



Local human pressures modulate turf sediment loads in a warm-temperate oceanic island

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ABSTRACT

In the Anthropocene, algal turfs are expected to replace macroalgal forests and coral cover as the dominant benthic state. These turf seascapes play a key role in regulating ecosystem processes through sediment retention, which carries significant ecological and socio-economic implications. However, our understanding of sediments trapped by turf on coastal reefs, particularly in oceanic islands, remains limited. In this study, we quantified turf seascape architecture (algal composition and mean height) and sediment properties (total particulate load, grain size distribution, and organic content) across a warm-temperate oceanic island. We further decoupled the role of geomorphological, anthropogenic, and turf algae structural predictors in explaining spatial variation in turf sediment properties. Our results revealed significant spatial variation in turf sediment loads, varying by three orders of magnitude ($\sim 1 \text{ g/m}^2$ to 2000 g/m^2), while organic load varied by two orders of magnitude ($\sim 1 \text{ g/m}^2$ to 100 g/m^2). Human pressure and turf algal composition were the strongest predictors of turf sediment load, highlighting the role of local human stressors in modulating sediment dynamics in emerging turf seascapes. Our study provides baseline information on the patterns and drivers of turf sediments in oceanic islands, a critical area to develop management plans that target the resilience of core ecosystem functions under altered reef configurations in the Anthropocene.

1. Introduction

Marine ecosystems are rapidly being reshaped in a human dominated era, caused directly by activities that extirpate species (Cardinale et al., 2012; Sherman et al., 2023) and indirectly by affecting Earth's climate (IPCC, 2021). Biodiversity change arisen from human activities often leads to novel ecosystem configurations with altered species interactions and ecosystem functions (Beaugrand et al., 2015; Bosch et al., 2022a), potentially altering the goods and services provided to human societies (Pech et al., 2017; Bonebrake et al., 2017). A clear example of such a process, is the widespread transformation of shallow reef systems from species with competitive life histories (K-strategists), such as tropical reef-building corals and temperate macroalgal forests, to opportunistic (r-strategists) carpet-like aggregations of low-lying macroalgae (herein, algal turfs) (O'Brien and Scheibling, 2018; Bellwood et al., 2019).

While the specific drivers of these ecosystem reconfigurations vary across the globe, from global warming to local pressures (e.g.,

eutrophication and sedimentation), several generalisable responses of ecological communities have been observed across tropical and temperate biomes (Filbee-Dexter and Wernberg, 2018; Connell et al., 2014). The loss of three-dimensional structure, for instance, can modify several key properties of habitat architecture that are critical for supporting associated organisms (Fraser et al., 2020a; b; Pessarrodona et al., 2021), as well as alter the transfer of energy through the food web (Pessarrodona et al., 2022a; Bosch et al., 2022b). Once established, turfs sustain their dominance through a series of reinforcing feedback mechanisms (Filbee-Dexter and Wernberg, 2018; O'Brien and Scheibling, 2018), such as: (i) quickly overgrowing and monopolising primary substrate, thus limiting suitable hard substratum for propagule settlement, and (ii) accumulating sediment, which reduces germination and survival rates of other habitat forming, foundational, species (Filbee-Dexter and Wernberg, 2018).

The nature of algal turfs, and the functions they underpin, is strongly shaped by the quantity and quality of sediments they trap (Tebbett et al.,

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2019). Turf algae retain and accumulate sediment by slowing water movement and using mucilage to bind deposited particles (Carpenter and Williams, 1993). The quantity of sediment retained by the turf varies greatly, as a function of both internal (i.e., compositional and structural variation) and external biophysical processes (i.e., biotic and abiotic determinants). Although traditionally perceived as relatively homogenous and structurally simple, turf seascapes encompass many phylogenetically diverse species, displaying varying morphologies, heights, and densities (Connell et al., 2014; Filbee-Dexter and Wernberg, 2018). This variability, in turn, determines the rate at which sediments are trapped (Gordon et al., 2016; Goatley et al., 2016; Tebbett et al., 2018a). For instance, the height of algal turfs is a critical driver of sediment accumulation, which underpins a key ecological transition, from short productive algal turfs (SPATs) to long sediment-laden algal turfs (LSATs) (Fong et al., 2018; Duran et al., 2019). Several external factors also modulate the quantity and size of sediments bounded within turf seascapes, including local sediment inputs (Browne et al., 2013; Tebbett et al., 2018b), reef geomorphology (Tebbett et al., 2017a), hydrodynamics (Bodde et al., 2014; Purcell, 2000), and the feeding activity of fishes (Goatley and Bellwood, 2010; Krone et al., 2010). The accumulation of algal turf sediments can have significant negative impacts, including hindering the recruitment of forest-forming species, affecting fish feeding behaviour, and the nutritional quality of algal resources (Goatley and Bellwood, 2012; Tebbett et al., 2017b, 2020).

Despite mounting evidence of these adverse impacts, knowledge on the patterns and processes underpinning sediment accumulation in turf seascapes are relatively scarce in both tropical (Tebbett and Bellwood, 2019; Schlaefer et al., 2021) and temperate reefs (Airoldi and Virgilio, 1998; Connell et al., 2014), relative to how abundant they are across the globe (Tebbett et al., 2023). These seascapes exhibit distinct compositions and architectures that vary widely across biogeographic regions, with cascading effects on ecological function (Pessarrodona et al., 2021). Oceanic islands are generally less resilient to biodiversity loss compared to continental regions, due to their isolation from mainland populations by vast geographic distances and abyssal barriers, which limit dispersal and recovery from disturbances (Kinlan et al., 2005). If a phase shift from either coral dominance or forest-forming macroalgae to turf-dominated seascapes occurs, recovery may be particularly challenging. This difficulty arises from feedback mechanisms, such as sediment trapping, that stabilize turf communities and hinder the recruitment of coral and macroalgal propagules, even when they are present (Goldberg et al., 2004; Martins et al., 2019). This calls for greater scientific attention on quantifying both the spatio-temporal patterns in turf sediments, as well as their implications for critical ecological processes that sustain coupled socio-ecological systems.

This study focuses on Gran Canaria Island, a warm-temperate oceanic island located at the biogeographic transition zone between the Atlantic-Mediterranean and the Tropical Eastern Atlantic. The region lies on the warm range edge of several temperate canopy-forming macroalgal forests of the genus *Cystoseira* and *Gongolaria sensu lato* in the northeast Atlantic Ocean (Valdazo et al., 2017). Forest-forming species have drastically declined in the last decades on the island, in response to Marine Heatwaves (MHWs) and intense coastal development (Valdazo et al., 2024). Despite these drastic habitat reconfigurations, it is unclear whether (or how much) turfs are expanding, and which drivers affect variability in their properties and associated sediments. This knowledge is critical for conservation, as turf expansion may hinder the recovery of *Cystoseira* and *Gongolaria* forests and affect the yields of socio-economically important targeted herbivorous fishes (e.g., the parrotfish *Sparisoma cretense*) (Tuya et al., 2006; Castro et al., 2019).

The goal of this study was to address these knowledge gaps, by quantifying key properties of turf algae (mean height, algal biomass and morpho-functional groups) and their associated sediments (particulate load, organic load, and grain size). Then, we modelled the relative importance of geomorphological, anthropogenic and turf algae structural predictors in shaping their spatial distribution, at the island scale.

These findings provide key insights for conservation and management, as understanding the distribution of turf seascapes is crucial for informing strategies aimed at mitigating their effects, and preserving the resilience of marine ecosystems in novel ecosystem configurations.

2. Materials and methods

2.1. Study context and experimental design

Surveys were conducted along the coast of Gran Canaria Island (Canary Islands, eastern Atlantic Ocean, 27° 44' N, 15° 35' W, Fig. 1a and b), at 12 shallow reef sites (range 1.53 m–15.12 m depth; 6.42 ± 3.71 m, mean \pm SD; Table S1) (Fig. 1c), during October–November 2023. Subtidal reefs on the island, located nearly 200 km off the northwest African coast, are mainly composed of basaltic rocky bottoms with steep slopes and sparse limestone reefs (Ramírez et al., 2008). The waters surrounding the coastal perimeter of the island are primarily oligotrophic, with the seasonal influence of cool-waters from the northwest African coast (Valdés and Déniz-González, 2015). At the local (i.e., site) scale, there is heterogeneity in the configuration of reefs, with north and western sides predominantly characterized by rocky cliffs and gravel beaches, while the eastern and south sides feature coastal platforms and sandy beaches (Valdazo et al., 2017; Di Paola et al., 2017). Coastal hydrodynamics, predominantly influenced by north-northwest swells and north-northeast trade winds (Sangil et al., 2013), strongly shape the composition and structure of benthic habitats on the island, which were historically dominated by frondose fucoid species in exposed shorelines and turf-algae in protected ones (Tuya and Haroun, 2006). During the last four decades, intense urban development in coastal areas, coupled with climate-related pressures (i.e., MHWs), have reshaped the configuration of shallow reefs, with drastic declines in the extent of complex marine forests of the genus *Gongolaria* (Valdazo et al., 2024). Our sampling design included the selection of these 12 sites to cover variations in the biophysical and anthropogenic factors that structure benthic habitats on the island, therefore providing an ideal model to test their relative role in shaping the composition and properties of turf seascapes.

2.2. Historical comparison

To examine the trajectory of shallow benthic assemblages in the last two decades, we resurveyed three sites that had historical data (Tuya and Haroun, 2006), with surveys conducted on the same reef area (based on GPS coordinates) and depth contour (2–8 m). These sites encompass exposed and sheltered reefs, thus capturing the interacting effects between climate warming and local hydrodynamic factors. The historical data, collected in 2005, consisted of 2 randomly selected sub-sites, between 10 and 100 m apart, within each site (Las Canteras, El Cabron and Sardina del Norte). At each sub-site, a SCUBA-diver haphazardly laid out four quadrats on the substrate ($n = 4 \times 2$ sub-sites) corresponding to 50×50 cm squares (0.25 m^2 area). The diver then estimated *in situ* the percent cover of benthic habitats, to the lowest taxonomic level possible, via the point-intercept method (121 points per quadrat).

For the 2023 data, three to six transects, of 25 m length \times 4 m wide (100 m^2 area), were deployed on each site. Briefly, the diver took images of the benthos at ca. 50 cm away from the substrate, corresponding to ca. 30×30 cm quadrats (0.09 m^2), approximately every 2.5 m along the transect line (10 photoquadrats per transect). Images were then analysed in the laboratory by overlaying a 5×5 squared grid, corresponding to 16 point-intercepts. Each habitat component was identified and then expressed for the quadrat, as a percentage. To minimise biases associated with species-area relationships (Triantis et al., 2011), we aggregated observations at the level of morpho-functional groups, following a similar approach to CATAMI (i.e., Collaborative and Annotation Tools for Analysis of Marine Imagery Video; Althaus et al., 2015), including: articulated (i.e., jointed or segmented, calcified algae; e.g. *Amphiroa* spp., *Cymopolia barbata*, *Jania* spp.), CCA (crustose coralline algae),

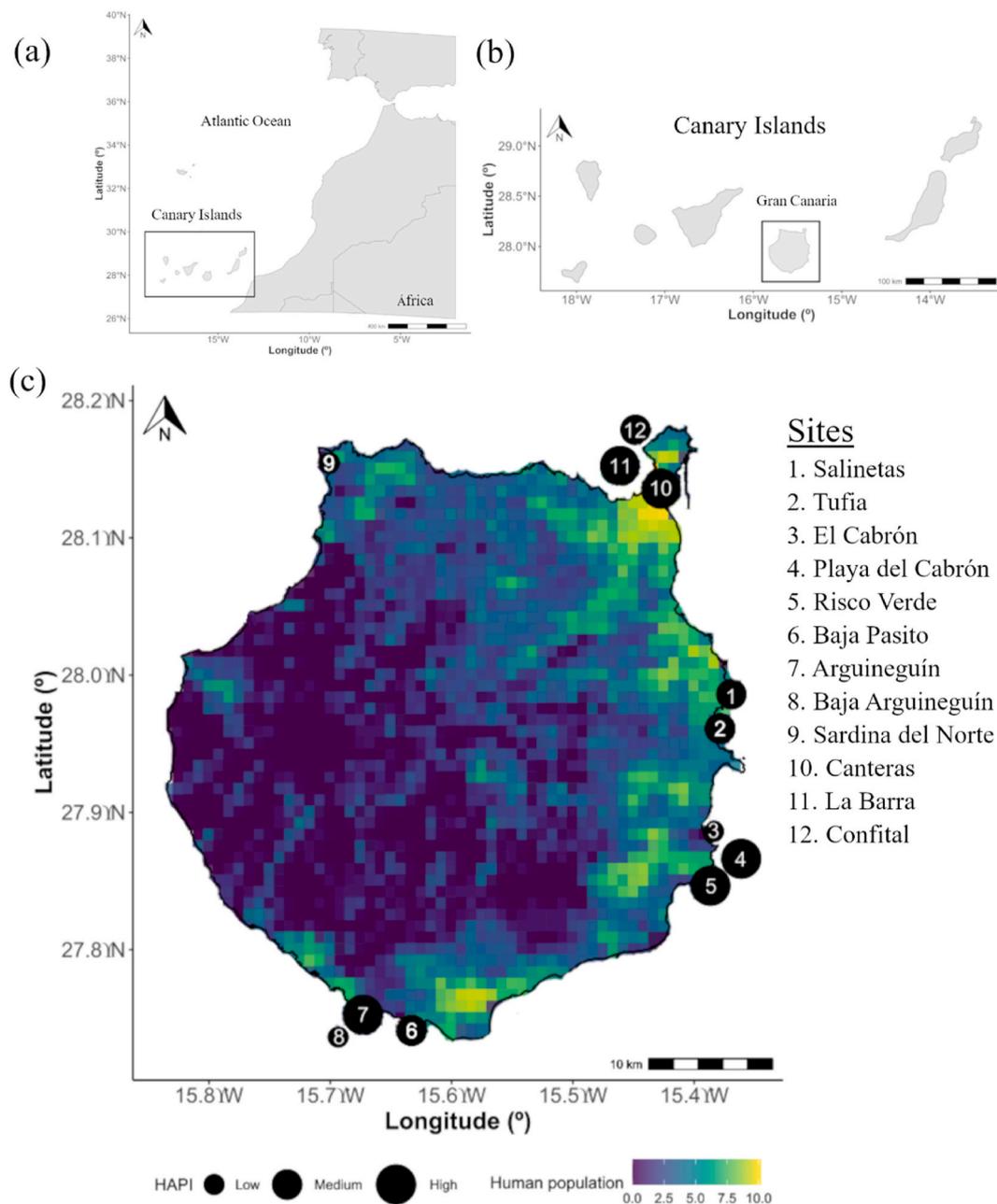


Fig. 1. Map of the study area showing (a) the geographical location of the Canary Islands within the northeast Atlantic Ocean, (b) the geographical location of the island of Gran Canaria within the Canary Islands, and (c) the twelve shallow reef sites sampled in Gran Canaria Island. Raster data represent human population density values ($\log_{10}(x + 1)$), with yellow tones indicating high-density areas and dark blue indicating low-density areas. The size of the dots represents the Human Activities and Pressure Index (HAPI) values for each site, with higher circles indicating high human pressures and smaller circles indicating low pressures. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

corticated (i.e., low profile, plate-like and lobed forms; e.g. *Padina pavonica*, *Lobophora variegata*, *Colpomenia sinuosa*), foliose (i.e., medium, <15 cm, flattened and sheet-like brown and red algae; e.g. *Dictyota* spp., *Taonia* spp.), leathery (i.e., distinct branching form with a vertical growth pattern, e.g. *Gongolaria*, *Cystoseira*, *Sargassum* spp.), red filamentous (e.g. *Asparagopsis taxiformis*, *Cottoniella filamentosa*) and turf algae (i.e., multi-taxon assemblage of short, low-lying (often <2 cm height) dense mats, composed of multispecies aggregations of algae, detritus, and cyanobacteria; Connell et al., 2014; Tebbett and Bellwood, 2019).

2.3. Structure of turf seascapes and particulate load

2.3.1. Turf samples collection

To quantify algal turfs properties and associated sediments, we haphazardly placed four 15×15 cm (0.0225 m^2) quadrats on reef substratum covered by algal turfs at each site, targeting flat (<20°) surfaces. This quadrat size matches the one used in several prior studies in coral and temperate reefs (Pessarrodona et al., 2021, 2023), whose area was visually greater than the structural pattern of the turf assemblage. All the algae and sediment within the quadrat were then collected using an airlift suction sampler with a cloth bag attached to the end ($26 \text{ cm} \times 32 \text{ cm}$, $125 \mu\text{m}$ mesh size) (Tebbett et al., 2022). Specifically, the sampler was initially positioned in direct contact with the substrate, and

all sediment particles within the quadrats were subsequently suctioned. Then, the sampler was lifted ca. 2 cm above the bottom, and all the non-encrusting algae was scraped off with a chisel and sucked using the Venturi pump. This procedure was then repeated in another area of the reef, at the same depth contour and at least 5 m apart, to minimise the non-independence between samples.

2.3.2. Turf samples processing

After collection, samples were kept in cool damp calico bags, stored in a cooler, and then transported to the laboratory within 6 h, where they were frozen (-18°C). Upon defrosting, samples were thoroughly washed with fresh water through a sieve column (2000, 1000, 500, 250 and $125\ \mu\text{m}$) to separate the algal components and the sediment fraction, which included inorganic and organic material $<2\ \text{mm}$, commonly called particulates. The algae, primarily retained in the coarse sieve, were then sorted into morpho-functional groups, including filamentous, foliose and corticated. Rocks, pebbles, free-living calcareous red algae (i.e., rhodoliths) and debris were discarded. We additionally quantified the height of each algal morpho-functional group, by taking measurements of the thallus of 2–5 randomly chosen individuals. Algal samples were then oven-dried, at 60°C for 48 h, for each morpho-functional group separately, to obtain the dry weight (g) per area (Fig. S1).

To determine particle size distribution and quantify the total benthic particulate load (defined here as the $125\text{--}2000\ \mu\text{m}$ fraction), the size fractions within each remaining sieve were subsequently re-suspended in individual glass beakers. Any observable algal fragments were removed, and the samples were then oven-dried, at 60°C for 48 h, before being individually weighed (i.e., dry weight, g). Then, we subjected the sediment samples to a bleaching process, using 30% hydrogen peroxide (H_2O_2), for at least 10 days, to eliminate any organic matter (Fig. S1) (Gordon et al., 2016). The process involved regular stirring, with fresh solution added periodically, until no bubbles were observed. After bleaching, the samples were rinsed with fresh water to eliminate salts, then blotted dry and reweighed separately. This procedure enabled us to quantify both the total mass (g) and proportion of organic vs. inorganic material in particulate loads. All measurements were standardized to m^2 to ensure comparability with other studies.

2.4. Geomorphological, anthropogenic and turf algae structural predictors

We investigated how geomorphological, anthropogenic, and turf algae structural characteristics influenced turf sediment loads and their properties. Geomorphological predictors were selected to capture interactions between reef geomorphology, orientation and hydrodynamics that affect sediment accumulation on reefs (Tebbett et al., 2023), and included: slope (i.e., maximum rate of change in elevation values), northness (i.e., orientation, -1 to $+1$, from south to north, respectively), eastness (i.e., orientation, -1 to $+1$, from west to east, respectively), rugosity (i.e., ratio of surface to planar area), and distance to the coast. These predictors were derived from a fine-scale digital model terrain of the study area, at a 5 m grid cell resolution, using the "MultiscaleDTM" R package (Ilich et al., 2023). For the analysis, slope and orientation values were averaged for grid cells within a 150 m radius, corresponding to a conservative distance where the reef slope typically transitions to soft bottoms across the study sites. The structure of turf algae included the mean height of turf algae and their morphological structure. For the latter, we applied a Principal Coordinate Analysis (PCoA), on a Bray-Curtis dissimilarity matrix summarizing variation in the structure (i.e., composition and biomass) of algal groups within each turf sample collected, via the "pco" function in the "labdsv" R package (Roberts, 2023) (Fig. S2). Then, we extracted the centroid of each sample (i.e., biomass-weighted position in the ordination space), using the two first dimensions, as they explained 42.91% and 20.93% of the variance, respectively, as explanatory variables in the models. Finally, we compiled proxies of human pressures from regional sources, including: human population density, the Human Activities and Pressure Index

(HAPI, Blanfuné et al., 2017), distance to ports, distance to sewage outfalls, and distance to aquaculture facilities. Given the HAPI index is an aggregated metric of cumulative human pressures from both terrestrial (urban, industrial, and agricultural areas) and marine (percentage of shoreline infrastructures, as well as aquaculture facilities and discharge of waste waters) environments, we decided to retain this for the analysis, which was previously developed for the island at a 5 km resolution (Valdazo et al., 2017, 2024). A detailed description of all predictor variables examined, including their measurement, underlying hypothesis, source, and grid resolution, is provided in Supplementary Table S2.

2.5. Data analysis

We tested for differences in benthic assemblage structure considering the combined effect of site and sampling year (2005 and 2023) using a Permutational Multivariate Analysis of Variance (PERMANOVA). This is a widely used approach when working with multivariate community data, as its permutation strategy for estimating p-values makes it robust to violation of normality assumptions (Anderson, 2001). To validate the results of the PERMANOVA, which are still sensitive to violations of homogeneity of variances among groups, we used the "Betadisper" function, applying a more conservative p-value threshold of <0.01 to minimise the risk of a Type I error. We ran a supplementary analysis to investigate how varying survey effort might have biased our statistical comparisons. For this, we carried out a resampling procedure, randomly selecting eight quadrats (i.e., the minimum effort at a site in any single year), without replacement. This procedure was iterated 99 times, and a PERMANOVA model was run within each iteration (i.e., where effort is standardized), to obtain a distribution of p-values. Multivariate analyses were carried out in the "vegan" R package (Oksanen et al., 2022).

To evaluate how turf sediment loads, composition, and organic loads varied in response to geomorphological, anthropogenic and turf algae structural predictors, we implemented a full-subset model selection approach (Fisher et al., 2018). For the sediment composition, we applied a Principal Coordinate Analysis (PCoA), on a Bray-Curtis dissimilarity matrix summarizing variation in the structure (i.e., composition and mass) of sediments within each turf sample, via the "pco" function in the "labdsv" R package (Roberts, 2023) (Fig. S3). Then, we extracted the centroid of each sample (i.e., mass-weighted position in the ordination space), using the two first dimensions, as they explained 66.73% and 14.38% of the variance, respectively. It is important to note that the y-axis corresponding to PCoA2 was used as the response variable in the analysis, as it distinguishes between different sediment sizes (Fig. S3). Specifically, this axis separates finer sediments ($125\ \mu\text{m}$ and $250\ \mu\text{m}$), which exhibit a more positive correlation, from coarser sediments (1 mm and 2 mm), which show a more negative correlation with PCoA2. Before analysis, we explored the presence of missing data and outliers, and continuous predictors were standardized (mean 0 and SD 1) to account for differences in scaling. To avoid multicollinearity issues, we excluded predictor variables with correlations >0.5 (Fig. S4), which resulted in the selection of 8 final predictors: slope, eastness, northness, distance to the coastline, HAPI, mean height of algae, habitat PCoA1 and habitat PCoA2. We note that the presence of two offshore reefs in the dataset, corresponding to depth outliers (Table S1), resulted in high correlation with distance to the coastline ($r = 0.7$), and moderate correlation with the HAPI index ($r = 0.5$), which challenges any potential causal inference on the effect of local human pressures (Fig. S4). To avoid potential confounding effects of depth on our inferences, we decided to remove these sites from the models, with the remaining sites displaying minimal depth variation (4.6 ± 1.37 , mean \pm SD).

We implemented Generalized Linear Mixed models (GLMMs), with a 'Gamma' error distribution and a "log" link function, using the "glmmTMB" R package (Brooks et al., 2017). All models incorporated sampling sites (i.e., $n = 12$), as a random effect, to account for the nested structure of the data (i.e., turf samples within sites) and unaccounted

predictors that might be spatially structured, thus resulting in spatial non-independence in model residuals. Model selection was conducted in the “MuMIn” R package (Barton, 2023), where the candidate model set comprised combinations of all predictor variables, limited to a maximum of four to prevent overfitting (Graham, 2003). We considered models within two units of the lowest AIC model, as having similar support (Burnham and Anderson, 2003). When competing models were present, we selected the model with the highest Akaike weights (ω AIC). Finally, model fit, and assumptions were evaluated using residual plots in the “DHARMA” R package (Hartig, 2022). Because the relative proportion of organics (i.e., organic load/total particulate load) is an informative measure on the nutritional quality of turf to consumers, we ran a supplementary analysis to test this relationship (relative organics ~ sediment load), using a GLM with a beta family and a “logit” link function. All analyses were performed using the statistical software R (R Core Team, 2023).

3. Results

3.1. Historical comparison

Our analysis revealed profound changes in benthic assemblage structure following the loss of canopy-forming species and the emergence of turf algae (Fig. 2). There was a significant change in benthic structure between years (PERMANOVA, $R^2 = 0.445$, $F = 141.74$, p -

value = 0.001), with significant site-to-site variations ($R^2 = 0.021$, $F = 3.33$, p -value = 0.018). Our supplementary analysis revealed that the effect of year was not confounded by varying sampling effort, with all the 99 iterations retrieving significant differences ($p < 0.001$).

Regarding site-to-site variations, we found that in 2005 the coverage of leathery algae (*Cystoseira* spp. and/or *Gongolaria* spp.) in the exposed shore of El Cabrón was 21%, while this macroalga was not observed in the contemporary surveys. The highest level of turf coverage in 2005 was found in Las Canteras (25.5 %), a sheltered embayment in the island’s metropolitan capital. Despite the overall heterogeneity in benthic habitat changes among sites, turf algae consistently increased from 2005 to 2023, by an average of 65.8 ± 1.30 % (Fig. 2).

3.2. Structure of turf seascapes and particulate loads

The properties of turf seascapes were heterogeneous across sites. The mean algal height ranged from 0.2 to 8.5 cm, with an average of 2.10 ± 1.66 cm. The largest algal heights were observed at La Barra and Confital, while the lowest at Sardina del Norte and Tufia (Fig. 3). When analysed by morpho-functional groups, filamentous algae were also significantly longer at La Barra and Confital (Fig. S5). Turf algal biomass varied over five orders of magnitude, from 0.004 to 152 g DW m^{-2} , with an average of $18.29 \pm 29.40 \text{ g DW m}^{-2}$. Confital and El Cabrón showed the highest algal biomass (Fig. 3), while Baja de Pasito and Las Canteras showed the lowest values. The particulate load varied over 3 orders of

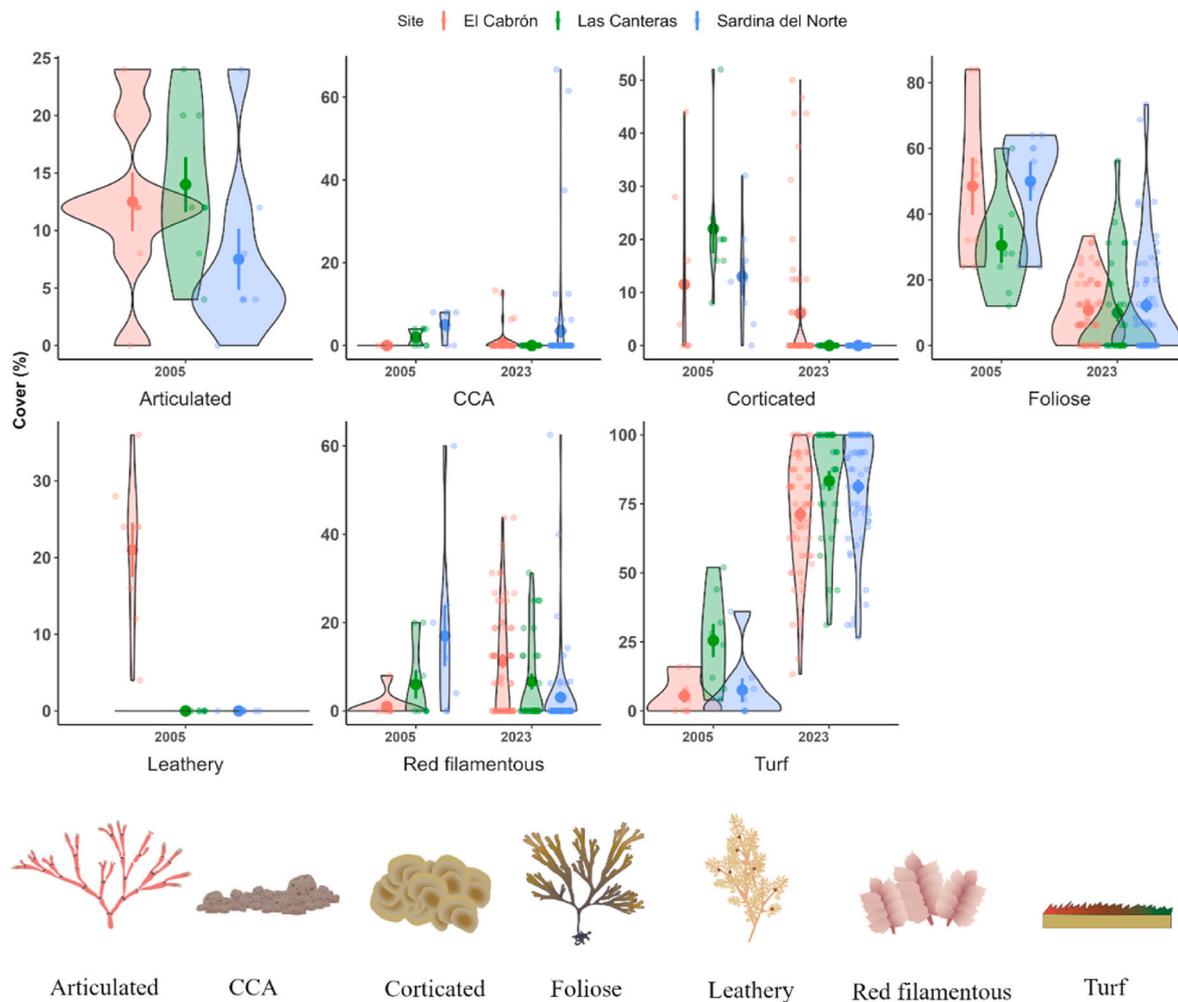


Fig. 2. Historical comparison of the benthic structure, according to morpho-functional groups, in Las Canteras, El Cabrón and Sardina del Norte, between 2005 and 2023. Larger dots represent mean values and whiskers SE errors. Violin plots and smaller dots are included within each panel to depict the distribution of replicate-level values. Image credit: Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/).

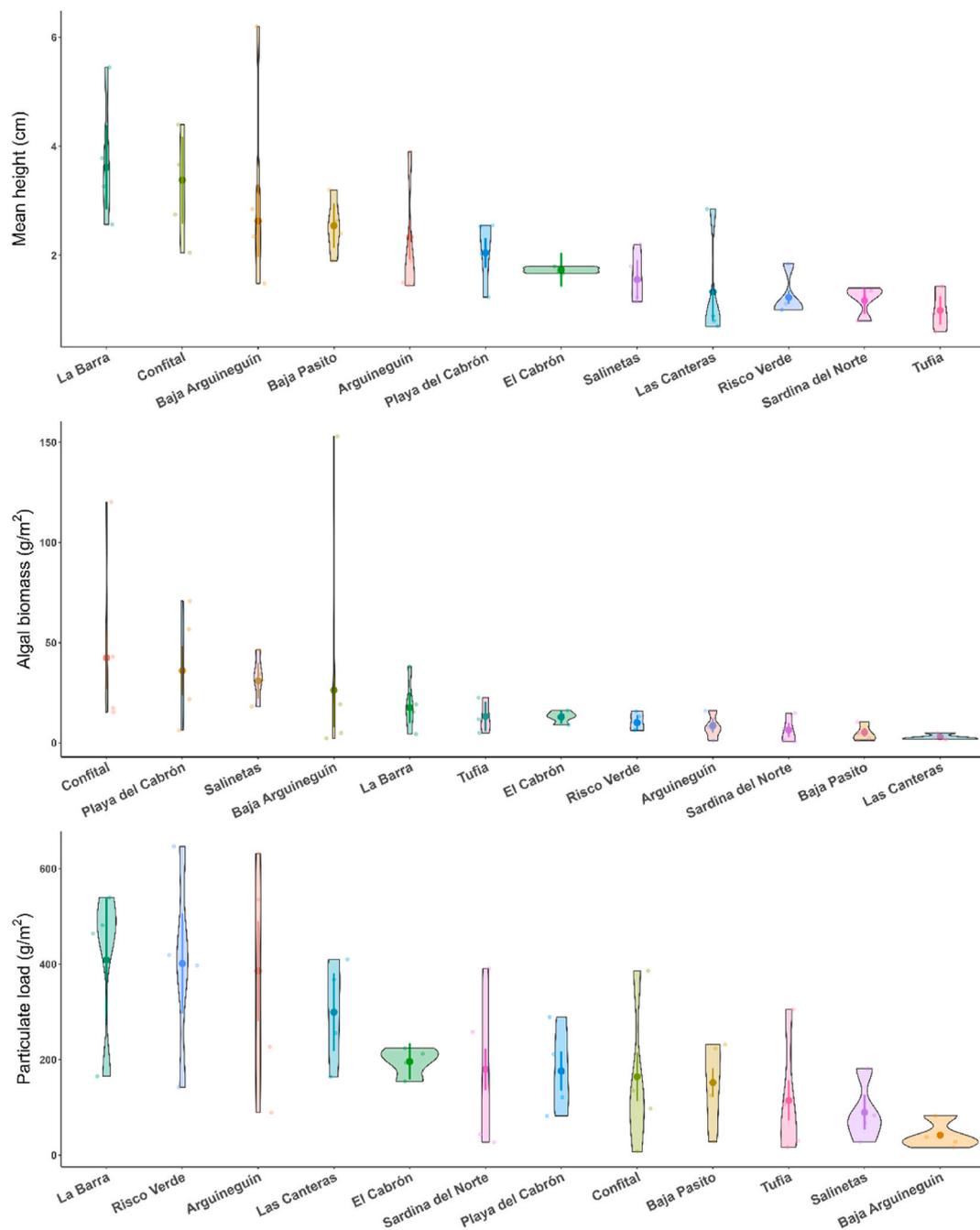


Fig. 3. Violin plots illustrating the mean height of algal turfs (cm), algal turf biomass (g/m^2), and particulate load (g/m^2) across sites, arranged in decreasing order. Larger dots indicate mean values, with whiskers representing SEs. The distribution of replicate-level values is visualized within each panel through violin plots and jittered points for raw data.

magnitude, from 0.86 to 1897 g DW m^{-2} , with an average particulate load of $215.22 \pm 317.97 \text{ g DW m}^2$. Risco Verde and La Barra had the highest particulate loads, while Salinetas and Baja de Arguineguín displayed the lowest values.

The relative biomass of the three distinct morpho-functional groups of algae exhibited substantial variation across sites (Fig. 4a). The proportion of filamentous algae varied across sites, but it was otherwise present in moderate to high relative biomass at all sites. For instance, filamentous algae was the dominant group in Baja Arguineguín, La Barra, Risco Verde and Tufia. Foliose algae ranked second in relative biomass, with also substantial spatial variability, although they did not prevail at all sites (i.e., Baja Pasito, Confital, Salinetas). Finally, corticated algae were only present in 3 sites (i.e., Arguineguín, Las Canteras

and Playa del Cabrón).

The relative masses of different sediment grain sizes were highly heterogeneous among sites (Fig. 4b). In La Barra and Las Canteras, the predominant grain size was fine sediment ($<250 \mu\text{m}$), with a sparse presence of coarser sediments ($>250 \mu\text{m}$). On the other hand, Baja Pasito, Confital and Salinetas were characterized by coarser sediments (1 and 2 mm), with a sparse presence of finer sediments ($125 \mu\text{m}$ and $250 \mu\text{m}$). The inorganic-to-organic matter ratio was generally more consistent across sites, varying from ~ 2 (Risco Verde) to 20% (La Barra) (Fig. 4c).

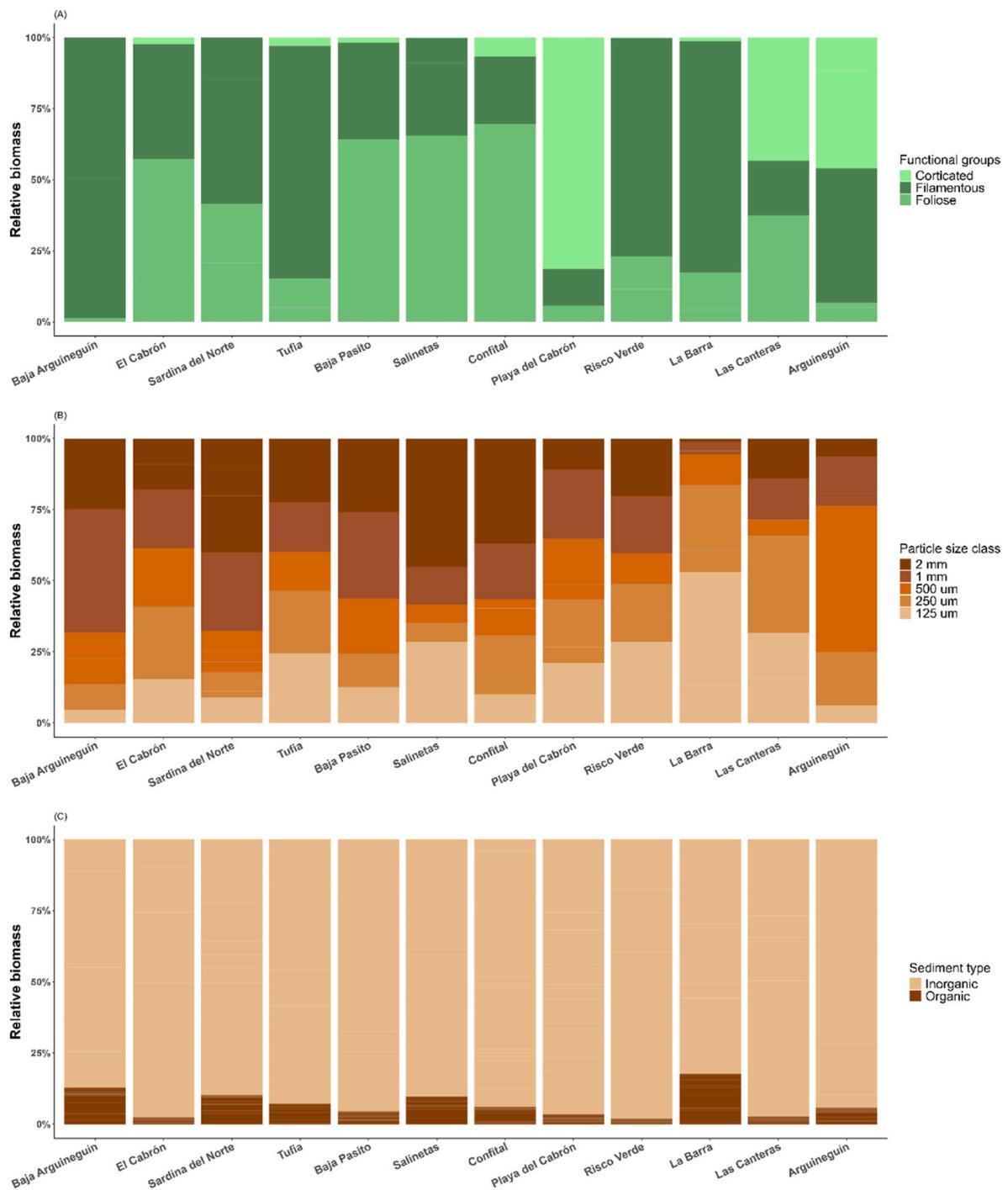


Fig. 4. (a) Relative biomass (percentage of total dry weight) of different algal groups (i.e., corticated, filamentous and foliose) at each site. (b) Relative mass (percentage of total dry weight) of the different particle grain sizes (i.e., sediment of 2 mm, 1 mm, 500 μm , 250 μm and 125 μm) at each site. (c) Relative mass (percentage of total dry weight) of the inorganic and organic fraction at each site. In all panels, sites are ordered in decreasing values of the HAPI index.

3.3. Drivers of turf sediment properties

The model with the best fit for predicting the quantity of sediment loads contained the effects of the HAPI index and the composition of turf algae morpho-functional groups (habitat PCoA1 and habitat PCoA2) ($\omega\text{AIC} = 0.43$, R^2 marginal = 0.579, R^2 conditional = 0.832) (Table 1). There was an additional model with substantial support (i.e., within 2 AICc units), containing the effects of turf algae composition and HAPI, with an additional contribution of the mean height of turf algae ($\omega\text{AIC} = 0.366$, R^2 marginal = 0.467, R^2 conditional = 0.537). The most parsimonious model explaining variation in fine sediment (125 μm)

(Sediment PCoA2) contained the effect of the mean height of turf algae ($\omega\text{AIC} = 0.134$, R^2 marginal = 0.133, R^2 conditional = 0.273). However, there was large uncertainty in the set of best models, with generally low support (ωAIC) and goodness-of-fit (R^2) for all models. Finally, the model with the best fit for predicting the total organic loads included the effect of eastness and the morpho-functional group of turf algae present ($\omega\text{AIC} = 0.186$, R^2 marginal = 0.186, R^2 conditional = 0.333). However, as in fine sediments, there was high variability in model support, and low variance explained by all models.

Model-averaged coefficients showed a positive relationship between the mean height of turf algae and sediment loads, with longer heights of

Table 1

Best (most parsimonious, within two units of the lowest AICc) GLMMs predicting variation in Sediment Load (SL), Sediment Composition (PCoA2) (SP2) and Organic Load (OL) of turf samples. The degrees of freedom (df), delta AICc, Akaike weights (w_{AICc}) and goodness-of-fit (R^2) marginal and conditional are provided for model comparisons.

Response	Best models	df	delta	w_{AICc}	R^2 marginal	R^2 conditional
SL	Habitat_PCoA1 + Habitat_PCoA2 + HAPI + (1 Site)	6	0	0.43	0.579	0.832
	Habitat_PCoA2 + HAPI + Mean_height + (1 Site)	6	0.323	0.366	0.467	0.537
	Habitat_PCoA2 + Mean_height + slope.150 + (1 Site)	6	1.484	0.205	0.417	0.496
SP2	Mean_height + (1 Site)	4	0	0.134	0.133	0.273
	eastness + (1 Site)	4	0.07	0.129	0.055	0.128
	dist_shore + (1 Site)	4	0.073	0.129	0.051	0.129
	HAPI + (1 Site)	4	0.586	0.1	0.056	0.13
	Habitat_PCoA1 + Mean_height + (1 Site)	5	0.908	0.085	0.162	0.265
	slope.150 + (1 Site)	4	1.159	0.075	0.024	0.128
	eastness + Mean_height + (1 Site)	5	1.187	0.074	0.158	0.27
	HAPI + Mean_height + (1 Site)	5	1.577	0.061	0.163	0.271
	dist_shore + HAPI + (1 Site)	5	1.773	0.055	0.083	0.131
	eastness + HAPI + (1 Site)	5	1.788	0.055	0.085	0.129
	HAPI + slope.150 + (1 Site)	5	1.881	0.052	0.084	0.132
	dist_shore + eastness + (1 Site)	5	1.92	0.051	0.07	0.128
	OL	eastness + Habitat_PCoA1 + (1 Site)	5	0	0.186	0.186
dist_shore + eastness + Habitat_PCoA1 + (1 Site)		6	0.154	0.172	0.228	0.313
eastness + Habitat_PCoA1 + Habitat_PCoA2 + (1 Site)		6	0.573	0.139	0.223	0.346
Habitat_PCoA1 + (1 Site)		4	0.664	0.133	0.098	0.352
eastness + Habitat_PCoA1 + Mean_height + (1 Site)		6	0.698	0.131	0.207	0.387
eastness + Habitat_PCoA1 + northness + (1 Site)		6	1.346	0.095	0.233	0.313
Habitat_PCoA1 + Habitat_PCoA2 + (1 Site)		5	1.827	0.074	0.127	0.370
Habitat_PCoA2 + (1 Site)		4	1.953	0.07	0.046	0.237

algal turfs trapping more sediment (Figs. 5a and 6a). Similarly, there was a significant positive effect of the HAPI index on sediment loads (Figs. 5b and 6b), which increased exponentially from low to high human pressure. We also found a significant negative effect of turf algae composition on sediment loads, suggesting that, when the biomass of foliose algae is high, they tend to trap less sediment (Figs. 5a and 6c). Conversely, when the biomass of foliose algae is low, sediment load increases, possibly due to trapping by filamentous algae (Figs. 5c and 6c, S2). Both the sediment size-frequency distribution, and total organic loads, were highly heterogeneous across our study sites and were not significantly predicted by any of the variables considered (Fig. 5b and c). We note, however, that there was a significant negative relationship between sediment loads and the relative proportion of organics (GLM, z -value = -4.73 , p -value = <0.001 , Fig. S6).

4. Discussion

Our study revealed substantial spatial heterogeneity of turf seascape properties at an oceanic island. This result challenges widespread assumptions that historical transitions from heterogenous upright seaweed communities in the region, including forest-forming algae of the genus *Cystoseira* and *Gongolaria sensu lato*, lead to seemingly homogenous seascapes (Valdazo et al., 2017). Previous research on turf seascapes have revealed large variation in its properties at several spatial scales, e. g., within sites, between habitats, and across large geographic areas, all of which can alter both their nutritional quality to consumers (Tebbett et al., 2018a, 2020; Goatley and Bellwood, 2012; Bellwood and Fulton, 2008), and their role as habitat for associated epifauna (Fraser et al., 2020a; Fraser et al., 2020b, 2021). We further show that variation in these attributes, particularly total sediment loads, were influenced by local human pressures, turf algal height and composition. The former provides direct evidence of the immediate role of local anthropogenic pressures in shaping sediment dynamics in turf seascapes, while the latter could reflect the indirect effects of climate change acting on the benthic community, through directional changes in the composition of morpho-functional groups of algae in the region. We note, however, that this inference remains purely speculative, given the lack of direct evidence linking climate to temporal variation in the morphological groups present here.

The resampling of historical sites revealed significant shifts in benthic habitat structure over the past two decades, with turf algae proliferating consistently at all sites, coinciding with a decline in the cover of upright foliose seaweeds and forest-forming leathery species (*Cystoseira* and *Gongolaria sensu lato*). This overarching effect of global warming — the decline of macroalgal forests and the rise of turf — can be further intensified by local hydrodynamics and anthropogenic pressures (Valdazo et al., 2017, 2024). For instance, the highest percent cover of turf algae in 2005 and 2023 was observed in Las Canteras, an urban beach protected by an intertidal sandstone reef located in one of the most densely populated areas of the island (Ferrer et al., 2023). Previous studies in the region have emphasized the role of hydrodynamics in shaping algal benthic structure, with turf algae tending to dominate protected shores (Tuya and Haroun, 2006). Therefore, the high levels of turf algae in the sheltered and human-impacted embayment of Las Canteras likely reflects the combined influence of hydrodynamic conditions and human activity on benthic structure. Although the protected sites had the highest levels of turf, it is important to note that the percentage increase was larger in the exposed sites, such as El Cabrón, where foliose seaweeds and forest-forming leathery species have experienced the most significant decline over time. This indicates that, despite the stronger hydrodynamic forces, turf has managed to dominate there.

Particulate loads associated with turf algae exhibited substantial variability across sites, ranging from 10s of $g\ m^{-2}$ to 1,000s of $g\ m^{-2}$. This range aligns with observations from other studies conducted on the Great Barrier Reef, which reported similar variability depending on the

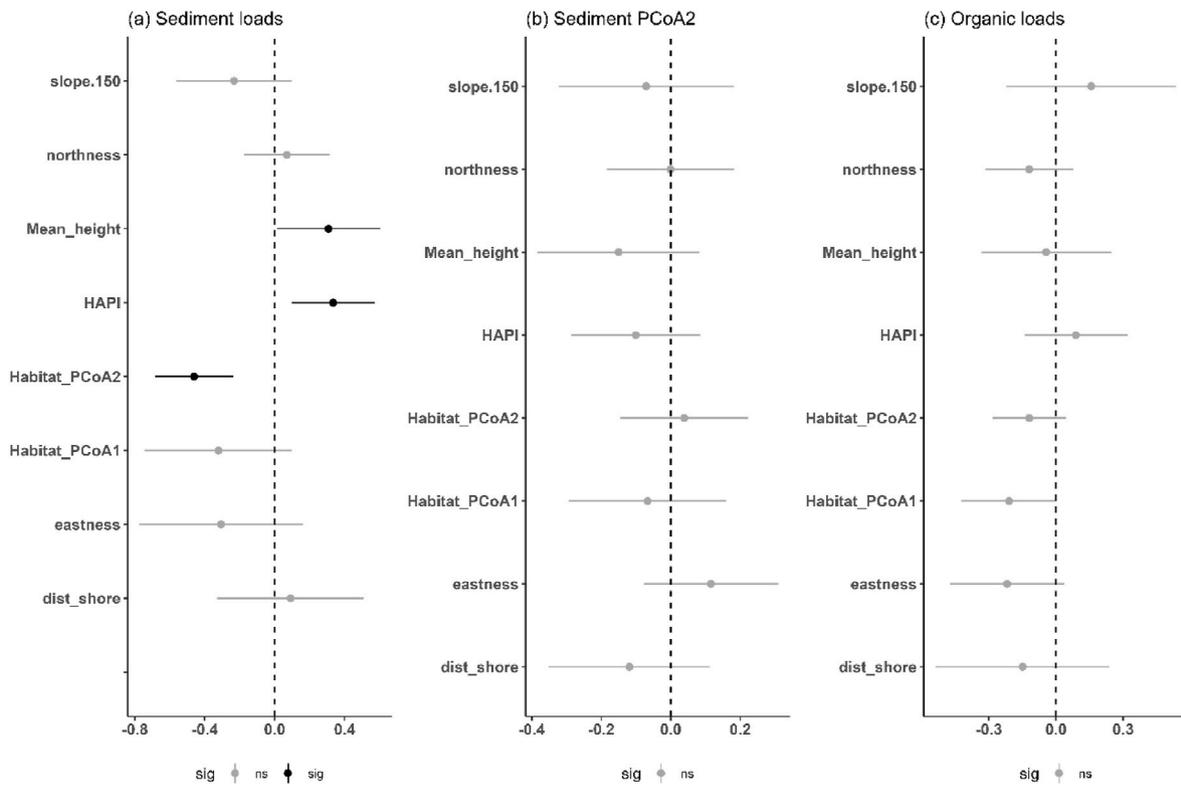


Fig. 5. Model-averaged coefficients from GLMMs testing the effect of each predictor variable in explaining variation on (a) sediment loads, (b) sediment composition (PCoA2), and (c) organic loads of turf samples. Dots represent averaged coefficients and bars represent $\pm 95\%$ confidence intervals.

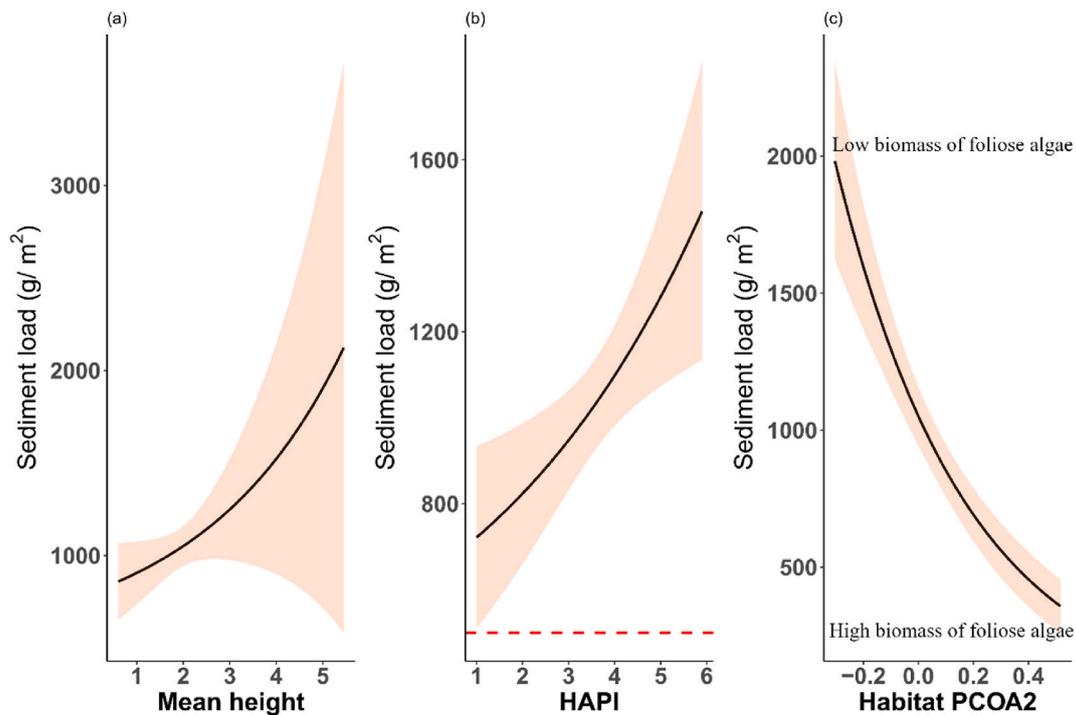


Fig. 6. Predicted relationship between the mean height of turf algae, HAPI index, habitat PCOA2 and sediment loads. Solid lines are predicted values from the most parsimonious GLMMs, and brown-shaded areas denote the 95% confidence interval. The dashed red line indicates the sediment load threshold beyond which a significant decline in fish abundance or feeding activity has been reported for tropical coral reefs (Tebbett et al., 2020). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

location of the reefs (Tebbett and Bellwood, 2019). However, other studies reported even higher ranges, from $<10 \text{ g/m}^2$ to $>10,000 \text{ g/m}^2$ (Tebbett et al., 2022). In this study, total particulate loads were strongly predicted by the HAPI index, turf algal height and composition, suggesting that both human pressures and the characteristics of turf algal mats strongly determine particulate loads. The HAPI index was consistently chosen within the set of supported models, indicating a strong role of human activities around the island in shaping the nature and structure of the turf seascapes and consequently, particulate accumulation. These findings indicate that proximity to urbanized areas leads to increased turf sediment accumulation due to human activities, a trend consistent with previous studies (Benedetti-Cecchi et al., 2001; Coleman et al., 2008).

The predicted relationship between the HAPI index and particulate loads suggests that only sites with minimal human pressure, below a hypothetical ecological threshold (i.e., tipping point above which ecosystem functions, such as herbivore, are severely undermined), could maintain their functionality. This result aligns with those reported by Tebbett et al. (2020), which showed that sediment loads above approximately $250\text{--}500 \text{ g/m}^2$ significantly reduced fish abundances and feeding activity (Fig. 6). Indeed, several studies revealed that increased sediment loads on turf algae reduce the grazing efficiency of herbivores, potentially destabilizing the ecosystem functions that support local fisheries (Goatley and Bellwood, 2013; Tebbett and Bellwood, 2019). We must note that these findings are largely based on tropical reef ecosystems, and the extent to which they can be generalized to subtropical or temperate reefs remains an important area of future research. Moreover, different herbivorous fish species show varying sensitivities to sediment accumulation on algal turfs (Pessarrodona et al., 2022b). For instance, fish ‘croppers’ such as surgeonfishes are more resilient to increased sediment levels since they can crop the tips of algal turfs, while scraping parrotfishes are more deterred by coarser sediments, likely because they interact more closely with sediments when scraping the reef with their beak-like teeth’ (Tebbett and Bellwood, 2019). These species-specific responses offer valuable insights into how sediment impacts feeding behaviour, highlighting the importance of maintaining sediment levels below critical thresholds to preserve the balance of herbivorous fish populations and, consequently, the overall health of reef ecosystems. Considering most scraping and grazing activity in the region comes from two species, the parrotfish *Sparisoma cretense* and *Sarpa salpa*, deciphering the effects of turf sediment loads on the feeding patterns and activities of these fishes is an important area of future research.

Our findings also corroborate the strong positive relationship between algal turf height and particulate loads, which may result from two possible mechanisms: (i) longer algal turfs developing first, thereby trapping more sediments, or (ii) the initial accumulation of sediments within algal turfs reduces herbivory (Latrille et al., 2019). This reduction in herbivory may facilitate the expansion of longer algal turfs, which in turn increases sediment retention (Goatley and Bellwood, 2013; Goatley et al., 2016). Additionally, high sediment loads can indirectly suppress herbivory by lowering the nutritional quality of turfs. This decline in quality may be due to reduced turf productivity (Tebbett et al., 2018a), or to the dilution of detritus concentration within the particulate mixture (Purcell and Bellwood, 2001), potentially leading to significant bottom-up ecological effects. Indeed, it is expected that algal turfs will increasingly trap sediment (Tebbett et al., 2020), potentially leading to reduced herbivory and diminished reef resilience (Bellwood and Fulton, 2008; Goatley and Bellwood, 2012; Goatley et al., 2016). This could result in a shift from a Short Productive Algal Turf (SPATs) state to a Long Sediment-Laden Algal Turf (LSATs) state (Goatley et al., 2016), posing significant threats to changing reef ecosystems by undermining their functionality and ability to provide key ecosystem services (Bellwood et al., 2019). Our study supports this notion, as we found increased sediment retention in turf diminishes the relative proportion of organics. In species-poor oceanic islands of the eastern Atlantic

Ocean, as the one studied here, deciphering both the bottom-up effects of turf on herbivores and the top-down effect of herbivores on turfs is a key area for future research, as two key herbivorous species (*Sparisoma cretense* and *Sarpa salpa*), which are both highly targeted by small-scale commercial fisheries, are solely responsible for the grazing and scraping function (Castro et al., 2019).

We also identified a significant relationship between algal turf composition and particulate loads, with higher particulate loads associated with filamentous algal turfs. Fine-branching filamentous forms may create a more tightly interwoven network of algal branches, which enhances their ability to trap and stabilize sediments more effectively than coarsely branching forms (O’Brien and Scheibling, 2018). This association may also be attributed to the rapid recovery rate of these filamentous forms following disturbances; indeed, these turf algae can fully regrow within just four days after being cropped by grazers (Bonaldo and Bellwood, 2010; Pessarrodona et al., 2023). Additionally, the vertical growth pattern of filamentous algae allows them to access light and thrive even under high particulate loads, whereas other morpho-functional groups, such as foliose, corticated, and articulated algae, which rely on horizontal growth pattern, may be less resilient conditions (Arjunwadkar et al., 2022).

Conversely to total particulate loads, the grain size distribution and total organic load, were not adequately predicted by the range of predictors considered here. The reason could be that other underlying factors may be at play, as numerous previous studies have consistently noted that finer sediments are typically associated with lower-energy environments (Gordon et al., 2016; Tebbett et al., 2017a). However, in our study we could not incorporate fine-scale quantitative measurements of local hydrodynamic forces that can interact with reef geomorphology to determine particulate deposition and retention (Bodde et al., 2014; Purcell, 2000; Tebbett et al., 2017b). For instance, steeper slopes are often associated with higher particulate accumulation, while high-energy reef crests tend to exhibit lower sediment retention due to stronger wave action and water flow (Tebbett et al., 2019). Further, the relative uniformity in total organic loads might be attributable to a lack of data on finer sediment fractions ($<63 \mu\text{m}$), potentially leading to an underestimation of organic loads. Fine sediments are particularly important ecologically, as they often contain higher levels of organic particulates (detritus), which are a crucial nutritional resource for grazing herbivorous fishes (Wilson et al., 2003). In contrast, coarser sediments ($>250 \mu\text{m}$) typically have lower organic content, which makes them less nutritious to potential consumers (Gordon et al., 2015, 2016). These findings highlight the complexity of sedimentation processes and the need to consider multiple environmental variables when assessing their impacts on coastal ecosystems.

Our study suffers from a series of caveats that should be considered when applying these results to other reef systems. A key methodological limitation stems from the airlift suction sampling technique used, which was constrained by the mesh size of the collection bag ($125 \mu\text{m}$). Consequently, finer sediment fractions ($<63 \mu\text{m}$), which often contain significant organic loads and detritus (Gordon et al., 2015), were not accurately collected. This exclusion likely underrepresents the total particulate load and the full spectrum of sediment-associated organic material, which plays crucial roles in nutrient cycling and serves as a vital food source for herbivorous fish (Wilson et al., 2003). This limitation is inherent to the airlift method (Tebbett et al., 2022), potentially leading to an underestimate of the total sediment load in these ecosystems that could obscure their role in food web dynamics, which is critical to understanding the ecological impacts of sediment composition. To address this, future studies should incorporate sampling methods that can capture finer sediment fractions, with smaller mesh sizes or alternative collection techniques (Tebbett et al., 2022). A further limitation is that we only considered turf properties at a single point in time, therefore ignoring environmental and biological processes that occurred through time that can influence sediment dynamics (Goatley et al., 2016). Expanding the geographic and temporal scope of future research,

including the incorporation of long-term monitoring data, would be essential for more accurately assessing these intra-regional differences and for developing effective conservation strategies.

Overall, our findings underscore the critical role of local human pressures and inherent algal turf properties in influencing the distribution and composition of particulate loads in oceanic, warm-temperate, reefs. The heterogeneous spatial patterns in sediment properties reported here at an island scale, could have important implications for reef ecological processes, such as herbivory and the recruitment of forest-forming species, ultimately destabilizing reef ecosystem functioning. The strong correlation between human pressures and increased particulate loads underscores the urgent need for targeted management strategies that halt local impacts, therefore mitigating the deleterious effects of sediment accumulation on reef-scale processes. This is particularly critical for oceanic islands, where the ecological consequences of turf expansion and sediment accumulation could be particularly severe, given the low number of species that support critical ecosystem functions (i.e., low functional redundancy) and the inherently limited connectivity to mainland populations that may promote recovery of habitat-forming species after natural and human driven disturbances. Our findings highlight the need for a comprehensive conservation approach that considers the complex interactions between herbivory, sediments, algal turfs and reef structures, all influenced by climate change and human activities. This approach is essential to safeguard the health and functionality of vulnerable oceanic reef systems.

CRediT authorship contribution statement

Mar Mourin: Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Data curation. **Iris Barroso:** Writing – review & editing, Investigation, Data curation. **Albert Pessarrodona:** Writing – review & editing, Investigation, Conceptualization. **Sandra Navarro-Mayoral:** Writing – review & editing, Investigation. **Fernando Tuya:** Writing – review & editing, Investigation, Funding acquisition. **Nestor E. Bosch:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare no conflict of interest.

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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.2025.107030>.

Data availability

Data will be made available on request.

References

- Airoldi, L., Virgilio, M., 1998. Responses of turf-forming algae to spatial variations in the deposition of sediments. *Mar. Ecol. Prog. Ser.* 165, 271–282. <https://doi.org/10.3354/meps165271>.
- Althaus, F., Hill, N., Ferrari, R., Edwards, L., Przeslawski, R., Schönberg, C.H.L., Stuart-Smith, R., Barrett, N., Edgar, G., Colquhoun, J., Tran, M., Jordan, A., Rees, T., Gowlett-Holmes, K., 2015. A standardised vocabulary for identifying benthic biota

- and substrata from underwater imagery: the CATAMI Classification Scheme. *PLoS One* 10 (10), e0141039. <https://doi.org/10.1371/journal.pone.0141039>.
- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* 26 (1), 32–46. <https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x>.
- Arjunwadkar, C.V., Tebbett, S.B., Bellwood, D.R., Bourne, D.G., Smith, H.A., 2022. Algal turf structure and composition vary with particulate loads on coral reefs. *Mar. Pollut. Bull.* 181, 113903. <https://doi.org/10.1016/j.marpolbul.2022.113903>.
- Barton, K., 2023. MuMIn: multi-model inference. R package version 1.47.5. Available at: <https://CRAN.R-project.org/package=MuMIn>.
- Beaugrand, G., Edwards, M., Raybaud, V., Goberville, E., Kirby, R.R., 2015. Future vulnerability of marine biodiversity compared with contemporary and past changes. *Nat. Clim. Change* 5 (7), 695–701. <https://doi.org/10.1038/nclimate2650>.
- Bellwood, D.R., Fulton, C.J., 2008. Sediment-mediated suppression of herbivory on coral reefs: decreasing resilience to rising sea-levels and climate change. *Limnol. Oceanogr.* 53 (6), 2695–2701. <https://doi.org/10.4319/lo.2008.53.6.2695>.
- Bellwood, D.R., Streit, R.P., Brandl, S.J., Tebbett, S.B., 2019. The meaning of the term ‘function’ in ecology: a coral reef perspective. *Funct. Ecol.* 33 (6), 948–961. <https://doi.org/10.1111/1365-2435.13265>.
- Benedetti-Cecchi, L., Pannacciulli, F., Bulleri, F., Moschella, P., Airoldi, L., Relini, G., Cinelli, F., 2001. Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores. *Mar. Ecol. Prog. Ser.* 214, 137–150. <https://doi.org/10.3354/meps214137>.
- Blanfuné, A., Thibaut, T., Boudouresque, C., Mácić, V., Markovic, L., Palomba, L., Verlaque, M., Boissery, P., 2017. The CARLIT method for the assessment of the ecological quality of European Mediterranean waters: relevance, robustness and possible improvements. *Ecol. Indic.* 72, 249–259. <https://doi.org/10.1016/j.ecolind.2016.07.049>.
- Bodde, W., Pomeroy, A., Van Dongeren, A., Lowe, R., Van Thiel de Vries, J., 2014. Hydrodynamic drivers of sediment transport across a fringing reef. *Coastal Engineering Proceedings* 1 (34), 37. <https://doi.org/10.9753/icce.v34.currents.37>.
- Bonaldo, R.M., Bellwood, D.R., 2010. Spatial variation in the effects of grazing on epilithic algal turfs on the Great Barrier Reef, Australia. *Coral Reefs* 30 (2), 381–390. <https://doi.org/10.1007/s00338-010-0704-4>.
- Bonebrake, T.C., Brown, C.J., Bell, J.D., Blanchard, J.L., Chauvenet, A., Champion, C., Chen, I., Clark, T.D., Colwell, R.K., Danielsen, F., Dell, A.I., Donelson, J.M., Evengård, B., Ferrier, S., Frusher, S., Garcia, R.A., Griffis, R.B., Hobday, A.J., Jarzyna, M.A., Pecl, G.T., 2017. Managing consequences of climate-driven species redistribution requires integration of ecology, conservation and social science. *Biol. Rev. Camb. Phil. Soc.* 93 (1), 284–305. <https://doi.org/10.1111/bvr.12344>.
- Bosch, N.E., McLean, M., Zarco-Perello, S., Bennett, S., Stuart-Smith, R.D., Vergés, A., Pessarrodona, A., Tuya, F., Langlois, T., Spencer, C., Bell, S., Saunders, B.J., Harvey, E.S., Wernberg, T., 2022a. Persistent thermally driven shift in the functional trait structure of herbivorous fishes: evidence of top-down control on the rebound potential of temperate seaweed forests? *Glob. Change Biol.* 28 (7), 2296–2311. <https://doi.org/10.1111/gcb.16070>.
- Bosch, N.E., Pessarrodona, A., Filbee-Dexter, K., Tuya, F., Mulders, Y., Bell, S., Langlois, T., Wernberg, T., 2022b. Habitat configurations shape the trophic and energetic dynamics of reef fishes in a tropical-temperate transition zone: implications under a warming future. *Oecologia* 200 (3–4), 455–470. <https://doi.org/10.1007/s00442-022-05278-6>.
- Brooks, M.E., Kristensen, K., Van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., et al., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9 (2), 378–400. <https://doi.org/10.32614/rj-2017-066>.
- Browne, N.K., Smithers, S., Perry, C., 2013. Carbonate and terrigenous sediment budgets for two inshore turbid reefs on the central Great Barrier Reef. *Mar. Geol.* 346, 101–123. <https://doi.org/10.1016/j.margeo.2013.08.011>.
- Burnham, K.P., Anderson, D.R., 2003. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer Science & Business Media.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. *Nature* 486 (7401), 59–67. <https://doi.org/10.1038/nature11148>.
- Carpenter, R.C., Williams, S.L., 1993. Effects of algal turf canopy height and microscale substratum topography on profiles of flow speed in a coral forereef environment. *Limnol. Oceanogr.* 38 (3), 687–694. <https://doi.org/10.4319/lo.1993.38.3.0687>.
- Castro, J.J., Divovich, E., Delgado de Molina Acevedo, A., Barrera-Luján, A., Riera, R., 2019. Reconstruction of marine small-scale fisheries captures in the canary islands (NE Atlantic Ocean) from 1950 to 2010. *Sci. Mar.* 83 (1), 7–17. <https://doi.org/10.3989/scimar.04837.18A>.
- Coleman, M.A., Kelaher, B.P., Steinberg, P.D., Millar, A.J.K., 2008. Absence of a large brown macroalga on urbanized rocky reefs around Sydney, Australia, and evidence for historical decline. *J. Phycol.* 44 (4), 897–901. <https://doi.org/10.1111/j.1529-8817.2008.00541.x>.
- Connell, S.D., Foster, Airoldi, L., 2014. What are algal turfs? Towards a better description of turfs. *Mar. Ecol. Prog. Ser.* 495, 299–307. <https://doi.org/10.3354/meps10513>.
- Di Paola, G., Auceili, P.P.C., Benassai, G., Iglesias, J., Rodríguez, G., Roszkopf, C.M., 2017. The assessment of the coastal vulnerability and exposure degree of Gran Canaria Island (Spain) with a focus on the coastal risk of Las Canteras Beach in Las Palmas de Gran Canaria. *J. Coast Conserv.* 22 (5), 1001–1015. <https://doi.org/10.1007/s11852-017-0574-9>.
- Duran, A., Adam, T.C., Palma, L., Moreno, S., Collado-Vides, L., Burkepille, D.E., 2019. Feeding behavior in Caribbean surgeonfishes varies across fish size, algal abundance, and habitat characteristics. *Mar. Ecol.* 40 (4). <https://doi.org/10.1111/maec.12561>.

- Ferrer, N., Santana, K., Martín, J., Valdazo, J., Bergasa, O., 2023. Holocene erosional processes in a highly exposed intertidal sandstone reef inferred from remote sensing data. *Remote Sens.* 15 (12), 2968. <https://doi.org/10.3390/rs15122968>.
- Filbee-Dexter, K., Wernberg, T., 2018. Rise of turfs: a new battlefield for globally declining kelp forests. *Bioscience* 68 (2), 64–76. <https://doi.org/10.1093/biosci/bix147>.
- Fisher, R., Wilson, S.K., Sin, T.M., Lee, A.C., Langlois, T.J., 2018. A simple function for full-subsets multiple regression in ecology with R. *Ecol. Evol.* 8 (12), 6104–6113. <https://doi.org/10.1002/ece3.4134>.
- Fong, C.R., Bittick, S.J., Fong, P., 2018. Simultaneous synergist, antagonistic and additive interactions between multiple local stressors all degrade algal turf communities on coral reefs. *J. Ecol.* 106 (4), 1390–1400. <https://doi.org/10.1111/1365-2745.12914>.
- Fraser, K.M., Lefcheck, J.S., Ling, S.D., Mellin, C., Stuart-Smith, R.D., Edgar, G.J., 2020a. Production of mobile invertebrate communities on shallow reefs from temperate to tropical seas. *Proc. Biol. Sci.* 287 (1941), 20201798. <https://doi.org/10.1098/rspb.2020.1798>.
- Fraser, K.M., Stuart-Smith, R.D., Ling, S.D., Edgar, G.J., 2021. High biomass and productivity of epifaunal invertebrates living amongst dead coral. *Mar. Biol.* 168 (7). <https://doi.org/10.1007/s00227-021-03911-1>.
- Fraser, K.M., Stuart-Smith, R., Ling, S., Heather, F., Edgar, G., 2020b. Taxonomic composition of mobile epifaunal invertebrate assemblages on diverse benthic microhabitats from temperate to tropical reefs. *Mar. Ecol. Prog. Ser.* 640, 31–43. <https://doi.org/10.3354/meps13295>.
- Goatley, C.H.R., Bellwood, D.R., 2010. Biologically mediated sediment fluxes on coral reefs: sediment removal and off-reef transportation by the surgeonfish *Ctenochaetus striatus*. *Mar. Ecol. Prog. Ser.* 415, 237–245. <https://doi.org/10.3354/meps08761>.
- Goatley, C.H.R., Bellwood, D.R., 2012. Sediment suppresses herbivory across a coral reef depth gradient. *Biol. Lett.* 8 (6), 1016–1018. <https://doi.org/10.1098/rsbl.2012.0770>.
- Goatley, C.H.R., Bellwood, D.R., 2013. Ecological consequences of sediment on high-energy coral reefs. *PLoS One* 8 (10), e77737. <https://doi.org/10.1371/journal.pone.0077737>.
- Goatley, C.H.R., Bonaldo, R.M., Fox, R.J., Bellwood, D.R., 2016. Sediments and herbivory as sensitive indicators of coral reef degradation. *Ecol. Soc.* 21 (1). <https://doi.org/10.5751/es-08334-210129>.
- Goldberg, N., Kendrick, G., Heine, J., 2004. Highway or country road: algal recruitment with distance from an island reef. *J. Mar. Biol. Assoc. U. K.* 84 (5), 879–882. <https://doi.org/10.1017/S0025315404010136h>.
- Gordon, S.E., Goatley, C.H.R., Bellwood, D.R., 2015. Low-quality sediments deter grazing by the parrotfish *Scarus rivulatus* on inner-shelf reefs. *Coral Reefs* 35 (1), 285–291. <https://doi.org/10.1007/s00338-015-1374-z>.
- Gordon, S.E., Goatley, C.H., Bellwood, D.R., 2016. Composition and temporal stability of turf sediments on inner-shelf coral reefs. *Mar. Pollut. Bull.* 111 (1–2), 178–183. <https://doi.org/10.1016/j.marpolbul.2016.07.013>.
- Graham, M.H., 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84 (11), 2809–2815. <https://doi.org/10.1890/02-3114>.
- Hartig, F., 2022. DHARMA: residual diagnostics for hierarchical (Multi-Level/mixed) regression models. R package version 0.4.6. Available at: <https://CRAN.R-project.org/package=DHARMA>.
- Ilich, A.R., Misiuk, B., Lecours, V., Murawski, S.A., 2023. MultiscaleDTM: an open-source R package for multiscale geomorphometric analysis. *Trans. GIS* 27 (4), 1164–1204. <https://doi.org/10.1111/tgis.13067>.
- Intergovernmental Panel on Climate Change (IPCC), 2021. In: Masson-Delmotte, V. (Ed.), *The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press.
- Kinlan, B.P., Gaines, S.D., Lester, S.E., 2005. Propagule dispersal and the scales of marine community process. *Divers. Distrib.* 11 (2), 139–148. <https://doi.org/10.1111/j.1366-9516.2005.00158.x>.
- Krone, R., Paster, M., Schuhmacher, H., 2010. Effect of the surgeonfish *Ctenochaetus striatus* (Acanthuridae) on the processes of sediment transport and deposition on a coral reef in the Red Sea. *Facies* 57 (2), 215–221. <https://doi.org/10.1007/s10347-010-0239-8>.
- Latrille, F.X., Tebbett, S.B., Bellwood, D.R., 2019. Quantifying sediment dynamics on an inshore coral reef: putting algal turfs in perspective. *Mar. Pollut. Bull.* 141, 404–415. <https://doi.org/10.1016/j.marpolbul.2019.02.071>.
- Martins, G.M., Harley, C.D., Faria, J., Vale, M., Hawkins, S.J., Neto, A.I., Arenas, F., 2019. Direct and indirect effects of climate change squeeze the local distribution of a habitat-forming seaweed. *Mar. Ecol. Prog. Ser.* 626, 43–52. <https://doi.org/10.3354/meps13080>.
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlenn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., Weedon, J., 2022. Vegan: community ecology package. R package version 2, 6–4. Available at: <https://CRAN.R-project.org/package=vegan>.
- O'Brien, J., Scheibling, R., 2018. Turf wars: competition between foundation and turf-forming species on temperate and tropical reefs and its role in regime shifts. *Mar. Ecol. Prog. Ser.* 590, 1–17. <https://doi.org/10.3354/meps12530>.
- Pecl, G., Araújo, M., Bell, J., Blanchard, J., Bonebrake, T., Chen, I., Clark, T., Colwell, R., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R., Griffis, R., Hobday, A., Janion-Scheepers, C., Jarzyna, M., Jennings, S., Williams, S., 2017. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* 355 (6332). <https://doi.org/10.1126/science.aai9214>.
- Pessarrodona, A., Filbee-Dexter, K., Alcoverro, T., Boada, J., Feehan, C.J., Fredriksen, S., Grace, S.P., Nakamura, Y., Narvaez, C.A., Norderhaug, K.M., Wernberg, T., 2021. Homogenization and miniaturization of habitat structure in temperate marine forests. *Glob. Change Biol.* 27 (20), 5262–5275. <https://doi.org/10.1111/gcb.15759>.
- Pessarrodona, A., Vergés, A., Bosch, N.E., Bell, S., Smith, S., Sgarlatta, M.P., Wernberg, T., 2022a. Tropicalization unlocks novel trophic pathways and enhances secondary productivity in temperate reefs. *Funct. Ecol.* 36 (3), 659–673. <https://doi.org/10.1111/1365-2435.13990>.
- Pessarrodona, A., Tebbett, S.B., Bosch, N.E., Bellwood, D.R., Wernberg, T., 2022b. High herbivory despite high sediment loads on a fringing coral reef. *Coral Reefs* 41 (1), 161–173. <https://doi.org/10.1007/s00338-021-02211-w>.
- Pessarrodona, A., Filbee-Dexter, K., Wernberg, T., 2023. Recovery of algal turfs following removal. *Mar. Environ. Res.* 192, 106185. <https://doi.org/10.1016/j.marenvres.2023.106185>.
- Purcell, S.W., 2000. Association of epilithic algae with sediment distribution on a windward reef in the northern Great Barrier Reef, Australia. *Bull. Mar. Sci.* 66, 199–214.
- Purcell, S., Bellwood, D., 2001. Spatial patterns of epilithic algal and detrital resources on a windward coral reef. *Coral Reefs* 20 (2), 117–125. <https://doi.org/10.1007/s003380100150>.
- R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: <https://www.R-project.org/>.
- Ramírez, R., Tuya, F., Haroun, R.J., 2008. El Intermareal Canario. Poblaciones de lapas, burgados y cañadillas. *BIOGES. Universidad de Las Palmas de Gran Canaria*, p. 52.
- Roberts, D.W., 2023. LabDsv: ordination and multivariate analysis for ecology. R package version 2.1-0. Available at: <https://CRAN.R-project.org/package=labdsv>.
- Sangil, C., Martín-García, L., Hernández, J.C., Concepción, L., Fernández, R., Clemente, S., 2013. Impacts of fishing and environmental factors driving changes on littoral fish assemblages in a subtropical oceanic island. *Estuar. Coast Shelf Sci.* 128, 22–32. <https://doi.org/10.1016/j.eess.2013.04.023>.
- Schlaefter, J.A., Tebbett, S.B., Bellwood, D.R., 2021. The study of sediments on coral reefs: a hydrodynamic perspective. *Mar. Pollut. Bull.* 169, 112580. <https://doi.org/10.1016/j.marpolbul.2021.112580>.
- Sherman, C.S., Simpfendorfer, C.A., Pacoureau, N., Matsushiba, J.H., Yan, H.F., Walls, R.H., et al., 2023. Half a century of rising extinction risk of coral reef sharks and rays. *Nat. Commun.* 14 (1), 15. <https://doi.org/10.1038/s41467-022-35091-x>.
- Tebbett, S.B., Bellwood, D.R., 2019. Algal turf sediments on coral reefs: what's known and what's next. *Mar. Pollut. Bull.* 149, 110542. <https://doi.org/10.1016/j.marpolbul.2019.110542>.
- Tebbett, S.B., Goatley, C.H.R., Bellwood, D.R., 2017a. The effects of algal turf sediments and organic loads on feeding by coral reef surgeonfishes. *PLoS One* 12 (1), e0169479. <https://doi.org/10.1371/journal.pone.0169479>.
- Tebbett, S.B., Goatley, C.H.R., Bellwood, D.R., 2017b. Algal turf sediments and sediment production by parrotfishes across the continental shelf of the Northern Great Barrier Reef. *PLoS One* 12 (1), e0170854. <https://doi.org/10.1371/journal.pone.0170854>.
- Tebbett, S.B., Bellwood, D.R., Purcell, S.W., 2018a. Sediment addition drives declines in algal turf yield to herbivorous coral reef fishes: implications for reefs and reef fisheries. *Coral Reefs* 37 (3), 929–937. <https://doi.org/10.1007/s00338-018-1718-6>.
- Tebbett, S.B., Goatley, C.H., Bellwood, D.R., 2018b. Algal turf sediments across the Great Barrier Reef: putting coastal reefs in perspective. *Mar. Pollut. Bull.* 137, 518–525. <https://doi.org/10.1016/j.marpolbul.2018.10.056>.
- Tebbett, S.B., Streit, R.P., Bellwood, D.R., 2019. A 3D perspective on sediment accumulation in algal turfs: implications of coral reef flattening. *J. Ecol.* 108 (1), 70–80. <https://doi.org/10.1111/1365-2745.13235>.
- Tebbett, S.B., Goatley, C.H., Streit, R.P., Bellwood, D.R., 2020. Algal turf sediments limit the spatial extent of function delivery on coral reefs. *Sci. Total Environ.* 734, 139422. <https://doi.org/10.1016/j.scitotenv.2020.139422>.
- Tebbett, S.B., Sgarlatta, M.P., Pessarrodona, A., Vergés, A., Wernberg, T., Bellwood, D.R., 2022. How to quantify algal turf sediments and particulates on tropical and temperate reefs: an overview. *Mar. Environ. Res.* 179, 105673. <https://doi.org/10.1016/j.marenvres.2022.105673>.
- Tebbett, S.B., Crisp, S.K., Evans, R.D., Fulton, C.J., Pessarrodona, A., Wernberg, T., et al., 2023. On the challenges of identifying benthic dominance on anthropocene coral reefs. *Bioscience* 73 (3), 220–228. <https://doi.org/10.1093/biosci/biad008>.
- Triantis, K.A., Guilhaumon, F., Whittaker, R.J., 2011. The island species–area relationship: biology and statistics. *J. Biogeogr.* 39 (2), 215–231. <https://doi.org/10.1111/j.1365-2699.2011.02652.x>.
- Tuya, F., Haroun, R., 2006. Spatial patterns and response to wave exposure of shallow water algal assemblages across the Canarian Archipelago: a multi-scaled approach. *Mar. Ecol. Prog. Ser.* 311, 15–28. <https://doi.org/10.3354/meps311015>.
- Tuya, F., Ortega-Borges, L., Sanchez-Jerez, P., Haroun, R., 2006. Effect of fishing pressure on the spatio-temporal variability of the parrotfish, *Sparisoma cretense* (Pisces: scaridae), across the Canarian Archipelago (eastern Atlantic). *Fish. Res.* 77 (1), 24–33. <https://doi.org/10.1016/j.fishres.2005.07.017>.
- Valdazo, J., Viera-Rodríguez, M.A., Espino, F., Haroun, R., Tuya, F., 2017. Massive decline of *Cystoseira abies-marina* forests in gran Canaria island (canary islands, eastern atlantic). *Sci. Mar.* 81 (4), 499. <https://doi.org/10.3989/scimar.04655.23a>.
- Valdazo, J., Coca, J., Haroun, R., Bergasa, O., Viera-Rodríguez, M.A., Tuya, F., 2024. Local and global stressors as major drivers of the drastic regression of brown

- macroalgae forests in an oceanic island. *Reg. Environ. Change* 24 (2). <https://doi.org/10.1007/s10113-024-02228-1>.
- Valdés, L., Déniz-González, I., 2015. Canary Islands eddies and coastal upwelling filaments off North-west Africa. Available at: <http://hdl.handle.net/1834/9181>.
- Wilson, S.K., Bellwood, D.R., Choat, J.H., Furnas, M.J., 2003. Detritus in the epilithic algal matrix and its use by coral reef fishes. *Oceanogr. Mar. Biol.* 41, 279–310.