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Composition, structure and diversity of fish assemblages across seascape types at Príncipe, an understudied tropical island in the Gulf of Guinea (eastern Atlantic Ocean)

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Coastal seascapes are often composed of a mosaic of interconnected habitats. Transitions between adjacent habitats are of special relevance to the ecology of many reef-associated organisms. In this study, we tested (i) whether the degree of similarity in the composition and structure of coastal fish assemblages differed between three interconnected seascape types, and (ii) whether differences in taxonomic and phylogenetic diversity of the fish assemblages were consistent between the seascape types. We sampled fish species from diverse habitats in the shallow coastal waters surrounding the island of Príncipe (Gulf of Guinea, eastern Atlantic Ocean), an understudied and remote tropical island. Specifically, video transects were carried out by SCUBA divers at three seascape types: rocky reefs, rocky reef–rhodolith bed transitions, and rocky reef–sandy bottom transitions, to extract presence/absence and ordinal abundance data, across a range of depths (9–31 m), covering the entire perimeter of the island. A total of 71 fish taxa were recorded. Both the composition and structure of the fish assemblages differed between the studied seascapes. The mean number of fish species (taxonomic diversity) was higher on 'reefs' than in both the 'reef–rhodolith bed' and 'reef–sandy bottom' transitions. In contrast, the taxonomic distinctness index (phylogenetic diversity) was higher for fish assemblages in both transitional seascape types than on rocky reefs. Hence, at the island-scale, the protection of local fish assemblages needs to consider a representative network of interconnected habitats, including at these seascapes boundaries where important ecological functions seem to occur.

Keywords: biodiversity, conservation, ecotones, equatorial West Africa, ichthyofauna, tropical reefs, underwater video, Wallacean shortfall

Introduction

Coastal landscapes, or seascapes, typically include a collection of reticulated habitats, such as rocky reefs, coral reefs, seagrass meadows, rhodolith beds and sandy seabeds, which create a complex matrix of habitat patches (Dorenbosch et al. 2005; Tuya et al. 2010; Cresswell et al. 2017). The abundance and composition of nearshore species is markedly influenced by the arrangement of such habitats, including the spatial distribution of fish associated with both hard and soft bottoms (Guidetti 2000; Tuya et al. 2010; Campbell et al. 2011; Espino et al. 2015). Notably, transitions between adjacent habitats—including edges or ecotones—are conspicuous seascape elements of coastal environments which alter the distributions and abundances of associated ichthyofauna (Valentine et al. 2008; Tuya et al. 2010; Espino et al. 2015). For example, several studies have documented differences in fish assemblage structure between reefs and surrounding sandy areas, in both tropical and temperate realms (Guidetti 2000; Mateo and Tobias 2007; Campbell et al. 2011). Typically, higher abundance and species richness (taxonomic diversity) are

found on reefs than on adjacent sandy bottoms (Barros et al. 2001; Mateo and Tobias 2007). However, we have limited knowledge on how other biodiversity facets (e.g. phylogenetic diversity) vary across habitat types (Bosch et al. 2017; Tuya et al. 2018), and to what extent there are spatial congruencies and/or mismatches among biodiversity facets at a range of spatial scales (Tucker et al. 2017; Wong and Kay 2019).

Within coastal seascapes, rhodolith-dominated areas and sandy seabeds are interspersed across temperate and tropical seas, and typically arranged in mosaics with rocky reefs (Otero-Ferrer et al. 2019). Rhodolith beds are underpinned by free-living, non-geniculate, calcareous red algae (Rhodophyta), which form nodules of rugged appearance and diverse morphology (Amado-Filho et al. 2007; Foster et al. 2013). Extensive rhodolith beds are found in many of the world's coastal areas (Amado-Filho et al. 2007; Foster et al. 2013), sustaining diverse invertebrate assemblages through the provisioning of food resources and refuges (Steller et al. 2003; de Figueiredo

et al. 2007; Otero-Ferrer et al. 2019, 2020). Although invertebrate assemblages associated with rhodolith beds have been extensively described (Grall et al. 2006; Amado-Filho et al. 2007; Foster et al. 2013), fish species living in these habitats are mostly unknown from an ecological perspective (Pereira-Filho et al. 2015).

Descriptions of local flora and fauna are key for understudied regions of the world's oceans, especially in species-rich tropical coastal areas (Alexandre et al. 2017; Haroun et al. 2018; Tuya et al. 2018; Vasco-Rodrigues et al. 2018). In this sense, filling knowledge gaps regarding the presence of species and their associated distribution patterns (the so-called Wallacean shortfall) might help to unravel large-scale biodiversity patterns, optimising transnational conservation planning (Whittaker et al. 2005; Bini et al. 2006; Hortal et al. 2015). This is the case regarding tropical western African coasts, including the Gulf of Guinea, which, despite being considered hotspots of marine biodiversity (Roberts et al. 2002), have many scientific gaps. From a biogeographic perspective, this tropical region is particularly relevant because the eastern and western Atlantic marine faunas are connected through the eastward-flowing Equatorial Counter Current (Wirtz et al. 2007).

The island of Príncipe (Democratic Republic of São Tomé and Príncipe) is a small tropical island (~136 km^2) near the equator, located within the Gulf of Guinea Islands marine ecoregion (eastern Atlantic Ocean) (Spalding et al. 2007), and was added to UNESCO's World Network of Biosphere Reserves in 2012. The island is understudied in terms of marine biodiversity, relative to its terrestrial flora and fauna (Jones 1994; Daniel 2010; Miller et al. 2012; Bell et al. 2015). Despite this, some fish inventories are available (e.g. Afonso et al. 1999; Wirtz et al. 2007; Maia et al. 2019), including a recent report of 130 fish species (Vasco-Rodrigues et al. 2018). These works, however, are based mostly on information collected from nearby São Tomé Island (Maia et al. 2019). The only quantitative study conducted in nearshore habitats of Príncipe was published recently by Tuya et al. (2018), focusing on changes in the diversity of reef-fish assemblages across depth gradients.

In this study, we surveyed nearshore fish species at three conspicuous seascape types across shallow coastal waters of Príncipe: rocky reefs, rocky reef–rhodolith bed transitions, and rocky reef–sandy bottom transitions. We used underwater video recordings made while SCUBA diving to determine (i) whether the degree of similarity in the composition and structure of fish assemblages differed between the three seascape types, and (ii) whether differences in taxonomic and phylogenetic diversity of fish assemblages were consistent between these habitats. We hypothesised that fish biodiversity, in terms of 'how much' taxonomic and phylogenetic diversity exists, would differ between the three habitats. In particular, we expected greater diversity on rocky reefs relative to the habitat transitions. Such baseline information is pertinent to promote conservation planning through the future establishment of marine protected areas within the framework of the UNESCO-designated Island of Príncipe Biosphere Reserve, especially since coastal resources targeted by local fisheries in the São Tomé and Príncipe islands have recently experienced declines in the abundance and mean body size of captures (Maia et al. 2018).

Materials and methods

Study area
The island of Príncipe (Figure 1) hosts a range of marine shallow-water (0–30 m depth) habitats, such as rocky reefs with sparse coral outcrops, sandy bottoms, and rhodolith biogenic beds (locally known as gla-gla) (Abreu et al. 2017; Maia et al. 2018). Rocky reefs have an irregular topography, including high-relief elements such as crevices, overhangs and caves (Lee et al. 2011; Carvalho et al. 2013). A total of 12 subtidal sites, along the island's entire perimeter, were surveyed in October and November of 2016 (Table 1), covering a depth range of 9–31 m. The sites encompassed a range of interspersed habitats, including rocky reefs adjacent to both rhodolith beds and sandy bottoms. Coralline algae and fleshy macroalgae dominated the benthic community structure on reefs, with sparse representation of filter-feeder colonies (e.g. sponges, and soft and hard corals) (Abreu et al. 2017). For the purpose of this study, we typified these habitat mosaics according to three seascape types: (i) transitions (incorporating edges) between rocky reefs and rhodolith beds; (ii) transitions (incorporating edges) between rocky reefs and sandy bottoms; and (iii) reefs (rocky reef areas >30 m from habitat edges) (Figure 2).

Fieldwork and data processing
Video transects with underwater cameras (GoPro7 Black, GoPro Inc., USA) were carried out by a SCUBA diver, swimming at a constant speed for 8 min, ~1 m above the bottom (wide-angle shooting at 133.9° diagonal field of view), at each of the three seascape types per site, if available. Video recordings are a useful method to extract presence/absence and ordinal abundance data on fish assemblages, avoiding *in situ* misidentifications of the relatively poorly known fauna of the region. Between two and six transects (samples) were carried out per seascape type and site, depending on their extent and availability as well as the intrinsic limitations of SCUBA diving with depth (Table 1). In the laboratory, each video was visualised three times using VLC 2.1+ software, which allows for light adjustments to improve fish identification. Fish species were identified following available checklists from São Tomé and Príncipe (i.e. Afonso et al. 1999; Wirtz et al. 2007; Vasco-Rodrigues et al. 2018). Only videos with a seawater visibility of >10 m were considered valid, for a total of 62 transects (14 for rocky reef–rhodolith transitions, 37 for rocky reef–sand transitions, and 11 for rocky reefs), equivalent to 10 h and 18 min of underwater observations. Individual fish that were distant from the camera, or appeared briefly and were blurred, were not considered. Some fish were not visually identified to species level, but were recorded at the genus level (i.e. *Kyphosus* spp., *Gobius* spp., *Lutjanus* spp. and *Thunnus* spp.) or family level (Pomacentridae). Each video was annotated with the depth (m) of the recording. From each video, we extracted two types of data: (i) a presence/absence list (compositional data), and (ii) abundance
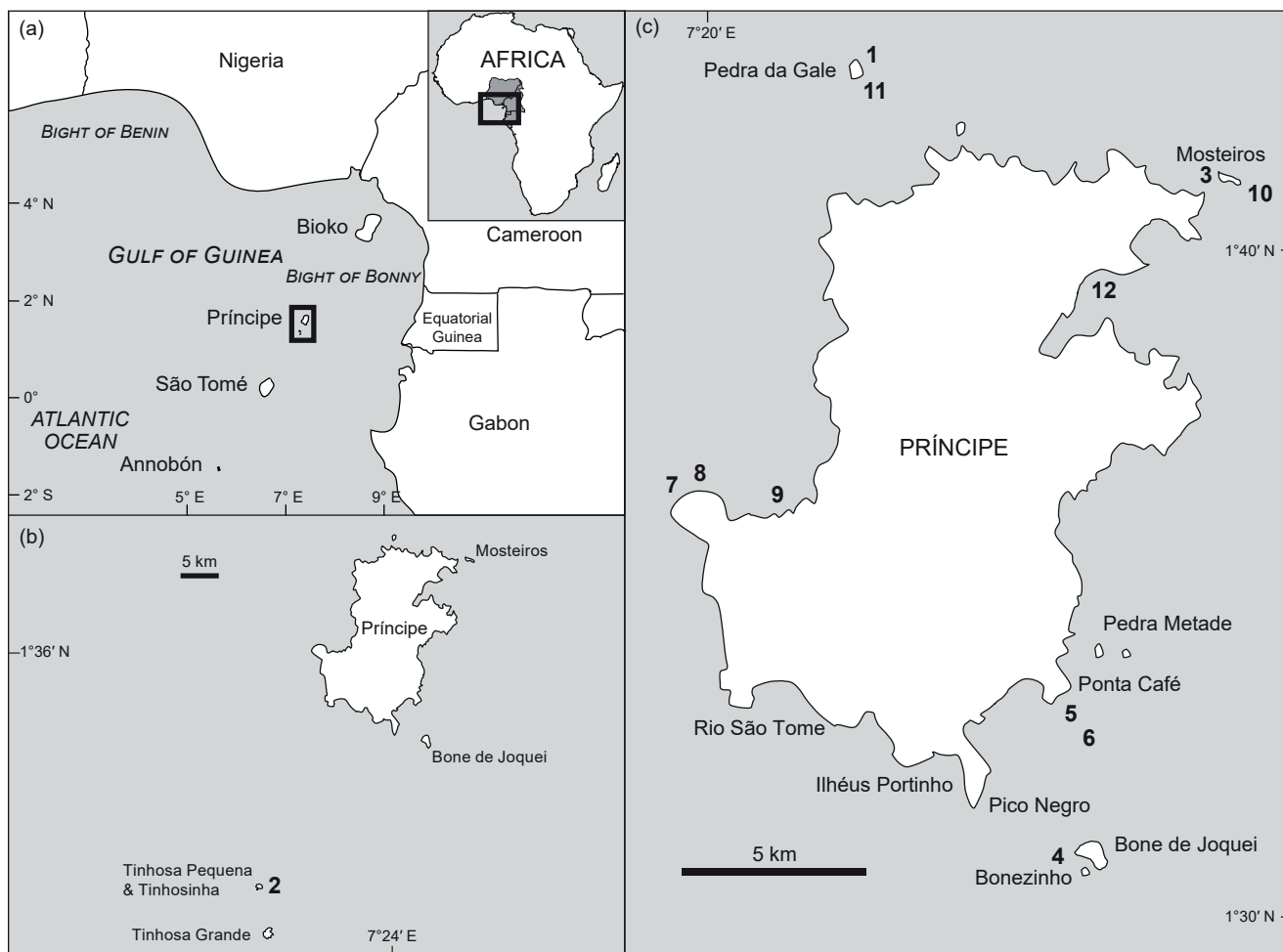
Figure 1: (a) Locations of the island of Príncipe in the Gulf of Guinea and (b, c) the sampled sites around the perimeter of the island: 1 – Pedra Galé; 2 – Ilhas Tinhosas; 3 – Mosteiros Oeste; 4 – Boné de Jóquei; 5 – Pedra Metade 1; 6 – Pedra Metade 2; 7 – Baía das Agulhas 1; 8 – Focinho de Cão; 9 – Baía das Agulhas 2; 10 – Mosteiros Este; 11 – Pedra Galé Sul; 12 – Pedra Medónia

Table 1: Location and depth of study sites at the island of Príncipe, Gulf of Guinea, for a survey of fish assemblages, in October to November 2016

Date	Depth (m)	Site	Latitude	Longitude
30 Oct 2016	31	Pedra Galé	1°43′35.45″ N	7°22′45.84″ E
31 Oct 2016	20	Ilhas Tinhosas	1°23′1.13″ N	7°17′0.80″ E
1 Nov 2016	9	Mosteiros Oeste	1°41′4.34″ N	7°28′3.17″ E
3 Nov 2016	13	Boné de Jóquei	1°30′52.08″ N	7°25′30.65″ E
4 Nov 2016	12	Pedra Metade 1	1°33′5.25″ N	7°25′9.67″ E
5 Nov 2016	18	Pedra Metade 2	1°33′0.80″ N	7°25′19.82″ E
6 Nov 2016	22	Baía das Agulhas 1	1°36′9.25″ N	7°20′45.94″ E
6 Nov 2016	17	Focinho de Cão	1°36′33.53″ N	7°20′1.23″ E
7 Nov 2016	15	Baía das Agulhas 2	1°36′7.82″ N	7°21′10.00″ E
8 Nov 2016	13	Mosteiros Este	1°41′5.34″ N	7°28′12.63″ E
9 Nov 2016	21	Pedra Galé Sul	1°43′26.04″ N	7°22′49.92″ E
10 Nov 2016	21	Pedra Medónia	1°41′29.24″ N	7°26′19.25″ E

information for each fish taxon, by considering five ordinal categories of abundance: 1 = >150 ind. per transect; 2 = 71–150 ind. per transect; 3 = 41–70 ind. per transect; 4 = 21–40 ind. per transect; 5 = 1–20 ind. per transect (Bosch et al. 2017).

Diversity estimates
Two indices capturing complementary aspects of the diversity of local communities (alpha-diversity) were calculated for each transect, according to the composition data (presence/absence) and assemblage structure
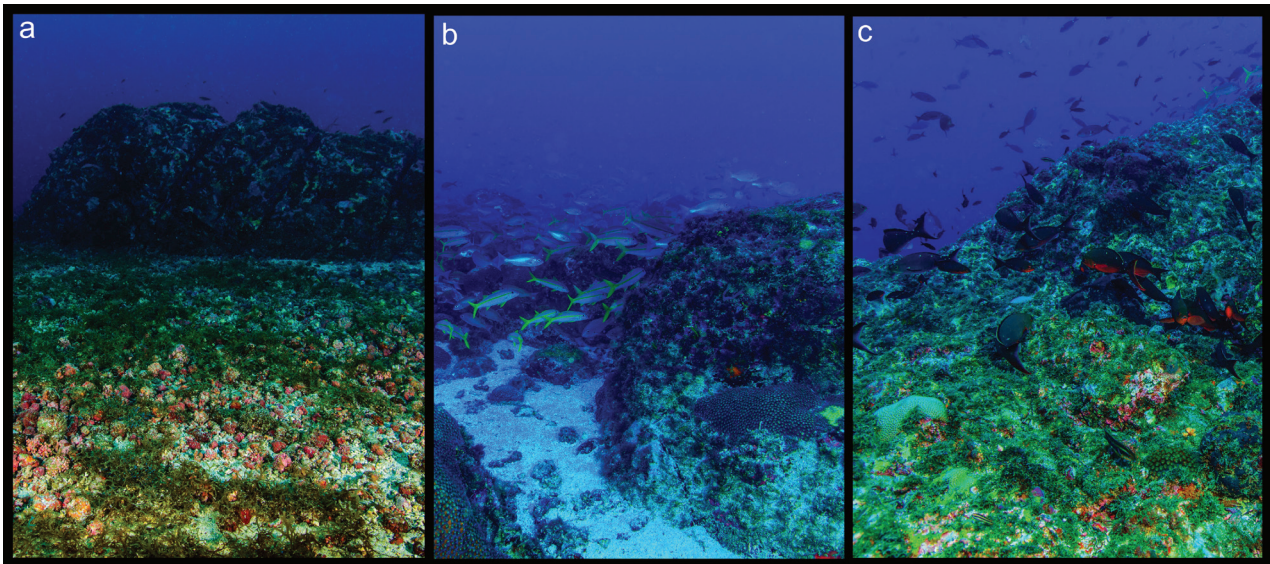
Figure 2: Seascape types at the island of Príncipe, surveyed during this study: (a) transitions between rocky reefs and rhodolith beds; (b) transitions between rocky reefs and sandy bottoms; (c) rocky reefs

data (composition and ordinal abundance). Taxonomic diversity (TD) was assessed through species richness (the number of fish taxa), whereas phylogenetic diversity was assessed through an index of taxonomic distinctness, Δ* (Clarke and Warwick 2001). This index considers the taxonomic distances along a Linnean classification tree between every pair of individuals drawn at random from the local community. The identification of fishes was initially validated via the World Register of Marine Species (WoRMS) 'match taxa' tool (www.marinespecies.org) and the available checklists for the nearby tropical areas (Afonso et al. 1999; Wirtz et al. 2007; Maia et al. 2019). The R package 'EcoIndR' (Guisande González 2017) implemented in R statistical software (R Core Team 2016) was further used to compute these two metrics of diversity. Phylogenetic diversity indices provided much greater resolution than traditional diversity indices, incorporating information on the 'relatedness' of species based on their evolutionary history (Cadotte et al. 2010). Increasingly used in conservation and ecology (Rogers et al. 1999; Ellingsen et al. 2005; Cadotte et al. 2010, 2012), their values are independent of the sampling effort, allowing objective comparisons between sites from studies where sampling effort is not standardised (Rogers et al. 1999).

Statistical analysis

Canonical analysis of principal coordinates (CAP) (Anderson and Willis 2003), implemented in PRIMER 6 (Clarke and Warwick 2001), was used as a constrained ordination to visualise differences in assemblage composition (i.e. according to presence/absence data) and structure (i.e. according to ordinal abundance categories) between the seascape types. By using CAP, axes were found in the multivariate space to maximise the separation between seascape types. Analyses were based on Jaccard and Bray–Curtis dissimilarities, which are ideal for compositional (presence/absence)

and abundance data, respectively (Clarke and Warwick 2001). The CAP routine also calculated miscalculation errors using the 'leave-one-out allocation' success (LoA): each sample was removed from the dataset, the CAP analysis re-run using the remaining observations, and then the removed sample classified to the nearest group centroid in the canonical space. Comparison of known groups with allocated groups provided miscalculation errors (Anderson and Willis 2003).

Generalised linear models (GLMs), using a negative binomial family-error structure because of overdispersion resulting from a large number of zeros, were fitted to both the matrices of species composition and species (ordinal) abundances via the R package 'mvabund' (Wang et al. 2012). The middle points of the five ordinal categories of abundance were considered. The depth of each video record was included in the models as a covariate. We tested the multivariate hypotheses that the composition and assemblage structure of fishes varied between habitats using the 'anova' function, which provided an analysis of deviance table. Probability values were then calculated using 999 resampling iterations via PIT-trap resampling. Diagnosis plots of residuals were visually inspected to check the appropriateness of fitted GLMs. Finally, GLMs were also fitted to both fish species richness and taxonomic distinctness, using the R package 'MASS' (Venables and Ripley 2002), to test for differences in species richness and taxonomic distinctness between seascape types. Poisson and Gamma family error structures, both with a log-link function, were selected to reach linear assumptions, respectively.

Results

A total of 71 fish taxa were recorded in this study (Table 2), which included the identification of 62 species, 59 genera and 35 families. Nearly half of the taxa (44%) were recorded in all three seascape types; ~30% of the taxa occurred in

Table 2: Checklist of fish taxa identified on each of the three seascapes types surveyed at the island of Príncipe (1 = present; 0 = absent), including the category of each species on the IUCN Red List of Threatened Species (DD = Data Deficient; LC = Least Concern; VU = Vulnerable)

Species	Rocky reef–rhodolith bed transitions	Rocky reef–sandy bottom transitions	Rocky reefs	IUCN Red List category
Abudefduf hoefleri	1	1	0	DD
Abudefduf saxatilis	0	1	1	LC
Acanthurus monroviae	1	1	1	LC
Aluterus scriptus	0	0	1	LC
Antennarius sp.	0	1	0	–
Apletodon wirtzi	0	1	0	LC
Apogon pseudomaculatus	0	1	1	LC
Balistes punctatus	1	1	1	VU
Bodianus pulchellus	1	1	1	LC
Bodianus speciosus	1	1	1	DD
Boops boops	0	1	0	LC
Bothus guibei	1	0	0	DD
Cantherhines pullus	1	1	1	LC
Canthidermis sufflamen	0	1	1	LC
Canthigaster supramacula	1	1	1	LC
Carangoides bartholomaei	1	1	1	LC
Caranx lugubris	1	0	1	LC
Cephalopholis nigri	0	1	1	LC
Cephalopholis taeniops	1	1	1	LC
Chaetodon robustus	0	0	1	LC
Chilomycterus reticulatus	0	0	1	LC
Chromis cadenati	1	0	0	LC
Chromis limbata	1	1	1	LC
Chromis multilineata	1	1	0	LC
Cirrhitus atlanticus	1	1	1	LC
Clepticus africanus	1	1	1	DD
Coris atlantica	1	1	1	LC
Echeneis naucrates	1	0	0	LC
Elagatis bipinnulata	1	1	1	LC
Epinephelus adscensionis	1	1	0	LC
Gobius spp.	1	1	1	–
Ginglymostoma cirratum	1	1	0	DD
Gnatholepis thompsoni	1	1	1	LC
Gorogobius nigricinctus	1	1	0	LC
Heteropriacanthus cruentatus	1	0	1	LC
Hippocampus algiricus	0	1	0	VU
Holacanthus africanus	1	1	1	LC
Holocentrus adscensionis	1	1	1	LC
Kyphosus spp.	1	1	1	–
Lutjanus spp.	1	1	1	–
Lutjanus agennes	0	1	1	DD
Lutjanus fulgens	0	1	0	LC
Melichthys niger	0	1	0	LC
Microspathodon frontatus	0	1	1	LC
Myrichthys pardalis	0	1	1	LC
Myripristis jacobus	1	1	1	LC
Mulloidichthys martinicus	1	1	1	LC
Muraena spp.	0	1	1	–
Muraena melanotis	0	1	1	LC
Oblada melanura	1	1	1	LC
Ophioblennius atlanticus	1	1	1	LC
Paranthias furcifer	1	1	1	LC
Pomacentridae	1	1	1	–
Pomadasys incisus	0	1	0	LC
Prionurus biafraensis	1	1	1	LC
Rypticus saponaceus	1	1	0	LC
Sargocentron hastatum	0	1	0	LC
Scarus hoefleri	1	1	1	LC
Scorpaena laevis	0	1	0	DD
Seriola rivoliana	0	1	0	LC
Serranus sp.	1	1	0	–
Sparisoma spp.	1	1	1	–
Sparisoma choati	1	1	1	–
Sparisoma rubripinne	0	1	0	LC
Sphyraena barracuda	1	1	1	LC
Stegastes imbricatus	1	1	0	LC
Taeniura grabata	1	1	0	DD
Thalassoma newtoni	1	1	1	LC
Thunnus spp.	1	0	0	–
Wheelerigobius wirtzi	0	1	1	LC
Xyrichtys novacula	1	0	0	LC

two seascape types; and ~27% of the taxa were restricted to a particular seascape (Figure 3). Rocky reefs and reef–sandy bottom transitions shared the greatest number of taxa (9), together with reef–sandy bottom transitions and reef–rhodolith bed transitions (9), when compared with rocky reefs and reef–rhodolith transitions (2) (Figure 3).

Both the composition and structure of fish assemblages differed between the three seascapes types (analysis of deviance: dev = 182.49, p = 0.002, df = 2; dev = 184.23, p = 0.01, df = 1, respectively) (Table 3). In particular, fishes associated with reef–rhodolith bed transitions differed
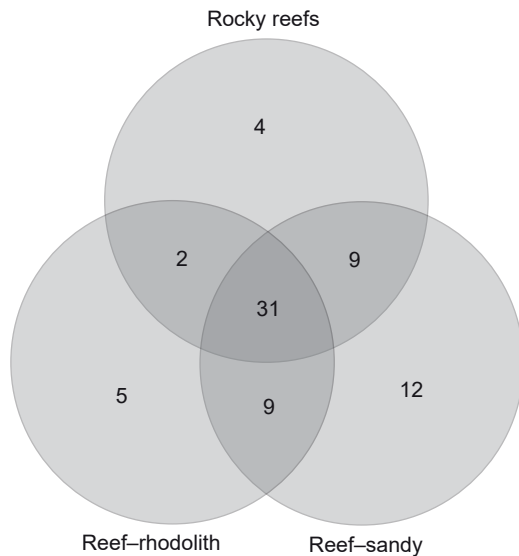
significantly in terms of both composition and assemblage structure to fishes from reef–sandy bottom transitions (Wald value = 5.66, p = 0.03; Wald value = 7.12, p = 0.03, respectively) (Table 4). However, though fishes from reef–sandy bottom transitions and rocky reefs differed in terms of their composition (Wald value = 6.09, p = 0.02), they did not differ in terms of their assemblage structure (Wald value = 5.18, p = 0.51) (Table 4).

These multivariate patterns are visualised in the CAP ordinations (Figure 4); samples corresponding to reef–rhodolith bed transitions cluster on the left-hand side of both ordinations, whereas samples corresponding to rocky reefs are on the right-hand side of both ordinations. Fish assemblages associated with reef–sandy bottom transitions are scattered across the entire ordination space.

Samples from rocky reefs had the lowest misclassification of the three seascape types (72.72% of corrected allocations, in terms of both fish composition and assemblage structure) (Table 5); when misclassified, all samples from rocky reefs were considered to be from reef–sandy bottom transitions. In contrast, samples from reef–rhodolith bed transitions had the larger degree of misclassification (57.14% and 50.0% of corrected allocations, respectively) (Table 5); when misclassified, samples from reef–rhodolith bed transitions were assigned primarily to reef–sandy bottom transitions (Table 5).

The mean number of fish species (species richness) per sample was larger on rocky reefs than in both reef–rhodolith beds and reef–sandy bottom transitions (GLM: estimate = 0.21, p = 0.02) (Figure 5a; Table 6). However, the taxonomic distinctness of fish assemblages was higher for both transition types relative to rocky reefs (GLM: estimate = −0.17, p = 0.08) (Figure 5b; Table 6).

Figure 3: Venn diagram showing the overlap in fish species composition in three nearshore seascape types surveyed at the island of Príncipe: reef–rhodolith = transitions between rocky reefs and rhodolith beds; reef–sandy = transitions between rocky reefs and sandy bottoms; and rocky reefs

Discussion

This study shows that the composition, assemblage structure and diversity of coastal fishes at Príncipe differed between

Table 3: Analysis of deviance testing the multivariate hypotheses that the composition and assemblage structure of fishes differed between the three landscape types, across a range of depths, at the island of Príncipe. df = degrees of freedom

Factor	df(Residual)	df	Composition		Assemblage structure	
			Deviation	p-value	Deviation	p-value
Intercept	61					
Depth	60	1	93.99	0.006	96.52	0.001
Habitat	58	2	182.49	0.002	184.23	0.01

Table 4: Results of multivariate generalised linear models predicting differences in the composition and assemblage structure of fishes between the three habitat types, across a range of depths, at the island of Príncipe. The reference level is 'reef–sandy' transitions

Factor	Composition		Assemblage structure	
	Wald value	p-value	Wald value	p-value
Intercept	10.56	0.001	13.10	0.001
Depth	7.35	0.08	10.85	0.05
Habitat [reef–rhodolith transitions]	5.66	0.03	7.12	0.03
Habitat [rocky reefs]	6.09	0.02	5.18	0.51

three types of nearshore seascapes. The two biodiversity dimensions we studied—taxonomic and phylogenetic diversity—both showed differences between the habitats.

Among the fish species recorded, some are listed as Vulnerable and others as Data Deficient on the IUCN Red List of Threatened Species, including, respectively, a heavily traded species of seahorse (*Hippocampus algiricus*) (Otero-Ferrer et al. 2017) and an economically important and probably overfished shark species (*Ginglymostoma cirratum*) (Maia et al. 2018). Our data highlight the need for additional biological
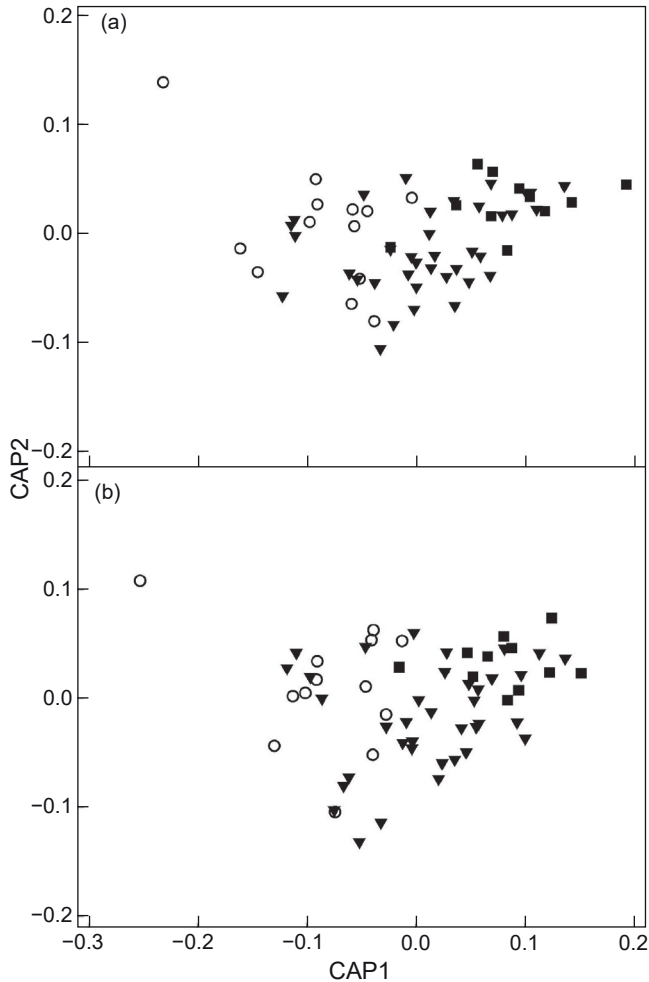

Figure 4: Canonical analysis of principal coordinates (CAP) bidimensional ordinations denoting differences in (a) fish composition and (b) fish assemblage structure, between seascape types in nearshore waters of the island of Príncipe. ○ = reef–rhodolith bed transitions; ▼ = reef–sandy bottom transitions; ■ = rocky reefs
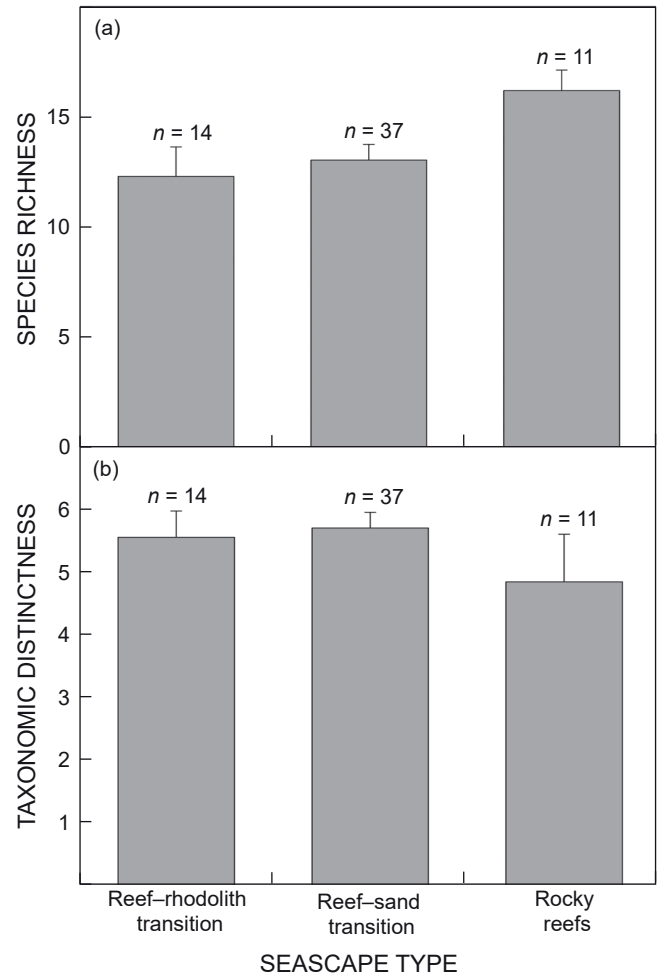

Figure 5: Differences in (a) fish species richness and (b) taxonomic distinctness between seascape types in nearshore waters of the island of Príncipe. Error bars represent +SE; *n* = number of underwater video transects

Table 5: Miscalculation errors (cross-validation), using the 'leave-one-out allocation' success, of samples according to their composition and assemblage structure, collected from each of three seascape types sampled at the island of Príncipe

Original group	Reef–rhodolith	Reef–sandy	Rocky reefs	Total	%Success	Total correct	Misclassification error
			Composition				
Reef–rhodolith	8	6	0	14	57.14	38/62 (61.29%)	38.71%
Reef–sandy	6	22	9	37	59.46		
Rocky reefs	0	3	8	11	72.73		
			Assemblage structure				
Reef–rhodolith	7	6	1	14	50	37/62 (59.68%)	40.32%
Reef–sandy	5	22	10	37	59.46		
Rocky reefs	0	3	8	11	72.73		

Table 6: Results of generalised linear models testing whether the species richness and the taxonomic distinctness of fish assemblages differed between the three seascape types, across a range of depths, at the island of Príncipe. The reference level is 'reef–sandy' transitions

	Estimate	SE	z-value	p-value
Species richness				
Intercept	2.59	0.14	18.33	<0.001
Depth	−0.001	0.007	−0.16	0.87
Habitat [reef–rhodolith]	−0.05	0.09	−0.58	0.56
Habitat [rocky reefs]	0.21	0.09	2.41	0.02
Taxonomic distinctness				
Intercept	1.79	0.15	12.32	<0.001
Depth	−0.002	0.007	−0.35	0.73
Habitat [reef–rhodolith]	0.05	0.09	0.59	0.56
Habitat [rocky reefs]	−0.17	0.10	−1.75	0.08

and ecological studies in the Prícipe seascape types to effectively implement management practices to conserve local fish populations. In terms of fish species richness, previous surveys carried out in the shallow subtidal habitats of Príncipe (Tuya et al. 2018) and São Tomé (Maia et al. 2019) provided similar results. In addition, the levels of fish taxonomic biodiversity registered here were similar to those observed at other oceanic islands in the tropical eastern Atlantic (e.g. Cabo Verde Archipelago, 67 species: Freitas et al. 2019) and in the western Atlantic (e.g. Virgin Islands, 71 species: Mateo and Tobias 2007), but were lower compared with those recorded at islands in the Caribbean and in the Indo-Pacific (Allen 2008; Acero et al. 2019). Islands in the Gulf of Guinea, including Annobón, São Tomé and Príncipe, together with Cabo Verde, have been considered important global hotspots for the conservation of marine biodiversity (Roberts et al. 2002), with high levels of endemism (~30%: Floeter et al. 2008). This fact is probably linked to their geographic isolation (Floeter et al. 2008; Cowman et al. 2017), but also to their oceanographic connectivity with the tropical western Atlantic through the Equatorial Counter Current (Wirtz et al. 2007; Floeter et al. 2008; Hachich et al. 2015; Herrero-Barrencua et al. 2019). Additionally, the cool Benguela Current to the south limits the movement of tropical species from the Indian Ocean, whereas the cold waters of the northeastern Atlantic also limit the northern range of tropical fish species (Floeter et al. 2008; Almada et al. 2013; Maia et al. 2019). Other factors that might contribute to high fish diversity in the region relative to other eastern Atlantic areas include the large diversity of habitats, such as seagrasses (Alexandre et al. 2017) and mangroves, that can serve as nursery areas for fishes (Haroun et al. 2018). In the case of Príncipe, several locations with mangroves have been identified (e.g. at Praia Caixão, Praia Grande and Praia Salgada), and these appear to be remnants of more extensive mangrove forests that once existed along the island's coast (Haroun et al. 2018). Some fish species recorded in our study have also been described in the mangrove fish assemblages of the island (e.g. *Pomadasys incisus*: Haroun et al. 2018).

Differences in fish composition and assemblage structure between the three seascape types can be attributed to differences in the physical structure of the habitats. Indeed, variability in the qualitative and quantitative attributes associated with different habitat types can alter patterns in the composition and structure of biological assemblages, as has been reported for other habitat transitions in nearshore waters (Guidetti 2000; Gullström et al. 2008; Campbell et al. 2011; Tuya et al. 2011, 2019; Otero-Ferrer et al. 2019). For example, rocky reefs contain many structural elements (e.g. crevices, overhangs) which are available as refuges against predators (Almany 2004; Tuya et al. 2019). In contrast, higher rates of competition and predation between fish species are found in habitat transitions, often with less structural complexity and fewer niches (Richardson et al. 2017; Tuya et al. 2019), resulting in lower taxonomic diversity when compared with rocky reefs. High rates of predation have been observed among fishes living in habitat edges around rocky reefs (Frazer et al. 1991; Barros et al. 2001; Dorenbosch et al. 2005; Tuya et al. 2010, 2011). Similar 'edge' effects were also observed for fish assemblages inhabiting coral reef–seagrass transitions on the island of Zanzibar (western Indian Ocean) (Dorenbosch et al. 2005).

Despite rocky reefs showing greater taxonomic diversity (i.e. high species richness) in comparison with the habitat transitions, the phylogenetic diversity (i.e. taxonomic distinctness index) of fish assemblages was greater in both transition types than on rocky reefs. Other studies have similarly shown that communities with low species richness do not necessarily have a lesser taxonomic distinctness than communities with many species (Ellingsen et al. 2005; Tuya et al. 2019), whereas the species richness and taxonomic distinctness of nearshore fishes would normally be expected to behave in the same way (Bosch et al. 2017). The mixing of biotas associated with interconnected habitats at their edges tends to increase diversity (Magura 2002; Ries et al. 2004). In turn, the higher misclassification error values observed here for habitat transitions can be explained because fish assemblages inhabiting boundaries between two habitats display great variability in terms of composition and species abundances, as a result of the mixing of biotas (Barros et al. 2001; Ries et al. 2004; Tuya et al. 2011). Greater phylogenetic diversity at habitat transitions, however, might be connected with lower availability of resources, which translates into higher degrees of interspecific competition between close relatives (i.e. 'limiting similarity' hypothesis: Macarthur and Levins 1967). Several studies have stressed, in this sense, the importance of competitive exclusion in shaping local assemblages of marine fishes (e.g. Ford and Roberts 2019; Vallée et al. 2019).

Our results revealed a discrepancy in fish diversity patterns across nearshore seascape types that was dependent on the diversity metric employed—which can have conservation implications, as we could obtain a more holistic understanding of biodiversity, particularly in the context of functional or evolutionary lineages (Tucker et al. 2017; Mazel et al. 2018; Tuya et al. 2019). In particular, both the 'reef–rhodolith bed' and the 'reef–sandy bottom' seascapes across Príncipe cannot be underestimated from a conservation perspective, because, despite their lower fish-species richness, these habitat transitions may accomplish other

important ecological functions (e.g. nursery or foraging areas) for reef-associated fishes, as has been indicated previously (e.g. Ries et al. 2004; Campbell et al. 2011). Considering the long tradition of marine resource exploitation by artisanal fishers in São Tomé and Príncipe (Maia et al. 2018; Tuya et al. 2018), future management plans, including the placement of MPAs, should also consider the preservation of these habitat boundaries.

In summary, this study demonstrates that the composition, structure and diversity of the coastal fish assemblages of Príncipe varied between three nearshore seascape types. The two biodiversity dimensions (taxonomic and phylogenetic) assessed across the seascapes provided relevant information to better understand ecosystem functioning and community assemblages in the shallow waters surrounding this tropical island.

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