Scale sensitivity of environmental effects on the temporal beta diversity of fishes in tropical coastal lagoons

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ABSTRACT: Disentangling multilevel sources of variation is critical for understanding of diversity patterns in high-variability environments. We investigated the scale sensitivity of short-term environmental effects on the temporal beta diversity of fishes in 3 tropical coastal lagoons in Southeastern Brazil. Environmental effects were investigated at 3 hierarchical levels (local, zone, and lagoon). An AICc-based model selection was applied to generalized linear mixed models relating abundance-based beta diversity (Bray-Curtis dissimilarity; β_{BC}) to environmental distances and random effects for other sources of variability. Abundance gradients (β_{BC-GRA}) contributed more for β_{BC} at all hierarchical levels, most likely due to random changes in the abundances of numerous rare marine-origin species. The temporal and spatial marine influences favored the balanced variation in the abundance of different species (β_{BC-BAL}), probably by allowing for marine species with different environmental tolerances and requirements. The freshwater vs. marine influences were primarily represented by short-term effects of salinity changes at the local and zone levels and tide height and accumulated rainfall at the lagoon level. Other environmental effects (e.g. pH and transparency) were representative of that balance depending on the β_{BC} component and hierarchical level. Random effects for morphometric features (local level, width of the connections between zones; lagoon level, distance from the ocean) and climate-related factors (local and zone levels, wind intensity and accumulated rainfall; lagoon level, changing seasons) were also relevant for the relationships between environmental variability and β_{BC}. This study evidenced major scale-related mechanisms driving the temporal beta diversity of fishes in tropical coastal lagoons.

KEY WORDS: Scale dependence · Short-term environmental variability · Fish assemblage structure · Multiscale sources of variation · Abundance-based dissimilarity

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1. INTRODUCTION

Coastal lagoons are shallow ecosystems widely subjected to environmental changes at different spatial and temporal scales, primarily associated with the regimes of temperature, precipitation, wind, and tides (Garcia et al. 2017, Pérez-Ruzafa et al. 2019). The importance of these climate- and ocean-related factors for spatial and temporal changes in water quality are influenced by the morphometric features

of the coastal lagoons, such as area, length of the main axis, and degree of connection with the ocean, as well as differences in riverine input (Petry et al. 2016, Hartz et al. 2019). These differences primarily influence the water renewal process, which may result in pronounced salinity gradients distinguishing zones with different levels of marine and freshwater influence (Knoppers et al. 1991, Franco et al. 2019). Likewise, the imbalance in the water-mediated exchange of energy, species, nutrients, and other materials may also represent great differences in the connectivity within and between the coastal lagoons and the ocean (Garcia et al. 2017, Netto & Fonseca 2017). In addition, land use changes and other human impacts resulting from the growing urban development typically associated with coastal areas also influence the environmental conditions in coastal lagoons (Guerra et al. 2011, Camara et al. 2019, Franco et al. 2019).

The environmental variability typical of transitional coastal ecosystems, such as estuaries and coastal lagoons, constitutes filters that select species for the local assemblages at different spatial and temporal scales (e.g. Sosa-López et al. 2007, Mouchet et al. 2013, Nelson et al. 2015). In the tropical region, the regional pool of fish species in coastal areas includes a variable mix of species belonging to families originating in freshwater habitats, but closely related to marine groups, and families that invaded the freshwater environment at different historical times, along with a high diversity of marine species (Reis et al. 2016). Fish species inhabiting transitional coastal ecosystems may, therefore, be widely distributed or restricted to areas with larger freshwater or marine influence, depending on their environmental tolerances and degrees of dependence on estuarine habitats (Elliott et al. 2007). Likewise, some fish species are rare or abundant over the entire annual cycle, whereas species that spend only particular stages of their life cycles in estuarine habitats occur or are more abundant in some periods throughout the year (Potter et al. 2015, Andrade-Tubino et al. 2020). Therefore, the life cycles of individuals strongly influence seasonal changes in species composition and abundance in such coastal ecosystems (Castillo-Rivera et al. 2010, Galaiduk et al. 2018). In this sense, it is likely that shorter-term changes may better reflect the species–environment relationships in terms of specific physiological limits and habitat requirements, as observed in short-term studies elsewhere (e.g. Netto & Fonseca 2017, Camara et al. 2018).

The biogeographic patterns inherent to coastal fish fauna in the tropical region have promoted a strong family-level dependence on the environmental tolerances and requirements associated with fish habitat use in transitional coastal ecosystems (Elliott et al. 2007, Reis et al. 2016). It is then reasonable to expect a high concordance between fish assemblages in tropical coastal lagoons related to the spatial and temporal changes in species composition and abundance associated with a given set of environmental effects (Heino 2010, Teichert et al. 2018). However, the morphometric features of coastal lagoons and riverine inputs strongly influence spatial heterogeneity and temporal variability in environmental conditions (Sheaves & Johnston 2009, Hartz et al. 2019). Unmeasured environmental effects, such as biotic interactions and landscape features, may also contribute to the variation in species composition and abundance in transitional coastal ecosystems (Henriques et al. 2017, Camara et al. 2019). These multiple influences may generate spatial dependence in the temporal effects, with the influence of environmental variability on fish assemblage structure dependent on spatial scale (Bergström et al. 2016, Östman et al. 2017). Therefore, unbiased estimates of species–environment relationships must consider the spatial and temporal dependencies resulting from these multiscale influences.

A better understanding of the critical aspects of ecosystem functioning associated with variation in species composition and abundance, or beta diversity, may be provided by qualitative (i.e. presence or absence) and quantitative (i.e. abundance) measures of dissimilarity (Legendre 2014, Baselga 2017). These measures may express variation in species composition (and abundance) as a non-directional change between sampling units (i.e. variation) or a directional change from one sampling unit to another (i.e. turnover; Anderson et al. 2011). Quantitative measures of dissimilarity are especially interesting to compare in assemblages that differ mostly by the abundance of their species (Legendre 2014). The directional measures of abundance-based dissimilarity assess diversity patterns and their possible causal mechanisms by distinguishing the replacement of the same number of individuals of different species between samples (i.e. balanced variation in abundance) and changes in the abundance between samples (i.e. abundance gradients; Baselga 2013). Therefore, information provided by abundance-based dissimilarity may maximize understanding of assembly processes supporting the diversity patterns where geographical proximity favors the species sharing between assemblages due to the higher probability of species dispersal and greater similarity

in the regional pool (Bender et al. 2017, Camara et al. 2019). Likewise, abundance-based dissimilarity measures are most likely more sensitive to the assemblage changes associated with short-term environmental variability, given the species responses based on their environmental tolerances and requirements. Studies on fish beta diversity in coastal lagoons are very scarce and, as far as we know, do not include directional abundance-based measures (e.g. Villéger et al. 2012, Camara et al. 2019). These measures are also rarely used in studies related to fish fauna in other types of coastal ecosystems (e.g. Lamy et al. 2015, Lazzari et al. 2020). Therefore, new insights on the ecological processes driving spatial and temporal variation in coastal fish assemblages may be achieved by directional abundance-based measures of beta diversity.

Considering the aforementioned scenario, we assume that disentangling the individual and shared roles of multiple environmental factors across a range of spatial scales is critical for a better understanding of the temporal variation in fish assemblage structure in tropical coastal lagoons. Likewise, given the different temporal scales associated with specific ecological processes, we believe that a better understanding of the assembly patterns must consider possible effects at different temporal scales. Based on these assumptions, this study investigated the sensitivity to the spatial scale of short-term environmental effects on the beta diversity (i.e. abundance-based dissimilarity) of fishes over an annual cycle in 3 tropical coastal lagoons. We considered directional changes between samples at the smallest temporal interval encompassed by the data set (i.e. 2 mo intervals) in order to identify as many hierarchically structured random sources of temporal variation (i.e. nested temporal effects) as possible. The short-term relationships were investigated at 3 spatial scales, herein named hierarchical levels (i.e. local, zone, and lagoon levels) comprising each sampling location nested in each zone within each coastal lagoon. We also investigated possible confounding effects on the relationships between short-term environmental variability and beta diversity at the local, zone, and lagoon levels. These effects included morphometric and hydrological features of the coastal lagoons and other sources of temporally and spatially dependent environmental variability, such as climate-related effects and hierarchical structure. We hypothesized that, depending on the hierarchical level, different environmental and/or confounding effects are relevant. Assessing and controlling for multiple sources of variation in temporal beta diversity, this study aims to provide unbiased estimates for the scale sensitivity of short-term environmental effects on the fish assemblage structure in tropical coastal lagoons.

2. MATERIALS AND METHODS

2.1. Study area

The 3 coastal lagoons (Maricá, Saquarema, and Araruama) are located on the coast of the Rio de Janeiro State, Southeastern Brazil (Fig. 1a). This tropical region contains a high number of coastal lagoons, which represent a common type of ecosystem on the Brazilian coast (Petry et al. 2016). The study area has an annual mean temperature of 22°C, and annual total rainfall ranges from 1000 to 1600 mm, peaking in the wet season (October to March) (Alvares et al. 2013). Despite the largest distance between 2 lagoons being less than 35 km, there is a climatic gradient, with rainfall decreasing from the Maricá to the Araruama lagoon (Knoppers et al. 1991). The studied coastal lagoons are formed by sets of cells oriented parallel to the coast, with reduced riverine input and single, narrow permanent connections with the ocean (Knoppers et al. 1991, Kjerfve 1994). As a consequence, water renewal is slow and strongly associated with wind, rainfall, and tidal fluctuations, which, in turn, are dependent on the distance from the sea (Knoppers et al. 1991, Franco et al. 2019). These characteristics lead to salinity gradients distinguishing zones with different levels of freshwater and marine influence, which are also related to morphometric differences (e.g. surface area, perimeter, longitudinal length, mean width, and channel mean length and width) between the coastal lagoons. These morphometric features were obtained for the studied lagoons from vectorial layers of hydrography (digital cartographic base of the Instituto Brasileiro de Geografia e Estatística; 1:50 000 scale) using a geographic information system (ArcGIS v.10.2; ESRI 2013).

The coastal lagoons are under increasing human pressures and are subjected to large sewage loads as a consequence of their proximity to urban areas of medium to high population density (Guerra et al. 2011, Camara et al. 2019). A large portion of the Araruama lagoon perimeter is also subjected to saline extraction (Franco et al. 2019). The native forest cover, represented by Restinga forest and swamps, is reduced and restricted to some portions of the coastal lagoons, which are also surrounded by different proportions of pasture cover (Camara et al. 2019).
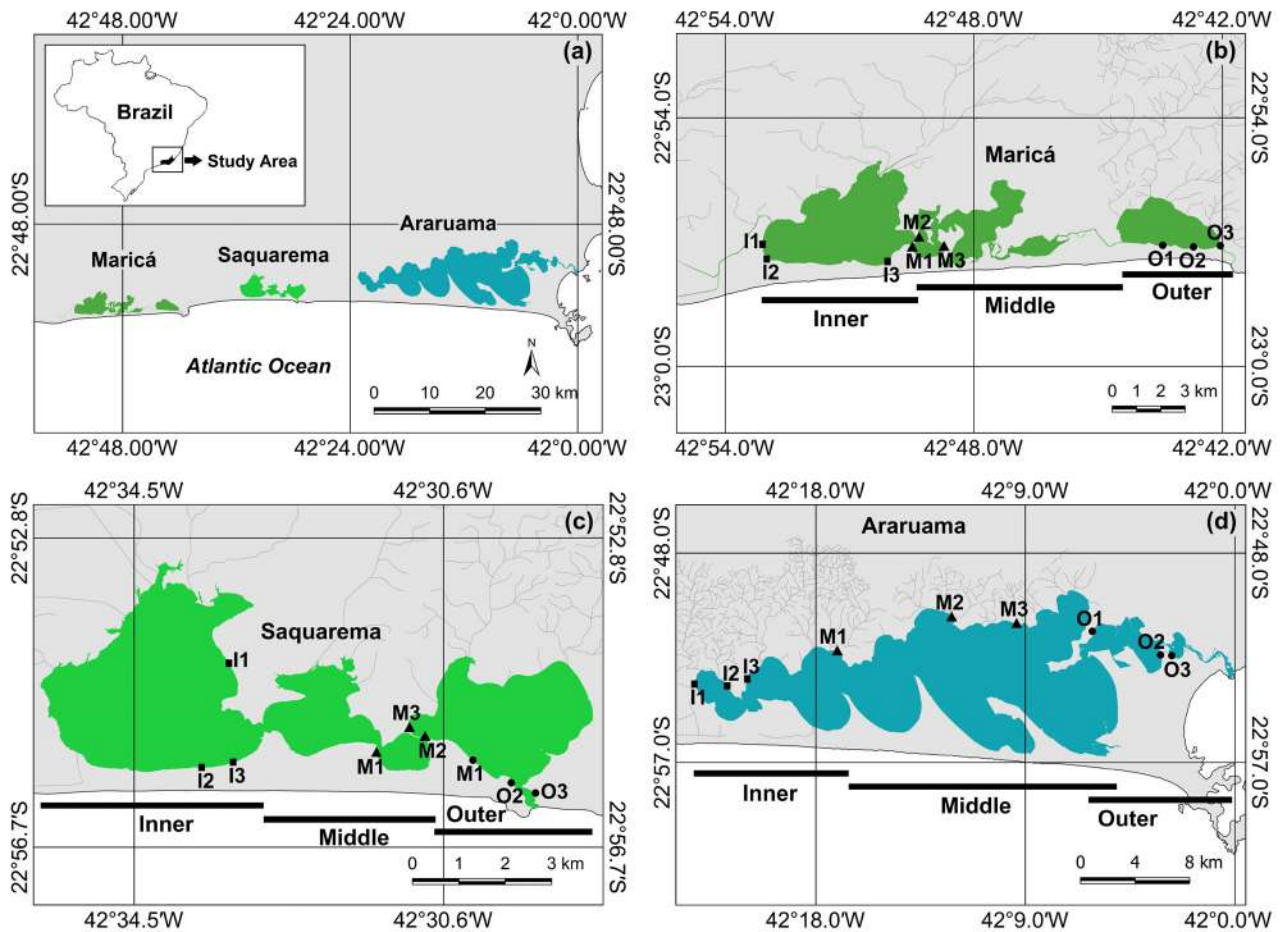
Fig. 1. (a) Study area showing the 3 coastal lagoons in Southeastern Brazil. Sampling locations and zones are represented for the (b) Maricá, (c) Saquarema, and (d) Araruama lagoons. Horizontal black bars: extensions considered for the inner, middle, and outer zones; black squares, triangles, and circles: sampling locations in the inner (I1, I2, and I3), middle (M1, M2, and M3), and outer (O1, O2, and O3) zones, respectively; light gray lines: fluvial input in each lagoon

Mesohaline conditions, with salinity ranging from 8 to 38 (mean value of 18), and a mean depth of 1.2 m characterize the Maricá lagoon (Franco et al. 2019). The lagoon system consists of 4 well defined and interconnected lagoons with a total area of 34 km², perimeter of 114 km, length of 19 km, and mean width of 1.7 km (Fig. 1b). The single channel connecting the lagoon to the ocean is 1.3 km long with a mean width of about 30 m. The drainage basin encompasses small streams and 3 main watersheds, 2 flowing to the most inner lagoon and another to the lagoon nearest from the connection with the ocean (Fig. 1b). The renewal time for 50% of the water in the Maricá lagoon varies between 27 and 7 d in the portions farthest and nearest from the connection with the ocean, respectively (Knoppers et al. 1991).

The Saquarema lagoon is a euhaline system with mean salinity of 35, formed by 4 interconnected lagoons with a mean depth of 1.2 m (Franco et al.

2019). The system encompasses 25 km² of surface area, with a perimeter of 59 km, length of 12 km, and mean width of 2.4 km (Fig. 1c). The channel that connects the Saquarema lagoon with the ocean is 1.1 km long and has a mean width of 118 m. Four small streams flow to the inner lagoon of the system, one flows to the intermediate lagoon, and 2 flow to the lagoon nearest the connection to the ocean (Fig. 1c). In the portion farthest from the connection to the ocean, the renewal time estimated for 50% of the water is 23 d, whereas in the nearest portion the estimate is 6 d (Knoppers et al. 1991).

The Araruama lagoon is a permanently hyperhaline coastal lagoon, with a mean salinity of approximately 50 (Kjerfve et al. 1996). This lagoon is formed by 7 elliptical cells with a total area of 217 km², perimeter of 223 km, length of 39 km, and mean width of 4.6 km (Fig. 1d). The Araruama lagoon has a mean depth of 3 m (Kjerfve et al. 1996) and is connected to

the ocean by a single 5.5 km long channel with mean width of 127 m. Riverine input consists of small and intermittent streams concentrated on the west portion of the lagoon (Fig. 1d). The entire lagoon has the highest renewal time for 50% of the water compared with the Maricá and Saquarema lagoons (i.e. approximately 84 d) (Kjerfve 1994, Kjerfve et al. 1996).

2.2. Fish sampling

Sampling was performed in the Maricá, Saquarema, and Araruama lagoons bimonthly between September 2017 and September 2018. For each lagoon, sampling was conducted at 3 locations in each of the 3 zones (i.e. inner, middle, and outer) (Fig. 1b–d). A total of 189 samples were obtained at the sampling locations (3 locations × 3 zones × 3 coastal lagoons × 7 periods).

Each sample comprised 3 replicates per location. For each replicate, fishes were collected with a beach seine (12 × 2.5 m; 5 mm mesh size) set parallel to the shore at approximately 1.5 m depth and dragging for 30 m perpendicular to the shore, covering a swept area of about 300 m^2. The collected fishes were fixed in 10% formalin, and after 48 h they were preserved in 70% ethanol. All fishes were identified to species level as described in Araújo et al. (2018), and voucher specimens were deposited in the Ichthyological Collection of the Laboratório de Ecologia de Peixes of the Universidade Federal Rural do Rio de Janeiro.

2.3. Measures of temporal beta diversity

The spatial and temporal variation in fish assemblages were firstly assessed by non-metric multidimensional scaling (NMDS; Legendre & Legendre 2012). The analysis aimed to identify hierarchical spatial and/or temporal structures associated with local assemblage patterns. The NMDS was based on Bray-Curtis dissimilarity in species composition and abundance per location and sampling period, which is appropriate for abundance data with many zeros, applied to a standardized and square-root transformed species abundance data matrix (Legendre & Gallagher 2001). The species abundance data matrix was standardized using Wisconsin double standardization, where abundance is divided by the maximum abundance of each species (column) and then divided by the total abundance of each sample (Oksanen et al. 2019). The stress indicates goodness-of-fit for samples in NMDS, and a maximum stress of 0.2 is considered indicative of high confidence in the observed distance between samples (Legendre & Legendre 2012). The spatial and/or temporal structures identified in the NMDS ordination were considered as random sources of variation in the following analyses.

Temporal beta diversity was estimated as the abundance-based assemblage dissimilarity between samples obtained in consecutive 2 mo intervals using the Bray-Curtis index (Baselga 2013, Legendre 2014). The total abundance-based dissimilarity between the consecutive 2 mo intervals (β_{BC}) was partitioned in 2 additive components: (1) the balanced variation in species abundances ($\beta_{BC\text{-}BAL}$), indicative of replacement of the individuals of some species in a given sample by the same number of individuals of different species in the following sample; and (2) the abundance gradient ($\beta_{BC\text{-}GRA}$), representing the loss or gain of individuals of all species from a given sample to the following sample (Baselga 2013). Compared to incidence-based dissimilarity measures, $\beta_{BC\text{-}BAL}$ is analogous to species replacement, as the observed changes in species abundances have different signs for different species and changes balance each other, whereas $\beta_{BC\text{-}GRA}$ is analogous to species nestedness, as the observed changes in species abundances have the same sign for all species (Baselga 2013, 2017). This procedure was performed for each sampling location (i.e. local level), each zone within a given coastal lagoon (i.e. zone level), and each coastal lagoon (i.e. lagoon level). Each measure of beta diversity (β_{BC}, $\beta_{BC\text{-}BAL}$, and $\beta_{BC\text{-}GRA}$) was obtained in the six 2 mo intervals between the 7 consecutive sampling periods for each location, zone, and lagoon. Therefore, each temporal beta diversity measure was obtained 162 times (3 locations × 3 zones × 3 coastal lagoons × 6 intervals) at the local level, 54 times (3 zones × 3 coastal lagoons × 6 intervals) at the zone level, and 18 times at the lagoon level (3 coastal lagoons × 6 intervals). The calculations were performed in R v.3.6.2 (R Core Team 2019) using the package 'betapart' (version 1.5.1; Baselga et al. 2018).

2.4. Environmental and morphometric variables

Environmental measures of physicochemical parameters and substrate were recorded at each location concurrently with fish sampling. Salinity, pH, and temperature (°C) were obtained with a HANNA HI 9829 multiprobe (HANNA Instruments), and depth (cm) was measured with a Speedtech model SM-5 digital probe (Speedtech Instruments). Transparency

(%) was measured with a Secchi disk and calculated as a percentage of Secchi depth/depth. Substrate type was classified considering the occurrence of clay + silt, fine sand, medium sand, coarse sand, gravel, and rocky bottom, estimated by visual census at 3 sampling points (1 and 0.5 m depth, and at the spread washing zone) within the approximately 300 m^2 area covered by the fish sampling. Classification was based on the scale defined by the granulometric analysis described in Camara et al. (2019). Substrate type was scored from 1 (clay + silt) to 6 (rocky bottom), and the mean value was calculated for each location.

Wind intensity was quantified following an observational classification of the wind effect on the physical environment, as follows: (1) absent, no movement perceived; (2) low, intermittent wind with little effect on leaves and surrounding shrub vegetation; (3) moderate, constant wind moving tree branches, but no effect on the effort needed for dragging the beach seine net is perceived; and (4) high, constant wind moving entire trees, and a higher effort needed for dragging with the beach seine net. For each location, 3 measures of wind intensity were obtained, one for each replicate of the fish sampling effort, and the mean value was then calculated. The classification did not consider the wind effect on the water surface to avoid any misunderstood effect of the tidal phase. For all cases, the classification was performed by the same observer.

The tide data set was obtained from the Centro de Previsão de Tempo e Estudos Climáticos/Instituto Nacional de Pesquisas Espaciais website (CPTEC/ INPE 2019). For each location, the tide height (m) was considered as the heights measured during the days and hours of sampling at the nearest stations from the channel that connects each coastal lagoon to the ocean. Therefore, the tide height was obtained at the Porto do Rio de Janeiro station, about 53 km from the Maricá lagoon, and at the Praia do Forno station, about 50 and 9 km from the Saquarema and Araruama lagoons, respectively. The mean value was calculated when more than one value was quantified during the sampling at a given location.

Accumulated rainfall (mm) was obtained for each coastal lagoon from the Instituto Nacional de Meteorologia website (INMET 2019). Values of accumulated rainfall were obtained for the sampling periods at the Forte de Copacabana station, about 31 km from the Maricá lagoon, and at the Arraial do Cabo station, about 8 km from the Araruama lagoon. For the Saquarema lagoon, the accumulated rainfall was calculated as the mean of the values recorded at the 2 stations.

Morphometric and hydrological features were obtained using a geographic information system (ArcGIS v.10.2; ESRI 2013). The geoprocessing procedures were based on vectorial layers of hydrography (1:50 000 scale; 2015–2016) provided through a partnership between the Instituto Brasileiro de Geografia e Estatística (IBGE) and the Instituto Estadual do Ambiente do Estado do Rio de Janeiro (INEA). The morphometric features included distance from the ocean (DO; km), measured for each location as the distance over water; mean width of the connections between adjacent zones (WZ; km), measured for each zone; and lagoon area (LA; km^2) and channel mean width (CW; km), both measured for each coastal lagoon. Hydrological features included riverine input per zone (RZ; km^{-1}), calculated as the ratio between the length of the riverine network in a given zone (km) and the respective zone area, and riverine input per lagoon (RL; km^{-1}), calculated as the ratio between the length of the riverine network in a given lagoon (km) and the respective lagoon area.

2.5. Data analysis

Generalized linear mixed models (GLMMs) were used to investigate the effects of short-term environmental variability (i.e. 2 mo intervals) on the beta diversity of fishes at 3 hierarchical levels (i.e. local, zone, and lagoon levels) (Bolker et al. 2009). GLMMs can control for the spatial and/or temporal dependence of data by using hierarchically structured random effects and can handle non-normal distributions by using link functions, which make the expected response linear and the expected variance homogeneous, so that the investigated relationships can be properly modeled by linear regressions (Gelman & Hill 2007, Bolker et al. 2009). Therefore, GLMMs are highly flexible and provide more accurate estimates for relationships influenced by multiple sources of random variation. In order to enjoy the benefits of that statistical approach, the predictor variables and the model structures were carefully specified, as described below.

Firstly, mean values of environmental variables measured at local and zone levels were calculated for the higher hierarchical levels. The environmental variables were centered and standardized to improve the parameter estimates and for fitting comparable models (Schielzeth 2010). The temporal variability of each environmental variable was then calculated as the pairwise Euclidean distance be-

tween the consecutive bimonthly samples (Oksanen et al. 2019). For all models, the gamma distribution, appropriate for positive continuous response variables and flexible enough to represent a variety of distribution shapes and dispersion patterns, was specified for the beta diversity measures representative of β_{BC} and its components, $\beta_{BC\text{-}BAL}$ and $\beta_{BC\text{-}GRA}$ (Ma 2017). The log-link function was used to ensure non-negative mean values for the gamma distribution and to make the expected response linear and the expected variance homogeneous (Gelman & Hill 2007, Bolker et al. 2009).

Prior to GLMM fitting, for each beta diversity measure per hierarchical level, the variance inflation factor (VIF) was calculated for each predictor variable in the full model (i.e. including all environmental distances) to avoid multicollinearity (Zuur et al. 2010). Generalized linear models (GLMs) were used for variable selection in this procedure, with full models including all environmental distances as fixed effects (Gelman & Hill 2007). At the local, zone, and lagoon levels, all full models included the environmental distances for salinity (Sa.d), pH (pH.d), temperature (Te.d), depth (De.d), transparency (Tr.d), substrate type (Su.d), and tide height (Ti.d). At the lagoon level, the full models also included the accumulated rainfall (Ra.d) due to expected differences as a result of the climatic gradient between the coastal lagoons. For all cases, almost all variables presented VIF < 2, and none had VIF > 4, which is indicative of negligible multicollinearity (Zuur et al. 2010).

The aforementioned environmental distances were then included as fixed effects in the GLMMs, whereas the morphometric and hydrological features and the hierarchical structure and climate-related factors were included as random effects to assess their possible confounding effects on the variances in the beta diversity measures (Bolker et al. 2009). At the local and zone levels, DO, WZ, and RZ were included as random effects. For each sampling location, the values of the morphometric and hydrological features were those related to their respective zones. DO was also included as a random effect at the lagoon level, as well as LA, CW, and RL. Based on the patterns observed in the NMDS ordination, random effects were also specified for the hierarchical structure to quantify unmeasured scale-dependent environmental effects at the local, zone, and lagoon levels, as well as their nested effects (i.e. sampling locations within zones and lagoons, and zones within lagoons; Schielzeth & Nakagawa 2013). Likewise, a random effect was specified for the occurrence of changing seasons (CS) between the 2 mo intervals to quantify

its possible influence on the variance in the beta diversity measures. The environmental distance for the wind intensity (Wi.d) was also included as a climate-related random effect in the models at the 3 hierarchical levels due to its possible influences on the physicochemical parameters and on fish occurrence and sampling (Bruno & Acha 2015, Pérez-Ruzafa et al. 2019). Finally, accumulated rainfall, included as a fixed effect at the lagoon level, was specified as a random effect in models at the local and zone levels to control for the spatial dependence associated with the single values recorded for each coastal lagoon per sampling period.

Considering that some of the random effects are most likely redundant, different combinations were specified at the local, zone, and lagoon levels. Therefore, random effects for zones and their nested effects within lagoons, and for lagoons themselves, were not included in the same models as their respective morphometric and hydrological features. At the local level, all full models included sampling location as a random effect to control for the statistical dependence of the temporal samples. However, random effects for the sampling locations within zones and lagoons and for the morphometric and hydrological features at the zone and lagoon levels were not included in the same models. At the local and zone levels, full models included all possible combinations of random effects for the morphometric and hydrological features, or the hierarchical structure, whereas other models also (or only) included one climate-related random effect (i.e. Wi.d, Ra.d, or CS). Similar combinations of random effects were included in models at the lagoon level, but as mentioned, Ra.d was specified as a fixed effect.

For each beta diversity measure per hierarchical level, a model selection procedure based on the corrected Akaike's information criterion (AICc), which corrects for the bias resulting from small sample sizes, was applied to compare the fitted models with different combinations of fixed and random effects and identify the best-supported models (Burnham & Anderson 2002). In a first step, the optimum random structure was defined by selecting the best models among the full models with different combinations of random effects. The set of candidate models also included full GLMs (i.e. models with no random effect). In a second step, an automated model selection procedure using the best full model (i.e. with random effects or not) as a start point was used to obtain the submodels with the most parsimonious combinations of fixed effects (Bartoń 2019). In both steps, the model with the lowest AICc was consid-

ered the best due to less information loss and a simpler structure (Burnham & Anderson 2002). Models were ranked according the AICc weight (*wi*) that represents the probability that the model is the best between the set of candidate models (Wagenmakers & Farrell 2004). The ΔAICc, which is the difference between the lowest AICc and the AICc of the model and represents the probability that the model minimizes the information loss, was used to select the models for interpretation (Burnham & Anderson 2002, Wagenmakers & Farrell 2004). All models with ΔAICc < 2 were considered with substantial support for interpretation (Burnham & Anderson 2002).

The goodness-of-fit of the selected models was expressed by the pseudo-R^2 based on the likelihood-ratio test (Magee 1990). For each selected model, the variance explained by the fixed effects was expressed by R^2 f, calculated as the ratio between the log-likelihood of the selected model and the log-likelihood of a null model including the intercept and the selected random effects. The variance explained by both the fixed and random effects was expressed by the R^2 f+r, calculated as the ratio between the log-likelihood of the selected model and the log-likelihood of a null model including only the intercept.

A model averaging approach was applied when more than one model was selected for the relationships between each temporal beta diversity measure and the environmental variability at the local, zone, and lagoon levels. Inferences across the selected models were combined by calculating model-averaged parameter estimates and the associated confidence intervals (Burnham & Anderson 2002). Therefore, the strength of the environmental effects based on their contributions to the average model was estimated by the model averaging approach. We used 85% confidence intervals because the model selection using the AICc supports additional variables over a null model at this level (Arnold 2010). Therefore, a parameter was considered informative if the 85% confidence interval did not overlap zero. The relative variable importance (RVI) for the parameter estimates in the average model was calculated by summing the *wi* of the selected models (recalculated without the other candidate models) including the predictor variable (Burnham & Anderson 2002).

Partial residuals based on the average coefficients estimated from the set of selected models were obtained for the relationships between the environmental distances and each beta diversity measure per hierarchical level. For each environmental distance considered informative (85% confidence interval), the partial residuals were calculated as the centered residuals of the full model plus the averaged coefficients resulting from the averaged model versus the respective environmental distance. Partial residual plots were constructed to visually compare the relationships between the informative environmental distances and the beta diversity measures (i.e. β_{BC}, $\beta_{BC\text{-}BAL}$, and $\beta_{BC\text{-}GRA}$) given the effects of the other environmental distances and random effects included in the GLMMs (i.e. partial residuals) at the local, zone, and lagoon levels.

All analyses were performed in R v.3.6.2 (R Core Team 2019) with the packages 'vegan' (version 2.5-6; Oksanen et al. 2019), 'car' (version 3.0-6; Fox & Weisberg 2019), 'lme4' (version 1.1-21; Bates et al. 2015), 'bbmle' (version 1.0.22; Bolker & R Core Team 2019), and 'MuMIn' (version 1.43.15; Bartoń 2019).

3. RESULTS

3.1. Spatial and temporal structures of the fish assemblages

A total of 99 fish species were collected during the annual cycle, including 40 families and 14 taxonomic orders mostly shared between all coastal lagoons (Table S1 in the Supplement at www.int-res.com/articles/suppl/m658p195_supp.pdf). Two fish species comprised 80% of the relative abundance of individuals in all coastal lagoons (*Atherinella brasiliensis*, 27% and *Anchoa januaria*, 53%; Table S1). A similar pattern was observed for the Maricá and Saquarema lagoons, whereas in the Araruama lagoon only one species, *A. brasiliensis*, accounted for 70% of the relative abundance. More species were representative considering the relative frequency in the samples, but only one species, *A. brasiliensis*, occurred in 100% of the samples (Table S1). Considering all coastal lagoons, 5 species had about 50% or more of relative frequency (*A. brasiliensis*, 100%; *A. januaria*, 58%; *Eucinostomus argenteus*, 56%; *Jenysia multidentata*, 50%; and *Elops saurus*, 47%). Among these species, only one was more frequent (i.e. occurred in at least about 50% of the samples) in all 3 coastal lagoons (*A. brasiliensis*), another was more frequent in both the Maricá and Saquarema lagoons (*A. januaria*), and 3 others were more frequent in only one lagoon (*J. multidentata*, Maricá; *E. argenteus*, Saquarema; and *E. saurus*, Araruama). Three more species were also more frequent in the Maricá lagoon (*Poecilia vivipara*, *Phalloptychus januarius*, and *Microgobius meeki*), and one more species in the Saquarema lagoon (*Diapterus rhombeus*). Despite a

concomitant large number of few representative species supporting spatial and temporal differences between the coastal lagoons, most families occurred in all systems, evidencing a high similarity at the family level (Table S1).

The spatial patterns in the NMDS ordination showed marked differences in species composition and abundance between the coastal lagoons, primarily associated with samples from the inner and middle zones in the Maricá and Araruama lagoon, and to a lesser extent, the Saquarema lagoon (Fig. 2a). Samples from the outer zone were generally more similar between all coastal lagoons (Fig. 2a). Samples from the inner and middle zones in the Saquarema lagoon, more widely distributed, were also similar to samples from the outer zones in the other lagoons, especially the Maricá lagoon (Fig. 2a). Therefore, the spatial gradient in species composition and abundance from the inner to the outer zone was more expressive in the Maricá and Araruama lagoons than the Saquarema lagoon (Fig. 2a). These spatial patterns demonstrated the hierarchical structure (i.e. organization patterns at locations within zones, zones within lagoons, and individual lagoons) of the fish assemblages.

The temporal differences observed in the NMDS ordination expressed very slight and gradual changes in species composition and abundance between consecutive seasons, but were strongly dependent on the spatial structure (Fig. 2a,b). These seasonal gradients were more marked only in the Araruama lagoon, with a greater distinction between samples from the winter and summer, regardless of zone (Fig. 2a,b). Seasonal differences in species composition and abundance were especially negligible in the inner and middle zones of the Maricá lagoon (Fig. 2a,b). Samples from the outer zones, in turn, were more associated with samples from the same season or consecutive seasons in all lagoons (Fig. 2a,b). In the Saquarema lagoon, regardless of a negligible seasonal trend, samples from the summer were more similar to samples from the outer zone of the Maricá lagoon (Fig. 2a,b).

3.2. Temporal beta diversity in multiple levels

At the local level, β_{BC} was higher in the Saquarema lagoon and, despite the similar values in the Maricá and Araruama lagoons, a greater variation was observed in the latter lagoon (Fig. 3a). The same tendency was observed for the values of β_{BC-BAL}, but the values varied more in the Saquarema lagoon and less in the Araruama lagoon (Fig. 3d). β_{BC-GRA} varied more in all lagoons, with a slight increase from the Maricá to the Araruama lagoon, indicative of a primary contribution of that process to β_{BC}, especially in the latter lagoon (Fig. 3g).

Beta diversity measures were similar at the local and zone levels, indicative of the strong influence of the environmental features of the zones (Fig. 3b,e,h). Regardless of that similarity, the variation between lagoons in the values of β_{BC} was more similar at the zone than the local level, primarily due to the smaller variation in the Araruama lagoon (Fig. 3b). In the Maricá and Saquarema lagoons, β_{BC-BAL} contributed more to smaller variation in the values of β_{BC} at the zone level compared with the local level, whereas in the Araruama lagoon, the smaller variation in the values of β_{BC-GRA} contributed more to that decrease (Fig. 3e,h). Despite the observed differences, at both the local and zone levels, β_{BC} was primarily associated with β_{BC-GRA} in the 3 coastal lagoons.

The beta diversity measures between consecutive 2 mo intervals were generally lower and varied less at the
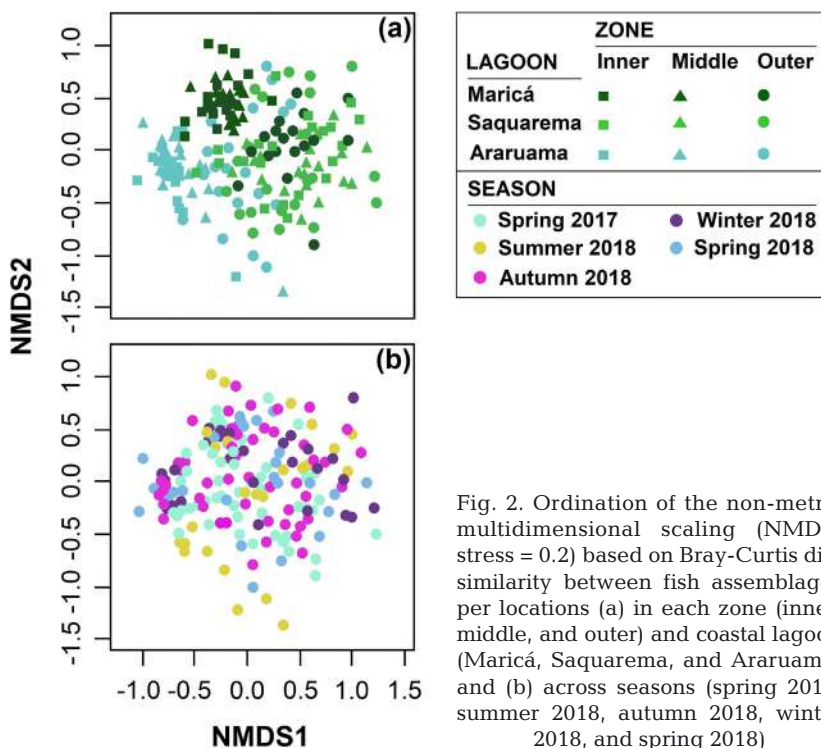

Fig. 2. Ordination of the non-metric multidimensional scaling (NMDS, stress = 0.2) based on Bray-Curtis dissimilarity between fish assemblages per locations (a) in each zone (inner, middle, and outer) and coastal lagoon (Maricá, Saquarema, and Araruama) and (b) across seasons (spring 2017, summer 2018, autumn 2018, winter 2018, and spring 2018)
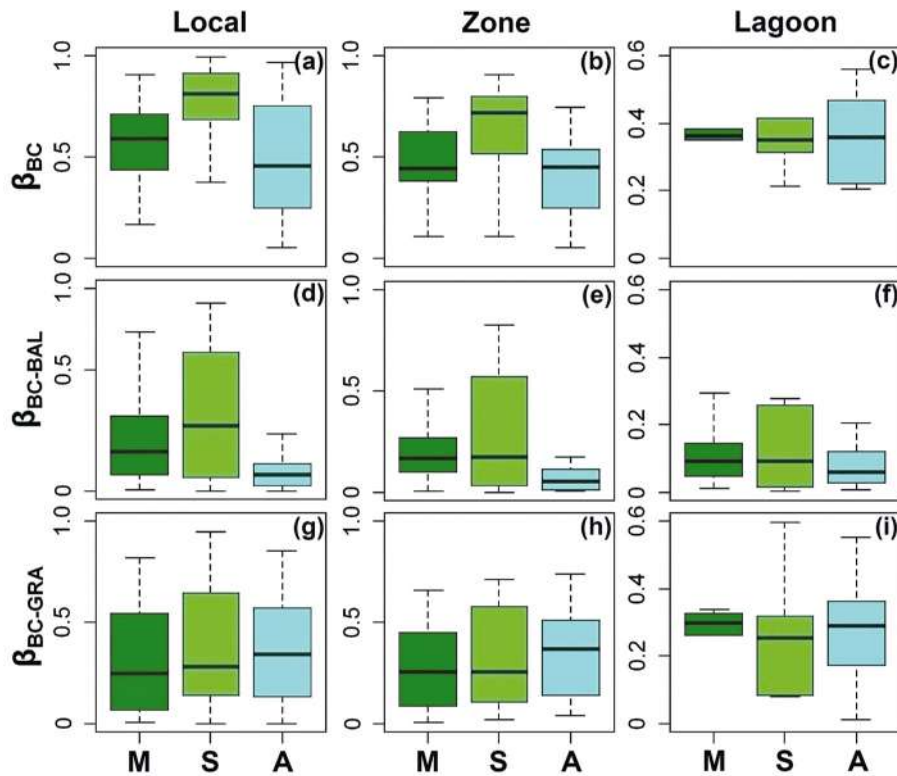
Fig. 3. Box-plots (median, lower and upper quartiles, and minimum and maximum values) of the variation in values of temporal beta diversity between consecutive 2 mo intervals during an annual cycle at the Maricá (M), Saquarema (S), and Araruama (A) lagoons. At the local, zone, and lagoon levels, measures express temporal changes in (a,d,g) each sampling location per lagoon, (b,e,h) zone per lagoon, and (c,f,i) each lagoon, respectively. Beta diversity measured as Bray-Curtis dissimilarity expresses the total abundance-based dissimilarity (β_{BC}), the balanced variation in the abundance of different species (β_{BC-BAL}), and the abundance gradients between consecutive 2 mo intervals (β_{BC-GRA})

lagoon level, especially in the Maricá lagoon (Fig. 3c,f,i). Therefore, both β_{BC-BAL} and β_{BC-GRA} were smaller considering the entire coastal lagoons, and there were no differences between lagoons (Fig. 3c,f,i). The values of β_{BC} varied less in the Saquarema lagoon than the Araruama lagoon due to the similar contribution of β_{BC-BAL} and β_{BC-GRA}, whereas in the latter lagoon the higher variation was primarily related to β_{BC-GRA} (Fig. 3c,f,i). Regardless of these differences, as with the other hierarchical levels, β_{BC} was primarily associated with β_{BC-GRA}.

3.3. Environmental variability

The greatest differences in local environmental conditions between the coastal lagoons were associated with salinity (Table 1). As expected, the highest salinity was observed in the Araruama lagoon, followed by intermediate values in the Saquarema lagoon and lower salinities in the Maricá lagoon. Depth and transparency also showed pronounced differ-

ences between coastal lagoons (Table 1). The values of depth were higher in the Araruama lagoon, followed by the Maricá lagoon and lower values in the Saquarema lagoon, whereas transparency was highest in the latter lagoon, followed by the Araruama lagoon, and the lowest in the Maricá lagoon (Table 1). Less pronounced environmental differences between the coastal lagoons were related to substrate type, which was slightly coarser in the Araruama lagoon than the Maricá and especially Saquarema lagoons (Table 1). Wind intensity, in turn, was much higher in the Saquarema lagoon, whereas accumulated rainfall decreased from the Maricá to the Araruama lagoon (Table 1). pH, temperature, and tide height were similar among the lagoons (Table 1).

Regarding morphometric features, DOs were greater in the Araruama lagoon, followed by the Maricá and Saquarema lagoons (Table 1). WZs were smaller in the Maricá lagoon than the other lagoons, with greater values observed in the Araruama lagoon (Table 1). The Araruama lagoon had a much larger LA than the other lagoons, but its CW was similar to

Table 1. Environmental, morphometric, and hydrological variables included in the generalized linear mixed models. Median, lower, and upper quartiles of the samples were obtained in 2 mo intervals during the annual cycle at sampling locations in the Maricá, Saquarema, and Araruama lagoons. (−) no information

Variable	Maricá			Saquarema			Araruama		
	Median	Lower	Upper	Median	Lower	Upper	Median	Lower	Upper
Environmental conditions									
Salinity	25.13	21.00	29.74	32.34	30.67	35.28	56.66	40.61	60.71
pH	8.89	8.56	9.29	8.48	8.32	8.72	8.33	8.22	9.55
Temperature (°C)	24.87	23.10	28.39	25.36	22.89	27.01	25.96	24.64	28.45
Depth (cm)	90.00	60.00	120.00	80.00	63.50	85.43	100.00	63.83	112.08
Transparency (cm)	46.67	32.00	70.00	75.33	56.67	96.17	70.67	45.17	86.00
Substrate type	3.00	2.00	3.30	2.00	2.00	3.00	4.00	3.00	4.50
Tide height (m)	0.70	0.60	0.80	0.70	0.60	0.75	0.65	0.55	1.00
Wind intensity	1.00	1.00	2.00	3.00	2.00	3.50	1.00	1.00	2.00
Accumulated rainfall (mm)	34.00	23.00	92.00	32.00	16.00	59.50	19.00	2.00	73.00
Morphometric features									
Distance from the ocean (km)	15.91	3.69	17.77	3.66	1.98	8.08	25.87	12.15	33.92
Mean width of the connection between adjacent zones	0.08	0.05	0.09	0.69	0.16	0.73	2.01	0.65	2.45
Lagoon area	33.7	–	–	25.0	–	–	216.5	–	–
Channel mean width	30.1	25.2	31.8	117.0	103.7	158.0	120.4	88.8	164.2
Hydrological features									
Riverine input per zone	11.00	0.00	23.19	18.53	13.56	20.48	1.31	0.00	26.90
Riverine input per lagoon	9.88	–	–	14.03	–	–	2.96	–	–

the Saquarema lagoon, which had the smallest area (Table 1). RZ and RL, in turn, were highest in the Saquarema lagoon, followed by the Maricá lagoon, and were much lower in the Araruama lagoon (Table 1).

3.4. Random structure of the variance in temporal beta diversity

At the local level, the random effects associated with sampling location, WZ, and Wi.d influenced more the variance in the response of β_{BC} (Table 2). The higher value of R^2 f+r (22%) compared with R^2 f (10%) was indicative of the relevance of these random effects to the relationship between β_{BC} and the environmental distances (Table 2). Likewise, the higher and varied values of WZ in the Araruama lagoon, with lower values in the Saquarema lagoon, and the lowest values in the Maricá lagoon, were indicative of the importance of WZ for the relationships between β_{BC} and the environmental variability between consecutive 2 mo intervals (Fig. 4a). The greater variation in the values of Wi.d in the Maricá lagoon and the higher values observed in the Saquarema lagoon compared with the other lagoons, in turn, were indicative of the relevance of climate-related factors for local-level differences in β_{BC} between coastal lagoons (Fig. 4c).

The random effects influencing the relationship between the environmental distances and β_{BC-BAL} at the local level were sampling location and Ra.d (Table 2). The higher value of R^2 f+r (32%) compared with R^2 f (4%) again indicated the high relevance of these random effects for the variance in the response of β_{BC-BAL}. No random effect otherwise influenced the relationships between the environmental distances and β_{BC-GRA} at the local level (Table 2). Therefore, the influence of sampling location on β_{BC} was related to its effect on β_{BC-BAL}. The higher and varied values of Ra.d in the Maricá lagoon compared with the Araruama lagoon were also indicative of the importance of climate-related factors for local-level differences in β_{BC} between coastal lagoons, based on its effect on β_{BC-BAL} (Fig. 4d).

Only Wi.d and Ra.d were relevant for the relationships between environmental distances and beta diversity at the zone level due to their random effects on the variance in the response of β_{BC-BAL} (Table 2). The higher value of R^2 f+r (47%) compared with R^2 f (22%) was indicative that the same climate-related relationships observed for β_{BC-BAL} at the local level may be assumed at the zone level (Table 2). The absence of random effects selected for the morphometric features, in turn, was indicative of differential effects of zones on the environmental conditions at their different sampling locations.

Table 2. Random effects included in the full generalized linear mixed models selected for the relationships between temporal beta diversity (Bray-Curtis dissimilarity) and environmental distances at the local, zone, and lagoon levels. The values of temporal beta diversity express the total abundance-based dissimilarity (β_{BC}), the balanced variation in abundance of different species ($\beta_{BC\text{-}BAL}$), and the abundance gradients ($\beta_{BC\text{-}GRA}$) between 2 mo intervals. Random effects: sampling locations (Lo), changing seasons (CS), mean width of the connections between adjacent zones (WZ), distance from the ocean (DO), and environmental distances for wind intensity (Wi.d) and accumulated rainfall (Ra.d). Fixed effects: environmental distances for pH (pH.d), transparency (Tr.d), temperature (Te.d), salinity (Sa.d), depth (De.d), substrate type (Su.d), tide height (Ti.d), and Ra.d. Results shown only for models with ΔAICc < 2. For all cases, only one model was considered informative given the data set and the candidate models. R^2 f: total variation explained by fixed effects (i.e. the likelihood-ratio-based R^2 of the global model calculated using a null model including the intercept plus random effects); R^2 f+r: total variation explained by fixed effects plus random effects (i.e. the likelihood-ratio-based R^2 of the global model calculated using a null model including only the intercept); *K*: number of factors (including intercept); LL: log likelihood; AICc *wi*: AICc weight; (−) no information

| Dependent variable | Effects | | R^2 f | R^2 f+r | *K* | LL | AICc | AICc *wi* |
	Fixed	Random						
Local level								
β_{BC}	pH.d, Tr.d, Te.d, Sa.d, De.d, Su.d, Ti.d	Lo, WZ, Wi.d	0.10	0.22	12	−2.51	31.25	0.28
$\beta_{BC.BAL}$		Lo, Ra.d	0.04	0.32	11	59.63	−95.39	0.32
$\beta_{BC.GRA}$		−		0.04	−	9	6.09	7.07	0.30
Zone level								
β_{BC}	pH.d, Tr.d, Te.d, Sa.d, De.d, Su.d, Ti.d	−	0.15	−	9	5.12	11.85	0.72
$\beta_{BC.BAL}$		Wi.d, Ra.d	0.22	0.47	11	39.82	−51.4	0.76
$\beta_{BC.GRA}$		−	0.11	−	9	11.50	−0.92	0.80
Lagoon level								
β_{BC}	pH.d, Tr.d, Te.d, Sa.d, De.d, Su.d, Ti.d, Ra.d	−	0.65	−	10	23.71	4.01	1.00
$\beta_{BC.BAL}$		CS, DO	0.90	0.92	12	43.07	0.25	0.99
$\beta_{BC.GRA}$		DO	0.54	0.59	11	13.15	39.70	0.66

At the lagoon level, the random effect for DO influenced both $\beta_{BC\text{-}BAL}$ and $\beta_{BC\text{-}GRA}$ (Table 2). In this sense, the higher and varied values of DO observed in the Araruama lagoon, followed by the Maricá lagoon, and the lower and less varied values in the Saquarema lagoon were indicative of its differential relevance between lagoons for the temporal dissimilarity in species composition and abundance (Table 2, Fig. 4b). Concurrently, the random effect of CS between 2 mo intervals on the response of $\beta_{BC\text{-}BAL}$ to the environmental variability was indicative of the relevance of specific ecological processes associated with longer-term intervals.

3.5. Multilevel environmental drivers of temporal beta diversity

According to model averaging, the positive effects of Sa.d and pH.d were the primary drivers of β_{BC} at the local level (Table 3). The positive relationship between pH.d and the partial residuals of its effect on β_{BC} given the other environmental and random effects was primarily supported in the Araruama lagoon (Fig. 5b). A greater contribution of the Araruama lagoon was also observed for the positive effect of Sa.d, but the values of β_{BC} were also positively
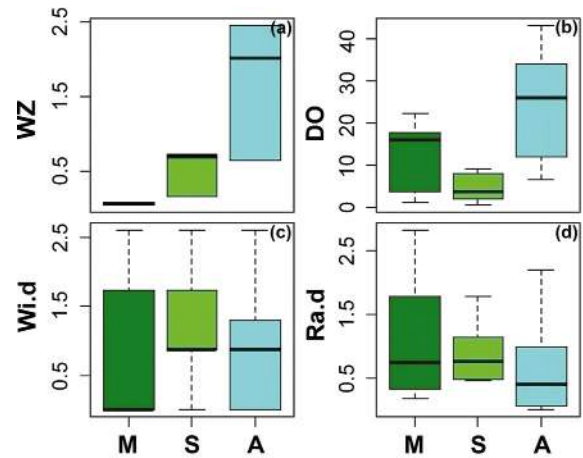

Fig. 4. Box-plots (median, lower and upper quartiles, and minimum and maximum values) of the variation in the random effects associated with the variance in the measures of temporal beta diversity between consecutive 2 mo intervals during an annual cycle in the Maricá (M), Saquarema (S), and Araruama (A) lagoons at the local, zone, and lagoon levels. The random effects are (a) the mean width of the connections between adjacent zones (WZ), (b) the distance from the ocean (DO), and the environmental Euclidean distances between 2 mo intervals for (c) wind intensity (Wi.d) and (d) accumulated rainfall (Ra.d)

associated with Sa.d in the other lagoons (Fig. 5a). These lagoon-dependent tendencies despite no random effect selected for the lagoon level against the

Table 3. Parameter estimates (with confidence intervals using a nominal level of 85%) and relative variable importance (RVI) based on the average of the generalized linear mixed models selected (ΔAICc < 2) for relationships between temporal beta diversity (Bray-Curtis dissimilarity) and the environmental distances at the local, zone, and lagoon levels. The values of temporal beta diversity express the total abundance-based dissimilarity (β_{BC}), the balanced variation in abundance of different species ($\beta_{BC\text{-}BAL}$), and the abundance gradients ($\beta_{BC\text{-}GRA}$) between 2 mo intervals. Estimates with confidence intervals that do not overlap zero in **bold**. Codes for the morphometric features and environmental distances included as random and fixed effects in Table 2. The number of models (n) including each parameter was indicated when more than one model was selected

Model parameter	β_{BC} Estimate	RVI	$\beta_{BC.BAL}$ Estimate	RVI	$\beta_{BC.GRA}$ Estimate	RVI
Local level	*Random effects: Lo, WZ, Wi.d*		*Random effects: Lo, Ra.d*			
Intercept	−0.810 (−1.139, −0.481)		−1.187 (−1.465, −0.908)		−1.250 (−1.508, −0.911)	
Sa.d	**0.307 (0.101, 0.513)**	1.00 (n = 7)			**0.433 (0.174, 0.693)**	0.79 (n = 2)
pH.d	**0.057 (0.007, 0.108)**	0.60 (n = 4)				
Su.d	−0.069 (−0.152, 0.014)	0.24 (n = 2)	0.070 (−0.046, 0.186)	0.16 (n = 1)		
De.d			−0.075 (−0.171, 0.020)	0.22 (n = 1)	**0.175 (0.057, 0.293)**	0.45 (n = 1)
Tr.d	0.075 (−0.007, 0.158)	0.29 (n = 2)	0.057 (−0.051, 0.165)	0.15 (n = 1)		
Te.d	−0.054 (−0.127, 0.019)	0.12 (n = 1)				
Ti.d			−0.049 (−0.140, 0.043)	0.15 (n = 1)		
Zone level			*Random effects: Wi.d, Ra.d*			
Intercept	−0.872 (−1.054, −0.690)		−1.709 (−2.181, −1.237)		−1.277 (−1.537, −1.018)	
Sa.d			**−0.488 (−0.799, −0.177)**	1.00 (n = 2)	**0.454 (0.036, 0.873)**	0.39 (n = 1)
pH.d	**−0.075 (−0.145, −0.005)**	0.33 (n = 1)				
Su.d					0.191 (−0.089, 0.471)	0.14 (n = 1)
De.d	0.086 (−0.023, 0.195)	0.22 (n = 1)				
Tr.d			**0.323 (0.141, 0.506)**	1.00 (n = 2)	0.180 (−0.025, 0.386)	0.31 (n = 2)
Te.d	**0.199 (0.073, 0.326)**	1.00 (n = 3)	**0.215 (0.055, 0.374)**	0.62 (n = 1)		
Lagoon level			*Random effects: CS, DO*		*Random effects: DO*	
Intercept	−1.431 (−1.587, −1.275)		−6.771 (−11.678, −1.865)		−1.465 (−1.922, −1.009)	
pH.d			**1.068 (0.991, 1.146)**			
Su.d			**−2.311 (−2.528, −2.094)**			
De.d			**−0.426 (−0.550, −0.302)**			
Tr.d			**1.868 (1.690, 2.045)**			
Te.d			**0.633 (0.479, 0.787)**			
Ti.d	**0.176 (0.106, 0.246)**				0.277 (−0.007, 0.560)	0.36 (n = 1)
Ra.d	**0.222 (0.125, 0.319)**		**2.067 (1.863, 2.272)**			

random effects related to sampling location, climate-related variability (i.e. Wi.d), and zone-level morphometric features (WC) evidence the importance of differences between lagoons in the effects of Sa.d and pH.d on β_{BC} at the local level (Tables 2 & A1 in the Appendix).

Also at the local level, the non-informative effects of temporal environmental variability on $\beta_{BC\text{-}BAL}$ evidenced the primary importance of random effects (sampling location and Ra.d; Tables 2, 3 & A1). The responses of $\beta_{BC\text{-}GRA}$, in turn, were positively related to Sa.d and De.d (Table 3), and these relationships were found for all coastal lagoons (Fig. 5c,d). However, considering the relationship between Sa.d and the partial residuals of its effect on $\beta_{BC\text{-}GRA}$, its positive effects were slightly more evident in the Araruama lagoon, especially considering the positive extreme of that relationship observed for some locations in the

inner and middle zones (Fig. 5c). To a lesser extent, an opposite tendency was observed for the positive effects of De.d on $\beta_{BC\text{-}GRA}$, with higher values of De.d associated with higher values of the partial residuals of its effect on $\beta_{BC\text{-}GRA}$ in some locations, primarily in the outer zones of the Maricá and Saquarema lagoons (Fig. 5d). The absence of random effects selected for the relationship between the environmental distances and $\beta_{BC\text{-}GRA}$ provides further evidence regarding the relevance of the effects of Sa.d and De.d (Table A1).

At the zone level, the negative effect of pH.d on β_{BC} was evident in the Araruama lagoon (Table 3; Fig. 6a). For the other coastal lagoons, primarily higher values of the partial residuals of the effect of pH on β_{BC} were associated with less varied and lower values of pH (Fig. 6a). The positive effect of Te.d on β_{BC}, in turn, did not show lagoon-related tendencies (Table 3,
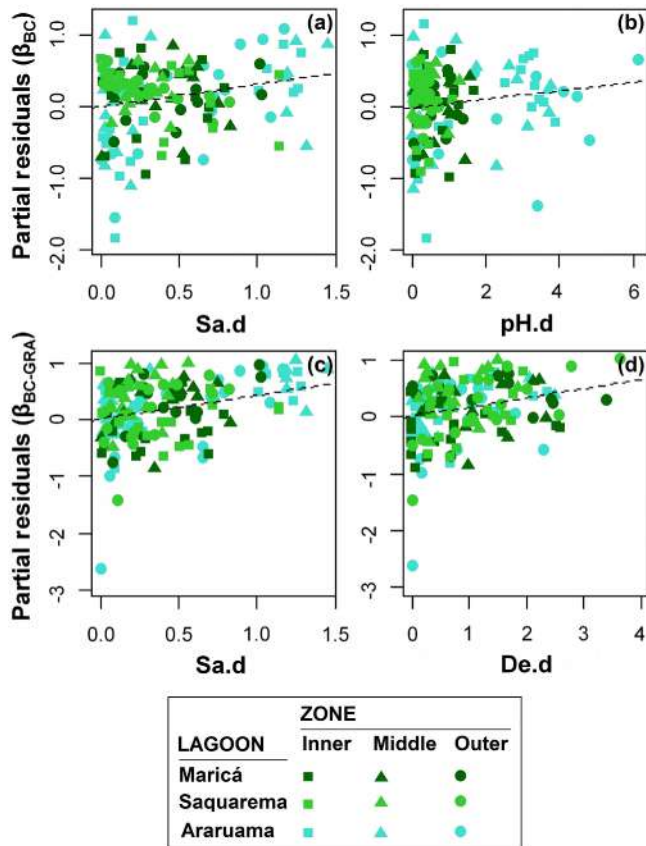
Fig. 5. Partial residual plots showing the relationships between the informative environmental distances and beta diversity measures (i.e. [a,b] total beta diversity between consecutive 2 mo intervals based on the Bray-Curtis index, β_{BC}, and [c,d] the abundance gradient, β_{BC-GRA}) given the effects of the other environmental distances and random effects included in the generalized linear mixed models at the local level. Partial residuals for the relationship between each environmental distance and beta diversity measure representing the centered residuals of the full model plus the averaged coefficients resulting from the averaged model versus the respective environmental distance. Environmental distances represented by the Euclidean distances between consecutive 2 mo intervals for salinity (Sa.d), pH (pH.d), and depth (De.d). Sampling locations identified according to their respective zones (inner, middle, and outer) and lagoons (Maricá, Araruama, and Saquarema)

Fig. 6b). The negative effect of Sa.d on β_{BC-BAL}, as well as the positive effects of Te.d and Tr.d, were supported in all coastal lagoons (Table 3, Fig. 6d–f). However, primarily low to intermediate values of Sa.d were associated with decreasing values of the partial residuals of its effect on β_{BC-BAL} in the Saquarema and especially Maricá lagoons, whereas a wider range negative relationship was observed for the Araruama lagoon (Fig. 6d). The relevance of the random effects for climate-related variability (Wi.d and Ra.d) most likely influenced these differ-

ences between the coastal lagoons (Tables 2 & A1, Fig. 4c,d). For β_{BC-GRA}, the positive effect of Sa.d indicated the primary relevance of salinity changes in determining the abundance gradient at the zone level (Table 3, Fig. 6c). That effect was also supported in all coastal lagoons — over a wider range for the Araruama lagoon, but in the Saquarema and especially Maricá lagoons, low to intermediate values of Sa.d were primarily associated with increasing values of the partial residuals of its effect on β_{BC-GRA} (Fig. 6c).

The positive effects of Ti.d and Ra.d on β_{BC} in the only selected model at the lagoon level evidenced the relevance of the balance between the marine and freshwater influences in all coastal lagoons (Tables 3 & A1, Fig. 7a,b). For β_{BC-BAL}, in turn, the strong effects of the several environmental distances included in the only selected model were indicative of the concordance between the coastal lagoons in terms of the multiple environmental effects on β_{BC-BAL} (Tables 3 & A1, Fig. 7c–h). The tendencies were equal for all coastal lagoons, but considering the range of environmental distances associated with the values of the partial residuals of their respective effects on β_{BC-BAL}, the responses were generally more similar between the Maricá and Saquarema lagoons compared with the Araruama lagoon (Fig. 7c–h). These patterns were primarily evident for the positive effect of pH.d and to a lesser extent the negative effect of De.d on β_{BC-BAL} (Fig. 7c,e). Differences between lagoons were less evident for the negative effect of Su.d and positive effects of Tr.d, Te.d, and Ra.d (Fig. 7d,f–h). Regardless of the high concordance between lagoons in terms of environmental distances associated with β_{BC-BAL}, lagoon-related differences in the ranges of these relationships highlighted the strength of their environmental differences. The absence of a relevant random effect for the lagoon level against the selected random effects for DO and CS provided further evidence in this sense (Table 2). The non-informative effects of environmental variability on β_{BC-GRA} were indicative of the primary relevance of DO for the abundance gradients at the lagoon level (Tables 2, 3 & A1).

4. DISCUSSION

The decrease in short-term beta diversity from the local to the lagoon level revealed the importance of spatial scale for ecological processes related to temporal changes in fish diversity in tropical coastal lagoons. The similar trends between coastal lagoons at the local and zone levels for β_{BC} are most likely a
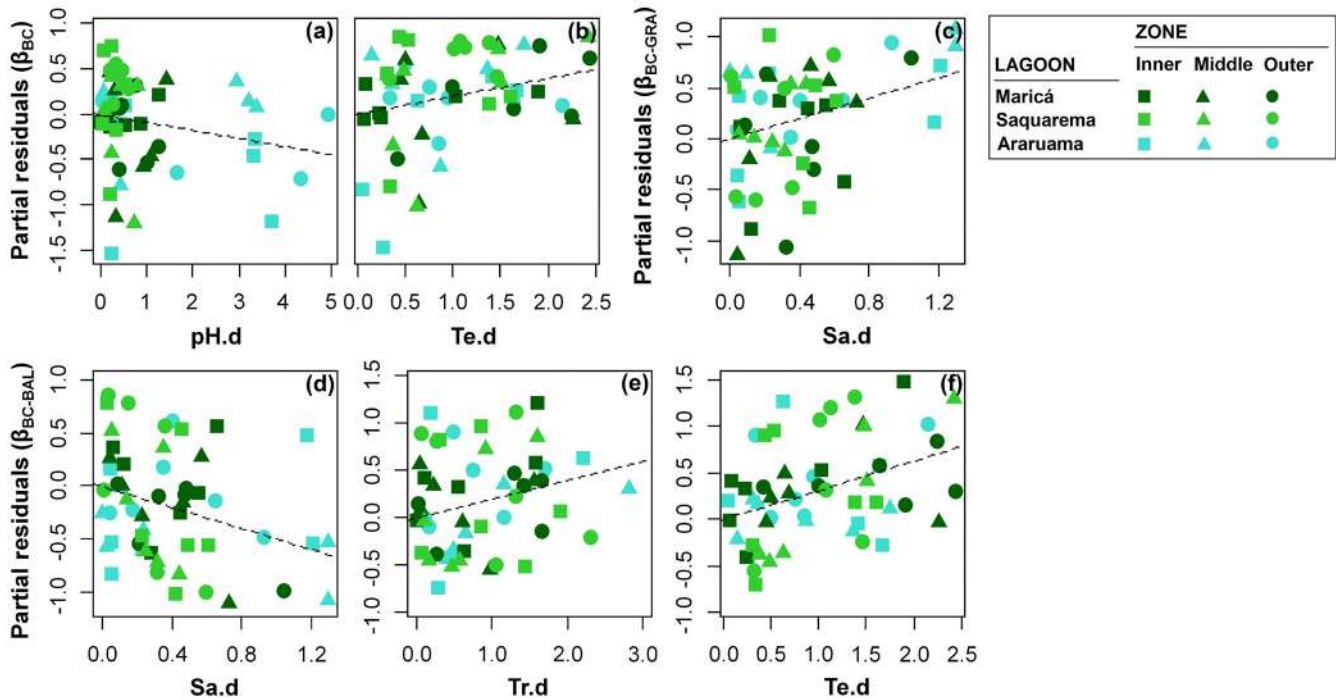
Fig. 6. Partial residual plots showing the relationships between the informative environmental distances and beta diversity measures (i.e. the total beta diversity between consecutive 2 mo intervals based on [a,b] the Bray-Curtis index, β_{BC}, [c] the abundance gradient, β_{BC-GRA}, and [d,e,f] the balanced variation in the abundance of different species, β_{BC-BAL}) given the effects of the other environmental distances and random effects included in the generalized linear mixed models at the zone level. Partial residuals for the relationship between each environmental distance and beta diversity measure representing the centered residuals of the full model plus the averaged coefficients resulting from the averaged model versus the respective environmental distance. Environmental distances represented by the Euclidean distances between consecutive 2 mo intervals for pH (pH.d), temperature (Te.d), salinity (Sa.d), and transparency (Tr.d). Zones (inner, middle, and outer) identified for each coastal lagoon (Maricá, Saquarema, and Araruama)

result of temporal consistency in the strong environmental differences between zones (Franco et al. 2019, Camara et al. 2020). Further evidence in this sense was provided by the greater differences associated with samples from locations in the inner and middle zones of the Maricá and Araruama lagoons in terms of spatial and temporal non-directional variation in species composition and abundance. At the lagoon level, the lower values of β_{BC} expressing the smaller changes in species composition and abundance between 2 mo intervals compared with the local and zone levels are most likely a result of the omission of within-lagoon spatial heterogeneity. A consequent greater synchrony at the lagoon level between the temporal dynamics of the fish assemblages and the regional species pool, highly shared for the study area, most likely explains the very similar values of β_{BC} between the coastal lagoons (Henriques et al. 2017, Araújo et al. 2018). The slighter spatial and temporal gradients related to the non-directional variation in species composition and abundance observed for sampling locations in the

Saquarema lagoon provide additional support for the influence of spatial heterogeneity on temporal beta diversity. In this smaller euhaline system, the greater and more constant marine influence provides higher temporal association between the fish assemblage and the regional species pool, which explains its generally higher and more variable values of β_{BC} at all hierarchical levels. Furthermore, considering that the Saquarema lagoon is closer to the Maricá lagoon than the Araruama lagoon, the greater similarity between its sampling locations in the summer and those from the outer zone of the Maricá lagoon further reinforces the importance of the regional species pool for the temporal β_{BC}.

The different levels of temporal interplay between fish assemblages in the coastal lagoons and the regional species pool were better assessed by the β_{BC} components. The generally greater contribution of β_{BC-GRA} to β_{BC} is most likely related to the random dispersal of numerous individuals of rare species, which represents most of the species richness in the coastal lagoons. The nearshore fish assemblages in these
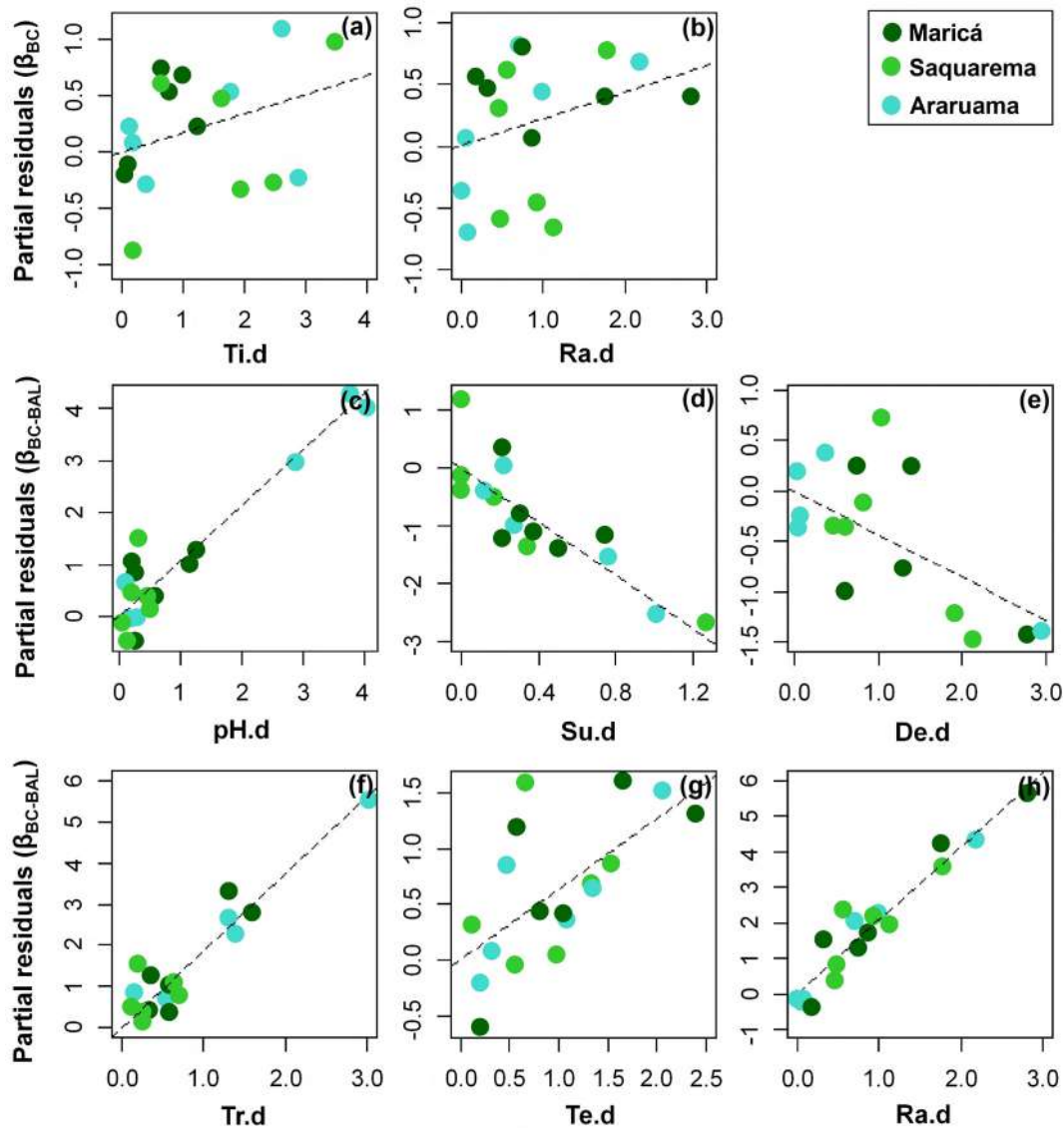
Fig. 7. Partial residual plots showing the relationships between the informative environmental distances and beta diversity measures (i.e. [a,b] total beta diversity between consecutive 2 mo intervals based on the Bray-Curtis index, β_{BC}, and [c–h] the balanced variation in the abundance of different species, $\beta_{BC\text{-}BAL}$) given the effects of the other environmental distances and random effects included in the generalized linear mixed models at the lagoon level. Partial residuals for the relationship between each environmental distance and beta diversity measure representing the centered residuals of the full model plus the averaged coefficients resulting from the averaged model versus the respective environmental distance. Environmental distances represented by the Euclidean distances between consecutive 2 mo intervals for tide height (Ti.d), accumulated rainfall (Ra.d), pH (pH.d), substrate type (Su.d), depth (De.d), transparency (Tr.d), and temperature (Te.d). Samples identified per coastal lagoon (Maricá, Saquarema, and Araruama)

coastal lagoons and other transitional ecosystems in this tropical region are characterized by a large number of marine straggler species (i.e. stenohaline species that occur in low numbers in estuaries), whose occurrence is especially rare in coastal lagoons and typically increases during periods of higher marine influence (Araújo et al. 2016, Camara et al. 2018, Andrade-Tubino et al. 2020). Araújo et al. (2019) observed the predominance of random assembly pro-

cesses for nearshore fish assemblages in this tropical region, providing further evidence for the role of rare species in the greater contribution of $\beta_{BC\text{-}GRA}$ to the β_{BC} patterns in the coastal lagoons.

Regardless of the overall lower contribution of $\beta_{BC\text{-}BAL}$ to β_{BC}, the higher and more varied values in the Saquarema lagoon than in the other lagoons are also indicative of the greater and more constant temporal interplay between its fish assemblage and

the regional species pool. As a consequence, this system is most likely more prone to provide shelter for species that use estuarine areas for spawning and/or feeding during particular periods of the year, contributing more to intra-annual changes in species composition and abundance (Castillo-Rivera et al. 2010, Andrade-Tubino et al. 2020). Such species groups encompass a high taxonomic diversity and a consequent wide range of specific environmental tolerances and requirements that most likely mediate the gradual transitions from individuals of some species to others (Elliott et al. 2007, Reis et al. 2016). In this sense, a greater temporal interplay with the regional species pool may be assumed in the Maricá lagoon compared with the Araruama lagoon, considering its slightly higher and more varied values of β_{BC-BAL}. The more marked gradients from estuarine to marine conditions in the Maricá lagoon may provide a wider range of suitable habitats for species with different habitat requirements, whereas the permanent hyperhaline conditions in the Araruama lagoon probably imposes a constant physiological limitation to several species (Franco et al. 2019).

The relationships between temporal environmental variability and the β_{BC} components at the local, zone, and lagoon levels provides further and strong support for the scale sensitivity of the mechanisms driving assembly processes in the coastal lagoons. The main mechanisms associated with the β_{BC} patterns were dependent on both of the different environmental effects selected to explain the β_{BC} components at the local, zone, and lagoon levels, and the multiple spatial and temporal scales of the fixed effects (i.e. environmental distances) and random effects (i.e. morphometric features, climate-related environmental distances, and changing seasons) selected to explain the β_{BC} components at each hierarchical level. The critical relevance of multiscale environmental drivers was shown by the effects of the morphometric features of the coastal lagoons and climate- and ocean-related factors on the short-term patterns of β_{BC} at the local, zone, and lagoon levels. These influences are represented primarily by the random effects for WZ and Ra.d on the relationships between environmental variability and the β_{BC} components at the local level, and the random effects for the local-level measure of Wi.d and Ra.d at the zone level. The importance of multiscale influences on the variance in the β_{BC} components were also supported at the lagoon level, given the random effects for DO, calculated as the mean of the local-level measures, and CS, that represents a temporal scale above the 2 mo intervals. Also at the lagoon level, fixed effects

of both local and regional (e.g. Ti.d and Ra.d) environmental conditions on the β_{BC} components provided even more evidence for the importance of considering multiscale sources of variation.

Each coastal lagoon has an unique signature based on the relevance of differences in the values and variations of their morphometric features for the short-term relationships. The influence of morphometric and hydrological features on the fish assemblage structure is widely documented in tropical transitional ecosystems (e.g. Pérez-Ruzafa et al. 2007, Sheaves & Johnston 2009, Petry et al. 2016, Hartz et al. 2019). Several studies have also assessed the effects of these features on environmental variability in coastal transitional ecosystems (e.g. Haines et al. 2006, Gunaratne et al. 2014). However, our study provides new information by assessing the effects of morphometric and hydrological features on the relationships between short-term environmental variability and the β_{BC} components. The random effect for WZ on the response of β_{BC} to the Sa.d and pH.d reflects the importance of differences between the coastal lagoons (i.e. lower values of WZ in the Maricá lagoon and higher and more variable values in the Araruama lagoon) to determine other environmental differences between sampling locations, possibly also related to the degree of marine influence. Likewise, the random effect for DO on the variances of β_{BC-BAL} and β_{BC-GRA} at the lagoon level reflects its overall influence on the mechanisms associated with the abundance-based beta diversity. These mechanisms are primarily related to the balance between the freshwater and marine influences represented by Ra.d and Ti.d, considering the small explanation added by the random effect for DO to their positive effects.

The absence of hydrological features as random effects in the selected models is most likely a result of the limited riverine input in all coastal lagoons (Knoppers et al. 1991, Kjerfve 1994). Otherwise, the relevance of climate-related sources of variation is partly supported by the random effect for Wi.d on the relationship between short-term environmental variability and β_{BC} at the local level, and β_{BC-BAL} at the zone level, which is most likely related to its determinant role on the local environmental conditions due to gas exchange associated with water mixing and sediment resuspension (Esteves et al. 2008, Pérez-Ruzafa et al. 2019). The random effect for Wi.d may also directly influence the abundance of fish larvae and juveniles by favoring their entrances into the coastal lagoons (Bruno & Acha 2015), primarily in their outer zones given

the greater probability of species exchange with the ocean. The relevance of climate-related sources of variation was also expressed by the random effect for Ra.d on $\beta_{BC\text{-}BAL}$ at both the local and zone levels, most likely as a result of a dilution effect that directly affects physicochemical parameters, primarily salinity levels (Kozlowsky-Suzuki & Bozelli 2004). Ra.d may also influence riverine inflow and consequently the input of dissolved organic carbon and other materials leached from nearby terrestrial environments (Farjalla et al. 2002). Evidence for the importance of these ecological relationships related to Wi.d and Ra.d is provided by the larger proportion of variance associated with their random effects on the responses of the β_{BC} components at local and zone levels. Therefore, as widely supported by several studies worldwide, the balance between freshwater and marine influences is a key factor for the prevalent environmental conditions and fish assemblage structure in coastal lagoons (Sosa-López et al. 2007, Garcia et al. 2017).

Further evidence for the relevance of freshwater and marine influences is provided by the positive effects of Ti.d and Ra.d on β_{BC} at the lagoon level, most likely favoring temporal beta diversity primarily due to the entrance of individuals by chance and mediated by specific environmental tolerances and requirements, respectively (Camara et al. 2018, 2020). Also at the lagoon level, the random effects for CS and DO on the variance in the response of $\beta_{BC\text{-}BAL}$ reinforces the importance of the freshwater–marine gradients throughout the year for changes in species composition and abundance, most likely influenced by the life cycles of species that spend only particular stages in the coastal lagoons (Reis-Filho et al. 2019). Considering the small explanation added by CS and DO to the positive effect of Ra.d on $\beta_{BC\text{-}BAL}$, their random effects are redundant with the variations in the values of Ra.d, most likely as a consequence of the typically dry and wet seasons in this tropical region and the marked rainfall gradient between the coastal lagoons that is coincident with their morphometric differences, respectively (Knoppers et al. 1991, Alvares et al. 2013).

The balance between freshwater and marine influences was also reflected by the positive effects of Sa.d and pH.d on β_{BC} at the local level. The positive effect of Sa.d is most likely related to the physiological limitation imposed on stenohaline species, primarily marine-origin species and to a lesser extent a few freshwater species that expand their occurrences in lower salinities (Franco et al. 2019). The effect of pH.d, in turn, may be indicative of a

positive influence of temporal variations on the intensity of acidification processes, as a result of changes in CO_2 levels by decomposition of riverine organic matter (Wallace et al. 2014). In this case, higher values of pH.d may influence species composition and abundance directly due to the physiological limitations of some species, or be an indirect indicator of a greater availability of feeding resources for opportunist species (Camara et al. 2018, Andrade-Tubino et al. 2020). Also at the local level, the positive effects of Sa.d and De.d on $\beta_{BC\text{-}GRA}$ highlight the relevance of the abundance gradients, primarily in areas with higher temporal changes in the marine influence (i.e. the Araruama lagoon and the outer zones in the other lagoons). Therefore, it is likely that unbalanced changes in the abundances of rare species are primarily related to the random dispersal of marine stragglers. These results are expected, given the relevance of these environmental differences, primarily the salinity gradients, to determine pronounced changes in the fish assemblage structure (Sosa-López et al. 2007, Garcia et al. 2017).

Similar relationships may be assumed at the zone level, considering the positive effect of Sa.d on $\beta_{BC\text{-}GRA}$, whereas its negative effect on $\beta_{BC\text{-}BAL}$ is most likely a result of a lower contribution of balanced changes in the abundance of species that use estuarine areas during particular stages of their life cycles for assembly processes under harsher environmental conditions represented by larger short-term changes in salinity. Therefore, the short-term dissimilarity in species composition and abundance at the zone level is related to unbalanced differences in the abundance due to the loss of individuals under critical salinity ranges (Whitfield et al. 2006, Sosa-López et al. 2007). To a lesser extent, other environmental distances also supported the relevance of the balance between marine and freshwater influences for beta diversity at the zone level. In this sense, considering that higher values of pH are indicative of more oligotrophic conditions under higher marine influence, the negative effect of pH.d on β_{BC} is most likely a primary result of lower $\beta_{BC\text{-}BAL}$ counterbalanced by higher $\beta_{BC\text{-}GRA}$ in higher salinity variations (Wallace et al. 2014). Likewise, transparency may be positively influenced by a larger input of organic matter under higher freshwater influence, whereas temperature is typically lower in areas with higher marine influence due to greater water exchange and volume (Farjalla et al. 2002, Esteves et al. 2008). Therefore, the positive effects of Te.d on β_{BC} and $\beta_{BC\text{-}BAL}$, and Tr.d on $\beta_{BC\text{-}BAL}$ are most likely a consequence of wider envi-

ronmental gradients throughout the year, providing more suitable habitats for different species inhabiting estuarine areas during specific stages of their life cycles (Reis-Filho et al. 2019).

Despite the greater concordance between the coastal lagoons on the short-term environmental effects on the β_{BC} components at the lagoon level, the relevance of their intrinsic features was evidenced by the random effects for their morphometric features and climate-related environmental factors, as well as the lagoon-related responses of β_{BC-BAL} to multiple environmental distances. In this sense, the negligible effects of Sa.d on the β_{BC} components at the lagoon level are most likely a result of the remarkable differences between the studied coastal lagoons, characterized as mesohaline (Maricá), euhaline (Saquarema), and hyperhaline (Araruama) systems (Franco et al. 2019). Therefore, the temporal β_{BC} is most likely more influenced by these permanent differences between the coastal lagoons than the less expressive short-term variation in the values of Sa.d. Regardless of that influence, and the more prominent differences between the coastal lagoons in the possible mechanisms related to their β_{BC} patterns at the local and zone levels, this study evidenced a concordance in the main environmental drivers of the assembly processes in the coastal lagoons, primarily related to a greater contribution of β_{BC-GRA} to β_{BC} and the freshwater vs. marine influences in all hierarchical levels. Furthermore, based on the effective identification and control of multiple scale-dependent sources of variation, the relationships observed in this study have great generalization power and may reflect key mechanisms working in other tropical coastal lagoons worldwide.

Considering the scarce number of studies focused on fish beta diversity in tropical coastal lagoons, and the complete lack of studies using abundance-based measures to express directional changes in fish assemblage structure in transitional ecosystems, our study opens a new avenue for a better understanding of the mechanisms associated with the temporal dynamic of assembly processes in such ecosystems. Scale-dependent spatial differences in the diversity components (alpha, gamma, and beta) expressed as changes in species richness, and the species composition and abundance of fish assemblages and habitat use groups were previously observed for these coastal lagoons and other transitional ecosystems in the studied region (Camara et al. 2019, 2020). However, the sensitivity to the spatial scale of temporal processes is a new finding with important implications in terms of reinforcing the need for multilevel assessments guiding management and conservation actions for coastal fish assemblages. In this sense, despite the extensive number of studies investigating spatial and temporal scales of variation in fish assemblage structures in coastal ecosystems, these studies focus primarily on assessing the species–environment relationships separately for these 2 dimensions, the interactions between spatial and temporal effects, or even the spatial synchrony of temporal trends (e.g. coastal lagoons, Gray et al. 2011; coral reefs, Lamy et al. 2015; soft-bottom coastal areas, Östman et al. 2017; bays, coastal lagoons, and oceanic beaches, Andrade-Tubino et al. 2020), and not on explicitly disentangling spatial, temporal, and environmental effects over a range of spatial scales (e.g. estuary, Garcia et al. 2012; soft-bottom coastal areas, Bergström et al. 2016; bays and coastal lagoons, Camara et al.2020). Therefore, all the mechanisms and environmental drivers assessed in this study constitute new achievements towards a better understanding of the roles of coastal lagoons in the maintenance of biodiversity and coastal fishery resources in the tropical region.

5. CONCLUSIONS

This study evidenced the scale sensitivity of short-term environmental effects on the temporal beta diversity of fishes in tropical coastal lagoons. The 3 main contributions of this study were the identification of (1) different assembly processes related to the temporal structure of the fish assemblages and (2) different multiscale environmental effects at (3) different hierarchical levels (i.e. local, zone, and lagoon). In this sense, the different assembly processes assessed by the directional measures of abundance-based dissimilarity in species composition and abundance (β_{BC}) also represents a new contribution for studies on fish assemblages in coastal lagoons.

A greater relevance of the β_{BC} component expressing abundance gradients (i.e. β_{BC-GRA}), with abundance changes independent of the species, compared with the balanced changes in the abundances of different species (i.e. β_{BC-BAL}) was observed in all hierarchical levels. The greater relevance of β_{BC-GRA} highlights the prevalence of a process analogous to species loss (or nestedness), but based on the loss (or gain) of individuals of different species between 2 mo intervals. The different contributions of the 2 assembly processes were highly induced by the degree of spatial and temporal marine influence in the tropical coastal lagoons, and mediated by the prevalence of

rare marine-origin species that are typically stenohaline and enter the coastal lagoons in low numbers during periods of higher marine influence. As a consequence, these species are probably mainly responsible for the greater contribution of $\beta_{BC\text{-}GRA}$ to β_{BC}. The greater and more constant marine influence in the Saquarema lagoon, in turn, led to higher values of $\beta_{BC\text{-}BAL}$ at all hierarchical levels — probably related to fish species that respond differentially to short-term environmental changes, primarily marine-origin species showing seasonal-mediated gradual changes in abundance as a consequence of their life cycles. Therefore, in a process analogous to species replacement, the higher short-term values of $\beta_{BC\text{-}BAL}$ in the Saquarema lagoon are most likely capturing gradual changes in the abundances balanced by individuals of different species, according to their specific environmental tolerances and requirements.

The relevance of the balance between freshwater and marine influences was supported by different environmental effects on β_{BC} components at all hierarchical levels. These relationships were primarily represented by effects of the Sa.d on the β_{BC} components at the local and zone levels, Ti.d and Ra.d at the lagoon level. Random sources of variation, in turn, were associated with morphometric and climatic differences between lagoons, which evidenced even more the relevance of investigating temporal effects at different spatial scales. The random influences of WZ and DO showed the relevance of connectivity between zones and with the marine environment for the β_{BC} patterns at the local and lagoon levels, respectively. Random effects for Wi.d and Ra.d, in turn, demonstrated that variations in such climatic-related characteristics differentially affect the relationships between the physicochemical parameters and beta diversity at the local and zone levels. Otherwise, the positive effects of short-term variations in Ra.d and Ti.d. on beta diversity at the lagoon level demonstrate a concordance in the relevance of the freshwater vs. marine influence between the coastal lagoons, with the strength of these relationships supported by the redundant random effects of CS and DO. Future investigations focused on more annual cycles may provide additional insights regarding the consequences of shifts in rainfall, tidal and other climate-related regimes on the structure of fish assemblages in tropical coastal lagoons. In this sense, considering that the negligible effect of the hydrological features was most likely related to reduced drainage basin in all coastal lagoons, future investigations focused on transitional ecosystems with larger differences in riverine inputs may also clarify its relevance for the balance between freshwater and marine influences. The concomitant incorporation of functional and/or phylogenetic information may also reinforce the importance of the main mechanisms identified in this study, and allow for the identification of other ecological processes structuring the fish assemblages in tropical transitional ecosystems.

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Appendix.

Table A1. Generalized linear mixed models selected for the relationships between temporal beta diversity (Bray-Curtis dissimilarity) and the environmental distances at the local, zone, and lagoon levels. The values of temporal beta diversity express the total abundance-based dissimilarity (β_{BC}), the balanced variation in abundance of different species (β_{BC-BAL}), and abundance gradients (β_{BC-GRA}) between 2 mo intervals. Random effects: sampling locations (Lo), changing seasons (CS), mean width of the connections between adjacent zones (WZ), distance from the ocean (DO), and environmental distances for wind intensity (Wi.d) and accumulated rainfall (Ra.d). Fixed effects: environmental distances for pH (pH.d), transparency (Tr.d), temperature (Te.d), salinity (Sa.d), depth (De.d), substrate type (Su.d), tide height (Ti.d), and Ra.d. Results shown only for models with the ΔAICc < 2. The best-supported model given the data set and the candidate models is in **bold**. R^2 f: total variation explained by fixed effects (i.e. the likelihood-ratio-based R^2 of the global model calculated using a null model including the intercept plus random effects); R^2 f+r: total variation explained by fixed effects plus random effects (i.e. the likelihood-ratio-based R^2 of the global model calculated using a null model including only the intercept); *K*: number of factors (including intercept); LL: log likelihood; AICc *wi*: AICc weight; (−) no information

Dependent variable	Model	Fixed	Random	R^2 f	R^2 f+r	K	LL	AICc	ΔAICc	AICc *wi*
Local level										
β_{BC}	**m1**	**Sa.d, pH.d**	**Lo, WC, Wi.d**	**0.08**	**0.20**	**7**	**−4.22**	**23.22**	**0.00**	**0.21**
	m2	Sa.d, Tr.d	Lo, WC, Wi.d	0.08	0.20	7	−4.52	23.80	0.58	0.16
	m3	Sa.d	Lo, WC, Wi.d	0.07	0.19	6	−5.70	23.98	0.76	0.14
	m4	Sa.d, pH.d, Su.d	Lo, WC, Wi.d	0.09	0.21	8	−3.51	24.02	0.80	0.14
	m5	Sa.d, pH.d, Tr.d	Lo, WC, Wi.d	0.09	0.21	8	−3.59	24.19	0.97	0.13
	m6	Sa.d, Te.d, pH.d	Lo, WC, Wi.d	0.09	0.21	8	−3.66	24.32	1.10	0.12
	m7	Sa.d, Su.d	Lo, WC, Wi.d	0.07	0.20	7	−4.99	24.74	1.52	0.10
$\beta_{BC.BAL}$	**m1**	**−**	**Lo, Ra.d**	**−**	**0.30**	**4**	**56.70**	**−105.13**	**0.00**	**0.32**
	m2	De.d	Lo, Ra.d	0.01	0.30	5	57.36	−104.31	0.82	0.22
	m3	Su.d	Lo, Ra.d	0.01	0.30	5	57.08	−103.75	1.38	0.16
	m4	Ti.d	Lo, Ra.d	0.00	0.30	5	57.00	−103.59	1.54	0.15
	m5	Tr.d	Lo, Ra.d	0.00	0.30	5	56.99	−103.57	1.56	0.15
$\beta_{BC.GRA}$	**m1**	**Sa.d, De.d**	**−**	**0.04**	**−**	**4**	**5.72**	**−3.16**	**0.00**	**0.45**
	m2	Sa.d	−	0.02	−	3	4.40	−2.64	0.52	0.35
	m3	−	−	−	−	2	2.84	−1.60	1.56	0.21
Zone level										
β_{BC}	**m1**	**Te.d**	**−**	**0.07**	**−**	**3**	**2.79**	**0.89**	**0.00**	**0.45**
	m2	Te.d, pH.d	−	0.10	−	4	3.67	1.48	0.59	0.33
	m3	Te.d, De.d	−	0.09	−	4	3.27	2.27	1.38	0.22
$\beta_{BC.BAL}$	**m1**	**Sa.d, Te.d, Tr.d**	**Wi.d, Ra.d**	**0.21**	**0.46**	**7**	**39.36**	**−62.28**	**0.00**	**0.62**
	m2	Sa.d, Te.d	Wi.d, Ra.d	0.16	0.42	6	37.53	−61.27	1.01	0.38
$\beta_{BC.GRA}$	**m1**	**−**	**−**	**−**	**−**	**2**	**8.45**	**−12.67**	**0.00**	**0.30**
	m2	Sa.d	−	0.03	−	3	9.37	−12.26	0.41	0.25
	m3	Tr.d	−	0.02	−	3	9.02	−11.56	1.11	0.17
	m4	Sa.d, Tr.d	−	0.06	−	4	9.97	−11.12	1.55	0.14
	m5	Su.d	−	0.01	−	3	9.79	−11.10	1.57	0.14
Lagoon level										
β_{BC}	**m1**	**Ti.d, Ra.d**	**−**	**0.61**	**−**	**4**	**22.61**	**−34.13**	**0.00**	**0.53**
$\beta_{BC.BAL}$	**m1**	**Tr.d, Te.d, pH.d, De.d, Su.d, Ra.d**	**CS, DO**	**0.91**	**0.92**	**10**	**43.56**	**−35.68**	**0.00**	**0.79**
$\beta_{BC.GRA}$	**m1**	**−**	**DO**	**0.30**	**0.33**	**3**	**5.19**	**−2.67**	**0.00**	**0.36**
	m2	Ti.d	DO	0.38	0.41	4	6.31	−1.54	1.13	0.21