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Sandy beach macrofauna along the shore of Fiji: Low species richness due to beach morphodynamics or low productivity in coastal waters?

M. Lastra [a,*], E. Jaramillo [b], J. López [a], J. Troncoso [a], I.F. Rodil [c], J. Vergara [b], A. Maracava [d]

[a] Centro de Investigación Mariña, Universidade de Vigo, EcoCost, 36310, Vigo, Spain
[b] Instituto de Ciencias de la Tierra, Facultad de Ciencias, Universidad Austral de Chile, Valdivia, Chile
[c] Departamento de Biología, Facultad de Ciencias del Mar y Ambientales, Campus Río San Pedro, Puerto Real (Cádiz), 11510, Spain
[d] University of the South Pacific, School of Marine Studies. Laucala, Suva, Fiji

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ABSTRACT

Six sandy beaches located on the south coast of Viti-Levu, Fiji, were sampled to provide as a first aim, an environmental description based upon their physical and biological attributes, to serve as a reference tool for further monitoring programs. Beach face slopes were measured at 4 replicated transects stretching from the front dunes or the seaward reach of the tree vegetation (upper shore level) to the low tide level. Samples for analyses of sand particle size were collected at 4 tidal levels: the upper shore, the drift and effluent lines, and the low tide level. Samples for macroinvertebrates were sampled at the dry, retention, and resurgence/swash zones. Beach sites were categorized in terms of their morphodynamic types by means of photographs taken on site and expert analysis, taking into consideration beach width, beach face slopes and mean grain sizes of sands. Three of the studied beaches were labeled as reflective, two were intermediate and one was in between these two morphodynamic types. The mean number of intertidal species and abundance of macroinvertebrates (dominated by crustaceans and polychaetes) across all sites were 4.1 taxa (±1.7, ranges = 2–6) and 917 individuals per linear meter of beach (m^{-1}) (±490, ranges = 133–1154). The second aim was to test the hypothesis that, along this coast, those biotic attributes are related to beach morphodynamic types. Our data allowed us to reject this hypothesis, since i) species richness and abundances of macroinvertebrates, did not differ significantly among beaches, ii) beach slope, beach width, and sediment grain size did not account for significant variations in the number of species and abundance of macroinvertebrates, and iii) multivariate analysis indicated that sediment grain size and beach slope just accounted for 31 % of the biotic richness variation. The third aim, was to evaluate the hypotheses that biotic richness in open ocean sandy beaches is not only affected by local environmental factors, but also by regional scale processes, such as ocean productivity. Thus, biotic information and coastal productivity data of ocean exposed sandy beaches along the tropical and subtropical belt at global scale were gathered from scientific literature. Based on upwelling and downwelling measurements, we conclude that oligotrophic ocean conditions, account for the low biodiversity and abundance of macroinvertebrate assemblages inhabiting the Fijian beaches studied. Our study establishes, for the first time, a reliable baseline for future studies and projects aimed at the protection of natural sandy beaches along the shores of the Fiji Islands and other isolated archipelagos of the tropical Pacific Ocean, where oligotrophic conditions prevail in their aquatic environment.

1. Introduction

Open ocean sandy beaches form an ecotone between sea and land, changing naturally in shape and width in response to variations in wave energy and sediment supply. With the current trend of coastal occupation worldwide, sandy beaches are amongst the most heavily threatened habitats, being under increasing pressure from escalating and expanding urban development, climate change, and sea level rise (Dugan et al., 2010; Carranza et al., 2020). Sandy beaches provide humans with numerous ecosystem services, including coastal protection (Mimura and Nun, 1998), and thus contribute to economic and ecological values that underpin the broader cultural architecture of many coastal societies

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* Corresponding author.
E-mail address: mlastra@uvigo.gal (M. Lastra).

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(Beaton, 1985; Barbier et al., 2011; Schlacher et al., 2014; Defeo et al., 2016; Carranza et al., 2020). Sandy beaches perform an extensive array of ecological functions that sustain biodiversity and faunal species with unique adaptations. These functions include the provision of shelter, food and nesting habitats for shorebirds, turtles, lizards, mammals, etc (Colombini and Chelazzi, 2003; Schlacher et al., 2013), as well as nutrient regeneration (Dugan et al., 2011; Barreiro et al., 2013).

It has been long argued that the ecological features of sandy beaches can be explained in terms of interaction between waves, tides, and sediment characteristics, i.e. beach morphodynamics. Thus, macroinvertebrate biodiversity and abundance increase along a continuum, from reflective, intermediate, to dissipative morphodynamic beach types (Short, 1996; McLachlan and Defeo, 2018). The interactions between physical and biotic variables indicate that wide surf zones, fine to medium sands, and flat beach face profiles (dissipative beaches) usually harbor a larger number of species and higher abundance and biomass of macroinvertebrates (McLachlan and Defeo, 2018). This tendency has been observed over a wide variety of beach types, tidal ranges, and biogeographical regions (Lewin et al., 1989; McLachlan, 1990; Defeo et al., 2017). However, when explaining deviations from the pattern predicted, latitudinal effects, biogeographical factors, and local events need to be considered (Rodil et al., 2012). For instance, coastal oceanographic productivity sustains the biotic characteristics of sandy beaches through subsidies of planktonic food (namely particulate and dissolved organic matter) (Defeo et al., 2017), as well as macroalgal wrack and carrion that provide food and shelter for highly mobile macroinvertebrates occupying several trophic guilds (Lastra et al., 2006; Duarte et al., 2014; Dugan et al., 2018; Schlacher et al., 2013). In this sense, species richness and abundance of macroinvertebrates are higher with increasing photopigment concentration in the water column, as demonstrated in beaches in different parts of the world (Lastra et al., 2006; Ortega-Cisneros et al., 2011; Rodil et al., 2012). Furthermore, it has been concluded that species interactions may well contribute to structuring and shaping biotic characteristics of sandy shores (Dugan et al., 2004).

From an ecological point of view, there is a generalized lack of information about the diversity and abundance of the macroinvertebrates that inhabit the tidal zone of both coral reef fringed beaches and open ocean sandy beaches in the vast geographic region of the tropical Pacific Ocean, including the sandy beach habitats of the Melanesian, Micronesian, and Polynesian countries (Yamada et al., 1995; Nunn and Mimura, 1997; Gombos et al., 2014). The paucity of ecological studies on sandy beaches in this region is alarming, not only because those beaches render important ecosystem services (Mimura, 1999; Singh, 2011), but also because many islands in the South Pacific present the world's highest rates of beach erosion and coastal squeeze as a consequence of sea level rise (Mimura and Nun, 1998; Mimura, 1999; Pachauri and Meyer, 2014). Thus, rates of sea level rise on some islands are four times the global average (Nunn, 2012). Coastal armoring has been the most frequently used strategy to counteract the negative effects of this accelerated change in certain areas (Hay, 2013; Nunn et al., 2021).

Fiji is the largest island nation in the South Pacific and it is home to about 800,000 people, 85 % of whom live along the coastal rim, relying significantly on marine resources and tourism. Fiji's tourism industry sustains around 40,000 jobs, attracting more than 900,000 visitors every year, who come to enjoy Fiji's white sandy beaches and coral reefs. Hence, the preservation of natural coastal protective ecosystems, such as sandy beaches, mangroves, and coral reefs, appears to be critical within the scope of the Integrated Coastal Management Framework of Fijian Government (Dumaru, 2011), intended to protect coastal areas against the predicted consequences of sea level rising and climate change.

Despite the above facts, studies on macroinvertebrates along the open ocean sandy shores of Fiji have been primarily restricted to species lists provided by taxonomical surveys that usually spanned different environments on large geographic scales (Boyko and Harvey, 2009; Oliverio, 2009; Boyko and McLaughlin, 2010; Poupin and Juncker, 2010; Mohammed and Coppard, 2008; Alfaro et al., 2009). As for sandy beaches –one of the most appreciated assets for scenic tourism– there are few studies dealing with the species richness and natural history of beach macroinvertebrates, which is an essential starting point to develop management and conservation programs in threatened coastal habitats.

We sampled six sandy beaches along the Coral Coast, on the southwest shore of Viti-Levu Island, Fiji. This stretch of coast accounts for 70% of the tourism in Fiji and concentrates around 15 beach resorts and most of the Fijian industry infrastructure (Dumaru, 2011). Due to the scant information on the ecology of this shore, our first aim was to provide a sound-based ecological description of the studied beaches that serves as a reference for further monitoring programs. The selection of the study sites was based on general beach features, such as beach face slopes and wave exposure. We tried to sample along the widest range of beach morphodynamic stages with the purpose to collect data to fullfill the second aim of this study, that is to evaluate the hypothesis, that beaches located near the reflective type of the morphodynamic spectrum harbor less species richness and abundance of macroinvertebrates than sites departing from that category, as shown by several studies around the world (e.g., Jaramillo, 1994; Jaramillo and McLachlan, 1993; McLachlan et al., 1993; McLachlan and Dorvlo, 2005). We also tested the influence of ocean productivity on the biological features of tropical beaches, either on islands or along the continental rim. We collected data from sandy beaches along the tropical ocean belt, where upwelling areas are unevenly distributed (e.g. Froyland et al., 2014). Consequently, we tested the hypothesis that sandy beaches located inside the upwelling areas harbor higher species richness and abundance than beaches located away from those areas (such as the coast of Fiji studied here), regardless of their morphodynamic state. By following this approach, we hope to provide valuable information to identify environmental factors responsible for biodiversity distribution in a poorly known coastal habitat in the tropics, namely, the ocean-exposed sandy beaches of the South Pacific islands.

2. Material and methods

2.1. General setting and study sites

The islands of Fiji are located in the region of Melanesia, Southeastern Pacific, an oceanic region characterized by low primary production and depleted nutrients availability (Morel et al., 2010; Boyce et al., 2010) (Fig. 1a). The stretch of coast studied belongs to the tropical humid bioclimatic zone, with average air temperature of 26 °C and over 2500 mm of rain annually (Fiji Meteorological Service; www.met.gov.fj).

Six ocean, non-urban sandy beaches, not directly fringed by coral reefs and not directly affected by riverine freshwater influences, were sampled along a coastal stretch spanning nearly 80 km on the southwest shore of Viti-Levu (Fig. 1b and c) to analyze species richness and abundance of the intertidal macroinvertebrates. Those beaches were Pacific Harbor (hereafter, PH) (18°15′6,7″S, 178°4′40,9″W), Wainiyabia Village (hereafter, WV) (18°15′46,0″S, 178°2′4,1″W), Sovi Bay (hereafter, SB) (18°10′48,6″S, 177°35′9,5″W), Sigatoka Dunes National Park (hereafter, Si) (18°10′24,1″S, 177°30′32,4″W), Shangri-La (hereafter, SL) (18°8′5,2″S, 177°25′10,9″W), and Natadola (hereafter, Nt) (18°6′1,6″S, 177°19′7,4″W) (Fig. 1c).

Since wave height and periods were not measured on site, morphodynamic beach stages based on Dean's parameter (*sensu* Wright and Short, 1983; McLachlan and Defeo, 2018) could not be determined. Thus, we used pictures and expert judgment (see Acknowledgments), as well as beach slope and beach width, to categorize the beaches studied as follows: SL and SB are reflective beaches (cf. Short, 2020) with narrow surf zones and waves breaking directly on the beach face (Fig. 2a and b) and located within enclosed embayments (Fig. 1c). Although PH

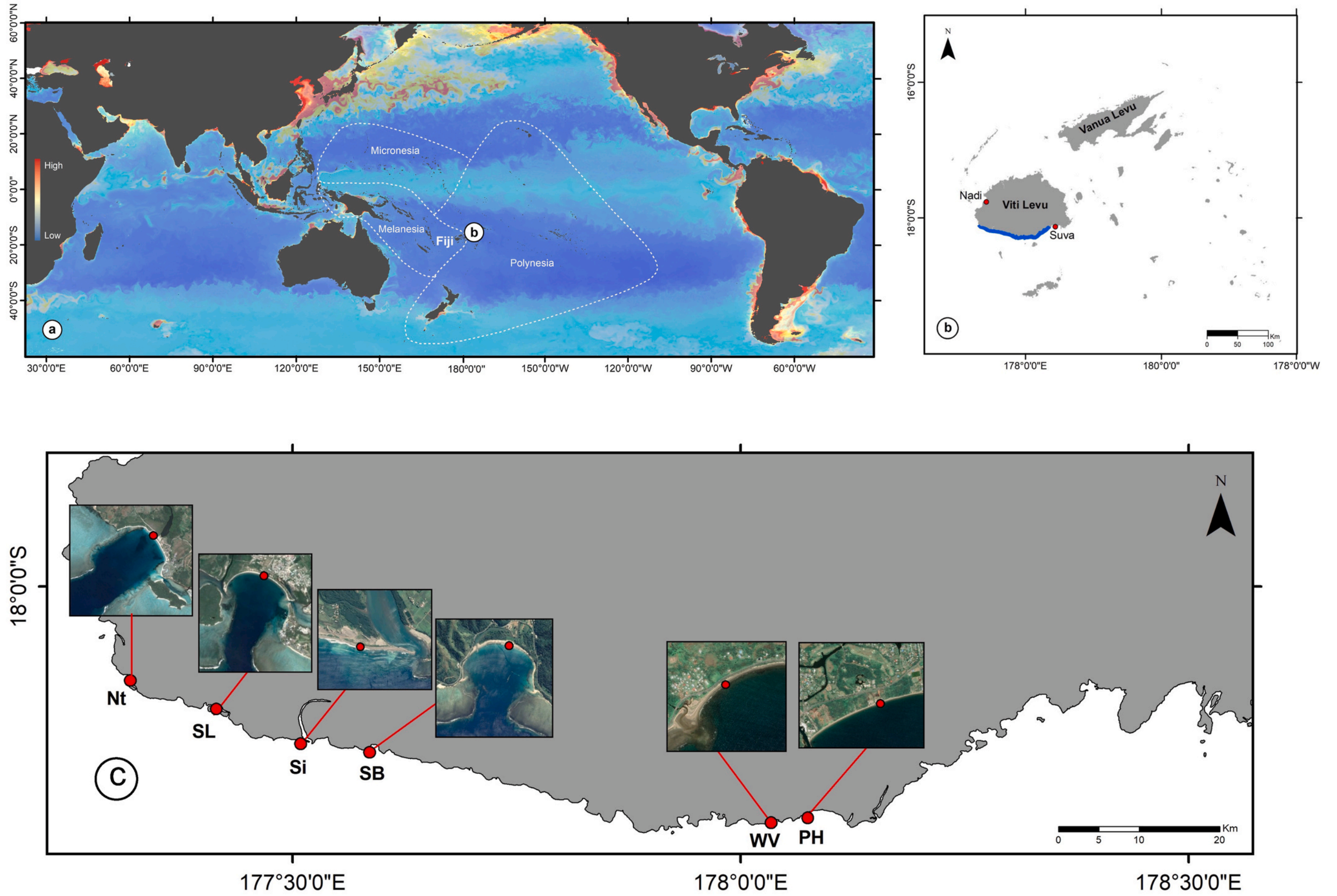

Fig. 1. a) Location of the Republic of Fiji in the low productive region of the west south tropical Pacific (east of Melanesia) (source for primary production layer: NASA Ocean Biology (OB.DAAC) (2018). Mean annual sea surface chlorophyll-a concentration for the period 2015–2018 (composite dataset created by UNEP-WCMC). Data obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua Ocean Color website (NASA OB.DAAC, Greenbelt, MD, USA)). b) The coastal range studied (thick blue line) along the southern coast of Viti-Levu, the main island of Fiji. c) Approximate locations and satellite images (source: GoogleEarth) of the study sites Nt, SL, Si, SB, WV, and PH.

(Fig. 2c) also presents reflective features, it is located in a more open coastal area (Fig. 1c). Nt presents a reflective zone in the upper and middle intertidal levels and a low tide terrace at the lower intertidal zone (cf. Short, 2020) (Fig. 2d). Si and WV fall into the category of intermediate beaches (cf. Short, 2020); while Si is a rhythmic beach with cusps and rips (Fig. 2e), WV is a low tide terrace intermediate beach (Fig. 2f), where waves break away from the beach intertidal. The tidal conditions at the sites studied were microtidal, reaching a 1.3 m range during spring tides (https://www.fijiports.com.fj). Human impact by recreational activities or other uses was assumed to be irrelevant at the sampling time.

2.2. Sampling of macroinvertebrates and description of beaches

All the fieldwork was performed during the low tides between 3rd and July 7, 2013, with a 10 cm tide variation between dates. Samples of macroinvertebrates (i.e., invertebrates retained on a 1 mm sieve) were collected along 4 replicated transects, perpendicular to the shoreline, spaced 5 m apart from each other, most of them located near the center of each beach. Each transect extended from the rear border of each beach (defined as the lower limit of coastal tree vegetation or the seaward base of the foredune system) to the low tide level or collapse point of breaking waves (i.e., the width of the whole beach) (Fig. 3). Three physical zones were distinguished across each transect: the dry or upper zone, between the rear border of the beach and the latest drift line (DL) or high tide mark; the retention zone, between DL and the effluent line (EL) or the upper limit of the resurgence zone; and the resurgence/swash zone, between EL and the low tide level (LT) or collapse point of breaking waves (cf. Salvat, 1964) (see Fig. 3). In each zone of each transect, five 10 cm diameter corers, placed equidistantly from one another, were used to collect samples of sediment to a depth of 20 cm (see Fig. 3). Samples belonging to each zone and transect were combined and sieved through 1 mm mesh and stored in 5% sea water-formalin until sorting. The lowest taxonomic level and number of macroinvertebrates were determined for each sample. The abundance per linear meter (ind m^{-1}) of those organisms was calculated as a linear interpolation between sampling levels and was therefore dependent on the species abundance and the width of each zone.

Beach height at each transect was calculated using Emery's profiling technique (Emery, 1961) and beach face slopes were then obtained for each site. Sediment samples for grain-size analysis were collected with a 3 cm diameter corer to a depth of nearly 5 cm at the base of the foredune or at the beginning of the sandy habitat immediately seaward of the tree vegetation, as well as at the DL, EL and LT of each beach and transect. Granulometry was performed using a settling tube (Emery, 1938) and the mean grain size of sands was calculated following the moment computational method (Seward-Thompson and Hails, 1973) and expressed in microns (Folk, 1980). The grain sizes collected at the abovementioned points were grouped as follows to characterize the different beach zones: the dry zone or upper beach (the average of mean sizes estimated for the rear border of the beach and DL), the retention zone (the average of mean sizes estimated for DL and EL), the

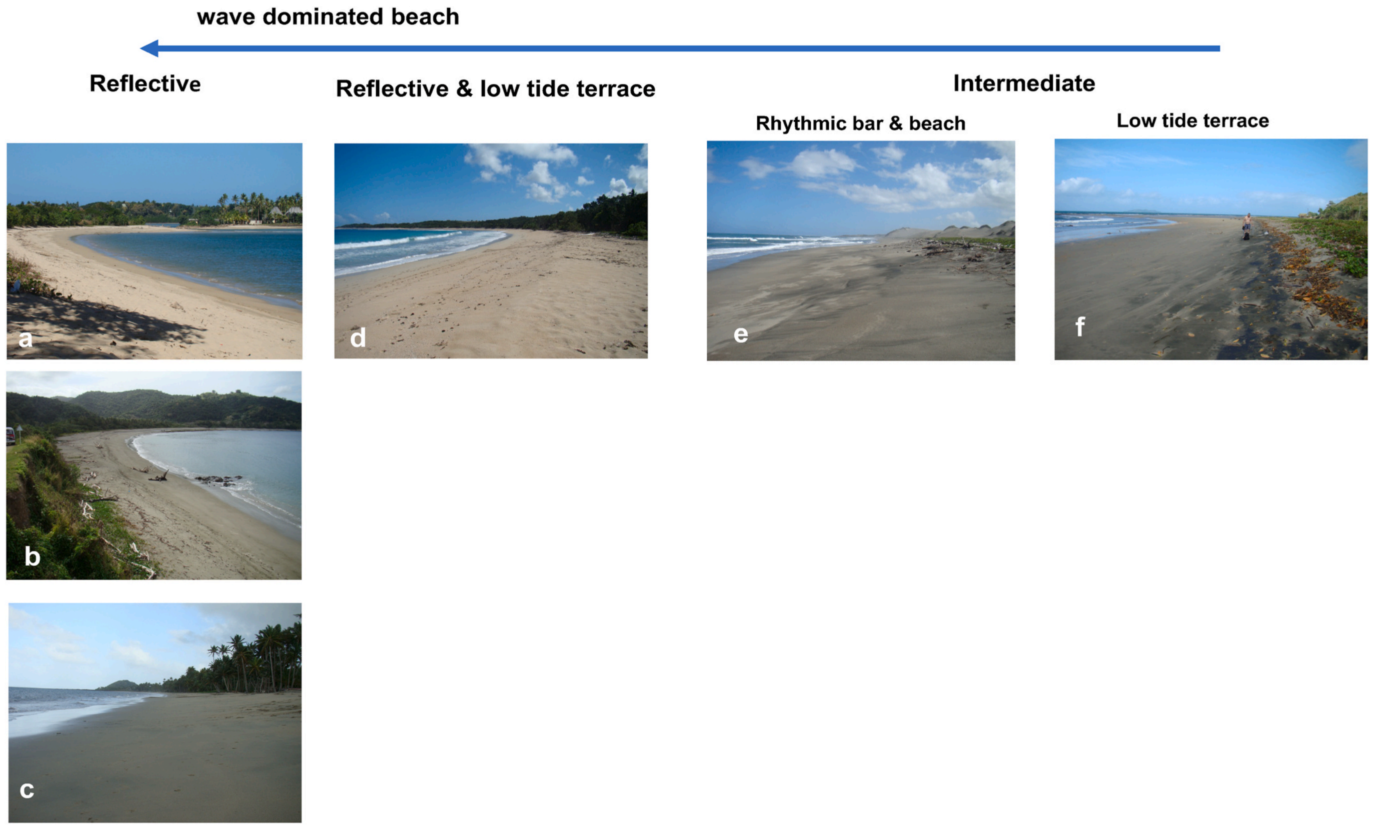

Fig. 2. Representative images of the sandy sites studied ordered according to beach morphodynamic types (see text): a) SL, b) SB, c) PH, d) Nt, e) Si, and f) WV.

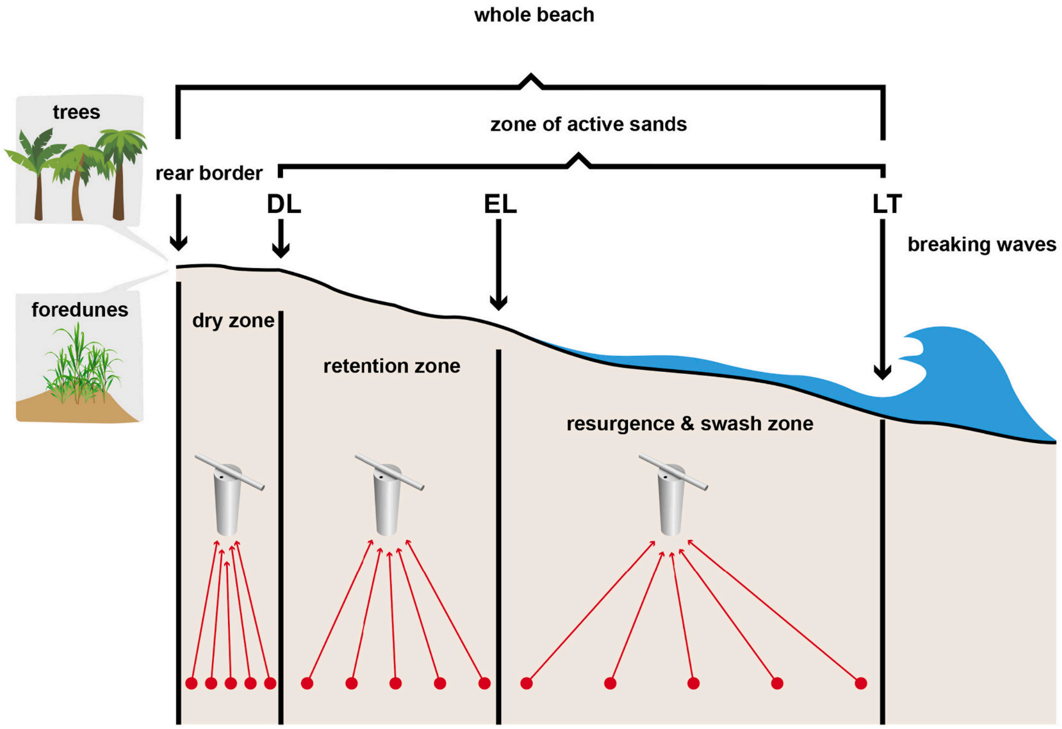

Fig. 3. Limits of the physical zones of beaches: the dry or upper zone between the rear border of the beach and the latest drift line (DL) or high tide mark; the retention zone between DL and the effluent line (EL) or the upper limit of the resurgence zone; and the resurgence/swash zone between EL and the low tide level (LT) or collapse point of breaking waves. Red dots represent the five samples collected with five 10 cm diameter corers, placed equidistantly from one another, in the dry, retention, and resurgence/swash zones (see text for further details).

resurgence/swash zone (the average of mean sizes estimated for EL and LT), and the zone of active sands or zone where sand grains are transported by waves and tides (the average of mean sizes estimated for DL, EL and LT) (Fig. 3).

2.3. *Macroinvertebrate species richness and near-ocean productivity*

Information on the ecology of tropical sandy beaches was used to assess the hypothesis that species richness of tropical sandy beach macroinvertebrates is affected not only by beach morphodynamics, but also by a bottom-up effect dependent on the inorganic nutrients that enhance primary production in the water column. Thus, upwelling data (m day $^{-1}$) were used as a proxy of the general productivity of coastal waters along the 30° equatorial belt. Values for the surrounding water of 24 beach sites were calculated as the average upwelling rate over 48 weeks, in accordance with the study published by Froyland et al. (2014, see Fig. 3a for detailed information) where short flow time trajectory data in a grid of 2° × 2° between 75° N and S is used to identify surface upwelling-downwelling distribution on a global scale. This method is based on a time-dependent horizontal velocity vector taken from the Ocean General Circulation Model for the Earth Simulator (OFES model). OFES is a global high-resolution model (Masumoto et al., 2004; Sasaki et al., 2008) configured on a 1/10° horizontal resolution grid with 54 vertical levels and forced with observed winds from the National Centers for Environmental Prediction (https://www.weather.gov/ncep/) and the National Center for Atmospheric Research (https://ncar.ucar.edu). Since current models indicate that coastal upwellings are stable in space over time (Barth, 1989; Haynes et al., 1993) –regardless of seasonality and short-term cycles that can operate from years to decades (e.g. ENSO)– we have assumed that the upwelling data obtained are widely representative of the ocean productivity in the areas studied. We obtained data related to the number of macroinvertebrate species on ocean exposed sandy beaches from 19 peer-reviewed papers which reported on studies conducted in the following places covering a latitudinal range close to 30° N and S of the Equator (Fig. 4, Table S1): Ecuador (Valdivia Bay) (Aerts et al., 2004), New Caledonia (Karitake beach) (Barón and Clavier, 1994), Atlantic coast of Costa Rica and Colombia (Dexter, 1974; Sibaja-Cordero et al., 2019), Pacific coast of Costa Rica and Colombia (Dexter, 1974; Sibaja-Cordero et al., 2019), Gulf of Mexico (Dexter, 1976), Pacific coast of México (Dexter, 1976), Atlantic coast of Panama (Dexter, 1979), Pacific coast of Panama (Dexter, 1979), coast of Brazil (Rio de Janeiro) (Soares-Ramalho-Fernandes and Soares-Gomes, 2006; Veloso et al., 1997; Veloso and Cardoso, 2001; Veloso et al., 2003), Australia East coast (Queensland) (McLachlan et al., 1996; Hacking, 2007), India East coast (Bay of Bengal) (McIntyre, 1968), Oman (McLachlan et al., 1998), Karavatti atoll (Narayanan and Sivadas, 1986), Cuba (East coast) (Ocaña et al., 2012), Kalvadevi (NW India) (Sivadas et al., 2012), Madagascar (N and SE coast) (Soares, 2003), and Peru (Lima) (Tarazona et al., 1986).

2.4. *Data analysis*

ANOVA and a Tukey's test were performed to explore eventual differences in the means of the abiotic and biotic factors studied for each beach (i.e., beach face slope, mean grain size of sands, and species richness and abundance of macroinvertebrates). The relationships among i) species richness and abundance of the macroinvertebrates versus beach features at the studied site, and ii) total species richness and species richness of Crustacea, Polychaeta and Bivalvia versus ocean productivity, were analyzed by regression analyses: step-wise selection procedure and R^2 criteria.

We examined the dissimilarity of the macrobenthic community composition (i.e. species-specific abundance) across the six beaches conducting a principal coordinate analysis (PCO) for centroids. The PCOs were based on the Bray-Curtis resemblance measure calculated from 4th-root transformed variables, followed by one-factor (beach as a fixed factor) non-parametric multivariate analyses of variance (PERMANOVA, unrestricted permutation of raw data, 9999 permutations). Only significant effects ($p < 0.05$) were further investigated through a series of pairwise comparisons using the appropriate terms in the model. When the number of unique permutations was low (i.e. less than 100), the Monte Carlo p-value was used. PERMDISP was used to check whether data showed homogeneity in multivariate dispersion.

The distribution of the abiotic variables (i.e., sediment characteristics, beach slope, and beach width) was first examined by the Draftsman plot routine to assess the degree of skewness and correlations. To ascertain how much of the overall change in the composition of the beach macrofauna community (fourth root-transformed abundance per linear meter, m^{-1}) can be explained by the abiotic variables (log (x+1) transformed), distance-based linear models (DistLM) were performed

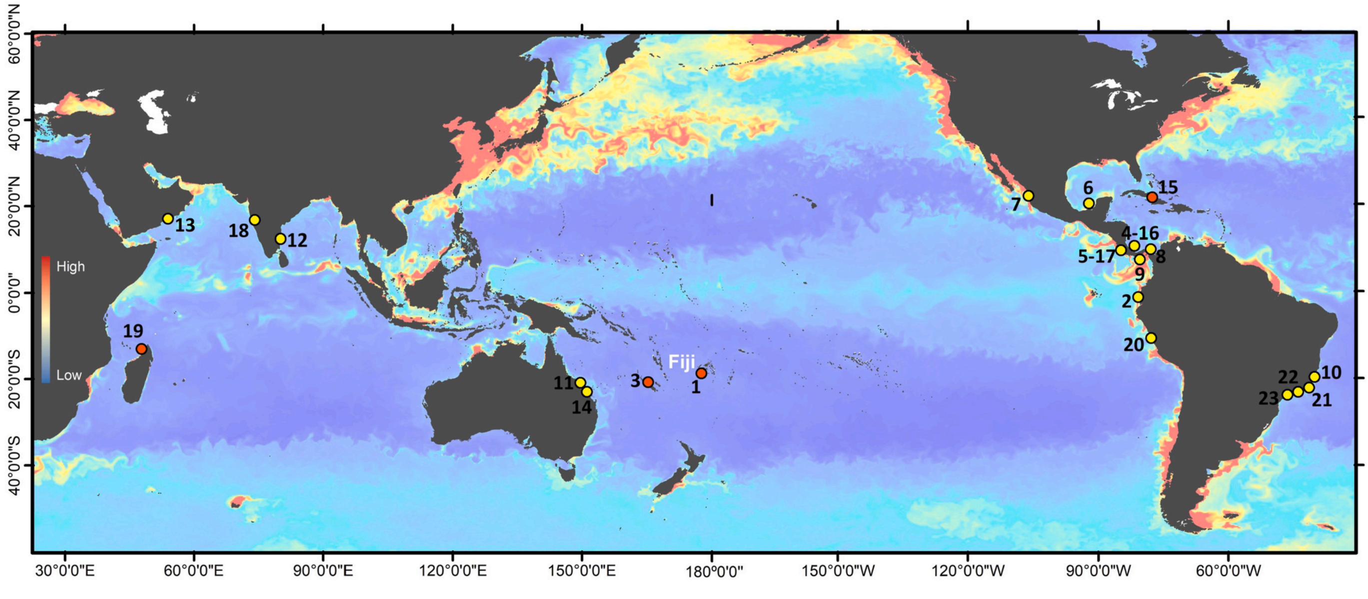

Fig. 4. Location of sites distributed along the 30° equatorial belt, from which data of macroinvertebrates were extracted to test the hypothesis that sandy beaches located inside the upwelling areas harbor higher species richness and abundance than beaches located away from those areas (see text and Supplementary Table S1 for name of sites).

(beach replicated transects as sampling units). DistLM performs a partitioning in the variation in data matrices similar to a regression, but it generates p-values by a permutation routine (9999 permutations). DistLM were fitted using the Best selection procedure and R^2 criteria. Distance-based redundancy analysis (dbRDA) was applied to visualize the position of the sites fitted to the significant predictor variables. All the multivariate analyses were performed using PRIMER7 (Anderson et al., 2008; Clarke and Gorley, 2015).

3. Results

3.1. Beach characteristics

Beach width ranged from 24 m (SL) to 40–41 m (SB, Si, and WV) (Table 1, Fig. 5). The widest dry zone occurred at SB (20 m) and the narrowest at WV and Nt (2 and 3 m, respectively). The width of the retention zones was similar (10 m) at SL, SB, and PH; while it was the highest at Nt (18 m), followed by Si (16 m) and WV (15 m). SL, SB and Si showed the narrowest resurgence zones (10–12 m), while WV had the widest resurgence zone (24 m) (Table 1, Fig. 5).

SL and Si had the steepest whole beach slopes (1/8.3 and 1/8.7, respectively), while WV showed the flattest slope (near 1/17) (Table 1, Fig. 5). Results of ANOVA and Tukey's test showed significant slope differences among beaches ($F = 507.5$, $p < 0,001$; Supplementary Table S2), with sites ranging from flatter to steeper as follows: WV > SB > PH > Nt = Si > SL (Supplementary Table S2; see also Fig. 5). The slopes of the resurgence/swash zones yielded significantly similar results ($F = 672.2$, $p < 0,001$; Supplementary Table S2), as for the whole beach slope: WV > SB=PH > Si > SL=Nt (Supplementary Table S2; see also Fig. 5).

The highest drift line was found at the beaches of Nt and Si: approximately, 410 and 293 cm above the low tide level (Table 1, Fig. 5), two sites with some of the steepest whole beach face slopes (1/9.0 m/m and 1/8.7) (Table 1). There were significant differences in drift line height among beaches ($F = 268.3$, $p < 0,001$; Supplementary Table S2), with sites ranging from the highest to the lowest drift lines above LT, as follows: Nt > Si > PH=SB=SL > WV (Supplementary Table S2; see also Fig. 5).The lowest drift line was found at WV (near 212 cm above the low tide level); the site with the flattest beach face slope (1/17.2 m/m) and the widest resurgence/swash zone (24 m; Fig. 5). Remarkably, the highest drift lines were measured in the steepest beaches, Si and Nt, a fact explained by the significant swell that occurred during the two consecutive days when sampling was conducted at these sites, what plausible pushed up the position of the drift line along the beach face.

Table 1
Widths (m) of the whole beach, dry, retention, and resurgence/swash zones (Dr, Rt and Rs & Sw, respectively); slopes of whole beach and that of the resurgence/swash zones; and height of drift line (DL) above low tide level (LT) (see Fig. 3 for locations and limits of those zones). The values for slopes and heights of DL above LT are means (n = 4 transects) with standard deviation in parentheses. Beaches are ordered according to beach morphodynamic types (see also Fig. 2). Acronyms for beaches as in Fig. 1.

sites	widths of:				slope of whole beach (m/m)	slope of Rs & Sw zone (m/m)	height of DL above LT (cm)
	whole beach	Dr	Rt	Rs & Sw			
SL	24	4	10	10	8.3 (0.2)	9.9 (0.3)	237.8 (5.0)
SB	40	20	10	10	12.2 (0.3)	13.5 (0.7)	240.5 (5.2)
PH	33	8	10	15	10.9 (0.2)	13.0 (0.2)	252.8 (10.2)
Nt	37	3	18	16	9.0 (0.3)	9.7 (0.4)	411.0 (15.6)
Si	40	12	16	12	8.7 (0.3)	12.5 (0.4)	293.3 (5.7)
WV	41	2	15	24	17.2 (0.4)	32.9 (0.6)	212.3 (5.1)

The mean grain size (MGS) analyses indicated that beach sediments belonged to the medium and coarse sand interval (250–500 μm and 500–1000 μm, respectively; Folk, 1980) (Table 2). There were significant MGS differences ($p < 0.001$) among beaches, with SB, Nt, and Si showing coarser sand than SL, PH, and WV (Supplementary Table S3).

3.2. The intertidal macroinvertebrates

Twelve taxa belonging to eight major taxa (Coleoptera, Amphipoda, Isopoda, Decapoda, Polychaeta, Oligochaeta, Bivalvia, and Gastropoda), were collected from the dry (upper beach), retention (middle beach) and resurgence/swash (lower beach) zones sampled at each site (Table 3). The sandy beach macroinvertebrate taxa were dominated by crustaceans (5 taxa) and polychaetes (3 taxa) (Table 3). Among crustaceans, talitrid amphipods and isopods from genus *Tylos* sp. were primarily found at the upper and middle beach, while the isopod *Euridyce wyuna* and the decapods *Hippa indica* and *Albunea steinitzi* were mostly found at the lower beach (Table 3). The most common polychaetes, *Scolelepis carunculatus* and *Scolelepis lamellicinta*, were primarily found at the lower beach, as happened with the bivalve *Donax* sp. and the gastropod *Hastula* sp. (Table 3).

Taxa richness was quite low, with a maximum of 5–6 taxa (PH, Si, and Nt) and mean values ranging from 0.8 (SB) to 2.3 taxa (SL and Nt, respectively) (Table 4) with no significant differences among beaches (Supplementary Table S4). There were no significant differences ($p > 0,05$) in the mean total abundance (Supplementary Table S4). The highest abundance was recorded at Nt and WV (means = 1144.8 and 1375.0 ind m^{-1}, respectively) and the lowest at SB (mean = 191.3, ±244.1) (Table 4). Among the two most abundant polychaetes, *Scolelepis carunculatus* showed higher abundance than *Scolelepis lamellicinta*, with mean abundances of up to 445.3 and 1126.8 ind m^{-1} at Nt and WV, respectively (Table 4). Those values were significantly higher ($p < 0.001$) than the abundance estimated for this polychaete at SL, SB, PH, and Si (Supplementary Table S4).

When considered individually, morphodynamic variables such as beach slope, beach width, and sediment grain size could not account for the significant variation in the number of species and abundance of the studied beaches ($p > 0.05$ in all cases).

The PCO showed discrimination of the macrofauna community composition (the first two axes explained 75.9 % of the variation) between beach sites (pseudo-$F_{5,18} = 3.59$; $p < 0.001$, PERMANOVA) based on dissimilarities among species-specific abundance (Fig. 6). The PERMDISP detected no significant multivariate dispersion of the macrofauna assemblages within beach sites ($F_{5,18} = 2.65$; $p = 0.170$). The largest dissimilarities in macrofauna assemblages when comparing two beaches were found between WV-Si, WV-SB and WV-SL (≤15%), and between SL-SB, SL-Nt, and SL-Si (≤30%) (Fig. 6, Supplementary Table S5). The macrofauna community of WV beach is dominated by *Scolelepis carunculata* ($F_{5,18} = 3.21$; $p < 0.05$), while SL beach is dominated by *S. lamellicincta* ($F_{5,18} = 8.42$; $p < 0.001$) and *Donax* sp ($F_{5,18} = 3.87$; $p < 0.05$) (Supplementary Fig. S1).

The DistLM highlighted the association between the macrofauna community composition and the abiotic variables of the beaches (the model accounted for almost 31% cumulative variation) (Supplementary Table S6). A significant part of the variation observed in the macrofauna community was explained by sediment characteristics (i.e. grain size at the resurgence/swash zones) and beach width (Table DISTLM). The first 2 dbRDA axes captured most of the salient patterns in the fitted model, with 100 % of the variability, and 31 % of the total variation in the data cloud (Supplementary Table S6). The resulting plot showed a pattern with a clear separation between the samples of the most reflective beaches (i.e. SB, PH, and SL) and the rest of the beaches (Fig. 7).

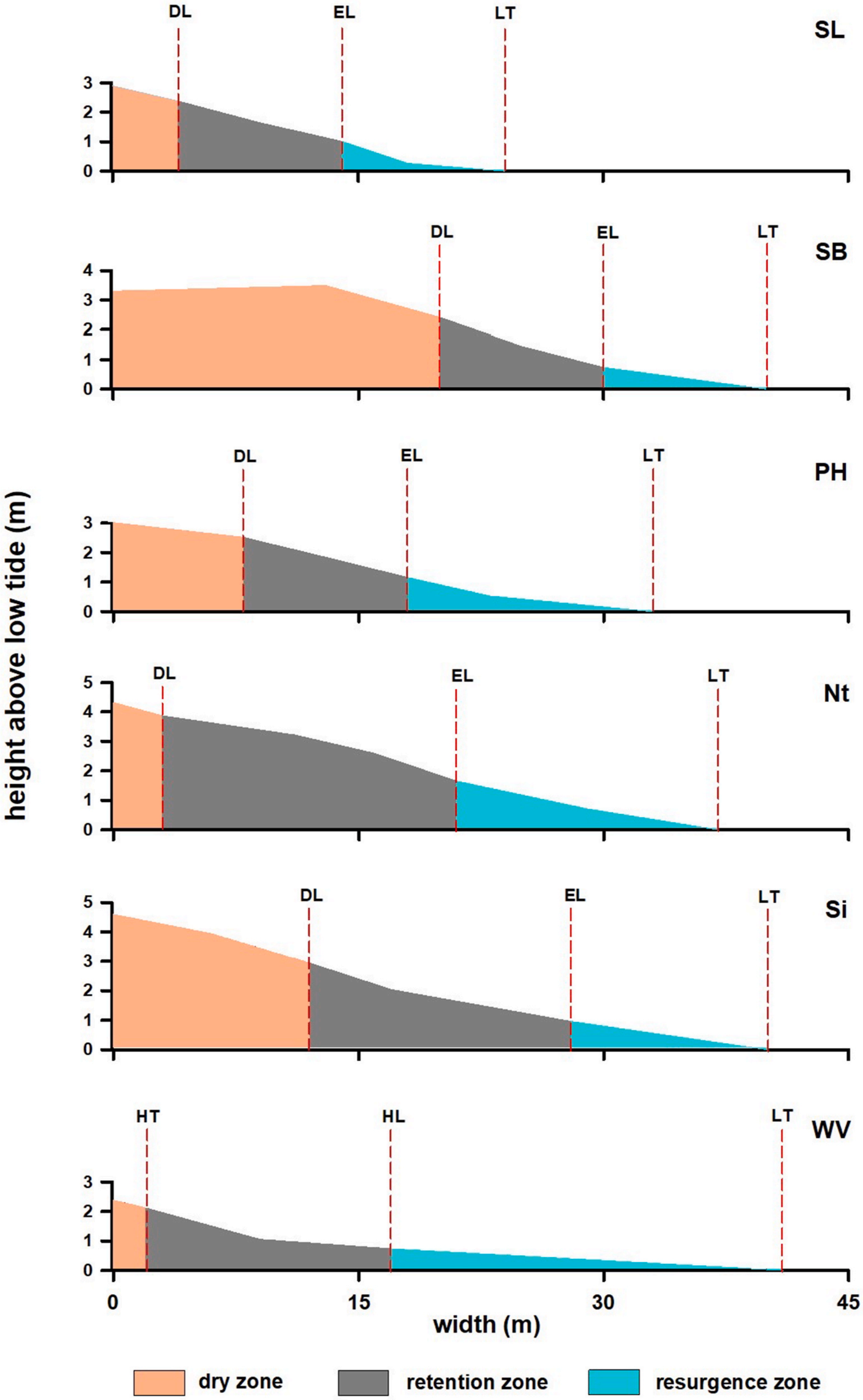

Fig. 5. Beach face slopes, widths of the whole beach and those of the dry, retention and resurgence zones at the study sites. suppAcronyms for beaches as in Fig. 1. DL = drift line, EL = effluent line and LT = low tide level. The zone above DL is the dry zone, that between DL and EL is the retention zone, and that between EL and LT is the resurgence zone. Beaches are ordered in terms of beach morphodynamic types (see also Fig. 2).

Table 2
Mean grain size (microns) of sand at the dry, retention, resurgence/swash, and active sands zones (see Fig. 3 for locations and limits of those zones). The values are means of four replicated samples with, standard deviation in parentheses. Beaches are ordered according to beach morphodynamic types (see also Fig. 2). Acronyms for beaches as in Fig. 1.

sites	dry zone (rear border to DL)	retention zone (DL to EL)	resurgence & swash zone (EL to LT)	zone of active sands (DL to LT)
SL	408 (90.3)	301.5 (30.6)	270.5 (25.1)	289.5 (35.3)
SB	696.1 (173.4)	668.1 (159.0)	786.0 (121.1)	717.8 (168.3)
PH	404.5 (75.6)	344.7 (45.3)	358.5 (68.2)	357.8 (57.0)
Nt	714.3 (45.9)	546.1 (163.0)	431.6 (74.5)	515.6 (138.6)
Si	503.1 (108.4)	523.1 (93.6)	617.4 (159.1)	597.8 (146.7)
WV	277.2 (23.9)	257.4 (12.7)	277.8 (28.4)	271.0 (25.8)

Table 3
List of taxa collected at the beaches studied. Major taxa are: IC= Insecta Coleoptera, CA= Crustacea Amphipoda, CI= Crustacea Isopoda, CD= Crustacea Decapoda, AP = Annelida Polychaeta, AO = Annelida Oligochaeta, MB= Mollusca Bivalvia, MG = Mollusca Gastropoda. Acronyms for beach zones are: Dr = dry zone or upper beach, Rt = retention zone or middle beach, and Rs & Sw = resurgence/swash zone or lower beach. Beaches are ordered according to beach morphodynamic types (see also Fig. 2). Acronyms for beaches as in Fig. 1.

lower taxa	SL	SB	PH	Nt	Si	WV
IC/undetermined species			Dr			
CA/Talitridae indet.				Dr/Rt		
CI/*Tylos* sp.				Rt	Rs & Sw	
CI/*Eurydice wyuna*				Rt/Rs & Sw		
CD/*Hippa indica*		Rs & Sw		Rs & Sw	Rt	
CD/*Albunea steinitzi*			Rs & Sw			
AP/*Scolelepis caruncultatus*	Rs & Sw	Rt	Rt	Rt/Rs & Sw	Rs & Sw	Rt/Rs & Sw
AP/*ScolelepIs lamellicinta*	Rs & Sw		Rs & Sw	Rs & Sw	Rt/Rs & Sw	
AP/*Harmothoe* sp.	Rs & Sw					
AO/undetermined species					Rs & Sw	
MB/*Donax* sp.	Rs & Sw					Rt/Rs & Sw
MG/*Hastula* sp.			Rs/Sw			

3.3. Macroinvertebrate species richness and ocean productivity

The number of taxa of macroinvertebrates found on tropical sandy beaches, according to peer-reviewed literature, was positively related to the upwelling rate measured in the surrounding coastal water (Fig. 8). Likewise, significant trends were observed for crustaceans and polychaetes species, but not for mollusks (Fig. 8, Supplementary Table S1). Data on macroinvertebrate taxa from Fiji (Fig. 8) fall in the lowest levels of the upwelling rates (m day^{-1}) and taxa richness of sand beach macroinvertebrates along the tropical belt analyzed (Supplementary Table S1).

Table 4
Community attributes of the macroinvertebrate fauna: highest and mean species richness and mean total abundances and abundances of the most common invertebrates in the study area (the polychaetes *Scolelepis caruncultatus* and *Scolelepis lamellicinta*). The values are means of four replicated samples, with standard deviation in parentheses. Beaches are ordered according to beach morphodynamic types (see also Fig. 2). Acronyms for beaches as in Fig. 1.

beaches	highest species richness	mean species richness	mean total abundance (ind m^{-1})	mean abundances of *Scolelepis caruncultatus* (ind m^{-1})	mean abundances of *Scolelepis lamellicinta* (ind m^{-1})
SL	4	2.3 (1.3)	637.5 (329.2)	63.8 (127.5)	191.3 (127.5)
SB	2	0.8 (1.0)	191.3 (244.1)	63.8 (127.5)	0
PH	5	1.3 (1.5)	637.8 (765.0)	127.5 (255.0)	63.8 (127.5)
Nt	6	2.3 (1.5)	1144.8 (912.3)	445.3 (353.4)	0
Si	5	2.0 (0.8)	943.3 (326.8)	76.5 (153.0)	76.5 (153.0)
WV	2	1.3 (0.5)	1375. (745.9)	1126.8 (631.2)	0

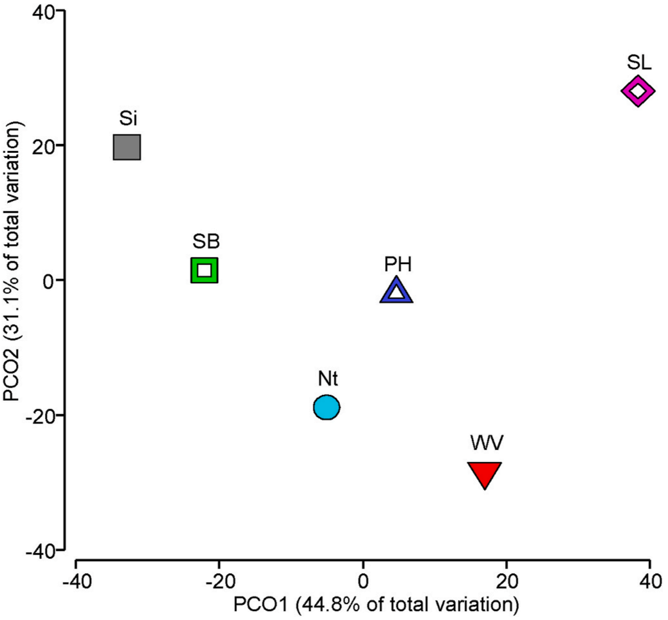

Fig. 6. Principal coordinate analysis (PCO) for centroids of the 4th-root transformed macrofauna community composition between beach sites based on the Bray-Curtis resemblance measure (9999 permutations).

4. Discussion

The beaches studied along the south shore of Viti-Levu harbor macroinvertebrate assemblages characterized by low taxa richness and abundance. As mentioned earlier, we categorized the beaches studied by expert judgment and beach slope and width. This categorization showed that morphodynamic features of exposed sandy beaches along the Fijian shore ranged from fully reflective (SL, SB, and PH) to intermediate (Si and WV). Dissipative beaches were absent along the studied coast. The extended presence of coral fringing reefs, prevents the high energy waves environment to reach the shore, which is necessary for the dissipative beaches to be formed. Dissipative beaches usually occur where waves exceed 2 m (McLachlan and Defeo, 2018), what is not common in beaches protected by reefs.

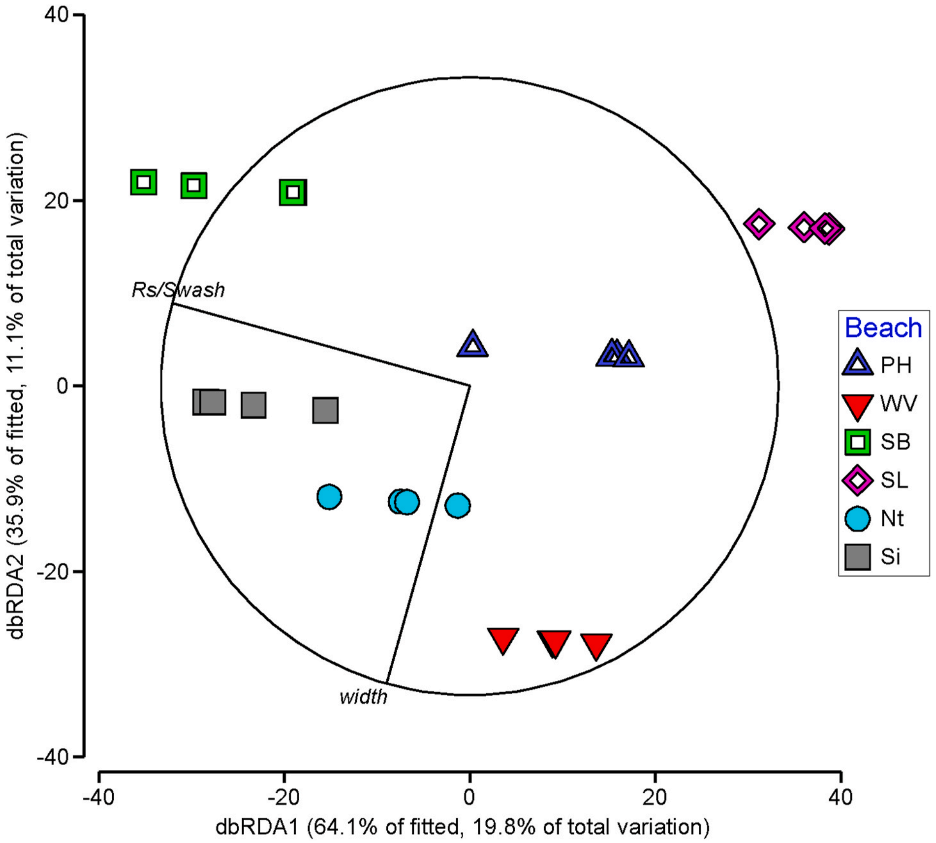

Fig. 7. dbRDA (distance-based redundancy analysis) ordination of the macrofauna community composition as predicted by the DistLM model. It shows the relationship between the abiotic predictors that best explain the variation in macrofauna composition in the six beaches studied.

In accordance with our hypothesis on community structure of intertidal macroinvertebrates *versus* beach types, we expected an increase in the number of macroinvertebrates taxa and abundance along the beach morphodynamic range studied; but there were no significant differences in taxa richness and total abundance of macroinvertebrates among beaches. Most probably, the morphodynamic range of beaches studied, included subtle differences which not result in notorious changes in the biotic variables studied here, a situation which may have been exacerbated by the absence of the dissipative type of beaches along the study area may have been exacerbated by the absence of the dissipative type of beaches along the study area.

In contrast with the univariate analyses, the multivariate evaluation performed to assess the relationships between the abiotic and biotic variables, did show that macroinvertebrate assemblages differed depending on the beach morphodynamic type. Thus, the beach site located at one of the extremes of our beach morphodynamic characterization (i.e., WV) was located far apart from the other sites in the PCO and dbRDA diagrams of the multivariate analysis. Those analyses revealed a relationship between the composition of the macroinvertebrate assemblages and basic features involved in beach morphodynamics, such the intertidal zone width and grain size. However, these variables can only account for 31% of the variability (see Table S6). The lack in explanatory power of the environmental variables used (31%), lead us to utilize the multicausal environmental severity hypothesis (Brazeiro, 2001) to provide a valid standpoint to clarify the role of the environment in explaining the differences in faunal assemblages. It is plausible that several factors, not included in the present study, are affecting differently to species with distinctive biotic characteristics. Consequently, we hypothesize that, when designing ecological studies of sandy beaches based on observational analyses, such as the present study, the main limitation might be that the geographic scale could not encompass a complete range of relevant environmental factors explicative of the biological trends."

It must be said that significant deviations from the paradigmatic relationship between beach morphodynamics and species richness and macrofauna abundance (e.g. Defeo et al., 1992; McLachlan, 1990; McLachlan et al., 1993, 1996; McLachlan and Dorvlo, 2005; McLachlan and Defeo, 2018) had been previously found by studies related to other coasts, in countries such as Spain and South Africa. Thus, Rodil et al. (2012, 2014) demonstrated that the macroinvertebrate community on the coast of northern Spain was not structured by a single physical factor, but instead by a complex set of drivers, including surrogates of food availability, such as chlorophyll-a. Similarly, it was found that the macrobenthic community on Mtunzini Beach, South Africa, is not structured mainly by physical factors, but instead by a complex and dynamic blend of nutritional, chemical, and physical drivers, including particulate organic matter, dissolved inorganic nutrients, and photopigment concentrations (Ortega-Cisneros et al., 2011). The results of these studies are aligned with the multicausal severity hypotheses (Brazeiro, 2001), which highlights the importance of assessing the beach climate in detail when explaining biological patterns, beyond those variables commonly used to characterize beach morphodynamics. In this regard, Rodil et al. (2012, 2014) and Ortega-Cisneros et al. (2011), demonstrated that oceanographic conditions need to be considered in the spatial analyses of the linkages between faunal assemblages and morphodynamic characteristics in ocean exposed sandy beaches, due to the bursting effect of nutrients availability and primary production on biotic richness. Moreover, we hypothesize that environmental control (i.e., filtering effect of the environment) at local-regional scale, and dispersal-connectivity among beaches, as part of the metacommunity dynamics theory (Gálvez et al., 2022), could have a strong influence on faunal assemblages and biodiversity. We did not include metacommunity analyses in our observational design, but we hypothesize that the distribution of beaches along the studied shore operates as

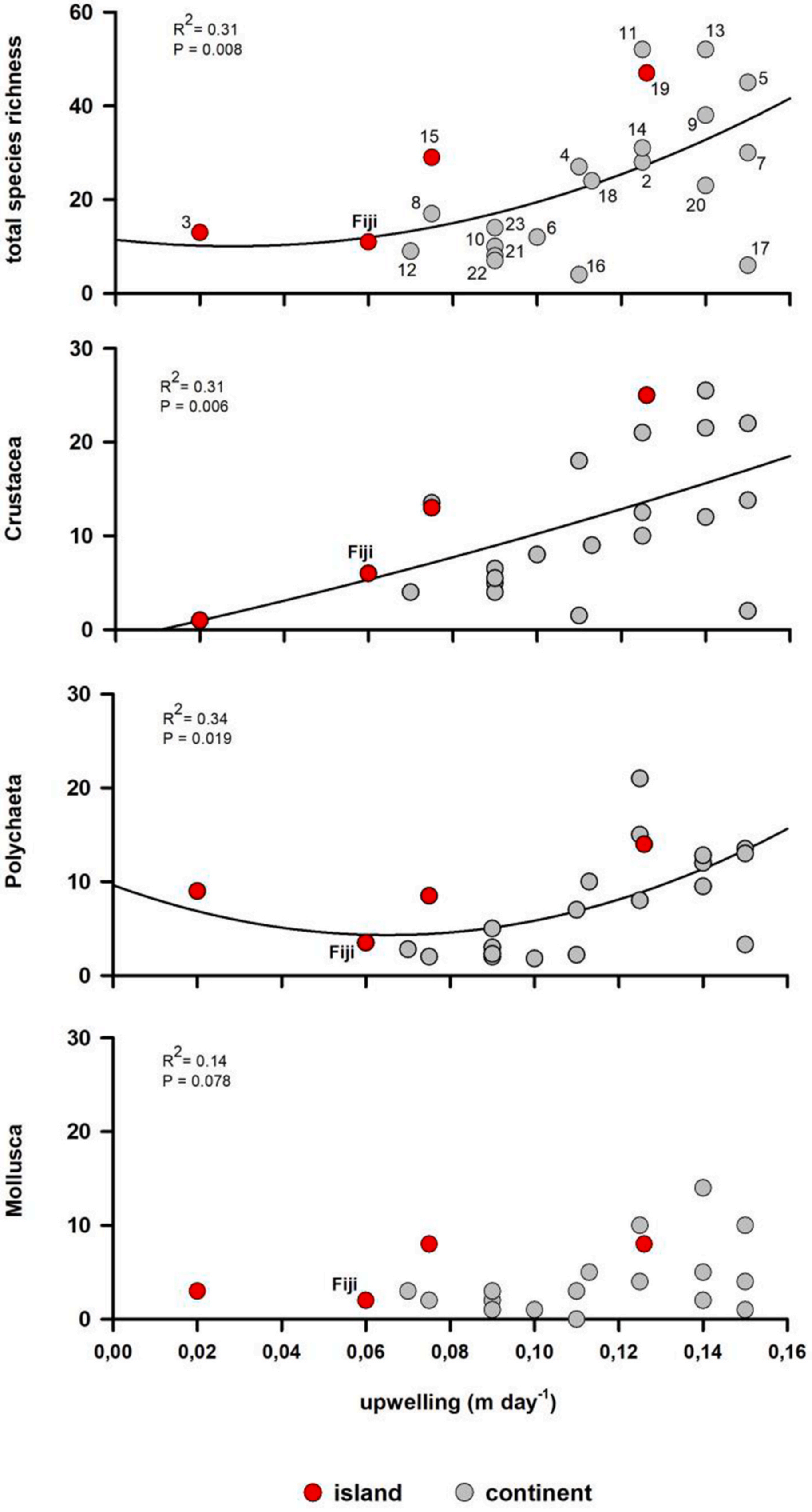

Fig. 8. Relationships between total species richness and species richness of Crustacea, Polychaeta, and Mollusca and upwelling rates across the tropical zone of the oceans. Upwelling calculated as the average rate over 48 weeks (m day^{-1}) in the surrounding coastal waters, according to Froyland et al. (2014) (see text for further details).

fragmented and heterogenous suitable habitats in a matrix of non-habitat for beach species (rocky headlands, mangrove forest, etc) (Leibold et al., 2004). Which types of species interactions are occurring at different spatial scales (within and among islands), as well as the assessment of the pre-recruit abundance and recruitment forecasting (Le Pape et al., 2020), are critical issues in further understanding on the ecology of sandy beaches of natural communities in tropical archipelagos of the South Pacific.

Shifting our analyses to a larger geographic scale, the second hypothesis of this study, that sandy beaches in upwelling areas harbor higher taxa richness and abundance of macroinvertebrates than beaches located away from those areas, can be tested. When comparing with other open-ocean tropical sandy beaches, biotic variables studied at the Fijian shore were within the range obtained on isolated islands located in oligotrophic regions of the Indo-Pacific Ocean, for instance, in New Caledonia (average 7.3 spp.; 15 spp. in total) (Barón and Clavier, 1994) or Kavaratti atoll (8 spp. in total) (Narayanan and Sivadas, 1986), among others. When comparing with sandy shores fringing continental plates, where nutrient supply prevails throughout the year, the number of species from the beaches of Viti-Levu was significantly inferior to the number of species found on beaches on the Pacific coast of Panama (60 spp.) (Dexter, 1979), Costa Rica (6–68 spp.) (Sibaja-Cordero et al., 2019) and on subtropical beaches on the coast of Oman (19–25 spp.) (McLachlan et al., 1998). Continental beaches along the tropical belt in oligotrophic waters harbor a similar number of species than those located on islands where downwelling oceanographic conditions or poor upwelling occurs; for instance, on the east coast of Australia (5–19 spp.) (Dexter, 1983; Hacking, 1998) and the northern coast of Spain (9–10 spp.) (Lastra et al., 2006).

Connections between biodiversity and food subsidies received from neighboring ecosystems have been demonstrated in the case of sandy beaches in temperate latitudes, where species richness is profoundly affected by the amount of algal wrack supply (Dugan et al., 2003; Rodil et al., 2019; Duarte et al., 2014). The effect of carrion on invertebrate assemblages in the intertidal beach have not been tested to date, but the studies at population level have demonstrated that conspicuous scavengers, such as ghost crabs (*Ocypode* sp.) (Schlacher et al., 2013) or Hippid crabs (*Hippa* spp.) (Wenner, 1977) responded strongly to carrion availability. In coral reef ecosystems, the dominance of coral over algae is associated with oligotrophic conditions and herbivore predominance, which prevents the proliferation of frondose macroalgae (Littler and Littler, 1994). Hence, the general scarcity of intertidal beach macrofauna observed in the beaches studied could be related to the lack of stranded marine macrophytes and carrion supplied by the dominant surrounding ecosystem, namely, the coral reef. In tropical sandy shores, the relationship between marine subsidies and biotic richness has been previously observed on Hawaiian beaches, where abundance of the scavenger crab (*Hippa pacifica*) was positively related to food supply estimated through edible C in the sediment (proteins + lipids + carbohydrates) (Lastra et al., 2016). Similarly, abundance and other biotic features, such as egg production, of *H. pacifica* on Hawaii and the Marshall Islands was mediated by the number of Portuguese man o'war *Physalia physalis*, the main prey of the scavenger crab (Wenner, 1977; Wenner et al., 1987). Besides algal wrack and carrion, the general productivity of coastal waters, measured as pigment concentration in the water column (Lastra et al., 2006; Ortega-Cisneros et al., 2011; Rodil et al., 2012) is a factor that can account for the observed trends. As many of the tropical islands in central South Pacific, Fiji is located in a low productive oceanographic region where chlorophyll concentration is low (Morel et al., 2010; Boyce et al., 2010), which is indicative of oligotrophic waters.

5. Conclusions

Taxa richness and total abundances of the sand beach macroinvertebrates assemblages were poorly related to the range of morphodynamic beach types studied on the coast of Viti-Levu. We postulate that the variability of macrofaunal assemblages was related with the synergistic effect of several environmental variables not included in the study, that exert different selective pressure depending on species characteristics, as stated by the multicausal environmental severity hypothesis. Beside this, we suggest that the scarcity of food subsidies received from nearshore waters was one of the factors responsible for the biotic depletion observed along the beach morphodynamic range analyzed. The lack of dissipative morphodynamic beach type along the studied shore, prevent to debate on the paradigmatic statement that the structure of the faunal community is primarily framed by beach morphodynamics. The evaluation of variability in nutrient supplies and species richness on a global scale showed that the tropical beaches included in our study harbor similar poor assemblages of species, which are comparable to those of tropical sandy beaches in low productive coastal areas, either on islands or along the continental rim.

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CRediT authorship contribution statement

M. Lastra: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **E. Jaramillo:** Writing – review & editing, Writing – original draft, Methodology, Data curation, Conceptualization. **J. López:** Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **J. Troncoso:** Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **I.F. Rodil:** Writing – review & editing, Writing – original draft, Supervision, Software, Methodology, Conceptualization. **J. Vergara:** Visualization, Validation, Software. **A. Maracava:** Investigation, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106850.

Data availability

Data will be made available on request.

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