



# Limited effects of marine protected areas on the distribution of invasive species, despite positive effects on diversity in shallow-water marine communities

Eva Cacabelos · Gustavo M. Martins · João Faria · Afonso C. L. Prestes · Tarso Costa · Ignacio Moreu · Ana I. Neto

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**Abstract** Marine protected areas (MPAs) can be an effective tool for the conservation and management of marine coastal habitats. MPAs have been shown to halt habitat degradation, enhance the biomass of exploited species and diversity in general. Yet, we still know little about its role in halting the spread of non-native species. In this study, we assessed the role of MPAs in the structure of shallow subtidal communities around São Miguel Island, in general, and particularly on distribution of the two species of genus *Asparagopsis*: *A. armata* and *A. taxiformis*. In the Azores, the former is a well-established invasive

species, whereas the status of *A. taxiformis* is still questionable. Overall, there was a significant greater diversity in terms of both species richness and number of macroalgal functional groups within MPAs. However, when considering the relative abundance of the various macroalgal functional groups, or the assemblage as a whole (multivariate analysis), there was no significant difference between areas within and outside MPAs. The cover of *A. taxiformis* was significantly greater within MPAs but not its biomass, whereas no significant variation was observed for *A. armata*. Overall, results suggest that surveyed MPAs had a positive effect on the diversity of shallow-water macroalgal communities. However, they have a limited role on the distribution of both *Asparagopsis* spp. and negligible effects when considering the relative abundances of macroalgal functional groups.

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E. Cacabelos (✉)  
MARE – Marine and Environmental Sciences Centre,  
Quinta do Lorde Marina, 9200-044 Caniçal,  
Madeira Island, Portugal  
e-mail: ecacabelos@mare-centre.pt

E. Cacabelos · G. M. Martins · J. Faria ·  
A. C. L. Prestes · T. Costa · I. Moreu · A. I. Neto  
Azorean Biodiversity Group, cE3c - Centre for Ecology,  
Evolution and Environmental Changes,  
9500-321 Ponta Delgada, Açores, Portugal

J. Faria · A. C. L. Prestes · T. Costa · I. Moreu ·  
A. I. Neto  
Departamento de Biologia, Faculdade de Ciências e  
Tecnologia, Universidade dos Açores,  
9500-321 Ponta Delgada, Açores, Portugal

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## Introduction

Many disturbed marine ecosystems worldwide are associated with habitat degradation, biodiversity loss, impairment of ecosystem functionality or with the spread of non-indigenous species (NIS) (Gianni et al. 2018). Marine protected areas (MPA) are an important

tool in coastal management, essential for ensuring the conservation of marine biodiversity and biomass, protecting or reducing degradation of habitats and ecosystems and for the maintenance of ecosystem functioning and resilience (Salm et al. 2000; FAO 2011; Bennet and Dearden 2014). MPAs can also have a positive impact on the local environment and economy benefiting local human populations (e.g. FAO 2011; Russi et al. 2016). MPAs are commonly used around the world to, via direct and indirect pathways, restore ecosystem services (e.g. coastal protection, fisheries, and opportunities for recreation and education, Leenhardt et al. 2015). MPAs have been found to be effective at increasing abundances, sizes, and biodiversity in coastal marine assemblages (e.g. Fraschetti et al. 2005; Micheli et al. 2005 and references therein, Alves et al. 2018; Topor et al. 2019) and limit the colonization success of invasive species (e.g. Ardura et al. 2016; Gestoso et al. 2017). MPAs can also assist in restoring the herbivory and maintenance of corals (Leenhardt et al. 2015), or in recovering sea urchin predators, in turn preventing overgrazing and leading to the recovery of macroalgal canopies (Sala et al. 1998; Goriup 2017). In the Azores, the established MPA network is also of key importance, providing several opportunities to enhance marine conservation, reducing user conflicts, and promoting sustainable development and research, although it must be effectively implemented and integrated into a wider marine management strategy for the region to achieve conservation goals (Abecasis et al. 2015).

On temperate rocky reefs, macroalgae are the main biological ecosystem engineers (Steneck et al. 2002; Neto et al. 2005) and play an important structuring role in intertidal and shallow subtidal communities by providing sheltering and substrate for a diverse suite of organisms (Davidson and Pearson 1996; Jenkins et al. 1999; Neto et al. 2005; Christie et al. 2009). Different pre- and post-recruitment processes, as well as environmental conditions or disturbances (see Sala et al. 1998; Tuya and Haroun 2006 and references therein) can influence the composition, distribution and structure of algal assemblages.

In the Azores, shallow subtidal macroalgal communities have been shown to be dominated by species with warm-temperate affinities (Sangil et al. 2018) and several NIS have been reported in the Azorean marine ecosystems (Cardigos et al. 2006). Among

macroalgae, the red alga *Asparagopsis armata* Harvey is probably the most conspicuous and widespread invasive macroalga present across the whole archipelago (Neto 1994; Cardigos et al. 2006; Martins et al. 2019a, b). Native to southern Australia and New Zealand (Horridge 1951), the first confirmed record of *A. armata* in the Azores dates back to 1952 (Tittley and Neto 2005). The species is currently widely distributed throughout the Atlantic and Mediterranean coasts from the British Isles to Senegal (Ní Chualáin et al. 2004; Andreakis et al. 2007a). The co-generic species *Asparagopsis taxiformis* (Delile) Trevisan was considered cosmopolitan in warm-temperate to tropical waters (Ní Chualáin et al. 2004). However, recent studies suggest that the highly invasive Indo-Pacific Mediterranean lineage (Lineage 2 in Andreakis et al. 2016), dominant in the central Mediterranean, has expanded its range to the southern coasts of Portugal (Andreakis et al. 2007a, b; Dijoux et al. 2014), representing a cryptic invasion in the Azores (Andreakis et al. 2016), co-existing here with the Atlantic lineage (Lineage 3 in Andreakis et al. 2016). The diploid epiphytic tetrasporophyte of both species is known as the 'Falkenbergia' stage, a small "pompon" that can be only distinguished by quantitative morphological features (Zanolla et al. 2014), and therefore never during field sampling.

Despite the wide distribution and spread rate of the *Asparagopsis* complex across the Macaronesian archipelagos, little is yet known about their potential ecological and/or economic impact, acting in isolation or in synchrony (but see Pacios et al. 2011; Guerra-García et al. 2012; Katsanevakis et al. 2014; Martins et al. 2019a, b). Analyses of its distribution are scarce (but see Martins et al. 2019a, b), although crucial to understand the drivers of its distribution (Underwood 1993). Studies of NIS often reveal that the invader seems to perform better than congeners in the invaded communities (Colautti et al. 2004), and, moreover, species with similar patterns of resource use and habitat requirements (as e.g. *A. armata* and *A. taxiformis*) are expected to increase interspecific competition.

Quantitative studies can be very useful in detecting changes in community structure, e.g. regarding the relative abundance of key species and associated ecosystem processes (Sangil et al. 2018). In the present study, a quantitative visual sampling, with a special focus on *Asparagopsis* spp., was done to

investigate the role of marine protected areas in structuring shallow subtidal macroalgal communities in general, and the distribution of *Asparagopsis* spp. in particular. Considering the effects of MPAs elsewhere (see description above), we hypothesized a greater abundance of canopy forming algae and overall diversity within MPAs, which in turn, would reduce the invasibility of macroalgal assemblages.

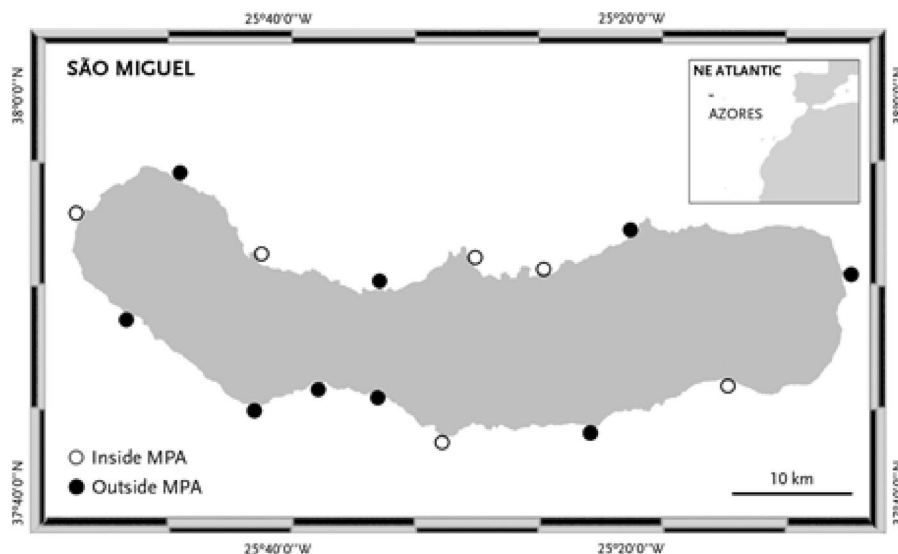
## Methods

### Study site and benthic community

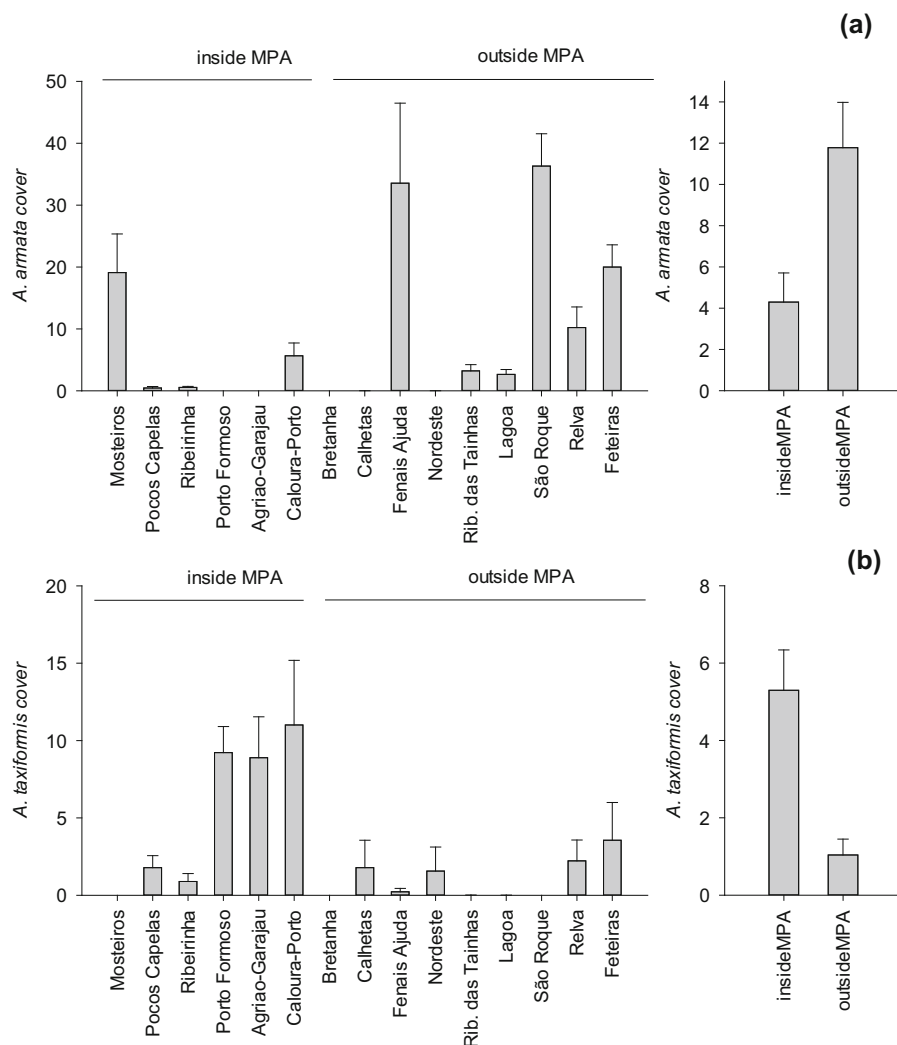
This study was done in São Miguel Island, Azores (37°51' to 37°42' N and 25°51' to 25°08' W, Fig. 1). Rocky shore shallow-water (5 m depth) benthic assemblages in the Azores are mostly dominated by macroalgae. The most abundant organisms at this depth include articulated calcareous (e.g. *Ellisolandia elongata* (J. Ellis & Solander) K.R. Hind), encrusting calcareous (e.g. *Lithophyllum* sp.), coarsely branched algae (e.g. *Halopteris scoparia* (Linnaeus) Sauvageau), and corticated foliose algae (e.g. *Dictyota* spp.) (Martins et al. 2008). This is also the depth at which the gametophytic phase of the invasive *A. armata* attains its highest biomass during its seasonal peak in abundance in late spring/early summer (Neto 2000, 2001).

### Sampling design

To examine the patterns of distribution of *A. armata* and *A. taxiformis* and associated assemblages across protected and non-protected areas of São Miguel Island, 15 exposed locations separated by kilometres were randomly sampled. Six of them were located within and nine outside marine protected areas (MPA) (Fig. 1). Within each location, nine quadrats of 50 × 50 cm were haphazardly placed on the sea bottom (a few metres apart). The assemblage in each quadrat was visually sampled using the method of Dethier et al. (1993) where a score of 0 (absent) to 4 (filled = 4%) was given to each taxa within each of the twenty-five 10 × 10 cm subquadrats. Organisms filling less than ¼ (= 1%) of all the twenty-five subquadrats were recorded as rare and later ascribed an arbitrary score of 0.5%. The specimens of the gametophytes *Asparagopsis* spp. present on the sampling quadrats were then collected for later determination of dry biomass. At the laboratory, samples were sorted (*A. armata* and *A. taxiformis*), cleaned of epiphytes, individually oven dried at 60 °C for 48 h and then weighted. All sampling was done between 22 and 30 June 2017, during the peak of *A. armata* abundance.



**Fig. 1** Sampled locations across the island. White dots indicate locations included within marine protected areas and black dots location with no protection status



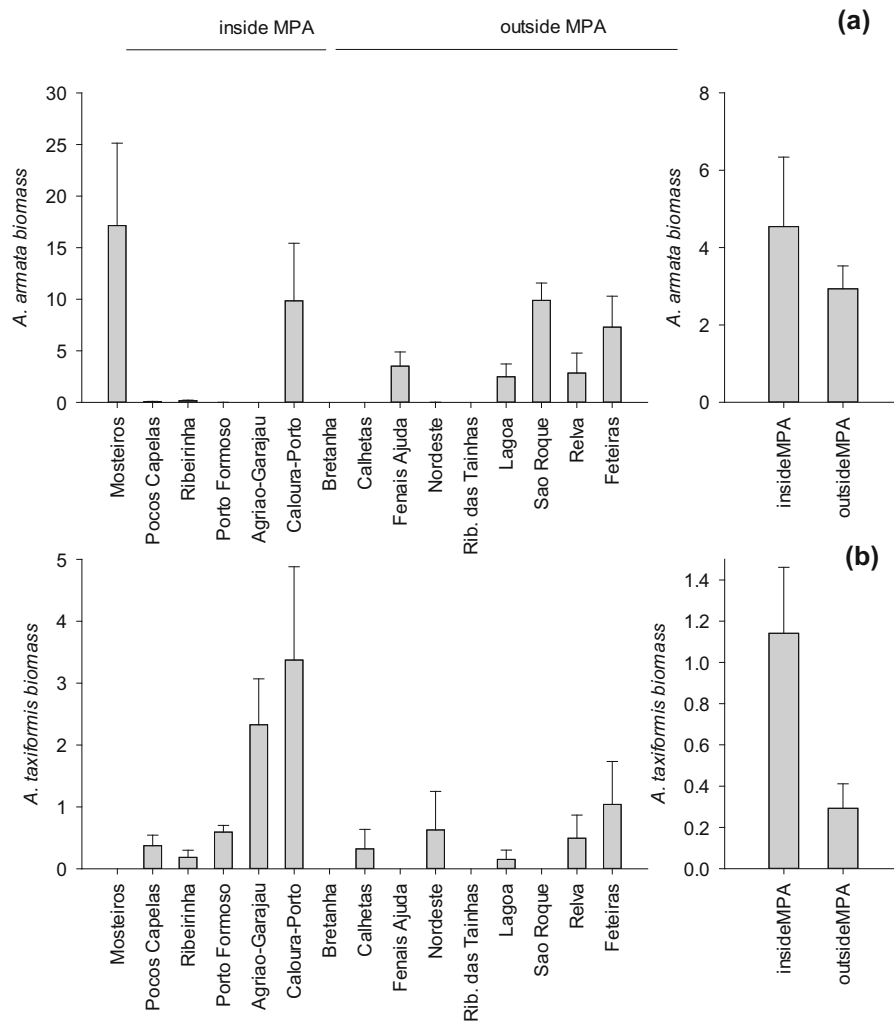
**Fig. 2** Mean (+SE) percentage cover of **a** *Asparagopsis armata* and **b** *Asparagopsis taxiformis* at the sampled locations both inside or outside marine protected areas (MPA)

### Data analysis

The algal assemblage was grouped into 7 morpho-functional groups (FG) adapted from Steneck and Dethier (1994): articulated calcareous algae (e.g. *Ellisolandia elongata*, *Jania* spp.), canopy forming algae (e.g. *Sargassum* spp., *Cystoseira* spp.), coarsely branched algae (e.g. *Halopteris* spp., *Plocamium cartilagineum*), corticated foliose algae (e.g. *Dictyota* spp.), encrusting algae (including both calcareous and non-calcareous species), foliose algae (e.g. *Ulva rigida*) and filamentous algae (e.g. *Cladophora* spp., *Polysiphonia* spp.).

To examine the role of MPA on the species richness and number of FG of macroalgae as well as on the abundance of *Asparagopsis* spp. (biomass and percentage cover) and each FG (percentage cover), we used a 2-way permutational ANOVA, with Protection as a fixed factor (2 levels) and Location as a random factor nested in Protection (PERMANOVA, Anderson 2001). PERMANOVA was run on Euclidean distances with 999 permutations. Prior to analysis, PERMDISP was used to check data for heterogeneity of variances, and transformations were applied where necessary.

Differences between protected and unprotected areas in the structure of assemblages were investigated as a whole using a similar design by running a



**Fig. 3** Mean (+SE) biomass (g of dry mass per 0.25 m<sup>2</sup>) of **a** *Asparagopsis armata* and **b** *Asparagopsis taxiformis* at the sampled locations, located inside or outside marine protected areas (MPA)

PERMANOVA using a Bray–Curtis similarity matrix of fourth-root transformed data (Clarke and Warwick 1994).

All analyses were run on the PRIMER-E v6 + PERMANOVA add-on (Clarke and Gorley 2006).

**Results**

The percentage cover of *A. armata* and *A. taxiformis* varied substantially across the island ranging between 0 and 36.33 ± 5.21 (mean ± SE) for *A. armata* and between 0 and 11.01 ± 4.18 for *A. taxiformis* (Fig. 2). Similarly, the biomass of *A. armata* and *A. taxiformis*

ranged between 0 and 17.15 ± 7.99 g (mean ± SE) and between 0 and 3.37 ± 1.51 g, respectively (Fig. 3). Percentage cover of *A. taxiformis* varied significantly with levels of protection (inside vs. outside MPA) and locations (*p* < 0.05 and 0.001 respectively; Table 1, Fig. 2) and was, overall, significantly greater inside MPAs (Fig. 2; percentage covers of 5.30 ± 1.03 vs. 1.04 ± 0.41). This difference between levels of protection, however, was not statistically significant when considering its biomass (*p* = 0.08; Table 1). In the case of *A. armata*, neither the percentage cover or its biomass varied significantly with protection (*p* = 0.28 and 0.64 respectively), although there was significant variation among

**Table 1** Permutational ANOVA comparing the percentage covers and biomass of *Asparagopsis armata* and *Asparagopsis taxiformis*, and the number of algal taxa (S) and functional groups (N FG) inside and outside marine protected areas (MPAs) and locations

	Source	df	MS	F	p
<i>Asparagopsis armata</i> cover	Protection	1	1814.6	1.307	0.28
	Location (Protection)	13	1388.3	8.779	<b>0.001</b>
	Residual	120	158.14		
P(perm) PERMDISP: 0.084					
<i>Asparagopsis taxiformis</i> cover	Protection	1	587.4	6.321	<b>0.027</b>
	Location (Protection)	13	92.94	3.724	<b>0.001</b>
	Residual	120	24.95		
P(perm) PERMDISP: 0.119					
<i>Asparagopsis armata</i> biomass	Protection	1	83.70	0.328	0.64
	Location (Protection)	13	254.87	3.731	<b>0.001</b>
	Residual	120	68.30		
P(perm) PERMDISP: 0.133					
<i>Asparagopsis taxiformis</i> biomass	Protection	1	23.34	3.188	0.084
	Location (Protection)	13	7.32	3.043	<b>0.002</b>
	Residual	120	2.41		
P(perm) PERMDISP: 0.062					
S	Protection	1	183.95	15.189	<b>0.001</b>
	Location (Protection)	13	12.11	4.984	<b>0.001</b>
	Residual	120	2.43		
P(perm) PERMDISP: 0.584					
N FG	Protection	1	47.91	14.384	<b>0.007</b>
	Location (Protection)	13	3.33	4.355	<b>0.001</b>
	Residual	120	0.7648		
P(perm) PERMDISP: 0.160					

Significant *p* values (< 0.05) are in bold  
*df* degrees of freedom, *MS* mean squares

locations ( $p < 0.001$  in both cases; Table 1; Figs. 2, 3).

A significant greater number of species and FGs found were found inside MPAs (mean  $\pm$  SE, species richness: inside MPA  $7.19 \pm 0.28$ , outside MPAs  $4.80 \pm 0.19$ ; Number of Functional Groups: inside MPAs  $4.72 \pm 0.92$ , outside MPAs  $3.51 \pm 0.11$ ;  $p < 0.001$  and  $p < 0.01$  respectively; Table 1, Fig. 4).

No significant variation was found on the abundance of the different macroalgal FGs with protection, although there was significant spatial variation in their abundance among locations (Table 2, Suppl. material).

When considering the macroalgal assemblage as a whole (multivariate data), there was also no significant variation in the structure of the macroalgal assemblage between MPAs and unprotected areas ( $p = 0.248$  considering all taxa and  $p = 0.426$  considering functional groups; Table 3).

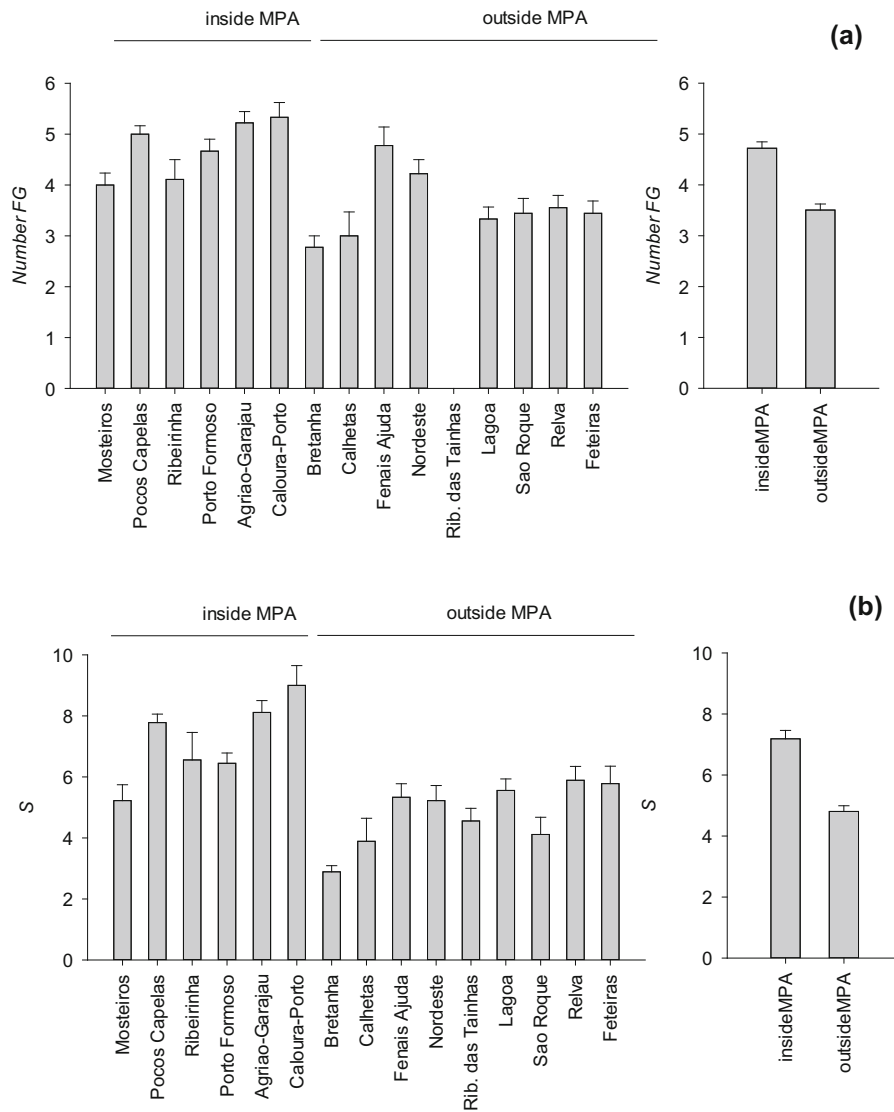
## Discussion

This study reveals a significant greater diversity, both in terms of species richness and numbers of macroalgal functional groups, inside MPA. This result is in accordance with the established idea that MPAs can

have a positive effect of the diversity of marine coastal habitats (Fraschetti et al. 2005; Gaines et al. 2010; Leenhardt et al. 2015). However, there was limited evidence, in our study, that MPAs influenced the relative abundance of macroalgal species. Moreover, there was limited evidence that MPAs had any effect on the distribution of species of *Asparagopsis*. Such a result is unexpected considering the biotic resistance hypothesis (Elton 1958), whereby more diverse communities are thought to be less susceptible to invasion because of a more complete utilization of resources, a result that has also been experimentally shown by Arenas et al. (2006). Such lack of effect of MPAs on the distribution of *A. armata* however, has also been documented by other authors (e.g. Blanco et al. 2018).

The role of MPA in preventing biological invasions, especially macroalgae, and the mechanistic importance of diversity in determining invasion success is poorly understood (Stachowicz et al. 2002; Blanco et al. 2018), when compared to other factors, e.g. predation, disturbance, productivity or propagule supply, which can also play an important role in determining patterns of invader distribution (Stachowicz et al. 2002).

Many macroalgal species are vulnerable to herbivory, which can have a structuring role in macroalgal communities (Ruitton et al. 2000; Gianni et al.



**Fig. 4** Mean (+SE) **a** number de macroalgal morpho-functional groups (FG) and **b** number of macroalgal taxa (S) at the sampled locations, located inside or outside marine protected areas (MPA)

2017, 2018; Martins et al. 2019a, b). In this context, the removal of natural predators may directly or indirectly influence these macroalgae communities through trophic cascades (Micheli et al. 2008, Alves et al. 2018). For example, mass occurrence of sea urchins, caused by human activities that overexploit their predators, is responsible for the depletion of macroalgal communities and the subsequent formation of extensive barren grounds (Tuya and Haroun 2006; Northerhaug and Christie 2009; Gianni et al. 2017). Although we considered sea urchins in our sampling, these macro herbivores were recorded in

such low densities that they were not analysed nor reported here. Worth considering is the herbivore fishes influence on algal species abundance and dynamics, facilitating the seasonal dominance of chemically-defended algal population such as *A. armata* (e.g. Sala and Boudouresque 1997), or their recently highlighted importance of in controlling the sublittoral algae (Ruitton et al. 2000; Gianni et al. 2017, 2018). Herbivore fishes could be therefore playing an important role in structuring macroalgal assemblages at our sampled depth, as in the Azores the hovering herbivore *Sparisoma cretense* and the spard

**Table 2** Permutational ANOVA comparing the abundance of each FG inside and outside MPA and locations

	Source	df	MS	F	p
Coarsely branched algae P(perm) PERMDISP: 0.215	Protection	1	94.97	0.026	0.862
	Location(Protection)	13	3697.6	12.074	<b>0.001</b>
	Residual	120	306.26		
Foliose algae P(perm) PERMDISP: 0.417	Protection	1	0.02	0.687	0.428 (P(MC))
	Location(Protection)	13	0.03	1.019	0.455 (P(MC))
	Residual	120	0.03		
Corticated foliose algae P(perm) PERMDISP: 0.459	Protection	1	331.39	0.304	0.587
	Location(Protection)	13	1091.20	4.187	<b>0.001</b>
	Residual	120	260.59		
Canopy forming algae P(perm) PERMDISP: 0.446	Protection	1	398.37	0.0593	0.825
	Location(Protection)	13	6722.70	16.872	<b>0.001</b>
	Residual	120	398.46		
Filamentous algae P(perm) PERMDISP: 0.230	Protection	1	4031.2	1.207	0.305
	Location(Protection)	13	3339.7	18.597	<b>0.001</b>
	Residual	120	179.59		
Articulated calcareous algae P(perm) PERMDISP: 0.084 (Fourth root)	Protection	1	1.84	0.160	0.68
	Location(Protection)	13	11.52	44.458	<b>0.001</b>
	Residual	120	0.26		
Encrusting algae P(perm) PERMDISP: 0.054	Protection	1	194.43	0.080	0.816
	Location(Protection)	13	2426.5	12.501	<b>0.001</b>
	Residual	120	194.1		

Significant *p* values (< 0.05) are in bold

*df* degrees of freedom, *MS* mean squares

**Table 3** Multivariate Permutational ANOVA testing for the effects of protection over the structure of macroalgal assemblage, based on fourth root abundance data of different taxa and FG

	Source	df	MS	F	p
Assemblage (Taxa) P(perm) PERMDISP: 0.001	Protection	1	24,298	1.279	0.248
	Location(Protection)	13	18,992	27.543	<b>0.001</b>
	Residual	120	689.53		
Assemblage (FG) P(perm) PERMDISP: 0.001	Protection	1	8991.6	1.002	0.426
	Location(Protection)	13	8974.7	24.67	<b>0.001</b>
	Residual	120	363.78		

Significant *p* values (< 0.05) are in bold

*df* degrees of freedom, *MS* mean squares

*Sarpa salpa* had the highest mean densities at 6 m (0.11/m<sup>2</sup> and 0.09/m<sup>2</sup>) among herbivores (Bertoncini et al. 2010). Similar mean densities (between 0.2 ind/m<sup>2</sup> and 0.04 ind/m<sup>2</sup>) have been recorded in different areas of the Mediterranean Sea (Gianni et al. 2017 and references therein), showing that the conservation of marine vegetated habitats should take into

consideration the role of herbivorous fishes and the assessment of their densities in space and time (Gianni et al. 2017, 2018). Changes in fishing pressure acting on top predators and negatively cascading down the food web (Sala et al. 1998; Gianni et al. 2013) and increasing of thermal habitat suitability of *S. salpa* due to the rising sea surface temperature (Marras et al.



2015) can also increase herbivore pressure on canopy forming algae (Gianni et al. 2018).

It is unclear if any such processes could be responsible for camouflaging the potential effects of MPAs on the distribution of these invasive species, or the nature of the relationship between the two *Asparagopsis* spp. across time, taking in consideration that they have very different seasonal dynamics. Such study should assess biomass. Further observational and experimental work, currently underway, may help shed light on the mechanisms determining the seasonal distribution and potential competition of the complex *Asparagopsis* spp. in the Azores.

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