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

UNIVERSIDADE DO ALGARVE

Faculdade de Ciências e Tecnologia

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Mestrado em Biologia Marinha

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Declaração de autoria de trabalho

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Declaro ser a autora deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída.

Assinatura

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Acknowledgements of the thesis

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Abstract

Human activities are rapidly altering the structure and functioning of ecosystems around the globe, but the magnitude and extent of ecological impacts remain poorly understood. Algal turfs are expected to replace macroalgal forests and coral reefs as the dominant benthic state in the Anthropocene, a process that is already occurring in many disparate temperate and tropical regions worldwide. Turf seascapes play a key role in regulating ecosystem processes through sediment retention. However, our understanding of sediments trapped by turf on coastal reefs, particularly in marginal oceanic islands, remains limited. Here, we quantified turf seascape composition (algal structure and mean height) and sediment properties (total particulate load, grain size distribution, and organic content) at an insular scale, using a densely populated warm-temperate oceanic island as a model system. We further decoupled the role of geomorphological, habitat, and anthropogenic predictors in explaining variation in turf seascape properties. We revealed significant spatial variation in turf seascape properties event at relatively small spatial scales, with turf sediment loads varying by three orders of magnitude (~ 1 g/m² to 2000 g/m²). In contrast, organic load varied considerably less (~ 1 g/m² to 100 g/m²) and displayed no significant variations across our study sites. Human pressure and algal composition were the strongest predictors of turf sediment load, highlighting the coupled role of global climate change and 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 marginal oceanic islands and calls for efforts to link variation in turf seascape properties with key ecological processes that maintain the functionality of these vulnerable systems.

Resumo

As alterações causadas pelos humanos estão a provocar uma redistribuição significativa da vida no planeta, desafiando paradigmas ecológicos estabelecidos e originando novas configurações nos ecossistemas. Estas novas configurações, frequentemente impulsionadas por novas interações emergentes entre espécies, estão a afetar o fluxo de energia e materiais nos ecossistemas, o que pode alterar os serviços que estes prestam à sociedade. Nos ecossistemas marinhos, espécies fundamentais, como os corais tropicais e as florestas de macroalgas em regiões temperadas, estão a ser substituídas por agregações de algas do tipo r, conhecidas como mantos de algas ou *turf*. Estas mudanças estão associadas a diversos fatores, como o aquecimento global, a eutrofização e a sedimentação. A perda da estrutura tridimensional dos habitats afeta as espécies que dela dependem e altera o fluxo de energia nos recifes. Uma vez estabelecidos, os mantos de algas reforçam o seu domínio através de mecanismos de *feedback*, como o rápido crescimento que impede a colonização de espécies fundamentais e a acumulação de sedimentos que reduz a germinação dessas espécies. As algas do tipo *turf* retêm sedimentos ao diminuir o movimento da água e ao usar mucilagem para aglutinar partículas. Esta acumulação de sedimentos pode dificultar a recuperação de espécies-chave e alterar o comportamento alimentar dos peixes, podendo potencialmente destabilizar as funções ecológicas que sustentam as pescarias locais. Apesar da crescente evidência dos efeitos adversos dos tapetes algais, os processos subjacentes à acumulação de sedimentos nestes ecossistemas receberam pouca atenção científica. Grande parte da investigação concentrou-se em sistemas de recifes bem estudados, como a Grande Barreira de Coral, neglegenciando regiões marginais, como as ilhas oceânicas, que são inerentemente mais vulneráveis à perda de biodiversidade. Nessas ilhas, as algas *turf* podem tornar-se o estado ecológico predominante, o que ressalta a necessidade de estudos detalhados sobre a composição destes habitats e os sedimentos que acumulam.

O nosso estudo foi realizado na ilha de Gran Canaria, localizada nas Ilhas Canárias (Atlântico Nordeste), onde inicialmente realizámos uma comparação histórica utilizando dados de fotocélulas de 2005 e 2023 para avaliar mudanças na configuração dos habitats bentônicos. As análises multivariadas de permutações (PERMANOVA) revelaram uma mudança significativa na estrutura da vegetação bentónica, destacando a esperada perda de algas formadoras de dossel e um aumento constante na cobertura de algas *turf*. Para o objetivo do nosso estudo, que era analisar as características do *turf* e o sedimento associado, selecionamos doze estações de amostragem com alta cobertura de mantos de algas (*turf*), representando diferentes condições biofísicas e antropogénicas. As amostras de algas e sedimentos foram coletadas por mergulho autónomo utilizando um coletor de sucção. No laboratório, as algas foram classificadas, pesadas e medidas em grupos morfofuncionais, enquanto o sedimento foi peneirado e tratado com peróxido de hidrogênio para eliminar a matéria orgânica. Posteriormente, analisámos vários preditores geomorfológicos, antropogénicos e do habitat para avaliar a sua influência na carga e composição dos sedimentos nos mantos de algas. Para isso, realizámos análises de coordenadas principais (PCoA) e ajustámos modelos lineares generalizados mistos (GLMM). Finalmente, foi realizada uma seleção de modelos com base no critério de informação de Akaike (AIC) para identificar os preditores mais relevantes.

Um dos modelos mais relevantes para prever a quantidade de sedimentos retidos pelas algas incluiu o índice HAPI (pressão humana acumulativa) e a composição dos habitats, mostrando que estas variáveis explicam grande parte da variabilidade nas cargas de sedimentos. O índice HAPI revelou-se consistentemente fundamental, destacando o impacto significativo das atividades humanas nos paisagens de algas *turf* e na acumulação de sedimentos. A correlação positiva entre o índice HAPI e a carga de sedimentos revela que um aumento na pressão humana está associado a um incremento exponencial na carga de sedimentos, de quase 395 g/m² a 1745 g/m² nas áreas mais afetadas. As áreas próximas à capital, Las Palmas de Gran Canaria, mostraram maiores acumulações de sedimentos, indicando que a urbanização intensifica a sedimentação, um achado corroborado por estudos anteriores. Esta acumulação de sedimentos impacta negativamente o comportamento alimentar dos peixes herbívoros, a qualidade das algas e o recrutamento de espécies-chave. O estudo também identificou que as áreas próximas à costa apresentavam maiores cargas de sedimentos, provavelmente devido a atividades humanas como dragagem e agricultura, o que gera stress nos ecossistemas recifais costeiros, afetando a biodiversidade e as funções ecológicas.

Este trabalho destaca ainda uma variabilidade significativa nas características dos mantos de algas, mesmo em escala de ilha. Em relação à composição dos habitats, observou-se uma correlação positiva entre a altura das algas *turf* e a quantidade de sedimentos retidos; as algas mais longas retêm mais partículas, o que pode dever-se à sua capacidade de capturar sedimentos ou ao efeito da sedimentação na redução da herbivoria.

Este ciclo de *feedback* pode perpetuar a dominância das algas *turf* em áreas afetadas pela sedimentação, alterando as interações ecológicas e a qualidade dos recursos para os peixes herbívoros. As algas filamentosas, devido à sua estrutura ramificada e rápida recuperação, foram particularmente eficazes na captura de sedimentos, destacando-se em relação a outras formas de crescimento menos resilientes sob altas cargas de sedimentos.

Em resumo, os nossos achados sublinham a importância das pressões humanas e das características dos mantos de algas na distribuição dos sedimentos em recifes temperados. A acumulação de sedimentos destabiliza funções ecológicas essenciais, afetando a herbivoria, o comportamento alimentar dos peixes e o recrutamento de espécies formadoras de florestas. Isto ressalta a necessidade urgente de estratégias de gestão que abordem tanto o aquecimento global quanto os impactos humanos locais, especialmente em ilhas oceânicas marginais, para proteger a saúde e funcionalidade destes ecossistemas recifais vulneráveis.

Table of contents

Index of Figures

Chapter 1 – General introduction

Chapter 2 - Manuscript

Index of Tables

Chapter 2 - Manuscript

List of abbreviations, acronyms and symbols

CATAMI - Collaborative and Annotation Tools for Analysis of Marine Imagery Video

CCA – Crustose Coralline Algae

DW – Dry Weight

EAC – Epilithic algal community

EAM – Epilithic algal matrix

GLMMs - Generalized Linear Mixed Models

HAPI – Human Activities and Pressure Index

IPCC - Intergovernmental Panel on Climate Change

LSATs - Long sediment-laden algal turfs

MHWs - Marine heatwaves

OL - Organic load

PCoA - Principal Coordinate Analysis

PERMANOVA - Permutational Multivariate Analysis of Variance

SL - Sediment load

SP2 - Sediment PCOA2

SPATs - Short productive algal turf

Chapter 1 - General Introduction

1. Climate change, human activities and redistribution of marine life

Earth has entered the Anthropocene, a new era in which human activities now rival natural processes in shaping ecosystems (Waters et al., 2016; Williams et al., 2016). Historically, disturbances have been recognized as essential components of ecosystem dynamics (Levin & Paine, 1974; Grime, 1977), but today, human-driven disruptions are altering these patterns in unprecedented ways (Turner, 2010). These activities are dramatically transforming terrestrial and marine ecosystems worldwide, leading to significant shifts in species distributions and profound impacts on biodiversity and ecosystem functioning (Beaugrand et al., 2015; Pecl et al., 2017). However, the long-term ecological consequences of these changes, and their effects on ecosystem services critical to human society, remain uncertain (Turner, 2010; Seidl et al., 2016).

A key aspect of this redistribution is the shift from K-strategist species, which are characterized by slower growth, lower reproductive rates, and longer lifespans, to r-strategist species, which reproduce rapidly, have shorter lifespans, and are more opportunistic (Pianka, 1970; Stearns, 1977). In stable environments with low disturbance, K-strategists typically dominate, shaping complex ecosystems with high biomass and biodiversity (Grime, 1977). These species possess traits that optimize resource capture in productive, crowded environments, often creating habitat structures that support diverse communities and regulate environmental conditions (Ellison et al., 2005). However, human activities have disrupted the conditions that favour these competitive species, instead promoting species that thrive in disturbed environments (Tilman & Lehman, 2001).

In recent decades, climate change and other human-induced stressors have led to significant declines in marine foundation species (K-strategists) and their communities, causing a loss of valuable ecosystem services (Wernberg et al., 2024). At the same time, the spread of fast-growing algal turfs (r-strategists) has been observed across various regions, contributing to increased coral mortality and a decline in kelp forest cover (Figure 1.1) (Goatley & Bellwood, 2011; Jouffray et al., 2015; Vergés et al., 2016; Feehan et al., 2019; Filbee-Dexter & Wernberg, 2018). Unlike corals and kelps, which are sensitive to environmental stressors, algal turfs are more resilient and thrive in human-altered environments, where they are expected to continue expanding (Hay, 1981; Falkenberg et al., 2015). This persistence is likely due to human-driven environmental changes, such as ocean warming, heatwaves, coastal eutrophication, sedimentation or ocean acidification, which promote the growth and survival of algal turfs (Hay, 1981; Falkenberg et al., 2015). Human-induced changes to disturbance regimes shift the balance of algal competition by directly enhancing turf growth and its competitive advantage, while disproportionately damaging canopy algae and corals (Strain et al., 2014). This indirect effect benefits turf algae and other organisms (Strain et al., 2014). As a result, many shallow reef ecosystems (temperate and tropical) are increasingly becoming dominated by algal turfs, which now play a key role in shaping these environments (Filbee-Dexter & Wernberg, 2018; Bellwood et al., 2019a; Pessarrodona et al., 2021).

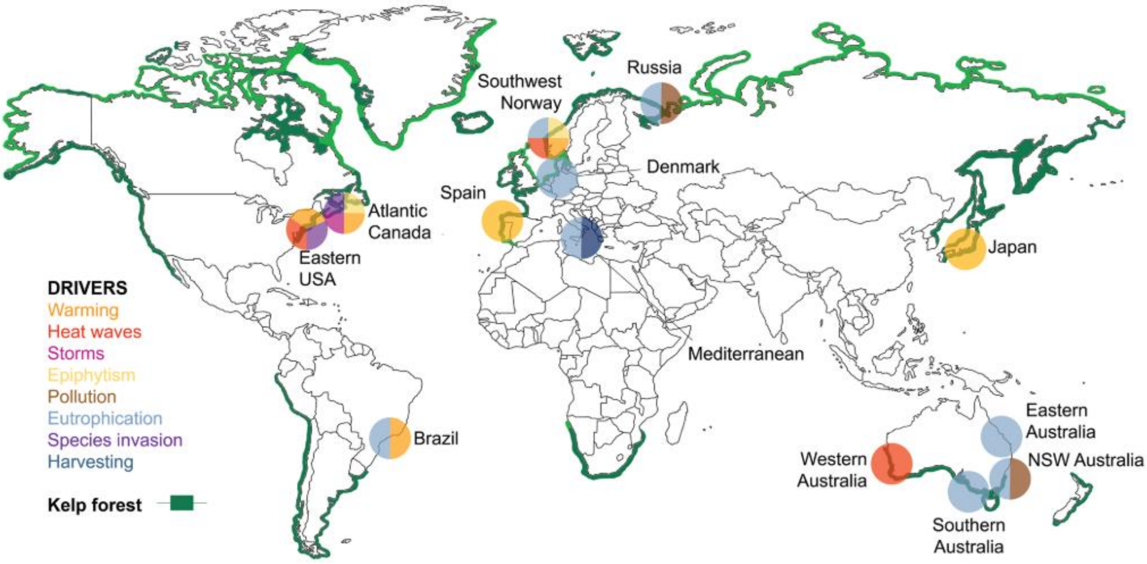

Figure 1.1. Global map showing the locations of shifts from habitat-forming macroalgae to algal turfs (circles) overlaid on the approximate distribution of global kelp forests (green). The slice colours of circles indicate different drivers implicated in the shift. Image reproduced from Filbee-Dexter & Wernberg. (2018).

In temperate shallow reefs, habitats once dominated by K-strategists species like canopy-forming species, are being replaced by warm-affinity species (Tanaka et al., 2012; Pessarrodona et al., 2018a), sea urchins (Ling et al., 2009; Filbee-Dexter & Scheibling, 2014), and particularly algal turfs – carpet-like aggregations of low-lying macroalgae-(Benedetti-Cecchi et al., 2001; Gorgula & Connell, 2004; Moy & Christie, 2012; Filbee-

Dexter & Wernberg, 2018). The shift from kelp forests to urchin barrens has been widely studied on temperate rocky reefs (Filbee-Dexter & Scheibling, 2014), often resulting from sea urchin population booms triggered by predator removal, recruitment pulses, or altered environmental conditions (Steneck et al., 2002; Filbee-Dexter & Scheibling, 2014). In some cases, kelp forests can recover after years or decades, as sea urchin populations decline and grazing pressure lessens (Watson & Estes, 2011; Filbee-Dexter & Scheibling, 2014). However, large-scale transitions from kelp forests to algal turfs appear to be more permanent, with reefs remaining in a degraded, turf-dominated state (Filbee-Dexter & Wernberg, 2018). This transformation reduces the structural complexity of these ecosystems, replacing the towering, forest-like environments with low-lying algal mats (Wernberg et al., 2016). These simplified habitats alter species interactions and lead to the emergence of novel biotic communities, where previously distinct species now coexist and interact in unpredictable ways (Pecl et al., 2017; Doney et al., 2012).

2. Turf algae definition

The description of turf algal mats has evolved over time, with various terms used in the literature. Initially, they were recognized as multispecies assemblages of short algae under the term ‘epilithic algal community’ (EAC) (Hatcher & Larkum 1983). Later, Wilson and Bellwood (1997) introduced the term ‘epilithic algal matrix’ (EAM) to emphasize the inclusion of non-algal components like organic detritus, inorganic sediments, microalgae, and microbes within the matrix. Since then, EAM has been widely adopted in the literature (e.g., Heenan et al., 2016; McAndrews et al., 2019; Rasher et al., 2011; Tebbett et al., 2017b; Wilson et al., 2003). Since the term “epilithic” comes from the Greek words ‘epi’ (meaning upon) and ‘lithic’ (meaning rock), some researchers have avoided this narrow terminology by combining both ‘turf’ and ‘epilithic’ (e.g., ‘epilithic algal turfs’; Bonaldo & Bellwood, 2010) or by using ‘turf’ as the primary term and listing ‘epilithic’ as a keyword (e.g., McCook 2001). Nowadays, the term turf algae (or ‘turfs’) is the most used term, following efforts by Connell et al. (2014) to standardize the definition. More recently, the terms ‘short productive algal turfs’ (SPATs) and ‘long sediment-laden algal turfs’ (LSATs) have been introduced to distinguish between two fundamental types of algal turfs: those that are relatively sediment-free and shorter, and heavily laden with sediments (Goatley et al., 2016). This evolution in terminology underscores the growing emphasis on the role of sediments within algal turfs.

3. Turf algae description

Turf algae are characterized by dense mats of small, multispecies assemblage of macroscopic algae that cover various substrates such as dead coral, rocks, and sandy areas (Connell et al., 2014). They grow in densely packed aggregations of thalli with reduced vegetation height (usually <10 cm), and exhibit a wide range of morphologies, from filamentous to foliose or branching forms (Airoldi, 2001). Despite being shorter than canopy-forming algae, turf algae encompass a diverse array of species with varying heights, densities, and structural complexity, which can resemble marine forests on a smaller scale (Connell et al., 2014). Algal turfs are globally widespread and compound a significant component of many tropical, subtropical, and temperate marine ecosystems (Connell et al., 2014; Filbee-Dexter & Wernberg, 2018; Tebbett & Bellwood, 2019), exhibiting significant heterogeneity across various spatial scales (Harris et al., 2015).

4. Ecological role of turf algae

Turf algae contribute to various ecosystem functions, such as recruitment, productivity, and supporting herbivory and detritivory (Alestra et al., 2014; Burek et al., 2018; Speare et al., 2019; Ng et al., 2021). However, the sediments trapped within algal turfs and increasing human pressures influence these functions and the ecosystem services reefs provide to humanity (Tebbett & Bellwood, 2019) (Figure 1.2).

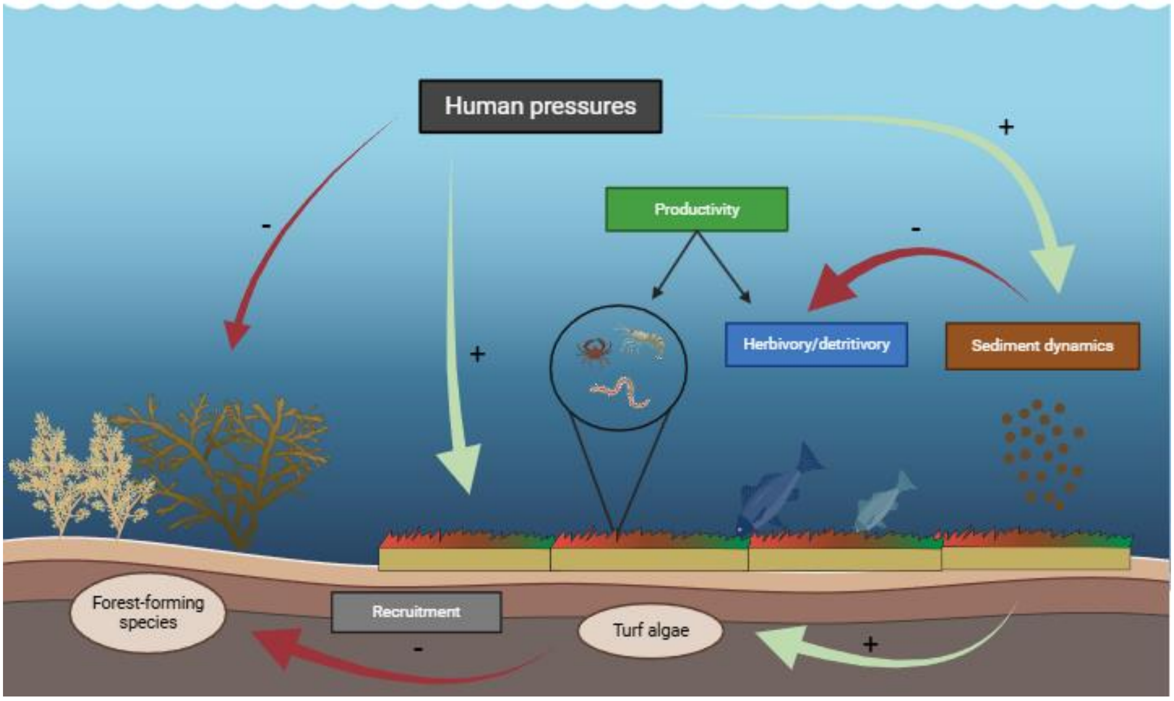

Figure 1.2. Schematic overview of how human pressures negatively impact forest-forming species while benefiting turf algae, and the ecosystem functions associated with turf algae. Arrows indicate the nature of the relationships, either positive or negative. Turf algae inhibit the recruitment and growth of forest-forming species but enhance productivity by providing food for herbivorous and detritivorous fish and habitat for epifauna. Additionally, turf algae trap sediments (a process enhanced by human pressures), which in turn negatively affects herbivory, productivity, and recruitment. Created with BioRender.com. Image credit: Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/).

4.1. Recruitment and competition

Canopy-forming seaweeds and corals typically outcompete turf algae in stable, low-stress environments (Irving & Connell, 2006) due to traits that allow them to displace turfs (O'Brien and Scheibling, 2018). For example, canopy-forming algae inhibit turf cover through shading or physical abrasion (whiplash) (Figure 1.3a,b) (Irving & Connell, 2006). However, natural disturbances such as warming events or storms often cause the death of these canopy-formers, creating open gaps that turf quickly colonize (Irving et al., 2004; Miller et al., 2009; Wernberg et al., 2020). Turf algae's rapid colonization of newly available spaces is a defining trait, enabling them to outcompete other benthic organisms (Vermeij et al. 2010; O'Brien and Scheibling, 2018; Liao et al. 2019). Their resilience to disturbance and stress (Hay, 1981) positions them to thrive as human activities increasingly impact marine environments (Falkenberg et al., 2015). Once established, turfs maintain dominance through self-reinforcing feedback mechanisms (Figure 1.3c,d) (Filbee-Dexter & Wernberg 2018; O'Brien and Scheibling 2018), including rapid overgrowth and monopolization of substrates (Falkenberg et al., 2015), which limits the availability of space for other species to settle (O'Brien and Scheibling 2018). Over time, turfs tend to accumulate sediment, which further strengthens their competitive edge by preventing the germination and survival of foundation species (Gorgula & Connell, 2004), therefore increasing post-settlement and/or post-recruitment mortality (O'Brien and Scheibling 2018). This sediment buildup creates conditions unfavourable for other species, reinforcing the dominance of turf algae (Filbee-Dexter & Wernberg, 2018; Gorman & Connell, 2009).

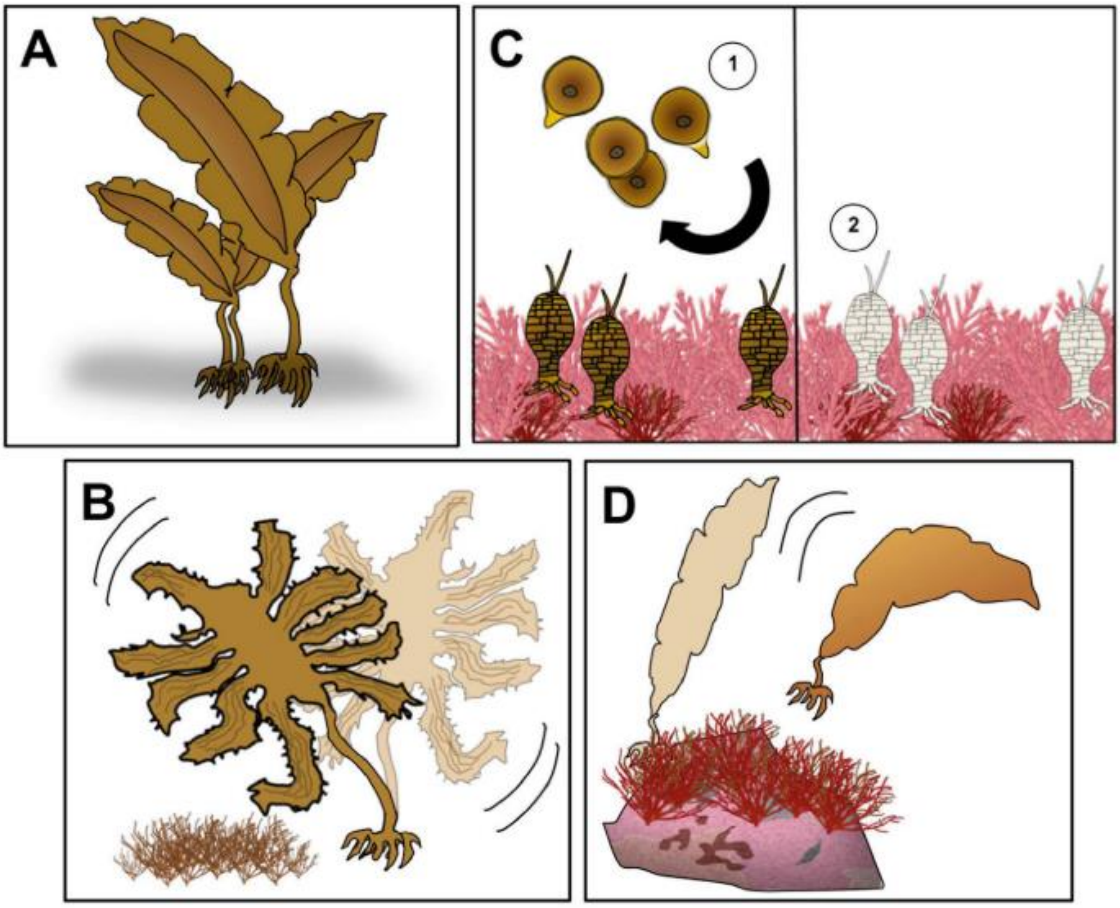

Figure 1.3. Mechanisms of competition between canopy-algae and turf-forming algae. Canopy algae suppress turf algae through (A) shading and (B) abrasion/whiplash. Turf algae (C) inhibit early life-history stages of canopy algae by (1) forming a settlement barrier or (2) increasing post-settlement mortality via sediment smothering, shading, overgrowth, or allelopathic exudates; and (D) causing post-recruitment mortality of macroscopic recruits via dislodgement/ sloughing. Image reproduced from O'Brien and Scheibling. (2018). Image credit: Dieter Tracey (filamentous algae). Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces. edu/imagelibrary/)

4.2. Productivity and herbivory/detritivory

The presence of turf algae is both natural and essential to the functioning of many reef ecosystems (Hatcher, 1988; Klumpp & McKinnon, 1992). Algal turfs are key primary producers (Tebbett & Bellwood, 2021) and play a crucial role in supporting essential trophic pathways, by transferring energy up the food chain, particularly through herbivorous fishes (Russ, 2003; Kelly et al., 2017; Tebbett et al., 2018). Their high productivity supports a diverse range of marine life, from herbivores that feed on the algae to detritivores that consume organic matter (Connell et al., 2014). Turf algae and detritus play a crucial role in maintaining fish biomass on coral reefs (McMahon et al., 2015) and temperate reefs undergoing tropicalization (Pesssarrodona et al., 2021).

Herbivorous fishes that exploit the nutritional resources contained within the EAM (e.g. algae, detritus, cyanobacteria) are the most diverse in terms of the functions they perform (e.g., sediment, algae removal) and the ways they feed and interact with the substratum, being partitioned into: scrapers, brushers, croppers, concealed croppers and sediment suckers (Adam et al., 2015; Marshell & Mumby, 2015; Bellwood et al., 2019b). The higher digestibility of algal turfs compared to macroalgae in marine forests is believed to promote increased fish herbivory, which may lead to greater overall fish biomass (Vergés et al., 2019).

Turf algae also contribute significantly to overall algal production, often surpassing the productivity of larger macroalgae by more than 15 times (Kelly et al., 2017). Herbivorous fish can consume 50%–100% of this primary production (Carpenter, 1986; Hay, 1981), helping to regulate algal growth and maintain ecological balance within turf algae communities.

Moreover, algal turfs play a key role in supporting secondary production by providing habitat for various epifaunal organisms, which serve as important food sources for higher-level consumers (Kramer et al., 2013). Globally, turfs have been shown to sustain diverse and abundant epifaunal communities (Kelaher & Castilla, 2005; Berthelsen et al., 2014; Martins et al., 2016; Fraser et al., 2021), primarily due to the creation of complex microhabitats with numerous small spaces that accommodate a wide range of invertebrates (Dijkstra et al., 2017). Additionally, meso-invertebrates inhabiting algal turfs provide an important food source for some invertivorous fish (Kramer et al., 2013).

4. Sediment dynamics

The characteristics and key ecosystem functions of algal turfs are greatly shaped by the amount and type of sediments they capture (Irving & Connell, 2002; Tebbett & Bellwood, 2019). The intricate structure of algal turfs creates a diffusive boundary layer that slows water movement, serving as the primary mechanism for sediment deposition and accumulation within these turfs (Carpenter and Williams, 1993; Latrille et al., 2019). Additionally, this process is likely enhanced by other factors, such as the secretion of mucilaginous sheaths by filamentous cyanobacteria within the EAM, which can bind sand particles together (Stal, 2003). Consequently, the EAM, and algal turfs in particular, demonstrate a remarkable ability to capture and retain sediments. In this context, various external factors influence the amount of sediment trapped within turf seascapes:

- Local sediment inputs: these sediment inputs are influenced by factors such as agricultural practices, coastal development, and nearshore dredging (Brodie & Pearson, 2016; Fisher et al., 2017; Tebbett et al., 2018b), that directly impact the amount and type of sediment delivered to a reef. This, in turn, determines how much sediment becomes trapped within turf seascapes (Browne et al., 2013).
- Reef morphology: geomorphological factors such as reef slope influence sediment trapping, with complex, uneven surfaces tending to accumulate more sediment than flat or smooth areas (Tebbett et al., 2017a).
- Hydrodynamics: wave action and water movement can displace sediments from algal turfs or promote sediment accumulation in calmer reef areas (Carpenter & Williams, 1993; Purcell, 2000). Also, the grain size distribution is influenced by reef morphology, with finer sediments in lower-energy habitats (Gordon et al., 2016)
- Feeding activity of fishes: Herbivorous fish are important in regulating sediment accumulation by grazing on algal turfs and helping to clear sediments (Hoey & Bellwood, 2007; Krone et al., 2010). The absence of these fish can lead to increased sediment trapping, which may affect the overall reef health (Goatley & Bellwood, 2010).

The presence of high turf sediment loads can significantly harm ecosystem functioning and resilience by disrupting essential ecosystem processes (e.g., recruitment and herbivory) (Ricardo et al. 2017; Tebbett et al. 2017a; Fong et al. 2018; Speare et al. 2019). The formation of an anoxic layer in turf sediments (Sousa et al 1981; Layton et al.

2019) can inhibit the recruitment of forest-forming species (Connell and Russell 2010), thus playing a key role in reinforcing turf dominance and preventing the recovery of canopy-dominated states (Filbee-Dexter & Wernberg, 2018).

Moreover, these sediments can also impact herbivory by altering fish-feeding behaviour and reducing the nutritional quality of algal resources, which may be diluted by the presence of inorganic sediments (Bellwood & Fulton, 2008; Goatley & Bellwood, 2012; Gordon et al., 2016; Pessarrodona et al., 2021; Tebbett et al., 2017b; Purcell & Bellwood, 2001; Tebbett et al., 2020). Even though fishes interact differently with sediments, in all cases, algal turf sediments appear to drive increased algal turf length by either i) reducing feeding rates (Goatley et al., 2016; Gordon et al., 2015; Tebbett et al., 2017a) or ii) limiting feeding to the 'above-sediment' portion of algal filaments (Adam et al., 2018; Tebbett et al., 2017c).

Algal turf sediments not only directly influence fish-feeding behaviour but also affect the ability of herbivorous fish to obtain adequate nutritional resources from the EAM. These sediments can: i) lower the productivity of the algal turfs (Tebbett et al., 2018a), ii) dilute the concentration of organic material within the algal turfs (Gordon et al., 2015; Purcell and Bellwood, 2001), and/or iii) promote the formation of LSATs, which likely reduce the availability of endolithic cyanobacteria for parrotfish (Clements et al., 2016; Hutchings et al., 2005).

If sediment retention and trapping increase within algal turfs, it can lead to the formation of LSATs (Gorgula and Connell 2004; Goatley et al. 2016; Filbee-Dexter and Wernberg 2018), which carries negative implications for the functioning of reef systems, and their ability to support key ecosystem services (Bellwood et al., 2019b). In relatively healthy reef systems, turf algae are characterized by SPATs, which are relatively free of sediments and support high-turnover herbivorous, particulate or detrital trophic pathways (Hatcher 1988; Klumpp and McKinnon 1992; Russ 2003; Wilson et al. 2003). However, overfishing of herbivorous fishes or increased sedimentation can shift the system to an alternate state, characterized by the proliferation of LSATs (Goatley et al. 2016). These LSATs are unproductive and trap additional sediment, further decreasing herbivory and initiating a positive feedback loop (Tebbett & Bellwood, 2019). This process triggers bottom-up effects on herbivorous fish populations (Tebbett et al., 2021), posing significant threats to shifting reef ecosystems by compromising their functionality and their capacity to deliver essential ecosystem services (Bellwood et al., 2019b).

5. Research questions

Despite its global prevalence, our understanding of the ecological impacts of turf expansion on reefs remains incomplete, particularly concerning the drivers that sustain turf-dominated systems and their associated sediments. While the definition of 'turf' in shallow reef ecosystems continues to be debated among ecologists (Connell et al., 2014), this knowledge gap is especially significant in temperate reefs, where research on turf algae began later than in tropical systems, resulting in fewer comprehensive studies.

Increased sedimentation, often driven by anthropogenic activities, exacerbates the complexity of these systems by intensifying the negative effects on reef ecosystems and accelerating turf expansion. Sediment accumulation within turf plays a critical and underexplored role in several key ecological processes, including nutrient cycling, habitat structure alteration, and the reduction of recruitment in key species, such as macroalgal forests (Ricardo et al. 2017; Tebbett et al. 2017a; Fong et al. 2018; Speare et al. 2019). These sediments can also act as physical barriers, trapping organic matter and nutrients, which enhance turf growth while simultaneously impairing the resilience of macroalgal forests (Filbee-Dexter & Wernberg, 2018).

Given the predicted expansion of turf-dominated ecosystems, understanding the multifaceted role of sediment in turf proliferation is a pressing priority for marine ecologists. Investigating how turf sediments influence ecological functions, such as nutrient dynamics and habitat modification, is essential to anticipate and mitigate the potential long-term impacts on reef resilience and ecosystem services.

This study addresses key knowledge gaps, with the overarching research question being ‘Which are the main drivers of turf sediments, and how do they influence key ecological processes in warming-temperate reef systems?’. To do so, we examined turf seascape composition and sediment properties on a warm-temperate island, assessing how geomorphological, habitat, and anthropogenic factors influence their variation.

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Chapter 2- Manuscript

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

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Keywords

Climate change, habitat reconfigurations, turf seascapes, local anthropogenic pressures, particulate load, ecosystem functions.

1. Abstract

Human activities are rapidly altering the structure and functioning of ecosystems around the globe, but the magnitude and extent of ecological impacts remain poorly understood. Algal turfs are expected to replace macroalgal forests and coral reefs as the dominant benthic state in the Anthropocene, a process that is already occurring in many disparate temperate and tropical regions worldwide. Turf seascapes play a key role in regulating ecosystem processes through sediment retention. However, our understanding of sediments trapped by turf on coastal reefs, particularly in marginal oceanic islands, remains limited. Here, we quantified turf seascape composition (algal structure and mean height) and sediment properties (total particulate load, grain size distribution, and organic content) at an insular scale, using a densely populated warm-temperate oceanic island as a model system. We further decoupled the role of geomorphological, habitat, and anthropogenic predictors in explaining variation in turf seascape properties. We revealed significant spatial variation in turf seascape properties event at relatively small spatial scales, with turf sediment loads varying by three orders of magnitude (~ 1 g/m² to 2000 g/m²). In contrast, organic load varied considerably less (~ 1 g/m² to 100 g/m²) and displayed no significant variations across our study sites. Human pressure and algal composition were the strongest predictors of turf sediment load, highlighting the coupled role of global climate change and 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 marginal oceanic islands and calls for efforts to link variation in turf seascape properties with key ecological processes that maintain the functionality of these vulnerable systems.

KEYWORDS: Climate change, habitat reconfigurations, turf seascapes, local anthropogenic pressures, particulate load, ecosystem functions.

2. Introduction

Modern humans (*Homo sapiens*) have inhabited earth ecosystems for approximately 300,000 years, just a blink of an eye of Earth's 4.54-billion-year history. Yet, human activities have severely decimated populations of wild species (Cardinale et al., 2012) and are causing the faster change in Earth's climate in the last 10,000 years

(IPCC, 2021). Climate-driven changes in species' geographic ranges and phenology are causing a major redistribution of life on earth (Beaugrand et al., 2015; Bosch et al., 2022), giving rise to novel ecosystem configurations where past ecological paradigms may be challenged (Hobbs et al., 2006; Williams et al., 2019). Emerging ecosystem configurations are often characterised by novel interactions between species that can alter energy and material flows (i.e., ecosystem functions) (Vergés et al., 2019; Pessarrodona et al., 2022b), potentially disrupting the goods and services provided to human societies (Pecl et al., 2017; Bonebrake et al., 2017). Understanding the processes that underpin the functioning of novel ecosystem configurations and their impacts on ecosystem functions and services is thus an emerging topic in ecological research.

In the marine realm, foundational species with competitive life histories (K-strategist), such as tropical reef-building corals and temperate macroalgal forests, are being increasingly replaced by opportunistic (r-strategist) carpet-like aggregations of low-lying macroalgae (herein algal turfs) (Falkenberg et al., 2015; Doubleday & Connell, 2018; O’Brien & Scheibling, 2018; Bellwood et al., 2019). While the 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 et al., 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 (Pessarrodona et al., 2021; Fraser et al., 2020), which in turn can alter the transfer of energy to reef consumers (Pessarrodona et al., 2022a,b; Bosch et al., 2022b). Once established, turfs sustain their competitive 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 spore settlement, and (ii) accumulating sediment, which reduces germination and survival rates of foundational species (Filbee-Dexter & Wernberg, 2018; Gorman & Connell, 2009).

Although traditionally perceived as relatively homogenous, structurally simple, habitat configurations, turf seascapes encompass many phylogenetically diverse species, displaying varying morphologies, heights, and densities (Connell et al., 2014; Filbee-Dexter & Wernberg, 2018). The variability found within turf seascapes determines key processes such as the rate at which sediment is trapped (Gordon et al., 2016; Clausing et al., 2014; Goatley et al., 2016; Tebbett et al., 2018), which in turn can alter consumer trophodynamics and the biomass production of important commercially targeted herbivorous fishes (Tebbett et al., 2018; Bellwood et al., 2018; Robinson et al., 2018). Turf algae retain and accumulate sediment by slowing water movement and using mucilage to bind deposited particles (Carpenter & Williams, 1993). Several external factors modulate the number 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; Carpenter and Williams, 1993; Purcell, 2000), and the feeding activity of fishes (Goatley & Bellwood, 2010; Hoey & Bellwood, 2008; Krone et al., 2010). The length of algal turfs is also a critical driver of sediment accumulation, which underpins a critical ecological transition from short productive algal turfs (SPATs) to long sediment-laden algal turfs (LSATs) (Goatley et al., 2016; Fong et al., 2018; Duran et al., 2019). 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 (Bellwood & Fulton, 2008; Goatley & Bellwood, 2012; Gordon et al., 2016; Pessarrodona et al., 2021; Tebbett et al., 2017b; Purcell & Bellwood, 2001; Tebbett et al., 2020).

Despite mounting evidence of these adverse impacts, the patterns and processes underpinning sediment accumulation in turf seascapes have garnered scant scientific attention and are seldom accounted for in ecosystem management and monitoring initiatives (Tebbett & Bellwood, 2019; Schlaefer et al., 2021). Most direct empirical quantifications of the quantity and quality of turf sediments, and their implications for reef dynamics, have been drawn from studies in well-known coral reef systems (e.g., the Great Barrier Reef) (Tebbett & Bellwood, 2019). Marginal reefs, defined as those under sub-optimal environmental conditions (Browne & Bauman, 2023; de O. Soares, M. et al., 2020), are at the forefront of ecological change, with many marine foundational species at their warm range edge experiencing severe population declines in response to long-term warming and intensifying marine heatwaves (MHWs) (Wernberg et al., 2016; Smith et al., 2023). Furthermore, oceanic islands are inherently less resilient to biodiversity loss than continental regions (Frankham, 2005), a phenomenon that is intensified in isolated systems separated from mainland populations by long geographic distances and abyssal barriers to dispersal (Kinlan et al., 2005). Turf seascapes could thus represent a permanent ecosystem state in marginal, isolated, oceanic islands, which 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.

Here, we augment our knowledge of algal turf properties and their sediments within marginal, isolated, oceanic islands. We focused on a warm-temperate oceanic island (Gran Canaria Island, Canary Islands, 27º 44´ N, 15º 35´ W), which constitutes a biogeographic transition zone between the Atlantic-Mediterranean and the Tropical Eastern Atlantic. The region lies on the warm range edge of several temperate macroalgal forests of the genus *Cystoseira* 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 MHWs and intense coastal development (Alfonso et al., 2021; Valdazo et al., 2024). To date, however, no study has quantified turf seascape composition and the properties of their sediments in the region, even though this can be a critical factor constraining the recovery of *Cystoseira* forest and modulating yields of socio-economically important targeted herbivorous fishes, such as the parrotfish *Sparisoma cretense* (Tuya et al., 2006; Castro et al., 2019). We quantified several key properties of turf algae (mean height, algae biomass and morpho-functional groups) and their sediments (particulate load, organic/inorganic ratio and grain size), and then modelled the relative importance of biotic, abiotic, and anthropogenic drivers in their spatial distribution at an island-scale. This study therefore represents an important first step to characterising turf seascapes in the region, which is key for developing management strategies in novel ecosystem configurations.

3. Materials and methods

3.1. Study context and experimental design

Surveys were conducted along the coast of Gran Canaria Island (Canary Islands, eastern Atlantic Ocean, Figure 2.1a, b), at 12 shallow reefs sites (up to 15 m) (Figure 2.1c), during October-November 2023. Subtidal reef ecosystems 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-water filaments from the northwest African coast and mesoscale island processes that generate upwelling (Valdés & 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 pocket beaches, while the eastern and south sides feature coastal platforms and 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 & Haroun, 2006). During the last four decades, intense urban development in the coastal area (mostly on Las Palmas de Gran Canaria and Maspalomas), coupled with climate-related pressures (i.e., long-term warming and marine heatwaves), have reshaped the configuration of shallow reefs, with drastic declines in the extent of complex marine forests of the genus *Cystoseira* (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.

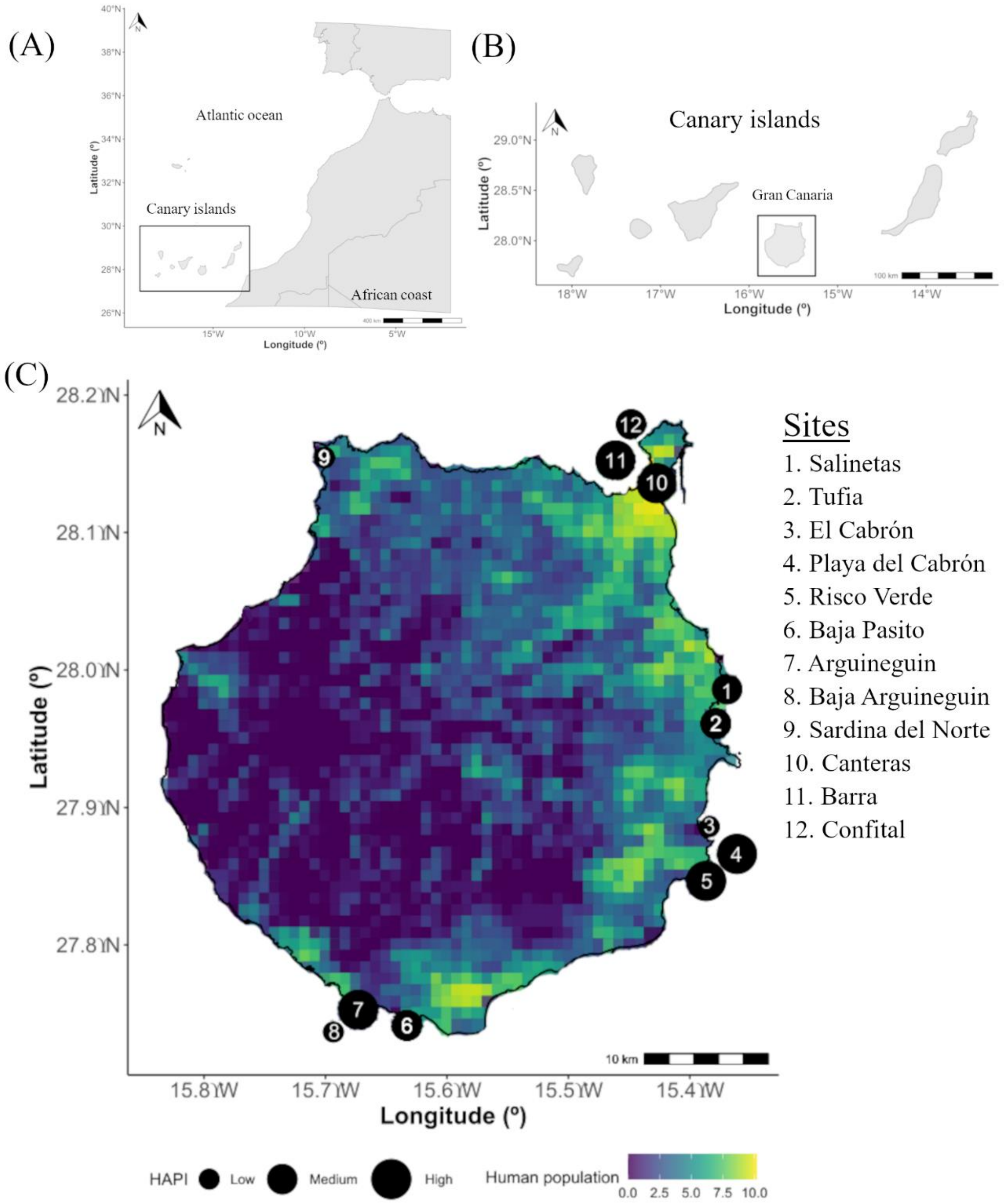

Figure 2.1. Map of the study context showing (A) the geographical location of the Canary Islands within the northeast Atlantic Ocean, (B) the geographical location of the island of Gran Canaria within the Canary Islands, and (C) the twelve shallow reef sites sampled within Gran Canaria Island. Raster 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 survey site, with higher circles indicating high human pressures and smaller circles indicating low human pressures.

3.2. Historical comparison

To examine shifts in benthic habitat configuration in the last two decades, we conducted quadrat surveys at three sites with historical data (Tuya & Haroun, 2006). 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 sites between 10 and 100 m apart within each location (Las Canteras, El Cabron and Sardina del Norte). At each site, a SCUBA-diver haphazardly laid out four quadrats in the substrate (n=4 x 2 sites) corresponding to ca. 50 × 50 cm squares (0.25 m^2). 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, (25 m transects length x 5 m wide) corresponding to 125 m^2 area, were deployed in each site. Briefly, the diver took images of the benthos ca. 60 cm away from the substrate, corresponding with ca. 30 x 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 x 5 squares grid corresponding to 16 point-intercepts. The habitat component was identified and then expressed for the quadrat as a percentage. We acknowledge that sampling protocols and quadrat area (0.25 vs. 0.09) were slightly different between periods. To minimise this source of bias, including island 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): articulated (i.e., jointed or segmented, calcified algae; e.g. *Amphiroa*, *Cymopolia barbata, Jania*), CCA (crustose coralline algae), corticated (i.e., low profile, plate-like and lobed forms; e.g. *Padina pavonica*, *Lobophora variegate, 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 habit. e.g. C*ystoseira*, *Sargassum spp*), red filamentous (e.g. *Asparagopsis taxiformis, Cotoniella filamentosa*) and turf algae (i.e., multi-taxon assemblage of short, low-lying dense mats, composed of multispecies aggregations of algae, detritus, and cyanobacteria; Connell et al., 2014; Tebbett and Bellwood, 2019).

3.3. Vegetation structure of turf seascapes and particulate load

3.3.1. Turf sample collection

To quantify algal turfs properties and associated sediments at each site, we haphazardly placed four 5 x 15 cm (225 cm^2) quadrats on reef substratum covered by algal turfs, targeting flat (< 20° from horizontal) surfaces. All the algae and sediment within the quadrat were then collected using an airlift suction sampler with a cloth bag attached at the end (26 cm x 32 cm, 125 um mesh size). 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, within the same depth contour, at least 5 m apart to minimise the non-independence between samples.

3.3.2. Turf sample processing

After collection, samples were kept in cool damp calico bags, stored in a cooler, and then transported to the laboratory within 6 hours, where they were frozen (-18º C). Upon defrosting, samples underwent a thorough washing with fresh water through a sieve column (2000, 1000, 500, 250 and 125 µm) to separate the algal components and the sediment fraction. The sediment fraction consists of inorganic and organic material <2 mm, commonly called particulates. The algae were (mostly) collected on the coarse sieve and subsequently separated into the following morphofunctional groups: filamentous, foliose and corticated. Rocks, pebbles, free-living calcareous red algae (i.e., rhodoliths) and debris were discarded. We additionally quantified the length of each algal morphofunctional group by taking measurements of the thallus of 2-5 randomly chosen individuals. Algal samples were oven-dried at 60°C for 48 h, for each morphofunctional group separately, to obtain the dry weight (g) (Figure 2.2).

To acquire the size-particle distribution and determine the total benthic particulate load (defined in this context as the 125–2000 µm fraction), the size fractions within each remaining sieve were subsequently re-suspended in individual glass beakers. Any observable algal fragments were eliminated, and the samples were oven-dried at 60°C for 48 hours 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 a minimum of ten days to eliminate any organic matter (Figure 2.2) (following 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 the among (g) and proportion of organic *vs.* inorganic material in particulate loads. All measurements were standardized to m^2 for comparability with other studies.

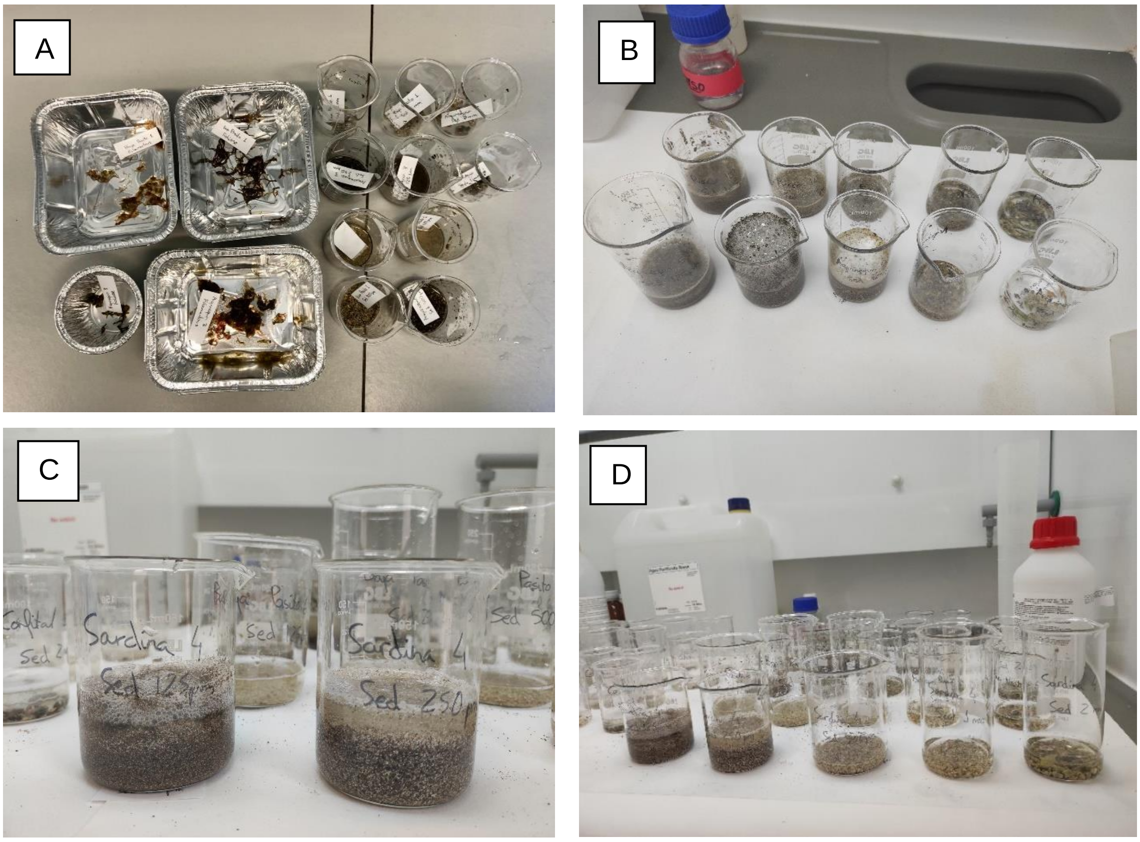

Figure 2.2. Algal and sediment samples were divided into morpho-functional groups and sediment particle sizes (A). Sediment samples were divided into glass beakers following different particle sizes with 30% hydrogen peroxide solution (H_20_2) (B, C, D).

3.4. Geomorphological, anthropogenic and habitat predictors

We sourced several geomorphological, anthropogenic, and habitat predictors expected to influence turf sediment loads and their properties. Geomorphological predictors included reef slope, northness, eastness and distance to the shore, and were calculated using geographic spatial analysis. The slope (i.e., maximum rate of change in elevation values), northness (i.e., orientation, -1 to +1, from south to north, respectively) and eastness (i.e., orientation, -1 to +1, from west to east, respectively) were derived from a fine-scale digital model terrain of the study area, at 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 250 m radius, corresponding to a conservative distance where the reef slope typically transitions to soft bottoms across the island. Distance to the coastline was obtained using functions available in the QGIS software (QGIS Development Team, 2024) We used the Human Activities and Pressure Index (HAPI, Blanfuné et al., 2017), previously developed for the island at 5 km grid cells (Valdazo et al., 2024), to characterize the magnitude of human perturbations. 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. Finally, habitat predictors included the mean height of turf algae and 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) (Figure S5). 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.

3.5. Data analyses

We tested for differences in benthic assemblage structure between the years 2005 and 2023, within each location independently, by using a Permutational Multivariate Analysis of Variance (PERMANOVA). PERMANOVA is a widely used approach when working with multivariate community data, as its permutation test for estimating p-values makes it robust to violation of normality assumptions (Anderson, 2001). To validate the results of the PERMANOVA, which are still sensible to violations of homogeneity of variances among groups, we used the Betadisper function, applying a more conservative p-value threshold of <0.01 to minimize the risk of Type I error. Analyses were carried out in the R statistical software (R Core Team, 2023), using the package “vegan” (Oksanen et al., 2022) and “tidyr” (Wickham et al., 2024).

To evaluate how turf sediment loads, composition, and organic load varied in response to geomorphological (i.e., slope, eastness, northness, distance to the coastline, rugosity), anthropogenic (i.e., HAPI, population (5 km), distance to the port, distance to aquaculture and sewage distance) and habitat (i.e., algal mean height and habitat PCoA axes) 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 biomass) of sediment component structure within each turf sample collected, via the pco function in the "labdsv" R package (Roberts, 2023) (Fig S6). 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 66.73% and 14.38% of the variance, respectively. Continuous predictors were standardized (mean 0 and SD 1) before analysis to account for differences in scaling. To avoid multicollinearity issues, we excluded predictor variables with correlations > 0.5, which resulted in the selection of 7 final predictors: eastness, northness, distance to the coastline, HAPI, mean height, habitat PCoA1 and habitat PCoA2. We implemented Generalized linear mixed models (GLMMs) with a 'Gamma' error distribution and a log link function using the "glmmTMB" R package (MollieE et al., 2017). All models incorporated sampling location (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 substantial support (Burnham & Anderson, 2003). When competing models were present, we selected the model with the highest Akaike weights (ωAIC). Finally, model fit, and assumptions were evaluated using residual plots in the "DHARMa" R package (Hartig, 2022). All analyses were performed using the statistical software R (R Core Team, 2023).

4. Results

4.1. Historical comparison

Our analyses revealed substantial changes in vegetation structure following the loss of canopy-forming species and the emergence of turf algae (Figure 2.3). There was a significant change in benthic structure between years ($R^2 = 0.445$, $F = 141.74$, p-value

= 0.001) with significant site-to-site variations ($R^2 = 0.021$, $F = 3.33$, p-value = 0.010); which are related to their degree of exposure to hydrodynamic and anthropogenic factors. Regarding site-to-site variations, we found that in 2005 the coverage of leathery algae (*Cystoseira*) in the exposed shore of El Cabron was 21% and is now extinct, whilst the highest levels of turf coverage were found in Las Canteras (25.5 %), a sheltered embayment within the island's capital. Despite the overall heterogeneity in benthic habitat change among sites, turf algae consistently increased by an average of 65.8 ±1.30 %, transitioning from 25.5% to 83.33% (increase 57.8%) in Las Canteras, from 5.5% to 71.19% (increase 65.7%) in El Cabron and from 7.5% to 81.27% in Sardina del Norte (increase 73.8%).

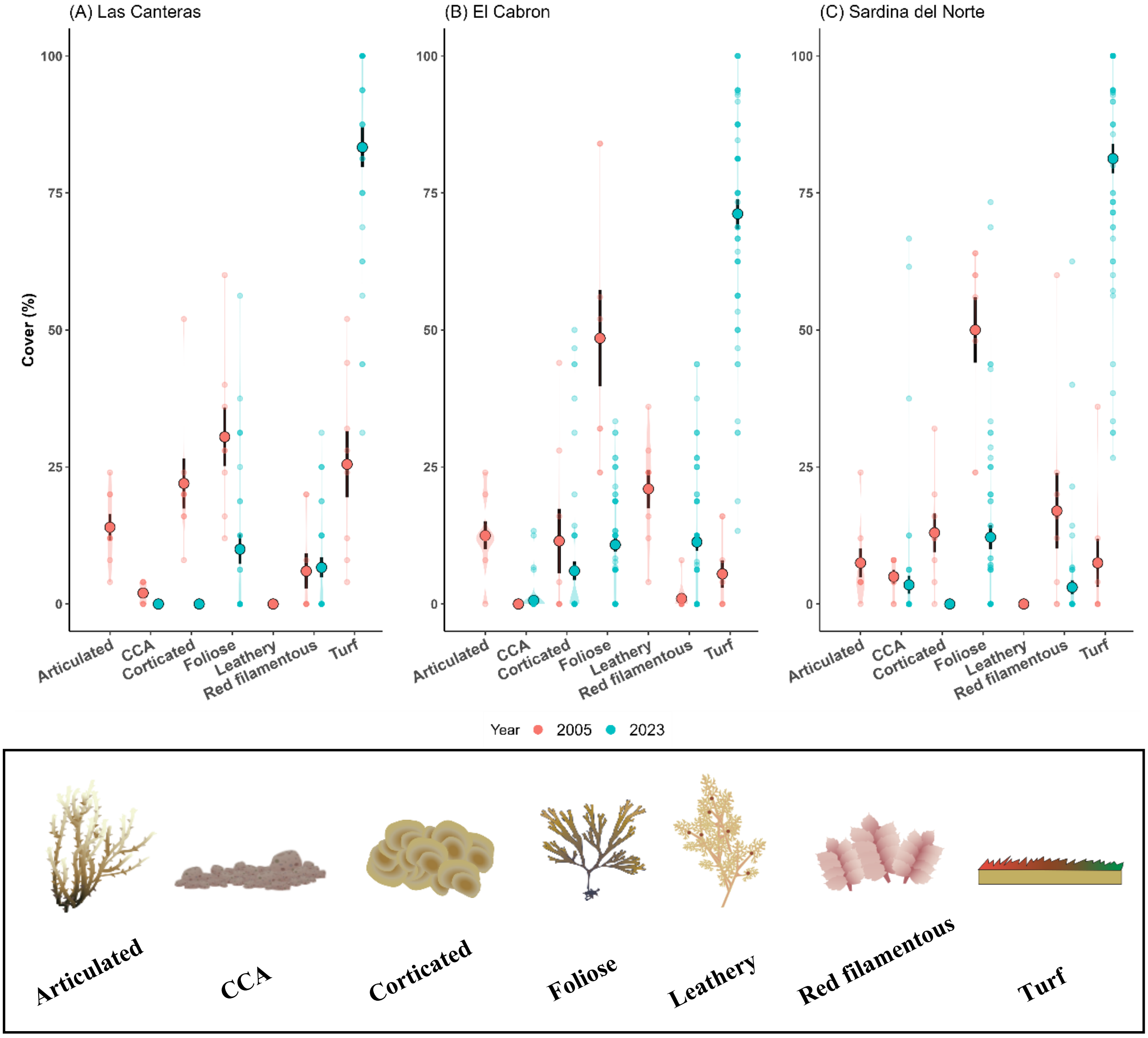

Figure 2.3. Historical comparison of the benthic composition in (A) Las Canteras, (B) El Cabron and (C) Sardina del Norte between 2005 and 2023. Larger dots are model-averaged predictions from GLMMs, and whiskers are SE around the predicted mean. Violin plots and smaller dots are included within each 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/).

4.2. Vegetation structure of turf seascapes and particulate load

The properties of turf seascapes were heterogeneous across sampling sites (Figure 4.2). The vegetation mean height varied from 0.2 to 8.5 cm, with an average of 2.10 ± 1.66 cm (Figure 2.4.a). Turf algal biomass varied from 0.004 to 152 g dry weight (DW) m^{-2}, with an average of 18.29 ± 29.40 g DW/m^2 (Figure 2.4.b). The particulate load ranged from 0.86-1897 g DW/m^2 (0.00086 - 1.9 kg), with an average particulate load of 215.22 ± 317.97 g DW/m^2 (Figure 2.4.c). The total organic loads ranged from 0.42 to 120.68 g DW/m^2, averaging 4.94 ± 11.59 g DW/m^2 (Figure 2.4.d). According to these results, organic loads tend to have values with less variation, suggesting a more consistent pattern and indicating that organic loads are relatively stable, whereas the particulate load may display greater fluctuations or variability.

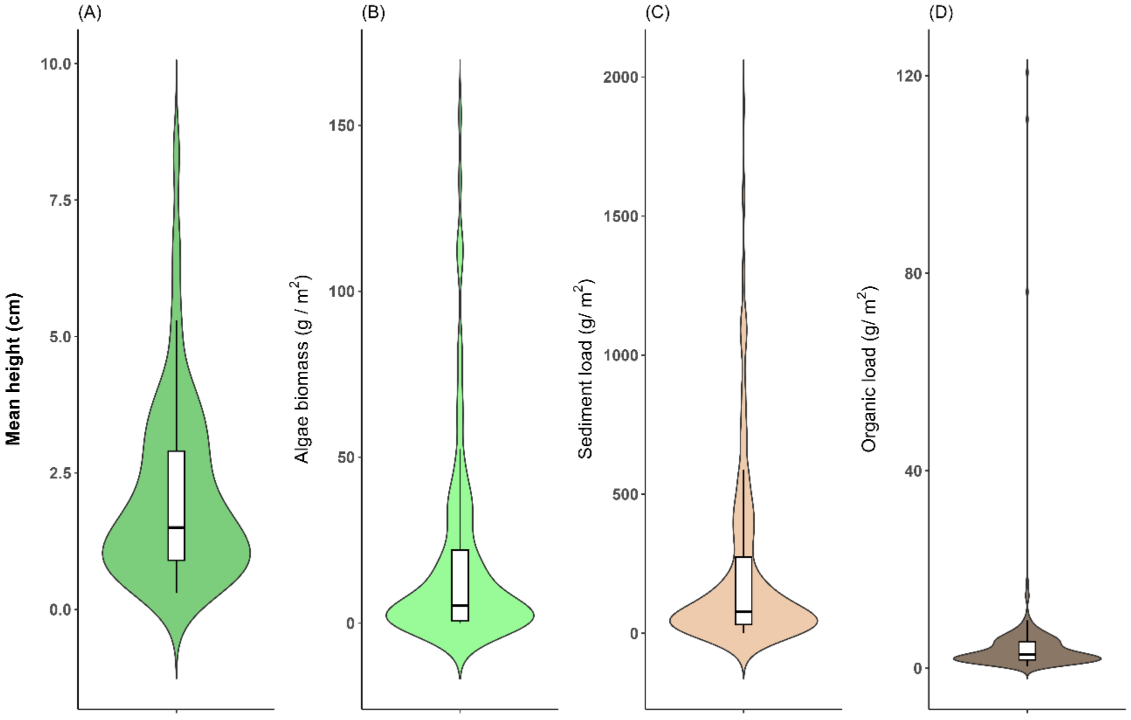

Figure 2.4. General results of (A) algae mean height, (B) algae biomass, (C) particulate load (C), and (D) organic load. Violin plots within each panel represent the distribution of replicate-level values. Boxplots represent the median value by the line inside the box, the quartiles (Q1 to Q3) by the length of the box, and the data spread or variability by the whiskers.

The relative biomass of the three distinct functional groups of algae exhibited significant variation across our sampling sites (Figure 2.5.a). Although the proportion of filamentous algae varied between sites, it is important to note that all sites had the presence of filamentous algae. Indeed, filamentous algae were the predominant group in Baja Arguineguin, la Barra, Risco Verde and Tufia. Foliose algae were the second group dominating, with a substantial effect, although they did not dominate all sites (i.e., Baja Pasito, Confital, Salinetas). Finally, corticated algae were only present in 3 sites (i.e., Arguineguin, Las Canteras and Playa del Cabron). Additionally, the relative biomass of different sediment grain sizes is highly heterogeneous among the twelve sites (Figure 2.5.b).

It is important to note that in la Barra and Las Canteras, the predominant group of grain size was thinner sediment (<250 µm), with a sparse presence of coarser sediments (>250 µm). On the other side, in Baja Pasito, Confital and Salinetas the predominant group of grain size was the coarser sediments (2 mm and 1 mm), with a sparse presence of thinner sediments (125 and 250 um). Conversely, the inorganic-to-organic matter ratio was remarkably consistent across sites (Figure 2.5.c), despite their inherently different turf seascape properties. Even though it was relatively constant, la Barra was the site with the highest organic load, whilst Risco Verde had the lowest organic load value.

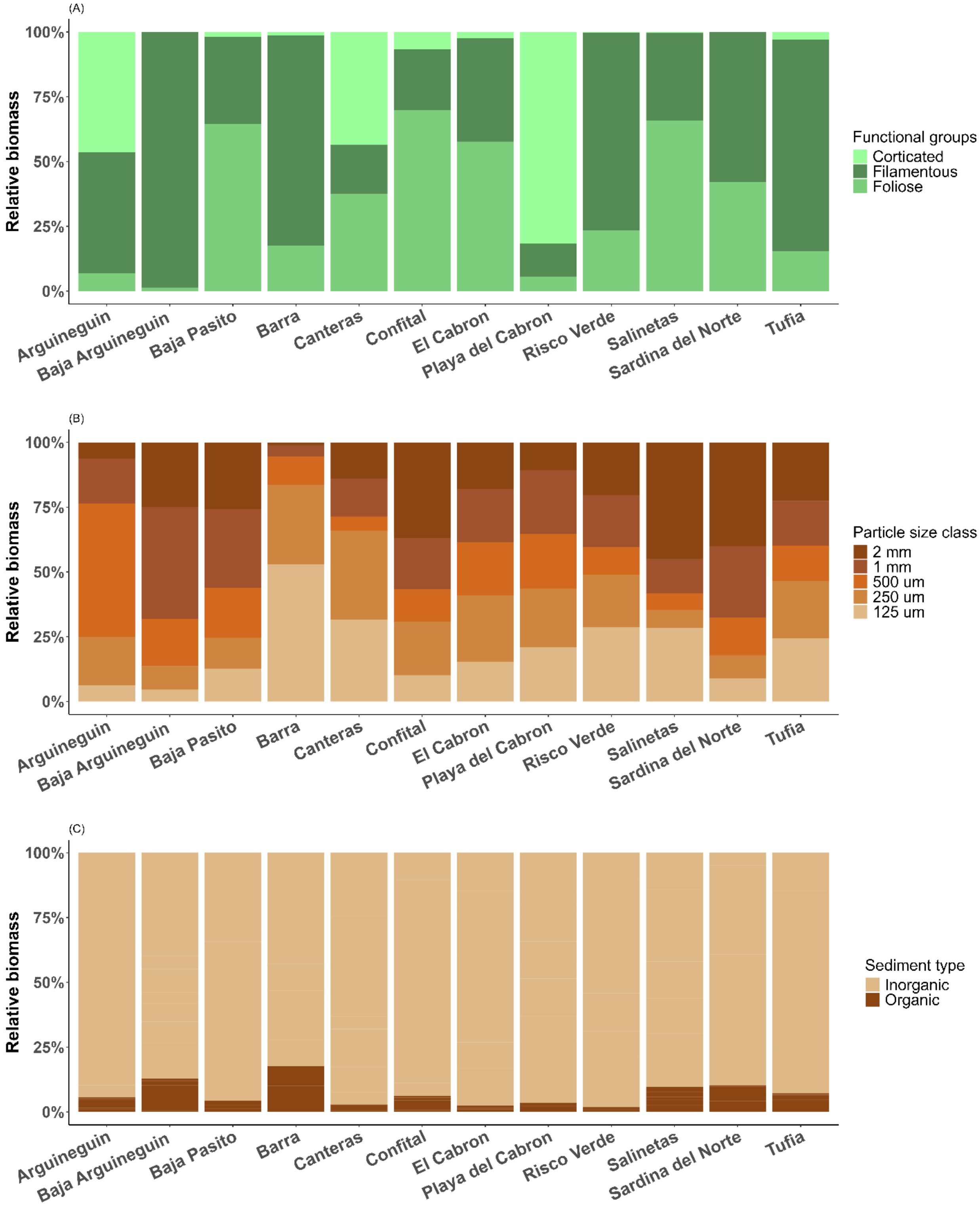

Figure 2.5. (A) Relative biomass (percentage of total dry weight) of different algal groups (i.e., corticated, filamentous and foliose) at each site. (B) Relative biomass (percentage of total dry weight) of the different particle grain sizes (i.e., sediment of 2 mm, 1 mm, 500 um, 250 um and 125 um) at each site. (C) Relative biomass (percentage of total dry weight) of the inorganic and organic fraction at each site.

4.3. Drivers of turf algae particulate loads

The model with the best fit for predicting the quantity of sediment load contained the effects of the HAPI index and the composition of habitat morphofunctional groups (habitat PCoA1 and habitat PCoA2) (ωAIC = 0.579, $R^2 = 0.552$) (Table 2.1). There was an additional model with substantial support (i.e., within 2 AICc units), containing the effects of habitat and HAPI with an additional contribution of distance to the coastline (ωAIC = 0.421, $R^2 = 0.565$). The most parsimonious model explaining variation in fine sediment (125 um) (Sediment PCoA2) contained the effect of the mean height of turf algae. This model had high support (ωAIC = 0.426, $R^2 = 0.100$), compared to other more complex models that had substantially lower *w*AICc values. Finally, the model with the best fit for predicting the quantity of organic load included the effect of eastness and the morpho-functional group of turf algae present. It is worth noting that although with variable support, the HAPI index was consistently chosen within the set of supported models, indicating a strong role of human activities on the island in shaping the nature and structure of turf seascape.

Table 2.1. Best (most parsimonious within two units of the lowest AICc) generalized linear mixed models (GLMM) predicting variation in sediment load (SL), sediment PCOA2 (SP2) and organic load (OL) of turf samples. The degrees of freedom (df), delta, Akaike weights (ωAICc) and goodness-of-fit (R^2) are provided for model comparisons.

Response	**Best models**	**df**	**delta**	***w* AICc**	**R^2**
SL	Habitat PCoA1 + Habitat PCoA2 + HAPI + (1 | Site)	6	0	0.579	0.552
	dist shore + Habitat PCoA2 + HAPI + (1 | Site)	6	0.641	0.421	0.565
SP2	Mean height + (1 | Site)	4	0	0.426	0.100
	HAPI + Mean height + (1 | Site)	5	1.415	0.21	0.122
	eastness + Mean height + (1 | Site)	5	1.617	0.19	0.118
	eastness + (1 | Site)	4	1.796	0.174	0.042
OL	eastness + Habitat PCoA1 + Habitat PCoA2 + (1 | Site)	6	0	0.379	0.358
	eastness + Habitat PCoA1 + (1 | Site)	5	1.579	0.172	0.317
	eastness + Habitat PCoA1 + northness + (1 | Site)	6	1.667	0.165	0.289
	Habitat PCoA1 + Habitat PCoA2 + northness + (1 | Site)	6	1.926	0.145	0.306
	Habitat PCoA1 + Habitat PCoA2 + (1 | Site)	5	1.993	0.14	0.375

Model-averaged coefficients showed a significant positive effect of the HAPI index on sediment load (Figure 2.6.a), which increased exponentially from nearly 395 g m^{-2} to 1745 g m^{-2} from low to high human pressure (Figure 2.7). We also found a significant negative effect of habitat composition on sediment load, overall, suggesting a transition from sediment-laden turf mats, when these were dominated by filamentous algae, to low sediment load, when these were dominated by foliose algae (Figure S5). Another indication of human pressures on sediment load is the significant effect of distance to the coastline, although there was high heterogeneity which resulted in confidence intervals overlapping zero (i.e., non-significance), with higher sediment accumulation closer to the shore. Similarly, there was also a positive relationship between the mean height of turf algae and sediment load, with longer heights of algae trapping more sediment, although this pattern was not discerned from a null expectation.

The sediment size-frequency distribution was highly heterogeneous across our study sites and was not significantly predicted by any of the variables considered. Still, we found some nuanced patterns with high ecological implications, such as the negative relationship with mean algal height, indicating that shorter algal turfs tend to trap the finer sediment particles. (Figure 2.6.b).

Finally, for the organic load, even though being homogeneous across our sampling sites, there was a significant negative trend of the morpho-functional group of turf algae (Figure 2.6.c), indicating that filamentous algae tend to trap more organic matter than more complex algae structures.

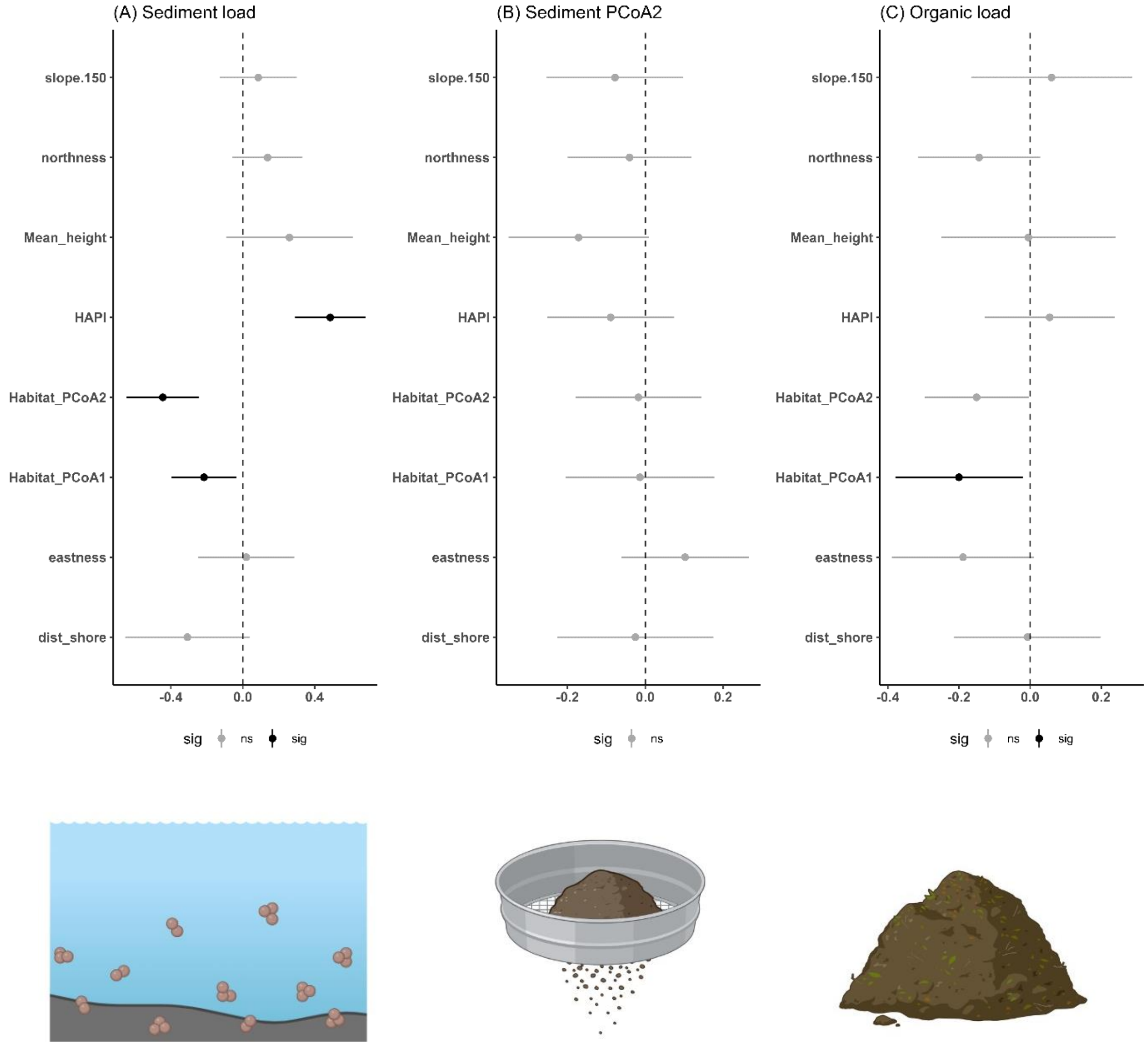

Figure 2.6. Model-averaged coefficients (SE) from generalized linear mixed models testing the effect for each predictor variable explaining variation on (a) sediment load, (b) sediment PCoA2, and (c) organic load of turf samples of the most parsimonious model. Dots represent means of coefficients while bars represent ± 95% confidence intervals. Image credit: Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces. edu/imagelibrary/).

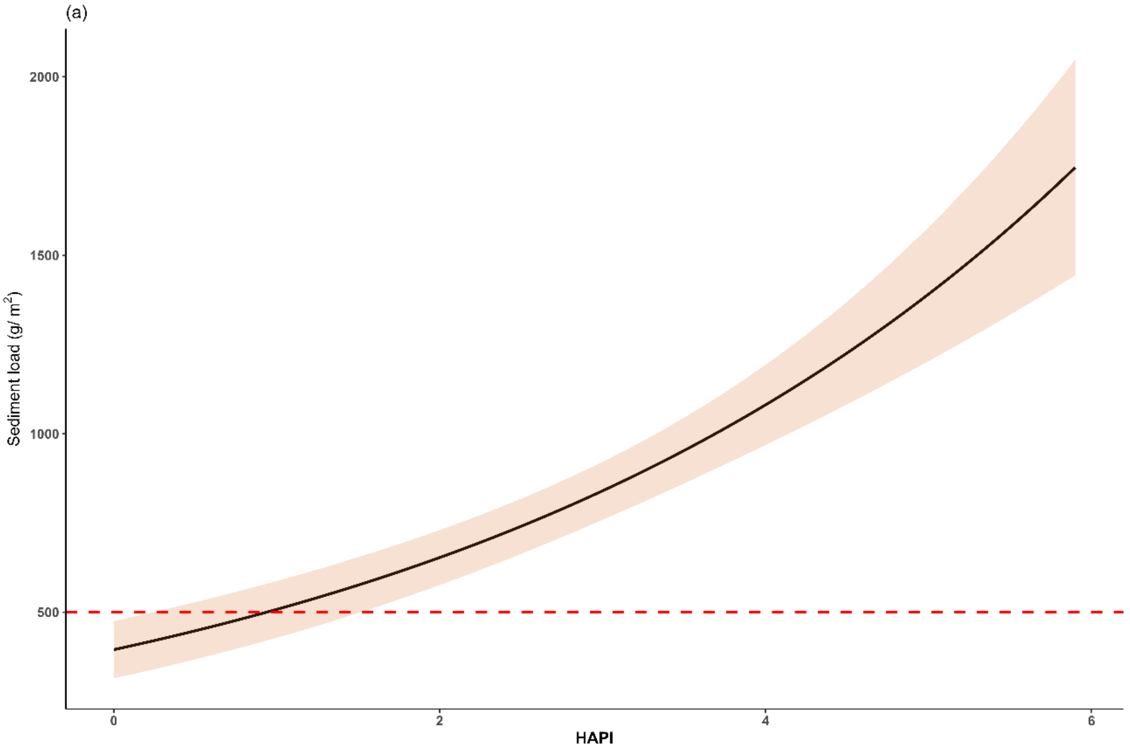

Figure 2.7. Predicted relationship between HAPI index and sediment load. Solid lines are predicted values from the most parsimonious generalized linear mixed models (GLMMs), and brown-shaded areas denote the 95% confidence interval. The dashed red line indicates the sediment load threshold beyond which a significant decline in fish abundance or feeding activity has been reported for tropical coral reefs (Tebbett et al., 2020).

5. Discussion

Our study revealed substantial spatial heterogeneity of turf seascape properties at small spatial scales in an oceanic island. This result challenges widespread assumptions that historical transitions from heterogenous up-right seaweed communities in the region, including forest-forming of the genus *Cystoseira* censu latu, result in seemingly homogenous seascapes (Valdazo et al., 2017). Although comparatively homogenous at the macro-scale, fine-scale investigation of turf seascapes has revealed substantial heterogeneity in their properties that can alter both their nutritional quality to consumers (Tebbett et al., 2018a, 2020; Goatley & Bellwood, 2012; Bellwood & Fulton, 2008) and their role as habitat for associated epifauna (Fraser et al., 2020a, b, 2021). We further show that variation in these attributes, particularly total sediment load, was best predicted by local human pressures and algal composition, highlighting the coupled role of indirect effects of climate and the direct impact of anthropogenic pressures in determining the structure and functioning of future turf seascape in the region.

The historical comparative analysis revealed significant shifts in benthic habitat structure over the past two decades, with turf algae proliferating consistently across all sites, coinciding with a decline in the cover of upright foliose seaweeds and forest-forming leathery species (*Cystoseira* 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. The highest levels of turf algae over time, for instance, were 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 benthic structures, with turf algae tending to dominate protected shores (Tuya & Haroun, 2006). Therefore, the increase in 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 changes over time. This indicates that, despite the stronger hydrodynamic forces, turf has still managed to dominate. Previous research has consistently shown that hydrodynamic forces play a critical role in determining particulate deposition and retention (Bodde et al., 2014; Purcell, 2000; Tebbett et al., 2017). However, contrary to these findings, we did not observe a significant effect of hydrodynamics on sediment load. This suggests that other geomorphological factors, such as topographic complexity, may have a stronger influence on sediment distribution. 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). These findings highlight the complexity of sedimentation processes and the need to consider multiple environmental variables when assessing their impacts on coastal ecosystems.

The particulate loads associated with turf algae exhibited significant variability across sites, ranging from 10s of g m^{-2} to 1000s of g m^{-2}. This range aligns with observations from other studies on the Great Barrier Reef, which have reported similar variability depending on the reef's location (Tebbett & Bellwood, 2019). However, other studies reported even higher ranges, from <10 g m^{-2} to >10000 g m^{-2} (Tebbett et al., 2022). Beyond particulate quantity, we also analysed grain size distribution, which displayed marked differences across habitats, with a subtle trend indicating that shorter algal turfs were more likely to capture finer sediment particles. Nevertheless, 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; Purcell & Bellwood, 2001; Tebbett et al., 2017). Notably, the proportion of organic load remained relatively constant across sites, in contrast to previous findings that reported a decrease in the proportion of detritus in total particulates as sediment loads increased (Tebbett et al., 2020). The uniformity in our results might be attributable to a lack of data on finer sediment fractions (<63 µm), potentially leading to an underestimation of organic load. 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 µm) are less nutritious due to the higher energetic costs associated with processing them (Gordon et al., 2016; Gordon et al., 2015).

The significant effect in the model of the HAPI index and habitat composition suggests that both human pressures and the composition of turf algal mats will strongly determine particulate loads. The HAPI index was consistently chosen within the set of supported models, indicating a strong role of human activities on the island in shaping the nature and structure of the turf seascape and consequently, particulate accumulation. The highest levels of these particulates were found in the island's most densely populated area, Las Palmas de Gran Canaria, particularly in samples from Las Canteras and La Barra. 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). Furthermore, our model demonstrates a negative relationship between distance from the coast and particulate load, with particulate levels generally decreasing as the distance from the shore increases (Tebbett & Bellwood, 2019). This pattern highlights the significant stress that increased sediment inputs impose on inshore reefs, particularly those closer to the coast (Latrille, 2019; Fabricius, 2005). These elevated sediment loads are often linked to agricultural runoff, coastal development, and nearshore dredging activities, further exacerbating the stress on these ecosystems (Brodie & Pearson, 2016; Fisher et al., 2017; Tebbett et al., 2018b). We must note, however, that in our study distance to the coast and depth (elevation) were strongly correlated. Elevated coastal surfaces face stronger currents and waves, causing sediments to be dislodged and accumulate in sheltered, lower areas farther from the coast (Tebbett et al., 2019). This interaction between hydrodynamics and anthropogenic pressures can complicate our understanding of sediment patterns in reef ecosystems. To better understand these patterns, further research is needed to disentangle the combined effects of these factors.

Our findings corroborate the strong positive relationship between algal turf length and particulate load, which may result from two possible mechanisms: (i) longer algal turfs develop first, thereby trapping more sediment, or (ii) the initial accumulation of sediments in 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 & Bellwood, 2013; Goatley et al., 2016). Additionally, high sediment loads can indirectly suppress herbivory by lowering the nutritional quality of the turf. This decline in quality may be due to reduced turf productivity (Tebbett et al., 2018) or to the dilution of detritus concentration within the particulate mixture (Purcell & Bellwood, 2001), potentially leading to significant bottom-up ecological effects. Indeed, it is anticipated 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). In the species-poor oceanic islands of the eastern Atlantic Ocean, including the isolated island studied here, deciphering both the bottom-up effects of turf on herbivores and the top-down effect of herbivores on turf is a key area for future research, as two key herbivorous species (*Sparisoma cretense* and *Sarpa salpa),* that are highly targeted by small-scale commercial fisheries are solely responsible for the grazing and scraping function (Castro et al., 2019).

The predicted relationship between the HAPI index and particulate loads suggests that only sites with minimal human pressure, below an ecological threshold, could maintain proper ecological functions. This result corresponds with Tebbett et al. (2020)

findings, who showed that sediment loads above approximately 250–500 g m^{-2} significantly reduced fish abundance and feeding activity in herbivorous fishes. Indeed, several studies revealed that the increased sediment loads on turf algae reduce the grazing efficiency of herbivores, potentially destabilizing the ecosystem functions that support local fisheries (Goatley & Bellwood, 2013; Tebbett & Bellwood, 2019). However, different herbivorous fish species show varying sensitivities to algal turf sediments. For instance, ‘croppers’ such as surgeonfishes are more resilient to sediment increases since they can crop the tips of algal turfs, while scraping parrotfishes are more deterred by coarser sediments, likely due to their beak-like teeth (Tebbett & 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.

We also identified a significant relationship between algal turf composition and particulate load, with higher particulate loads being 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 & 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 & Bellwood, 2010; Pessarrodona et al., 2023). Additionally, the vertical growth habit of filamentous algae allows them to access light and thrive despite high particulate loads, whereas other morpho-functional groups, such as foliose, corticated, and articulated algae, which rely on horizontal growth, may be less resilient under such conditions (Arjunwadkar et al., 2022).

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 µm). Consequently, finer sediment fractions (<63 µm), 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, as noted by Tebbett et al. (2022), potentially leading to a biased understanding of sediment dynamics in these ecosystems. However, since all samples were collected under the same conditions, valid comparisons between them remain possible. To address this, future studies in this region should incorporate sampling methods that can capture finer sediment fractions, with smaller mesh sizes or alternative collection techniques. Such methods would provide a more comprehensive assessment of sediment composition and enhance our understanding of sediment dynamics, particularly concerning their broader ecological impacts, including food web interactions and reef resilience. A further limitation is that we only considered turf properties at a single time point in time, and therefore ignored environmental and biological processes that occurred across 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 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 marginal, oceanic, warm-temperate reefs. The heterogenous spatial patterns in sediments properties reported here, even at small intra-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 address both global climate change and local human impacts to mitigate the potential negative ecological impacts of sediment accumulation in turf seascapes in reef-scale ecological processes. This is particularly critical for marginal and isolated oceanic islands, where the ecological consequences of turf expansion and sediment accumulation could be particularly severe, leading to long-term damage that may be difficult to reverse. As our findings indicate, the ongoing transformation of these ecosystems demands a comprehensive approach to conservation that considers the complex interactions between herbivory, sediments, algal turfs and reef structures linked to climate-driven changes and human activities, to safeguard the health and functionality of these vulnerable reef systems.

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Appendixes

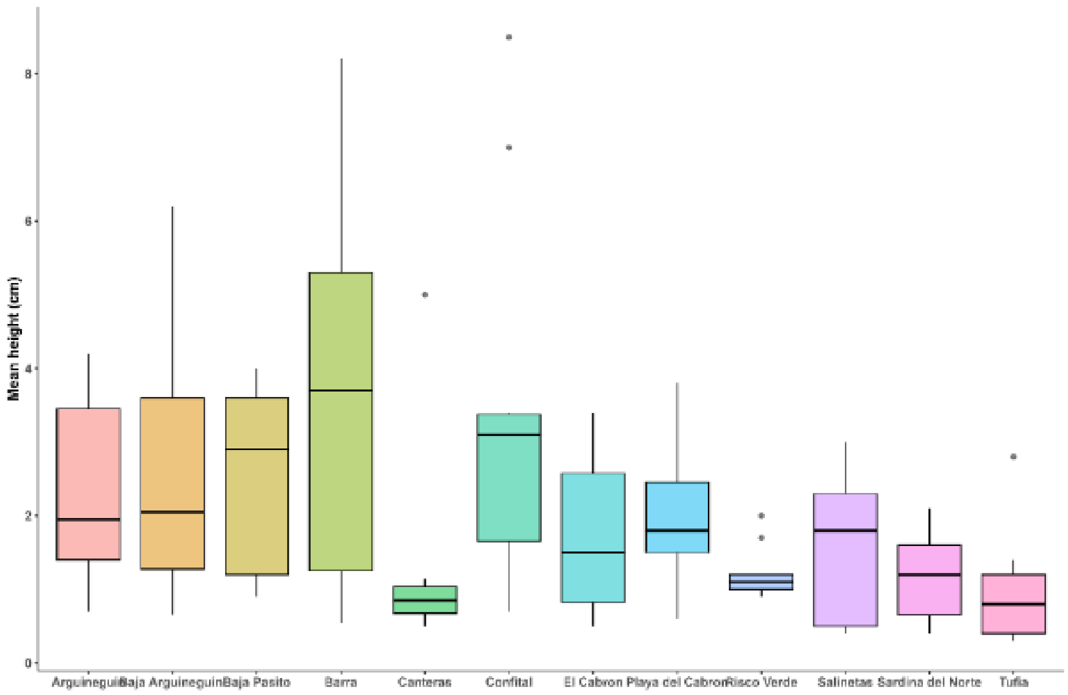

Figure S1. Exploratory boxplot of the mean height of turf algae (cm) per site.

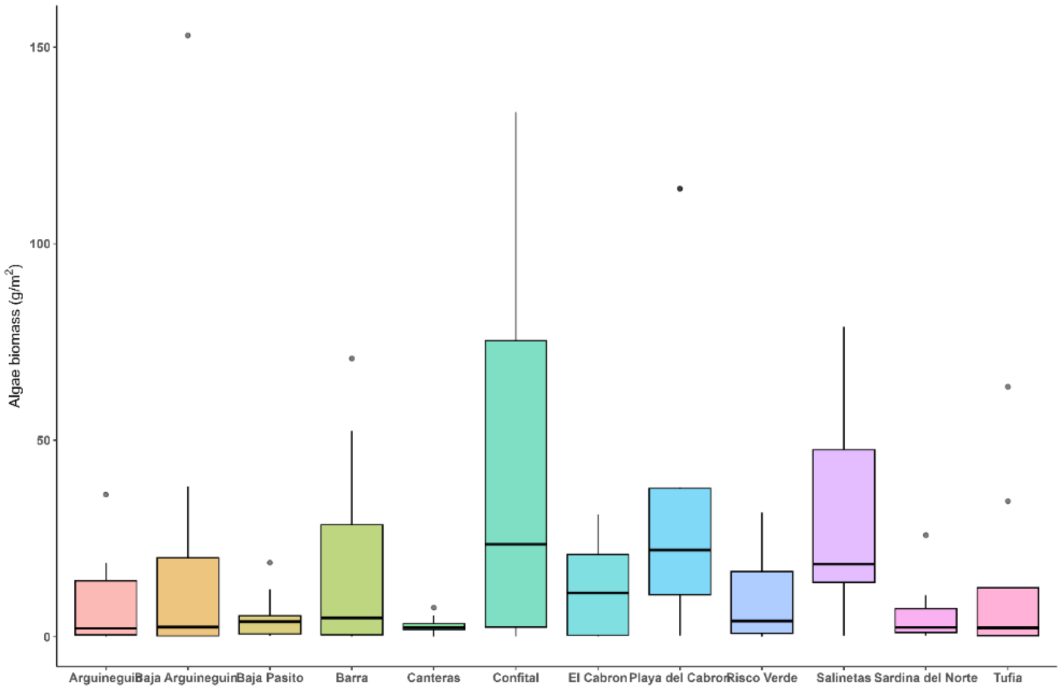

Figure S2. Exploratory boxplot of turf algae biomass (cm) per site.

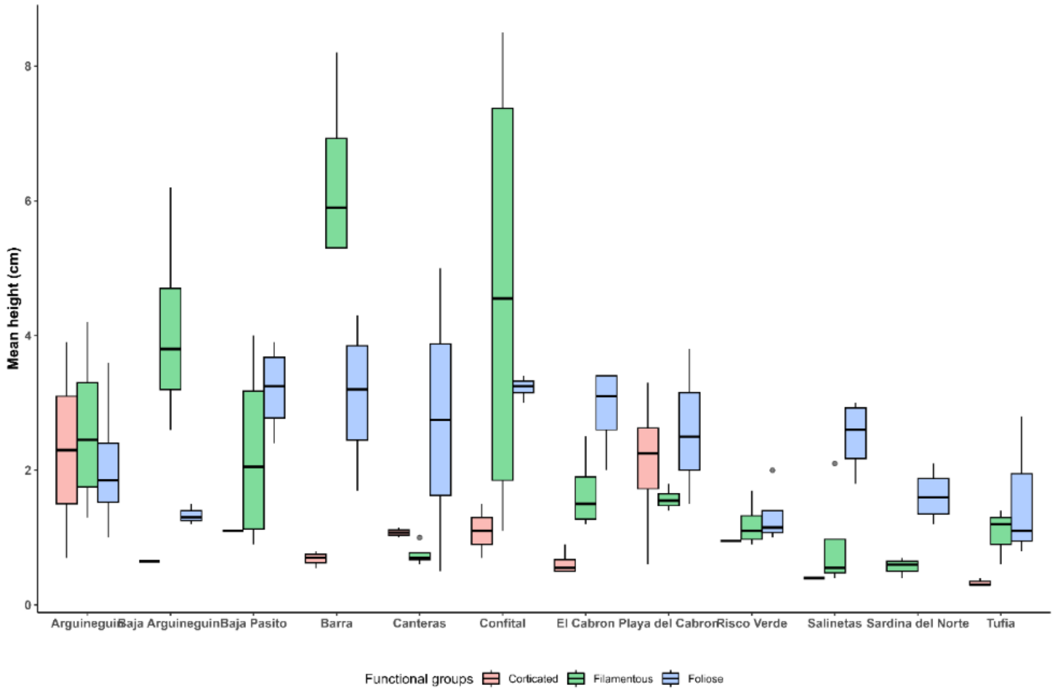

Figure S3. Exploratory boxplot of turf algae mean height according to the different functional groups per site.

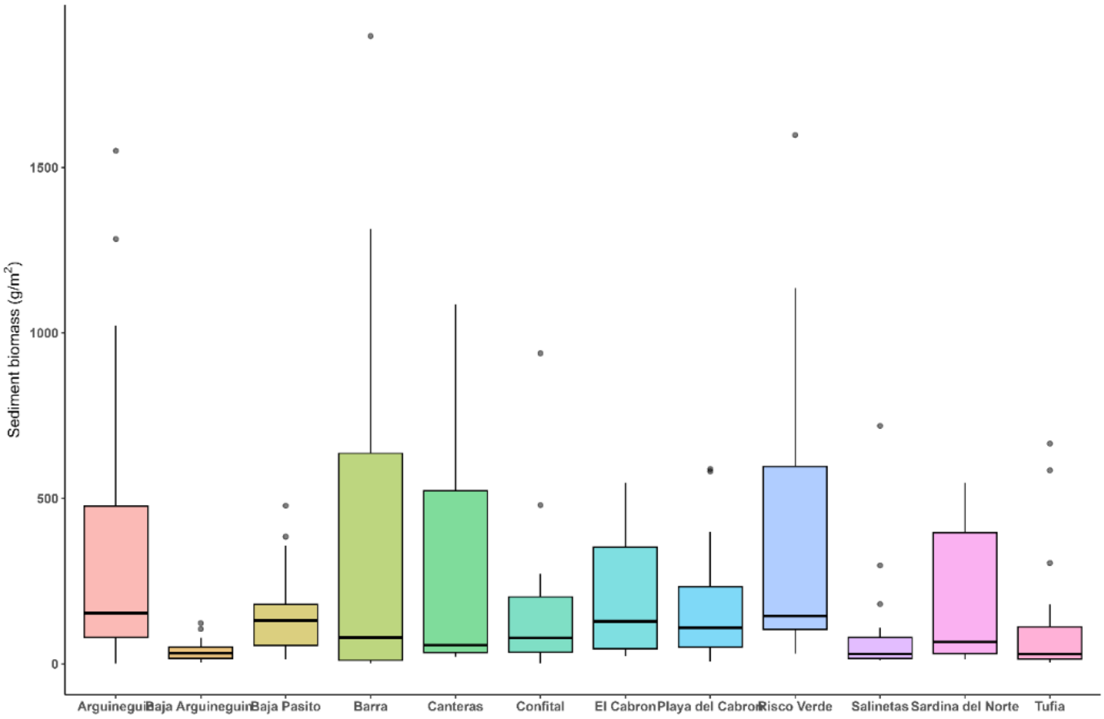

Figure S4. Exploratory boxplot of sediment biomass per site

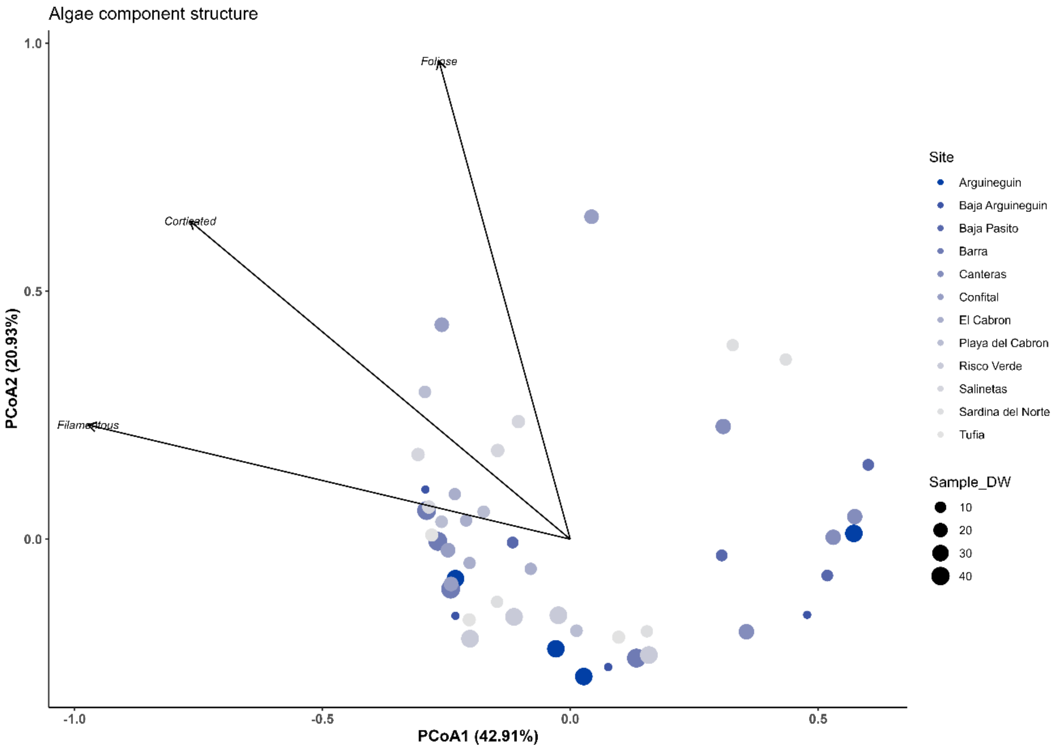

Figure S5. Principal coordinate analysis (PCoA) based on the Bray-Curtis dissimilarities across turf samples depicting variation in turf habitat structure. Different colours represent the sample sites, the size of the circles represents the sample algae dry weight, while biplot vectors show the morphological algal groups.

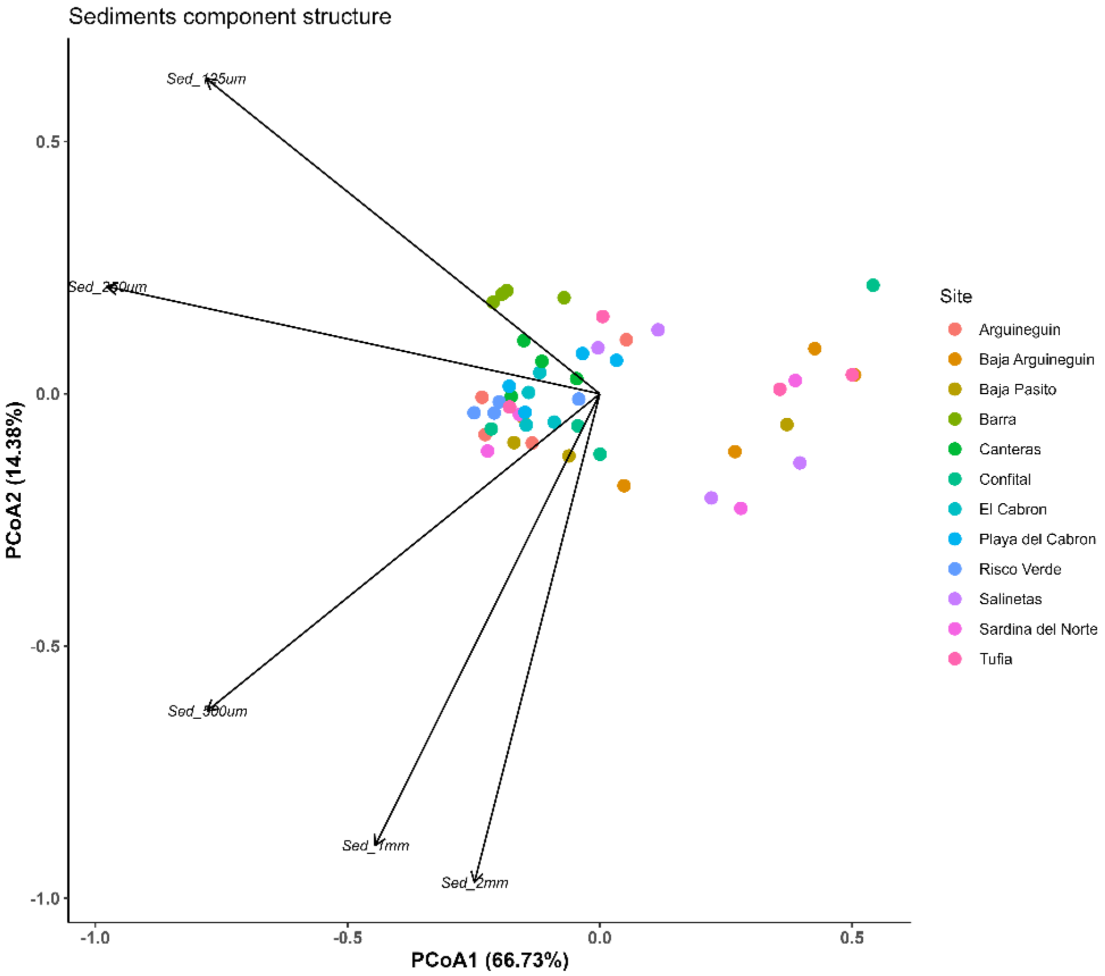

Figure S6. Principal coordinate analysis (PCoA) based on the Bray-Curtis dissimilarities across turf samples depicting variation in sediment components. Different colours represent the sample sites, while biplot vectors show the particle distribution.

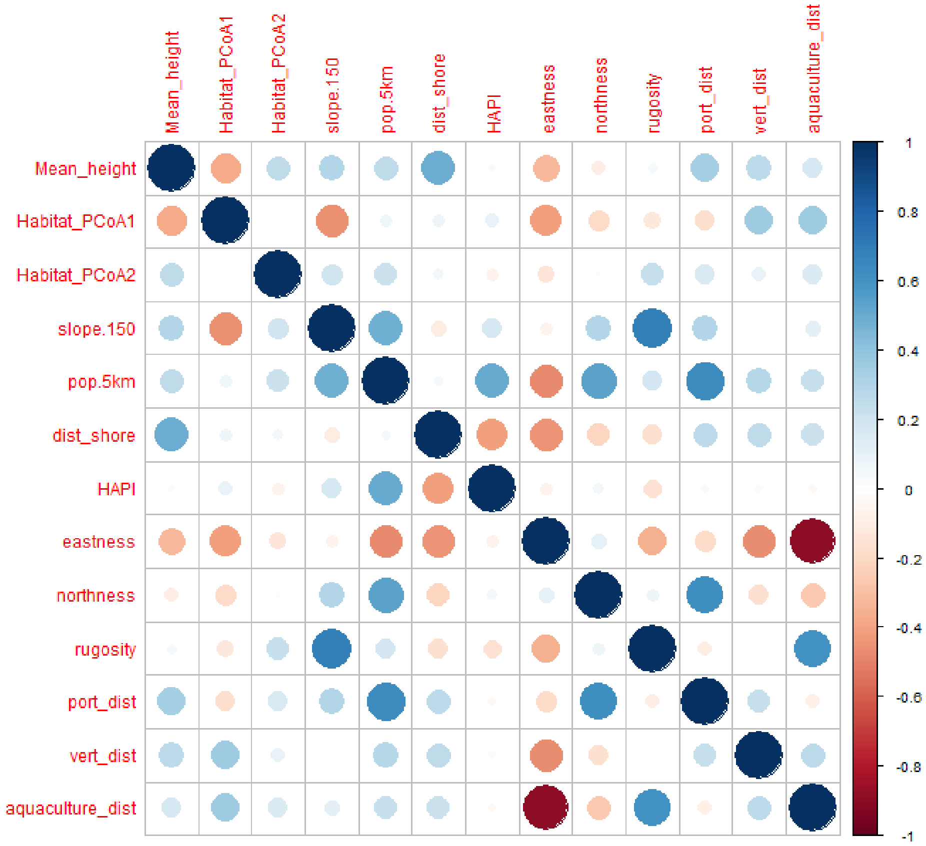

Figure S7. Correlation matrix of environmental. The size of the circles indicates the Pearson correlation coefficients between the pairs of variables. The color of the variable differs between 1 and -1 indicating a strong correlation close to 1, while numbers close to 0 show a weak correlation.