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## Shallow subtidal macroalgae in the North-eastern Atlantic archipelagos (Macaronesian region): a spatial approach to community structure

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### ABSTRACT

Shallow subtidal macroalgal communities in the North-eastern Atlantic archipelagos (Azores, Madeira, Canaries and Cape Verde) were studied in order to identify their spatial organization patterns and the main drivers of change. Fifteen islands and 145 sites across 15° of latitude and 2850 km were sampled. We found high spatial variability across the scales considered (archipelago, island and site). The structure of macroalgal communities differed among archipelagos, except between Madeira and the Canaries, which were similar. Across a latitudinal gradient, macroalgal communities in the Azores were clearly separated from the other archipelagos; communities in Madeira and the Canaries occupied an intermediate position, while those in Cape Verde appeared at the opposite end of the gradient. In the Azores, species with warm-temperate affinities dominated communities. Cape Verde communities were, in contrast, dominated by tropical taxa, whereas in the subtropical Canaries and Madeira there was a mixture of species with colder and warmer affinities. Apart from crustose coralline algae, the Dictyotales were the group with greatest cover; larger and longer-lived species were progressively replaced by short-lived species along a latitudinal gradient from north to south. The perennial species *Zonaria tournefortii* dominated the sea-bottom in the Azores, the semi-perennial *Lophophora variegata* in the Canaries, the filamentous algae in Madeira and the ephemeral *Dictyota dichotoma* in Cape Verde. We hypothesized that the differences among archipelagos could be explained by synergies between temperature and herbivory, which increased in diversity southwards, especially in Cape Verde. This was supported by the predominance of non-crustose macroalgae in the Azores and of crustose macroalgae in Cape Verde, as would be predicted from the greater herbivore activity. At the scale of islands and sites, the same set of environmental variables drove differences in macroalgal community structure across all the Macaronesian archipelagos.

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**KEY WORDS** community structure; Dictyotales; latitudinal gradient; Macaronesian archipelagos; seaweed; spatial distribution

### Introduction

In coastal marine systems, abundance estimates of different taxa are commonly made at spatial scales ranging from small- (a few or hundreds of metres) to meso-scale (a few to hundreds of km). At smaller spatial scales, many studies have linked community structure with variation in environmental factors (e.g. local oceanographic conditions, depth, sedimentation, pollutants) and species interactions (e.g. Díez *et al.*, 2003; Martins *et al.*, 2013; Sangil *et al.*, 2014a; Bermejo *et al.*, 2016). However, at larger biogeographic scales, studies mostly comprise general descriptions of biota, or analyses of presence/absence data, whilst abundance data are scant.

These large-scale studies are valuable either for characterizing biogeographic regions (Eckman, 1953; Briggs, 1974; Gaines & Lubchenco, 1982; Liuzzi *et al.*, 2011) or examining latitudinal and longitudinal patterns of richness and diversity (Tuya & Haroun, 2009). They have also highlighted the key role of temperature as a major driver of species distribution in the marine environment, as well as that of environmental variables such as ocean currents, geographic isolation and coastal geomorphology (Lüning, 1990). Yet studies based on presence/absence data are insufficient, particularly when more complex ecological questions are considered. For instance, they provide little information regarding

variation in community structure, including the relative abundance of key species and their importance in ecosystem processes.

Hard-bottom macroalgae are key primary producers and many species are considered as foundation species, supporting a diverse assemblage of benthic biodiversity around them (Bruno *et al.*, 2005). Their development is strongly influenced by temperature, which affects growth, photosynthetic performance and survival and plays a central role in shaping patterns of biogeographic distribution (Eggert, 2012). Despite the ecological importance of macroalgae, there are still gaps in the knowledge of large-scale distribution patterns. Progressive changes in abundance (cover or biomass) at larger spatial scales may be a consequence of latitudinal or longitudinal shifts in community organization (e.g. Wernberg *et al.*, 2011; Sales *et al.*, 2012; Schils *et al.*, 2013; Lathlean *et al.*, 2015). Quantitative approaches can be very useful in detecting sudden changes in the structure of communities, and thus help establish biogeographic regions with greater reliability (Wernberg *et al.*, 2003; Blanchette *et al.*, 2008; Connell & Irving, 2008; Porter *et al.*, 2013). They can be especially important when assessing the effects of global warming on species range limits and abundance, and for detecting phase shifts (Harley *et al.*, 2006; Lima *et al.*, 2007).

Among the Macaronesian archipelagos, the macroalgal floras of the Canaries and Madeira have been shown to be compositionally very similar (Prud'homme van Reine & van den Hoek, 1990). In contrast, those of the Azores and Cape Verde have been separated from them in terms of composition. According to van den Hoek (1975, 1984), the Azores, Madeira and Canaries are included in the Warm Temperate North-eastern Atlantic Region, while Cape Verde is within the Tropical Eastern Atlantic Region. More recently, Tuya & Haroun (2009) divided Lusitanian Macaronesia into two major biogeographic areas: one comprising the Canaries, and the other comprising Azores, Madeira and the Selvagens. Additionally, based on species composition, oceanographic characteristics and presence of specific ecosystems, Spalding *et al.* (2007) considered the Azores, Madeira and the Canaries as one province within the Lusitanian ecoregion, and Cape Verde as a province within the West African Transition Ecoregion. All these previous studies agree that there is a clear distinction in the composition of the macroalgal flora between the warm-temperate (Madeira, Canaries) and tropical archipelagos (Cape Verde).

In our study, we used quantitative data to examine patterns of spatial variability in macroalgal community structure in the shallow rocky subtidal zone of the Macaronesian archipelagos (Azores, Madeira, Canaries and Cape Verde) by sampling 145 sites in 15 islands, spanning 15° of latitude and 2850 km (Fig. 1). The

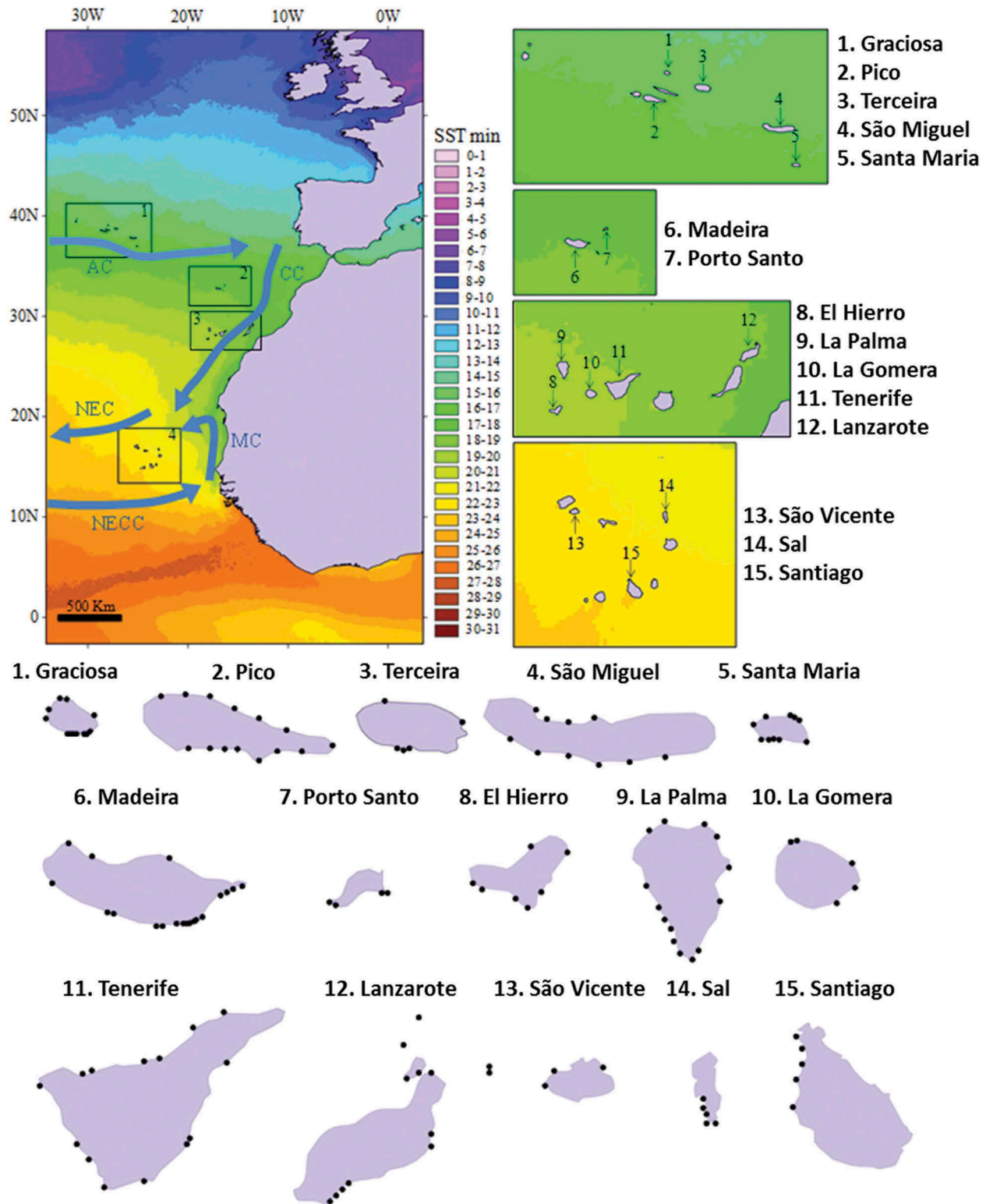
potential role of temperature in driving observed patterns of macroalgal community structure was examined, along with that of other environmental variables such as nutrients, solar radiation, herbivore richness, island size and human population density. Patterns of species distribution and community structure have never been investigated using a quantitative approach at the Macaronesian scale. In the present study, we predict that such use of quantitative data, rather than merely presence/absence, should provide a clearer vision of Macaronesian biogeography, and help identify key species and their relative importance in macroalgal community structure. Specifically, we aimed to: (i) evaluate the patterns of variability in subtidal macroalgal community structure at several spatial scales (archipelago, island and site), identifying the species responsible for differences among archipelagos; (ii) assess spatial variation in macroalgal morphotypes; and (iii) identify potential environmental drivers of spatial variation in macroalgal community structure.

## Materials and methods

### Site description

The NE Atlantic archipelagos, known as the Macaronesian region, comprise five groups of islands: the Azores, Madeira, Selvagens, the Canaries and Cape Verde. They differ in distance from the nearest continent – from 90 km (the Canaries) to 1380 km (the Azores) and are situated between latitudes 39.73° and 24.70°N (Table 1). The farthest distance between islands is approximately 2850 km. These archipelagos have biological, geological, climatological and oceanographic aspects in common. They are all of volcanic origin and have emerged from the ocean basin independently of continents, as a result of successive eruptions. Ocean currents, notably the Azores and Canary currents, link these archipelagos from Azores to Cape Verde, creating a route for the spread of organisms from north to south. In addition, the North Equatorial current and counter-current and the Mauritanian current directly affect the Cape Verde archipelago (Aristegui *et al.*, 2009).

Considering the SST<sub>min</sub> (Sea Surface Temperature), latitudinal changes in temperature can exceed 8°C (Fig. 1, Table 1), with the annual SST<sub>mean</sub> varying slightly more than 6°C (Tyberghein *et al.*, 2012). Availability of nutrients is also highly heterogeneous in the area (Table 1). Colder waters surrounding the Azores are mesotrophic, unaffected by upwelling. In Madeira the waters are oligotrophic, as in most of the Canaries where only the eastern islands are slightly affected by a nutrient increase through the upwelling 'filaments'. In contrast, the waters of Cape Verde are nutrient-enriched because they are affected by a strong upwelling plume from the coast of Senegal and Mauritania (Hoepffener *et al.*, 2014).



**Fig. 1.** Location of the archipelagos, islands and sampling sites. Blue arrows indicate the major current systems in the study area. AC = Azores current, CC = Canary Current, NEC = North equatorial current, NECC = North equatorial counter current, MC = Mauritanian current, based on Aristegui *et al.* (2009). Minimum sea surface temperature (SSTmin) derived from Tyberghein *et al.* (2012).

### Data collection

Fieldwork was carried out by scientific scuba diving at 15 islands: five in the Azores (Graciosa, Pico, Terceira, São Miguel and Santa Maria), two in Madeira (Madeira and Porto Santo), five in the Canaries (El Hierro, La Palma, La Gomera, Tenerife and Lanzarote)

and three in Cape Verde (São Vicente, Sal and Santiago). Altogether 145 sites were sampled from 2007 to 2013 (3–18 sites per island; Fig. 1), mainly in summer to avoid seasonal effects on macroalgal community structure. Percentage benthic macrophyte cover was estimated *in situ* on rocky reefs at 5–25 m



**Table 1.** Summary of geographic position, oceanographic conditions and the richness of herbivores in the Macaronesian archipelagos.

	Azores	Madeira	Canaries	Cape Verde
Latitude	39.72 to 36.92N	33.10 to 32.40N	29.41 to 27.63N	17.21 to 14.80N
Longitude	−31.79 to −24.77W	−17.26 to −16.27W	−18.16 to −13.33W	−25.36 to −22.66W
SSTmin <sup>a</sup>	15.39–16.40°C	17.47–18.14°C	18.06–19.87°C	21.82–23.51°C
SSTmean <sup>a</sup>	18.42–19.46°C	20.30–21.10°C	20.22–22.14°C	23.95–24.90°C
Nutrients and productivity <sup>a</sup>	Mesotrophic nitrate 1.20–1.60 $\mu\text{mol l}^{-1}$ Chl <i>a</i> 0.16–0.29 $\text{mg m}^{-3}$	Oligotrophic nitrate 0.67–0.73 $\mu\text{mol l}^{-1}$ Chl <i>a</i> 0.11–0.16 $\text{mg m}^{-3}$	Oligotrophic nitrate 0.56–0.68 $\mu\text{mol l}^{-1}$ Chl <i>a</i> 0.12–0.18 $\text{mg m}^{-3}$	Mesotrophic nitrate 1.39–1.850 $\mu\text{mol l}^{-1}$ Chl <i>a</i> 0.25–0.39 $\text{mg m}^{-3}$
Herbivores	Low diversity 3 sea urchins 5 fish	Poorly diversified 4 sea urchins <sup>b</sup> 5 fish	Poorly diversified 4 sea urchins <sup>b</sup> 5 fish	High diversity 5 sea urchins 11 fish

<sup>a</sup>Data obtained from Tyberghein *et al.* (2012). Herbivore data were obtained from World Echinoidea Database (Kroh & Mooi, 2017) and FishBase (Froese & Pauly, 2017). <sup>b</sup>In Madeira and Canaries there are large populations of the sea urchin *Diadema africanum* (Alves *et al.*, 2001; Hernández *et al.*, 2008).

depth. At each site, 14–24 replicate 0.25 m<sup>2</sup> quadrats were sampled once (total  $n = 2825$ ). Quadrats were randomly located at least 10 m apart, within the studied depth range. Relative species abundance was recorded *in situ*. The dominant seaweeds were estimated using the visual scanning method including over- and understory layers (Sangil *et al.*, 2014a). All taxa were identified to species or genus level, except filamentous blue-green algae ('cyanophytes'), crustose coralline algae, crustose non-coralline algae and small filaments (mainly Ceramiales such as *Ceramium*, *Polysiphonia* and *Herposiphonia*). For further analysis, taxa were grouped into non-crustose macroalgae (sum of all non-crustose species) and morpho-functional groups. Species with the same morphology usually have a similar phenology, and respond similarly to environmental conditions (Steneck & Dethier, 1994). For this study, we grouped species together as filaments and small turfs, and ephemeral, perennial, semi-perennial, erect calcified and crustose macroalgae (Table 2).

For each island, oceanographic, biological, geographic and anthropogenic parameters were used as predictor variables in the multivariate analyses. The parameters were: annual sea surface temperature (SSTMin and SSTmean), dissolved nitrate ( $\mu\text{mol l}^{-1}$ ), chlorophyll *a* (Chl *a*) concentration ( $\text{mg m}^{-3}$ ), photosynthetically available radiation (PAR,  $\text{mol m}^{-2} \text{day}^{-1}$ ), sea-urchin and herbivorous fish richness (which may be related to the variability in coastal habitats), island size ( $\text{km}^2$ ), human population (density for each island, reflecting possible anthropogenic impacts), and the latitude of each site sampled. SSTmin, SSTmean, nitrate, Chl *a* and PAR were obtained from Bio-Oracle, a geospatial database compiling worldwide oceanographic and climatic data (Tyberghein *et al.*, 2012). Geographic and demographic data were obtained from government websites. Sea-urchin and herbivorous fish richness data were obtained from databases (Froese & Pauly, 2017; Kroh & Mooi, 2017). Quantitative data for herbivores were not available for all islands.

## Analyses

Spatial variation in community structure was examined using permutational analysis of variance (PERMANOVA; Anderson *et al.*, 2008) on the square-root transformed cover data. The resemblance matrices were obtained using Bray–Curtis dissimilarities. The design consisted of a three-way analysis, with 'Archipelago' (four levels: Azores, Madeira, Canaries, Cape Verde) treated as a fixed factor, 'Island' (15 levels) as a random factor nested in 'Archipelago' and 'Site' (145 levels) as a random factor nested in 'Archipelago' and 'Island'. *A posteriori* pairwise comparisons per 'Archipelago' and 'Island' were performed. Pseudo-*F* values were obtained from a maximum of 4999 random permutations. The species that contributed most to observed differences among archipelagos were identified using similarity percentages (SIMPER; Clarke & Gorley, 2006). To visualize spatial patterns in community structure, non-metric multidimensional scaling ordination (nMDS) was used (Clarke & Gorley, 2006). These analyses were based on the mean species cover pooled among samples for each of the studied sites. After analysis, macroalgal cover per island was also averaged and a Bray–Curtis similarity matrix and new nMDS, as well as a group-average agglomerative hierarchical clustering (CLUSTER), were performed to visually depict relationships between islands. These ordination and classification analyses were also based on square-root matrices.

Differences in the mean cover of macroalgal morpho-functional groups (defined above), and the total cover of non-crustose macroalgae (obtained from the sum of each non-crustose species) were examined using permutational ANOVAs (Anderson *et al.*, 2008). Resemblance matrices were generated using the Euclidean distances of the data (Anderson & ter Braak, 2003) and data analysed using the same design as described above. Prior to analyses, data were also square-root transformed. Sums of squares type III were employed, both in the permutational ANOVAs and the PERMANOVA, to account for unbalanced design (Anderson *et al.*, 2008).

**Table 2.** Mean percentage cover ( $\pm$  SE) of macroalgae identified in the Eastern Atlantic archipelagos studied.

	Azores	Madeira	Canaries	Cape Verde
<b>Crustose macroalgae</b>				
Crustose coralline algae	7.77 $\pm$ 0.68	15.96 $\pm$ 0.68	26.95 $\pm$ 0.93	48.40 $\pm$ 0.96
Crustose non-coralline algae	1.06 $\pm$ 0.28	0.33 $\pm$ 1.63	0.61 $\pm$ 0.10	
Maërl ( <i>Lithothamnion corallioides</i> , <i>Phymatolithon calcareum</i> )		1.09 $\pm$ 0.17	0.002 $\pm$ 0.001	
<i>Pseudolithoderma adriaticum</i>			1.27 $\pm$ 0.112	
<i>Peyssonnelia</i> spp.	0.51 $\pm$ 0.17		0.03 $\pm$ 0.02	0.18 $\pm$ 0.06
<b>Perennial and semiperennial macroalgae</b>				
<i>Asparagopsis armata</i>	3.83 $\pm$ 0.50	0.07 $\pm$ 0.04		
<i>Asparagopsis taxiformis</i>	2.08 $\pm$ 0.38	0.39 $\pm$ 0.14	0.67 $\pm$ 0.13	0.07 $\pm$ 0.03
<i>Caulerpa racemosa</i>			<0.001	1.09 $\pm$ 0.19
<i>Caulerpa sertularoides</i>				0.46 $\pm$ 0.11
<i>Codium adherens</i>	0.36 $\pm$ 0.19			
<i>Codium elisabethae</i>	0.20 $\pm$ 0.08			
<i>Cystoseira abies-marina</i>	0.06 $\pm$ 0.02		1.90 $\pm$ 0.36	
<i>Cystoseira compressa</i>			1.68 $\pm$ 0.32	
<i>Cystoseria foeniculacea</i>			0.01 $\pm$ 0.01	
<i>Cystoseira</i> sp1			0.72 $\pm$ 0.18	
<i>Dasya baillouviana</i>			0.10 $\pm$ 0.03	0.03 $\pm$ 0.02
<i>Dictyopteris polypodioides</i>	0.03 $\pm$ 0.02		0.007 $\pm$ 0.004	
<i>Dictyopteris</i> sp		0.005 $\pm$ 0.14		
<i>Gelidium latifolium</i> *	0.02 $\pm$ 0.02			
<i>Lobophora variegata</i>		0.26 $\pm$ 0.06	22.88 $\pm$ 1.15	0.36 $\pm$ 0.07
<i>Halopteris scoparia</i>	6.48 $\pm$ 0.62	4.90 $\pm$ 0.56	0.14 $\pm$ 0.04	
<i>Halopteris filicina</i>		10.47 $\pm$ 23.61		
<i>Plocamium cartilagineum</i>	0.23 $\pm$ 0.10		0.01 $\pm$ 0.007	
<i>Pterocladia capillacea</i>	0.33 $\pm$ 0.13		0.04 $\pm$ 0.01	
<i>Sargassum desfontainesii</i>			0.02 $\pm$ 0.01	
<i>Sargassum flavifolium</i>			0.60 $\pm$ 0.13	
<i>Sargassum vulgare</i>		0.002 $\pm$ 0.002		
<i>Sargassum</i> sp.1	0.004 $\pm$ 0.004			
<i>Sargassum</i> sp.2			0.37 $\pm$ 0.08	
<i>Sargassum</i> sp.3				0.007 $\pm$ 0.007
<i>Sphaerococcus coronopifolius</i>	0.23 $\pm$ 0.11			
<i>Stypopodium zonale</i>			0.78 $\pm$ 0.13	<0.001
<i>Zonaria tournefortii</i>	29.65 $\pm$ 1.44		0.51 $\pm$ 0.21	
<b>Ephemeral macroalgae</b>				
<i>Canistrocarpus cervicornis</i>			1.30 $\pm$ 0.18	
<i>Codium vermilara</i>	0.008 $\pm$ 0.008			
<i>Colpomenia sinuosa</i>	1.20 $\pm$ 0.23	0.007 $\pm$ 0.003	0.06 $\pm$ 0.02	
<i>Dictyota bartayresiana</i>				0.22 $\pm$ 0.07
<i>Dictyota crenulata</i>			0.01 $\pm$ 0.006	
<i>Dictyota dichotoma</i>	16.95 $\pm$ 0.99		0.39 $\pm$ 0.05	17.09 $\pm$ 0.92
<i>Dictyota fasciola</i>			0.006 $\pm$ 0.002	
<i>Dictyota implexa</i>				0.33 $\pm$ 0.08
<i>Dictyota jamaicensis</i>				0.05 $\pm$ 0.02
<i>Dictyota linearis</i>			0.005 $\pm$ 0.003	
<i>Dictyota menstrualis</i>				0.01 $\pm$ 0.006
<i>Dictyota pfaffii</i>			0.23 $\pm$ 0.03	0.04 $\pm$ 0.01
<i>Dictyota pulchella</i>			0.006 $\pm$ 0.004	
<i>Dictyota</i> sp.			<0.001	
<i>Dictyota</i> sp.1		0.29 $\pm$ 2.09		
<i>Dictyopteris delicatula</i>				0.36 $\pm$ 0.07
<i>Ganonema lubrica</i>				
<i>Ganonema farinosa</i>				0.01 $\pm$ 0.01
<i>Halymenia</i> sp.				0.01 $\pm$ 0.01
<i>Hydroclathrus clathratus</i>		0.012 $\pm$ 0.39	0.003 $\pm$ 0.001	
<i>Liagora distenta</i>			0.001 $\pm$ 0.001	
<i>Liagora tetrasporifera</i>	0.12 $\pm$ 0.08		0.17 $\pm$ 0.07	
<i>Liagora</i> sp.		0.27 $\pm$ 3.30		
<i>Liebmannia leveillei</i>	0.008 $\pm$ 0.008			
<i>Padina pavonica</i>	1.02 $\pm$ 0.21	0.18 $\pm$ 0.04	0.22 $\pm$ 0.05	
<i>Rosenvingeia intricata</i>				0.001 $\pm$ 0.001
<i>Scinaia</i> sp.	0.004 $\pm$ 0.004			
<i>Scinaia complanata</i>	0.02 $\pm$ 0.02			
<i>Taonia atomaria</i>			0.02 $\pm$ 0.01	
<b>Filaments and small turfs</b>				
<i>Aglaozonia parvula</i>	0.35 $\pm$ 0.10			
<i>Anadyomene saldanhae</i>	0.08 $\pm$ 0.02			
<i>Anadyomene stellata</i>				0.08 $\pm$ 0.03
<i>Asparagopsis</i> sp. (sporophyte)			<0.001	<0.001
<i>Asteromenia peltata</i>	0.004 $\pm$ 0.004			
<i>Bryopsis hypnoides</i>			<0.001	
<i>Bryopsis</i> sp.				<0.001
<i>Caulerpa webbiana</i>		0.013 $\pm$ 0.007	<0.001	
<i>Chaetomorpha</i> sp.			0.003 $\pm$ 0.002	
<i>Champia parvula</i>				0.003 $\pm$ 0.03

(Continued)

Table 2. (Continued).

	Azores	Madeira	Canaries	Cape Verde
<i>Chlorodesmis</i> sp.				0.06±0.02
<i>Chondria</i> sp.				<0.001
<i>Cladophora liebethuthii</i>			0.03±0.02	
<i>Cladophora</i> sp.	0.28±0.17			
<i>Coelothrix irregularis</i>				<0.001
<i>Cottoniella filamentosa</i>	0.52±0.16	2.90±0.43	0.25±0.07	0.08±0.05
Cyanophytes ( <i>Blenothrix</i> spp., <i>Lyngbya</i> spp., <i>Schizothrix</i> spp.)		0.003±0.051	0.19±0.02	1.42±0.18
<i>Dasya hutchinsiae</i>			0.005±0.002	
<i>Dasycladus vermicularis</i>		0.032±0.009	0.002±0.009	
<i>Derbesia</i> sp.				<0.001
<i>Ernodesmis verticillata</i>			0.03±0.009	
<i>Gelidiopsis intricata</i>			0.03±0.008	0.45±0.06
Filamentous macroalgae ( <i>Aglaothamnion</i> spp., <i>Anotrichium</i> spp., <i>Ceramium</i> spp., <i>Crouania</i> , <i>Herposiphonia</i> spp., <i>Polysiphonia</i> spp.)	4.04±0.58	12.43±0.87	0.43±0.04	0.83±0.07
<i>Gelidium pusillum</i>			0.005±0.005	
<i>Halopithys incurvus</i>		1.08±0.26		
<i>Halydictyon mirabile</i>				<0.001
<i>Heterosiphonia crispella</i>			<0.001	<0.001
<i>Hypnea spinella</i>			0.003±0.001	0.04±0.17
<i>Laurencia dendroidea</i>			0.005±0.003	0.20±0.04
<i>Laurencia</i> sp.1				0.001±0.001
<i>Laurencia</i> sp.2			<0.001	
<i>Lophocladia trichoclados</i>		1.00±7.69	1.24±0.25	5.07±0.35
<i>Meredithia microphylla</i>	0.26±0.13			
<i>Microdictyon calodictyon</i>			0.002±0.002	
<i>Nemacystus hispanicus</i>			<0.001	
<i>Neomeris annulata</i>				0.04±0.01
<i>Parvocaulis polyphysoides</i>			<0.001	
<i>Parvocaulis</i> sp.		0.10±0.02		
<i>Platysiphonia caribaea</i>				<0.001
<i>Pseudochlorodesmis furcellata</i>			0.11±0.01	0.001±0.001
<i>Pseudotetraspora marina</i>			0.20±0.05	
<i>Pterosiphonia pennata</i>			0.002±0.002	
<i>Rhodymenia holmesii</i>			<0.001	
<i>Sphacelaria cirrosa</i>			0.006±0.003	
<i>Sphacelaria rigidula</i>			0.001±0.001	
<i>Spyridia hypnoides</i>			0.012±0.006	
<i>Ulva rigida</i>		0.007±0.004		
<i>Valonia utricularis</i>		0.019±0.010		
<i>Ventricaria ventricosa</i>				<0.001
<i>Wrangelia argus</i>			0.02±0.01	
<i>Wrangelia penicillata</i>			0.004±0.003	
<b>Erect calcified macroalgae</b>				
<i>Amphiroa fragilissima</i>			0.06±0.01	2.80±0.26
<i>Corallina caespitosa</i>	5.91±0.68		0.03±0.01	
<i>Corallina</i> sp.		0.009±0.006		
<i>Galaxaura rugosa</i>			0.02±0.01	0.01±0.01
<i>Halimeda tuna</i>				0.03±0.03
<i>Halitilton virgatum</i>			0.10±0.02	
<i>Jania pumila</i>			0.04±0.01	
<i>Jania</i> spp. ( <i>J. adhaerens</i> , <i>J. capillacea</i> )	5.52±0.70		1.64±0.16	0.19±0.09
Unidentified erect calcified		0.04±0.73		

\*Currently regarded as a synonym of *Gelidium spinosum* (S.G.Gmelin) P.C.Silva (Guiry & Guiry, 2017).

In order to identify the contribution of each predictor variable to the spatial variability of macroalgae among Macaronesian archipelagos, a distance-based linear model routine (DistLM; Legendre & Anderson, 1999) was applied. This method performs multivariate multiple regressions on the basis of any distance measure, making a forward selection of the predictor variables, either individually or in specified sets, with tests by permutation. In our study, the DistLM analysis was based on similarity matrices of macroalgal cover data and data from the 10 environmental variables selected (detailed above). The method used stepwise selection, an adjusted  $R^2$  criterion and 9999

permutations. Prior to the DistLM analysis, the draftsman plot method with the corresponding Pearson's correlation coefficients was used to explore the relationships between environmental variables (Clarke & Gorley, 2006). The draftsman plot test was performed so that any strongly correlated predictor variables ( $R > 0.5$ ) could be excluded. In our case, high collinearity meant that SSTmean and Chl *a* were excluded from the DistLM. Following recommendations by Clarke & Gorley (2006), macroalgal cover data were square-root transformed and environmental variable data were normalized. A distance-based redundancy analysis (dbRDA) was used to

visualize the relationship between macroalgal data and predictor variables, which is the best way to represent the multivariate regression model and multidimensional space generated by the DistLM analysis in a simplified, two-dimensional plot (McArdle & Anderson, 2001). These analyses show the percentage cover of the 15 most abundant taxa.

All statistical analyses were performed using PRIMER-E® v.6 + PERMANOVA+ ([www.primer-e.com](http://www.primer-e.com); Clarke & Gorley, 2006).

## Results

Analyses of the dataset for macroalgal cover showed significant variation for all factors: 'archipelago', 'island' and 'site' (Table 3a). An *a posteriori* test for 'archipelago' showed that there were significant differences between all pairs of archipelagos, except between Madeira and the Canaries (Table 3b). For the term 'island', significant differences in the structure of macroalgal assemblages was found between most islands within each archipelago (Supplementary table 1S). The SIMPER procedure (Table 3c) revealed

that variation in the abundance of *Zonaria tournefortii*, crustose coralline algae, *Dictyota dichotoma*, filamentous algae, *Halopteris scoparia*, *Lobophora variegata* and *Lophocladia trichoclados* explained most of the spatial variability in macroalgal assemblage structure between archipelagos. Inspection of the nMDS (Fig. 2) showed that samples from the Azores were clearly segregated from those from the remaining archipelagos, while those from Madeira and the Canaries partly overlapped. The same analysis also revealed a wide dispersion (high variability) among sites within each archipelago, except in Cape Verde where samples tended to overlap closely. The nMDS island ordination (Fig. 3a) showed a significant separation between groups of islands belonging to each archipelago, especially for the Azores, which were apart from the remainder. Within each archipelago, islands were generally grouped together, except in Madeira, where Madeira itself and Porto Santo appeared segregated. Hierarchical cluster analysis (Fig. 3b) showed that islands belonging to the same archipelago were in the same clade; at 50% similarity, the islands within the Azores, Canaries and Cape

**Table 3.** (a) Results of distance-based permutational three-way PERMANOVA comparing algal assemblages structure using 'archipelago' (four levels) fixed factors, 'island' (15 levels) as random factor nested in 'archipelago', and 'site' (145 levels; see Fig. 1) as random factor nested in 'archipelago' and 'island'. (b) Results of pairwise analyses for the factor 'archipelago'. (c) SIMPER procedure shows species that most contribute to the differences in algal assemblages between archipelagos.

(a) PERMANOVA analysis					
Source of variation	df	MS	Pseudo- <i>F</i>	<i>P</i> (perm)	
Ar	3	6.5493E5	4.287	0.0002	
Is(Ar)	11	1.3225E5	6.357	0.0002	
Si(Is(Ar))	130	20447	16.957	0.0002	
Res	2824	1205.8			
Total					
(b) Pairwise analyses					
	<i>t</i>		<i>P</i>		
Az - Ma	1.811		0.0088		
Az - Ca	3.231		0.0002		
Az - CV	2.979		0.0002		
Ma - Ca	1.292		0.0956		
Ma - CV	1.773		0.036		
Ca - CV	2.238		0.0006		
(c) SIMPER analyses					
	Dissimilarity (%)				
	Az - Ma	Az - Ca	Az - CV	Ma - CV	Ca - CV
<i>Zonaria tournefortii</i>	17.99	15.07	14.46		
Crustose coralline algae	14.30	15.82	22.07	22.68	16.32
<i>Dictyota dichotoma</i>	13.49	11.27	11.86	18.53	17.33
Filamentous algae	8.61	3.44	4.24	9.11	3.28
<i>Halopteris scoparia</i>	7.70	4.89	4.68	3.18	
<i>Jania</i> spp.	6.65	5.04	3.34	4.82	3.36
<i>Dictyota pfaflfii</i>	3.95			4.45	
<i>Halopteris filicina</i>	3.86	3.27	3.19		
<i>Corallina caespitosa</i>	3.64	3.16	3.06		
<i>Lobophora variegata</i>		11.56			14.03
<i>Pseudolithoderma adriaticum</i>		2.73			3.22
<i>Asparagopsis armata</i>		2.64	2.59		
<i>Asparagopsis taxiformis</i>		2.06			
<i>Lophocladia trichoclados</i>			7.12	9.82	8.96
<i>Amphiroa fragilissima</i>			4.17	5.52	5.19
Cyanophytes				3.35	3.38
<i>Gelidiopsis intricata</i>					2.19
<i>Canistrocarpus cervicornis</i>					1.85
<i>Caulerpa racemosa</i>					1.69

Ar = Archipelago, Is = island, Si = site, Az = Azores, Ma = Madeira, Ca = Canaries, CV = Cape Verde.



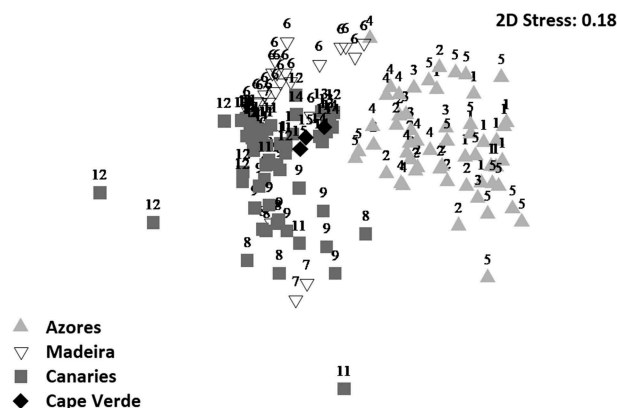


Fig. 2. Non-metric MDS ordination based on the mean percentage cover of macroalgal species at each of the sites studied with numbers indicating islands (see Fig. 1).

Verde were close together. Only the islands of Madeira and Porto Santo showed lower similarity, although they shared the same clade.

The composition and relative abundance of species differed from one archipelago to another (Table 2). In the Azores, the communities were dominated by *Z. tournefortii* and *D. dichotoma* with a mean percentage cover ( $\pm$  SE) of  $29.65 \pm 1.44$  and  $16.95 \pm 0.99\%$  respectively. Other taxa such as crustose coralline algae, *Halopteris scoparia*, *Corallina caespitosa*, *Jania* spp. and *H. filicina* were common elements in the communities of this archipelago. In Madeira, the dominant species were the crustose coralline ( $15.96 \pm 0.68\%$ ) and filamentous ( $12.43 \pm 0.87\%$ ) algae, followed by others such as *H. filicina*, *H. scoparia* and *Cottoniella filamentosa*. In the Canaries, the most important taxa were the crustose coralline algae ( $26.95 \pm 0.93\%$ ), *L. variegata* ( $22.88 \pm 1.15\%$ ), and *C. abies-marina*, *Cystoseira compressa*, *Jania* spp., *Canistrocarpus cervicornis* and *L. trichoclados*. However in Cape Verde, the communities were dominated by crustose coralline algae ( $48.40 \pm 0.96\%$ ) and *D. dichotoma* ( $17.09 \pm 0.92\%$ ), followed by *L. trichoclados*, *Amphiroa fragilissima*, cyanophytes, *Caulerpa racemosa* and filamentous algae.

Variation in cover of the non-crustose macroalgae and macroalgal morpho-functional groups depended on spatial scale. The abundance of non-crustose macroalgae varied significantly among 'archipelagos', 'islands' and 'sites' (Table 4). Cover was greatest in the Azores (Fig. 4, Table 4); *a posteriori* tests showed significant differences between the Azores and the other archipelagos (Table 4). Within each archipelago, variation in non-crustose macroalgal cover between islands was particularly high in Madeira and the Canaries (Supplementary table 2S, Fig. 5), whilst no significant variation was found at this scale in Cape Verde. The cover of crustose macroalgae varied significantly among 'archipelagos', 'islands' and 'sites' (Table 4). The cover of these

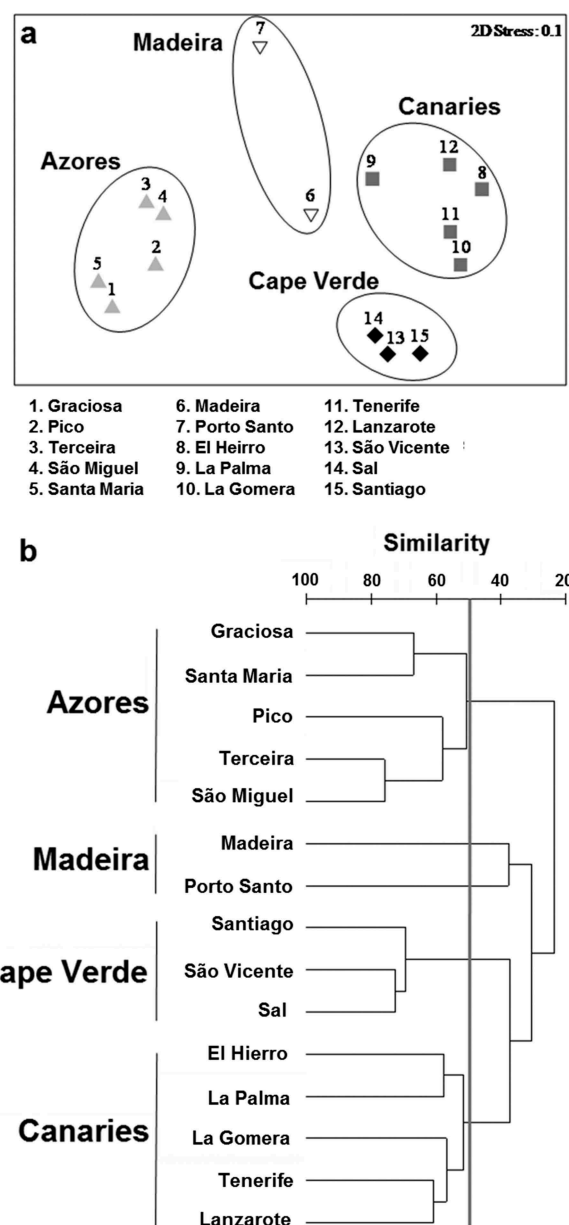


Fig. 3. Non-metric MDS ordination (a), and hierarchical cluster analysis (b) based on the mean percentage cover of macroalgal species at each of the islands studied.

macroalgae generally increased from the Azores to Cape Verde (Fig. 4). *A posteriori* tests showed there was significant variation between the Azores and the other archipelagos, between Madeira and Cape Verde and also between the Canaries and Cape Verde (Table 4). Significant variation in the cover of crustose macroalgae at the scale of islands was particular great in the Azores and Madeira (Supplementary table 2S, Fig. 5). The cover of perennial and semi-perennial macroalgae also varied significantly at the three spatial scales examined (Table 4). The largest cover of these algae was recorded in the Azores, followed by the Canaries (Fig. 4); *a posteriori* tests found significant variation between the pairs Azores–Madeira and Azores–Cape Verde (Table 4). At the scale of islands, variation in the cover of perennial

**Table 4.** Results of distance-based permutational three-way ANOVAs comparing the percentage of macroalgal cover of different groups using ‘archipelago’ (four levels) fixed factors, ‘island’ (15 levels) as random factor nested in ‘archipelago’, and ‘site’ (145 levels; see Fig. 1) as random factor nested in ‘archipelago’ and ‘island’; and results of pairwise analyses for the factor ‘archipelago’.

Non-crustose macroalgae							
ANOVA analysis					Pairwise analyses		
Source of variation	df	MS	Pseudo- <i>F</i>	<i>P</i> (perm)		<i>t</i>	<i>P</i>
Ar	3	2427.20	3.290	0.036	Az - Ma	2.983	0.010
Is(Ar)	11	638.94	6.463	0.0002	Az - Ca	3.164	0.007
Si(Is(Ar))	130	97.16	20.679	0.0002	Az - CV	8.186	0.0002
Res	2680	4.69			Ma - Ca	0.090	0.932
Total	2824				Ma - CV	0.236	0.841
					Ca - CV	0.331	0.754
Crustose macroalgae							
ANOVA analysis					Pairwise analyses		
Source of variation	df	MS	Pseudo- <i>F</i>	<i>P</i> (perm)		<i>t</i>	<i>P</i>
Ar	3	2263.7	6.400	0.003	Az - Ma	0.828	0.449
Is(Ar)	11	304.51	5.378	0.0002	Az - Ca	3.465	0.005
Si(Is(Ar))	130	55.65	19.438	0.0002	Az - CV	5.195	0.0004
Res	2680	2.86			Ma - Ca	1.698	0.115
Total	2824				Ma - CV	3.366	0.023
					Ca - CV	2.201	0.041
Perennial and semi-perennial macroalgae							
ANOVA analysis					Pairwise analyses		
Source of variation	df	MS	Pseudo- <i>F</i>	<i>P</i> (perm)		<i>t</i>	<i>P</i>
Ar	3	2683.30	3.990	0.017	Az - Ma	4.244	0.001
Is(Ar)	11	581.87	6.317	0.0002	Az - Ca	1.088	0.304
Si(Is(Ar))	130	90.52	27.113	0.0002	Az - CV	5.293	0.0002
Res	2680	3.33			Ma - Ca	1.347	0.194
Total	2824				Ma - CV	0.614	0.606
					Ca - CV	1.677	0.120
Ephemeral macroalgae							
ANOVA analysis					Pairwise analyses		
Source of variation	df	MS	Pseudo- <i>F</i>	<i>P</i> (perm)		<i>t</i>	<i>P</i>
Ar	3	976.59	2.913	0.056			
Is(Ar)	11	293.03	9.601	0.0002			
Si(Is(Ar))	130	29.99	13.556	0.0002			
Res	2680	2.21					
Total	2824						
Filaments and small turfs							
ANOVA analysis					Pairwise analyses		
Source of variation	df	MS	Pseudo- <i>F</i>	<i>P</i> (perm)		<i>t</i>	<i>P</i>
Ar	3	184.49	0.940	0.434			
Is(Ar)	11	165.77	3.035	0.008			
Si(Is(Ar))	130	53.69	13.236	0.0002			
Res	2680	4.050					
Total	2824						
Erect calcified macroalgae							
ANOVA analysis					Pairwise analyses		
Source of variation	df	MS	Pseudo- <i>F</i>	<i>P</i> (perm)		<i>t</i>	<i>P</i>
Ar	3	105.12	0.2933	0.824			
Is(Ar)	11	317.43	15.29	0.0002			
Si(Is(Ar))	130	20.39	9.938	0.0002			
Res	2680	2.05					
Total	2824						

and semi-perennial macroalgae was particularly high in the Canaries (Supplementary table 2S, Fig. 5), while values were more similar in the other archipelagos. The cover of ephemeral macroalgae, filaments and small turfs, and erect calcified macroalgae only varied significantly at the scale of islands and sites (Table 4, Fig. 4). At the scale of islands there was significant variation in their cover in about 40% of the comparisons (Supplementary table 2S, Fig. 5). The relative abundance of the morpho-functional

groups (Fig. 6a) and their relative contribution to total algal cover (Fig. 6b) showed clear changes in macroalgal community structure across the study region. Some of these changes followed a clear latitudinal gradient, most obviously for the crustose macroalgae, with a progressive increase from Azores to Cape Verde. An inverse pattern was also found to some extent for perennial and semi-perennial macroalgae, although mean values were lower in Madeira than in the Canaries. Erect calcified macroalgae also

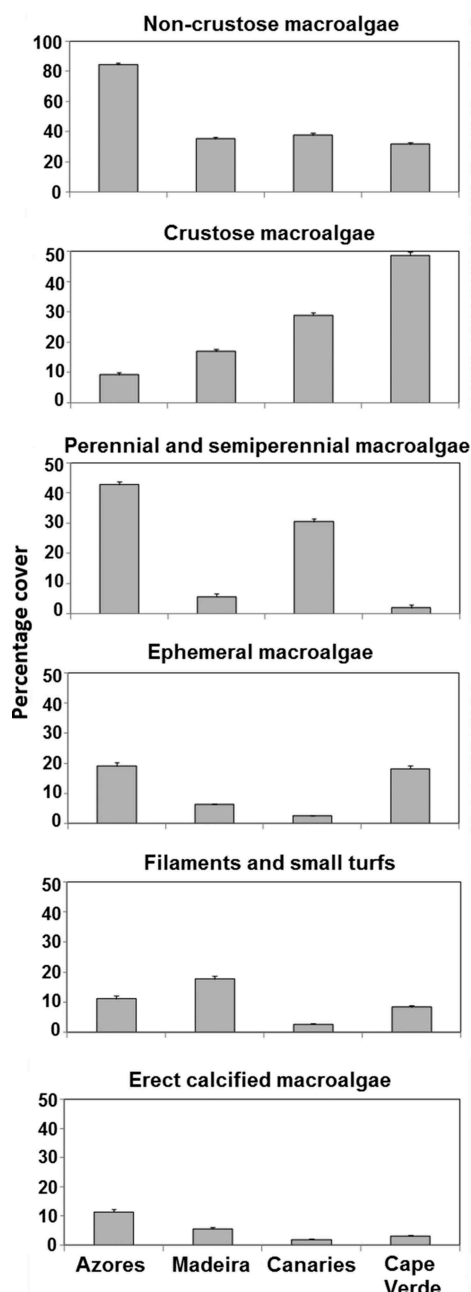


Fig. 4. Percentage cover of non-crustose macroalgae and each functional group in the archipelagos studied.

decreased towards the Canaries and Cape Verde, although, as revealed by ANOVAs, there were no significant variations among archipelagos. Lastly the contribution of ephemeral macroalgae, and filaments and small turfs was dissimilar between archipelagos.

The DistLM analysis detected significant variation between macroalgal assemblage structure and all predictor variables, except for latitude (Table 5). Marginal tests (Table 5a) revealed significant variation in the structure of macroalgal assemblages and also in each variable alone. The relative contribution of each environmental variable to macroalgal assemblage structure was as follows: sea urchin diversity (21.18%), nitrate (20.32%), PAR (19.85%), SSTmin (18.90%), human population (12.15%), island size (11.97%) and herbivorous fish

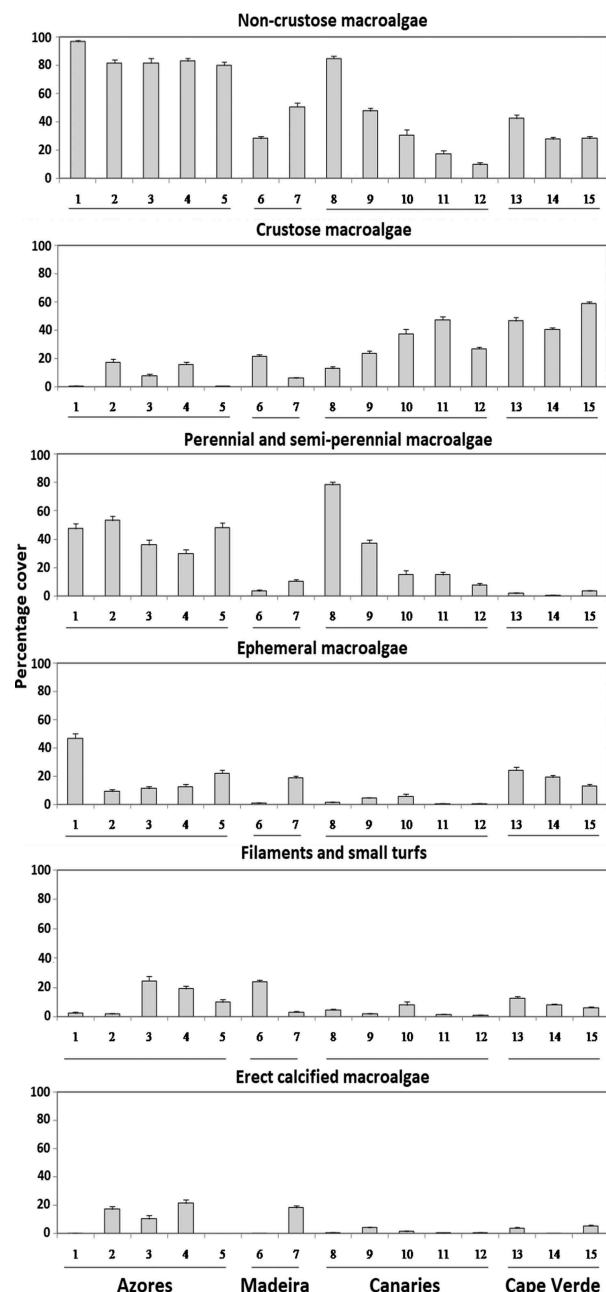


Fig. 5. Percentage cover of non-crustose macroalgae and each functional group in the studied islands.

(5.36%). The sequential test (Table 5b) evaluating the effect of all predictor variables combined found the following contributions: sea urchin (14.57%), island size (11.97%), herbivorous fish (9.61%), SSTmin (4.46%), human population (2.10%), PAR (1.77%) and nitrate (1.19%). These seven variables explained 45.70% of the total variability. The dbRDA analysis (Fig. 7a) showed that island size, sea urchins, SSTmin and PAR were partially positively correlated with the first axis, while nitrate was partially negatively correlated. Herbivorous fish and human population were partially negatively correlated with the second axis. The ordination plot also showed that samples from the Azores segregated from the remaining archipelagos along the first axis, while Madeira, the Canaries and Cape Verde

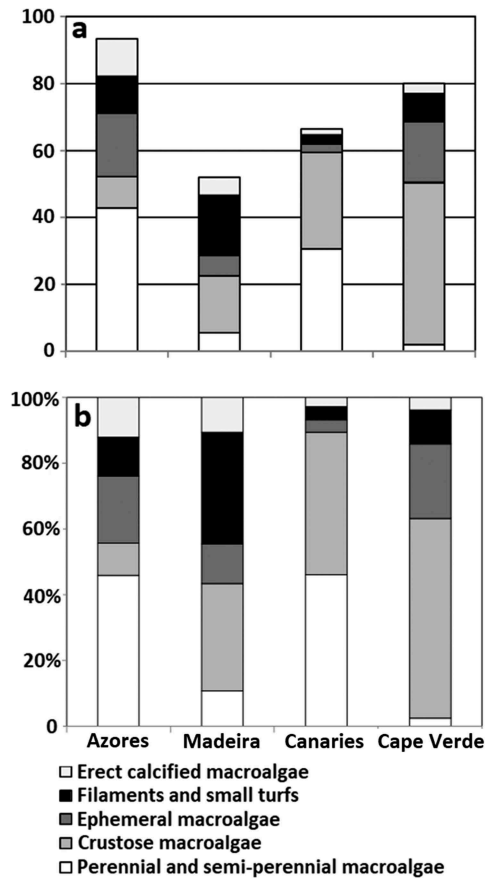


Fig. 6. Cumulative abundance (percentage cover) of each functional group in the archipelagos studied (a); and their contribution (%) to the total macroalgal cover (b).

were mainly ordered along the second axis. The overlaid trajectory of variation in algal cover (Fig. 7b) showed that *Z. tournefortii*, *C. caespitosa*, *H. scoparia*, *H. filicina*, *Asparagopsis taxiformis*, *Asparagopsis armata*, *Jania* spp., *C. filamentosa* and *D. dichotoma* increased their cover along the negative values of the first axis. Crustose coralline algae and *L. trichoclados* showed a partial correlation with positive values on the first axis and with negative values on the second axis. *Lobophora variegata* was partially correlated with positive values on both axes. Filamentous macroalgae increased their cover following negative values of the second axis.

## Discussion

Analyses of the macroalgal assemblage structure based on the entire species dataset (PERMANOVA) showed high spatial variability across the NE Atlantic archipelagos, with significant variation in the structure of macroalgal assemblages detected at all the spatial scales considered (archipelago, island and site). At the largest spatial scale of archipelagos, significant variation was found among all archipelagos except between Madeira and the Canaries, the two geographically closest archipelagos. Such large-scale variation in community structure at spatial scales > 1000 km was previously

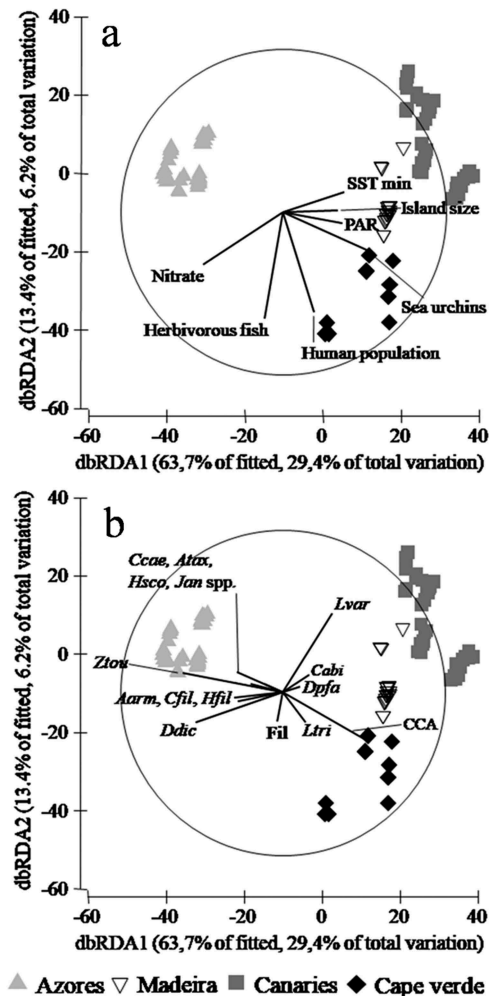


Fig. 7. Distance-based redundancy analysis (dbRDA). (a) Relationships between the ordination of samples based on species cover and predictor variables. (b) Direction of increasing cover of the most abundant taxa. *Ztou* = *Zonaria tournefortii*, CCA = crustose coralline algae, *Lvar* = *Lobophora variegata*, *Ddic* = *Dictyota dichotoma*, *Hsco* = *Halopteris scoparia*, *Hfil* = *Halopteris filicina*, *Atax* = *Asparagopsis taxiformis*, *Aarm* = *Asparagopsis armata*, *Ccae* = *Corallina caespitosa*, *Jan* spp. = *Jania* spp., *Cfil* = *Cottoniella filamentosa*, *Dpfa* = *Dictyota pfaffii*, *Ltri* = *Lophocladia trichoclados*, *Fil* = filamentous macroalgae.

documented elsewhere for both intertidal (Blanchette *et al.*, 2008) and subtidal (Schiel, 2011; Wernberg *et al.*, 2011; Porter *et al.*, 2013) macroalgae. As found in those studies, there can be dramatic changes over wide latitudinal gradients in the relative abundance of species, which dominate some sites and are scarce or absent in others. In our case, such large-scale variation was mostly generated by variation in the relative abundance of a few taxa like *Z. tournefortii*, crustose coralline algae, *D. dichotoma*, filamentous algae, *H. scoparia*, *L. variegata* and *L. trichoclados*. Our results suggest that the structure of macroalgal communities in Macaronesia can be divided into three large groups: the Azores, Madeira plus Canaries, and Cape Verde.

**Table 5.** Results of DistLM (distance-based linear model routine) considering species cover. (a) Test for relationships between individual predictor variables and species cover. (b) Test for relationships between predictor variables and species cover considering all environmental variables integrated in a multiple regression model.

(a) Marginal test				
Variable	Pseudo- <i>F</i>	<i>P</i>	% var	
SSTmin	33.339	0.0001	18.90	
Nitrate	36.471	0.0001	20.32	
PAR	35.428	0.0001	19.85	
Sea urchin	38.446	0.0001	21.18	
Herbivorous fish	8.109	0.0001	5.36	
Latitude	0.989	0.4314	0.68	
Island size	19.460	0.0001	11.97	
Human population	19.790	0.0001	12.15	
(b) Sequential test				
Variable	Pseudo- <i>F</i>	<i>P</i>	% var	Com. % var
Sea urchin	28.181	0.0001	14.57	14.57
Island size	19.460	0.0001	11.97	26.55
Herbivorous fish	21.249	0.0001	9.61	36.17
SSTmin	10.544	0.0001	4.46	40.63
Human population	5.330	0.0001	2.10	42.74
PAR	4.344	0.0001	1.77	44.51
Nitrate	2.853	0.0003	1.19	45.70

Although we have not included data for the Selvagens in this study, these islets could probably be included in the Madeira–Canaries group.

As expected, variation in the structure of macroalgal assemblages among islands (within archipelagos) was lower than variation among islands belonging to different archipelagos. The above grouping of Macaronesian archipelagos differs from that obtained using presence/absence data by Prud'homme van Reine & van den Hoek (1990) who included Madeira, Canaries and Azores as part of the same clade (60% similarity). On the one hand, the macroalgal assemblage structure of the Azores resembles that of warm temperate areas of the north-eastern Atlantic and Mediterranean (Guiry & Guiry, 2017) dominated by species such as *Z. tournefortii*, *H. scoparia*, *H. filicina* and *C. caespitosa*. Although there are kelp populations, these are restricted to certain deep-water biotopes (Amorim *et al.*, 2015). On the other hand, Cape Verde supports an assemblage of macroalgae dominated by tropical taxa, e.g. crustose coralline algae, cyanophytes, *A. fragilissima*, *Caulerpa* spp. and *L. trichoclados*. Despite such differences, the abundance of some taxa was remarkably similar among archipelagos, which could be evidence of a larger Macaronesian grouping. For instance, the cover of *Dictyota dichotoma* was similar in the Azores and Cape Verde (the two most distant archipelagos). This may reflect this species' ability to tolerate a wide range of environmental conditions such as temperature (Eggert, 2012). Indeed, its cover was, surprisingly, much lower in Madeira and the Canaries. It is however possible that the taxon '*Dictyota dichotoma*'

comprises more than one species, as in the case for other *Dictyota* 'species' in the region (Tronholm *et al.*, 2010). The macroalgal assemblages of the Canaries and Madeira occupy an intermediate position between the warm temperate and tropical regions, as already suggested for the Canaries (Sangil *et al.*, 2011). In these archipelagos, taxa with affinity for colder waters (e.g. *Cystoseira* spp. and *H. scoparia*) coexist with those preferring warmer waters (e.g. *L. variegata*, *L. trichoclados* and *C. cervicornis*).

Crustose coralline algae were grouped together owing to difficult *in situ* identification, but differentiating them to species level would probably have contributed to a more comprehensive biogeographic differentiation among archipelagos, since it is an especially diverse and variable group of species (Sangil *et al.*, 2014b). Apart from crustose corallines, Dictyotales were the most abundant group and best reflected the variation among Macaronesian archipelagos. Larger and longer-lived species were replaced by short-lived species from north to south: the perennial species *Z. tournefortii* dominated in the Azores, the semi-perennial *L. variegata* in the Canary Islands, and the ephemeral *D. dichotoma* in Cape Verde. Similar variation has also been described for the Fucales in New Zealand and South Western Australia (Wernberg *et al.*, 2003; Schiel, 2011), where larger species with greater longevity are replaced by smaller and shorter-lived species toward warmer latitudes. It is well known that the biogeographic distribution of macroalgae is directly influenced by climate (Bartsch *et al.*, 2012). Temperature can have strong effects on the geographic distribution of macroalgae, and is often assumed to be the main abiotic driver in species abundances (Eggert, 2012). In our study, it is very likely that differences in macroalgal assemblage structure across the Macaronesian archipelagos were a response to temperature changes, although the potential role of factors other than temperature cannot be ruled out.

Multivariate analysis also showed significant variation in macroalgal assemblage structure at the scale of islands and sites. In the Canaries, variability in the structure of macroalgal communities among islands has previously been attributed to the longitudinal thermal gradient (2°C) across the archipelago, as well as to variation in the population sizes of *Diadema africanum* (Hernández *et al.*, 2008; Sangil *et al.*, 2011), the main benthic herbivore around the Canaries and Madeira (Hernández *et al.*, 2012). In the Azores, it has been shown that variation at the scale of islands may be based on differences in the biotopes (Martins *et al.*, 2008; Wallenstein *et al.*, 2008). Although not tested to date, temperature could also contribute to differences among the Azores, although the thermal gradient from east to west is smaller there (1°C). In Madeira, variation between Madeira itself



and Porto Santo may be caused by their geomorphological differences: sedimentary environments predominate on the latter, which would prevent high densities of *D. africanum* (Hernández *et al.*, 2008). At the scale of sites, differences in community structure have been linked to changes in wave exposure (Tuya & Haroun, 2006) and sedimentation, besides their interaction with local densities of *D. africanum* (Hernández *et al.*, 2008; Sangil *et al.*, 2011). Depth and wave exposure were also identified as important factors for community structure in the Azores (Martins *et al.*, 2013), whereas in Madeira, wave exposure, sedimentation, depth and grazing by *D. africanum* have been identified as the main variables affecting macroalgal communities (Bianchi *et al.*, 1998; Alves *et al.*, 2001). Cape Verde was the archipelago with the greatest similarity in community structure among islands (e.g. no significant differences were found between São Vicente and Sal or between sites). It is possible that spatial variation in environmental conditions is lower there, however sampling effort in this archipelago was also lower.

The grouping of macroalgal species into different functional groups, a tool employed in biogeographic studies (e.g. Schils *et al.*, 2013), reveals additional spatial patterns. Although differences between some groups were greater than others, in temperate and warm-temperate regions non-crustose macroalgae are favoured over sessile organisms due to temperature, nutrient concentration and lower herbivore pressure (Johannes *et al.*, 1983; Wohlenberg-Miller, 1998). In our results, non-crustose macroalgal cover was significantly greater in the Azores, where it exceeded 80%. This contrasts with the rest of the archipelagos, where cover did not reach 40%. The inverse pattern was observed in crustose macroalgae, which could be related to grazing pressure increasing latitudinally towards Cape Verde, mainly due to sea urchins. Under these conditions the crustose morphotype has a major competitive advantage, since herbivores are unable to consume them easily (Carpenter, 1986; Andrew, 1993). Although there was variation in the abundance of perennial and semi-perennial macroalgae among archipelagos, the latitudinal pattern was not as clear. Ephemeral macroalgae, filaments and small turfs, and erect calcified macroalgae did not vary among archipelagos; perhaps this was due to their overall lower abundance, hence low statistical contribution. Variation in the abundance of morpho-functional groups at the smaller spatial scales of islands and sites was also high. Spatial variation was particularly noticeable in Madeira and Canaries for non-crustose, crustose, perennial and semi-perennial macroalgae, which were most closely correlated with variation in the densities of *D. africanum*.

The multiple regression models (DistLM analysis) showed that variability in community structure was significantly related to all the variables considered, except latitude. This is probably due to the longitudinal gradients generated in some archipelagos like the Canaries (see Sangil *et al.*, 2014a), which blur latitudinal changes in their structure. When considered separately, the environmental variables SSTmin, nitrate concentration, PAR and sea-urchin richness were the most significant contributors to community variation. However, when considered together, herbivore richness (both urchin and fish) and island size explained most of the spatial variation. The two regression models (separated or combined variables) point to the role of environmental variables (SSTmin, nitrate concentration, PAR) and herbivory as the principal drivers of change throughout the Macaronesian archipelagos. The dbRDA analysis showed the varying influence of the different variables on the archipelagos. All factors, except nitrate concentration, were opposed or partially opposed to the samples from the Azores, which at the same time were positioned apart from those from the rest of the archipelagos. These parameters are presumably the cause of macroalgal communities in the Azores being significantly different from the rest. Here, community development is linked to the lowest water temperature, mesotrophic waters and the least solar radiation reaching the bottom. As already noted here, these factors may cause these macroalgal communities to become lusher, with higher cover and predominance of perennial elements. Herbivores are less diverse in the Azores, and although grazing by the urchins *Paracentrotus lividus* and *Arbacia lixula* has been demonstrated in warm-temperate ecosystems (Bulleri *et al.*, 1999), their ability to control macroalgal growth is not comparable to *D. africanum*. This large urchin causes extensive urchin barrens, particularly in Madeira and the Canaries (Alves *et al.*, 2001; Hernández *et al.*, 2008). Although *D. africanum* has recently been found in the Azores, in Santa Maria, the southernmost island (Minderlein & Wirtz, 2014), it is virtually absent elsewhere in that archipelago. Specialized fish herbivores are also scarce there (Harmelin-Vivien *et al.*, 2001; Menezes *et al.*, 2006). The worldwide negative relationship between latitude and richness and relative abundance of herbivorous fishes has been discussed extensively (Floeter *et al.*, 2005). Towards the south, it is clear that macroalgal community structure is driven by synergies between environmental factors, especially temperature and grazing. In the tropics, interactions between macroalgae and herbivores may be more important than the environmental conditions affecting them (Keith *et al.*, 2014). Indeed, temperate macroalgae produce significantly lower concentrations of defensive compounds

than their tropical sister species (Hay, 1998). In Madeira and the Canaries urchin grazing generates two types of subtidal vegetation (Hernández *et al.*, 2008): urchin barrens dominated by crustose algal communities when the sea-urchin density is  $> 2\text{--}2.5$  individuals  $\text{m}^{-2}$  and upright macroalgal beds when the density is low (Sangil *et al.*, 2014a). Fish seem to have little ability to control macroalgal communities (González *et al.*, 2012), although a more experimental approach is necessary to test this. The *D. africanum* density in Cape Verde is generally lower than 1 individual  $\text{m}^{-2}$  (Entrambasaguas *et al.*, 2008), in contrast to Madeira and Canaries where it can reach 3–4 individuals  $\text{m}^{-2}$  (Alves *et al.*, 2001; Hernández *et al.*, 2008). However, herbivorous fish in Cape Verde are more diverse and more abundant (authors' unpublished data), e.g. there are three species of scarids, two surgeonfish and one damselfish, all absent from the other archipelagos. In any case, both temperature and grazing are higher in Cape Verde. The temperature increase would favour the development of species with tropical affinities (Bolton *et al.*, 2004), and herbivores would promote the development of crustose macroalgae via the elimination of perennial macroalgal species. On the other hand, the higher primary productivity in the tropics permits the development of macroalgae with high turnover rates (Ferreira *et al.*, 2004), which in Cape Verde are represented by filamentous macroalgae (mainly *Ceramiales*) and *L. trichoclados*. Nutrient concentrations, due to local oceanographic conditions, are greater in the Azores and Cape Verde, which may be correlated with more abundant filamentous species and small turfs. Human population is essentially a variable that explains differences among islands within each archipelago (see dbRDA analysis). In the Canaries, this variable was strongly correlated with *D. africanum* densities at each island, which probably reflect trophic cascades: greater human population, greater fishing intensity and a consequent lower abundance of *D. africanum* predators (Hernández *et al.*, 2008). Finally, island size could be related to the environmental diversity of each island, which results in more variable communities at the scale of sites.

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## Disclosure statement

No potential conflict of interest was reported by the author(s).

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## Author contributions

C. Sangil: original concept, data, data analysis, drafting and editing manuscript; G. M. Martins: data and editing manuscript; J.C. Hernández: data, drafting and editing manuscript; F. Alves: data; A. I. Neto: data; C. Ribeiro: data; K. León-Cisneros: data; J. Canning-Clode: data; E. Rosas-Alquicira: data; J.C. Mendoza: data; I Tittley: data; F. Wallenstein: data; R. P. Couto: data; M. Kaufmann: data and editing manuscript.

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