

The scale-dependent effect of environmental filters on species turnover and nestedness in an estuarine benthic community

ANDRÉ MENEGOTTO ^{1,4,*} CRISTIAN S. DAMBROS ² AND SÉRGIO A. NETTO ¹

¹Laboratório de Ciências Marinhas, Universidade do Sul de Santa Catarina, Tubarão, Santa Catarina 88704-900 Brazil

²Departamento de Ecologia e Evolução, Universidade Federal de Santa Maria, Santa Maria, Rio Grande do Sul 97105-900 Brazil

*Programa de Pós-Graduação em Ecologia e Evolução, Universidade Federal de Goiás, Goiânia, Goiás 74690-900 Brazil

Citation: Menegotto, A., C. S. Dambros, and S. A. Netto. 2019. The scale-dependent effect of environmental filters on species turnover and nestedness in an estuarine benthic community. *Ecology* 100(7):e02721. 10.1002/ecy.2721

Abstract. Environmental filtering is a major mechanism structuring ecological communities. However, it is still not clear how different abiotic drivers composing the environmental filter interact with each other to determine local species assemblage and create spatial patterns in species distribution. Here, we evaluated the effects of two strong and uncorrelated environmental variables (salinity and sediment properties) on the β -diversity of an estuarine macrobenthic community while accounting for spatial effects. Our results show that the benthic community composition has a strong spatial structure along the estuary, which can be greatly explained by salinity and sediment variation. Salinity is most associated with species replacement (turnover), whereas sediment is more important for species loss (nestedness). However, the effects of sediment variation on nestedness are mainly detected at a smaller spatial scale (estuarine sectors), whereas the effects of salinity on species turnover are stronger as spatial scale increases (entire estuary). Our findings suggest that environmental filters can drive both turnover and nestedness components of β -diversity, but that their relative importance depends on the spatial scale of investigation. Although abiotic drivers associated with detrimental effects (sediment) usually result in nestedness, larger spatial scales encompass abiotic drivers associated with different suitable conditions (salinity), increasing the relative importance of the replacement component of species β -diversity.

Key words: abiotic filter; beta-diversity; brackish water; coastal lagoon; community assembly; hierarchical environmental filter; macrofauna.

INTRODUCTION

A fundamental goal of community ecology is to understand the processes driving the assembly of biological communities from regional to local pools of species. According to a niche-based theoretical model, species from the regional pool must pass through three main ecological filters to colonize a local community successfully: dispersal, environmental, and biotic filters (Keddy 1992, Belyea and Lancaster 1999, HilleRisLambers et al. 2012). Traditionally, the concept of ecological filters has been investigated focusing on which of these three mechanisms is governing the assembly process of a focal community, especially the importance of the environment compared to dispersal or biotic filters in structuring local assemblages and community β -diversity (Arellano et al. 2016, Cao et al. 2016, Duan et al. 2016). However, these approaches usually assume the effects of an environmental filter as a single and discrete

constraint, even though it may be composed by different abiotic drivers acting on different spatial scales (Poff 1997, de Bello et al. 2013). A less-explored subject, though, is how different abiotic factors interact to determine local species assemblage, i.e., the hierarchical nature of the environmental filter.

The idea of a hierarchical environmental filter was already present at the birth of the ecological filter metaphor (Keddy 1992, Belyea and Lancaster 1999). For example, Keddy (1992) highlighted how a sequence of environmental drivers progressively select species best adapted to local conditions in a wetland community. Similarly, a meta-analysis revealed that different abiotic factors interact to determine plant community composition and concluded that the importance of each environmental driver is associated with the spatial scale of observation (Siefert et al. 2012). However, few studies have explored how the hierarchical influence of environmental drivers may affect community β -diversity (Poff 1997, Fernandez-Goñi et al. 2013). More precisely, it is still not clear if these filters act by reducing the number of species in some communities (species loss), or by selecting species with different environmental requirements at each local community (species turnover).

Manuscript received 24 August 2018; revised 24 December 2018; accepted 4 March 2019. Corresponding Editor: Jonathan H. Grabowski.

⁴E-mail: andre.menegotto@gmail.com

Here, we evaluated the effects of two strong and uncorrelated environmental variables (salinity and sediment properties) on the species composition of an estuarine macrobenthic community. The estuarine system is ideal to test the environmental filter hypothesis because of its harsh conditions (i.e., at least for most of the aquatic species). Under stressful conditions, environmental filters become more important than dispersal limitation for community assembly (Chase 2007). In addition, salinity and sediment are known to be the most important abiotic variables for estuarine benthic species (Teske and Wooldridge 2003, Nanami et al. 2005). In our study area, salinity and sediment gradients are completely orthogonal (see details below), allowing us to test their independent effects on the composition of local communities. Specifically, we tested the importance of each environmental variable on benthic β -diversity at broad and fine spatial scales and evaluated how each variable affects the loss and replacement of species as spatial scale increases.

METHODS

Study area

We conducted the study in the Laguna Estuarine System, a choked coastal lagoon in southern Brazil (Fig. 1). The lagoon has an area of 184 km², a mean depth of 2 m, and it is isolated from the ocean by a sand barrier to the east. Small rivers to the west contribute freshwater

input and sediment delivery. The particular geomorphology of the lagoon creates a west–east axis of sedimentary variation, with surface sediments varying from silty and poorly sorted grains with high organic and water content to the west, and well-sorted fine sand with low organic content to the east (Appendix S1: Fig. S1). Sediment inflow of the elongated and shore-parallel Laguna Estuarine System generated a series of cusped divisions (separation) due to wind waves that build spits segmenting the lagoon into separate basins (Woodroffe 2002). Water exchange between the lagoon and the ocean occurs through a single and narrow channel in the south. The connection with the sea in the outer sector creates a south–north salinity gradient (perpendicular to sedimentary variation), with high salinity values in the south decreasing toward the inner north. During the course of the study, salinity varied from 30.02 psu (practical salinity unit) in the outer sector to 2.23 psu in the inner sector (Appendix S1: Fig. S1).

Sampling

We sampled 39 sublittoral sites (mean depth of 1.7 m) throughout the whole estuarine system in order to cover both environmental gradients of salinity and sediment (Fig. 1). In early August 2008, three samples of sediment were collected at each sampling site for analysis of benthic community composition. Samples were collected using a 15 cm diameter PVC core tube pushed into the sediment to a depth of 10 cm. After collection, samples were fixed in 10% formalin for at least 48 h, sieved on a 0.5-mm mesh net, preserved in 70% ethanol, and sorted using a dissecting microscope. All invertebrates were identified to the lowest possible taxonomical level and counted.

At each sampling site, we also measured the bottom water salinity with an YSI 556MPS multiparameter instrument (YSI Inc., Yellow Springs, Ohio, USA) and collected three samples of sediment to characterize the sedimentary environment. For each sample of sediment, we determined the mean grain size, sorting, skewness, fine (silt + clay) and sand percentages, total organic matter, water content and heterogeneity. Details on sediment processing and analysis, as well as spatial distribution of sedimentary variables and salinity, are provided in Appendix S1.

Data analysis

The composition of species can be determined by niche processes when individual species are strongly adapted to a narrow range of environmental conditions (Keddy 1992, Chase 2007). However, neutral processes, such as random colonization and local extinction, can also determine how species are spatially distributed so that areas close to each other share similar composition of species (Hubbell 2001). To disentangle the effects of environmental variables on the composition of benthic communities from the effect of other processes that

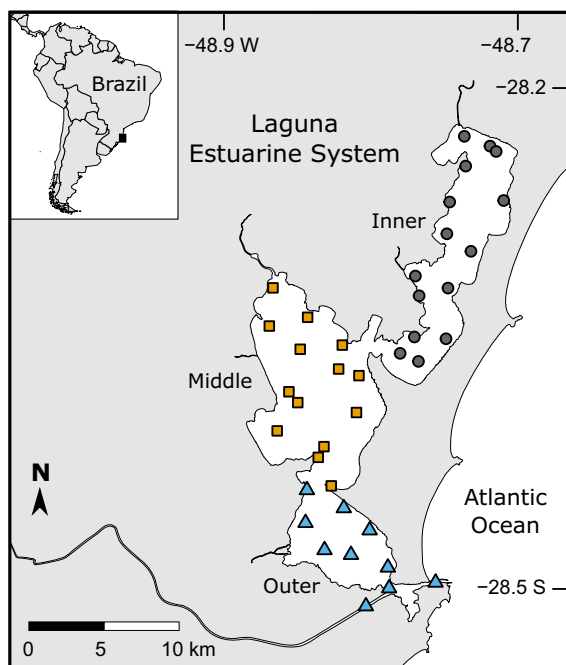


FIG. 1. Map of the Laguna Estuarine System with the sampling stations in the inner (grey circles), middle (orange squares), and outer (blue triangles) sectors.

could cause spatial autocorrelation (e.g., neutral processes), we tested for the association between species composition and the salinity and sedimentary gradients, and the geographic positioning of sampling sites.

Sedimentary variables were highly correlated with each other (above 79%, except skewness), and the first axis of a principal component analysis (PCA) summarizing these variables was used as a predictor variable representing the sedimentary gradient (Appendix S1). The first PCA axis accounted for 79% of variation in sedimentary variables. Salinity was only weakly correlated to any sedimentary variable ($-0.19 < r < 0.15$) or with the PCA axis representing the sedimentary gradient ($r = 0.04$). Therefore, salinity and the PCA axis of sediment were used as independent environmental predictor variables in all analyses.

To determine how the environment and the spatial positioning of sites were associated with the composition of species, we performed a redundancy analysis (RDA) using Sørensen similarity matrix based on presence/absence species data as response variable and sediment (PCA axis), salinity, and spatial predictors as predictor variables. Spatial predictors were obtained from site coordinates using Moran eigenvector maps (MEMs) based on a Gabriel graph (Dray et al. 2012, Legendre and Legendre 2012). MEMs are linear variables representing all possible configurations of spatial autocorrelation. Each MEM represents a different spatial scale ranging from the broadest (MEM with highest associated eigenvalue) to the finest (MEM with lowest associated eigenvalue). We used scalograms to project the correlation between sites scores of the two first axes of the RDA, and the residual axes of the same RDA, with the spatial basis formed by 38 MEMs to identify the main scales of spatial variation in the response data. Scalograms are presented in smoothed version with 19 spatial components formed by groups of two successive MEMs (R^2 values summed). To test if the maximum observed R^2 value is significantly higher than values obtained in the absence of spatial autocorrelation, we used a permutation procedure with 999 repetitions. Spatial analyses were performed using the “spdep” (Bivand 2018) and “spacemakeR” (Dray 2013) R packages. A forward selection based on adjusted R^2 values was used to select only those MEMs with strong explanatory power for benthic species composition (Blanchet et al. 2008). The selected MEMs were divided into two groups corresponding to broad and fine scale MEMs. We performed variation partitioning (Borcard et al. 1992) of the RDA axes representing the main changes in community composition to quantify the association of species composition with salinity, sediment, and broad-scale and fine-scale MEMs. Multivariate analyses (PCAs and RDAs) and variation partitioning were performed using the “vegan” R package (Oksanen et al. 2018).

In addition to the RDA analyses, we evaluated the effects of spatial and environmental drivers on the turnover (species replacement) and nestedness (species loss)

components of β -diversity (Baselga 2010). Total β -diversity, which was calculated here with the Sørensen similarity index (β_{sor}), may be caused by both turnover and richness differences. Because the Simpson similarity index (β_{sim}) is unaffected by difference in species richness, it is used to describe the contribution of spatial turnover. The resulting difference between β_{sor} and β_{sim} , therefore, yields an estimate of the nestedness (β_{nes}). These metrics were calculated with the presence/absence species data using the “betapart” package (Baselga et al. 2018). Geographic coordinates were used to calculate the pairwise geographic distance matrix. Environmental distance matrices were created independently based on differences of salinity and sediment between all pairs of sites. To quantify the association of the Sørensen similarity index and each component of benthic β -diversity with geographic and environmental matrices we applied a multiple regression on distance matrices (MRM) using the “ecodist” package (Goslee 2017) in the R program (R Core Team, 2018). Because structuring factors may affect community assembly at different spatial scales (Barton et al. 2013), we explored the MRM models for the entire estuary and separately for each estuarine sector.

RESULTS

We recorded 51,364 individuals from 39 species/morpho-species of macrobenthic invertebrates including Polychaeta (18 spp.), Crustacea (8 spp.), Mollusca (6 spp.), as well as five other taxonomic groups with one species each. The microgastropod *Heleobia australis* was the most abundant species, with 76.68% of the total abundance, followed by the bivalve *Erodona mactroides* (12.04%), and the polychaete *Paraprionospio pinnata* (3.41%). We found a minimum of 4 species and a maximum of 18 species per site. Overall, species richness was higher in sandy (12.64 ± 3.58 , mean $\pm$ SD) than muddy sites (7.4 ± 2.73 ; $F_{2,36} = 11.59$, $P < 0.001$), and increased from the inner to the outer sector (7.4 ± 2.67 ; 9.58 ± 2.95 ; 14.8 ± 2.35 ; $F_{2,36} = 22.9$, $P < 0.001$).

Environmental and spatial effects on community composition at different spatial scales

The first two axes of RDA accounted for 76.9% and 23.1% of the total variability in species composition, and were strongly correlated with salinity ($r_{\text{sal}} = 0.98$ and 0.21) and sediment variation ($r_{\text{sed}} = 0.25$ and -0.97 ; $R^2_{\text{sal+sed}} = 0.38$, $P = 0.001$ based on 999 permutations; Appendix S2: Figs. S1–S3). The scalograms for the first two axes of the RDA revealed that both axes exhibited a broad-scale nonrandom spatial pattern ($R^2_{\text{Max}} = 0.80$, $P = 0.001$; $R^2_{\text{Max}} = 0.30$, $P = 0.004$; Appendix S2: Fig. S4). After the removal of the effects of salinity and sediment on the RDA axes of species composition, there was still a significant broad-scale spatial pattern for the first axis that could not be explained by salinity and

sediment ($R^2_{\text{Max}} = 0.26$, $P = 0.004$; Appendix S2: Fig. S4). The forward selection procedure chose only one broad-scale spatial predictor (MEM 1), whereas no spatial predictor corresponding to fine scales was selected. The selected MEM representing spatial structure at broad-scale explained 64% of the total variance in community composition, from which 53% could be attributed to salinity and only 1% to sediment (Fig. 2). Although most of the fraction explained by salinity was spatially structured, sediment explained 15% of the variation in species composition independently of any spatial predictor. The most inclusive model, with environmental and spatial components, explained 80% of the species variation within the estuary, with only 10% corresponding to a pure spatial fraction (Fig. 2).

Relationships between β -diversity and geographic and environmental distance

Because salinity is highly correlated with geographic distance (salinity: $r = 0.84$; sediment: $r = 0.09$), we conducted the MRM analysis twice, once including geographic distance and once using exclusively the environmental variables. The results show that the similarity in species composition measured by the Sørensen similarity index decreased with geographic distance and differences in salinity and sediment (Table 1). Considering the turnover and nestedness components of β -diversity separately, the turnover component was mainly associated with geographic distance and differences in salinity, whereas the nestedness component was more strongly associated with differences in sediment (Table 1, Fig. 3). However, the strength of these associations differed across scales. For the entire estuary, we found a

strong correlation between the similarity in species composition and geographic and salinity matrices. In contrast, the difference in sediment was the best predictor of species composition when MRM analysis was run separately for each estuarine sector (Table 1, Fig. 4). It is noteworthy that the significance test of our analysis using only environmental variables could be initially influenced by residual autocorrelation, because we removed the spatial predictor from the model. However, a mantel test of the spatial structure in the residuals revealed that geographic distance accounted for only 6% of the residual variation in the model for the entire estuary. In the model of the inner and middle sectors, such influence is lower than 1%. Spatial structure in the residuals was relatively high only in the model of the outer sector (22%), where no environmental variable was associated with β -diversity. Therefore, we believe that the results of our MRM analysis are robust to the effects of spatial autocorrelation.

DISCUSSION

In order to investigate how environmental filters drive species distribution, we evaluated the changes in an estuarine benthic community along two strong and independent environmental gradients of salinity and sediment, while accounting for spatial effects. No signal of fine-scale variation in species composition was detected in our analyses, suggesting absence of patchy distributions within the estuary. Both environmental predictors were strongly associated with broad-scale spatial patterns in species distribution. However, only the effects of salinity were spatially structured, since sediment disposition within the study area reduces the spatial structure of the sedimentary gradient. Salinity was the most influential environmental predictor of benthic β -diversity at broad scale and was associated with a strong turnover in species composition. However, when we conducted the analysis separately for each estuarine sector, a broad but smaller scale, sediment became a better predictor of β -diversity. Contrary to salinity, sediment variation was related to species loss from sandy to muddy sites. Overall, our results revealed a clear dependence of spatial scale in the strength of each environmental driver on community composition. Consequently, the relative importance of each component of β -diversity was also scale-dependent: whereas the salinity gradient determines species turnover across the entire estuary, sediment variation determines species loss within the estuarine sectors. Our findings suggest that environmental filters can drive both the turnover and nestedness components of β -diversity, but the relative importance of each component depends on the spatial scale of investigation.

Spatial turnover is assumed to indicate the existence of dispersal limitation or selective differentiation between communities (Simpson 1943, Baselga 2010). Although dispersal limitation explains some of the patterns observed here (Dray et al. 2012, Legendre and

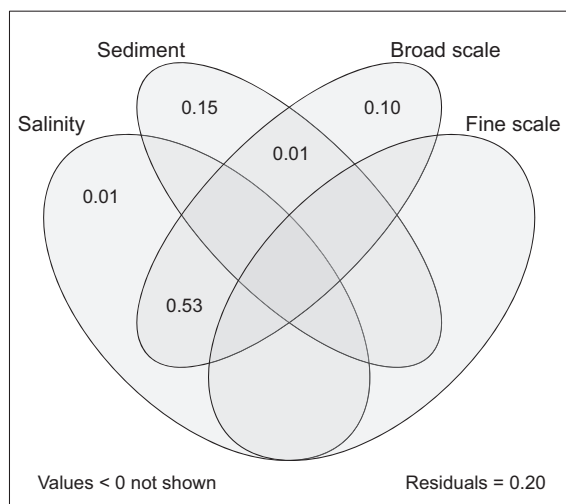


FIG. 2. Variation partitioning results of benthic community composition showing the fraction explained by salinity and sediment (environmental component), and broad and fine-scale Moran eigenvector maps (spatial component).

TABLE 1. Standardized regression coefficient for the influence of geographic and environmental distance on total β -diversity (β_{sor}), turnover (β_{sim}), and nestedness (β_{nes}) of benthic invertebrates across the entire estuary and for each estuarine sector.

	Geographic distance	Salinity distance	Sediment distance	<i>F</i>	<i>R</i> ² (%)
Entire estuary					
1 – β_{sor}	–0.098***	0.004 (–0.078***)	–0.024** (–0.033***)	231.88 (199.42)	49*** (35***)
1 – β_{sim}	–0.081***	–0.004 (–0.071***)	0.008 (–0.000)	82.66 (83.39)	25*** (18***)
1 – β_{nes}	–0.018	0.008 (–0.007)	–0.031*** (–0.033***)	19.40 (26.86)	07*** (07***)
Inner					
1 – β_{sor}	–0.008	–0.018 (–0.024*)	–0.053*** (–0.054**)	14.20 (21.21)	30*** (29**)
1 – β_{sim}	0.004	–0.033 (–0.030*)	0.041*** (0.041***)	6.99 (10.55)	17** (17***)
1 – β_{nes}	–0.012	0.014 (0.006)	–0.094*** (–0.094***)	33.43 (49.77)	50*** (49***)
Middle					
1 – β_{sor}	–0.005	–0.037 (–0.041***)	–0.055*** (–0.058***)	21.82 (32.97)	43*** (43***)
1 – β_{sim}	–0.014	–0.037 (–0.046**)	0.026 (0.020)	6.45 (9.41)	18* (18*)
1 – β_{nes}	0.009	–0.001 (0.005)	–0.081** (–0.078**)	36.36 (54.56)	55** (55**)
Outer					
1 – β_{sor}	–0.058**	0.000 (–0.005)	0.004 (–0.017)	4.91 (0.50)	26 (02)
1 – β_{sim}	–0.060*	–0.004 (–0.010)	0.005 (–0.016)	4.15 (0.46)	23 (02)
1 – β_{nes}	0.002	0.005 (0.005)	–0.001 (–0.001)	0.17 (0.24)	01 (01)

Notes: Values in parentheses are results excluding geographic distance from the model. See Appendix S2: Table S1 for regression coefficients calculated with unstandardized variables.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

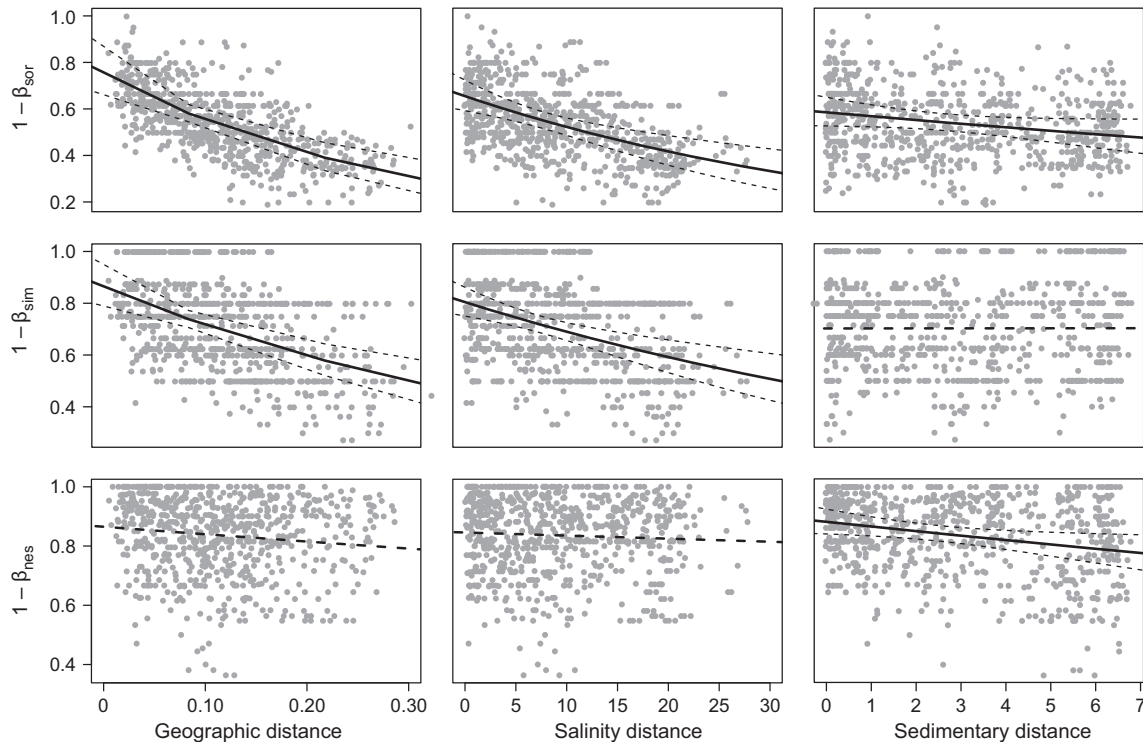


FIG. 3. Changes of Sørensen similarity index ($1 - \beta_{\text{sor}}$), turnover ($1 - \beta_{\text{sim}}$), and nestedness ($1 - \beta_{\text{nes}}$) components of β -diversity with geographic, salinity, and sedimentary pairwise distance matrices at the full estuary scale. Plots indicate significant (solid lines + 95% confidence interval) and nonsignificant (dashed lines) results in the MRM analysis. Lines were modeled fitting a generalized linear model using a binomial log-link function.

Legendre 2012), macrobenthic species usually have high dispersal capacity in wind-wave dominated shallow systems (Lundquist et al. 2006, Pilditch et al. 2015). In addition, most of the spatial variation in species

composition observed in our study could be attributed to salinity alone. The large salinity variation (0–30 psu) represents a physiological barrier for many species that are adapted to specific salinity conditions, which limit

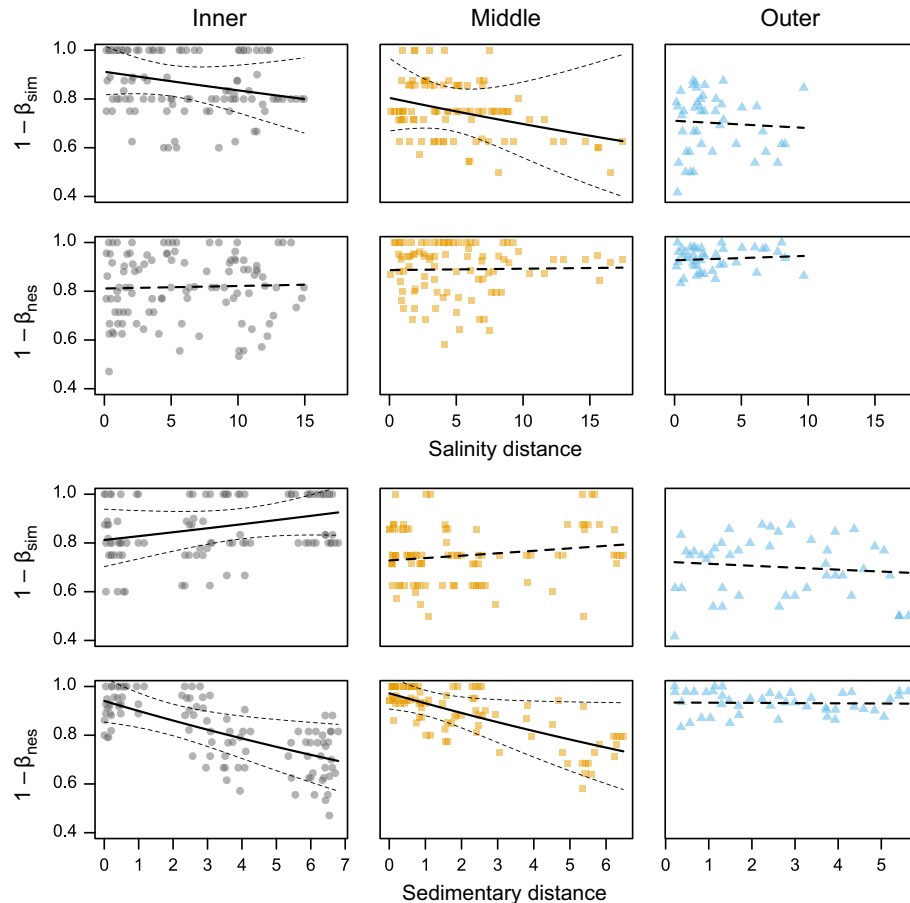


FIG. 4. Changes of turnover ($1 - \beta_{\text{sim}}$) and nestedness ($1 - \beta_{\text{nes}}$) components of the β -diversity with salinity and sedimentary pairwise distance matrices for the inner (grey circles), middle (orange squares), and outer (blue triangles) sectors of the estuary. Plots indicate significant (solid lines + 95% confidence interval) and nonsignificant (dashed lines) results in the MRM analysis. Lines were modeled fitting a generalized linear model using a binomial log-link function.

their spatial distribution along the estuary (Cognetti and Maltagliata 2000, Telesh and Khlebovich 2010). In accordance with this theoretical expectation, our study shows that benthic β -diversity across the whole estuarine system reflects mainly the replacement of oligohaline species in the inner by polyhaline species in the outer sector. These species are adapted to particular levels of salinity on which they can control osmotic pressure and ionic concentration with low energy cost (Medeiros et al. 2016, Rivera-Ingraham and Lignot 2017). Therefore, considering that each species has physiological adaptations to different levels of salinity and they are allowed to freely track those conditions (Josefson 2016, Medeiros et al. 2016), the result must be a spatial change in species composition along the estuary.

Our study indicates that for this estuarine benthic community, nestedness derives from detrimental effects along the sedimentary gradient. Contrary to the salinity gradient, which represents a transition along distinct but suitable conditions for life in aquatic systems, several factors make one end of the sedimentary gradient highly

inhospitable for many species. In mud bottoms, superficial fine sediment acts as physical barrier that increases the contribution of anaerobic pathways to the overall decomposition and relocates the reoxidation of reduced solutes upwards (Hohai et al. 2014, Mestdagh et al. 2018). Under this circumstance, oxygen penetration depth never exceeds a few centimeters and becomes a major limiting factor for sediment-dwelling organisms (Mestdagh et al. 2018). In addition, sessile or less motile benthic fauna that lives on the substratum or in tubes often have a limited capacity to escape the constant deposition of sediments, and suspension feeders risk damaging their respiratory apparatus (Stevens 1987, Mestdagh et al. 2018). Experiments have shown that even thin layers of deposition may reduce species diversity by nearly 50%, with the strongest effect on those taxa living on the sediment–water interface (Lohrer et al. 2004). Consequently, the macrofauna in these locations is typically depauperated or characterized by dense benthic assemblages consisting of only a few generalist species (Magni et al. 2005, Mestdagh et al. 2018; Appendix S2: Fig. S5).

Interestingly, such effects were only noticed when we reduced the analyses to a sector scale within the estuary. Thus, our results suggest that once the salinity range is small enough to allow the coexistence of species adapted to similar osmotic conditions (same species pool), reducing species replacement along the salinity gradient, variation from sandy to muddy sediments will act as a secondary environmental filter, contributing to the community β -diversity through species loss.

Despite the importance of species loss associated with sediment variation within the estuarine sectors, it should be noted that the nestedness pattern was detected in only two of three sectors of the study area. We did not find any effect of sediment or salinity on β -diversity in the outer sector, where the estuary experiences large oscillations in salinity due to tide and wind effects on marine and freshwater inputs (Netto et al. 2018). It is possible that the large and unpredictable variation in salinity in this sector leads to physiological stressful conditions, which may mask the spatial effects of environmental drivers (Sanders 1968). Previous studies have suggested that estuarine areas subjected to great salinity oscillations are occupied by basically euryhaline species, whose populations have developed a broad tolerance to the unpredictability of the environment and have lost the substrate specificity that usually characterizes species in relatively stable waters (Cognetti 1982). Therefore, we suggest that temporal instability and unpredictability may be important factors in the detection of nestedness pattern in natural communities.

The hierarchical influence of different environmental drivers reported here is similar to results from studies conducted in the terrestrial realm (Siefert et al. 2012). However, by partitioning the β -diversity our study went further and showed how uncorrelated variables are affecting the community composition at different scales. Until now, only a few metacommunity studies have investigated the relative importance of nestedness and turnover in determining dissimilarity patterns (Gianuca et al. 2016, Soininen et al. 2018), especially considering the spatial scaling of β -diversity (Barton et al. 2013). In most of these studies, nestedness has been considered simply a byproduct of geographic isolation (Gianuca et al. 2016, Hill et al. 2017). Although this process may be important to explain β -diversity patterns at biogeographical scale, where nestedness may reflect the extinction/colonization dynamics resulting from past glaciations (Dobrovolski et al. 2012), our study reveals that nestedness may also arise from species sorting operating through niche mechanisms in relatively small and connected communities. In this sense, the absence of an impressive nestedness in some metacommunity studies (Hill et al. 2017) may reflect the absence of a detrimental environmental variable selecting for the subset of opportunist species or, alternatively, the overshadow of this process by another variable determining turnover, which tends to be more common as the spatial scale of analysis increases (Soininen et al. 2018).

By demonstrating how β -diversity components vary across spatial scales, we hope contribute to the development of a more general framework for testing the process structuring ecological communities. Overall, our results support the predictions that nestedness pattern emerges from species sorting process over short environmental gradients ranging from suitable to marginal conditions (e.g., sandy to muddy sediments). Yet, a gradient that ranges between two distinct but suitable conditions (e.g., marine to freshwater) will result in turnover (Svenning et al. 2011; Appendix S2: Fig. S6). We show that increasing the spatial scale of the study will encompass larger variation of suitable conditions, involving more than one species pool (Patterson and Brown 1991, Cutler 1998, Svenning et al. 2011) and increasing the relative importance of species turnover and the reduction in nestedness.

ACKNOWLEDGMENTS

We thank to André Francisco and Israel Valgas for their invaluable assistance in the field work and Márcia Kurtz for helping with granulometric analysis. A. Menegotto was supported by the 'Artigo 170' scholarship program from Santa Catarina State, and S. A. Netto by the Brazilian National Council for Scientific and Technological Development (CNPq).

LITERATURE CITED

- Arellano, G., J. S. Tello, P. M. Jørgensen, A. F. Fuentes, M. I. Loza, V. Torrez, and M. J. Macia. 2016. Disentangling environmental and spatial processes of community assembly in tropical forests from local to regional scales. *Oikos* 125:326–335.
- Barton, P. S., S. A. Cunningham, A. D. Manning, H. Gibb, D. B. Lindenmayer, and R. K. Didham. 2013. The spatial scaling of beta diversity. *Global Ecology and Biogeography* 22:639–647.
- Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* 19:134–143.
- Baselga, A., D. Orme, S. Villeger, J. De Bortoli, and F. Leprieux. 2018. betapart: partitioning beta diversity into turnover and nestedness components. R package version 1.5.0. <https://CRAN.R-project.org/package=betapart>
- Belyea, L., and J. Lancaster. 1999. Assembly rules within a contingent ecology. *Oikos* 86:402–416.
- Bivand, R. 2018. Spatial dependence: weighting schemes, statistics and models. R package version 0.7–7. <https://CRAN.R-project.org/package=spdep>
- Blanchet, F. G., P. Legendre, and D. Borcard. 2008. Forward selection of explanatory variables. *Ecology* 89:2623–2632.
- Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73:1045–1055.
- Cao, P., J. T. Wang, H. W. Hu, Y. M. Zheng, Y. Ge, J. P. Shen, and J. Z. He. 2016. Environmental filtering process has more important roles than dispersal limitation in shaping large-scale prokaryotic beta diversity patterns of grassland soils. *Microbial Ecology* 72:221–230.
- Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences USA* 104:17430–17434.
- Cognetti, G. 1982. Adaptive strategy of brackish-water fauna in pure and polluted waters. *Marine Pollution Bulletin* 13:247–250.

- Cognetti, G., and F. Maltagliata. 2000. Biodiversity and adaptive mechanisms in brackish water fauna. *Marine Pollution Bulletin* 40:7–14.
- Cutler, A. H. 1998. Nested patterns of species distribution: processes and implications. Pages 212–231 in M. L. McKinney and J. A. Drake, editors. *Biodiversity dynamics: turnover of populations, taxa, and communities*. Columbia University Press, New York, New York, USA.
- de Bello, F., S. Lavorel, S. Laverigne, C. H. Albert, I. Boulangeat, F. Mazel, and W. Thuiller. 2013. Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. *Ecography* 36:393–402.
- Dobrovolski, R., A. S. Melo, F. A. S. Cassemiro, and J. A. F. Diniz-Filho. 2012. Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* 21:191–197.
- Dray, S. 2013. *spacemakeR: spatial modelling*. R package version 0.0-5. https://r-forge.r-project.org/R/?group_id=195
- Dray, S. et al. 2012. Community ecology in the age of multivariate multiscale spatial analysis. *Ecological Monographs* 82:257–275.
- Duan, M., Y. Liu, Z. Yu, J. Baudry, L. Li, C. Wang, and J. C. Axmacher. 2016. Disentangling effects of abiotic factors and biotic interactions on cross-taxon congruence in species turnover patterns of plants, moths and beetles. *Scientific Reports* 6:23511.
- Fernandez-Goñi, B. M., S. P. Harrison, B. L. Anacker, and H. D. Safford. 2013. Climate interacts with soil to produce beta diversity in Californian plant communities. *Ecology* 94:2007–2018.
- Gianuca, A. T., S. A. J. Declerck, P. Lemmens, and L. De Meester. 2016. Effects of dispersal and environmental heterogeneity on the replacement and nestedness components of β -diversity. *Ecology* 98:525–533.
- Goslee, S. 2017. *ecodist: dissimilarity-based functions for ecological analysis*. R package version 2.0.1. <https://CRAN.R-project.org/package=ecodist>
- Hill, M. J., J. Heino, I. Thornhill, D. B. Ryves, and P. J. Wood. 2017. Effects of dispersal mode on the environmental and spatial correlates of nestedness and species turnover in pond communities. *Oikos* 126:1575–1585.
- HilleRisLambers, J., P. B. Adler, W. S. Harpole, J. M. Levine, and M. M. Mayfield. 2012. Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics* 43:227–248.
- Hohaia, A., K. Vopel, and C. A. Pilditch. 2014. Thin terrestrial sediment deposits on intertidal sandflats: effects on pore-water solutes and juvenile bivalve burial behaviour. *Biogeosciences* 11:2225–2235.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Josefson, A. B. 2016. Species sorting of benthic invertebrates in a salinity gradient—importance of dispersal limitation. *PLoS ONE* 11:e0168908.
- Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* 3:157–164.
- Legendre, P., and L. Legendre. 2012. *Numerical ecology*. Third edition. Elsevier, Amsterdam, The Netherlands.
- Lohrer, A. M., S. F. Thrush, J. E. Hewitt, K. Berkenbusch, M. Ahrens, and V. J. Cummings. 2004. Terrestrially derived sediment: response of marine macrobenthic communities to thin terrigenous deposits. *Marine Ecology Progress Series* 273:121–138.
- Lundquist, C. J., S. F. Thrush, J. E. Hewitt, J. Halliday, I. MacDonald, and V. J. Cummings. 2006. Spatial variability in recolonisation potential: influence of organism behaviour and hydrodynamics on the distribution of macrofaunal colonists. *Marine Ecology Progress Series* 324:67–81.
- Magni, P., S. Micheletti, D. Casu, A. Floris, G. Giordani, A. N. Petrov, G. De Falco, and A. Castelli. 2005. Relationships between chemical characteristics of sediments and macrofaunal communities in the Cabras lagoon (Western Mediterranean, Italy). *Hydrobiologia* 550:105–119.
- Medeiros, C. R., L. U. Hepp, J. Patrício, and J. Molozzi. 2016. Tropical estuarine macrobenthic communities are structured by turnover rather than nestedness. *PLoS ONE* 11:e0161082.
- Mestdaghe, S., L. Bagaço, U. Braeckman, T. Ysebaert, B. De Smet, T. Moens, and C. Van Colen. 2018. Functional trait responses to sediment deposition reduce macrofauna-mediated ecosystem functioning in an estuarine mudflat. *Biogeosciences* 15:2587–2599.
- Nanami, A., H. Saito, T. Akita, K. Motomatsu, and H. Kuwahara. 2005. Spatial distribution and assemblage structure of macrobenthic invertebrates in a brackish lake in relation to environmental variables. *Estuarine, Coastal and Shelf Science* 63:167–176.
- Netto, S. A., P. R. Pagliosa, A. Colling, A. L. Fonseca, and K. M. Brauko. 2018. Benthic estuarine assemblages from the Southern Brazilian Marine Ecoregion. Pages 177–212 in P. C. Lana and A. F. Bernardino, editors. *Brazilian estuaries: a benthic perspective*. Springer, Cham, Switzerland.
- Oksanen, J. et al. 2018. *vegan: community ecology package*. Package version 2.5-3. <http://CRAN.R-project.org/package=vegan>
- Patterson, B. D., and J. H. Brown. 1991. Regionally nested patterns of species composition in granivorous rodent assemblages. *Journal of Biogeography* 18:395–402.
- Pilditch, C. A., S. Valanko, J. Norkko, and A. Norkko. 2015. Post-settlement dispersal: the neglected link in maintenance of soft-sediment biodiversity. *Biology Letters* 11:20140795.
- Poff, N. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* 16:391–409.
- R Core Team. 2018. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org
- Rivera-Ingraham, G. A., and J. H. Lignot. 2017. Osmoregulation, bioenergetics and oxidative stress in coastal marine invertebrates: raising the questions for future research. *Journal of Experimental Biology* 220:1749–1760.
- Sanders, H. L. 1968. Marine benthic diversity: a comparative study. *American Naturalist* 102:243–282.
- Siefert, A. et al. 2012. Scale dependence of vegetation-environment relationships: a meta-analysis of multivariate data. *Journal of Vegetation Science* 23:942–951.
- Simpson, G. G. 1943. Mammals and the nature of continents. *American Journal of Science* 241:1–31.
- Soininen, J., J. Heino, and J. Wang. 2018. A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecology and Biogeography* 27:96–109.
- Stevens, P. M. 1987. Response of excised gill tissue from the New Zealand scallop *Pecten novaezelandiae*. *New Zealand Journal of Marine and Freshwater Research* 21:605–614.
- Svenning, J. C., C. Fløjgaard, and A. Baselga. 2011. Climate, history and neutrality as drivers of mammal beta diversity in Europe: insights from multiscale deconstruction. *Journal of Animal Ecology* 80:393–402.

- Telesh, I. V., and V. V. Khlebovich. 2010. Principal processes within the estuarine salinity gradient: a review. *Marine Pollution Bulletin* 61:149–155.
- Teske, P. R., and T. H. Wooldridge. 2003. What limits the distribution of subtidal macrobenthos in permanently open and temporarily open/closed South African estuaries? Salinity vs. sediment particle size. *Estuarine, Coastal and Shelf Science* 57:225–238.
- Woodroffe, C. D. 2002. *Coasts: form, process and evolution*. Cambridge University Press, Cambridge, UK.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2721/supinfo>

DATA AVAILABILITY

Data and R scripts are available on Zenodo: <https://doi.org/10.5281/zenodo.2588430>