

Macrobenthic Community Changes of Intertidal Sandy Shores after a Mega-Disturbance

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Abstract Large-scale events of destruction and mortality trigger abrupt changes in the structure of natural communities. Testing the magnitude of such effects and the resilience of the impacted communities is difficult, however, because large-scale disturbances are generally unpredictable and thus available data are rare. Here, we studied the spatiotemporal variation of intertidal sandy-shore communities in relation to the Maule earthquake and tsunami that hit the south-eastern Pacific shore on the 27 February 2010. We analysed a dataset of four sampling times conducted over a period of 23 months, in which macrobenthic (>1 mm) species abundances were sampled before and consecutively three times after the Maule earthquake and tsunami took place. Our results indicated that the Maule earthquake and tsunami triggered abrupt and significant changes in species richness, total abundance, and community structure within the southern rupture area. Immediately after the earthquake and tsunami, sites within the southern rupture area of the earthquake showed significant changes in community structure, reaching up to 91 % dissimilarity with the pre-earthquake state. However, this high

dissimilarity gradually decreased throughout time, indicating that the community subsequently tended to return toward its pre-event structure. Accordingly, a statistical model predicting a return toward the initial multivariate structure significantly fitted to our dataset. We suggest that the changes of intertidal sandy-shore communities are the result of the high abundance of species with high mobility and short generation times, producing populations that are highly dynamics. These traits may constitute therefore a negative feedback preventing the establishment of alternative community states after large-scale disturbances.

Keywords Macrofauna · Sandy beaches · Disturbance · Diversity · Functional traits · Earthquake · Tsunami

Introduction

The frequency and intensity of destructive events, such as hurricanes, droughts, and fires, are predicted to increase during the next century in association with climate change (Pachauri et al. 2014). Accordingly, the question of how communities respond to massive disturbances is becoming increasingly relevant for ecologists and policy makers (Prach and Walker 2011; Barnosky et al. 2012; Cardinale et al. 2012). Answering this question requires us to accurately determine the magnitude of the effects of major disturbances and also to determine the resilience of the impacted communities (e.g. Magurran et al. 2010; Matthews et al. 2013). This task becomes difficult to achieve in nature, because such disturbance events are in general unpredictable and pre-disturbance data of population abundances and community structure are rarely available.

After a disturbance, species' functional traits, such as high mobility and shorter generation times, can influence the

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temporal variation of the local assemblages (Dittmann 1999; Matthews et al. 2013). Short generation times allow species to recover population numbers between frequent disturbances (e.g. Valdivia et al. 2005). In addition, highly mobile organisms rapidly re-colonise recently disturbed areas, resulting in a fast recovery of the assemblage (Dittmann, 1999). High turnover rates of amphipods allow, for example, recently disturbed populations to recover within few days (Edgar 1992; Taylor 1998). Such turnover rates, added to consistent propagule rain (Berlow 1997), could assure a permanent supply of settlers and provide the assemblage with a high resilience, that is, a strong tendency to return to a pre-disturbance state.

In marine ecosystems, intertidal sandy shores can be exposed to cyclic erosion and accretion of sand, which result in a highly dynamic matrix habitat (Gallop et al. 2013; Jackson et al. 2013). Nevertheless, these systems can harbour a moderately high diversity and abundance of organisms with high mobility and short generation times, producing populations that are highly dynamics (Cardoso and Defeo 2004; Defeo and McLachlan 2013). In intertidal sandy shores, therefore, we might expect rapid changes of population numbers after drastic physical changes in the environment, due to the dominance by functional traits that allow the local populations to withstand dynamic environmental conditions.

Co-seismic coastal changes can trigger abrupt shifts in intertidal and subtidal assemblages (Jaramillo et al. 2012; Hernández-Miranda et al. 2014). The 2010 rupture of the plate boundary off central Chile, known as the Maule earthquake, resulted in significant uplifts and subsidence along ca. 500 km of the coast (Fariás et al. 2010). This geological modification brought secondary effects such as tsunamis, vertical displacements of land, and erosion of sediments following the earthquake, which altered community composition and produced massive mortality events of coastal organisms (Castilla et al. 2010; Jaramillo et al. 2012; Sepúlveda and Valdivia 2016). For intertidal and shallow-subtidal organisms, a coastal uplift severely enhances the physiological stress related with aerial exposure, leading to drastic reductions of population numbers. Sepúlveda and Valdivia (2016) determined that the co-seismic effects of the Maule earthquake—derived from a shore uplift and further tsunami—on the local communities were highly localised at the spatial scale of tens to hundreds of kilometre. However, the authors analysed mostly short to intermediate temporal community responses (Sepúlveda and Valdivia 2016). The temporal variation of these impacted communities, therefore, still remains unclear.

Here, we present the results of a natural experiment in which we tested the general model that species assemblages inhabiting highly dynamic habitats show a significant change after a major disturbance. After 23 months, a dataset of species abundances obtained in four intertidal sandy shores before and consecutively after the Maule earthquake and tsunami was used to test the specific predictions that (i) the Maule

earthquake and tsunami triggered an abrupt change in community structure and diversity and that (ii) the disturbed assemblages progressively tended to return toward the pre-disturbance structure.

Materials and Methods

Study Area and Sampling Design

Our study took advantage of an on-going monitoring programme of intertidal sandy shores in south-central Chile, which allowed us to quantify species abundances before and after the Maule earthquake and tsunami. The epicentre of this earthquake (Mw 8.8) was located ca. 120 km north-east of Concepción (36° 49' S, 73° 03' W) and took place in 27 February 2010. The earthquake and tsunami caused significant geomorphological changes, including shore uplifts of ca. 200 cm, increases of beach width, and decreases of beach slopes within the rupture area (Fariás et al. 2010; Jaramillo et al. 2012; Sepúlveda and Valdivia 2016). Four sandy beaches were studied during a period of 23 months. Two intertidal sandy shores (Hualpén and Llico) were located and sampled within the southern rupture area (~36.5° S, and <150 km from the earthquake epicentre, Fig. 1), and two intertidal sandy shores (Mehuín and La Misión) were located in a control area (~39.5° S, >400 km away from the earthquake epicentre, Fig. 1) in order to compare species richness, abundance, and community structure.

These four sites were selected, from a pool of ten available sandy beaches, according to similar morphodynamic characteristics such as orientation to prevailing south-western winds, mild slopes (1/slope < 40), widths of ca. 50 m, and mean grain sizes between 150 and 300 µm. According to these characteristics, our sampling sites can be described as “intermediate” sandy shores following Jaramillo et al. (2001). Circumscribing our study to a single sandy-shore model allowed us to reduce potential confounding effects of beach morphology on the spatiotemporal patterns of community structure.

Samplings of species abundances in the intertidal sandy shores were conducted during austral summers, starting on early February 2010 (before the Maule earthquake). Temporal replicates were sampled during March 2010, March 2011, and January 2012. At each shore and sampling event, five transects spaced from one another by 10 m were extended from high (MHW) to low tidal (MLW) heights. Along each transect, ten samples of sediment, equally spaced across the intertidal zone, were collected independently burying 0.3 m depth a metallic corer of 0.1 m diameter (equalling 0.0023 m³ per corer). The sand obtained was screened through a 1-mm sieve mesh to collect all macroinfauna, which were preserved in a 70 % ethanol solution until further taxonomic classification. Classification was done to the lowest possible

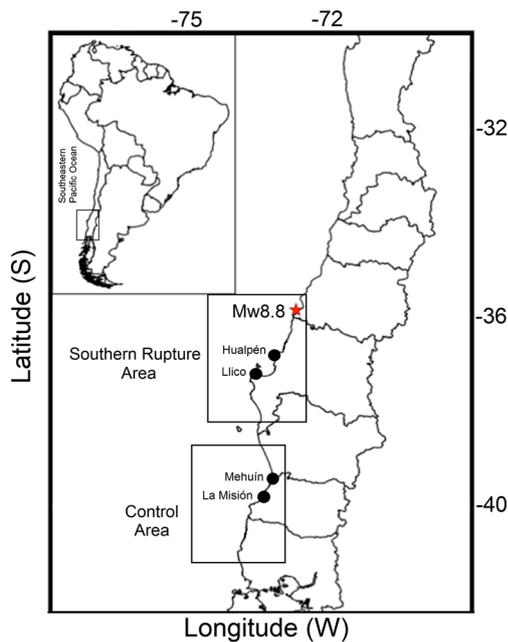


Fig. 1 Map of the sampling sites in the central Chilean coast. The Maule earthquake epicentre is indicated by a star. Hualpén and Llico were located within the earthquake southern rupture area and <150 km of lineal distance from the epicentre (~36° S), while Mehuín and La Misión were located within the control area and >400 km away from the epicentre (~39° S)

taxonomic level, usually species, with aid of a binocular microscope. In order to analyse all organisms along the sandy-shore community zonation, the ten core samples of each transect were pooled to obtain abundances per transect (i.e. number of individuals/0.023 m³ of sediment).

Data Analysis

We calculated the number of species and individuals as diversity components to obtain trends for species richness and abundance over time, respectively (Magurran 1988). Additionally, the contribution of each taxon to the temporal variation in community structure was evaluated with similarity percentage routines (SIMPER, Clarke and Warwick 2001). In this procedure, we estimated Bray-Curtis dissimilarities between and within sampling times in the entire dataset of species abundances. The average between-group dissimilarities were then broken down into separate contributions from each taxon. For each taxon with the highest contribution, we estimated the proportion of individuals found 2 years after earthquake (January 2012) in relation to that in the pre-earthquake sampling time (February 2010) in order to establish differences in abundances per species before and 2 years after earthquake.

The differences for species richness, abundance, and community structure were assessed separately by means of

permutational multivariate analyses of variance (PERMANOVA, Anderson 2001) using time (i.e. February 2010, March 2010, March 2011, and January 2012) and area (i.e. rupture and control) as fixed factors and site (i.e. Hualpén and Llico within the southern rupture area and Mehuín and La Misión within the control area) nested in area as a random factor to test the prediction that (i) the Maule earthquake triggered an abrupt change in community structure and diversity within the impacted area. Additionally, in the PERMANOVA, we generated a temporal planned contrast to compare the immediate effect between “before” (February 2010) and “after” (i.e. March 2010) the Maule earthquake.

Permutational analysis of multivariate dispersions (PERMDISP, Anderson 2006) was used to test for differences in within-group heterogeneity between the February 2010 and March 2010 groups (temporal contrast) and between the groups in the time × site interaction. PERMDISP showed homogeneity of multivariate dispersions between the February 2010 and March 2010 groups ($F_{(1, 38)} = 0.168$, $P_{\text{perm}} = 0.707$). The analysis showed heterogeneity of multivariate dispersions between some groups in the time × site interaction ($F_{(7, 32)} = 5.765$, $P_{\text{perm}} = 0.005$); notwithstanding, previous simulations demonstrate that the null-hypothesis rejection rate of PERMANOVA is highly robust to heterogeneity in dispersions when the sampling or experimental design is balanced (Anderson and Walsh 2013), as in our case.

For all analyses, probability values of significant fits were derived from a pseudo- F distribution calculated through 10,000 permutations of the original dataset; when the simulated permutations were <1000, the probability value was obtained through Monte-Carlo simulations (Anderson 2001). Univariate (log-transformed species richness and abundance) and multivariate ($\sqrt{\sqrt{\cdot}}$ -transformed species abundance) PERMANOVAs were based on Euclidean and Bray-Curtis similarity matrices, respectively. Statistically, significant contrast between before and after under the interaction [time × site(area)] would support the hypothesis (i).

Independently for each intertidal sandy shore, we estimated the average between-group similarity, which was compared to the initial within-group similarity (pre-disturbance condition) to test the prediction that (ii) the disturbed assemblages progressively tended to return toward the pre-disturbance structure. A consecutive increase in the between-group similarity would support the hypothesis (ii). In order to further test the hypothesis (ii), the macrofauna similarity matrix of each site was compared individually against a cyclicality (statistical) model to test whether community structure tended to return gradually to its initial, pre-disturbance state. These fits were conducted with RELATE analyses based on Spearman rank correlations (ρ) between the original dissimilarity matrices and the dissimilarity model matrix that would result from a perfect cycle of inter-sample distances of the same number of

observations, which were evaluated through statistical tests using 10,000 permutations. The temporal trajectories of community structure ($\sqrt{\sqrt{\cdot}}$ -transformed data) of the sandy intertidal shores were visualised by means of principal coordinates analyses (PCO, Gower 2005) ordination plots based on Bray-Curtis dissimilarity matrices. All analyses were performed using PERMANOVA+ for the PRIMER6 statistical package (Clarke and Gorley 2006; Anderson et al. 2008).

Results

Species Composition of the Intertidal Sandy Shores

A total of 3236 invertebrate individuals, belonging to 19 species, were identified at the four sites during the sampling period. Three species contributed over 88 % of the total abundance across all sites: the talitrid amphipod *Orchestoidea tuberculata* (31.8 %), the anomuran crab *Emerita analoga* (31.3 %), and the cirrolanid isopod *Excirrolana hirsuticauda* (25.2 %). At some sites and times, the opheliid polychaete *Thoracophelia heterocirrus* (6.7 %) and the cirrolanid isopod *Excirrolana braziliensis* (2.0 %) were highly represented (Table 1).

In both sites within the southern rupture area, three species showed high abundances before the Maule earthquake. Immediately after the disturbance, the species abundance decreased drastically (especially in Llico) and then showed fluctuating patterns throughout time, reaching relatively high proportions of individuals toward the end of this study (Table 1). Particularly, the three species with non-planktonic development (i.e. *O. tuberculata*, *E. braziliensis*, and *E. hirsuticauda*) showed a relatively high proportion of their pre-earthquake abundance by January 2012. On the other hand, the species with the highest dispersal potential (i.e. *E. analoga*) showed a low recovery of its pre-earthquake abundance (Table 1). In sites within the control area, the four species indicated above showed fluctuating abundances throughout time, reaching relatively low and high proportions of individuals toward the end of this study for Mehuín and La Misión, respectively (Table 1). The exception was *E. braziliensis*, which showed low mean abundance before earthquake and was not found during the post-disturbance periods in La Misión (Table 1).

Temporal Dynamics of Community Structure

Community structure significantly differed between sampling times and sites nested in area (pseudo- $F_{(6, 64)} = 3.32$, $P_{perm} < 0.001$, CV = 22.4 %; Table 2 (a)). Moreover, there was a significant effect for temporal [before vs. after \times site(area)] planned contrast on community structure (Table 2 (a)).

Llico, the site with values of zero ind. 0.023 m^{-3} after the earthquake (Table 1), showed wide temporal variations in community structure, evidenced by the long distances between sampling times in the PCO ordination plot (Fig. 2: compare the length of site-specific trajectories). Immediately after the earthquake and tsunami (March 2010), the assemblage of Llico showed a 91 % of dissimilarity with respect to its initial state (Fig. 2). The before-after impact dissimilarities for Llico decreased until reaching a 35 % 2 years after the earthquake and tsunami (Fig. 2). The other site within the southern rupture area (i.e. Hualpén) in addition to those sites within the control area showed between-group dissimilarities fluctuating between 20 and ~40 % toward the end of the study (Fig. 2). The RELATE tests showed significant correlations between the similarity matrices and the perfect cyclicity model matrices for Hualpén and Llico within the southern rupture area and La Misión within the control area (Fig. 2).

Species Richness of the Intertidal Sandy-Shore Assemblages

The sites showed varying degrees of change in species richness, with Llico, the site with the strongest co-seismic coastal uplift in the southern rupture area (Sepúlveda and Valdivia 2016), showing the steepest change from before to after the earthquake and tsunami. Within the southern rupture area, the number of intertidal sandy-shore species at Hualpén decreased slightly from before to after the Maule earthquake during the next two periods (March 2010 and March 2011), increasing slightly after 2 years from the earthquake (Fig. 3a). At Llico, the number of species decreased drastically from before to immediately after the disturbance. On January 2012, the mean species number reached similar values to those registered in the pre-disturbance period (Fig. 3b). Within the control area, the number of species at Mehuín decreased after the earthquake and then oscillated throughout time around a mean value of ca. 3.5 species (Fig. 3c). At La Misión, the number of species decreased from before to after the disturbance, then increased and remained similar during the next two years (Fig. 3d). Species number showed a statistically significant response to the time \times site(area) interaction (pseudo- $F_{(6, 64)} = 4.48$, $P_{perm} = 0.001$; component of variation (CV) = 34.1 %). In addition, the results showed that there was a significant effect for temporal [before vs. after \times site(area)] planned contrast (Table 2 (b)).

Abundance of Intertidal Sandy-Shore Organisms

The number of individuals showed varying patterns across the region (Fig. 4). Sites within both areas showed decreases in abundance from before to after the earthquake took place; however, only Llico, in the southern rupture area, reached values of zero ind. 0.023 m^{-3} (see also Table 1). Within the

Table 1 Intertidal sandy-shore mean abundances from SIMPER analysis for the four species with the highest contribution to the average between-group Bray-Curtis dissimilarity in the time

Area	Species per site	Intertidal zone	Development type	Feb10	Mar10	Mar11	Jan12	Abundance ratio
Southern rupture	Hualpén							
	<i>Emerita analoga</i>	Low	P	49.0	62.4	19.4	14.0	0.3
	<i>Thoracophelia heterocirrus</i>	Mid-	P	16.6	3.0	4.6	18.4	1.1
	<i>Exciorolana hirsuticauda</i>	Mid-	NP	10.2	2.0	14.0	7.2	0.7
	<i>Orchestoidea tuberculata</i>	High	NP	3.4	9.6	15.2	27.0	7.9
	Llico							
	<i>Emerita analoga</i>	Low	P	14.6	0.4	0.0	3.4	0.2
	<i>Exciorolana hirsuticauda</i>	Mid-	NP	14.2	0.0	33.8	11.6	0.8
Control	Mehuín							
	<i>Orchestoidea tuberculata</i>	High	NP	11.6	0.8	2.0	2.0	0.2
	<i>Exciorolana hirsuticauda</i>	Mid-	NP	9.4	4.6	5.2	2.2	0.2
	<i>Emerita analoga</i>	Low	P	6.8	3.2	2.8	2.8	0.4
	<i>Exciorolana braziliensis</i>	Mid-	NP	6.2	0.4	0.6	0.8	0.1
	La Misión							
	<i>Orchestoidea tuberculata</i>	High	NP	32.4	19.0	35.6	31.2	1.0
	<i>Exciorolana hirsuticauda</i>	Mid-	NP	17.0	3.3	13.6	15.8	0.9
	<i>Emerita analoga</i>	Low	P	11.0	2.3	4.2	7.0	0.6
	<i>Exciorolana braziliensis</i>	Mid-	NP	2.0	0.0	0.0	0.0	0.0

Feb10 corresponds to the abundances measured before (27 February 2010) and Mar10, Mar11, and Jan12 to those abundances measured after the Maule earthquake. The abundance ratio is the proportion of individuals found 2 years after earthquake (January 2012) in relation to that found before earthquake (February 2010). Mean abundances are expressed as individuals per transect (0.023 m^{-3})

P Planktonic, NP Non-planktonic

southern rupture area, the number of individuals at both sites showed different degrees of variation between before and immediately after the earthquake. Hualpén did not show differences in the mean abundance between before and immediately

after, while Llico showed a drastic decline in abundance after the earthquake (Fig. 4a, b). Within the control area, the mean abundances decreased in both sites after the earthquake but never reaching low mean abundances as those in Llico in the

Table 2 PERMANOVA outputs for the species richness, abundance, and community structure of the intertidal sandy-shore communities in central Chile

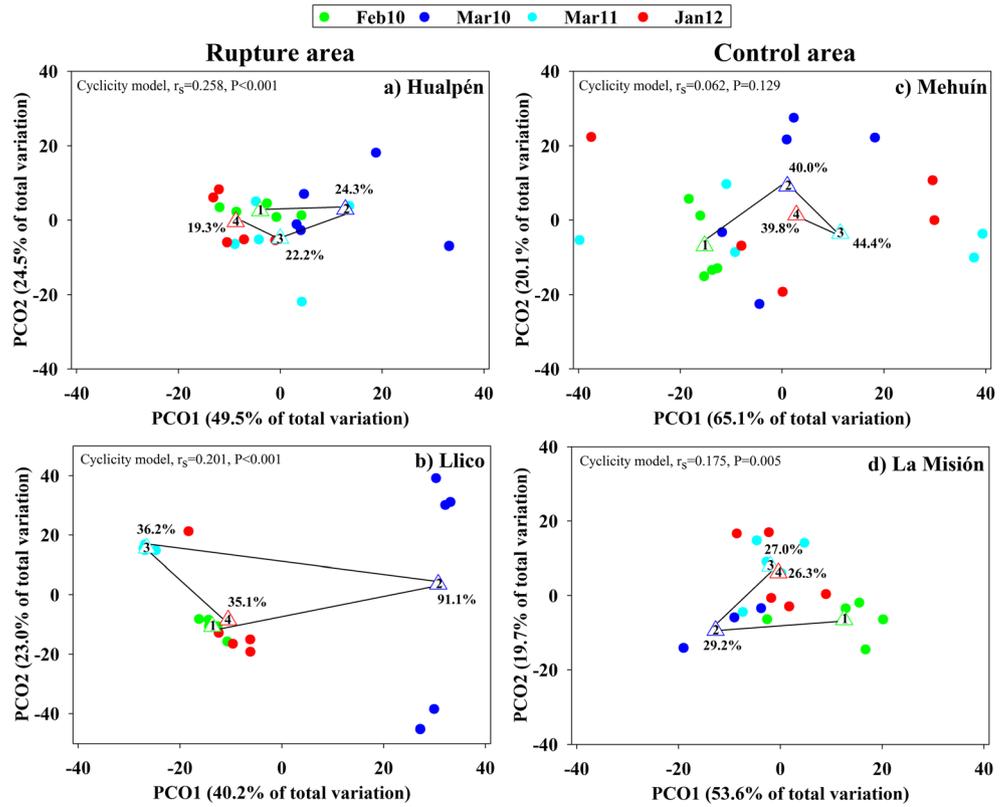
Source of variation	df	a) Community structure				b) Species richness				c) Abundance			
		Pseudo-F	P_{perm}	Perm	CV	Pseudo-F	P_{perm}	Perm	CV	Pseudo-F	P_{perm}	Perm	CV
Time	3	1.18	0.346	9949	1.5	1.86	0.242	9959	9.5	1.53	0.292	9956	5.3
*Before vs. after	1	1.72	0.202**	798		3.42	0.213**	798		3.78	0.196**	798	
Area	1	0.81	0.577**	3	0.0	0.05	0.853**	3	0.0	0.15	0.729**	3	0.0
Site(area)	2	12.05	<0.001	9928	26.7	4.02	0.021	9951	7.4	54.86	<0.001	9945	42.6
Time × area	3	1.07	0.429	9952	1.1	0.53	0.687	9967	0.0	0.22	0.884	9961	0.0
*Before vs. after × area	1	0.65	0.693**	801		0.28	0.645**	798		0.02	0.903**	800	
Time × site(area)	6	3.32	<0.001	9894	22.4	4.48	0.001	9951	34.1	12.45	<0.001	9944	36.3
*Before vs. after × site(area)	2	4.14	<0.001	9903		5.23	0.008	9957		13.28	<0.001	9957	
Residual	64				48.3				49.0				15.8

Perm number of unique permutations performed, CV components of variation (%)

*Temporal planned contrast (February 2010 vs. March 2010)

**Probability based on Monte-Carlo simulations (P_{MC})

Fig. 2 Principal coordinates analysis (PCO) plots showing the temporal variation of dissimilarities (%) for the intertidal sandy-shore community structures. Transects (*filled circles*) and multivariate centroids (*open triangles*) showing the temporal variation of the community structure before (Feb10) and after (Mar10 to Jan12) the Maule earthquake/ tsunami of 27 February 2010. The centroids of consecutive samplings were connected by *lines* and *correlative numbers* (1–4) to facilitate the interpretation of the community structure temporal trajectories



southern rupture area (Fig. 4c, d). A statistically significant effect of the time \times site(area) interaction on the mean abundance was observed (pseudo- $F_{(6, 64)} = 12.45$, $P_{perm} < 0.001$; CV = 36.3 %). In addition, the results showed that there was a significant effect for the temporal [before vs. after \times site(area)] planned contrast (Table 2 (c)).

Discussion

The results showed significant changes of the intertidal sandy-shore assemblages after the occurrence of the mega-disturbance. Assemblages located at both, the southern rupture and control areas, significantly varied in terms

Fig. 3 Temporal trends of the mean species number for the intertidal sandy-shore communities in central Chile. Values are given as mean \pm 1 S.E. Grey dotted line indicates when the earthquake/tsunami took place (27 February 2010)

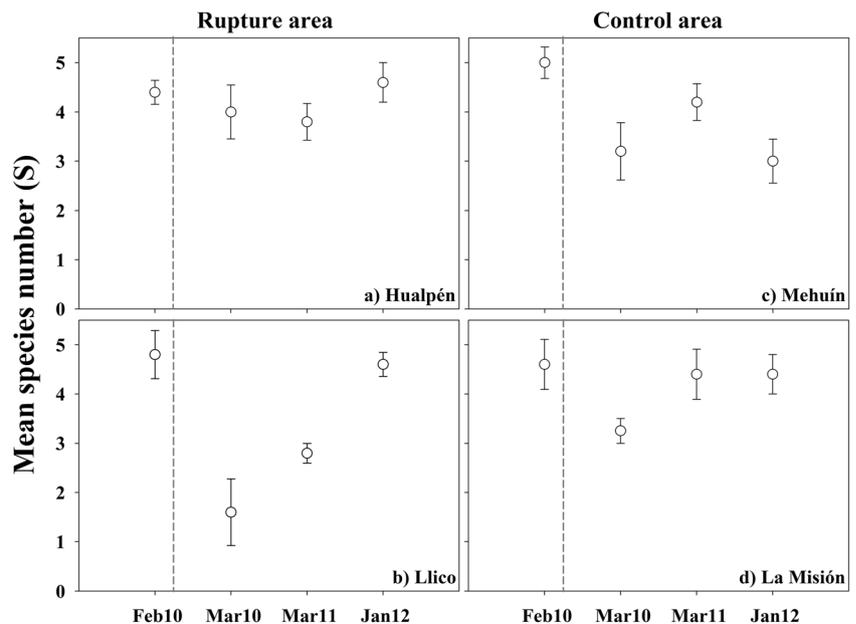
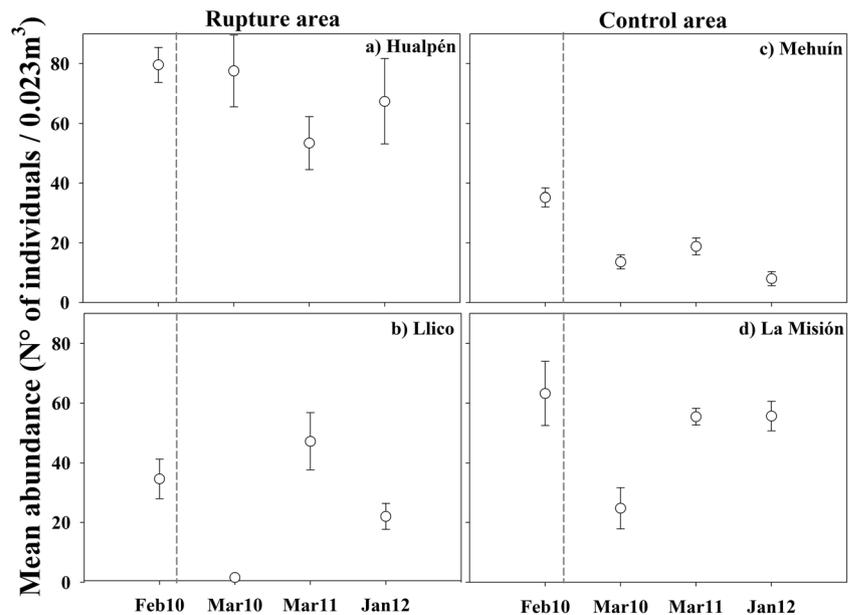


Fig. 4 Temporal trends of the mean number of individuals (per 0.023 m³) for intertidal sandy-shore communities in central Chile. Values are given as mean \pm 1 S.E. Grey dotted line indicates when the earthquake/tsunami took place (27 February 2010)



of community structure, richness, and abundance. Nevertheless, these changes were stronger at Llico, the site that showed the strongest co-seismic coastal uplift and tsunami exposure in the impact area (e.g. Farías et al. 2010; Sepúlveda and Valdivia 2016). The assemblages within the control area did not show measurable geomorphological responses to the Maule earthquake (Jaramillo et al. 2012; Sepúlveda and Valdivia 2016); therefore, the significant temporal variation in community structure observed in this area was likely influenced by other environmental factors, such as sediment dynamic, and changes in beach morphology and organic matter concentration (see Jackson et al. 2013; Veas et al. 2013 for examples).

Co-seismic processes such as coastal uplift and the concomitant tsunami that affected the shore can explain the patterns observed at Llico, the site that showed the strongest variations in multivariate community structure in our study. First, coastal uplift was maximal at Llico. Shore uplift implies that exposition of marine organisms to UV radiation, heat, hypoxia, and desiccation is significantly enhanced. For example, Castilla et al. (2010) reported a significant relationship between the coastal uplift and the percentage cover of dead shallow-subtidal organisms in rocky shores in the rupture area. Second, the tsunami that followed the earthquake deposited and eroded large amounts of sediments on some shores located in the rupture area (Jaramillo et al. 2012). Llico was directly exposed to the tsunami impact, and in this area, the mechanical abrasion caused by the tsunami razed the vegetation and manmade structures, changing also the composition and stratification of sediments (Vargas et al., 2011; Sepúlveda pers. obs.). Therefore, co-seismic interactive processes are key to understand the significant, and spatially localised, ecological effects of the Maule earthquake.

A key finding of our study was that the impacted assemblage at Llico showed a significant tendency to return to a pre-earthquake state already after 12 months, and after 23 months, the pre- and post-disturbance assemblages were no longer different. Also, the pattern of variation of the impacted assemblage of Llico was almost undistinguishable from those of the other sites, which was evidenced by the significant fit of the “cyclicality” statistical model to all-but-one sites. According to these results, the effect of the Maule mega-earthquake on the structure of the macrobenthic intertidal communities was likely of limited duration. A longer sampling period would have allowed us to clearly distinguish between these short- and other (potential) long-term legacies of the disturbance. Nevertheless, the analysed communities are dominated by organisms with short generation times (e.g. Cardoso and Defeo 2004 and see the following paragraphs below), which makes our sampling period appropriate to track the development of these assemblages.

The cyclic erosion and accretion of sand pose drastic environmental changes to the local biota in sandy shores (Jackson et al. 2013). Accordingly, the dominant taxa at sandy shores are characterised by short generation times and high mobility that allow them to recover their populations under dynamic physical conditions (e.g. Cardoso and Defeo 2004). Indeed, our study indicated that the dominant species with the highest abundance ratios were those characterised by high mobility at the local scale. For instance, the cirrolanid isopod *E. braziliensis* can show significant patterns of variation in their life-history traits over geographical scales, suggesting a high population dynamic (e.g. Cardoso and Defeo 2004). In general, peracarid crustaceans show population turnover rates between 30 and 100 % per day, indicating that these organisms are able to recover the entire population density after 24 h

(Poore 2005). These abilities could have helped to the dominant peracarid populations to recover in numbers after the abrupt environmental change triggered by the Maule earthquake and tsunami, providing the assemblage with a high potential for resilience. As expressed above, longer population time series in the region are necessary to determine any long-term effect of this mega-disturbance.

In addition to the dominant functional traits in local assemblages, horizontal and vertical migrations of larvae, juveniles, and adults from other areas might also have influenced the population- or community-level temporal patterns. For example, neighbouring zones that showed non-significant or even positive responses to the Maule earthquake (e.g. armoured zones in Llico; Jaramillo et al. 2012) could have served as a “source” of individuals migrating into the impacted zones within a given site. In this study, the abundance of peracarid crustaceans (particularly *E. hirsuticauda* and *O. tuberculata*) showed variations in abundance between one and two orders of magnitude among different time periods, showing in general higher abundances during late summer and autumn. The ability of peracarids to actively move among different intertidal zones could help to rapidly increase the size of the population after a disturbance (Sepúlveda and Valdivia 2016). Since peracarid crustaceans are direct developers (non-planktonic stages) with extended parental care, most (particularly amphipods) inhabit transitional zones with terrestrial habitats and are capable of burrowing; it is likely that the recolonisation is the result of active migration of adult peracarids from the neighbouring sites and further establishment in the re-invaded habitat. Specific traits of these species make them less vulnerable to environmental variability during early life stages, allowing for the persistence and abundance of peracarid crustaceans in highly dynamic systems (e.g. Barboza et al. 2012; Sepúlveda and Valdivia 2016). Such source-sink dynamics have been used to explain the assembly and structure of communities occurring in patchy habitats connected by dispersion (Leibold et al. 2004; Gothe et al. 2013). On the other hand, species such as the mole crab *E. analoga* with indirect development (planktonic stages) and the ability to burrow in intertidal zones did not recover in the site most affected by the Maule earthquake and tsunami. It is likely that the large amounts of sand deposited by the tsunami altered the physical features of intertidal sandy shores; this, in turn, could have affected the burrowing rate of *E. analoga* and therefore the chance of survival (Veas et al. 2013, 2014). Further manipulative work is needed to assess the dispersal strategies of dominant species in sandy beaches (Munguia et al. 2007).

According to what is discussed above, assemblages dominated by mobile species might be more resilient than those dominated by sessile species. For example, mobile invertebrates can re-colonise a disturbed area more rapidly than sessile species (e.g. Valdivia et al. 2014). In addition, highly

mobile invertebrates usually have shorter generation times than dominant sessile species. Assemblages dominated by sessile species, like rocky shores, generally need comparatively long periods to recover from large-scale disturbances (e.g. 12 years, Jenkins et al. 2004; 9 years, Petraitis et al. 2009), and alternative stable states have been described in some cases (Paine and Trimble 2004; Petraitis et al. 2009). Therefore, sandy shores might show a higher resilience than rocky shores, despite the former usually harbour fewer species than the latter. Mobility, as a species’ trait affecting community resilience, should be included in new models of ecosystem stability.

In summary, our results suggest that the community-level “footprints” of the Maule mega-disturbance were, in addition to spatially confined (Sepúlveda and Valdivia 2016), relatively limited in time. The analysis of longer time series of macrobenthic populations would allow us to determine potential long-term legacies of the disturbance on the structure of these communities. Nevertheless, the fact that, here and worldwide, the dynamic intertidal sandy-shore communities are characterised by species with high mobility and short generation times allows us to suggest that these functional traits might constitute a negative feedback preventing the system to exceed its elastic limit (sensu Tett et al. 2013) and a further shift toward an alternative community state. Therefore, species’ traits can exert a relevant role in maintaining the stability of these valuable ecosystems.

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