Storm effects on intertidal invertebrates: increased beta diversity of few individuals and species (#15810)

First revision

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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 of the fauna 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. Invertebrates assemblages appeared to recover within a short interval (weeks to months) after storms months, 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.

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

2   **species**

3

4   **Short title: Storm effects on intertidal invertebrates**

5

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25

26   **Abstract**

27

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
33   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 of the fauna increased
36   after storms. This higher β-diversity was primarily driven by species losses. Significantly fewer species at
37   a significantly lower density occurred within days to weeks after storms. Negative density and biomass
38   responses to storm events were most prominent in crustaceans. Invertebrates assemblages appeared to
39   recover within a short interval (weeks to months) after storms months, highlighting that most species
40   typical of sedimentary shorelines are, to some degree, resilient to short-term changes in wave energy.
41   Given that storm frequency and intensity are predicted to change in the coming decades, identifying
42   properties that determine resilience and recovery of ecosystems constitute a research priority for
43   sedimentary shorelines and beyond.

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1. Introduction

Extreme weather events, including changes to storm frequency and intensity, are predicted to increase over the 21st century (IPCC 2013, Lin and Emanuel 2016, Walsh et al. 2016). These global changes to ecosystem physical and chemical conditions are having numerous and widespread biological impacts in the sea and on land (Weatherdon et al. 2016). In the global oceans, climate change is expected to substantially alter the provision of ecosystems services critical to humankind, such as coastal protection and capture fisheries (Gattuso et al. 2015), but many responses in marine ecosystems still remain incompletely understood (Hauser et al. 2016, Nagelkerken and Munday 2016).

Storms may cause massive changes to coastal environments, particularly on sedimentary shorelines (Mateo and Garcia-Rubies 2012), often causing the translocation of sediment from the beach and dunes, and the landwards movement of the coastline (Masselink et al. 2016). These large habitat changes are usually accompanied by impacts to faunal assemblages, best documented for benthic invertebrates, seagrass meadows and algal communities (Lucrezi et al. 2010, Jaramillo et al. 2012, Mateo and Garcia-Rubies 2012).

The unpredictable nature of storms generally precludes the use of a rigorous experimental design to specifically test for storm effects, meaning that nearly all published 'storm studies' are largely opportunistic (Harris et al. 2011). In addition, often only a few or no data points are available immediately before a storm, post-storm sampling can be truncated, and for large storms it is challenging or impossible to find control areas that were not affected by the event (Posey et al. 1996); arguably, this makes attribution of ecological patterns to storm effects somewhat weak. An alternative is to make *a priori* predictive hypotheses based on knowledge of the biology of species and their likely response to large disturbance events in their habitat (Harris et al. 2011).

Here, we combine oceanographic, sediment and biological data to investigate how storms can affect the sedimentary habitat of a tidal flat in Southeast Brazil and the macrobenthic assemblages inhabiting it. Specifically, we tested four complementary, predictive hypotheses:

1. Higher wave energy during storms may translocate and disperse large sediment volumes (Masselink et al. 2016). We therefore predict that habitat heterogeneity (i.e. the spatial variation in seafloor properties amongst sampling sites) would be reduced after storms.

2. Habitat heterogeneity can be a major determinant for ecological assemblages, typically promoting 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   3.   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   4.   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, 23º 49'S, 45º 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 Araçá Bay are subject to physical forcing by

102 frontal systems, when current speeds can increase eightfold (Fo 1990). At the region, the highest storm

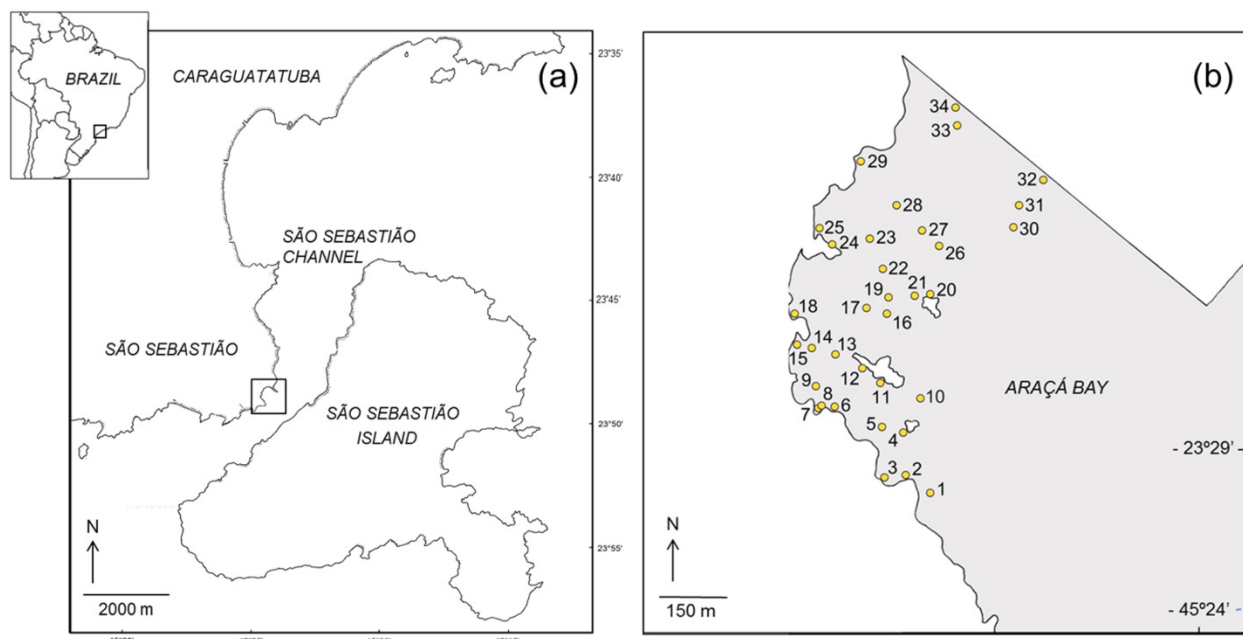103 waves are associated to cold fronts and reaching offshore significant wave heights of 6.4m (Pianca et

104 al.2010).

105

106

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

108

109

2.2 Field sampling

111   Field work was done during spring tides on four times, at ca. three month intervals, from September 2011

112   to July 2012 (25 September 2011, 5 February 2012, 7 May 2012, and 29 July 2012). Three storm events

113   occurred during the study (22 November 2011, 06 May 2012, 18 July 2012; Fig. 2), all accompanied by

114   torrential rain, strong winds, flooding, and building damages. We sampled on the first spring tide after the

115   storms in May and July 2012 (one-day lag in May and 11 days in July).

116

117   During each event, field work was done early in the morning of two consecutive days, collecting fauna

118   from 34 sites. The sampling sites were positioned to encompass habitat diversity of the tidal flat (i.e.

119   different sediment types over a range of depths), and to achieve a reasonable dispersion and spatial

120   coverage (Fig. 1). The position of each sampling site was recorded with a GPS (Garmin eTrex Legend,

121   *datum* WGS84) and the same locations (+/- 1 m) were sampled during each of the four sampling events.

122   Three faunal samples (corer: 20 cm inner diameter, 20 cm depth) and one sediment sample (corer: 3 cm

123   inner diameter, 20 cm deep) were collected per site and event.

124

2.2 Biological and environmental data

126   Fauna cores were washed on the same day of collection through a 0.3 mm mesh sieve, and the retained

127   fauna was fixed in 70% ethanol. Sediment granulometric analysis was performed with standard dry

128   sieving described by Suguio (1973). Sediment statistics were calculated with SysGran software (Camargo

129   2006) using the classifications of Folk and Ward (1957). Organic matter content was determined by

130   weight losses of dried samples (60°C for 24 h) after incineration (550°C for 6 h). Calcium carbonate

131   content was determined by 10% HCl digestion.

132

133   Sediment temperature and interstitial water salinity were measured *in situ* with a digital thermometer and

134   an analog refractometer (precision of 0.01 and 0.1 units, respectively). Wave height and period for the

135   region were obtained for 24.5 S and 45.5 W from the global wave generation model WaveWatch III

136   (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

137   kg/m^3), g the acceleration due to gravity (9.81 m/s^2), H the wave height (m), and T the wave period (s)

138   (Herbich 2000). We considered wave height and power for the three days before each sampling event.

139   This time lag was found to show the strongest correlation between wave height/power and changes in

140   macrobenthic species in the area (Turra et al. 2016).

141

142   All work was done in accordance with permit No. 19887-1 issued by the federal environmental agency,

143   Ministério do Meio Ambiente, Instituto Chico Mendes de Conservação da Biodiversidade.

144

2.3 Data analysis

146 We tested for differences in habitat heterogeneity and fauna β–diversity amongst times with permutational

147 analysis of multivariate dispersion (PERMDISP, Anderson 2006). In this analysis, higher multivariate

148 dispersions is an indication of higher variability (i.e., higher habitat heterogeneity and β–diversity) among

149 sampling sites (Anderson 2006). For habitat heterogeneity, the test was based on Euclidean distances

150 calculated from normalized sediment data. For fauna β–diversity, the test was based on Hellinger

151 transformation (Legendre and De Cáceres 2013) calculated from abundance data for the full suite of

152 species. PERMDISP analysis was done using Primer 6 software (Clarke and Gorley 2006). Ordination

153 plots (nMDS) were computed with the vegan package in R (Oksanen 2017) to illustrate differences in

154 habitat heterogeneity and β–diversity (i.e. dispersion of sampling sites) between sampling events.

155

156 We tested for differences in species richness, abundance and biomass of invertebrate assemblages

157 amongst times using general linear models with 'Time' as fixed factors. Models were adjusted using the

158 negative binomial distributions for count data (species richness and abundance) and gamma distributions

159 for continuous data (biomass). We used Tukey post-hoc tests to examine differences among sampling

160 times using the MASS package in R (Ripley et al. 2013). This framework was used to investigate

161 differences in the whole assemblage and also in the main groups of intertidal macrofauna (i.e., molluscs,

162 polychaetes and crustaceans) separately.

163

164 We used the Similarity percentage analysis (SIMPER) based on Bray-Curtis distance to investigate the

165 contribution of each individual species to the differences in species assemblages among sampling

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

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

168

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

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

171 calculates compositional differences among communities (β_{total}) and partitions it into β diversity attributed

172 to species replacement (β_{repl}) and β diversity attributed to species loss or gain (β_{rich}). This analysis was

173 done with the R package BAT (Cardoso et al. 2015)

174

3. Results

176

177 Seawater temperature varied seasonally, whereas salinity and organic matter content of the sediment

178 changed relatively little over time (Table 1). The silt-, clay-, and fine sand fraction of the sediment

179 increased between Sep. 2011 and July 2012 (Table 1). Waves were higher and more powerful before
180 samplings in May and July 2012 (Table 1, Figure 2).
181

182 **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 (10^4W/s)	20.1 (1.7)	18.1 (7.3)	42.8 (5.3)	30.4 (3.4)

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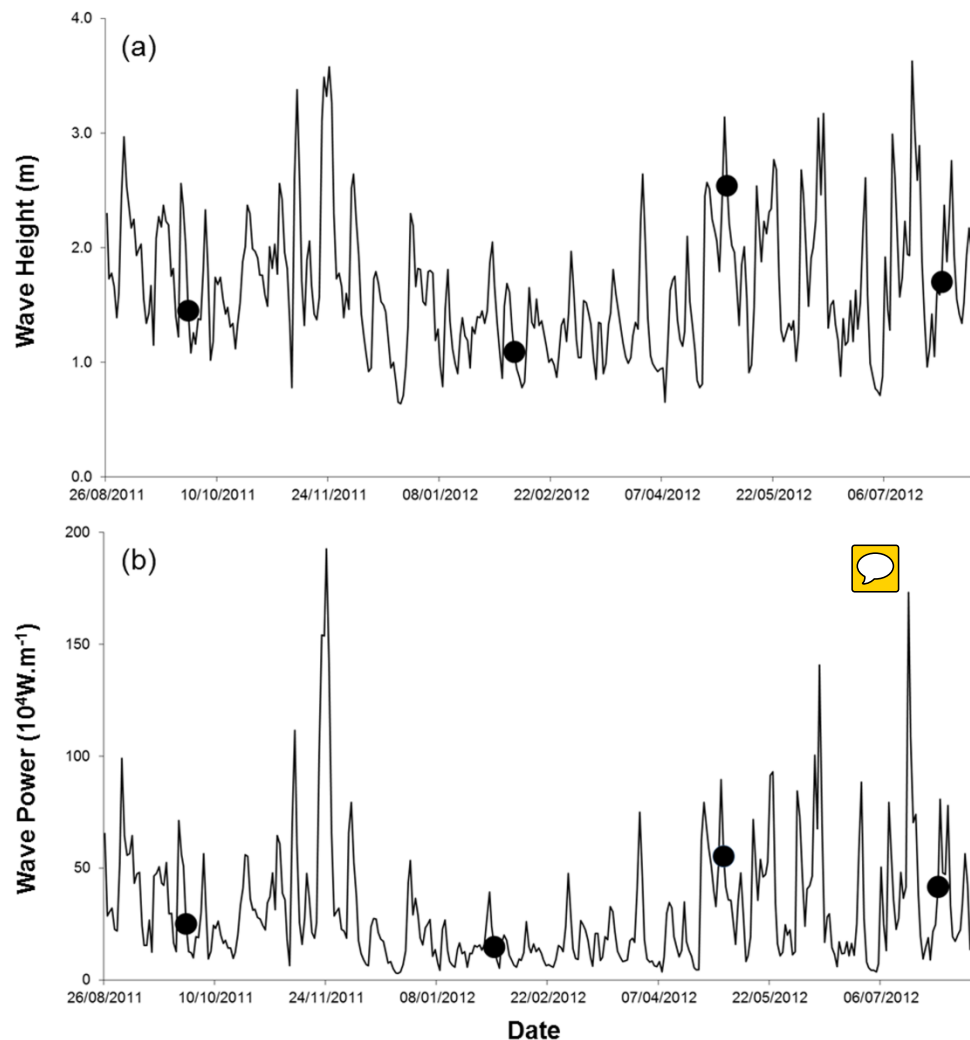
Fig. 2 Wave height (a) and wave power (b) during the study period (sampling events are shown by dots).

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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).
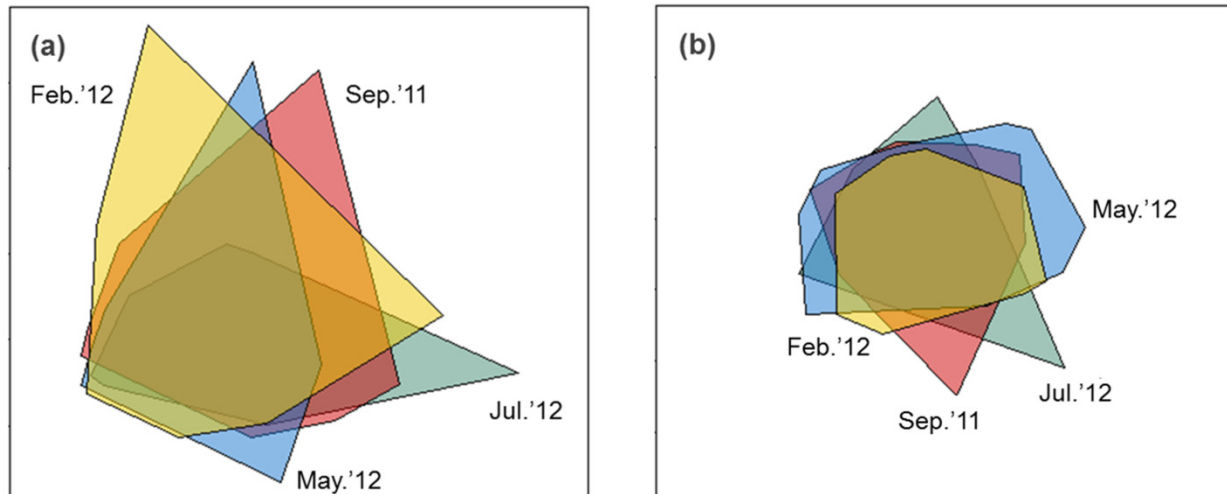
Fig. 3 nMDS biplot of Euclidean distance based normalized environmental data (a) and nMDS biplot of Hellinger disimilarity matrix based on macrobenthic abundance data (b). Samples from September 2011 are located inside the polygon plotted in red, from February 2012 in yellow, from May 2012 in blue, and from July 2012 in green. Stress for these ordination are 0.10 (a) and 0.19 (b).
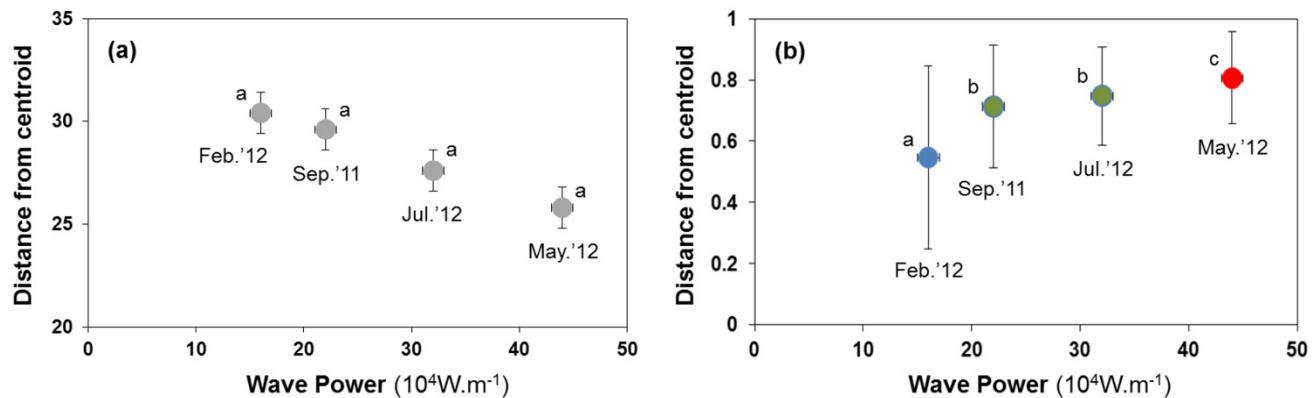
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Fig. 4 Habitat heterogeneity (a) and β–diversity of macrobenthic assemblages (b) during four sampling events
associated with significant variation in wave energy preceding each event. Measure of habitat heterogeneity and
β–diversity is the distance 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.

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H2: Β–diversity declines after storms due to more homogenous sediment matrix.

210

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

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

212

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

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

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

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abundance following storm events (Tables 2 & 3).

216

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

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differences in species assemblages among sampling periods.

219

	Monokalliapseudes Schubarti	*Capitella 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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224 **Table 3.** Temporal variation in the density (ind.m^{-2}) of species that accounted for most of the assemblage-wide

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

	September 2011	February 2012	May 2012	July 2012
	mean (se)	mean (se)	mean (se)	mean (se)
Monokalliapseudes schubartii	2151 (635)	3264 (571)	1776 (79)	538 (276)
Capitella sp.C	114 (68)	521 (257)	667 (428)	768 (336)
Heteromastus filiformis	23 (9)	32 (11)	47 (12)	133 (36)
Scoloplos sp1	112 (30)	63 (14)	35 (10)	87 (19)
Armandia hossfeldi	50 (25)	7 (4)	47 (19)	224 (74)

226

227

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

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

232 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).
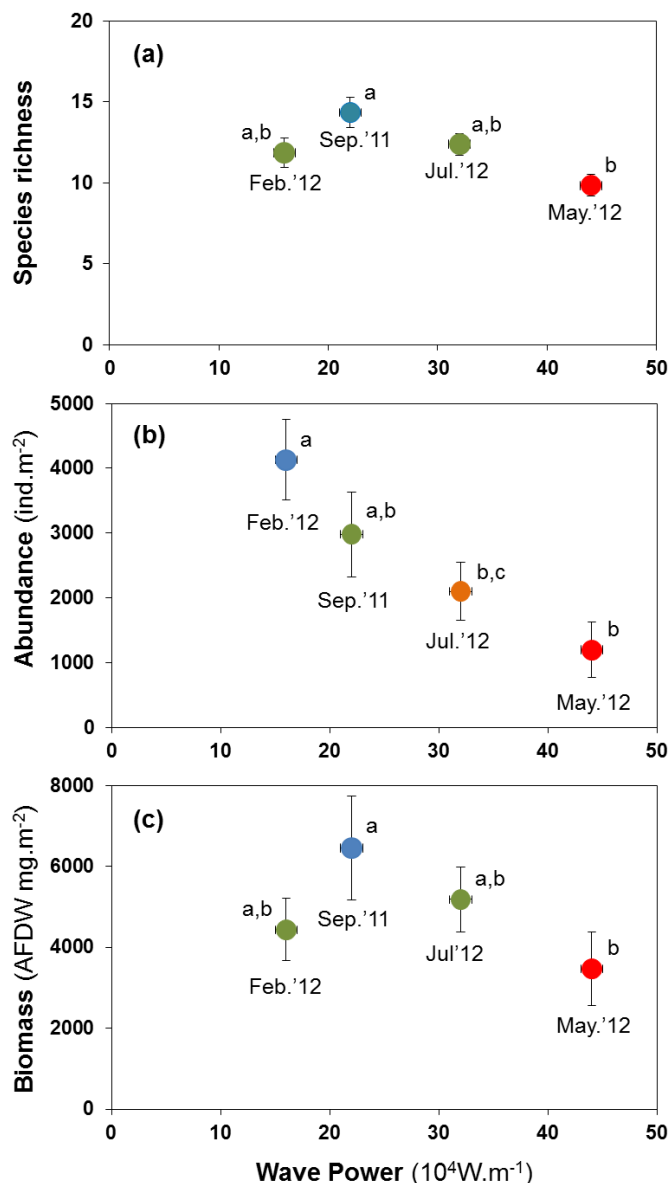
234
235 **Fig. 5** Variation in the mean number of species per site (a), mean abundance (b) and mean biomass (c) of
236 macrobenthic assemblages at four sampling events associated with significant variation in wave energy preceding
237 each event. Letters and colours denote different groups in generalized linear models (P<0.05). Error bars denote
238 standard errors.
239

240 All major groups of intertidal macrofauna (i.e. molluscs, polychaetes, crustaceans) were affected by
241 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).

24
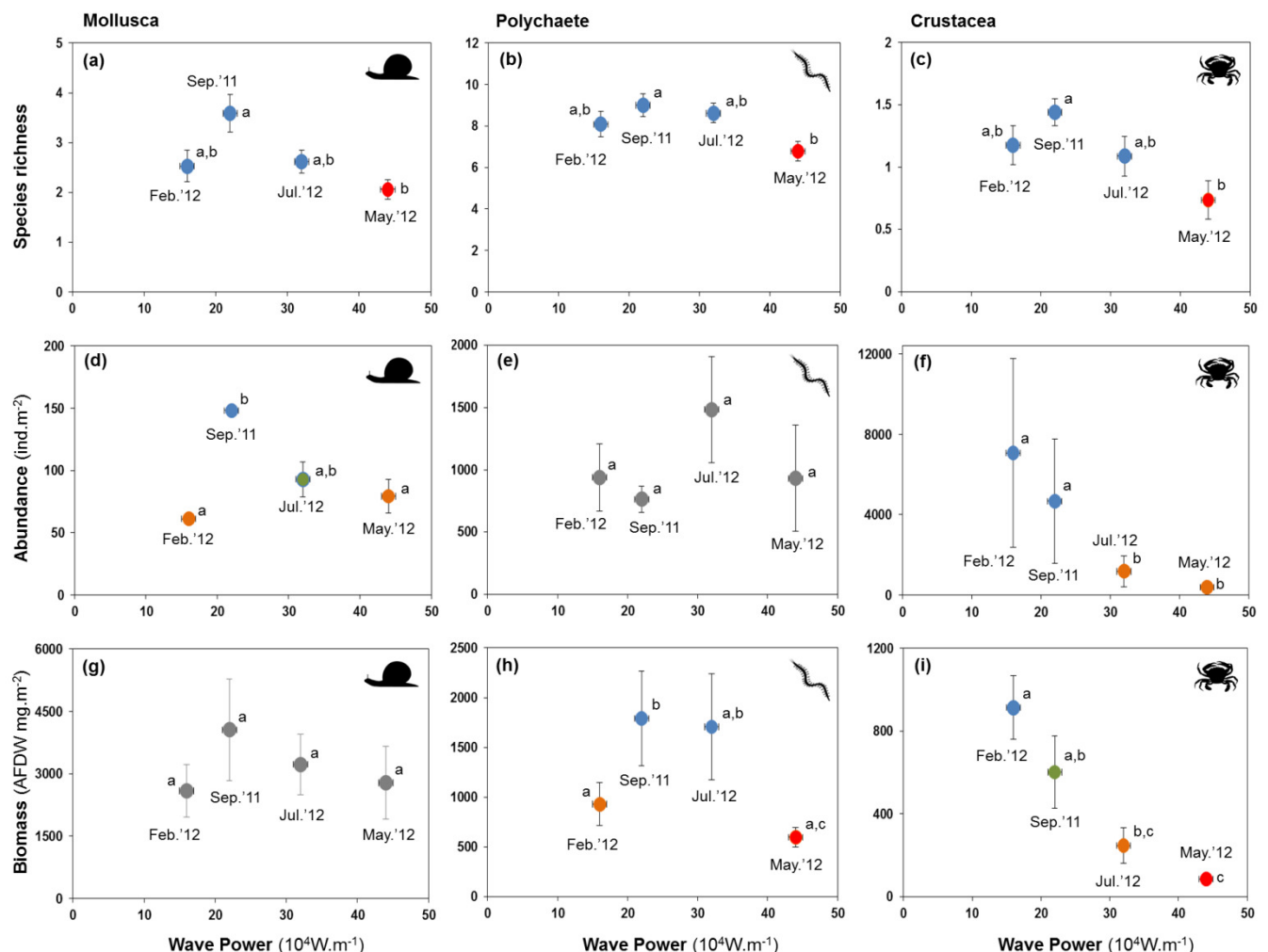
Fig. 6 Variation in the mean number of species, abundance, and biomass of molluscs (a, d & g), polychaetes (b, e & h), and crustaceans (c, f & i) at four sampling events associated with significant variation in wave energy preceding each event. Letters and colours denote different groups in generalized linear models (P<0.05). Error bars denote standard errors.

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254   *H4: Species losses drive most of the change in β–diversity.*

255   Declines in species numbers accounted for most of temporal β–diversity in the macrobenthos, and its

256   contribution was higher shortly after storms (Table 4). By contrast, species replacement was less

257   important.

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264 **Table 4** – Β–diversity and β–diversity partitioning among sampling periods. Higher values of β–diversity denote
265 greater differences in the composition of species and number of individuals between two consecutive sampling
266 times. Percentages indicate the amount of variation between periods attributable to species losses or species
267 replacement.

	Total β diversity (β_{total})	Species replacement / substitution (β_{repl})	Species loss / gain 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 %

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269

4. Discussion

271

272 Significant changes in macrobenthic species richness, abundance and biomass in a tropical tidal flat were
273 associated with temporal variation in wave energy. This resulted in significant changes to fauna
274 β–diversity over time that was mainly attributable to species losses, but, apparently, unlinked to variation
275 in habitat heterogeneity.

276

277 Previous studies about the influence of storms on coastal soft-sediment ecosystems have shown that
278 storms may have stronger impacts on environmental features than on the fauna (e.g. Saloman and
279 Naughton 1984, Cochôa et al. 2006, Alves and Pezzuto 2009, Harris et al. 2011), and that offshore
280 sediment transport is the dominant geo-morphological response of sedimentary shores to increased wave
281 energy (Masselink et al. 2016). These studies, however, were mostly done on exposed ocean beaches,
282 habitats with fewer species that are well adapted to high-energy conditions (Brown 1996, Schlacher et al.
283 2008). By contrast, our results showed that under more sheltered conditions, storm impacts were more
284 evident in the fauna than in the environment.

285

286 The observed decrease in the number of species, individuals and biomass of macrobenthic assemblages
287 may have been caused by accretion and redistribution of sediments, burying fauna at some site and
288 winnowing them at others. Waves and currents may suspend fine-grained sediments (Lohrer et al. 2006),
289 and alongshore sediment distribution within the same system or accretion of sediment in washover

290   deposit can occur after storms (Masselink et al. 2016). Moreover, Alcantará-Carrió et al. (2017) showed
291   that the seaward transport of terrigenous sediment after intense rains in combination with resuspension of
292   sediments by storm waves and transport by wind-driven currents alter the sedimentary features in the
293   São Sebastião Channel. These hypothesized mechanisms mechanisms of fauna change are functionally
294   supported by studies showing significant changes to the macrobenthos following sediment deposition and
295   substantial alterations in hydrodynamic regimes (Jaramillo et al. 2012, Cummings et al. 2003, Rodil et al.
296   2011, Schlacher et al. 2012).
297

298   Whilst storms were followed by decreases in species richness in all major groups of the macrobenthos,
299   richness changes were more pronounced in crustaceans which also declined strongly in abundance and
300   biomass. This was mainly a consequence of massive (-95%) declines of the tanaid *Monokalliapseudes*
301   *schubarti*. *M. schubarti* is small (ca. 5 mm) and builds tubes that rarely extend for more than 5 cm into the
302   sediment, possibly making it more susceptible to sediment erosion (Nucci et al. 2001), In fact,
303   morphological traits of benthic invertebrates have been suggested to modulate storms impacts (Mateo
304   and Garcia-Rubies 2012), with small-bodied individuals and those with low mobility thought to be more
305   susceptible to storms (Negrello Filho and Lana 2013, Urabe et al. 2013).
306

307   Fewer species of polychaetes were recorded at lower biomass after storm events. Some species, mostly
308   small and tubiculous forms, such as the *Isolda pulchella* (Müller in Grube, 1858), were also less
309   numerous after storms. By contrast, opportunistic polychaete species (e.g. *Capitella* sp.C, *Heteromastus*
310   *filiformis* (Pearson and Rosenberg 1978)) increased in abundance after storms. We did not reccord
311   significant changes in the biomass of molluscs, possibly a consequence of heavier, shelled forms of the
312   macrobenthos being less likely to be displaced by turbublent currents associated with storms.
313

314   Storm effects appeared to be influenced by the timing of a storm in relation to the tidal regime. Masselink
315   et al. (2016) found that storms impacts on the south-west coast of England were highest when the peak
316   storm waves coincided with spring high tides. In our study, this was likely the case in May 2012 when the
317   height of the storm passed during a spring tide. The observed effects of storms on the macrobenthic
318   fauna of Araçá Bay also appeared to be stronger during a short time after storms. We found that
319   differences in environmental and biotic characteristics were most pronounced in May 2012, when
320   samples were taken one day after the storm had passed.
321

322   Most species typical of sedimentary shorelines are, to some degree, adapted to high-energy conditions
323   and hence may recover relatively quickly (e.g. within days to weeks) from most storm events (Harris et al.
324   2011, Schlacher and Thompson 2013; Machado et al. 2016). For example, in a subtropical coastal soft-
325   sediment ecosystem in South Brazil, Gallucci and Netto (2004) found that abundance and number of
326   species of macrobenthic organisms declined during the passage of a cold front, but all values were back

327   to pre-frontal conditions 24 h later. Similarly, Machado et al. (2016) found recovery of macrobenthic

328   assemblages inhabiting tropical ocean exposed beaches within seven weeks of a storm. It is important to

329   emphasize, however, that recovery depends on the magnitude, spatial scale and return frequency of the

330   disturbance events in soft-sediment environments and other marine systems (Lucrezi et al. 2010,

331   Urabe et al. 2013, McClain and Schlacher 2015, Schlacher et al. 2015). The most powerful storms may

332   cause ecological changes that require years to recover and may compromise the spatial and trophic

333   structure of the ecosystems (Jaramillo et al. 1987, Mateo and Garcia-Rubies 2012).

334

335   **5. Conclusion**

336

337   Here we show that storms can cause significant changes to macrobenthic assemblages inhabiting a tidal

338   flat. Decreases in species richness, abundance and biomass of invertebrate assemblages were related to

339   increase wave power. Species losses drove changes to higher β–diversity but the fauna appeared to

340   recover within a few weeks. Changes to habitat features were comparatively smaller. Given that storm

341   activity, location and intensity are predicted to change over the coming decades in a warming world (Lin

342   and Emanuel 2016, Walsh et al. 2016), ecological changes attributed to altered storm properties are likely

343   expected. Unfortunately, the functional consequences of altered storm regimes for coastal ecosystems

344   are fundamentally unknown, including the continued provision of ecosystem services such as coastal

345   protection and capture fisheries. Thus, future work shall prioritise investigations of how ecological

346   processes in coastal ecosystems respond to extreme events and which features may determine their

347   resilience and recovery.

348

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354

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