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Identifying key-conservation areas for *Posidonia oceanica* seagrass beds

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ABSTRACT

The configuration of a habitat often reflects its conservation status and, to be effective, the conservation actions to be implemented must be adapted to local environmental conditions and human activities. Here, we take advantage of a fine resolution map (1:10000) of marine habitats to study the spatial configuration of *Posidonia oceanica* seagrass beds, a marine habitat of great ecological and economic importance. Six different composition and landscape descriptors were calculated at different resolutions (grid cells of 400 m × 400 m, 200 m × 200 m and 100 m × 100 m) between 0 and 40 m deep along 1700 km of French Mediterranean coastline (mainland and Corsica). A Random Forest approach was applied to relate these landscape descriptors to anthropogenic and environmental factors and to assess their relative importance. The best predictive power of the Random Forests models was obtained for 100 m × 100 m grid cells with models explaining 87% of the variance of the decline index and 70% of the variance of the cohesion index. The identification of threshold points for all environmental variables allowed to localize seagrass beds in either good or bad environmental conditions. We also identified sites whose spatial configuration is degraded despite good environmental conditions. These are sites with greater influence from human activities that could benefit from proactive conservation measures.

1. Introduction

Human activities have strongly modified the environment: global warming, sea level rise and loss of biodiversity are signs of this global impact (UNEP-MAP-RAC/SPA, 2010; Khare et al., 2019). Major climate and ecological changes affect the world's oceans leading to a number of responses including increasing water temperatures, changing weather patterns, shrinking ice-sheets, temperature-driven shifts in marine species ranges and the disappearance of species (Jagers et al., 2019). In addition to being impacted by climate change, marine biodiversity is strongly impacted by other human activities and their consequences, mainly fishing, chemical pollution and eutrophication, physical degradation of habitats and invasion of alien species (Amara, 2011; Glover and Smith, 2003).

The Mediterranean Sea, because of its location, is strongly affected by climate change and by many anthropogenic factors. At the crossroads of Africa, Europe and Asia, the Mediterranean coasts have experienced the apogee and decline of many civilizations. The region has always been an important route for merchants and travelers, allowing trade and cultural exchange. Human influence has been present in the Mediterranean for several millennia but it has become increasingly important with technological advances (Coll et al., 2010). Its coastline stretches 21 states and is one of the main tourist destinations in the world, with 200 million tourists a year. Mediterranean-type ecosystems, with their characteristic and unique weather patterns of mild, wet winters and hot, dry summers, are present only in five regions of the world: in California, central Chile, the Cape South Africa, and in southwestern and southern Australia. It is therefore a unique geographical, cultural, historical and economic context. About 7% of the world's population lives in the Mediterranean coastal countries, i.e. 460 million inhabitants.

The Mediterranean coasts and the ecosystems they shelter are therefore subject to some of the most important human pressures on the planet even though it is a marine diversity hotspot with approximately 17,000 species listed (Coll et al., 2010). One ecosystem is particularly recognized to contribute to most of the biodiversity, productivity and ecosystem services of the French Mediterranean coast: *Posidonia oceanica* (L.) Delile seagrass beds meadows (UNEP/MAP, 2009). The extensive marine grasslands constituted by *P. oceanica*, recognized as being a habitat of community interest (92/43/EEC Habitats Directive, habitat codes 1120: Posidonia).

Seagrass bed ecosystems play an essential ecological role (Cullen-Unsworth et al., 2014) and provide valuable services such as protection against coastal erosion, contribution to fisheries by supporting food

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webs or the absorption of pollutants by water filtration (Waycott et al., 2009). Seagrass beds are sentinel species (i.e. species whose sensitivity serves as an early indicator of changes in the environment of a given ecosystem): any change in their spatial distribution (e.g. a reduction in the maximum depth limit, or a loss of covered areas) reflects a change in the state of the environment (Orth et al., 2006). Because of global changes, seagrass bed ecosystems have shown a widespread decline over the last decades (Selig et al., 2014; Waycott et al., 2009). For *P. oceanica*, a protected, endemic and most common seagrass bed species in the Mediterranean (Boudouresque et al., 2012), the loss of cover is estimated to be about 10% over the last 100 years with a 50% decrease in density over the last 20 years (Marbà et al., 2014; Telesca et al., 2015). *P. oceanica* declines are mainly observed near urban areas (Boudouresque et al., 2012; Holon et al., 2018) and are mainly related to human activities: 67.6% of the cover decreases are attributed to physical impacts from human activities (Boudouresque et al., 2009; Marbà et al., 2014), and its degradation status is explained at 71% by anthropogenic pressures (Holon et al., 2018). *P. oceanica*, spatial extent and density are also influenced by light (Elkalay et al., 2003). Moreover, *P. oceanica* suffers from desalination (i.e. water salinity < 33 psu) (Ben Alaya, 1972) and does not bear extreme temperatures (< 9.0 °C and > 29.2 °C (Augier et al., 1980). The seascapes made of *P. oceanica* are thus strongly influenced by natural and anthropogenic factors that determine their shape and functioning at different spatial scales (Abadie et al., 2018).

The trajectory of seagrass beds in Europe since 1869 has shown a serious trajectory of decline but a recent study (de los Santos et al., 2019) recently revealed a weak reversal of trend in their extent and density, especially for *P. oceanica* (increase of 0.5% in area) (de los Santos et al., 2019). This seagrass bed recovery was mostly (68%) attributed to management actions (de los Santos et al., 2019).

One of the challenges in seagrass bed conservation is getting accurate information about their health condition (Unsworth et al., 2018). However, spatial and temporal data on seagrass bed extent and density are normally scattered or scarce in most regions, as well as disparate in terms of the metrics of change assessed. Another challenge is to adapt and prioritize management actions as well as possible to the local conditions since local environmental conditions and human activities influence the spatial extent and density of *P. oceanica* seagrass beds (see above). The present work aims at addressing these challenges and investigates how to link the spatial configuration of *P. oceanica* to anthropogenic pressures and environmental conditions to more systematically assess its conservation status and better orientate management actions.

Previous studies have assessed the influence of anthropogenic pressures and changes in environmental conditions on the ecosystem conservation status or degradation status trough a landscape approach (Abadie et al., 2015; Pittman, 2017). Several landscape indices have been proposed to study the spatio-temporal configuration, fragmentation and connectivity of seagrass beds (Sleeman et al., 2005). Most studies so far have focused on the impact of particular pressures on seagrass beds, such as fish farming (Cancemi and De Falco, 2003; De Espinardo et al., 1999), the introduction of foreign nutrients into the environment (Hughes et al., 2018), and the damage caused by 10-m-long anchors on the structural characteristics and spatial dynamics of *P. oceanica* (Abadie et al., 2019). Holon et al. (2018) estimated the cumulative effect of several coastal anthropogenic pressures on the degradation status of *P. oceanica* along the French Mediterranean coastline. However, direct environmental factors, such as salinity, temperature, turbidity or chlorophyll A, known to influence the distribution and ecological status of seagrass beds (Boudouresque et al., 2006; Telesca et al., 2015; Montefalcone et al., 2016), have not been taken into account in this previous study. Holon et al. (2018), showed that the influence of anthropogenic pressures on degradation was not linear: thresholds were detected and passing these thresholds could put *P. oceanica* in a critical management status. Studies have shown that once certain thresholds of various global stressors (Hughes et al., 2018) or of external elements (nutrient enrichment (Connell et al., 2017) are passed, seagrass beds could completely change their conservation status. However, to our knowledge, no study has investigated so far the impact of several anthropogenic and environmental variables simultaneously on the seagrass bed conservation status.

The aim of this present study is to assess the relative influence of multiple anthropogenic pressures and environmental factors on the conservation status of *P. oceanica* along the French Mediterranean coast. Therefore, different landscape indices related to the conservation status of *P. oceanica* were calculated at different spatial scales in order to select the most representative ones. The threshold values found for anthropogenic pressures and environmental variables were used to classify the seagrass beds according to their conservation status. This allowed a fine-scale definition of priority areas that required special attention in conservation measures. We focused on the French Mediterranean, which represents 1700 km (of which about 700 km for Corsica; Source: www.shom.fr) of the 46,000 km of Mediterranean coastline.

2. Methodology

2.1. Study zone and spatial distribution data of P. oceanica

This study was carried out along the 1700 km of French Mediterranean coast (including Corsica), between 0 and 40 m depth which is the bathymetric growth limit of *P. oceanica* in France (Boudouresque et al., 2012). The distribution data of *P. oceanica* and dead matte (which is what remains of the plant after its death) come from the 1:10000 map of 11 marine biocenoses available on the MEDTRIX platform (www.medtrix.fr, Project DONIA expert, see Holon et al. (2015a, 2015b) for details concerning data and map building). Briefly, after compiling a bibliographic synthesis, data were gathered and homogenized from 1:10000 habitat maps; these data were collected by different organizations and programs (see Acknowledgements). Campaigns were led between 2005 and 2014 using classical methods: aerial or satellite photography, side-scan sonar survey, sonar survey and validation through direct observations ("ground-truth points") based on classical dives and/or towed dives. The raster of 11 marine biocenoses was reclassified into three biocenoses, namely: 1 = *P. oceanica*, 2 = dead matte and 3 = nine other habitats. We divided our study area into cells of identical and joined size using the QGIS software version 18.02.16. Three data sets were built depending on the dimensions of the cells, i.e. 100 m × 100 m, 200 m × 200 m or 400 m × 400 m. Landscape indices, pressures and environmental values (see after) were calculated for each cell of different dimensions from their respective raster previously transformed into points; the average value was extracted using the software ArcGIS 10.3.1. Smaller cell dimensions were not used because they did not permit to properly compute all the landscape indices.

2.2. Human pressure data

We used the map of anthropogenic pressures made by Holon et al. (2015a, 2015b) at a resolution of 20 m along the French Mediterranean coasts and available on the MEDTRIX platform (www.medtrix.fr, Project IMPACT). Nine pressures (based on quantitative data), on which local decision-makers can have an influence, were considered: human-made coastline (big harbours/harbours/artificial beaches, ports of refuge/pontoons, groynes, land- fills and seawalls areas), urbanization (Number of people per municipality), costal population (size and density considering the inhabitants-residents), aquaculture (total area of aquaculture farms), agriculture (land cover), coastline erosion (land cover), urban effluents (capacity, output), boat anchoring (number and size of boats observed during summer), and fishing (traditional and recreational fishing areas). These pressures have an impact on seagrass beds by changing the clarity of the water and/or the water current and/or directly causing irreparable physical damages (Boudouresque et al., 2012). Indeed, urban and industrial discharges, coastal erosion or shoreline artificialization contribute to the supply or re-suspension of the mineral and organic matter (Waycott et al., 2009), while agricultural areas can increase erosions and phytoplankton production when leaching nitrogen and phosphorus inputs. This induces an increase in water turbidity and contributes to the reduction of light diffusion in the water column (Waycott et al., 2009). However, accessibility to light has a direct impact on the survival capacities and metabolism of *P. oceanica*. Secondly, pressures such as fishing and mooring have more immediate and localized destructive effects, since anchors, seines and trawls (trawling which has been prohibited over seagrass beds by the European Regulatory Council since 2006) can deteriorate or tear up the seagrass beds (Boudouresque et al., 2012), almost irreversibly.

Data about the origin and the intensity of these pressures came from published databases (MEDAM, CORINE land cover, INSEE and MEDOBS) and from the Water Agency RMC and IFREMER. Satellite images and unpublished data from Andromède Océanologie were also analyzed.

2.3. Environmental data

The environmental variables considered for this study were: seawater salinity, sea surface temperature, chlorophyll A, and turbidity. They were provided by the PREVIMER weather-France project (available on http://marc.ifremer.fr/). We used annual average values for 2010–2012 years.

2.4. Landscape indices

Six landscape indices were calculated from the raster of the three biocenoses maps to characterize the landscape configuration of *P. oceanica*: i) the average area of patches, ii) the percentage of seabed coverage, iii) the fragmentation index, iv) the aggregation index, v) the cohesion index and vi) the decline index (Table 1). The computation of the five first landscape indices recommended by Sleeman et al. (2005) for the monitoring of seagrass beds fragmentation was done with the SDMtools package (Vanderwal et al., 2019), using R statistical software (R Core Team, 2018). For each index, values are expected to vary according to the conservation status of the habitat (Table 1). The decline index was calculated with R based on Holon et al. (2018), who used it to estimate the degradation status of the seagrass beds. A principal component analysis (ACP) was then done to visualize how the meadows were characterized according to the landscape indices. Following this ACP, we retained for further analyses the indices that were not correlated and better characterized the seagrass beds.

2.5. Choice of scale

The collinearity between the pressures was tested through the calculation of the Inflation Factors of Variance (VIF), realized with the package ‘usdm’ (Naimi, 2017). Variables with a VIF greater than a threshold value of 5 (VIF $>$ 5) were considered to generate collinearity and were excluded from the analysis. Each landscape index selected by ACP was modelled according to anthropogenic pressures and environmental variables using Random Forests (called RF thereafter) as previously described by (Breiman, 2001). RF is a machine learning method that builds a set of classification or regression trees. RF have been found to be ideally suited to ecological data as they do not require linear relationships, they effectively model variable interactions, can handle missing data and correlated variables, are more stable than traditional regression trees to minor changes in input data and have high predictive power (Breiman, 2001; Catherine et al., 2010; Cutler et al., 2007; Holon et al., 2018; Parravicini et al., 2012).

Random Forests were built using 1000 trees to stabilize the ‘out-of bag’ error and allow for random testing of three potential splitting variables at each node. For each dataset (dimensions of, 100 m × 100 m, 200 m × 200 m, 400 m × 400 m), a model was built and the predictive capacities of the three models were compared using the percentage of explained variance. The scale (cell dimension) producing the highest explained variance was used thereafter.

2.6. Estimation of the relative influence of predictive variables on the selected landscape indices

In RF, the relative importance of a predictive variable is quantified by comparing the accuracy of the model's predictions using the original variable with the accuracy of the same model using a randomly permuted variable (Siroky, 2009). We used “IncNodePurity”, which is the average total decrease in node impurity attributed to splitting on each measured variable using the residual sum of squares; it provides an indication of node prediction accuracy attributed to each variable. Partial dependence diagrams of the random forest were used to visualize the influence (importance, slope value, shape) of each variable on each selected landscape index, while taking into account the average effects of all interactions with other explanatory variables.

Table 1
Landscape indices used for the study of *P. oceanica* seagrass beds configuration. See (Rutledge, 2003) for the expected landscape index values for a habitat in a good conservation status.

Landscape indices	Formula	Components	Maximum expected value for a habitat in a good conservation status
Average area of patches	$\frac{\sum_{i=1}^{n} a_{pi}}{n_p}$	a_{pi}: Area of *P. oceanica* patches in a quadrats np: number of *P. oceanica* patches in a quadrat	-
Percentage of *seabed coverage*	$\frac{\sum_{i=1}^{n} a_{pi}}{A_p} \times 100$	a_{pi}: Area of *P. oceanica* patches in a quadrat A_p: Area of *P. oceanica* patches and other patches in a quadrat	100
Fragmentation index	$1 - \sum_{i=1}^{n}\left(\left(\frac{a_{pi}}{A_p}\right)^2\right)$	a_{pi}: Area of *P. oceanica* patches in a quadrat A_p: Area of *P. oceanica* patches and others patches in a quadrat	0
Aggregation index	$\left(\frac{g_p}{\max(g_p)}\right) \times 100$	g_p: number of contacts between *P. oceanica* pixels	100
Cohesion index	$\left[1 - \frac{\sum_{i=1}^{n} p_{pi}}{\sum_{i=1}^{n}(p_{pi} \times \sqrt{a_{pi}})}\right] \times \left[1 - \frac{1}{\sqrt{A_p}}\right]^{-1} \times 100$	P_{pi}: perimeter of each *P. oceanica* patch a_{pi}: Area of *P. oceanica* patches in a quadrat A_p: Area of *P. oceanica* patches and others patches in a quadrat	100
Decline index	$\frac{Am}{Am + Ap} \times 100$	A_m: Area of the dead matte A_p: *P. oceanica* patches area	0

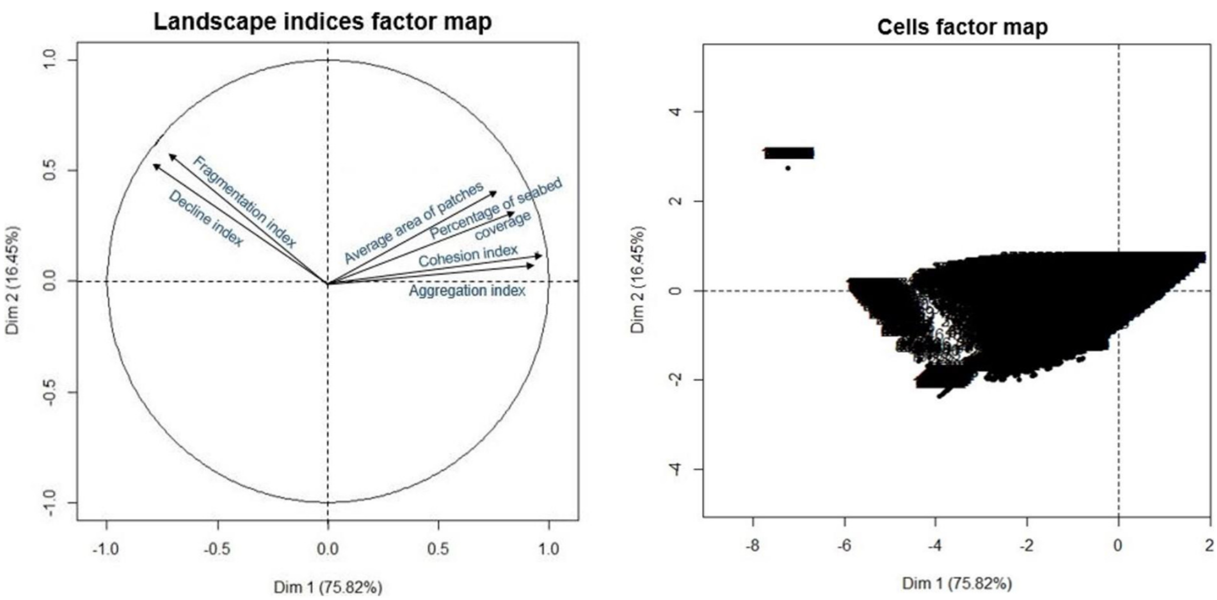

Fig. 1. ACP graph showing the characterization of 100 × 100 m seagrass cells by landscape indices (114,282 cells).

2.7. Detection of thresholds and visualization of the results

Thresholds (i.e. points at which the statistical properties of a sequence of observations change abruptly) were searched for each of the environmental variables and anthropogenic pressures using the package "strucchange" (Leisch et al., 2019). According to Zeileis et al. (2015), the research and test of existing thresholds (breakpoints) is based on a dynamic programming approach based on Bellman's principle (Bellman, 2008). More details on this dynamic programming algorithm can be found in Bai and Perron (2003). The main computational effort is to compute a triangular RSS (Residual Sum of Squares) matrix, which gives the sum of the residual squares for a series of observations starting at observation i and ending at i' with $i < i'$. From a simple linear regression model, the "breakpoints" function of the package calculates an object of type "breakpointsfull", which contains all the possible threshold points. This contains in particular the rectangular matrix of the sum of the residual squares and the functions making it possible to extract an optimal segmentation. A summary of this object gives the threshold points for all segmentations as well as the associated RSS and the associated BIC test statistic (Bayesian Information Criteria) (Leisch et al., 2019).

A threshold value can be interpreted as the value (of an environmental variable or anthropogenic pressure) above or below which the spatial configuration of *P. oceanica* (and thus its conservation status) would change radically. In case where thresholds are identified, we can thus distinguish two categories of sites for each environmental variable or human pressure considered depending to whether it is above or below the threshold identified. A first map was built to show *P. oceanica* (living and dead matte) classified into two categories: i) cells where a threshold is exceeded for any of the environmental variables and ii) cells where the threshold is exceeded for at least one environmental variable. Depending on the spatial configuration of *P. oceanica* characterized by landscape index, these values were expected to be linked with *P. oceanica* in more or less good conservation status (see Table 1). Second, we built a map to identify the cells of low correspondence between the landscape index (and conservation status) and the environmental variables within the previous categories.

The map consequently showed cells in four categories: i) cells where the environmental variables and the landscape index are "good", ii) cells where environmental variables are good (under the threshold) and the landscape index is not in favor of a good conservation status, iii) environmental variables are bad (threshold crossed) but the landscape index is in favor of a good conservation status and iv) environmental variables (threshold crossed) and the landscape index are not in favor of a good conservation status.

The limit threshold for each landscape index was fixed at 50.

2.8. Showing congruences and incongruities between the conservation status and the explaining variables

The cohesion index was used to represent the conservation status of the *P. oceanica* at the study scale and its links with the environmental variables depending on the threshold measured. This index that measures the connectivity between *P. oceanica* patches well reflects the processes of ecological degradation within a landscape (Rutledge, 2003), and assesses well its state of conservation (Opdam et al., 2003).

Using the cohesion index calculated on each grid cells, we associated the location of *P. oceanica* with respect to the environmental conditions and the *P. oceanica* cohesion index. We defined that cells with cohesion Index ≤50 are in a bad conservation status whereas cells with a cohesion Index > 50 are in a good conservation status. We classified all cells in four categories namely: 1) *P. oceanica* patches are in good environmental conditions and present a good cohesion, 2) *P. oceanica* patches are in good environmental conditions but present a bad cohesion, 3) *P. oceanica* patches are in poor environmental conditions but present a good cohesion, 4) *P. oceanica* patches are in poor environmental conditions and present a poor cohesion. For each of these four categories, different conservation actions were defined, ranging from inaction to urgent restoration measures.

3. Results

All anthropogenic pressures and environmental variables were kept for the analyses because the collinearity test showed that they all had a VIF value weaker than 5. The principal component analysis was performed with the six landscape indices for all cell sizes and explained 92.7% of the total inertia with the first two axes. Cells characterized by only the presence of dead matte were very noticeable in the PCA because they were far removed from other cells on both axes of the PCA. The first axis alone explained 75.8% of the total inertia. Independent of the cell size chosen, the first axis clearly contrasted two landscape indices, namely the decline index and the cohesion index (see Fig. 1). Both of these indices were retained to characterize the configuration of the seagrass beds for all further analyses. The other landscape indices

Table 2
Summary of percentage of variance explained by Random forest models for each landscape index retained to characterize the spatial configuration of *P. oceanica* seagrass beds and for each cell dimension.

Cell dimension	Decline index			Cohesion index		
	100 m	200 m	400 m	100 m	200 m	400 m
Percentage of variance explained	87%	82%	75%	70%	42%	48%

were therefore removed from the analyses.

The RF models showed that the scale of 100 × 100 m was associated with the highest explained variance: 87% for the decline index and 70% for the cohesion index (Table 2).

For both landscape indices, environmental variables were more strongly linked to the spatial configuration of *P. oceanica* seagrass beds than anthropogenic pressures with, in order of importance: temperature, salinity, turbidity and then chlorophyll A (Fig. 2).

A grid cell size of 100 × 100 m and the associated data set were thus retained for the following analyses.

The partial dependence curves of the decline index as a function of the different explaining variables all exhibited non-linear relationships (Fig. 3). This means that thresholds can be identified for all of them. Over the thresholds value, the decline index decreased with the temperature, increased with increasing values of turbidity and chlorophyll A, and was weak between two values of salinity (Fig. 3). The decline index also globally increased with increasing anthropogenic pressures through non-linear patterns. Similarly, the partial dependence plots for the model explaining the cohesion index showed non-linear patterns and thresholds were detected for all variables. Patterns were opposite to the ones observed for the decline index.

Regardless of the landscape index considered question, the detected thresholds for environmental variables values were similar. Landscape indices were in favor of *P. oceanica* being in good conservation status (low decline index, high cohesion index) for temperatures superior to 16.5 °C, salinity between 33 psu and 41 psu, turbidity inferior to 1.5 NTU and chlorophyll A below 1.7 µg/L. These values were used to visualize on a map of living *P. oceanica* beds and dead matte localized in areas below or above one, two, three or four of the environmental thresholds (Fig. 4). This map suggests that almost all *P. oceanica* located east of the longitude 6° E (Cap Carqueiranne) were associated to good environmental conditions.

Urbanization and coastal population were the two anthropogenic pressures most related to the decline of *P. oceanica* with a decline, which, beyond a threshold, decreased as urbanization and population size increased (Figs. 2 and 3). In comparison with other anthropogenic pressures - i.e. human-made coastline, coastal erosion, fishing, urban effluents, boat anchoring and aquaculture - the decline of *P. oceanica* increased linearly when these different pressures were high (see thresholds on Fig. 3).

For all anthropogenic pressures, the cohesion between *P. oceanica* patches decreased linearly when the pressures increased. Cohesion was thus used to visualize where the good conservation status of *P. oceanica* based on the cohesion index (linearly linked with anthropogenic pressures) matched good or bad environmental conditions (Fig. 5).

The erroneous matches were the most interesting to locate; they were between 5° (around the Rhône River) and 7° E and especially between 5° and 6° E. In this region, cohesion was good despite of bad environmental conditions, and the values of the anthropogenic pressures were more important, except for aquaculture and agriculture, than in the regions where environmental conditions were good and the cohesion bad (Fig. 6).

On the contrary, in the Eastern part, some areas presented good environmental conditions but a bad cohesion. In these areas, the average value of some pressures such as human-made coastline, coastal population, fishing, urban effluents, coastal erosion aquaculture where higher than in areas presenting good environmental conditions but a good cohesion (*P*-value $\leq$2.2.e-16 associated to Wilcoxon Test).

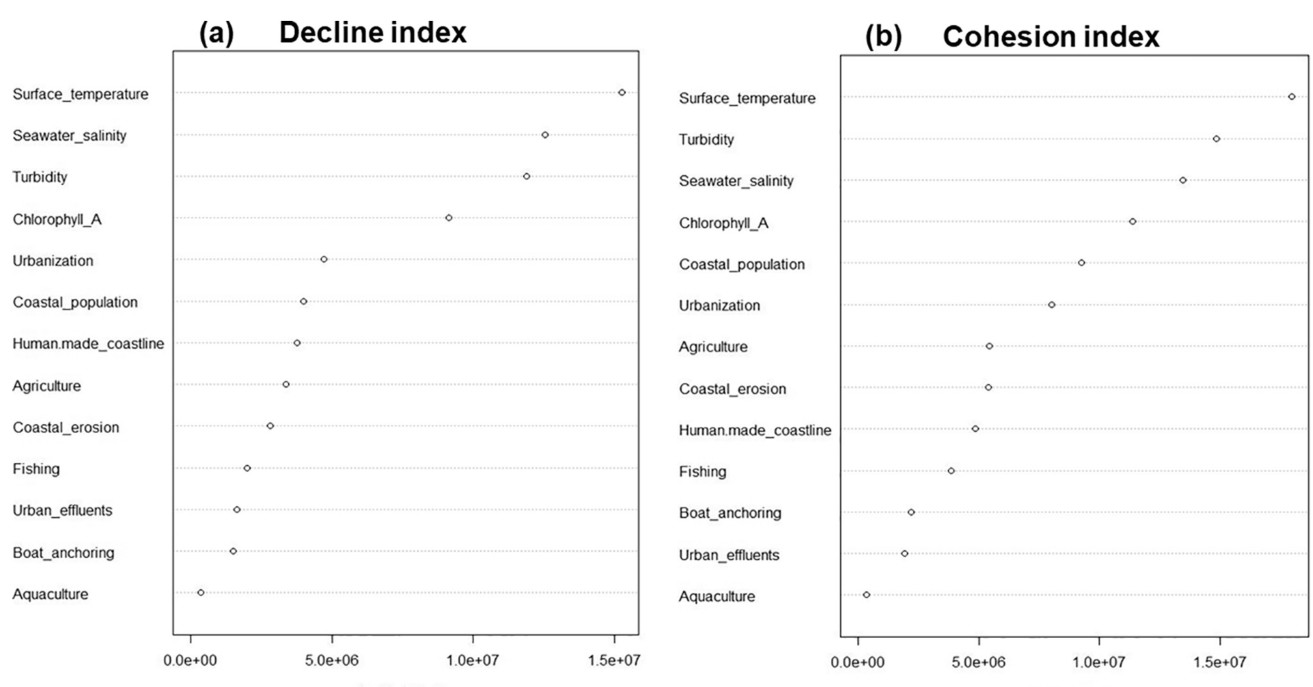

Fig. 2. Importance of each explaining variable relative to the seagrass decline index (a) and cohesion Index (b) with the Random Forest model respectively explaining 87% and 70% of the variance (grid cell size = 100 × 100 m).

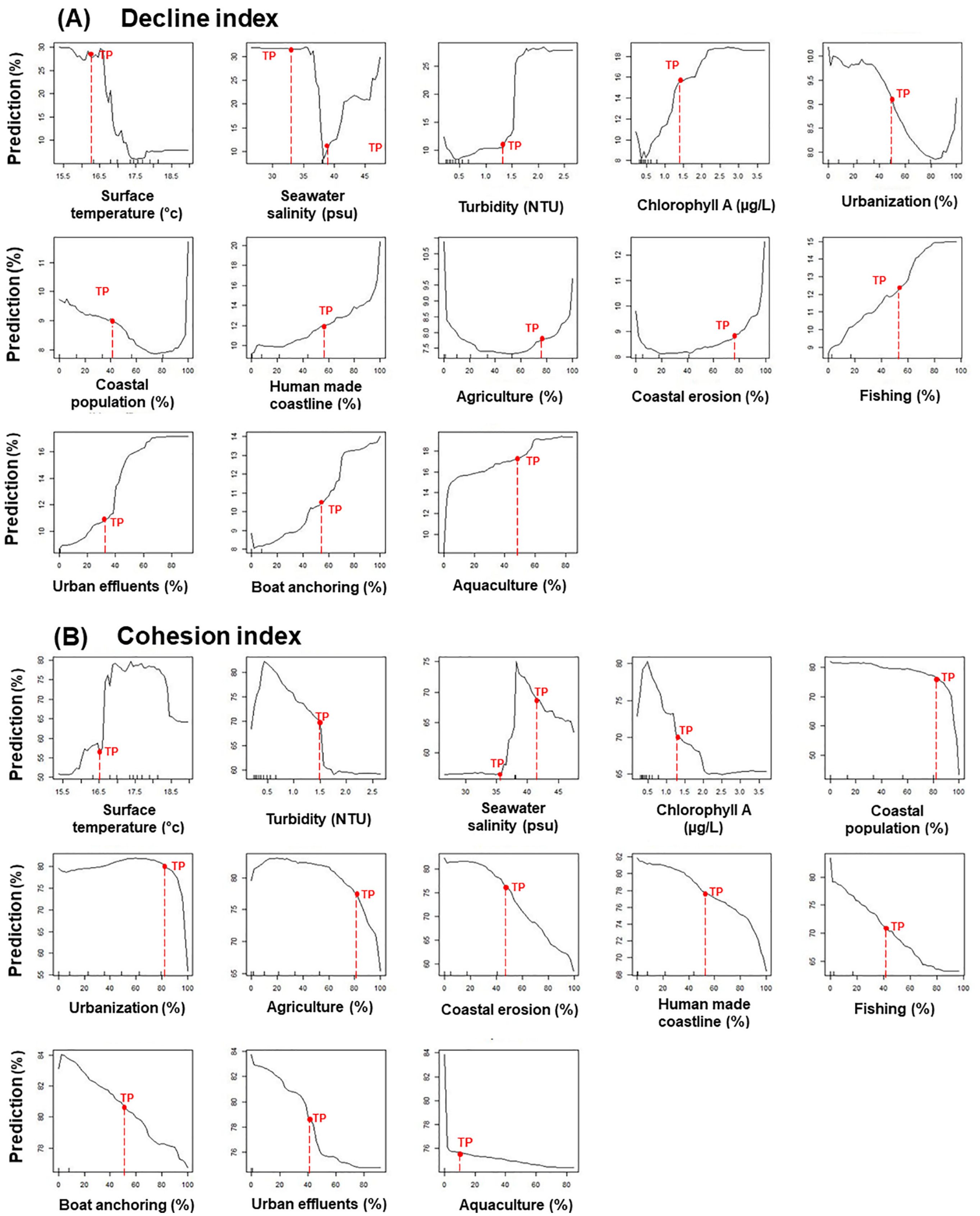

Fig. 3. Influence and response curves of each explaining variable on A) the decline index and B) the cohesion index of *P. oceanica* seagrass beds through the Random Forest model with 100 × 100 m cells. Thresholds (TP) are indicated in red. Note that to improve visualization, the Y axis scale is adapted to each variable. The graphs are ordered according to the influence of the different factors on the indices (see Fig. 2). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

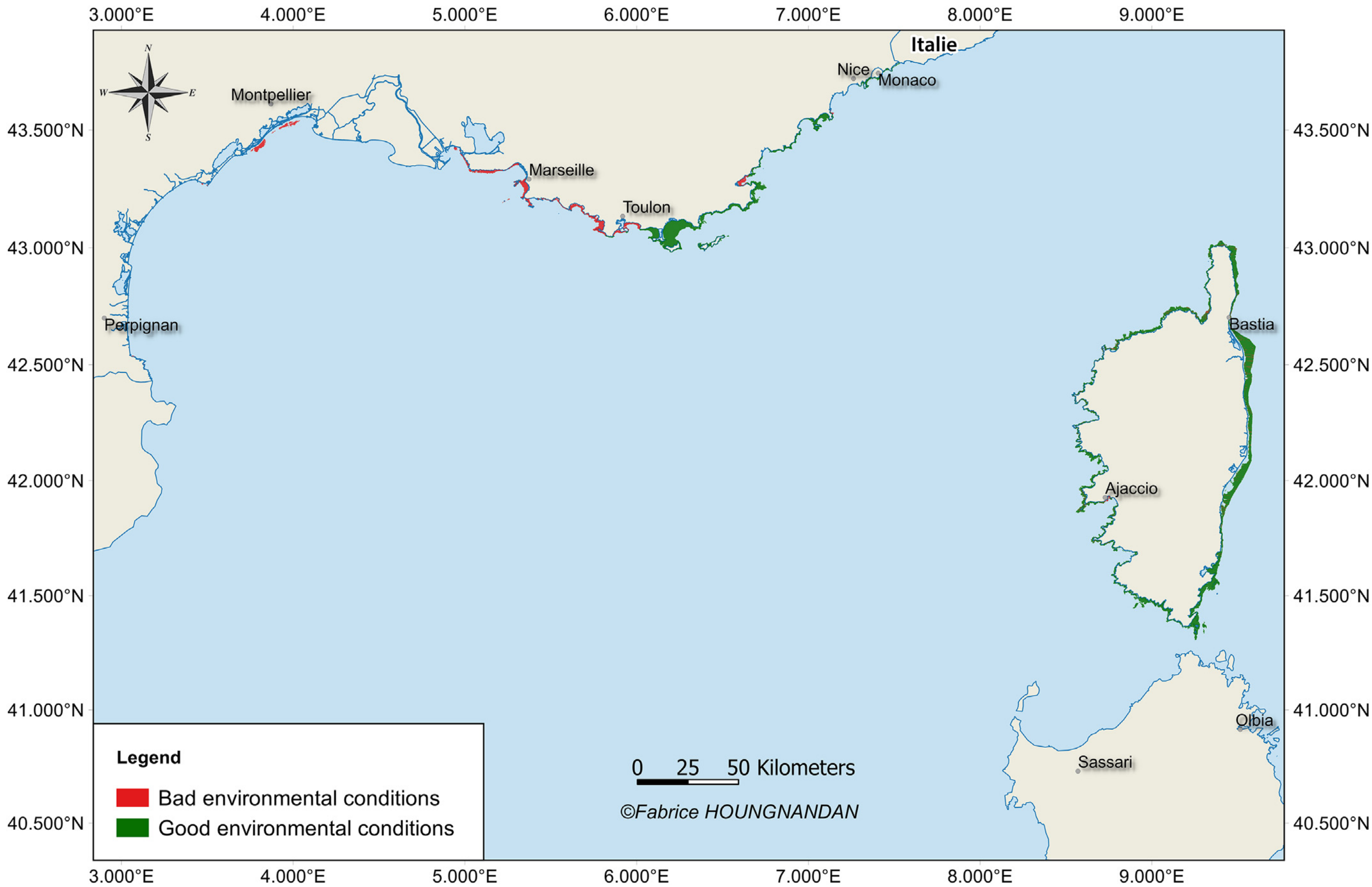

Fig. 4. Distribution of *P. oceanica* beds (living and dead matte) according to the threshold of environmental variables. In green: cells where all the environmental variables (temperature, salinity, turbidity and chlorophyll A) are good. In red: cells where the threshold is exceeded for at least one environmental variable. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. Anthropogenic pressures and environmental variables influence P. oceanica conservation status

Using data from the 1700 km French Mediterranean coastline (including Corsica), the aim of this study was to assess the relative influence of multiple anthropogenic pressures and environmental factors on the conservation status of *P. oceanica* seagrass beds through using their spatial configuration, and then to use these results to classify the seagrass beds according to management needs. In the study area, the conservation status defined by the spatial configuration of *P. oceanica* seagrass beds was better characterized by two opposite landscape indices: the decline index and the cohesion index. The first index measures the spatial coverage of *P. oceanica* in a cell and the second one measures the connectivity between *P. oceanica* patches. A reduction in patch cohesion can occur if *P. oceanica* suffers a significant direct physical impact, which subsequently reduces its spatial coverage in synergy with the effect of several other pressures. The decline of *P. oceanica* is therefore a progressive process that follows the reduction of connectivity between the *P. oceanica* patches.

Mixing anthropogenic and environmental pressures, our model was able to explain *P. oceanica* landscape indices, especially the decline index, with excellent performances (87% of the variance explained). A similar model with only anthropogenic pressures accounted for 71.3% overall variance of the decline index (Holon et al., 2018). As expected, the decline index increased with increasing anthropogenic pressures, contrary to the cohesion index which showed an opposite pattern. Among these anthropogenic pressures, urbanization and population density were the most important variables to explain the landscape indices. Our results also showed a more direct influence of environmental factors on the conservation status of *P. oceanica*. This is strengthened by the fact that even if almost no seagrass beds is free of physical impacts due to human activities (Marbà et al., 2014), environmental conditions, and especially temperature, still remain the most important constraints for the conservation status of *P. oceanica*. Our results are in agreement with recent studies, which highlighted that the rise in sea temperature caused by climate change was one of the main reasons for the global decline of seagrass beds, and particularly *P. oceanica*, in the French Mediterranean (Marbà and Duarte, 2010; Pergent et al., 2014).

4.2. Thresholds for environmental variables and anthropogenic pressures define P. oceanica conservation status

Thresholds were identified for the influence of each anthropogenic pressure and environmental variable on the decline index and the cohesion index of *P. oceanica*. The values of anthropogenic pressures and environmental variables above the thresholds represent the areas at most risk of decline for *P. oceanica* in the French Mediterranean.

The threshold values identified by our models for all the environmental variables were very similar to those found in the literature for temperature (≤ 10 °C) (Boudouresque et al., 2012) and salinity (≤ 33 psu and ≥ 41 psu) (Ben Alaya, 1972). *P. oceanica*'s absence from the Levantine coast (eastern Mediterranean) and its scarcity in the northern Adriatic and along the French western coastline was already assumed to be due to respectively summer and winter temperatures (Boudouresque and Meinesz, 1982). Moreover, our results showed that

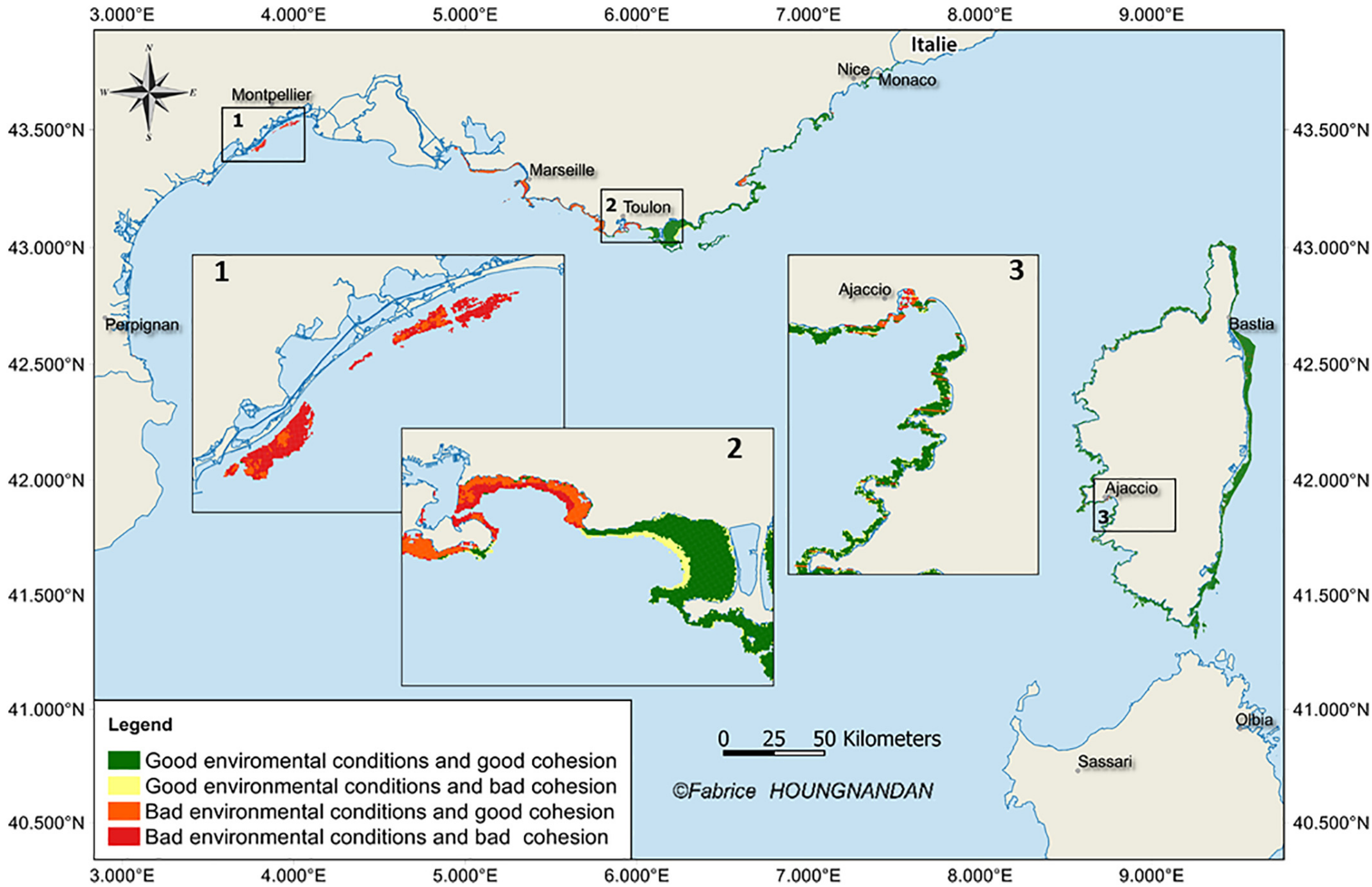

Fig. 5. Distribution of *P. oceanica* (100-m grid cells) according to the cohesion index (value > 0.5 = good cohesion; ≤0.5 = bad cohesion) and environmental variables (value above the threshold for at least one environmental variable = bad environmental conditions; value under the threshold for all environmental variables = good environmental conditions).

the decline of *P. oceanica* increased linearly with high turbidity and chlorophyll A levels in the water column although no threshold value was clearly reported in the literature. The thresholds identified in the present study were 1.5 for turbidity and 1.7, for chlorophyll A. The increases in turbidity and chlorophyll A result in a decrease in illumination and then a reduction in the cover and density of seagrass beds leading to the death of *P. oceanica* (Ruiz and Romero, 2003). Threshold values obtained for anthropogenic pressures compared with those found by Holon et al. (2018), who used another detection method, are in the same range especially for human-made coastline, coastal population, erosion, and urban effluents. The largest differences were found for local pressures, certainly highly influenced by the grid size used; the grid size was smaller (50 × 50 m) with Holon et al. (2018) who only focused on anthropogenic pressures. The direct negative impact of local pressures, like aquaculture and anchoring, is recognized but limited in space (Cancemi and De Falco, 2003; Ganteaume et al., 2005; Pasqualini et al., 2000; Ruiz and Romero, 2001), even if the impacted areas could be higher than previously thought (Deter et al., 2017). The direct action of anchors, by tearing out *P. oceanica* shoots or sections of" matte", reduces the cover of the meadow, and encourages the forming of erosive" intermattes" that can later spread (because of hydrodynamism) and join together, thus fragmenting the meadow (Pasqualini et al., 2000). The anchoring of big ships (cruise ships, warships) provokes particularly spectacular ploughing of the" matte" (Ganteaume et al., 2005).

4.3. Spatial location of priority areas and localized management actions

Regarding the environmental variables, the Rhône river, often assumed to be the origin of the poor development of *P. oceanica* in its Western part (Boudouresque et al., 2012) because of its influence on water turbidity, seemed not to be such an important barrier for the spatial configuration of existing seagrass beds. Our results showed that the border is more East: so-called "Cape of Carqueiranne".

On the eastern part of the cape of Carqueiranne, environmental conditions were good and should permit seagrass beds with a good cohesion and a poor decline, whereas the western part of cap de Carqueiranne presented one of four bad environmental conditions, that should not permit seagrass beds in a good conservation status. *P. oceanica* located in the eastern part of the cape of Carqueiranne were in a best conservation status (higher cohesion index and weakest decline index) than the ones located on the Western part.

Despite their localization in good environmental conditions, some seagrass beds still presented a bad conservation status that could be due to human activities. The area between 5° (around the Rhône River) and 7° E and especially between 5° and 6° E was particularly interesting because of the high concentration of mismatch between landscape indices and environmental values. Where cohesion was good despite the bad environmental conditions, historical data (if they exist) would be needed to test the existence of a delay effect with either environmental data (environmental conditions are becoming better and better explaining the good cohesion) or cohesion (the cohesion is still good despite the environmental data getting bad). On the contrary, at the Eastern part, where the environmental conditions were good but the cohesion was bad, the anthropogenic pressures should be targeted and rehabilitation or restoration might be possible.

It is also important to stress the fact that, at a human scale, unlike disturbances which are reversible (oil spills), the disappearance of a *P.*

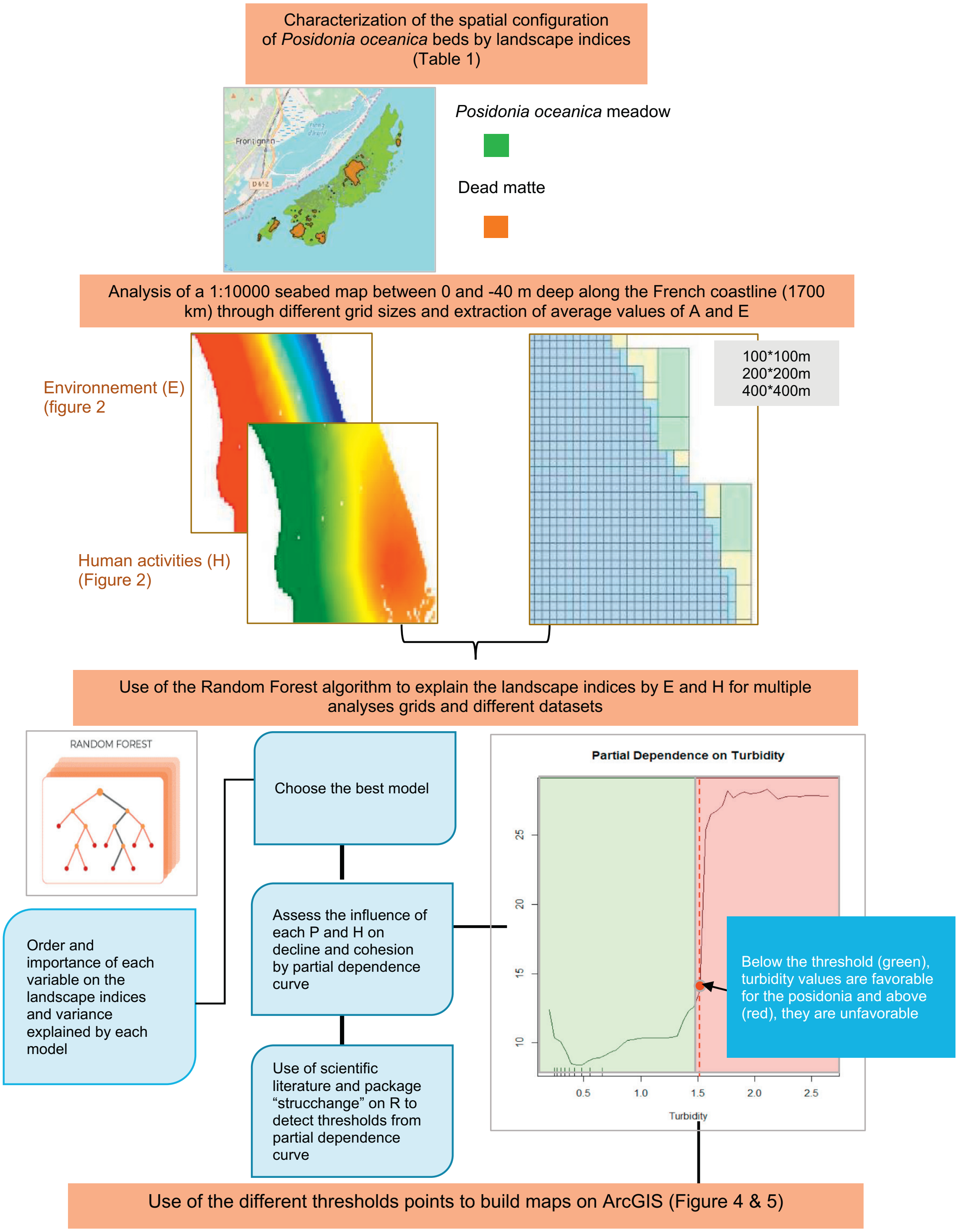

Fig. 6. Overview of the processing steps followed in this study.

oceanica can be considered irreversible because natural recolonization takes centuries (Boudouresque et al., 2012). It is therefore a priority to protect this species in order to avoid any destruction. There are direct and indirect protection measures. *P. oceanica* is already directly protected by international conventions ratified by most Mediterranean countries. The Habitats Directive particularly benefits *P. oceanica*, a species resistant to disturbances but with an extremely low recovery capacity (O'Brien et al., 2018). Many indirect measures also protect the *P. oceanica*: Marine Protected Areas (Boudouresque et al., 2004) and measures intended to curb pollutant discharge. Some management measures to improve water quality have reversed the decline of seagrass beds. For example in the Provence-Alpes-Côte d'Azur region (French Mediterranean), the *P. oceanica* Monitoring Network (RSP) has reported an increase in the number of progressive meadow limits since almost all the waste water has started going through treatment plants (Boudouresque et al., 2000). In Denmark, reduced nutrient inputs in fjords has led to an increase in the depth limit of eelgrass (Riemann et al., 2016). In Portugal, the decrease in nitrogen inputs to an estuary in 1998 reversed the decreasing trajectory of *Z. noltei* after severe eutrophication events in the 1980s and early 1990s (Cardoso et al., 2010).

Along the Catalonia coasts in Spain, it resulted in significant improvements of water quality and of the biochemical indicators of *P. oceanica* (Roca et al., 2015).

The importance of the regression of seagrass beds, coupled with the slow rate of natural recolonization, has led to the idea that it may be necessary to carry out reimplantation of *P. oceanica* (Calumpong and Fonseca, 2001). It may be necessary in areas where there has been a considerable decline in seagrass beds. Of course, it must first be ascertained that the causes of the regression of the seagrass beds have ceased to act. Considering local constraints and the conservation status of seagrass meadows, our results can help to target these areas.

5. Conclusion

In this study, we evaluated the relative influence of environmental factors and anthropogenic pressures on the conservation status of *P. oceanica*, which is one of the most important ecosystems of the Mediterranean Sea. Our statistical models explained the spatial configuration of *P. oceanica* beds with excellent performances. Environmental conditions, before anthropogenic pressures, mostly influenced the conservation status of this marine plant. Combining thresholds identified for the environmental variables with cohesion index, we established a descriptive map that helps making conservation decisions. This map showed four categories of seagrass beds, i.e. four sectors, in totally different conditions that should now be targeted for further studies interested in understanding the functioning of this ecosystem, the local human impacts or rehabilitation possibilities.

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