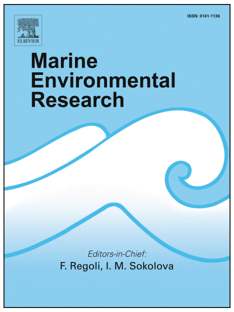

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PII: S0141-1136(22)00204-5

DOI: https://doi.org/10.1016/j.marenvres.2022.105759

Reference: MERE 105759

To appear in: *Marine Environmental Research*

Received Date: 2 May 2022

Revised Date: 20 September 2022

Accepted Date: 22 September 2022

Please cite this article as: Martín García, L., Rancel-Rodríguez, N.M., Sangil, C., Reyes, J., Benito, B., Orellana, S., Sansón, M., Environmental and human factors drive the subtropical marine forests of *Gongolaria abies-marina* to extinction, *Marine Environmental Research* (2022), doi: https://doi.org/10.1016/j.marenvres.2022.105759.

Environmental and human factors drive the subtropical marine forests of *Gongolaria abies-marina* to extinction

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Abstract

Large brown macroalgae are foundational threatened species in coastal ecosystems from the subtropical northeastern Atlantic, where they have exhibited a drastic decline in recent years. This study describes the potential habitat of *Gongolaria abies-marina*, its current distribution and conservation status, and the major drivers of population decline. The results show a strong reduction of more than 97% of *G. abies-marina* populations in the last thirty years and highlight the effects of drivers vary in terms of spatial heterogeneity. A decrease in the frequency of high waves and high human footprint are the principal factors accounting for the long-term decline in *G. abies-marina* populations. UV radiation and sea surface temperature have an important correlation only in certain locations. Both the methodology and the large amount of data analyzed

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in this study provide a valuable tool for the conservation and restoration of threatened macroalgae.

Keywords: Algae; *Gongolaria abies-marina;* Sargassaceae; distribution model; temporal variability; drivers of decline; Multivariate analysis; geographically weighted regression; Canary Islands.

1. Introduction

Large brown algae are among the most important foundational species in the Mediterranean and adjacent warm-temperate northeastern Atlantic coasts, particularly the species of *Cystoseira sensu lato*, which are currently included in three genera *Cystoseira*, *Ericaria,* and *Gongolaria* (Sargassaceae, Fucales), with the Mediterranean harbouring the area with the highest biodiversity (Bruno de Sousa et al., 2019; Draisma et al., 2010; Orellana et al., 2019). Species of *Cystoseira s.l.* are erect perennials, and some of them are among the most long-lived macroalgae (Ballesteros et al., 2009; Capdevila et al., 2016; Navarro et al., 2012), having a key role by providing diverse ecosystem services for a high number of invertebrates, fishes, and other algal species (Giakoumi et al., 2012; Sala et al., 2012). Most species thrive in shallow photophilic rocky reefs and form distinctive forests dominated by one or a few species (Sales et al., 2012; Thibaut et al., 2005; Verdura et al., 2021). In the Mediterranean, all species of *Cystoseira s.l.*, except *Cystoseira compressa,* are considered highly threatened as they have experienced a severe decline in recent decades (UNEP-PAM-RAC/SPA, 2012), and some local extinctions have been reported in this basin (Blanfuné et al., 2016; Thibaut et al., 2015).

Habitat transformation, eutrophication, pollution, overgrazing, marine heat waves (Fabbrizzi et al., 2020; Soltan et al., 2001; Thibaut et al., 2014, 2015; Verdura et al., 2021), and competition with other marine species, such as mussels (Thibaut et al., 2005) and other macroalgae, have been proposed as factors responsible for the decrease in the extension of forests of *Cystoseira s.l.* The lower abundance of these macroalgae and their replacement by more opportunistic species on shorelines altered by human activity has been reported on numerous occasions (Arévalo et al., 2007; Kletou et al., 2018; Mancuso et al., 2018; Mangialajo et al., 2008; Rodríguez-Prieto and Polo, 1996; Sales and Ballesteros, 2009). Long-term studies link increased anthropogenic stress with the collapse of algal populations, both in the Mediterranean Sea (Blanfuné et al., 2016; Thibaut et al., 2005, 2014, 2015) and the NE Atlantic Ocean (Bernal-Ibañez et al., 2021). The recovery of forests of *Cystoseira s.l.* following re-oligotrophication (Iveša et al., 2016; Soltan et al., 2001) as well as the unviability of transplanting individuals to polluted zones (Sales et al., 2011) support the hypothesis that populations of *Cystoseira s.l.* require good water quality for their development (Arévalo et al., 2007; Bermejo et al., 2016; Pinedo et al., 2007).

Changes in seawater temperature are causing important shifts in the distribution and abundance of large brown algae worldwide, including some Fucales (e.g., Beas-Luna et al., 2020; Pfister et al., 2017; Voerman et al., 2013; Wernberg et al., 2010). In particular, the species and lineages of *Cystoseira s.l.* are considered sensitive organisms that can survive only within a relatively narrow range of environmental conditions and disappear from sites that undergo environmental changes (Arévalo et al., 2007; Dauvin et al., 2010). The direct relationship between an increase in temperature and a decrease in the populations of *Cystoseira s.l.* has recently been demonstrated following recent marine heat wave episode in the Mediterranean (Verdura et al., 2021). Thus, future projections point to the vulnerability and extirpation of some species in some areas (Buonomo et al., 2018), although local-scale climatic refugia have been also suggested

(Verdura et al., 2021). In the Atlantic, the increase in temperature has had a positive effect on populations of *Cystoseira s.l.* at the northern limit of its distribution. For example, populations of *Cystoseira foeniculacea* have expanded in southern Ireland since the late 20th century in coincidence with rising temperatures, although the expansion has also been favored by declining populations of the sea urchin *Paracentrotus lividus* (Trowbridge et al., 2011), a trend that is mirrored by populations of *Gongolaria baccata* in northern Spain (Méndez-Sandín and Fernández, 2016). Contrary to the expansion of these species, others, such as *Gongolaria abies-marina, Cystoseira humilis,* or *Ericaria selaginoides,* are suffering a sharp decline in distribution and population size (Bernal-Ibáñez et al., 2021; Sansón et al., 2014; Valdazo et al., 2017).

Gongolaria abies-marina, one of the few Atlantic species of *Cystoseira s.l.* with marginal populations in the Mediterranean, has been barely mentioned in the Balearic Islands, Murcia, and the area situated between Sicily and Libya. In the Atlantic, it is distributed along Macaronesia and at some sites along the adjacent northwestern coasts of Africa (Guiry and Guiry, 2022; Rodríguez-Prieto et al., 2013). Populations in the Canary Islands, Salvages, Madeira and Azores reach high development, making it a foundational species (Bernal-Ibáñez et al., 2021; Sangil et al., 2011, 2018). Particularly in the Canary Islands, populations of *G. abies-marina* were so abundant three decades ago that they formed dense forests from the beginning of the sublittoral zone along an extensive part of the rocky coasts of the islands (Gil-Rodríguez et al., 1992; Reyes et al., 2000). Nonetheless, populations are currently severely reduced to patches mostly occurring in a few sites exposed to waves on the north side of the islands (Sangil et al., 2011; Tuya and Haroun, 2006), with the loss of most of the forests mapped in the 1980s (Wildpret et al., 1987). The serious decline of *G. abies-marina* populations supported by scientific data has led to its inclusion in the Spanish Catalog of Threatened Species under the category of vulnerable (B.O.E., 2019), according to IUCN criteria.

Even though the decrease in populations of *Gongolaria abies-marina* in the Canary Islands is presumably related to an increase in surface seawater temperature and an increase in the densities of the sea urchin *Diadema africanum* in shallow rocky bottoms (Martínez et al., 2015a; Riera et al., 2014), no study provides clear evidence of the factors that have led to the near disappearance of this species. In this assessment, supported by a historical cartography of the dominant macroalgae beds on the Canary Islands (Wildpret et al., 1987), and samples obtained along the entire perimeter of the western islands, spatial information regarding possible drivers of decline of this species was gathered, with the purpose of solving four key aspects about the habitat and the long-term spatial trend of *G. abies-marina*: (1) its potential habitat, (2) its current distribution, (3) the magnitude of the decline and current conservation status, and (4) the specific factors most likely driving its loss.

2. Materials and methods

2.1. Study area

The Canary Islands are a subtropical archipelago located in the eastern North Atlantic Ocean (**Fig. 1**). As a result of the adjacent African upwelling, these islands show a longitudinal gradient of temperature and nutrients. Sublittoral forests of *Cystoseira s.l.* change according to this gradient, with communities monopolized by *Gongolaria abies-marina* on the western islands and mixed populations of several species, such as *G. abies-marina*, *Ericaria selaginoides*, *Cystoseira foeniculacea* and *C. compressa*, on the eastern islands (Sangil et al., 2014). In general, *Cystoseira s.l.* are located in rocky photophilic bottoms and do not exceed 3-6 m in depth, although in some exceptional areas, they exceed 30 m in depth (Martín-García et al., 2016; Reyes et al., 2000). Populations of *G. abies-marina* are more prevalent on the northern and northeastern coasts of the islands, which are more exposed to trade winds and strong swells (Elejabeitia and Afonso-Carrillo, 1994; Muñoz et al., 2007; Pinedo and Afonso-Carrillo, 1994; Sangil et al., 2006). Our study area includes all shallow sublittoral habitats of the westernmost Canary Islands, where *G. abies-marina* is potentially the most common species.

2.2. Data collection

The historical distribution of populations of *Gongolaria abies-marina* was compiled from a set of cartographic data from samplings performed along the entire coast of the Canary Islands between 1986 and 1987 (Wildpret et al., 1987). Maps were made by transferring field annotations to hard-copy paper cartography. Data were digitized into a file shape format (shp) using QGIS software, a free and open-source geographic information system (GIS) (http://www.qgis.org). The current distribution of *G. abies-marina* populations was recorded during 2017 by sampling the entire coastline of the four western islands (1079 km: 164 km from El Hierro, 274 km from La Palma, 133 km from La Gomera, and 508 km from Tenerife), which represents 46.14% of the total perimeter of the Canary Islands. Populations were distributed on rocky coasts from the upper limit of low tides to the shallow sublittoral, so samplings were performed during maximum low tides to avoid missing any populations. Fieldwork was conducted by boats, walking tours, visual inspection, snorkeling, and georeferenced photographs. The underwater television system Deep Blue Pro was used to locate the maximum depth of some populations. Data were recorded on a Tablet LENOVO 10.1” with an integrated GPS and the application MapIt (https://mapit-gis.com/) installed to collect mapping information together with a survey form designed for this study. The form includes the extension of *Gongolaria abies-marina* populations and photographs linked to each location. Subsequently, information was imported into QGIS to create the distribution area in shape format. Last, data were transferred to 0.25 km^2 grids (a polygonal vector in geopackage format) that divide the coastline of the western islands (**Fig. 1**). In total, 1427 grids present data on populations of *G. abies-marina* in 1987 and 2017. Data on the extension of populations were transformed to percent coverage considering the available hard substrate mapped in previous studies (Barquín-Diez and Martín-García, 2015).

2.3. Distribution model of *Gongolaria abies-marina* in the Canary Islands

The random forest (RF; Breiman, 2001) algorithm was used to model the spatial distribution of *Gongolaria abies-marina* using presence and absence data. The model was built, evaluated, and projected using the *sdm* package (Naimi and Araújo, 2016). For the modeling, a total of 400 points (locations with x, y positions) were used, corresponding to locations where the species is known to be present or absent in this study and in previous floristic and cartographic studies in the Canary Islands (Barquín-Diez and Martín-García, 2015; Martín-García et al., 2015, 2016; Rodríguez et al., 2008; Wildpret et al., 1987). A total of 119 points of presence correspond to the centroids of current and widespread areas or populations of *G. abies-marina* (**Fig. 1**). The other 291 points are absent where other communities or habitats had developed.

For the RF model, it is also necessary to use a set of variables related to physical and oceanographic descriptors, in this case: depth, slope, eastness, northness, distance to hard substrate, benthic position index (BPI; with a scale factor of 500 m), fetch and sea surface temperature (SST). These variables have been selected to obtain an independent model of stational or temporal changes. Except for fetch and SST, all other variables were extracted from the digital terrain models (DTMs) created by the Spanish Ministry of the Environment during several eco-mapping projects between 2003 and 2006. BPI describes the landscape on change in slope position, e.g., on ridges, flats, or slopes (Lundblad et al., 2006). More details about the topographic parameters are explained in Martín-García et al. (2013). Fetch, which is a common exposure parameter for coastal locations (Bekkby et al., 2009; Martín-García et al., 2014), was calculated as the average distance in meters from each site to the nearest shoreline in the 16 directions of the compass rose, with a maximum distance of 200 km. SST was also included in the model because of the Northwestern African upwelling that maintains a constant and longitudinal gradient of temperature on the surface waters of the Canary Islands (Barton et al., 1998). Mean values of the last ten years (2007-2017) were obtained from the global product Group for High Resolution Sea Surface Temperature (GHRSST) Level 4 sea surface temperature analysis (JPL OurOcean, 2010). All variables were in raster asci format and had an initial resolution of 5 m but were resampled to 100 m to facilitate analysis and computation time. Before computing the model, variables were evaluated for collinearity using the variance inflation factor (VIF) and used for habitat model construction. Data, variables, and results were manipulated or created with QGIS and R software.

The resulting model was evaluated with the area under the curve (AUC) of the receiver operating characteristic (Fielding and Bell, 1997) with bootstrapping (random sampling with replacement; Efron and Tibshirani, 1993) resampling 100 times. The evaluation was calculated using the *dismo* package and the result was reported as a mean of the AUC with the confidence limits. The true skills statistics maximization approach (Max. TSS, sensitivity and specificity combined; Allouche et al., 2006) was used as a threshold to convert the model into a binary raster and make possible a comparison with the cartography in 1987. Finally, the cartography of 1987 in shape format was also transformed into a raster with the same resolution of the model (100 m) to calculate a confusion matrix using the R package caret (Kuhn, 2020) to analyze the relationship, similarities and differences between the model and these historical data.

2.4. Driving factors for spatiotemporal changes in *Gongolaria abies-marina* population distribution

Climatic and anthropogenic factors were gathered and evaluated as possible causal drivers of the strong decline in populations of this species. Of them, sea surface temperature (SST), percentage of waves with significant height greater than 4 m (hereinafter Hs4 m) and ultraviolet radiation (UV) were selected because they are known to influence the status of sublittoral communities (Sangil et al., 2011) and provide the temporal ranges of the sampling periods (1987 and 2017). Monthly mean, minimum and maximum values were calculated for each of these three variables and each period. Variables that showed a higher relationship with the coverage differences of the species were selected. Then, data were analyzed as an average for the periods between 1982-1987 and 2012-2017 to obtain the average conditions that existed when the sampling was performed and for the region between latitudes 27 and 29 north and longitudes 13 and 19 west (**Fig. 1**). Finally, the differences between values of these two periods were used for the analysis. The human footprint is another variable included in the analysis although there is no available time series and thus, only a spatial analysis was performed. Other data sources about human impact on the coast of the study area were considered: distance to sewage outfalls, population density or distance to urban centers, among others. However, the resolution of these variables was not enough for this study or there was no data time series. Data on herbivory of the most abundant sea urchin *Diadema africanum* were not considered because of its deeper distribution (Sangil et al., 2011, 2014). Details about each variable are explained below.

Sea surface temperature (SST). Data were obtained from the Global Product Group for High Resolution Sea Surface Temperature (GHRSST) Level 4 Sea Surface Temperature analysis (JPL OurOcean Project, 2010), which is produced daily with a spatial resolution of 0.01 degrees (1 km) by the JPL OurOcean group using satellite data from several sensors and *in situ* data from drifting and moored buoys. Mean values of SST for both summer/warmest months (July, August, September) and winter/coldest months (January, February, March) were calculated for the two periods 1982-1987 and 2012-2017.

Hs4 m. Tables with monthly wave heights for the SIMAR database were obtained from a considerable time series of wind and swell parameters from numerical models provided by “Puertos del Estado” (http://www.puertos.es/en-us, Appendix A). These datasets have a spatial resolution of approximately 12.5 km. Data were downloaded from 76 points from the SIMAR grid around the western Canary Islands, and the relative frequency of waves exceeding the 4 m threshold in significant height (Hs) was selected after evaluating all the parameters offered by the SIMAR database and its correlation with the coverage differences of the species. This significant wave height threshold was established to be considered an indicator of wave exposure in extreme events that affect the species. Similar data have been used for other regions and species (Borja et al., 2018).

Human Footprint. The footprint raster layer provides a global map of cumulative human pressure on the environment in 2009, with a spatial resolution of ~1 km. The dataset is supplied by the Data Center in NASA's Earth Observation System Data and Information System (EOSDIS) and produced by Venter et al. (2016). This database is only available for the pressures in 1993 and 2009 and does not cover the temporal range analyzed in this study. However, it has been considered spatial data of human pressure without any temporal analysis. Human pressure is measured using eight variables, including urbanized environments, population density, electrical power infrastructure, farmlands, grasslands, roads, railways, and waterways. This is a terrestrial variable, but this parameter may have a direct relationship with *Gongolaria abies-marina* since it is a coastal species that grows in the shallow rocky sublittoral.

UV radiation at the sea surface. Sea surface UV radiation is one of the data products of the European Centre for Medium-Range Weather Forecasts (ECMWF) atmospheric reanalysis ERA5 and is available from the webpage https://cds.climate.copernicus.eu/. This is the amount of UV radiation (J/m^2) with a wavelength of 0.20-0.44 μm reaching the sea surface. It is a monthly averaged reanalysis with a resolution of 0.25 degrees (approximately 25 km) and was downloaded only for the Canary Islands and converted to watts per square meter (W/m2), divided by the accumulation period (one day) expressed in seconds.

The values of all the selected variables were included in the grid of 500 m resolution (1427 cells) as the differences between the values of 1987 and 2017, except for the human footprint since its historical data were not available, then the last version of 2009 was used and included to analyze its spatial influence. Cartographic data about the coverage differences of *Gongolaria abies-marina* between each period were also included in the grid. QGIS and R software (packages *Raster* and *ncdf4*) were used for further transformations of variables and the inclusion of data in the grid around the western Canary Islands.

2.5. Data analysis of driving factors.

A multivariate geographically weighted regression (GWR) model was used to analyze the relationship between changes in the distribution of *Gongolaria abies-marina* from 1987 to 2017 and changes in environmental and human factors considering spatial heterogeneity. In a global regression model, data values are independent of geographical location, there is no spatial correlation, and the sample data are balanced. Then, global analysis could mask possible relations that occur or take place only in certain regions of the study area, since the relationship between variables may change spatially. GWR describes a family of regression models in which the coefficients are allowed to vary spatially (Fotheringham et al., 2002) by reviewing the sample point or zone centroid and, therefore, are estimated based on the samples in the local window at that moment, which is centered on the current point. The GWR fitted model equation is as follows (Nakaya, 2016):

$$y_i = \beta_0(u_i, v_i) + \sum_k \beta_k\,(u_i, v_i) X_{k,i} + \varepsilon_i$$

where y_i is the dependent variable of sample i, the individual sample; (u_i, v_i) is the coordinates of sample i; $\beta_k(u_i, v_i)$ is the k^{th} regression parameter of sample i; $X_{k,i}$ is the k^{th} independent variable for sample i; and ε_i is the random error at location i.

The spatial kernel controlling the distance-decay function can take either a fixed (distance) or adaptive (number of samples) approach to establish the radius of the local GWR model, in effect creating a moving window regression for each observation point in the study area (Fotheringham et al., 2002; Windle et al., 2010). All the samples in the local window are weighted according to their distances from the corresponding current point. The size of the kernel bandwidth has a substantial impact on the outcome of the GWR analysis and should be selected carefully. In this study, the adaptive kernel function is used to calculate bandwidth, and the Gaussian kernel is used to weight the observations and run the GWR function. The kernel bandwidth was determined by minimizing the cross-validation (CV) score for the fitted regression model. The multivariate GWR model and kernel bandwidth were developed using the *spgwr* package (Bivand et al., 2020) of R software.

3. Results

3.1. Changes in spatial distribution areas

Data from 1987 show that *Gongolaria abies-marina* populations were distributed around almost the entire perimeter of the western Canary Islands, with a total extension of 4402 ha (**Table 1**), forming continuous belts and/or beds on the rocky sublittoral zone of each island. La Palma showed lower coverage, highlighting the absence of assemblages along the northeast coasts, where conditions are favorable for the species. This is because it was impossible to sample due to bad meteorological/oceanographic conditions, as explained in the technical data source used. One location in the north of La Gomera (Los Órganos) was also not sampled for the same reason. Tenerife was the island with the largest extensions of *G. abies-marina*. By default, all populations represented in this cartography have a bathymetric limit of 10 m depth, since the study did not use technologies that would allow sampling at greater depths.

Data from 2017 shows that *Gongolaria abies-marina* populations are located almost exclusively in the north and northeastern sides of the islands in wave-exposed coasts. The distribution area is extremely fragmented, forming small patches (< 2 m^2) or belts (< 2 m width) at the beginning of the sublittoral zone. Only 9 populations showed an extension higher than 1 ha, representing 71% of the total extension (129 ha) (**Table 1**). The largest population is located in the north of Tenerife (Punta del Hidalgo), with an extension of 66 ha (51% of the total area) from the low tide limit to 9-16 m depth. The other largest populations are found close by the previous one (Anaga, S/C de

Tenerife), a second in northwest El Hierro (Baja de Los Negros, Frontera) and a third in northeast La Palma (Barlovento), in the area that was not sampled in 1987.

Comparison of data between 1987 and 2017 shows a strong decline, greater than 97% in the entire coastline of the four islands (**Fig. 2**). Populations in northern La Palma and La Gomera are again exceptions, as *G. abies-marina* was not registered in 1987 because of logistical constraints.

3.2. Model distribution

The resulting RF model has an AUC value of 0.96 and a TSS of 0.84. The three variables that most contributed to the model were northness (23%), distance to soft bottom (16%) and BPI 500 (9.3%) (**Fig. 3**). Model parameters show that areas with a high probability of occurrence are slope and rocky platforms, away from soft bottoms, in the north facing shores (**Fig. 4**). The value of max TSS (0.51) was used as the threshold to convert the model into a binary raster (**Fig. 2**). A visual comparison between the two maps shows that the predicted distribution and the cartography of 1987 have an important level of concordance in the north of the islands, especially in some areas where there are wide belts of *Gongolaria abies-marina* in both 1987 and 2017 (**Fig. 2**).

The confusion matrix obtained between the model and cartography 1987 had a high value of accuracy and specificity but a low value of sensitivity and Kappa (**Table 2**). These results show that the model has a correct prediction of the true absences, but the prediction accuracy is lower for true presences, since almost 70% of the presence data in 1987 cartography was classified as absence in the model (**Table 1**). This happens because the model does not include most of the beds in the south of the islands, especially in Tenerife, the only island with a smaller potential distribution area than cartography in 1987 (**Table 1**). On the other hand, the model includes locations with

Gongolaria populations represented in 2017 cartography and cited in other studies but not included in 1987 due to limited access to the sites or the presence of meadows beyond 10 m depth.

3.3. Exploratory analysis of drivers of decline

The four variables considered in this study show highly significant differences in the spatial or temporal comparison, especially for SST and UV radiation (**Fig. 5**). Spatially, both variables show increasing values from Tenerife to El Hierro. The coasts of El Hierro have warmer waters and higher radiation values than the others, and Tenerife holds the coldest waters and the lowest radiation levels. These parameters have an important local variation at each island, showing higher values on the southwest coasts (**Fig. 6**). Temporarily, parameters tend to rise significantly in all the islands, drastically for SST. Again, these differences in both variables UV radiation and SST are more remarkable on the southwestern coasts (**Fig. 6**).

Wave exposure (Hs4 m) presents a greater range of variation in Tenerife and La Palma, which have a greater coastal perimeter. These islands also show the highest wave values, especially on their northern coasts (**Fig. 6**). In contrast, La Gomera, which is protected by Tenerife from prevailing winds and currents, exhibits the lowest values and lowest temporal changes. This parameter tends to decrease significantly in all the islands over time, except in La Gomera. The northeast coast of Tenerife presented the greatest decrease in Hs4 m between 1987 and 2017 (**Fig. 6**).

Footprint also shows high differences between islands, with the greatest human impact in Tenerife and the lowest values in El Hierro (**Fig. 6**). This parameter presents significant local differences: Tenerife has areas with a low human footprint in the northeast and northwest ends of the island, comparable to El Hierro or La Gomera, but other areas with the highest values (**Fig. 6**).

3.4. Analysis of the multivariate GWR model

The initial global multivariate model (R^2 = 16.6%) shows significant relationships between the differences in *Gongolaria* coverage and changes in Hs4 m and the human footprint and UV radiation but with a higher p value (**Table 3**). However, there is no significant relationship with SST.

Even so, the GWR model (with an adaptative quantile of 8.6% and R^2 = 0.214) shows that the effects of variables on *Gongolaria* coverage are significantly different in terms of spatial heterogeneity. Descriptive statistics for local parameter coefficients produced by GWR reveal much variation in parameter values (**Table 4**), suggesting the presence of spatial nonstationarity (it means that the statistical properties change through space) in relationships between the decline in *Gongolaria* coverage and the explanatory variables of temporal changes. The GWR presents low R^2 but shows that even noisy, high-variability data have a significant trend with low p values, indicating a true relationship between the significant predictors and the response variable.

Footprint and Hs4 m have the greatest relationship on species coverage at a spatial scale. Footprint has a significant negative relationship in Tenerife and La Palma, with the highest values in this parameter (**Fig. 7**). Therefore, a high human footprint is related to a high coverage loss. In the case of Hs4 m, the lower proportion of high waves has a meaningful relationship with the decrease in *Gongolaria* over time, and it is especially important north of Tenerife and west of La Gomera. UV radiation is significant in Tenerife and northeast La Palma, where the increase in radiation in the last 30 years has a strong relationship with the decrease in algal coverage. Changes in SST were only significant in small areas in the north and southeast of Tenerife, where SST increased by 0.4-0.5 °C (**Fig. 7**).

4. Discussion

Our study shows that both environmental and human drivers have a direct and clear relationship with the reduction in *Gongolaria abies-marina* forests. Our comparisons between data from 1987 and 2017 highlight a drastic decline of more than 97% of their former extension in the western Canary Islands, which indicates a serious threat toward the extinction of this species. Historically, populations of *G. abies-marina* formed extensive forests in the shallow sublittoral zone of the islands up to more than 10 m depth (Wildpret et al., 1987). However, populations are currently highly fragmented; they have disappeared from many localities, and when they are present, they are mostly relegated to the uppermost sublittoral zone. It seems to be no exception. Other macaronesian archipelagos, such as Madeira, are registering an important decline of different species of Sargassaceae family (Bernal-Ibáñez et al., 2021). Drastic reduction of these species is observed in Azores, although there are no references to the conservation status. Several studies conducted both in the NE Atlantic and Mediterranean have shown similar regressions in populations of other species of *Cystoseira*, *Ericaria*, and *Gongolaria*, which also formed underwater forests decades ago. Among them, at least seven habitat-forming species of *Ericaria*, seven species of *Gongolaria*, and six *Cystoseira* spp. have been documented to be in progressive decline during the last decades (Bernal-Ibáñez et al., 2021; Blanfuné et al., 2016; Mariani et al., 2019; Thibaut et al., 2005, 2014, 2015; Valdazo et al., 2017; **Tables 5-7**). The magnitude of the population decline and the conservation status differ depending on the species and localities.

According to our model, *Gongolaria abies-marina* forests persist in habitats with rocky sloped platforms, away from soft seabeds and mainly on the northern coasts exposed to waves. Other species of *Cystoseira s.l.* grow on similar bottoms, and others inhabit sheltered habitats and rocky pools (**Tables 5-7**). The distribution model of

Gongolaria abies-marina shows a high correlation with the cartography of the populations in 1987. This model allows an understanding of the suitability of localities that could not be sampled (e.g., some localities in 1987). The model can thus offer relevant information in regions where there is no historical mapping of distribution, showing the state of conservation with high accuracy. Similar modeling tools have been used to identify the potential distribution of algae, whether invasive (Banerjee et al., 2019) or foundational species (Fabbrizzi et al., 2020; Martínez et al., 2015b), and reproduce the distribution area of the species at a broad scale.

Our results show that the resilient populations of Canarian *Gongolaria abies-marina* are in the north side of the islands, which can function as local climatic refugia, similar to the results shown by Verdura et al. (2021) for populations of *Ericaria crinita* in a Mediterranean locality. Similar spatial inequalities have been detected in other Mediterranean species. For example, populations of *Ericaria amentacea* have undergone a slight reduction (Soltan et al., 2001; Thibaut et al., 2014, 2015), while *E. brachycarpa* has suffered a notable decline (Thibaut et al., 2005, 2015). *Ericaria crinita* has been extirpated in some locations (Thibaut et al., 2005) but not in others (Sales & Ballesteros, 2009; Verdura et al., 2021). In contrast, some species have increased their coverage, such as *Cystoseira compressa* (Thibaut et al., 2005) and *Cystoseira corniculata* (Tsiamis et al., 2013).

Similar changes in the distribution and abundance have been observed in other groups of canopy-forming macroalgae on the temperate coasts of the Atlantic Ocean (Martínez et al., 2015a). Among the brown algae, other Fucales (*Ascophyllum nodosum, Fucus guiryi, F. serratus, F. vesiculosus, Himanthalia elongata*) (Díez et al., 2012; Fernández, 2011; Jueterbock et al., 2013; Viejo et al., 2011) and Laminariales (*Laminaria hyperborea, L. occhroleuca, Saccorhiza polyschides, S. latissima*)

(Fernández, 2011; Voerman et al., 2013) are much less abundant or have disappeared in locations where they were dominant. Some habitat-forming red algae, such as *Gelidium corneum* and *Chondrus crispus*, have also suffered a drastic decrease in their distribution and coverage in the temperate NE Atlantic region (Borja et al., 2013; Díez et al., 2012; Martínez et al. 2015a). In particular, two endemic *Gelidium* species (*G. canariense* and *G. arbuscula*) from shallow rocky sublittoral areas on highly exposed coasts of the Canary Islands show a similar pattern of decline (Alfonso et al., 2021), including locations where they were exploited for industrial purposes in the past (Afonso-Carrillo, 2003).

Here, we show that wave exposure and the human footprint are key drivers of the current distribution and temporal changes in *Gongolaria abies-marina* populations. As the human footprint and wave exposure have the highest relation on coverage loss, UV radiation and SST only seem critical in specific locations. Our results, in contrast with those obtained by Valdazo et al. (2017), point to human footprint affects the conservation status of these forests, especially in Tenerife the most overcrowded island, even if it shows differences between localities. Although it was not possible to analyze temporal changes in this parameter, it is obvious that there has been an increase in human pressure on littoral sites in the Canary Islands in recent decades (ISTAC, 2021). For instance, the human population in Tenerife has increased by 275,556 people between 1987 and 2017, according to official statistics (ISTAC, 2021). The spatial relation between human pressure and loss of *G. abies-marina* populations suggests that if footprint data from 30 years ago had been available, we would also have obtained a temporal significant correlation. **Figure 8** shows areas where the human impact has increased in the last 30 years (two different areas of Tenerife), which correspond to areas with highest human footprint values, and total disappearance of *G. abies-marina* populations in recent decades. On the contrary, areas with lowest human footprint values (in La Gomera and La Palma), human activities have not changed over time and populations are still present. In any case, it would be interesting to complement these studies with future analysis of more specific data about temporal changes on human activity in coastal zones.

Wave exposure is one of the main drivers affecting the coastal environment (Sierra and Casas-Prat, 2014) and has important effects on benthic species (Borja et al., 2018; Burrows, 2012). However, the use of this parameter in species distribution studies is limited, probably because of reduced information and lack of consensus in some areas and climate projections (Morim et al., 2018). Our study shows that wave exposure tends to decrease significantly over the years in the Canary Islands, in agreement with the results of Morim et al. (2018), which show a decrease in wind waves over the North Atlantic based on the revision of wave climate projection studies. Wave exposure also has a greater variation between islands, with the northern coasts being the most exposed, so it could play a key role in the conservation of *G. abies-marina* forests in the archipelago. For example, the current largest (66 ha) and deepest populations, which represent half of what remains, are concentrated in a single locality (Punta del Hidalgo) north of Tenerife. The particular geomorphological and oceanographic conditions of this locality, with large shallow rocky platforms and high exposure, help maintain large macroalgae assemblages and exuberant populations of *Gongolaria*, although with a decrease in the size of individuals over time (Sansón et al., 2014).

On the other hand, both SST and UV radiation vary along the oceanographic east–west gradient of the islands and have increased over time. These two variables influence all stages in macroalgal life cycles (Sierra and Casas-Prat, 2014) and are also regarded as major factors determining the zonation of seaweeds in shallow waters

(Bischof et al., 1998; Dring et al., 1996; Maegawa et al., 1993). Geppi and Riera (2022) found that the increase in sea temperature seems to affect the morphology of some algae in the Canary Islands. Nevertheless, our results indicate only local effects on populations of certain islands or even on small sites on the islands.

Discrete periods of high anomalies temperatures in the ocean, called marine heatwaves (MHWs), are becoming more frequent and intense (Hobday et al., 2016; Oliver et al., 2021; Smale et al., 2019) and have significant impact on marine life, including marine forests (Filbee-Dexter et al., 2020). A worldwide evaluation of MHWs found moderate to low incidence of these events for Macaronesia and adjacent continental shores (Oliver et al., 2018; Holbrook et al., 2019). Regional studies show that although MHWs are becoming more intense and frequent (Bernal-Ibánez, 2022; Castrillo-Acuña 2021), they present important spatial variations (Castrillo-Acuña 2021) with the Canary basin as the least favorable region to suffer these events. This region presents permanently warm waters between 21 and 24 °C with intense anticyclonic eddies that lead to a deepening of the mixed layer (Sangrá et al. 2009) and favor heat dissipation (Castrillo-Acuña, 2021). Using these features as a reference, an additional analysis was carried out to test the relation between MHWs and the decline of *G. abies-marina*. Using a daily global 5km-resolution Marine Heatwave category data from Satellite and Information Services about Coral Reef Watch (https://coralreefwatch.noaa.gov/product/marine_heatwave/), we get and compare the maximum intensity of heatwaves for the periods between 1985-1987 and 2015-2017. This data confirms that the heatwaves have increased especially in certain areas like the African coast and but they present low frequency and intensity in the western islands of the Canary archipelago (see Figure 9) with 1-2 events per year and intensity of between 1.5-2.5 °C respectively. In any case, the spatial distribution of this parameter did not present a correlation with the coverage of *G. abies-marina* and its decline; therefore, this variable was not analyzed as a possible driver of change in the algae populations. This result is consistent with the tolerance temperature threshold of *G. abies-marina*. This species can grow over a wide range of temperatures up to a maximum of 25 ºC (Sangil et al., 2018). Then, it grows at temperatures higher than those normally recorded in the western Canary Islands and at the level of MHWs that have been recorded in this area. All evidence indicates that the species can grow under the conditions of the current MHWs.

Studies about the possible causes of the decline of this species in other Macaronesian archipelagos are still scarce. Bernal-Ibáñez et al. (2021) suggest that the increase of urbanization and tourism, associated with habitat destruction and the degradation of water quality, may impact on the canopy-forming brown macroalgae in Madeira. Changes in the light and turbidity regimes represent other possible detrimental impacts (Bernal-Ibáñez et al. 2021). However, the effect of these impacts has not yet been proven. The present study is the first to show a cause effect relationship between human and environmental variables and the drastic changes in the distribution of a sublittoral fucalean species in Macaronesia.

In the Canary Islands, species of *Gongolaria* (*G. abies-marina* and *G. mauritanica*) and *Ericaria selaginoides* are regionally protected within the framework of the Canary Islands Checklist of Protected Species (Law 4/2010, of 4 June 2010). From 2019, and thanks to data provided by this study, these species are now included in the Spanish Checklist of Threatened Species as vulnerable. Nevertheless, the rapid and strong decline of *G. abies-marina* forests studied here and considering the difficulty of reducing or eliminating the causes of this decline, we have reported this situation to the competent authorities to increase its protection category and dedicate more effort on strategies for the conservation and restoration of these macroalgae forests. Currently our studies are focused on mitigating the loss of these underwater algae forests, carrying out a detailed monitoring of the macroalgal communities and colonization experiments in the best areas detected throughout this study on each island of the Canary archipelago.

Acknowledgments

We are grateful to all the skippers who took us around each of the islands during the project: Juan, Cristopher and Denis (La Gomera), Adrián, Raquel, Alexander, Víctor, Vilayta and the fishermen Don Antonio, Norberto and Adán (Tenerife), Joseba and Irving Landaeta (El Hierro), and Miguel and Yajaira (La Palma). We are also grateful to Tamia Brito and the staff of Marine Reserves of La Palma and El Hierro for their help and company during the sampling on these islands, to Leopoldo Moro for his support throughout the project and Pablo Martín-Sosa for the revision of the manuscript. This research was co-funded by the Canary Government (*Dirección General de Protección de la Naturaleza, Viceconsejería de Medio Ambiente del Gobierno de Canarias*) and the European Regional Development Fund (ERDF).

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Tables

Table 1. Extension of *Gongolaria abies-marina* populations (in hectares) and relative percentage between extension in 1987, 2017 and RF model. True + correspond to data of 1987 represented in the model.

	El Hierro	La Gomera	La Palma	Tenerife	Total
1987	655.6	306.4	555.0	2885.3	4402.5
Model	721.0	333.9	796.1	2390.5	4241.5
True +	376.3	101.5	201.4	669.1	1348.4
2017	20.9	3.9	4.5	99.6	128.9
% 2017 vs 1987	3.2	1.3	0.8	3.5	2.9
% 2017 vs model	2.9	1.2	0.6	4.2	3.0
% 1987 vs model	57.4	33.1	36.3	23.2	30.6

Table 2. Results of confusion matrix obtained between the model and data of *Gongolaria abies-marina* populations in 1987.

Accuracy	0.9371
95% CI	(0.9361, 0.9382)
Kappa	0.2352
Sensitivity	0.2065
Specificity	0.980
Balanced Accuracy	0.593

Table 3. Parameter estimates for the global regression model of *Gongolaria abies-marina* populations

	Estimate	Std. Error	t value	p-value	
Intercept	5.16	4.29	1.20	0.229	
Dif. Radiation	-11.81	7.06	-1.67	0.095	.
Dif. HS4	21.20	1.79	11.85	0.000	***
FootPrint	-0.28	0.04	-6.82	0.000	***
Dif. SST	-1.62	3.91	-0.41	0.680	

982 **Table 4.** Summary statistics of the GWR coefficient estimates.

	Minimum	**Lower quartile**	**Median**	**Upper quartile**	**Maximum**	**Global**
Intercept	-14.923	2.067	12.713	44.865	62.736	11.225
Dif.Radiation	-128.509	-100.084	-32.380	-1.597	33.377	-23.654
Dif. Hs4	13.032	16.473	18.358	29.046	34.116	21.528
Footprint	-0.616	-0.360	-0.148	-0.064	0.287	-0.273
Dif. SST	-3.203	4.595	10.080	15.393	28.928	6.940

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Table 5. Documented status of populations of species of *Ericaria* in Northeastern Atlantic Ocean and Mediterranean Sea. *Different trends of populations register in different sites in the same study and habitat. Abbreviations: n.d., not defined.

Species	**Ecological role**	**Habitat**	**Locality/country**	**Time period**	**Trend/status**	**Method/data available**	**Driver of change**	**Reference**
E. amentacea (C.Agardh) Molinari and Guiry	Habitat-forming species	Shallow rocky wave-exposed zones	Marseille, France, NE Mediterranean	1972-1974 1995-1996	Slight decline	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Soltan et al., 2001
	Habitat-forming species	Shallow rocky wave-exposed zones	Corsica, France, WE Mediterranean	1700 2008-2009 2010-2011	Slight decline	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Thibaut et al., 2014
	Habitat-forming species	Shallow rocky wave-exposed zones	France, NW Mediterranean	1826 2007-2013	Slight decline	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Thibaut et al., 2015
	Belt-forming species	Shallow sublittoral, 2-3 m depth, wave-exposed habitats	W Istria, N Adriatic	1950-2013	Well established	Revisit historical records	Eutrophication levels	Ivesa et al., 2016
E. brachycarpa (J.Agardh) Molinari and Guiry	Photophilic species	Shallow sublittoral, 0-4 m depth, sheltered habitats	France, W Mediterranean	1907, 2003	Decline	Revisit historical records	Habitat transformation, pollution, overgrazing, competition vs mussels	Thibaut et al., 2005
	Photophilic species	Littoral pools and sublittoral, moderately exposed habitats	France, NW Mediterranean	1899 2007-2013	Decline	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Thibaut et al., 2015
	n.d.	n.d.	Girona, Spain, W Mediterranean (several sites)	1907-2019	Present – Unknown*	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Mariani et al., 2019
E. crinita (Duby) Molinari and Guiry	Accompanying species, locally abundant	Sheltered rocky pools	France, W Mediterranean	1905, 2003	Extinct	Revisit historical records	Habitat transformation, pollution, overgrazing, competition vs mussels	Thibaut et al., 2005
	Belt-forming species	Very shallow and sheltered habitats	Corsica, France, WE Mediterranean	1958-2007	Well established	Quantitative and historical data	n.d.	Sales and Ballesteros, 2010
	Accompanying species, locally abundant	Sheltered rocky pools	France, NW Mediterranean	1826 2007-2013	Dramatic decline	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Thibaut et al., 2015
	Belt-forming species	Very shallow and sheltered habitats	Marseille, France, NE Mediterranean	1700 2010-2016	Decline (few individuals)	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Blanfuné et al., 2016
			Var, France, NE Mediterranean	1821 2010-2016	Well established			
			Corsica, France, WE Mediterranean	1822 2010-2016	Well established			

E. crinita (Duby) Molinari and Guiry	Belt-forming species	Very shallow and sheltered habitats	France, NW Mediterranean	1824 2010-2016	Decline	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Blanfuné et al., 2016
			Languedoc, France, N Mediterranean	1834 2010-2016	Decline (only 1-2 m^2)			
			French Catalonia, France, W Mediterranean	1883 2010-2016	Extinct			
	Belt-forming species	Shallow sublittoral to 40 m depth, sheltered and wave-exposed habitats	W Istria, N Adriatic	1950-2013	Well established	Revisit historical records	Eutrophication levels	Ivesa et al., 2016
	n.d.	n.d.	Girona, Spain, W Mediterranean (several sities)	Since 1907	Present – No present *	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Mariani et al., 2019
		Sublittoral cove		Since 1982	Decline			
		Rock pool		Since 2002	Present – Stable*			
	Habitat-forming species	Upper rocky sublittoral, wave-sheltered	Girona, Spain, W Mediterranean	2014-2017	High mortality	Quantitative and historical data	Marine heat wave	Verdura et al., 2021
					Population unimpacted			
E. funkii (Schiffner ex Gerloff and Nizamuddin) Molinari and Guiry	n.d.	Sublittoral (12-30 m depth)	France, W Mediterranaean	1908-2003	Extinct	Revisit historical records	Habitat transformation, pollution, overgrazing, competition vs mussels	Thibaut et al., 2005
E. mediterranea (Sauvageau) Molinari and Guiry	Belt-forming species	Shallow sublittoral (0-1 m depth)	France, W Mediterranaean	1904, 2003	Decline (50%)	Revisit historical records	Habitat transformation, pollution, overgrazing, competition vs mussels	Thibaut et al., 2005
E. selaginoides (Linnaeus) Molinari and Guiry	Belt-forming species	Intertidal and shallow rocky sublittoral, exposed habitats	Madeira, Portugal, SE Atlantic Ocean	1980-2021	Decline	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Bernal-Ibánez et al., 2021
E. zosteroides (C.Agardh) Molinari and Guiry	n.d.	Sublittoral (12-30 m depth)	France, W Mediterranaean	1907, 2003	Decline	Revisit historical records	Habitat transformation, pollution, overgrazing, competition vs mussels	Thibaut et al., 2005
	Accompanying species	Sublittoral to 80 m depth	France, NW Mediterranean	1929 2007-2013	Stable	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Thibaut et al., 2015

Table 6. Documented status of populations of species of *Gongolaria* in Northeastern Atlantic Ocean and Mediterranean Sea. *Different trends of populations register in different sites in the same study and habitat. Abbreviations: n.d., not defined.

Species	**Ecological role**	**Habitat**	**Locality/country**	**Time period**	**Trend/status**	**Method/data available**	**Driver of change**	**Reference**
G. abies-marina (S.G.Gmelin) Kuntze	Belt-forming species	Shallow sublittoral to 10 m depth, sheltered to wave-exposed habitats	Gran Canaria, Canary Islands, NE Atlantic	1980-2010	Dramatic decline	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Valdazo et al., 2017
	Belt-forming species	Rocky infralittoral to upper circalittoral	Madeira, Portugal, SE Atlantic Ocean	1980-2021	Decline	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Bernal-Ibánez et al., 2021
G. baccata (S.G.Gmelin) Molinari and Guiry	n.d.	n.d.	France, NW Mediterranean	Before 1950; 2007-2013	Exclude	Revisit historical records	Habitat transformation, pollution, overgrazing, competition vs mussels	Thibaut et al., 2015
	Belt-forming species	Low intertidal	Bañugues , Spain, NE Atlantic	1977; 2007	Increase	Quantitative data	n.d.	Méndez-Sandín and Fernández, 2016
G. barbata (Stackhouse) Kuntze	Accompanying species, locally abundant	Sheltered shallow sublittoral to 5 m depth, with sediments	France, W Mediterranean	1906-2003	Extinct	Revisit historical records	Habitat transformation, pollution, overgrazing, competition vs mussels	Thibaut et al., 2005
	Accompanying species, locally abundant	Sheltered shallow sublittoral	France, NW Mediterranean	1825 2007-2013	Dramatic decline	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Thibaut et al., 2015
	Dense forests	Sheltered shallow sublittoral to 3m depth	W Istria, N Adriatic	1950-2013	Well established	Revisit historical records	Eutrophication levels	Ivesa et al., 2016
	n.d.	Mainly sandy and most rocky shores	Girona, Spain, W Mediterranean (several sities)	1836-2019	Present – Absent – Not present*	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Mariani et al., 2019
G. elegans (Sauvageau) Molinari and Guiry	Accompanying belt-forming species	Sheltered rock pools to 2-4 m depth	France, W Mediterranean	1891, 2003	Almost extint	Revisit historical records	Habitat transformation, pollution, overgrazing, competition vs mussels	Thibaut et al., 2005
	Accompanying belt-forming species	Sheltered rock pools to 2-4 m depth	France, NW Mediterranean	1912-2013	Locally extinct	Revisit historical records	Habitat transformation, pollution, overgrazing, competition vs mussels	Thibaut et al., 2015
	Accompanying belt-forming species	Sheltered rock pools to 2-4 m depth	Medes I.; Girona, Spain, W Mediterranean	2001-2016	Stable	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Medrano et al., 2019
	n.d.	n.d.	Girona, Spain, W Mediterranean (several sities)	1907, 1978, 1982	Not present	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Mariani et al., 2019
		Deep exposed habitats		1979-2019	Present			
		Rock pool		Unknown	Present			

Species	**Ecological role**	**Habitat**	**Locality/country**	**Time period**	**Trend/status**	**Method/data available**	**Driver of change**	**Reference**
G. montagnei (J.Agardh) Kuntze	n.d.	Sheltered deep rock pools	France, W Mediterranean	1905-2003	Extinct			Thibaut et al., 2005
	Accompanying species	Shallow exposed sublittoral (to 1 m depth)	France, NW Mediterranean	Before 1950; 2007-2013	Stable? or increasing	Revisit historical records Quantitative and historical data	Habitat transformation, pollution, overgrazing, competition vs mussels	Thibaut et al., 2015
	n.d.	Rock pools to 30-50 m depth			Locally extinct			
		Sublittoral to 70 m depth			Dramatic decline			
	Belt-forming species	Shallow sublittoral to 40 m depth, sheltered and wave-exposed habitats	W Istria, N Adriatic	1950-2013	Well established	Revisit historical records	Eutrophication levels	Ivesa et al., 2016
	n.d.	n.d.	Girona, Spain, W Mediterranean	Unknown	Present	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Mariani et al., 2019
G. sauvageauana (Hamel) Molinari and Guiry	Accompanying species	Innermost areas	Languedoc, France, NW Mediterranean	1883-1937	Extinct	Revisit historical records Quantitative and historical data	Habitat transformation, pollution, overgrazing, competition vs mussels	Thibaut et al., 2005
	Accompanying species	Innermost areas	France, NW Mediterranean	1940 2007-2013	Decline	Revisit historical records	Habitat transformation, pollution, overgrazing, competition vs mussels	Thibaut et al., 2015
	Belt forming species	Mainly sandy and most rocky shores	Girona, Spain, W Mediterranean (several sities)	Unknown	Present	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Mariani et al., 2019
				1836-2019	Not present			
G. squarrosa (De Notaris) Kuntze	n.d.	Sea surface and prots	France, NW Mediterranean	1842 2007-2013	Not present	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Thibaut et al., 2015

Table 7. Documented status of populations of species of *Cystoseira* in Northeastern Atlantic Ocean and Mediterranean Sea. *Different trends of populations register in different sites in the same study and habitat. Abbreviations: n.d., not defined.

Species	Ecological role	Habitat	Locality/country	Time period	Trend/status	Method/data available	Driver of change	Reference
C. compressa (Esper) Gerloff and Nizamuddin	Locally abundant	Shallow sublittoral, sheltered and exposed habitats	France, W Mediterranean	1905-2003	Increase	Revisit historical records	Habitat transformation, pollution, overgrazing, competition vs mussels	Thibaut et al., 2005
	Belt-forming species	Upper sublittoral	Saronikos Gulf, N Aegean	1998-2010	Decline	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Tsiamis et al., 2013
	Locally abundant	Shallow sublittoral, sheltered and exposed habitats	France, NW Mediterranean	1839 2007-2013	Stable	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Thibaut et al., 2015
	Dense forests	Shallow sublittoral to 40 m depth, sheltered and wave-exposed habitats	W Istria, N Adriatic	1950-2013	Well established	Revisit historical records	Eutrophication levels	Ivesa et al., 2016
	Belt-forming species	Upper sublittoral	Girona, Spain, W Mediterranean	2001-2016 (except: 2006, 2007, 2011, 2015)	Decline	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Medrano et al., 2019
C. corniculata (Turner) Zanardini	Belt-forming species	n.d.	Outer Saronikos Gulf, S Aegean	1998-2010	Slight increase	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Tsiamis et al., 2013
	n.d.	n.d.	France, NW Mediterranean	Before 1950-2013	Exclude	Revisit historical records	Habitat transformation, pollution, overgrazing, competition vs mussels	Thibaut et al., 2015
	Belt-forming species	Upper sublittoral to 40 m depth, sheltered and wave-exposed habitats	W Istria, N Adriatic	1950-2013	Well established	Revisit historical records	Eutrophication levels	Ivesa et al., 2016
C. crinitophylla Ercegovic	Belt-forming species	n.d.	Inner Saronikos Gulf, S Aegean	1998-2010	Decline	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Tsiamis et al., 2013
C. dubia Valiante	n.d.	n.d.	France, NW Mediterranean	Before 1950-2013	Exclude	Revisit historical records	Habitat transformation, pollution, overgrazing, competition vs mussels	Thibaut et al., 2015
C. foeniculacea (Linnaeus) Greville	Accompanying species	Shallow sheltered rock pools	France, W Mediterranean	1883-2003	Extinct	Revisit historical records	Habitat transformation, pollution, overgrazing, competition vs mussels	Thibaut et al., 2005

Species	Ecological role	Habitat	Locality/country	Time period	Trend/status	Method/data available	Driver of change	Reference
C. foeniculacea (Linnaeus) Greville	Belt-forming species	Shallow sublittoral to several m depth	SW Ireland, Barloge Creek, Celtic Sea	1960-2011	Well established	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Trowbridge et al., 2011
	Dense forests	Shallow sublittoral to 110 m depth, sheltered and wave-exposed habitats	France, NW Mediterranean	1825, 1929 2007-2013	Stable? locally near extinct	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Thibaut et al., 2015
	Dense forests	Shallow sublittoral to 110 m depth, sheltered and wave-exposed habitats	W Istria, N Adriatic	1950-2013	Well established	Revisit historical records	Eutrophication levels	Ivesa et al., 2016
	Belt forming species	Mainly sandy and most rocky shores	Girona, Spain, W Mediterranean (several sities)	1835-2019 n.d.	Not present	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Mariani et al., 2019
	Belt forming species	Intertidal and shallow rocky sublittoral, exposed habitats	Madeira, Portugal, SE Atlantic Ocean	1980-2021	Decline	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Bernal-Ibáñez et al., 2021
C. humilis Schousboe ex Kützing	Belt forming algae	Rocky intertidal and shallow sublittoral, wave-exposed habitats	Madeira, Portugal, SE Atlantic Ocean	1980-2021	Decline	Quantitative and historical data	Habitat transformation, pollution, overgrazing	Bernal-Ibáñez et al.., 2021

Figures

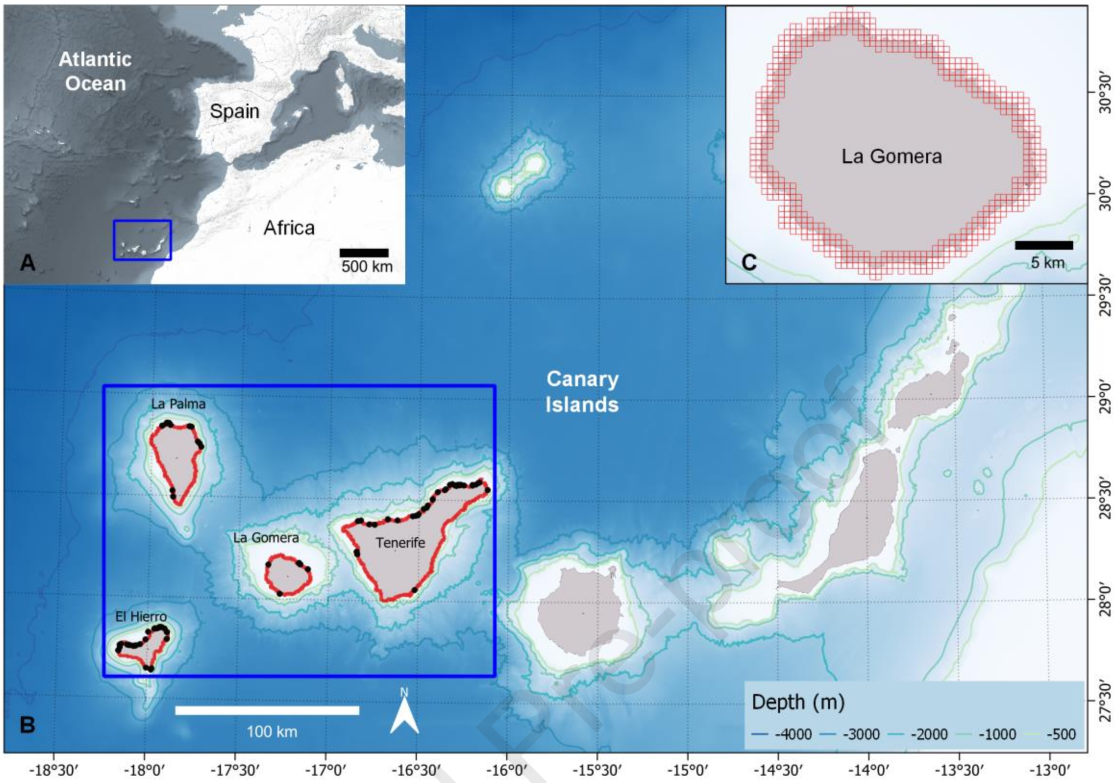

Figure 1. Location of the Canary Islands (A), the western islands in a blue rectangle (B). For the comparative analysis of coverage of *G. abies-marina*, the grid used appears in red and the centroid points used as presences in modeling as black points. The zoom in La Gomera island (C) allows a better view of the limits and distribution of the grid.

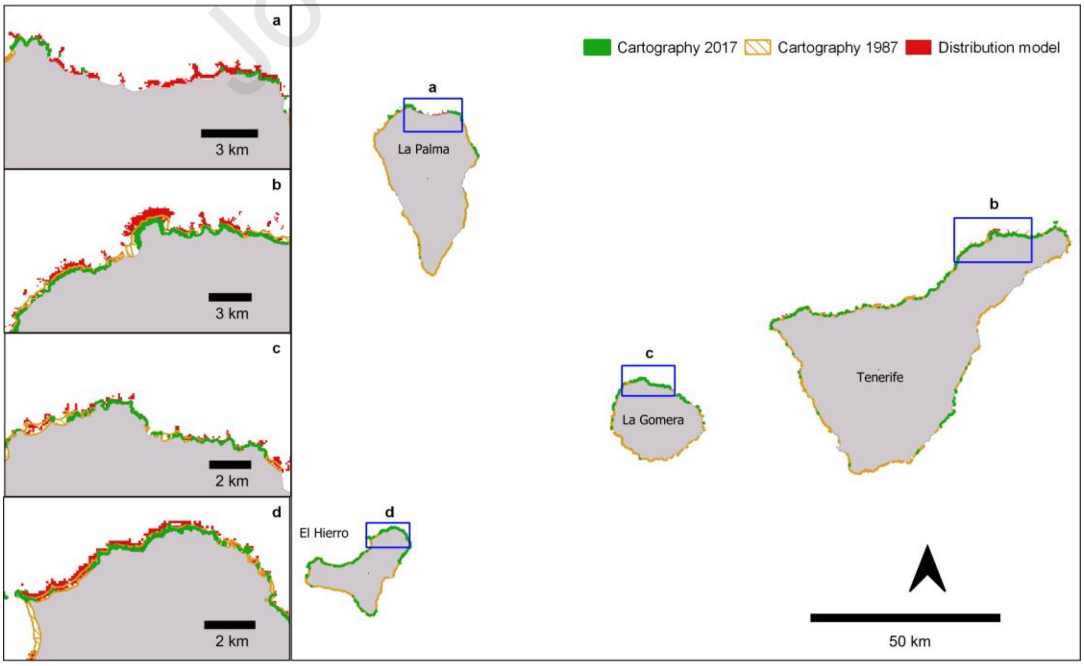

Figure 2. Distribution maps of *Gongolaria abies-marina* in the western Canary Islands in 1987, 2017 and the distribution model.

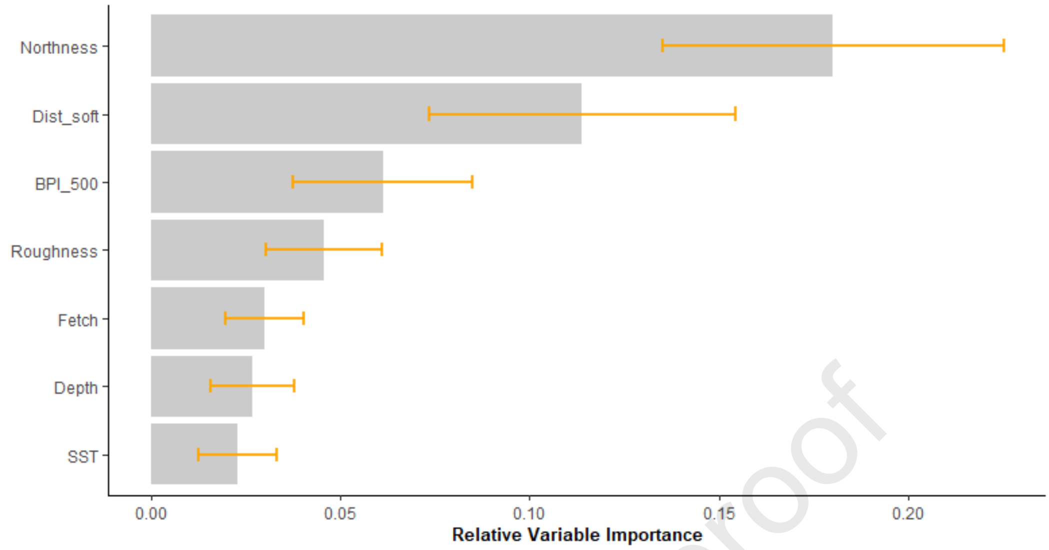

Figure 3. Importance of the variables in the RF model. Error bars in yellow.

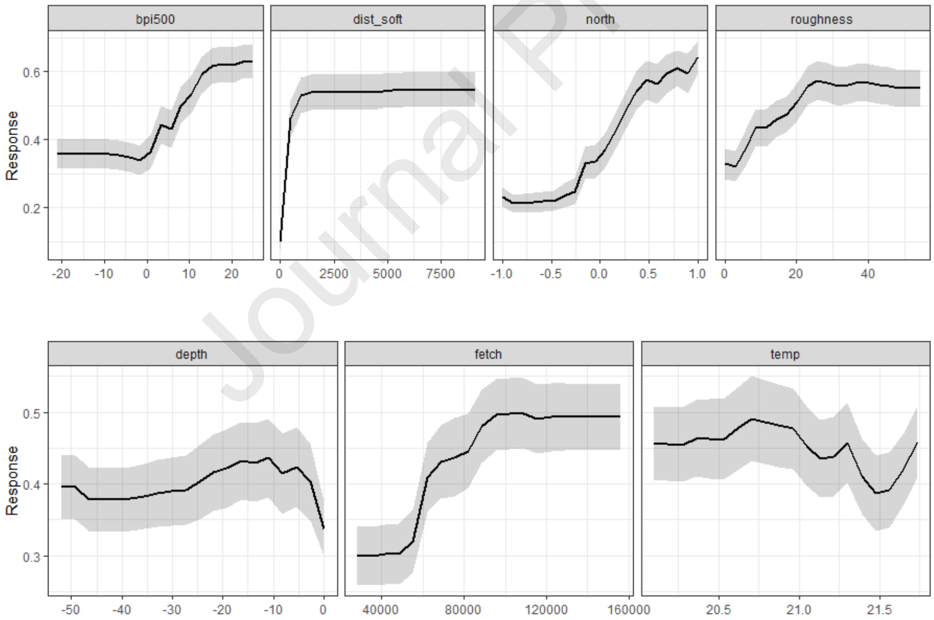

Figure 4. Response curves of each variable for the RF model.

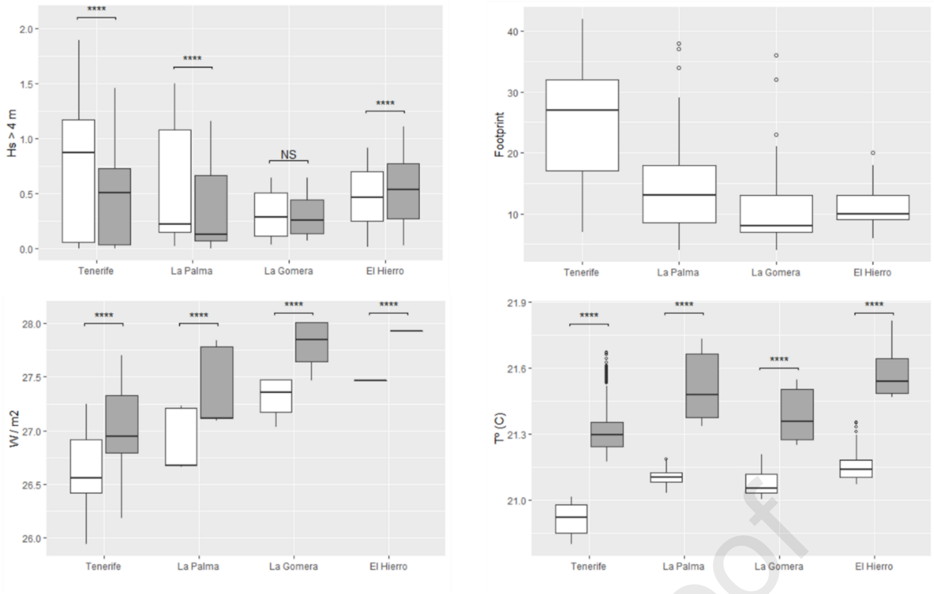

Figure 5. Boxplot of drivers of decline of *Gongolaria abies-marina* forests. The symbols show the significant level in temporal comparisons using t-test. Comparisons between islands are all significant.

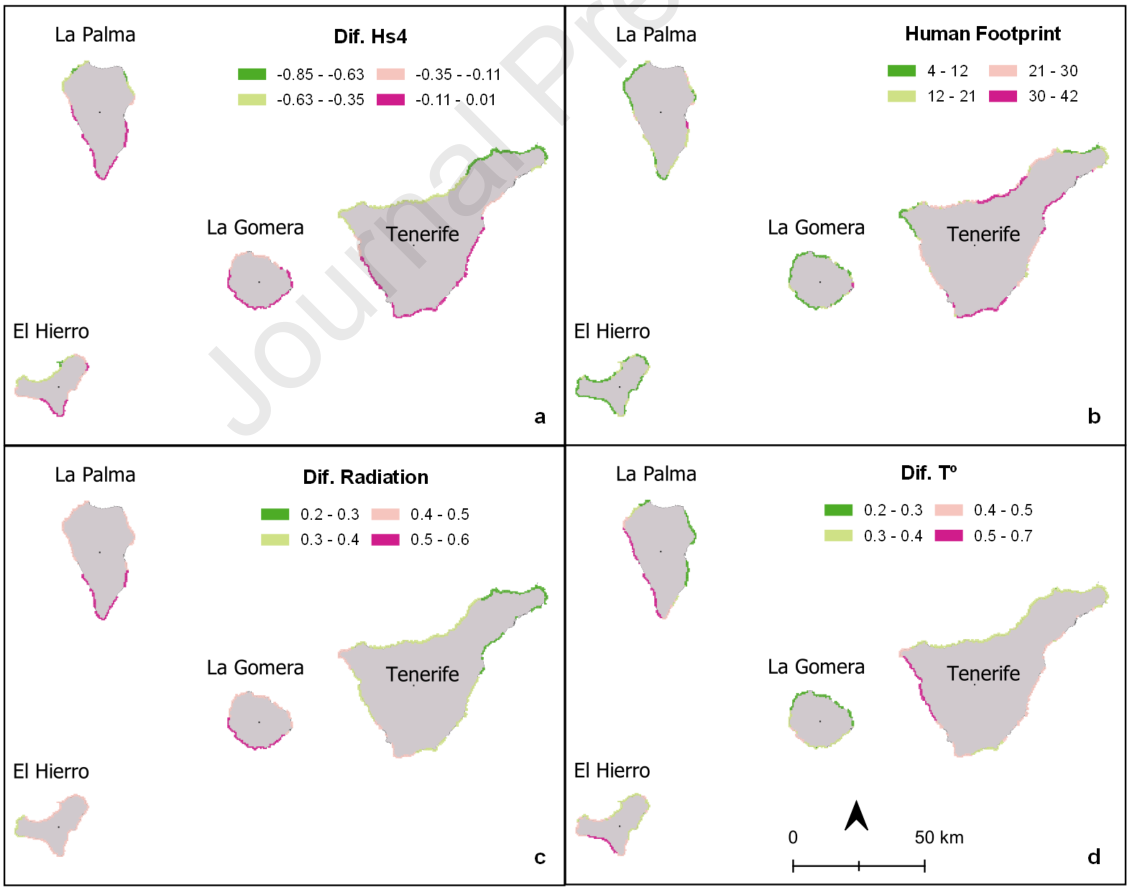

Figure 6. Distribution map of the differences between values of 1987 and 2017 for each variable considered a driver of decline of *Gongolaria abies-marina*. Footprint does not have temporal analysis.

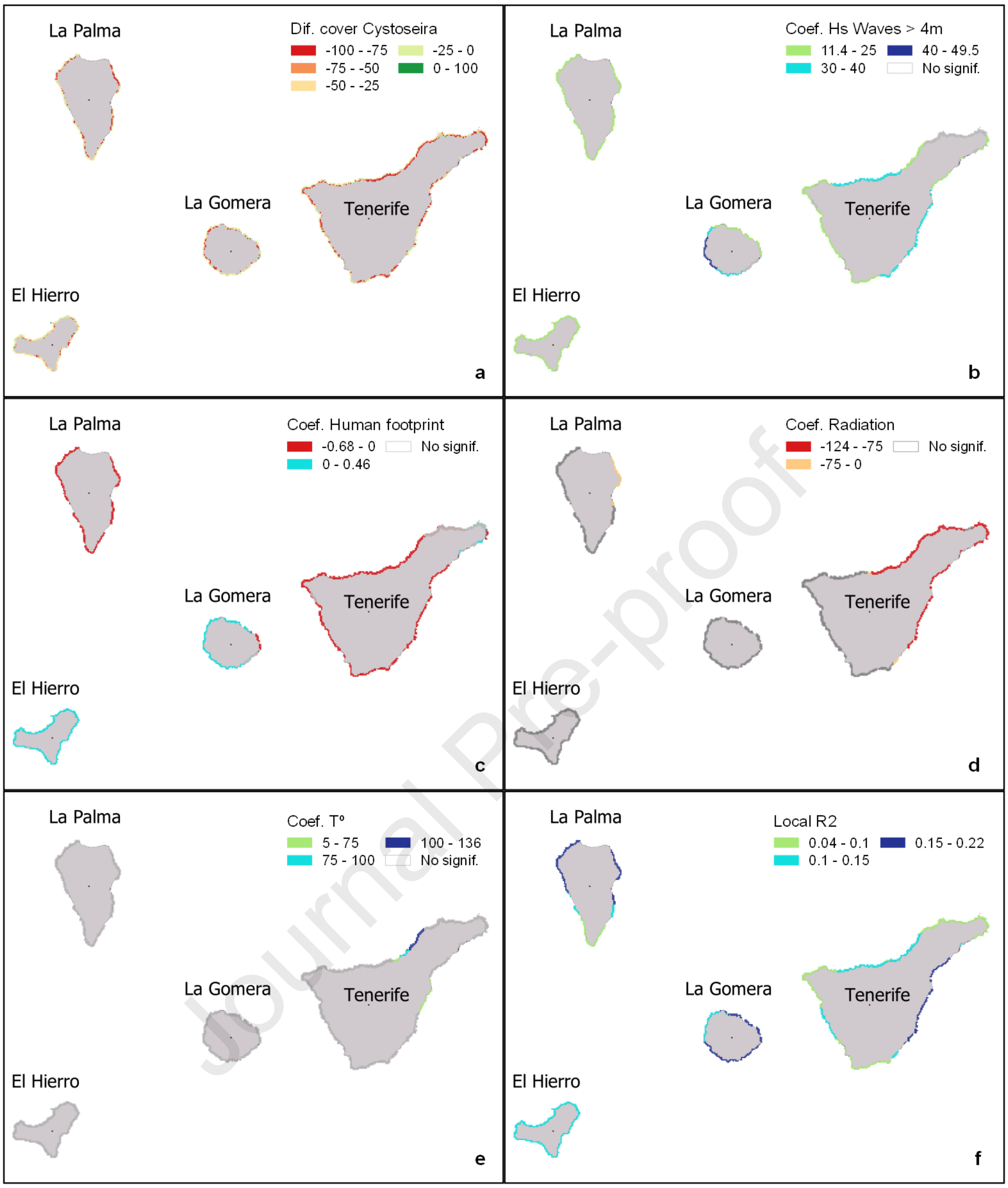

Figure 7. Differences in *G. abies-marina* coverage between 1987 and 2017 (a); Coefficients of the Geographically Weighted Regression (GWR) model for each environmental factor (b-e) and R^2 of the GWR model (f). To facilitate the interpretation of the figure, orange-red ramps have been used for negative values, green-blue for positive and grids without any color for not significance.

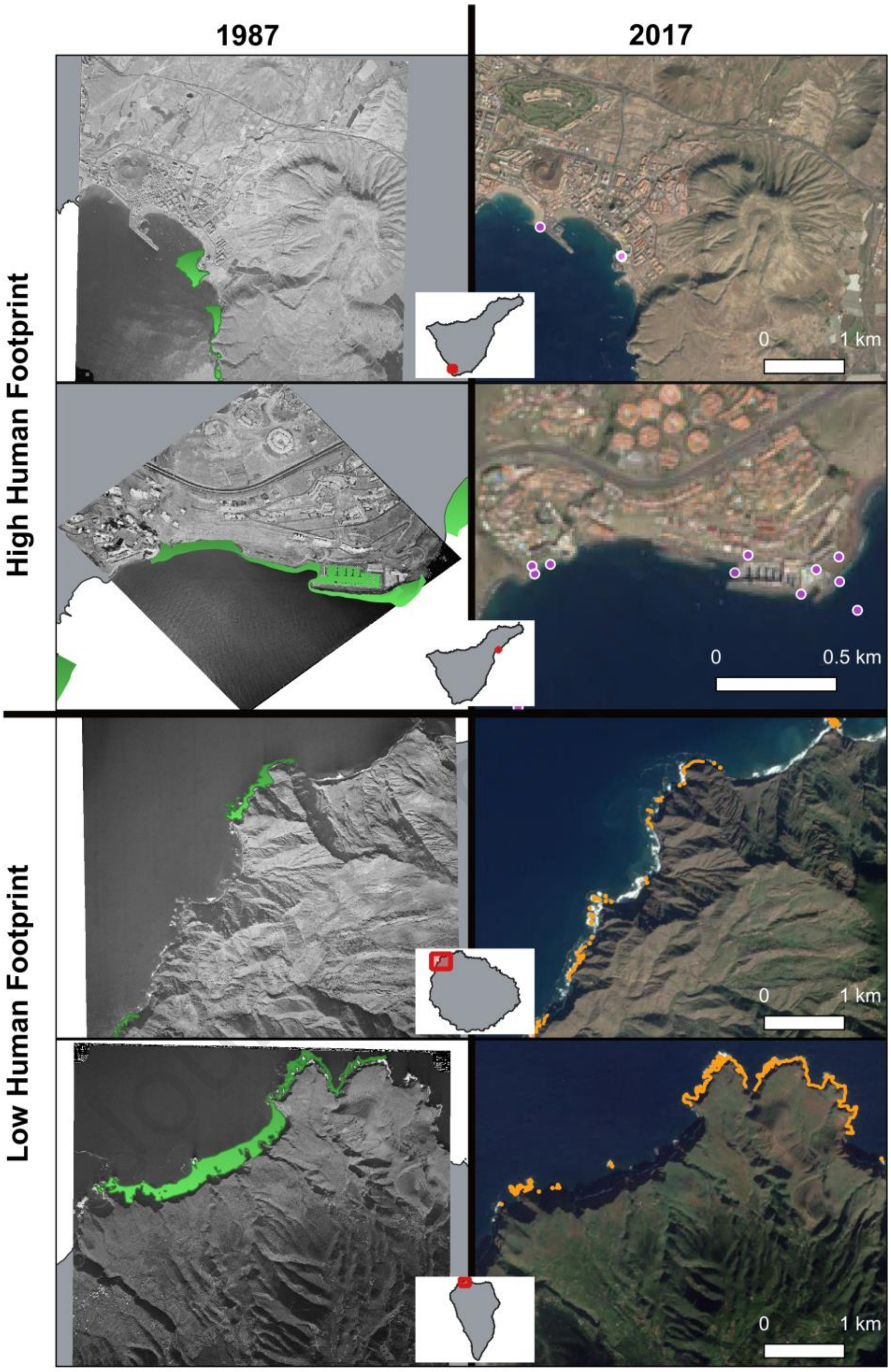

Figure 8. Comparative aerial photographs between locations with high (Tenerife) and low (La Gomera and La Palma) human footprint and between the years 1987 and 2017**.** *Gongolaria abies-marina* populations are represented in green for 1987 and in orange for 2017. Violet circles represent sewage outfalls. Tenerife locations do not present any population of *G. abies-marina* in 2017.

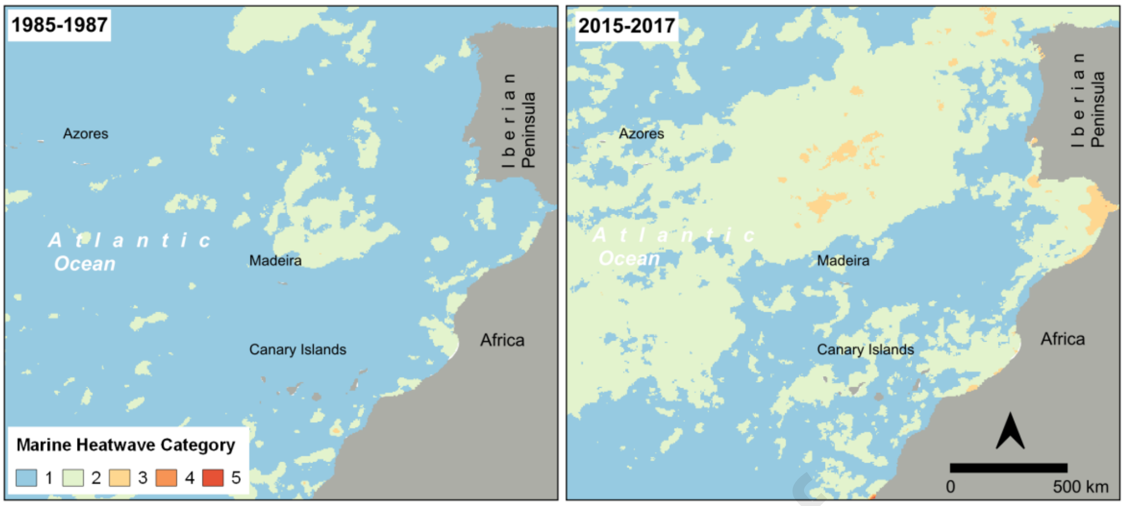

Figure 9. Maximum category of Marine Heatwaves (MHWs) in the Macaronesia region during the warmest months (July, August, and September) for the periods 1985–1987 and 2015–2017..

Appendix A

Additional data about the SIMAR database provided by “Puertos del Estado” (http://www.puertos.es/en-us).

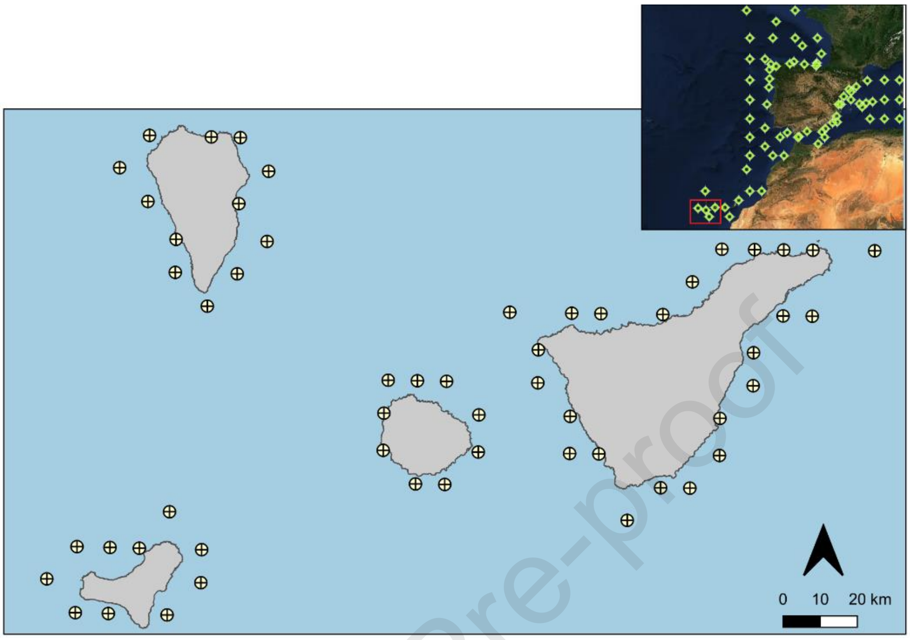

Figure 1A. Location of the SIMAR points around the western Canary Islands selected to download the wave data.

Table 1A. Swell and waves parameters included in SIMAR database that were considered as possible drivers of decline of *G. abies-marina*. In bold, the selected variable Hs4 (relative frequency of waves exceeding the 4 m threshold in significant height).

Parameter	Type of waves	Description	Unit	Mean 1987	Mean 2017
Hm0	Wind and Swell	Spectral significant height (m)	meters (m)	1.19	1.37
Tm02		Mean period (s), moments 0 and 2	seconds (s)	5.94	5.58
Tp		Peak period (s)	seconds (s)	9.13	9.68
DirM		Mean direction that waves come from. Direction is given on a 16 point compass scale	0-360 (0=N,90=E)	164.62	154.52
Calm sea		Relative frequency, the number of times exceeding the threshold in significant height (Hs)	%	2.65	0.43
Hs4				**0.61**	**0.51**
Hs4.5				0.25	0.17
Hs5				0.10	0.07
Hs>5				0.05	0.04
Hm0_V	Wind	Spectral significant height (m)	meters (m)	1.24	0.86
DirM_V		Mean direction that waves come from (0=N,90=E)	0-360 (0=N,90=E)	69.68	98.56
Hm0_F2	Swell	Spectral significant height (m)	meters (m)	0.39	0.45
DirM_F2		Mean direction that waves come from	(0=N,90=E)	220.93	207.67

Highlights

- *Gongolaria abies-marina* is one of the few Atlantic species of *Cystoseira s.l.*
- Its populations present a strong decline greater than 97% in the last thirty years.
- The potential habitat of the species is comparable to historical mapping.
- A lower proportion of high waves and human footprint are the main drivers.
- UV radiation and sea surface temperature are important only in certain locations.

Author statement

Laura Martín García: Conceptualization, Visualization, Data Curation, Methodology, Investigation, Writing - Review & Editing; **Nereida M. Rancel-Rodríguez:** Investigation, Resources, Data Curation; **Carlos Sangil:** Conceptualization, Investigation; **Javier Reyes:** Investigation, Data Curation; **Blas Benito:** Formal analysis, Methodology; **Sharay Orellana:** Investigation, Resources, Data Curation; **Marta Sansón:** Conceptualization, Visualization, Investigation, Writing - Review & Editing, Supervision, Funding acquisition.

Declaration of interests

☐ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☒ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Marta Sanson reports financial support was provided by European Regional Development Fund.