



Macroalgae niche modelling: a two-step approach using remote sensing and in situ observations of a native and an invasive *Asparagopsis*

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Received: 16 July 2020 / Accepted: 29 April 2021
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Abstract We are facing a global loss of biodiversity due to climate change. This will lead to unpredictable changes in ecosystems, affecting the goods and services they provide introduction of non-indigenous marine species. This represents one of the major threats to marine biodiversity and therefore, there is a strong need to assess, map and monitor these alien species. The appearance of non-indigenous species is especially dangerous in fragile ecosystems and it is of great importance to better understand the invasion mechanisms of these invasive species. This is the case for invasive alga *Asparagopsis armata*, present in the Azores Archipelago. In this study we propose a methodology to define the realized ecological niche of this invasive alga, alongside the native *Asparagopsis taxiformis*, to understand better its distribution and

potential impact on native communities and ecosystem services. These objectives comply with the EU Biodiversity strategy for 2020 goals and the need to map and assess ecosystems and their services. The lack of reliable high-resolution data makes this a challenging task. Within this scope, we propose a combination of Remote Sensing, Unmanned Aerial Vehicle based imagery together with in-situ field data to build ecological niche modelling approaches as a cost-effective methodology to identify and characterize vulnerable marine ecosystems. Our results show that this combination can help achieve monitoring, leading to a better understanding of ecological niches and the consequences of non-indigenous species invasion in fragile ecosystems, like small islands, when faced with limited data.

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Keywords *Asparagopsis armata* · *Asparagopsis taxiformis* · Ecological niche modelling · Remote sensing · Unmanned aerial vehicle

Introduction

The global decline in marine biodiversity coupled with the rapidly changing climate leads to shifts in marine organisms' distributions (Poloczanska et al. 2013; Sunday et al. 2012). This may lead to unpredictable changes in the provision of associated ecosystem services, with potentially severe impacts on society and the economy, such as reducing fisheries or loss of recreational opportunities (Beaumont et al. 2008) and the apparition of non-indigenous-marine-species (NIMS). Macroalgae are amongst the most invasive NIMS (Schaffelke et al. 2006). They are considered one of the greatest threats to native marine biodiversity and the ocean's resource value (Norse 1993, M. Vitousek et al. 1997).

The NE Atlantic is a hot spot of ocean warming, with temperature increases measured between 0.3° and 0.8° C per decade (MCCIP 2010). The Azores Archipelago, located in this region, composes nine volcanic islands along with many islets, positioned in three main groups on the mid-Atlantic ridge (França et al. 2003). The geologically recent formation of the islands, coupled with its isolated location make the marine and coastal environment of the Azorean Archipelago of high interest, particularly given its biodiversity-rich coastal ecosystems (Santos et al. 1995). However, small islands are known to be vulnerable to climate change (Veron et al. 2019), and the threat of alien species invasion for small islands is well documented (Nurse et al. 2014; IPCC 1995).

This is the case of the invasive *Asparagopsis armata*. *A. armata* was introduced to the Azores in the early twentieth century in the Atlantic and Mediterranean. It is widely distributed in the eastern North Atlantic Ocean, including Canaries and Macaronesia (Dijoux et al. 2014), where it is also considered invasive (Martins et al. 2019). It shows a tropical-to warm-temperate distribution, presenting biomass peaks in spring and summer (Andreakis et al. 2004).

NIMS have been linked to the reduction of ES provision, which is often termed Ecosystem

Disservices (EDS), functions or properties of ecosystems that cause effects that are perceived as harmful, unpleasant or unwanted (Von Döhren and Haase 2015). The relation between the NIM *A. armata* and its related ES and EDS has only been recently studied, but it is known to affect natural ecosystem functioning and to provide EDS (Katsanevakis et al. 2014). One disservice could be the potential impact on other native seaweeds, such *Asparagopsis taxiformis*. *A. taxiformis* is considered a cosmopolitan species in warm-temperate to tropical waters (Ní Chualáin et al. 2004). However, distinct geographical lineages indicate regional differentiation within this species (Ní Chualáin et al. 2004; Andreakis et al. 2004).

There is a strong need to monitor native and invasive seaweeds' distribution, but this can be time-consuming, resource intensive, and often limited to small areas (Werdell and Roesler 2003). Moreover, in NE Atlantic, we can find a lack of regional-scale distribution data resulting in a more challenging detection of ecological impacts over local communities (Smale et al. 2013; Rodrigues, 2015). Knowledge of the socio-economic effects of invasive seaweed is poor, and economic impacts derived from seaweed invasion are mainly based on mitigation costs, rather than long term socio-economic impacts (Schaffelke and Hewitt 2007).

Methods such as remote sensing (RS) could be the answer to achieve cost-effective methodologies to map and monitor seaweed distribution at regional and global scales (Green et al. 1996; Topouzelis et al. 2018; Wabnitz et al. 2008; Traganos and Reinartz, 2017). RS has been used to map seaweeds (Dogan et al. 2013; Casal et al. 2013; Hoang et al. 2016), although studying heterogeneous coasts constitutes a much more difficult task because of the lack of suitable satellite imagery with adequate spectral and spatial resolutions (Brodie et al. 2018). Previous studies have attempted to map the coastline of São Miguel with low-cost Unmanned Aerial Vehicle (UAV) imagery, to obtain red–green–blue (RGB or “real colour”) images with very high resolution (Kellaris et al. 2019).

An alternative approach to direct monitoring is the characterization of species' (realized) niches, which can help assess invasion capabilities of NIMS. Given a set of environmental variables known to influence directly a certain species physiology, the environmental fundamental niche can be understood as the

physiological responses of that species to those environmental variables, where its growth rate is identified as positive.

Assuming all environmental drivers are identified, we can predict geographic areas where the species of interest could establish and thrive, (assuming no significant competitive interactions (Clark et al. 2007), and no dispersal limitations (Barve et al. 2011)). Assessing a species' fundamental niche based on field observations is virtually impossible, but the realized niche can be retrieved with in-situ data. Realized niche can be described as the fundamental niche after a series of constraints are applied. These constraints can be identified as (i) the accessibility to geographic locations and (ii) the interactions between species (biotic interactions) in that area. Furthermore, the geographic scope of the study area can influence our interpretations if the full environmental range of the species is not seen in the area of study. However, the realized niche of a species, assessed for a certain geographic area with different accessibility characteristics and biotic interactions, can be used to determine the invasiveness capabilities for any NIMS in a given geographic area.

Our goal is to infer the realized ecological niche of the invasive red alga *Asparagopsis armata*, and its native co-generic species *Asparagopsis taxiformis* around São Miguel Island using presence records from all over Azores Archipelago. This will allow a better understanding of this species' potential geographic spread and its socio-economic consequences.

For this purpose, we use a combination of RS, UAV imagery and in-situ field data together with ecological niche modelling approaches to monitor and forecast the potential distribution of these important seaweeds. This will help take the first step towards a deeper comprehension of the ES loss and ecosystem disservices related to NIMS establishment within local communities.

Methods

Study area

The study area (Fig. 1) comprise Pico, Flores, Terceira and São Miguel islands within the Azores Archipelago. They are located in west (Flores) and the central Azores (Terceira and Pico), which are affected by the

Gulf stream. São Miguel island belongs to the eastern region, where the Azores current has the most substantial influence over the whole archipelago. The Azores Archipelago is a confluence zone with notable influence over the oceanographic and biological characterization of the North Atlantic region (Caldeira and Reis 2017). It is considered a highly productive marine region with highly seasonal variations of nutrient cycles (Amorim et al. 2017). In concordance with global climate change patterns (Karl et al. 2000), temperature and precipitation levels in the Azores have been measurably on the rise (Santos et al. 2004).

Environmental variables

Two sets of environmental variables were produced for this study, along with two different modelling approaches. An initial set of 6 environmental variables characterizing the abiotic conditions of São Miguel island were considered. These variables were derived from a DEM, taken from the EMODnet Bathymetry portal. We generated: Aspect, Depth, Fetch, Roughness, Slope and Topographic Position Index (TPI), restricted to a 3 km buffer from the shoreline. Aspect, roughness, slope and TPI were processed using *Aspect*, *Roughness*, *Slope* and *Topographic Position Index* Raster tools in *QGIS 3.4.1 Madeira*, at an output spatial resolution of 100 m x 100 m. Depth values were obtained directly from the DEM at a resolution of 100 m x 100 m. The Fetch (a measure of coastal exposure derived from spatial proximity to shorelines) was calculated using *R studio* 1.1.463B (Yesson et al. 2015).

The second set of environmental variables used in a presence/absence approach contained photoperiod, depth and temperature values. Depth and temperature values were obtained via in situ measures recorded with a *MARES Mission Puck 3* dive computer by scuba divers in 2016, 2017 and 2018 in Pico, Terceira, Flores and São Miguel islands. Photoperiod values corresponding to these survey's day were calculated using the *daylength* function in the *geosphere* R package (Forsythe et al. 1995). Table 1 shows both sets of variables.

We undertook a Variance Inflation Factor (VIF) analysis to test for spatial correlation of the environmental variables, to set aside those predictors spatially correlated. We ran the analysis using the VIF function

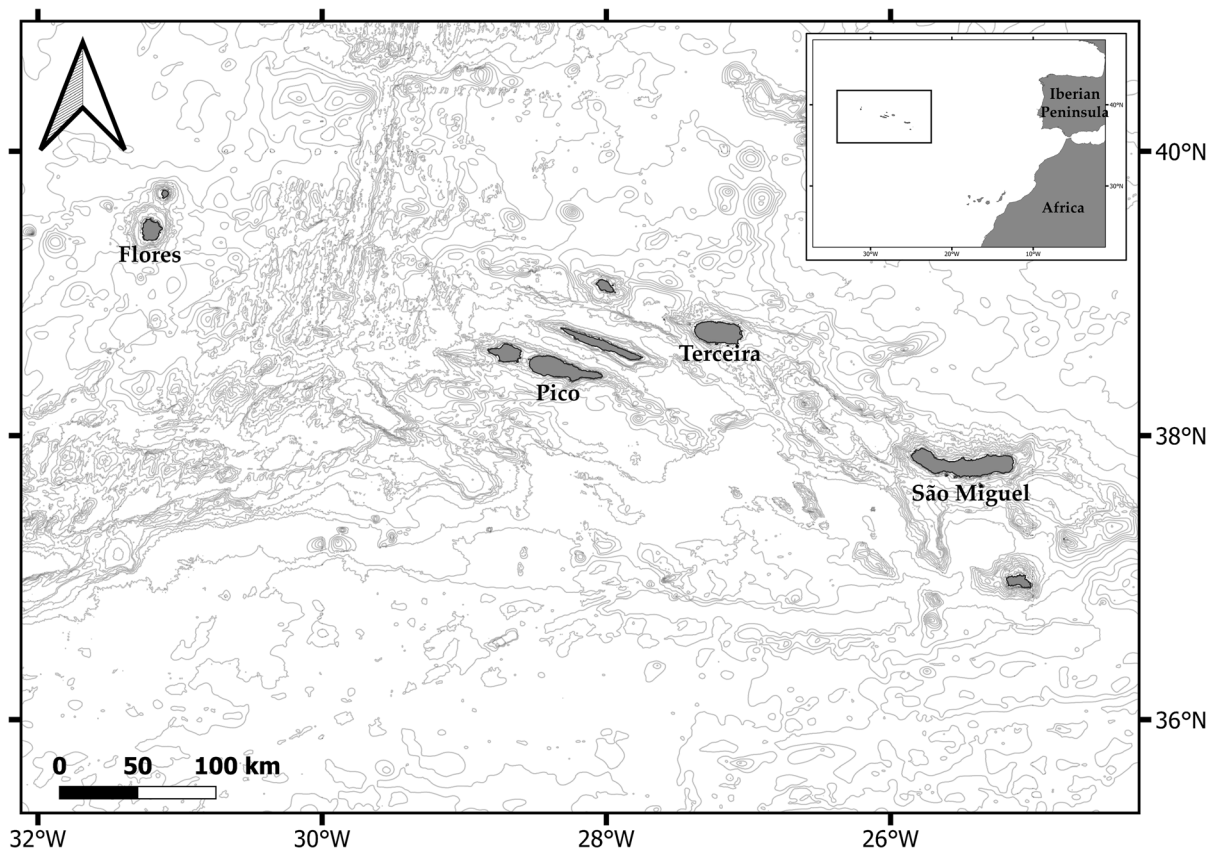


Fig. 1 Azores Archipelago

implemented in the R *sdm* package (Naimi et al. 2014). This analysis showed that roughness and TPI were highly correlated (with VIF values greater than 10), so TPI was removed from subsequent analysis.

Species occurrence data

Distribution models are based on statistical approaches that study the linkage of occurrence data and environmental variables (Marcelino and Verbruggen 2015).

Occurrence data can be considered as georeferenced locations where the species have been found, while absence data are georeferenced points where the species has been surveyed and not found. Absence data are rarely available (Loiselle et al. 2003) but pseudo-absence or background data can be used as an alternative (Marcelino and Verbruggen 2015). Due to the characteristics of the data acquisition, while undertaking Ecological Niche Modelling (ENM) for

invasive species, it is a common procedure to use only presence data (Marcelino and Verbruggen 2015). For our modeling approaches, we constructed two different occurrence datasets. (i) Presence-only data derived from remote sensing imagery classification to run Presence/background models with our first set of environmental variables to be used with MAXENT and (ii) Presence/absence dataset obtained from a sampling survey in 2016, 2017 and 2018 in 4 islands of Azores Archipelago. A series of spots were revisited during those years to assess the presence of the species and the abiotic conditions (Table 1). This dataset was used to run the generalized linear models (GLM) detailed below.

Remote sensing derived presence data

Occurrence data was supplemented by data inferred from a UAV survey (Kellaris et al. 2019). Images were taken with an unmanned aerial vehicle (UAV) in three

Table 1 Environmental variables

Variables	Source	Spatial resolution	Model
Aspect (°)	Processed from EMODnet Digital Elevation Model with <i>Aspect</i> Raster Tool in <i>QGIS 3.4.1 Madeira</i>	100 m x 100 m	Presence/ Background
Depth_1 (m)	Extracted directly from Digital Elevation Model available in EMODnet Bathymetry portal Digital Elevation Model (http://emodnet-bathymetry.edu)	100 m x 100 m	Presence/ Background
Fetch (m)	Calculated using <i>R studio 1.1.463</i> as implemented in (Yesson et al. 2015)	100 m x 100 m	Presence/ Background
Roughness (m)	Processed from EMODnet Digital Elevation Model with <i>Roughness</i> Raster Tool in <i>QGIS 3.4.1 Madeira</i>	100 m x 100 m	Presence/ Background
Slope (°)	Processed from EMODnet Digital Elevation Model with <i>Slope</i> Raster Tool in <i>QGIS 3.4.1 Madeira</i>	100 m x 100 m	Presence/ Background
TPI (m)	Processed from EMODnet Digital Elevation Model with <i>Topographic Position Index</i> Raster Tool in <i>QGIS 3.4.1 Madeira</i>	100 m x 100 m	Presence/ Background
Depth_2 (m)	In situ measures	N/A	Presence/ Absence
Temperature (°C)	In situ measures	N/A	Presence/ Absence
Photoperiod (hours)	Calculated using <i>daylength</i> function in <i>geosphere</i> R package (Forsythe et al. 1995)	N/A	Presence/ Absence

São Miguel island regions, using a DJI Phantom 3 Professional quadcopter drone that carries a visible light camera. The survey was carried out at low tide, considering optimal conditions (low cloud coverage and low wave speed) at 114 m altitude, achieving a spatial resolution of $4.93 \text{ cm} \cdot \text{pixel}^{-1}$. Surveys were carried out in May and June 2018, in Caloura, Mosteiros and Lagoa coasts (Fig. 2), along with ground-truth surveys by kayak and scuba divers to test the image classification. Support Vector Machine (SVM) image classification was used as our source of occurrence data. The DroneDeploy software (DroneDeploy, San Francisco, CA, USA) was used to design the flight plan with image overlaps set to 85% frontlap, 80% sidelap and Pix4Dmapper (Pix4D SA, Lausanne, Switzerland) was used to construct photomosaics.

This classification presented an accuracy of 0.998 with a standard deviation of 6.42×10^{-4} in Kappa statistics (Kellaris et al. 2019). We used the *Point Sampling Tool* plugin in *QGIS 3.4.1* to extract presence sites from these classified UAV images. First, we constructed a 100 m x 100 m square rectangle grid and the UAV survey areas with *Create Grid* tool and then used *Centroids* to obtain a point grid consisting of those squares' centroids. With these

centroids, we extracted the UAV classification output to obtain presence and absence of the target algae. We selected 100 m x 100 m resolution for our sample point grid to match the spatial resolution of our environmental variables and our presence records.

A random subset selection of presence points for *A. armata* and *A. taxiformis* using the *Subset Features* geostatistical Analysis tool in *ArcGIS 10.4*, to avoid spatial correlation between presence records. This resulted in 29 and 30 presence records for *A. armata* and *A. taxiformis*, respectively (Fig. 2).

Survey sampling data

Four islands (from 65 to 513 km apart) were selected among the three island groups (eastern, central, and western) of the archipelago, chosen to be representative of the three groups and span the entire length of the archipelago. Sampling surveys were carried out in 2016, 2017 and 2018 (Fig. 3). Within each island, 3 sites were randomly selected, with no prior identification of the algae's presence, with surveys conducted depths of 5-, 10- and 15-m depth. Within each site, three $50 \times 50 \text{ cm}$ quadrats were placed on the seabed and visually sampled by scuba divers using the method of Dethier et al. (1993), recording depth and

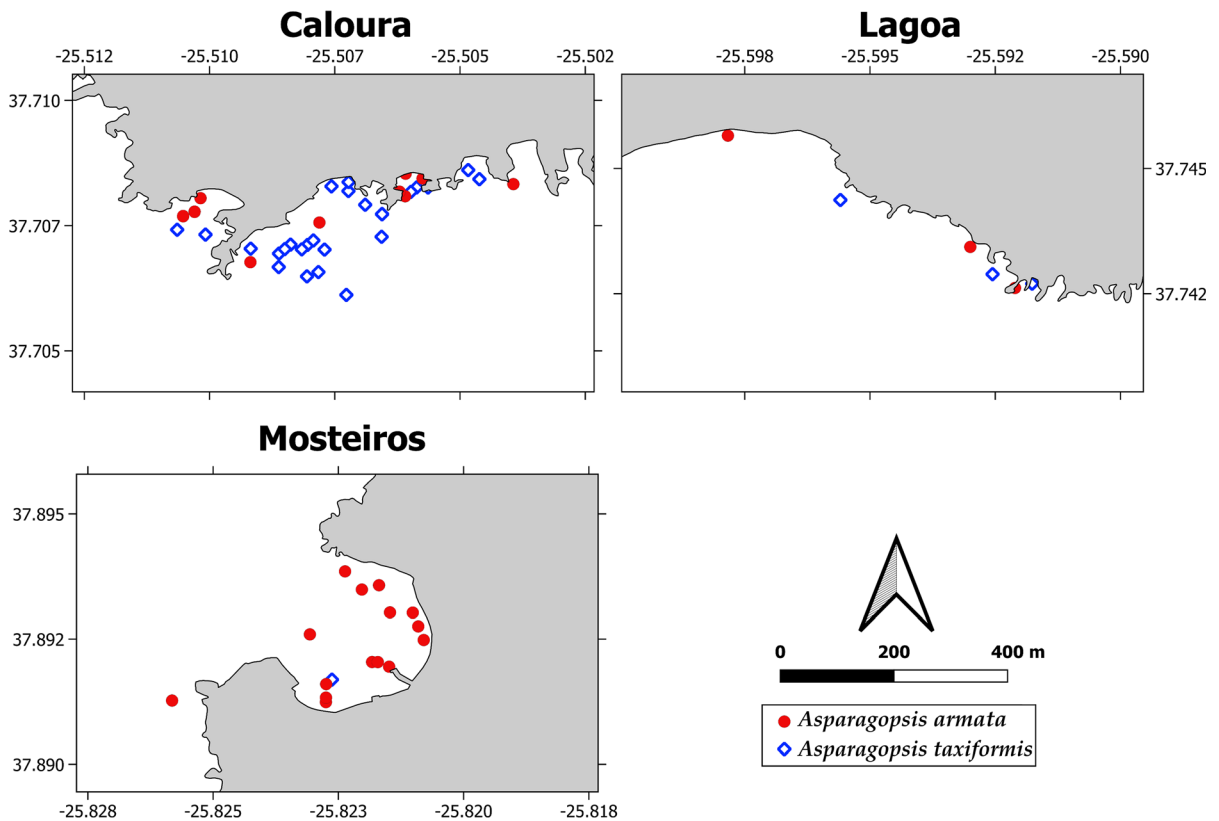


Fig. 2 Presence data derived from UAV classification images in Caloura, Lagoa and Mosteiros bays (São Miguel island)

temperature values with a *MARES Mission Puck 3* dive computer.

Each location was surveyed repeatedly for a total of 73 different sampling days over three years. Quadrant position was randomly chosen in each survey and by the end of the process, 1265 observations were recorded. The species presence/absence data set consisted of 70 records in 2016, 955 records in 2017 and 240 records in 2018 (Table 2). This set of presence data was constructed considering photoperiod and sampling sites' values along with sampled temperature and depth (categorized as deeper or shallower than 10 m) and used to run three different kinds of presence/absence models.

Ecological niche modelling approaches

Species distribution models (SDMs) are widely used in ecology and conservation with a vast variety of methodologies and approaches (Elith et al. 2006). An SDM algorithm is a mathematical expression that can

be used to estimate species distribution using environmental predictor variables. Among the most commonly used methods, we can find regression algorithms that make use of absence and presence data, such as: Generalized linear models (GLM), Generalized additive models (GAM), multivariate adaptive regression splines and boosted regression trees; or algorithms that only use presence data together with background data such as SVMs (Drake et al. 2006) and MAXENT (Kearney et al. 2008).

In this context, we propose a two-step approach to characterize the species ecological niche. A “geographic approach” focuses on how species distribution is affected by topographical variables and an “environmental approach” to understand the species' temporal dynamics.

On the one hand, in-situ observations provide a robust dataset of the species' presence and absence over time, with extensive temporal coverage but limited geographic extent. This continuous monitoring of the species allowed us to study how changes in

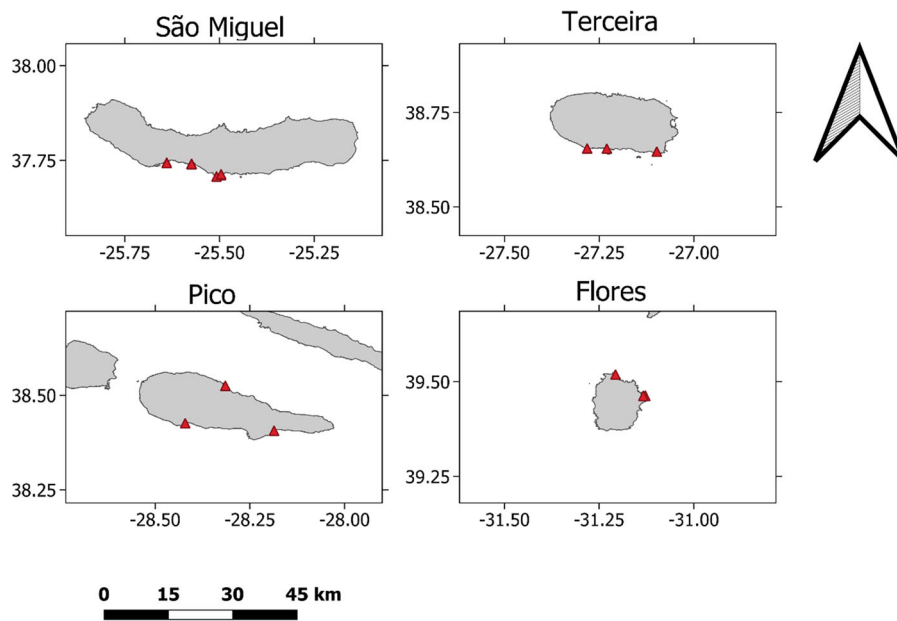


Fig. 3 Sampling sites (red triangles) in different islands of the Azores Archipelago during 2016, 2017 and 2018

Table 2 Presence records per surveyed year

	2016	2017	2018
January	0	60	0
February	0	60	0
March	0	60	0
April	0	60	0
May	0	160	60
June	0	315	60
July	0	60	60
August	0	60	60
September	0	60	0
October	0	50	0
November	60	10	0
December	10	0	0

dynamic variables, such as SST or photoperiod, affect species distribution, although providing little information regarding the species' response to different abiotic environmental characteristics. On the other hand, a remote sensing-based dataset lacks temporal coverage, but its geographic extent, with surveys in three different bays of the island, allows us to characterize how species distribution is affected by terrain variables changes.

Presence/background approach

First, to characterize the algae distribution response, we worked with MAXENT, using the first set of 6 topographic variables with presence data derived solely from remote sensing. These variables were used to assess the response of *A. armata* and *A. Asparagopsis* to different topographic characteristics. Environmental variables were not used for this model as their spatial resolution was too coarse in comparison to the topographic data. As presence records were retrieved from three different coasts limited to São Miguel island, the extent for model validation was limited to this island as well. This analysis will provide estimates of the species' topographic preferences, to be then used along with results of presence/absence models.

MAXENT has been broadly used to model species distribution. It is based on a maximum entropy approach, predicting the species occurrence by minimizing the estimated relative entropy from presence data only (Phillips et al. 2006) which has been shown to perform well with limited datasets. Samples With Data (SWD) tables were constructed using the *Point Sampling Tool* plugin in *QGIS 3.4.1 Madeira*, extracting environmental variables corresponding to each presence record. Localities where the algae were not

present in the UAV classification maps were selected as background (or pseudo absence) data. The KUENM package (Cobos et al. 2019) with R studio 1.1.463 was used to undertake an automated calibration process using MAXENT software creating a certain number of candidate models, taking into consideration all possible combinations of setting parameters. A single set of variables was used, comprising all six topographic variables, Beta multiplier range values were selected from 0.1 to 9.7 (with increasing steps of 0.4) and all possible combinations of setting parameters were used in the automated process. Then, partial ROC, omission rates and Akaike's Information Criterion (AIC) were assessed to find statistically significant models (Cobos et al. 2019).

Presence/absence approach

Secondly, we undertook a species habitat suitability characterization using the presence/absence dataset to study how these species' distributions respond to dynamic environmental variables. Before final model selection, GAM, RF and GLM algorithms were constructed, and performances compared, based on this initial assessment the GLM algorithm was selected to undertake the presence/absence approach.

The extent considered for model validation should be set according to geographic areas where the species had accessibility. In this particular case, a more limited extent was taken into consideration (Barve et al. 2011).

The relatively recent arrival of *A. armata*, would point to a more limited extent being considered, in keeping with its short term expansion capabilities (Barve et al. 2011). However, resource availability limited the study area to 4 islands of the archipelago (Fig. 3).

To study the different responses to changes in temperature, photoperiod and depth, the sites were revisited over three years to characterize the physiological response to annual variability of those abiotic factors, along with potential preferences over any particular location.

Four variables were used to calibrate the models: (i) Temperature, (ii) Photoperiod, (iii) Depth and (iv) Sampling site. Recorded temperatures reached minimum levels of 15 and 23 °C for the 3-year period, with photoperiod values ranging between 9.53 and 14.76 h

and registered depths of 5, 10 and 15 m, then classified in two classes (< 10 m and > 10 m).

Model evaluation

Both models' performance was evaluated using Area Under the Curve (AUC) values and by assessing how predictors contribute to explain and determine the species distribution.

For the MAXENT model (Presence/background), variable contributions were calculated using a Jack-knife approach implemented in *MAXENT 3.4.1* and 40 models were run using a 20% bootstrap random subsample selection test.

After assessing and evaluating our models, two suitability maps were constructed graphically explaining how *A. armata* and *A. taxiformis* geographic distribution is affected and explained by topographic environmental variables, and spatial explicit species geographic distribution maps were constructed. Then, species response to environmental variables was characterized and species realized ecological niche was inferred with the combination of both outputs.

Results

Direct observations of *Asparagopsis armata* span 426 sites totalling 1265 observations. The native *Asparagopsis taxiformis* was seen in 793 sites within the same 1265 observations (Fig. 3). Presence/background data was also generated from classified drone imagery 29/30 presence records for *A. armata*/*A. taxiformis* respectively and 2355/2356 background records.

Presence/background approach

A total of 493 MAXENT models were generated for *A. armata* and *A. taxiformis* for parameter optimization. Model selection criteria were based on: (i) Partial Receiver Operating Characteristic (ROC), with values lower than 1 showing statistical significance, (ii) Omission rates, with values lower than 5% related to the best performance and (iii) Lowest delta AIC pointing to the single best model finding the best trade-off between data fitting and model complexity, avoiding both overfitting and underfitting (Peterson

et al. 2008; Snipes and Taylor 2014; Cobos et al. 2019). Model parameters are presented in Table 3.

Depth was the most crucial variable for the *A. taxiformis* model, followed by Roughness, and all other variables were excluded after Jackknife analysis. The species was associated with 5 and 20 m of depth and low values of roughness, suggesting a preference for smoother bottoms. In contrast, for *A. armata*, Depth, and Fetch were the variables with a higher relative contribution to habitat prediction, with Depth the most important again (Table 4). For *A. armata*, we

found response to depth similar to *A. taxiformis*, with preferences for shelter and shoreward areas (lower Fetch). The maximum preference appears to values closer to 100 m, dramatically decreasing when fetch reaches values greater than 10,000 m. All other variables were discarded for modeling processes as they were negatively impacting model performance.

When optimal parameter settings were characterized, we run the MAXENT model 40 times. Both *A. taxiformis* and *A. armata* models had an excellent

Table 3 MAXENT parameter settings

	<i>A. armata</i>	<i>A. taxiformis</i>
Beta Multiplier	1.1	1.2
Hinge features threshold	0.45	0.5
Beta threshold	1.63	1.86
L/Q/P ^a features	1.4	1.5

^aLinear, quadratic and product features*

Table 5 AUC results for *A. Armata* and *A. taxiformis* presence/absence models

Species	Model	Mean value	Standard deviation
<i>A. armata</i>	GAM	0.89	0.01
<i>A. armata</i>	GLM	0.88	0.02
<i>A. armata</i>	RF	0.91	0.02
<i>A. taxiformis</i>	GAM	0.74	0.02
<i>A. taxiformis</i>	GLM	0.74	0.02
<i>A. taxiformis</i>	RF	0.76	0.01

Table 4 MAXENT variable contributions

		Variable contribution (%)	Variable permutation importance (%)
<i>A. armata</i>	Depth	72.1	55.3
	Fetch	27.9	44.7
<i>A. taxiformis</i>	Depth	62.5	63.75
	Roughness	37.5	36.25

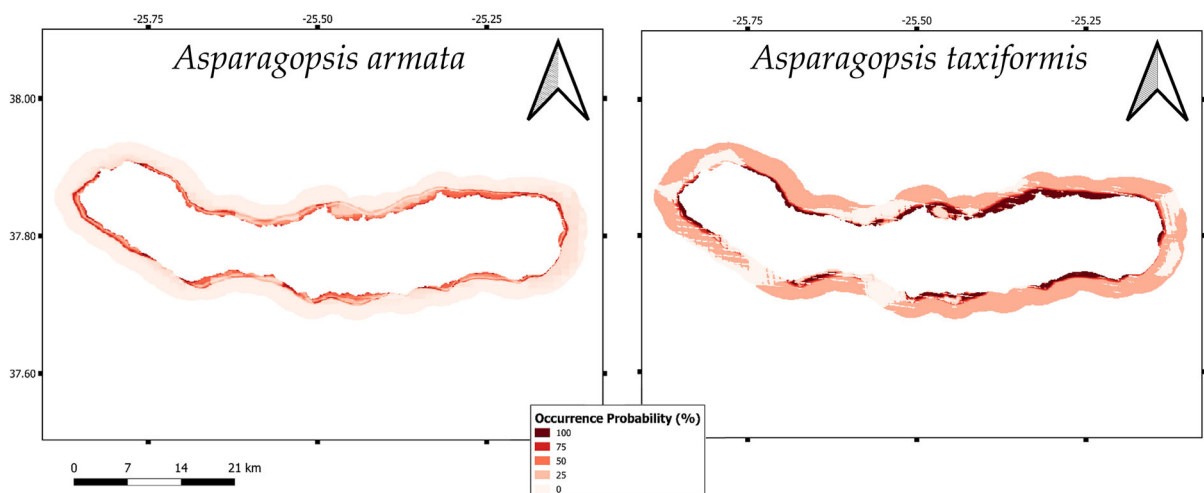
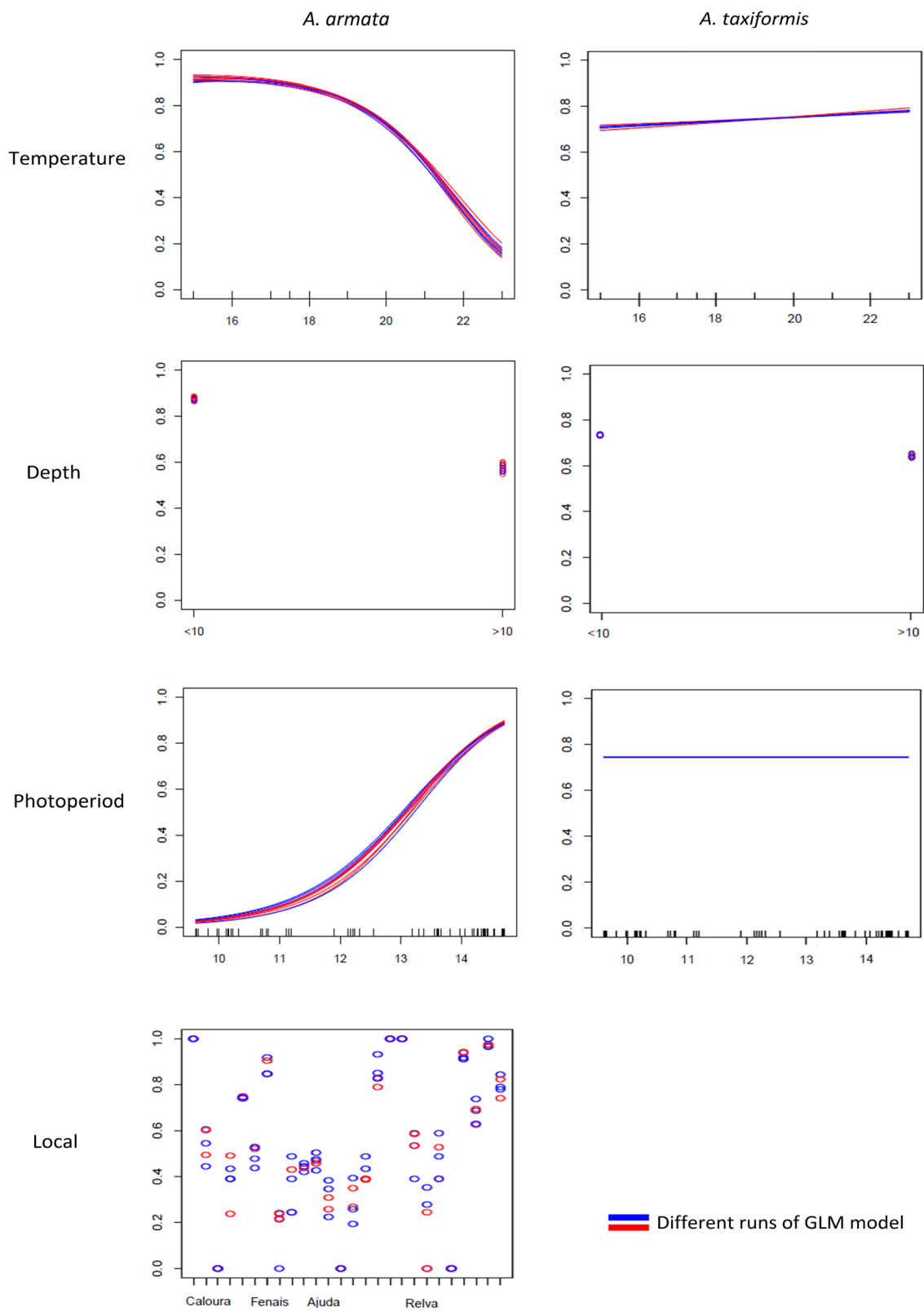


Fig. 4 MAXENT predicted potential geographic distribution in São Miguel island



◀ **Fig. 5** Species response to depth, photoperiod and temperature environmental predictors for 10 different runs for GLM model

performance, with a mean AUC value of 0.806 and 0.823.

The model prediction estimates show a more homogeneous geographic distribution for *A. armata* without a clear preference in any region with lower habitat suitability values in São Miguel island. For *A. taxiformis*, we can observe higher suitability values over the north-northeast part of the Island (Fig. 4).

Presence/absence approach

Model performance for the presence/absence approach was relatively similar across all methods (Table 5). Simpler models should be preferred over complex ones (Guisan et al. 2002) therefore, based on models' similar performance and taking into consideration GLM more straightforward explanation and results in interpretation, we focus on the GLMs to present variable species response. Model evaluation was carried out with a cross-validation method implemented in the *Biomod* R package, with ten different runs.

Photoperiod and temperature have the greatest influence on the *A. armata* model. At the same time, Depth barely affects the species response and sampling site slightly affecting *A. taxiformis* distribution but has negligible influence over *A. armata* (Figs. 5 and 6). Maximum suitability is expected when medium–high values of photoperiod (starting at 13 h per day) meet low to medium temperature values (around 15.5–18.5 °C). High values of temperature are unsuitable for *A. armata*. The results are less clear for *A. taxiformis* (Figs. 5 and 6), which shows a relative weak response to photoperiod.

Discussion

In NE Atlantic, *Asparagopsis armata*'s known northern and southern distribution boundaries can be found in UK and Senegal, respectively. Along with this known geographic distribution, we can find optimal growth temperatures between 10 and 21 °C, with lethal limits at 5 and 27 °C (Mata et al. 2006). In the

Azores Archipelago, these limits are very unlikely to be reached. Photoperiod values range from 9.5 to 14.76 h, with the temperature reaching its minimum at 15 °C with an annual maximum at 24 °C. All possible fundamental abiotic environmental requirements for the species to be present are not met in the Azorean archipelago. As expected from mechanistic modeling approaches, the species' fundamental niche is extremely unlikely to be captured by a modeling effort based only on Azores distribution data.

On the contrary, our approach aimed to understand better and characterize the realized niche of the species within the archipelago. Aside from the abiotic environmental requirements present in any given geographic area, other particularities such as biotic interactions and species accessibility play an essential role when shaping the realized niche of a species. Such particularities are not explicitly captured by the model itself (Barve et al. 2011). However, the species' inferred realized niche identifies its suitability to the abiotic environmental variables available in a given geographic area.

For the specific set of variables considered in the model, *A. armata*'s distribution is best explained by two key variables: (i) Photoperiod and (ii) Temperature. The realized niche of the species, given the variables considered, can be found when specific values of photoperiod (13 h) meet temperatures between 15.5 and 18.5 °C.

Compared to its co-generic species, *A. armata*'s niche is much narrower than the *A. taxiformis*'. *A. taxiformis* is far less affected by changes in depth than *A. armata* and shows a generalist profile, in concordance with findings from the southern coast of Spain (Zanolla et al. 2018), where they found different cohorts overlapping in time. *A. taxiformis* distribution cannot be explained with confidence by any of the environmental variables considered. However, there appears to be a geographic preference to locations such as Caloura beach. *A. armata*'s optimal temperatures and photoperiod values are expected to be met earlier in the year in latitudes closer to the equator, and later as we get farther north as Kraan and Barrington (2005) results show for the Irish coast.

A. armata's optimal environmental conditions in Azores Archipelago can be expected to be achieved in the early summer with explosive blooms when optimal conditions are met, and starting to decay after summer (Mata et al. 2006). Therefore, we could predict intense

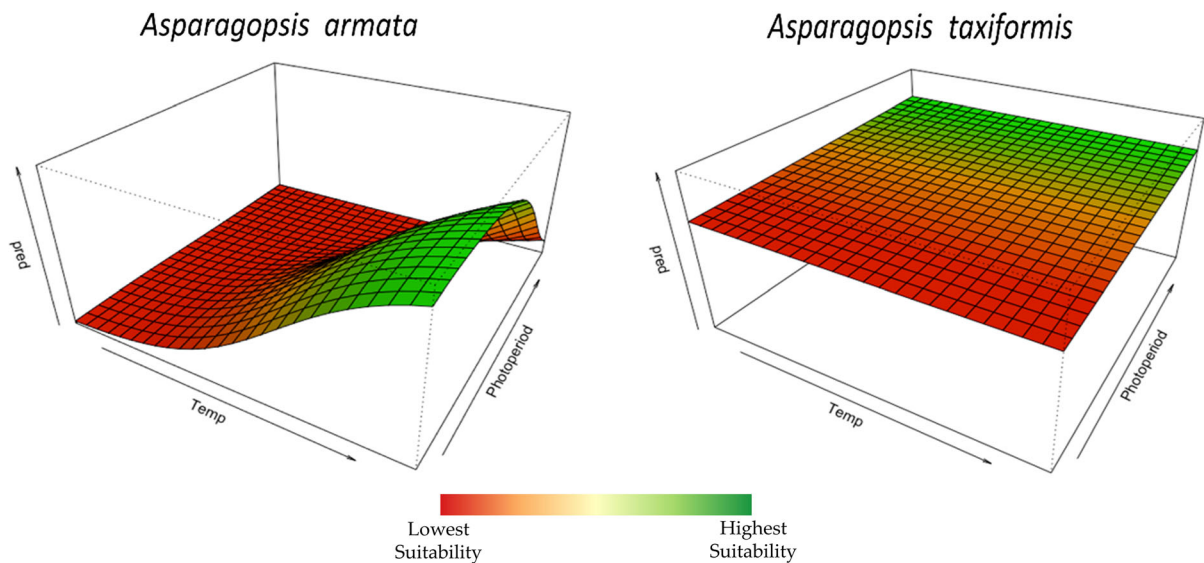


Fig. 6 *A. taxiformis* and *A. armata* response to photoperiod and temperature environmental predictors

blooms when the water stays relatively cold in early-summer period (with high photoperiod values). When these criteria are met, we can expect suitable areas for *A. armata*'s gametophytic stage to overlap with *A. taxiformis*'. However niche preferences of the two species are quite different to allow for a significant overlap. Nevertheless, other algal blooms may occur at various times over the year, not necessarily overlapping year on year, pointing out that photoperiod alone may not be a reliable predictor of blooms by itself (Martins et al. 2019).

A. armata does not show distribution preferences over any region of the São Miguel coast and this is something we might expect from a geographically wide-ranging invasive species. This feeds the narrative that *A. armata* shows opportunistic characteristics with explosive blooms when climatic conditions are met in late spring-early summer, growing all over the coast regardless of the environment's geographical characteristics. Conversely, *A. taxiformis* shows a specific preference over the north-northeast coast when analyzing its geographic distribution. *A. taxiformis* models are not very robust, and we may be lacking essential predictor variables. Other studies have shown the importance of variables such as primary productivity, surface salinity, nutrient concentrations, Chlorophyll-a, and pH for invasive seaweeds (Karl et al. 2000; Miller et al. 2019; Guerra-García et al. 2012). Variables such as SST or sea

surface salinity are freely available from remote sensing datasets but at a much broader spatial resolution than the data used in this study. Spatial resolution strongly affects model predictive capabilities (Guisan et al. 2007).

The relationship between the spatial resolution of species occurrence data and environmental variables is a crucial aspect for consideration. For instance, coarse resolution environmental variables may fail to identify the habitat where the species occurs, and changes in spatial resolution of environmental variables can alter our understanding of presence patterns (Guisan et al. 2007), especially when considering highly dynamic oceanographic processes.

On the contrary, when considering coarse-scale occurrence datasets, such as historical collections with inherent spatial uncertainties, the use of finer-scale environmental data is not advised (Graham et al. 2004).

Our case study worked with two datasets of two different natures, with presence records of high spatial resolution and low location uncertainties. The spatial resolution of our remote-sensing derived occurrences made this dataset unfit to be used with coarser freely available environmental variables (Guisan et al. 2007). However, it proved to be important when undertaking ecological modeling of invasive algae. Considering this limitation, along with its poor temporal resolution (our records being limited to a

small window of time where abundance peaks were expected), we decided to model our species response to solely topographic variables, at a convenient native resolution of 100 m x 100 m. UAV imagery allowed us to get a wide “screenshot” where representative values of the species’ topographic preferences could be easily and cost-effectively retrieved, compared to the logistic and human resources demanded for an extensive sampling field survey.

On the other hand, while lacking the capacity to assess topographic preferences, the in-situ dataset allowed us to determine species preferences for specific conditions of photoperiod and temperature, independent of the topographic characteristics, (which remained constant over the 3 years of sampling). In contrast to the remote-sensing dataset, the in-situ dataset provide the temporal resolution needed to study dynamic variables. The in-situ dataset was unfit to be used with coarse resolution environmental data (Guisan et al. 2007) but convenient to characterize species response to abiotic dynamic factors. Due to the limitations of environmental variable availability (outlined above), two different models were run in two separate steps of a sole modeling approach. Firstly, we assessed the species physiological response to dynamic variables, characterizing the realized niche related to those abiotic factors, in an attempt to empirically locate the time of potential peaks of abundance in the archipelago. In a second step, we sought to characterize species response to topographic variables, which is intrinsically linked to expected abundance peaks.

With the outputs of these two modeling steps, we inferred the realized niche of the species, identifying, on the one hand, the periods of the year where invasive *A. armata* could pose a real threat to native *A. taxiformis*. On the other hand, studying the species’ topographic preferences where this peak of abundance is expected, providing spatially explicit assessments of its invasion mechanics. This spatially explicit information aims to be a convenient tool to better understand the species’ invasiveness capabilities and anticipate the expected locations where explosive blooms may occur.

It is essential to consider that the presence/background model was constructed with observations from the South and West Coasts of São Miguel island, with no data in the North or East coast of São Miguel (due to weather constraints limiting survey sampling

capabilities). This sampling procedure may have introduced a bias in the presence records. For this reason, the presence/background model was not projected to other islands of the archipelago (Stolar and Nielsen 2015).

Also image classifications used in the present study indicated overfitting in the training data. Nevertheless, remote sensing-based occurrence data proved a convenient tool to predict potential geographic distribution, allowing us to infer species niche when working in parallel with in situ datasets.

While not explicitly captured in the model, the biotic interactions affecting species’ establishment can be considered an intrinsic characteristic of any given geographic area. This local competition will ultimately effect species’ realized niche. This study aimed to assess the invasiveness trait of *A. taxiformis* in the Azores Archipelago by defining and studying its realized niche. Given the nature and the purpose of this modeling approach itself, caution is advised when considering extending these results to the whole species potential distribution (Malanson et al. 1992).

While the two-step approach modeling with different datasets provided good results, demonstrating its potential application when facing data scarcity scenarios, other approaches might be helpful in the present study. For example, it could be interesting to broaden study areas, even attempting to undertake a complete UAV image classification of the whole island, considering different times of the year. This will permit construction of a species niche model based entirely on remote sensing-based data sets although depending on the time of the year this approach may not be feasible due to weather constraints (Kellaris et al. 2019). Nonetheless, although solely relying on UAV imagery may not be possible, it remains an excellent complementary tool.

Furthermore, once the realized niche of the invasive species is identified and possible locations for the species to appear anticipated, UAV imagery could represent a ready-to-use tool to reaffirm and validate the hypothetical locations more likely to be invaded, and so be used as an early alarm system.

As stated, our results may lack the capabilities to drive firm conclusions about the geographic distribution of the species outside the Azorean archipelago. For these purposes, historical presence datasets, with a much broader spatial resolution (and location uncertainties) could be used with other sets of freely

available remote-sensing derived environmental variables, in an attempt to assess the potential distribution of these species in a wider geographic area, with coarser resolutions. This approach would allow us to get closer to the fundamental niche of the species. However, some problematic issues would need to be considered, such as the presence of potential different genetic lines of the species, that could be included in the same occurrence dataset. Other genetic lines of the species may represent different adaptations to various environments and hence, dissimilarities in niche characteristics. This issue may affect not only the model performance but the proper identification of its niche. Nonetheless, this approach would allow us to compare the potential distribution of the species with the assessed realized niche in the Azores Archipelago, and help better understand the invasive capabilities of *A. armata*.

Eventually, as a consequence of ocean warming, optimal day lengths (photoperiod) will no longer match optimal temperatures for the species to thrive. Optimal photoperiod values will occur along with less suitable SST values (warmer sea surface). These conclusions are in concordance with the leading results in (Martínez et al. 2018), showing that rising values of Sea Surface Temperature (SST) are related to the ecological niche narrowing of temperate seaweeds, with solid distribution range contractions and shifts in distributions. While that may appear positive, as an invasive species may no longer find suitable habitat in the Azores with the consequent apparition of ecosystem disservices, it should be noted that many natives will suffer the same fate with severe socio-economic impacts. This is further evidence of the vital need to monitor not only invasive but native species in coastal ecosystems as a tool to inform policymakers and provide proof evidence of socio-economic advantages derived from natural ecosystem protection and restoration.

Conclusions

Further steps need then to be taken, and explicit spatial maps of both ES and EDS provided by *A. armata* and *A. taxiformis* should be produced as a critical tool for marine and coastal conservation, following the EU Biodiversity strategy for 2020. The Outermost Regions (ORs) of Europe, such as Azores

Archipelago, are expected to undertake this MAES procedure, but a lack of reliable and high-resolution data usually makes this kind of assessment and valuation infeasible.

In this context, ecological niche modeling characterization represents one of the first steps of MAES in the region, helping to identify and characterize impacts and losses of ES related to Coastal ecosystems in remote and data-scarce scenarios. Future MAES procedures and spatially explicit ES assessments will strongly depend on ecological and socio-economic data, which in combination with ecological niche modeling methodologies will set a feasible scenario for MAES in the Macaronesian bioregion.

Acknowledgements This study is a contribution to the research project ‘ASP AZOR— Ecosystem impacts and socio-economic benefits of *Asparagopsis armata* in the Azores’ (Ref. ACORES-01-1045-FEDER-00060) funded through FEDER (85%) and regional funds (15%) via ‘Programa Operacional Açores 2020’. CY is supported by Research England. All authors dedicate this work to the memory of our beloved co-author, Prof. Ana Neto. May she rest in peace.

Author Contributions Using the initials of every co-author, as in: EC, MF, AG, CY, AP, IM, AN, MA. EC, MF, AG, CY and AN conceived the main research idea. MA contributed to the integration and development of the MAES approach into the main research idea. EC, MF, AG, IM and AP contributed to the production, collection and selection of field and modeling data. EC and MF developed the theory and performed the computations. EC, CY and MF verified the analytical methods. All authors discussed the results and contributed to the final manuscript.

Funding The funding sponsors had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, and in the decision to publish the results

Declarations

Conflicts of interest The authors declare no conflict of interest.

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