urbanization (AICcw = 1.00; Figure 2e). The model explained 45.7% of the deviance in fish abundance.

### 3.3 | Functional diversity

As with species richness and abundance, the functional diversity of fish assemblages was also strongly influenced by breaker wave height, chlorophyll-a levels and urbanization (Table 1; Figure 5). Additionally, the distance to and size of the mouth of the closest river also exerted a significant effect on the selection of fish functional traits.

The number of singular species decreased linearly with wave breaker height (AICcw = 1.00; Figure 3a) and increased with higher levels of Chl-a (AICcw = 1.00; Figure 3b). Functional richness (FRic) also decreased linearly with wave height (AICcw = 1.00; Figure 3c). Functional dispersion (FDis) was higher in sites further away from rivers (AICcw = 0.87; Figure 3d), in sites with a low level of urbanization (AICcw = 0.95; Figure 3e) (although it showed low values in the more pristine sites), and at sites with a gentler slope (AICcw = 0.63; Figure 3f). Spatial structure was generally significant and selected in the top set of models (AICcw = 0.65, Table 1). In contrast to FRic and FDis, changes in functional evenness (FEve) were not related to any of the environmental variables.

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**FIGURE 2** Smoothers curves (S) showing the relationship (solid line) between (a) waves, (b) chlorophyll-a, (c) urbanization and taxonomic species richness, (d) wave, (e) urbanization and fish abundance. Shaded areas indicate standard errors of the smooth curve. The ‘rug plots’ on the x-axis indicate the range of variables over which measurements were taken.
or degree of urbanization. Thus, sites with higher wave energy, resulted in fish communities with fewer and less extreme trait modalities, although the distribution of individuals among these modalities did not change (a function of individuals clustering near the centre of trait space, likely defined by common and schooling fishes present across most sites). The models explained 42.1% of the deviance for Sing.sp., 18% for FRic, 54.4% for FDis, and for 13.7% Feve (Table 1).

The comparisons of the single-trait CWM values between habitats showed that changes in environmental characteristics resulted in significant shifts in functional traits of sandy beach fish assemblages (Table 1). The water column feeding position was mainly influenced by Chl-α, distance to the closest river, urbanization and waves. Benthic fishes were slightly more abundant further away from rivers (AICcw = 0.79; Figure 4a) and in areas with intermediate wave height (AICcw = 0.52; Figure 4b) (30.2% of deviance explained). Demersal fishes were more abundant with increasing Chl-α level (AICcw = 1.00; Figure 4c) and increasing urbanization (AICcw = 0.58; Figure 4d). Spatial structure was generally significant and selected in the top set of models explaining demersal fish distribution (AICcw = 0.93; Table 1) (33.3% of deviance explained). Pelagic fishes decreased in abundance with increasing Chl-α level (AICcw = 0.94; Figure 4e), wave height (AICcw = 0.65; Figure 4f) and distance to river (AICcw = 0.60; Figure 4g). They were also driven by urbanization (AICcw = 0.78; Figure 4h), with lower abundance in intermediate levels of urbanization, while increasing with beach inclination (AICcw = 0.58; Figure 4i) (30.8% of deviance explained). Surface feeding fishes were not related to any of the measured environmental variables or degree of urbanization.

The abundance of particular trophic groups was mainly driven by wave height. Detritivorous (16.4% of deviance explained) and phytoplanktivorous species were less abundant at sites with increasing wave height (AICcw = 0.91; AICcw = 0.85; Figure 4j,k) (22.4% of deviance explained). Zooplanktotrophic species were slightly less abundant with increasing wave height (AICcw = 0.52; Figure 4m) and with increasing distance to river (AICcw = 0.66; Figure 4n) (12.7% of deviance explained). For zoobenthivorous fish, we observed higher abundance at intermediate wave heights (Tot.AICcw = 1.00; Figure 4o), and a positive influence of Chl-α (AICcw = 1.00; Figure 4p) (35.9% of deviance explained). Piscivorous fishes increased in abundance
as wave height increased (Tot.AICcw = 1.00; Figure 4q) and as the river size increased (AICcw = 0.83; Figure 4r) (44.7% of deviance explained).

Small fishes (L_{med} 5–20 cm) were more abundant close to river mouths (AICcw = 0.72; Figure 4s) (26.6% of deviance explained). Large fishes (L_{med} >40 cm) were mostly spatially structured (AICcw = 1.00, Table 1) (54.8% of deviance explained), while medium sized fishes (L_{med} 20–40 cm) were not related to any of the measured environmental variables or degree of urbanization. Association (solitary/schoolforming) was also not related to any of the environmental variables or degree of urbanization.

4 | DISCUSSION

Despite surf zones having ecological importance for many fishes and supporting significant fisheries (Schlacher et al., 2015), few studies to date have addressed how environmental and anthropogenic variables shape surf zone taxonomic and functional fish biodiversity patterns on a regional scale (Andrade-Tubino et al., 2020). We show that surf zone fish communities are mainly structured by wave breaker height and proximity to human impacts and that these variables tended to reduce taxonomic and functional diversity to a few generalist predatory fish species, a consequence of their ability to explore multiple resources, which allows them to effectively forage in less diverse or impoverished conditions caused by anthropic impacts. In addition to wave height and urbanization, we also found that chlorophyll-a levels and proximity to rivers may significantly influence the taxonomic and functional patterns of fish species in sandy beach surf zones.

Abundance and number of species of surf fish has been hypothesized to be higher in areas with intermediate wave action since it may enhance schooling (Valesini et al., 2004) and liberate benthic prey species from the sediment (Pessanha and Araújo,
Our results, however, showed that the number of species and individuals of nearshore fish assemblages was linearly and negatively related to wave height. As a consequence, fish richness and abundance are likely higher in sheltered conditions, possibly due to a calmer surf climate which may favour the occurrence of several species, and in dissipative beaches, areas with wider surf zones where wave energy is dissipated through. Dissipative beaches are also known to have larger number of microhabitats such as runnels and bars along the benthic environment (Mosman et al., 2020), characteristic that tends to increase fish richness and abundance (Layman, 2000; Marin Jarrin & Miller, 2016). Higher fish richness and diversity in sheltered or dissipative beaches have been previously reported by Clark (1997) and Andrade-Tubino et al. (2020), reinforcing that habitats with lower wave energy on the beach face may be the most beneficial for nearshore fish diversity (Beyst et al., 2001).

Importantly, we found urbanization to be a fundamental driver of nearshore fish assemblages with an overall negative effect on their number of species and individuals. Similarly, Araújo et al. (2017) registered a decrease in species richness and abundance of fishes in a sandy beach after coastal industrialization while Reyes-Martínez et al. (2015) and Costa et al. (2017a) found low fish richness with high levels of visitation and beach maintenance, suggesting that impacted beaches are avoided by surf zone fishes. Human disturbances may also negatively affect fish assemblages by reducing water quality (Huijbers et al., 2015) and food availability (Costa et al., 2017b; Schlacher & Thompson, 2012) and simplifying food webs in comparison to non-urbanized beaches (Reyes-Martínez et al., 2015). Nevertheless, we found the influence of urbanization on fish richness and abundance to have a non-linear relationship, with stabilization at moderate levels of urbanization, suggesting that reduction of just a few of these direct or indirect impacts is unlikely to generate significant effects on fish assemblages.

### Table 1

| Overall Akaike weights (AICcw) for each variable | Waves | Chl-a | UI | Distance river | River size | Slope | Lat, Long | %Variance Explained |
|---|---|---|---|---|---|---|---|---|
| **Taxonomic Diversity** | | | | | | | | |
| Richness | 1.00 | 0.92 | 0.52 | 0.16 | 0.15 | 0.14 | 0.00 | 41.8% |
| Abundance | 1.00 | 0.14 | 1.00 | 0.41 | 0.21 | 0.42 | 0.07 | 45.7% |
| **Functional Diversity** | | | | | | | | |
| Sing.sp | 1.00 | 1.00 | 0.26 | 0.11 | 0.21 | 0.14 | 0.00 | 42.1% |
| Fric | 1.00 | 0.13 | 0.14 | 0.13 | 0.12 | 0.10 | 0.00 | 18.0% |
| Fdis | 0.24 | 0.19 | 0.95 | 0.87 | 0.18 | 0.63 | 0.96 | 54.4% |
| Feve | 0.11 | 0.16 | 0.22 | 0.19 | 0.10 | 0.12 | 0.25 | 13.7% |
| **CWM** | | | | | | | | |
| Association | | | | | | | | |
| Solitary | 0.25 | 0.13 | 0.12 | 0.17 | 0.15 | 0.24 | 0.05 | 23.0% |
| Schoolforming | 0.26 | 0.13 | 0.12 | 0.17 | 0.17 | 0.16 | 0.05 | 23.0% |
| Water | | | | | | | | |
| Benthic | 0.52 | 0.10 | 0.26 | 0.79 | 0.35 | 0.10 | 0.00 | 30.2% |
| column Demersal | 0.29 | 1.00 | 0.58 | 0.41 | 0.25 | 0.15 | 0.93 | 33.3% |
| Feeding | Pelagic | 0.65 | 0.94 | 0.78 | 0.60 | 0.17 | 0.58 | 0.00 | 30.8% |
| Position | Surface | 0.13 | 0.09 | 0.11 | 0.19 | 0.10 | 0.37 | 0.46 | 23.3% |
| Diet | Detritivorous | 0.91 | 0.39 | 0.13 | 0.13 | 0.17 | 0.13 | 0.00 | 16.4% |
| Phytoplanktivorous | 0.85 | 0.40 | 0.74 | 0.19 | 0.17 | 0.11 | 0.00 | 22.4% |
| Zooplanktivorous | 0.52 | 0.33 | 0.18 | 0.66 | 0.20 | 0.15 | 0.08 | 12.7% |
| Zoobenthivorous | 1.00 | 1.00 | 0.21 | 0.15 | 0.11 | 0.33 | 0.13 | 35.9% |
| Piscivorous | 1.00 | 0.09 | 0.27 | 0.22 | 0.83 | 0.20 | 0.21 | 44.7% |
| **Length** | | | | | | | | |
| L<sub>med</sub> 5-20cm | 0.30 | 0.41 | 0.22 | 0.72 | 0.22 | 0.35 | 0.37 | 26.6% |
| L<sub>med</sub> 20-40cm | 0.16 | 0.46 | 0.31 | 0.14 | 0.16 | 0.30 | 0.00 | 10.5% |
| L<sub>med</sub> >40cm | 0.07 | 0.00 | 0.12 | 0.38 | 0.00 | 0.16 | 1.00 | 54.8% |
substantial change. Besides wave height and urbanization, chlorophyll-α levels in sandy beach surf zones also significantly influenced the species richness of fish assemblages. Reflecting the role of phytoplankton production as an important food resource for many surf-zone fishes, number of species was higher in sites with higher chlorophyll-α levels, likely due to increased food resources and more links in the local trophic web (Bergamino et al., 2011).

As with taxonomic diversity, wave height, urbanization and chlorophyll-α levels were also the main drivers of functional diversity of nearshore fish assemblages. The higher number of species in sites with lower waves and higher chlorophyll-α levels resulted in higher values of FRic and singular species, showing that fish assemblages in these sites have a wider range of functional traits. The urbanization effect, however, was not so clear. We found higher values of Fdis at sites with low (between 1 and 2) and high (>3) UI, suggesting that, despite having lower species richness and abundance of individuals, fish assemblages in urbanized sites may maintain high functional diversity (Sousa Gomes-Gonçalves et al., 2020; Teichert et al., 2018). Also, beaches with a steep slope have short, deep surf zones that consist of less microhabitats (like runnels and bars) (Wright & Short, 1984), which can explain the decrease of functional dispersion, since less ecological niches are available to be filled by distinct functional groups. Fdis was also lower at sites close to river mouths, likely reflecting the lower and more variable salinity which could prevent the occurrence of marine/stenohaline species. In fact, variations in salinity resulting from local freshwater discharges have shown to strongly modify the structure of sandy beach macrofaunal assemblages (Lercari & Defeo, 2006) and our results suggest that this effect may be extended to the nektonic diversity.

The analyses of the single-trait CWM enabled us to further dissect how environmental variables and human actions affect the functional diversity of nearshore assemblages. Higher waves reduced the abundance of pelagic, detritivorous, phyto- and zooplanktivorous species, likely due to the lower primary productivity and deposition of organic matter linked to higher hydrodynamics in the shallow areas of the surf zone (Brown & McLachlan, 2010; McLachlan et al., 1981; Odebrecht et al., 2014). Conversely, the abundance of piscivores (e.g. Strongylura timucu (Walbaum, 1792) and Carcharhinus limbatus (Müller & Henle, 1839)), increased with wave height, highlighting the ability of predatory species to withstand or migrate away from these harsher environmental conditions as necessary (Stewart & Jones, 2001). Interestingly, the abundance of benthic and zoobenthivorous species was higher in areas with intermediate wave height, suggesting that the hypothesis of higher fish abundances in areas with moderate wave action may be true for these species traits.

We also observed that pelagic fishes were more abundant in sites with lower Chl-α levels, while demersal and zoobenthivorous fishes showed the opposite trend. Although studies show that natural Chl-α levels for sandy beaches are commonly found to be low (0.05–9.16 μg L⁻¹, Menéndez et al., 2016), some isolated values registered in our study are quite high: up to 80 μg L⁻¹. Many sites in the study area (e.g. Itagua & Itamambuca beaches) experience sewage discharges from neighbouring areas (CETESB – Environmental Agency of the State of São Paulo), either from local outfalls or from rivers contaminated by anthropic discharges along its path, resulting in an ongoing nutrient enrichment process, which has been shown to profoundly affect phytoplankton species composition and production (Aktan et al., 2005) and fishes (Guidetti et al., 2002). Since the majority of the pelagic fish in our study were planktivorous, this contrasts with other studies that found these groups to be more abundant in areas with nutrient enrichment associated with sewage discharge (Palacios-Sánchez et al., 2019). This discrepancy highlights that even though the input of nutrient-rich water creates favourable phytoplankton growth conditions (Grimes & Finucane, 1991), there might be a limit for it to be considered ‘favourable’ for pelagic species, while still benefiting demersal and zoobenthivorous species. Nevertheless, more studies are required to investigate the underlying mechanisms that generate the observed effects of phytoplankton abundance on the functional diversity of fishes.

Benthic fishes were more abundant far from river mouths, while sites close to river mouths had higher abundance of small fishes (Lmed: 5–20 cm), zooplanktivorous and pelagic fishes. Sandy beach surf zones contain many transitory species (e.g. Diapterus rhombeus (Cuvier, 1829) and Eucinostomus melanopterus (Bleeker, 1863)) that enter estuaries during the initial or reproductive phases of their lives, which may explain the occurrence of small-bodied species closer to rivers. Furthermore, rivers modify the functioning of the coastal system processes by discharging large amounts of nutrients and sedimentary material into the water column, which are then distributed by marine currents and alongshore transport (Herrera & Bone, 2011). These nutrient inputs can be facilitated by the numerous small river tributary mouths (0.006–0.3 km) present near almost all of the beaches in our study. These river tributaries may also serve as a source of organic and inorganic contamination derived from human activities, for especially due to discharges along its course, such as found in rivers in the study area (CETESB 2019), which can benefit some but limit other functional groups.

In summary, our results show that surf-zone fish assemblages are structured by an interplay between environmental and anthropogenic factors and highlight the importance of considering both drivers in ecological assessments. They also reaffirm the importance of considering functional traits to complement taxonomic assessments, since environmental and anthropic variables affect species with specific functional traits differently in ways that are not always reflected in the total species richness. Targeting low-wave sites with low urbanization is an important strategy to protect communities taxonomically and functionally more distinct. In particular, species which are of critical conservation importance (e.g. rays of the genus Dasyatis), were only found at sites with low waves and urbanization. However, this strategy would miss trophic categories, such as piscivorous fishes (e.g. blacktip reef shark, Carcharhinus limbatus or several species of the genus Trachinotus), which were most abundant in...
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CONFLICT OF INTEREST

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data is made available as supplementary material.

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REFERENCES

Aktan, Y., Tüfekçi, V., Tüfekçi, H., & Aykulu, G. (2005). Distribution patterns, biomass estimates and diversity of phytoplankton in Izmit Bay (Turkey). Estuarine, Coastal and Shelf Science, 64(2-3), 372-384. https://doi.org/10.1016/j.ecss.2005.03.003
Araújo, F. G., de Azevedo, M. C. C., de Araújo Silva, M., Pessanha, A. L. M., Gomes, I. D., & da Cruz-Filho, A. G. (2002). Environmental influences on the demersal fish assemblages in the Sepetiba Bay, Brazil. Estuaries, 25(3), 441-450. https://doi.org/10.1007/BF02695986
Araújo, F. G., Pinto, S. M., Neves, L. M., & de Azevedo, M. C. C. (2017). Inter-annual changes in fish communities of a tropical bay in southeastern Brazil: What can be inferred from anthropogenic activities? Marine Pollution Icorcu, 114(1), 102-113. https://doi.org/10.1016/j.marpollbul.2016.08.063
Azevedo, M. C. C., de Sousa Gomes-Gonçalves, R., Mattos, T. M., Uehara, W., Guedes, G. H. S., & Araújo, F. G. (2017). Taxonomic and functional distinctness of the fish assemblages in three coastal environments (bays, coastal lagoons and oceanic beaches) in Southeastern Brazil. Marine Environmental Research, 129, 180-188. https://doi.org/10.1016/j.marenvres.2017.05.007
Barton, K., & Barton, M. K. (2015). Package ‘MuMln’. Version, 1, 18.
Begossi, A., May, P. H., Lopes, P. F., Oliveira, L. E., Da Vinha, V., & Silvano, R. A. (2011). Compensation for environmental services from artisanal fisheries in SE Brazil: Policy and technical strategies. Ecological Economics, 71, 25-32. https://doi.org/10.1016/j.ecolecon.2011.09.008
Bergamino, L., Lercari, D., & Defeo, O. (2011). Food web structure of sandy beaches: temporal and spatial variation using stable isotope analysis. Estuarine, Coastal and Shelf Science, 91(4), 536-543. https://doi.org/10.1016/j.ecss.2010.12.007
Beyst, B., Hostens, K., & Mees, J. (2001). Factors influencing fish and icocrustacean communities in the surf zone of sandy beaches in Belgium: Temporal variation. Journal of Sea Research, 46(3-4), 281-294.
Borcard, D., & Legendre, P. (2002). All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecological Modelling, 153(1-2), 51-68.
Borland, H. P., Schlacher, T. A., Gilby, B. L., Connolly, R. M., Yabsley, N. A., & Olds, A. D. (2017). Habitat type and beach exposure shape
Teichert, N., Lepage, M., Chevillot, X., & Lobry, J. (2018). Environmental drivers of taxonomic, functional and phylogenetic diversity (alpha, beta and gamma components) in estuarine fish communities. *Journal of Biogeography*, 45(2), 406–417. https://doi.org/10.1111/jbi.13133

Tejerina-Garro, F. L., Maldonado, M., Ibañez, C., Pont, D., Roset, N., & Oberdorff, T. (2005). Effects of natural and anthropogenic environmental changes on riverine fish assemblages: a framework for ecological assessment of rivers. *Brazilian Archives of Biology and Technology*, 48(1), 91-108. https://doi.org/10.1590/S1516-8913005000100013

Valesini, F. J., Potter, I. C., & Clarke, K. R. (2004). To what extent are the fish compositions at nearshore sites along a heterogeneous coast related to habitat type? *Estuarine, Coastal and Shelf Science*, 60(4), 737–754. https://doi.org/10.1016/j.ecss.2004.03.012

Vargas-Fonseca, E., Olds, A. D., Gilby, B. L., Connolly, R. M., Schoeman, D. S., Huibers, C. M., Hyndes, G. A., & Schlacher, T. A. (2016). Combined effects of urbanization and connectivity on iconic coastal fishes. *Diversity and Distributions*, 22(12), 1328–1341. https://doi.org/10.1111/ddi.12495

Villéger, S., Miranda, J. R., Hernández, D. F., & Mouillot, D. (2010). Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications*, 20(6), 1512-1522.

von der Heyden, S. (2017). Making evolutionary history count: biodiversity planning for coral reef fishes and the conservation of evolutionary processes. *Coral Reefs*, 36(1), 183–194. https://doi.org/10.1007/s00338-016-1512-2

Wood, R. J. (2006). Erosion–corrosion interactions and their effect on marine and offshore materials. *Wear*, 261(9), 1012–1023. https://doi.org/10.1016/j.wear.2006.03.033

Wood, S. (2012). mgcv: Mixed GAM Computation Vehicle with GCV/ AIC/REML smoothness estimation.

Wright, L. D., & Short, A. D. (1984). Morphodynamic variability of surf zones and beaches: a synthesis. *Marine Geology*, 56, 93–118. https://doi.org/10.1016/0025-3227(84)90008-2

Yabsley, N. A., Gilby, B. L., Schlacher, T. A., Henderson, C. J., Connolly, R. M., Maxwell, P. S., & Olds, A. D. (2020). Landscape context and nutrients modify the effects of coastal urbanisation. *Marine Environmental Research*, 158, 104936. https://doi.org/10.1016/j.marenvres.2020.104936

Zuur, A. F., Leno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3-14.

**Biosketch**

The multi-institutional research group ([www.manejo.io.usp.br](http://www.manejo.io.usp.br)) made up of marine scientists is focused on the ecology of coastal ecosystems. The aim of their shared research project is to provide baseline data on biodiversity and the main drivers of this biodiversity in order to contribute essential information for conservation measures. This specific work will serve as a crucial record for including sandy beaches in the coastal management plan. The study offers the first evidence for site prioritization and provides subsidies for understanding patterns at larger scales in order to incorporate the results in further integrated coastal management plans.

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**Supporting Information**

Additional supporting information may be found in the online version of the article at the publisher’s website.

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