Storm effects on intertidal invertebrates: increased beta diversity of few individuals and species

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Climate change is predicted to lead to more extreme weather events, including changes to storm frequency, intensity and location. Yet, the ecological responses to storms are incompletely understood for sandy shorelines, the globe's longest land-ocean interface. Here we document how storms of different magnitude impacted the invertebrate assemblages on a tidal flat in Brazil. We specifically tested the relationships between wave energy and spatial heterogeneity, both for habitat properties (habitat heterogeneity) and fauna (β -diversity), predicting that larger storms redistribute sediments and hence lead to spatially less variable faunal assemblages. The sediment matrix tended to become less heterogeneous across the flat after high-energy wave events, whereas β -diversity increased after storms. This higher β -diversity was primarily driven by species losses. Significantly fewer species at a significantly lower density occurred within days to weeks after storms. Negative density and biomass responses to storm events were most prominent in crustaceans. Invertebrate assemblages appeared to recover within a short time (weeks to months) after storms, highlighting that most species typical of sedimentary shorelines are, to some degree, resilient to short-term changes in wave energy. Given that storm frequency and intensity are predicted to change in the coming decades, identifying properties that determine resilience and recovery of ecosystems constitute a research priority for sedimentary shorelines and beyond.



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26 Abstract

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- 28 Climate change is predicted to lead to more extreme weather events, including changes to storm
- 29 frequency, intensity and location. Yet, the ecological responses to storms are incompletely understood for
- 30 sandy shorelines, the globe's longest land-ocean interface. Here we document how storms of different
- 31 magnitude impacted the invertebrate assemblages on a tidal flat in Brazil. We specifically tested the
- 32 relationships between wave energy and spatial heterogeneity, both for habitat properties (habitat
- heterogeneity) and fauna (β -diversity), predicting that larger storms redistribute sediments and hence lead
- 34 to spatially less variable faunal assemblages. The sediment matrix tended to become less
- 35 heterogeneous across the flat after high-energy wave events, whereas β -diversity increased after storms.
- 36 This higher β -diversity was primarily driven by species losses. Significantly fewer species at a
- 37 significantly lower density occurred within days to weeks after storms. Negative density and biomass
- 38 responses to storm events were most prominent in crustaceans. Invertebrate assemblages appeared to
- 39 recover within a short time (weeks to months) after storms , highlighting that most species typical of
- 40 sedimentary shorelines are, to some degree, resilient to short-term changes in wave energy. Given that
- 41 storm frequency and intensity are predicted to change in the coming decades, identifying properties that
- 42 determine resilience and recovery of ecosystems constitute a research priority for sedimentary shorelines
- 43 and beyond.
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47 1. Introduction

48

49 Extreme weather events, including changes to storm frequency and intensity, are predicted to increase 50 over the 21st century (IPCC 2013, Lin and Emanuel 2016, Walsh et al. 2016). These global changes to 51 ecosystem physical and chemical conditions are having numerous and widespread biological impacts in 52 the sea and on land (Weatherdon et al. 2016). In the global oceans, climate change is expected to 53 substantially alter the provision of ecosystems services critical to humankind, such as coastal protection 54 and capture fisheries (Gattuso et al. 2015), but many responses in marine ecoystems still remain 55 incompletely understood (Hauser et al. 2016, Nagelkerken and Munday 2016). 56 57 Storms may cause massive changes to coastal environments, particularly on sedimentary shorelines 58 (Mateo and Garcia-Rubies 2012), often causing the translocation of sediment from the beach and dunes, 59 and the landwards movement of the coastline (Masselink et al. 2016). These large habitat changes are 60 usually accompanied by impacts to faunal assemblages, best documented for benthic invertebrates, 61 seagrass meadows, and algal communities (Lucrezi et al. 2010, Jaramillo et al. 2012, Mateo and Garcia-62 Rubies 2012). 63 64 The unpredictable nature of storms generally precludes the use of a rigorous experimental design to 65 specifically test for storm effects, meaning that nearly all published 'storm studies' are largely 66 opportunistic (Harris et al. 2011). In addition, often only a few or no data points are available immediately 67 before a storm, post-storm sampling can be truncated, and for large storms it is challenging or impossible 68 to find control areas that were not affected by the event (Posey et al. 1996); arguably, this makes 69 attribution of ecological patterns to storm effects somewhat weak. An alternative is to make a priori 70 predictive hypotheses based on knowledge of the biology of species and their likely response to large 71 disturbance events in their habitat (Harris et al. 2011). 72 73 Here, we combine oceanographic, sedimentary and biological data to investigate how storms can affect 74 the sedimentary habitat of a tidal flat in Southeast Brazil and the macrobenthic assemblages inhabiting it. 75 Specifically, we tested four complementary, predictive hypotheses: 76 77 1. Higher wave energy during storms may translocate and disperse large sediment volumes 78 (Masselink et al. 2016). We therefore predict that habitat heterogeneity (i.e. the spatial variation in 79 seafloor properties amongst sampling sites) would be reduced after storms. 80 81 Habitat heterogeneity can be a major determinant for ecological assemblages, typically promoting 82 beta diversity (i.e. variability in species composition among sampling units for a given area)



83 (Anderson et al. 2006, Schlacher et al 2007, McClain and Barry 2010, Meager et al. 2011). 84 Therefore, we expect that storms lower beta diversity of the fauna. 85 86 Disturbance caused by storms has been reported to detrimentally affect populations of benthic 87 species (Jaramillo et al. 1987, Mateo and Garcia-Rubies 2012). Accordingly, we expect lower 88 species richness, abundance, and biomass of invertebrates after storms. 89 90 Given that we expect lower β-diversity (prediction 2) and reduced number of species after storms 91 (prediction 3), we predict that changes in β -diversity may be mainly attributable to species losses 92 rather than species replacement. 93

- 94 2. Material and Methods
- 95

96 2.1 Study area

97 This study was done on the intertidal flats of Araçá Bay (Brazil, 23° 49'S, 45° 24'W; Fig. 1), a sheltered 98 and heterogeneous intertidal flat adjacent to the São Sebastião Channel, Southeast Brazil (Amaral et al. 99 2010). The area is relatively small (ca. 750 m wide and long) and protected from the prevailing swell by 100 São Sebastião Island (Fig. 1). It is one of few tide-dominated environments along the southeastern coast 101 of Brazil (Dottori et al. 2015). Hydrographic properties of Aracá Bay are subject to physical forcing by 102 frontal systems, when current speeds can increase eightfold (Fo 1990). At the region, the highest storm 103 waves are associated to cold fronts and reaching offshore significant wave heights of 6.4m (Pianca et 104 al.2010).



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108 109 2.2 Field sampling 110 Field work was done during spring tides on four times, at ca. three month intervals, from September 2011 111 to July 2012 (25 September 2011, 5 February 2012, 7 May 2012, and 29 July 2012). Three storm events occurred during the study (22 November 2011, 06 May 2012, 18 July 2012; Fig. 2), all accompanied by 112 113 torrential rain, strong winds, flooding, and building damages. We sampled on the first spring tide after the 114 storms in May and July 2012 (one-day lag in May and 11 days in July). 115 116 During each sampling event, field work was done early in the morning of two consecutive days, collecting 117 fauna from 34 sites. The sampling sites were positioned to encompass habitat diversity of the tidal flat 118 (i.e. different sediment types over a range of depths), and to achieve a reasonable dispersion and spatial 119 coverage (Fig. 1). The position of each sampling site was recorded with a GPS (Garmin eTrex Legend, 120 datum WGS84) and the same locations (+/- 1 m) were sampled during each of the four sampling events. 121 Three faunal samples (corer: 20 cm inner diameter, 20 cm depth) and one sediment sample (corer: 3 cm 122 inner diameter, 20 cm deep) were collected per site and event. 123 124 2.2 Biological and environmental data 125 Fauna cores were washed on the same day of collection through a 0.3 mm mesh sieve, and the retained 126 fauna was fixed in 70% ethanol. Sediment granulometric analysis was performed with standard dry 127 sieving described by Suguio (1973). Sediment statistics were calculated with SysGran software (Camargo 128 2006) using the parameters of Folk and Ward (1957). Organic matter content was determined by weight 129 losses of dried samples (60°C for 24 h) after incineration (550°C for 6 h). Calcium carbonate content was 130 determined by 10% HCl digestion.

Fig. 1 Map showing the location of the study area (a) and the sampling sites in the intertidal area of Aracá Bay (b).

131

Sediment temperature and interstitial water salinity were measured *in situ* with a digital thermometer and an analog refractometer (precision of 0.01 and 0.1 units, respectively). Wave height and period for the region were obtained for 24.5 S and 45.5 W from the global wave generation model WaveWatch III (NCEP/NOAA). Wave power (P_w) was calculated as: $P_w = \rho g^2 H^2 T / 32\pi$, where ρ is water density (1,027 kg/m³), g the acceleration due to gravity (9.81 m/s²), H the wave height (m), and T the wave period (s) (Herbich 2000). We considered wave height and power for the three days before each sampling event. This time lag was found to show the strongest correlation between wave height/power and changes in macrobenthic species in the area (Turra et al. 2016).

- 139 140
- 141 All work was done in accordance with permit No. 19887-1 issued by the federal environmental agency,
- 142 Ministério do Meio Ambiente, Instituto Chico Mendes de Conservação da Biodiversidade (ICM-Bio).
- 143

144 2.3 Data analysis

145 We tested for differences in habitat heterogeneity and fauna β -diversity amongst times with permutational 146 analysis of multivariate dispersion (PERMDISP, Anderson 2006). In this analysis, higher multivariate 147 dispersion is an indication of higher variability (i.e., higher habitat heterogeneity and β -diversity) among 148 sampling sites (Anderson 2006). For habitat heterogeneity, the test was based on Euclidean distances 149 calculated from normalized sediment data. For fauna β -diversity, the test was based on Hellinger 150 transformation (Legendre and De Cáceres 2013) calculated from abundance data for the full suite of 151 species. PERMDISP analysis was done using Primer 6 software (Clarke and Gorley 2006). Ordination 152 plots (nMDS) were computed with the vegan package in R (Oksanen 2017) to illustrate differences in 153 habitat heterogeneity and β -diversity (i.e. dispersion of sampling sites) between sampling events. 154 155 We tested for differences in species richness, abundance and biomass of invertebrate assemblages 156 amongst times using general linear models with 'Time' as fixed factors. Models were adjusted using the 157 negative binomial distributions for count data (species richness and abundance) and gamma distributions 158 for continuous data (biomass). We used Tukey post-hoc tests to examine differences among sampling 159 times using the MASS package in R (Ripley et al. 2013). This framework was used to investigate 160 differences in the whole assemblage and also in the main groups of intertidal macrofauna (i.e., molluscs,

- 161 polychaetes and crustaceans) separately.
- 162

We used the Similarity percentage analysis (SIMPER) based on Bray-Curtis distance to investigate thecontribution of each individual species to the differences in species assemblages among sampling

165 periods. Data was log(x+1) transformed before analysis to reduce influence of abundant species.

166 SIMPER was done in Primer 6 software (Clarke and Gorley 2006).

167

168 We used the β -diversity partitioning framework of Podani and Schmera(2011) and Carvalho et al. (2012)

169 to investigate compositional changes of macrobenthos (i.e. β -diversity) over time. This framework

- 170 calculates compositional differences among communities (β_{total}) and partitions it into β diversity attributed
- 171 to species replacement (β_{repl}) and β diversity attributed to species loss or gain (β_{rich}). This analysis was
- 172 done with the R package BAT (Cardoso et al. 2015)
- 173

174 **3. Results**

175

Seawater temperature varied seasonally, whereas salinity and organic matter content of the sediment changed relatively little over time (Table 1). The silt-, clay-, and fine sand fraction of the sediment increased between Sep. 2011 and July 2012 (Table 1). Waves were higher and more powerful before samplings in May and July 2012 (Table 1, Fig. 2).

180

181 **Table 1.** Environmental parameters recorded.

	September 2011	February 2012	May 2012	July 2012
	mean (se)	mean (se)	mean (se)	mean (se)
Temperature (°C)	21.9 (0.2)	27.4 (0.2)	25.0 (0.2)	20.4 (0.1)
Salinity	32.3 (0.3)	31.7 (0.9)	30.6 (0.7)	29.9 (0.6)
Mean grain size (ϕ)	2.5 (0.7)	2.7 (0.7)	2.7 (0.5)	2.8(0.64)
Silt and clay (%)	4.2 (0.6)	4.7 (0.6)	4.8 (0.6)	5.7 (0.9)
Fine sand (%)	68.4 (3.2)	73.5 (3.2)	74.1 (3.8)	74.7 (3.1)
Coarse sand (%)	10.7 (1.6)	9.5 (1.7)	7.9 (1.3)	7.3 (1.6)
Pebbles (%)	6.2 (1.4)	3.7 (1.1)	3.2 (0.9)	3.2 (1.0)
Organic matter (%)	1.6 (0.1)	1.7 (0.2)	1.7 (0.2)	1.9 (0.2)
CaCO ₃ (%)	4.9 (0.4)	4.4 (0.4)	3.8 (0.5)	3.5(0.3)
Height of waves (m)	1.5 (0.06)	1.6 (0.04)	2.1 (0.11)	1.7 (0.04)
Power of waves (10 ⁴ W/s)	20.1 (1.7)	18.1 (7.3)	42.8 (5.3)	30.4 (3.4)





187 We recorded 126 species from 33,320 individuals during the study (supplementary data). Polychaetes,

188 molluscs and crustaceans made up 94% of species (polychaetes: 67 species; molluscs: 34 species;

189 crustaceans: 18 species). Crustaceans were the most abundant group, comprising 56.5% of all

190 individuals, mainly because of the high number of the tanaidacean Monokalliapseudes schubartti (Mañé-

191 Garzón, 1949); polychaetes made up 39.6%, and molluscs 3.7% of catches (supplementary data).

192

193 H1: Lower habitat heterogeneity after storms

194 Sediment properties were spatially more homogeneous after periods of higher wave power (Fig. 3a), but

195 differences between sampling times were not significant (Fig. 4a; PERMDISP P = 0.586).

Fig. 2 Wave height (a) and wave power (b) during the study period (sampling events are shown by dots. Red dots
 correspond to storm sampling events).

¹⁸⁶









Fig. 4 Habitat heterogeneity (a) and β -diversity of macrobenthic assemblages (b) during four sampling events associated with significant variation in wave energy preceding each event. Measure of habitat heterogeneity and β -diversity is the distance from centroids across all sites at a time. Letters and colours denote different groups (P<0.05) in permutational analysis of multivariate dispersion (PERMDISP). Error bars denote standard errors.

210 H2: *B*-diversity declines after storms due to more homogenous sediment matrix.

211 Macrobenthic assemblages showed a significantly higher β diversity following periods of higher wave

212 power (Fig. 3b and 4b; PERMDISP P = 0.001). Species that contributed most to differences in

213 macrobenthic assemblages among sampling periods are listed in Table 2 & 3. Storm effects appear to be

214 driven mainly by large declines in the abundance of the tanaid Monokalliapseudes schubartti, whereas

215 polychaetes (i.e. Capitella sp.C, Heteromastus filiformis, Armandia hossfeldi) tended to increase in

- abundance following storm events (Tables 2 & 3).
- 217

218 **Table 2.** Similarity percentage (SIMPER) analysis showing the contribution (%) of the five most important species to

219	differences	in species	assemblages	among	sampling	periods
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	Monokalliapseudes Schubarti	<i>Capitella</i> sp. C	Heteromastus filiformis	Scoloplos sp1	Armandia hossfeldi	Mean dissimilarity
Sep vs. Feb	10.98	4.96	n/a	5.34	n/a	68.1
Sep vs. May	11.14	6.55	n/a	5.46	n/a	74.9
Sep vs. Jul	9.65	6.85	5.51	5.27	6.47	69.3
Feb vs. May	16.03	8.17	5.04	5.44	n/a	75.3
Feb vs. Jul	12.75	7.9	5.9	5.37	7.24	71.6
May vs. Jul	8.29	8.97	6.63	6.22	8.04	69.9

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Table 3. Temporal variation in the density (ind.m⁻²) of species that accounted for most of the assemblage-wide

September 2011	February 2012	May 2012	July 201 <i>2</i>
mean (se)	mean (se)	mean (se)	mean (se)
2151 (635)	3264 (571)	1776 (79)	538 (276)
114 (68)	521 (257)	667 (428)	768 (336)
23 (9)	32 (11)	47 (12)	133 (36)
112 (30)	63 (14)	35 (10)	87 (19)
50 (25)	7 (4)	47 (19)	224 (74)
	September 2011 mean (se) 2151 (635) 114 (68) 23 (9) 112 (30) 50 (25)	September February 2011 2012 mean (se) mean (se) 2151 (635) 3264 (571) 114 (68) 521 (257) 23 (9) 32 (11) 112 (30) 63 (14) 50 (25) 7 (4)	SeptemberFebruaryMay201120122012mean (se)mean (se)mean (se)2151 (635)3264 (571)1776 (79)114 (68)521 (257)667 (428)23 (9)32 (11)47 (12)112 (30)63 (14)35 (10)50 (25)7 (4)47 (19)

225 differences in macrobenthic assemblages among sampling events (cf. Table 2).

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228 H3: Storm disturbance results in lower abundance, biomass, and species richness

229 Abundance, species richness and biomass were significantly lower in samples taken shortly after high-

230 energy wave events (Fig. 5). The mean number of species per site was lowest at 9.82 species after the

strongest wave event, compared with 11.82 to 14.35 species at other times (Fig. 5a). Abundance peaked

at 4126 ind.m⁻² in Feb. 2012, declining to 1195 ind.m⁻² after the storm in May 2012 (Fig. 5b). Biomass

233 declined from 6.5 to 3.5 gAFDW.m⁻² between September 2011 and May 2012 (Fig. 5c).

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Fig. 5 Variation in the mean number of species per site (a), mean abundance (b) and mean biomass (c) of
 macrobenthic assemblages at four sampling events associated with significant variation in wave energy preceding
 each event. Letters and colours denote different groups in generalized linear models (P<0.05). Error bars denote
 standard errors.

239

240 All major groups of intertidal macrofauna (i.e. molluscs, polychaetes, crustaceans) were affected by

storms (Fig. 6). The mean number of species per site of all groups was significantly lower after the

242 strongest wave event (P < 0.05) (Fig. 6a-c). Temporal patterns of changes in abundance and biomass

243 did, however, differ between groups. Crustaceans showed the most pronounced density (Fig. 6f) and

244 biomass (Fig. 6i) response, declining strongly after storms. Molluscs showed a broadly similar density

- 245 pattern to crustaceans, albeit being less pronounced (Figs. 6d & 6g), whereas the abundance of
- 246 polychaetes tended to increase following periods of higher wave energy (Figs. 6e & 6h).



Fig. 6 Variation in the mean number of species, abundance, and biomass of molluscs (a, d & g), polychaetes (b, e & h), and crustaceans (c, f & i) at four sampling events associated with significant variation in wave energy preceding each event. Letters and colours denote different groups in generalized linear models (P<0.05). Error bars denote standard errors.

- 252
- 253 H4: Species losses drive most of the change in β -diversity.
- 254 Declines in species numbers accounted for most of temporal β -diversity in the macrobenthos, and its
- 255 contribution was higher shortly after storms (Table 4). By contrast, species replacement was less
- 256 important.
- 257

Table 4 – B–diversity and β –diversity partitioning among sampling periods. Higher values of β –diversity denote

259 greater differences in the composition of species and number of individuals between two consecutive sampling

260 times. Percentages indicate the amount of variation between periods attributable to species losses or species

261 replacement.

	Total β diversity (β_{total})	Species replacement /	Species loss / gain		
		substitution (β _{repl})	richness differences (β _{rich})		
Sep. vs Feb.	0.45	44.4%	56.4%		
Feb. vs May	0.79	16.4 %	83.6 %		
May vs July	0.47	11.7 %	89.3 %		
mean	0.57	24.2 %	76.4 %		

262 263

264 4. Discussion

265

Significant changes in macrobenthic species richness, abundance and biomass in a tropical tidal flat were associated with storms. This resulted in significant changes to fauna β -diversity over time that was mainly attributable to species losses, but not strongly linked to variation in habitat heterogeneity.

269

270 Previous studies about the influence of storms on coastal soft-sediment ecosystems have shown that 271 storms may have stronger impacts on environmental features than on the fauna (e.g. Saloman and 272 Naughton 1984, Cochôa et al. 2006, Alves and Pezzuto 2009, Harris et al. 2011), and that offshore 273 sediment transport is the dominant geo-morphological response of sedimentary shores to increased wave 274 energy (Masselink et al. 2016). These studies were, however, mostly done on exposed ocean beaches, habitats with fewer species that are well adapted to high-energy conditions (Brown 1996, Schlacher et al. 275 276 2008). By contrast, our results showed that under more sheltered conditions, storm impacts were more 277 evident for the fauna than for the environment.

278

279 The observed decrease in the number of species, individuals and biomass of macrobenthic assemblages 280 may have been caused by accretion and redistribution of sediments, burying fauna at some site and 281 winnowing them from others. Waves and currents may suspend fine-grained sediments (Lohrer et al. 282 2006), and alongshore sediment distribution within the same system or accretion of sediment in washover 283 deposit can occur after storms (Masselink et al. 2016). Moreover, Alcantará-Carrió et al. (2017) showed 284 that the seaward transport of terrigenous sediment after intense rains in combination with resuspension of 285 sediments by storm waves and transport by wind-driven currents alter the sedimentary features in the 286 São Sebastião Channel. These hypothesized mechanisms of fauna change are functionally supported by 287 studies showing significant changes to the macrobenthos following sediment deposition and substantial



alterations in hydrodynamic regimes (Jaramillo et al. 2012, Cummings et al. 2003, Rodil et al. 2011,
Schlacher et al. 2012).

290

291 Whilst storms were followed by decreases in species richness in all major groups of the macrobenthos. 292 changes in species richness were more pronounced in crustaceans, which also declined strongly in 293 abundance and biomass. This was mainly a consequence of massive (-95%) declines of the tanaid 294 Monokalliapseudes schubarti. M. schubarti is small (ca. 5 mm) and builds tubes that rarely extend for 295 more than 5 cm into the sediment, possibly making it more susceptible to sediment erosion (Nucci et al. 296 2001). In fact, morphological traits of benthic invertebrates have been suggested to modulate storms 297 impacts (Mateo and Garcia-Rubies 2012), with small-bodied individuals and those with low mobility 298 thought to be more susceptible to storms (Negrello Filho and Lana 2013, Urabe et al. 2013). 299

Fewer species of polychaetes were recorded at lower biomass after storm events. Some species, mostly small and tubiculous forms such as *Isolda pulchella* (Müller in Grube, 1858), were less numerous after storms. By contrast, opportunistic polychaete species (e.g. *Capitella* spp, *Heteromastus filiformis* (Pearson and Rosenberg 1978)) increased in abundance after storms. We did not reccord significant changes in the biomass of molluscs, possibly a consequence of heavier, shelled forms of the macrobenthos being less likely to be displaced by turbublent currents associated with storms. 306

307 The relationship between wave power and changes in macrobenthic fauna metrics approximated in 308 several cases a bell-shaped curve, suggesting a resemblance with the "intermediate disturbance 309 hypothesis" (IDH, Connel 1978); a core prediction of IDH is that at high disturbance levels species 310 intolerant of the disturbance become locally extirpated whereas more intense competition limits species 311 numbers at low disturbance intensity and frequency. Consequently, the highest number of species is 312 expected to occur at intermediate levels of disturbance (but see Fox (2013), Sheil and Burslem (2013), 313 and Huston (2014) for discussions on the validity of the IDH). Arguably, disturbance by wave energy at 314 intermediate levels may have enhanced species richness and productivity at sedimentary coastal 315 ecosystem by reducing competition. Nevertheless, as pointed out by Huston (2014), the causes of high 316 diversity go beyond the simple effects of disturbances slowing the process of competitive exclusion and 317 must include multiple ecological and evolutionary processes. In sedimentary shorelines, especially in 318 sheltered environments, intermediate disturbance caused by waves is expected to increase water 319 circulation processes and may also enhance biodiversity and productivity of macrobenthic assemblages 320 by increasing the amount of food available in the water column, and/or reducing the concentration of 321 nutrients in the sediment, resulting in lower eutrophication processes (Cloern 2001, Corte et al. 2017). 322 323 Storm effects appeared to be influenced by the timing of a storm in relation to the tidal regime. Masselink

324 et al. (2016) found that storms impacts on the south-west coast of England were highest when the peak



325 storm waves coincided with spring high tides. In our study, this was likely the case in May 2012 when the

- 326 height of the storm passed during a spring tide. The observed effects of storms on the macrobenthic
- 327 fauna of Araçá Bay also appeared to be stronger during a short time after storms. We found that
- 328 differences in environmental and biotic characteristics were most pronounced in May 2012, when
- 329 samples were taken one day after the storm had passed.
- 330

331 Most species typical of sedimentary shorelines are, to some degree, adapted to high-energy conditions 332 and hence may recover relatively quickly (e.g. within days to weeks) from most storm events (Harris et al. 333 2011, Schlacher and Thompson 2013; Machado et al. 2016). For example, in a subtropical coastal soft-334 sediment ecosystem in South Brazil, Gallucci and Netto (2004) found that abundance and number of 335 species of macrobenthic organisms declined during the passage of a cold front, but all values were back 336 to pre-frontal conditions within a day. Similarly, Machado et al. (2016) found recovery of macrobenthic 337 assemblages inhabiting tropical ocean exposed beaches within seven weeks of a storm. It is important to 338 emphasize, however, that recovery depends on the magnitude, spatial scale and return frequency of the 339 disturbance events in soft-sediment environments and other marine systems (Lucrezi et al. 2010, Urabe 340 et al. 2013, McClain and Schlacher 2015, Schlacher et al. 2015). The most powerful storms may cause 341 ecological changes that require years to recover and may compromise the spatial and trophic structure of 342 the ecosystems (Jaramillo et al. 1987, Mateo and Garcia-Rubies 2012).

343

344 **5. Conclusion**

345

346 Here we show that storms can cause significant changes to macrobenthic assemblages inhabiting a tidal 347 flat. Decreases in species richness, abundance, and biomass of invertebrate assemblages were related 348 to increases in wave power. Species losses drove changes towards higher β -diversity, but the fauna 349 appeared to recover within a few weeks. Changes in habitat features were comparatively smaller. Given 350 that storm activity, location and intensity are predicted to change over the coming decades in a warming 351 world (Lin and Emanuel 2016, Walsh et al. 2016), ecological changes attributed to altered storm 352 properties are likely. Unfortunately, the functional consequences of altered storm regimes for coastal 353 ecosystems are largely unknown, including the continued provision of ecosystem services such as 354 coastal protection and capture fisheries. Thus, future work shall prioritise investigations of how ecological 355 processes in coastal ecosystems respond to extreme events and which features may determine their 356 resilience and recovery.

357

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365 **References**

- Alcántara-Carrió J, Sasaki DK, de Mahique MM, Taborda R, and de Souza LAP (2017) Sedimentary constraints on
 the development of a narrow deep strait (São Sebastião Channel, SE Brazil). *Geo-Marine Letters*, 1-14.
- Alves ES, and Pezzuto PR (2009) Effect of cold fronts on the benthic macrofauna of exposed sandy beaches with contrasting morphodynamics. *Brazilian Journal of Oceanography* 57:73-94.
- Amaral, A. C. Z., A. E. Migotto, A. Turra & Y. Schaeffer-Novelli, 2010. Araçá: biodiversidade, impactos e ameaças.
 Biota Neotropica 10: 219–264.
- 372 Anderson MJ (2006) Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62:245-253.
- Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. (2006). Multivariate dispersion as a measure of beta
 diversity. *Ecology letters*, *9*: 683-693.
- Anderson MJ, Crist TO, Chase JM, Vellend M, Inouye BD, Freestone AL, Sanders NJ, Cornell HV, Comita LS,
 Davies KF, Harrison SP (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing
 ecologist. *Ecology letters* 14:19-28.
- Brown AC (1996) Behavioural plasticity as a key factor in the survival and evolution of the macrofauna on exposed
 sandy beaches. *Revista Chilena de Historia Natural* 69:469-474.
- Camargo MG (2006) Sysgran: um sistema de código aberto para análises granulométricas do sedimento. *Revista Brasileira de Geociências* 36: 371–378.
- Cardoso P, Rigal F, and Carvalho JC (2015) BAT Biodiversity Assessment Tools, an R package for the
 measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods in Ecology and Evolution* 6:232-236.
- Carvalho JC, Cardoso P, and Gomes P (2012) Determining the relative roles of species replacement and species
 richness differences in generating beta-diversity patterns. *Global Ecology and Biogeography* 21:760-771.
- 387 Clarke KR, Gorley RN (2006) PRIMER V6: user manual-tutorial. Plymouth Marine Laboratory
- Cloern, JE (2001) Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series* 210: 223-253
- Cochôa AR, Lorenzi I, and Borzone aCAA (2006) A Influência da Passagem de uma Frente Meteorológica na
 Distribuição da Macrofauna Bentônica Mesolitoral de uma Praia Arenosa Exposta. *Tropical Oceanography* 34:59-71.
- 392 Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310.
- Corte GN, Coleman RA, Amaral AC (2017) Environmental influence on population dynamics of the bivalve
 Anomalocardia brasiliana. *Estuarine, Coastal and Shelf Science* 187:241-8.
- 395 Cummings V, Thrush S, Hewitt J, Norkko A, and Pickmere S (2003) Terrestrial deposits on intertidal sandflats:
- Sediment characteristics as indicators of habitat suitability for recolonising macrofauna. *Marine Ecology Progress* Series 253:39-54.



- Dottori M, Siegle E, and Castro BM (2015). Hydrodynamics and water properties at the entrance of Araçá Bay,
 Brazil. Ocean Dynamics 65: 1731-1741.
- 400 Fo C (1990) Wind driven currents in the Channel of São Sebastião: winter, 1979. *Boletim do Instituto Oceanográfico* 401 38:111-132.
- 402 Folk,RL and Ward WC (1957) Brazos River Bar: a study in the significance of grain-size parameters. *Journal of* 403 *Sedimentary Petrology* 27: 3–26.
- Fox, J. W. 2013. The intermediate disturbance hypothesis should be abandoned. *Trends in Ecology and Evolution* 28:86–92
- Gallucci F, and Netto SA (2004) Effects of the passage of cold fronts over a coastal site: An ecosystem approach.
 Marine Ecology Progress Series 281:79-92.
- 408 Gattuso JP, Magnan A, Billé R, Cheung WWL, Howes EL, Joos F, Allemand D, Bopp L, Cooley SR, Eakin CM,
- Hoegh-Guldberg O, Kelly RP, Pörtner HO, Rogers AD, Baxter JM, Laffoley D, Osborn D, Rankovic A, Rochette J,
 Sumaila UR, Treyer S, and Turley C (2015) Contrasting futures for ocean and society from different anthropogenic
 CO2 emissions economics Science 240
- 411 CO2 emissions scenarios. *Science* 349.
- 412 Harris L, Nel R, Smale M, and Schoeman D (2011) Swashed away? Storm impacts on sandy beach macrofaunal 413 communities. *Estuarine Coastal and Shelf Science* 94:210-221.
- 414 Hauser DDW, Tobin ED, Feifel KM, Shah V, and Pietri DM (2016) Disciplinary reporting affects the interpretation of 415 climate change impacts in global oceans. *Global Change Biology* 22:25-43.
- 416 Herbich JB (2000) Handbook of coastal engineering. McGraw-Hill, New York
- Huston MA (2014). Disturbance, productivity, and species diversity: empiricism vs. logic in ecological
 theory. *Ecology*, 95:2382-2396.
- 419 IPCC (2013) Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth
- 420 Assessment Report of the Intergovernmental Panel on Climate Change. [Stocker, T.F., D. Qin, G.-K. Plattner, M.
- Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press,
 Cambridge, UK
- 423 Jaramillo E, Croker RA, and Hatfield EB (1987) Long-term structure, disturbance, and recolonization of macroinfauna 424 in a New Hampshire sand beach. *Canadian Journal of Zoology* 65:3024-3031.
- Jaramillo E, Dugan JE, Hubbard DM, Melnick D, Manzano M, Duarte C, Campos C, and Sanchez R (2012)
 Ecological implications of extreme events: Footprints of the 2010 earthquake along the Chilean coast. *PLoS ONE*7:e35348. doi:35310.31371/journal.pone.0035348.
- Legendre P, Cáceres M. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning.
 Ecology Letters. 2013 Aug 1;16(8):951-63.
- 430 Lin N, and Emanuel K (2016) Grey swan tropical cyclones. *Nature Climate Change* 6:106-111.
- 431 Lohrer A M, Hewitt JE, and Thrush SF (2006). Assessing far-field effects of terrigenous sediment loading in the 432 coastal marine environment. *Marine Ecology Progress Series* 315:13-18.
- Lucrezi S, Schlacher TA, and Robinson W (2010) Can storms and shore armouring exert additive effects on sandybeach habitats and biota? *Marine and Freshwater Research* 61:951-962.
- 435 Machado PM, Costa LL, Suciu MC, Tavares DC, and Zalmon IR (2016) Extreme storm wave influence on sandy 436 beach macrofauna with distinct human pressures. *Marine Pollution Bulletin*.



- 437 Masselink G, Scott T, Poate T, Russell P, Davidson M, and Conley D (2016) The extreme 2013/2014 winter storms:
- 438 Hydrodynamic forcing and coastal response along the southwest coast of England. *Earth Surface Processes and* 439 *Landforms* 41:378-391.
- Mateo MA and Garcia-Rubies T (2012). Assessment of the ecological impact of the extreme storm of Sant Esteve's
 Day (26 December 2008) on the littoral ecosystems of the north Mediterranean Spanish coasts. *Final Report (PIEC* 200430E599).
- 443 McClain CR, Barry JP (2010) Habitat heterogeneity, disturbance, and productivity work in concert to regulate 444 biodiversity in deep submarine canyons. *Ecology* 91:964-76.
- 445 McClain CR, and Schlacher TA (2015) On some hypotheses of diversity of animal life at great depths on the sea 446 floor. *Marine Ecology* 36:849-872.
- 447 Meager J, Schlacher TA, and Green M (2011) Topographic complexity and landscape temperature patterns create a 448 dynamic habitat structure on a rocky intertidal shore. Marine Ecology Progress Series 428:1–12.
- Nagelkerken I, and Munday PL (2016) Animal behaviour shapes the ecological effects of ocean acidification and
 warming: Moving from individual to community-level responses. *Global Change Biology* 22:974-989.
- 451 Negrello Filho OA, and Lana PC (2013) Short-term stability of estuarine benthic assemblages: Are storms pattern-452 defining events? *Zoologia* 30:266-272.
- 453 Nucci PR, Turra A., and Morgado EH (2001) Diversity and distribution of crustaceans from 13 sheltered sandy
- 454 beaches along Sao Sebastiao Channel, south-eastern Brazil. *Journal of the Marine Biological Association of the* 455 *United Kingdom* 81:475-484.
- 456 Oksanen J, Kindt R, Legendre P, O'Hara B, Stevens MH, Oksanen MJ, Suggests MA (2007) The vegan package.
 457 Community ecology package.
- Pianca C, Mazzini PL, Siegle E (2010) Brazilian offshore wave climate based on NWW3 reanalysis. Brazilian Journal
 of Oceanography 58:53–70
- Podani J, and Schmera D (2011) A new conceptual and methodological framework for exploring and explaining
 pattern in presence absence data. *Oikos* 120:1625-1638.
- Posey M, Lindberg W, Alphin T, and Vose F (1996) Influence of storm disturbance on an offshore benthic community.
 Bulletin of Marine Science 59:523-529.
- 464 Ripley B, Venables B, Bates DM, Hornik K, Gebhardt A, Firth D, Ripley MB (2013) Package 'MASS'. Cran R.
- Rodil IF, Lohrer AM, Chiaroni LD, Hewitt JE, and Thrush SF (2011) Disturbance of sandflats by thin terrigenous
 sediment deposits: Consequences for primary production and nutrient cycling. *Ecological Applications* 21:416-426.
- Saloman CH, and Naughton SP (1984) Beach restoration with offshore dredged sand: effects on nearshore
 macroinfauna. NOOA Technical Memorandum NMFS-SEFC-133
- 469 Schlacher TA, and Thompson L (2013) Environmental control of community organisation on ocean-exposed sandy 470 beaches. *Marine and Freshwater Research* 64:119-129.
- 471 Schlacher TA, Schoeman DS, Dugan JE, Lastra M, Jones A, Scapini F, and McLachlan A (2008) Sandy beach
- 472 ecosystems: key features, sampling issues, management challenges and climate change impacts. Marine Ecology 29
- 473 (S1):70–90.Schlacher TA, Noriega R, Jones A, and Dye T (2012) The effects of beach nourishment on benthic
- invertebrates in eastern Australia: Impacts and variable recovery. *Science of the Total Environment* 435:411-417.
- 475 Schlacher TA, Weston MA, Schoeman DS, Olds AD, Huijbers CM, and Connolly RM (2015) Golden opportunities: A
- 476 horizon scan to expand sandy beach ecology. Estuarine, Coastal and Shelf Science 157:1-6.



- 477 Sheil D, Burslem DF (2013) Defining and defending Connell's intermediate disturbance hypothesis: a response to
 478 Fox. *Trends in Ecology and Evolution* 28:571-2.
- 479 Turra A, Pombo M, Petracco M, Siegle E, Fonseca M, Denadai MR (2016) Frequency, Magnitude, and Possible
- 480 Causes of Stranding and Mass-Mortality Events of the Beach Clam Tivela mactroides (Bivalvia: Veneridae). PLoS
- 481 ONE 11(1): e0146323. doi:10.1371/journal.pone.0146323
- 482 Urabe J, Suzuki T, Nishita T, and Makino W (2013) Immediate Ecological Impacts of the 2011 Tohoku Earthquake
 483 Tsunami on Intertidal Flat Communities. *PLoS ONE* 8.
- Walsh KJE, McBride JL, Klotzbach PJ, Balachandran S, Camargo SJ, Holland G, Knutson TR, Kossin JP, Lee Tc,
 Sobel A, and Sugi M (2016) Tropical cyclones and climate change. *Wiley Interdisciplinary Reviews: Climate Change*7:65-89.
- Weatherdon LV, Magnan AK, Rogers AD, Sumaila UR, and Cheung WWL (2016) Observed and projected impacts of
 climate change on marine fisheries, aquaculture, coastal tourism, and human health: An update. *Frontiers in Marine Science* 3.
- 490
- 491