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Research Article

Patterns of distribution of the invasive alga *Asparagopsis armata* Harvey: a multi-scaled approach

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Abstract

Human activities are contributing to the homogenization of the world's biota by transporting thousands of species to areas outside their native range. Some of these species can lead to profound changes in the structure and function of natural ecosystems in areas where they are introduced, with dramatic economic and ecological impacts. The red alga *Asparagopsis armata* is considered an invasive species in Europe, but can be particularly abundant in the Azores (NE Atlantic), where there is virtually no information on its ecology. Here, we investigate the patterns of spatial distribution and impacts of *A. armata* in the Azores, as a first step to understand its potential spread. Adopting a hierarchical design, we surveyed the distribution of *A. armata*, and associated assemblages, at a range of spatial scales (from islands (10s of km apart), locations (kms apart), sites (10s of m apart) to quadrats (m apart)). Results showed that the abundance of *A. armata* varied significantly among locations and that there was substantial variability in its abundance among islands, locations and quadrats and little variability among sites. At the scale of locations, the abundance of *A. armata* did not correlate with any of our predictor variables (sea urchin density, Latitude, Longitude and sea temperature). However, at the quadrat scale, there was a significant and negative correlation between the abundance of *A. armata* and diversity of associated macrophytes, as well as, with the abundance of the conspecific *A. taxiformis* and the abundance of most of the remainder macroalgal groups. The potential role of biotic and abiotic factors in generating the observed patterns is discussed. This study further highlights the suitability of the analytical tools used here to examine patterns of distribution over a range of spatial scales and its applicability in the field of aquatic invasions.

Key words: Azores, hierarchical analysis, invasion, macroalgae, shallow-water macroalgal communities

Introduction

Human activities are contributing to the homogenisation of the world's biota by transporting thousands of species to areas outside their native range (Hallegraeff and Bolch 1992; Ruiz et al. 2000). Some of these species can overcome the ecological barriers of the new habitat and become

established. Such non-indigenous species are considered invasive, due to their dominance and rate of spread in the new habitat (Lonsdale 1999) and can potentially have significant ecological and economic impacts (Williamson 2006; Simberloff et al. 2013).

In the Azores (NE Atlantic archipelago), several non-indigenous species have been reported in terrestrial (Silva et al. 2008), freshwater (Raposeiro et al. 2012) and marine (Cardigos et al. 2006) ecosystems. Among the later, the red alga *Asparagopsis armata* Harvey, 1855 was first confirmed in the Azores in 1952 (Tittley and Neto 2005). This species is probably the most conspicuous and widespread of all the non-indigenous marine species reported so far, occurring in all the nine islands of the archipelago (Neto 1994; Cardigos et al. 2006). It has a diplohaplontic heteromorphic life cycle (Feldmann and Feldmann 1939, 1942; Chihara 1961, 1962), in which the free-living, filamentous diploid sporophyte (“Falkenbergia” stage) produces haploid spores via meiosis, and these develop into erect, usually benthonic, male or female haploid gametophytes that produce male or female gametes. Fertilization occurs on the female reproductive structures and gives rise to a diploid zygote that develops into a multicellular carposporophyte, which remains dependant on the female thallus (Feldmann and Feldmann 1939). The benthonic gametophytes are seasonal in the Azores, where they generally peak in abundance in late spring or early summer (Neto 1997, 2000).

Asparagopsis armata is thought to be native to southern Australia and New Zealand (Horridge 1951). In Europe, it is widely distributed throughout the Atlantic and Mediterranean coasts, from the British Isles to Senegal, including the Azores, Canary and Madeira Islands (Ni Chualáin et al. 2004; Andreakis et al. 2007), where it is considered an invasive species (South and Tittley 1986; Sala and Bouderesque 1997; Bouderesque and Verlaque 2002). Despite its wide distribution and spread rate, compared to other invasive seaweeds (i.e., *Caulerpa* spp.), little is known about its potential ecological and/or economic impacts (but see Pacios et al. 2011; Guerra-García et al. 2012; Katsanevakis et al. 2014; Nyberg and Wallentinus 2005). Analyses of its distribution across multiple spatial scales are even scarcer, although crucial to understand the drivers of its distribution, assess its potential impact and contribute for future management and mitigation strategies (Underwood 1993; Bishop et al. 2002). Grazers can play an important role in structuring macroalgal assemblages (Lubchenco and Gaines 1981; Hawkins and Hartnoll 1983). The alga *A. armata* is generally perceived as being relatively unpalatable to most herbivores although some studies report that sea hares, abalones and some fish can indeed feed on *A. armata* (Sala and Bouderesque 2002; Katsanevakis et al. 2014; Greff et al. 2017). Unlike the above, we still know little about the potential role of sea-urchins, which are regarded as key structuring agents of subtidal communities in temperate and tropical regions (Paine and Vadas 1969; Morrison 1988), in controlling the distribution of this species.

Table 1. Predictor variables at sampled locations.

Island	Location	Latitude (decimal degrees)	Longitude (decimal degrees)	Seawater temperature (°C)	Sea urchin density (n.m ⁻²) (mean ± SE)
Flores	Boqueirão	39.4630	31.1277	17	0.00 ± 0.00
	Ponta Delgada	39.5216	31.2066	17	0.00 ± 0.00
	São Pedro	39.4630	31.1330	17	0.35 ± 0.19
Pico	São Roque	38.5244	28.3144	17	0.00 ± 0.00
	Santa Cruz	38.4061	28.1858	17	0.40 ± 0.57
	São Caetano	38.4261	28.4205	17	0.15 ± 0.15
Terceira	Monte Brasil	38.6541	27.2300	16	0.05 ± 0.07
	Negrilo	38.6547	27.2816	15	0.00 ± 0.00
	Salga	38.6461	27.0977	16	0.00 ± 0.00
São Miguel	Galera	37.7072	25.5075	19	0.00 ± 0.00
	Caloura	37.7127	25.4955	19	0.00 ± 0.00
	Lagoa	37.7400	25.5733	20	0.00 ± 0.00

Three aspects are generally perceived as being important in determining the successful establishment of non-indigenous species in their new habitat: the biology of the non-indigenous species (species invasiveness), the number and frequency of introductions (propagule pressure) and the susceptibility of the recipient native community to invasion (community invasibility) (Lonsdale 1999; Vaz-Pinto et al. 2014a). Here we investigate the patterns of distribution of *A. armata* in the Azores at a range of spatial scales and assess its potential interaction with the remaining macroalgal and sea urchin communities. This is a preliminary first step to explore the influence of potential factors (e.g. competition and grazing pressure) driving its distribution and successful establishment in the Azores.

Materials and methods

Study site and community structure

The study was done in the Azorean archipelago, which comprises 9 volcanic islands organised into 3 groups (eastern, central and western) located between 37° to 40°N and 25° to 31°W (Table 1). Sampling was performed within shallow-water communities (5 m depth), which, in this region, are mostly dominated by macroalgae. The most abundant organisms at this depth include articulated corallines (e.g. *Ellisolandia elongata* (J.Ellis and Solander) K.R. Hind), encrusting corallines (e.g. *Lithophyllum* sp.), coarsely branched algae (e.g. *Halopteris scoparia* (Linnaeus) Sauvageau, *Asparagopsis taxiformis* (Delile) Trevisan) and corticated foliose algae (e.g. *Zonaria tournefortii* (J.V. Lamouroux) Montagne, *Dictyota* spp.) (Martins et al. 2013). 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

A spatially structured hierarchical design (Underwood and Chapman 1996) was adopted to examine the patterns of distribution of *A. armata* and

associated macroalgal assemblages at 4 islands separated by 65 to 515 km. Islands were randomly selected, but stratified to include at least one island per group (eastern, central and eastern), so that sampling spanned the entire length of the archipelago.

For each island, 3 exposed locations, separated by kilometres (5–40 km) were randomly selected. Within each location, 2 sites (10s of m apart) were randomly selected and within each site, 10 50 × 50 cm quadrats (metres apart) were haphazardly placed on the seabed at about 5 m depth. 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 25 10 × 10 cm subquadrats. Organisms filling overall less than $\frac{1}{4}$ (= 1%) of a single subquadrat were recorded as rare and later ascribed an arbitrary score of 0.5%. All sampling was done within a month (20th May to 23rd June 2017) during the peak of *A. armata* abundance.

At each location, we also recorded sea temperature at the seabed using a portable thermometer, latitude and longitude (Table 1). The density of conspicuous macroinvertebrate grazers, such as sea-urchins (e.g. *Sphaerechinus granularis*) was also recorded in 10 randomly laid 1 × 1 m quadrats per site to assess the relationship between the density of these species and the percentage cover of *A. armata* (Table 1).

Data analysis

To examine patterns of spatial variation in the distribution of the invasive alga *A. armata*, a 3-way fully nested permutational ANOVA (PERMANOVA, Anderson 2001) was used. Factors were island (random, 4 levels), location (random, 3 levels) and site (random, 2 levels) with 10 replicates. Logistical constraints meant that at one of the sampling sites, only 8 replicate quadrats (instead of 10) were sampled. For this reason, we used permutational ANOVA, rather than a traditional ANOVA, since the latter is more affected by unbalanced designs (Underwood 1997). Permutational ANOVA was run on Euclidean distances with 999 permutations. Prior to analysis, PERMDISP was used to check data for heterogeneity of variances. Since heterogeneity of variances persisted, even after attempts to transform the data, we ran the analyses on the untransformed data, but used a more conservative P-value ($\alpha = 0.01$) to determine significance. All analyses were run on the PRIMER-E v6 + PERMANOVA add-on (Clarke and Gorley 2006).

Mean squares (MS) estimates were used to assess the variation associated with each scale. This was done by dividing the difference between the MS of the term of interest and the MS of the term hierarchically below by the product of the levels of all terms below that of interest (Underwood and Chapman 1996; Fletcher and Underwood 2002). Estimates of spatial variations were reported as actual variances, to guarantee independence and allow comparisons with other studies, but also as relative percentages, to ascertain the relative contribution of each scale to the overall variability.

Table 2. Fully nested permutational ANOVA comparing *Asparagopsis armata* abundance at a hierarchy of spatial scales (islands, locations and sites) and the associated estimates of variance (ω^2) and their relative (%) contribution to each scale.

Source	df	MS	F	P	ω^2	%
Island	3	33537.00	3.02	0.056	377.95	33
Location (Island)	8	88756.00	38.09	0.001	545.40	47
Site (Island \times Location)	12	291.33	1.34	0.207	7.43	1
Residual	214	217.68			217.68	19

At the scale of quadrats, the Pearson Product-Moment Correlation (PPMC) was used to measure the strength of a linear association between the percentage cover of the invasive *A. armata* and the percentage cover of the associated flora. For this purpose, the algal assemblage was grouped into 7 morpho-functional groups adapted from Steneck and Dethier (1994): articulated coralline algae (e.g. *Ellisolandia elongata*, *Jania rubens*), canopy-forming algae (e.g. *Sargassum* spp., *Cystoseira* spp.), coarsely branched algae (*Asparagopsis taxiformis*, *Halopteris* spp., *Plocamium cartilagineum*), corticated foliose algae (e.g. *Dictyota* spp., *Zonaria tournefortii*), encrusting algae (including both calcareous and non-calcareous species), filamentous algae (e.g. *Cladophora* spp., *Polysiphonia* spp.) and coenocytic algae (e.g. *Codium* spp.). We also correlated: (i) the percentage cover of *A. armata* with the cover of *A. taxiformis*, to explore the possibility of competition between the invasive (*A. armata*) and the congeneric species complex (*A. taxiformis*); and (ii) the percentage cover of *A. armata* and total species number (richness) to explore the potential relationship between the extent of susceptibility of the existing community to invasion by *A. armata*.

At the scale of locations, we used PPMC to measure the strength of a linear association between the percentage cover of *A. armata* and sea temperature, latitude, longitude and the density of sea urchins. For this purpose, the percentage cover of *A. armata*, as well as, the densities of sea urchins were averaged among all quadrats ($n = 20$) within each location. This analysis was done only at the scale of locations since this was the only spatial scale at which there was significant variation in the abundance of *A. armata* (see Table 2).

PPMC derived P-values were corrected for multiple comparisons using the Holm-Bonferroni Sequential correction (Holm 1979) separately for analyses done at the scale of quadrats and locations.

Results

Across the islands, the percentage cover of *A. armata* ranged from 0.15 ± 0.10 to 77.30 ± 4.98 (mean \pm SE) (Figure 1). Despite the substantial variation between the islands, significant variation in the percentage cover of *A. armata* was only found at the scale of locations (i.e., km) (Table 2). The largest variation in the abundance of *A. armata* among locations ranged between 70.35 ± 4.49 in São Miguel, compared with 0.15 ± 0.10 in Pico Island.

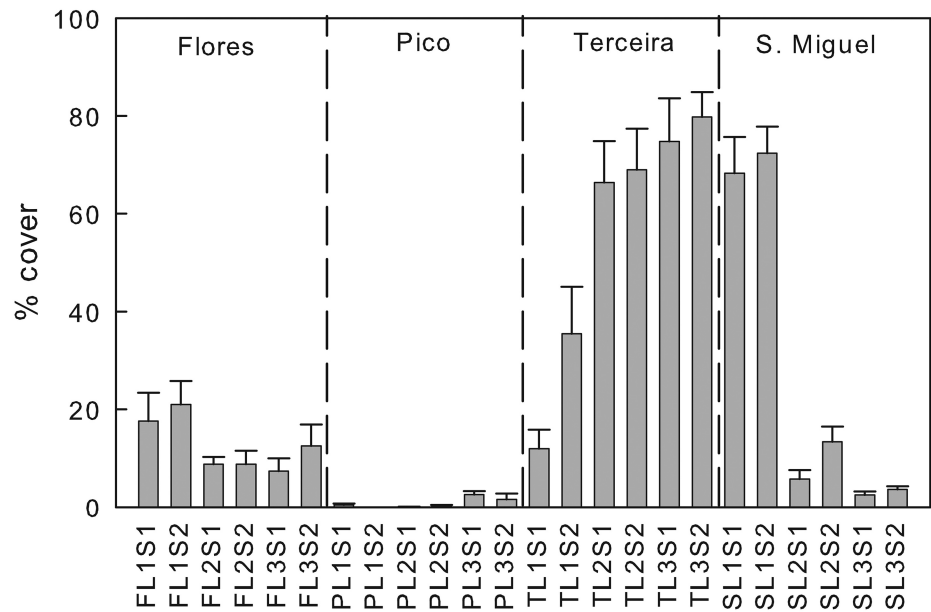


Figure 1. Mean (+SE) percentage cover of *Asparagopsis armata* at the sampled locations. Each bar is the mean cover in that site. First letter stands for island (F – Flores, P – Pico, T – Terceira and S – São Miguel); second letter stands for each of the three locations sampled within each island (L1 – Location 1, L2 – Location 2 and L3 – Location 3), and; third letter stands for each of the two sites sampled within each location (S1 – Site 1 and S2 – Site 2).

Table 3. Pearson Product-Moment Correlation between the percentage cover of *Asparagopsis armata* and the percentage cover of other macroalgal morpho-functional groups (at the scale of quadrats; 236 degrees of freedom) and environmental variables (at the scale of locations; 10 degrees of freedom). *P – Holm-Bonferroni sequentially corrected P-values. n.a. – not applicable. Significant correlation ($P < 0.05$) in bold.

	r	t	P	*P
Quadrat scale				
Algal richness	-0.69	-14.68	< 0.001	< 0.001
<i>Asparagopsis taxiformis</i>	-0.33	-5.33	< 0.001	< 0.001
Corticated foliose algae	-0.40	-6.72	< 0.001	< 0.001
Articulated coralline algae	-0.32	-5.27	< 0.001	< 0.001
Coarsely branched algae	-0.30	-4.84	< 0.001	< 0.001
Encrusting algae	-0.30	-4.83	< 0.001	< 0.001
Canopy-forming algae	-0.14	-2.21	0.028	0.056
Filamentous algae	-0.10	-1.51	0.132	0.134
Location scale				
Sea urchins	-0.38	-1.31	0.219	n.a.
Longitude	+0.34	1.14	0.279	n.a.
Sea temperature	-0.30	-1.01	0.338	n.a.
Latitude	-0.12	-0.38	0.710	n.a.

Inspection of the components of variation showed that variability in the abundance of *A. armata* was mostly associated with the scale of locations, islands and, to a smaller extent, quadrats (Table 2). Variability in the abundance of *A. armata* at the scale of sites was negligible.

At the quadrat scale, after the correction of P-values for multiple comparisons, the abundance of *A. armata* was negatively and significantly correlated with the abundance of the congeneric *A. taxiformis*, algal richness and the cover of articulated coralline, coarsely branched, corticated foliose and encrusting algae (Table 3). The only groups of algae that did not correlate with *A. armata* were canopy-forming algae and filamentous algae (Table 3).

At the scale of locations, none of our predictor variables (temperature, latitude, longitude and sea urchin density, see Table 1) significantly correlated with the abundance of *A. armata* (Table 3).

Discussion

Characterization of spatial scales of variation is a preliminary step to the experimental testing of a hypothesis. It allows the identification of the appropriate scales of variation, ensuring that attention is focused on the most relevant processes (Underwood and Chapman 1996; Benedetti-Cecchi 2001; Martins et al. 2008). The present study shows that, in the Azores, the abundance of the invasive alga *A. armata* varies mostly at the scale of locations (i.e. km). This result suggests that processes operating at the km scale are potentially the main drivers of the distribution of this invasive alga, a pattern that is widely common among subtidal taxa (Fraschetti et al. 2005; Tuya and Haroun 2006; Martins et al. 2013). Unlike in the Azores (our study), Tuya and Haroun (2006), only found significant variation in the cover of *Asparagopsis* spp. at the scale of sites in the Canaries. It should be noted, however, that these authors collapsed the two congeneric species (*A. armata* and *A. taxiformis*) into a single group for analysis, and so comparability between studies is not straightforward.

Despite the observed significant variation in the distribution of *A. armata* among locations, none of our studied variables significantly correlated with its abundance at this spatial scale. Therefore, variations in sea temperature among locations, factors associated with changes in latitude and longitude, as well as variation in the abundance of grazers (sea urchins) among locations are unlikely to explain the observed variability in the cover of *A. armata*. Although not directly measured in this study, changes in exposure to wave action among locations, are also unlikely to explain the observed variation in the abundance of *A. armata* (Tuya and Haroun 2006; Martins et al. 2013). The ability of this species, however, to disperse with water currents, either during its tetrasporophyte stage ("*Falkenbergia rufolanosa*") or gametophyte stage attached to floating objects, suggests that shoreline configuration and local currents may play an important role in determining its distribution at the location (km) scale (Archambault and Bourget 1999). However, the exact process which determines the distribution of *A. armata* in the Azores still requires further investigation.

Biological interactions (e.g. competition, predation) can also play an important role in determining the distribution of species (i.e. Connell 1961; Dayton 1971; Menge 1976; Steneck et al. 1991; Benedetti-Cecchi et al. 2001) and are often associated with distributional changes occurring at the smaller spatial scales of quadrats (but see also i.e. Ritchie et al. 2009; Wisz et al. 2013 for evidence of the role of biotic interactions in determining the distribution of species and assemblages at larger spatial scales). In agreement

to this, we found a number of significant and interesting correlations between the abundance of *A. armata* and the remaining biota at the scale of quadrats.

First, we found a negative correlation between the abundance of *A. armata* and algal richness. This result is in agreement with the idea that more diverse communities should be less susceptible to invasion because of a more complete utilization of resources; a concept that is known as “biotic resistance” proposed by Elton (1958). Despite the intuitive nature of this concept, observational studies attempting to relate the frequency of invasion to community diversity are scale-dependent, showing variable, and even contrary results, with more diverse communities having more, not fewer, non-indigenous species (e.g., Lonsdale 1999), constituting the so-called “invasion paradox” (Fridley et al. 2007). Moreover, experimental approaches appear to suggest that species identities, particularly the identity of macroalgal functional groups, may be more important than richness in determining the ability of macroalgal communities to resist invasion (Arenas et al. 2006). It is thus unclear whether this pattern is evidence of biotic resistance or something else. Another potential explanation for the negative correlation between the abundance of *A. armata* and diversity is that the former may have a strong negative influence in the remaining macroalgal assemblage, in turn, leading to a lower diversity. This view is supported by the fact that the abundance of *A. armata* was negatively correlated with the abundance of most macroalgal morpho-functional groups (see Table 3). Such a result, where the abundance of invasive species is negatively correlated with the abundance of native taxa, is also supported by the study of Vaz-Pinto et al. (2014b). Again, future experimental exclusions of *A. armata* from invaded patches (such as those done to test the effects of other invaders; e.g. Piazzini and Ceccherelli 2006; Bulleri et al. 2010) must be carried out if we are to better understand the nature of this relationship.

Second, there was a negative correlation between the abundance of *A. armata* and *A. taxiformis*. Morphologically, the two congeneric species are very similar and they can easily be misidentified unless for the presence of harpoon-like hooks in *A. armata* (Andreakis et al. 2004). Even though the two species of *Asparagopsis* differ in their response to sea temperature (Ni Chualáin et al. 2004), the lower and upper critical limits of temperature of both species are unlikely to be met in the Azores (mean monthly SST ranging between 15–23 °C, Amorim et al. (2017)). As such, the negative correlation between the two *Asparagopsis* spp. may be tentatively interpreted as evidence that they are competing, as already suggested by Tittley and Neto (2005). In fact, *A. taxiformis* was an uncommon component of the marine algal flora of the Azores (Tittley and Neto 2005), but it probably occurs nowadays across almost all Azorean Islands (Cardigos et al. 2006).

Although *A. armata* may have displaced *A. taxiformis* in the past (Tittley and Neto 2005), recent observations suggest otherwise (Tittley and Neto 2005; Cardigos et al. 2006). The nature of the relationship between the two *Asparagopsis* spp. in the Azores thus needs to be experimentally tested taking in consideration that there are different lineages of *A. taxiformis*, including a worldwide invasive lineage (Dijoux et al. 2014). Such study should also assess if competition between the two species varies with seasonal changes in temperature.

It should also be noted (and formerly investigated) that variation in species interactions, occurring at smaller spatial scales, may also influence patterns of distribution at larger spatial scales (i.e. locations) (Ritchie et al. 2009; Wisz et al. 2013). If *A. taxiformis* effectively competes with the invasive *A. armata*, as is suggested by the negative correlation found between the two (see results and also Zanolla et al. 2018), it is possible that variation in the abundance of *A. taxiformis* at the scale of locations ($F_{8,12} = 10.978$, $P < 0.001$) can also impact the cover of *A. armata* at this spatial scale. This could easily happen via space pre-emption since *A. taxiformis* recruits earlier than *A. armata* in the Azores (authors personal observation).

In summary, this is the first step to understanding the processes driving the distribution and the potential ecological consequences of the invasive alga *A. armata* in the Azores. We report that *A. armata* was found throughout the archipelago and showed a high variation in abundance at the scale of locations (km). Seawater temperature, latitude and longitude, urchin density were not found to influence *A. armata* abundance. A negative correlation was found, however, between *A. armata* and macroalgal species richness and certain functional groups at the quadrat scale. Future studies to better understand the nature of the relationship between *A. armata* and the macroalgal community should benefit from an experimental approach where the presence of *A. armata*, alone or in combination with other components of the assemblage, is manipulated. A more in-depth investigation of the dispersive tetrasporophyte stage ("*Falkenbergia rufolanosa*") of the alga may also help explaining the spatial variability in the distribution of the gametophytic stage of the alga.

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